

The inflorescences structure of *Cyperus* L. section *Luzuloidei* Kunth (Cyperaceae)

N. J. Guarise, A. C. Vegetti

Morfología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional del Litoral, Esperanza, Santa Fe, Argentina

Received 10 May 2007; Accepted 13 June 2007; Published online 26 October 2007
© Springer-Verlag 2007

Abstract. In the present work the inflorescences of 12 species of *Cyperus* sect. *Luzuloidei* Kunth sensu Kükenthal were analyzed using the methodology and terminology of Troll's school. All the inflorescences studied are polytelic (indeterminate). The inflorescences are anthela-like or capitate, and can be terminal or pseudolateral. Below the main florescence a paracladial zone is present. In this zone three types of branching were observed, i.e. normal, accessory-axillar and prophyllar branching, whose position vary among the different species. In the paracladial zone a subzone of long paracladia and a subzone of short paracladia were observed. In the short paracladial subzone the spikelets are clustered in fascicles, which can be serial, prophyllar or mixed. Variation in length and position of prophylls, length of prophyll, number and degree of branching were noticed. The systematic value of the inflorescence in the section *Luzuloidei* is discussed.

Keywords: Inflorescences; typology; *Cyperus* sect. *Luzuloidei*; branching pattern; fascicles; phyllotaxis; systematic

Cyperus L., comprising about 550 species is the second largest genus in the family (Tucker

1994, Goetghebeur 1998). *Cyperus* is not a monophyletic group and presents several taxonomic problems, and there is no general agreement in its circumscription and infrageneric division (Muasya et al. 1998, 2000, 2002). Of the 28 sections proposed by Kükenthal (1935–36) the section *Luzuloidei* Kunth includes species from the American continent (Denton 1978).

The section *Luzuloidei* presents difficulties in its taxonomical delimitation and in the distinction of some of its members (Denton 1978); for that reason the elucidation of its limits is necessary. Kükenthal (1935–36) included 18 species and several varieties in the section *Luzuloidei*. The species circumscribed by Kükenthal present generally compound or decompound anthelic inflorescences; rarely simple or contracted ones. Spikelets are oblong to ovate, more or less compressed, usually in congested clusters, with wingless rachilla, and have dense or laxly imbricate glumes. Denton (1978) excluded some of the species and varieties considered by Kükenthal (1935–36), therefore the section *Luzuloidei* is

now reduced to 10 species and 5 varieties; some of them have been elevated to species (Tucker 1994, Carter et al. 1999).

Among the characters considered to characterize the subdivision of *Cyperus*, the inflorescence has been used at infrageneric levels (Clarke 1908; Kükenthal 1935–36; Barros 1925, 1938). However, the use of the inflorescences as characters for the division of the genera has been criticized by several authors (Goetghebeur 1989, Muasya et al. 2002). The inflorescences of the genera *Cyperus* have been described in many ways (Barros 1925, 1938, 1947; Kükenthal 1935–36; Haines and Lye 1983; Tucker 1983, 1994; Adams 1992; Guaglianone 1996), but always from a descriptive point of view. Typological studies of *Cyperus* inflorescences are rare (Mora Osejo 1960, Heinzen and Vegetti 1994, Perreta and Vegetti 2002) and they include a few species, without implementing a comparative study within infrageneric categories.

To solve the taxonomic problems and the relationships in *Cyperus*, a precise morphological study at the level of species is required (Muasya et al. 2000). In order to provide new and useful data which may be used in the revision of the genera, a re-evaluation could be made on structural characters of the different parts of the inflorescence.

In this context the typology-based system developed by Troll (1964) and Weberling (1989) has proved to be useful for describing inflorescences (Mora Osejo 1987, Rua 1999) as well as for providing characters with phylogenetic value (Nickol 1995, Aagesen 1999, Rua and Aliscioni 2002, Tortosa et al. 2004, Liu et al. 2005). In a typological interpretation of the inflorescence, the terminal spikelet of the main axis of the inflorescence is the main florescence (HF; Figs. 1–4). The lateral branches preceding the main florescence are known as paraclades; each paracladium consists of a short hypopodium, a prophyll, an epipodium of variable length and a terminal spikelet, named co-florescence (cof; Figs. 1–4). The paraclades can be represented by only one spikelet (short paraclades,

sPc; Figs. 1–4) or by a more complex structure of ramifications (long paraclades, lPc; Figs. 1–4). The paraclades form the paracladial zone (PZ; Figs. 1–4) below the main florescence; the paracladial zone and the main florescence constitute the inflorescence. The paracladial zone is usually composed of subzones of short paraclades (sPcZ) and long paraclades (Figs. 1–4).

The aim of this work is to analyze the inflorescences of *Cyperus* belonging to the section *Luzuloidei* from a typological point of view as a way to contribute to the knowledge of the inflorescence of the genera and also provide characters with potential use in further taxonomic and phylogenetic research.

Materials and methods

Specimens belonging to 12 of 18 species of *Cyperus* sect. *Luzuloidei* sensu Kükenthal (1935–36) (Table 1) were examined and a series of characters related with the inflorescence were recorded (Tables 2–4). Inflorescences were either obtained from herbarium specimens (BAA, BAB, LIL, SF and SI; Table 1) or collected in the field from living plants, which were preserved in 70% alcohol. The dry material was boiled in water for a short period. Mature inflorescences were dissected under a NIKON SMZ-10 stereoscopic microscope, and photographed with a digital camera Nikon COOLPIX 990. The results were schematized and tables were made to register the results in a comparative way. The number of branches of primary, second, third, etc. order were counted for each ramification pattern (Table 4). The position of the different types of branching was observed and schematized (Figs. 1–4). The length of the proximal branch was measured from the insertion until the apex of its terminal spikelet (Table 3). A branch with evident epipodium was considered when it was recognizable (Table 2).

In *C. hieronymi* and *C. pseudovegetus* we could not perform a complete qualitative study like in the others species due to the lack of sufficient herbarium material. In *C. pseudovegetus* only a part of the inflorescence could be studied and in *C. virens* var. *drummondii* only one inflorescence could be analyzed completely.

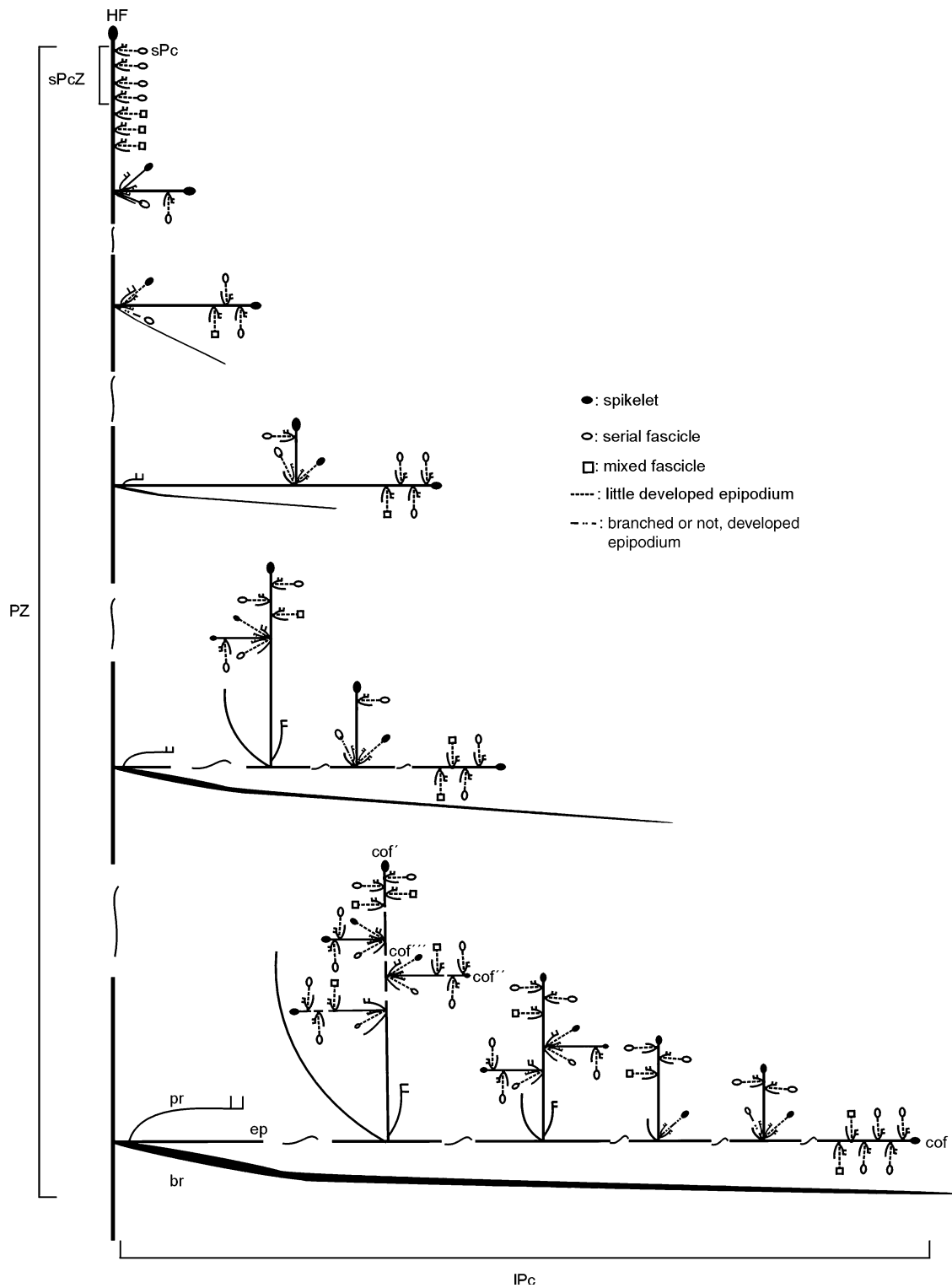


Fig. 1. Structure of the flowering unit of *Cyperus* section *Luzuloidei* with accessory-axillar branches in distal portion of the main axis. *br* perophyll; *cof* cincinnate of 1st order; *cof'* cincinnate of 2nd order; *cof''* cincinnate of 3rd order; *cof'''* cincinnate of 4th order; *ep* epipodium; *HF* main florescence; *IPc* long paracladium; *pr* prophyll; *PZ* paracladial zone; *sPc* short paracladium; *sPcZ* subzone of short paracladia

