

García-Moro Pablo (Orcid ID: 0000-0002-8331-4771)
Otero Ana (Orcid ID: 0000-0002-3354-2979)
Benítez-Benítez Carmen (Orcid ID: 0000-0003-4956-0343)
Martín-Bravo Santiago (Orcid ID: 0000-0003-0626-0770)
Naczi Robert F.C. (Orcid ID: 0000-0002-3985-0059)
Jiménez-Mejías Pedro (Orcid ID: 0000-0003-2815-4477)

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Biogeography and systematics of *Carex* subgenus *Uncinia* (Cyperaceae): A unique radiation for the genus *Carex* in the Southern Hemisphere

Pablo García-Moro,^{1,2} Ana Otero,^{3,4} Carmen Benítez-Benítez,⁵ Lucas Costa,⁶ Santiago Martín-Bravo,⁵ Robert F.C. Naczi,⁷ Anton A. Reznicek,⁸ Eric H. Roalson,⁹ Julian R. Starr¹⁰ & Pedro Jiménez-Mejías^{1,2}

1 Department of Biology (Botany), Universidad Autónoma de Madrid, Campus Cantoblanco, 28049, Madrid, Spain

2 Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, 28049, Madrid, Spain

3 Department of Biodiversity and Conservation, Real Jardín Botánico (RJB-CSIC), 28014, Madrid, Spain

4 Grainger Bioinformatics Center, Department of Science and Education Botany, The Field Museum, 1400 South Lake Shore Drive, Chicago, Illinois 60605-2496, U.S.A.

5 Área de Botánica, Departamento de Biología Molecular e Ingeniería Bioquímica, Universidad Pablo de Olavide, carretera de Utrera Km 1 s.n., 41013, Seville, Spain

6 Laboratory of Plant Cytogenetics and Evolution, Department of Botany, Federal University of Pernambuco, 50670-420, Recife, Pernambuco, Brazil

7 New York Botanical Garden, Bronx, New York, New York 10458-5126, U.S.A.

8 University of Michigan Herbarium, 3600 Varsity Drive, Ann Arbor, Michigan 48108-2228, U.S.A.

9 School of Biological Sciences, Washington State University, Pullman, Washington 99164-4236, U.S.A.

10 Department of Biology, University of Ottawa, Ottawa, Ontario, K1N 6N5, Canada

Address for correspondence: Pablo García-Moro, pablogarciamoro@gmail.com

Abstract *Carex* subg. *Uncinia* (Cyperaceae) constitutes one of six currently recognized *Carex* subgenera. This subgenus is mainly distributed on the American continent and in the Pacific region, and it is the only subgenus almost entirely absent from the Old World and primarily diversified in the Southern Hemisphere. It includes some of the few *Carex* species with clear epizoochoric traits: the representatives of *C.* sect. *Uncinia* possess utricles with an exserted and hooked rachilla that allows the diaspores to attach to feather or hair. We performed phylogenetic (ITS, ETS-1f, *matK*), biogeographic, and ancestral state reconstruction analyses to elucidate the systematic structure, origin and dispersal routes, and major morphological evolutionary patterns of the different lineages within the subgenus. Our phylogenetic reconstructions revealed that the subgenus comprises seven different clades that mostly match previously recognized sections. One of the clades, however, represents a new section described herein as *C.* sect. *Wheelerianae*. Unispicate lineages evolved repeatedly from ancestors bearing multispicate inflorescences, while the presence of a rachilla, often pictured as a plesiomorphy in *Carex*, seems to have developed four independent times in the evolution of *C.* subg. *Uncinia*. The origin of the subgenus

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dates back to the beginning of the Miocene, probably in North America from where it colonized the Southern Hemisphere. It first dispersed to South America during the Early Miocene. Later, in the Middle Miocene, representatives of *C.* sect. *Uncinia* would reach the Pacific Southwest region (New Zealand, Australasia) from South America in at least two independent dispersal events. The vast majority of the biogeographic events seem to be explained by long-distance dispersal. The remarkable dispersal ability of *C.* sect. *Uncinia* enabled by the hooked rachilla has allowed it to reach remote archipelagos in the Pacific and Subantarctic regions, probably bird-mediated.

Keywords ancestral area reconstruction; epizoochory; long-distance dispersal; Pacific Southwest; phylogeny; rachilla; Southern Hemisphere; *Uncinia*

Supporting information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

Systematics and evolution of *Carex*. — *Carex* L. (Cyperaceae), with more than 2000 species, is one of the three largest angiosperm genera in the world (excluding apomictic groups; Roalson & al., 2021). It originated during the Eocene in Eastern Asia (Martín-Bravo & al., 2019). This region has been considered the *Carex* diversity cradle from where it established its main colonization routes, effectively spreading around the world. The impressive migration ability of *Carex* has allowed it to colonize all biogeographical regions except Antarctica (Martín-Bravo & al., 2019), becoming a nearly cosmopolitan genus. The adaptation of *Carex* to temperate and cold climates seems to have favored its establishment primarily in temperate and high latitudes, as well as extra-temperate cold-climate areas, such as tropical mountain ranges (Gehrke & Linder, 2009).

Systematic treatment of the genus *Carex* and allied genera has changed significantly over the last 100+ years. Kükenthal (1909) first arranged tribe Cariceae, grouping *Carex* together with the genera *Schoenoxiphium* Nees, *Kobresia* Willd. and *Uncinia* Pers. In turn, he divided *Carex* into four different subgenera: (1) *C.* subg. *Primocarex* Kük. (= *C.* subg. *Psyllophorae* (Degl.) Peterm. s.l.), (2) subg. *Vignea* (P.Beauv. ex T.Lestib.) Peterm., (3) subg. *Indocarex* Kük. (= *C.* subg. *Vigneastra* (Tuck.) Kük.), and (4) “subg. *Eucarex* Kük.” (not validly published, = subg. *Carex*). Kükenthal’s division of Cariceae into different genera was based on three primary morphological characters (Reznicek, 1990; Global Carex Group, 2015): (i) the structure of the inflorescence, (ii) the morphology of the perigynium, and (iii) the grade of development of the rachilla. The perigynium is the fertile prophyll of an extremely reduced last-order inflorescence branch, often consisting of a single female flower contained within the perigynium, which can have open or fused margins to the apex forming an utricle (Jiménez-Mejías & al., 2016a; Léveillé-Bourret & al., 2018). The rachilla constitutes a remnant of the axis of that last-order inflorescence branch (Fig. 1), and in tribe Cariceae it may be sterile or consist of one to a few male flowers at its apex which represent a terminal male spikelet. Outside Kükenthal’s Cariceae treatment, a fifth genus, *Cymophyllus* Mack. ex Britton & A.Br., was later erected to segregate *Carex fraseriana* Ker Gawl., and remained in use until recently (Reznicek, 2002).

In his revision paper, Reznicek (1990) set the foundation for a major reconsideration of generic limits within Cariceae. He only recognized three subgenera within *Carex*: subg. *Carex*, subg. *Indocarex*, and subg. *Vignea*. He considered *C.* subg. *Primocarex* as a heterogeneous clustering of species whose placement needed further study. He also considered the genera *Cymophyllus*, *Kobresia* and *Uncinia* to be included within this group even though their status was still in need of revision. Later molecular phylogenetic studies (Roalson & al., 2001; Starr & al., 2004; Waterway & Starr, 2007) confirmed all the Cariceae satellite genera to be nested within *Carex*. This led to the eventual enlargement of *Carex* engulfing *Cymophyllus*, *Kobresia*, *Schoenoxiphium*, and *Uncinia* (Global Carex Group, 2015). A recent phylogenomic analysis (Villaverde & al., 2020) has led to further adjustments in the classification of *Carex*, recognizing six subgenera: *C.* subg. *Siderostictae* Waterway, subg. *Psyllophorae* s.str., subg. *Euthyceras* Peterm. (both formerly included within a broadly delimited *C.* subg. *Psyllophorae* s.l.), subg. *Uncinia* (Pers.) Peterm., subg. *Vignea*, and subg. *Carex*. Given the large size of *Carex*, each subgenus has traditionally been organized into multiple sections (Roalson & al., 2021), which circumscribe groups of relatively similar species, making the genus more manageable from an organizational point of view (Jiménez-Mejías & al., 2016b).

Systematics and biogeography of *Carex* subg. *Uncinia*. — From being considered an independent genus to its eventual merging within *Carex*, the systematic placement of the former genus *Uncinia* has been quite problematic (Table 1). The former genus *Uncinia* was easily recognized from all Kükenthal's (1909) Cariceae genera by having an exerted, hooked rachilla. In contrast, species that Kükenthal placed in *Carex* had an undeveloped rachilla, or a very reduced rachilla that is contained within the utricle (Fig. 1) (Starr & al., 2008), with the only exception of *C. microglochis* Wahlenb., whose rachilla effectively protrudes from the utricle beak.

The first named *Uncinia* species were described under *Carex* (e.g., *C. uncinata* L.f. [Linnaeus, 1782], *C. erinacea* Cav. and *C. phleoides* Cav. [Cavanilles, 1791]) but were soon transferred to their own genus (Persoon, 1807). That placement remained unaltered until Sanger sequencing-based phylogenetic methods demonstrated that species in the genus *Uncinia* formed a well-supported clade nested within *Carex*. It was found to be placed among the members of the so-called “Unispicate clade”, together with other genera of the tribe such as *Kobresia* and *Cymophyllus* and a number of species from *C. subg. Psyllophorae* s.l. (Roalson & al., 2001; Starr & al., 2004; Waterway & Starr, 2007; Jiménez-Mejías & al., 2016b). Thus, *Uncinia* was formally transferred to *Carex* (Global Carex Group, 2015), although a sectional classification following that placement was not formulated at that time. In Villaverde & al.'s (2020) phylogenomic work and subsequent phylogenies (e.g., Martín-Bravo & al., 2019), the former genus *Uncinia* was not nested within the majority of the Unispicate clade *Carex* species, but was found to be part of a clade (*Uncinia* clade) sister to the *C. subg. Vignea* clade. This novel placement also showed that the *Uncinia* clade included a few *Carex* sections together with the former genus *Cymophyllus*. Currently, the *Uncinia* clade is recognized as a distinct subgenus (*C. subg. Uncinia*; Villaverde & al., 2020), comprising 96 species belonging to six recently accepted sections (Roalson & al., 2021) (Fig. 2): *C. sect. Firmiculmes* (Kük.) Mack., *sect. Leucocephalae* Mack. (equivalent to the former monotypic genus *Cymophyllus*), *sect. Phyllostachys* (Torrey & A.Gray ex Carey) L.H.Bailey., *sect. Psilocarpae* Kük., *sect. Schiedeanae* Kük. p.p. (Neotropical species), and *sect. Uncinia* (Pers.) Baill., the latter entirely equivalent to the former genus *Uncinia* (Table 1). As currently circumscribed, *C. subg. Uncinia* is the fourth-largest subgenus of *Carex*, after *C. subg. Carex*, *subg. Vignea*, and *subg. Euthyceras* (Villaverde & al., 2020; Roalson & al., 2021).

Martín-Bravo & al. (2019) explored colonization patterns from a global perspective, hypothesizing that colonization events from the Northern to the Southern Hemisphere are at much higher frequency than those in the opposite direction. Accordingly, it has been inferred that *Carex* colonized the Southern Hemisphere several times independently from different regions (Gehrke & Linder, 2009; Martín-Bravo & al., 2019). Because of that, it was suggested that the Northern Hemisphere acted as a diversity cradle and the Southern Hemisphere acted as a colonization sink for *Carex*. This pattern has been studied in other pan-temperate elements that originated in regions of the Northern Hemisphere and dispersed to regions of the Southern Hemisphere, such as *Myosotis* L. (which colonized New Zealand from Eurasia; Winkworth & al., 2002), *Astragalus* L. (which entered South America from North America in two colonization events; Scherson & al., 2008) and *Poa* L. (originated in Eurasia and dispersed to all regions of the Southern Hemisphere; Soreng, 1990; Hoffmann & al., 2013; Giussani & al., 2016). The major diversity of *C. subg. Uncinia* is concentrated outside the Old World and has most of its diversity in the Southern Hemisphere (Roalson & al., 2021).

However, the biogeographic history of *Carex* subg. *Uncinia* remains unclear. Using a representative sampling of the group (65.6% of all accepted species), Martín-Bravo & al. (2019) inferred that the subgenus originated in the Americas during the Early Miocene, but they were unable to resolve whether this took place in North or South America. During Early and Middle Miocene, the group soon split into some of its main lineages. However, this study did not include representatives of *C. sect. Psilocarpae*, and only one species of the South American representatives of *C. sect. Schiedeanae* was included. In the particular case of *C. sect. Uncinia*, it appears to have originated in South America, and then spread through the Pacific region, colonizing the Pacific Southwest and a number of Pacific archipelagos. In fact, many species of *C. sect. Uncinia* (34 of the total 72) inhabit New Zealand (Martín-Bravo & al., 2019). The authors argued that the wide distribution of *C. subg. Uncinia* was probably mediated by epizoochory, since migratory birds could have transported the utricles attached to feathers by the hooked rachilla as a long-distance dispersal (LDD) mechanism.

Aims. — The current study has four main objectives: (1) to unravel the infrageneric relationships in *Carex* subg. *Uncinia* using molecular phylogenetic analyses; (2) to reconstruct its biogeographical history at a regional scale, disentangling its ancestral area, main dispersal routes, and establishment across the Pacific and circum-Antarctic archipelagos; (3) to clarify the evolutionary patterns of its diagnostic morphological features (inflorescence and rachilla); and (4) to propose a revised formal taxonomic framework and arrange the subgenus into sections.

