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Structure of the inflorescences of selected South American species of *Abildgaardia* Vahl, *Bulbostylis* Kunth, and *Fimbristylis* Vahl (Abildgaardieae-Cyperoideae-Cyperaceae)

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Abstract Abildgaardieae poses several taxonomic challenges, because there is no general agreement on its circumscription and infrageneric divisions. With the objective of providing data with taxonomic and phylogenetic value, the structures of the inflorescences of *Abildgaardia*, *Bulbostylis*, and *Fimbristylis* were analyzed following the methodology and terminology of Troll's school. The inflorescences studied are polytelic and may comprise only the main florescence or may also show a paracladial zone below it. They are unispiculate, anthela-like, or capitate, and can be terminal, pseudolateral, or in an intermediate position. Normal and prophyllar branching patterns are observed. The acropetal reduction in the order and number of ramifications, and the length of bracts and prophylls were recorded. Foliose structures with an intermediate form between a setaceous bract and a glume are frequently found at the spikelet base. Hypotheses of the homology of these structures, and a list of inflorescence characteristics and character states are presented. The branching pattern of the inflorescence seems to be the main characteristic with potential taxonomic and phylogenetic implications at genus level. The rest of the characteristics could possibly be useful for infrageneric divisions.

Keywords Inflorescences · *Abildgaardia* · *Bulbostylis* · *Fimbristylis* · Typology · Branching pattern · Systematics

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Introduction

The tribe Abildgaardieae comprises about 420 species (Goetghebeur 1998) which are mainly distributed in the tropical and temperate regions of Africa, Australia, Asia, and America (Goetghebeur and Coudijzer 1984; Gordon-Gray 1971). Based on morphological (Bruhl 1995) and combined morphological and DNA sequence data (Muasya et al. 2000), this tribe appears as a monophyletic group with moderate to weak support. However, analyses based only on DNA sequence data portray Abildgaardieae as non-monophyletic and closely related to the tribe Arthrostylideae (Ghamkhar et al. 2007; Muasya et al. 1998, 2009; Simpson et al. 2007).

Abildgaardieae poses several taxonomic problems and there is no general agreement on its circumscription and infrageneric divisions (Bruhl 1995; Ghamkhar et al. 2007; Muasya et al. 1998, 2000; Simpson et al. 2007). According to several authors, the tribe Abildgaardieae consists of six or seven genera (Bruhl 1995; Goetghebeur 1998; Goetghebeur and Coudijzer 1984). Among those genera, *Abildgaardia*, *Bulbostylis*, and *Fimbristylis* have posed difficulties for morphological delimitation. To distinguish them, different characteristics have been used, including deciduous or persistent style-base, embryo type, shape and size of the fruits, fruit wall ornamentation, phyllotaxy of the glumes, shape and size of the spikelets, presence or absence of long hairs within the orifice of the leaf sheath, and shape and structure of the inflorescences (Haines and Lye 1983; Goetghebeur and Coudijzer 1984, 1985; Guaglianone 1970; Lye 1973, 1974a, 1974b, 1981, 1982, 1983; Pedersen 1969; Svenson 1957; Van der Veken 1965). However, the fact that *Abildgaardia*, *Bulbostylis*, and *Fimbristylis* share many of those characteristics (Barros 1947; Kral 1971; Prata and López 2003) has led some authors such as Bentham (1883)

and Koyama (1961) to consider them as one single genus, namely *Fimbristylis* s.l. At present, molecular phylogenetic data support the division of *Abildgaardia*, *Bulbostylis*, and *Fimbristylis*, but the relationships among these genera are still unclear (Ghamkhar et al. 2007). Molecular phylogenetic analyses of the family Cyperaceae (Muasya et al. 1998, 2000, 2009; Simpson et al. 2007) depict *Abildgaardia* and *Fimbristylis* as more closely related to each other than to the genus *Bulbostylis*—an observation also shared by Ghamkhar et al. (2007). According to Ghamkhar's work, *Fimbristylis* is paraphyletic, and seems to be related to some *Crosslandia* and *Abildgaardia* species, whereas *Bulbostylis* is monophyletic and sister to the other Abildgaardieae, or Abildgaaardieae + Arthrostylideae. This work by Ghamkhar et al. (2007) is the only hypothesis available concerning molecular phylogeny for the tribe Abildgaardieae, although it is mostly limited to Australian taxa. No molecular phylogenetic cladogram is available for species included in Own's study.

Although several authors (e.g., Gordon-Gray 1971; Lye 1973) have questioned the use of inflorescence characteristics for morphological delimitations of taxa, research on inflorescence structure has clarified several morphological homology questions (Heinzen and Vegetti 1994; Guaglianone 1970; Guarise and Vegetti 2007; Mora-Osejo 1960, 1987; Vegetti 1992, 1994). In this sense, Troll's typology, enriched by the ideas of several authors, for example Weberling, Kukkonen, Rua and Vegetti, has proven useful for describing inflorescences (Mora-Osejo 1987; Rua 1999) and for providing characteristics with phylogenetic and taxonomic value (Aagesen 1999; Cavalcanti and Rua 2008; Guarise and Vegetti 2008; Liu et al. 2005; Nickol 1995; Rua and Aliscioni 2002; Tortosa et al. 2004). Our study is a first step toward a re-evaluation of inflorescence structure in species of *Abildgaardia*, *Bulbostylis*, and *Fimbristylis*, which we intend to carry out by:

1 describing, by means of the typological terminology, the inflorescence structure of species belonging to these three challenging genera; and
2 providing characteristics which may be useful for the purposes of taxonomic and cladistic studies.

Materials and methods

Inflorescences of species of *Abildgaardia*, *Bulbostylis*, and *Fimbristylis* sensu Barros (1947), with the subsequent contributions made by López (1996) and López et al. (2007) regarding *Bulbostylis*, and those made by Adams (1994) in connection with *Fimbristylis* (Table 1) were examined and a series of characteristics related to the

inflorescence were recorded (Tables 2, 3, 4). Inflorescences were either obtained from herbarium specimens (BA, BAA, CORD, CTES, and SF) or collected in the field, and samples were preserved in 70% ethanol. Dry material was boiled in water for a short period. Mature inflorescences were dissected under a Nikon SMZ-10 stereoscopic microscope, and photographed using a Nikon Coolpix 990 digital camera. The number of spikelets and branches of first, second, third, etc. order were counted (Table 3).

For the typological interpretation, the terminology followed Troll (1964), Weberling (1985, 1989), Kukkonen (1994), Rua (1999), and Vegetti (2003).

Results

In all the species studied the following zones can be distinguished on the whole plant: innovation zone (IZ), inhibition zone (HZ), and the inflorescence or unit of inflorescence (UIF) (Fig. 1a). The IZ bears reduced leaves with axillary buds, which produce new shoots with a similar structure to that of the mother shoot. Above this region is the HZ, which shows well-developed leaves with axillary buds that do not develop. The internode above the distal vegetative leaf often elongates, forming the scape, which still belongs to the inhibition zone. In the distal portion of the shoot is the UIF, formed by the terminal spikelet of the main axis (main florescence HF) and, in most cases, by the paracladial zone (PZ) below it (Fig 1b–d). Important qualitative and quantitative inflorescence data representative of the species of Abildgaardieae studied are listed in Tables 2 and 3.

The inflorescences are constituted only by the HF (*Abildgaardia ovata*, *Bulbostylis capillaris* var. *microstachys*), by the HF and a PZ reduced to buds (*B. brevifolia*), or, more commonly, by the HF and a well-developed PZ (Table 2; Fig. 2). The PZ is generally divided into a subzone of short paraclades (sPZ) and a subzone of long paraclades (lPZ), but at times it can be constituted only by the sPZ or only by the lPZ (Table 2; Fig. 2).

The inflorescences are unispiculate (Fig. 3a, b) or, more commonly, paucispicate or plurispicate (Table 3; Fig. 3c–j). The latter have either an anthela-like shape (anthelodium; indeterminate inflorescences) or they can be reduced to a more or less contracted head, like a capitulum (Fig. 3; Table 2). The anthelodium can be lax or congested and can have paraclades of first (simple anthelodium), second (compound anthelodium), and even third order (decompound anthelodium) with an evident epipodium. The capituliform inflorescence does not have developed epipodia.

