



## Mycosphere Essays 13 – Do xylariaceous macromycetes make up most of the Xylariomycetidae?

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### Abstract

In this essay, we focus on the micro-xylariaceous genera (with inconspicuous ascomata and asexual morphs) in the Xylariomycetidae, with special emphasis on Xylariaceae. Are micro-xylariaceous less diverse than macro-xylariaceous genera (with conspicuous stromata) genera? This paper also reviews their taxonomic significance and current systematic relationship and evaluates different characters used in their taxonomic placement. So far, only a few micro-xylariaceous taxa have been studied in detail in comparison with the stromatic macroscopic xylariaceous taxa and the reasons for this are discussed. It is hoped that further sampling and study of different substrata and habitats, with greater emphasis on sequence data, may lead to the discovery of many more micro-xylariaceous genera.

**Key words** – Ascomycetes – micro-Xylariaceae – taxonomy – phylogeny – Xylariales

### Introduction

The family Xylariaceae (Sordariomycetes, Xylariomycetidae, Xylariales) comprises 87 genera and more than 1300 species (Maharachchikumbura et al. 2015, 2016). The Xylariaceae is one of the largest and well known families of Ascomycota, and has a worldwide distribution (Maharachchikumbura et al. 2015, 2016). The Xylariaceae are important wood degraders, but some are endophytes and others plant pathogens (Petrini et al. 1995, Edwards et al. 2003). Most xylariaceous species inhabit wood, while others are encountered on dung or associated with insect nests, such as termites and ants, with several species being economically important as plant pathogens (Edwards et al. 2003, Visser et al. 2009, Hsieh et al. 2010). Xylariaceae species exhibit a great diversity in tropical regions, from where many new taxa are described (Whalley et al. 1996, Rogers 2000, Stadler et al. 2013, Kuhnert et al. 2014, Daranagama et al. 2014, 2015 a, c, Liu et al. 2015, Ariyawansa et al. 2015, Li et al. 2016). Species delimitation in Xylariaceae is complicated as they exhibit a diverse range of morphological characters, ranging from massive, stalked or sessile

stromata, to minute rudimentary stromata with ascomata immersed in the substrata. Typically xylariaceous species are characterized by pigmented, aseptate ascospores, frequently with a germ slit. The asci, which have a conspicuous apical apparatus, are usually found in perithecia embedded in stromata of Xylariaceae species (Stadler 2011, Maharachchikumbura et al. 2016).

Intrageneric and intergeneric relationships of Xylariaceae with other related families in Xylariomycetidae are not well-studied (Stadler 2011). The lack of available data for this large group is a major drawback in establishing the boundaries among genera, as well as families. However, recent comprehensive phylogenetic studies have contributed much knowledge towards the interpretation of generic and familial relationships of the Xylariomycetidae (Stadler et al. 2013, Daranagama et al. 2015a, b, Maharachchikumbura et al. 2015, 2016, Senanayake et al. 2015).

Most stromatic Xylariaceae are well-studied and characterized based on morphology and phylogeny. Genera such as *Annulohypoxylon*, *Daldinia*, *Entonaema*, *Hypoxylon*, *Rhopalostroma* and *Xylaria* have been studied extensively for their morphology and phylogeny, as well as chemical profiles and chemotaxonomic relationships (Ju & Rogers 1996, Hsieh et al 2005, 2010, Stadler et al. 2010a, b, 2014a, b, Daranagama et al. 2014, 2015c, Kuhnert et al. 2014, 2015). Unfortunately, most of the non stromatic, microscopic genera in Xylariaceae are less well-studied, and their affinities to other genera and families are poorly established. *Appendixia*, *Calceomyces*, *Emarcea*, *Halorosellinia*, *Helicogermis*, *Indurata* and *Xylotumulus* are a few examples. Most of these genera are only known from their type collections and some are restricted to specific localities or habitats (Figures 1, 2), while some are recently collected and monotypic. Therefore, they have not been phylogenetically analyzed for their taxonomic placements. In this paper we address the reasons why the non stromatic xylariaceous fungi have been neglected and are less well-studied.

### **Micro-Xylariaceae and Macro-Xylariaceae**

The concept of defining the xylariaceous fungi as micro-Xylariaceae and macro-Xylariaceae is rather subjective. There is no established protocol or a set of guidelines for this distinction. It is also noteworthy that some species in genera that mainly contain taxa usually characterized by conspicuous stromata can have species with relatively minute ones. For example, in the genus *Xylaria*, species such as *X. albocincta* (Rehm) Y.M. Ju et al., *X. carabayensis* (Mont.) Y.M. Ju et al. and *X. discolor* (Berk. & Broome) Y.M. Ju et al. have small, discoid to pulvinate, soft stromata (Ju et al. 2012). On the other hand, several asexual states are classified in the genera known as “larger” Xylariaceae. Likewise the precise circumscriptions of the genera may not be possible at this stage with the available data. Thus our attempt at defining micro-Xylariaceae and macro-Xylariaceae genera may be suspended until more data are available and more taxa are discovered especially with the recollected type species.

