Mycosphere 7 (5): 570–581 (2016) www.mycosphere.org ISSN 2077 7019

Article

Doi 10.5943/mycosphere/7/5/4

Mycosphere Essays 12. Progress in the classification of the water-cooling tower ascomycete *Savoryella* and a tribute to John Savory: a review

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Jones EBG, To-anun C, Suetrong S, Boonyuen N 2016 – Mycosphere Essays 12. Progress in the classification of the water–cooling tower ascomycete *Savoryella* and a tribute to John Savory: a review. Mycosphere 7(5), 570–581, Doi 10.5943/mycosphere/7/5/4

Abstract

The genus *Savoryella* belongs in the family *Savoryellaceae* (Savoryellales, Hypocreomycetidae, Sordariomycetes) and its species have a worldwide distribution. A natural classification was not possible when the genus was introduced, since it predated molecular phylogenetic studies; therefore morphology-based descriptions only were provided. In this review we discuss the history and significance of the genus, illustrate its morphology and discuss its role in the colonization and biodeterioration of lignocellulosic materials. Molecular analyses of SSU, LSU and RPB2 sequence data placed the genus in the Hypocreomycetidae with high support and resulted in the introduction of the order Savoryellales. The role of *Savoryella* in the soft rot decay of wood is also discussed.

Key words – Phylogeny – *Savoryellaceae* – taxonomy – water cooling towers – wood decay

Introduction

The senior author first came across *Savoryella* (an unidentified member of the Ascomycota) as an undergraduate student in 1957 on a vacation placement at the Princes Risborough Research Laboratory, near Aylesbury, Bucks., UK. The senior author was assigned to John Savory to learn aspects of soft rot of timber in water cooling towers and came across a number of unidentified fungi. My undergraduate project was on soft rot decay of marine fungi, a little known group at that time.

During 1960-1962, I was commissioned to examine timber from water cooling towers with circulating brackish water and documented fungi on both treated and untreated wood (Jones 1962, unpublished data). Timbers in these towers showed extensive decay, premature failure of the wood preservative treatment and it was necessary to identify the causative organisms. Many of these were marine fungi, but others could not be identified; however, time did not allow a more detailed study as I was studying for my Ph.D. on the physiology of marine fungi.

Submitted 9 August 2016, Accepted 5 September 2016, Published online 25 September 2016

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Fig. 1 – Typical water cooling tower.