As regards the position of the inflorescence in relation to the scape, both terminal inflorescences, with the main axis following the same direction as the scape, and

Table 1 Material studied

Abildgaardia Vahl

  Abildgaardia ovata (Burm. f.) Kral: A.G. Reutemann 33; 54 (SF); M.G. López and A.G. Reutemann 377 (CTES); Krapovickas A. et al. 21531; Parodi 9803 (BAA); Venturi S. 2823 (BA); Yörgensen 2870

Bulbostylis Kunth

  Bulbostylis brevifolia Palla: M.G. López et al. 338; Vanni et al. 4598 (CTES)

  B. capillaris (L.) C.B. Clarke var. *capillaris* Barros: Castellanos 34353a (BA); Arbo 8665; Vanni et al. 4540 (CTES)

  B. capillaris (L.) C.B. Clarke var. *contracta* (Kük. ex Osten) Barros: Núñez J. A. 28210 (BA)

  B. capillaris (L.) C.B. Clarke var. *elatior* (Griseb.) Osten: Castellanos 33477; Agusti E. 91737 (BA)

  B. capillaris (L.) C.B. Clarke var. *microstachys* (Boeck.) Barros: M.G. López and R. Vanni 382 (CTES)

  B. major Palla: M.G. López et al. 250; 251(CTES)

  B. consanguinea (Kunth) C.B. Clarke: Yörgensen P. 3314 (BA)

  B. hirtella (Schrad. ex Schult.) Urb.: M.G. López et al. 270 (CTES)

  B. juncoides (Vahl) Kük. ex Herter var. *ampliceps* Kük. ex Osten: Castellanos 10314; Daella Jurado 22475 (BA)

  B. juncoides (Vahl) Kük. ex Herter var. *juncoides*: Boelcke and Nicora 8109 (BAA); Vanni et al. 4563 (CTES)

  B. juncoides (Vahl) Kük. ex Herter var. *lorentzii* (Boeck.) Kük. ex Osten: Castellanos 17151; Niederlein G. 6036 (BA); Parodi L. R. 6900 (BAA); Vanni et al. 4595, 4574 et al. (CTES); ejemplar no. 6027 (CORD)

  B. rugosa M. G. López: M.G. López 104 (CTES)

  B. scabra (J. Presl & C. Presl) C.B. Clarke: Arbo 8672-2; 8719 (CTES); M.G. López et al. 187 (CTES)

  B. sphaerocephala (Boeck.) C.B. Clarke: Vanni 4616 (CTES)

Fimbristylis Vahl

  Fimbristylis autumnalis (L.) Roem. & Schult.: Ejemplars no. K67, 16985 y 10049 (CORD)

  F. complanata (Retz.) Link.: M.G. López and A.G. Reutemann 375; 361 (CTES)

  F. dichotoma (L.) Vahl: M.G. López and A.G. Reutemann 376; Vanni and A.G. Reutemann 4630 (CTES)

  F. spadicea (L.) Vahl: Yörgensen P. 2871 (BA); M.G. López 371 (CTES)

  F. squarrosa Vahl: M.G. López and A.G. Reutemann 374 (CTES)

pseudolateral inflorescences, with the lower bract and their paraclade pointing to the same direction as the scape and thus turning the main axis aside (Table 2), may be observed. Intermediate dispositions between the above-mentioned are also frequent in inflorescences.

The shape and length of the bracts and prophylls are variable. Within the same inflorescence, the bracts vary from setiform and well-developed to glumaceous and reduced toward the apex of the inflorescence and toward the distal portion of each paraclade, whereas the prophylls vary from tubular and well-developed to glumaceous and more reduced. The branching order and the number and length of the paraclades also reduce toward the apex of the inflorescence and toward the distal portion of each paraclade (Fig. 2b, c, 3c–j).

The paraclades can originate from (Table 2; Fig. 4):

1 axillary buds of the bracts disposed over the main axis or over the long paraclades (normal branching);
2 axillary buds of the prophylls (prophyllar branching); and/or
3 accessory buds, which generate paraclades between a normal branch and its bract.

The prophyllar productions can be represented by the following structures (Fig. 4d–j):

1 one small bud (in most cases);
2 a sessile spikelet with or without a bud, or a vestigial spikelet in the axil of its prophyll; or
3 a more complex system formed by normal and prophyllar ramifications.

Commonly within the same species, same variety, and even in the same inflorescence are prophyllar productions represented by 2 or 3 of these structures (Table 2).

In the inflorescences of *Bulbostylis* and *Fimbristylis*, the paraclades are generally disposed in a spiral arrangement. The disposition of the paraclades can follow a right-handed or left-handed spiral and generally exhibits a homodromic arrangement where both the primary paraclades and the secondary paraclades spiral in the same manner (Fig. 5). However, primary and secondary paraclades with anti-dromic arrangement can sometimes be observed.

In *Abildgaardia ovata* and in the species of *Fimbristylis* studied the spikelets usually have wingless rachilla (Table 4). In *Bulbostylis,* the rachilla bears expansions but these are smaller than in the other two genera (Table 4). Most species show, at the base of the spikelets, foliose structures with an aspect that is intermediate between a setaceous bract and a glume, with the more distal ones resembling glumes to a greater extent (Fig. 6a–i). Such

Table 2 Qualitative inflorescence data for *Abildgaardia*, *Bulbostylis*, and *Fimbristylis*

Species	Shape of the inflorescence	Structure of the inflorescence	Ramification patterns	Prophyllar structures	Position of the inflorescence	Maximum order normal ramification[a]	Maximum order prophyllar ramification[b]
Abildgaardia ovata	Unispiculate or [c]simple anthelodium	HF or HF + PZ (PZ only with sPZ)	Normal	–	Pseudolateral Terminal	1°	–
B. brevifolia	Unispiculate; simple, compound or decompound anthelodium	HF + PZ (PZ reduced to a b, with sPZ + IPZ, or only with sPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll	Pseudolateral	3°	4°
B. capillaris var. *capillaris*	Simple or [c]compound anthelodium	HF + PZ (PZ with sPZ + IPZ, or only with sPZ)	Normal and Prophyllar	b	Pseudolateral [c]Terminal	2°	3°
B. capillaris var. *contracta*	Fascicle of spikelets; simple or [c]compound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll	Pseudolateral Terminal	2°	3°
B. capillaris var. *elatior*	[c]Simple or compound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll, or fsc of sp	Pseudolateral Terminal	2°	4°
B. capillaris var. *microstachys*	Unispiculate or simple anthelodium	HF or HF + PZ (PZ only with sPZ)	Normal	–	Pseudolateral	1°	–
B. major	Compound or decompound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b	Pseudolateral Terminal, and Pseudolateral-Terminal	3°	4°
B. consanguinea	Simple anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b	Pseudolateral [c]Terminal	1°	3°
B. hirtella	[c]Compound or decompound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar (and perhaps Accessory)	b	Pseudolateral [c]Terminal	3°	4°
B. juncoides var. *ampliceps*	Simple anthelodium	HF + PZ (PZ with sPZ + IPZ, or only with IPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll, or fsc of sp	Pseudolateral Terminal	1°	2°
B. juncoides var. *juncoides*	Capitate	HF + PZ (PZ with sPZ + IPZ, or only with sPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll	Pseudolateral Terminal	–	3°
B. juncoides var. *lorentzii*	Capitate	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll, or fsc of sp	Pseudolateral [c]Terminal	–	4°
B. rugosa	Compound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll	Pseudolateral Terminal	2°	3°

Table 2 continued

Species	Shape of the inflorescence	Structure of the inflorescence	Ramification patterns	Prophyllar structures	Position of the inflorescence	Maximum order normal ramification[a]	Maximum order prophyllar ramification[b]
B. scabra	Compound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b, or sp with b or other sp in the axil of its prophyll, or fsc of sp	[c]Pseudolateral Terminal	2°	4°
B. sphaerocephala	Capitate	HF + PZ (PZ with sPZ + IPZ)	Normal and Prophyllar	b	Terminal	–	3°
F. autumnalis	[c]Compound or decompound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal	–	Pseudolateral	4°	–
F. complanata	[c]Compound or decompound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal	–	Pseudolateral	5°	–
F. dichotoma	Simple, compound or decompound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal	–	Pseudolateral and Pseudolateral-Terminal	3°	–
F. spadicea	Simple, compound or decompound anthelodium	HF + PZ (PZ with sPZ + IPZ, or only with sPZ)	Normal	–	Pseudolateral [c]Terminal	3°	–
F. squarrosa	Compound anthelodium	HF + PZ (PZ with sPZ + IPZ)	Normal	–	Pseudolateral	2°	–

