

Phylogenetics, ancestral state reconstruction, and a new infrageneric classification of *Scleria* (Cyperaceae) based on three DNA markers

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Abstract The genus *Scleria* (Cyperaceae), with ca. 250 species, is placed in the monotypic tribe Sclerieae. It has a primarily pantropical distribution. Previously, infrageneric classifications have been proposed but none has been based on molecular phylogenetic evidence and most studies have treated the genus from only one geographical region. In this study, DNA portions from 101 species of *Scleria* from across its distributional range and all infrageneric groups were extracted and amplified for three molecular markers: the coding chloroplast marker *ndhF*, the chloroplast intron *rps16* and the nuclear ribosomal region ITS. Phylogenetic hypotheses were constructed using Bayesian inference and maximum likelihood approaches. Additionally, ancestral states of four morphological characters were reconstructed at important nodes using the program BayesTraits. A new infrageneric classification based on molecular evidence and supported by morphology is presented. *Scleria* is confirmed as monophyletic and sister to tribe Bisboeckelereae. A subdivision of *Scleria* into four subgenera (*S.* subg. *Browniae*, *S.* subg. *Hypoporum*, *S.* subg. *Scleria*, *S.* subg. *Trachylomia*) is supported by our results. In this paper, twelve major clades are recovered within *Scleria* subg. *Scleria*. Clear morphological diagnostic features match these clades. Ancestral state reconstruction indicates that androgynous spikelets, a zoniform hypogynium, a paniculate inflorescence with staminate and subandrogynous spikelets, and normal linear leaves are ancestral in *Scleria*. Androgynous spikelets are found in the three first-branching subgenera, while in *S.* subg. *Scleria* an evolutionary shift towards subandrogynous and strictly unisexual spikelets is noted. Hypogynia are generally well developed with the exception of *S.* subg. *Hypoporum*, where the hypogynium is reduced or even lost. Inflorescences in *Scleria* vary from short, densely paniculate and pyramidal to subcapitate, only in *S.* subg. *Hypoporum* a glomerate-spicate inflorescence is found. The pseudopremorse leaf habit arose only once within *S.* subg. *Scleria*. *Scleria* sect. *Scleria* shows a reversal to normal leaf tips.

Keywords ancestral states; BayesTraits; Cyperoideae; molecular phylogeny; *Scleria*; Sclerieae; sedge family

Supplementary Material Electronic Supplement (Figs. S1–S9; Tables S1, S2; Appendix S1) and DNA sequence alignment are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

Scleria P.J.Bergius (1765), commonly known as nut rushes or razor grasses, is with its ca. 250 species one of the major genera of the sedge family (Cyperaceae). The genus is placed in the monotypic tribe Sclerieae and has a primarily pantropical distribution, locally extending into warm-temperate regions. Approximately 113 species are known from the Americas, 97 from Africa and 59 from Asia and Oceania (Govaerts & al., 2015). Throughout their range, species of *Scleria* occur in open places in forest, but they are more commonly collected from areas undergoing secondary succession, grasslands, road- and riversides, swamps, etc. Although *Scleria* does occur on fertile soils, they have a preference for moist, poor soils, and they are more frequently found in humid and warm climates than

in drier, more temperate climates (Camelbeke, 2001). Most species grow in the tropical zone, below 1600 m. Some species have considerable local ecological or economic significance (Simpson & Inglis, 2001).

Goetghebeur (1986, 1998) proposed four subfamilies for the Cyperaceae, i.e., Caricoideae, Cyperoideae, Mapanioideae and Sclerioideae. His subfamily Sclerioideae comprised four closely related tribes: Bisboeckelereae, Cryptangieae, Sclerieae and Trilepideae. However, Bruhl (1995) only recognised two subfamilies, Cyperoideae and Caricoideae, with tribe Sclerieae included in the latter. Recent molecular studies (e.g., Muasya & al., 2009; Hinchliff & Roalson, 2013; Jung & Choi, 2013) agreed upon two subfamilies (Mapanioideae, Cyperoideae), with the Sclerieae included in subfamily Cyperoideae where they formed a separate clade together with tribe Bisboeckelereae.

Although most authors recognise a distinct tribe Sclerieae based on morphological characters, the classification and exact circumscription of Sclerieae are controversial. Over the years, several authors have included one or more tribes in Sclerieae: e.g., Bisboeckelerae (e.g., Fenzl, 1836; Chermezon, 1937; Koyama, 1969; Hooper, 1973; Kern, 1974), Bisboeckelerae and Cryptangieae (e.g., Nees, 1834, 1842), Bisboeckelerae, Cryptangieae and Trilepideae (e.g., Clarke, 1908; Koyama, 1961), or even more tribes (e.g., Kunth, 1837; Steudel, 1855).

One of the first infrageneric classifications of tribe Sclerieae was proposed by Nees (1834, 1842), who placed the species in 18 separate genera (Fig. 1). Eleven of those genera are currently included in the genus *Scleria* and the other seven are part of different tribes. However, his genus *Scleria* did not include one of the two species from the original generic description by Bergius (1765). The recent lectotypification of *Scleria* by Camelbeke & al. (2001) therefore renders Nees's *Omoscleria* congeneric with *Scleria*. Only few authors followed Nees's classification (e.g., Fenzl, 1836; Liebmann, 1850; Walpers, 1852). Most agreed upon a broadly circumscribed *Scleria* including the genera raised by Nees (1834, 1842). However, some of the generic names published by Nees (1834, 1842) are still used at a subgeneric or sectional level (Fig. 1). Later on, Clarke (1908) structured the genus by creating seven subgenera and seven sections (Fig. 1). His classification was almost entirely based on nutlet characters plus a restricted number of morphological characters. In a study of the North, Central and South American species of *Scleria*, Core (1936) largely followed Clarke's (1908) classification. In Core's (1936) treatment, *Scleria* was divided in five sections (Fig. 1). Kern (1961), dissatisfied with most previous classifications, arranged the Asian species of *Scleria* into nine sections, some based on Clarke's (1908) classification, others completely new (Fig. 1). Two of his sections, *S. sect. Diplacrum* (R.Br.) J.Kern and *S. sect. Sphaeropus* (Boeckeler) J.Kern, are now included in the genus *Diplacrum* R.Br. from tribe Bisboeckelerae. Examples of other classifications include those of Rafinesque (1830; three sections), Bentham for Australian *Scleria* (1878; six series), Nelmes for African *Scleria* (1955, 1956; four sections), Robinson for African *Scleria* (1966; two subgenera), Haines & Lye for East African *Scleria* (1983; six sections), Camelbeke for Central and South American species (2001; five sections), and several more. All these classifications, except those of Nees (1834), Steudel (1855) and Clarke (1908), were published in regional floristic accounts. They agreed on some sections, but a detailed classification of the whole genus was still lacking. In his provisional account of the genus *Scleria* for the *Flora Zambesiaca*, Robinson (1966: 487) stated: "Indeed, a world-wide revision of the genus is long overdue."

In recent years, most authors have agreed upon two subgenera: *S. subg. Hypoporum* (Nees) C.B. Clarke and *S. subg. Scleria* (e.g., Camelbeke, 2001; Ahumada & Vegetti, 2009). The latter is often divided into several sections, depending on the region where the author was working (e.g., Core, 1936; Kern, 1961; Camelbeke, 2001). An overview of the most important past and current views on Sclerieae and the genus *Scleria* is shown in Fig. 1. In Camelbeke & al. (2001) a complete list of

generic and infrageneric names within *Scleria* was published together with their typification.

Species of *Scleria* constitute several growing forms going from small, slender, narrow-leaved annual herbs with numerous fibrous roots to medium-sized or tall, more or less robust, rhizomatous perennial herbs. Less often they are caespitose, and sometimes conspicuously broad-leaved (Camelbeke, 2001). The smallest *Scleria* species are found among the annuals, e.g., mature specimens of *S. pulchella* Pilg. only 6 cm tall have been observed (K. Bauters, pers. obs.). The tallest species of *Scleria* have a climbing habit, with a record for *Scleria tenacissima* (Nees) Steud. of 14 m (Camelbeke, 2001). The leaves are arranged in three ranks along the culm. Sometimes, normally developed long internodes alternate with much shortened ones, resulting in the middle leaves being arranged in pseudowhorls. The pseudowhorled condition is only encountered in some Asian and Australian species. The apex of the leaf is generally acute, but in several species of *S. sect. Ophryoscleria* (Nees) C.B. Clarke and *S. sect. Schizolepis* (Schrad. ex Nees) C.B. Clarke a broad 5-nerved proximal end of the blade is rather abruptly narrowing into a 3-nerved distal part, a leaf form described as pseudopremorse (Chermezon, 1926). The inflorescence is paniculate (Fig. 2O). However, due to differences in the degree of development many variations on the paniculate theme do occur. Camelbeke (2001) recognised eight different inflorescence types, all derived from a paniculate progenitor. The most specialised inflorescence type is found in *S. subg. Hypoporum* with an inflorescence consisting of a linear spike of distant, sessile spikelet clusters subtended by glume-like or short foliate bracts (Fig. 2L, M). The flowers are always unisexual and arranged in staminate, pistillate or (sub)androgynous spikelets. In staminate spikelets, the lower empty glumes are distichously placed, while the higher fertile ones are spirally arranged (Fig. 2D, E). The strictly pistillate spikelets have all their glumes arranged distichously with one fertile pistillate flower in the highest glume (Fig. 2E). The androgynous spikelet has a combination of both (Fig. 2A, B): a lower part with distichously arranged empty glumes and one pistillate flower, and a top part of many, spirally arranged glumes with staminate flowers. The subandrogynous condition is similar to the androgynous one. However, only the female part is well developed, while the male part is limited to one or two empty glumes (Fig. 2C). Species of *Scleria* have unilocular, tricarpetate, indehiscent, one-seeded dry fruits (Camelbeke, 2001). The nutlet always has a hard, bony pericarp. At the base of the mature nutlet a structure, the hypogynium, is attached. Kukkonen (1967) interpreted this hypogynium as vestigial perigonal bristles or staminate organs. Other authors have stated that it is a greatly modified perianth (e.g., Core, 1936; Blaser, 1941) or a receptacle (Blaser, 1941). Franklin Hennessy (1985) considered the hypogynium as a new modification of the stipe of the nutlet and not a vestigial structure. However, no explanation seems satisfactory at this point. All species of *S. subg. Scleria* have a hypogynium. This hypogynium more or less develops into a conspicuously three-lobed structure (Fig. 2H–K), with the lobes placed equidistantly around the base of the ovary, each opposite a fruit rib (Camelbeke, 2001). Some species, e.g., in

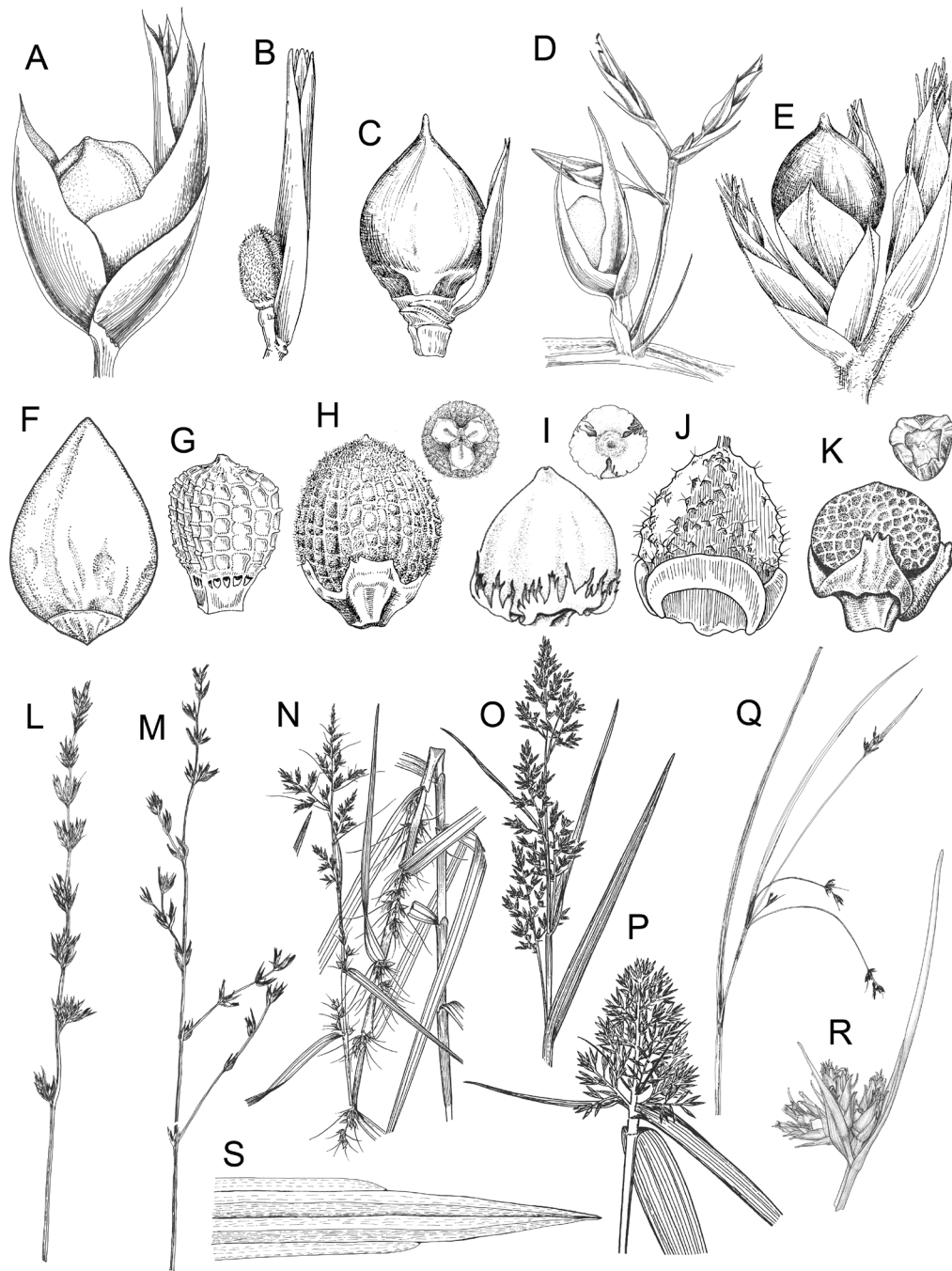


Fig. 2. **A**, Androgynous spikelet of *Scleria rehmannii* (Bauters 2013-097, GENT); **B**, Androgynous spikelet of *S. fulvipilosa* with lower glumes removed (Robinson 4712, K); **C**, Subandrogynous spikelet of *S. porphyrocarpa* with lower glumes removed (Robinson 3849, BR); **D**, Staminate and pistillate spikelet of *S. vaginata* (Ancush 1060, MO); **E**, Staminate and subandrogynous spikelet of *S. porphyrocarpa* (Robinson 3849, BR); **F**, Lateral view of nutlet of *S. corymbosa* with zoniform hypogynium; **G**, Nutlet with hypoporum type of hypogynium of *S. zambesica* (Robinson 6578, MO); **H**, Lateral and basal view of nutlet with trilobed hypogynium of *S. patula* (Robinson 3684, K); **I**, Lateral and basal view of nutlet with lacinate hypogynium of *S. rubrostriata* (Lucas & al. 859, K); **J**, Nutlet of *S. triquetra* with hypogynium with recurved margins (de Granville & al. 9777, US); **K**, Lateral and basal view of *S. scrobiculata* with trilobed hypogynium with recurved margins; **L**, *S. dregeana*: Hypoporum s.str. inflorescence type (Bauters 2015-098, GENT); **M**, *S. rehmannii*: Hypoporum s.l. (branched) inflorescence type (Bauters 2015-097, GENT); **N**, *S. bracteata*: Bracteata inflorescence type; **O**, *S. camatrensis*: Paniculate inflorescence with staminate and subandrogynous spikelets; **P**, *S. cyperina*: Short, densely paniculate inflorescence type; **Q**, *S. unguiculata*: Truncated inflorescence type (Bauters 2015-019, GENT); **R**, *S. baldwinii*: Subcapitate inflorescence type; **S**, *S. depressa*: pseudopremorse leaf (Botanical Garden Ghent University). — A, D, L, M, Q & S drawn by Judit Fehér; B, C, E, G, H (drawn by Mary Grierson) & I (drawn by Margaret Tebbs) reproduced with permission of the Board of Trustees, Royal Botanic Gardens, Kew; F & K reproduced from Kern (1961) with permission of Naturalis Biodiversity Centre; J drawn by Cathy Pasquale, Department of Botany, Smithsonian Institution, reproduced with permission; images N–P reproduced with permission of Missouri Botanical Garden Press; R drawn by Juliet Beentje (Royal Botanic Gardens, Kew).

