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Inflorescence Structure in Koyamaeae and its Relationship with Sclerieae, Bisboeckelereae, Cryptagieae and Trilepideae Tribes (Cyperoideae-Cyperaceae)

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Abstract This paper aims to interpret and characterize the inflorescence of Koyamaeae tribe from the typological point of view in order to establish homologies and promote comparative studies and the use of inflorescence characters in future phylogenetic studies. The Koyamaeae tribe is comprised of one monotypic *Koyamaea* W. Thomas & Davidse genus, with *K. neblinensis* W. Thomas & Davidse. *Koyamaea neblinensis* has a synflorescence type II and/or type III made up by a many-noded culm, covered by sheaths, usually unbranched (synflorescence type II), but occasionally with 1–2 branches from the upper half (synflorescence type III). The inflorescence of *Koyamaea* shows a main axis leading to a terminal spikelet (main florescence) and a primary branch (primary paraclade) arising from the axillary bud of the single involucral bract. Accordingly, the inflorescence is composed of the main florescence and a highly reduced paracladial zone. This paracladial zone is reduced to one node where a single primary paraclade is inserted. This primary paraclade consists of a short hypopodium, a prophyll, an epipodium and a terminal spikelet (or coflorescence). The axillary bud of the prophyll develops a secondary branch (secondary paraclade) with a similar structure to that of the primary paraclade. All subsequent higher-order branches also arise in the axils of prophylls. Inflorescence characters of this tribe are discussed in relation to related tribes *Sclerieae*, *Bisboeckelereae*, *Cryptangieae* and *Trilepideae* (sensu Goetghebeur, 1998).

Keywords *Koyamaea* · Cyperoideae · Cyperaceae · Inflorescence

I. Abstract
II. Introduction
III. The Structure of the Plant
IV. Inflorescence Structure
V. Branching Patterns
VI. Comparison of the inflorescence structure in *Koyamaea* and related genera
VII. Conclusions
VIII. References

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Introduction

The Koyamaeae tribe (sensu Thomas & Davidse, 1989) is comprised of one monotypic *Koyamaea* W. Thomas & Davidse genus, with *K. neblinensis* W. Thomas & Davidse. According to Thomas and Davidse (1989), this genus is so distinctive that it would be out of place in any existing tribe of Sclerioideae (sensu Goetghebeur, 1998), so they propose a new Koyamaeae tribe for this genus in the Sclerioideae subfamily. Goetghebeur (1998) considers this subfamily may be heterogeneous and identifies within it 4 tribes and two unclassified genera (*Exochogyne* C.B. Clarke and *Koyamaea*), listed as *insertae sedis*. In the phylogeny stated by Muasya et al. (2009), only two subfamilies are recognized for Cyperaceae: Mapanioideae and Cyperoideae. In this study, only some of the tribes identified by Goetghebeur (1998) within the Scleroideae subfamily are recognized as belonging to the Cyperoideae subfamily, and this phylogeny does not include the *Koyamaea* genus.

Koyamaea neblinensis is endemic in Cerro de la Neblina (SE Venezuela and adjacent Brazil), in dry scrubs or in more mesic savannahs (Thomas & Davidse, 1989; Goetghebeur, 1998). This species shows a capitate inflorescence with few-several bisexual spikelets with unisexual flowers (Thomas & Davidse, 1989; Goetghebeur, 1998) and it exhibits a prophyllar branching pattern (Thomas & Davidse, 1989). These authors provide a description of the inflorescence in *Koyamaea*; in such description, the genus has a different inflorescence structure than that observed in many of the genera to which it is related. In view of this, this review aims to interpret and characterize the inflorescence of Koyamaeae tribe from the typological point of view in order to establish homologies and promote comparative studies and the use of inflorescence characters in future phylogenetic studies. Inflorescence characters of this tribe are discussed in relation to related tribes *Sclerieae*, *Bisboeckelereae*, *Cryptangieae* and *Trilepideae* (sensu Goetghebeur, 1998).

