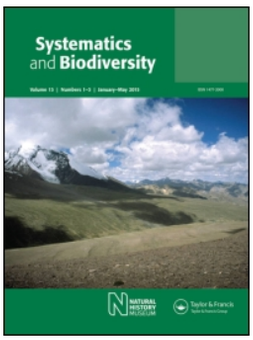


Systematics and Biodiversity

ISSN: 1477-2000 (Print) 1478-0933 (Online) Journal homepage: http://www.tandfonline.com/loi/tsab20

Diversity, systematics, and evolution of Cynodonteae inflorescences (Chloridoideae – Poaceae)

Vanesa Pilatti, SebastiÁn E. Muchut, Nora G. Uberti-Manassero, Abelardo C. Vegetti & Renata Reinheimer

To cite this article: Vanesa Pilatti, SebastiÁn E. Muchut, Nora G. Uberti-Manassero, Abelardo C. Vegetti & Renata Reinheimer (2017): Diversity, systematics, and evolution of Cynodonteae inflorescences (Chloridoideae – Poaceae), Systematics and Biodiversity, DOI: 10.1080/14772000.2017.1392371

To link to this article: https://doi.org/10.1080/14772000.2017.1392371

Systematics and Biodiversity (2017), 1–15

Research Article

Diversity, systematics, and evolution of Cynodonteae inflorescences (Chloridoideae – Poaceae)

VANESA PILATTI[1,2,†], SEBASTIÁN E. MUCHUT[1,2], NORA G. UBERTI-MANASSERO[3,5], ABELARDO C. VEGETTI[1,3] & RENATA REINHEIMER[3,4]

[1]Morfología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional del Litoral, CONICET, FBCB, Santa Fe, Argentina
[2]Fellow of Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET)
[3]Member of Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET)
[4]Instituto de Agrobiotecnología del Litoral, Universidad Nacional del Litoral, CONICET, FBCB, Santa Fe, Argentina
[5]Biología Celular, Facultad de Ciencias Agrarias, Universidad Nacional del Litoral, CONICET, FBCB, Santa Fe, Argentina

(Received 29 December 2016; accepted 26 September 2017; published online 20 November 2017)

The species of the Cynodonteae tribe show great morphological diversity in their reproductive structures. Previous studies where inflorescences were comparatively analysed in the context of phylogeny have shown that although grass inflorescences seem to be excessively variable, there are certain aspects of inflorescences that store relevant information on the evolution and systematics in Poaceae. We have analysed and compared the inflorescence structures of species belonging to the Hilariinae, Monanthochloinae, Scleropogoninae, and Muhlenbergiinae subtribes. Considering the most relevant morphological characters, the most recurrent types of inflorescences in the lineage were determined by means of a principal coordinates analysis. To understand the evolution of inflorescence morphology, ancestral reconstructions of inflorescence characters were performed using the Bayesian inference method. The results obtained demonstrate that the processes of homogenization and truncation might account for the diversity observed in adult inflorescences. Five different types of inflorescences were identified out of 36 theoretical possibilities. Amongst these, inflorescence type 1 (panicle of spikelets, with a terminal spikelet, non-homogenized, and bearing third- or higher-order branches) was found to be the most frequent in the studied group. Ancestral reconstructions of morphological characters allowed us to suggest that the ancestor of the group might have had an inflorescence with the form of a raceme of spikelets, non-truncated and bearing first-order branches. More complex inflorescences bearing no terminal spikelets and having branches of higher order might have diverged this lineage.

Key words: Chloridoideae, Cynodonteae, evolution, inflorescence, morphology, Poaceae, systematics

Introduction

The Chloridoideae subfamily comprises approximately 131 genera and 1,601 species distributed in subtropical and tropical regions with their centre of radiation in Africa, Australia and Asia (GPWG II, 2012; Jacobs, Kingston, & Jacobs, 1999; Peterson, Romaschenko, & Johnson, 2010a; Soreng et al., 2015, 2017). At present, five monophyletic tribes are recognized within Chloridoideae: Centropodieae, Triraphideae, Eragrostideae, Zoysieae, and Cynodonteae (Bell & Columbus, 2008; Bouchenak-khelladi et al., 2008; Columbus et al., 2007; Hilu & Alice, 2001; Hilu & Wright, 1982; Ingram & Doyle, 2004, 2007; Liu et al., 2007; Peterson, Columbus, & Pennington, 2007, 2010a, 2011, 2012, 2014; Roodt-Wilding & Spies, 2006; Soreng et al., 2015, 2017; Van den Borre & Watson, 1997). Amongst these, the Cynodonteae tribe has the largest number of species, including 839 species grouped into 93 genera and 18 subtribes (Soreng et al., 2015, 2017). The lineage composed of the Hilariinae, Monanthochloinae, Boutelouinae, Scleropogoninae, and Muhlenbergiinae subtribes, mostly represented by New World species, is the most derived one of the Cynodonteae tribe. In terms of morphology, this lineage shows wide variations amongst inflorescences, ranging from loose (e.g.

Correspondence to: Renata Reinheimer. E-mail: renatarein@fca.unl.edu.ar;
Correspondence to: Vanesa Pilatti. E-mail: vanesapilatti@hotmail.com
†Current address: Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Agropecuaria Rafaela, Ruta 34 km 227, Cp: 2300, Santa Fe, Argentina

ISSN 1477-2000 print / 1478-0933 online

http://dx.doi.org/10.1080/14772000.2017.1392371

Muhlenbergia asperifolia, *Muhlenbergia porteri*, *Muhlenbergia purpusii*, *Scleropogon brevifolius*, etc.) or dense (e.g. *Distichlis. spicata*, *Muhlenbergia rigens*, *Muhlenbergia rigida*, etc.) panicles with a large number of spikelets to simple, single-spikelet inflorescences (e.g. *Distichlis acerosa*, *Distichlis littoralis*, and *Distichlis australis*) (Clayton & Renvoize, 1986; Liu, Zhao, & Hao, 2005; Nicora & Rugolo de Agrasar, 1987; Peterson et al., 2007; Watson & Dallwitz, 1992). Inflorescence characters are of the most widely used in grass systematics (Clayton & Renvoize, 1986; Kellogg, 2015; Perreta, Ramos, & Vegetti, 2009). Previous studies where inflorescences were comparatively analysed in the context of species phylogeny have shown that although grass inflorescences seem to be excessively variable at first sight, there are certain aspects of inflorescences that store relevant information on the evolution and systematics of the groups within the family (Reinheimer, Amsler, & Vegetti, 2013a; Reinheimer, Vegetti, & Rua, 2013b). Particularly, Panicoideae inflorescences have been found to share evolutionary trends and patterns, rather than evolving randomly (Reinheimer et al., 2013a, 2013b). So far, Cynodonteae inflorescences have not been characterized comparatively. Current literature only offers comprehensive inflorescence descriptions of a few species within this group (Liu et al., 2005; Pilatti & Vegetti, 2014).

With the aim of studying inflorescence morphology of the most derived Cynodonteae subtribes from an evolutionary perspective, we intend to: (1) make a detailed analysis of the adult inflorescence structure; (2) establish the most common inflorescence types; (3) discuss the evolution of the ancestral states of the most significant morphological traits; and (4) assess the systematic value of inflorescence characters in the segregation of the various taxonomic groups under study.

Materials and methods

Morphological analysis of the inflorescence

This study involved 68 species representing seven (out of nine) genera from the selected group. Inflorescences were analysed from species of *Distichlis* (10/11), *Muhlenbergia* (47/182), *Blepharidachne* (1/4), *Scleropogon* (1/1), *Erioneuron* (3/3), *Munroa* (4/5), and *Hilaria* (2/10) (Table S1, see online supplemental material. The morphological study consisted in describing the branching systems of the vegetative and reproductive structures that make up the plant, using the typological terminology proposed by Troll (1964), Weberling (1985, 1989), and later contributions (Rúa, 1999). The inflorescences were dissected and characterized using a Nikon SMZ-10 stereoscopic microscope and photographed with a Canon A640 digital camera. When necessary, observations were made using a scanning electron microscope (SEM) following the methodology reported by Lucero et al. (2014).

In order to identify the types of inflorescences present in the group, a principal coordinates analysis (PCoA) was performed using Infostat v. 2010 software (Di Rienzo et al., 2010) following the methodology reported by Reinheimer et al. (2013a). Four morphological characters were selected for this study based on our personal observations and previous reports (Kern, Guarise, & Vegetti, 2008; Reinheimer & Vegetti, 2008; Reinheimer et al., 2013a, 2013b; Salariato, Zuloaga, Giussani, & Morrone, 2010): (1) form of inflorescence (0: panicle of spikelets, 1: panicle of spiciform primary branches, 2: raceme of spikelets); (2) absence/presence of terminal spikelet at the end of the central axis (0: absence, 1: presence); (3) homogenization (Rúa, 1999), meaning similarity amongst inflorescence branches (0: homogenized, 1: non-homogenized), and (4) maximum degree of ramification (0: first-order, 1: second-order, 2: third- or higher-order of branching) (Table S2, see online supplemental material). Data of *Bouteloua* species were retrieved from the work by Pilatti and Vegetti (2014). Taxa that showed polymorphism in any character were duplicated. Species with missing characters were not included in the analysis. Then, the proportion of taxa corresponding to each type of inflorescence identified and to the states of each character studied was determined.

Phylogenetic reconstruction and the evolution of inflorescence

The selection of ingroup and outgroup taxa was based on recent studies (Bell, 2010; Bell & Columbus, 2008; Columbus et al., 2007; Peterson et al., 2010a, 2010b, 2012; Siqueiros-Delgado, Ainouche, Columbus, & Ainouche, 2013). Ninety-one species (out of a total of 278) were included as ingroup, representing all genera of the Monanthochloinae, Boutelouinae, Hilariinae, and Muhlenbergiinae subtribes, and most of the genera of Scleropogoninae. As outgroup, we used 16 species belonging to the Tripogoninae, Pappophorinae, and Traginae subtribes (Peterson et al., 2010a, 2012). A list of the species, voucher material, and GenBank accession numbers used in the molecular study is presented in Table S3 (see online supplemental material).