S. sect. Corymbosae, have an unlobed zoniform hypogynium (Fig. 2F). In *S. subg. Hypoporum* this hypogynium is reduced or even absent (Fig. 2G). According to Franklin Hennessey (1985) the hypogynium is absent in *S. subg. Hypoporum*, while others (e.g., Camelbeke, 2001) saw it as a strongly reduced or obsolete structure. The hypogynium is supported by an outer structure, the cupule, which, similar to the hypogynium, generally develops into a more or less three-lobed organ, with the lobes of the hypogynium and cupule always opposite (Camelbeke, 2001). The hypogynium and the cupule are developing as one structure without a marked abscission zone. However, at maturity a marked abscission zone is formed separating the cupule and the hypogynium (Camelbeke, 2001; K. Bauters, unpub.). While in many *Scleria* species the cupule then appears to push the glumes aside to facilitate the dispersal of the nutlets by swelling, this has not been observed in *S. subg. Hypoporum*.

No previous attempt has been made to reconstruct a molecular phylogeny of *Scleria*. However, selected *Scleria* species have been included in the sampling of larger Cyperaceae phylogenies. Most of these studies show *Scleria* to be the sister taxon of tribe Bisboeckelereae (Muasya & al., 1998; Hirahara & al., 2007; Hinchliff & al., 2010; Jung & Choi, 2013; Viljoen & al., 2013), while other studies point towards Sclerieae nested in a paraphyletic Bisboeckelereae (Muasya & al., 2009; Hinchliff & Roalson, 2013). In Hinchliff & Roalson (2013), 12 species of *Scleria* were included, but no morphologically recognisable groupings were retrieved.

In this paper, we present a molecular phylogenetic study of *Scleria* based on sequence data from the nuclear ribosomal internal transcribed spacer region (ITS), the coding *ndhF* chloroplast

gene and the chloroplast *rps16* intron. The objectives of this study are: (1) to construct a molecular phylogeny of *Scleria*, and (2) to reconstruct evolution of taxonomically important characters. By addressing these aims we (1) obtain insights in the evolution of *Scleria* species, and (2) have a sound basis for establishing a new infrageneric classification for the whole genus.

■ MATERIALS AND METHODS

Taxon sampling.— Sampling for this study consists of 118 samples, representing 101 species of *Scleria* and 4 outgroup taxa (Appendix 1). Taxon sampling was based on Clarke (1908), Core (1936), Nelmes (1955, 1956), Kern (1961), Robinson (1966) and Camelbeke & al. (2001) to cover all the geographical regions and to ensure all described subgenera and sections were represented. The sampling contained 9 samples from North America, 7 from Central America, 32 from South America, 39 from Africa, 7 from Madagascar, 14 from Asia and 10 from of Australia and Oceania. For all known subgenera, sections and lower ranks, a specimen representing the type was included following Camelbeke & al. (2001). Since a complete and thorough classification of *Scleria* was not available, we sampled as widely as possible following the literature cited above. Furthermore, taxa were sampled to span as much morphological variation as possible, including taxa that have distinctive and unusual morphologies (e.g., *S. bequaertii* De Wild. and *S. bracteata* Cav.). To ensure complete coverage of the morphological variation, 2997 specimens representing 239 species were studied (Electr. Suppl.: Appendix S1).

Table 1. Primers used in this study.

Marker / Primer name	Primer sequence (5'–3')	Reference
<i>ITS</i>		
ITS-L	TCGTAACAAGGTTTCCGTAGGTG	Hsiao & al. (1994)
ITS-A	GGAAGGAGAAGTCGTAACAAGG	Blattner & al. (1999)
ITSsef17	ACGAATTCATGGTCCGGTGAAGTGT	Sun & al. (1994)
ITS-D	CTCTCGGCAACGGATATCTCG	Blattner & al. (1999)
ITS-C	GCAATTCACACCACGTATCGY	modified from Blattner & al. (1999)
ITS4	TCCTCCGCTTATTGATATGC	White & al. (1990)
<i>ndhF</i>		
ndhF-A	TATGGTTACCTGATGCCATGGA	Hinchliff & al. 2010
indhFIF2	GCBTGTTCCTGGTCTAAAGATG	This study
ndhhFIR3	GAGRRAATAGCATAGTATTRTC	This study
ndhFiF3	GAYAATACTATGCTATTYYCTC	This study
ndhF-D1	CTATRTAACCRGATTATATGACCAA	Hinchliff & al. 2010
<i>rps16</i>		
rps16F_ox	GTGGTAGAAAGCAACGTGCGACTT	Oxelmann & al. 1997
rps16R_ox	TCGGGATCGAACATCAATTGCAAC	Oxelmann & al. 1997
rps16F_in1	GTRGAACGGGAGTGAATTYTT	This study
rps16R_in2	CTTCGGGGACCTTAATCCTT	This study

Appendix 1 lists all taxa included with voucher information, geographic origin and GenBank accession numbers. Most of the samples for DNA extraction were collected from herbarium specimens in GENT and MO. Silica gel-dried samples from Australia, Thailand and the U.S.A., and specimens from the Ghent University Botanical Garden were also used. Where possible, leaf material was sampled. All specimens were newly sampled for this study. As outgroup, representatives of the four genera of the Bisboeckelerae were chosen (*Becquerelia* Brongn., *Bisboeckelera* Kuntze, *Calyptrocarya* Nees, *Diplacrum*).

DNA extraction, amplification, and sequencing. — After tissue homogenisation (Mixer Mill, Retsch, Haan, Germany), total DNA was extracted from 5–20 mg of dried material using innuPREP Plant DNA Kit (Analytik Jena, Jena, Germany) following the manufacturer's protocol. Amplifications were performed in volumes of 25 µl containing a GeneAmp 10× PCR buffer with 100 mM Tris-HCl, pH 8.3, 500 mM MgCl₂, 0.01% (w/v) gelatin (Applied Biosystems, Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.), dNTP solution of 10 mM (5-prime), ampliTaq DNA polymerase (Lifetechnologies, Carlsbad, California, U.S.A.) with 5 U/µl, primer solution with a concentration of 10 µM, 1 µl bovine serum albumin (BSA) and 1 µl of unquantified DNA. For this study, ten primers from previous studies were used and five new internal primers were developed (see Table 1 for all primers used). The following primer combinations were used initially: ITS-L & ITS4; *ndhF*-A & *ndhF*-D1; *rps16F_ox* & *rps16R_ox* (Table 1). Where necessary, internal primers were constructed (Table 1). For ITS, two additional forward primers were used (ITS-A & ITSsef17) when first attempts failed to result in usable PCR products. Initial denaturation was set to 3:00 min at 96°C. After this polymerase chain reaction (PCR) was performed for 30 cycles (40 for *ndhF*) of denaturation (0:30 min at 95°C [ITS], 0:45 min at 95° [*rps16*, *ndhF*]), primer annealing (0:30 min at 52° [ITS], 0:45 min at 95° [*rps16*, *ndhF*]), and primer extension (1:30 min at 72° [ITS], 1:00 min at 72° [*rps16*, *ndhF*]). Finally, an elongation period of 7 min at 72°C ended the reaction. The PCR products were electrophoresed on 1% agarose gels in 1× Tris-acetate-EDTA (TAE) buffer (pH 8.0) and stained with ethidium bromide to confirm a single product. Afterwards, the cleaned PCR products were sent to Macrogen Europe (Amsterdam, Netherlands) for sequencing on ABI3730XL machines using the same primers as in the PCR reactions.

Sequence alignment and phylogenetic reconstruction.

— Sequences were read into Sequencher v.5.0.1 (Gene Codes Corporation, Ann Arbor, Michigan, U.S.A.) and sequence ends were trimmed automatically. After this, contigs were constructed and loaded into PhyDE v.0.9971 (Müller & al., 2010). Sequences then were aligned using MAFFT v.7.215 (Katoh & al., 2002, 2009) with “maxiterate” and “tree rebuilding number” set to 100 (long run), afterwards, alignments were checked manually. For *ndhF*, sequences were also converted into amino acids (AA) using PhyDE to verify that no stop-codons occurred in one of the sequences. Insertions and deletions (indels) were coded following the simple indel coding scheme of Simmons & Ochoterena (2000) available in SeqState v.1.4.1 (Müller, 2005).

Tree topologies were searched for using maximum likelihood (ML) and Bayesian inference (BI) methods. These analyses were performed on the different datasets: (1) the single-marker alignments, (2) a matrix with combined chloroplast markers without ITS and (3) a concatenated matrix with all three markers included. Two taxa (three specimens) were removed (SC121 *S. williamsii*, SC135 *S. gaertneri*, SC271 *S. gaertneri*) from the concatenated matrix due to uncertain position in the single-locus analyses following suggestions by Pirie (2015). Before analysing the data, appropriate models were chosen using jModelTest v.2.1.6 (Darriba & al., 2012), with the Bayesian information criterion selected. jModelTest selected GTR+I+G for ITS and GTR+G for *rps16* as best fitting model. For *ndhF*, the nucleotide alignment was loaded in Partitionfinder v.1.1.1. (Lanfear & al., 2012). The best partition scheme grouped first and second codon positions of *ndhF* into one partition with GTR+G as best model; the third codon of *ndhF* was in a second partition with GTR+I+G as best model. ML analyses for all datasets were carried out in RAxML v.7.2.8 (Stamatakis, 2006), setting partitions (see below) for each region. The model was set to GTRGAMMA and the bootstrap analysis to 1000 replicates.

BI gene tree analyses were conducted on individual matrices using MrBayes v.3.2 (Huelsenbeck & Ronquist, 2003). Four runs were conducted for 50 million generations, sampling every 1000th generation. The results were reviewed in Tracer v.1.5 (Drummond & Rambaut, 2007) to check for convergence and to obtain burn-in values. The first 25% of trees were discarded as burn-in, with remaining trees used to construct a 50% majority-rule consensus tree. Trees were checked manually for incongruences. The dataset with the combined chloroplast markers was partitioned in 4 partitions: (1) codon position one and two of *ndhF*, (2) codon position three of *ndhF*, (3) *rps16* and (4) indels. The concatenated matrix was partitioned in five partitions: (1) codon position one and two of *ndhF*, (2) codon position three of *ndhF*, (3) ITS, (4) *rps16* and (5) indels. For both analyses parameters were unlinked and analysis was run for 50 million generations over four runs, sampling every 1000th generation. The first 25% of trees were discarded as burn-in, with remaining trees used to construct a 50% majority-rule consensus tree. jModelTest and MrBayes were run on CIPRES (<http://www.phylo.org/index.php/portal/>; Miller & al., 2010). Resulting trees were visualised and modified in TreeGraph2 v.2.0.52 (Stöver & Müller, 2010).

Geographical range and four morphological characters (spikelet type, hypogynium type, inflorescence type, leaf tip type) were mapped to the BI tree to illustrate positions of state modification in the tree. The geographical range was obtained from Govaerts & al. (2015).

Ancestral state reconstruction. — Four discrete morphological characters were chosen for ancestral state reconstruction:

(1) spikelet type (Camelbeke, 2001)—Androgynous type (Fig. 2A, B): only bisexual spikelets; Subandrogynous type (Fig. 2C, E): staminate and subandrogynous spikelets; Unisexual type (Fig. 2D): staminate and/or pistillate spikelets; Trachylomia type (Fig. 2A–C): androgynous, subandrogynous and staminate spikelets, often occurring on the same specimen;

(2) hypogynium type (this paper)—Zoniform type (Fig. 2F): annular unlobed hypogynium; Hypoporum type (Fig. 2G): hypogynium strongly reduced or absent, not visible; Trilobed type (Fig. 2H): hypogynium with three distinct lobes, margins not recurved; Trilobed with recurved margin type (Fig. 2J, K): hypogynium with three distinct lobes which have a recurved margins, often connate with the lower tissue; Lacinate type (Fig. 2I): hypogynium with lobes deeply incised;

(3) inflorescence type—Hypoporum s.str. type (Fig. 2L): linear spike of distant clusters subtended by glume-like or short foliate primary bracts (Camelbeke, 2001; spiciform type of Ahumada & Vegetti, 2009); Branched Hypoporum s.l. type (Fig. 2L): linear spike of spikelet clusters which is branched (Camelbeke, 2001; paniculate with spiciform branches type of Ahumada & Vegetti, 2009); Bracteata type (Fig. 2N): staminate spikelets restricted to upper part of inflorescence, subandrogynous spikelets restricted to lower part of inflorescence (Camelbeke, 2001; Ahumada & Vegetti, 2009); Paniculate with staminate & subandrogynous spikelets type (Fig. 2O): inflorescence of a repeatedly branched main axis, each side branch repeats the structure of the main axis and is composed of spikes (or spikelets) (Camelbeke, 2001; “Fifth group” of Ahumada & Vegetti, 2009); Short densely paniculate & pyramidal type (Fig. 2P): inflorescence mostly very densely paniculate, main inflorescence axis barely visible, pyramidal, pistillate spikelets lowermost in each side branch, staminate spikelets mostly on distinct long peduncles (Hymenolytrum type of Camelbeke, 2001; “Seventh group” of Ahumada, 2009); Truncated type (Fig. 2Q): main inflorescence truncated, not developed (Ahumada, 2009); Subcapitate type (Fig. 2R): almost head-like inflorescence in pseudolateral position; and

(4) leaf tip type—Normal type; Pseudopremorse type (Fig. 2S).

These characters are of major importance in diagnosing different sections and species in *Scleria*. Character states for spikelet-, hypogynium- and leaf-tip type were chosen by studying ca. 3000 specimens (Electr. Suppl.: Appendix S1), the character states for the inflorescence types are largely based on Ahumada & Vegetti (2009) and Camelbeke (2001). All characters are binary or multistate and were analysed alike. Character states for each specimen analysed are shown in Electr. Suppl.: Table S1.

BayesTraits v.1.0 (Pagel & al., 2004; Pagel & Meade, 2006) was used to perform ancestral state reconstructions. The sampled trees from independent runs (.t-files) of the BI analysis on the concatenated matrix (see above) were loaded in Mesquite v.2.75 (Maddison & Maddison, 2011). For all four .t-files the first 12,500 trees were discarded as burn-in and 500 trees were randomly sampled out of the remaining trees and merged in a separate file, resulting in 2000 sampled trees. The outgroup was used to root the trees and was pruned afterwards. Next, 26 well-supported nodes were chosen for ancestral state reconstruction. The command lines for these 26 nodes were generated in BayesTrees v.1.3 (Meade, 2011). The 2000 sampled trees were used for analysing each character separately using the Multistate module as implemented in BayesTraits. Initially, a ML analysis was run to derive empirical priors. After setting these priors, a BI analysis was performed using a MCMC approach, 50 million

generations, sampling every 1000th generation, discarding the first 25% as burn-in. Acceptance rates were checked manually and RateDev parameters were varied to reach acceptance rate values between 20%–40% to ensure adequate mixing. Ancestral states were plotted on the concatenated BI 50% majority-rule consensus tree using pie charts in TreeGraph2.

■ RESULTS

Phylogenetic reconstruction. — The data matrices contained 111 ITS, 118 *ndhF* and 111 *rps16* sequences, all newly obtained for this study. For 107 taxa, all three gene regions were successfully sequenced, for 9 taxa two regions and for 2 taxa only one region could be obtained. The length for aligned individual gene datasets respectively were 777, 1484 and 1198 nucleotide characters for ITS, *rps16* and *ndhF*. Simple indel coding (Simmons & Ochoterena, 2000) resulted in the addition of 197, 268 and 17 binary characters, respectively. The resulting chloroplast and concatenated data matrices contained 2681 nucleotide bases and 285 indel characters and 3459 nucleotide bases and 382 indel characters respectively.

