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to mainland Africa**

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Cover illustration: *Scleria racemosa* Poir. in Ankarafantsika National Park, Madagascar
(Photo by: Javier Galán).

***Scleria* diversity in Madagascar: evolutionary links to mainland Africa**

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Abstract

A taxonomic revision of the genus *Scleria* (Cyperoideae, Cyperaceae) in Madagascar is presented, supported by a phylogeny based on the markers *ndhF*, *rps16* and ITS. Collections from K, P and MO have been examined and 424 specimens identified to species level. Our results recognise 25 species of *Scleria* from Madagascar, including two varieties: six endemics, one near endemic, 10 African species and eight tropical widespread taxa. *Scleria achtenii* is reported for the first time in Madagascar and *S. rosea* is taken out of synonymy of *S. trialata*. Distribution maps, preliminary conservation assessments, and notes on synonymy, ecology and ethnobotany are provided. Nine species have been typified. Three rare endemic species: *S. andringitrensis*, *S. madagascariensis* and *S. perpusilla*, are assessed as threatened. The most diverse sections: *Abortivae* and *Hypoporum*, which include 13 species in total and 52% of the vouchers examined, showed strong differences in habitat preference.

ADDITIONAL KEYWORDS: conservation -- Cyperaceae -- Cyperoideae -- Sclerieae -- sedges -- typification -- taxonomy

INTRODUCTION

Cyperaceae is a cosmopolitan family which includes 94 genera and 5539 species of annual and perennial herbs (Govaerts *et al.*, 2017). This family, commonly known as the sedge family, has its centre of diversification in the tropics. However, sedges play a fundamental role in the ecology of seasonal and permanent wetlands at all latitudes. *Scleria* P.J.Bergius (1965), also known as nut rushes or razor grasses, is the sixth largest genus in the family with 257 species (Govaerts *et al.*, 2017), it is monophyletic (Bauters *et al.*, 2016), and the only genus in the tribe Sclerieae (subfamily Cyperoideae) (Franklin Hennessy, 1985; Simpson *et al.*, 2007). Although most species of *Scleria* occur in tropical Africa, South America and Asia, 35 species are found in North America (Govaerts *et al.*, 2017).

Scleria encompasses herbs with very variable habits, from tiny annuals with fibrous roots to perennial climbers more than ten metres long. Perennial habit is achieved by means of a stoloniferous rhizome or bulbs, and certain species develop aerial adventitious roots at stem nodes as an adaptation to flooded habitats (Jacono, 2008). Culms are trigonous or triquetrous. Leaves are alternate and spirally arranged, often persistent at the base, and finely serrate at least along the distal third of the margins, rarely entire. In certain groups, leaves are abruptly narrowed down or pseudopraemorse. Sheaths are sometimes winged, and usually topped by a contraligule or lingula (Haines & Lye, 1983), opposite to the blade. Flower-bearing branches develop at distal nodes, and are usually subtended by leafy bracts (Robinson, 1966). Flowers are always unisexual and enclosed by at least 3 glumes (Haines & Lye, 1983). Glumes are spirally arranged in staminate flowers, and distichous in pistillate flowers (Ahumada & Vegetti, 2009). Flowers group in spikelets, where the pistillate flower is always proximal. There are four types of spikelets in *Scleria* (Eiten, 1976; Ahumada & Vegetti, 2009): unisexual, i.e. pistillate or staminate; androgynous; and subandrogynous, when vestiges of male flowers are found in the form of empty glumes. The inflorescence is a panicle that, depending on which clade, shows different degrees of development (Ahumada & Vegetti, 2009; Bauters *et al.*, 2016). It can be summarized in true panicles (Figure 1A–C); truncated, when the main axis is underdeveloped (Figure 1D–F), and spicate-glomerulate (Figure 1G). The fruit is a nutlet, smooth or ornamented, subtended by a cupule and frequently surrounded by a hypogynium (Figure 2). In general, *Scleria* from Madagascar can be classified in two groups. The first encompasses plants with androgynous spikelets arranged in terminal spikes, and nutlets without a hypogynium. The second covers plants with lateral and terminal panicles made of subandrogynous or unisexual spikelets, and nutlets with a conspicuous hypogynium.

The hypogynium is taxonomically the most informative character and access to fruiting material is critical for identifying specimens at infrageneric level. Many authors have hypothesized about the origin of this structure but its origin remains obscure (Bauters *et al.*, 2016). The presence of a hypogynium led many authors to infer inaccurate relationships between genera within the tribes Sclerieae and Bisboeckelereae (Chermezon, 1937; Haines & Lye, 1983). Eiten (1976) focused on the sex of the flowers and branching pattern of the inflorescence to separate *Scleria* from the four genera in Bisboeckelereae. This approach was supported by Franklin Hennessy (1985), who proposed maintaining the tribe Sclerieae as monotypic. Currently, molecular analyses support this approach and place *Sclerieae*, as monotypic, however the phylogenetic relationship between Sclerieae and Bisboeckelereae remains unclear (Simpson *et al.*, 2007; Hinchliff *et al.*, 2010). Some authors place them as sister tribes (Jung & Choi, 2013), while others place Sclerieae inside Bisboeckelereae in a paraphyletic clade (Muasya *et al.*, 2009; Hinchliff & Roalson, 2013). For a long time, the genus *Acriulus* Ridl. (3 species; Clarke, 1908), was placed either in or close to *Scleria*. It was finally placed in *Scleria griegifolia* (Ridl.) C.B. Clarke (Kern, 1963). Many authors followed this approach (Robinson, 1966; Franklin Hennessy, 1985), and this has been recently verified in molecular analyses (Bauters *et al.*, 2016). Bauters *et al.* (2016) have recently published a complete infrageneric reconstruction of *Scleria* based on the markers ITS, *ndhF* and *rps16* where four subgenera and 15 sections are recognised.

Ecological considerations

Scleria grows in wet and open areas usually below 1700 m, from swamps to forest gaps and grasslands. Many species thrive in disturbed habitats, such as roadsides and field margins, and are therefore considered weeds. This is the case for *S. boivinii* Steud in Africa (Holm, 1979), *S. gaertneri* Raddi in Central and South America (Holm, 1979; Clavo Peralta, 1993), *S. poaeformis* Retz. in Asia and Australia (Holm, 1979; Naczi & Ford, 2008), *S. lithosperma* (L.) Sw. in West Polynesia (Holm, 1979), *S. tessellata* Willd. (Naczi & Ford, 2008) and *S. lacustris* C. Wright in Florida (Jacono, 2008). However, little is known about precise ecological aspects and relationships of *Scleria*.

Although wind pollination occurs in the genus (Hurst, 1972; Rosales *et al.*, 1997), many studies have shown the importance of insects as vectors for pollination. This is the case for some species of flies and wasps in America (Mexzón, 1997; Mexzón-Vargas & Chinchilla-López, 2003) and China (Jongjitvimol & Poolprasert, 2014). Nevertheless, relationships between insects and *Scleria* go beyond pollination. Leafhopper nymphs of the genus

Dorydiella from the Everglades feed on the stems of *Scleria* (DeLong, 1923), and other species of this genus in Canada are known to inhabit very specific prairies rich in *Scleria* and *Eleocharis* R.Br. (Paiero *et al.*, 2010). In Australia and Puerto Rico, larvae of many species of skippers of the family *Hesperiidae* feed on *Scleria* (Symon, 1980; Torres, 1992).

Insects also act as dispersal agents. Van der Pijl (1982) hypothesized that the hypogynium of some *Scleria* species resembles an elaiosome of the hepatica type, and in the Appalachians, seeds of *S. triglomerata* Michx. were removed by ants of the species *Aphaenogaster rudis* in 73% of the encounters (Gaddy, 1986). In wetlands, many birds eat *Scleria* nutlets (Olson & Blum, 1968; Hurst, 1972; Bruzual & Bruzual, 1983; Delany *et al.*, 2000), and epizoochory is an effective mechanism of dispersion in these habitats, where nutlets get stuck to the feet and legs of birds (Razi, 1950; Mossman, 2009). In the Galapagos, fruits of *S. distans* Poir. have been found in dung of turtles of the genus *Chelonoidis* (Blake *et al.*, 2012). Also, in the Mexican tropical rainforest, frugivorous birds and bats disperse the nutlets of *S. gaertneri* (Galindo-González, Guevara, & Sosa, 2000). However, seed buoyancy studies and germination tests from ingested seeds are needed to weigh the importance of hydrochory and endozoochory as dispersal mechanisms.

The genus *Scleria* in Madagascar

The first efforts to explore Madagascan sedge diversity started at the end of the nineteenth century with Rev. Richard Baron. In his *Compendium des plantes Malgaches* (Baron, 1906), he already recognized ten species of *Scleria* plus *Acriulus*. However, it was in 1937 when Henri Chermezon published the first major revision of the Cyperaceae of Madagascar, which was included in Henri Humbert's *Flore de Madagascar et des Comores*. Chermezon (1937) recognized four genera in the tribe Sclerieae: *Eriospora* Hochst. ex A.Rich., (now *Coleochloa*), *Diplacrum*, *Acriulus* and *Scleria*. In this publication, which constitutes the only revision of *Scleria* from Madagascar published to date, Chermezon identified 22 species and two varieties of *Scleria*, 12 of which were endemic. Currently, Govaerts *et al.* (2017) lists 26 species as occurring in Madagascar, with six endemics, two near-endemic, nine species also occurring on mainland Africa and nine more widely distributed species. *Scleria* is the second largest genus of sedges in Madagascar, and is one of the three genera highlighted in the Catalogue of the Vascular Plants of Madagascar (2017) where taxonomic revision is necessary.

Objectives

Using herbarium material, this study aims to: (1) update the taxonomy of the genus *Scleria* in Madagascar, (2) study the distribution of the species and elaborate preliminary conservation assessments, and (3) explore the phylogenetic relationships between species from Madagascar and their overseas relatives.

MATERIAL AND METHODS

Morphological study

All specimens and records were studied from BM, C, K, MNHN, MO, PI and TAN (Thiers, continuously updated). Definitions of all botanical terms follow Beentje (2016), unless specified otherwise. In total, 424 specimens were identified to species level, 355 of which were included in the distribution maps. Subgenera and sections here presented follow Bauters *et al.* (2016). The characters included in the descriptions were studied using a stereo optical microscope Leica S6 E with an amplification up to 40x.

DNA extraction, amplification and sequencing

For the phylogenetic analyses, 109 sequences were obtained from Bauters *et al.* (2016), 54 sequences facilitated by Kenneth Bauters are here used for the first time, DNA from 11 specimens was newly extracted and 18 sequences obtained for this study. Voucher information and GenBank accession numbers are provided in Appendix 2. Because of the poor quality of the DNA, four species could not be included in the analyses: *Scleria achnteei*, *S. andringitrensis*, *S. rutenbergiana* and *S. trialata*. DNA was sequenced using Sanger sequencing. Three markers were used: two from the chloroplast (*rps16* and *ndhF*) plus one nuclear (ITS). For ITS, only two primers were used (ITS-4 and ITS-L), whereas internal primers were necessary for *rps16* and *ndhF*: *ndhFA*, *ndhFIR1*, *ndhFIF2* & *ndhFD1*; *rps16F*, *rps16Rin2*, *rps16Fin1* & *rps16R2* (Bauters *et al.*, 2016).

Leaf samples between 15-20 mg were obtained from herbaria material and homogenized in a ball bearing grinder Retsch MM301. DNA was extracted with Qiagen Dneasy® Plant Mini Kit as explained in the protocol. PCRs were performed using 1 or 2 µL of total DNA in a total volume of 25 µL. Each reaction required 5.50 µL of H₂O, 12.50 µL of Premix Dream Taq™ (4.0 mM MgCl₂), 5 µL of TBT 5X buffer (Samarakoon, Wang, & Alford, 2013) and 0.50 µL of each primer at 0.2 µM. For ITS, 0.5 µL of DMSO (D₂H₆OS) were added. The initial

conditions followed Bauters *et al.* (2016). For ITS, initial denaturation and Taq activation occurred for 3 min at 96°C; followed by 30 cycles of denaturation (95°C-00:30 min), annealing (52°C-00:30 min) and extension (72°C-01:30 min); and final extension at 72°C for 7 min. A second round was performed at 94°C-2 min; 94°C-1 min, 47°C-00:30 min, 72°C-01:50 min (30 cycles); and 72°C-4 min. Although better results were generally achieved, because of lowering excessively the annealing temperature, second bands appeared during the electrophoresis. For *rps16*, initial denaturation and Taq activation was done at 96°C during 3 min; followed by 30 cycles of denaturation (95°C-00:45 min), annealing (57°C-00:45 min) and extension (72°C-01:00 min); and final extension (72°C-7 min). For *ndhF*, initial denaturation and Taq activation occurred at 96°C during 3 min; followed by 40 cycles of denaturation (95°C-00:45 min), annealing (50°C-00:45 min) and extension (72°C-01:00 min); and final extension (72°C-7 min). The electrophoresis gel was prepared by diluting 1 gr of agarose in 100 ml of Tris-acetate 1X buffer and stained with 4 µL of ethidium bromide.

DNA purification was done using silica-gel columns. Firstly, 125 µL of Qiagen PB binding buffer was added to the PCR product, loaded into the columns and centrifuged for 1 min at 13.000 rpm. Secondly, it was washed using 750 µL of Qiagen PE washing buffer and centrifuged two times, each for 1 min at 13.000 rpm. Finally, the DNA was diluted in 30 µL of elution buffer (10 mM Tris-Cl, pH 8.5).

Cycle-sequencing was performed in volumes of 5 µL. The reaction included 0.25-2.25 µL of H₂O and 1.00-3.00 µL of DNA, plus 1 µL of sequencing buffer 5X (400 mM of Trizma Base and 10 mM MgCl₂, pH 9.0), 0.25 µL of Big Dye® Premix 3.1 (ThermoFischer) and 0.50 µL of primer (1.0pmol/ µL). For ITS, 0.10 µL of DMSO 2% were added. This was followed by 26 cycles of denaturation, 00:10 min at 96°C; annealing, 00:05 min at 50°C; and extension, 04:00 min at 60°C. Concentration of total DNA was measured with a spectrophotometer NanoDrop 2000. Plates were read in an AB 3730 DNA Analyzer.

Phylogenetic analyses

Sequences were read and assembled in GENEious v10.2.3 (Kearse *et al.*, 2012), compiled in PhyDE-1 v0.9971 (Müller *et al.*, 2010), and aligned in MAFFT v7.310 (Katoh *et al.*, 2002; Katoh, Asimenos & Toh, 2009). The analyses were run in CIPRES (Miller, Pfeiffer, & Schwartz, 2010). The outgroup is represented by one species for each genus of the tribe Bisboeckelereae. Maximum likelihood (ML) and Bayesian Inference (BI) were performed for

each marker individually to check incongruences. Finally, analyses were run for the concatenated dataset.

ML analyses were performed in RAxML HPC Black Box v 7.2+ which applies the GTRGAMMA model for bootstrapping and inference of the best tree (Alexandros Stamatakis, 2006; Stamatakis, Hoover, & Rougemont, 2008). BI analyses were performed in MrBayes v3.2 (Ronquist *et al.*, 2012). BI analyses were run for 10 million generations on two runs, sampling every 1000th generation, and discarding the first 25% of trees as burn-in. For the concatenated set analyses, PartitionFinder v2.1 (Lanfear *et al.*, 2016) was used for model selection, which, using the Akaike Information Criterion, selected GTR+G as best fitting model for each of the three markers.

Trees were read in TreeGraph 2 (Stöver & Müller, 2010). Although only nodes with bootstrap (BS) values over 0.75 and posterior probability (PP) values higher than 0.95 are considered as well supported, any BS over 0.70 and PP above 0.80 are shown.

Mapping and preliminary conservation assessments

Distribution maps were produced with QGIS v2.18. Coordinates for non-georeferenced specimens were retrieved, where possible, from the *Gazetteer to Malagasy botanical collecting localities* (Schatz *et al.*, 2003). The only two specimens of *S. distans* var. *distans* could not be georeferenced, so no distribution maps are provided. The primary vegetation map, used to explore ecological preferences in the distribution of the species and sections, was downloaded from the Kew GIS unit Madagascar Project (Puy & Moat, 1996). The ecoregions map was retrieved from The Nature Conservancy (Majka & Platt, 2009).

For the preliminary conservation assessments, the IUCN Red List Categories and Criteria: Version 3.1 (2012) and its guidelines (IUCN Standards and Petitions Subcommittee, 2017) were followed. Area of Occupancy (AOO) and Extent of Occurrence (EOO) were calculated with GeoCAT (Bachman *et al.*, 2011). For endemic species known from three or less georeferenced collections, a precautionary principle has been applied as proposed by Callmander *et al.* (2011).



Figure 1. Main types of inflorescences of *Scleria* from Madagascar. A, inflorescence of *S. rosea* (Ramandimbimanana & Randimbiarison 460, K). B, inflorescence of *S. trialata* (Lance 30, K). C, inflorescence of *S. angusta* (Mogg 288898, K). D, truncated panicle of *S. melanomphala* (Brummit & Singe 232, K). E, truncated panicle of *S. griegifolia* (Bossert 15031, K). F, truncated panicle of *S. foliosa* (Raynal 7664, K). G, spicate-glomerulate inflorescence of *S. distans* (Croat 29582, K). H, panicle of *S. hilsenbergii* (Rajaonary 45, K). I, inflorescence of *S. lithosperma* (Frontier-Tanzania Coastal Programme Research Forest 412, K).

RESULTS

25 taxa, including two varieties, of *Scleria* from Madagascar were identified in the morphological study: six endemics; one restricted to Madagascar, the Comoros and Mayotte; 10 African species; five also present in America; two Asian and Australian; and one pantropical. The species belonged to two subgenera (*Scleria* and *Hypoporum*) and 10 sections. Sections *Abortivae*, *Hypoporum* and *Foveolidia* encompass 18 species in total, and 52% of the records correspond to the first two. Previous publications allowed to cover almost all the morphological variability observed in the studied herbarium specimens, consequently, there was a much reduced number of vouchers that showed enough morphological variability to be considered as new taxa. Because rare specimens were only found in single vouchers, potential new species have been excluded from this study until new collections are examined and further molecular work is done.

Most taxonomic changes are due to our broader knowledge of the genus and recent molecular evidence (Bauters *et al.*, 2016). Nine species are typified here (Appendix 1), including eight lectotypes and one neotype. *Scleria achtenii* is reported for the first time in Madagascar, and *S. abortiva* is here considered to be a synonym of *S. trialata*. Also, we propose to recognise the taxon *Scleria rosea* Cherm. (Figure 2G-H) as a species delimited morphologically and supported in the phylogenetic analyses. This taxon, described in 1923, was previously considered a variety, and finally a synonym, of *Scleria trialata*. There are four species for which, despite being listed in Madagascar (Govaerts *et al.*, 2017; Schatz *et al.*, 2017), we could not find any evidence of its occurrence. These are *Scleria bambariensis*, *S. lacustris*, *S. hirtella* and *S. secans*. The last two are restricted to Central and South America (Bauters *et al.*, 2016), but are very similar to their African relatives *Scleria distans* and *S. boivinii*. Descriptions for all the 25 taxa, including notes on distribution, habitat, phenology, and ethnobotanical considerations, are provided in Appendix 1.