To supplement sequences available in online databases from previous works (Bell, 2010; Bell & Columbus, 2008; Columbus et al., 2007; Peterson et al., 2010a, 2010b, 2012; Siqueiros-Delgado et al., 2013), we generated 53 sequences for 14 additional species, including one species of *Erioneuron*, *Distichlis*, *Muhlenbergia*, and *Tragus*, two species of *Munroa*, and eight species of *Bouteloua* (Table S3, see online supplemental material). To that

end, total DNA was isolated from silica dried leaves using a modified (CTAB) protocol by Doyle and Doyle (1987), or from herbarium material using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Six plastid DNA sequences (*ndhA* intron, *ndhF*, *rps16-trnK*, *rps16* intron, *rps3*, and *rpl32-trnL*) and a single nuclear ITS DNA sequence were amplified by polymerase chain reaction (PCR) using primers and amplification conditions specified by Peterson et al. (2010a). Amplifications were performed in a TGradient Thermocycler (Biometra, Göttingen, Germany). PCR products were cleaned and sequenced by Macrogen Inc. using the ABI PRISM BigDye Terminator Cycle Sequencing Kits with AmpliTaq DNA polymerase (Applied Biosystems, Seoul, Korea). Single-pass sequencing was performed using the same primers used for PCR reactions.

The sequences were assembled and edited in BioEdit v. 7.1.3.0 (Hall, 1999) and aligned using Muscle v. 3.8 (Edgar, 2004a, 2004b). Ambiguous regions were excluded from the analysis, while all gaps were treated as missing data. We conducted a phylogenetic analysis under Bayesian inference (BI) using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003). The best-fit model (GTR + G + I) was inferred with jModeltest v. 2.1.4 (Darriba, Taboada, Doallo & Posada, 2012) based on the Akaike Information Criterion (AIC) for a cpDNA, ITS, and combined cpDNA + ITS datasets. We ran four chains of the Markov Chain Monte Carlo (MCMC) for 4 million generations for ITS and cpDNA datasets, and 2 million generations for the combined dataset, and one tree per 1,000 generations was sampled in two independent runs (nchains = 4, nruns = 2; chain temperature = 0.2; sample frequency = 1,000), until the convergence diagnostic (standard deviation of split sequences) dropped below 0.01. The fraction of the sampled values discarded as burn-in was set at 0.25. We estimated the 50% majority-rule consensus of the remaining trees (6002 for ITS and cpDNA datasets, and 3002 for the combined dataset) and used posterior probability (PP) to evaluate nodal support.

We reconstructed ancestral character states using BI and the trees generated before. Character states were estimated for nodes with a posterior probability equal to/higher than 0.95 (Fig. S5, see online supplemental material). For the analyses, we used the MCMC method and the 'multistate' module in BayesTraits (Pagel, Meade, & Barker, 2004). The ranges of the hyperprior varied 1–46 for absence/presence of terminal spikelet, 1–28 for homogenization, 0–20 for maximum degree of ramification and form of inflorescence. The values of ratedev were 8 for absence/presence of terminal spikelet and homogenization, and 6 for maximum degree of ramification and form of inflorescence. The significance between one state and another was estimated using the Bayes Factor (BF) in the Tracer v. 1.5.0 software (Rambaut & Drummond, 2007). A value of BF between 2 and 5 indicates 'positive' support, between 5 and 10 'strong' support, and any value >10 means 'very strong' support.

We calculated the transition rates of each character state in the entire tree using MCMC runs. The statistical differences amongst rates were studied using the analysis of variance (ANOVA) in the Infostat program (Di Rienzo et al., 2010) followed by Tukey's test.

Results

Structure of the plant

In the species studied, the synflorescence consists of: a distal region, the anthotagma (AT), which comprises the inflorescence, and a proximal region, the trophotagma (TT), which extends from the basal leaves of the shoot to the most distal leaf (Troll, 1964) (Fig. 1).

Typically, the TT region shows a proximal area made up by short internodes that corresponds to the innovation zone (IZ) and a distal area with long internodes, which may behave as an inhibition zone (HZ) or partially as an enrichment zone (EZ) (Fig. 1). In particular, the IZ shows cataphylls whose axillary buds give origin to new shoots (innovations) with a similar structure to that of the parent shoot, generating plants with a caespitose appearance (Fig. 1.1; Table S4, see online supplemental material). Sometimes, the IZ may develop underground stems (rhizomes) (Fig. 1.2) or a system of plagiotropic aerial shoots (stolons) (Fig. 1.3; Table S4, see online supplemental material). The HZ is located above the IZ and it has leaves with developed sheath and lamina whose axillary buds never develop lateral shoots (Fig. 1). The EZ comprises the internodes and the most distal leaves of the trophotagma, whose axillary buds initiate lateral branches or

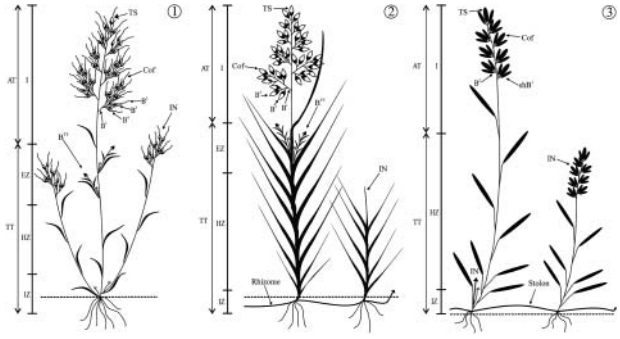


Fig. 1. Synflorescence schemes. **(1.1)** *Muhlenbergia microsperma*; **(1.2)** *Distichlis spicata*; **(1.3)** *Hilaria cenchroides*. Abbreviations: AT, anthotagma region; B^1, branch of first order; B^2, branch of second order; B^3, branch of third order; B^4, branch of fourth order; B^{TT}, branch of trophotagma; Cof, coflorescence; EZ, enrichment zone; HZ, inhibition zone; I, inflorescence; IN, innovation; IZ, innovation zone; shB^1, short primary branch; TS, terminal spikelet; TT, trophotagma region.

trophotagma branches (B^{TT}). These branches develop a prophyll, a varying number of true leaves and commonly end in an inflorescence (Figs 1.1 and 1.2). The development of this zone varies amongst species and it is sometimes absent (Fig. 1.3; Table S4, see online supplemental material).

Variations in the inflorescence

The differences found between the branching systems of the inflorescences in the studied species are summarized in Table S5 (see online supplemental material).

Inflorescence forms

In the lineage studied, two forms of inflorescences were recognized in addition to the panicle of spiciform primary branches that had already been described for species of *Bouteloua* (Pilatti & Vegetti, 2014; Fig. 2.1). One of these forms of inflorescence, the panicle of spikelets, is composed of a main axis bearing ramified lateral branches, where spikelets are inserted (Fig. 2.2). The other form of inflorescence, the raceme of spikelets, has a main axis with non-ramified first-order branches ending in a spikelet (Fig. 2.3). The inflorescence form of *D. acerosa*, *D. littoralis*, and *D. australis* could not be determined because only one spikelet is developed (Fig. 2.4). In general, the inflorescence form does not vary within each species, however, we have found that in *D. bajaensis* the inflorescence could be a panicle or a raceme of spikelets depending on the studied specimen.

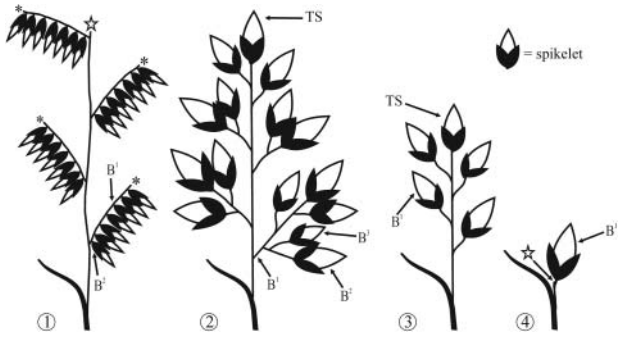


Fig. 2. Simplified scheme of inflorescence diversity. **(2.1)** Panicle of spiciform primary branches (e.g. *Bouteloua barbata*) described by Pilatti & Vegetti, 2014; **(2.2)** Panicle of spikelets (e.g. *Muhlenbergia fastigata*); **(2.3)** Raceme of spikelets (e.g. *Scleropogon brevifolius*); **(2.4)** One spikelet (e.g. *Distichlis acerosa*). Abbreviations: B^1, branch of first order; B^2, branch of second order; B^3, branch of third order; TS, terminal spikelet. The stars indicate absence of a terminal spikelet on the main inflorescence. The asterisks indicate absence of a terminal spikelet on the branch of first order.

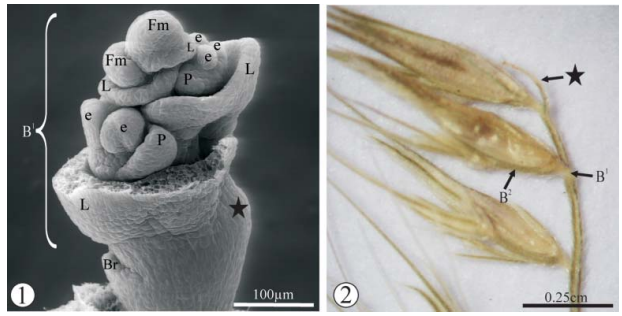


Fig. 3. Absence of terminal spikelet at the end of the central axis of the inflorescence. **(3.1)** Scanning electron micrograph of early stage of development of *Distichlis acerosa* inflorescence; **(3.2)** Mature inflorescence of *Muhlenbergia bryophilus*. Abbreviations: Br, bract; B^1, branch of first order, B^2, branch of second order; e, stamens; Fm, floral meristem; L, lemma; P, palea. The stars indicate absence of a terminal spikelet on the main axis of the inflorescence.