ML and BI analyses of the individual markers produced largely congruent trees (Electr. Suppl.: Figs. S1–S6). Supported nodes are defined as nodes with posterior probability (PP) values ≥ 0.90 and bootstrap (BS) values ≥ 75 . Two taxa, *Scleria gaertneri* (SC135, SC271) and *Scleria williamsii* (SC121), were recovered in *S. sect. Scleria* for *ndhF* and *rps16* but were recovered in *S. sect. Schizolepis* in the results of the ITS analyses. Because of this incongruence, they were removed from the concatenated analyses, following suggestions by Pirie (2015).

ML and BI analyses of the combined chloroplast markers produced congruent trees (Electr. Suppl.: Figs. S7, S8). Supported nodes are defined as in the single-marker gene trees. *Scleria gaertneri* (SC135, SC271) and *S. williamsii* (SC121) were recovered in *S. sect. Scleria* contrasting again with their position in the results of the ITS analyses.

Both ML and BI analyses for the concatenated matrix resulted in largely congruent trees with minor incongruences near the terminal taxa (Fig. 3; Electr. Suppl.: Fig. S9). These incongruences are mainly caused by the lower resolution rate of the ML analysis, resulting in some polytomies, where in the BI phylogenetic hypothesis relationships within clades are better resolved. Since the main focus of this paper is to deal with *Scleria* at sectional level, these minor incongruences could be used because they mainly were found at species level and did not influence the backbone of the *Scleria* phylogeny. Incongruences are discussed below and marked in figures (Electr. Suppl.: Figs. S1–S9).

In the results of all analyses, *Scleria* was maximally supported as monophyletic and *S. subg. Browniae* (C.B. Clarke) C.B. Clarke was sister to the three other subgenera, with *S. subg. Hypoporum* sister to both *S. subg. Trachylomia* and *S. subg. Scleria* (Figs. 3, 4). All four subgenera were monophyletic and strongly supported (PP ≥ 0.90 , BS ≥ 75). Within *S. subg. Browniae*, relationships between species varied depending on which marker was analysed, but support values were generally

low within this clade. Delimitation of *S.* subg. *Hypoporum* was the same in all phylogenetic hypotheses although species relationships are sometimes unclear (e.g., *S. sobolifer*). Within *S.* subg. *Hypoporum*, the pantropical *S. lithosperma* is always found in its own clade as sister taxon to all other species of *S.* subg. *Hypoporum*. Next, a clade with *S. castanea* and *S. virgata* is retrieved in all phylogenetic hypothesis. Additionally, three more clades can be distinguished within this subgenus, all sharing some morphological characters. The all-American *S.* subg. *Trachylomia* was also recovered in all phylogenetic hypotheses with largely congruent relationships at species level. The largest subgenus, *S.* subg. *Scleria*, was further divided into 12 clades (Fig. 3). The mainly Asian *S.* sect. *Corymbosae* was sister to all other sections of this subgenus. Relationships at species level were the same in all trees except in the results of the combined chloroplast analyses where *S. corymbosa* was resolved in a polytomy with the other species of *S.* sect. *Corymbosae* and the remainder of *S.* subg. *Scleria*. A clade comprising *S.* sect. *Margaleia* and *S.* sect. *Acriulus* was found to be sister to the remaining *Scleria* species, only in the ITS BI tree (Electr. Suppl.: Fig. S2) both sections were in a polytomy with the remainder of *S.* subg. *Scleria*. Within *S.* sect. *Acriulus*, relationships between species were not well supported and *S. transvaalensis* was sometimes found in a polytomy with *S.* sect. *Margaleia* (Electr. Suppl.: Figs. S1, S2, S5). Next, a well-supported *S.* sect. *Melanomphalae* is found including only *S. melanomphala*. The split between *S.* sect. *Hymenolytrum* and other sections of *Scleria* is well supported and found in the results of all analyses. Within this section, species delimitation was unclear in the single-marker analyses, but the same sectional delimitation was recovered for all alignments. *Scleria* sect. *Foveolidia* was found to be sister to the remaining five sections. *Scleria biflora* was always recovered as sister to the other species of this section. Relationships within this section were congruent in all analyses. It occurs mainly in Africa with a few outliers in America and Asia. *Scleria* sect. *Naumannianae* was recovered in the same position in all phylogenetic hypotheses. The Asian and Australian *S.* sect. *Elatae* was well supported as sister group to the remaining four sections of *S.* subg. *Scleria*, only in both ITS trees this section was recovered in a polytomy with the remaining sections (Electr. Suppl.: Figs. S1, S2). Relationships within *S.* sect. *Elatae* were largely congruent although some polytomies occurred. An all-African-Malagasy *S.* sect. *Abortivae* was found as sister clade to the three remaining sections in the results of *ndhF*, the combined chloroplast analyses and the concatenated analyses (Electr. Suppl.: Figs. S3, S4, S7–S9). In the ITS and *rps16* trees this section was recovered in a polytomy with *S.* sect. *Schizolepis*, sect. *Scleria* and sect. *Ophryoscleria* (Electr. Suppl.: Figs. S1, S2, S5, S6). In the results of the ML analyses for ITS, *rps16*, *ndhF*, the combined chloroplast analyses and the concatenated data matrix, and in the results of the BI analyses of ITS, *ndhF*, the combined chloroplast data matrix and the concatenated data matrix, *S.* sect. *Schizolepis* and sect. *Scleria* were recovered as sister clades (Electr. Suppl.: Figs. S1–S5, S7–S9). In the BI tree for *rps16*, both sections were recovered in a polytomy with *S.* sect. *Abortivae* and sect. *Ophryoscleria* (Electr. Suppl.: Fig.

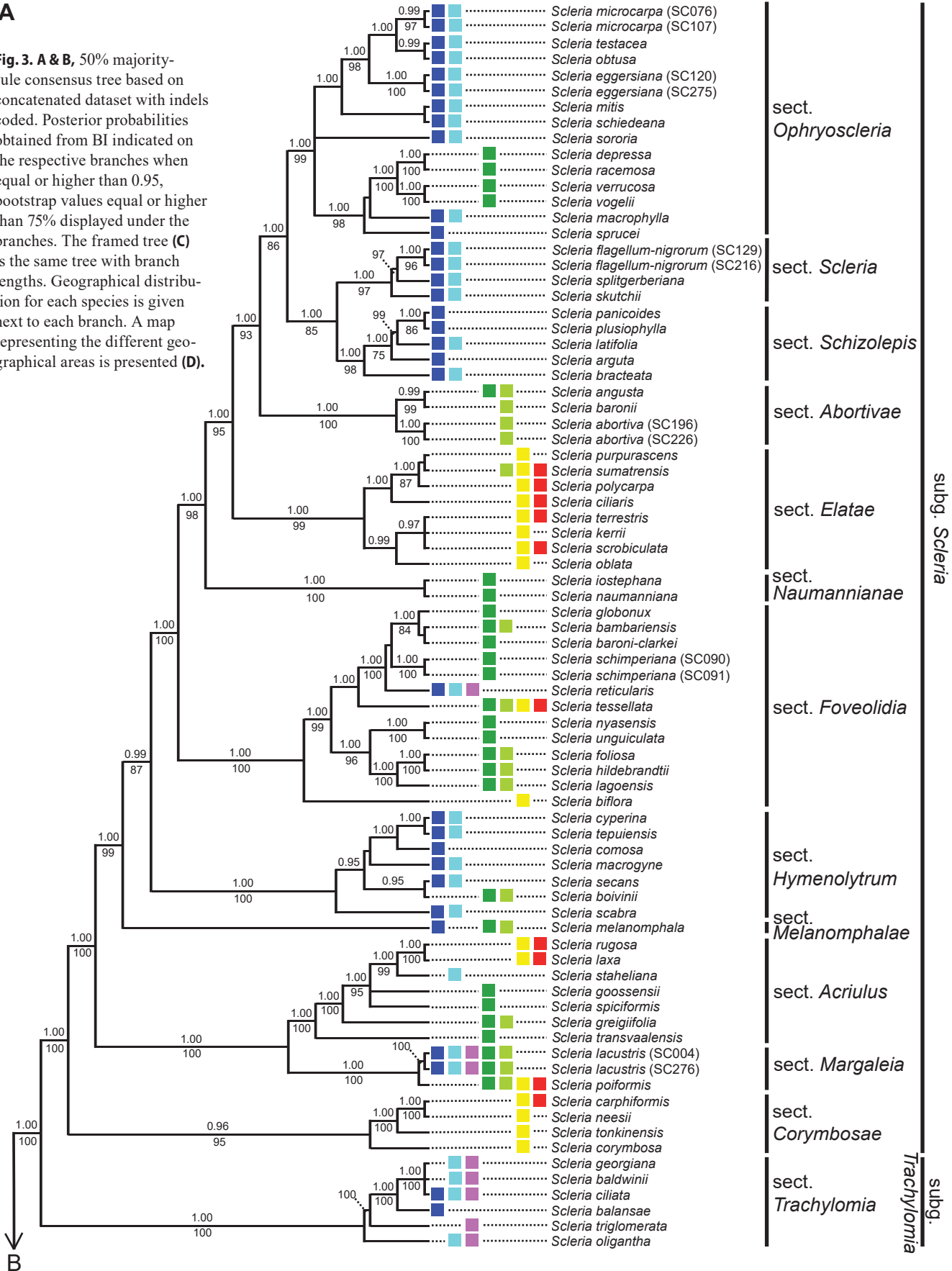
S6). The latter section, *S.* sect. *Ophryoscleria* was recovered as a supported clade in all phylogenetic hypotheses except for the ML trees of *rps16* and *ndhF* and the BI tree of *ndhF* where different clades of this section were retrieved in the polytomy with *S.* sect. *Schizolepis* and sect. *Scleria* (Electr. Suppl.: Figs. S3–S5, S7, S8). Relationships within *S.* sect. *Ophryoscleria* were largely congruent throughout all analyses. In total, four subgenera were recovered in the phylogeny with only *S.* subg. *Scleria* encompassing more than one section (Fig. 3).

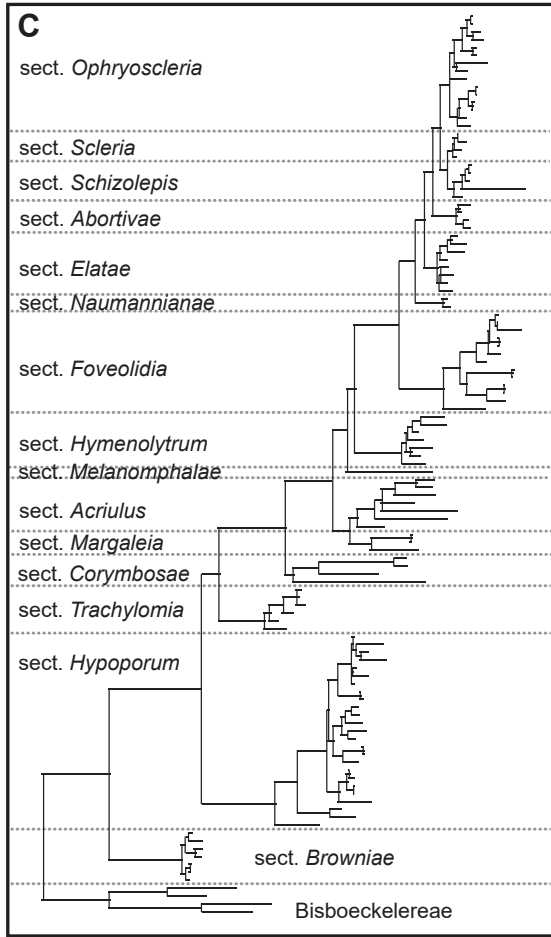
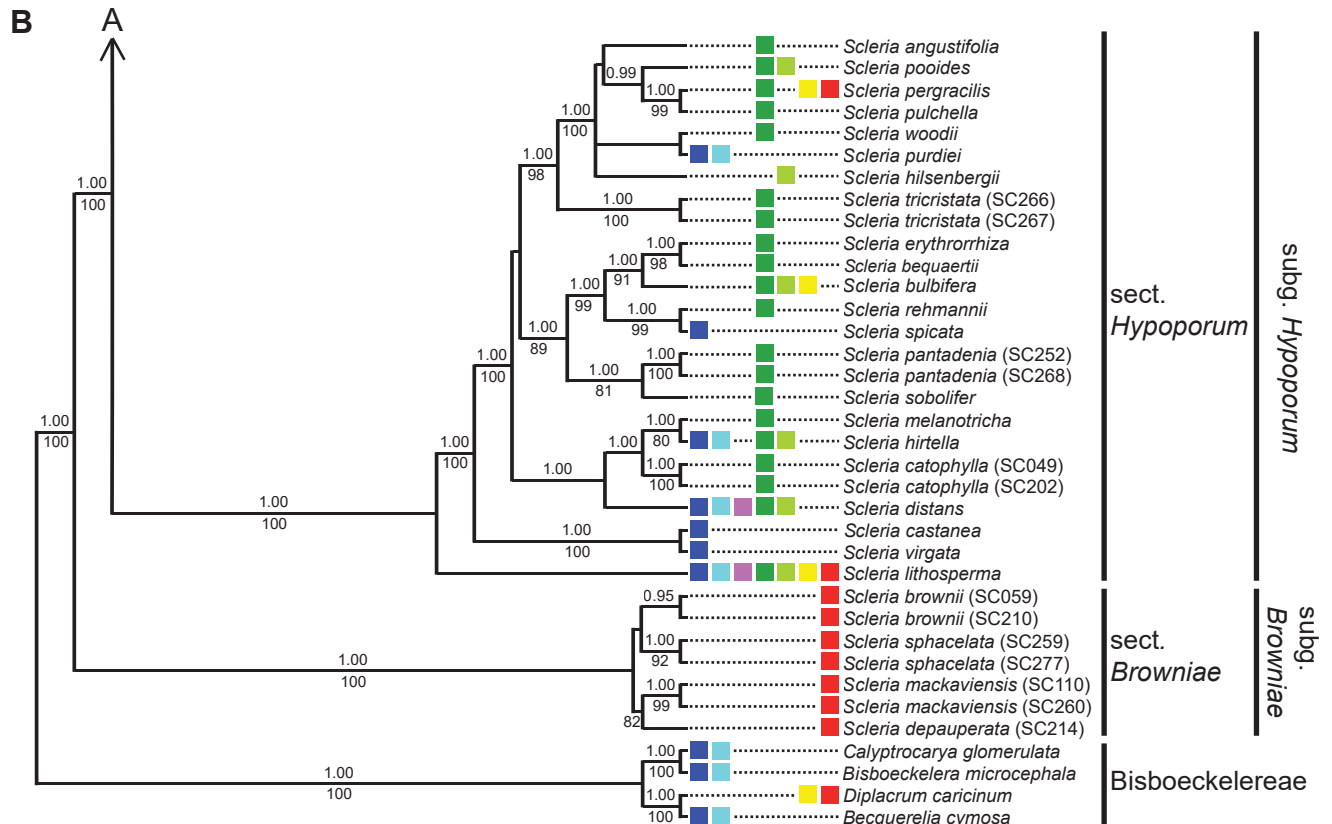
Ancestral state reconstruction. — Ancestral character state reconstruction showed that the androgynous spikelets type is most likely ancestral in *Scleria* with probabilities higher than the *Trachylomia* type (Fig. 4, node 1, 60% versus 40%). The androgynous spikelet type is mainly found in the early divergent lineages of *S.* subg. *Browniae* (Fig. 4, node 2, 98%) and *S.* subg. *Hypoporum* (Fig. 4, node 4, 93%). Species having androgynous, subandrogynous and male spikelets (*Trachylomia* type) are only found in *S.* subg. *Trachylomia* (Fig. 4, node 6, 100%). The ancestral spikelet state of *S.* subg. *Scleria* is the androgynous type (Fig. 4, node 7, 84%) evolving into the subandrogynous type for the largest part of the subgenus (Fig. 4, node 9, 92%). Unisexual spikelets evolved two times independently within *S.* subg. *Scleria*: once in *S.* sect. *Corymbosae* and another time in *S.* sect. *Hymenolytrum* (Fig. 4).

