Flora 210 (2015) 3–12

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Inflorescence development in Abildgaardieae (Cyperaceae, Cyperoideae)

Andrea G. Reutemann[a,b,*], Abelardo C. Vegetti[a,b], Raúl Pozner[c]

[a] Morfología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional Del Litoral, Kreder 2805, 3080 Esperanza, Santa Fe, Argentina
[b] Instituto de Agrobiotecnología del Litoral (UNL-CONICET), Kreder 2805, 3080 Esperanza, Santa Fe, Argentina
[c] Instituto de Botánica Darwinion (IBODA-CONICET), Labardén 200, CC 22 San Isidro, Buenos Aires, Argentina

ARTICLE INFO

Article history:
Received 7 June 2014
Received in revised form 6 October 2014
Accepted 28 October 2014
Edited by Rainer Lösch.
Available online 29 November 2014

Keywords:
Abildgaardieae
Homology
Inflorescence
Meristem
Phyllotaxis

ABSTRACT

Inflorescences in Cyperaceae are a source of characters with significant systematic value; however, the structure and primary homologies pose a challenge to their interpretation. The relationships among members of Abildgaardieae are not clear due to the absence of a phylogeny with strong support, comprising a representative number of species. Establishing correct primary homologies of inflorescences within Abildgaardieae might help to clarify the relationships among its members, as well as to find synapomorphies for the most important clades. Variations in the mature inflorescences within Abildgaardieae have been related to their "shape" and "structure", and preliminary phylogenetic studies in species of *Bulbostylis* have shown that inflorescence structure traits are phylogenetically informative, but this is not true for the mere shape. While similar structures in the adult inflorescences of the members of different clades within Abildgaardieae might be considered homologous, it must be ascertained whether such similar structures share the same developmental process or have different developmental patterns. By studying the development of inflorescences in selected species of Abildgaardieae using SEM, we were able to show that inflorescences with homologous structures share a similar developmental process and, therefore, the adult structure of inflorescences may be relied on for establishing correct primary morphological homologies in this plant group. Most structural variations of inflorescences in Abildgaardieae depend on the degree of development of processes shared by the studied species. While phyllotaxis in the main axis of *Cyperus* may be modified during inflorescence development after primordial inception, variations in the phyllotactic patterns of leaves on vegetative shoots (=nomophylls) and of leaves on fertile shoots (=bracts or hypsophylls) within Abildgaardieae, might establish deeper differences in inflorescence structure, since they depend on changes in the shape of the apical meristem.

Introduction

In Cyperaceae, reproductive structures have often shown to be a source of systematic, reliable, diagnostic traits (Guarise et al., 2012, and citations therein). The basic reproductive units within the family are the spikelets (Richards, 2002; Richards et al., 2006; Vrijdaghs, 2006), which bear highly simplified flowers. Spikelets are arranged in inflorescences that are generally compound and have a structure and primary homologies (=conjectures of homologies; De Pinna, 1991) hard to determine (Goetghebeur, 1998; Reutemann et al., 2012a; Vegetti, 2003). Comparative developmental studies within Cyperaceae have proved to be a suitable approach to interpret flower and spikelet structures and their primary homologies (Bruhl, 1991; Gehrke et al., 2012; Mora-Osejo, 1987; Nijalingappa and Goetghebeur, 1989; Reutemann et al., 2012b; Reynders et al., 2012; Richards, 2002; Richards et al., 2006; Vrijdaghs et al., 2004, 2005a,b, 2006, 2007, 2009, 2010, 2011; Vrijdaghs, 2006). However, only a few developmental studies have been published on inflorescences of Cyperaceae beyond the spikelet level. Among those papers, only Guarise et al. (2012) considered the whole process of inflorescence development and showed how developmental studies can reveal and clarify primary homologies valuable for systematics in *Cyperus*.

Abildgaardieae is a complex Cyperaceous group with inconclusive evolutionary relationships (Ghamkhar et al., 2007). In its more restricted circumscription, Abildgaardieae is composed of six genera (*Abildgaardia*, *Bulbostylis*, *Crosslandia*, *Fimbristylis*, *Nelmesia* and *Nemum*), and among those genera, *Abildgaardia*, *Bulbostylis* and *Fimbristylis* have the most controversial limits. Both the structural

* Corresponding author at: Morfología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional Del Litoral, Kreder 2805, 3080 Esperanza, Santa Fe, Argentina. Tel.: +54 3496 426400; fax: +54 3496 426400.
E-mail address: areutemann@fca.unl.edu.ar (A.G. Reutemann).

http://dx.doi.org/10.1016/j.flora.2014.10.009
0367-2530/

Table 1
Main differences observed in the structure of adult inflorescences in Abildgaardieae previously recorded by Reutemann et al. (2009) and Reutemann (2012).

Species	Presence of normal branches	Maximum branching order of the species	Presence of prophyllar branches	Bract phyllotaxis	Inflorescence symmetry
B. communis	Yes	3rd	Yes	Stable	Radial
B. conifera	No	–	No	Stable	Radial
B. juncoides	Yes	2nd	Yes	Stable	Radial
B. sphaerocephala	Yes	3rd	No/yes[a]	Stable	Radial
F. autumnalis	Yes	4th	No	Stable	Radial
F. dichotoma	Yes	3rd	No	Stable	Radial
F. ovata	No/yes[a]	1st	No	Variable	Mixed
F. spadicea	Yes	3rd	No	Stable	Radial
F. squarrosa	Yes	2nd	No	Stable	Radial

[a] Rarely.

similarity found in the species gathered under these three genera and the existence of transitional species have raised the question of whether it is correct to consider this group of species as separate genera (Goetghebeur and Coudijzer, 1984). On a molecular basis, *Abildgaardia* is included into *Fimbristylis*, while *Bulbostylis* is considered an independent genus (Govaerts et al., 2007). Also, the structure and development of the style base do not support a clear difference between *Abildgaardia* and *Fimbristylis* (Reutemann et al., 2012b).

The morphology of adult inflorescences within Abildgaardieae has been analyzed by Reutemann et al. (2009), and Reutemann (2012). These studies revealed that the main variations in the mature inflorescences are related to the inflorescence "shape" and "structure". The shape of the inflorescences (whether they are capitate or anthelate; i.e., congested, or lax and with proximal branches overtopping the terminal spikelet and the distal branches – see Reutemann et al., 2012a) is basically determined by the length of the epipodium (=the internode after prophyll on an inflorescence branch) of branches of different orders, whereas the structure of the inflorescences depends on the presence or absence of branches, the branching degree they reach, the bracts phyllotaxis, the inflorescence symmetry, and the existence of special types of branching, such as prophyllar branching (Fig. 1A–E; Table 1). Guarise et al. (2012) showed in *Cyperus* that the same mature inflorescence features may result from independent developmental sequences, differing by: (1) the timing in the development and elongation of the main axis and branches, (2) position of second-order branching initiation and, (3) phyllotaxis changes during development. In Poaceae, for instance, a similar mature inflorescence structure may be produced by deeper developmental differences, such as the acropetal/basipetal inception and differentiation of second-order branches (Reinheimer, 2007; Reinheimer et al., 2009).