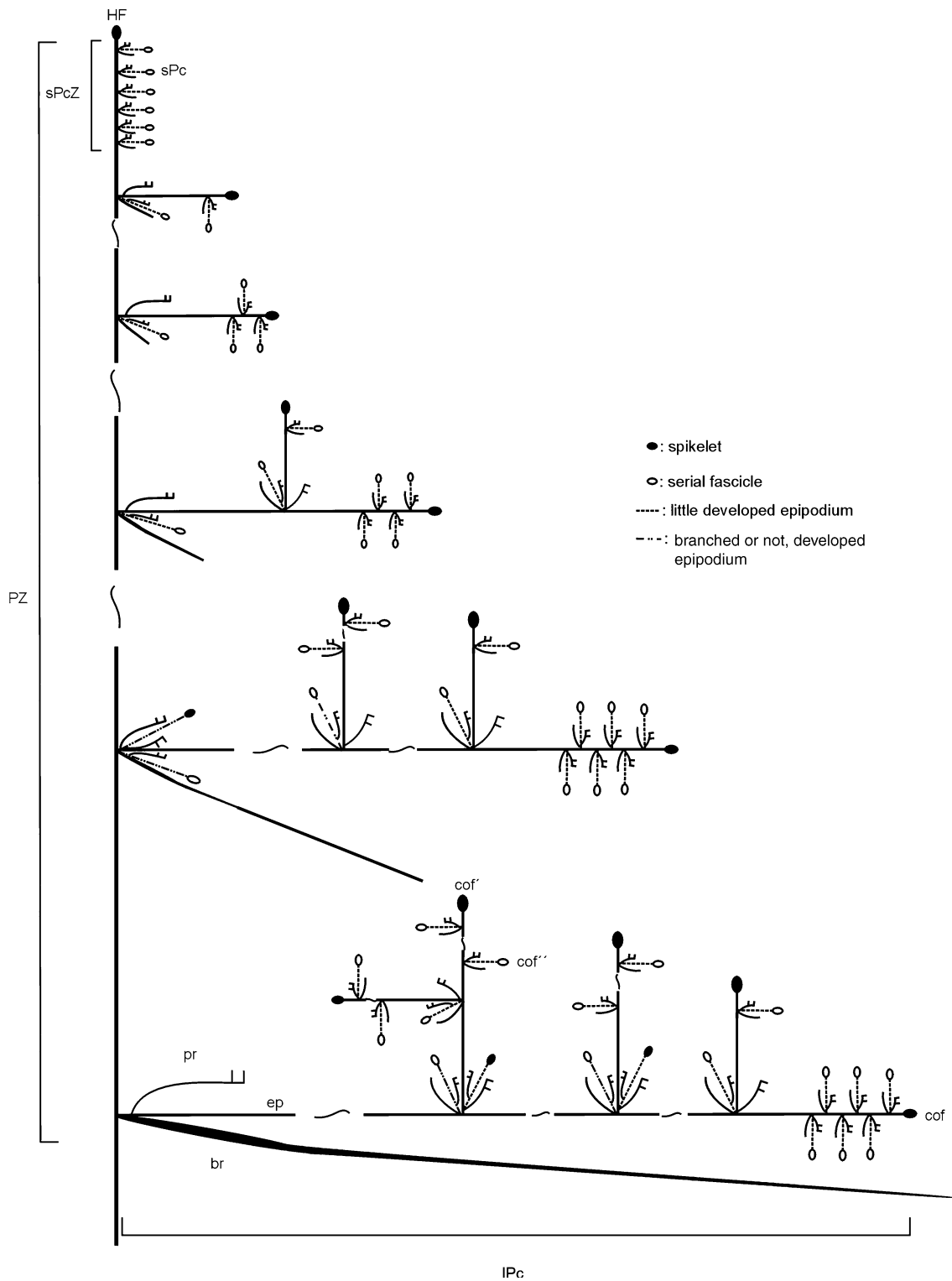


Fig. 2. Structure of the flowering unit of *Cyperus* section *Luzuloidei* with accessory-axillar and prophyllar axes from the middle portion of the main axis. *br* perophyll; *cof* coflorescence of 1st order; *cof'* coflorescence of 2nd order; *cof''* coflorescence of 3rd order; *ep* epipodium; *HF* main florescence; *IPc* long paracladia; *pr* prophyll; *PZ* paracladial zone; *sPc* short paracladia; *sPcZ* subzone of short paracladia

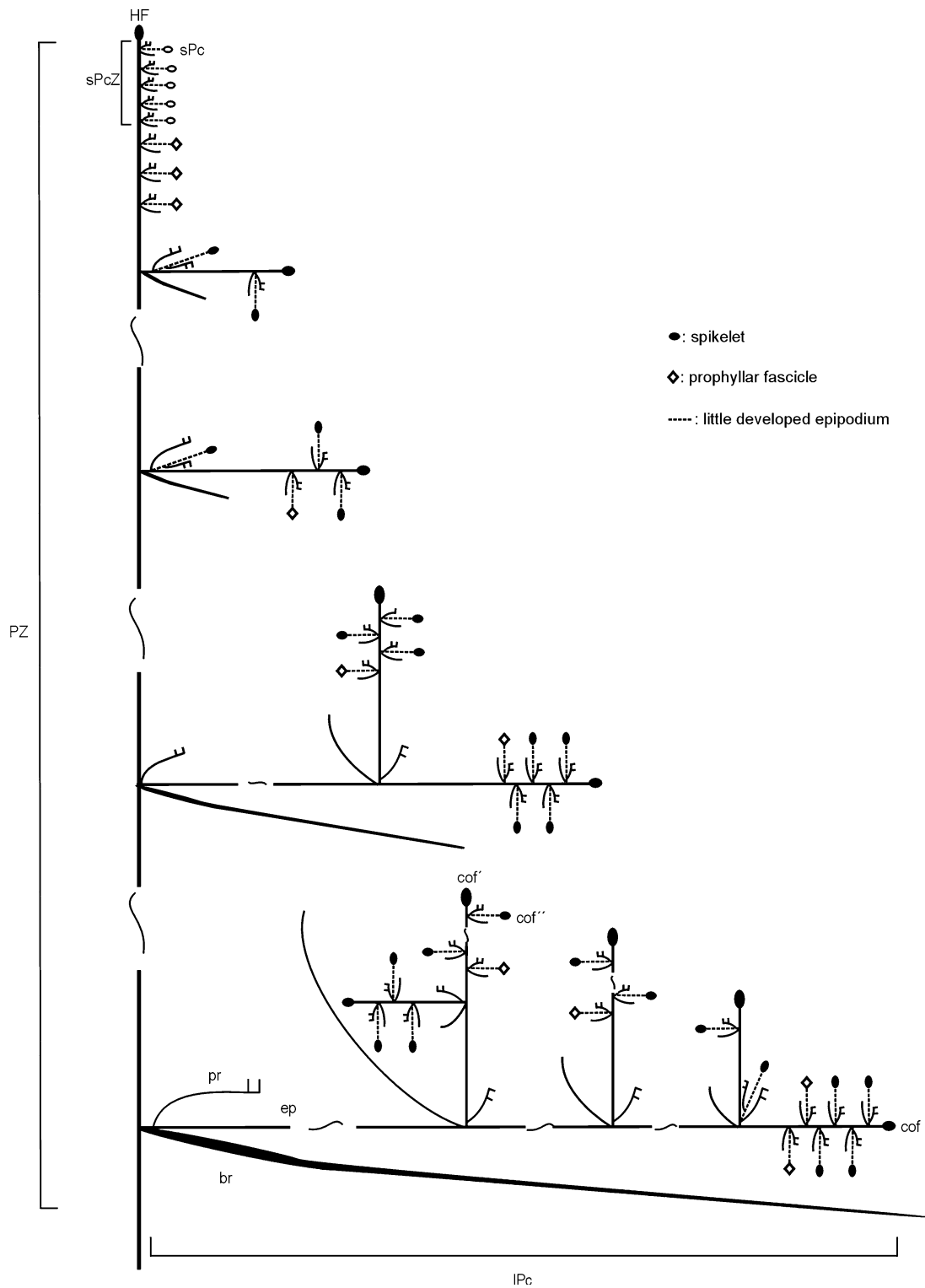


Fig. 3. Structure of the flowering unit of *Cyperus ochraceus*. *br* perophyll; *cof'* cofilament of 1st order; *cof''* cofilament of 2nd order; *cof'''* cofilament of 3rd order; *ep* epipodium; *HF* main florescence; *lPc* long paracladium; *pr* prophyll; *PZ* paracladial zone; *sPc* short paracladium; *sPcZ* subzone of short paracladia

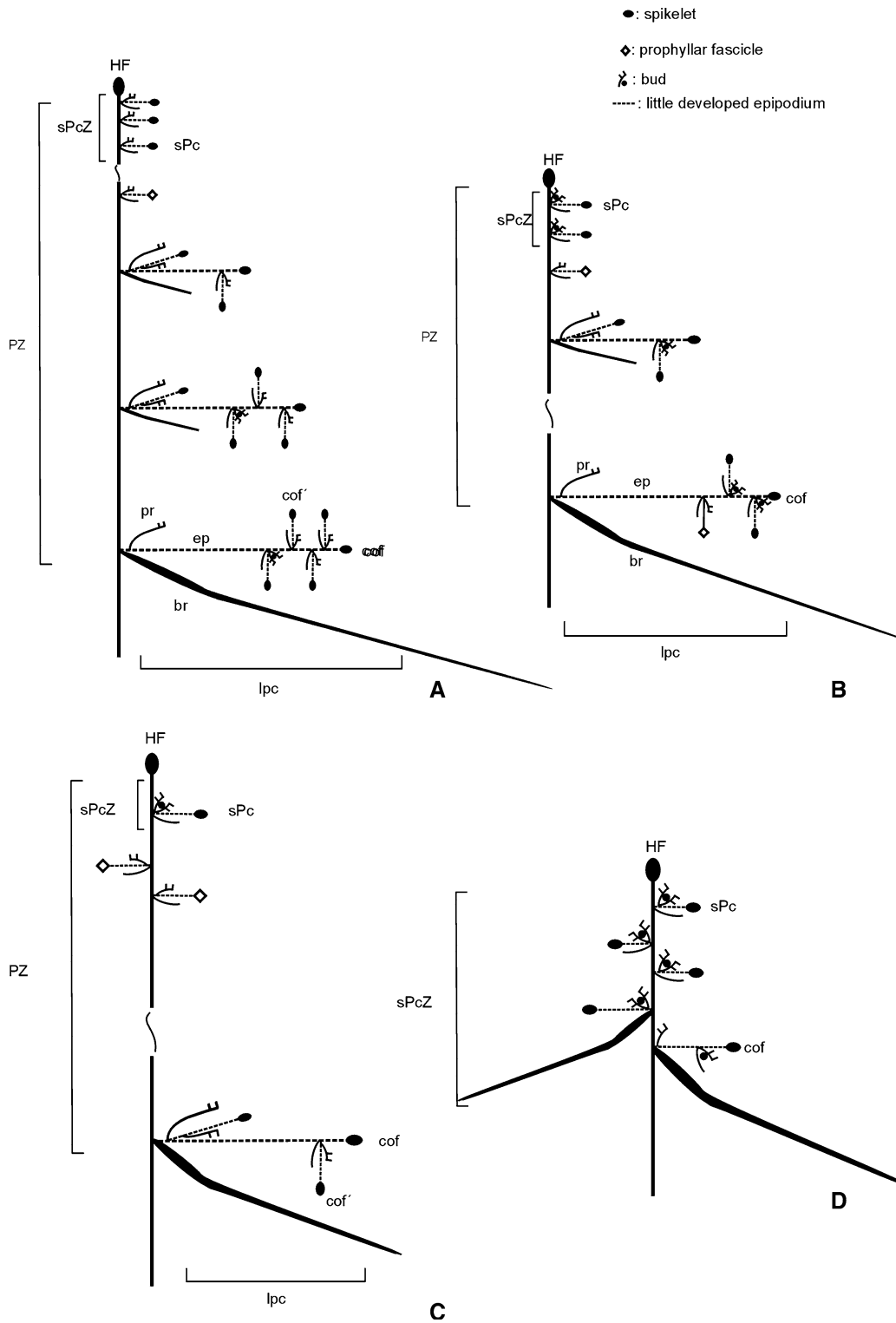


Fig. 4. Variation of the flowering unit of *Cyperus incomtus* var. *incomtus*. **A-C** no fully homogenized inflorescence; **D** fully homogenized inflorescence. *br* prophyll; *cof* cofiloflorescence of 1st order; *cof'* cofiloflorescence of 2nd order; *ep* epipodium; *HF* main florescence; *lpc* long paracladium; *pr* prophyll; *PZ* paracladial zone; *sPc* short paracladium; *sPcZ* subzone of short paracladia

