Monilochaetes and allied genera of the Glomerellales, and a reconsideration of families in the Microascales

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Abstract: We examined the phylogenetic relationships of two species that mimic Chaetosphaeria in teleomorph and anamorph morphologies, Chaetosphaeria tulasneorum with a Cylindrotrichum anamorph and Australiasca queenslandica with a Dischloridium anamorph. Four data sets were analysed: a) the internal transcribed spacer region including ITS1, 5.8S rDNA and ITS2 (ITS), b) nc28S (ncLSU) rDNA, c) nc18S (ncSSU) rDNA, and d) a combined data set of ncLSU-ncSSU-RPB2 (ribosomal polymerase B2). The traditional placement of Ch. tulasneorum in the Microcales based on ncLSU sequences is unsupported and Australiasca does not belong to the Ceratocystidaceae. Both holomorph species are nested within the Glomerellales. A new genus, Reticulascus, is introduced for Ch. tulasneorum with associated Cylindrotrichum anamorph; another species of Reticulascus and its anamorph in Cylindrotrichum are described as new. The taxonomic structure of the Glomerellales is clarified and the name is validly published. As delimited here, it includes three families, the Glomerellaceae and the newly described Australiasaceae and Reticulascaceae. Based on ITS and ncLSU rDNA sequence analyses, we confirm the synonymy of the anamorph genera Dischloridium with Monilochaetes. Consequently Dischloridium laeïnse, type species of the genus, and three related species are transferred to the older genus Monilochaetes. The teleomorph of D. laeïnse is described in Australiasca as a new species. The Plectosphaerellaceae, to which the anamorph genus Stachylium is added, is basal to the Glomerellales in the three-gene phylogeny. Stibellia annulata also belongs to this family and is newly combined in Acrostalagmus. Phylogenetic analyses based on ITS, nLSU and nSSU, and combined nLSU-nSSU-RPS2 sequences clarify family relationships within the Microcales. The family Ceratocystidaceae is validated as a strongly supported monophyletic group consisting of Ceratocystis, Cornuvesica, Thielaviopsis, and the type species of Ambrosiella. The new family Gondwanamycteaceae, a strongly supported sister clade to the Ceratocystidaceae, is introduced for the teleomorph genus Gondwanamyceae and its Custinaphora anamorphs. Four families are accepted in the Microcales, namely the Ceratocystidaceae, Gondwanamycteaceae, Halosphaeriaceae, and Microascales. Because of a suggested affinity of a Faurelina indica isolate to the phylogenetic position of the Chaetofaudiellaceae is reevaluated. Based on the results from a separate nLSU analysis of the Dothideomycetes, Faurelina is excluded from the Microcales and placed in the Pleosporales.

Key words: Australiasca, Australiasaceae, Ceratocystidaceae, Cylindrotrichum, Dischloridium, Gondwanamycteaceae, Reticulascus, Reticulascaceae, phylogeny, Plectosphaerellaceae.

Taxonomic novelties: New order: Glomerellales Chafeef. ex Réblová, W. Gams & Seifert, ord. nov. New families: Australiasaceae Réblová & W. Gams, fam. nov., Ceratocystidaceae Loq. ex Réblová, W. Gams & Seifert, fam. nov., Gondwanamycteaceae Réblová, W. Gams & Seifert, fam. nov., Reticulascaceae Réblová & W. Gams, fam. nov. New genera: Reticulascus Réblová & W. Gams, gen. nov., New species: Australiasca laeïnse Réblová & W. Gams, sp. nov., Cylindrotrichum setosum Seifert, sp. nov., Reticulascus clavatus Réblová & Fournier, sp. nov. New combinations: Acrostalagmus annulatus (Berk. & Broome) Seifert, comb. nov., Hyalocylindropsora rosea (Petch) Réblová & W. Gams, comb. nov., Monilochaetes baccinvaria (Matsush.) Réblová & Seifert, comb. nov., Monilochaetes camelliae (Alcorn & Sivan.) Réblová, W. Gams & Seifert, comb. nov., Monilochaetes laeïnse (Matsush.) Réblová, W. Gams & Seifert, comb. nov., Monilochaetes regenerans (Bhat & W.B. Kendr.) Réblová & Seifert, comb. nov., Reticulascus tulasneorum (Réblová & W. Gams) Réblová & W. Gams, comb. nov.

INTRODUCTION

The genus Chaetosphaeria (Chaetosphaeriaceae, Chaetosphaeriaceae) is a cosmopolitan genus of nonstromatic, perithecial ascomycetes (Réblová 2000, Réblová & Winka 2000, Fernández et al. 2006). It is characterised by dark, opaque, usually subglobose to conical perithecia. The asci are uniloculate, short-stipitate with a dichiasis anamorph. The genus has been characterised by dark, opaque, usually subglobose to conical perithecia, asci, ascospores, and branching and anastomosing filiform paraphyses. Periphyses are cylindrical, and rarely fragment into part-spores. Periphyses are bicolorous, 1- to several-septate, ellipsoidal to fusoid, sometimes cylindrical, and rarely fragment into part-spores. Periphyses and paraphyses are persistent, cylindrical, seldom branching, septate, and longer than the asci. The genus has been characterised by dark, opaque, usually subglobose to conical perithecia, asci, ascospores, and phialidic, dematiaceous hyphomycetes. Recognising these species as distinct from Chaetosphaeria is difficult based purely on morphology. In most cases, their systematic placement can be ascertained by DNA sequence data, which suggest that the morphological similarities are a result of convergent evolution.

Chaetosphaeria tulasneorum was experimentally linked to its anamorph Cylindrotrichum oligospermum by Réblová & Gams (1999). Based on nLSU rDNA sequence data, Ch. tulasneorum was segregated from the core species of Chaetosphaeria in the Chaetosphaeriaceae (Réblová & Winka 2000) and tentatively placed in the Microcales, along with Cylindrotrichum hennebertii, a non-setose counterpart of C. oligospermum. Chaetosphaeria tulasneorum colonises decaying wood and forms minute, black perithecia containing uniloculate, short-stipitate ascii with an imamylloid apical ring, 2–4-celled ellipsoid to ellipsoid-fusoid ascospores, and branching and anastomosing filiform paraphyses forming a "network" within the centrum. The reticulate paraphyses and the 1-septate, cylindrical conidia of the Cylindrotrichum anamorph are the only deviating morphological characters between Ch. tulasneorum and other core Chaetosphaeria species.
The phialidic, dematiaceous hyphomycete Dischloridium laènse, described originally from dead leaves of Musa paradisiaca in Papua New Guinea (Matsushima 1971), is common on dead palm spathes in Australia. In some respects it is similar to species of Chloridium, a well-established anamorph genus associated with Chaetosphaeria, but the microscopic structures are much larger. On material from Australia and England, perithecia of Australiasca (Sivanes & Alcorn 2002) were associated with fertile conidiophores of D. laènse. This teleomorph was first reported from England by Kirk (1986) on stems of Dicksonia antarctica, but never described or illustrated. Sivanes & Alcorn (2002) erected the monotypic ascomycete genus Australasica including the type species, A. queenslandica, and named its anamorph Dischloridium camelliae. The fungus was isolated from leaves, stems, and branches of Camellia sinensis and the connection between the morphs was proven experimentally in vitro. They distinguished D. camelliae from D. laènse by longer conidia and larger conidiophores. Sivanes & Alcorn (2002) compared Australasica with genera in the morphologically similar families Chaetosphaeriaceae and Lasiosphaeriaceae. At that time, no molecular data were available to confirm placement in either family.

The Australasica teleomorph of D. laènse is morphologically similar to species of Chaetosphaeria in perithecial and anamorphic characters. Dischloridium laènse, the type of its genus, produces effuse colonies of single to fasciculate, macronematous conidiophores with a stromatic base. The conidiophores are dark brown but paler towards the apex. The phialidic conidiogenous cells are terminally integrated bearing an indistinct collarette producing brown but paler towards the apex. The phialidic, dematiaceous hyphomycete Dischloridium is phylogenetically well-defined and validated to a well-established anamorph genus associated with Dothideomycetes (Halsted 1890), recently revised and delimited from the type species, A. queenslandica, never described or illustrated. Sivanes & Alcorn (2002) compared Australasica with genera in the morphologically similar families Chaetosphaeriaceae and Lasiosphaeriaceae. At that time, no molecular data were available to confirm placement in either family.

To assess the higher level phylogenetic relationships of Ch. tulasneorum and related species of Cylindrotrichum, Australasica, Dischloridium, and Monilochaetes, we analysed members from 19 orders or families of perithecial ascomycetes. We used DNA sequence data from the nuclear large (ncLSU rDNA) and small subunit (ncSSU rDNA) subunits in independent analyses and combined these with the second largest subunit of RNA polymerase (RPB2) for a multigene analysis.

Based on the phylogenies presented here, several new and strongly supported families and orders are proposed. The order Monilochaetes is morphologically defined and validated to include three families, the Glomerellaceae and the newly described Australasaceae and Reticulascaceae. The internal transcribed spacer region (ITS including ITS1, 5.8S and ITS2) was used to further analyse the phylogenetic relationships among species of Dischloridium and Monilochaetes. Within the Microascales, we accept four families, i.e. Ceratocystidaceae, which is validated here, and the newly described Gondwanamycetaceae, Halosphaeriaceae, and Microascales. We discuss the family and order affinities of Faurelina attributed to the Chaedefaudiellaceae of the Microascales by von Arx (1978) and by Tang et al. (2007). We examined authentic material, specifically the in vitro ex-type and another strain of F. indica, and analysed ITS and ncLSU sequence data. Based on results from a ncLSU analysis of the Dothideomycetes, Faurelina (Chafeaufaudiellaceae) is excluded from the Microascales and placed in the Pleosporales (Dothideomycetes).

MATERIAL AND METHODS

Morphological observations

All herbarium specimens examined and cultures studied are listed under each treated species. Dried specimens were rehydrated in water; material was examined with an Olympus SXZ12 dissecting microscope and centrum material including asci, ascospores, and paraphyses was mounted in Melzer’s reagent or 90 % lactic acid. Hand sections of the perithecial wall were studied. When present, conidiophores, conidiogenous cells, and conidia were examined in water, Melzer’s reagent, or 90 % lactic acid. All measurements were made in Melzer’s reagent. Means ± standard errors (s.e.) based on 25 measurements are given for ascospore, ascal, and conidial dimensions. Images were captured using differential interference (DIC) or phase contrast (PC) microscopy using an Olympus DP70 Camera operated by Imaging Software Cell* on an Olympus BX51 compound microscope or an Evolution MP digital camera operated by ImagePro v. 6.0 on an Olympus BX50 compound microscope. Conidia and conidiogenous cells of Australasica queenslandica were photographed in the living state using an FEI Quanta 200 Environmental Scanning Electron Microscope (ESEM). A ca. 2 × 2 mm cube of agar with mycelium was observed at 20kV after the sample chamber achieved local thermodynamic equilibrium: chamber pressure 200 Pa, sample temperature from -15 °C to -16 °C. A Gaseous Secondary Electron Detector (GSED) was used for signal detection. Cooling of the specimen in the chamber was achieved using a PC-controlled Peltier cooling stage with external water chiller (JT Manufacturing, Hudson, NH, USA). Images were processed with Adobe Photoshop CS4 Extended or Adobe Photoshop CS2.

