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Inflorescence structure in *Rhynchospora* Vahl (Cyperaceae)

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ABSTRACT

We investigated the inflorescence structure of *Rhynchospora* following the methodology and terminology of Troll's school, with the objective of providing a characterization of the inflorescence suitable to evaluate the processes responsible for the diversity observed. Homogenization of inflorescence structures may occur fully or partially. In the first case, all branches of the inflorescence are homogeneous, while in the later, distal and proximal parts of the inflorescence bear homogeneous branches, but in the middle portions of the inflorescence non-homogeneous branches exist. Other characters leading to different forms of inflorescences are branching degree, internode elongation along the main axis of the synflorescence, degree of epipodium elongation of distal paraclades, development of bract and prophyll, and development of prophyllar paraclades. We identified three main types of inflorescences: (1) partially homogeneous paniculodia, (2) partially homogeneous capitate heads, and (3) a fully homogeneous capitate head. Within the first type, four subtypes were also recognized. Finally, we discuss how these processes can operate to produce the variation of the inflorescence shape.

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Introduction

Rhynchospora Vahl is a cosmopolitan genus of Cyperaceae. The diversity of the genus comprises at least 250 species mainly restricted to the Americas (Strong, 2006; Thomas et al., 2009), and most diverse in northern South America (Araujo et al., 2003; Koyama, 1972), particularly in savanna habitats. In the phylogenetic hypotheses of Muasya et al. (2009) for Cyperaceae, *Rhynchospora* appears as sister to *Pleurostachys*, forming the tribe Rhynchosporeae.

Rhynchospora has been recognized as a genus for more than two-hundred years (Vahl, 1806). In the worldwide taxonomic revision of the genus made by Kükenthal (1949, 1950, 1951) several infrageneric categories were proposed. Two subgenera were distinguished based on the morphology of the style: a deeply divided style for *Rhynchospora* subgenus *Haplostyleae* and a shallowly divided style for *Rhynchospora* subgenus *Diplostyleae* (today called subgenus *Rhynchospora*). Within subgenus *Haplostyleae*, Kükenthal recognized seven sections and also two groups which he called "Pars" (lat. "part"; a classification level between subgenus and section). Within subgenus *Rhynchospora*, he recognized three groups as "Pars" and twenty-one sections. Since Kükenthal (1949, 1950, 1951), no revision of this infrageneric classification has been attempted, and currently it is admitted that both subgenera are

artificial and an extensive phylogenetic study of the genus is needed (e.g., Strong, 2006).

Recently, a preliminary phylogenetic hypothesis for the Rhynchosporeae was proposed based on *trnL* intron and *trnL-F* intergenic spacers, including 41 species of *Rhynchospora* (Thomas et al., 2009). Although many of Kükenthal's infrageneric divisions were moderately to well supported, it was clear that the infrageneric divisions of *Rhynchospora* needed to be re-evaluated. The genus *Pleurostachys*, for instance, was found to be deeply embedded within *Rhynchospora* with the consequence that for *Pleurostachys* to be maintained as a genus, *Rhynchospora* would have to be splitted into several new genera (Thomas et al., 2009).

According to Strong (2006), inflorescences in *Rhynchospora* can vary from a single terminal, solitary head of spikelets to large compound panicles of many spikelets, often composed of a terminal and a series of one to several lateral, partial panicles. A common circumscription of the inflorescence in *Rhynchospora* is that it possesses a series of repeated axillary inflorescences beneath the terminal inflorescence (Guaglianone, 1979, 1980, 1981, 1982, 2001; Strong, 2006; Thomas et al., 2009). But the description of inflorescences in *Rhynchospora* is confusing; several different authors may refer to the inflorescence of the same species with different terms.

It has been suggested that the inflorescence structure in angiosperms is the result of evolutive processes, such as homogenization, truncation and racemization (Cámara Hernández and Rua, 1991; Rua, 1996; Troll, 1964; Weberling, 1985, 1989). A typology-based system was elaborated by Troll (1964) in order to describe the inflorescence in a way useful to evaluate the occurrence of the evolutionary processes mentioned (see Fig. 1 for further explanation of

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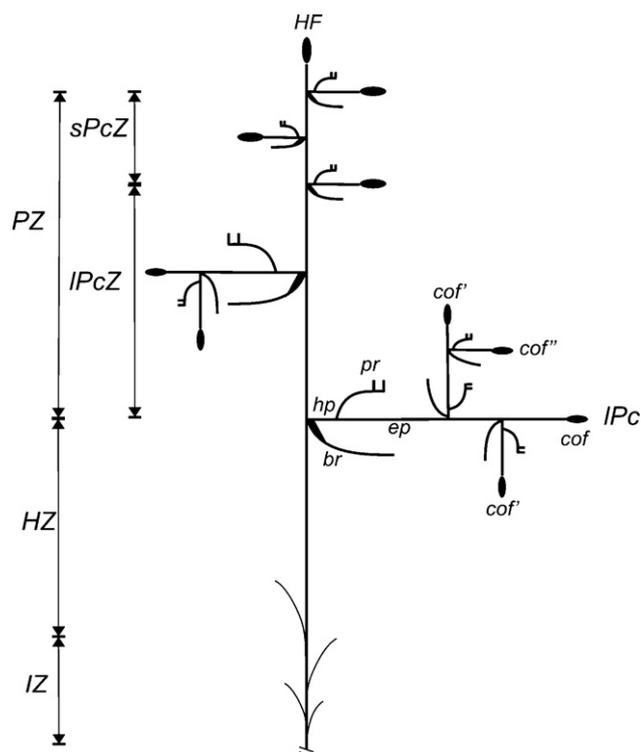


Fig. 1. Troll's typology system: the synflorescence is the floriferous axis produced from the apical meristem or an innovation bud, originated in the innovation zone (IZ) which is followed by the inhibition zone (HZ). When the main axis ends in a florescence (main florescence, HF), lateral branches, called paraclades (Pc), can develop below the HF. Each paraclade originates from the axil of a bract (br), and consists of a hypopodium (hp), a prophyll (pr), an epipodium (ep) of variable length, and a terminal spikelet, the co-florescence (cof). The Pc can be represented by a single spikelet (in Cyperaceae) – short paraclades (sPc), or by a more complex, branching structure – long paraclades (lPc). The paraclades form the paracladial or enrichment zone (PZ) below the HF; the PZ and the HF together constitute the inflorescence. The PZ can be composed of subzones of short paraclades (sPcZ) and long paraclades (lPcZ) or can be represented by either one of them.

this typology system). The typological analysis was useful to understand the structure of the inflorescences in some taxa of Cyperaceae (Ahumada and Vegetti, 2009; Browning and Gordon Gray, 1999; Guarise and Vegetti, 2008a,b; Kukkonen, 1984, 1986, 1994; Mora Osejo, 1960; Perreta and Vegetti, 2002; Reutemann et al., 2009; Vegetti, 1992, 1994, 2002, 2003).