Presence or absence of the main axis terminal spikelet

In most of the studied species, the inflorescence main axis ends in a terminal spikelet (Figs 2.2 and 2.3). However, some species had inflorescences without a terminal spikelet (Fig. 2.4), in a similar way to species of *Bouteloua* (Pilatti & Vegetti, 2014). When this is the case, the most distal primary branch is frequently observed to adopt the terminal position of the main axis as if it were a continuation of it (Fig. 3.1); alternatively, the main axis may end in a sterile prolongation (Fig. 3.2).

Inflorescence homogenization and degree of ramification

Inflorescences in the studied species may be classified as non-homogenized or homogenized. Non-homogenized inflorescences have proximal primary branches that may reach several degrees of ramification (from third to fifth order) (Fig. 4.1). On the other hand, homogenized inflorescences have all primary branches with the same degree of ramification (in general, first and second order) (Figs.4.2–4). In turn, homogenized inflorescences can be disjunct or not disjunct. The former show both long first-order branches and short first-order branches or either type (Figs 4.2 and 4.3). On the contrary, in non-disjunct homogenized inflorescences, the difference between the types of primary branches is not clear (Fig. 4.4).

Number and arrangement of first-order branches in the inflorescence

In most of the studied genera, the total number of first-order branches varies significantly amongst species and

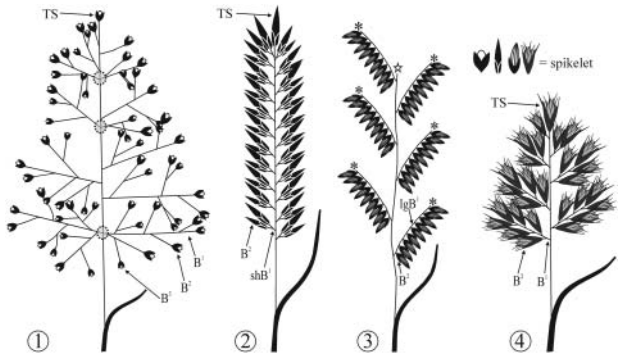


Fig. 4. Diagrams of non-homogenized and homogenized inflorescences. **(4.1)** Non-homogenized inflorescence of *Muhlenbergia asperifolia*; **(4.2)** Homogenized and disjunct inflorescence with short first-order branches of *Muhlenbergia phalaroides*; **(4.3)** Homogenized and disjunct inflorescence with long first-order branches of *Bouteloua trifida* (Pilatti & Vegetti, 2014); **(4.4)** Homogenized and non-disjunct inflorescence of *Erioneuron avenaceum*. Abbreviations: B^1, branch of first order; B^2, branch of second order; B^3, branch of third order; lgB^1, long branch of first order; shB^1, short branch of first order; TS terminal spikelet. Circles with dotted lines indicate pseudoverticils of branches of first order. The stars indicate absence of a terminal spikelet on the main inflorescence. The asterisks indicate absence of a terminal spikelet on the branch of first order.

even amongst analysed specimens. Some species showed inflorescences with one first-order branch and this state was consistent in all of its examined specimens (Figs 2.4 and 3.1).

First-order branches on the main axis of the inflorescence follow an alternate arrangement. However, some inflorescences were observed to have a differential lengthening in the internodes of the main axis, forming occasional pseudoverticils of first-order branches (Fig. 4.1).

Identification of inflorescence types

The inflorescences of species included in the PCoA have been grouped into five different types (Table 1) amongst the 36 theoretical possibilities (forms of inflorescences × absence/presence of terminal spikelet × homogenization × maximum degree of ramification [3 × 2 × 2 × 3 = 36]). The dispersion diagram shows that the two main axes account for 91.6% (CP1 = 73.1%; CP2 = 18.5%) of total variation (Fig. S1, see online supplemental material).

Proportion of inflorescence types and character states amongst the species studied

Type 1 is the most frequent one in the studied group (Fig. S2.1, see online supplemental material) (Table 1). This type of inflorescence describes most of the species of the Muhlenbergiinae subtribe (Fig. S2.2, see online supplemental material). Type 2 inflorescences are characteristic of all species of the Hilariinae subtribe and, to a lesser extent, of the Monanthochloinae and Scleropogoninae subtribes (Figs S2.3–5, see online supplemental material). Inflorescence type 3 is found in 6% of the species of the Muhlenbergiinae subtribe (Fig. S2.2, see online supplemental material). Inflorescence type 4 defines all species belonging to the Boutelouinae subtribe (Fig. S2.6, see online supplemental material). Inflorescence type 5 predominates amongst species of the Monanthochloinae and Scleropogoninae subtribes (Figs S2.4–5, see online supplemental material). Table S6 (see online supplemental material) shows the proportion of character states for each subtribe.

Evolution of inflorescences

Phylogeny. The ITS and the cpDNA tree separately cannot resolve deep nodes (Figs S3 and S4); however all the subtribes are well supported, except by Scleropogoninae in the cpDNA tree. The relationship between Boutelouinae and Monanthochloinae is supported by the cpDNA tree only. The cpDNA and the ITS trees were manually inspected for conflicting nodes with posterior probabilities (PP) 0.95 or more. As no supported conflicts were found, we proceeded to analyse the combined dataset. When ITS and cpDNA are combined the resolution of the tree substantially increases (Fig. S5, see online supplemental material). Similar results have been shown previously using the same molecular markers in Cynodonteae (Peterson, Romaschenko, & Herrera Arrieta, 2016). The

Table 1. Five inflorescence types found by principal coordinate analysis (PCoA). *Abbreviation: TS* terminal spikelet.

Type	*Inflorescence form*	*Absence/Presence of TS*	*Homogenization*	*Maximum degree of ramification*	*Species (example)*
1	Panicle of spikelets	Present	Non-homogenized	3rd or higher order	*Muhlenbergia tricholepis*
2	Panicle of spikelets	Present	Homogenized	2nd order	*Muhlenbergia diversiglumis*
3	Panicle of spikelets	Absent	Homogenized	2nd order	*Muhlenbergia geminiflora*
4	Panicle of spiciform primary branches	Absent	Homogenized	2nd order	*Bouteloua williamsii*
5	Raceme of spikelets	Present	Homogenized	1st order	*Scleropogon brevifolius*

majority-rule consensus inferred from the combined dataset and Bayesian analysis shows a highly supported monophyletic lineage (PP = 0.99) composed of the Hilariinae, Monanthochloinae, Boutelouinae, Scleropogoninae, and Muhlenbergiinae subtribes (Fig. S5, see online supplemental material). This lineage is divided early into clade I (PP = 0.95) and clade II (PP = 0.99). Two groups may be identified within clade I: clade A (PP = 0.73), including species belonging to the subtribes Hilariinae and Scleropogoninae, and clade B (PP = 0.99), made up by species of the Monanthochloinae and Boutelouinae sister subtribes. Clade II includes all species of the *Muhlenbergia* genus (Muhlenbergiinae subtribe). All subtribes belonging to the most derived lineage of Cynodonteae were retrieved as monophyletic groups (PP = 0.99–1.00).

Ancestral reconstruction and transition rates of inflorescence characters. The evolution of inflorescence characters was assessed on the tree recovered from the combined ITS + cpDNA dataset. The ancestor of the most derived group within Cynodonteae (Clades I + II) may have had an inflorescence of a raceme of spikelets (Fig. 5.1; PP = 0.95; lnFB = 2). The panicle of spikelets may have evolved at least six independent times during the specific diversification of the clade: at the base of the Hilariinae subtribe (PP = 0.92; lnFB = 2.85), in the *B. benthamiana* species, in the *Erioneuron* genus (PP = 1.00; lnFB = 6.1), in the *D. laxiflora* species, in the clade composed of *D. spicata* and *D. palmeri* (PP = 0.99; lnFB = 3.2) and at the base of Muhlenbergiinae (PP = 0.98; lnFB = 3). The panicle of spiciform primary branches may have evolved independently at the origin of the Boutelouinae subtribe (PP = 0.99; lnFB = 2.5).

State reconstruction analyses estimate that the ancestor of Clades I + II had an inflorescence with a terminal spikelet on the distal end of the main axis, with a 100% probability and lnFB~ 4.5 depending on the strategy applied (Fig. 5.2). During species diversification, inflorescences have lost their terminal spikelet at least three different times: at the base of the subtribe Boutelouinae (PP = 0.99; lnFB = 2), in the *D. acerosa* species of the Monanthochloinae subtribe and in the clade composed of *M. bryophilus*, *M. cenchroides*, and *M. geminiflora* (PP = 0.99; lnBF ≃ 4.5).

As regards homogenization of the inflorescence (Fig. 5.3), Bayesian analyses were ambiguous in the reconstruction at the basal node (lnFB = 1.38). Clade I ancestor may have had homogenized inflorescences (PP = 98.5; lnFB ≃ 3). This condition remained in most of the specimens studied from clade I, with the exception of *D. spicata*, which had a non-homogenized inflorescence. Additionally, the Muhlenbergiinae ancestor may have had (PP = 1.00; lnBF > 5) non-homogenized inflorescences that evolved into homogenized inflorescences at least four independent times: in the *M. brevis*, *M. alopecuroides*, and *M. diversiglumis* species and in the clade made up by *M. bryophilus*, *M. cenchroides*, and *M. geminiflora* (PP = 0.99; lnBF = ~ 2.3).

The reconstruction of the maximum degree of ramification suggests that the ancestral inflorescence of the studied group may have had first-order branches (Fig. 5.4; PP = 0.92; lnFB = 3). Inflorescences that bear up to second-order branches may have evolved at least five independent times during the specific diversification of clade I (at the base of the Hilariinae subtribe (PP = 0.90; lnFB = 2.9), in the *B. benthamiana* species and *Erioneuron* (PP = 1.00; lnFB = 6.5), in the *D. laxiflora* and *D. palmeri* species, and at the base of the Boutelouinae (PP = 0.87; lnFB = 1)), and four independent times during the specific diversification of Muhlenbergiinae (in the *M. brevis*, *M. alopecuroides*, and *M. diversiglumis* and in the clade made up by *M. bryophilus*, *M. cenchroides*, and *M. geminiflora* (PP = 0.98; lnFB = 3.4)). Inflorescences with third- or higher-order branches evolved at least two independent times: in the *D. spicata* and at the base of the Muhlenbergiinae subtribe (PP = 1.00, lnFB = 3.5).