Single-ascospore isolates were obtained from fresh material with the aid of a single-spore isolator (Meopta, Prague, Czech Republic). Isolates were grown on potato carrot agar (PCA), oatmeal agar (OA), and 2 % malt extract agar (MEA) (Gams et al. 1998). Colonies were examined after 7, 21, and 30 d at 25 °C in the dark and under near-UV light source (12 h light: 12 h dark). Two strains of Faurelina indica were grown on Blakeslee’s malt extract agar (Gams et al. 1998) and OA and incubated under ambient room conditions for two mo to induce the arthroconidial anamorph. Cultures are maintained at BRIP (Plant Pathology Herbarium, Queensland, Australia), CBS (CBS Fungal Biodiversity Center, Utrecht, the Netherlands), DAOM (Canadian Collection of Fungal Cultures, Agriculture and Agri-Food Canada, Ottawa, Canada), and the Institute of Botany, Academy of Sciences, Průhonice, Czech Republic.

DNA extraction, amplification and sequencing

DNA was isolated with an UltraClean Microbial DNA Kit (MoBio Laboratories, Inc., Canada) using mycelium removed from PCA or MEA cultures following the manufacturer’s protocol for filamentous fungi. All PCR experiments were carried out using a PTC-200 thermal cycler (MJ Research Inc., Watertown, MA, USA). PCR reactions containing 2–4 mM MgSO4 were performed using Platinum Taq DNA polymerase High Fidelity (Invitrogen, Carlsbad, CA, USA) in 25 mL volume reactions. PCR conditions were as follows: for ncSSU 2 min at 94 °C; 35 cycles of 30 s at 94 °C, 30 s at 55 °C and 150–300 s at 68 °C; for ITS and ncLSU 2 min at 94 °C, 35 cycles of 30 s at 94 °C, 30 s at 55–60 °C, and 165–270 s at 68 °C; and for RPB2 2 min at 94 °C; 35 cycles of 30 s at 94 °C, 30 s at 55–61 °C.
alignments and bases 1–59 were excluded from the analysis of the RPB2 alignment, because of the incompleteness of the 5′-end of the majority of the available sequences. An additional 69 bases in the RPB2 part of the alignment, which were difficult to identify as homologous, were also excluded. All alignments are deposited in TreeBase (10538).

The three genes for the combined analysis (ncLSU-ncSSU-RPB2) were tested for heterogeneity among data partitions before combining them for the total evidence analysis. We used the partition homogeneity/incongruence-length difference test implemented in PAUP (Swoford 2002) to determine if different partitions of the data gave significantly different signals. Because combining data with value $P > 0.01$ generally improves phylogenetic accuracy (Cunningham 1997) and our data did not show significant heterogeneity ($P = 0.01$), the sequences were combined for further analysis.

Maximum parsimony analyses were conducted with PAUP v. 4.0b10 (Swoford 2002). A heuristic search was performed with the stepwise-addition option with 1 000 random taxon addition replicates and TBR branch swapping. All characters were unordered and given equal weight. Gaps were treated as missing data. Branch support was estimated on the recovered topologies by performing a heuristic search of 1 000 bootstrap replicates consisting of ten random-addition replicates for each bootstrap replicate.

Bayesian analysis was performed in a likelihood framework, as implemented by the MrBayes v. 3.0b4 software package, to reconstruct phylogenetic trees (Huelsenbeck & Ronquist 2001). The program MrModeltest2 v. 2.3. (Nylander 2008) was used to infer the appropriate substitution model that would best fit the model of DNA evolution for our sequence data sets. Bayesian searches using Metropolis-coupled Markov chain Monte Carlo sampling were conducted. One cold and three heated Markov chains were used in the analysis. Bayesian analyses were run for 5 M generations with trees sampled every 1 000 generations. The first 20 000 trees representing the “burn-in” phase were discarded. To estimate posterior probabilities (PP) of recovered branches (Larget & Simon 1999), 50 % majority rule consensus trees were produced from the remaining trees using PAUP.

**PHYLOGENETIC RESULTS**

The first analysis was restricted to the ncLSU. The alignment consisted of the two first thirds of the ncLSU region for 99 sequences representing 91 species in 19 ascomycetous families and orders and 1 283 total characters: 615 constant, 140 not parsimony-informative, and 453 parsimony-informative. A maximum parsimony (MP) heuristic search produced 16 most parsimonious trees (MPTs) with a length of 3 303 steps (CI = 0.303, RI = 0.665, HI = 0.696). One of these trees is shown in Fig. 1. The GTR+I+G substitution model was selected for the Bayesian analysis. The order *Glomerales* forms a monophyletic clade (82 % bootstrap support /0.7 posterior probability) with three families recognised, the Australiasaceae (90/1.0), Glomerales (85/0.83), and Reticulascaceae (97/1.0). Within the Reticulascaceae, Cylindrotrichum setosum is sister to the Reticulascus clavatus clade (95/1.0). *R. tulaneorum* forms a well-supported clade (75/1.0), and *Kylindria peramazonei* and *Porosphaerella* are nested at the base of the Reticulascaceae (97/1.0). The order *Microascales* as presently conceived appears to be polyphyletic. The monophyletic *Ceratoctydialcaceae* (100/1.0) and *Gondwanamycetales* (100/1.0) form a clade (92/1.0) as a
### Table 1. Sources and accession numbers of isolates

| Teleomorph                              | Anamorph                      | M           | Source* | Substrate and Locality                                | GenBank accession numbers ** |
|-----------------------------------------|-------------------------------|-------------|---------|------------------------------------------------------|-------------------------------|
| Australiasca laeënsis                  | Monilochaetes laeënsis        | ● DAOM 226788 | Australia, dead fronds of a tree fern               | GU180623 GU180641 GU180610 – |
| Monilochaetes laeënsis                 | ● PRM 915720                  |             | UK, stem of Dicksonia antarctica                   | GU180624 GU180642 – –        |
| Australiasca queenslandica             | Monilochaetes camelliae       | ● BRIP 24607a | A. antarctica, branch of Camellia sinensis         | HM237327 HM237324 – –        |
| Monilochaetes camelliae                | ○ BRIP 24334c                |             | A. antarctica, branch of Camellia sinensis         | HM237326 – –                 |
| Calosphaeria pulchella                 | Calosphaeriophora pulchella   | ● CBS 115999 | France, wood and bark of Prunus avium              | – – AY761078** AY761071** GU180661 |
| Ceratosphaeria lampadophora             | Harpophora-like               | ● CBS 117555 | France, decayed wood                               | – – GU180618 – –            |
| Chaetosphaeria ciliata                 | Menispora ciliata             | ● ICMP 18253 | New Zealand, decayed wood                          | – – GU180637 GU180614 GU180659 |
| Chaetosphaeria curvispora              | Chloridium-like               | ● ICM 18255 | New Zealand, decayed wood                          | – – GU180636 AY502933** GU180655 |
| Faurelina indica                       | Arthrographis sp.             | ● CBS 126.78 | India, dung of goat                                | – – GU180653 – –            |
|                                       | Arthrographis sp.             | ● CBS 301.78 | India, dung of cow                                 | – – GU180654 – –            |
| Reticulascus clavatus                 | Cylindrotrichum clavatum     | ● CBS 125296 | France, submerged wood of Alnus glutinosa           | GU180627 GU180643 GU180622 – |
| Cylindrotrichum clavatum              | ○ CBS 125239                  |             | France, submerged wood of Platanus sp.             | GU180633 GU180649 GU180615 – |
| Cylindrotrichum clavatum              | ○ CBS 125297                  |             | France, submerged wood of Fraxinus sp.             | GU180634 GU180650 – –       |
| Cylindrotrichum clavatum              | ○ CBS 426.76                  |             | Sweden, decayed wood of Ulmus scabra               | GU201799 – – –               |
| Reticulascus tulasneorum              | Cylindrotrichum oligospermum  | ○ CBS 561.77 | Netherlands, twig of Fraxinus excelsior            | GU291801 – – –               |
| Reticulascus tulasneorum              | Cylindrotrichum oligospermum  | ○ CBS 570.76 | Germany, dead twig of Symphoricarpus albus          | – – AF178560** – –          |
| Reticulascus tulasneorum              | Cylindrotrichum oligospermum  | ○ CBS 557.74 | Czech Republic, wood of Salix purpurea             | – – – – – –                 |
| Reticulascus tulasneorum              | Cylindrotrichum oligospermum  | ● CBS 101319 | Czech Republic, wood of Sambucus nigra             | – – AF178547** – –          |
| Togniniella acerosa                   | Phaeocrella acerosa           | ● ICM 18256 | New Zealand, decayed wood of Nothofagus sp.         | – – AY761078** AY761073** GU180660 |
| tu                                      | Acrostalagmus annulatus       | ○ DAOM 212126 | Germany, soil and roots                            | GU180632 GU180646 GU180611 GU180662 |
| tu                                      | Cylindrotrichum gonii         | ○ CBS 879.85 | Sweden, dead stem of Urtica dioica                 | HM237328 HM237322 – –       |
| tu                                      | Cylindrotrichum setosum       | ○ DAOM 229246 | Australia, wood and bark mulch on the ground       | GU180635 GU180652 GU180617 – |
| tu                                      | Custingophora olivacea        | ○ CBS 335.68 | Germany, compost                                   | – – – – – – –               |
| tu                                      | Kylindria penarumazinensis    | ○ CBS 838.91 | Cuba, leaf litter of Bucida palustris               | GU180628 GU180638 GU180609 GU180656 |
| tu                                      | Kylindria penarumazinensis    | ○ CBS 421.95 | Cuba, leaf of Bucida palustris                      | GU291800 HM237325 – –       |
| tu                                      | Gibellulopsis nigrescens      | ○ DAOM 226890 | Canada, Ontario, soil                              | GU180631 GU180648 GU180613 GU180664 |
| tu                                      | Monilochaetes guadalcanensis  | ○ CBS 346.76 | Solomon Islands, leaf of Musa                       | GU180625 GU180640 – –       |
| tu                                      | Monilochaetes infuscans       | ○ CBS 379.77 | New Zealand, Ipomoea batatas                       | – – GU180645 GU180619 GU180619 – |
| tu                                      | Monilochaetes infuscans       | ○ CBS 869.96 | South Africa, Ipomoea batatas                      | GU180626 GU180639 GU180620 GU180657 |
| tu                                      | Monilochaetes infuscans       | ○ CBS 870.96 | South Africa, Ipomoea batatas                      | – – GU180644 GU180621 –     |
| tu                                      | Plectosporium tabacinum       | ○ DAOM 229828 | Canada, Ontario, soil straw of Orzya sativa imported from Canada | GU180630 GU180647 GU180612 GU180663 |
| tu                                      | Stachylium bicolor            | ○ DAOM 226658 | – – – – – – – –                                       | – GU180651 GU180616 –     |

* BRIP = Plant Pathology Herbarium, Queensland, Australia; CBS = Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; DAOM = Canadian Collection of Fungal Cultures, Agriculture and Agri-Food Canada, Ottawa.

** These sequences were published elsewhere (Réblová & Winka 1999, Réblová & Seifert 2004, Réblová et al. 2004).

* M: morph of material available: • = teleomorph, ◦ = anamorph.

