Radiation and repeated transoceanic dispersal of Schoeneae (Cyperaceae) through the Southern Hemisphere

Jan-Adriaan Viljoen, A. Muthama Muasya,
Russell L. Barrett, Jeremy J. Bruhl,
Adele K. Gibbs, Jasper A. Slingsby,
Karen L. Wilson, G. Anthony Verboom

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Premise of the study: The broad austral distribution of Schoeneae is almost certainly a product of long-distance dispersal. Owing to the inadequacies of existing phylogenetic data and a lack of rigorous biogeographic analysis, relationships within the tribe remain poorly resolved and its pattern of radiation and dispersal uncertain. We employ an expanded sampling of taxa and markers, and a rigorous analytic approach, to address these limitations. We evaluate the roles of geography and ecology in stimulating the initial radiation of the group, as well as its subsequent dispersal across the Southern Hemisphere.

Methods: A dated tree was reconstructed using reversible-jump MCMC with a polytomy prior and molecular dating, applied to data from two nuclear and three cpDNA regions. Ancestral areas and habitats were inferred using dispersal–extinction–cladogenesis models.

Key results: Schoeneae originated in Australia in the Palæocene. The existence of a "hard" polytomy at the base of the clade reflects the rapid divergence of six principal lineages ca. 50 Ma within Australia. From this ancestral area, Schoeneae have traversed the austral oceans with remarkable frequency, a total of 29 distinct dispersal events being reported here. Dispersal rates between landmasses are not explicable in terms of the geographical distances separating them. Transoceanic dispersal generally involved habitat stasis.

Conclusions: Although the role of dispersal in explaining global distribution patterns is now widely accepted, the apparent ease with which such dispersal may occur has perhaps been under-appreciated. In Schoeneae, transoceanic dispersal has been remarkably frequent, with ecological opportunity, rather than geography, being most important in dictating dispersal patterns.

Key words: biogeography; dispersal–extinction–cladogenesis; habitat shift; transoceanic dispersal; niche conservatism; polytomy prior

Introduction

Biologists since the time of Hooker have been intrigued by the phytogeographic affinities of Australia, southern Africa, and South America (Hooker, 1853; Levyns, 1964; Crisci et al., 1991; Crisp et al., 1999; Galley and Linder, 2006; Moreira-Muñoz, 2007). Vicariance associated with the break-up of Gondwana by ca. 120 Ma (Ali and Krause, 2011) was previously considered to be the leading cause of this pattern (Levyns,

1964; Raven and Axelrod, 1974), but more recent evidence from fossils and molecular dating (Sanmartín and Ronquist, 2004; Linder et al., 2003; Cook and Crisp, 2005; Pirie et al., 2008; Sauquet et al., 2009) has made it clear that many plant lineages showing this disjunct distribution originated after the break-up, implicating long-distance dispersal (Raven and Axelrod, 1974; de Queiroz, 2005; but see Heads, 2011). The schoenoid sedges (Cyperaceae: Schoeneae) are one such group: the sedge family as a whole has a crown age of ca. 75 Ma (Janssen and Bremer, 2004; Besnard et al., 2009), and tribe Schoeneae (over 450 species) is distributed throughout the southern continents, with particularly high endemism in Australia and South Africa (data from Govaerts et al., 2011). Verboom (2006) concluded that at least five transoceanic dispersal events must have taken place in Schoeneae over the last 40 Ma. The precise number and direction of these dispersal events remains unclear, however, due to incongruence between published phylogenies, incomplete resolution, and the lack of rigorous biogeographic analysis. We address these issues by presenting robust phylogenetic and biogeographic reconstructions for the tribe.

Morphological classification has been problematic in many clades of Cyperaceae owing to the severe reduction of floral parts and the rampant convergence of traits in the family, emphasizing the utility of molecular phylogenies in sedge systematics (Muasya et al., 1998, 2009b). The cpDNA phylogenies of Verboom (2006) and Muasya et al. (2009a) and the cpDNA + ITS tree of Jung and Choi (2013) demonstrate that Schoeneae, as defined by both Bruhl (1995) and Goetghebeur (1998), is not monophyletic, on account of their inclusion of *Cladium, Carpha,* and *Trianoptiles.* Schoeneae sensu Goetghebeur (1998) contains five further genera shown by Muasya et al. (2009a) to fall outside the core Schoeneae clade. These are *Arthrostylis, Actinoschoenus, Trachystylis, Pleurostachys,* and the large genus *Rhynchospora,* which, on the basis of cpDNA data, belongs in a separate clade containing Cypereae and Cariceae. Hinchliff and Roalson's (2013) tree of Cyperaceae agrees with the exclusion of these five genera from Schoeneae, but supports the inclusion of *Cladium, Carpha,* and Cryptangieae in Schoeneae. Support for the monophyly of Schoeneae s. s. is also equivocal. The maximum-parsimony tree of Muasya et al. (2009a),

based on *rbc*L and *trn*L–F data, found no support for Schoeneae as a clade, or even for their stricter "Schoeneae 1" group, which includes *Carpha* + *Trianoptiles* and *Scleria*. In contrast, Verboom's (2006) Bayesian tree, based on *rbc*L, *rps*16, and *trn*L–F, weakly supports the monophyly of Schoeneae excluding *Carpha* + *Trianoptiles* and *Scleria* ($PP = 0.96$), a circumscription of Schoeneae not recovered by Muasya et al. (2009a). This clade was recovered by (Jung and Choi, 2013) and (Hinchliff and Roalson, 2013), with $PP = 1.00$ in the former but with very weak support in the latter ($BP = 0.58$). These conflicting interpretations of the tribal limits of Schoeneae based on cpDNA data indicate the need for data from independently assorting loci.

A striking feature of existing phylogenies is the high support at deep and shallow nodes combined with a complete lack of support for any resolution between the six main subclades of Schoeneae (detailed in Table 1, which are themselves well supported ($PP = 1.00$ in Verboom, 2006; $BP \geq 0.75$ in Muasya et al., 2009a; $BP \geq 0.97$ in Hinchliff and Roalson, 2013). This polytomy at the base of the Schoeneae may be "soft", reflecting insufficient information to recover the true relationships between the lineages, or "hard", reflecting near-instantaneous divergence of these six clades (Lewis et al., 2005). Lewis et al. (2005) developed a reversible-jump MCMC procedure that enables sampling of trees with one or more polytomies during Bayesian phylogeny reconstruction. Although the motivation for this method was to prevent the inflation of support for nodes above very short branches (the "star tree paradox"), it also allows the posterior probability of a hard polytomy at a particular node to be calculated as the proportion of sampled trees with a polytomy at the position of interest (Nagy et al., 2012).

If the different clades of Schoeneae were found to have distinct geographic distributions, the rapid divergence between them might be interpreted as the result of simultaneous dispersal to different regions of the globe, followed by peripatric differentiation and local speciation (Darwin, 1859; Jordan, 1905). An alternative scenario is that the clades diverged into different ecological niches, either within the ancestral area or associated with long-distance dispersal among the southern continents (sympatry: Darwin, 1859; Bush, 1969; Givnish et al., 2009; parapatry:

Jain and Bradshaw, 1966; Cracraft, 1982).

The fact that Schoeneae are widespread south of the equator (Govaerts et al., 2011) suggests that their distribution is not limited by dispersal ability. On the other hand, they are almost entirely confined to the Southern Hemisphere and are most prevalent on oligotrophic soils in temperate rather than tropical zones, leading us to postulate a significant role for habitat filtering (i. e., ecological constraints on where populations can be established; (Endler, 1982; Cavender-Bares et al., 2006)) in their biogeographic history.

The specific aims of the present study are as follows:

- to re-evaluate the monophyly of Schoeneae, particularly with regard to the placement of the *Carpha* and *Scleria* clades, by adding nuclear sequence data to existing chloroplast data sets and by increasing taxon sampling;
- to resolve the relationships of the principal schoenoid lineages or else to evaluate whether their polytomous relationship is "hard", reflecting rapid divergence;
- to estimate (taking phylogenetic uncertainty into account) the times of divergence of the principal lineages and the timing and directionality of transoceanic dispersal events in Schoeneae;
- to test whether differentiation of the principal schoenoid lineages coincided with intercontinental dispersal and/or specialization to different habitats (i. e., whether the radiation was adaptive); and
- to explore the roles of geography vs. habitat conservatism on dispersal in Schoeneae.

Materials and methods

Species and marker sampling

Species were selected in such a way as to ensure that the concatenated sequence matrix was as complete as possible and that genera (or mono-

phyletic portions of genera) were represented proportionally to their size while capturing their biogeographic distribution (Table 1). As outgroups we sampled at least one taxon from each major non-schoenoid lineage of Cyperaceae, including two representatives of Hypolytreae, so that their most recent common ancestor could be used as a calibration point (see BEAST analysis below). For Schoeneae, we made use of previously published sequence data (Zhang et al., 2004; Chacón et al., 2006; Slingsby and Verboom, 2006; Verboom, 2006; Muasya et al., 2009a), supplementing these with new sequences, principally from the external and internal transcribed spacers (ETS and ITS) of the nuclear ribosomal gene region (nrDNA), but also filling some cpDNA gaps (Appendix 1). ETS and ITS have been used to resolve relationships in Cariceae and Cypereae, and in regional studies (Waterway and Starr, 2007; Larridon et al., 2013; Jung and Choi, 2013), the latter being shown to have higher information content than most cpDNA markers in the sedges (Hinchliff and Roalson, 2013).

DNA extraction, PCR amplification, and sequencing

Silica-dried leaf and culm material was pulverized for ca. 20 min at 30 Hz in an MM400 oscillating mill (Retsch GmbH, Haan, Germany). DNA was extracted using the CTAB method (Doyle and Dickson, 1987; Gawel and Jarret, 1991). The chloroplast regions were amplified with the primer combinations used by Verboom (2006). The ETS region was amplified with primers ETS-1F and 18S-R (Starr et al., 2003) and ITS with primers ITS-4 and ITS-A (at UNE) or ITS-L (at UCT) (White et al., 1990; Hsiao et al., 1994; Blattner, 1999). PCR reagents were mixed to the following concentrations: *Taq* buffer with dye 1×, $MgCl_2$ 2 mM in total, each dNTP 0.2 mM, each primer 0.3 mM, *Taq* polymerase 1 U (KAPA Biosystems, Ltd., Cape Town, RSA). To promote amplification of the nuclear markers, dimethyl sulphoxide and bovine serum albumen were added to 2 % (v/v) and 0.04 % (w/v) respectively. PCR reactions were done in AB2720 thermal cyclers (Applied Biosystems, Inc., Foster City, California, USA) using the following programme: initial denaturation at 94 °C for 2 min; 32 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s, ex-

tension at 72 °C for 90 s; and a final extension step at 72 °C for 7 min. PCR products were cleaned and sequenced on ABI3730XL cycle sequencers at the University of Stellenbosch DNA Sequencing Unit (Stellenbosch, RSA).

Matrix assembly

Contigs of forward and reverse sequences were assembled with SeqMan v. 7.0.0 (DNASTAR, Inc.). (New sequences are deposited on GenBank with accession numbers KF553442–KF553627.) These were aligned with previously published sequences downloaded from GenBank (Appendix 1) using Muscle v. 3.8.31 (Edgar, 2004), and the resulting alignments edited by hand in BioEdit v. 7.0.9 (Hall, 1999). Ambiguously aligned regions, noted in all matrices except *rbc*L, were excluded from downstream analyses.

Model testing

The best-fitting model of sequence evolution for each gene region was selected on the basis of BIC values (Luo et al., 2010) calculated by MrAIC v. 1.4.4 (Nylander, 2004), which uses PhyML v. 3.0 (Guindon and Gascuel, 2003) to optimize parameters on the maximum-likelihood (ML) tree for each model. The selected models were as follows: GTR+Γ for ETS, ITS, and *rps*16; HKY+Γ for *rbc*L and *trn*L. The proportions of variable sites were 574/713 (81 %) for ETS, 457/844 (54 %) for ITS, 386/1430 (27 %) for *rbc*L, 538/1204 (45 %) for *rps*16, and 622/1285 (48 %) for *trn*L.

Phylogeny reconstruction

The phylogeny was reconstructed using Bayesian MCMC algorithms, both sampling and not sampling polytomous trees. We first inferred the gene trees for each of the five regions separately to identify potential incongruence. As there were no instances of conflict at well supported nodes (Appendix S1), the matrices of the five regions were concatenated and partitioned by gene for the downstream analyses. The phylogeny was reconstructed in MrBayes v. 3.2.1 (Ronquist et al., 2012), averaging over all submodels of the GTR relative substitution rate model (using

"`nst=mixed`") and modelling rate heterogeneity with a gamma distribution with four rate categories. All parameters except topology and branch lengths were unlinked across partitions. The MCMC sampler was run four times simultaneously for 4×10^7 generations with four Metropolis-coupled chains at a temperature setting of 0.2, sampling 10^4 parameter estimates in each run. Tracer v. 1.5 (Rambaut and Drummond, 2009) was used to calculate the effective sample size of each parameter. These were all above 2000, indicating that the MCMC algorithm had been run long enough, and all four runs had converged on the same parameter estimates. The average standard deviation of split frequencies reached 0.01 after 1.1×10^7 generations, indicating topological convergence. The first 50 % of samples were discarded as burn-in and a consensus tree was created from the post-burn-in samples in MrBayes, with posterior probabilities (*PP*) of nodes indicating clade support. (The sequence alignments and trees produced are deposited in TreeBase at `http://purl.org/phylo/treebase/phylows/study/TB2:S14725`.)