Table 1. Material studied

<i>Cyperus entrerianus</i> Boeck.: Guarise 58, 106, 110, 111, 119, 121, 210, 232, 233, 247 (SF), Vegetti & Guarise 1268, 1269, 1271 (SF).
<i>C. eragrostis</i> Lam. var. <i>compactus</i> (E. Desv.) Kük.: Garaventa 1756 (BAA).
<i>C. eragrostis</i> Lam. var. <i>eragrostis</i> : Guarise: 60, 61, 109, 116, 117, 118, 122, 123, 124 (SF).
<i>C. fraternus</i> Kunth: Burkart 7927 (SI), Fernandez 947 (SI), Guaglianone et al. 710 (SI), Guarise 18. (SF), Schulz 10550 (SI), Venturi 8858. (SI).
<i>C. hieronymi</i> Boeck.: Cabrera et Farris 17457 (BAA), Herbario Instituto Miguel Lillo 10108. (LIL), Burkart & Troncoso 11246 (SI). Parodi 14558 (BAA).
<i>C. incomtus</i> Kunth var. <i>incomtus</i> : Cano & Cámara-Hernández 670 (BAA), Dinelli 791 (BAB), Guarise 112, 225, 226, 243 (SF), Spegazzini 14027 (BAB).
<i>C. intricatus</i> (Schrad.) ex Schult: Guaglianone, Tur et Carrillo 1139 (SI).
<i>C. luzulae</i> (L.) Retz.: Arenas P. 2336 (SI), Guaglianone et al. 3200 (SI), Parodi 9024 (BAB), Pipoly 9088 (SI), Saravia Toledo & Nelson Joaquín 10519 (SI).
<i>C. ochraceus</i> Vahl: Callejas, S 2256 (SI), Guaglianone, Galiano et Tur 1958 (SI), Krapovickas et al. 19391 (SI), Schulz & Varela 5236 (LIL).
<i>C. pseudovegetus</i> Steudel.: Fisher 372 (SI), Fisher 37232. (SI)
<i>C. reflexus</i> Vahl: Bacigalupo & Fortunato 1954 (SI), Burkart 19917 (SF), Lewis & Collantes 882 (SF), Nicora 4997 (SF), Nicora 5424 (SF), Troncoso et al. 3535 (SF).
<i>C. surinamensis</i> Rottb.: Guarise 15, 20, 30, 51, 55, 102, 105, 108, 406 (SF), Martinez Crovetto & Grondona 4418 (BAB), Vegetti & Perreta 1239 (SF).
<i>C. virens</i> Michx var. <i>drummondii</i> (Torrey & Hooker) Kükenthal: González et al. 7091 (SF).
<i>C. virens</i> Michx var. <i>montanus</i> (Boeck.) Denton: Guarise 328 (SF).
<i>C. virens</i> Michx. var. <i>virens</i> : Guarise 29, 56, 66, 98, 142, 157, 173, 200, 223 (SF).

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

Results

Tables 2, 3 and 4 show important qualitative and quantitative inflorescence parameters representative of *Cyperus* sect. *Luzuloidei*. In all species studied the following zones can be distinguished on the whole plant: innovation zone, inhibition zone, paracladial zone and main florescence. The innovation zone is the basal region of the shoot. Generally it is constituted by reduced leaves, and the buds in this zone develop into lateral shoots similar to the structure of the mother shoot. The inhibition zone, located above the innovation zone, is constituted by a sequence of sterile nodes; the leaves within the inhibition zone display well developed blades and sheaths. In the distal portion of the inflorescence the axis

ends in a spikelet (main florescence), below this a paracladial zone is developed. Each paracladium in the paracladial zone can be branched or reduced to its cofillorescence. In *C. virens* var. *virens* and *C. eragrostis* var. *eragrostis* some paracladia display a reduced or vestigial cofillorescence (Fig. 5A).

The inflorescences may present either an anthela-like form (anthelodium; indeterminate inflorescences; Troll 1964) (Fig. 6A, B, C) or it can be reduced to a more or less contracted head, like a capitulum (Fig. 6D). These are the fundamental forms of the inflorescences in the species studied. The anthelodium can have paracladia of first (simple anthelodium), second (compound anthelodium) and up to third order (decompound anthelodium) with an evident epipodium (Table 2). The appearing, number and length of the paracladia with an evident epipodium is variable among the species and varieties (Tables 2, 3). In *C. entrerianus* the inflorescence form is considerably influenced by the environmental conditions.

Table 2. Important qualitative inflorescence parameters of *Cyperus* sect. *Luzuloidei*

Species	Maximum order with evident epipodium	Maximum order ramification	Types of fascicles	Order of the Pca-a with branching	Order of the Pcp with branching
<i>C. entrierianus</i>	(none-1 st -) 2 nd	(4 th -) 5 th	Mixed & Serial	–	–
<i>C. eragrostis</i> var. <i>compactus</i>	none	2 nd (-3 rd)	Mixed & Serial	–	–
<i>C. eragrostis</i> var. <i>eragrostis</i>	1 st (-2 nd)	3 rd (-4 th)	Serial	1 st	–
<i>C. fraternus</i>	(none-)1 st (-2 nd)	3 rd (-4 th)	Serial	1 st - 2 nd	–
<i>C. hieronymi</i>	(none-) 1 st - 2 nd	5 th	Mixed & Serial	1 st - 2 nd	–
<i>C. incomtus</i> var. <i>incomtus</i>	none	(1 st -) 2 nd (-3 rd)	Prophyllar	–	2 nd (a)
<i>C. intricatus</i>	1 st	3 rd	Serial	–	–
<i>C. luzulae</i>	1 st -2 nd	4 th	Mixed & Serial	1 st -2 nd	3 rd (a)
<i>C. ochraceus</i>	2 nd	4 th	prophyllar	–	–
<i>C. pseudovegetus</i>	(none-1 st -) 2 nd (-3 rd)	?	Serial	?	?
<i>C. reflexus</i>	none (-1 st)	3 rd	Serial	1 st -2 nd	–
<i>C. surinamensis</i>	2 nd (-3 rd)	(3 rd -) 4 th	Serial	1 st -2 nd	2 nd -3 rd
<i>C. virens</i> var. <i>drummondii</i>	1 st (-2 nd)	4 th	Serial	2 nd	–
<i>C. virens</i> var. <i>montanus</i>	3 rd	6 th	Mixed & Serial	–	–
<i>C. virens</i> var. <i>virens</i>	(1 st -) 2 nd (-3 rd)	4 th	Serial	1 st -2 nd	2 nd

Pca-a accessory-axillar paracladia; Pcp prophyllar paracladia; ^(a) less frequently; ? missing data

This species frequently displays a compound anthelodium, but in unfavorable conditions the inflorescences may be either a simple anthelodium or a capitate one.

In the distal region of 1st, 2nd and 3rd order paracladia with an evident epipodium there are clusters (glomerulous) of spikelets. Such glomerules are constituted by paracladia with a reduced epipodium and a variable branching order (from 2nd to 6th), depending on the maximum degree of ramification of the species and their position in the inflorescence.

The position of the inflorescence in relation to the scape, can be terminal (Fig. 6A), as in most species of the section, or pseudolateral. In pseudolateral inflorescences the lower pherophyll and paracladium points into the same direction as the stem, turning the main axis aside (eg. *C. surinamensis*; Fig. 6B) or not (eg. *C. fraternus* and *C. reflexus*; Fig. 6C).

Foliaceous, laminar, setiform and glumaceous pherophylls are observed in clear acropetal sequence. All the species displayed the four types of pherophylls, with variations in the length of the proximal one (Table 3).

In the species studied the prophylls display an acropetal variation in size and form: tubular (cladoprophyll), laminar and glumaceous. All of them are two-keeled, a hardly observable character in the glumaceous ones. The length of the lowermost prophyll varies among the species (Table 3), whereas the length of the distal ones (glumaceous) is smaller than 0,1 cm in all species studied. The occurrence of the different types of pherophylls and prophylls varies according to the region of the inflorescence; on the main axis the different types of pherophylls and prophylls are present.

Table 3. Important quantitative parameters of *Cyperus* section *Luzuloidei* Kunth (all measurements in cm)

Species	Length of first order paracladium	Length of long evident paracladium, different to 1rs	Length of the lowermost bract	Length of the lowermost prophyll
<i>C. entrerianus</i>	(3,5-) 7-12,2	2 nd : 1,65-3,1	(14-) 43-45	(0,15-) 1,5-1,6
<i>C. eragrostis</i> var. <i>compactus</i>	1,3-1,5	-	4-5	0,2-0,4
<i>C. eragrostis</i> var. <i>eragrostis</i>	5,5-8	2 nd : 1,2-1,4	25-40	0,6-1
<i>C. fraternus</i>	2,2-5,4	2 nd : 0,9-1	13,2-15	0,35-0,6
<i>C. hieronymi</i>	(4,1-) 6-8 (-10)	2 nd : (0,8-) 1,3-1,5 (-2,5)	28-40	1,2-1,7
<i>C. incomtus</i> var. <i>incomtus</i>	1-1,65	-	12,5-32	0,2-0,5
<i>C. intricatus</i>	3-3,2	-	20-23	0,5-0,6
<i>C. luzulae</i>	1,4-4	2 nd : 1-1,4	30-38	0,5-0,6
<i>C. ochraceus</i>	5-8	2 nd : 1,7-1,8	38-55	0,7-0,8
<i>C. pseudovegetus</i>	1,5-7,2	2 nd : 0,8-1,2	20-36	0,7-1,6
<i>C. reflexus</i>	1,1-1,3 (-4,2)	-	(2,8-) 6,4-9,4	0,3-0,5
<i>C. surinamensis</i>	5,4-5,8 (-9)	2 nd : 1,8-1,9 (-3,3) 3 rd : 0,8	17-25,5	1-1,1
<i>C. virens</i> var. <i>drummondii</i>	3,4	2 nd : 1,6	32	0,7
<i>C. virens</i> var. <i>montanus</i>	14-16	2 nd : 1-1,6	35-40	1,9-2,3
<i>C. virens</i> var. <i>virens</i>	6,2-8,5	2 nd : 1,8 (-2,6) 3 rd : 0,9	(25,2-) 30-52	1-1,8

The following **ramification patterns** were observed in the paracladial zone of the inflorescences studied of *Cyperus* sect. *Luzuloidei*:

Axillar and Normal branching. Paracladium is produced by an axillary bud of a prophyll (Fig. 7A, B).

Prophyllar branching. Paracladium is produced by a prophyllar bud (Fig. 7A, B). The prophyllar branch, its prophyll and the main nerve of the prophyll, are all in the same plane. This branching type never repeats several times. This means that the prophyllar branching pattern never results in a series of prophyllar paracladia.

In a few cases, the prophyll of some spikelets in *C. entrerianus*, *C. luzulae* and *C. virens* var. *virens* enclosed a flower (hermaphrodite or female) in its axil (Fig. 5B, C). This flower appeared almost in the position of the remain flowers of the spikelet. In all the cases when this flower is present in the axil of a prophyll, the first glume, normally inserted in a transversal plane (with respect to the prophyll) was found to be always absent (Fig. 5B, C).

Accessory-axillar branch. New paracladia are observed between an axillary branch and its prophyll. These axes have a basipetal

development and maturation. Only one prophyll protected the accessory paracladia (Fig. 7C, D) and each of these accessory axes has its own prophyll in the axils of which a prophyllar branch can be produced.

The prophyllar and accessory-axillar branches can be either ramified or reduced to their cincinnasces (Table 2). In the different species accessory-axillar and prophyllar axes are arranged in different modes along the inflorescence and the long paracladia (Figs. 1-4). In some species accessory-axillar axes of 1st order can be developed from the proximal region upwards throughout the main axis (*C. eragrostis* var. *compactus*, *C. fraternus*, *C. reflexus*, *C. surinamensis*) (Fig. 2), in the middle-distal region (*C. eragrostis* var. *eragrostis*, *C. intricatus*, *C. luzulae*, *C. virens* var. *drummondii* and *C. virens* var. *virens*) or just in the distal region of the main axis (*C. entrerianus*, *C. hieronymi*, *C. virens* var. *montanus* and var. *virens*) (Fig. 1).