HF, main florescence; PZ, paracladial zone; sPZ, subzone of short paraclades; IPZ, subzone of long paraclades; b, bud; sp, spikelet; fsc, fascicle; Prllar, prophyllar

[a] Only paraclades with evident epipodium are considered

[b] Prophyllar buds are also considered

[c] Less frequently

Table 3 Quantitative inflorescence data for *Abildgaardia*, *Bulbostylis*, and *Fimbristylis* (measurements in cm)

Species	No. spikelets	Spikelet length	No. pc 1°ᵃ	No. pc 2°ᵃ	No. pc 3°ᵃ	No. pc 4°ᵃ	No. pc 5°ᵃ	Length ep of first pc1°	Length of the lowermost bract	Length of the uppermost bract	Length of the lowermost prophyll	Length of the uppermost prophyll
Abildgaardia ovata	Low	Long-medium	Low	0	0	0	0	Short	Short	?	Short-medium	?
B. brevifolia	Low	Medium-short	Low	0-low	0-low	0	0	Short-medium	Short	Medium-long	Medium	Medium-long
B. capillaris var. *capillaris*	Low	Medium-short	Low	0-low	0	0	0	Short	Short	Medium-long	Short-medium	Medium
B. capillaris var. *contracta*	Low	Medium-short	Low	0-low	0	0	0	Short	Short	Medium-long	Short-medium	Medium
B. capillaris var. *elatior*	Low	Medium-short	Low-medium	0-low	0	0	0	Short	Short	Medium-long	Medium	Medium-long
B. capillaris var. *microstachys*	Low	Short	Low	0	0	0	0	Short	Short	Long	Short	Medium
B. major	Medium-low	Medium-short	Low	Low-medium	0-low	0	0	Short-long	Short-long	Long	Medium-long	Long
B. consanguinea	Low	Medium-short	Low	0	0	0	0	Medium	Medium-long	Long	Medium-long	Long
B. hirtella	Medium-low	Short	Medium	Low-high	0-low	0	0	Short-medium	Short-medium	Short-medium	Medium	Medium
B. juncoides var. *ampliceps*	Low	Medium-short	Low-medium	0	0	0	0	Short	Short-medium	Long	Medium	Medium
B. juncoides var. *juncoides*	Low	Medium-short	0	0	0	0	0	0	Short	Medium-long	Medium	Medium
B. juncoides var. *lorentzii*	Medium-low	Medium-short	0	0	0	0	0	0	Short	Medium-long	Medium	Medium
B. rugosa	Low	Long-medium	Low-medium	Low	0	0	0	Short	Short	Long	Medium	Medium-long
B. scabra	Low	Medium-short	Low-medium	Low	0	0	0	Short	Short	Medium-long	Medium	Medium-long
B. sphaerocephala	Medium-low	Short	0	0	0	0	0	0	Short-medium	?	Medium	Short-medium
F. autumnalis	Very high-medium	Medium-short	Medium	Medium	0-medium	0-medium	0	Short-long	Short-medium	Medium	Medium	Medium-long
F. complanata	Very high-medium	Medium-short	Medium-high	Low-high	0-high	0-high	0–1	Short-long	Medium-long	Medium	Medium	Short-medium
F. dichotoma	Low	Medium-short	Low-medium	0-low	0-low	0	0	Short-medium	Short-medium	Medium-long	Medium	Medium
F. spadicea	Low	Medium-short	Low-medium	0-low	0-low	0	0	Short-medium	Short-medium	Medium	Medium	Medium

Table 3 continued

Species	No. spikelets	Spikelet length	No. pc 1°ᵃ	No. pc 2°ᵃ	No. pc 3°ᵃ	No. pc 4°ᵃ	No. pc 5°ᵃ	Length ep of first pc1°	Length of the lowermost bract	Length of the uppermost bract	Length of the lowermost prophyll	Length of the uppermost prophyll
F. squarrosa	Low	Medium-short	Low-medium	Low	0	0	0	Short-medium	Short-medium	Medium-long	Medium	Medium-long

No. spikelets: low 1–49, medium 50–99, high 100–149, very high 150–200; Spikelet length: short 0.1–0.49, medium 0.5–0.99, long 1–1.5; No. pc 1°: low 1–6, medium 7–13, high 14–21; No. pc 2°: low 1–23, medium 24–47, high 48–72; No. pc 3°: low 1–31, medium 32–63, high 64–96; No. pc 4°: low 1–9, medium 10–19, high 20–30; Length ep of first pc1°: short 0.1–1.69, medium 1.7–3.3, long 3.4–5.1; Length of the lowermost bract: short 0.1–2.49, medium 2.5–4.99, long 5–7.5; Length of the uppermost bract: short 0.03–0.13, medium 0.14–0.27, long 0.28–0.42; Length of the lowermost prophyll: short 0.03–0.24, medium 0.25–0.49, long 0.5–0.75; Length of the uppermost prophyl:l short 0.03–0.09, medium 0.1–0.19, long 0.2–0.3

No., number of; 1°, 2°, …, order of ramification; pc, paraclade; ep, epipodium; ?, unknown date

ᵃ Only paraclades with evident epipodium are considered

structures may be absent in some species (*Bulbostylis juncoides*), but this is not often the case. When they are present, they may be empty, bear a bud in their axil, or a paraclade with a slightly developed epipodium (Table 4); these productions seem to be protected by a glumaceous prophyll. In some cases, said foliose structures bear a flower in their axils (*B. capillaris* var. *microstachys* and *Fimbristylis squarrosa*) (Fig. 6j, k). In *Bulbostylis* and *Fimbristylis*, the glumes also show a spiral disposition; also, the basal foliose structures of the spikelet appear to respect the spiral-wise sequence of the glumes as much as the spiral arrangement of the proximal ramifications of the axis on which they are found (Fig. 5). If these ramifications are not present (in short paraclades), the foliose structure is always situated opposite to the prophyll of the axis that bears it (Fig. 6d–h). In *Abildgaardia*, the basal foliose structures of the spikelet and the lower glumes are disposed in a distichous fashion whereas the upper glumes are disposed in a spiral arrangement (Fig. 6a, b).

Discussion

The morphological diversity that may be observed in the inflorescences of the species studied is mainly because of (Tables 2, 3; Figs. 2, 3, 4):

1. the presence or absence of PZ and its subdivision into an sPZ and an lPZ;
2. the number and maximum branch degree of the paraclades;
3. the branching patterns;
4. the internode length of the paraclades and the main axis; and
5. the position of the inflorescence.

In all species the inflorescences are polytelic (indeterminate), as in most Cyperaceae (Alves et al. 2000; Heinzen and Vegetti 1994; Guarise and Vegetti 2008; Kukkonen 1984, 1986; Vegetti 1992, 1994; Vegetti and Tivano 1991; Vrijdaghs 2006; Vrijdaghs et al. 2003, 2004, 2005a, 2005b, 2007), and monocotyledonous (Alves 2000; Weberling 1985). The HF is always present, thus the inflorescences are heterothetic (Rua 1999), i.e., non-truncate. They have both homocladic inflorescences (Rua 1999), which are always unispiculate, and heterocladic inflorescences (Rua 1999), formed by the HF and the PZ.

In the PZ, the acropetal reduction of the order of ramification, number, and length of the paraclades is a common feature in the family (Browning and Gordon-Gray 1999; Haines 1966; Heinzen and Vegetti 1994; Kukkonen 1984, 1986; Vegetti 1992, 1994, 2003; Vegetti and Tivano 1991). The phyllotaxis of normal paraclades is similar to that observed by Guarise and Vegetti (2007) for *Cyperus* L.