As reversible-jump MCMC sampling of trees containing polytomies is not implemented in MrBayes, the phylogeny reconstruction was repeated in Phycas v. 1.2.0 (Lewis et al., 2005), using the same partitions and the models selected with MrAIC, with the polytomy prior in effect and the prior on the resolution classes set to 1 (i. e., all trees equally probable *a priori*). This ensured that there was no sampling bias in favour of resolved trees due to the greater number of possible dichotomous than multichotomous trees for a given number of terminals. The analysis was run twice for 2×10^5 cycles with a single chain, saving 2×10^3 samples in each run. The parameter summaries and plot of split probabilities indicated that the MCMC chain had converged and the first 5×10^4 cycles were discarded as burn-in. The post-burn-in trees were summarized, annotated, and plotted using NCLconverter distributed with the Nexus Class Libraries (Lewis and Holder, 2008), the Newick Utilities (Junier and Zdobnov, 2010), and the packages ape v. 3.0-8 (Paradis et al., 2004) and phyloch v. 1.5-3 (Heibl, 2008) for R v. 3.0.1 (R Core Team, 2013). The Bayesian node support values were supplemented with nonparametric bootstrap proportions (*BP*) calculated from 1000 bootstrap samples using RAxML v. 7.4.4 through the CIPRES Science Gateway (Stamatakis et al.,

2008; Miller et al., 2010), applying a GTR+Γ_{25} model to each partition.

To establish the effect of incomplete or inconsistent sampling in the sequence matrix, we also ran the MrBayes and Phycas analyses on the subset of taxa for which both nuclear and at least two chloroplast gene regions had been sampled. This subset comprised 18 taxa representing all clades. The models with the best BIC scores for this subset were GTR+Γ for ETS, ITS, *rbc*L, and *rps*16; HKY+Γ for *trn*L. MCMC settings were as above except that the analysis converged rapidly enough that it was run for only 5×10^4 cycles in Phycas, discarding the first 2.5×10^4 as burn-in.

Molecular dating

To estimate divergence dates in Schoeneae, node ages were coestimated with the phylogeny and other model parameters using an uncorrelated relaxed-clock model in BEAST v. 1.7.5 (Drummond and Rambaut, 2007). The data set was partitioned as above and analysed with the same substitution models, using the MrBayes consensus tree as the starting tree.

Mapanioideae and Cyperoideae were constrained to be reciprocally monophyletic and the split between them (i. e., the crown age of Cyperaceae) was calibrated as a prior with a uniform distribution between 67 and 83 Ma, corresponding to the error range of Besnard et al.'s (2009) estimate for this node from a tree of the commelinoids (mainly Poaceae and Cyperaceae) that incorporated six fossil calibrations. The mid-Eocene fossil of *Volkeria messelensis* S.Y.Smith et al. described by Smith et al. (2009) was used to set a lognormal prior of $\mu = 6$ Ma offset by 36.5 Ma, with $\ln \sigma = 1$ Ma, on the crown age of the Hypolytreae (represented by *Hypolytrum nemorum* (Vahl) Spreng. and *Mapania cuspidata* (Miq.) Uittien in our data set), yielding a 95 % prior HPD interval of 60–37 Ma (lower- to mid-Eocene; Gradstein et al., 2004).

Gamma-distributed priors with shape = 1 and scale = 1 were set on the means of the uncorrelated log-normal relaxed clocks of each partition, as well as on the birth and death rates of the birth-death diversification model (Drummond et al., 2006; Gernhard, 2008). All other priors were kept at their default settings.

Analyses were run four times for 10^8 generations, saving 10^4 samples in

each run. Convergence was assessed with Tracer v. 1.5 and the first 5×10^7 generations were discarded as burn-in. The maximum-clade-credibility tree was annotated with medians and 95 % HPD intervals of node ages using TreeAnnotator v. 1.7.5.

Ancestral area reconstruction

Ancestral areas were reconstructed using dispersal–extinction–cladogenesis (DEC) models in Lagrange (Ree et al., 2005; Ree and Smith, 2008), which makes use of branch length information to infer the maximum-likelihood (ML) combination of areas at each node of the tree. The species in the tree were scored as present or absent in each botanical region (Level 2 of Brummitt, 2001) as indicated in the World Checklist of Monocotyledons (Govaerts et al., 2011). To facilitate analyses, the number of states was reduced as follows: the various Pacific regions (including New Caledonia but excluding New Zealand) were combined into a single area, as were Central and South America, and Malesia and Southeast Asia. The seven retained states were thus Southern Africa, Madagascar, Southeast Asia, Australia, New Zealand, Pacific Islands, and South America. The Eurasian and North American regions were excluded from the analysis since *Schoenus nigricans* L. is the only species in our data set to occur there. Its documented occurrence in South America is based on a single record from Uruguay, regarded by Osten (1931) as "*sin duda introducida accidentalmente*", so this taxon was scored as absent from this region.

Lagrange C++ v. 0.20-28 (downloaded from `http://www.github.com/blackrim/lagrange`) was used to optimize tree-wide dispersal and extinction parameters of the biogeographic model and to infer ancestral areas. All combinations of areas were allowed as ancestral states and the dispersal rates were set to equal on the basis of the model test results (see below). To account for phylogenetic uncertainty (Lutzoni et al., 2001), especially at the base of Schoeneae, the Lagrange analysis was run over 1000 trees randomly selected from the posterior distribution sampled with BEAST. The Lagrange output was parsed and the mean proportional likelihoods of ancestral states calculated in R, making use of the packages ape and phyloch. (The R code is available at

https://github.com/javiljoen/phylojjeny.)

To test whether dispersal rates in Schoeneae were determined by geographic distance, the likelihoods of the following models were compared on the maximum-clade-credibility dated tree: (A) all rates equal, (B) all rates different (estimated), (C) rates inversely proportional to minimum distance between regions, and (D) rates inversely proportional to squared distance (i. e., dispersal is limited by propagule density, assuming homogeneous radial diffusion from the source area). The pairwise minimum Great-Circle distances in the latter two models were calculated with the R packages sp v. 1.0-9 (Pebesma and Bivand, 2005) and rgdal v. 0.8-9 (Bivand et al., 2013), using shapefiles from http://www.kew.org/gis/tdwg (R code at https://github.com/javiljoen/phylojjeny). Model weights were calculated from the differences between AIC values as

$$\omega_i = \frac{e^{-0.5\times\Delta_i}}{\sum e^{-0.5\times\Delta_i}},$$

where $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{min}$ (Table 2).

Ancestral habitat reconstruction

The distributions of lineages may be constrained more by ecological opportunity than dispersal ability (Crisp et al., 2009) and shifts to distinct habitats may be associated with cladogenesis. We therefore felt justified in treating habitat types as "areas" under a biogeographic DEC model. Lagrange has the additional advantage that it allows the inference of polymorphic ancestral states. Habitat descriptions for each species were extracted from the available literature and supplemented with our own observations (Appendix S2). Habitats were coded as perennially wet or seasonally dry (or both) and closed or open (or both). Therophytes in seasonally wet habitats were classified as wet-adapted species, while hemicryptophytes in such habitats were considered dry-adapted because they must survive a dry season, during which nutrient uptake and carbon fixation are limited. Habitats described as forest or woodland were considered closed, whereas grasslands, streamsides, bogs, alpine vegetation, heathland, and scrub were coded as open. Australian usage of the term

"swamp" (Sainty and Jacobs, 2003) is more or less equivalent to African "marsh", and both were coded as open unless specifically described as closed. The phylogenetic signal in the two variables was assessed to determine whether ancestral states could sensibly be reconstructed. The ML estimate of the tree transformation parameter λ was calculated using fitDiscrete in the R package geiger v. 1.3-1 (Harmon et al., 2008) (modified to allow λ values > 1), where $\lambda = 1$ corresponds to Brownian motion and $\lambda = 0$ indicates that trait evolution is random with respect to phylogeny (i. e. no phylogenetic signal) (Pagel, 1999). Vegetation type and habitat moisture at ancestral nodes were reconstructed as described above for ancestral areas, except that an asymmetric (all-rates-different) dispersal rate matrix was optimized separately on each of the 1000 trees.

Results

Circumscription and monophyly of Schoeneae

The phylogenetic tree reconstructed with MrBayes, Phycas, and RAxML is shown in Figure 1. All three analyses excluded *Cladium, Scleria, Rhynchospora,* and *Arthrostylis* from Schoeneae with $PP/BP = 1.00$. *Cladium* was resolved as sister to all the other Cyperoideae, the next most basal split being the divergence of the *Scleria* + Bisboeckelereae clade from the remainder of the Cyperoideae. *Rhynchospora* and *Arthrostylis* resolved closer to Cariceae and Cypereae than to Schoeneae.

Schoeneae s. s. (henceforth, Schoeneae) had support of $PP = 1.00/1.00$ (MrBayes/Phycas) and $BP = 1.00$ (RAxML). *Trianoptiles* formed a clade with *Carpha* that was sister to Schoeneae, but the Schoeneae + *Carpha* clade was not supported by any of the three analyses ($PP < 0.90$, $BP = 0.65$). In the analyses of the more fully sampled taxa (Fig. 2), Schoeneae was once again supported by all three methods ($PP = 0.99/0.99$, $BP = 0.83$), as was the monophyly of Schoeneae + *Carpha* clade + *Lagenocarpus* ($PP = 1.00/1.00$, $BP = 1.00$). The relationships between Schoeneae, *Carpha* clade, and *Lagenocarpus* were not resolved using either data set.

The MrBayes and Phycas trees were largely congruent, although the Phycas analysis returned lower support values at all supergeneric nodes

except that subtending *Caustis* + *Lepidosperma* + *Tricostularia* clades ($PP = 0.80/0.95$), a node not recovered in the ML analysis ($BP < 0.50$), nor in the Phycas analysis of the well-sampled taxa. The nodes that collapsed in the Phycas analysis were generally poorly supported in MrBayes and were subtended by short branches (< 0.01 substitutions per site).

Relationships within Schoeneae

The six main subclades were all well supported ($PP/BP = 1.00$), as were clades within them that roughly correspond to named genera (or monophyletic portions of genera). Relationships between these main clades, however, were weakly supported and inconsistent across analyses, including in the analyses run on the subset of taxa that had been fully sampled (Fig. 2). This lack of resolution was also apparent in the individual gene trees (Appendix S1), indicating that it is the result of low phylogenetic signal, rather than gene tree conflict. The sole exception is the Bayesian support for *Gahnia* + *Lepidosperma* clade in the *trn*L data ($PP = 0.99$, but $BP = 0.66$), which was not recovered (but also not contradicted) by the other data sets. Of the trees sampled by Phycas, 73 % had a polytomy at the base of Schoeneae (82 % in the more densely sampled subset). None was completely unresolved (a hexachotomy), but the only supported node was *Caustis* + *Lepidosperma* + *Tricostularia* ($PP = 0.95$), which was unsupported in the other analyses, as mentioned above.

Our results confirm the polyphyly of the genera *Schoenus, Tetraria,* and *Costularia. Schoenus* consists of at least two clades, one containing most of the species of *Schoenus*, as well as *Tetraria* s. s. (*Schoenus* clade), and the other in *Tricostularia* clade with reticulate-sheathed *Tetraria*. The Australian *T. octandra* (Nees) Kük. and *T. capillaris* (F.Muell.) J.M.Black were not resolved near either of the African clades of *Tetraria,* but near *Morelotia* (*Tricostularia* clade) and *Neesenbeckia* (*Lepidosperma* clade), respectively. *Costularia arundinacea* (Sol. ex Vahl) Kük., classified as a member of subgenus *Lophoschoenus* was placed in the *Tricostularia* clade, rather than with its congeners (all members of subgenus *Costularia*). And the species of *Costularia* and *Oreobolus* in the *Oreobolus* clade were not consistently recovered as clades corresponding to genera.

Molecular dating

The well supported nodes in the MrBayes and Phycas analyses were also recovered by BEAST (Appendix S3). Along the backbone of Schoeneae, the BEAST analysis additionally supported the monophyly of *Caustis* + *Lepidosperma* + *Tricostularia* ($PP = 1.00$).

Schoeneae had split from the *Carpha* clade by the Palæocene 95% HPD [71.4–53.6] Ma) and the six main subclades diverged in the space of ca. 5.5 Ma in the late-Palæocene–Eocene (between [60.1–43.6] Ma and [56.1–38.7] Ma). Within the *Tetraria* s. s. and the *Oreobolus* clades, the bulk of extant species diversity is recent (≤ 10 Ma), while in the other clades it is older.

Ancestral areas and habitats

Schoeneae was unambiguously reconstructed as originating in Australia (Fig. 3, Appendix S4). Furthermore, the initial split into the six subclades was found to have taken place within that continent, with each subclade still containing Australian representatives today.

Dispersal of five of the six lineages to the other austral continents commenced in the Oligocene. During the Oligocene–Miocene, the Pacific islands were colonized four times from Australia (Fig. 3, Appendix S4). Dispersal to southeast Asia (including Malesia) and New Zealand started in the Miocene, and Madagascar was colonized by two lineages in the late Miocene. The African mainland was reached by three different Australian and Pacific lineages during the Oligocene and Miocene, by *Capeobolus*–*Cyathocoma* from an uncertain origin, and by Malagasy *Costularia* in the Pliocene. While most changes in distribution were reconstructed as range expansion events, eleven vicariance events were also inferred, e. g. between *Tetraria capillaris* and *Neesenbeckia punctoria* (Vahl) Levyns.

The model in which each dispersal rate was estimated separately (B) had a higher likelihood ($\ln L = -120.3$; Table 2) than that assuming a single dispersal rate between all areas ($\ln L = -147.0$), though this did not represent a significantly better fit (model weight $\omega = 2.18 \times 10^{-7}$) on account of the 42 extra free parameters and the absence of some

dispersal categories from the data (e. g. South America to Madagascar). This comparison thus fails to provide support for differences in dispersal rate. Setting rates to the reciprocals of the minimum distances or squared distances was also not justified ($\omega = 9.54 \times 10^{-7}$ and $\omega = 3.39 \times 10^{-29}$, respectively), indicating that the dispersal rates between pairs of areas was not related to the distance between them.