The importance of truncation and homogenization processes were recognized in Cyperaceae (Guarise and Vegetti, 2008b). Truncation consists in loss of the distal portion of the inflorescence. Homogenization is the specialization of distal portions of the inflorescence in such a way that the lateral branches become homogeneous throughout (Rua, 1999), producing similarities in the ramification degree among the inflorescence branches (Reinheimer and Vegetti, 2008). In non-homogenized inflorescences branches present different degrees of ramification along the inflorescence and do not present specialization, while in the fully homogenized inflorescences the degree of ramification is the same for all branches (Rua, 1996, 1999; Troll, 1964; Weberling, 1985, 1989). When homogenization is only partial, some branches present similar branching degree and other have a different branching degree (Reinheimer and Vegetti, 2008; Rua, 1996, 1999). The resulting inflorescence has been considered in Poaceae as a transitional or intermediate form between the non-homogeneous inflorescence and a fully homogeneous inflorescence (Reinheimer and Vegetti, 2008; Rua, 1996; Rua and Weberling, 1998). Partially homogenized inflorescences were never recognized in Cyperaceae so far.

Although the inflorescence in *Rhynchospora* is diverse, a comprehensive typological study relating it to the occurrence of the evolutive processes mentioned above has never been attempted. The present work has the following objectives: (1) to describe the synflorescence structure of *Rhynchospora* from a typological point of view as a form to contribute to the knowledge of the inflorescence of the genus; (2) to identify the processes responsible for the diversification of the inflorescence in the genus.

Materials and methods

Specimens examined were collected from the field and deposited at the herbarium of the Universidad del Litoral (SF), or obtained from different herbaria (CORD, LIL, LP, SI and SF). We examined the synflorescences of 23 species of *Rhynchospora*, including species from both subgenera, all five "Pars", and 12 different sections (of a total of 27 recognized by Kükenthal; Table 1) that represent the diversity of the inflorescence structure in the genus. Mature inflorescences were dissected using a Nikon SMZ-10 stereoscopic microscope, and photographed using a Canon A640 digital camera.

In the interpretation of synflorescences we used mainly the terminology proposed by Troll (1964), but with additional contributions taken into account (Kukkonen, 1994; Rua, 1999; Vegetti, 2003; Weberling, 1985).

Results

Synflorescence structure

In all species examined the plant has a distal region, the anthotagma (the region that bears the floral axis) and a proximal region, the trophotagma (the region that usually has a vegetative function): Figs. 1–3. The trophotagma has an innovation zone (IZ) at or near the base of the shoot comprised of short internodes, followed by an inhibition zone (HZ) that is characterized by the absence of axillary axes, the presence of long internodes bearing leaves with sheaths, and well-developed blades. The buds present at the IZ can develop into a new synflorescence that repeats the structure of the main shoot (Fig. 4).

The inflorescence always ends in a spikelet which is the main florescence (HF, terminal spikelet). Below it, a paracladial zone (PZ) develops, where paraclades originate from the axils of bracts. (Figs. 2 and 3). Each paraclade (Pc) ends in a coflorescence (cof, terminal spikelet of the paraclade) and possesses a short hypopodium (hp), a prophyll (pr), and an epipodium (ep). In the PZ, two subzones can be distinguished; a short distal paracladial subzone (sPcZ) that bears sPc reduced to its cof in the distal region below the HF, and, below the sPcZ, a long paracladial subzone (lPcZ) that also bears lPc of different branching degrees (Fig. 2).

With respect to the PZ, two main structures were found, a proximal lPcZ and a distal sPcZ (Fig. 2). Branching degree decreased distally along the lPcZ, until paraclades are reduced to cof in the sPcZ. In Fig. 3, only short paraclades are depicted in the PZ.

Homogenization

Differences in the PZ were found with regard to the degree of homogenization. Fig. 2 shows an inflorescence where the PZ has both a sPcZ and a lPcZ and in which the process of homogenization is only partial (Table 2). These inflorescences have a distal homogeneous region (Dhr) in which the sPc bears only short paraclades reduced to cof; the first proximal long paraclades in the lPcZ are also homogenized. As a result, the inflorescence has also a proximal homogeneous region (Phr), and a middle inhomogeneous

Table 1
Species studied and respective infrageneric classification according to Kükenthal (1949, 1950, 1951).

Subgenus	Pars	Section	Species	
Haplostylis	Anthelata	<i>Paniculatae</i> Boeck	<i>R. hieronymii</i> Boeck	
		<i>Longirostres</i> Kunth	<i>R. corymbosa</i> (L.) Britton	
			<i>R. scutellata</i> Grises	
			<i>R. trispicata</i> (Nees) Schrad. ex Steud.	
			<i>R. asperula</i> (Nees) Steud.	
		<i>Polycephalae</i> C.B. Clarke	<i>R. holoschoenoides</i> (Rich.) Herter	
			<i>R. exaltata</i> Kunth	
		<i>Pseudocapitatae</i>	<i>R. recurvata</i> (Nees) Steud	
			<i>R. pilosa</i> Boeckeler	
	Capitatae	<i>Pluriflorae</i> Kük.	<i>R. globosa</i> (Kunth) Roem. & Schult.	
			<i>R. terminalis</i> (Nees) Steud	
Diplostylis	Eu-Rhynchospora	<i>Mariscalae</i> Kük.	<i>R. consanguinea</i> (Kunth) Boeck.	
			<i>R. marisculus</i> Nees	
		<i>Stenophyllae</i> Kük.	<i>R. barrosiana</i> Guaglianone	
			<i>R. rugosa</i> (Vahl) Gale	
			<i>R. britonii</i> Gale	
	Psilocaryae	<i>Globulares</i> Gale	<i>R. velutina</i> (Kunth) Boeck	
			<i>R. praecincta</i> Maury	
		<i>Eu-Psilocarya</i> (Torr.) C.B. Clarke	<i>R. emaciata</i> (Nees) Boeck.	
			<i>Luzuliformes</i> Kük.	<i>R. tenuis</i> Link
			<i>Tenues</i> Kük.	<i>R. tenella</i> (Nees) Boeck.
Dichromena	<i>Dichromena</i> (Michx.) Vahl	<i>R. nervosa</i> (Vahl) Böckeler		
		<i>R. setigera</i> (Kunth) Boeck		

region (*MNhr*) where branching degree decreases distally (Fig. 2). This type of inflorescence presents two different subzones (*sPcZ* and *lPcZ*) and is considered disjunct. The *Phr* (Fig. 2) is characterized by the presence of a few long paraclades which possess the same maximum degree of branching and even the same number of secondary paraclades (Fig. 2). The *Dhr* only have *sPc*.

