

# *Savoronala*, a new genus of Malmideaceae (Lecanorales) from Madagascar with stipes producing sporodochia

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**Abstract** The new genus and species *Savoronala madagascariensis* is a lichenized hyphomycete characterized by its pale glaucous placodioid thallus with erect, short but robust stipes apically producing sporodochia with brown, sub-spherical conidia, whose cells are wrapped around a single chlorococcoid algal cell. Phylogenetic analyses using nuLSU and mtSSU sequences place *Savoronala* in the Malmideaceae (Lecanorales). The new species was collected on *Erica* stems and inhabits coastal dunes near Taolanaro (southeast Madagascar). *Lecidea floridensis* is shown to belong to *Malmidea* whereas *Lecidea cyrtidia* and *L. plebeja* are also resolved in the Malmideaceae. The genus *Sporodochiolichen* Aptroot & Sipman is reduced into synonymy with *Tylophoron*.

**Keywords** Anamorphic fungi · Lecanoromycetes · *Sporodochiolichen* · Madagascar · Phylogeny

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## Introduction

Madagascar is one of the world's most important biodiversity hotspots (Myers et al. 2000). The island harbors a very rich and diverse angiosperm flora with an estimation of c. 12,000 species (Schatz et al. 1996), with c. 80% considered to be endemic. Indeed, all segments of the biodiversity of the island are very rich in species, most of them being endemic (Goodman and Beanstead 2003). The rate of discovery of new taxa is unabated, including in supposedly well-known groups such as the lemurs (discovery of a further new species of *Microcebus* in 2012: Radespiel et al. 2012), or the chameleons (a puzzling number of cryptic species has just been demonstrated in the dwarf genus *Brookesia*: Glaw et al. 2012).

This contrasts sharply with the lichen flora as a mere 157 species are included in the only available check-list (Aptroot 2012); an unpublished list by the same author has 368 accessions. During a field trip in 2008, we could prospect several biomes, e.g. montane rainforests, rock outcrops and coastal sand dunes, and could make numerous new records for the island. New species were discovered such as *Syncesia madagascariensis* (Ertz et al. 2010) that was eventually found in La Réunion (van den Boom et al. 2011). Most of the new records, however, comprise widespread species not confined to Madagascar. Endemism is thus most probably much lower than in vascular plants. As an example, the dry spiny forests around the city of Toliara are a hotspot for endemic angiosperms while the lichen flora is rather species-poor. Important areas for lichen diversity seem to be situated in the montane rainforests where urgent conservation measures are needed. Another area that proved to be very rich in lichens are the coastal sands near the city of Taolanaro (southeast Madagascar) where we collected a very puzzling lichenized hyphomycete with stipes producing

sporodochia that represents a new species for science, being considered a genus of its own. The aim of the present paper is to describe it and to determine its phylogenetic position.

## Material and methods

Hand-made sections were investigated light-microscopically in water and 5% KOH. Microscopical measurements all refer to material examined in 5% KOH, which dissolves surrounding crystals. Chemical reactions were tested using KOH (K) and Lugol's reagent without (I) or with (K/I) pretreatment with K. Thin-layer chromatography (TLC) of acetone extracts was performed in solvent systems B and G (Orange et al. 2001). Air-dried herbarium material for study by SEM was mounted on polished aluminium stubs using a transparent two-component epoxy glue, gold-coated in a Balzers Union SCD 040 sputter and examined in a Cambridge Stereoscan S 200 scanning electron microscope.

Two well-preserved specimens of the new taxon lacking any visible symptoms of fungal infection were sampled for DNA isolation. Extraction of DNA and PCR amplification were performed following the protocol of Cubero et al. (1999). The following primers were used: for mtSSU: mrSSU1 and mrSSU3R (Zoller et al. 1999); for nuLSU: LIC2044, LR0R, LR3R, LR3, and LR6 (Kauff and Lutzoni 2002; Rehner and Samuels 1994; Vilgalys and Hester 1990). Amplicons were sequenced by Macrogen<sup>®</sup>. Sequence fragments were assembled with Sequencher v.4.9 (Gene Codes, Ann Arbor, MI, USA). Sequences were subjected to MEGABLAST searches to detect potential contamination.

We first built a matrix of LSU sequences retrieved from GenBank and representing all major clades of the Ascomycota following Schoch et al. (2009), to assess that our material actually belongs to the Lecanoromycetes as expected. The sampling covered the whole phylogenetical variation of the Ascomycota, including representatives of Taphrinomycetes, Saccharomycetes, Pezizomycetes, Orbiliomycetes, Arthoniomycetes, Dothideomycetes, Eurotiomycetes, Lecanoromycetes, Lichinomycetes, Leotiomyces, and Sordariomycetes. A single maximum likelihood (ML) analysis was performed with GARLI (v.0.951 for OSX; Zwickl 2006) and the branches of the single most likely tree produced were evaluated with 100 pseudoreplicates (data not shown). As our material was resolved within the Lecanoromycetes, albeit with weak support, we could proceed with phylogenetical analyses focusing on that clade.

A selection of taxa having both nuLSU and mtSSU sequences were chosen from the studies of Schmult et al. (2011) and Kalb et al. (2011) to generate a phylogenetic tree including the main groups of the Lecanoromycetidae. The taxa listed in Table 1 were aligned manually using MacClade 4.05 (Maddison and Maddison 2002). The outgroup species

**Table 1** DNA sequences used in this study; GenBank accession numbers in bold (4) refer to sequences generated by this project, all other sequences (148) were obtained directly from GenBank

