

Synflorescence typology in Cyperaceae

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This work presents the basis for typological study of the inflorescences in Cyperaceae. Inflorescence variation in this family are analyzed and discussed from the typological point of view. However, this review does not intend to comprise all of the variation present in the inflorescence structure of the Cyperaceae.

Key words: Cyperaceae, inflorescence, typology

Introduction

The morphology of inflorescences has played an important role in plant taxonomy and systematics; however, comparative typological analysis started later, with the work of W. Troll and his collaborators (Troll 1964, Weberling 1965, 1985, 1989).

In previous works by Mora-Osejo (1960), Kukkonen (1984, 1986, 1990), Vegetti and Tivano (1991), Vegetti (1992, 1994), Heinzen and Vegetti (1994) and Browning and Gordon-Gray (1999), Troll's typological interpretation was used as a basis to analyze the structural variation in the Cyperaceae inflorescences.

The inflorescence morphology of Cyperaceae is diverse and complex. Misapplication of terms in formal taxonomical descriptions has led to morphologically erroneous examples, since a uniform and stable terminology has not been established (Browning & Gordon-Gray 1999). The main problems in the interpretation of the inflorescence structure result from studies, which did not consider the entire inflorescence; instead, attention was restricted to the position and

arrangement of flowers in the final units of the often copiously branched inflorescence (Kukkonen 1984). A typological analysis may help to find the correct interpretation of the branching systems in these inflorescences, and that is the aim of this paper.

Synflorescence type

According to Troll (1964), the wide diversity of inflorescences in angiosperms is due to variation of two basic types: monotelic and polytelic. In monotelic inflorescences the apex of the main axis commonly ends with a terminal flower, but this condition is not always evident.

In the Cyperaceae, the inflorescence axes generally end in a group of flowers, which in most taxa is a spikelet (Mora-Osejo 1960, Kukkonen 1984, 1986, Vegetti 1992, 1994, Goetghebeur 1998). Essentially, the spikelets of Cyperaceae consist of an open axis (rachilla) bearing one to many glume(s), which may subtend a sessile flower. There is no terminal flower and the inflorescence is thus polytelic.

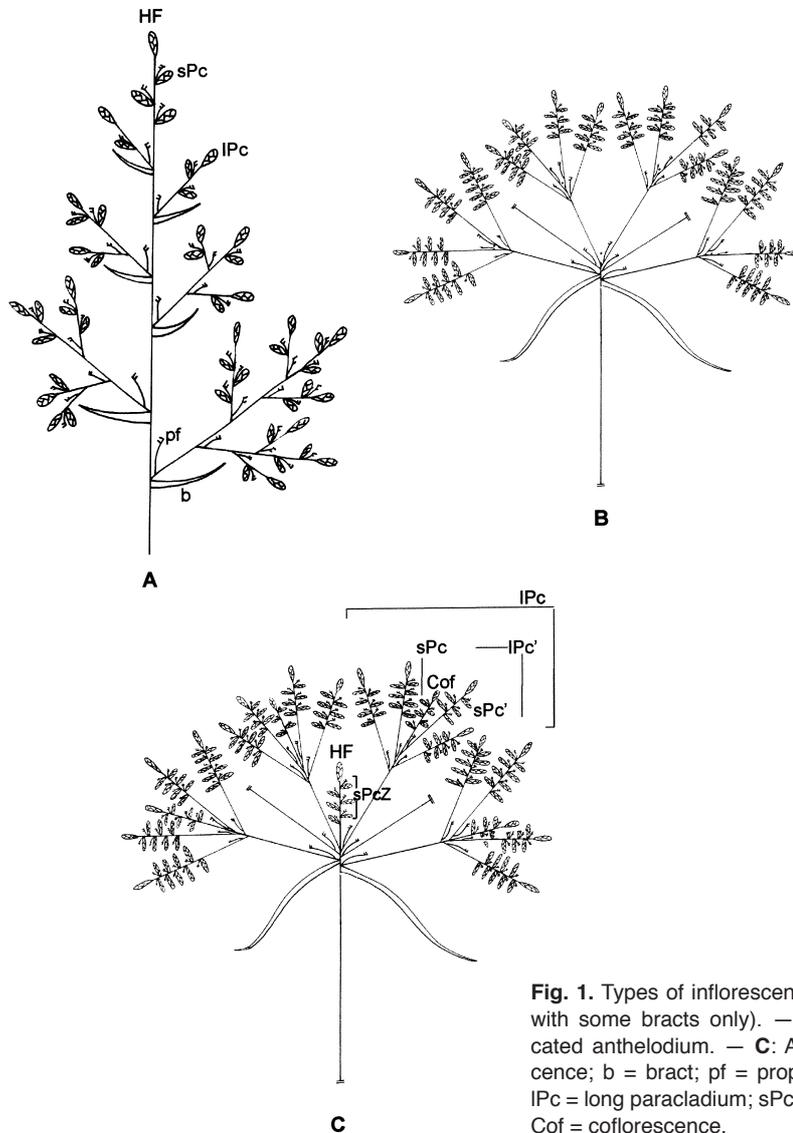


Fig. 1. Types of inflorescences in Cyperaceae (schematic, with some bracts only). — **A:** Paniculodium. — **B:** Truncated anthelodium. — **C:** Anthelodium. HF = main florescence; b = bract; pf = prophyll; sPc = short paracladium; IPc = long paracladium; sPcZ = short paracladium subzone; Cof = coflorescence.

