Systematic Botany (2021), 46(2): pp. 304–320
© Copyright 2021 by the American Society of Plant Taxonomists
DOI 10.1600/036364421X16231782047442
Date of publication August 11, 2021

Systematics of the Giant Sedges of *Carex* Sect. *Rhynchocystis* (Cyperaceae) in Macaronesia with Description of Two New Species

Mónica Míguez,[1] Pedro Jiménez-Mejías,[2,3] Carmen Benítez-Benítez,[1] Hanno Schaefer,[4] and Santiago Martín-Bravo[1,5]

[1]Área de Botánica, Departamento de Biología Molecular e Ingeniería Bioquímica, Universidad Pablo de Olavide, ctra. de Utrera km 1 sn, 41013, Seville, Spain

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

[3]Departamento de Biología (Botánica), Facultad de Ciencias Biológicas, Universidad Autónoma de Madrid, C/Darwin 2, 28049, Madrid, Spain

[4]Plant Biodiversity Research, Department of Ecology and Ecosystem Management, Technical University of Munich, Emil-Ramann Strasse 2, 85354, Freising, Germany

[5]Author for correspondence (smarbra@upo.es)

Communicating Editor: Nádia Roque

Abstract—Populations of *Carex* sect. *Rhynchocystis* (Cyperaceae) from the Macaronesian archipelagos (Azores and Madeira) have traditionally been treated either as a variety of the widely distributed Western Palearctic *C. pendula*, or directly synonymized under it. However, recent phylogenetic studies have shown that Azorean populations of *C. pendula* display a certain degree of differentiation from mainland plants, while the phylogenetic relationships of Madeiran populations remain unclear. Here we perform an integrated systematic study focused on the Macaronesian populations of *Carex* sect. *Rhynchocystis* to elucidate their phylogenetic relationships and taxonomic status. We reconstructed a molecular phylogeny based on five DNA regions and conducted a multivariate morphological analysis. Divergence time estimates show that the Macaronesian populations can be traced back to a Plio-Pleistocene origin. Our results suggest that these island populations of *C. pendula* are better treated as two distinct species within *Carex* sect. *Rhynchocystis* (i.e. ***C. leviosa*** from the Azores and ***C. sequeirae*** from Madeira). We provide morphological characters to differentiate the new species from *C. pendula* s. s., detailed descriptions of the three taxa, a revised key for the entire section, as well as detailed analytical drawings of the two newly described species. We also perform a critical evaluation of the taxonomic diversity of *Carex* in the Azores and Madeira. Finally, we informally assessed the conservation status of the new species at a global scale under IUCN categories and criteria, resulting in the proposal of the categories Least Concern for *C. leviosa* and Critically Endangered for *C. sequeirae*.

Keywords—Azores, budding speciation, island endemism, Madeira, taxonomy.

The Macaronesian archipelagos consist of a series of oceanic islands west of the European coast and North Africa, namely from north to south, the Azores, Madeira, Savage Islands, Canary Islands, and Cabo Verde. Macaronesia is considered one of the 10 Mediterranean Basin hotspots for plant biodiversity (Médail and Quezel 1997) and is rich in endemics (Sánchez-Pinto et al. 2005; Jardim and Menezes de Sequeira 2008; Acebes-Ginovés et al. 2010; Silva et al. 2010). The high endemism in these archipelagos is partly due to some of them sheltering a particular kind of cloud forest, the so-called "laurisilva." These lauroid forests have long been thought to be remnants of the vegetation that once covered Europe during the Neogene (Engler 1879; Axelrod 1975; Barbero et al. 1980). This assumption has been made mainly due to the temperate oceanic climate of these islands. Some studies have proposed that some species might date back to the Neogene and thus would be relictual elements (i.e. paleoendemics) in the Macaronesian archipelagos (Engler 1879; Maire 1957; Aigoin et al. 2009; Manen et al. 2010; Kondraskov et al. 2015; Mairal et al. 2018). Nevertheless, it has been revealed by molecular approaches, that the majority of the species found at laurisilva forests seem to have a more recent Plio-Pleistocene origin (Aigoin et al. 2009; Kondraskov et al. 2015; Schüßler et al. 2019).

According to the checklists of both archipelagos, *Carex* L. (Cyperaceae) is represented in the Azores by 20 taxa, of which 11 are native, three of them endemic, eight introduced, and one of doubtful status (Silva et al. 2010). Alternatively, 11 taxa have been reported for Madeira, all of them native, two of them endemic (Jardim and Menezes de Sequeira 2008). Furthermore, Madeira and Azores are reported to share at least one Macaronesian *Carex* endemic taxon (Jardim and Menezes de Sequeira 2008; Silva et al. 2010). However, differences in the number and identity of the reported taxa are apparent in the more recent official Portuguese checklist (Menezes de Sequeira et al. 2012) and floristic treatments (Jiménez-Mejías and Luceño 2011; Govaerts et al. 2020). Chorological novelties and taxonomic rearrangements have also affected the account of *Carex* in Azores and Madeira (Jiménez-Mejías et al. 2014; Martín-Bravo et al. 2019b).

Carex sect. *Rhynchocystis* Dumort. (Cyperaceae) currently comprises five species and two subspecies of giant sedges. The members of this section are disjunctly distributed in the Western Palearctic (i.e. *C. agastachys* L.f., *C. microcarpa* Bertol. ex Moris, and *C. pendula* Huds.) and sub-Saharan Africa [i.e. *C. bequaertii* subsp. *bequaertii* De Wild. from East Tropical Africa, *C. bequaertii* subsp. *mossii* (Nelmes) Míguez, Gehrke, Martín-Bravo and Jim.-Mejías from South Africa, and *C. penduliformis* Cherm. from Madagascar]. The systematics of the group has recently been studied, based on both molecular and morphological data (Míguez et al. 2017, 2018, respectively). Míguez et al. (2017) recovered *Carex* sect. *Rhynchocystis* as monophyletic, and showed that the group diversified during the middle-late Miocene in Europe. Consequently, the Western Palearctic species have been considered relict elements whose origin predates the onset of the Mediterranean climate (Milne and Abbott 2002). The authors also demonstrated that in its traditional circumscription, *C. pendula* included two distinct but hitherto overlooked lineages: 1) *C. pendula* s. s., mainly from western Europe and the Mediterranean basin; and 2) *C. agastachys*, mainly from eastern Europe and southwestern Asia (Jiménez-Mejías et al. 2017; Míguez et al. 2017, 2018).

In the past, Macaronesian populations of *C. pendula* s. l. were treated under the illegitimate name *C. myosuroides* Lowe (Lowe 1833; Seubert 1844) or as a variety of *C. pendula* (i.e. *C. pendula* var. *myosuroides* Boott; Boott 1867; Kükenthal 1909; Schaefer 2005). In the phylogeny presented by Míguez et al. (2017), the few included samples from Madeira and Azores appeared nested within *C. pendula* s. l. and thus were considered to belong to this taxon. However, the two sampled Azores populations constituted a remarkably well-supported clade, distinct from the rest of *C. pendula*. In contrast, the single sampled Madeira population was recovered as an isolated lineage, at the base of the *C. pendula* clade. Nonetheless, both relationships lacked significant statistical support (Míguez et al. 2017). In the morphometric study of *Carex* sect. *Rhynchocystis* (Míguez et al. 2018), three samples belonging to populations from Madeira, and two samples from Azores were included. All of them were recovered within the variability of *C. pendula* s. s. Regardless, the few Macaronesian samples included in these previous molecular and morphological studies (Míguez et al. 2017, 2018) were insufficient to draw a robust conclusion about their phylogenetic relationship or their taxonomic status.

In this paper, we present a detailed reevaluation of the taxonomic status and phylogenetic relationships of the Macaronesian populations of *C. pendula* by expanding the sampling of Macaronesian populations and genetic markers. This approach may allow us to reach reliable phylogenetic and taxonomic conclusions about the islands' populations that we were unable to attain in previous studies (Míguez et al. 2017, 2018). We use DNA sequence data from three chloroplast regions (cDNA) (*atpIH*, *matK* and *rpl32-trnL*^{UAG}), and two nuclear regions (nDNA) (ETS and ITS), together with micro- and macromorphological data, to: 1) elucidate whether there are significant molecular/morphological differences between Macaronesian and mainland *C. pendula* populations; and 2) assess the taxonomic status of the Macaronesian populations.

Materials and Methods

Phylogenetic Analyses—Samples of all species of *Carex* sect. *Rhynchocystis* were used to representatively cover its range (see Míguez et al. 2018). We sampled the following populations (1 specimen per population): 1) six of *C. agastachys*; 2) five of *C. bequaertii* subsp. *bequaertii* and three of *C. bequaertii* subsp. *mossii*; 3) three of *C. microcarpa*; 4) eight of *C. pendula*; 5) one of *C. penduliformis*; 6) five of *C. pendula* from the Azores, treated by us as *C. leviosa*; 7) five of *C. pendula* from Madeira, treated by us as *C. sequeirae*; and 8) two species from each of the closely related *Carex* sect. *Ceratocystis* Dumort., *Carex* sect. *Phacocystis* Dumort., *Carex* sect. *Sylvaticae* Rouy, and *Carex* sect. *Spirostachyae* (Drejer) L.H.Bailey, as outgroups (Míguez et al. 2017; Appendix 1). We sequenced and analyzed three cDNA (*atpIH, matK*, and *rpl32-trnL*^{UAG}) and two nDNA (ETS and ITS) regions, which have been successfully used in molecular studies for *Carex* sect. *Rhynchocystis* and close groups (Waterway and Starr 2007; Escudero and Luceño 2009; Jiménez-Mejías et al. 2012, 2016b; Villaverde et al. 2015). Many sequences were obtained from the previous phylogeny of *Carex* sect. *Rhynchocystis* by Míguez et al. (2017). We newly produced a total of 72 sequences (see Appendix 1) from herbarium material and freshly collected material from both archipelagos. The PCR conditions and primers followed Míguez et al. (2017) for ITS, ETS, *matK,* and *rpl32-trnL*^{uag}, and Shaw et al. (2007) for *atpIH*. The PCR products were cleaned and sequenced, as described in Míguez et al. (2017). Likewise, raw sequences were edited, assembled, and the matrices aligned and manually adjusted, as indicated in Míguez et al. (2017). IUPAC symbols were used to represent nucleotide ambiguities in ETS and ITS sequences. Edited sequences were deposited in GenBank (Appendix 1). Five matrices were built for phylogenetic analyses: 1) ETS; 2) ITS; 3) combined nDNA; 4) combined cDNA; and 5) combined nDNA-cDNA. We performed Bayesian inference (BI) and maximum likelihood (ML) analyses for all matrices. For BI analyses, substitution models were calculated for each DNA region separately under the Akaike information criterion (AIC) in jModeltest v. 2.1.3 (Darriba et al. 2012). Given the relatively few indels within the matrices, informative ones were coded manually as a fifth binary character state and analyzed with BI with the F81 model of sequence evolution as specified in the MrBayes manual (Ronquist and Huelsenbeck 2003). We set two runs each of four chains with 10 million generations in MrBayes v. 3.2.7a (Ronquist et al. 2012) as implemented in CIPRES Science Gateway (Miller et al. 2010), with a 20% burn-in. For ML, matrices were analyzed with RAxML v. 8.2.12 (Stamatakis 2014), also implemented in CIPRES, under a GTR-GAMMA model, with 1000 bootstrap replicates, and indels coded as specified above. To obtain the combined nDNA-cDNA matrix (44 accessions), samples that lacked more than one DNA region were discarded, resulting in 4.5% missing data (6.8% missing in *atp*IH, 4.5% in ITS, 0% in ETS, 4.5% in *matK* and 2.2% in *rpl32-trnL*^{UAG}). Phylogenetic analyses for the combined nDNA-cDNA matrix were performed with and without coding indels to explore its effect in the topology. The obtained trees were compared and checked for incongruences of supported nodes with Bayesian posterior probabilities > 0.95 and bootstrap support $> 75\%$ (Gehrke et al. 2010).

Haplotype Network—Genealogical relationships between plastid haplotypes were obtained for a sampling subset that included only species of the monophyletic group formed of *C. agastachys*, *C. leviosa*, *C. pendula*, and *C. sequeirae* (lineage B; see phylogenetic results and Míguez et al. 2018). We compiled a new matrix of 49 concatenated sequences of plastid markers (*atpIH-matK-rpl32-trnL*^{UAG}). Accessions lacking one or several of these markers were excluded from that matrix. In total, we obtained four concatenated sequences of *C. leviosa*, four of *C. sequeirae*, 24 of *C. pendula,* and 14 of *C. agastachys* (see Appendix 1). Statistical parsimony analysis was performed using TCS v. 1.21 (Clement et al. 2000). The maximum number of differences resulting from individual substitutions between haplotypes was calculated with 95% confidence limits. The matrix was analyzed with and without coding indels, in the same way as in the phylogenetic analyses.

Divergence-Time Estimation—We constructed a matrix of 16 combined *atpIH*-ETS-ITS-*matK-rpl32-trnL*^{UAG} sequences (aligned length 3519 sites): eight from *Carex* sect. *Rhynchocystis* (one sequence per taxon), plus eight outgroups (see Appendix 1). A dated phylogeny was estimated using BEAST v. 2.6.1 (Bouckaert et al. 2019), through the CIPRES Science Gateway (Miller et al. 2010), following Míguez et al. (2017), unless otherwise noted. Two calibration points were enforced: 1) a fossil (*C. limosioides* Negru from the early Miocene; Jiménez-Mejías et al. 2016b) to constrain the crown node of *Carex* sect. *Rhynchocystis*, since its characteristics perfectly match those found within the lineage (Jiménez-Mejías et al. 2016b); and 2) a secondary calibration obtained from Martín-Bravo et al. (2019a) to constrain the clade including *Carex* sect. *Rhynchocystis*, *Carex* sect. *Sylvaticae*, *Carex* sect. *Ceratocystis*, and *Carex* sect. *Spirostachyae*, implemented under a normal distribution with a mean of 17.04 Ma, and a deviation of 1.0. Three independent runs of 10 million generations each were conducted under a Yule tree prior. Convergence, mixing of MCMC chains, ESS values, and burn-in were checked in Tracer v. 1.7.1 (Rambaut et al. 2018). The resulting tree files from the different runs were combined in a single file with Logcombiner v. 2.6.2 (Bouckaert et al. 2019), which was subsequently used to obtain a single Maximum clade credibility tree with TreeAnnotator v. 2.6.2 (Bouckaert et al. 2019).

Macromorphological Study—The morphological study included a total of 75 herbarium specimens from 13 herbaria (E, BM, K, LISU, M, MADJ, MADM, MHA, P, SEV, TUM, UPOS, UPS; Appendix 2, Míguez et al. 2021; abbreviations follow Thiers 2020). Our sampling was designed to explore the morphological variation within the monophyletic group formed by *C. agastachys*, *C. leviosa*, *C. pendula*, and *C. sequeirae* (lineage B; see phylogenetic results), and to specifically provide insights into the relationships of the Macaronesian taxa of *C. pendula*, which grouped in previous morphometric works (Míguez et al. 2018). Herbarium vouchers were selected to representatively cover the distribution range of the four species (see Míguez et al. 2018): 23 specimens of *C. agastachys*; 28 specimens of *C. pendula*; nine specimens of *C. leviosa*, representing five populations from four different Azorean Islands (São Miguel, Faial, Pico, and Santa Maria; Appendix 2, Míguez et al. 2021); and 15 specimens of *C. sequeirae*, representing at least eight different populations from Madeira (some vouchers did not indicate the exact location). All the material was manually measured, except the three Madeiran specimens from K (Appendix 2, Míguez et al. 2021), which were measured from high-resolution digital images. In our morphological study, we considered 25 quantitative continuous (including one ratio), seven quantitative discrete, and two qualitative characters (Table 1). They were mainly based on the characters used in our previous taxonomic revision of the section (Míguez et al. 2018). Five characters were newly measured, based on our observations of the Macaronesian specimens: two quantitative continuous, LTPS (Length of the awn of the pistillate glume) and LAPSMF (Length of the male part of the proximal-most lateral spike);

TABLE 1. List of characters measured in the macromorphometric study.

