

Inflorescence structure in species of *Scleria* subgenus *Hypoporum* and subgenus *Scleria* (Sclerieae-Cyperaceae)

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Abstract The objective of this study was to realize a typology approach toward the inflorescences in *Scleria* in order to provide characters that would have potential use in further taxonomic and phylogenetic research and that would allow identification of the tendencies and processes that could have yielded the variations within *Scleria* inflorescences. The majority of species studied present a main florescence; *Scleria reticularis* and *S. melanophala* have truncated inflorescences. The variations are related to the grade of development reached by the main florescence and the different parts of the paracladial zone. Major inflorescence variability was found in section *Scleria*. A change in spikelet sexuality can occur toward the distal parts. There were variations in the distinct species with respect to the hierarchy of the paracladia where the change occurs. Future investigations should center on the ontogenetic aspects of inflorescence development of *Scleria*, integrating these results, together with those of adult inflorescences, into taxonomic and phylogenetic investigations.

Keywords Inflorescence · *Scleria* · Sclerieae · Cyperaceae

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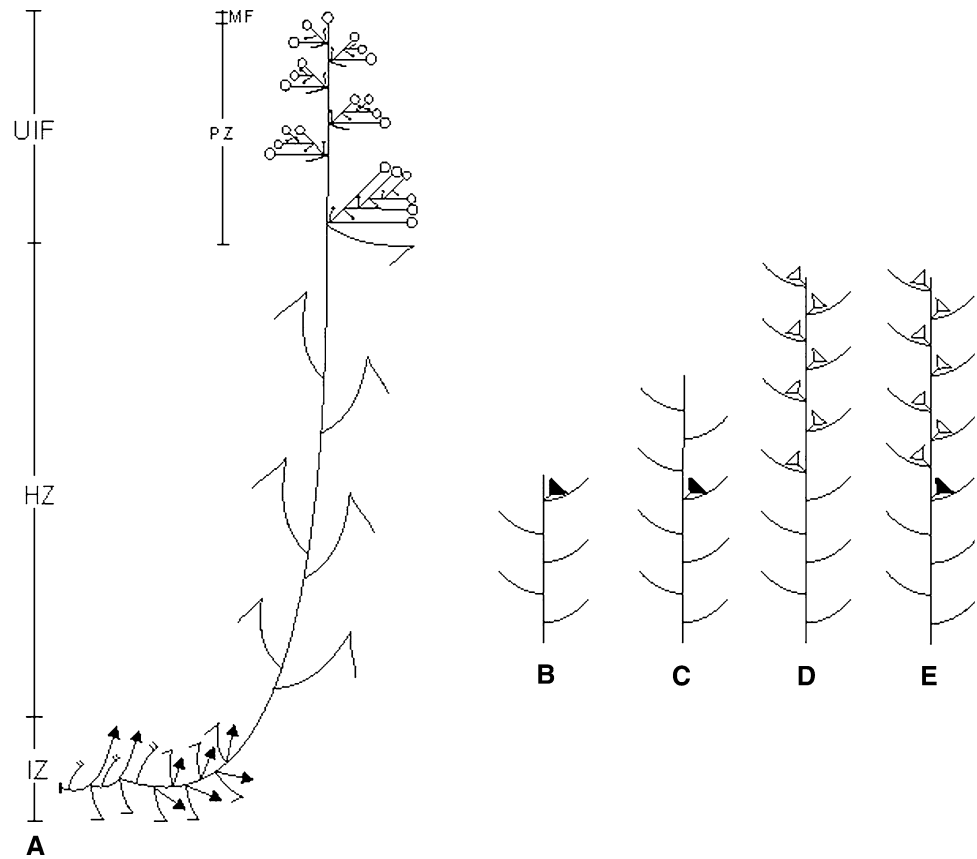
Introduction

The genus *Scleria* P. J. Bergius is distributed mainly in tropical and warm-temperate regions. It includes about 250 species (Goetghebeur 1998). A worldwide revision of the genus is long overdue. Until modern times, classification systems at the infrageneric level within *Scleria* were largely subjective (Camelbeke 2001–2002). Camelbeke incorporated phylogenetic (cladistic) principles into the infrageneric systematics for the American species of *Scleria*. His study confirmed the existence of the two subgenera and the sections *Hypoporum* (Nees) C.B. Clarke, *Ophryoscleria* (Nees) C.B. Clarke, *Hymenolytrum* (Schrad. ex Nees) Core, and *Schizolepis* (Schrad. ex Nees) C.B. Clarke, but indicated that the section *Scleria* s.l. is polyphyletic and that various smaller monophyletic clades could be recognized in this unnatural group. Consequently, the taxonomy and the phylogeny of *Scleria* need deep revision.

The basically paniculate inflorescence of *Scleria* (Fig. 1) is extremely polymorphic due to differences in the degree of development of its different parts. Therefore, the external morphology of the inflorescence in *Scleria* is an important diagnostic character (Camelbeke 2001–2002; Yano and Hoshino 2007). Consequently, studies of the inflorescences can provide new data to integrate into future taxonomic and phylogenetic investigation. However, very few previous works have resulted in information about the inflorescence structure of the genus (Holm 1898; Kern 1961; Haines and Lye 1972; Camelbeke 2002).

The main problems in the interpretation of the inflorescence structure result from studies that did not consider the entire inflorescence (Kukkonen 1984). Important data can be obtained from a study of the entire system of ramification of the inflorescence and from the variation of

Fig. 1 **a** Synflorescence structure in *Scleria*. **b** Pistillate spikelet. **c** Subandrogynous spikelet. **d** Staminate (or male) spikelet. **e** Androgynous spikelet. *HZ* Inhibition zone, *IZ* innovation zone, *MF* main florescence, *PZ* paracladial zone, *UIF* inflorescence unit, circles indicate spikelets, arrowheads indicate active vegetative meristems, ▼ indicates pistillate flower, ▽ indicates staminate flower



its constituent parts. In this context, the typology-based system developed by Troll (1964) and Weberling (1989) has proven to be useful for describing Cyperaceae inflorescences (Kukkonen 1984, 1986; Vegetti 1992, 2003; Vegetti and Tivano 1991; Browning and Gordon-Gray 1999; Perreta and Vegetti 2002; Guarise and Vegetti 2008) as well as for providing characters with phylogenetic value (Nickol 1995; Aagesen 1999; Rua and Aliscioni 2002; Rua 2003; Tortosa et al. 2004; Liu et al. 2005).

The aims of this work are (1) to analyze the inflorescences of *Scleria* from a typological point of view as a form to contribute to the knowledge of the inflorescence of the genus and also provide characters with potential use in further taxonomic and phylogenetic research and (2) to identify tendencies and processes that could have operated in the establishment of the variations within *Scleria* inflorescences.

Materials and methods

The typology developed by Troll (1964, 1969) and Weberling (1989) has been applied to the interpretation of the inflorescences of the species of *Scleria*.

Live plants from field collections and herbarium specimens from various herbaria [B, BA, BAA, BAB, BAF,

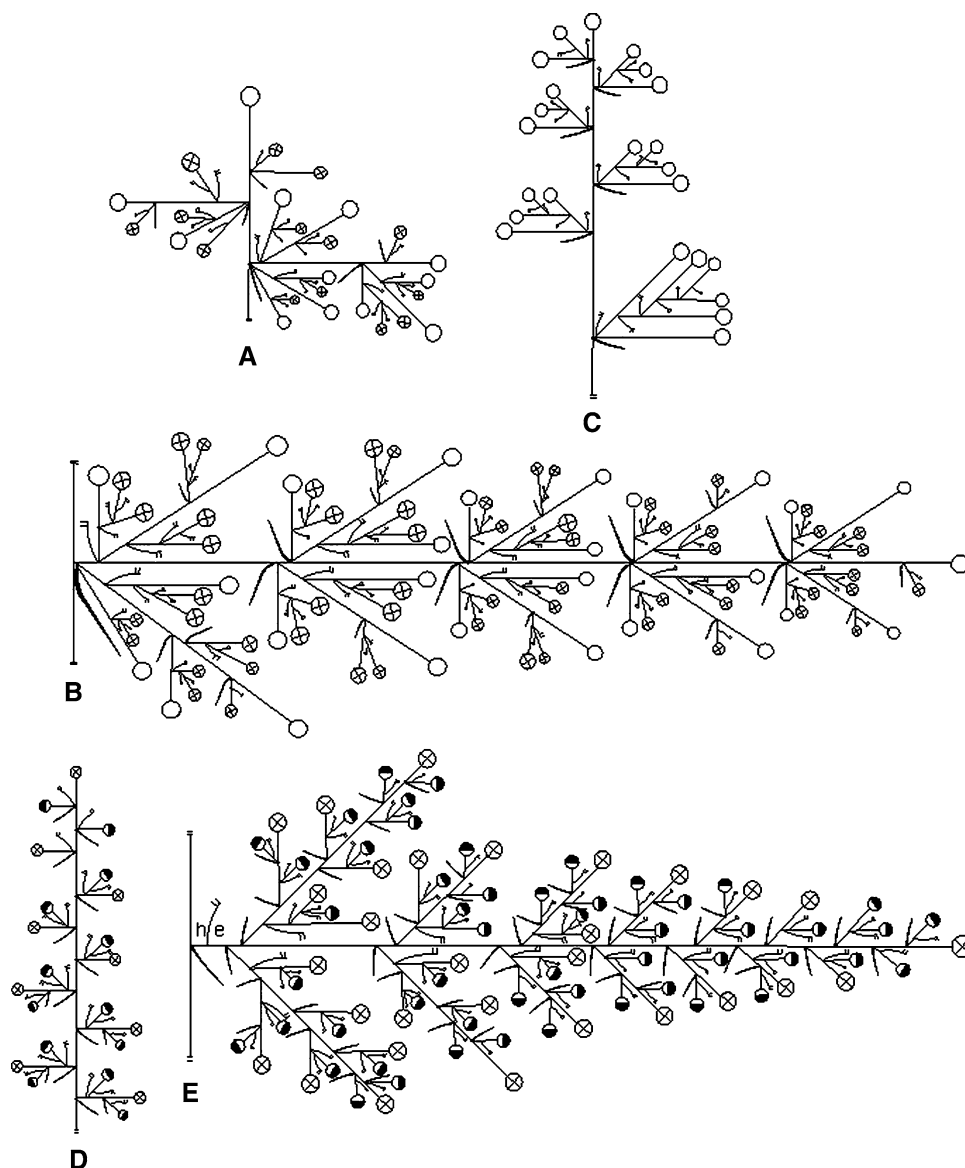
BM, BR, CTES, FCQ, G, GENT, JUA, K, LIL, LP, LPB, M, MNES, MVM, P, PY, SI, UNR (abbreviations from Index Herbariorum)] were studied using a stereoscopic microscope (see “Appendix”). Comparative observations were organized according to the characteristics of the distinct zones of the synflorescences: characteristics of the main florescence, of the paracladial zone, and of each paracladial type individually. At least ten specimens for each species were investigated.

Results

General typological plan

In all of the species studied, the following typological zones were recognized (Fig. 2a): (1) innovation zone (IZ): formed by the rhizomes and the basal part of the aerial shoots whose axillary buds develop new shoots (innovations); (2) inhibition zone (HZ): comprised the portion of the aerial shoot whose leaves present axillary buds that do not develop; (3) paracladial zone (PZ): disposed above the inhibition zone and formed by flowering shoots or paracladia; and (4) main florescence (MF): represented by the terminal spikelet of the main axis of the inflorescence. The main florescence and the

Fig. 2 Inflorescence of *S. variegata*: **a** distal part, **b** basal paracladium. **c** Inflorescence of *S. leptostachya*. Inflorescence of *S. latifolia*: **d** distal part, **e** basal paracladium. *e* Epipodium, *h* hypopodium, \odot androgynous spikelet, \otimes staminate (or male) spikelet, \oplus subandrogynous spikelet



paracladial zone together form the unit of inflorescence (UIF).

The UIF of *Scleria* is formed by a group of dense fascicles of spikelets that are repeated along the length of the main axis and, in various species, also along the length of the ramifications (Figs. 1, 2).

The paracladial zone is formed by a variable number of primary paracladia (= inflorescence branch), disposed helicoidally, that arise from the axillary bud of the bracts (glumiform or foliaceous) disposed over the main axis (Fig. 2). Each primary paracladium consists of a short hypopodium (only in a few cases well developed), an adaxial prophyll, an epipodium of variable development, and a variable number of bracts and their co-flourescence (terminal spikelet of the paracladium) (Fig. 2e).

Secondary paracladia are generated from the axillary bud of the prophyll and from the bracts present in the primary paracladia, and in this mode, there can exist a continual generation of a variable number of paracladia of tertiary and subsequent orders. Ramification from the axillary bud of the prophylls of the secondary paracladia and of the following orders is very frequent. So there is formed in each primary paracladium a cymose system of ramification (Fig. 2 a–c) that together constitutes the denominated fascicles of spikelets.

The development of the paracladial zone is acropetal. Over the main axis and over each one of the paracladia, a reduction in the length of the internodes, in the number and development of the bracts, and in the number and grade of branching of the paracladia occurred. Consequently, in the

distal portions, paracladia are reduced to hypopodium, prophyll, epipodium, and co-florescence, i.e., they lack bracts, and consequently, the following paracladium is generated from the axillary bud of the prophyll or is not developed (Fig. 2). In the latter case, the distal paracladium consists only of its co-florescence.

Due to the acropetal development of the inflorescence, the basal and middle paracladia are recognized to have a higher grade of ramification than those paracladia near to the apex (Fig. 2). The paracladia near the apex present the minimum grade of ramification (denominated here as distal paracladia) and differ in number and structure in the different species (Table 1).

The length of the internodes is highly variable among the species. The main variations presented are in the length of the epipodium and, in some species, the length of the hypopodium. The characteristics associated with the length of the rest of the internodes are responsible for the general appearance of the inflorescences, which can be lax or dense.

In the species studied, the main florescences are developed and do not exhibit homogenization in most cases. Exceptions occur for *S. reticularis* Michx. and *S. melanomphala* Kunth (Table 1), which presented truncated inflorescences formed exclusively by the two to three basal paracladia, and for *S. obtusa* Core, which presents partial homogenization in the middle and distal portions.