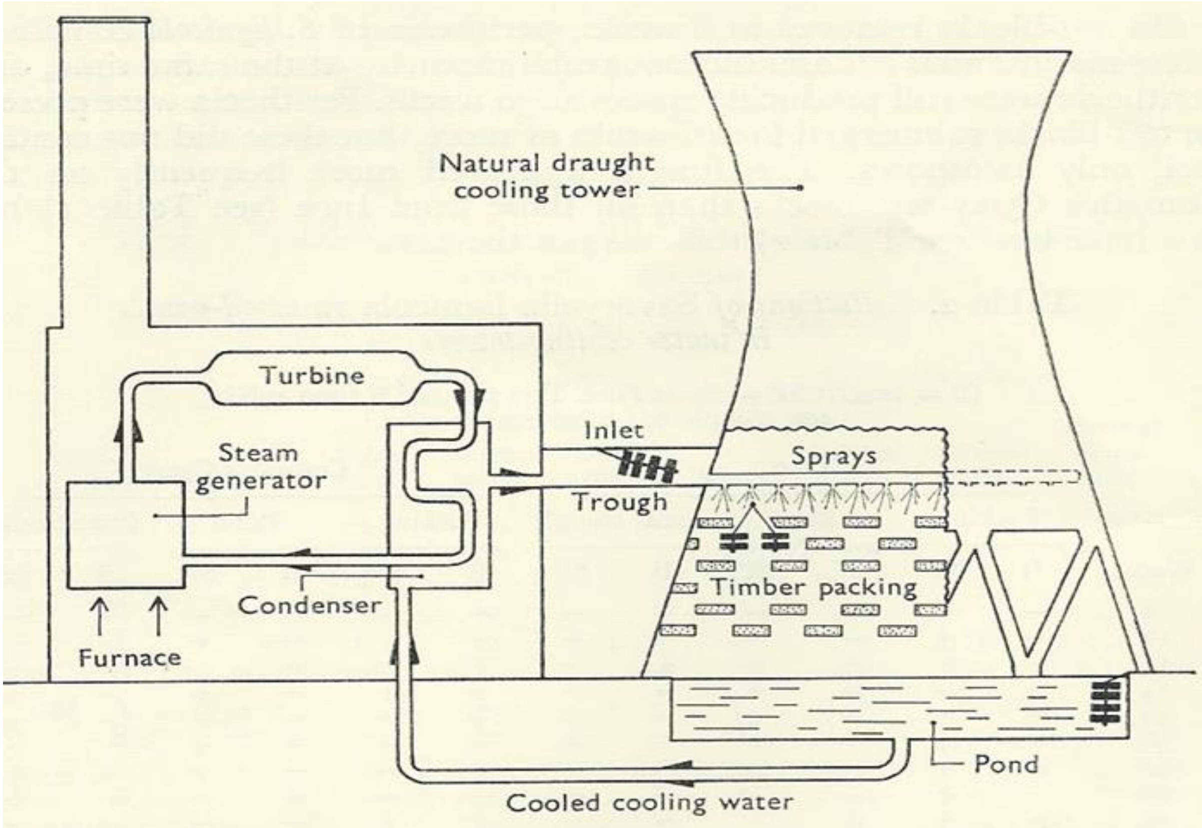

Fig. 2 – Diagram of water cooling tower indicating sampling positions in the inlet trough, timber packing and pond.

Clearly, timber in water cooling towers supported a rich and unique micro fungal community, which had not been investigated in any detail (Baechler & Richards 1961, Baker 1950, 1951, 1954, Findlay & Savory 1950). Thus, on completion of my Ph.D., I started as a lecturer at the Portsmouth Regional Technical College and in due course took on my first postgraduate students. Rod Eaton was one of my first postgraduate students and was set the task of documenting the ecology and taxonomy of the fungi colonizing timber in water cooling towers.

A comprehensive study was undertaken to document the fungi on treated and untreated timber from a wide range of cooling towers spread across the UK, the exposure of treated and untreated wood test blocks at selected towers, determine the wood decay ability of isolated fungi and a chemical analysis of water used in the various cooling towers. Mechanical draught water cooling towers have a distinctive appearance (Fig. 1) and were attached to electric-generating power stations to cool down water circulating through the condensers.

The warm water was piped to the cooling tower and sprinkled over a stack of wooden slats and the water collected in ponds below the packing and recirculated to the condensers (Fig. 2). Air was drawn through the towers; thus cooling the water running through the wooden slats. Some 16 cooling towers, mainly in the north of England, were sampled for the micro fungi growing on their timbers (Eaton & Jones 1971a, b, Eaton 1972).

A recurring species in the study was an ascomycete and after much debate, it was decided to introduce a new genus, namely *Savoryella* with *S. lignicola* as the type species (Jones & Eaton 1969) (Fig. 3).

Title – *Savoryella lignicola* gen. et sp. nov., from water cooling towers. (1969) Transactions of the British Mycological Society 52: (1), 161–174.

Savoryella gen.nov.

Perithecia solitaria vel gregaria, substrato immersa vel partim immersa, pallido vel atro brunnea, collo brevi, periphysato. Asci unitunicati, cylindracei et aparaphysati. Ascospori octo, triseptati, loculis extremis hyalinis et loculis mediis brunneis. Species typica: *S. lignicola* Jones & Eaton.

Savoryella lignicola sp.nov. (Pl. 9).

Perithecia 200–345 × 120–180 μm, collo 80–165 × 72 μm, solitaria vel gregaria, substrato immersa vel partim immersa, pallido vel atro brunnea, membranacea et aparaphysata. Asci 128–180 × 16–24 μm unitunicata, longo-cylindracei. Ascospori octo, 24·5–33·5 (43·0) × 8·5–12·5 μm, ellipsoidei, triseptati, loculis extremis hyalinis (2·6–6·0 μm) et loculis mediis brunneis (10·6–16·0 μm).

Perithecia 200–345 × 120–180 μm, neck 80–165 × 72 μm, solitary to aggregated, immersed or partly immersed in the substratum, globose, pale to dark brown in colour, membranous with well defined wall and aparaphysate. Asci 128–180 × 16–24 μm, long-cylindrical with a short foot, 8-spored and unitunicate. Ascospores 24·5–33·5 (43·0) × 8·5–12·5 μm, ellipsoidal, triseptate, central cells brown (10·6–16·0 μm) and the end cells hyaline (2·6–6·0 μm).