A special problem arises with taxa that might have a terminal flower (Cĕlakovský 1887, Eiten 1976a, 1976b, Browning & Gordon-Gray 1995b, Goetghebeur 1998). *Scirpodendron* and *Chrysitrix* are some of the very few Cyperaceae where the axis apparently terminates in a flower (Goetghebeur 1998). Consequently, inflorescences in these genera would be termed monotelic. The nature of the inflorescence (monotelic or polytelic) commonly is characteristic and consistent in a given family. However, some largely polytelic families contain monotelic species and *vice versa* (Weberling 1985). In monocotyledons

polytely is a very common feature (Weberling 1989).

Structure of the synflorescence

In Cyperaceae the plants are composed of a group of shoots of consecutive ramification order (main shoot and axillary shoots). Normally, each of these shoots ends in an inflorescence and according to Troll's (1964) system it should be considered a synflorescence.

The proximal portion of the synflorescence,

the trophotagma (Hagemann 1990), has leaves that are sometimes preceded by cataphylls. In the basal zone, the leaf size increases toward the apex, and the leaves have buds in their axils. These buds develop into lateral shoots with a structure similar to the mother shoot during the same growth period (sylleptic ramification) or the next one (cataleptic ramification). In this zone, called the innovation zone, the internodes are short, except in species forming rhizomes and stolons (Mora-Osejo 1960).

The floral scape forms the inhibition zone and it is the internode that has the maximal intercalary growth. In some species this internode achieves a length of 2–3(–5) m.

In bract axils, floriferous shoots, called paracladia, are originated and these as a whole constitute the paracladial zone.

The main axis ends in a terminal spikelet: the main florescence (Fig. 1C). The paracladial zone and the main florescence form the flowering unit (Sell 1969).

Structure of the flowering unit

The inflorescence of Cyperaceae appears as a “panicle” of spikelets (Raynal 1971), but it is often modified into a ramification form similar to an anthela contracted into a capitulum, or a spike-like structure, or reduced to a single spikelet (Goetghebeur 1998). Partial inflorescences of the first, second, third, and higher order may be present and may correspond to any of these forms, in many different combinations. In these inflorescences the spikelets terminate the main axis and the branches (Goetghebeur 1998). Anthela and panicle are defined as inflorescences whose terminal and lateral axes have terminal flowers (Troll 1964). In Cyperaceae, however, these axes do not end in terminal flowers but in spikelets (florescences). For that reason Troll (1964) proposed to denominate them *anthelodium* (Figs. 1C and 3–9) and *paniculodium* (Fig. 1A), respectively.

The primary prophylls are often described as involucre bracts. The lowermost ones are usually foliar (sheathing or not) and the uppermost are bracteose and very small. The bracts of the ultimate branchlets (spikelet bracts) are often

barely distinct from glumes (Goetghebeur 1998). In some genera the lower bract points into the same direction as the stem, appearing as its continuation (Figs. 6–9) and also assumes a stem-like appearance, turning the inflorescence aside to a pseudolateral position (Vegetti & Tivano 1991, Vegetti 1992).

Branching in the floral region usually starts from the primary bract axils (Goetghebeur 1998). The prophyll of each branch is commonly sterile but in some taxa a prophyllate bud develops (Guaglianone 1970, Kukkonen 1986, Vegetti & Tivano 1991); these buds generate secondary and higher-order branching (prophyllar branching pattern, Figs. 2E, 7 and 9) (Guaglianone 1970, Meert & Goetghebeur 1979, Vegetti & Tivano 1991, Vegetti 1992, Goetghebeur 1998).

In a polytelic inflorescence, the floral group at the end of the main axis and of the paracladia of different orders is called a florescence. In Cyperaceae, florescences are represented by spikelets (Figs. 1C, 3C and D, 4A and E, 5). The florescence on the main axis is the main florescence and the florescence on each paracladium is a coflorescence (Troll 1964, Weberling 1965, 1985, 1989).

