

# A synopsis of the androgynous species of *Carex* subgenus *Vignea* (Cyperaceae) in South America

PEDRO JIMÉNEZ-MEJÍAS<sup>1,2,\*</sup>, SANTIAGO MARTÍN-BRAVO<sup>3</sup>,  
JOSÉ IGNACIO MÁRQUEZ-CORRO<sup>3</sup>, SABINA DONADÍO<sup>4</sup>, ERIC H. ROALSON<sup>5</sup> and  
ROBERT F. C. NACZI<sup>6</sup>

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

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

<sup>3</sup>Área de Botánica, Department of Molecular Biology and Biochemical Engineering, Universidad Pablo de Olavide, Ctra de Utrera km 1 s.n., 41013 Sevilla, Spain

<sup>4</sup>Instituto de Botánica Darwinion (IBODA-CONICET), calle Labardén 200, C.C. 22, B1642HYD, San Isidro, Argentina

<sup>5</sup>School of Biological Sciences, Washington State University, PO Box 644236, Pullman WA 99164, USA

<sup>6</sup>The New York Botanical Garden, 2900 Southern Blvd, Bronx, NY 10458–5126, USA

Received 19 February 2020; revised 2 September 2020; accepted for publication 1 November 2020

This is the first work of a series of thorough studies into the taxonomy and systematics of *Carex* in South America. Here, we present the systematic placement, biogeographic insights, taxonomic accounts, formal typifications and summarized distributions for the 24 species of *Carex* subgenus *Vignea* with androgynous spikes in the continent. We performed a phylogenetic study using the barcode markers ETS, ITS and *matK* to check the placement of 22 of these species on a previous tree with > 1000 *Carex* spp. We examined > 600 specimens from 38 herbaria and conducted an exhaustive nomenclatural survey consulting all pertinent literature. South American androgynous species of subgenus *Vignea* are grouped in seven distinct lineages, corresponding with the same number of inferred colonizations. Most groups seem to have colonized South America during the Plio-Pleistocene, except for species of section *Bracteosae*, a local radiation that dates back to the Late Miocene. All colonizations by native species seem to have originated from North America. The two putatively introduced taxa are western Palaearctic species. An identification key is provided for the studied species. We make 19 new typifications and a new species (*Carex pedicularis*) is described.

ADDITIONAL KEYWORDS: Andes – boreotemperate – Neotropics – Patagonia – sedges – Southern Cone – taxonomy.

## INTRODUCTION

*Carex* L. (Cyperaceae) is one of the hyperdiverse plant genera. With *c.* 2000 species, it ranks among the three largest genera of plants and one of the two largest of monocots (Govaerts *et al.*, 2020+; POWO, 2020). It is known to have diversified in the temperate areas of the Northern Hemisphere from which it colonized the Southern Hemisphere repeatedly (Martín-Bravo

*et al.*, 2019). *Carex* is readily characterized from all other genera of Cyperaceae by its unisexual flowers, the female flowers being enclosed in a prophyll (the perigynium), which in the vast majority of the species has its margins closed, forming a utricle (Jiménez-Mejías *et al.*, 2016a). The flowers are arranged in spikelet-like spikes, which in turn may be organized in a variety of inflorescences: paniculate, racemose, spike-like or capitate.

The only monographic treatment for *Carex* in South America is that of Kükenthal (1899), which he soon modified with additions and nomenclatural

\*Corresponding author. E-mail: [pjimmej@gmail.com](mailto:pjimmej@gmail.com)

rearrangements (Kükenthal, 1904, 1905). To date, the most complete compendium of South American *Carex* remains Kükenthal's (1909) slightly later world monograph. Despite the existence of a number of regional treatments published during the subsequent 100 years (e.g. Barros, 1935, 1947; Macbride, 1936; Barros, 1947; Pedersen, 1968; Barros, 1969; Moore, 1983; Reznicek, 1995; Wheeler, 2007, 2009; Silveira & Longhi Wagner, 2012; Jiménez-Mejías & Silva, 2020) the current knowledge of the group is still quite scattered. There are indeed a number of valuable taxonomic works by the prolific author Wheeler (1987, 1988, 1996a, b, 2002, 2006, among many others) that unfortunately remain mostly unconnected, holding back the integrated understanding of *Carex* as a whole in South America.

*Carex* subgenus *Vignea* (P.Beauv. ex T.Lestib.) Peterm. is perhaps the best morphologically defined large group in the genus. With the exception of two problematic species (*Carex baldensis* L. and *Carex curvula* All.) that were recently transferred to subgenus *Psyllophora* (Degl.) Peterm. (Villaverde *et al.*, 2020), subgenus *Vignea* has been recovered as a well-supported monophyletic group in phylogenetic analyses based on Sanger sequencing (e.g. Roalson, Columbus & Friar, 2001; Hendrichs *et al.*, 2004; Waterway & Starr, 2007; Ford *et al.*, 2012; Jiménez-Mejías *et al.*, 2016b; among many others) and further confirmed by genomic analyses (Villaverde *et al.*, 2020). The relatively dense spike-like inflorescences with sessile bisexual spikes and (almost always) distigmatic flowers make subgenus *Vignea* a readily diagnosable group easy to differentiate from all the other remaining subgenera of *Carex*. One of the most remarkable diagnostic characters for the taxonomy of subgenus *Vignea* is the sex distribution within spikes, which remains more or less constant in most groups. Indeed, most identification keys soon split between species with androgynous spikes and those with gynaecandrous spikes (e.g. Egorova, 1999; Ball & Reznicek, 2002; Luceño, Escudero & Jiménez-Mejías, 2008, Dai *et al.*, 2010). Recent phylogenetic analyses have demonstrated that groups entirely formed by gynaecandrous species [sections *Deweyanae* (Tuck. ex Mack.) Mack., *Gibbae* Kük., *Glareosae* G.Don, *Cyperoideae* G.Don (= *Ovales* Kunth), *Remotae* C.B. Clarke and *Stellulatae* (Kunth) Christ] have arisen several times during the diversification of subgenus *Vignea* (Ford *et al.*, 2012; Jiménez-Mejías *et al.*, 2016b). In addition, there are two groups in which the sex distribution may vary between species or even between individuals [sections *Ammoglochin* Dumort. s.s. and *Holarrhenae* (Döll) Pax]. Although it is clear that androgynous or gynaecandrous species cannot be regarded as natural groups, their consideration has a

practical base in terms of taxonomic ordination and systematics. Among Neotropical species of subgenus *Vignea*, androgynous species (Fig. 1) have been recurrently assigned to a few sections: *Ammoglochin* (Kükenthal 1909; Wheeler 1988), *Divisae* Lemcke (Kükenthal, 1899; Wheeler 2006), *Foetidae* (Tuck. ex L.H. Bailey) Kük. (Kükenthal, 1909; Wheeler 1987, 1996a) and *Phaestoglochin* Dumort. s.l. (Wheeler 1996b, 2002). These classifications have been problematic since the sectional arrangement within *Vignea* has been shown to be highly polyphyletic and in much need of revision (Hendrichs *et al.*, 2004; Ford *et al.*, 2012; Jiménez-Mejías *et al.*, 2016b; Roalson *et al.* in press).

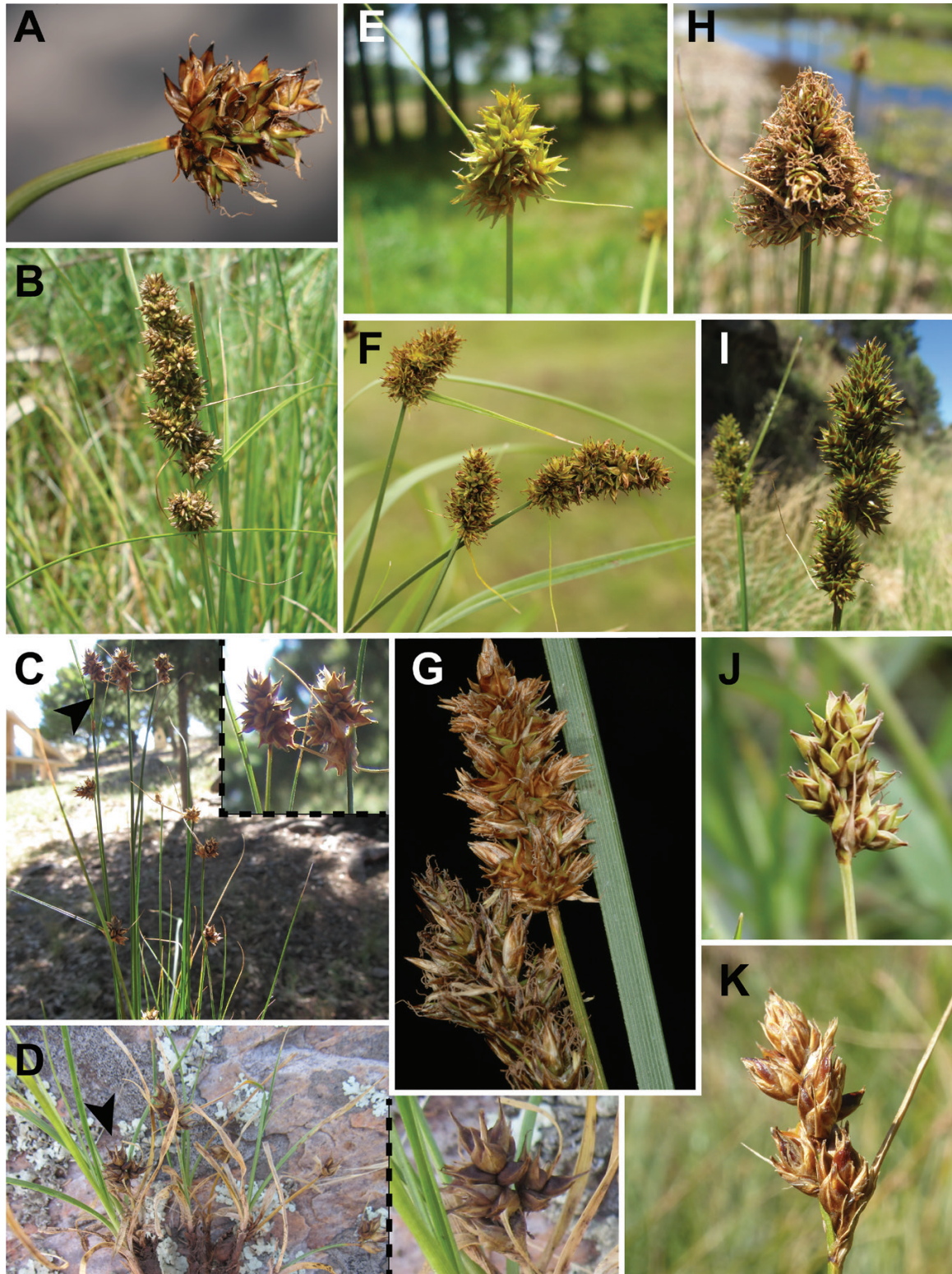
In recent years, large digitization projects have made available on the Internet thousands of old bibliographic references and detailed images of type material. Such unprecedented availability of resources is facilitating the thorough revision of taxonomic groups that otherwise would have taken longer to complete because of the need of visiting herbaria or requesting material on loan (Cellinese & Beaman, 2012; Jiménez-Mejías, Cohen & Naczi, 2017a; Soltis, 2017).

The present work is the first paper of a series of contributions towards an exhaustive clarification on the taxonomy and systematics of *Carex* in South America. Here we aim to clarify the taxonomy of the South American androgynous species of *Carex* subgenus *Vignea* (Table 1). Among other species of subgenus *Vignea*, this work excludes *Carex canescens* L. and *Carex skottsbergiana* Kük. (both from *Carex* section *Glareosae* G.Don), *Carex turumiquirensis* Steyerem. (*Carex* section *Stellulatae* Kunth) and the the monophyletic *Carex* section *Cyperoideae* G.Don (approximately ten currently accepted species in South America), all taxa that invariably bear gynaecandrous spikes. Due to their particular and intricate taxonomic controversies we do not treat those groups here, and additional studies will be performed towards a thorough treatment in the future. In this publication we elucidate the phylogenetic placement and relationships of most of the androgynous South American species of subgenus *Vignea* (22 out of 24; see *Results*), provide an identification key for them covering the entire continent and present a summarized treatment including an exhaustive nomenclatural revision, geographical distributions and relevant observations.

## MATERIAL AND METHODS

### TAXONOMIC REVISION

During the last five years, the first author of the present work, with the support of all the other co-authors in different cases, has carried out a comprehensive study



**Figure 1.** Representative images of living specimens of South American androgynous species of *Carex* subgenus *Vignea*. A, *C. melanocystis* (Argentina, Tierra del Fuego, San Sebastián). B, *C. feddeana* (Argentina, Entre Ríos, Gualaguaychú). C, *C. fossa* (Argentina, Buenos Aires, Saavedra). D, *C. rupicola* (Argentina, Buenos Aires, Abra del Hinojo). E, *C. sororia* (Argentina, Entre Ríos, La Aurora del Palmar). F, *C. subdivulsa* (Argentina, La Rioja, Chilecito). G, *C. gayana* (Chile,

of the full Neotropical *Carex* collections at MICH, MO, NY and US (codes according to *Index Herbariorum*, Thiers, 2020+), which together account for the largest Cyperaceae Neotropical collections in North America. Material was also newly collected during three fieldwork expeditions, one to Argentinian Patagonia in 2010 by S.M.-B. (material deposited at SI and UPOS), one to central and northern Argentina in 2015 by P.J.-M., S.M.-B. and S.D. (material deposited at MCNS, NY, SI, UPOS and WS) and one to south-eastern and southern Brazil in 2018 by P.J.-M. (material deposited at FLOR, RB, UFP and UPOS). In addition, we have studied specimens on loan from A and E, plus a number of additional collections housed at B, MA, MCNS, SI and UPOS. An extensive search of digitized images was also performed in the online repository JSTOR Global Plants (<https://plants.jstor.org/>) and on the websites of B, F, K, P and the National Herbarium of the Netherlands. In total, > 600 specimens have been examined.

Material was identified according to all the specialized literature cited in the Taxonomic Treatment, with special reference to several of Wheeler's works (1987, 1988, 1996a, b, 2002, 2006, 2009) focusing on Neotropical species of subgenus *Vignea*. Distributions have been revised according to specimens and all pertinent literature we have located (see Taxonomic Treatment). Representative iconography (plates and pictures) is cited when available. Photographs of representative inflorescences and utricles are newly provided to illustrate all the species in the study group.

Digital images of original material of every accepted name and most involved synonyms have been located in digital repositories or have been requested from various herbaria. Stafleu & Cowan (1976–2009) provided the starting point for tracing non-digitized material. We searched for formal lectotypifications exhaustively and new lectotypifications were made when necessary.

#### PHYLOGENETIC PLACEMENT

We explored the phylogenetic placement of 22 of the 24 androgynous species of subgenus *Vignea* known from South America according to our own results (we were unable to include only material of the rare Chilean endemic *Carex nebularum*, and from introduced populations of the European *Carex divisa*). We used the Martín-Bravo *et al.* (2019) matrices as the starting point. In that study the authors prepared two matrices of concatenated

sequences from three markers (nuclear ribosomal ETS and ITS and plastid *matK*): (1) a multiple tips matrix (4467 sequences), containing multiple accessions for 1312 *Carex* spp.; and (2) a singletons matrix, containing only the longest concatenated sequence of each species. With the singletons matrix, the authors intended to reduce the amount of missing data in the multiple tips matrix, and thus produced a better-resolved topology. For the present study we combined data from the two matrices to give further insights into the phylogenetic structure of the androgynous species of subgenus *Vignea*. We retained the singletons matrix and added additional sequences from the multiple tips matrix. The newly added sequences were those of the study species, plus those of the most closely allied taxa according to the phylogeny in Martín-Bravo *et al.* (2019). With this strategy we aimed to gain insights into the monophyly of species and to understand relationships with their closest relatives.

For the phylogenetic reconstruction, we resorted to the scaffolding approach used in Jiménez-Mejías *et al.* (2016b). First, only those accessions containing ETS and ITS were considered for constructing the maximum likelihood tree using RAxML (Stamatakis, 2014). Then, we placed all the excluded accessions using the evolutionary placement algorithm (Berger, Krompass & Stamatakis, 2011), as implemented in RAxML. Support was evaluated by the Shimodaira-Hasegawa implementation of the approximate likelihood-ratio test (Anisimova & Gascuel, 2006). Phylogenetic analyses were conducted in CIPRES Science Gateway (Miller *et al.*, 2010).

## RESULTS

### TAXONOMIC REVISION

Twenty-four species were identified among all the studied material of androgynous *Carex* subgenus *Vignea* from South America. One is here formally described (*Carex pedicularis* sp. nov., see below). Indications of the original material are provided for every accepted name and for the vast majority of the synonyms. Twenty-four new typifications of accepted names and synonyms are made here. Plates summarizing representative inflorescence (Fig. 2) and utricle morphology (Fig. 3) are presented.

---

Magallanes, Torres del Paine; bisexual inflorescence). H, *C. firmicaulis* (Argentina, Neuquén, Epu Lauquen). I, *C. brongniartii* (Argentina, Buenos Aires, Abra de la Ventana). J, *C. ownbeyi* (Argentina, Tucumán, Tafi del Valle). K, *C. divisa* (Chile, Valparaíso, Quintay). Pictures: J. Calvo (K), S. Donadio (B, E), P. Jiménez-Mejías & G.E. Rodríguez-Palacios (F, J), M. Luceño (A, G) and S. Martín-Bravo (C, D, H, I).

