



Synflorescence Architecture studies in some Indian Cypereae (Cyperaceae)

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Abstract

The tribe cypereae comprises 19 genera and 900 species, of which the genus *Cyperus* is the largest having a cosmopolitan distribution. There are differences in opinion on the delimitation of the genus. The comparative typological analysis of synflorescence has proved to be a major source of reliable diagnostic traits for the same. In this context, synflorescence variations in more than 35 taxa of Cypererae. were analyzed during present investigations and systematic value is discussed in detail. In the phenetic analyses all the studied taxa were grouped in to two major groups based on synflorescence and achene characters. Furthermore, type of inflorescence, rachilla disarticulation and spikelet prophylls are found to be most functional characters. The results show *Cyperus s.s.* to be polyphyletic, and merging of all the segregated taxa into *Cyperus s.l.* and recognizing as subgenera would make a monophyletic entity.

Keywords: *Cyperus*, *Courtoisina*, *Kyllinga*, *Pycnus*, *Queenslandiella*, synflorescence

Introduction

Cyperaceae are the third largest monocotyledonous family comprising 109 genera and about 5,500 species. It constitutes two large genera- *Carex* L. (1757 spp.) and *Cyperus* L. (686 spp.) having a cosmopolitan distribution (Govaerts *et al.*, 2011; Muasya *et al.*, 1998). Cyperaceae are resolved as monophyletic and originated from Juncaceae, with Mapanioideae (Plunkett *et al.*, 1995; Goetghebeur, 1998). Modern classifications for the family proposed by Goetghebeur (1986) and Bruhl (1995) are based on morphological, anatomical, embryological, phytochemical and physiological characters. Goetghebeur (1986) subdivided the family into 4 subfamilies and 17 tribes on the basis of cladistic analyses, while, Bruhl (1995) classified the family into 2 subfamilies and 12 tribes, based on cladistic and phenetic analyses using DELTA datasets (Dallwitz *et al.*, 1993). Several phylogenetic analyses based on molecular data suggested various relationships between and within the taxa (Muasya *et al.*, 1998, 2002, 2009; Starr *et al.*, 2004; Ford *et al.*, 2006; Simpson *et al.*, 2007). However, phylogenetic analyses based on morphological data remain scarce in the absence of adequate number of valuable morphological characters in sedges (Goetghebeur & Borre, 1989; Guarise & Vegetti, 2008b; Naczi, 2009; Reutemann *et al.*, 2009).

Traditional infrageneric classification of the genus *Cyperus* comprises six sub-genera, i.e., *Cyperus*, *Mariscus*, *Torulinium*, *Pycnus*, *Juncellus* and *Kyllinga* (Kukenthal, 1936). Recent studies in Cypereae recognize two major groups, the *Fiania* and *Cyperus* clades. *Cyperus* is the core genus, in the *Cyperus* clade in which the thirteen segregate genera (*Alinula*, *Androtrichum*, *Ascolepis*, *Courtoisina*, *Kyllinga*, *Kyllingiella*, *Lipocarpha*, *Oxycaryum*, *Pycnus*, *Queenslandiella*, *Remirea*, *Sphaerocyperus* and *Volkiella*) are embedded (Muasya *et al.*, 2009). As inflorescence diversification play a pivotal role in understanding the relationship between different taxa, it appears appropriate to consider it as a new viewpoint, and it also provides the significant values for phylogenetic analyses (Tucker & Grimes, 1999; Liu *et al.*, 2005; Rua & Aliscioni, 2002; Tortosa *et al.*, 2004; Urdampilleta *et al.*, 2005). Thus, in the last few years, structure of inflorescences being studied by many cyperologists. The establishment of homologies among different types of inflorescences is one of the main concerns of the researchers (Raynal, 1971; Eiten, 1976; Reutemann *et al.*, 2009; Guarise *et al.*, 2012; Desai & Raole, 2013). In these circumstances, comparative typological analysis was started with the work of Troll (1964) and Weberling (1989), and revised by Vegetti (2003) and Reutemann *et al.* (2012) for the Cyperaceae.

In a typological interpretation, 'a system of flower bearing branches and their relative positions on a plant is called as Synflorescence' (Troll 1964). More precisely, the term 'inflorescence' is deliberately kept rather imprecise in order to have a convenient word, for each inductive attempt at the analysis of an unknown inflorescence system. On the other hand, use of the term 'synflorescence' requires the analysis of structure of a given inflorescence within the context of the whole branching system of a taxon and its allies for their relationships (Weberling, 1992). Studies on *Cyperus* inflorescences are rare (Heinzen & Vegetti, 1994; Perreta & Vegetti, 2002) and they include very few species, without implementing a comparative study within infrageneric categories except the work of Guarise & Vegetti (2008b). To solve the taxonomic problems and the relationships in *Cyperus*, a precise morphological study at species level is required (Muasya *et al.*, 2000). In addition to that, Muasya *et al.* (2009) also raised the point to incorporate inflorescence characters of cyperaceae members for phylogenetic studies. In this context, the present study is a step towards the re-evaluation of synflorescence structure in species of *Cyperus s.l.* in order to provide new useful data which may be used in further revision of the genus. In addition to above, it also helps to provide new characteristic features for the taxonomic, phenetic and cladistic studies for this family.

Synflorescence Architecture

Plants of sedges are composed of shoots of consecutive order of ramification and terminate in an inflorescence (Moore & Mooser, 1995). According to the typological system, each one of these shoots constitutes inflorescences and the entire system is called synflorescence (Troll, 1964; Vegetti, 2003). In the synflorescence two principal parts are recognized: proximal portion is the trophotagma (TT) and the distal one is unit of inflorescence (UIF) (Vegetti & Muller-Doblies, 2004). The trophotagma has an innovation zone (IZ) at/near the base of shoot, which bears proximally cataphylls and foliage leaves, and comprised of a basal zone of short internodes (SIZ) and a distal zone of long internodes (LIZ) (Rua & Weberling, 1998; Tivano *et al.*, 2009). The LIZ can constitute an inhibition zone (HZ), an extension of the enrichment zone (EZ) or a region that behaves in part as HZ and in part as EZ (Rua & Weberling, 1998), and is characterized by the absence of axillary axes, the presence of leaves with sheaths and well-developed blades.

The main florescence (HF) and paraclades (Pc) of various magnitudes make up the enrichment zone (EZ) or paracladial zone. The enrichment axes originating in the distal region of the LIZ normally bears a prophylls and developed leaves called trophotagma (Rua & Weberling, 1998; Vegetti & Weberling, 1996) and terminate in an UIF similar to that of the relative mother axis that supports them. These axes have been denominated 'paraclades of the trophotagma' (Vegetti & Muller-Doblies, 2004), 'long paraclades of second order' (Weberling & Muller-Doblies, 1993) or 'paraclades with trophotagma' (Vegetti & Weberling, 1996). From the axillary buds of the trophotagma of these enrichment axes, new axes of similar structure can be originated. In this mode, the LIZ can contribute to increase the number of flowering branches of the plant (Rua & Weberling, 1998).

In sedges, the unit of inflorescence (UIF) is composed of group of flowers on indefinite growth axis (spikelet), thus the synflorescence is polytelic, such as those found in other monocots (Troll 1964, Camara-Hernandez & Rua, 1991; Vegetti, 1993). It has both homothetic inflorescences, which are always unispiculate (only terminal spikelet- HF), and heterothetic inflorescences, formed by the HF and the PZ (Rua, 1999). Here, spikelets functionally replace the individual flowers of a 'panicle' (Raynal, 1971; Weberling, 1992; Kukkonen, 1994; Goetghebeur, 1998). In his treatment of inflorescences, Troll (1964) proposed that the panicle gives rise to the anthela, by lengthening of paraclades over main axis. For polytelic inflorescences he coined the terms 'paniculodium', and 'anthelodium' respectively for cyperoid taxa.

