

Tubisorus, a new genus of smut fungi (*Ustilaginomycetes*) for *Sorosporium pachycarpum*

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Abstract. A new genus of smut fungi, *Tubisorus*, is proposed for *Sorosporium pachycarpum* on *Mnesithea rottboellioides*, *Poaceae*.

Key words: molecular analysis, new combination, new genus, smut fungi, taxonomy, *Tubisorus*, *T. pachycarpus*

Introduction

A peculiar smut fungus, *Sorosporium pachycarpum* was described by H. Sydow (in Sydow & Petrak 1928) on *Rottboellia ophiuroides* (= *Mnesithea rottboellioides*), from the Philippines. The sori are very long, tubiform, in the axis of spikes with aborted spikelets. They are filled with a black, granular powdery mass of spore balls. The spore balls are permanent, composed of globoid, thick-walled, ornamented spores. The fungus was placed into the genus *Tolyposporella* by Ling (1949), and into the genus *Endosporisorium* by Vánky (1995); the latter genus turned out to be a synonym of *Macalpinomyces*. Thirumalachar *et al.* (1967: 395) treated it also under *Tolyposporella*. Vánky (1998: 93–95) considered the genus *Sorosporium* F. Rudolphi to be a synonym of *Thecaphora* Fingerh., parasitising only dicotyledonous host plants.

Based on the peculiar sorus, spore ball and spore morphology, as well as on molecular phylogenetic analyses of ITS and LSU rDNA sequences, a new genus is proposed for *S. pachycarpum*.

Materials and methods

The following specimens were examined for the present work: Philippines, Luzon, Pampanga Prov., Stotsenberg, XI.1923, coll. M.S. Clemens 2313 (BPI 180089; syntype); Papua New Guinea, Morobe, 19.XI.1939, coll. M.S. Clemens

(BPI 71558, H.U.V. 10504 & 16772); PNG, Moresby, 20.III.1998, coll. R.G. Shivas, G.R. Kula, C. & K. Vánky, in Vánky, Ust. exs. No. 1036 (H.U.V. 18515 & 18606); PNG, Port Moresby, 21.III.1998, coll. R.G. Shivas, C. & K. Vánky (H.U.V. 18520); PNG, Finschhafen, 31.III.1998, coll. R.G. Shivas, G.R. Kula, C. & K. Vánky (H.U.V. 18521); Australia, Queensland, Townsville, James Cooke Univ. Campus, coll. C. Bretzel, IX.1996 (H.U.V. 18206); Queensland, Cape York Peninsula, 3 km N of Bamaga, coll. R.G. Shivas, C. & K. Vánky (H.U.V. 19237); Queensland, 65 km S of Cairns, Eubenangee Swamp, 17.VIII.2006, coll. R.G. Shivas, C. & K. Vánky (H.U.V. 21582); Australia, Northern Territory, between Pine Creek and Adelaide River, 12.4 km off Stuart Hwy, Dorat Road, coll. M. & R.G. Shivas, Y.C. Tran, T. & K. Vánky, 23.IV.2011 (H.U.V. 21891).

The nomenclatural novelty was registered in MycoBank (www.Mycobank.org, Crous *et al.* 2004).

Morphological examination

Sorus structure and spore characteristics were studied using dried herbarium specimens. For microscopic studies of the soral, spore ball and spore characters, young sori were rehydrated in hot water, fixed in 2% glutaraldehyde in 0.1 M Na-cacodylate buffer at pH 7.2 for several days. After six transfers in 0.1 M Na-cacodylate buffer, the material was postfixed in 1% osmiumtetroxide in the same buffer for 1 h

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in the dark, washed in distilled water, and stained in 1% aqueous uranyl acetate for 1 h in the dark. After five washes in distilled water, the material was dehydrated in acetone series, embedded in Spurr's plastic and sectioned with a diamond knife. Semi-thin sections were stained with new fuchsin and crystal violet, mounted in "Entellan" and studied in a light microscope. For light microscopy (LM) spore balls were dispersed in a small droplet of lactophenol, covered with a cover glass, gently heated to boiling point to rehydrate the spores and expel air bubbles from the preparation, and studied at 1000 $\times$ magnification. For scanning electron microscopy (SEM), spore balls were placed on double-sided adhesive tape, mounted on a specimen stub, sputter-coated with gold-palladium, *ca* 35 nm, and examined in a SEM at 10 kV.