Both habitat traits showed significant phylogenetic signal. The rates of change from seasonal to perennially wet habitat and vice versa were not significantly different ($\delta = 2 \times \ln(L_1/L_2) = 0.92, \mathrm{df} = 1, P = 0.336$), habitat moisture regime evolving according to a Brownian motion process ($\hat{\lambda} = 1.01$). Vegetation type, conversely, changed asymmetrically, with transitions to open habitat occurring at a significantly higher rate than to forest ($\delta = 9.92, \mathrm{df} = 1, P = 0.002$), and the estimated phylogenetic signal in this character ($\hat{\lambda} = 0.47$) differed from both the expectation under Brownian motion ($P \leq 0.001$) and that without phylogenetic structure ($P = 0.027$).

Most of the deep nodes within Schoeneae were reconstructed as occupying perennially moist or both perennial and seasonal habitats (Fig. 4A). The *Tricostularia* clade, *Mesomelaena*, and *Cyathochaeta* have specialized to dry environments, while *Machaerina* and *Oreobolus* associate predominantly with perennially wet environments. In *Gahnia, Costularia, Lepidosperma* and the *Schoenus* clade, generalist ancestors have differentiated into wet- and dry-adapted lineages. The dry-adapted lineages mostly occur in Australia and South Africa.

The ancestor of Schoeneae was inferred to have inhabited open vegetation. The main transitions into forest were in *Gahnia* and *Costularia,* both in the last 10 Ma, with *Machaerina* and *Lepidosperma* becoming generalists ≥ 20 Ma (Fig. 4B). Adaptation to shade is associated with dispersal to the Pacific, Southeast Asia, and Madagascar. The shade-tolerant clades tend to be found in perennially moist environments, but not all wet-adapted lineages are found in shady habitats; for example, *Neesenbeckia, Oreobolus,* and some *Lepidosperma* inhabit open wetlands.

Numerous habitat shifts were inferred in Schoeneae, involving both generalization ("dispersal") and specialization ("vicariance"). Habitat shifts taking place within a geographical area did not show a directional

bias along either habitat axis (Fig. 6). When geographical dispersal was accompanied by a habitat shift, however, it was more often into drier (3/3) and/or more open (3/4) habitats. Nevertheless, most of the dispersal events (22/29) did not involve any habitat shift.

Discussion

Morphological classification in Cyperaceae suffers from uncertainty in character homology, especially pertaining to reproductive structures (e. g. Bruhl, 1991; Vrijdaghs et al., 2007; Reutemann et al., 2012). While analyses of floral ontogeny are helping to cut this Gordian knot (Vrijdaghs et al., 2009, 2010; Prychid and Bruhl, 2013), they are most useful in secondary homology assessment, requiring an *a priori* phylogenetic hypothesis based on independent data, such as those provided by DNA sequences. Goetghebeur (1998) classified *Cladium, Rhynchospora,* and *Arthrostylis* as members of Schoeneae on the basis of inflorescence morphology, but our results place the latter two closer to core Cyperoideae (the clade containing Cypereae, Cariceae, and Abildgaardieae) and *Cladium* as sister to all other Cyperoideae, consistent with Bruhl (1995), Ghamkhar et al. (2007), and Jung and Choi (2013). Hinchliff and Roalson (2013) placed *Rhynchospora* as sister to core Cyperoideae and *Arthrostylis* in Abildgaardieae. However, they found strong support for *Cladium* as sister to Schoeneae + Cryptangieae + *Carpha.* This appears to be based on cpDNA and ITS data for about a dozen species in *Cladium, Schoenus, Gahnia,* and *Oreobolus* and cpDNA data for other members of Schoeneae (detailed information is not provided), so our conflicting results may be due to the denser nrDNA sampling in this study, or our sparser sampling of outgroup taxa. The conflict may also be the result of the difference in computational method used, as Hinchliff and Roalson (2013) used ML, while the more modestly sized data sets (Verboom, 2006; Jung and Choi, 2013; and this study) were analysed by Bayesian inference, which incorporates model uncertainty to a greater degree by producing a posterior distribution of trees associated with a distribution of parameter values.

In agreement with Bruhl's (1995) morphological analysis, Verboom's

(2006) cpDNA Bayesian analysis, Jung and Choi's (2013) cpDNA + ITS Bayesian analysis, and Hinchliff and Roalson's (2013) ML analysis, but contra the cpDNA hypothesis of Muasya et al. (2009a), our analyses confirm that the genera *Becquerelia, Calyptrocarya, Diplacrum* (Bisboeckelereae) and *Scleria* (Sclerieae) fall outside the Schoeneae clade. The discordance between Muasya et al.'s (2009a) and Verboom's (2006) cpDNA trees may be due to the simplistic model of sequence evolution implicit in the parsimony method employed by the former (which causes, inter alia, long-branch attraction) and/or because they used only two plastid regions, whereas Verboom (2006) used three. The low bootstrap support at the deeper nodes of the Muasya et al. (2009a) tree indicates insufficient variability in the *rbc*L and *trn*L–F regions used by them, since conflict in the data would have manifested in our results as well.

Schoeneae was strongly supported as monophyletic in all analyses ($PP = 0.99$–1.00, $BP = 0.83$–1.00), with *Trianoptiles* and *Carpha* forming a clade sister to Schoeneae. Verbelen (1970) and Goetghebeur (1986) described distinct embryo types for *Schoenus* and *Carpha,* which supports the reclassification of the *Carpha* clade as a separate tribe, Carpheae. Our results do not support the *Lagenocarpus* clade (Cryptangieae) as separate from the *Carpha* clade + Schoeneae, so the separation of Carpheae from Schoeneae also argues for the maintenance of Cryptangieae, pending further work on this undersampled group.

While Jung and Choi (2013) and Hinchliff and Roalson (2013) used ITS data for members of three of the main subclades of Schoeneae, the present study is the first to include sufficient sampling of nuclear regions to provide independent evidence for testing relationships in the tribe. The six main subclades identified by Verboom (2006) were also supported by our ETS and ITS data, in both separate and combined analyses. While robust on genetic grounds, these clades appear to lack phenotypic apomorphies and none was recovered in Bruhl's (1995) comprehensive cladistic analysis of morphological characters in the family. We, therefore, refrain from treating them formally and instead continue to use the provisional clade names in Fig. 1. Forthcoming work will deal with this and related taxonomic issues, such as the polyphyly of *Tetraria, Schoenus,* and *Costularia,* noted by Zhang et al. (2004) and Verboom (2006). Rela-

tionships between these clades remain unresolved, despite the increased marker and taxon sampling. The added nrDNA regions were highly informative, contributing disproportionately to the variability in the data set. Nevertheless, no nodes along the Schoeneae backbone were supported in the MrBayes analysis, despite this method being biased in favour of resolved trees (Lewis et al., 2005). In addition, the majority of the trees sampled by the Phycas analysis were polytomous or inconsistently resolved, indicating a near-instantaneous divergence at the base of the clade, dated as taking place between [38.7–56.1] and [43.6–60.1] Ma.

Schoeneae was reconstructed as originating in Australia, its initial radiation taking place on that continent. Australia had already separated from all neighbouring landmasses except Papuasia at this time and had yet to approach the Sundaland and Philippine Sea Plates (Wilford and Brown, 1994; Neall and Trewick, 2008), so the broad austral distribution of Schoeneae and the divergence of its major lineages cannot be explained as a product of the separation and isolation of once-contiguous subpopulations due to tectonic shifts (i. e., vicariance). Within Australia, open habitats, inferred as ancestral, would initially have been sparsely distributed (Crisp et al., 2004), but there are records of Cyperaceae in mid-Eocene seasonally dry forest in the Lake Eyre basin in south-central Australia (Martin, 2006). Diversification of Schoeneae may have been enabled by the increasing appearance of more open, sclerophyllous vegetation from this period onwards, especially after the initiation of the Antarctic Circumpolar Current ca. 38–28 Ma, which is thought to have caused drier and more seasonal climates in Australia (Quilty, 1994; Crisp et al., 2004; Martin, 2006). However, as no shifts into closed vegetation were inferred for the early Schoeneae, the initial divergence of the major lineages was probably not the result of adaptation to distinct vegetation types.

Starting in the Palæocene, Australia experienced diverse rainfall regimes with a seasonally arid central zone, an arid northwest, and humid rainforest on the rest of the continent (Quilty, 1994; Crisp et al., 2004; Martin, 2006). The variation in the moisture niches of the principal schoenoid lineages suggests that they may have radiated into different moisture niches. Our reconstructions are ambiguous at the deeper nodes, however,

with the result that niche partitioning at the time of the radiation lacks clear support.

Another possibility is that radiation was non-adaptive, with initial divergence being driven primarily by geographic isolation within Australia, a real possibility if the ancestral habitat was patchily distributed. Unfortunately, testing for intracontinental allopatry is problematic, as the reconstruction of palæodistributions is precluded by the sparseness of the fossil record for Cyperaceae and for the Australian flora as a whole (Quilty, 1994). Moreover, current distributions are unlikely to retain a signal of historical allopatry after 50 Ma (Losos and Glor, 2003). To understand the initial radiation in Schoeneae, more precise studies of microhabitat are needed. Investigation of substrate characteristics is likely to prove especially fruitful, as several instances of edaphic specialization are known (e. g. in *Lepidosperma:* Barrett, 2013). In addition, study has begun on non-ecological mechanisms of reproductive isolation such as polyploidization.

Dispersal of Schoeneae out of Australia commenced in the Oligocene and has been ongoing, accounting for at least fourteen dispersal events to the Pacific Islands, New Zealand, Southeast Asia, Southern Africa, and possibly South America (Fig. 5). Southern New Guinea is on the Australian tectonic plate, which had already come into contact with the Pacific and Asian plates by the Miocene (Sanmartín and Ronquist, 2004; Neall and Trewick, 2008), potentially allowing Papuasia and Malesia to be colonized in relatively short steps by "island-hopping". Likewise, while New Caledonia is thought to have been completely submerged following the separation of Zealandia from Australia, its re-emergence had already started by the Oligocene (Pelletier, 2007; Cluzel et al., 2012), with volcanic islands possibly serving as stepping stones for various plant lineages (Wilford and Brown, 1994; Ladiges and Cantrill, 2007), e. g. Monimiaceae (Renner et al., 2010). Dispersal to New Caledonia and New Zealand, however, has mostly taken place in the last 20 Ma (Winkworth et al., 2002; Cook and Crisp, 2005), a pattern also apparent in Schoeneae. A number of species of *Lepidosperma* not included in our analyses also occur in New Caledonia, their presence there almost certainly being due to recent long-distance dispersal (Barrett, 2012). Dispersal of Schoeneae

to Southern Africa, South America, and New Zealand took place long after direct contact with Australia had been broken and must, therefore, have been transoceanic. Long-distance dispersal between the southern continents has now been reported for a number of plant groups, including from Madagascar to New Caledonia in *Acridocarpus* (Davis et al., 2002); from Australia to New Caledonia, New Zealand, and the Indian Ocean islands in Monimiaceae (Renner et al., 2010); from New Zealand to Australia and other areas (Winkworth et al., 2002); from Australasia to southern Africa in Restionaceae (Linder et al., 2003), Iridaceae (Goldblatt et al., 2002), Ehrharteae (Verboom et al., 2003), and Proteaceae (Barker et al., 2007); and in the opposite direction in gnaphaloid Asteraceae, Danthonioideae, and six other taxa (Bergh and Linder, 2009; Pirie et al., 2012). The schoenoid sedges are, however, exceptional in terms of the sheer number of transcontinental dispersal events that have taken place since the mid-Miocene.

In light of this high dispersal ability, it seems surprising that no Schoeneae, other than *Schoenus nigricans* and *S. ferrugineus* L., have crossed the tropics into the Northern Hemisphere. Since our model comparisons indicate a limited role for geographic distance in determining dispersal rates in Schoeneae (in contrast to the situation in Danthonioideae; Linder et al., 2013), other factors are required to explain this pattern. Of likely importance is niche conservatism, a phenomenon whose biogeographic influence has been demonstrated in a range of plant groups, from both the Northern and Southern Hemispheres (Donoghue, 2008; Crisp et al., 2009). In Schoeneae, limited dispersal into the Northern Hemisphere has likely been constrained by the association of this lineage with the cool-temperate, nutritionally-deficient conditions that typify the austral zone. Although we have not tested this idea directly, our analyses do demonstrate significant phylogenetic conservatism (signal) in habitat moisture and vegetation openness, with Schoeneae dispersing into areas with the same habitat in 22 out of 29 cases (Fig. 6). In some instances, dispersal only took place after adaptation to novel habitats (e. g. dispersal to tropical China and India following adaptation to shaded habitats in *Machaerina, Gahnia*), while in others no change was involved (e. g. dispersal to South America and Southern Africa). Although denser species sampling, especially of

Lepidosperma, might alter our interpretation, these results argue for the general importance of ecological opportunity in structuring historical dispersal in Schoeneae.

In this context, palæoenvironmental perturbations operating at a regional scale have likely been influential in generating opportunities for dispersal, and in dictating the timing of such dispersal. The colonization of South America by *Oreobolus,* for example, coincided with Andean uplift and the opening up of the oligotrophic páramo vegetation type (Chacón et al., 2006), these changes likely enhancing the invasive success of this lineage. Similarly, the establishment of fynbos vegetation and its associated fire regime on the more nutrient-deficient substrates of the South African Cape, ca. 20 Ma or earlier (Bytebier et al., 2011), likely facilitated entry into the region by the progenitors of the *Tetraria* s. s. (23.0–37.5 Ma) and reticulate-sheathed *Tetraria* (10.7–20.7 Ma) clades. Members of both lineages resprout vigorously in the wake of fire (Slingsby, 2011) and, like closely related *Schoenus* (Shane et al., 2006), probably possess dauciform roots, reflecting adaptation to conditions of nutrient deficiency.