The zoniform hypogynium type (Fig. 5D–J) is ancestral in *Scleria* (Fig. 4, node 1, 71%). This zoniform hypogynium is also found in the ancestor of *S.* sect. *Trachylomia*, *S.* sect. *Corymbosae* and in the common ancestor of *S.* sect. *Acriulus* and *S.* sect. *Margaleia*. In *S.* subg. *Browniae*, all species have a tri-lobed hypogynium (Fig. 5A) and the ancestor probably had a tri-lobed hypogynium type (Fig. 4, node 2, 100%). The hypogynium became strongly reduced or even absent (*Hypoporum* type) one time in the ancestor of *S.* subg. *Hypoporum* (Fig. 4, node 4, 100%) (Figs. 2G, 5C). Species with tubercle-like appendages above the zoniform hypogynium all group together in *S.* subg. *Trachylomia* (Fig. 5D–G). Only *S. baldwinii* has lost these tubercles. In this study these tubercles were seen as outgrowths of the pericarp and not as part of the hypogynium (Fig. 5D–F, arrows). *Scleria* subg. *Scleria* has an ancestor with a zoniform hypogynium type (Fig. 4, node 7, 100%). This zoniform hypogynium type (Figs. 2F, 5I) again evolved into a tri-lobed hypogynium, mainly in *S.* sect. *Hymenolytrum* (Fig. 4, node 13, 100%) and sect. *Foveolidia* (Fig. 4, node 15, 98%). A further evolved type is the tri-lobed hypogynium with a recurved margin type found in the ancestors of *S.* sect. *Naumannianae* (Fig. 4, node 17, 100%; Fig. 5X), *S.* sect. *Elatae* (Fig. 4, node 18, 100%; Figs. 2K, 5O, P) and *S.* sect. *Scleria* (Fig. 4, node 24, 100%; Fig. 2J). The tri-lobed hypogynium type is also found in *S.* sect. *Ophryoscleria* although in this section it is always covered by a corky swollen cupule. In *S.* sect. *Ophryoscleria*, the hypogynium can only be seen when this cupule is removed (Fig. 5W). The ancestral state reconstruction in this study, however, recovered a trilobed hypogynium with recurved margins as ancestral state for this clade (Fig. 4, node 26, 65%). The lacinate hypogynium type (Figs. 2I, 5Q–S) can be found in two sections, namely *S.* sect. *Abortivae* (Fig. 4, node 21, 100%) and *S.* sect. *Schizolepis* (Fig. 4, node 25, 100%).

A

Fig. 3. A & B, 50% majority-rule consensus tree based on concatenated dataset with indels coded. Posterior probabilities obtained from BI indicated on the respective branches when equal or higher than 0.95, bootstrap values equal or higher than 75% displayed under the branches. The framed tree (C) is the same tree with branch lengths. Geographical distribution for each species is given next to each branch. A map representing the different geographical areas is presented (D).





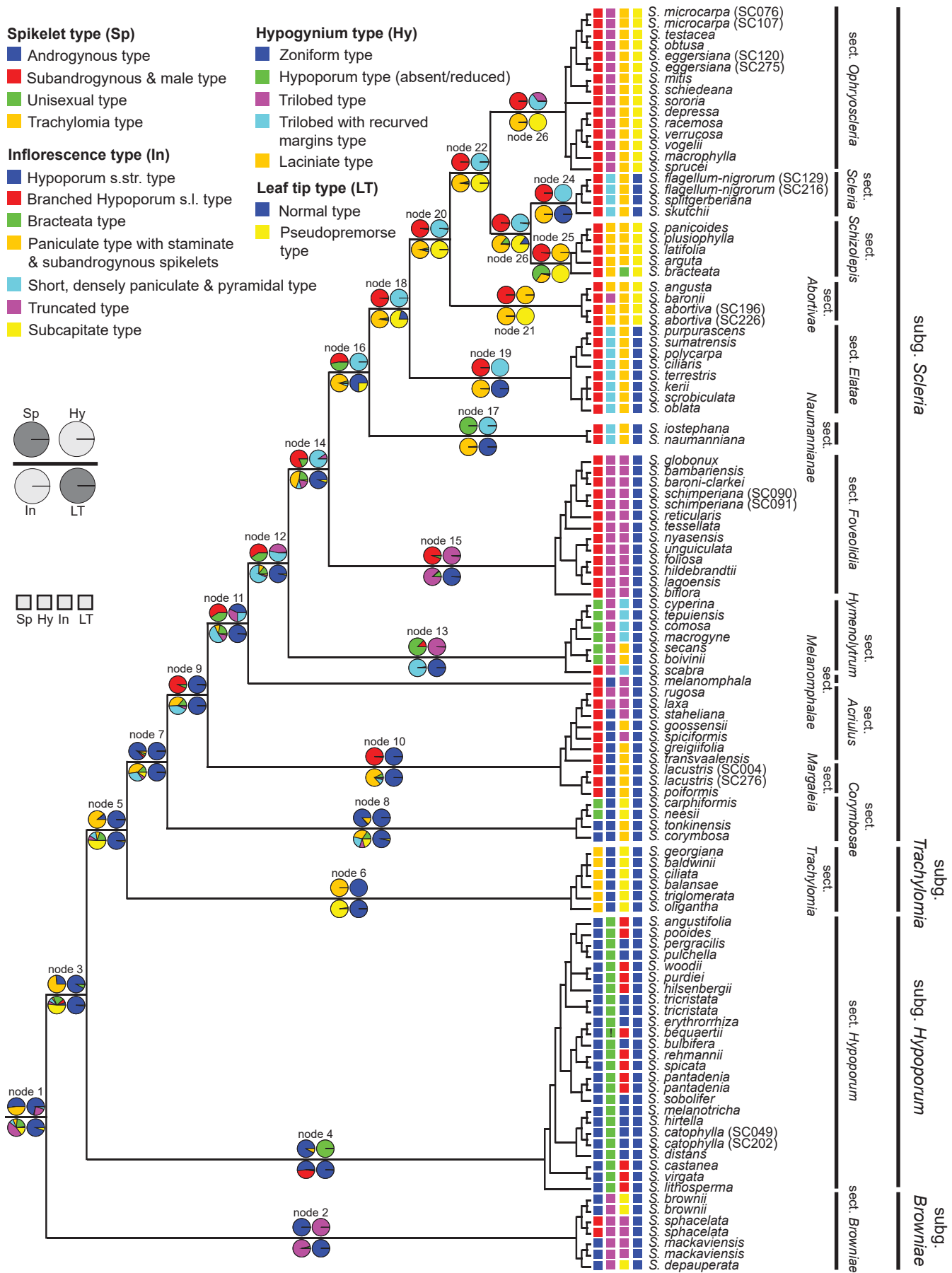


Fig. 4. 50 % majority-rule consensus tree of the concatenated BI ITS-*ndhF-rps16* analysis. Phylogenetic hypothesis with ancestral state reconstruction for four morphological characters; ! = *S. bequaertii* has a soft, spongy tissue possibly representing the hypogynium. Pie diagrams show the probability of the different character states.

The ancestral state for inflorescence type most likely is the truncated type with two or three basal lateral branches (Fig. 4, node 1, 46%). This type is also found at the base of *S.* subg. *Browniae* (Fig. 4, node 2, 96%). In *S.* subg. *Hypoporum*, two types of inflorescences are found, the *Hypoporum* s.str. type (Fig. 2L) and the branched *Hypoporum* s.l. type (Fig. 2M). The ancestral state most likely is the *Hypoporum* s.str. type (Fig. 4, node 4, 52% vs. 45%). The subcapitate inflorescence (Fig. 2R) type is ancestral in *S.* sect. *Trachylomia* (Fig. 4, node 6, 97%). A paniculate inflorescence with staminate and subandrogynous spikelets (Fig. 2O) is found in the ancestor of *S.* subg. *Scleria* (Fig. 4, node 7, 40%). This type evolved into several types: a short, densely paniculate and pyramidal type (Fig. 2P) in *S.* sect. *Hymenolytrum* (Fig. 4, node 13, 98%) and truncated type (Fig. 2Q) in *S.* sect. *Foveolidia* (Fig. 4, node 15, 88%). For *S.* sect. *Naumanniana*, sect. *Elatae*, sect. *Abortivae*, sect. *Scleria* and sect. *Ophryoscleria*, the paniculate type with staminate and subandrogynous spikelets is ancestral (Fig. 4, node 17, 98%; node 19, 99%; node 21, 99%; node 24, 99%; node 26, 98%). In *S.* sect. *Schizolepis*, the Bracteata type is recovered as ancestral state (Fig. 4, node 25, 65%; Fig. 2N).

Pseudopremorse leaves (Fig. 2S) arose only once in *Scleria* (Fig. 4, node 20, 100%). A reversal to a normal linear leaf tip shape occurred in *S.* sect. *Scleria* (Fig. 4, node 24, 100%).

Results of the ancestral state reconstruction are portrayed in Electr. Suppl.: Table S2.

■ DISCUSSION

Subgeneric relationship in *Scleria*. — This study presents the most comprehensive phylogenetic hypothesis of *Scleria* to date. Within *Scleria* we found strong support for the following subgenera and sections: *S.* subg. *Browniae* (*S.* sect. *Browniae*), *S.* subg. *Hypoporum* (*S.* sect. *Hypoporum*), *S.* subg. *Trachylomia* (*S.* sect. *Trachylomia*), *S.* subg. *Scleria* (*S.* sect. *Abortivae*, sect. *Acriulus*, sect. *Corymbosae*, sect. *Elatae*, sect. *Foveolidia*, sect. *Hymenolytrum*, sect. *Margaleia*, sect. *Melanomphalae*, sect. *Naumanniana*, sect. *Ophryoscleria*, sect. *Schizolepis*, sect. *Scleria*). As sister to all other *Scleria*, a group of Asian, Australian and Oceanian species is found, i.e., *S.* subg. *Browniae*, originally described by Clarke (1900) as a section and more elaborately discussed by Kern (1961) at sectional level. Next, *S.* subg. *Hypoporum* is found as sister group of *S.* subg. *Trachylomia* and subg. *Scleria*. Although the combined chloroplast marker and concatenated analyses resulted in a well-resolved phylogenetic hypothesis for *S.* sect. *Hypoporum*, the results of the single-marker analyses indicate some incongruences as to the relationships within the clades of *S.* sect. *Hypoporum*. From the alignments, it is evident that the molecular markers used in this study do not contain enough variation within this subgenus and a more elaborate study of the phylogenetics and morphology of *S.* subg. *Hypoporum* is needed (K. Bauters, K. Meganck, P. Goetghebeur, I. Larridon, unpub. data).

While strictly androgynous spikelets are the rule in the two previously discussed subgenera, it seems that in *S.* subg. *Trachylomia* a transition took place from androgynous to

subandrogynous spikelets. Some specimens have strictly androgynous spikelets while in other specimens only subandrogynous ones are found. Often the male parts are reduced to one stamen with one reduced glume. Also, intermediates are found with both androgynous and subandrogynous spikelets.

Within *S.* subg. *Scleria* relationships were recovered with high support values, but relationships between *S.* sect. *Abortivae*, sect. *Ophryoscleria*, sect. *Schizolepis* and sect. *Scleria* were not resolved in the phylogenetic hypotheses based on several of the single-marker analyses. However, the results of the concatenated ML and BI analyses were congruent and support for the relationships between these four sections was high. Only *S.* sect. *Ophryoscleria* was not always resolved as a monophyletic clade. However, based on the results of the ITS and the concatenated analyses, the monophyly of this section was confirmed. Moreover, this section is easily recognised by its morphology, mainly by its pseudopremorse leaves and the corky swollen cupula covering the tri-lobed hypogynium.

Two taxa, *S. gaertneri* (SC135, SC271), and *S. williamsii* (SC121) were excluded from the concatenated data matrix since their position is incongruent in the single-marker phylogenetic hypotheses. Their position in *S.* sect. *Scleria*, however, is well supported in the results of the combined chloroplast analyses (Electr. Suppl.: Figs. S7, S8). Moreover, the placement in *S.* sect. *Schizolepis* in the results of ITS can be explained by the lack of variation in the ITS sequences of *S.* sect. *Ophryoscleria*, *S.* sect. *Schizolepis* and *S.* sect. *Scleria*. In the ITS sequences of the species of *S.* sect. *Schizolepis* and *S.* sect. *Scleria* only 59 variable sites were recovered of which only 13 are informative. Consequently, the low resolution in the results of the ITS analyses for these sections may be explained by this lack of informative sites. Based on the results of the combined chloroplast trees and their morphological distinctness we choose to keep *S.* sect. *Schizolepis* and *S.* sect. *Scleria* as separated sections. All species included in *S.* sect. *Schizolepis* have a lacinate hypogynium (see Figs. 2I, 5R), this hypogynium type is the least obvious in *S. bracteata*, but still visible (Fig. 5S). In contrast, all species of *S.* sect. *Scleria* have a trilobed hypogynium with recurved margin (Figs. 2J, 5T, 5U). This trilobed hypogynium always has a smooth edge. Another striking difference is the presence of four sterile, distichous glumes below the fertile glume in the spikelet of species of *S.* sect. *Scleria*, where in *S.* sect. *Schizolepis* (and all other *Scleria*) only one or two sterile glumes are found below the fertile one. Finally, the leaf tips of species of *S.* sect. *Schizolepis* are always pseudopremorse, a character that is never found in the members of *S.* sect. *Scleria*. Morphology of both sections is discussed more elaborately below.

All subgenera and sections recovered in this paper will be discussed below under “Taxonomic Treatment”. For each subgenus and each section diagnostic features, distribution, included species and notes are given.

Ancestral state reconstruction. — The common ancestor of *Scleria* probably had an androgynous spikelets type (Fig. 4, node 1, 60%), since the *Trachylomia* type (Fig. 4, node 1, 40%) does not occur in the two earliest diverging clades. If this *Trachylomia* type represents the ancestral state, the assumption must be made that it disappeared in *S.* subg. *Browniae* and

