











Research Article

A framework infrageneric classification of *Carex* (Cyperaceae) and its organizing principles

Global *Carex* Group

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Abstract Phylogenetic studies of *Carex* L. (Cyperaceae) have consistently demonstrated that most subgenera and sections are para- or polyphyletic. Yet, taxonomists continue to use subgenera and sections in *Carex* classification. Why? The Global *Carex* Group (GCG) here takes the position that the historical and continued use of subgenera and sections serves to (i) organize our understanding of lineages in *Carex*, (ii) create an identification mechanism to break the ~2000 species of *Carex* into manageable groups and stimulate its study, and (iii) provide a

framework to recognize morphologically diagnosable lineages within *Carex*. Unfortunately, the current understanding of phylogenetic relationships in *Carex* is not yet sufficient for a global reclassification of the genus within a Linnean infrageneric (sectional) framework. Rather than leaving *Carex* classification in its current state, which is misleading and confusing, we here take the intermediate steps of implementing the recently revised subgeneric classification and using a combination of informally named clades and formally named sections to reflect the current state of our knowledge. This hybrid classification framework is presented in an order corresponding to a linear arrangement of the clades on a ladderized phylogeny, largely based on the recent phylogenies published by the GCG. It organizes *Carex* into six subgenera, which are, in turn, subdivided into 62 formally named Linnean sections plus 49 informal groups. This framework will serve as a roadmap for research on *Carex* phylogeny, enabling further development of a complete reclassification by presenting relevant morphological and geographical information on clades where possible and standardizing the use of formal sectional names.

Key words: *Carex*, clades, classification, sections, subgenera.

1 Classification Principles

Most subgenera and sections of the large genus *Carex* L. (Cyperaceae), ca. 2000 species, have been demonstrated to be polyphyletic (Starr et al., 1999; Yen & Olmstead, 2000; Roalson et al., 2001; Ford et al., 2006; Starr & Ford, 2009; Waterway et al., 2009, 2015a; Jiménez-Mejías et al., 2016a; Villaverde et al., 2020). Despite this fact, infrageneric classification of the genus helps to organize our understanding of phylogeny, identify species groups, and stimulate additional study of the genus. Our current understanding of *Carex* phylogeny is not yet sufficient for a global reclassification of the genus. Rather than leaving *Carex* classification in its current state, we here erect a taxonomic framework using a combination of informally named clades and formally named sections, organized within the subgeneric classification proposed by Villaverde et al. (2020), which reflects the current state of our knowledge of *Carex* lineages.

Our work builds on a long tradition of naming subgenera and sections to organize the complex diversity in *Carex* (e.g., Linnaeus, 1753; Schweinitz & Torrey, 1825; Kunth, 1837; Tuckerman, 1843; Bailey, 1887). The most complete classification frameworks to date include the worldwide revision of Cariceae by Kükenthal (1909), the North American revision by Mackenzie 1931–(1931–1935), the U.S.S.R treatment by Kreczetowicz (1935), the Russian treatment by Egorova (1999), the *Flora of North America* (Ball & Reznicek, 2002; hereafter FNA), and the *Flora of China* (Dai et al., 2010f; hereafter FOC). Citations of any of the treatments within FNA or FOC are referred to the use of these general abbreviations, with individual treatments of sections and their individual references provided in Tables 1 and 2, respectively. In addition, numerous sectional and subgeneric names have been published, particularly in floristic treatments, leading to a confusing array of hundreds of sectional names, despite many authors recognizing ~70 sections for the genus (Kükenthal, 1909; Mackenzie, 1931–1931–1935; Egorova, 1999; however, see Jiménez-Mejías et al., 2016a, which compiled 126 sections from the available treatments).

The proposed framework also builds on recent molecular progress into the circumscription of the genus and its

subgenera. The realignment of *Carex* to include the segregate genera *Cymophyllus*, *Kobresia*, *Schoenoxiphium*, and *Uncinia* (Waterway et al., 2015a) has somewhat complicated the infrageneric classification; however, infrageneric units have rarely been used for these segregate genera. A recent revision of subgeneric classification based on phylogenomic data provides the subgeneric framework used here (Villaverde et al., 2020). We present some taxonomic synonymy for those groups receiving formal classification ranks, but we do not attempt to provide an exhaustive synonymy here. That work will await more detailed studies of subgenera, named clades, and sections.

The Global *Carex* Group framework classification recognizes two formal Linnaean taxonomic levels, subgenera and sections, in addition to informally named clades. In this classification, we apply subgeneric and sectional names to accord as closely as possible with their historical use, but they are often applied here more broadly or more narrowly than historical usage where necessary to define monophyletic groups. In the process, we winnow those sectional names most widely used (following Egorova, 1999, FNA, and FOC, unless otherwise indicated) to identify names with priority, which are sometimes not the best known or most widely used names. In an effort to cover the entire genus, we do not endeavor to provide a comprehensive formal system of sectional names. Untangling intricate nomenclature and identifying types for the many available sectional names are beyond the scope of the current study. Instead, we here take the significant first step of identifying the clades to which the most widely used names apply, facilitating easier communication, and providing a clear link between the phylogeny and previously published works.

Informal clade names are used to represent clades that either have the potential to be described as formal sections eventually, but that are not currently recognized due to uncertainty about nomenclature or morphological diagnosability of the clade, or are strongly supported by molecular data—the only data we are considering for delimiting clades in this classification—but morphologically heterogeneous and probably best subdivided into readily recognized and diagnosable sections. Each informal name for terminal clades—clades that do not

Table 1 Treatments for *Carex* and segregate genera from the *Flora of North America*

Treatment	Reference
<i>Carex</i> L.	Ball & Reznicek (2002)
Sections	
<i>Acrocystis</i> Dumortier	Crins & Rettig (2002)
<i>Albae</i> (Ascherson & Graebner) Kükenthal	Ball (2002a)
<i>Ammoglochin</i> Dumortier	Reznicek (2002a)
<i>Anomalae</i> J.Carey	Cochrane (2002a)
<i>Aulocystis</i> Dumortier	Ball & Mastrogiuseppe (2002)
<i>Bicolores</i> (Tuckerman ex L.H.Bailey) Rouy	Ball (2002b)
<i>Capituligerae</i> Kükenthal	Murray (2002a)
<i>Carex</i> L.	Reznicek & Catling (2002a)
<i>Careyanae</i> Tuckerman ex Kükenthal	Bryson & Naczi (2002a)
<i>Ceratocystis</i> Dumortier	Crins (2002a)
<i>Chlorostachyae</i> Tuckerman ex Meinshausen	Ball (2002c)
<i>Chordorrhizae</i> (Heuffel) Meinshausen	Reznicek & Catling (2002b)
<i>Circinatae</i> Meinshausen	Murray (2002b)
<i>Clandestinae</i> G.Don	Crins (2002b)
<i>Collinsiae</i> (Mackenzie) Mackenzie	Standley (2002a)
<i>Cyperoideae</i> G.Don	Mastrogiuseppe (2002a)
<i>Deweyanae</i> (Tuckerman ex Mackenzie) Mackenzie	Naczi (2002)
<i>Dispermae</i> Ohwi	Toivonen (2002a)
<i>Divisae</i> H.Christ ex Kükenthal	Reznicek & Catling (2002c)
<i>Dornera</i> Heuffel	Murray (2002c)
<i>Filifoliae</i> (Tuckerman) Mackenzie	Mastrogiuseppe (2002b)
<i>Firmiculmes</i> (Kükenthal) Mackenzie	Crins (2002c)
<i>Foetidae</i> (Tuckerman ex L.H.Bailey) Kükenthal	Reznicek (2002b)
<i>Glareosae</i> G.Don	Toivonen (2002b)
<i>Glaucescents</i> Reznicek	Standley (2002b)
<i>Granulares</i> (O.Lang) Mackenzie	Cochrane & Naczi (2002)
<i>Griseae</i> (L.H.Bailey) Kükenthal	Naczi & Bryson (2002)
<i>Hallerianae</i> (Ascherson & Graebner) Rouy	Ball (2002d)
<i>Heleglochin</i> Dumortier	Cochrane (2002b)
<i>Hirtifoliae</i> Reznicek	Ball (2002e)
<i>Hispidae</i> Mackenzie ex Reznicek	Standley (2002c)
<i>Holarrhenae</i> (Döll) Pax	Reznicek & Catling (2002d)
<i>Hymenochlaenae</i> (Drejer) L.H.Bailey	Waterway (2002)
<i>Inflatae</i> Kükenthal	Standley (2002d)
<i>Lamprochlaenae</i> (Drejer) L.H.Bailey	Ball & Murray (2002)
<i>Laxiflorae</i> (Kunth) Mackenzie	Bryson & Naczi (2002b)
<i>Leptocephalae</i> L.H.Bailey	Cochrane (2002c)
<i>Leuchoglochin</i> Dumortier	Cochrane (2002d)
<i>Limosae</i> (Heuffel) Meinshausen	Ball (2002f)
<i>Longicaules</i> Mackenzie ex Reznicek	Mastrogiuseppe (2002c)
<i>Lupulinae</i> Tuckerman ex J. Carey	Reznicek (2002c)
<i>Macrocephalae</i> Kükenthal	Mastrogiuseppe (2002d)
<i>Mitratae</i> Kükenthal	Standley (2002e)
<i>Multiflorae</i> (J.Carey) Kükenthal	Standley (2002f)
<i>Nardinae</i> (Tuckerman) Mackenzie	Murray (2002d)
<i>Obtusatae</i> (Tuckerman) Mackenzie	Murray (2002e)
<i>Ovales</i> Kunth	Mastrogiuseppe et al. (2002)
<i>Paludosae</i> G.Don	Reznicek & Catling (2002e)
<i>Paniceae</i> G.Don	Rothrock & Reznicek (2002)
<i>Phacocystis</i> Dumortier	Standley et al. (2002)
<i>Phaestoglochin</i> Dumortier	Ball (2002g)
<i>Phyllostachyae</i> Tuckerman ex Kükenthal	Crins et al. (2002)
<i>Physoglochin</i> Dumortier	Cochrane (2002e)
<i>Pictae</i> Kükenthal	Ball (2002h)

Continued

Table 1 Continued

Treatment	Reference
<i>Porocystis</i> Dumortier	Ball (2002i)
<i>Racemosae</i> G.Don	Murray (2002f)
<i>Rhynchocystis</i> Dumortier	Reznicek (2002d)
<i>Rostrales</i> Meinschausen	Reznicek (2002e)
<i>Rupestres</i> (Tuckerman) Meinschausen	Ball (2002j)
<i>Schiedeanae</i> Kükenthal	Reznicek (2002f)
<i>Scirpinae</i> (Tuckerman) Kükenthal	Dunlop (2002)
<i>Scitae</i> Kükenthal	Murray (2002g)
<i>Shortianae</i> (L.H.Bailey) Mackenzie	Cochrane (2002f)
<i>Spirostachyae</i> (Drejer) L.H.Bailey	Crins & Reznicek (2002)
<i>Squarrosae</i> J.Carey	Ford & Reznicek (2002)
<i>Stellulatae</i> Kunth	Reznicek (2002g)
<i>Thuringiaca</i> G.Don	Standley (2002g)
<i>Triquetrae</i> (L.H.Bailey) Mackenzie	Ball (2002k)
<i>Vesicariae</i> (Heuffel) J.Carey	Reznicek & Ford (2002)
<i>Vulpinae</i> (Heuffel) H.Christ	Standley (2002h)
Other genera	
<i>Cymophyllus</i> Mackenzie	Reznicek (2002h)
<i>Kobresia</i> Willdenow	Ball (2002l)

contain additional nested named clades—is based on a representative species name, which is selected because it may be (i) the oldest or one of the oldest specific epithets in the clade, (ii) widely known, (iii) geographically widespread, and/or (iv) not easily confused with other formal or informal clade names. For example, the clade that includes the type species of *Carex* includes a heterogeneous assemblage of species and previously recognized sections (e.g., *Lupulinae*, *Pseudocypereae*, *Vesicariae*, etc.) and is here referred to as the “Hirta Clade,” since *Carex hirta* L. is the oldest name in the clade and the type species of the genus (see informal group VI.X.1. under subgenus *Carex* below for details). Clades that, in turn, contain other named clades are named using any two of the embedded clades.

The following list presents our proposed classification in an order corresponding to a linear arrangement of the clades on a ladderized phylogeny (largely following Jiménez-Mejías et al., 2016a; Martín-Bravo et al., 2019; Villaverde et al., 2020; Fig. 1). To avoid redundant and continuous citation of these three works, we will not make further reference to them, except as needed to address particularities. Conversely, additional relevant phylogenetic studies are cited where they provide insights into clade composition or whenever the accepted clade does not match the groupings shown by the above cited phylogenies. Similarly, comments about morphology rely primarily on the synopses and keys provided in Egorova (1999), FNA, and FOC, which are consequently not cited for morphological descriptions. However, where morphological comments are derived from other works, they have been cited.

Notes on circumscription are presented following many of the formal and informal classification units. At each classification level, lists of *incertae sedis* species are presented at the beginning of the recognized groups at

their respective classification level. Under each clade, corresponding validly published sectional names that overlap with or are included within the clade are listed (i.e., whenever the clade includes the type species of the section). Species affiliated with the sections or informal groups are listed in Appendix SI. The “Circumscription” field under each clade indicates the number of world’s *Carex* interpreted as being in the section/clade, based on both phylogenetic and morphological data, and the number of sampled taxa that we include based on any of the phylogenetic studies we have inspected is indicated in parentheses after the global number.

Throughout the study, we have assumed several terminological conventions to ease comparisons between clades and limit regional differences in terminology. Thus, inflorescence units are referred to as spikes rather than spikelets. Floral bracts are referred to as scales. Inflorescence prophylls are referred to as cladoprophylls, and flower prophylls under either the generic term perigynia (for clades whose perigynia are either all incompletely closed or vary in degree of closure) or the more specific utricle (only for clades in which all species have closed perigynia; see Jiménez-Mejías et al., 2016b). Throughout the study, the fruit is referred to as a nutlet.

Formal and informal classification units follow the following conventions: Roman numerals (I, II, etc.) correspond to the subgenera of Villaverde et al. (2020). Nested within the subgenera are unranked clades and named sections, organized as an outline with letter designations (A, B, C, etc.), and Arabic numerals (1, 2, 3, etc.), with a notable exception: species and clades of an uncertain placement are designated IS (*incertae sedis*), or where there is more than one in the same lineage they are designated IS1, IS2, etc., and placed in the outline where they fall in the guide tree (Fig. 1). The label “ISO” is reserved for taxa that have not been sequenced and cannot be reliably placed within any clade.

Table 2 Treatments for *Carex* and segregate genera from the *Flora of China*

Treatment	Reference
<i>Carex</i> L.	Dai et al. (2010f)
Sections	
<i>Acrocystis</i> Dumortier	Dai & Koyama (2010a)
<i>Albae</i> (Ascherson & Graebner) Kükenthal	Dai & Koyama (2010b)
<i>Anomalae</i> J.Carey	Dai & Koyama (2010c)
<i>Aulocystis</i> Dumortier	Liang & Koyama (2010a)
<i>Capituligerae</i> Kükenthal	Tang et al. (2010a)
<i>Carex</i> L.	Dai & Koyama (2010d)
<i>Careyanae</i> Tuckerman ex Kükenthal	Liang et al. (2010a)
<i>Chlorostachyae</i> Meinshausen	Dai & Koyama (2010e)
<i>Clandestinae</i> G.Don	Dai et al. (2010a)
<i>Confertiflorae</i> Franchet ex Ohwi	Dai et al. (2010b)
<i>Cryptostachyae</i> Franchet	Tang et al. (2010b)
<i>Cyperoideae</i> G.Don	Liang et al. (2010b)
<i>Debiles</i> (J.Carey) Ohwi	Dai & Koyama (2010f)
<i>Decorae</i> (Kükenthal) Ohwi	Liang et al. (2010c)
<i>Dispermae</i> Ohwi	Liang et al. (2010d)
<i>Echinochloomorphae</i> Y.L.Chang ex S.Yun Liang	Liang et al. (2010e)
<i>Euprepes</i> Nelmes & Airy Shaw	Zhang & Koyama (2010a)
<i>Foetidae</i> (Tuckerman ex L.H.Bailey) Kükenthal	Liang et al. (2010f)
<i>Forficulae</i> (Franchet ex Kükenthal) Raymond	Liang et al. (2010g)
<i>Gibbae</i> Kükenthal	Liang et al. (2010h)
<i>Glareosae</i> G.Don	Liang et al. (2010i)
<i>Glauciformes</i> Ohwi	Dai & Koyama (2010g)
<i>Graciles</i> Kükenthal	Dai & Koyama (2010h)
<i>Grallatoriae</i> Kükenthal	Tang et al. (2010c)
<i>Hangzhouenses</i> C.Z.Zheng, X.F.Jin & B.Y.Ding	Zhang & Tucker (2010)
<i>Heleoglochin</i> Dumortier	Liang et al. (2010j)
<i>Hemiscaposae</i> C.B.Clarke	Zhang et al. (2010a)
<i>Hirtae</i> Tuckerman ex Kükenthal	Dai & Koyama (2010i)
<i>Holarrhenae</i> (Döll) Pax	Liang et al. (2010k)
<i>Hymenochlaenae</i> (Drejer) L.H.Bailey	Dai et al. (2010c)
<i>Hypolytroides</i> Nelmes	Zhang & Koyama (2010b)
<i>Indicae</i> Tuckerman	Zhang et al. (2010b)
<i>Japonicae</i> Kükenthal	Zhang & Koyama (2010c)
<i>Lageniformes</i> (Ohwi) Nelmes	Tang et al. (2010h)
<i>Lamprochlaenae</i> Drejer	Dai & Koyama (2010j)
<i>Leuchoglochin</i> Dumortier	Tang et al. (2010d)
<i>Limosae</i> Meinshausen	Dai & Koyama (2010k)
<i>Macrocephalae</i> Kükenthal	Liang et al. (2010l)
<i>Mitratae</i> Kükenthal	Tang et al. (2010i)
<i>Molliculae</i> Ohwi	Dai et al. (2010d)
<i>Mundae</i> Kükenthal	Zhang & Koyama (2010d)
<i>Occlusae</i> C.B.Clarke	Dai & Koyama (2010l)
<i>Ovales</i> Kunth	Liang et al. (2010m)
<i>Paludosae</i> G.Don	Dai & Koyama (2010m)
<i>Paniceae</i> G.Don	Dai & Koyama (2010n)
<i>Phacocystis</i> Dumortier	Liang et al. (2010n)
<i>Phleoideae</i> Meinshausen	Liang et al. (2010o)
<i>Physodeae</i> H.Christ ex Kükenthal	Liang et al. (2010p)
<i>Physocarpae</i> Drejer ex L.H.Bailey	Dai et al. (2010e)
<i>Physoglochin</i> Dumortier	Tang et al. (2010e)
<i>Planatae</i> Akiyama	Liang et al. (2010q)
<i>Polystachyae</i> Tuckerman	Zhang & Koyama (2010e)
<i>Praelongae</i> (Kükenthal) Nelmes	Liang et al. (2010r)
<i>Pseudocypereae</i> Tuckerman ex Kükenthal	Dai & Koyama (2010o)

Continued

Table 2 Continued

Treatment	Reference
<i>Racemosae</i> G.Don	Liang & Koyama (2010b)
<i>Radicales</i> (Kükenthal) Nelmes	Dai & Koyama (2010p)
<i>Rarae</i> C.B.Clarke	Tang et al. (2010f)
<i>Remotae</i> C.B.Clarke	Liang et al. (2010s)
<i>Rhizopodae</i> Ohwi	Tang et al. (2010j)
<i>Rhomboidales</i> Kükenthal	Liang et al. (2010t)
<i>Rupestres</i> (Tuckerman) Mackenzie	Tang et al. (2010g)
<i>Scabrellae</i> Kükenthal	Zhang & Koyama (2010f)
<i>Secalinae</i> (O.Lang) O.Lang ex Kükenthal	Dai & Koyama (2010q)
<i>Siderostictae</i> Franchet ex Ohwi	Tang et al. (2010k)
<i>Stellulatae</i> (Kunth) Christ	Liang et al. (2010u)
<i>Surculosae</i> Raymond	Zhang & Koyama (2010g)
<i>Thomsonianae</i> Y.L.Chang ex S.Yun Liang	Liang et al. (2010v)
<i>Tuminenses</i> Y.L.Chang	Liang & Koyama (2010c)
<i>Vulpinae</i> (Heuffel) H.Christ	Liang et al. (2010w)
Other genera	
<i>Kobresia</i> Willdenow	Zhang & Noltie (2010)

2 A New Framework Infrageneric Classification of *Carex*

Carex L., Sp. Pl. 2: 972. 1753.