Table 4 Flower and spikelet data for *Abildgaardia*, *Bulbostylis*, and *Fimbristylis*

Species	Duration style base	Style-branches	Achene shape	No. stamens	No. fertile glumes	No. foliose "glumaceous-bractiform" structures and production in their axils	Rachilla
Abildgaardia ovata	Deciduous	3	Trigonous	3	Low	3 or more, empty	Winged
B. brevifolia	Persistent	3	Trigonous	3	Medium-low	1, empty or with a bud	Winged
B. capillaris var. *capillaris*	Deciduous	3	Trigonous	2	Low	1–2, empty or with a bud, a sp or a pc with evident ep	Winged
B. capillaris var. *contracta*	Persistent	3	Trigonous	2–3	Medium-low	1, empty or with a bud	Winged
B. capillaris var. *elatior*	Deciduous	3	Trigonous	2	Low	1, empty or with a bud	Winged
B. capillaris var. *microstachys*	Deciduous	3	Trigonous	3	Low	1–2, the lowermost: empty or with a bud; the uppermost: flower	Winged
B. major	Persistent	3	Trigonous	3	Low	1–2, empty or with a bud	Winged
B. consanguinea	Persistent	3	Trigonous	3	Low	1, empty or with a bud	No winged
B. hirtella	Persistent	3	Trigonous	2	Low	1–2, empty or with a bud, a sp or a pc with evident ep	Winged
B. juncoides var. *ampliceps*	Persistent	3	Trigonous	3	Medium	0	Winged
B. juncoides var. *juncoides*	Persistent	3	Trigonous	3	Low	0	Winged
B. juncoides var. *lorentzii*	Persistent	3	Trigonous	3	Low	0	Winged
B. rugosa	Persistent	3	Trigonous	3	Medium	1–2, empty	No winged
B. scabra	Persistent	3	Trigonous	2–3	Low	1, empty or with a bud	Winged
B. sphaerocephala	Persistent	3	Trigonous	3	Low	?	Winged
F. autumnalis	Deciduous	3	Trigonous	1–3	Low	1, empty or with a bud	Winged
F. complanata	Deciduous	3	Trigonous	1–3	Medium-low	1, empty or with a bud	Winged
F. dichotoma	Deciduous	2	Lenticular	1–2	High-low	1-2-3, empty	Winged
F. spadicea	Deciduous	2	Lenticular	2–3	Medium-low	1-2-3, empty	Winged
F. squarrosa	Deciduous	2	Lenticular	1	High	1–2, flower	No winged

No. fertile glumes: low 1–18, medium 19–37, high 38–57

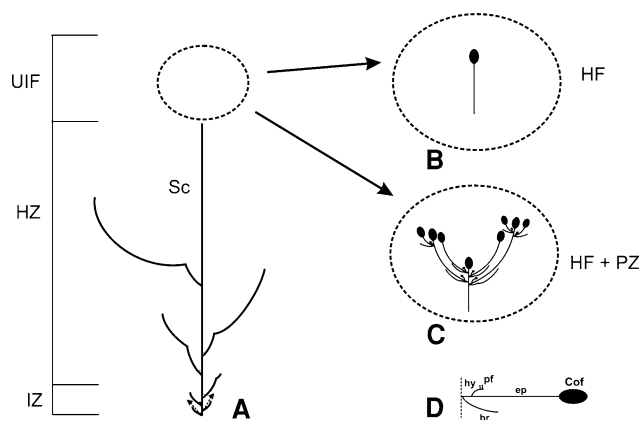No., number of; sp, spikelet; pc, paraclade; ep, epipodium; ?, unknown date

Fig. 1 Typological interpretation of the vegetative and reproductive shoot system of Abildgaardieae. **a** Structure of the synflorescence. **b** Unit of the inflorescence composed only of the terminal spikelet of the main axis of the inflorescence: main florescence. **c** Unit of the inflorescence comprising the main florescence and the paracladial zone; the lateral branches preceding the main florescence are the paraclades. **d** Detail of a paraclade, consisting of a short hypopodium, a prophyll, an epipodium of variable length, and a terminal spikelet, which is named co-florescence. *IZ*, innovation zone; *HZ*, inhibition zone; *Sc*, scape; *UIF*, unit of the inflorescence; *PZ*, paracladial zone; *HF*, main florescence; *Cof*, coflorescence; *hy*, hypopodium; *pf*, prophyll; *ep*, epipodium; *br*, bract

section *Luzuloidei* Kunth. However, in the species of *Cyperus*, the normal paraclades are disposed in an anti-dromic arrangement, whereas in the inflorescences of Abildgaardieae the homodromic arrangement is more frequent.

In the species under study, normal branching is observed, although *Bulbostylis* additionally shows pro-phyllar branching. The prophyllar productions increase the development of the PZ and the number of spikelets of the inflorescence. Prophyllar ramifications have already been observed in other species of Cyperaceae (Kukkonen 1986; Meert and Goetghebeur 1979; Vegetti 1994) and in *Bulbostylis* (Guaglianone 1970). Accessory ramifications produced by multiple buds are present within the family (Alves et al. 2000; Guarise and Vegetti 2005; Mora-Osejo 1960) but have not been reported for any of the genera analyzed. Here, in a single inflorescence of *Bulbostylis hirtella,* an accessory paraclade produced by a serial bud has been observed (Fig. 4k–m). This paraclade constitutes a novelty within the genus, and within the tribe, but as it was observed only once, it may be an isolated case and not a typical kind of branching of the species. This should be clarified by future studies based on further evidence.

Diverse forms of the inflorescences are observed, which are caused by variations in the internode length of the paraclades and the main axis (Guarise and Vegetti 2008; Vegetti 2003). Frequently, an inflorescence shape is pre-dominant for each species, but there is mostly quite a broad range of variation (Table 2). The position of the

inflorescence in relation to the scape is also a varying aspect within the same species and even within the same plant. In addition to terminal and pseudolateral inflorescences, some species show intermediate position inflorescences. Such inflorescences bear the lower bract and their paraclade in the same direction as the scape but the main axis is not twisted with respect to it, as opposed to what may be seen in pseudolateral inflorescences (Guarise and Vegetti, unpublished data).

The main florescence and the co-florescences are the spikelets (Rua 1999). These are plurifloral with perfect flowers (Table 4) and bear fertile glumes generally arranged in a spiral fashion; however, in *Abildgaardia ovata* the lowest glumes and the glumaceous-bractiform foliaceous structures of the base of the spikelets are sub-distichous. (Fig. 6a, b).