The Structure of the Plant

In *Koyamaeae neblinensis*, as in most Cyperaceae species, the plant is composed of shoots of consecutive branching order (Fig. 1). One of the shoots is the main axis of the plant and the others are axillary shoots (innovations=basal branches) generated in the basal zone of short internodes. Each of these shoots should be considered, in a morphological sense, as a synflorescence (Troll, 1964; Rua, 1999; Vegetti, 2003).

During the vegetative phase, the apical meristems of the main axis and the axillary basal shoots generate leaves and shoots and, following floral induction, the terminal inflorescence (Fig. 1, tIn). This inflorescence appears in most of the Cypereae genera in the terminal portion of a long internode (scape) (Fig. 1a); however, the terminal inflorescence can sometimes be at the end of a foliate stem with somewhat developed internodes (Fig. 1b and c). The axillary buds in the foliate stem may develop (Fig. 1c) or not (Fig. 1b); thus, in some species, the tIn appears alone in the distal portion of such a foliate stem (Fig. 1b), while in other few species, when this happens, the axillary buds develop floriferous shoots (enrichment shoots, Fig. 1c). Each of these enrichment shoots ends in an inflorescence (lateral inflorescence, lIn).

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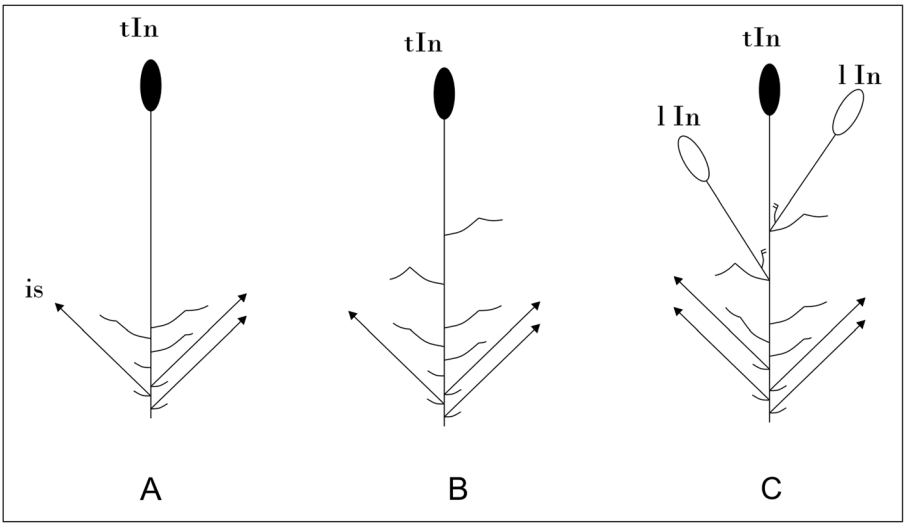

Fig. 1 Structure of synflorescence in Cyperaceae: **a** Synflorescence with aphyllous scape and terminal inflorescence (synflorescence type I); **b** Synflorescence with foliate stem and terminal inflorescence (synflorescence type II); **c** Synflorescence with foliate stem and terminal (filled oval) and lateral (empty oval) inflorescence (synflorescence type III). References: is, innovation shoot; lIn, lateral inflorescence; tIn, terminal inflorescence

Based on the aforementioned, the following synflorescence types may be recognized in the Cyperaceae (Reutemann et al., 2012): (1) a synflorescence with a scape and one single inflorescence (tIn), as in most species of Cyperaceae (synflorescence type I, Fig. 1a; (2) a synflorescence with only a tIn and a foliate stem, as in some species of *Ficinia* Schrad. and *Kyllinga* Rottb. (synflorescence type II, Fig. 1b); and (3) a synflorescence with a foliate stem with a tIn and a variable number of lIns (synflorescence type III, Fig. 1c), as in some species of *Ficinia* and *Cyperus blysmoides* C.B.Cl. The synflorescence types I and II have a single inflorescence (the terminal inflorescence); the synflorescence type III has a variable number of inflorescences (terminal inflorescence and lateral inflorescences).