C. incomtus var. *incomtus* and *C. ochraceus* have prophyllar paracladia only. In both species, these paracladia are placed in the distal region of the main axis (Figs. 3, 4B). In *C. incomtus* var. *incomtus* also prophyllar

Table 4. Number of paracladia and spikelets in *Cyperus* section *Luzuloidei* Kunth

Character	<i>C. entrieanus</i>	<i>C. eragrostis</i> var. <i>compactus</i>	<i>C. eragrostis</i> var. <i>eragrostis</i>	<i>C. fraternus</i>	<i>C. incomtus</i> var. <i>incomtus</i>	<i>C. intricatus</i>	<i>C. luzulae</i>
N° pc 1 st axillar	(10-) 20-23 (-29)	8-10	(13-) 15-18 (-22)	13-18	7-14	18-22	(21-) 23-25 (-26)
N° pc 1 st accessory-axillar	(11-) 16-19 (-23)	9-14	(8-) 15-20 (-26)	(7-) 23-25 (-37)	0	19-24	(12-) 14-17
N° pc 2 nd axillar	(37-) 167-179 (-324)	16-18	(37-) 56-76 (-131)	(40-) 70-89	(0-) 2-6 (-32)	75-86	(150-) 161-169 (-180)
N° pc 2 nd accessory-axillar	(50-) 220-295 (-431)	20-21	(43) 120-180 (253)	(85-) 166-174	0	107-120	(139-) 156-190 (-208)
N° pc 2 nd prophyllar	(3-) 7-8 (-12)	4-7	0 (-2)	0-1 (-3)	(0-) 5-7	0	4-8
N° pc 3 rd axillar	(34-) 437-714 (-800)	0	(28-) 50-100 (-183)	(12) 47 (111)	0	46-52	(290-) 303-330 (-342)
N° pc 3 rd accessory-axillar	(31-) 707-857 (-1645)	0	(8-) 47-87 (-290)	(22) 63-86 (185)	0	55-60	263-267
N° pc 3 rd prophyllar	(25-) 100-146 (-216)	0 (-2)	0 (-5)	0	(0-) 3-5	0	(95-) 104-120 (-130)
N° pc 4 th axillar	(13-) 154-201 (-576)	0	0 (-2)	0 (-2)	0	0	30-32
N° pc 4 th accessory-axillar	(26-) 200-260 (-798)	0	0 (-2)	0 (-3)	0	0	(13-) 17-25 (-29)
N° pc 4 th prophyllar	(21-) 260-340 (-652)	0	0 (-2)	0-1	0	0	(74-) 94-133 (-153)
N° pc 5 th axillar	2-5 (-11)	0	0	0	0	0	0
N° pc 5 th accessory-axillar	(1-) 9-10	0	0	0	0	0	0
N° pc 5 th prophyllar	74-92 (-330)	0	0	0	0	0	0
N° pc 6 th prophyllar	0	0	0	0	0	0	0
N° spikelets	(247-) 2400-2600 (-5854)	70-90	(140-) 300-500 (-900)	(196-) 311-602	15-27 (-58)	788-800	1231-1272

N° pc 1 st axillar	19-22	13-19	15-17	20	30-41	21-25
N° pc 1 st accessory-axillar	0	(17-) 24 (-36)	35-47 (-62)	18	5-7	(9-)-15-18 (-33)
N° pc 2 nd axillar	89-90	50-70 (-112)	(90-) 120-165	131	288-300	150-200
N° pc 2 nd accessory-axillar	0	(51-) 158-234	(290-) 346-530 (-568)	124	132-145	170-320
N° pc 2 nd prophyllar	6-9	(0-) 1-3 (-5)	(0-) 7-12	0	4-6	0 (-5)
N° pc 3 rd axillar	64-86	(12-) 80 -117	(77) 250-335	257	1148-1200	310-530
N° pc 3 rd accessory-axillar	0	(11-) 137-226	(236-) 520-730 (-1200)	405	750-766	(430-) 570-700 (-970)
N° pc 3 rd prophyllar	29-58	(0-) 9	0-3 (-34)	0	95-100	0-2 (-30)
N° pc 4 th axillar	0-2	0-1 (-10)	(0-) 20-54	47	1290-1312	60-90 (-151)
N° pc 4 th accessory-axillar	0	0 (-18)	(0-) 39-58 (-115)	64	893-900	70-90 (-247)
N° pc 4 th prophyllar	13-62	0 (-2)	0-1 (-10)	0	510-545	0 (-10)
N° pc 5 th axillar	0	0	0	0	168-174	0
N° pc 5 th accessory-axillar	0	0	0	0	126-130	0
N° pc 5 th prophyllar	0	0	0	0	608-650	0
N° pc 6 th prophyllar	0	0	0	0	40-44	0
N° spikelets	247-299	200 - 500 (-788)	(755-) 1350-2500	1106	5689-6100	1260-1600 (-2436)

Abbreviation: pc paracladio; N° number of; 1°, 2°, ... order of ramification

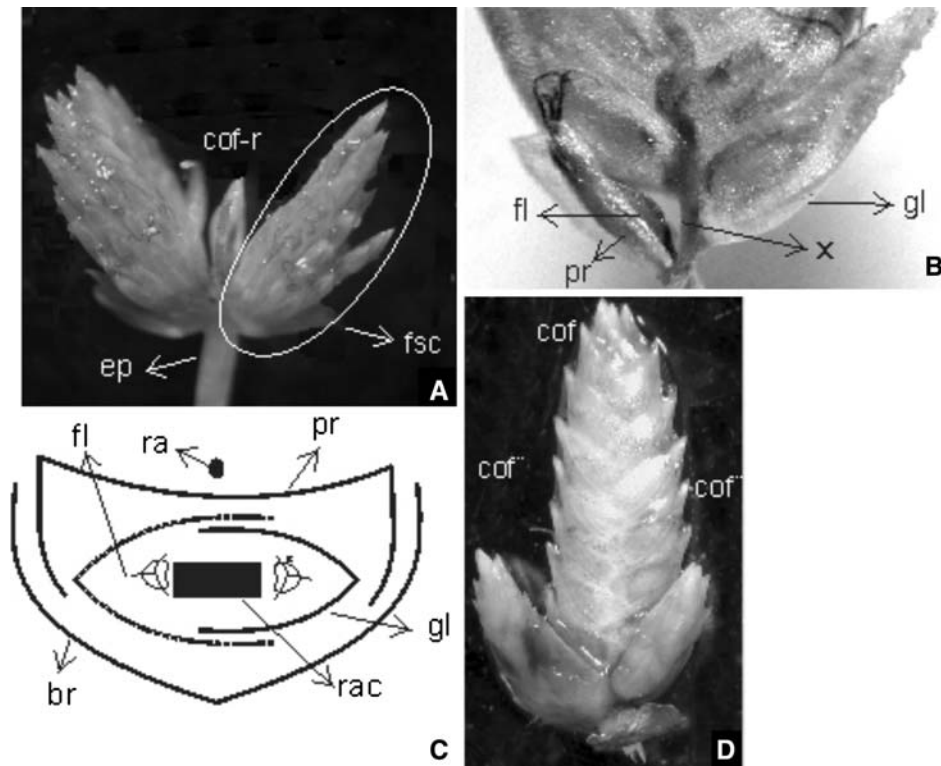


Fig. 5. A atrophied coflorescence in *C. eragrostis* var. *eragrostis*; B, C axillary flower of prophyll of *C. entrerianus*; D long paracladium of *C. incomtus* var. *incomtus*; br pherophyll; cof coflorescence of n-order; cof' coflorescence of n+1 order; cof-r rudimentary coflorescence; ep epipodium; fl flower; fsc fascicle (enclosed by the solid white line); gl glume; pr prophyll; ra rachis; rac rachilla; X indicate the position of the first absent glume. In C, broken line indicate the position of the absent glume

paracladia of 2nd order were observed throughout the main axis of the inflorescence, with the exception of the short paracladial subzone (Fig. 4A, C).

Fascicles of spikelets. Species studied in section *Luzuloidei* are characterized by spikelets grouped in fascicles (Fig. 8). These fascicles can be prophyllar (Fig. 8A, B), serial (Fig. 8C, D) and mixed (Fig. 8E, F) fascicles.

Prophyllar fascicles. They are constituted by two spikelets where the prophyllar ramification is not repeated successively. One of them originates in the axillary bud of a pherophyll and the other one in the axillary bud of the prophyll of the spikelet (Fig. 8A, B).

Serial fascicles. The spikelets are arranged one below the other, and all are protected by a single basal pherophyll (Figs. 5A, 8C, D). In

such type of fascicles a spikelet size hierarchy and a basipetal development sequence is observed, which can end in a bud or rudimentary spikelet. In some fascicles of *C. virens* var. *virens*, some spikelets do not display the basipetal sequence.

Mixed fascicles. The three types of ramification are conjugated (Fig. 8E, F). The number of accessory-axillary spikelets is variable, whereas the number of prophyllar spikelets is just one per prophyll, because this branching type never is repeated several times. In *C. entrerianus* and *C. virens* var. *montanus* two spikelets could be observed in the axil of the prophyll of a normal spikelet; these spikelets are arranged in a serial way (Fig. 8E and F).

The presence of one or another fascicle type varies with the species and varieties (Table 2). In the three types of fascicles