Type *Carex hirta* L. (designated by Hitchcock & Green, 1929: 187).

- = *Cymophyllus* Mack.
- = *Kobresia* Willd.
- = *Schoenoxiphium* Nees
- = *Uncinia* Pers.

I. *Carex* subg. *Siderosticta* Waterway, in Villaverde et al., Bot. J. Linn. Soc. 194: 156. 2020.

This subgeneric name was created, as multiple studies support this clade as the sister lineage to the rest of *Carex* (Waterway et al., 2009; Starr et al., 2015; Jiménez-Mejías et al., 2016a; Martín-Bravo et al., 2019; Uzma et al., 2019; Villaverde et al., 2020). This is a highly variable clade whose distribution is entirely restricted to East and Southeast Asia.

I.A. *Carex* sect. *Siderostictae* (Franch.) Ohwi, Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 11: 428. 1936.

This clade includes all species traditionally placed in sects, *Hemiscaposae*, *Siderostictae*, and *Surculosae*, but those sectional circumscriptions are not supported by current phylogenetic hypotheses. Whereas red plant bases are only known from subg. *Carex*, some species of traditional sect. *Siderostictae* are pink-red at the base of the plant or at the base of leaves and bracts, sometimes more widespread throughout the plant. This pink-red appears to be present in all sect. *Siderostictae* and is also present in some species of sect. *Hemiscaposae*, such as *Carex scaposa* (Starr J & Ford B, pers. obs.). This clade is further distinguished from the sister sect. *Hypolytroides* by its bisexual spikes and leafless fertile culms appearing to arise laterally to leaf rosettes. It is also one of the few *Carex* groups containing species with unequivocally entomophilous traits.

Despite its small size, this group is morphologically heterogeneous with inflorescences varying from simple to highly compound. Similarly, leaves can be relatively narrow

and lanceolate to extremely wide and pseudopetiolate. The widest leaves in Cyperaceae (up to 12 cm) are found in this group (Starr et al., 2015).

Circumscription 27 species (19 sampled).

Other known Sectional Names *Hemiscaposae* C.B.Clarke, *Surculosae* Raymond.

Geographic Distribution East and Southeast Asia.

Additional relevant literature Waterway et al. (2009), Yano et al. (2014), and Starr et al. (2015).

I.B. *Carex* sect. *Hypolytroides* Nelmes, Kew Bull. 6: 121. 1951.

The two species of sect. *Hypolytroides* form the sister lineage to sect. *Siderostictae* (I.A.). They are easily recognized by their highly compound inflorescences with unisexual spikes, the staminate ones often distally disposed; true leafy stems lacking basal leaves; and utricles with honey-combed deposit of epicuticular wax, giving them a distinct grayish-blue color.

Circumscription 2 species (2 sampled): *Carex hypolytroides*, *C. moupinensis*.

Geographic Distribution East and Southeast Asia.

Non-*Siderosticta* *Carex*

Euthyceras–*Psyllophorae* Clade

Current phylogenetic hypotheses based on Sanger sequencing usually resolve a clade comprising subgenera *Euthyceras* and *Psyllophorae* with the *Curvula* Clade. This group has been recognized in previous publications as the "Caricoid clade" (Waterway & Starr, 2007). Phylogenomic approaches did not recover that clade (Villaverde et al., 2020).

II. *Carex* subg. *Psyllophorae* (Degl.) Peterm., Deutschl. Fl.: 602. 1849.

Current phylogenetic hypotheses resolve three major clades in this subgenus (Benítez-Benítez et al., in prep.). Although the recent megaphylogenies resolved several of the species in that subgenus as independent lineages or intermingled within other clades, it seems that this was due to incomplete marker sampling. The subgenus shows a striking disjunct distribution, with one clade centered in the

Western Palearctic, another in South America, and another in Southern Africa. It is a relatively old group with deep phylogenetic branches.

II.IS1. *Curvula* Clade

Current phylogenetic hypotheses place a clade including *C. baldensis* and *C. curvula* as sister to subgenus *Psyllophorae*, but on a short branch (Martín-Bravo et al., 2019; Villaverde et al., 2020). Accordingly, they have been provisionally placed in that subgenus. This group has a more-or-less capitate inflorescence, androgynous spikes, three stigmas, and well-developed, but not protruding, rachilla. *Carex baldensis* displays white scales and utricles,

and it is one of the few *Carex* species with unequivocal entomophilous traits.

Circumscription 2 species (2 sampled): *Carex baldensis*, *C. curvula*.

Known Sectional Names *Baldenses* Kük., *Curvulae* (Pax.) Asch. & Graebn.

Geographic distribution Mountains of Europe.

II.A. *Carex* sect. *Psyllophorae* Degl. in J.-L.-A. Loisel., Fl. Gallica, ed. 2, 2: 282. 1828.

This well-defined group includes species with uni- to multispicate inflorescences, due apparently to inflorescence reduction. The rachilla is sometimes visible and, in

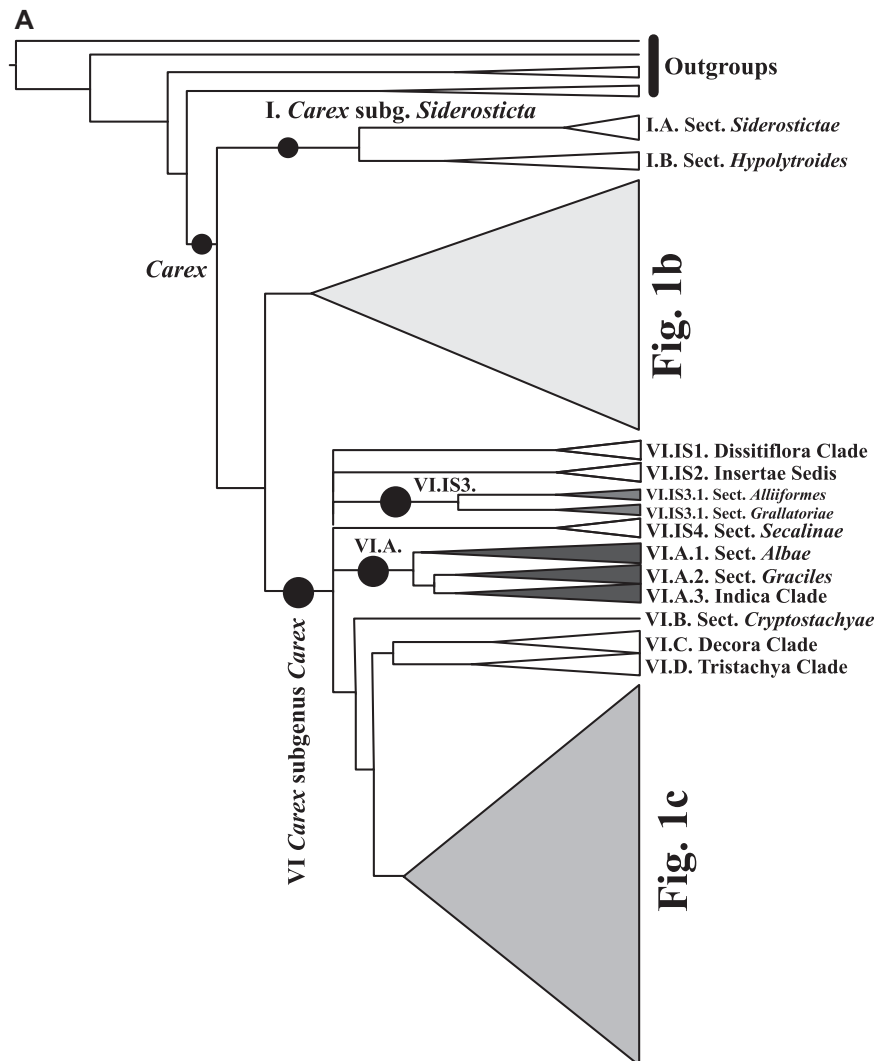


Fig. 1. Phylogenetic scaffold for the *Carex* classification based on a composite understanding of lineages (Jiménez-Mejías et al., 2016a; Martín-Bravo et al., 2019; Villaverde et al., 2020). **A**, Root, early branching events in *Carex*, *Carex* subgenus *Siderosticta*, and early branching events in *Carex* subgenus *Carex*. **B**, *Carex* subgenera *Euthyceras*, *Psyllophorae*, *Uncinia*, and *Vigna*. **C**, *Carex* subgenus *Carex*. Roman numeral/letter/number combinations refer to recognized sections/clades in the classification. Black dots on internal branches marked with Roman numeral/letter designations are clades recognized in the classification where subclades are recognized. To make it easier to visually recognize named subclades within clades, subclades are given the same gray shading to visually contrast the subclades recognized within clades with other clades. “E–P Clade” = *Euthyceras*–*Psyllophorae* Clade, “V–U Clade” = *Vigna*–*Uncinia* Clade.

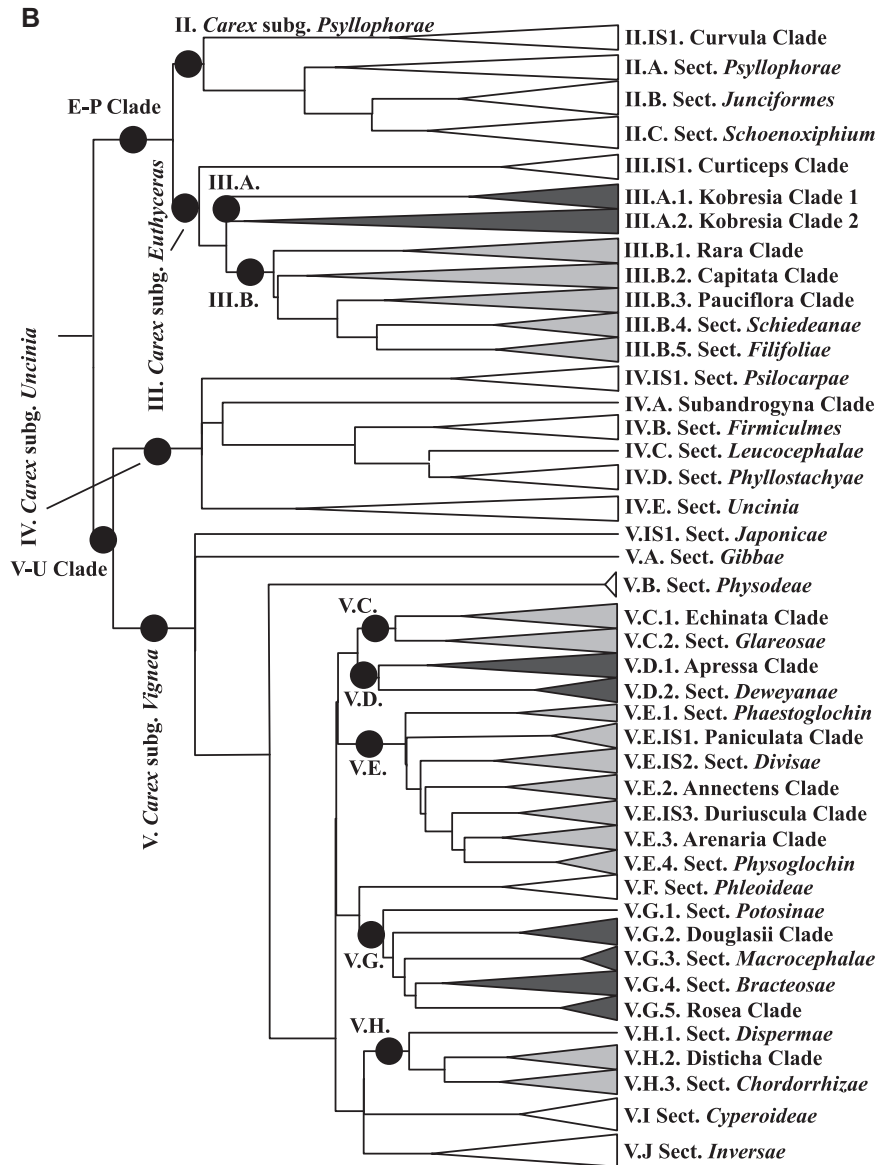


Fig. 1. Continued

some cases, gives rise to a staminate spike, whereas in most cases, it is vestigial. Cladophylls range from absent to funnelform or, rarely, fertile and utricle-like. Synapomorphies for this group include androgynous spikes with the staminate part linear and pistillate scales promptly deciduous.

Circumscription 7 species (7 sampled).

Other known sectional names *Caryotheca* V.I.Krecz. ex T.V.Egorova.

Geographic distribution Europe, Mediterranean Basin, Macaronesia, and East Tropical Africa.

II.B. *Carex* sect. *Junciformes* (Boeckeler) Kük. in H.G.A.Engler, Pflanzenr. IV, 20 (Heft 38): 82.

This section includes the species ascribed to sects. *Aciculares* and *Junciformes*, plus *C. phalaroides* and allies and *C.*

camptoglochin (Benítez-Benítez et al., in prep.). Most species in this group are characterized by inflorescences with a single, androgynous, usually dense spike having an inconspicuous staminate tip comprising up to six flowers above the 2–25-flowered pistillate portion. The exception is *C. phalaroides* and allies, which bear multispicate racemose inflorescences that would have evolved from unispicate ancestors.

Circumscription 28 species (23 sampled).

Other known sectional names *Aciculares* (Kük.) G.A.Wheeler.

Geographic distribution South America, in the Andes and Patagonia, reaching marginally Central America; three species in New Zealand.

II.C. *Carex* sect. *Schoenoxiphium* (Nees) Baill., Hist. pl., monogr. Cypér.: 345. 1894.