Abbreviations	Quantitative continuous variables
ACHL	Achene length
ACHL/ACL	Ratio ACHL/ACL
ACHW	Achene width
ACL	Length from the achene base to the maximum width
ASL	Apical spike length
ASW	Apical spike width
CLMW	Culm width
DSFS	Distance between the two uppermost lateral spikes
FSLP	Peduncle length of the proximal-most lateral spike
PSL	Most proximal spike length
PSW	Most proximal spike width
LAPSMF	Length of the apex in the proximal-most lateral spike where male flowers are found
LTPS	Length of the tips of the pistillate glume
LIGL	Ligule length
LUMWD	Length from the utricle base to its maximum width
MAXCLPM	Maximum length of the pistillate glume colored margin
PSCLL	Pistillate glume length
PSCLW	Maximum pistillate glume width
SLEAFW	Maximum leaf width
SSCLL	Glume length
SSCLW	Maximum staminate glume width
UBL	Utricle beak length
UL	Utricle length
UMW	Utricle maximum width
USL	Utricle stalk length
	Quantitative discrete variables
ASN	Apical spikes number
LSN	Lateral spikes number
PSDFS	Peduncle scabrousness of the distal lateral spike (measured in prickles per 0.5 cm^2)
PSPFS	Peduncle scabrousness of the proximal lateral spike (measured in prickles per 0.5 cm^2)
SAP	Scabrousness of the awn of the pistillate glume (number of prickles in the bristle)
SBL	Scabrousness of the basal leaf (measured in prickles per 25 mm^2)
SLI	Scabrousness of the lower bract of the inflorescence (measured in prickles per 25 mm^2)
	Qualitative variables
DLC	Distal ligule color
PLC	Proximal ligule color

and three quantitative discrete, SBL (Scabrousness of the basal leaf (measured in prickles per 25 mm^2)), SAP (Scabrousness of the awn of the pistillate glume (number of prickles on the awn)), and SLI (Scabrousness of the lower bract of the inflorescence (number of prickles per 25 mm^2)). The number of prickles on the female spike peduncle was counted on the 0.5 cm distal portion of the peduncles of the proximal and distal female spike. Two or three mature stems were measured per specimen, and their averages included in the analyses. Species descriptions were prepared according to a previous taxonomic treatment of *Carex* sect. *Rhynchocystis* (Míguez et al. 2018). The use of specific terminology regarding the utricle follows the recommendations established by Jiménez-Mejías et al. (2016a).

Statistical Analyses—Principal components analysis (PCA), discriminant function analysis (DFA), and the Mann-Whitney U Test were carried out. Multivariate analyses were conducted following procedures by Míguez et al. (2018). Analyses were performed using the software IBM SPSS statistics v. 22 (Chicago, IL, USA).

PRINCIPAL COMPONENT ANALYSIS (PCA)—We followed the sequential PCA approach performed by Míguez et al. (2017) for *Carex* sect. *Rhynchocystis* and inspired by Valcárcel and Vargas (2010) and Jiménez-Mejías et al. (2014). Consecutive PCA were used to identify morphogroups. The PCA were conducted using a correlation matrix to scale the characters (Manly 1994). To achieve the best split among morphogroups, we first performed an exploratory PCA-I starting with the 32 quantitative variables and including all the samples, retaining later only those with the highest principal component (PC) loadings and with the highest correlation coefficients, whenever the correlation between characters was found not to be redundant. This character purge allowed identifying morphogroups, i.e. separate clusters containing more than one species. The samples on the morphogroups formed by more than one species were split as a new subset and subsequently re-analyzed separately, including again all the characters and performing a new character purge. Kaiser-Meyer-Olkin's measure of sampling adequacy (KMO) and Bartlett's test of sphericity were estimated to evaluate the suitability of the data for finding structure and only principal components with eigenvalues greater than 1 were retained (Valcárcel and Vargas 2010; Jiménez-Mejías et al. 2014). The process was repeated until only pairs of species were retained for a PCA analysis. Details of the subsequent PCAs were as follows:

For PCA-I, we used the complete dataset, which was composed of 75 specimens from the four species (*C. agastachys, C. leviosa, C. pendula*, and *C. sequeirae*). After the character purge, a total of 11 variables were kept for the final analysis (ACHL, ACHW, ASL, DLC, LSN, PLC, PSDFS, PSL, SAP, SLI, and UMW). Since *C. agastachys* split from the other three species, which overlapped in a single morphogroup (see results), the next subsequent analyses excluded *C. agastachys*.

For PCA-II, we used 51 specimens of *C. pendula*, *C. leviosa*, and *C. sequeirae*. A total of 10 variables were kept for the final analysis (ACHL, ACHW, ACL, ASL, LAPSMF, LSN, LTPS, LUMWD, SAP, and UL). Since *C. pendula* split from the Macaronesian species, which still overlapped forming a single morphogroup (see results), the next subsequent analyses excluded *C. pendula*.

For PCA-III, we used 24 specimens belonging to *C. leviosa* and *C. sequeirae*. A total of 9 variables were kept for the final analysis (ACHL, DLC, FSLP, LAPSMF, PLC, PSCLL, PSCLW, PSW, and UBL).

The final morphogroups obtained at the end of each chain of consecutive PCA were considered indicative of morphological distinctiveness within the previously known phylogenetic framework of the section, implying we consider these groups as homogeneous morphogroups.

DISCRIMINANT FUNCTION ANALYSIS (DFA)—After the identification of homogeneous morphogroups, DFA was performed using the variables included in PCA-I, to assess taxonomically significant morphogroups as described in Jiménez-Mejías et al. (2014). We considered as potentially significant those groups correctly classified for 80% of excluded cases. We randomly selected 70% of all samples to perform the DFA using a cross-validation of the model over these samples. Then, the remaining 30% of the samples were randomly excluded from the analyses and used as a confirmatory blind control.

MANN-WHITNEY U TEST—To check for the most significant differences among the two newly described species and *C. pendula* (where these were previously subsumed), we performed a Mann-Whitney *U* test. The Shapiro-Wilk normality test was carried out, which showed that most of our data did not meet the assumption of normality. The Mann-Whitney *U* test is a non-parametric test analog to the two-sample *t* test (Campbell and Swinscow 2009). The level of significance was set at $p < 0.01$. These analyses were run in R (R Development Core Team 2019).

Micromorphological Study—Micromorphology of the achene was examined under scanning electron microscopy following the same procedure as described in Míguez et al. (2018). We applied this treatment to 13 achenes (i.e. three from *C. agastachys*, five from *C. leviosa,* three from *C. sequeirae*, and six from *C. pendula*; Appendix 2).

Informal Conservation Assessment—We evaluated the conservation status of *C. leviosa* and *C. sequeirae* at the global level following criteria, categories, and guidelines from IUCN (2012, 2017). Area of occupancy (AOO) and extent of occurrence (EOO) were calculated for *C. sequeirae* using the GeoCAT tool (Bachman et al. 2011).

RESULTS

Phylogenetic Analyses—The aligned matrix of the concatenated *atpIH*-ETS-ITS-*matK*-*rpl32*-*trnL*^{UAG} DNA regions consisted of 44 sequences (Appendix 1) and 3536 sites, 13 of which corresponded to coded indels (i.e. three in *atpIH*, ETS, and *rpl32*-*trnL*^{UAG} each, and four in ITS). The nucleotide substitution model that best fit each DNA region based on jModelTest results were: K80 for ITS 5.8S, HKY for *matK*, GTR for *atpIH*, GTR + G for *rpl32*-*trnL*^{UAG}, and ETS, GTR + I + G for ITS1 and ITS2. Matrices with and without coding indels yielded very similar topologies (Fig. 1, Appendix 3, Míguez et al. 2021, respectively) but slight differences in nodal support and phylogenetic relationships within the *C. pendula* s. l. clade (see below). Analyses performed on the matrices with individual markers (ETS Fig. S1, ITS Fig. S2 in Appendix 4, Míguez et al.

2021), and nuclear and plastid concatenated datasets (cDNA Fig. S3, nDNA Fig. S4 in Appendix 4, Míguez et al. 2021), were congruent with the topology of the combined nDNA-cDNA matrix with coded indels. For the sake of simplicity, we will discuss topological relationships based on the topology recovered from that last, most comprehensive matrix (Fig. 1). BI and ML analyses strongly supported the monophyly of *Carex* sect. *Rhynchocystis* with 1.0 posterior probability (PP) and 100% bootstrap support (BS), and *Carex* sect. *Sylvaticae* as its sister group (1 PP, 97% BS). The monophyly of all species within *Carex* sect. *Rhynchocystis* was strongly supported (1 PP, > 98% BS), except for *C. penduliformis* (only one sample) and mainland populations of *C. pendula* (i.e. *C. pendula* s. s., see below). Two main lineages were moderate to strongly supported within *Carex* sect. *Rhynchocystis*: (lineage A) including the Mediterranean endemic *C. microcarpa* as sister to the African *C. bequaertii*/*C. penduliformis* (0.97 PP, 68% BS); and (lineage B) a Western Palearctic lineage with *C. agastachys* as sister to the *C. pendula* s. l. clade, which contained *C. pendula* s. s. and the Macaronesian taxa (0.95 PP, 80% BS). Within the *C. pendula* s. l. clade, three main clades emerge: 1) *C. pendula* s. s. excluding samples from Morocco and Cyprus; 2) *C. sequeirae*; and 3) *C. leviosa*. The first was strongly supported by BI (1 PP) but not by ML (58% BS), whereas the other two were strongly supported (1 PP, > 99% BS). Populations from Morocco and Cyprus showed an isolated phylogenetic placement that varied whether indels were coded or not, and that produced a paraphyletic *C. pendula* s. s. (Fig. 1; Appendix 3, Míguez et al. 2021). Interestingly, when indels were coded, the population from Cyprus appeared as sister to *C. sequeirae* (with support only in BI with 0.95 PP), whereas that from Morocco was placed as sister to the remainder of *C. pendula* s. s., but without support (Fig. 1). On the other hand, if indels were not coded, the accessions from Morocco and Cyprus were retrieved as successive sisters to both Macaronesian species, but only the sister relationship of the population from Cyprus received high BI support (0.97 PP, Appendix 3, Míguez et al. 2021).

Haplotype Analyses—When analyzing the plastid sequences of the *C. pendula* lineage (i.e. *C. agastachys*, *C. leviosa*, *C. pendula*, and *C. sequeirae*) with statistical parsimony, 15 haplotypes were identified when coding indels, all of them species-specific (Fig. 2; Appendix 1). When indels were not coded (results not shown), the retrieved haplotype network was almost identical, except for a population of *C. leviosa* (AZO2) displaying the same haplotype as three other populations (H14) instead of a different one (H13) in the net obtained when indels were coded (Fig. 2). As expected, *C. agastachys* haplotypes were very different from those from *C. pendula* s. l. Three different haplotypes were found for *C. leviosa* (H13–H15) and five for *C. sequeirae* (H8–H12). *Carex leviosa* and *C. sequeirae* were interconnected through *C. pendula* by the haplotype H2. The isolated *C. pendula* haplotypes H2–H4 corresponded to *C. pendula* samples from Morocco (H3), Cyprus (H4), and continental Portugal (H2).

Divergence-Time Estimation—Diversification of *Carex* sect. *Rhynchocystis* (crown node) was estimated to have begun 16.13 Ma (95% highest posterior density (HPD) interval 15.97–16.5 Ma; Early-Middle Miocene; Fig. 3). Remarkably synchronous diversification times, dated to the Middle-Late Miocene, were retrieved for the two main lineages within the section (lineage A: 11.5 Ma, 95% HPD 6.16–16.0 Ma; lineage B: 11.6 Ma, 95% HPD 6.15–16.0 Ma; Fig. 3). An Early Pliocene mean age (4.49 Ma) was obtained for the *C. pendula* s. l. clade, although with a wide confidence interval spanning from the Pleistocene to the Late Miocene (95% HPD 1.19–8.65). Finally, the split between the Macaronesian *C. leviosa* and *C. sequeirae* was dated around the end of the Plio-Pleistocene (2.22 Ma, 95% HPD 0.39–4.75 Ma).

Macromorphological Analyses—In all datasets, Kaiser's measure of sampling adequacy was > 0.5, and Barlett's test of sphericity was significant. This implies that the sampling size is suitable to be explored using PCA (Valcárcel and Vargas 2010; Jiménez-Mejías et al. 2014). Principal components extracted in each PCA are referred to as PC and numbered using roman numerals. Three separate analyses of the morphological data were conducted using different combinations of taxa. For the first analysis, all taxa were included. Subsequent analyses removed distinctive morphogroups in order to investigate finer patterns of variation in the data.

Principal Component Analysis (PCA)—In the PCA-I, we extracted three principal components (PC) that accounted for 68.26% of the total variance (39.87%, 18.72%, and 9.67% respectively). The scatter-plot PC-1 vs. PC-2 revealed a general structure with two major groups (Fig. 4A). One morphogroup included the studied samples of *C. pendula* s. s., *C. leviosa,* and *C. sequeirae* and the second morphogroup included all samples of *C. agastachys* (Fig. 4A). The characters that contributed the most to the first two components were ACHL, ACHW, and PLC (Table 1).

In the PCA-II we extracted three principal components (PC) that accounted for 69.28% of the total variance (35.53%, 22.96%, and 10.79%, respectively). The scatter-plots PC-1 vs. PC-2 revealed a general underlying structure with two morphogroups, one including the samples of *C. pendula* s. s. and another morphogroup, including *C. leviosa* and *C. sequeirae* (Fig. 4B). The characters that contributed the most to the first two components were ACL, LTPS, and SAP (Table 1).

In the PCA-III, we extracted three principal components (PC) that accounted for 71.95% of the total variance (42.33%, 17.53%, and 12.09%, respectively). The scatter-plots PC-1 vs. PC-2 revealed a clear separation between *C. leviosa* and *C. sequeirae* (Fig. 4C). The characters that contributed the most to the first two components were PSCLL, FSLP, and PSGLW (Table 1).

Discriminant Function Analysis (DFA)—DFA analysis correctly classified 100% of the originally selected cases and 78.7% in the cross-validation (Appendix 5, Míguez et al. 2021). The analysis of unselected cases retrieved 82.6% of samples correctly classified (Appendix 5, Míguez et al. 2021). For each of the four a priori groups (*C. agastachys*, *C. leviosa*, *C. pendula,* and *C. sequeirae*), DFA retrieved more than 80% of excluded cases correctly classified, except for *C. pendula* (75%; Appendix 5, Míguez et al. 2021).

Mann-Whitney U Test—This test retrieved significant differences (p value < 0.01) between *C. pendula* and *C. leviosa* in eight of 32 characters (Table 2). The remaining characters overlapped in the range between both morphogroups. Similarly, the Mann-Whitney *U* test retrieved significant differences (p value < 0.01) in nine characters of 32 between *C. pendula* and *C. sequeirae* (Table 2). Between *C. leviosa* and *C. sequeirae,* the Mann-Whitney *U* test retrieved significant differences (p value $<$ 0.01) in four characters of 32 (Table 2). Boxplots of the most discriminant characters retrieved by DFA or with less than 25% overlap are shown in Fig. 5.