MATERIALS AND METHODS

Sampling. — We have compiled a representative sampling of *Carex* subg. *Uncinia* covering all the sections according to Roalson & al. (2021). Sequences were taken from two sources: the dataset of Martín-Bravo & al. (2019) and newly sequenced material from silica-gel dried fresh material as well as herbarium vouchers (Appendix 1). Final sampling implied 75 species (78.1% of the total species) of the subgenus over the 63 species (65.6%) previously sampled by Martín-Bravo & al. (2019). Also, for the first time, representatives of *C. sect. Psilocarpae* were included in a molecular phylogenetic analysis.

DNA amplification and sequence editing. — Whenever possible, we sequenced three markers for each sample: two nuclear (ETS-1f, ITS) and one plastid (*matK*) region. These markers have already been used successfully to reconstruct phylogenetic relationships within *Carex* (Jiménez-Mejías & al., 2016b; Martín-Bravo & al., 2019). As outgroup, we chose different taxa belonging to the other five subgenera of *Carex* (Appendix 1), allowing us to represent all the main lineages within *Carex*.

Newly sequenced material was processed at Washington State University (Pullman, Washington, U.S.A.) and Pablo de Olavide University (Seville, Spain). DNA was extracted from leaf tissue following a modified CTAB procedure (Doyle & Doyle, 1987). PCR amplification was performed using the same protocols and primers as in Jiménez-Mejías & al. (2016b).

All the obtained raw sequences were processed using Geneious Prime v.2020.1.2 (<https://www.geneious.com>). Chromatograms with low quality and incomplete sequences were discarded. All the sequences of each marker were aligned individually using MUSCLE (Edgar, 2004) as implemented in Geneious Prime, obtaining three matrices (one per marker). Indels were coded as binary data using SeqState v.1.4.1 (Müller, 2005) according to the Simmons & Ochoterena (2000) simple coding method. These three matrices were concatenated into a fourth matrix (all-Data matrix). Since not all the markers amplified for all samples, the concatenated matrix contained a considerable proportion of missing data (Table 2) which yielded trees with unexpectedly low statistical support for some branches. In order to overcome this problem, we prepared a fifth matrix (all-nrDNA matrix) where all sequences contained at least sequences of both ETS-1f and ITS markers regardless of whether the accession had *matK* or not (nuclear DNA). Eventually, we created a last matrix (final matrix) adding to the all-nrDNA matrix the longest available concatenated sequence of the lacking species from the all-Data matrix.

Phylogenetic analyses. — The best evolutionary model for each individual marker was estimated using jModelTest v.2.1.6 (Guindon & Gascuel, 2003; Darriba & al., 2012), except for the coded indels, for which we implemented the model JC, as explained in MrBayes manual (Ronquist & al., 2012). We run Bayesian inference (BI) and maximum likelihood (ML) phylogenetic analyses on all the matrices. For the BI analyses, MrBayes v.3.2.7a (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) was used. We set 10 million generations and four simultaneous Markov Chain Monte Carlo runs, with a sample frequency of one tree every 1000 generations. A burn-in of 25% was applied before computing the 50% majority-rule consensus tree and after confirming the analyses had reached stationarity. ML was performed using RAxML-HPC BlackBox v.8.2.12 (Stamatakis, 2014) with parameters set to default. As RAxML-HPC BlackBox does not recognize matrices with binary indels, we excluded that partition from the analyses.

All phylogenetic analyses were run on the CIPRES Science Gateway (Miller & al., 2010).

Divergence time estimation. — We performed divergence time estimation as implemented in BEAST v.1.10.4 using the final matrix. Calibration points were selected according to Martín-Bravo & al. (2019) using three fossils (Jiménez-Mejías & al., 2016c) and a secondary calibration for *Carex* subg. *Uncinia* (Table 3). We excluded the coded indels as we ought to reduce the number of partitions of our matrix, while we already knew that these indels just slightly increased the support of some already well-supported branches. As a result, we considered only three partitions (one per marker). We followed the same procedure but used some different parameters than Otero & al. (2019a). We ran four independent runs, each one of 20 million generations, sampling every 2000 generations. Also, we assigned two different uncorrelated Log-normal relaxed clocks, one to *matK* (uniform distribution = 1.0×10^{-4} to 1.0×10^{-2}) and the other to ETS-1f and ITS (uniform distribution = 5.0×10^{-4} to 5.0×10^{-2}) (Otero & al., 2019a). Effective sample sizes (ESS) for each run were assessed through Tracer v.1.7 and considered appropriate above 200 (Rambaut & al., 2018). LogCombiner v.1.10.4 (Suchard & al., 2018) was used to combine all trees generated from each independent run. TreeAnnotator v.1.10.4 (Suchard & al., 2018), by selecting the “maximum clade credibility tree” option, allowed us to obtain the final, dated tree. For the subsequent reconstruction analyses, we used this dated tree after pruning the outgroup and leaving only one terminal per

taxon.

Morphological ancestral state reconstruction. — We estimated ancestral states for rachilla and inflorescence, two of the most important diagnostic characters in tribe Cariceae (see Introduction) and traditionally considered of great evolutionary significance. First, we checked for the best model of evolution using the function “fitDiscrete” implemented in the R package *geiger* v.2.0.7 (Pennell & al., 2014). Rachilla states were coded as “undeveloped”, “contained within the utricle” or “exserted and hooked”, while inflorescence states were coded as “unispicate”, “branched” or “sometimes branched/sometimes unispicate”. For both traits, we tested the equal rates (ER), all rates different (ARD) and symmetrical (SYM) models and one custom model adjusted after observing the Q matrix from the best model of a first test with the previous models. For rachilla, the custom model was derived from the SYM model, but the rate transitions for vestigial-present and vestigial-absent were different. For inflorescence, the custom model was derived from the ARD model, but with equal rate for transitions from the unispicate state. The best-fitting model was chosen according to the Akaike information criterion. The reconstruction (based on the best-fitting model) was carried out by MCMC-sampling of the posterior distributions of 10,000 stochastic character maps using the “make.simmap” function implemented in the R package *phytools* v.0.7-70 (Revell, 2012).

Biogeographic reconstruction. — Biogeographic reconstruction was performed using the BioGeoBEARS package (Matzke, 2018) on RStudio. We tested DEC and DIVALIKE models and did not consider the “+J” parameter. The major concerns regarding conceptual and statistical issues described for the +J parameter (Ree & Sanmartín, 2018) led us to avoid the use of this parameter in our biogeographic models. We built a biogeographical matrix in which we coded the regions where the study group is distributed. These regions comprised specific areas within the American continent, the Pacific and sub-Antarctic region (Table 1) according to patterns of diversity of *Carex* subg. *Uncinia* in the area after checking distributions in WCSP (Govaerts & al., 2020). This regionalization was finer than the one used in Martín-Bravo & al. (2019) and allowed us to perform a more detailed study to find out the specific areas where the different groups originated and expanded to. We performed two different ancestral area reconstructions. First, nine geographic areas were delimited: (1) WNA, Western North America; (2) ENA, Eastern North America; (3) CA, Central America; (4) ASA, Atlantic South America; (5) And, extra-Patagonian Andes (from herein simply referred as “Andes”); (6) Pat, Patagonia; (7) PI, Pacific islands; (8) Sub, sub-Antarctic archipelagos; and (9) PSW, Pacific Southwest (including Australia, New Zealand and Tasmania). However, as the high number of areas sometimes produced considerable uncertainty in the inferred ancestral area for some nodes, a second biogeographic analysis was performed where certain areas were merged to produce just six potential ancestral areas. The selected regions were: (1) N, North America (WNA + ENA); (2) CA, Central America; (3) S, South America (ASA + And + Pat); (4) PI, Pacific Islands; (5) Sub, sub-Antarctic archipelagos; and (6) PSW, Pacific Southwest.

RESULTS

Phylogenetic analyses. — The final matrices contained 179 different specimens from *Carex* subg. *Uncinia* sequenced successfully for the following markers: ETS-1f (124; 42 newly obtained for this study), ITS (122; 29 new sequences), and *matK* (109; 35 new sequences) (suppl. Appendices S1–S3). After removing sequences with excessive missing data (suppl. Appendices S4, S5), the final concatenated matrix for all three markers contained 109 sequences (suppl. Appendix S6). Additional characteristics of each of the matrices are presented in Table 2. The best evolutionary model for each marker was selected according to AIC scores as obtained from jModelTest. These models were: HKY+I+ Γ for ETS-1f and GTR+ Γ for ITS and *matK*.

ML and BI analyses of each matrix resulted in similar topologies (suppl. Figs. S1–S10) without significant incongruences within our ingroup. For significant incongruences, we understood those involving well-supported lineages conflicting among trees (clades with BS [bootstrap support] > 75 or PP [posterior probability] > 0.90; Gehrke & al., 2010). This supported our concatenation approaches. Results are primarily based on the final matrix (Fig. 3), as it yielded the highest-supported topology. Species from the same subgenus grouped together in well-supported clades in our phylogeny. Accordingly, *Carex* subg. *Uncinia* formed a highly supported clade (PP = 1; BS = 88). This clade was in turn subdivided into two main clades: clade 1 (PP = 1; BS = 99) and clade 2 (PP = 1; BS = 83). Clade 1 contained two main subclades: *C. sect. Leucocephalae* clade (PP = 1; BS = 100) and *C. sect. Phyllostachys* clade, which was monophyletic but poorly

supported (PP = 0.70; BS = 61) in both analyses. Clade 2 contained the rest of the subgenus. The first diverging clade in clade 2 contained the current *C. sect. Firmiculmes* (PP = 1; BS = 95), while the second clade diverging from this node (PP = 0.97) contained the rest of the groups. The next diverging group corresponded to *C. sect. Psilocarpae* clade I (PP = 1; BS = 99). This clade was sister to a clade (PP = 0.91; BS = 50) that again contained the remainder of the subgenus. From this last node, the *C. sect. Psilocarpae* clade II (PP = 1; BS = 100), which contained only *C. sellowiana* Schldl., was sister to a clade (PP = 0.96; BS = 61) comprising the South American representatives of *C. sect. Schiedeanae* (hereafter referred to as South American sect. *Schiedeanae*; PP = 1; BS = 96) and *C. sect. Uncinia* (PP = 1; BS = 97), one sister to the other. Within the *C. sect. Uncinia* clade, we found four main lineages (Fig. 3). The first, lineage A, included our only accession of *C. kingii* (R.Br. ex Boott) Reznicek as sister to a strongly supported clade (PP = 1; BS = 100) containing all remaining lineages. Lineage B was a well-supported clade (PP = 1; BS = 99) mainly composed of species from South America, with the remarkable exception of two species from the Pacific Southwest (*C. subtilis* K.A.Ford, *C. parvispica* K.A.Ford). Lineage C (PP = 1; BS = 98) included only two South American species with articulated glumes, *C. firmula* and *C. subsacculata* (G.A.Wheeler & Goetgh.) J.R.Starr. And finally, lineage D (PP = 1; BS = 99) was composed largely of members of *C. sect. Uncinia* from the Pacific Southwest.

Divergence-time analysis. — The tree topology obtained by Beast (Fig. 4) was almost identical to the tree obtained using MrBayes (Fig. 3) with the exception of *Carex* sect. *Psilocarpae* clades I and II, which here are sister clades, although poorly supported. The origin of *C. subg. Uncinia* was inferred at 22.88 mya (95% HPD: 20.99–24.70 mya), at the beginning of the Miocene (Fig. 4). Both clade 1 and clade 2 diversified during the Miocene at 9.09 (3.67–17.27) mya (Late Miocene) and 20.63 (17.79–23.28) mya (Early Miocene) respectively. Within clade 1, divergence between *C. sect. Leucocephalae* and sect. *Phyllostachys* was inferred at 9.09 (3.67–17.27) mya (Late Miocene). Within clade 2, ancestors of each main group diverged during the Miocene: Middle Miocene for *C. sect. Firmiculmes* at 12.93 (6.07–19.88) mya, sect. *Psilocarpae* clade II at 15.48 (9.97–20.30) mya, and sect. *Uncinia* at 14.41 (10.99–17.85) mya; and Late Miocene for South American *C. sect. Schiedeanae* at 10.14 (5.37–15.09) mya and sect. *Psilocarpae* clade I at 7.91 (2.84–13.56) mya. The divergence of *C. kingii* (lineage A) from the rest of *C. sect. Uncinia* took place during the Middle Miocene at 14.41 (10.99–17.85) mya. The rest of the main lineages within *C. sect. Uncinia* diversified during Late Miocene (lineage B at 9.16 [6.15–12.02] mya, and lineage D at 8.13 [5.65–10.75] mya) and along the Mio-Pliocene boundary (lineage C at 4.68 [1.73–8.35] mya).

Morphological ancestral state reconstruction. — Our custom models for rachilla and inflorescence evolution provided the best fit for our data according to the AIC values (suppl. Table S1). An “undeveloped” rachilla was inferred as the ancestral state for the group, with few transitions to “contained within the utricle” close to the tips and one single transition to “exserted and hooked” for the ancestor of the *Carex* sect. *Uncinia* clade (Fig 5). No reversions of state were observed, indicating that dwarfing of a developed rachilla may not be possible. Although most species presented “unispicate” inflorescences, the ancestral state was retrieved to be probably “branched” with transitions to the other states all along the phylogeny (Fig 5). Although there were reversions between “branched” and “sometimes branched/unispicate” states, once “unispicate” was acquired, there were no state reversions, indicating an evolutionary tendency for this type of inflorescence.