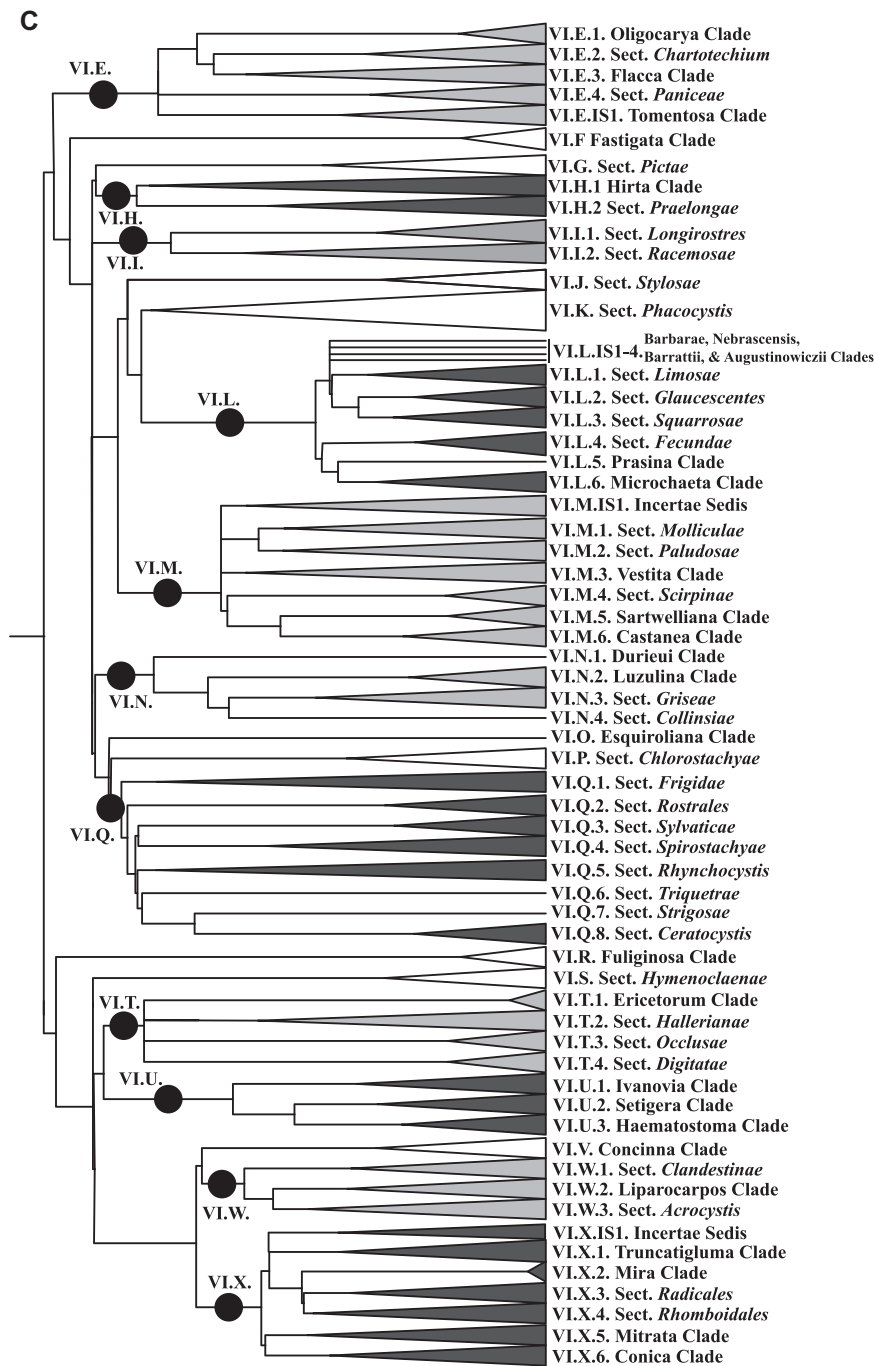


Fig. 1. Continued

This section comprises species formerly placed in the obsolete genus *Schoenoxiphium* Nees, but with the inclusion of *C. acocksii*. The section is defined by paniculate inflorescences that branch up to five times or are rarely unbranched or reduced to a single spike. Prophylls in this section have closed lateral margins, but the morphology varies depending on their position in the inflorescence: (i) tubular sterile cladoprophylls at the base of first-order branches; (ii) fertile and wide-mouthed (funnelform), prominently veined utriculiform cladoprophylls in intermediate or second-to-last-order branches; and (iii) last branching order

prophylls fully transformed into prominently veined and beaked utricles.

Circumscription 19 species (18 sampled).

Geographic distribution The center of diversity is in southeastern parts of Africa with a few species extending to southwestern Africa, East Tropical Africa, Madagascar, and southwestern Arabian Peninsula.

Additional relevant literature Gehrke et al. (2010), Villaverde et al. (2017b, 2021), Márquez-Corro et al. (2017, 2020), and Luceño et al. (2021).

III. *Carex* subg. *Euthyceras* Peterm., *Deutschl. Fl.* 602. 1849.

III.ISo. Incertae Sedis

Carex bucharica is a Central Asian species showing a striking resemblance to species from the North American sect. *Filifoliae* (e.g., filiform leaves and puberulent utricles). While poorly explored, connections between the Western North American and Central Asian floras have been previously reported (Weber, 2003). *Carex bucharica* has also been classified as a *Kobresia*.

Circumscription 1 species (0 sampled): *Carex bucharica*.

Known sectional names *Cardioperae* V.I.Krecz. ex T.V.Egorova.

Geographic distribution Central Asia.

III.IS1. Curticeps Clade

Two species traditionally placed in *Kobresia* form a modestly supported clade that is sister to the rest of subg. *Euthyceras*. These species share closed perigynia, forming utricles, and lax, branched inflorescences. The odd-looking *C. kobresioidea* from Sumatra may also belong to this clade.

Circumscription 3 species (2 sampled): *Carex curticeps*, *C. kobresioidea*, *C. prainii*.

Geographic distribution Himalayas and Southeast Asia.

III.A. Kobresia Clade

The *Kobresia* Clade embraces the majority of the species in the obsolete genus *Kobresia*, vaguely characterized by mostly having perigynia with margins open and rachillas sometimes branching in staminate spikes (Waterway et al., 2015a). The *Kobresia* Clade, as here defined, is composed of two large clades that are treated separately as *Kobresia* Clade 1 (III.A.1.) and *Kobresia* Clade 2 (III.A.2.). The placement of the unsampled species must be considered doubtful, awaiting clarification from molecular phylogenetic studies. The morphological affinities between the two clades are also uncertain. Both clades include paniculate *Kobresia* species that seem to have evolved from unispicate ancestors. *Kobresia* Clade 2 (III.A.2.) has more paniculate species than *Kobresia* Clade 1 (III.A.1.), and those species in *Kobresia* Clade 1 that are paniculate form a single clearly derived subclade. Morphological variation across the two clades needs more study before deciding whether they should be recognized as one section or two.

III.A.ISo. Kobresia Incertae Sedis

This includes four species originally described in the genus *Kobresia*, but they are uncertain in their relationships to the two recognized *Kobresia* clades.

Circumscription 4 species (0 sampled).

Geographic distribution Indian Himalaya.

III.A.1. Kobresia Clade 1

All members of this clade were traditionally placed in the obsolete genus *Kobresia*. This clade comprises a majority of the species of that former genus that bear unispicate unbranched inflorescences with open perigynia.

Circumscription 32 species (26 sampled).

Geographic distribution Himalaya to western and northern China, with a few species distributed into the Caucasus, one entering western North America, and another circumboreal.

III.A.2. Kobresia Clade 2

This clade includes two species formerly thought to belong to *Carex* sect. *Leucoglochin*, along with the majority of the

former *Kobresia* species with branched inflorescences. The perigynium structure in the clade is highly variable, ranging from open and scale-like to having the margin closed, and thus forming a utricle.

Circumscription 21 species (19 sampled).

Geographic distribution Central Asia, Himalaya to western and northern China, with few species distributed south into Southeast Asia as well as one circumboreal species.

III.B. Capitata–Schiedeanae Clade

This clade is further divided into five named clades, with each clade grouping species from one or more similar sections, comprising species mostly with unbranched terminal spikes, with the exception of sect. *Schiedianae*, which tends to have branching inflorescences.

III.B.1. Rara Clade

This clade combines the monotypic sect. *Leptocephalae* with sect. *Rarae*. Current sampling places *C. leptalea* (sect. *Leptocephalae*) sister to the samples included from *Rarae*, but almost half of that section has not yet been sampled. In addition, *C. rhizopoda*, type of sect. *Rhizopodae*, has also been found to be allied to the Rara Clade (Jin X-F et al., pers. comm.). Whether this clade is best treated as one or several sections, it requires more complete sampling and a more detailed morphological study.

Circumscription 27 species (16 sampled).

Known sectional names *Leptocephalae* L.H.Bailey, *Rarae* C.B.Clarke, *Rhizopodae* Ohwi.

Geographic distribution Asia and Australasia, except *C. leptalea*, which is mainly North American.

Additional relevant literature Oda et al. (2019).

III.B.2. Capitata Clade

This informal group is loosely defined by plants with a single terminal androgynous spike and with membranaceous, thin-walled veinless utricles (with the exception of *C. obtusata*, whose utricle is strongly coriaceous and conspicuously veined). The clade comprises the type and associated species of several sections, as well as *C. microglochin* from sect. *Leucoglochin*. The arrangement of the different sections within the clade is mostly unresolved, even though sect. *Capituligerae* plus the two species of sect. *Longespicatae* (*C. monostachya* and *C. runssoroensis*) form a strongly supported clade (Villaverde et al., 2015b). Denser gene sampling is needed before proposing a formal taxonomic treatment.

Circumscription 11 species (10 sampled).

Known sectional names *Capituligerae* Kük., *Longespicatae* Kük., *Nardinae* (Tuck.) Mack., *Obtusatae* (Tuck.) Mack., *Petraeae* (O.Lang) Kük.

Geographic distribution Mainly circumboreal, with disjunct species or populations in East Tropical Africa and Austral South America.

III.B.3. Pauciflora Clade

This is another somewhat heterogeneous assemblage of unispicate species. This clade includes the type and associated species of the previously recognized sects. *Circinatae*, *Dornera*, and *Inflatae*, as well as the type of sect. *Leucoglochin*, *C. pauciflora*. Further study is needed to figure out whether multiple sections should be considered here. All sampled species are from the Northern Hemisphere, but

some species from the sections represented in this clade are distributed in Southeast Asia, Australia, and New Zealand. Those non-North American species need to be sampled to determine whether or not they belong to this clade.

Circumscription: 14 species (10 sampled).

Known sectional names: *Circinatae* Meisn., *Dornera* Heuff., *Inflatae* Kük., *Leucoglochin* Dumort.

Geographic distribution: Holarctic with a few species disjunct in Southeast Asia, eastern Australia, and New Zealand.

III.B.4. *Carex* sect. *Schiedeanae* Kük., in H.G.A.Engler, *Pflanzenr.* 20[IV,38]: 255. 1909.

Species in this distinctive clade of dry-adapted *Carex* typically have branched inflorescences unlike other clades in the Capitatae–Schiediana Clade (III.B.) of subg. *Euthyceras*. This reacquisition of branched inflorescences from a putative unispicate ancestor is similar to the evolutionary pattern found in the Kobresia Clade (III.A.) in this same subgenus. They are all small caespitose species with compact inflorescences of uniformly short, androgynous spikes, with utricles variously short-pubescent, and often tuberculate and papillose as well. It is a remarkable group from an ecological point of view, with most species adapted to dry, even desert habitats, including one extreme calciphile (*C. gypsophila*). This section has, at times, included species from South America, but those species are a part of the Subandrogyna Clade (IV.A.) in subgenus *Uncinia*.

Circumscription 15 species (13 sampled). Ten of these have been recently described (Reznicek et al., 2021).

Geographic distribution Mexico and southwestern United States.

III.B.5. *Carex* sect. *Filifoliae* (Tuck.) Mack., in N.L.Britton et al., *N. Amer. Fl.* 18: 177. 1935.

This section forms the sister lineage to sect. *Schiedeanae*, which has a similar geographic distribution. Section *Filifoliae* is a small group readily characterized by narrow, flat to filiform-involute leaves, broad scales, and utricles thin-walled and hirsute, puberulent or antrorsely hispid, at least distally. Additionally, plants of this section tend to grow in dry habitats, including cliffs and rocky slopes, dry prairies, bluff crests, rocky slopes, and even desert habitats.

Circumscription 5 species (2 sampled).

Geographic distribution North America south to Mexico.

Vigna–Uncinia Clade

Current phylogenetic hypotheses resolve a clade comprising subgenera *Vigna* and *Uncinia*.

IV. *Carex* subg. *Uncinia* (Pers.) Peterm., *Deutschl. Fl.* 602. 1849.

Most species in this subgenus are unispicate, except a few taxa placed in the Subandrogyna Clade (IV.A.) and sect. *Phyllostachyae* (IV.D.). It is the only *Carex* subgenus almost entirely absent from the Eastern Hemisphere. The primarily amphitropical distribution of the group suggests a long-distance dispersal; however, further work is needed to figure out whether the dispersal or dispersals were North to South, vice-versa, or both.

IV.IS1. *Carex* sect. *Psilocarpae* Kük., in H.G.A. Engler, *Pflanzenr.* IV, 20(Heft 38): 89.

Recent unpublished results (García-Moro, Jiménez-Mejías, and collaborators, in prep.) support the inclusion of these unusual unispicate sedges among members of subg. *Uncinia*. Some of its members show a striking resemblance to species in sect. *Phyllostachyae*. More studies are needed to figure out the true relationships among these groups of plants.

Circumscription 6 species (4 sampled).

Geographic distribution Temperate and subtropical Atlantic South America, from northern Argentina to eastern Brazil.

IV.A. Subandrogyna Clade

Phylogenetic analyses support the South American members of sect. *Schiediana* as distantly related to core *Schiediana* (subg. *Euthyceras*, see III.B.4.) and morphologically distinguishable from them (Jiménez-Mejías & Escudero, 2016; Jiménez-Mejías & Reznicek, 2018). Additional studies are necessary to figure out whether the Subandrogyna Clade should be treated as a distinct section or as merged within another section.

Circumscription 4 species (3 sampled).

Geographic distribution Tropical and subtropical Andean South America.

IV.B. *Carex* sect. *Firmiculmes* (Kük.) Mack., in N.L.Britton et al., *N. Amer. Fl.* 18: 221. 1935.

Although this section has been traditionally hard to place, it is clearly supported as the sister lineage to sect. *Phyllostachyae*, with which it shares an absence of bracts and presence of foliaceous pistillate scales. The inflorescence is reduced to a terminal androgynous spike that is so lax that it may easily be misinterpreted as racemose.

Circumscription 3 species (3 sampled): *Carex geyeri*, *C. multicaulis*, *C. tompkinsii*.

Geographic distribution Western North America.

IV.C. *Carex* sect. *Leucocephalae* Holm, *Amer. J. Sci.* 14: 62. 1902.

Formerly classified in its own genus (*Cymophyllus*), *C. fraseriana* strongly contrasts with any other *Carex* species by its broad, oblong, ciliate and serrulate-margined, evergreen leaves that lack a ligule, sheath, and midvein—a leaf morphology that is unique in Cyperaceae. Flowering stems bear leaves reduced to expanded bladeless sheaths. Its bright white unispicate inflorescences suggest entomophily, which is found in only a few other *Carex* groups.

Circumscription 1 species (1 sampled): *Carex fraseriana*.

Geographic Distribution Central Appalachian Mountains.

IV.D. *Carex* sect. *Phyllostachyae* Tuck. ex Kük., in H.G.A.Engler, *Pflanzenr.* 20[IV,38]: 642. 1909.

Molecular and morphological data provide strong support for monophyly of this section (e.g., Ford et al., 2008; Pham et al., 2016). All species favor mesic deciduous forests. Most species in sect. *Phyllostachyae* bear linear leaves, with winged culms and peduncles that are dilated at apices. Inflorescences vary from unispicate to racemose, with proximal scales (possibly bracts) large and foliaceous. The terminal spike is androgynous, whereas lateral spikes are pistillate and the utricles are conspicuously beaked.

Circumscription 10 species (10 sampled).

Geographic Distribution North America north of Mexico.

IV.E. *Carex* sect. *Uncinia* (Pers.) Baill., Hist. Pl. (Baillon): 345. 1894.

Section *Uncinia* is here delimited to match the limits of the obsolete genus *Uncinia*. The group is readily distinguished by its unispicate inflorescences and long, hooked rachilla protruding from the tip of each perigynium and ending in a hook formed by a retrorse inrolled glume (Kukkonen, 1967; Reznicek, 1990; Waterway et al., 2015a). The rachilla in sect. *Uncinia* is the only unequivocal epizoochorous trait found in the genus *Carex*. The section is organized into two well-supported subclades, for the most part corresponding to *U.* section *Uncinia* (= *Stenandrae* Clarke) with mostly Australasian species and *U.* section *Platyandrae* Clarke with mostly South American species (Clarke, 1883; Kükenthal, 1909; Hamlin, 1958, 1959).

Circumscription 74 species (49 sampled).

Geographic distribution South America and New Zealand, reaching marginally Mexico, the Caribbean, Pacific, South Atlantic, and circum-Antarctic archipelagos. It is the only group of sedges native to true Antarctic lands (South Georgia and Kerguelen archipelagos; Govaerts et al., 2020).

Additional relevant literature Starr et al. (2003, 2008) and Wheeler (1994).

V. *Carex* subg. *Vignea* (P.Beauv. ex T.Lestib.) Heer, Mitth. Geb. Theor. Erdk. 1: 426. 1836.

Subgenus *Vignea* is the most morphologically cohesive of the six subgenera, with the vast majority of its species having distigmatic flowers and inflorescences with sessile spikes and without cladophylls. We split subgenus *Vignea* into 11 primary clades/sections. Several of these clades are then more finely split into clades/sections. *Vignea* has required a significant reorganization due to several problematic characters, including inflorescence complexity and rhizome length and behavior. These problems are particularly evident in those traditional sections with androgynous inflorescence spikes, whereas those with gynecandrous spikes have required fewer changes. The gender distribution of the spikes (i.e., androgynous or gynecandrous) seems to be homoplasious, with gynecandry having arisen several times in subgenus *Vignea* (Ford et al., 2006, 2012).

V.ISo. Incertae Sedis Species

The following five species are likely to be in subg. *Vignea*, but their placement within the subgenus is unknown: *C. chlorantha*, *C. esquirollii*, *C. fuscolutea*, *C. klaphakei*, and *C. ochrochlamys*.

V.IS1. *Carex* sect. *Japonicae* Kük., in H.G.A.Engler, Pflanzenr. IV, 20(Heft 38): 252. 1909.

This clade is named after the section of the only species known to be in the lineage, *Carex satsumensis*. It is an early-diverging branch that some analyses have placed as sister to subg. *Vignea* (Yano et al., 2014; Starr et al., 2015; Léveillé-Bourret & Starr, 2019; Zhang, pers. obs.) or to all non-Siderostictae subgenera (Léveillé-Bourret et al., 2018), but it has traditionally been placed in subg. *Vigneastra* (now mostly included in subg. *Carex*). It shares with subg. *Vignea* sessile primary inflorescence units, whereas the primary inflorescence units are usually peduncled in other species historically placed in subg. *Vigneastra*. Therefore, until new data shed light on the placement of this lineage, it has been provisionally placed in subg. *Vignea* (Villaverde et al., 2020). This species is distinctive; it is strongly rhizomatous, grows in sandy areas, and has numerous androgynous spikes and flowers with three stigmas.

Circumscription 1 species (1 sampled): *Carex satsumensis*.

Other known sectional names *Pacificae* Ohwi.

Geographic distribution Japan, Vietnam, the island of Taiwan, and the Philippines.