Micromorphological Study—Two pictures with different zoom were taken from each sample: an image of the entire achene to visualize its shape (Fig. 6A–D), and a second picture

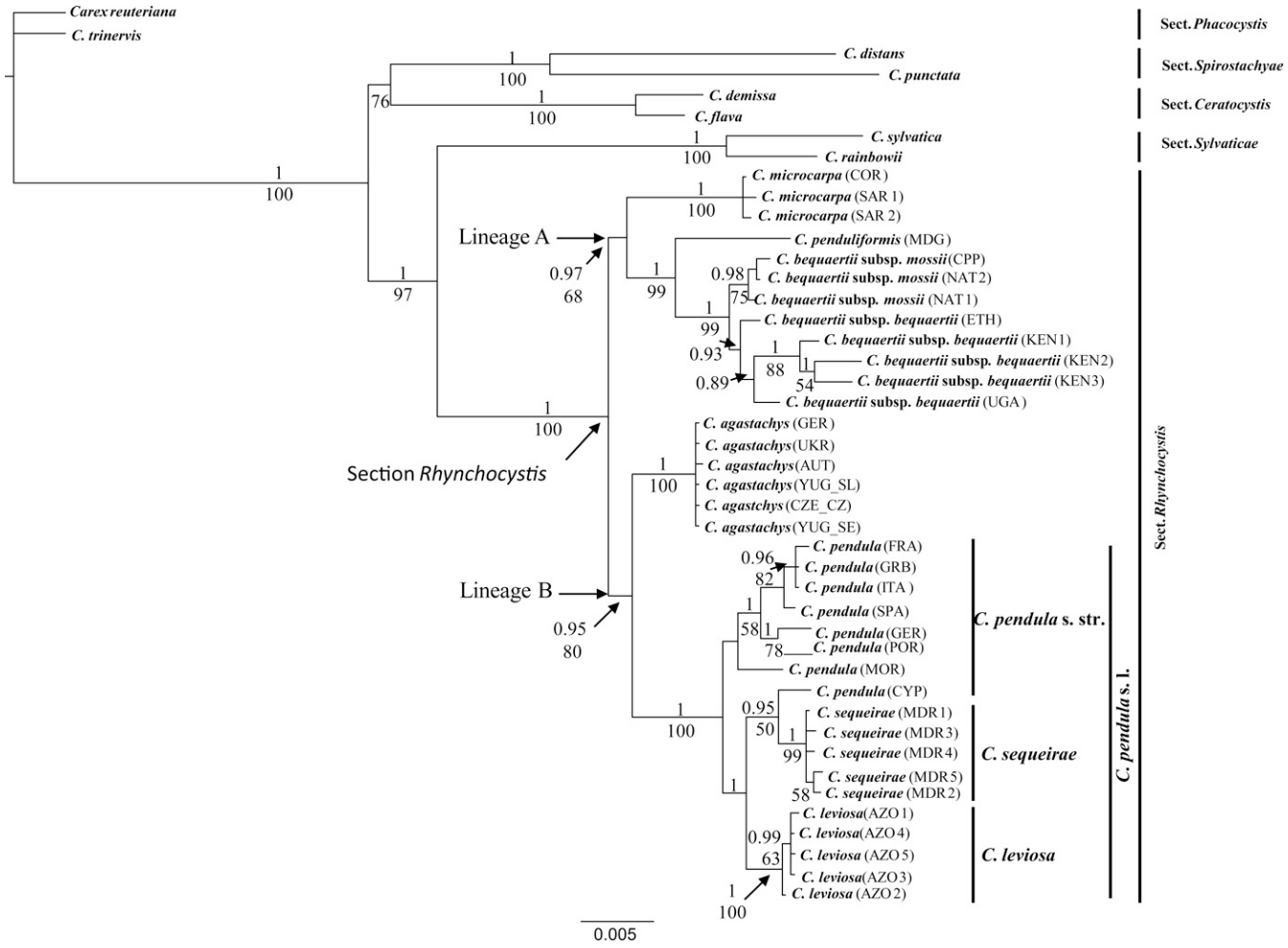

FIG. 1. Majority-rule consensus tree of *Carex* sect. *Rhynchocystis* inferred under Bayesian inference using the combined nDNA-cDNA matrix (*atpIH*, ETS, ITS, *matK*, and *rpl32-trnL*^{UAG} regions) with indels coded. Numbers above and below the branches indicate clade support values: Bayesian posterior probability and bootstrap, respectively. Tip labels indicate species names and codes of the source regions (in parentheses), following "botanical countries" as in Brummitt (2001) and including a number when there is more than one sample from the same region. Scale bar indicates substitutions per site.

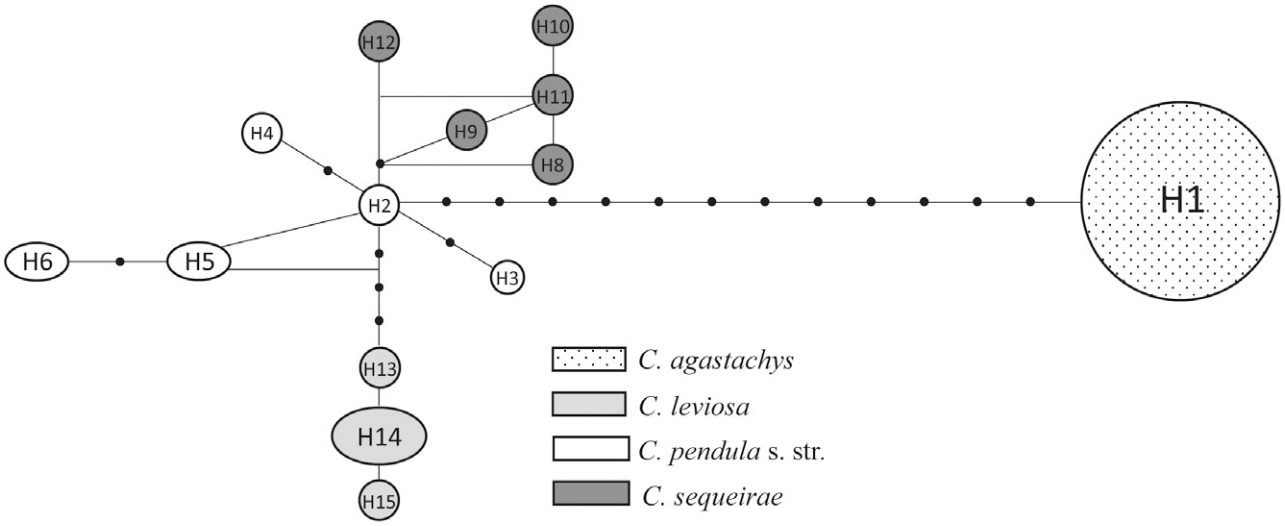

FIG. 2. Statistical parsimony network of the 15 haplotypes retrieved from the analysis of the combined cDNA matrix (*atpIH-matK-rpl32-trnL*^{UAG}) with indels coded. Small black circles represent extinct or unsampled haplotypes, and each line between haplotypes represents a single mutational step. Circle size is proportional to the number of samples displaying the corresponding haplotype. Specific haplotypes obtained for each sample are given in Appendix 1.

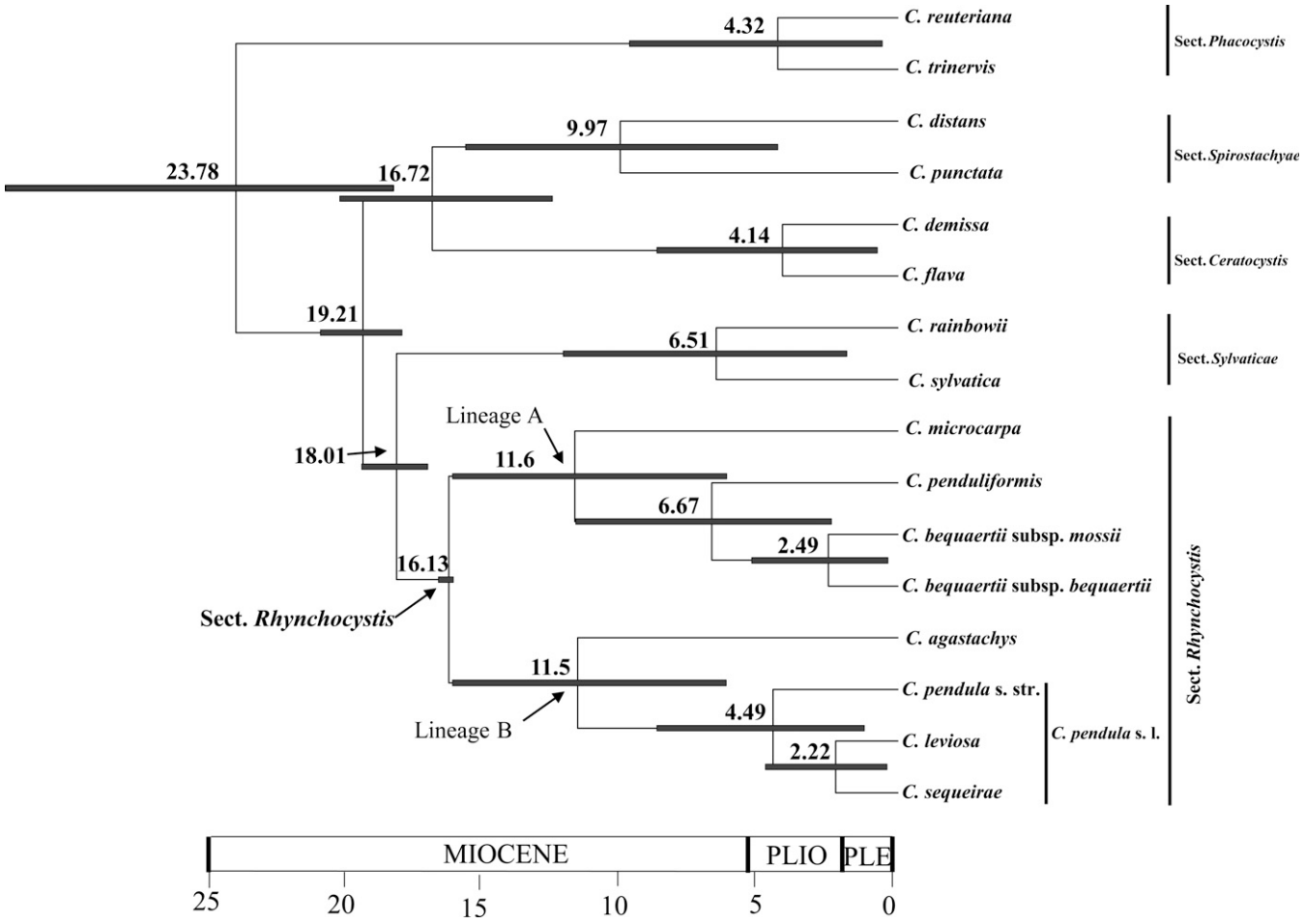

FIG. 3. Maximum clade credibility tree from the molecular dating analysis of *Carex* section *Rhynchocystis* under an uncorrelated lognormal relaxed clock model using a matrix of combined *atpIH*-ETS-ITS-*matK*-*rpl32*-*trnL*^{UAG} regions. Node bars represent 95% highest posterior density (HPD) intervals for the divergence time estimates of each node with posterior probabilities higher than 0.9. PLIO = Pliocene; PLE = Pleistocene.

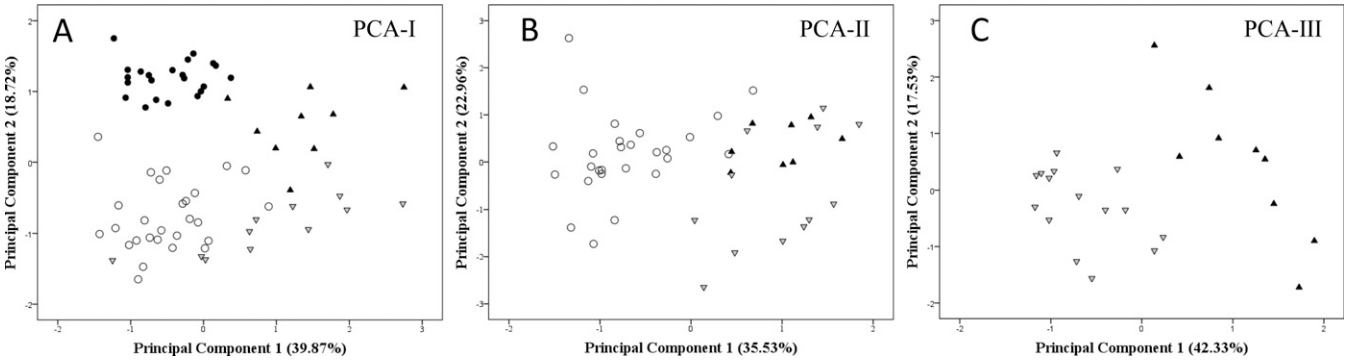

FIG. 4. Scatter plot of the first principal components extracted from the PCA. A. (PCA-I) *C. agastachys*, *C. leviosa*, *C. pendula*, and *C. sequeirae*. B. (PCA-II) *C. leviosa*, *C. pendula*, and *C. sequeirae*. C. (PCA-III) *C. leviosa* and *C. sequeirae*. Symbols depict the different species considered: *C. agastachys* = black circles; *C. leviosa* = black triangles; *C. pendula* = white circles; *C. sequeirae* = white triangles.

showing the micromorphological features of the achene in detail (Fig. 6E–H). Achenes of C. leviosa were narrowly elliptical, and those of C. sequeirae oblong-obovate. The epidermic cells micromorphology was similar in all the studied species, as already known for the other taxa in the section (Míguez et al. 2018). Epidermic cells were polygonal, more or less isodiametric, with straight anticlinal walls, a flattened to slightly concave silica platform, and only one large central silica body. No smaller silica bodies or double central bodies were observed.

DISCUSSION

Two New Species From Macaronesia Overlooked Within C. pendula s. l.—Our results show that there are two distinct insular lineages (from Azores and Madeira) within *C. pendula*

TABLE 2. Comparison among *C. pendula*, *C. leviosa,* and *C. sequeirae* based on the studied macromorphological variables. Characters that display less than 25% overlap in pairwise comparisons at species level are marked by an asterisk (Character abbreviations specified in Table 1). Characters found to be significantly different by the Mann-Whitney *U* test are marked with a hash (#). Those fulfilling both conditions are highlighted in bold.

	C. leviosa	C. pendula
C. pendula	ASL$^{\#}$, DSFS$^{\#}$, LAPSMF$^{\#}$, LTPS$^{\#}$, PSCLL$^{\#}$, PSGLL*, **SAP$^{\#*}$**, SLEAFW$^{\#}$, **UMW$^{\#*}$**	
C. sequeirae	LAPSMF$^{\#}$, LSN*, PSCLL$^{\#}$, PSGLL*, PSW$^{\#}$, UBL$^{\#}$, UMW*	ACHW$^{\#}$, FSLP$^{\#}$, LAPSMF$^{\#}$, LSN*, LTPS$^{\#}$, PSCLL$^{\#}$, PSL$^{\#}$, **SAP$^{\#*}$**, SLI*, UL$^{\#}$, **UMW$^{\#*}$**

s. l. that deserve taxonomic recognition: *C. leviosa* and *C. sequeirae*, respectively. Different lines of evidence, genetic and morphological, support the rank of species for the populations of each of the two Macaronesian archipelagos. The obtained phylogenetic relationships for *Carex* sect. *Rhynchocystis* (Fig. 1; Appendix 3, Míguez et al. 2021) show that each of the two insular population groups from Azores and Madeira constitute strongly supported monophyletic groups nested within a paraphyletic *C. pendula* s. s. (Fig. 1; Appendix 3, Míguez et al. 2021). All individual and combined nuclear and plastid matrices also yielded monophyletic groups for each Macaronesian population set (Appendix 4, Míguez et al. 2021). Each of them has specific plastid haplotypes different between them and *C. pendula* s. s. (Fig. 2). In addition, significant morphological differences have been found between them and *C. pendula* s. s. and *C. agastachys*. Our sequential PCA approach clearly separated samples from Azores and Madeira from those of mainland *C. agastachys* and *C. pendula* s. s. (Fig. 4). Furthermore, DFA confirmed the taxonomic validity of the identified morphogroups corresponding to each of the studied species (> 80% of excluded cases correctly classified; Appendix 5, Míguez et al. 2021), except for *C. pendula* (75%), which was attributed to the low number of excluded cases, since the taxonomic validity of this species has been previously tested with DFA for a more extensive sampling (Míguez et al. 2017). Finally, up to seventeen of the measured characters were found to be different among the two newly described species and *C. pendula* (Fig. 5; Table 2). Moreover, the characterization of the bioclimatic niche (Sanz-Arnal et al. unpubl. data) suggests that *C. leviosa* and *C. sequeirae* are also ecologically differentiated from *C. pendula* s. s.