Biogeographic analyses. — We selected the DEC model as the best fit for our data in the 9-area analysis (lnL = -146.7; AIC = 297.4) (Fig. 4), and a DIVALIKE model for the 6-area analysis (lnL = -84.01; AIC = 172.19) (suppl. Fig. S11). The ancestral area of *Carex* subg. *Uncinia* has been recovered as equivocal between three areas in the Americas (Eastern North America, Western North America, and Andes) in our 9-area analysis (Fig. 4), while our 6-area analysis (suppl. Fig. S12) recovered the region of North America as the most probable area (65.8%) for its origin and a combination of both North and South America as the second most probable area (33.7%). For the sake of simplicity, we will refer to the ancestral areas of the rest of the tree according to the 9-area analysis unless otherwise specified.

The clade 1 (*Carex* sect. *Leucocephalae* and sect. *Phyllostachys*) ancestral area was placed in Eastern North America (71.69%). The *C. sect. Phyllostachys* ancestor was probably distributed in Eastern North America (59.15%) where it diversified, but also colonized Western North America from its ancestral area by at least one colonization event.

The ancestral area for clade 2 was also equivocal with two possible areas recovered: Western North America and Andes (Fig. 4). Our 6-area analysis also recovered a combination of regions (in this case North America and South America) as the most probable ancestral area (Fig. S12). The *Carex* sect. *Firmiculmes* ancestor was placed in Western North America (Fig. 4). The rest of the groups diverged from a South American ancestor whose area was recovered as ambiguous between Patagonia and the Andes. The poorly supported clade encompassing *C. sect. Psilocarpae* clades I and II recovered Atlantic

South American and Andean regions, while the ancestor of the *C. sect. Psilocarpae* clade II was already entirely restricted to Atlantic South America. The ancestor of the two remaining South American groups, *C. sect. Schiedeanae* and sect. *Uncinia*, seems to have its common ancestral area in the Andes (Fig. 4). The current South American *C. sect. Schiedeanae* remained entirely within this region, while *C. sect. Uncinia* greatly expanded its range.

The ancestral area of *Carex* sect. *Uncinia* was recovered ambiguous between Patagonia and the Andes. *Carex kingii* (lineage A; Fig. 4) is now entirely confined to Patagonia, but the other three groups colonized other South American areas and spread to the Pacific and sub-Antarctic regions. The common ancestral area of lineages B, C, and D was recovered as a heterogeneous area that mainly included the Andean region and Patagonia in the 9-area analysis. Our 6-area analysis (suppl. Fig. S12) confirmed that this ancestor originated in South America. The ancestral area of lineage B was placed in the Andes (Fig. 4), later spreading to Patagonia, Atlantic South America, Central America, New Zealand, Pacific Islands, and sub-Antarctic archipelagos. The ancestral area of lineage C was also placed in the Andes (Fig. 4). The ancestor of lineage D (Fig. 4) was restricted to the Pacific Southwest, with later dispersal events to Pacific islands and sub-Antarctic archipelagos. Our results show at least two colonization events of the Pacific Southwest from South America, and multiple colonizations of Pacific and sub-Antarctic archipelagos from different source areas.

DISCUSSION

***Carex* subg. *Uncinia* phylogeny and correspondence with existing taxonomic treatments.** — Our phylogenetic results show seven monophyletic groups within *Carex* subg. *Uncinia* organized in two main clades: clade 1, grouping the monotypic *C. sect. Leucocephalae* clade sister to the *C. sect. Phyllostachys* clade; and clade 2, grouping the remaining five groups, i.e., *C. sect. Firmiculmes* clade, sect. *Psilocarpae* clade I, sect. *Psilocarpae* clade II, South American sect. *Schiedeanae* clade, and sect. *Uncinia* clade (Fig. 3). The main clades found in our phylogeny, as well as the phylogenetic relationships among them, agree with those presented in previous works (Martín-Bravo & al., 2019; Villaverde & al., 2020; Roalson & al., 2021). These seven clades corresponded differently to *Carex* sections or independent genera over the years (Table 1). Thus, species belonging to the *C. sect. Uncinia* clade were originally considered as an independent genus within the tribe Cariceae (Kükenthal, 1909) until its transfer to *Carex* (Global Carex Group, 2015), and now it constitutes the current *C. sect. Uncinia* (Roalson & al., 2021). With the exception of *C. sect. Uncinia*, most species in this subgenus were originally included in *Carex* and placed in the former *C. subg. Primocarex* (= subg. *Psyllophorae* s.l.) by Kükenthal (1909) due to the presence of a single terminal spikelet as the inflorescence. Only *C. sect. Phyllostachys* and sect. *Schiedeanae* were placed in other subgenera (subg. *Carex* and subg. *Indocarex* [= subg. *Vigneastrae*], respectively) as these sometimes have multispicate inflorescences.

Carex sect. *Leucocephalae* appears in our analyses as a monotypic distinct clade sister to a poorly supported *C. sect. Phyllostachys* (Fig. 3). Initially described as a species of *Carex*, *C. fraseriana* is a North American endemic from the Appalachians. It was placed within *C. subg. Primocarex* and sect. *Leucocephalae* by Kükenthal (1909). Because of the strongly deviant morphological characteristics of leaves and inflorescences (Reznicek, 2002), it was soon transferred to its own genus, *Cymophyllus* (Britton & Brown, 1913), which was recognized until recently (Reznicek, 2002). Starr & al.'s (2008) phylogeny already revealed the nested position of *C. fraseriana* within *Carex*, being placed in a clade that also included the former genus *Uncinia*. Because of that, the genus *Cymophyllus* was dismissed and re-merged within *Carex* during the re-arrangement of the genus (Global Carex Group, 2015). The close relationship of *C. sect. Leucocephalae* with sect. *Phyllostachys* was solidly established in Jiménez-Mejías & al. (2016b) and Martín-Bravo & al. (2019), where both sections formed a clade in turn sister to another clade containing the former genus *Uncinia* and *C. sect. Firmiculmes*. Our work agrees with the previous placement of *C. sect. Leucocephalae* closely related to *C. sect. Phyllostachys* and as part of *C. subg. Uncinia*.

Carex sect. *Phyllostachys* is a morphologically cohesive group (Naczi & al., 1998; Crins & al., 2002) and it is recovered as monophyletic but poorly supported in some of our analyses (Fig. 3). It is entirely endemic to North America and was initially placed in *C. subg. Carex* (“*Eucarex*”) by Kükenthal (1909). While some other phylogenies have failed in recovering *C. sect. Phyllostachys* as a monophyletic group (Jiménez-Mejías & al., 2016b), it is well-supported in some of our single-marker analyses (suppl. Figs. S1, S10) as well as other previous analyses (Martín-Bravo & al., 2019). This fact, added to the morphological coherence present in the whole group, leads us to consider it as a single section awaiting further data.

The early-diverging clade within clade 2 of *Carex* subg. *Uncinia* (Fig. 3) conforms to the current *C. sect. Firmiculmes* (Roalson & al., 2021), which is endemic from Western North America. The section was initially placed within *C. subg. Primocarex* and sect. *Psilocarpae*, as subsect. *Firmiculmes* (Kükenthal, 1909). It is a morphologically well-defined group (Crins, 2002). Starr & al.'s (2008) phylogeny placed it within the Unispicate clade. Later works recovered *C. sect. Firmiculmes* also within the core Unispicate clade of the tribe Cariceae and closely related to the former genus *Uncinia* (Jiménez-Mejías & al., 2016b; Martín-Bravo & al., 2019). Our results agree in recognizing *C. sect. Firmiculmes* as an independent section within *C. subg. Uncinia*.

Carex sect. Psilocarpae appears split into two well-supported clades in our phylogeny: *C. sect. Psilocarpae* clade I and *C. sect. Psilocarpae* clade II. Phylogenetic reconstructions recovered *C. sect. Psilocarpae* clade I as the sister group of the clade including *C. sect. Psilocarpae* clade II plus a monophyletic South American *C. sect. Schiedeanae* and sect. *Uncinia*, although marginally supported (Fig. 3). Thus, *C. sect. Psilocarpae* as traditionally defined would be a paraphyletic group. Species within it were primarily placed in *C. subg. Primocarex sect. Psilocarpae*, in subsect. *Seticulmes* (Kükenthal, 1909). Superficial morphological characteristics of the included species led to their grouping into a single section (Kükenthal, 1905; Kükenthal, 1909, Silveira & Longhi-Wagner, 2012), but no phylogenetic reconstruction of this section has been previously conducted. Biogeographical analyses (Fig. 4) also show that these two groups inhabit different regions (species of *C. sect. Psilocarpae* clade I are confined to Atlantic South America, being endemic from southern and southeastern Brazil, while the monotypic *C. sect. Psilocarpae* clade II is also present there but reaches the Andes through the Chaco; see below). Both groups also display distinct characteristics, with *C. sellowiana* (*C. sect. Psilocarpae* clade II) having an ovate spike, with the staminate portion of the spike much shorter than the pistillate one, often concealed by it, while the other species have spikes cylindrical, with the staminate portion conspicuously elongated and often as long as the female one (Kükenthal, 1909; Jiménez-Mejías & Silva, 2020). Eventually, although our reconstructions have some uncertainty and both clades may show alternative relationships using other markers, the long branch supporting *C. sellowiana* (Fig. 4) shows a split deeper between it and *C. sect. Psilocarpae* clade I than between any other couple of groups here considered at sectional level. According to all these differences, we suggest that *C. sect. Psilocarpae* should be treated as two separate sections.

South American representatives placed in *Carex sect. Schiedeanae* (Jiménez-Mejías & Escudero, 2016; Jiménez-Mejías & Reznicek, 2018; Roalson & al., 2021) were recovered as a well-supported clade sister to the *C. sect. Uncinia* clade in our work. The taxonomic history of this set of species dates back to the relatively recent description of *C. subandrogyna* G.A. Wheeler & Guagl. (Wheeler & Guaglianone, 2003). The initial placement of *C. subandrogyna* within *C. sect. Schiedeanae* implied its recognition as a member of *C. subg. Indocarex*, since Kükenthal (1909) placed that section in this subgenus. However, recent phylogenies revealed that this species was more closely related to other *Carex* groups than to the rest of representatives of *C. sect. Schiedeanae* (Martín-Bravo & al., 2019; Villaverde & al., 2020). In this work, we have increased the sampling of allies of *C. subandrogyna* and have found that the South American *C. sect. Schiedeanae* species form a monophyletic group. Since the rest of *C. sect. Schiedeanae* species, all of North American distribution (Roalson & al., 2021), are placed in a different subgenus (*C. subg. Euthyceras*; Martín-Bravo & al., 2019; Villaverde & al., 2020; Roalson & al., 2021), *C. sect. Schiedeanae* as traditionally conceived would constitute a polyphyletic group. We propose that this group should be treated as a new and independent section.

Carex sect. Uncinia is the largest clade in our phylogeny. It comprises most species of *C. subg. Uncinia*, and, so far, all the included species from the former genus *Uncinia*. Starr & al.'s (2008) phylogeny revealed for the first time the placement of *Uncinia* within *Carex*. In that work, *C. kingii* was already recovered as the sister lineage of the rest of the entire group. That topology was also confirmed by later phylogenetic hypotheses (Jiménez-Mejías & al., 2016b; Martín-Bravo & al., 2019; Villaverde & al., 2020). Recent works (Roalson & al., 2021) already accepted the treatment of the former genus *Uncinia* as *Carex sect. Uncinia*. Our phylogeny largely agrees with other phylogenies in the internal phylogenetic structuring of *C. sect. Uncinia* (Fig. 3), with *C. kingii* as the sister lineage to the core sect. *Uncinia* clade (lineage A; Fig. 3), which the latter organized in three different and highly supported clades (lineages B, C and D; Fig. 3) (Starr & al., 2008; Jiménez-Mejías & al., 2016b, Martín-Bravo & al., 2019). Our biogeographic analyses (Fig. 4) also support these three groups as primarily inhabiting different geographic regions (lineages B and C mostly in South America, and lineage D in New Zealand; see below). A more comprehensive sampling is needed to figure out if these should be considered as infrasectional taxonomic partitions or if additional clades may be awaiting discovery. A few species (e.g., *C. austrocompacta*, *C. erinacea*, *C. hamata*, and *C. phleoides*) appear as not monophyletic in our phylogenies. This illustrates the intricate taxonomy of *C. sect. Uncinia*. Future biosystematic studies may help to resolve these taxa.

We are aware that our Sanger-based approach may have some limitations, especially regarding the internal phylogenetic resolution of some clades. Future genomic studies should improve the resolution of the phylogenetic relationships within *Carex*, and may support or reject what is proposed here. Still, we believe that our work makes an incremental contribution to understanding the evolution of the genus.

Morphological evolution of *Carex* subg. *Uncinia*: unispicate inflorescence and rachilla. — The presence of the exerted and hooked rachilla and the unispicate inflorescence of *Carex* subg. *Uncinia* are characters considered of great evolutionary relevance in *Carex*, and that have been used in Cariceae to delimitate genera, subgenera, or sections (Kükenthal, 1909; Reznicek, 1990; Egorova, 1999). As explained in the introduction, the rachilla in *Carex* is the remnant of the last-level inflorescence branch, whose subtending prophyll is actually the utricle (Reznicek, 1990; Global Carex Group, 2015). The presence of well-developed rachillas has been considered a plesiomorphic state, while extreme reduction would be an apomorphic state in the genus (Reznicek, 1990; Starr & al., 2008). Similarly, truly branched inflorescences have been considered ancestral in *Carex*, while simplified (unispicate) ones have been regarded as derived (Reznicek, 1990; Starr & Ford, 2009), as already reported in other groups of sedges closely related to Cariceae (e.g., tribes Dulichieae and Scirpeae; Léveillé-Bourret & al., 2014). It should be noted that since the perigynium is a prophyll, it implies that the rachilla—even if “undeveloped”—is actually always present. Thus, even unispicate inflorescences in *Carex* are ultimately inflorescences branched at the last level.