In a paracladial zone (PZ), paraclades as a rule originate from the axils of a leaf (phyllome), which is called 'subtending leaf/ bract/ spathe/ pherophyll'. Thus, a pherophyll is defined by its position, and not by its shape (Endress, 2010). Pherophylls are not restricted to inflorescences, but are of general occurrence in a ramifying flowering plant. The first phyllome on each lateral branch commonly remains small and has the shape of bracts, called 'prophyll/ bracteole/ spatheole' (Endress, 2010). Both bracts and prophylls may be foliaceous, laminar, setiform, tubular (cladoprophyll) or glumaceous, according to their position and function. At the base of the prophylls (of spikelets and/or inflorescence branches), a swelling body or pulvinus is present (Haines, 1967). This play a role in the expansion of the paraclades or spikelets, and it related to wind pollination. Thus, each paraclade (Pc) possesses a short hypopodium (internode

between the bract subtending the spikelet and the prophyll, a prophyll (pr), and a long epipodium (internode between the prophyll and the second glume) and ends in a coflorescence (Cof, terminal spikelet of the paraclade).

In addition to above, PZ comprises two subzones; a short distal paracladial subzone (sPcZ) that bears sPc reduced to its Cof in the distal region below the HF, and a long paracladial subzone (lPcZ) that also bears lPc of different branching degrees. Branching degree decreased distally along the lPcZ, until paraclades are reduced to Cof in the sPcZ (Vegetti, 2003). Kellogg (2006) considers that the variations observed in the phyllotaxis of the primary inflorescence branches and in the inflorescence symmetry should be further looked into in future developmental studies. Besides that, paraclades of the 2nd order or above can show the same phyllotaxis pattern as the main axis; i.e., homodromic arrangement or the arrangement can differ from the main axis; i.e., antidromic arrangement (Weberling, 1992). For a proper interpretation of the inflorescence, it is important to know the inflorescence ramification pattern (Haines, 1967; Meert & Goetghebeur, 1979; Vegetti & Tivano, 1991) and the branch position in the inflorescences (Guarise & Vegetti, 2008b). In the inflorescence, three types of branching can be observed:

Normal branching: the branch is produced by an axillary bud of a bract

Prophyllar branching: the branch is produced by a prophyllar bud

Accessory branching: new branches are observed between an axillary branch and its bract.

It is well accepted that the spikelet is composed of an indefinite axis (rachilla), which bears flowers in lateral position. Although it is often hard to rule out the possibility of a tiny residual inflorescence meristem; in this case the 'terminal' flower would actually be lateral (Malcomber *et al.*, 2006). Vrijdaghs *et al.* (2010, 2011) have given general developmental model for spikelet structure and suggested the process of epicaulescence for the winged rachilla and its effect on the orientation of the pistil (dorsiventral or lateral) in the tribe Cypereae.

Materials and Methods

Thirty five taxa of *Cyperus* s.l. (Kukenthal, 1936) were examined and their nomenclature was followed given by World Checklist of Monocotyledons

(Govaerts *et al.*, 2011). Specimens were either collected from the field or obtained from BARO Herbarium. All the collected materials were mounted on the herbarium sheets were deposited at BARO (Table 1). Mature inflorescences were dissected under Olympus SZ61 stereo-microscope, and photographed with a digital camera Cannon SLR500D and Olympus FE-5010. For the typological interpretation the terminology described by Vegetti (2003), Guarise & Vegetti (2008b) and Vrijdaghs *et al.* (2010) have been followed. Morphological study of each taxa has been done for 20 plants. Average measurements have been recorded for 28 characters of reproductive parts of specimens only. A series of characters related with the synflorescence and spikelets were recorded (Table 3, 4) and results were schematized in Table 2. The number and position of different types of branching were observed for each ramification pattern. The length of the proximal branch was measured from the insertion until the apex of its terminal spikelet. Based on the results, possible hypothetical processes responsible for the structural diversity of inflorescence and evolutionary trends within or between studied taxa are presented in Fig. 3 with the help of (Guarise & Vegetti, 2008a). For the phenetic analyses, coding of the morphological characters has been done after Bruhl (1995) and Naczi (2009) and provided in Table 4. The dendrogram depicting the relationship of the taxa were constructed on the basis of quantitative and qualitative characters. Square Euclidean distance was used as a measure of similarity for the cluster analysis. Correlation coefficients were estimated with the help of SPSS ver.21 software (Ingrouille, 1986).

Results

In all the species studied, following zones can be distinguished on the whole plant: innovation zone, inhibition zone, paracladial zone and main florescence. In the distal portion of the inflorescence the axis ends in a spikelet (main florescence), and below there is a well developed paracladial zone. Each paracladium in the paracladial zone can be developed as branched or reduced coflorescence. Table 2 show important qualitative and quantitative inflorescence parameters in taxa studied.

Four major type of inflorescence are observed in the paracladial zone with various subtypes: Anthelodium (A), Capitata (C), Spike (S) and Unispicate (U).

A. Anthelodium: It is a cymose corymb, crateriform indeterminate inflorescence, with the terminal

Table 1. List of studied taxa (Govaerts, 2011)