* tu = teleomorph unknown

GU1806XX–GU1806YY are sequences newly generated in this study.
Fig. 1. One of 16 most parsimonious trees from a heuristic analysis of nLSU rDNA sequences. Thickened branches indicate posterior probability values ≥ 1.0 PP and 100 % bootstrap support. Bootstrap support values ≥ 50 % and Posterior probability values ≥ 0.5 are included at the nodes. Branch lengths are drawn to scale. An asterisk above or below a branch marks branches that collapse in the strict consensus tree.
Fig. 2. One of the 14 most parsimonious trees from a heuristic analysis of ncSSU rDNA sequences. Details as in Fig. 1.
sister to the *Plectosphaerellaceae* (100/1.0). The other two families of the *Microascaceae* form a separate clade (82/1.0) containing the *Microascales* (97/1.0) and the *Halosphaeraceae* (88/1.0). The second analysis was restricted to the ncSSU. The alignment consisted of the whole gene for ncSSU for 71 sequences representing 67 species in 19 ascomycetous orders and families and 1 777 total characters: 1 102 constant, 195 not parsimony-informative, and 405 parsimony-informative. A maximum parsimony heuristic search produced 14 MPTs with a length of 2 267 steps (Cl = 0.390, RI = 0.697, HI = 0.609), one of which is shown in Fig. 2. For the Bayesian analysis, the GTR+I+G substitution model was selected. The *Glomerellales* form a monophyletic, strongly supported clade (81/0.98) containing representatives of three families, the *Australiasiacaeae* (78/1.0), *Glomerellaceae* (100/1.0), and *Reticulacaceae* (94/1.0). The *Plectosphaerellaceae* form a separate, strongly supported clade (100/1.0) basal to the *Microascaceae*. The *Microascaceae* appear as a monophyletic clade (100/1.0) including two strongly supported subclades. The first subclade (78/1.0) contains the *Halosphaeraceae* (65/-) and *Microascaceae* (81/1.0) and the second subclade (83/1.0) contains the *Ceratocystidaceae* (80/1.0) and *Gondwanamycetaceae* (100/1.0).

In the third analysis, a combination of the ncLSU and ncSSU data sets plus RPB2 sequences was assessed for 54 taxa representing 52 species in 18 ascomycetous orders and families. The alignment of the combined set of ncLSU-ncSSU-RPB2 DNA sequences consisted of 4 224 total characters: 2 148 constant, 314 not parsimony-informative, and 1 484 parsimony-informative. A maximum parsimony heuristic search produced two MPTs with a length of 11 688 steps (Cl = 0.278, RI = 0.476, HI = 0.722); one is shown in Fig. 3. For the Bayesian analysis the GTR+I+G substitution model was selected. The *Glomerellales* are a monophyletic, well-supported clade (100/0.81) with the *Plectosphaerellaceae* as a sister group (100/1.0). The *Microascaceae* appear as a monophyletic, strongly supported clade (88/1.0), again with two subclades; the first (87/1.0) contains the *Halosphaeraceae* (94/1.0) and *Microascaceae* (88/1.0) while the other (100/1.0) comprises the *Ceratocystidaceae* (100/1.0) and *Gondwanamycetaceae* (99/1.0).

The fourth analysis included ITS1, 5.8S, and ITS2 regions of species of the *Glomerellales* and *Plectosphaerellaceae*. The alignment consisted of 38 sequences representing 29 species in five families and 574 total characters: 277 constant, 75 not parsimony-informative, and 222 parsimony-informative. A maximum parsimony heuristic search produced nine MPTs with a length of 786 steps (Cl = 0.592, RI = 0.821, HI = 0.407). One is shown in Fig. 4. The GTR+I+G substitution model was inferred for the Bayesian analysis. Following the results of our other analyses, two *Chaetosphaeria* species (*Chaetosphaeria*) were used as outgroups. The order *Glomerellales* is a strongly supported monophylum (95/0.99) containing three strongly supported families, the *Australiasiacaeae* (99/1.0), *Glomerellaceae* (99/0.97), and *Reticulacaceae* (96/1.0). The *Plectosphaerellaceae* (100/1.0) appears as a strongly supported sister clade to the *Glomerellales*. Six strains represent the *Australiasiacaeae* in the analysis: two strains of *Australiasia queenslandica*, two strains of *A. laeënsis*, and one strain each of *Monilochaetes infuscans* and *M. guadalcanalensis*. The *Reticulacaceae* are represented by four strains of *Reticulascus clavatus* (anamorph *C. clavatum*), four strains of *R. tulasneorum* (anamorph *Cylindrothrichum oligospernum*), *C. setosum*, *C. gori*, and two strains of *Kylindersia perumazonensis*. The two conidial (CBS 125239, CBS 125287) and single ascospore (ex-type strain CBS 125296) isolates of freshwater *R. clavatus* plus one terrestrial isolate (CBS 428.76) formed a strongly supported monophylum (100/1.0). Another strongly supported monophyletic clade (97/1.0) included one ascospore- (ex-type strain CBS 101319) and three conidial isolates of *R. tulasneorum* (CBS 557.74, CBS 561.77, ex-type strain of *C. henneberti* CBS 570.76). The anamorphic *C. setosum* (ex-type strain DAOM 229246), *C. gori* (CBS 879.85), and *K. perumazonensis* (CBS 421.95, CBS 838.91) were basal to the rest of the clade on separate branches.

A fifth analysis of the ncLSU rDNA sequences was run to determine the relationship of two strains of *Faurellinia indica* with members of the *Dothideomycetes* and *Eurotiomycetes*. The alignment consisted of the first two thirds of the ncLSU for 68 species representing 66 species in 11 orders and families and 1 229 total characters: 716 constant, 76 not parsimony-informative, and 362 parsimony-informative. A maximum parsimony heuristic search produced 66 MPTs with a length of 1 593 steps (Cl = 0.433, RI = 0.760, HI = 0.567). One is shown in Fig. 5. The GTR+I+G substitution model was selected for the Bayesian analysis. The two strains of *Faurellinia* form a monophyletic clade (88/0.9), which is a sister to the *Didymellaceae* (96/1.0). The suggested relationship of *Faurellinia* with the *Eremomycetaceae* and *Testudinacea* could not be confirmed; the families grouped on separate branches with no close relationship to each other. *Faurellinia* appears to be a member of the *Pleosporales* within the *Dothideomycetes* unrelated to the *Microascaceae*.

### TAXONOMY

#### Glomerellales

Chadefaud (1960) proposed the order "Glomerellales" for a group of endophytic fungi and parasites of living plants with ascomata varying from endostromatal to apostromatal and ascospores that are often unicellular and hyaline. No Latin diagnosis was provided for the order. Within the order he suggested an evolution of the apical apparatus from an initial condition of the periocular thickening of the apical dome lacking a pronounced chitinoid ring to derived conditions of either the apical thickening converted into an apical cushion reduced to a simple lens-shaped disc or with the initial of a chitinoid ring developing in the periocular thickening. According to the texture and pigmentation of the ascomata, he further divided the order into two groups: a) "Eu-Glomerellales", which included genera with a non-fleshy black stroma i.e. *Gibellina, Glomerella, Phyllachora, and Physalospora*; and b) "Polystigmatales" as "Glomerellales nectrioides", which comprised one genus, *Polystigma*, with a orange to red, fleshy stroma. After this invalid introduction of the name *Glomerellales*, the order was also cited by Lanier *et al.* (1978) and later by Locquin (1984), when he listed the *Glomerellales* and *Polystigmatales* as separate orders, again without a Latin diagnosis. After the validation of the *Glomerellales* in Zhang *et al.* (2006), we validate here the phylogenetically delimited order *Glomerellales*, excluding the earlier validated but unrelated *Phyllachorales*.

Three families are accepted in the *Glomerellales*, namely the *Glomerellaceae, Australiasiacaeae*, and *Reticulacaceae*. The latter two families are newly described below based on cultural studies, detailed morphological comparisons of the holomorphs, and newly generated ITS, ncLSU, ncSSU, and RPB2 sequences.
Glomerellales Chadef. ex Réblová, W. Gams & Seifert, ord. nov. MycoBank MB515429.

Glomerellales Chadef., Traité de botanique systématique. Tome I, p. 613. 1960 (also in Lanier et al., Mycol. Pathol. Forest. I: 292. 1978; Locquin, Mycol. Gén. Struct., p. 170. 1984) nom. inval., Art. 36.

Ascomata perithecia, brunnea usque nigra, nonnumquam sclerotidea, ostiolum perispheum. Pariete ascomatum 2–3-stratosis. Hamathecium paraphyses verae. Glomerellales, ord. nov. MycoBank MB515429.

Asci unitunicati, brevi-stipitati, parte apicali iodo non reagente. Ascosporeae hyalinae vel pallide pigmentatae, 0-pluri-cellulares. Anamorphe: conidia modo phialidico

Typus: Glomerellaceae Locq. ex Seifert & W. Gams, Mycologia 98: 1083. 2007 [2006].

Perithecia darkly pigmented, sometimes becoming ± sclerotial. Perithecial wall 2–3-layered, ostiolum perispheum. Interascal tissue of thin-walled, tapering paraphyses. Asci unitunicate, thin-
This family accommodates the teleomorph genus Glomerella and its Colletotrichum anamorphs. For discussion and description refer to Zhang et al. (2006).

**Glomerellaceae**

This family accommodates the teleomorph genus Glomerella and its Colletotrichum anamorphs. For discussion and description refer to Zhang et al. (2006).

Glomerellaceae Locq. ex Seifert & W. Gams in Zhang et al., Mycologia 98: 1083. 2007. [2006].

**Australiascaceae** Réblová & W. Gams, fam. nov. MycoBank MB515430.

Stromata absent. Ascomata perithecia, brunnea usque nigra, ostiolum periphysatum. Pariete ascomatum fragilis, 2-stratato. Interascal tissue of thin-walled, tapering paraphyses. Asci uniloculati, 8-spored, cylindrical-clavate, apical ring distinct, inamylloid. Ascospores hyaline, septate. Anamorph: Monilochaetes; conidios of 0(–3)-septate, hyalinis modo phialidico orientibus.

Typus: Australiasca Sivan. & Alcom, Aust. Syst. Bot. 15: 742. 2002.

**Stroma** absent. **Perithecia** brown to black, ostiolum periphysate. **Perithecial wall** 2-layered, fragile. **Interascal tissue** of thin-walled, tapering paraphyses. **Asci** uniloculati, 8-spored, cylindrical-clavate, annulo apicali lodo non reagente. Ascospores hyaline, septate. Anamorph: *Monilochaetes*; conidios of 0(–3)-septate, aggregated in slime or in chains.

The Australiascaceae accommodates the holomorph genus Australiasca and anamorphic *Monilochaetes*. The molecular data for Australiasca (Figs 1–3) confirm that the genus is unrelated to the Chaetosphaeriaceae or Lasiosphaeriaceae as suggested by Sivanesan & Alcom (2002). However, the Australiascaceae, like

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**Glomerellales** & Microascales

**Fig. 4.** One of the nine most parsimonious trees from a heuristic analysis of ITS rDNA operon of the Glomerellales and the Plectosphaerellaceae. The accession numbers of strains of the newly described Australiascaceae and Reticulascaceae are indicated. Details as in Fig. 1.
Fig. 5. One of 66 most parsimonious trees from a heuristic analysis of ncLSU rDNA of Faurelina indica and Dothideomycetes. Details as in Fig. 1.
the Reticulascaceae, accommodates telemorphs that mimic Chaetosphaeria and which are almost indistinguishable from its perithecia on morphological grounds. The anamorphs are phialidic, dematiaceous hyphomycetes with hyaline, slimy conidia, which are also similar to anamorphs of Chaetosphaeria.