Koyamaea neblinensis has a synflorescence type II and/or type III made up by a many-noded culm, covered by sheaths, usually unbranched (synflorescence type II), but occasionally with 1–2 branches from the upper half (synflorescence type III); these branches end in a lateral inflorescence similar to the terminal inflorescence.

Inflorescence Structure

Based on the description by Thomas and Davidse (1989), the inflorescence of *Koyamaea* shows a main axis leading to a terminal spikelet (main florescence) and a primary branch (primary paraclade) arising from the axillary bud of the single involucral bract. Accordingly, the inflorescence is composed of the main florescence and a highly reduced paracladial zone. This paracladial zone is reduced to one node where a single primary paraclade is inserted. This primary paraclade consists of a short hypopodium, a prophyll, an epipodium and a terminal spikelet (or coflorescence).

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The axillary bud of the prophyll develops a secondary branch (secondary paraclade) with a similar structure to that of the primary paraclade. All subsequent higher-order branches also arise in the axils of prophylls (Fig. 2a and b). As a result, there is one prophyll subtending each of the spikelets (Thomas & Davidse, 1989) except for the main florescence, which is on the main axis.

The inflorescence forms a solitary head terminating the main culm and branches. The head bears 2–9 spikelets (Thomas & Davidse, 1989). The inflorescence formed by 2 spikelets consists of the main florescence and one single primary paraclade. This paraclade lacks prophyllar branches. The inflorescence with 9 spikelets consists of the main florescence, one primary paraclade and subsequent higher-order paraclades, and may even have an eighth paraclade. The variations in the branching degree of the single primary paraclade determine the spikelet number in the inflorescence of *Koyamaea neblinensis*.

The main florescence is taken to a lateral position by the development of the single primary paraclade which, in turn, is taken to a lateral position by the development of the secondary paraclade, and so on, until the rudiment of the highest-order paraclade appears as pseudo-terminal. Because of this, the *Koyamaea neblinensis* inflorescence is typically pseudo-lateral (Fig. 2a).

Florescences (spikelets) show differential development based on the branching degree of the paraclades supporting them. The most-developed florescences (the main florescence and the co-florescence of the primary paraclade) consist of 16–26 glumes. The uppermost 1–2 and the lowermost 4–7 glumes are sterile, the lowest fertile glume bears a pistillate flower and the subsequent 10–16 glumes bear staminate flowers (Thomas & Davidse, 1989). The co-florescences (terminal spikelets) of paraclades of second order and subsequent orders are more reduced, with a smaller number of male flowers (Thomas & Davidse, 1989).

Branching Patterns

The *Koyamaea* inflorescence displays a prophyllar branching pattern (Thomas & Davidse, 1989). The single primary paraclade originates from the axillary bud of the involucral bract; the rest of the paraclades (1–8) originate from the axillary bud of the prophylls (Fig. 2a and b). The inflorescence in *Koyamaea neblinensis* consists of a terminal spikelet (main florescence) and a fascicle of spikelets of prophyllar nature (primary paraclade=paracladial zone).

In the Cyperaceae inflorescence, three types of branching patterns can be observed (Meert & Goetghebeur, 1979; Guarise & Vegetti, 2007; Reutemann et al., 2012), namely (a) normal branching: the branch is produced by an axillary bud of a bract; (b) prophyllar branching: the prophyllar branch is produced by a prophyllar bud; and (c) accessory branching: new branches are observed between an axillary branch and its bract.

Prophyllar productions may have varying degrees of development in different species and even within one species (Reutemann et al., 2009); also, they may repeat themselves several times; thus, the prophyllar branching pattern may or may not result in a whole series of prophyllar branches (Reutemann et al., 2012). A whole series of prophyllar branches occurs in the *Koyamaea* inflorescence (Fig. 2a and b). Normal and