The cardinal feature of Xylariaceae is perithecial ascoma embedded in more or less well-developed stromata (Rogers 2000) although some micro-Xylariaceae taxa even lack stromata (eg. *Anthostomella*, *Brunneiperidium*, *Lunatiannulus*, *Occultitheca*). Except for a few micro-xylariaceous, asexual genera discovered in earlier decades, most of the common xylariaceous species discovered by early mycologists possessed massive stromata, for example, *Daldinia*, *Entonaema*, *Engleromyces*, *Hypoxylon*, *Sarcoxydon*, *Squamotubera* and *Xylaria*. These large-sized Xylariaceae are often referred to as “macrofungi” in the popular mycological literature. However, several xylariaceous species lack stromata or have reduced stromata, and are usually referred to as “microfungi”. These microfungi taxa are immersed in the host tissue, visible only as blackened dots or areas even under a stereoscope. Some examples are *Anthostomella*, *Appendixia*, *Brunneiperidium*, *Cannonia*, *Fasciatispora*, *Lunatiannulus*, *Nipicola*, *Occultitheca*, *Pandanicola*, *Pyriformiascoma*, *Sabalicola* and *Spirodecospora*.

**Table 1** Comparison of Micro-Xylariaceae and Macro-Xylariaceae and their major studies

Genus	Molecular data	Key references
• Micro-Xylariaceae		
<i>Amphirosellinia</i> <sup>§</sup>	Yes	Ju et al. (2004)
<i>Anthocanalis</i> <sup>§</sup>	Yes	Daranagama et al. (2015a)
<i>Anthostomella</i>	Yes	Francis (1975) Francis et al. (1980) Hyde (1996) Lu & Hyde (2000a) Lu & Hyde (2000b) Daranagama et al. (2015a) Jones et al. (2015)
<i>Appendixia</i>	No	Lu et al. (2000c)
<i>Areolospora</i>	No	Jong et al. (1974) Hawksworth (1980)
<i>Ascotricha</i> <sup>§</sup> = <i>Dicyma</i> = <i>Puciola</i>	Yes	Hawksworth (1971) Berkeley (1838) Cheng et al. (2015)
<i>Astrocystis</i> <sup>§</sup>	Yes	Berkeley & Broome (1873) Læssøe et al. (1994) Dulymamode et al. (1998) Jones et al. (2015)
<i>Barrmaelia</i>	Yes	Rappaz (1995)
<i>Brunneiperidium</i> <sup>§</sup>	Yes	Daranagama et al. (2015a)
<i>Calceomyces</i> <sup>§</sup>	Yes	Udagawa & Ueda (1988)
<i>Cannonia</i>	No	Taylor & Hyde (1999)
<i>Chaenocarpus</i>	No	Rebentisch (1804)
<i>Collodiscula</i> <sup>§</sup> = <i>Acanthodochium</i>	Yes	Hino et al. (1955) Réblová et al. (2016)
<i>Coniolariaella</i> <sup>§</sup> = <i>Coniolaria</i>	Yes	García et al. (2006)
<i>Cyanopulvis</i>	No	Fröhlich & Hyde (2000)
<i>Emarcea</i> <sup>§</sup>	Yes	Duong et al. (2004)
<i>Fasciatispora</i> <sup>§</sup>	Yes	Hyde (1991) Alias et al. (1994)
<i>Halorosellinia</i> <sup>§</sup>	Yes	Whalley et al. (2000) Schlingham et al. (1998) Xia et al. (2007)
<i>Helicogermisli</i>	No	Hawksworth & Lodha (1983)
<i>Hypocopra</i>	Yes	Kirk (1867) Spegazzini (1880) Saccardo & Saccardo (1905) Krug & Cain (1974)
<i>Hypocreodendron</i> = <i>Discoxylaria</i> <sup>*§</sup>	No	Lindqvist & Wright (1964) Rogers et al. (1995) Réblová et al. (2016)
<i>Leptomassaria</i>	No	Petrak (1914) Ahmad & Lodhi (1953) Munk (1957)
<i>Lunatiannulus</i> <sup>§</sup>	Yes	Daranagama et al. (2015a)
<i>Myconeisia</i>	No	Kirschstein (1936)
<i>Nipicola</i>	No	Hyde (1992) Hyde & Taylor (1996) Fröhlich & Hyde (2000) Jones et al. (2015)
<i>Nodulisporium</i> ** = <i>Pleurographium</i>	Yes	Cox et al. (1994) Stadler et al. (2013)