In polytelic inflorescences, below the main florescence terminating the main axis, paracladia, or branches with a structure similar to that of the main axis, can occur. They may be reduced to a coflorescence only (short paracladium, sPc) or second order paracladia may originate below the coflorescence and, in this way, the ramification of the system continues (long paracladium, lPc) (Figs. 1C and 3–9).

The inflorescence of *Schoenoplectus californicus* (Figs. 6 and 7) has a main florescence (HF) and a paracladial zone. The latter is formed of primary paracladia (Pc), some of which are reduced to coflorescences and others having paracladia of a higher (up to fifth) order. This species always has one paracladium per node. Each paracladium is composed of a short hypopodium, a prophyll, a long epipodium, a variable number of bracts and a coflorescence at the end. From the axillar bud of the prophyll and of the bracts, the branching system of each paracladium may be continued. Within the paracladial zone, the degree of ramification of the paracladia usually is diminished acropetally, and a gradual reduction of the

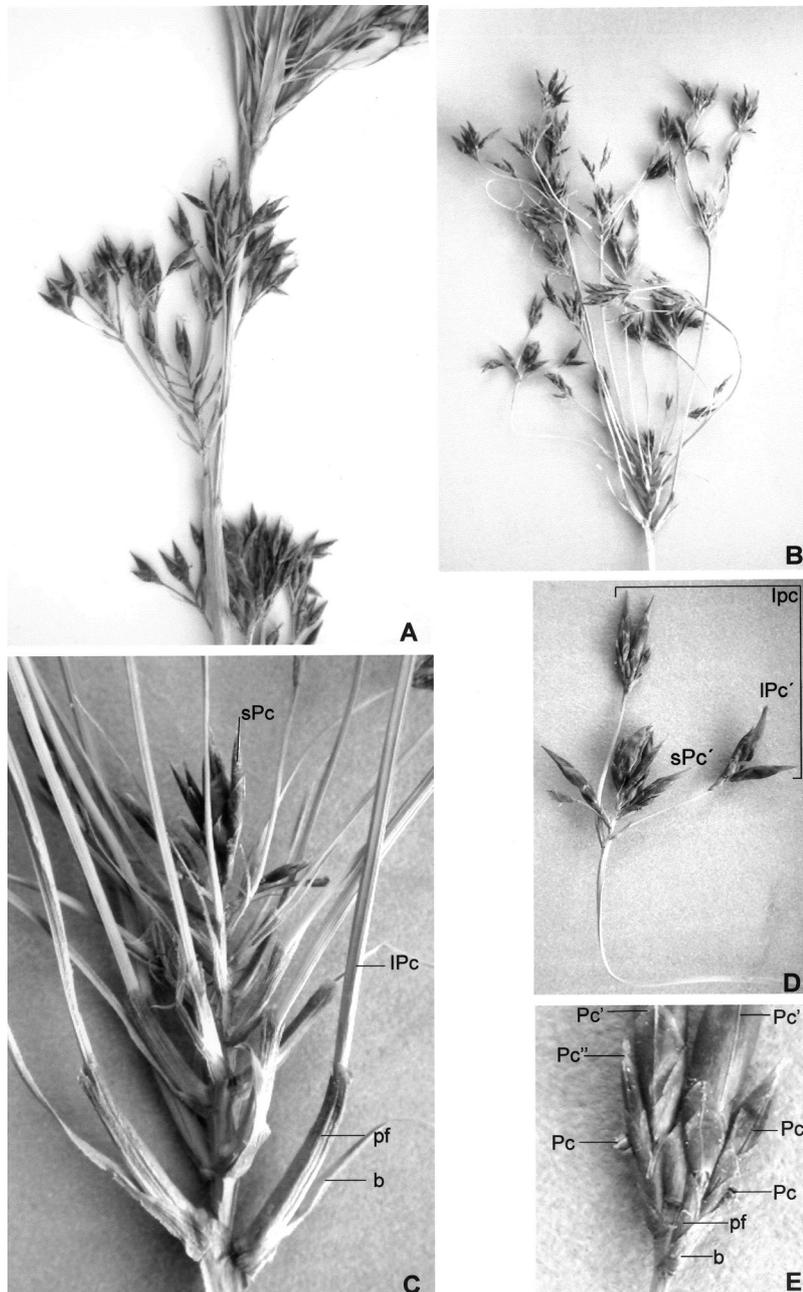


Fig. 2. *Rhynchospora corymbosa*. — **A**: Panicle. — **B** and **C**: Distal part. — **D**: Long paracladium. — **E**: Prophyllate paracladia. Pc, Pc', Pc'' = paracladia of consecutively higher order; the others as in Fig. 1.

epipodium length and of the prophyll development can be observed. The prophyll is tubular in the proximal paracladia (cladoprophyll) and it is barely developed in distal paracladia, appearing as a glume (Vegetti & Tivano 1991).