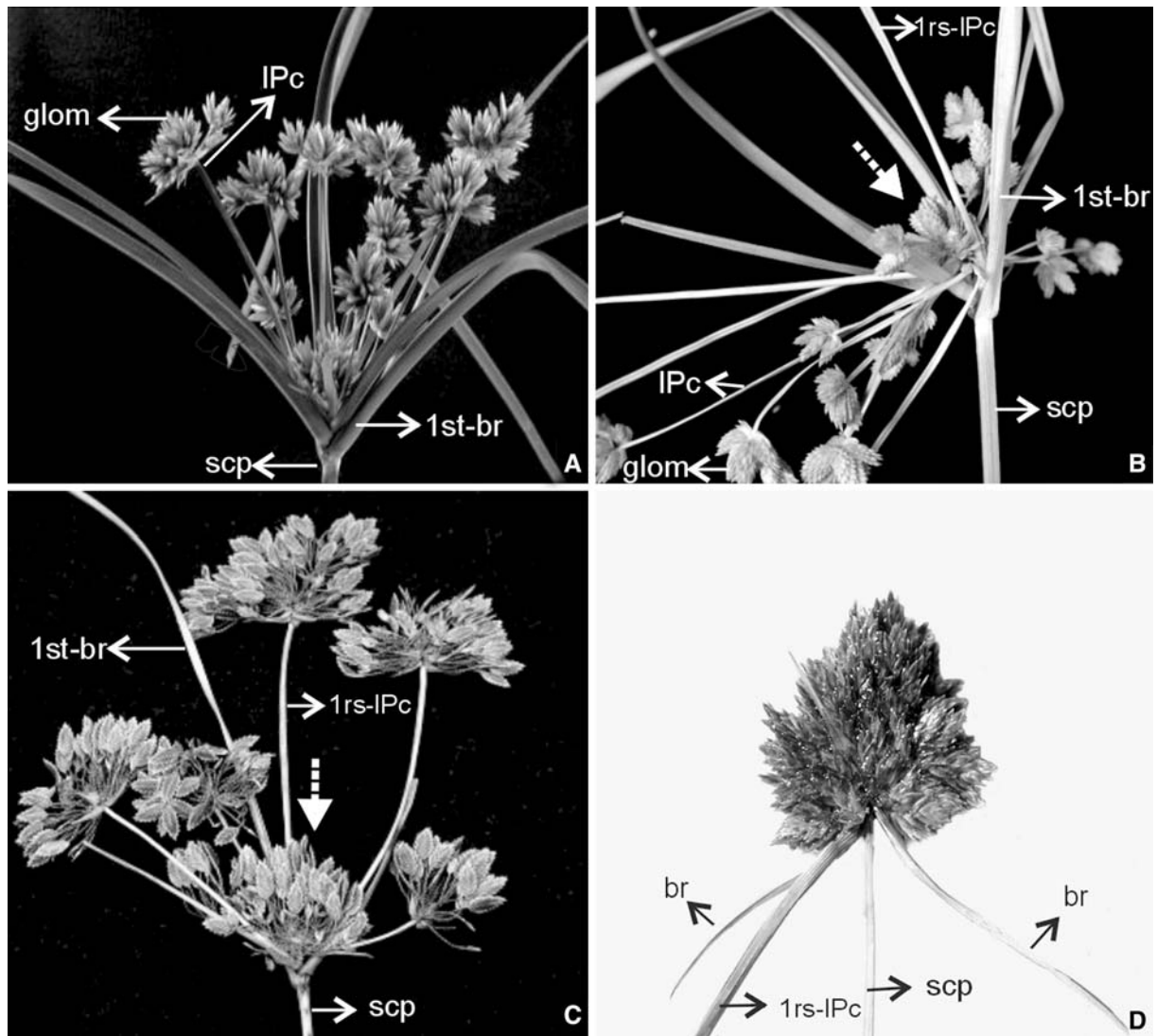


Fig. 6. Variation in the form and position of the inflorescences. **A** *C. eragrostis* var. *eragrostis*; **B** *C. surinamensis* var. *surinamensis*; **C** *C. fraternus*; **D** *C. reflexus*. *1st-br* first pherophyll; *1st-IPc* first long paracladium; *br* pherophyll; *glom* glomerulous; *IPc* long paracladium; *scp* scape. In **B** and **C** the broken white arrow shows the terminal head in the inflorescences and the position of the main axis

described the spikelets are arranged in the same plane formed by the only subtending pherophyll and the middle part of the prophyll (Fig. 8).

Paracladial zone. The paracladial zone can be divided in a subzone of short paracladia and a subzone of long paracladia (Figs. 1–4). The inflorescences studied (except, some *C. incomtus* var. *incomtus* inflorescences;

Fig. 4D) do not show a strong homogenization process. Hence the short paracladial subzone is small.

Generally the subzone of short paracladia presents only serial fascicles (Figs. 1, 2), but sometimes single spikelets can be observed (e.g. *C. enterianus*, *C. eragrostis* var. *eragrostis*, *C. hieronymi*, *C. luzulae*, *C. reflexus* and *C. virens* var. *montanus*). Rarely this subzone is

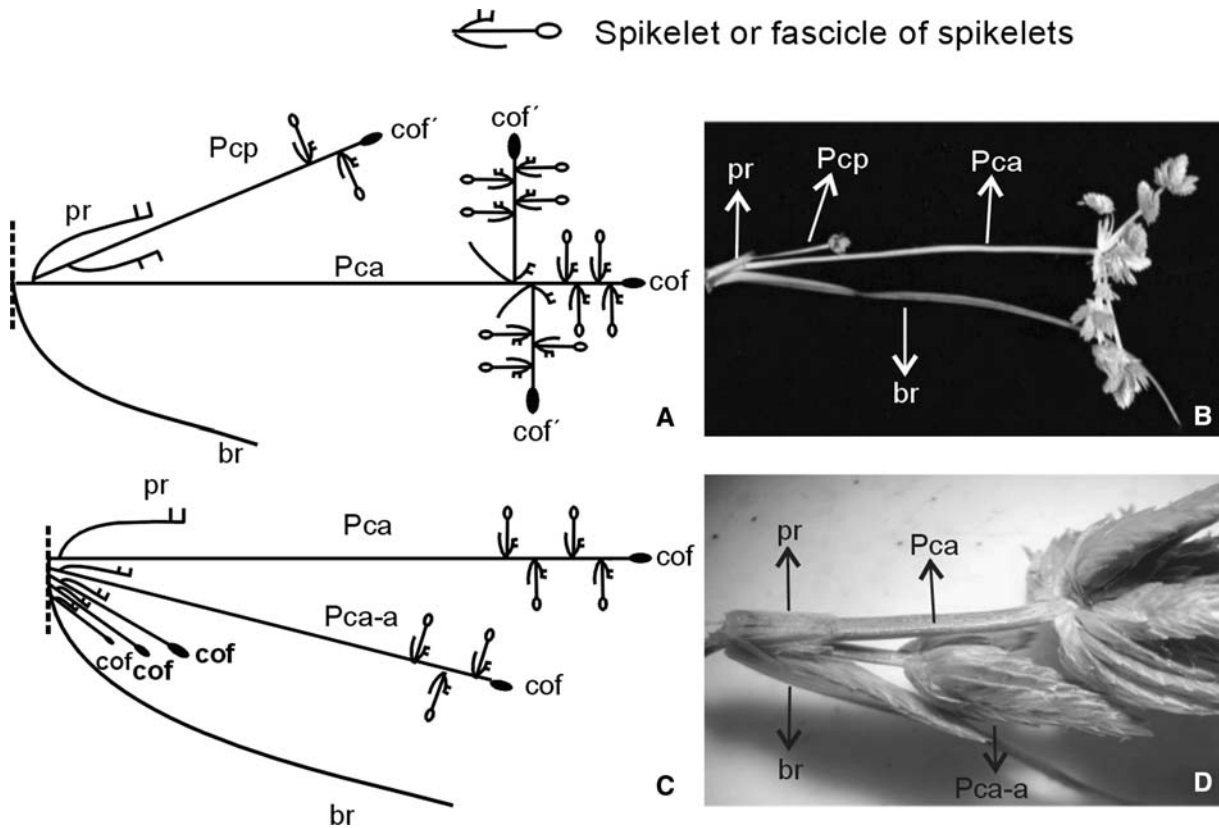


Fig. 7. Types of ramification. **A** scheme of prophyllar ramification; **B** prophyllar ramification of *C. surinamensis*; **C** scheme of accessory-axillar ramification; **D** accessory-axillar ramification of *C. eragrostis* var. *eragrostis*. *br* pherophyll; *cof* coflorescence of n-order; *cof'* coflorescence of n+1 order; *Pca* axillar paracladium; *Pca-a* accessory-axillar paracladium; *Pcp* prophyllar paracladium; *pr* prophyll

formed by mixed fascicles (*C. entrerianus*). Only in *C. incomtus* var. *incomtus* and *C. ochraceus*, this subzone is only constituted by single spikelets (Figs. 6, 7). In *C. entrerianus*, *C. eragrostis* var. *compactus*, *C. hieronymi*, *C. luzulae* and *C. virens* var. *montanus* the subzone of short paracladia is preceded by mixed fascicles (Fig. 1), which are not part of the homogenized subzone. In *C. incomtus* var. *incomtus* and *C. ochraceus* the subzone of short paracladia is preceded by prophyllar fascicles (Figs. 3, 4A–C). In some inflorescences of *C. incomtus* var. *incomtus* all the paracladia are reduced to their coflorescences (these paraclades present poorly developed buds in the axils of the prophylls); for that reason the inflorescences are completely

homogenized and only constituted by the main florescence and a short paracladial subzone (Fig. 4D).

Below the subzone of short paracladia, a subzone of long paracladia is observed. This subzone is constituted by paracladia that repeat the structure of the inflorescences (Figs. 1–4). This subzone displays variations in the order of ramification, length of paraclades, number of paraclades and spikelets (Tables 2–4). Variation in the type of ramification, in the arranged of the prophyllar and accessory-axillar branching along the main axis, and whether these are branching or not, is also observed (Table 2). These features can be useful for the differentiation of some of the species and varieties.

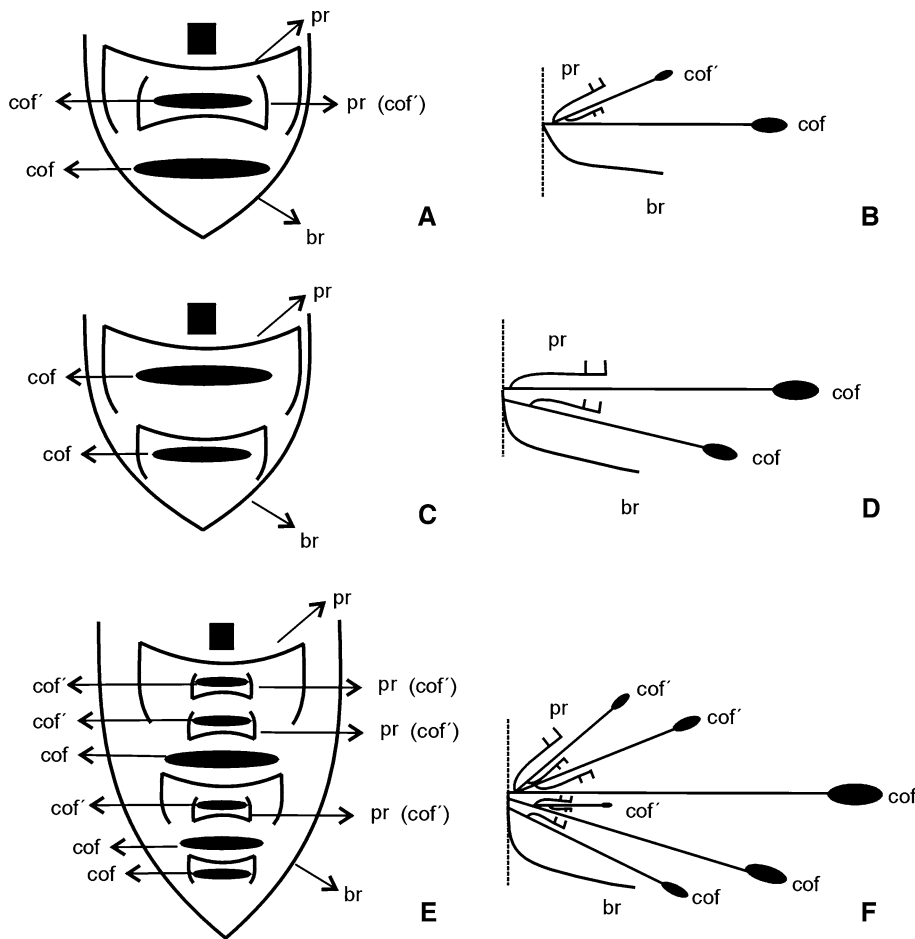


Fig. 8. Types of fascicles. **A, B** prophyllar fascicle; **C, D** serial fascicle; **E, F** mixed fascicle. *br* perophyll; *cof* coflorescence of 1st order; *cof'* coflorescence of 2nd order; *pr* prophyll; *pr (cof')* prophyll of the coflorescence of 2nd order

In the paracladial zone, the order, number and length of the paracladia decrease acropetally. In some inflorescences of *C. incomtus* var. *incomtus* a hierarchy in size of the main florescence over the first order co-florescence and the latter over the second order ones is observed. On certain occasions the spikelet of second order is less developed (Fig. 5D); this difference may be due to a differential development of the spikelet plus the observation of not completely mature inflorescences.