The development of the florescences (spikelets) along the length of the total inflorescence is variable within the same species and among the distinct species. Because of this, the following types of florescences are recognized within the genus (Fig. 2 b–e):

Pistillate (or female) spikelet: a much reduced rachilla top is observed above the glume that encloses the single pistillate flower. All the glumes are disposed distichously (Fig. 2b).

Subandrogynous spikelet: functionally unisexual female spikelets with a (more or less) conspicuous rachilla that

Table 1 Main characteristics of the inflorescences of species of *Scleria*

Sections and species	MF	UIF length (cm)	Pc (n)	Max Pc branching order	Bract type	Max spikelets (n)	dPc (n)	Spikelets/dPc (n)	Spikelet type
<i>Hypoporum</i>									
<i>S. composita</i>	A	4.5–9	9–12	4	Gl	33	1	2	A
<i>S. distans</i>	A	2.3–10	4–9	4	Gl	10	1	3	A
<i>S. leptostachya</i>	A	3–11	4–14	6	Gl	7	1	2	A
<i>S. variegata</i>	A	8.5–16	4–15	5	F–Gl	87	1	2	A–S
<i>Ophryoscleria</i>									
<i>S. macrophylla</i>	S	36–48	19–25	5	F–Gl	64	4	1	P–S
<i>S. microcarpa</i>	S	9–21	10–17	5	F–Gl	50	1	2	SA–S
<i>S. mitis</i>	S	35–74	27–33	5	F–Gl	150	1	1	SA–S
<i>S. obtusa</i>	S	11–26	8–13	6	F–Gl	40	1	3	SA–S
<i>Schizolepis</i>									
<i>S. latifolia</i>	S	6–54	13–25	5	F–Gl	83	3	1	SA–S
<i>S. panicoides</i>	S	28–52	13–30	5	F–Gl	200	2	1	SA–S
<i>S. plusiophylla</i>	S	17–45	15–25	6	F–Gl	70	1	3	SA–S
<i>Scleria</i>									
<i>S. bracteata</i>	S	51–90	30–35	5	F–Gl	430	3	1	S–SA–A
<i>S. ciliata</i>	A–S	1.5–42	3–5	8	F–Gl	30	1, 3	–5	A–SA–S
<i>S. flagellum-nigrorun</i>	S	38–55	10–20	5	F–Gl	70	2	1	S–SA
<i>S. lacustris</i>	S	25–35	16–20	6	F–Gl	106	1	2	SA–S
<i>S. melaleuca</i>	S	13–38	10–20	6	F–Gl	55	2	3	SA–S
<i>S. melanomphala</i>	–	52–76	2–3	7	F–Gl	115	–	–	SA–S
<i>S. reticularis</i>	–	31–54	2–3	7	F–Gl	40	–	–	SA–S
<i>S. scabra</i>	S	7–12	12–17	4	F–Gl	20	2	1	SA–S
<i>S. secans</i>	S	7–38	10–15	5	F–Gl	25	3	1	S–P
<i>S. sellowiana</i>	A–SA	1.5–60	3–5	5	F–Gl	15	1–2	4	SA–A

A Androgynous, dPc distal primary paracladia, F foliaceous, Gl glumiform, Max maximum, MF main florescence, P pistillate, Pc primary paracladia, S staminate, SA subandrogynous, UIF unit of inflorescence

possess empty glumes that are more or less well developed and disposed helicoidally, topped by the glume that encloses the single pistillate flower; the pistillate flower and the empty glumes below it, are disposed distichously. On occasion, these empty glumes are not present (Fig. 2c).

Staminate (or male) spikelet: the glumes located distally that enclose the staminate flowers are disposed spirally, and the empty glumes located in the proximal part are disposed distichously (Fig. 2d).

Androgynous spikelet: distal from the female flower, the rachilla bears glumes subtending staminate flowers. The sterile glumes below the glume subtending female flower (fructiferous glume) are disposed distichously, whereas the glumes located distally, which bear staminate flowers, are disposed spirally (Fig. 2e).

According to the typological pattern described here, the species of *Scleria* show a great variation in the structure of their inflorescences as a function of the grade of development reached by the main florescence and the different parts of the paracladial zone. These variations were analyzed for each taxonomic section as described below.

Inflorescences of the species of subgenus *Hypoporum* (Nees) C.B. Clarke, section *Hypoporum*

Within section *Hypoporum*, *Scleria variegata* (Nees) Steud. is distinguished by having the inflorescence of greatest length with respect to the other three species (Table 1). A great variation in the number of primary paracladia has been observed, with *S. leptostachya* Kunth and *S. variegata* as the species that have the largest number of primary paracladia.

Scleria variegata (Fig. 2a, b) shows an important development of prophyllar paracladia and has paracladia that bear the greatest number of bracts, consequently presenting the most developed inflorescence within the section.

The paracladia of *S. leptostachya* (Fig. 2c) lack bracts, consequently all of the secondary paracladia and paracladia of the following orders emerge from the axillary bud of the prophylls (Table 2). In the rest of the species, the paracladia have prophyllar origin only, including tertiary paracladia (*S. distans*) or quaternary paracladia (*S. composita* and *S. variegata*).

The maximum grade of ramification of the paracladia (Table 1) ranges from the fourth order (*Scleria distans* and *S. composita*) to the sixth order (*S. leptostachya*).

The number of distal paracladia is one in all of the species. The number of spikelets of this distal paracladium is two to three (Table 1).

With respect to the internode length of the inflorescences, *Scleria variegata* presents paracladia with an important intercalary growth between the internodes, which determines the lax appearance of its inflorescences. In the other three species, in contrast, the reduced length of the internodes, especially that of the epipodium, determined that all of the primary paracladia are presented as dense fascicles of spikelets along the main axis.

In the basal and middle primary paracladia, *Scleria variegata* (Fig. 2a, b) presents a fascicle of spikelets formed from the prophyll of the primary paracladium and a series of fascicles, originating from the axillary bud of the bracts, separated from the base by the development of the epipodium. It was further observed that in some of the basal paracladia, there are two branches of important development, one is the primary paracladium and the other branch might be a branch originating from an accessory bud.

The main florescence is androgynous. The sexuality of the rest of the florescences (spikelets, Tables 1, 2; Fig. 2c) is androgynous in *Scleria distans*, *S. composita*, and *S. leptostachya* and is androgynous and staminate in *S. variegata*. The variation in the sexuality of this species occurs distally and in the paracladia of higher orders of ramification (Tables 1, 2; Fig. 2a, b).

Inflorescences of the species of the subgenus *Scleria*

Section *Ophryoscleria* (Nees) C.B. Clarke

The largest variation in the length of the UIF is observed in *Scleria mitis* P.J. Bergius, which has both the largest length and the greatest number of primary paracladia, whereas *S. obtusa* core has the smallest number of paracladia (Table 1).

The maximum grade of ramification of the paracladia is the fifth order, with the exception of *Scleria obtusa*, which produces paracladia of the sixth order (Table 2; Fig. 3a). In all the studied species of this section, the paracladia have prophyllar origin as of the quaternary paracladia (Table 2).

The distal paracladia consist of one to three spikelets; these distal paracladia are present in the primary order (*S. microcarpa*, *S. mitis*, and *S. obtuse*) or quaternary (*S. macrophylla*) (Table 1; Fig. 3).

Scleria mitis and *S. macrophylla*, with inflorescences of greater length, are generally found with well-developed hypopodium in the basal primary paracladia. *S. macrophylla* presents a well-developed epipodium. The first prophyllar secondary paracladium originates from the first basal primary paracladia in *S. microcarpa* and *S. obtusa*, and later, from the third basal primary paracladium in *S. mitis* and *S. macrophylla*.

Table 2 Main characteristics of the paracladia of the species of *Scleria*

Sections and species	1° Pc		2° Pc		3° Pc		4° Pc		5° Pc		6° Pc		7° Pc		8° Pc		
	Cof	Or	Cof	Or	Cof	Or	Cof	Or	Cof	Or	Cof	Or	Cof	Or	Cof	Or	Cof
<i>Hypoporum</i>																	
<i>S. composita</i>	A	Pr Br	A	Pr Br	A	Pr	A	–	–	–	–	–	–	–	–	–	–
<i>S. distans</i>	A	Pr Br	A	Pr	A	Pr	A	–	–	–	–	–	–	–	–	–	–
<i>S. leptostachya</i>	A	Pr	A	Pr	A	Pr	A	Pr	A	Pr	A	–	–	–	–	–	–
<i>S. variegata</i>	A	Pr Br	A–S ^a	Pr Br	A–S	Pr	S	Pr	S	–	–	–	–	–	–	–	–
<i>Ophryoscleria</i>																	
<i>S. macrophylla</i>	S	Pr Br	S–P ^a	Pr Br	S–P ^c	Pr	S–P	Pr	S–P	–	–	–	–	–	–	–	–
<i>S. microcarpa</i>	S, A ^b	Pr Br	S–SA ^c	Pr Br	SA–S ^c	Pr	SA	Pr	SA	–	–	–	–	–	–	–	–
<i>S. mitis</i>	S	Pr Br	S–SA ^a	Pr Br	S–SA ^c	Pr Br	SA	Pr	SA	–	–	–	–	–	–	–	–
<i>S. obtusa</i>	S–SA ^a	Pr Br	S–SA	Pr Br	SA	Pr	SA	Pr	SA	Pr	SA	–	–	–	–	–	–
<i>Schizolepis</i>																	
<i>S. latifolia</i>	S	Pr Br	S–SA	Pr Br	SA–S ^c	Pr	SA	Pr	SA	–	–	–	–	–	–	–	–
<i>S. panicoides</i>	S	Pr ^a Br	S	Pr Br	S–SA ^a	Pr Br	SA–S ^c	Pr Br	SA	Pr	–	–	–	–	–	–	–
<i>S. plusiophylla</i>	S	Pr Br	S–SA ^c	Pr Br	S–SA	Pr	SA	Pr	SA	Pr	SA	–	–	–	–	–	–
<i>Scleria</i>																	
<i>S. bracteata</i> ^c	S–SA ^a	Pr Br	S–SA–A ^c	Pr Br	SA–S–A ^a	Pr Br	SA–S	Pr	SA–S	–	–	–	–	–	–	–	–
<i>S. ciliata</i>	S–A	Pr Br ^d	S–A ^c –SA ^a	Pr	SA–S ^c –A ^a	Pr	SA–S ^a	Pr	SA	Pr	SA	Pr	SA	Pr	SA	Pr	SA
<i>S. flagellum-nigrorun</i>	S	Pr ^d Br	S–SA ^a	Pr Br	S–SA ^c	Pr Br	SA–S ^a	Pr	SA	–	–	–	–	–	–	–	–
<i>S. lacustris</i>	S	Pr Br	S–SA ^a	Pr ^d Br	SA–S ^c	Pr	SA	Pr	SA	Pr	SA	–	–	–	–	–	–
<i>S. melaleuca</i>	S–SA ^a	Pr Br	S–SA ^c	Pr Br ^d	SA–S ^c	Pr Br	SA	Pr	SA	Pr	SA	–	–	–	–	–	–
<i>S. melanomphala</i>	S	Pr Br	S	Pr Br	S–SA	Pr Br	SA–S	Pr Br ^a	SA–S ^c	Pr Br ^d	SA–S ^c	Pr	SA	–	–	–	–
<i>S. reticularis</i>	S	Pr Br	S–SA ^c	Pr Br	SA–S ^c	Pr Br ^a	SA–S ^a	Pr	SA	Pr	SA	Pr	SA	Pr	SA	–	–
<i>S. scabra</i>	S	Pr ^d Br	S–SA ^c	Pr Br ^a	SA–S ^a	Pr	SA	–	–	–	–	–	–	–	–	–	–
<i>S. secans</i>	S	Pr Br	S–P ^c	Pr Br	S–P	Pr	P	Pr	P	–	–	–	–	–	–	–	–
<i>S. sellowiana</i>	A–SA	Pr Br ^d	SA	Pr	SA	Pr	SA	Pr	SA	–	–	–	–	–	–	–	–

A Androgynous, Br axillary bud of bract, Cof cofillorescence, Or origin, P pistillate, 1° Pc–8°Pc paracladia of first through eighth orders, Pr prophyllar, S staminate, SA subandrogynous

^a Rarely

^b Only once

^c At times

^d Few

^e For the Pc of both spikelet types, only

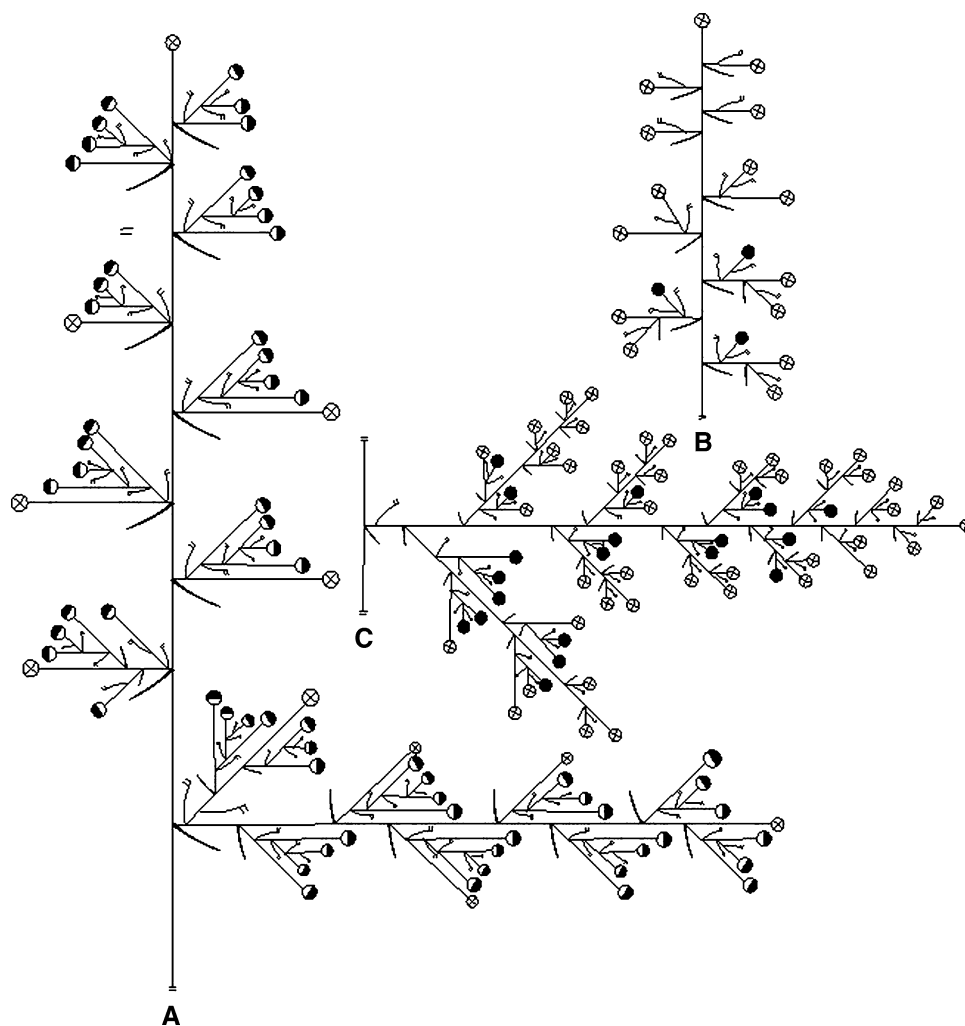
Scleria mitis, *S. obtusa* (Fig. 3a), and *S. microcarpa* have staminate and subandrogynous spikelets. In contrast, *S. macrophylla* (Fig. 3b, c) possesses a staminate and pistillate one. The main florescence and the paracladia of lesser order of ramification have staminate spikelets. Distally over the main axis and over each paracladium, the spikelets are subandrogynous, with the exception of *S. macrophylla*, which bears pistillate spikelets on some paracladia of the ultimate order of branching (Tables 1, 2; Fig. 3).