Our ancestral state reconstructions partly contradict these observations. Regarding the inflorescence, our study seems to agree in an evolutionary tendency to complexity reduction (Fig. 5). When unispicate inflorescence is fixed within a clade it does seem to be an “evolutionary end” with no observed reversion to truly branched, at least in *Carex* subg. *Uncinia*. On the other hand, the rachilla underwent the opposite change: the undeveloped rachilla is plesiomorphic in our reconstructions and its development implies an evolutionary innovation (Fig. 5). Considering that the rachilla implies that a unispicate inflorescence is actually branched at its last level, it seems that non-branching by itself is irreversible, but re-branching at higher-to-last levels once a unispicate inflorescence has been reached. Acquisition of additional levels of branching in *Carex*, however, seems possible if the inflorescence still has more than one level of branching (e.g., Márquez-Corro & al., 2020), and it has been proposed to happen in very rare instances under particular selective pressures (e.g., entomophily in *C. baldensis* L.; Starr & Ford, 2009). The complete lack of reversals from rachilla exerted and hooked to undeveloped in *C.* sect. *Uncinia* can be hypothesized due to the functionality of the rachilla as an epizoochoric appendage, and thus its loss would be strongly negatively selected. While formal statistical approaches are missing, it seems that a developed rachilla in other *Carex* groups (e.g., former genus *Kobresia*) might be lost and acquired multiple times (see phylogenies in Jiménez-Mejías & al., 2016b; Martín-Bravo & al., 2019).

Biogeography of *Carex* subgenus *Uncinia*: origin and journeys across the seas. — Our results unequivocally placed the origin of *Carex* subg. *Uncinia* in the American continent (Fig. 4; Fig S12) during the Early Miocene. This supports the previous estimates of the origin and timing in Martín-Bravo & al. (2019). Nonetheless, our 9-area analysis failed to discriminate in which continent (North America or South America) *C.* subg. *Uncinia* originated, or whether the ancestor was actually widespread on both landmasses. However, additional evidence based on the coding of 6 areas (suppl. Fig. S12) points to North America as the ultimate origin of the group (65.8%), with that region being the most probable area and a combination of North and South America (33.7%) the second most probable area. Additionally, all other subgenera of *Carex* had their origin in the Northern Hemisphere (Martín-Bravo & al., 2019), which ultimately supports a northern origin for *C.* subg. *Uncinia*.

Clade 1 (Fig. 4) seems to have originated and entirely evolved and diversified in North America. According to our results, the most probable ancestral area for this lineage would be Eastern North America, where it diversified into the current *Carex* sect. *Leucocephalae* (which is endemic to this area) and sect. *Phyllostachys* during the Late Miocene (approximately 9.09 [3.67–17.27] mya). The inferred divergence age agrees with Martín-Bravo & al. (2019), who provided a mean age for this event of 9.21 myr. *Carex* sect. *Phyllostachys* seems to have also dispersed to Western North America in at least one colonization event at the beginning of the Pliocene (5.4 [3.67–17.27] mya).

The ancestral area of clade 2 (Fig. 4) also includes, as the most probable area, a combination of some North and South American regions, which matches with our 6-area analysis that recovered both North and South America as the most probable ancestral area (Fig. S12). Our study inferred that *Carex* sect. *Firmiculmes* diverged and established in Western North America, while the ancestor of the other three sections dispersed to South America by LDD mechanisms due to the fact that this dispersal happened during the Early Miocene (20.63 [17.79–23.28] mya). In this epoch, the Panama Isthmus

was still open (Haug & Tiedemann, 1998; Coates & Stallard, 2013). It was not until its closure in the Late Pliocene (approximately 2.8 mya; O’Dea & al., 2016) when North and South Americas were connected.

Diversification in the Southern Hemisphere may have been related to geological events such as the Andean orogeny. It is known that during the Early Miocene there were floristic interchanges between the Andes and Central America (Luebert & Weigend, 2014), and this could have facilitated the entry of *Carex* sect. *Psilocarpae*, South American sect. *Schiedeanae*, and sect. *Uncinia* ancestors into South America. The Andes seems to be the main region of diversification for South American *Carex* sections (Fig. 4). According to Luebert & Weigend (2014), the Andean uplift would have favored the colonization of the other mentioned South American areas, allowing some genera to establish in new habitats. *Carex* subg. *Uncinia* could have also dispersed from the Andes to other South American regions during this geological time frame (Early Miocene). Another palaeogeological event to consider is the appearance of the Drake passage (49 to 17 mya; Scher & Martin, 2006); this event caused the cooling of the Southern Hemisphere and Antarctica glaciation (Barker & Burrell, 1977; Toggweiler & Samuels, 1995; Scher & Martin, 2006). The cooling of South American regions could have been a determining factor for plants colonization. Given the (generally) cold-adapted preferences of *Carex* (including *C.* subg. *Uncinia*), this would have likely favored the colonization of South America by *Carex* lineages.

Carex sect. *Uncinia* was the only lineage within *C.* subg. *Uncinia* able to colonize the entire South American continent and to spread outward to the Pacific Southwest, Pacific islands, and sub-Antarctic archipelagos. This was probably facilitated by the hooked rachilla as a key innovation of *C.* sect. *Uncinia* (see other parallel cases in Otero & al., 2019b), a feature not present in the other lineages of the subgenus, which are confined to mainland America. Lineages B and C (Fig. 4) are mainly composed of South American species, while lineage D is almost entirely distributed in the Pacific Southwest.

Colonization of the Pacific Southwest region (primarily New Zealand) took place at least twice (lineages B and D; Fig. 4) during the Late Miocene and Pliocene (8.13 and 3.94 mya, respectively). While the colonization of New Zealand by lineage B yielded only two species (*C. parvispica*, *C. subtilis*), lineage D resulted in a large radiation, creating in this region a major diversity center for *C.* sect. *Uncinia*. The significantly reduced diversity of lineage B in comparison with lineage D in the Pacific Southwest could be due to the later arrival of the former (Fig. 4), which has had less time to diversify, and/or the fact that most ecological niches were already filled by lineage D species, preventing the establishment of lineage B (high-density blocking; Waters & al., 2013). It is unclear whether the dispersal occurred east to west or vice-versa, but it undoubtedly took place in two independent LDD events, since Antarctica already lacked suitable habitats at this time (tundra became extinct during the Middle Miocene, 14.07 ± 0.05 mya; Lewis & al., 2008). Remarkably, despite its much larger size, Australia and Tasmania harbor much less *C.* sect. *Uncinia* diversity than New Zealand, which seems to point to processes of evolutionary radiation in this latter archipelago (Martín-Bravo & al., 2019).

Colonization of the Pacific islands by *Carex* sect. *Uncinia* took place by two different routes: from New Zealand to Hawaii (lineage D, *C. uncinata*; Fig. 4) and from South America to the Juan Fernández archipelago (lineage B, *C. macloviformis* (G.A.Wheeler) J.R.Starr, *C. phleoides* Cav. subsp. *phleoides*, *C. fernandesiana* (Nees ex Boeckeler) J.R.Starr, and lineage C, *C. firmula*; Fig. 4). The case of the sub-Antarctic archipelagos is similar to that of the Pacific region. These archipelagos were colonized multiple times from both South American (lineage B, *C. meridensis* (Steyerm.) J.R.Starr, *C. brevicaulis* Thouars; Fig. 4) and Pacific Southwest regions (*C. erebus* K.A.Ford, *C. dikei* K.L.Wilson, *C. austrocompacta* K.L.Wilson p.p.) from both east to west and west to east, presumably by LDD mechanisms. Unlike the previous case, colonization of the sub-Antarctic region seemed to have happened during the late Pleistocene (Fig. 4). This led us to hypothesize that Pleistocene glaciations could have favored dispersal and diversification events into these areas by cold-adapted lineages such as *C.* sect. *Uncinia*.

Between South America and New Zealand, several routes of migratory birds (principally shorebirds and albatrosses) are well-established (Wilson, 1986; Dingle, 2008). Undoubtedly, bird epizoochory facilitated by the hooked rachilla must be one of the LDD mechanisms that allowed *Carex* sect. *Uncinia* to reach remote locations from its source areas in South America and New Zealand (e.g., Thorsen & al., 2009).

Taxonomic treatment. — Our phylogeny supports the recognition of seven distinctive lineages at sectional level within *Carex* subg. *Uncinia*. Five of these are already recognized as sections, one has been newly recognized and the other raised from subsection to section rank. Below we formally delimited the seven lineages as sections, provide descriptions, and provide the most significant morphological, geographical, and ecological features for each.

Carex sect. ***Firmiculmes*** (Kük.) Mack. in Jepson, Fl. Calif. 1: 225. 1922 ≡ *Carex* subsect. *Firmiculmes* Kük. in Engler, Pflanzenr. IV. 20 (Heft 38): 93. 1909 – Type (designated by Reznicek in Novon 11: 455. 2001): *Carex geyeri* Boott.

Description. – Plants usually caespitose, with short or inconspicuously elongated rhizomes. Culms trigonous, brown or red, smooth or scabrous distally, erect, with fibrous basal sheaths. Leaves basal, blades flattish or V-shaped in cross section. Inflorescence consisting of a single androgynous spike, lax, bractless. Staminate portion of the spike separated from the pistillate portion by short but conspicuous internodes or sessile, no more than 15-flowered. Pistillate portion of the spike few-flowered, often lax. Pistillate glumes with apex short or long awned, chartaceous. Utricles narrowly obovate, trigonous, slightly hairy, with a short truncate beak. Stigmas 3. Achenes trigonous, almost as large as the utricle bodies. Rachilla present, contained within the utricle, linear (description according to Kükenthal, 1909; Crins, 2002). (Fig. 2A)

Circumscription. – Three species (Crins, 2002; Roalson & al., 2021).

Geographical distribution. – Western North America (Crins, 2002; Roalson & al., 2021).

Carex sect. ***Leucocephalae*** Holm in Amer. J. Sci. 14: 62. 1902 ≡ *Cymophyllus* Mack. in Britton & Brown, Ill. Fl. N. U.S., ed. 2, 1: 441. 1913 – Type: *Carex fraseriana*.

Description. – Plants caespitose. Culms compressed, smooth, erect at flowering and dropping at maturity, with sheaths whitish to straw colored. Leaves basal, blades flattish, ciliate-serrulate at margins. Inflorescence consists of a single androgynous spike, lax, bractless. Staminate portion of the spike cylindrical to oblong, often with numerous staminate flowers without glumes. Pistillate portion of the spike with 20–30 flowers, dense, globose. Pistillate glumes whitish. Utricles inflated, whitish, glabrous, with a short truncate beak. Stigmas 3. Achenes trigonous, smaller than the utricle bodies. Rachilla vestigial, reduced (description modified from Reznicek, 2002). (Fig. 2B)

Circumscription. – One species (Roalson & al., 2021).

Geographical distribution. – Central Appalachian Mountains (Eastern North America) (Roalson & al., 2021).

Carex sect. ***Phyllostachys*** (Torrey & A.Gray ex Carey) L.H.Bailey. in Bot. Gaz. 10(1): 208. 1885 ≡ *Carex* [unranked] *Phyllostachys* Torrey & A.Gray ex Carey in Gray, Manual: 536, 538. 1848 – Type (designated by Catling & al. in Syst. Bot. 18: 497. 1993): *Carex backii* Boott.

Description. – Plants usually caespitose, with short or inconspicuously elongated rhizomes. Culms trigonous, smooth or hairy, winged, erect, with dilated at apices, basal sheaths, pale to medium brown. Leaves basal, blades V-shaped or slightly M-shaped in cross section, glabrous or papillose. Inflorescence consisting of a single spike or racemose with up to 5 spikes, lateral spikes pistillate or androgynous, terminal spike always androgynous, bracts absent. Staminate portion of the spike 2–5-flowered, elongated to cylindrical. Pistillate portion of the spike 3–14-flowered. Proximal pistillate glumes foliaceous, distal pistillate glumes scale-like and ovate. Utricles trigonous, lanceolate to oblong-lanceolate, rounded-trigonous, beak flattened-triangular. Stigmas 3. Achenes trigonous, as large as or smaller than utricle bodies. Rachilla undeveloped, abnormally present (description according to Naczi & al., 1998; Starr & al., 1999; Crins & al., 2002; Ford & al., 2008). (Fig. 2C)

Circumscription. – Ten species (Roalson & al., 2021).

Distribution. – North America (north of Mexico).

Notes. – *Carex* sect. *Phyllostachyae* and *Carex* sect. *Phyllostachys* have been treated as two different names based on their different Latin suffixes (see discussion at Naczi & Ford, 2001). However, according to ICN Art. 53.2, Ex. 11 (Turland & al., 2018), both names should be treated as confusingly similar and so as synonyms. The first time the name *Phyllostachys* was validly published for an infrageneric taxon of *Carex* was by Carey (1848). However, the ambiguous ranking of this taxon forces us to consider it as unranked. Previously, Tuckerman (1843) used the spelling '*Phyllostachyae*'; however, it is a nomen nudum. The first time the name was published at sectional rank was by Bailey (1885), who explicitly cited Carey's work. Accordingly, Bailey's sectional name must be treated as a combination of Carey's name, and thus it should be typified according to Carey's delimitation of the group, as already done by Catling & al. (1993). This way, the traditional taxonomic use of the name *Carex* sect. *Phyllostachys* is maintained, which excludes *Carex phyllostachys* C.A.Mey. from its delimitation.

