

## The Flowering Unit in the Synflorescences of Amaranthaceae

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**Abstract** The structure of the synflorescence and the flowering units in Amaranthaceae are characterized. The synflorescence is polytelic. In the flowering unit we recognize the main florescence and the enrichment zone. The florescences may consist of: (1) Fully developed partial florescences bearing three or more flowers; (2) Partial florescences reduced to one or a few fertile flowers having prophylls with more or less modified axillary productions; or (3) No partial florescences but solitary flowers having prophylls with no axillary productions. We described the flowering unit in species with florescences bearing a solitary flower and the flowering unit in species with florescences bearing partial florescences. Hypothesized developmental processes are described, with a view to finding relationships among different models characterized in the family as well as defining characters for cladistic studies, which may be useful to depict all the variations observed.

**Keywords** Amaranthaceae · Synflorescence · Flowering Unit · Inflorescence

### Introduction

The typology-based system developed by Troll (1964) and Weberling (Weberling, 1965, 1989) has proved to be useful for describing inflorescences (Rua, 1999) as well as for providing characters for cladistic analyses (Nickol, 1995; Rua & Aliscioni, 2002; Tortosa et al., 2004; Reinheimer, 2007).

In fact, Troll's key contribution was highlighting the necessity for a comparative morphological approach to discovering homology (Tortosa et al., 2004), which, in turn, he considered central to assess phylogenetic relationships (Troll, 1951). In their research on the inflorescences of *Nassauvia* Comm. ex Juss., Tortosa et al. (2004) have proved that a typological approach may not only be compatible with a cladistic treatment of characters, but also a necessary first step

towards constructing hypotheses on primary homology (De Pinna, 1991) which may be suitable for testing through cladistic analysis (Rua, 1999).

In the typology-based analysis of inflorescences proposed by Troll (1964) and Weberling (1989), the concept of flowering unit introduced by Sell (1976) becomes useful. The flowering unit represents the characteristic inflorescence within one species, i.e. the minimum possible flowering expression in any given species. It may be one flower, one florescence, or a more complex branch system (Rua, 1999).

The complete flowering branch system produced by an apical bud of the embrional axis or an innovation bud during a growth season is called synflorescence (Troll, 1964; Weberling, 1965, 1989). The synflorescence bears a terminal flowering unit, which ends the main axis of the plant, and the axillary flowering units, which are found in the apical region of the lateral branches (Sell & Cremers, 1987).