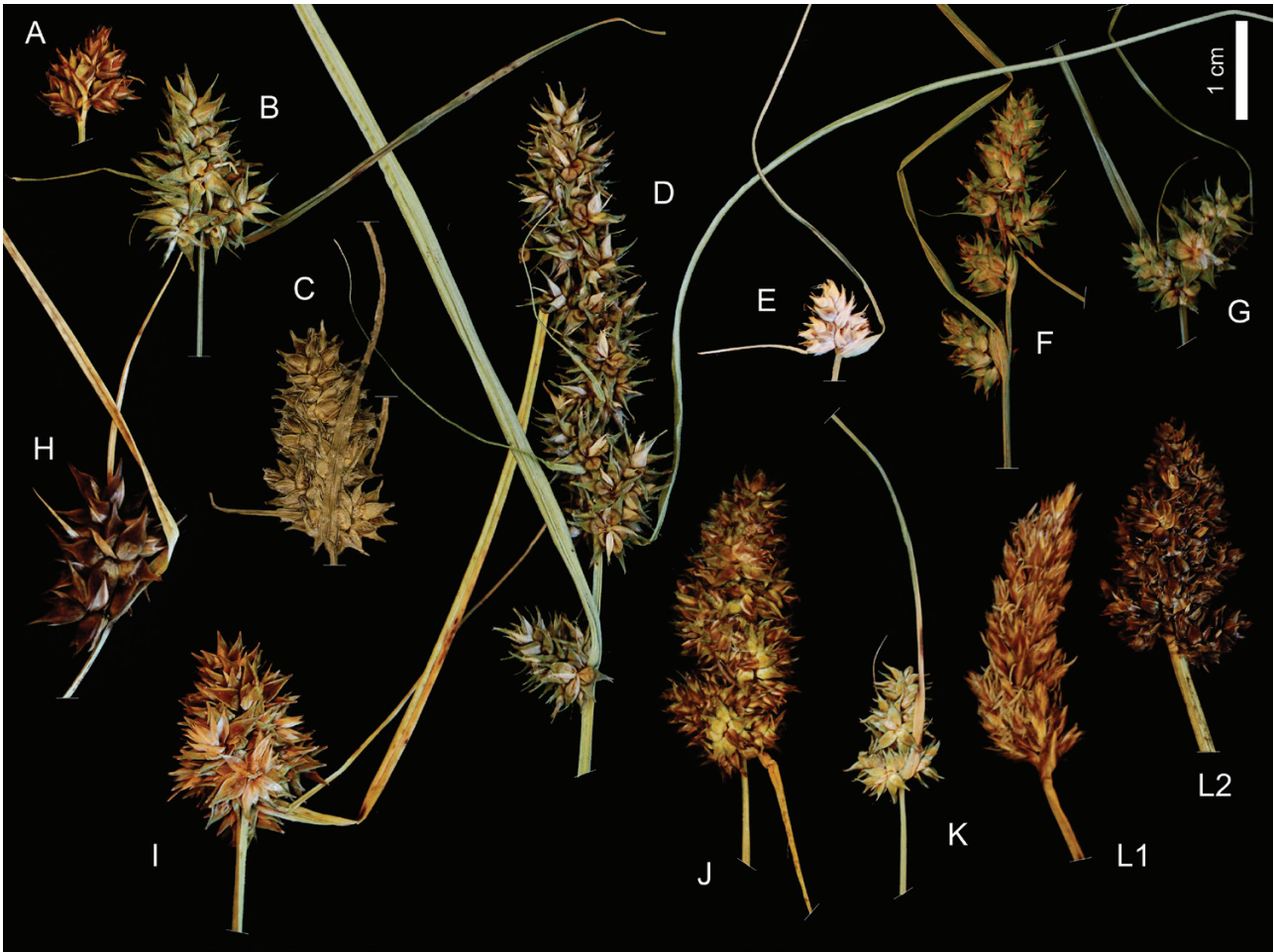
**Table 1.** Taxonomic summary of the androgynous South American species belonging to *Carex* subgenus *Vignea*. Taxa not native to the continent are marked with an asterisk (\*). Relatively narrowly distributed species are marked with a hash (#).

|   | Distribution  |
|---|---|
| <b><i>Carex maritima</i> group</b>  |   |
| <i>Carex melanocystis</i> É.Desv. (previously treated as <i>C. maritima</i> Gunnerus) | Patagonia and Andes, becoming scattered north of central Chile and north-western Argentina                  |
| <b><i>Carex</i> section <i>Bracteosae</i> Pax</b>                                     |   |
| <i>Carex bonariensis</i> Desf. ex Poir.   | From northern Patagonia, north to south-eastern Brazil, scattered in the tropical Andes to southern Ecuador |
| <i>Carex bracteosa</i> (Rchb.) Kunze#   | Central and southern Chile  |
| <i>Carex feddeana</i> H.Pfeiff  | Northern Argentina to south-eastern Brazil and southern Bolivia   |
| <i>Carex giovanniana</i> Jim.-Mejías#   | North-western Argentina to south-western Bolivia  |
| <i>Carex fossa</i> G.A.Wheeler  | Confirmed only for north-eastern Argentina and northern Argentinian Patagonia                               |
| <i>Carex pedicularis</i> Jim.-Mejías & Naczi  | Argentina north to Paraguay and Uruguay   |
| <i>Carex rupicola</i> (Pedersen) G.A.Wheeler#   | North-eastern Argentina and Uruguay   |
| <i>Carex sororia</i> Kunth  | Argentina to south-eastern Brazil   |
| <i>Carex subdivulsa</i> (Kük.) G.A.Wheeler#   | North-western Argentina   |
| <i>Carex uruguensis</i> Boeckeler   | North-eastern Argentina to southern Brazil  |
| <b><i>Carex gayana</i> group</b>  |   |
| <i>Carex gayana</i> É.Desv.   | Patagonia and Andes, north to Peru  |
| <b><i>Carex nebularum</i> group</b>   |   |
| <i>Carex firmicaulis</i> Kalela   | Patagonia to north-eastern Argentina  |
| <i>Carex hypoleucos</i> É.Desv.   | Patagonia   |
| <i>Carex nebularum</i> Phil. #  | Central and southern Chile  |
| <i>Carex pleioneura</i> G.A.Wheeler#  | Central Chile and north-western Argentina   |
| <i>Carex reichei</i> Kük.   | Patagonia   |
| <b><i>Carex praegracilis</i> group</b>  |   |
| <i>Carex ecuadorica</i> Kük.  | Andes from north-western Argentina to Ecuador   |
| <i>Carex macrorrhiza</i> Boeckeler  | Central Argentina to northern Chile and Bolivia   |
| <i>Carex subfuegiana</i> G.A.Wheeler  | Eastern Patagonia to central Argentina  |
| <b><i>Multiflorae-Vulpinae</i> alliance</b>   |   |
| <i>Carex brongniartii</i> Kunth   | Central Chile and northern Argentina to south-eastern Brazil  |
| <i>Carex ownbeyi</i> G.A.Wheeler  | Andes, from north-western Argentina to Colombia   |
| <b><i>Carex</i> section <i>Divisae</i> Christ ex Lemcke</b>                           |   |
| <i>Carex divisa</i> Huds.*  | Western Palaearctic, introduced in Río de la Plata region and central Chile                                 |
| <b><i>Carex</i> section <i>Phaestoglochin</i> Dumort.</b>                             |   |
| <i>Carex divulsa</i> Stokes*  | Western Palaearctic, introduced in north-eastern Argentina  |

## PHYLOGENETIC PLACEMENT

The phylogenetic analyses provided well-supported placement for the 22 included species (Fig. 4; Supporting Information, Appendix S1). All the samples were recovered in the subgenus *Vignea* clade. Two sets of species were recovered forming respectively monophyletic groups: the representatives of *Carex* section *Bracteosae* Pax [*Carex bonariensis* Desf. ex Poir., *Carex bracteosa* (Kunze ex Rchb.) Kunth, *Carex giovanniana* Jim.-Mejías, *Carex feddeana* H.Pfeiff., *Carex fossa* G.A.Wheeler, *Carex pedicularis* Jim.-Mejías & Naczi sp. nov. (described below), *Carex rupicola*

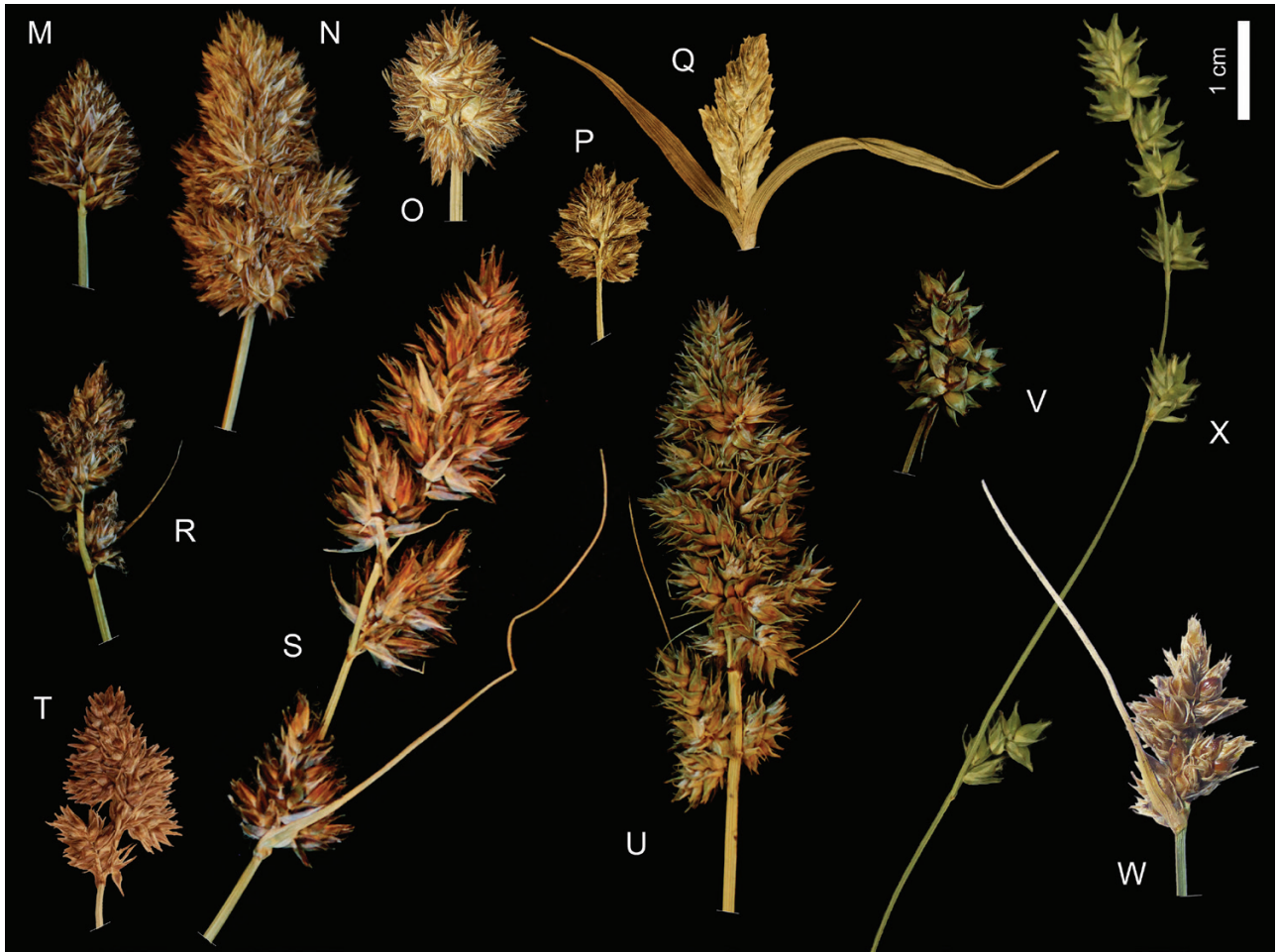
(Pedersen) G.A.Wheeler, *Carex sororia* Kunth, *Carex subdivulsa* (Kük.) G.A.Wheeler and *Carex uruguensis* Boeckeler] and the group of *C. nebularum* Phil. (*Carex firmicaulis* Kalela, *Carex hypoleucos* É.Desv., *Carex pleioneura* G.A.Wheeler and *Carex reichei* Kük.). *Carex ecuadorica* Kük., *Carex macrorrhiza* Boeckeler and *Carex subfuegiana* G.A.Wheeler were recovered unresolved in a shallow clade with other superficially similar North American *Carex* spp. (*Carex alma* L.H.Bailey, *Carex chihuahuensis* Mack., *Carex pansa* L.H.Bailey and *Carex praegracilis* W.Boott). *Carex gayana* É.Desv. was found in a clade unresolved with the North American *Carex*



**Figure 2.** Representative inflorescence variation displayed by all the South American androgynous species of *Carex* subgenus *Vigneia*. A, *C. melanocystis* (Argentina, San Juan, Paso de las Aguas Negras, *Martín-Bravo et al. 94SMB15*, UPOS). B, *C. bonariensis* (Argentina, Entre Ríos, Gualaguaychú, *Rodríguez-Palacios et al., 105GERP15*, UPOS). C, *C. bracteosa* (Chile, Valparaíso, Concón, *Pöppig 249*, BM, lectotype). D, *C. feddeana* (Argentina, Entre Ríos, Gualaguaychú, *Rodríguez-Palacios et al., 106GERP15*, UPOS). E, *C. fossa* (Argentina, Buenos Aires, Saavedra, *Martín-Bravo et al. 22SMB15*, UPOS). F, *C. giovanniana* (Argentina, Salta, Campo Quijano, *Rodríguez-Palacios et al., 21GERP15*, UPOS, isotype). G, *C. pedicularis* (Argentina, Entre Ríos, La Jaula, *Rodríguez-Palacios et al., 104GERP15*, UPOS). H, *C. rupicola* (Argentina, Buenos Aires, Sierra de la Ventana, *Martín-Bravo et al. 11SMB15*, UPOS). I, *C. sororia* (Argentina, Entre Ríos, La Aurora del Palmar, *Rodríguez-Palacios et al., 93GERP15*, UPOS). J, *C. subdivulsa* (Argentina, La Rioja, Chilecito, *Martín-Bravo et al. 107SMB15*, UPOS). K, *C. uruguensis* (Argentina, Entre Ríos, Paraná, *Rodríguez-Palacios et al., 102GERP15*, UPOS). L, *C. gayana* (Argentina, Neuquén, Pino Hachado, *Martín-Bravo et al. 60SMB15*, UPOS; L1, staminate inflorescence; L2, pistillate inflorescence). M, *C. firmicaulis* (Argentina, Neuquén, Epu Lauquen, *Martín-Bravo et al. 71SMB15*, UPOS). N, *C. hypoleucos* (Argentina, Neuquén, Pino Hachado, *Martín-Bravo et al. 61SMB15*, UPOS). O, *C. nebularum* (Chile, Bio-Bío, Ñuble, Termas de Chillán, *Rechinger & Rechinger 64330*, B). P, *C. pleioneura* (Chile, Coquimbo, Illapel, *Looser 2141*, GH, holotype). Q, *C. reichei* (Chile, Maule, Curicó, *Reiche 514*, SGO, lectotype). R, *C. ecuadorica* (Argentina, Jujuy, Tres Cruces, *Rodríguez-Palacios et al., 88GERP15*, UPOS). S, *C. macrorrhiza* (Argentina, San Juan, Paso de las Aguas Negras, *Martín-Bravo et al. 98SMB15*, UPOS). T, *C. brongniartii* (Argentina, Santa Cruz, Lago Buenos Aires, *Barros 2169*, SI). U, *C. brongniartii* (Argentina, Buenos Aires, Abra de la Ventana, *Martín-Bravo et al. 14SMB15*, UPOS). V, *C. ownbeyi* (Argentina, Tucumán, Tafí del Valle, *Rodríguez-Palacios et al., 70GERP15*, UPOS). W, *C. divisa* (Chile, Valparaíso, Quintay, *Calvo & Escobar 8014*, SGO). X, *C. divulsa* (Argentina, Capital Federal, Costanera Sur, *Jiménez-Mejías & Rodríguez-Palacios 2BPJM15*, UPOS).

*simulata* Mack., to which it is close morphologically. The South American samples formerly ascribed to *Carex maritima* (presented in our study as *Carex melanocystis*)

formed a monophyletic group within the clade containing the other species from its homonymous group. *Carex brongniartii* Kunth and *Carex ownbeyi* G.A. Wheeler



**Figure 2.** Continued.

formed independent monophyletic groups, both nested within a clade containing North American species mostly belonging to sections *Multiflorae* (J.Carey) Kük. and *Vulpinae* (Heuff.) H.Christ. Finally, the Argentinian samples of *Carex divulsa* Stokes were placed together with other conspecific samples as unresolved among the European accessions of section *Phaestoglochin* s.s. (relationships of that introduced species not shown in Fig. 4). The molecular data also confirmed that the recently described *C. giovanniana* (Jiménez-Mejías, Fabbroni & Haigh, 2020a) is a distinct species sister to *C. subdivulsa*.

## DISCUSSION

### PHYLOGENETIC AND BIOGEOGRAPHIC RELATIONSHIPS IN SOUTH AMERICAN ANDROGYNOUS CAREX SUBGENUS VIGNEA

Systematic relationships are discussed according to our results. Biogeographic relationships and ages follow

Martín-Bravo *et al.* (2019), whose trees are entirely congruent with ours at the relevant phylogenetic levels. Reported ages are intervals of mean ages, since the time divergence analyses performed in that study did not account for uncertainty.

### *Carex* section *Bracteosae*, a Miocene South American radiation

Defined by Kükenthal (1909) to accommodate mainly Neotropical species, section *Bracteosae* has been variously treated by different authors as independent or as part of a broadly conceived section *Phaestoglochin*. The species of South American section *Bracteosae* are here demonstrated to compose a monophyletic group that diversified in the continent (Fig. 4B): *C. bonariensis*, *C. giovanniana*, *C. feddeana*, *C. fossa*, *C. pedicularis*, *C. rupicola*, *C. sororia*, *C. subdivulsa* and *C. uruguensis*. Despite several species possessing the unusual character



**Figure 3.** Representative utricles variation displayed by all the South American androgynous species of *Carex* subgenus *Vignea*. For each species the left picture shows the adaxial face of the utricles, and the right image shows the abaxial one. A, *C. melanocystis* (Argentina, San Juan, Paso de las Aguas Negras, *Martín-Bravo et al.* 94SMB15, UPOS). B, *C. bonariensis* (Argentina, Tucumán, Tafí del Valle, *Rodríguez-Palacios et al.*, 67GERP15, UPOS). C, *C. bracteosa* (Chile, Valdivia, *Cumming*, s.n. NY). D, *C. feddeana* (Argentina, Córdoba, Quebrada del Condorito, *Rodríguez-Palacios et al.* 48GERP15, UPOS). E, *C. fossa* (Argentina, Buenos Aires, Saavedra, *Martín-Bravo et al.* 22SMB15, UPOS). F, *C. giovanniana* (Argentina, Salta, Campo Quijano, *Rodríguez-Palacios et al.*, 21GERP15, UPOS, isotype). G, *C. pedicularis* (Argentina, Entre Ríos, Uruguay, *Pedersen* 7205, NY). H, *C. rupicola* (Argentina, Buenos Aires, Abra del Hinojo, *Martín-Bravo et al.* 24SMB15, UPOS). I, *C. sororia* (Argentina, Entre Ríos, La Aurora del Palmar, *Rodríguez-Palacios et al.*, 93GERP15, UPOS). J, *C. subdivulsa* (Argentina, La Rioja, Chilecito, *Martín-Bravo et al.* 107SMB15, UPOS). K, *C. uruguensis* (Argentina, Entre Ríos, Paraná, *Rodríguez-Palacios et al.*, 102GERP15, UPOS). L, *C. gayana* (Argentina, San Juan, Paso de las Aguas Negras, *Martín-Bravo et al.* 98SMB15, UPOS). M, *C. firmicaulis* (Argentina, Neuquén, Epu Lauquen, *Martín-Bravo et al.* 72SMB15, UPOS). N, *C. hypoleucos* (Argentina, Neuquén, Pino Hachado, *Martín-Bravo et al.* 61SMB15, UPOS). O, *C. nebulareum* (Chile, Bio-Bío, Ñuble, Termas de Chillán, *Rechinger & Rechinger* 64330, B). P, *C. pleioneura* (Argentina, San Juan, Iglesia, *Chiapella* 2408 & *Vitek* 09-0423, NY). Q, *C. reichei* (Argentina, Santa Cruz, Río Gallegos, *Boelcke* 12343, SD). R, *C. ecuadorica* (Argentina, Jujuy, Cochino, *Ruthsatz* 538/4, NY). S, *C. macrorrhiza* (Argentina, San Juan, Paso de las Aguas Negras, *Martín-Bravo et al.* 88SMB15, UPOS). T, *C. subfuegiana* (Argentina, Santa Cruz, Tehuelches, *Donat* 81, NY). U, *C. brongniartii* (Argentina, Buenos Aires, Abra de la Ventana, *Martín-Bravo et al.* 14SMB15, UPOS). V, *C. ownbeyi* (Argentina, Tucumán, Tafí del Valle, *Rodríguez-Palacios et al.*, 70GERP15, UPOS). W, *C. divisa* (Argentina, Buenos Aires, Magdalena, *Torres Robles & García* 976, MO). X, *C. divulsa* (Argentina, Capital Federal, Costanera Sur, *Jiménez-Mejías & Rodríguez-Palacios* 2BPJM15, UPOS).

of verrucose utricles, these species do not seem to constitute a monophyletic group within the clade. In our analysis, the sister group of the South American species of section *Bracteosae* is the North American