The reconstructions of transition rates indicate that some changes in the inflorescence character states appear in the tree more frequently than others. Figure 6 illustrates the comparison of transition rates for each character.

Discussion

Structure of the plant

The synflorescence of the studied species has different zones already described in other grasses: (1) innovation zone, (2) inhibition zone, (3) enrichment zone (not developed in some species), and (4) inflorescence (Cámara Hernández & Rúa, 1991; Perreta et al., 2009; Reinheimer, 2007; Reinheimer & Vegetti, 2008; Rúa, 1999; Troll, 1966, 1969; Troll & Weberling, 1989; Vegetti & Anton, 1996; Weberling, Muller Doblies, Muller Doblies, & Rúa, 1997). The innovation zone guarantees perenniality and the vegetative growth of the plant (Rúa & Weberling, 1998). Most species studied are densely caespitose and produce sylleptic innovations, that is, lateral axes that develop and flower at the same time as the parent axis (Rúa, 1999). In turn, the following year, perennial species will produce cataleptic innovations from the axillary buds of the sylleptic innovations (Cámara Hernández & Rúa, 1991; Rúa, 1999). This type of caespitose growth is highly frequent amongst grasses (Rúa & Weberling, 1998). Additionally, some of the studied species develop stolons and rhizomes, whose buds produce sylleptic and cataleptic shoots. These structures make the innovation zone larger, promoting the vegetative propagation of the plants and increasing the number of inflorescences (Cámara Hernández & Rúa, 1991).

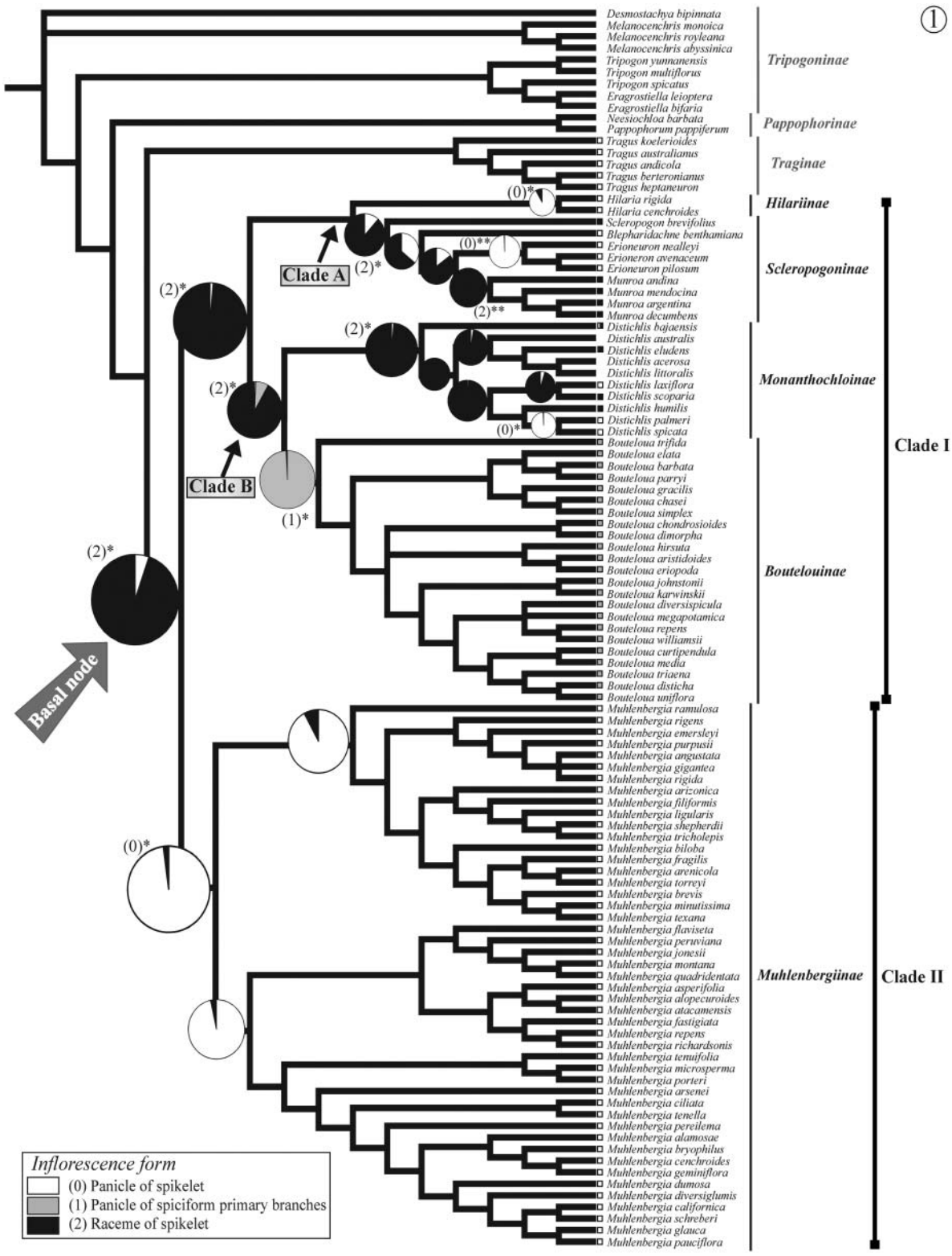


Fig. 5. Reconstructed ancestral character states on the Bayesian MCMC majority-rule consensus tree. Pie charts indicate Bayesian ancestral character posterior probabilities at selected nodes. Numbers in parentheses indicate the state with the highest likelihood based on the Bayes factor (BF) results. Two or more numbers in parentheses indicate an ambiguous assignation of the ancestral character state. *, BF between 2 and 5 (positive support); **, BF between 5 and 10 (strong support). **(5.1)** Optimization of inflorescence form character states; **(5.2)** Optimization of the presence/absence of the terminal spikelet character states; **(5.3)** Optimization of the homogenization character states; **(5.4)** Optimization of the maximum degree of ramification character states.

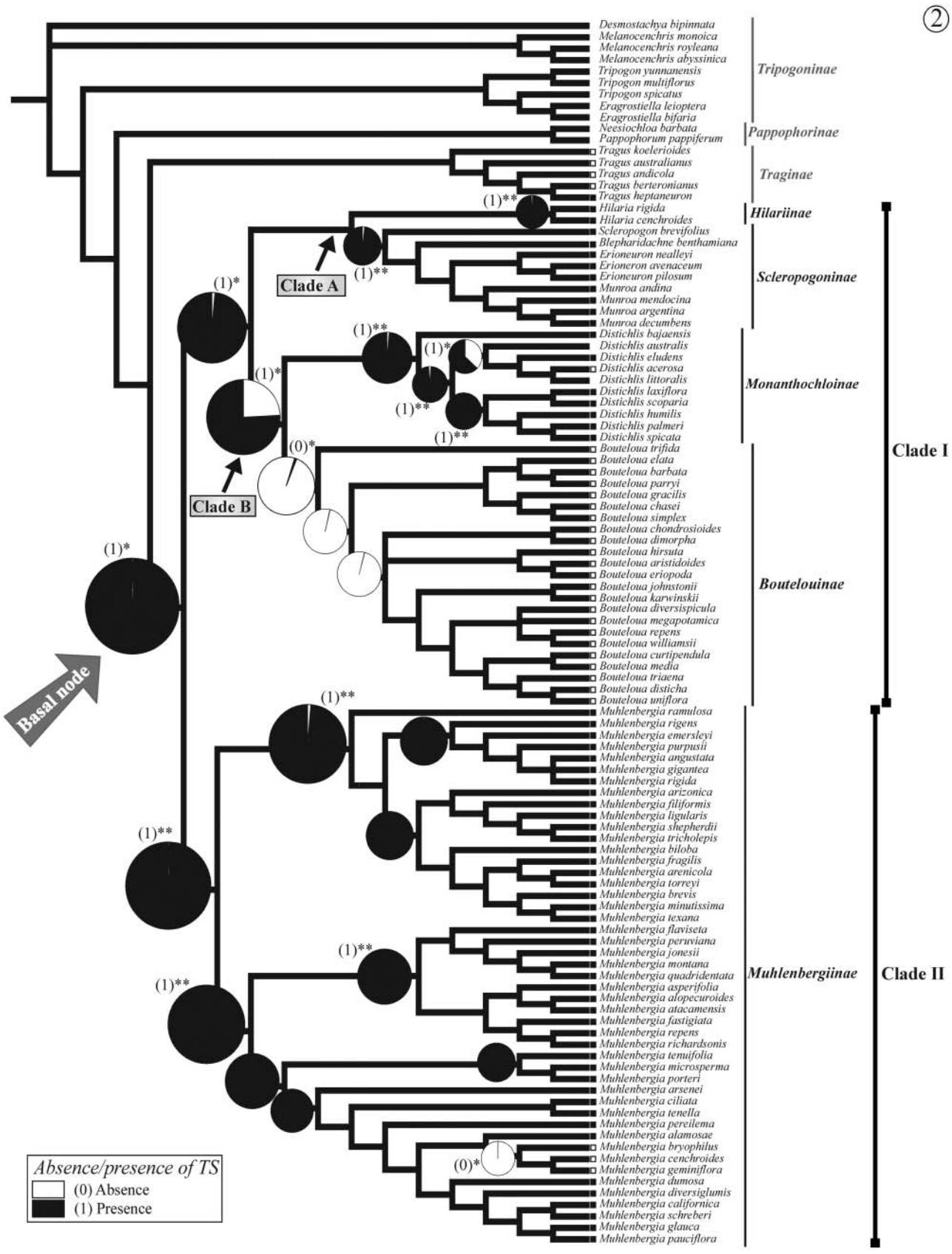


Fig. 5. (*Continued*)