Taxa	nuLSU	mtSSU
<i>Bacidia rosella</i> (Pers.) De Not.	37960788	32141050
<i>Bacidina arnoldiana</i> (Körb.) V. Wirth & Vězda	119514008	119514020
<i>Bryoria trichodes</i> (Michx.) Brodo & D. Hawksw.	119513961	119514140
<i>Buellia punctata</i> (Hoffm.) A. Massal.	119513966	119514131
<i>Byssoloma leucoblepharum</i> (Nyl.) Vain.	59323706	50082856
<i>Calopadia foliicola</i> (Fée) Vězda	59323707	50082860
<i>Catolechia wahlenbergii</i> (Ach.) Flot.	119514004	119514021
<i>Cladia retipora</i> (Labill.) Nyl.	34148718	34148561
<i>Cladonia rangiferina</i> (L.) Weber ex F.H. Wigg.	46852258	32141054
<i>Crocynia pyxinoides</i> Nyl.	46411442	46411380
<i>Degelia plumbea</i> (Lightf.) P.M. Jørg. & P. James	119643345	119642269
<i>Evernia prunastri</i> (L.) Ach.	6318536	15987426
<i>Fellhanera bouteillei</i> (Desm.) Vězda	59323777	50082865
<i>Fellhanera subtilis</i> (Vězda) Diederich & Sérus.	59323710	50082864
<i>Frutidella caesioatra</i> (Schaer.) Kalb	59323778	50082843
<i>Hypogymnia physodes</i> (L.) Nyl.	123979301	123979249
<i>Hypotrachyna caraccensis</i> (Taylor) Hale	119643035	119641533
<i>Imshaugia aleurites</i> (Ach.) S.L.F. Mey.	119513963	119514121
<i>Japewia tornensis</i> (Nyl.) Tønsberg	113473520	HQ660559
<i>Lecania cyrtella</i> (Ach.) Th. Fr.	37960799	32141064
<i>Lecanora achariana</i> A.L. Sm.	123979298	123979247
<i>Lecanora contractula</i> Nyl.	119513956	119514155
<i>Lecanora fuscescens</i> (Sommerf.) Nyl.	HQ660532	HQ660555
<i>Lecanora hybocarpa</i> (Tuck.) Brodo	110666897	119641323
<i>Lecanora intumescens</i> (Rebent.) Rabenh.	37960800	32141065
<i>Lecanora muralis</i> (Schreb.) Rabenh.	HQ660533	HQ660556
<i>Lecanora polytropa</i> (Ehrh.) Rabenh.	119514002	119514017
<i>Lecidea berengeriana</i> (A. Massal.) Nyl.	HQ660537	HQ660562
<i>Lecidea cyrtidia</i> Tuck.	HQ660538	HQ660563
<i>Lecidea floridensis</i> Nyl.	HQ660540	HQ660565
<i>Lecidea fuscoatra</i> (L.) Ach.	119642943	119641368
<i>Lecidea nylanderii</i> (Anzi) Th. Fr.	HQ660545	HQ660572
<i>Lecidea plebeja</i> Nyl.	HQ660549	HQ660577
<i>Lecidea pullata</i> (Norman) Th. Fr.	HQ660546	HQ660574
<i>Lecidea roseotincta</i> Coppins & Tønsberg	HQ660547	HQ660575
<i>Lecidea turgidula</i> Fr.	59323712	50082866
<i>Lecidella meiococca</i> (Nyl.) Leuckert & Hertel	37960801	32141066
<i>Lepraria incana</i> (L.) Ach.	119514005	119514022
<i>Lobaria scrobiculata</i> (Scop.) P. Gaertn.	46411444	46411386
<i>Malmidea coralliformis</i> Kalb	HM447627	HM447597
<i>Malmidea eeuuae</i> Kalb	HM447628	HM447601
<i>Masonhalea richardsonii</i> (Hook.) Kärnefelt	123979302	123979250
<i>Megalalaria grossa</i> (Pers. ex Nyl.) Hafellner	59323785	58891484
<i>Megalospora tuberculosa</i> (Fée) Sipman	46411439	46411388

**Table 1** (continued)

Taxa	nuLSU	mtSSU
<i>Micarea adnata</i> Coppins	59323715	50082829
<i>Micarea alabastrites</i> (Nyl.) Coppins	59323716	50082842
<i>Micarea doliiformis</i> (Coppins & P. James) Coppins & Sérus.	HQ660534	HQ660557
<i>Micarea (Leimonis) erratica</i> (Körb.) Hertel, Rambold & Pietschm.	59323717	50082815
<i>Micarea micrococca</i> (Körb.) Gams ex Coppins	59323719	50082827
<i>Micarea sylvicola</i> (Flot.) Vězda & V. Wirth	59323720	50082847
<i>Mycoblastus sanguinarius</i> (L.) Norman	119642962	119641393
<i>Neophyllis melacarpa</i> F. Wilson	34148734	34148585
<i>Niebla cephalota</i> (Tuck.) Rundel & Bowler	119513972	119514150
<i>Parmotrema reticulatum</i> (Taylor) M. Choisy	119643103	119641619
<i>Peltigera degenii</i> Gyeln.	46411446	46411393
<i>Phaeophyscia orbicularis</i> (Neck.) Moberg	119643263	119641752
<i>Placynthium nigrum</i> (Huds.) Gray	15216685	46411472
<i>Porpidia albocaerulescens</i> (Wulfen) Hertel & Knoph	119513967	119514128
<i>Protoblastenia calva</i> (Dicks.) Zahlbr.	46852266	119514161
<i>Protopannaria pezizoides</i> (Weber) P.M. Jørg. & S. Ekman	119643399	119642318
<i>Pseudevernia furfuracea</i> (L.) Zopf	50953329	15987445
<i>Psilolechia leprosa</i> Coppins & Purvis	59323722	50082808
<i>Psilolechia lucida</i> (Ach.) M. Choisy	59323723	50082807
<i>Psora decipiens</i> (Hedw.) Hoffm.	119513970	119514120
<i>Pyrrhospora quereana</i> (Dicks.) Körb.	37960817	32141081
<i>Ramalina complanata</i> (Sw.) Ach.	113707378	123979257
<i>Rhizocarpon geographicum</i> (L.) DC.	62005347	29837334
<i>Savoronala madagascariensis</i> 537	<b>KC020142</b>	<b>KC020144</b>
<i>Savoronala madagascariensis</i> 538	<b>KC020143</b>	<b>KC020145</b>
<i>Scoliciosporum umbrinum</i> (Ach.) Arnold	52699715	32141084
<i>Solorina saccata</i> (L.) Ach.	123979315	123979265
<i>Sphaerophorus globosus</i> (Huds.) Vain.	119513977	119514123
<i>Sporastatia testudinea</i> (Ach.) A. Massal.	52699717	46411480
<i>Stereocaulon tomentosum</i> Th. Fr.	34148745	34148600
<i>Tephromela atra</i> (Huds.) Hafellner	119513974	119514151
<i>Xanthoria elegans</i> (Link) Th. Fr.	119643441	119642386