In Fig. 3, the inflorescence structure is fully homogeneous bearing only short paraclades (*sPc*) reduced to its *cof* and, as a consequence, disjunction is absent.

Degree of branching

The degree of branching presents great variation in the *Rhynchospora* species studied. In the case of partially homogeneous inflorescences, the degree of branching decreases distally. The maximum number of normal branches found is up to the fifth degree in *Rhynchospora marisculus*. Fully homogeneous inflorescences only have paraclades of the first degree, as in *R. nervosa* (Table 2).

Phyllotaxis

Along the main axis, the phyllotaxis of the paraclades is spirotristichous in all species studied, despite the differences in branching degree mentioned above (Fig. 5). Paraclades of the 2nd order or above can show the same phyllotaxis pattern as the main axis (homodromic arrangement) or the arrangement can differ from the main axis (antidromic arrangement). Both possibilities can be found in different specimens of the same species or even in the same individual (Fig. 5).

Epipodium elongation

Variation with regard to epipodium development of primary paraclades (*Pc*¹) was distinguished qualitatively. The epipodium of some species is not elongated, as in *Rhynchospora nervosa* or *R. globosa* (Table 2). When elongation is significant, an easily to recognize *ep* can be present at distal and/or proximal-median paraclades (e.g., only *lPc* in *R. hieronymii*; *lPc-sPc* in *R. corymbosa*; Table 2). In species in which an elongation of *ep* occurs, the degree of elongation varies in the distal *Pc*¹ depending on species, resulting in three different types of epipodia: (1) those not surpassing the HF, (2) those reaching the HF, and (3) those surpassing the HF (Table 2).

Internode elongation along the main axis

In the PZ, internodes at the first proximal *Pc*¹ can be elongated; they decrease in length acropetally along the main axis, being shortest at the distal paraclades. Species like *Rhynchospora nervosa* and *R. globosa* never display elongated internodes at the proximal *Pc*¹ (Table 2). The number of elongated internodes at proximal branches shows little variation within species (Table 2). Long paraclades of the proximal homogeneous region (*Phr*) have elongated internodes, whereas in the middle non-homogeneous region (*MNhr*) and the distal homogeneous region (*Dhr*), internodes are reduced (Fig. 2).

Contrary to the PZ, in the innovation zone (*IZ*) internode length increases distally. The inhibition zone (*HZ*), between the *IZ* and the PZ, shows variation between and within species. In general, the *HZ* is represented by only one internode of variable length (e.g., *R. corymbosa*), although in some species it may consist of more than one, as in *R. setigera*.

Bract and prophyll

The two types of bracts differ in shape and consistency. The foliaceous type has a basal portion sheathing the shoot and a distal leaf-like blade. The other type of bract is more or less setiform, smaller than the foliaceous type, and not sheathing. Along the main shoot, bract length decreases acropetally. The proximal and median *Pc*¹ have leafy bracts and the distal *Pc*¹ have setiform ones. In some species, setiform bracts are the only type of bract present in the inflorescence (e.g., *R. globosa*; Table 2). Sheathing bracts are common in PHP inflorescences (Table 3). When proximal *Pc*¹ in PHP inflorescences (see below in this section) are separated by elongated internodes, these paraclades are originated from foliaceous bracts.

In *Rhynchospora*, prophylls are two-keeled while bracts are one-keeled. In the species studied, the prophylls display an acropetal variation in size and even shape. Two types can be found, tubular prophylls (cladoprophyll) and glumaceous prophylls (Fig. 6). Some species have both forms of prophylls (*R. corymbosa*) and others only have the glumaceous form (*R. setigera*) – Table 2. All prophylls are two-keeled, while bracts are one-keeled, as it occurs also in other Cyperaceae.

Table 2
Main characteristics of the inflorescences of the studied species of *Rhynchospora*. Pc, paracladia (Pc^1 1st order paracladia); LPc, long paracladium; SPc, short paracladium; NA, not applicable; NE, not elongated; NS, not surpassing the HF; R, reaching the HF; S, surpassing the HF; Cl, cladoprophyll; Gl, gluma-like prophyll.

Species	Number of Pc^1	Maximum branch degree	Prophyllar branching	Epipodium of Pc^1 elongated	Degree of epipodium elongation of distal Pc^1	Number of internodes elongated at proximal Pc^1	Prophyll form	Sheathing bract
<i>R. asperula</i>	18–26	3	Yes	LPc-SPc	S	2–6	Cl-Gl	Yes
<i>R. barrosiana</i>	9–18	3	Yes	LPc	S	(1)–2	Cl-Gl	Yes
<i>R. brittonii</i>	(12–) 13–14	3	Yes	LPc-SPc	R	2–4	Cl-Gl	Yes
<i>R. consanguinea</i>	14–17	1	No	NE	NA	0	Gl	No
<i>R. corymbosa</i>	9–20	4	Yes	LPc-SPc	S	1–4	Cl-Gl	Yes
<i>R. emaciata</i>	11–14	3	No	LPc-SPc	S	(1)–2–3	Gl	Yes
<i>R. exaltata</i>	12–15	2	Yes	LPc	NS	3–5	Gl	Yes
<i>R. globosa</i>	12–15	2	Yes	NE	NA	0	Gl	No
<i>R. hieronymii</i>	13–15	4	No	LPc	NS	2–3	Gl	Yes
<i>R. holoschoenoides</i>	9–11	3	Yes	LPc	S	0–3	Gl	Yes
<i>R. marisculus</i>	17–18	5	Yes	LPc-SPc	S	2–3	Cl-Gl	Yes
<i>R. nervosa</i>	8–10	1	No	NE	NA	0	Gl	No
<i>R. pilosa</i>	8	1	Yes	NE	NA	0	Gl	No
<i>R. praecincta</i>	14–16	3	No	LPc	NS	(1)–2	Gl	Yes
<i>R. recurvata</i>	30	2	No	NE-LPc	NA	0	Gl	Yes
<i>R. rugosa</i>	9	3	Yes	LPc-SPc	S	1–2	Cl-Gl	Yes
<i>R. scutellata</i>	12–13–15	3	Yes	LPc	S	2–4	Cl-Gl	Yes
<i>R. setigera</i>	8–12	3	No	NE	NA	0–(1)	Gl	No
<i>R. tenella</i>	15	4	Yes	LPc-SPc	S	1–2	Gl	Yes
<i>R. tenuis</i>	(13–) 15–16	4	Yes	LPc-SPc	S	(1)–2	Gl	Yes
<i>R. terminalis</i>	(–19) 8–13	1	No	NE	NA	0	Gl	No
<i>R. trispicata</i>	13	4	Yes	LPc-SPc	S	1	Cl-Gl	Yes
<i>R. velutina</i>	7–11	3	No	LPc-SPc	R	1–2	Cl-Gl	Yes