| No. | Taxa | Synonyms | Voucher specimens at BARO |
|-----|--|--|--|
| 1 | <i>Courtoisina cyperoides</i> (Roxb.) Soják | <i>Kyllinga cyperoides</i> Roxb. <i>Cyperus pseudokyllingioides</i> Kuk. <i>Mariscus cyperoides</i> (Roxb.) Dietr. | RJD 186, 330, 637; Bedi 391, 1588, 1951 |
| 2 | <i>Cyperus alulatus</i> J. Kern | <i>Cyperus iria</i> var. <i>rectangularis</i> Kuk. <i>Cyperus rectangularis</i> (Kuk.) Bennet | RJD 225, 373, 506; JVJ 322; Sabnis 154, 181, 238; ASARI 77 |
| 3 | <i>Cyperus arenarius</i> Retz. | <i>Scirpus glomeratus</i> B.Heyne ex Wall. | JVJ 227, 871; RJD 225, 373, 506; KSR 714, 910, 1211; Sabnis 81, 81; PPB 772 |
| 4 | <i>Cyperus bulbosus</i> Vahl | <i>Cyperus stolonifer</i> Willd. ex Kunth <i>Cyperus rotundus</i> var. <i>pendulus</i> Nees | RJD 78, 633, 669; KSR 344, 856, 919; Sabnis 43, 90 |
| 5 | <i>Cyperus compactus</i> Retz. | <i>Mariscus compactus</i> (Retz.) Bold. | Sabnis 412, 442; RJD 453, 513, 631 |
| 6 | <i>Cyperus compressus</i> L. | <i>Cyperus pectiniformis</i> R. & S. <i>Cyperus dilutus</i> Vahl | JVJ 177, 318; RJD 122, 356, 508; Bedi 1, 522, 1621, 2924; KSR 219; DNT 59, 603; Sabnis 293, 301, 446 |
| 7 | <i>Cyperus corymbosus</i> Rottb. | <i>Cyperus diphyllus</i> Retz. <i>Cyperus nudus</i> Roxb. | RJD 507, 900, 905; Sabnis 313, 373, 399, 418, 421 |
| 8 | <i>Cyperus cuspidatus</i> Kunth | <i>Cyperus uncinatus</i> sensu C.B.Clarke <i>Cyperus capitatus</i> Retz. | RJD 115 |
| 9 | <i>Cyperus cyperoides</i> subsp. <i>cyperoides</i> (L.) Kuntze | <i>Kyllinga sumatrensis</i> Retz. <i>Mariscus sumatrensis</i> (Retz.) Raynal | Bedi 2708; DNT 220, 642 |
| 10 | <i>Cyperus difformis</i> L. | <i>Cyperus viridis</i> Willd. ex Kunth | JVJ 224, 288; RJD 77, 279, 348; Bedi 88, 1041, 2017, 3590; Sabnis 153, 295, 376; DNT 651, 1273 |
| 11 | <i>Cyperus digitatus</i> Roxb. | <i>Cyperus dives</i> Delile <i>Cyperus exaltatus</i> var. <i>dives</i> (Delile) C.B.Clarke | Bedi 2720; RJD 892 |
| 12 | <i>Cyperus esculentus</i> L. | <i>Pycneus esculentus</i> (L.) Hayek | JVJ 870; RJD 168, 653, 740; Bedi 254, 1590, 2585, 2641; Sabnis 27, 307, 334, 440; DNT 708 |
| 13 | <i>Cyperus exaltatus</i> var. <i>exaltatus</i> Retz. | <i>Cyperus alopecuroides</i> J. König ex Roxb. | JVJ 219; RJD 429, 616, 727, 889; Sabnis 7, 141, 171, 329 |
| 14 | <i>Cyperus iria</i> L. | <i>Cyperus parviflorus</i> Nees <i>Cyperus iria</i> var. <i>paniciformis</i> C.B.Clarke | JVJ 178; RJD 118, 464, 503; Bedi 186, 1076, 1625, 2761; KSR 304; Sabnis 158, 279, 322 |
| 15 | <i>Cyperus laevigatus</i> L. | <i>Juncellus laevigatus</i> (L.) C.B.Clarke | Sabnis 87; JVJ 180; KSR 249, 936, 483; Sabnis 36, 234, 442 |
| 16 | <i>Cyperus meeboldii</i> Kuk. | <i>Cyperus adamii</i> Raymond | DNT 1040 |
| 17 | <i>Cyperus microiria</i> Steud. | <i>Cyperus iria</i> var. <i>parviflorus</i> Miq. | RJD 335, 423, 505; Sabnis 103; PPB 804 |

| No. | Taxa | Synonyms | Voucher specimens at BARO |
|-----|---|---|---|
| 18 | <i>Cyperus nutans</i> var. <i>eleusinoides</i> (Kunth) Haines | <i>Cyperus eleusinoides</i> Kunth | RJD 240, 544, 899; JVJ 181, 1174; Bedi 1585, 3584; DNT 1739, 1757; Sabnis 172, 241, 469 |
| 19 | <i>Cyperus pangorei</i> Rottb. | <i>Cyperus tegetum</i> Roxb. | RJD 146, 380, 890; JVJ 220, 357, 432; Bedi 339; PPB 1163, Sabnis 184 |
| 20 | <i>Cyperus paniceus</i> (Rottb.) Boeck. | <i>Kyllinga panacea</i> Rottb. <i>Mariscus paniceus</i> (Rottb.) Vahl | DNT 1223; 862, 888, 891; Bedi 33; RJD 862, 888, 891 |
| 21 | <i>Cyperus pulcherrimus</i> Willd. ex Kunth | <i>Cyperus eumorphus</i> Steud. | JVJ 1635; RJD 405, 420, 630 |
| 22 | <i>Cyperus rotundus</i> subsp. <i>retzii</i> Kük. | <i>Cyperus retzii</i> Nees <i>Cyperus bifax</i> C.B. Clarke | RJD 227, 637, 682 |
| 23 | <i>Cyperus rotundus</i> subsp. <i>rotundus</i> L. | <i>Cyperus stoloniferus</i> var. <i>pallidus</i> Boeck. | RJD 16, 103, 175; DNT 16, 668; Sabnis 6, 40, 342, 427 |
| 24 | <i>Cyperus tuberosus</i> Rottb. | <i>Cyperus rotundus</i> subsp. <i>tuberosus</i> (Rottb) Kük. | RJD 8, 316, 370; Sabnis 105, PPB 3, 575 |
| 25 | <i>Cyperus squarrosus</i> L. | <i>Cyperus aristatus</i> Rottb. <i>Mariscus squarrosus</i> (L.) C.B. Clarke | RJD 284, 441, 535; JVJ 319, 872; Bedi 124, 138, 1603, 3487; KSR 424, 1302; Sabnis 118, 438; DNT 1097 |
| 26 | <i>Cyperus tenuispica</i> Steud. | <i>Cyperus flavidus</i> sensu C.B. Clarke <i>Cyperus delicatulus</i> Steud. | RJD 260, 446, 610; JVJ 228; Bedi 1902, 1945 |
| 27 | <i>Kyllinga brevifolia</i> Rottb. | <i>Cyperus brevifolius</i> (Rottb.) Hassk. | RJD 116, 399, 406; Bedi 58, 2018, 2638; Sabnis 68, ASARI 74 |
| 28 | <i>Kyllinga bulbosa</i> P. Beauv. | <i>Kyllinga triceps</i> Rottb. <i>Cyperus triceps</i> (Rottb.) Endl. <i>Kyllinga tenuifolia</i> Steud. | RJD 245, 479, 572; JVJ 230; Bedi 56, 2014, 2016, 2717; KSR 372, 681 |
| 29 | <i>Kyllinga squamulata</i> Vahl | <i>Kyllinga metzii</i> Hochst. ex Steud. <i>Cyperus metzii</i> (Hochst. ex Steud.) Mattf. & Kük. | Sabnis 241 |
| 30 | <i>Pycreus flavidus</i> (Retz.) T. Koyama | <i>Cyperus flavidus</i> Retz. <i>Pycreus globosus</i> Rchb. <i>Cyperus globosus</i> All. | JVJ 729, 1192; RJD 237, 457, 894; Sabnis 233, 245, 247 |
| 31 | <i>Pycreus membranaceus</i> (Vahl) Govind. | <i>Cyperus membranaceus</i> Vahl <i>Pycreus pumilus</i> var. <i>membranaceus</i> (Vahl) Karthik. <i>Cyperus pumilus</i> var. <i>membranaceus</i> (Vahl) C.B. Clarke | RJD 896, 897, 898; DNT 880, 1100; Sabnis 282, 340, 464 |
| 32 | <i>Pycreus pumilus</i> (L.) Nees | <i>Cyperus pumilus</i> L. <i>Pycreus punctatus</i> Govind. | JVJ 324; RJD 66, 306, 494, 600; Bedi 84, 1034, 1467, 1787, 3488 |
| 33 | <i>Pycreus puncticulatus</i> (Vahl) Nees | <i>Cyperus puncticulatus</i> Vahl <i>Pycreus</i> <i>baccha</i> Nees | JVJ 329 |
| 34 | <i>Pycreus sanguinolentus</i> (Vahl) Nees | <i>Cyperus sanguinolentus</i> Vahl | RJD 392, 785, 895; Sabnis 191, 199, 242 |
| 35 | <i>Queenslandiella hyalina</i> (Vahl) Ballard | <i>Cyperus hyalinus</i> Vahl <i>Pycreus pumilus</i> var. <i>substerilis</i> E.G. Camus | RJD 482, 724, 639; Sabnis 250, 253, 335, 395 |

