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The sooty moulds

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Abstract Sooty moulds are a remarkable, but poorly understood group of fungi. They coat fruits and leaves superficially with black mycelia, which reduces photosynthesis rates of host plants. Few researchers have, however, tried to quantify their economic importance. Sooty moulds have been well-studied at the morphological level, but they are poorly represented in a natural classification based on phylogeny. Representatives are presently known in *Antennulariellaceae*, *Capnodiaceae*, *Chaetothyriaceae*, *Coccodiniaceae*, *Euantennariaceae*, *Metacapnodiaceae* and *Trichomeriaceae* and several miscellaneous genera. However, molecular data is available for only five families. Most sooty mould colonies comprise numerous species and thus it is hard to confirm relationships between genera or sexual and asexual states. Future studies need to obtain single spore isolates of species to test their phylogenetic affinities and linkages between morphs. Next generation sequencing has shown sooty mould colonies to contain many more fungal species than expected, but it is not clear which species are dominant or active in the communities. They are more common in tropical, subtropical and warm temperate regions and thus their prevalence in temperate regions is likely to increase with global warming. Sooty moulds are rarely parasitized by fungicolous taxa and these may have biocontrol potential. They apparently grow in extreme environments and may be xerophilic. This needs testing as xerophilic taxa may be

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of interest for industrial applications. Sooty moulds grow on sugars and appear to out-compete typical "weed" fungi and bacteria. They may produce antibiotics for this purpose and their biochemical potential for obtaining novel bioactive compounds for medical application is underexplored.

Keywords Antibiotics · *Capnodiales* · *Chaetothyriales* · Global warming · Life cycle · Phylogeny · Xerophiles

Introduction

The sooty moulds are a group of well over 200 epifoliar fungal species that live on plant surfaces where sap-feeding insects feed on plant foliage. The insects excrete honeydew as a waste product. The honeydew drips on the foliage below and covers leaves, twigs and even plants, soil and rocks below with a sticky sugary coating. Honeydew is largely composed of sugars with smaller amounts of amino acids, proteins, minerals, vitamins and other organic compounds (Auclair 1963). The sooty moulds grow on this and produce a thin superficial network of dense, dark hyphae (Hughes 1976; Faull et al. 2002, Fig. 1).

Sooty moulds are most common in tropical and subtropical regions around the world. Most of the sooty moulds have hyphae with mucilaginous outer walls. These readily absorb water and thus maintain moisture on leaf surfaces for long periods (Batista and Ciferri 1963b). Hyphae of different taxa of sooty moulds are often mixed together in a sooty mould colony on the host surface. These usually include asexual and sexual stages of the same or different species, but not all sooty moulds produce a sexual state (Hughes 1972, 1976; Hughes and Seifert 2012). Species delimitation is a major issue in sooty moulds as they frequently grow together and show noticeable pleomorphy. Some species are thought to produce as many as three asexual states, which have been allied to one sexual state (Hughes 1976). However, this information is based on direct observation rather than on cultural or molecular proof.

Historically, the term 'sooty mould' was first used by Berkeley and Desmazières (1849) in their detailed study of some members of the genus *Fumago*. They based their work on herbarium specimens from Sri Lanka, i.e. 'coffee leaves with a deep black colour of sooty mould related with coccus or bug', on 'the serious sooty mould on citrus leaves in the Azores and Madeira', and on *Citrus* species grown in greenhouses in France. The term was later popularized in the US plant pathology literature, starting with Weber's paper in 1897 (Hughes 1976; Faull et al. 2002). It is generally understood that sooty moulds are fungi that grow on honeydew secreted by insects in the Order Hemitera, suborder Homoptera, which includes aphids, whiteflies, soft scales, mealy bugs, leafhoppers and psyllids, living on plants and other surfaces, such as rocks below plants (Barr 1987). The sponge-like layers formed by sooty moulds are usually the result of an interaction between sap-feeding insects and non-parasitic fungi (Hughes 1976). Sooty moulds are fairly harmless saprobes living on honeydew but reduce plant photosynthesis. The honeydew-producing immature and adult stages of the insects, however, cause harm by sucking the sap from plants.

Historical background of research on sooty moulds

Persoon (1822) described the first sooty mould, *Fumago vagans*, recognizing its black mycelium with small pycnidium covering the leaves of lime, elm, poplar, ash and willow. Spegazzini (1918) reorganized sexual states of sooty moulds to belong to seven families in the order *Perisporiales*, including the *Capnodiaceae* and *Chaetothyriaceae* with sooty moulds forming ostiolate perithecia. Asexual states were named as "Deutocapnodieas", with pycnidial forms placed in "Asbolisieas" and hyphomycetous forms in "Hypasbolisieas". Batista and Ciferri (1963a) transferred some of Spegazzini's anamorphic Asbolisieas to Hypasbolisieas because of their elongated pycnidia or synnematous form.

The above concepts prevailed for much of the previous century, until Hughes (1976) collected and monographed many sooty moulds from New Zealand. Reynolds (1998) provided some information on the phylogeny of the sooty moulds, with capnodiacean isolates constituting a monophyletic group, which are represented by both asexual and sexual states.

Sooty moulds are presently known in the families *Antennulariellaceae*, *Capnodiaceae*, *Chaetothyriaceae*, *Coccodiniaceae*, *Euantennariaceae*, *Metacapnodiaceae* and *Trichomeriaceae* (Reynolds 1998; Winka et al. 1998; Chomnunti et al. 2012a, b; Hughes and Seifert 2012; Hyde et al. 2013). Recently, the *Schifferulaceae* was described as a new sooty mould family for saprobic fungi from India (Hosagoudar and Riju 2011). However, species of *Schifferulaceae* cannot be cultured, so their systematic arrangement has not been ascertained with molecular techniques. They produce hyphopodia which is present in many species with affiliation to the *Asterinaceae*, *Englerulaceae* and *Meliolaceae*, families which have not been included in the study.

The taxonomic treatment of sooty moulds has been rather unsatisfactory because they exist as communities on plant surfaces. Comprising many different asexual and sexual states which are often linked on the basis on host association, the connections between these states are still largely unproven and unclear. Traditionally, the name sooty mould was associated with the families *Capnodiaceae* and *Chaetothyriaceae* (McAlpine 1896; Faull et al. 2002). Their ascomata are black, ovoid to ellipsoidal or dome-shaped perithecia that may have setae (Chomnunti et al. 2012a, b). They contain a type of bitunicate ascus with eight hyaline to brown septate ascospores. Their asexual reproductive structures have been interpreted as synnemata by some authors.

Fig. 1 Sooty moulds on various hosts. **a** *Sapotaceae*. **b** *Dracaenaceae*. **c** *Convallariaceae*. **d** *Euphorbiaceae*. **e** *Acanthaceae*. **f** *Euphorbiaceae*. **g** *Asteraceae*. **h** *Rubiaceae*

In recent times, mycologists have used molecular techniques as well as biochemical characters to confirm the identity of fungi (Webster and Weber 2007; Maharachchikumbura et al. 2012; Udayanga et al. 2012; Hyde et al. 2013). However, using molecular phylogeny is still problematic, because most type materials are unavailable for DNA extraction. In addition to

describing herbarium materials, epitypification using fresh material is therefore also needed to stabilise the status of some genera or species. The freshly collected epitype helps to interpret new features or attributes of specimens. For a definition of what is an epitype one should consult Article 9.8 of the latest edition of the *International Code of Nomenclature for Algae, Fungi, and Plants* (Melbourne Code) (McNeill et al. 2012; see also: http://www.iapt-taxon.org/nomen/main.php). Thus, re-examination of type materials and establishment of epitypes with living cultures is essential for taxonomic progress. Multi-gene analysis combined with the assessment of distinctive morphological characters are needed to develop a strong species-based taxonomic system (Phillips et al. 2006, 2007; Crous et al. 2007; Shenoy et al. 2007; Alves et al. 2008; Chomnunti et al. 2011; Hughes and Seifert 2012; Liu et al. 2012).

During the International Botanical Congress XVIII (IBC) held in Melbourne, Australia (July 2011), it was agreed that a fungus can only have one name and this is now reflected in the new *International Code of Nomenclature for Algae, Fungi, and Plants* (Gams et al. 2012; Stadler et al. 2013). This change is directly linked to the advances in molecular phylogenetic analysis, because a more natural systematic classification can be obtained through molecular evidence. Comparison of DNA sequence data has made it possible to reliably connect asexual morphs to their sexual states. It is now expected that with each species having only one name, there will be much less confusion which previously resulted from the dual classification system (Hawksworth et al. 2011; McNeill and Turland 2011; Rossman and Seifert 2011; Wingfield et al. 2012). An example of this is the sooty mould *Fumago citri*. The species was introduced by Persoon in 1822, but because it was considered not to be described in a 'complete' way, it was transferred to the genus *Polychaeton* by Léveillé (1847). However, Berkeley & Desmazieres (1849) transferred all the species once known in the genus *Fumago*, and by default *F. citri*, to *Capnodium*. Accordingly, the species became known as *Capnodium citri*. Its generic name is used for fungi showing ascus and ascospores, the sexual stage, which is not often observed. So, the name *Polychaeton* was still used as long as the sooty mould did not produce ascospores. With the advent of molecular techniques we can now show that both morphs with different names are the same organism. Therefore, there is no need to continue using different names and *Capnodium citri* is preferred. More information on the adoption of a single name for this fungus can be found in Art. 57 of the Melbourne Code (2012).

The present taxonomy of each of the sooty mould families is outlined and discussed below, and list of genera included in each family also presented in Table 1.

Fossil sooty moulds

Fossil evidence indicates that sooty moulds have been around for at least 100–113 millions years. Schmidt et al. (2014) reviewed previous and presented new fossil evidence to trace the fossil record of sooty moulds for about 100 million years, from the early Cretaceous (Albian, about 100 to 113 million years ago), to the early Miocene (17 million years ago). They illustrated convincing micrographs showing *Metacapnodiaceae*-like species. In one micrograph (Fig. 6) they show the asexual states of *Metacapnodium succinum* from the Baltic (middle or late Eocene) and Bitterfeld ambers (late Oligocene amber). The fossil fungi grew on leaves and bark of different conifer and angiosperm trees in ancient tropical to temperate coastal forests. Thus, capnodialean sooty moulds appear to have occupied their specialized niche since the early angiosperms appeared in the fossil record (Schmidt et al. 2014).

Early Cretaceous sooty moulds are morphologically similar to asexual extant capnodialean taxa suggesting a long evolutionary history. Acccordingly, sooty moulds might represent a very ancient component of humid forest ecosystems. Sap sucking insects are believed to have evolved long before the Cretaceous, since the oldest aphid record is from the middle Triassic (Szwedo and Nel 2011). Hemipterans and palaeodictyopterans with sucking beaks are known from the Carboniferous (Labandeira 2006; Nel et al. 2013). Thus, associations between sooty moulds and plant-sucking, presumably and honeydew-producing insects may have evolved in pre-Cretaceous times (Schmidt et al. 2014).

It is interesting that sooty moulds in *Chaetothyriales* are related to rock-inhabiting black yeasts (Gueidan et al. 2008, 2011; Voglmayr et al. 2011). Honeydew from insects on the plants may have dropped on to rocks beneath the plants and may have been the vehicle in early evolution by which the rock-inhabiting fungi eventually evolved to occupy the extreme rock-dwelling habitats. This is quite feasible, considering that sooty moulds were probably already xerophilic and could have relatively easily have adapted to an extreme life as rock-dwelling fungi. Several *Capnodiales* have also been isolated as rock-dwelling fungi (Ruibal et al. 2009; Selbmann et al. 2014), and it is equally feasible that some of these taxa evolved from capnodiaceous sooty moulds.

Sooty moulds and insects

Sooty moulds have intricate relationships with plant sucking insects, as they grow on secreted honeydew. However, it is not known if these relationships are plant or insect host-specific, non-specific, or as we suspect, a combination of all three. There have been relatively few studies of the fungi associated with sap feeding insects, however He (2011) examined the fungal and bacterial species associated with armoured scale insects and investigated the insect microbiota by cultivation and identified the associates by phylogenetic analysis. He (2011) found 76 putative fungal operational taxonomic units (OTUs) and 58 putative bacterial OTUs. While these numbers

Table 1 Genera of sooty moulds in the different families. Combined and modified after Lumbsch & Huhndorf (2010), Kirk et al. (2008) and Hyde et al. (2013)

Antennulariellaceae	*Capnodiaceae*	*Chaetothyriaceae*	*Coccodiniaceae*	*Euantennariaceae*	*Metacapnodiaceae*	*Trichomeriaceae*
Achaetobotrys	*Capnodium*	*Actinocymbe*	*Coccodinium*	*Antennatula*	*Capnocybe*	*Trichomerium*
Antennulariella	*Capnophaeum*	*Ceramothyrium*	*Dennisiella*	*Capnokyma*	*Capnophialophora*	
Capnofrasera	*Leptoxyphium*	*Chaetothyriomyces*	*Limacinula*	*Euantennaria*	*Capnosporium*	
	Phragmocapnia	*Chaetothyrium*		*Hormisciomyces*	*Hormiokrypsis*	
	Scorias	*Euceramia*		*Rasutoria*	*Hyphosoma*	
		Microcallis		*Strigopodia*	*Metacapnodium*	
		Phaeosaccardinula		*Trichothallus*		
		Treubiomyces		*Trichopeltheca*		
		Yatesula				

appear to be high, the role of most of these microorgansims also remains unclear. Such alpha taxonomic studies must be taken with caution and need to be further elaborated by using more concise barcoding approaches. The results, however, do point towards a very high biodiversity that in all likelihood can only be resolved by culturing as many of these OTUs as possible. They may include causal inhabitants, adhering fungal spores, sooty moulds, internal or external pathogens, ingested fungi and/or fungi growing on the host cuticle.

There have been several records of scale insect associated fungi with perhaps one of the earliest ones from Oise amber in France, dating back to the early Eocene (52–55 millions years ago) (Schmidt et al. 2014). These authors illustrate a *Uzelothrips eocenicus* thrips species with apparent sooty mould fragments attached to the cuticle. These thrips appeared to use the sooty moulds both as their microhabitat and as a food source, and hyphal fragments have often been seen attached to their cuticles (Schmidt et al. 2014).

There have been other reports of pathogens of scale insects and these are discussed in a later section, but few on scale insect associated fungi. He et al. (2013) described a new species of black yeast, *Knufia aspidiotus* (*Chaetothyriaceae*, *Chaetothyriales*) from scale insects, during an investigation of the microbial communities associated with the scale insects.

Methods to study sooty moulds

Field collection and morphological studies

Random collections of sooty moulds can be made in the field by looking for sooty or blackened area on leaves (Fig. 1), twigs, stems and surrounding areas (any material) beneath the infected plant. Recently developed colonies comprise fewer species and therefore provide optimum sampling for obtaining isolates of the dominant species. Collected material should be placed in paper bags and all collection details noted (i.e. location, collector, collecting date, habitat and host). Any insects and honeydew secretions present should be recorded. If insects/mould relationships are to be investigated the insects should also be collected by placing in 75 % alcohol with 0.5~1 % glycerol. In the laboratory, the specimens can be stored for several weeks, if maintained in a relatively dry atmosphere. In plastic bags samples will "sweat" and soon be overgrown by other fungi.

Samples should be first viewed under a dissecting microscope to determine the age of colonies, the number of fungi present and the suitability of specimens for further study. If the sooty mould specimens are too old, it may be impossible to gain much data or isolates from the colonies. If the freshly collected specimens are not sporulating they can be placed in moist chambers (sterilized boxes with moistened sterile tissues) for 1 to 2 days to induce sporulation. However, the colonies are likely overgrown by other fungi after prolonged incubation times. Specimens can be stored dry until examination, but viability of spores will be reduced over time.

Microscopy

One or two fruiting bodies should be transferred to slides by using fine needles or forceps and rehydrated in water, 3–5 % KOH, and/or lactophenol with cotton blue reagent prior to examination. Sections of ascomata are best made free-hand and mounted in lactic acid. Observations and hand sections can be examined under a microscope; such as a Nikon ECLIPSE 80i/Ni with differential interference contrast microscopy. Measurements are best obtained from digital photographs manually or through imaging software. In the case of asexual fungi, it is essential to establish how the spores are produced (conidiogenesis).

Single spore isolation

Most of the sooty moulds collected will be blackened colonies on the surface of leaves and each sooty mould sample will contain blackened areas comprising asexual and sexual states of multiple species. It is therefore essential that careful single

spore isolation of each species, including both its asexual and sexual states is carried out (see below). In this way it is possible to establish which sexual and asexual spores can be linked and how many species actually exist within a colony. Initially, molecular data will be needed to establish link morphs of single species, but later this will be possible using morphology.