Section *Schizolepis* (Schr. ex Nees) C.B. Clarke

Scleria latifolia Sw. is the species that possesses the largest range of variation in the length of the UIF and

also the greatest length of that structure (Table 1). *Scleria latifolia* and *S. panicoides* Kunth show (Table 1) the greatest variation in the number of primary paracladia. The maximum value occurs in *S. panicoides* and the minimum value occurs in *S. latifolia*. The grade of ramification for these paracladia can reach the fifth order (*S. latifolia* and *S. panicoides*) or the sixth order (*S. plusiophylla* Steud.). The maximum number of bracts in the primary and secondary paracladia is greatest in *S. panicoides* and is reduced in *S. plusiophylla*. Consequently, *S. panicoides* presents a greater number of spikelets per primary paracladium (200) with relation to *S. latifolia* (83) and *S. plusiophylla* (70) (Table 1).

Fig. 3 **a** Inflorescence of *S. obtusa*; inflorescence of *S. macrophylla*; **b** distal part, **c** basal paracladium. ♀ Pistillate (or female) spikelet; for other symbols, see Fig. 2



In this section, the paracladia have prophyllar origin (Table 2), as of the fourth order (*S. latifolia* and *S. plusiophylla*) or fifth order (*S. panicoides*).

The number of distal paracladia ranges from one to three. These paracladia consist of one spikelet (*S. panicoides* and *S. latifolia*) or of three spikelets (*S. plusiophylla*) (Table 1).

The hypopodium of the basal paracladia is well developed in the three to five proximal paracladia of *S. latifolia*, *S. panicoides*, and *S. plusiophylla* when development of the prophyllar paracladia is not observed. The epipodium of the paracladia is of variable development, long in the basal ones and reduced acropetally.

The main florescence is staminate (Table 1). The coflorescences of the paracladia can be staminate or subandrogyne (Table 2); the change from staminate to subandrogyne occurs distally along the length of the main axis and in the paracladia of greater orders of ramification (Table 2; Fig. 2d, e).

Section Scleria s.l.

Scleria ciliata Michx., *S. sellowiana* Kunth, *S. bracteata* Cav., and *S. secans* (L.) Urb. show a large variation in the length of the UIF. *Scleria bracteata* and *S. melanomphala* possess greater lengths in their inflorescences, with the former species having the greatest. *Scleria scabra* Willd. is the species with the smallest inflorescence length for the entire section (Table 1).

Scleria bracteata possesses the highest number of primary paracladia (Table 1). A group very homogeneous for the maximum number of primary paracladia is formed by *S. lacustris*, *S. secans*, *S. melaleuca*, *S. flagellum-nigrorum*, and *S. scabra*. *S. flagellum-nigrorum* and *S. melaleuca* have the greatest mean length of the inflorescence in this group, which indicates that the paracladia are distanced from one another by long internodes (Table 1). *Scleria scabra* presents an important number of paracladia in a UIF of much reduced length; consequently, the main axis presents

reduced internodes and the inflorescence is dense. Another group is formed by *S. ciliata*, *S. sellowiana*, *S. melanomphala*, and *S. reticularis*, which have a very low average number of primary paracladia (Table 1). *Scleria melanomphala* (Fig. 4a) and *S. reticularis* have a low number of primary paracladia (Table 1) despite occupying the second and fourth ranks, respectively, for the lengths of their inflorescences. Consequently, the internodes of the main axis in both species are long.

The number of bracts is very variable in the section *Scleria*. The maximum grade of ramification (Table 1) is from fourth order (*S. scabra*) to eighth order (*Scleria ciliate*, Fig. 4a).

In this section, the paracladia are of prophyllar origin only (Table 2) and include tertiary paracladia (*S. sellowiana*, *S. ciliate*), quaternary paracladia (*S. lacustris*, *S. scabra*, *S. secans*), paracladia of fifth order (*S. bracteata*, *S. flagellum-nigrorum*, *S. melaleuca*, *S. reticularis*), and paracladia of the seventh order (*S. melanomphala*).

The number of distal paracladia ranges from one to three. These distal paracladia can present one to five spikelets. In *S. reticularis* and *S. melanomphala*, the distal paracladia are not developed (Table 1).

S. bracteata, *S. secans*, *S. melaleuca*, and *S. scabra* in the basal primary paracladium present developed epipodia; *Scleria lacustris* presents developed epipodia from the third to fourth proximal paracladia; and *S. flagellum-nigrorum* presents developed epipodium from the sixth to seventh proximal paracladia. In *S. reticularis* and *S. melanomphala*, the epipodia in all of the primary paracladia are more developed in comparison with the rest of the species. *Scleria bracteata* and *S. flagellum-nigrorum* develop the first prophyllar secondary paracladium later between the 8th and the 13th primary paracladium.

The majority of the species of the section have the main florescence developed (Table 1). Exceptions to this are *Scleria reticularis* and *S. melanomphala*, which have the UIF truncated (Fig. 4a).

In this section, four groups of species can be distinguished according to the sexuality of the spikelets (Tables 1, 2). In the first group is *Scleria bracteata* (Fig. 5), which is the only species of all those studied with proximal paracladia that possess exclusively subandrogynous spikelets and distal paracladia with staminate spikelets. There always exists an intermediate paracladium, which has subandrogynous spikelets on the basal part and staminate spikelets in the terminal part; this paracladium marks the limit between those paracladia exclusively “subandrogynous” and those exclusively “staminate.”

In the second group is *Scleria secans* (Fig. 4b, c), the only species of this section with pistillate spikelets and staminate spikelets.

The third group is formed by *Scleria ciliata*, with androgynous, subandrogynous, and staminate spikelets (Fig. 6), and *S. sellowiana*, with subandrogynous and androgynous spikelets. These taxa present distinct types of inflorescences. The first species presents four types of inflorescences according to the sexuality of the spikelets (Fig. 6). In *S. sellowiana*, two types of inflorescences are present.

Scleria lacustris, *S. flagellum-nigrorum*, *S. melaleuca*, *S. reticularis*, *S. melanomphala* (Fig. 4a), and *S. scabra* form the fourth group, with staminate and subandrogynous spikelets in the same inflorescence.

The sexuality of the main florescence (Table 1) differs in the different species, being staminate in the majority of them, androgynous or staminate in *Scleria ciliate* (Fig. 6), and androgynous or subandrogynous in *S. sellowiana*. The sexuality of the co-florescences (Table 2) in the majority of species are staminate changing to subandrogynous. They are all subandrogynous in the inflorescence type B of *S. sellowiana*, staminate changing to pistillate in *S. secans* (Fig. 4b, c), androgynous changing to subandrogynous in inflorescence type A of *S. sellowiana* and type B of *S. ciliate* (Fig. 6b), androgynous changing to staminate in inflorescence type C of *S. ciliate* (Fig. 6c), and staminate changing to pistillate and later to subandrogynous in the basal paracladia in inflorescence type A of *S. ciliate* (Fig. 6a). The change in sexuality occurs distally along the principal axis and on the paracladia and occurs in different levels in the different species.

Discussion

The species studied of *Scleria* have a paniculiform inflorescence, with the exception of most species of the section *Hypoporum*, which present inflorescences that are partially contracted (Haines and Lye 1972; Camelbeke 2001–2002). This paniculodium is terminal in all species of *Scleria* studied here; it appears to take a lateral position in *S. ciliata* and *S. sellowiana*, but in fact the unit of inflorescence is pseudolateral in these two species. The pseudolateral position of the inflorescence can occur in isolated cases within a genus, as occurs in *Scleria* or in *Cyperus* (Heinzen and Vegetti 1994; Guaglianone 1996), or it can constitute a common feature of all the species belonging to a genus as in *Schoenoplectus* (Rchb.) Palla (Vegetti and Tivano 1991; Vegetti 1992) and *Isolepis* (Vegetti 1994).

In the majority of species of *Scleria*, the main axis and the paracladia end in a spikelet; therefore, to determine the inflorescence type (Troll 1964), it is necessary to analyze the structure of this spikelet. Some authors consider that the spikelet of *Scleria* presents a terminal flower (Pax

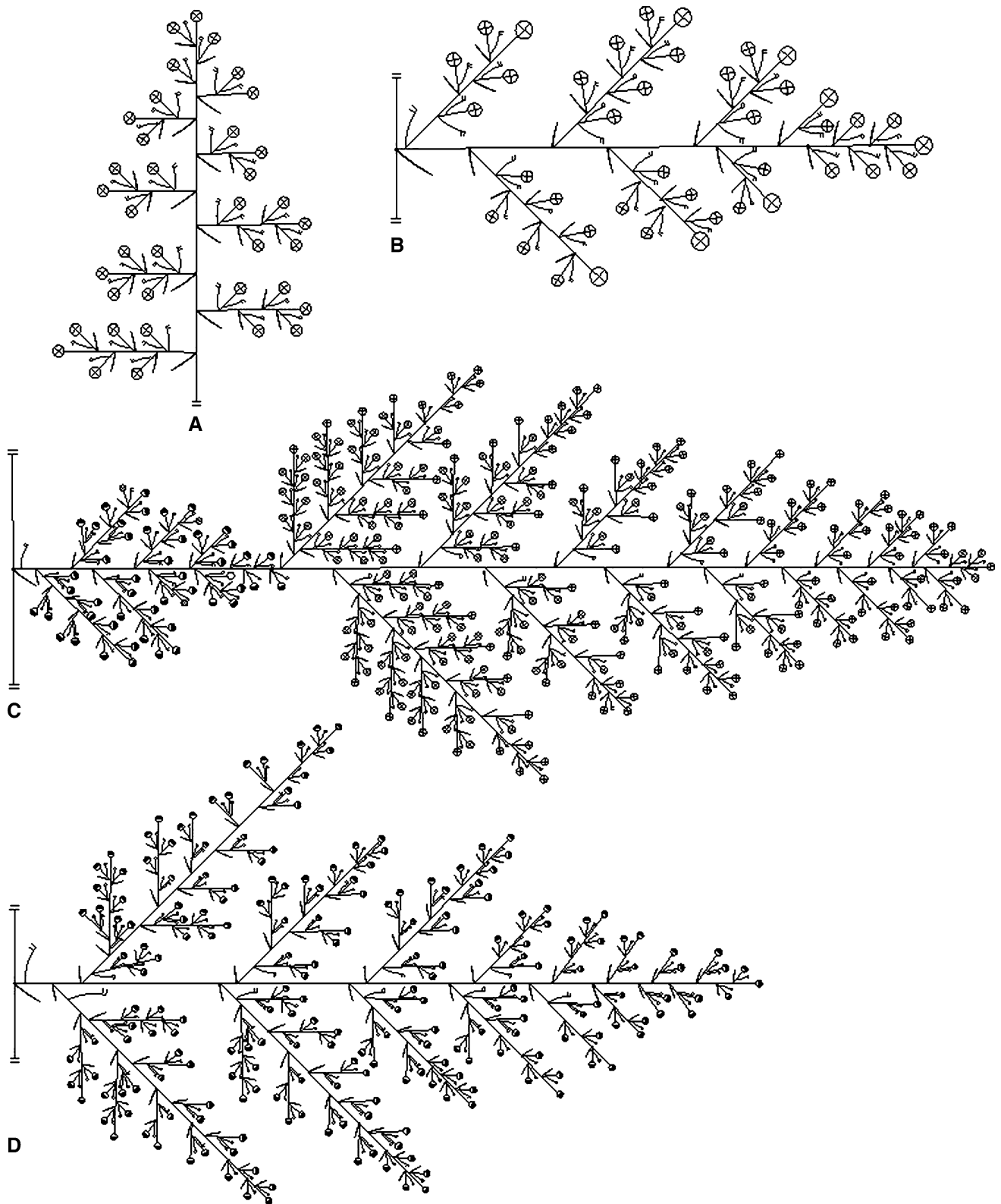
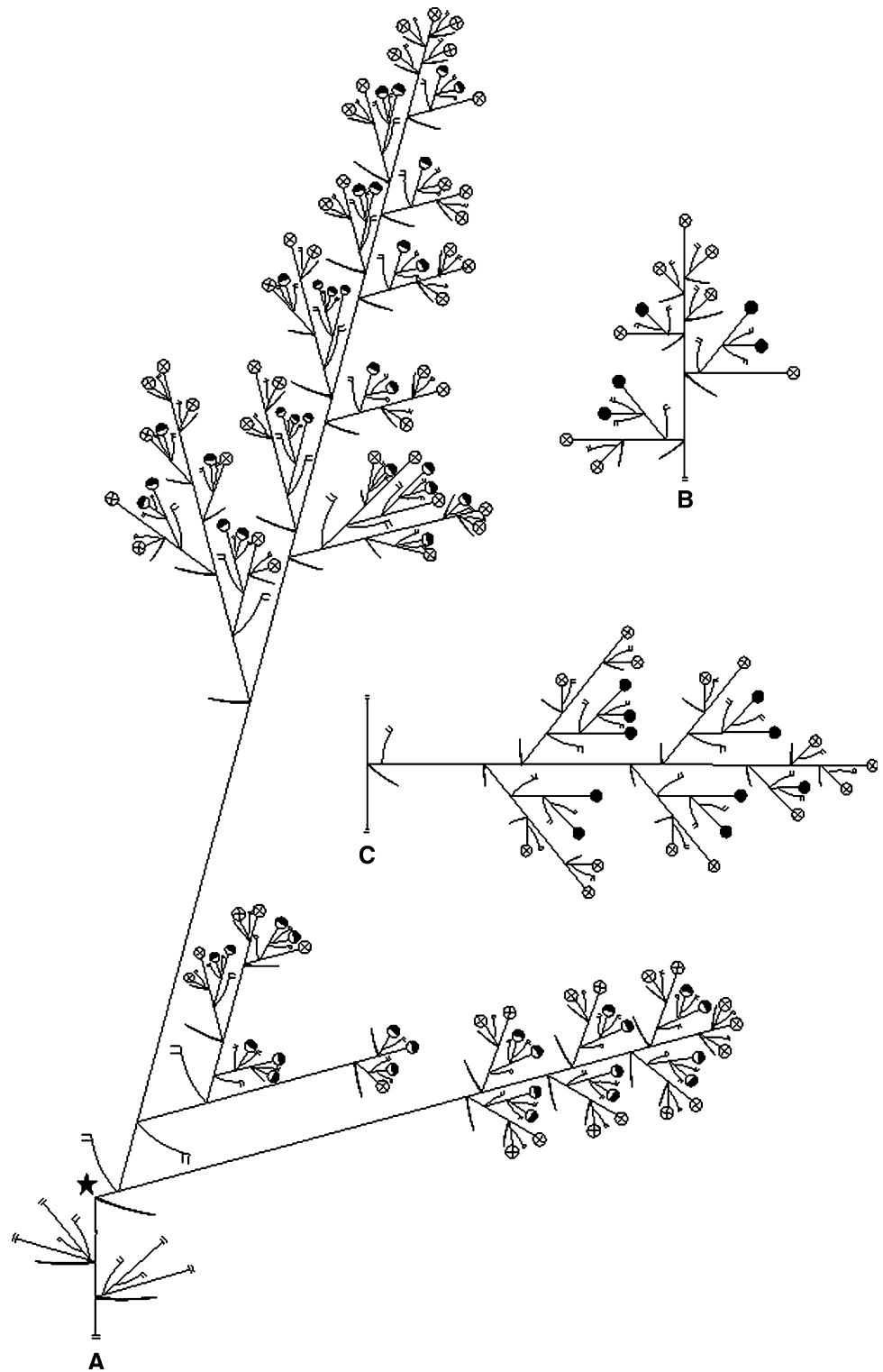


