Inflorescence structure in *Rhynchospora* Vahl (Cyperaceae)

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**A B S T R A C T**

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 prophyllary paraclades. We identified three main types of inflorescences: (1) partially homogeneous paniculodia, (2) partially homogeneous capitule heads, and (3) a fully homogeneous capitule 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 Rhynchosporae.

*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 *Haplostylaea* and a shallowly divided style for *Rhynchospora* subgenus *Diplostylaea* (today called subgenus *Rhynchospora*). Within subgenus *Haplostylaea*, 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 *Rhynchospora* 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 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 split 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 circumscripting 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, 1988). 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...
The infructescence (Vegetti, 2008; 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 infructescence. Homogenization is the specialization of distal portions of the infructescence in such a way that the lateral branches become homogeneous throughout (Rua, 1999), producing similarities in the ramification degree among the infructescence branches (Reinhheimer and Vegetti, 2008). In non-homogenized infructescences branches present different degrees of ramification along the infructescence and do not present specialization, while in the fully homogenized infructescences 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 (Reinhheimer and Vegetti, 2008; Rua, 1996, 1999). The resulting infructescence has been considered in Poaceae as a transitional or intermediate form between the non-homogeneous infructescence and a fully homogeneous infructescence (Reinhheimer and Vegetti, 2008; Rua, 1996; Rua and Weberling, 1998). Partially homogenized infructescences were never recognized in Cyperaceae so far.

Although the infructescence 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 infructescence of the genus; (2) to identify the processes responsible for the diversification of the infructescence 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 infructescence structure in the genus. Mature infructescences were dissected using a Nikon SMZ-10 stereochemical 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 (Kükten, 1994; Rua, 1999; Vegetti, 2003; Weberling, 1985).

Results

Synflorescence structure

In all species examined the plant has a distal region, the antheridium (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 paracladal zone (PZ) develops, where paraclades originate from the axis of bracts. (Figs. 2 and 3). Each paraclade (Pc) ends in a coflorescence (cof, terminal spikelet of the paraclade) and possesses a short hypodiopodium (hp), a prophyll (pr), and an epidiopodium (ep). In the PZ, two subzones can be distinguished: a short distal paracladal subzone (sPcZ) that bears spF reduced to its cof in the distal region below the HF, and, below the sPcZ, a long paracladal subzone (IPcZ) that also bears lPc of different branching degrees (Fig. 2).

With respect to the PZ, two main structures were found, a proximal IPcZ and a distal sPcZ (Fig. 2). Branching degree decreased distally along the IPcZ, 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 infructescence where the PZ has both a sPcZ and a lPcZ and in which the process of homogenization is only partial (Table 2). These infructescences have a distal homogeneous region (Dhr) in which the sPcZ bears only short paraclades reduced to cof; the first proximal long paraclades in the lPcZ are also homogenized. As a result, the infructescence 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).

<table>
<thead>
<tr>
<th>Subgenus</th>
<th>Pars</th>
<th>Section</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Haplostylis</td>
<td>Anthelata</td>
<td>Paniculatae Boeck</td>
<td>R. hieronymii Boeck</td>
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<td></td>
<td></td>
<td>Longirostres kunth</td>
<td>R. corymbosa (L.) Britton</td>
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<td></td>
<td></td>
<td>Polycephalae C.B. Clarke</td>
<td>R. scutellata Griseb.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pseudopachytopae</td>
<td>R. risipicata (Nees) Schrad. ex Steud.</td>
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<td></td>
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<td></td>
<td>R. asperula (Nees) Steud.</td>
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<td></td>
<td></td>
<td></td>
<td>R. holochonemos (Rich.) Herter</td>
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<td></td>
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<td></td>
<td>R. exiliflora Kunth</td>
</tr>
<tr>
<td>Capitatae</td>
<td></td>
<td></td>
<td>R. recurvata (Nees) Steud.</td>
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<td></td>
<td>R. pilosa Boeckeler</td>
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<td></td>
<td></td>
<td></td>
<td>R. globosa (Kunth) Roem. &amp; Schult.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>R. terminalis (Nees) Steud.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>R. consanguinea (Kunth) Boeck.</td>
</tr>
<tr>
<td>Diplostylis</td>
<td>Eu-Rhynchospora</td>
<td>Mariscula Kük.</td>
<td>R. marisculus Nees</td>
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<td>Stereophyllae Kük.</td>
<td>R. barroisiana Guaglanione</td>
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<td>Globulares Gale</td>
<td>R. rugosa (Vahl) Gale</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Eu-Pulicaria (Tor.) C.B. Clarke</td>
<td>R. britonii Gale</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Luzuliformes Kük.</td>
<td>R. velutina (Kunth) Boeck</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tenues Kük.</td>
<td>R. praecincta Maury</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>R. emaciata (Nees) Boeck.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>R. tenuis Link</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>R. tenella (Nees) Boeck.</td>
</tr>
<tr>
<td></td>
<td>Dichromena</td>
<td>Dichromena (Michx.) Vahl</td>
<td>R. nervosa (Vahl) Böckeler</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>R. setigera (Kunth) Boeck</td>
</tr>
</tbody>
</table>