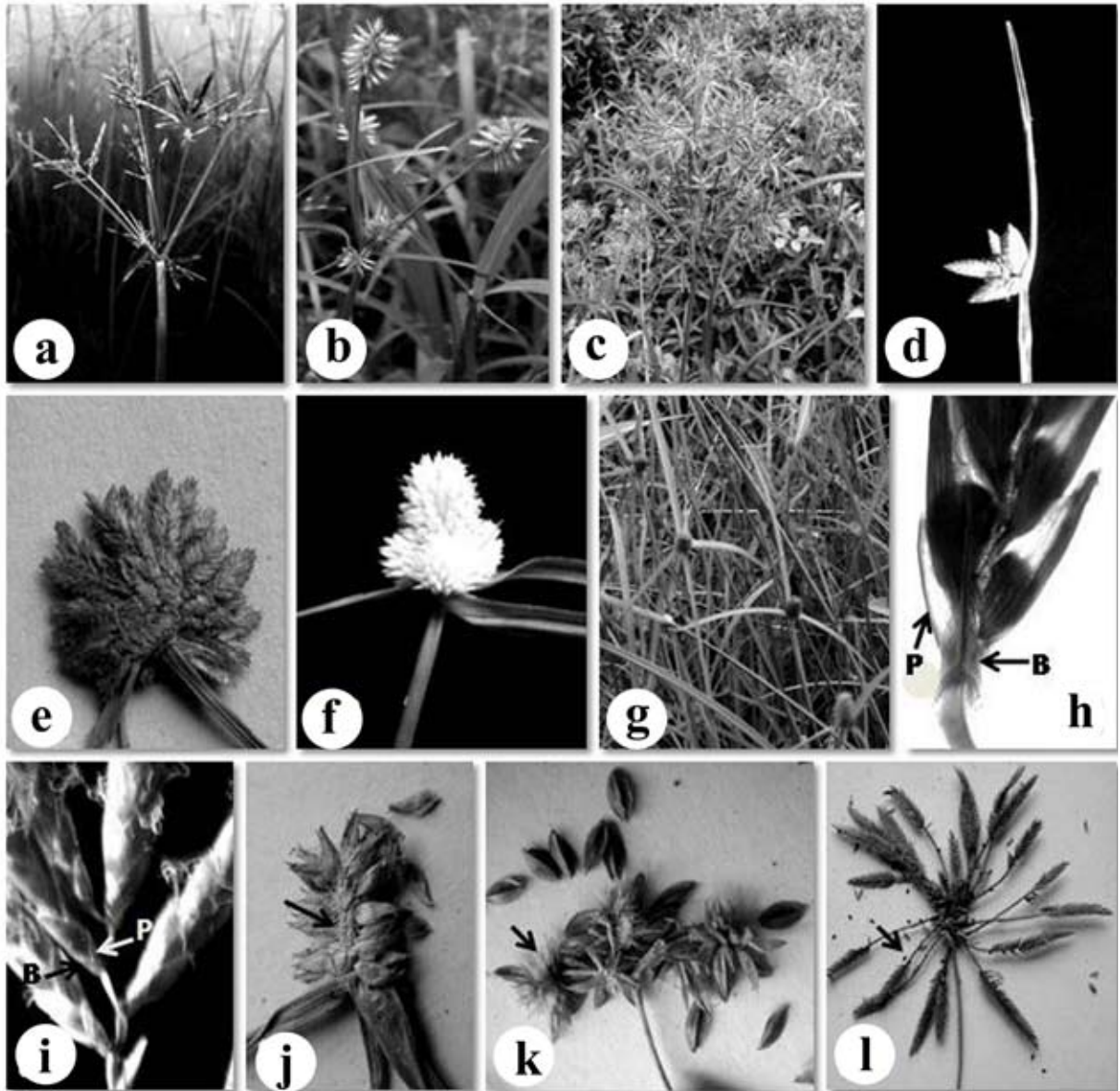


Fig. 1. a. Simple anthelodium of *Cyperus rotundus* subsp. *rotundus*; b. Anthelodium with glomerules of spikelets in *C. squarrosus*; c. Decompound anthelodium of *C. esculentus*; d. Pseudolateral inflorescence of *C. levigatus*; e. Capitata inflorescence of *C. meeboldii*; f. Spike of Spiklets of *Kyllinga bulbosa*; g. Spike of *K. brevifolia*; h. Close-up of *Cyperus compressus* spikelet showing vertical orientation of bract against prophyll; i. Close-up of *C. rotundus* subsp. *rotundus* spikelet showing transverse orientation of bract against prophyll; j-l. Disarticulation of rachilla, j. *Kyllinga brevifolia* showing complete deciduous rachilla, k. *Courtoisina cyperoides* showing deciduous rachilla leaving prophyll and bract, l. *Pycreus membranaceus* showing persistent rachilla. (P - Prophyll, B - Bract).

spikelet and the short and distal branches hidden among the long and proximal ones, which overtop them. The anthela of spikelets may be simple, compound, and decompound depending on the branching order with expanded epipodium (either first, second, or third and above, respectively).

1). Decompound anthelodium (A_1 -subtype): The short-paraclades and the successive order long-

paraclades are completely non-homogenized. The IPC (third order) or higher order long paraclades develop from the proximal portion of the basal long-paraclades: *Cyperus alulatus*, *C. exaltatus*, *C. iria*, *C. nutans*, *C. pangorei*, *C. rotundus* ssp. *retzii*

2). Compound anthelodium (A_2 -subtype): The short-paraclades and the successive order long paraclades are partially homogenized. The IPC

Table 2. Important qualitative inflorescence parameters of Cyperaceae

| No. | Taxa | Maximum order of ramification | Length of 1 st Pc (cm) | Lower most bract Length (cm) | Number of Flower per spikelet | Number of Glumes per Spikelet | Number of Prophyll per Spikelet | Spikelet orientation against Bract | Number of Stamen | Number of Stigma |
|-----|---|-------------------------------|-----------------------------------|------------------------------|-------------------------------|-------------------------------|---------------------------------|------------------------------------|------------------|------------------|
| 1 | <i>Courtoisina cyperoides</i> | 2-3 | 5-10 | 10-17 | 1 | 2 | 2 | T | 3 | 3 |
| 2 | <i>Cyperus alulatus</i> | 3-4 | 15-25 | 55-70 | 6-12 | 1 | 1 | T | 2 | 2 |
| 3 | <i>C. arenarius</i> | 1 | 1-2 | 8-15 | 12-28 | 1 | 1 | T | 3 | 3 |
| 4 | <i>C. bulbosus</i> | 1 | 2-4 | 7-11 | 14-28 | 1 | 1 | T | 3 | 3 |
| 5 | <i>C. compactus</i> | 2 | 5-12 | 25-34 | 4-8 | 1 | 2 | V | 3 | 3 |
| 6 | <i>C. compressus</i> | 2-3 | 5-15 | 15-28 | 16-28 | 1 | 2 | V | 3 | 3 |
| 7 | <i>C. corymbosus</i> | 2-3 | 9-15 | 52-68 | 12-30 | 2 | 2 | V | 3 | 3 |
| 8 | <i>C. cuspidatus</i> | 2 | 2-7 | 3-7 | 20-50 | 1 | 1 | T | 3 | 3 |
| 9 | <i>C. cyperoides</i> subsp. <i>cyperoides</i> | 1 | 4-8 | 24-32 | 80-120 | 1 | 1 | T | 3 | 3 |
| 10 | <i>C. difformis</i> | 2 | 5-9 | 14-22 | 20-50 | 1 | 1 | T | 2 | 3 |
| 11 | <i>C. digitatus</i> | 3-4 | 10-25 | 60-110 | 30-70 | 1 | 1 | T | 3 | 3 |
| 12 | <i>C. esculentus</i> | 2-3 | 10-18 | 24-36 | 12-26 | 1 | 1 | T | 3 | 3 |
| 13 | <i>C. exaltatus</i> var. <i>exaltatus</i> | 3-4 | 18-30 | 64-97 | 8-14 | 1 | 1 | T | 3 | 3 |
| 14 | <i>C. iria</i> | 2-3 | 3-8 | 7-18 | 6-12 | 1 | 1 | T | 3 | 3 |
| 15 | <i>C. laevigatus</i> | 1 | 0.3-0.5 | 5-12 | 14-36 | 1 | 2 | V | 3 | 2 |
| 16 | <i>C. meeboldii</i> | 1 | 0.2-0.4 | 7-16 | 16-24 | 1 | 2 | V | 3 | 3 |