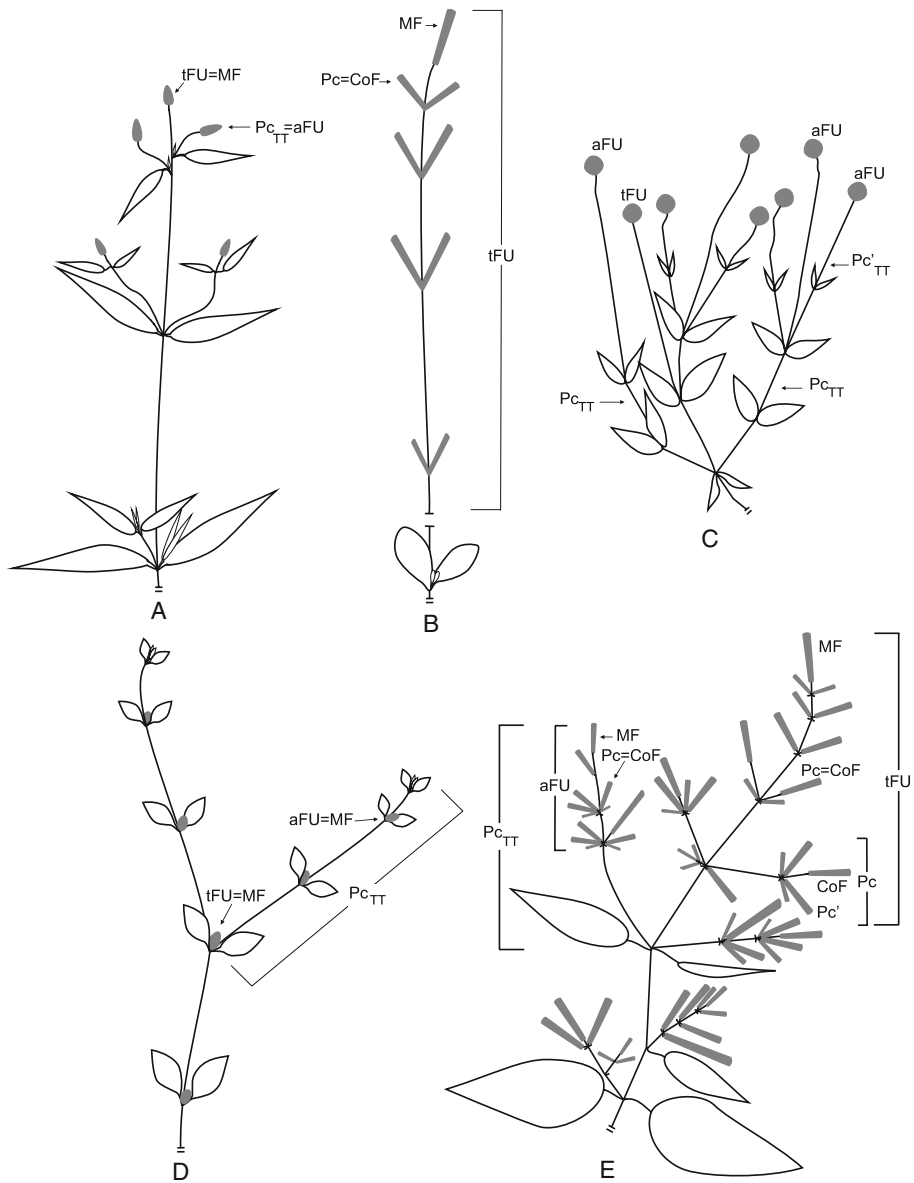
Amaranthaceae Juss. (in the sense of Schinz, 1934) comprises 77 genera with a total of approximately 840 species, mainly distributed throughout tropical and subtropical latitudes (Müller & Borsch, 2005b). Only a few genera occur in temperate regions, the most prominent of which is *Amaranthus* L. Centers of diversity are Central and South America, tropical and South Africa, and Australia. The family contains annuals, herbaceous perennials, shrubs, woody lianas, and even small trees (Kadereit et al., 2003). Amaranthaceae are characterized by having solitary flowers, cymose or variously compound (modified cymose) inflorescences, often subtended by bracts or bracteoles (Cronquist, 1981; Kadereit et al., 2003). Some characters of great taxonomic importance include the reproductive organs and the structure and typology of the inflorescences (Eckardt, 1976; Cronquist, 1981).

In this work, we analyze the structure of the synflorescence and, particularly, the structure of the flowering unit in Amaranthaceae. To this end, we describe hypothesized developmental processes, with a view to finding relationships among different models characterized in the family as well as defining characters for cladistic studies, which may be useful to depict all the variations observed.