Conclusion

The six principal schoenoid lineages were differentiated during a dramatic radiation event taking place within Australia ca. 50 Ma, the rapid tempo of lineage divergence at this time accounting for a lack of phylogenetic resolution at the base of Schoeneae. From this starting point, members of the lineage dispersed freely, colonizing most landmasses in the Southern Hemisphere, sometimes repeatedly. We report a minimum of 29 transoceanic dispersal events since the Oligocene. Since dispersal rates are not related to geographic distance, factors other than geography are required to explain the australly biased distribution of this group. We propose a key role for niche conservatism, demonstrating that most transoceanic dispersal in Schoeneae has proceeded without change in the habitat variables examined. Further work is needed to test this idea more fully, however, specifically investigating the role of edaphic and climatic niche conservatism as a determinant of the distribution of the schoenoid sedges.

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Appendix 1. Vouchers

For each taxon, information is displayed in the following sequence: **Species,** *Voucher* (supplied only for new sequences), GenBank accession numbers: ITS, ETS, *rbc*L, *rps*16, *trn*L. New sequences KF553442–KF553627 are in bold.

***Arthrostylis aphylla* R.Br.,** —, —, AY506757, AY725939, —, AY506700. ***Becquerelia cymosa* Brongn.,** *Thomas et al. 10284 (K),* **KF553533,** —, Y12948, **KF553464, KF553496. *Calyptrocarya* sp. (ITS, ETS), *bicolor* (H.Pfeiff.) T.Koyama (*rbc*L),** *Kew 11301 (K),* **KF553534, KF553442,** EF178540, —, —. ***Capeobolus brevicaulis* (C.B.Clarke) Browning,** *Verboom 646,* **KF553535, KF553443,** DQ058343, DQ058324, DQ058303. ***Carex magellanica* Lam.,** —, AY757655, AY278292, GQ469849, EU541818, AY757521. ***Carpha alpina* R.Br.,** —, —, DQ385557, AF307909, —, AY230010. ***Carpha capitellata* var. *bracteosa* (C.B.Clarke) Kük.,** *Muasya 4759,* **KF553536,** —, **KF553598, KF553465, KF553497. *Carpha glomerata* Nees,** ITS, ETS: *Muasya 5863; rps*16: *Muasya 1176,* **KF553537, KF553444,** AY725941, **KF553466,** AY230024. ***Caustis dioica* R.Br.,** *MW Chase 2225 (K),* **KF553538,** —, Y12976, **KF553467, KF553498. *Chrysitrix capensis* L.,** *Muasya 3333,* **KF553539,** —, AJ419938, AY344148, AY344171.

***Cladium mariscus* (L.) Pohl,** *MJC 292 (K),* **KF553540,** —, DQ058338, DQ058319, AY344172. ***Costularia arundinacea* (Sol. ex Vahl) Kük.,** —, —, —, —, —, AY230036. ***Costularia fragilis* (Däniker) Kük.,** —, —, —, EU828589, —, —. ***Costularia laxa* Cherm.,** —, —, DQ450465, —, —, DQ456955. ***Costularia leucocarpa* (Ridl.) H.Pfeiff.,** *Larridon et al. 2010-0140,* **KF553541,** —, **KF553599, KF553468, KF553499. *Costularia natalensis* C.B.Clarke,** *Verboom 773,* **KF553542, KF553445,** DQ058345, DQ058326, DQ058305. ***Costularia nervosa* J.Raynal,** —, —, —, —, —, AY230032. ***Costularia pantopoda* (Baker) C.B.Clarke, var. *pantopoda*,** *Larridon et al. 2010-0144,* **KF553543,** —, **KF553600, KF553469, KF553500. *Costularia pantopoda* var. *baronii* (C.B.Clarke) Kük.,** *Larridon et al. 2010-0139,* **KF553544,** —, **KF553601, KF553470, KF553501. *Costularia* sp. 1,** *Larridon et al. 2010-0153,* **KF553545,** —, **KF553602, KF553471, KF553502. *Costularia* sp. 2,** *Larridon et al. 2010-0219,* **KF553546,** —, —, **KF553472, KF553503. *Costularia* sp. 3,** *Larridon et al. 2010-0249,* **KF553547,** —, **KF553603, KF553473, KF553504. *Cyathochaeta avenacea* (R.Br.) Benth.,** *Verboom 1248,* **KF553548,** —, **KF553604, KF553474, KF553505. *Cyathochaeta diandra* (R.Br.) Nees,** *Wilson 9468,* **KF553549,** —, —, —, AY230042. ***Cyathocoma hexandra* (Nees) Browning,** *Verboom 648,* **KF553550,** —, DQ058344, DQ058325, DQ058304. ***Cyperus rigidifolius* Steud.,** —, —, —, Y13016, AF449535, AY040600. ***Diplacrum caricinum* R.Br. (ITS), *africanum* (Benth.) C.B.Clarke (*rbc*L),** —, —, AB261688, AY725942, —, —. ***Epischoenus cernuus* Levyns,** *Verboom 707,* **KF553551,** —, **KF553605, KF553475, KF553506. *Epischoenus gracilis* Levyns,** *Verboom 636,* **KF553552,** —, DQ058349, DQ058332, DQ058311. ***Epischoenus villosus* Levyns,** *Verboom 1144,* **KF553553,** —, **KF553606, KF553476, KF553507. *Eriophorum vaginatum* L.,** —, AY242009, AY242008, Y12951, AF449553, AY757692. ***Evandra aristata* R.Br.,** ITS: *Bruhl 2108;* ETS: *Wilson 8974; trn*L: *Barrett 5356,* **KF553554, KF553446,** AY725944, —, **KF553508. *Ficinia paradoxa* (Schrad.) Nees,** ETS, ITS: *Verboom 534; rps*16: *Tshiila 13,* **KF553555, KF553447,** DQ058354, **KF553477,** DQ058317. ***Gahnia aspera* (ITS) var. *globosa* (*trn*L) (R.Br.) Spreng.,** —, —, AB261676, —, —, AF285073. ***Gahnia baniensis* Benl,** *Simpson 2737 (K),* **KF553556,** —, DQ058342, DQ058323, DQ058302. ***Gahnia trifida* Labill.,** *Verboom 1228,* **KF553557,** —, **KF553607, KF553478,**

KF553509. *Gahnia tristis* Nees ex Hook. & Arn., *Shaw 885 (K),* **KF553558,** AB261677, —, **KF553479, KF553510. *Hypolytrum nemorum* (Vahl) Spreng.,** —, —, AY242046, Y12958, AY344142, AJ577325. ***Lagenocarpus albo-niger* (A.St.-Hil.) C.B.Clarke,** *Thomas et al. 11111 (K),* **KF553559, KF553448,** AY725949, **KF553480, KF553511. *Lepidosperma* aff. *filiforme* Labill.,** ITS: *Bruhl 1898A;* ETS: *Barrett 4463,* **KF553560, KF553449,** —, —, AF285074. ***Lepidosperma laterale* R.Br.,** *Hosking 1786,* **KF553561,** DQ385587, —, —, **KF553512. *Lepidosperma longitudinale* Labill.,** ITS: *Hodgon 345;* ETS, *rbc*L, *rps*16, *trn*L: *Verboom 1236,* **KF553562, KF553450, KF553608, KF553481, KF553513. *Lepidosperma tortuosum* F.Muell.,** ITS: *Bruhl 2357;* ETS, *rps*16, *trn*L: *Coveny 17470 (K),* **KF553563, KF553451,** AY725950, **KF553482, KF553514. *Machaerina iridifolia* (Bory) T.Koyama,** *Ah-Peng 1742,* **KF553564,** —, **KF553609, KF553483, KF553515. *Machaerina juncea* (R.Br.) T.Koyama,** ETS: *Barrett 3352; rbc*L, *rps*16, *trn*L: *Verboom 1229,* **KF553565,** —, **KF553610, KF553484, KF553516. *Machaerina mariscoides* (Gaudich.) J.Kern,** *Johns 9195 (K),* **KF553566,** —, DQ058340, DQ058321, DQ058300. ***Machaerina rubiginosa* (Spreng.) T.Koyama,** ETS, *trn*L: *Bruhl 1859; rbc*L: *Wilson 9456,* **KF553567,** AB261679, **KF553611,** —, **KF553517. *Mapania cuspidata* (Miq.) Uittien,** —, —, —, DQ058337, DQ058318, DQ058297. ***Mesomelaena pseudostygia* (Kük.) K.L.Wilson,** *Barrett 5279,* **KF553568,** —, DQ058341, DQ058322, DQ058301. ***Mesomelaena tetragona* (R.Br.) Benth.,** *Chase 2227 (K),* —, —, Y12949, **KF553485, KF553518. *Morelotia gahniiformis* Gaudich.,** ITS: *Morden 2117; trn*L: *Morden s.n.,* —, **KF553452,** EF178576, —, **KF553519. *Neesenbeckia punctoria* (Vahl) Levyns,** ITS: *Bruhl 1731;* ETS: *Verboom 650,* **KF553569, KF553453,** AY725952, DQ058327, DQ058306. ***Oreobolus distichus* F.Muell.,** *Coveny 5373 (K),* **KF553570,** DQ450468, —, —, AY230030. ***Oreobolus kuekenthalii* Steenis ex Kük.,** —, —, AY242047, Y12972, —, EF178536. ***Oreobolus obtusangulus* Gaudich.,** —, —, DQ450472, AF307926, —, DQ456962. ***Oreobolus oligocephalus* W.M.Curtis,** —, —, DQ450473, —, —, DQ456963. ***Oreobolus pectinatus* Hook.f.,** —, —, DQ450475, AF307927, —, DQ456965. ***Pseudoschoenus inanis* (Thunb.) Oteng-Yeb.,** *Muasya 4384,* —, —, **KF553612, KF553486, KF553520. *Ptilothrix deusta* (R.Br.) K.L.Wilson,** ITS: *Bruhl 2055;* ETS: *Gibbs 46,* **KF553571, KF553454,** —, —, AY230041. ***Rhynchospora rugosa***

subsp. *brownii* (Roem. & Schult.) T.Koyama, *Verboom 616,* **KF553572, KF553455,** DQ058353, DQ058336, AY230043. ***Schoenus bifidus* (Nees) Boeckeler,** ITS: *Hodgon 784; rps*16, *trn*L: *Verboom 1249,* —, **KF553456,** —, **KF553487, KF553521. *Schoenus caespititius* W.Fitzg.,** *Verboom 1255,* **KF553573,** —, —, **KF553488, KF553522. *Schoenus curvifolius* (R.Br.) Roem. & Schult.,** ITS: *Barrett 4174;* ETS, *rbc*L, *rps*16, *trn*L: *Verboom 1240,* **KF553574, KF553457, KF553613, KF553489, KF553523. *Schoenus efoliatus* F.Muell.,** ITS: *Barrett 5341;* ETS, *rbc*L, *rps*16, *trn*L: *Verboom 1235,* **KF553575, KF553458, KF553614, KF553490, KF553524. *Schoenus grandiflorus* (Nees) F.Muell.,** ITS, *trn*L: *Wilson 8847;* ETS: *Barrett 3364,* **KF553576, KF553459,** —, —, **KF553525. *Schoenus nigricans* L.,** *Haase et al. s.n. (K),* —, **KF553460,** Y12983, DQ058331, DQ058310. ***Schoenus nitens* (R.Br.) Roem. & Schult.,** *Gibbs 133,* **KF553577, KF553461,** —, —, **KF553526. *Schoenus pennisetis* S.T.Blake,** *Verboom 1237,* **KF553578,** —, **KF553615, KF553491, KF553527. *Schoenus rigens* S.T.Blake,** *Barrett 5234,* **KF553579,** GU386455, —, —, **KF553528. *Scleria distans* Poir.,** *Muasya 1023,* —, **KF553462,** DQ058339, DQ058320, DQ058299. ***Tetraria bolusii* C.B.Clarke,** *Verboom 606,* **KF553580,** —, **KF553616,** DQ058335, DQ058315. ***Tetraria capillaris* (F.Muell.) J.M.Black,** ETS, *rbc*L: *Wilson 9464; trn*L: *Bruhl 2484,* **KF553581,** DQ385604, **KF553617,** —, **KF553529. *Tetraria compacta* Levyns,** *Verboom 614,* **KF553582,** —, DQ058351, **KF553492,** DQ058313. ***Tetraria compar* (L.) P.Beauv.,** *Verboom 549,* **KF553583,** —, DQ058350, DQ058333, DQ058312. ***Tetraria crassa* Levyns,** *Verboom 507,* **KF553584,** —, DQ058352, DQ058334, DQ058314. ***Tetraria cuspidata* (Rottb.) C.B.Clarke,** *Verboom 520,* **KF553585,** —, **KF553618,** DQ419897, DQ419865. ***Tetraria exilis* Levyns,** *Verboom 623,* **KF553586,** —, **KF553619,** DQ419898, DQ419866. ***Tetraria flexuosa* (Thunb.) C.B.Clarke,** *Verboom 505,* **KF553587,** —, **KF553620,** DQ419891, DQ419859. ***Tetraria involucrata* (Rottb.) C.B.Clarke,** ETS: *Verboom 1283; rbc*L: *Verboom 661,* **KF553588,** —, **KF553621,** DQ419884, DQ419852. ***Tetraria microstachys* (Vahl) H.Pfeiff.,** *Verboom 640,* **KF553589,** —, DQ058347, DQ058328, DQ058307. ***Tetraria nigrovaginata* (Nees) C.B.Clarke,** *Verboom 500,* **KF553590,** —, **KF553622,** DQ419889, DQ419857. ***Tetraria picta* (Boeckeler) C.B.Clarke,** *Verboom 524,* **KF553591,** —, **KF553623,** DQ419899, DQ419867. ***Tetraria sylvatica* (Nees) C.B.Clarke,** *Verboom*

515, **KF553592,** —, **KF553624,** DQ419896, DQ419864. ***Tetraria triangularis*** **(Boeckeler) C.B.Clarke,** *Verboom 518,* **KF553593,** —, —, DQ419885, DQ419853. ***Tetraria ustulata*** **(L.) C.B.Clarke,** *Verboom 664,* **KF553594,** —, **KF553625,** DQ419893, DQ419861. ***Tetraria variabilis*** **Levyns,** *Verboom 508,* **KF553595,** —, **KF553626, KF553493, KF553530. *Tetrariopsis octandra*** **(Nees) C.B.Clarke,** *Verboom 1242,* —, —, **KF553627, KF553494, KF553531. *Trianoptiles capensis*** **(Steud.) Harv.,** *Muasya 3160,* **KF553596, KF553463,** —, **KF553495, KF553532. *Tricostularia pauciflora*** **(R.Br.) Benth.,** *Gibbs 53,* **KF553597,** —, AY725954, —, AY230038.