Prophyllar branching

In addition to the axillary paracladia (originated in the axil of bracts), in some species additional paracladia can be produced from buds positioned in the axil of prophylls (Fig. 6A; Table 2), called from here prophyllar paracladia. On the other hand, some species only have axillar branching (e.g., *R. hieronymii*, *R. velutina*, and *R. nervosa*; Table 2). In the species which present the two forms of prophylls, prophyllar branching takes place in glumaceous prophylls but not in tubular prophylls (Table 2).

Synflorescence shape/type

Three main types of synflorescences can be recognized in *Rhynchospora*: partially homogeneous paniculodia (PHP); partially homogeneous capitate heads (PHch); and fully homogeneous capitate head (FHch). The PHP type can be divided into four subtypes of synflorescences (Table 2; Fig. 7): partially homogeneous panicles of anthelodia (PHPa), partially homogeneous panicles of corymbodia

(PHPc), partially homogeneous panicles of fascicles (PHPf), and partially homogeneous panicles of capitate heads (PHPch).

Partially homogeneous paniculodia (PHP), always exhibit a PZ with $sPcZ$ and $lPcZ$, sheathing bracts at proximal Pc^1 , internodes elongated at proximal Pc^1 , and elongation of ep at distal Pc^1 . Long primary paraclades and the degree of ep elongation at distal Pc^1 are the characters that allow the differentiation of three of the four subtypes of PHP. Formation of a PHPc occurs when the summit of long paraclades takes the form of a corymb and spikelets at distal Pc^1 reach the HF by elongation of ep (e.g., *R. brittonii* and *R. velutina*; Table 2; Fig. 7). When the end of a long paraclade takes the form of an anthelodium and the coflorescences (spikelets) of the distal Pc^1 surpass the HF by ep elongation, a PHPa is formed (e.g., *R. corymbosa* and *R. tenuis*; Table 2; Fig. 7). In the PHPf subtype, the end of a long paraclade takes the form of a fascicle. When long distal paraclades are separated by short internodes and also have the ep elongated so that the main florescence is surpassed by lPc , the synflorescence ends in an anthelodium (*R. scutellata*, *R. rugosa* and *R. barrosiana*; Tables 2 and 3; Fig. 7).

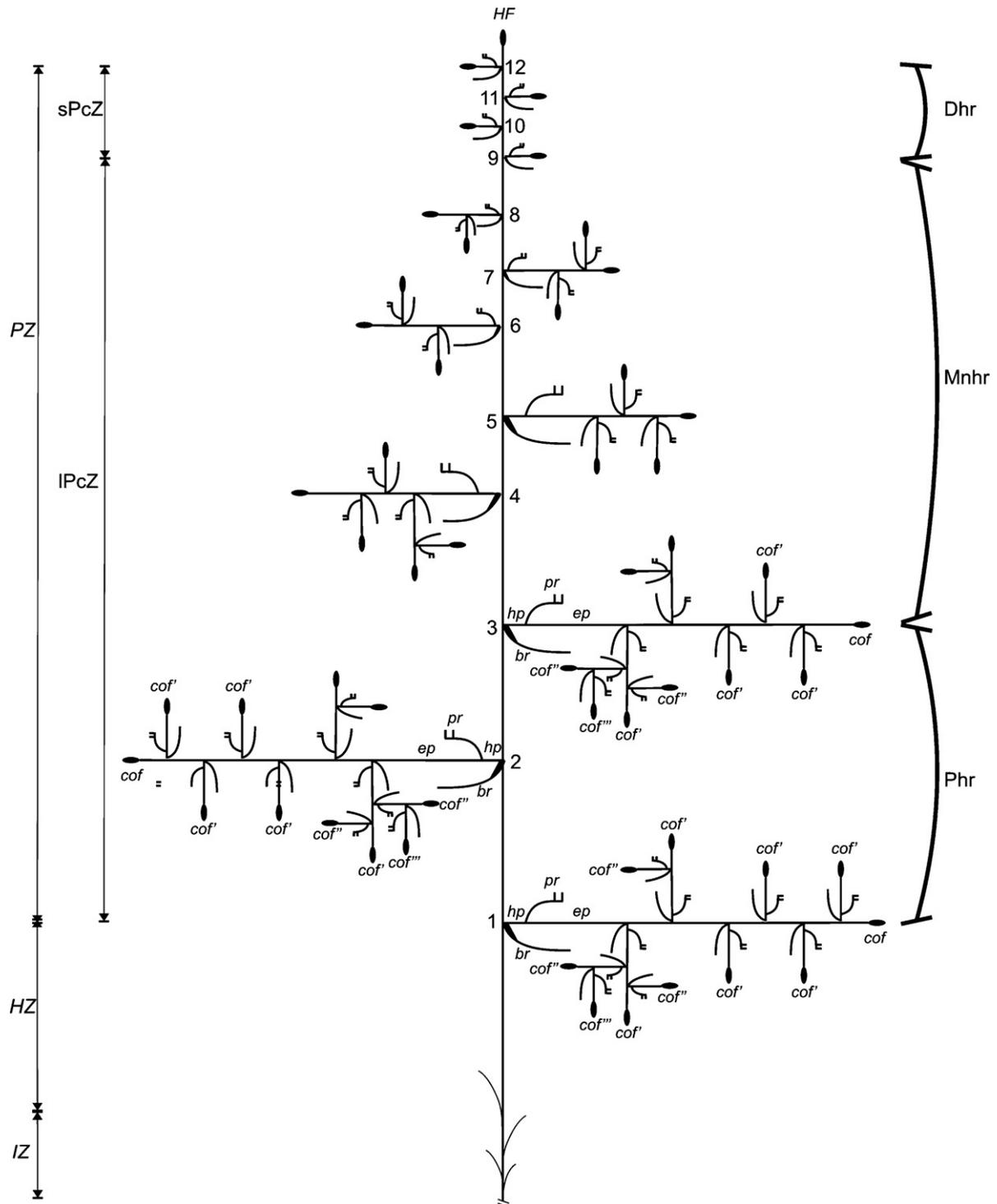


Fig. 2. Structure of a partially homogenized synflorescence: *br* pherophyll; *cof*, *cof'*, *cof''* and *cof'''*, cymose of paracladium of successive order; *ep* epipodium; *HF* main inflorescence; *pr* prophyll; *PZ* paracladial zone; *IPcZ* long paracladial subzone; *sPcZ* short paracladial subzone; *HZ* inhibition zone; *IZ* innovation zone; *Dhr* distal homogenized region; *Mnhr* middle not homogenized region; *Phr* proximal homogenized region.