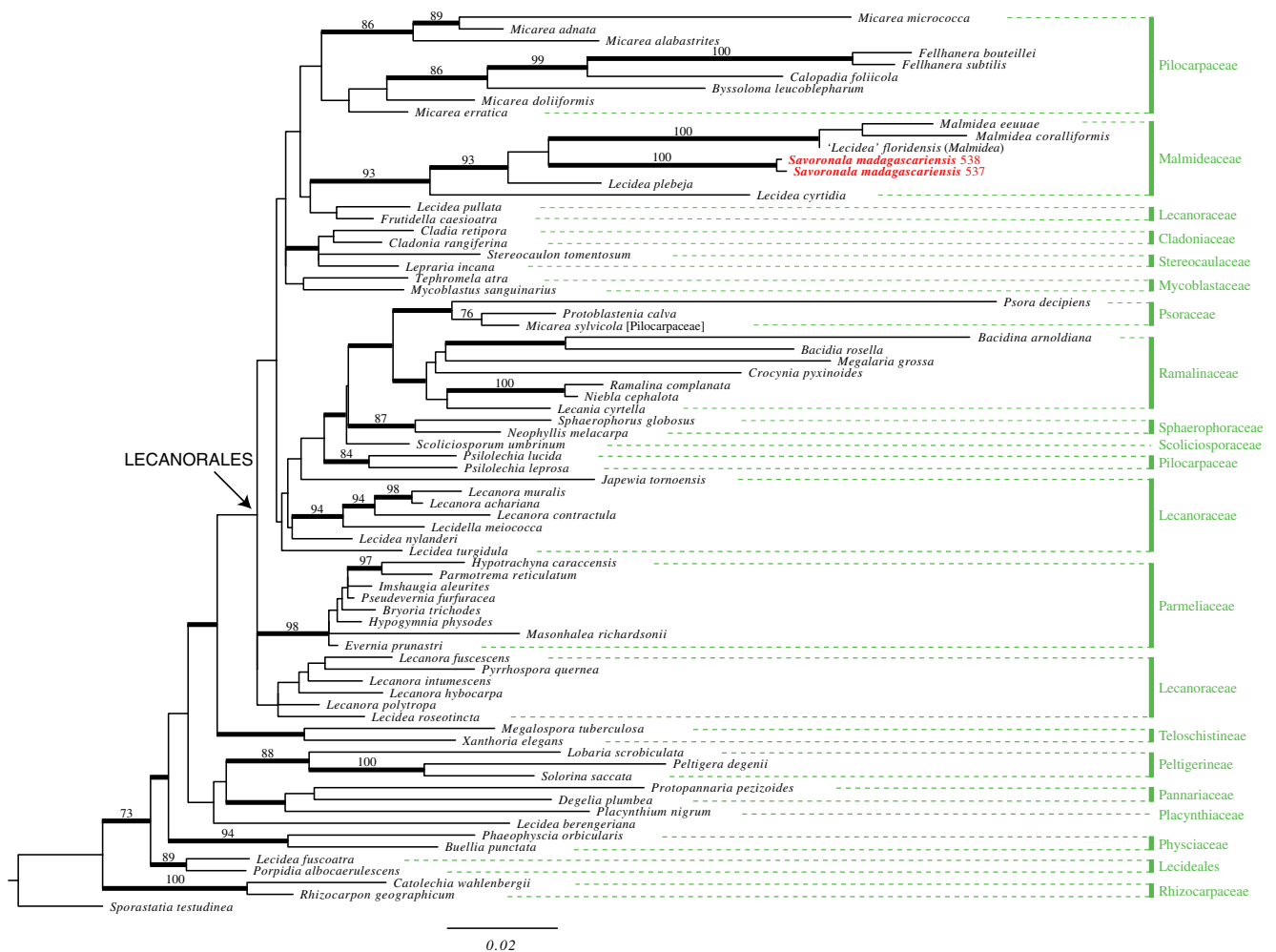
*Sporastatia testudinea* was chosen based on Schmull et al. (2011). Ambiguous regions and introns representing a total of 2,867 bp were delimited on the alignment of Schmull et al. (2011) retrieved from the AFTOL website and excluded from the analyses after realigning the portions that were ambiguous in the larger dataset.

Analyses for topological incongruence among loci were carried out using 1,000 replicates of neighbor-joining bootstrapping (NJ-bs) with distance measure estimated by maximum likelihood under a six-parameter (GTR) best-fit evolutionary model for nucleotide substitution (Cunningham et al. 1998; Liò and Goldman 1998; Yang et al. 1994) using

PAUP\* 4.0b10 (Swofford 2002). Best-fit evolutionary models were estimated for all NJ analyses using Akaike Information Criterion (AIC) as implemented in Modeltest v.3.06 (Posada and Crandall 1998). The GTR+I+G model was selected for the nuLSU and the mtSSU datasets. All topological bipartitions with NJ-bs values  $\geq 70\%$  were compared for the two loci. A conflict was assumed to be significant if two different relationships (one being monophyletic and the other being non-monophyletic) for the same set of taxa were both supported with bootstrap values  $\geq 70\%$  (Mason-Gamer and Kellogg 1996). Based on this criterion, no conflict was detected and therefore the nuLSU and mtSSU datasets were concatenated. The combined two-loci dataset consisted of 76 taxa and 1,624 unambiguously aligned sites, 1,171 for nuLSU and 453 for mtSSU.

Bayesian analyses were carried out on the two-loci dataset using the Metropolis-coupled Markov chain Monte Carlo method (MCMCMC) in MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) on the CIPRES portal (Miller et al. 2010). Analyses were run under the selected model for each gene partition using a gamma-distributed rate parameter and a proportion of invariable sites. Two parallel MCMCMC runs were performed each using four independent chains and 20 million generations, sampling trees every 1,000th generation. TRACER v.1.5 (Rambaut and Drummond 2007) was used to ensure that stationarity was reached by plotting the log-likelihood values of the sample points against generation time. Posterior probabilities (PP) were determined by calculating a majority-rule consensus tree generated from the 30,000 post-burnin trees of the 40,000 trees sampled by the two MCMCMC runs using the sumt option of MrBayes. The ML analysis was performed on the two-loci dataset using GARLI (v.0.951 for OSX; Zwickl 2006) with default settings, and a single most likely tree was produced ( $-\ln L = 130,69.1812$ ). One thousand bootstrap pseudoreplicates were used to calculate a majority rule consensus tree in PAUP\* to assess the ML bootstrap values (ML-bs). The Bayesian tree did not contradict the ML tree topology for the strongly supported branches and hence only the majority rule consensus tree of the ML analysis is shown here with the branches supported by the Bayesian analysis represented by thicker lines (Fig. 1).  $ML\text{-}bs \geq 70\%$  and  $PP > 90\%$  were considered to be significant. Phylogenetic trees were visualized using FigTree v.1.3.1 (Rambaut 2012).