The dematiaceous hyphomycete genus Monilochaetes was described and illustrated for a single species, M. infuscans (Halsted 1890, Harter 1916), which causes scurf disease or soil stain of Ipomoea batatas (sweet-potato). Another saprobic species, M. guadalcanalensis, collected on leaves of Musa sp., originally described in Catenulaira, was recently added (Rong & Gams 2000) and this classification is confirmed here by molecular data. Monilochaetes includes species with solitary, erect, sometimes curved or geniculate, macromatous conidiophores, darker near the base, becoming paler towards the apex, with prominently darkened septa, terminal, wide monophaeides with a shallow collarette, and aseptate, rarely septate, hyaline conidia adhering in basipetal chains or heads. Rong & Gams (2000) distinguished Monilochaetes from the other two similar dematiaceous hyphomycete genera Dischloridium (Sutton 1976) and Exochalaria (Gams & Holubová-Jechová 1976) by aspects of conidiophore branching and fasciculation and conidial shapes and dimensions. The present ITS and nLSU phylogenies confirm that Dischloridium and the morphologically similar other genus Monilochaetes, which up to now was only known as asexual, are congeneric. Therefore, Dischloridium laeënsis, type of the genus, is transferred to Monilochaetes and Dischloridium becomes a generic synonym of Monilochaetes.

The teleomorph-anamorph connections of Australiasca queenslandica, type species of the genus, with M. camelliae and of the newly described A. laeënsis with M. laeënsis were experimentally established (Sivanesan & Alcorn 2002, this study). The other four species accepted in Monilochaetes are presently only known to be anamorphic. A further species of Monilochaetes is described by Réblová et al. (2011).

KEY TO THE SPECIES OF AUSTRALIASCA AND MONILochaetes IN THE AUSTRALIsCAceae

1. Conidia hyaline, ellipsoidal, aseptate, rarely 1–3-septate, longer than 26 μm .......................................................... 2
2. Conidia hyaline, ellipsoidal, aseptate, rarely 1-septate, shorter than 26 μm .......................................................... 3
3. Conidia 0–1-septate, rhomboid–ellipsoidal to obovoidal, usually forming chains .......................................................... 5
4. Conidia aseptate, ellipsoidal to oblong, usually in small clusters, aggregated in slimy droplets .......................................................... 4
5. Conidia 0–1-septate, rhomboid–ellipsoidal to obovoidal, usually forming chains .......................................................... 5

Australiasca laeënsis Réblová & W. Gams, sp. nov. MycoBank MB518384, Fig. 6A–K. Anamorph: Monilochaetes laeënsis (Matsush.) Réblová, W. Gams & Seifert, comb. nov. MycoBank MB515431.
Basionym: Chloridium laeënse Matsush., Bull. Natl. Sci. Mus. Tokyo 14: 462. 1971.
≡ Dischloridium laeënse (Matsush.) B. Sutton, Kavaka 4: 47. 1976.

Etymology: Epithet from the anamorph species, originally derived from the type locality, Lae in Papua-New Guinea (Matsushima 1971).

Stromata absentia. Perithecia superficialia, gregarious vel solitaria, atrca, conica usque obpyriformia, 200–320 μm diam, 340–450 μm alta, ostiolum peripheriastum. Paries ascomatum fragilis, 2-stratostatus. Paraphyses septatae, hyalinae, sursum angustatae, ascos superantes. Asci uniloculati, cylindraceo-clavati, 130–148 × 18–20 μm (in medio ± s.e. = 137.6 ± 5.3 × 19.3 ± 0.6 μm), 8-loculati, brevi-stipitati, apice truncato. Ascospores ellipsoideae usque ovoideae, 24.5–31.5(–33) × (8–)9–9.5 μm (in medio ± s.e. = 15.7 ± 0.2 × 4.4 ± 0.04 μm), hyalinae, 0–1-septatae. Anamorph Monilochaetes laeënsis.

Perithecia 200–320 μm diam, 340–450 μm high, gregarious to solitary among conidiophores, superficial, base slightly immersed, conical to obpyriform, with a short beak, black, glabrous or with setae. Setae scanty, acute, thick-walled, dark brown, paler to subhyaline towards apex, sometimes on upper half of perithecium, 90–155 × 5–7 μm; longer, thicker-walled setae, arising from base of perithecium, 300–420 × 10–11 μm. Perithecial wall 16–22 μm thick, becoming 45–54 μm thick towards base, fragile, 2-layered: outer layer of textura prismatica consisting of thick-walled, brick-like cells, cells becoming polyhedral towards base; inner layer of hyaline, compressed cells. Paraphyses ca. 2.5–3 μm wide, persistent, hyaline, septate, branching, longer than ascii. Asci 130–148 × 18–20 μm (mean ± s.e. = 137.6 ± 5.3 × 19.3 ± 0.6 μm), uniloculate, cylindrical-clavate, short-stipitate, apex truncate, with a distinct, shallow annulus, ca. 6 μm wide, 1–1.5 μm high, 8-spored. Ascospores 24.5–31.5(–33) × (8–)9–9.5 μm (mean ± s.e. = 28.4 ± 0.6 × 8.9 ± 0.1 μm), ellipsoidal to oblong, apiculate at both ends, 1-celled, becoming transversely 1–3-septate after discharge, smooth, germinating with germ tubes at both ends, hyaline, irregularly 2-seriate in ascus.
Colonies in vivo dark, hairy, effuse. Conidiophores 200–600 μm long, 6.5–9 μm wide, arising in small fascicles or small loose groups of 2–6 or solitary from a minute stroma, macronematous, percurrently proliferating, dark brown, 5–15-septate; base occasionally bulbous with smaller, thick-walled, adjacent pseudoparenchymatous cells forming stromatic tissue in substratum. Conidiogenous cells monophialidic, 50–70 × 4.5–8(–10) μm, terminal, cylindrical, hardly tapering at apex, subhyaline; collarette ca. 1–2 μm high, minute, conidiogenous locus located at base of collarette. Conidia 22–26 × 10–12 μm (mean ± s.e. = 23.2 ± 0.2 × 10.8 ± 0.2 μm), ellipsoidal to cylindrical-ellipsoidal, broadly rounded, sometimes obtuse at base, hyaline, basal scar 3.5–4 μm diam, smooth-walled.

Colonies in vitro after 14 d on PCA at 25 °C 15–20 mm diam, felty, stromatic tissue absent, aerial mycelium olive-brown, margin entire; reverse pale greyish-brown. Colonies readily sporulating, beginning...
after 5 d on PCA at 25 °C under near-UV light (12 h light: 12 h dark). Conidiophores, phialides, and conidia morphologically identical to those on natural substratum. Conidiophores 40–160 × 7–8 μm, pale brown throughout, with none or 1 percurrent proliferation, 2–5-septate; in about 28 d, longer conidiophores developing, ca. 160–280 μm long, dark brown, subhyaline towards apex, with 1–4 percurrent proliferations, up to 2–15-septate. Conidigenous cells mononialdiades 31–58 × (6–)7–9 μm, tapering to 6–6.5 μm just below collarette; collarette ca. 1.5 μm high and (5.5–)6–8 μm wide. Conidia (15.5–)18–22.5(–23.5) μm long, 7.5–9(–10) μm wide (mean ± s.e. = 20.9 ± 1.82 ± 0.3 μm), ellipsoidal to cylindrical-ellipsoidal, rounded, sometimes obtuse at base, hyaline, basilar scar 2–3.5 μm diam, smooth-walled.

Specimens examined (anamorph and teleomorph): Australia, New South Wales, Blue Mountains, Mt. Tomah Botanical Garden, S 33 32.4, E 150 25.4, 1197 m a.s.l., on dead stipes and spathes of a tree fern in a rain forest, 17 Aug. 1997, K.A. Seifert no. 884 and G.J. Samuels, DAOM 228788. UK, England, West Cornwall, Penjerrick House Gardens, 22 June 2000, dead stipes of Dicksonia antarctica, B. Candy, PRM 915720, holotype of A. laeënsis.

Notes: Based on the results from ITS and LSU rDNA phylogenies, Australiasca laeënsis and A. queenslandica are distinct species, although they are morphologically similar. Australiasca queenslandica and its M. camelliae anamorph were originally described and isolated from culture, stems and branches of Camellia sinensis; perithecium containing mature asc and ascospores formed in vitro (Sivanesan & Alcorn 2002). The ascospores released by A. queenslandica were often observed to be 1–3-septate, becoming dicytoseptate, and some produced phialides with hyaline microconidia in vitro. The recently collected material of A. laeënsis from England and Australia documents perithecium produced on the host associated with the conidiophores of its M. laeënsis anamorph. The ascospores were observed to be transversely 1–3-septate after discharge, but never became dicytoseptate or exhibited phialidic germination. Australiasca laeënsis is described here based on our observations on the host and the anamorph in culture.

The range of conidial lengths of M. camelliae and M. laeënsis overlap, but those of the former species are usually longer. Monilochaetes camelliae produces conidia 18–35 × 8–13 μm in culture on Sachs agar + maize leaves (Sivanesan & Alcorn 2002) or 20.5–24(–26.5) × (10–)11–12(–13) μm on PCA (this study). The conidia of M. laeënsis are 22–26 × 10–12 μm on the host and (15.5–)18–22.5(–23.5) μm × 7.5–9(–10) μm (this study). Therefore, the conidia of M. camelliae from Sachs agar overlap in length with conidia of M. laeënsis, but exceed its upper range by nearly 10 μm, while on PCA the conidia of M. camelliae are only slightly longer than those of M. laeënsis. The conidial dimensions for M. laeënsis from our collections correspond with measurements of the type and other specimens on host substrata from different localities, e.g. Sutton (1976, conidia 15–20 × 8–10 μm), Matsuhashi (1971, 17–26 × 8–12 μm), and Holubová-Jechová (1982, 14.5–24 × 6.5–10 μm). The conidia of M. laeënsis are hyaline, aseptate, and arise singly from the conidiogenous locus, usually in slimy heads. The conidia of M. camelliae were described as occasionally 1–3-septate, produced in heads or chains (Sivanesan & Alcorn 2002). The conidiophores of M. camelliae are also slightly longer, often swollen subapically (Sivanesan & Alcorn 2002).

Monilochaetes laeënsis has been collected on dead leaves in Papua New Guinea (Matsuhashi 1971), Sri Lanka (Sutton 1976, Bhat & Sutton 1985), and Cuba (Holubová-Jechová 1982), dead leaves or twigs and dead palm spathes in Australia, Ethiopia, India and Malaysia (Bhat & Sutton 1985), and dead fern spines in the United Kingdom (Kirk 1986). Only the European and recent Australian material contained perithecia with mature asc and ascospores. Kirk (1986) noted that Dischloridium does not occur naturally in the British Isles but was probably introduced into gardens where it was found along with its host Dicksonia antarctica. He also suggested that the prevailing colder temperatures may have triggered sexual reproduction in nature; our own teleomorph specimen was collected in a cool, humid valley in the Australian winter.

Australiasca queenslandica Sivan. & Alcorn, Aust. Syst. Bot. 15: 742. 2002. Figs 7A–R, 8A–G. Anamorph: Monilochaetes camelliae (Alcorn & Sivan.) Réblová, W. Gams & Seifert, comb. nov. MycoBank MB513835. Basionym: Dischloridium camelliae Sivan. & Alcorn, Aust. Syst. Bot. 15: 743. 2002.

Colonies in vitro on MEA after 14 d at 25 °C with 22–25 mm radial growth, more or less planar, surface dark brown, covered with abundant, pale grey, lanose to cottytony aerial mycelium, margin smooth and entire, reverse grey, sterile. Colonies on PCA after 14 d at 25 °C with 23–25 mm radial growth, planar, surface brown, covered with pale grey, lanose to cottytony aerial mycelium, margin smooth and entire, reverse dark grey, sterile.