*Carex arkansana* (L.H. Bailey) L.H. Bailey, a taxon that shares with the Neotropical species the character of having the proximal bract(s) much longer than the entire inflorescence ([Ball & Reznicek, 2002](#)), and





**Figure 3.** Continued.

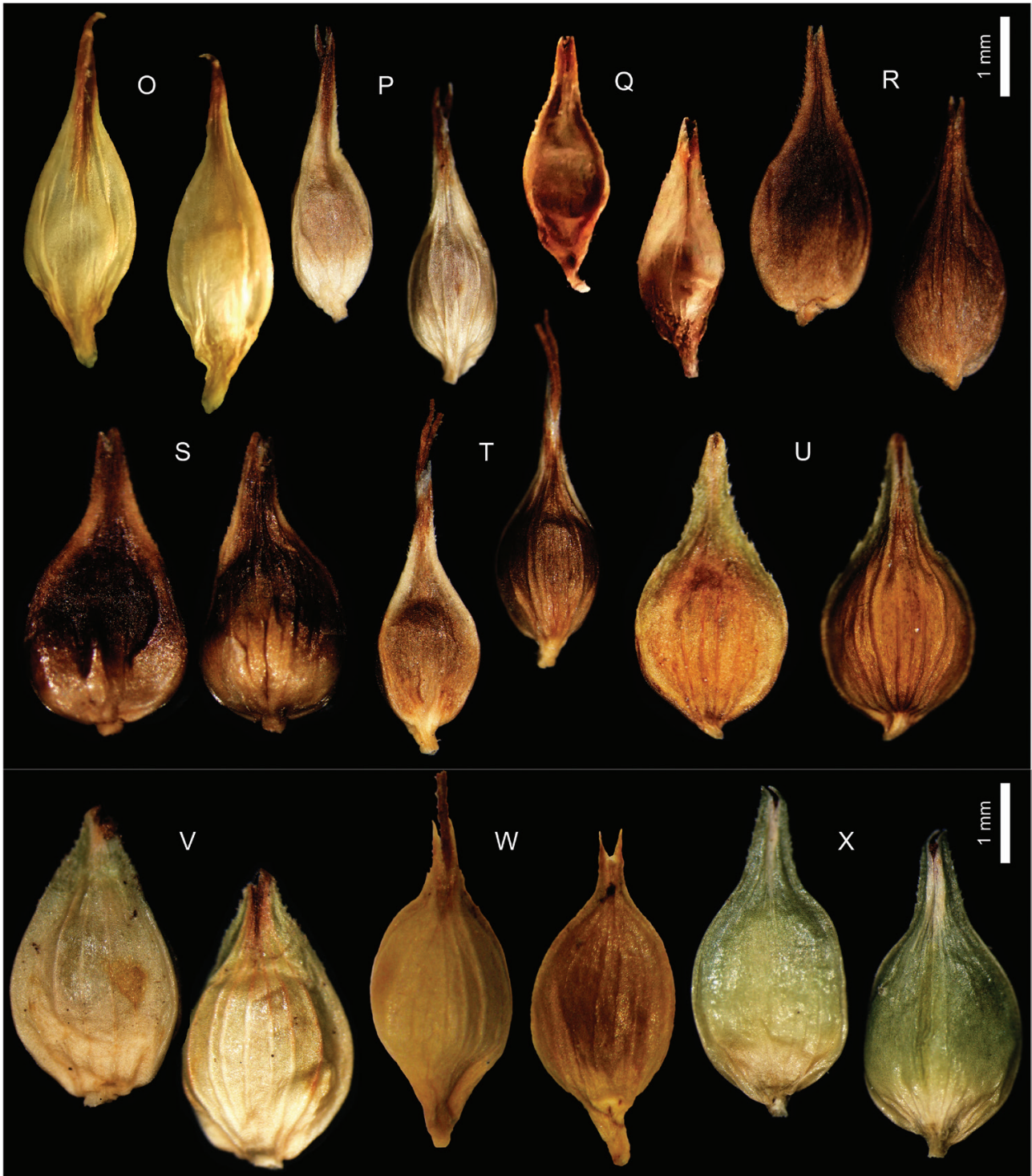
that may well be included in section *Bracteosae*. The group colonized South America from North America 9.6–9.2 Mya (Tortonian, late Miocene). Section *Bracteosae* in the most strict circumscription currently extends from moderate latitudes in the Southern Cone north to Ecuador through the Andes, with a centre of diversity in north-eastern Argentina. All of the species inhabit wet or mesic habitats, with the remarkable exception of *C. rupicola*, that transitioned to arid environments.

*Pliocene-Pleistocene colonization by species previously ascribed to sections Ammoglochin, Divisae and Foetidae*

In our analyses, species usually (and variously) classified in sections *Ammoglochin*, *Divisae* and *Foetidae* were found in four distinct phylogenetic placements within subgenus *Vignea*. This supports at least three independent colonization events, all of them also from North American ancestors.

The group including *C. ecuadorica*, *C. macrorrhiza* and *C. subfuegiana* (Fig. 4E) formed an unresolved radiation involving similar species from North America (*C. pansa* and *C. praegracilis*) also placed in section *Divisae*, plus the morphologically deviant *C. alma* and *C. chihuahuhensis*, which have larger inflorescences. This close relationship of the South American species to some of the North American representatives of section *Divisae* was previously noted in earlier works that extensively recorded *C. praegracilis* (usually under its synonym *Carex marcida* Boott) from South America. These records are clearly ascribable to the Neotropical species (e.g. [Kükenthal, 1899](#); [Macbride, 1936](#)). The entrance of the group into South America was relatively recent, happening during the Late Pliocene-Pleistocene (2.2–1.6 Myr).

The group formed by the closely related *C. firmicaulis*, *C. hypoleucos*, *C. nebularum*, *C. pleioneura* and the dwarf *C. reichei*, was recovered as another monophyletic group sister to the western North American *Carex nervina* L.H.Bailey (Fig. 4C). It seems to be another group of recent entrance into and

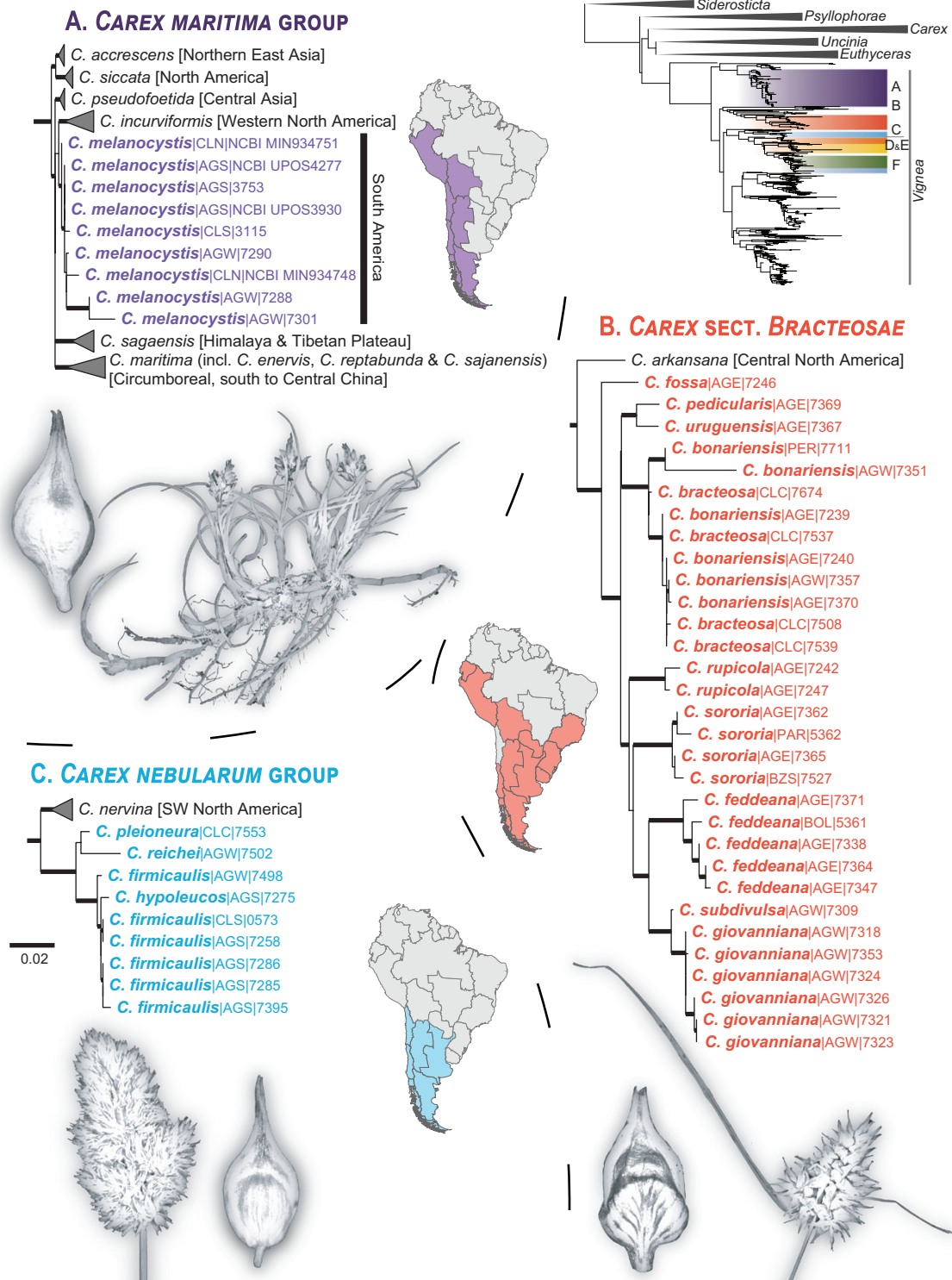


**Figure 3.** Continued.

radiation in South America, with divergence ages also dating to the Late Pliocene-Pleistocene (2.6–1.7 Mya)

*C. gayana* was recovered in an unresolved clade with the North American *C. simulata* Mack.

(Fig. 4D). These taxa share obvious morphological similarities, one of the most remarkable ones being dioecy (which seems facultative in *C. gayana*). Indeed, [Kükenthal \(1909\)](#) regarded some populations in



**Figure 4.** Representative ETS-ITS-*matK* maximum likelihood (ML) *Carex* phylogenetic tree with a focus on *Carex* subgenus *Vigneae* shown in the right corner. The clades including the Neotropical species studied (A-F) are highlighted in different colours. Bold thick branch lines represent non-parametric bootstrapping (BS) clade support > 75%. The labeling of the accessions includes species name, TDWG geographical code and accession number according to [Martín-Bravo et al. \(2019\)](#). The distribution areas of the species group, section or alliance are shown in coloured maps according to TDWG regions ([Brummitt, 2001](#)). Representative image sketches (not to scale) of both inflorescence and utricle of the species are depicted.

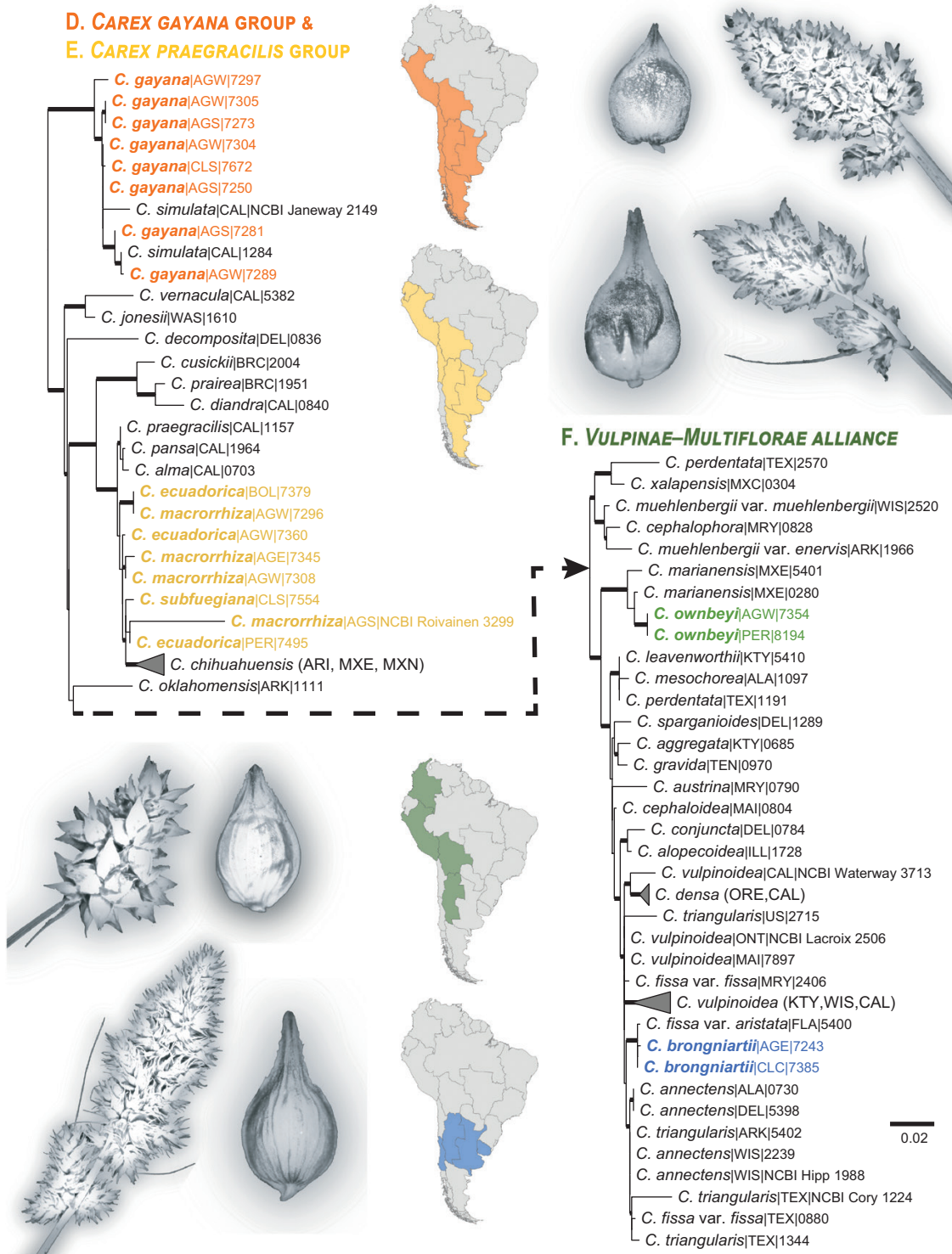


Figure 4. Continued.

western North America to be *C. gayana*. The origin of the *C. gayana*–*C. simulata* lineage can be traced to the early Pliocene (5.2 Mya), although further

studies are needed to clarify the relationships between the North and South American taxa and thus the direction of the colonization.

Villaverde *et al.* (2015) showed that the Neotropical populations usually ascribed to *C. maritima* Gunnerus (named here as *C. melanocystis* É.Desv.) seem to be closely related to the western North American *Carex incurviformis* Mack., both in turn allies of *C. maritima* (Fig. 4A). Lines of evidence in Martín-Bravo *et al.* (2019) about the origin of the South American plants were inconclusive, although these do not contradict the results of the detailed study by Villaverde *et al.* (2015), which reported a north to south migration to account for the colonization of South America. The inferred age for this colonization event is considerably different in each study (1.80 Mya vs. 0.23 Mya, respectively), a result possibly due to the different calibrations used in each study, although both ages fall entirely in the Pleistocene. Regarding the taxonomic structure of *C. maritima* and its allies, our increased taxonomic sampling sheds light about the systematic relationships within the group. The North American *C. incurviformis*, the Himalayan *Carex sagaensis* Y.C.Yang, the Central Asian *Carex pseudofortida* Kük. and the South American *C. maritima*-like plants form clades (Fig. 4A). On the other hand, the circumboreal *C. maritima* s.s. also forms a well-supported clade, but in this case associated with several northern Asian species [*Carex enervis* C.A.Mey., *Carex reptabunda* (Trautv.) V.I.Krecz. and *Carex sajanensis* V.I.Krecz.]. This result points to the distinctiveness of the South American populations and their re-evaluation as a distinct species (*C. melanocystis*). In any case, the relationships among species of the *C. maritima* group are in need of revision, particularly to elucidate whether the northern Asian species must be considered independent from *C. maritima* s.s. or not.

#### *Not diversified (yet): the orphans C. brongniartii and C. ownbeyi*

*C. ownbeyi* was described by Wheeler (2002) as a member of section *Phaestoglochin* on the basis of its androgynous spikes and spreading utricles longer than the subtending glumes. However, in our tree, this species is allied to a different group of North American species mainly traditionally placed in sections *Multiflorae* and *Vulpinae* (*Multiflorae-Vulpinae* alliance; Fig. 4F). *Carex ownbeyi* is also the result of another colonization event from North America that happened during the Late Pliocene or the Pleistocene (2.7–0.7 Mya). *Carex ownbeyi* was placed in our phylogenetic analyses as sister to the Mexican *C. marianensis* Stacey, a taxon much larger in size that occurs at lower elevations. This biogeographical disjunction between Mexican

sierras and the Andes is already known for a few other *Carex* spp. [e.g. *Carex boliviensis* Van Heurck & Müll. Arg. (Reznicek & González-Elizondo 2001); *Carex mandoniana* Boeckeler-*Carex peucophila* Holm (A.A. Reznicek, pers. comm.)]. Reduction of size of as an adaptation to high mountain environments has been also suggested in other *Carex* spp. (Jiménez-Mejías *et al.*, 2017b, 2018).

The taxonomically distinct *Carex brongniartii* was also recovered as part of the *Multiflorae-Vulpinae* alliance, apparently closely related to *Carex fissa* Mack var. *aristata* F.J.Herm. from the south-eastern USA (Fig. 4F). However, interspecific relationships at the specific level within this subclade are unclear and several taxa appear as non-monophyletic. Kükenthal (1899, 1909) already suggested the affinity of *C. brongniartii* with species in section *Multiflorae*, which was otherwise expected due the morphology of *C. brongniartii* utricles and the transversely wrinkled sheaths. Our study further confirms the relationship of *C. brongniartii* with this North American group. The colonization of South America by the ancestor of *C. brongniartii* seems to have happened from North America at relatively recent times during the Pleistocene (c. 0.5 Mya).

#### *Western Palaearctic aliens in temperate South America*

Two of the studied species (*C. divisa* and *C. divulsa*) are broadly distributed in the western Palaearctic and appear disjunctly in the Río de la Plata region and central Chile. From these two, we have been able to confirm molecularly the identity of *C. divulsa*, which has been recovered as unresolved in the section *Phaestoglochin* s.s. clade among the European accessions of the same species (Supporting Information, Appendix S1). The presence of these two species in South America could well be the result of recent introductions, as typically reported for *C. divulsa* (Pedersen, 1968). However, a direct dispersal from the western Palaearctic to South America is known to have happened in other plant groups, including at least three independent events in *Carex* (Escudero *et al.*, 2009; Martín-Bravo *et al.*, 2019). Further studies are needed to confirm the introduced status of these populations.

#### VARIABILITY OF TAXONOMIC CHARACTERS AMONG ANDROGYNOUS REPRESENTATIVES OF CAREX SUBGENUS VIGNEA IN SOUTH AMERICA

During our revision we have detected a few recurrent problems that have misled previous taxonomic decisions. These include the following.