Table 1. Sizes, distributions, and habitats of the main clades in Schoeneae and extent of sampling in this study.

Clade	Taxa included	No. of species	Number sampled	Proportion	Distribution	Distribution sampled	References	Habitat
Carpha	*Carpha*	15	3	0.2	SE Aus; NZ; Pap; Japan; S+E+C Afr; Masc; Mad; S Am	Aus; NZ; S Afr	Zhang et al. (2004)	In swamps from low to high altitudes, often along stream sides or rivulets
	Trianoptiles	3	1	0.3	S Afr	S Afr	Zhang et al. (2004)	In wetland
Caustis	*Caustis*	5	1	0.2	Aus	Aus		In open forest or scrub, on dry sandy soil, also at the edge of streams
	Evandra	2	1	0.5	Aus	Aus		On wet spots in heathland
Gahnia	*Gahnia*	40	4	0.1	Aus; NZ; China; Mal; NC; Hawaii	Aus; Mal; NC		In swampy to wet places in lowland and at high altitude
	Cyathochaeta	5	2	0.4	Aus	Aus		In marshes
	Mesomelaena	5	2	0.4	Aus	Aus		In heath formations
	Ptilothrix	1	1	1	Aus	Aus		In open vegetation
Lepidosperma	*Lepidosperma*	66	4	0.1	Aus; NC; NZ; China; Mal	Aus; NZ		Along rivers and in woodland, rarely in mountain heath vegetation
	Machaerina	51	4	0.1	Aus; Mal; China; Pacific; NZ; C+S Am; E Afr; Mad; Masc	Aus; Mal; NC; NZ; Mad		In wetlands, sometimes as floating mats, or in woodlands, often at higher altitudes
	Tetraria capillaris complex	9	1	0.1	Aus; NZ	Aus; NZ	Barrett et al., in prep.	Along creeks and in woodland and heath formations
	Neesenbeckia	1	1	1	S Afr	S Afr		At stream sides
Oreobolus	*Oreobolus*	16	5	0.3	Aus; Mal; NZ; S Am; Hawaii	Aus; Mal; NZ; S Am	Seberg (1988)	In wet alpine and subantarctic vegetation
	Costularia subgenera *Costularia* & *Chamaedendron*	15	6	0.4	S Afr; Mad; NC	S Afr; Mad; NC	Raynal (1974)	In scrubby vegetation on rocky ground, rarely in forest fringes
	Capeobolus	1	1	1	S Afr	S Afr		Fynbos (heath)
	Cyathocoma	3	1	0.3	S Afr	S Afr		On mountain slopes
Schoenus	*Schoenus* s. s.	105	7	0.1	Aus; NZ; Japan; China; Mal; S Afr; Eur; W Asia; S US; C Am; S Am	Aus; NZ; Mal; S Afr	Bruhl et al., in prep.	Often in humid grassland or woodland
	Tetraria s. s.	30	9	0.3	S Afr	S Afr	Levyns (1947)	In rather dry, sandy, or rocky places on mountain slopes, more rarely in marshy places
	Epischoenus	7	2	0.3	S Afr	S Afr	Levyns (1959)	In damp to marshy places, often low- to mid-montane
Tricostularia	*Tricostularia*	5	1	0.2	Aus; NC; Mal	Aus		In open heath or scrubland, on humid sandy soils
	Morelotia	2	1	0.5	NZ; Hawaii	Hawaii		On dry open hillsides
	Tetraria octandra	1	1	1	Aus	Aus		Sedgeland, heath, woodland

	Schoenus p. p.	3	2	0.7	Aus	Aus	Bruhl et al., in prep.	Often in humid grassland or woodland
	Reticulate-sheathed *Tetraria*	46	6	0.1	S+E Afr	S Afr	Slingsby (2011)	In rather dry, sandy, or rocky places on mountain slopes, more rarely in marshy places
	Epischoenus cernuus	1	1	1	S Afr	S Afr		Seasonal swamps, open heath
	Costularia subgen. *Lophoschoenus*	9	1	0.1	NC; Mal; Pap; Seychelles	NC	Raynal (1974)	In scrubby vegetation on rocky ground, rarely in forest fringes
Unknown	*Reedia*	1	0	0	Aus	—		In swamps
	Gymnoschoenus	2	0	0	Aus	—		Swamps, sedgeland or heathlike vegetation
Ingroup total		450	69	0.15				

Notes: Species from polyphyletic genera were assigned to clades on the basis of published and preliminary results (listed references and Verboom, 2006). Clade sizes and distributions were inferred from the World Checklist of Monocotyledons (Govaerts et al., 2011) and the listed references. Habitat descriptions are from Goetghebeur (1998) and our own observations. Afr, Africa; Am, America; Aus, Australia; Mad, Madagascar; Mal, Malesia; Masc, Mascarenes; NC, New Caledonia; NZ, New Zealand; Pap, Papuasia.

Table 2. Comparison of dispersal models, showing that incorporating geographic distance did not result in better model fit and that the large number of parameters in the most complex model (B) was not justified by a sufficient increase in the likelihood.

Model	Global dispersal rate	Global extinction rate	$\ln L$	No. of parameters	AIC	Model weight ω
A. All rates equal	0.004	0.000	−147.0	2	298.0	1.00
B. All rates estimated separately	0.276	0.000	−120.3	44	328.7	2.18×10^{-7}
C. Rates inversely proportional to minimum distance	0.030	0.000	−160.8	2	325.7	9.55×10^{-7}
D. Rates inversely proportional to minimum distance squared	0.042	0.000	−212.5	2	429.1	3.39×10^{-29}

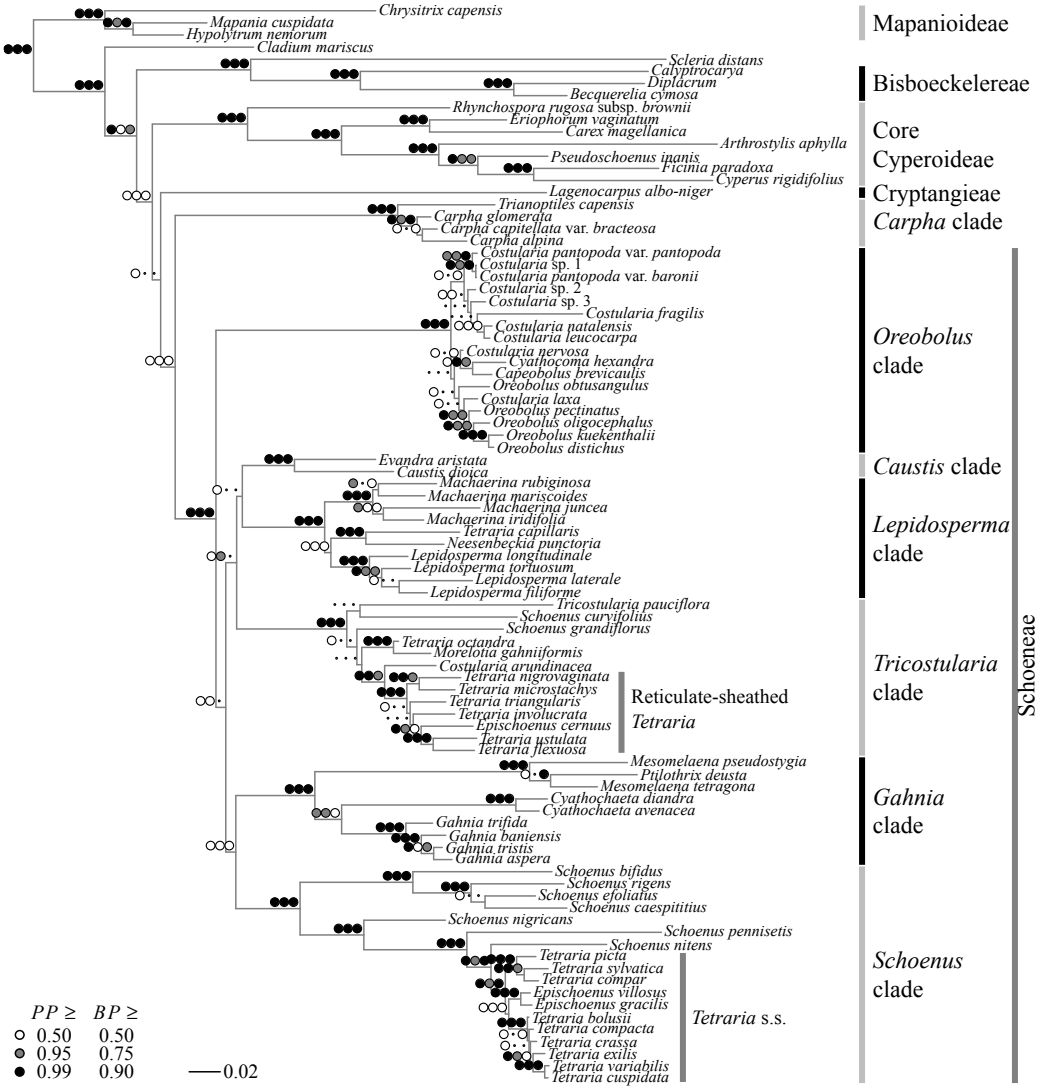


Fig. 1. Bayesian tree of Schoeneae based on ETS, ITS, *rbc*L, *rps*16, and *trn*L. The tree is plotted with the branch lengths estimated in MrBayes. The scale bar is in substitutions per site. Shaded points on each branch represent, from left to right, *PP* values from MrBayes, *PP* values from Phycas, and *BP* values from RAxML. Clades in Schoeneae are labelled with the informal names used in the text.

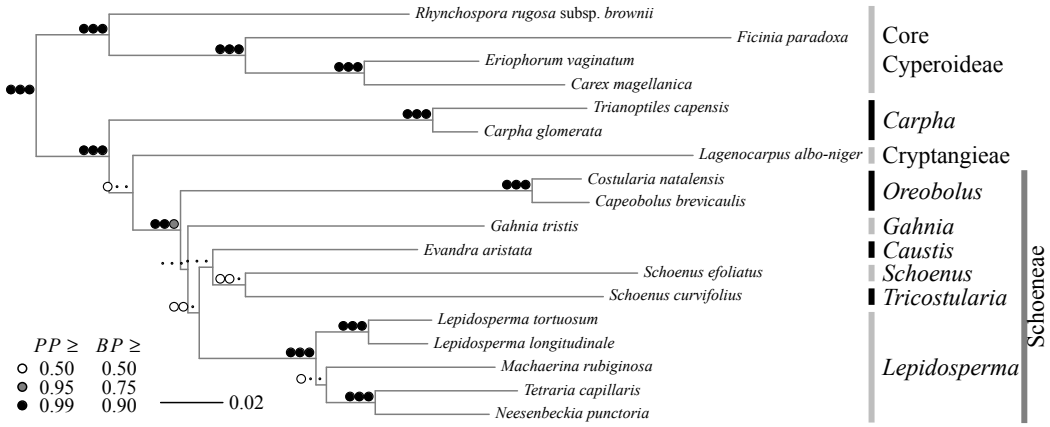


Fig. 2. Bayesian tree for the subset of taxa that were sampled for both nuclear and at least two cpDNA markers.
Other details as in Fig. 1.