In Cyperaceae, the paracladia are diminished in acropetal sequence and, as stated by Timonen

(1993), the numeration of the axes must consequently be from base to apex (Mora-Osejo 1960, Meert & Goetghebeur 1979, Vegetti & Tivano 1991, Vegetti 1992, Heinzen & Vegetti 1994, Vegetti 1994) rather than *vice versa* (Kukkonen 1984, 1986, 1990, Browning & Gordon-Gray 1999).

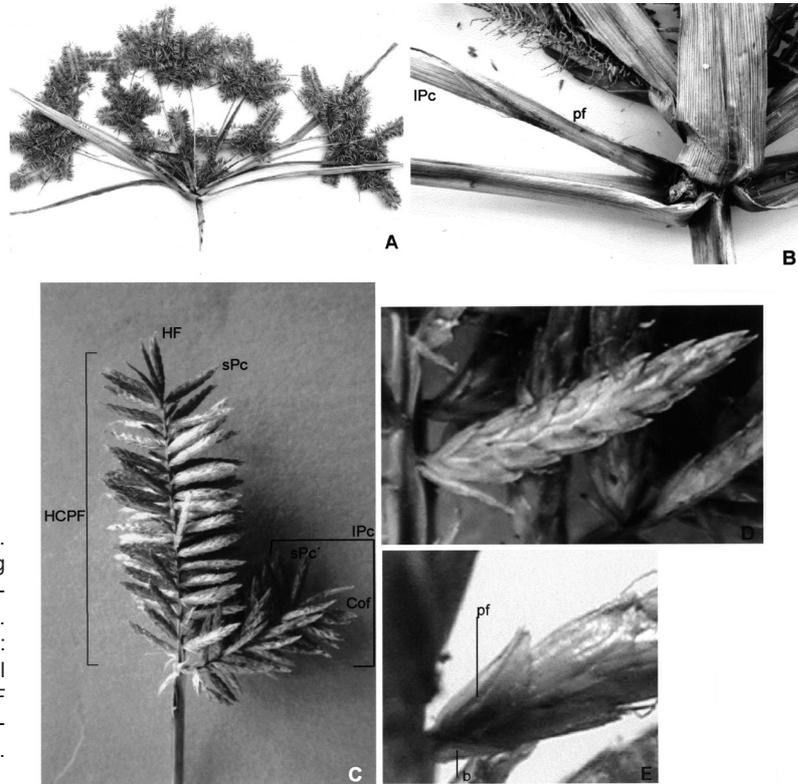


Fig. 3. *Cyperus digitatus*. — **A:** Anthelodium. — **B:** Long paracladium with its cladoprophyll. — **C:** Distal part. — **D:** Axillary spikelet. — **E:** Subtending bract and prophyll of the axillary spikelet. HCPF = main central partial florescence; the others as in Figs. 1 and 2.

At the base of axillary spikelets (short paracladia), a well developed prophyll (Fig. 3D and E) is present (since it is an axillary shoot). In terminal spikelets this is not the case (neither on the main axis nor on the long paracladia).

In the anthelodia the main florescence and the distal paracladia form a central, contracted group of spikelets (Figs. 1C, 3C, 4E and F). Browning and Gordon-Gray (1999) called this structure the main central partial florescence.

Variations in the flowering unit structure

Variation in the structure of the flowering unit may be analyzed in the main florescence and in the paracladial zone. In general, a main florescence is present. It shows variation in length and morphology of the rachilla, in the number and the size of the glumes and in the sexual condition of the flowers. In addition, some species exhibit differences in the disarticulation of rachilla or

glumes. The literature on the spikelet structure in Cyperaceae is abundant (Holttum 1948, Mora-Osejo 1966, Kukkonen 1967, Eiten 1976a, 1976b, Haines & Lye 1977, Hooper 1986, Nijalingappa & Goetghebeur 1990, Browning 1994, Browning & Gordon-Gray 1995a, 1995b).

The main florescence can be missing if truncation has taken place (Weberling 1989). Then the inflorescence is called truncate. This is the case in *Cyperus papyrus* (Mora-Osejo 1960), *C. prolifer* (Raynal 1971, Haines & Lye 1983) and *C. giganteus* (Fig. 1B; Perreta & Vegetti 2001).

However, the most important variation is observed in the paracladia. Thus variation of the synflorescence may either consist of many spikelets arranged in a complex branching system, or a few spikelets or even a single spikelet. In the latter case, the paracladial zone is not developed and the flowering unit comprises of the main florescence only, as in *Eleocharis* (Fig. 5E) and some species of *Schoenoplectus* (Figs. 8 and 9; Vegetti 1992), *Isolepis* (Vegetti 1994) and *Bolboschoenus* (Browning & Gordon-Gray 1999).