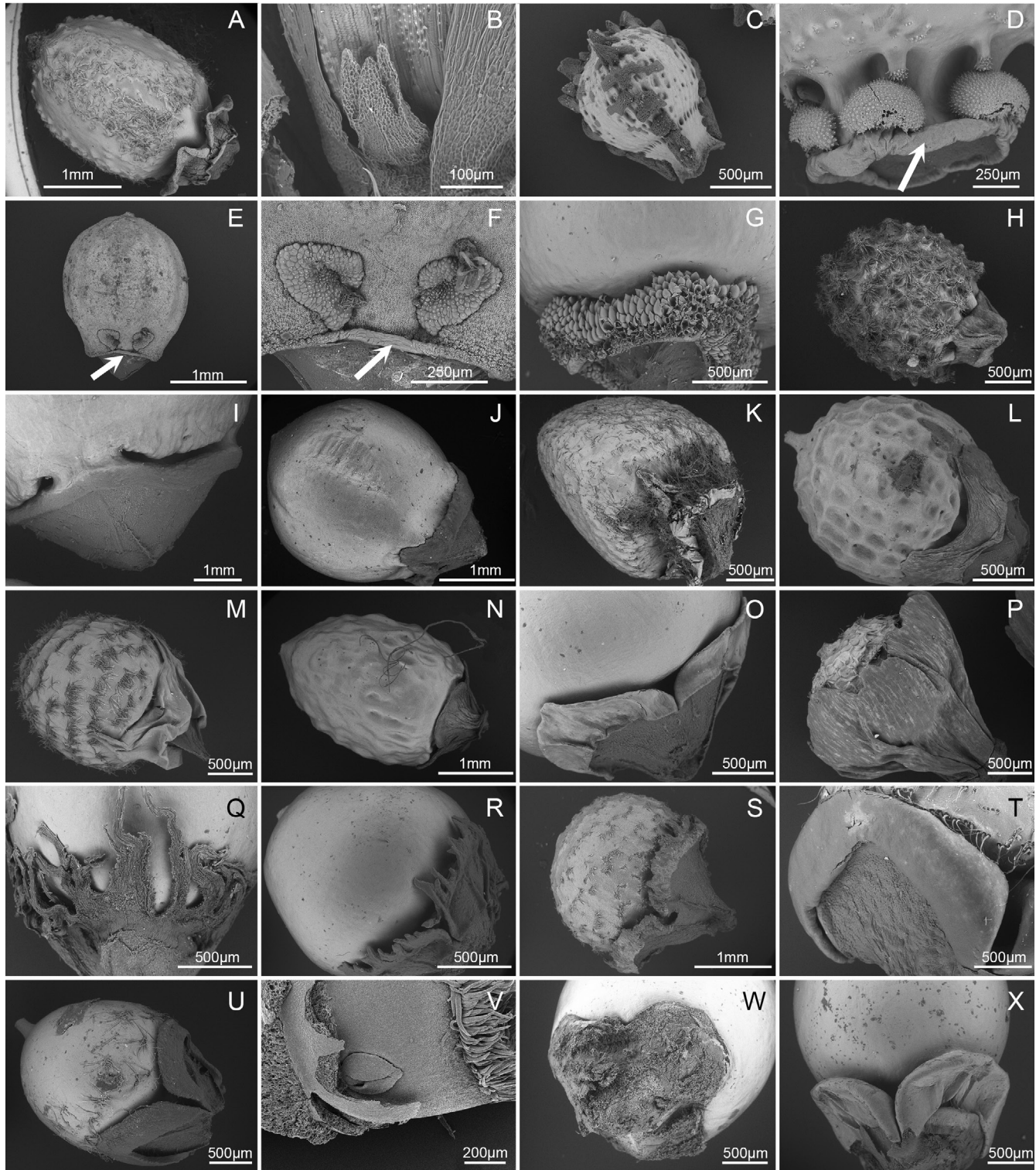


Fig. 5. SEM micrographs of fruits of *Scleria*. **A**, *S. brownii*, nutlet with loosely trilobed hypogynium (Michel C.R. & Deichmann B. 3027, MO); **B**, *S. sphacelata*, subandrogynous spikelet with reduced pistillate flower (Michell C.R. 3026, MO); **C**, *S. tricristata*, nutlet with reduced or absent hypogynium of the Hypoporum type (Bidgood S. & al. 6083, MO); **D**, *S. ciliata*, tubercles on nutlet, zoniiform hypogynium indicated by arrow (McKenzie P.M. 2008, MO); **E**, *S. georgiana*, nutlet, zoniiform hypogynium indicated by arrow (Bauters K. & Coenen J. 2013-045, GENT); **F**, *S. georgiana*, detail of tubercles, zoniiform hypogynium indicated by arrow (Bauters K. & Coenen J. 2013-045, GENT); **G**, *S. triglomerata*, tuberculate rim covering a zoniiform hypogynium (Kral R. 50517, MO); **H**, *S. neesii*, nutlet with zoniiform hypogynium (Larsen K. & al. 45846, MO); **I**, *S. lacustris*, zoniiform hypogynium (Hansen B. 12894, US); **J**, *S. poiiformis*, zoniiform hypogynium (Wilson K.L. 7508, GENT); **K**, *S. cyperiana*, nutlet with trilobed hypogynium (Liesner R. 23711, GENT); **L**, *S. reticularis*, nutlet with trilobed hypogynium (Sorrie B.A. 10750, US); **M**, *S. unguiculata*, ►

S. subg. *Hypoporum* only to reappear again in *S.* subg. *Trachylomia*. Both *S.* subg. *Browniae* and *S.* subg. *Hypoporum* are characterised by androgynous spikelets with subandrogynous spikelets only in *S. sphacelata*. Spikelets in *S.* subg. *Trachylomia* are androgynous, subandrogynous and staminate (*Trachylomia* type). Sometimes both androgynous and subandrogynous spikelet types are found in the same specimen. Often, the spikelets appear to be subandrogynous but when closely examined one fertile stamen can be found, subtended by a minute glume. The subandrogynous spikelet is a reduction of the androgynous spikelet, with staminate parts reduced to one or few empty glumes (Fig. 2C). This subandrogynous type of spikelet arose near the base of *S.* subg. *Scleria* (Fig. 4, node 9, 92%). In the whole of *S.* subg. *Scleria*, subandrogynous spikelets are found with androgynous unisexual spikelets only in *S.* sect. *Corymbosa*, and in *S.* sect. *Hymenolytrum* a further reduction to complete unisexual spikelets. Until now, no remnants of male parts have been found in the female spikelets of *S.* sect. *Hymenolytrum*, suggesting a complete reduction of the male flowers.

The common ancestor of *Scleria* most likely had a hypogynium. This is not surprising since in the sister group of the Sclerieae, the Bisboeckeleraeae, a similar structure is present near the base of the nutlet. This structure might be homologous with the cupule of *Scleria*, but this assumption is currently not supported by ontogenetic evidence, although the most parsimonious interpretation would be to suggest that these structures are homologous in the two tribes. The common ancestor of *Scleria* had a zoniform hypogynium following our analysis.

A note must be made on the tubercles found near the base in *S.* subg. *Trachylomia*. Although most authors described them as part of the hypogynium, these tubercles seem to form a separate structure not necessarily associated with the hypogynium. The tubercles seem to be an outgrowth of the pericarp of the nutlet. Following this assumption the real hypogynium is the narrow, zoniform rim at the base of the nutlet, below the tubercles (Fig. 5D–F, arrow). This zoniform hypogynium is covered by the tubercles in *S. triglomerata*, but can be seen when these tubercles are removed. The common ancestor of *S.* subg. *Scleria* had a zoniform hypogynium (Fig. 4, node 7, 100%), which evolved at least two times towards a tri-lobed hypogynium. A normally tri-lobed hypogynium is common to both *S.* sect. *Hymenolytrum* (Fig. 5K; Fig. 4, node 13, 100%) and *S.* sect. *Foveolidia* (Fig. 5L–N; Fig. 4, node 15, 98%). Also, *S.* sect. *Ophryoscleria* is characterised by a simple tri-lobed hypogynium, but in all species, except in *S. sororia*, this hypogynium is covered by a corky swollen cupule and only visible when the cupule is removed. In *S.* sect. *Elatae*, all species have a tri-lobed hypogynium with recurved margins clearly seen

in *S. oblata* (Fig. 5O). In some species, this margin is folded back all the way, appearing like a simple tri-lobed hypogynium (Fig. 5P). However, in these species the folded nature can be seen when studied carefully. *Scleria* sect. *Scleria* is also characterised by a recurved or folded hypogynium (Fig. 5T, U), although species of this section are easily distinguished from *S.* sect. *Elatae* by the deeply cut tri-lobed nature of the hypogynium. A homoplasy is found between *S.* sect. *Abortivae* and sect. *Schizolepis*. While not forming a monophyletic clade, both sections have a remarkably similar lacinate hypogynium (Fig. 5Q–S). This lacinate type arose twice independently and misled many authors to place species from the two sections into one group.

The truncated inflorescence type was most likely present in the common ancestor of *Scleria* (Fig. 4, node 1, 46%). In *S.* subg. *Browniae*, both truncated and subcapitate types are found and the truncated one is suggested to be ancestral (Fig. 4, node 2, 96%). Two inflorescence types are found in *S.* subg. *Hypoporum*, a strictly unbranched Hypoporum s.str. type and the branched Hypoporum s.l. type. The unbranched Hypoporum s.str. type in our analysis is slightly preferred as ancestral (Fig. 4, node 4, 52% vs. 45%). Both types arose multiple times independently, suggesting that they can easily be altered in evolution. *Scleria* subg. *Trachylomia* clearly has a subcapitate inflorescence type as ancestral state (Fig. 4, node 6, 97%), while in *S.* subg. *Scleria* the paniculate type is most probable (Fig. 4, node 7, 40%). The paniculate inflorescence type with staminate and subandrogynous spikelets is the most common inflorescence type in *S.* subg. *Scleria*, occurring in the common ancestors of *S.* sect. *Corymbosae* (Fig. 4, node 8, 31%), *S.* sect. *Naumannianae* (Fig. 4, node 17, 98%), *S.* sect. *Elatae* (Fig. 4, node 19, 99%), *S.* sect. *Abortivae* (Fig. 4, node 21, 99%), *S.* sect. *Scleria* (Fig. 4, node 24, 99%), *S.* sect. *Ophryoscleria* (Fig. 4, node 26, 98%) and in the common ancestor of both *S.* sect. *Acriulus* and *S.* sect. *Margaleia* (Fig. 4, node 10, 79%). The short, densely paniculate and pyramidal type only occurs in *S.* sect. *Hymenolytrum*, which makes it a valid diagnostic feature of this section. All species of *S.* sect. *Foveolidia* are characterised by the truncated inflorescence type.

Pseudopremorse leaves are very characteristic for *S.* sect. *Abortivae*, sect. *Ophryoscleria* and sect. *Schizolepis*. It seems unlikely that this character state evolved multiple times and the single origin of the pseudopremorse leaf tips was confirmed by our analysis (Fig. 4, node 20, 100%). However, these three sections form a paraphyletic grade with *S.* sect. *Scleria* nested among them, suggesting that the pseudopremorse state reverted to normal in this section. The results indicate that this, indeed, is the case and that the reversal took place in the ancestor of *S.* sect. *Scleria* (Fig. 4, node 24, 100%).

- ▶ nutlet with trilobed, acuminate hypogynium (Bauters K. 2015–213, GENT); **N**, *S. foliosa*, nutlet with trilobed hypogynium (Bidgood S. & al. 6396, MO); **O**, *S. oblata*, hypogynium with recurved margins (Desfayes M. 980427-15, GENT); **P**, *S. sumatrensis*, aril-like hypogynium (Procter J.E.A. 4267, MO); **Q**, *S. angusta*, lacinate hypogynium (Smook L. 6086, MO); **R**, *S. latifolia*, lacinate hypogynium (Camelbeke K. & Goetghebeur P. 913, GENT); **S**, *S. bracteata*, nutlet with slightly lacinate hypogynium (Toriola-Marbot D. 330, GENT); **T**, *S. williamsii*, trilobed hypogynium with recurved margins (Rivero E. 445, GENT); **U**, *S. gaertneri*, nutlet with trilobed hypogynium with recurved margins (Laegaard S. 71318, GENT); **V**, *S. depressa*, subandrogynous spikelet with male rudiments and ciliated cupule (Goetghebeur P. 12128, GENT); **W**, *S. eggersiana*, trilobed hypogynium after removing cupule (Piepenbring M. & al. 2728, GENT); **X**, *S. iostephana*, trilobed hypogynium with recurved margins (Hess H. & E. 52/1229, GENT).

■ TAXONOMIC TREATMENT

Species followed by an asterisk (*) are placed in the section based on morphology. For additional specimens examined, see Electr. Suppl.: Appendix S1.

Scleria* subg. *Browniae (C.B.Clarke) C.B.Clarke in Bull. Misc. Inform., Addit. Ser. 8: 132. 1908 – Type: *S. brownii* (R.Br.) Kunth, Enum. Pl. 2: 349. 1837.

Diagnosis. – *Scleria* subg. *Browniae* is characterised by its perennial habit, slightly reddish and inflated leaf sheaths, androgynous spikelets (Fig. 2A, B), a simple tri-lobed hypogynium with lobes not adpressed to the nutlet (Fig. 5A) and truncated to subcapitate inflorescences.

Species included (9 species). – *Scleria brownii* Kunth, *S. cyathophora* Holttum*, *S. densispicata* (C.B.Clarke) J.Kern*, *S. depauperata* Boeckeler, *S. mackaviensis* Boeckeler, *S. motleyi* C.B.Clarke*, *S. neocaledonica* Rendle*, *S. papuana* J.Kern*, *S. sphacelata* F.Muell.

Distribution. – Asia, Australia and Oceania.

Note. – Kern (1961) had concerns about the distinction between *Scleria brownii* and *S. mackaviensis*, since the latter often seems to be merely a slightly altered form of *S. brownii*. However, Wilson (on PlantNET, 2015) maintains *S. brownii* separate from *S. mackaviensis*. Also, we find sufficient support to treat them as separate species. *Scleria sphacelata* is often described as strictly dioecious, although Mueller (1875) did not mention this in his original description. In this study, both subandrogynous specimens and staminate specimens were observed. In the staminate specimens, small rudiments of a female flower can be found near the base of the spikelet (Fig. 5B). The spikelets of *S. sphacelata* in this study therefore were treated as subandrogynous. Kern (1961) also found a specimen of *S. brownii* with strictly male spikelets; it is possible that there is a tendency towards dioecism in this subgenus.

Scleria* subg. *Hypoporum (Nees) C.B.Clarke in Hooker, Fl. Brit. India 6: 685. 1894 – Type: *S. pergracilis* (Nees) Kunth, Enum. Pl. 2: 354. 1837.

Diagnosis. – *Scleria* subg. *Hypoporum* can be recognised by its annual or perennial habit, androgynous spikelets, a reduced hypogynium (Fig. 5C) and unbranched Hypoporum s.str. (Fig. 2L) or the branched Hypoporum s.l. inflorescence type (Fig. 2M). The inflorescence is a linear spike of distant, sessile spikelet clusters subtended by a short glume-like or foliate bract.

Species included (66 species). – *Scleria afroreflexa* Lye*, *S. andringitrensis* Cherm., *S. angustifolia* E.A.Rob., *S. aromatica* Core*, *S. bequaertii* De Wild., *S. bicolor* Nelmes*, *S. bourgeauii* Boeckeler*, *S. bradei* Gross*, *S. bulbifera* Hochst. ex A.Rich., *S. burchellii* C.B.Clarke*, *S. calcicola* E.A.Rob.*, *S. castanea* Core, *S. catophylla* C.B.Clarke, *S. composita* (Nees) Boeckeler*, *S. cuyabensis* Pilg.*, *S. delicatula* Nelmes*, *S. distans* Poir., *S. dregeana* Kunth*, *S. erythrorrhiza* Ridl., *S. filiculmis* Boeckeler*, *S. flexuosa* Boeckeler*, *S. fulvipilosa* E.A.Rob.*, *S. glabra* Boeckeler*, *S. guineensis* J.Raynal*, *S. hilsenbergii* Ridl., *S. hirtella* Sw., *S. hispidior* (C.B.Clarke) Nelmes*, *S. hispidula* Hochst. ex A.Rich.*, *S. interrupta*

Rich.*, *S. killipiana* Britton*, *S. kindtiana* Graebn.*, *S. laxiflora* Gross*, *S. leptostachya* Kunth*, *S. lithosperma* (L.) Sw., *S. longispiculata* Nelmes*, *S. melanotricha* Hochst. ex A.Rich., *S. melicoides* Schldl.*, *S. minima* C.B.Clarke*, *S. monticola* Nelmes ex Napper*, *S. motemboensis* Britton*, *S. pantadenia* Meganck & Bauters, *S. paupercula* E.A.Rob.*, *S. pergracilis* (Nees) Kunth, *S. perpusilla* Cherm.*, *S. polyrrhiza* E.A.Rob.*, *S. pooides* Ridl., *S. procumbens* E.A.Rob.*, *S. pulchella* Ridl., *S. purdiei* C.B.Clarke, *S. pusilla* Pilg.*, *S. rehmannii* C.B. Clarke, *S. richardsiae* E.A.Rob.*, *S. robinsoniana* J.Raynal*, *S. sheilae* J.Raynal*, *S. sobolifer* E.F.Franklin, *S. spicata* (Spreng.) J.F.Macbr., *S. tenella* Kunth*, *S. tricristata* Meganck & Bauters, *S. valdemuricata* Kük.*, *S. variegata* (Nees) Steud.*, *S. verticillata* Muhl.*, *S. veseyfitzgeraldii* E.A.Rob.*, *S. virgata* (Nees) Steud., *S. welwitschii* C.B.Clarke*, *S. woodii* C.B. Clarke, *S. zambesica* E.A.Rob.*.

Distribution. – Africa, the Americas, Asia, Australia, Madagascar and Oceania.