DNA extraction, PCR, and sequencing

Genomic DNA was isolated directly from the herbarium specimen (H.U.V. 21891). For methods of isolation and crushing of fungal material, DNA extraction, amplification, purification of PCR products, sequencing, and processing of the raw data see Lutz *et al.* (2004). ITS 1 and ITS 2 regions of the rDNA including the 5.8S rDNA (ITS) were amplified using the primer pair ITS1-F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990). The 5'-end of the nuclear large subunit ribosomal DNA (LSU) was amplified using the primer pair NL1 and NL4 (O'Donnell 1993). Primers were used for both PCR and cycle sequencing. For amplification the annealing temperature was adjusted to 48 °C. DNA sequences determined in this study were deposited in GenBank (accession numbers: ITS: JN871718/LSU: JN871717).

Phylogenetic analyses

Blast searches (Altschul *et al.* 1997) for both the ITS and LSU sequence revealed closest similarity to members of the *Macalpinomyces/Sporisorium/Ustilago*-group. To further elucidate the phylogenetic position of *Sorosporium pachycarpum*, its ITS and LSU sequence was analysed against the combined ITS/LSU-dataset of Stoll *et al.* (2005). For this analysis, the dataset was reduced to one specimen per species; the ITS and LSU sequences of *Anomalomyces panici* (Vánky *et al.* 2006) were added. GenBank accession numbers of sequences used in the molecular analyses are included in Fig. 8.

Sequence alignment was obtained using MAFFT 6.853 (Katoh *et al.* 2002, 2005; Katoh & Toh 2008) using the L-INS-i option. As suggested by Giribet & Wheeler (1999) and Gatesy *et al.* (1993), respectively, to obtain reproducible results manipulation of the alignment by hand as well as manual exclusion of ambiguous sites were avoided. Instead, highly divergent portions of the alignment were omitted using GBlocks 0.91b (Castresana 2000) with the following options: 'Minimum Number of Sequences for a Conserved Position' to 50, 'Minimum Number of Sequences for a Flank



Fig. 1. *Tubisorus pachycarpus* on *Mnesithea rottboellioides* (Papua New Guinea, H.U.V. 16 772) – young sori in much elongate, tubular axis of the spikes, with aborted spikelets. Habit. Bar = 1 cm

Position' to 50, 'Maximum Number of Contiguous Non-conserved Positions' to 8, 'Minimum Length of a Block' to 5 and 'Allowed Gap Positions' to 'With half'.

The resulting alignment [new number of positions: 1160 (65% of the original 1779 positions) number of variable sites: 372] was used for phylogenetic analyses using a Bayesian Approach (BA) and Maximum Likelihood (ML). For BA a Markov chain Monte Carlo technique was used as implemented in the computer program MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck

2003). Four incrementally heated simultaneous Markov chains were run over 5 000 000 generations using the general time reversible model of DNA substitution with gamma distributed substitution rates and estimation of invariant sites, random starting trees and default starting parameters of the DNA substitution model as recommended by Huelsenbeck & Rannala (2004). Trees were sampled every 100th generation, resulting in an overall sampling of 50 001 trees. From these, the first 5 001 trees were discarded (burnin = 5 001). The trees sampled after the process had reached stationarity (45 000 trees) were used to compute a 75 % majority rule consensus tree to obtain estimates for the *a posteriori* probabilities of groups of species. This Bayesian approach to phylogenetic analysis was repeated five times to test the independence of the results from topological priors (Huelsenbeck *et al.* 2002).

ML analysis (Felsenstein 1981) was conducted with the RAXML 7.2.8 software (Stamatakis 2006), using raxmlGUI (Silvestro & Michalak 2010), invoking the GTRCAT and the rapid bootstrap option (Stamatakis *et al.* 2008) with 1000 replicates.