Spikelets. The structure of spikelets in the species studies is remarkably homogeneous. The spikelets have hermaphrodite and female flowers; the latter do not display a determinate

position within the spikelet. The glumes are generally arranged on a transversal plane formed by the perophyll and the prophyll (Fig. 9A, B). In *C. ochraceus* (Fig. 9E) and *C. incomtus* var. *incomtus*, due to a torsion epipodium of the spikelets, some spikelets appear with the glumes in the same plane as the perophyll and prophyll, or in an intermediate position. In *C. hieronymi* spikelets with the glumes disposed in one or another type as described above, are observed. However, unlike *C. ochraceus* and *C. incomtus* var. *incomtus*, the spikelets with the perophyll, prophyll and glumes in the same plane, do not show any evidence of torsion in the rachilla base (Fig. 9C, D).

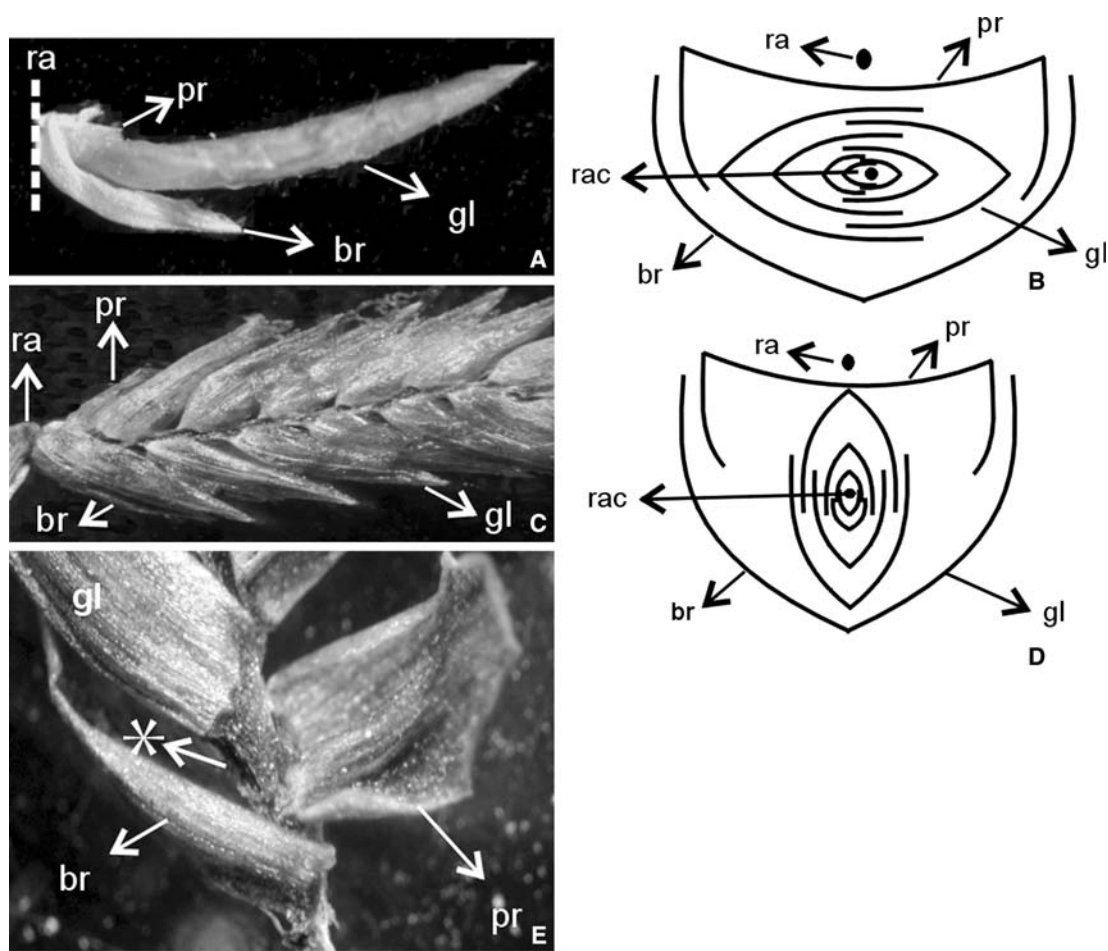


Fig. 9. Spikelets of *Cyperus* section *Luzuloidei*. **A, B** spikelets with the arranged on a transversal plane formed by the periphyll and the prophyll; **C, D** spikelets of *Cyperus hieronymi* with the glumes in the same plane as the periphyll and prophyll; **E** torsion of the epipodium of the spikelet of *Cyperus ochraceus* (indicated by an asterisk). *br* periphyll; *gl* glume; *pr* prophyll; *ra* rachis; *rac* rachilla

The number of spikelets is very variable between the species, even between the inflorescences of the same species (Table 4).

Phyllotaxis. The phyllotaxis varies along the synflorescence (main shoot); the disposition of the leaves in the trophotagma (vegetative zone) is tristichous (phyllotaxis $1/3$), whereas in the paracladial zone the periphylls, and their paraclades, have a spiral arrangement (Fig. 10), with a divergence fraction of $3/8$.

In the paracladial zone the formation of more than three orthostichies can be observed. Each of this orthostichies is conformed by paraclades from the basal and distal region of the inflorescences; whereas the paraclades of

the middle region are not positioned over any orthostichies (Fig. 10A). If the number of primary branches in the main axis is not nine or more than nine, there are no orthostichies (e.g. some *C. incomtus* var. *incomtus* inflorescences).

In the axillar (Fig. 10A) and prophyllar branching, the disposition of paraclades can follow a right-hand or left-hand spiral; showing an antidromic arrangement. This antidromic arrangement was not observed in the accessory-axillar ramification (Fig. 10C).

Another change in the phyllotaxis is observed at the last order branching (spikelet), in which, except for the prophyll, the

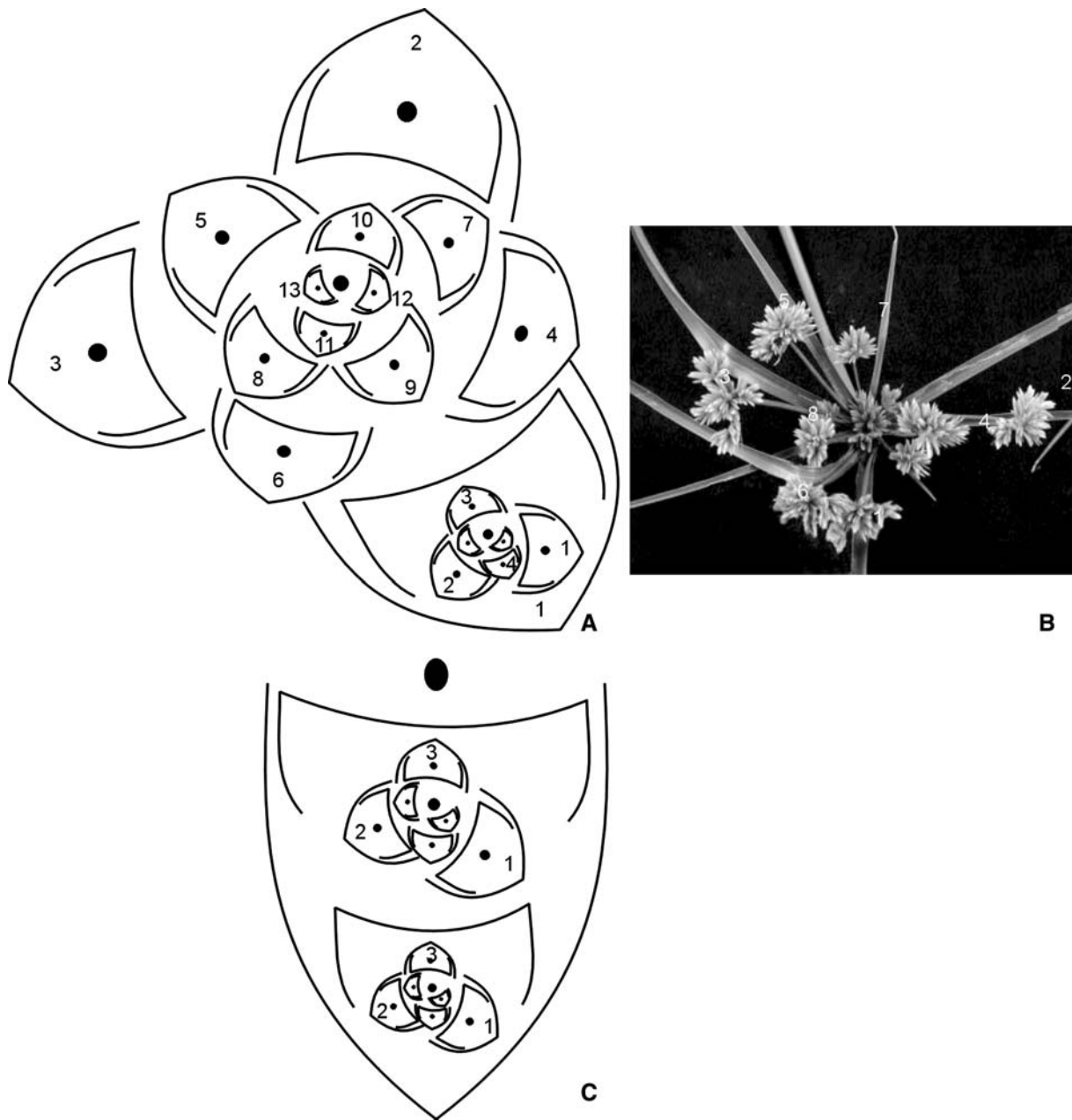


Fig. 10. Phyllotaxis. **A** disposition of the paraclades of first order in the main axis and paraclades of second order; **B** disposition of the paraclades of first order in the main axis in *C. eragrostis* var. *eragrostis*; **C** disposition of paraclades in the normal and accessory-axillary ramification; the numbers indicate the appearing order of appearance of paraclades

glumes have a distichous arrangement ($1/2$ phyllotaxis) (Fig. 10B). The distichous disposition of the glumes would indicate a change in the inflorescence phyllotaxis, from a spiral arrangement ($3/8$ phyllotaxis) to a distichous

phyllotaxis ($1/2$ phyllotaxis). This switch can be mediated by the prophyll of the spikelets in a transitional position, because it forms an angle of 90° with respect to the glumes. In *C. hieronymi* some spikelets present the pro-

phylls in a distichous position respective to the arrangement of the glumes (see spikelets) (Fig. 9C, D).

Discussion

The inflorescences of the species of *Cyperus* section *Luzuloidei* are polytelic (indeterminate inflorescence) as in most Monocotyledons (Weberling 1985, Alves 2000) and Cyperaceae (Mora-Osejo 1960, 1987; Kukkonen 1984, 1986; Vegetti and Tivano 1991; Vegetti 1992, 1994; Heinzen and Vegetti 1994; Alves et al. 2000; Vrijdaghs et al. 2003, 2004, 2005 a, b). In the basal portion of the principal axis each synflorescence (Troll 1964, Rua 1999) presents vegetative leaves. This is the trophotagma (Hagemann 1990). Within this trophotagma one can recognize an innovation and an inhibition zone. The internode above the distal vegetative leaf often elongates forming the scape (Mora-Osejo 1960, Heinzen and Vegetti 1994, Alves 2000), which still belongs to the inhibition zone (Vegetti 2003). In the distal portion of the inflorescence the axis ends in a spikelet (main florescence), below a paraclade zone is developed (Troll 1964, Weberling 1985, Rua 1999). In the paraclade zone, the acropetal reduction of the order of ramification, number and length of the paracladia is a common feature in the family (Haines 1966; Kukkonen 1984, 1986, Vegetti and Tivano 1991; Vegetti 1992, 1994; Heinzen and Vegetti 1994; Browning and Gordon-Gray 1999; Vegetti 2003).

