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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 wellsupported 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 unispicate 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, 179, 1-42.

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ADDITIONAL KEYWORDS: classifications – *Cymophyllus* – Cyperoideae – generic limits – inflorescence morphology – *Kobresia* – new combinations – nomenclature – phylogenetic relationships – *Schoenoxiphium* – taxonomic revision – *Uncinia* – *Vesicarex*.

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. 2150species (Goetghebeur, 1998). Bruhl included a sixth genus, the monotypic Vesicarex 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 unispicate 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 & Lve, 1983; Egorova, 1999; Dai & Liang, 2000; Ball, Reznicek & Murray, 2002; Luceño, 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.) Peterm. (= subgenus *Primocarex* Kük.), subgenus Vignea (P.Beauv ex T.Lestib.) Peterm., subgenus Vigneastra (Tuck.) Kük. [= subgenus Indocarex (Baill.) Kük.] and subgenus *Carex* (= subgenus *Eucarex* Peterm.). 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, Bayer & Ford, 1999; Yen & Olmstead, 2000; Roalson, 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 Cyperaceae, 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; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Léveillé-Bourret *et al.*, 2014), as predicted by evidence from associations with parasitic smut fungi in the genus *Anthracoidea* (Kukkonen & Timonen, 1979), rather than sister to previously suggested tribes having unisexual flowers, such as Sclerieae (Haines & Lye, 1972; Smith & Faulkner, 1976) or Rhynchosporeae (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) subgenera Carex and Vigneastra, named the core 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 unispicate 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 multispicate species in either the Vignea clade or the core 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 unispicate clade) was moderately supported in that analysis,

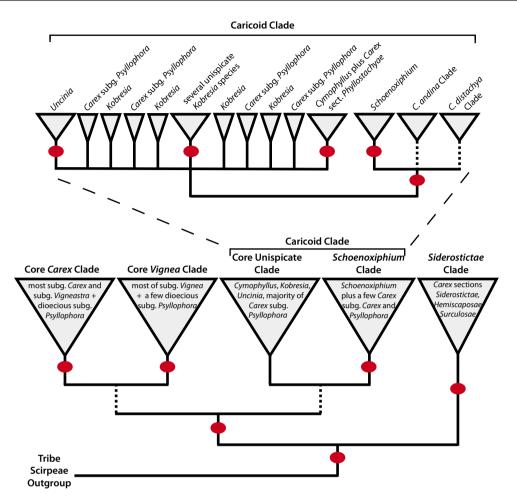


Figure 1. Generalized phylogenetic tree of Cyperaceae tribe Cariceae based on molecular phylogenetic studies to date. Full lines show relationships that are supported by all or most studies. Dotted branches show relationships that are frequently seen but more inconsistent among studies. Branches with 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.

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.

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 Vesicarex 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; Holttum, 1948; Kukkonen, 1967, 1984, 1990; Kern, 1974; Eiten, 1976; Smith & Faulkner, 1976; Goetghebeur, 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

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the inflorescence. The terminology used to describe inflorescences in Cariceae 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 Cariceae, 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 Cariceae, 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 (Vrijdaghs *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 Cariceae, 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 subtends a spikelet or group of spikelets.

Spikelets in Cariceae 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 Cariceae, 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; Luceño 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 nonhomologous 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 Cariceae (e.g. Tuckerman, 1843; Bailey, 1886; Holm, 1903; Ivanova, 1939; Bruhl, 1995; Ball & Reznicek, 2002; Vrijdaghs 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 Cariceae.

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; Vrijdaghs 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 Cariceae 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 Cariceae arises because these reduced spikelets of Cariceae, 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

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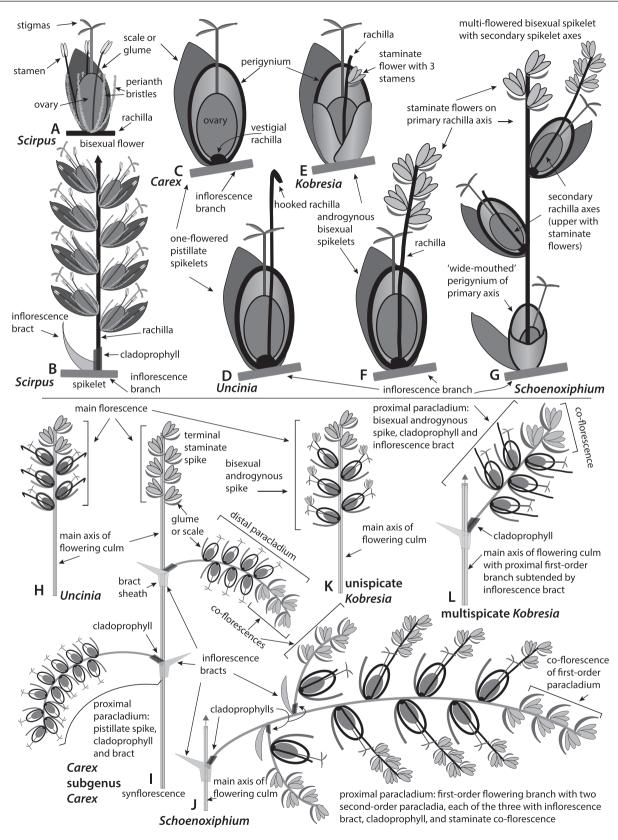


Figure 2. See caption on next page.

Figure 2. Diagrammatic representations, not to scale, of flower and inflorescence structure in Cyperaceae tribe Cariceae with comparison to tribe Scirpeae in A and B. Axes are exaggerated in length and spacing of flowers so that the structure can be clearly seen. Diagrams above the horizontal line show flower and spikelet structure, whereas those below the line show the arrangement of the spikelets and staminate flowers into inflorescences. It should be noted that, for simplicity, all ovaries are drawn with three stigmas, although two stigmas are also frequently seen, especially in Carex subgenera Vignea and Psyllophora. All axes are shown in progressively darker shades of grey indicating higher order branching, with the highest order branches (rachillae) shown in black. All prophylls (including cladoprophylls and perigynia) are also drawn in black. Scale-like glumes that subtend staminate flowers or perigynia are shown in medium grey, whereas inflorescence bracts at the base of primary and secondary inflorescence axes are shown in light grey. The perianth (only in A, B) is also shown in light grey. The gynoecium is shown in a slightly darker shade of grey than the androecium. A, Flower structure of a typical species in tribe Scirpeae. B, Spikelet structure in tribe Scirpeae. C, One-flowered pistillate spikelet typical of Carex s.s. and Cymophyllus, but also sometimes found in Schoenoxiphium and Kobresia. Here and elsewhere, the black ellipse represents a flask-like perigynium that is closed except for an apical orifice through which styles, stigmas and sometimes rachillae emerge. D, One-flowered pistillate spikelet of Uncinia, showing hooked rachilla protruding from the perigynium. E, Bisexual spikelet with perigynium not fully sealed and containing a fertile pistillate flower and a small staminate flower on the persistent rachilla, typically found in some Kobresia inflorescences. F, Bisexual spikelet with one fertile pistillate flower and multiple staminate flowers borne on an elongated rachilla protruding from the perigynium, found in *Schoenoxiphium* and some *Kobresia*. The number of staminate flowers varies from one to several. G, Spike of spikelets resulting from additional branching of the primary rachilla after producing the first perigynium at the base, resulting in two additional spikelets, one pistillate and one bisexual, proximal to the distal staminate flowers of the primary rachilla (redrawn based on fig. 3 in Gehrke et al., 2012). This proliferation of branching of the rachilla after producing a fertile perigynium can be found in *Schoenoxiphium* and blurs the distinction between rachis and rachilla. Note that what we label as the primary rachilla here is called the rachis of the spike of spikelets in Gehrke et al. (2012). We show it in black and refer to it as a primary rachilla to emphasize the structural similarity between rachis and rachilla in this case. H-L, Examples of various types of inflorescence or parts thereof, using both traditional and typological terminology to label them. H, Unispicate inflorescence of Uncinia, comprising only the main florescence, which is an androgynous terminal spike. This type of unispicate inflorescence is also found in Cymophyllus and Carex subgenus *Psyllophora*, but with short or vestigial rachillae rather than the hooked rachillae of *Uncinia*. I. Typical synflorescence found in Carex subgenus Carex, showing the main florescence (terminal spike) and two paracladia to illustrate terms describing these structures. J, Typical example of proximal paracladium (lowest first-order branch and subtending bract) in Schoenoxiphium ecklonii (redrawn based on Levyns, 1945). K, Main florescence of the unispicate Kobresia myosuroides (redrawn based on Kern, 1958). L, Proximal paracladium of the multispicate Kobresia simpliciuscula (redrawn based on Kern, 1958).

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, androgynous (perigynia proximal and staminate flowers distal on the spike axis), gynecandrous (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 unispicate and multispicate inflorescences.

Although terms such as spike, unispicate and multispicate 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 multipseudospicate, 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

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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 guite 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-Linnean 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-Linnean 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, in subsequent floristic manuals, fewer subgenera have been recognized by others (Ohwi, 1936; Koyama, 1962). Many rejected Psyllophora as a distinct subgenus, dispersing these species among subgenera Carex and Vignea, or even into Uncinia, Kobresia or Schoenoxiphium (see below for details). The recognition of subgenus Vignea has been almost universal, the most notable change being the merger of a few dioecious, unispicate species from subgenus *Psyllophora* into it (e.g. section Physoglochin Dumort.). Carex subgenera Carex and Vigneastra have been treated as a single subgenus by some (Ohwi, 1936; Koyama, 1962; Kern & Noteboom, 1979). There have also been suggestions that subgenus Vigneastra is ancestral to one or more of the other Carex subgenera (Nelmes, 1951, 1952, 1955; Hamlin, 1959; Nannfeldt, 1977), and possibly derived from Schoenoxiphium (Haines & Lye, 1972) or from a 'primitive Kobresia-Schoenoxiphium stock' (Smith & Faulkner, 1976) based on the similarity of inflorescence structure in these groups.