A single capitate head or an anthelodium of capitate heads placed at the end of *Pc*¹ makes up the fourth subtype of PHP, a panicle of capitate heads (PHPch). The first case is evident in *R. exaltata* where, in general, *ep* of proximal and middle *Pc*¹ are elongated. In contrast, in *R. holoschoenoides*, commonly an anthelodium of capitate heads is placed at the proximal and middle *Pc*¹, but only single capitate heads are formed by the distal *Pc*¹; in both species *ep* of *sPc*¹ are never elongated. Prophyllar branching can be present in the PHPa, PHPf and PHPc subtypes, but only axillar branching was

found in the PHP type, such as in *R. hieronymii* and *R. praecincta* (Table 2).

In the partially homogeneous capitate (PHch) inflorescence type, as the homogenization process is only partial, in the paracladial zone, the *sPcZ* is distal and the *IPcZ* is basal (Fig. 2). Inflorescences of this type are characterized by absence of long internodes at the proximal *Pc*¹, a maximum branching degree of second order, and the *ep* of *Pc*¹ that are not elongated. This type of congested inflorescence either displays only axillar branching,

Table 3
Homogenization degree, synflorescence types and shape of the species of *Rhynchospora* studied.

Species	Homogenization degree	Synflorescence type	Synflorescence shape	Inflorescence polymorphism
<i>R. asperula</i>	Partial	PHPa	Paniculodium of antelodia	No
<i>R. barrosiana</i>	Partial	PHPf	Paniculodium of fascicles	No
<i>R. britonii</i>	Partial	PHPc	Paniculodium of corymbodia	No
<i>R. consanguinea</i>	Full	FHch	Capitate head	^a
<i>R. corymbosa</i>	Partial	PHPa	Paniculodium of antelodia	No
<i>R. emaciata</i>	Partial	PHPa	Paniculodium of corymbodia	No
<i>R. exaltata</i>	Partial	PHPch	Paniculodium of capitate heads	No
<i>R. globosa</i>	Partial	PHch	Capitate head	No
<i>R. hieronymii</i>	Partial	PHP	Paniculodium	No
<i>R. holoschoenoides</i>	Partial	PHPch/Ach	Paniculodium of antelodia of capitate heads/Antelodium of capitate heads	Yes
<i>R. marisculus</i>	Partial	PHPa	Paniculodium of antelodia	No
<i>R. nervosa</i>	Full	FHch	Capitate head	No
<i>R. pilosa</i>	Full	FHch	Capitate head	^a
<i>R. praecincta</i>	Partial	PHP	Paniculodium	No
<i>R. recurvata</i>	Partial	PHch	Capitate head	^a
<i>R. rugosa</i>	Partial	PHPf	Paniculodium of antelodia	^a
<i>R. scutellata</i>	Partial	PHPf	Paniculodium of fascicles	No
<i>R. setigera</i>	Partial	PHch/PHPch	Capitate head/Paniculodium of capitate heads	Yes
<i>R. tenella</i>	Partial	PHPa	Paniculodium of antelodia	No
<i>R. tenuis</i>	Partial	PHPa	Paniculodium of antelodia	No
<i>R. terminalis</i>	Full	FHch	Capitate head	No
<i>R. trispicata</i>	Partial	PHPa/A	Paniculodium of antelodia/Antelodium	Yes
<i>R. velutina</i>	Partial	PHPc	Paniculodium of corymbodia	No

^a Missing data.

as in *R. setigera*, or can have prophyllar branching, as in *R. globosa*. Bracts can be large or reduced, but never sheathing the main shoot (Table 2).

The fully homogeneous capitate (FHch) inflorescence type (Fig. 3), as in the PHch type, is characterized by the absence of long

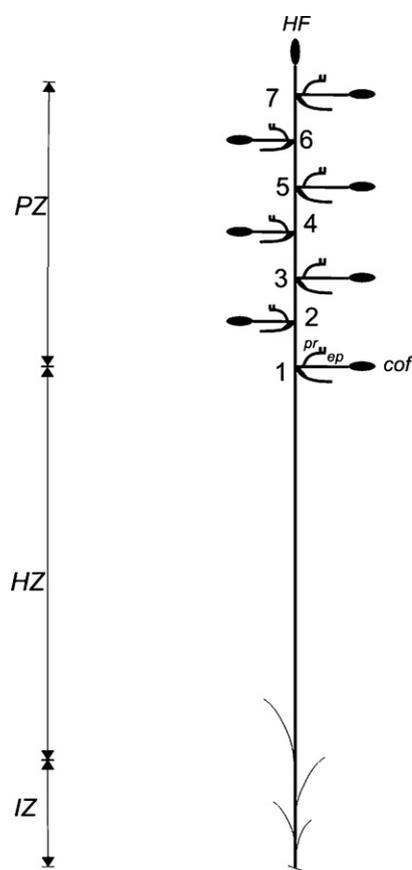


Fig. 3. Structure of a fully homogenized synflorescence: *br* prophyll; *cof* coflorescence of 1st order; *ep* epipodium; *HF* main inflorescence; *pr* prophyll; *PZ* paraclyadial zone.

internodes at the proximal Pc^1 , and has the *ep* of Pc^1 not elongated. Absence of long paraclades and the strong process of homogenization are the main characteristics of this type of inflorescence; as a result, the *PZ* of the FHch inflorescence type only has a *sPcZ* with extremely short internodes between *sPc*, with only branches of the first order reduced to *cof* (Table 2; Fig. 3). The phyllotaxis pattern is identical to the partially homogeneous inflorescences types (Figs. 1–3). In general, only axillary branching is present in the FHch type, with the exception of *R. pilosa* (Table 2) which also possesses prophyllar branching. The shape of capitate inflorescences can be an extremely condensed fascicle of spikelets to an almost globose form in either PHch or FHch types.