Considering that preliminary phylogenetic studies in *Bulbostylis* have shown that characters of the mature inflorescence structure are important from a phylogenetic point of view since they can usually be seen as synapomorphies in trees (Reutemann, 2012), we propose a comparative study of inflorescence development among selected members of Abildgaardieae to test how reliably structural features of mature inflorescences are to be used to establish primary homologies within this tribe, analyzing whether species from different subclades or groups of Abildgaardieae reach similar mature inflorescence features through shared or independent developmental patterns.

Materials and methods

We studied the inflorescence development of nine species of Abildgaardieae with similar characters in their mature inflorescence structure (according to Reutemann, 2012; Reutemann et al., 2009; Table 1 and Fig. 1A–E), but belonging to two different subclades of Abildgaardieae, as based on Ghamkhar et al. (2007), listed in Table 2: (a) the clade including *Bulbostylis* species (hereafter "clade 1"); and (b) the clade including species of *Fimbristylis* and *Crosslandia* and also, in some analyses, species from the Arthrostylideae tribe (hereafter "clade 2"). Among the studied species, *B. conifera* (from clade 1) and *F. ovata* (from clade 2) were selected to compare the development of inflorescences without branching (=unispicate); *B. communis*, *B. juncoides*, *B. sphaerocephala* (clade 1) and *F. autumnalis*, *F. dichotoma*, *F. spadicea*, *F. squarrosa* (clade 2) were selected to analyze the development of branched inflorescences (=plurispicate); while *B. communis*, *B. conifera*, *B. juncoides*, *B. sphaerocephala* (clade 1) and *F. autumnalis*, *F. dichotoma*, *F. spadicea*, *F. squarrosa* (clade 2) were chosen to compare inflorescences with stable bract phyllotaxis and radial symmetry. Additionally, inflorescences of *B. communis* and *B. juncoides* (both from clade 1) were used to study the development of prophyllar branches, exclusive of *Bulbostylis*. Finally, *F. ovata* was also selected to understand the development of bracts with variable phyllotaxis, only found in this species (in comparison with the stable phyllotaxis found in the remaining species).

Table 2
Species and specimens included in this study, presented as based on the Abildgaardieae subclade they belong to, according to the phylogeny proposed by Ghamkhar et al. (2007). For details about the botanical nomenclature of species, see Govaerts et al. (2007).

Clade 1
Bulbostylis communis MG López and D Simpson: Reutemann 02; 182 (SF)
B. conifera (Kunth) Beetle: AAI 26 (HRCB)
B. juncoides (Vahl) Kük. ex Herter: Reutemann et al., 07; 12 (SF)
B. sphaerocephala (Boeck.) Lindm.: Dematteis 2708 (CTES); Reutemann et al. 157; 161 (SF)

Clade 2
Fimbristylis autumnalis (L.) Roem. and Schult.: Lucero et al. 28; Reutemann et al. 28; 64 (SF)
F. dichotoma (L.) Vahl: López and Reutemann 376 (CTES); Lucero et al. 24; Reutemann et al. 79 (SF); Martins and Oriani 353 (HRCB)
F. ovata (Burm. f.) J. Kern: Reutemann et al. 33; 54 (SF); Reutemann and Acosta 173 (SF)
F. spadicea (L.) Vahl: Reutemann 76; Reutemann and Acosta 73; Reutemann et al. 22 (SF)
F. squarrosa Vahl: Reutemann et al. 63; 95 (SF)

For each species, between 20 and 40 samples of fresh, young inflorescences obtained from plants collected in wild populations were used for scanning electron microscopy (SEM) studies. Inflorescences at different early stages of development were fixed in formalin–acetic acid–ethanol (FAA; Ruzin, 1999), dissected in 70% ethanol under an OLYMPUS SZH10 stereomicroscope, and dehydrated with a graded ethanol series (80%, 96%, 99.5%) plus two final changes of 100% acetone. The dehydrated material was critical-point dried in an EMITECH K850 critical point dryer, using CO_2 as intermediate fluid, and then coated with gold-palladium. All samples were observed and photographed with a Philips XL30 scanning electron microscope from the Electron Microscopy Service of

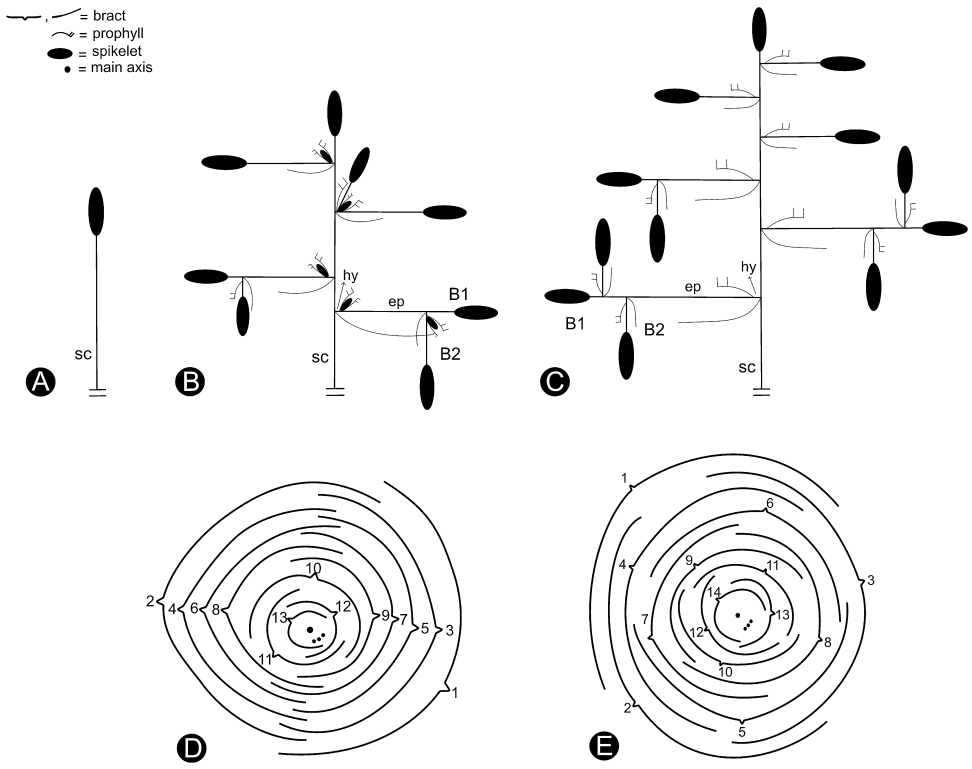

Fig. 1. Mature inflorescence structure in Abildgaardieae previously described by Reutemann et al. (2009) and Reutemann (2012). (A) Inflorescence with terminal spikelet, but without branches (=unispicate inflorescence). (B) Inflorescence with terminal spikelet, and normal and prophyllar branches, i.e., branches produced by the development of the axillary bud of a bract, or of a prophyll, respectively (=plurispicate inflorescence). (C) Inflorescence with terminal spikelet, and only normal branches (=plurispicate inflorescence). (D) Mixed symmetry inflorescence (=with the basal part somewhat bilateral, and the medial and distal portions radial), which bears bracts with variable phyllotaxis (being spirodistichous in the proximal region, and spiral in the medial and distal regions). (E) Radial symmetry inflorescence, which bears bracts with stable phyllotaxis (being spiral throughout the inflorescence). *Abbreviations*: B1, primary branch; B2, branch of second order; ep, epipodium; hy, hypopodium; sc, scape. Line length in the diagrams does not match the actual length of internodes. The ellipsis in (D) and (E) indicates the phyllotactic continuity for the rest of the distal bracts.

the "Bernardino Rivadavia" Natural Science Museum (Buenos Aires, Argentina).