The morphology of the inflorescence in subgenus *Vignea* is often a good diagnostic character. There are a number of species in different groups that differ by characters such as inflorescence length or length of internodes between proximal spikes (e.g. Molina, Acedo & Llamas, 2008). However, these characters seem to be quite variable in species of section *Bracteosae*. For example, Wheeler (2002) considered that *C. fossa* and *C. sororia* were distinguished, among other characters, by their inflorescence configuration, with *C. fossa* having a short, congested inflorescence and *C. sororia* having larger, more elongated inflorescences. This posed a conflict with some northern forms of *C. sororia* that have congested inflorescences, which Wheeler (2002) cited as *C. fossa*. However, detailed examination of the utricles of these northern populations reveals a morphological continuity with *C. sororia* and noticeable differences from typical specimens of *C. fossa*. Something similar occurs in *C. subdivulsa*. Wheeler (2002) reported it to have an oblong elongated inflorescence with the lowermost spike distant, whereas our collections from the Argentinian Province of La Rioja revealed that, within a single population, a number of differently configured inflorescences could be found: from spikes forming elongated oblong and disrupted inflorescence, to inflorescences congested and short. Another taxon affected by taxonomic overpartition is *C. uruguensis*, from which different varieties (see Taxonomic Treatment) have been described based on inflorescence variation. Our observations confirm that utricle morphology in *C. uruguensis* seems constant; however, the inflorescence may vary considerably, from a small, congested head to an elongated spike with separated pseudospikelet clusters in a similar fashion to *C. divulsa*.

Another character that may display variability is the presence of a corky bulge at the base of the utricles. This can be differently developed, depending on the species. In *C. feddeana* (Fig. 2D), for example, this bulge often has the shape of an inverted U that covers most of the proximal half of the utricle body. In *C. uruguensis* (Fig. 2K) this corky base varies from a linear bulge to a broad V-shaped inflated structure. The corky base can only be properly observed when the utricle is fully developed. In immature specimens it can still be identified as the utricle base is collapsed and wrinkled, as drawn for the utricle of *C. uruguensis* in Silveira & Longhi-Wagner (2012).

#### TAXONOMIC TREATMENT

The presented taxonomic treatment is based in our own data but also critically accounts for the information provided by previous works. Distributions by botanical countries are summarized using TDWG codes at botanical country level (Brummitt, 2001). Representative studied material (at least one voucher per botanical country) is provided in the Supporting Information (Table S1). Specimens that have been

seen are indicated by exclamation marks “!”; if the material was seen from a digital image it has been explicitly mentioned as “digital image!”.

The identification key was built according to our own observations and considering the variation presented by Wheeler (1987, 1988, 1996a, b, 2002, 2006, 2009), especially regarding the distinction of species of section *Bracteosae* and the *C. nebularum* group. We intentionally include several species of section *Abditispicae* G.A.Wheeler (subgenus *Carex*) because the extremely congested inflorescences and utricles with two stigmas can be easily mistaken for species of subgenus *Vignea* (see Jiménez-Mejías *et al.*, 2020).

For the most accurate identification of samples the specimens should bear ripe fruits and, whenever possible, several inflorescences from the same population should be examined. In order to simplify, we intentionally used 2-D shape terms to refer to the outline of 3-D organs. Utricle and inflorescence width should be measured at their widest point.

#### CAREX MARITIMA GROUP

Formerly ascribed to section *Foetidae* (Tuck. ex L.H.Bailey) Kük., the phylogenetic placement of the type species (*Carex foetida* All.) in a different lineage (Jiménez-Mejías *et al.*, 2016b; Roalson *et al.* In press.) apparently leaves the distinctive group of *C. maritima* without a formal name. This set of species displays a remarkable bipolar disjunction (Villaverde *et al.*, 2015), being widely distributed in the boreal areas of the Northern Hemisphere and with *C. melanocystis* distributed in South America south to high latitudes.

As mentioned above the South American accessions formed a monophyletic group in our phylogenetic reconstructions (Fig. 4A). In addition, other Asian and North American accepted species of the complex form monophyletic groups also at the same branching level of the phylogenetic tree. This clearly points to the taxonomic distinctiveness of the austral populations. Accordingly, we treat them at species rank as *C. melanocystis*.

1. *Carex melanocystis* É.Desv. in C.Gay, *Fl. Chil.* 6: 203 (1854)

*Carex incurva* var. *melanocystis* (É.Desv.) Kük. in H.G.A.Engler (ed.), *Pflanzenr.*, IV, 20(38): 114 (1909). *Holotype*: CHILE: Chili, C. Gay (P-032665 digital image!).

*Carex psammogaea* Steud., *Syn. Pl. Glumac.* 2: 187 (1855).

*Holotype*: CHILE: Sandy Point, Dec, Lechler 1134a (P-00306909 digital image!); *isotype*: S-07-12239 digital image!).

ARTIFICIAL KEY TO THE ANDROGYNOUS SPECIES OF *CAREX* SUBG. *VIGNEA* IN SOUTH AMERICA

1. Inflorescence formed by a single unbranched spike..... Other *Carex* groups
- 1'. Inflorescence with more than one spike..... 2
2. Spikes unisexual ..... 11. *C. gayana* (in part)
- 2'. Spikes bisexual..... 3
3. Stigmas three ..... Other *Carex* groups
- 3'. Stigmas two ..... 4
4. Lateral spikes pedunculate, with a tubular or funnel-form prophyll at base..... Other *Carex* groups
- 4'. Lateral spikes sessile, without a prophyll at base or with a reduced scale-like one only at the lowermost spikes ..... 5
5. Terminal spike male or gynaeandrous, lateral ones androgynous, female or gynaeandrous ..... Other *Carex* groups
- 5'. Terminal and lateral spikes all androgynous ..... 6
6. Glumes blackish to purplish-brown and inflorescences paniculate ..... *Carex* section *Fecundae* (in part)
- 6'. Glumes whitish, stramineous, ferrugineous, brown or reddish-brown and inflorescences capitate or spike-like, rarely branched at base, if glumes darker, then inflorescences capitate or spike-like..... 7
7. Flowering stems shortly developed, the inflorescence sessile or even buried among leaves ..... 8
- 7'. Flowering stems more or less well developed, the inflorescence exerted above the leaves..... 12
8. Leaf blades < 1.5 cm long; utricles 4–8 mm long, oblong; nutlets rhomboidal.....  
..... *Carex collumanthus* [section *Abditispicae*, subgenus *Carex*]
- 8'. At least some leaf blades > 1.5 cm long; utricles ≤ 4.6 mm long, ovate to elliptic; nutlets ovate to elliptic ..... 9
9. Leaf blades filiform or incurved, 0.5–1.5(2.5) mm wide; most utricles longer than the glumes, the glumes brown; inflorescence globose, pyramidal or broadly ovate ..... 10
- 9'. Leaf blades flat, 1.2–4.0 mm wide; utricles shorter than or equalling glumes, the glumes stramineous to pale brown; inflorescence oblong to ovate ..... 11
10. Inflorescence bractless or with glumaceous bracts embracing the lowermost spikes but not the entire inflorescence; utricles nerveless or faintly nerved at the base ..... 1. *C. melanocystis* (in part)
- 10'. Inflorescence with a setaceous bract embracing its base, usually longer than the inflorescence; utricles conspicuously nerved..... *C. ruthsatziae* (in part) [section *Abditispicae*, subgenus *Carex*]
11. Utricle surface papillose, with beak smooth; inflorescence short-ovate, sometimes buried among the basal leaves..... *C. humahuacaensis* [section *Abditispicae*, subgenus *Carex*]
- 11'. Utricle surface smooth, with beak scabrid distally; inflorescence oblong to narrowly ovate, exerted above the leaves ..... 17. *C. reichei* (in part)
12. Leaf sheaths transversely wrinkled distally on the side opposite blade insertion; inflorescence ≥ 2.5 cm; utricles suborbicular, flattish, with the margins profusely serrulate at least on its distal half and the faces nerved, smooth ..... 21. *C. brongniartii*
- 12'. Leaf sheaths smooth, not wrinkled; inflorescence length variable, but often < 2.5 cm; utricles ovate, obovate, elliptical or suborbicular, the margins serrulate or smooth, the faces nerved or nerveless, smooth or verrucose..... 13
13. Inflorescence lax, with several of the proximal spikes distant, separated by internodes > 2× times longer than the spikes, the utricles not verrucose nor having a corky bulge at base; proximalmost bracts narrowly leaf-like or bristle-like, longer than its spike, usually shorter than the inflorescence..... 24. *C. divulsa*
- 13'. Inflorescence congested or lax, when lax proximalmost spike(s) separated by an internode often < 2× as long as the spikes, the utricles verrucose or not, with a corky bulge at base or not, if lowest spike separated by internodes > 2× the spike length, then utricles verrucose or with a corky bulge at base; proximalmost bract leaf-like, bristle-like or glume-like, longer or shorter than the inflorescence..... 14
14. Proximal-most bract bristle-like or glume-like, shorter than its spike to equalling the whole inflorescence, if surpassing it, then bract bristle-like with a glume-like base and stems often inconspicuous (the inflorescence buried among basal leaves); utricles with faces smooth, not verrucose..... 15
- 14'. Proximal-most bract leaf-like, clearly overtopping the inflorescence, sometimes narrow but then bract not glume-like at the base and flowering stems conspicuous; utricles with faces smooth or verrucose ..... 28

- 15 . Utricles  $\leq 3$  mm long, markedly ovate, widest at base or immediately above it, nerveless or abaxially nerved in its lower half; beak  $< 1.2$  mm, long incised abaxially, the incision often extending into the utricle body; rhizomes elongate .....12. *C. gayana* (in part)
- 15'. Utricles  $> (2.5)2.8$  mm long, ovate to elliptical, widest towards base or middle, nerveless, nerved at base, or with nerves running most of the length of the utricle body; beak  $> 0.7$  mm, not incised or incision not entering the utricle body; rhizomes elongate or short and plant tussock-forming .....16
- 16 . Adaxial face of utricles with (three) four to ten raised nerves running most of the length of the utricle body .....17
- 16'. Adaxial face of utricles nerveless or with up to three faint nerves.....19
- 17 . Utricle body elliptic to obovate; utricle conspicuously constricted at apex into a  $< 1$  mm beak, usually bidentate .....23. *C. divisa* (in part)
- 17'. Utricle body ovate to elliptic; utricle not constricted at apex into the beak or constricted into a  $> 1$  mm beak, truncate or obscurely bidentate .....18
- 18 . Utricles  $2.8\text{--}3.6 \times 0.8\text{--}1.3$  mm; most pistillate glumes as long as or longer than the utricles.....  
.....16. *C. pleioneura* (in part)
- 18'. Utricles  $3.5\text{--}4.0 \times 1.2\text{--}1.9$  mm; pistillate glumes conspicuously shorter than the utricles .....  
.....22. *C. ownbeyi* (in part)
- 19 . Plants with short rhizomes, tussock-forming to loosely caespitose; flowering stems well-developed .....20
- 19'. Plants with rhizomes conspicuously elongate; flowering stems well-developed or inconspicuous and then the inflorescence almost sessile .....23
- 20 . Utricles  $0.8\text{--}1.3$  mm wide, the abaxial face with several nerves running its entire length .....  
.....16. *C. pleioneura* (in part)
- 20'. Utricles  $1.4\text{--}2.4$  mm wide, the abaxial face nerveless or faintly nerved at base.....21
- 21 . Inflorescence outline orbicular to ovate,  $7\text{--}14(17) \times 7\text{--}12$  mm; widest utricles  $1.4\text{--}1.6$  mm wide .....  
.....13. *C. firmicaulis*
- 21'. Inflorescence outline ovate to oblong-ovate,  $15\text{--}40 \times 10\text{--}20$  mm; widest utricles  $1.6\text{--}2.4$  mm wide.....22
- 22 . Nutlets  $1.3\text{--}1.5 \times 0.7\text{--}0.9$  mm; utricles ovate; glumes with a narrow hyaline margin or without hyaline margin.....15. *C. nebularium*
- 22'. Nutlets  $1.5\text{--}1.8 \times 1\text{--}1.5(2)$  mm; utricles obovate, elliptic or broadly ovate; glumes with broad hyaline margin or almost completely hyaline .....14. *C. hypoleucos*
- 23 . Leaf blades filiform,  $0.5\text{--}1.5(2.5)$  mm wide, often incurved; most utricles longer than the glumes, the glumes brown, and inflorescence globose, pyramidal or broadly ovate, often shorter than the leaf blades .....24
- 23'. Leaf blades filiform to flat, often  $> 1.5$  mm wide, usually  $\pm$  straight; most utricles as long as or shorter than glumes, the glumes hyaline, brown or ferruginous, and inflorescence globose, elliptical or oblong, surpassing the leaf blades or not .....25
- 24 . Inflorescence bractless or with glumaceous bracts embracing the lowermost spikes but not the entire inflorescence; utricles nerveless or faintly nerved at the base .....1. *C. melanocystis* (in part)
- 24'. Inflorescence with a setaceous bract embracing its base, usually longer than the inflorescence; utricles conspicuously nerved..... *C. ruthsatziae* (in part) [section *Abditispicae*, subgenus *Carex*]
- 25 . Exserted portion of the flowering stems up to 3 cm long, usually much shorter, inflorescence appearing sessile above leaves; utricle body elliptical, gradually attenuated into a deltoid beak .....17. *C. reichei*
- 25'. Exserted portion of the flowering stems usually  $> 3$  cm, inflorescence elevated above leaves; utricle body ovate, elliptical or oblong, attenuated or constricted into the beak .....26
- 26 . Utricle outline triangular, the body markedly ovate, thus widest at base or immediately above it, gradually attenuating into the beak, rarely weakly constricted into the beak; margins of the utricle scabrid in distal half .....19. *C. macrorrhiza* (in part)
- 26'. Utricle outline bottle-shaped, the body elliptical, oblong or obovate, thus widest near middle or above it, rarely more or less ovate and widest towards base, constricted at apex into the beak; margins of the utricle scabrid or smooth in distal half.....27
- 27 . Glumes pale ferruginous.....20. *C. subfuegiana*
- 27'. Glumes true brown, straw-coloured or hyaline.....18. *C. ecuadorica*
- 28 . Utricles verrucose at least adaxially .....29
- 28'. Utricles adaxially smooth, not verrucose .....32



- 29 . Utricles  $\geq 5$  mm long; base of the flowering culms usually bulbiform..... 8. *C. rupicola*
- 29'. Utricles  $< 5$  mm long; base of the flowering culms not or scarcely swollen..... 30
- 30 . Utricle body broadly ovate to suborbicular (occasionally the margins folded inward, thus the utricle becoming oblong); widest utricles in each inflorescence  $3.0\text{--}4.0 \times (1.8)2.0\text{--}2.5$  mm, abruptly contracted into a more or less parallel-sided beak; inflorescence up to  $1.5(2.5)$  cm long, congested, rarely the proximal-most spikes separated; glumes whitish-hyaline or pale brown-tinged near the middle nerve....  
..... 7. *C. pedicularis*
- 30'. Utricle body ovate to oblong; widest utricles in each inflorescence  $3.7\text{--}5 \times 1.6\text{--}2$  mm, attenuate or scarcely contracted into a deltoid beak; inflorescence up to  $7.2$  cm long, congested or the proximal-most spikes separated; at least upper glumes of each spike brownish, rarely all whitish-hyaline..... 31
- 31 . Largest utricles  $(3.5)3.7\text{--}5 \times 1.6\text{--}2$  mm, including the stipitate base, margins scabrid or smooth; nutlets  $(1.8)1.9\text{--}2.2 \times 1.3\text{--}1.6$ ; inflorescence usually  $< 3.5$  cm long..... 2. *C. bonariensis*
- 31'. Largest utricles  $2.8\text{--}3.9 \times 1.2\text{--}1.8$  mm, including the stipitate base, margins scabrid, very rarely smooth; nutlets  $1.4\text{--}1.9 \times 0.9\text{--}1.3$  mm; inflorescence often  $> 3$  cm long, up to  $7.2$  cm ..... 4. *C. feddeana* (in part)
- 32 . Plant with elongate rhizomes, pistillate glumes stramineous to reddish-brown, and utricles elliptical, with faces strongly nerved and without a corky adaxial bulge at its base ..... 23. *C. divisa* (in part)
- 32'. Without the above combination of characters ..... 33
- 33 . Most utricles shorter than the glumes and concealed by them; utricle body ovate, attenuated distally into a broadly deltoid beak ..... 19. *C. macrorrhiza* (in part)
- 33'. Utricles longer than the glumes, apparent; utricle body ovate, elliptic or orbicular, attenuated or constricted distally into a narrowly deltoid or parallel-sided beak ..... 34
- 34 . Utricles  $3.5\text{--}5$  mm long with a conspicuous corky adaxial bulge at base  $> 1$  mm long, the adaxial face with the nerves running into the distal half, the abaxial face with conspicuous raised nerves .....  
..... 3. *C. bracteosa*
- 34'. Utricles  $2.7\text{--}5.0$  mm long without a corky bulge at base, the faces of the utricles nerveless or nerved, if utricles with a corky bulge at base, then adaxial nerves confined to utricle base and abaxial face nerveless or faintly nerved..... 35
- 35 . Abaxial face of the utricles conspicuously nerved, with four to six raised nerves running uninterruptedly from the utricle base to the beak (although sometimes faint at middle); glumes reddish-brown; mature stems usually curved..... 22. *C. ownbeyi* (in part)
- 35'. Abaxial face of the utricles nerveless or nerved only at base, rarely some nerves running to the beak, but then glumes pale brown to whitish-hyaline; mature stems usually straight..... 36
- 36 . Utricles  $3.0\text{--}3.5 \times 2\text{--}2.4$  mm, body orbicular to broadly ovate, the distal margins scabrid, with a narrow flat margin, the nutlet almost completely filling the entire utricle width; inflorescence congested, conical; glumes whitish-hyaline ..... 5. *C. fossa*
- 36'. Utricles  $2.7\text{--}5.0 \times 0.8\text{--}2.0(2.5)$  mm, body elliptical to ovate, with or without a flat margin, the nutlet filling the entire utricle width or not; inflorescence congested or elongate, subglobose and head-like to oblong; glumes whitish-hyaline, straw-coloured, brown or reddish brown ..... 37
- 37 . Utricles  $(3.5)3.8\text{--}5.0 \times 1.5\text{--}2.0(2.5)$  mm, elliptic; inflorescence  $(0.6)0.8\text{--}1.5$  cm wide..... 9. *C. sororia*
- 37'. Utricles  $2.7\text{--}3.6(4.0) \times 0.8\text{--}1.5(1.6)$  mm, ovate or elliptic; inflorescence  $0.4\text{--}1.0(1.2)$  cm wide..... 38
- 38 . Utricle body ovate, widest at or near the base, or oblong, with an inflated corky base, gradually attenuate into the beak, which gives to the entire utricle a narrowly triangular outline; rhizomes more or less elongate..... 39
- 38'. Utricle body elliptic, widest at or near the middle, without a corky base or with a very slightly inflated one, more or less constricted into the beak, which gives the entire utricle a bottle-shaped outline; rhizomes densely caespitose, rarely shortly elongate ..... 40
- 39 . Utricle with a corky base formed by a basal flattened or V-shaped bulge ..... 11. *C. uruguensis*
- 39'. Utricle with a corky base formed by an inverted U-shaped bulge centered in the utricle lower half, often reaching utricle middle ..... 4. *C. feddeana* (in part)
- 40 . Glumes reddish-brown, with a narrow hyaline margin only at apex or without a differentially coloured margin; leaf blades  $2.5\text{--}5$  mm wide ..... 10. *C. subdivulsa*
- 40'. Glumes pale brown to straw-coloured, with a broad hyaline margin from base to apex; leaf blades  $\leq 3$  mm wide ..... 6. *C. giovanniana*

*Carex misera* Phil., Fl. Atacam.: 53 (1860), nom. illeg., non *Carex misera* Buckley (1843).

*Carex melanocystis* var. *misera* Kük., Bot. Jahrb. Syst. 27: 499 (1899).