Our studies on *Carex* sect. *Rhynchocystis* have revealed unexpected taxonomic findings, all emphasizing that *C. pendula* in its traditional concept (i.e. Kükenthal 1909; Egorova 1999) contained neglected (i.e. *C. agastachys*; Míguez et al. 2018) or undescribed species (i.e. *C. leviosa* and *C. sequeirae*; this study). Remarkably, *C. pendula* used to be considered a taxonomically well-known and clearly defined species, with little (if any) taxonomical controversy around it. Previous studies in *Carex* have also uncovered new or neglected taxa from within supposedly well-known species (e.g. Naczi et al. 1998; Benítez-Benítez et al. 2017) which suggests that unrecognized diversity may be still waiting to be unveiled in *Carex*. This indicates that we are far from a complete taxonomic overview of the planetary

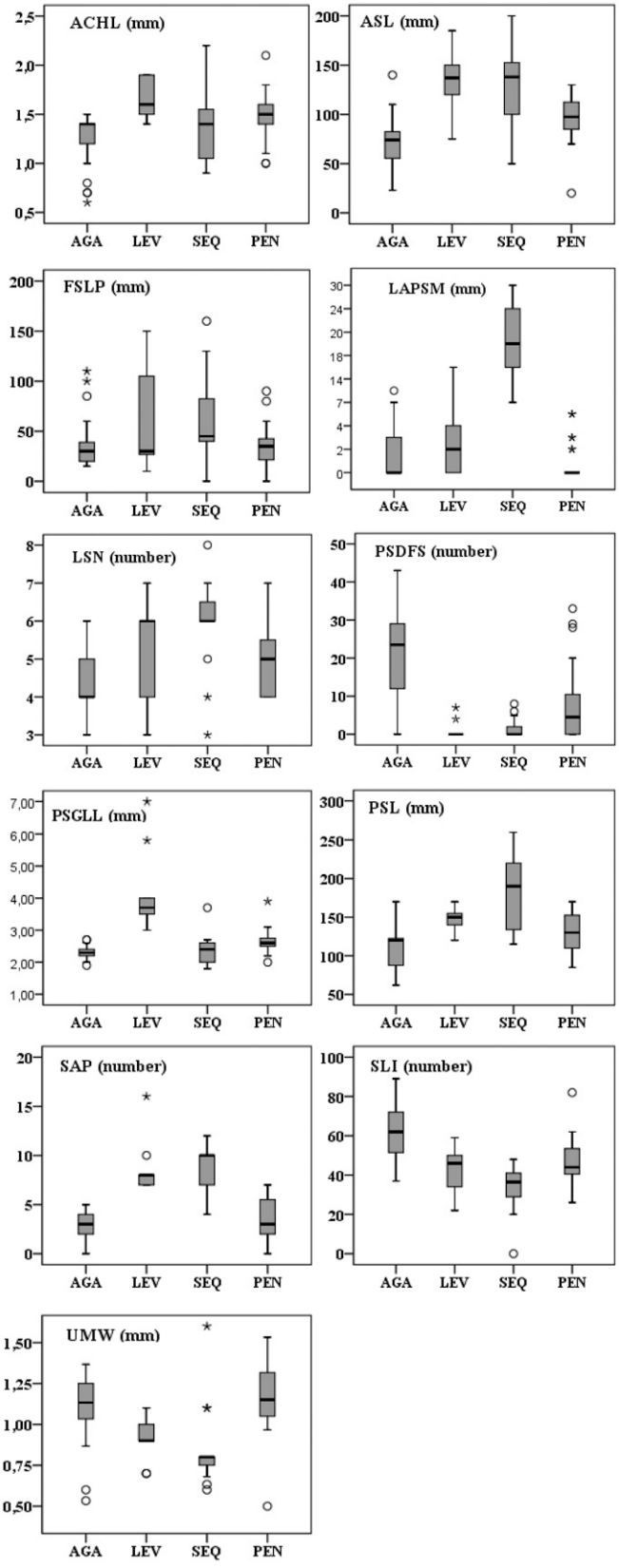

FIG. 5. Boxplots of the most discriminant characters retrieved by DFA or with less than 25% overlap. The X-axis represents the considered species labeled as follows: AGA (*C. agastachys*), LEV (*C. leviosa*), SEQ (*C. sequeirae*), PEN (*C. pendula*). The boxes cover 50% of the data values ranging between the 25th and 75th percentiles, and the lines show 90% of the values between the fifth and 95th percentiles. The line within the box represents the median. Outlying values are indicated by small "o", and extreme values are indicated by asterisks.

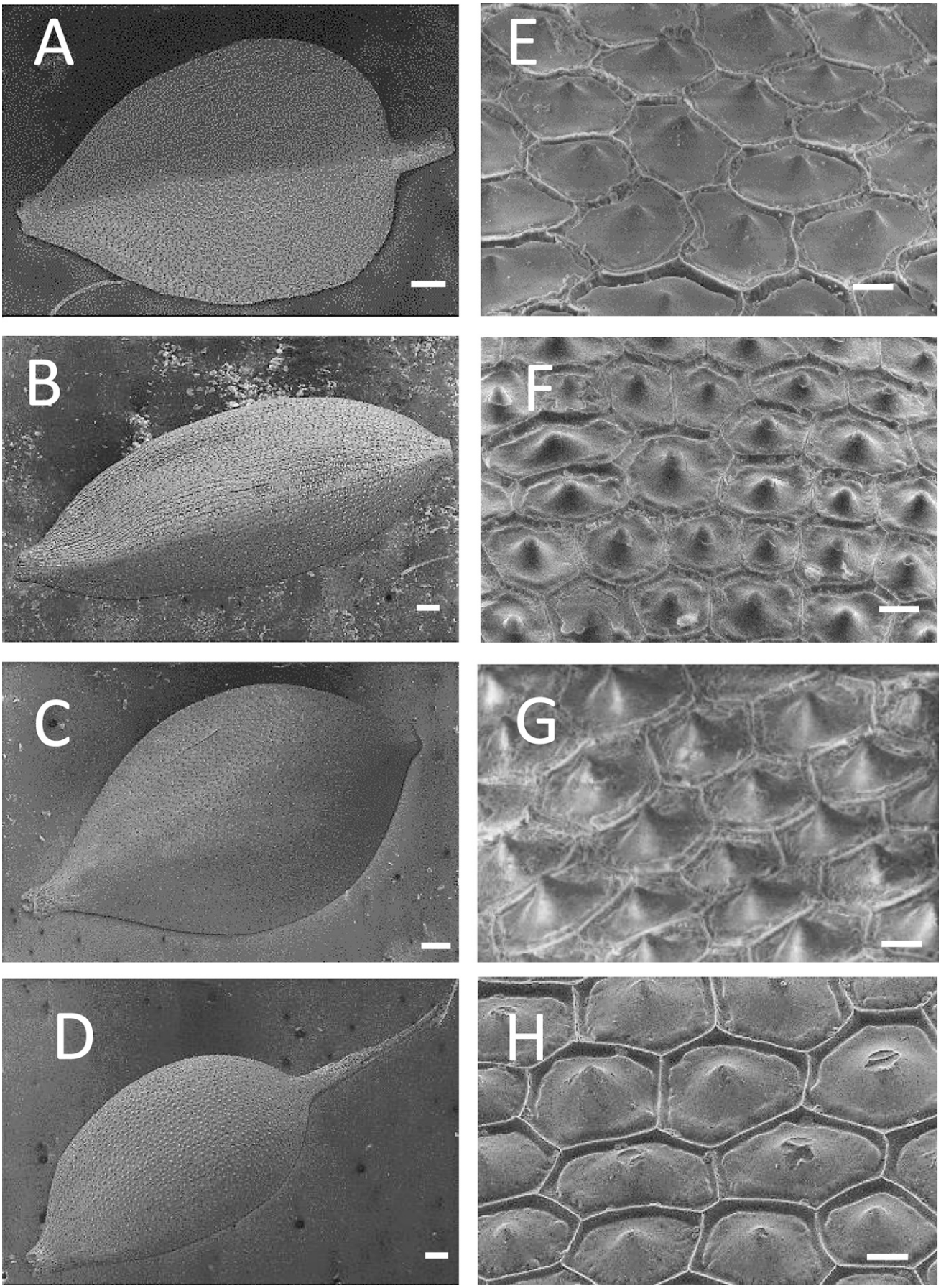

FIG. 6. Scanning electron micrographs of the entire achene (A–D; scale bar 100 µm) and detail of the achene surface (E–H; scale bar 10 µm) in *C. agastachys* (A, E); *C. leviosa* (B, F); *C. pendula* (C, G); and *C. sequeirae* (D, H). Specimens used for the micromorphological study are indicated in Appendix 2 (Míguez et al. 2021).

biodiversity and that integrative taxonomic revisionary works (i.e. including different sources of evidence, such as phylogenetics, morphology, ecology and geography) are still much needed even in allegedly well-known areas like the Western Palearctic.

Paraphyly of C. pendula s. s.: Evolutionary and Taxonomic Implications—While most populations of mainland *C. pendula* s. s. clustered in our study, forming a well-supported monophyletic group, the phylogenetic placement of the samples from Morocco and Cyprus rendered *C. pendula* s. s. paraphyletic (Fig. 1; Appendices 3, 4). All considered species within *Carex* sect. *Rhynchocystis* to date were found to constitute monophyletic groups (Míguez et al. 2017, 2018; except for *C. peduliformis* for which monophyly has not been tested yet). The recognition of paraphyletic taxa in biological classifications has been a long-standing debate (e.g. Rieseberg and Brouillet 1994; Crisp and Chandler 1996; Nordal and Stedje 2005; Velasco 2008; Schmidt-Lebuhn 2012; among many others). However, the phylogenetic scenario we obtained can be explained by taking into account the evolutionary history of *C. pendula* s. l., and in particular, the phylogenetic imprints of oceanic island speciation. The finding of oceanic island endemic species nested within a paraphyletic mainland ancestor is an expected outcome of relatively recent peripatric speciation (also called budding speciation) involving peripherally isolated populations (Emerson 2002; Funk and Omland 2003; Crawford 2010; Anacker and Strauss 2014; Stuessy et al. 2014). The two Macaronesian species match well with this pattern, in which two different founder events could have taken place in Azores and Madeira after colonization of the archipelagos by *C. pendula*-like ancestors. This would have conveyed reproductive isolation and genetic drift of the island populations, with subsequent genetic differentiation resulting in two strongly-supported lineages (Fig. 1; Appendix 3, Míguez et al. 2021), with exclusive haplotypes (Fig. 2) and clear morphological differentiation between them and *C. pendula* s. s. (Fig. 4). Morocco and Cyprus *C. pendula* s. s. populations responsible for its paraphyly likely belong to the ancestral mainland genetic stock which has not yet disappeared due to incomplete lineage sorting (Funk and Omland 2003; Vanderpoorten and Long 2006). With time, extinction and sorting of ancestral haplotypes may likely result in a monophyletic *C. pendula* s. s. (Crawford 2010; Anacker and Strauss 2014). This way, paraphyly in *C. pendula* s. s. could be considered a natural transition stage in its evolution (Hörandl and Stuessy 2010). Paraphyletic species are widely accepted as natural products of the evolutionary process (Brummitt 2002; Hörandl 2006; Hörandl and Stuessy 2010). Furthermore, paraphyletic species have also been detected and accepted in *Carex* (King and Roalson 2009; Maguilla et al. 2015). We agree that species delimitation should not solely be based on the phylogenetic species concept, but it should also take into account cohesiveness and distinctiveness (Stuessy et al. 2014).

As argued above, while a paraphyletic *C. pendula* does not seem to pose too much of a conflict for the recognition at species rank of *C. leviosa* and *C. sequeirae*, we cannot completely rule out that the *C. pendula* populations from Cyprus and Morocco might constitute cryptic taxa yet to be described. Future biosystematic studies focusing on *C. pendula* in the Mediterranean basin must elucidate whether these populations deserve taxonomic recognition.

Colonization of Macaronesia by Carex sect. Rhynchocystis—The haplotype network (Fig. 2) indicates at least two independent colonizations of Macaronesia from the mainland, each accounting for the colonization of one archipelago (Azores and Madeira). This is inferred by the fact that: 1) the two sets of island populations do not share any haplotype (or ribotype; see Míguez et al. 2017); and 2) they are not directly related and appear as derived from those of *C. pendula* s. s. from different parts of the network (Fig. 2). These colonizations could have taken place by means of two long-distance dispersal events of *C. pendula*-like ancestors from the Western Palearctic during the Plio-Pleistocene (2.22 Ma, 95% HPD 0.39–4.75 Ma; Fig. 3). Most documented Macronesian plant colonizations have been inferred to have originated in the Mediterranean region (Carine et al. 2004). The divergence time of the clade, including *C. leviosa* and *C. sequeirae,* is congruent with the geological origin of both the Azores archipelago (between ca. 0.3 and 6 Ma) and Madeira island (< 5.6 Ma) (Borges et al. 2008; Moura et al. 2019). Only one other section of *Carex*, the closely related *Carex* sect. *Spirostachyae* (Fig. 1), is also represented by different endemic species in the Macaronesian archipelagos (Appendix 6, Míguez et al. 2021): *C. lowei* Bech (Madeira), *C. hochstetteriana* J. Gay ex Seub. (Azores), and *C. perraudieriana* (Kük. ex Bornm.) Gay ex Kük. (Canary Islands), all of them laurisilva-dwelling plants as *C. leviosa* and *C. sequeirae*. However, in this case, the number of involved colonizations of Macaronesia is not clear (Escudero et al. 2009; Martín-Bravo and Escudero 2012). In addition, the divergence time of at least some of these endemic species (i.e. *C. lowei* and *C. hochstetteriana*) could date back to the Late Miocene (Escudero et al. 2009; Martín-Bravo et al. 2019a). Interestingly, the two other sections of *Carex* closely related to *Carex* sect. *Rhynchocystis* also have one Azorean endemic each: *C. vulcani* Hochst. ex Seub. (*Carex* sect. *Sylvaticae*), and *C. demissa* subsp. *cedercreutzii* (Fagerstr.) J.Koopman (*Carex* sect. *Ceratocystis*). In this case, the origin of these taxa seems to be placed in the Pleistocene (Martín-Bravo et al. 2019a). Previous studies have also remarked other shared biogeographic patterns between these closely related sections of *Carex* (Martín-Bravo et al. 2013; Míguez et al. 2017), which may reflect a common evolutionary history. While *C. lowei* and *C. hochstetteriana* could constitute paleoendemic species, the Plio-Pleistocene origin inferred for *C. sequeirae*, *C. leviosa, C. vulcani*, *and C. demissa* subsp. *cedercreutzii* suggests they could represent neoendemics (Kondraskov et al. 2015; Mairal et al. 2018). This highlights the remarkable historical contribution of the genus *Carex* to the assemblage of the Macaronesian flora from Neogene times, and in particular, to laurisilva endemicity.