On Scots pine test-blocks placed for 168 days (16 June, 1966–1 December, 1966) amongst the packing timber of a water-cooling tower at Connah's Quay, Flintshire, North Wales. Type: **IMI** 129784.

Phylogenetic placement of *Savoryella lignicola*

At that time, the genus could not be assigned to any higher order taxon, and subsequently various authors attempted its classification, based on morphological features: Sphaeriales *incertae sedis* (Kohlmeyer & Kohlmeyer 1979), Xylariales (Eriksson & Hawksworth 1986), Halosphaeriales (Read et al. 1993), Sordariales (Jones & Hyde 1992) and Hypocreales (Vijaykrishna et al. 2006). The current classification of the genus *Savoryella* is shown as follows:

Phylum: ASCOMYCOTA
Class: SORDARIOMYCETES
Subclass: HYPOCREOMYCETIDAE
Order: SAVORYELLALES
Family: *SAVORYELLACEAE*
Genus: *SAVORYELLA*
Type species: *Savoryella lignicola* EBG Jones & RA Eaton

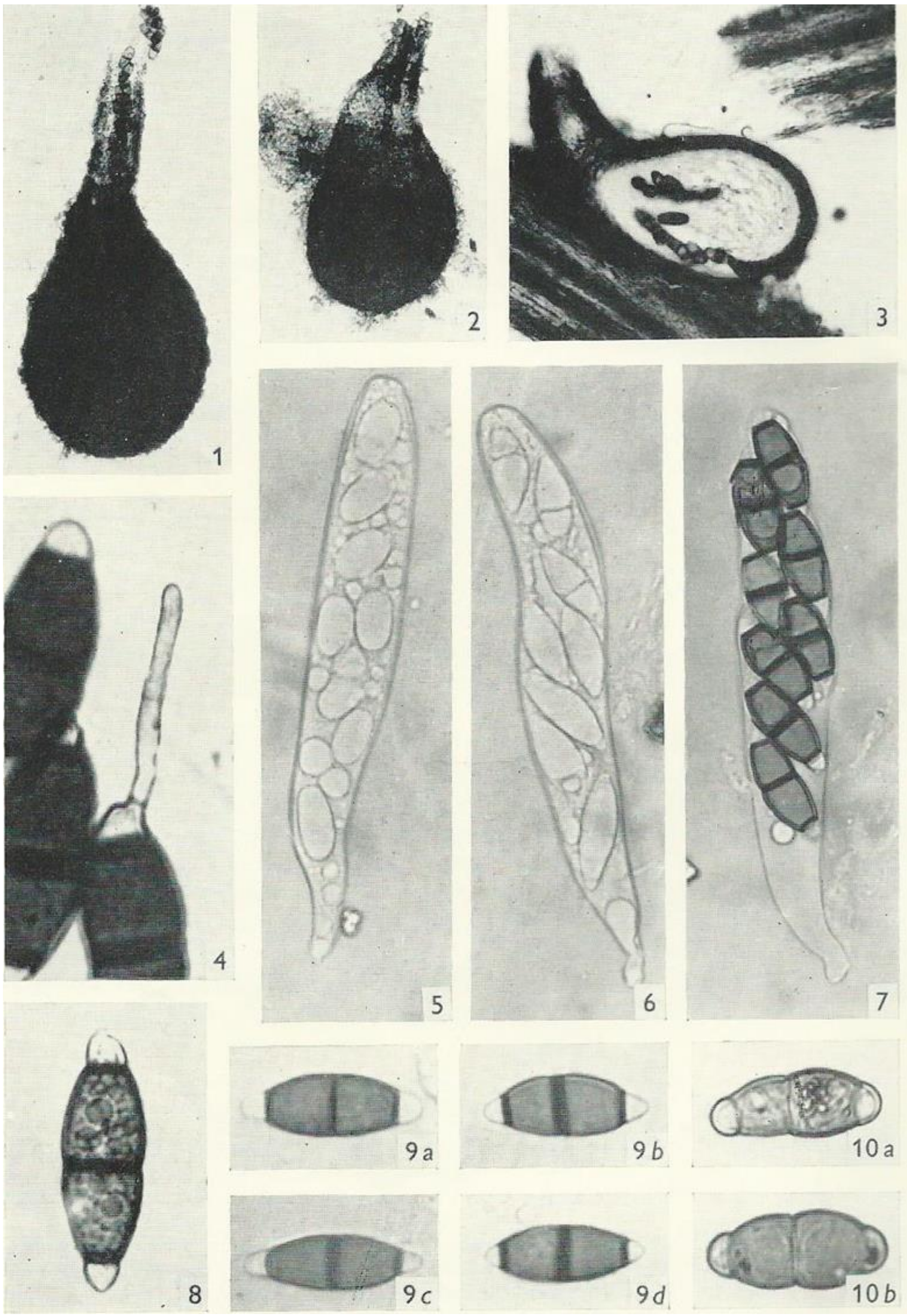

Fig. 3 – Original illustration of *Savoryella lignicola*, reproduced with permission of the British Mycological Society.