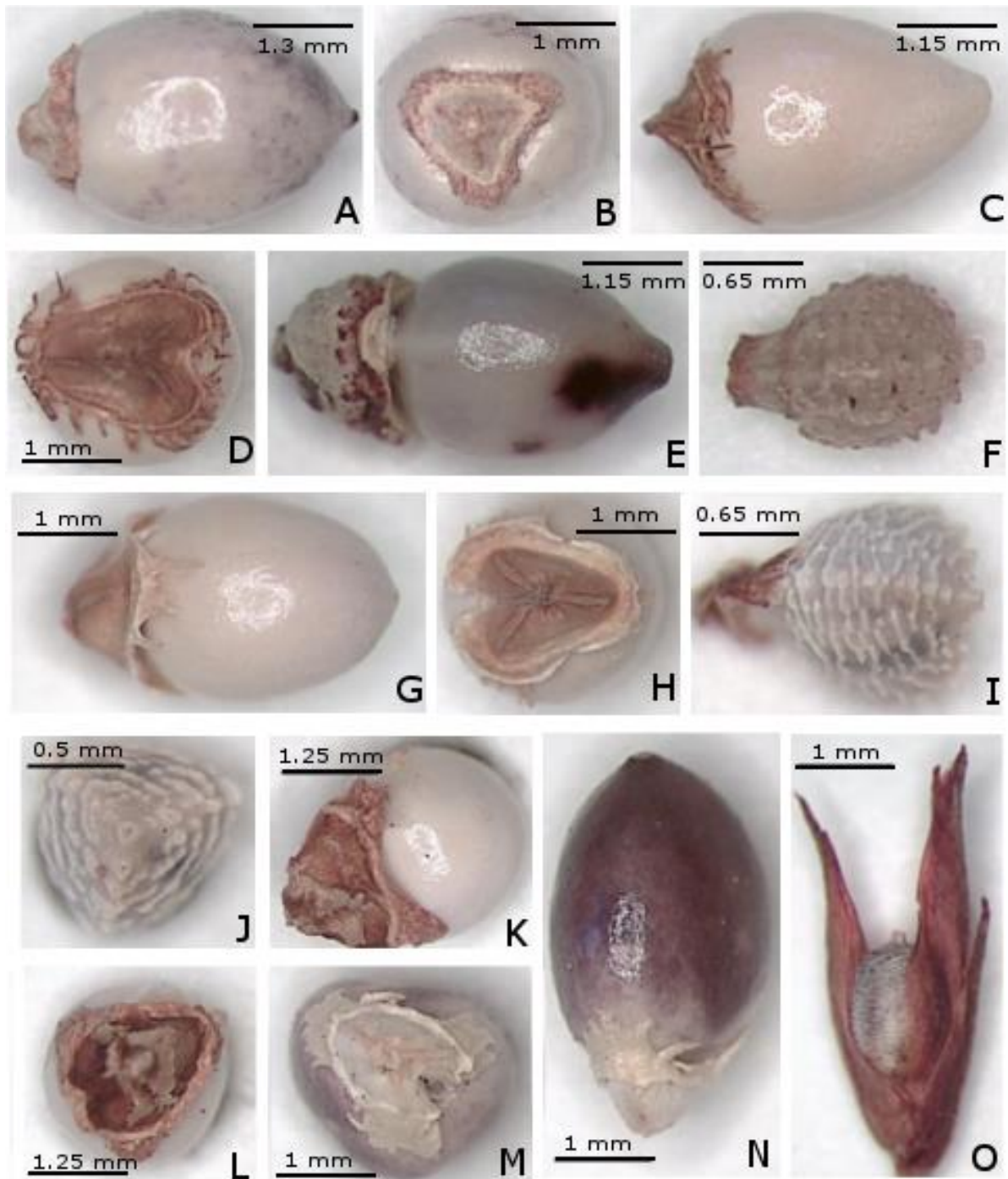


Figure 2. Nutlets of *Scleria* species occurring in Madagascar. A, B, *S. madagascariensis* (Rakotozafy 2741, K). C, D, *S. trialata* (Lance 30, K). E, *S. baronii* (Hoffman 221, K). F, *S. perpusilla* (Decary 7695, K). G, H, *S. rosea* (Ranarivelo 282, K). I, J, *S. hilsenbergii* (Rajaonary 45, K). K, L, *S. rutenbergiana* (Wilkin 941, K). M, N, *S. angusta* (Boivin s.n., K). O, *S. andringitrensis* (Perrier de la Bathie 14385, K).

KEY TO *SCLERIA* SPECIES FROM MADAGASCAR

- | | | |
|-----|---|---|
| 1 | Most spikelets androgynous; hypogynium absent (sect. <i>Hypoporum</i>)..... | 2 |
| 1' | Most spikelets unisexual or subandrogynous; hypogynium conspicuous (except for <i>S. baronii</i>)..... | 8 |
| 2 | Inflorescence with lateral panicles subtended by leafy bracts (Figure 1I); nutlets smooth with 3 depressions at the base; caespitose..... | (19) <i>S. lithosperma</i> |
| 2' | Inflorescence made of a single terminal spike or panicle..... | 3 |
| 3 | Inflorescence a terminal lax panicle; nutlets ornamented..... | 4 |
| 3' | Inflorescence a terminal spicate-glomerate panicle..... | 5 |
| 4 | Glomerules with 2–5 spikelets (Figure 1H); nutlets 1–1.3 mm × 0.7–1 mm in diameter, trigonous, wrinkles arranged mainly transversally (Figure 2I–J); culms puberulous at least at the base; annual plants | (18) <i>S. hilsenbergii</i> |
| 4' | Single spikelets held by slender and flexuous branches; culms glabrous; perennial plants, rhizomatous..... | (21) <i>S. pooides</i> |
| 5 | Inflorescence a reduced spike; culm < 10 cm; nutlet < 1.5 mm long, wrinkled (Figure 2F); annual plants..... | (20) <i>S. perpusilla</i> |
| 5' | Terminal spike 5–10 cm long, made of 4–10 glomerules; perennial plants..... | 6 |
| 6 | Glomerules erect; nutlets smooth to slightly verrucose; conspicuous bulb present at the base of the stem..... | (15) <i>S. bulbifera</i> |
| 6' | Glomerules reflexed; glumes villose (Figure 1G); rhizomatous..... | 7 |
| 7 | Nutlets smooth..... | (16) <i>S. distans</i> var. <i>distans</i> |
| 7' | Nutlets ornamented..... | (17) <i>S. distans</i> var. <i>chrondrocarpa</i> |
| 8 | Inflorescence a single terminal dense panicle, small lateral panicles rarely present; 10–20 cm long, 5–10 cm wide; stem > 1 m; leaves 40–70 × 1–3 cm; nutlets smooth, 3–3.5 × 2–2.5 mm; aquatic perennial, rhizomatous..... | (22) <i>S. poaeformis</i> |
| 8' | Inflorescence always with leafy bracts (flower-bearing branches therefore in terminal and lateral position)..... | 9 |
| 9 | Panicles truncated (main axis underdeveloped, Figure 1D–E)..... | 10 |
| 9' | True panicles, pyramidal or at least main axis well developed Figure 1A–C)..... | 16 |
| 10 | Hypogynium loosely attached to the nutlet; nutlet frequently ornamented; culm < 1 m; leaves; annual plants or perennials with short rhizome (sect. <i>Foveolidia</i>)..... | 11 |
| 10' | Hypogynium appressed; nutlets smooth; inflorescences clearly pedunculated; perennials with thick rhizome..... | 15 |
| 11 | Nutlet 3.5 × 1.7–2 mm wide, oblong, smooth, often very slightly pitted, white; hypogynium without conspicuous lobes, margin obscure with red dots; usually two panicles per node; tufted..... | (10) <i>S. hildebrandtii</i> |
| 11' | Hypogynium with lobes; nutlets not like that..... | 12 |
| 12 | Hypogynium with three slender lobes; nutlets 2.5–3.5 × 1.8–2.2 cm, slightly pitted, hairy underneath; leaves > 30 cm; culm triquetrous perennial..... | (11) <i>S. lagoensis</i> |
| 12' | Nutlets clearly pitted or reticulated, at least at the basal half..... | 13 |
| 13 | Perennial with reddish rhizome; nutlet white, pitted, hairy; hypogynium with long lobes, 2–3fid; leaves 20–25 × 0.4–0.5 cm, sheath scabrid..... | (8) <i>S. achtenii</i> |
| 13' | Annual plants; leaves < 30 cm long..... | 14 |
| 14 | Lateral panicles in pairs, peduncle 3–15 cm; nutlet ovoid, 3.5 × 2.5 mm, reticulated but smooth at the apex; hypogynium with lobes rounded..... | (9) <i>S. foliosa</i> |
| 14' | Lateral panicles solitary; nutlet oblong, 3–3.5 × 1.5–2 mm, regularly tessellate, white..... | (12) <i>S. tessellata</i> |

- 15 Nutlets 4–4.5 × 2–3 mm, beaked; hypogynium embracing the stipe; peduncle up to 20 cm, flexuous (Figure 1E); leaves glabrous; contraligule absent; glumes densely ciliate inside.....(6) *S. griegifolia*
- 15' Nutlets 3–3.5 × 2–2.5 mm oblong, smooth, apex dark (Figure 1D); peduncle > 15 cm; glumes glabrous inside and hairy externally.....(23) *S. melanomphala*
- 16 Hypogynium heart-shaped, lobes laciniate; leaves pseudopraemorse..... 17
- 16' Hypogynium never laciniate..... 19
- 17 Culm > 1.5 m, rachilla and prophyll red/purple; glumes straw coloured, margin ciliate; lateral panicles shorter than the internode (Figure 1A).....(4) *S. rosea*
- 17' Plants > 1.5 m; stem, rachilla and glumes straw coloured or brown..... 18
- 18 Glumes strictly straw coloured, ciliate at the base; lateral panicles generally shorter than the internode (Figure 1C); leaves 30–40 × 1.2–2 cm, largely acuminate, pleated when pressed; nutlet often purple, smooth (Figure 2M-N)...(1) *S. angusta*
- 18' External glumes and prophyll purple/blackish; inflorescence, densely branched, lateral panicles longer than the internode (Figure 1B); nutlet ovoid, smooth, white (Figure 2C-D).....(5) *S. trialata*
- 19 Hypogynium clearly trilobed..... 20
- 19' Hypogynium without 3 distinctive lobes..... 22
- 20 Inflorescence totally red: glumes, prophyll and rachilla; leaves pseudopraemorse; sheaths winged; contraligule membranous; nutlet ovoid; hypogynium with lobes short and dentate (Figure 2A-B)..... (3) *S. madagascariensis*
- 20' Inflorescence straw coloured..... 21
- 21 Nutlet hairy underneath; hypogynium deeply trilobed, margin revolute; panicle little branched; rachilla reddish, flattened; glumes straw coloured with reddish margin and green midrib(25) *S. gaertneri*
- 21' Nutlet smooth; lobes of hypogynium truncated (Fig. 2K-L)...(7) *S. rutenbergiana*
- 22 Perennial climber up to 15 m, tufted at the base; leaves very sharp; bracts 1–1.5 times longer than the spikelet; long staminal crest (1 mm); nutlet minutely hairy; hypogynium revolute.....(13) *S. boivinii*
- 22' Stout perennials; leaves pseudopraemorse..... 23
- 23 Nutlet 4.5–5 mm × 3–4 mm, style persistent; hypogynium finely ciliate; cupule thickened; stem up to 3 m; sheaths winged; leaves 30–60 × 1.5–3 cm(24) *S. racemosa*
- 23' Nutlet 2.5–3 × 2–2.5 mm; hypogynium extremely reduced, white to purplish (Figure 2E); leaves 30–40 cm long.....(2) *S. baronii*

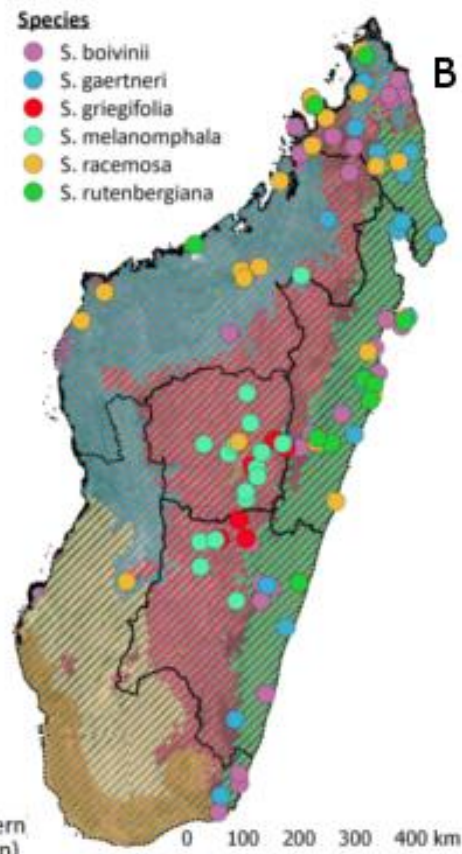
The results and discussion mainly refer to the ML analysis of the concatenated alignment with BS and PP values, shown in Figure 3, all single marker and concatenated analyses are available in Appendix 3. Sections *Scleria* and *Schizolepsis* were only well resolved in the BI analysis of the concatenated alignment (Appendix 3 Figure 8), and showed inconsistencies across the other analyses. Bauters *et al.* (2016) already commented on the incongruences found in these clades. Nevertheless, the species *S. gaertneri* was well supported in every analysis except for BI and ML of the marker rps16 (BS = 62, PP = 0.85). Sections *Ophryoscleria* and *Abortivae* were supported in all the analyses (BS > 95, PP = 1). However, *Abortivae* infrageneric relationships were not resolved. *Scleria angusta* from Africa and Madagascar did not form a

well supported clade in any analyses. *S. rosea* was well supported in the analyses of the marker *ndhF* (BS = 97, PP = 1) and the concatenated alignment (PP = 0.96). Sections *Foveolidia*, *Hymenolytrum*, *Melanomphalae*, *Margaleia*, *Acriulus* and *Hypoporum* clustered in well supported clades throughout all the analyses (BS > 99, PP 1), with the only exception of sections *Acriulus* and *Margaleia* in the analysis of the single marker ITS (BS = 73, PP = 0.89). Regarding the infrageneric relationships of the pantropical species, African and American specimens of *S. poaeformis*, *S. gaertneri* and *S. distans* formed one single supported clade for each species. *S. lagoensis* was not monophyletic in any of the analyses. Instead, American and African specimens showed significant differences in the ML analysis of the single marker *rps16* and ML and BI analyses of the concatenated alignment. *Scleria distans* var. *chondrocarpa* was only well supported in BI of the marker ITS (PP = 0.99). *Scleria hilsenbergii* and *S. pooides* were sister species in all analyses but were only well supported as individual species in the concatenated analyses and the single marker ITS. *Scleria bulbifera* includes three consistent clades throughout all the analyses, except in the concatenated and ITS analyses where only two of them are well supported.

Figure 4 shows all the localities where each species has been collected. *Scleria* occurs in all Madagascan ecoregions, however, a spatial bias is very evident, with most vouchers collected in easily accessible spots along the main road network. Seven species are known from up to four georeferenced localities (Figure 4A). Of these seven species, four are widespread outside Madagascar and three are endemic: *S. madagascariensis* (Figure 2A-B), *S. perpusilla* (Figure 2F) and *S. andringitrensis* (Figure 2O). Additional research is needed to assess the extinction risk of these species. Nevertheless, because none of them have been collected in the last 30 years, we propose to assess them as threatened until new evidence becomes available (see Appendix 1). The remaining taxa can provisionally be listed as least concern (LC).



Figure 3. ML analysis of the concatenated alignment. BS values and PP are displayed at the left and right side of the slash respectively. The box includes the same tree with branch lengths. The squares represent the areas where the species occurs.



Ecoregions

- Dry Deciduous Forests (Western)
- Succulent Woodlands (Western)
- Subhumid Forests & Grasslands (Central)
- Lowland Forests (Eastern)
- Spiny Thickets (Southern)

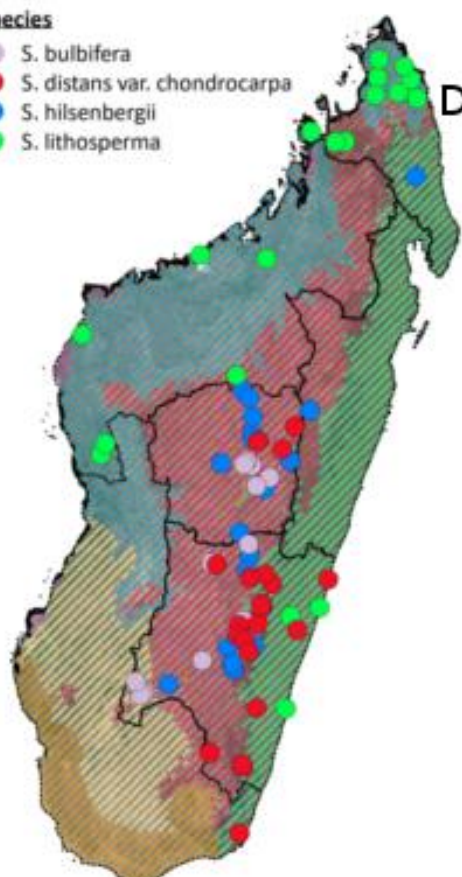
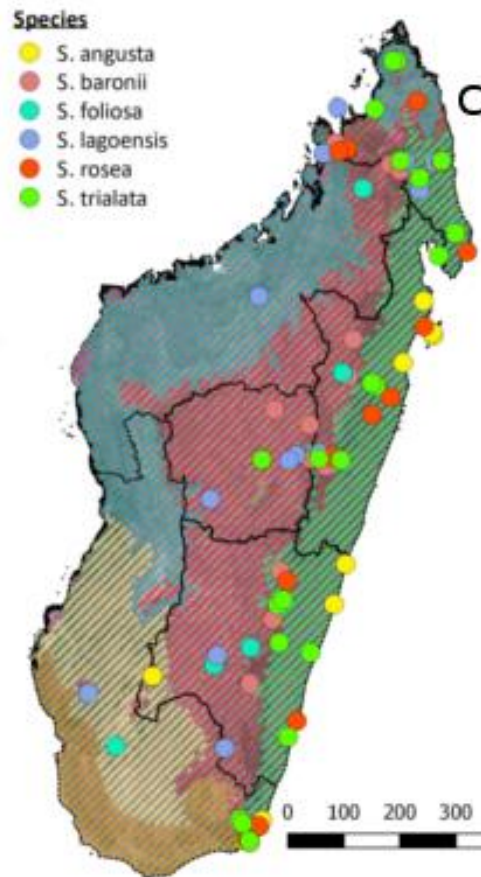


Figure 4. Distribution maps for all *Scleria* species known to occur in Madagascar. The points represent herbarium vouchers from P, K and MO. The black line separates the six provinces of Madagascar. The coloured areas represent the seven ecoregions of Madagascar (Majka & Platt, 2009). A. Species known from less than four georeferenced collections. Triangles represent species preliminary assessed as threatened. B. Species that belong to sections with only one species in Madagascar. C. Species from the sections *Abortivae* and *Foveolidia*. D. Species within the section *Hypoporum*.