There are two main groups of sooty mould fungi, i.e. ascomycetes and hyphomycetes, which have different types of fructifications. The methods for isolation may therefore be different.

Isolation via spore suspension

Ascomata are removed from the substrate surface using fine forceps or laterally cut and spore masses are transferred with a sterilized needle or fine forceps to a drop of sterile water on a small glass container or a flamed microscope slide. Asexual spores of hyphomycetes or coelomycetes can also be treated this way (Fig. 3). Spores of coelomycetes often ooze from the conidiomata neck and can be transferred to a water drop using a sterile needle. With hyphomycetes, a superficial scrap of the surface, using a needle, should dislodge spores that will stick to the needle and can be placed in a drop of water. The drop of water is then examined under a dissecting microscope to establish that enough and the correct spores have been transferred.

The agitated spore suspension is then sucked into a Pasteur pipette or syringe. Small drops are placed on agar in the centre of pre-marked squares in a grid on the bottom of a Petri dish. As isolation media, 2 % water agar (WA) or malt extract agar (MEA) (Fig. 2a) are well suited. The plates are usually incubated overnight at room temperature or in an incubator (25 °C). The plates are examined for single germinated spores under a dissecting microscope at high magnification. Germinating spores are transferred separately to at least three new MEA plates. Spores normally germinate within 12–24 h and should be transferred immediately by picking up single spores with a small piece of agar using a fine needle. If left any longer than 2 days, contaminants will probably overgrow the plates and it will be impossible to guarantee that single spore cultures of the correct species have been obtained. Some spores should be examined under a compound microscope to confirm the correct spore types or species has been obtained. By photographing germinating spores, germination traits may be documented, which may be morphologically informative (Fig. 3f–j). A maximum of six spores can be placed equidistant, at opposite sides of the Petri-dishes. The number may be chosen individually, but with more spores, the chance of contamination increases. If identical spores have been picked for the initial Petri dishes all colonies should be similar (see Fig. 2e). This is a good way to confirm one has isolated conspecific strains.

Once colonies have reached about 1 cm diameter (Fig. 2e) they should be transferred to fresh media. Some strains may require special treatment for production of sexual or asexual states, for which, e.g., agar supplemented with honey may be appropriate (Ng 1963). Plates should then be prepared for photography, morphological and molecular study. They should also be deposited in culture collections, at early stage of the project to avoid confusion and contamination of strains. At least two strains of each species should be obtained. Cultures can be usually grown on MEA agar at 25–28 °C for 12 h of light/12 h of dark for routine maintenance. Colour and colony characteristics can be assessed after 2 weeks, or earlier if the fungus grows very quickly. Colony size and shape are measured, recorded and photographed. After 1 month, the cultures can be observed under a microscope and all characters recorded (Fig. 2f).

Preparation of herbarium material

Preparation of herbarium material is essential for describing new species and important to keep records so that published data are verifiable. Herbarium material should also be prepared as early as possible by taking a small piece of material of the species of interest. The material is immediately dried and transferred to the curator of a herbarium. Ideally, the leaf is cut into parts containing single species, rather than depositing samples with multiple species. Herbarium material can also be obtained from dried cultures. All dried material should be placed in containers or herbarium packets, labelled and deposited in the herbarium as soon as possible as it may deteriorate if left in the laboratory. Herbarium material is best prepared from freshly collected samples, while fragments are separated for study, as colonies will quickly be overgrown if left for example, in a moist chamber.

Storage of isolates

The major issues when working with fungal cultures are contaminations by other fungi and mites. The risk increases with incubation time. The best practice is therefore to deposit strains in culture collections as soon as practical. There are several methods to store cultures and these are outlined in CBS Laboratory Manual Series 1 (Crous et al. 2009a, b), which the researcher should consult. However, we recommend from experience that

1. Cultures are placed in a culture collection as early as possible, and not only when a culture collection number is needed for a publication.
2. Cultures are placed in more than one culture collection including 1–2 collections in other countries.
3. Cultures are maintained in at least triplicates and applying different conservation procedures (e.g. frozen, under water, in vials, in liquid nitrogen) during the study.

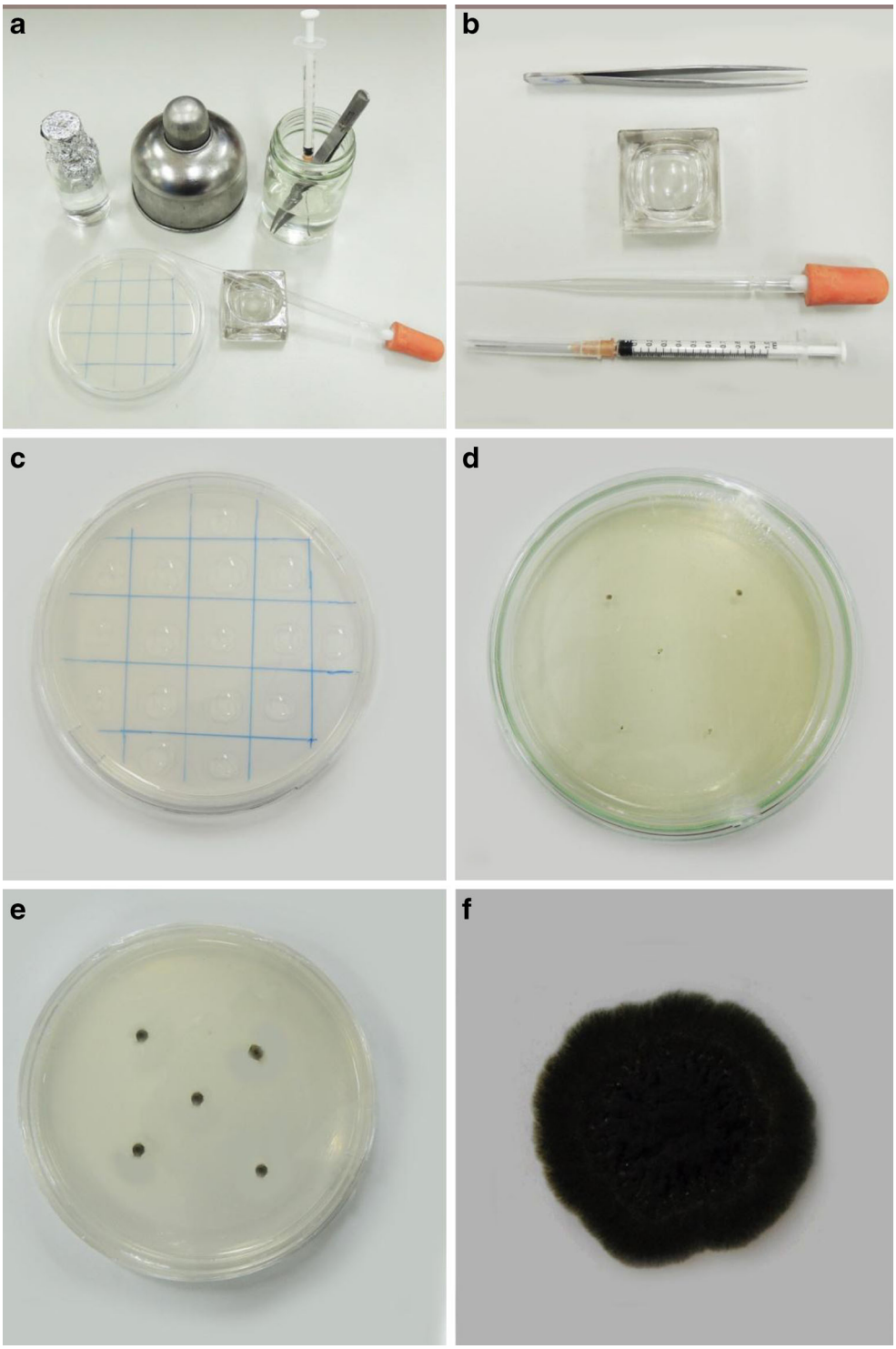

Fig. 2 **a-f** Single spore isolation. **a, b** Tools for isolation: Alcohol lamp, extra fine forceps, small glass container, Pasteur pipette with teat and syringe. **c** Spore suspensions (shiny drops) on agar in the centre of squares marked on the base of MEA plates. **d** Small colonies on MEA plates. **e** Fungal colonies of about 0.5 cm in diameter. Note that at this stage it is possible to establish if they are similar and represent the same species. **f** Pure culture of *Leptoxyphium* sp

Although the herbarium material for sooty moulds is essential for publication purposes, they have limited scientific value as it is hard to obtain sequence data from a herbarium specimen and the specimen may contain a complex of species. A dried culture and more importantly a living culture is therefore extremely important as material for complementary work.

Environmental scanning electron microscopy (ESEM)

The local microenvironment may play a critical role for sooty moulds. Unfortunately little research has been undertaken to evaluate the importance of the microenvironmental conditions for these mixed species communities. Traditional and molecular methods usually homogenise samples, which separate the

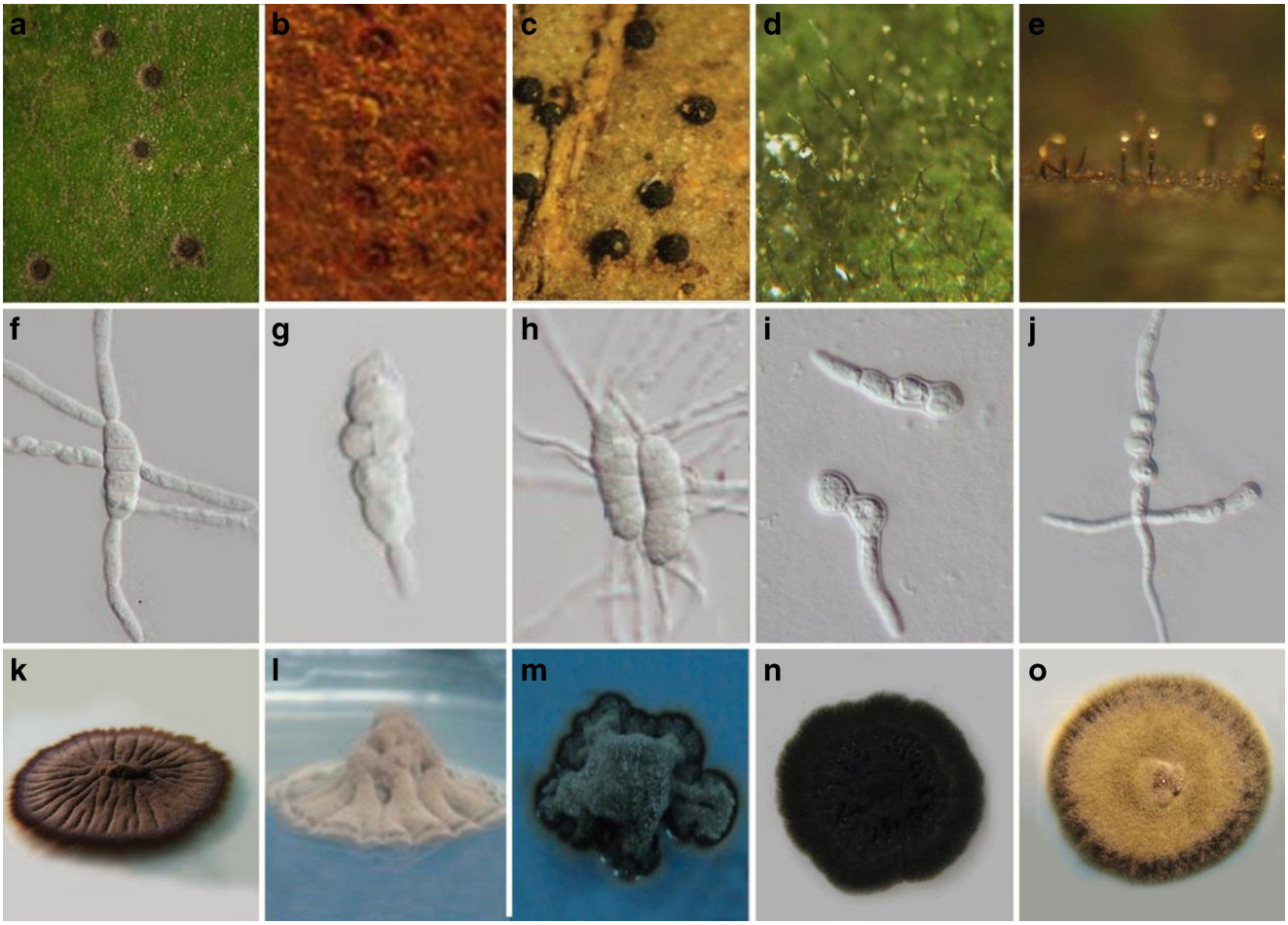

Fig. 3 Macro- and microscopic features of different species of sooty moulds (**a**, **f**, **k** *Ceramothyrium* sp., **b**, **g**, **l** *Chaetothyrium brischofiacola*, **c**, **h**, **m** *Phaeosaccardinula ficus*, **d**, **i**, **n** *Leptoxyphium* sp., **e**, **j**, **o** *Phragmocapnias* sp.) **a-c** Ascomata superficial on host. **d-e** Pycnidia superficial on host. **f-h** Germinating ascospores. **i**, **j** Germinating conidia. **k-o** Colonies of sooty moulds on MEA after 4 weeks incubation at 27 °C in the dark

organisms from its microcosm, while culturing and single spore isolation selects individual species. These techniques have merits in the kind of information they provide, but remove the species from the context of its environmental existence.

The visual study of fungi by light microscopy provides more information, as multiple species may be observed simultaneously. The process of sample preparation, such as mounting and separating tissues, however, usually disturbs the natural occurrence and relationships of the fungi. Developments in the field of scanning electron microscopy now allow observation of microbial communities in a near-original state (Collins et al. 1993). Fragile environments such as bacterial biofilms (Priester et al. 2007) and mycorrhizospheres (Nurmiaho-Lassila et al. 1997) have been visualised and photographed without destructive processing, which may disrupt the organisms natural state. Environmental scanning electron microscopy (ESEM) requires little in terms of sample preparation and allows magnification up to 12,000 times, providing extensive detail on form and structure of organisms of interest. Fungal hyphae can be viewed in their natural state, as dehydration is not essential.

In the case of New Zealand sooty moulds, this technique has provided deep insights into their communities (Figs. 4, 5, 6, 7, and 8). The intertwining hyphae of several different morphotypes are immediately apparent, revealing an intimate relationship between different fungi (Figs. 5 and 6). The three dimensional structural detailing of spores and spore-cups lends a novel perspective to the physical aspects of these fungi (Fig. 6). This micro-community level of visual detail can be compared to that of a bacterial biofilm. Whether this translates into functional inter-dependency is another question, since such a communal view of sooty moulds has been largely speculative in the past. Identification of the functional roles of the fungal morphotypes observed via ESEM may help to reach a realistic understanding of the community ecology of sooty moulds (Figs. 4, 5, 6, 7, and 8).

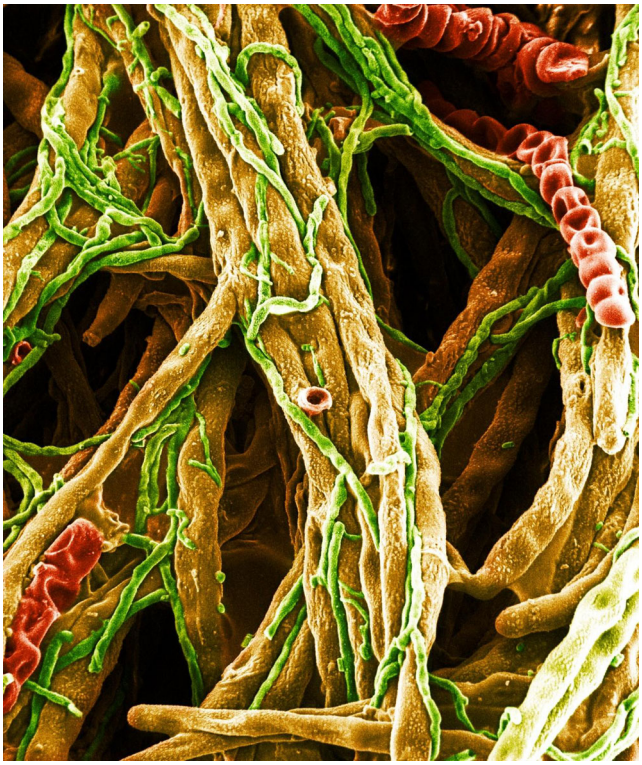

Fig. 4 Section from sooty mould community on leaf of black beech (*Nothofagus solandri* var. *solandri*) infested with the scale insect *Ultracoelostoma brittini* at Mt Richardson, New Zealand. Several morphotypes are immediately apparent, some with smooth other with coarse hyphae. Some fruiting structures can also be seen (*in red*). The image was taken on a FEI Quanta Environmental Scanning Electron Microscope (ESEM) and artificially coloured according to morphology. Magnification 800×. Adapted from Dhami et al. (2013)

Fig. 5 Section from sooty mould community on branch of black beech (*Nothofagus solandri* var. *solandri*) infested with the scale insect *Ultracoelostoma brittini* at Mt Richardson, New Zealand. A cluster of fruiting structures is visible in the center (*red*) and surrounded by fungal hyphae. The image was taken on a FEI Quanta ESEM and artificially coloured according to morphology. Magnification 200×. Adapted from Dhami et al. (2013)

Next generation sequencing

Next generation sequencing (NGS) techniques, such as 454-pyrosequencing and Illumina®, have revolutionised the field of molecular phylogenetics in the past few years, removing barriers that have previously impeded the study of complex communities. This parallel sequencing of multiple targets in (meta) genomic DNA extracts, has been successfully applied for fungal community analyses of phyllosphere samples (for review see Rastogi et al. 2013), but only once to sooty mould communities (Dhami et al. 2013). NGS technology has also reduced the cost of whole genome sequencing, although eukaryotic organisms still prove challenging (Schmutz 2013). In the case of fungi, advances in genome sequencing have been made, but are limited so far to culturable species (DiGuistini et al. 2009). In future, environmental fungi, such as sooty moulds could greatly benefit from the application of NGS aided genome sequencing.