Genus	Molecular data	Key references
<i>Occultitheca</i>	No	Rogers & Ju (2003)
<i>Ophiorosellinia</i>	No	Rogers et al. (2004)
<i>Pandanicola</i>	No	Hyde (1994)
<i>Paramphisphaeria</i>	No	Fernández et al. (2004)
<i>Paucithecium</i>	No	Lloyd (1923)
<i>Pyriformiascoma</i> <sup>§</sup>	Yes	Daranagama et al. (2015a)
<i>Rosellinia</i> <sup>§</sup>	Yes	De Notaris (1844)
= <i>Dematophora</i>		Saccardo (1913)
= <i>Vrikshopama</i>		Ellis & Everhart (1890)
		Smith & Ramsbottom (1915)
		Rappaz (1995)
		Spegazzini (1898)
		Petrini (2003)
		Petrini (2013)
		Réblová et al. (2016)
<i>Sabalicola</i>	No	Hyde (1995)
<i>Spirodecospora</i>	No	Lu et al. (1998)
<i>Striatodecospora</i>	No	Zhou et al. (2000)
<i>Virgaria</i> <sup>§</sup> = <i>Ascovirgaria</i>	Yes	Rogers & Ju (2002)
		Réblová et al. (2016)
• Macro-Xylariaceae		
<i>Annulohyoxylon</i> <sup>§</sup>	Yes	Ju & Rogers (1996)
		Hsieh et al. (2005)
<i>Biscogniauxia</i> <sup>§</sup>	Yes	Kuntze (1891)
		Ju et al. (1998)
<i>Camillea</i>	Yes	Fries (1849)
= <i>Basidiobotrys</i>		Læssøe et al. (1989)
= <i>Masoniomyces</i>		Whalley et al. (1998)
= <i>Xylocladium</i>		San Martín et al. (1993)
<i>Chlorostroma</i>	No	Miller et al. (2007)
<i>Daldinia</i> <sup>§</sup>	Yes	Cesati & De Notaris (1863)
= <i>Annellosporium</i>		Stadler et al. (2014a)
= <i>Versiomyces</i>		Réblová et al. (2016)
<i>Durotheca</i>	No	Læssøe et al. (2013)
<i>Engleromyces</i>	No	Hennings (1900)
		Whalley et al. (2010)
<i>Entoleuca</i>	Yes	Sydow & Petrak (1922)
		Ju et al. (2004)
<i>Entonaema</i>	Yes	Möller (1901)
		Martin (1938)
		Rogers (1981)
		Sihanonth et al. (1998)
<i>Euepixylon</i> <sup>§</sup>	Yes	Füisting (1867)
		Læssøe & Spooner (1994)
<i>Gigantospora</i>	No	Lu & Hyde (2003)
<i>Guestia</i>	No	Smith & Hyde (2001)
<i>Hypoxylon</i> <sup>§</sup>	Yes	Bulliard (1791)
= <i>Pyrenopolyporus</i>		Saccardo (1882)
= <i>Triplicaria</i>		Berkeley & Broome (1883)
= <i>Nodulisporium</i>		Martin (1967)
		Martin (1976)
		Jones et al. (2015)
		Rogers & Samuels (1985)
		Ju & Rogers (1996)
		Ju et al. (2005)
		Réblová et al. (2016)
<i>Induratia</i>	No	Samuels et al. (1987)
<i>Kretzschmaria</i> <sup>§</sup>	Yes	Fries (1849)
= <i>Holttumia</i>		Saccardo (1883)