Results

Vegetative growth and transition to the reproductive state

During the vegetative stage of all species studied, the shoot apical meristem (SAM) produces nomophyll primordia, which outgrow the SAM as they develop and envelop it completely (Figs. 2A and 3A). During this stage, the SAM shape in the different genera correlates with the initial leaf arrangement. Flat-shaped SAMs, composed of two opposite faces, which are typical for the studied species of *Fimbristylis*, produce vegetative leaf primordia in an almost distichous pattern (Figs. 2A, B and 3A, B; Table 3); while conical SAMs, with three roughly flat faces, characteristic for the studied species of *Bulbostylis*, generate nomophyll primordia on three planes (Figs. 2I and 4A; Table 3). However, between each plastochrone, the differentiating leaves twist slightly, which results in a spirodistichous nomophyll phyllotaxis instead of distichous in *Fimbristylis*, and a spirotristichous nomophyll phyllotaxis instead of tristichous in *Bulbostylis* (Figs. 2A, B, I; 3A, B; 5A, B and 6A, B; Table 3). In all the species studied, the SAM elongates above the latest leaf primordium after producing a variable number of nomophylls, and becomes an inflorescence meristem (IM), thus starting the reproductive stage (Figs. 2C, D, J; 3G and 4B).

Regardless of its shape during the vegetative stage, the SAM changes its appearance when it turns into an IM, consistently acquiring the shape of a dome (i.e., no flat faces) (Figs. 2J; 3G and 4B; Table 3). The change of shape of the apical meristem takes place later only in *F. ovata*, so the IM initially keeps the flat shape, which is typical of the SAM in the vegetative zone of this species (Fig. 2D), but following some activity time, it finally acquires the shape of a dome (Fig. 2E; Table 3). In all cases, the change of shape of the apical meristem occurs along with a change in the leaf initiation arrangement, which begins generating as a spiral (Figs. 2F, J, K; 3C, D; 4C, G, H; 5A, B and 6A, B; Table 3).

Development of the inflorescence main axis

Unispicate inflorescences

In the species with unispicate inflorescences covered in this study (Tables 1 and 2), the IM initially produces sterile bracts, and later produces fertile bracts (=glumes), each one bearing a floral meristem in its axil. Such glumes and their floral meristems initiate and differentiate acropetally.

Differences between *B. conifera* and *F. ovata* development occur when the apical meristem changes its shape, which occurs simultaneously with the beginning of the reproductive stage in *B. conifera*, but happens later in *F. ovata* (Fig. 2D and J; Table 3). This phenomenon determines the bract phyllotaxis to be stable (consistently spiral) in *B. conifera* throughout the inflorescence, but variable in *F. ovata* (i.e., spirodistichous at the beginning of the reproductive stage and later spiral) (Fig. 2G, H, L and M; Table 3).

Plurispicate inflorescences

In species with plurispicate inflorescences (Table 1), the IM activity begins with the production of bract primordia with branch meristems (BM) in their axils, which will later develop into each of the primary branches (Figs. 3C, D and 4C, D, G, H). Such bracts