Currently, ten species are known and worldwide in their distribution:

1978: *Savoryella verrucosa* Minoura & T. Muroi
1982: *Savoryella paucispora* (Cribb & JW Cribb) J Koch
1992: *Savoryella appendiculata* KD Hyde & EBG Jones
1992: *Savoryella longispora* EBG Jones & KD Hyde
1993: *Savoryella aquatica* KD Hyde
1994: *Savoryella grandispora* KD Hyde
1997: *Savoryella curvispora* WH Ho, KD Hyde & Hodgkiss
1997: *Savoryella fusiformis* WH Ho, KD Hyde & Hodgkiss
1998: *Savoryella limnetica* HS Chang & SY Hsieh (now referred to *Ascotaiwania*)
2000: *Savoryella melanospora* Abdel-Wahab & EBG Jones

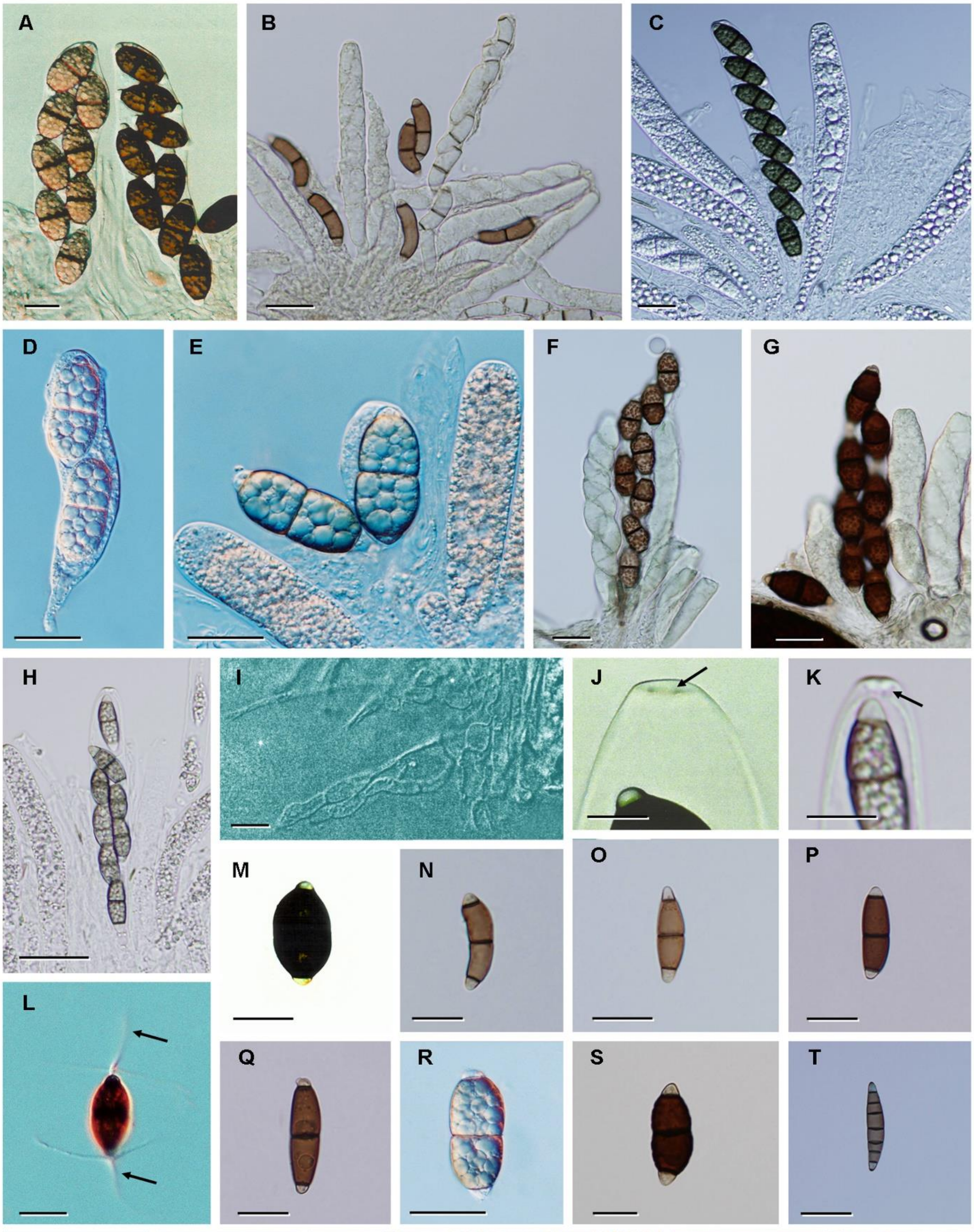

Fig. 4 – *Savoryella* and its related species from (Boonyuen et al. 2011 in Mycologia and Jones & Hyde 1992 in Botanica Marina). A. *Savoryella aquatica*. B. *S. curvispora*. C. *S. lignicola*. D–E. *S. paucispora*. D. Young two spored ascus. E. Mature and immature asci and paraphyses. F–G. *S. verrucosa*. H. *Ascothailandia grenadoidea*. I. *S. longispora*. J. *S. aquatica* (apical ring, arrow). K. *A. grenadoidia* (apical ring, arrow). L. *S. appendiculata* (ascospore with appendages, arrow). M. *S. aquatica*. N. *S. curvispora*. O. *S. fusiformis*. P. *S. lignicola*. Q. *S.* l*ongispora*. R. *S. paucispora*. S. *S. verrucosa*. T. *Ascotaiwania lignicola*. Scale bars A–E, L–T = 20 µm, F–H = 25 µm, I–K = 10 µm. Reproduced from Mycologia with permission of the Mycological Society of America.

Other cooling tower fungi

Some 58 and 29 microfungi were found growing on beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) test blocks, respectively, at the 16 water cooling towers sampled over a three-year period, but only a few could be fully identified (Eaton 1972). This was a new environment to be sampled for fungi and a number of new taxa were described: *Delitschia bispora* RA Eaton & EBG Jones, *Phaeonectriella lignicola* RA Eaton & EBG Jones, *Taeniolella longissima* RA Eaton & EBG Jones, *Phaeonectriella lignicola* RA Eaton & EBG Jones, and *Tricladium varium* EBG Jones & RJ Stewart (Eaton & Jones 1970, Jones et al. 2002, Jones & Stewart 1972).