Note. – The presence or absence of a hypogynium in *Scleria* subg. *Hypoporum* always has been a major issue of debate. Franklin Hennessey (1985) stated that the absence of a hypogynium reflects the ancestral state in *Scleria*, while Camelbeke (2001) hypothesised that the hypogynium is not absent but only rudimentary and is therefore a derived state. Our results support the hypothesis by Camelbeke (2000) that the reduced or absent hypogynium represents a derived character state since the ancestral state in *Scleria* is a zoniform hypogynium (Fig. 4, node 1, 71%) Although extremely reduced, the hypogynium forms a shallow triquetrous stipe in *S. subg. Hypoporum*. Here, the nutlets remain attached to the spikelets and they reach the substrate only during winter when aerial parts die back (Franklin Hennessey, 1985). In *S. bequaertii*, the supposed hypogynium consists of a soft, white and spongy tissue of ca. 1 mm length, almost as broad as the nutlet (Robinson, 1966), a strong indication for the presence and highly reductive nature of a hypogynium in *S. subg. Hypoporum*.

Scleria* P.J.Bergius subg. *Scleria – Type: *S. flagellum-nigrorum* P.J.Bergius in Kongl. Vetensk. Acad. Handl. 26: 144, pl. 4–5. 1765.

Diagnosis. – *Scleria* subg. *Scleria* can be recognised by its annual or perennial habit. Most commonly spikelets are subandrogynous but androgynous (*S. corymbosa*, *S. tonkinensis*) and unisexual spikelets (*S. sect. Hymenolytrum*, *S. carphiformis*, *S. neesii*) are also found. Hypogynia are zoniform (*S. sect. Acriulus*, *S. sect. Corymbosae*, *S. sect. Margaleia*, *S. sect. Melanomphalae*), tri-lobed (*S. sect. Acriulus*, *S. sect. Foveolidia*, *S. sect. Hymenolytrum*, *S. sect. Ophryoscleria*, *S. baronii* of *S. sect. Abortivae*), tri-lobed with recurved margins (*S. sect. Elatae*, *S. sect. Naumanniana*, *S. sect. Scleria*) or lacinate (*S. sect. Abortivae*, *S. sect. Scleria*). Inflorescences are paniculate (*S. sect. Abortivae*, *S. sect. Acriulus*, *S. sect. Corymbosae*, *S. sect. Elatae*, *S. sect. Hymenolytrum*, *S. sect. Margaleia*, *S. sect. Naumanniana*, *S. sect. Ophryoscleria*, *S. sect. Schizolepis*, *S. sect. Scleria*), truncated (*S. sect. Acriulus*, *S. sect. Foveolidia*, *S. sect. Melanomphalae*), short and densely pyramidal paniculate (*S. sect. Hymenolytrum*),

subcapitate (*S. sect. Corymbosae*) or of the Bracteata type (*S. bracteata* – *S. sect. Schizolepis*).

Species included (149 species). – See details in the following treatment of sections.

Distribution. – North, Central and South America, Africa, Madagascar, Asia, Australia and Oceania.

Scleria (subg. *Scleria*) sect. ***Abortivae*** Cherm. ex Bauters, **sect. nov.** – “*Scleria* sect. *Abortivae* Cherm.” in Humbert, Fl. Madagasc. 29: 262. 1937, nom. nud. – Type: *S. abortiva* Nees ex Kunth, Enum. Pl. 2: 346. 1837.

Diagnosis. – Species in this section are robust perennials with subandrogynous and male spikelets, a paniculate inflorescence, a lacinate hypogynium (Fig. 5Q) (tri-lobed in *Scleria baronii*) and pseudopremorse leaves.

Species included (6 species). – *Scleria abortiva* Nees ex Kunth, *S. angusta* Nees ex Kunth, *S. baronii* C.B. Clarke ex Cherm., *S. madagascariensis* Boeckeler*, *S. sieberi* Nees*, *S. trialata* Poir*.

Distribution. – Tropical Africa, Madagascar.

Notes. – Based on the lacinate hypogynium and the pseudopremorse leaves, most authors included the above species in *Scleria* sect. *Schizolepis* (e.g., Nelmes, 1956). Indeed, based on morphology alone it is difficult to separate this section from *S. sect. Schizolepis*. However, leaf sheaths are never winged in *S. sect. Abortivae*, while in *S. sect. Schizolepis* all species have broadly winged leaf sheaths. Also, the taxa have distinct distributions: *Scleria* sect. *Abortivae* occurs only in Madagascar or in the case of *S. angusta* also on mainland Africa while *S. sect. Schizolepis* is only found in Central and South America.

In *Scleria baronii*, the lacinate hypogynium is absent and a more common tri-lobed hypogynium is found, which misled Chermeson (1937) to place it in *S. sect. Elatae*. The pseudopremorse leaves together with its distribution, however, point towards *S. sect. Abortivae*, assuming this pseudopremorse character state arose only once.

Scleria (subg. *Scleria*) sect. ***Acriulus*** (Ridl.) R.W. Haines & Lye, Sedges Rushes E. Afr.: 357. 1983 – Type: *S. acriulus* C.B. Clarke (= *S. greigiifolia* (Ridl.) C.B. Clarke in Oliver, Fl. Trop. Afr. 8: 509. 1902).

Diagnosis. – This section is mainly characterised by its subandrogynous and male spikelets, the zoniform hypogynium (Fig. 5I, J) and a truncated or paniculate inflorescence with staminate and subandrogynous spikelets.

Species included (12 species). – *Scleria goossensii* De Wild., *S. greigiifolia* (Ridl.) C.B. Clarke, *S. induta* Turrill*, *S. laxa* R.Br., *S. natalensis* Boeckeler ex C.B. Clarke*, *S. pachyrryncha* Nelmes*, *S. rugosa* R.Br., *S. setulosociliata* Boeckeler*, *S. spiciformis* Benth., *S. staheliana*, *S. thwaitesiana* Boeckeler*, *S. transvaalensis* E.F. Franklin.

Distribution. – Africa, Asia, Australia, Central America and Madagascar.

Notes. – Species of this section have caused some confusion in the past. Different authors placed these species in different sections. Kern (1961) placed *Scleria laxa* and *S. rugosa* in *S. sect. Tessellatae* (now *S. sect. Foveolidia* by priority).

Both species indeed do resemble species from that section. The sometimes reticulate pattern of the nutlets and the general appearance of these plants can get them easily confused with *S. sect. Foveolidia*. Several species were placed in *S. sect. Scleria*: *S. staheliana* (Camelbeke, 2001), *S. goossensii* (De Wildeman, 1926), *S. spiciformis* (Clarke, 1908) and *S. transvaalensis* (Franklin Hennessy, 1985). *Scleria greigiifolia* was even described its own genus *Acriulus* by Ridley (1883) as a close relative of *Scleria*. It was Clarke (1902) who included *Acriulus* in *Scleria*. Surprisingly neither Nelmes (1956) nor Piérart (1953) followed this view. Kern (1963) wrote a detailed paper on the inclusion of *Acriulus* in *Scleria*. *Scleria* sect. *Acriulus* was originally based on two or three species, now all merged under *S. greigiifolia*. Surely, *S. sect. Acriulus* is highly heterogenous with plants of only 15 cm height with poorly developed panicles (e.g., *S. rugosa*) up to plants of 2 m height with well-developed nodding panicles (e.g., *S. greigiifolia*).

Scleria (subg. *Scleria*) sect. ***Corymbosae*** Pax in Engler & Prantl, Nat. Pflanzenfam. II(2): 121. 1888 – Type: *S. corymbosa* Roxb., Fl. Ind., ed. 1832, 3: 574. 1832.

Diagnosis. – In *Scleria corymbosa* and *S. tonkinensis*, the spikelets are androgynous and the inflorescence is paniculate with staminate and subandrogynous spikelets, whereas in *S. carphiformis* and *S. neesii* strictly unisexual spikelets are found, arranged in a subcapitate inflorescence. In all species, the hypogynium is a brown to reddish, slightly triangular, narrow, minutely glandular band, described by Kern (1961) as obsolete. In this paper, we treat the hypogynium as zoniform. Both *S. carphiformis* and *S. neesii* are easily recognised by their unisexual spikelets, subcapitate inflorescence, densely hairy stems and leaves, and their tuberculate nutlets with tufts of hairs on top of the tubercles (Fig. 5H).

Species included (5 species). – *Scleria carphiformis* Ridl., *S. corymbosa* Roxb., *S. neesii* Kunth, *S. porphyrocarpa* E.A. Rob., *S. tonkinensis* C.B. Clarke.

Distribution. – Asia and Australia, *S. porphyrocarpa* is found in the Democratic Republic of the Congo and Zambia.

Notes. – Clarke (1908) placed these species in *Scleria* subg. *Hypoporum* based on the “absence” of a hypogynium. However, the hypogynium of *S. sect. Corymbosae* is clearly visible as an unlobed rim (Fig. 5H) and the hypogynium is therefore described as zoniform here. Kern (1961) distinguished two different sections for these species: *S. corymbosa* was placed in the *S. sect. Corymbosae* while *S. carphiformis* and *S. neesii* were united in *S. sect. Carphiformes*. However, our results indicate that the two sections can be merged into one *S. sect. Corymbosae*. A remarkable member of this section is *S. porphyrocarpa*, a species growing up to 5 m tall, only known from the Democratic Republic of Congo and Zambia. This species is very similar in its general appearance to *S. corymbosa* with corymb-like partial inflorescences. However, it differs in its stouter habit and the shiny purple nutlets.

Scleria (subg. *Scleria*) sect. ***Elatae*** C.B. Clarke in Hooker, Fl. Brit. India 6: 689. 1894 – Type: *S. elata* Thwaites, Enum. Pl. Zeyl.: 353. 1864 (= *S. terrestris* (L.) Fasset).

Diagnosis. – Species of this section are characterised by their robust habit, thick woody and often nodulose rhizomes, the middle leaves are organised in pseudowhorls or at least are approximating each other, subandrogynous and staminate spikelets, paniculate inflorescences with subandrogynous and staminate spikelets and a hypogynium with recurved margins often connate with the lower tissue. This hypogynium has recurved margins but in a quite different way from that in *S. sect. Scleria* (Fig. 5O, P). The hypogynium lobes are folded back (Fig. 5O) and are often connate with the lower hypogynium tissue (Fig. 5P). In some species this hypogynium forms an aril-like cupule around the nutlet (e.g., *S. sumatrensis*) (Fig. 5P).

Species included (24 species). – *Scleria anomala* (Steud.) J.Raynal*, *S. ciliaris* Nees, *S. dulungensis* P.C.Li*, *S. fauriei* Ohwi*, *S. harlandii* Hance*, *S. indica* D.M.Verma & Veena*, *S. jiangchengensis* Y.Y.Qian*, *S. junghuhniana* Boeckeler*, *S. kerrii* Turrill, *S. khasiana* Boeckeler*, *S. levis* Retz.*, *S. lingulata* C.B.Clark*, *S. millespicula* T.Koyama*, *S. oblata* S.T. Blake ex J.Kern, *S. ovinux* J.Raynal ex Fosberg*, *S. polycarpa* Boeckeler, *S. psilorrhiza* C.B.Clark*, *S. purpurascens* Steud., *S. radula* Hance*, *S. rutenbergiana* Boeckeler*, *S. scrobiculata* Nees & Meyen, *S. suffulta* C.B.Clark*, *S. sumatrensis* Retz., *S. terrestris* (L.) Fassett.

Distribution. – This section mainly occurs in Asia and Oceania although *S. sumatrensis* is also known from the Seychelles.

Notes. – Although Clarke (1894) seemed to be correct in putting these species into a separate section, almost no other authors followed him in this and most synonymised *Scleria* sect. *Elatae* with *S. sect. Scleria*. Chermeson (1937) did use *S. sect. Elatae* but all the species he included can now be put in a different section. He characterised this section mainly by the pyramidal paniculate inflorescence, a character found in most sections of *S. subg. Scleria*.

Scleria (subg. *Scleria*) sect. ***Foveolidia*** Raf. in Bull. Bot., Geneva 1: 219. 1830 – Type: *S. reticularis* Michx., Fl. Bor.-Amer. 2: 167. 1803.

Diagnosis. – All species in this section are rather small to moderately sized annuals or perennials with a very short rhizome. Furthermore, they have subandrogynous spikelets, a pale greenish tri-lobed hypogynium and truncated inflorescences with 2 or 3 lateral panicles. The hypogynium is nearly always loosely adpressed to the nutlet (Fig. 5L–N) and is, in most cases, distinctly tri-lobed, all in a similar way (Fig. 5L, N). However, sometimes the lobes are slender or even acuminate (Fig. 5M).

Species included (33 species). – *Scleria achtenii* De Wild.*, *S. adpressohirta* (Kük.) E.A.Rob.*, *S. anceps* Liebm.*, *S. annularis* Steud.*, *S. arcuata* E.A.Rob.*, *S. aurantiaca* Lye*, *S. bambariensis* Cherm., *S. baroni-clarkii* De Wild., *S. benthamii* C.B.Clark*, *S. biflora* Roxb., *S. chlorocalyx* E.A.Rob.*, *S. clathrata* Hochst. ex A.Rich.*, *S. foliosa* Hochst. ex A.Rich., *S. globonux* C.B.Clark*, *S. gracillima* Boeckeler*, *S. hildebrandtii* Boeckeler, *S. lagoensis* Boeckeler, *S. lucentinigricans* E.A.Rob.*, *S. mikawana* Makino*, *S. muehlenbergii* Steud.*, *S. multilacunosa* T.Koyama*, *S. novae-hollandiae*

Boeckeler*, *S. nyasensis* C.B.Clark*, *S. parvula* Steud.*, *S. patula* E.A.Rob.*, *S. reticularis* Michx., *S. scabriuscula* Schltldl.*, *S. schimperiana* Boeckeler, *S. stocksiana* Boeckeler*, *S. tessellata* Willd., *S. tricuspidata* S.T.Blake*, *S. unguiculata* E.A.Rob., *S. xerophila* E.A.Rob.*

Distribution. – *Scleria* sect. *Foveolidia* is a clade with mostly African and Malagasy representatives. Some species, however, occur in the Americas or Asia and Australia.

Notes. – Although Robinson (1961) thought this section comprised only annuals, we can confirm the presence of some perennial species such as *Scleria nyasensis*, *S. unguiculata* and *S. lagoensis*. According to Robinson (1961, 1966) the number of lateral panicles on the nodes is an important character to identify species. These narrow, lateral panicles can be erect or pendulous. Most species of *S. sect. Foveolidia* have nutlets with a reticulate or lacunose-tessellate surface that is often hairy. However, species with a glabrous, smooth nutlet surface are also found (e.g., *S. baroni-clarkii*, *S. schimperiana*).

A more commonly used name for this section is *Scleria* sect. *Tessellatae*. This name was published by Clarke (1894) and subsequently used by other authors (e.g., Kern, 1961; Robinson, 1961). However, Rafinesque (1830) published a section named *Foveolidia* where he included “*S. reticulata* Michx.” He was referring to *S. reticularis* Michx., making this species the valid type of this section. Until now, this section by Rafinesque has always been overlooked and never used in practice, but since it is validly published it should be used instead of the name *Tessellatae*.

Scleria (subg. *Scleria*) sect. ***Hymenolytrum*** (Schrad. ex Nees) Core in Brittonia 2: 10. 1936 – Type: *S. cyperina* Willd. ex Kunth, Enum. Pl. 2: 345. 1837.

Diagnosis. – *Scleria* sect. *Hymenolytrum* is characterised by its stout habit, the strictly unisexual spikelets (except *S. scabra*, which has subandrogynous and staminate spikelets), a short, densely paniculate and pyramidal inflorescence (truncated in *S. boivinii* and *S. secans*), a tri-lobed hypogynium and a distinctive obtuse to ovate contraligule with a membranous appendage. Although this appendage is not found in *S. cyperina* and *S. tepuiensis*, the other characters of these two species fit this description well and both are easily recognised as *S. sect. Hymenolytrum*. Also characteristic for the section are the nodulose stem base and the minutely hairy nutlet. Moreover, the pistillate spikelets are sessile and near the base in each branch while the staminate spikelets are on distinctly long peduncles.

Species included (15 species). – *Scleria boivinii* Steud., *S. comosa* (Nees) Steud., *S. cyperina* Kunth, *S. macrogyne* C.B. Clarke, *S. martii* (Nees) Steud.*, *S. poeppigii* (Nees) Steud.*, *S. ramosa* C.B.Clark*, *S. robusta* Camelb. & Goetgh.*, *S. scabra* Willd., *S. secans* (L.) Urb., *S. stenophylla* Core*, *S. stipularis* Nees*, *S. tepuiensis* Core, *S. vaginata* Steud.*, *S. violacea* Pilg.*

Distribution. – This section comprises species from both Central and South America with the exception of *Scleria boivinii* which is found in tropical Africa and Madagascar.