*Carex incurva* var. *misera* (Kük.) Kük. in H.G.A.Engler (ed.), Pflanzenr., IV, 20(38): 114 (1909).

*Holotype*: CHILE: Zorras (SGO-000000860 digital image!).

*Carex oligantha* Phil., Anales Mus. Nac. Santiago de Chile 2: 80 (1891), nom. illeg., non *Carex oligantha* Steud. (1855).

*Lectotype* (here designated): CHILE: Colorados, Jan 1885, *Philippi* (SGO-000000871 digital image!; isolectotypes: SGO000000872 digital image!, P-00306908 digital image!).

*Iconography*: [Figures 1A, 2A, 3A](#). Additional figures in [Gay \(1854: tab. 73, fig. 5\)](#), [Barros \(1935: 179, as \*Carex incurva\* and \*C. incurva\* var. \*melanocystis\*\)](#), [Barros \(1947: tab. 174, as \*C. incurva\*, \*C. incurva\* var. \*melanocystis\* and \*Carex incurva\* var. \*misera\*\)](#), [Wheeler \(2009: 330, fig. 295, as \*C. maritima\*\)](#), [Jiménez-Mejías et al. \(2020, as \*C. maritima\*\)](#).

*Distribution*: From Tierra del Fuego north to Peru. Erroneously cited from Ecuador (see notes) [83 BOL PER 85 AGS AGW CLC CLN CLS].

*Etymology*: From the Greek *melano*, black, and *kystis*, bladder, presumably in reference to the darkened ripe utricles that some populations of this species may develop.

*Notes*: [Jørgensen, Nee & Beck \(2014\)](#) considered *C. ruthsatziae* G.A.Wheeler to be a synonym of *C. maritima*. Despite the striking resemblance of the two taxa, they belong to different taxonomic groups, with *C. ruthsatziae* being a member of section *Abditispicae* in subgenus *Carex*, as supported by recent molecular results ([Martín-Bravo et al., 2019](#)). The two species can be distinguished by the characters mentioned in the key. See also [Jiménez-Mejías et al. \(2020\)](#) for additional comments on the differences between the two species.

The citation of *C. maritima* from Ecuador ([Jørgensen & León-Yáñez, 1999](#)) is erroneous. After the study of detailed digital images of the material on which the citation is based (ECUADOR: Chimborazo, *Laegaard 52718*, QCNE-26066) we concluded that it is *C. ecuadorica* beyond any doubt.

Detailed comparison of Northern Hemisphere true *C. maritima* with *C. melanocystis* reveals subtle but rather constant differences between them. The two taxa can be distinguished by the shape of the ripe utricles. In *C. maritima* these are biconvex, not or with an inconspicuous, narrow flattened margin adaxially,

attenuated from the top of the nutlet to the beak into a more or less deltoid beak that is not constricted at its sides. The South American material has utricles convex abaxially and flattish to concave adaxially, the adaxial face bearing a narrow but conspicuous flat margin at its distal half, and the beak noticeably constricted at the top of nutlet. *Carex incurviformis*, also closely related, can be distinguished from the other two species by its narrower utricles (1.1–1.4(1.6) mm wide, with a ratio 2.4–3.7 times as long as wide) with many raised nerves on each face.

*Selected additional references*: [Wheeler \[\(2009\) description\]](#), [Jiménez-Mejías et al. \[\(2020\) taxonomic notes\]](#).

CAREX SECTION BRACTEOSAE PAX IN H.G.A. ENGLER & K.A.E. PRANTL, NAT. PFLANZENFAM. 2(2): 123

A relatively well-defined group from the morphological point of view, mostly characterized by the spreading utricles and the presence of a leaf-like lowermost bract surpassing the inflorescence. Despite initially being conceived to accommodate only Neotropical species ([Kükenthal, 1909](#)), the phylogenetic data may suggest the inclusion here of at least the North American *Carex arkansana*. That Nearctic species has usually been placed in section *Phaestoglochin* and displays the above-mentioned combination of characters.

2. *Carex bonariensis* Desf. ex Poir. in J.B.A.M. de Lamarck, *Encycl., Suppl.* 3: 250 (1813)

*Holotype*: ARGENTINA: Buenos Aires, *P. Commerson s.n.* (FI-012272 digital image!; isotypes: MPU-020514 digital image!, P-00303478 digital image!).

*Carex papillosa* Nees, J. Bot. (Hooker) 2: 398 (1840). *Type*: ARGENTINA: Buenos Aires, Tweedie [implicit in the protologue] (not found, presumably at B and destroyed).

*Neotype* (here designated): Boott, Ill. Gen. Carex 2 (1860): tab. CCIX.

*Carex trachycystis* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 314 (1879).

*Lectotype* (here designated): ARGENTINA: Concepción del Uruguay, Apr 1876, *Lorentz 1007* (GOET-006367 digital image!; isolectotypes: CORD-00005859 digital image!, GOET-006367 digital image!).

*Carex bonariensis* var. *tolimensis* Maury, J. Bot. (Morot) 2: 423 (1888).

*Lectotype* (here designated): COLOMBIA: Cerca de Piedras, in decliv. or. montis, Tolima, alt. 390 m, *André 1883* (K-001129612 digital image!).

*Carex bonariensis* var. *remota* Kük., Bot. Jahrb. Syst. 27: 513 (1899).

*Carex bonariensis* f. *remota* (Kük.) Kük. in H.G.A. Engler (ed.), Pflanzenr., IV, 20(38): 151 (1909).  
Type: ARGENTINA: Prov. Entreríos [Entre Ríos], Concepción del Uruguay, Lorentz 768 (not found, presumably at B and destroyed).

*Carex bonariensis* f. *pumila* Osten, Anales Mus. Hist. Nat. Montevideo, ser. 2, 3: 237 (1931).

Type: URUGUAY: Durazno, in pratis humidis in ripa flum. Yf, 23 XII 1900, Osten 4319 (not seen, presumably at MVM).

Iconography: Figures 2B, 3B. Additional figures in Barros (1935): 206, as *C. bonariensis* var. *trachycystis* and Silveira & Longhi-Wagner (2012): 380.

Distribution: From northern Patagonia, north to south-eastern Brazil on the eastern coast and much scattered to southern Ecuador through the Andes [83 BOL ECU PER 84 BZL BZS 85 AGE AGS AGW CLC URU].

Etymology: From Buenos Aires.

Notes: The name *Carex trachycystis* Griseb. has been used to refer to *C. pedicularis*, but the type material clearly matches *C. bonariensis*. Indeed Küenthall (1909) referred to *C. bonariensis* var. *trachycystis* as having utricles “anguste ovati” [narrowly ovate], while the plants that have been referred to by Wheeler (1996a) as *C. trachycystis* display suborbicular ones. See additional comments under *C. pedicularis*.

Although we have not found the type materials of *Carex papillosa* Nees and *C. bonariensis* var. *remota* Kük., we list those names under the synonymy of *C. bonariensis* according to Küenthall (1909), who almost certainly studied the types of the two names. The neotypification of *C. papillosa* Nees is intended to fix the taxonomic concept of *C. bonariensis* to Nees’s name.

Cited from southern Chile (CLS) by Govaerts *et al.* (2020+), but the citation seems to be erroneous (see Rodríguez *et al.*, 2018). Reports from Argentinian Patagonia (AGS) seem to be based on material from northern Rio Negro (Barros, 1935, 1947) which we have not studied. The report from Paraguay (Zuloaga *et al.*, 2020+) is erroneous, as it was based on *C. feddeana* collections (e.g. Canindeyú, Sierra de Maracayú, 2 Oct 1960, Hassler 5252, P-00303468 digital image!; Presidente Hayes, Chacoí, 28 Oct 1989, Schinini 26669, U-1225801 digital image!).

Selected additional references: Wheeler [(1996) taxonomic notes], Silveira & Longhi-Wagner [(2012) description].

3. *Carex bracteosa* (Kunze ex Rchb.) Kunth, Enum. Pl. 2: 379 (1837)

*Vignea bracteosa* Kunze ex Rchb. in J.C. Mössler & H.G.L. Reichenbach, Handb. Gewächsk. ed. 2, 3: 1619 (1830) [basionym].

Lectotype (*here designated*): CHILE. In fossis paludosis prope Concon, Pöppig 249 (BM 000888080 digital image! (Fig. 2C); isolectotypes: F-0BN013388 digital image!, HAL-0109836 digital image!, MO-2246492 digital image!, P-00303498 digital image!).

*Carex illustranda* Steud., Syn. Pl. Glumac. 2: 190 (1855).

Holotype: CHILE: In arenosis udis prope urbem Valdivia, 1822, Philippi 194 (P-00303502 digital image!; isotypes: BM-000901287 digital image!, FI-012270 digital image!, GOET-002799 digital image!, P-00303500 digital image!, P-00303501 digital image!, S-07-12261 digital image!).

Iconography: Figures 2C, 3C. Additional figures in Boott (1858–1867: tab. 401, 403), Gay (1854: tab. 73, fig. 8), and Wheeler & Muñoz-Schick (2007: 19).

Distribution: Central Chile [85 CLC].

Etymology: From the Latin *bracteosus*, bracteate, presumably in reference to the leaf-like lowermost bract, that usually surpasses the inflorescence.

Notes: *Carex bracteosa* has been recovered in our analyses nested within *C. bonariensis* in our phylogenetic study, which points to a close relationship between the two taxa. Given their morphological distinctiveness, we retain both taxa at the species rank, although further studies would be desirable to ascertain the true relationships between *C. bracteosa* and *C. bonariensis*.

Wheeler & Muñoz-Schick (2007) designated a lectotype for *C. bracteosa*. However, they did not note that *C. bracteosa* was to be treated as a combination of the earlier *Vignea bracteosa* Kunze ex Rchb. through the attribution of both names in their respective protologues to Kunze (ICB Art. 41.3, Ex. 3, Turland *et al.*, 2018). Accordingly, *V. bracteosa* was still in need of typification. We proceed to designate the lectotype for that name using the same voucher that Wheeler & Muñoz-Schick (2007) designated as the type of *C. bracteosa*.

Cited from southern Chile (CLS) by Govaerts *et al.* (2020+), the citation seems to be erroneous (see Rodríguez *et al.*, 2018).

Selected additional references: Wheeler & Muñoz-Schick [(2007) description, taxonomic notes].

4. *Carex feddeana* H.Pfeiff., Repert. Spec. Nov. Regni Veg. 17: 30 (1921)

*Lectotype* (designated by [Wheeler, 1996a](#)): BRAZIL. Paraná, prope Pinhaes, locis subpaludosis, *G. Jönsson 1134a* (BREM, not seen; isolectotypes: G-00098284 digital image!, GH-00101838 digital image!, MO-2246490 digital image!, NY-00011463!, S-07-12248 digital image!).

*Carex bonariensis* var. *achalensis* Kurtz ex Kük., Bot. Jahrb. Syst. 27: 513 (1899).

*Lectotype* (here designated): ARGENTINA: Prov. Córdoba, Sierra Achala, *Kurtz 2888* (CORD-00002080 digital image!).

*Iconography*: [Figures 1B, 2D, 3D](#). Additional figures in [Barros \(1935: 204, as \*Carex bonariensis\* var. \*achalensis\*\)](#) and [Silveira & Longhi-Wagner \(2012: 387\)](#).

*Distribution*: From northern Argentina to southern Bolivia and southern Brazil [83 BOL 84 BZL BZS 85 AGE AGW PAR URU].

*Etymology*: Commemorating Friedrich K.G. Fedde, 1873–1942, a German botanist based at the Berlin Botanical Museum.

*Notes*: Rarely, fully ripe specimens of this species may have utricles smooth instead of verrucose. In this case, the specimens would key to *C. uruguensis*, but then such specimens can be distinguished by the characters indicated in the key.

Cited for AGW from Catamarca Province ([Barros, 1935; Zuloaga et al., 2020+](#)). We have not seen any material from that region.

*Selected additional references*: [Wheeler \[\(1996a\) taxonomic notes\]](#), [Silveira & Longhi-Wagner \[\(2012\) description\]](#).

##### 5. *Carex fossa* G.A. Wheeler, *Darwiniana* 40: 205 (2002)

*Carex involucrata* Boott, Ill. Gen. Carex 2: 76 (1860), nom. illeg., non *Carex involucrata* Boeckeler (1855).

*Carex sororia* var. *involucrata* Kük. in H.G.A. Engler (ed.), Pflanzenr., IV, 20(38): 150 (1909).

*Holotype*: America Meridionalis [ARGENTINA?], *Gillies*, Herb. Hookerianum (K-000584724 digital image!).

*Iconography*: [Figures 1C, 2E, 3E](#). Additional figures in [Boott \(1858–1867: tabs. 209–2010, as \*Carex involucrata\*\)](#) and [Barros \(1935: 202, as \*C. sororia\*?\)](#).

*Distribution*: Argentina, at least from Buenos Aires and Pampa, south to Chubut, other records north of

the indicated area in Argentina, Paraguay, Uruguay and Brazil are here considered doubtful (see notes below) [84 BZS? 85 AGE AGS AGW? PAR? URU].

*Etymology*: From the Latin *fossa*, literally, ditch or pit, a term chosen by [Wheeler \(2002\)](#) to refer to the ‘weedy’ habitat of this species, often occurring in roadside verges, ditches or along railroad embankments.

*Notes*: The illegitimate name *Carex involucrata* Boott remained in synonymy under *C. sororia* until [Wheeler \(2002\)](#) resurrected the taxon with the new name *C. fossa*. He presented a putative combination of characters including utricles and inflorescences distinctive of *C. fossa* and reported the species as occurring from the Argentinian Patagonia north to Salta, Paraguay and Uruguay. Wheeler did not study any actual voucher from the northern areas, and he entirely relied on bibliographic records reporting *C. involucrata* from there. He also mentioned a doubtful entity from northern Argentina and southern Brazil, *C. sororia* var. *pseudobracteosa* (Kük.) Kük., somehow intermediate between what he considered *C. fossa* and *C. sororia*. We have studied vouchers identified by Wheeler as *C. fossa* from the entire area, including Paraguay, Uruguay and Brazil. Whereas the specimens from the southern half of the range seems to us to be more or less constant and distinct from *C. sororia*, we agree with Wheeler that the delimitation of *C. fossa* becomes much problematic in the northern part of the alleged range (Paraguay, Brazil). The populations of what he called *C. sororia* var. *pseudobracteosa*, with relatively broad perigynia, blur the delimitation between *C. sororia* and Wheeler’s ‘true’ *C. fossa*, although we still believe that these are a much closer match to *C. sororia*. Here we adopt a compromise solution and consider as *C. fossa* s.s. only the Argentinian plants from the temperate-cold central provinces. The group would much benefit from a proper biosystematic study to set the limits between the two taxa.

*Selected additional references*: [Wheeler \[\(1996\) description \(perhaps including some \*C. sororia\* variation\), taxonomic notes\]](#).

##### 6. *Carex giovanniana* Jim.-Mejías, *Kew Bull.* 75-24: 3 (2020)

*Holotype*: ARGENTINA. Salta Prov.: Rosario de Lerma Dpt., Campo Quijano, Corralito, 1750–1850 m, 24°58’54” S 65°43’40” W, 3 Feb 15, Rodríguez-Palacios et al. 21GERP15 (SI!, isotypes at MCNS! UPOS! WS!).

*Iconography*: [Figures 2F, 3F](#). See additional figures in [Jiménez-Mejías et al. \(2020\)](#).

*Distribution:* North-western Argentina (Tucumán and Salta, probably also in Jujuy) and southern Bolivia [83 BOL 85 AGW].

*Etymology:* Commemorating Giovanni E. Rodríguez-Palacios, an amateur caricologist born in Zacatecoluca (El Salvador, 1977) and collector of the holotype.

*Notes:* Previously confused with *C. subdivulsa* (Jiménez-Mejías *et al.*, 2016c), *C. sororia* and *C. uruguensis* (see notes under these latter two species). *Carex giovanniana* can be easily distinguished from these species by the characters presented in the identification key. See additional comments in Jiménez-Mejías *et al.* (2020).

*Selected additional references:* Jiménez-Mejías *et al.* [(2020) description, taxonomic notes].

### 7. *Carex pedicularis* Jim.-Mejías & Naczi, *sp. nov.*

*Diagnosis:* This new species is similar to *C. bonariensis*, from which it differs by the broadly ovate to suborbicular utricule body, abruptly contracted into a parallel-sided beak.

*Holotype:* ARGENTINA: Entre Ríos, Pre-Delta National Park edges, La Jaula, meadows in forest edge, with *Parkinsonia* and *Phytolacca dioica*, 47 m, 32° 6' 52.78" S, 60° 36' 35.92" W, 16 Feb 2015, G. Rodríguez-Palacios, S. Donadio & P. Jiménez-Mejías 104GERP15 (SI!; isotypes at UPOS! WS!).

*Paratypes (selected studied material):* ARGENTINA: Corrientes, C.L. Cristóbal *et al.* 1318, 28 Sep 1975 (NY-2861945!); Entre Ríos, T.M. Pedersen 7205, 19 Nov 1964 (NY-2861950!); Tucumán, S. Venturi 10251, 30 Mar 30 (US-02140651!). PARAGUAY: Presidente Hayes, E. Zardini *et al.*, 2650, 25 May 1987 (MO-5787367!). URUGUAY: Florida, Gallinal *et al.* PE-5202, 22 Apr 1943 (NY-02861942!).

*Carex bonariensis* var. *glabrescens* Kurtz ex Kük., Bot. Jahrb. Syst. 27: 512 (1899).

*Lectotype (here designated):* ARGENTINA: Prov. Córdoba, Rio Primero, Kurtz 4817 (CORD 00002081 digital image!).

*Description:* Plant caespitose, rhizomes with short internodes, rarely some internodes slightly elongate. Fertile culms (10)15–50(60) cm, slightly shorter than or equalling the leaves, rarely slightly exceeding them, sharply trigonous, the faces sulcate, the angles smooth for most of its length, antrorsely scabridulous towards the apex, (0.2)0.5–1.0(1.1)

mm wide at the middle of its length; basal sheaths brown to dark brown, early decomposing into fibres. Leaf blades 1.2–2.0(2.5) mm wide, flat, glabrous, margins and nerves antrorsely-scabrid for most of their length; ligule truncate to rounded, protruding into the blade 0.5–1.5 mm, the free portion hyaline to reddish-brown. Inflorescence (0.5)0.8–1.5(2.5) cm long, 6–1(14) mm wide, congested, suborbicular to shortly ovate, rarely elliptical, the spikes aggregated or rarely the lowermost one slightly separated by an internode shorter than it, still overlapping with the spike(s) immediately above; proximal-most bract leaf-like to filiform (2.5)5.0–11.0 cm × 0.5–1.0(1.8) mm, long exceeding the inflorescence, the immediately adjacent bract long-filiform, also surpassing the inflorescence. Spikes three to six, androgynous, with five to 12 spreading utricles, the distal ones the smallest, crowded and almost undistinguishable, the proximal ones larger and more conspicuous, compound spikes absent. Female glumes 2.3–3.0 × 1.4–1.5 mm, shorter than to equalling the utricles, ovate, acute or subulate, almost entirely whitish-hyaline or pale brown-tinted near the midnerve, with one to three nerves at the middle, the grooves between nerves greenish to stramineous; male glumes c. 2.0 × 0.5 mm, elliptic, subulate to mucronate, entirely whitish hyaline, with a narrow inconspicuous greenish or stramineous middle nerve. Utricles 2.5–4.0 × (1.8)2.0–2.5 mm, plano-convex, the body broadly ovate to suborbicular, pale greenish to stramineous, the margins antrorsely-scabridulous for most of their lengths, especially towards apex, abruptly constricted into a 0.5–1.0 mm shallowly bidentate beak with parallel sides, the faces profusely verrucose to almost muricate, nerveless to faintly nerved distally, the base with a three- to six-nerved corky bulge that may reach the middle of the utricule body. Nutlets narrowly biconvex, suborbicular to broadly ovate, yellowish to brownish, 1.5–1.8 × 1.5–1.6 mm, closely enveloped by the utricule, the base constricted to form a substipitate base, the style base shortly conical.