New subgenera in *Carex s.s.* have been proposed by various 20th century botanists. The monotypic subgenus Altericarex H.St.John & C.S.Parker was described to accommodate Carex concinnoides, a North American species with four stigmas and tetragonous nutlets (St. John & Parker, 1925). Subgenus Kuekenthalia Savile & Calder was proposed for those species with more or less inflated perigynia and often persistent styles [sections such as Lupulinae Tuck. ex J.Carey, Paludosae G.Don, Vesicariae (Heuff.) J.Carey etc., plus a few unispicate species] (Savile & Calder, 1953). Another subgenus of Carex, Kreczetoviczia T.V.Egorova, was segregated from subgenus Carex to accommodate species with two stigmas, but mostly unisexual spikes [e.g. sections Phacocystis Dumort. s.l., Graciles (Tuck. ex Kük.) Ohwi and *Abditispicae* G.A.Wheeler] (Egorova, 1985). None of these subgenera has, however, been widely adopted.

Relationships 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 androgynous, leading to an early theory that unispicate *Carex* spp. are primitive and multispicate 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 multispicate 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 rachillabearing unispicate species only, referring to this group as 'true *Primocarex*', and moved the remaining unispicate 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 *Kukenthalia*. 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 cladoprophylls 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 *Psyl*lophora was polyphyletic, comprising species with unispicate 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 distignatic 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, Schoenoxophium and Uncinia in one genus, recognizing each of them at the subgeneric level in genus Carex s.l., but without making valid nomenclatural transfers.

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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 Vesicarex has been shown to be related to species of Carex section Abditispicae (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 *Vigneastra* 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 Vigneastra) 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 Vigneastra show that representatives from other sections of subgenus Vigneastra form one (Gehrke & Linder, 2009) or more (Waterway et al., 2009; Starr et al., 2015) earlydiverging lineages in the core Carex clade. None of these groups of subgenus Vigneastra 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* + *Hypol*- vtroides 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 Vignea 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 Vigneastra 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 Vignea) 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-florescences 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 Hemiscaposae and Surculosae have paniculiform inflorescences with higher order branching. Each node of the reproductive culm in section Hemiscaposae 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 cladoproin C. surculosa phylls 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 Vigneastra 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 *Vigneastra*, 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. 2I). 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 gynecandrous 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 Vigneastra 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 Vigneastra 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 distignatic flowers [Phacocystis s.l., Bicolores (Tuck. ex L.H.Bailey) Rouy, Abditispicae] 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 firstorder 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 cladoprophylls 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 gynecandrous 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 unispicate, 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 Kükenthal'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 androgynous 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. and ina and C. distachva clades form a monophyletic group, but differ strongly in morphology and distribution. Schoenoxiphium is endemic to eastern and southern Africa, the C. and ina 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. and ina clade and some in the C. distachya clade have at least some unispicate 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 unispicate 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 unispicate Carex. Many of these small groups already have names at the generic level as these highly reduced unispicate 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 unispicate 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; 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 Vigneastra 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 Vigneastra. 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 unispicate individuals of normally multispicate Carex spp. (e.g. C. flacca Schreb.) has also been found sporadically in natural Carex populations and can be easily induced by the application of 2,3,5triodobenzoic 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 have 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 multiflowered 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 distignatic 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 phyllotaxy (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 unispicate 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 caricoid 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., Hymenochlaenae s.l., Porocystis, Phacocystis s.l., Racemosae, Mitratae Kük., Rhomboidales, Laxiflorae (Kunth) Mack., Paniceae G.Don, Bicolores, Careyanae Tuck. ex Kük., Griseae (L.H.Bailey) Kük., Granulares (O.Lang) Mack., Rostrales Meinsh., Vesicariae, Paludosae, Carex, Lupulinae, Squarrosae 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.

Replaced synonym: Carex brevicaulis Mack., Bull. Torrey Bot. Club 40: 547. 1913, nom. illeg. Carex deflexa var. brevicaulis B.Boivin, Le Naturaliste Canadien 94(4): 522. 1967; non Carex brevicaulis Thouars (1808).

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.

Carex fraseriana *Ker Gawl., Bot. Mag. 33: t. 1391. 1811.*

Cymophyllus fraserianus (Ker Gawl.) Kartesz & Gandhi, Rhodora 93: 138. 1991.

Carex fraseri Andrews, Bot. Repos. 10: t. 639. 1811. Olamblis fraseri (Andrews) Raf., Good Book: 26. 1840. Cymophyllus fraseri (Andrews) Mack. in N.L.Britton & A.Brown, Ill. Fl. N. U.S., ed. 2, 1: 441. 1913.

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

Carex lagopus Muhl., Descr. Gram.: 265. 1817.

Distribution: eastern USA (southern Appalachian Mts.).

TRANSFERS FROM KOBRESIA WILLD. TO CAREX L.

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

Replaced synonym: Elyna humilis C.A.Mey. ex Trautv., Trudy Imp. S.-Peterburgsk. Bot. Sada 1: 21. 187. 1871. Kobresia humilis (C.A.Mey. ex Trautv.) Serg. in Schischkin, Fl. URSS 3: 111. 1935. Kobresia royleana (Nees) Boeckeler var. humilis (C.A.Mey. ex Trautv.) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 46. 1909; non Carex humilis Leyss. (1761).

Kobresia persica Kük. & Bornm., Oesterr. Bot. Z. 47: 133. 1897; non *Carex persica* Nelmes (1939).

Kobresia royleana (Nees) Boeckeler var. *parvinux* T.Koyama, Acta Phytotax. Geobot. 16: 168. 1956.

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.

Replaced synonym: Kobresia prainii Kük., Bull. Herb. Boissier, sér. 2, 4: 50. 1904; non *Carex prainii* Kük. (1903).

Kobresia utriculata C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 67. 1908; non *Carex utriculata* Boott (1939).

Kobresia prainii Kük. var. elliptica Y.C.Yang in C.Y.Wu, Fl. Xizang. 5: 387, f. 217. 1987.

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.

Basionym: Kobresia bistaminata W.Z.Di & M.J.Zhong, Acta Bot. Boreal.-Occid. Sin. 6(4): 275. 1986. Kobresia myosuroides (Vill.) Fiori ssp. bistaminata (W.Z.Di & M.J.Zhong) S.R.Zhang, Novon, 9: 453. 1999.

Kobresia kashgarica Dickoré, Stapfia, 39: 79. 1995.

Distribution: From Karakorum to western China.

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

Basionym: Kobresia bonatiana Kük., Bull. Géogr. Bot. 22: 250. 1912.

Kobresia fragilis C.B.Clarke, J. Linn. Soc., Bot. 36: 267. 1903. Schoenoxiphium fragile (C.B.Clarke) C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 67. 1908. non Carex fragilis Boott (1858).

Carex curvata Boott, Ill. Gen. Carex 1: 2, pl. 5. 1858, non Knaf (1847). Kobresia curvata C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 68. 1908.

Schoenoxiphium clarkeanum Kük., Bull. Herb. Boissier, sér. 2, 4: 49. 1904. Kobresia clarkeana (Kük.) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 48. 1909; non Carex clarkeana Kük. (1904).

Kobresia clarkeana (Kük.) Kük. var. megalantha Kük., Bull. Géogr. Bot. 22: 249. 1912.

Kobresia hispida Kük., Acta Horti Gothob. 5: 39. 1930.

Kobresia yuennanensis Hand.-Mazz., Symb. Sin. 7: 1256. 1936.

Kobresia curticeps (C.B.Clarke) Kük. var. gyirongensis Y.C.Yang in C.Y.Wu, Fl. Xizang. 5: 391, f. 222. 1987.

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.

Replaced synonym: Kobresia sibirica (Turcz. ex Ledeb.) Boeckeler, Linnaea 39: 7. 1875. Elyna sibirica Turcz. ex Ledeb., Fl. Ross. 4(2): 262. 1852; non Carex sibirica Willd. ex Kunth (1837).

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

Kobresia macrocarpa Clokey ex Mack., N. Amer. Fl. 18: 5. 1931. Kobresia bellardii (All.) Degl. ex Loisel. var. macrocarpa (Clokey ex Mack.) H.D.Harr., Man. Pl. Colorado 641. 1954; non Carex macrocarpa Phil. (1858).

Kobresia smirnovii N.A.Ivanova, Bot. Zhurn. S.S.S.R. 24: 480. 1939; non *Carex smirnovii* V.I.Krecz. (1935).

Kobresia hyperborea A.E.Porsild, Bull. Natl. Mus. Canada 121: 103. 1951; non *Carex hyperborea* Drejer (1841).

Kobresia hyperborea A.E.Porsild var. alaskana Duman, Bull. Torrey Bot. Club 83: 194. 1956.

Kobresia hyperborea A.E.Porsild var. lepagei Duman, Bull. Torrey Bot. Club 83: 194. 1956. Kobresia schoenoides (C.A.Mey.) Steud. var. lepagei (Duman) B.Boivin, Naturaliste Canad. 94: 525. 1967.

Distribution: Subarctic to north-western USA.

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. Basionym: Kobresia brandisii C.B. Clarke ex Jana & R.C.Srivast., J. Jap. Bot. 89: 205, f. 1&2. 2014.

Distribution: Western Himalaya (India).

Carex breviprophylla O.Yano, nom. nov.