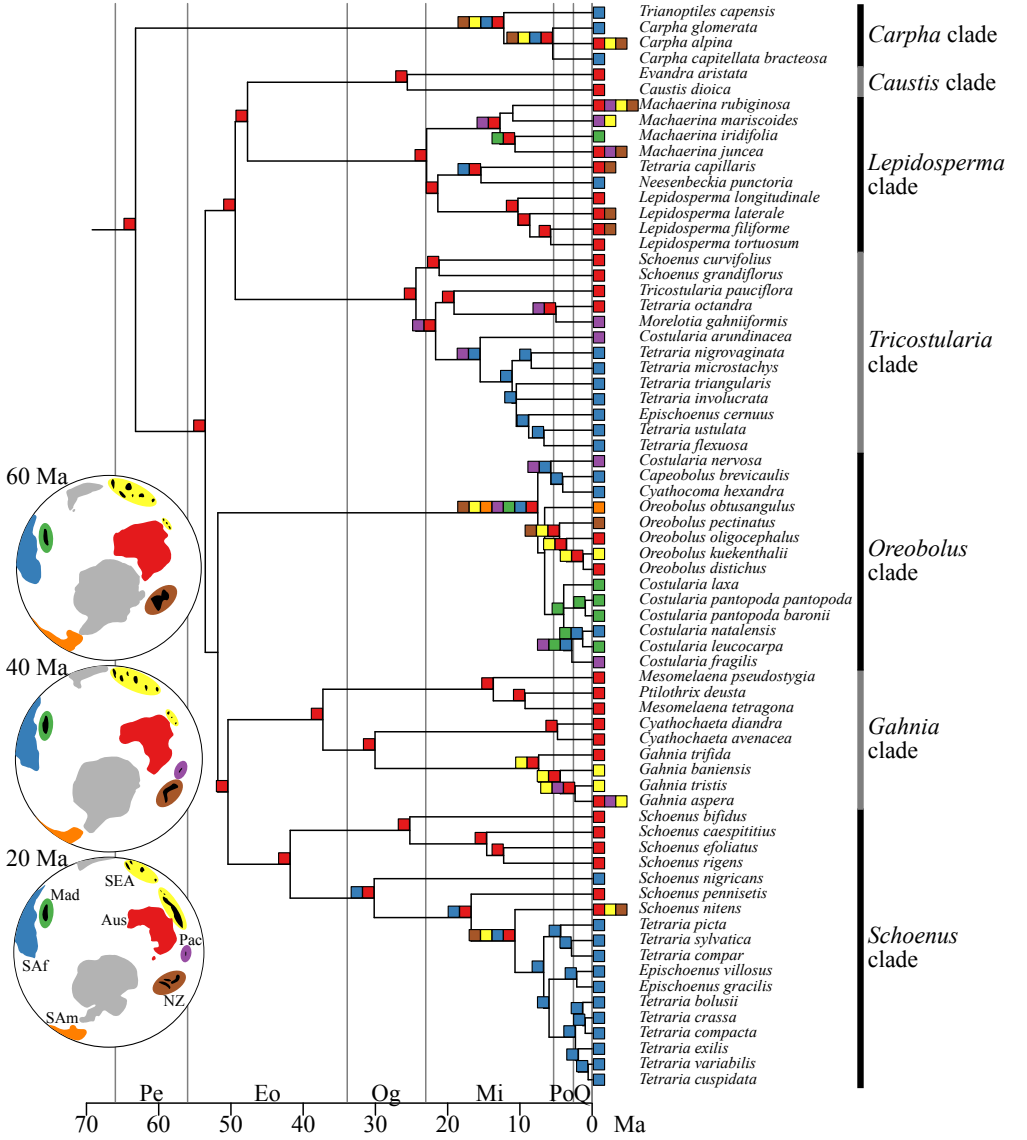


Fig. 3. Maximum-likelihood reconstruction of ancestral distributions in Schoeneae. Coloured boxes indicate the areas with a proportional likelihood (averaged over 1000 BEAST trees and summed over all distribution ranges containing the area) of $pL \geq 0.50$ at each node, plotted on the consensus tree (nodes with $PP < 0.50$ collapsed). Note that three of the nodes had no areas with total $pL \geq 0.50$. Please see Appendix S4 (online) for the pL values of each combination of areas. Maps are based on Wilford and Brown (1994). Geological epochs follow Gradstein et al. (2004) and are indicated with the standard abbreviations. Aus, Australia; Mad, Madagascar; Pac, Pacific Islands; NZ, New Zealand; SAf, Southern Africa; SAm, South America; SEA, Southeast Asia.

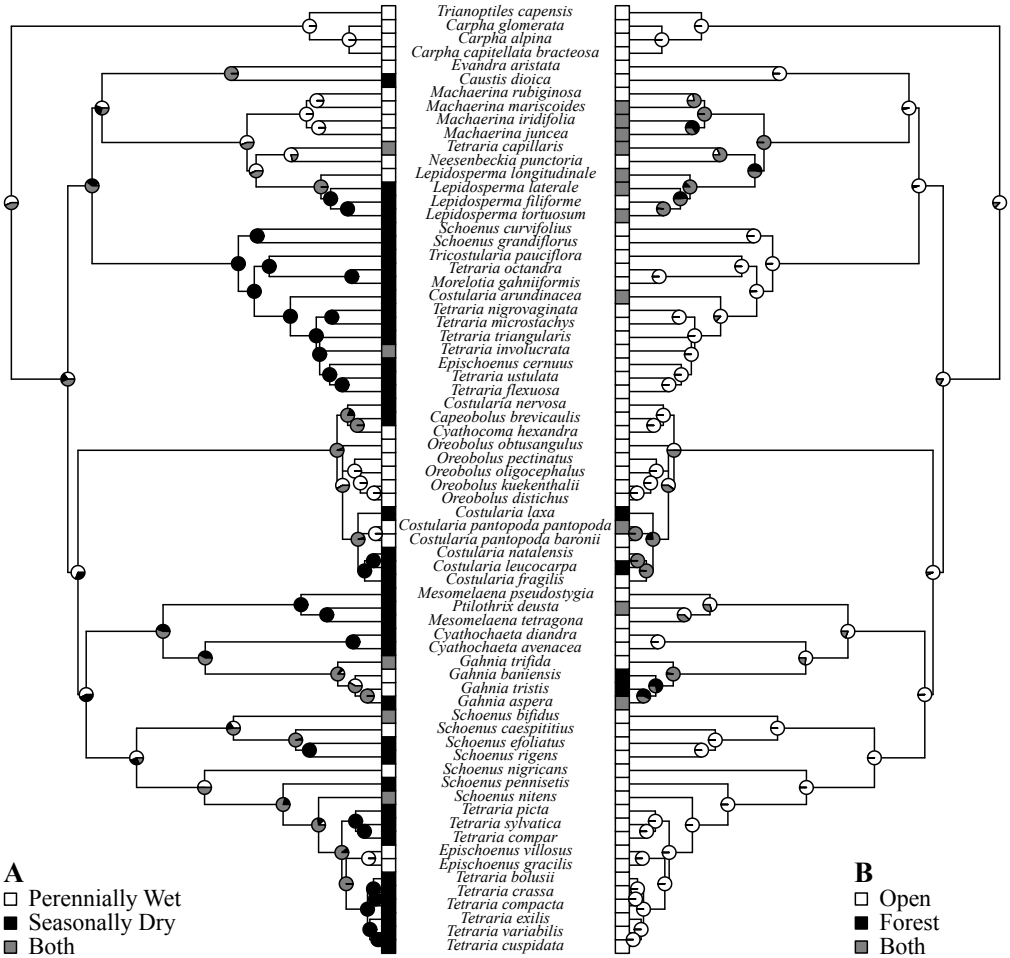


Fig. 4. Maximum-likelihood reconstructions of ancestral habitats in Schoeneae, shown as the proportional likelihood of each state at ancestral nodes. (A) Moisture regime. (B) Vegetation type.

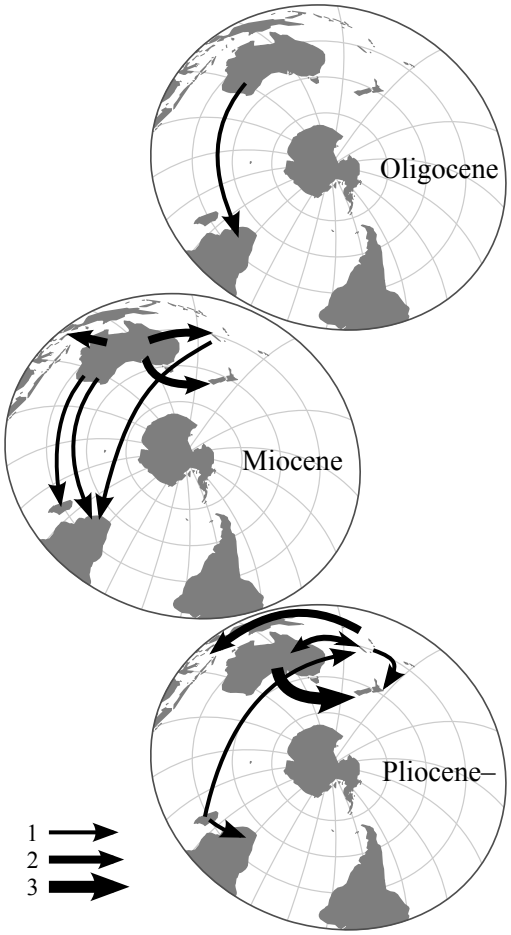


Fig. 5. Inferred dispersal events in Schoeneae.
Arrow thickness is proportional to the number of events. The six dispersal events in the *Oreobolus* clade for which the source area was ambiguously reconstructed have been omitted. Maps were drawn using the R packages maps v. 2.2-6 and mapproj v. 1.1-8.3.

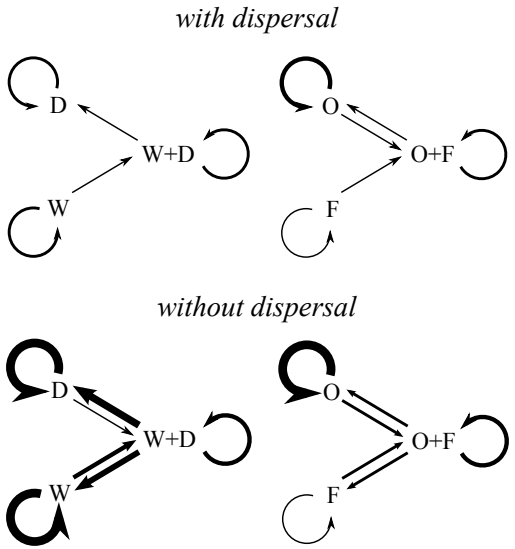
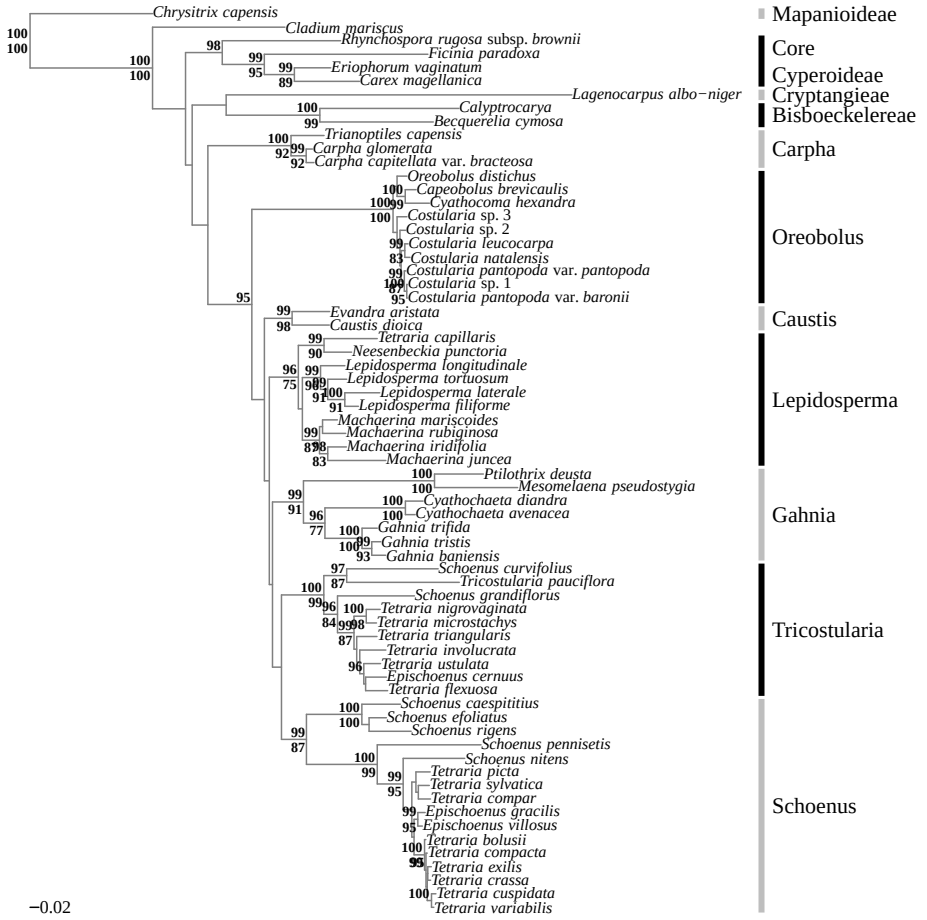
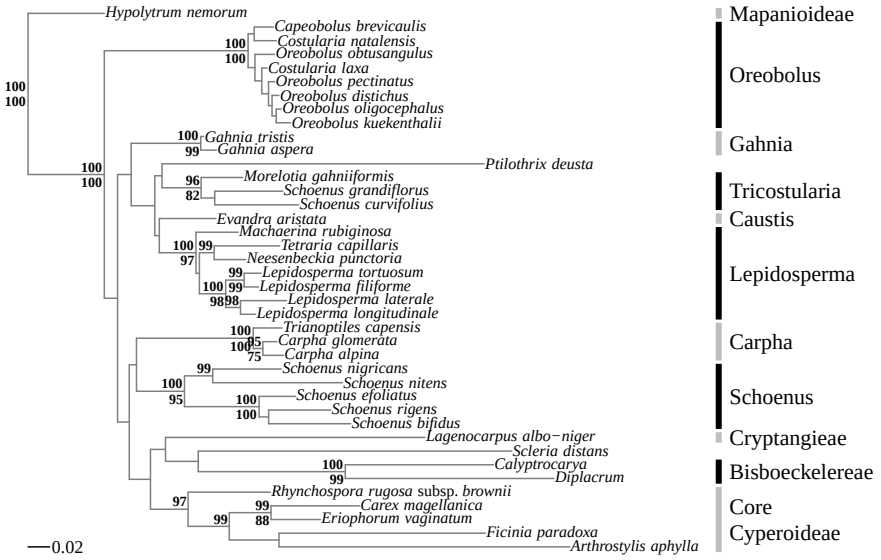


Fig. 6. Number of habitat shifts along branches with and without dispersal events. Counts were binned into classes of width 3; arrow thickness is proportional to the class mean. Loops represent branches where no shift occurred. D, seasonally dry; W, perennially wet; F, forest (closed-canopy) vegetation; O, open vegetation.