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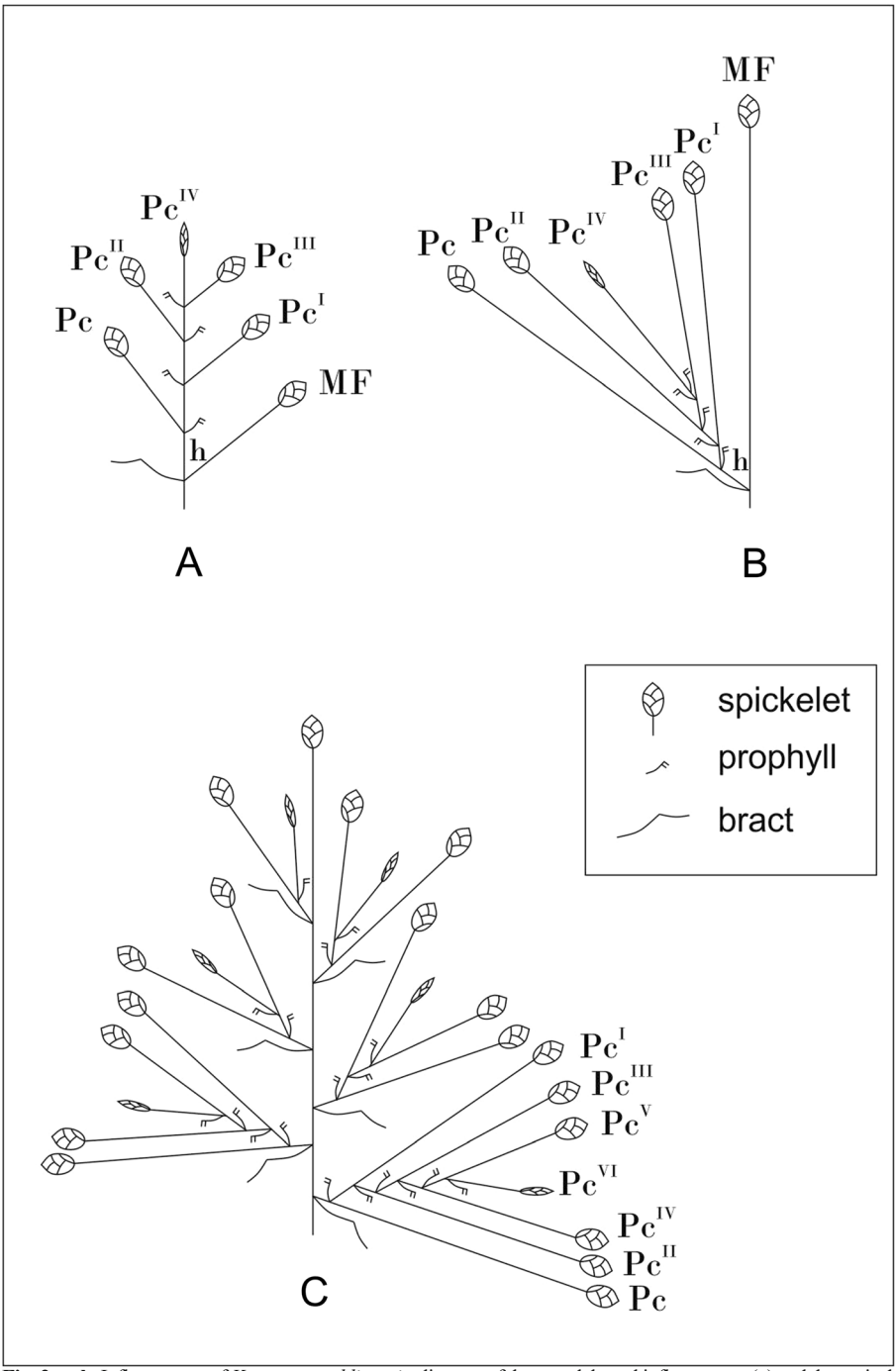

Fig. 2 **a**-**b**, Inflorescence of *Koyamaea neblinensis*: diagram of the pseudalateral inflorescence (**a**) and theoretical diagram of the inflorescence with its prophyllar branching pattern (**b**). **c**, Diagram of the inflorescence of *Scleria leptostachya*. References: *MF* main florescence, *Pc* primary paraclade, *Pc′*, *Pc″*, *Pc‴*, Pc^{IV}, Pc^{V}, Pc^{VI}, prophyllar paraclades of subsequent order. Adapted of: **a**, Thomas and Davidse (1989); **c**, Ahumada and Vegetti (2009)