The major difference of NGS to other molecular technologies is that taxa or Operational Taxonomic Units (OTUs) are no longer separated prior to sequencing by cultivation or subcloning of PCR products (mostly Intergenic Transcribed Spacer region ribosomal RNA or ITS rRNA gene amplicons), but the molecules of interest are only separated in the sequencing process itself (for reviews see Lindahl et al. 2013; Mardis 2013). Such NGS analyses may then yield thousands to billions of sequences from a single DNA extraction (Ratan et al. 2013). At first sight, it may seem questionable if NGS approaches are suitable for the analyses of sooty mould communities, which are composed of a limited number of taxa. However, it is possible to label hundreds of samples differentially during PCR and analyze

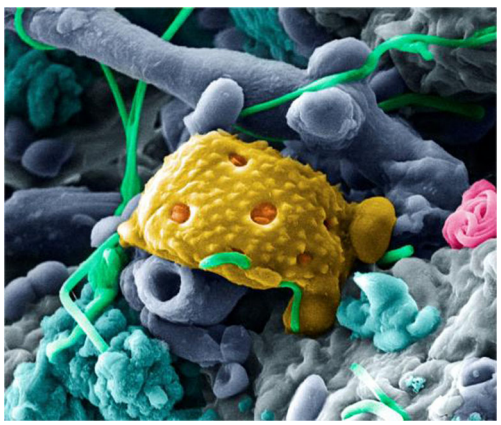

Fig. 6 Section from sooty mould community on kānuka (*Kunzea ericoides*) branch infested with scale insect *Coelostomidia wairoensis*. A solitary fruiting structure surrounded by morphologically diverse fungal hyphae is visible. Image is artificially coloured according to morphology. Magnification 8,000×, using FEI Quanta environmental scanning electron microscope. Adapted from Dhami et al. (2013)

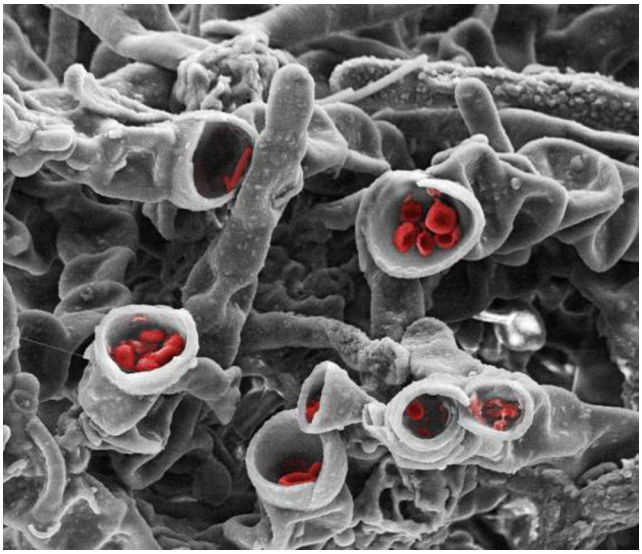

Fig. 7 Section from sooty mould community on kānuka (*Kunzea ericoides*) branch infested with scale insect *Coelostomidia wairoensis*. Fruiting structures with possible spores (in *red*) surrounded by morphologically diverse fungal hyphae. Spores are artificially coloured. Magnification 3,000× using FEI Quanta environmental scanning electron microscope. Adapted from Dhami et al. (2013)

them simultaneously in a single sequencing run (e.g., Peršoh 2013). Such analyses are by far more cost-efficient and less laborious than multiple individual analyses of single targets by Sanger sequencing. Furthermore, the first NGS analysis of sooty mould communities indicated a much higher species richness in sooty mould communities than previously thought, i.e. >200 OTUs in a single sample

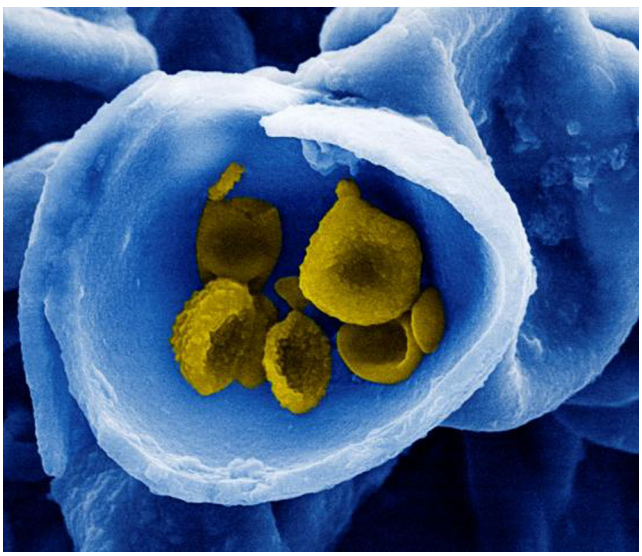

Fig. 8 Single mature fruiting structure with up to six possible spores visible. Environmental scanning electron micrograph of sooty moulds from kānuka (*Kunzea ericoides*) branch infested with scale insect *Coelostomidia wairoensis*. Image was artificially coloured. Magnification 12,000× using FEI Quanta environmental scanning electron microscope. Adapted from Dhami et al. (2013)

(Dhami et al. 2013). However, authentic reference data are only available for relatively few genera or species of Ascomycota, i.e. few reference strains have been accurately named or provided with detailed modern morphological treatments. Thus, very few environmental sequences can be accurately named to species or genus level.

Fungi-specific NGS has relied heavily on the variability of the ITS region across taxa owing to its inter-intraspecific barcode gap (Nilsson et al. 2009; Schoch et al. 2012). There are examples where this insufficiently represents true phylogeny (Lindner and Banik 2011), but for majority of diversity analyses the ITS region has been used reliably. There have been limited investigations for other gene markers (Seifert et al. 2007; Chen et al. 2010), but so far none share the same widespread usage as the ITS. Usage of the ITS region in NGS however, comes with limitations. The length variability of ITS across taxa makes it not only difficult to align, but can also profoundly impact on the inferred phylogeny (Min and Hickey 2007). Caution must be applied, as it is possible to obtain meaningless phylogenies biased by length polymorphism of the ITS. Nevertheless, these data may provide accurate taxon identification with the use of current tools (Porter and Golding 2011), given that a suitable taxonomy informed reference database is available. The UNITE database, with over 350,000 ITS sequences, in conjunction with the analysis workbench PlutoF (Abarenkov et al. 2010), are tailored specifically for fungal NGS analysis. An understanding of the biases and methods to refine NGS data are essential to remove errors inherent to this technology. Standardised guidelines are now available and should inform NGS data analysis (Nilsson et al. 2011), especially for environmental fungi such as sooty moulds, as it is crucial to separate novel diversity from erroneous sequences with confidence.

A vast proportion of fungal diversity resides in the environmental sources such as soil, water, air or dust. Despite this, roughly 8 % of the sequences in the UNITE database originate from these environments. Most other sequences are either mycorrhizae or associated with plants (diseases), animals or other specialist hosts. Taxonomic identification of environmental fungi and their genetic characterisation must therefore complement each other for this revolutionary technology to realise its full potential. However, due to the erroneous nature of many sequences in GenBank (Cai et al. 2009), and as relatively few named Ascomycota, with sequence data in GenBank have been morphologically characterized, this has become a major challenge for mycologists.

Phylogeny of sooty moulds

The sooty moulds presently comprise seven families and several orphaned genera of ascomycota. These include *Antennulariellaceae*, *Capnodiaceae*, *Euantennariaceae* and

Metacapnodiaceae of Class Dothideomycetes, and *Chaetothyriaceae*, *Coccodiniaceae* and *Trichomeriaceae* of Class Eurotiomycetes. Chomnunti et al. (2011, 2012a, b) studied the systematics of sooty moulds in Thailand, based on morphological characters using sequences from type species as references and molecular analysis of DNA sequence data. They found tropical sooty moulds belong to *Capnodiaceae*, *Chaetothyriaceae* and *Trichomeriaceae*. However, this was the first comprehensive study of this group of fungi in a tropical country, and further study is clearly needed. In northern Thailand most of the sooty mould infections are caused by *Capnodiaceae*.

For this review, large subunit ribosomal RNA (LSU rRNA) gene sequences from 46 isolates from sooty mould taxa belonging to the families *Antennulariellaceae*, *Capnodiaceae*, *Chaetothyriaceae*, *Euantennariaceae* and *Trichomeriaceae* were downloaded from GenBank and aligned using MAFFT version 7 (Katoh et al. 2009) with a further 47 isolates (Supplementary Table 1). The alignment was optimized manually to allow maximum alignment and maximum sequence similarity using Bioedit (Hall 1999) and Clustal X 2.0.11 (Thompson et al. 1997). A maximum likelihood analysis was performed with RAxML (Stamatakis et al. 2005; 2008) RAxMLGUI v.0.9b2 interface (Silvestro and Michalak 2012). The search was subjected to rapid bootstrapping and likelihood scores were estimated under the GTR + G substitution model. The number of replicates was automatically inferred using the stopping criterion (Pattengale et al. 2009). In addition Bayesian analyses were carried out with MrBayes v. 3.0b4 (Huelsenbeck and Ronquist 2001) as described in Hongsanan et al. (2014). *Sordaria fimicola* was used as outgroup taxon in all phylogenetic analyses. Trees were visualised in Treeview v. 1.6.6 (Page 2001) and edited with Powerpoint. The maximum likelihood tree is presented in Fig. 9, with bootstrap values (>50) and Bayesian posterior probabilities (>0.9).

In the resulting tree, family *Capnodiaceae* comprised 26 strains which clustered with 100 % ML bootstrap support and 100 % posterior probability (PP) and is placed within *Capnodiales* under Dothideomycetes (Hyde et al. 2013). Other families in *Capnodiales* include *Dissoconiaceae*, *Euantennariaceae*, *Mycosphaerellaceae* and *Piedraiaceae*. The two representatives of *Myriangiales* form the sister group to *Capnodiales*. Species of the genus *Capnodium* cluster with species of *Conidioxyphium*, *Microxyphium* and *Polychaeton* (100 % ML bootstrap support and 100 % PP) with two species (four strains) of *Scorias* being basal. The *Capnodiaceae* clade includes one sequence of *Antennulariellaceae*, *Antennariella placitae*, which has a close relationship with *Microxyphium theae*. However, morphologically, *A. placitae* is distinct from members of the clade, so future studies are needed to clarify its placement.

Trichomeriaceae and *Chaetothyriaceae* cluster together with *Herpotrichiellaceae* in the *Chaetothyriales* clade, which is in agreement with Chomnunti et al. (2011). The *Trichomeriaceae* clade includes three species (six strains) of *Trichomerium* and four not further identified strains of *Chaetothyriales*. The *Chaetothyriaceae* clade includes two species (five strains) of the genus *Ceramothyrium* with 86 % ML bootstrap support and 100 % PP, and is related to *Vonarxia vagans* and *Phaeosaccardinula ficus* with 92 % ML bootstrap support and 100 % PP. *Chaetothyriales* sp. strain TRN436 is also placed in *Chaetothyriaceae*.

The phylogenetic tree includes no representatives from *Coccodiniaceae*, as no LSU rRNA sequences are as yet available in the international databases. While the *Coccodiniaceae* are represented by a single ITS sequence. *Metacapnodiaceae*, as recently discussed by Hughes et al. (2012), have not been sequenced at all. This underlines the paucity of sequence data available for sooty moulds and calls for a concerted effort to obtain sequence data from representative families and genera. In addition, more loci should be sequenced as ITS or Elongation Factor 1 (EF1) do not appear to resolve all species well (Yang et al. 2013).

Sooty mould communities

Temperate versus tropical sooty moulds

The core groups composing sooty mould communities, i.e. the families discussed below, seem to be mostly restricted to tropical, subtropical and Mediterranean climates (cf. Olejnik et al. 1999; Faull et al. 2002). They have only been reported from temperate regions directly adjacent to these zones, i.e. from northern Iran (Byrami et al. 2013) and New Zealand (Hughes 1976). The few studies restricted to strictly temperate climates have reported rather uniform community compositions from central Europe (Friend 1965a, b; Flessa et al. 2012). Sooty moulds seem to be predominantly composed of *Aureobasidium* (*Dothioraceae*) and *Cladosporium* (*Davidiellaceae*) there, sometimes accompanied by *Epicoccum* (*Pleosporaceae*). An exception is *Capnocheirides* (*Capnodiales incertae sedis*), being a sooty mould associated with European *Rhododendron* spp. (Crane and Hughes 1982; Flessa and Rambold 2013).

Cultivation versus direct sequencing

As oligo-species communities, sooty moulds fall, in technical terms, in between single (e.g., fruiting bodies, plant pathogens, and mycorrhizal fungi) and multi-species communities, such as soil inhabiting or endophytic fungi. Because the majority of sooty mould taxa form reproductive structures on the substrate, direct morphological characterization of the