Taxonomic Diversity of Carex in Azores and Madeira—Despite recent intense efforts towards an exhaustive biodiversity checklist of these Macaronesian archipelagos (Borges et al. 2008, 2010), their catalog of life appears far from complete, as exemplified by *Carex*. We performed a comparison between the recent *Carex* checklists for Madeira and Azores (Jardim and Menezes de Sequeira 2008; Silva et al. 2010, respectively), and the national checklist (Menezes de Sequeira et al. 2012), as well as chorological databases compiled by taxonomic experts (Jiménez-Mejías and Luceño 2011; Govaerts et al. 2020), and specific works dealing with the evolution of Azorean flora (Schaefer 2002; Schaefer et al. 2011). Surprisingly, this comparison revealed incongruences for up to 20 of the 29 taxa reported for both archipelagos by these relevant checklists (Appendix 6, Míguez et al. 2021). These affect not only the number and identity of *Carex* taxa present in the archipelagos but also their native and taxonomic status (Appendix 6, Míguez

et al. 2021). We integrate all the available information and present an updated and cross-checked diversity account of *Carex* for the Azores and Madeira (Appendix 6, Míguez et al. 2021; including the species herein described). We recognize 20 taxa for the Azores, of which 12 are native (five endemic), four introduced, and four of doubtful occurrence and/or status. For Madeira, we recognize 11 taxa, of which ten are native (two endemic), and one of doubtful status. Nonetheless, a critical revision of *Carex* in Macaronesia is needed.

The number of vascular plant taxa, particularly of native and endemics, is considerably lower in Azores (1120 taxa, 209 native, 69 endemics; Schaefer pers. obs.) than in Madeira (1204 taxa, 708 native, 154 endemics; Jardim and Menezes de Sequeira 2008). However, taking into account only native species, the degree of endemism in Azores is comparatively higher than in Madeira (33.2% vs. 21.7%, respectively). In addition, few Azorean endemics are restricted to a single island; most are widespread within the archipelago. These features have been termed the "Azores diversity enigma" (Carine and Schaefer 2010), which has been explained by geological, geographical, and ecological attributes of the archipelago (Triantis et al. 2012), as well as to an incomplete taxonomic knowledge of Azorean plant diversity (Schaefer et al. 2011; Connor et al. 2013; Moura et al. 2019). Interestingly, *Carex* displays an opposite pattern of taxonomic diversity, with more native (12 vs. 10) and endemic (five vs. two) taxa in Azores than in Madeira (Appendix 6, Míguez et al. 2021). This could be related to the inverted latitudinal species richness gradient, which is well-known at the global level in *Carex* (Escudero et al. 2012). It could also be applicable at the regional level in Macaronesia, especially taking into account that the diversity of *Carex* in the Canary Islands (11 taxa, of which two are endemic; Acebes-Ginovés et al. 2010, Martín-Bravo et al. 2019b) and Cape Verde (two taxa, both endemic; Sánchez-Pinto et al. 2005) is progressively lower.

Taxonomic Treatment

The following treatment accounts for the variation of *Carex* sect. *Rhynchocystis* in the Macaronesian archipelagos of Azores (*C. leviosa*) and Madeira (*C. sequeirae*) (Table 3). Since the newly considered taxa are split from a formerly more widely conceived *C. pendula*, we also included a description of the resulting more narrowly circumscribed *C. pendula*.

Carex leviosa Míguez, Jim.-Mejías, H. Schaef. & Martín-Bravo, sp. nov. Type: Azores. São Miguel Island, NW part of the island, between Mosteiros and Pilar de Bretanha, João Bom, about 500 meters before the village; dry stream in ravine, humid and shady understory in lauroid forest with many introduced species. 26 August 2015. *S. Martín-Bravo and L. Bellón 136SMB15* (holotype: UPOS-6520!, isotypes: MA!, MADJ!).

Carex leviosa differs from *C. pendula* mainly (Table 3) by its pistillate glumes conspicuously longer than the utricles (vs. equaling or shorter than the utricles), with a long and scabrid awn and with hyaline margins (vs. acute or mucronate, glabrous in all of its surface, and without hyaline margin).

Stems 150–250 cm × 2–4 mm, smooth. **Leaf-blades** 10–20 mm wide. **Ligule** (10–)15–32(–40) mm long, reddish to purple-reddish, apex acute or emarginated. **Basal sheaths** reddish to purple-reddish entire and scale-like. **Inflorescence** racemose with 1 male spike and 1 female spike clustered at the apex and (3–)4–6(–7) lateral female spikes; lowest bract leaf-like slightly shorter than the inflorescence. **Male spike** (75–)115–151(–185) × 3–5 mm, entirely male, fusiform, nodding, sessile. **Lateral spike** 120–170 × 5–7 mm, entirely female rarely very shortly androgynous, long cylindrical, nodding to pendulous, long-pedunculated with peduncle (10–)18–107(150) mm long distal ones with the peduncle progressively shorter sparsely scabrid, all with a tubular cladoprophyll at the base. **Staminate glumes** 3.4–7.5 × 0.7–1.1 mm linear oblong or narrowly obovate, brown, midrib prolonged in a scabrid awn. **Pistillate glumes** 3–4.9(–7) × 0.7–1.2 mm, narrowly ovate to narrowly obovate, body longer than the utricles, brown with hyaline margins, midrib pale prolonged into a scabrid awn (0.4–)0.7–1 mm long. **Utricles** 2.5–3.1 × 0.7–1.1 mm, ellipsoid, prominently veined, greenish to brown at maturity, apex gradually attenuated into a beak, beak 0.2–0.5 mm long. **Achenes** (1.1–)1.4–1.9 × 0.7–0.9 mm, narrowly elliptical, brown. Figure 7.

Distribution—*Carex leviosa* is endemic to the Azores archipelago (Portugal) [AZO], where it is distributed in all nine main islands (Corvo, Faial, Flores, Graciosa, Pico, Santa Maria, Terceira, Sao Miguel, and Sao Jorge).

Habitat—The species is found in shady and humid laurisilva forest understory (often dominated by the invasive Australian *Pittosporum undulatum*); also in coastal *Morella-Picconia* forest and old plantations of the Japanese Cedar (*Cryptomeria japonica*), at 0–800 m a. s. l.

Phenology—Plants flower from July to September.

Etymology—The species epithet was proposed by Paula and Raquel Herrero Míguez, Mónica Míguez's daughters. It refers to the magic levitation spell "Wingardium Leviosa" (pronounced "leviOsa, not leviosA," as quoting Hermione in the book *Harry Potter and the Sorcerer's Stone*), from J. K. Rowling's Harry Potter universe, as the thick lateral spikes of *C. leviosa* hang from thin long-peduncles looking like they are levitating in the air. The resulting term is analogous to the meaning of the epithet of the species in which *C. leviosa* was included until now (i.e. *C. pendula*), which means 'hanging.' The selected epithet intends to commemorate Paula and Raquel, who are great fans of the Harry Potter book series and movies. At the same time, we want the epithet to also serve as a tribute to J. K. Rowling, writer of the Harry Potter books, because of her dedication and concern about conservation of nature and wildlife as expressed in her work *Fantastic Beasts and Where to Find Them* (Rowling 2001).

Informal Conservation Status—The species is distributed in all Azores islands, and with numerous populations across most of them (Schaefer pers. obs). It has been considered not endangered and common in Azores (Schaefer et al. 2011), although it can be locally scarce on the drier islands (Santa Maria and Graciosa; Schaefer 2002; Schaefer pers. obs.). Therefore, the species does not appear to fulfill any of the IUCN criteria (IUCN 2012) required to be classified as endangered, and we hypothesize that if a formal conservation assessment were performed the conservation status would be Least Concern (LC).

Carex pendula Huds. Fl. Angl.: 352 (1762). Type: Morison. 1699. Pl. Hist. Univ. Oxon. 3m, sect. 8. tab. 12. Fig. 4. (Neotype designated by Egorova (1999)). England. London, Hampstead Heath, between Hampstead and Highgate, Ken Wood lake –vc 21, Middlesex. *M. A. Spencer MAS-2012–040* (epitype:

TABLE 3. Comparison of the main diagnostic morphological characters distinguishing *C. leviosa*, *C. pendula*, and *C. sequeirae*.

	C. leviosa	*C. pendula*	*C. sequeirae*
Stems	150–250 cm × 2–4 mm	50–180(240) cm × 2–4(6) mm	< 100 cm × (1.4)1.9–2.8(3.4) mm
Peduncle of lowermost spike	(10)18–107(150) mm, sparsely scabrid	(0)20–45(90) mm, smooth or sparsely scabrid	(0)40–95(160) mm, usually smooth
Inflorescence spike composition	1 male spike and 1 female spike clustered at the apex, and (3–)4–6(–7) female lateral spikes, exceptionally shortly androgynous	Inflorescence with 1(2) male apical spikes, and 4–6(7) female, lateral spikes exceptionally shortly androgynous	Inflorescence with 1–2(5) male spikes at the apex, and 4–6(8) androgynous lateral spikes, with a male tip 10–30 mm long
Pistillate glume	Conspicuously longer (3–4.9(7) mm long) than the utricles, ratio utricle length/pistillate glume length < 1; apex long-awned, with hyaline margin	Equal to or shorter (2.5–2.8(3.9) mm long) than the utricle, ratio utricle length/pistillate glume length ≥ 1; apex acute or mucronate, without hyaline margin	Generally shorter (1.8–2.6(3.7) mm long) than the utricles or shortly surpassing it, utricle length/pistillate glume length ≥ 1; apex usually awned, without hyaline margin
Utricle	2.5–3.1 × 0.7–1.1 mm	(1.4)2–3.6 × (0.5)1.1–1.5 mm	(1.4)2.2–2.5(3.1) × 0.6–0.8(1.6) mm
Achene	Narrowly ellipsoid (1.1)1.4–1.9 × 0.7–0.9 mm	Ellipsoid (1)1.4–1.7(2.1) × (0.4)0.7–1(1.5) mm	Oblong-obovate 0.9–1.6(2.2) × (0.3)0.5–1 mm

BM-001074530!, designated by Jiménez-Mejías et al. 2017; isoepitype: UPOS-5004!).

Carex maxima Scop., Fl. Carniol. ed. 2. 2: 229 (1772). TYPE: SLOVENIA. Carniola. *G.A. Scopoli s.n.* (lectotype: LINN-1100.94!; designated by Jiménez-Mejías et al. 2017).

Stems 50–180(–240) cm × 2–4(–6) mm smooth or slightly scabrid distally. **Leaf-blades** (6–)10–14(–19) mm wide. **Ligule** 20–37(–65) mm long, whitish hyaline becoming brownish when dry rarely slightly reddish-tinged, apex acute to subacute. **Basal sheaths** inconspicuous dark brown or reddish; often the stem bases covered by marcescent leaves light brown. **Inflorescence** with 1(–2) male spikes at the apex and 4–6(–8) lateral female spikes rarely shortly androgynous; lowermost bract leaf-like equaling or slightly shorter than the inflorescence. **Male spike** (20–)85–113(–130) × (2.5–)4–6(–9) mm, fusiform or cylindrical erect, spreading or nodding, sessile or subsessile, sometimes with a peduncle up to 2.5 cm. **Lateral spikes** (85–)110–155(–170) × 3–6(–8) mm, entirely female rarely very shortly androgynous and then with male tips < 5 mm, long-cylindrical, flexuose, spreading or pendulous, subsessile or with peduncles (0–)20–45(–90) mm, usually smooth rarely sparsely scabrid. **Staminate glumes** 3.6–6.6(–9.8) × 0.5–1(–1.9) mm, linear, oblong or narrowly obovate, apex acute, reddish-brown with a hyaline midrib. **Pistillate glumes** 2.5–2.8(–3.9) × 0.7–1.2 mm, narrowly ovate to narrowly obovate, mucronate, the body generally shorter than the utricles or shortly surpassing them, reddish-brown with a greenish midrib, tipped by a mucro 0–0.5 mm long. **Utricles** (1.4–)2–3.6 × (0.5–)1.1–1.5 mm, ovoid or ellipsoid, greenish or yellowish-green, beak 0.2–0.5 mm, apex truncate. **Achenes** (1–)1.4–1.7(–2.1) × (0.4–)0.7–1(–1.5) mm, elliptical with the maximum width at the middle or slightly above it, brown to straw-colored . See Míguez et al. 2018, Fig. 8, for detailed iconography.

Distribution—*Carex pendula* is found in Europe and the Mediterranean, including northwestern Africa and the Mediterranean shores of southwestern Asia, introduced in New Zealand and North America. ALB, ALG, BGM, cal, chs, COR, CYP, DEN, EAI, FRA, GER, GRB, GRC, BEL, DEN, HUN, IRE, IRQ?, ITA, KRI, LBS, MOR, NET, nzs, ore, PAL?, POR, SAR, SIC, SPA, swe, SWI, TUN, TUR, YUG_CR, YUG_MN, YUG_SL (geographic region abbreviations follow Brummitt 2001).

Habitat—The species is usually found in riparian forests beside streams on damp clayish soils, at 25–1370 m a. s. l.

Phenology—Plants flower from (March) April to August (December).

Etymology—The specific epithet is from the Latin "pendulus" meaning hanging, in reference to the pendulous lateral spikes.

Informal Conservation Status—The wide distribution of *C. pendula* and a large number of known populations across the Western Palearctic prevents the application of any of IUCN endangered categories. We therefore hypothesize that if a formal conservation assessment were performed, the conservation status would be Least Concern (LC).

Carex sequeirae Míguez, Jim.-Mejías, Benítez-Benítez & Martín-Bravo., sp. nov. TYPE: MADEIRA. Madeira Island, Ilha, road that goes down the riverbank from the town center; 279 m a. s. l, 32°48'30.8"N, 16°55'13.4"W; near a waterfall, accompanying vegetation: ferns, rhododendrons. 1 June 2018. *C. Benítez-Benítez and M. Míguez 66CBB18* (holotype: UPOS-10570!, isotypes: MA!, MADJ!).

Carex myosuroides Lowe, Trans. Cambridge Philos. Soc. 4(1): 10 (1833), nom. illeg., non *Carex myosuroides* Vill., Prosp. Hist. Pl. Dauphiné: 17 (1779). Type: Madeira. '653. *Carex myosuroides*, from Rev. M. Lowe. 1837' (neotype: K-000363419!; designated by Míguez et al. 2018).

Carex pendula var. *myosuroides* Boott., Ill. Gen. Carex 4: 197 (1867). TYPE: MADEIRA. '653. *Carex myosuroides*, Madeira, from Rev. M. Lowe. 1837'. (lectotype: K-000363419!; designated by Míguez et al. 2018).

Carex sequeirae differs from *C. pendula* (Table 3) by its invariably androgynous lateral spikes, terminated in a narrowly conical tip 10–30 mm long of staminate flowers (vs. lateral spikes female, exceptionally shortly androgynous), and by its oblong-obovate nutlets (vs. elliptical in *C. pendula*).