Replaced synonym: Kobresia gandakiensis Rajbh. & H.Ohba in H. Ohba & S. B. Malla (eds.), Himal. Pl. 2: 132, f. 4h-o. 1991; non *Carex gandakiensis* Katsuy. (2008).

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.

Basionym: Kobresia burangensis Y.C.Yang in C.Y.Wu, Fl. Xizang. 5: 374, f. 208. 1986.

Distribution: South-western China (western Tibet).

Carex capillifolia (Decne.) S.R.Zhang, comb. nov. Basionym: Elyna capillifolia Decne. in Jacquemont, Voy. Inde. 4(Bot.): 173. 1844. Kobresia capillifolia (Decne.) C.B.Clarke, J. Linn. Soc., Bot. 20: 378. 1883.

Elyna spicata Boiss., Fl. Orient. 5: 394. 1882, non Schrad. (1806).

Kobresia brunnescens Boeckeler, Beitr. Cyper. 1: 40. 1888.

Kobresia elata Boeckeler, Beitr. Cyper. 2: 32. 1890.
Kobresia macrolepis Meinsh., Trudy Imp.
S.-Peterburgsk. Bot. Sada 18: 276. 1901. Elyna macrolepis (Meinsh.) Fomin & Woronow, Opred. Rast.
Kavk. 1: 173. 1909.

Kobresia capilliformis Ivanova, Bot. Zhurn. SSSR 24: 484. 1939.

Kobresia thomsonii Maxim. ex Ivanova, Bot. Zhurn. SSSR 24: 486. 1939, pro syn.

Kobresia oviczinnikovii T.V.Egorova in Grubov, Pl. As. Centr. 3: 33. 1967, syn. nov.

Kobresia yushuensis Y.C.Yang, Acta Biol. Plateau Sin. 2: 6. 1984.

Distribution: From Caucasus to western China.

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

Kobresia cercostachys (Franch.) C.B.Clarke, J. Linn. Soc., Bot. 37: 267. 1903.

Kobresia stiebritziana Hand.-Mazz., Akad. Wiss. Wien, Math.-Naturwiss. Kl., Anz. 57: 54. 1920.

Kobresia nepalensis (Nees) Kük. var. stiebritziana (Hand.-Mazz.) R.C.Srivast., Novon 8(2): 203. 1998.

Distribution: Bhutan, Sikkim, south-western China.

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

Replaced synonym: Kobresia duthiei C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 697. 1894; non Carex duthiei C.B.Clarke (1894).

Kobresia rostrata C.B.Clarke ex Ivanova, Bot. Zhurn. SSSR 24: 500. 1939, nom. nud., pro syn.; non *Carex rostrata* Stokes (1787).

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.

Basionym: Kobresia coninux F.T.Wang & Tang, Acta Phytotax. Sin. 1: 182. 1951.

Kobresia pusilla Ivanova, Bot. Zhurn. SSSR 24: 496. 1939; non Carex pusilla Arv.-Touv. (1872).

Kobresia helanshanica W.Z.Di & M.J.Zhong, Acta Bot. Boreal.-Occid. Sin. 5 (4): 311, f. 1. 1985.

Kobresia daqingshanica X.Y.Mao, Acta Sci. Nat. Univ. Intramongol. 19(2): 341, f. 1. 1988.

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

Kobresia curticeps (C.B.Clarke) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 47. 1909.

Distribution: Central & eastern Himalaya to southern Tibet.

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

Basionym: Kobresia deasyi C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 68. 1908.

Kobresia schoenoides (C.A.Mey.) Steud., Syn. Pl. Glumac. 2: 246. 1855. *Elyna schoenoides* C.A.Mey., Verzeichn. Pfl. Cauc. Casp.: 29. 1831; non *Carex* schoenoides Schrank (1789).

Kobresia pamiroalaica Ivanova, Bot. Zhurn. SSSR 24: 481. 1939.

Kobresia pamiralaica Ivanova in R.R. Schreder, Fl. Uzbekist. 1: 347, 540. 1941.

Kobresia septatonodosa Koyama, Acta Phytotax Geobot. 16: 168. 1956.

Kobresia maquensis Y.C.Yang, Acta Biol. Plateau Sin. 2: 4, f. 3. 1984.

Kobresia lacustris P.C.Li, Acta Bot Yunnan. 12(1): 14. 1990.

Kobresia glaucifolia F.T.Wang & Tang ex P.C.Li, Acta Phytotax. Sin. 37(2): 153. 1999.

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.

Basionym: Kobresia esbirajbhandarii Rajbh. & H.Ohba, J. Jap. Bot. 62: 272. 1987.

Distribution: Nepal.

Carex esenbeckii Kunth, Enum. Pl. 2: 522. 1837 Kobresia esenbeckii (Kunth) Noltie, Edinburgh J. Bot. 50(1): 43. 1993. Kobresia esenbeckii (Kunth) F.T.Wang & Tang ex P.C.Li in W.T.Wang, Vasc. Pl. Hengduan Mount. 2: 2352. 1994, later isonym.

Carex trinervis Nees in Wight, Contr. Bot. India 120. 1834, non Degl. (1807). Kobresia trinervis (Nees) Boeckeler, Linnaea 39: 4. 1875. Hemicarex trinervis (Nees) C.B.Clarke, J. Linn. Soc., Bot. 20: 382. 1883.

Kobresia seticulmis Boeckeler, Linnaea 39: 3. 1875. Holmia seticulmis (Boeckeler) Fedde & J.Schust., Just's Bot. Jahresber. 41(2): 10. 1913 (publ. 1918).

Kobresia hookeri Boeckeler, Linnaea 39: 4. 1875. Hemicarex hookeri (Boeckeler) Benth., J. Linn. Soc., Bot. 18: 367. 1881.

Carex mutans Boott ex C.B.Clarke, J. Linn. Soc., Bot. 20: 383. 1883.

Carex polygyna Boeckeler, Beitr. Cyper. 1: 40. 1888. Kobresia hookeri Boeckeler var. dioica C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 695. 1894.

Kobresia angusta C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 695. 1894.

Kobresia foliosa C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 696. 1894.

Kobresia trinervis (Nees) Boeckeler var. foliosa (C.B.Clarke) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 43. 1909. Distribution: Himalaya to south-western China.

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

Replaced synonym: Hemicarex filicina C.B.Clarke, J. Linn. Soc., Bot. 20: 384. 1883. Kobresia filicina (C.B.Clarke) C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 696. 1894; non Carex filicina Nees (1834).

Kobresia filicina (C.B.Clarke) C.B.Clarke var. subfilicinoides P.C.Li, Acta Phytotax. Sin. 37(2): 155. 1999; non Carex subfilicinoides Kük. (1930).

Distribution: Eastern Himalaya, south-western China.

Etymology: The first part of the name, *fili-*, threadlike, 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.

Basionym: Kobresia fissiglumis C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 696. 1894. Kobresia esenbeckii (Kunth) Noltie var. fissiglumis (C.B.Clarke) Noltie, Edinburgh J. Bot. 50(1): 43. 1993.

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

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

Basionym: Kobresia gammiei C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 68. 1908.

Kobresia williamsii Koyama, Bot. Mag. (Tokyo) 86 (1004): 279, pl. 3. 1973.

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

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

Basionym: Kobresia handel-mazzettii Ivanova, Bot. Zhurn. SSSR 24: 494. 1939.

Kobresia capillifolia (Decne.) C.B.Clarke var. condensata Kük., Notes Roy. Bot. Gard. Edinburgh 7: 134. 1912.

Kobresia condensata (Kük.) S.R.Zhang & Noltie, Fl. China 23: 274. 2010.

Kobresia royleana (Nees) Boeckeler var. himalaica Rajbh. & H.Ohba in H. Ohba & S. B. Malla (eds.), Himal. Pl. 2: 150. 1991.

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

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

Basionym: Kobresia harae Rajbh. & H.Ohba, J. Jap. Bot. 62: 193 (1987), as 'harai'.

Distribution: India, Nepal.

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

Basionym: Kobresia hohxilensis R.F.Huang, Biol. & Human Physiol. Hoh Xil Region, 101. 1996.

Kobresia stolonifera Y.C.Tang ex P.C.Li, Acta Phytotax. Sin. 37(2): 154. 1999.

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

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

Replaced synonym: Kobresia graminifolia C.B.Clarke, J. Linn. Soc., Bot. 36: 268. 1903; non Carex graminifolia Cherm. (1923).

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

Basionym: Kobresia kanaii Rajbh. & H.Ohba in H. Ohba & S. B. Malla (eds.), Himal. Pl. 2: 135, f. 6. 1991.

Distribution: Nepal, Sikkim.

Carex kangdingensis S.R.Zhang, **nom. nov.** Replaced synonym: Kobresia falcata F.T.Wang & Tang ex P.C.Li, Acta Bot. Yunnan 12 (1): 18, f. 9. 1990; non *Carex falcata* Turcz. (1838).

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. Basionym: Schoenoxiphium kobresioideum Kük., Bull. Jard. Bot. Buitenzorg III 16: 312. 1940. Kobresia kobresioidea (Kük.) J. Kern, Acta Bot. Neerl. 7: 795. 1958. Distribution: Northern Sumatra.

Carex kokanica (Regel) S.R.Zhang, comb. nov.

Basionym: Elyna kokanica Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 7: 563. 1880.

Trilepis royleana Nees, Linnaea 9: 305. 1834; non Carex royleana Nees (1834). Kobresia royleana (Nees) Boeckeler, Linnaea 39: 8. 1875. Kobresia stenocarpa (Kar. & Kir.) Steud. var royleana (Nees) C.B.Clarke, J. Linn. Soc., Bot. 20: 381. 1883.