| No. | Taxa | Maximum order of ramification | Length of 1 Pc (cm) | Lower most bract Length (cm) | Number of Flower per spikelet | Number of Glumes per Spikelet | Number of Prophyll per Spikelet | Spikelet orientation against Bract | Number of Stamen | Number of Stigma |
|-----|--|-------------------------------|---------------------|------------------------------|-------------------------------|-------------------------------|---------------------------------|------------------------------------|------------------|------------------|
| 17 | <i>C. microiria</i> | 3-4 | 13-28 | 57-68 | 6-14 | 1 | 1 | T | 3 | 3 |
| 18 | <i>C. nutans</i> var. <i>eleusinooides</i> | 4 | 13-21 | 44-57 | 20-40 | 1 | 1 | T | 3 | 3 |
| 19 | <i>C. pangorei</i> | 3-4 | 8-15 | 16-24 | 12-22 | 1 | 1 | T | 3 | 3 |
| 20 | <i>C. paniceus</i> | 1 | 0.5-1 | 12-18 | 60-100 | 1 | 1 | T | 3 | 3 |
| 21 | <i>C. pulcherrimus</i> | 3-4 | 3-7 | 10-22 | 10-20 | 1 | 1 | T | 2 | 3 |
| 22 | <i>C. rotundus</i> subsp. <i>retzii</i> | 3-4 | 12-23 | 34-52 | 8-12 | 1 | 1 | T | 3 | 3 |
| 23 | <i>C. rotundus</i> subsp. <i>rotundus</i> | 2-3 | 5-10 | 12-24 | 20-40 | 1 | 2 | V | 3 | 3 |
| 24 | <i>C. squarrosus</i> | 3 | 2-4 | 3-6 | 16-28 | 1 | 1 | T | 1 | 3 |
| 25 | <i>C. tenuispica</i> | 3 | 3-12 | 12-26 | 20-50 | 1 | 1 | T | 3 | 3 |
| 26 | <i>C. tuberosus</i> | 3-4 | 7-15 | 35-48 | 12-24 | 1 | 2 | V | 3 | 3 |
| 27 | <i>Kyllinga brevifolia</i> | 0 | 0 | 3-9 | 1 | 1 | 1 | T | 2 | 2 |
| 28 | <i>K. bulbosa</i> | 2 | 0.2-0.5 | 6-11 | 1 | 1 | 1 | T | 2 | 2 |
| 29 | <i>K. squamulata</i> | 0 | 0 | 6-12 | 1 | 1 | 1 | T | 2 | 2 |
| 30 | <i>Pycnus flavidus</i> | 1-2 | 0.5-1.5 | 22-34 | 20-40 | 1 | 1 | T | 2 | 2 |
| 31 | <i>P. membranaceus</i> | 1 | 7-12 | 18-24 | 30-60 | 1 | 2 | V | 2 | 2 |
| 32 | <i>P. pumilus</i> | 2 | 1-2 | 4-7 | 20-32 | 1 | 2 | V | 2 | 2 |
| 33 | <i>P. puncticulatus</i> | 3-4 | 4-7 | 15-28 | 12-18 | 1 | 1 | T | 2 | 2 |
| 34 | <i>P. sanguinolentus</i> | 2 | 2-4 | 10-18 | 10-18 | 1 | 1 | T | 2 | 2 |
| 35 | <i>Queenslandiella hyalina</i> | 2 | 1.5-4 | 7-12 | 12-18 | 1 | 1 | T | 2 | 2 |

Table 3. List of Characters and character state used for phylogenetic analysis

| No. | Character with character state |
|-----|---|
| 1 | Inflorescence position: Terminal (0), Pseudo-lateral (1) |
| 2 | Inflorescence type: Anthelodium (0), Capitata (1), Spike (2), Unispicate (3) |
| 3 | Inflorescence: Elongated (0), Contracted (1) |
| 4 | Lateral Inflorescence branches: Elongated (0), Contracted (1) |
| 5 | Maximum order of ramification: ≥ 4 (0), 3-2 (1), 1 (2), 0 (3) |
| 6 | Lower most paracladial length: $>15\text{cm}$ (0), 14-5cm (1), $<5\text{cm}$ (2) |
| 7 | Spikes in glomerules: Absent (0), Present (1) |
| 8 | Spikes on longest paracladia: ≥ 5 (0), 4-2 (1), 1 (2) |
| 9 | Shape of solitary spike: Linear (0), Pyriform-Ovoid (1), Globose (2) |
| 10 | Rachilla: Deciduous as a whole (0), Deciduous leaving spikelet bract and prophyll (1), Persistent (2) |
| 11 | Spikelet compression: Lateral (0), Dorsal (1), Terete (2) |
| 12 | Number of spikelet bract: 0 (0), 1 (1), 2 (2) |
| 13 | Bract orientation with respect to spikelet: Transverse (0), Vertical (1) |
| 14 | Spikelet prophyll no.: 0 (0), 1 (1), 2 (2) |
| 15 | Spikelet prophyll size with spikelet bract: Longer (0), Equal (1), Shorter (2) |
| 16 | Number of Perigynia: >50 (0), 49-25 (1), 24-1 (2) |
| 17 | Perigynia nature: Hyaline (0), Membranous (1), Chartaceous (2) |
| 18 | Perigynia max. width: near base (0), near middle (1), near apex (2) |
| 19 | Perigynia apex: Obtuse (0), Acute (1), Acuminate- mucronate (2), Aristate (3) |
| 20 | Perigynia apex angle: Bent (0), Straight (1) |
| 21 | Number of Perigynia nerves: 15-11 (0), 10-5 (1), 4-1 (2) |
| 22 | Perigynia colour: Green-yellow (0), Brown-straw (1), Red-purple (2) |
| 23 | Number of Stamen: 3 (0), 2 (1), 1 (3) |
| 24 | Number of Stigma: 3 (0), 2 (1), 1 (3) |
| 25 | Number of Achene per spikelet: 1-5 (0), 6-20 (1), >20 (2) |
| 26 | Achene shape: Trigonous (0), Lenticular (1), Linear-lanceolate (2) |
| 27 | Achene texture: Glabrous (0), Papillose (1) |
| 28 | Achene colour: White-brown (0), Purple-red (1), black (2) |

(second order) develop from primary long-paraclades: *Cyperus compactus*, *C. esculentus*, *C. corymbosus*, *C. difformis*, *C. compressus*, *C. microiria*, *C. pangorei*, *C. pulcherrimus*, *C. rotundus* ssp.

rotundus, *C. tenuispica*, *C. tuberosus*, *Courtoisina cyperoides*, *Pycreus* spp.