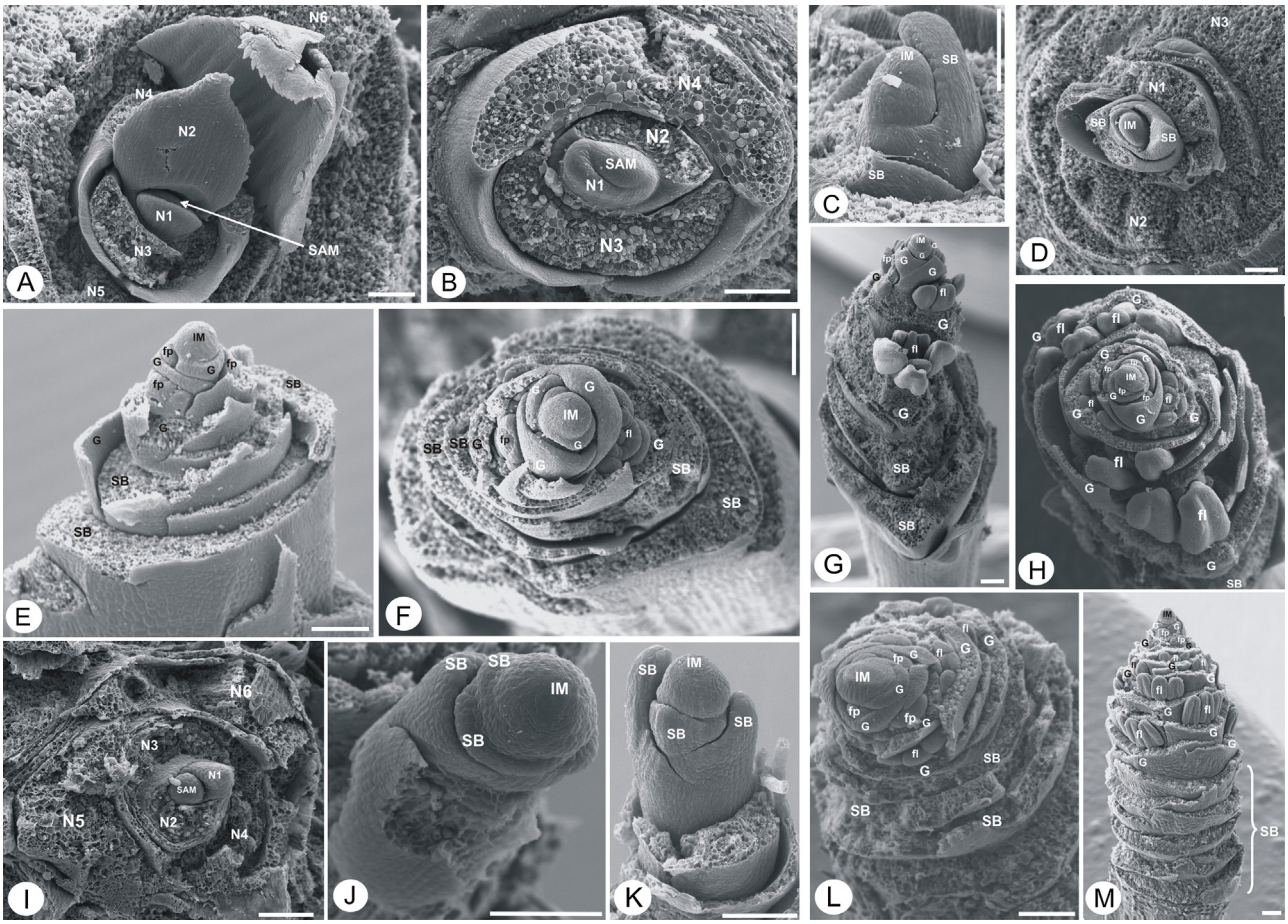

Fig. 2. Scanning electron micrographs of inflorescence development in *Fimbristylis ovata* (A–H) and *Bulbostylis conifera* (I–M). (A) Vegetative stage with the shoot apical meristem protected by the nomophylls that have just initiated. (B) Vegetative stage where the nomophylls have been removed and the flat apical meristem can be seen producing vegetative leaves on two planes. (C) Elongation of the apical meristem during transition to the flowering phase. (D) Early flowering phase with the inflorescence meristem keeping the flat shape that is typical of the apical meristem in the vegetative phase. (E) and (F) Early inflorescence development stage, when the inflorescence meristem already looks like a dome and produces organs in spiral fashion. (G) and (H) Next inflorescence development stage in which the mixed symmetry of the inflorescence may be clearly recognized, with a bilateral basal region, and radial medial and distal zones. (I) Vegetative phase where the shoot apical meristem has a conical shape and produces vegetative leaves on three planes. (J) Elongation of the apical meristem, initiating the flowering phase; note that the inflorescence meristem has a dome shape at an early time. (K) Early inflorescence development stage, with the dome-shaped inflorescence meristem producing organs in spiral fashion. (L) and (M) Inflorescence during later stages of development, with radial symmetry and stable phyllotaxis bracts. *Abbreviations*: SB, sterile bracts; fl, flower; fp, flower primordium; G, glume; IM, inflorescence meristem; N1–6, nomophylls 1–6; SAM, shoot apical meristem in vegetative state. Bar = 100 μm.

Table 3
Nomophyll and bract phyllotaxis, and shape of the apical meristems in Abildgaardieae.

Species	Phyllotaxis				Change of phyllotaxis on the main axis	SAM shape	IM shape
	Nomophylls	Br1 and B1	Br2 and B2 (and higher orders)	Glumes and sterile bracts			
B. communis	ST	S	[a]	S	ST–S	C	Do
B. conifera	ST	–	–	S	ST–S	C	Do
B. juncoides	ST	S	[a]	S	ST–S	C	Do
B. sphaerocephala	ST	S	[a]	S	ST–S	C	Do
F. autumnalis	SD	S	S	S	SD–S	F	Do
F. dichotoma	SD	S	S	S	SD–S	F	Do
F. ovata	SD	–	–	Proximal: SD, distal: S	SD–S	F	Initiation: F, next: Do
F. spadicea	SD	S	S	S	SD–S	F	Do
F. squarrosa	SD	S	S	S	SD–S	?	Do

Note: B1, primary branch; B2, secondary branch; Br1, primary bract; Br2, secondary bract; C, conical; Do, dome; F, flat; IM, inflorescence meristem; S, spiral; SAM, shoot apical meristem; SD, spiro-distichous; ST, spiro-tristichous; ?, no data.

[a] The phyllotaxis cannot be determined because there are not enough secondary branches (1–2 in *B. communis* and *B. juncoides*; 1–3 in *B. sphaerocephala*).