Stems < 100 cm × (1.4–)1.9–2.8(–3.4) mm, smooth. **Leaf-blades** 9–16 mm wide; **ligule** (10–)18–25(–32) mm long, whitish hyaline becoming brownish when dry, apex acute to subacute; basal sheaths scale-like reddish. **Inflorescence** with 1–2(–5) male spikes at the apex and 4–6(8) lateral androgynous spikes; lowermost bract leaf-like equaling or slightly shorter than the inflorescence. **Male spikes** (50–)100–155(–200) × 4–6 mm

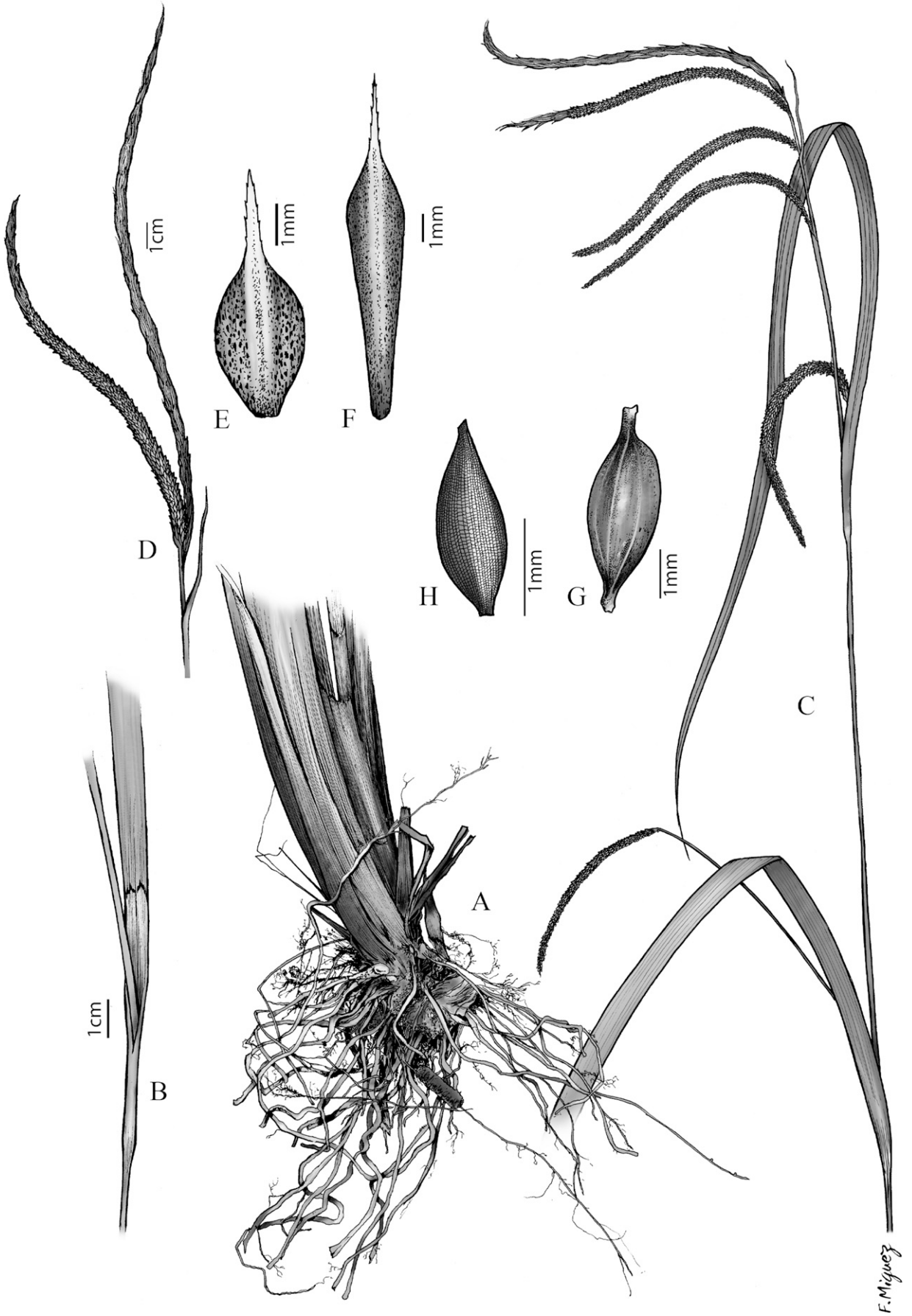

FIG. 7. Botanical illustration of the holotype of *Carex leviosa* Míguez et al. Portugal, Azores, San Miguel, NW of the island, between Mosteiros and Pilar de Bretanha, 26 August 2015, *S. Martín-Bravo and L. Bellón 136SMB15* (UPOS-6520). A. Culm base. B. Ligule. C. Inflorescence. D. Male and female spikes clustered at apex. E. Pistillate glume. F. Staminate glume. G. Utricle. H. Achene. Drawing by F. Míguez.

long-fusiform, nodding, subsessile. **Lateral spikes** (115–)130–240(–260) × 3–5(–8) mm frequently shortly androgynous and finished in a conical tip (7–)15–24(–30) mm containing staminate flowers; long-cylindrical, flexuose, spreading or pendulous. Distal spikes sessile or subsessile, proximal spikes with peduncle longer as lower the spike, peduncle (0–)40–95(–160) mm usually smooth. **Staminate glumes** (3.4–)4.6–7(0.35) × 0.6–0.9(–1.2) mm linear oblong or narrowly obovate, apex acute to subrounded, brownish with a midrib. **Pistillate glumes** 1.8–2.6(–3.7) × 0.5–1 mm, narrowly ovate to narrowly obovate, the body generally shorter than the utricles or shortly surpassing them, reddish-brown with a greenish midrib prolonged in a scabrid awn 0.4–0.7 mm. **Utricles** (1.4–)2.2–2.5(–3.1) × 0.6–0.8(–1.6) mm ovoid or ellipsoid, greenish, red-dotted; beak 0.1–0.3 mm, apex truncated. **Achenes** 0.9–1.6(–2.2) × (0.3–)0.5–1 mm oblong-obovate, brownish to yellowish. Figure 8.

***Distribution*—**The species is found on Madeira island [MDR].

Habitat*—Carex sequeirae* is found on wet soils in shaded laurisilva understory mainly along irrigation channels (levadas) and streams, at 130–600 m a. s. l.

***Phenology*—**Plants flower from April to June.

***Etymology*—**The specific epithet, *sequeirae*, honors Prof. Dr. Miguel Pinto da Silva Menezes de Sequeira (born 1964), renowned Portuguese botanist living and working in Madeira and Professor of the University of Madeira. We would like to acknowledge him for his passionate and tireless activity in favor of the study and conservation of Madeiran native flora.

***Informal Conservation Status*—**In contrast to *C. leviosa*, *C. sequeirae* is a rare and restricted species with very few known persisting populations (four) in the north of Madeira, all of them comprising very few individuals. A total of at least eight populations were deduced from the studied material (Appendix 2, Míguez et al. 2021). However, during recent fieldwork in Madeira (Míguez and Benítez-Benítez pers. obs.; Menezes de Sequeira pers. obs.), we could only confirm the persistence of four populations, the destruction of at least one historical population near the capital (Funchal) by infrastructure development, and the apparent absence of living individuals in the remaining three populations, although further exhaustive field surveys are needed to search for additional individuals/populations. The four known populations are enclosed in an extent of occurrence (EOO) of only 10.64 km^2. This would point to the application of criteria B1 of the Critically Endangered (EN) category (threshold of 100 km^2; IUCN 2012). In addition, the destruction of at least one population also conveying a reduction in the EOO, AOO, and the number of individuals fulfills condition B1b (i, ii, iv, v). However, the number of locations (i.e. four) does not fulfill the condition and, therefore, prevents the application of CR category since two conditions of criteria B must be fulfilled. Nonetheless, we could only observe a total of 28 living individuals in the field (ranging between 5–10 per population), which would qualify the species as critically endangered (CR) under criterion D. Therefore, with the currently available data, we hypothesize that if a formal conservation assessment were performed, the conservation status of this species would be CR (D). Interestingly, an abnormally high proportion of the individuals observed in the field displayed aborted achenes and morphological aberrations possibly caused by fungal infestation (Menezes de Sequeira pers. obs.), which could be related to genetic problems derived from the extremely low population size (e.g. inbreeding depression; Kariyat et al. 2012).

Despite being a restricted and endangered endemic, the conservation of *C. sequeirae* has been neglected due to its masking under *C. pendula*, a widespread and frequently abundant species across its range. Given the alarming likely conservation status of this species, we stress here the urgent need of both in-situ and ex-situ conservation programs, as well as its inclusion in conservation legislation to enforce legal protection in order to safeguard its future.

Key to the Species of Carex Section Rhynchocystis

1. Uppermost spike with male and female flowers intermingled, rarely entirely male. . . . . *C. bequaertii*
   2. Pistillate glumes brown, middle nerve usually lighter than the sides; ligule subacute, sometimes emarginated. . . . . *C. bequaertii* subsp. *bequaertii*
   2. Pistillate glumes light brown, middle nerve usually darker than the sides; ligule emarginated. . . . . *C. bequaertii* subsp. *mossii*
1. Uppermost spike entirely male, rarely bearing female flowers intermingled with the male ones 3
   3. All spikes erect or slightly spreading, subsessile, rarely the lowermost one with a peduncle up to 50 mm; leaves strongly coriaceous, 4–9 mm wide; stems 40–100 cm long; peduncle of the proximal female spike smooth . . . . . *C. microcarpa*
   3. At least the lowermost spike conspicuously pendulous when mature, with a peduncle (0)25–100(160) mm; leaves herbaceous, not coriaceous, (6)9–20 mm wide; stems usually more than (50)100 cm long; peduncle of the proximal female spike smooth to scabrid 4
      4. Uppermost two to five lateral spikes sessile or subsessile, closely arranged, separated by short internodes 5–7 mm long; mature utricles and achenes dark-brown to blackish. . . . . *C. penduliformis*
      4. Uppermost two lateral spikes usually pedunculate, rarely sessile or subsessile, separated by conspicuous internodes (2)20–100 mm long, most proximal ones with internodes even longer; mature utricles and achenes greenish, yellowish, or brown. 5
         5. Pistillate glume conspicuously longer than the utricles, with ratio utricle length/pistillate glume length < 1; pistillate glume long-awned (awn (0.4–)0.7–1 mm long); inflorescence with 1 male spike and 1 female spike clustered at the apex, and 4–7 lateral spikes, female or exceptionally shortly androgynous . . . . . *C. leviosa*
         5. Pistillate glume equaling or shorter than the utricle, with ratio utricle length/pistillate glume length ≥ 1; pistillate glume apex acute, mucronated or awned (awn 0–0.7 mm long); inflorescence with 1(2) male apical spikes, and (3)4–6(8) lateral spikes, female or androgynous. . . 6
            6. Achene markedly obovate, with the widest point near the top; ligule of the upper leaves and bracts conspicuously red or reddish purple; peduncle of the lowermost spike conspicuously scabrid; utricle beak bidentate or truncate . . . . . *C. agastachys*
            6. Achene ellipsoid or oblong-obovate, with the widest point at the middle or slightly above it; ligule of the upper leaves and bracts whitish hyaline, becoming pale brown or orangish when dry, very rarely slightly reddish-tinged; peduncle of the lowermost spike smooth or very sparsely scabrid; utricle beak truncate 7
               7. Lateral spikes female, sometimes the proximal-most one(s) shortly androgynous and then with a male tip < 5 mm long; pistillate glumes acute or mucronate, mucro 0–0.5 mm long. . . . . *C. pendula*
               7. All lateral spikes androgynous, tipped by a narrowly conical male part (7–)15–24(–30) mm long; pistillate glumes awned, awn 0.4–0.7 mm long. . . . . *C. sequeirae*

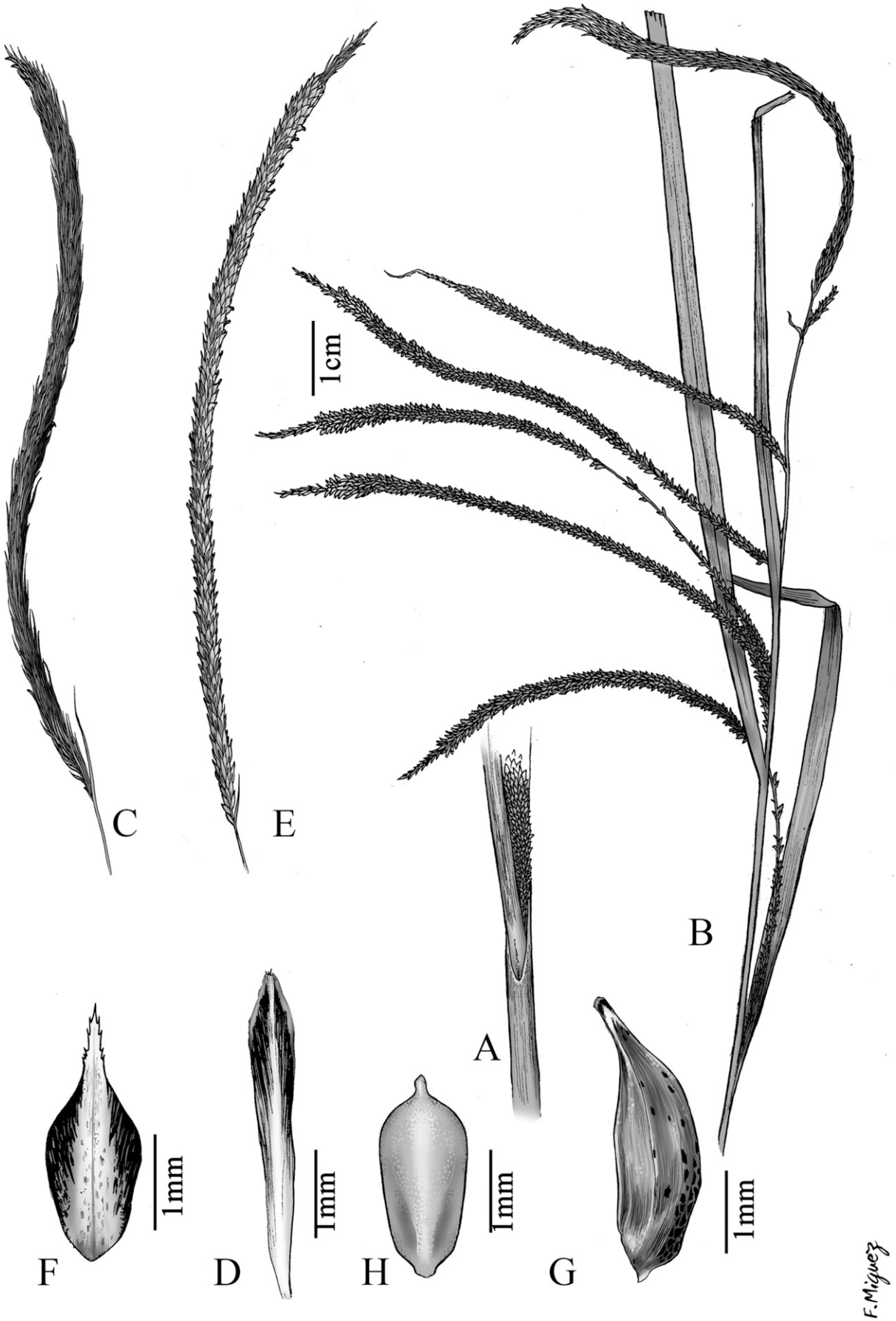

FIG. 8. Botanical illustration of *Carex sequeirae* Míguez et al. Portugal, North side of Madeira by rivulets, 1837. *J. Boott s.n.* (K-000363417). A. Ligule. B. Inflorescence. C. Male apical spike. D. Staminate glume. E. Uppermost lateral spike. F. Pistillate glume. G. Utricle. H. Achene. Drawing by F. Míguez.

Acknowledgments

The authors thank all staff from herbaria E, BM, G, K, LISU, M, MADJ, MADM, MHA, P, SEV, TUM, UPOS, UPS for granting us access to their collections and for providing plant material; M. Sequeira (Universidade da Madeira) for providing plant material and for help with fieldwork in Madeira; L. Bellón for help during fieldwork in Azores; F. Míguez for the illustrations of specimens; the staff of UPOS botanical laboratory and Universidad Pablo de Olavide microscopy service, in particular to E. Ritoré, C. Barciela, and F. Rodríguez Rojas for technical support. This research was supported by the Spanish Ministry of Science and Technology through the project CGL2016-77401-P.

Author Contributions

SM-B and PJ-M conceived the idea, collected plant material, analyzed data, and drafted the manuscript; MM collected plant material, carried out the laboratory work, and analyzed the data; CBB collected plant material; HS provided critical materials and revised the writing of the manuscript. All authors contributed to the writing of the final version.

Literature Cited

Acebes-Ginovés, J. R., M. C. León-Arencibia, M. L. Rodríguez Navarro, M. A. Aguilar, A. García, P. L. Pérez de Paz, O. Rodríguez-Delgado, V. E. Martín Osorio, and W. Wildpret de la Torre. 2010. Pteridophyta, Spermatophyta. Pp. 122–172 in *Lista De Especies Silvestres De Canarias. Hongos, Plantas Y Animales Terrestres*, eds. M. Arechavaleta, S. Rodríguez, N. Zurita and A. García. Tenerife: Gobierno de Canarias.