There is much controversy over the origin of the foliar structures present at the base of the spikelets. Within the family, similar structures at the base of the spikelets having an intermediate aspect between a glume and a bract, with buds, branches, or flowers as axillary productions, have been recorded. These structures have sometimes been treated as glumes and, other times, as bracts (Browning and Gordon-Gray 1999; Kukkonen 1984, 1986). Within the Abildgaardieae tribe, some authors have made reference to the presence of "sterile glumes" at the base of the spikelets of species of *Abildgaardia* (Haines and Lye 1983; Kral and Strong 1999), *Bulbostylis* (Barros 1947; Kral and Strong 1999; López 2006), *Fimbristylis* (Barros 1947; Haines and Lye 1983), and *Nelmesia* (Goetghebeur 1998), which are generally described as being different in size and shape from the fertile superior glumes (Barros 1947; Kral and Strong 1999). We consider most of these structures to be homologous to bracts in *Bulbostylis* and *Fimbristylis*, owing to the fact that they commonly develop a spikelet or a bud protected by a glumaceous prophyll in their axils. Homologizing these structures to bracts is also supported by the variation observed in the inflorescence of *B. brevifolia*. In this species, the inflorescences frequently have a well-developed PZ, but at times the inflorescence can be reduced to the HF beneath which develop four of these foliose structures, each with a bud in its axil. In such a case, it can be assumed that the PZ appears as reduced to buds, which may lead to considering said foliose structures as bracts whose buds, if developed, have generated branches and not flowers. Only in *Fimbristylis squarrosa* and *Bulbostylis capillaris* var *microstachys* do these structures always bear a flower, which might make them homologous to glumes, despite their different shape from the upper glumes. In *Abildgaardia ovata*, these structures were always empty, which prevents us from hypothesizing about their nature (are they bracts or glumes?). They might as well be sterile glumes as bracts. The presence of one to two
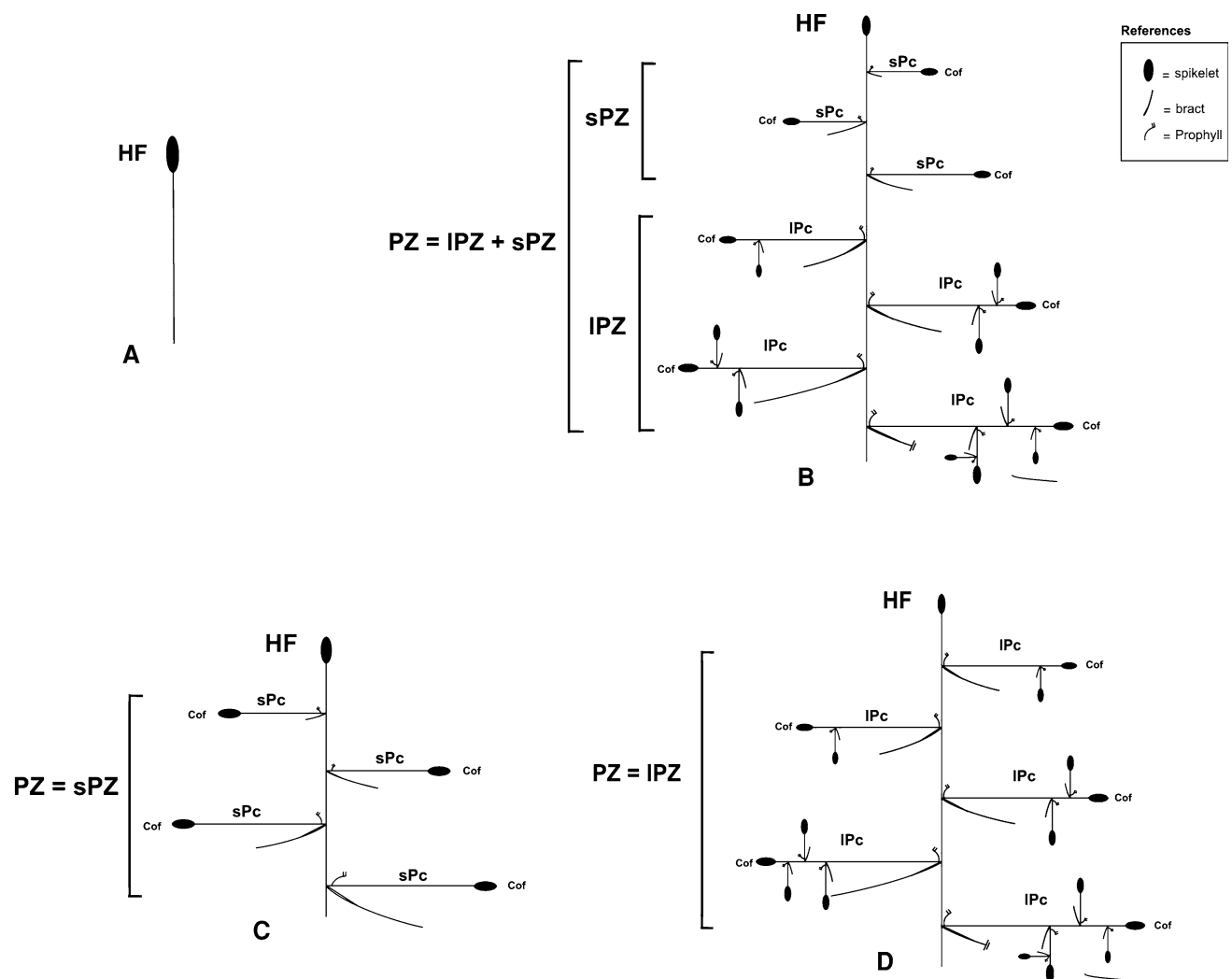
Fig. 2 Variation in the structure of the unit of inflorescences of Abildgaardieae. **a** Inflorescence reduced to the main florescence. **b** Inflorescence comprising the main florescence and the paracladial zone composed of subzones of short paraclades (consisting of paraclades represented by only one spikelet) and long paraclades (consisting of paraclades with a more complex structure of ramifications). **c** Inflorescence composed of the main florescence and only of the subzone of short paraclades. **d** Inflorescence composed of the main florescence and only of the subzone of long paraclades. *HF*, main florescence; *Cof*, coflorescence; *PZ*, paracladial zone; *lPZ*, subzone of long paraclades; *sPZ*, subzone of short paraclades; *lPc*, long paraclade; *sPc*, short paraclade

paraclades below the HF in a few inflorescences of *Abildgaardia ovata* may lead us to conclude that these structures, or at least those found further toward the base, are homologous to bracts rather than to glumes (Fig. 7). Ontogenetic studies should be carried out in order to clarify the homologies of the abovementioned structures.

Winged rachillas are usually found in the species studied. Within the family, various genera have winged rachilla, which allows for different interpretations. At present, there is much controversy over these structures and their relationship to the monopodial or sympodial organization of the spikelets (Celakovsky 1887, Holttum 1948; Vrijdaghs 2006; Vrijdaghs et al. 2007; Zhang et al. 2004). Celakovsky (1887) considers that the winged expansions in *Schoenus*