3). Simple anthelodium (A_3 -subtype): The short-

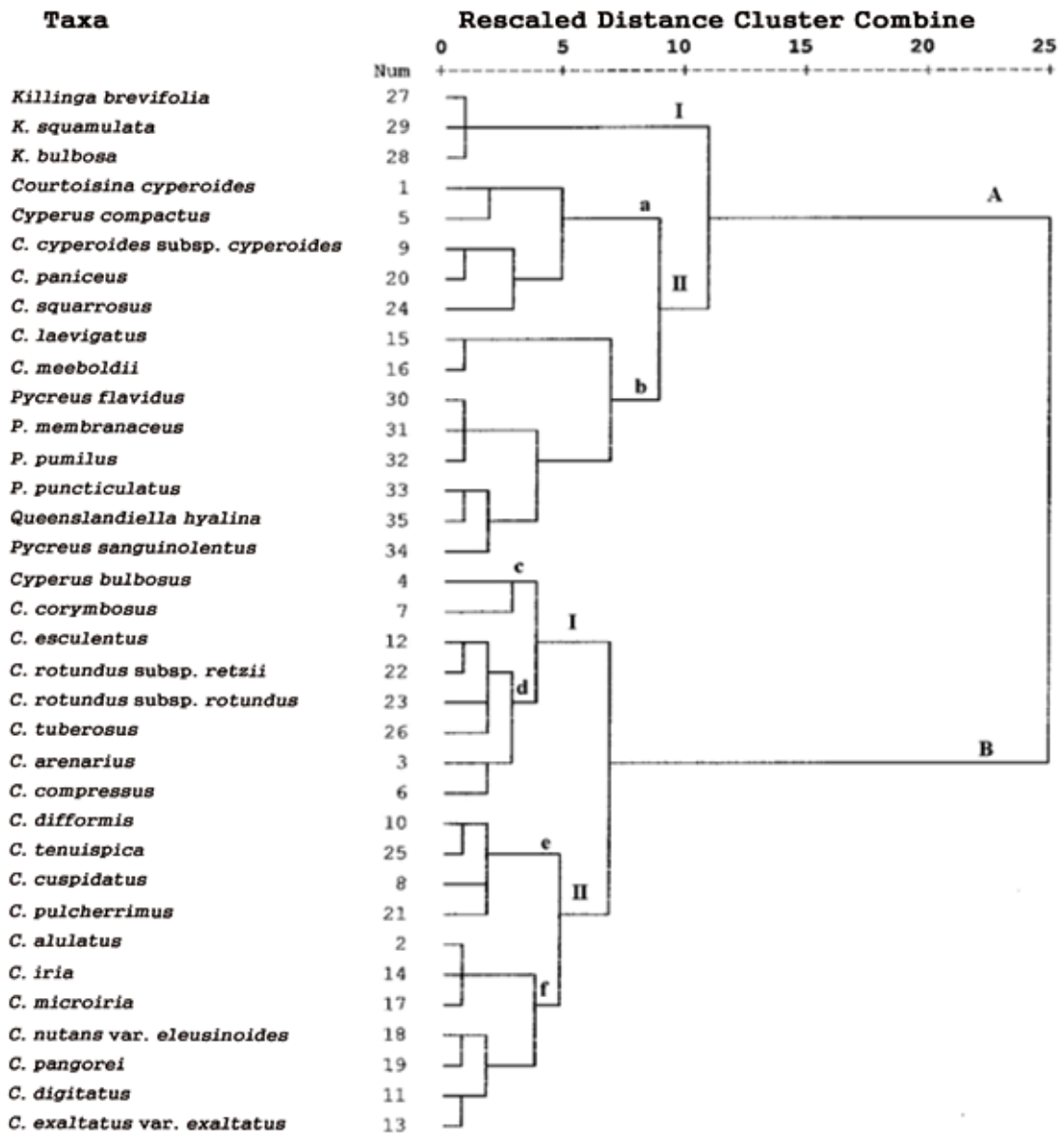


Fig. 2. Dendrogram showing the relationship of 35 taxa of Cyperaceae.

paraclades and primary long paraclades are partially homogenized: *Cyperus paniceus*, *C. squarrosus*, *C. bulbosus*

4). Fasciculate (A_4 -subtype): It developed from the above mentioned anthelodia by the decrease in internodal length of main axis and paracladia: *Cyperus bulbosus*, *C. arenarius*

B. Capitate: Indeterminate inflorescence, similar to a capitulum or head, due to a pronounced shortening of the internodes on the main axis and

branches of different order. In some cases, there is also a reduction of the branching degree: *Cyperus meeboldii*, *C. laevigatus*

C. Unispicate: It is a kind of inflorescence in which glumes are directly arranged along the main axis, and all florescences are homogamous. The inflorescence lacks branches and consists of the terminal spikelet only: *Kyllinga brevifolia*

D. Spike of spikelets: Indeterminate inflorescence with spikelets disposed sessile on the main axis: *Kyllinga bulbosa*, *K. squamulata*

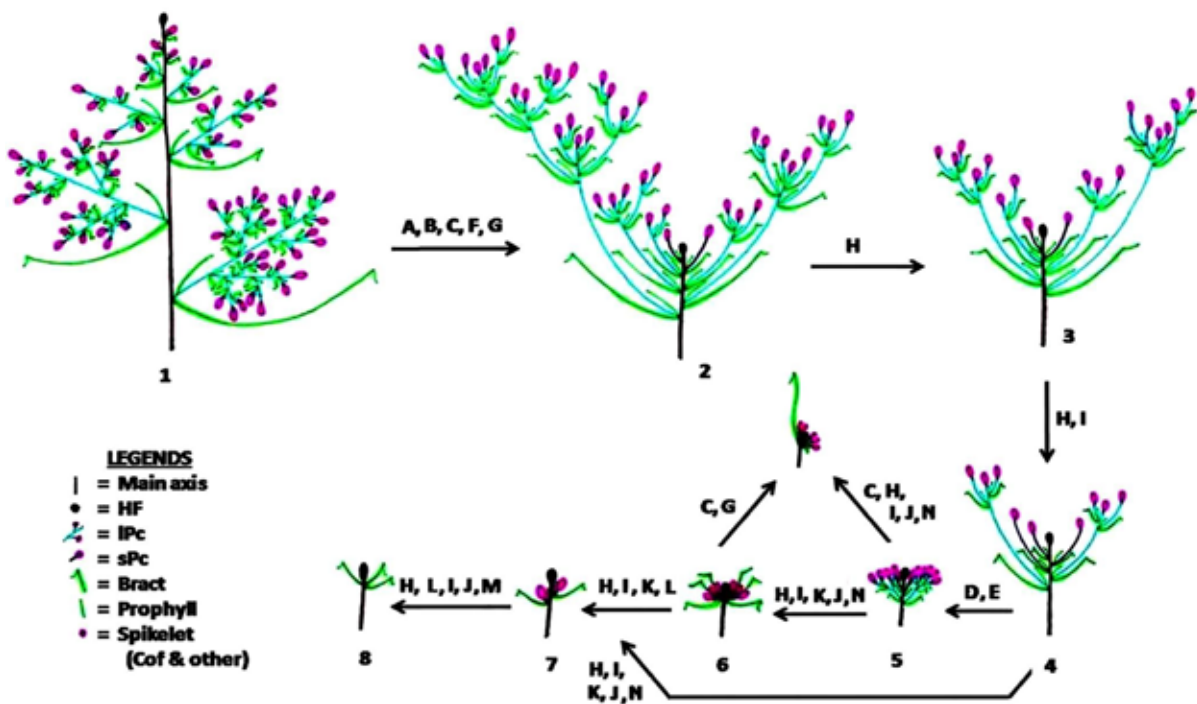


Fig. 3. Hypothetical processes responsible for the synflorescence diversification in Cyperaceae.