Aigoin, D. A., N. Devos, S. Huttunen, M. S. Ignatov, J. M. Gonzalez-Mancebo, and A. Vanderpoorten. 2009. And if Engler was not completely wrong? Evidence for multiple evolutionary origins in the moss flora of Macaronesia. *Evolution* 63: 3248–3257.

Anacker, B. L. and S. Y. Strauss. 2014. The geography and ecology of plant speciation: Range overlap and niche divergence in sister species. *Proceedings. Biological Sciences* 281: 20132980.

Axelrod, D. 1975. Evolution and biogeography of the Madrean Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* 62: 280–334.

Barbero, M., A. Benabid, C. Peyre, and P. Quézel. 1980. Sur la presence au Maroc de *Laurus Azorica*. *Anales del Jardin Botanico de Madrid* 37: 467–472.

Bachman, S., J. Moat, A. W. Hill, J. de la Torre, and B. Scott. 2011. Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126.

Benítez-Benítez, C., M. Míguez, P. Jiménez-Mejías, and S. Martín-Bravo. 2017. Molecular and morphological data resurrects the long neglected *Carex laxula* (Cyperaceae) and expands its range in the Western Mediterranean. *Anales del Jardin Botanico de Madrid* 74: 57.

Boott, F. 1867. *Illustrations of the Genus Carex*, vol. 4. London: William Pamplin.

Bouckaert, R., T. G. Vaughan, J. Barido-Sottani, S. Duchêne, M. Fourment, A. Gavryushkina, J. Heled, G. Jones, D. Kühnert, N. De Maio, M. Matschiner, F. K. Mendes, N. F. Müller, H. A. Ogilvie, L. du Plessis, A. Popinga, A. Rambaut, D. Rasmussen, I. Siveroni, M. A. Suchard, C.-H. Wu, D. Xie, C. Zhang, T. Stadler, and A. J. Drummond. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 15: e1006650.

Borges, P. A. V., C. Abreu, A. M. F. Aguiar, P. Carvalho, R. Jardim, I. Melo, P. Oliveira, C. Sergio, A. R. M. Serrano, and P. Vieira. 2008. *A List of the Terrestrial Fungi, Flora and Fauna of Madeira and Selvagens Archipelagos*. Funchal and Angra do Heroísmo, Portugal: Direccão Regional do Ambiente da Madeira and Universidade dos Açores.

Borges, P. A. V., R. Gabriel, A. M. Arroz, A. Costa, R. T. Cunha, L. S. Silva, E. Mendonca, A. M. F. Martins, F. Reis, and P. Cardoso. 2010. The Azorean Biodiversity Portal: An internet database for regional biodiversity outreach. *Systematics and Biodiversity* 4: 423–434.

Brummitt, R. K. 2001. *World Geographical Scheme for Recording Plant Distributions*, ed. 2. Pittsburgh: Hunt Institute for Botanical Documentation, Carnegie Mellon University.

Brummitt, R. K. 2002. How to drop up a tree. *Taxon* 51: 31–41.

Campbell, M. J. and T. D. V. Swinscow. 2009. *Statistics at Square One*, ed. 11. London: BMJ Books.

Carine, M. A. and H. Schaefer. 2010. The Azores diversity enigma: Why are there so few Azorean endemic flowering plants and why are they so widespread? *Journal of Biogeography* 37: 77–89.

Carine, M. A., S. J. Russell, A. Santos-Guerra, and J. Francisco-Ortega. 2004. Relationships of the Macaronesian and Mediterranean floras: Molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany* 91: 1070–1085.

Clement, M., D. Posada, and K. A. Crandall. 2000. TCS: A computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1660.

Connor, S. E., W. O. Van der Knaap, J. F. N. van Leeuwen, and P. Kuneš. 2013. Holocene palaeoclimate and palaeovegetation on the islands of Flores and Pico. Pp. 149–162 in *Climate Change Perspectives from the Atlantic: Past, Present and Future*, eds. J. M. Fernández-Palacios, L. de Nascimento, J. C. Hernández, S. Clemente, A. González, and J. P. Díaz-González. La Laguna: Servicio de Publicaciones, Universidad de La Laguna.

Crawford, D. J. 2010. Progenitor-derivative species pairs and plant speciation. *Taxon* 59: 1413–1423.

Crisp, M. and G. Chandler. 1996. Paraphyletic species. *Telopea* 6: 813–844.

Darriba, D., G. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772.

Egorova, T. V. 1999. *The Sedges (Carex L.) of Russia and Adjacent States (Within the Limits of The Former USSR).* Saint Louis: Missouri Botanical Garden Press.

Emerson, B. C. 2002. Evolution on oceanic islands; molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology* 11: 951–966.

Engler, A. 1879. *Versuch Einer Eintwicklungsgeschichte, Insbesondere Der Florengebiete Seit Der Tertiärperiode*, vol. 1. *Die extra-tropischen Gebiete der nördlischen Hemisphär*e. Leipzig: W. Engelmann.

Escudero, M. and M. Luceño. 2009. Systematics and evolution of *Carex* sects. *Spirostachyae* and *Elatae* (Cyperaceae). *Plant Systematics and Evolution* 279: 163–189.

Escudero, M., V. Valcárcel, P. Vargas, and M. Luceño. 2009. Significance of ecological vicariance and long-distance dispersal in the diversification of *Carex* sect. *Spirostachyae* (Cyperaceae). *American Journal of Botany* 96: 2100–2014.

Escudero, M., A. L. Hipp, M. J. Waterway, and L. M. Valente. 2012. Diversification rates and chromosome evolution in the most diverse angiosperm genus of the temperate zone (*Carex*, Cyperaceae). *Molecular Phylogenetics and Evolution* 63: 650–655.

Funk, D. J. and K. E. Omland. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 34: 397–423.

Gehrke, B., S. Martín-Bravo, M. Muasya, and M. Luceño. 2010. Monophyly, phylogenetic position and the role of hybridization in *Schoenoxiphium* Nees (Cariceae, Cyperaceae). *Molecular Phylogenetics and Evolution* 56: 380–392.

Govaerts, R., P. Jiménez-Mejías, J. Koopman, D. A. Simpson, P. Goetghebeur, K. L. Wilson, T. Egorova, and J. J. Bruhl. 2020. World Checklist of Cyperaceae. Facilitated by the Royal Botanic Gardens, Kew. http://wcsp.science.kew.org/ (last accessed January 2020).

Hörandl, E. 2006. Paraphyletic versus monophyletic taxa — Evolutionary versus cladistic classifications. *Taxon* 55: 564–570.

Hörandl, E. and T. F. Stuessy. 2010. Paraphyletic groups as natural units of biological classification. *Taxon* 59: 1641–1653.

IUCN. 2012. IUCN red list categories and criteria, version 3.1. Ed. 2. Gland, Switzerland and Cambridge, UK: IUCN.

IUCN. 2017. Guidelines for using the IUCN red list categories and criteria, version 13. Cambridge, UK: IUCN Standards and Petitions Subcommittee.

Jardim, R. and M. Menezes de Sequeira. 2008. Lista Das Plantas Vasculares (Pteridophyta And Spermatophyta). Pp. 179–208 in *A List of The Terrestrial Fungi, Flora and Fauna of Madeira and Selvagens Archipelagos*, eds. P. A. V. Borges, C. Abreu, A. M. F. Aguiar, P. Carvalho, R. Jardim, I. Melo, P. Oliveira, C. Sérgio, A. R. M. Serrano, and P. Vieira. Funchal and Angra do Heroísmo: Direcção Regional do Ambiente da Madeira & Universidade dos Açores.

Jiménez-Mejías, P. and M. Luceño. 2011. Cyperaceae. Euro+Med Plantbase. The information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/.

Jiménez-Mejías, P., S. Martín-Bravo, and M. Luceño. 2012. Systematics and taxonomy of *Carex* sect. *Ceratocystis* (Cyperaceae) in Europe: A molecular and cytogenetic approach. *Systematic Botany* 37: 382–398.

Jiménez-Mejías, P., M. Luceño, and S. Martín-Bravo. 2014. Species boundaries within the southwest Old World populations of the *Carex flava* group (Cyperaceae). *Systematic Botany* 39: 117–131.

Jiménez-Mejías, P., M. Hahn, K. Lueders, J. R. Starr, B. H. Brown, B. N. Chouinard, K.-S. Chung, M. Escudero, B. A. Ford, K. A. Ford, S. Gebahauer, B. Gehrke, M. H. Hoffmann, X.-F. Jin, J. Jung, S. Kim, M. Luceño, E. Maguilla, S. Martín-Bravo, M. Míguez, A. Molina, R. Naczi, J. E. Pender, A. A. Reznicek, T. Villaverde, M. J. Waterway, K. L. Wilson, J.-C. Yang, S. Zhang, A. L. Hipp, and E. H. Roalson (Global Carex Group). 2016a. Megaphylogenetic specimen-level approaches to the *Carex* (Cyperaceae) phylogeny using regions ITS, ETS, and *matK*: Implications for classification. *Systematic Botany* 41: 500–518.

Jiménez-Mejías, P., E. Martinetto, A. Momohara, S. Popova, S. Y. Smith, and E. H. Roalson. 2016b. A commented synopsis of the pre-Pleistocene fossil record of *Carex* (Cyperaceae). *Botanical Review* 82: 258–345.

Jiménez-Mejías, P., M. Míguez, M. A. Spencer, C. E. Jarvis, and S. Martín-Bravo. 2017. Typification of 18th century names in *Carex* sect. *Rhynchocystis* (Cyperaceae): *Carex pendula* and allies. *Taxon* 66: 973–975.

Kariyat, R. R., C. M. De Moraes, A. G. Stephenson, and M. C. Mescher. 2012. Inbreeding increases susceptibility to powdery mildew (*Oidium neolycopersici*) infestation in horsenettle (*Solanum carolinense* L). *Plant Signaling & Behavior* 7: 803–806.

King, M. G. and E. H. Roalson. 2009. Discordance between phylogenetics and coalescent-based divergence modeling: Exploring phylogeographic patterns of speciation in the *Carex macrocephala* species complex. *Molecular Ecology* 18: 468–482.

Kondraskov, P., N. Schütz, C. Schüßler, M. Menezes de Sequeira, A. S. Guerra, J. Caujapé-Castells, R. Jaén-Molina, A. Marrero-Rodríguez, M. A. Koch, P. Linder, J. Kovar-Eder, and M. Thiv. 2015. Biogeography of Mediterranean hotspot biodiversity: Re-evaluating the 'tertiary relict' hypothesis of Macaronesian laurel forests. *PLoS One* 10: e0132091.

Kükenthal, G. 1909. Cyperaceae-Caricoidae in *Das Pflanzenreich*, vol. 4, 20 (Heft 38), ed. A Engler. Leipzig: Wilhelm Engelmann.

Lowe, R. 1833. *Transactions of The Cambridge Philosophical Society*, vol. 4. Cambridge: Phylosophical Society.

Maguilla, E., M. Escudero, M. J. Waterway, A. L. Hipp, and M. Luceño. 2015. Phylogeny, systematics, and trait evolution of *Carex* section *Glareosae*. *American Journal of Botany* 102: 1128–1144.

Mairal, M., J. Caujapé-Castells, L. Pellissier, R. Jaén-Molina, N. Álvarez, M. Heuertz, and I. Sanmartín. 2018. A tale of two forests: Ongoing aridification drives population decline and genetic diversity loss at continental scale in Afro-Macaronesian evergreen-forest archipelago endemics. *Annals of Botany* 122: 1005–1017.

Maire, R. 1957. *Flore de l'Afrique du Nord*, vol. 4. Paris: Paul Lechevalier.

Manen, J. F., G. Barriera, P. A. Loizeau, and Y. Naciri. 2010. The history of extant *Ilex* species (Aquifoliaceae): Evidence of hybridization within a Miocene radiation. *Molecular Phylogenetics and Evolution* 57: 961–977.

Manly, B. F. J. 1994. *Multivariate Statistical Methods: A Primer*, ed. 18. London: Chapman and Hall Publishers.

Martín-Bravo, S. and M. Escudero. 2012. Biogeography of flowering plants: A case study in Mignonettes (Resedaceae) and sedges (*Carex*, Cyperaceae). Pp. 257–290 in *Global Advances in Biogeography*, ed. D. L. Stevens. Croatia: Intech, Rijeka.

Martín-Bravo, S., M. Escudero, M. Míguez, P. Jiménez-Mejías, and M. Luceño. 2013. Molecular and morphological evidence for a new species from South Africa: *Carex rainbowii* (Cyperaceae). *South African Journal of Botany* 87: 85–91.

Martín-Bravo, S., P. Jiménez-Mejías, T. Villaverde, M. Escudero, M. Hahn, D. Spalink, E. Roalson, A. Hipp, C. Benítez-Benítez, L. P. Bruederle, E. Fitzek, B. A. Ford, K. A. Ford, M. Garner, S. Gebauer, M. H. Hoffman, X. F. Jin, I. Larridon, E. Léveillé-Bourret, Y.-F. Lu, M. Luceño, E. Maguilla, J. L. Márquez-Corro, M. Míguez, R. Naczi, A. Reznicek, and J. R. Starr. 2019a. A tale of worldwide success: Behind the scenes of *Carex* (Cyperaceae) biogeography and diversification. *Journal of Systematics and Evolution* 57: 695–718.

Martín-Bravo, S., M. Míguez, C. Benítez-Benítez, M. Menezes De Sequeira, and P. Jiménez-Mejías. 2019b. *Carex canariensis* Kük. +Md(M). *Willdenowia* 49: 100–101.

Médail, F. and P. Quezel. 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean basin. *Annals of the Missouri Botanical Garden* 84: 112–127.

Menezes de Sequeira, M., D. Espírito-Santo, C. Aguiar, J. Capelo, and J. Honrado. 2012. *Checklist da Flora de Portugal (Continental, Açores e Madeira)*. Lisboa: Associação Lusitana de Fitossociologia.

Míguez, M., B. Gehrke, P. Jiménez-Mejías, and S. Martín-Bravo. 2017. *Carex* sect. *Rhynchocystis* (Cyperaceae): A Miocene subtropical relict in the western Palaearctic showing a dispersal derived Rand Flora pattern. *Journal of Biogeography* 44: 2211–2224.

Míguez, M., S. Martín-Bravo, and P. Jiménez-Mejías. 2018. Reconciling morphology and phylogeny allows an integrative taxonomic revision of the giant sedges of *Carex* section *Rhynchocystis* (Cyperaceae). *Botanical Journal of the Linnean Society* 188: 34–58.

Míguez, M., P. Jiménez-Mejías, C. Benítez-Benítez, H. Schaefer, and S. Martín-Bravo. 2021. Data from: Systematics of the giant sedges of *Carex* sect. *Rhynchocystis* (Cyperaceae) in Macaronesia with description of two new species. Dryad Digital Repository. https://doi.org/10.5061/dryad.37pvmcvj3.

Miller, M. A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 in *Proceedings of the Gateway Computing Environments* (GCE). New Orleans: Gateway Computing.

Milne, R. I. and R. J. Abbott. 2002. The origin and evolution of tertiary relict floras. *Advances in Botanical Research* 38: 281–314.

Moura, M., P. Catalán, A. Brehm, and M. M. De Sequeira. 2019. Colonization routes, microevolutionary genetic structure and conservation concerns in a remote widespread insular endemic grass: The case of the Azorean tussock grass *Deschampsia foliosa*. *Botanical Journal of the Linnean Society* 191: 365–380.

Naczi, R. F. C., A. A. Reznicek, and B. A. Ford. 1998. Morphological, geographical, and ecological differentiation in the *Carex willdenowii* complex (Cyperaceae). *American Journal of Botany* 85: 434–447.