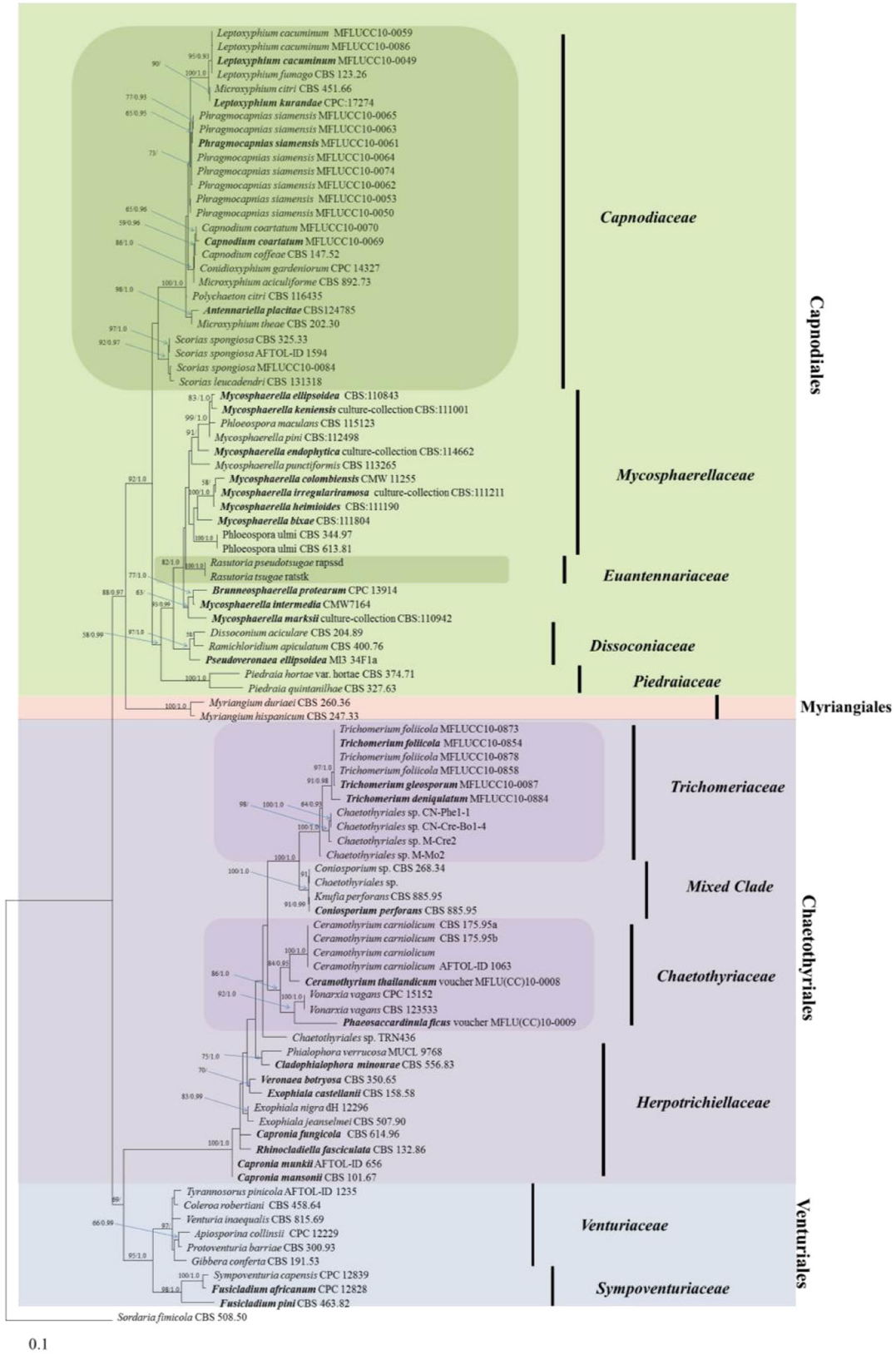

Fig. 9 Phylogenetic relationships among sooty moulds and related taxa. Most likely tree found by Randomized Axelerated Maximum Likelihood (RAxML). RAxML bootstrap support values (BP >50) and Bayesian posterior probabilities (PP >90) are given for the nodes (BP/PP). Type strains are emphasized in bold. Taxon names are followed by culture collection numbers. *Sordaria fimicola* (CBS 508.50) is used as outgroup

communities is technically feasible (e.g., Byrami et al. 2013). However, such analyses are confined to identification of sporulating taxa, because vegetative characters (i.e. hyphal morphology) are insufficient for species delimitation (Faull et al. 2002). Accordingly, cultivation approaches are supposed to result in higher identification rates and also allow for experimental assessment of biological, physiological and ecological traits. The major challenge for cultivation approaches is the isolation of all taxa, to obtain a realistic assessment of the sooty mould community. Since fragment plating will only reveal the fungi growing most quicklest under the (artificial) cultivation conditions, application of high-throughput cultivation techniques, such as dilution-to-extinction-cultivation (Collado et al. 2007; Unterseher and Schnittler 2009), is an ideal additional technique to obtain comprehensive insights into community composition.

Cultivation-independent characterization of fungal communities usually uses the barcoding gene, i.e. the ITS rRNA gene, for taxon delimitation (Schoch et al. 2012). However, ITS sequence data are not suitable for species discrimination in many fungal genera (Wikee et al. 2011; Maharachchikumbura et al. 2011). This seems to apply also for the major families of sooty moulds, which lack sufficient interspecific and/or possess to high intraspecific variability for molecular species delimitation (Yang et al. 2013). Accordingly, the resolution power of Molecular Operational Taxonomic Units (MOTUs) may be limited. However, this may still be sufficient to assess most factors shaping sooty mould community composition, such as geographical location, climatic conditions, and taxonomic affiliation of the host plants and honeydew producing insects. The latter may be concertedly classified to MOTUs by supplementary analyses of the DNA-extracts targeting barcoding genes of plants and insects.

Assignment of the MOTUs to taxa will remain a major challenge, as molecular assessments of sooty mould communities revealed an enormously high proportion of unidentifiable MOTUs, indicating a considerable deficiency of reference data (Dhami et al. 2013). The fact that this also applies for New Zealand, where sooty mould are certainly best studied due to the work of S. J. Hughes indicates that even though individual sooty mould communities are composed of a limited number of species, the overall species diversity of sooty moulds is extremely high. Accordingly, it may be feasible to use molecular methods to assess distribution patterns first on a MOTU-basis, followed by targeted isolation of species for identification and physiological characterization, or vice versa.

While qualitative assessment of even the most complex microbial communities with molecular methods is nowadays routinely applied (e.g., Soon et al. 2013; Rastogi et al. 2013), quantification of the taxa involved remains a major challenge (Raidl et al. 2005; Tellenbach et al. 2010). Such data are, in particular, important for sooty mould communities which differ only quantitatively, but not qualitatively (Flessa et al. 2012). A comprehensive study on the applicability of different markers to estimate fungal biomass revealed that comparability of estimates derived from ITS copy numbers, ergosterol and different phospholipid fatty acids content is rather limited (Baldrian et al. 2013). Technical reasons for the inconsistent results regarding ITS copy numbers are manifold, including the variability of ITS copy numbers among fungal genomes and sequence variation at the primer binding sites and within the ITS region in general (cf. Amend et al. 2010). Furthermore, it has been argued that fungal activity, rather than fungal biomass, is most relevant for certain aspects of fungal community analyses (Peršoh 2013). For sooty moulds it seems of particular importance to establish whether the MOTU's identified are active in the community or just single spores which have happened to fall there.

To solve these problems, i.e. to establish the required conversion parameters, sooty moulds actually possess some traits, which would qualify them as model communities. They may be sampled without compromising integrity, they are composed of manageable species diversity, and they are directly observable microscopically. This allows for the combination of genomic and transcriptomic analyses with morphological and cultivation based assessments. Furthermore, fluorescence-in-situ-hybridisation (FISH) is applicable to differentiate between morphologically unidentifiable hyphae (Nakada et al. 2013).

Families of sooty moulds

Capnodiales

The order *Capnodiales* includes the sooty mould families *Antennulariellaceae*, *Capnodiaceae*, *Euantennariaceae* and *Metacapnodiaceae*.

Antennulariellaceae Woron.

This is a poorly known family of sooty moulds which was described by Woronichin (1925) in *Capnodiales*, and currently includes up to six genera with 27 species (Kirk et al. 2008). Lumbsch and Huhndorf (2010), however, listed only two genera and Hyde et al. (2013) listed three genera (Table 1). Species in the family have a widespread distribution, and are found in warm temperate to tropical regions, where they grow as black sooty moulds on plants (Cannon and Kirk 2007). Woronichin (1925) mentioned that *Antennulariellaceae*, based on *Antennulariella*, was one of the families that represented *Capnodiales* best, because the species have, along with *Capnodiaceae* and *Coccodiniaceae*, ostiolate ascomata. This was later also mentioned by Hughes (1976). *Antennulariellaceae* differ from *Coccodiniaceae* in having completely closed ascomata and irregular hyphae in the sexual and conidial

states (Woronichin 1925). *Achaetobotrys* (Fig. 10) is a genus with two species that was added to this family by Woronichin (1926). The asexual states of *Antennulariaceae* have been described as pycnidial in *Antennariella* Bat. & Cif. Conidia are small and dark brown, subglobose to obovoid, and produced intercalary or terminally on a short stalks. Pycnidia possess a short neck and ostioles at maturity and the pycnidial wall is pseudoparenchymatous, smooth or roughened (Hughes 1976). *Capnodendron*, again, is hyphomycetous, producing somewhat lateral conidiophores (Hughes 2000). Hughes (2003) included a further hyphomycetous sooty mould genus, *Capnofrasera*, in *Antennulariellaceae*. This

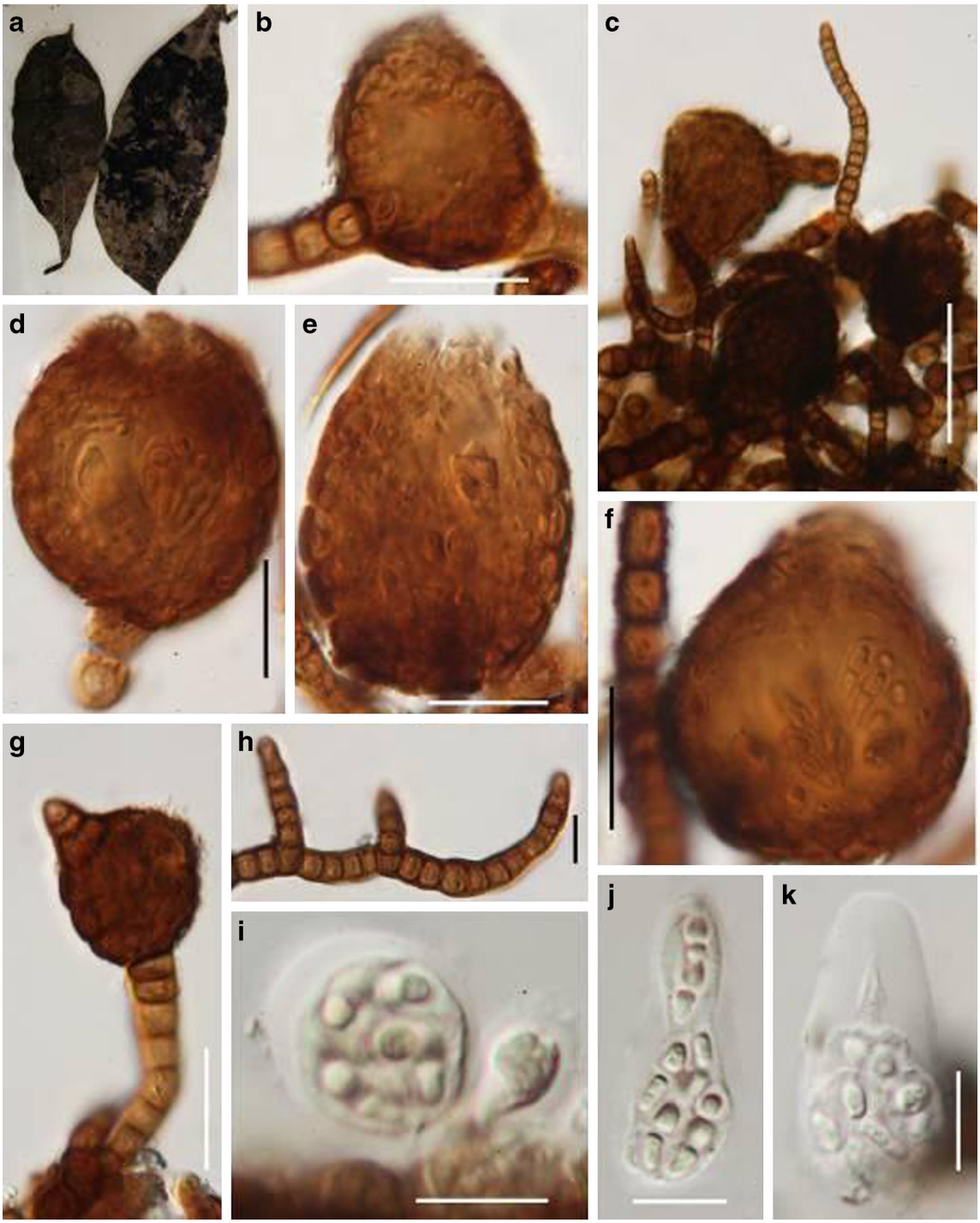

Fig. 10 *Achaetobotrys affinis* (Material examined: Australia, New South Wales, Mitchell River District, between Grafton and Glen Innes, on living leaf of *Rhodosphaeria rhodanthema*, January 1935. L. Fraser, isotype). **a** Sooty mould on host. **b–f** Ascomata. **g** Ascomata developing from repeated divisions of hyphae. **h** Septate hyphae. **i–k** Asci with ascospores. *Bars*: c=50 μm, b, d–g=20 μm, h–k=10 μm

genus is known from Brazil, Canada, Chile, New Zealand, Venezuela and the USA. Hughes and Crane (2006) re-examined *Torula glutinosa* from sooty moulds on leaves and stems of *Eriodictyon* spp. in California and transferred the species to *Hetoroconium glutinosum* (Cooke & Harkness) S. Hughes & J.L. Crane. *Antennulariella concinnata* (Fraser) Hughes (1976) was neotypified, illustrated and described by Hughes (2007) with a *Heteroconium* synanamorph . Few sequences for *Antennulariaceae* are available in GenBank, comprising two LSU and ITS sequences of *Antennariella placitae* (Cheewangkoon et al. 2009) and one small subunit ribosomal RNA (SSU rRNA) sequence of *Antennariella californica* (Reynolds 1998). Molecular data is therefore required to establish the ordinal placement of this family, and relationships between the sexual and asexual states of its various possible asexual genera.

Capnodiaceae Höhn. ex Theiss.

This family is probably the most specioise and common family of sooty moulds. Kirk et al. (2008) stated that it includes 26 genera and 117 species, although Lumbsch and Huhndorf (2010) accepted only 13 genera. The family name was introduced by Höhnel (1910) and validated by Theissen (1916). von Arx and Müller (1975) and Hughes (1976) circumscribed the family on the basis of ecological characters.

The first major monographic review of capnodiaceous sooty moulds was by Fraser (1935) who based it on sexual and asexual species, and placed the species in the *Eucapnodiaceae*. Afterwards Batista and Ciferri (1963a) monographed the *Capnodiaceae* as *Capnodiales*. Hughes (1976) reviewed and re-classified *Capnodiaceae*, characterizing the species by the structure of the hyphae, the presence or absence of paraphyses and by deviating conidial states. Crous et al. (Crous et al. 2009a, b) used molecular methods to classify the members of the *Capnodiales* and included three genera of *Capnodiaceae* in their study. They concluded that the order probably contained diverse lineages, and some of these might merit a new family, but more sequence data was needed to support this. Chomnunti et al. (2011) used a RAxML maximum likelihood tree based on combined LSU and SSU rRNA genes to show that *Capnodium*, *Leptoxyphium*, *Phragmocapnias* and *Scorias* are well-defined genera in *Capnodiaceae*.

Chomnunti et al. (2011) moved many genera from *Capnodiaceae* to other families based on morphological characters of type specimens, thus only five genera are now accepted in *Capnodiaceae* (Table 1). Species in the family have a widespread distribution, especially in tropical and subtropical regions worldwide. For example, *Capnodium* species are the most commonly found sooty moulds in gardens and landscapes (Laemmlen 2011). The taxa of this family can be recognized by their superficial black mycelia with septate, cylindrical, dark-brown hyphae (Fig. 11). They form bitunicate asci. The asexual stages form elongated pycnidia. Pycnidia have short or long narrow necks with a conspicuous oval swelling. Near the base, middle or apex of the pycnidia, minute, unicellular and hyaline conidia are produced (Chomnunti et al. 2011).

Euantennariaceae S. Hughes & Corlett ex S. Hughes

This family was introduced by Hughes (1972) and comprises nine genera and 28 species according to Kirk et al. (2008). Hyde et al. (2013) accepted four genera (Table 1). Taxa in this family are recognized by superficial, brown, cylindrical mycelium, consisting of septate hyphae with smooth to coarsely roughened walls, lightly constricted at septa (Hughes 1972). The ascostromata are subglobose, darkly pigmented with thick walls, and ostiolate at maturity. They bear cylindrical hyphal appendages (Figs. 12 and 13). Asci are bitunicate, usually 8-spored, and ellipsoid. Ascospores are pale brown to dark brown, ellipsoid to broadly ellipsoid, and 3- to multiseptate (Figs. 12 and 13).

The asexual state has two forms of conidia in *Euantennariaceae*, and sometimes both asexual morphs are formed by species of *Euantennaria* (Figs. 12 and 13). *Strigopodia* (Fig. 14) is similar to *Euantennaria* and molecular data are needed to test possible conspecificity. Ameroconidia are also found in *Hormisciomyces* within conidiophores having terminal whorls of globose phialides, whereas phragmoconidial synanamorphs are found in *Antennatula*, *Capnokyma* and *Trichothallus*. *Capnokyma* is recognized by its erect setae-like conidiophores, while discrete conidiophores are not formed by *Antennatula*. The phragmoconidia are blastic and sessile, subhyaline to dark brown, 3- to multiseptate, ellipsoidal to subcylindrical, tapered towards the end, and straight or curved (Eriksson 1981; Hughes 1976; Hughes and Seifert 2012). Seifert and Hughes (2000) introduced *Spiropes dictyosporus* (hyphomycete) from the North Island of New Zealand. The taxon was associated with with *Euantennaria mucronata* and *Capnodyma coricola* in sooty mould colonies. Hughes (2002) also introduced *Capnokyma rossmanae* as a new species from Cerro de la Neblina, Venezuela. It shows the typical morphology of unbranched conidiophores, but smaller conidia with less septa when compared to the type species *C. coricale*.