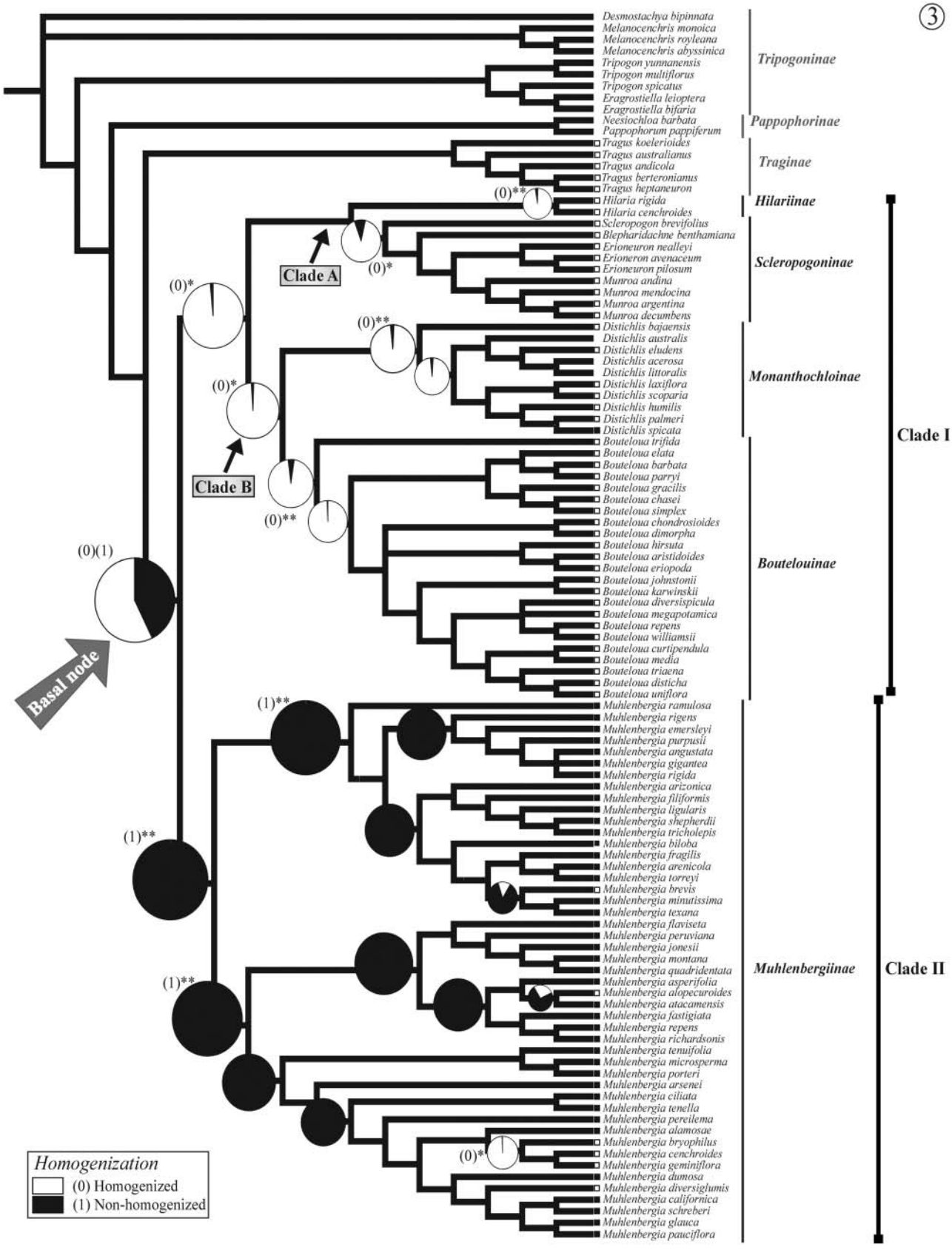


Fig. 5. (*Continued*)

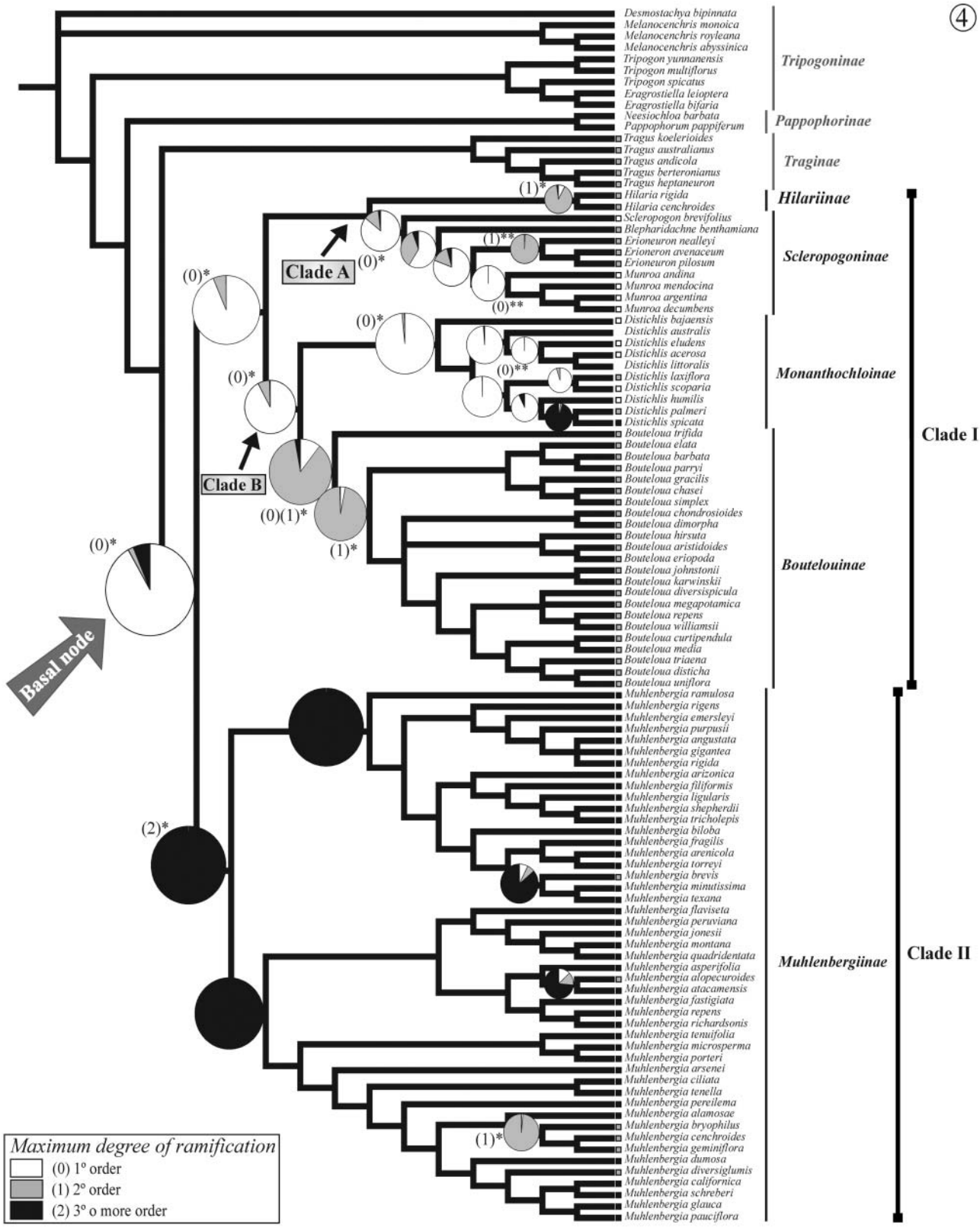
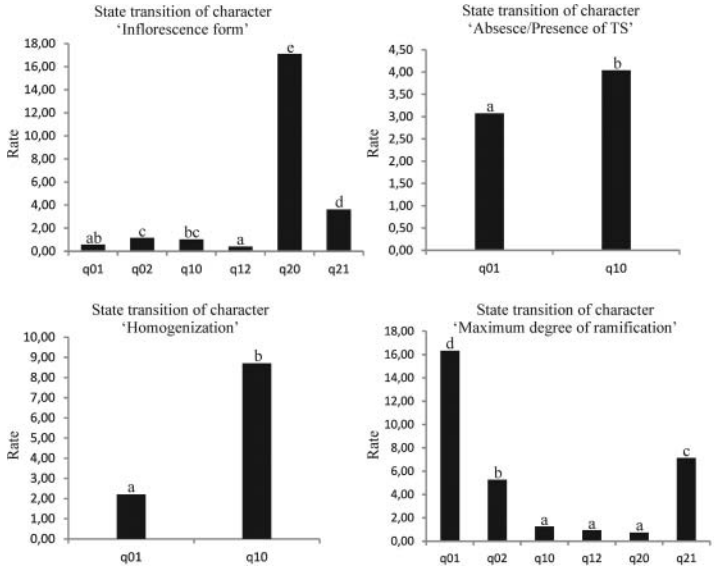


Fig. 5. (*Continued*)



Character	*Character state transition*	*Mean value*	*Standard deviation*	*Min. value*	*Max. value*
Inflorescence form	q01	0,57	0,59	0,00	4,17
	q02	1,15	1,18	0,00	7,87
	q10	1,02	1,06	0,00	9,36
	q12	0,41	0,44	0,00	2,88
	q20	17,11	7,09	1,71	50,36
	q21	3,61	2,71	0,02	17,31
Absence/ Presence of TS	q01	3,07	2,14	0,02	13,87
	q10	4,04	1,96	0,38	12,67
Homogenization	q01	2,20	1,42	0,07	10,72
	q10	8,70	3,80	1,38	26,53
Maximum degree of ramification	q01	16,33	6,92	1,82	46,61
	q02	5,26	3,63	0,25	20,80
	q10	1,26	1,25	0,00	8,85
	q12	0,93	0,92	0,00	6,96
	q20	0,73	0,78	0,00	6,32
	q21	7,14	3,13	0,86	22,15

Fig. 6. Transition rate values of each morphological character. Different letters above bars indicate statistical differences amongst state transitions ($P<0.01$). Abbreviations: Max., maximum; Min., minimum; TS, terminal spikelet.