Elyna stenocarpa Kar. & Kir., Bull. Soc. Imp. Naturalistes Moscou 15(3): 526. 1842; non Carex stenocarpa Turcz. ex Krecz. (1935). Kobresia stenocarpa (Kar. & Kir.) Steud., Synop. Pl. Glum. 2: 246. 1854.

Kobresia stenocarpa (Kar. & Kir.) Steud. var. simplex Y.C.Yang in C.Y.Wu, Fl. Xizang. 5: 395, f. 224. 1987.

Kobresia paniculata Meinsh., Trudy Imp. S.-Peterburgsk. Bot. Sada 18(3): 279. 1901. Kobresia royleana (Nees) Boeckeler var. paniculata (Meinsh.) Kük, in Engler (ed.), Pflanzenr. 38(IV, 20): 46. 1909.

K. minshanica F.T.Wang & Tang ex Y.C.Yang, Acta Biol. Plateau Sin. 2: 1. 1984. Kobresia royleana (Nees) Boeckeler ssp. minshanica (F.T.Wang & Tang ex Y.C.Yang) S.R.Zhang, Novon 9: 453. 1999.

K. menyuanica Y.C.Yang, Acta Biol. Plateau Sin. 2: 3. 1984.

Distribution: Western Asia (Afghanistan), Central Asia, Himalaya, western China.

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

Carex lepidochlamys (F.T.Wang & Tang ex P.C.Li) S.R.Zhang, comb. nov.

Basionym: Kobresia lepidochlamys F.T.Wang & Tang ex P.C.Li, Acta Bot. Yunnan. 12(1): 15, f. 6. 1990.

Kobresia cuneata Kük., Acta Horti Gothob. 5: 39. 1930; non Carex cuneata Ohwi (1931).

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

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

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

Replaced synonym: Kobresia kuekenthaliana Hand.-Mazz., Symb. Sin. 7: 1258. 1936. Schoenoxiphium kuekenthalianum (Hand.-Mazz.) Ivanova, Bot. Zhurn. SSSR 24: 501. 1939; non Carex kuekenthaliana Appel & A.Brückn. (1891).

Distribution: South-western China (Sichuan).

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.

Basionym: Kobresia littledalei C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 67. 1908. Kobresia tibetica Maxim. var. littledalei (C.B.Clarke) P.C.Li in W.T.Wang, Vasc. Pl. Hengduan Mount. 2: 2349. 1994.

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

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

Basionym: Kobresia filifolia (Turcz.) C.B.Clarke var. macroprophylla Y.C.Yang, Acta Biol. Plateau Sin. 2: 8, f. 5. 1984. Kobresia macroprophylla (Y.C.Yang) P.C.Li in L.K.Dai & S.Y.Liang, Fl. Reipubl. Popul. Sin. 12: 17. 2000.

Kobresia filifolia (Turcz.) C.B.Clarke, J. Linn. Soc., Bot. 20: 381. 1883. Elyna filifolia Turcz., Bull. Soc. Imp. Naturalistes Moscou 28(1): 353. 1855; non Carex filifolia Nutt. (1818). Kobresia capillifolia (Decne.) C.B.Clarke var. filifolia (Turcz.) Kük., Finska Vet.-Soc. Föhr. 65(8): 1. 1902–1903.

Kobresia gracilis Meinsh., Acta Horti Petrop. 18: 276. 1901; non Carex gracilis Curtis (1782).

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.

Basionym: Kobresia mallae Rajbh. & H.Ohba, J. Jap. Bot. 62: 270. 1987.

Distribution: Nepal.

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

Kobresia myosuroides (Vill.) Fiori in Fiori et al., Fl. Anal. Ital. 1: 125. 1896. *Elyna myosuroides* (Vill.) Fritsch ex Janch., Mitt. Naturwiss. Vereins Univ. Wien 5: 110. 1907.

Carex bellardii All., Fl. Pedem. 2: 264. 1785. Kobresia bellardii (All.) Degl. ex Loisel., Fl. Gall. 2: 626. 1807.

Carex hermaphrodita J. F. Gmel, Syst. Nat. 2: 138. 1791.

Kobresia scirpina Willd., Sp. Pl. ed. 4, 4(1): 205. 1805.

Elyna spicata Schrad., Fl. Germ. 1: 155. 1806.

Carex affinis R.Br., Bot. App. 750. 1823.

Kobresia nardina Hornem. in G. C. Oeder & al., Fl. Dan. 74. 1827.

Kobresia filiformis Dewey, Amer. J. Sci. Arts 29: 253. 1836.

Elyna filiformis Steud., Syn. Pl. Glumac. 2: 245. 1855.

Carex vulcanicola Nakai, Bot. Mag. (Tokyo) 28: 327. 1914.

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

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

Replaced synonym: Kobresia nepalensis (Nees) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 46: 40, f. 9. 1909. Uncinia nepalensis Nees in Wight, Contr. Bot. India 129. 1834; non Carex nepalensis Spreng. (1826).

Carex linearis Boott, Ill. Gen. Carex 1: 51, pl. 136. 1858, non Clairv. (1811). *Hemicarex linearis* (Boott) Benth., J. Linn. Soc., Bot. 18: 367. 1881.

Carex linearis Boott var. elachista C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 713. 1894. Kobresia nepalensis (Nees) Kük. var elachista (C.B.Clarke) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 40. 1909.

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.

Replaced synonym: Kobresia woodii Noltie, Edinburgh J. Bot. 50(1): 48, f. 1h-l. 1993; non Carex woodii Dewey (1846).

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.

Basionym: Blysmocarex nudicarpa Y.C.Yang, Acta Bot. Yunnan. 4(4): 325. 1982. Kobresia nudicarpa (Y.C.Yang) S.R.Zhang, Acta Phytotax. Sin. 33(2): 160. 1995. Kobresia macrantha Boeckeler var. nudicarpa

(Y.C.Yang) P.C.Li in L.K.Dai & S.Y.Liang, Fl. Reipubl. Popul. Sin. 12: 26. 2000. *Blysmocarex macrantha* (Boeckeler) Ivanova ssp. *nudicarpa* (Y.C.Yang) D.S.Deng, Guihaia 22: 120. 2002.

Kobresia macrantha Boeckeler, Beitr. Cyper. 1: 39. 1888. Blysmocarex macrantha (Boeckeler) Ivanova, Bot. Zhurn. SSSR 24: 502. 1939; non Carex macrantha Boeckeler (1888).

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

Basionym: Kobresia paramjitii Jana, Noltie, R.C.Srivast & A.Mukh., Indian J. Plant Sci. 3 (online): 106. 2014.

Distribution: Sikkim.

Carex parvula O.Yano, nom. nov.

Replaced synonym: Kobresia pygmaea (C.B.Clarke) C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 696. 1894. Hemicarex pygmaea C.B.Clarke, J. Linn. Soc., Bot. 20: 383. 1883; non Carex pygmaea Boeckeler (1876).

Kobresia pygmaea C.B.Clarke var. filiculmis Kük., Acta Horti Gothob. 5: 37. 1930; non *Carex filiculmis* Franch. & Sav. (1878).

Kobresia microstachya Ivanova, Bot. Zhurn. SSSR 24: 488. 1939; non Carex microstachya Ehrh. (1784).

Kobresia koelzii Kük. ex Ivanova, Bot. Zhurn. SSSR 24: 498. 1939, pro syn.

Distribution: From Himalaya to northern and western China.

Etymology: The specific epithet refers to the dwarf habit.

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

Replaced synonym: Kobresia inflata P.C.Li, Acta Bot. Yunnan. 12(1): 16. 1990; non Carex inflata Huds. (1762). *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 prainii Kük., Bull. Herb. Boissier, sér. 2, 4: 51. 1903

Replaced synonym: Kobresia sikkimensis Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 47. 1909; non Carex sikkimensis C.B.Clarke (1894).

Distribution: Nepal to Assam.

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

Replaced synonym: Kobresia loliacea F.T.Wang & Tang ex P.C.Li, Acta Bot. Yunnan. 12(1): 13. 1990; non *Carex loliacea* L. (1753).

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.

Basionym: Kobresia pseudolaxa C.B.Clarke, J. Linn Soc., Bot. 20: 381. 1883.

Kobresia laxa Nees in Wight, Contr. Bot. India 119. 1834; non Carex laxa Wahlenb. (1803). Elyna laxa (Nees) Kunth, Enum. Pl. 2: 534. 1837. Hemicarex laxa (Nees) Benth., J. Linn. Soc., Bot. 18: 367. 1881. Schoenoxiphium laxum (Nees) Ivanova, Bot. Zhurn. SSSR 24: 501. 1939.

Schoenoxiphium hissaricum Pissjauk., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR. 12: 72. 1950. Kobresia hissarica (Pissjauk.) Soják, Nár. Mus. Odd. Prír. 148: 194. 1979 (publ. 1980). Kobresia laxa Nees ssp. hissarica (Pissjauk.) Kukkonen, Ann. Naturhist. Mus. Wien, B 98B(Suppl.): 91. 1996.

Kobresia afghanica Raymond, Dansk Bot. Ark. 14: 17. 1965.

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.

Basionym: Kobresia pseuduncinoides Noltie, Edinburgh J. Bot. 50(1): 47, f. 1a-g. 1993.

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.

Basionym: Kobresia rcsrivastavae Jana, Indian J. Fundam. Appl. Life Sci. 2: 256. 2012.

Distribution: India (Uttaranchal).

Carex sanguinea Boott, Proc. Linn. Soc. London 1: 285. 1846

Kobresia sanguinea (Boott) Raymond, Biol. Skr. 14(4): 19. 1965.

Distribution: Eastern Afghanistan to western Himalaya.