Metacapnodiaceae S. Hughes & Corlett

This family was introduced by Hughes (1972) and includes six genera and 19 species (Kirk et al. 2008). It is represented by *Metacapnodium* and species are widespread in tropical regions (Kirk et al. 2008, Table 1). The superficial mycelium forms a spongy subiculum. Hyphae are brown to dark brown, moniliform, i.e. constricted at the septa, and branched, with terminal cells usually tapering towards the apex (Fig. 15, and Hughes and Seifert 2012). Ascomata are immersed in a subiculum, broadly ellipsoidal or globose, surrounded by appendages and the peridium cells appear to be composed of a *textura angularis* (Fig. 15). *Asci* are 8-spored, bitunicate,

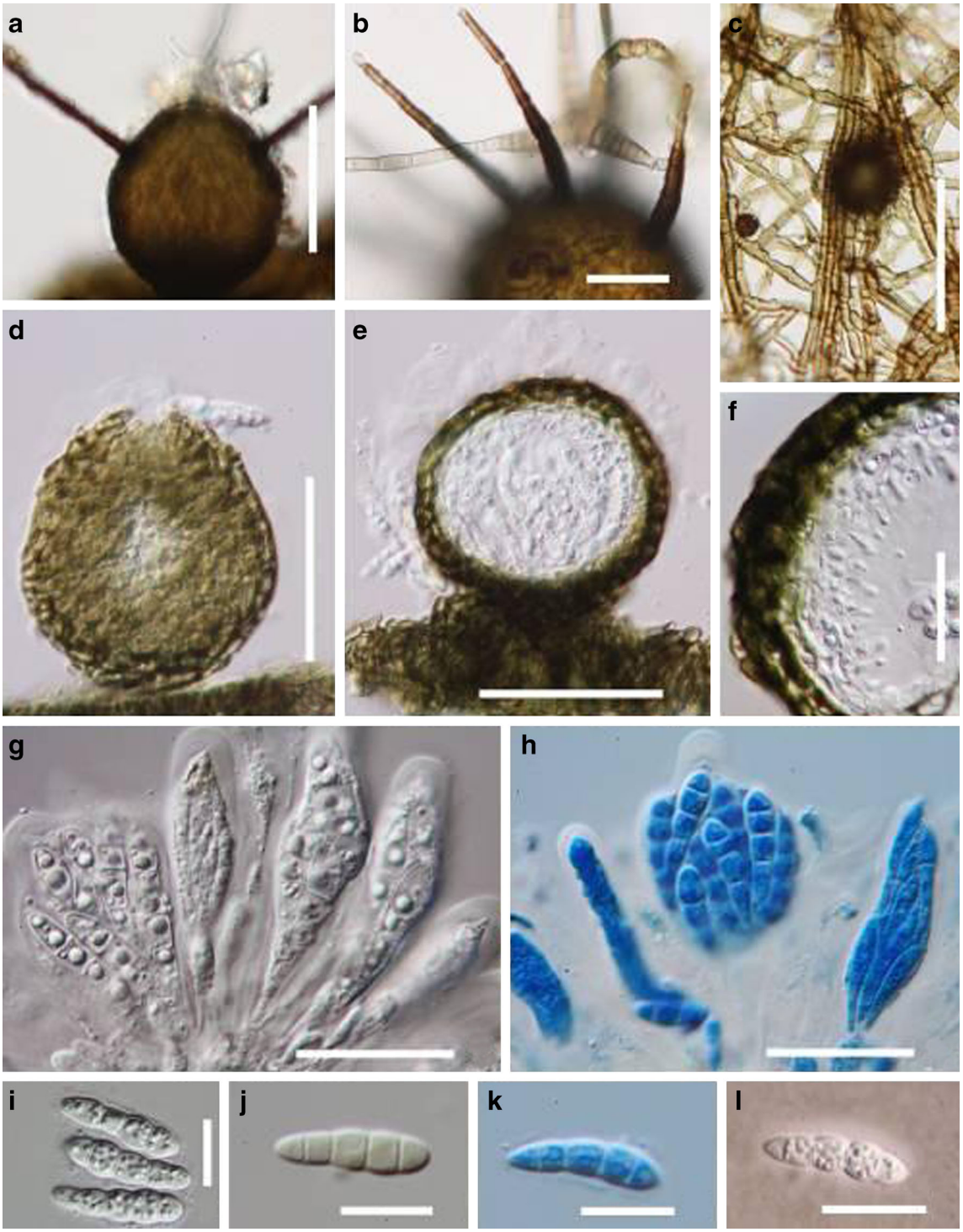

Fig. 11 *Phragmocapnias betle* (Material examined: THAILAND, Chiang Rai, on living leaf of *Sapotaceae*, 27 December 2011, Saowanee Wikee, MFLU11-1155). **a, d** Superficial ascomata on host. **b** Setae. **c** Hyphae. **e** Vertical section through ascoma. **i** Peridium. **g** Asci. **h** Asci stained in Cotton blue reagent. **i** Ascospores. **j** Ascospore stained in Melzer's reagent. **k** Ascospore stained with cotton blue reagent. **l** Ascospore in Indian ink. *Bars*: a, c–f=50 μm, b, g, h=20 μm, i–l=10 μm

ellipsoidal and have a pedicel. Ascospores are ellipsoidal with somewhat conical end cells, trans-septate, thick-walled, brown to dark brown, and darker at the septa (Fig. 15, and Hyde et al. 2013).

Metacapnodiaceae have hyphomycetous conidial asexual states, which distinguishes it from *Capnodiaceae* (Hughes 1972). They can produce several synanamorphs, all forming a thick, brown to black, dense subicula arranged in a

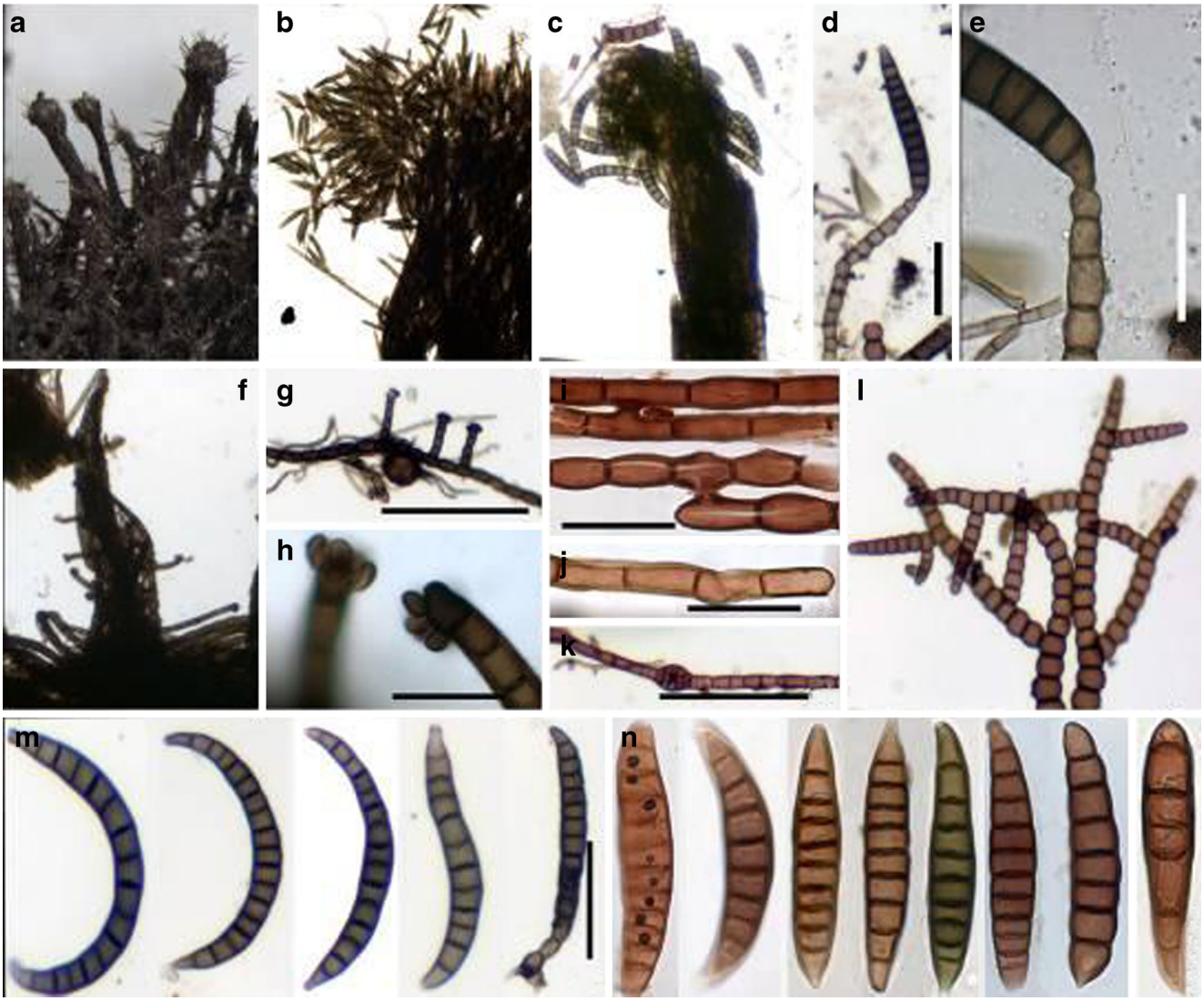

Fig. 12 *Euantennaria mucronata* (Material examined: NEW ZEALAND, Canterbury, on *Nothofagus solandri* var. *cliffortioides*, 14 May 1963, S.J. Hughes, PDD 21317a). **a** Synnemata. **b, c** Synnema with head of conidia. **d, e** Hyphae from teased, mature synnema with conidia. **f, h** Conidiophores. **i** Anastomosed hyphae. **j** Hyphal appendages on ascostromata. **k, l** Septate hyphal. **m, n** Conidia. *Bars*: e, h–j=20 μm, k, m, n=50 μm, g=200 μm

pseudoparenchymatous cushion. Asexual states have been reported in *Capnophialophora*, *Capnocybe*, *Capnosporium*, *Hormiokrypsis* and *Hyphosoma*. All *Metacapnodiaceae* species share a *Capnophialophora* asexual state, which is characterised by plump, ampulliform phialides, developing on the narrowing parts of the moniloid conidiophores, producing small ameroconidia. *Hormiokrypsis* has solitary dry stauroconidia, *Capnocybe* has slimy heads of phragmoconidia, and *Capnosporium* has solitary, dry phragmoconidia, which produce phialides and microconidia (Batista and Nascimento 1957; Hughes 1966; Hughes and Seifert 2012; Hyde et al. 2013). However, as more than one sooty mould species will grow on a leaf, the relationships of these asexual states with *Metacapnodium* needs molecular confirmation or detailed culture studies (Chomnunti et al. 2011; Hughes and Seifert 2012).

Chaetothyriales

The order *Chaetothyriales* includes the sooty mould families *Chaetothyriaceae*, *Coccodiniaceae* and *Trichomeriaceae*.

Chaetothyriaceae Hansf. ex M.E. Barr

This family comprises nine genera (Table 1) according to Lumbsch and Huhndorf (2010), while 13 genera and 98 species were reported by Kirk et al. (2008). Chaetothyriaceous species are often confused with capnodiaceous sooty moulds, which are associated with insects and have similar characters on various hosts (Hansford 1946). Studies on *Chaetothyriaceae* have been mainly conducted by C.G Hansford, S.J. Hughes and A.C. Batista and colleagues from 1940 to 1970, and there have been few studies since. The family is poorly circumscribed and most previous work consists of brief descriptions with line drawings

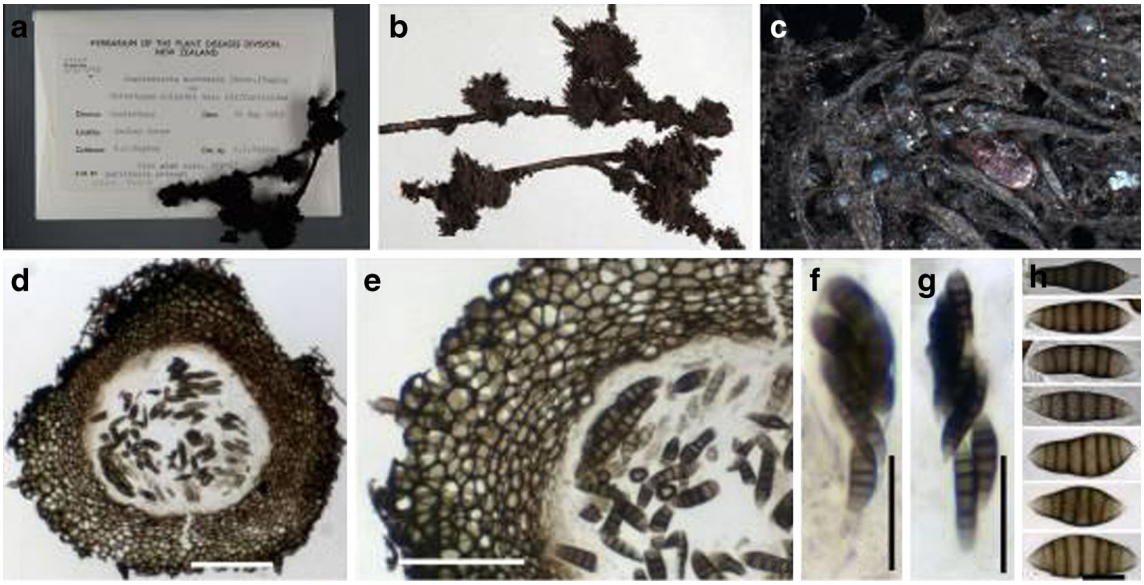

Fig. 13 *Euantennaria mucronata* (Material examined: NEW ZEALAND, Canterbury, on *Nothofagus solandri* var. *cliffortioides*, 14 May 1963, S.J. Hughes, PDD 21317). **a** Type collection packet. **b** Type specimen. **c** Perithecia. **d, e** Vertical section of ascostroma. **f, g** Asci. **h** Ascospores. *Bars*: f–n=20 μm, d, e=100 μm

(Hansford 1946; Batista and Ciferri 1962). The basis for arrangement of genera is hard to follow and perhaps rather subjective, because it is based on the weight the individual authors attached to certain characters, such as spore septation, presence of ascomata setae and mycelium colour (Batista and Ciferri 1962; Hughes 1976).

The genera are characterized by ascomata which form beneath a mycelia pellicle lying on the leaf surface (Fig. 16). The pellicle is attached to the upper part of ascomata, and ascomata are subglobose to globose with or without setae. Asci are bitunicate, clavate or pyriform and short pedicellate. Ascospores are clavate, muriform, hyaline to light brown, and with or without mucilaginous sheath (Fig. 16). *Chaetothyriaceae* are easily discriminated form other sooty moulds on leaf surfaces by the shape of the ascomata (Fig. 16). In *Capnodiaceae* ascomata are single, subglobose to globose, with or without setae, while in *Chaetothyriaceae* they form ascostromata, i.e. the ascomata are surrounded by a pellicle of superficial mycelium, and are often multilocular. In addition, phylogenetic analyses from LSU and ITS sequence data have clearly shown them to be unrelated, placing the families in two separate classes: *Dothideomycetes* and *Eurotiomycetes*, respectively (Schoch et al. 2006, 2009; Geiser et al. 2006; Chomnunti et al. 2012a, b).

Coccodiniaceae Höhn., ex O.E. Erikss.

This family of sooty moulds was described by Eriksson (1981) and currently comprises three genera: the type genus *Coccodinium*, *Dennisiella* and *Limacinula* (Lumbsch and Huhndorf 2010). Kirk et al. (2008) recognized five genera, which include the asexual genera *Bisbyopeltis* and *Microxiphium*, while Hyde et al. (2013) accepted three genera (Table 1). In his re-classification of sooty moulds, Hughes (1976) did not include *Coccodiniaceae*. The family is characterised by limacinuloid ascomata (dark brown collabent ascomata) on living leaves and sometimes other plant parts (Fig. 17). The fungi develop on a scanty or well-developed subiculum or darkened hyphae usually surrounded by a very loose arrangement of hyphae. These appear light to whitish macroscopically, are individually connected, and form a hyphae at the lower portion of the fruit body wall. Ascomata are sessile on a subiculum, globose to subglobose, brownish, uniloculate, thick-walled, and with periphysate ostioles. Asci are bitunicate and 8-spored. Ascospores are irregularly arranged, saccate and stalked. They are ellipsoid or clavate, fusiform, transversely septate or muriform, constricted at septa, hyaline or dark brown. The hyphomycetous asexual states develop on rosettes of phialides, with mycelium forming a thin setose pellicle, of aseptate hyphae, which curve at the tips (Reynolds 1971; Reynolds and Gilbert 2005) as in species of *Microxyphium* and *Bisbyopeltis*.