Sections *Abortivae* and *Hypoporum* show different preferences in habitat. The first are mostly restricted to the eastern evergreen forests, and the latter to dryer vegetation types of Central Madagascar (Figure 5).

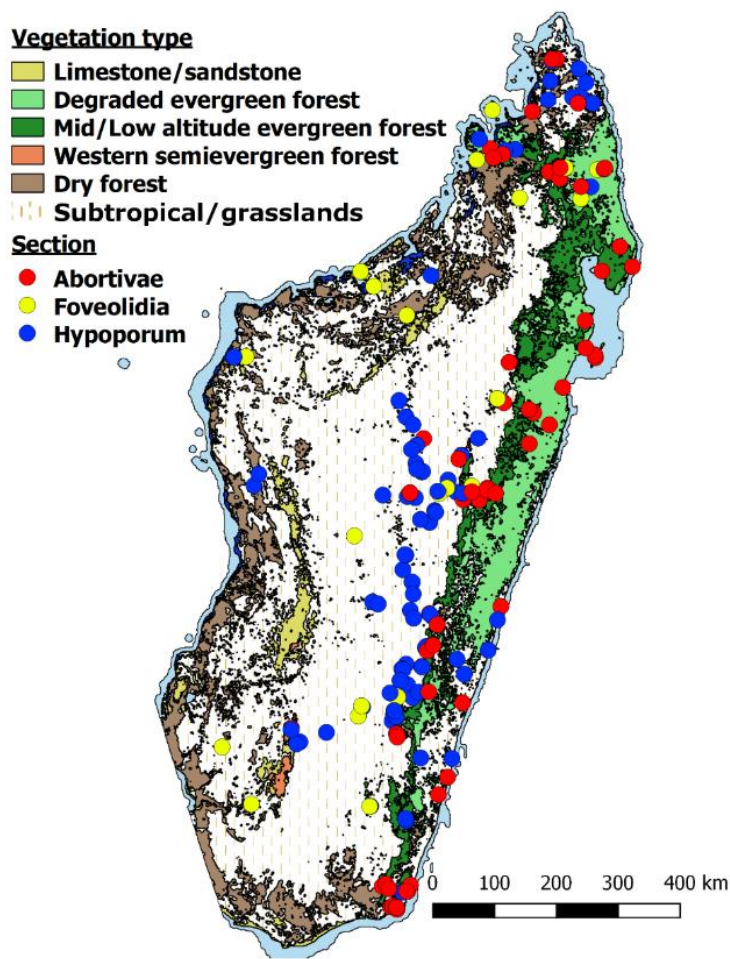


Figure 5. Sections *Abortivae* and *Hypoporum* plotted against the map of primary vegetation (Puy & Moat, 1996).

DISCUSSION

Callmander *et al.* (2011) estimated that, of the 1698 native but non-endemic Malagasy species of angiosperms, 654 are exclusively shared with Africa and 41 are also present in Asia and the New World. Our results show that 10 of the 24 species of *Scleria* found on Madagascar also

occur in Africa, and eight in tropical America, Asia or Australia, a higher proportion than most genera. Gautier & Goodman (2003) hypothesized that, given the long isolation of Madagascar, there is a large number of plant genera (around one third) that show pantropical distribution, which can be explained by means of efficient dispersal mechanisms. Our results reinforce this hypothesis in two ways. Firstly, Figure 3 shows that at least three different *Scleria* lineages diversified in Madagascar. The ancestors of these lineages probably arrived by hydrochory (Jacono, 2008) and avian epi/endozoochory (Bruzual & Bruzual, 1983; Delany *et al.*, 2000; Mossman, 2009). Further molecular research is necessary to evaluate if there is a common Madagascan ancestor to *S. perpusilla*, *S. andringitrensis* and *S. hilsenbergii*, or whether they are descendent from different African relatives. Another uncertain point is the origin of *S. rutenbergiana*. Our morphological study agrees with both Chermezon (1937) and Bauters *et al.* (2016) that *S. rutenbergiana* seems related to certain species in section *Elatae*, such as *S. terrestris*. However, section *Elatae* only occurs in Asia and Oceania, with the only exception of *S. sumatrensis*, which is also present in Seychelles, but very different to *S. rutenbergiana*.

Secondly, the large non endemic element in *Scleria* (76% of the species) must be recent additions that arrived, apart from the means previously explained, intentionally or accidentally by humans during the last 2000 years (Binggeli, 2003). There are many recorded uses of *Scleria* by local peoples from Africa and India that support this idea (Appendix 1). These two findings, besides the ability of *Scleria* to thrive in most wet and open habitats (Holm, 1979), may explain the high proportion of African and Asian species of *Scleria* widespread in Madagascar compared to other genera.

The opposite process has also occurred, in which species that have diversified in Madagascar have colonised other regions through long distance dispersal. This is the case of section *Abortivae*, which includes one species also present in the Comoros and Mayotte (*S. trialata*), one in South Africa (*S. angusta*) and one endemic to Seychelles and Mascarenes (*S. sieberi*) as well as three Madagascar endemics (*S. baronii*, *S. madagascariensis* and *S. rosea*). A more in-depth sampling of populations from South Africa, Madagascar and nearby islands is needed to unveil the phylogenetic relationships between species in section *Abortivae*. African and Madagascan populations of *S. angusta* have a great similarity in morphology and habitat preference (both occur in wetlands along the coast (Gordon-Gray, 1995), which suggests that they indeed belong to the same species. Although there is considerable variability within *S. trialata*, no evidence was found to separate *S. abortiva* and *S. trialata* as traditionally circumscribed. This approach is also followed by Schatz *et al.* (2017). Many *Scleria* specimens

found in the Seychelles and the Mascarenes have been identified as *S. sieberi* Nees or as its synonym *S. angusta* Nees var. *seychellensis*. However, the taxonomic status of this taxon is uncertain and it needs to be typified. Most specimens from the Seychelles and the Mascarenes can be identified as *S. trialata*. *S. sieberi* sensu C.B. Clarke is closely related to, and probably the same species as, *S. rosea* bearing largely acuminate leaves, white to purple nutlets with a lacinate hypogynium, spikelets with conspicuous bracts and inflorescences with a reddish rachilla and straw coloured glumes. If both taxa are merged, *S. sieberi* has priority over *S. rosea*, however, collections from the Seychelles and Mauritius have to be examined. Not all species in the genus have a lacinate hypogynium; in *S. madagascariensis* it is trilobate and dentate, whereas in *S. baronii* it is an extremely reduced one.

The phylogenetic results presented here confirm that the pantropical taxa *S. gaertneri*, *S. distans* and *S. poaeformis* each represent a monophyletic species as was suggested based on morphological similarity. However, more extensive sampling is needed to assess if genetic differences have started arising between populations from different continents. On the other hand, Robinson (1966) already referred to the relationship between the morphological variants of *S. lagoensis* and their distribution; a statement that is now supported with molecular data (Figure 3). Although a more extensive sampling is needed to address this issue, this proves that molecular evidence is critical in delineating species of *Scleria* with a wide distribution range, and caution should be taken before merging two species. Thus, additional sampling is necessary to evaluate the status of *S. lithosperma* and *S. tessellata*. On the other hand, *S. bulbifera*, shows an internal consistent variability throughout the analyses (see Appendix 3), which along with the morphological variability observed in the specimens and noted by previous authors (Gordon-Gray, 1995), suggests that the presence of a conspicuous bulb may be characteristic to a whole clade rather than to a single species.

Differences in phenology can be inferred from the data. Whereas species which occur in the East, fruit throughout the year, species in Central Madagascar typically fruit during the wet season (November to April), possibly due to an increase in seasonality. Our results show that there is a strong relationship between phylogeny and habitat preferences (Figure 5), which has important considerations in conservation assessments; populations of species restricted to the eastern evergreen forests, an ecosystem threatened by deforestation, need to be evaluated. As *Scleria* has proved to succeed in disturbed areas (Holm, 1979), it seems unlikely that deforestation will cause an imminent extinction of any of its species. However, the status of *S. andringitrensis*, *S. madagascariensis* and *S. perpusilla* need to be immediately reassessed.

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APPENDIX 1. Species descriptions, distribution and preliminary conservation status

SCLERIA (SUBG. *SCLERIA*) SECT. *ABORTIVAE* *Cherm. ex Bauters*

(1) *Scleria angusta* Nees ex Kunth in Enum. Pl. 2: 346 (1837). *Type*: MADAGASCAR. Cap. b. Spei., 1.iii.1832, *Drège 4246* (lectotype, designated here: MNHN-P-00462002!; isoelectotypes: MNHN-P-P00462000!, MNHN-P-P00462001!, K000363518! and K000363519!).

Perennial. Culm 1–2.5 m long, 3–4 mm thick, triangular, mainly glabrous, sheath occasionally puberulent. Leaves 30–40 cm long, 1.2–2 cm wide, largely acuminate, pleated when pressed, pseudopraemorse. Medium leaves closely arranged, sheaths completely covering the culm. Antrorse prickly-hairs usually present along margins and distal third of the central nerves on the abaxial side. Contraligule triangular, rounded, puberulous, purplish. Panicle with leafy bracts, pyramidal, terminal 7–12 cm long, laterals solitary and at least the most basal shorter than the internode (Figure 1C). Peduncle only visible in the basal panicles, generally less than 5 cm long. Rachilla pale brown to greenish, sometimes reddish, flattened. Prophyll, rachilla and bracts of the spikelet glabrous, sometimes hairy. Spikelets unisexual or subandrogynous. Male glume 3–4 mm long, female 3 mm, shortly mucronate, beige, mucronate, ciliate at the base. Nutlet ovoid to piriform, 2–2.5 mm long, 1.5–2 mm in diameter, white to purple, smooth, shiny. Hypogynium heart-shaped, lacinate, especially on the lobes (Figure 2M–N).

Distribution and habitat: South Africa and Madagascar. South Africa: patchy distribution along the coast of Natal, in swamp forest (Gordon-Gray, 1995). Madagascar: along the east coast, in wetlands, most rarely close to rivers and lakes in the Central region. 0–700 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR: L'Ouest de l'Isalo, 30.vii.1928, *H. Humbert 5055* (TAN001250, MNHN-P-P0189809, K); 700–800 m, i.ii.1934, *H. Humbert 13750* (MNHN-P-P01898854) ; **Antananarivo**: x.1882, *R. Baron 1435* (K, MNHN-P-P01707789); **Antsiranana**: Daraina, Antsahabe Forest, 550 m, 11.i.2004, *L. Nusbaumer LN916* (K); **Toamasina**: Tamatave, 26.vii.1912, *K. Afzelius s.n.* (K); **Toliara**: Tôlanaro, Ste. Luce, 10 m, 20.x.1989, *R. Rabehovitra 2062* (K, MO); Soomierana, 10.x.1932, *M. R. Decary 10768* (K).

(2) *Scleria baronii* C.B. Clarke in Consp. F. Afr. 5: 669 (1895). *Type*: MADAGASCAR, Antananarivo: 1889, *R. Baron 4296* (lectotype, designated here: K000363341!; isoelectotype: MNHN-P-P00457088!).

Perennial with a robust rhizome. Culm 1–2.5 m, 5–6 mm thick. Leaves 30–40 cm long, over 2.5 cm wide, pseudopraemorse, glabrous. Contraligule triangular, puberulous on the surface, margin membranous and reddish, inner nerves curved outwards following the margin. Inflorescence with leafy bracts, lateral panicles always solitary at the nodes. Panicles lax, copiously branched, basal secondary branches over 4 cm long. Laterals 10–12 cm long, peduncle 3 cm, longer than the internode. Spikelets unisexual or subandrogynous. Glumes 3–4 mm long, dark purple, female mucronate, glabrous, prophyll puberulous. Nutlet ovoid, 2.5–3 mm long, 2–2.5 mm in diameter, white to purplish, smooth, shiny. Hypogynium very reduced, cupule very thick and dark (Figure 2E).

Distribution and habitat: endemic to Madagascar, in mid and low altitude evergreen forests. 800–1700 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antananarivo:** 1889, *R. Baron* 4296 (K000363341, MNHN-P-P00457088); **Antsiranana:** DIANA, 500 m, 3409, *H. Perrier de la Bâthie* 2632 (MNHN-P-P00457087); **Fianarantsoa:** Ambohimombo Forest, i.1895, *Forsyth Major* 205 (K); RS Ivohibe, Marovitsika Forest, 17.x.2000, *P. Hoffman et al.* 221 (K, MNHN-P-P01898846); **Toamasina:** 11 .xii.1958, *Réserves Naturelles* 9632 (MNHN-P-P01896595, MNHN-P-P01896596); Alaotra-Mangoro, 987 m, 14.ii.2007, *P. Antilahimena* 5872 (MO, MNHN-P-P01708459, TAN); Alaotra-Mangoro, 993 m, 14.ii.2007, *P. Antilahimena* 5349 (MO, MNHN-P-P01670451, TAN); Toamasina: 900 m, ix.1953, *J. M. Bosser* 6569 (MNHN-P-P01896592, MNHN-P-P020640250) 900–1200 m, ix.1937, *H. Humbert* 18035 (MNHN-P-P02640249).

Notes: The reduced hypogynium led Chermeson (1937) to place it in the section *Elatae*.

(3) *Scleria madagascariensis* Boeckeler in Bot. Jahrb. Syst. 5: 514 (1884). *Type:* MADAGASCAR, Antananarivo: Ost-Imerina: Andrangoloaka, xi.1880, *J.M. Hildebrandt* 3745 (lectotype, designated here: K00363342!; isolectotypes: MNHN-P-P00457089! and MNHN-P-P00457090!).

Perennial with conspicuous rhizome. Culm 1.5–2 m long, 2.5–3.5 mm wide, triquetrous, scabridulous, edges red. Internodes of the inflorescence completely red. Leaves 20–30 cm long, 1.2–1.4 cm wide, pseudopraemorse, arranged every 10 cm along the culm. Sheaths glabrous or puberulous, winged. Prickle hairs present all along the margin and wings, retrorse, reddish, antrorse along the veins, only at the apical part, scarce. Contraligule triangular,

rounded, margin red, membranous. Inflorescence red, with leafy bracts. Panicle pyramidal, one terminal plus 3–4 laterals, 8–13 cm long, each lateral as long as the internode, the basal pedunculate. Spikelets unisexual or subandrogynous. Glumes 3–4 mm long, slightly mucronate, reddish, finely ciliate along the margin and hairy at the base. Conspicuous bracts, 2–6 cm long. Prophyll completely purple, puberulous. Nutlet 3–3.5 mm long, 2–2.5 mm wide, ovate, smooth, white, apex purplish. Hypogynium trilobed, dentate, white with red dots (Figure 2A-B).

Distribution and habitat: Endemic to Madagascar. Only known from four localities. Evergreen forest. 1200–1400 m.

Conservation status: EN B1ab(ii,iii) +B2ab(ii,iii). AOO is 12 km² and is known from less than 5 localities. It was recorded for the last time in 1991. Since all localities are along the western border of the eastern evergreen forest, a reduction of the AOO and quality of its habitat can be inferred from the primary and remaining primary vegetation maps (Puy & Moat, 1996).

Representative specimens examined: MADAGASCAR, **Antananarivo:** Anjozorabe Forest, 1400 m, 3.ix.1991, A. Rokotozafy et al. 2741 (MO, K); Ost-Imerina: Andrangoloaka, xi.1880, J.M. Hildebrandt 3745 (K000363342); **Central:** x.1881, R. Baron 452 (K).

Notes: There are many misidentifications between *S. madagascariensis* and *S. rosea*. However, *S. madagascariensis* is a very rare species that always shows winged sheaths, reddish glumes, spikelets with long bracts and a dentate hypogynium.

(4) *Scleria rosea* Cherm., Bull. Soc. Bot. France 70: 298 (1923). *Scleria trialata* var. *rosea* (Cherm.) Cherm. *Type:* MADAGASCAR, Andorovanto: Anivorano R. Viguier & H. Humbert 574, 8.x.1912 (lectotype, designated here: MNHN-P-P00457097!; isolectotype: B 10 0166745!). Malagasy: *vendranala*, *lamiera*.

Perennial, rhizome well lignified. Culm 0.8–1.5 m long, 2–3.5 mm wide, triquetrous, scabridulous, reddish. Leaves 15–25 cm long, 1–1.4 cm wide, glabrous but puberulous towards the mouth, pseudopraemorse. Sheaths sometimes winged. Margin and distal part of the veins scabrid, reddish. Contraligule triangular, apex rounded, margin dark, ciliate. Inflorescence with terminal and lateral panicles subtended by leafy bracts. Panicles pyramidal to spiciform (Figure 1A). Peduncle very short, almost entirely inside the sheath. Laterals shorter than the internodes, solitary. Rachilla reddish. Spikelets unisexual or subandrogynous. Glumes 2–3.5 mm long, shortly mucronate, straw coloured to dark purple/reddish, margin

ciliate. Prophyll purple, puberulous. Nutlet ovoid, 2.5–3 mm long, 1.5–2 mm wide, white, smooth. Hypogynium heart-shaped, white, lacinate (Figure 2G-H).

Distribution and habitat: Endemic to Madagascar. On littoral and mid altitude evergreen forests. 0–1000 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antsiranana:** Ambahatra, 800 m, 3.iii.1999, *L. Gautier et al. LG3457* (GENT, K, MNHN-P-P01888410); Ambre Mount, 850 m, 29.iii.2012, *S. D. Ramandimbomanana et al. SDR460* (GENT, K); Bekolosy, 850 m, 20.v.1995, *L. Gautier & C. Chatelain LG2737* (K, MNHN-P-P01888409); Daraina, 800 m, 3.xii.2004, *L. Gautier & R. Claude LG4821* (GENT, K, MNHN-P-P01708460); 400 m, 4.v.2010, *C. Birkinshaw et al. 1769* (MO, K); **Fianarantsoa:** Ivohimonitra Forest, 1896, *Forsyth Major 90* (K); RS Manombo, 20 m, 20.ix.2005, *R. Razakamalala et al. 2175* (MO, K); *R. Razakamalala et al. 776* (MNHN-P-P01888402, MO); **Toamasina:** Maroantsetra, 100–200 m, 1.xi.2001, *O. Poncy 1549* (K, MNHN-P-P00373065); Maroantsetra, 4 m, 5.ix.2009, *H. Ralimanana RLII285* (K); RS Mangerivola, 491 m, 23.vii.2006, *T. Ranarivelo et al. RTI282* (K); **Toliara:** Anosy, 0–10 m, 29.iv.1989, *R. E. Gereau et al. 3434* (MO, K, MNHN-P-P01888401); Manantanteli Forest, 60–300 m, 22.ix.1928, *H. Humbert 5820* (K, MNHN-P-P01888400).