V.A. *Carex* sect. *Gibbae* Kük., in H.G.A.Engler, Pflanzenr. 20[IV,38]: 238. 1909.

This monotypic section is consistently found to be the sister lineage to the rest of subgenus *Vignea*. It is morphologically distinctive, with leaf-like bracts and gynecandrous spikes, and anomalous within the subgenus due to its tristigmatic flowers, trigonous utricles, and the fact that cladophylls are present, sometimes with an abortive pistillate flower (Su, 1994).

Circumscription: 1 species (1 sampled): *Carex gibba*.

Geographic distribution: China, Japan, and Korea.

V.B. *Carex* sect. *Physodeae* Christ, in Acta Horti Petropol. 18: 312. 1901.

A remarkable group of species from arid habitats, with elongated rhizomes, filiform leaves, and utricles with extremely thin walls. In *C. physodes* and *C. subphysodes*, the utricles are strongly inflated and balloon-like, probably for wind dispersal (Abudurehman et al., 2018).

Circumscription 3 species (3 sampled): *Carex pachystylis*, *C. physodes*, *C. subphysodes*.

Geographic distribution Eastern Europe and southeast to Central Asia.

V.C. Echinata–Glareosae Clade

This clade includes members traditionally placed in sects. *Glareosae* and *Stellulatae*, as well as a few other species. These gynecandrous, morphologically similar sections have long been considered to be closely related (Reznicek & Ball, 1980; Naczi, 2009).

V.C.1. Echinata Clade

This clade includes all the gynecandrous species traditionally placed within sect. *Stellulatae* as well as the androgynous *C. elongata* and *C. foetida*. Further study is needed on circumscription of this clade.

Circumscription 13 species (11 sampled).

Known sectional names *Elongatae* Kunth, *Foetidae* (Tuck. ex L.H.Bailey) Kük., *Stellulatae* Kunth.

Geographic distribution Circumboreal, widespread in the northern temperate zone.

V.C.2. *Carex* sect. *Glareosae* G.Don, in J.C.Loudon, Hort. Brit. 376. 1830.

This section constitutes a well-supported clade defined by inflorescences usually racemose, but sometimes capitate or reduced to a single spike; spikes gynecandrous, rarely pistillate; and utricles thin, coriaceous or membranous, plano-convex, wingless, smooth or minutely papillose, usually nerved, with beak emarginate to truncate.

Circumscription 28 species (26 sampled).

Other known sectional names *Canescentes* Fr., *Heleonastes* Kunth.

Geographic distribution Mainly circumboreal, in cold and temperate regions of Europe, Asia, and North America, with disjunct species in South America and southwestern Pacific islands.

Additional relevant literature Maguilla et al. (2015, 2018) and Villaverde et al. (2017a).

V.D. Appressa–Deweyanae Clade

This clade comprises two strikingly different groups of species: the Appressa Clade, with predominantly compound, androgynous spikes, and the monophyletic section *Deweyanae*, with few-flowered gynecandrous spikes.

V.D.1. Appressa Clade

This clade includes species traditionally placed in sects. *Heleoglochin*, *Phaestoglochin*, and *Vulpinae*. However, they are not closely allied to European and North American species from these sections, with the exception of *C. appropinquata*, which is the only European member of this clade. These are medium-to-large cespitose plants, sometimes forming trunk-like bases up to 1.5 m tall (Ford K, pers. obs.), with leaves channeled, inflorescences mostly spiciform or occasionally laxly paniculate, and utricles ovate or elliptic, flattened to biconvex, with margins distinctly denticulate, tapered into a shortly bifid beak.

Circumscription 10 species (8 sampled).

Geographic distribution Predominantly distributed in Australia and New Zealand, with some species reaching Malaysia and elsewhere in the southwestern Pacific, *C. appropinquata* distributed in Eurasia, and *C. vulpinaris* distributed from Afghanistan to western Himalaya.

Additional relevant literature Molina et al. (2015).

V.D.2. *Carex* sect. *Deweyanae* Tuck. ex Mack., in N.L. Britton & A. Brown, III. Fl. N. U.S. ed. 2, 1: 352. 1931.

Both morphologic and molecular data provide strong support for monophyly of this section, which is diagnosed by spikes gynecandrous, proximal utricles in each spike ascending to appressed; utricles 2.5–6.7 times as long as wide, with the distal portion of utricle body only one cell thick and beaks at least one-third the length of the utricle; and culms with chlorenchyma present between bundle cap and epidermis for at least two of three vascular bundles at the angles of the culm. Two species that have traditionally been placed in sect. *Deweyanae*, *C. kreczetoviczii* and *C. laeviculmis*, are here placed in section *Glareosae* (V.C.2.).

In molecular studies (Martín-Bravo et al., 2019), *Carex bromoides* has appeared allied to sect. *Inversae* (V.J.) due, apparently, to phylogenetic incongruence between markers (especially the phylogenetic signal of ETS with respect to other markers; Jiménez-Mejías P, pers. obs.; Waterway M, pers. obs.) that may indicate ancient intersectional hybridization. The situation of that species may require further research to determine its origins and classification placement.

Circumscription 6 species (6 sampled).

Geographic Distribution North America, and one species disjunct in Japan.

Additional relevant literature Naczi (2002, 2009).

V.E. Phaestoglochin–Annectens Clade

We split this clade into seven named lineages, three of which we refer to as *incertae sedis* clades based on their uncertain relationships to the other larger clades recognized here. It is unclear whether these are best treated as separate from the other clades. This clade includes a large number of species traditionally placed in sects. *Divisae*, *Multiflorae*, *Phaestoglochin*, *Physoglochin*, and *Vulpinae*, among others; however, the clades generally do not follow traditional sectional boundaries with the exception of *Physoglochin*.

V.E.IS1. Paniculata Clade

Carex paniculata is differentiated from the other European sedges by its combination of large, highly branched paniculate inflorescences and pyriform utricles. Both the relationships of *C. paniculata* to other lineages and the species limits of *C. paniculata* in relation to its named infraspecific taxa need further study to determine the appropriate classification.

Circumscription 1 species (1 sampled): *Carex paniculata*.

Known sectional names *Paniculatae* G. Don

Geographic distribution Western Palearctic, with two subspecies in the Canary and Cabo Verde Islands.

Additional relevant literature Molina et al. (2015).

V.E.IS2. *Carex* sect. *Divisae* H. Christ ex Kük., in H.G.A. Engler, Pflanzenr. 20[IV,38]: 119. 1909.

It is a morphologically cohesive group that comprises species with creeping rhizomes and coriaceous utricles with raised nerves and bifid beaks. The traditional placement of *Carex erythrorrhiza* in section *Stenorhynchae* (see V.E.2.) seems to be primarily due to assumed biogeographic affinities with other species.

Circumscription 3 species (2 sampled): *Carex consanguinea*, *C. divisa*, *C. erythrorrhiza*.

Geographic distribution Europe and the Mediterranean Basin, Eastern Africa, and Southern Africa.

V.E.IS3. Duriuscula Clade

This clade comprises two species with a close morphological affinity for dry habitats, whose species limits are in need of further study. These species have traditionally been placed in sect. *Divisae*, but current phylogenetic hypotheses place them as sister to the *Arenaria* Clade (V.E.3.) + sect. *Physoglochin* (V.E.4.).

Circumscription 2 species (2 sampled): *Carex duriuscula*, *C. stenophylla*.

Geographic distribution Circumboreal.

V.E.1. *Carex* sect. *Phaestoglochin* Dumort., Fl. Belg. 146. 1827.

It is a clade mostly comprising the Eastern Hemisphere species of sect. *Phaestoglochin* plus two species of *Vulpinae*, including the type of the section, *C. vulpina*, as well as a few species whose traditional placement in other sections was based on biogeography rather than morphological similarities. Previous placement of *C. paniculata* subsp. *calderae* in this clade (Molina et al., 2015; Martín-Bravo et al., 2019) was a mistake due to sequencing of a misidentified *C. canariensis* (Jiménez-Mejías P, pers. obs.). As here delimited, sect. *Phaestoglochin* is characterized by short rhizomes, inflorescences spicate (rarely distally branched), spikes androgynous, and utricles wingless. Further work is needed to establish morphological differences between this clade and other clades whose species have traditionally been placed in sects. *Phaestoglochin* and *Vulpinae* in part (e.g., the Annectens Clade, V.E.2.).

Circumscription 19 species (14 sampled).

Other known sectional names *Echinochloomorphae* Y.L. Chang ex S. Yun Liang, *Vulpinae* (Heuffel) Christ.

Geographic distribution Primarily Western Palearctic, with one species in Southern Africa, and entering southern Asia east to the Himalayas.

V.E.2. Annectens Clade

This clade is essentially a combination of parts of sects. *Phaestoglochin* and *Vulpinae* (but excluding the type species

of both sections), along with species usually placed in sects. *Multiflorae* and *Stenorhynchae*, among others. It is a heterogeneous assemblage of species, in which small sets of species seem to constitute subclades with morphological coherence. However, there is a limited understanding at this time to propose a new sectional arrangement.

Circumscription 53 species (49 sampled).

Known sectional names *Multiflorae* (J.Carey) Kük., *Stenorhynchae* Kük.

Geographic distribution Predominantly North American, with several South American species, a monophyletic Tropical African clade, and a single circumboreal species (*C. diandra*, which is also in New Zealand). The Annectens Clade is one of the few *Carex* groups that display an unusual disjunction between North America and sub-Saharan Africa.

V.E.3. *Arenaria* Clade

This clade comprises species traditionally assigned to two highly distinctive sets of species. On the one hand, species placed in sects. *Planatae* and *Remotae* are mostly caespitose with lax, elongate, spicate inflorescences of gynecandrous spikes, the proximal ones distant and long-leafy bracted, with diminutive wingless utricles. On the other hand, sect. *Ammoglochin* species mostly have elongated rhizomes, with inflorescences spicate but short, spikes overlapping and variable bracts and distribution of genders, and utricles flattened and broadly winged. Each group could constitute a good taxonomic section, except *C. remota* (type of sect. *Remotae*), which falls sister to sect. *Ammoglochin*, both, in turn, sister to the rest of the *Planatae*–*Remotae* assemblage. Further work is needed to understand the reasons for the odd phylogenetic placement of *C. remota* with respect to the rest of the species in the section and whether *Ammoglochin* and *Remotae* are better treated as one taxonomic group or more.

Circumscription 15 species (13 sampled).

Known sectional names *Ammoglochin* Dumort., *Planatae* Akiyama, *Remotae* (Aschers.) C.B.Clarke.

Geographic distribution Eurasia. Species assigned to sect. *Remotae* and *Planatae* are predominantly Asian (with the exception of *C. remota*), whereas species assigned to sect. *Ammoglochin* are predominantly European.

V.E.4. *Carex* sect. *Physoglochin* Dumort., Fl. Belg. 145. 1827.

This distinctive section of alpine, arctic, and boreal regions is strongly supported by both molecular and morphological characters. All species are of small stature with slender rhizomes and unispicate with primarily unisexual spikes.

Circumscription 5 species (4 sampled).

Geographic distribution Northern latitudes and high elevations of North America and Eurasia.

V.F. *Carex* sect. *Phleoideae* Meinsh., Trudy Imp. S.-Petersburgsk. Bot. Sada 18: 281, 322. 1901.

This section is monophyletic as traditionally delimited, based on a sample of six species and with the addition of *Carex unisexualis* (sect. *Holarrhenae*, sequenced) and possibly *C. thomsoniana* (sect. *Thomsoniana*, not sequenced). *Carex unisexualis* was considered a variety of a *Phleoideae* species by Kükenthal (as *Carex fluviatilis* var. *unisexualis* (C.B.Clarke) Kük.), but placed into sect. *Holarrhenae* in FOC, apparently based on its long-creeping rhizomes and monoecy. The placement of *C. thomsonii* here is tentative; however, its

inflorescence and utricles share clear morphological affinities with the rest of sect. *Phleoideae*, the only character separating it from them apparently the thickened, bulb-like stem bases.

Section *Phleoideae* is defined by culms tufted; proximal bracts usually leaf-like; inflorescences spicate, simple, cylindrical, typically densely aggregated, with spikes androgynous; and utricles membranous, veined, winged on margin or thickened, with bifid beaks, and outlets not filling the utricles.

Circumscription 10 species (7 sampled).

Other known sectional names *Thomsoniana* Y.L.Chang ex S.Yun Liang.

Geographic distribution East and Southeast Asia.

V.G. *Rosea*–*Macrocephala* Clade

This clade encompasses a wide morphological range and needs further study. There are some subtle trends that need to be further explored: for example, the first three small lineages include species with long rhizomes, and most of the early lineage divergences are centered on Mexico and western North America, with subsequent movement to eastern North America, South America, and East Asia.

V.G.1. *Carex* sect. *Potosinae* Mack., in N.L.Britton et al., N. Amer. Fl. 18: 39. 1931.

Section *Potosinae* has not previously had clear affinities to other groups. Its placement within the *Rosea*–*Macrocephala* Clade is not surprising, however, as it shares traits characteristic of the other lineages, including long rhizomes (in sect. *Macrocephalae* [V.G.3.] and the Douglasii Clade [V.G.2.]) and few-flowered inflorescences (in the *Rosea* Clade [V.G.5.]). Section *Potosinae* has the rare feature of tuberculate utricles, shared with a few species of sect. *Bracteosae* (V.G.4.). It is the only lineage of the *Rosea*–*Macrocephala* Clade to be arid-adapted.

Circumscription 1 species (1 sampled): *Carex potosina*.

Geographic distribution Mexico.

V.G.2. Douglasii Clade

There is no clear morphological justification for why these two species form a lineage, and its validity needs further study. The more narrowly distributed *C. perglobosa* is within the broader range of *C. douglasii*, but the two species do not co-occur as *C. perglobosa* occurs at much higher elevations.

Circumscription 2 species (2 sampled): *Carex douglasii*, *C. perglobosa*.

Geographic distribution Western North America.

V.G.3. *Carex* sect. *Macrocephalae* Kük., in H.G.A.Engler, Pflanzenr. 20[IV,38]: 186. 1909.

This clade is morphologically distinctive, comprising two strongly rhizomatous coastal dune endemics (North Pacific Rim, but with introductions to eastern North American coast), most typically with separate staminate and pistillate spikes, though occasionally androgynous. It is one of only two groups within subg. *Vigneae* having flowers with three stigmas (the other being sect. *Gibbae* [V.A.]) and has utricles that usually exceed 1 cm in length.

Circumscription 2 species (2 sampled): *Carex kobomugi*, *C. macrocephala*.

Geographic distribution Pacific rim from eastern China, Russia, and Japan to Oregon.

V.G.4. *Carex* sect. *Bracteosae* Pax, in H.G.A.Engler & K.A.E.Prantl., Nat. Pflanzenfam. 2: 123.

It is a morphologically homogeneous group with the exception of *C. vallicola*; all other species in this clade bear several leafy bracts that surpass the inflorescence. All species share androgynous spikes and utricles with spongy bases that sometimes form a conspicuous large bulge. Several South American species display the unusual feature of tuberculate utricles, a feature shared with sect. *Potosinae* (V.G.1.). The two North American species form a grade leading to the South American clade, suggesting a North American origin of the Neotropical species.

Circumscription 12 species (12 sampled).

Geographic distribution Predominantly South American but with two species in western/central North American.

Additional relevant literature Jiménez-Mejías et al. (2021a).

V.G.5. Rosea Clade

This clade is endemic to eastern North American deciduous or mixed forests. The morphological coherence of this lineage has been recognized with the same name since the study of Mackenzie (1916) reviewed in Webber & Ball (1984) and is strongly supported in all phylogenetic analyses. The Rosea Clade is morphologically and geographically distinct from all other members of *Phaestoglochin* and can be distinguished from the latter by its slender (typically <5 mm wide), elongate inflorescences; spikes that are typically not overlapping; and utricles with spongy thickened bases, often divergent at maturity.

Circumscription 6 species (6 sampled).

Geographic distribution Eastern North America.

V.H. Disticha–Chordorrhizae Clade

The clade is marked by long rhizomatous or, at least in *C. chordorrhiza* and *C. pseudocuraica*, stoloniferous growth, except for species traditionally classified in sect. *Phaestoglochin* (in the Disticha Clade [V.H.2.]), which are strictly cespitose.

Circumscription 31 species (25 sampled).

Geographic distribution Primarily circumboreal, mainly at temperate latitudes.

V.H.1. Carex sect. Dispermae Ohwi, Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 11: 237. 1936.

Carex disperma is a distinctive species traditionally placed in sect. *Glareosae* (despite having androgynous spikes) or treated as a monotypic section. Plants have slender rhizomes and racemose inflorescences with few-flowered androgynous spikes with plump, shiny, spreading short-beaked utricles.

Circumscription 1 species (1 sampled): *Carex disperma* Dewey.

Geographic distribution Circumboreal.

V.H.2. Disticha Clade

This clade encompasses parts of sect. *Ammoglochin*, most of sects. *Foetidae* (excluding its type) and *Holarrhenae*, and nearly all species of sect. *Phaestoglochin* that are restricted to North America west of the Mississippi river (except *C. vallicola*). With the exception of those traditionally placed in *Phaestoglochin*, species in this clade are defined in part by being colonial from creeping rhizomes. The western North American *Phaestoglochin* species (*C. hoodii*, *C. hookeriana*, *C. occidentalis*, and *C. tumulicola*) are all strictly cespitose.

Spikes are mostly androgynous; however, variable distribution of staminate and pistillate flowers in the spikes is common in species of sects. *Holarrhenae* as well as in *C. siccata*. Unisexual (sometimes both pistillate and staminate) and androgynous spikes can be found on the same plant in several species, with the spikes often overlapping enough to be nearly indistinguishable from one another.

No traditional section corresponds to this group, even though all included members of sect. *Holarrhenae* and those placed in *Foetidae* each form a single clade within this group. Phylogenetic data suggest that the traditional sections may provide guidelines to cleave two or three sections out of this clade, but more work is needed to define sectional limits.

Circumscription 27 species (22 sampled).

Known sectional names *Holarrhenae* (Döll) Pax.