It is remarkable that the transition from tristichous disposition, being characteristic for the leaves of the trophotagma region, to spiral arrangement in the paracladial zone is a relevant feature. Variation in the phyllotaxis along the inflorescence and its ramification was observed in grasses (Vegetti and Anton 1995; Cámara-Hernández 2001a, b; Reinheimer and Vegetti 2004; Kern et al. 2005; Reinheimer et al. 2005).

The inflorescences are anthela-like or of a capitate form, and can be terminal or pseudo-lateral. The variation in the internode lengths

of the paracladia and the main axis produce variation in the form of the synflorescences (Vegetti 2003). The degree of development of the different structures, especially the length of the paracladial epipodium has systematic (Denton 1978) and taxonomic relevance (Carter 1990, Tucker 1994).

Different kinds of perophylls and prophylls can be observed. On the main axis, the different types of perophylls and prophylls are not limited to the inflorescence subzones as happens in species of *Cyperus* subg. *Cyperus* (Lucero et al. 2005), where the homogenization process includes the foliar structures.

In the inflorescences of the species studied normal, prophyllar and accessory-axillar branching patterns were observed. Normal and prophyllar branching patterns have been described by several authors (Blazer 1944; Haines 1966; Guaglianone 1970, 1980, 1981, 1982; Meert and Goetghebeur 1979; Bruhl 1995; Goetghebeur 1998; Vegetti and Guaglianone 2005).

Guaglianone (1970) and Vegetti (1992) named the paracladia originating in the axil of a tubular prophyll “intraprophyllar” and those placed in the axils of a laminar prophyll “prophyllar”. The utility of the terms described above is confusing and we suggest to designate such structures as just “prophyllar”.

An accessory-axillar pattern is produced by serial buds. Evidence for the interpretation as serial buds is the lack of antidromic arrangement of these branches. The antidromic arrangement is typical of the successive ramification (Mora-Osejo 1960), and it was observed in the axillar and prophyllar branching present in the inflorescences studied. Further ontogenic studies allow us to explain the origin of these accessorial structures. Branches arising from accessory serial buds are observed in *Hypolytrum* Rich. (Alves et al. 2000) and *Cladium mariscus* R. Br. (Mora-Osejo 1960); while accessory collateral buds are observed in *Schoenus ferrugineus* (L.) (Mora-Osejo 1960) and in *Coleochloa setifera* (Ridley) Gilly (Kukkonen 1986).

In some species of section *Luzuloidei*, flowers in the axil of prophylls were observed. These axillary flowers have been also described by Meert and Goetghebeur (1979), Kukkonen (1984, 1986, 1990) and Timonen (1985). There is an intense controversy on the origin of the axillary flower in the prophyll. Koyama (1961) considered the prophyll in the Cyperaceae spikelets as a modified glume whose axillary flower aborts secondarily. However, Dahlgren et al. (1985) considered the flower in the axil of the prophyll to represent the axillary flower of the first undeveloped glume and not as part of a prophyllar bud. They did not mention the position of the undeveloped glume with respect to the prophyll of the spikelet. According to our observation (the relation of the prophyllar product and the position of the flower in the axil of the prophyll), it is reasonable to consider the prophyll as being homologous to a pherophyll and not to a glume. For that reason the prophylls in the species of *Cyperus* sect. *Luzuloidei*, independently of their form and position in the inflorescence, are modified pherophylls whose axillary buds may or may not produce a branch, but never a flower.

The spikelets are the florescences (Rua 1999), which, in Cyperaceae, have been considered as flowering unit (Eiten 1976), partial inflorescence (Pedersen 1969, Haines and Lye 1983) or fundamental inflorescence (Kral 1971). The spikelets bear hermaphrodite and female flowers; the latter, as observed by Barnard (1957), do not display a determinate position within the spikelet. The glumes are generally arranged on a transversal plane formed by the pherophyll and the prophyll (dorsiventrally compressed spikelet). In *C. hironymi* some spikelets have the pherophyll, prophyll and glumes on the same plane (laterally compressed spikelet).

In the section *Luzuloidei*, the spikelets are grouped in small fascicles; i.e. serial, prophyllar and mixed fascicles. In the three types of fascicles described, the spikelets are arranged in the same median plane formed by the only subtending pherophyll and the middle part of the prophyll. This disposition is not the most

generalized in the prophyllar branching pattern (Meert and Goetghebeur 1979). The serial fascicles of the species belonging to *Cyperus* section *Luzuloidei* resemble to the tandem pattern branching proposed by Meert and Goetghebeur (1979), and recognized by Bruhl (1995), but differ from these in the origin and the position of the branching. In the latter all ramifications are prophyllar and originate opposite to one of prophyllar keels; this condition is considered primitive (Haines 1966). Haines (1966) used the term "tandem branching" to describe a serial branching pattern, which is similar to the structure described in this work; in order to avoid the misapplication of terms relative to the serial structure we decided to call them fascicle.

Systematic value

The species of the section *Luzuloidei* appear to form a natural group (Denton 1978). The accessory-axillar and prophyllar branch, and the spikelets grouped in fascicles described in this work were not observed in other species of *Cyperus*. These characters can be distinctive features at sectional level. Probably one or more of these characters could be a synapomorphy of the section. According to the in-group comparison, the accessory-axillar branch appears to represent a primitive character within the section.

Notwithstanding that many characters observed in the inflorescences of the section are suitable to distinguish species or varieties (Tables 2–4), the ramification pattern, the types of fascicles, the constitution of the subzone of short paracladia and whether this is preceded by fascicles or not (and the type of these fascicles), are the best states of characters to delimit the following two groups:

Group 1: formed by species with accessory-axillar branch and subzone of short paracladia constituted by serial fascicles; inside of this group two subgroups can be recognized:

- a. mixed and serial fascicles, and subzone of short paracladia preceded by mixed fasci-

cles (Fig. 1): *C. entrerianus*, *C. eragrostis* var. *compactus*, *C. hieronymii*, *C. luzulae* and *C. virens* var. *montanus*.

- b. with only serial fascicles and subzone of short paracladia not preceded by mixed or prophyllar fascicles (Fig. 2): *C. eragrostis* var. *eragrostis*, *C. fraternus*, *C. intricatus*, *C. pseudovegetus*, *C. reflexus*, *C. surinamensis*, *C. virens* var. *drummondii* and *C. virens* var. *virens*.

Group 2: formed by species without serial branches, only with prophyllar fascicles, the subzone of short paracladia constituted by single spikelets and preceded by prophyllar fascicles (Figs. 3, 4); this is observed in *C. incomtus* var. *incomtus* and *C. ochraceus*; subzone of short paracladia.

A comprehensive treatment of the section *Luzuloidei* was published by Denton (1978). Many of the relationships and groups established in her work, and other treatments (Denton 1983, Carter et al. 1996, Araujo and Longhi-Wagner 1997), are incongruent with the groups proposed here, being based in similarities of the inflorescences.

Of the species considered within the subgroup 1-a, *C. entrerianus*, *C. luzulae* and *C. hieronymii* appear to be closely related (perhaps represent the same evolutionary line), whereas the inflorescence of *C. virens* var. *montanus* and *C. eragrostis* var. *compactus* could be the result of a parallel evolution. The close relationship between *C. entrerianus* and *C. luzulae* has been proposed by Carter (1990) and Tucker (1994), on the basis of vegetative and reproductive characters. *C. hieronymii* presents some spikelets with its perophyll, prophyll and glumes in the same plane (laterally compressed); this is the most distinctive character of this species. Denton (1978) excluded *C. hieronymii* from the section *Luzuloidei*, while Barros (1925, 1938) included it in his section *Chorystachys* (now included in the subgenus *Cyperus*). Despite that, form, ramification patterns and the inflorescence structure of *C. hieronymii* are very similar to the remaining species studied here. This especially applies

to *C. entrerianus*. Considering this, the exclusion of the section *Luzuloidei* is not supported by the inflorescence characters.

According to Denton's system (1978), all species included in our subgroup 1-b, except *C. pseudovegetus*, constitute a distinctive group, distantly related to the rest of the species of the section *Luzuloidei*. Inside this group, *C. reflexus* and *C. fraternus* on one hand, and *C. virens* s.l. on the other hand, constitute two distinctive groups (Denton 1978, 1983); related to *C. virens* s.l. are *C. intricatus* and *C. surinamensis* (Denton 1978). These relationships are supported by the structure of the inflorescence, except for *C. virens* var. *montanus* and *C. intricatus*. The first species shows clear differences to the remaining varieties studied here, and the second species shows similarities with *C. eragrostis* var. *eragrostis*.

C. pseudovegetus appears more closely related to *C. luzulae* (Denton 1978, 1983), however the inflorescence of *C. pseudovegetus* presents intermediate characters between *C. eragrostis* var. *eragrostis* and *C. luzulae*. *C. eragrostis* var. *compactus* is recognized by Barros (1947) but not by Denton (1978). The difference observed in the inflorescences supports the distinction of two varieties.

C. incomtus var. *incomtus* and *C. ochraceus* are the most distinctive species in the section. *C. incomtus* var. *incomtus* has been excluded from the section by Denton (1978) to appear most similar to the section *Glutinosi* (with C_4 anatomy). Similarities in the inflorescence of *C. incomtus* var. *incomtus* with *C. ochraceus* and in its anatomical character with other species of the *Luzuloidei* section (Araujo and Longhi-Wagner 1997) do not support the exclusion proposed by Denton (1978). Further studies are necessary to determine the position of *C. incomtus* var. *incomtus*. There is no doubt, that inflorescence structure has a definite systematic value for the section. However, this consideration must be handled with care. The inflorescence typology provides a valuable tool for making hypotheses of primary homology (De Pinna 1991). It is advisable to test

such hypotheses by a cladistic analysis. Despite of the treatment of Denton (1978), there is no comprehensive phylogenetic analysis of the section *Luzuloidei*. For that reason, the relationships established in this work are preliminary and further cladistic analyses of the section that include inflorescences characters, are needed.

The authors are grateful to Prof. E. R. Guaglianone for the critical reading of the manuscript and suggested improvements and Dr. Focko Weberling for help us in the translation of the manuscript.