Notes: This is probably the same species as *S. sieberi* Nees sensu C.B. Clarke (SEYCHELLES: 1874, J. Home 636 K000363347; J. Home 636 642 K000363348). *S. sieberi* is endemic to Mascarenes and Seychelles. However, further exploration is necessary of collections from the Mascarenes and the Seychelles.

(5) *Scleria trialata* Poir. in J.B.A.M. de Lamarck, Encycl. 7: 6 (1806). *Scleria abortiva* Nees ex Kunth, *Scleria abortiva* var. *planifolia* Cherm. Type: MADAGASCAR, L.M.A. du Petit-Thouars s.n. (holotype: MNHN-P-P00457082!; isotype: MNHN-P-P00457083!). Malagasy: *tsivendrambendrana*, *verradrady*.

Perennial. Culm 1.5–2 m, 3–6 mm wide, triangular, puberulous, soft, with appressed hairs scattered all over specially near the mouth. Leaves 25–35 cm long, 1.4–2 cm wide, pseudopraemorse, arranged every 5–7 cm. Prickle hairs present, antrorse, along the margin and distal part of veins. Blade sometimes rough, covered by a dense indumentum of stiff appressed antrorse hairs. Sheaths loose, covering almost completely the culm. Contraligule triangular, apex rounded, puberulous, margin ciliate, internal veins curved outwards

sometimes straight at the mouth. Conspicuous inflorescence, densely branched (Figure 1B). Terminal panicle 7–12 cm long. Laterals longer than the internode, solitary. Peduncle usually less than 3–5 cm, sometimes covered by the sheath. Rachilla straw coloured. Spikelets unisexual or subandrogynous. Male glume 3.5–4 mm long, female 3–3.5 mm, mucronate, margin entire or finely ciliate. External mainly brownish, purple/red on the margins, internals completely purplish. Bracts less than 2 cm long, scabrid. Prophyll straw coloured, puberulent. Nutlet ovoid, 2.5–3 mm long, 1.5–2 mm wide, smooth, white. Hypogynium heart-shaped, yellowish brown, lacinate (Figure 2C-D).

Distribution and habitat: Madagascar, the Comoros, Mascarenes and Mayotte. Restricted to the northern and eastern wet forests. 0–1000 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antananarivo:** 950 m, 13.viii.1968, *J. H. McWhirter 120* (K); Ankazobe, 23.xii.1947, *M. P. Saboreau 1185* (K); x.1882, R. Baron 1424 (K, MNHN-P-P01875262, MNHN-P-P01875263); **Antsiranana:** Doany, 1250 m, 26.x.2001, *L. Gautier et al. LG3944* (GENT, K, MNHN-P-P01708454); **Fianarantsoa:** Ranomafana Forest, 1200 m, 29.vii.1987, *P. Phillipson 2169* (MO); **Toamasina:** Alaotra-Mangoro, 1085 m, 10.ii.2008, *A. Rakotondrafara 533* (MO, MNHN-P-P01668985, TAN); NW Masoala Peninsula, 550 m, 10.x.1986, *P. P. Lowry II et al. 4062* (MO, K); Antaralava Besalampy Forest, 958 m, 15.xi.2008, *P. Antilahimena et al. 6906* (K, MO); Masoala Peninsula, 0–10 m, vi.1993, *M. L. Zjhra & J. Hutcheon 238* (K, MO); 470 m, 19.ix.1993, *K. Lance 30* (K); Moramanga, 900 m, 11.xi.1938, *Lam & Meeuse 5375* (K); Perinet Reserve, 5.v.1988, *D.A. Simpson 88/112* (K); Vavatenina, 300–350 m, 12.vii.2003, *A. Rakotondrafara et al. 234* (K, MO); **Toliara:** Andohahela, 200–700 m, 4-24.v.1993, *B. Randriamampionona 328* (K, MNHN-P-P01875304); Massif de Bezavona, 28.viii.1919, *M.R. Decary 10434* (K, MO, MNHN-P-P01898905); Pic St Louis., 9.vii.1932, *M.R. Decary 9954* (K, MO). **MAYOTTE, Grande-Terre:** Mamoudzou, 1.vii.2003, F. Barthelat 1204 (K); Reserve Forestiere de Majimbini, 18.vi.2002, F. Barthelat 934 (K). **REUNION, Sainte- Rose:** 300 m, iii.1957, J. Bossier 11954 (K).

Notes: *S. trialata* differs from *S. angusta* in its larger panicles, generally longer than the internodes, dark glumes, and broader scabrid leaves. In Madagascar, it was used to treat toothaches (Chermeson, 1937).

SCLERIA (SUBG. *SCLERIA*) SECT. *ACRIULUS* (Ridl.) R. W. Haines & Lye

(6) *Scleria griegifolia* (Ridl.) C.B. Clarke in D. Oliver & auct. suc. (eds.), Fl. Trop. Afr. 8: 509 (1902). *Acriulus greigiifolius* Ridl. Type: ANGOLA, Huilla: marshes on the river Cacolobar, near lake Ivantala, ii.1860, Welwitsch 6959 (holotype: BM000922708!). Malagasy: *vendrana*.

Perennial with a thick rhizome. Culm 0.75–1.5 m long, 2–3 mm thick. Basal leaves persistent. Leaves 25–40 cm long, 5–8 mm wide, scabridous to glabrous. Antrorse prickly hairs present on margins and central nerve, up to 0.5 mm. Contraligule absent. Sheath closed, V shaped, partially membranous. Panicle truncated (Figure 1E), terminal and lateral, several per node, secondary branches very short. Rachilla purple, dentate. Peduncle up to 20 cm, flexuous, reddish. Spikelets unisexual or subandrogynous. Glumes densely ciliate on the inner surface, male 3–4 mm, female 4.5–5 mm, purple on the lower half, straw coloured at the top, margin finely ciliate. Nutlet 4–4.5 mm long, 2–3 mm in diameter, beaked, smooth, white. Hypogynium present, margin revolute, embracing the stipe, red dotted.

Distribution and habitat: Tropical and southern Africa, Madagascar. Grasslands and savannahs of Central High Plateau. 1300–1700 m.

Conservation status: LC (Thacker & Juffe Bignoli, 2013).

Representative specimens examined: MADAGASCAR, xii.1958, *J. Bosser* 12395 (K000455296); **Antananarivo:** 17.i–22.iv.1955, *H. Humbert* 28167 (MO, MNHN-P-P01921102, TAN); Andrangoloaka, Ost-Imerina, xi.1880, *J. M. Hildebrandt* 3751 (K000363343); Ankaratra, Lac Froid, 1650 m, 24.iv.2010, *I. Larridon et al.* 2010-0336 (GENT, K); near Carion iii.1961, *J. Bosser* 15031 (K000455295, MNHN-P-P01896547); **Central:** x.1882, *R. Baron* 1870 (K000363344); xii.1883, *R. Baron* 3331 (K000455294); xi.1885, *R. Baron* 4102 (K000455293); **Fianarantsoa:** near Ambatofinandrahana, 1400–1500 m, 16.i.1955, *H. Humbert & R. Capuron* 28123 (K, MO, MNHN-P-P01896548); Ambositra, 3.xii.1995, *M. Desfayes* 95.3121 (GENT); RN 7, 113–116 km N of Fianarantsoa, 1580–1590 m, 28.i.1975, *T. B. Croat* 29973 (MO, MNHN-P-P01896564); West Itremo, 17.i–22.iv.1955, *H. Humbert* 30062 (MNHN-P-P01896546).

Notes: In Madagascar, a preparation from the leaves is drunk to treat fevers (Rasoanaivo *et al.*, 1992).

SCLERIA (SUBG. *SCLERIA*) SECT. *ELATAE* C.B. Clarke in Hooker, *Fl. Brit. India* 6: 689 (1894)

(7) *Scleria rutenbergiana* Boeckeler, Abh. Naturwiss. Vereins Bremen 7: 40 (1880). Type: MADAGASCAR, Antsiranaan: Manongarivo Massif, 1909, Perrier de la Bathie 2643 (neotype, designated here: MNHN-P-P01888459!).

Perennial rhizomatous. Culm 1–2 m long, 2–3 mm thick, glabrous, scabridous along the edges, reddish. Leaves 20–30 cm long, 1.2–1.5 mm wide, pseudopraemorse, glabrous, margin entire to scabridous. Contraligule triangular, apex rounded, glabrous. Panicle in lateral and terminal position, 5–15 cm long, lax. Bracts leafy. Lateral panicles usually less than 5 cm long, the most basal isolated. Spikelets unisexual or subandrogynous. Bract of the spikelet ciliate at the base, up to 2 cm. Glumes, 3 mm, straw coloured. Rachilla reddish, scabrid. Nutlet 2.5–3 mm in diameter, globose to ovoid, white, smooth. Hypogynium trilobed, lobes truncated, yellowish brown (Figure 2K-L).

Distribution and habitat: Endemic to Madagascar, most frequently along the eastern and north-western coasts. 0–1200 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR: RN70, 27 (MNHN-P-P01888460, MNHN-P-P0188846, MNHN-P-P01888461, MNHN-P-P01888462); **Antsirananana:** NossiBe, xii.1857, *Boivin s.n.* (MNHN-P-P01888464); PN Montagne d'Ambre, 1400–1475 m, 9–13.iv.1993, S. Malcomber *et al.* 2371 (MO, K); **Fianarantsoa:** km23 RN25 Mananjary-Ifanadiana, 30 m, 16.xii.1997, P. Wilkin *et al.* 941B (MNHN-P-P01888458); Analamazaota, 1908, *d'Alleizette s.n.* (MNHN-P-P01888447); km23 RN25 Mananjary-Ifanadiana, 30 m, 16.xii.2017, P. Wilkin *et al.* 941B (K, MNHN-P-P01888458); **Tananarive:** Fotsimano, xii.1962, *J. Bosser 17028* (MNHN-P-P01888449); Toamasina: iii.1954, *J. Bosser 163* (MNHN-P-P01888450); near **Toamasina**, 20.ix.1912, *R. Viguiet et H. Humbert 195* (MNHN-P-P01888454, MNHN-P-P01888455); Ste. Marie, v.1847, *M. Boivin 1645B* (NHN-P01888445).

SCLERIA (SUBG. *SCLERIA*) SECT. *FOVEOLIDIA* Raf. in Bull. Bot., Geneva 1:2019 (1830)

(8) *Scleria achtenii* De Wild. in Rev. Zool. Bot. Africaines 14 (Suppl. Bot.): 16 (1926). Type: DCR, Kasai: Achten 97B (holotype: BR-863890!). First time cited in Madagascar.

Perennial with reddish rhizome, 6 cm long, 0.3 cm thick. Culm 0.45–0.70 meters long, 0.7–1.1 mm thick, slightly swollen at the base. Leaves 20–25 cm long, 0.4–0.5 cm wide,

pseudopraemorse, scabrid, with retrorse prickly hairs along the margin and central nerves. Contraligule membranous, reddish. Sheath winged, scabrid. Panicle truncated, reduced, several terminals and solitary laterals. Peduncle 2–6 cm. Spikelets unisexual or subandrogynous. Male glumes 4–4.5 mm long, female 4.5–5.5, straw coloured. Nutlet white, pitted, hairy. Hypogynium with long lobes, 2–3fid, white.

Distribution and habitat: Tropical and South Africa, Madagascar. Only one locality in Madagascar, on a sandy embankment in mid altitude evergreen forest. 1127 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Fianarantsoa:** Ranomafana National Park, 1127 m, 21.iv.2010, *I. Larridon et al. 2010-0228B* (GENT).

Notes: It differs from *S. niasensis* C.B. Clarke because of its bifid/trifid lobes and single panicles in each node.

(9) *Scleria foliosa* Hochst. ex A. Rich. in Tent. Fl. Abyss. 2: 509 (1850). *Scleria perrieri* Cherm. *Type:* ETHIOPIA, Afar: 18.ix.1838, G. W. Schimper 1232 (holotype: BM000758637!).

Annuals with a poorly developed root system. Culm 0.35–0.8 m long, 2–3 mm thick. Leaves 15–30 cm long, 3–4 mm wide, glabrous, antrorse prickly hairs on the central veins of the distal part, margin scabrid, three conspicuous central nerves central, pleated when dried. Contraligule rounded, glabrous, margin entire, surface slightly ciliate towards the mouth. Terminal and lateral panicles, truncated (Figure 1F), two per node. Leafy bracts present, much longer than the inflorescence on the basal panicles, at least as long on the terminal. Laterals with a peduncle 3–15 cm, longer towards the base. Spikelets unisexual or subandrogynous. Glumes straw coloured with midrib green, male 4.5–5 mm long, female 5 mm long and 2.5–3 mm wide. Nutlet ovoid, 3.5 mm long and 2.5 mm in diameter, reticulated but smooth towards the distal third, white. Hypogynium cream–coloured, loosely attached to the nutlet, trilobed, lobes rounded to orbicular.

Distribution and habitat: Tropical and South Africa, Madagascar. Madagascar: open forest and grasslands. 500–1300 m.

Conservation status: LC (Mani, 2011).

Representative specimens examined: MADAGASCAR, **Antananarivo:** iii.1960, *J. M. Bosser 13623* (TAN); ii.1961, *J. M. Bosser 14870* (TAN); **Fianarantsoa:** iv.1960, *J. M. Bosser 14115*

(TAN, MNHN-P-P01707650, MNHN-P-P01707651, MNHN-P-P01707652, MNHN-P-P01707653); **Mahajanga**: Betainkankana, Ankaizina, iii.1952, *J. Bosser 2771* (MNHN-P-P01707649); **Toamasina**: iv.1962, *J. M. Bosser 15912* (TAN, MNHN-P-P01707648); **Toliara**: Analavelona Forest, 950–1250 m, iii.1934, *H. Humbert 14233* (K, TAN); near Onilahi River (Benenitsa), vii.1919, *H. Perrier de la Bâthie 12704* (MNHN-P-P00346037, MNHN-P-P00346038, MNHN-P-P00346039).

Notes: Chermezon identified the Malagasy specimens as *S. perrieri*, based on the fade reticulation of the nutlet and its attached hypogynium. However, the rest of characters are identical to *S. foliosa*. Used as fodder in Sudan (Simpson & C.A., 2001) and as a treatment for gonorrhoea in Tanzania (Burkill, 1985).

(10) *Scleria hildebrandtii* Boeckeler in Flora 63: 454 (1880). *Type*: Lectotype: KENYA, Fessland von Mombassa: viii.1877, J. M. Hildebrandt 2044 (lectotype, designated here: MNHN-P00465972!; isolectotype: MNHN-P-P00465973!).

Annual with short rhizome, tufted, many basal leaves persistent as scales. Culm 40–60 cm long, 1.5–2 mm wide. Leaves 15–20 cm long, 5–8 mm wide, glabrous. Prickles hairs present along the margin on the distal half, antrorse. Margin scabrid. Contraligule truncated, membranous and puberulous on the surface. Sheaths can be shortly winged. Inflorescence a truncated panicle with leafy bracts. Usually two panicles per node. Leafy bracts much longer than the inflorescence on the basal panicles, and at least as long in the terminal. Spikelets unisexual or subandrogynous. Glumes straw coloured to reddish, 5–5.5 mm long. Nutlets 3.5 mm long, 1.7–2 mm wide, oblong, smooth, although sometimes very slightly pitted, white. Hypogynium without conspicuous lobes as the other species, margin obscure with red dots.

Distribution and habitat: Eastern coast of Africa and northeast coast of Madagascar, where it is only known from two localities in the province of Mahajanga. On limestone and sandy soils at sea level.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Mahajanga**: ii.1908, *H. Perrier de la Bâthie 2485* (MNHN-P-P01888605); environs de Marovoray (Boïar), v.1925, *H. Perrier de la Bâthie 17252* (MNHN-P-P01888604, K, TAN001259).

Notes: It has been confused with specimens of *S. foliosa* with smooth nutlets. However, the nutlet of *S. hildebrandtii* is cylindrical to oblong, whereas *S. foliosa* shows an ovoid fruit, slightly apiculate.

(11) *Scleria lagoensis* Boeckeler in Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1869: 151 (1869). *Scleria canaliculatotriquetra* Boeckeler, *Scleria mayottensis* C.B.Clarke. Type: BRAZIL, Lagoa Santa, 2.iii.1864, Warming 494 (holotype: C10010663!). Malagasy: *zamana*.

Perennial. Culm 0.8–1 m, 1–2 mm thick, distinctly triquetrous. Leaves 40–60 cm long, 0.4–1 cm wide, glabrous but prickly hairs present on the distal part. Contraligule rounded, membranous, veins well marked, glabrous, with red dots. Sheaths markedly winged, Panicle 6–8 cm long, truncated, terminal and lateral. Spikelets unisexual or subandrogynous. Glumes straw coloured. Nutlets 2.5–3.5 cm long, 1.8–2.2 cm wide, subtly pitted, hairy underneath, ovoid. Hypogynium with three slender lobes, sometimes red at the tip.

Distribution and habitat: Tropical and South Africa, South America and Madagascar. Madagascar: widespread, from low altitude evergreen and dry forests on the north, to 1400 m on Central Madagascar. Tolerant to dry soils.

Conservation status: LC

Representative specimens examined: MADAGASCAR: i.1899, *H. Perrier de la Bâthie* 883 (K, MNHN-P-P01888566); **Antananarivo:** iii.1960, *J. M. Bosser* 13620 (TAN); 18.iii.1951, *H. Humbert & R. Capuron* 25622 (MO); Andraisoro, 11.iii.1919, *R. Decary s.n.* (MNHN-P-P01888559); **Antsiranana:** Bemarivo, Boina, ii.1907, *H. Perrier de la Bâthie* 2408 (MNHN-P-P01888555); Nosy Be, *Boivin* 1990; **Mahajanga:** Tsaramandroso, 12.iii.1965 *Jacqueline & Maurice Peltier* 5209 (MNHN-P-P01888552); **Toliara:** Analavelona Forest, 950–1250 m, iii.1934, *H. Humbert* 14233 (MNHN-P1888560).

Notes: Vegetative parts of African and American specimens are practically identical. However, nutlets of plants from Brazil (where the type comes from) are frequently hairy all over and more globose than its African relatives. They could be different species or subspecies, as previously noted by Robinson (1966). Nevertheless, further research is required.

(12) *Scleria tessellata* Willd. in Sp. Pl. 4: 315 (1805). Type: INDIA. Herb Willdenow 17323 (holotype: B-W17323-010!).

Tufted annual, completely glabrous. Culm 30–80 cm. Leaves 10–20 cm long, 3–4 mm wide. Antrorse prickly hairs present in the distal part of the leaf. Contraligule truncated, membranous, glabrous, red dotted. Panicle in terminal and lateral position, truncated, laterals solitary. Spikelets unisexual or subandrogynous. Glumes 5–6 mm long, straw-coloured. Male flowers with two stamens. Nutlets oblong, 3–3.5 mm long, 1.5–2 mm wide, regularly tessellate, white. Hypogynium strongly trilobed, loosely appressed to the nutlet, yellowish brown.