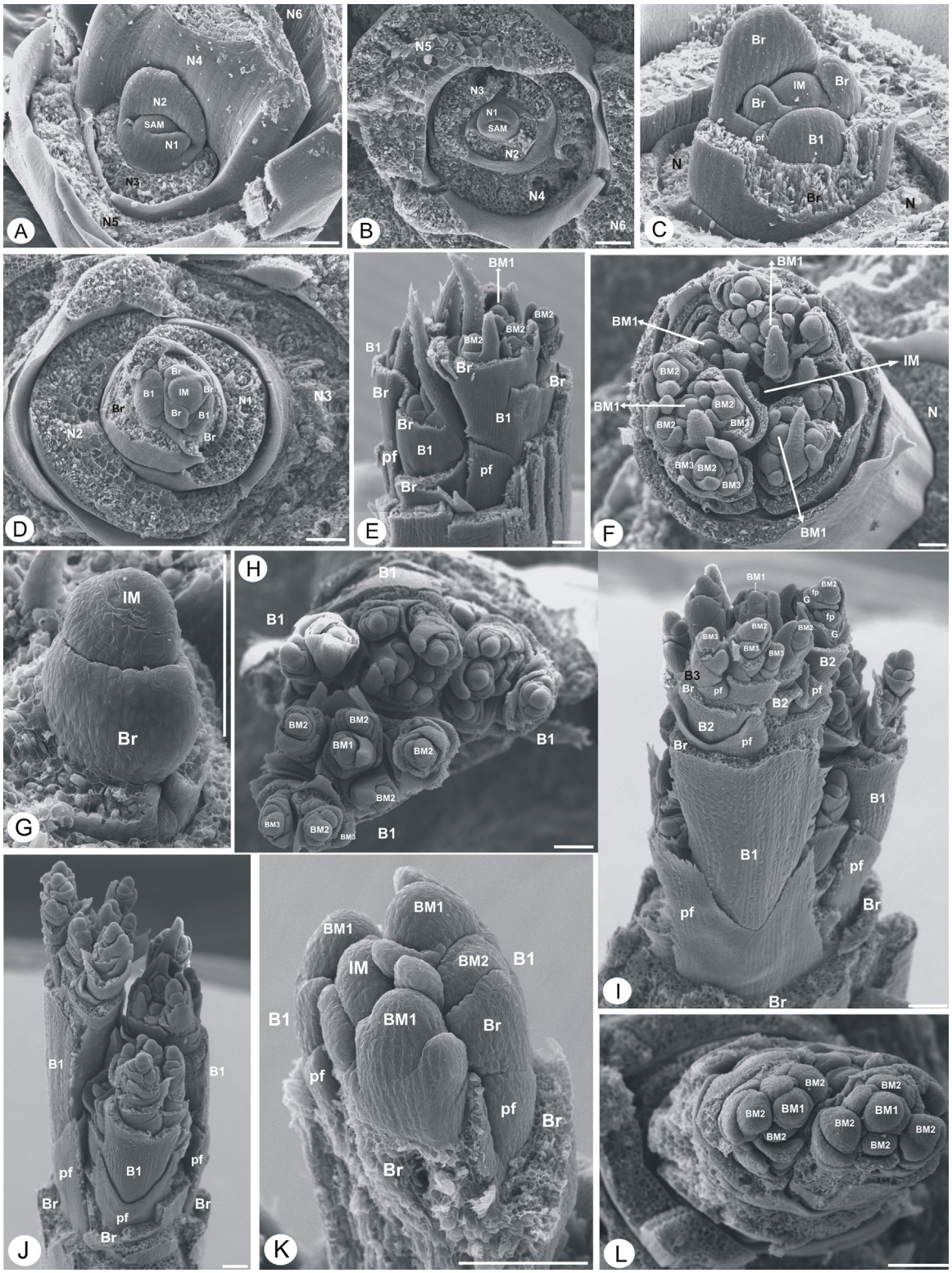

Fig. 3. Scanning electron micrographs of inflorescence development in *Fimbristylis spadicea* (A–F) and *F. autumnalis* (G–L). (A) and (B) Vegetative stage, when the flat shoot apical meristem produces nomophylls distichously, which cover the meristem early. (C) and (D) Early inflorescence development stage, with the dome-shaped inflorescence meristem producing bracts and primary branch meristems in acropetal and spiral fashion. (E) Differentiation of primary branches and initiation of second order branches. (F) Differentiation of second order branches and initiation of third order branches. (G) Elongation of the apical meristem, which adopts its dome shape during the transition to the flowering phase. (H–J) Advanced state of inflorescence development, where first, second and third order branches may be observed. (K) Initiation and differentiation of primary branches. (L) Initiation and differentiation of secondary branches. *Abbreviations*: B1, primary branch; B2, branch of second order; B3, branch of third order; BM1, primary branch meristem; BM2, branch meristem of second order; BM3, branch meristem of third order; Br, bract; fp, flower primordium; G, glume; IM, inflorescence meristem; N1–6, nomophylls 1–6; pf, prophyll; SAM, shoot apical meristem in vegetative state. Bar = 100 μm.

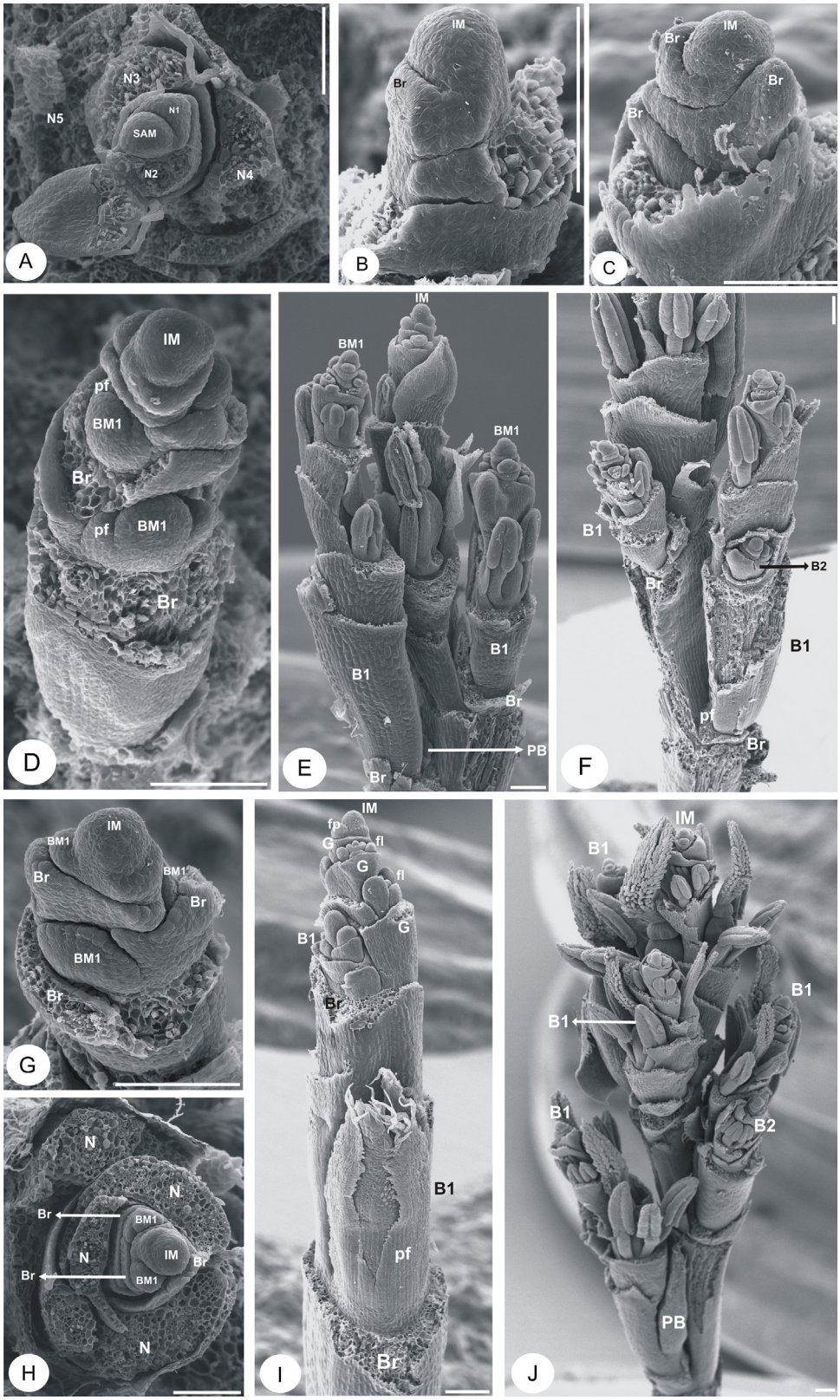

Fig. 4. Scanning electron micrographs of inflorescence development in *Bulbostylis communis* (A–F) and *B. juncoides* (G–J). (A) Vegetative stage, when the shoot apical meristem has a conical shape and produces vegetative leaves on three planes. (B) Elongation of the apical meristem, which adopts its dome shape during the transition to the flowering phase. (C) Early inflorescence development stage, with the dome-shaped inflorescence meristem producing bracts in spiral fashion. (D) Initiation of primary branches. (E) Differentiation of primary branches; the arrow indicates the initiation of a prophyllar branch at the base of a primary branch. (F) Initiation of secondary branches. (G) and (H) Early inflorescence development stage, with the dome-shaped inflorescence meristem producing bracts and primary branch meristems in acropetal and spiral fashion. (I) Early differentiation state of primary branches. (J) Advanced differentiation state of primary branches, and formation of secondary branches. *Abbreviations*: B1, primary branch; B2, branch of second order; BM1, primary branch meristem; Br, bract; fl, flower; fp, flower primordium; G, glume; IM, inflorescence meristem; N1–5, nomophylls 1–5; PB, prophyllar branch; pf, prophyll; SAM, shoot apical meristem in vegetative state. Bar = 100 μm.