Colonies in vitro on PCA sporulating in 14 d at 25 °C in darkness. Setae absent. Conidiophores 200–720 μm long, 9–10(–10.5) μm wide near base and 6.5–7.5(–8.5) μm wide in middle, pale to dark brown, subhyaline towards apex, with none or 1 percurrent proliferation, up to 20-septate. Conidigenous cells mononialdiate, subhyaline, paler towards collar, ampulliform to cylindrical, slightly swollen, 36–45(–60) μm long, 6.5–9(–9) μm wide at widest part, tapering to ca. 3–4 μm just below collar; collarate 4.5–5.5 μm wide and ca. 1.5–2 μm high. Conidia 20.5–24(–26.5) × (10–)11–12 μm (mean ± s.e. = 22.5 ± 0.3 × 11.8 ± 0.1), 0–1-septate, ellipsoidal to cylindrical-ellipsoidal, broadly rounded at end, obtuse at base, basilar scar 3–5 μm diam, some conidia with a laterally displaced hilum, hyaline, smooth-walled.

After 6 mo on PCA at 25 °C in darkness, producing minute conidiophores with microconidia. Setae absent. Conidiophores more or less erect, arising from aerial mycelium, simple or sparingly branched, pale brown to subhyaline, 40–60 μm long and 2–2.5 μm wide, with terminally integrated or intercalary conidiogenous cells. Conidigenous cells mononialdiate, subhyaline to pale brown, usually paler towards apex, ampulliform to cylindrical, 8–20 μm long, 2.5–3.5 μm wide at widest part, tapering to ca. 1.5 μm just below collar; collarate 2.5–3 wide, ca. 2 μm high. Conidia 4.5–3.5 × 3.5–μm (mean ± s.e. = 4.5 ± 0.1 × 3.2 ± 0.1), aseptate, thick-walled, broadly ellipsoidal to subglobose, rounded at ends, base slightly tapering, obtuse with a minute abscission scar, accumulating in small, clear to whitish droplets, hyaline, smooth-walled. Chlamydospores not observed.

Specimens examined (anamorph only): Australia, Queensland, Malanda, isolated from branch of Camellia sinensis, 19 Feb. 1997, D. Steel M. 8982c, BRIP 24334c; Queensland, Brisbane, S 27 30, E 152 58, isolated from branch of Camellia sinensis, 10 July 1997, J.L. Alcorn, BRIP 24607a.

Notes: Two isolates of M. camelliae were examined and ITS and nLSU sequences were generated (Table 1). One of these is an authentic, single-ascospore isolate listed among specimens examined in the protologue of Dischloridium camelliae (Sivanesan & Alcorn 2002).

The ESEM photographs of conidia of M. camelliae (Fig. 8A, B, F, G) demonstrate well that there is a continuum between conidial chains and slimy heads on the phialides. The osmolarity of the medium may influence the relative proportion of chains and slimy heads as seen particularly in Chloridium, where chains, cirrhi, and
slimy heads are all observed in one genus or even one species (W. Gams, unpubl. data). The conidial chains of *M. camelliae* were difficult to observe in squash mounts from agar, but were visible directly in the Petri dish by light microscopy.

**Additional species of Monilochaetes**

Since its description the original generic concept of *Dischloridium* has been expanded with the addition of fifteen species having variable morphology of conidia and conidiophores including several species with brown, distoseptate conidia. To be consistent with the morphological delimitation of *Monilochaetes* indicated by phylogeny, we accept only two of the fourteen remaining species previously included in *Dischloridium* for transfer to *Monilochaetes*, namely *D. basicurvatum* and *D. regenerans*. Other species are newly transferred to or accepted in other hyphomycete genera, such as *Crasedodidymum*, *Hyalocylindrophora*, or *Paradischloridium*, and a few cannot presently be reassigned.

After revising type material, cultivation studies, and molecular data of *Exochalara longissima*, the type species of that genus, we
confirm that the species is unrelated to *Monilochaetes* (material and isolates examined: IMI 18047 holotype of *Chalara longissima*; IMI 167413 holotype of *Catenuaria piceae*; CBS 980.73, cited as the only strain in the description of *E. longissima* by Gams & Holubová-Jechová 1976, and CBS 393.82). The true relationship of the genus *Exochalara* lies with the *Helotiales* of the *Leotiomycetes* (Réblová et al. 2011). The strain studied by Rong & Gams (2000), CBS 662.82, with pronounced branching of the short conidiophores, is not conspecific with or related to *E. longissima*.

**Monilochaetes** Halst., New Jersey Agric. Exp. Stn. Bull. 76: 27. 1890.
≡ *Dischloridium* B. Sutton, Kavaka 4: 47. 1976.

**Monilochaetes basicurvata** (Matsush.) Réblová & Seifert, *comb. nov.* MycoBank MB515432.
*Basionym:* *Dischloridium basicurvatum* Matsush., Matsush. Mycol. Mem. 8: 18. 1995.

**Monilochaetes guadalcanalensis** (Matsush.) I.H. Rong & W. Gams, Mycotaxon 76: 455. 2000.
*Basionym:* *Catenuaria guadalcanalensis* Matsush., Microfungi of the Salomon Islands and Papua New Guinea, Kobe, p. 10. 1971.
≡ *Exochalara guadalcanalensis* (Matsush.) W. Gams & Hol.-Jech., Stud. Mycol. 13: 58. 1976.

**Monilochaetes infuscans** Ellis & Halst., New Jersey Agric. Exp. Stn. Bull. 76: 27. 1890. Fig. 9A–I.
≡ *Dischloridium cylindrosporum* S.K. Srivast., Sydowia 39: 217. 1986.

**Monilochaetes regenerans** (Bhat & W.B. Kendr.) Réblová & Seifert, *comb. nov.* MycoBank MB515433.
*Basionym:* *Dischloridium regenerans* Bhat & W.B. Kendr., Mycotaxon 49: 48. 1993.
Species excluded from Dischloridium and Monilochaetes, but not reclassified

Accepted names are printed in bold.

Dischloridium keniense P.M. Kirk, Mycotaxon 23: 30. 1985.
Basionym: Craspedodidymum keniense (P.M. Kirk) Bhat & W.B. Kendr., Mycotaxon 49: 37. 1993.

Dischloridium roseum (Petch) Seifert & W. Gams, Mycotaxon 24: 459. 1985.
Basionym: Acremonium roseum Petch, Ann. Royal Bot. Gard. Peradeniya 7: 317. 1922.
≡ Hyalocylindrophora rosea (Petch) Réblová & W. Gams, comb. nov. MycoBank MB515434
≡ Hyalocylindrophora venezuelensis J.L. Crane & Dumont, Canad. J. Bot. 56: 2616. 1978.
≡ Dischloridium venezuelense (J.L. Crane & Dumont) Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 725. 1985.

Notes: With this new combination the combining authors accept the argument by Holubová-Jechová (1990) that this hyaline species should not be considered congeneric with similar pigmented species. The species has not been cultured or sequenced.

Dischloridium triseptatum Hol.-Jech, Česká Mykol. 41: 110. 1987. Fig. 10A–J.
≡ Paradischloridium ychaffrei Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 723. 1985.

Dischloridium venezuelense (J.L. Crane & Dumont) Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 725. 1985.
≡ Hyalocylindrophora rosea (Petch) Réblová & W. Gams (see above).

Dischloridium ychaffrei (Bhat & B. Sutton) Hol.-Jech., Česká Mykol. 42: 204. 1988.
Basionym: Paradischloridium ychaffrei Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 723. 1985. Fig. 10A–J.
≡ Dischloridium triseptatum Hol.-Jech, Česká Mykol. 41: 110. 1987.

Notes: Paradischloridium was erected for phialidic dematiaceous hyphomycetes reminiscent of Dischloridium, but with conidiophores that are not fasciculate and do not arise from stromatic tissue. The phialides lack even remnants of a collarette and conidia are brown with 3-distosepta (Bhat & Sutton 1985). The conidiogenesis of \textit{P. ychaffrei} is particularly interesting. Fig. 10C–F show the conidiogenous locus sitting deeper in the venter of the cylindrical phialide than is typical for \textit{M. laeïnsis} or other Monilochaetes species; it is located more towards the bottom of the conidiogenous cells. Fig. 10C, D show young, hyaline conidia formed within the venter. In Fig. 10B, F, the top of a new phialide appears to be proliferating through the old phialide and collarette to form a new functional phialide. Similar phialidic structures and conidium ontogeny were described, for example, in species of Catenularia,
Chloridium, and Sporoschismopsis (Holubová-Jechová & Hennebert 1972). No living culture of *P. ychaffrei* was available to further assess the phylogenetic relationships of this genus.

**Dischloridium species of uncertain status**

A few *Dischloridium* species remain that cannot be transferred to *Monilochaetes* or other genera. Three of these form a group of morphologically similar taxa with features intermediate between *Monilochaetes* and *Colletotrichum*, viz. *Dischloridium*
**Trophis racemosa**

Microfungorum a Matsushima lectorum, Kobe, p. 69. 1975.

Sci. Bull. 3: 39. 1897.

Univ. Waterloo Biol. Ser. 35: 50 (fig. 29). 1991.

This family contains two holomorph genera, *Reticulascus* and *Porosphaerellopsis*. Although these genera differ morphologically, ontogeny and morphology of the centrum and interthecial filaments unite them and partially define the family. The interthecial tissue is formed of filiform branching and anastomosing filaments, forming a "network" among the asci. They are attached to the hymenium and to the top of the ascomatal wall. This structure was first described and illustrated by Samuels & Müller (1978) for *Porosphaerellopsis spiroroschismophora* and is documented here for *Reticulascus tulasneorum* and *R. clavatus*. The second species in the genus *Porosphaerellopsis*, *P. bipolaris* (Ranghoo et al. 2001), collected on submerged wood in a stream in China, does not form this "network", and has paraphyses that are wider and simple. The link between *P. bipolaris* and a *Sporoschismopsis* anamorph suggested by Ranghoo et al. (2001) has not been established convincingly.

**Reticulascaceae** Réblová & W. Gams, fam. nov. MycoBank MB515435.

Stromata minute nonnumquam formata. Ascomata perithecia, fusca usque nigra, ostiolum peripherale. Pariete ascomatum 2-stratato. Hamathecium paraphysatum vereae; paraphyses septatae, hyalinae, ramosae, anastomosantes, sursor angustatae, ascosuperantes. Ascis uniseriates, cylindrical-clavati, 8-spores, annulo apicali iodo non reagente. Ascosporae hyalinae vel atrobrunneaes, ellipsoidae usque fusiformes, septatae, nonnumquam utrinque poro praeditae. Anamorphae: Cylindrotrichum, Sporoschismopsis; conidigenesis phialidica.

**Reticulascus** Réblová & W. Gams, gen. nov. MycoBank MB515436.

Etymology: from the Latin ascus and reticulum, referring to the network of interthecial filaments.

Stromata absent. Perithecia brown to black. Ostiolum peripherale. Perithelial wall 2-layered. Interascal tissue of thin-walled, tapering, branching and anastomosing paraphyses. Ascis uniseriates, 8-spored, cylindrical-clavate, apical ring inamyloid. Ascosporae hyalinae or dark brown, ellipsoidal to fusiform, sometimes with end pores. Anamorphs: Cylindrotrichum, Sporoschismopsis; conidigenesis phialidica.