In grasses, the synflorescence may or may not have branches of the trophotagma along the enrichment zone (Vegetti & Müller−Doblies, 2004). These branches help increase the number of floriferous branches, especially in species that bear a largely reduced terminal inflorescence (Rúa & Weberling, 1998; Vegetti, 1994, 1999; Vegetti & Müller-Doblies, 2004). In the clades studied, the presence of branches of the trophotagma varies amongst species and is not unique to a genus. It has also been observed that there are species with perennial and annual plants that may or may not develop branches of the trophotagma. Accordingly, the presence of branches of the trophotagma does not seem to be related to the life cycle. Similar conclusions were drawn from the analysis of synflorescences of the Panicoids grasses (tribe Paniceae-Panicoideae) (Reinheimer, 2007; Reinheimer & Vegetti, 2008). The development of branches of the trophotagma in the synflorescences might be regulated by hormones, genes, and mostly environmental conditions where plants grow (Doust, 2007; McSteen, 2009; Rúa & Gróttola, 1997).

Variations in the inflorescence

From a comparative morphological point of view, adult inflorescences show variations in terms of: (1) inflorescence form, (2) loss (truncation) or presence of the terminal spikelet on the main axis, (3) homogenization, and (4) number, arrangement and maximum degree of ramification of first-order branches.

The most common inflorescence form amongst the studied species is the panicle of spikelets, as in most grasses (Kellogg, 2015; Liu et al., 2005). However, the inflorescence of the *S. brevifolius*, *D. humilis*, *D. scoparia*, and *D. eludens* species and *Munroa* is a raceme of spikelets, as determined for other grasses such as *Brachypodium*, *Danthonia*, *Lepturus*, and *Odyssea* amongst others (Allred, 1982; Kellogg, 2015; Liu et al., 2005). The inflorescence form of *D. acerosa*, *D. littoralis*, and *D. australis* could not be determined because only one spikelet is developed. An extreme reduction has also been observed in the inflorescence of the *Aciachne* genus (tribe Stipeae, Pooideae) (Vegetti & Tivano, 1991).

Truncation is the loss of different inflorescence structures (Rúa, 1999). This process has been described for many grass genera: *Chloris*, *Cynodon* (Liu et al., 2005; Vegetti, 1986), *Eleusine* (Gasser & Vegetti, 1997), *Leptochloa* (Perreta & Vegetti, 1998), *Paspalum* (Rúa & Weberling, 1998), *Digitaria* (Cámara Hernández, 2001), *Setaria* (Pensiero & Vegetti, 2001; Vegetti & Pensiero, 1990), *Urochloa*, *Brachiara, Eriochloa*, *Thuarea* (Reinheimer, 2007; Reinheimer & Vegetti, 2008), and *Bouteloua* (Pilatti & Vegetti, 2014). A few species of *Distichlis* and *Muhlenbergia* bear inflorescence without a terminal spikelet at the tip of the main axis. In addition, it has been reported that *Bouteloua* present a second level of truncation given that their inflorescences also lack the terminal spikelet at the tip of primary branches (Pilatti & Vegetti, 2014).

Homogenization is a process whereby first-order branches have the same degree of ramification (Rúa, 1999). This evolutionary process, which generally defines the inflorescence appearance, has been described for different groups of Poaceae both in species belonging to the Chloridoideae (Cámara Hernández, 2001; Liu et al., 2005; Perreta & Vegetti, 1998; Pilatti & Vegetti, 2014; this

work), Ehrhartoideae (Vegetti, 2000; Vegetti & Pensiero, 1999), and Panicoideae subfamilies (Pensiero & Vegetti, 2001; Reinheimer & Vegetti, 2008; Rúa, 1993, 1996; Rúa & Weberling, 1998; Vegetti, 1999). As a result of the homogenization process, homogenized inflorescences may be disjunct (Rúa, 1999). This means that inflorescences show a distal zone of short first-order branches and a proximal zone of long first-order branches (Rúa, 1999). This classification has been applied to several genera of Paniceae (Reinheimer, 2007; Rúa & Weberling, 1998). In this work, we have observed that there are disjunct homogenized inflorescences made up only by long first-order branches, as in *Bouteloua* (Pilatti & Vegetti, 2014), or short first-order branches, as in the species studied of *Scleropogon*, *Hilaria*, *Munroa*, and some species of *Distichlis* and *Muhlenbergia*.

The truncation process has generally been associated with the homogenization process (Perreta et al., 2009; Rúa & Weberling, 1998; Vegetti & Anton, 2000). Truncated inflorescences characterized to date in Poaceae are homogenized (revised in Perreta et al., 2009), as it has been observed in some species of *Muhlenbergia.* This correlation between truncation and homogenization also occurs in the *Setaria* (Pensiero & Vegetti, 2001), *Leptochloa* (Perreta & Vegetti, 1998), and *Digitaria* (Cámara Hernández, 2001), in most of the species of *Paspalum* (Rúa, 1996), in *Andropogoneae* (Vegetti, 1999), *Eriochloa*, *Thuarea involuta*, in certain species of *Brachiaria* and *Urochloa* (Reinheimer & Vegetti, 2008), *Spartina* (Kern et al., 2008), and *Bouteloua* (Pilatti & Vegetti, 2014). However, the studied species of *Hilaria*, *Munroa*, *Erioneuron*, *S. brevifolius*, *B. benthamiana*, and some species of *Distichlis*, and *Muhlenbergia* show an asymmetric relation between homogenization and truncation processes, given that inflorescences are homogenized and show no signs of truncation. This correlation has also been observed in members of Panicoid grasses (for example, *Brachiaria*, *Urochloa*, *Chaetium*, and *Panicum phanopyrum*) (Reinheimer & Vegetti, 2008; Reinheimer et al., 2013a).

Generally speaking, the total number and the ramification pattern of first-order branches is a polymorphic character amongst individuals of one species. Studies that include comparative data on the number and ramification of first-order branches show that these traits vary widely amongst grass species and genera (Doust & Kellogg, 2002; Kern et al., 2008; Perreta & Vegetti, 2004; Pilatti & Vegetti, 2014; Reinheimer & Vegetti, 2008; Reinheimer, Astegiano, & Vegetti, 2005b; Reinheimer, Pozner, & Vegetti, 2005a; Tivano & Vegetti, 2004).

The first-order branches of the studied species are arranged in an alternate fashion along the inflorescence main axis. However, some species of *Muhlenbergia* show a differential lengthening of internodes on the inflorescence main axis, forming pseudoverticils that appear interspersed with alternate first-order branches. This characteristic has been observed in species of *Leptochloa* (Perreta & Vegetti, 1998), *Eleusine* (Gasser & Vegetti, 1997), *Chloris*, and *Cynodon* (Cámara Hernández & Rúa, 1991; Vegetti, 1986), *Megathyrsus*, and *Melinis* (Reinheimer et al., 2005a Reinheimer & Vegetti, 2008; Reinheimer, Zuloaga, Vegetti, & Pozner, 2009).

Types of inflorescence

Through the PCoA we identified five out of the 36 putative inflorescence types, of which highly branched panicles, non-truncated, and non-homogenized are most frequently observed in the lineage. These results demonstrate that not all theoretical combinatorial patterns of inflorescence character states are found in Cynodonteae. Similar observations were made for the Panicoideae grasses (Reinheimer et al., 2013a). When the incidence of a given inflorescence type is analysed considering each subtribe separately, we found that each has preferentially adopted one type of inflorescence over others. Interestingly, inflorescence types that are present in one subtribe are not well represented in the others. For instance, *Muhlenbergia* and Boutelouinae bears exclusively types 1 and 4, respectively. Similar results have been found when the occurrence of character states are analysed separately. It would be interesting to investigate whether similar types can be found in other grass lineages. Such investigations would reveal to what extent the inflorescence types described here can be comprehensive to other groups.

Evolution of inflorescences

The phylogeny obtained in this work shows results that are consistent with those published by Peterson et al. (2012, 2012, 2015) and Snow et al. (2013). All the subtribes were retrieved as monophyletic groups. Our results suggest that the ancestor of the most derived lineage of Cynodonteae may have had a raceme of spikelets, with terminal spikelet and non-ramified first-order branches. In particular, the ancestral reconstruction of the inflorescence form suggests that inflorescences may have evolved from simpler (raceme of spikelets with non-ramified first-order branches) to more complex (panicle of spikelets with ramified first-order branches). Interestingly, the inflorescence form of a panicle of spiciform primary branches evolved exclusively from a raceme of spikelets in the Boutelouinae subtribe and is thus a synapomorphy of the group.

The terminal spikelet has disappeared from the top of the inflorescence main axis many independent times during the diversification of the studied lineage. This character state has been acquired by most species that compose clade B (*D. acerosa* and at the base of the Boutelouinae subtribe) and by some species of *Muhlenbergia* of clade II. The evolutionary tendency towards truncated

inflorescences has also been observed in other grasses such as in Panicoideae (Reinheimer et al., 2013a, 2013b).

The reconstruction of homogenization showed two contrasting evolutionary tendencies in the analysed group. In clade I, most species showed no changes in their homogenized inflorescences, except for *D. spicata*, which shifted from homogenized to non-homogenized. Conversely, in clade II the inflorescences have evolved several times from non-homogenized to homogenized. Reports in other grass lineages indicate that the most frequent transition happened from non- to homogenized inflorescences and the inverse transition was rarely observed (Reinheimer et al., 2013a, 2013b; Salariato et al., 2010).