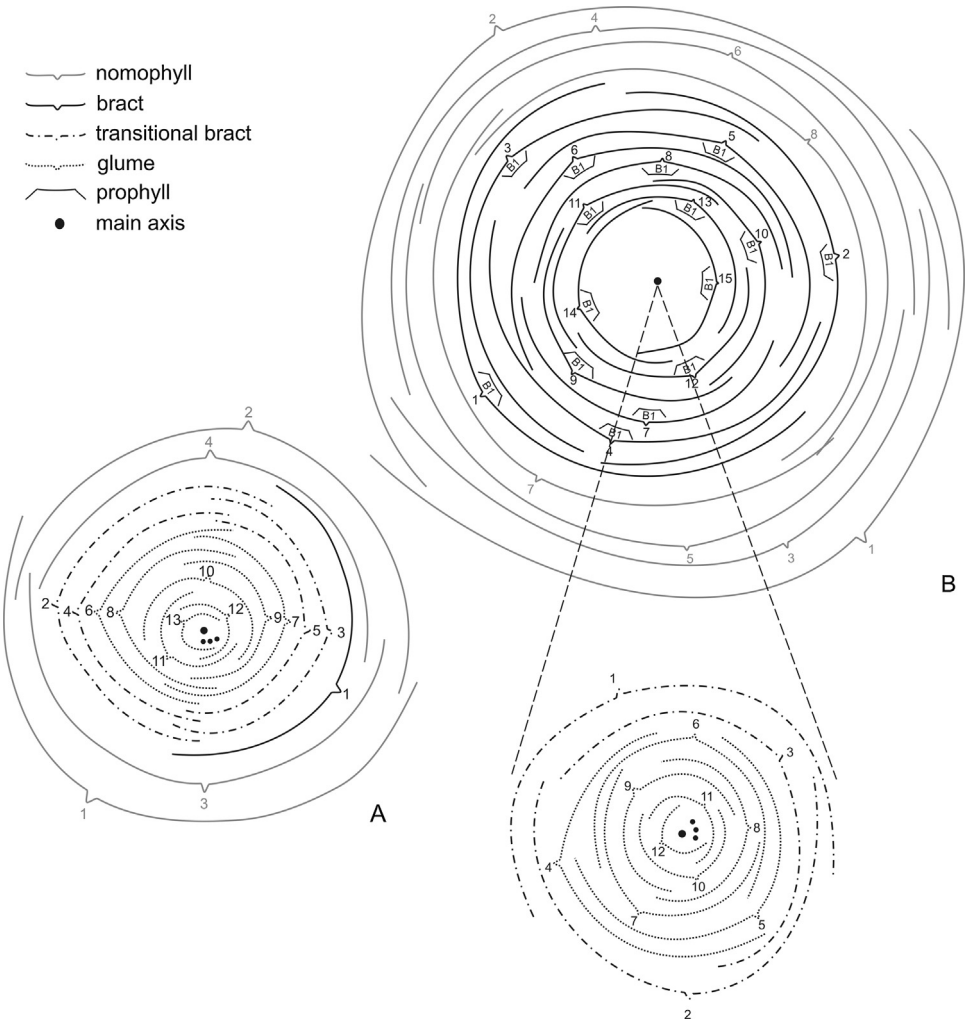

Fig. 5. Phyllotaxis of nomophylls and bracts on the plant main axis in *Fimbristylis ovata* (A) and *F. autumnalis* (B). The ellipsis indicates the phyllotactic continuity for the rest of the distal bracts; the portion in (B) between dotted lines is shown below because of space constraint. *Abbreviation*: B1, primary branch.

and their BM initiate acropetally and start differentiating (acropetal differentiation) as they are produced, while the IM continues its activity.

Coinciding with the initiation of the primary branches, the main axis internodes may or may not experience a slight elongation, which determines a different distance between the primary branch primordia. Among the studied species, only the inflorescences of *Bulbostylis* show an early elongation of the main axis internodes, because of which the differentiating primary branches are notoriously apart from one another, unlike what has been observed in species of *Fimbristylis* (Figs. 3D and 4D).

In all cases, following the production of a variable number of bracts and their branch meristems, the IM may or may not generate transitional bracts (i.e., having a mixed shape of a non-floriferous bract and a glume) with BM that initiate but remain vestigial, or they just do not develop. Finally, the IM starts forming glumes with floral meristems (FM) in their axils, which will together become the inflorescence terminal spikelet. Both the non-floriferous bracts and the transitional bracts and glumes develop in a helical pattern from a dome-shaped IM; this spiral is continuous in all the types of leaves generated by the IM on the main axis (Figs. 5B and 6B; Table 3).

Both in unispicate and plurispicate species, the IM stops its activity after forming the terminal spikelet on the main axis, but remains "open", that is to say, it does not end with the production of one terminal flower (Figs. 2H, M and 4E, J).

Development of the primary branches

The primary branch meristems begin their activity by initiating a prophyll and may then: (1) differentiate into a complex branch, that is, produce a variable number of bracts with axillary meristems of secondary branches, generate transitional bracts, and finally produce glumes and FM that will form the terminal spikelet on the primary branch (Figs. 3H–J and 4J, F); or (2) only develop the terminal spikelet on the primary branch, after forming, or not, transitional bracts (Fig. 4E, J).

Due to the fact that primary branches of the inflorescences initiate and differentiate acropetally, proximal branches usually become more differentiated (that is, more branched and reach a higher branching degree) than distal branches.

Development of the second- and third-order branches

Whenever secondary branches are observed in the inflorescences, they emerge firstly on the most proximal primary branch and continue initiating and differentiating on the higher primary branches of the inflorescence (Figs. 3E, K, L and 4F, J). On one single primary branch, secondary branches and their bracts initiate and differentiate acropetally, as it occurs with primary branches on the main axis (Fig. 3F, H–J, L). Regardless, whether the BM of the primary branch originates a complex branch or a branch reduced to