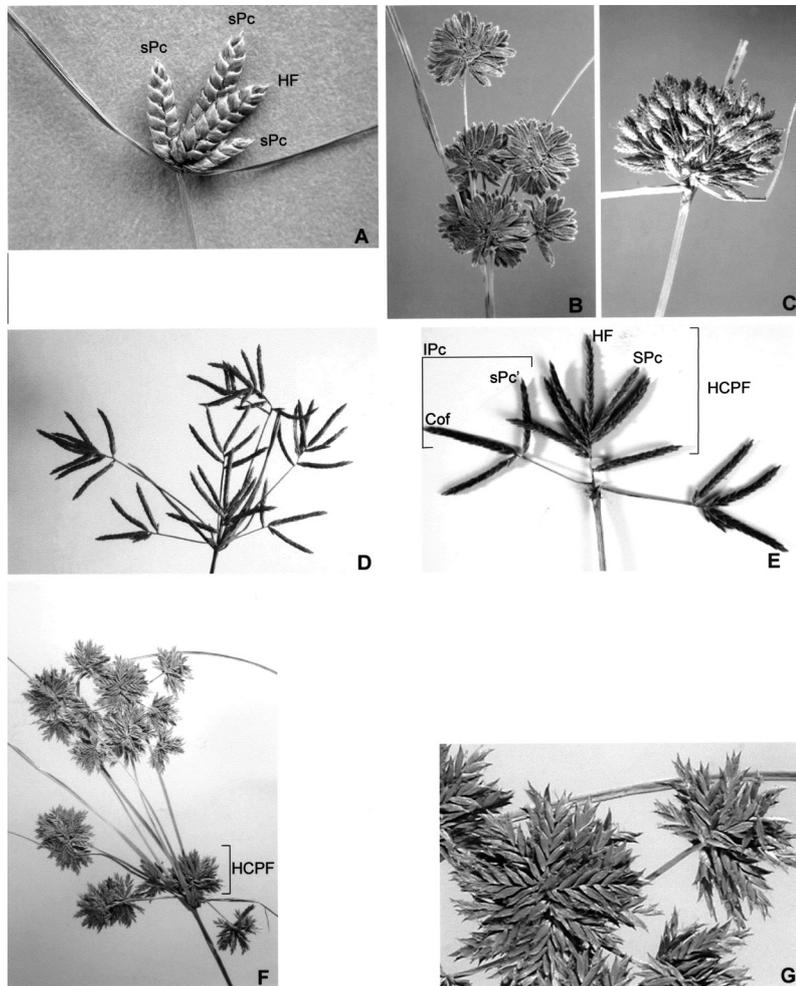


Fig. 4. Inflorescences of species of *Cyperus*. — **A:** *C. incomtus*. — **B and C:** *C. reflexus*. — **D and E:** *C. rotundus* (in **E** distal part of **D** without long paracladia). — **F and G:** *C. oxylepis* (**G** is part of a primary long paracladium of **F**). Symbols as in Figs. 1 and 2.

The variation in paracladial can concern:

1. The number of paracladia arranged on the main axis, e.g. anthelodia with “few radiuses” (Figs. 4D and 5A), and others with “many radiuses” (Figs. 3A and 4F).
2. The degree of development of primary paracladia, which may be (a) reduced to a cofillorescence (Fig. 4A), or (b) consisting of the cofillorescence and paracladia of higher order (secondary only or of “n” order), e.g. composite anthelodia or paniculodia with branches of diverse ramification order (Figs. 1A and C, 2, 5A–D and 6–9).
3. The development of bracts and prophylls.
4. The development of prophyllary buds (Figs. 2E and 6–9);
5. The intercalary growth of internodes, both on the main axis and on paracladia of diverse orders, especially the internodes of the main axis and of the epipodium in the long paracladia. Strong suppression of the intercalary growth of the internodes leads to flowering units arranged in a capitulum (Fig. 6D).
6. The stimulation of basipetal-mesotonic development of the buds. This, combined with the variation mentioned above causes that the main florescence (Figs. 1C, 2, 4 and 5), remains hidden among the long paracladia (anthelodium).

The inflorescences of Cyperaceae are a good example of the “principle of variable proportions” (Troll 1964). Although they show a dif-