Winka et al. (1998) studied the morphology of *Coccodiniaceae* and found the asexual state to be reminiscent of a *Capnodendron* species, which is a conidial state of sooty moulds in the family *Antennulariellaceae*. However, molecular data to test the phylogenetic relationship between *Coccodiniaceae* and *Antennulariellaceae* are missing. While *Microxyphium* has been linked to *Dennisiella* in *Coccodiniaceae* (Schoch et al. 2006; Crous et al. 2007; Ruibal et al. 2009), phylogenetic data of Chomnunti et al. (2011) indicate that *Microxyphium citri* is a member of *Capnodiaceae*. Our molecular analysis (Fig. 9) reveals further

Fig. 14 *Strigopodia piceae* (Material examined: USA, Maine, Mt. Desert Island, on *Picea rubra*, 30 June 1929, D.S. Johnson, determined by A.C. Batista (BPI 618549). **a** Voucher label. **b** Ascomata. **c** Hyphae on ascoma. **d** Section of ascoma. **e** Peridium. **f** Pseudoparaphyses. **g-i** Immature and mature asci. **j-l** Immature and mature ascospores. **m-q** Conidia and short conidiogenous cell present, conidiophores absent. *Bars*: b, d=100 μm, c=10 μm, e=50 μm, f=5 μm, g-q=20 μm

Fig. 15 *Metacapnodium spongiosum* (Material examined: SPAIN, W from Jimena de la Frontera close to Las Cañillas, at the road 3331, on bark of *Erica arborea*, 21 March 2011, H. Voglmayr & W. Jaklitsch, MFLU12-0140). **a** Thick woolly black mass of mycelium on *Erica arborea*. **b, c** Section through globose ascoma. **d** Peridium. **e** Hyphae. **f, g** *Capnophialophora* state. **h, j** Ascospores. **k–m** *Capnocybe* state. *Bars*: a=100 μm, c, e=50 μm, f–g=20 μm, i–m=10 μm

Microxiphium species as members of *Capnodiaceae*, indicating that this poorly understood family and its associated genera require further research at the morphological, cultural and molecular level.

Trichomeriaceae Chomnunti & K.D. Hyde

This family was placed by Chomnunti et al. (2012a, b) in *Chaetothyriales* with *Trichomerium* as type of the family (Table 1) and presently contains 23 species (Kirk et al. 2008). The fungi have ascostromata with a thin-walled peridium covered with setae, developing on loosely interwoven mycelial masses of dark brown hyphae. Asci are bitunicate and ascospores are hyaline, fusoid, septate, and, in some species, possess longitudinal septa. Species are similar to those in *Capnodiaceae* and *Chaetothyriaceae* but phylogenetic analysis clearly show that they cluster separate from these families (Chomnunti et al. 2012a, b). *Trichomerium* species can be distinguished from *Capnodiaceae* species by the loose mycelium beneath the ascomata and abundant setae surrounding the ascomata (Fig. 18). Asci are cylindrical to clavate with an apical ring, and ascospores are fusoid with three transverse septa or sometimes with longitudinal septa (Fig. 18).

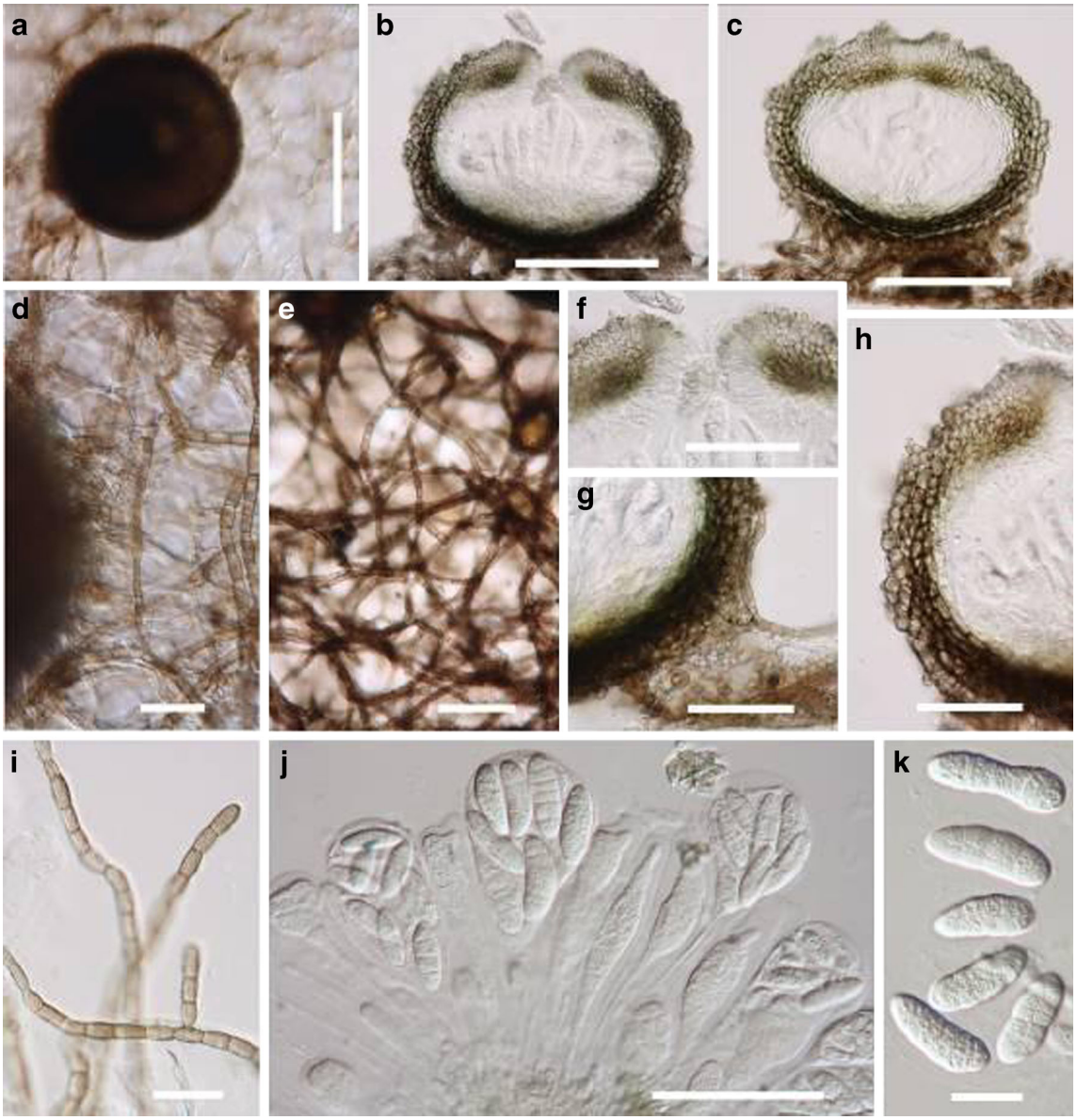

Fig. 16 *Phaeosaccardinula ficus* (Material examined: THAILAND, Chiang Mai, on living leaf of *Ixora* sp., 12 October 2010, Ratchadawan Cheewangkul, MFLU09-0643). **a** Black superficial ascoma on living leaves. **b, c** Vertical section through ascoma with ostiole. **d, e, i** Hyphal network, septate hyphae and possible conidia. **f** Ostiole. **g** Subiculum−like structure of mycelia at the base of the ascoma. **h** Peridium. **j** Obovoid to clavate asci. **k** Muriform ascospores. *Bars*: a–c=100 μm, e=50 μm, d, f–j=20 μm, k=5 μm

Miscellaneous genera of sooty moulds

Many species of sooty moulds are pleomorphic, their colonies on the host often merge and many spore types can be observed in sooty moulds colonies. Therefore it is often difficult to distinguish and to confirm where a spore is formed and to which entity it belongs (Seifert et al. 2011). As a consequence, the status of many sooty mould species and genera is still uncertain. Some Chaetothyriaceae and Coccodiniaceae are called "sooty moulds" but may be biotrophic rather than growing on honey dew. Extraction of DNA directly from sooty mould colonies is one method to establish the presence of species in sooty mould colonies and establish their taxonomic affiliations. Dhami et al. (2013) observed the diversity of sooty moulds associated with scale insects by using scanning electron microscopy in combination with Terminal-Restriction Fragment Length Polymorphism (T-RFLP) and ITS-based tag-pyrosequencing. They provided data on the diversity of sooty mould community, but were unable to distinguish the morphology or metabolic activity of the OTU's. The following genera are miscellaneous genera of sooty moulds. Very little is known about each of these genera and they are in urgent need of further study.

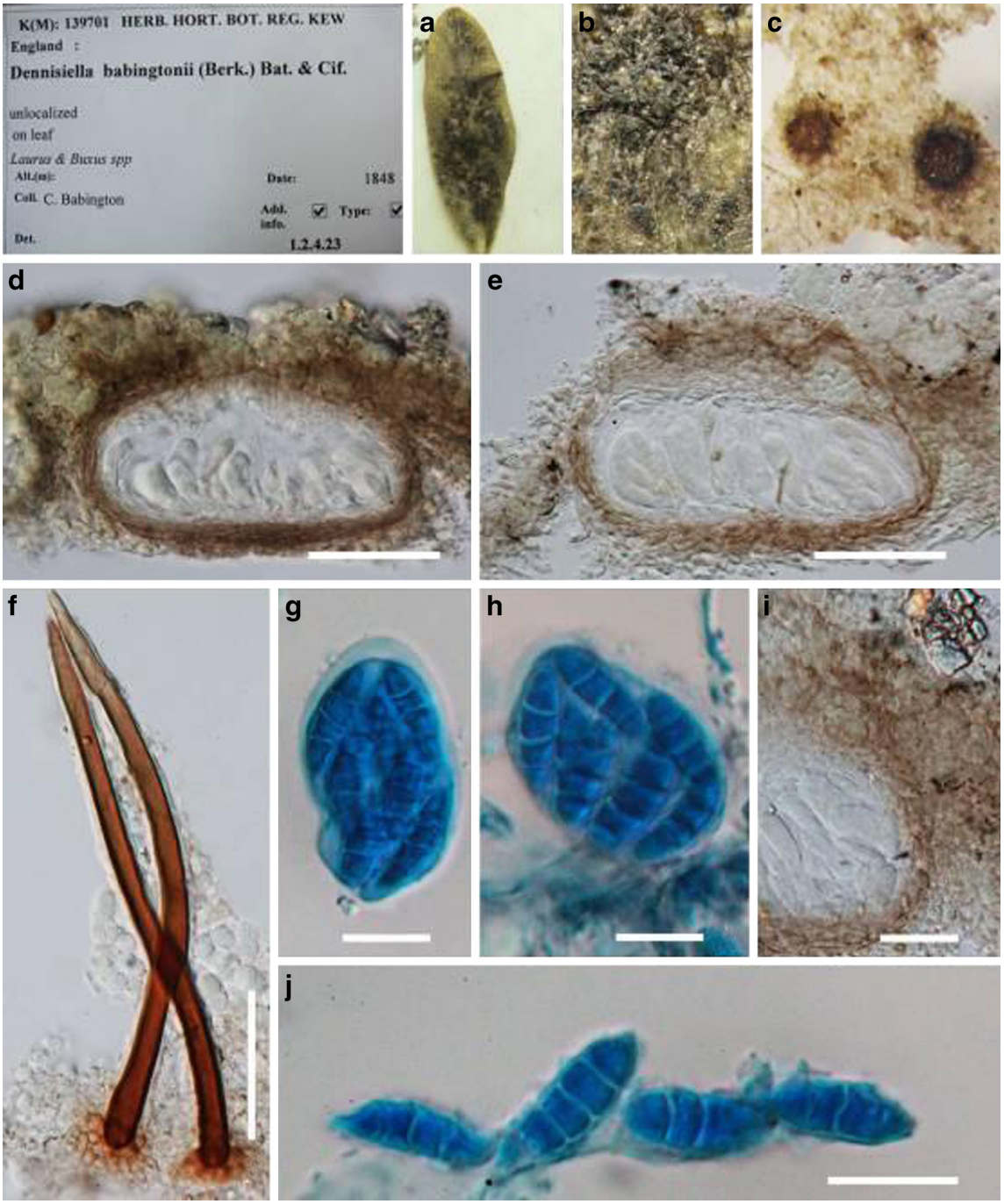

Fig. 17 *Dennisiella babingtonii* (Material examined: UK, unlocalized, on leaves of *Laurus* and *Buxus* spp., 1848, C. Babington, K(M) 139701). **a–c** Ascostromata and setae on host surface. **d, e** Vertical section of ascostromata. **f** Setae. **g, h** Asci stained with cotton blue. **i** Peridium connect with mycelium. **j** Ascospores stained with cotton blue. *Bars*: d–f=50 μm, i=20 μm, g–h, j=10 μm

Asteridiella McAlpine

Type species: ***Asteridiella solani*** McAlpine, Proc. Linn. Soc. N.S.W. 22(1): 38 (1897)

Nieves-Rivera et al. (2002) studied sooty moulds of southwestern Puerto Rico and found flat colonies of *Asteridiella sepulta* (*Meliolaceae*) with a spongy subiculum on the surface of leaves, twigs and small branches of *Avicennia germinana.* The fungus was associated with sugary honeydew from the planthopper *Petrusa marginata* (Homoptera, Flatidae).

Baudoinia J.A. Scott & Unter.

Type species: ***Baudoinia compniacensis*** (Richon) J.A. Scott & Unter., in Scott et al.

≡ *Torula compniacensis* Richon, 3: 17 (1881)

This species causes dark, sooty colonies on twigs worldwide, but also grows on the exterior of buildings as well as on

Fig. 18 *Trichomerium foliicola* (Material examined: THAILAND, Chiang Rai, Baan Du, on living leaf of *Psidium* sp., 20 October 2010, Putarak Chomnunti, MFLU10-0002). **a**. Macroscopic appearance on guava leaves. **b**. Ascostromata with setae **c**, **d**. Vertical section through ascostromata, peridium. **e**. Setae. **f**. Hyphae. **h**, **i**. Asci. **g**. Conidia. **k** = Ascospores. **j** = Spore germination. *Scale bars*: c–d=100 μm, e=50 μm, h, i, f=20 μm, g, j, k=10 μm

interior walls of alcohol maturation houses, which are subjected to large temperature variations, periodic high humidity and wetting (Scott et al. 2007). *Baudoinia compniacensis* can use glucose and ethanol as energy source, and utilize inorganic and organic forms of nitrogen Ewaze et al. (2007). Its morphology resembles other sooty moulds in having dark-brown, septate or uniseptate conidia with coarsely roughened walls that are borne in unbranched chains. Analysis of SSU rRNA

sequences showed the genus to belong to *Capnodiales*. It is interesting that with the exception of honeydew secretions, its preconditions for growth are similar to those of most sooty moulds (Scott et al. 2007)

Capnocheirides J.L. Crane & S. Hughes

Type species: ***Capnocheirides rhododendri*** (Kunze) J.L. Crane & S. Hughes, Mycologia 74(5): 753 (1982)

≡ *Torula rhododendri* Kunze, in Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) 2: 95 (1829)

Capnocheirides is a monotypic European sooty mould genus. The species is host specific on *Rhododendron* and most collections are from alpine regions of Western Europe including Austria, Belgium, France, Germany, Italy, Switzerland and Yugoslavia. The sooty mould produces condensed black hyphae on leaf scales on the lower surface of *Rhododendron ferrugineum* and *R. hirsutum* leaves and occasionally on twigs. The mycelium comprises superficial, branched, dark brown, septate hyphae. Conidiophores are mostly absent. Arthroconidia are multiseptate, sessile or short stalked, thick-walled, brown to dark brown with rough walls (Crane and Hughes 1982). There has been no molecular data generated for this genus.

Helicosingula P.S. van Wyk et al.

Type species: ***Helicosingula leucadendri*** P.S. van Wyk et al., Trans. Br. mycol. Soc. 84(1): 183 (1985)

Helicosingula produces sooty black colonies on the living leaves of *Leucadendron tinctum* in South Africa. The narrow, brown hyphae, penetrate the host cuticle. It's tightly coiled helicosporous conidia arise from globose conidiogenous cells which are produced directly from the vegetative hyphae and remain as cup-shaped cells after conidial secession. Scanning electron micrographs show that the helicospores are coiled in three dimensions, and that the genus might accordingly be related to *Helicorhoidion* (Van Wyk et al. 1985).

Kameshwaromyces Kamal et al.

Type species: ***Kameshwaromyces globosus*** Kamal et al., Mycotaxon 25(1): 248 (1986)

Kameshwaromyces is sooty mould genus reported from *Elephantopus scaber* from India. The species produce a ubiquitous network of anastomosing hyphae on leaves of *Elephantopus scaber* thayt do not invade the host. *Kameshwaronmyces* is characterized by micronematous conidiophores, monoblastic conidiogenous cells, and conidia which arise terminally and laterally on the hyphae. Conidia are globose, thick-walled, brown to dark brown, muriform and multicellular, and appear as shiny, black balls. *Kameshwaronmyces* is similar to *Dictyopolyschema*, but differs in having discrete tretic conidiogenous cells (Kamal and Morgan-Jones 1986).