Inflorescence polymorphism

The inflorescences types and subtypes described above represent the plant architecture for a given species, although some species can show alternative forms in regard to this architecture (Table 3). For instance, the generalized type of inflorescence in *Rhynchospora setigera* is a solitary capitate head (PHch type), but occasionally a second head could develop from an axillary bud forming a reduced panicle of heads (PHPch subtype) – Table 3. Another case of inflorescence polymorphism is found in *R. holoschoenoides* where proximal Pc^1 can be repressed. As a result,

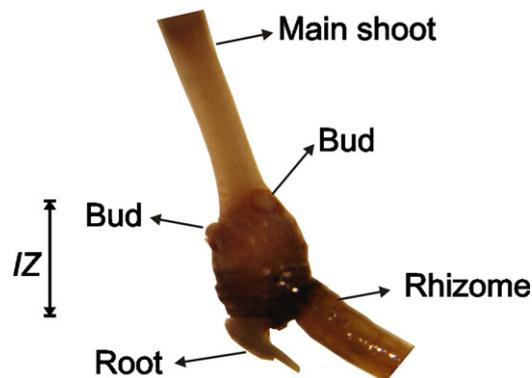


Fig. 4. Basal portion of the synflorescence of *R. tenuis*. Basal leaves were removed.

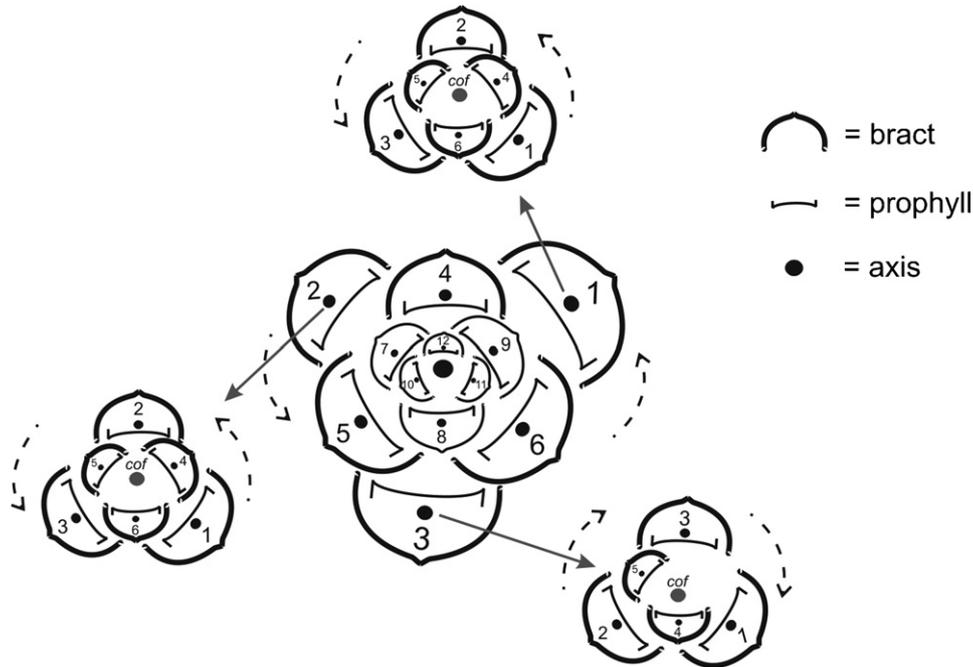


Fig. 5. Disposition of the paraclades of first order in the main axis, and disposition of paraclades of second order of the three most proximal primary paraclades of Fig. 2; cof coflorescence of 1st order.

the inflorescence shape is an anthela of heads instead of the typical panicle of head (Table 3).

Discussion

The morphology of the inflorescences and the establishment of homologies among different types of inflorescences is of importance in order to structure the morphology of Cyperaceae (Raynal, 1971), and is the concern of this paper.

Synflorescence structure in the studied species of *Rhynchospora* always has an innovation zone (IZ) and an inhibition zone (HZ), which belong to the trophotagma (Figs. 2 and 3). Above this portion and below the main florescence (HF), a paracladial zone can be recognized which possesses short and long paraclades (Fig. 2) or short paraclades exclusively (Fig. 3). This zonation is in agreement with that found in other groups of Cyperaceae (Guarise and Vegetti, 2008b; Reutemann et al., 2009; Vegetti, 2003).

Of the three processes suggested as being responsible for structural diversity of the inflorescences in angiosperms, homogenization is the only process that takes part in the diversification of the inflorescence in *Rhynchospora*. Partial homogenization of the distal portion of the inflorescence, is recognized here for first time in Cyperaceae – but with structural differences in comparison with Poaceae, were partially homogeneous inflorescences present a distal homogeneous region and a proximal non-homogeneous region (Reinheimer and Vegetti, 2008; Rua, 1996; Rua and Weberling, 1998). In *Rhynchospora*, partially homogeneous inflorescences have two homogeneous regions separated by a middle non-homogeneous region (Fig. 2). Although in the basal region (Phr) long primary paraclades bear secondary paraclades of different branching degree, first order paraclades all possess the same maximum branch degree and a similar number of secondary paraclades, producing the same appearance as the inflorescence shape.

Axillary branching is present in all the species, but the branching degree shows remarkable variation. The minimum degree of branching observed was only of first order in fully homogeneous inflorescences, whereas branching degree in partially

homogeneous inflorescences varied from 2nd to 5th order (Table 2). It must be noted that the different types of inflorescences can also be characterized by degree of branching. The PHch subtype only has branches (paraclades) of 2nd or 3rd order (e.g., *R. globosa* and *R. setigera*, respectively), whereas in the PHP type and its four subtypes (PHPf, PHPa, PHPc and PHPch) branching degree varies from 3rd to 5th order (e.g., *R. asperula* and *R. marisculus*, respectively): Figs. 2, 3 and 7; Table 2.