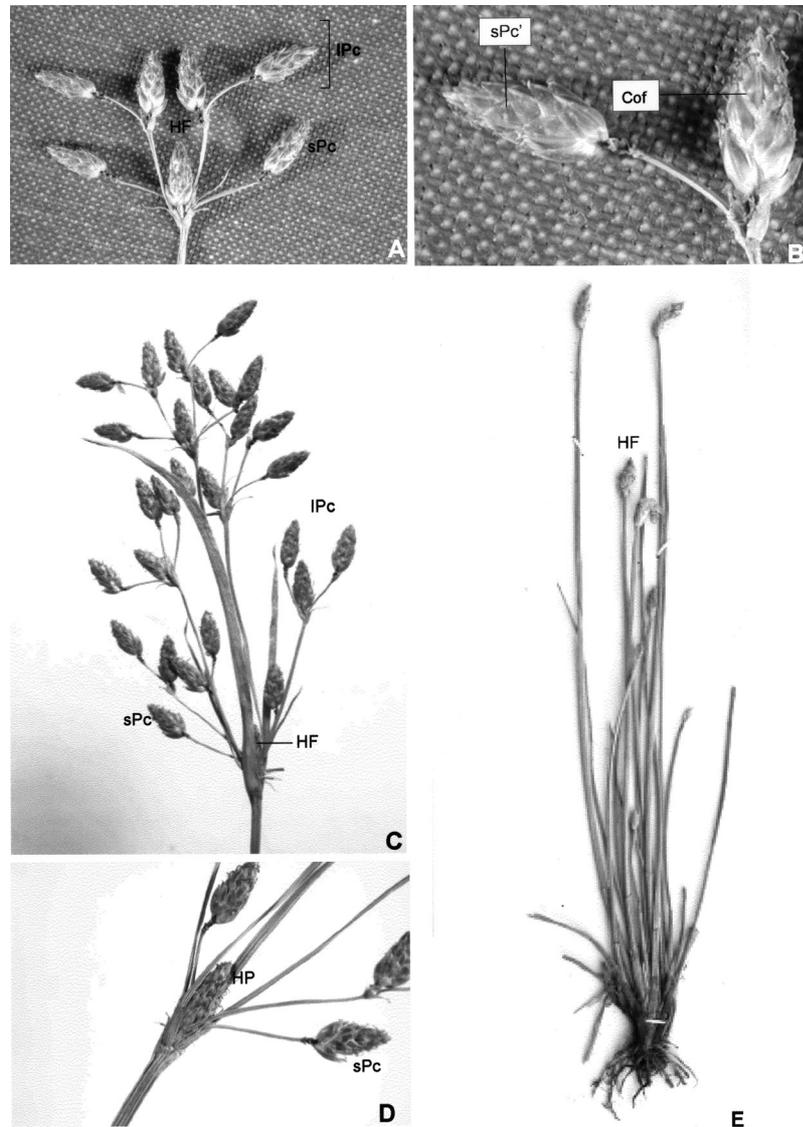


Fig. 5. A–D: *Fimbristylis dichotoma*. — **A** and **C**: Inflorescence. — **B**: Long paracladium of **A**. — **D**: Main inflorescence and short paracladia of **C**. — **E**: *Eleocharis obtusa*. Symbols as in Fig. 1 and 2.

ferent appearance, a careful observation of the branching system reveals a common structural pattern with different degrees of development among their components (especially the internode length of the main axis and of the epipodia), the level of ramification of the paracladia, and the development of bracts and prophylls. Raynal (1971) considered that the anthelodium and paniculodium have a common structural plan but different intercalary growth of the internodes (Fig. 1A and C).

In some genera, inflorescences are very homogeneous, as in *Eleocharis*, where they are

composed of single spikelets (main florescence), or in the tribe Trilepideae, with a paniculodium of dense spikes, each spike comprising of many small spikelets (Goetghebeur 1998). In other genera, even when they maintain a common structural pattern, important variation in the degree of development of their components are observed. This is the case in *Schoenoplectus* (Figs. 6–9; Vegetti & Tivano 1991, Vegetti 1992), *Isolepis* (Vegetti 1994), and *Bolboschoenus* (Browning & Gordon-Gray 1999). In the latter genus a considerable range of variation of anthelodia is represented by an inflorescence



Fig. 6. *Schoenoplectus californicus*. — **A–C:** *S. californicus* var. *californicus*. — **D:** *S. californicus* var. *spoliatus*. Symbols as in Fig. 2.

comprising a solitary spikelet only, to complex structures, with branches of third or occasionally even fourth ramification order, that altogether may bear more than 400 spikelets. According to Browning and Gordon-Gray (1999), in southern African species of *Bolboschoenus* variation in the degree of development of the paracladial zone and consequently in the number of spikelets is observed, even within a single species.

A very particular structural pattern can be seen in *Cyperus giganteus* (Fig. 1B). The inflo-

rescence displays truncation of the main florescence and of the distal short paracladia. Consequently, the inflorescence consists exclusively of ramified primary paracladia (Perreta & Vegetti 2001). This pattern is also present in *C. papyrus* (Mora-Osejo 1960, Raynal 1971, Haine & Lye 1983) and *C. prolifer* (Raynal 1971, Haine & Lye 1983).