In line with Stoll *et al.* (2005), trees were rooted with sequences of *Eriomoeszia eriocauli* and *Moesziomyces bullatus*.

Results

Phylogenetic analyses

The different runs of BA that were performed and the ML analyses yielded consistent topologies in respect to well supported branchings. To illustrate the results, the consensus tree of one run of the Bayesian phylogenetic analyses is presented (Fig. 8). Estimates for *a posteriori* probabilities are indicated on branches before slashes, numbers on branches after slashes are ML bootstrap support values.

In all analyses *Sorosporium pachycarpum* clustered within the *Macalpinomyces/Sporisorium/Ustilago*-group as sister taxon of *Ustilago bouriquetii* and *U. maydis* within a group consisting of *Macalpinomyces loudetiae*, *M. simplex*, *M. trichopterygis*, *M. tristachya*, *Sporisorium trachypogonis-plumosi*, and *U. vetiveriae*.

Taxonomy

Tubisorus Vánky & M. Lutz, **gen. nov.**

MYCOBANK # 563575

Sori formationes tubulares plantarum nutrientium familiae Poacearum. Massa atra granuloso-pulverea glomerulorum sporarum conferti, columella et cellulae steriles nullae. *Glomeruli sporarum* e sporis tantum compositi. *Sporae* pigmentatae (brunneae, sine violaceo nec rubro tincto). *Sporae verae* hyalinae, in matrice carassa, gelatinosa, hyalina immittae, strato externo tenui, pigmentato, ornamentis velatis.

Typus generis: T. pachycarpus.

Sori tubular on host plants in the *Poaceae*, filled with dark, granular powdery mass of spore balls, columella and sterile cells lacking. **Spore balls** composed of spores only. **Spores** pigmented (brown, without violet or red tint). The proper spore is hyaline and embedded in a thick, gelatinous, hyaline substance, coated by a thin, pigmented, ornamented outer layer of spore wall.

Type of the genus: *T. pachycarpus*.

Tubisorus pachycarpus (Syd.) Vánky & M. Lutz, **comb. nov.**
MYCOBANK # 563576

Basionym: *Sorosporium pachycarpum* Syd., in Sydow & Petrak, Ann. Mycol. 26: 431, 1928; *Tolyposporella pachycarpa* (Syd.) L. Ling, Sydowia 3: 133, 1949; *Endosporisorium pachycarpum* (Syd.) Vánky, Mycotaxon 56: 213, 1995. – Syntype on *Rottboellia ophiuroides* (= *Mnesithea rottboelliioides*), Philippines, Luzon, Pampanga Prov., Stotsenberg, XI.1923, coll. M.S. Clemens 2313 (BPI 180089!) (another syntype is probably lost).