Carex sargentiana (Hemsl.) S.R.Zhang, comb. nov.

Basionym: Kobresia sargentiana Hemsl., J. Linn. Soc., Bot. 30: 139. 1894. Kobresia robusta Maxim. var. sargentiana (Hemsl.) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 36. 1909.

Kobresia robusta Maxim., Bull. Acad. Imp. Sci. St.-Petersbourg, n.s., 29: 218. 1883; non *Carex robusta* F. Nyl. (1844).

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.

Basionym: Kobresia setschwanensis Hand.-Mazz., Symb. Sin. 7: 1254. 1936.

Kobresia longearistita P.C.Li, Acta Bot. Yunnan. 12(1): 16, f. 8. 1990.

Kobresia pinetorum F.T.Wang & Tang ex P.C.Li, Acta Bot. Yunnan: 12(1): 14, f. 5. 1990.

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

Carex siamensis (Ohwi) S.R.Zhang, comb. nov.

Basionym: Kobresia siamensis Ohwi, Acta Phytotax. Geobot. 23: 109. 1968.

Kobresia curvirostris (C.B.Clarke) C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 699. 1894. *Hemicarex* curvirostris C.B.Clarke, J. Linn. Soc., Bot. 20: 384. 1883; non Carex curvirostra Hartm. (1832).

Distribution: Eastern Himalaya to northern Thailand.

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

Carex simpliciuscula Wahlenb., Kongl. Vetensk.

Acad. Nya Handl. 24(2): 141. 1803

Kobresia simpliciuscula (Wahlenb.) Mack., Bull. Torrey Bot. Club 50: 349. 1923.

Carex bipartita All., Fl. Pedem. 2: 265. 1785, nom. rej. *Kobresia bipartita* (All.) Dalla Torre, Atlas Alpenfl. 2: 216. 1882.

Schoenus monoicus Sm., Engl. Bot. t. 1410. 1805. Kobresia caricina Willd., Sp. Pl. ed. 4, 4: 206. 1805.

Carex lacustris Balbis ex Willd., Sp. Pl. ed. 4, 4: 206. 1805, pro syn.

Carex hybrida Schuhr ex Willd., Sp. Pl. 4: 206. 1805, pro syn.

Carex mirabilis Host, Icon. Descr. Gram. Austriac. 4: 44, pl. 78. 1809.

Elyna caricina Mert. et Koch in Röhling, Deutschl. Fl. ed. 3, 1: 458. 1823.

Carex lobata Willd. ex Kunth, Enum. Pl. 2: 533. 1837, pro syn.

Kobresia simpliciuscula (Wahlenb.) Mack. var. americana Duman, Bull. Torrey Bot. Club 83: 194. 1956.

Kobresia filifolia (Turcz.) C.B.Clarke ssp. subfilifolia T.V.Egorova, Jurtzev & V.V.Petrovsky, Bot. Zhurn. (Moscow & Leningrad) 66(7): 1042. 1981. Kobresia simpliciuscula (Wahlenb.) Mack. ssp. subfilifolia (T.V.Egorova, Jurtzev & V.V.Petrovsky) T.V.Egorova, Novosti Sist. Vyssh. Rast., 20: 84. 1983. Kobresia simpliciuscula (Wahlenb.) Mack. var. subfilifolia (T.V.Egorova, Jurtzev & V.V.Petrovsky) A.E.Kozhevn., Sosud. Rast. Sovet. Dal'nego Vostoka, 3: 229. 1988.

Kobresia simpliciuscula (Wahlenb.) Mack. ssp. subholarctica T.V.Egorova, Novosti. Sist. Vyssh. Rast., 20: 83. 1983. Kobresia simpliciuscula (Wahlenb.) Mack. var. subholarctica (T.V.Egorova) A.E.Kozhevn., Sosud. Rast. Sovet. Dal'nego Vostoka, 3: 229. 1988. Kobresia subholarctica (T.V.Egorova) T.V.Egorova, Bot. Zhurn. (Moscow & Leningrad) 76(12): 1736 1991.

Distribution: Europe to Caucasus, subarctic America to western USA.

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

Basionym: Kobresia squamiformis Y.C.Yang, Acta Biol. Plateau Sin. 2: 9, f. 6. 1984, published as: 'squmaeformis'.

Kobresia setschwanensis Hand.-Mazz. ssp. squamiformis (Y.C.Yang) S.R.Zhang, Novon 9: 453. 1999.

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

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

Replaced synonym: Kobresia tibetica Maxim., Bull. Acad. Imp. Sci. St.-Petersbourg, n.s., 29: 219. 1884.

Kobresia capillifolia (Decne.) C.B.Clarke var. tibetica (Maxim.) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 36. 1909; non *Carex thibetica* Franch., orth. var. (1887).

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.

Basionym: Kobresia tunicata Hand.-Mazz., Symb. Sin. 7: 1254. 1936.

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

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

Kobresia uncinoides (Boott) C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 698. 1894.

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

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

Basionym: Kobresia vaginosa C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 695. 1894. Kobresia nepalensis (Nees) Kük. var. vaginosa (C.B.Clarke) Kük. in Engler, Pflanzenr. 38(IV, 20): 40. 1909. Kobresia nepalensis (Nees) Kük. ssp. vaginosa (C.B.Clarke) Koyama in Hara et al., Enum. Fl. Pl. Nepal 1: 113. 1978. Kobresia nepalensis (Nees) Kük. var. vaginosa (C.B.Clarke) R.C.Srivast., Fl. Sikkim 1: 225. 1996.

Kobresia cercostachys (Franch.) C.B.Clarke var. capillacea P.C.Li, Acta Bot. Yunnan. 12(1): 17. 1990. Distribution: Nepal, Sikkim, south-western China.

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

Basionym: Kobresia vibhae Jana, R.C.Srivast & Bhaumik, Indian J. Plant Sci. 3 (online): 110, pl. 5. 2014.

Distribution: South-eastern Himalaya.

Carex vidua Boott ex C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 713. 1894

Kobresia vidua (Boott ex C.B.Clarke) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 40. 1909.

Kobresia prattii C.B.Clarke, J. Linn. Soc., Bot. 36: 268. 1903.

Kobresia harrysmithii Kük., Acta Horti Gothob. 5: 37. 1930.

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

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

Basionym: Kobresia yadongensis Y.C.Yang in C.Y.Wu, Fl. Tibet. 5: 388, f. 219. 1987.

Distribution: South-western China (southern Tibet).

Carex yangii (S.R.Zhang) S.R.Zhang, comb. nov. Basionym: Kobresia yangii S.R.Zhang, Acta Phytotax. Sin. 33(2): 160. 1995.

Kobresia gracilis Y.C.Yang, Acta Biol. Plateau Sin. 2: 11, f. 7. 1984, non Meinsh. (1901).

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

TRANSFERS FROM SCHOENOXIPHIUM NEES TO CAREX L.

Carex basutorum (Turrill) Luceño &

Martín-Bravo, comb. nov.

Basionym: Schoenoxiphium basutorum Turrill, Bull. Misc. Inform. Kew 1914: 19. 1914.

Distribution: South Africa (Free State), Lesotho.

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

Basionym: Schoenoxiphium burkei C.B.Clarke, J. Linn. Soc. Bot. 20: 386. 1883.

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

Carex capensis Thunb., Prodr. Pl. Cap.: 14. 1794 Schoenoxiphium ecklonii Nees, Linnaea 10: 200. 1836. Archaeocarex ecklonii (Nees) Pissjauk., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 12: 83. 1950. Kobresia ecklonii (Nees) T.Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8: 80. 1961.

Schoenoxiphium thunbergii Nees, Linnaea 9: 305. 1834. Archaeocarex thunbergii (Nees) Pissjauk., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 12: 83. 1950.

Schoenoxiphium altum Kukkonen, Notes Roy. Bot. Gard. Edinburgh 43: 365. 1986.

Carex bisexualis C.B.Clarke in Harvey & auct. suc. (eds.), Fl. Cap. 7: 302. 1898.

Carex capensis Schkuhr, Beschr. Riedgräs. 2: 39. 1806, nom. illeg.

Carex zeyheri C.B.Clarke in Harvey & auct. suc. (eds.), Fl. Cap. 7: 303. 1898.

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

Distribution: South Africa (Cape Province).

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

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

Replaced synonym: Schoenoxiphium gracile Cherm., Bull. Soc. Bot. France 70: 300. 1923; non Carex gracilis Curtis (1782).

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. Basionym: Schoenoxiphium distinctum Kukkonen, Bot. Not. 131: 263. 1978.

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

Carex killickii Nelmes, Kew Bull. 10: 89. 1955 Replaced synonym: Schoenoxiphium filiforme Kük., Bull. Misc. Inform. Kew 1910: 129. 1910; non Carex filiformis L. (1753). Schoenoxiphium strictum Kukkonen, Notes Roy. Bot. Gard. Edinburgh 43: 366. 1986.

Schoenoxiphium molle Kukkonen, Notes Roy. Bot. Gard. Edinburgh 43: 366. 1986.

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

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

Replaced synonym: Schoenoxiphium buchananii C.B.Clarke ex C.B.Clarke in Harvey & auct. suc. (eds.), Fl. Cap. 7: 305. 1898. Carex buchananii (C.B.Clarke ex C.B.Clarke) C.B.Clarke in Harvey & auct. suc. (eds.), Fl. Cap. 7: 305. 1898, nom. illeg.; non Carex buchananii Bergr. (1880). Kobresia buchananii (C.B.Clarke) T.Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8: 80. 1961.

Distribution: South Africa (Natal), Lesotho.