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, to distichous arrangement of glumes on spikelet is an observed relevant feature. Foliaceous, laminar, setiform and glumaceous prophylls are observed in clear acropetalous sequence in all the studied taxa, with variations in the length of the proximal one. Among them, largest one is observed in *Cyperus digitatus* and *C. exaltatus* var. *exaltatus* (60-110cm) and the smallest in *Cyperus cuspidatus*, *C. squarrosus*, *Kyllinga brevifolia*, and *P. puncticulatus* (3-10cm). In all the species studied the prophylls display an acropetal variation in size and form: tubular (cladoprophyll), laminar and glumaceous and two-keeled, a hardly observable character in the glumaceous ones. The occurrence of the different types of prophylls and prophylls varies according to the region of the inflorescence. Moreover, number of glumaceous prophylls and prophylls varies from 1-2 (Table 4). The shape and length of the bracts and prophylls are also variable.

Discussion

Today, there are differences in opinion on whether to recognize to genus *Cyperus*, in a very broad sense (*sensu lato*) with a number of subgenera (e.g.

Kukenthal, 1936; Tucker, 1983, 1994), or in a narrow sense (*sensu stricto*) with various segregate genera (e.g. Goetghebeur, 1998; Bruhl, 1995). The topology of most of the *Cyperus* clade shows a number of significant features, notably the polytomy formed by species of *Cyperus* subg. *Cyperus* (including *Mariscus*), *Juncellus*, *Kyllinga* and *Pycreus*. The status of these genera is under debate, of them, many authors (e.g. Goetghebeur, 1986; Simpson *et al.*, 2007; Bruhl, 1995; Vrijdaghs *et al.*, 2011) accepting *Juncellus* as a distinct genus, whereas others, notably Kukenthal (1936) and Haines & Lye (1983), have treated them as subgenera within *Cyperus*. To solve these taxonomic problems and the relationships in *Cyperus*, a precise morphological study at the species level is required (Muasya *et al.*, 2000).

In the present work 35 members of tribe Cyperaceae belonging to *Cyperus* (27), *Courtoisina* (1), *Kyllinga* (2), *Pycreus* (4) and *Queenslandiella* (1) are evaluated for their inflorescence architecture. An anthelodium has been recorded in 30 species, unispicate in *Kyllinga brevifolia*, spike of spikelets in *K. bulbosa* and *K. squamulata*, capitate in *Cyperus meeboldii*; whereas *C. leavigatus* is distinct due to its pseudolateral inflorescence (Fig. 1, Table 4). Most of the anthelodium depict paracladia of first, second and up to third order with an

evident epipodium (Table 2). In the distal region of paracladia with glomerules of spikelets were observed in *Cyperus cyperoides*, *C. compactus*, *C. cyperoides* subsp. *cyperoides*, *C. difformis*, *C. pulcherrimus* and *C. paniceus* (Table 4, Fig. 1). In all the species of Cyperaceae, the normal paraclades are disposed in an antidromic arrangement and have normal ramifications, as already been observed in other species of Cyperaceae (Reutemann *et al.*, 2009; Desai & Raole, 2013). The prophyllar productions increase the development of the PZ and the number of spikelets of the inflorescence (Kukkonen, 1986; Meert & Goetghebeur, 1979; Vegetti, 1994) and also observed in this study, which are mainly responsible for the diversification of synflorescence. Homogenization, truncation and racemization are the three main processes occurring during the development of synflorescence, which may occur independently or in combinations.

Processes in the Cyperaceae Synflorescence:

Process A: Upright lengthening of epipodium in acropetalous order; i.e., lower most Pc bears largest length over preceding ones (which is responsible for the formation of an anthelodium from paniculodium).

Process B: Inhibition of the development of Pc from the axils of the upper leaves of the long internode zone (i.e. Pc with UIF).

Process C: Upright positioning of the lowermost primary bract and Pc, continuing the direction of the stem- the inflorescence is bent over, suggesting a pseudo-lateral/ lateral position, phenomenon called 'Metatopies'.

Process D: Development of Pc below the main florescence in the UIF.

Process E: Increase of the number of Pc of the UIF.

Process F: Increase of branching degree.

Process G: Increase of the internodal growth of the Pc.

Process H: Reduction of the internodal growth of the Pc.

Process I: Reduction of the number of Pc of the UIF.

Process J: Diminishing of branching degree.

Process K: Inhibition of the development of the IPc in the UIF; the UIF is formed by sPc only (constituting a spike of spikelets).

Process L: Inhibition of the development of the Pc: the UIF is formed by the main florescence only (sometimes, when there is not IPc subzone, this process represents the inhibition of the short-Pc subzone).

Process M: Truncation of the region of sPc of the UIF.

Process N: Truncation of the distal region of the IPc of the UIF.

Raynal (1971), Goetghebeur (1998) and Guarise & Vegetti (2007) considered the panicle as the basic cyperaceous inflorescence which can be modified through the elongation or contraction of the internodes in various reduction trends. Leafy stems with evenly spaced inflorescence branches and distal branches distinctly higher than the proximal branches together with spikelets of many bisexual florets arranged with few or no sterile glumes suggest a peculiarly specialized type of panicle, rather than a relatively primitive form, suggested by Mattfeld (1938). The hermaphrodite paniculodium (Fig. 3-1), evolved early in basal groups of the family. Indeterminate inflorescence with the terminal spikelet and short distal branches which overtopped by proximal long branches called anthelodium (Fig. 3.2), is results from the inhibited lengthening of the main axis internodes and the distal branch epipodium, with an important development of the basal branch epipodium. The anthela of spikelets may be simple (Fig. 1A, B; 3.4), compound (Fig. 3.3) or decomposed (Fig. 1C, 3.2), depending on the branching order with expanded epipodium (either first, second or third, fourth and above, respectively). This variation in the form of the anthela of spikelets has been described in other species of *Cyperus* (Wilson, 1991; Guaglianone, 1996; Guarise & Vegetti, 2007, 2008) and *Fimbristylis* (Reutemann *et al.*, 2009; Desai & Raole, 2013). Generally, there is a gradual transition in the number of spikelets in each inflorescence and in the branching order of the inflorescence branches. The branching degree becomes distally reduced and the branches become progressively shorter toward the apex (Fig. 3.5). In many inflorescences of Cyperaceae, most of the primary branches have a lower similar order of branching, except for the very distal ones, which are reduced either to the minimum branching degree or to the terminal spikelet. These inflorescences with many branches of similar branching order are homogenized inflorescences. The variations in the anthela of spikelets depend on the length of the epipodium of their branches. The internode growth from the