References

- Aagesen L (1999) Phylogeny on the tribe Colletiae, Rhamnaceae. *Bot J Linn Soc* 131: 1–43
- Adams CD (1992) *Cyperaceae*. Flora Trinidad and Tobago 3(5): 383–562. Government Printer, Port of Spain
- Alves MV (2000) Abordagem Tipológica das Inflorescências em Monocotiledóneas. Tópicos Atuais em Botânica. 51º Congresso Nacional de Botânica. Brasília, DF. pp 17–22
- Alves MV, Wanderley MGL, Thomas WW (2000) Typology of the inflorescence in species of *Hypolytrum* Rich. (*Cyperaceae*) from Brazil. *Beitr Biol Pflanzen* 72: 59–73
- Araújo AC, Longhi-Wagner HM (1997) Anatomia foliar e micromorfologia da superfície do fruto na taxonomia de *Cyperus* L. (*Cyperaceae*) *Iheringia*, ser Bot 48: 103–120
- Barnard C (1957) Floral histogenesis in the Monocotyledons. II. The *Cyperaceae*. *Austral J Bot* 5: 115–128
- Barros M (1925) *Ciperáceas Argentinas*. Clave para la determinación de los géneros. *Revista Centro de Estudiante Agron y Vet* 125–126: 641–667
- Barros M (1938) *Ciperáceas argentinas III*, géneros *Androtrichum*, *Lipocarpha*, *Ascolepis* y *Cyperus*. *An Mus Cienc Nat Buenos Aires* 39: 253–381
- Barros M (1947) *Cyperaceae*. In: Descole H (ed) *Genera et Species Plantarum Argentinae*. Tomo IV (I y II). Buenos Aires, pp 1–539
- Blazer HW (1944) Studies in the morphology of the *Cyperaceae*. II. The prophyll. *Amer J Bot* 31: 53–64
- Browning J, Gordon-Gray KD (1999) The inflorescence in southern African species of *Bolboschoenus* (*Cyperaceae*). *Ann Bot Fennici* 36: 81–97
- Bruhl J (1995) Sedge genera of the world: relationships and a new classification of the *Cyperaceae*. *Austral Syst Bot* 8: 125–305
- Cámara Hernández J (2001a) La polistiquia en las inflorescencias de las Poáceas. *Bol Soc Argent Bot* 36 (Supl.): 9–10
- Cámara Hernández J (2001b) Morfología de las inflorescencias de *Diplachne* y *Leptochloa* (*Poaceae*). *Bol Soc Argent Bot* 36: 267–278
- Carter R (1990) *Cyperus entrerianus* (*Cyperaceae*), an overlooked species in temperate North America. *Sida* 14: 69–77
- Carter TB, Bryson TC, Andreas L (1999) The taxonomy of *Cyperus virens* and *Cyperus drummondii* (*Cyperaceae*) in the southeastern United States. *Sida* 18: 1049–1063
- Clarke CB (1908) New genera and species of *Cyperaceae*. *Kew Bull Add series VIII*
- Dahlgren RMT, Clifford HT, Yeo PF (1985) The families of the Monocotyledons: Structure, evolution and taxonomy, VI–XII, Springer Berlin, pp 1–520
- Denton MA (1978) A taxonomic treatment of the *Luzulae* group of *Cyperus*. *Contr Univ Michigan Herb* 11: 197–271
- Denton MA (1983) Anatomical studies of the *Luzulae* group of *Cyperus* (*Cyperaceae*). *Syst Bot* 8: 250–262
- De Pinna MCC (1991) Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7: 367–394
- Eiten LT (1976) Inflorescence units in the *Cyperaceae*. *Ann Missouri Bot Gard* 63: 113–112
- Goetghebeur P (1989) Studies in *Cyperaceae* 9. Problems in the Lectotypification and Infrageneric Taxonomy of *Cyperus* L. *Bull Soc R Bot Belg* 122: 103–114
- Goetghebeur P (1998) *Cyperaceae*. In: Kubitzki K, Huber H, Rudall PJ, Stevens PS, Stützel T (eds) *The families and genera of vascular plants*, vol 4, Springer Berlin, pp 141–190
- Guaglianone ER (1970) Un nuevo carácter útil en la distinción genérica entre *Fimbristylis* Vahl y *Bulbostylis* Kunth (*Cyperaceae*). *Darwiniana* 16: 40–48
- Guaglianone ER (1980) Contribución al estudio del género *Rhynchospora* Vahl (*Cyperaceae*) II. *Darwiniana* 22: 449–509

- Guaglianone ER (1981) Contribución al estudio del género *Rhynchospora* Vahl (Cyperaceae) III. Darwiniana 23: 489–506
- Guaglianone ER (1982) Contribución al estudio del género *Rhynchospora* Vahl (Cyperaceae). IV. *Rhynchospora iberae* nueva especie de América Austral. Darwiniana 24: 469–473
- Guaglianone ER (1996) Cyperaceae. In: Lahitte HBJ, Hurrell A (eds) Las Plantas Hidrófilas de la Isla Martín García Buenos Aires. Ser Informes 52: 70–96, 217
- Hagemann W (1990) Comparative morphology of acrogeous branch systems and phylogenetic considerations. II Angiosperms Acta Biotheor 38: 207–242
- Haines RW (1966) Prophylls and branching in Cyperaceae. Journ E Afr Nat Hist Soc 26: 51–78
- Haines RW, Lye KA (1983) The sedges and rushes of East Africa. East African Natural History Society, Nairobi, p 404
- Heinzen FA, Vegetti AC (1994) Typology of the inflorescence in *Cyperus corymbosus* var. *subnodosus* and *C. rotundus* (Cyperaceae). Beitr Biol Pflanzen 68: 263–273
- Kern V, Guarise NJ, Vegetti AC (2005) Estructura de la inflorescencia en especies de *Spartina* Schreb. (Poaceae: Chloridoideae: Cynodonteae). Soc Argent Bot 40 (Supl.): 175
- Koyama T (1961) Classification of the family Cyperaceae I. J Faculty Sci Univ Tokyo 8: 37–148
- Kral R (1971) A treatment of *Abildgaardia*, *Bulbostylis* and *Fimbristylis* (Cyperaceae) for North America. Sida 4: 57–227
- Kükenthal G (1935–1936) Cyperaceae-Scirpoideae-Cypereae. In: Engler A (ed) Pflanzenr. 4, 20 (101): 1–160. 1935; 161–671. 1936
- Kukkonen I (1984) On the inflorescence structure in the family Cyperaceae. Ann Bot Fennici 21: 257–264
- Kukkonen I (1986) Special features of the inflorescence structure in the family Cyperaceae. Ann Bot Fennici 23: 107–119
- Kukkonen I (1990) The inflorescence, structure of *Kobresia myosuroides* and related species of sect. *Elyna* (Cyperaceae). Ann Bot Fennici 27: 159–167
- Kukkonen I (1994) Definition of descriptive terms for the Cyperaceae. Ann Bot Fennici 31: 37–43
- Liu Q, Zhao N, Hao G (2005) Inflorescence structures and evolution in subfamily Chloridoideae (Gramineae). Pl Syst Evol 251: 183–198
- Lucero JJ, Guarise NJ, Vegetti AC (2005) Tipología de la Inflorescencia de *Cyperus* sección *Chlorocyperus* (Cyperaceae). Soc Argent Bot 40 (Supl.): 46
- Meert M, Goetghebeur P (1979) Comparative floral morphology of Bisboeckelereae and Cariceae (Cyperaceae) on the basis of the anthoid concept. Bull Soc Roy Bot Belg 112: 128–143
- Mora-Osejo LE (1960) Beiträge zur Entwicklungsgeschichte und vergleichenden Morphologie der Cyperaceen. Beitr Biol Pflanzen 35: 293–341
- Mora-Osejo LE (1987) Estudios morfológicos autoecológicos y sistemáticos en Angiospermas. Acad. Colombiana de Ciencias Exactas, Físicas y Naturales. Ser Jorge Álvarez Lleras 1, Bogotá, p 195
- Muasya AM, Simpson DA, Chase MW, Culham A (1998) An assessment of suprageneric phylogeny in Cyperaceae using *rcbL* DNA sequences. Pl Syst Evol 211: 257–271
- Muasya AM, Brulh JJ, Simpson DA, Chase MW, Culham A (2000) Suprageneric phylogeny of Cyperaceae: a combined analysis. In: Wilson KL, Morrison DA (eds) Monocots: Systematics and evolution, pp 610–614
- Muasya AM, Simpson DA, Chase MW (2002) Phylogenetic relationships in *Cyperus* L. s.l. (Cyperaceae) inferred from plastid DNA sequence data. Bot J Linn Soc 138: 145–153
- Nickol M G (1995) Phylogeny and inflorescences of Berberidaceae, a morphological survey. Pl Syst Evol (Suppl) 9: 327–340
- Pedersen TM (1969) Cyperaceae. In: Cabrera AL (ed) Flora de la Provincia de Buenos Aires. Tomo IV (I). Colección Científica del I.N.T.A. Buenos Aires, pp 315–421
- Perreta MG, Vegetti AC (2002) The inflorescence of *Cyperus giganteus* Vahl (Cyperaceae). Feddes Rept 113: 256–260
- Reinheimer R, Vegetti AC (2004) The inflorescences of South American species of *Panicum* subg. *Phanopyrum* sect. *Laxa* (Poaceae: Panicoideae: Paniceae). Beitr Biol Pflanzen 73: 185–199
- Reinheimer R, Zuloaga F, Vegetti A, Pozner R (2005) Desarrollo temprano y homologías de las inflorescencias en el clado PCK (Poaceae: Panicoideae: Paniceae). Soc Argent Bot 40 (Supl.): 178
- Rua GH (1999) Inflorescencias. Bases Teóricas para su Análisis. Sociedad Argentina de Botánica. Buenos Aires. p 100

- Rua GH, Aliscioni SS (2002) A morphology-based cladistic analysis of *Paspalum* sect. *Pectinata* (Poaceae). *Syst Bot* 27: 489–501
- Rua GH, Weberling F (1995) Growth form and inflorescence structure of *Paspalum* L. (Poaceae, Paniceae): A comparative morphological approach. *Beitr Biol Pflanzen* 69: 363–431
- Timonen T (1985) Synflorescence morphology and anatomy in *Kobresia laxa* (Cyperaceae). *Ann Bot Fennici* 12: 153–171
- Tortosa RD, Rua G, Bartoli A (2004) A typological analysis of the inflorescences of the genus *Nassauvia* (Asteraceae). *Flora* 199: 42–46
- Troll W (1964) Die Infloreszenzen, Typologie und Stellung im Aufbau des Vegetationskörpers, vol 1. Gustav Fischer, Jena
- Tucker GC (1983) The taxonomy of *Cyperus* (Cyperaceae) in Costa Rica and Panama. *Syst Bot Monogr* 2: 1–85
- Tucker GC (1994) Revision of the Mexican species of *Cyperus* (Cyperaceae). *Syst Bot Monogr* 43: 213
- Vegetti AC (1992) Typology of the inflorescence in species *Schoenoplectus* (Cyperaceae) in Austral America. *Beitr Biol Pflanzen* 67: 241–249
- Vegetti AC (1994) Typology of the inflorescence of *Isolepis*. *Beitr Biol Pflanzen* 68: 21–26
- Vegetti AC (2002) Typological reinterpretation of the inflorescences in Cariceae (Cyperaceae). *Phyton* 42: 159–168
- Vegetti AC (2003) Synflorescence typology in Cyperaceae. *Ann Bot Fennici* 40: 35–46
- Vegetti AC, Anton AM (1995) Some evolution trends in the inflorescence of Poaceae. *Flora* 190: 225–228
- Vegetti AC, Guaglianone ER (2005) Estructura de las inflorescencias en especies de *Rhynchospora* Vahl (Cyperaceae) de América. *Austral Bol Soc Argent Bot* 40 (Suppl.): 48
- Vegetti AC, Tivano JC (1991) Inflorescence typology in *Schoenoplectus californicus* (Cyperaceae). *Beitr Biol Pflanzen* 66: 323–345
- Vrijdaghs A, Goetghebeur P, Smets E, Caris P (2003) The unusual development of the gynoeceum of *Cladium mariscus* (L.) Pohl (Cyperaceae). Symposium for Biodiversity and Evolutionary Biology at Frankfurt, Germany
- Vrijdaghs A, Goetghebeur P, Muasya MA, Smets E, Caris P (2004) The nature of the perianth in *Fuirena* (Cyperaceae). *South Afr J Bot* 70: 587–594
- Vrijdaghs A, Caris P, Goetghebeur P, Smets E (2005a) Floral ontogeny in *Scirpus*, *Eriophorum* and *Dulichium* (Cyperaceae), with special reference to the perianth. *Ann Bot* 95: 1199–1209
- Vrijdaghs A, Goetghebeur P, Muasya MA, Caris P, Smets E (2005b) Floral Ontogeny in *Ficinia* and *Isolepis* (Cyperaceae), with Focus on the Nature and Origin of the Gynophore. *Ann Bot* 96: 1247–1264
- Weberling F (1985) Aspectos modernos de la morfología de las inflorescencias. *Bol Soc Argent Bot* 24: 1–28
- Weberling F (1989) Morphology of flowers and inflorescences. Cambridge Univ Press, London. p 405