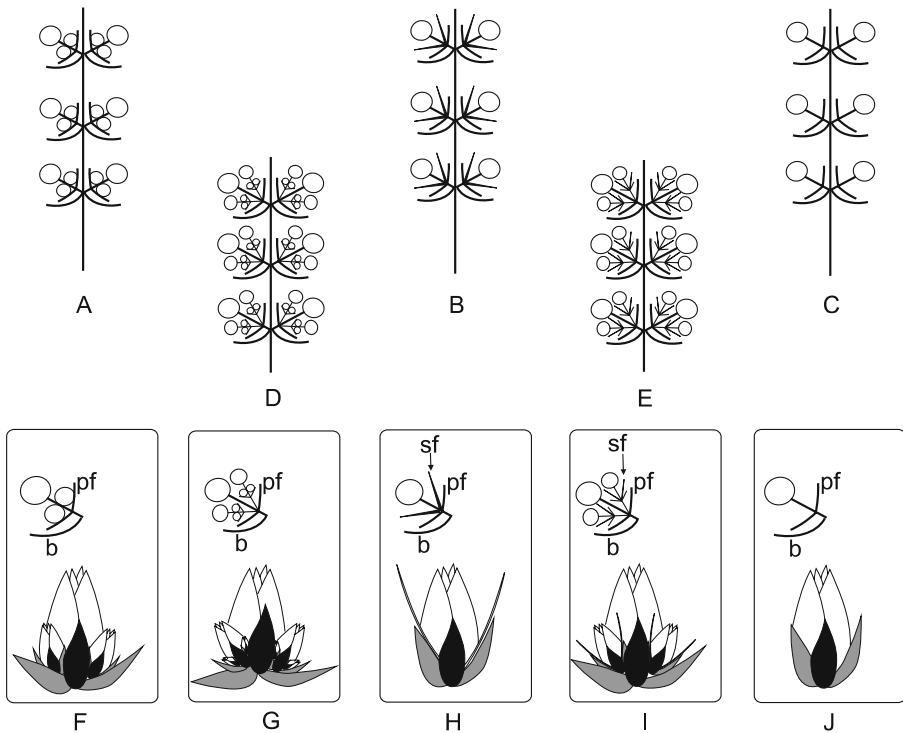
## The Structure of the Synflorescence

These are annual or perennial species. Each synflorescence has a distal region, the anthotagma, that is, the terminal flowering unit (tFU= terminal inflorescence), and a proximal region, the trophotagma, which usually has a vegetative function (Fig. 1). The trophotagma is the region of the synflorescence that bears well-developed leaves. The axillary buds of the trophotagma may develop branches (paraclades of the trophotagma, branches of the trophotagma or enrichment axes, Fig. 1). Consequently, the trophotagma region commonly shows an enrichment zone. These paraclades end in a flowering unit (lateral or axillary FU, aFU) similar to the FU of the main axis (tFU).

In the Amaranthaceae synflorescence, the terminal and axillary flowering units lack terminal flowers, but they bear a cluster of lateral flowers (Fig. 2); therefore, the synflorescence in this family is polytelic (Troll, 1964).



**Fig. 1** Synflorescences in Amaranthaceae: A, *Pseudoplantago friesii* Suess. (Covas, 1939); B, *Froelichia tomentosa* (Mart.) Moq. (Pedersen, 1987); C, *Pfaffia gnaphaloides* (L.f.) Mart. (Carrizo & Isasmendi, 1998); D, *Alternanthera kurzii* Schinz ex Peders. (Pedersen, 1987); E, *Hebanthe occidentalis* Borsch et Pedersen (Carrizo & Isasmendi, 1998). Key: aFU, axillary flowering unit; tFU, terminal flowering unit; Pc, Pc', paraclades of the flowering unit of consecutive order; Pc<sub>TT</sub>, Pc'<sub>TT</sub>, paraclades of the trophotagma of consecutive order; MF, main florescence; CoF, coflorescence



**Fig. 2** Florescences of Amaranthaceae: A, partial florescence with cyme bearing 3 fertile flowers; B, partial florescence with cyme bearing one fertile flower and 2 sterile lateral flowers; C, partial florescence with solitary flowers; D, partial florescence with more than 3 fertile flowers; E, partial florescence with more than one fertile flower and sterile lateral flowers; F, G, H, I and J, details of the units for each florescence shown in A, D, B, E and C, respectively

## The Flowering Unit

In the flowering unit we recognize the main florescence and the enrichment zone (or paracladial zone), which is composed of a variable number of paraclades (paraclades of the flowering unit, Pc Fig. 1).

### The Main Florescence

The main florescence is the terminal flowering grouping on the main axis. In Amaranthaceae, the flowering axis of the florescences (Fig. 2) may be simple (reduced to one flower with its two prophylls) or branched in the axil of its prophylls, thus making up partial florescences (Troll, 1964; Weberling, 1985; Rua, 1999). In the same genera, (*Sericocomopsis* Schinz ex Gilg, *Indobanalia* A.N. Henry & B. Roy), the axillary bud of the prophylls generates one flower; consequently, the florescence is formed by dichasia. The cymose branching may repeat itself from the axillary bud of the prophylls in each flowering axis of the following order, and then some partial florescences (cymes) may show a complex structure (Rua, 1999). Lateral cymes may then become increasingly compound and

complex (as in *Nelsia* Schinz and *Amaranthus* species) (Townsend, 1993) owing to the development of the axillary bud of the prophylls of the lateral flowers of different order (Fig. 2).