Production of prophyllar and accessory buds can take place in species of Cariceae, Cyperaceae, Hypolytreae, and Rhynchosporeae of the Cyperaceae family (Alves, 2000; Guarise and Vegetti, 2008a; Haines, 1966; Meert and Goetghebeur, 1979; Mora Osejo, 1960; Raynal, 1971). In the species of *Rhynchospora* studied, we found only prophyllar buds that develop into branches (Fig. 6A; Table 2). This is a common feature in species with the PHP subtypes of inflorescences (PHPa; PHPc; PHPf; PHPch; Fig. 7). On the other hand, in the FHch type, the prophyllar branching is absent except in *R. pilosa*. Also, there were two species with the PHP inflorescence type in which we did not find prophyllar branching, *R. hieronymii* and *R. praecincta* (Table 2). As mentioned before, in the inflorescences with prophyllar branching, prophyllar branching is related to prophyll form; we did not find branching in tubular prophylls (Fig. 6A and B).

Important differences were noticed with respect to the epipodium (*ep*). In capitate inflorescences (PHch and FHch), *ep* are never elongated; this, along with reduced branching, is a major factor in the formation of this type of congested structure (Fig. 7; Tables 2 and 3). The role of the epipodium is also important in the formation of inflorescence shape of the PHP inflorescence type (Tables 2 and 3). Elongated *ep* are present in all PHP subtypes, with variation in the degree of elongation. When *ep* of distal *Pc* were elongated and surpassed the HF (main florescence), an anthelodium resulted. In the formation of the corymbodium shape, *ep* elongate at the same position of the HF, and when *ep* elongated less, a fascicle shape is formed (Fig. 7; Tables 2 and 3).

Internode elongation of basal (proximal) paraclades of the first order is rather variable. In PHP type and all PHP subtypes, the internodes of proximal paraclades are elongated; the length of

internodes decreases from the proximal to the distal portion. In capitate inflorescences (PHch and FHch), the internodes are extremely contracted (Fig. 7). When internode elongation of the proximal Pc^1 occurs, the number of elongated internodes in a species may be characteristic (Table 2).

Partially homogeneous inflorescences with short and long paraclade subzones are considered disjunct ones. As stated by Rua (1999), proximal branches can reach the appearance of individual inflorescences if disjunction is present along with internode elongation. But, as all these branches are derived from the same apical bud, in the sense of Troll (1964) it should be treated as only one inflorescence (The “synflorescence”). This argument may explain why this type of inflorescence in *Rhynchospora* has been described as having a terminal inflorescence, and lateral inflorescences as different, below it. Floristic and taxonomic treatments of the genus commonly refer to PHP inflorescences as having a terminal inflorescence and a certain number of lateral inflorescences. We consider this a misinterpretation and in this work we perform a typological approach in order to clarify the inflorescence structure in *Rhynchospora* in a consistent way. According to Weberling (1985), without a comparative basis it is impossible to understand the architecture of inflorescences. In taxonomic works, it has been common to distinguish between lateral and terminal inflorescences in the genus (Abreu Ferreira and Eggers, 2008; Guaglianone, 2001; Koyama, 1972; Rocha and Luceño, 2002; Strong, 2006), but misinterpreting the inflorescence structure will preclude the study of primary homology (De Pinna, 1991).

One of the critics against the typological concept of Troll was that he rejected the idea of transitional forms. Later, Weberling (1989) recognized that in many plant families the huge diversity of inflorescences show transitions from the monotelic to the polytelic type. A more modern view of Troll's ‘types’ is to see them as ‘classes’ characterized by sharp limits (Claßen-Bockhoff, 2001). These sharp limits are reflected in the present typological approach to *Rhynchospora* (Fig. 7; Table 2). Some authors have shown that polymorphic characters provide phylogenetic signals and that they are useful in resolving phylogenies (Kornet and Turner, 1999; Wiens and Servedio, 1997). In *Rhynchospora* we observed inflorescence polymorphism in at least two species studied, *R. holoschoenoides* and *R. setigera* (Table 3). In present work, we describe the inflorescence of *R. trispicata* as PHPa subtype. According to the description of the inflorescence of Guaglianone (2001), however, *R. trispicata* also shows inflorescence polymorphism. Guaglianone (2001) described this inflorescence as an anthela, which suggest that the proximal Pc with elongated internode is repressed.

Trends of the structure and shape of the inflorescence

As mentioned earlier, typically the inflorescence in *Rhynchospora* possesses a series of repeated axillary inflorescences beneath the terminal inflorescence. The typological approach shows that in fact, the synflorescence possesses lateral branches (paraclades) separated by long internodes, instead of several inflorescences. The shape of the inflorescence is related to the structural characters and processes mentioned earlier; here we recognize three main types of inflorescences and four subtypes (Table 3; Fig. 7). Raynal (1971) and Goetghebeur (1998) considered the panicle as the basic cyperaceous inflorescence which can be modified by the elongation or contraction of the internodes and various reduction trends. In reviewing the processes responsible for synflorescence diversity in sedges (Cyperaceae), Guarise and Vegetti (2008b) use the term ‘paniculodium’ instead of ‘panicle’, taking into account that inflorescences in the family end in a spikelet (polytelic inflorescence). In his treatment of inflorescences, Troll (1964) proposed that the panicle gives rise to the anthela and the corymb,

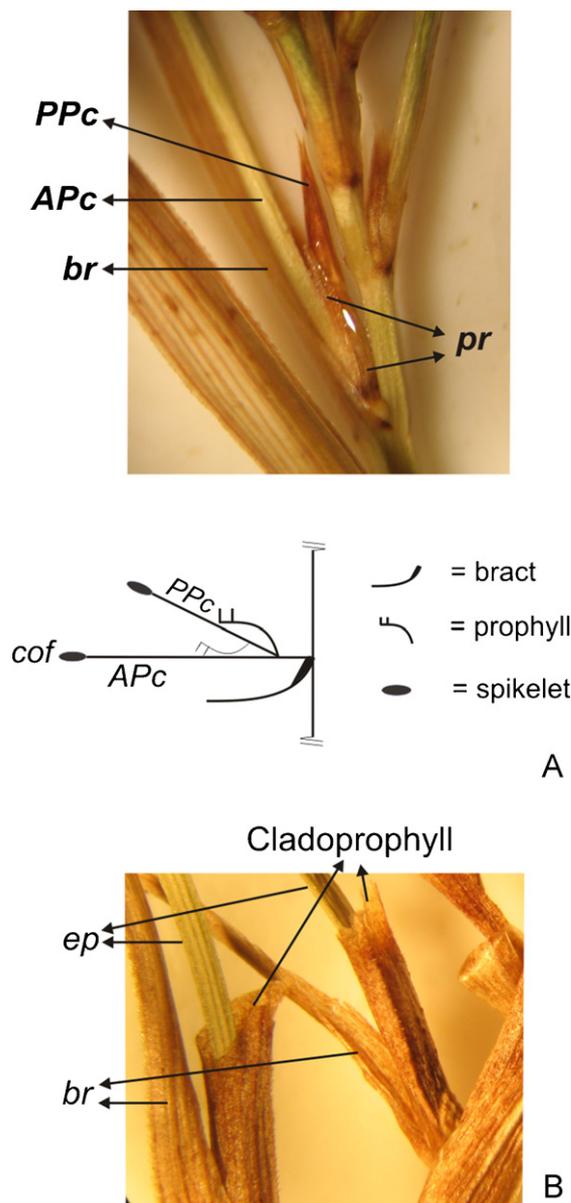


Fig. 6. (a) Prophyllar branching in *R. britonii*. *APc* axillary paracladium; *PPc* prophyllar paracladium; *br* bract; *pr* prophyll. (b) Presence of cladoprophyll in *R. corymbosa*. *IZ* innovation zone; *ep* epipodium; *br* bract.