A further dataset was assembled with all mtSSU accessions of *Malmidea* Kalb, Rivas Plata & Lumbsch in Kalb et al. (2011) together with the same loci accessions of *Lecideia cyrtidia* and *L. floridensis* in Schmull et al. (2011) and our sequences of *Savoronala*. An unweighted maximum parsimony analysis was run under PAUP\* (Swofford 2002), using heuristic searches with 1,000 random addition replicates, with tree bisection–reconnection (TBR) branch-swapping, steepest descent not in effect and MulTrees



**Fig. 1** Phylogenetic relationships among 76 taxa within Lecanoromycetidae based on a combined dataset of nuLSU and mtSSU sequences that resulted from a maximum likelihood analysis. ML-bs values  $\geq 70$  are shown above internal branches. Internal branches with a PP  $> 90\%$

resulting from a Bayesian analysis are considered strongly supported and represented by *thicker lines*. The two specimens of the new genus *Savoronala* are in *red and bold*

option in effect. Gaps were treated as missing data. The strength of support for individual branches was estimated using bootstrap values drawn from the 50% consensus tree constructed from all optimal trees saved during 100 pseudoreplicates heuristic searches.

## Results

### Phylogenetic analyses

Our phylogenetic tree is largely congruent with the well-supported lineages in Schumler et al. (2011) (Fig. 1). Some basal groups are strongly supported by both analyses such as the Rhizocarpaceae (ML-bs=100; PP=100), the Lecideales (ML-bs=89; PP=100), the Physciaceae (ML-bs=94; PP=100) and the Peltigerineae (ML-bs=88; PP=100), but the relationships between them are not supported. The Lecanorales

including most of the terminals are not supported. Families within the Lecanorales are often poorly supported except only for the Parmeliaceae (ML-bs=98; PP=100), the Malmideaceae (ML-bs=93; PP=100) and, the Sphaerophoraceae (ML-bs=87; PP=100) the three being well-supported by our analyses. When treated in the sense of Schumler et al. (2011), the Lecanoraceae and Pilocarpaceae are polyphyletic.

The two *Savoronala* specimens are resolved in a strongly supported clade (ML-bs=100; PP=100) with *Lecidea cyrtidia* Tuck., *L. floridensis* Nyl., *L. plebeja* Nyl. (= *L. sp.1* in Schumler et al. 2011), *Malmidea coralliformis* Kalb and *M. eeuuae* Kalb as part of the Lecanorales. In our phylogenetic tree, the latter clade (named here the Malmideaceae, thus including *Lecidea cyrtidia*, *L. floridensis*, *L. plebeja*, *Savoronala*, and two species of *Malmidea*) is sister to two Lecanoraceae, *Frutidella caesioatra* and *Lecidea pullata*, but this relationship is not supported. The clade *Frutidella-Malmidea* is sister to 9 representatives of the Pilocarpaceae



(5 *Micarea*, *Byssoloma leucoblepharum*, *Calopadia foliicola* and 2 *Fellhanera*) but this relationship is not supported either. In the six-loci phylogenetic tree by Schmull et al. (2011), the clade *Lecidea cyrtidia*, *L. floridensis* and *L. plebeja* (= *L. sp. 1*) (without support) together with *Micarea doliiformis* (Coppins & P. James) Coppins & Sérus. (without support) is sister (without support) to the core group of Pilocarpaceae (*Byssoloma*, *Calopadia*, *Fellhanera* and *Micarea*) and considered as being part of this family. However, the genus *Malmidea* was missing in the study by Schmull et al. (2011) because sequences of this genus only recently became available (Kalb et al. 2011). The placement of the genus *Malmidea* in the well-supported group including *Lecidea cyrtidia*, *L. floridensis*, *L. plebeja* and *Savoronala* led us to consider *Savoronala* as being part of the Malmideaceae recently described by Kalb et al. (2011).

Finally, the analysis with all mtSSU accessions of *Malmidea*, including *Lecidea cyrtidia*, *L. floridensis*, and *Savoronala*, could resolve with strong support *Lecidea floridensis* within a clade including all accessions of *Malmidea* (Kalb et al. 2011; tree not shown).

#### Taxonomy

*Savoronala madagascariensis* Ertz, Eb. Fisch., Killmann, Razafin. & Sérus., **gen. et sp. nov.** (Figs 2–3)