Many others remain to be recollected and described, as this is a unique habitat for fungi. The most common fungus reported was *Monodictys putredinis* (Wallr.) S Hughes, present at all sites and at each sampling period over the three years. *Chaetomium globosum* Kunze ex Fr., *Graphium* spp. and *Doratomyces microsporus* (Sacc.) FJ Morton & G Sm., were also common, but at fewer test sites. The only other studies that documented fungi in water cooling towers are those of Natarajan and Udaiyan (1978), and Udaiyan and Manian (1991a, b) who replicated the studies carried out in the UK. This study was probably instigated by CV Subramanian who visited Portsmouth to learn more about marine fungi. They listed 103 species (4 Zygomycota, 26 Ascomycota, 3 Basidiomycota and 73 asexual morphs) on beech and Scots pine test blocks exposed at a water cooling tower in Madras, India. Only eight species were common to both studies, including the new species *S. lignicola* and *Ph. lignicola*.

In both the UK and Indian studies, beech test blocks supported a greater diversity of species when compared to Scots pine and this has been reported in other studies (Byrne & Jones 1974). In total, some 150 fungi have now been recorded from this unique habitat; however, few of these large water cooling towers remain in the UK as the old electric-generating power stations are decommissioned and pulled down.

The genus *Savoryella*

Currently, ten *Savoryella* species have been described as listed above. Boonyuen et al. (2011), in a combined phylogenetic analysis (LSU, SSU, 5.8S rRNA genes, rpb1, rpb2, and tef1 genes) of *Savoryella* species, showed that they formed a monophyletic group in the Sordariomycetes, but showed no affinities with accepted orders. All are reported from submerged wood in aquatic habitats: six from freshwater, four from marine or brackish water (including water cooling towers), while *S. melanospora* is known on driftwood from coastal sand dunes in Australia (Abdel-Wahab & Jones 2000, Jones et al. 2015).