Notes. – Nees (1842) raised some of these species to generic level and established the genus *Hymenolytrum* to accommodate

them. However, other authors (e.g., Core, 1936; Camelbeke, 2001) did not accept this genus and placed it at sectional level. Until now, all authors followed a narrow circumscription of this section, which is now extended by the inclusion of *S. boivinii*, *S. scabra*, and *S. secans*.

Apart from their distribution, it is nearly impossible to distinguish *Scleria boivinii* and *S. secans*. Boivin, who collected the type specimen of *S. boivinii*, identified this specimen as *S. reflexa*, referring to the species described by Kunth (1816), which is now a synonym of *S. secans*. Rakotonirina & al. (on label) identified the same specimen in MO as *S. secans*, confirming Boivin's original idea about this specimen. We choose to treat them separately based on the distinct geographical distribution, pending a broader molecular study.

***Scleria* (subg. *Scleria*) sect. *Margaleia* Raf. in Bull. Bot., Geneva 1: 219. 1830 – Lectotype (designated by Camelbeke & al. in Taxon 50: 483. 2001): *S. poiformis* Retz., Observ. Bot. 4: 13. 1786.**

Diagnosis. – *Scleria* sect. *Margaleia* can be characterised by its stout aquatic habit, subandrogynous and male spikelets, a zoniform hypogynium (Fig. 5I, J) and a paniculate inflorescence with staminate and subandrogynous spikelets. The finely divided floating roots of *S. lacustris* and the broad and thick leaves of *S. poiformis* easily separate both species.

Species included (3 species). – *Scleria chevalieri* J.Raynal*, *S. lacustris* C.Wright, *S. poiformis* Retz.

Distribution. – Tropical Africa, tropical America, Asia, Australia and Madagascar.

Notes. – The position of both species has varied over time. Nelmes (1955) believed *Scleria lacustris* was a true *S.* subg. *Hypoporum* species based on the androgynous spikelets. However, all the specimens examined for the present study have subandrogynous spikelets. The same species was placed in *S.* sect. *Tessellatae* by Clarke (1900, 1908) and in *S.* sect. (*Eu*)*Scleria* by Core (1936) and Franklin Hennessy (1985). Also *S. poiformis* was placed in *S.* sect. *Scleria* by Franklin Hennessy (1985).

***Scleria* (subg. *Scleria*) sect. *Melanomphalae* Bauters, **sect. nov.** – Type: *S. melanomphala* Kunth, Enum. Pl. 2: 345. 1837.**

Diagnosis. – *Scleria* sect. *Melanomphalae* is characterised by its subandrogynous and male spikelets, a zoniform hypogynium and a truncated inflorescence.

Species included (1 species). – *Scleria melanomphala* Kunth.

Distribution. – Africa, Madagascar, and South America

Notes. – *Scleria melanomphala* is isolated and has no close relative in our study. This species occurs in South America as well as in tropical and South Africa where it is widespread. Robinson (1966) synonymised this species with *S. longigluma* Kük. from South America. However, Camelbeke (2001) treated this species as separate based on the smaller and more rounded nutlet. Based on their geographical distributions it would make sense to treat the two as separate species: *S. longigluma* from South America and *S. melanomphala* from tropical and South Africa. No molecular data was available to test this hypothesis,

which was a reason for us to keep it merged in *Scleria melanomphala*. Future research will hopefully resolve this issue.

***Scleria* (subg. *Scleria*) sect. *Naumanniana* Bauters, **sect. nov.** – Type: *S. naumanniana* Boeck. in Bot. Jahrb. Syst. 5: 94. 1884.**

Diagnosis. – This section contains species with subandrogynous and male spikelets, a tri-lobed hypogynium with reflexed margins (Fig. 5X) and paniculate inflorescences with staminate and subandrogynous spikelets. The subandrogynous spikelet is almost becoming unisexual in all four species. The remnants of the male parts are always extremely reduced or even absent.

Species included (4 species). – *Scleria canescens* Boeckeler*, *S. chlorantha* Boeckeler*, *S. iostephana* Nelmes, *S. naumanniana* Boeckeler.

Distribution. – All species occur in tropical Africa.

Notes. – Piérart (1951) treated both *S. iostephana* and *S. naumanniana* as *S. naumanniana* s.l. It was Nelmes (1956) who separated them and described *S. iostephana*. The latter always has bluish-purple nutlets and can easily be distinguished from *S. naumanniana* by that character. The hypogynium with reflexed margins is similar to that in *S.* sect. *Scleria*. However, our phylogenetic hypothesis does not suggest any affinity between these two species and *S.* sect. *Scleria*, implying that this type of hypogynium arose multiple times independently.

***Scleria* (subg. *Scleria*) sect. *Ophryoscleria* (Nees) C.B. Clarke in Urban, Symb. Antill. 2: 138. 1900 – Type: *S. racemosa* Poir. in Lamarck, Encycl. 7: 6. 1806.**

Diagnosis. – All species are tall perennials with staminate and subandrogynous spikelets. The hypogynium is simply tri-lobed (Fig. 5W) but in nearly all species (except *Scleria sororia*) covered with a swollen cupule, totally hiding the hypogynium. This cupula has a ciliate margin (Fig. 5V). The simple tri-lobed hypogynium can only be seen when the corky cupule is removed (Fig. 5W). Inflorescences are paniculate with staminate and subandrogynous spikelets and leaves are always pseudopremorse.

Species included (18 species). – *Scleria depressa* (C.B. Clarke) Nelmes, *S. eggersiana* Boeckeler, *S. macrophylla* J.Presl & C.Presl, *S. microcarpa* Nees ex Kunth, *S. mitis* P.J.Bergius, *S. mucronata* Poir.*, *S. obtusa* Core, *S. oligochondra* Nelmes*, *S. racemosa* Poir., *S. schiedeana* Schltld., *S. sororia* Kunth, *S. sprucei* C.B. Clarke, *S. testacea* Nees ex Kunth, *S. tropicalis* M.T.Strong*, *S. uleana* Boeckeler*, *S. verrucosa*, *S. vichadensis* F.J.Herm.*, *S. vogelii* C.B. Clarke.

Distribution. – Central and South America with four species with an African distribution.

Notes. – Little disagreement is found in the literature about this section. The ciliate cupule covering the tri-lobed hypogynium, combined with the pseudopremorse leaves, make species in this section easy to recognise. Robinson (1966: 487) did not use a sectional classification for *Scleria*, but he did use *S.* subg. *Ophryoscleria*, even suggesting that it could possibly be raised to generic level. In some species the style base remains attached to the nutlet (e.g., *S. depressa*, *S. racemosa*, *S. verrucosa*, *S. vogelii*) while in others the style base remains attached at

first but becomes deciduous after a while (e.g., *S. microcarpa*). African representatives of this section all group together in a well-supported clade.

Scleria (subg. *Scleria*) sect. ***Schizolepis*** (Schrad. ex Nees) C.B. Clarke in Hooker, Fl. Brit. India 6: 694. 1894 – Type: *S. latifolia* Sw., Prodr.: 18. 1788.

Diagnosis. – All species except *Scleria bracteata* are characterised by a stout perennial habit with subandrogynous and staminate spikelets, a lacinate hypogynium, paniculate inflorescence and pseudopremorse leaves with broadly winged leaf sheaths. *Scleria bracteata* is the exception, not only in this section, but in the whole genus *Scleria*. Spikelets are always staminate and subandrogynous and separated in different parts of the inflorescence, which is of the Bracteata type (Camelbeke, 2001), with the staminate spikelets restricted to the upper part and the subandrogynous spikelets to the lower part of the inflorescence.

Species included (15 species). – *Scleria acanthocarpa* Boeckeler*, *S. arguta* (Nees) Steud., *S. assamica* (C.B. Clarke) D.M. Verma*, *S. atrogumis* D.A. Simpson*, *S. bracteata* Cav., *S. buekiana* Schldl.*, *S. camatrensis* Core*, *S. foveolata* Cav.* *S. latifolia* Sw., *S. myricocarpa* Kunth*, *S. neogranatensis* C.B. Clarke*, *S. orchardii* C.D. Adams, *S. panicoides* Kunth, *S. plu-siophylla* Steud., *S. rubrostriata* A.C. Araujo & N.A. Brummitt*.

Distribution. – Central and South America.

Notes. – No other *Scleria* species shows the remarkable separation of male and subandrogynous spikelets as found in *S. bracteata*. Therefore *S. bracteata* was previously classified in its own genus *Macrolomia* Schrad. ex Nees (1842). However, *S. bracteata* does have a slightly lacinate hypogynium and pseudopremorse leaves, which links the species to *S. sect. Schizolepis*.

Nees (1842) described *Schizolepis* as a new genus and Clarke (1908) and Chermeson (1937) treated it as a subgenus. However, most authors have used it at sectional level (e.g., Core, 1936; Camelbeke, 2001). Kern (1961) in his work on Malaysian *Scleria* remarked that the lacinate margin of the hypogynium is not a valid character for this subgenus. He stated that there are several Asian species of *Scleria* with lacinate hypogynium margins, referring to some species of *S. sect. Elatae*. However, the nature of the lacinate hypogynium in *S. sect. Schizolepis* is distinctly different from the hypogynium of those species in *S. sect. Elatae* (K. Bauters, unpub. data). In *S. sect. Schizolepis* the margins of the hypogynium are clearly fringed, while in *S. sect. Elatae* these margins are sometimes dentate, but never fringed as in *S. sect. Schizolepis*.

Scleria (subg. *Scleria*) sect. ***Scleria*** – Type: *S. flagellum-nigrorum* P.J. Bergius in Kongl. Vetensk. Acad. Handl. 26: 144, pl. 4–5. 1765.

Diagnosis. – All species in this section are tall, often climbing perennials with staminate and subandrogynous spikelets, these spikelets always having four empty glumes below the fertile glume. The hypogynium is characterised by three lobes with recurved margins (Fig. 5T, U), sometimes folded back so far that they reach the cupule (e.g., *Scleria flagellum-nigrorum*).

The hypogynium itself is deeply incised, forming three distinctive lobes. In most species a patently paniculate inflorescence (Camelbeke, 2001; merged under paniculate type in this paper) with staminate and subandrogynous spikelets is found, with the patent position of the branches caused by a swollen prophyll near the base of the axis. No pseudopremorse leaves are observed. This section is distinguished from *S. sect. Naumanniana* by the four empty glumes below the fertile glume in *S. sect. Scleria*, while in *S. sect. Naumanniana* only 2 empty glumes are found below the fertile glume.

Species included (13 species). – *Scleria amazonica* Camelb., M.T. Strong & Goetgh.*, *S. flagellum-nigrorum* J.P. Bergius, *S. gaertneri* Raddi, *S. huberi* C.B. Clarke*, *S. macbrideana* Gross*, *S. scandens* Core*, *S. skutchii* M.T. Strong & J.R. Grant, *S. splitgerberiana* Henrard ex Uittien, *S. stipitata* Uittien*, *S. tenacissima* (Nees) Steud.*, *S. triquetra* M.T. Strong*, *S. warmingiana* Boeckeler*, *S. williamsii* Gross.

Distribution. – *Scleria* sect. *Scleria* is restricted to Central and South America with *S. gaertneri* also occurring in Africa and Madagascar.

Notes. – Previously, *Scleria* sect. *Scleria* was a heterogeneous, polyphyletic group in the genus. Species not matching other sections were included in this section, which made characterising the section almost impossible (e.g., Clarke, 1908; Core, 1936; Nemes, 1956). Our results suggest a much narrower circumscription of the section, which is now mainly characterised by the deeply cut tri-lobed hypogynium with recurved margins (Fig. 5T, U).

Scleria subg. ***Trachylomia*** (Nees) Bauters, **comb. & stat. nov.**

≡ *Trachylomia* Nees in Martius, Fl. Bras. 2(1): 174. 1842 –

Type: *S. triglomerata* Michx., Fl. Bor.-Amer. 2: 168. 1803.

Diagnosis. – The subgenus can be characterised by its subcapitate inflorescence with few androgynous, subandrogynous and staminate spikelets and small papillose structures near the base of the nutlet, often in tubercles (Fig. 5D). Spikelets are arranged in the inflorescence following the *Trachylomia* type.

Species included (13 species). – *Scleria alpina* Core*, *S. balansae* Maury ex Micheli, *S. baldwinii* (Torr.) Steud., *S. bellii* LeBlond*, *S. ciliata* Michx., *S. colorata* Core*, *S. georgiana* Core, *S. havanensis* Britton*, *S. minor* (Britton) W. Stone*, *S. oligantha* Michx., *S. pauciflora* Muhl. ex Willd.*, *S. sellowiana* Kunth*, *S. triglomerata* Michx.

Distribution. – Species in this subgenus all occur in somewhat cooler climates of both the Northern and Southern Hemispheres in the Americas (Core, 1934), although most species are also found in more tropical regions (e.g., Florida, West Indies).

Notes. – Core (1934, 1936) placed the species with tubercles near the base of the nutlet in an unranked group named “Tuberculatae”. He failed, however, to include *Scleria georgiana* in this group, not realising that the six pores he described near the nutlet base of this species are actually six tubercles sunken in the surface of the nutlet (Fig. 5E, F). Together with *S. baldwinii*, he placed this species in *S. sect. Hypoporum* based on the assumption that *S. georgiana* did not have any tubercles. Admittedly, *S. baldwinii* is the odd one out in this subgenus and lacks any sign of papillose structures, so it might easily be

mistaken for a true species of *S. subg. Hypoporum*. However, the general subcapitate appearance of the inflorescence and the longitudinal ridges on the nutlet, which it has in common with *S. georgiana*, does place *S. baldwinii* in *S. subg. Trachylomia*. In *S. georgiana* the tubercles are somewhat reduced, while in *S. baldwinii* this reduction is complete. Also, *S. triglomerata* is related to this “Tuberculatae” group. Although it does not have pronounced tubercles, the papillose rim near the base of the nutlet (Fig. 5G) is built in the same way as the proper tubercles in *S. balansae*, *S. ciliata*, *S. georgiana* and *S. oligantha*. This last species is often confused with *S. triglomerata* since its nine tubercles often seem to form a closed rim in young specimens or in dried nutlets. The function of these papillose structures and tubercles is still not clear. Gaddy (1986) reported that nutlets of *S. triglomerata* are collected by ants, and a possible explanation could be that the papillose structures function as an elaiosome. Further research is needed to clarify the nature and purpose of these tuberculate structures. Most authors describe these papillose tubercles or rims as being part of the hypogynium. However, SEM imaging reveals that the position of the tubercles is an outgrowth of the pericarp and not of the hypogynium (Fig. 5D–F). Thus, it seems more likely that these structures are separate from the hypogynium and that the actual hypogynium is zoniform.

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Appendix 1. Vouchers information and GenBank accession numbers included in this study. All sequences were newly generated for this study.

Abbreviation used for analyses, taxon, collector plus number (herbarium code), origin and GenBank accession numbers ITS, *ndhF*, *rps16*.