In the inflorescences of Cariceae (Fig. 10) truncation of the main florescence and homogenization of the distal paracladia have taken place,

Fig. 7. Schematic representation of the inflorescence of *Schoenoplectus californicus*. Symbols: 1 = lower node; 2–8, successive nodes of main axis; B₁ = lower bract; B_{2–8} = bracts of nodes 2–8; Pc₁ = paracladium developed at node 1; Pc_{2–8} = paracladia developed at nodes 2–8; Pc'₁–Pc'₅ = paracladia of succeeding orders corresponding to paracladium Pc₁; Pf₁ and Pf'₁ = prophylls; epi = epidium; CoF = coflorescence; HF = main florescence.

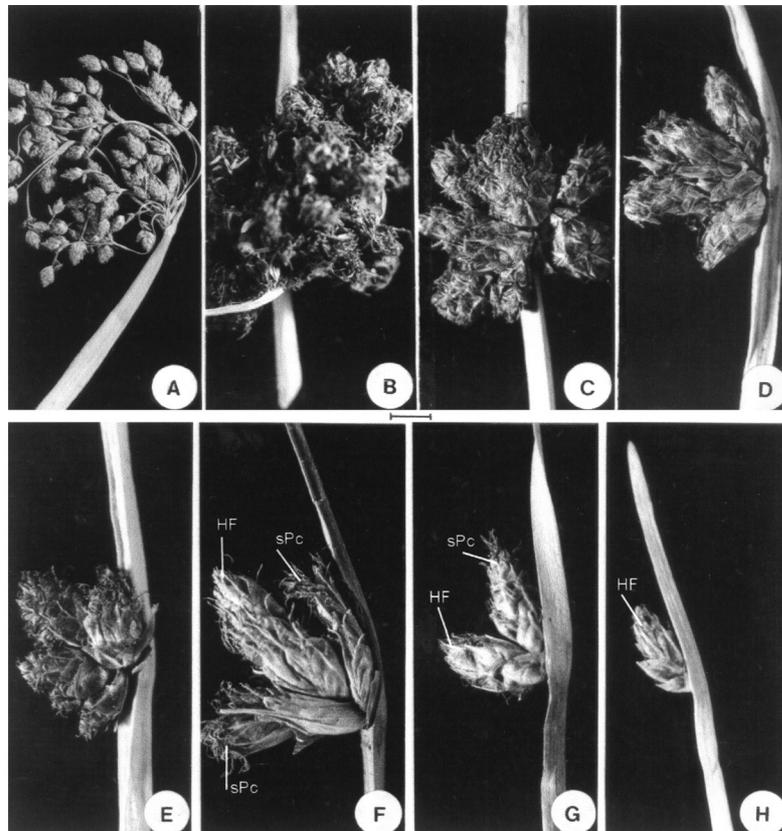
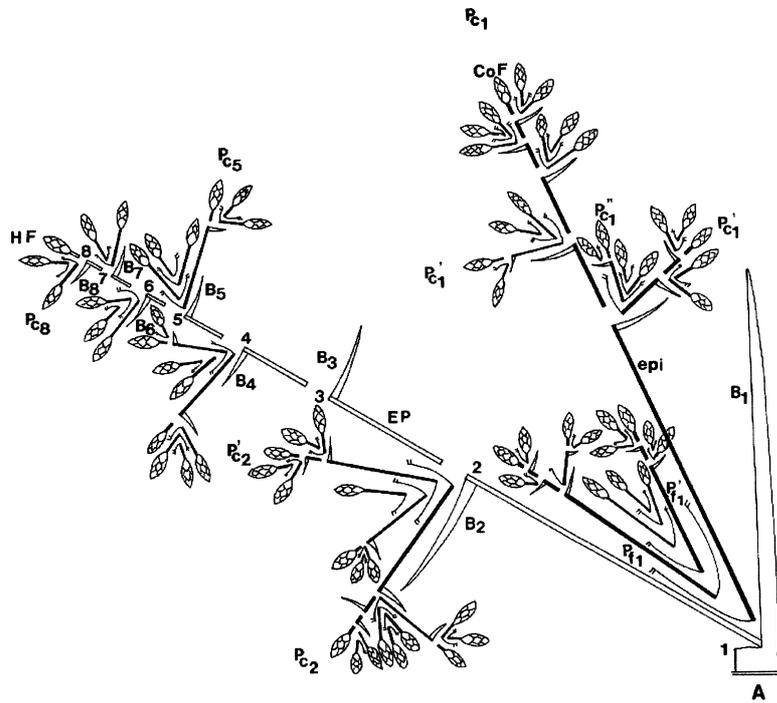


Fig. 8. Inflorescences of species of *Schoenoplectus*. — **A**: *S. tabernaemontani*. — **B**: *S. californicus* var. *spoliatus*. — **C** and **E**: *S. pungens* var. *longispicatus*. — **D**, **F**–**H**: *S. pungens* var. *badius*.