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prophyllar branching patterns have been described by several authors (Blaser, 1944; Haines, 1966; Guaglianone, 1970, 1980, 1981, 1982; Meert & Goetghebeur, 1979; Vegetti & Tivano, 1991; Vegetti, 1992; Bruhl, 1995; Goetghebeur, 1998; Lucero & Vegetti, 2012; Reutemann et al., 2012). Prophyllar axillary productions can be either branched or reduced to their terminal spikelet. Although normal branching takes place along the inflorescence, the presence and position of prophyllar branches in the inflorescences may vary. In this context, whereas prophyllar branching is an important feature of the main branching system of the inflorescence, it is relatively rare in the spikelet clusters (Haines, 1966), except in the spikelet clusters of some species of *Cyperus* L. section *Luzuloidei* (Guarise & Vegetti, 2007), *Bulbostylis* Kunth (Reutemann et al., 2009), *Rhynchospora* Vahl (Haines, 1966; Lucero & Vegetti, 2012), *Scleria* P.J. Bergius and in the single spikelet fascicle of *Koyamaea* (Fig. 2a and b).

In different species, prophyllar axes may or may not be arranged in different ways along the main inflorescence axis and branches (Guarise & Vegetti, 2007; Reutemann et al., 2012). In *Bulbostylis*, the development of prophyllar productions does not occur in a given region of the inflorescence, whereas in some species of *Cyperus incomtus* Kunth var. *incomtus* and *C. ochraceus* Vahl, these branches are located in different parts of the inflorescence (Guarise & Vegetti, 2007). Given the limited development of the paracladial zone in *Koyamaea neblinensis*, the prophyllar pattern always appears in a similar region of the inflorescence (Fig. 2a and b).

Comparison of the Inflorescence Structure of Koyamaeae and Related Tribes

Given the characteristics of its flowers and spikelets, Koyamaeae was placed within the Scleroideae subfamily (sensu Goetghebeur, 1998), which is related to the genera of the tribes *Sclerieae*, *Bisboeckelereae*, *Cryptangieae* and *Trilepideae* (sensu Goetghebeur, 1998).

The inflorescences of the *Scleria* species were studied from a typological point of view (Ahumada, 2006; Ahumada & Vegetti, 2009). They show similarities and differences with respect to the *Koyamaea* inflorescence. The *Scleria* inflorescences are mostly paniculate and, in some species, they are spiciform. Their paracladial zone has a varying number of primary paraclades: 4–15 in species of the subgen. *Hipoporum* sect. *Hypoporum*; 8–33 in species of the subgen. *Scleria* sect. *Ophryoscleria*, 13–30 in species of the subgen. *Scleria* sect. *Schizolepis* and 2–35 in species of the subgen. *Scleria* sect. *Scleria*. The branching degree varies 4–5° in species of the sect. *Hypoporum*, 5–6° in species of the sect. *Ophryoscleria* and sect. *Schizolepis* and 4–8° in species of the sect. *Scleria*. In connection with such variations, the maximum number of spikelets of the primary paraclades ranges from 7 to 430 in species of *Scleria. Scleria* inflorescences show normal branching and prophyllar branching (Ahumada & Vegetti, 2009). In *Scleria leptostachya*, (Fig. 2c) the primary paraclades lack bracts and, as a result, all the secondary and subsequent order paraclades present prophyllar branching, similarly to what is observed in the single primary paraclade of the inflorescence of *Koyamaea* (Fig. 2a and b). The different species of *Scleria* show variations in terms of when only prophyllar branching takes place in the paraclades of the subsequent order.

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The hypopodium of the primary paraclades is poorly developed in species of *Scleria* subgen. *Hypoporum* sect. *Hypoporum*, in *Scleria* subgen. *Scleria* sect. *Scleria* and *S. obtusa* sect. *Ophryoscleria*. There are also variations in the development of the epipodium in the different species of *Scleria*. A higher degree of development of the hypopodium and the epipodium determines whether inflorescences are looser or denser. In *Koyamaea*, the hypopodium and the epipodium of all the paraclades are reduced.