*Iconography:* Figures 2G, 3G. See additional figures in Kükenthal (1909: 151, as *Carex bonariensis*).

*Distribution:* Southern South America [85 AGE AGS AGW CLC? PAR URU].

*Etymology:* From the Latin *pediculus*, louse, meaning 'belonging to the lice', as the tiny rounded utricles with scabrid margins somewhat resemble lice; a parallel construction to the name of *Carex pulicaris* L., which is named after the flea (*pulex*).

*Notes:* *C. pedicularis* was already considered by Wheeler (1996a) as a species distinct from *C. bonariensis*, but he used the name *C. trachycystis* to refer to it, probably because of the congested inflorescences of the type collection of the latter name. However, careful examination of the original material of *C. trachycystis* revealed that these plants are *C. bonariensis* specimens with congested inflorescences, with utricles clearly ovate-oblong, attenuate to the beak, and with a maximum width of c. 1.5 mm. Accordingly, we synonymize *C. trachycystis* with *C. bonariensis*, and publish the new species *C. pedicularis* to accommodate the plants that were called *C. trachycystis* by Wheeler (1996a).

This species has been cited from Central Chile [CLC, Bío-Bío Province (Rodríguez *et al.*, 2018; Zuloaga *et al.*, 2020+); both as *C. trachycystis*] and from Patagonia [AGS, Río Negro Province (Barros, 1935), as *C. bonariensis* var. *trachycystis*; (Zuloaga *et al.*, 2020+) as *C. trachycystis*] but we have not studied material from these areas. Given the problematic taxonomy of *C. trachycystis* these records need to be confirmed.

*Selected additional references:* Wheeler [(1996a) as *Carex trachycystis*, key].

8. *Carex rupicola* (Pedersen) G.A. Wheeler, *Hickenia* 2: 180 (1996)

*Carex bonariensis* var. *rupicola* Pedersen, Colecc. Ci. Inst. Nac. Tecnol. Agropecu 4(1): 332 (1969) [basonym].

*Holotype:* ARGENTINA: Buenos Aires, Partido Tornquist, Sierra de la Ventana, La Pileta, 5 Nov 1941, Cabrera 7353 (LP digital image!).

*Iconography:* Figures 1D, 2H, 3H. See additional figures in Wheeler (1996a: 180).

*Distribution:* Endemic from the low elevation dry ranges of Buenos Aires Province and Uruguay [85 AGE URU].

*Etymology:* From the Latin *rupis*, rock, and *-cola*, cultivation, referring to the rocky habitats where this species grows.

*Selected additional references:* Wheeler [(1996a) taxonomic notes, key].

*Notes:* A remarkable species among all the representatives of *Carex* subgenus *Vignea*, found in dry rocky soils growing with cacti, a quite unusual habitat for a *Carex* species. As a notable vegetative character, sterile shoots are strongly thickened at the base forming a corm.

9. *Carex sororia* Kunth, *Enum. Pl.* 2: 379 (1837)

*Holotype:* URUGUAY: Montevideo, Sellow 564 (photograph of B material [destroyed in World War II] FI photograph!, MO photograph!).

*Neotype (here designated):* URUGUAY: Florida, Cerro Colorado, Estancia San Pedro, Gallinal *et al.* B-758, Dec 1936 (NY-00636803!).

*Carex involucrata* var. *submuricata* C.B. Clarke ex Kük., Bot. Jahrb. Syst. 27: 510 (1899).

*Lectotype (here designated):* ARGENTINA: Concepción del Uruguay, Sep 1877, Lorentz 1119 (K-000584726 digital image!; isolectotypes: K-000584725 digital image!, P-00314641 digital image!).

*Carex involucrata* var. *pseudobracteosa* Kük., Bot. Jahrb. Syst. 25: 510 (1899).

*Carex sororia* var. *pseudobracteosa* (Kük.) Kük. in H.G.A. Engler (ed.), Pflanzenr., IV, 20(38): 150 (1909).

*Type:* ARGENTINA: Entreríos [Entre Ríos], Concepción del Uruguay, Lorentz 457. Apparently deposited at B, destroyed.

*Carex apiahyensis* Palla, Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 79(1): 199 (1908).

*Holotype:* BRAZIL: Apiahy [São Paulo], Herbarium Palla 107 (GZU-000006134 digital image!).

*Carex sororia* f. *paupera* Osten, Anales Mus. Hist. Nat. Montevideo, ser. 2, 3: 236 (1931).

*Type:* URUGUAY: Canelones, Independencia, campos de piedra, 4-1910, Osten 5318. (not seen, presumably at MVM).

*Iconography:* Figures 1E, 2I, 3I. See additional figures in Boott (1858–1867: tab. 117), Barros (1947: tab. 178) and Pedersen (1968: 325).

*Distribution:* Southern South America [84 BZL BZS 85 AGE AGS? AGW? PAR URU].

*Etymology:* From the Latin *sororius*, ‘from the sister’, perhaps meaning morphological resemblance to other *Carex* spp.

*Notes:* We could not study the material that support the citation of *C. sororia* from Ecuador (Jørgensen & León-Yáñez, 1999), which we consider highly doubtful. The only other collection of *Carex* subgenus *Vignea* we studied from the same locality (Azuay, Sevilla de Oro) belongs to *Carex bonplandii* Kunth (Camp 4722, NY!). Accordingly, we remove *C. sororia* among the list of Ecuadorian plants. We could not confirm

either the presence of the taxon in southern (Río Negro) or in north-western (Catamarca, Tucumán) Argentina (Barros, 1935, 1947; Zuloaga *et al.*, 2020). However, we have confirmed that materials of *C. fossa* and *C. giovanniana* from these areas have been cited under the name of *C. sororia*. Accordingly, we consider the presence of *C. sororia* in AGS and AGW also as doubtful and in need of confirmation.

*Selected additional references:* Wheeler [(2002) taxonomic notes], Silveira & Longhi-Wagner [(2012) description].

10. *Carex subdivulsa* (Kük.) G.A. Wheeler; *Darwiniana* 40: 203 (2002)

*Carex involucrata* var. *subdivulsa* Kük., Bot. Jahrb. Syst. 27: 511 (1899) [basonym].

*Carex sororia* f. *subdivulsa* (Kük.) Kük. in H.G.A. Engler (ed.), Pflanzenr., IV, 20(38): 150 (1909). *Neotype* (designated by Wheeler, 2009): ARGENTINA: La Rioja, Dpto. Famatina, Sierra Famatina, 28° 20'S, 67° 55'W, La Hoyada, c. 2500 m.s.m., 24–31 Jan 1908, Kurtz 15000 (MIN; isoneotypes, CORD, SI!).

*Iconography:* Figures 1F, 2J, 3J. See additional figures in Wheeler (2009: 331, fig. 297).

*Distribution:* North-western Argentina, local in the provinces of La Rioja and Tucumán [85 AGW].

*Etymology:* From the Latin *sub-*, close to, 'close to [*Carex*] *divulsa*'.

*Notes:* Previous reports from Salta and Jujuy (Jiménez-Mejías *et al.*, 2016c) belong to *C. giovanniana*.

*Selected additional references:* Wheeler [(2002) description, taxonomic notes; (2009) description].

11. *Carex uruguensis* Boeckeler, Bot. Jahrb. Syst. 7: 277 (1886)

*Carex sororia* subsp. *uruguensis* (Boeckeler) Luceño & M. Alves, Anales Jard. Bot. Madrid 57: 173 (1999).

*Holotype* (destroyed): ARGENTINA: Entre Ríos, Paso de Duranguillo, 24 Jan 1878, Lorentz 1564 (B, photograph at F-0BN013409!).

*Lectotype* (here designated): ARGENTINA: Entre Ríos, Paso de Duranguillo, 24 Jan 1878, Lorentz 1564 (CORD-00002111 digital image!). Remaining syntypes: ARGENTINA: Entre Ríos, Concepción del Uruguay, Quinta de Sagastume, Oct 1885, Lorentz 1685, CORD-00002110 digital image! photograph at F (F-0BN013409!) and US.

*Carex involucrata* var. *angustata* Kük., Bot. Jahrb. Syst. 27: 511 (1899).

*Carex uruguensis* var. *angustata* (Kük.) Kük. in H.G.A. Engler (ed.), Pflanzenr., IV, 20(38): 149 (1909).

*Type:* ARGENTINA: Buenos Aires, in silva prope San Isidro (*Bettfreund n. 2b, 70, 71, Bettfreund et Isolina Köster n. 276, 59*), Bañados de Flores (*Spegazzini*) (not seen).

*Carex pseudoechinata* Boeckeler, Beitr. Cyper. 2: 34 (1890).

*Carex uruguensis* var. *pseudoechinata* (Boeckeler) Kük., Bot. Jahrb. Syst. 27: 512 (1899).

*Type:* ARGENTINA: Corrientes, *Niederlein n. 2118* (photograph at F F-0bn013410! and US!, original apparently destroyed).

*Iconography:* Figures 2K, 3K. See additional figures in Barros (1947: tab. 178) and Silveira & Longhi-Wagner (2012: 410, utricle with the corky base underdeveloped).

*Distribution:* Northern Argentina to southern Brazil, unknown from Paraguay but potentially present [84 BZS 85 AGE AGW? PAR? URU].

*Etymology:* From Uruguay.

*Notes:* *C. uruguensis* is a poorly understood taxon. Herbarium vouchers have been often misidentified as *C. sororia*. In addition, the name has been also used to refer to the superficially similar *C. giovanniana*, from which it clearly differs by the utricle characters indicated in the key. The different varieties described and accepted by different authors seem to correspond with variation in the inflorescence configuration (see *Discussion*) and utricle size, and probably have little taxonomic value (if any).

*Carex uruguensis* seems to be confined to the lowlands of the Paraná and Uruguay river basins, reaching a few coastal stations in Brazil at its northernmost limit (Silveira & Longhi-Wagner, 2012; Jiménez-Mejías & Silva, 2020). The reports from Bolivia (Jørgensen *et al.*, 2014) are based on specimens of *C. giovanniana* (Jiménez-Mejías *et al.*, 2020). It has been also cited from AGW (Tucumán; Barros, 1935, 1947; Zuloaga *et al.*, 2020) but these records are potentially misidentifications too and need confirmation. A thorough revision of herbarium material would be desirable to better define the geographical limits of the species.

*Selected additional references:* Barros [(1935) description], Silveira & Longhi-Wagner [(2012)

description (apparently limited to few specimens, thus recorded variation probably not representative of the species)].

#### CAREX GAYANA GROUP

The phylogenetic placement of *C. gayana* in a morphologically diverse clade prevents us proposing a formal sectional placement until more data is available. Because of the phylogenetic analyses and morphological affinities, it seems clear to us that the South American *C. gayana* and the Nearctic *C. simulata* are closely related (perhaps even conspecific) and form what we call here “*Carex gayana* group”.

12. *Carex gayana* *É.Desv. in C.Gay, Fl. Chil.* 6: 205 (1854)

*Lectotype (here designated):* Gay (1854, tab. 73, fig. 3).

*Epitype (here designated):* CHILE. Prov. Coquimbo, Cordillera de los Patos, 1837, *C. Gay* 300 (SGO-000000845 digital image!).

*Carex schedonautos* Steud., *Syn. Pl. Glumac.* 2: 189 (1855).

*Carex gayana* var. *schedonautos* (Steud.) Kük. in H.G.A.Engler (ed.), *Pflanzenr.*, IV, 20(38): 123 (1909).

*Holotype:* CHILE. Oazy Harbour, détroit de Magellan, *W. Lechler* 1228 (P-00305113 digital image!; isotypes: K-000584714 digital image!, K-000584715 digital image!, K-000584716 digital image!, MICH-1109200 digital image!, P-00305112 digital image!, P-00305114 digital image!, S-07-12256 digital image!).

*Carex diclina* Phil., *Linnaea* 33: 271 (1865).

*Lectotype (here designated):* CHILE. Cord. de Santiago, Las Arañas, Nov. 1861, *Philippi* s.n. (SGO-000000838, digital image!; isolectotype: SGO-000000837 digital image!).

*Carex nitens* Phil. *Anales Univ. Chile* 43: 557 (1873).

*Holotype:* CHILE. Valle del Yeso, *Philippi* s.n. (SGO-000000868 digital image!).

*Carex taurina* Phil., *Anales Univ. Chile* 93: 489 (1896).

*Carex gayana* var. *rufa* Kük., *Bot. Jahrb. Syst.* 27: 501 (1899).

*Carex gayana* var. *taurina* (Phil.) Kük. in H.G.A.Engler (ed.), *Pflanzenr.*, IV, 20(38): 123 (1909).

*Carex gayana* var. *taurina* (Phil.) Kük. in H.G.A.Engler (ed.), *Pflanzenr.*, IV, 20(38): 123 (1909).

*Lectotype (here designated):* CHILE. In montibus Doña Ana l. d. Baños del Toro invenit Febr. 1883, *F. Philippi* s.n. (SGO-000000889 digital image!; isolectotype: SGO-000000888 digital image!).

*Carex gayana* var. *densa* Kük., *Bot. Jahrb. Syst.* 27: 501 (1899).

*Lectotype (here designated):* CHILE. In Andibus prov. Coquimbo, *Volckmann* s.n. (SGO-000000846 digital image!).

*Iconography:* Figures 1G, 2L, 3L. See additional figures in Gay (1854, tab. 73, fig. 3), Boott (1858–1867: tab. 411), and Barros (1935:181; 1947: tab. 176, as *Carex gayana* var. *taurina*), Wheeler (2009: 327, fig. 29).

*Distribution:* Widespread from Tierra del Fuego to southern Peru [83 BOL PER 85 AGE AGS AGW CLC CLN CLS].

*Etymology:* Commemorating Claude Gay, 1800–1873, a French botanist who studied the Chilean flora.

*Notes:* This species shows great morphological variability regarding size, inflorescence configuration and glume colour. This has led to the description of different specific and infraspecific names. The most striking extreme is the existence of populations where the inflorescences are entirely pistillate or staminate (Fig. 2L1, L2), a feature that is also shared with the closely related *C. simulata* (see *Discussion*). The available genetic studies point to that genetic partitions detected within *C. gayana* that match geographic distribution rather than morphological variation (Pfeiffer *et al.*, 2018).

Underdeveloped stages of the utricle might be taken as elliptical, as the immature utricle seems cuneate towards the basal stipe. These plants are usually misclassified as species in the *C. nebularum* or *C. praegracilis* groups.

*Selected additional references:* Wheeler [(2009) description].

#### CAREX NEBULARUM GROUP

A group vaguely defined by its more or less tussock-forming habit, congested inflorescences, hyaline to pale brown glumes and ascending utricles, usually shorter than glumes. This morphology also agrees with the affinity of the Neotropical species of the group with the closely related North American *C. nervina* L.H.Bailey. This assemblage of species may well deserve to be treated as a section on its own.

13. *Carex firmicaulis* Kalela, *Ann. Acad. Sci. Fenn., Ser. A* 54(5): 53 (1940)

*Lectotype (designated by Jiménez-Mejías et al., 2016c):* ARGENTINA. Neuquén, Rahue, 21-XII-1937,



*Kalela* 1539 (H-1066601, digital image!; isolectotype: H-1066600, digital image!).

*Carex pycnostachya* var. *major* Kük., Bot. Jahrb. Syst. 27: 503 (1899).

*Carex nebularum* f. *major* (Kük.) Kük. in H.G.A.Engler (ed.), Pflanzenr., IV, 20(38): 118 (1909).

*Lectotype* (here designated): ARGENTINA: Córdoba, en las pendientes del Cerro Champaquí, mas arriba del Rio del Catre, Sierra de Achala, 30 Jan 1877, *Hieronymus* 789 (CORD-00002104 digital image!; isotype CORD-00002105 digital image!). Remaining syntypes: ARGENTINA: Córdoba, Sierra de Achala, Cerro Champaquí, c. 2600 msm, 18 Dec 1885, *Kurtz* 3024a (CORD-00002106 digital image!, CORD-00002107 digital image!).

*Carex macrorrhiza* var. *simplex* Kük. in H.G.A.Engler (ed.), Pflanzenr., IV, 20(38): 127 (1909).

*Lectotype* (designated by [Barros, 1947](#)): ARGENTINA: Cordillera de Mendoza, El Planchón, *Kurtz* 7635. Second-step lectotypification (here performed): Mendoza, Río Salado Superior, Valle Hermoso, 5–6 Feb 1893, *Kurtz* 7635 (CORD-00002096 digital image!; isolectotype: CORD-00002097 digital image!).

*Carex andicola* G.A.Wheeler, *Hickenia* 2: 196 (1996). *Holotype*: ARGENTINA: Neuquén, Los Lagos, Estancia Fortín Chacabuco, Mallín Frison, 20 Jan 1951, *Boelcke* 4542 (BAA-00004831 digital image!).

*Paratypes*: ARGENTINA: Neuquén, Minas, a 21 km de Las Ovejas, camino a las lagunas Epu-Lauquén, arroyo Las Bandurrias, 1250 m, 14 Jan 1964, *Boelcke et al.*, 10796 (SI-000211!). Córdoba, Calamuchita, Sierra Grande, Falda este del Cerro Champaquí, 15 Jan 1952, *Hunziker* 9632 (CORD-00002077 digital image!).

*Iconography*: [Figures 1H, 2M, 3M](#). See additional figures in [Barros \(1935\)](#): 193, as *C. nebularum* f. *major*; 1947: tab. 175, as *C. nebularum* s.s.).

*Distribution*: Argentinian Patagonia and Tierra del Fuego, north to Mendoza Province and central Chile, disjunct in Sierra de Achala (Córdoba Province), apparently absent from Chilean Patagonia [85 AGE AGS AGW CLC CLS].

*Etymology*: From the Latin *firmus*, firm, strong, and *caulis*, stem, ‘of the firm stem’, possibly referring to the erect, stiff flowering stems.

*Selected additional references*: [Wheeler \[\(1996b\)\]](#) description, as *Carex andicola*.

14. *Carex hypoleucos* *É.Desv.* in *C.Gay, Fl. Chil.* 6: 206 (1853)

*Lectotype* (here designated): CHILE: Chili. *C. Gay* s.n. (P-032657 digital image!).

= *Carex kurtziana* Kük., Bot. Jahrb. Syst. 27: 503 (1899).

*Carex nebularum* var. *kurtziana* (Kük.) Kük. in H.G.A.Engler (ed.), Pflanzenr., IV, 20(38): 118 (1909).

*Lectotype* (here designated): ARGENTINA: Prov. de Mendoza, Arroyo negro, pr. “Laguna ocho”, Cordillera de Malal-hué [Malargüe], 18 Jan 1888, *Kurtz* 5746 (CORD-00002095 digital image!). Remaining syntypes: ARGENTINA: Prov. de Mendoza, inter Rio grande et Arroyo Calqueque, Cordillera de Malal-hué [Malargüe], 30 Jan 1888, *Kurtz* 5937 (CORD-0000293 digital image! CORD-00002094 digital image!).

*Iconography*: [Figures 2N, 3N](#). See additional figures in [Gay \(1854\)](#): tab. 73, fig. 4).

*Distribution*: Argentinian Patagonia, north to Mendoza, also in adjacent central-southern Chile [85 AGS CLC CLS?].