Genus	Molecular data	Key references
		Martin (1976)
		Rogers & Ju (1998)
		Pereira et al. (2009)
		Hladki & Romero (2001)
<i>Kretzschmariella</i>	No	Viégas (1944)
		Ju & Rogers (1994)
<i>Leprieuria</i>	No	Læssøe et al. (1989)
<i>Nemania</i> <sup>§</sup>	Yes	Gray (1821)
= <i>Geniculisyneema</i>		Pouzar (1985)
= <i>Geniculosporium</i>		Ju & Rogers (2002)
		Ju et al. (2005)
		Rogers et al. (2006)
		Jones et al. (2015)
		Réblová et al. (2016)
<i>Obolarina</i> <sup>§</sup>	Yes	Pouzar (1986)
		Mirabolfathy et al. (2013)
<i>Phylacia</i>	Yes	Léveillé (1845)
		Dennis (1957)
		Speer (1980)
		Rodrigues & Samuels (1989)
		Medel et al. (2006)
<i>Podosordaria</i> <sup>§</sup>	Yes	Holway (1897)
		Krug & Cain (1974)
		Martin (1976)
		Rogers & Læssøe (1992)
		Hyde et al. (1996)
		Rogers et al. (1998)
<i>Poroleprieuria</i>	No	González et al. (2004)
<i>Poronia</i>	Yes	Willdenow (1787)
= <i>Lindquistia</i>		Möller (1901)
		Patouillard (1906)
		Sydow et al. (1911)
		Rogers et al. (1998)
		Hembrom et al. (2013)
<i>Pyrenomoxa</i>	Yes	Morgan (1895)
= <i>Pulveria</i>		Stadler et al. (2005)
<i>Rhopalostroma</i>	Yes	Hawksworth (1977) Hawksworth et al. (1979)
		Hawksworth & Whalley (1985)
		Whalley et al. (1998)
		Kaur & Ojha (2000)
		Stadler et al. (2010a)
		Daranagama et al. (2014)
<i>Rostrhypoxylon</i> <sup>§</sup>	Yes	Fournier et al. (2010)
<i>Ruwenzoria</i> <sup>§</sup>	Yes	Stadler et al. (2010c)
<i>Sarcoxydon</i> <sup>§</sup>	Yes	Cooke (1883)
		Petch (1924)
		Patouillard (1927)
		Rogers (1981)
<i>Squamotubera</i>	No	Hennings (1903)
		Rogers (1981)
<i>Stromatoneurospora</i> <sup>§</sup>	Yes	Jong & Davis (1973)
<i>Stilbohypoxydon</i>	Yes	Hennings (1902)
		Rogers & Ju (1997)
		Hladki & Romero (2003)
		Petrini (2004)
		Pereira et al. (2009)
<i>Thamnomyces</i>	Yes	Nees von Esenbeck (1820)
		Montagne (1834)
		Cooke (1884)

Genus	Molecular data	Key references
<i>Theissenia</i> <sup>\$</sup>	Yes	Lloyd (1920) Stadler et al. (2010b) Maublanc (1914) Ju et al. (2003) Ju et al. (2007)
<i>Thuemenella</i>	Yes	Penzig & Saccardo (1897) Boedijn (1964) Rifai & Webster (1965) Dennis (1970)
<i>Vivantia</i>	No	Rogers et al. (1996)
<i>Wawelia</i>	No	Namyslowski (1908) Minter & Webster (1983) Lundqvist (1992) Webster et al. (1999)
<i>Xylaria</i> <sup>\$</sup> = <i>Moelleroclavus</i> = <i>Padixonina</i> = <i>Pseudoxylaria</i> = <i>Xylocoremium</i>	Yes	Schrank (1789) Gray (1821) Rogers et al. (1988) San Martín et al. (1989) San Martín et al. (2001) Ju & Hsieh (2007) Hladki & Romero (2010) Hsieh et al. (2010) Réblová et al. (2016)
<i>Xylocrea</i>	No	Möller (1901) Smith (1901) Rick (1906)
<i>Xylotumulus</i> <sup>\$</sup>	Yes	Rogers et al. (2006)

\$ – Reliable sequences of the respective type species are available

\*– Sexual morph and stromatic Xylariaceae

\*\*– Asexual state of several stromatic Xylariaceae

### Microfungal genera in Xylariaceae

According to the outline provided by Maharachchikumbura et al. (2015) the family Xylariaceae comprises 87 genera and more than 1300 species. Among these, over 30 genera may be considered as microfungal with reduced reproductive structures or lacking stromata. Unlike the well-known stromatic genera in Xylariaceae, the above mentioned microfungal genera have been less well-studied and neglected by mycologists over a long time. Microfungal genera account for almost 1/3 of the currently accepted genera of Xylariaceae, but databases such as Index Fungorum and MycoBank, provide little data on these fungi.