Savoryella melanospora has recently been collected on intertidal mangrove wood, in Colva, India by Borse et al. (2016). Although *Savoryella* species are worldwide in their distribution, most records are from the tropics/subtropics. All possess ellipsoidal, 3-septate ascospores, central cells brown, end cells hyaline, with or without polar appendages (Fig. 4). *Savoryella appendiculata* is the only species with bipolar tetraradiate appendages that are formed on release from the ascomata. Read et al. (1993) demonstrated at the ultrastructural level, that the appendages are formed as an outgrowth of the hyaline apical cell of the ascospore. This species is generally found growing on wood associated with sand, and may aid in the dispersal of ascospores.

The order Savoryellales

Boonyuen et al. (2011) showed that *Savoryella* species formed a unique clade in Hypocreomycetidae, Sordariomycetes, along with the genera *Ascotaiwania*, *Ascothailandia* and *Canalisporium*. With the one fungus-one name ruling (Hawksworth 2011, Taylor 2011), the genus Canalisporium had priority and thus *Ascothailandia* was synonymized under that name (Nawawi & Kuthubutheen 1989, Sri-indrasutdhi et al. 2010, Réblová et al. 2016a, b). The Savoryellales clade forms a sister clade to the orders Coronophorales and Melanosporales, with strong statistical support.