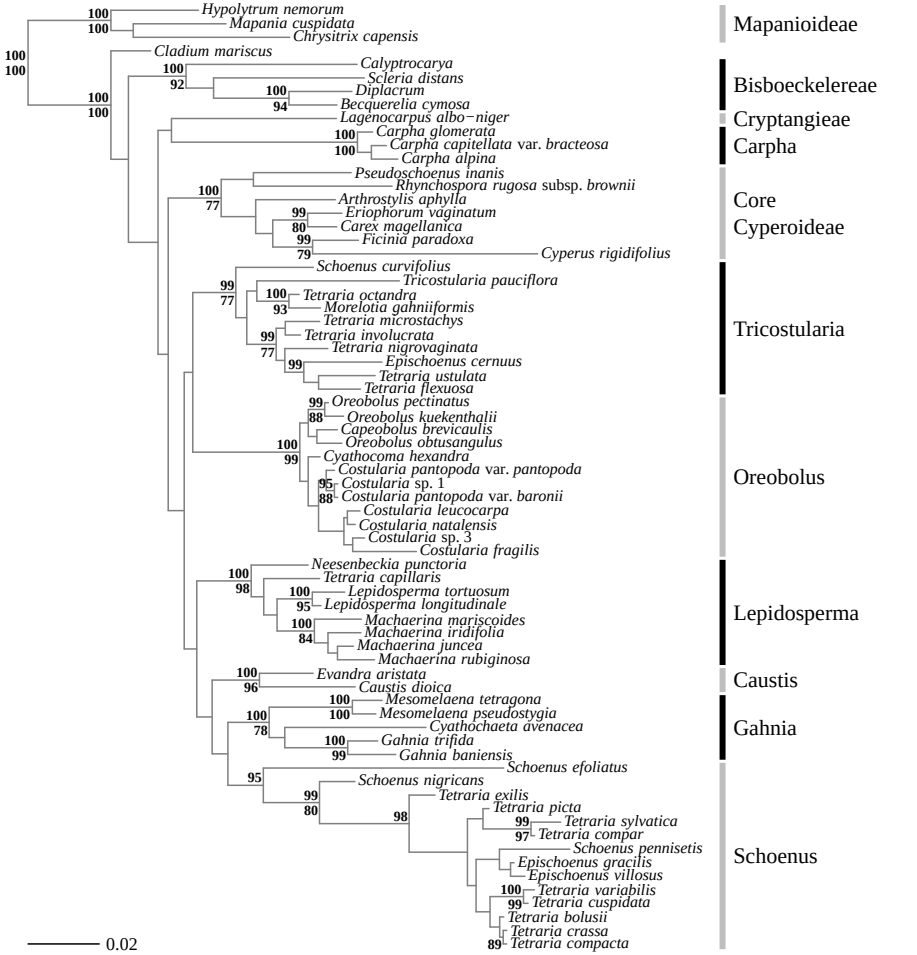
(a) ETS

Appendix S1. Gene trees of Schoeneae inferred with MrBayes and RAxML. Scale bar is in substitutions per site. Node support is indicated by *PP* values above subtending branches and *BP* values below. Clades in Schoeneae are labelled with the informal names used in the text.



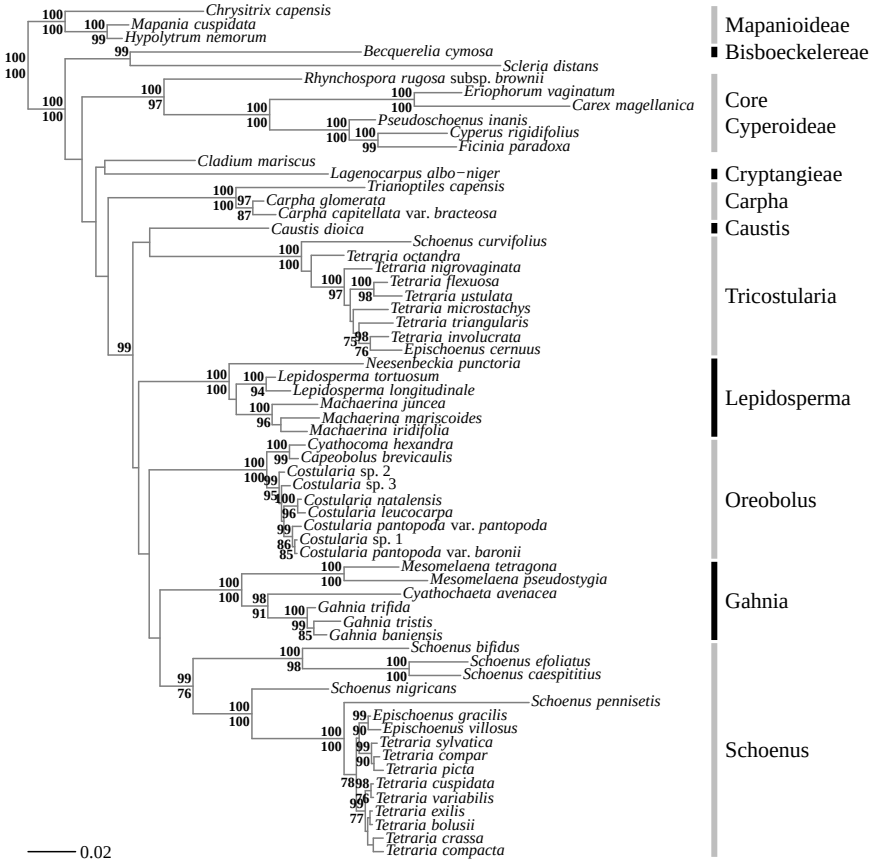
(b) ITS

Appendix S1. Gene trees (continued).



(c) *rbc*L

Appendix S1. Gene trees (continued).

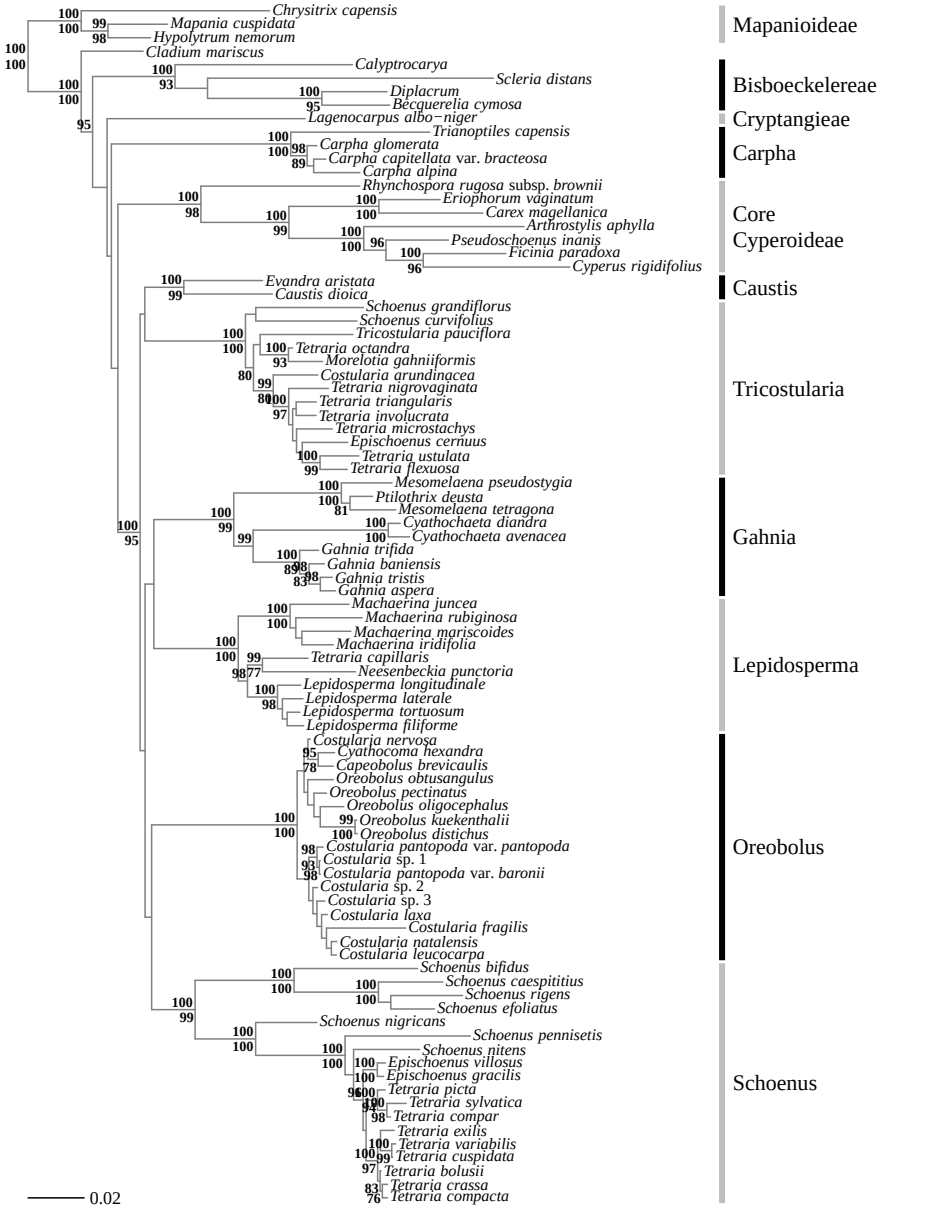


(d) *rps*16

Appendix S1. Gene trees (continued).

(e) *trn*L

Appendix S1. Gene trees (continued).



(f) Concatenated cpDNA

Appendix S1. Gene trees (continued).

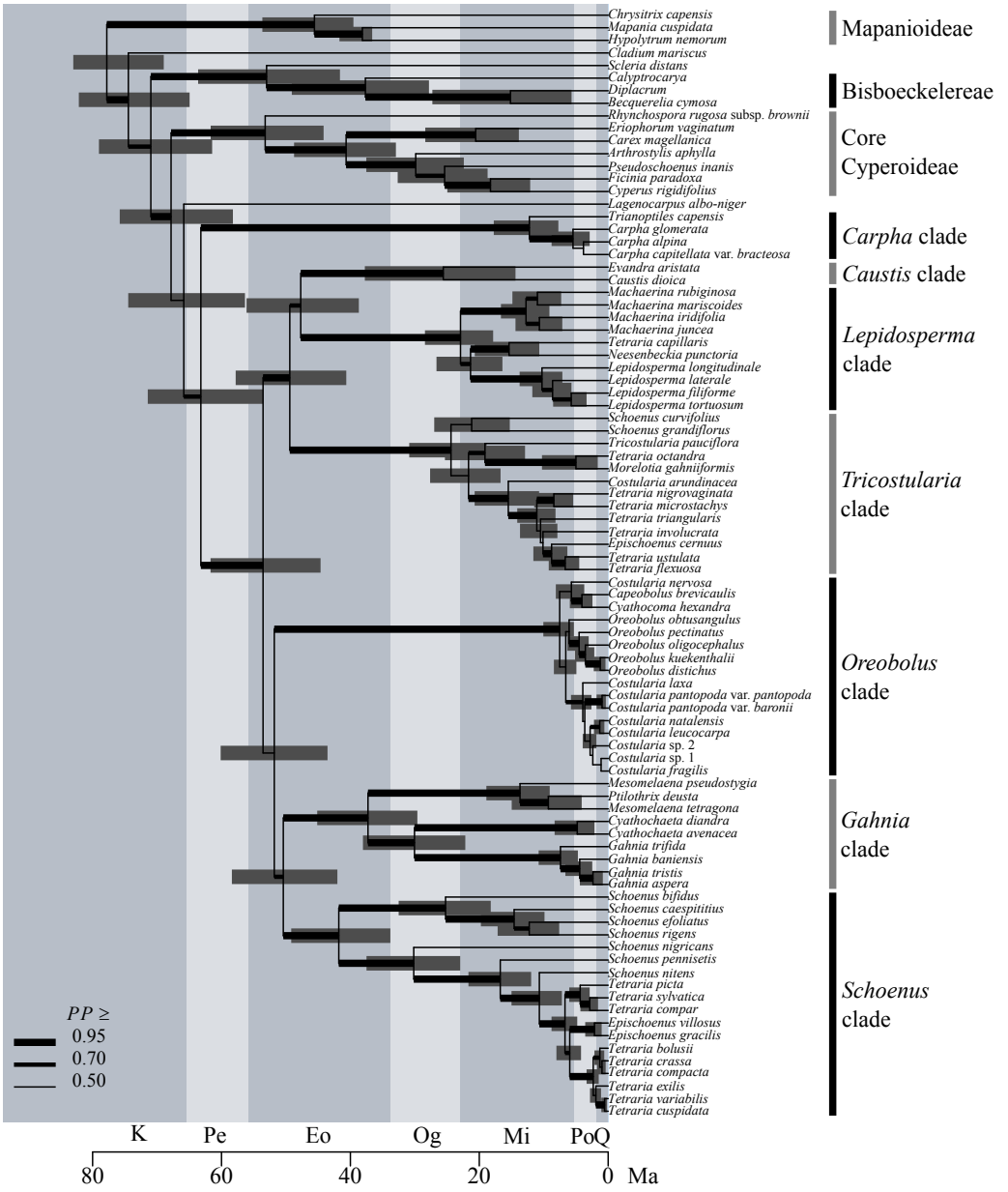
Appendix S2. Habitat descriptions from the literature and coding for reconstruction of ancestra

Species	Description	Reference
Capeobolus brevicaulis	Rocky slopes in mountain *fynbos* below 1600 m	Archer (2000)
Carpha alpina	Common in bogs in mountain districts, 300–1800 m; at sea level in Southland; *pakihi*-land	Edgar (1970)
Carpha capitellata var. *bracteosa*	Marshy places, flats, and lower slopes	Levyns (1950)
Carpha glomerata	Streamsides, flats, and lower mountain slopes	Levyns (1950)
Caustis dioica	In sand; usually in heath or *Banksia* woodland	Rye (1987); Wheeler et al. (2002)
Costularia arundinacea	Maquis ensoileillés ou léger sous-bois, sur sols variés; 0–1500 m	Raynal (1974)
Costularia fragilis	Rocailles et maquis steppiques; 0–1400 m	Raynal (1974)
Costularia laxa	Forêts, brousse éricoïde, 1400–2000 m	Chermezon (1937)
Costularia leucocarpa	Forêts, rochers siliceux, 700–2000 m	Chermezon (1937)
Costularia natalensis	In rough grassland or in remnants of forest margin, frequently among rocks	Gordon-Gray (1995)
Costularia nervosa	Maquis ensoleillés sur péridotites	Raynal (1974)
Costularia pantopoda var. *pantopoda*	Forêts, rocailles humides, marais, 1200–2500 m	Chermezon (1937)
Costularia pantopoda var. *baronii*	Rocailles siliceuses humides, marais, *savoka,* 600–2400 m	Chermezon (1937)
Cyathochaeta avenacea	Heath and woodland, often bordering swamps or watercourses	Wheeler et al. (2002)
Cyathochaeta diandra	Sandstone; in heath	Beadle et al. (1982)
Cyathocoma hexandra	Marshes and water courses on mountain slopes below 800 m	Archer (2000)
Epischoenus cernuus	Damp sandy places, 180–1530 m; mountain slopes	Levyns (1959); Archer (2000)
Epischoenus gracilis	Marshy places, 300–1670 m	Levyns (1959)
Epischoenus villosus	Damp places, 180–1830 m	Levyns (1959)
Evandra aristata	Swamps and winter-wet heath	Wheeler et al. (2002)
Gahnia aspera	In drier situations in rainforest, dry sclerophyll forest, and woodland	Wilson (1993)
Gahnia baniensis	In thickets on hills and mountain ridges, in open country among bracken, mostly 900–2100 m, rarely down to 200 m; swampy to wet places in lowland and at high altitude	Kern (1974)