*Etymology*: From the Greek *hypo-*, under, beneath, below, and *leukos*, light-coloured, white, ‘whitish beneath’, probably referring to the pale glumes with broad hyaline margins.

*Notes*: Cited from southern Chile (CLS, Magallanes Province) by [Rodríguez et al. \(2018\)](#). Given the problematic taxonomy of the group, the presence of *C. hypoleucos* at such a disjunct location needs to be confirmed.

*Additional literature*: [Wheeler \[\(1996b\)\]](#), as *Carex kurtziana*, key].

15. *Carex nebularum* *Phil.*, *Anales Univ. Chile* 93: 492 (1896)

*Lectotype* (here designated): CHILE: Valle de las Nieblas, Jan 1877, *Philippi* 502 (SGO-000000867 digital image!; isolectotype: SGO-000000866 digital image!).

*Iconography*: [Figures 2O, 3O](#).

*Distribution*: Apparently endemic from northern Chilean Patagonia north to central Chile. Previous reports from Argentina seem to correspond to confusion with *C. firmicaulis* (Wheeler, 1996) or *C. hypoleucos* [85 CLS CLC].

*Etymology*: From the Latin *nebula*, mist, fog, in reference to the locus classicus, ‘Valle de las Nieblas’, that translates to English as ‘Valley of the Mists’.

*Notes*: A rarely collected and poorly understood species. Its name has been widely misused to refer to *C. firmicaulis* on the Argentinean side of the Andes (Wheeler, 1996b). The taxon in its most strict sense is probably a Chilean endemic.

Cited from southern Chile (CLS, Aisén Province) by Rodríguez *et al.* (2018). Given the problematic taxonomy of the group, it would be desirable to confirm the presence of *C. nebularium* in that region.

*Selected additional references*: Wheeler [(1996b) key].

16. *Carex pleioneura* G.A. Wheeler, *Aliso* 11: 533 (1987)

*Holotype*: CHILE: Coquimbo, Dpto. Illapel, Hacienda Cuncumén, cajón de los Pelambres, 3000 m, suelo pantanoso, 9–12 Jan 1932, *Looser 2141* (GH-00101841 digital image!). *Paratypes*: ARGENTINA: San Juan, Dpto. Calingasta, Pachón, valle del Río Pachón, 3300 m., Feb 1982, *Maqueda 10085* (SI-000227 digital image!, SI-000228 digital image!, SI-000229 digital image!). CHILE: Aconcagua, Dpto. Petorca, 5 hours by horse southeast of Patagua Mine, ca. 18 km east of La Ligua, 1900 m, 30 Dec 1938, *Morrison 17038* (SI-030193 digital image!).

*Carex pycnostachya* Desv. in C. Gay, Fl. Chil. 6: 204 (1854), nom. illeg., non *Carex pycnostachya* Kar. & Kir. (1842).

*Lectotype (here designated)*: CHILE: P. de Coquimbo, Cordillera de los Patos, Jan 1838, *Gay 655* (P-00312850 digital image!).

*Iconography*: Figures 2P, 3P. See additional figures in Wheeler (2009: 331, fig. 296).

*Distribution*: High Andes of central Chile, with a known single location in Argentina (San Juan Province) [85 AGW CLC].

*Etymology*: From the Greek *pleion*, many, and *neuro*, nerves, ‘many nerved’ referring to the nerved utricles of this species.

*Notes*: The name *Carex pycnostachya* Desv. has been often listed as a synonym of *C. nebularium*. However, after the examination of the digital image of the selected lectotype specimen, spike and utricle dimensions point to *C. pleioneura* as a much better match. This also agrees with the geographical location of the types of

the two names. The illustration associated with the protologue shows a nerveless utricle. However, the protologue also specifies that the utricles are nerveless but before ripening (“Utrículo sin nerviosidades antes de la madurez”). We confirm that the selected lectotype specimen bears unripe utricles, but even so, some nerves are observable in two of the utricles in the envelope. This agrees with our identification of the specimen as *C. pleioneura*.

*Selected additional references*: Wheeler [(1987) description, (1996b) key, (2009) description].

17. *Carex reichei* Kük., *Bot. Jahrb. Syst.* 27: 504 (1899)

*Lectotype (designated by Wheeler, 1988)*: CHILE: Cordillera de Curicó, 2500 msm, *Reiche 514* (SGO-00000883 digital image!).

*Carex aueri* Kalela, *Ann. Acad. Sci. Fenn.*, Ser. A 54(5): 60 (1940).

*Lectotype (designated by Wheeler, 1988)*: CHILE: Territ. Magallanes, Carpa Manzana – Seno Skyring, Etel. Laguna Blanca, 9 Feb 1928, *Kalela 2221* (H-1066609 digital image!; isolectotypes: H-1066608 digital image!, S-07-12247 digital image!).

*Iconography*: Figures 2Q, 3Q. See additional figures in Barros (1949: 165, as *Carex aueri*; 1969: 76, fig. 66, as *C. aueri*).

*Distribution*: Patagonia, north to central Chile [85 AGS AGW CLC CLS].

*Etymology*: Commemorating Karl (Carlos) F. Reiche, 1860–1939, a German botanist settled in Santiago (Chile), collector of the type specimens of this species.

*Notes*: Dwarf forms of *C. gayana* or *C. subfuegiana* have been sometimes classified as *C. reichei*.

*Selected additional references*: Barros [(1949) description, as *C. aueri*], Wheeler [(1988) taxonomic notes, description].

#### CAREX PRAEGRACILIS GROUP

A vaguely defined group of plants with creeping rhizomes, more or less congested inflorescences, hyaline to pale brown glumes and utricles ascending, usually shorter than glumes. The Neotropical species are phylogenetically and also morphologically allied to North American species usually placed in section *Divisae* (as *C. praegracilis* and *C. pansa*). Other species

in the same clade display disparate morphologies, which prevent us from further speculating about other affinities and from proposing a formal sectional treatment.

*Carex ecuadorica*, *C. macrorrhiza* and *C. subfuegiana* form a taxonomically complex group of morphologically similar plants. The distinction of the three taxa in austral South America has been quite problematic. The first citation of *C. ecuadorica* in Argentina (Wheeler, 1996b) was later reported to be the then undescribed *C. subfuegiana* (Wheeler, 2006), which is now reported in Argentina from Patagonia to San Juan Province. Wheeler (2006) removed *C. ecuadorica* entirely from the South Cone and considered it to be an exclusively northern Andean species. All the remaining records of *C. ecuadorica*-like plants from northern Argentina, Bolivia and Chile were ascribed by him to *C. macrorrhiza*. However, later Jiménez-Mejías et al. (2016c) cited *C. ecuadorica* from northern Argentina (Salta and Jujuy) after comparison with additional material.

We agree that taxonomic limits among the three species are problematic and still need re-evaluation. As a compromise solution, we have decided to rely for our taxonomic treatment on how the studied specimens fit to the observable morphological characters (inflorescence and utricle) displayed by the respective type specimens. However, we admit that the taxonomic picture may be more complex. We consider that all the studied Bolivian specimens match *C. ecuadorica* better than *C. macrorrhiza*. We also confirm that the report of *C. ecuadorica* from northern Argentina by Jiménez-Mejías et al. (2016c) is based on morphologically unequivocal specimens. There are problematic populations at least in northern Chile. The northern Chilean plants are somewhat transitional between *C. ecuadorica* and *C. macrorrhiza* (e.g. CHILE: Tarapacá, Mamiña, 22 Oct 1960, Montero 6335, CONC-68517!). Further studies would be desirable to clarify the situation of the three taxa in Chile, Argentina and Bolivia.

18. *Carex ecuadorica* Kük., *Beibl. Bot. Jahrb. Syst.* 78: 7 (1904)

*Lectotype* (designated by Jiménez-Mejías et al., 2016c): ECUADOR: In Andibus Ecuadoriensibus, Sep 1857, Spruce 5908 (C-10010040 digital image!; isolectotypes: E-00502223 digital image!, K-000584631 digital image!, P-00304724 digital image!, P-00304725 digital image!, S-R-916, digital image!). Remaining syntypes: ECUADOR: In prov. Riobamba ad basim occid. mont. Altar, Sep 1891, Sodiro 199/60 (F-0BN000148 F-0BN013392 F-0045462F, photo!, P-00304723 digital image!). ECUADOR: Auf noffum Lasabodan um Lataeum ga und Meulalo 2800–3000 m, Lehmann 7689 (K-000584636 digital image!, US-2140966!).

*Iconography*: Figures 2R, 3R.

*Distribution*: North-western Argentina to Ecuador [83 BOL ECU PER 85 AGW].

*Etymology*: Belonging to Ecuador.

*Notes*: The lectotype collection Spruce 5908 is apparently mixed, at least one specimen (GH-00027529 digital image!) belongs to *Carex phalaroides* Kunth.

Most materials, if not all, from the northern Andes reported as *C. praegracilis* (e.g. Macbride 1936) belong to *C. ecuadorica*.

19. *Carex macrorrhiza* Boeckeler, *Beitr. Cyper. 1: 43* (1888)

*Lectotype* (designated by Wheeler, 2006): ARGENTINA: La Rioja, Sierra Famatina, en las cercanías de la quebrada, 2 a 4 leguas arriba del Vallecito, 21 Jan 1878, Hieronymus & Niederlein 600 (S-07-12262 digital image!; isolectotype: SI digital image!, photograph at F!).

*Carex curvifolia* Boeckeler, *Beitr. Cyper. 1: 41* (1888). *Type*: ARGENTINA. Sierra Tamative [Famatina], prov. de la Rioja, Hieronymus et Niederlein (presumably at B, destroyed).

*Iconography*: Figures 2S, 3S. See additional figures in Barros (1947: tab. 173) and Wheeler (2009: 332, fig. 298).

*Distribution*: Southern Andes, from Mendoza Province in Argentina, north to northern Argentina, disjunct in Sierra de Achala (Córdoba Province) and local in northern Chile (although see comments under *C. ecuadorica*), doubtful in Bolivia [83 BOL? 85 AGE AGW CLN].

*Etymology*: From the Greek *makros*, long, large, and *rhiza*, root, 'large rooted', referring to the thick elongated rhizomes of this species.

*Notes*: Kükenthal (1909) presumably studied at B the original material of the names *C. macrorrhiza* and *C. curvifolia* (now destroyed), synonymizing the latter to the former. We follow Kükenthal (1909) and Wheeler (2006) and keep *C. curvifolia* as synonym of *C. macrorrhiza*.

The plant pictured in Barros (1935: 196) does not match the characters of *C. macrorrhiza* regarding the utricle, although the plant that is represented for the whole habit strongly resembles the species. The plate might represent a large specimen of *C. ecuadorica* or a mix of different taxa.

The records from Uruguay (Zuloaga *et al.*, 2020; Govaerts *et al.*, 2020+) seem to be at least partly based on specimens of *C. divisa* (e.g. URUGUAY: Soriano, Herter 94293, US-02141036!). Wheeler considered such records doubtful (Wheeler, 2006). The presence of *C. macrorrhiza*, an Andean species, in Uruguay also seems improbable to us, so we do not include the country under the distribution of the species. All the studied records from Bolivia are here identified as *C. ecuadorica*, thus the presence of specimens morphologically assignable to *C. macrorrhiza* in Bolivia needs confirmation.

*Selected additional references:* Wheeler [(2006) taxonomy, (2009) description].

20. *Carex subfuegiana* G.A.Wheeler, *Hickenia* 3: 260 (2006)

*Holotype:* ARGENTINA: Chubut, Dpto. Río Senguerr, Río Mayo, Estancia Zootécnica, 30 Jan 1954, Grondona 3567 (MIN; isotype: SI-006971 digital image!).

*Iconography:* Figures 2T, 3T. See additional figures in Wheeler (2009: 333, fig. 299).

*Distribution:* Argentina, from Patagonia north to San Juan Province through the Andes [85 AGS AGW].

*Etymology:* From the Latin *sub-*, close to, referring to the fact that most populations of the species occur in the Patagonia immediately north of Tierra del Fuego (Wheeler 2006).

*Notes:* Previously confused with *C. macrorrhiza* and *C. ecuadorica* (Wheeler, 2006), species to which *C. subfuegiana* is similar.

*Selected additional references:* Wheeler [(2006) description, (2009) description].

THE MULTIFLORAE-VULPINAEE ALLIANCE

Under this name we conceive a clade of subgenus *Vignea* that groups American species previously placed in sections *Multiflorae* and *Vulpinae*, but also in section *Phaestoglochin*. Although relatively morphologically diverse, the set of species in this clade share a few characters, like the rotund utricle bodies with margins scabrid towards the apex. Other characters traditionally considered for the different individual sections, like wrinkled sheath fronts or elongated inflorescence (Ball & Reznicek, 2002) are not apomorphic to the entire group. The two South American species that we place here are

quite disparate in morphology: *C. brongniartii*, a large plant from low and medium elevations and *C. ownbeyi*, a diminutive plant from High Andean environments.

21. *Carex brongniartii* Kunth, *Enum. Pl.* 2: 380 (1837)

*Holotype:* CHILE. J. S. C. Dumort d'Urville s.n. (P-00303580 digital image!; isotype: P-00303579 digital image!).

*Carex hypoxanthos* Steud., *Syn. Pl. Glumac.* 2: 193 (1855).

*Holotype:* CHILE. In pascuis prope coloniam Arique in prov. Valdivia, Lechler 738 (P-032661 digital image!; isotypes: GOET-002800 digital image!, K-000584723 digital image!).

*Iconography:* Figures 1I, 2U, 3U. See additional figures in Gay (1854: tab. 73, fig. 10), Barros (1935: 198; 1947: tab. 177), and Silveira & Longhi-Wagner (2010; 2012: 383).

*Distribution:* Central Chile and northern Argentina, north to south-eastern Brazil (Rio Grande do Sul) [84 BZS 85 AGE AGW CLC URU].

*Etymology:* Commemorating Adolphe T. Brongniart, 1801–1876, a leading French plant taxonomist of the 19<sup>th</sup> century.

*Notes:* Originally cited by Brongniart (1833) as *Carex muhlenbergii* Willd. The taxon was soon recognized as an independent species.

*Selected additional references:* Pedersen [(1968) description], Silveira & Longhi-Wagner [(2010) ecology, (2012) description].

22. *Carex ownbeyi* G.A.Wheeler, *Darwiniana* 40: 200 (2002)

*Holotype:* BOLIVIA: Cochabamba, Prov. Quillacollo, camino Sipe Sipe-Lipichi, 2800 m.s.m., 9 Apr 1990, Hensen 731 (MIN; isotype: LPB digital image!).

*Iconography:* Figures 1J, 2V, 3V. See additional figures in Wheeler (2002: 202).

*Distribution:* Sparsely distributed across the Tropical and Subtropical Andes, from Tucumán to Colombia (Wheeler, 2002; Jiménez-Mejías *et al.*, 2016c, 2018, 2020). Probably much under-collected [83 CLM ECU? 84 BOL PER 85 AGW].

*Etymology:* Commemorating Gerald B. Ownbey, 1916–2010, Professor of botany at the University of Minnesota, one of the mentors of Gerald A. Wheeler.

*Notes:* Not recorded from Ecuador, but its presence in the Andean part of the country seems probable.

*Selected additional references:* Wheeler [(2002) description].

CAREX SECTION *DIVISAE* CHRIST EX LEMCKE, BEITR.  
CAREX 96. 1892

Here considered in its narrowest possible sense, as the type species is the Eurasian *C. divisa*.

23. *Carex divisa* Huds., *Fl. Angl.*: 348 (1762)

*Lectotype* (designated by Molina *et al.*, 2006): Herb. Sloane 127: 47, second specimen from right, *Sherard s.n.* (BM-SL!). *Epitype* (designated by Molina *et al.*, 2006): UNITED KINGDOM. Isle of Sheppey, *Goodenough s.n.* (K-000960405, digital image!).

*Iconography:* Figures 1K, 2W, 3W. See additional figures in Ball & Reznicek (2002: 203), Jermy *et al.* (2007: 255).

*Distribution:* Native from Eurasia and North Africa, apparently introduced in the Río de la Plata Region (Buenos Aires Province in Argentina and Uruguay) and central Chile [85 age clc uru] (Jiménez-Mejías *et al.*, 2018; Calvo & Jiménez-Mejías, 2020).

*Etymology:* From the Latin *divisus*, divided, probably in reference to the head-like inflorescences, that are often lobed.

*Notes:* This taxon has been previously cited from South America as *Carex marcida* Boott (= *C. praegracilis* Boott) (see Jiménez-Mejías *et al.*, 2018). The sparse material from Argentina, Chile and Uruguay that we have examined matched the characters reported to distinguish *C. divisa* from *C. praegracilis* (Ball & Reznicek, 2002). *Carex divisa* has become naturalized in other parts of the world (Ball & Reznicek, 2002; Govaerts *et al.*, 2020+), thus the South American populations could also well be the result of human introduction.

*Selected additional references:* Ball & Reznicek (2002), Jermy *et al.* (2007), Luceño *et al.* (2008) (descriptions).

CAREX SECTION *PHAESTOGLOCHIN* DUMORT., FL.  
BELG. 146. 1827

Here considered in its narrowest sense as delimited in Molina (2008) and Roalson *et al. in press*. It is an Old World group mainly diversified in the western Palaearctic. It must be expanded from its traditional concept to accommodate at least the widespread Eurasian *Carex otrubae* Podp. and *Carex vulpina* L., the Macaronesian *Carex canariensis* Kük, the South African *Carex glomerata* Thunb. and the Himalayan *Carex wallichiana* Spreng. The only species present in South America (*C. divulsa*, presumably introduced) is unequivocally placed in that group.

24. *Carex divulsa* Stokes in W. Withering, *Bot. Arr. Brit. Pl. ed. 2*, 2: 1035 (1787)

*Lectotype* (designated by Molina *et al.*, 2008): ‘*Carex nemorosa*, fibrosa radice, caule exquisite triangulari, spica longa divulsa seu interrupta, capitulis solitariis praeterquam ultimo’ in Micheli, *Nov. Pl. Gen.*: t. 33, f. 10. 1729. *Epitype* (designated by Molina *et al.*, 2008): ‘Gram. Cyp. spicatum minus spicâ longâ/divulsâ seu interrupta Ray 1279. 2 Petiver’ (No. 17274, FI-M).

*Iconography:* Figures 2X, 3X. See additional figures in Barros (1935: 208; 1947: tab. 182), Pedersen (1968: 331) and Molina *et al.* (2008: 396).

*Distribution:* Native to western Eurasia and North Africa, apparently introduced in north-eastern Argentina (Buenos Aires and Entre Ríos Provinces) [85 age].

*Etymology:* From the Latin *divulsus*, parted, in reference to the elongated inflorescences, with long internodes between the lower spikes.

*Notes:* This species has been reported a long time ago as an introduced species in Argentina (Barros, 1935). The Argentinian plants are a fairly good fit for the narrowest concept of *C. divulsa* as presented in Molina *et al.* (2008). Thus the South American populations fall within the largest portion of the variation of the species. In any case, further genetic studies would be desirable to confirm the status of the Río de la Plata plants.

*Selected additional references:* Ball & Reznicek (2002), Jermy *et al.* (2007), Luceño *et al.* (2008) and Molina *et al.* (2008) (descriptions).

## CONCLUSIONS

The different groups of androgynous species of *Carex* subgenus *Vignea* from South America show a predominant pattern of *in situ* diversification, with all the native species being endemic to the continent. Ancestors are inferred to have North American provenance. Patagonia and the High Andes of Chile and Argentina together account for most of the diversity. Another centre of diversification are the plains and hills between north-eastern Argentina and southern Brazil, where the diversity of section *Bracteosae* is concentrated. The tropical central and northern Andes account for little diversity. This is in line with the markedly cold-temperate character of species of subgenus *Vignea* (see subgenus distribution in Martín-Bravo *et al.*, 2019). Most species are relatively widespread over large regions, with the exception of the relatively narrowly distributed *Carex bracteosa*, *C. giovanniana*, *C. nebularum*, *C. pleioneura*, *C. rupicola* and *C. subdivulsa*. Only the presence of two species (*C. divisa* and *C. divulsa*) may be the result of recent introductions.