Fig. 9. Schematic representations of the inflorescences of species of *Schoenoplectus*. — **A:** *S. californicus* var. *spoliatus*. — **B:** *S. californicus* var. *tereticulmis*. — **C:** *S. pungens* var. *badius*. — **D, E, G and H:** *S. pungens* var. *longispicatus*. — **F:** *S. tabernaemontani*. Symbols as in Fig. 1.

producing a pseudoflorescence: the pseudospikelet (Vegetti 2001). Moreover, according to this author, in *Kobresia* the pseudoflorescence is very reduced and it is truncated in *K. macrolepis* and *K. pygmaea* var. *filiculmis*.

It is evident that the reductive processes do not always affect specific and/or equivalent areas. Indeed, in some cases, it is the proximal part of the inflorescence which is reduced; in extreme cases, the result is that only the main florescence remains (Vegetti 1992, 1994, Browning & Gordon-Gray 1999). In other cases the distal part of the inflorescence is reduced; this reduction can affect both the main florescence and the subzone of short paracladia (Perreta & Vegetti 2001, Vegetti 2001). Thus, in the latter case, the inflorescence is composed only of long

paracladia, as in *Cyperus giganteus* (Perreta & Vegetti 2001).

This typological analysis suggests usage of terms that may at first seem complicated, but when they are clear, they can be applied easily and effectively, as was demonstrated in the typological studies performed by Mora-Osejo (1960), Kukkonen (1984, 1986), Vegetti and Tivano (1991), Vegetti (1992, 1994), Heinzen and Vegetti (1994), and Browning and Gordon-Gray (1999).

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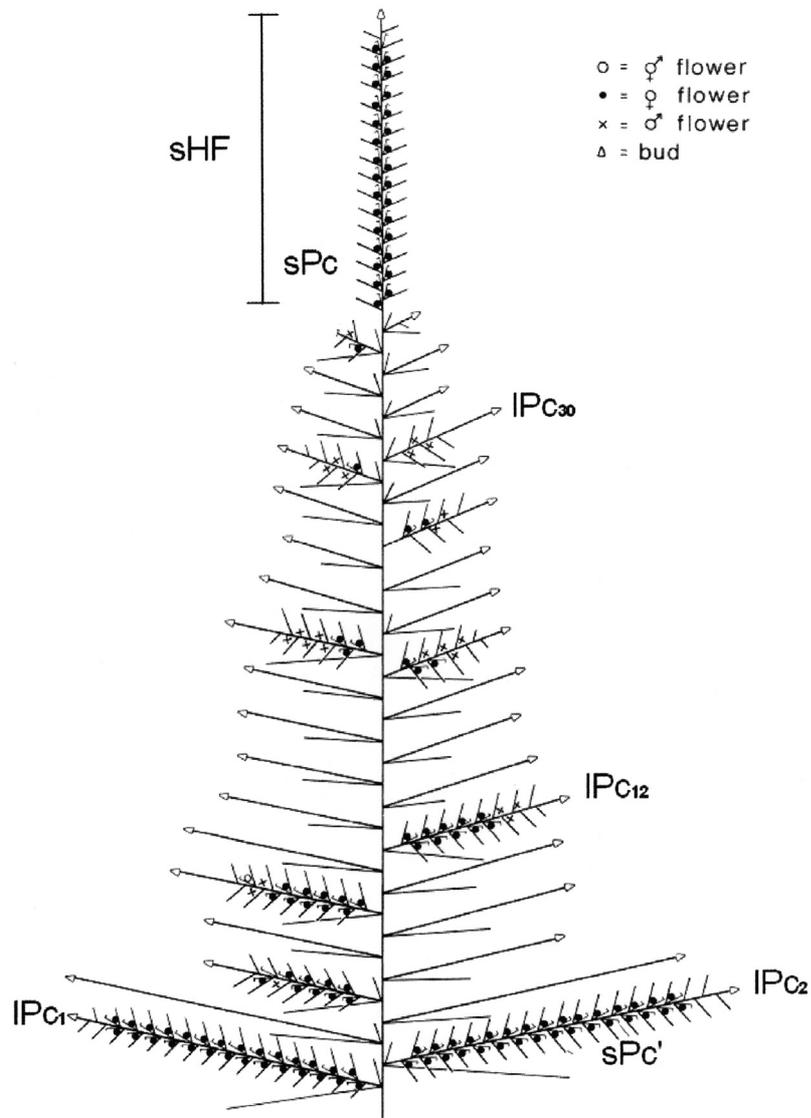


Fig. 10. Inflorescence of *Carex disticha* (modified from Kukkonen 1984). Symbols: sHF = pseudoflorescence; the others as in Fig. 1. Reproduced from Kukkonen (1984: fig. 5) with the permission of The Finnish Zoological and Botanical Publishing Board.

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