It is worth noting that species of *Scleria* have fascicles of spikelets similar to the inflorescence of *Koyamaea. Scleria leptostachya* Kunth (subg. *Hypoporum* sect. *Hypoporum*) shows primary paraclades lacking bracts and, consequently, bears secondary paraclades and paraclades of the subsequent order of prophyllar nature (Fig. 2c); *S. obtusa* Core (sect. *Ophryoscleria*), *S. ciliata* Michx and *S. sellowiana* Kunth (sect. *Scleria*) display a limited number of bracts on the primary paraclades and, consequently, most of the secondary paraclades arise from the axillary buds of the prophylls. The latter two species, in turn, show a very small number of primary paraclades (3–5).

It should be mentioned that when paraclades lack bracts, all the paraclades originating on such paraclades arise from the axillary bud of the prohyll, forming the typical fascicles of spikelets observed in the single primary paraclade of the inflorescence of *Koyamaea* (Fig. 2a and b), as well as in the 4–14 primary paraclades of *S. leptostachya* (Fig. 2c)..

Koyamaea neblinensis shows one type of bisexual spikelet with unisexual flowers (Fig. 3a). The species of *Scleria* (Ahumada & Vegetti, 2009) show 4 spikelet types with varying arrangements in different parts of the inflorescences and also in different species (Fig. 3b–e). In *Koyamaea*, the inflorescence is composed of a terminal spikelet (main florescence) and one spikelet fascicle of prophyllar nature. This spikelet fascicle is also present in the inflorescences of *Scleria* (Fig. 2c), but in these genera, unlike what occurs in *Koyamaeae* (Fig. 2a), the main florescence appears in terminal position and the spikelet fascicles are located in lateral position

The species of *Calytrocarya* Nees (Bisboeckelereae, sensu Goetghebeur, 1998) show a paniculate or a capitate inflorescence with few-many spikelets. Partial inflorescences are corymbose to capitately contracted, with many lateral bisexual or functionally male or female spikelets, terminal spikelets being male or female (Goetghebeur, 1998). Davidse and Kral (1988) describe two new species of *Calytrocarya* and characterize their inflorescence morphology. These two new species have synflorescence type III, that is, they show a tIn and several lIns. The inflorescence is a congested head composed of globose clusters of compound spikelets; the lower 2–3 compound spikelets in a globose cluster are male, the upper 5–8 compound spikelets are female (Fig. 3f and h). The male compound spikelets are usually unbranched (Fig. 3g), and they consist of a hypopodium, a 2-keeled prophyll, an epipodium, and 6–10 bracts that subtend male flowers. In *C. monocephala* Hochst. ex Steud., the male compound spikelets are branched (Fig. 3i); the branch is borne in the axil of a bract. The female compound spikelets may be branched or unbranched (Fig. 3f and h); the branches are borne in the axil of bracts. In the inflorescences of *Calytrocarya*, the buds of prophylls do not develop (Davidse & Kral, 1988).

In the species of the Bisboeckelereae tribe, all the inflorescence axes terminate in a unisexual unit (male or female "flower"). This structure is terminal given that no rudimentary rachilla tip is observed (Meert & Goetghebeur, 1979). In these species,