Outgroup: **SC281** *Becquerelia cymosa* Brongn., *Van Andel T.R. & al. 4473* (GENT), Suriname, LN886915, LN887033, LN887144; **SC282** *Bisboeckelera microcephala* (Boeck.) T.Koyama, *Billiet F. & al. 1850* (BR), French Guiana, LN886916, LN887034, LN887145; **SC106** *Calyptrocarya glomerulata* (Brongn.) Urb., *De Wilde Bart 7* (TCD), Guyana, LN886843, LN886954, LN887070; **SC279** *Diplacrum caricinum* R.Br., *Sungkaew S. & Teerawatananon A. 636* (Thailand Natural History Museum), Thailand, LN886913, LN887031, –; **Ingroup:** **SC196** *Scleria abortiva* Nees ex Kunth, *Archer R.H. 3816* (MO), Madagascar, LN886879, LN886995, LN887110; **SC226** *S. abortiva, Razakamalala R. & al. 3309* (MO), Madagascar, LN886891, LN887007, LN887120; **SC072** *S. angusta* Nees ex Kunth, *Browning J. 390* (GENT), South Africa, LN886828, LN886939, LN887056; **SC008** *S. angustifolia* Robinson, *Hess H.&E. 52/597* (GENT), Angola, LN886807, LN886918, LN887036; **SC125** *S. arguta* (Nees) Steud., *Perry A. 1195* (GENT), Bolivia, LN886852, LN886964, LN887079; **SC203** *S. balansae* Maury, *Pedersen C. 2262* (MO), Brazil, LN886881, LN886997, –; **SC187** *S. baldwinii* (Torr.) Steud., *Bauters K. & Coenen J. 2013-038* (GENT), U.S.A., –, LN886992, LN887107; **SC204** *S. bambariensis* Cherm., *Biggood S. & al. 5695* (MO), Tanzania, LN886882, LN886998, LN887112; **SC205** *S. baroni-clarkei* De Willd., *Walters G. & al. 878* (MO), Gabon, LN886883, LN886999, –; **SC206** *S. baronii* C.B.Clarke ex Cherm., *Antilahimena P. & al. 5872* (MO), Madagascar, LN886884, LN887000, LN887113; **SC207** *S. bequaertii* De Willd., *Robinson E.A. 4260* (MO), Zambia, LN886885, LN887001, LN887114; **SC108** *S. biflora* Roxb., *Sungkaew S. & Teerawatananon A. 256* (Thailand Natural History Museum), Thailand, LN886845, LN886956, LN887072; **SC209** *S. boivinii* Steud., *Mamadou N. & al. 10* (MO), Gabon, LN886886, LN887002, LN887115; **SC068** *S. bracteata* Cav., *Toriola-Marbot D. 330* (GENT), French Guiana, LN886827, LN886938, LN887055; **SC059** *S. brownii* (R.Br.) Kunth, *Wilson K.L. 8098* (GENT), Australia, LN886823, LN886934, LN887052; **SC210** *S. brownii*, *Michell C.R. & Deichmann B. 3027* (MO), Australia, LN886887, LN887003, LN887116; **SC265** *S. bulbifera* Hochst. ex A.Rich., *Reekmans M. 6830* (GENT), Burundi, LN886904, LN887022, LN887134; **SC062b** *S. carphiformis* Ridl., *Wilson K.L. 8223* (GENT), Australia, LN886825, LN886936, –; **SC047** *S. castanea* Core, *Beck St. G. 22851* (GENT), Bolivia, LN886818, LN886929, LN887047; **SC049** *S. catophylla* C.B.Clarke, *Hess H.&E. 51/139* (GENT), Angola, LN886819, LN886930, LN887048; **SC202** *S. catophylla* C.B.Clarke, *Carvalho M.F. 4674* (MO), Equatorial Guinea, LN886880, LN886996, LN887111; **SC060** *S. ciliaris* Nees, *Wilson K.L. 8231* (GENT), Australia, LN886824, LN886935, LN887053; **SC189** *S. ciliata* Michx., *Bauters K. & Coenen J. 2013-042* (GENT), U.S.A., –, LN886993, LN887108; **SC063b** *S. comosa* (Nees) Steud., *Haase R. 753* (GENT), Bolivia, LN886826, LN886937, LN887054; **SC096** *S. corymbosa* Roxb., *Bart De Wilde & al. 02-199* (TCD), Thailand, LN886836, LN886947, LN887064; **SC127** *S. cyperina* Kunth, *Beck St. G. 133* (GENT), Brazil, LN886853, LN886965, LN887080; **SC214** *S. depauperata* Boeck., *Raynal J. & Jaffré T. 16510* (MO), New Caledonia, LN886888, LN887004, LN887117; **SC054** *S. depressa* (C.B.Clarke) Nelmes, *Goetghebeur P. 12128* (GENT), Cameroon, LN886821, LN886932, LN887050; **SC177** *S. distans* Poir., *Bauters K. & Coenen J. 2013-007* (GENT), U.S.A., LN886989, LN887104; **SC120** *S. eggersiana* Boeck., *Piepenbring M. & al. 2728* (GENT), Panama, LN886850, LN886961, LN887077; **SC275** *S. eggersiana*, *Camelbeke K. & Goetghebeur P. 939* (GENT), Costa Rica, LN886909, LN887027, LN887139; **SC025** *S. erythrorrhiza* Ridl., *Hess H.&E. 52/289* (GENT), Angola, LN886810, LN886921, LN887039; **SC216** *S. flagellum-nigrorum* P.J.Bergius, *Guillén R. & al. 1635* (MO), Bolivia, LN886889, LN887005, LN887118; **SC129** *S. flagellum-nigrorum*, *Moraes M. & al. 1785* (GENT), Bolivia, LN886854, LN886966, LN887081; **SC130** *S. foliosa* Hochst. ex A.Rich., *Malaisse F. & Goetghebeur P. 418* (GENT), Democratic Republic of the Congo, LN886855, LN886967, LN887082; **SC135** *S. gaertneri* Raddi, *Pott A. s.n.* (GENT), Brazil, LN886858, LN886970, LN887085; **SC271** *S. gaertneri*, *Camelbeke K. & Goetghebeur P. 903* (GENT), Costa Rica, LN886908, LN887026, LN887138; **SC186** *S. georgiana* Core, *Bauters K. & Coenen J. 2013-033* (GENT), U.S.A., –, LN886991, LN887106; **SC133** *S. globonux* C.B.Clarke, *Hess H.&E. 52/696* (GENT), Angola, LN886856, LN886968, LN887083; **SC134** *S. goossensii* De Willd., *Smith T.B. 585-52* (GENT), Cameroon, LN886857, LN886969, LN887084; **SC075** *S. greigiifolia* (A.Rich.) C.B.Clarke, *Desfayes M. 95-3121* (GENT), Madagascar, LN886829, LN886940, LN887057; **SC137** *S. hildebrandtii* Boeck., *Zwaenepoel A. 508* (GENT), Kenya, LN886859, LN886971, LN887086; **SC032** *S. hilsenbergii* Ridl., *Larridon I. & al. 2010-0138* (GENT), Madagascar, LN886812, LN886923, LN887041; **SC034** *S. hirtella* Sw., *Larridon I. & al. 2010-0241* (GENT), Madagascar, LN886813, LN886924, LN887042; **SC140** *S. iostephana* Nelmes, *Hess H. & E. 52/1229* (GENT), Angola, LN886860, LN886972, LN887087; **SC102** *S. kerrii* Turrill, *Bart De Wilde & al. 02-325* (TCD), Thailand, LN886840, LN886951, LN887067; **SC004** *S. lacustris* C.Wright, *Guareco I. 409* (GENT), Bolivia, LN886806, LN886917, LN887035; **SC276** *S. lacustris*, *Jacono C.C. 344* (GENT), U.S.A., LN886910, LN887028, LN887140; **SC224** *S. lagoensis* Boeck., *Gereau R.E. & al. 4306* (MO), Tanzania, LN886890, LN887006, LN887119; **SC141** *S. latifolia* Sw., *Camelbeke K. & Goetghebeur P. 913* (GENT), Costa Rica, LN886861, LN886973, LN887088; **SC142** *S. laxa* R.Br., *Wilson K.L. 7338* (GENT), Australia, LN886862, LN886974, LN887089; **SC182** *S. lithosperma* (L.) Sw., *Bauters K. & Coenen J. 2013-019* (GENT), U.S.A., –, LN886990, LN887105; **SC110** *S. mackaviensis* Boeck., *Wilson K.L. 9871* (NE), Australia, LN886847, LN886958, LN887074; **SC260** *S. mackaviensis*, *Waterway M. 2012-027* (NE), Australia, –, LN887021, LN887133; **SC104** *S. macrogyne* C.B.Clarke, *Bart De Wilde 26* (TCD), Guiana, LN886841, LN886952, LN887068; **SC145** *S. macrophylla* J.Presl & C.Presl, *Laegaard S. 101080* (GENT), Ecuador, LN886863, LN886975, LN887090; **SC112** *S. melanophala* Kunth, *Muasya M.A. 96/167* (GENT), Tanzania, LN886848, LN886959, LN887075; **SC028** *S. melanotricha* Hochst. ex A.Rich., *Desfayes M. 95-17115* (GENT), Madagascar, LN886811, LN886922, LN887040; **SC076** *S. microcarpa* Nees ex Kunth, *Desfayes M. 970117-21* (GENT), Paraguay, LN886830, LN886941, LN887058; **SC107** *S. microcarpa*, *Bart De Wilde 19* (TCD), Guiana, LN886844, LN886955, LN887071; **SC148** *S. mitis* P.J.Bergius, *Thomas W.W. & al. 11399* (GENT), Brazil, LN886865, LN886977, LN887092; **SC150** *S. naumanniana* Boeck., *Laegaard S. 16894* (GENT), Senegal, LN886866, LN886978, LN887093; **SC230** *S. neesii* Kunth, *Larsen K. & al. 45846* (MO), Thailand, –, LN887008, –; **SC232** *S. nyasensis* C.B.Clarke, *Rwaburindore P.K. 3708* (MO), Uganda, LN886892, LN887009, LN887121; **SC093** *S. oblata* S.T.Blake, *Bart De Wilde & al. 02-110* (TCD), Thailand, LN886834, LN886945, LN887062; **SC154** *S. obtusa* Core, *Beck. St. G. 46* (GENT), Bolivia, LN886867, LN886979, LN887094; **SC236** *S. oligantha* Michx., *Brant A.E. 4716* (MO), U.S.A., LN886893, LN887010, LN887122; **SC155** *S. panicoides* Kunth, *Solomon J.C. 18411* (GENT), Bolivia, LN886868, LN886980, LN887095; **SC252** *S. pantadenia* Meganck & Bauters, *Biggood S. & al. 5550* (MO), Tanzania, LN886902, LN887019, LN887131; **SC268** *S. pantadenia*, *Biggood S. & al. 8133* (MO), Tanzania, LN886907, LN887025, LN887137; **SC173** *S. pergracilis* (Nees) Kunth, *Madsen J.E. 5987* (GENT), Burkina Faso, LN886876, LN886988, LN887103; **SC239** *S. plusiophylla* Steud., *Zardini E. & Guerrero L. 37110* (MO), Paraguay, LN886894, LN887011, LN887123; **SC280** *S. poiiformis* Retz., *Bart*

Appendix 1. Continued.

De Wilde b89 (TCD), Thailand, LN886914, LN887032, LN887143; **SC122** *S. polycarpa* Boeck., *Turner H. 174* (GENT), Indonesia, –, LN886963, –; **SC019** *S. pooides* Ridl., *Hess H.&E. 52/281* (GENT), Angola, LN886809, LN886920, LN887038; **SC241** *S. pulchella* Ridl., *Bidgood S. & al. 5723* (MO), Tanzania, LN886895, LN887012, LN887124; **SC053** *S. purdiei* C.B.Clarke, *Beck St. G. 13542* (GENT), Bolivia, LN886820, LN886931, LN887049; **SC094** *S. purpurascens* Steud., *Bart De Wilde & al. 02-177* (TCD), Thailand, LN886835, LN886946, LN887063; **SC109** *S. racemosa* Poir., *Billiet F. S3802* (BR), Africa, LN886846, LN886957, LN887073; **SC009** *S. rehmannii* C.B.Clarke, *Laegaard S. 15729* (GENT), Zimbabwe, LN886808, LN886919, LN887037; **SC192** *S. reticularis* Michx., *Bauters K. & Coenen J. 2013-050* (GENT), U.S.A., LN886878, LN886994, LN887109; **SC043** *S. rugosa* R.Br., *De Dapper M. 81/1* (GENT), Indonesia, LN886817, LN886928, LN887046; **SC088** *S. scabra* Willd., *Luceño M. 282* (GENT), Brazil, LN886831, LN886942, LN887059; **SC242** *S. schiedeana* Schldtl., *Tellez O.V. 12761* (MO), Mexico, LN886896, LN887013, LN887125; **SC090** *S. schimperiana* Boeck., *Friis I. & al. 8034* (GENT), Ethiopia, LN886832, LN886943, LN887060; **SC091** *S. schimperiana*, *Smith P.A. 4309* (GENT), Botswana, LN886833, LN886944, LN887061; **SC100** *S. scrobiculata* Nees & Meyen, *Bart De Wilde & al. 02-99* (TCD), Thailand, LN886839, LN886950, LN887066; **SC105** *S. secans* (L.) Urb., *Bart De Wilde 10* (TCD), Guiana, LN886842, LN886953, LN887069; **SC244** *S. skutchii* M.T.Strong & J.R.Grant, *Grant J.R. & Rundell J.R. 92-02062* (MO), Costa Rica, LN886897, LN887014, LN887126; **SC040** *S. sobolifer* E.F.Franklin, *Reid C. 531* (GENT), South-Africa, LN886814, LN886925, LN887043; **SC259** *S. sphacelata* F.Muell., *Bruhl J.J. 2467* (NE), Australia, LN886903, LN887020, LN887132; **SC277** *S. sphacelata*, *Michell C.R. 3026* (MO), Australia, LN886911, LN887029, LN887141; **SC041** *S. spicata* (Spreng.) J.F.Macbr., *Harley R.M. 24658* (GENT), Brazil, LN886815, LN886926, LN887044; **SC246** *S. spiciformis* Benth., *Harris D.J. 8223* (MO), Gabon, LN886898, LN887015, LN887127; **SC162** *S. splitgerberiana* Henrard ex Uittien, *Gottsberger G. & Döring J. 126-19186* (GENT), Brazil, LN886869, LN886981, LN887096; **SC146** *S. sororia* Kunth, *Tenorio P.L. & al. 14638* (GENT), Guatemala, LN886864, LN886976, LN887091; **SC163** *S. sprucei* C.B.Clarke, *Saldias M. & al. 2703* (GENT), Bolivia, LN886870, LN886982, LN887097; **SC164** *S. staheliana* Uittien, *Cremers G. 12187* (GENT), French Guyana, LN886871, LN886983, LN887098; **SC097** *S. sumatrensis* Retz., *Bart De Wilde & al. 02-198* (TCD), Thailand, LN886837, LN886948, LN887065; **SC167** *S. tepuiensis* Core, *Gröger A. 1127* (GENT), Venezuela, LN886873, LN886985, LN887100; **SC055** *S. terrestris* (L.) Fassett, *Goetghebeur P. 12129* (GENT), Philippines, LN886822, LN886933, LN887051; **SC166** *S. tessellata* Willd., *De Smet K. 7714* (GENT), Burkina Faso, LN886872, LN886984, LN887099; **SC278** *S. testacea* Nees ex Kunth, *Schessl M. 3006* (GENT), Brazil, LN886912, LN887030, LN887142; **SC098** *S. tonkinensis* C.B.Clarke, *Bart De Wilde & al. 02-173* (GENT), Thailand, LN886838, LN886949, –; **SC168** *S. transvaalensis* E.F.Franklin, *Reid C. 1815* (GENT), South-Africa, LN886874, LN886986, LN887101; **SC266** *S. tricristata* Meganck & Bauters, *Bidgood S. & al. 6083* (MO), Tanzania, LN886905, LN887023, LN887135; **SC267** *S. tricristata*, *Bidgood S. & al. 5846* (MO), Tanzania, LN886906, LN887024, LN887136; **SC249** *S. triglomerata* Michx., *Kral R. 94078* (MO), U.S.A., LN886899, LN887016, LN887128; **SC250** *S. unguiculata* E.A.Robinson, *Bidgood S. & al. 5577* (MO), Tanzania, LN886900, LN887017, LN887129; **SC171** *S. verrucosa* Willd., *Hepper F.N. & Maley J. 7752* (GENT), Ivory Coast, LN886875, LN886987, LN887102; **SC118** *S. virgata* Steud., *Irwin H.S. & al. 20762* (GENT), Brazil, LN886849, LN886960, LN887076; **SC251** *S. vogelii* C.B.Clarke, *Jongkind C.C.H. 8509* (MO), Liberia, LN886901, LN887018, LN887130; **SC121** *S. williamsii* Gross., *Rivero E. 445* (GENT), Bolivia, LN886851, LN886962, LN887078; **SC042** *S. woodii* C.B.Clarke, *Dyer M.E. 753* (GENT), Nigeria, LN886816, LN886927, LN887045.