region (MNhr) where branching degree decreases distally (Fig. 2). This type of inflorescence presents two different subzones (sPCZ and iPCZ) 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 co/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 (Pc1) 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 IPC in R. hieronymii; IPC-sPC in R. corymbosa; Table 2). In species in which an elongation of ep occurs, the degree of elongation varies in the distal Pc1 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 Pc1 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 Pc1 (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 Pc1 have leafy bracts and the distal Pc1 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 Pc1 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 (Table 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*. Lc, paracladia (Pc1 1st order paracladia); Lc, long paracladia; SPC, short paracladia; NA, not applicable; NE, not elongated; NS, not surpassing the HF; R, reaching the HF; S, surpassing the HF; CL, clado prophyll; Gl, gluma-like prophyll.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Pc1</th>
<th>Maximum branch degree</th>
<th>Prophyllar branching</th>
<th>Epipodium of Pc1 elongated</th>
<th>Degree of epipodium elongation of distal Pc1</th>
<th>Number of internodes elongated at proximal Pc1</th>
<th>Prophyll form</th>
<th>Sheathing bract</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. asperula</em></td>
<td>18–26</td>
<td>3</td>
<td>Yes</td>
<td>Lc-SPc</td>
<td>S</td>
<td>2–6</td>
<td>Cl-Gl</td>
<td>Yes</td>
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<tr>
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<td>9–18</td>
<td>3</td>
<td>Yes</td>
<td>Lc</td>
<td>S</td>
<td>(1)–2</td>
<td>Cl-Gl</td>
<td>Yes</td>
</tr>
<tr>
<td><em>R. britonii</em></td>
<td>(12–) 13–14</td>
<td>3</td>
<td>Yes</td>
<td>Lc-SPc</td>
<td>R</td>
<td>2–4</td>
<td>Cl-Gl</td>
<td>Yes</td>
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<td><em>R. consanguinea</em></td>
<td>14–17</td>
<td>1</td>
<td>No</td>
<td>NE</td>
<td>NA</td>
<td>0</td>
<td>Gl</td>
<td>No</td>
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<tr>
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<td>9–20</td>
<td>4</td>
<td>Yes</td>
<td>Lc-SPc</td>
<td>S</td>
<td>(1)–2–3</td>
<td>Gl</td>
<td>Yes</td>
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<td>11–14</td>
<td>3</td>
<td>No</td>
<td>Lc-SPc</td>
<td>S</td>
<td>(1)–2–3</td>
<td>Gl</td>
<td>Yes</td>
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<td>2</td>
<td>Yes</td>
<td>Lc</td>
<td>NS</td>
<td>3–5</td>
<td>Gl</td>
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<td>12–15</td>
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<td>0</td>
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<td>NS</td>
<td>2–3</td>
<td>Gl</td>
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<td>Lc</td>
<td>S</td>
<td>0–3</td>
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<td>5</td>
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<td>S</td>
<td>2–3</td>
<td>Cl-Gl</td>
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<td>8–10</td>
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<td>NA</td>
<td>0</td>
<td>Gl</td>
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<td>8</td>
<td>1</td>
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<td>0</td>
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<td>NS</td>
<td>(1)–2</td>
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<td>0</td>
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<td>1–2</td>
<td>Cl-Gl</td>
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<td>12–13–15</td>
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<td>Yes</td>
<td>Lc</td>
<td>S</td>
<td>2–4</td>
<td>Cl-Gl</td>
<td>Yes</td>
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<td>8–12</td>
<td>3</td>
<td>No</td>
<td>NE</td>
<td>NA</td>
<td>0–(1)</td>
<td>Gl</td>
<td>No</td>
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<tr>
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<td>15</td>
<td>4</td>
<td>Yes</td>
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<td>S</td>
<td>1–2</td>
<td>Gl</td>
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<td>(13–) 15–16</td>
<td>4</td>
<td>Yes</td>
<td>Lc-SPc</td>
<td>S</td>
<td>(1)–2</td>
<td>Gl</td>
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<td>8–13</td>
<td>1</td>
<td>No</td>
<td>NE</td>
<td>NA</td>
<td>0</td>
<td>Gl</td>
<td>No</td>
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<tr>
<td><em>R. trispicata</em></td>
<td>13</td>
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<td>Yes</td>
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<td>No</td>
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<td>R</td>
<td>1–2</td>
<td>Cl-Gl</td>
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</table>