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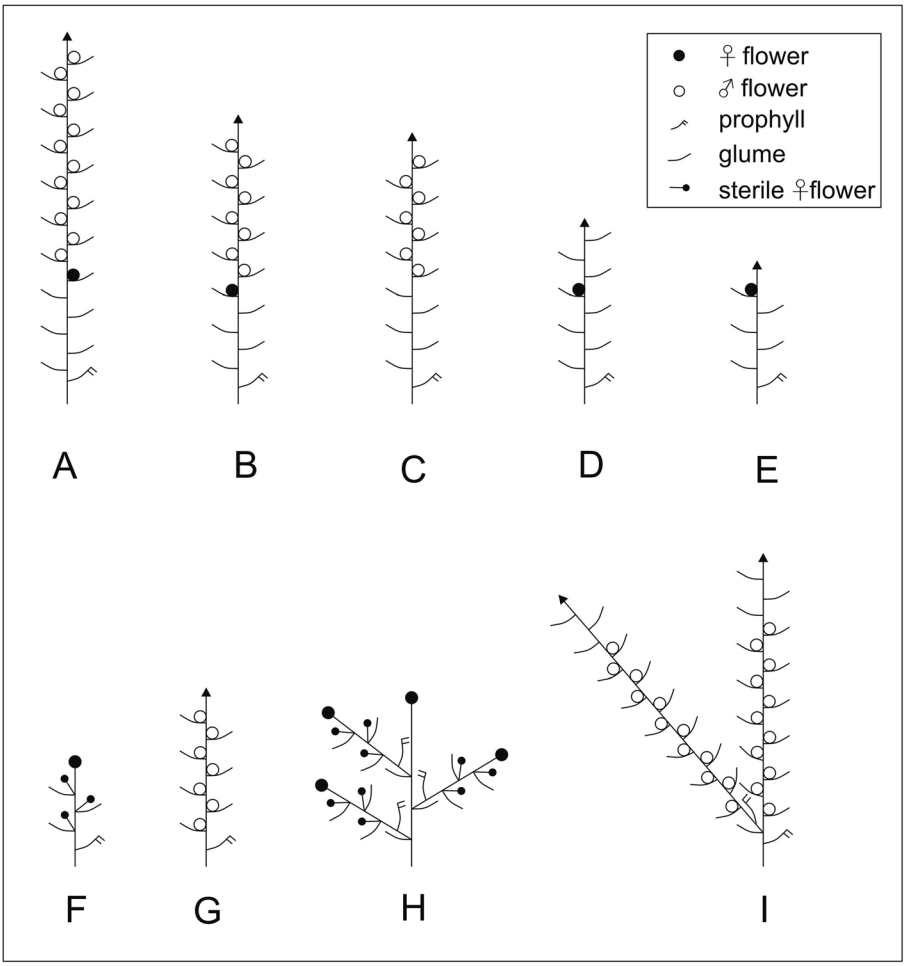

Fig. 3 Spikelet structure in *Koyamaea neblinensis* y some related genera: **a**, Spikelet of *Koyamaea neblinensis*; **b-e**, Spikelet types in *Scleria*: androgynous spikelet (**b**), staminate spikelet (**c**), subandrogynous spikelet (**d**), pistillate spikelet (**e**); F-I, Diagrams of *Calytrocarya* species. Adapted of: **a**, Thomas and Davidse (1989); **b-e**, Ahumada and Vegetti 2009; **f-i**, Davidse and Kral (1988)

the bud of the prophyll does not develop (Meert & Goetghebeur, 1979; Kukkonen, 1986). In *Becquerelia cymosa* Brongniart (Bisboeckelereae, sensu Goetghebeur, 1998), all nodes of the main axis of the inflorescence show two branches in the axil of the same leaf-like bract (Kukkonen, 1986). According to this author, the two branches are born from serial buds.

Conclusions

The inflorescence of *Koyamaea* is polytelic, not truncated and not homogenized. It is the result of significant reduction processes that have affected the paracladial zone. This

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zone has been reduced to a single node with a single primary paraclade lacking bracts and can make subsequent prophyllar paraclades up to the eighth order. All the paraclades are formed by a co-florescence (terminal spikelet of the paraclade) and one prophyllar paraclade. The prophyllar branching pattern determines the formation of a fascicle of spikelets. This fascicle of spikelets is similar to those present in the inflorescences of *Scleria* species where bract paraclades are not present, as is the case of *Scleria leptostachya*.

The inflorescences of genera belonging to the Crytangieae, Trilepidae, Sclerieae and Bisboeckelereae tribes (Scleroideae, sensu Goetghebeur, 1998) related to *Koyamaea* are paniculate or capitate (Goetghebeur, 1998), with few-several primary paraclades bearing prophylls and bracts. In all of these genera, the inflorescence is more highly developed than the inflorescence of *Koyamaea*.

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