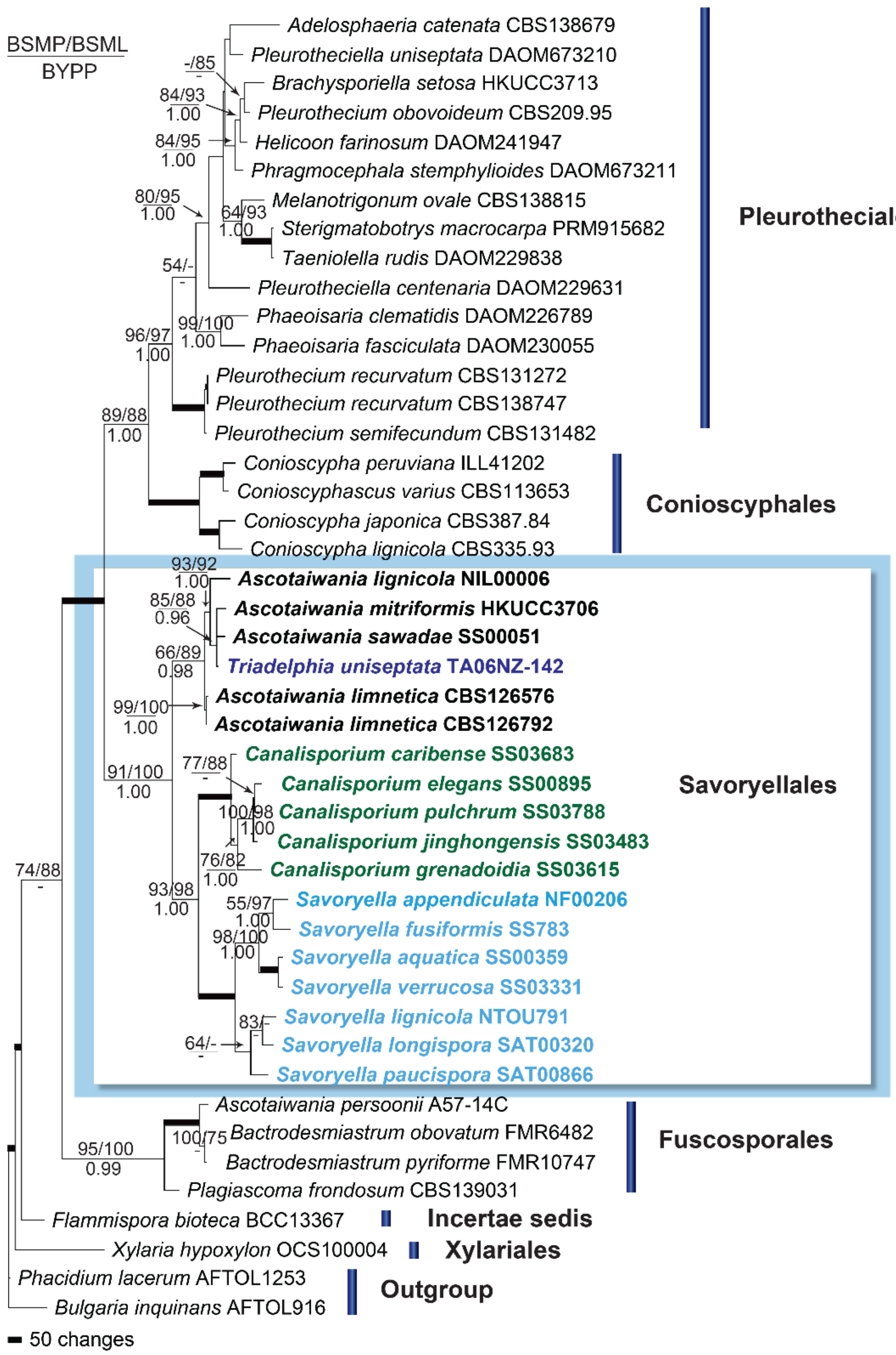

Fig. 5 – A single maximum parsimony tree inferred from combined SSU, LSU rDNA and rpb2 sequence data generated with maximum parsimony analysis. Maximum parsimony (BSMP, left) and likelihood (BSML, right) bootstrap values greater than 50% are given above the node. Bayesian posterior probabilities greater than 0.95 are given below each node (BYPP). The internodes that are highly supported by all bootstrap proportions (100%) and posterior probabilities (1.00) are shown as a thicker line.

Ascotaiwania was shown to be polyphyletic with two species grouping with the type species *A. lignicola* Sivan. & H.S. Chang, while *Ascotaiwania hughesii* Fallah, J.L. Crane & Shearer did not group within the Savoryellales, but formed a separate clade in the Hypocreomycetidae (Boonyuen et al. 2011). Likewise, *Ascotaiwania persoonii* Fallah, J.L. Crane & Shearer, has also been shown to group distant to the Savoryellales (Réblová & Seifert 2004). Réblová et al. (2012)

noted that *Helicoön farinosum* Linder (asexual morph of *Ascotaiwania hughesii*) grouped in the *Helicoön sensu lato* clade. Maharachchikubura et al. (2015), with wider sampling of other genera, included *Carpoligna pleurothecii* F.A. Fernández & Huhndorf, *Conioscyphascus varius* Réblová & Seifert, *Conioscypha japonica* Udagawa & Toyaz. and *Pleurothecium semifecundum* Réblová, Seifert & J. Fourn. in the Savoryellales clade. However, in the text *Carpoligna*, *Conioscypha*, *Flammispora* and *Sterigmatobotrys* were referred to as Savoryellales *incertae sedis* (Maharachchikubura et al. 2015), while Zelski et al. (2015) placed *Conioscypha* and *Conioscyphascus* species as a sister clade to the Savoryellales (Hypocreomycetidae *incertae sedis*). A more recent classification of the Hypocreomycetidae is published by Maharachchikubura et al. (2016).

Réblová et al. (2016a) have shown that *Triadelphia uniseptata* (Berk. & Broome) P.M. Kirk nested within the monophyletic *Ascotaiwania* clade as a sister to *A. mitriformis* Ranghoo & K.D. Hyde while *Ascotaiwania persoonii* nested in the *Bactrodesmiastrum* clade with high support, while *Helicoön farinosum* nested in the Pleurotheciales. More recently, Yang et al. (unpublished data) propose a new order Fuscosporales that accommodates the *Bactrodesmiastrum* clade, including *Ascotaiwania persoonii* and a number of new dematiaceous hyphomycetes.

Currently, *Conioscypha* and *Pleurothecium* have been referred to the new orders Conioscyphales and Pleurotheciales, respectively as shown in Fig. 5 (Réblová et al. 2016a, b). Many *Ascotaiwania* and *Triadelphia* species have not been sequenced and further alignments can be expected with the discovery of new genera and sequencing of other taxa.

The family *Savoryellaceae*

Jaklitsch and Réblová (2015) introduced this family to accommodate *Savoryella* species, unaware that Boonyuen et al. (2011) had introduced the order Savoryellales. Taxa currently assigned to the family based on Index Fungorum (2016), MycoBank (Crous et al. 2004), Faces of Fungi database (Jayasiri et al. 2015) and NCBI (http://www.ncbi.nlm.nih.gov/nuccore) are listed in Table 1.