Fig. 4 Inflorescence of *S. bracteata*. **a** Distal part, **b** paracladium in distal region, **c** medial paracladium, **d** basal paracladium. See Fig. 2 for symbols

Fig. 5 Inflorescence of *S. melanomphala*: **a** the most distal paracladium. Inflorescence of *S. secans*: **b** distal part, **c** basal paracladium. ★ indicates the truncated main axis; see Figs. 2 and 3 for the other symbols



1886; Kern 1961; Schultze-Motel 1964; Mora-Osejo 1960; Koyama 1967, 1969) whereas others (Nees 1842; Holm 1898; Holttum 1948; Eiten 1976; Koyama 1961; Goetghebeur 1986; Camelbeke 2001–2002; Vrijdaghs et al. 2007) affirm that it is monopodial and that the flowers are lateral. The apparent terminal position of the pistillate

flower in the androgynous spikelets is related to the fact that during growth, when the ovary develops into the fruit, the distal staminate part of the spikelet is pushed aside (Camelbeke 2001–2002). This can be observed in the lateral position of the flowers of *Scleria*. In this way, it can be confirmed that the inflorescence in *Scleria* is polytelic like

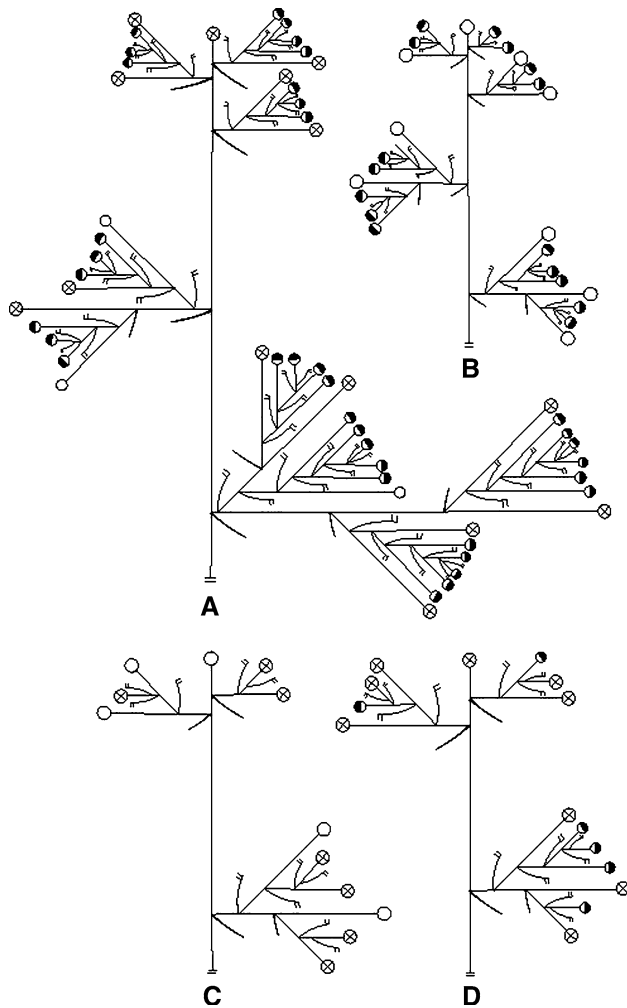


Fig. 6 Inflorescences of *S. ciliata*: **a** type A, **b** type B, **c** type C, **d** type D. See Figs. 2 and 3 for symbols

all of the rest of the inflorescences of Cyperaceae that have been analyzed to date (Mora-Osejo 1960; Vegetti 2003; Vrijdaghs 2006).

When the main axis develops a terminal spikelet, the polytelic inflorescence is nontruncated, whereas when the main axis lacks the terminal spikelet, the inflorescence becomes truncated (Troll 1964; Weberling 1989; Vegetti 2003). The truncation can affect the main florescence only, or the distal, medial, or proximal paracladia too (Kunze 1989). *Scleria reticularis* and *S. melanomphala* do not have a main florescence or distal and medial paracladia, thus the inflorescence in these two species is truncated (Fig. 4a). In grasses, truncated inflorescence may be determined by two different main-axis development patterns: (1) when the apical meristem of the inflorescence main axis ceases its activity immediately after the transition to flowering (basipetal initiation and differentiation of primary paracladia) or (2) when the main axis arrests its growth and the truncated structures never form (main florescence, distal

and medial paracladia) (Reinheimer et al. 2005, 2009; Liu et al. 2007).

Homogenization, that is the development of similarities among the inflorescence branches, is an evolutionary process that determines, in part, the general appearance of the inflorescence (Reinheimer and Vegetti 2008). Different degrees of homogenization are found in some taxa, including non-homogenized, partially homogenized, and completely homogenized inflorescences (Rua 1996; Rua and Weberling 1998). In the species of *Scleria* studied, the paracladia showed acropetalous development, not presenting homogenization of the paracladia, with the exception of *S. obtusa* (Fig. 3a), which presents partial homogenization in the middle and distal portions of the inflorescence.

The phyllotaxis varies along the synflorescence (main shoot); the disposition of the leaves in the vegetative zone is tristichous (phyllotaxis 1/3), whereas in the paracladial zone, the bracts and their paraclades have a spiral arrangement with a divergence fraction of 3/8. Another change in the phyllotaxis is observed at the last order of branching (spikelet), in which the proximal glumes have a distichous arrangement (1/2 phyllotaxis). The distichous disposition of the glumes would indicate a change in the inflorescence phyllotaxis from a spiral phyllotaxis. The change from distichous to spiral is generally abrupt.

In the pistillate spikelets, the glumes are disposed distichously; the subandrogynous spikelet, staminate spikelet, and androgynous spikelet have one proximal portion with glumes disposed distichously and one distal portion with glumes disposed spirally. In the species with the latter type of spikelet, considering each axis separately (the main axis and the branched paracladia), the phyllotaxy pattern changes first from spiral to distichous and then again from distichous to spiral. It is remarkable that the transition from tristichous disposition, being characteristic of the leaves of the vegetative region, to spiral arrangement in the paracladial zone is a relevant feature (Guarise and Vegetti 2008). But it is very unusual to have such a double and bidirectional change in phyllotaxy pattern along the same morphological axis as occurs in the inflorescences of *Scleria* with subandrogynous, staminate, or androgynous spikelets. Extensive spikelet and floral ontogenetic research is needed to clarify these phyllotaxy changes.

In the species studied of *Scleria*, a system of cymose ramification denominated as fascicles of spikelets is formed from the axillary bud of the prophylls. The cymose system of prophyllar ramification that is represented in the inflorescences of *Scleria* has been characterized by Haines and Lye (1972). In section *Hypoporum*, the most characteristic mode of the fascicles of spikelets is observed, that of inflorescences with predominantly prophyllar ramification. The fascicles of spikelets in the distal portions of the

main axis and of the paracladia in the species in which exclusively prophyllar paracladia predominate (as occurs in *S. mitis*) can clearly be observed. The number of spikelets that integrate the fascicle differ according to the position of the fascicle and by species. For example, the better developed fascicles have three (*S. mitis*, *S. macrophylla*, *S. secans*) or four spikelets (*S. plusiophylla*, *S. lacustris*, *S. melaleuca*).

The majority of the species present only one type of inflorescence in regard to the sexuality of spikelets. Some have only one type of spikelet (such is the case in the majority of species of section *Hypoporum*); most species have inflorescences presenting two types of spikelet sexuality. The inflorescence type A of *Scleria ciliata* (Fig. 6a) presents three different types of spikelets. With respect to spikelet sexuality, *Scleria sellowiana* and *S. ciliata* (Fig. 6) possess two and four types of inflorescences, respectively. In the inflorescences that show two or more types of spikelets, the change in sexuality occurs toward the distal parts. There are variations in the distinct species with respect to the hierarchy of the paracladia where the change occurs. These determine changes in the proportion of each spikelet type in the total inflorescence.

The species studied of section *Hypoporum* have androgynous spikelets with the exception of *Scleria variegata*, which presents staminate spikelets toward the distal portions, coinciding with those proposed by Haines and Lye (1972). In the species of section *Ophryoscleria*, the spikelets are staminate and toward the distal portions subandrogynous, with the exception of *S. macrophylla*, which presents staminate spikelets and, toward the distal portions, pistillate spikelets. This last situation was also observed by Haines and Lye (1972) for *S. racemosa* Poir. and *S. verrucosa* Willd. In the section *Schizolepis*, the spikelets are staminate and toward the distal portions subandrogynous. Greater variation is observed in section *Scleria* presenting staminate, subandrogynous, androgynous, and pistillate spikelets. Haines (1983) indicated that androgynous spikelets were not represented in section *Scleria*, although noting that this type of spikelet was reported for *S. nyasensis* C.B. Cl. This character was found in some of the species studied in this work, such as *S. sellowiana* and *S. ciliata*. Within this section it is notable that *S. bracteata* presents spikelets that are subandrogynous in the middle and basal paracladia and staminate spikelets in the distal paracladia, with an intermediate paracladia distributed with both types of spikelets, the subandrogynous ones on the basal paracladia and the staminate ones on the distal paracladia (Fig. 5).

All of the *Scleria* species studied with unisexual spikelets are monoecious. Camelbeke (2001–2002) cites three species of *Scleria* that are dioecious in the neotropics:

S. amazonica Camelb., M.T. Strong and Goetgh., *S. tenacissima* Steud., and *S. sphacelata* F. Muell.

The different types of spikelets described in *Scleria* represent a reduction series, with the bisexual spikelets considered as ancestral and the subandrogynous spikelets intermediate between the bisexual and the unisexual spikelets (Haines and Lye 1983; Camelbeke 2001–2002).

Changes in sexuality occur frequently, and the gain or loss of unisexuality apparently is a common feature (Malcomber and Kellogg 2006). The most relevant data in *Scleria* are the changes in spikelet sexuality towards the distal portions of the inflorescence. Timonen (1998) suggested that rudimentary stamens may occur in female flowers as well as rudimentary gynoecia in male flowers. Unisexual flowers generally are generated by a pattern of organ abortions (Ainsworth 2000; Reinheimer 2007). The sexual expression induces the control of the development of floral organs, stopping or activating an existing functional development path (Malcomber et al. 2006). These authors state that in the absence of evolutionary covariation between the stamens and gynoecia abortions, or even in the same plant, the production of staminate flowers occurs by different mechanisms than those of the production of pistillate flowers. The variation observed in the development of staminate flowers and neutral ones led some authors (Malcomber and Kellogg 2006) to raise the possibility that there is no single pattern of sexual expression and that it has changed several times and in different ways through evolution.

The grade of ramification is reduced acropetally over both the main axis and over the paracladia. As the prophyll is the basal leaf of the paracladia, their axillary production is the last to be reduced, and consequently, in the distal portions (to the main axis and the branched paracladia) of all species, the ramification (if present) is prophyllar only.