In several genera (*Digera* Forssk., *Pleuropterantha* Franch., *Sericostachys* Gilg & Lopriore, *Centema* Hook. f.), the prophyllar flowers of the partial florescence either are modified sterile flowers of very diverse forms (spines, wings or hairs, Fig. 2B, H) or they do not develop (Fig. 2C, J). When the former occurs, the main florescence is composed of partial florescences made up by the central flower and 1–2 sterile flowers growing from the axil of 1–2 prophylls (*Pseudoplantago* Suess., *Digera*., *Kyphocarpa* (Fenzl) Lopr., *Cyathula* Blume, *Allmaniopsis* Suess., *Daysphaera* Volkens ex Gi). Branching from the prophylls, cymes may become even more complex, to the extent that some genera show a varying number of fertile flowers and sterile flowers (Fig. 2E, I) (*Centema*, *Kyphocarpa*, *Nelsia*, *Neocentema* Schinz, Cavaco, 1962). In *Rosifax* C. Townsend, the partial florescence consists of a solitary hermaphrodite flower and a solitary small sterile flower formed by a large-celled, spongy, ventrally floccose cylinder tipped with small greenish processes present within and scarcely exceeding one bracteole, with the second bracteole empty (Townsend, 1993). In *Sericorema* (Hook. f.) Lopr., sterile flowers depicted as branched spines are in fact a small bud (Cavaco, 1962). If the partial florescence bears more than 3 flowers, it may have 1–3 hermaphrodite flowers with 1–2 lateral modified sterile flowers (*Pseudoseriocoma* Cavaco, Townsend, 1993).

In the Gomphreneae and Celosieae tribes, several genera of the Aervinae subtribe (*Sericocoma*, *Arthraerua* Schinz, *Aerva* Forssk., *Polyrhabda* C.C.Townsend, *Trichuriella* Bennet, *Nothosaerva* Wight) and the genus *Charpentiera* Gaudich. (subtribe Amaranthinae), the main florescence consists of an assembly of solitary flowers along the main axis (no partial florescences may be observed, as in the above-mentioned cases). In all of these species, the flower has prophylls but has not developed axillary buds (Fig. 2C, J).

The development of partial florescences in the main florescence is highly variable and influenced by the environment where the plants grow (Cremers & Sell, 1986); however, in Amaranthaceae, the development of the partial florescence and that of solitary flowers in the florescence seem to be genetically determined for different groups.

Sterile flowers and partial florescence axes go through significant modifications, so that, in some cases, the partial florescence falls as one unit (Townsend, 1993). According to this author, the lateral sterile modified flowers fuse with the indurate base of the partial florescence so that the whole unit falls as a burr in *Sericorema*, or in *Centema* and *Cyathula*, with the partial florescence falling wholly or partly as a burr in fruit.

Accordingly, florescences in the Amaranthaceae family may consist of:

- (1) Fully developed partial florescences bearing three or more flowers (Fig. 2A, D, F, G);
- (2) Partial florescences reduced to one or a few fertile flowers having prophylls with more or less modified axillary productions (Fig. 2B, E, H, I); or
- (3) No partial florescences but solitary flowers having prophylls with no axillary productions (Fig. 2C, J).

## The Paracladial Zone of the Flowering Unit

Some species (Fig. 1B, E) bear a varying number of flowery branches underneath the main florescence (primary paraclades). Each primary paraclade ends in a structure that is similar to the one described for the main axis (coflorescence = florescence of the paraclade) and may, in turn, have paraclades of the following order.

## Variations in the Structure of the Flowering Unit

The inflorescences (= flowering units) of the Amaranthaceae have been described as a dense head, spike, raceme or panicle, or a loose or spike-like thyrse (Eliasson, 1988; Townsend, 1993). In this family, the flowering unit may be either reduced to the florescence (Fig. 1A, C, D) or it may also have a paracladial zone (Fig. 1B, E). Thus, the most significant variations of the flowering unit within this family relate to the florescence structure and the degree of development of the paracladial zone.