Carex sect. ***Psilocarpae*** Kük. in Engler, Pflanzenr. IV. 20 (Heft 38): 89. 1909 – **Type (designated here):** *Carex sellowiana* Schldl.

Description. – Plants cespitose, with short or inconspicuously elongated rhizomes. Culms flattened-trigonous, scabrid, erect or dropping, with dark purplish sheaths. Leaves basal, blades flattish. Inflorescence consisting of a single androgynous spike, usually elliptic, rarely oblong, bractless or with a linear bract. Staminate portion of the spike 6–10-flowered, often concealed by the pistillate portion. Pistillate portion 6–20-flowered, dense. Pistillate glumes lanceolate, mucronate to aristate. Utricles trigonous, elliptic to obovate, glabrous, with a short truncate beak. Stigmas 3. Achenes trigonous, subtended by a conspicuous 3-lobed cup-like elaiosome. Rachilla undeveloped (description modified from Kükenthal, 1909; Silveira & Longhi-Wagner, 2012). (Fig. 2E)

Circumscription. – One species (*Carex sellowiana*).

Geographical distribution. – Temperate and subtropical South America, from south Brazil to northern Argentina, west to Bolivia through chaco regions (Govaerts & al., 2020; Jiménez-Mejías & Silva, 2020).

Carex sect. ***Seticulmes*** (Kük) Jim.-Mejías & García-Moro, **stat. nov.** ≡ *Carex* subsect. *Seticulmes* Kük. in Engler, Pflanzenr. IV. 20 (Heft 38): 90. 1909 – Type: *Carex seticulmis* Boeckeler (Art. 10.8).

Description. – Plants cespitose, with short or inconspicuously elongated rhizomes. Culms trigonous, with scarcely scabrid or smooth margins, erect, with stramineous or hyaline sheaths. Leaves basal, blades flattish. Inflorescence consisting of a single androgynous spike, elliptic or lanceolate to oblong-lanceolate, often embraced or concealed by involucre bracts. Staminate portion of the spike many-flowered, cylindrical, usually clearly exerted from the pistillate portion. Pistillate portion of the spike 2–8-flowered, dense. Pistillate glumes elliptic, oblong, lanceolate, mucronate. Utricles trigonous, elliptic, stramineous, membranaceous, slightly hairy distally, with a short beak truncate to slightly bidentate. Stigmas 3. Achenes trigonous, almost as large as the utricles. Rachilla undeveloped (description modified from Kükenthal, 1909). (Fig. 2D)

Circumscription. – Five species (Roalson & al., 2021; excluding *Carex sellowiana*).

Geographical distribution. – Temperate and subtropical South Atlantic regions of Brazil (Jiménez-Mejías & Silva, 2020; Roalson & al., 2021).

Carex sect. ***Uncinia*** (Pers.) Baill., Hist. Pl. 12: 345. 1894 ≡ *Uncinia* Pers., Syn. Pl. 2: 534. 1807 – Type (designated by Pfeiffer, Nomencl. Bot. 2(2): 1529. 1874–1875): *Carex uncinata* L.f.

Description. – Plants cespitose, with short or inconspicuously elongated rhizomes. Culms trigonous, scabrous or smooth, erect or slightly curved, with brown to reddish brown basal sheaths. Leaves basal or few cauline, blades flattish or channeled. Inflorescence consisting of a single androgynous spike, clavate to cylindrical, rarely elliptical, bractless or rarely with a leaf-like bract at its base. Staminate portion of the spike, 5- to many-flowered. Pistillate portion of the spike with few to >100 flowers, lax to tightly compact. Pistillate glumes broadly ovate, often coriaceous, usually persistent after the utricles is dispersed, rarely deciduous. Utricles trigonous to plano-convex, glabrous or hairy, with a short beak or sometimes almost beakless. Stigmas 3. Achenes trigonous to compressed-trigonous, narrowly oblong, as long as or shorter than the utricles body. Rachilla present, exerted, ended in a hooked tip (description according to Clarke, 1883; Wheeler, 2007). (Fig. 2G)

Circumscription. – 72 species (Roalson & al., 2021).

Geographical distribution. – Mainly in South America and New Zealand but also found in Central America, the Caribbean, and sub-Antarctic, South Atlantic and Pacific archipelagos. It reaches marginally Mexico and the Philippines (Roalson & al., 2021).

Carex sect. ***Wheelerianae*** Jim.Mejías, Martín-Bravo & Reznicek, **sect. nov.** – Type: *Carex subandrogyna* G.A.Wheeler & Guagl.

Description. – Plants cespitose, rarely with elongated rhizomes. Culms trigonous, somewhat winged beneath the inflorescence, scabrid, erect or slightly curved, with brown to dark brown basal sheaths. Leaves basal, blades flattened. Inflorescence consisting of (1)2–3 spikes, the lowest one sometimes concealed by the lowermost bract, lateral spikes pistillate or androgynous, terminal spike always androgynous. Staminate portion of the spike few-flowered, shortly oblong, often concealed by the pistillate part. Pistillate portion of the spike with up to 40–50 flowers, dense, cylindrical. Pistillate glumes mucronated or awned. Utricles trigonous, obovate to elliptic, glabrous, with shortly cylindrical beak. Stigmas 3, conspicuously curled backwards. Achenes trigonous, as large as the utricles bodies. Rachilla contained within the utricles, undeveloped or conspicuously present (description according to Wheeler & Guaglianone, 2003; Wheeler & Guaglianone,

2006; Jiménez-Mejías & Escudero, 2016; Jiménez-Mejías & Reznicek, 2018). (Fig. 2F)

Circumscription. – Four species are known (Jiménez-Mejías & Reznicek, 2018).

Geographical distribution. – Andean South America, south to northern Argentina (Roalson & al., 2021).

Etymology. – Dedicated to G.A.Wheeler (1940–2018), a prolific botanical author who published an enormous amount of taxonomic studies on South American *Carex*, forming the basis for modern knowledge of the genus in the continent.

AUTHOR CONTRIBUTION

PG-M and PJ-M conceived the idea and drafted a first version of the manuscript. PJ-M and LC collected the material used in this work from different herbaria and fieldwork. Labwork was performed by PJ-M and CB-B, with support from SM-B and EHR. PG-M and CB-B edited the sequences and built the matrices. PG-M, AO, CB-B, LC, and PJ-M performed bioinformatic analyses. Taxonomic treatment was designed and discussed by PG-M, PJ-M, JRS, EHR, AAR and RFCN. All the authors contributed to the writing of the final version of the manuscript. — PG-M, <https://orcid.org/0000-0002-8331-4771>; AO, <https://orcid.org/0000-0002-3354-2979>; CB-B, <https://orcid.org/0000-0003-4956-0343>; LC, <https://orcid.org/0000-0002-4798-097X>; SM-B, <https://orcid.org/0000-0003-0626-0770>; RFCN, <https://orcid.org/0000-0002-3985-0059>; AAR, <https://orcid.org/0000-0002-9467-6225>; EHR, <https://orcid.org/0000-0003-1655-3681>; JRS, <https://orcid.org/0000-0002-6069-9437>; PJ-M, <https://orcid.org/0000-0003-2815-4477>

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Appendix 1. Species list genetic material used in this study.

Taxon (names follow revised taxonomy); ID code; country, *collector with collection number* and (herbarium code); GenBank no. ETS; ITS; *matK*. Sequences obtained in this study are marked with an asterisk (*). Missing sequence data is indicated by a dash (–).

Carex alba Scop.; spm00000584; Spain, Lleida, *P. Jiménez-Mejías & al. 128PJM13* (UPOS); MN760667; MN762295; MN763219. *Carex stricta* K.A.Ford; spm00004420; New Zealand, Westland Land District, (CHR-458892); MN761369; MN762315; MN763437. *Carex aucklandica* (Hamlin) K.A. Ford; spm00004410; New Zealand, Southland Land District, *B.D. Rance s.n.* (CHR-580900); MN759812; MN762316; MN763443. *Carex austrocompacta* K.L.Wilson 1; spm00005217; Australia, Tasmania; AY244540; AY244539; –. *Carex austrocompacta* 2; spm00005930; U.K., Tristan da Cunha, *Gremmen-T07 0114* (E-00348927); MN759809; MN762207; MN763363. *Carex austroflaccida* K.L.Wilson; spm00005091; Australia; AY012644; AY012643; –. *Carex backii* Boot in W.J.Hooker 1; spm00002007; Canada, British Columbia, *V.J. Kranija, J. Pojar & C. Parsons s.n.* (UBC-150083); MN760838; MN761841; GU172571. *Carex backii* 2; spm00005330; Canada, Manitoba, *Naczi & Ford 9913* (DOV); –; –; FJ597182. *Carex backii* 3; spm00005331; Canada, Manitoba, *Naczi & Ford 9846* (DOV); –; –; FJ597183. *Carex backii* 4; spm00005329; U.S.A., Michigan, *Naczi 1326* (DOV); –; –; FJ597184. *Carex backii* 5; spm00005116; Canada, Ontario; AY241968; –; –. *Carex backii* 6; Waterway_3689; Canada, Québec; AY757398; AY757402; –. *Carex banksiana* K.A.Ford 1; spm00005085; New Zealand; AY012635; AY012634; MN762992. *Carex banksiana* 2; spm00005086; New Zealand; AY012638; AY012637; –. *Carex basiantha* Steud. 1; spm00005335; U.S.A., Alabama, *Ford & Naczi 95* (WIN); –; –; FJ597261. *Carex basiantha* 2; spm00005334; U.S.A., Georgia, *Naczi 9174* (WIN); –; –; FJ597185. *Carex basiantha* 3; spm00005333; U.S.A., Arkansas, *Bryson & Bryson 21475* (DOV); –; –; FJ597186. *Carex basiantha* 4; spm00000637; U.S.A., New York, *A.B. Pittman & A.R. Darr 6150007* (DOV-040375); MN760877; –; GU172584. *Carex basiantha* 5; *Naczi_2946*; U.S.A., Mississippi; –; AF027431, AF027471; –. *Carex brevicaulis* Thouars 1; *Solbrig_3434*; –; AF284987; U.K., Tristan da Cunha; –. *Carex brevicaulis* 2; spm00005216; U.K., Tristan da Cunha; AY244534; –; –. *Carex brevicaulis* 3; spm00005215; U.K., Tristan da Cunha; –; AY244534; –. *Carex brevicaulis* 4; spm00005931, *WSU_803*; U.K., Tristan da Cunha, *Gremmen, T07 0495* (E-00348919); MN759881; MN762272; MN763350. *Carex brevicaulis* 5; spm00005932, *WSU_804*; U.K., Tristan da Cunha, *Gremmen T07 0377* (E-00348938); MN759882; MN762269; MN763351. *Carex camptoglochis* V.I.Krecz; spm00005210; Ecuador; AY244520; AY244519; MN763057. *Carex canescens* L. subsp. *canescens*; spm00005994; Finland, *M. Kääntönen 156/94* (H-691346); KP980244; KP980431; KP980061. *Carex capitellata* Boiss. & Balansa in P.E.Boissier; spm00003459; Turkey, Sarigöl-Jusufeli, *W. Lang s.n.* (M-57954); MN761079; MN762699; MN763677. *Carex cordillerana* Saarela & B.A.Ford 1; spm00001544; Canada, British Columbia, *B.A. Ford & J.M. Saarela 135* (WIN-67266); MN760140; MN761840; FJ597201. *Carex cordillerana* 2; spm00005234; U.S.A., Utah, *Naczi & Thieret 3433* (WIN); DQ115133; DQ115132; –. *Carex cordillerana* 3; spm00005336; U.S.A., Utah, *Saarela & Roe 196* (WIN); –; –; FJ597202. *Carex cordillerana* 4; spm00005337; U.S.A., Utah, *Naczi & Thieret 3433* (WIN); –; –; FJ597200. *Carex corynoidea* K.A.Ford; spm00005087; New Zealand; AY012647; AY012646; –. *Carex crispa* K.A.Ford; spm00004422; New Zealand, Otago Land District, *A.P. Druce APD1751* (CHR-476015); MN759872; –; MN763436. *Carex cyanea* K.A.Ford; spm00005097; New Zealand; AY012632; AY012631; –. *Carex delacosta* Kuntze 1; spm00006490, *WSU_942*; Chile South, Los Lagos, Palena, *Fernández Alonso & al. JLF30793* (UPOS); –; OL629363*; OL676777*. *Carex delacosta* 2; spm00007650, *WSU_1960*; Chile South, Isla Englefield, *Pisano & Cardenas 4914* (A); OL629320*; –; OL676778*. *Carex dikei* (Nelmes) K.L.Wilson; spm00003482; South Africa, Marion-Prince Edward Island, *Hertel 24387* (M-223512); MN759810; MN762533; MN763777. *Carex distachya* Desf.; spm00000588; Spain, Cádiz, *P. Jiménez-Mejías & al. 89PJM04* (UPOS-2150); MN760248; MN762299; MN763811. *Carex dolichophylla* J.R.Starr; spm00007649, *WSU_1959*; Chile Central, Chaichuin, *H. Gunckel 3035* (A); –; –; OL676779*. *Carex drucei* (Hamlin) K.A.Ford; spm00004418; New Zealand, Southland Land District, *B.D. Rance s.n.* (CHR-586921); MN761259; MN762198; MN763431. *Carex ecuadorensis* (G.A.Wheeler & Goetgh.) J.R.Starr; spm00005088; Ecuador, Cotacachi; AY012662; AY012661; MN762991. *Carex edura* K.A.Ford; spm00002184; New Zealand, Nelson Land District, *K.A. Ford s.n.* (CHR-489463); MN759875; –; MN762989. *Carex egmontiana* (Hamlin) K.A.Ford; spm00004416; New Zealand, Westland Land District, *N. Zviagina, s.n.* (CHR-458898); MN761238; MN762200; MN763589. *Carex erebus* K.A.Ford; spm00004424; New Zealand, Southland