Species	Description	Reference
Gahnia trifida	Along the margins of estuaries and watercourses, in coastal heaths, and bordering swamps, often in saline soils	Wheeler et al. (2002)
Gahnia tristis	In swampy to wet places in lowland and at high altitude; in dry spots near the sea, on riverbanks, also in rocky places and along trails in the mountains, up to 1200 m in the Malay Peninsula, up to 2000 m in Borneo	Kern (1974)
Lepidosperma filiforme	Lowland on poor clay hills and in sandy soil in *Leptospermum* scrub or in *pakihi;* in heath, woodland, and forest on sandy soils	Edgar (1970); Wilson (1993)
Lepidosperma laterale s. l.	Lowland on poor clay hills, or in damp sand, or in *Leptospermum* scrub; in a range of habitats, especially woodland and forest, mostly on sandy soils, often on rocky hillsides	Edgar (1970); Wilson (1993)
Lepidosperma longitudinale	In winter-wet depressions and along watercourses; swamps	Rye (1987); Beadle et al. (198
Lepidosperma tortuosum	Sandy soil; in mountain heath and woodland	Beadle et al. (1982); Wilson (1993)
Machaerina iridifolia	Les montagnes des Mascareignes et des Seychelles; on forest margins at high altitude and on lava flows on Réunion	Raynal (1972)
Machaerina juncea	Lowland swamps, salt marshes, damp sand on lake margins and river estuaries, 0–275 m	Edgar (1970)
Machaerina mariscoides	In secondary forests, on open hillsides, at low altitudes, up to 350 m; in wetlands, sometimes as floating mats, or in woodlands, often at higher altitudes	Kern (1974)
Machaerina rubiginosa	Swampy places and lake margins; sometimes dominant over wide of the marsh, 0–2650 (3225?) m	Kern (1974)
Mesomelaena pseudostygia	In the coastal sandplain heaths and scrub heaths	Wilson (1981)
Mesomelaena tetragona	Heath and woodland on sand and laterite, sometimes in low-lying winter-wet areas	Wheeler et al. (2002)
Morelotia gahniiformis	On dry open hillsides; on lava fields and in dry forest, mesic forest and subalpine shrubland, 520–2380 m	Wagner et al. (1999)
Neesenbeckia punctoria	Streamsides on lower slopes to 800 m	Archer (2000)
Oreobolus distichus	Moist places in the alpine zone, 1100–2400 m	Seberg (1988)
Oreobolus kuekenthalii	In mountain heaths in dry or somewhat moist localities, also in open places on rocks, sometimes dominant; in the Malay Peninsula 1600–2150 m, in Sumatra 2450–3460 m	Kern (1974)
Oreobolus obtusangulus	Moorland, e. g. *Astelia* and *Sphagnum* bogs, 0–2400 m (Chilean/Argentine subsp. *obtusangulus*); in cushion and *Sphagnum* bogs in páramo, 3000–4000 m (Andean subsp. *unispicus*)	Seberg (1988)
Oreobolus oligocephalus	In wet alpine and subantarctic vegetation	Curtis (1985)

Species	Description	Reference
Oreobolus pectinatus	In bogs, 900–1500 m, descending to sea level in Southland; on the bare and exposed faces of hills; moist habitats, 0–2150 m	Edgar (1970); Seberg (1988)
Ptilothrix deusta	In seasonally wet heath and dry sclerophyll forest and woodland, on sandy soil	Wilson (1993)
Schoenus bifidus	Swamps, watercourses, and winter-wet depressions in heath and woodland	Wheeler et al. (2002)
Schoenus caespititius	Heath, shrubland, woodland and coastal heath, usually in winter-wet areas	Wheeler et al. (2002)
Schoenus curvifolius	*Banksia* and jarrah woodland and heath, sometimes in winter-wet areas	Wheeler et al. (2002)
Schoenus efoliatus	Often in humid grassland or woodland; swamps and winter-wet areas in heath and woodland, sometimes in water	Wheeler et al. (2002)
Schoenus grandiflorus	In jarrah and *Banksia* woodland in sandy soil	Wheeler et al. (2002)
Schoenus nigricans	Marshes and water courses on flats and lower slopes below 200 m	Archer (2000)
Schoenus nitens	Damp areas near sea-shores, estuaries and salt-lakes, usually associated with limestone	Wheeler et al. (2002)
Schoenus pennisetis	Delicate annual; clay soils in winter-wet flats or swampy depressions	Wheeler et al. (2002)
Schoenus rigens	In sandy soil in winter-wet depressions	Rye (1987)
Tetraria bolusii	Below 1200 m	Archer (2000)
Tetraria capillaris	Swampy ground or *pakihi,* or in dry sand or scrub, 0–600 m; in gravelly soils in jarrah woodlands (but see Barrett & Wilson, forthcoming)	Edgar (1970); Rye (1987)
Tetraria compacta	Bushy slopes	Levyns (1950)
Tetraria compar	Sandy lower slopes and coastal *fynbos*	Archer (2000)
Tetraria crassa	Lower mountain slopes	Archer (2000)
Tetraria cuspidata	Sparse grassland, often among rocks and mostly in sandstone-derived soils, 1500–2500 m	Gordon-Gray (1995)
Tetraria exilis	Widely scattered among bushes on the flats and mountains but never very abundant	Levyns (1947)
Tetraria flexuosa	Flats and mountains	Levyns (1950)
Tetraria involucrata	Moist sandstone slopes to 2000 m	Archer (2000)
Tetraria microstachys	Flats and mountains, in dry sandy places	Levyns (1950)
Tetraria nigrovaginata	Sandy mountain slopes and plateaux to 1200 m	Archer (2000)
Tetraria octandra	In sandy heath and woodland, and on hillsides with granitic rocks	Wheeler et al. (2002)
Tetraria picta	Moist sands above 1200 m	Archer (2000)
Tetraria sylvatica	Sandy and gravelly places on flats and mountains	Levyns (1950)
Tetraria triangularis	Bushy places on the eastern part of the summit of Table Mt.	Levyns (1950)
Tetraria ustulata	Sandy flats, lower slopes, and plateaux to 1200 m	Archer (2000)
Tetraria variabilis	Sandy places from Smitswinkel Bay southwards	Levyns (1947)

Species	Description	Reference
Trianoptiles capensis	Damp places on flats and lower mountain slopes	Levyns (1950)
Tricostularia pauciflora	Sandstone; swampy places	Beadle et al. (1982)



Appendix S3. Dated tree of Schoeneae reconstructed in BEAST.
Branch thickness indicates node support. Nodes with $PP < 0.5$ have been collapsed. Grey bars indicate 95 % HPD intervals of node ages. Geological epochs follow Gradstein et al. (2004) and are indicated with the standard abbreviations.

Appendix S4. Proportional likelihoods of ancestral areas at each node of the Schoeneae tree. (See inset for node numbers and Fig. 3 for area codes.)

Node	SAf	Mad	Aus	Pac	SEA	SAf Mad	SAf Aus	SAf Pac	Mad Aus	Mad Pac	Aus NZ	Aus Pac	Aus SEA	Pac SEA	SAf Mad Pac	SAf Aus NZ	SAf Aus Pac	SAf Aus SEA	SA NZ SE
1			0.09				0.1				0.06		0.06			0.09		0.08	
2			0.54																
3			0.41																
4			0.7																
5			0.81				0.12												
6							0.71									0.07		0.07	
7			0.04				0.33									0.19		0.19	
8							0.17									0.2		0.2	
9	1																		
10	0.86																		
11	1																		
12	0.56																		
13	1																		
14	0.92																		
15	0.55																		
16	1																		
17	1																		
18	1																		
19			1																
20			1																
21			0.8																
22			0.99																
23			0.94																
24			0.29									0.04	0.42						
25					0.08								0.5						
26					0.05								0.35						
27			1																
28			1																
29			0.96																
30																			
31																			
32		0.42				0.05				0.15					0.21				
33										0.19					0.51				
34						0.88													
35		1																	
36											0.27								
37			0.27										0.7						
38													1						
39								0.58											
40	0.99																		
41			0.96																
42			0.48				0.08					0.27					0.13		
43			0.06				0.09					0.37					0.16		
44								0.98											
45	1																		
46	0.55																		
47	1																		
48	1																		
49	1																		
50			0.44									0.29							
51												1							

Appendix S4. Proportional likelihoods of ancestral areas at each node of the Schoeneae tree (continued).

Node	Aus NZ SEA	Aus Pac SEA	SAf Aus NZ SEA	Mad Aus NZ Pac	Mad Aus NZ SAm	Mad Aus Pac SEA	Aus NZ Pac SEA	SAf Mad Aus NZ SAm	SAf Mad Aus Pac SAm	SAf Mad NZ Pac SAm	SAf Aus NZ SAm SEA	Mad Aus NZ Pac SAm	Mad Aus NZ Pac SEA	Mad Aus NZ SAm SEA	Aus NZ Pac SAm SEA	SAf Mad Aus NZ Pac SAm	SAf Mad Aus NZ Pac SEA	SAf Mad Aus NZ SAm SEA	SA Au NZ Pa SA SE
1	0.06		0.09																
2																			
3																			
4																			
5																			
6																			
7			0.2																
8			0.38																
9																			
10																			
11																			
12																			
13																			
14																			
15																			
16																			
17																			
18																			
19																			
20																			
21																			
22																			
23																			
24		0.24																	
25		0.38																	
26		0.55																	
27																			
28																			
29																			
30								0.02	0.13	0.02	0.02	0.02			0.03	0.02	0.02	0.12	0.0
31					0.03				0.07					0.25	0.02				
32																			
33																			
34																			
35																			
36	0.66																		
37																			
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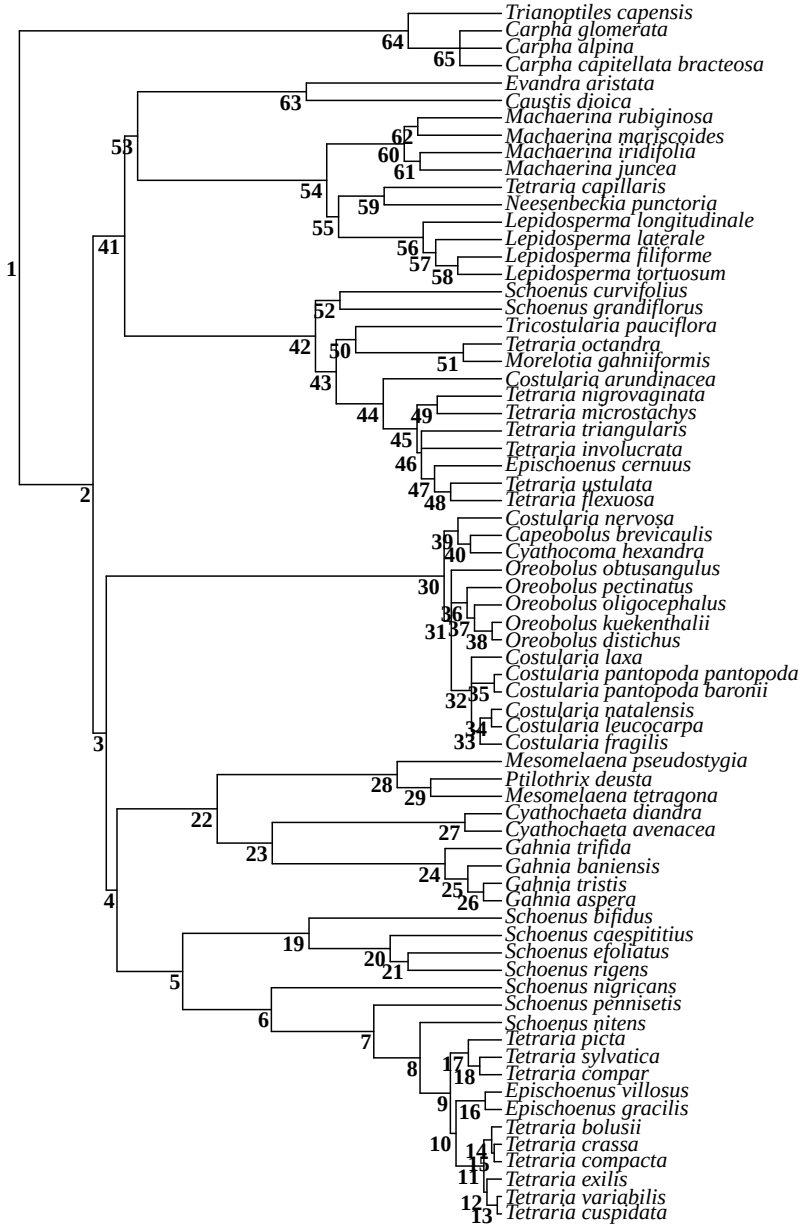

Inset: Node numbers used in Appendix S4.