In sections *Scleria*, *Schizolepis*, and *Ophryoscleria*, foliaceous and glumiform bracts are present, as they are in *Scleria variegata* of section *Hypoporum*. The rest of the species in the latter section show only glumiform bracts. *Scleria leptostachya* lacks bracts in the paracladia, and *S. ciliata* and *S. sellowiana* possess very few (one or two); consequently all of the secondary paracladia and those of the following orders are prophyllar in the first species, and the majority of the paracladia are prophyllar in the other two species. However, little development of the prophyllar paracladia has been observed in *S. scabra*.

In all of the species, the paracladia are located one per node. In *S. variegata*, two basal paracladia are observed at the same node. One is interpreted as the primary paracladium originating in the axillary bud of the bract located at this node; the other paracladium, considering its location, possibly originated as part of an accessory bud. Haines and

Lye (1983) mention the presence of two paracladia at the same level in *S. racemosa* and *S. verrucosa* but do not clarify the origin of these two branches. Developmental studies will help us to determine if this paracladium of *S. variegata* is accessory-axillar. Ramifications from supernumerary buds of serial type have been observed in *Hypolytrum* Rich. (Alves et al. 2000), *Cladium mariscus* R. Br. (Mora-Osejo 1960), and *Cyperus* L. section *Luzuloide* Kunth (Guarise and Vegetti 2008).

In summary, we found the following characters that differ across the different species in the genus: (1) total number of the primary paracladia, (2) maximum branch degree of the primary paracladia, (3) characterization of the bract (glumiform or foliaceous), (4) number of bracts of the paracladia, (5) origin of the successive paracladia (non-prophyllar or prophyllar), (6) differences in main axis and paracladium internode length, (7) total number of the most distal primary paracladia, (8) ramification degree of the most distal primary paracladia, (9) degree of homogenization of the inflorescence, (10) presence or absence of the terminal spikelet of the main axis, (11) position of the inflorescence (terminal or pseudolateral), (12) sexuality of the spikelets along the length of the inflorescence, (13) maximum number of fascicles of spikelets, (14) total number of spikelets, (15) phyllotaxis of the glumes, (16) maximum inflorescence length, and (17) position of the first prophyllar secondary paracladium.

Inflorescences in the genus *Scleria* differ extensively in the number of primary paracladia, the maximum inflorescence length, the number of paracladium bracts, the number of the most distal primary paracladia, and the total number of spikelets. These characters diverge among species within the same genus, and among specimens of the same species.

Among the different structures found in the inflorescence of the genus *Scleria*, we identified different evolutionary trends that have already been described for Cyperaceae (Vegetti 2003; Guarise and Vegetti 2008). These trends are, at least in part, responsible for the diversity of the *Scleria* inflorescences and include the following: (1) reduction of the number of primary paracladia; (2) reduction of the paracladium branching order; (3) reduction of the number of bracts of each paracladium; (4) reduction/elongation of the internodes both in the main axis as well as the paracladia, especially the epipodium, which produces important variations in the appearance of the inflorescence; (5) development of the prophyllar paracladia; (6) reduction in the development of the florescences and the consequent change in the sexuality of the spikelets; (7) truncation of the main florescence and the distal and medial paracladia (*S. reticularis* and *S. melanomphala*); and (8) homogenization of paracladia (*S. obtusa*). These

processes possibly may have occurred, independently or combined, more than once, and in different ways.

Systematic value

In his cladistic study, Camelbeke (2001–2002) confirmed the subgenera *Hypoporum* and *Scleria*; the first is monophyletic and the latter is polyphyletic. This author confirmed the sections *Hypoporum*, *Hymenolytrum*, *Ophryoscleria*, *Schizolepis*, and *Scleria*.

The section *Hypoporum* is distinguished from the rest by generally presenting inflorescences of the spiciform type or the paniculate type with spiciform branches; and with spikelets exclusively androgynous or androgynous and staminate. Within this section, the majority of the species studied present only androgynous spikelets and primary paracladia reduced in the axil of the glumiform bracts; with secondary paracladia only of prophyllar origin (*Scleria leptostachya*) or originating from the axillary bud of the bracts (*S. distans* and *S. composita*). *Scleria distans* showed primary paracladia nutants, pendulous, up to 10 spikelets. These primary paracladia are loose arrangements; whereas *S. composita* has erect primary paracladia with up to 30 spikelets, those of *S. distans* are densely disposed. *Scleria variegata* is differentiated from the rest of the species of the section by spikelets that are androgynous and staminate and by primary paracladia that are more developed, spiciform, and bearing secondary paracladia that are reduced. Consequently, two main inflorescence types are recognized in the section *Hypoporum*: (1) spiciform inflorescence of sessile spikelet clusters (paracladia) subtended by glume-like or short foliate primary bracts (*S. distans*, *S. composita*, and *S. leptostachya*) and (2) paniculate inflorescence with spiciform primary paracladia that form spikes of spikelet clusters similar to the inflorescence of the first type (*S. variegata*).

Camelbeke (2001–2002) characterized the inflorescences of the section *Ophryoscleria* as paniculate with staminate and subandrogynous spikelets. In our work, the inflorescences of *S. macrophylla* were shown to have staminate and pistillate spikelets; the hypopodium and the epipodium of the basal paracladium are developed; and the species presented the first prophyllar secondary paracladium on the third primary one. *S. microcarpa* presents reduced inflorescences with few bracts and short internodes; *S. obtusa* showed partial homogenization. *S. mitis*'s primary paracladia could present up to 150 spikelets, with the four to five proximal paracladia very distanced from the main axis by long internodes; this is the species with the longest UIF and the highest primary paracladia number of this section.

The section *Schizolepis* is monophyletic and sister of *Ophryoscleria* (Camelbeke 2001–2002). In section *Schizolepis* subandrogynous and staminate spikelets are present, with predominance of staminate ones in *Scleria panicoides* and of subandrogynous ones in *S. plusiophylla* and *S. latifolia*. In these latter two, fascicles with a greater number of spikelets are formed by two spikelets in *S. latifolia* and by four in *S. plusiophylla*.

The position of the remainder of the species in Camelbeke's cladogram makes *Scleria* section *Scleria* polyphyletic. The majority of species are found in this section, as is the major inflorescence variability. Based on characters of the inflorescence, we propose the following groups among species of the section *Scleria*:

First group: *S. bracteata*. The inflorescence shows remarkable arrangement of the staminate and subandrogynous spikelets in separate portions of the inflorescence; the first prophyllar secondary paracladium appears in the eighth- to thirteenth-order primary paracladium. This inflorescence type, which is unique in the genus, seems to justify the recognition of a distinct section *Macrolomia* as proposed by Camelbeke (2001–2002).

Second group: *S. melanomphala* and *S. reticularis* with truncated inflorescences, formed by two or three basal paracladia.

Third group: *S. ciliata* and *S. sellowiana*. Both species present distinct types of inflorescences according to the sexuality of the spikelets. *S. ciliata* presents four types of inflorescences and *S. sellowiana* two types. Also, in these species the unit of the inflorescence is pseudolateral. Both species have low numbers of paracladia, with maximum eighth-order branching in *S. ciliata* and maximum fifth-order branching in *S. sellowiana*.

Fourth group: *S. melaleuca*. The only species in the section *Scleria* and the genus with staminate flower with one stamen.

Fifth group: *S. secans* and *S. flagellum-nigrorum*. These are large climbers with many-noded stems scrambling in trees and shrubs up to several meters high by means of minute reflexed prickles on the angles of the leaf sheaths and margins and midrib of the leaf blades (Ahumada 2007). In the inflorescence of *S. flagellum-nigrorum*, the five to seven proximal primary paracladia lack prophyllar secondary paracladia, and the number of staminate spikelets is higher than the number of subandrogynous spikelets. *S. secans* from Argentina and Paraguay has pistillate and staminate spikelets; *S. flagellum-nigrorum* has subandrogynous and staminate spikelets. However the specimens of *S. secans* from other countries (Bolivia, Brazil, Colombia, Ecuador, Guianas, Perú, Venezuela) (Camelbeke 2001–2002) have subandrogynous and

staminate spikelets, as does *S. flagellum-nigrorum*. The androgynous spikelets are regarded as ancestral and the subandrogynous spikelets intermediate between the bisexual and the strictly unisexual spikelets. Therefore we considered that pistillate spikelets from *S. secans* specimens from Argentina and Paraguay are subandrogynous spikelets that changed to pistillate ones at the limit of the species's southern distribution area.

Sixth group: *S. lacustris*. This species is aberrant within section *Scleria* due to its annual habit. The inflorescence presents staminate and subandrogynous spikelets and paracladia with maximum sixth-order branching. It has a fruit with hypogynium obscurely three-lobed, lobe-margin entire, and margin narrow (Ahumada 2007). Some species from section *Hypoporun* have this kind of hypogynium, so Nelmes (1955) located *S. lacustris* within section *Hypoporun*. We accept Robinson's (1966) placement, locating it within section *Scleria*. However future research about this point is necessary.

Seventh group: *S. scabra*. This species has inflorescences that are very short, very densely paniculate and pyramidal, with the main inflorescence axis barely visible. Camelbeke (2001–2002) wrote that some specimens of *S. scabra* could be interpreted as belonging to section *Hymenolytrum*, in which case they should be called *S. cerradicola* T. Koyama. In the material he studied, there seemed to be a range of almost sessile to clearly peduncled staminate spikelets. The name *S. scabra* has been used awaiting a thorough study and demarcation of section *Hymenolytrum*. Most likely *S. cerradicola* will prove to be a synonym of *S. scabra*. We are in agreement with Camelbeke's opinion.

In the section *Hypoporun*, the spiciform inflorescence type (*S. composite*, *S. distans*, and *S. leptostachya*) appears to represent a reduction from the paniculate inflorescence with spiciform branches (*S. variegata*) by progressive contraction of the side branches (Camelbeke 2001–2002). Haines and Lye (1983) consider that the fascicles of spikelets and the reduced inflorescences that characterize the species of the section *Hypoporun* are more specialized than the inflorescences in the rest of the sections. But the Camelbeke cladogram gives no information on whether *Scleria* subg. *Hypoporun* is more primitive or more derived within subg. *Scleria* (Camelbeke 2001–2002). A new cladistic study of the genus, including a greater number of species, is necessary (Camelbeke 2001–2002). A new study could combine molecular and morphological data, and we strongly consider that the characters of the inflorescences analyzed in this work shall be used.

The diversity of forms of inflorescences observed in the adult state is determined by differences in the patterns of development (Albert et al. 1998; Doust and Kellogg 2002a,

b). Doust and Kellogg (2002a, b) observe that inflorescences that are morphologically similar in adult states can develop by very different processes, or that small changes during the development can yield a considerable range of variation in the adult morphology of the inflorescences. Undoubtedly, developmental studies constitute a powerful source of characters that are necessary for understanding inflorescence morphology and diversification (Doust and Kellogg 2002a, b; Reinheimer 2007). Characters from ontogenetic analyses are very useful in taxonomic and phylogenetic research (Albert et al. 1998; Kellogg 2000; Doust and Kellogg 2002a, b; Kellogg et al. 2004; Bess et al. 2005). Additional developmental studies of the *Scleria* inflorescence are needed. Two features could be relevant in these studies: the change in phyllotaxy pattern along the same morphological axis and the acropetal change of spikelet sexuality.

It is known that the inflorescence is the result of early patterns and spatial patterns of genetic expression that control the process of morphological development (Kellogg 2000; Reinheimer 2007). Future investigations should focus attention on the ontogenetic and genetic aspects of inflorescence development of *Scleria*, integrating the results of these studies, together with those relative to adult inflorescences, into taxonomic and phylogenetic investigations. Together they would permit the understanding of how, when, and where modifications during development occur to create the extensive inflorescence variation seen in *Scleria*.

Appendix

Section *Hypoporum*

Scleria composita (Nees) Boeck.: Ekman 1297 (B, SI); Steinbach 6981 (B, BM, G, SI); Glaziou 22354 (BR, G); Pedersen 816 (BR, CTES); Pedersen 4510 (BR, CTES, G, K, LP); Herrera 420 (CTES); Krapovickas et al. 24746 (CTES); Nicora 5257 (CTES, SI); Quarín 469 (CTES); Schinini et al. 21775 (CTES, JUA); Beck 13175 (GENT, JUA, LPB); Irwin et al. 24393 (K); Ahumada et al. 6664 (JUA); Ahumada et al. 6666 (JUA); Ahumada et al. 7633 (JUA); ídem. 7643 (JUA); Ahumada et al. 7886 (JUA); Guillén et al. 416 (JUA, MNES); Killeen 1597 (LPB); Guaglianone et al. 846 (SI); Pedersen 13466 (SI); Rojas 14051 (SI).