which are modifications of the panicle. For polytelic inflorescences he coined the terms ‘paniculodium’, ‘anthelodium’ and ‘corymbodium’, respectively. Later, Raynal (1971) stated that the anthela and paniculodium have a common structural plan but different intercalary growth of the internodes. As pointed out by Guarise and Vegetti (2008b), a capitate inflorescence may derive from a paniculodium, an anthela, or from a spike of spikelets for the reduction of the internodes length of the main axis and Pc . The same authors, however, stated that there is no reason to suppose that the reverse pathway might not happen, producing a type of inflorescence with Pc developed from any more congested shape.

The diversity in the structure of the inflorescences in *Rhynchospora* is due to variations in the following characters and processes: (1) homogenization process; (2) branching degree; (3) internode elongation along the main axis of the synflorescence; (4) elongation of Pc^1 epipodium; (5) degree of epipodium elongation of distal Pc^1 ; (6) development of bract and prophyll; (7) development of prophyllar paraclades (Fig. 7; Tables 2 and 3).

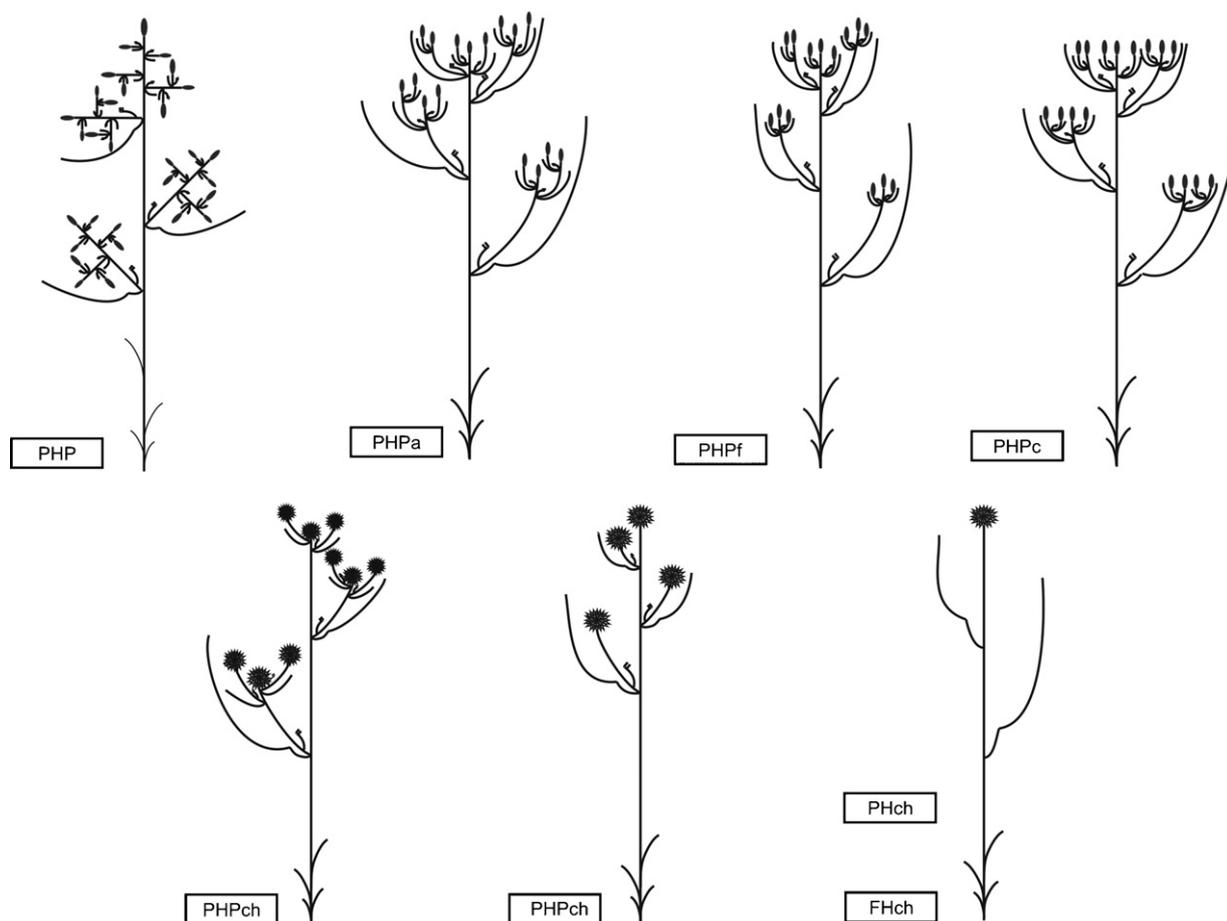


Fig. 7. Synflorescence diversity in *Rhynchospora*. Partially homogenized paniculodium type (PHP type); partially homogenized paniculodium of antelodia subtype (PHPa subtype); partially homogenized paniculodium of corymbodia subtype (PHPc subtype); partially homogenized paniculodium of fascicles subtype (PHPf subtype); partially homogenized paniculodium of capitate heads subtype (PHPch subtype); partially homogenized capitate head type (PHch type); fully homogenized capitate head type (FHch type).

The quantitative and qualitative characters of the inflorescence in the genus *Rhynchospora* recognized here (Tables 2 and 3), are useful to describe its inflorescence structure, and to recognize the processes involved in the diversification of the inflorescence. These characters are of potential use in future phylogenetic studies of the group. Nevertheless, before an extended molecular and morphological phylogenetic study of *Rhynchospora* would be achieved, we are still unable to suggest convincingly evolutive pathways that may have occurred in the diversification of the inflorescence in the group.

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