### “The Problem” with micro-xylariaceous genera

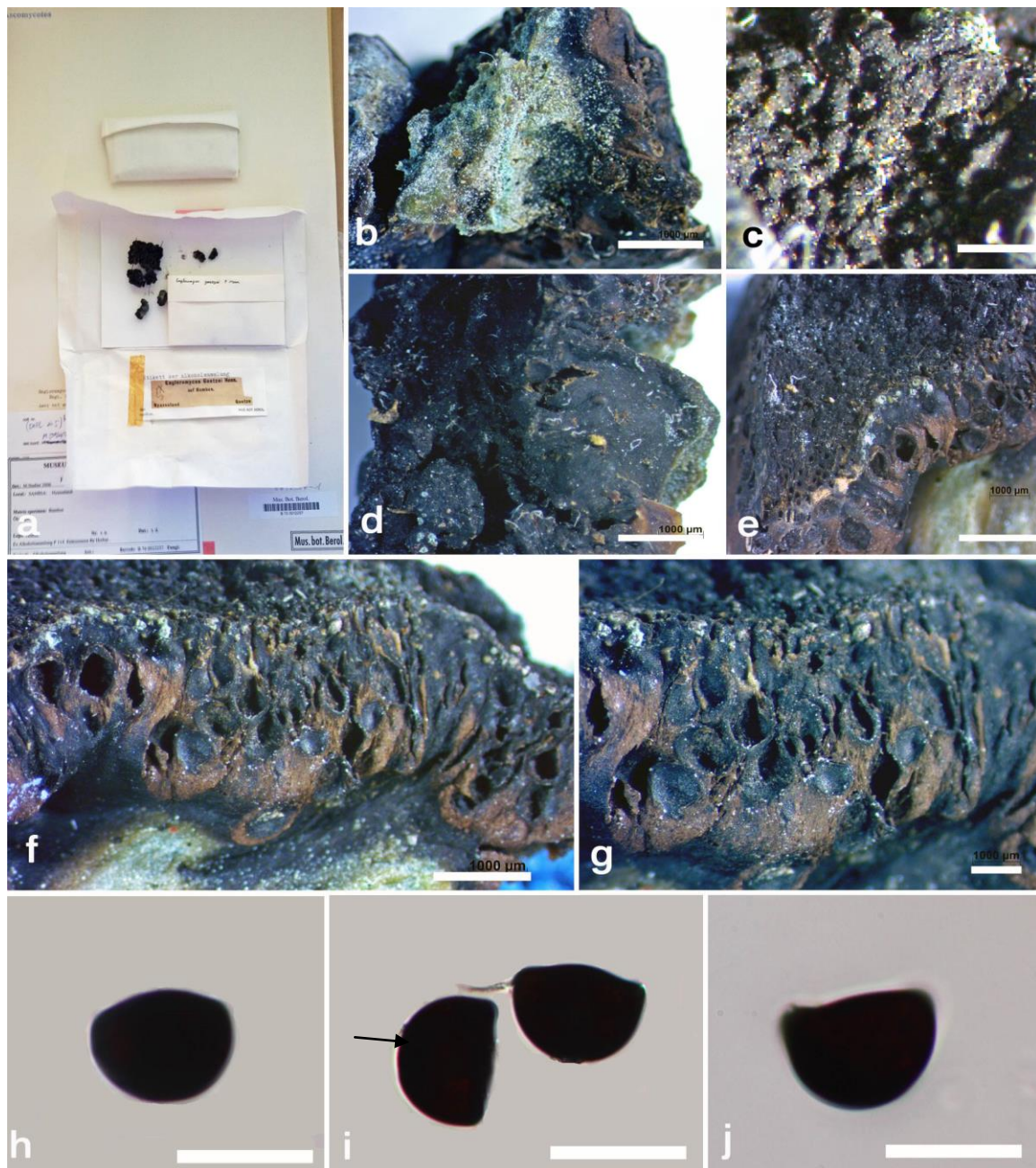
Stromatic Xylariaceae with their massive (up to 10 cm tall and sometimes even more), conspicuous, highly developed stromata are well-represented in the tropics, while the less conspicuous microfungal genera in Xylariaceae and other families of Xylariomycetidae, including Amphisphaeriaceae, Apiosporaceae, Cainiaceae, Clypeosphaeriaceae, Coniocessiaceae, Hyponectriaceae, Diatrypaeaceae, Melogrammataceae, Myelospermataceae and Vialaeaceae are less collected and therefore poorly studied (Carroll 1988, Hyde and Wong 2000, Carmarán et al. 2006, Daranagama et al. 2015a). Most stromatic Xylariaceae are readily visible to the unaided eye and are often collected and well-characterized macroscopically. This is especially true in Xylariaceae in which the gross morphology of the stromata has been described in detail, while microscopic characters, such as ascomatal shape, peridium and ascus characters, have been less well-documented (Miller 1961, Rogers 1981, Læssøe 1994, Rogers et al. 1997). However, with the recent development of molecular phylogeny and chemical profiling, these stromatic Xylariaceae genera are well-characterized and easily identified (Triebel et al. 2005, Stadler et al. 2008, 2010a, 2014a, Daranagama et al. 2014).



**Fig. 1 – *Appendixia closterium* (Holotype)** a. Herbarium details. b, c. Stromata in wood. d. Cross section of stromata showing perithecia encased in stromatal tissue. e. Peridium. f, g. Mature asci. h. Asci with apical apparatus slightly bluing in Melzer's reagent. i, j. Ascospores with polar appendages. Scale bars: d= 100 µm, e = 20 µm, f= 50 µm, g-h = 25 µm.