### The Flowering Unit in Species with Florescences Bearing a Solitary Flower

In some species, the FU lacks a paracladial zone and is only composed of the main florescence (MF). In such cases, when the florescence consists of solitary flowers arranged along an axis, the FU is either a spike (or spiciform inflorescence) or a raceme. *Deeringia* R. Br., *Henonia* Moq., *Hermbstaedtia* Rchb., *Pseudodigera* Chiov., *Arthraerua*, *Chionothrix* Hook. f., *Psilotrichum* Blume, *Achyranthes* L., *Pandiaka* Hook. f., *Alternanthera* Forssk., and *Gomphrena* L. (Cavaco, 1962) bear spikes; some specimens of *Deeringia* (Cavaco, 1962) bear racemes.

In other species, the FU is composed of the main florescence and a varying number of paraclades ( $Pc_{FU}$ ). In these cases, the FU consists of a complex branching system with a main axis and branches; it is a paniculiform inflorescence with spiciform or racemose branches, depicted as a branched spike (Townsend, 1993), a panicle (Standley, 1917; Eliasson, 1987; Robertson, 1981), a paniculiform complex inflorescence (Borsch, 2001) or a synflorescence of racemes (Sánchez-del Pino & Flores Olivera, 2006). Examples of such structure may be found in *Deeringia*, *Lagrezia* Moq., *Aerva*, *Chionothrix*, *Psilotrichum*, *Achyranthes*, *Achyropsis* Hook. f., *Pleuropetalum* Hook. f., *Irenella* Suess. (Cavaco, 1962; Townsend, 1993).

### The Flowering Unit in Species with Florescences Bearing Partial Florescences

When the FU lacks a paracladial zone and is only composed of the main florescence, if the florescences comprise partial florescences arranged along an axis, then the FU is a spike-like thyrse, such as occurs with *Amaranthus*, *Digera*, *Chamissoa* Kunth, *Pleuropterantha* Franch., *Saltia* R. Br., *Nelsia*, *Marcelliopsis* Schinz, *Kyphocarpa*, *Centema*, *Neocentema*, *Pupalia* Juss. (Cavaco, 1962; Townsend, 1993; Sánchez-del Pino & Flores Olivera, 2006). If the FU bears paraclades, it may be described as a panicle (Standley, 1917; Eliasson, 1987; Robertson, 1981) or, in practical terms, as a

“paniculiform complex inflorescence” (Borsch, 2001); however, following a strict terminology, it as a synflorescence of thyrsoid paracladia (Sánchez-del Pino & Flores Olivera, 2006). Examples may be found in *Iresine* P. Browne and *Sericostachys* (Cavaco, 1962; Townsend, 1993).

In the thyrses-type synflorescence, the partial florescence may be either dichasium or may then become increasingly compound and complex (as in the *Amaranthus* species).

### Other Considerations on the Flowering Unit

Many genera have a very reduced inflorescence axis to form capitula that may be condensed-spiciform (as in various *Brayulinea* Small, *Mechowia* Schinz, *Pandiaka*, *Philoxerus* R. Br., *Gomphrena* and *Alternanthera* species) or condensed-thyrsoid (as in *Allmania* R. Br. ex Wight) (Townsend, 1993). Such inflorescences have been described as globose heads, subglobose or short to elongate capitate or glomerate spikes by some authors (Standley, 1917; Mears, 1977; Eliasson, 1987; Henrickson, 1987; Borsch, 2001). In other genera, it is the paraclade axes that are much reduced to form capitula that may be condensed-spiciform (*Celosia* L.) or condensed-thyrsoid (*Amaranthus*, *Pseudoseriocoma*, *Leucosphaera* Gilg, *Cyathula*, *Dasysphaera* Volkens ex Gilg).

Depending on the degree of development of the paracladial zone within a certain genus, inflorescences may be spike-like to lax and paniculate (*Ptilotus* R. Br., *Psilotrichum*, *Psilotrichopsis* C.C. Townsend, *Achyranthes*, *Pfaffia* Mart. *Chionothrix*, *Stilbanthus* Hook. F. (Townsend, 1993). In some cases, the terminal flowering unit (tFU) bears branches and, consequently, a main florescence and paraclades of consecutive order are present, whereas the axillary flowering units (aFU) are barely branched or bear only a main florescence. Thus, it is possible to find paniculiform inflorescences with spiciform branches and simple spike-like inflorescences in one species (*Froelichia* Moench and *Hebanthe* Mart.).