Distribution and habitat: Tropical Africa, Madagascar, Australia, India and South East Asia. Very common taxon that thrives in wetlands, grasslands and rice fields (Naczi & Ford, 2008). Madagascar: only two localities. Its distribution area overlaps with *S. hildebrandtii*. On wet and sandy prairies, at sea level. Chermezon (1937) thought it was probably introduced.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Mahajanga:** near Majunga, iv.1908, *H. Perrier de la Bâthie* 2595 (K, MNHN-P-P01888413, MNHN-P-P01888414); iii.1927, *H. Perrier de la Bâthie* 17945 (TAN001257, K).

Notes: Kühn (1982) noted that this taxon originally comes from Madagascar, a statement totally unfounded. *Scleria tessellata* resembles *S. hildebrandtii* and *S. foliosa*. It can be distinguished because of the oblong and completely reticulate nutlet, and the deeply trilobed hypogynium with oblong lobes are oblong. The pits are not as deep as in *S. foliosa*. It has also been misidentified with *S. bambariensis* Cherm. However, there is no evidence of *S. bambariensis* in Madagascar. The misunderstanding probably comes from a misidentification of *H. Perrier de la Bâthie* 17945 (see above) by E. A. Robinson.

***SCLERIA* (SUBG. *SCLERIA*) SECT. *HYMENOLYTRUM* (Schrad. ex Nees) Core in Brittonia 2: 10 (1936)**

(13) *Scleria boivinii* Steud. in Syn. Pl. Glumac. 2: 173 (1855). *Scleria reflexa* Benth., *Scleria barteri* Boeckeler. *Type:* MADAGASCAR, Toamasina: Sainte Marie, Lafondrou Forest (Tafondro) 1849, *M. Boivin* 1643 (lectotype: MNHN-P-P04021507!; isotype: K!). Malagasy: *vondranditi, sambi havitra, filelatra, diti.*

Perennial climber, tufted at the base. Culm 2–10 m long, 1.5–2 mm thick, triquetrous, bulbous at the base. Leaves 30–35 cm long, 2–3 mm wide, glabrous except but main vein villose. Prickle hairs present in margins and central costa of the leaf, antrorse along the distal part, the rest retrorse. Sheath puberulent on the abaxial side. Contraligule large, obtuse, membranous at the margin, ciliate at the base. Inflorescence with conspicuous leafy bracts. Panicles pyramidal, erect, 6–10 cm long, in terminal and lateral position, grouped at the top of the culm. Spikelets unisexual or subandrogynous. Bract 1–1.5 times longer than the spikelet. Male glume 3–4.5 mm, female 4.5–6 mm, brown, glabrous, midrib scabrid and purplish, straw-coloured in between. Staminal crest very developed, up to 1 mm. Nutlet 2.5–3.5 mm long, 1.5–2.5 mm wide, trigonous, minutely hairy, white. Hypogynium cream-coloured, rotund, margin revolute, brown.

Distribution and habitat: Tropical Africa, Madagascar and the Comoros. This species is recorded as invasive in Ghana (Holm, 1979). In Madagascar is very common and forms dense populations on edges and canopy gaps of wet forest. 0–2000 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antsiranana:** Reserve speciale of Monongarivo, Bekolosy, 22.v.1995, *L. Gautier & C. Chatelain* LG2766 (MO, K, MNHN-P-P01888433); 7–12.xii.1992, *S. Malcomber et al.* 1975 (MNHN-P-P01888419, MO, K); Betsitsika Forest, 149 m, 12.1.2009, *M. Y. Ammann et al.* MYA247 (K); SAVA, 940 m, 15.i.2004, *L. Nusbaumer* 993 (G); **Fianarantsoa:** 12 km E of Ifanadiana, 600 m, 18.xii.1997, *P. Wilkin et al.* 946 (GENT, TAN, K, MNHN-P-P01888423); Ambilandrano, 450 m, 9.i.1993, *H. Beentje* 4802 (K, TAN); Soanierana, 100 m, 30.xi.1938, *Lam & Meeuse* 5556 (K, MNHN-P-P01888425); **Toamasina:** 10 km south of Foulpointe, 12.xii.1984, *L. J. Dorr & L. C. Barnett* 3394 (MO, K, MNHN-P-P01888432); Sainte Marie, Lafondrou Forest (Tafondro) 1849, *M. Boivin* 1643 (MNHN-P-P04021507, K); Vallée de la Fanjahirana, 19.ix.1932, *M. R. Decary* 10647 (K, MNHN-P-P01888420); MADAGASCAR, **Toliara:** Fort-Dauphin, Ivohibe Forest, 386 m, xi.2005, *R. Razakamalala et al.* 2476 (MO, K); near Fort-Dauphin, Manantantely Forest, 60–300 m, 22.ix.1928, *H. Humbert* 5780 (MNHN-P-P01888422, K).

Notes: It is closely related to *Scleria secans* (L.) Urb, morphologically and molecularly (Bauters *et al.*, 2016). This has led to many misidentifications. However, *S. boivinii* is an African taxon, whereas *S. secans* only occurs in South America. It is locally used in many ways. Nutlets are used as beads in necklaces in Ghana (Abbiw, 1990). In Tropical Africa, macerates and decoctions of leaves and stems are used to ease childbirth (Lebbie & Guries, 1995), treat coughs, blennorrhoea, toothache, snakes bites (Burkill, 1985), headaches (Betti, 2004; Idu, Erhabor & Ovuakporie-Uvo, 2014), onchocerciasis (Abondo, Mbenkum & Thomas, 1990).

SCLERIA SUBG. HYPOPORUM (Nees) C.B. Clarke in Hooker, Fl. Brit. India 6: 685 (1984)

(14) *Scleria andringitrensis* Cherm. in Bull. Soc. Bot. France 70: 297 (1923). *Type:* MADAGASCAR, Fianarantsoa: Massif de l'Andringitra, 2200 m, iii.1922, *H. Perrier de la Bâthie* 14385 (lectotype, designated here: MNHN-P-P00457098!; isolectotypes: K000363345!, TAN000431!, MNHN-P-P00457099! and MNHN-P-P00457100!).

Perennial, caespitose. Stems 20–30 cm long, 0.5–0.8 mm wide. Inflorescence a 15 cm spike with unbranched glomerules spread every 2–3 cm. Each glomerule consists of 1–3 erect

androgynous spikelets. Glumes 5–5.5 mm long, glabrous, reddish. Nutlet 1.3 mm long, 1 mm in diameter, white, conspicuously transversally striated (Figure 2O).

Distribution and habitat: Endemic to the Andringitra Massif. Ericoid forest. 900–2200m.

Conservation status: VU D2. AOO is 8 km². This species is only known from two collections, the latest made in 1970. Although its only location is a protected area, we propose to assess the species as Vulnerable until further explorations allow us to reassess its status.

Representative specimens examined: MADAGASCAR, **Fianarantsoa:** Massif de l'Andringitra, iii.1922, *H. Perrier de la Bâthie* 14385 (K); 1700 m, 2.iii.1970, *J. L. Guillaumet* 3502 (MNHN-P-P01898843).

(15) *Scleria bulbifera* Hochst. ex A.Rich. in Tent. Fl. Abyss. 2: 510 (1850). *Scleria buchananii* Boeckeler; *Scleria atosanguinea* Hochst. ex Steud.; *Scleria schweinfurthiana* Boeckeler.: *Type:* ETHIOPIA: 3.x.1937, W. Schimper 327 (holotype: MNHN-P-P00465919!).

Perennial. Stems bulbous at the base, bulb 0.5–1.0 cm thick, brown, covered by old leaves. Culm glabrous to puberulous, 50–70 cm long. Leaves 20–30 cm long, 0.2–0.5 cm wide, puberulous, pale green. Inflorescence a terminal spike, 10 cm long, made of 4–10 erect unbranched glomerules. Basal glomerulus with bracts less than 1.5 cm long. Spikelets androgynous. Glumes 4–5mm long, purple, scabrid, sometimes with hairs. Nutlet 1–1.5 mm diameter, smooth to slightly verrucose, with tubercles transversally arranged.

Distribution and habitat: Tropical and South Africa, Madagascar and Arabian Peninsula. Madagascar: restricted to the Central Plateau and Highlands. Grasslands and savannah, on siliceous soils. 800–1600 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antananarivo:** Antsirabe, Sahatsiho, 1600 m, 24.xii.1928, *H. Humbert* 7124 (MNHN-P-P01707777, K); 1500 m, x.1913, *Perrier de la Bâthie* 2661 (MNHN-P-P01707770); **Central Madagascar:** x.1882, *R. Baron* 2003 (K, MNHN-P-P01707771, MNHN-P-P01707772); **Fianarantsoa:** Massif de l'Andringitra, 1600–2000 m, xi–xii.1924, *H. Humbert* 3636 (MNHN-P-P01707773, MNHN-P-P01707774); Ihosy, Isalo, 856 m, 23.i.2008, *M. Andriamahay & S. Rokotoarisoa* SNGF1859 (SNGF, TEF, K); **Toliara:** Antanimena-Itremo, 4.xii.2012, *F. Rakotonasolo* RNF2093 (K, TAN, MNHN-P-P01063613).

Notes: Gordon-Gray (1995) pointed that *S. bulbifera* shows a wide range of nutlet morphologies. Further research is needed to assess the internal variation within this taxon.

(16) *Scleria distans* Poir. var. *distans* in J.B.A.M.de Lamarck, *Encycl.* 7: 4 (1806). *Scleria nutans* Willd. ex Kunth; *Scleria bojeri* C.B.Clarke.: *Type:* PUERTO RICO: A. P. Ledru 110 (lectotype: MNHN-P-P00274452!; isolectotypes: MNHN-P-P00274453!, MNHN-P-P00274454!).

Rhizome 2–3mm in diameter. Thin stems arise every 1–2cm, 20–50cm long, 1 mm thick. Sometimes forms dense stands. Leaves 10–15cm long, puberulous, less often glabrous. Contraligule strongly ciliate. Inflorescence a terminal spike, 8–10cm long, with 6–8 glomerules. Glomerules unbranched, reflexed (Figure 1G). Spikelets androgynous. Glumes 4–4.5mm, straw coloured, villose, awned. Hairs white, dark towards the apex. Nutlets smooth.

Conservation status: LC

Distribution and habitat: America, Tropical Africa and Madagascar. Madagascar: Central High Plateau. Most vouchers of *S. distans* in Madagascar belong to the variety *chondrocarpa*.

Representative specimens examined: MADAGASCAR, 1867, Lyall 209 (K); Lyall s.n. (K); **Central Madagascar:** xii.1883, R. Baron 397 (K).

Notes: The rhizome is smashed and drunk as mate or tereré, to treat diabetes and intestinal parasites (Pin *et al.*, 2009).

(17) *Scleria distans* var. *chondrocarpa* (Nelmes) Lye, *Nordic J. Bot.* 3: 243 (1983). Holotype: UGANDA, Bugala Island: Kalangala, 1150 m, 5.vi.1932, A. S. Thomas 95 (K000321076). Isotype: KAW.

Stems thickened at the base. Nutlet 1.5 × 1mm, always ornamented, either transversely wrinkled or tuberculate. Although the ornamentation is not equally patent across the specimens.

Conservation status: LC

Distribution and habitat: Eastern Africa and Madagascar. Madagascar: canopy gaps and degraded mid altitude evergreen forest, grasslands, 700–1600 m. Less frequent along the low altitude evergreen forest.

Representative specimens examined: MADAGASCAR, 7.v.1912, P. A. Methuen s.n. (K); **Antananarivo:** Ankazobe, 25.iii.1930, R. Decary 7711 (TAN, MNHN-P-P01707753); Ivato,

1365 m, 25.i.1975, *T. B. Croat* 29582 (MO, K, MNHN-P-P01896575); Intremo Massif, 1300–1400 m, 27.i.1975, *T. B. Croat* 29888 (MO, K, MNHN-P-P01896573); **Central Madagascar**: x.1881, *R. Baron* 801 (K); viii.1880, *G. W. Parker* 23 (K); **Fianarantsoa**: Ranomafana National Park, 1205 m, 21.iv.2010, *I. Larridon et al.* 2010-0241 (GENT); 1128 m, 21.iv.2010, *I. Larridon et al.* 2010-0229 (GENT); 1178 m, 21.iv.2010, *I. Larridon et al.* 2010-0248 (GENT); RN 7, PK 294, 1717 m, 22.iv.2010, *I. Larridon et al.* 2010-0279 (GENT); Ambohimombo Forest, 1350–1440 m, i.1895, *Forsyth Major* 226 (K); 33 km south of Irondro 600 m, 26.iii.1993, *D. Turk & M. Beck* 367 (K); Ambohimahasina, 1941, *Herbier. Jard. Bot* 4550 (TAN, K); South Midongy National Park, 2.iii.1927, *M. Decary* 4980 (K); **Toamasina**: 15.ii.1930, M.R. Decary 7137 (MNHN-P-P01707752).

Notes: The material studied has a bulb less than 0.5 cm wide, whereas the types established by Nelves have bulbs between 0.5–1 cm. The drooping glomerules with black hairs make it very similar to the annual *Scleria melanotricha* Hochst. & A.Rich. However, *S. melanotricha* does not have a creeping rhizome and the fruit has three conspicuous tubercles mixed with three smooth bands and an orange rugose rim on the stipe. It is restricted to mainland Africa. In addition, it has been confused many times with *S. hirtella*, another annual very similar in appearance but is a strictly American species (*Camelbeke et al.*, 2001; Raynal, 1976).

(18) *Scleria hilsenbergii* Ridl. in *J. Bot.* 22: 16 (1884). *Type*: MADAGASCAR: Hilsenberg & Bojer s.n. (holotype: BM000922714!).

Annual. Culms puberulous at least at the base, 30–40 cm long. Leaves 10–15 cm long, 1–1.5 mm wide, glabrous to puberulent. Inflorescence is a terminal lax panicle, 5–10 cm long (Figure 1H). Glomerules with 2–5 spikelets, held by thin erect branches up to 4 cm long. Spikelets androgynous. Glumes 4–4.5 mm long, straw coloured or reddish, glabrous. Glumes of the female flower mucronate (0.5–1 mm). Nutlet 1–1.3 mm long, 0.7–1 mm in diameter, trigonous, densely tuberculate, wrinkles arranged mainly transversally (Figure 2I–J).

Distribution and habitat: Endemic to Central Madagascar, 1000–1700 m. Wetlands, degraded grasslands and secondary forest patches.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antananarivo**: Analamanga Region, 9.iii.2010, *F. A. Rajaonary* 45 (MO, K); vi.1961, *J. Bosser* 15071 (K, TAN); Ankatso, 10.ii.1923, *M. Decary* 382 (K, MNHN-P-P01888589); Itasy Region, Lake Itasy, i.1931, *G. F. Scott Elliot* 1908 (K, MNHN-P-P01888593); Antsirabe, Vontovorona, 2035 m, 1.iv.1971,

K. A. Lye 5947 (K); **Fianarantsoa**: iv.2010, I. Larridon et al. 2010-0268 (GENT); Andringita National Park, 1581 m, iv.2010, I. Larridon et al. 2010-0122 (GENT); **Toamasina**: Besakay, iv.1992, A. Dhondt 7 (GENT).

(19) *Scleria lithosperma* (L.) Sw. var. *lithosperma* in Prodr. Veg. Ind. Occ.: 18 (1788). Type: *Kaden-pullu* in Rheede, Hort. Malab., 12: 89, t. 48 (1693) (lectotype).

Caespitose perennial. Culm 60–80 cm, glabrous to puberulous. Leaves 15–20 cm long, 2–4 mm wide, puberulent. Contraligule triangular, densely ciliate. Inflorescence with lateral and terminal panicles. Bracts leafy, shorter towards the apex. Inflorescence spiciform, terminal and lateral, unbranched, with 3–5 glomerules (Figure 1I). Spikelets androgynous. Nutlet 2 mm long, 1.5 mm in diameter, ovoid to obovoid, smooth, trigonous, with three depressions at the base.

Distribution and habitat: Pantropical. It is a very widespread plant that can grow in semi-dry grasslands, crops and disturbed areas (Simpson & C.A., 2001; Naczi & Ford, 2008). In West Polynesia, it is a weed (Holm, 1979). Madagascar: present along the south eastern and northwest coast, rarely over 400 meters. Low altitude dry and semideciduous forest.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antsiranana**: Daraina, 81 m, 2.iii.2005, L. Nusbaumer & P. Ranirison LN1526 (K, G); Bassin de Biromba, 217 m, 28.v.2001, S. Wholhauser & H. Andriamalaza SW448 (K, G); Daraina, 204 m, 20.iii.2004, L. Gautier et al. LG4654 (K, G); Daraina, 325 m, 5.iii.2003, L. Gautier et al. LG4230 (K, G).

Notes: Because of its leafy bracts and lateral panicles, it has been previously included in its own section *Lithospermae* (Chermezon, 1937) and section *Corymbosae* (Haines & Lye, 1983). The other variety, *Scleria lithosperma* var. *linearis* Benth., is restricted to tropical Asia and Australia. It is used to treat skin infections and diseases in India (Vijayan et al., 2007; Chendurpandy, Mohan, & Kalidass, 2010; Rani et al., 2011). In Tanzania it is utilized in treatments for dysmenorrhoea and to help during childbirth (Burkill, 1985).

(20) *Scleria perpusilla* Cherm. in Bull. Soc. Bot. France 76: 557 (1929). Type: MADAGASCAR, Antananarivo: 1500 m, ii.1928, H. Perrier de la Bâthie 18433 (lectotype, designated here: BR0000013180607!; isoelectotypes: MNHN-P-P00346040!, MNHN-P-P00346041!).

Annual. Stems 3–8cm long, 0.3–0.5mm thick, glabrous. Leaves 1.5–2.5cm long, glabrous. Inflorescence a reduced, terminal spike. Spikelets androgynous. Glumes 3.5–4.5cm, dark purple, glabrous. Nutlet 1.2 mm long, 1 mm in diameter, white, ornamentation transversely wrinkled to reticulated (Figure 2F).

Distribution and habitat: Endemic to Central Madagascar. On rocky soils, 1200–1500 m.

Conservation status: VU D2. The AOO is 12 km² and the number of locations 3. This taxon is probably little represented in the collections because of its habit. However, it was collected for the last time in 1962. Therefore, we propose to assess it as Vulnerable until new evidence appears.

Representative specimens examined: MADAGASCAR, Antananarivo: 1500 m, ii.1928, *H. Perrier de la Bâthie 18433* (BR, MNHN-P-P00346040, MNHN-P-P00346041); Ankazobe, iii.1930, *M. R. Decary 7695* (K, MNHN-P-P01888491); iii.1962, *J. Bosser 15968* (MNHN-P-P01888490).

Notes: There are only two specimens collected for this species, both examined by H. Chermeson for his revision of *Scleria* from Madagascar (1937?). Since then, there are no records for this taxon.