Land District., *S.J. Wagstaff 121* (CHR-624015); MN761283; MN762204; MN763440. ***Carex erinacea* Cav. 1**; spm00005214; Chile Central; AY244532; AY244531; -. ***Carex erinacea* 2**; spm00007400, WSU_1710; Chile Central, Osorno, *L. Zollitach 52* (M); OL629321*; -. ***Carex erinacea* 3**; spm00007403, WSU_1713; Chile Central, Valdivia, *T.Christian & al.,253* (E); OL629322*; -. ***Carex erinacea* 4**; Vann_3569; Chile South, Los Lagos; AY244532; AY244531; -. ***Carex erinacea* 5**; spm00007736, WSU_2046; Chile South, Arauco, Region VIII, *M. Rosas & al. 5329* (K); OL629323*; OL629364*; -. ***Carex erythrovaginata* K.A.Ford**; spm00005096; New Zealand; AY012623; AY012622; -. ***Carex fernandesiana* (Nees ex Boeckeler) J.R.Starr 1**; spm00007396, WSU_1706; Chile, Juan Fernández, *E. Ugarte & O. Parra 9163* (M); OL629324*; -. ***Carex fernandesiana* 2**; spm00007564, WSU_1874; Chile, Juan Fernández, *T. Stuessy & D. Crawford 15212* (CONC); OL629325*; OL629365*; OL676782*. ***Carex fernandesiana* 3**; spm00007565, WSU_1875; Chile, Juan Fernández, *T. Stuessy & M. Garcia, 11670* (CONC); OL629326*; OL629366*; OL676783*. ***Carex fernandesiana* 4**; spm00007651, WSU_1961; Chile, Juan Fernández, *O.T. Solbrig & al. 3824* (A); OL629327*; -. ***Carex firmula* (Kük.) J.R.Starr 1**; spm00005110; Chile South, Region XII, *Pisano & Dollenz 5801* (G); AY012659; AY012658; -. ***Carex firmula* 2**; spm00006492, WSU_940; Chile South, Los Lagos, *J.L. Fernandez Alonso & al. RM2792* (UPOS); -. ***Carex firmula* 3**; spm00007609, WSU_1919; Chile South, Antarctica chilena, *W.R.Buck, 57466* (NY); OL629328*; OL629368*; OL676785*. ***Carex firmula* 4**; spm00007646, WSU_1956; Chile South, Seno Otway, *Pisano 3392* (A); OL629329*; -. ***Carex firmula* 5**; spm00005111; Ecuador, *Øllgaard 98225* (AAU); AY012656; AY012655; -. ***Carex firmula* 6**; spm00007610, WSU_1920; Ecuador, Napo, *B. Lojnant & U. Molau 12947* (NY); OL629330*; -. ***Carex firmula* 7**; spm00007608, WSU_1918; Chile South, Magallanes, *M. Bonifacino 4228* (NY); OL629331*; OL629369*; OL676788*. ***Carex flava* L.**; spm00001483; Canada, Newfoundland, *C. Hanel & N. Djan Chekar CH010808 11* (MT); MN760068; MN761801; GU172872. ***Carex fraseriana* Ker Gawl. 1**; spm00000952; U.S.A., Maryland, *W.D. Longbottom, R.F.C. Naczi & G. Van Velsir 6000* (DOV-051066); MN760136; MN761870; GU172896. ***Carex fraseriana* 2**; spm00005189; U.S.A., Tennessee; AY241970; AY241969; -. ***Carex fraseriana* 3**; spm00005190; U.S.A., Tennessee; -. ***Carex geyeri* Boott 1**; spm00000942; Canada, Alberta, *B.A. Ford & J.M. Saarela 110* (DOV-021808); MN759795; MN761822; GU172909. ***Carex geyeri* 2**; spm00005152; U.S.A., Montana; AY244527; AF027434, AF027474; -. ***Carex geyeri* 3**; spm00007899; U.S.A., Montana, *Starr MT96039* (WIS); -. MN762960; MN762990. ***Carex goetghebeurii* J.R.Starr 1**; spm00007611, WSU_1921; Ecuador, Zamora-Chincipe, *G. Wheeler & Goetghebeur 18526* (NY); OL629332*; -. ***Carex goetghebeurii* 2**; spm00007739, WSU_2049; Ecuador, Zamora-Chincipe, *S. Laegaard 18526* (K); OL629333*; -. ***Carex hamata* Sw. 1**; spm00007359, WSU_1669; Argentina, Tucumán, *G. Rodriguez-Palacios & P. Jiménez-Mejías 87GERP15* (UPOS); OL629335*; OL629371*; -. ***Carex hamata* 2**; spm00007489, WSU_1799; Bolivia, Florida, *C.E. Hinchliff 761* (WS); OL629319*; OL629360*; OL676776*. ***Carex hamata* 3**; spm00007397, WSU_1707; Bolivia, La Paz, Nor Yungas, *G. Beck 17684* (M); OL629336*; -. ***Carex hamata* 4**; spm00007618, WSU_1928; Colombia, Cundimarca, *A.M. Cleef 4829* (NY); OL629337*; -. ***Carex hamata* 5**; spm00005093; Ecuador, *Starr 99032*; AY012665; AY012664; -. ***Carex hamata* 6**; spm00007619, WSU_1929; Ecuador, Napo, *J. Luteyn & M. Gavilanes, 14378* (NY); OL629338*; -. ***Carex hamata* 7**; spm00007317, WSU_1627; Argentina, Tucumán, *G. Rodriguez-Palacios & P. Jiménez-Mejías, 6GERP15B*; OL629334*; OL629370*; -. ***Carex hamlinii* K.A.Ford**; Gardner_333; New Zealand; -. EU812836; -. ***Carex healyi* K.A.Ford**; spm00005107; New Zealand, *Ogle 2854* (CHR); AY012626; AY012625; -. ***Carex hilairei* Boott**; spm00007453, WSU_1763; Brazil South, Paraná, Rio de Janeiro, *J.C. Lindeman & J.H. de Haas, 5132* (NY); OL629339*; OL629372*; -. ***Carex hilaireioides* C.B. Clarke ex Kük.**; spm00007456, WSU_1766; Brazil East, *H.S. Irwin & al. 29206* (NY); OL629340*; OL629373*; OL676774*. ***Carex horizontalis* (Colenso) K.A.Ford**; spm00005106; New Zealand; AY012641; AY012640; -. ***Carex imbecilla* K.A.Ford**; spm00004419; New Zealand, Nelson Land District, *P. Knightbridge s.n.* (CHR-596652); MN759877; MN762532; MN763398. ***Carex jamesii* Schwein. 1**; spm00000630; U.S.A., Alabama, *R.F.C. Naczi 1020* (DOV-02803); MN761088; -. FJ597225. ***Carex jamesii* 2**; spm00005340; U.S.A., Maryland, *Naczi & al. 9320* (DOV); -. FJ597223. ***Carex jamesii* 3**; spm00005341; U.S.A., Oklahoma, *Naczi & Ford 9656* (DOV); -. FJ597224. ***Carex juniperorum* Catling 1**; Naczi_2937; U.S.A., Kentucky; -. AF027419, AF027461; -. ***Carex juniperorum* 2**; spm00000631; U.S.A., Kentucky, *R.F.C. Naczi & A.E. Trauth 5538* (DOV-026418); MN760823; MN762011; FJ597226. ***Carex juniperorum* 3**; Naczi_2934; U.S.A., Ohio; -. AF027460; -. ***Carex juniperorum* 4**; spm00005343; U.S.A., Ohio, *Naczi, Trauth, Dalton & McAllister 5508* (DOV); -. FJ597227. ***Carex kingii* (R.Br. ex Boott) Reznicek 1**; spm00005221; Chile South, Isla Hoste, *Pisano 5530* (GH); AY244526; AY244525; -. ***Carex kingii* 2**; spm00007562, WSU_1872; Chile South, Capitan Prat, *N. Garcia 156148* (CONC); -. OL629375*; OL676791*. ***Carex kingii* 3**; spm00007563, WSU_1873;

Chile South, Magallanes, *CEQUA-PNBO 1075* (CONC); –; OL629376*; OL676792*. *Carex kirinensis* W.Wang &/ Y.L.Chang; spm00003366; China, Xizang, *B. Dickoré 11487* (MSB-140860); MN761078; MN762698; MN763776. *Carex laegaardii* J.R.Starr 1; spm00007614, WSU_1924; Colombia, Arauca, *A.M. Cleef 9153* (NY); –; OL629377*; OL676793*. *Carex laegaardii* 2; spm00007615, WSU_1925; Ecuador, Napo, *G. Wheeler & Goetghebeur 38475* (NY); OL629341*; OL629378*; OL676794*. *Carex latebracteata* Waterf. 1; spm00001383; U.S.A., Arkansas, *R.F.C. Naczi & B.A. Ford 7023* (DOV); MN760142; MN761898; FJ597232. *Carex latebracteata* 2; spm00005345; U.S.A., Arkansas, *Naczi & Ford 9664* (DOV); –; –; FJ597233. *Carex latebracteata* 3; spm00005346; U.S.A., Oklahoma, *Naczi & Ford 9649* (DOV) –; –; FJ597231. *Carex lechleriana* (Steud.) J.R.Starr; spm00003118; Chile South, Magallanes, Punta Arenas, *M. Luceño 184ML05* (UPOS 1802); –; GU176169; –. *Carex lepida* Boott 1; 4E7CBB18; Bolivia, *Adolfo M. 258* (US); OL629356*; –; –. *Carex lepida* 2; 6E7CBB18; Colombia, *L.E. Mora 2452* (US); OL629357*; OL629379*; OL676795*. *Carex lepida* 3; 5E7CBB18; Ecuador, *R. Valencia 204* (US); –; –; OL676775*. *Carex leporina* L.; spm00001780; U.S.A., Wisconsin, *E.J. Judziewicz 6689* (WIS-41373); MN760316; MN761726; GU173336. *Carex leptalea* Wahlenb. 1; spm00001032; U.S.A., Michigan, *Reznicek & F.W. Case 11370* (DOV-041345); MN761081; MN761825; GU173113. *Carex leptalea* 2; spm00007381, WSU_1691; Venezuela, Mérida, *B.F. Oberwinkler 12424* (M); OL629318*; –; –. *Carex longifructus* (Kük.) K.A.Ford; spm00004426; New Zealand, Westland Land District, *K.A.Ford 27/98* (CHR-515889); MN759874; –; MN763397. *Carex macloviformis* (G.A.Wheeler) J.R.Starr; spm00007617, WSU_1927; Chile, Juan Fernández, *I.C. Skottsberg 169* (NY); OL629342*; –; OL676796*. *Carex madida* J.R.Starr; spm00005095; Ecuador; AY012674; AY012673; –. *Carex megalepis* K.A.Ford; spm00005089; New Zealand; AY012650; AY012649; –. *Carex meridensis* (Steyerm.) J.R.Starr 1; spm00007399, WSU_1709; Bolivia, La Paz, Sud Yungas, *G. Beck & B. Ruthsatz, 21803* (MSB); OL629343*; –; OL676797*. *Carex meridensis* 2; spm00003133; Chile South, Magallanes-Antarctica chilena, *M. Luceño 1ML06* (UPOS 10810); –; GU176170; –. *Carex meridensis* 3; Starr_3461; Ecuador; AY244536; AY244535; –. *Carex minor* (Kük.) K.A.Ford; spm00004412; New Zealand, Westland Land District, *P.J. Bellingham & L.E. Burrows 1734* (CHR-565338); MN761311; MN762538; MN763439. *Carex multicaulis* L.H.Bailey 1; Roalson_3226; –; AF285028; –. *Carex multicaulis* 2; Ford_1635; U.S.A., California; –; AF027435_AF027475; –. *Carex multicaulis* 3; spm00001092; U.S.A., California, *D. Castaner 10243* (DOV-039651); MN760145; MN761823; –. *Carex multifaria* (Nees ex Boott) J.R.Starr 1; spm00005101; Chile Central, *Vann 9083* (FHO); AY012668; AY012667; –. *Carex multifaria* 2; Vann_SM00014; Chile South, AY012667; –; –. *Carex multifaria* 3; spm00006493, WSU_939; Chile South, Los Lagos, *J.L. Fernandez Alonso & al. JLF30739* (UPOS); –; OL629380*; OL676798*. *Carex negerii* (Kük.) J.R.Starr; spm00007557, WSU_1867; Chile Central, *H. Gunckel 13978* (CONC); –; –; OL676799*. *Carex obtusifolia* (Heenan) K.A.Ford; spm00004428; New Zealand, Southland Land District, *H.D. Wilson 789-317* (CHR-359448); MN759811; MN762331; MN763441. *Carex pachamamae* Jim.-Mejías & Reznicek; spm00007430, WSU_1740; Bolivia, Cavallero, *J.R.I. Wood 13628* (NY); OL629344*; –; OL676800*. *Carex parvispica* K.A.Ford; spm00004427; New Zealand, Canterbury Land District (CHR-607514); MN761401; –; MN763434. *Carex penalpina* K.A.Ford; Gardner_335; New Zealand; –; EU812838; –. *Carex perplexa* (Heenan & de Lange) K.A.Ford 1; spm00004409; New Zealand, North Auckland Land District, *P.J. de Lange & M. Ritchie 4185* (CHR-536482); MN761282; MN762206; MN763430. *Carex perplexa* 2; Gardner_340; New Zealand; –; DQ385605; –. *Carex phleoides* Cav. subsp. *phleoides* 1; spm00007312, WSU_1622; Argentina, Tucumán, *G. Rodríguez-Palacios & P. Jiménez-Mejías 1GERP15*; OL629345*; OL629381*; –. *Carex phleoides* subsp. *phleoides* 2; spm00007314, WSU_1624; Argentina West, *G. Rodríguez-Palacios & P. Jiménez-Mejías 3GERP15*; OL629346*; OL629382*; –. *Carex phleoides* subsp. *phleoides* 3; spm00005103; Chile Central, *Vann 9801*; AY012671; AY012670; –. *Carex phleoides* subsp. *phleoides* 4; Vann_SM00015; Chile South; AY012670; –; –. *Carex phleoides* subsp. *koyamae* (Gómez-Laur.) Jim.Mejías; spm00007613, WSU_1923; Ecuador, Pichincha, *S. Laegaard 2112* (NY); OL629347*; –; OL676801*. *Carex potens* K.A.Ford; spm00004430; New Zealand, Wellington Land District, *C.C. Ogle 4194* (CHR-565655); MN759879; MN762201; MN763433. *Carex punicea* K.A.Ford; spm00005105; New Zealand; AY012629; AY012628, –. *Carex purpurata* (Petrie) K.A.Ford; spm00004431; New Zealand, Southland Land District, *B.D. Rance s.n.* (CHR-541292); MN759876; MN762209; MN763406. *Carex pyrenaica* Wahlenb.; spm00000582; Spain, Huesca, *P. Jiménez-Mejías & al. 410PJM05* (UPOS-2826); MN760878; MN762484; MN763762. *Carex salticola* J.R.Starr; spm00000581; Argentina, Neuquén, *T. Villaverde & J. Starr P22-5 10027* (UPOS_3944) MN759880; MN762262; MN763703. *Carex saximontana* Mack. 1; spm00001727; U.S.A., Colorado, *T. Hogan 3675* (COLO-474788); MN760141; MN761857; GU173508. *Carex saximontana* 2; spm00005347; Canada, Manitoba, *Naczi & Ford 9929* (DOV); –; –; FJ597250. *Carex saximontana* 3; spm00005348; Canada, Manitoba, *Naczi & Ford 9883* (DOV); –; –; FJ597248. *Carex*