Etymology: The epithet honours Ilkka Kukkonen, a Finnish botanist who studied *Schoenoxiphium* and described several species.

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

Basionym: Schoenus lanceus Thunb., Prodr. Pl. Cap.: 17. 1794. Schoenoxiphium lanceum (Thunb.) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 28. 1909. Kobresia lancea (Thunb.) Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3. Bot. 8: 80. 1961.

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

Schoenoxiphium capense Nees, Linnaea 7: 533. 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 rufum Nees in Linnaea 10: 201. 1836. Carex rufa (Nees) Baill., Hist. Pl. 12: 340. 1894, nom. illeg., non Lam. (1779), non Schrank (1789). Archaeocarex rufus (Nees) Fedde & J.Schust., Just's Bot. Jahresber. 41(2): 7. 1913 (publ. 1918). Kobresia rufa (Nees) T.Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8: 80. 1961.

Schoenoxiphium dregeanum Kunth, Enum. Pl. 2: 529. 1837; non Carex dregeana Kunth (1837).

Schoenoxiphium rufum var. pondoense Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 31. 1909.

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 & Martín-Bravo, nom. nov.

Replaced synonym: Schoenoxiphium madagascariense Cherm., Bull. Soc. Bot. France 70: 299. 1923; non Carex madagascariensis Boeckeler (1884).

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

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

Carex perdensa (Kukkonen) Luceño &

Martín-Bravo, comb. nov.

Basionym: Schoenoxiphium perdensum Kukkonen, Bot. Not. 131: 265. 1978.

Distribution: South Africa (Cape Province, Natal).

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

Replaced synonym: Schoenoxiphium burttii Kukkonen, Notes Roy. Bot. Gard. Edinburgh 43: 365. 1986; non Carex burttii Noltie (1993).

Distribution: South Africa (Natal).

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

Carex schimperiana Boeckeler, Linnaea 40: 373. 1876

Schoenoxiphium schimperianum (Boeckeler) C.B.Clarke in Bull. Misc. Inform. Kew, Addit. Ser. 8: 67. 1908.

Carex densenervosa Chiov. in Ann. Bot. (Rome) 9: 149. 1911.

Schoenoxiphium bracteosum Kukkonen in Notes Royal Botanic Garden Edinburgh 43: 365. 1986. *Distribution:* Ethiopia to South Africa, Arabian Peninsula.

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

Basionym: Schoenoxiphium schweickerdtii Merxm. & Podlech, Mitt. Bot. Staatssamml. München 3: 529. 1960.

Distribution: South Africa (Natal).

Carex spartea Wahlenb., Kongl. Vetensk. Acad. Nya Handl. 1803: 149. 1803

Schoenoxiphium sparteum (Wahlenb.) C.B. Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 67. 1908. Archaeocarex spartea (Wahlenb.) Pissjauk. Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 12: 83. 1950. Kobresia spartea (Wahlenb.) T. Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8: 80. 1961. Uncinia spartea (Wahlenb.) Spreng., Syst. Veg. 3: 830. 1826.

Schoenoxiphium kunthianum Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 31. 1909. Archaeocarex kunthiana (Kük.) Pissjauk., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 12: 83. 1950. Kobresia kunthiana (Kük.) T. Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8: 80. 1961.

Carex bolusii C.B.Clarke in Harvey & auct. suc. (eds.), Fl. Cap. 7: 304. 1898.

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.

Schoenoxiphium caricoides C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 67. 1908.

Schoenoxiphium caricoides var. major (C.B.Clarke) C.B.Clarke, Bull. Misc. Inform. Kew, Addit. Ser. 8: 67. 1908.

Uncinia sprengelii Nees, Linnaea 10: 205. 1836, nom illeg.; Carex sprengelii (Nees) Boeckeler, Linnaea 40: 371. 1876, nom. illeg.

Distribution: Uganda, Kenya, South Africa, Madagascar.

Carex uhligii K.Schum. ex C.B.Clarke, Bot. Jahrb. Syst. 38(2): 136. 1906

Replaced synonym: Schoenoxiphium lehmannii (Nees) Kunth ex Steud., Syn. Pl. Glumac. 2: 245. 1855. Uncinia lehmannii Nees, Linnaea 10: 206. 1836. Schoenoxiphium sparteum var. lehmannii (Nees) Kük. in Engler, Pflanzenr. 38(IV, 20): 32. 1909. Kobresia

lehmannii (Nees) T.Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8: 80. 1961; non *Carex lehmannii* Drejer (1844).

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.

Basionym: Uncinia aspericaulis G.A.Wheeler, Darwiniana 45: 131. 2007.

Distribution: Juan Fernández Islands (Alejandro Selkirk).

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

Replaced synonym: Uncinia caespitosa Colenso ex Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 287. 1853; non Carex caespitosa L. (1753).

Uncinia caespitosa var. collina Petrie, Trans. & Proc. New Zealand Institute 52: 19. 1920.

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.

Basionym: Uncinia auceps de Lange & Heenan, Phytotaxa 104 (1): 12–20. 2013.

Distribution: New Zealand (Chatham Islands).

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

Basionym: Uncinia aucklandica Hamlin, Domin. Mus. Bull. 19: 63. 1959.

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

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

Replaced synonym: Uncinia compacta R.Br., Prodr. Fl. Nov. Holl.: 241. 1810. Carex compacta (R.Br.) Poir. in Lamarck, Encycl., Suppl. 3: 282. 1813, nom. illeg.; non Carex compacta Lam. (1779).

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 Brown's original epithet, which presumably refers to the dense inflorescences of this species, to provide a link between the new name and the original name.

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

Replaced synonym: Uncinia flaccida S.T.Blake, Proc. Roy. Soc. Queensland 51: 49. 1939 (publ. 1940); non Carex flaccida Sw. ex Kunth (1837).

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 Blake's 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.

Replaced synonym: Uncinia sulcata K.L.Wilson, Telopea 5: 620. 1994; non Carex sulcata Schur (1858).

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.

Replaced synonym: Uncinia tenella R.Br., Prodr. Fl. Nov. Holl.: 241. 1810.

Carex 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.

Replaced synonym: Uncinia banksii Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 287. 1853. Uncinia riparia

var. banksii (Boott) C.B.Clarke, J. Linn. Soc., Bot. 20: 392. 1883; non Carex banksii Boott (1846).

Uncinia capillaris Colenso, Trans. & Proc. New Zealand Institute 20: 210. 1888; non Carex capillaris L. (1753).

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'Acugna: 35. 1808

Uncinia brevicaulis (Thouars) Kunth, Enum. Pl. 2: 528. 1837.

Uncinia breviculmis Carmich., Trans. Linn. Soc. London 12: 508. 1819.

Uncinia rigida Boeckeler, Flora 65: 64. 1882. Uncinia brevicaulis var. rigida (Boeckeler) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 52. 1909.

Uncinia cylindrica Franch., Miss. Sci. Cap Horn 5: 379. 1889. Uncinia macloviana var. cylindrica (Franch.) Kük., Bot. Centralbl. 76: 212. 1898.

Uncinia phleoides var. laticarpa Kük., Bot. Centralbl. 82: 130. 1900. Uncinia brevicaulis var. laticarpa (Kük.) Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 52. 1909.

Uncinia brevicaulis f. montana Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 52. 1909.

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

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

Basionym: Uncinia cheesemanniana Boeckeler, Bot. Jahrb. Syst. 5: 521. 1884.

Uncinia nervosa Boott in J.D.Hooker, Fl. Tasman. 2: 102. 1858. Uncinia compacta var. nervosa (Boott) C.B.Clarke, J. Linn. Soc., Bot. 20: 395. 1883.

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.

Replaced synonym: Uncinia clavata (Kük.) Hamlin, Domin. Mus. Bull. 19: 68. 1959. Uncinia australis var. clavata Kük. in Cheeseman, Man. New Zealand Fl.: 802. 1906. Uncinia uncinata var. clavata (Kük.) Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 62. 1909; non Carex clavata Thunb. (1794).

Distribution: New Zealand (North & South Islands).

Etymology: From the Greek *koryne*, club or mace, Latinized as *coryne*, plus the adjectival suffix *-oideus*, *-a*, *-um*, indicating resemblance of this species' spikes to small clubs.

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

Replaced synonym: Uncinia involuta Hamlin, Domin. Mus. Bull. 19: 49. 1959; non Carex × involuta (Bab.) Syme (1870).

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

Etymology: The name refers to the curled leaf tips in this species.

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

Replaced synonym: Uncinia leptostachya Raoul, Ann. Sci. Nat., Bot., III, 2: 116. 1844; non Carex leptostachya Boiss. (1882).

Distribution: New Zealand (North & South Islands).

Etymology: The name refers to the bluish colour of the leaves; from the Latin *cyaneus*, dark blue.

Carex dawsonii (Hamlin) K.L.Wilson, comb. nov. Basionym: Uncinia dawsonii Hamlin, Trans. Roy. Soc. New Zealand, Bot. 2: 128. 1963.

Distribution: New Caledonia.

Carex debilior (F.Muell.) K.L.Wilson, comb. nov. Basionym: Uncinia debilior F.Muell., Fragm. 8: 151. 1874. Uncinia filiformis var. debilior (F.Muell.) W.R.B.Oliv., Trans. & Proc. New Zealand Institute 49: 128. 1917.

Distribution: Australia (Lord Howe Island).

Carex delacosta Kuntze, Revis. Gen. Pl. 3(2): 332. 1898

Replaced synonym: Uncinia macloviana Gaudich., Voy. Uranie: 412. 1829. Uncinia gracilis var. macloviana (Gaudich.) C.B.Clarke, J. Linn. Soc., Bot. 20: 400. 1883. Uncinia brevicaulis var. macloviana (Gaudich.) Kük. in Engler (ed.), Pflanzenr. 38(IV, 20): 52. 1909; non Carex macloviana d'Urv. (1826).