ferrugineus are evidence that the *Schoenus* spikelet is a cymose inflorescence, in which the wings are the result of the fusion of the new lateral axis and the basal portion of the bract of this axis. Unlike Celakovsky, Holttum (1948) considers the wings to be often arranged in monopodial distichously organized spikelets and to be glumes whose basal portions are expanded and enclose the lower internode. For *Fimbristylis* s.l., Koyama (1961) has already referred to the presence of wings considering them formed by the decurrent base of the glume that continues with the wings of the winged rachilla. Monopodial organization of the spikelet seems to be most appropriate for the species of Abildgaardieae, but developmental studies are necessary to interpret the origin of these "wings" adequately.
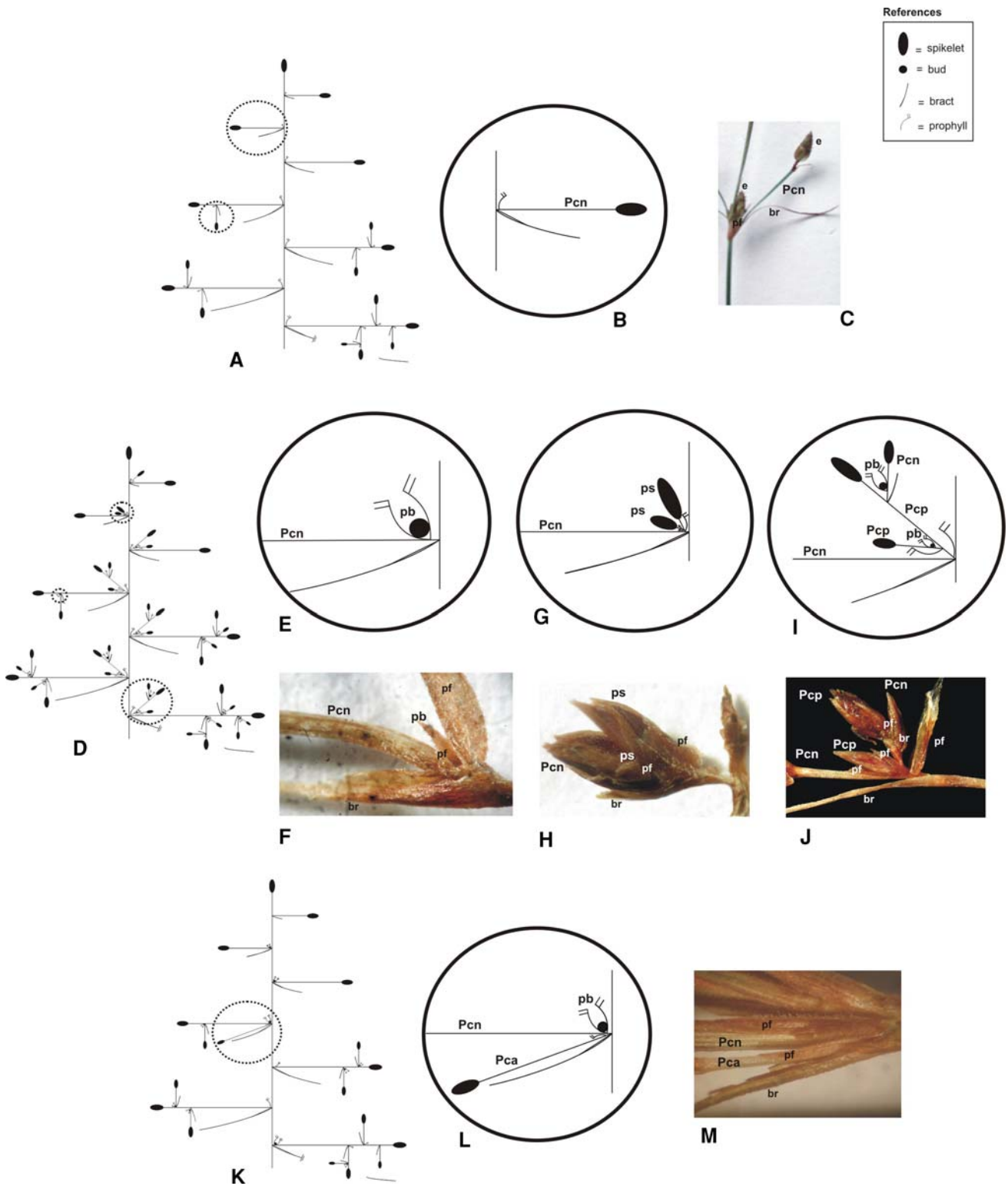
Fig. 3 Different ramification patterns recognized in the inflorescences of Abildgaardieae. **a–c**, normal branching; **d–j**, prophyllar branching, represented by a bud (**e**, **f**); a spikelet with or without a bud, or a vestigial spikelet in the axil of its prophyll (**g**, **h**), or a more complex system formed by normal and prophyllar ramifications (**i**, **j**); **k–m** accessory-axilar branching produced by serial buds. *Pcn*, normal paraclade; *Pcp*, prophyllar paraclade; *Pca*, accessory paraclade; *pb*, prophyllar bud; *ps*, prophyllar spikelet; *pf*, prophyll; *br*, bract; *e*, spikelet
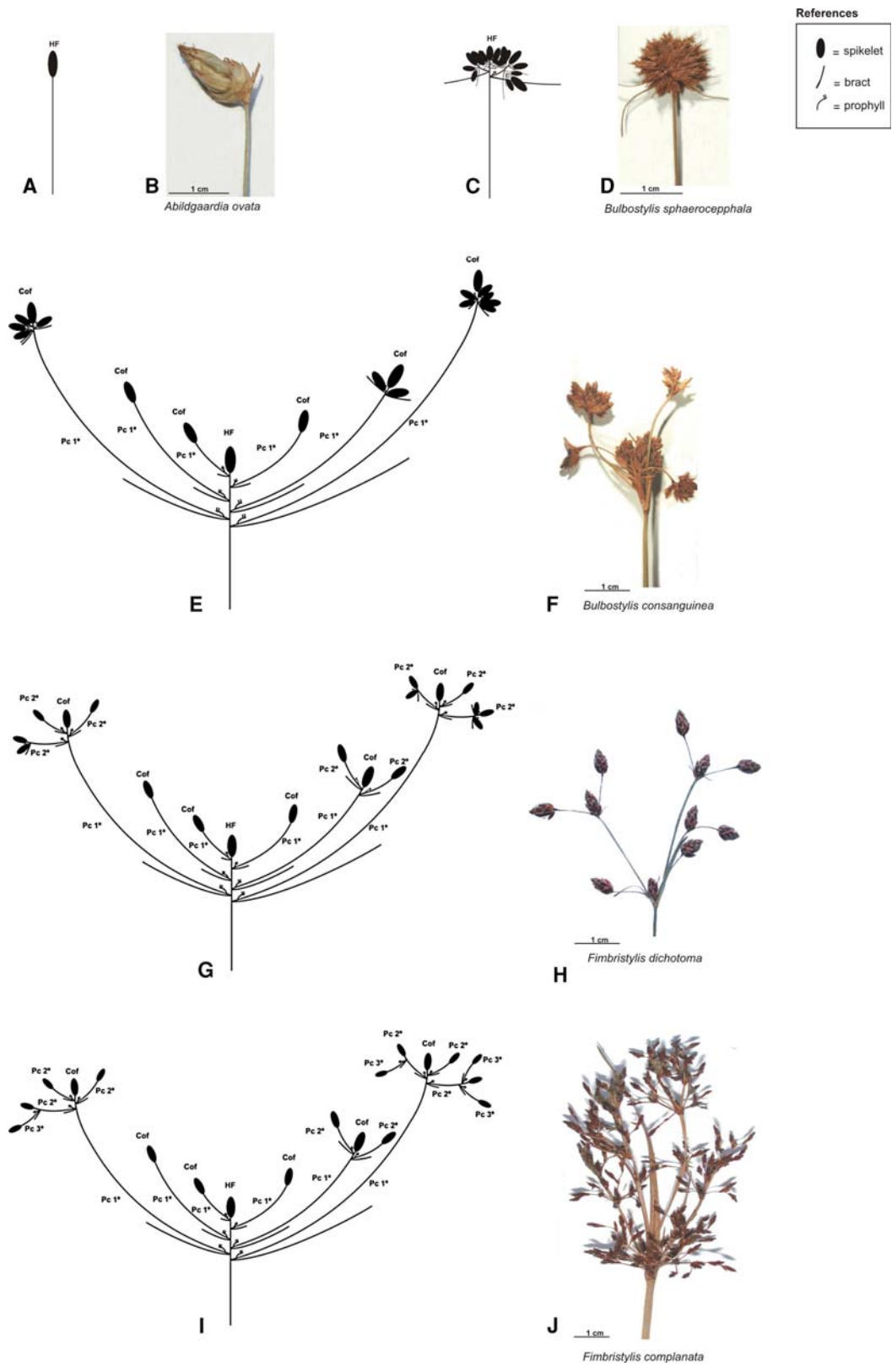
Fig. 4 Form of the inflorescences. **a**, **b**, unispicate inflorescence; **c**, **d**, capituliform inflorescence; **e**, **f**, simple anthelodium; **g**, **h**, compound anthelodium; **i**, **j**, decompound anthelodium. *HF*, main florescence; *Cof*, coflorescence; *Pc1°*, primary paraclade; *Pc2°*, secondary paraclade; *Pc3°*, tertiary paraclade
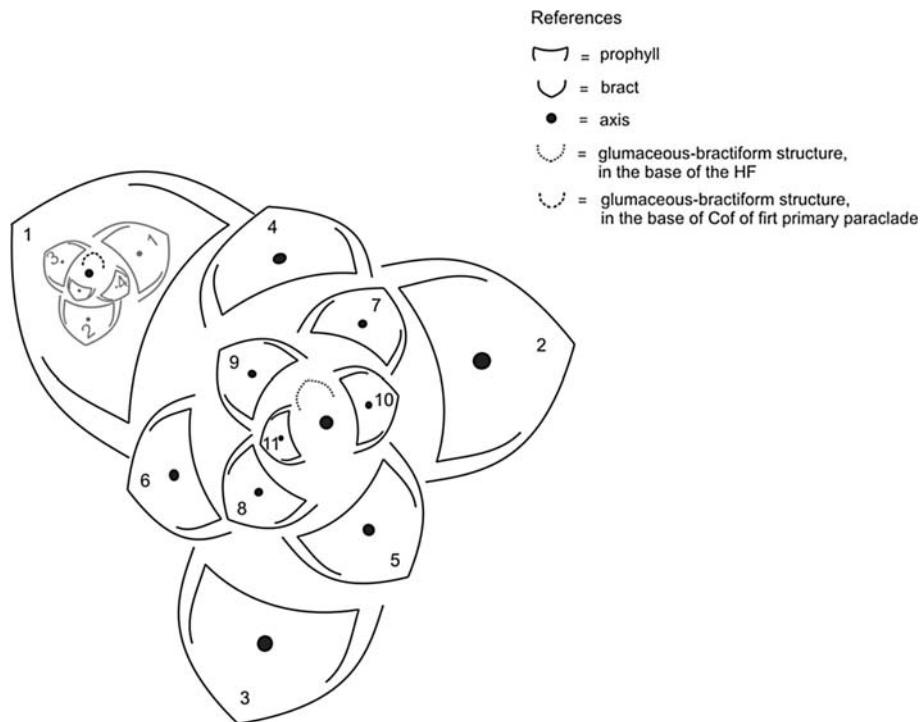
Systematic value

Of all the inflorescence characteristics discussed, the branching pattern of the inflorescence seems to be the main characteristic with potential taxonomic and phylogenetic implications at genus level. Prophyllar productions are never found in *A. ovata* or in the studied species of *Fimbristylis*, but they are usually observed in *Bulbostylis* (Table 2). This characteristic is likely to be a synapomorphy of the genus. The presence or absence of such productions and the degree to which they develop must be carefully accounted for in more species of *Bulbostylis*, because this may become a new tool for infrageneric divisions.

The other inflorescence characteristics do not allow establishing distinct limits among genera, but they do allow making a few generalizations. Thus, for instance, in relation to inflorescence structure, the PZ does not generally develop in *A. ovata*, but when it does, it is only limited to one to two short paraclades. In *Fimbristylis*, inflorescences always have a PZ divided into an sPZ and an lPZ, except in *F. squarrosa*, where the inflorescence also develops with a PZ reduced to an sPZ. Higher structural variations may be seen in *Bulbostylis*, given that different species may have inflorescences lacking a PZ, as observed in *A. ovata* (*B. capillaris* var. *microstachis*); or inflorescences composed both of the sPZ and the lPZ, or only composed either by the sPZ or the lPZ (Table 2; Fig. 2).