saximontana 4; spm00005349; Canada, Manitoba, *Naczi & Ford 9912* (DOV); –; –; FJ597249. *Carex scabrada* J.R.Starr; spm00007555, WSU_1865; Chile South, Aysén, *N. Garcia 4058* (CONC); –; OL629383*; OL676802*. *Carex sellowiana* Schltld. 1; spm00007463, WSU_1773; Argentina, Misiones, *S.G. Tressens 1997* (A); OL629348*; OL629384*; OL676772*. *Carex sellowiana* 2; spm00007457, WSU_1767; Brazil South, Paraná, *G. Hatsobach 24931* (NY); OL629349*; OL629385*; –. *Carex sellowiana* 3; spm00007458, WSU_1768; Brazil South, Rio Grande du Sur, M.Sobral 5171 (NY); OL629350*; –; OL676773*. *Carex sellowiana* 4; spm00008230, 10E7CBB18; Paraguay, *E. Zardini s.n.* (MO-864163); –; OL629386*; –. *Carex seticulmis* Boeckeler 1; spm00008231, 24E1ERV19; Brazil Southeast, *P. Jiménez-Mejías 6bPJM18* (UPOS); OL629358*; –; OL676771*. *Carex seticulmis* 2; spm00007459, WSU_1769; Brazil Southeast, Santa Teresa, *L. Kollman & al. 4638* (NY); OL629359*; OL629374*; –. *Carex siderosticta* Hance; spm00007900; Cultivated, *Léveillé-Bourret 545* (WIS); MN761119; MN762653; MN763050. *Carex silvestris* (Hamlin) K.A.Ford; spm00004421; New Zealand, Otago Land District, *M. Thorsen 140/09* (CHR-607868); MN761239; MN762317; MN763405. *Carex strictissima* (Kük.) K.A.Ford; spm00004413; New Zealand, Wellington Land District, *G. La Cock s.n.* (CHR-616074); MN759878; MN762205; MN763432. *Carex subandrogyna* G.A.Wheeler & Guagl. 1; spm00007313, WSU_1623; Argentina, Tucumán, *G. Rodríguez-Palacios & P. Jiménez-Mejías 2GERP15* (WS); OL629351*; OL629387*; OL676803*. *Carex subandrogyna* 2; spm00007316, WSU_1626; Argentina, Salta, *G. Rodríguez-Palacios & P. Jiménez-Mejías 5GERP15* (WS); MN761392; MN762864; MN763577. *Carex subandrogyna* 3; spm00007320, WSU_1630; Argentina, Salta, *G. Rodríguez-Palacios & P. Jiménez-Mejías 17GERP15* (WS); OL629352*; OL629388*; –. *Carex subandrogyna* 4; spm00007325, WSU_1635; Argentina, Salta, *G. Rodríguez-Palacios, M. Fabbroni & P. Jiménez-Mejías 30GERP15* (WS); OL629353*; OL629389*; –. *Carex subandrogyna* 5; spm00007356, WSU_1666; Argentina, Salta, *G. Rodríguez-Palacios & P. Jiménez-Mejías 78GERP15* (WS); OL629354*; OL629390*; OL676804*. *Carex subsacculata* (G.A.Wheeler & Goetgh.) J.R.Starr; spm00005108; Ecuador, *Starr 99035*; AY012653; AY012652; –. *Carex subtilis* K.A.Ford; spm00004415; New Zealand, Otago Land District, *P.N. Johnson 1066* (CHR-479158); MN759873; MN762539; MN763435. *Carex subviridis* K.A.Ford; spm00004429; New Zealand, Westland Land District, *M. Smale s.n.* (CHR-616782); MN761284; MN762199; MN763438. *Carex superata* Naczi, Reznicek & B.A.Ford 1; spm00005350; U.S.A., Florida, *Naczi 6226* (DOV); –; –; FJ597252. *Carex superata* 2; spm00005351; U.S.A., Georgia, *Mears s.n.* (DOV); –; –; FJ597253. *Carex superata* 3; spm00005352; U.S.A., Georgia, *Naczi 9170* (DOV); –; –; FJ597251. *Carex superata* 4; spm00000632; U.S.A., Kentucky, *Naczi & Reznicek 7406* (DOV-020809); MN759796; MN761897; GU173653. *Carex timida* Naczi & B.A.Ford 1; spm00000625; U.S.A., Alabama, *R.F.C. Naczi 10883* (DOV-049843); MN760139; MN762123; FJ597258. *Carex timida* 2; spm00005354; U.S.A., Arkansas, *Naczi & Ford 9681* (DOV); –; –; FJ597257. *Carex tompkinsii* J.T.Howell 1; B1076; U.S.A., California, *Janeway 7874* (CHSC-86115); MK581990; MK581537; –. *Carex triangula* J.R.Starr 1; ARG; Chile South, *M. Luceño 185ML08* (UPOS-1803); –; –; KP996355. *Carex triangula* 2; spm00003121; Chile South, Magallanes, *M. Luceño 185ML05* (UPOS); –; GU176171; –. *Carex triangula* 3; spm00005219; Chile South; –; AY244541; –. *Carex triangula* 4; spm00007645, WSU_1955; Chile South, Magallanes-Antarctica chilena, *Pisano 5381* (A); OL629355*; –; OL676805*. *Carex umbricola* K.L.Wilson; spm00005220; Australia, AY244538; AY244537; –. *Carex uncinata* L. 1; Gustafson_1898; –; AF284988; –. *Carex uncinata* 2; spm00005112; New Zealand; AY244543; AY242054; –. *Carex willdenowii* Willd. 1; Naczi_2933; U.S.A., Kentucky; –; AF027426, AF027467; –. *Carex willdenowii* 2; spm00000624; U.S.A., Kentucky, *R.F.C. Naczi 10927* (DOV-052598); MN760138; MN761839; FJ597260. *Carex willdenowii* 3; Naczi_2936; U.S.A., Ohio; –; AF027424, AF027466; –. *Carex willdenowii* 4; spm00005130; U.S.A., Pennsylvania, *Naczi s.n.*; –; AF027425; –. *Carex willdenowii* 5; spm00005358; U.S.A., Pennsylvania, *Naczi 9601* (DOV); –; –; FJ597259. *Carex zotovii* (Hamlin) K.A.Ford; spm00004411; New Zealand, Westland Land District, *N. Zviagina s.n.* (CHR-503448); MN761260; MN762203; MN763442.

FIGURE LEGENDS

Figures are in final size: Fig. 1: one column wide; Fig. 2: two columns wide; Fig. 3: landscape orientation, 160 mm high, 217 mm wide; Fig. 4: two columns wide; Fig. 5: in landscape orientation, 160 mm high, 220 mm wide

Fig. 1. All rachilla (highlighted) configurations that appear within *Carex* subg. *Uncinia*: undeveloped, contained within the utricle, and exerted and hooked (modified from Starr & al., 2008).

Fig. 2. Representative variation of the seven main groups detected by our phylogeny (see Results) within *Carex* subg. *Uncinia*: **A**, *Carex geyeri* (sect. *Firmiculmes*) (Colorado, U.S.A.); **B**, *C. fraseriana* (sect. *Leucocephalae*) (cultivated) **C**, *C. juniperorum* (sect. *Phyllostachys*); **D**, *C. seticulmis* (sect. *Psilocarpae* [subsect. *Seticulmes* = sect. *Seticulmes*, stat. nov.]), Parque Nacional do Itatiaia (Brazil); **E**, *C. sellowiana* (sect. *Psilocarpae*), Paraná (Brazil); **F**, *C. subandrogyna* (South American sect. *Schiedeanae* [= sect. *Wheelerianae*, sect. nov.]), Parque Nacional Los Alisos (Tucumán, Argentina); **G**, *C. edura* K.A.Ford (sect. *Uncinia*), The Remarkables (Queenstown, New Zealand). — A by J.R. Starr; B & C by A.A. Reznicek; D–F by P. Jiménez-Mejías; G by S. Martín-Bravo.

Fig. 3. Phylogenetic reconstruction based on the BI analysis of the Final Matrix dataset. Branch supports are expressed in PP (posterior probability) values from the BI analysis (black) and in BS (bootstrap support) values from the ML analysis (red). Only high support (BS \geq 75; PP \geq 0.90) is shown. The six main clades within *Carex* subg. *Uncinia*, main lineages within *C. sect. Uncinia*, and outgroup's subgenera are marked at the right.

Fig. 4. BioGeoBEARS DEC 9-area biogeographic reconstruction and divergence-time analysis. Areas selected (see Materials and Methods) are: Pat, Patagonia; And, extra-Patagonian Andes; ASA, Atlantic South America; CA, Central America; WNA, Western North America; ENA, Eastern North America; PSW, Pacific Southwest; PI, Pacific islands; Sub, sub-Antarctic archipelagos. Numbers in red correspond to the combinations of ancestral areas inferred by BioGeoBEARS, see legend. *C. phl.* = *Carex phleoides*.

Fig. 5. Geiger morphological state reconstruction for the diagnostic characters of *Carex* subg. *Uncinia* (rachilla, left; inflorescence, right) and their different configurations proposed in this study: undeveloped (yellow), contained within the utricle (red), and exerted and hooked (blue) for the rachilla; unispicate (orange), sometimes unispicate/branched (pink), and branched (green) for the inflorescence.

SUPPLEMENTARY MATERIALS

Fig. S1. Phylogenetic reconstruction using Bayesian inference analyses of the ETS-1f dataset.

Fig. S2. Phylogenetic reconstruction using maximum likelihood analyses of the ETS-1f dataset.

Fig. S3. Phylogenetic reconstruction using Bayesian inference analyses of the ITS dataset.

Fig. S4. Phylogenetic reconstruction using maximum likelihood analyses of the ITS dataset.

Fig. S5. Phylogenetic reconstruction based on the Bayesian inference analyses of the *matK* dataset.

Fig. S6. Phylogenetic reconstruction based on the maximum likelihood analyses of the *matK* dataset.

Fig. S7. Phylogenetic reconstruction based on the Bayesian inference analyses of the all-Data dataset.

Fig. S8. Phylogenetic reconstruction based on the maximum likelihood analyses of the all-Data dataset.

Fig. S9. Phylogenetic reconstruction based on the Bayesian inference analyses of the all-nrData dataset.

Fig. S10. Phylogenetic reconstruction based on the maximum likelihood analyses of the all-nrData dataset.

Fig. S11. Raw results of BioGeoBEARS ancestral area reconstruction for our 9-area and 6-area analyses.

Fig. S12. BioGeoBEARS DIVALIKE 6-area biogeographic reconstruction and divergence-time analysis. Areas selected (as explained in Materials and Methods) are: N, North America; S, South America; CA, Central America; PSW, Pacific Southwest; PI, Pacific islands; Sub, sub-Antarctic archipelagos.

Appendix S1. ETS matrix; 124 aligned sequences.

Appendix S2. ITS matrix; 122 aligned sequences.

Appendix S3. *matK* matrix; 109 aligned sequences.

Appendix S4. allData matrix; includes all sequences of matrices in suppl. Appendices S1–S3 (ETS-1f, ITS, *matK*); 179 concatenated aligned sequences.