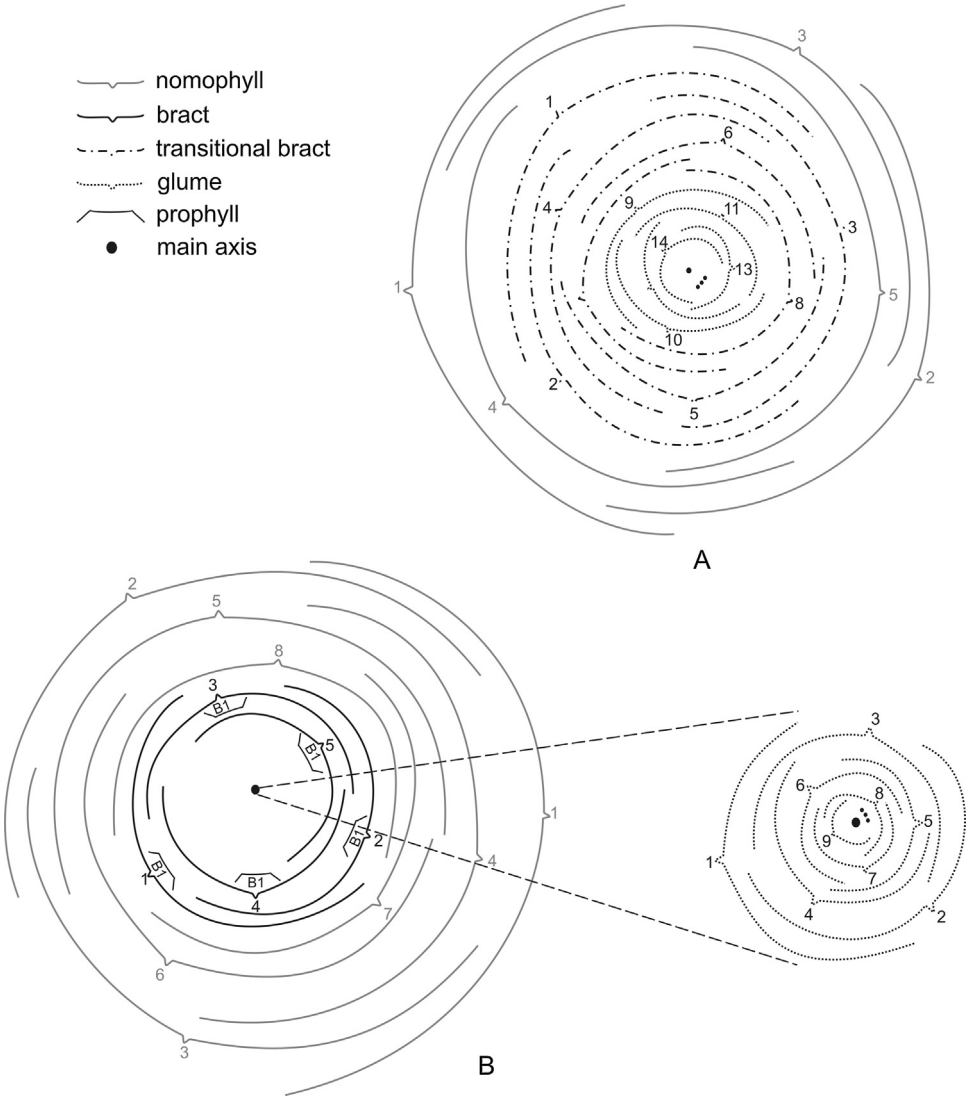

Fig. 6. Phyllotaxis of nomophylls and bracts on the plant main axis in *Bulbostylis conifera* (A) and *B. sphaerocephala* (B). The ellipsis indicates the phyllotactic continuity for the rest of the distal bracts; the portion in (B) between dotted lines is shown on one side because of space constraint. *Abbreviation*: B1, primary branch.

its terminal spikelet, it is always dome-shaped and the bracts it produces are arranged in one single helix (Table 3).

Within the studied species, whenever third-order branches are generated, they initiate and differentiate as previously mentioned for primary and secondary branches (Fig. 3F, H–J).

Development of prophylls and prophyllar branches

From a BM of any order, the prophyll initiates as two lateral protuberances, which then meet on a continuous edge on the adaxial side of the BM (Fig. 4D). This edge and both lateral protuberances lengthen, while another edge begins taking shape on the abaxial side of the developing branch. This second edge becomes thicker from the sides inwards until it finally becomes a continuous edge (Fig. 7A). The prophyll continues growing around the developing branch and gradually acquires its two-keeled form, with the lateral appendages projecting and two notches, one adaxial and the other abaxial, the latter always being more noticeable (Figs. 3E, I, J and 4I, J).

In the studied species with branches in the prophyll axil (Table 1), prophyllar branches emerge from a dome-shaped meristem (i.e., Prophyllar Branch Meristem, PBM), which begins its activity by producing a prophyll (within which a new PBM may form or not), and then generates bracts and their corresponding axillary meristems acropetally and spirally, just like the normal branch meristems do (Fig. 7A–D). In all cases, prophyllar structures initiate after the emergence of the normal inflorescence branches of highest order (2nd, this is observed both in *B. communis* and *B. juncoides*), and the fact that they are less differentiated than normal branches is possibly due to their late initiation (Fig. 4E, J). Nevertheless, prophyllar structures usually mature over time and may even bear fruit.

Late development of the inflorescence

Once all the structures that make up the inflorescence have initiated, the inflorescence begins emerging from the nomophylls as a consequence of the scape lengthening. With the emergence of the inflorescence, a differential lengthening of the internodes of branches of different orders takes place, based on the shape the inflorescence will eventually take. In capitate inflorescences, the epipodia of branches of all orders remain contracted, while they lengthen in anthelodia. Such elongation begins in primary branches and it may or may not reach secondary and tertiary branches.