Scleria distans Poir.: Buchtein 7163 (B); Edwal 9206 (B); Ekman 1798 (B); Ekman 6205 (B); Herter 344 (B, CTES, G, LIL, M, SI); Lombardo Marchesi Mus. Botan. Montev. 1839 (B); Mutis 6109 (B); Osten 7414 (B); Osten 8835 (B, MVM); Osten 16088 (B); Steinbach 6861 (B, BM, G, K); Steinbach 6982 (B, BM, G, K); Partridge

60808 (BA); Rabello et Barbosa 197a (BA, MVM, SI); Hatschbach 2073 (BAA, SI); sin coleccionista (BAA 1054); Jörgensen-Hansen 702 (BAB); Martínez Crovetto et Milano 5001 (BAB); Balansa 448a (BAF, BM, G, K); Klein 3834 (BAF); Molfino s.n. (BAF); Reitz et Klein 16449 (BAF); Dusén 13490 (BM); Fiebrig 4840 (BM, G, K, P); Hassler 3575 (BM, G, K, P); Hassler 5633 (BM, G, K, P); Hassler 8254 (BM, G); Hassler 8794 (BM, G, K); Marín et Giménez GM518 (BM, SI); Morong 424 (BM, K); Spruce s.n. (BM); Zardini et Park guard 15500 (BM, PY); Balansa 448 (BR, G, K, P); P. Claussen 427 (BR); Kummrow 2129 (BR); Pedersen 499 (BR, G, K, LP, P); Pedersen 3652 (BR, G); Stephan s.n. (BR); Wullschlägel 655 (BR); Ahumada 1931 (CTES); Ahumada 2240 (CTES); Arbo et al. 1227 (CTES); Arbo et al. 6228 (CTES); Arbo et al. 6391 (CTES, JUA); Arbo et al. 6773 (CTES); Arbo et al. 7110 (CTES, JUA); Barros 2430 (CTES, LIL, SI); Bordas et Schmeda 4112 (CTES, FCQ); Carnevali 2404 (CTES); Carnevali 3901 (CTES); Carnevali 4380 (CTES); Carnevali 5482 (CTES); Carnevali 6231 (CTES); Carnevali 6332 (CTES); Fernández 977 (CTES); Ferrucci et al. 259 (CTES); Hatschbach 26214 (CTES); Jorgensen 3508 (CTES); Krapovickas et Cristóbal 13515 (CTES); Krapovickas et al. 25337 (CTES); Krapovickas et Schinini 36325 (CTES); Neiff 812 (CTES); Pedersen 7895 (CTES); Pedersen 12761 (CTES); Quarín et al. 2443 (CTES); Quarín et al. 2730 (CTES); Rambo 38818 (CTES); Rambo 44558 (CTES); Rosengurt B-4319 (CTES, MVM, SI); Schinini 22943 (CTES); Schinini et al. 29334 (CTES, G, JUA); Schwindt 931 (CTES, LIL); Sparre et Vervoorst 986 (CTES); Swartz 9007 (CTES, LIL); Tressens et al. 920 (CTES); Cavalcante 926 (Herbario Emilio Göeldi); Basualdo 5442 (FCQ); Basualdo 5852 (FCQ); Degen 1731 (FCQ); Mereles 3479 (FCQ); Soria 4451 (FCQ); Soria 5834 (FCQ); Nicora et al. 9914 (FCQ, SI); Zardini et Velásquez 26597 (FCQ); Balansa 448b (G, P); Eggers 2491 (G, M); Fiebrig 437 (G, K, M, P); Hassler 32 (Herb. Hassler 2420) (G, SI); Hassler 1315 (G, K, P); Osten 4409 (G); Osten 5352 (G, MVM); Poeppig s.n. (G); Reitz et Klein 8424 (G); Riedel s.n. (G, SI 1805); Sellow s.n. (G); Steinbach 5327 (G, MVM); Steinbach 5495 (G); Beck 13137 (GENT); Ahumada 6340 (JUA); Ahumada et al. 6655 (JUA); Ahumada et al. 6660 (JUA); Ahumada et al. 6662 (JUA); Ahumada et al. 6663 (JUA); Ahumada et al. 7428 (JUA); Zardini et al. 641 (JUA, LP, SI); Troncoso et Bacigalupo 2985 (JUA, SI); Hasse 880 (K); Jorgensen 3588 (K); Lindeman 1899 (K); Montes 3291 (K, SI); Pedersen 7696 (K, P, SI); Wood 9373 (K); Wood et Goyder 15406 (K); Woolston 577 (K, SI); Woolston 1427 (K); Rambo 38514 (LIL); Duarte 6339 (LP, SI); Jorgensen 3588a (LP, SI); sin coleccionista 50729 (LP); Abott et Isaacs 16507 (LPB); Beck et al. 9867 (LPB); Beck 14860 (LPB); Beck 17196 (LPB); Beck 17458 (LPB); Beck 17561 (LPB); Beck

17866 (LPB); Beck 18381 (LPB); Bruderreck 16 (LPB); Buchtein 7165 (LPB); García et al. 2121 (LPB); Killeen 1763 (LPB); Müller 9456 (LPB); Legrand 22 (MVM); Osten 21865 (MVM, SI); Rosengurt 971 (MVM); Rosengurt 975 (MVM); Bonpland s.n. (P); Croat 24024 (P); Ellenberger 1457 (P); Poeppig 34 (P); Reitz et Klein 17825 (P, SI); Saint-Hilaire 2358 (P); Ule 1344 (P); Brian Abrell 68 (PY); Zardini et forest ranger 10277 (PY); Archer et Rojas 4852 (SI); Barros 2405 (SI); Barros 2451 (SI); Bartlett 21235 (SI); Burkart 17322 (SI); Burkart 19419 (SI); Burkart 21534 (SI); Burkart 25074 (SI); Burkart et al. 29212 (SI); Burkart et al. 29213 (SI); Burkart et al. 29765 (SI); Burkart et al. 29779 (SI); Burkart et al. 30735 (SI); Chebataroff 727 (SI); Glaziou 13303 (SI); Hatschbach 2073 (SI); Hatschbach 3692 (SI); Hatschbach 6699 (SI); Joly 367 AB5 (SI); Klein 744 (SI); Klein 2545 (SI); Klein et al. 5924 (SI); MG N° 24670 (SI); Ocemago 12399 (SI); Rambo 32454 (SI); Reitz et Klein 399 (SI); Reitz 5338 (SI); Reitz et Klein 5668 (SI); Reitz et Klein 16593 (SI); Reitz et Klein 10304 (SI); Rojas 1032 (SI); Rojas 6661 (SI); Smith et Klein 7518 (SI); Smith et al. 9391 (SI); Türckheim 197 (SI); Zardini et Velázquez 24691 (SI); Zardini et Tilleria 31510 (SI).

Scleria leptostachya Kunth: Steinbach 5300 (B, G, MVM, SI); Steinbach 6864 (B, G, K); Steinbach 6927 (B, BM, G, K, SI); Reitz et Klein 16422 (BAF); Gardner s.n. (BM); Hassler 8210 (BM, G); Riedel 2990 (BM); Caballero Marmori 1353 (CTES); Hatschbach 26041 (CTES, LP); Schwindt 2348 (CTES, LIL); Balansa 456 (G, P); Sellow s.n. (G); Irwin et al. 11690 (GENT); Irwin et al. 25930 (GENT); Schessl 3142 (GENT); Ahumada 7578 (JUA); Burkart 14759 (JUA, K, SI); Glaziou 20052 (K); Ratter et Bertolda 1034 (K); Riedel 158 (K); Wood 14322 (K); Rambo 30816a (LIL); Regnell Ser. III, 1321 (LIL, P); Bruderreck 125 (LPB); Killeen 2041 (LPB); Duarte 7755 (M, SI); Regnell s.n. (P); Riedel 2990 (P); Weddell s.n. (P); Araujo 58 (SI); Fontana F177-34 (SI); Hatschbach 3687 (SI); Irwin et al. 10234 (SI); Irwin et al. 16399 (SI); Irwin et al. 18660 (SI); Klein 4604 (SI); Rambo 30816 (SI); Reitz et Klein 11983 (SI); Riedel 1833 (SI); Rojas 6846 (SI); Smith et Klein 10864 (SI); Smith et Klein 10991 (SI).

Scleria variegata (Nees) Steud.: Brade 11191 (B); Hoehne 19492 (B); Hatschbach 24052 (CTES); Vanni et al. 3156 (CTES, JUA); Ahumada et al. 6658 (JUA); Martius s.n. (M); Herter 4319 (MVM); Atala 269 (SI); Castellanos 22697 (SI); Guaglianone et Gatusso 2504 (SI); Martinelli et al. 10860 (SI).

Section *Ophryoscleria*

Scleria macrophylla J. Presl & C. Presl: Pipoly et al. 11702 (B); Sagot 1172 (BM, K, P); Steinbach 8021 (BM, G, K); Billiet et Jadin 6001 (BR); Morrone et M. Belgrano 5058 (CTES); Gardner 1858. (G); Gardner 1895 (G, K); Huker

7753 (G); Leblond s.n. (G); Pittier 4882 (G); Salzmänn s.n. (G); Beck et al. 19107 (GENT); Beck 20717 (GENT); Croat et Rosas 62688A (GENT); Smith et al. 13645 (GENT, LPB); Beck et al. 19630 (K); Burchell 5489 (K); Gardner 1875 (K); Feurer 6480 (LPB); Gonzáles 85 (LPB); Wood 15012 (LPB); Janssen 581 (M); Martius s.n. (M); Prance et Silva 59012 (M); sin coleccionista s.n. (M); Raynal-Roques 20176 (P); Richard s.n. (P); sin coleccionista s.n. (P); Soubirou s.n. (P); Soubirou s.n. (P); Soubirou s.n. (P); Rojas 3689 (SI).

Scleria microcarpa Nees ex Kunth: Ekman 2115 (B); Ekman 4378 (B); Ekman 11232 (B); Ekman 13260 (B); Ekman 15893 (B); Ekman 17369 (B); Ekman 17115 (B); Killeen et Guillén 6837 (B); Pickel 335 (B); Pickel 3453 (B); Pickel 3160 (B); Rojas 7420 (B); Sampaio 5617 (B); Sampaio 5897 (B); Steinbach 7564 (B, BM, G, K); Hassler 8081 (BM, G, K, LIL, P); Ridley et al. s.n. (BM); Sagot 897 (BR, K, P); Schomburgk 660 (BR, K); Wright 723 (BR); Encarnación 26480 (G); Gehriger 279 (G); Kallunki et al. 483 (G); Poeppig 3062 (G); Anderson 10671 (GENT); Chonono et Saavedra 257 (GENT, LPB); Focke 910 (GENT); Focke 1069 (GENT); Jardim et al. 241 (GENT); Killeen et Guillén 6877 (GENT); Luceño 122 (GENT); Moraes 250 (GENT, LPB); Moraes et al. 1770 (GENT); Hasse 895 (K); Beck et al. 19348 (K); Lowe 4221 (K); Sperling 6559 (K, LPB); Traill 1206 (K, P); Ule 5298 (K); Martius s.n. (M); Sintenis 781 (M); Croat 24024 A (P); Benoist 1407 (P); Cremers 7836 (P); Leprieur 77 (P); Mélinon s.n. (P); Mélinon 18 (P); Poeppig s.n. (P); Schomburgk s.n. (P); Sintenis 78 (P); sin coleccionista s.n. (P); Anderson 10600 (SI); Rojas 1017 (SI); Rojas 2288 (SI).

Scleria mitis P.J. Bergius, Kongl.: Gregory et al. 10313 (BAA); Hassler 10041 (BAF, G, K, LIL, P); Sintenis 6659 (BAF); Jiménez et Marín, G 1955BJ (BM, SI); Weigelt s.n. (BM, G); Martius s.n. (BR); Ferrucci et al. 1426 (CTES, JUA); Ferrucci et al. 1634 (CTES, JUA); Hatschbach et al. 58618 (CTES); Krapovickas et Schinini 31779 (CTES); Krapovickas et Schinini 31994 (CTES); Mereles et Geisslu 3972 (CTES); Pedersen 12154 (CTES); Schinini et al. 29268 (CTES, G); Schinini et Dematteis 33297 (CTES); Mereles 3472 (FCQ); Broadway 7731 (G); Salzmänn s.n. (G); Steinbach 5512 (G); Irwin et al. 14364 (GENT); Luceño 68 (GENT); W. Thomas et al. 11399 (GENT); Asplund 9328 (K); Asplund 19321 (K); Hage et al. 2292 (K); Kallunki et al. 483 (K); Spruce s.n. (K); Cabrera et Zardini 29985 (LP); Luetzelburg s.n. (M); Martius s.n. (M); Claussen 990 (P); Cremers et al. 12486 (P); L. C. Richard s.n. (P); Sagot s.n. (P); Salzmänn s.n. (P); Solomon et al. 6903 (PY); Filgueiras et Zuloaga 2192 (SI).

Scleria obtusa Core: Fiebrig 4728. (G, K, M, P); Beck 3308 (GENT); Beck et Hasse 10131 (GENT, LPB); Beck 15032 (GENT, JUA, K); Beck et Hasse 9923 (LPB);

Bruderreck 110 (LPB); Gutierrez et al. 1881 (LPB); Hasse 388 (LPB); Orellana et Beck 46 (LPB); Orellana et Beck 208 (LPB); Orellana 361 (LPB); Orellana et al. 566 (LPB); Orellana et al. 686 (LPB); Saavedra et Chonono 357 (LPB).

Section *Schizolepis*

Scleria latifolia Sw.: Barros 2343 (B, CTES, SI); Bartlett 11718 (B); Buchtein 388 (B); Buchtein 7161 (B); Camargo 2712 (B); Edwalli 9237 (B); Herter 4328 (B, MVM); Irwin et Soderstrom 6277 (B); Jensen-Jacobs et al. 257 (B); Jensen-Jacobs et al. 343 (B); Jürgens s.n. (acc. 1946 Herb. Rudolf Gross) (B); Loefgren et Edwalli 9232 (B); Rambo 57151 (B); Rambo 57157 (B); Swallen 3180 (B); Usteri 9247 (B); Walter 210 (B); Kermes 2463 bis (BAB, BAF); Múlgura et al. 595 (BAB, SI); Rodríguez 289 (BAB); Hassler 11302 (BAF, BM, G, K, P, SI); Hassler 8685 (BM, G, K, P, SI); Zardini et Velázquez 15780 (BM, PY); Ahumada 3689 (CTES); Araujo 808 et Peixoto 614, Herb. RB 172106 (CTES); Arbo 464 (CTES); Caballero Marmorini s.n., Herb. Itaipú Binacional 1727 (CTES); Correa et al. 5417 (CTES); Guaglianone et al. 2911 (CTES, JUA, SI); Hatschbach et al. 35945 (CTES); Irwin et al. 18295 (CTES); João et Rohr s.n. (CTES 63168, LIL 201324); Krapovickas et al. 17214 (CTES); Krapovickas et al. 26431 (CTES); Krapovickas et Cristóbal 38532 (CTES); Lindeman et al., serie 26.13, Herb. ICN 28216 A y B (CTES); Pallarés 208 (CTES); Pedersen 5968 (CTES, K, P SI); Pedersen 9303 (CTES, K); Pérez 357 (CTES, PY); Pipoly et al. 11216 (B, CTES); Quarín 480 (CTES, LP, P); Quarín 487 (CTES, LIL); Quarín et al. 2765 (CTES); Quarín 3376 (CTES); Schinini et Carnevali 10602 (CTES); Schinini et al. 11230 (CTES); Schinini et al. 23755 (CTES, JUA); Schinini et Caballero Marmorini 27105 (CTES); Sparre et Vervoorst 518 (CTES); Tressens et al. 384 (CTES, K); Tressens et al. 883 (CTES); Tressens 2925 (CTES); Valls et Irgang 2979 A y B (CTES); Basualdo 2275 (FCQ); Mereles 3638 (FCQ); Zardini 6757 (FCQ, GENT, SI); Zardini et Aguayo 8494a (FCQ); Belanger 407 (G); Broadway 565 (G); Broadway 4755 (G, P); Broadway 5508 (G); Fiebrig 418 (G); Gaudichaud 85 (G, P); Hahn 1281 (G); Hart a.1896 (G); Hassler 10439 (G); Herminier 16 (G); Huber 1901 (G); Jardim et al. 737 (G); Kuniyoshi and Kuniyoshi 1620 (G); Molina et al. 17331 (G); Riedel s.n. (G); Schinini 4416 (G); Shotsky s.n. (G); Stutz 2079 (G); Tonduz 12776 (G); Tonduz 12853 (G); Weddell 1132 (G); Beck 27629 (GENT); Beck 13654 (GENT, JUA, LPB); Gentry et al. 59140 (GENT); Luceño 17 (GENT); Solomon 10818 (GENT); Zardini et Tilleria 28495 (GENT); Zardini et Aquino 32861 (GENT); Zardini et Vera 42643 (GENT); Ahumada 6338 (JUA); Burchell 980 (K); Lira et al. 71 (K); Rodríguez et al. 42 (K); Rodrigues et al. 49 (K); Sales de