Microxyphispora Manohar. et al.

This genus was introduced by Manoharachary et al. (2004), with *M. corticola* as the type species. Sooty mould species of *Microxyphispora* are found on dried twigs of *Albizzia odorotissina* in India. They produce cylindrical pycnidia and ostioles with subulate extensions. The pycnidiospores or conidia are broad ellipsoidal, two- to four- celled, pseudoseptate, hyaline, which are covered with a mucilaginous sheath (Manoharachary et al. 2004).

Raizadenia S.L. Srivast., Indian Phytopath. 34(3): 335 (1981)

Type species: ***Raizadenia garhwalensis*** S.L. Srivast., Indian Phytopath. 34(3): 335 (1981)

Raizadenia is a monotypic sooty mould genus found on leaves of *Triticum aestivum* in India. *Raizadenia garhwalensis* is characterized by a mycelium composed of cylindrical cells, which are generally longer than wide. The mycelium is raised and produces synnematous conidiomata with long and narrow conidiogenous cells. The phragmoseptate conidia are produced in a terminal capitulum (Seifert et al. 2011).

Sarcinella Sacc., Michelia 2(no. 6): 31 (1880)

Type species: ***Sarcinella heterospora*** Sacc., Fungi italica autogr. del. 1–4: Tab. 126 (1877)

Hosagoudar and Riju (2011) introduced the new family *Schiffnerulaceae* for the placement of black mildews which are host-specific. They produce black colonies and invade leaves, soft stems and petioles. Hosagoudar and Riju (2011) reported from India 39 species of *Sarcinella*, 10 *Questieriella* spp., a *Mitteriella* sp., and one species of *Digitosarcinella* as synanamorphs of *Schiffnerula*, which is the type of the family. Seifert et al. (2011) include these four genera as hyphomyceteous sooty mould genera and Hyde et al. (2013) synonymized *Schiffnerulaceae* with *Englerulaceae*.

Staurospores

Hyphomycetous staurospores are often found associated with sooty moulds and were placed in *Triposporiopsidaceae* by Hughes and Seifert (2012). Hyphomycetous stauroconidia similar to the Ingoldian fungi are mostly found in freshwater environments (Ando 1992; Descals et al. 1995). Gönczöl and Révay (2006) studied the diversity of rainborne hyphomycete conidia from living trees in forests of Germany, Hungary, Romania and Sweden and found 62 species with stauroconidia, such as *Trifurcospora irregularis*, *Retiarius bovicornutus*, *Titae complexa*, and *Tripospermum camelopardus*. Tubaki (1957) found stauroconidia associated with a large number of hyphomycetous asexual aquatic fungi, such as *Trinacrium* and *Tripospermum*. *Tripospermum porosporiferum* and *T. variablile* were first reported as sooty moulds on longan (*Dimocarpus longan*) in Puerto Rico (Serrato-Díaz et al. 2010). We have found these spores associated with capnodiaceous and chaetothyrialean taxa. Hongsanan et al. (2014) also found the same spores associated with the newly described genus *Chaetothyriothecium* in *Microthyriaceae*. This indicates that these spores may originate

from generalistic epiphyllous fungi, from fungicolous fungi on foliar epiphytes or, less likely, sooty moulds. Their asexual relationship with ascomycetous sooty moulds, however, must be questioned, and molecular data is needed to unravel their phylogenetic relationships.

Other genera

We have examined type specimens of *Cleistosphaera macrostegia*, *Eumela chiococcae*, *Hyalomeliolina guianensis Phaeostigme picea*, *Stomatogene agaves* and *S. yuccae*. These are also reminiscent of sooty moulds in producing copious, brown, superficial hyphae on leaves. However, they also resemble species of *Asterinaceae* and *Meliolaceae* and further studies are needed to establish whether they are biotrophs or associated with honeydew from scale insects. *Podonectria coccicola* was also reported to be associated with scale insects, as were species of *Myrangium*. Whether or not these taxa represent sooty moulds requires further investigation.

Life cycle of sooty moulds

Spores of sooty moulds are usually dispersed by wind or rain splash. It is not known if insects serve as vectors, although one species has been isolated from an insect (Nelson 2008; He et al. 2013). After germination on a honeydew-coated substrate, sooty moulds grow on the surface and turn the substrate surface black (Fig. 1) (Hughes 1976; Reynolds 1999; Nelson 2008).

As the sooty mould colonies develop, they grow across the leaf surface, often fusing with colonies of the same or other species (Fig. 19). Together, these colonies may form biofilms covering entire leaves or even plants (Hughes 1983; Laemmlen 2011). The first reproductive structures to appear are the asexual stages and, as the colonies mature, the sexual states may also develop.

In 3 years of collecting sooty moulds in northern Thailand we assembled more than 100 collections of leaves colonized by sooty moulds, of which 70 % showed only asexual states.

Ecology, distribution and control

Ecology

Occurrence and biodiversity

Sooty moulds can grow under a wide range of environmental conditions, but conducive temperature and moisture are fundamental. They are common in warm to tropical regions and the diversity of species is generally higher in warmer climates (Jouraeva et al. 2006; Nelson 2008; Dhami et al. 2013). In fact, in every visit to a small area of forest, orchard or gardens one will invariably find numerous sooty mould infections. The frequency of sooty moulds appears to be greater after the rainy season as the honeydew may be washed off leaves during heavy rains, while it will persist for long periods during dry periods (Batista and Ciferri 1963a). In general, sooty moulds do not infect the plant tissues and their damage is just cosmetic. However, the numbers of species actively involved in an infection may range from one to many. Perez et al. (2009) found that persistent sooty mould deposits on citrus that have classically been referred to as *Capnodium citri* (and related asexual morphological forms) actually comprise a myriad of fungal species including many saprobes and potential fruit and foliar pathogens of citrus. Mehrotra (1997) report numerous diseases on *Paulownia* in India, including sooty moulds that were present on the upper surface of leaves with *Cladosporium cladosporioides* on the lower surfaces. The sooty mould, *Isariopsis inidica* var. *zizyphi* infects leaves of *Ziziphus mauritiana* in India and causes sooty or black spots (Jamadar et al. 2009). Gong (1993) reported sooty moulds on rattan in China.

Impact on photosynthesis rate

The science of plant pathology treats sooty moulds as plant disease agents because of their negative effects on photosynthesis: they block sunlight from leaf chloroplasts, thus reducing the plants' energy production (Nelson 2008; Laemmlen 2011). Reduction of photosynthesis by sooty moulds results in lower growth rates and thus reduced yields. Sooty mould colonies on pecan foliage were found to reduce the light reaching the leaves by 50 % (Smith and Tedders 1978). Filho & Paiva (2006) reported similar effects of sooty moulds on mahogany (*Seietenia macrophylla*). Santos et al. (2013) showed that sooty moulds on leaves of olive trees (*Olea europaea*) decrease the fluorescence parameters, foliar free gas exchanges, and water content. They concluded that the decrease of light reaching the leaves affects the normal physiological metabolism of the plant (as photosynthesis), with consequences for olive fruit production. When compared to non-infected leaves, sooty mould covered leaves of olive trees showed an increased iron concentration (Fiori 2001). Furthermore, sooty mould colonies on fruits or vegetables reduce their market value due to the unattractive appearence (Stover 1975).

Interactions between predators, herbivores, plants and sooty moulds

There is almost no information on the interactions between plants, honeydew producing insects and sooty moulds or the way sooty moulds can influence phyllosphere communities.

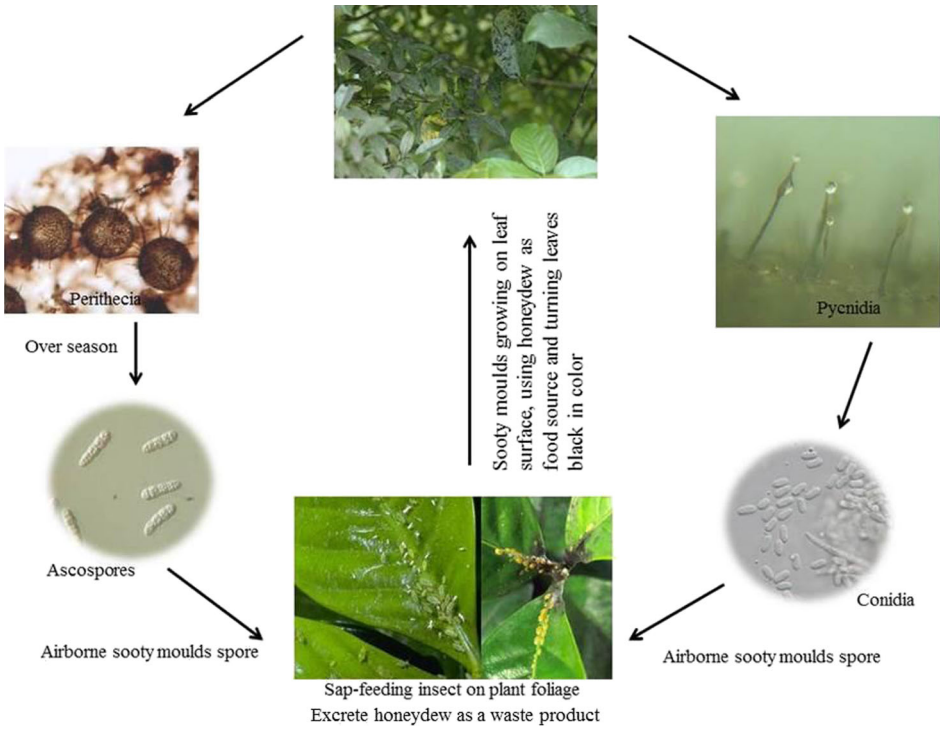

Fig. 19 Generalised life cycle of sooty moulds

Perez et al. (2009) investigated the interactions between a parasitoid, an insect herbivore, and the fungal phyllosphere community. The results suggest that the presence of the parasitoid may lead to a top-down trophic cascade affecting phyllosphere fungal community diversity and structure. Clearly, much more research is needed on these relationships.

Sooty moulds and polycyclic aromatic hydrocarbons (PAHs) and heavy metal accumulation on leaves

The accumulation of fine-particle-associated polycyclic aromatic hydrocarbons (PAHs) and heavy metals on leaves of deciduous trees was investigated by Jouraeva et al. (2006). *Tilia* x *euchlora* which is frequently infected, and *Pyrus calleryana* which is unaffected by sooty moulds have similar leaf morphology and were exposed to identical environmental conditions. Leaves with sooty moulds accumulated significantly higher amounts of PAHs and metals than unaffected leaves. This may be assigned to physico-chemical properties of epicuticular waxes on leaves. The presence of sooty molds on deciduous leaves alters either the accumulation modes and/or degradation pathways of PAHs. Aragao et al. (2012) used energy dispersive X-ray fluorescence to observe the peak areas of chemical elements in healthy and infected samples and scanning electron microscopy (SEM) to study the damage caused by sooty moulds on olive tree leaves. Leaves infected with sooty moulds had a metabolic imbalance with high concentrations of Fe^{2+} and low concentrations of Ca^{2+}. Infected leaves developed a thin layer of glucose (cyclodextrin) on their surface.

New Zealand sooty moulds

In
New Zealand, sooty moulds form characteristic communities in beech forests of the South Island by growing on honeydew on leaves and branches. Several beech species harbour endemic scale insects (family Coelostomidiidae) that produce copious amounts of nutrient-rich honeydew (Beggs et al. 2005; Dhami et al. 2011). These insects remove a substantial amount of nutrients from the trees and make the nutrients available to the insects, birds, mammals and the sooty moulds (Murphy and Kelly 2003; Dungan et al. 2007). Honeydew composition is a key factor for the composition of New Zealand sooty mould communities (Dhami et al. 2013). Sooty moulds grow on the honeydew producing a thick spongy hyphal growth, which provides nutrients as well as shelter to a range of invertebrates (Carlton and Leschen 2007; Leschen et al. 2008). There is evidence of consumption of sooty moulds by stream invertebrates living in beech forests of New Zealand (Smith and Collier 2000; Chadderton et al. 2003). On the other hand, the thick cover of sooty moulds in the honeydew splash zones has been implicated in reducing litter decomposition (Wardhaugh and Didham 2006). This exemplifies a generally overlooked facet of the sooty moulds in a healthy ecosystem where they may play an important role in nutrient cycling and other key ecosystem processes.

Distribution and control

Sooty moulds are found on almost any host, have a wide distribution and occur on both wild and cultivated plants, including greenhouse plants (Zopf 1879). Detection of sooty moulds by infrared imagery was used in glasshouse propagated plants and might be useful in large-scale greenhouse production (Summy and Little 2008). The main factor determining the distribution of sooty moulds are the insects (Batista and Ciferri 1963a). Laboratory experiments showed that pycnidiospores of asexual *Capnodiales*, *Chaetothyriales* and *Micropeltidaceae* germinated well in solutions of honeydews secreted by aphids and scale insects, as well as in some plant decoctions (Yamamoto 1956; Batista 1959). Srivastava and Thakre (1997) observed the sooty mould *Capnodium citri* on orange leaf surfaces associated with the insects *Aleurocanthus woglumi*, *Dialeurodes citri* and *Diapohorina citri*. The honeydew-producing insects were abundant in the rainy season but less abundant in the summer.

A study of 270 collections of sooty moulds from major herbaria and fungaria by Olejnik et al. (1999) found that the samples came from 34 countries on all continents except for Antarctica. Fifty four per cent of them were from Borneo, Cuba, India, Malaysia, and the Philippines, and a few specimens from other tropical or sub-tropical regions thus confirming that these groups of fungi are distributed from the Mediterranean to tropical regions.

As early as 1849, Gardner reported that coccus or bugs were associated with sooty moulds on coffee plants in Sri Lanka (Gardner 1849). His observations were in accordance with the appearance of scale insects and sooty moulds on leaves of exotic plants in England and the serious outbreaks in the orange plantations of the Azores and Madeira, and on leaves of *Arbutus* in British Columbia (Berkeley and Desmazières 1849). *Limacinia fernandeziana*, is the sooty mould found on wild plant in the forests of Juan Fernandez (Johow 1896). Sooty moulds are also common in Europe and parts of North America, especially on *Tilia*, *Salix* and *Ulmus* trees (Hughes 1976), and in Australia. Hughes (1966) described *Capnocybe* and *Capnophialophora* from New Zealand and mentioned that sooty moulds occur in abundance in this country. He collected over 500 specimens in the year 1963 alone. Later Hughes (1972) investigated the sooty moulds from New Zealand further and described two new families: *Euantennariaceae* and *Metacapnodiaceae*.

In cool-temperate climates, evergreen substrata provide suitable environments for the growth of sooty moulds, particularly ornamental shrubs such as species of *Camellia*, *Rhododendron*, and *Prunus laurocerasus* (Royal Botanic Gardens, Kew, UK National Collection of Dried Fungi, unpublished data). However, the *Capnodiaceae* are scarce during the winter. The number of sooty moulds in the UK is low, 13 species have been recorded, the most common being *Capnodium salicinum* and *Denisiella babingtonii* (Cannon et al. 1985, Royal Botanic Gardens, Kew, UK National Collection of Dried Fungi, unpublished data). On the other hand, the warm-temperate climates in Australia and the Mediterranean countries provide an abundance of perennial foliage on which the sooty moulds are able to establish themselves during the winter, and so persist from one season to the next (Fraser 1935; Reynolds and Gilbert 2005). Flessa et al. (2012) studied sooty patches on deciduous and evergreen leaves in Germany using spread plate culture techniques, and sequencing analysis of ITS rDNA gene, and found eight different fungal taxa. Their study did not show any host-specificity or preference among the fungi involved. In the north of tropical Thailand we have found 11 species of sooty moulds, many being undescribed species and as yet not established as host-specific.

Since sooty moulds are phylogenetically diverse fungal communities, it is highly likely that competition and resource partitioning play a crucial role in their survival. Sooty mould community composition may be influenced by a range of factors, such as insect honeydew composition (Dhami et al. 2013) or microclimate. It is also likely that different fungal species may be specialists of different stages of sooty mould formation on host plants, such as initial infection or pioneers, secondary species followed by stable climax community. However, there is little information available on the succession of this community.