The analysis of inflorescence evolution also documented that reversion to ancestral character states in traits such as form of inflorescence, presence/absence of a terminal spikelet and maximum degree of ramification is unlikely in the studied group. Interestingly, transition rates counts suggested that clade I and clade II have inherited different abilities to change the morphology of their inflorescences. Clade I has been more liable to change in its inflorescences in terms of form and branching, while clade II had more capacity to modify its homogenization condition and the development of the terminal spikelet of the inflorescence.

In conclusion, this work explores inflorescence diversity within a set of grass subtribes in an evolutionary context. The methods used allowed us to analyse and compare the morphological diversity of adult inflorescences, determine the types of inflorescences occurring most frequently, identify inflorescence characters with systematic value, and hypothesize on the evolutionary tendencies of the inflorescence characters in the lineage. Our results are in concordance with those published for the disparate Panicoids grasses, suggesting that similar macroevolutionary trends created the grass inflorescence diversity shown today. It would be interesting to extrapolate this type of comparative study to other groups of grasses in order to uncover new insight into the evolutionary tendencies that resulted in inflorescence diversity.

Acknowledgements

The authors thank the curators of the ASU, BA, CTES, K, LIL, LP, MEXU, RSA, SF, SI, and UNSL herbaria for providing plant material. We would also like to thank Dr Juan Carlos Tivano for accompanying the authors on numerous field expeditions. We are also grateful to anonymous reviewers for critically reading the manuscript.

This work was supported by the Agencia Nacional de Promoción Científica y Tecnológica Argentina under Grant PICT-2011-0590 to A.V. and Grant no. PICT 2013-0757 to R.R.; Universidad Nacional del Litoral under Grant UNL-CAID + D 2011 50120110100213LI to R.R.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Fondo para la Investigación Científica y Tecnológica [grant number PICT 2013-0757], [grant number PICT-2011-0590]; Universidad Nacional del Litoral [grant number CAID+D 2011 - 50120110100213LI].

Supplemental data

Supplemental data for this article can be accessed here: https://doi.org/10.1080/14772000.2017.1392371.

References

Allred, K. W. (1982). Describing the grass inflorescence. *Journal of Range Management, 35*, 672–675.

Bell, H. L. (2010). A new species of *Distichlis* (Poaceae, Chloridoideae) from Baja California, Mexico. *Madroño, 57*, 54–63.

Bell, H. L., & Columbus, J. T. (2008). Proposal for an expanded Distichlis (Poaceae, Chloridoideae): Support from molecular, morphological, and anatomical characters. *Systematic Botany, 33*, 536–551.

Bouchenak-khelladi, Y., Salamin, N., Savolainen, V., Forest, F., van der Bank, M., Chase, M. W., & Hodkinson, T. R. (2008). Large multi-gene phylogenetic trees of the grasses (Poaceae): Progress towards complete tribal and generic level sampling. *Molecular Phylogenetics and Evolution, 47*, 488–505.

Cámara Hernández, J. (2001). Morfología de la inflorescencia de *Digitaria sanguinalis* (Poaceae). *Boletín de la Sociedad Argentina de Botánica, 36*, 87–95.

Cámara Hernández, J., & Rúa, G. H. (1991). The synflorescence of Poaceae. *Beitrage zur Biologie der Pflanzen, 66*, 297–311.

Clayton, W., & Renvoize, S. A. (1986). Genera *Graminum* Grasses of the World. *Kew Bulletin additional series, 13*, 1–389.

Columbus, J. T., Cerros-Tlatilpa, R., Kinney, M. S., Siqueiros-Delgado, M. E., Bell, H. L., Griffth, M. P., & Refulio-Rodriguez, N. (2007). Phylogenetics of Chloridoideae (Gramineae): A preliminary study based on nuclear ribosomal internal transcribed and chloroplast trnL-F sequences. In J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, & M. G. Simpson (Eds.), *Monocots: Comparative biology and evolution-Poales* (pp. 565–579). Claremont, California: Rancho Santa Ana Botanic Garden, *Aliso 23*.

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

Di Rienzo, J. A., Casanoves, F., Balzarini, M. G., Gonzalez, L., Tablada, M., & Robledo, C. W. (2010). InfoStat versión 2010. Argentina: Grupo InfoStat, FCA, Universidad Nacional de Córdoba. Retrieved from http://www.infostat.com.ar/ (accessed 2 October 2017).

Doyle, J. J., & Doyle, J. L. (1987). A rapid DNA isolation procedure for small quantities of fresh leaf material. *Phytochemical Bulletin, 19*, 11–15.

Doust, A. N. (2007). Grass architecture: Genetic and environmental control of branching. *Current Opinion in Plant Biology, 10*, 21–25.

Doust, A. N., & Kellogg, E. A. (2002). Inflorescence diversification in the panicoid "bristle grass" clade (Paniceae, Poaceae): Evidence from molecular phylogenies and developmental morphology. *American Journal of Botany, 89*, 1203–1222.

Edgar, R. C. (2004a). MUSCLE: A multiple sequence alignment method with reduced time and space complexity. *BioMedCentral Bioinformatics, 5*, 113.

Edgar, R. C. (2004b). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research, 32*, 1792–1797.

Gasser, M., & Vegetti, A. C. (1997). Inflorescence typology in *Eleusine indica* and *Eleusine tristachya* (Poaceae). *Flora (Germany), 192*, 17–20.

Grass Phylogeny Working Group (GPWG II). (2012). New grass phylogeny resolves deep evolutionary relationships and discovers C4 origins. *New Phytologist, 193*, 304–312.

Hall, T. A. (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series, 41*, 95–98.

Hilu, K. W., & Alice, L. A. (2001). A phylogeny of Chloridoideae (Poaceae) based on matK sequences. *Systematic Botany, 26*, 386–405.

Hilu, K. W., & Wright, K. (1982). Systematics of Graminae: A cluster analysis study. *Taxon, 31*, 9–36.

Ingram, A. L., & Doyle, J. J. (2004). Is *Eragrostis* (Poaceae) monophyletic? Insights from nuclear and plastid sequence data. *Systematic Botany, 29*, 545–552.

Ingram, A. L., & Doyle, J. J. (2007). *Eragrostis* (Poaceae) monophyly and infrageneric classification. In J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, & M. G. Simpson (Eds.), *Monocots: Comparative biology and evolution-Poales* (pp. 595–604). Claremont, California: Rancho Santa Ana Botanic Garden. *Aliso* 23.

Jacobs, B. F., Kingston, J. D., & Jacobs, I. I. (1999). The origin of grass−dominated ecosystems. *Annals of the Missouri Botanical Garden, 86*, 590-−643.

Kellogg, E. A. (2015). Flowering plants. Monocots: Poaceae. In K. Kubitzki (Ed.), *The families and genera of vascular plants*. Germany: Springer.

Kern, V., Guarise, N., & Vegetti, A. (2008). Typology of the inflorescence in *Spartina* (Poaceae: Eragrostoideae*). Plant Systematics and Evolution, 273*, 51–61.

Liu, Q., Peterson, P. M., Columbus, J. T., Zhao, N., Hao, G., & Zhang, D. (2007). Inflorescence diversification in the 'Finger Millet Clade' (Chloridoideae, Poaceae): A comparison of molecular phylogeny and developmental morphology. *American Journal of Botany, 94*, 1230–1247.

Liu, Q., Zhao, N. X., & Hao, G. (2005). Inflorescence structures and evolution in subfamily Chloridoideae (Gramineae). *Plant Systematics and Evolution, 251*, 183–198.

Lucero, L. E., Vegetti, A. C., & Reinheimer, R. (2014). Evolution and development of the spikelet and flower of *Rhynchospora* (Cyperaceae). *International Journal of Plant Sciences, 175*, 186–201.

McSteen, P. (2009). Hormonal regulation of branching in grasses. *Plant Physiology, 149*, 46–55.

Nicora, E. G., & Rúgolo de Agrasar, Z. E. (1987). *Los géneros de gramíneas de América Austral*. Buenos Aires, Argentina: Hemisferio Sur.

Pagel, M., Meade, A., & Barker, D. (2004). Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology, 53*, 673–684.

Pensiero, J. F., & Vegetti, A. C. (2001). Inflorescence typology in *Setaria* p. beauv. (Poaceae, Paniceae*). Feddes Repertorium, 112*, 371–385.

Peichoto, M. C., & Vegetti, A. C. (2007). Synflorescences of species related to *Schizachyrium condensatum* (Poaceae). *Flora-Morphology, Distribution, Functional Ecology of Plants, 202*, 503–512.

Perreta, M., & Vegetti, A. C. (1998). Tipología de la inflorescencia en *Leptochloa chloridiformis*, *Leptochloa virgata* y *Leptochloa mucronata* (Poaceae). *Kurtziana, 26*, 135–144.

Perreta, M. G., & Vegetti, A. C. (2004). Estructura de las inflorescencias en especies de *Melica* (Meliceae, Pooideae, Poaceae). *Darwiniana, Nueva Serie, 42*, 37–49.

Perreta, M., Ramos, J., & Vegetti, A. C. (2009). Development and structure of the grass inflorescence. *The Botanical Review, 75*, 377–396.

Peterson, P. M., Columbus, J. T., & Pennington, S. J. (2007). Classification and biogeography of new world grasses: Chloridoideae. In J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, & M. G. Simpson (Eds.), *Monocots: Comparative biology and evolution-Poales* (pp. 580–594). Claremont, California: Rancho Santa Ana Botanic Garden.

Peterson, P. M., Romaschenko, K., Barker, N. P., & Linder, H. P. (2011). Centropodieae and *Ellisochloa*, a new tribe and genus in Chloridoideae (Poaceae). *Taxon, 60*, 1113–1122.

Peterson, P. M., Romaschenko, K., & Johnson, G. (2010a). A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. *Molecular Phylogenetics and Evolution, 55*, 580–598.