## ACKNOWLEDGEMENTS

The authors would like to thank curators and staff of the herbaria A, B, BAA, CONC, E, GZU, K, LP, LPB, LPS, MA, MCNS, MICH, MO, NY, QCNE, SI, UPOS, UPS, US and WS for assistance when visiting their collections, sending or receiving material on loan, searching for critical specimens and providing high resolution images when found, and/or granting permission to extract DNA; A. Marticorena (CONC) and S. Beck (LPB) for their particular attention to us, locating a number of particular vouchers and photodocumenting them; the curators and staff from FLOR, MCNS, SI, UFP, UPOS and WS for processing collections; also the curators and staff of a countless number of herbaria that have kindly (and sometimes repeatedly) confirmed the absence of material of interest during multiple consultations; the Argentinian and Brazilian National Parks Authorities and regional federal governments for granting permission to collect material; C.C. Coates, M. Hahn, M. Míguez, J.B. Ponsford, W. Roberts and C.A. Robinson for technical support during processing of the samples for PCR amplification; J. Gauffin, M. Fabbroni, M. Lechowiz and M. Waterway for their critical help during fieldwork in Argentina, and L. Costa and L.P. Silva for help and organization of fieldwork in Brazil; M. Merello and J. Prusky (MO) and I. Larridon (K) for helping with light microscopy pictures of material of *C. divisa* and *C. nebularum*, respectively; A.A. Reznicek for discussion on the taxonomy and biogeography of Neotropical *Carex*, financial and logistical support for a visit to study the MICH collection and critical comments

on an earlier version of this manuscript; B. Ruthsatz for sending specimens from her private herbarium on loan and for the interesting discussion about fieldwork observations; V. Valcárcel for support in shipping and receiving material to MAUAM; J. Calvo and M. Luceño for permission to reproduce their living plant pictures; an anonymous reviewer for comments that helped improving the quality of our manuscript, and G.E. Rodríguez-Palacios for his selfless help, assistance and care during visits to herbaria and fieldwork.

We want to make an especial mention and explicitly acknowledge here the importance in the preparation of this paper of the late Dr. G.A. Wheeler's (1940–2018) immense revisionary work that has remained unpublished. He was the one who detected and marked many of the type vouchers that we here formally lectotypify. Being marked by him, those materials were digitized with priority, which made them readily available and easily traceable on the Internet. Without this previous work by Wheeler the present publication would have been much harder to prepare.

This study has been possible by funding received from the Regional Government of Madrid, Spain (*Macondo*, Award# SI1/PJI/2019-00333 to P.J.-M.), the National Science Foundation (Award #1256033 to E.H.R.), the Spanish Ministry of Economy and Competitiveness (Award# CGL2016-77401-P to S.M.-B. and a predoctoral fellowship BES-2017-079621 to J.I.M.-C.) and a postdoctoral fellowship from the Smithsonian Institution to P.J.-M.

## REFERENCES

- Anisimova M, Gascuel O. 2006. Approximate likelihood-ratio test for branches: a fast, accurate and powerful alternative. *Systematic Biology* **55**: 539–552.
- Ball PW, Reznicek AA. 2002. *Carex*. In: Flora of North America Editorial Committee, eds. *Flora of North America*. New York: Oxford University Press, 254–572.
- Barros M. 1935. Ciperáceas argentinas II, géneros *Kyllinga* Rottb., *Scirpus* L., y *Carex* L. *Anales del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* **38**: 133–264.
- Barros M. 1947. Cariceae. In: Descole HR, ed. *Genera et species plantarum Argentinae. Tomus IV. Pars II*. Buenos Aires: Guillermo Kraft, 370–490.
- Barros M. 1949. Notas Ciperológicas. V. *Darwiniana* **9**: 163–168.
- Barros M. 1969. Cyperaceae. In: Correa MN, ed. *Flora Patagónica, Parte II, Typhaceae a Orchidaceae (excepto Gramineae)*. Buenos Aires: Instituto Nacional de Tecnología Agropecuaria, 38–92.
- Berger SA, Krompass D, Stamatakis A. 2011. Performance, accuracy, and web server for evolutionary placement of short sequencereads under maximum likelihood. *Systematic Biology* **60**: 291–302.

- Boott F. 1858–1867.** *Illustrations of the genus Carex*. London: W. Pamplin.
- Brongniart AT. 1833.** *Carex*. In: Duperrey LI, ed. *Voyage autour du monde. Botanique, Phanérogamie f. 11*. Paris: A. Bertrand, 149–158.
- Brummitt RK. 2001.** *World geographical scheme for recording plant distributions edition 2*. International Working Group on Taxonomic Databases for Plant Sciences (TDWG).
- Calvo J, Jiménez-Mejías P. 2020.** *Carex divisa*, una nueva ciperácea naturalizada en Chile. *Collectanea Botanica* **39**: e008.
- Cellinese N, Beaman R. 2012.** Mass digitization of scientific collections: new opportunities to transform the use of biological specimens. *ZooKeys* **209**: 7–17.
- Dai LK, Liang SY, Zhang SR, Tang YC, Koyama T, Tucker GC. 2010.** *Carex* Linnaeus. In: Wu ZY, Raven PH, Hong DY, eds. *Flora of China* **23**. Beijing, St. Louis: Science Press, Missouri Botanical Garden Press, 285–461.
- Egorova TV. 1999.** *The sedges (Carex L.) of Russia and adjacent states (within the limits of the former USSR)*. St. Petersburg, St. Louis.: St. Petersburg State Chemical-Pharmaceutical Academy, Missouri Botanical Garden.
- Escudero M, Valcárcel V, Vargas P, Luceño M. 2009.** Significance of ecological vicariance and long-distance dispersal in the diversification of *Carex* sect. *Spirostachyae* (Cyperaceae). *American Journal of Botany* **96**: 2100–2114.
- Ford BA, Ghazvini H, Naczi RFC, Starr JR. 2012.** Phylogeny of *Carex* subg. *Vignea* (Cyperaceae) based on amplified fragment length polymorphism and nrDNA data. *Systematic Botany* **37**: 913–925.
- Gay C. 1854.** *Atlas de la historia física y política de Chile* **1**. Paris: E. Thunot.
- Govaerts R, Jiménez-Mejías P, Koopman J, Simpson D, Goetghebeur P, Wilson K, Egorova T, Bruhl J. 2020+.** *World checklist of Cyperaceae*. Kew: The Board of Trustees of the Royal Botanic Gardens. Available at: <https://wcp.science.kew.org/home.do>
- Hendrichs M, Michalski S, Begerow D, Oberwinkler F, Hellwig FH. 2004.** Phylogenetic relationships in *Carex*, subgenus *Vignea* (Cyperaceae), based on ITS sequences. *Plant Systematics and Evolution* **246**: 109–125.
- Jermey J, Simpson DA, Foley M, Porter M. 2007.** *Sedges of the British Isles*. London: Botanical Society of the British Isles.
- Jiménez-Mejías P, Alegría-Olivera JJ, Beltrán HW, Cano A, Granada-Paucar A, Maldonado Fonkén MS, Riva-Regalado S, Ruthsatz B, Escudero M. 2020.** Chorological and nomenclatural notes on Peruvian *Carex* (Cyperaceae). *Caldasia* **41**.
- Jiménez-Mejías P, Benítez-Benítez C, Fernández-Mazuecos M, Martín-Bravo S. 2017b.** Cut from the same cloth: the convergent evolution of dwarf morphotypes of the *Carex flava* group (Cyperaceae) in Circum-Mediterranean mountains. *PLoS One* **12**: e0189769.
- Jiménez-Mejías P, Cohen JI, Naczi RFC. 2017a.** The study of online digitized specimens revalidates *Andersonglossum boreale* as a species different from *A. virginianum* (Boraginaceae). *Phytotaxa* **295**: 22.
- Jiménez-Mejías P, Fabbroni M, Donadio S, Rodríguez-Palacios GE, Hilpold A, Martín-Bravo S, Waterway MJ, Roalson EH. 2016c.** Taxonomic and distribution notes on *Carex* (Cyperaceae) from the Neotropics. *Boletín de la Sociedad Argentina de Botánica* **51**: 727–739.
- Jiménez-Mejías P, Fabbroni M, Haigh A. 2020a.** Chorological, nomenclatural and taxonomic notes on *Carex* (Cyperaceae) from Bolivia and northern Argentina. *Kew Bulletin* **75**: 24.
- Jiménez-Mejías P, Hahn M, Lueders K, Starr JR, Brown BH, Chouinard BN, Chung K-S, Escudero M, Ford BA, Ford KA, Gebauer S, Gehrke B, Hoffman MH, Jin X-F, Jung J, Kim S, Luceño M, Maguilla E, Martín-Bravo S, Míguez M, Molina A, Naczi RFC, Pender JE, Reznicek AA, Villaverde T, Waterway MJ, Wilson KL, Yang J-C, Zhang S, Hipp AL, Roalson EH. 2016b.** Megaphylogenetic specimen-level approaches to the *Carex* (Cyperaceae) phylogeny using ITS, ETS, and *matK* sequences: implications for classification. *Systematic Botany* **41**: 500–518.
- Jiménez-Mejías P, Luceño M, Wilson KL, Waterway MJ, Roalson EH. 2016a.** Clarification of the use of the terms perigynium and utricle in *Carex* L. (Cyperaceae). *Systematic Botany* **41**: 519–528.
- Jiménez-Mejías P, Pereira-Silva L. 2020b.** *Carex* in Flora do Brasil 2020 under construction. Jardim Botânico do Rio de Janeiro. Available at: <http://reflora.jbrj.gov.br/reflora/floradobrasil/FB7161>. Accessed 17 December 2020.
- Jiménez-Mejías P, Strong M, Gebauer S, Hilpold A, Martín-Bravo S, Reznicek AA. 2018.** Taxonomic, nomenclatural and chorological reports on *Carex* (Cyperaceae) in the Neotropics. *Willdenowia* **48**: 117–124.
- Jørgensen PM, León-Yáñez S, eds. 1999.** Catalogue of the vascular plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* **75**: 1–1152.
- Jørgensen PM, Nee M, Beck SG, eds. 2014.** Catálogo de las plantas vasculares de Bolivia. *Monographs in Systematic Botany from the Missouri Botanical Garden* **127**: 1–1741.
- Kükenthal G. 1899.** Die *Carex* vegetation des außertropischen Südamerika (ausgenommen Paraguay und Südbrasilien) (A Engler, Ed.). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **27**: 485–563.
- Kükenthal G. 1904.** Aloysius Sodiro, S. J.: Plantae ecuadorenses. III. Cariceae. *Beiblatt zu den Botanischen Jahrbüchern* **78**: 6–9.
- Kükenthal G. 1905.** Die von E. Ule gesammelten brasilianischen Carices (E Gilg, A Weisse, and T Loesener, Eds.). *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*: 204–210.
- Kükenthal G. 1909.** Cyperaceae: Caricoideae. In: Engler A, ed. *Das Pflanzenreich*. IV. Vol. 20. Leipzig: Wilhelm Englemann, 1–824.
- Luceño M, Escudero M, Jiménez-Mejías P. 2008.** *Carex*. In: Castroviejo S, ed. *Flora Iberica XVIII*. Madrid: Consejo Superior de Investigaciones Científicas, 109–250.
- Macbride JF. 1936.** Cyperaceae. In: Dahlgren BE, ed. *Flora of Peru. Part I*. Chicago: Field Museum of Natural History, 261–320.

- Martín-Bravo S, Jiménez-Mejías P, Villaverde T, Escudero M, Hahn M, Spalink D, Roalson EH, Hipp AL, the Global Carex Group. 2019.** A tale of worldwide success: behind the scenes of *Carex* (Cyperaceae) biogeography and diversification. *Journal of Systematics and Evolution* **57**: 695–718.
- Miller MA, Pfeiffer WT, Schwartz T. 2010.** Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway computing environments workshop (GCE)*. New Orleans: 1–8.
- Molina A, Acedo C, Jarvis C, Llamas F. 2006.** Typification of some of Hudson's plant names in *Carex* L. *Taxon* **55**: 1009–1013.
- Molina A, Acedo C, Llamas F. 2008.** Taxonomy and new taxa of the *Carex divulsa* aggregate in Eurasia (section *Phaestoglochin*, Cyperaceae). *Botanical Journal of the Linnean Society* **156**: 385–409.
- Moore DM. 1983.** *Carex*. In: Nelson A, ed. *Flora of Tierra del Fuego*. Shrewsbury: Anthony Nelson, 330–340.
- Pedersen TM. 1968.** Cyperaceae. In: Cabrera AL, ed. *Flora de la Provincia de Buenos Aires. Parte I. Pteridófitas, Gimnospermas y Monocotiledóneas (excepto Gramíneas)*. Buenos Aires: Instituto Nacional de Tecnología Agropecuaria, 315–421.
- Pfeiffer VW, Ford BM, Housset J, McCombs A, Blanco-Pastor JL, Gouin N, Manel S, Bertin A. 2018.** Partitioning genetic and species diversity refines our understanding of species–genetic diversity relationships. *Ecology and Evolution* **8**: 12351–12364.
- POWO. 2019.** *Plants of the World Online*. Kew: Royal Botanic Gardens. Available at: <http://www.plantsoftheworldonline.org>
- Reznicek AA. 1995.** The *Carex lurida* group (Cyperaceae) in the Neotropics. *Contributions from the University of Michigan Herbarium* **20**: 217–230.
- Reznicek AA, González-Elizondo MS. 2001.** *Carex* section *Porocystis* in Mexico and Central America. *Contributions from the University of Michigan Herbarium* **23**: 339–348.
- Roalson EH, Columbus JT, Friar EA. 2001.** Phylogenetic relationships in Cariceae (Cyperaceae) based on ITS (nrDNA) and *trnT-L-F* (cpDNA) region sequences: assessment of subgeneric and sectional relationships in *Carex* with emphasis on section *Acrocystis*. *Systematic Botany* **26**: 318–341.
- Rodríguez R, Marticorena C, Alarcón D, Baeza C, Cavieres L, Finot VL, Fuentes N, Kiessling A, Mihoc M, Pauchard A, Ruiz E, Sánchez P, Marticorena A. 2018.** Catálogo de las plantas vasculares de Chile. *Gayana Botanica* **75**: 1–430.
- Roalson E, Jiménez-Mejías P, Hipp AL, Benítez-Benítez C, Bruederle LP, Chung K-S, Escudero M, Ford BA, Ford K, Gebauer S, Gehrke B, Hahn M, Hayat MQ, Hoffman MH, Hoffman HH, Jin X-F, Kim S, Larridon I, Lévêille-Bourret É, Lu Y-F, Luceño M, Maguilla E, Márquez-Corro JI, Martín-Bravo S, Masaki T, Míguez M, Naczi RFC, Reznicek AA, Spalink D, Starr JR, Uzma, Villaverde T, Waterway MJ, Wilson KL, Zhang S.** In press. A framework infrageneric classification of *Carex* (Cyperaceae) and its organizing principles. *Journal of Systematics and Evolution*.
- Silveira GH, Longhi-Wagner HM. 2010.** New records in the genus *Carex* L. (Cyperaceae) for Brazil and Rio Grande do Sul. *Acta Botanica Brasilica* **24**: 229–231.
- Silveira GH, Longhi-Wagner HM. 2012.** O gênero *Carex* L. (Cyperaceae) no Rio Grande do Sul, Brasil. *Revista Brasileira de Biociências* **10**: 373–417.
- Soltis PS. 2017.** Digitization of herbaria enables novel research. *American Journal of Botany* **104**: 1281–1284.
- Stafleu FA, Cowan RS. 1976–2009.** *Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types, 2nd edn*. Utrecht: Bohn, Scheltema & Holkema.
- Stamatakis A. 2014.** RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.
- Thiers B. 2020+.** *Index herbariorum: a global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available at: <http://sweetgum.nybg.org/science/ih/>
- Turland N, Wiersema J, Barrie F, Greuter W, Hawksworth D, Herendeen P, Knapp S, Kusber WH, Li DZ, Marhold K, May T, McNeill J, Monro A, Prado J, Price M, Smith G. 2018.** *International Code of nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Glashütten: Koeltz Botanical Books.
- Villaverde T, Escudero M, Luceño M, Martín-Bravo S. 2015.** Long-distance dispersal during the middle-late Pleistocene explains the bipolar disjunction of *Carex maritima* (Cyperaceae). *Journal of Biogeography* **42**: 1820–1831.
- Villaverde T, Jiménez-Mejías P, Luceño M, Waterway MJ, Kim S, Lee B, Rincón-Barrado M, Hahn M, Maguilla E, Roalson EH, Hipp AL, the Global Carex Group. 2020.** A new classification of *Carex* subgenera supported by a HybSeq backbone phylogeny. *Botanical Journal of the Linnean Society* **194**: 141–163.
- Waterway MJ, Starr JR. 2007.** Phylogenetic relationships in tribe Cariceae (Cyperaceae) based on nested analyses of four molecular data sets. *Aliso* **23**: 165–192.
- Wheeler GA. 1987.** A new species of *Carex* (Cyperaceae) from western South America and a new combination in the genus. *Aliso* **11**: 533–537.
- Wheeler GA. 1988.** Taxonomic notes on *Carex* (Cyperaceae) of austral South America. *Aliso* **12**: 97–102.
- Wheeler GA. 1996a.** A new combination in South American *Carex* (Cyperaceae) and additional notes on the genus. *Hickenia* **2**: 179–184.
- Wheeler GA. 1996b.** Three new species of *Carex* (Cyperaceae) from Argentina and a range extension for *C. ecuadorica*. *Hickenia* **2**: 189–200.
- Wheeler GA. 2002.** *Carex* (Cyperaceae) from South America: three new species and some name changes. *Darwiniana* **40**: 199–208.
- Wheeler GA. 2006.** A new species of *Carex* (Cyperaceae) from austral South America and the status and distribution of *C. macrorrhiza*. *Hickenia* **3**: 259–266.



- Wheeler GA. 2007.** *Carex* and *Uncinia* (Cyperaceae, Cariceae) from the Juan Fernández Archipelago, Chile. *Darwiniana* **45**: 120–141.
- Wheeler GA. 2009.** *Carex*. In: Kiesling R, Guaglianone R, Cialdella AM, E R de AZ, eds. *Flora de San Juan: República Argentina. Vol. 4, Monocotiledóneas*. San Juan: Editorial Fundación Universidad Nacional de San Juan, 323–338.
- Wheeler GA, Muñoz-Schick M. 2007.** *Carex bracteosa* (Cyperaceae) from Chile and its lectotypification. *Noticiario Mensual del Museo Nacional de Historia Natural* **358**: 17–21.
- Zuloaga FO, Morrone O, Belgrano MJ, Marticorena C, Marchesi E, eds. 2020+.** *Catálogo de las plantas vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay)*. Available at: <http://www.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm>

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Complete ETS-ITS-*matK* concatenated tree built to test the phylogenetic placement of multiple accessions of South American androgynous species of *Carex* subgenus *Vigneae*. For details about the construction of the tree see Material and Methods.

**Table S1.** Selected representative specimens of the studied material. One or two vouchers per TDWG area (Brummit, 2001) are presented to justify the record in each botanical country. When a country is not represented in this list, the reader is referred to the notes under the corresponding species treatment.