Geographic distribution Widespread in North America and temperate Eurasia. The *Carex maritima* lineage is bipolar; most species are circumboreal in distribution reaching the southwestern European Alps, Himalaya, and southern Rocky Mountains, whereas *C. melanocystis* inhabits southern South America (Jiménez-Mejías et al., 2021a).

Additional relevant literature Villaverde et al. (2015a).

V.H.3. Carex sect. Chordorrhizae (Heuffel) Meinsh., Trudy Imp. S.-Petersburgsk. Bot. Sada 18: 2. 1901.

This strongly supported clade includes two species that are both long-stoloniferous plants with procumbent vegetative shoots; however, *C. pseudocuraica* has typically been separated from *C. chordorrhiza* based on the presence of unisexual spikes and placed in sect. *Holarrhenae* (Egorova, 1999). Both species have short ovoid spikes crowded toward the tips of wiry culms, with leaves borne proximally and much shorter than the culms.

Circumscription 2 species (2 sampled): *Carex chordorrhiza*, *C. pseudocuraica*.

Geographic distribution Circumboreal.

V.I. Carex sect. Cyperoideae G. Don, in J.C. Loudon, Hort. Brit. 376. 1830.

This is the largest traditional section in subg. *Vignea* that has been consistently recognized in morphological and phylogenetic studies (Reznicek, 1993; Hipp et al., 2006; Hipp, 2008). Section *Cyperoideae* is a highly distinctive clade that is defined by short rhizomes (rarely elongated), true vegetative culms (i.e., vegetative shoots with conspicuously elongated internodes; Reznicek & Catling, 1986), gynecandrous spikes, and utricles usually with typically serrulate wings. The attribution of species to sect. *Ammoglochin* (*C. balfourii* and *C. iljinii*) seems to be based on the fact that these are Western Palearctic taxa as well as on the presence of longer rhizomes. Stoloniferous growth from the previous season's culms is present at least in *Carex leporina* (Wilson et al., 2014), *C. projecta*, *C. tribuloides*, *C. harfordii* (Hipp A, pers. obs.), *C. longii* subsp. *meridionalis* (Jiménez-Mejías P, pers. obs.), and perhaps other species.

The group has been widely known under the name of sect. *Ovales* (type *C. leporina*). As the type species of the formerly segregated sect. *Cyperoideae* (*C. bohémica*) has been shown to be embedded within the larger sect. *Ovales*, it is clear that *Cyperoideae* is the name with priority for this clade.

Circumscription 94 species (87 sampled).

Other known sectional names: *Leporinae* Fr., *Ovales* Kunth.

Geographic distribution Predominantly North America, with ca. 5 species in Eurasia and ca. 10 in Central and South America.

V.J. *Carex* sect. *Inversae* Kük., in H.G.A.Engler, Pflanzenr. 20[IV,38]: 187. 1909.

This group is strongly supported in all analyses conducted to date, both with and without the addition of *C. maackii* Maxim., a species that has previously been consistently classified in sect. *Cyperoideae*. This clade is characterized by gynecandrous or androgynous spikes that bear winged or unwinged utricles; in the latter case, plants are mostly creeping rhizomatous with foliose inflorescence bracts. Some New Zealand species also have papillose utricles. The position of *C. maackii* needs additional investigation, as its placement as sister to the remainder of *Inversae* raises difficulties for identifying synapomorphies for both *Cyperoideae* and *Inversae*.

Circumscription 14 species (10 sampled).

Geographic distribution Predominantly Australia and New Zealand (*Inversae* s.s.), with one East Asian species (*C. maackii*).

VI. *Carex* subg. *Carex*

Most species of this subgenus bear flowers with three stigmas and spikes primarily unisexual, except in the groups where otherwise indicated. It is by far the largest and most morphologically variable of the subgenera. There are ca. 100 species in this subgenus whose sectional placement remains to be addressed with further work.

VI.IS1. *Dissitiflora* Clade

Recent analyses place *C. dissitiflora* and *C. bostrychostigma* together as an early-diverging lineage (Jiménez-Mejías et al., 2016a; Martín-Bravo et al., 2019) or as sister to the rest of subg. *Carex* (Waterway et al., 2015b; Léveillé-Bourret et al., 2018; Léveillé-Bourret & Starr, 2019; Zhang, pers. obs.). The two species have been placed in sects. *Mundae* and *Debiles*, respectively, and differ in inflorescence morphology (androgynous spikes in *C. dissitiflora* versus terminal staminate plus lateral pistillate spikes in *C. bostrychostigma*), as well as in features of the leaves, utricles, and nutlets (Hoshino et al., 2011). The placement and circumscription of this clade need further study. Until new data shed light on the placement of this lineage, it has been provisionally placed in subg. *Carex* due to the morphological affinities with species in that subgenus (Villaverde et al., 2020).

Circumscription 2 species (2 sampled): *Carex bostrychostigma*, *C. dissitiflora*.

Geographic distribution East Asia.

VI.IS2. *Insertae Sedis*

It is a group of nine species from several traditional sections that are sometimes recovered as satellite lineages of the *Flacca*–*Panicaceae* Clade (VI.E.), but their placements are poorly supported and unstable among phylogenetic reconstructions. It includes tropical species with long slender spikes that are often fastigiate and narrow utricles with elongated beaks. Three are European species traditionally placed in sect. *Aulocystis* (*C. kitaibeliana*, *C. macrolepis*, and *C. mucronata*).

Circumscription 9 species (8 sampled).

Geographic distribution Europe, eastern Mediterranean, East Africa, and Himalayan Asia.

VI.IS3. *Alliiformes-Grallatoriae* Clade

Sections *Alliiformes* (VI.IS3.1.) and *Grallatoriae* (VI.IS3.2.) are often recovered as sister lineages. However, the relationship of this clade to other groups is uncertain, as it has been found allied to different clades in different reconstructions (Martín-Bravo et al., 2019; Lu et al., 2021).

VI.IS3.1. *Carex* sect. *Alliiformes* Akiyama, Caric. Far East. Reg. As. 143. 1955.

This is currently considered a monotypic group. *Carex alliiformis* is a multispicate sedge that morphologically strongly resembles species from sects. *Molliculae* (VI.M.1.) or *Paludosae* (VI.M.2.), whereas it is quite different morphologically from its sister group, the unispicate sect. *Grallatoriae* (VI.IS3.2.). Other similar species from East Asia may also belong to sect. *Alliiformes* (e.g., *C. wenshanensis*; Jin & Lu, pers. obs.), but until more evidence is available, we provisionally list them as unplaced.

Circumscription 1 species (1 sampled): *Carex alliiformis*.

Geographic distribution Pacific East Asia, south to Vietnam.

VI.IS3.2. *Carex* sect. *Grallatoriae* Kük., in H.G.A.Engler, Pflanzenr. 38(IV. 20): 88. 1909.

Section *Grallatoriae* is monotypic, only including the diminutive unispicate species, which can be either androgynous or dioecious, and is endemic to insular East Asia.

Circumscription 1 species (1 sampled): *Carex grallatoria*.

Geographic distribution Archipelago of Japan and the island of Taiwan.

VI.IS4. *Carex* sect. *Secalinae* (O. Lang) O.Lang. ex Kük., in H.G.A.Engler, Pflanzenr. 38(IV. 20): 679. 1909.

It is a very characteristic group of sedges with stiff coriaceous leaves and large utricles that are 5–10 mm long with long bifid beaks, and it is primarily found on temporarily inundated soils. Although this seems to constitute a natural group, their placement among the different phylogenetic reconstructions seems quite unstable.

Other known sectional names *Hordeiformes* (Asch. & Graebn.) Rouy., *Kuekenthalia* (Börner) V.Krecz.

Circumscription 3 species (2 sampled): *Carex eremopyroides*, *C. hordeistichos*, *C. secalina*.

Geographic distribution Medium latitudes of temperate Europe east to Central Asia.

VI.A. *Albae-Indica* Clade

A clade encompassing the circumboreal sect. *Albae* with two groups of mainly tropical species. This clade has been informally named “Small Core *Carex* Clade” and recovered as sister to the rest of subg. *Carex* (Starr et al., 2015; Villaverde et al., 2020).

VI.A.1. *Carex* sect. *Albae* (Asch. & Graebn.) Kük., in H.G.A.Engler, Pflanzenr. 38(IV. 20): 499. 1909.

It is a small morphologically well-defined group. Species in sect. *Albae* have small inflorescences with few loosely flowered spikes and utricles inflated, shiny, with a truncate beak.

Circumscription 4 species (3 sampled).

Geographic Distribution Circumboreal.

VI.A.2. *Carex* sect. *Graciles* Kük., in H.G.A.Engler, Bot. Jahrb. Syst. 27: 516. 1899.

Section *Graciles* species have a well-defined morphology that makes it easy to distinguish these species from other

Carex lineages. They have slender, lax pistillate spikes, two stigmas, and small lenticular utricles with a well-developed elongated bifid beak. Inflorescences range from racemose to highly compound.

Circumscription 32 species (11 sampled).

Geographic Distribution East and southern Asia, reaching marginally East Africa, Madagascar, the Mascarenes, Australia, and Pacific archipelagos.

VI.A.3. Indica Clade

This clade encompasses a wide range of morphological diversity, but it has a strong geographic component, being one of the few primarily tropical *Carex* clades. The Indica Clade and the Decora Clade (VI.C.) include most of the diversity of the historically recognized subg. *Vigneastra* (*Indocarex*). They both include species formerly placed in some of the same sections; however, the Indica Clade is dominated by species traditionally placed in sections *Euprepes*, and *Mapaniifoliae*, among others, whereas the Decora Clade comprises predominantly those species traditionally placed in sects. *Decorae* and *Indicae* (even though the type of this section, *C. indica* L., seems to actually be in the Indica Clade).

The diversity of form and structure in the Indica Clade is impressive and largely parallels the diversity of rare *Carex* forms seen in subg. *Siderosticta*. For example, some species have true leafy stems, lacking basal leaves, and some have exceptionally wide pseudopetiolate leaves. In addition, species may have complex paniculate or simple androgynous multispicate inflorescences, which may or may not possess utriculiform cladophylls. The Indica Clade is also one of the few *Carex* groups containing species with unequivocal entomophilous traits. Significant work is needed to understand the evolution of diversity in this clade.

Circumscription 29 species (16 sampled).

Known sectional names *Euprepes* Nelmes & Airy Shaw, *Indicae* Tuck., *Mundae* Kük., *Mapaniifoliae* Nelmes & Airy Shaw.

Geographic Distribution Predominantly South and Southeast Asia, with some species reaching West Pacific islands.

Additional relevant literature Starr et al. (2015).

VI.B. *Carex* sect. *Cryptostachyae* Franch., *Nouv. Arch. Mus. Hist. Nat.*, ser. 3, 10: 106. 1898.

Analyses place *C. cryptostachys* as an isolated lineage in the early-diverging grade of subgenus *Carex*. The trigonous nutlets that are constricted on the angles, with faces excavated, are unique. Its numerous androgynous spikes on short lateral culms are also unusual for the genus.

Circumscription 1 species (1 sampled): *Carex cryptostachys*.

Geographic Distribution Eastern China and Southeast Asia, south to northeastern Australia.

VI.C. Decora Clade

This is a large clade that embraces most species traditionally placed in sects. *Decorae* and *Indicae*; however, it does not include the type of *Indicae* (material assignable to *C. indica* has been recovered in the Indica Clade [VI.A.3.]). This clade and the Indica Clade (VI.A.3.) include most of the diversity of the obsolete subg. *Vigneastra* (*Indocarex*). The Decora Clade is one of the few groups of *Carex* primarily diversified in tropical areas. Most species in this clade display large inflorescences, often paniculate

or fastigiate; utriculiform cladophylls; and androgynous spikes. It is a taxonomically complicated group with subtle diagnostic characters and broad intraspecific variation. The majority of the accepted species are yet to be sequenced, and, thus, some species may be transferred to the Indica Clade (VI.A.3.) in the future.

Circumscription 110 species (41 sampled).

Known sectional names *Cruciatae* (C.B.Clarke) Nelmes, *Decorae* (Kük.) Ohwi, *Filicinae* (C.B.Clarke) Nelmes, *Scabrellae* Kük., *Stramentitiae* Boott ex Boeckeler

Geographic distribution Circumtropical.

VI.D. Tristachya Clade

This small clade comprises mostly Asian species traditionally placed in sects. *Mitratae* and *Lageniformes*, and they share similar distinctive nutlet features (see VI.X. Rhomboidales–Mitrata clade below) that are quite different from those of other species in this part of the phylogeny (Jin XF, pers. obs.). Additional sampling and analyses are needed to determine if their isolated placement here is supported or whether it is an analysis artifact.

Circumscription 8 species (4 sampled).

Geographic distribution East Asia, Australia (Queensland).

VI.E. Flacca–Paniceae Clade

This clade represents species from a large range of sections with a diverse morphology, and significant work is still needed to determine the best application of sectional concepts.

VI.E.IS1. Tomentosa Clade

Carex tomentosa has traditionally been placed in sect. *Acrocystis*. Its placement is still somewhat unclear, other than the odd affinity to *C. desponsa* reported in recent phylogenies. The two taxa bear no evident resemblance to each other, and so they are treated as an *insertae sedis* clade. Their putative relatedness should be taken with caution, deserving further study.

Circumscription 2 species (2 sampled): *Carex desponsa*, *C. tomentosa*.

Geographic distribution Europe to central Asia (*C. tomentosa*) and eastern Himalaya (*C. desponsa*).

VI.E.1. Oligocarya Clade

Dickoré (1995) discussed the similarity of *C. alajica* and *C. oligocarya*, the two taxa placed in this group. He noted that they mainly differ only in the size of the utricles, which may best be regarded as geographically differentiated subspecies.

Circumscription 2 species (2 sampled): *Carex alajica*, *C. oligocarya*.

Geographic distribution Mountains of Central Asia east to western Himalaya and western China (Xinjiang).

VI.E.2. *Carex* sect. *Chartoteuchium* (Börn.) V.I.Krecz., in Komarov, *Flora SSSR*. 3: 279. 1935.

The species in this clade have often been placed in sect. *Aulocystis*. They share the common feature of having broad ovate spikes that are often pendant and nutlets elevated on a well-developed conspicuous carpophore.

Circumscription 6 species (6 sampled).

Geographic distribution Predominantly mountains of Central Asia, east to the Himalayas and the Tibetan Plateau to central China, with one species circumpolar.

VI.E.3. Flacca Clade

This is an apparently well-supported clade comprising ca. 27 *Carex* species formerly ascribed to up to eight different sections, including at least the types of five of them: *Thuringiaca*, *Ferrugineae*, *Depauperatae*, *Abditispicae*, and *Pellucidae* (see below). This clade is one of the most heterogeneous assemblages in *Carex*. Species range from large and robust forms to those that are dwarf or even acaulescent. Utricles vary among species from membranaceous to coriaceous, glabrous to scabrid, and long-beaked to beakless. The only character that seems to be more or less shared by a number of species is the bluish-green leaves. A few species in sect. *Abditispicae* have connate anther filaments (Wheeler, 1987), a character unique in the entire genus *Carex*.

Circumscription 28 species (25 sampled).

Known sectional names *Abditispicae* G.A.Wheeler, *Aulocystis* Dumort., *Depauperatae* Meinsh., *Ferrugineae* (Tuck.) Kük., *Pellucidae* G.A.Wheeler, *Schizochlaenae* V.I.Krecz., *Thuringiaca* G.Don.

Geographic distribution Highly disjunct, Western Palearctic, southern North America, Andean South America, and Patagonia. Two clear centers of diversity with a number of local endemics are found in the mountains of southern and central Europe, and South America.

VI.E.4. *Carex* sect. *Paniceae* G.Don, in J.C.Loudon, Hort. Brit. 376. 1830.

Section *Paniceae*, which is considered here in the broad sense, includes sects. *Laxiflorae* and *Bicolores*, which have typically been considered closely allied sections. Current phylogenetic hypotheses support a monophyletic *Bicolores* within a clade of *Paniceae* species that is, in turn, nested in *Laxiflorae*, which is nested in a broader sampling of *Paniceae*. Although there is a *Bicolores* clade and a clade including most of *Laxiflorae*, the grade of multiple lineages of various *Paniceae* and *Laxiflorae* species would not be easily treatable. We consider it best treated as one section, based on currently available data. Most species within this group have bluish-green leaves and lax pistillate spikes with inflated utricles, often with more or less elevated epidermal cells that sometimes rise as conspicuous papillae. Most species inhabit moist-to-wet temperate forests, with some species occurring in open wetlands in the same biomes.

Circumscription 46 species (37 sampled).

Other known sectional names *Bicolores* (Tuck. ex L.H.Bailey) Rouy, *Laxiflorae* (Kunth) Mack.

Geographic distribution Predominantly North America, also East Asia and Europe; two species reaching Central and South America.

VI.F. Fastigiata Clade

This is a fairly isolated clade of unclear affinity and circumscription that currently includes only *C. fastigiata* and *C. yunnanensis*. Whereas utricles of the two species are similar, *C. yunnanensis* has unbranched lateral inflorescence branches and *C. fastigiata* has rebranching lateral branches with multiple spikes.

Circumscription 2 species (2 sampled): *Carex fastigiata*, *C. yunnanensis*.

Geographic distribution Central and western China and west into Himalayan Asia.

VI.G. *Carex* sect. *Pictae* Kük., in H.G.A.Engler, Pflanzenr. 20[IV,38]: 82. 1909.

This small clade corresponds to sect. *Pictae*, but with a slight expansion to include *C. pedunculata*. It has been previously noted that *C. pedunculata* (often placed in sect. *Clandestinae* [FNA]) shares morphological similarities with sect. *Pictae*, such as the reddish culm bases, sheathless or shortly sheathing bracts, and pubescent utricles, short-beaked or beakless, with enlarged fleshy bases.

Circumscription 4 species (4 sampled).

Geographic distribution and habitat Eastern and northern North America (3 species) and East Asia (1 species).