Peterson, P. M., Romaschenko, K., & Johnson, G. (2010b). A phylogeny and classification of the Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae) based on plastid and nuclear DNA sequences. *American Journal of Botany, 97*, 1532–1554.

Peterson, P. M., Romaschenko, K., & Herrera Arrieta, Y. (2014). A molecular phylogeny and classification of the Cteniinae, Farragininae, Gouiniinae, Gymnopogoninae, Perotidinae, and Trichoneurinae (Poaceae: Chloridoideae: Cynodonteae). *Taxon, 63*, 275–286.

Peterson, P. M., Romaschenko, K., Snow, N., & Johnson, G. (2012). A molecular phylogeny and classification of *Leptochloa* (Poaceae: Chloridoideae: Chlorideae*) sensu lato* and related genera. *Annals of Botany, 109*, 1317–1329.

Peterson, P. M., Romaschenko, K., & Herrera Arrieta, Y. (2015). Phylogeny and subgeneric classification of *Bouteloua* with a new species, *B. herrera−arrietae* (Poaceae: Chloridoideae: Cynodonteae: Boutelouinae). *Journal of Systematics and Evolution, 53*, 351–366.

Peterson, P. M., Romaschenko, K., & Herrera Arrieta, Y. (2016). A molecular phylogeny and classification of the Cynodonteae (Poaceae: Chloridoideae) with four new genera: *Orthacanthus*, *Triplasiella*, *Tripogonella*, and *Zaqiqah*; three new subtribes: Dactylocteniinae, Orininae, and Zaqiqahinae; and a subgeneric classification of *Distichlis. Taxon, 65*, 1263–1287.

Pilatti, V., & Vegetti, A. (2014). Diversity of inflorescences in the Boutelouinae subtribe (Poaceae: Chloridoideae: Cynodonteae). *Flora, 209*, 426–434.

Rambaut, A., & Drummond, A. J. (2007). BEAST: Bayesian evolutionary analysis by ampling trees. *BioMedCentral Evolutionary Biology, 7*, 214.

Reinheimer, R. (2007). Desarrollo y estructura de la inflorescencia de *Brachiaria y Urochloa* (Poaceae: Panicoideae: Paniceae) y sus implicancias sistemáticas (Tesis doctoral). Santa Fe, Argentina: Universidad Nacional del Litoral. Facultad de Bioquímica y Ciencias Biológicas.

Reinheimer, R., Pozner, R., & Vegetti, A. C. (2005a). Inflorescence, spikelet, and floral development in *Panicum maximum* and *Urochloa plantaginea* (Poaceae). *American Journal of Botany, 92*, 565–575.

Reinheimer, R., Astegiano, M. E., & Vegetti, A. C. (2005b). Typology of the inflorescence in species of *Sporobolus* (Sporobolinae-Eragrostideae-Poaceae). *Kurtziana, 31*, 7–19.

Reinheimer, R., & Vegetti, A. C. (2008). Inflorescence diversity and evolution in the PCK clade (Poaceae: Panicoideae: Paniceae). *Plant Systematics and Evolution, 275*, 133–167.

Reinheimer, R., Zuloaga, F. O., Vegetti, A. C., & Pozner, R. (2009). Diversification of inflorescence development in the PCK Clade (Poaceae: Panicoideae: Paniceae). *American Journal of Botany, 96*, 549–564.

Reinheimer, R., Amsler, A., & Vegetti, A. C. (2013a). Insights into panicoid inflorescence evolution. *Organisms Diversity & Evolution, 13*, 97–110.

Reinheimer, R., Vegetti, A. C., & Rúa, G. H. (2013b). Macroevolution of Panicoid inflorescences: A history of contingency and order of trait acquisition. *Annals of Botany, 112*, 1613–1628.

Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics, 19*, 1572–1574.

Roodt-Wilding, R., & Spies, J. J. (2006). Phylogenetic relationships in southern African chloridoid grasses (Poaceae) based on nuclear and chloroplast sequence data. *Systematics and Biodiversity, 4*, 401–415.

Rúa, G. H. (1993). The synflorescence of *Paspalidium rarum* (Poaceae) and an alternative hypothesis about the evolution of some Poaceous inflorescences. *Australian Systematic Botany, 6*, 261–267.

Rúa, G. H. (1996). The inflorescences of *Paspalum* (Poaceae, Paniceae): The Quadrifaria group and the evolutionary pathway towards the fully homogenized, truncated common type. *Plant Systematics and Evolution, 201*, 199–209.

Rúa, G. H. (1999). *Inflorescencias: Bases teóricas para su análisis*. Buenos Aires: Sociedad Argentina de Botánica.

Rúa, G. H., & Gróttola, M. C. (1997). Growth form models within the genus *Paspalum* L. (Poaceae, Paniceae). *Flora, 192*, 65–80.

Rúa, G. H., & Weberling, F. (1998). Growth form and inflorescence structure of *Paspalum* L. (Poaceae: Paniceae): A comparative morphological approach. *Beitrage zur Biologie der Pflanzen, 69*, 363–431.

Salariato, D. L., Zuloaga, F. O., Giussani, L. M., & Morrone, O. (2010). Molecular phylogeny of the subtribe Melinidinae (Poaceae: Panicoideae: Paniceae) and evolutionary trends in the homogenization of inflorescences. *Molecular Phylogenetics and Evolution, 56*, 355–369.

Siqueiros-Delgado, M. E., Ainouche, M., Columbus, J. T., & Ainouche, A. (2013). Phylogeny of the *Bouteloua curtipendula* complex (Poaceae: Chloridoideae) based on nuclear ribosomal and plastid DNA sequences from diploid taxa. *Systematic Botany, 38*, 379–389.

Snow, N., Peterson, P. M., & Romaschenko, K. (2013). Systematics of *Disakisperma* (Poaceae, Chloridoideae, Chlorideae). *PhytoKeys, 26*, 21–70.

Soreng, R. J., Peterson, P. M., Romaschenko, K., Davidse, G., Zuloaga, F. O., Judziewicz, E. J., … Morrone, O. (2015). A worldwide phylogenetic classification of the Poaceae (Gramineae). *Journal of Systematics and Evolution, 53*, 117–137.

Soreng, R. J., Peterson, P. M., Romaschenko, K., Davidse, G., Teisher, J. K., Clark, L. G., … Zuloaga, F. O. (2017). A worldwide phylogenetic classication of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. *Journal of Systematics and Evolution, 55*, 259–290. doi:10.1111/jse.12262

Tivano, J. C., & Vegetti, A. (2004). Synflorescence typology in Pappophoreae (Eragros- toideae – Poaceae). *Beitrage zur Biologie der Pflanzen, 7*, 157–174.

Troll, W. (1964). *Die Infloreszenzen, Typologie und Stellung im Aufbau des Vegetationskörpers,* 1. Jena: G. Fischer.

Troll, W. (1966). Botanischer Teil. In *Kommission für biologische Forschung* (pp. 110–131). Bericht. Jb. 1965. Mainz: Akademie der Wissenschaften und der Literatur.

Troll, W. (1969). Botanischer Teil. In *Kommission für biologische Forschung* (pp. 88–105). Bericht. Jb. 1968. Mainz: Akademie der Wissenschaften und der Literatur.

Troll, W., & Weberling, F. (1989). *Infloreszenzuntersuchungen an monotelen Familien: Materialien zur Infloreszenzmorphologie*. Stuttgart: G. Fischer.

Van den Borre, A., & Watson, L. (1997). On the classification of the Chloridoideae (Poaceae). *Australian Systematic Botany, 10*, 491–531.

Vegetti, A. C. (1986). Contribución al conocimiento de las inflorescencias en Chloris y Cynodon (Poaceae). *Kurtziana, 18*, 109–120.

Vegetti, A. C. (1994). Typology of the inflorescence in species of Isolepis. *Beitrage zur Biologie der Pflanzen, 68*, 21–26.

Vegetti, A. C. (1999). Typology of the synflorescence of Andropogoneae (Poaceae), additional comments. *Feddes Repertorium, 110*, 111–126.

Vegetti, A. C. (2000). Typology of synflorescence in Oryzeae (Poaceae). *Phyton (Austria), 40*, 71–88.

Vegetti, A. C., & Anton, A. M. (1996). The synflorescence concept in Poaceae. *Flora, 191*, 231–234.

Vegetti, A. C., & Anton, A. M. (2000). The grass inflorescence. In S. W. L. Jacobs & J. Everett (Eds.), *Grasses: Systematics and evolution* (pp. 29–31). Melbourne, Australia: CSIRO Publishing.

Vegetti, A. C., & Muller-Doblies, D. (2004). The inhibition areas within the synflorescence of Poaceae. *Beitrage zur Biologie der Pflanzen, 73*, 51–74.

Vegetti, A. C., & Pensiero, J. F. (1990). Typology of the inflorescence in Setaria poiretiana (Poaceae). *Beitrage zur Biologie der Pflanzen, 65*, 313–318.

Vegetti, A. C., & Pensiero, J. F. (1999). Tipología de la inflorescencia en Zizaniopsis (Poaceae, Oryzeae). *Darwiniana, 37*, 345–349.

Vegetti, A. C., & Tivano, J. C. (1991). The inflorescence of Aciachne (Poaceae). *Boletín de la Sociedad Argentina de Botánica, 27*, 91–96.

Watson, L., & Dallwitz, M. J. (1992). *The grass genera of the world*. Wallingford, UK: C.A.B. International.

Weberling, F. (1985). Aspectos modernos de la morfología de las inflorescencias. *Boletín de la Sociedad Argentina de Botánica, 24*, 1–28.

Weberling, F. (1989). The architecture of inflorescences in the Myrtales. *Annals of the Missouri Botanical Garden, 75*, 226–310.

Weberling, F., Muller Doblies, U., Muller Doblies, D., & Rúa, G. H. (1997). Towards a descriptive and a comparative morphological terminology for complex inflorescences). *Boletín de la Sociedad Argentina de Botánica, 32*, 171–184.

Associate Editor: Nadia Bystriakova