**Reticulascaceae**

This family contains two holomorph genera, *Reticulascus* and *Porosphaerellopsis*. Although these genera differ morphologically,
Several anamorphic species are related to this clade. The delimitation of Cylindrotrichum, typified by C. oligosporum, and morphologically similar genera of dematiaceous hyphomycetes has been controversial, with varying concepts proposed by Gams & Holubová-Jechová (1976), DiCosmo et al. (1983), Ramíbeli & Onofri (1987), Arambargi & Cabello (1989), and Holubová-Jechová (1990). The Cylindrotrichum anamorphs of Reticulascus species generally resemble the dematiaceous, phialidic hyphomycetous anamorphs linked with Chaetosphaeria (Rěbová 2000, 2004), but the presence of cylindrical, 1-septate conidia seems to be a deviating character. The conidia are formed from conspicuously sympodially proliferating, terminally integrated phialides within shallow collarettes (Gams & Holubová-Jechová 1976: 48, figs 23, 24; Rěbová & Gams 1999: 34, fig. 16). Based on a nLSU phylogeny, Rěbová & Winka (2000) showed that several species included in Cylindrotrichum by Gams & Holubová-Jechová (1976) belong to the Chaetosphaeriaceae (Chaetosphaeriales), but others are phylogenetically unrelated with a possible affinity with the Microascales. Our molecular analyses of ITS, nLSU, ncSSU, and the combined data set of three genes (Figs 1–4) confirms that Reticulascus tulasneorum is the anamorph of C. oligosporum. C. clavatus/C. clavatum, the newly described anamorphic C. setosum, previously known species C. goni, Kylindria peramazonensis, and Poroschismopsis (anamorph Sporoschismopsis) group outside the Chaetosphaeriaceae and Microascales. They form a monophyletic group that we recognize as a new family within the Glomerellales.

The dematiaceous hyphomycete genera Cylindrotrichum, Kylinidria, and Sporoschismopsis, linked as anamorphs with the Reticulascaceae, possess conidia that vary in shape, colour, and size, and, although conidiogenesis is phialidic, the position and size, and, although conidiogenesis is phialidic, the position of the conidiogenous locus is phialidic, the position of the conidiogenous locus within the collarette also varies. In Sporoschismopsis, the first and a few subsequent conidia arise endogenously and are formed in basipetal succession from the apical portion of the phialide from deep-set conidiogenous loci within a deep collarette. After formation of several conidia, the phialide proliferates through the collarette to form a new functional phialide (Holubová-Jechová & Hennebert 1972: 385, fig. 1). Similar conidium ontogeny also occurs in Catenularia and Chloridium anamorphs of Chaetosphaeria species and in species of Cadophora or Phialophora.

The remaining 18 species previously classified in Cylindrotrichum, including those transferred to Kylinidria (13 species) and Xenokylinidria (3 species) by DiCosmo et al. (1983), are putative members of the Chaetosphaeriales for which the name Kylinidria was given preference by Rěbová (2000). In fact, the Cylindrotrichum-like anamorphs linked with Chaetosphaeria are variations on the Chloridium theme and do not represent a unique or unusual pattern within the Chaetosphaeriaceae. If future analyses confirm the placement of K. triseptata in the Reticulascaceae, Kylinidria will be excluded from the anamorphs linked with Chaetosphaeria and separated from Xenokylinidria.

Kylinidria peramazonensis did not group in the same clade as the four Cylindrotrichum species, rather it formed a poorly supported branch with Poroschismopsis at the base of the Reticulascus/Cylindrotrichum clade (Figs 1, 4). This species is discussed and illustrated below and is the only typical representative of the genus Kylinidria included in our analysis. Unlike Cylindrotrichum species of Kylinidria have oblong, longer, and wider, 1-several-septate, often asymmetrical conidia and wider and shorter conidiophores terminating with a monopodial swollen in its upper part with or without a collarette. The phialides occasionally elongate above the collarette with several percurrent extensions. These characters contrast with Cylindrotrichum having 1-septate, symmetrical, cylindrical conidia and narrower, longer, and often seta-like conidiophores with cylindrical mono- or polyphialides that never elongate above the collarette. Because of the morphological characters distinguishing Kylinidria and Cylindrotrichum and results from the ITS and nLSU phylogenetic analyses, we prefer to keep these anamorph genera separate.

Reticulascus tulasneorum (Rěbová & W. Gams) Rěbová & W. Gams, comb. nov. MycoBank MB515437. Fig. 11.
Basionym: Chaetosphaeria tulasneorum Rěbová & W. Gams, Czech Mycol. 51: 32, 1999.
Anamorph: Cylindrotrichum oligospermum (Corda) Bonord., Handb. Allg. Mykol. p. 88. 1851.
=Cylindrotrichum hennebertii R. Gams & Hol-Jech., Stud. Mycol. 15: 50, 1976.

For a full description and more information, refer to Rěbová & Gams (1999).

Species examined: Czech Republic, South-western Bohemia, Javornická hornatina Mts., Strašín near Sušice, on dead branch of Sambucus nigra, 21 Oct. 1997, M. Sršček, PRM 842978, holotype of Chaetosphaeria tulasneorum, ex-type strain CBS 101319.

Notes: Reticulascus tulasneorum produces minute, black, nonstromatic ascomata growing on decaying wood. The ascosporas are hyaline, narrowly ellipsoidal, 1- to rarely 3-septate, and glabrous at maturity, similar to those of R. clavatus having slightly verruculose ascosporas. In the features of asci, interthecal filaments, and perithecial wall, these species are indistinguishable. The morphological characters of the associated anamorphs are diagnostic. The teleomorph is known from only one locality (Rěbová & Gams 1999).

Cylindrotrichum hennebertii (ex-type strain CBS 570.76) groups with R. tulasneorum including its anamorph C. oligospermum. The former taxon was described for specimens with only a short layer of conidiophores (Gams & Holubová-Jechová 1976; 50, fig. 24), contrasting with the development of two strata of conidiophores for the latter species. The layering of the conidiophores described in the protologue of C. hennebertii seems to be quite variable depending on substrate and age of the material. With the further evidence of their identical ITS sequences, C. hennebertii is now regarded as a synonym of C. oligospermum, the anamorph of Reticulascus tulasneorum.

Reticulascus clavatus Rěbová & Fournier, sp. nov. MycoBank MB515652. Figs 11F–M, 12A–F.
Anamorph: Cylindrotrichum clavatum W. Gams & Hol.-Jech., Stud. Mycol. 43: 54, 1976.

Etymology: Epithet taken from that of the anamorph species, derived from the shape of conidia.

Perithecia 150–170 μm alta, 120–200 μm diam, superfiicialia, solitaria, subglobosa vel conica, minute papillata, ostiolata, glabra. Canalis ascomaticus perithecialis, 15 μm crassus, bistratus. Paraphyses copiosae, filiformes, septatae, ramosae, anastomosantes, reticulum formantes, hyalinae, 1.5 μm latae, ultra ascorum apices protrudentes. Asci 87–108 × 7–8.5 μm (in medio ± s.e. = 95.5 ± 0.2 × 7.5 ± 0.2 μm), cylindrici vel clavati, breviter stipitati. Ascosporae 14–18(–19) × 4–4.5 μm (in medio ± s.e. = 15.7 ± 0.2 × 4.4 ± 0.04 μm), fusiformes, bi- vel quadri-cellulares, verruculose, hyalinae, 1–2-seriatae in asco.

Perithecia 150–170 μm high, 120–200 μm diam, scattered among conidiophores, superficial, solitary, subglobose to conical, with
minute papilla, glabrous, ostiolum lined with periphyses. 

Perithecial wall brittle, heavily sclerotised in upper part, sclerotisation weakens towards base. Lateral wall ca. 15 μm thick, 2-layered: outer layer of thin-walled, dark brown, brick-like cells; inner layer of flattened, elongated hyaline cells. 

Paraphyses ca. 1.5 μm wide, copious, filiform, sparsely septate, not constricted at septa, forming a network, hyaline, longer than asci. 

Asci 87–108 × 7–8.5 μm (mean ± s.e. = 95.5 ± 0.2 × 7.5 ± 0.2 μm), cylindrical to clavate, slightly

Fig. 11. A–E. Reticulas tus tulasneorum. A, B. Asci containing ascospores. C. Ascos pores. D. Interthecial filaments. E. Perithecia on the host. F–M. Reticulas tus clavatus. F, L. Asci with ascospores. G. Vertical section of the perithecial wall. H–J. Perithecia with conidiophores of the anamorph on the host. K. Interthecial filaments. M. Ascos pores. A–E from PRM 842978 (holotype); F–M from PRM 915717 (holotype). Scale bars: A = A–D, F, K–M = 10 μm; E, H–J = 250 μm; G = 50 μm. DiC: A–C, E–J, L, M; PC: D, K.
**Fig. 12.** A–F. *Cylindrotrichum clavatum* anamorph of *Reticulascus clavatus*. A. Conidia. B–D. Conidiophores of the lower layer (shorter conidiophores) with sympodially extending sporiferous apices, in culture. E–F. Conidiophores ending into a monophialide on the host. A–C from ex-type strain CBS 125296 (PCA, 14 d old), E–F from PRM 915717 (holotype). G–M. *Cylindrotrichum gorii*. G, H. Conidiophores, in culture. I. Conidia, in culture. J–L. Conidiophores, on the host. M. Conidia, on the host. G–M from CBS 879.85 (PCA, 14 d old). Scale bars: A = 10 μm; B–F = 20 μm; G, H, J–L = 20 μm; I, M = 10 μm. DIC: A–F, G–M.

Conidiophores truncate to broadly rounded at apex, short-stipitate, ascal apex with inamyloid apical annulus, 3–3.5 μm wide, 1–1.5 μm deep, 8-spored. Ascospores 14–18(–19) × 4–4.5 μm (mean ± s.e. = 15.7 ± 0.2 × 4.4 ± 0.04 μm), fusiform, 2–4-celled, with a delayed formation of second and third septa, slightly constricted at septa, mature ascospores finely verruculose, 1–2-seriate in ascus.
Colonies in vivo brown to black, hairy, effuse. Setae absent. Conidiophores macronematous, mononematous, cylindrical, straight, forming two layers. Conidiophores of lower layer shorter, 60–135 × 4.5–5 μm, pale brown, subhyaline towards apex, 2–5-septate; longer conidiophores forming an upper layer, 200–360 × 5–5.5 μm, mid to dark brown, subhyaline towards apex, up to 10-septate; conidiophores of both layers ending in a monophialide or polyphialide. Conidiogenous cells 25–37 × 3.5–5 μm, usually monophialidic, rarely polyphialidic with up to two lateral openings; collarette hyaline to subhyaline, 1.5–2 μm wide, ca. 1.5 μm high. Conidia 10.5–11 × 4–4.5 μm (mean ± s.e. = 10.2 ± 0.2 × 4.2 ± 0.04 μm), cylindrical, rounded at apex, slightly tapering, obtuse at base, 1-septate, not constricted at septum, hyaline, smooth.

Colonies in vitro after 14 d on PCA at 25 °C 14–17 mm diam, cushion-like, aerial mycelium greyish brown, margin entire, reverse dark brown. Colonies sporulating after 7–10 d
on PCA at 25 °C in darkness. 

Conidiophores macronematous, mononematous, solitary, erect, forming two layers: conidiophores of lower layer 50–100 × 2.5–3 μm, cylindrical, straight or slightly flexuous, 2–10-septate, pale brown, subhyaline to hyaline towards apex; conidiophores of upper layer up to 260 μm long, 3.5–4 μm wide, mid brown, subhyaline towards apex. 

Conidigenous cells integrated, terminal or intercalary, with up to 30 lateral phialidic openings arising from synapodial elongation, fertile apices 15–70 μm long; collettes hyaline to subhyaline, 1–1.5 μm wide, ca. 1.5 μm high. Conidia 9–12.5(−13.5) × 2.5–3 μm (mean ± s.e. = 11.6 ± 0.3 × 2.7 ± 0.05 μm), cylindrical, rounded at apex, slightly tapering, obtuse at base, 1-septate, not constricted at septum, hyaline, smooth. In PDA culture, conidia slightly smaller, 8.5–10.5 × 2.5(−3) μm (mean ± s.e. = 9.3 ± 0.1 × 2.6 ± 0.03 μm).