Uncinia montana Phil., Anales Univ. Chile 1865(2): 322. 1865. Uncinia macloviana var. montana (Phil.) Kük., Bot. Centralbl. 82: 132. 1900; non Carex montana L. (1753).

Uncinia delacosta Steud. in W.Lechler, Berberid. Amer. Austral.: 52. 1857, nom. nud.

Distribution: Chile to southern Argentina.

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.

Basionym: Uncinia dikei Nelmes, Kew Bull. 4: 377. 1949.

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.

Replaced synonym: Uncinia macrophylla Steud., Syn. Pl. Glumac. 2: 244. 1855; non Carex macrophylla Hochst. ex Steud. (1855).

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

Uncinia phalaroides Boott ex C.B.Clarke, J. Linn. Soc., Bot. 20: 396. 1883; non *Carex phalaroides* Kunth (1837).

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. Basionym: Uncinia drucei Hamlin, Domin. Mus. Bull.

19: 58. 1959.

Uncinia drucei var. payciflora Hamlin, Domin. Mus. Bull. 19: 59. 1959.

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

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

Basionym: Uncinia ecuadorensis G.A.Wheeler & Goetgh., Aliso 15: 10. 1996 (publ. 1997).

Distribution: Northern and central Ecuador.

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

Replaced synonym: Uncinia divaricata Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 286. 1853. Uncinia compacta var. divaricata (Boott) Hook.f., Handb. N. Zeal. Fl. 1: 309. 1864; non Carex divaricata Kük. (1903).

Uncinia clarkei Petrie, Trans. & Proc. New Zealand Institute 20: 185. 1888. Uncinia compacta var. clarkei (Petrie) Cheeseman, Man. New Zealand Fl.: 800. 1906. non Carex clarkii E.W.Berry, Am. Nat. 39: 347 (1905).

Uncinia compacta var. Petriei C.B.Clarke in Cheeseman, Man. New Zealand Fl.: 800. 1906. Uncinia divaricata var. Petriei (C.B.Clarke) Hamlin, Domin. Mus. Bull. 19: 57. 1959.

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.

Basionym: Uncinia egmontiana Hamlin, Domin. Mus. Bull. 19: 33. 1959.

Uncinia silvestris var. squamata Hamlin, Domin. Mus. Bull. 19: 28. 1959.

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

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

Replaced synonym: Uncinia hookeri Boott in J.D.Hooker, Fl. Antarct.: 91. 1844. Uncinia riparia var. hookeri (Boott) Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 63. 1909; non Carex hookeri Kunth (1837).

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

Uncinia erinacea (Cav.) Pers., Syn. Pl. 2: 534. 1807. Agistron erinacea (Cav.) Raf., Good Book: 28. 1840.

Uncinia longifolia Kunth, Enum. Pl. 2: 527. 1837. Uncinia longiaristata Steud., Syn. Pl. Glumac. 2: 243. 1855.

Uncinia philippii Hohen. ex Steud., Syn. Pl. Glumac. 2: 243. 1855.

Uncinia macrotricha Franch., Miss. Sci. Cap Horn 5: 379. 1889.

Uncinia erinacea var. angustata Kük., Bot. Centralbl. 82: 101. 1900.

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 douglasii Boott in J.D.Hooker, Fl. Antarct. 2: 369. 1846. Uncinia macloviana var. douglasii (Boott) Kük., Bot. Centralbl. 82: 133. 1900.

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 douglasii*.

Carex firmula (Kük.) J.R. Starr, comb. & stat. nov.

Basionym: Uncinia tenuis f. firmula Kük., Repert. Spec. Nov. Regni Veg. 16: 433. 1920.

Uncinia tenuis Poepp. ex Kunth, Enum. Pl. 2: 525. 1837; non Carex tenuis Rudge (1804). Uncinia gracilis Decne. in Dumont d'Urville, Voy. Pôle Sud, Atlas: t. 6, f. B. 1843; non Carex gracilis Curtis (1782). Distribution: Central America to Falkland Islands.

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

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

Replaced synonym: Uncinia tenuifolia G.A.Wheeler & Goetgh., Aliso 14: 144. 1995; non Carex tenuifolia Poir. (1789).

Distribution: South-eastern Ecuador.

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

Carex hamata Sw., Prodr. Veg. Ind. Occ.: 18. 1788 Uncinia hamata (Sw.) Urb., Symb. Antill. 2: 169. 1900.

Carex jamaicensis Poir. in Lamarck, Encycl., Suppl. 3: 246. 1813.

Carex uncinata Schkuhr ex Steud., Nomencl. Bot., ed. 2, 1: 297. 1840.

Uncinia phleoides C.A.Mey., Bull. Acad. Roy. Sci. Bruxelles 9(2): 249. 1842, nom. illeg.

Uncinia jamaicensis Liebm., Mexic. Neldeagt. Pl., V, 2: 272. 1851, nom. illeg.

Uncinia mexicana Steud., Syn. Pl. Glumac. 2: 243. 1855. Uncinia hamata var. mexicana (Steud.) Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 54. 1909.

Uncinia galeottii Boott ex C.B.Clarke, J. Linn. Soc., Bot. 20: 400. 1883.

Uncinia multifolia Boeckeler, Bot. Jahrb. Syst. 8: 207. 1887.

Uncinia hamata f. angustifolia Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 54. 1909.

Distribution: Mexico to Tropical America.

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

Replaced synonym: Uncinia astonii Hamlin, Domin. Mus. Bull. 19: 64. 1959; non Carex astonii Hamlin (1968).

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.

Replaced synonym: Uncinia scabra Colenso ex Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 285. 1853; non Carex scabra Hoppe (1800).

Uncinia disticha Colenso, Trans. & Proc. New Zealand Institute 20: 210. 1888; non *Carex disticha* Huds. (1762).

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.

Basionym: Uncinia horizontalis Colenso, Trans. & Proc. New Zealand Institute 15: 334. 1883.

Uncinia rupestris Raoul, Ann. Sci. Nat., Bot., II, 2: 117. 1844; non Carex rupestris All. (1785).

Uncinia compacta var. viridis C.B.Clarke, J. Linn. Soc., Bot. 20: 395. 1883. Uncinia caespitosa var. viridis (C.B.Clarke) Hamlin, Domin. Mus. Bull. 19: 52. 1959. Uncinia viridis (C.B.Clarke) Edgar in Moore & Edgar Fl. N. Zeal. 2: 229. 1970.

Uncinia compacta var. caespitiformis Kük. in L.Cockayne, Rep. Bot. Surv. Stewart I.: 42. 1909.

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.

Replaced synonym: Uncinia gracilenta Hamlin, Domin. Mus. Bull. 19: 47. 1959; non Carex gracilenta Boott ex Boeckeler (1877).

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.

Basionym: Uncinia koyamae Gómez-Laur., Brenesia 18: 92. 1980.

Distribution: Mexico (Chiapas), Costa Rica.

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

Replaced synonym: Uncinia paludosa G.A.Wheeler & Goetgh., Aliso 14: 142. 1995; non Carex paludosa Gooden. (1794).

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 & Goetghebeur, 1995, 1997).

Carex lechleriana (Steud.) J.R.Starr, comb. nov.

Basionym: Uncinia lechleriana Steud., Syn. Pl. Glumac. 2: 244. 1855.

Distribution: Chile to southern Argentina.

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

Replaced synonym: Uncinia filiformis Colenso ex Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 286. 1853; non Carex filiformis L. (1753).

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.

Basionym: Uncinia tenella var. longifructus Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 66. 1909. Uncinia longifructus (Kük.) Petrie, Trans. & Proc. New Zealand Institute 52: 17. 1920.

Distribution: New Zealand (North & South Islands).

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

Basionym: Uncinia macloviformis G.A.Wheeler, Darwiniana 45: 136. 2007.

Distribution: Juan Fernández Islands (Alejandro Selkirk).

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

Replaced synonym: Uncinia chilensis G.A.Wheeler, Aliso 15: 1. 1996 (publ. 1997); non Carex chilensis Brongn. (1833).

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.

Replaced synonym: Uncinia lacustris G.A.Wheeler, Aliso 14: 141. 1995; non Carex lacustris Willd. (1805).

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.

Replaced synonym: Uncinia ferruginea Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 288. 1853. Uncinia australis var. ferruginea (Boott) C.B.Clarke in Cheeseman, Man. New Zealand Fl.: 802. 1906. Uncinia unciniata var. ferruginea (Boott) Kük. in Pflanzenr. 38: 62. 1909; non Carex ferruginea Scop. (1772).

Uncinia nigra Colenso, Trans. & Proc. New Zealand Institute 17: 253. 1885; non *Carex nigra* (L.) Reichard (1778).

Uncinia variegata Colenso, Trans. & Proc. New Zealand Institute 20: 211. 1888; non Carex variegata (All.) Lam. (1792).

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.

Basionym: Uncinia meridensis Steyerm., Fieldiana, Bot. 28(1): 61. 1951.

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

Uncinia smithii Philcox, Kew Bull. 15: 229. 1961.

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. Basionym: Uncinia caespitosa var. minor Kük. in

T.F.Cheeseman, Man. New Zealand Fl.: 802. 1906. Uncinia angustifolia Hamlin, Domin. Mus. Bull. 19:

42. 1959.

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.

Basionym: Uncinia multifaria Nees ex Boott in J.D.Hooker, Fl. Antarct. 2: 369. 1846.

Uncinia macrostachya É.Desv. in C.Gay, Fl. Chil. 6: 229. 1854. Uncinia multifaria var. macrostachya (É.Desv.) Kük., Bot. Centralbl. 82: 102. 1900.