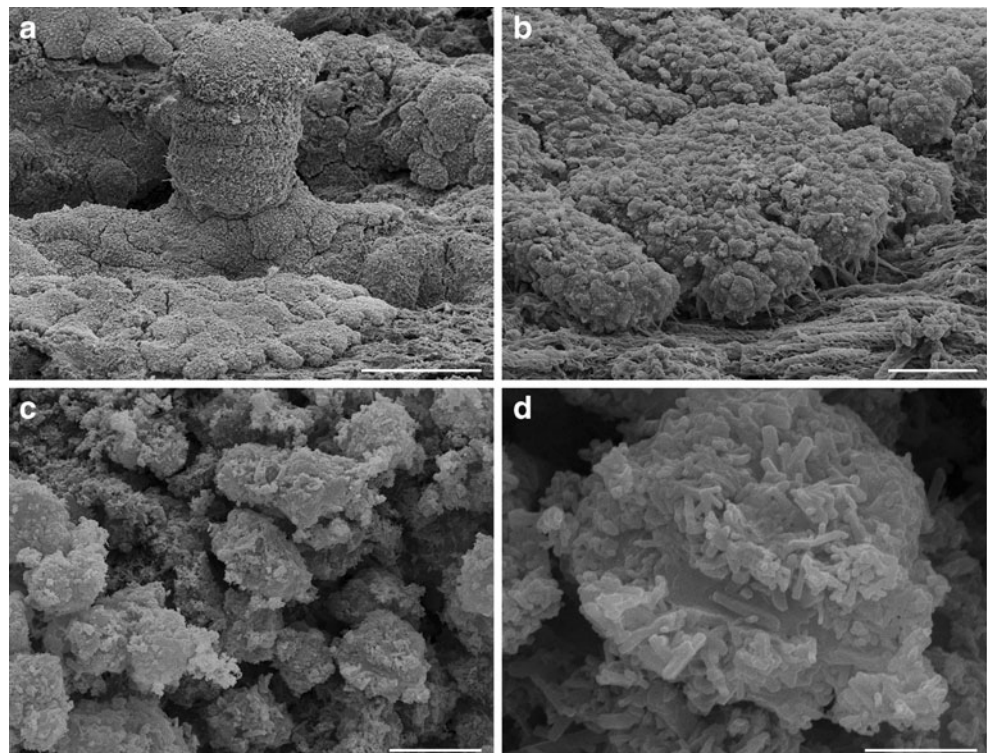
Mycobank MB 801909 & MB 801910

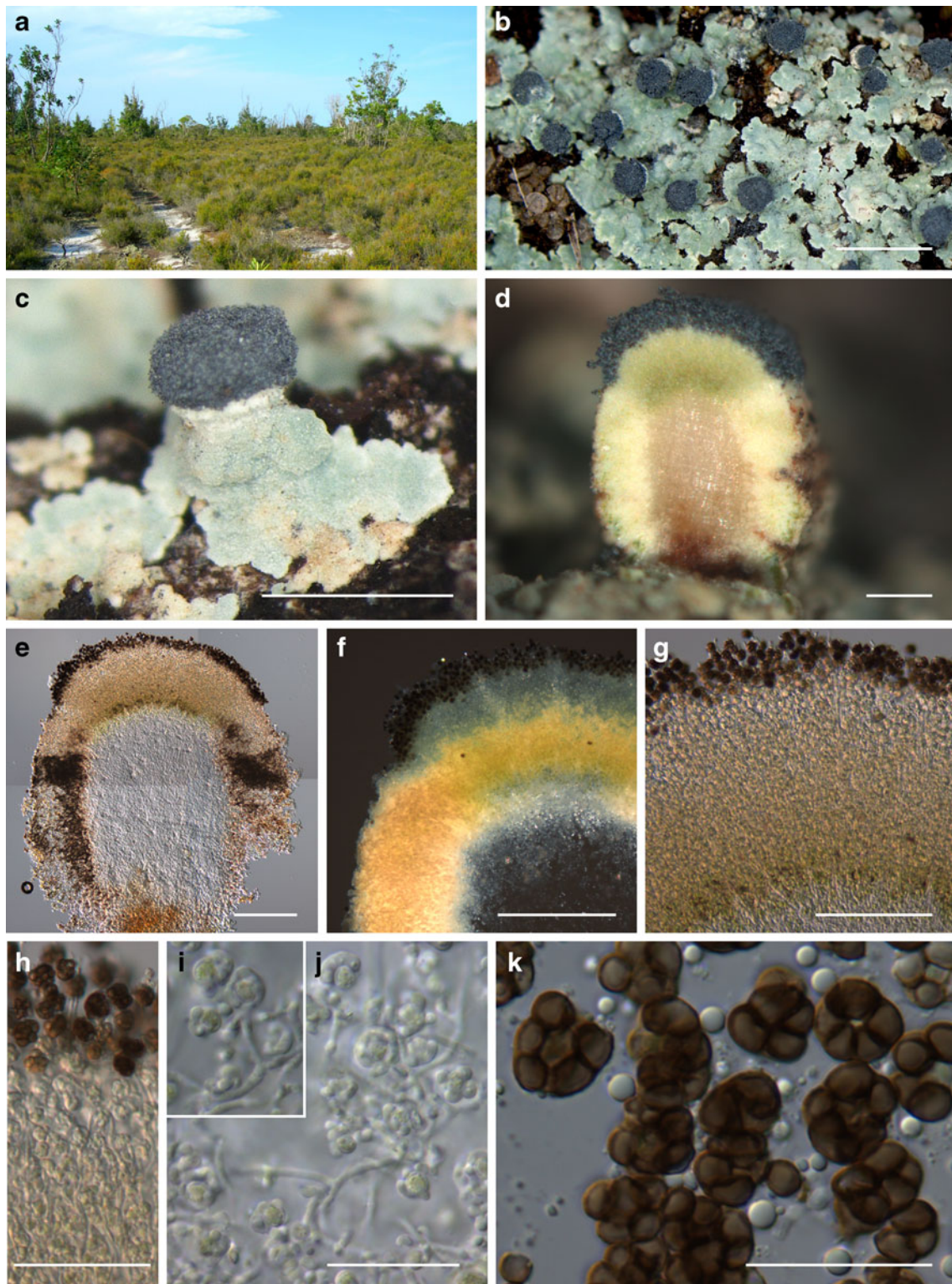
Diagnosis: Genus novum ab omnibus generibus ascomycotarum lichenisatarum combinatione signorum sucessivorum differt: thalli parvi placoides pallide glauci, photobiontes chlorococcoidei, formatio stipium pallide fulvorum cum sporodochia caeruleo-canescens in apice et conidia fusca cum cellula algarum.

Type: Madagascar, NE Taolanaro (Fort Dauphin), 22 m alt., 24°56'55.2"S, 47°00'33.2"E, on base of a stem of *Erica*, 11 Oct. 2008, D. Ertz 13139, E. Fischer, D. Killmann, V. Razafindrahaja & E. Sérusiaux (BR–holotypus; TAN, LG, KOBL—isotypi).

*Thallus* crustose, placodioid, adnate and ±tightly attached on bark, forming rosettes and with sporodochia-producing stipes when only reaching (0.5–)1 mm diam., coalescing to form patches up to 3 cm diam., pale glaucous green, covered with distinct pruina (easily seen when dry), outer lobes closely contiguous, flat to convex, with a smooth to verruculose, matt surface, esorediate, ecorticate; lobe ends not incurved; medulla hyphae irregularly branched, hyaline, mainly 1.5–2 µm thick, covered by many hyaline crystals dissolving in K; prothallus absent. *Photobiont* chlorococcoid, cells green, subsphaerical, (4–)5–7(–9) µm in the thalline lobes, 3–5(–6) µm at the apex of the stipes. Sporodochia forming at the apex of erected stipes; stipes single (rarely two contiguous), developing at the centre of the thallus, never branched, pale cream (sometimes dark brown when covered by other microorganisms), with a verruculose

**Fig. 2** *Savoronala madagascariensis* (isotype KOBL), SEM photographs. **a** Thallus and a sporodochium on a stipe. **b** Thallus margin. **c** 'Mature' conidia. **d** One 'mature' conidium, showing the many tiny crystals at its surface. Scale bars (a) 500 µm, (b) 80 µm, (c) 10 µm, (d) 3 µm





**Fig. 3** *Savoronala madagascariensis* (**b, c** isotype LG; **d–k** holotype). **a** Habitat, coastal heathland on dunes with *Erica* shrubs. **b, c** Thallus and sporodochia on stipes. **d, e** Section through a stipe and sporodochium (**e** in KOH). **f** Section through the upper part of a stipe and sporodochium view in polarized light (in H<sub>2</sub>O). **g, h** Conidiogenesis

(in KOH). **i, j** Wrapping of the algae at the beginning of the conidiogenesis (in KOH). **k** 'Mature' conidia (in KOH). Scale bars (**a**) *Erica* shrubs of about 1 m high, (**b**) 2 mm, (**c**) 1 mm, (**d–f**) 200  $\mu$ m, (**g**) 100  $\mu$ m, (**h**) 50  $\mu$ m, (**i–k**) 20  $\mu$ m



surface, sometimes slightly constricted at the base that is sometimes covered by thalline lobes, 200–700(–900)  $\mu\text{m}$  tall and 350–600(–800)  $\mu\text{m}$  thick when fully developed but sometimes almost absent; sporodochium convex, grayish blue, the same diameter or slightly wider than the stipe; upper surface uneven when covered by conidial agglomerations, when eroded becoming pale glaucous green.