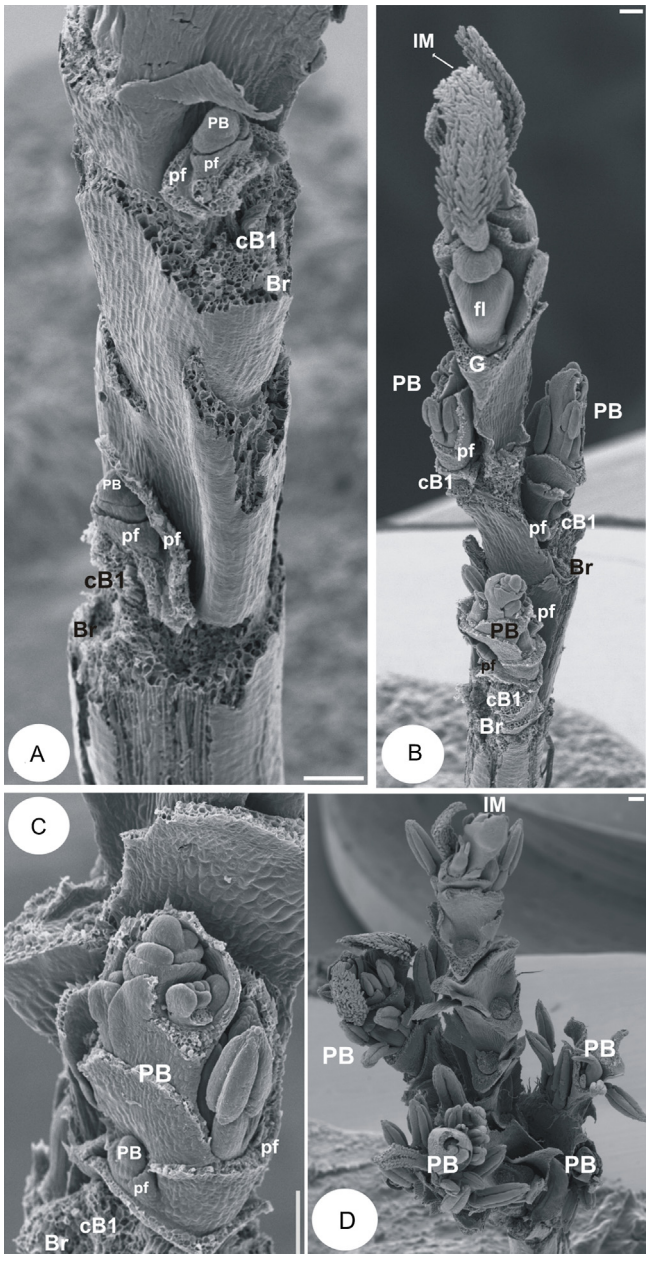

Fig. 7. Scanning electron micrographs of prophyllar branches development in *Bulbostylis juncoides*. (A) Early stages of prophyllar branch development. (B) and (C) Next prophyllar branch development stage. (D) Advanced differentiation state of prophyllar branches. *Abbreviations*: Br, bract; cB1, scar of primary branch; fl, flower; G, glume; IM, inflorescence meristem; PB, prophyllar branch; pf, prophyll. Bar = 100 μm.

Discussion

The morphology of a mature inflorescence is the end product of an array of contributing developmental processes (Vollbrecht and Schmidt, 2009), which are not always shared by similar adult inflorescences (Doust and Kellogg, 2002a, 2002b; Reinheimer, 2007; Reinheimer et al., 2009). In this regard, Doust and Kellogg (2002b) consider it may be preferable to look for homologies on the level of development rather than in the morphology of mature inflorescences. However, this does not seem to apply to Abildgaardieae, where similar adult inflorescences belonging to species in different clades follow shared ontogenetic development paths. Unispicate inflorescences of *B. conifera* and *F. ovata* show similar organogenesis, where the IM gives origin to foliar organs and axillary flowers that initiate and differentiate acropetally. On the other hand, plurispicate inflorescences of all the studied species show normal branches (of the first-, second- and third-order), which emerge and differentiate acropetally from dome-shaped BMs located in bract axils. Finally, species of different Abildgaardieae clades showing inflorescences with stable phyllotaxis and radial symmetry acquire such mature characteristics as a consequence of the existence of dome-shaped IMs that keep their shape unchanged throughout development. In view of this, given that similar characters of adult inflorescences among species of both Abildgaardieae clades are produced similarly, the mature inflorescence structure of this group of plants may be reliably used to establish correct primary morphological homologies.

Within one clade (clade 1), species of *Bulbostylis* with prophyllar productions also generate their prophyllar branches similarly: from dome-shaped axillary branch meristems (=PBM), which, like branch meristems, initiate their activity by generating a prophyll, and then produce organs in acropetal and helical manner. Nevertheless, despite the uniform development of inflorescences within Abildgaardieae, our studies have revealed stable differences in the timing of internode lengthening along the main axis among species of both clades. This heterochrony had already been observed by Guarise et al. (2012), who showed the taxonomic value of this character in *Cyperus*. But such heterochrony is first reported here for Abildgaardieae.

Regarding the variable phyllotaxis (spiro-distichous and then spiral) and mixed symmetry (bilateral in the basal part, and radial in the medial and distal portions) of *F. ovata* inflorescences, we found that this phenomenon is related to IM changing from a flat to a dome-shaped form during inflorescence development, which differs from all other species studied, where the IM remains (dome-shaped) unchanged throughout the reproductive stage. This connection between phyllotaxis and shape of the apical meristem might well be useful to account for phenomena such as the mixed phyllotaxis of the inflorescence branches of certain species of Abildgaardieae (e.g., *B. pilosa* (Willd.) Cherm, *B. laniceps* C. B. Clarke ex T. Durand and Schinz, *F. adenolepis* J. Kern, *F. cinnamometorum* (Vahl) Kunth, *F. fulvescens* (Thwaites) Thwaites, among others; Goetghebeur and Coudijzer, 1985; Haines and Lye, 1983; Kern, 1974) with spiral bracts and distichously-arranged glumes, simply as a result of a dome-shaped branch meristem shifting into a flat branch meristem.

In this study, in the vegetative zone, spirodistichous phyllotaxis is associated with flat meristems, while the spirotristichous phyllotaxis involves conical meristems. Some authors have already mentioned the apex shape as one of the factors affecting the initial position of new foliar primordia (Dengler, 1999; Kirchoff, 2000; Guarise et al., 2012). The position of new leaf formation depends both on the location of the preceding primordia and the availability of a minimum space or volume for the new primordium to become organized (Sachs, 1991). It has recently been proposed that there are peaks in auxin concentration in the plant apex, as determined by the PIN carrier proteins, regulated in turn by three redundant PLETHORA (PLT) proteins, which establish the sites where new organs will be formed in *Arabidopsis* (Reinhardt, 2005; Prasad et al., 2011). Parameters affecting the available space for new leaf formation, such as meristem size and extension growth, may influence phyllotaxis, because they indirectly influence auxin transport and the size of the field in which auxin operates (Reinhardt, 2005). In the species studied, the transition from a flat or conical meristem to a dome-shaped meristem might account for a similar effect in the phyllotaxis along the plant main axis.

Inflorescence phyllotaxis and symmetry had not been used as taxonomic and systematic characters in Cyperaceae up until the work by Guarise et al. (2012), who showed that, in the *Cyperus* genus, these characters are useful both in mature and in

developing inflorescences. Now, the results of this study also show that the phyllotaxis and the shape of the apical meristem in the vegetative stage and at the beginning of the reproductive stage provide additional data which are likely to be useful for studies within Cyperaceae.

As result of our first comparative analysis of the development of inflorescences in Abildgaardieae, we have been able to identify two new morphological characters that could support phylogenetic relationships within Abildgaardieae: (1) shape of the SAM, and phyllotaxis, (2) heterochrony of internodes lengthening along the main axis. The spirodistichous phyllotaxis (associated with flat meristems) of nomophylls in *Fimbristylis*, on the one hand, and the spirotristichous phyllotaxis (associated with conical meristems) of nomophylls in *Bulbostylis*, on the other hand, support the separation of both genera. In the same regard, the early lengthening of the main axis internodes in the plurispicate inflorescences of *Bulbostylis*, as opposed to the absence of such internode lengthening in the inflorescences of *Fimbristylis*, is a distinguishing character between both genera. Additionally, there is no evidence based on inflorescence development to support the position of *Abildgaardia* as an individual genus; instead, our findings support a close relationship between *Abildgaardia* and *Fimbristylis*, which is in line with the current proposal to consider them as one single genus (Govaerts et al., 2007).

Acknowledgements

We would like to thank F. Tricarico for his assistance with SEM photography, and also A. Amsler for her assistance in the preparation of Figs. 5 and 6. Funding was provided by Agencia Nacional de Promoción Científica y Tecnológica – PICT 464 to A. C. Vegetti, and Universidad Nacional del Litoral – CAID+D 2011 to A. G. Reutemann.

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