Nordal, I. and B. Stedje. 2005. Paraphyletic taxa should be accepted. *Taxon* 54: 5–6.

R Development Core Team. 2019. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.r-project.org/.

Rambaut, A., A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.

Rieseberg, L. H. and L. Brouillet. 1994. Are many plant species paraphyletic? *Taxon* 43: 21–32.

Ronquist, F. and J. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Systematic Biology* 61: 539–542.

Rowling, J. K. 2001. *Fantastic Beasts and Where to Find Them.* New York. Arthur A. Levine- Scholastic.

Sánchez-Pinto, L., M. L. Rodríguez, S. Rodríguez, K. Martín, A. Cabrera, and M. C. Marrero. 2005. Pteridophyta, Spermatophyta. Pp. 38–57 in *Lista Preliminar de Especies Silvestres de Cabo Verde (Hongos, Plantas y Animals Terrestres)*, eds. M. Arechavaleta, N. Zurita, M. C. Marreno and J. L. Martín-Esquivel. Santa Cruz de Tenerife: Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias.

Schaefer, H. 2002. Chorology and diversity of the Azorean flora. *Dissertationes Botanicae* 374: 1–130.

Schaefer, H. 2005. Endemic vascular plants of the Azores: An updated list. *Hoppea. Denkschriften der Regensburgischen Botanischen Gesellschaft* 66: 275–283.

Schaefer, H., O. J. Hardy, L. Silva, T. G. Barracloug, and V. Savolainen. 2011. Testing Darwin's naturalization hypothesis in the Azores. *Ecology Letters* 14: 389–396.

Schmidt-Lebuhn, A. N. 2012. Fallacies and false premises — A critical assessment of the arguments for the recognition of paraphyletic taxa in botany. *Cladistics* 28: 174–187.

Schüßler, C., M. Thiv, C. Bräuchler, J. A. Reyes-Betancort, and M. A. Koch. 2019. Island biogeography of the Macaronesian Gesnouinia and Mediterranean Soleirolia (Parietarieae, Urticaceae) with implications for the evolution of insular woodiness. *Taxon* 68: 537–556.

Seubert, M. 1844. *Flora Azorica Quam Ex Collectionibus Schedisque Hochstetteri Patris Et Filii.* Bonnae: Apud A. Marcum.

Shaw, J., E. B. Lickey, E. E. Schilling, and R. L. Small. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms The tortoise and the hare III. *American Journal of Botany* 94: 275–288.

Silva, L., M. Moura, H. Schaefer, F. Rumsey, and E. F. Dias. 2010. Tracheobionta. Pp. 117–146 in *A List of the Terrestrial and Marine Biota from the Azores*, eds. P. A. V. Borges, A. Costa, R. Cunha, R. Gabriel, V. Gonçalves, A. F. Martins,V. Vieira. Cascais, Portugal: Princípia.

Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.

Stuessy, T. F., K. Takayama, P. López-Sepúlveda, and D. J. Crawford. 2014. Interpretation of patterns of genetic variation in endemic plant species of oceanic islands. *Botanical Journal of the Linnean Society* 174: 276–288.

Thiers, B. 2020. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ science/ih/(last accessed November 2019).

Triantis, K. A., J. Hortal, I. Amorim, P. Cardoso, A. M. C. Santos, R. Gabriel, and P. A. V. Borges. 2012. Resolving the Azorean knot: A response to Carine and Schaefer 2010. *Journal of Biogeography* 39: 1179–1184.

Valcárcel, V. and P. Vargas. 2010. Quantitative morphology and species delimitation under the general lineage concept: Optimization for *Hedera* (Araliaceae). *American Journal of Botany* 97: 1555–1573.

Vanderpoorten, A. and D. G. Long. 2006. Budding speciation and neotropical origin of the Azorean endemic liverwort, *Leptoscyphus azoricus*. *Molecular Phylogenetics and Evolution* 40: 73–83.

Velasco, J. D. 2008. Species concepts should not conflict with evolutionary history, but often do. *Studies in History and Philosophy of Science Part C Studies in History and Philosophy of Biological and Biomedical Sciences* 39: 407–414.

Villaverde, T., M. Escudero, M. Luceño, and S. Martín-Bravo. 2015. Long-distance dispersal during the middle-late Pleistocene explains the bipolar disjunction of *Carex maritima* (Cyperaceae). *Journal of Biogeography* 42: 1820–1831.

Waterway, M. J. and J. R. Starr. 2007. Phylogenetic relationships in tribe Cariceae (Cyperaceae) based on nested analyses of four molecular data sets. *Aliso* 23: 165–192.

Appendix 1. List of studied material. Sample label includes "botanical country" as in Brummitt (2001). Information about collecting locality, voucher, and GenBank accession numbers for ITS, ETS, *atpIH*, *matK* and *rpl32-trnL*^{UAG}, respectively, is provided. An asterisk (*) indicates that the sequence for the corresponding region was not obtained. A hash (#) indicates those sequences newly obtained in this study. Samples used in the phylogenetic (PA) and dating analyses (DA) are indicated, together with the plastid haplotype number obtained in the analysis of the combined *atpIH-matK-rpl32-trnL*^{UAG} matrix of lineage B of sect. *Rhynchocystis* (*C. agastachys*, *C. leviosa*, *C. pendula* and *C. sequeirae*).

Ingroup: Section *Rhynchocystis* Dumort. *Carex agastachys* L.f: C. *agastachys* (AUT), Austria, Vorarlberg, Hermannsberg, W. Lippert *15027,* M-0177708, KU939626, KU939551, #MW296191, KU939705, KU939780, H1, PA. *C. agastachys* (CZE_CZ), Czech Republic, Moravia Centralis, J. Dvorák *s.n.,* M-0151978, KU939632, KU939557, #MW296192, KU939711, KU939787, H1, PA. *C. agastachys* (GER1), Germany, Kreis Traunstein. W. Lippert *MTB8142/3,* M-0177733, KU939642, KU939564, #MW296193, KU939720, KU939797, H1, PA, DA. *C. agastachys* (UKR), Ukraine, Veliky Berezny, A.K.Skvortsov *s.n.,* M-0151973, KU939650, KU939574, #MW296195, KU939729, KU939806, H1, PA. *C. agastachys* (YUG_SE), Serbia, Miroc Mountains, P. Jiménez-Mejías *86PJM10,* UPOS-4208, KU939660, KU939584, #MW296194, KU939738, KU939816, H1, PA. *C. agastachys* (YUG_SL), Slovenia, Podravksa, Ptju, M.Thulin *s.n.,*UPS-V571925, KU939672, KU939597, #MW296196, KU939750, KU939828, H1, PA. ***Carex bequaertii* subsp. *bequaertii*** De Wild: *C. bequaertii* subsp. *bequaertii* (ETH), Ethiopia, Gaysay Valley, B. Gehrke *BG 240*, Z, KU939606, KU939530, #MW296197, KU939685, KU939764, PA. *C. bequaertii* subsp. *bequaertii* (KEN1), Kenya, Naro Moru route, M. Muasya & B. Gehrke *BG79*, Z-000081200/01, EU288572, KU939532, #MW296198, KU939687, KU939765, PA. *C. bequaertii* subsp. *bequaertii* (KEN2), Kenya, Sirimon Route path, M. Muasya & B. Gehrke *BG98*, Z-000081202, EU288573, KU939533, #MW296199, KU939688, KU939766, PA, DA. *C. bequaertii* subsp. *bequaertii (*KEN3), Kenya, Koroborte, M. Muasya & B. Gehrke, *BG145*, Z-000081203, EU288574, KU939534, #MW296200, KU939689, KU939767, PA. *C. bequaertii* subsp. *bequaertii* (UGA), Uganda, Rwenzori Mountains, B. Gehrke & H.P.Linder *BG352*, Z-000081205, KU939612, KU939536, #MW296201, KU939691, MW286378, PA. ***Carex bequaertii* subsp. *mossii*** (Nelmes) Míguez, Martín-Bravo & Jim.-Mejías*:* *C. bequaertii* subsp. *mossii* (CPP), South Africa, Hogsback, C. Reid *Reid1204*, UPOS-3080, KU939621, KU939547, #MW296205, KU939702, KU939777, PA, DA. *C. bequaertii* subsp. *mossii* (NAT1), South Africa, Kwazulu-Natal, Bushmańs Nek, S. Martín-Bravo et al. *169SMB08*, UPOS-13908, KU939617, KU939617, #MW296206, KU939697, KU939774, PA. *C. bequaertii* subsp. *mossii* (NAT2), South Africa, Kwazulu-Natal, Monk's cowl, M. Luceño et al. *73ML08,* UPOS-4725, KU939618, KU939542, #MW296207, KU939698, KU939775, PA. ***Carex microcarpa*** Bertol ex Moris: *C. microcarpa* (COR), France, Corsica, Ghisome, M. Escudero & M.Luceño *88ME07,* UPOS-4730, KU939614, KU939538, #MW296202, KU939693, KU939770, PA. *C. microcarpa* (SAR1), Italy, Sardinia, Ogliastra, Pira river, Urbani & Calvia *s.n.*, SS, MW366386, MW366394, #MW296203, KU939695, KU939772, PA, DA. *C. microcarpa* (SAR2), Italy, Sardinia, Ogliastra, Urbani & Calvia *s.n.*, SS, KU939616, KU939540, #MW296204, KU939696, KU939773, PA. ***Carex leviosa*** Míguez, Jim.-Mejías, H. Schaef. & Martín-Bravo: *C. leviosa* (AZO1), Portugal, Azores, Ilha do Pico, H. Schaefer, *Schaefer2013/89*, TUM, KU939628, KU939553, #MW296208, KU939707, KU939782, H15, PA, DA. *C. leviosa* (AZO2), Portugal, Azores, Santa Maria, H. Schaefer, *Schaefer2013/90*, TUM, KU939629, KU939554, #MW296209, KU939708, KU939783, H13, PA. *C. leviosa* (AZO3), Portugal, Azores, Saõ Miguel, S. Martín-Bravo & L. Bellón, *136SMB15*, UPOS-6520(1/3), #MW366380, #MW366387, #MW296210, *, #MW286371, H14, PA. *C. leviosa* (AZO4), Portugal, Azores, Saõ Miguel, S. Martín-Bravo & L. Bellón, *143SMB15,* UPOS-6830(1/7), #MW366381, #MW366388, #MW296211, #MW286366, #MW286372, H14, PA. *C. leviosa* (AZO5), Portugal, Azores, Faial, Salgueiro et al. *385,* SEV-275671, *, #MW366389, #MW296212, #MW286367, #MW286373, H14, PA. ***Carex pendula*** Huds.: *C. pendula* (CYP), Cyprus, Stavros-tis-Psokas, G. Alziar 0977, SEV-251911, KU939631, KU939556, #MW296213, KU939710, KU939786, H4, PA. *C. pendula* (FRA), France, Haute-Normandie, Eure, P. Jiménez-Mejías *15PJM10,* UPOS-4099, KU939634, KU939559, #MW296214, KU939712, KU939789, H7, PA. *C. pendula* (GER), Germany, Kreis Freising, J. Sellma *MTB 7837/3*, M-0177729, KU939645, KU939567, #MW296215, KU939722, KU939799, H6, PA. *C. pendula* (GRB), United Kingdom, London, Hampsted, M.A. Spencer, MAS/2012/040, UPOS-5004, KU939648, KU939572, #MW296216, KU939727, KU939799, H5, PA, DA. *C. pendula* (ITA), Italy, Torino, Puente de Valle Ceppi, P. Jiménez-Mejías et al. *105bisPJM12*, UPOS, KU939653, KU939576, #MW296217, KU939731, KU939809, H6, PA. *C. pendula* (MOR), Morocco, Chefchaouèn, M. Ait Lafkih et al. 61, BM-340, KU939658, KU939582, #MW296218, KU939736, KU939814, H3, PA. *C. pendula* (POR), Portugal, Sintra, J.C. Zamora *s.n.*, UPOS-13505, KU939657, KU939581, #MW296224, KU939735, KU939813, H2, PA. *C. pendula* (SPA), Spain, Jaén, Aldeaquemada road, P. Jiménez-Mejías, *62PJM09,* UPOS-4720, KU939664, KU939588, #MW296225, KU939741, KU939820, H5, PA. ***Carex penduliformis*** Cherm.: *C. penduliformis* (MDG), Madagascar, Mahajanga Bealanana, S. Wohlhauser et al. *795*, P-01874870, *, KU939600, #MW296226, KU939833, KU939755, PA, DA. ***C. sequeirae*** Míguez, Jim.-Mejías, Benítez-Benítez & Martín-Bravo: *C. sequeirae* (MDR1), Portugal, Madeira, Santana, M. Sequeira *MS7806*B, UPOS-5182, KU939656, KU939579, #MW296219, KU939734, KU939812, H8, PA. *C. sequeirae* (MDR2), Portugal, Madeira, Ribeira do Inferno, C. Benítez-Benítez *53CBB18(1)*, UPOS-12625, #MW366382, #MW366390, #MW296220, #MW286368, #MW286374, H10, PA, DA. *C. sequeirae* (MDR3), Portugal, Madeira, Levada do Rei, C. Benítez-Benítez *47CBB18(1*), UPOS-12626, #MW366383, #MW366391, #MW296221, *, #MW286375, H9, PA. *C. sequeirae* (MDR4), Portugal, Madeira, Ribeira do Inferno, C. Benítez-Benítez *50CBB18(1),* UPOS-12627, #MW366384, #MW366392, #MW296222, #MW286369, #MW286376, H12, PA. *C. sequeirae* (MDR5), Portugal, Madeira, Ilha, C. Benítez-Benítez *66CBB18(1),* UPOS-10570, #MW366385, #MW366393, #MW296223, #MW286370, #MW286377, H11, PA.

Outgroup: *Carex demissa* Hornem.: *C. demissa* (MOR), Morocco, Rif, P. Jiménez-Mejías et al. *93PJM07*, UPOS-3517, JN634656, KU939524, *, KU939680, KU939759, PA, DA. ***Carex flava*** L: *C. flava* (NOR), Norway, Laponia, Skjervoy, M. Luceño & M. Guzmán *4005ML,* UPOS-403, AY278310, KU939525, #MW296187, KU939681, KU939760, PA, DA. ***Carex reuteriana*** Boiss.: *C. reuteriana* (SPA), Spain, Cáceres, P. Jiménez-Mejías *57PJM07,* UPOS-5957, KU939602, KU939520, #MW296186, KU939676, JN222833, PA, DA. ***Carex trinervis*** Dumort.*: C. trinervis* (SPA), Spain, Huelva, P. Jiménez-Mejías *43PJM07,* UPOS-2205, KU939603, KU939521, #MW296188, KU939677, KU939756, PA, DA. ***Carex distans*** L.: *C. distans* (IRA), Iran, Azerbaijan, Paygham-Marzrou, M. Amini Rad *s.n.,* IRAN-38662/1, EU812723, KU939522, *, KU939678, KU939757, PA, DA. ***Carex punctata*** Gaudin: *C. punctata* (KRI), Greece, Crete, Chania, S. Martín-Bravo & M. Luceño *381SMB05*, UPOS-257, DQ384178, KU939523, *, KU939679, KU939758, PA, DA. ***Carex sylvatica*** Huds.: *C. sylvatica* (SWI), Switzerland, Basel, Lechowicz *s.n.*, MTMG, AY757599, AY757660, #MW296190, JN896090 (U.K, Glamorgan NMW175, s.n.), KU939761, PA. DA. ***C. rainbowii*** Luceño, Jim.-Mejías, M. Escudero & Martín-Bravo: *C. rainbowii* (NAT), South Africa, Rainbow Gorge, S. Martín-Bravo & M. Luceño *120SMB11*, UPOS-5030, KC122380, KC122388, #MW296189, KU939682, KU939762, PA, DA.