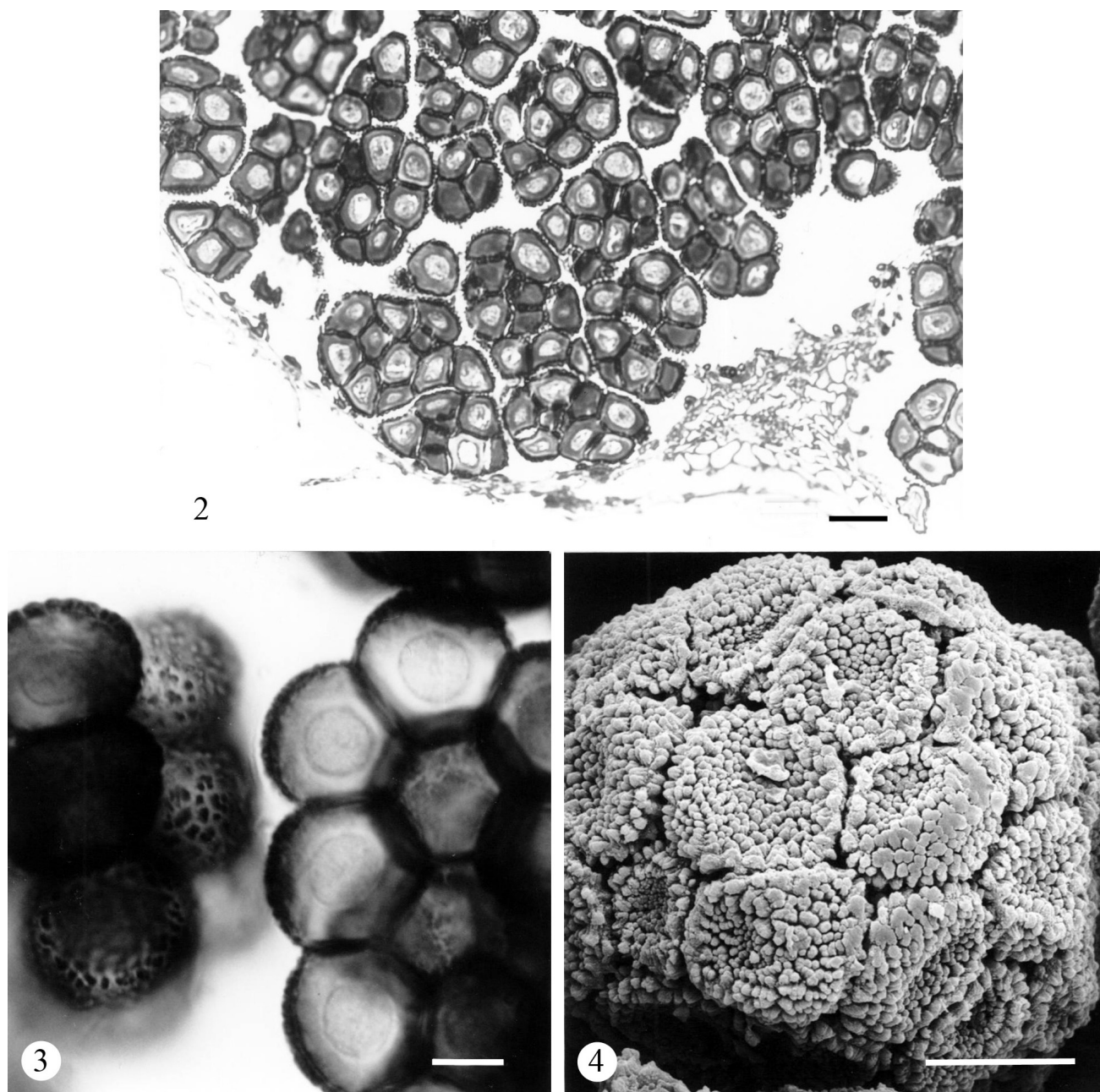
Sori (Figs 1, 7) in much elongated axis of the spikes with aborted spikelets, tubular, 0.5–1.5 mm wide, up to 20–25 cm long, yellowish to greyish brown, at maturity rupture longitudinally, on several places between the veins, exposing the black, granular-powdery mass of spore balls. **Spore balls** (Figs 2–5) globoid, long ellipsoidal to irregular, composed of 5–50 or more spores, apparently loose but rather permanently connected, 25–50 (–65) × 45–100 (–150) µm, dark olivaceous brown. **Spores** (Figs 3–5) subglobose, ovoid or irregular with one or several flattened contact sides, 12–20 × 16–24 µm, olivaceous brown; wall 3-layered (Figs 3, 5): outer layer 1.5–2 µm thick, pigmented, densely provided with irregular, prismatic warts, c. 1 µm high on the free surface, smaller and finer on the contact sides; middle layer hyaline, gelatinous, homogenous, 2.5–7 µm thick; inner layer 0.5–1.5 µm thick, smooth, surrounding the finely granular, hyaline proper spores which in squashed spores are liberated (Fig. 6). These are subglobose, broadly ellipsoidal, ovoid, subpolyhedrally irregular or elongated, (7–) 8–10.5 × 9–14.5 µm; wall 0.5–1 µm thick, composed of a very thin inner layer and a hyaline sheath, smooth. **Spore germination** unknown.