Soft rot decay of wood

Many *Savoryella* species have been shown to cause soft rot decay of wood (Eaton & Jones 1971a, b, Leightly & Eaton 1977, Mouzouras 1986, Leightly 1980). This type of decay is prevalent where wood is exposed to wet conditions, such as submerged wood in marine and freshwater habitats (Jones 1972, Bucher et al. 2004a), water cooling towers (Findlay & Savory 1950, Savory 1954a, b), archeological timbers (Jones & Jones 1993), and terrestrial environments (Duncan 1960).

The term ‘soft rot’ was coined by Savory (1954a, b) for fungi that caused decay of the secondary wood cell wall layers. This was described in timbers from water cooling tower packing and characterized by chains of biconical cavities in the S2 cell wall layer. These cavities are helically orientated in the wood cell wall, following the microfibrillar arrangement in the S2 layer and best observed in the microscope under polarized light. Hale and Eaton (1985) have shown that the cavities are formed by the activities of lignolytic enzymes released from the hypha within the S2 layer by a process of ‘start-stop’ oscillatory growth of fine hyphae and subsequent widening around these hyphae to form the cavities (Leightly & Eaton 1977).

While soft rot of wood under field conditions can be quite high 31.7 to 40.3 % of beech and Scots pine test blocks over 54 weeks, losses under laboratory conditions on agar media can be as low 5.4% (Eaton 1969, Mouzouras 1989). When weight losses caused by soft rot fungi and basidiomycetes are compared, the former do poorly: 17.4% (*Savoryella lignicola*), with 73% weight loss by the basidiomycete *Pycnoporus sanguineus* (L.) Murrill (Bucher et al. 2004b). The latter has a much wider spectrum of lignolytic enzymes for the decay of wood (Pointing et al. 2000). *Savoryella aquatica* and *S. lignicola* have both been shown to cause soft rot of wood causing weight losses of 5.4-14.3-17.4 % (Mouzouras 1989, Bucher et al. 2004a, b).

Table 1 Genera referred to the Savoryellales

Genus	Current number Species	Species sequenced
Ascotaiwania	13	7
Canalisporium (sexual morph *Ascothailandia*)	12	7
Savoryella	10	7
Triadelphia	18	2

Fig. 6 – John Savory, a research scientist at the Forest Products Research Laboratory, Princes Risborough.

John Savory

This essay has been written to pay tribute to John Savory who devoted much of his research work on the characterization of soft rot decay in timber (Savory 1954a, b). He was pivotal in the introduction of the senior author to soft rot fungi, water cooling towers and experimental studies of these economically import group of fungi. Thus, the many studies on water cooling tower fungi that were initiated led to the discovery of the genus *Savoryella*, and named in his honour. John was a remarkable man, affable, good humored, a ready wit, a wonderful teacher and scientist. John Savory was not to know how widespread this genus was worldwide and its key position in the classification of the Ascomycota, as these developments took place after his death (Fig. 6).

Conclusion

The *Savoryella* story is a classic example of how the discovery of a single fungus can lead to such exciting results. This has led to the establishment of a well-supported order, which in turn has helped to resolve a whole range of genera, indeed families and orders. Many asexual genera, not previously classified, now find a home in well-established families/orders: *Conioscypha* (Conioscyphales), *Carpoligna*, *Helicoön*, *Pleurothecium* and *Sterigmatobotrys* (Pleurotheciales), *Bactrodesmiastrum* and *Ascotaiwania persoonii* (*Bactrodesmiastrum* clade) all having a relationship with the order Savoryellales (*Canalisporium* and *Triadelphia*) (Réblová & Seifert 2004, Sri-indrasutdhi et al. 2010, Boonyuen et al. 2011, Réblová et al. 2012, Zelski et al. 2015, Hernandez-Restrepo et al. 2015, Réblová et al. 2016a).

The order Savoryellales was first thought to be a sister clade of the Coronophorales and Melanosporales (Boonyuen et al. 2011), but is now known to form a wider relationship with Conioscyphales, Pleurotheciales and Fuscosporales (*Bactrodesmiastrum* clade) with high statistical support (Réblová et al. 2016a, Yang et al. unpublished data). Therefore, the study of a little known aquatic ascomycete has resolved the taxonomy of a wide range of other taxa.

Acknowledgements

We are grateful to the following who have contributed in different ways on various aspects of this project: Drs. Rod Eaton, Somsak Sivichai, Ka-Lai Pang, Veera Sri-indrasutdhi, Sue Read and Kevin Hyde. Gareth thanks Cynthia Savory for the photograph of John, for her hospitality and for many shared memories of a wonderful man.

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