Characteristics such as achene shape, style-branches, spikelet number, maximum order of normal ramification, number of the glumaceous-bractiform structures at the spikelet base and the production in their axils, may have taxonomic implications for grouping species into *Fimbristylis*. Among these characteristics, "the branches into which the style is divided" and "the achene shape" have often been used to maintain sections within *Fimbristylis* (Clarke 1900, 1908; López, unpublished data; Osten 1931). Among the species studied, many characteristics are shared between *F. autumnalis* and *F. complanata* on the one hand, and between *F. dichotoma* and *F. spadicea*, on the other. Closeness among these species has already been observed. Thus, for example, Barros (1947) treats *F. autummalis* and *F. complanata* as only one species considering the latter as a taxonomic variety of *F. autumnalis*; whereas Kral (1971) mentions how frequently *F. autumnalis* has been confused with *F. complanata*, species that differ primarily in their annual or perennial habit and the length of their anthers. Regarding *F. dichotoma* and *F. spadicea*, López (unpublished data) argues that they may be considered separately based only on small differences in the surface of the achene, and on the presence of a ligule in *F. dichotoma* and not in *F. spadicea*.

For the genus *Bulbostylis*, many problems are faced in identification of varieties within *B. capillaris* and *B. juncoides* because of the presence of specimens with intermediate characteristics (López, personal communication). In
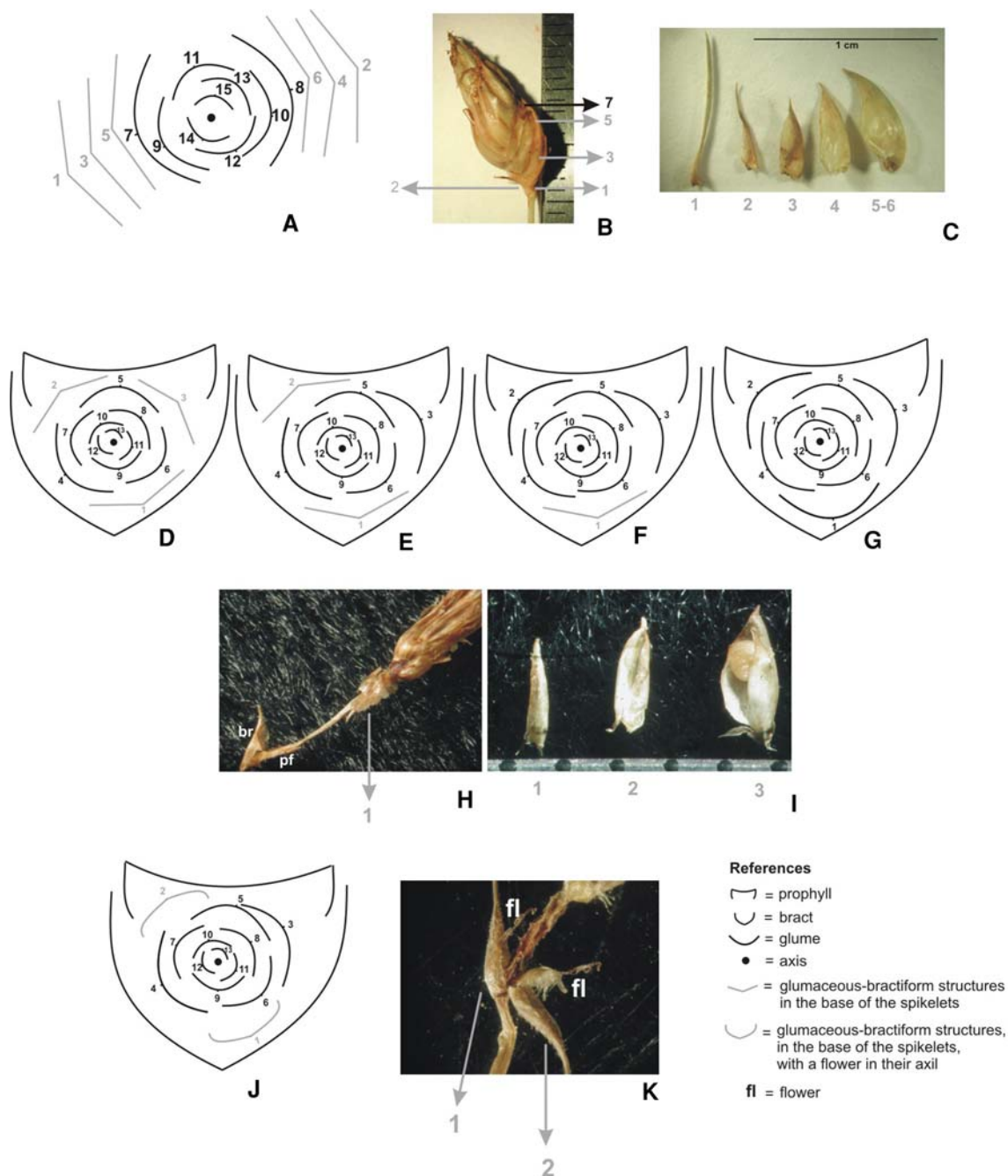
Fig. 6 Phyllotaxis of the glumes in Abildgaardieae and their relationship to the disposition of bracts, prophylls, and the basal glumaceous-bractiform structures of the spikelets. **a, b**: *Abildgaardia ovata*, main florescence with basal glumaceous-bractiform structures and basal glumes disposed in distichous arrangement, and upper glumes with a spiral arrangement. **c** *Abildgaardia ovata*, variation on the form of the basal glumaceous-bractiform structures. **d–g** *Bulbostylis* and *Fimbristylis*, basal glumaceous-bractiform structures and glumes disposed in spiral arrangement. **h** Detail of a basal glumaceous-bractiform structure in *Fimbristylis autumnalis*. **i** Variation on the form of the basal glumaceous-bractiform structures in *Fimbristylis dichotoma*. **j, k** *Fimbristylis squarrosa*, with two of said structures with a flower in their axil

Bulbostylis capillaris, for example, the varieties *capillaris*, *contracta*, and *elatior* share important characteristics, for example the form of the inflorescence (except in the var. *contracta*, which shows fasciculate spikelets that are not observed in the other varieties), the branching patterns, and the maximum order of branching of the inflorescences. Such characteristics confirm a close relationship among these three varieties and set them apart from the var. *microstachys*, which has highly marked differences in other aspects. However, these differences could be attributable to differences in the
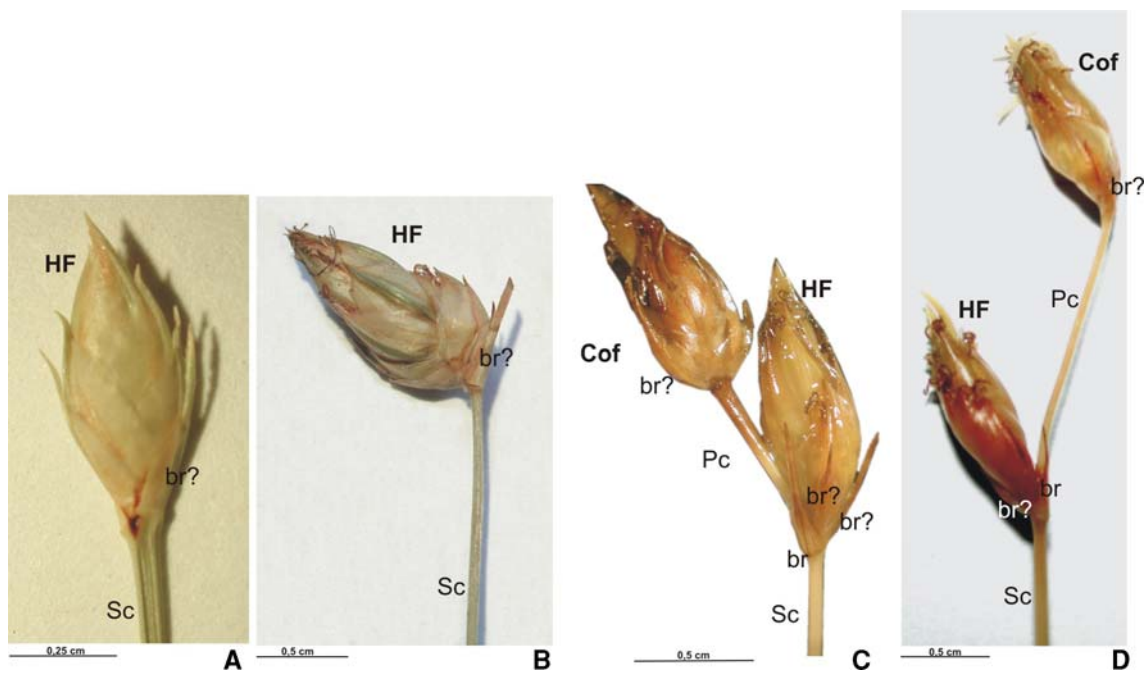
Fig. 7 Variation of the inflorescence of *Abildgaardia ovata*. **a** Young inflorescence. **b** Adult unispiculate inflorescence, with pseudolateral position. **c** Adult inflorescence formed by two spikelets, with terminal position. **d** Adult inflorescence formed by two spikelets, with pseudolateral position. *HF*, main florescence; *Cof*, coflorescence; *Sc*, scape; *br*, bract; *br?*, bract or glume?