VI.H. Hirta–Praelongae Clade

This clade reflects the sister relationship of the Hirta Clade (VI.H.1.) and sect. *Praelongae* (VI.H.2.) recovered in several Sanger-based phylogenetic trees (M.J. Waterway, unpublished results; S. Kim, unpublished results). However, genomic data place sect. *Praelongae* as most closely related to the similar-looking sect. *Phacocystis* (Villaverde et al., 2020). Additional data are necessary to determine the best placement of sect. *Praelongae*.

VI.H.1. Hirta Clade

This group contains *Carex hirta* L., the type species of the genus *Carex*, as well as of subg. *Carex* and sect. *Carex*. If the Hirta Clade is to be regarded as a section in the future, the sectional name “*Carex*” would have priority. This clade has been recovered in numerous previous molecular phylogenetic studies (e.g., Roalson et al., 2001; Hendrichs et al., 2004; Waterway & Starr, 2007; Gehrke & Linder, 2009; Waterway et al., 2009, 2015b; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Lipnerová et al., 2013; Gebauer et al., 2014). As defined here, this clade represents one of the largest in the genus and is formed by species usually placed in up to eight different sections. A close relationship among these sections has long been suggested by morphological similarities, putative intersectional hybrids, smut parasitism data, and molecular data (e.g., Kükenthal, 1909; Kreczetowicz, 1935; Savile & Calder, 1953; Hylander, 1966; Nilsson, 1985; Cayouette & Catling, 1992; Kukkonen, 1998; Egorova, 1999; Gebauer et al., 2014). The majority of the currently accepted sections more or less correspond to largely monophyletic subclades when using additional markers (Waterway et al., unpubl. data; Gebauer S et al., unpubl. data). However, the current state of knowledge prevents a reclassification at this point.

Species in the Hirta Clade display a series of morphological similarities. Most are large-to-medium-size plants with leaves having transverse septate-nodulose venation. Utricles are large, inflated, with conspicuously bifid beaks, and they loosely contain the nutlet within. Nutlets are mostly trigonous and, in most species, the style is strongly lignified and persistent, which makes it one of the *Carex* groups most conspicuous in fossil assemblages (Jiménez-Mejías et al., 2016c). It is one of the few *Carex* groups with adaptations that seems to point to epizoochory, such as the recurved utricule beak teeth in *C. capricornis* and *C. comosa*, and potentially the deeply bifid beak of a number of the other species. The inflated utricles loosely containing the nutlets probably also aid in hydrochory (Waterway MJ, personal obs.). Nearly all species inhabit inundated or wet soils, and many are strongly rhizomatous,

forming large monospecific stands in ponds, lakes, and other wetlands. The clade is one of the few in *Carex* with extensive hybridization (e.g., Cayouette & Catling, 1992; Egorova, 1999; Jermy et al., 2008; Pedersen et al., 2016; among others).

Circumscription 106 species (67 sampled).

Known sectional names *Ampullaceae* (Rouy) T.V.Egorova, *Carex*, *Hirtae* Tuck. ex Kük., *Lasiocarpae* Fr. ex Christ, *Lupulinae* Tuck. ex J.Carey, *Odontostomae* Fr. ex Pax, *Physocarpae* Drej. ex L.H.Bailey, *Pseudocypereae* Tuck. ex Kük., *Vesicariae* (Heuff.) J.Carey.

Geographic distribution Widely distributed in cold and temperate regions of both hemispheres, with distribution centers in Eurasia and North America, and with a few montane species in the tropics.

Additional relevant literature Luceño (2008a, 2008b, 2008c) and Gebauer et al. (2014).

VI.H.2. *Carex* sect. *Praelongae* (Kük.) Nelmes, Reinwardtia 1:421. 1951.

This is a widespread, morphologically cohesive group characterized by the elongate and staminate terminal spike, and the elongated, narrowly to broadly cylindrical lateral spikes that are typically densely flowered in a very regular pattern. Lateral inflorescence branches are typically arching to drooping and pistillate, but distal ones are often androgynous. Scales are often mucronate to aristate, and the gynoeceum has two stigmas. The utricles are usually nerved, sometimes red-punctate or covered by high papillae, and attenuated at the top. Species in sect. *Praelongae* inhabit wet-to-moist habitats.

Circumscription 33 species (26 sampled).

Geographic distribution Predominantly East Asia, but with species reaching western Himalayas, and Southeast Asia, and a few disjunct taxa in tropical and southern Africa and Madagascar as well as in Pacific archipelagos.

Additional relevant literature Benítez-Benítez et al. (2021).

VI.I. Longirostres–Racemosae Clade

This clade includes the small sect. *Longirostres* (VI.I.1.) and its sister sect. *Racemosae* (VI.I.2.), both predominantly circumboreal groups.

VI.I.1. *Carex* sect. *Longirostres* (Kük.) Mack., N. Amer. Fl. 18: 297. 1935.

This strongly supported clade falls sister to sect. *Racemosae* in most molecular phylogenies, distant from any other clade that contains species formerly placed in sect. *Hymenochlaena*. This group consists of relatively robust species that are characterized by densely to loosely caespitose clumps with short, thickened fibrillose rhizomes resembling fraying rope; flowering culms with one or more distal staminate spikes and two or more cylindrical pistillate spikes on drooping peduncles; and smooth nerveless utricles abruptly narrowed to cylindrical, and often slightly curved beaks longer than the utricle body.

Circumscription 3 species (3 sampled): *Carex arnellii*, *C. hondoensis*, *C. sprengelii*.

Geographic distribution Broadly distributed across northern U.S.A. and southern Canada, west to British Columbia, and across temperate Asia as far east as European Russia.

VI.I.2. *Carex* sect. *Racemosae* G.Don, in J.C.Loudon, Hort. Brit. 376. 1830.

It is a strongly supported clade, but the number of species is difficult to establish, as species delineation within this taxonomically challenging group is often difficult and varies considerably among treatments. Taxa usually placed within other sections but often considered morphologically deviant within them have recently been found to be a part of sect. *Racemosae* (e.g., *C. heterostachya* placed in sect. *Paludosae*; *C. atrofusoides* and *C. psychrophila* from sect. *Aulocystis*), whereas others traditionally considered a part of *Racemosae* had to be transferred to other groups (e.g., *C. mertensii*, *C. stylosa*, among others). Section *Racemosae* is characterized by sheathless bracts with basal auricles, spikes often broadly elliptic, the terminal one in most cases staminate or gynecandrous, usually dark-colored scales, utricles thin-walled, and nutlets abruptly constricted to a sub-stipitate base.

Circumscription 74 species (65 sampled).

Other known sectional names *Atratae* Fr. ex Pax, *Microrynchae* Drej. ex L.H.Bailey and *Loxaniza* (Raf.) V.I.Krecz.

Distribution Circumboreal; predominantly in high mountains and arctic tundra, four species disjunct in the Southern Hemisphere, from the southern Andes to Tierra del Fuego.

Additional relevant literature: Gebauer et al. (2015), Massatti et al. (2016), Jiménez-Mejías et al. (2021b), and Gebauer et al. (in prep.).

VI.J. *Carex* sect. *Stylosae* (T.V.Egorova) S.Gebauer & M.H.Hoffm., Syst. Bot. 40: 444. 2015.

This group combines some species of sect. *Stylosae* with morphologically allied species that have typically been included within sect. *Phacocystis*. All the species share strongly lignified persistent styles, but some have three stigmas, whereas others have only two.

Circumscription 8 species (7 sampled).

Geographic distribution Circumboreal, but predominantly East Asia and eastern North America.

VI.K. *Carex* sect. *Phacocystis* Dumort., Fl. Belg. 146. 1827.

This is a morphologically homogeneous clade that mostly amalgamates species traditionally placed in sect. *Phacocystis* and some of its segregates (e.g., sects. *Forficulae*, *Temnemis*, or *Tuminenses*, as conceived by Egorova (1999)), as well as species formerly treated in sects. *Podogyneae* and *Scitae*. Section *Phacocystis* roughly matches the circumscription of Egorova's (1999) obsolete *Carex* subg. *Kreczetoviczia* T.V.Egorova, excluding sects. *Praelongae* and *Abitispicae*. As circumscribed here, this clade is one of the largest of the genus, comprising about 110 species; however, some of the Asian species not yet sequenced may eventually be transferred to sect. *Praelongae* (VI.H.2.) or sect. *Stylosae* (VI.J.). *Phacocystis* is remarkable for its high rate of hybridization and includes species of a well-documented hybrid origin.

Section *Phacocystis* is characterized by sheathless bracts with membranous auricles at their bases; cylindrical spikes, terminal ones usually staminate and lateral ones pistillate or androgynous; two stigmas (except in a few species); and glabrous to more or less papillose utricles, with a shortly truncate beak or beakless (except in species formerly placed in sect. *Forficulae*, which bear well-developed bifid utricle beaks).

Circumscription 109 species (87 sampled).

Other known sectional names *Forficulae* (Kük.) Raymond, *Podogynae* Holm., *Scitae* Kük., *Temnemis* (Raf.) Krecz., *Tuminenses* Y.L.Chang & Y.L.Yang.

Geographic distribution Primarily circumboreal, with disjunct species in Central and South America, and Australasia south to New Zealand. Conspicuously absent from sub-Saharan Africa.

Additional relevant literature Faulkner (1972), Chater (1980), Cayouette & Morisset (1985), Cayouette (1987), Standley (1987, 1990), Volkova et al. (2008), Dragon & Barrington (2009), Korpelainen et al. (2010), Jiménez-Mejías et al. (2011, 2012a, 2014b), Nowak et al. (2020), Benítez-Benítez et al. (2021), and Pender et al. (2021).

VI.L. Glaucescentes–Fecundae Clade

This clade includes various small sections and species often placed within or associated with sect. *Phacocystis*. Here, we treat these separately from sect. *Phacocystis*, in part because it includes a number of distinctive groups traditionally recognized at the sectional level. All of them are medium-to-large plants from aquatic or wet habitats, with the only obvious synapomorphy being sheathless bracts. Clades VI.L.IS1–4 below consist of single species or pairs of species whose placements are highly problematic, even unstable between different phylogenetic reconstructions (see placement of the species in Benítez-Benítez et al., 2021).

VI.L.IS1. Barbarae Clade

Carex barbarae has been considered to have morphological characters similar to *C. obnupta* and *C. nebrascensis* (sect. *Phacocystis*), and to be largely sterile, suggesting that it may be a hybrid (FNA). Given its unstable and somewhat intermediate placement between the clades of the two species with which it shares morphological similarities, the possibility of a hybrid origin needs further study.

Circumscription 1 species (1 sampled): *Carex barbarae*.

Geographic distribution Western North America.

Additional relevant literature Benítez-Benítez et al. (2021).

VI.L.IS2. Nebrascensis Clade

The two species in this clade have usually been placed in sect. *Phacocystis*.

Circumscription 2 species (2 sampled): *Carex endlichii*, *C. nebrascensis*.

Geographic distribution Western North America, including Mexico.

Additional relevant literature Benítez-Benítez et al. (2021).

VI.L.IS3. Barrattii Clade

Carex barrattii has been included in sect. *Limosae*, with which it shares a superficially similar appearance, but the lateral spikes of *C. barrattii* are androgynous rather than pistillate. It is an uncommon and local species of acidic wetlands.

Circumscription 1 species (1 sampled): *Carex barrattii*.

Geographic distribution Eastern U.S.A.

Additional relevant literature Benítez-Benítez et al. (2021).

VI.L.IS4. Augustinowiczii Clade

The species of this clade have been included in sect. *Racemosae*, because the terminal spike is sometimes gynecandrous and has three stigmas.

Circumscription 2 species (2 sampled): *Carex augustinowiczii*, *C. curvicollis*.

Geographic distribution East Asia.

Additional relevant literature Benítez-Benítez et al. (2021).

VI.L.1. *Carex* sect. *Limosae* (Heuffel) Meinsh., Trudy Imp. S.-Peterburgsk. Bot. Sada 18: 283. 1901.

This clade includes most species of sect. *Limosae*, which has traditionally been recognized to include ca. six species. It is a morphologically coherent group of loosely cespitose to stoloniferous slender plants with lax inflorescences, the short lateral spikes pendant at the end of filiform peduncles, and utricles beakless and minutely papillose. They are most often found in wet, peaty habitats and have a characteristic yellow indumentum on their roots.

Circumscription 4 species (4 sampled).

Geographic distribution Higher latitudes and elevations in the Northern Hemisphere, except for *C. limosa*, which also occurs in the mountains of Hispaniola in the Caribbean, and in the Venezuelan Andes, and the bipolar *C. magellanica*, which also occurs in Patagonia and Tierra del Fuego in austral South America.

Additional relevant literature Benítez-Benítez et al. (2021).

VI.L.2. *Carex* sect. *Glaucescentes* Reznicek, Novon 11: 457. 2001.

It is a small well-supported clade that is also morphologically distinctive, formed by robust sedges with glaucous leaves, large cylindrical pistillate spikes, and more or less flattened utricles.

Circumscription 4 species (4 sampled).

Geographic distribution Amphitropical distribution with three species found in the southeastern U.S.A. to Texas and one species found in southern Brazil to northeastern Argentina (*C. brasiliensis*).

Additional relevant literature Benítez-Benítez et al. (2021).

VI.L.3. *Carex* sect. *Squarrosae* J.Carey, Carices North. U.S., 564. 1847.

This clade includes two species traditionally included in sect. *Squarrosae* (the other two have been found to be part of the Hirta Clade [VI.H.1.]), plus the single representative of sect. *Shortianae*. The three species have been reported to hybridize (FNA), which is perhaps not surprising in light of their morphological similarity to one another. The three species have medium-to-large sedges, with inflorescences bearing erect spikes, the terminal one invariably gynecandrous and the lateral gynecandrous or pistillate, and utricles strongly appressed within the very congested spikes.

Circumscription 3 species (3 sampled): *Carex shortiana*, *C. squarrosa*, *C. typhina*.

Other known sectional names *Shortianae* (L.H.Bailey) Mack.

Geographic distribution Central to eastern North America.

Additional relevant literature Benítez-Benítez et al. (2021).

VI.L.4. *Carex* sect. *Fecundae* Kük., in H.G.A.Engler, Pflanzenr. 20[IV,38]: 401. 1909.

Section *Fecundae* is one of the few mainly tropical *Carex* clades and the only one entirely confined to tropical America.

It is a well-supported clade with a relatively well-defined morphology. They are mostly robust plants, including perhaps the largest species of the genus (stems >3 m; Reznicek AA, pers. obs.). Scales are mostly dark colored and utricles are subcoriaceous with a bifid beak. The stigma number varies from two to three, sometimes even on a single plant. The inflorescence structure is probably the most diverse for any *Carex* clade of almost any size, ranging from simple racemose inflorescences to profusely branching ones (Reznicek, 1990), with spikes much-branched on well-developed peduncles or forming congested inflorescences where branches are tightly packed.

Circumscription 20 species (9 sampled), even though the taxonomy of the group is much in need of revision and new species might await discovery.

Geographic distribution Neotropical, from southern Mexico, to Andean South America, reaching south to northwestern Argentina, with a clear center of diversity in southern Mexico.

VI.L.5. *Prasina* Clade

Some phylogenetic hypotheses have placed *Carex prasina* as sister to the Microchaeta Clade (VI.L.6), but others have shown that the placement of this species is quite unstable and needs further study (Benítez-Benítez et al., 2021). This species has been traditionally placed in sect. *Hymenochlaenae*, but previous workers (Waterway, 2002) already considered this to be an anomalous placement based on morphology.

Circumscription 1 species (1 sampled): *Carex prasina*.

Geographic distribution Eastern North America.

VI.L.6. *Microchaeta* Clade

This clade nearly matches Egorova's concept of sect. *Scitae*, excluding the type of the section (*C. scitae*) that is placed in sect. *Phacocystis* (see also Benítez-Benítez et al., 2021). It also accommodates several species previously placed in sects. *Phacocystis*, *Racemosae*, and *Limosae*.

Circumscription 8 species (8 sampled).

Geographic distribution: Western North America and East Asia.

VI.M. *Molliculae*–*Castanea* Clade

This large clade is organized into six named clades/sections and three species of uncertain placement categorized as *Insertae Sedis*. Four of the clades largely diversified in or are endemic to the Western Hemisphere, and the others are primarily Eurasian in distribution with disjunctions to North America and Australia.

VI.M.IS1. *Incertae Sedis*

Here, we list four species whose affinities to the *Mollicula*–*Castanea* Clade (VI.M.) seem clear, but whose exact placement among the different clades remains unresolved.

Circumscription: 4 species (3 sampled).

Geographic distribution East Asia and Eastern North America.

VI.M.1. *Carex* sect. *Molliculae* Ohwi, Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 11: 450. 1936.

Species in sect. *Molliculae* have been often transferred (or the entire section merged) to the group here named sect. *Paludosae* (VI.M.2.). Here, we delimitate the section following Lu et al. (2021).

Circumscription 11 species (11 sampled).

Geographic distribution East Asia.

VI.M.2. *Carex* sect. *Paludosae* G.Don in J. C. Loudon, Hort. Brit. 377. 1830.

This is a group of large sedges, mostly found growing in wet soils. It has been long recognized in East Asia taxonomy as sect. *Confertiflorae*, but it is here enlarged to include a few non-Asian species according Lu et al. (2021). Consequently, the group needs to be renamed as sect. *Paludosae*, as it includes the type of that name (*C. acutiformis*).

Other known sectional names *Acutiformes* T.V.Egorova, *Confertiflorae* Franch. ex Ohwi, *Dispalatae* Ohwi, *Ischnostachyae* Ohwi.

Circumscription 23 species (18 sampled).

Geographic distribution Primarily East Asia, marginally reaching Europe and Africa (*C. acutiformis*) and Western North America (*C. amplifolia*).

VI.M.3. *Vestita* Clade

A clade embracing two species with coriaceous, tomentose utricles, and that are found growing in dry-to-moist soils. Its placement as an independent clade is provisional due to these species unstable placement in different phylogenetic reconstructions (Waterway MJ, pers. obs.).

Known sectional names *Globulares* Meinsh.

Circumscription 2 species (2 sampled): *Carex globularis*, *C. vestita*.

Geographic distribution Eastern North America and northeastern Europe to northeastern Asia.