Melo et al. 228 (K); Silva et al. 125 (K); Tschá et al. 311 (K); Husnot 1868 (M); Martius s.n. (M); Meier et al. 2007 (M); Othmer s.n. (M); Prance et Silva 59590 (M); sin coleccionista s.n. (M); Swartz s.n. (M); Vogl A 21 (M); Rojas 2285 (MVM, SI); Dwyer et Lieser 12081 (P, SI); Glaziou s.n. (P); Lourteig 1935 (P); Nadeaud s.n. (P); Levy 1407 (P); Questel 4101 (P); Le Gallo 2847 (P); Raynal 15565 (P); Raynal 19571 (P); Raynal s.n. (P); Zardini et Benítez 3412 (PY); Zardini 7567 (PY); Zardini et park guard 11819 (PY); Zardini 15998 (PY); Joly et al. 681ABJ (SI); Koyama et al. 14141 (SI); Martinelli et al. 10950 a (SI); Montes 104 B (SI); Mori et al. 13773 (SI); Morrone et al. 1432 (SI); Múlgura et al. 1884 (JUA, SI); Múlgura et al. 1928 (SI); Múlgura et al. 2650 (SI); Múlgura et al. 3283 (JUA, SI); Muniz 354 (SI); Rambo 37920 (SI); Reitz et Klein 10960 (SI); Rojas 8095 (SI).

Scleria panicoides Kunth: Brade 10755 (B); Brade 10897 (B); Brade 12650 (B); Buchtein 5101 (B); Gehtr 7864 (B); Gross 20136 (B); Hoehne 3914 (B); Hoehne 9242 (B); Rambo 41854 (B); Hauman 22516 (BA); Jørgensen 4490 (BA); Pérez Moreau 21058 (BA); Bang 2350 (BM, G, K); Lindeman et Hass 1942 (BR); Orth 704 (BR, K); Amarilla et al. 75 (CTES); Castellanos 21662 (CTES); Eskuche et al. 5-126 (CTES, SI); Hatschbach 16491 (CTES); Honfi 53 (CTES, K); Keller et F. Moskovich (CTES); Keller 2797 (CTES); Herb. Orchioni 4913 (CTES); Pedersen 7791 (CTES); Quarín 1147 (CTES, LIL); Reitz 1796 (CTES); Schinini et al. 28746 (CTES, JUA); Schinini et al. 31390 (CTES); Tressens et al. 5389 (CTES); Tressens 5838 (CTES); Keel 1495 (FCQ); Reitz et Klein 8912 (G, SI); Solomon 18411 (GENT); Guaglianone et al. 2892 (JUA, SI); Rodríguez et al. 566 (JUA, MNES); Rodríguez et al. 847 (JUA, MNES); Ball s.n. (K); Custódio Filho et Franco 2743 (K); Glaziou 11658 (K, P); Hunt 6351 (K); sin coleccionista (K); Bertoni 2786 (LIL); Rodríguez 371 (LP, SI); Martius s.n. (M); Martius s.n. (M); Gaudichaud 84 (P); Lindeman et Hass 5111 (P); Lourteig 2349 (P); Mexia 4686 (P); Weddel 366 (P); Castellanos 24428 (SI); Deginani et al. 1258 (SI); Reitz et Klein 4293 (SI); Reitz et Klein 6789 (SI).

Scleria plusiophylla Steud.: Brade 12171 (B); Henkel et al. 5599 (B, GENT); Hoehne 9240 (B); Jørgensen 4490 (B, MVM, SI); Rojas 5030 (B, SI); Hauman 1923 (BA); Perrone 54115 (BA); Perrone 54117 (BA); Benítez 56 (BAA, CTES, LIL, LP); Correa et al. 5417 (BAB, CTES, SI); Fernández et al. 184 (BAB, CTES, LIL); Molina et al. 4103 (BAB, PY); Hassler 6365 (BM, G); Arenas 685 (CTES); Guaglianone et al. 2818 (CTES, JUA, SI); Krapovickas et Cristóbal 28753 (CTES); Mereles 3607 (CTES, FCQ); Ortiz 233 (CTES); Múlgura et al. 3514 (CTES, JUA, SI); Schinini 5606 (CTES); Schinini et Fernández 6076 (CTES); Schinini 8045 (CTES, G); Schinini et Bordas 20230 A y B (CTES); Schinini et al. 21927

(CTES); Schinini et Caballero Marmorini 27023 (CTES); Schinini et M. Quintana 36342 (CTES); Vanni et al. 2719 (CTES, K, LIL); Ahumada 6343 (JUA); Ahumada et al. 6657 (JUA); Ahumada O. et al. 6668 (JUA); Beck 24722 (JUA, LPB); Cabral et al. 262 (JUA, CTES); Guaglianone et al. 3004 (JUA); Seidel et Vargas 1143 (JUA, LPB); Tur et Guaglianone 1974 (JUA, SI); Mereles 1125 (FCQ); Mereles 3606 (FCQ); Schinini 4416a (FCQ, G); Soria 1789 (FCQ, G); Soria 3086 (FCQ); Zardini et Degen 3667 (FCQ); Zardini et Salina 26153 (FCQ, GENT); Balansa 460 (G); Degen 223 (G, SI); Bertoni 976 y 976a (G); Chodat 269 (G); Fernández Casas et Molero 3755 (G); Hassler 901 (G); Hatschbach 45855 (G); Pedersen 14697 (G, SI); Beck 17294 (GENT, JUA, LPB); Zardini et Park guard 15511 (GENT, PY); Zardini et Gerrero 37110 (GENT); Glaziou 18593 (K, P); Hassler 8685b (K); Silva et al. 51 (K); Solomon 18411 (LPB); Brunner 1501 (PY); Zardini et forest ranger 10302 (PY); Zardini et Velásquez 15344 (PY); Zardini et Velásquez 15630 (PY); Boelcke 6743 (SI); Cabrera et al. 28894 (SI); Morrone et al. 1455 (SI); Morrone et al. 1633 (SI); Morrone et al. 2044 (SI); Pavetti et Rojas 9723 b (SI); Zardini et Aguayo 8494 (SI); Zardini et Benítez 47341 (SI); Zuloaga et al. 5162 (SI).

Section *Scleria*

Scleria bracteata Cav.: Bang 762 (BM, G); Buchtein 3652 (B, M); Buchtein 5102 (B); Buchtein 5103 (B); Buchtein 5104 (B); Buchtein 7163 (B); Buchtein 7164 (B); Buchtein 8067 (B); Buchtein 8068 (B); Faz, Loefgren 1359 (B); Hoffmannsegg s.n. (B–W 17341); Irwin et Soderstrom 6549 (B); Mass et al. 7204 (B); Mexia 6593 (B); Mexia 9145 (B); Pickel 644 (B); Pickel 3142 (B); Pilger 723 (B); Pipoly et al. 11458 (B); Sampaio 5567 (B); Steinbach 7038 (B, G, K, LIL); Ule 8540 (B, K); Hassler 11294 (BM, G, P); Ridley et al. s.n. (BM); Williams 1652 (BM); Martius s.n. (BR, K); Pittier et Durand 3693 (BR); Pohl s.n. (BR); Schomburgk 108 (BR, G, K); Wright 725 (BR). Blanchet 692 (G); Holton 109 (G); Johnston 203 (G); Jurgensen 659 (G); Krukoff 7135 (G); Pavon s.n. (G); Pittier 8093 (G); Pittier 9450 (G); Poeppig s.n. (G); Sagot 1350 (G). Salzmänn s.n. (G, K); Salzmänn 937 (G); Tnduz 4640 (G). Ule 8540 (G); Beck 12101 (GENT, LPB, SI); Beck et Ruthsatz 21813 (GENT); García 835 (GENT); Grifo et Solomon 809 (GENT); Luceño et Alves 87 (GENT); Luceño 133 (GENT); Mendes 195 (GENT); Mendes 2895 (GENT); Vargas et Seidel 441 (GENT); Beck 27883 (JUA, LPB); Bang 267 (K, M); da Silva et al. 3078 (K); Noblick et al. 2357 (K); Pulle 510 (K); Beck 1786 (LPB); Beck 2243 (LPB); Beck 17765 (LPB); Beck 22767 (LPB); Beck 24723 (LPB); Foster et Ribera 12323 (LPB); Lützelburg 134 (M); Lützelburg 136 (M); Lützelburg 192 (M); Martius 862 (M); Martius 2950 (M); Martius 2951 (M);

Martius 2952 (M); Martius 2953 (M); Martius 2954 (M); Martius 2955 (M); Martius 2956; Spruce s.n. (M); Martius 2957. (M), Martius 2958 (M); Othmer s.n. (M); Pereira et al. 9221 (M); Prance et Silva 59495 (M); Reiche 424 (M); Wagner s.n. (M); Bonpland s.n. (P); de Grosourdy 18 (P); Pentland s.n. (P); Richard s.n. (P).

Scleria ciliata Michx.: Pedersen 4277 (BR, G, K, SI); Hatschbach 25353 (CTES); Pedersen 8518 (CTES, K); Tressens et al. 4202 (CTES); Davidse et al. 35117 (GENT); Ahumada 6341 (JUA); Ahumada et al. 6654 (JUA); Ahumada et al. 6661 (JUA); Ahumada et al. 6665 (JUA); Ahumada et al. 7406 (JUA); Ahumada et al. 7437 (JUA); Ahumada et al. 7454 (JUA); Ahumada et al. 7577 (JUA); Honfi 616 (JUA, MNES); Troncoso et al. 2012 (JUA, SI); Godfrey 48108 (LIL); Bacigalupo et al. 369 (SI); Bacigalupo et al. 554 (SI); Bacigalupo et al. 846 (SI); Bacigalupo et al. 1036 (SI); Burkart et al. 29214 (SI); Burkart et al. 29215 (SI); Fredholm 5041 (SI); Fredholm 5769 (SI); Guaglianone et al. 3049 (SI); Smith et Klein 7478 (SI); Smith et Klein 8558 (SI); Umbach 252 (SI).

Scleria flagellum-nigrorum P.J. Bergius: Schulz 6333 (BAA); Bertoni 5083 (CTES); Bertoni 5321 (CTES, LIL); Carnevali 3524 (CTES); Krapovickas et al. 24273 (CTES); Keel 1210 (FCQ); Keel et Vera 1277 (FCQ); Hassler 2904 (G); Mexia 6423 (G); Prance et al. 3489 (G); Tessmann 3277 (G); Simpson et al. 668 (G); Guillén et Coria 1635 (GENT); Schessl 2407 (GENT); Burchell 2723 (K); Sagot 991 (K); Sellow s.n. (K); Pott et al. 5833 (LP); Moraes et al. 1785 (LPB); Janssen et Gemtchujnicov 400 (M).

Scleria lacustris C. Wright: Ekman 11583 (B); Ekman 17741 (B); Ekman 17916 (B); Hassler 8081 a (BM, G); Beck 15035 (GENT, JUA, K, LPB); Franken 187 (GENT, LPB); Guareco 409 (GENT, LPB); Orellana 247 (GENT, LPB); Pott et al. 5739 (LP); Moraes et Sarmiento 1276 (LPB); Orellana 803 (LPB); Robinson 4700 (M); Weddell 3300 (P); Rojas 6817 (SI).