(21) *Scleria pooides* Ridl. in Trans. Linn. Soc. London, Bot. 2: 170 (1884). *Scleria multispiculata* Boeckeler. *Type:* ANGOLA: Huilla, November 1859, Welwitsch 7142 (holotype: LISU222777!; isotypes: BM000922698!, K000363388! and LISU222778!).

Perennial, rhizomatous. Culm glabrous, 30–40 cm long. Leaves 12–17 cm long, 0.5–1.5 mm wide, glabrous. Inflorescence a terminal lax panicle, 4–8 cm long. Glomerules formed by a single androgynous spikelet, on the tips of thin flexuous branches. Glumes of the female flower 2–3 mm long, glabrous, dark. Nutlet 1–1.5 mm long, tuberculate.

Distribution and habitat: Tropical Africa and Madagascar. Prairies of central Madagascar, 1400–1600 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antananarivo:** environs de Antsirabe, i.1914, *H. Perrier de la Bâthie 2727* (MNHN-P-P01888480); i.1956, *J. Bosser 8921* (TAN, MNHN-P-P01888479); Mont Lombony, environs de Antsirabe, 1500 m, i.1920, *H. Perrier de la Bâthie 12982* (TAN001211, MNHN-P-P01888481); forêt de la Mandraka, 1909, *d'Alleizetle 328* (MNHN-P-P01888482).

Notes: There are only four collections from Madagascar. H. N. Ridley named this species after the genus *Poa*, because of the slender and flexuous branches that hold the solitary spikelets. It can be distinguished from *S. hilsenbergii* due to its smaller glumes, solitary spikelets and shorter and crowded panicle.

SCLERIA SUBG. SCLERIA SECT. MARGALEIA Raf. In Bull. Bot., Geneva 1:219 (1830)

(22) *Scleria poaeformis* Retz. in Observ. Bot. 4: 13 (1786). *Scleria oryzoides* J.Presl & C.Presl. Type: SRI LANKA, J.G. König s.n. (holotype: C10010679!).

Aquatic perennial with strong rhizome. Culm 1.3–2m long, 3–10 mm wide. Leaves 40–70 cm long, 1–3 cm wide. Inflorescence a single terminal panicle, many times branched, dense, 10–20 cm long, 5–10 cm wide. Spikelets unisexual or subandrogynous. Sometimes small lateral panicles present. Glumes brown, dark. Nutlet smooth, ovoid, white, 3–3.5 mm long, 2–2.5 mm in diameter.

Distribution and habitat: Tropical Africa, Asia, Australia, South Africa and Madagascar. Madagascar: along the east coast, at sea level. It has become a weed in Australia, Thailand, Vietnam and Indonesia, where it grows in swamps, wet savannah and in croplands (Holm, 1979; Simpson & C.A., 2001; Naczi & Ford, 2008).

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Fianarantsoa:** i.1964, *J. Bosser 19017* (TAN, MO, MNHN-P-P01888489); **Toamasina:** environs de Tamatave, 10.i.1933, *Decary s.n.* (MNHN-P-P01888488); environs de Tamatave, 27.ix.1912, *R. Viguier & H. Humbert 431* (MNHN-P-P01888485); Vatomandry, xi.1921, *H. Perrier de la Bâthie 14102* (TAN, MNHN-P-P01888484).

Notes: It is used in West Africa, for polishing wood and reduce abdominal inflammation (Burkill, 1985).

SCLERIA (SUBG. SCLERIA) SECT. MELANOMPHALAE Bauters in Taxon 65(3): 461

(23) *Scleria melanomphala* Kunth in Enum. Pl. 2: 345 (1837). *Scleria melanocephala* Drège, *Scleria centralis* Cherm., *Scleria tisserantii* Cherm., *Scleria longigluma* Kük. Types: SOUTH AFRICA, Eastern Cape: between the Bashee river and Morley, 300–600 m, ii.1840, *J. F. Drège 4379* (lectotype, designated here: K000363499!; isolectotypes: MNHN-P-P00465985!, MNHN-P-P00465986!).

Perennial with well developed rhizome, 4–6 mm thick. Tufted, many leaves and stems with hairy margins and edges persist. Culm 0.5–1.3 m long, 1–2 mm thick, edges pilose at the base. Leaves 25–35 cm long, 0.3–0.5 cm wide, margin ciliate at the proximal part (1 mm). Contraligule truncated, obtuse, slightly membranous on the margin, glabrous or ciliate. Inflorescence a truncated panicle (Figure 1D), in terminal and lateral position, sometimes more than one per node. Peduncle 2–15 cm. Spikelets unisexual or subandrogynous. Glumes 0.8–1.2 cm long, mucronate, glabrous inside and hairy on the external side, purplish with a green brownish midrib. Bracts 2–3 cm long, shorter than the inflorescence, straw-coloured or purplish. Nutlet 3–3.5 mm long, 2–2.5 mm in diameter, ovoid to elliptic, smooth, apex dark. Hypogynium with lobes barely marked, yellowish brown.

Distribution and habitat: Africa, South America and Central Madagascar, in open wet places (Simpson & C.A., 2001). In Central Madagascar, between 900–1700 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR: *Herbier du Jardin Botanique de Tananarive 331.9* (MNHN-P-P01888503); *Herbier du Jardin Botanique de Tananarive 331.10* (MNHN-P-P01888505); **Antananarivo:** 16.iii.1930, *R. Decary 7590* (MNHN-P-P01784488, TAN); Ambotolampy, 14.ii.1930, *J. Peltier & M. Peltier 1875* (MNHN-P-P01888511); Antsirabe, Vontovorona, 2020–2050 m, 1.iv.1971, *K. A. Lye 5945* (K); Manankazo, Ankazobe, 9.i.1913, *H. Perrier de la Bâthie 2692* (MNHN-P-P01888513); Ankaratra, Lake Froid, 1650 m, 24.iv.2010, *I. Larridon et al. 2010-0336B* (GENT); Mandraka Forest, viii.1906, *Herbier de Ch. d'Alleizette 1013* (MNHN-P-P01888507); Mandraka Forest, 16.viii.1906, *Herbier L. Rotereau s.n.* (MNHN-P-P01888510); Soamahamanina, 1200 m, 3.ii.2000, *A. Raynal-Roques et al. 24936* (MO, TAN, MNHN-P-P01888500); **Central Madagascar:** Betsileo, i.1881, *J. M. Hildebrandt 4015* (K, MNHN-P-P01888508); x.1882, *R. Baron 2007* (K, MNHN-P-P01888499); **Fianarantsoa:** 14 km au sud de Fianarantsoa, 22.x.1970, *M. Keraudren-Aymonin & G. G. Aymonin 25103* (MNHN-P-P01888509); near Ambatofinandrahana (Betsileo), 1400–1500 m, 16.i.1955, *H. Humbert & R. Capuron 28118* (MNHN-P-P01888498); West Itremo, 1500–1700 m, 17-22.i –18-22.iv.1955, *H. Humbert 300?2* (MNHN-P-P01888502); *H. Humbert 28168* (MNHN-P-P01888504).

Notes: This was found in Middle Stone Age settlements along with *S. natalensis*, used for bedding (Wadley et al., 2011). Burkill (1985) recorded its use as treatment for disorders of the urinary system.

SCLERIA (SUBG. *SCLERIA*) SECT. *OPHYROSCLERIA* (Nees) C.B. Clarke in Urban, *Symb. Antill.* 2: 138 (1990)

(24) *Scleria racemosa* Poir. in J.B.A.M.de Lamarck, *Encycl.* 7: 6 (1806) *Scleria ciliolata* Boeckeler, *Ophryoscleria racemosa* (Poir.) Nees. Type: MADAGASCAR, A.A. du Petit-Thouars s.n. (holotype: MNHNP00346044!; isotype: MNHN-P-P00346045!). Malagasy: *sirosera*.

Perennial with strong rhizome. Culm 1.5–3 m long, 4–6 mm wide. Leaves 30–60 cm long, 1.5–3 cm wide, pseudopraemorse, glabrous. Prickle hairs present along distal third of margins and nerves of the abaxial side, antrorse, conspicuous, up to 0.2 mm. Contraligule triangular, glabrous, margin membranous. Sheath winged. Inflorescence a terminal panicle and several smaller laterals, do not overlap with each other, barely branched. Spikelets unisexual or subandrogynous. Male glume 4–4.5 mm long, female 4–5 mm, straw coloured outside with brown red dots at the top, purplish inside, puberulous. Bracts ciliate at the base. Nutlet 4.5–5 mm long, 3–4 mm wide, smooth, beige, style persistent. Hypogynium regularly ciliate. Cupule swollen, cup shaped, yellowish brown.

Distribution and habitat: Tropical and East Africa, Madagascar, the Comoros and Mayotte. Widespread across the wetlands of the northern half Madagascar. Associated to *Raphia farinifera* (Gaertn.) Hyl. 0–1000 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, A.A. du Petit-Thouars s.n. (MNHNP-P00346044); 10.x.1969, B. Descoings 1198 (MNHNP-P01888436); Moquin-Tandon, Christian Horace Bénédicte Alfred s.n. (MNHNP-P00346045); **Antsiranana:** Ambilobé, Mahavary, 31.vii.1939, R. Decary 14767 (MNHNP-P01888468, TAN); Antsakoamanondro, 17.v.1960, J. Peltier & M. Peltier 2432 (MNHNP-P01888443); Nossi-Be, 28.i.1841, A. Pervillé 485 (MNHNP-P01888476, MNHNP-P01888477, TAN); viii.1841, A. Pervillé 248 (K); iv.1879, J. M. Hildebrandt 2921 (K000363350, MNHNP-P01888440); v.1879, J. M. Hildebrandt 2984 (K000363351, MNHNP-P01888441); vi.1847, M. Boivin 1991 (MNHNP-P01888466, MNHNP-P01888467); vi.1907, L. Rotureau s.n. (MNHNP-P01888444); J. M. C. Richard 924 (MNHNP-P01888472); Sava, 1190 m, 4.v.2006, R. Razakamalala & et al. 2814 (MO, TAN, K, MNHNP-P01888437); **Mahajanga:** 1932, H. Perrier de la Bâthie 638 (MNHNP-P01888469); 27.v.1912, K. Afzelius s.n. (K); Ambatoboeny, 125 m, 18.v.2001, R. Randrianaivo et al. 638 (K, MO); Ampijoara, Natural Reserve, 12.xi.1995, M. Desfayes

95.12111 (GENT); Ampombimanangy, 113 m, 24.vii.2006, *M. Andriamahay & S. Rakotoarisoa 1446* (K); Analalava, 15 m, 5.x.2012, *S. E. Rakotoarisa et H. Randrianavsoa SNGF3069* (TAN, K000753248, MO, MNHN-P); Befandriana-Nord, 29.vii.1942, *Herbier du Jardin Botanique de Tananarive 5175* (MNHN-P-P01888439); North: i.1892, *R. Baron 6371* (K); North-West: ix.1887, *R. Baron 3787* (K); **Toamasina**: *M. Bojer* (MNHN-P-P01888474); Besinkara, 300 m, 23.vi.1994, *L. Gautier et al. LG2411* (G, MO, TAN, MNHN-P-P01888465); Analamazaotra Forest, x.1909, *A. C. D'Alleizette 681* (MNHN-P-P01888471); Ste. Marie, *M. Boivin 1647* (MNHN-P-P01888442).

SCLERIA* (SUBG. *SCLERIA*) SECT. *SCLERIA

(25) *Scleria gaertneri* Raddi in Atti Reale Accad. Lucchese Sci. 2: 331 (1823). *Scleria longifolia* Boeckeler, *Scleria pterota* C.Presl ex C.B.Clarke, *Scleria melaleuca* Rchb. ex Schldl. & Cham., *Scleria margaritifera* Wild. Type: BRAZIL. Rio de Janeiro, *Raddi s.n.* (holotype: PI!). Malagasy: *vendrmario, serosera nbambo*.

Tufted perennial with strong rhizome. Culm 35–80 cm long, 1.3–1.6 mm wide. Leaves 10–30 cm long, 5–8 mm wide, generally glabrous but central vein ciliate, some basal leaves with few but conspicuous hairs, margins scabrid. Spine-like prickly hairs present along the distal part of the leaves, antrorse. Sheaths slightly winged. Contraligule triangular, glabrous, sometimes puberulous, strongly ciliate along the margin. Panicle spiciform, little branched, rachilla reddish, flattened, completely glabrous. One or two terminal panicles, up to 5 cm long. Laterals solitary, generally two or three, distal panicle close to the terminal, basal much shorter than the internode. Peduncle up to 5 cm. Spikelets unisexual, mostly 75% female. Male glume 2.5–3.5 mm long, female 3–3.5 mm, both straw coloured with reddish margin and green midrib. Nutlet globose, 2–3 mm in diameter, smooth, hairy underneath, shiny, white. Hypogynium deeply trilobed, margin revolute.

Distribution and habitat: Africa, Central and South America, and Madagascar. It is as a weed in Peru (Clavo Peralta, 1993), Costa Rica, Honduras, Trinidad and Dominican Republic (Holm, 1979). In a study based in Brazil, Silva *et al.*, 2001 noted that *S. gaertneri* establishes arbuscular mycorrhizae in some environments. Madagascar: littoral and mid altitude wet forest. 0–1200 m.

Conservation status: LC

Representative specimens examined: MADAGASCAR, **Antsiranana**: 400 m, 28.v.1995, *L. Gautier & C. Chatelain 2829* (MO, TAN); Ankarana Massif, 170 m, 31.i.2003, *M. Bardot-*

Vaucoulon et al. 1385 (K, MO, TAN); Besinkaram 350 m, 2.iv.1996, *L. Gautier & S.T. Be LG2959* (G, MO, TAN, K); Maroantsetra, 28.ii.1988, *D. A. Simpson 88/87* (MO, TAN, K); Nossi Be, iv.1879, *J.M. Hildebrandt 2924* (JE, K, MNHN-P-P01888534) SAVA, 1190 m, 3.iii.2006, *R. Razakamalala & et al. 2709* (MO, K); **Fianarantsoa**: km 23 RN25 Mananjary-Ifanadiana, 30 m, 16.xii.2017, *P. Wilkin et al. 941* (K); **Toamasina**: Maroantsetra, Andranofotsy river, 11.ii.1988, *D. A. Simpson & M. R. Cheek 88/19* (TAN, K); route Fotsimaro-Ambodiriano, xii.1962, *J. M. Bosser 17021* (TAN, K).

Notes: In South America, it has been utilised as a stimulant of the nervous system and to treat constipation (Alcorn, 1984) and snake poisoning (Soares *et al.*, 2004). In Tanzania, it is locally used as a medicine to treat dysmenorrhoea and colds in humans, and rinderpest in cattle (Burkill, 1985).

APPENDIX 2. Vouchers and GenBank accession numbers. ** Unpublished sequences facilitated by Kenneth Bauters. * Newly generated sequences.

Taxon (reference)	Voucher (herbarium)	Country	ITS	<i>ndhF</i>	<i>rps16</i>
<i>Becquerelia cymosa</i> Brongn. (SC281)	Van Andel T.R. & al. 4473 (GENT)	Suriname	LN886915	LN887033	LN887144
<i>Bisboeckelera microcephala</i> (Boeck.) T.Koyama (SC282)	Billiet F. & al. 1850 (BR)	French Guiana	LN886916	LN887034	LN887145
<i>Calyptrocarya glomerulata</i> (Brongn.) Urb. (SC106)	De Wilde Bart 7 (TCD)	Guyana	LN886843	LN886954	LN887070
<i>Diplacrum caricinum</i> R.Br. (SC279)	Sungkaew S. & Teerawatananon A. 636 (Thailand Natural History Museum)	Thailand	LN886913	LN887031	-
<i>Scleria angusta</i> Nees ex Kunth (JG20)	Rabevohitra 2062 (K)	Madagascar	*	-	-
<i>Scleria angusta</i> Nees ex Kunth (SC072)	Browning J. 390 (GENT)	South Africa	LN886828	LN886939	LN887056
<i>Scleria bambariensis</i> (SC204)	Bidgood S. & al. 5695 (MO)	Tanzania	LN886882	LN886998	LN887112
<i>Scleria bambariensis</i> Cherm. (SC064b)	Coppejans E. 8350 (GENT)	Kenya	-	**	-
<i>Scleria baronii</i> C.B.Clarke ex Cherm (SC206)	Antilahimena P. & al. 5872 (MO)	Madagascar	LN886884	LN887000	LN887113
<i>Scleria boivinii</i> Steud. (SC056)	Breteler 5339 (GENT)	Ivory Coast	-	**	-
<i>Scleria boivinii</i> Steud. (SC057)	Viane R. 1057 (GENT)	Ivory Coast	-	**	-
<i>Scleria boivinii</i> Steud. (SC209)	Mamadou N. & al. 10 (MO)	Gabon	LN886886	LN887002	LN887115
<i>Scleria brownii</i> (R.Br.) Kunth (SC059)	Wilson K.L. 8098 (GENT)	Australia	LN886823	LN886934	LN887052
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC026)	Reekmans M. 4745 (GENT)	Burundi	**	-	-
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC035)	Reekmans M. 8724 (GENT)	Burundi	**	-	-
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC265)	Reekmans M. 6830 (GENT)	Burundi	LN886904	LN887022	LN887134
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC285)	Laegaard S. 16215 (GENT)	Zimbabwe	**	**	-
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC306)	Gereau R.E. & al. 4306 (MO)	Tanzania	-	**	-
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC355)	Bauters K. 2015-071 (GENT)	Zambia	-	**	-
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC378)	Bauters K. 2015-163 (GENT)	Zambia	**	**	**
<i>Scleria bulbifera</i> Hochst. ex A.Rich (SC438)	Bauters K. 2015-163 (GENT)	Zambia	-	**	**
<i>Scleria corymbosa</i> Roxb. (SC096)	Bart De Wilde & al. 02-199 (TCD)	Thailand	LN886836	LN886947	LN887064
<i>Scleria cyperina</i> Kunth (SC127)	Beck St. G. 133 (GENT)	Brazil	LN886853	LN886965	LN887080
<i>Scleria distans</i> Poir. var. <i>distans</i> (SC178)	Bauters K. & Coenen J. 2013-008 (GENT)	Florida	**	**	**
<i>Scleria distans</i> Poir. var. <i>distans</i> (SC036)	Reekmans M. 10474 (GENT)	Burundi	**	-	-
<i>Scleria distans</i> Poir. var. <i>distans</i> (SC037)	Reekmans M. 7239 (GENT)	Burundi	**	**	**
<i>Scleria distans</i> Poir. var. <i>distans</i> (SC039)	Gonto R. & Fernandez A. 147 (GENT)	Venezuela	**	-	-
<i>Scleria distans</i> Poir. var. <i>distans</i> (SC177)	Bauters K. & Coenen J. 2013-007 (GENT)	U.S.A.	LN886877	LN886989	LN887104
<i>Scleria distans</i> Poir. var. <i>distans</i> (SC253)	Bauters K. & Coenen J. 2013-009 (GENT)	Florida	-	**	**
<i>Scleria distans</i> var. <i>chondrocarpa</i> (Nelmes) Lye (SC033)	Larridon I. et al. 2010-0279 (GENT)	Madagascar	**	**	**
<i>Scleria distans</i> var. <i>chondrocarpa</i> (Nelmes) Lye (SC031)	Larridon I. et al. 2010-0229 (GENT)	Madagascar	**	**	**
<i>Scleria distans</i> var. <i>chondrocarpa</i> (Nelmes) Lye (SC034)	Larridon I. et al. 2010-0241 (GENT)	Madagascar	LN886813	LN886924	LN887042
<i>Scleria flagellum nigrorum</i> Berg. (SC129)	Moraes M. & al. 1785 (GENT)	Bolivia	LN886854	LN886966	LN887081
<i>Scleria foliosa</i> Hochst. Ex A. Rich. (SC130)	Malaisse F. & Goetghebeur P. 418 (GENT)	DCR	LN886855	LN886967	LN887082