*Stipes* in longitudinal section, when well developed, with a hyaline and loose medulla in the center surrounded by a cortex; medulla of *textura intricata* composed of 1- to 1.5- $\mu\text{m}$ -thick hyphae in a gel matrix, without or with very few crystals, up to c. 480  $\mu\text{m}$  in diam.; algal layer present albeit poorly differentiated (only a few algal cells present between the medulla and the cortex), except under the conidiophores where the algal cells are numerous and compact; cortex c.120–200  $\mu\text{m}$  thick, composed of anticlinal,  $\pm$  in parallel arranged hyaline hyphae; hyphae covered by minute crystals dissolving in K (best seen under polarized light); conidiophores irregularly branched, anastomosing, of 1–1.5  $\mu\text{m}$  thick, forming a rather dense, hyaline, layer of c.110–190  $\mu\text{m}$  thick with many hyaline conidia.

*Conidia* subspherical, first hyaline becoming dark brown when ‘mature’ at the surface of the stipes where they are easily detached to act as diaspores, covered by many tiny crystals dissolving in K, formed by mostly (3–)5–8(–10) fungal cells, (6–)7–10(–12)  $\mu\text{m}$  in diam. when brown, wrapping around a single algal cell, easily seen at early stages of the diaspores formation and before the fungal cells become brown; individual fungal cells shortly elongate, often curved and reniform, smooth, mostly 4–7 $\times$ 2–3  $\mu\text{m}$  in brown conidia. *Ascomata* and *pycnidia* unknown.

**Chemistry.** Thallus K–, C–, P+ pale yellow (weak), UV–. Stipes and thallus in section entirely I–, K/I–. TLC: zeorin and usnic acid and several unidentified UV spots after application of 10% sulfuric acid and heating (solvents B, G) (no fatty acid detected).

**Distribution and ecology:** Known only from the type locality in Madagascar where it was collected several times on *Erica* stems of a coastal *Erica*-grassland mosaic (Virah-Sawmy et al. 2009) on dunes composed of quartzitic sand. The open sandy places between the *Erica* shrubs were partly covered by large and conspicuous *Cladonia* cushions including *C. centrophora* Müll. Arg., *C. cinereorubens* des Abb., *C. confusa* (R. Sant.) Follm. & Ahti, *C. medusina* (Bory) Nyl., *C. praetermissa* A.W. Archer, *C. perplexa* des Abb. (type locality at Fort Dauphin, which is the earlier name of Taolanaro) and *C. perrieri* des Abb.

The type locality belongs to the littoral forest of Madagascar which occurs on the sandy coastal plains of the eastern part of the island and represents one of the smallest and most diverse habitats (De Gouvenain and Silander 2003; Ganzhorn et al. 2001). Beside *Erica*, dominant shrubs include *Canthium* sp., *Indigofera* sp., *Psorospermum revolutum*, *Ravenala madagascariensis* and *Vernonia nudicaulis*. The locality is also famous for large populations of *Nepenthes madagascariensis* growing in some freshwater swamps and also on the quartzitic sand dunes. Evidence from various proxies (geochemical analyses, diatoms, pollen and charcoal) indicates that the coastal environment of eastern Madagascar has been highly dynamic over the last 6,500 years, including higher sea level (up to 1–3 m higher than present; Virah-Sawmy et al. 2009).

The coastal heathlands and forests are under tremendous threats (Consiglio et al. 2006) because of woodland destruction, charcoal production and the recent opening of a giant mine of ilmenite (c.6,000 ha) and the associated titane production unit by Rio Tinto Ltd. (<http://www.riotintomadagascar.com>).

***Tylophoron*** Nyl. ex Stizenb.

Ber. Thät. St. Gallen Naturwiss. Ges. 1861–1862: 177 (1862). Type: *Tylophoron protrudens* Nyl.

**Syn. nov.** *Sporodochiolichen* Aptroot & Sipman, Lichenologist 43: 358 (2011). Type: *Sporodochiolichen lecanoricus* Aptroot & Sipman

***Tylophoron hibernicum*** (D. Hawksw., Coppins & P. James) Ertz, Diederich, Bungartz & Tibell, Lichenologist 43: 354 (2011).

Basionym: *Blarneya hibernica* D. Hawksw., Coppins & James, Bot. J. Linn. Soc. 79: 358 (1979).

**Syn. nov.** *Sporodochiolichen lecanoricus* Aptroot & Sipman, Lichenologist 43: 358 (2011). Type: Papua New Guinea, Eastern Highlands Prov., Mount Gahavisuka Provincial Park, 11 km N of Goroka, alt. 2,300–2,450 m, on bark in mountain forest, 11 August 1992, A. Aptroot 31060 (BR-holotype!)

## Discussion

*Savoronala madagascariensis* is easy to recognize by the following combination of characters: (1) the small, pale glaucous placodioid thalli, (2) the chlorococcoid photobiont, (3) the formation of pale cream stipes bearing grayish blue sporodochia at the apices, and (4) conidia associated and dispersed with an algal cell and dark brown when ‘mature’. No other taxa throughout the lichenized fungi can be confused with *Savoronala*. In combination with the

phylogenetic results, discussed in the following, we consider these differences as sufficient for the recognition of a new genus.

In our molecular analyses (Fig. 1), *Savoronala* was shown to be part of the family Malmideaceae where the closely related *Lecidea cyrtidia*, *L. floridensis* and *L. plebeja* can be included. These species share no obvious phenotypical characters with *Savoronala*. To our knowledge, none of these species are known to produce any kind of vegetative diaspores, nor conidia, and all have a crustose thallus (not placodioid). The three species are of uncertain generic position and need to be accommodated in other genera because the generic type [*Lecidea fuscoatra* (L.) Ach.] forms, with other species of *Lecidea* sensu stricto and *Porpidia*, a distinct lineage outside the Lecanorales and referred to as the Lecideales (Schmull et al. 2011).