Comparatively very few micro-Xylariaceae have been carefully examined and even fewer have been thoroughly studied using both morphology and phylogeny. The major reason for this omission is the microscopic nature of the ascomata with apparent lack of any visible stromata. Therefore, fewer micro-Xylariaceae have been collected over the past 100 years. Unlike the stromatic Xylariaceae, the differences of micro-Xylariaceae mostly lie in their microscopic characters such as, shape, size of ascomata, peridium characters, morphology of apical apparatus, length and configuration of germ slits and also morphology of ascospores (Lu and Hyde 2000a, b Réblová and Seifert 2004, Petrini 2013, Réblová 2013, Daranagama et al. 2015a, Senanayake et al. 2015). Therefore, earlier mycologists focused mainly on external morphological characters of these microfungi. Several of the micro-Xylariaceae have been observed only once (e.g. *Appendixia closterium* (Berk. & M. A. Curtis) B.S. Lu & K.D. Hyde (Figure 1), *Areolospora* S.C. Jong & E.E. Davis, *Calceomyces lacunosus* Udagawa & S. Ueda and *Emarcea* Duong et al.), and then superficially (e.g. *Stereosphaeria americana* (M.E. Barr & Samuels) K.D. Hyde et al.). This can be seen in the number of micro-Xylariaceae recorded over the years, and fewer than half of those have any sequence data available (Table 1). It is only recently that they have been intensively studied with emphasis on ultrastructural characters and molecular phylogeny.





**Fig. 2** – *Engleromyces goetzei* (Holotype **a**. Herbarium details, **b**. Stromata with faded white flesh **c**. Stromatal surface with ostioles, **d and e**. Roughened stromatal surface, **f and g**. Cross section of stromata showing perithecia encased in stromatal tissue **h and j**. Ascospores, **i**. Ascospores with appendage present at one end (arrow head). Scale bars: b–e = 2 mm, f, g = 1mm, h–j = 20  $\mu$ m.

### Limitations in the studies of microfungi

The major limitation in understanding the micro-Xylariaceae is the lack of fresh collections, especially from tropical locations from where majority of the known species have been described. Therefore, progress in our understanding of the micro-Xylariaceae should come with more intensive collecting, particularly of habitats and substrates other than wood, and greater emphasis on obtaining sequence data. The lack of stromata means greater emphasis must be placed on ascocal anatomy, peridium structure, asci and ascospore morphology and ultrastructure. The lack of dichotomous keys, with reliance on single characters, is another problem in their taxonomic discourse. Thus, the importance of molecular approaches has been highlighted in order to determine the phylogenetic relationships (Stadler et al. 2013, Daranagama et al. 2015a, Maharachchikumbura et al. 2015).



The second problem in the study of micro-Xylariaceae is that many species were described long ago and have never been recollected (*Engleromyces*, *Sarcoxydon*, and *Squamotubera*). Stadler et al. (2013) highlighted that many type species of xylariaceous genera are only known from their original collections or else from the drawings made many years ago, for example, the holotype material of *Engleromyces goetzei* Henn., collected from Zambia in 1899 and deposited in B herbarium is now hard and degraded and not suitable for morphological observation (Figure 2). Also, *Podosordaria mexicana* Ellis & Holw., collected in 1896 on cow dung, is highly deteriorated. Similarly, the genus *Squamotubera* is only known from its short Latin prologue by Hennings (1903) with no illustrations. The types of the genera *Appendixia*, *Cannonia*, *Fasciatispora*, *Occultitheca* and *Sabalicola* have been encountered in earlier decades, but attempts to recollect them have so far failed as they were often isolated from specific hosts or from remote localities. For example, the monotypic genera *Appendixia* and *Sabalicola* were encountered from USA around 1893 and 1882, respectively. However, so far they have not been reported again.

The third problem with micro-Xylariaceae genera is that their spores are often difficult to germinate and thus many were not isolated into axenic culture. Unlike macrofungi, multi spore isolation or sterile tissue culture is not possible with microfungi, which leaves single spore isolation as the only option. For example, Lu and Hyde (2000b) and Daranagama et al. (2015a) addressed the difficulty of obtaining cultures from *Anthostomella* species. Many other Xylariaceae, such as *Kretzschmaria* and *Camillea* spp., are difficult to culture from ascospores. *Anthostomella* can be considered as the most frequently collected and well-studied micro-Xylariaceae genus (Eriksson 1966, Francis 1975, Francis et al. 1980, Hyde and Goh 1999, Lee and Crous 2000, Lu and Hyde 2000a, b, c, Daranagama et al. 2015a). However, most of these studies were only based on morphology (Eriksson 1966, Francis 1975, Francis et al. 1980, Hyde and Goh 1999, Lu and Hyde 2000a, b, c.). Lu and Hyde (2000b) examined more than 2600 anthostomella-like specimens from 35 herbaria in their monograph. They accepted 86 species, while 95 species were synonymized, 105 taxa were relocated to other genera and 65 species were regarded as doubtful. The genus clearly shows considerable morphological diversity and is thought to be a heterogeneous group. Daranagama et al. (2015a) used a multi gene approach to show that the genus is polyphyletic. This highlights the need to study other micro-Xylariaceae at the molecular level. These fungi should be recollected and cultured to generate sequence data. Only then can their familial affinities and species numbers can be accurately established.