It should be noted that, in some genera, the flowery shoots have an inflorescence that has been described (Townsend, 1993) as solitary or clustered axillary spikes (*Nothosaerva* Wight); solitary or fasciculate (*Alternanthera*); with very small hermaphrodite flowers, in few axillary flowered sessile clusters or in dichasia (*Tidestromia* Standley, Sánchez-del Pino & Flores Olivera, 2006); with hermaphrodite flowers, either solitary or paired in the axils of upper leaves (*Polyrhabda*).

Usually, one branch (paraclade) arises per leaf at each node from the respective axillary bud; however, in *Gomphrena boliviana* Moq. var. *boliviana* f. *robusta* (Hicken) Pedersen, *G. ferruginea* Pedersen var. *rustica* Pedersen, *G. tomentosa* (Griseb) R.E. Fr., *G. pallida* (Suess.) Pedersen subsp. *pallida*, *Iresine diffusa* Humb. & Bonpl. ex Willd. var. *diffusa* (Pedersen, 1976, 1990; Acosta, pers. com.), in some species of *Charpentiera* and *Froelichia* (Townsend, 1993; Borsch and Pedersen, 1997; Sánchez-del Pino & Flores Olivera, 2006), two or more branches arise per leaf at each node, which may lead to consider the possibility of branches developing from accessory buds (*Hebanthe*, Fig. 1, E).

The varying intercalary growth determines variations in the florescence axis, in its peduncle and in the enrichment zone. Accordingly, FUs may be extremely dense or extremely lax, shortly or long pedunculate, with paraclades closer to or farther away



along the main axis, and axillary flowering units closer to or farther away along the paraclades.

Paraclades differ in number and degree of branching. There are also differences in the number of leaves in each paraclade and in the gradual reduction, or lack of it, of the leaves that become bracts.

Bracts in each partial florescence and prophylls may be persistent or deciduous. The shape and hair density of the prophylls and the sterile flowers in the partial florescences contribute to fruit dissemination by the wind (Cavaco, 1962; Engler, 1964).

### Hypothesized Developmental Processes

Differences among the models of synflorescences present in Amaranthaceae may be explained in terms of the following processes: development of the florescence prophyllar bud; reduction of flower number in the florescences; reduction of the number of partial florescences in the florescences; shortening of internodes of the florescences; shortening of the basal internode of the partial florescences; shortening of the basal internode (peduncle) of the florescences; reduction of the paraclade number; reduction of the branching degree of the paraclades; shortening of the internodes of the main axis and of the paraclades; reduction of the number of leaves along the main axis and in each paraclade. These processes seem to have taken place, independently or in combination, more than once and in different ways.

As no development evidence is currently available supporting correlation between such processes in Amaranthaceae, each of them should be treated as an independent character in cladistic studies. The treatment of the inflorescence type as a single compound character seems to be somewhat hazardous, since inflorescence configurations may have resulted from the combination of several developmentally independent characters (Tortosa et al., 2004).

### Taxonomic and Phylogenetic Considerations

The Amaranthaceae classification and circumscription are currently under discussion (Rodman, 1990; Downie & Palmer, 1994; Manhart & Rettig, 1994; Judd et al., 1999; Cuénoud et al., 2002; Müller & Borsch, 2005b). Cavaco's (1962) proposed new system largely based on inflorescence characters and embryology, with two additional subfamilies (Brayulinoideae, Celosioideae), remained mostly unaccepted by authors afterward (Townsend, 1993).

The currently accepted classification by Townsend (1993) is largely based upon the work of Schinz (1893, 1934), who recognized two subfamilies, the Amaranthoideae and the Gomphrenoideae. The *Pseudoplantago* genus, displaying a mixture of amaranthoid and gomphrenoid floral morphology, was classified within its own tribe (Covas, 1939) and considered intermediate between the two subfamilies (Eliasson, 1988; Townsend, 1993). Because of its gomphrenoid unilocular anthers; however, the Pseudoplantageae tribe was classified within Gomphrenoideae (Townsend, 1993).