Appendix S5. allnrData matrix; includes all taxa sequences with both nuclear markers amplified (ETS-1f, ITS), and those who also had *matK*; 93 concatenated aligned sequences.

Appendix S6. Final matrix; used to perform all phylogenetic, dating, and biogeographic analyses; 109 concatenated aligned sequences.

Table 1. Comparison between the treatment proposed in this paper and relevant former treatments of the sections of *Carex* subg. *Uncinia*, and geographical distribution according to Roalson & al. (2021).

Accepted treatment	Former treatments		Regional distribution (Roalson & al., 2021)
	Section/Subsection	Genus/Subgenus	
<i>Carex</i> sect. <i>Firmiculmes</i>	Sect. <i>Psilocarpae</i> subsect. <i>Firmiculmes</i> (Kük) Mack. (Kükenthal, 1909; Crins, 2002)	<i>Carex</i> subg. <i>Primocarex</i> Kük. (Kükenthal, 1909)	Western North America
<i>Carex</i> sect. <i>Leucocephalae</i>	Sect. <i>Leucocephalae</i> (Kükenthal, 1909)	<i>Carex</i> subg. <i>Primocarex</i> (Kükenthal, 1909)	Central Appalachian Mountains

	N/A	<i>Cymophyllus</i> (Reznicek, 1990; Reznicek, 2002)	
<i>Carex</i> sect. <i>Phyllostachys</i>	Sect. <i>Phyllostachyae</i> Tuck. ex. Kük. (Kükenthal, 1909)	<i>Carex</i> sect. <i>Phyllostachys</i>	North America north of Mexico
<i>Carex</i> sect. <i>Psilocarpae</i>	Sect. <i>Psilocarpae</i> subsect. <i>Seticulmes</i> Kük. p.p. (Kükenthal, 1909)	<i>Carex</i> sect. <i>Psilocarpae</i>	Temperate and subtropical Atlantic South America; from NE Argentina and SE Bolivia to E Brazil
<i>Carex</i> sect. <i>Seticulmes</i>	Sect. <i>Psilocarpae</i> subsect. <i>Seticulmes</i> Kük. p.p. (Kükenthal, 1909)	<i>Carex</i> subg. <i>Primocarex</i> (Kükenthal, 1909)	Temperate and subtropical Atlantic South America; from NE Argentina and SE Bolivia to E Brazil
<i>Carex</i> sect. <i>Uncinia</i>	N/A	<i>Uncinia</i> Pers. (Kükenthal, 1909; Reznicek, 1990)	South and Central America, New Zealand, Australia, the Caribbean, Pacific, South Atlantic and circum-Antarctic archipelagos, reaching marginally Mexico and the Philippines
<i>Carex</i> sect. <i>Wheelerianae</i>	<i>Carex</i> sect. <i>Schiedeanae</i> Kük. (Wheeler & Guaglianone, 2003; Wheeler & Guaglianone, 2006; Jiménez-Mejías & Escudero, 2016; Jiménez-Mejías & Reznicek, 2018)	<i>Carex</i> subg. <i>Indocarex</i> (Kükenthal, 1909)	Andean South America

Table 2. Summary of the six matrices used in this work.

Matrix	Number of sequences	Length (bp)	Number of indels coded	Total length (bp)	% Identical sites	Missing data (%) **
ETS-1f	124	628	48	676	13.9	10.7
ITS	122	644	53	697	0*	10.4
<i>matK</i>	109	817	4	821	40.8	18.6
all-Data (all ETS-1f, ITS and <i>matK</i> sequences)	179	2089	153	2194	19.6	44.4
all-nrDNA (specimens with ETS-1f and ITS available, regardless they whether or not had <i>matK</i>)	93	2089	153	2194	28.4	25.6
Final matrix	109	2089	153	2194	20.5	8.2

* The lack of identical sites in the ITS matrix is due to the presence of fragmentary ITS-1 and ITS-2 sequences.

** Missing data calculated in matrices with coded indels.

Table 3. Calibrations used in the dating analysis according to Jiménez-Mejías & al. (2016c) and Martín-Bravo & al. (2019).

Calibration	Age (mya)	Placement
<i>Carex colwellensis</i> Chandler (fossil)	Eocene (38.0–33.9)	Crown node of genus <i>Carex</i> (tree root)
<i>Carex marchica</i> Mai (fossil)	Early Miocene (23.0–16.0)	Crown node of <i>C.</i> subg. <i>Vignea</i>

Carex hartauensis Mai (fossil)

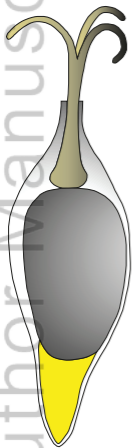
Late Oligocene (28.1–23.0)

Crown node of *C.* subg. *Carex*

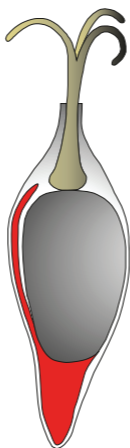
Secondary calibration (Martín-Bravo & al., 2019)

Early Miocene (22.91)

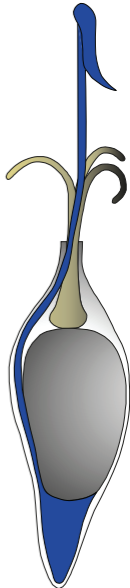
Crown node of *C.* subg. *Uncinia*



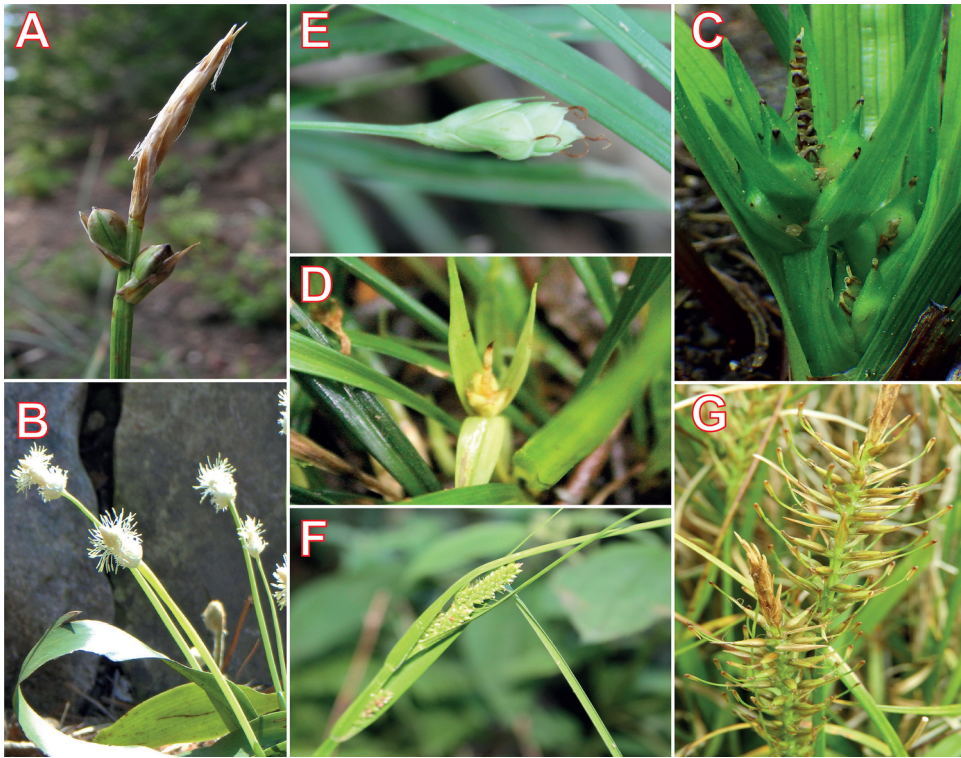
Undeveloped



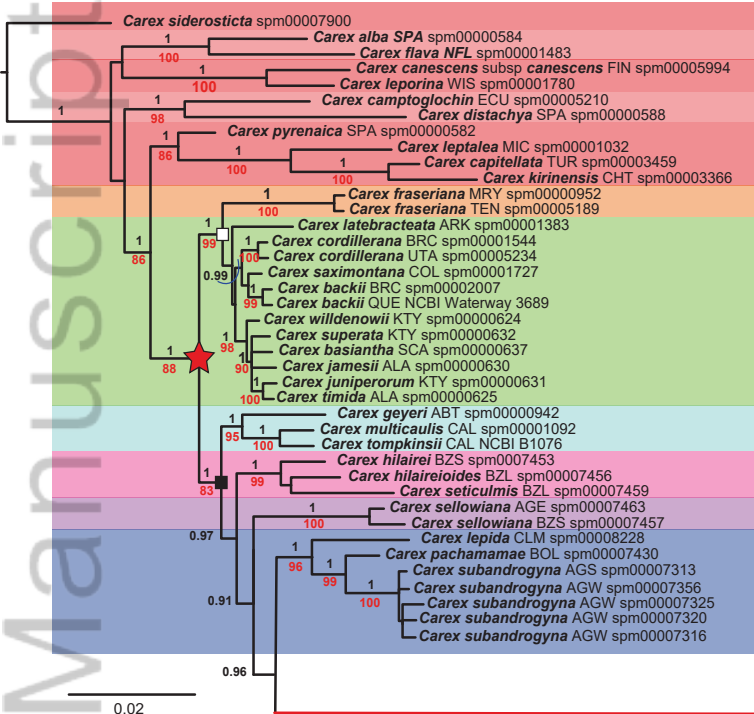
Contained within
the utricle



Exserted and
hooked

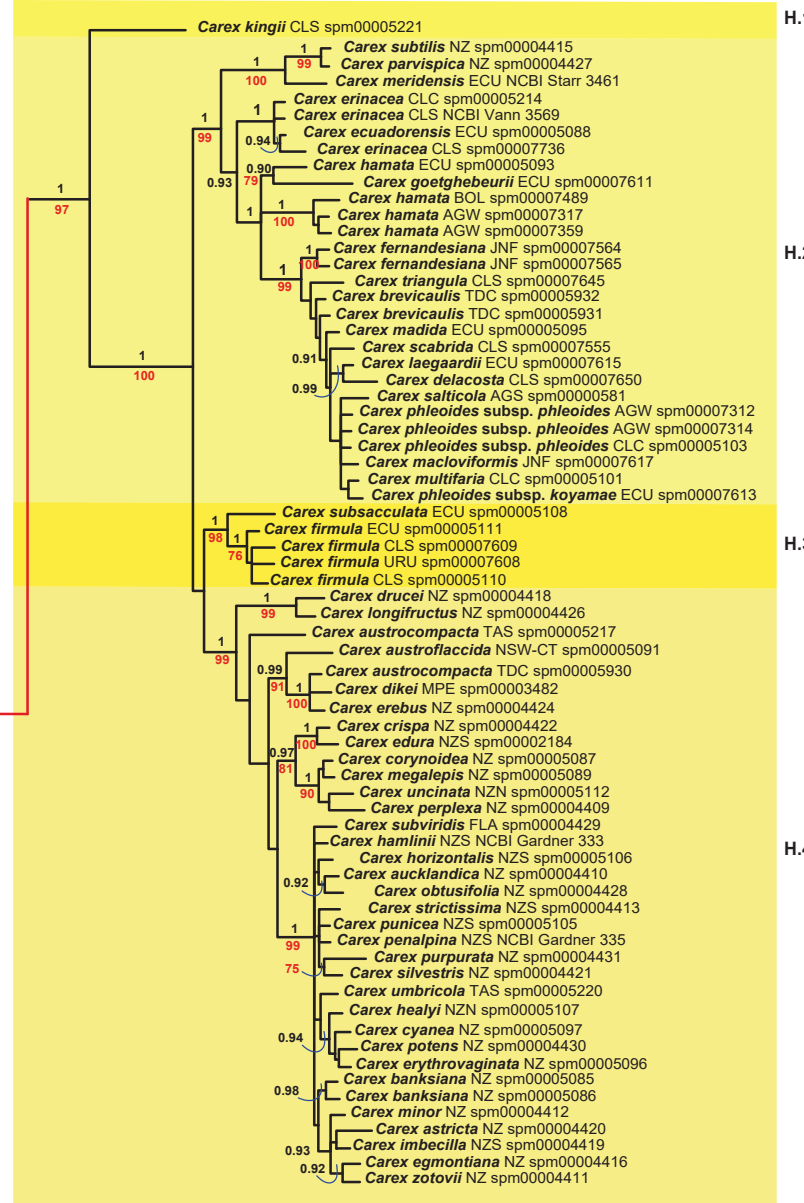


TAX_12678_Figure_2_RGB.jpg



A.1
A.2
A.3
A.4
A.5
B
C
D
E
F
G

- A.1 Subg. *Siderostictae*
 - A.2 Subg. *Carex*
 - A.3 Subg. *Vigneae*
 - A.4 Subg. *Psyllophorae*
 - A.5 Subg. *Euthyceras*
- OUTGROUP**
- B Sect. *Leucocephalae*
 - C Sect. *Phyllostachys*
 - D Sect. *Firmiculmes*
 - E Sect. *Psilocarpae* clade I = Sect. *Seticulmes* stat. nov.
 - F Sect. *Psilocarpae* clade II
 - G South American sect. *Schiedeanae* = Sect. *Wheelerianae* sect. nov.
- H.1 Sect. *Uncinia* - Lineage A
 - H.2 Sect. *Uncinia* - Lineage B
 - H.3 Sect. *Uncinia* - Lineage C
 - H.4 Sect. *Uncinia* - Lineage D
- ★ Subg. *Uncinia*
- Clade 1
- Clade 2



A.1
A.2
A.3
A.4
A.5
B
C
D
E
F
G

H.1
H.2
H.3
H.4