Distribution: South-central & southern Chile.

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

Basionym: Uncinia negeri Kük., Bot. Centralbl. 76: 210. 1898.

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.

Basionym: Uncinia nemoralis K.L.Wilson, Telopea 5: 620. 1994.

Distribution: South-eastern Australia.

Carex obtusifolia (Heenan) K.A.Ford, comb. nov. Basionym: Uncinia obtusifolia Heenan, New Zealand J. Bot. 34 (1): 11. 1996.

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

Carex papualpina K.L.Wilson, nom. & stat. nov. Replaced synonym: Uncinia compacta var. alpina Noot., Blumea 24: 519. 1978; non Carex alpina Schrank (1789).

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 Boott in J.D.Hooker, Handb. N. Zeal. Fl. 1: 309. 1864; non Carex sinclairii Boott 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.

Replaced synonym: Uncinia fuscovaginata Kük., Bull. Herb. Boissier, II, 4: 50 (1904). Uncinia purpurata var. fuscovaginata (Kük.) Cheeseman, Man. New Zealand Fl.: 801. 1906; non Carex fuscovaginata Kük. (1904).

Uncinia fuscovaginata var. caespitans Hamlin, Domin. Mus. Bull. 19: 21. 1959.

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.

Basionym: Uncinia perplexa Heenan & de Lange, New Zealand J. Bot. 39 (3): 376. 2001.

Distribution: New Zealand (North Island).

Carex phleoides Cav., Icon. 5: 40. 1799

Uncinia phleoides (Cav.) Pers., Syn. Pl. 2: 534. 1807.

Agistron phleoides (Cav.) Raf., Good Book: 28. 1840. Uncinia trichocarpa C.A.Mey., Cyperac. Nov.: 11.

1831. Uncinia phleoides var. trichocarpa (C.A.Mey.) C.B.Clarke, J. Linn. Soc., Bot. 20: 399. 1883.

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 durvillei Steud., Syn. Pl. Glumac. 2: 243. 1855.

Uncinia urvillei Steud., Syn. Pl. Glumac. 2: 243. 1855.

Uncinia longispica Boeckeler, Flora 41: 650. 1858. Uncinia trichocarpa var. longispica (Boeckeler) Kük., Bot. Centralbl. 82: 131. 1900.

Uncinia montteana 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 longifolia Phil. ex C.B.Clarke, J. Linn. Soc., Bot. 20: 399. 1883.

Uncinia phleoides var. nux-nigra C.B.Clarke, J. Linn. Soc., Bot. 20: 399. 1883.

Uncinia phleoides f. longispica Franch., Miss. Sci. Cap Horn 5: 378. 1889.

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

Uncinia phleoides var. brachytricha Speg., Revista Fac. Agron. Univ. Nac. La Plata 3: 626. 1897.

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.

Replaced synonym: Uncinia costata Kük., Repert. Spec. Nov. Regni Veg. 16: 433. 1920; non Carex costata Schwein. (1824).

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.

Replaced synonym: Uncinia affinis (Colenso ex C.B.Clarke) Hamlin, Domin. Mus. Bull. 19: 30. 1959. Uncinia riparia var. affinis Colenso ex C.B.Clarke, J. Linn. Soc., Bot. 20: 392. 1883. non Carex affinis R.Br. in J.Richardson, Bot. App: 750 (1823).

Uncinia purpurata var. subcaespitosa Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 61. 1909.

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.

Replaced synonym: Uncinia rubra Colenso ex Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 287. 1853; non Carex rubra H.Lév. & Vaniot (1909).

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.** Basionym: Uncinia purpurata Petrie, Trans. & Proc. New Zealand Institute 17: 272. 1885.

Distribution: New Zealand (South Island).

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

Basionym: Uncinia rapaensis H.St.John, Nordic J. Bot. 4: 60. 1984.

Distribution: Austral Islands (Rapa-Iti).

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

Basionym: Uncinia × rubrovaginata Hamlin, Domin. Mus. Bull. 19: 24. 1959. U. fuscovaginata × U. rubra.

Distribution: New Zealand (North Island).

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

Replaced synonym: Uncinia andina G.A.Wheeler, Hickenia 2: 218. 1997; non Carex andina Phil. (1896).

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.

Replaced synonym: Uncinia scabriuscula G.A.Wheeler, Hickenia 2: 215. 1997; non Carex scabriuscula Mack. (1908).

Distribution: Southern Chile to south-western Argentina.

Etymology: The epithet for the new name means somewhat scabrous in Latin, and is used to highlight the characteristically scabrid culms of this species (Wheeler, 1997a)

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

Basionym: Uncinia sclerophylla Nelmes, Kew Bull. 4: 143 (1949).

Uncinia ohwiana T.Koyama, Bot. Mag. (Tokyo) 69: 214 (1956).

Distribution: New Guinea highlands.

Carex silvestris (Hamlin) K.A.Ford, comb. nov. Basionym: Uncinia silvestris Hamlin, Domin. Mus. Bull. 19: 26. 1959.

Distribution: New Zealand (North Island).

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

Basionym: Uncinia rubra var. strictissima Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 64. 1909. Uncinia strictissima (Kük.) Petrie, Trans. & Proc. New Zealand Institute 47: 55. 1915.

Uncinia rigida Petrie, Trans. & Proc. New Zealand Institute 17: 271. 1885, nom. illeg.

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

Carex subsacculata (G.A.Wheeler & Goetgh.)

J.R.Starr, comb. nov.

Basionym: Uncinia subsacculata G.A.Wheeler & Goetgh., Aliso 14: 145. 1995.

Distribution: Ecuador (Pichincha).

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

Replaced synonym: Uncinia elegans (Kük.) Hamlin, Domin. Mus. Bull. 19: 11. 1959. Uncinia sinclairii var. elegans Kük. in Cheeseman, Man. New Zealand Fl.: 799. 1906. Uncinia macrolepis var. elegans (Kük.) Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 60. 1909; non Carex elegans Willd. (1787).

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

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

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

Basionym: Uncinia subtrigona Nelmes, Kew Bull. 4: 144 (1949).

Uncinia riparia var. stolonifera Kük. & Steen., Bull. Jard. Bot. Buitenzorg, III, 13: 213 (1934).

Distribution: Borneo (Mt Kinabalu), Philippines (Mt Apo), New Guinea highlands.

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

Replaced synonym: Uncinia distans Colenso ex Boott in J.D.Hooker, Fl. Nov.-Zel. 1: 286. 1853; non Carex distans L. (1759).

Uncinia nelmesii Hamlin, Trans. Roy. Soc. New Zealand, Bot. 2: 127. 1963; non Carex nelmesii H.E.Hess (1953).

Distribution: New Zealand (North Island).

Etymology: The name refers to the light green leaves of this species.

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

Replaced synonym: Uncinia triquetra Kük., Bot. Centralbl. 82: 97. 1900. Uncinia lechleriana var. triquetra (Kük.) Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 58. 1909; non Carex triquetra Boott (1846).

Distribution: Magellan Region of South America.

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

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

Replaced synonym: Uncinia austroamericana G.A.Wheeler, Darwiniana 43: 271. 2005; non Carex austroamericana G.A.Wheeler (1986).

Distribution: Southern Chile to Tierra del Fuego.

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

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

Replaced synonym: Uncinia riparia R.Br., Prodr. Fl. Nov. Holl.: 241 (1810). Carex riparia (R.Br.) Poir. in Lamarck, Encycl., Suppl. 3: 282 (1813), nom. illeg., non Carex riparia Curtis (1783).

Distribution: South-eastern Australia.

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

Carex uncinata L.f., Suppl. Pl.: 413. 1782

Uncinia uncinata (L.f.) Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 62. 1909.

Uncinia australis Pers., Syn. Pl. 2: 534. 1807, nom. illeg.

Carex hamosa Thouars, Esquisse Fl. Tristan d'Acugna: 35. 1808, nom. illeg.

Uncinia scaberrima Nees, Linnaea 9: 305. 1834, nom. inval.

Uncinia lindleyana Kunth, Enum. Pl. 2: 526. 1837. Uncinia rigidula Steud., Syn. Pl. Glumac. 2: 245. 1855.

Uncinia alopecuroides Colenso, Trans. & Proc. New Zealand Institute 15: 335. 1883.

Uncinia bractata Colenso, Trans. & Proc. New Zealand Institute 16: 341. 1884.

Uncinia pedicellata Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 61. 1909. Uncinia uncinata var. pedicellata (Kük.) Petrie, Trans. & Proc. New Zealand Institute 47: 54. 1915.

Uncinia uncinata var. laxior Carse, Trans. & Proc. New Zealand Institute 48: 240. 1916.

Uncinia uncinata var. uliginosa Skottsb., Acta Horti Gothob. 15: 328. 1944.

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

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

Replaced synonym: Uncinia araucana G.A.Wheeler, Aliso 15: 3. 1996 (publ. 1997); non Carex araucana Phil. (1896).

Distribution: South-central Chile (La Araucaria).

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 *Carex* (including *Uncinia*) in South America.

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

Basionym: Uncinia zotovii Hamlin, Domin. Mus. Bull. 19: 37. 1959.

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

TRANSFER FROM VESICAREX STEYERM. TO CAREX L.

Carex collumanthus (Steyerm.) L.E.Mora, Acta Biol. Colomb. 1: 40. 1982 Basionym: Vesicarex collumanthus Steyerm., Fieldiana, Bot. 28(1): 63. 1951.

Distribution: Western South America to north-western Venezuela.

INCERTAE SEDIS

Uncinia obtusata Colenso, Trans. & Proc. New Zealand Institute 16: 341. 1884.

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