On *Poaceae*: *Mnesithea rottboelliioides* (R. Br.) de Koning & Sosef (*Coelorachis rottboelliioides* (R. Br.) A. Camus; *Manisuris rottboelliioides* (R. Br.) Kuntze; *Rottboellia ophiuroides* Benth.).

Geographic distribution: Australia, Papua New Guinea, Philippines (comp. Sydow & Petrak 1928: 431; Shivas *et al.* 2001: 335; Vánky & Shivas 2008: 105).

Discussion

H. Sydow (in Sydow & Petrak 1928: 431) described *Sorosporium pachycarpum* to be in the leaves of the host plant. Ling (1949: 133) also considered that the sori are in the leaves, which was the reason that he transferred the fungus into the genus *Tolyposporella*. Zundel (1953: 68) described the sori on the abaxial side of the leaves, and treated the fungus under

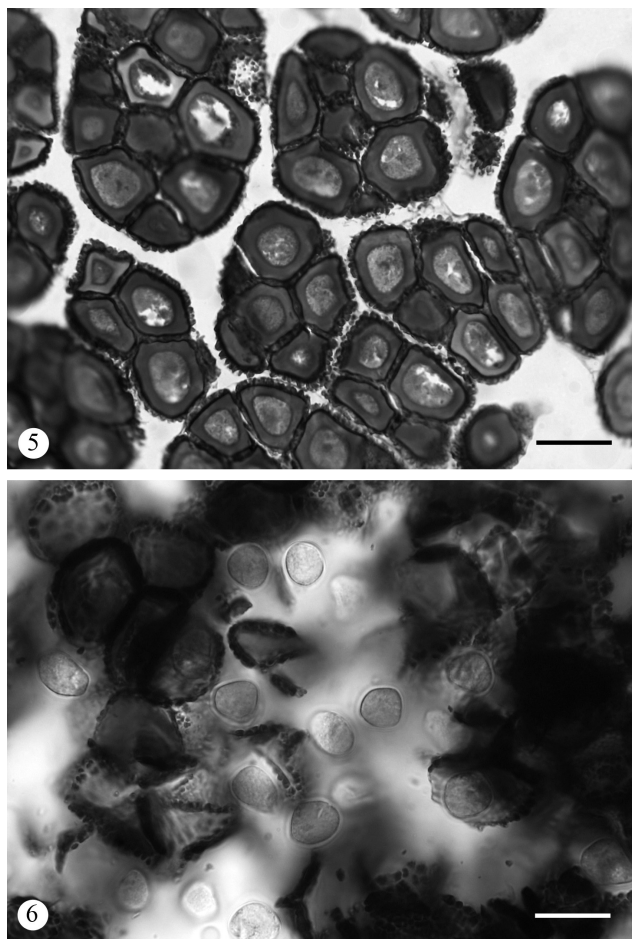


Figs 2–4. *Tubisorus pachycarpus* on *Mnesithea rottboellioides* (Papua New Guinea, H.U.V. 16772). 2. Semi-thin, stained, transversal section of a part of a sorus with sectioned spore balls. Bar = 25 μm . 3–4. Spores balls and spores in LM and in SEM. Bars = 10 μm

the genus *Sorosporium*. Despite the fact that Thirumalachar *et al.* (1967: 395) wrote that “Many *Sorosporium* species are foliicolous . . .” and that “The smut was correctly placed in the genus *Sorosporium* by Sydow”, they treated it as *Tolyposporella pachycarpa* (Syd.) Ling. Vánky & Shivas (2008: 166) wrote that the sori of *Tolyposporella pachycarpa* are “in the axis of aborted inflorescence”, which is inaccurate. The exact place of the sori is first described by Vánky (2012: 995).