The placement of *Lecidea floridensis* in the strongly supported clade with *Malmidea coralliformis* and *M. eeuuae* suggest that the species might belong to the genus *Malmidea*. Examination of the material used by Schmull et al. (2011) of *Lecidea floridensis* confirmed that it belongs to the recently described genus *Malmidea* (Kalb et al. 2011), and more precisely to the *M. piperis* aggr. (Cáceres 2007; Lücking 2008). Indeed, it has a smooth or slightly rugose thallus reacting UV+pale yellow, apothecia biatorine, round or slightly undulating, 0.8–1.2 mm in diam, with a dark brown disc, a slightly prominent and pale bluish black margin, excipulum paraplectenchymatous, brown, made of radiating hyphae, slightly constricted at septa, with hydrophobic granules, paraphyses simple or more rarely branched and anastomosing, with a slightly swollen apex, clavate asci with a distinct tubular structure in the tholus, ascospores 8/ascus, simple, ellipsoid,  $9\text{--}16 \times 5.5\text{--}6.5 \mu\text{m}$ , halonate.

It is easily distinguished from *Malmidea piperis* (Spreng.) Kalb et al. by its whitish K- medulla (orange-red medulla K+purple in *M. piperis*). It could be a synonym of the neotropical and widespread species *M. vinosa* (Eschw.) Kalb et al. as we could not detect any significant morphological or anatomical difference, except for slightly smaller ascospores. We thus refrain from making the combination of *Lecidea floridensis* into *Malmidea* as the epithet may represent a mere synonym of *M. vinosa*. Both *M. piperis* and *M. vinosa* have been reported from Florida, USA (Lücking et al. 2011). As a conclusion, the specimen of *Lecidea floridensis* used in the phylogenetic study by Schmull et al. (2011) is a species of *Malmidea* Kalb et al. (2011).

*Lecidea cyrtidia* is saxicolous on well-lit siliceous rocks and is reported from North America (Esslinger 2011) and

from Belgium and Denmark in Europe (Søchting and Alstrup 2002; Sérusiaux et al. 1999), while *L. plebeja* is corticolous or lignicolous, mainly on conifer stems in boreal and alpine-montane environments in North America (Esslinger 2011) and north and central Europe (Hafellner and Türk 2001; Santesson et al. 2004). These two species have an excipulum, hamathecium and ascospores very similar to those of *Malmidea*; they mainly differ by the absence of any lichen metabolites in the thallus (in *Malmidea*, the thallus can produce atranorin, norsolorinic acid, anthraquinones, biphenyls and xantholepinones; Kalb et al. 2011), excipulum outer parts comprizing cells 3–5  $\mu\text{m}$  wide and with dark brown apical caps, paraphyses apices slightly swollen and with brown caps, and smaller ascospores ( $<10 \mu\text{m} \times 2.5\text{--}4 \mu\text{m}$ ) (Coppins and Muhr 1997; Sérusiaux et al. 1999). They most probably represent an undescribed genus within the Malmideaceae.

We decided to name as ‘conidia’ the vegetative propagules produced at the stipes of *Savoronala* despite the fact that one algal cell is wrapped and completely surrounded by the fungus hyphae, and is thus dispersed altogether with the fungal ‘conidia’. A process of conidiogenesis is indeed visible and the cells of mature conidia strongly differ from those of the ‘carrying hyphae’ (=conidiophores), becoming slightly larger and dark brown. The conidiogenesis can be compared with that of the aeroaquatic hyphomycete *Spirosphaera* Beverw. (Marvanová and Bärlocher 1998); the conidia arise apically or laterally on undifferentiated conidiophores, and are rapidly septate and inflating, and further coiling up. In *Savoronala*, a single algal cell, out of those present within the conidiophores-producing tissue, is wrapped up by the coiling conidia; the conidia cells further become larger and brown.

Dispersal of conidia together with algal cell is a rare phenomenon in lichenized fungi, being so far restricted to highly specialized conidiomata structures. Indeed, only the hyphophores within the subfamily Gomphilloideae (Rivas Plata et al. 2012) and the campylidia within the Pilocarpaceae (Sérusiaux 1986; Lücking 2008; Vězda 1986) can disperse their conidia and algal cells all together. In the Gomphilloideae, several genera produce conidia or conidia-like “diahyphae” in specialized conidiomata, here named hyphophores, that are dispersed with algal cells, usually mixed up within the conidial mass, but not genuinely wrapped up by conidia. The following genera are concerned: *Actinoplaca* Müll. Arg., *Calenia* Müll. Arg., *Gyalectidium* Müll. Arg. and *Jamesiella* Lücking, Sérus. & Vězda (Lücking et al. 2005).

Within the Pilocarpaceae s.l., several genera produce campylidia in which algal cells occur within the conidiogenous layer. In those genera, algal cells are expelled



with conidia, sometimes in a sticky mass that can be seen at the opening of the campylidium (Sérusiaux 1986). The following genera are concerned: *Sporopodium* Mont., *Tapellaria* Müll. Arg. and *Tapellariopsis* Lücking (Sanders and Lücking 2002; Lücking 2008). In the genus *Sporopodiopsis* Sérus. (Sérusiaux 1997), the campylidia are organized in such a way that, although algal cells are not present within the campylidia cavity, conidia can “collect” algal cells on their way out and disperse with them.

Malme (1935) could observe conidia being wrapped up by filiform conidia in *Calopadia perpallida* (Nyl.) Vězda, but recent studies (Lücking 2008) could not confirm this observation; we suspect that Malme was observing the campylidia of a species of *Tapellaria* or *Sporopodium*. Sanders and Lücking (2002) featured filiform conidia encircling algal cells at a very early stage of the thallus growth in *Tapellariopsis octomera*; association between conidia and algal cells in this species could merely be the result of the conidia being strongly curved (Lücking 1999). With the data available, formation and dispersal of conidia wrapping up tightly algal cells (here always a single one) have never been documented for lichenized fungi.

We also addressed the question that the stipes of *Savoronala* might represent highly modified campylidia, but we did not find any obvious character to support this hypothesis. The diaspores of *Savoronala*, being a firmly attached assemblage of the photo- and mycobionts, are also reminiscent of ‘goniocyst’, a term that has been used for different types of diaspores containing algae (see Sérusiaux et al. 2006 for detailed discussion about the origin and use of the term ‘goniocyst’). However, it is usually applied for tiny thallus granules, always without any process of conidiogenesis. As examples, the thallus of most *Malmidea* species is composed of goniospores (Kalb et al. 2011) and *Nyungwea* Sérus., Eb. Fisch. & Killmann produces goniospores on erected stipes, but here the stipes are made entirely of loose hyphae and the photobiont belongs to *Trentepohlia* (Sérusiaux et al. 2006). The diaspores of *Gallaicolichen* Sérus. & Lücking (Sérusiaux and Lücking 2007) represent a very different morphological pattern, as here the photobiont (belonging to the genus *Phycopeltis*) is the wrapping up agency as it does envelop its mycobiont partner; those diaspores are named peltidia.