Control of sooty moulds

The first step in the control of sooty moulds is to rinse any sticky surfaces on the leaves with a jet of water and to wash off honeydew before the mould can grow. Sooty moulds can be indirectly controlled by reducing populations of sucking insects that excrete honeydew. If one of the horticultural oils is used for control, it also has the advantage of helping to loosen sooty moulds from the plant surface. This hastens the weathering away of the sooty moulds. Horticultural oils formulated by many companies are available through garden centres, hardware stores, and similar establishments (Lamborn 2009). Cultural practices to control sooty moulds include early detection and control of the insect pests, prevention of further insect and sooty mould infestation; over-pruning, over-watering and directly taking out insect pests from the plant (Laemmlen 2011).

Ant management is also an important consideration to halt development of sooty moulds. Ants are attracted to and use honeydew as a food source. In fact, ants often farm the aphids, and harvest the honeydew before other predators and parasites feed on it. The presence of ants is a good indicator of honeydew being produced by insects (Nelson 2008; Lamborn 2009). Because sooty moulds are more common in warmer

regions, the higher temperatures and increased drought stress that will occur with global warming are expected to increase the prevalence of sooty moulds. During drought, aphid populations and their honeydew production typically increase on foliage undergoing moisture stress. Under dry conditions, less rain would be available to remove or dilute honeydew concentrations, which promotes sooty mould. During the extended summer drought of 1988, sooty moulds were more prevalent throughout the Northeastern USA (Kessler 1992, see also: http://www.na.fs.fed.us/spfo/pubs/howtos/ht_sooty/ht_sooty.htm)

Srivastava and Thakre (1996) mention that growth and development of sooty moulds on Mandarin oranges (*Citrus reticulata*) is dependent on honeydew. They showed that management of sooty moulds using fungicides (Baycor, Captaf, Contaf, Fytoan, Thiride and Zebtane) is effective and can control their growth and development. Dalvi et al. (2002) showed that a bleaching solution with 0.05–0.1 % NaOCl is effective in removing sooty moulds from postharvest fruit skins.

Pathogens of sooty moulds

Sooty moulds are also hosts to pathogens, although their effect on the colonies is unclear. Such parasitism (at least in northern Thailand) appears to be uncommon as we found a single species, *Rhombostilbella rosea*, parasitizing a single collection of *Chaetothyrium*. This fungus has been known to parasitize *Chaetothyriaceae* and *Capnodiaceae* from Indonesia and south-eastern United States (Pohlad 1988).

In this study, we made collections of *Phaeosaccardinula* sp. on *Brischofia* leaves and 80 % were infected with *R. rosea* (Figs. 20 and 21). In the infected sooty mould colonies, nearly all ascomata were colonized by the parasite. It formed distinct thickened and yellowish synnemata on the ascomata. *Hyphae* of 2 μm in width were formed at the basal part within the ascomata and infection was first noticeable when conidia were released from the ostioles (Pohlad 1988). *Synnemata* were 200–250 μm long and 50–70 μm in diameter, comprising dense hyphae. They produced hyaline to rose conidiophores at maturity (Fig. 21). *Conidiophores* of 2 μm in width were appressed spirally or twisted when immature, and formed around the top or along the sides of the synnemata when mature. Proliferation was sympodial and they boreconidia at the apices (Fig. 21). *Conidia* of 20–30×6–11 μm were formed at the apex of the conidiophores as swellings. They were globose to subglobose when immature, and became tapered at both ends at maturity as well as enlarged at the centre or rhomboid, with short appendages at the spores apices (Fig. 21).

Sooty moulds and disease

Sooty mould may cause asthmatic and rhinitic reactions (Santilli et al. 1985; Guarneri et al. 2008). They rarely cause diseases in humans handling infected fruits. A male laborer in Italy who handled sooty mould-covered citrus fruits developed hypo- and hyperpigmented areas on his hands, without signs of inflammation or allergic reaction, together with several episodes of bronchial asthma (Guarneri et al. 2008). It was suggested that intracutaneous penetration of a melanoid fungal pigment might have caused hyperpigmentation, while fungal products that are toxic/apoptosis-inducing for melanocytes and/or that interfere with melanogenesis could have caused hypopigmentation. Research on sooty mould-related human diseases may be needed, and the above case underlines the importance of education, use of protection devices, and prevention of sooty mould infestation in individuals exposed to these fungi.

Industrial potential of sooty moulds

Sooty moulds develop on sugary solutions called honeydew, excreted by sap sucking insects. If malt extract agar or other media high in sugars are exposed to the air, they will quickly be colonized by airborne fungi such as *Aspergillus* and *Pencillium*. Yet the sugary excretions on leaves are colonized only by sooty moulds and the common airborne fungi are absent. There are two probable reasons for the dominance of the sooty moulds. Firstly we suspect that the sooty moulds will produce antibiotic and antifungal agents, which will prevent the common airborne fungi from developing. If this is the case then the sooty moulds should be screened to establish which antimicrobials they produce and if they might have any medicinal importance. Interestingly, one tropical sooty mould (*Capnodium* sp.) is known to produce antibiotics, such as tetramic acid, methiosetin and epicorazin A (Herath et al. 2012). Secondly, the sugary excretions are likely to dry rapidly and therefore the fungi that can grow on this nutritious food resource are likely to be limited to those that can grow at low water activity. We therefore suspect that the sooty moulds are xerophilic. Thus if industry requires fungi that can perform functions at low water activity levels the sooty moulds may be appropriate candidates.

The amount of compounds known from sooty moulds is remarkably low (Laatsch 2012). This is probably due to a lack of studies, rather than poor capabilities of the fungi to produce chemical compounds, as sooty moulds have been poorly researched for most aspects. The novel antibiotic methiosetin, a new tetramic acid, was produced in a culture of *Capnodium* sp., a tropical sooty mould (Herath et al. 2012). Epicorazine A was also discovered from the same fungus and is a known antibiotic (Baute et al. 1978; Deffieux et al. 1978). In the so-called Fitness Test Screening, Methiosetin showed poor antibacterial activity against *Staphylococcus aureus* (MIC 256 μg/mL), while Epicorazine A had significantly better activity against *Haemophilus influenzae* (MIC 0.5 μg/mL). The discovery of new antibiotic agents that are effective

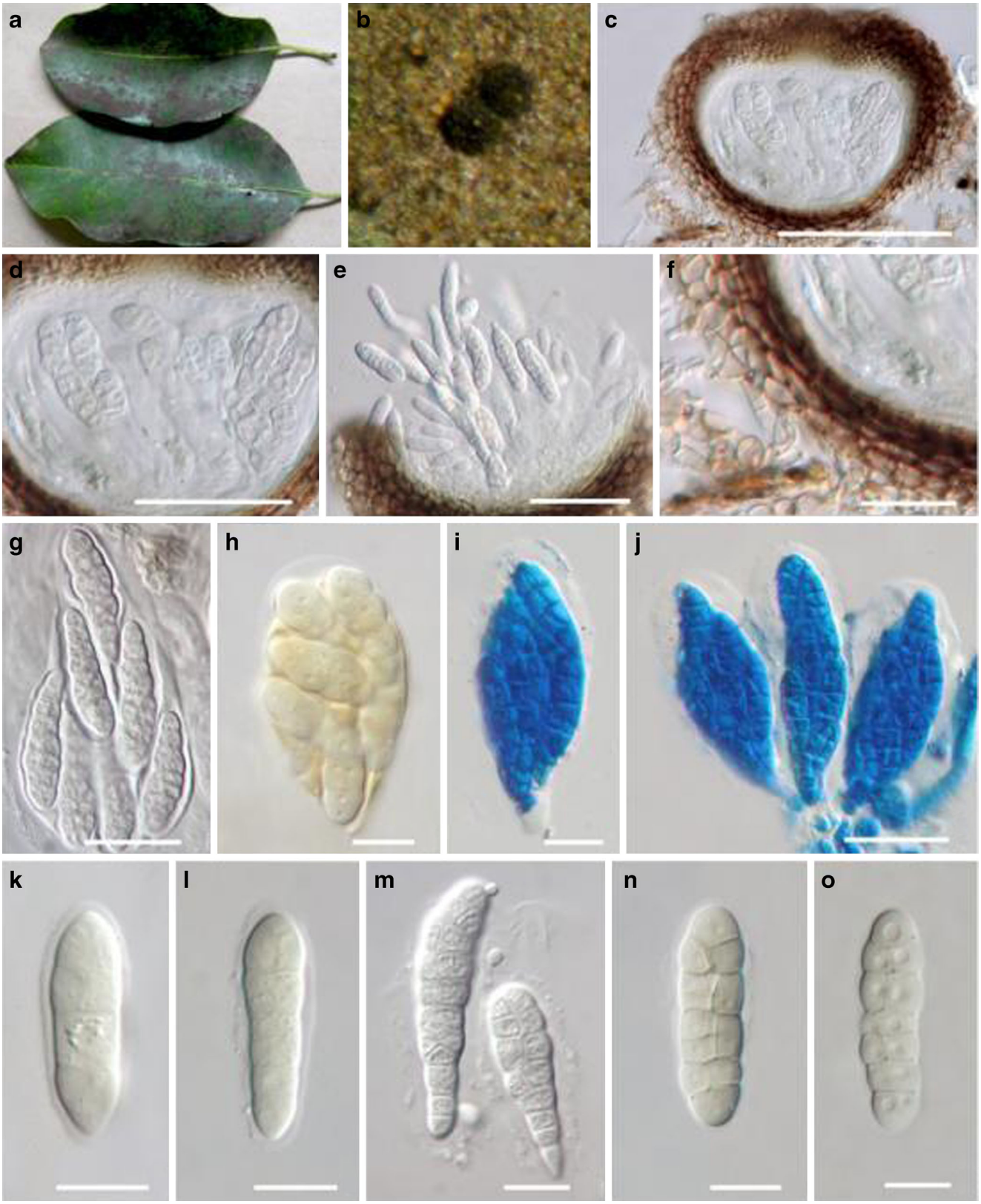

Fig. 20 *Phaeosaccardinula sp.* without *Rhombostilbella* infection (Material examined: THAILAND, Chiang Rai, Mae Fah Luang campus, on living leaf of *Mimusops elengi*, 24 April 2011, Huang Zhang 24/4/11). **a** Specimens. **b** Ascomata on surface of host. **c** Section through ascoma. **d** Asci arrangement inside ascoma. **e, m** Ascospores. **f** Peridium. **g** Asci. **h** Asci stained with Melzer's reagent. **i–j** Asci stained with cotton blue reagent. **k–l** Immature ascospore stained with Melzer's reagent. **m** Ascospores at maturity. **n–o** Mature ascospores stained with Melzer's reagent. *Bars*: c=100 μm, d, e=50 μm, f, g, j=20 μm, h, i, k–o=10 μm

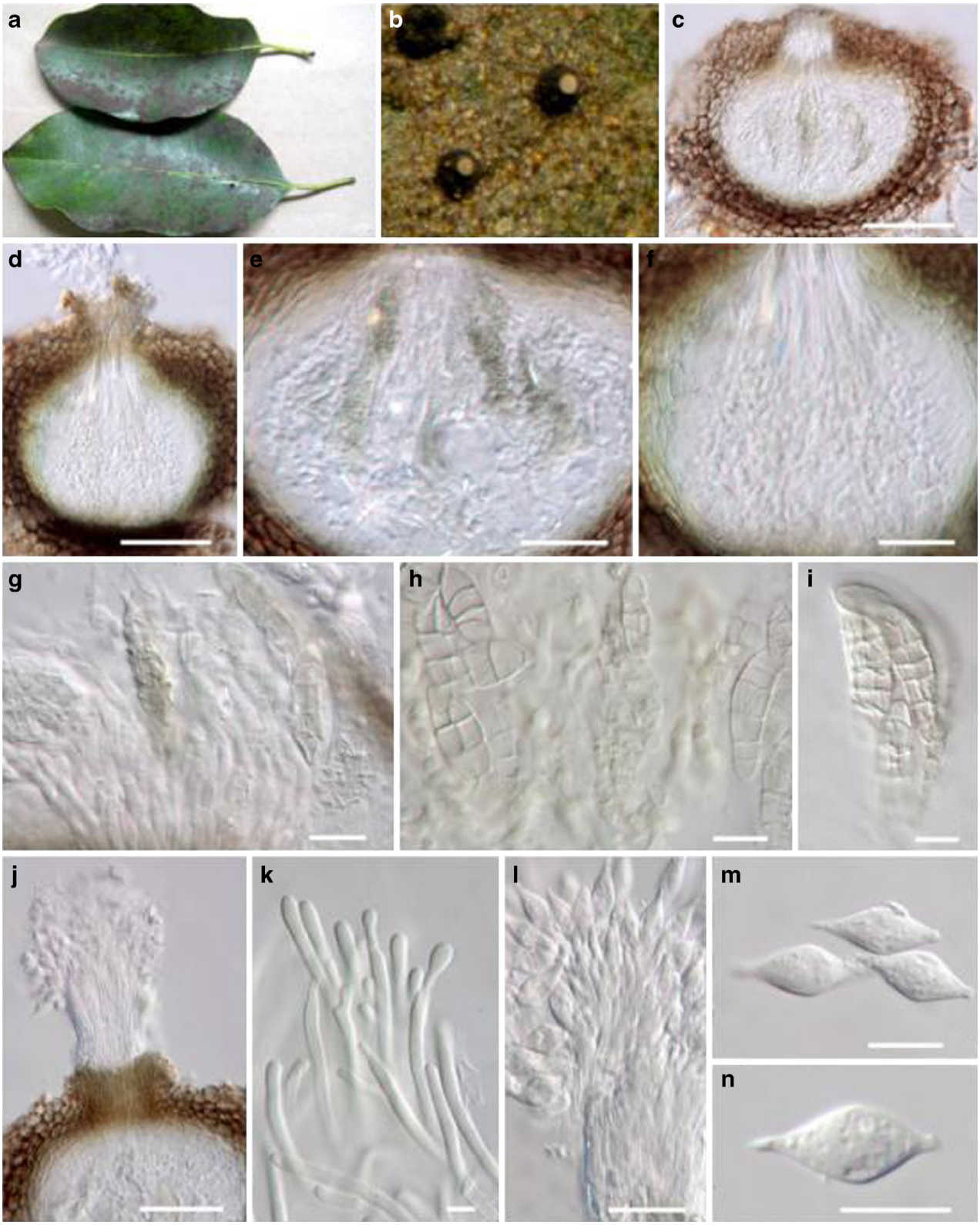

Fig. 21 *Phaeosaccardinula* sp. with *Rhombostilbella rosea* infection (Material examined: THAILAND, Chiang Rai, Mae Fah Luang campus, on living leaf of *Mimusops elengi*, 24 April 2011, Huang Zhang, MFLU11-1116). **a** Specimens. **b** Parasite raising on ascomata of host. **c–f** Section through ascomata, with hyphae of parasite developing inside. **g–i** Asci disintegrated by infection of parasite. **j–n** *R. rosea*. **j** Synnemata protruding from ostiole. **k** Conidiophores forming immature conidia at the tip. **l** Conidiophores bearing mature conidia. **m–n** Conidia at maturity. *Bars*: c, d, j, l=50 μm, e–g, i=20 μm, h, k, m, n=10 μm

against drug-resistant micro-organisms is an important challenge (Herath et al. 2012). The compounds involved in sooty moulds interactions are presently unknown and research is needed to establish if they have any industrial potential.

Some species of sooty moulds are commercially and agriculturally important, for example, *Caldariomyces fumago* is used to produce an extracellular industrial chloroperoxidase, which belongs to the class of heme glycoproteins (Pickard et al. 1991; Faull et al. 2002). This enzyme may be used as a catalyst for chlorination reactions, as well as a catalase or a peroxidase. Mwenje and Mguni (2001) found that isolates of *Capnodium* that caused preharvest soft rot of avocado fruits (*Persea americana*) in Zimbabwe produced pectinases and cellulases. Bussaban et al. (2011) reported an edible gelatinized sooty mould species from Thailand; this is a first report of an edible sooty mould and the practice generates income for the villagers.

Conclusion and future work

Sooty moulds are a remarkable, but poorly understood group of fungi. They cause disease by coating fruit and leaves with a black mycelial covering that reduces photosynthetic ability. However few researchers have tried to quantify their economic importance. Sooty moulds have been well-studied at the morphological level, but they are poorly represented in a natural classification based on phylogeny. Most sooty mould colonies comprise numerous species and thus it is hard to confirm relationships between genera or sexual and asexual states. Future studies need to obtain single spores isolates of species to test their phylogenetic affinities and linkages between morphs. Next generation sequencing has shown sooty mould colonies to contain many more fungal species than expected. Sooty moulds appear to grow in extreme environments and it should be tested if they are xerophilic. Growing on energy-rich sugars, they appear to out-compete typical weed fungi and bacteria. They may produce antibiotics for this purpose and may be potential creative organisms to obtain novel compounds of medicinal potential and this deserves further research.

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