The type of the genus *Tolyposporella* G.F. Atk. is *T. chrysopogonius* G.F. Atkinson (1897) on *Sorghastrum nutans* (L.) Nash, USA. Its sori form linear, more or less confluent,

initially subepidermal, later bursting striae on the inner surface of leaf sheaths. The spore balls are composed of firmly agglutinated, smooth spores with unevenly thickened wall. It is quite different from the smut on *Mnesithea*. *Tolyposporella* is a genus of five species, four on *Poaceae*, and one on *Eriocaulaceae*, which probably does not belong to this genus (comp. Vánky 2012). All *Tolyposporella* species have spores with smooth, unevenly thick, multilamellar wall and sori on the surface of the leaves or leaf sheaths. In contrast, the spore wall of *Tubisorus pachycarpus* is ornamented and three-layered (for description see above). Similar spore wall structure, in which



Figs 5–6. *Tubisorus pachycarpus* on *Mnesithea rottboellioides* (Papua New Guinea, H.U.V. 16772). 5. Sectioned and stained spore balls and spores showing the thin, pigmented, ornamented outer spore wall, the thick, homogenous mass in which the thin-walled proper spores with granular content are embedded. Bar = 10 µm. 6. Ruptured outer, pigmented spore walls permitting the thin-walled, hyaline proper spores to emerge. Bar = 10 µm

the proper spore is embedded in a gelatinous layer and coated by a thin, pigmented outer layer occurs in the smut fungi only in the genus *Kuntzeomyces* Henn. ex Sacc., with two closely related species in the spikelets of *Rhynchospora* (Cyperaceae; comp. Piepenbring 2001). In them, however, the spores are smooth and single. These characters of the spores, in addition to the soral characters, exclude *Tubisorus pachycarpus* from *Tolyposporella*. *Tubisorus* neither belongs to the genus *Sporisorium* Ehrenb. ex Link, nor to *Macalpinomyces* Langdon & Full., in which sterile cells, or groups of sterile cells, and in the sori often also columella/ae are present (comp. Vánky 2002).

Piepenbring *et al.* (1998: 210, Fig. 28) reported presence of germ pores in the spores of “*Sorosporium*” *pachycarpum*, which could not be confirmed.

Molecular phylogenetic analyses based on BA and ML analyses of ITS + LSU rDNA sequence data suggest a



Fig. 7. Mature sori of *Tubisorus pachycarpus* on *Mnesithea rottboellioides* (Photo: Christine Vánky)

common ancestor of *Tubisorus pachycarpus* and the *Ustilago maydis*/*U. bouriquetii* clade. *U. maydis* (DC.) Corda produces galls on the stems, leaves or inflorescence of *Zea* (including *Euchlaena*) species (subtribe *Tripsacinae*, tribe *Andropogoneae*, subfam. *Panicoideae*), filled with single spores. *U. bouriquetii* Maubl. & Roger produces considerably hypertrophied filaments of *Stenotaphrum* species (subtribe *Setariinae*, tribe *Paniceae*, subfam. *Panicoideae*), filled by single spores.

Mnesithea Kunth belongs to the subtribe *Rottboelliinae* of the tribe *Andropogoneae*, subfam. *Panicoideae* (Clayton & Renvoize 1986: 368). Three other known smut fungi on members of this genus are: *Sporisorium operculatum* Vánky & R.G. Shivas (2001: 154; Australia), *S. perforatum* Vánky (2004: 104; India), and *S. mnesithea* (Mishra) Vánky (2004: 107; India). None of these, including *Ustilago maydis* and *U. bouriquetii* is similar to *Tubisorus pachycarpus*.