Specimens examined: France, Haute Garonne, Manciou, along road D635 on the way to Frechet, on submerged wood of Alnus glutinosa, 28 Feb. 2009. J. Fournier no. J.F. 09009, PRM 915717, holotype, ex-type strain CBS 125296; Rimont, Le Baup, on submerged wood of Fraxinus sp., 12 June 2009, J. Fournier no. J.F. 09154, PRM 915718, living culture CBS 125297; Auros, Rimont, road D18, 1.5 km south of the village, Le Baup, 500 m a.s.l., on submerged wood of Platanus sp., associated with Achroconiosporidium potamiae, Cosmospora sp., Savorrella immetica, 23 May 2008, J. Fournier & M. Delport no. J.F. 08139, PRM 915719, living culture CBS 125239.

Notes: Reticulascus clavatus is a common dweller of submerged wood in lotic sites in France. The anamorph does not always occur on freshly collected material, although fertile conidiophores usually appear after incubation in a moist chamber for 1–2 wk (J. Fournier, unpubl. data).

Reticulascus clavatus differs from the closely related R. tulasneorum and its C. oligospermum anamorph by verrucose mature ascospores, absence of setae among the conidiophores, which terminate with a monophialide in vivo and only rarely a polyphialide. In axenic culture (PCA, PDA) of R. clavatus, the lower layer of conidiophores terminates in polyphialides with up to 30 lateral openings (Fig. 12C, D).

Cylindrotrichum setosum Seifert, sp. nov. MycoBank MB515589. Fig. 13A–L.

Colonies in agaro farinae avenae confecto post 20 dies radium 6–7 mm attingentes, in agaro maltoso 4–5 mm. Conidiophora simplicia vel raro ramosa, stipite subhyalin vel dilute brunneo ad 200 μm longo, 1.5–2.5 μm lato, vel cellulae conidiogenae ex hyphis fasciculatis dilute brunneis, 3.5–8 μm latis singulae vel acervatae orisitae; setae seu conidiophora suprarenterans seu ex hyphis aggregatis perpendicularly orisitae, 45–80 μm longae, simplices, brunneae vel fuscae, accurulare, in parte inferiori 3.5–4 μm latae, sarcum acutum. Cellulae conidiogenae monoc- vel polyphialides, subhyalines vel dilute brunneae, amphiophores vel subulate, 6–13 μm longae, parte inferioris ellipsoidae, 3.5–7 × 2–4 μm, rachide recta vel geniculata ad 7 × 1.5–2.5 μm, 1–6 foramina conidiogena sessilia vel < 3 μm longa ferente, collare inconspicuum, rachide recta vel geniculata ad 7 × 1.5–2.5 μm, 1–6 foramina conidiogena sessilia vel < 3 μm longa ferente, collare inconspicuum, 6–13 μm longae, 1–6 foramina conidiogena sessilia vel < 3 μm longa ferente, collare inconspicuum, 6–13 μm longae. Setae sterile, pointed, distinct from the ampulliform to subulate conidiogenous cells; setae present or absent .......................... 3

Notes: Cylindrotrichum setosum is unique in the genus because of the physical separation of the conidiogenous cells in the setae. In other species, the conidiophores are seta-like and have a terminal phialide or polyphialide at the apex. In C. setosum, the conidiogenous cells tend to be clustered at the base of the setae in a manner reminiscent of species of Circinotrichum or Gyrothrix. However, the proliferation of the conidiogenous cells and the morphology of the 1-septate conidia resemble other species of Cylindrotrichum. Unlike C. setosum, microconidia have not been reported in other Cylindrotrichum species.

KEY TO ACCEPTED SPECIES OF CYLINDROTRICHUM

1. Conidia cylindrical to slightly clavate, usually wider than 2.5 μm; conidiophores seta-like but sterile setae absent ......................................... 2
2. Conidia longer than 9 μm; 8.5–13 × 3–4 μm in vivo and 9–12.5(−13.5) × 2.5–3 μm in vitro; teleomorph R. clavatum ............ C. clavatum
3. Conidia shorter than 9 μm; (5)–5.5–7.5(−9) × 3–3.5 in vivo and 7–9(−9.5) × 3–3.5 μm in vitro; teleomorph unknown .............................................. C. gori (Lunghini 1979)
4. Setae sterile, pointed, distinct from the ampulliform to subulate conidiogenous cells; telomorph unknown ........................................ C. setosum
5. Conidiophores often seta-like, with a terminal mono- or polyphialide at the apex; teleomorph R. tulasneorum .................. C. oligospermum

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GLOMERELLALES & MICROASCALES
Species phylogenetically related to *Cylindrotrichum*

**Kylindria peruamazonensis** Matsush., Matsush. Mycol. Mem. 7: 56. 1993. Fig. 14.

Specimens examined: *Cuba*, Clínaga de Zapata Matanzas, on leaf litter of *Bucida palustris*, Dec. 1991, R.F. Castañeda, INIFAT C91/111, living culture CBS 838.91; Sandi Spiritus. Las V., on leaf of *B. palustris*, 25 Aug. 1994, R.F. Castañeda, INIFAT C94/84R, living culture CBS 421.95.

**Notes:** Two strains identified as *Kylindria triseptata* were analysed (CBS 838.91, 421.95), but neither matches the fungus described by Matsushima (1975) as *Cylindrotrichum triseptatum* Matsush. in the morphology of conidiogenous cells and conidial dimensions. Our cultural observations suggest that the conidiophores, conidiogenous cells, and conidia of these strains match the description of *Kylindria peruamazonensis*. The apex of the phialide terminates with a funnel-shaped collarette unlike that of *C. triseptatum*, in which the monophasial discs lack a collarette and may elongate slightly and possess apical densely annellate proliferations. Previously such proliferations were observed in *Cacumini sorium capitulum*, the anamorph of *Chaetosphaeria decastyla*, and in the so-called *Cylindrotrichum* anamorph of *Ch. acutata* (Réblová & Gams 1999); these were considered a diagnostic character of *Xenokylindria* (DiCosmo et al. 1983). *Kylindria ellisi* also has 3-septate hyaline conidia, but differs from *K. peruamazonensis* by a hardly visible collarette and symmetrical, 3-septate conidia rounded at both ends, without an apiculus.

Unlike *K. peruamazonensis*, cylindrical to oblong, septate conidia with a tapering, obtuse to papillate base with a laterally displaced hilum are typical of several *Kylindria* species, namely *K. excentrica*, *K. pluriseptata*, and *K. triseptata*. *Kylindria excentrica* has 3-septate conidia, but differs from *K. peruamazonensis* in absence of a collarette and much larger conidia (27.5–35 × 7.5–8 μm; Bhat & Sutton 1985). *Kylindria peruamazonensis* is probably the species morphologically most similar to *K. triseptata*; it differs from the latter by the presence of a collarette, either lacking or with a very short elongation of the phialides above the collarette, with several percurrent proliferations, the unusual formation of imbricate conidia, and production of a microconidial form in *vitro* (macroconidia 12.5–23 × 4–7.5 μm; Matsushima 1993). Symphalial proliferation of the apex of the conidiogenous cell was not observed in cultures of *K. peruamazonensis* and *K. triseptata* (Matsushima 1975, 1993). Unlike *K. peruamazonensis*, *K. pluriseptata* has 6–8-septate and much longer conidia (35–40 × 5–6 μm; Castañeda 1987).

**Additional anamorph species affiliated with the Plectosphaerellaceae**

Our phylogenetic analyses place the anamorph species *Stachylyidium bicolor* (DAOM 226658) in a basal position in the family *Plectosphaerellaceae* (Figs 1–3). Several anamorph genera in this family have verticillate conidiophores such as *Acrostalagmus* and *Verticillium*. *Stachylyidium bicolor*, the type of its genus, produces erect, roughened, verticillate conidiophores, often with additional verticillate axes emerging from the main stipe; this results in a more complex conidiophore than in other similar genera. As with the species of the other genera, the conidiogenous cells are phialidic but taper strongly near the tip, and the conidia are oblong-ellipsoidal and accumulate in slime. We consider *S. bicolor* sufficiently distinct both morphologically and phylogenetically from *Acrostalagmus* and *Verticillium* to continue to be recognised as a distinct genus.

The phylogenetic analyses demonstrate that the common tropical hyphomycete described and illustrated by Seifert (1985) as *Stilbella annulata* is a member of the *Plectosphaerellaceae* and a sister species to *Acrostalagmus luteoalbus*, the type of the genus. Both *S. annulata* and *A. luteoalbus* produce auroconidia in bright orange to reddish slimy masses; in both species the reddish pigmentation sometimes also colours the phialides. The conidiophore branching of *S. annulata* lacks the regular verticillate aspect of *A. luteoalbus*, being intermediate between verticillate and penicillate. The synnemata of *S. annulata* and their conspicuously lobed marginal hyphae are also deviating characters from the present generic concept of *Acrostalagmus*. Given the well-supported phylogenetic relationship between these two species, it seems preferable to focus on the similarities between these species rather than the differences and to transfer *S. annulata* to *Acrostalagmus* rather than propose a new genus. This modifies the generic concept of *Acrostalagmus* to include synnematosus species:

**Acrostalagmus annulatus** (Berk. & Broome) Seifert, comb. nov. MycoBank MB518663. Basionym: *Stilbum annulatum* Berk. & Broome, Grevillea 3: 63. 1874. (holotype: no. 6045, on Brassica sp., Car. Inf., herb. Berkeley, 1879, K.

≡ *Stilbella annulata* (Berk. & Broome) Seifert, Stud. Mycol. 27: 58. 1985

**Note:** For full synonymy and examined material, refer to Seifert (1985).

**MICROASCALLES**

Kirk et al. (2008) and Cannon & Kirk (2007) included four families in the Microascales, i.e. Ceratocystidaceae, Chadeaufiellaceae, Halosphaeriaceae, and Microasaceae, although the Ceratocystidaceae is not validly published and was not listed among accepted fungal families by Hawksworth & David (1988). On the basis of our results from nCSU rDNA and three-gene phylogenies (Figs 2, 3), the following families are accepted in the order, Microascales, Halosphaeriaceae, Ceratocystidaceae, which is validated here, and Gondwanamycetaceae fam. nov. We accept the Halosphaeriaceae as a family of the Microascales (Kirk et al. 2008), although they are often placed separately in their own order (Spatafora et al. 1998).

Recent studies by Spatafora et al. (1998), Kong et al. (2000), and Zhang et al. (2006) suggested that the Microascales may prove to be paraphyletic or polyphyletic. In our study, the cladogram based on nCSU rDNA sequences (Fig. 1) provided no support for any of the backbone branches of the four families that we accept in the order. In the phylogenies based on nCSU rDNA and the combined nCSU-nCSU-RPB2 data sets (Figs 2, 3), the Microascales appear as a monophyletic grouping of four families, all with high branch support. In both phylogenies the Microascales are divided into two major subclades, one containing the Halosphaeriaceae and Microasaceae and a second subclade with the Ceratocystidaceae and Gondwanamycetaceae. The nCSU and the three-gene phylogeny did not support the putative para- or polyphyletic of the Microascales.