<i>Scleria gaertneri</i> Raddi (JG11)	Razakamalala R. 2709 (K)	Madagascar	-	-	*
<i>Scleria gaertneri</i> Raddi (JG25)	M. Bardot-Vaucoulon et al. 1385 (K)	Madagascar	-	*	-
<i>Scleria gaertneri</i> Raddi (SC135)	Pott A. s.n. (GENT)	Brazil	LN886858	LN886970	LN887085
<i>Scleria gaertneri</i> Raddi (SC271)	Camelbeke K. & Goetghebeur P. 903 (GENT)	Costa Rica	LN886908	LN887026	LN887138
<i>Scleria griegifolia</i> (Ridl.) C.B. Clarke (SC075)	Desfayes M. 95-3121 (GENT)	Madagascar	LN886829	LN886940	LN887057
<i>Scleria hildebrandtii</i> Boeckeler (SC137)	Zwaenepoel A. 508 (GENT)	Kenya	LN886859	LN886971	LN887086
<i>Scleria hilsenbergii</i> Ridl. (SC032)	Larridon I. & al. 2010-0138 (GENT)	Madagascar	LN886812	LN886923	LN887041
<i>Scleria hilsenbergii</i> Ridl. (SC298)	Dhondt 7 (GENT)	Madagascar	**	**	-
<i>Scleria lacustris</i> C. Wright (SC004)	Guareco I. 409 (GENT)	Bolivia	LN886806	LN886917	LN887035
<i>Scleria lacustris</i> C. Wright (SC276)	Jacono C.C. 344 (GENT)	U.S.A.	LN886910	LN887028	LN887140
<i>Scleria lagoensis</i> Boeckeler (JG02)	Hunt & Ferreira Ramos 6061 (K)	Brazil	*	-	*
<i>Scleria lagoensis</i> Boeckeler (SC224)	Gereau R.E. & al. 4306 (MO)	Tanzania	LN886890	LN887006	LN887119
<i>Scleria latifolia</i> Sw. (SC141)	Camelbeke K. & Goetghebeur P. 913 (GENT)	Costa Rica	LN886861	LN886973	LN887088
<i>Scleria lithosperma</i> var. <i>lithosperma</i> (L.) Sw. (JG10)	L. Nusbaumer & P. Ranirison LN1526 (K)	Madagascar	*	-	-
<i>Scleria lithosperma</i> var. <i>lithosperma</i> (L.) Sw. (SC003)	Stevens W.D. & Martinez S. 25260 (GENT)	Guatemala	-	**	**
<i>Scleria lithosperma</i> var. <i>lithosperma</i> (L.) Sw. (SC182)	Bauters K. & Coenen J. 2013-019 (GENT)	U.S.A.	-	LN886990	LN887105
<i>Scleria lithosperma</i> var. <i>lithosperma</i> (L.) Sw. (SC183)	Bauters K. & Coenen J. 2013-026 (GENT)	U.S.A.	-	**	**
<i>Scleria lithosperma</i> var. <i>lithosperma</i> (L.) Sw. (SC184)	Bauters K. & Coenen J. 2013-027 (GENT)	U.S.A.	-	**	**
<i>Scleria madagascariensis</i> (JG23)	Rokotozafy 2741 (K)	Madagascar	*	-	*
<i>Scleria melanomphala</i> Kunth (JG17)	Larridon et al. 2010-0336B (GENT)	Madagascar	-	-	*
<i>Scleria melanomphala</i> Kunth (SC112)	Muasya M.A. 96/167 (GENT)	Tanzania	LN886848	LN886959	LN887075
<i>Scleria naumanniana</i> Boeck. (SC150)	Laegaard S. 16894 (GENT)	Senegal	LN886866	LN886978	LN887093
<i>Scleria oligantha</i> Michx. (SC236)	Brant A.E. 4716 (MO)	U.S.A.	LN886893	LN887010	LN887122
<i>Scleria poaeformis</i> Retz. (JG15)	Mogg A.O.D. 28820 (K)	Madagascar	-	*	*
<i>Scleria poaeformis</i> Retz. (SC280)	De Wilde B. b89 (TCD)	Thailand	LN886914	LN887032	LN887143
<i>Scleria pooides</i> Ridl. (SC019)	Hess H.&E. 52/281 (GENT)	Angola	LN886809	LN886920	LN887038
<i>Scleria pooides</i> Ridl. (SC020)	Hess H.&E. 51/169 (GENT)	Angola	**	**	-
<i>Scleria pooides</i> Ridl. (SC264)	Merrett L. 1027 (GENT)	Zambia	**	**	**
<i>Scleria pooides</i> Ridl. (SC364)	Bauters K. 2015-119 (GENT)	Zambia	**	**	**
<i>Scleria pooides</i> Ridl. (SC365)	Bauters K. 2015-122 (GENT)	Zambia	**	**	-
<i>Scleria pooides</i> Ridl. (SC367)	Bauters K. 2015-129 (GENT)	Zambia	**	**	-
<i>Scleria pooides</i> Ridl. (SC386)	Bauters K. 2015-189 (GENT)	Zambia	**	**	**
<i>Scleria pooides</i> Ridl. (SC391)	Bauters K. 2015-207(GENT)	Zambia	**	-	-
<i>Scleria racemosa</i> Poir. (JG18)	Desfayes M. 95-1211 (GENT)	Madagascar	*	*	*
<i>Scleria racemosa</i> Poir. (SC109)	Billiet F. S3802 (BR)	Africa	LN886846	LN886957	LN887073
<i>Scleria rosea</i> Cherm. (SC196)	Archer R.H. 3816 (MO)	Madagascar	LN886879	LN886995	LN887110
<i>Scleria rosea</i> Cherm. (JG12)	SDR460 (K)	Madagascar	*	*	*
<i>Scleria sphacelata</i> F. Muell. (SC277)	Michell C.R. 3026 (MO)	Australia	LN886911	LN887029	LN887141
<i>Scleria</i> spp. sect. <i>Abortivae</i> (JG24)	Rakotomalaza P. J. & Ravelomanantsoa D.2128 (K)	Madagascar	-	*	-
<i>Scleria terrestris</i> (L.) Fassett (SC055)	Goetghebeur P. 12129 (GENT)	Philippines	LN886822	LN886933	LN887051
<i>Scleria tessellata</i> Willd. (SC166)	De Smet K. 77/14 (GENT)	Burkina Faso	LN886872	LN886984	LN887099
<i>Scleria triglomerata</i> Michx. (SC249)	Kral R. 94078 (MO)	U.S.A.	LN886899	LN887016	LN887128

APPENDIX 3. Single marker and concatenated analyses.

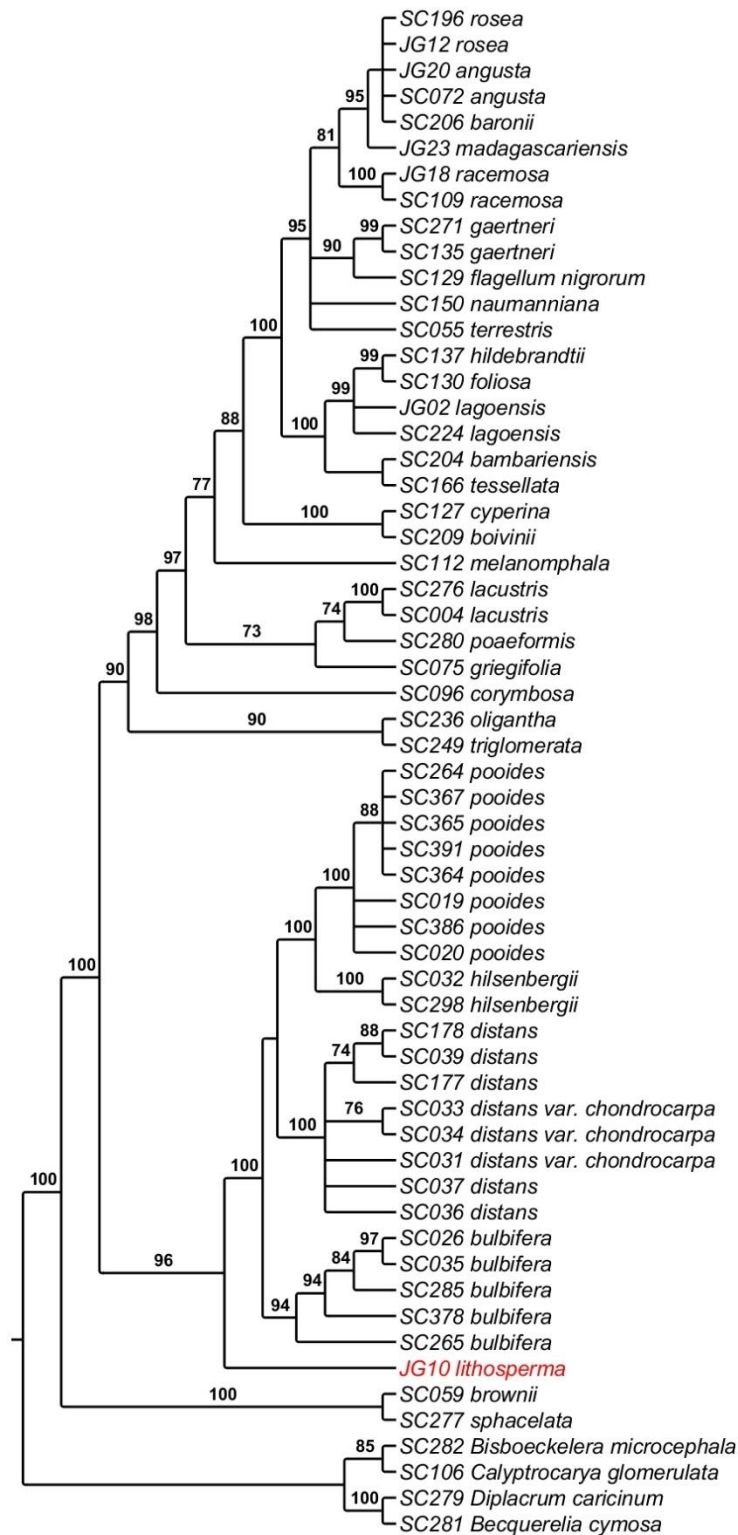


Figure 1. ML analysis of the marker ITS. The cladogram shows all the sequences included in the alignment. BS values equal or higher than 70% are displayed. Species in red are not included in the concatenated analyses.

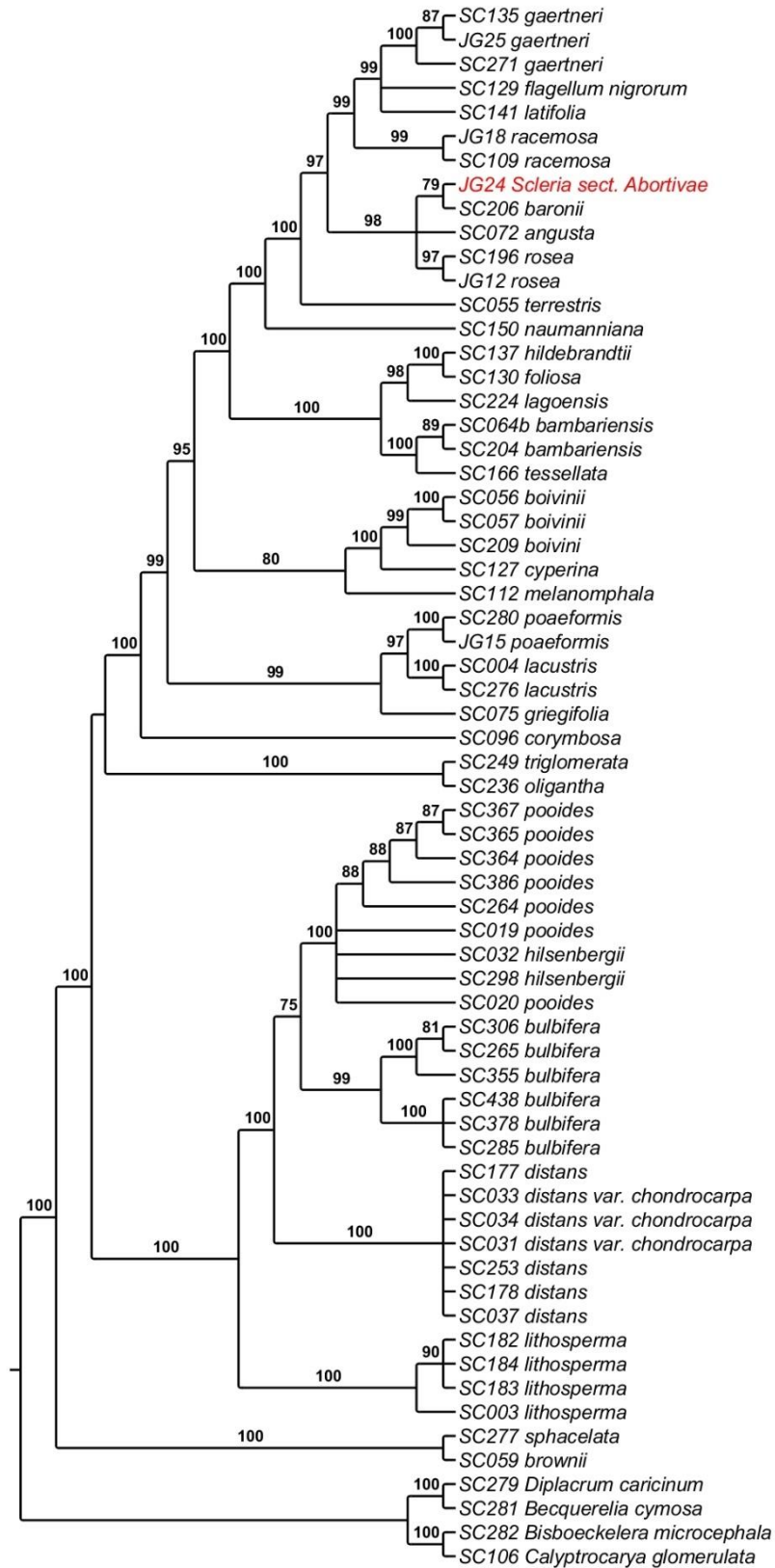


Figure 2. ML analysis of the marker *ndhF*. The cladogram shows all the sequences included in the alignment. BS values equal or higher than 70% are displayed. Species in red are not included in the concatenated analyses.

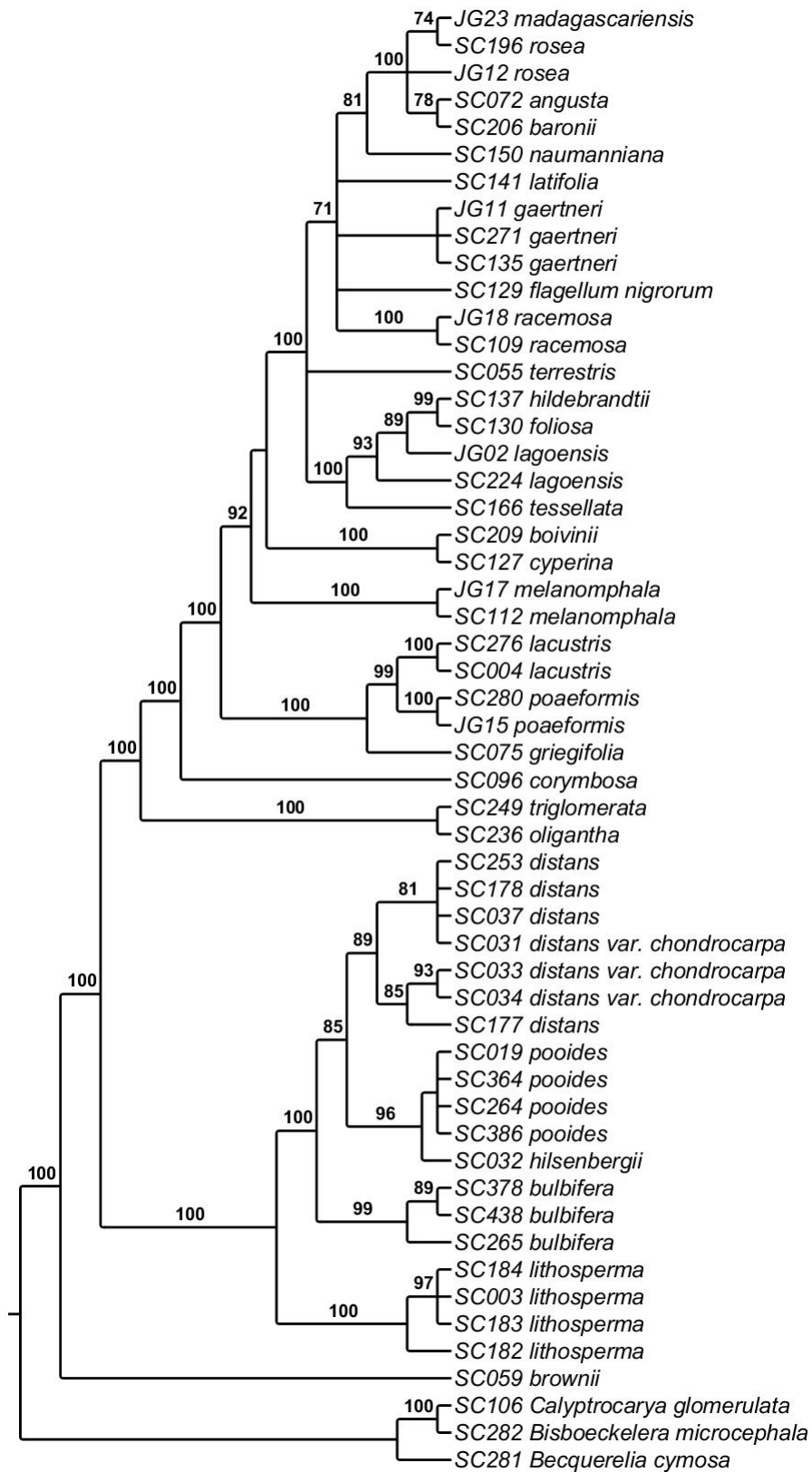


Figure 3. ML analysis of the marker *rps16*. The cladogram shows all the sequences included in the alignment. BS values equal or higher than 70% are displayed.