altitude where these plants grow, because the var. *microstachys* is commonly found around 2,000 m above sea level, where all plants tend to develop less. As regards the varieties of *B. juncoides*, they have no glumaceous-bractiform structures of uncertain nature present at the base of the spikelets, and they are similar with regard to the number and length of paraclades and spikelets, the length of bracts and prophylls, the number of stamens, and the characteristics of the prophyllar productions. However, slight differences can be observed in the form of their inflorescence (simple anthelodia in the variety *ampliceps* vs. capituliform inflorescences in the varieties *juncoides* and *lorentzii*) and in their structures (the three varieties are generally heterocladic and are formed by the sPZ and the lPZ, but the variety *ampliceps* can often have inflorescences constituted only by long paraclades, and the variety *juncoides* can have inflorescences composed only of short paraclades).

In this work, we note that *A. ovata* and the studied species of *Fimbristylis* share more similarities among themselves than with the species of *Bulbostylis*. The most stable characteristics observed that group *Abildgaardia* and *Fimbristylis* together are the presence of a deciduous style base and the absence of prophyllar ramifications. The development of small winged expansions on the rachilla of the species of *Bulbostylis* studied, and the presence of indumentum on the glumes also contribute to distancing *Bulbostylis* from *Abildgaardia* and *Fimbristylis*, where, in general, the wings of the rachilla are well developed and the glumes are glabrous.

This close relationship observed between the inflorescences of *Abildgaardia* and *Fimbristylis*, with regard to *Bulbostylis*, concurs with data obtained in a phylogenetic analysis of the group (Ghamkhar et al. 2007; Muasya et al. 1998, 2000, 2009; Simpson et al. 2007) and with morphological studies in which *Abildgaardia* is treated as a section of *Fimbristylis* (Barros 1947; Clarke 1900, 1908; Osten 1931; Kern 1974).

However, some authors have considered *Abildgaardia* and *Bulbostylis* to have greater affinity (Haines and Lye 1983; Lye 1973; Van der Veken 1965), principally on the basis of embryological characteristics, but also owing to the existence of species with intermediate characteristics between these two genera (such as type of embryo, deciduous style base, large spikelets, and/or distichous glumes). The presence of unispicate inflorescences in *Abildgaardia* and *Bulbostylis* only could support a closer relationship between these two genera; however, inflorescences of *Fimbristylis* with one spikelet have been reported by other authors (Haines and Lye 1983).

Conclusions

The typological system conceived by Troll was originally criticized by his contemporaries because it turned out to be a rigid system which mixed both empirical findings

Table 5 Characteristics and character states with potential phylogenetic value

Inflorescences

  Inflorescence shape: unispiculate (0), simple anthelodium (1), compound anthelodium (2), decompound anthelodium (3), fasciculate (4), capitate (5)

Inflorescence structure: only HF (0), HF + PZ with lPZ and sPZ (1), HF + PZ with only lPZ (2), HF + PZ with only sPZ (3)

Inflorescence position: terminal (0), pseudolateral (1), intermediate (2)

Ramification pattern: normal (0), prophyllar (1)

Intraprophyllar productions: bud (0), spikelet with a bud or other spikelet in the axil of its prophyll (1), fascicle of spikelets (2)

Maximum order of normal ramification: 1° (0), 2° (1), 3° (2), above 3° (3)

Maximum order of prophyllar ramification: 2° (0), 3° (1), 4° (2)

Number of spikelets per inflorescence: low: 1–49 (0), medium: 50–99 (1), high: 100–149 (2), very high: 150–200 (3)

Number of pc 1° with evident epipodium: none (0), low: 1–6 (1), medium: 7–13 (2), high: 14–21 (3)

Number of pc 2° with evident epipodium: none (0), low: 1–23 (1), medium: 24–47 (2), high: 48–72 (3)

Number of pc 3° with evident epipodium: none (0), low: 1–31 (1), medium: 32–63 (2), high: 64–96 (3)

Number of pc 4° with evident epipodium: none (0), low: 1–9 (1), medium: 10–19 (2), high: 20–30 (3)

Pc 5° with evident epipodium: absent (0), present (1)

Length of the epipodium of the first pc 1° (cm): 0 (0), short: 0.1–1.69 (1), medium: 1.7–3.3 (2), long: 3.4–5.1 (3)

Length of the lowermost bract (cm): short: 0.1–2.49 (0), medium: 2.5–4.99 (1), long: 5–7.5 (2)

Length of the uppermost bract (cm): short: 0.03–0.13 (0), medium: 0.14–0.27 (1), long: 0.28–0.42 (2)

Length of the lowermost prophyll (cm): short: 0.03–0.24 (0), medium: 0.25–0.49 (1), long: 0.5–0.75 (2)

Length of the uppermost prophyll (cm): short: 0.03–0.09 (0), medium: 0.1–0.19 (1), long: 0.2–0.3 (2)

Spikelets

  Spikelet length (cm): short: 0.1–0.49 (0), medium: 0.5–0.99 (1), long: 1–1.5 (2)

Number of fertile glumes: low: 1–18 (0), medium: 19–37 (1), high: 38–57 (2)

Number of foliose "glumaceous-bractiform" structures: none (0), one (1), two (2), three or more (3)

Production in the axil of the foliose "glumaceous-bractiform" structures: empty (0), with a bud (1), with a spikelet or a pc well developed (2), with a flower (3)

Rachilla: winged (0), not winged (1)

Flowers

  Duration of the style base: deciduous (0), persistent (1)

  Style-branches: two (0), three (1)

(This characteristic and the characteristic *achene shape* are not independent, thus only one of them needs to be considered)

  Number of stamens: one (0), two (1), three (2)

HF, main florescence; PZ, paracladial zone; lPZ, subzone of long paraclades; sPZ, subzone of short paraclades; 1°, 2°, … , order of ramification, pc, paraclade

and subjective concepts (Claßen-Bockhoff 2001). Later, the typological approach was reduced to a "scientific procedure for abstracting general rules from the individuals" (Claßen-Bockhoff 2001). It is currently a valuable first step toward establishing hypotheses of primary homology (De Pinna 1991), which should then be subjected to developmental, genetic, and phylogenetic analyses.

Table 5 shows a list of potentially useful inflorescence characteristics and character states, and other spikelet and flower characteristics observed in this work. As far as inflorescence characteristics are concerned, "the branching pattern of the inflorescence" seems to be the main characteristic with potential taxonomic and phylogenetic implications at genus level. The rest of the characteristics

could possibly be useful for infrageneric divisions. We plan to include these characteristics in a morphological data matrix, in combination with other morphological characteristics derived from anatomical and ontogenetic studies, to assess their potential phylogenetic value through a cladistic analysis. Subsequently, we will produce a molecular phylogeny of Abildgaardieae including the species in this study, with the objective of carrying out morphological and molecular data combined analysis and hypothesizing on the evolution of the inflorescence characteristics observed in this study.

Foliose structures present at the base of the spikelets in *Bulbostylis* and *Fimbristylis* seem to be homologous with bracts, excepting *F. squarrosa*, where such structures bear a flower and may thus be considered homologous with

glumes. The nature of those structures in *Abildgaardia ovata* will remain uncertain until ontogenetic studies in this species are carried out.

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