The family Microasaceae and order Microascales were introduced by Luttrell (1951) and were later validated with Latin descriptions by Malloch (1970) and Benny & Kimbrough (1980),
respectively. Luttrell (1951) described the Microascaceae for taxa with beaked ascomata and evanescent, nonstipitate asci disposed irregularly throughout the filamentous centrum. Corlett (1963, 1966) confirmed the observations of Luttrell (1951) and described the asci of Microascus and Petriella as developing directly from the cells of the ascogenous hyphae and not from croziers. Members of the Microascaceae appear to have evolved away from a hymenial configuration; in the microascaceous centrum a peripheral layer of paraphysoidal elements develops that grows inward towards the ascogenous hyphae (Benny & Kimbrough 1980). Malloch (1970) redefined the Microascaceae to include both ostiolate and nonostiolate taxa; ascocarps are darkly pigmented, usually hairy, rarely glabrous; asci arise singly or in chains, without croziers, evanescent, irregularly disposed throughout the centrum; ascospores are reddish brown to copper-coloured with germ pores, dextrinoid when young and smooth. The genera of the Microascaceae differ in the manner of ramification of ascogenous hyphae and the formation of asci among the interthecial elements. The associated anamorphs are of the anellidic type, e.g. Cephalotrichum and Scopulariopsis. Aleuricconidia as in Petriella and arthroconidia as in Kernia also occur (Malloch 1970, 1971).

**Ceratocystidaceae**

The family level classification of Ceratocystis has been discussed since the genus was removed from the Ophiostomatales (Barr 1990, Samuels 1993). In recent literature the genus has sometimes been placed in the Chadefauduellaceae, while other authors placed it in its own family, the Ceratocystidaceae, as proposed by Locquin (1972, as "Ceratocystaceae"). The name Chadefauduellaceae predates
the *Ceratocystidaceae*, but these families are phylogenetically distinct (see below). The *Ceratocystis* clade is a monophyletic group centred on species of *Ceratocystis* or anamorphic species of the *Chalara*-like genus *Thielaviopsis*. *Ambrosiella xylebori*, type of this anamorphic genus, occurs in a monophyletic clade together with *Ceratocystis*, now separated from similar anamorphs of the *Ophiostomatales* that are classified in *Raffaelea* (Cassar & Blackwell 1996, Jones & Blackwell 1998, Harrington et al. 2010).

The teleomorph genus *Curnuvesica* shares similar characters of centrum ontogeny, ascospore morphology, evanescent asci, and associated anamorphs with *Ceratocystis*, and may belong to the same clade. Because there are no available nLSU sequences for *Curnuvesica*, its relationship to *Ceratocystis* and *A. xylebori* could only be explored with the nCSSU rDNA phylogeny (Fig. 2). *Curnuvesica falcata*, with a *Chalara*-like anamorph (Viljoen et al. 2000), falls in a basal position with these taxa in a monophyletic clade.

These four genera, *Ambrosiella*, *Ceratocystis*, *Curnuvesica*, and *Thielaviopsis*, constitute a family of their own, which has no valid name. The family name *Ceratocystidaceae* (as "Ceratocystaceae") proposed by Locquin (1972) was never validly published. It is phylogenetically well-established and is validated here.

**Ceratocystidaceae** Locq., ex Réblová, W. Gams & Seifert, fam. nov. MycoBank MB515438.

*Ceratocystaceae* Locq., Rev. Mycol., Supplément, 1 Table. 1972, nom. inval., Art. 36.

Stromata absent. Ascomata perithecia, fusca usque nigra, saepe aggregata, collo longo angustato et hyphis ostiolaris prostrudentibus, divergentibus praedita. Paries tenuis. Structura interrascals nulla. Asci unimicroni, catenati, saepe evanescentes, 8-spori. Ascosporae hyalinae, forma variabiles, 0–1-septatae, saepe pariete partim tenuis. Structura interascalis nulla. Asci unitunicati, catenati, saccati, evanescentes, longo angustato et hyphis ostiolaribus protrudentibus, divergentes praedita. Paries ascomatum fragilis. Filamenta interthecialia nulla. Asci unitunicati, evanescentes.

**Ceratocystaceae** nov.

**Gondwanamycetaceae**

Species of *Gondwanamycetes* and their *Custinghamophora* anamorphs form a strongly supported monophyletic clade (Figs 1–3) that is sister to the *Ceratocystidaceae*. The diagnostic characters of this clade include the apparent absence of interascal filaments in the ascomatal centrum and hyaline, allantoid ascospores with a hyaline sheath giving the spore a falcate to lunate appearance. The teleomorphs, described either from infructescences of *Protea* (Wingfield et al. 1988, Marais et al. 1998) or from sapwood associated with *Scolytidae* (bark beetles) (Bright & Torres 2006, Kolařík & Hulcr 2008), produce dark, globose perithecia with a long, filiform neck, evanescent asci, and hyaline, fusiform ascospores with or without a gelatinous sheath.

Detailed observations on the ontogeny of *asci* and centrum of *Gondwanamycetes* are lacking. Based on the phylogenetic position of the genus, it is likely to be similar to that of the *Ceratocystidaceae*. The morphology of the anamorphs of *Gondwanamycetes* is distinctive. The conidiophores are erect, darkly pigmented, paler towards the apex, and either monoverruculate, sometimes with a terminal vesicle or divergently penicillate with whorls of phialides producing hyaline conidia. The conidigenous locus is located at the base of the shallow collarette. The terminal vesicle was not observed in the anamorph of *Gondwanamycetes scolytodis* and *Custinghamophora cetrics*, both associated with bark beetles in *Cecropia* (Kolařík & Hulcr 2008). The conidogenesis of *Custinghamophora* (as *Knoxdaviesia proteae*), the anamorph of *Gondwanamycetes proteae*, observed with fluorescence microscopy, TEM, and SEM, was illustrated by Mouton et al. (1993). After discharge, conidia adhere in slimy droplets on the phialide apices. In contrast, the phialidic conidia of species of the *Ceratocystidaceae* are formed in long chains deep within the venter of the cylindrical phialide.

The taxonomic relationships of the anamorph genera *Knoxdaviesia* and *Custinghamophora*, both phylogenetically related to this family, have been discussed by others, e.g. Viljoen et al. (1999), Kolařík & Hulcr (2008). Although the genera appear morphologically identical as originally described, they differ in their ecological behaviour. Species of *Custinghamophora* occur in compost, whereas species of *Knoxdaviesia* associated with *Gondwanamycetes* were first observed in infructescences of *Protea* spp. infested by insects (Wingfield et al. 1988, Marais et al. 1998). The fact that some recently described species of *Gondwanamycetes* and *Custinghamophora* are associated with *Scolytidae* (bark beetles) (Bright & Torres 2006, Kolařík & Hulcr 2008) raises the possibility that the originally reported ecological distinction might have been an artifact of intense sampling of *Protea* in a relatively narrow geographical area in the Western Cape Province of South Africa. Based on molecular and morphological features, Kolařík & Hulcr (2008) considered *Knoxdaviesia* and *Goidanichia* to be synonyms of *Custinghamophora*. We prefer to recognise *Goidanichia* as distinct because of the *Aspergillus*-like vesicles on the conidiophores of the only species, *G. barroni*.

We recognise this clade as a distinct family in the *Microascales*, proposed here as the *Gondwanamycetaceae*.

**Gondwanamycetaceae** Réblová, W. Gams & Seifert, fam. nov. MycoBank MB515439.

Stromata absent. Ascomata perithecia, nigra, collo comparate longo praedita, apicem versus angustata, ostiolum hyphis divergentibus praeditum. Paries ascomatum fragilis. Flamenta interthecialis nulla. Asci unimicroni, evanescentes. Ascosporae hyalinae, aseptatae, fusiformes, lunatae vel falcatae, vagina gelatinosa...
Chadefaudiellaceae

Chadefaudiellaceae was described and validly published by Benny & Kimbrough (1980) for the coprophilous genus Chadefaudia. Cannon & Kirk (2007) added a second genus to the family, Faureлина (Locquin-Linard 1975). Locquin-Linard (1973) and Parguey-Leduc (1977) placed the Chadefaudia in the Microascales because of its perithecial acomata, catenate asci, and characteristic centrum structures, i.e. asci arising from a fertile layer lining the bottom of the cavity, aseptate hyphae ramifying upwards, asci differentiated without croziers and liberated by basal dissolution to float free in the centrum (Benny & Kimbrough 1980). Ascospores are 1-celled, nondextrinoid, striate, and lack germ pores. No anamorph has been reported. Faureлина was described for coprophilous, cleistothecial fungi, otherwise reminiscent of Chadefaudia, but differing by dextrinoid ascospores, and the absence of apical anastomosing setae on its ascomata. The ascomatal wall of Faureлина is cephalothecid and the asci are catenate, irregularly disposed in the centrum at maturity, characters reminiscent of Chadefaudia (Udagawa & Furuya 1973, Furuya 1978, von Arx et al. 1981). Von Arx (1978) and von Arx et al. (1981) regarded the anamorph of Faureлина as similar to the Arthrographis anamorph of Pithoascus langeronii, producing arthroconidia and secondary small blastoconidia in axenic culture (CBS 126.78).

The classification of Faureлина has been problematic. Despite the similarities with Chadefaudia noted by Locquin-Linard (1975), Parguey-Leduc & Locquin-Linard (1976) concluded that Faureлина should be placed in the Loculoascomycetes. Faureлина was later transferred by von Arx (1978) to the Microascales because of its dextrinoid ascospores, which lack germ pores. He speculated on a relationship with Neurospora in the Sordariaceae (Sordariomycetes), which is characterised by elongate, striate ascospores with apical germ pores, and an anamorph with 1-celled, inflated arthroconidia or perhaps even with the Testudinaceae (Dothideomycetes). Benny & Kimbrough (1980) accepted Faureлина in the Pithoascaceae (= Microascales fide Kirk et al. 2008), a family erected for members of the Microascales with arthroconidial anamorphs and narrowly fusoid or naviculate ascospores. Recently both genera were placed in the Chadefaudiellaceae, Microascales (Cannon & Kirk 2007). This was in part based on the conclusions of Tang et al. (2007), who sequenced a single strain of Faureлина indica (CBS 126.78) and obtained nLSU, nSSU, and RP2 sequences identical to those of Ceratocystis fimbiıata, the type species of Ceratocystis.

We studied two authentic strains of Faureлина indica, the ex-type strain CBS 126.78 and CBS 301.78. They both grew slowly and mature ascomata did not develop on OA after 2 mo, but an arthroconidial anamorph with 0–1-septate conidia was observed similar to that illustrated by von Arx et al. (1981). No structures resembling phialidic or Ceratocystis-type ascomata were produced. We generated new ITS and nLSU sequences (ITS: GU291802; nLSU: GU180653, GU180654) for these two strains. Phylogenetic analysis of nLSU sequences (Fig. 5) suggests a relationship with the Didymellaceae (Pleosporales, Dothideomycetes). ITS sequences (phylogeny not shown) were similar to those of Erremomyces and Arthrographis species (90–91% overall similarity), which also have arthroconidial anamorphs. We are confident that our sequences represent the fungus described by von Arx et al. (1981); those reported by Tang et al. (2007) were based on a different fungus. Our morphological and molecular studies fail to support the phylogenetic relationship of Faureлина with Ceratocystis suggested by Tang et al. (2007).

Based on these results, we confirm the hypothesis originally proposed by Parguey-Leduc & Locquin-Linard (1976) that Faureлина originated in the group of fungi with ascolocular development. Based on nLSU sequences, we cannot confirm a close relationship of Faureлина with the Testudinaceae (von Arx 1978) or the Erremomyctaceae; the latter includes the morphologically similar Arthrographis (Fig. 5).

This phylogenetic reevaluation eliminates the Chadefaudiellaceae as an appropriate family name for the Ceratocystis clade. Chadefaudia is morphologically slightly different from Faureлина. A further molecular analysis may lead to a re-establishment of the Chadefaudiellaceae in the Microascales, but with the exclusion of Faureлина from the family and distinct from the Ceratocystidaceae.

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