The lichenized hyphomycete *Dictyocatenulata alba* Finley & E.F. Morris (Aptroot and Schiefelbein 2003; Diederich et al. 2008; Lendemmer and Harris 2004) also produces subspherical, muriform conidia at the apices of stipes; however, the species differs strongly from

*Savoronala* by a very thin, crustose thallus with trentepohlioid algae, synnematal conidiomata and hyaline conidia not associated with any algal cell. *Cheiromycina* B. Sutton is a small lichen-forming hyphomycete genus of uncertain affiliation that produces sporodochia and has a chlorococcoid photobiont (Aptroot and Schiefelbein 2003; Hawksworth and Poelt 1990; Printzen 2007; Sutton and Muhr 1986); it differs from *Savoronala* by sessile sporodochia with hyaline, rarely pale brown at the base, palmately branched conidia not associated to any algae and subspherical to shortly ellipsoid conidiogenous cells (with *C. globosa* Aptroot & Schiefelbein being atypical for the genus by having unicellular, globose to slightly ellipsoid conidia, whereas conidiogenous cells were not recognized by the authors).

Several other lichenized taxa are known to produce sporodochia (Table 2). Among the Lecanorales, *Byssoloma gahavisukanum* Sérus. differs by its epiphyllous and very thin thallus forming sessile bluish sporodochia with vertical chains of up to 20, ellipsoid to slightly lacrimiform conidia (Aptroot et al. 1997); *Micarea adnata* Coppins differs by a pale gray-green, ± waxy thallus producing simple, cylindrical to oblong ellipsoid macroconidia in non-stipitate, whitish sporodochia (Coppins 1983); the monotypic genus *Xyleborus* R. C. Harris & Ladd [type species *X. sporodochifer* (Harris and Ladd 2007)], placed in the Stereocaulaceae, differs by a pale to olivaceous thallus producing globose, hyaline conidia in white, hemispherical to subglobose, sessile sporodochia. All these taxa are also known to produce apothecia. Several lichenized taxa producing sporodochia are also known among the Arthoniales, but all have trentepohlioid photobionts; e.g., *Milospium* (Aptroot and Sipman 2001), *Reichlingia* (Diederich and Coppins 2009), ‘*Sclerococcum*’ *griseisporodochium* Etayo (Etayo 1995; the generic affiliation of this Arthoniales needs further study since the generic type of *Sclerococcum*, *S. sphaerale*, was resolved in the Eurotiomycetes by Diederich et al. 2012), *Tylophoron* (Ertz et al. 2011; Tibell 1991). *Sporodochiolichen* Aptroot & Sipman includes four species (Aptroot and Sipman 2011), but the generic type (*S. lecanoricus* Aptroot & Sipman) is obviously conspecific with *Tylophoron hibernicum* (D. Hawksw., Coppins & P. James) Ertz, Diederich, Bungartz & Tibell, despite the photobiont was said to be myrmecoid. As a consequence, the genus *Sporodochiolichen* is here reduced into synonymy with *Tylophoron* (see “Results”). The three other species of *Sporodochiolichen* differ from *Savoronala* by golden yellow or pink, sessile sporodochia and generally simple or 1-distoseptate conidia; their phylogenetic position remains to be determined.

**Table 2** Comparison of *Savoronala* with other lichenized taxa producing sporodochia (or synnemata)

	Ascomata		Sporodochia		Sporodochial conidia			Accompanying algae
	Photobiont		Sporodochia	Color and surface	Shape	Septation		
<i>Byssoloma gahavisukanum</i> Sérus.	Apothecia	Chlorococcoid	Sessile, bluish	Hyaline, smooth?	Ellipsoid to slightly lacrimiform	In chains	Absent	
<i>Cheiromycina</i> B. Sutton	Unknown	Clorococcoid	Sessile, white, bluish grey, grey or olivaceous	Hyaline, rarely brown below, smooth	Globose or palmately branched	Simple or multicellular	Absent	
<i>Dictyocatenulata</i> Finley & E. F. Morris	Unknown	Trentepohlioid	Stipitate, white (synnemata)	Hyaline, smooth	Subspherical	Muriform	Absent	
<i>Micareea adnata</i> Coppins	Apothecia	Micareoid	Sessile, whitish	Hyaline, smooth	Ellipsoid to oblong	Simple	Absent	
<i>Milospium</i> D. Hawksw.	Unknown	Trentepohlioid	Sessile, dark brown to black	Brown, smooth	Generally strongly curved	Simple or multicellular	Absent	
<i>Psammia palmata</i> Earl.-Benn. & D. Hawksw.	Unknown	Coccoid or absent	Sessile, brownish	Hyaline, smooth	Palmately branched in a single plane	Usually simple	Absent	
<i>Reichlingia</i> Diederich & Scheid.	Unknown	Trentepohlioid	Sessile, reddish to chocolate brown	Brown, verrucose	Irregularly branched	Multicellular	Absent	
<i>Savoronala</i> Ertz et al.	Unknown	Chlorococcoid	Stipitate, greyish blue	Brown, smooth	Subspherical	Multicellular	Single algal cell wrapped up by conidia	
' <i>Sclerococcum</i> ' <i>griseisporodochium</i> Etayo	Unknown	Trentepohlioid	Sessile, greyish mauve to dark violet	Brown, verrucose	Forming chains of up to 5–8 globose cells	1(–2) distoseptum	Absent	
' <i>Sporodochiolenchen</i> ' Aptroot & Sipman ( <i>S. lecanoricus</i> excluded)	Unknown	Myrmecioid	Sessile, golden yellow or pink	Hyaline, smooth or papillate	Generally ellipsoidal or clavate with one end pointed	Simple or 1-distoseptate	Absent	
<i>Tylophoron</i> Stizenb.	Apothecia	Trentepohlioid	Sessile, rarely stipitate, pale or brown	Hyaline or brown, smooth to slightly roughened	Ellipsoid or oblong	0–1-septate	Absent	
<i>Xyleborus</i> R. C. Harris & Ladd	Apothecia	Chlorococcoid	Sessile, white	Hyaline, smooth	Globose, forming short, irregular chains/groups	Simple	Absent	

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