Table 4. Character state of studied taxa (Character no. as per Table 3)

| No. | Character No. → | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | | |
|-----|---|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|
| | Taxa ↓ | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | <i>Courtoisina cyperoides</i> | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 2 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| 2 | <i>Cyperus alulatus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 3 | <i>C. arenarius</i> | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| 4 | <i>C. bulbosus</i> | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | |
| 5 | <i>C. compactus</i> | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | |
| 6 | <i>C. compressus</i> | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | |
| 7 | <i>C. corymbosus</i> | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | |
| 8 | <i>C. cuspidatus</i> | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 1 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | |
| 9 | <i>C. cyperoides</i> subsp. <i>cyperoides</i> | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | |
| 10 | <i>C. difformis</i> | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | |
| 11 | <i>C. digitatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | |
| 12 | <i>C. esculentus</i> | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | |
| 13 | <i>C. exaltatus</i> var. <i>exaltatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | |
| 14 | <i>C. iria</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | |
| 15 | <i>C. laevigatus</i> | 1 | 1 | 1 | 1 | 3 | 1 | 0 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | |
| 16 | <i>C. meeboldii</i> | 0 | 1 | 1 | 1 | 3 | 2 | 0 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | |
| 17 | <i>C. microtria</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | |

| No. | Character No. → | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | |
|-----|---|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|
| | Taxa ↓ | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 18 | <i>C. nutans</i> var. <i>eleusinoides</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 19 | <i>C. pangorei</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 20 | <i>C. panicus</i> | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 21 | <i>C. pulcherrimus</i> | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| 22 | <i>C. rotundus</i> subsp. <i>retzii</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 2 |
| 23 | <i>C. rotundus</i> subsp. <i>rotundus</i> | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 0 |
| 24 | <i>C. squarrosus</i> | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 3 | 0 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 |
| 25 | <i>C. tenuispica</i> | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 |
| 26 | <i>C. tuberosus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 2 |
| 27 | <i>Kyllinga brevifolia</i> | 0 | 3 | 1 | 1 | 3 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 3 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| 28 | <i>K. bulbosa</i> | 0 | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 0 | 2 | 2 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 29 | <i>K. squamulata</i> | 0 | 2 | 1 | 1 | 3 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 3 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 30 | <i>Pycurus flavoides</i> | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 2 | 2 | 2 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 |
| 31 | <i>P. membranaceus</i> | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 |
| 32 | <i>P. pumilus</i> | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| 33 | <i>P. puncticulatus</i> | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| 34 | <i>P. sanguinolentus</i> | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 1 | 2 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| 35 | <i>Queenslandiella hyalina</i> | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |

inflorescence branch axes (except the epipodium) affects the inflorescence shape, especially in the manner in which branches group in the distal portion of an inflorescence branch with a developed epipodium; these groups can be simply described as a contracted head or glomerulous (*C. squarrosus*, *C. difformis*; Fig. 1B), lax (*C. esculentus*, Fig. 1C) or congested spikes (*C. arenarius*, *C. bulbosus*; Fig. 3.5). Guarise & Vegetti (2008b) have suggested presence of one or another type of ramification pattern within species and varieties for *Cyperus* sect. *Luzuleoidei*. In the same manner, during the present work ramification (branching) from the axil of normal bracts or mixed type (*C. difformis* and *C. pulcherrimus*) was recorded.

Inflorescence with spikelets disposed sessile on the main axis called spike of spikelets. The spike of spikelets is composed of spikelets with perfect flowers in *Kyllinga bulbosa* (Fig. 1F, 3.7). In some cases, there is also a reduction of the branching degree. A capitate inflorescence may derive from a paniculodium, an anthelodium or from a spike of spikelets because of pronounced shortening of the internodes on the main axis and branches of different order as seen in *C. meeboldii* (Fig. 1E, 3.6) (Reutemann *et al.*, 2012). In that process the inflorescence meristem produces lateral meristems which may behave either wholly as spikelet meristem and, consequently, do not produce other branches and end immediately in a spikelet. There is no reason to suppose that the reverse pathway might happen to produce a type of inflorescence with an epipodium developed from any more congested form (Guarise & Vegetti, 2007).

Although the synflorescence shows different appearance, a careful observation of the branching system reveals a common structural pattern, but difference in the number of paracladia arranged on the main axis and others and the development of bracts and prophylls (Table 1). Type of inflorescence, rachilla disarticulation and number and size of spikelet prophylls are found to be most functional character to segregate the studied taxa. The corymbose and anthelodium appears to be the basic structure from which the most evolved stage capitate and a globose spike is evolved due to truncation of the intercalary growth of the internodes. The major trend of synflorescence evolution among and within the genera is reductive, but the possibility of the occurrence of amplification within or between the groups must not be neglected (Guarise & Vegetti, 2008a).

Phenetic analysis of presently studied taxa based

on inflorescence and achene characters were segregated into two major groups. Group **AI** separates from **AII** due to presence of capitate inflorescence and deciduous nature of the rachilla without leaving prophylls and bract (Fig. 1J-L, 2; Table 4). Group **AII** further divided into **a** & **b** on the basis of glomerules nature of spikes, deciduous nature of rachilla and achene structure. Group **b** is further segregating on the basis of type of inflorescence, maximum order of ramification, size of prophyll with respect to spikelet bract and stamen number. *C. cyperoides* ssp. *cyperoides*, *C. compactus*, *C. paniceus*, *C. squarrosus* are formerly included in *Mariscus* which is also noticed in the dendrogram. The segregation of *Courtoisina cyperoides* from *Cyperus* spp. (including *Mariscus*) on the basis of 2-8 flowered spikelets in glomerules, dorsally compressed spikelet and prophylls and 2 bracts per spikelet (Fig. 2, Table 4). In reference to *Courtoisina*, Vorster (1986) suggested conserving the name *Courtoisina* on the basis of deciduous spikelet and persistence of 2 glumes along with the annual life cycle. In addition to above presence of anthelate inflorescences, laterally compressed spikelets, multiple flowers, bifid style and lenticular achene in *Q. hyalina* shows close relationship with *Pycneus* than *Cyperus* (Fig. 2, Table 4). *C. leavigatus* and *C. meeboldii* depict overall similarities except position & type of inflorescence (Fig. 1), stigma number and achene shape (Table 4). Hence, the retention of *Juncellus* as *Cyperus* is supported by the present statistical analysis and rbcL studies of Muasya *et al.* (2009).

Group **B** divided into **BI** & **BII** on the basis of number of spikelet prophyll and achene colour (Fig. 2). Group **BI** is further segregated into group **c** & **d** on the basis of number of spikes on longest paracladia and size of spikelet prophyll. Within the group **d** *C. esculentus*, both the subspecies of *C. rotundus* and *C. tuberosus* are forming a single cluster due to elongated lateral inflorescence branches, ovoid-pyriform spikes and deciduous nature of rachilla leaving prophyll and bract (Fig. 1J-L, 2; Table 4). **BII** is further divided into subgroup **e** & **f** on the basis of inflorescence type and maximum order of ramification. Furthermore, *C. iria*, *C. microiria* and *C. alulatus* segregated from rest other species by spikelet prophyll size, achene colour, perigynia colour and apex (Fig. 2, Table 4). According to Naczi (2009), morphology based phylogenetic analyses for sedges do produce trees with similar level of informative as other flowering plants. Evidently, application of morphological characters only in the broadest sense does provide enough information to yield well resolved trees

with good to strong support for a substantial number of the branches in the present study.

The results show *Cyperus s.s.* to be polyphyletic, and merging all the segregated taxa into broadly circumscribed *Cyperus s.l.* and recognizing various segregates as subgenera would make a monophyletic entity. This conclusion is supported by phylogenetic studies based on molecular (Muasya *et al.*, 1998; Plunkett *et al.*, 1995), morphological (Bruhl, 1995; Simpson, 1995) and combined data analysis (Muasya *et al.*, 2000). However, this option is not favored because it would result in a big genus (c. 900 species) and reduce taxonomic clarity. Therefore, present investigation supports Goetghebeur's *Cyperus s.s.* (1998) and recognizing the segregate taxa at generic level (Table 1). Further, more intensive phylogenetic studies involving character homology of more species at molecular level are warranted to get a full resolution of their relationships.

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