A survey of the pollen morphology of Amaranthaceae points to the polyphyly of most of Schinz's tribes (Borsch, 1998). Since the subfamilial and tribal classification traditionally employed (Schinz, 1893, 1934; Townsend, 1993), in particular for the diverse Amaranthoideae subfamily, this is not reflected by the tree presented by Kadereit et al. (2003) and Müller and Borsch (2005b). These recent molecular analyses of Amaranthaceae (Kadereit et al., 2003; Müller & Borsch, 2005b) have corroborated many of the suggestions made in the palynological study (Müller & Borsch, 2005a). According to these analyses, only the Gomphrenoideae subfamily and the Celosieae tribe were supported as monophyletic, while Amaranthoideae were found to be paraphyletic, and Amarantheae, Amaranthinae, Aervinae, Gomphreneae, Gomphreninae, and Froelichiinae were polyphyletic. Trees based on *matK/trnK* sequence data clearly show that most of the entities recognized at the tribal or subtribal level by previous authors (Schinz, 1893, 1934; Townsend, 1993) do not reflect natural groups (Müller & Borsch, 2005b). The Aervinae (Amarantheae, Amaranthoideae) subtribe constitutes the most speciose group in the system of Townsend (1993), consisting of 38 genera out of 69 distinguished by him. The group otherwise appears morphologically highly divergent. In addition, it is in this group that a great diversity in partial florescence structure is observed.

The evolution of morphological characters previously used for classification as well as of some pollen characters was analyzed by Müller and Borsch (2005a) based on the *matK/trnK* tree. One of the characters they analyzed was the partial inflorescence structure, for which they recognized only two states: there may be present only fertile flowers and modified sterile flowers. In Müller and Borsch's work (2005b), four independent gains of a type of partial inflorescence architecture are reconstructed. According to these authors, while the independence of the gain in *Pseudoplantago* is assured, the three gains traced in the Achyranthoids again depend on a topology that is not entirely certain.

In his new system, largely based on inflorescence characters, Cavaco (1962) analyzes the flower and inflorescence morphology in Amaranthaceae and explains variations observed in the structure of partial florescences (which he calls "partial" or "elementary" inflorescences). As we understand it, in many Amaranthaceae genera, partial florescences are cymes and, as such, lateral flowers are axillary products of the prophylls (Troll, 1964). A special case, which should be further researched into, is that of the *Sericocoma pungens* Fenzl species, which bears 4 prophylls by "elementary inflorescence" (Cavaco, 1962). They probably constitute two prophylls and two bracts, just as this author proposes for *Marcellopsis* (Cavaco, 1962). As Cavaco (1962) describes *Marcellopsis* structure, it may indicate that such "elementary inflorescence" is not a partial florescence but a paraclade; accordingly, the synflorescence structure in that genus should be examined more thoroughly.

Based on our study, the terminal and axillary flowering units should be delimited and characterized and the florescence structure should be analyzed by recognizing:

- Solitary flowers (Fig. 2C, J);
- Partial florescences

#### Simple cymes

bearing three fertile flowers (Fig. 2A, F)

bearing one fertile flower and two modified sterile lateral flowers (Fig. 2B, H)

## Compound cymes

bearing fertile flowers (Fig. 2D, G)

bearing fertile flowers and sterile lateral flowers (Fig. 2E, I) .

## Conclusion

In order to establish a suite of characters to deal satisfactorily with general inflorescence form, we recommend carefully determining the zones and regions of the synflorescence, paying special attention to the flowering unit and the structure of the paraclades of the trophotagma. In the flowering unit, the following characters must be considered: 1) development of the prophyllar bud of the primary flowers; 2) development degree of the partial florescences; 3) number of primary paraclades of the FU; 4) branching degree of these paraclades and 5) arrangement of these paraclades on the main axis.

Undoubtedly, developmental studies constitute a powerful source of characters that are necessary toward understanding inflorescence morphology and diversification (Doust & Kellogg, 2002a, b; Reinheimer, 2007) as well as extremely useful in taxonomic and phylogenetic research (Albert et al., 1998; Kellogg, 2000; Doust & Kellogg, 2002a, b; Kellogg et al., 2004; Bess et al., 2005).

In Amaranthaceae, new combined morphological and molecular phylogenetic analyses, with a dense sampling, will be required; these analyses must include information of inflorescence characters. We strongly believe it will be useful to incorporate into such analyses the characters of the inflorescences discussed in this work.

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