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 prophyllary paracladia. On the other hand, some species only have axillary 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 paniculodua (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 Caryobodia (PHPc), partially homogeneous panicles of fascicles (PHPf), and partially homogeneous panicles of capitulate heads (PHCh).

Partially homogeneous paniculodia (PHP), always exhibit a PZ with sPZ and lPZ, sheathing bracts at proximal Pc1, internodes elongated at proximal Pc1, and elongation of ep at distal Pc1. Long primary paraclades and the degree of ep elongation at distal Pc1 are the characters that allow the differentiation of three of the four subtypes of PHP. Formation of a PHCh occurs when the summit of long paraclades takes the form of a corymb and spikelets at distal Pc1 reach the HF by elongation of ep (e.g., *R. britonii* 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 Pc1 surpass the HF by ep elongation, a PHCh is formed (e.g., *R. corymbosa* and *R. tenais*; Table 2; Fig. 7). In the PHCh 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 IpC, the synflorescence ends in an anthelodium (*R. scutellata*, *R. rugosa* and *R. barrosiana*; Tables 2 and 3; Fig. 7).
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 axillary 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 $lPcZ$ 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 axillary branching,
Table 3
Homogenization degree, synflorescence types and shape of the species of Rhynchospora studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Homogenization degree</th>
<th>Synflorescence type</th>
<th>Synflorescence shape</th>
<th>Inflorescence polymorphism</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. asperula</td>
<td>Partial</td>
<td>PHPa</td>
<td>Paniculodium of antelodia</td>
<td>No</td>
</tr>
<tr>
<td>R. barrosiana</td>
<td>Partial</td>
<td>PHPf</td>
<td>Paniculodium of fascicles</td>
<td>No</td>
</tr>
<tr>
<td>R. britoni</td>
<td>Partial</td>
<td>PHPc</td>
<td>Paniculodium of corymbodia</td>
<td>No</td>
</tr>
<tr>
<td>R. consanguinea</td>
<td>Full</td>
<td>PHPch</td>
<td>Capitate head</td>
<td>No</td>
</tr>
<tr>
<td>R. corymbosa</td>
<td>Partial</td>
<td>PHPa</td>
<td>Paniculodium of antelodia</td>
<td>No</td>
</tr>
<tr>
<td>R. emaculata</td>
<td>Partial</td>
<td>PHPa</td>
<td>Paniculodium of corymbodia</td>
<td>No</td>
</tr>
<tr>
<td>R. exaltata</td>
<td>Partial</td>
<td>PHPch</td>
<td>Paniculodium of capitate heads</td>
<td>No</td>
</tr>
<tr>
<td>R. globosa</td>
<td>Partial</td>
<td>PHPch</td>
<td>Capitate head</td>
<td>No</td>
</tr>
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<td>R. hieronymii</td>
<td>Partial</td>
<td>PHP</td>
<td>Paniculodium</td>
<td>No</td>
</tr>
<tr>
<td>R. holoschoenoides</td>
<td>Partial</td>
<td>PHPch/Ach</td>
<td>Paniculodium of antelodia/Antelodium of capitate heads</td>
<td>Yes</td>
</tr>
<tr>
<td>R. marisculus</td>
<td>Partial</td>
<td>PHPa</td>
<td>Paniculodium of antelodia</td>
<td>No</td>
</tr>
<tr>
<td>R. nervosa</td>
<td>Full</td>
<td>PHPch</td>
<td>Capitate head</td>
<td>No</td>
</tr>
<tr>
<td>R. pilosa</td>
<td>Full</td>
<td>PHPch</td>
<td>Capitate head</td>
<td>No</td>
</tr>
<tr>
<td>R. praecincta</td>
<td>Partial</td>
<td>PHP</td>
<td>Paniculodium</td>
<td>No</td>
</tr>
<tr>
<td>R. recurvata</td>
<td>Partial</td>
<td>PHPch</td>
<td>Capitate head</td>
<td>No</td>
</tr>
<tr>
<td>R. rugosa</td>
<td>Partial</td>
<td>PHPf</td>
<td>Paniculodium of antelodia</td>
<td>No</td>
</tr>
<tr>
<td>R. scutellata</td>
<td>Partial</td>
<td>PHPf</td>
<td>Paniculodium of fascicles</td>
<td>No</td>
</tr>
<tr>
<td>R. setigera</td>
<td>Partial</td>
<td>PHPch/PHPch</td>
<td>Capitate head/Paniculodium of capitate heads</td>
<td>Yes</td>
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<td>R. tenella</td>
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<td>Paniculodium of antelodia</td>
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<tr>
<td>R. tenuis</td>
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<td>PHPa</td>
<td>Paniculodium of antelodia</td>
<td>No</td>
</tr>
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<td>R. terminalis</td>
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<td>PHPch</td>
<td>Capitate head</td>
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<tr>
<td>R. trispicata</td>
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<td>PHPa/A</td>
<td>Paniculodium of antelodia/Antelodium</td>
<td>Yes</td>
</tr>
<tr>
<td>R. velutina</td>
<td>Partial</td>
<td>PHPc</td>
<td>Paniculodium of corymbodia</td>
<td>No</td>
</tr>
</tbody>
</table>