VI.M.4. *Carex* sect. *Scirpinae* (Tuck.) Kük., in H.G.A.Engler, Pflanzenr. 20[IV,38]: 81. 1909.

Plants are typically unispicate and unisexual, rendering species in this section dioecious; culms are strongly reddish brown at the base. Dunlop & Crow (1999) found the placement of *C. scabriuscula* in sect. *Scirpinae* to be problematic due to high polymorphism in purportedly diagnostic traits within the species (e.g., plants less commonly have 1–2 reduced lateral spikes).

Circumscription 3 species (3 sampled): *Carex curatorum*, *C. scabriuscula*, *C. scirpoidea*. Phylogenomic data reveal a cryptic geographic variation in *C. scirpoidea*, which requires further study (Westergaard et al., 2019).

Geographic distribution Predominantly North American, with the exception of *C. scirpoidea* subsp. *scirpoidea* that, as currently circumscribed, displays amph-Beringian (Yana-Kolyma and Chukotka in eastern Russia) and amph-Atlantic (very local in only three locations in Norway, Westergaard et al., 2019) disjunctions.

Additional relevant literature Dunlop (1990, 2002).

VI.M.5. *Sartwelliana* Clade

This clade comprises two species endemic to California that are typically placed in sect. *Paludosae*. Reznicek & Catling (2002e) suggested that their placement in *Paludosae* was anomalous and recommended placement elsewhere or in their own section. Species in this clade share similarities with some western North American species in the sister *Castanea* Clade (VI.M.6.): basal sheaths tinged with reddish-purple, pubescent leaf sheaths and blades, erect cylindrical spikes, and small, pubescent utricles with short bidentulate hyaline beaks; however, pistillate bracts are sheathless or short sheathing with shorter blades than those found in most of the *Castanea* Clade.

Circumscription 2 species (2 sampled): *Carex congdonii*, *C. sartwelliana*.

Geographic distribution California.

VI.M.6. Castanea Clade

Species in this strongly supported clade have been previously placed in sects. *Hymenochlaenae*, *Porocystis*, *Fecundae*, *Halleriana*, *Longicaules*, and the monotypic *Hirtifoliae*. The group can be separated into two sets of species. Species in the larger subclade are defined by (i) reddish- or purplish-brown culm bases and basal bladeless sheaths; (ii) leaf sheaths and sometimes blades pubescent, (iii) inflorescences usually with staminate or gynecandrous terminal spikes and few to several peduncled lateral pistillate spikes, and (iv) obtusely trigonous, green, membranaceous, multi-veined, short-beaked to beakless utricles, sometimes pubescent, and many with red crystalline inclusions. The smaller subclade differs in having terminal spikes androgynous, gynecandrous, staminate, or androgynecandrous, and lateral spikes either mostly pistillate or mostly androgynous. We have tentatively included seven unsampled species in this subclade, because they belong to species complexes with representatives that have been sampled (*C. mackenziana* complex; Reznicek, 1990, Reznicek & González-Elizondo, 1997; *C. flexirostris* complex; Reznicek & González-Elizondo, 1999).

The distinction between the two subclades is weak, and a better understanding of relationships will require additional sampling of Mexican and Central American species.

Circumscription 58 species (41 sampled).

Known sectional names *Longicaules* Mack. ex Reznicek, *Hirtifoliae* Reznicek, *Porocystis* Dumort.

Geographic distribution Largely Western Hemisphere. The larger subclade is predominantly North American and disjunct between eastern temperate North America and the Pacific Coast, reaching Mexico and Central America, with rare outliers in South America (south to northern Argentina). Most of the common and widespread species are in eastern North America. The Pacific coastal, southwestern, and Mexican species typically have more restricted distributions, and many of those in the Neotropics are narrow endemics or known only from their type localities. The smaller subclade comprises mainly Mexican and Central American species.

Additional relevant literature Reznicek (1986), Jones & Reznicek (1992), Reznicek & González-Elizondo (2001), Waterway (1990a, 1990b, 1994, 2002), Smith & Waterway (2008a, 2008b), Jiménez-Mejías et al. (2018).

VI.N. Luzulina–Griseae Clade

This clade is predominantly North American except for *C. durieui*, which is found in Europe and whose placement here needs confirmation.

VI.N.1. Durieui Clade

Carex durieui does not have obvious morphological affinities with other members of the broader clade or other species in Europe. It was traditionally included in sect. *Ceratocystis* on the basis of the superficial resemblance of their inflorescences until its exclusion on the basis of molecular phylogeny (Jiménez-Mejías et al., 2012b).

Circumscription 1 species (1 sampled): *Carex durieui*.

Distribution Northwest Iberian Peninsula.

VI.N.2. Luzulina Clade

The species in this clade have typically been considered members of sect. *Aulocystis*. The section is distinguished from other lineages formerly placed in sect. *Aulocystis* by its green to purple but never blackish utricles.

Circumscription 4 species (4 sampled).

Geographic distribution Mountains of western North America from British Columbia to California.

VI.N.3. *Carex* sect. *Griseae* (L.H.Bailey) Kük., in H.G.A.Engler, Pflanzenr. 20[IV,38]: 516. 1909.

We combine the sections *Granulares*, *Griseae*, and *Careyanae* into a single taxon, sect. *Griseae*, because the sections are phylogenetically entangled and are morphologically very similar. *Careyanae* traditionally included species with more sharply trigonous utricles; *Granulares* traditionally included species with inflated utricles with plane or raised nerves; and *Griseae* species traditionally were recognized as having more or less terete or bluntly trigonous utricles with distinctly impressed nerves, whether fresh or dried. As here defined, all members of sect. *Griseae* share lateral spikes in which the utricles have a face (instead of an angle) opposite to the axis of the spike, chlorenchyma with scattered pigment cells, and utricles with a large proliferation of nerves (40–60 in most species). Section *Griseae* species differ from the similar-looking species formerly placed in sect. *Laxiflorae* (here merged with sect. *Paniceae*, VI.E.4.) by having obtusely trigonous culms, rather than the acutely trigonous or even slightly winged culms of the *Laxiflorae*.

Most of the species in this group are from deciduous broadleaf forest understories. *Carex conoidea* and the few species formerly placed in sect. *Granulares* are exceptions, being mostly from open habitats.

Circumscription 35 species (34 sampled).

Other known sectional names *Granulares* (O.Lang) Mack., *Careyanae* Tuck. ex Kük.

Distribution Predominantly in eastern North America, with a few species extending to western North America, and three occurring in Mexico and Guatemala.

Additional relevant literature Bryson & Naczi (2002a), Cochrane & Naczi (2002), Naczi & Bryson (2002), and Naczi (2009).

VI.N.4. *Carex* sect. *Collinsiae* (Mack.) Mack., in N.L.Britton et al., N. Amer. Fl. 18: 425. 1935.

Carex collinsii is morphologically distinct (FNA), with unique hooked utricle beak teeth that seem to be an adaptation for epizoochoric dispersal (A.A.Reznicek, pers. obs.).

Circumscription 1 species (1 sampled): *Carex collinsii*.

Distribution Eastern U.S.A.

VI.O. Esquiroliana Clade

Recent analyses place *C. esquiroliana*, usually included in sect. *Siderostictae*, as an isolated lineage within subg. *Carex*. Other species assigned to sect. *Siderostictae* on the basis of broad and pseudopetiolate leaves appear also to be more closely related to subg. *Carex* than to the early-diverging subg. *Siderosticta*. These species share unisexual spikes and beaked utricles, and hence are tentatively placed here (Léveillé-Bourret E, pers. obs.; X.-F. Jin, pers. obs.).

Circumscription 4 species (1 sampled).

Distribution Southern China and Vietnam.

VI.P. *Carex* sect. *Chlorostachyae* Tuck. ex Meinh., Trudy Imp. S.-Petersburgsk. Bot. Sada 18: 283. 1901.

This highly supported clade is exclusively formed by a set of morphologically similar species traditionally placed in sect. *Chlorostachyae*. Plants in this section are small, slender sedges with short leaves, thin stems, and sheathing bracts with short blades. The spikes are lax, with the terminal one staminate or bisexual, and the lateral ones pistillate on long filiform peduncles that may become pendant or contorted. Utricles are diminutive, smooth, and often shiny. *Carex handelii*, traditionally placed in this section, is excluded because recent phylogenetic analyses place it in the Indica Clade (VI.A.3.).

Circumscription 13 species (6 sampled).

Other known sectional names *Capillares* (Asch. & Graebn.) Rouy.

Geographic distribution Circumboreal, on montane to alpine belts of mountain ranges.

VI.Q. *Ceratocystis*–*Spirostachyae* Clade

This large clade is consistently found across phylogenetic studies (e.g., Waterway & Starr, 2007; Waterway et al., 2009; Jiménez-Mejías et al., 2016a; Martín-Bravo et al., 2019), and hence is recognized as a clade here.

VI.Q.1. *Carex* sect. *Frigidae* Fr. ex Kük., in H.G.A.Engler, Pflanzenz. 20[IV,38]: 531. 1909.

The earlier broad conception of this section (Kükenthal, 1909) included a diverse array of species now assigned to several sections within subgenus *Carex*. The two species we now include in this recircumscription of sect. *Frigidae* were most recently treated in sect. *Aulocystis*, but recent phylogenetic studies show sect. *Aulocystis* to be polyphyletic. These two species are separable from all other species previously placed in sect. *Aulocystis* by the combination of short creeping rhizomes, yellowish old leaf remains, and short cylindrical to linear pistillate spikes with dark, often reddish scales, hanging from arching flowering culms.

Circumscription 2 species (2 sampled): *Carex frigida*, *C. stenantha*.

Geographic distribution Disjunct between western and central Europe (*C. frigida*) and East Asia (*C. stenantha*).

VI.Q.2. *Carex* sect. *Rostrales* Meinh., Trudy Imp. S.-Petersburgsk. Bot. Sada 18: 283. 1901.

This section is a small morphologically well-defined group characterized by the relatively lax, few-flowered pistillate spikes with spreading long and slender utricles, tapering to a beak and loosely enclosing the nutlet.

Circumscription 5 species (5 sampled).

Other known sectional names *Folliculatae* Mack.

Geographic distribution Eastern and central North America, disjunct to East Asia, Papua New Guinea, and New Zealand.

Additional relevant literature Wujek & Menapace (1986).

VI.Q.3. *Carex* sect. *Sylvaticae* Rouy, Fl. Fr. 13: 470. 1912.

This small, relatively well-defined section includes species previously placed in sect. *Hymenochlaena* (Chater, 1980) or an expanded concept of sect. *Sylvaticae* that included other species not considered part of the section in this treatment (e.g., *C. arnellii*, *C. bostrychos-*

tigma; Egorova, 1999). Species in this group are distinguished from other Eastern Hemisphere sedges by their mostly cylindrical lax and flexuous pistillate spikes, and slender, nerved, smooth, and shiny utricles that are long attenuated into a long bifid beak.

Circumscription 6 species (6 sampled).

Geographic distribution Western Palearctic east to the Caucasus, including North Africa and Macaronesia (Azores), and eastern South Africa.

Additional relevant literature Martín-Bravo et al. (2013) and Benítez-Benítez et al. (2017).

VI.Q.4. *Carex* sect. *Spirostachyae* Drej. ex L.H.Bailey, Proc. Amer. Acad. Arts Sci. 22: 109. 1887.

This clade is consistently well supported (Waterway & Starr, 2007; Escudero et al., 2008; Escudero & Luceño, 2009). It includes about 100 species, the majority of which have traditionally been placed in sects. *Spirostachyae*, *Elatae*, and *Echinochlaena* (Kükenthal, 1909). Within the clade, three subclades are supported, two of which encompass most species from sects. *Spirostachyae* and *Elatae* mixed together. On the basis of these results, sects. *Spirostachyae* and *Elatae* were merged into a single sect. *Spirostachyae* (Escudero & Luceño, 2009). The third subclade comprises species mostly from sect. *Echinochlaena* that are here formally transferred to sect. *Spirostachyae*. All the species share, among other characters, sheathing bracts, cylindrical spikes, acute to awned scales, profusely reddish punctulate utricles, attenuated into relatively short bifid beaks, and elliptical nutlets.

Circumscription 102 species (78 sampled).

Other known sectional names *Echinochlaena* Kük., *Elatae* Kük. These two names would apply to two of the three clades in which sect. *Spirostachyae* is organized, the third containing the type species of sect. *Spirostachyae*.

Geographic distribution One of the most broadly distributed groups of species in the genus, sect. *Spirostachyae* is primarily distributed in the Western Palearctic, East Tropical Africa, and New Zealand, with disjunct taxa in Mexico, South America, South Africa, Atlantic islands (Azores, Madeira, Canary Isles, Santa Helena, and Tristan da Cunha archipelagos), Madagascar, the Mascarenes, and Australia.

VI.Q.5. *Carex* sect. *Rhynchocystis* Dumort., Fl. Belg. 147. 1827.

This small but morphologically well-defined section includes plants that are among the largest known in the genus, with robust flowering stems that can easily surpass 2 m length in some species (Martín-Bravo S, pers. obs.). Pistillate spikes are cylindrical, dense and large, frequently flexuose and pendant, and utricles are small and abruptly narrowed into a small tubular beak.

Circumscription 5 species (5 sampled).

Geographic distribution Southwestern Palearctic, including North Africa and Macaronesia (Azores and Madeira), eastern sub-Saharan Africa, and Madagascar.

Additional relevant literature Míguez et al. (2017, 2018, accepted).

VI.Q.6. *Carex* sect. *Triquetrae* (L.H.Bailey) Mack., in N.L.Britton et al., N. Amer. Fl. 18: 215. 1935.

Section *Triquetrae* is monotypic with unclear phylogenetic and morphological affinities. *Carex triquetra* is a species with

coriaceous foliage from Mediterranean habitats in the California floristic province.

Circumscription 1 species (1 sampled): *Carex triquetra*.

Geographic distribution California and Baja California.

VI.Q.7. *Carex* sect. *Strigosae* Fr. ex Christ, Bull. Soc. Bot. Belg. 24, 2: 13. 1885.

A monotypic section that is sometimes placed as a subsection within sect. *Sylvaticae*. Current phylogenetic hypotheses place it as sister to sect. *Ceratocystis*.

Circumscription 1 species (1 sampled): *Carex strigosa*.

Geographic distribution Temperate Europe and Caucasus.

VI.Q.8. *Carex* sect. *Ceratocystis* Dumort., Fl. Belg. 147. 1827.

A morphologically well-defined clade that includes mostly short-lived plants, and it is characterized by globose to shortly cylindrical pistillate spikes, acute to very shortly mucronate scales, utricles constricted in a long bifid beak that is often bent, and obovate nutlets. This section of *Carex* has frequent hybridization between species, and it also includes one of the few species that may behave as annuals (*C. oederi* is able to flower in its first year). Circumscription of this section has remained stable for a long time, with exclusion of *C. duriei* being the only exception.

Circumscription 16 species (13 sampled).

Geographic distribution Mainly circumboreal, with disjunct taxa in Andean South America, Patagonia, South Africa, Australia, and New Zealand. The section has a clear amphiatlantic center of diversity.

Additional relevant literature Crins & Ball (1988, 1989a, 1989b), Bruederle & Jensen (1991), Hedrén (2002), Derieg et al. (2008), Luceño & Jiménez-Mejías (2008), Jiménez-Mejías et al. (2012b), Derieg et al. (2013), Jiménez-Mejías et al. (2014a, 2017), and Nygaard et al. (2021).

VI.R. Fuliginosa Clade

As defined here, the Fuliginosa Clade has been supported in recent phylogenetic studies and includes morphologically similar species, but its relationship to other clades remains somewhat unclear.

Circumscription 5 species (4 sampled).

Geographic distribution Mountains of south-central Asia to central China, with one species in Southwest Asia, and another circumboreal and also reaching the mountains of Europe.

VI.S. *Carex* sect. *Hymenochlaenae* (Drejer) L.H.Bailey, in J.M.Coulter, Man. Bot. Rocky Mt. 379. 1885.

The accumulating DNA evidence suggests that sect. *Hymenochlaenae*, as lectotypified by Reznicek (1986) with *C. cherokeensis* Schwein, is a relatively small section with a broad but disjunct geographic distribution. This contrasts with Kükenhal's (1909) broadly defined sect. *Hymenochlaenae*, in which he treated 49 species with diverse traits from five continents within six subsections. Of the eight species treated as sect. *Hymenochlaenae* here, only two were included in the section by Kükenhal (1909) (*C. longibrachiata* was treated in sect. *Elatae* and four were described later). These eight species form a morphologically coherent group, with culm bases displaying various shades of brown from pale or yellow-brown to chestnut or dark brown, but not reddish, and tending to be fibrillose; inflorescences with several linear to cylindrical spikes, 1–5 per node, the distal one several staminate or gynecan-

drous, erect, sessile, or short pedunculate, and the lateral ones pistillate or rarely gynecandrous, nodding or drooping on long filiform peduncles; and green ellipsoid, obovoid or fusiform utricles tapering to bidentate beaks, glabrous or at least partially hispid in some species. A majority of the other species previously treated in sect. *Hymenochlaenae* are here placed in the Castanea Clade (VI.M.4.), whereas those in subsections. *Capillares* and *Graciles* form coherent morphological groups and are treated here in other groups (sect. *Chlorostachyae*, VI.P.; and the *Graciles* Clade (VI.A.2.)), respectively. Other species are scattered across several clades, mainly within subg. *Carex*.

Circumscription 8 species (6 sampled). Additional species, especially from China, may belong here (Jin et al., 2007).

Geographic distribution North America, disjunct from Southeast U.S.A. to local endemics in southern California and Chiapas, Mexico; eastern and southeastern Australia; and East Asia (Korea, southern Japan, southern China, and the island of Taiwan).

VI.T. Hallerianae–Digitatae Clade

This clade of four lineages includes members previously placed in *Acrocystis*, *Hallerianae*, *Occlusae*, and *Clandestinae*. It is not clear what level of division makes the most sense for sectional recognition without a more detailed morphological study. All species in this clade display diversely pubescent utricles. With the exception of species placed in sect. *Occlusae*, the rest of the taxa in this clade inhabit mesic–dry to semiarid environments.