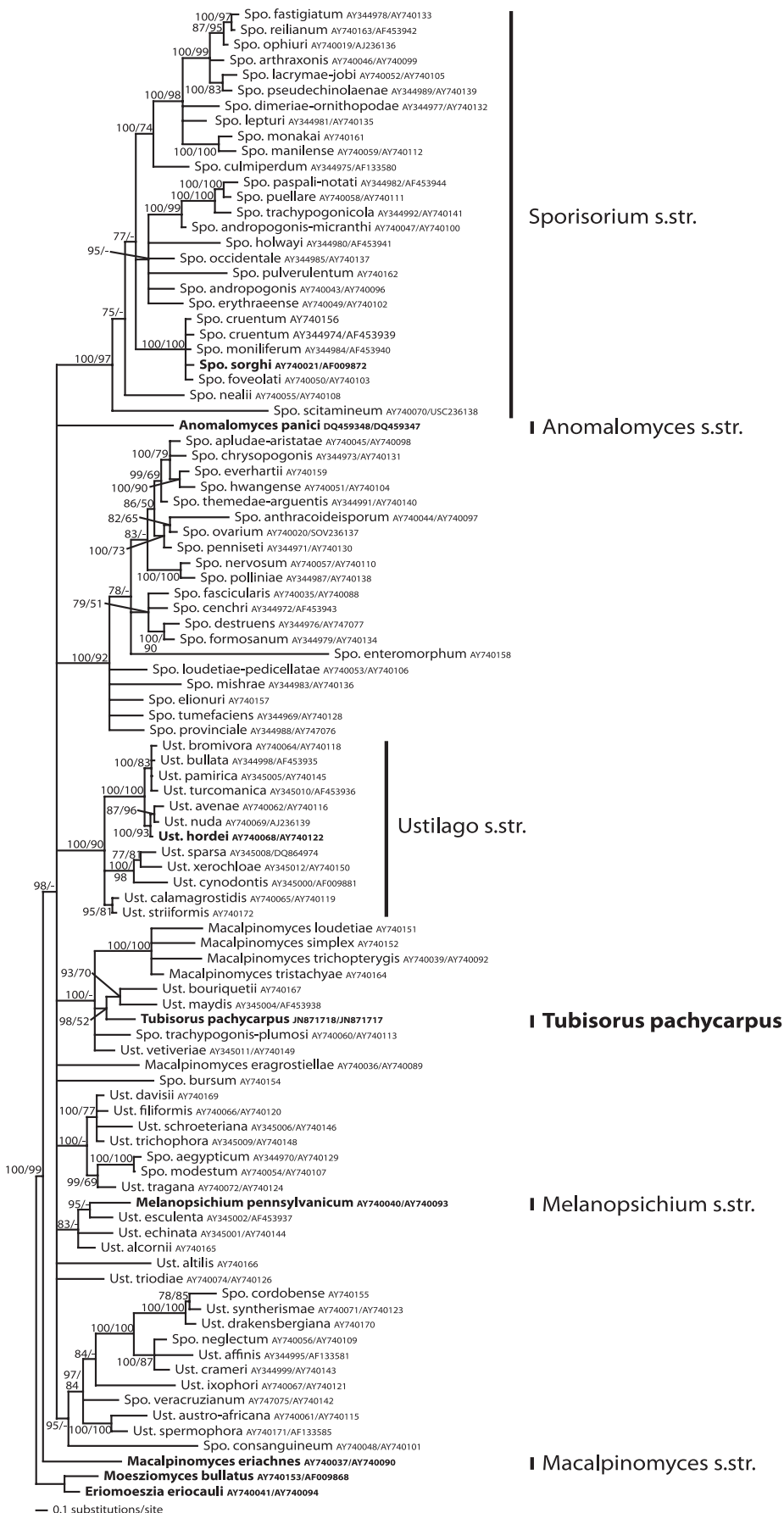


Fig. 8. Bayesian inference of phylogenetic position of *Sorosporium pachycarpum*: Markov chain Monte Carlo analysis of an alignment of concatenated ITS + LSU base sequences using the GTR+I+G model of DNA substitution with gamma distributed substitution rates and estimation of invariant sites, random starting trees and default starting parameters of the DNA substitution model. A 75 % majority-rule consensus tree is shown computed from 45 000 trees that were sampled after the process had reached stationarity. The topology was rooted with sequences of *Eriomoeszia eriocauli* and *Moesziomyces bullatus*. Numbers on branches before slashes are estimates for a *posteriori* probabilities, numbers on branches after slashes are ML bootstrap support values. Branch lengths were averaged over the sampled trees. They are scaled in terms of expected numbers of nucleotide substitutions per site. *Spo.* = *Sporisorium*, *Ust.* = *Ustilago*

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