The fourth problem, closely tied to the previously described one, is the lack of reliable sequence data of representative micro-xylariaceous fungi. Very few morphologically validated strains are deposited in public databases such as, GenBank. Most of the sequences belonging to Xylariomycetidae species deposited in public databases are not derived from type specimens or cultures. Most of the sources of these sequences are always missing, and the specimens or cultures never deposited in public collections. It is pertinent to point out that many sequences of Xylariaceae are misidentifications, a common feature of sequences in GenBank (Bridge et al. 2005). Stadler et al. (2013) highlighted the mislabeled strain ATCC 42768 which has continuously been referred to as *Xylaria hypoxylon* in many studies, but it actually corresponds to *X. longiana* Rehm. It was only very recently that the generic type of Xylariaceae (*Xylaria hypoxylon* (L.) Grev.) was formally epitypified and an ex-epitype strain deposited with authentic sequences (Stadler et al. 2014b). However, not only this species, but many other generic types in Xylariaceae, are in need of proper epitypification with living cultures and authentic sequence data.

When we blast the GenBank database for Xylariaceae there are more than 5000 hits of which more than 2000 correspond to *Xylaria*. The actual problem occurs when these data are used in molecular studies. Only about 15–20% of data can be considered as authentic, thus their use in other studies is highly questionable, devaluing the accuracy of the analysis. Many sequences from different genes representing the stromatic Xylariaceae genera, such as *Annulohypoxylon*, *Daldinia*, *Hypoxylon* and *Xylaria* are now available in GenBank because of the extensive studies carried out recently on these genera (Hsieh et al. 2005, 2010, Visser et al. 2009, Kuhnert et al. 2014, Stadler et al. 2014a). However, the opposite applies to the micro-Xylariaceae. For example, *Barrmaelia*

comprises seven species, but sequences for only two species are available in GenBank. Data for over half of the genera listed in Table 1 have no sequence data e.g. *Appendixia*, *Cannonia*, *Occultitheca*, *Sabalicola*, *Spirodecospora*, *Nipicola* and *Pandanicola*. Stadler (2011) reported that about 80% of the cultures belonging to *Annulohyphoxylon*, *Daldinia* and *Hypoxydon*, have morphological, chemotaxonomic and molecular data available for their species. In the case of micro-Xylariaceae the opposite is the case because of the practical difficulties in DNA extraction from fruiting bodies. In the case of stromatic genera, their massive stromata can also be used in DNA extraction and thus direct sequencing.

A fifth problem is that a significant number of xylariaceous fungi occur as asexual morphs (for example: *Arthroxyllaria*, *Dicyma*, *Discoxyllaria*, *Lindquistia*, *Muscodor*, *Padixonia*, *Virgaria* and *Xylocoremium*) and some have not been connected to their sexual morphs, e.g. *Muscodor*. These taxa have been isolated from soil or other substrata and attempts to obtain the sexual morphs have been unsuccessful. The asexual morphs of other sexual genera may yet still be discovered.

A further issue is that many xylariaceous taxa have been isolated as endophytes with some remaining sterile, while others have been identified as the asexual morphs: e.g. *Surculiseria* and *Muscodor* (Okane et al. 2001). Cultures of *Muscodor* are sterile and its position in Xylariaceae is not yet confirmed, therefore Maharachchikumbura et al. (2016) placed *Muscodor* in the Xylariales *incertae sedis*. *Surculiseria rugispora* Okane, Nakagiri & Tad. Ito, is an endophytic asexual taxon isolated from the leaves of the mangrove tree *Bruguiera gymnorhiza* (L.) Lam.

The stromatic Xylariaceae genera are of great interest as sources for novel compounds, thus they have been extensively investigated for their secondary metabolites. The well-developed, massive, conspicuous stromata are a rich source of secondary metabolites and lend themselves to study (Stadler 2011). However, the same is not the case for micro-Xylariaceae genera with the exception of *Halorosellinia oceanica* (S. Schatz) Whalley et al. from which a wide range of new chemical structures have been reported (Schillingham et al. 1998, Chinworrungsee et al. 2005, Xia et al. 2007, Jones 2008, 2013). Since they lack stromata, where most novel chemicals have been derived, the micro-Xylariaceae has generally been neglected in the search for new chemical metabolites.