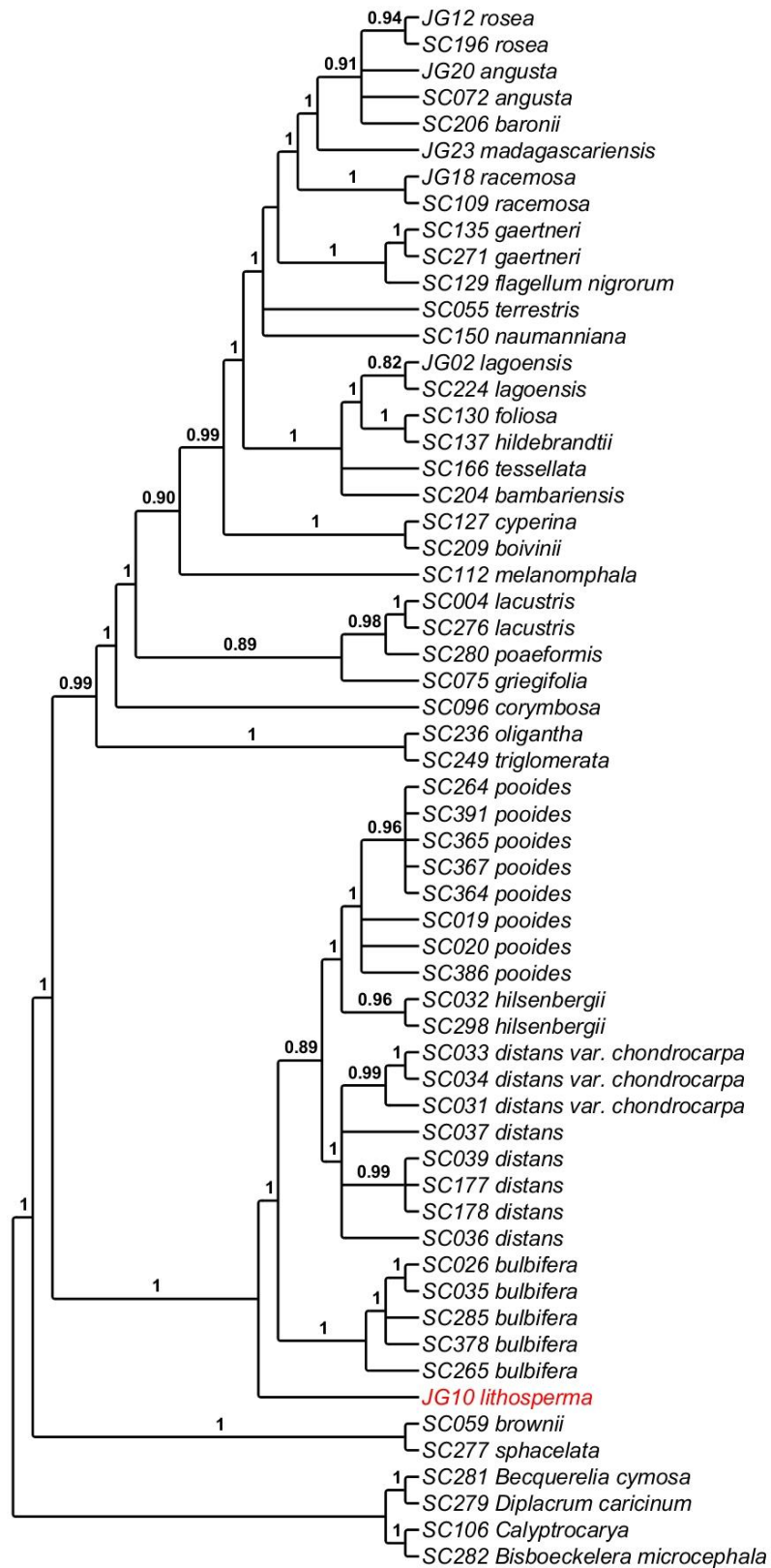


Figure 4. BI analysis of the marker ITS. The cladogram shows all the sequences included in the alignment. PP values equal or higher than 0.80 are displayed. Species in red are not included in the concatenated analyses.

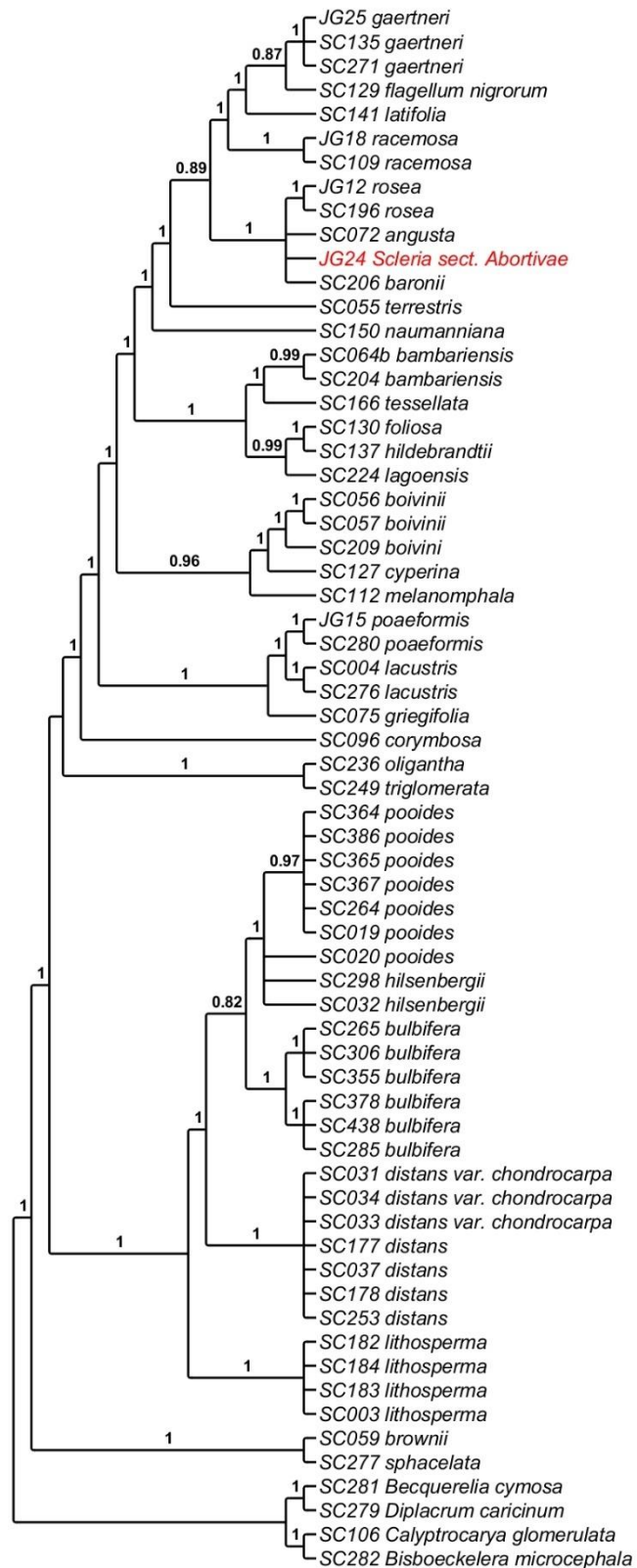


Figure 5. BI analysis of the marker *ndhF*. The cladogram shows all the sequences included in the alignment. PP values equal or higher than 0.80 are displayed. Species in red are not included in the concatenated analyses.

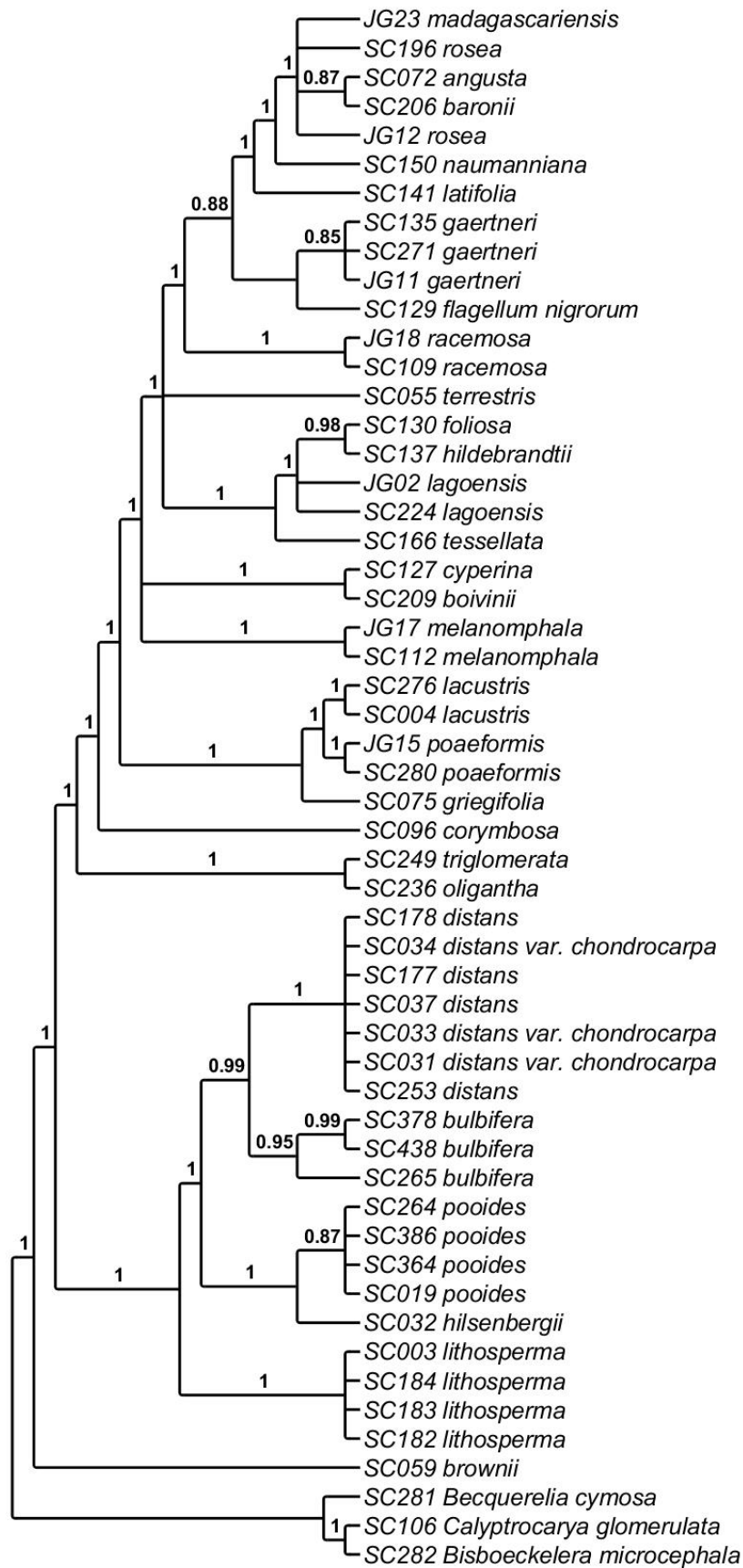


Figure 6. BI analysis of the marker *rps16*. The cladogram shows all the sequences included in the alignment. PP values equal or higher than 0.80 are displayed.

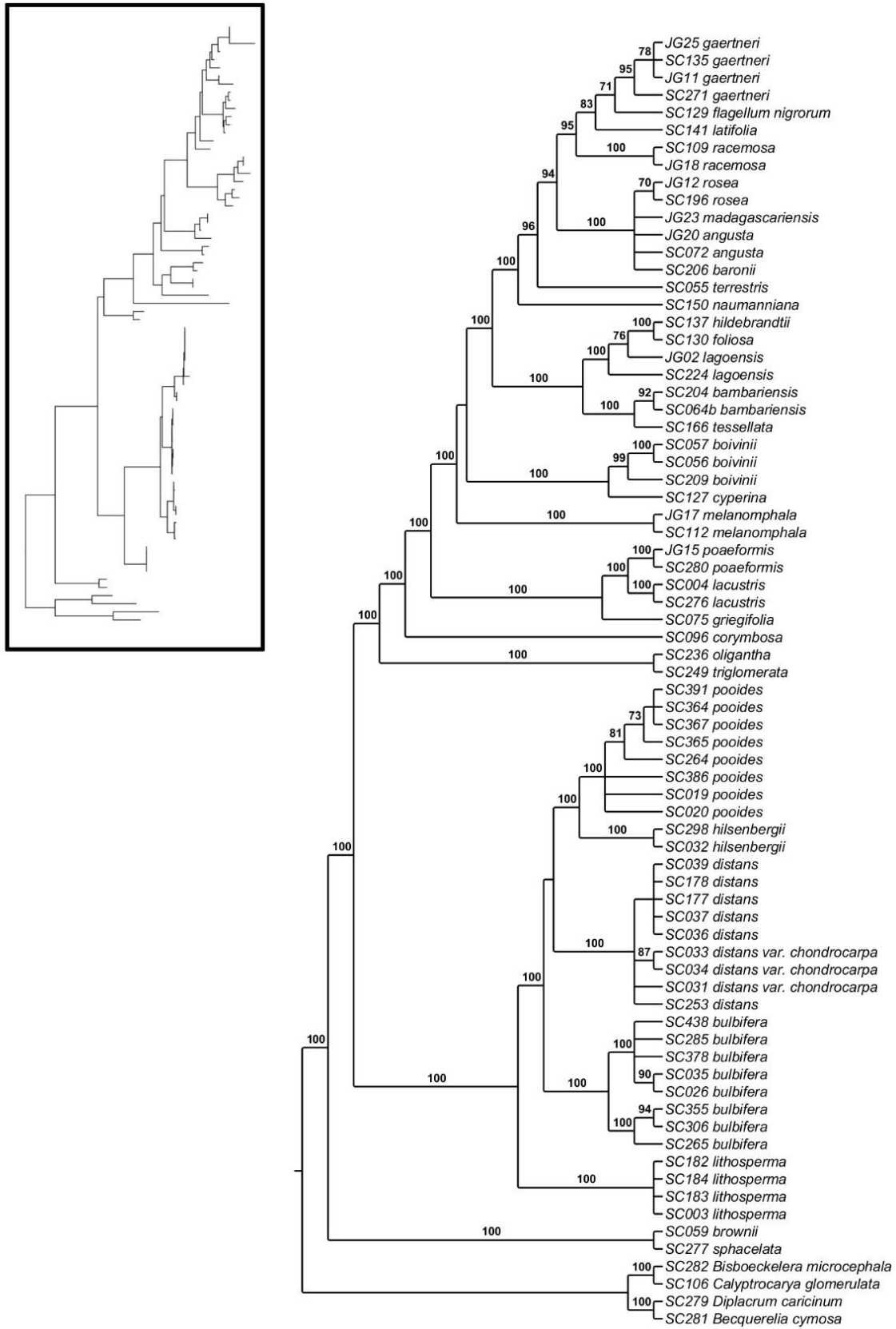


Figure 7. ML analysis of the concatenated alignment. The cladogram shows all the sequences included in the alignment. BS values equal or higher than 70% are displayed. The box includes the same tree with branch lengths.

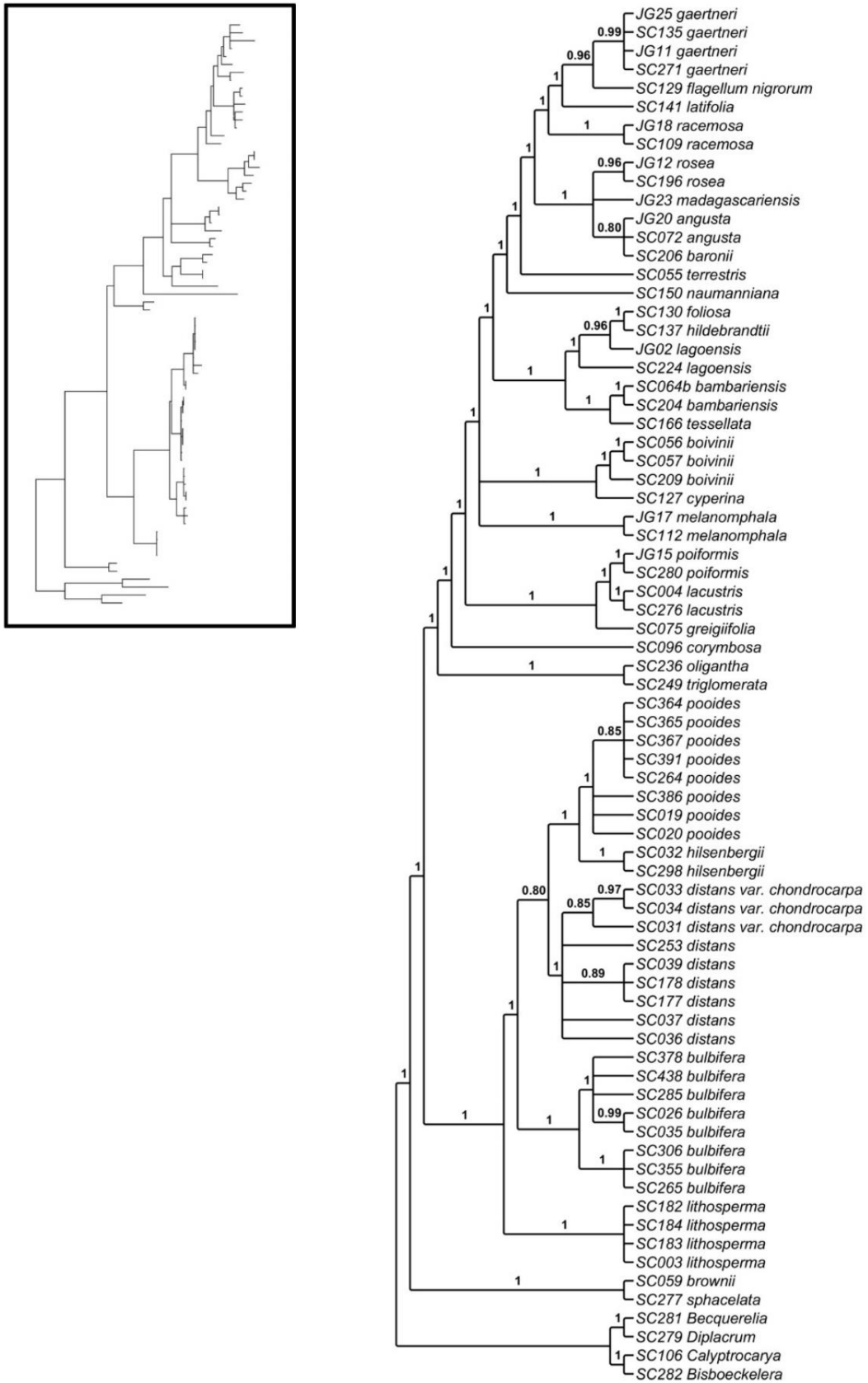


Figure 8. BI analysis of the concatenated alignment. The cladogram shows all the sequences included in the alignment. PP values equal or higher than 0.80 are displayed. The box includes the same tree with branch lengths.