VI.T.1. Ericetorum Clade

This clade comprises two closely related species that are traditionally placed in sect. *Acrocystis*. Both species have distinctive verrucose–muricate utricles.

Circumscription: 2 species (2 sampled): *Carex ericetorum*, *C. melanocarpa*.

Geographic distribution Mountains of Europe to central and East Asia.

VI.T.2. *Carex* sect. *Hallerianae* (Aschers. & Graebn.) Rouy, in G.Rouy et al., Fl. France 13: 439. 1912.

This is a well-defined monophyletic group of dry-adapted sedges with narrow leaves and laxly hairy utricles with fleshy bases.

Circumscription 5 species (5 sampled).

Geographic distribution The group displays a remarkable Madrean–Tethyan disjunction pattern, with two species present in central and southwestern North America (south to Guatemala) and the others distributed in southern Europe and the Mediterranean (east to the Caucasus). It is the only *Carex* group that has diversified locally on Mediterranean islands, with a few species endemic to the Balearic Islands and Corsica.

VI.T.3. *Carex* sect. *Occlusae* C.B.Clark, Bull. Misc. Inform. Kew, Addit. Ser. 8: 147. 1908.

It is another small group that is very well defined from a morphological point of view. Species in sect. *Occlusae* bear true leafy stems, inflorescences with overlapping spikes, and densely hairy utricles.

Circumscription 8 species (3 sampled).

Geographic distribution East, South, and Southeast Asia.

VI.T.4. *Carex* sect. *Digitatae* (Fr.) Christ, Bull. Soc. Bot. Belg. 24(2): 13. 1885.

This is a group of poorly differentiated species bearing lateral leafless culms that are apparently prone to hybridization.

Circumscription 4 species (4 sampled).

Geographic distribution Predominantly Europe, with one species reaching East Asia.

VI.U. *Setigera*–*Haematostoma* Clade

This clade is formed by a morphologically diverse set of species that share the common biogeographic feature of being mainly diversified in the mountains of Central, South, and East Asia.

VI.U.1. *Ivanoviae* Clade

The two high-altitude species comprising this clade form an isolated lineage within the *Setigera*–*Haematostoma* Clade and need further comparative study to determine how they are related to the rest of the clade.

Circumscription 2 species (2 sampled): *Carex herbacoeli*, *C. ivanoviae*.

Geographic distribution Central Asia and Himalayas.

VI.U.2. *Setigera* Clade

Despite diverse habits and inflorescence diversity, the placement of members from sects. *Polystachyae* and *Setigerae*, together with several Asian species from sect. *Aulocystis*, as well as *C. rufulistolon* (sect. *Thuringiaca*) from Nepal, is consistent with morphology. The clade is characterized by cylindrical, often androgynous spikes; utricles more or less inflated and usually pubescent; and, in most species, a continuous style that merges directly into the nutlet, the style base sometimes slightly thickened or contorted. This group contains *C. baccans*, whose red fleshy utricles may be adapted to endozoochory.

Circumscription 13 species (10 sampled).

Known sectional names *Polystachyae* Tuck. ex Kük., *Setigerae* Kukkonen.

Geographic distribution South, East, and Southeast Asia, westwards through the Himalayas to Central Asia (Russia) and Southwest Asia (Turkey).

VI.U.3. *Haematostoma* Clade

All species placed in this clade have previously (or currently) been classified in sect. *Aulocystis*. Whether this should be recognized at the sectional level is dependent on characterizing it in relation to the *Ivanoviae* Clade (VI.U.1.) and *Setigera* Clade (VI.U.2.).

Circumscription 22 species (11 sampled).

Known sectional names *Nigellae* Nelmes.

Geographic distribution Central Asia east to Himalaya and central China, with only one boreal species (*C. petricosa*) displaying an almost circumpolar distribution.

VI.V. *Concinna* Clade

This clade comprises three species traditionally placed in sect. *Clandestinae*. It includes the remarkable *C. concinnoides*, the only known *Carex* species with four stigmas.

Circumscription 3 species (3 sampled): *Carex concinna*, *C. concinnoides*, *C. richardsonii*.

Geographic distribution Northern North America.

VI.W. *Acrocystis*–*Clandestinae* Clade

It is a heterogeneous group whose members are mostly short in stature with short cylindrical unisexual or androg-

ynous spikes and have utricles that are mainly pubescent with short beaks. Many species display enlarged, somewhat fleshy utricle bases that may play a role in dispersal by ants. Most of the plants in this clade inhabit mesic or mesic–dry environments.

VI.W.1. *Carex* sect. *Clandestinae* G. Don, in J.C. Loudon, Hort. Brit. 376. 1830.

Almost half of the species in this clade have traditionally been classified in sect. *Clandestinae* (14 species). Most of the others have previously been classified in sects. *Aulocystis* or *Decorae* and display trigonous utricles covered by short soft hairs, traits that distinguish them from other species in these two sections. Several other species traditionally treated in *Aulocystis* or *Clandestinae* may belong here, but we list them as *incertae sedis*, because more study is needed to place them, given the extreme polyphyly exhibited by those sections.

Circumscription 31 species (22 sampled).

Geographic distribution Europe and Asia, with species in North, Central, Himalayan, and East Asia, and southeast to Papua New Guinea.

VI.W.2. *Liparocarpos* Clade

Currently, three species are recognized here, but there are several species of sect. *Lamprochlaenae* that are *incertae sedis* and may also belong here.

Circumscription 3 species (3 sampled): *Carex liparocarpos*, *C. tangulashanensis*, *C. turkestanica*.

Geographic distribution Europe and North Africa, and east to West/Southwest Asia, Central Asia, and Himalaya.

VI.W.3. *Carex* sect. *Acrocystis* Dumort., Fl. Belg. 147. 1827.

This clade is a broad circumscription of sect. *Acrocystis*, but it excludes some species previously placed in *Acrocystis* that instead group with other clades in current molecular analyses. Furthermore, a handful of species from other sections fall within sect. *Acrocystis*, as defined here, including four *Lamprochlaenae* species, one *Mitratae*, and one *Hymenochlaenae*.

In its current definition, this clade includes *C. zekogensis* (previously placed in sect. *Hymenochlaenae*) from China as sister to a pair of clades; one clade includes the type species (*C. montana*) and is predominantly European and Asian in distribution, and the other clade has the European *C. pilulifera* as sister to a North American clade. These patterns suggest that the section may have originated in Eurasia with a later dispersal, possibly through a Europe/North Atlantic route to North America.

Circumscription 45 species (36 sampled).

Other known sectional names *Lamprochlaenae* (Drejer) L.H. Bailey.

Geographic distribution North America, East and Central Asia, and Europe.

Additional relevant literature Roalson et al. (2001) and Roalson & Friar (2004a, 2004b).

VI.X. *Rhomboidales*–*Mitrata* Clade

This clade includes a number of recognizable sections and other clades that need further assessment, as the best arrangement for the formal classification of these taxa is not yet clear. Most of the species included in this group display striking nutlet morphologies, including rhomboidal nutlets,

sometimes with invaginate angles or concave faces, in some species prolonged at the apex in a diversely shaped beak (from cylindrical and thickened to annulate), and frequently with the style thickened at its base forming a stylopodium. It is expected that some of the general *incertae sedis* species might also be placed in this clade.

VI.X.IS1. *Incertae Sedis*

Here, we list 11 species that are likely a part of the broader Rhomboidales–Mitrata Clade, nine of which have been previously placed in sect. *Mitratae*, but whose placement in the clades recovered here is unclear. They are likely placed in either Mitrata Clade (VI.X.5.) or the Conica Clade (VI.X.6.). The other two species have recently been placed in sect. *Infossae* (Su, 2009, Cen et al., 2016). More than a dozen species previously classified in *Rhomboidales*, *Careyanae*, or *Clandestinae* were synonymized to the two species included here, *C. blinii* and *C. oxyphylla*. DNA data place *Carex oxyphylla* as sister to the Mitrata Clade, so it is possible that these species can be placed in the same section as the rest of that clade, but more sampling is needed to determine if sect. *Infossae* should be maintained or not.

Circumscription 12 species (3 sampled).

Geographic distribution These unplaced species are distributed throughout most of Asia, but the majority are from China.

VI.X.1. *Truncatigluma* Clade

This small clade comprises two subclades, both well supported: one that groups species previously included in sects. *Aulocystis* and *Decorae* and another with species from sects. *Mitratae* and *Lageniformes*. Species in the first group tend to have narrowly ellipsoid, stipitate, short to long-beaked bidentate, puberulent or pubescent utricle, and narrowly ellipsoid to cylindrical nutlets with distinctly stipitate bases, and at least slightly thickened or elongate persistent style bases. The two species from sect. *Decorae* that are placed in this subclade, however, differ in inflorescence structure with all spikes androgynous in both species and complex paniculate inflorescences in *C. morii*. *Carex morii* also grows in tropical forests, whereas the other species in the clade are most often found in rocky areas in the mountains including streamsides, meadows, moors, volcanic slopes, and mountain summits. Species in the second subclade are similar to sect. *Mitratae* in their cespitose growth form and inflorescence structure, but the nutlets are distinctive, with concave or excavated faces both above and below the middle and persistent thickened style bases forming cylindrical or flaring “necks,” some up to 1 mm long. *Carex pudica*, from traditional sect. *Mitratae*, is placed in this group by DNA data, but it does not share these unique features of the nutlets; rather, it has the annulate discoid persistent style base, typical of species in both the Mitrata and Conica Clades. More sampling is needed to determine the full composition of this clade and whether it is most appropriately treated as one or more sections.

Circumscription 12 species (6 sampled).

Geographic distribution East Asia to Southeast Asia, but predominantly in Japan, the island of Taiwan, and the Korean Peninsula.

VI.X.2. *Mira* Clade

This clade comprises a small group of Asian species traditionally placed in sect. *Acrocystis* that current phylogenetic

studies place closer to sect. *Rhomboidales* and the *Truncatigluma* Clade. They are small, cespitose plants with narrow (< 2.5 mm wide), often scabrous leaves and flowering culms longer than the leaves. The inflorescence is crowded distally with a single, terminal staminate spike that is usually longer than the 1–2 sessile, short cylindrical, few-flowered pistillate spikes. Utricles are ellipsoid, short-beaked, pubescent, or scabrous, tightly enclosing small (<2 mm) ellipsoid or obovoid nutlets. The styles are deciduous but slightly thickened at the base, leaving a very short, persistent, cylindrical beak on the nutlet, smaller but reminiscent of the apices of species in the *Truncatigluma* Clade. Culm bases and both staminate and pistillate scales are reddish-purple in most species of this clade.

Circumscription 5 species (4 sampled).

Geographic distribution Japan, Korea, and the island of Taiwan, with two species extending northward to the Russian Far East and Siberia.

VI.X.3. *Carex* sect. *Radicales* (Kük.) Nelmes, Reinwardtia 1: 389. 1951.

Although this clade does not consistently receive strong support in our DNA analyses, nearly all sampled species of sect. *Radicales* were placed in this clade on the basis of current phylogenetic analyses. Section *Radicales* is a morphologically consistent group with plants cespitose from short, sometimes thickened rhizomes, usually covered with persistent dark brown bracts; 1–6 androgynous spikes, the lowermost basal or borne from below the middle of the flowering culm; leaf-like involucral bracts, longer than the inflorescence; short-beaked compressed trigonous, variously pubescent utricles, and short stipitate nutlets with persistent thickened styles (Zhou & Jin, 2014; Jin et al., 2015). *Carex tsoi*, which differs from typical *Radicales* by its filiform culms, ovoid rather than cylindrical spikes, smaller nutlets, and the inflated brown-punctulate styles is placed in the Conica Clade in our current analyses, but its morphology does not fit well there either, so we treat it here as *incertae sedis*, pending further study.

Circumscription: 15 species (6 sampled).

Geographic distribution: Predominantly distributed in East Asia, with some species occurring in South Asia and Malesia.

VI.X.4. *Carex* sect. *Rhomboidales* Kük., in H.G.A.Engler, Pflanzenr. 38[IV,20]: 622. 1909.

Carex sect. *Rhomboidales*, as treated here includes all 40 species that were included in the most recent revision based on morphology of the species from East Asia (Jin & Zheng, 2013), plus three species described after 2013, five Japanese species treated as subspecific taxa by Jin & Zheng (2013), but at the species level by Hoshino et al. (2011), and one species each from Malaysia and the Philippines. On the basis of published molecular phylogenetic studies and as yet unpublished sequence data (Waterway MJ, pers. obs.), we have included in sect. *Rhomboidales* two species from Europe and Western Asia that were previously classified in sect. *Depauperatae* (*C. brevicollis* and *C. michelii*); two Chinese species traditionally classified in sect. *Careyanae* (*C. baimaensis* and *C. giraldiana*); and two species that Jin & Zheng (2013) had explicitly transferred from sect. *Rhomboidales* to sect. *Mitratae* (*C. dipledon* and *C. kobresiformis*). *Carex chinensis*, for which no DNA data are yet available, was also transferred to sect. *Mitratae* by Jin & Zheng (2013), but it is

here retained in sect. *Rhomboidales* due to its similarity to *C. kobresiiiformis*.

As detailed in Jin & Zheng (2013), most species here included in the section grow in cespitose clumps from short, ligneous rhizomes, even though a few have longer or creeping rhizomes. They usually have leaves at least 5 mm wide, often scabrous on margins and inflorescences with a single terminal staminate spike (rarely androgynous), and 2–7 erect, pedunculate, lateral pistillate, or androgynous spikes usually borne singly at each node with long sheathing involucre bracts with short blades. Utricles are generally at least 5 mm long, ellipsoid to ovoid or rhomboid and obtusely trigonous, tapering to a distinct beak with bidentate or rarely obliquely truncate orifices, the teeth short to long. Nutlets are trigonous and usually rhombic ovoid in shape, mitrate or hastate at the apex with the majority of species having constrictions or invaginations on the angles, and some also concave or excavated on the faces, either above or below the middle, or both.

Circumscription 59 species (22 sampled).

Geographic distribution East and Southeast Asia, with two species occurring from Europe to western Asia.

Additional relevant literature: Jin et al. (2014).

VI.X.5. Mitrata Clade

This clade, which includes the type for sect. *Mitratae* (*C. mitrata*), is comprised predominantly of species that are traditionally placed in that section. However, the majority of species from sect. *Mitratae* are found in the Conica Clade (VI.X.6.; see below). It may be that these two clades are sister groups and might best be treated together as sect. *Mitratae*; however, current phylogenetic hypotheses show only weak support for each clade and only group the two together weakly, with a very short branch. Hence, we here treat them as two different clades. Species in both clades are of small to medium size, characterized by inflorescences with terminal staminate spikes and usually erect linear to cylindrical spikes, lightly veined and often pubescent, short-beaked utricles, and generally obovoid or narrowly ovoid nutlets, usually with a persistent annulated discoid stylopodium. Those in the Mitrata Clade are generally smaller in stature than those in the Conica Clade with, on average, narrower leaves and shorter pistillate spikes that are more crowded distally. Species circumscriptions in this clade vary widely. We have used Hoshino et al. (2011) as the source for names of Japanese species, FOC for the Chinese species, and Egorova (1999) for the Eurasian species.

Circumscription 28 species (16 sampled).

Known sectional names *Mitratae* Kük.

Geographic distribution Temperate and tropical Asia, Australia and New Zealand, with the center of species diversity in East Asia, a few species reaching Europe and the Mediterranean region, and a few naturalized in North America and perhaps elsewhere.

Additional relevant literature: Akiyama (1955), Hoshino et al. (2011), Katsuyama (2015), and Jin (2017).

VI.X.6. Conica Clade

Most of the species traditionally classified in sect. *Mitratae* that have not been placed in the Mitrata Clade are placed here, along with a few species previously classified in sect. *Rhomboidales*. This clade is predominantly comprised of species that have traditionally been placed in sect. *Mitratae*. Although the Conica

Clade is not strongly grouped with the Mitrata Clade (VI.X.5.), it is sister to the latter in some analyses, and further study is needed to determine whether it is best treated in a broadly defined sect. *Mitratae* or as a separate section. Species in this clade are similar to those in the Mitrata Clade, but they tend to have inflorescences with longer erect or arching lateral spikes that are not crowded distally, instead more or less evenly dispersed along the upper half of the flowering culms (more rarely nearly basal), subtended by more leaf-like, usually short sheathing bracts. Lateral spikes are generally pistillate, but sometimes androgynous, and vary from narrowly linear, relatively few-flowered spikes to more densely flowered, cylindrical spikes. The leaf width is also much more variable in the Conica Clade than in the Mitrata Clade, with some species having leaves as wide as 20 mm or as narrow as 0.5 mm. Utricles are similar to those in the Mitrata Clade, and the nutlets also have the characteristic annulate discoid style bases, mitrate beaks, or more rarely, a thickened style base that resembles a collar or neck. Some have nutlets with concave or excavated faces, as in sect. *Rhomboidales*, and a few exhibit the invaginations typically found in that section. Species circumscriptions also vary widely in this clade, so we have used the same sources for species names as in the Mitrata Clade.

Circumscription 48 species (14 sampled).

Geographic distribution Mainly East Asia, particularly diverse in Japan; a few species reach Europe, and western and northern Asia.

Additional relevant literature Akiyama (1955), Hoshino et al. (2011), and Katsuyama (2015).

VII. Incertae Sedis

There are 113 species that we have not been able to place in a clade with any confidence and are here listed under VII. Incertae Sedis (Appendix S1). These names are generally from sections that are polyphyletic and, therefore, difficult to assess for placement in a clade, section, or portion of a section. Furthermore, many of these species are of Asian origin and have not been studied in much detail; as such, more work is needed to place them in the classification.

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Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.12722/supinfo>:

Appendix SI. *Carex* species list organized by the linear classification presented in the manuscript. Species marked with an asterisk (*) are those sampled in molecular phylogenetic studies. Accepted names follow the World Checklist of Seed Plants (WCSP) unless recent treatments suggest that a different taxonomy is warranted. Deviations from WCSP are described in the text.