### **Current status of the micro-Xylariaceae**

In many phylogenetic analyses of Xylariaceae only the macro-Xylariaceae genera have been investigated (Smith et al. 2003, Pelaéz et al. 2008, Tang et al. 2009), and many have been monographed and revised (Rodrigues and Samuels 1989, Ju and Rogers 1996, Hsieh et al. 2005, Stadler et al. 2010b, 2014a, Petrini 2013, Jacklitsch et al. 2014) using morphology, molecular and even chemical data. Many microfungus genera in the Xylariales (ex Xylariaceae) have been extensively studied including *Anthostomella*, *Amphisphaeria*, *Arecophila*, *Kiliophora*, *Pestalotiopsis* and *Seimatosporium* (Hyde 1996, Lu and Hyde 2000b, Wang et al. 2004, Barber et al. 2011, Maharachchikumbura et al. 2014, Daranagama et al. 2015a, Norphanphoun et al. 2015). The examples given above should certainly be sufficient to indicate that the microfungus genera have so far been neglected.

### **Phylogenetic relationships between families in Xylariomycetidae**

The phylogenetic affinities of families in the Xylariomycetidae have not been clearly established (Rogers 2000, Senanayake et al. 2015). Likewise, the assignment of genera to families sometimes cannot be done with certainty only using morphology, in which similar taxa are grouped together. However, in many cases the phylogenetic relationship of genera is not clear either. For example, xylariaceous genera such as *Biscogniauxia* and *Camellia* have bipartite stromata and this is also found in some species of Diatrypaceae; e.g. *Diatrype stigma* (Hoffm.) Fr. The interrelationship between Xylariaceae and Diatrypaceae has long been the topic of study (Munk 1957, Acero et al. 2004, Stadler et al. 2013). For example, the genera *Creosphaeria* and *Lopadostoma* with libertella-like asexual morphs were included in Xylariaceae, but others opined

affinities with Diatrypaceae (Acero et al. 2004, Daranagama et al. 2015a). More recently these two genera were referred to the family Lopadostomataceae based on phylogeny and morphology by Senanayake et al. (2015) and Maharachchikumbura et al. (2016) *Jumillera* and *Whalleya* were introduced to encompass taxa based on morphological differences of their asexual morphs (Rogers et al. 1997). However, both genera produce scolecosporous conidia, which is a characteristic feature of *Lopadostomaceae*. Some *Jumillera* species produce libertella-like asexual morphs and species such as *J. cinerea* (Ellis & Everh.) J.D. Rogers et al. produce geniculosporium-like synanamorphs in culture (Rogers et al. 1997). *Whalleya microplaca* (Berk. & M.A. Curtis) J.D. Rogers et al. produced a similar asexual morph to *Lopadostoma pouzarii* Granmo & L.E. Petrini (Granmo and Petrini 1996). Therefore, *Jumillera* and *Whalleya* have affinities with both *Xylariaceae* and *Lopadostomaceae*. Therefore their phylogenetic placement remains to be established as fresh material and molecular data becomes available.

*Pyriformiascoma* is a new xylariaceous genus with unknown affinities, which appeared to be in a basal clade to other xylariaceous genera (Darangama et al. 2015a). However, this genus may be better referred to other families in the Xylariales or to others when there are enough strains collected in the future. For example, Krug (1977) introduced the family Cainiaceae to accommodate *Cainia* a genus often placed in Amphisphaeriaceae. *Cainia* obviously has affinities with both the Amphisphaeriaceae and Xylariaceae as reported by Rogers (1994), and Kang et al. (1998, 1999a, 1999b). Therefore it is evident that there are several evolutionary interfaces that have been observed in this group and many of these microfungial genera represent unrecognized evolutionary lineages. On the other hand formalization of these evolutionary patterns based on the few data available may not be wise. Therefore additional studies are clearly needed to clarify this issue.

## Conclusion

Although research studies have mostly focused on the larger Xylariaceae it is unlikely they are the most diverse forms in Xylariomycetidae. This essay indicates that future studies should focus on the micro-fungi in Xylariales. Many of these micro-fungi have not been studied due to lack of material, especially sequence data. Many new lineages in the Xylariomycetidae remain to be introduced and wider collecting, modern descriptions and illustrations are required, along with sequence data. In particular, early described genera need recollecting and epitypifying so as to obtain a better knowledge of lineages within Xylariomycetidae. A culture-based study of endophytes associated with rubber trees in Peru yielded a new genus and species: *Xylona heveae* Gazis & P. Chave., resulting in the introduction of a new class of Pezizomycotina: Xylonomycetes (Gazis et al. 2012). This shows that many more xylariaceous and other endophytic taxa remain to be collected and characterized.

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