Scleria melaleuca Rchb. ex Schldtl. & Cham.: Buchtein 388 (B); Buchtein 4283 (B); Ekman 1801 (B); Ekman 2283 (B); Ekman 4327 (B); Dupré s.n. (B); Ekman 15816 (B); Günther 331 (B, P); Günther 334 (B); Günther 335 (B); Howard 9528 (B); Irwin et al. 21443 (B); Irwin al. 26255 (B); Pickel 3321 (B); sin coleccionista s. n. (B); Steinbach 6860 (B, BA, BM, G, K); Steinbach 14994 (B); Hauman 33278 (BA); Jörgensen 3312 (BA, SI); Jörgensen 3578 (BA, BAB, LIL, SI); Steinbach 2367 (BA); Nicora et Cámara Hernández 627 (BAA); Parodi 5456 (BAA, SI); Parodi 7088 (BAA); Bacigalupo et al. 1102 (BAB, FCQ); Cabral et Molina 1014 (BAB, CTES); Fortunato et al. 2491 (BAB); Kermes (404) 5.800 bis (BAB); Llamas BAB 27007 (BAB); Petetín et Molina 1465 (BAB); Ramella et al. 3033 (BAB); Spigazzini 17843 (BAB); Spigazzini, C. et P. Spigazzini 19332 (BAB); Spigazzini 19333 (BAB); Spigazzini 19355 (BAB); Spigazzini 19356

- (BAB); Spegazzini 19357 (BAB); Balansa 3028 (BAF, P); Kermes s.n. (BAF); Hassler 491 (BM, G, K, P); Hassler 8667 (BM, G, K, P); Jiménez et Marín 65 (BM, CTES, JUA, SI); Morong 246 (BM, K); Schomburgk 876 (BM, K); Triana s.n. (BM); Zardini et Velázquez 16867 (BM); de Gryse 36 (BR); Husnot 41 (BR); Eggers 190 (BR); Johnson s.n. (BR); Martius s.n. (BR); Pedersen 533 (BR, K, LP, P); Pedersen 3203 (BR, G); Pedersen 3204 (BR); Pittier et Durand 2715 (BR); Sieber 269 (BR); Wright 726 (BR); Arenas 1147 (CTES); Bordas 3035 (CTES); Bordas 4169 (CTES); Bordón s.n. (CTES); Croat 18077 (CTES); Carnevali 6005 (CTES); Duré 482 (CTES); Heinonen et al. 74 (CTES); Honfi 65 (CTES, MNES); Krapovickas et Cristóbal 11342 (CTES); Krapovickas et al. 23904 (CTES); Krapovickas et al. 24274 (CTES, LIL); Krapovickas et al. 25467 (CTES); Krapovickas et Schinini 36319 (CTES); Liddell 274 (CTES); Mereles 794 (CTES, FCQ, G); Morel 3503 (CTES); Mroginski et al. 327 (CTES); Pedersen 15001 (CTES); Pedersen 16044 (CTES, G); Quarín 212 (CTES, LIL); Quarín et Schinini 1068 (CTES); Quarín et al. 2603 (CTES); Ramalho Campelo et Costa Silva 1846 (CTES); Revilla 41 A (CTES); Schinini 5710 (CTES, FCQ); Schinini 5862 (CTES, G); Schinini 8161 (CTES); Schinini 21053 (CTES, JUA); Schinini 23144 (CTES, G, JUA); Schinini et Carnevali 23323 (CTES, JUA); Schinini et Bordas 25141 (CTES); Schinini et Vanni 25977 (CTES, G); Schinini 27542 (CTES); Schinini et al. 27708 (CTES); Schinini et al. 27871 (CTES); Schinini et Caballero Marmorì 29947 (CTES); Schinini et Caballero Marmorì 30225 (CTES, G); Schulz 2914 (CTES, SI); Schulz 6333 (CTES, JUA); Schulz 11741 (CTES); Smith 2195 (CTES); Sparre et Vervoorst 1018 (CTES); Sparre et Vervoorst 1652 (CTES); Schwarz 4046 (CTES); Schwarz 4336 (CTES); Schwarz 7088 (CTES); Schwarz 11739 (CTES); Tressens et al. 5189 (CTES, JUA, SI); Vanni et al. 1587 (CTES, LIL); Soria 1526 (FCQ); Mereles et al. 391 (FCQ, G); Mereles et al. 395 (FCQ); Mereles 1122 (FCQ); Mereles 3686 (FCQ); Mereles 3877 (FCQ); Mereles 4399 (FCQ); Zardini 7968 (b) (FCQ); Zardini et Velásquez 8944 (FCQ); Zardini et Velásquez 10755 (FCQ); Zardini et Velásquez 26702 (FCQ, GENT); Zardini et Velásquez 27120 (FCQ); Zardini et Velásquez 27205 (FCQ); Zardini et Velásquez 27332 (FCQ); Balansa 458 (G, K, P); Ekman 1271 (G); Fiebrig 418 b (G); Fiebrig 730 (G); Fiebrig 4728a (G); Garvizu et Fuentes. 387 (G); Hahn 2073 (G, PY); Hassler 2407 (G); Lossau 260 (G); Lossau 268 (G); Mamaní et al. 1400 (G); Mereles 2360 (G); Pittier et Tonduz 8393 (G); Piittier et Tonduz 8524 (G); Ritter 3121 (G); Rojas 169 (G); Schunke 2697 (G); Schunke 4540 (G); Solomon et al. 6868 (G, PY); Steinbach 5230 (G); Stern et al. 321 (G); Tonduz 8529 (G); Tonduz 14617 (G); Alves et al. 2295 (GENT); Beck et al. 372 (GENT); Beck 13192 (GENT, JUA, LPB); Chonono et Saavedra 257 (GENT, LPB); Focke 1220 (GENT); Gottsberger et Posey 43-22183 (GENT); Guareco 277 (GENT); Guillén et Choré 1525 (GENT); Guillén et Choré 3121 (GENT); Jardim et al. 173 (GENT); Luceño 16 (GENT); Schessl 315/1-3 (GENT); Schessl 268/1-6 (GENT); Schessl et Gottsberger 3035 (GENT); Solomon 17158 (GENT); Zardini et Velásquez 20505 (GENT); Zardini et Aquino 30195 (GENT, SI); Zardini et Aquino 31652 (GENT); Zardini et Guerrero 33763 (GENT); Zardini et Guerrero 41737 (GENT); Ahumada 6336 (JUA); Ahumada 6339 (JUA); Ahumada 6344 (JUA); Ahumada et al. 6659 (JUA); Ahumada et al. 6670 (JUA); Ahumada et al. 7384 (JUA); Ahumada et al. 7673 (JUA); Ahumada et al. 7772 (JUA); Honfi 258 (JUA, MNES); Múlgura et al. 3048 (JUA, SI); Seijo et al. 580 (JUA, MNES); André 494 (K); Baur 320 (K); Burchell 9938 (K); da Silva et al. 2917 (K); Fiebrig 418 (K); Glaziou 1424 (K); Glaziou 14373 (K); Guaglianone et al. 417 (K, SI); Martius s.n. (K); Pedersen 7548 (K, P); Sagot 627 (K); Salzmänn s.n. (K, P); Sellow s.n. (K); Spruce s.n. (K); Stannard 122 (K); Woolston 463 (K); Villalba s.n. (LIL); Hatschbach 24325 (LP); Hatschbach 24170 (LP); La Plata 12857 (LP); Schwuabe 704 (LP); Beck 3266 (LPB); Chonono et Saavedra 124 (LPB); Luetzelburg 15604 (M); Martius s.n. (M); Ex herbario Schwargrichen 318 (M); Swartz s.n. (M); Debeaux 72 (P); Eggers 6596 (P); Ledru s.n. (P); Leprieur s.n. (P); Mandon 96 (P); Raynal 15846 (P); Raynal 18275 (P); Riedel s.n. (P); Rodríguez 1560 (P); Rodríguez 2850 bis (P); sin coleccionista s.n. (P); Hahn et al. 1062 (PY); Hahn 2336 (PY); Soria 5497 (PY); Zardini et Velásquez 10387 (PY); Zardini et park guard 11798 (PY); Buchtein 1236 (SI); Filgueiras et Zuloaga 2244 (SI); Guaglianone et Múlgura 2117 (SI); Jiménez 52 (SI); Mereles 963 (SI); Meyer 255 (SI); Meyer 448 (SI); Morrone et Pensiero 321 (SI); Riedel 909 (SI); Smith et al. 6328 (SI); Tur et Guaglianone 2017 (SI); Zardini et Guerrero 35340 (SI); Zardini et Guerrero 37771 (SI); Zuloaga et al. 2244 (SI).
- Scleria melanomphala* Kunth: Ekman 1303 (B, G); Hassler 8889 (BM, G, K, P); Hassler 10144 (BM, G, K, P); Fiebrig 6298 a (G, SI); Callejas 7048 (GENT); Irwin et al. 16470 (GENT); Sneidern 1342 (G); Woolston 1104 (K, SI); Anderson 9554 (LIL); Hatschbach 34223 (LP); Guaglianone et al. 843 (SI).
- Scleria reticularis* Michx.: Ekman 11952 (B); Howard 9933 (B); Mass et al. 7362 (CTES); Pedersen 2611 (CTES); Quarín 471 (CTES); Steinbach 5425 (G); Ule 8065 (G); Ahumada et al. 9457 (JUA); Rambo 46182 (LIL); Sloughs, Umbach 4604 (LIL); Tracy 7127 (LIL); Sigle 19 (LPB); Bruderreck 241 (LPB); Assene 2686 (P); Assene 8434 (P); Feuillet 990 (P); Biltomore Herb. 3287a (SI); Black et al. 57-19758 (SI); Black 50-9989 (SI); Brevard 6038 (SI); Umbach 250 (SI).
- Scleria scabra* Willd.: Brade 9057 (B); Buchtein 330 (B); Ekman 17858 (B); Ekman 18063 (B); Spruce s.n. (BM,

G, K); Schinini et Dematteis 33855 (CTES, JUA); Araujo et al. 1232 (G); Hatschbach 31900 (G); Hatschbach et al. 64884 (G); Hatschbach et al. 69016 (G); Ramella 2757 (G); Beck 18598 (GENT, JUA, LPB); Guillén et Centurión 874 (GENT); Luceño et al. 282 (GENT); Arbo et al. 5642 (K); Burchell 7013 (K); Hunt 5655 (K); Wood et Goyder 15383 (K); Loeffgren 1223 (P); Huber 2135 (SI).

Scleria secans (L.) Urb.: Buchtein 329 (B, P); Ekman 2801 (B); Ekman 3878 (B); Ekman 11495 (B); Jörgensen 3585 (B, BA, MVM, SI); Jürgens 162 (B); Piruibe, Loeffgren 9235 (B); Swallen 3135 (B); Schwacke 123 (B); Perez Moreau 48166 (BA, CTES); Balansa 3027 (BAF); Marín et Jiménez GM293 (BM); Spruce s.n. (BM, K); Williams 771 (BM); Husnot s.n. (BR); Alvim 270 (CTES); Eskuche 425 (CTES, SI); Gentry et Revilla 16197 (CTES); Hatschbach 25791 (CTES); Nee 8987 (CTES); Ratter et al. 6363 (CTES); Revilla 63 (CTES); Schinini 4322 (CTES, FCQ, LIL); Schinini et Bordas 20357 (CTES); Schinini et al. 21926 (CTES, JUA); Schinini 23126 (CTES, G); Schinini 23987 (CTES, G); Schinini et Caballero Marmorì 27022 (CTES); Mereles 1124 (FCQ); Zardini 6724 (FCQ); Zardini 7433 (FCQ); Chodat 267 (G); Chodat 291 (G); Hahn 1740 (G, PY); L' Herminier s.n. (G); Salzmänn s.n. (G); Schunke 3716 (G); Sellow s.n. (G); Steinbach 5308 (G, MVM); Webster et Wilson 5028 (G); Weigelt s.n. (G); Killeen et al. 4802 (GENT); Beck et Foster 13948 (GENT, JUA, LPB); Zardini et Velásquez 15759 (GENT, PY); Zardini et Telleria 28387 (GENT); Ahumada 6337 (JUA); Ahumada 6342 (JUA); Ahumada et al. 6669 (JUA); Ahumada et al. 7651 (JUA); Ahumada et al. 7778 (JUA); Guaglianone et al. 3006 (JUA, SI); Burchell 1844 (K); Burchell 9273 (K, P); Hostman 837 (K); Lanjouw et Lindeman 930 (K); Mueller s.n. (K); Noblick 1808 (K); Sagot 626 (K); Salzmänn s.n. (K); Helme 432 (LPB); Gröger et al. 1334 (M); Martius s.n. (M); Pohl s.n. (M); Swartz s.n. (M); Leblond s.n. (P); Ledru 788 (P); Salzmänn s.n. (P); Smith et Klein 7977 (P, SI); Zardini 7269 (PY, SI); Zardini 12609 (PY); Beck 7339 (SI); Burkart 15346 (SI); Guaglianone et al. 1076 (SI); Guaglianone et Múlgura 2168 (SI); Hatschbach 2511 (SI); Klein 2643 (SI); Klein et al. 5912 (SI); López et Conradt 203 (SI); Martinelli et al. 11046 (SI); Múlgura et al. 2806 (SI); Reitz 2269 (SI); Reitz et Klein 2292 (SI); Reitz et Klein 3794 (SI); Reitz et Klein 9191 (SI); Rojas 5256 (SI); Scolnik 1180 (SI); Smith et Klein 7572 (SI); Traill s.n. Santos et al. 1469 (SI).

Scleria sellowiana Kunth: Ekman 1282 (B, G); Herter 611a (B); Jürgens 38 (B); Lombardo 3563 (B); Osten 6572 (B, LIL); Osten 6932 (B, BA, LIL); Rambo 48857 (B); Hauman 33279 (BA); Parodi 12377 (BAA, SI); Pedersen 1881 (BR, CTES, LP, P); Pedersen 10013 (BR, CTES, G); Ahumada et al. 6656 (CTES); Fernández 473 (CTES); Goldfarb s.n. CTES. 353009 (CTES); Lindeman et al. 21161 (CTES); Montes 9819 (CTES, LIL); Montes 11106

(CTES, LP); Montes 12913 (CTES, LP); Montes 12949 (CTES, LP); Rambo 44237 (CTES, JUA); Rambo 49057 (CTES, SI); Schinini 16065 (CTES); Schinini et Caballero Marmorì 30163 (CTES, JUA); Schinini et al. 35.687 (CTES); Schulz 2971 (CTES, SI); Herter 4353 (G, M, SI); Beck 17863 (GENT); Ahumada et al. 6667 (JUA); Bacigalupo et al. 1060 (JUA, SI); Bacigalupo et Guaglianone 1523 (JUA, SI); Bacigalupo et Guaglianone 1526 (JUA, SI); Guaglianone et al. 787 (JUA, SI); Montes 15255 (JUA, SI); Balansa 459a (K); Castellanos 11754 (LIL, P); Jörgensen 3312 (LIL); Legrand 3612 (MVM); Osorio 225 (MVM); Rosengurt B-2768 (MVM, SI); Pérez et Aguayo 2371 (PY); Arechavaleta 4392 (SI); Barros 2429 (SI); Barros 2450 (SI); Burkart 7932 (SI); Chebataroff 4512 (SI); Gallinal et al. 4548 (SI); Klein 3716 (SI); Osten 22295 (SI); Rambo 54528 (SI); Reitz et Klein 5139 (SI); Rosengurt B-422 (LP, SI); Rosengurt B-3183 (SI); Rosengurt B-4217 (SI); Sehnem 5039 (SI); Pire 1940 (UNR).

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