* 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 internodes at the proximal Pc1, and has the ep of Pc3 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 sPc 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 Pc1 can be repressed. As a result,
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 trophagma (Figs. 2 and 3). Above this portion and below the main florescence (HF), a paracladal 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 Veggetti, 2008b; Reutemann et al., 2009; Veggetti, 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 Veggetti, 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.

Auxiliary 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. mariscus, respectively): Figs. 2, 3 and 7; Table 2.

Production of prophyllar and accessory buds can take place in species of Cariceae, Cyperaceae, Helyporetaceae, and Rhynchosporaeae of the Cyperaceae family (Alves, 2000; Guarise and Veggetti, 2008a; Haines, 1966; Meert and Goetghheber, 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; PHPch; PHPf; 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 capitulate 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 capit- 
ite inflorescences (PHch and FHch), the internodes are extremely 
contracted (Fig. 7). When internode elongation of the proximal Pc1 
occurrs, the number of elongated internodes in a species may be 
characteristic (Table 2).

Partially homogeneous inflorescences with short and long par-
acle subzones are considered disjunct ones. As stated by Rua 
(1999), proximal branches can reach the appearance of individ-
ual 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 inflo-
rescences as different, below it. Floristic and taxonomic treatments 
of the genus commonly refer to PHP inflorescences as having a ter-
minal 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 struc-
ture 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; Guaglione, 2001; 
Koyama, 1972; Rocha and Luceño, 2002; Strong, 2006), but mis-
interpreting 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 diver-
sity 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 (Cläßen-Bockhoff, 
2001). These sharp limits are reflected in the present typologi-
cal 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 stud-
ied, 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 polymor-
phism. 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 Rhyn-
chospora possesses a series of repeated axillary inflorescences 
beneath the terminal inflorescence. The typological approach 
shows that in fact, the synflorescence possesses lateral branches 
(paracles) separated by long internodes, instead of several in-
florescences. 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 pan-
icle 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 syn-
florescence 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) pro-
posed that the panicle gives rise to the anthela and the corymb, 
which are modifications of the panicle. For polytelic inflorescences 
he coined the terms ‘paniculodium’, ‘anthelodium’ and ‘corymbo-
dium’, respectively. Later, Raynal (1971) stated that the anthela 
and paniculodium have a common structural plan but different inter-
calary growth of the internodes. As pointed out by Guarise and 
Vegetti (2008b), a capitate inflorescence may derive from a pan-
iculodium, 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 Rhyn-
chospora is due to variations in the following characters and pro-
cesses: (1) homogenization process; (2) branching degree; (3) 
internode elongation along the main axis of the synflorescence; (4) 
elongation of Pc1 epipodium; (5) degree of epipodium elongation of 
distal Pc1; (6) development of bract and prophyll; (7) development 
of prophyllar paracles (Fig. 7; Tables 2 and 3).
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 evolutionary pathways that may have occurred in the diversification of the inflorescence in the group.

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References


