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An updated multigene phylogeny of *Leotiomycetes*

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Abstract: A paper by Johnston and others published in 2019 provided three *Leotiomycetes*-wide phylogenies, one based on genomes, one a multigene phylogeny with up to 15 genes, and one based on ITS sequences. The genomic and multigene phylogenies provided a backbone phylogeny for the class that has proven to be robust, providing a phylogenetically stable concept for the large order *Helotiales*. However, a lack of genomic data for the clades outside of *Helotiales*, towards the root of the tree, meant that relationships in this part of the tree remained somewhat poorly resolved. The ITS phylogeny, although phylogenetically much less informative, provided a wider taxon coverage, focussing on the type species of genera not otherwise treated for which ITS data was available. This paper treats genera listed as *Leotiomycetes* in the Outline of Fungi 2024. It incorporates newly available DNA sequence data and taxonomic changes, especially for genera, families, and orders published since 2019, into the 2019 multigene and ITS analyses. The genomic phylogeny is not updated.

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INTRODUCTION

The pre-molecular classification of fungi now recognised as *Leotiomycetes* was developed almost entirely based on the morphology of the sexual states. In a few cases, such as the pezicula-like fungi and *Sclerotiniaceae*, where links between sexual and asexual morphs of several groups of plant pathogens have long been recognised, the asexual morphology had also been incorporated into historical taxonomic concepts.

Following the widespread use of molecular sequencing technologies, it has been recognised that the morphological diversity of asexual morphs of *Leotiomycetes* is very wide, and that many genera known from their asexual morphs alone are *Leotiomycetes*. The taxa with no known sexual morph were often first detected in cultures grown from host tissue where they live as pathogens, leaf and root endophytes, mycorrhizas, and from fresh water.

Molecular phylogenies allow both the morphologically rich sexual morphs and the often morphologically cryptic asexual morphs to be incorporated into phylogenies and hence into a modern, phylogenetically-based *Leotiomycetes* classification. These phylogenies also allow environmental DNA sequence data to be linked to taxa with a known lifestyle, hence enabling ecological interpretation of the unnamed diversity detected in environmental DNA sampling projects. *Leotiomycetes* are often amongst the most frequently detected species in such projects, perhaps because of the diversity of lifestyles found amongst *Leotiomycetes* (Johnston *et al.* 2019, Quandt & Haelewaters 2021, Wijayawardene *et al.* 2024).

To maintain the utility of phylogenetic identification methods, reinterpretation of relationships suggested by newly generated DNA sequence data, and the impact those data have on existing classifications, need to be continually updated. This paper updates the 15 gene multigene and ITS-based phylogenies published by Johnston *et al.* (2019). In recent years, the rate of description of new genera and families has increased (Table 1). Since the Johnston *et al.* (2019) paper was published, four new orders have been proposed, 17 new families established and approximately 84 new genera described. Most of these new taxa have DNA sequence data available. In addition, several taxa treated only in the ITS-based phylogeny provided by Johnston *et al.* (2019), now have multigene data available. As well as expanded taxon coverage, 93 additional genomes are available for the analyses presented here. These are important because several of the most informative genes used

Table 1. Number of new *Leotiomycetes* families and genera described over the last 65 years, average number of taxa per year across 10-year periods. Based on data in Index Fungorum 19 of the *Leotiomycetes* families in current use were named between the years 1826 and 1960, from 1960 to 2024 an additional 38 families were named.

Period	Average number new taxa per year	
	Genera	Families
1960s	2.8	0.1
1970s	5.5	0.2
1980s	6.3	0.3
1990s	3.7	0.2
2000s	3.4	0.2
2010s	7.7	2.5
2020s	12.2	1.2

in the Johnston *et al.* (2019) multigene analysis cannot be amplified using Sanger sequencing because reliable primers are not available, but they can be readily extracted from draft genome assemblies. These highly informative genes were selected based on a phylogenetic informativeness analysis using PhyDesign (López-Giráldez & Townsend 2011) to select genes likely to be most informative at deep levels within the phylogeny.

MATERIALS AND METHODS

GenBank and JGI were searched for DNA sequence data that had been generated for the genera listed as *Leotiomycetes* in the '2024 Outline of Fungi and fungus-like taxa' (Hyde *et al.* 2024). Wherever possible, sequence data for these genera were derived from type specimens of the generic types, or from specimens identified as those species. Where multiple records were available for a generic type, the ITS sequences were compared to ensure that they represented the same species. Where they represented more than one species, the source of the DNA sequences was checked and an ad-hoc assessment was made regarding the reliability of the identifications of the specimens. Whenever possible, identifications of the specimens used to generate genomes were checked using single gene phylogenies incorporating selected genes extracted from the genomes.

For the newly generated genomes, genomic DNA was extracted from fungal cultures by first harvesting mycelium and drying it using a concentrator plus vacuum centrifuge (Eppendorf). The dried tissue was ground into a fine powder using a 2 mm steel bead and a MM400 bead mill (Retsch GmbH). Genomic DNA was then extracted using the QIAamp DNA Mini Kit (Qiagen) on a QIAcube Connect automated system (Qiagen). The extracted DNA was further purified using AMPure XP magnetic beads (Beckman Coulter). The DNA quality and quantity were assessed using a Qubit fluorometer (Thermo Fisher Scientific), a spectrophotometer, and agarose gel electrophoresis. Sequencing was performed by Macrogen (South Korea) or Genewiz (China), using the Illumina Truseq Nano DNA kit and the VAHTS Universal Pro DNA Library Prep kit respectively. Libraries were prepared and sequenced using 150 bp paired-end reads on the Illumina NovaSeq 6000 platform. Each sample yielded over 5 Gb of raw sequencing data, with > 93 % of bases achieving a Q30 quality score. Read trimming and adapter removal were performed using fastp v. 0.23.2 (Chen *et al.* 2018). De novo genome assembly was carried out using SPAdes v. 4.0.0 (Prjibelski *et al.* 2020) with the "isolate" option. Assemblies were polished with Pilon v. 1.24 (Walker *et al.* 2014) and contigs shorter than 500 bp were removed. Genome assembly completeness was assessed using BUSCO v. 5.8.2 (Manni *et al.* 2021) against the "fungi_odb10" lineage dataset.

Methods for the multigene analysis follow Johnston *et al.* (2019). The sequences available for each gene were aligned using MAFFT (Katoh & Standley 2013) as implemented in Geneious v. 10 (Dotmatics, New Zealand). The ends were manually trimmed and introns were removed manually; all remaining data were then concatenated using Geneious v. 10. Maximum likelihood (ML) analyses were run with IQ-TREE (Nguyen *et al.* 2015, Chernomor *et al.* 2016), using models selected by ModelFinder (Kalyaanamoorthy *et al.* 2017) for each partitioned gene; ultrafast bootstrap (BS) analysis with 1000 replicates estimated branch support in the ML tree (Hoang *et al.* 2018). *Xylaria hypoxylon* and *Neurospora crassa* were used as outgroups. The taxa and genes included in the alignment are provided in Table S1 and the partitions and models used for the multigene analysis are in Table S2 (https://doi.org/10.7931/e59n-b194).

The DNA sequences used for the ITS phylogeny are provided in Table S3. Sequences were aligned using MAFFT, trimmed to begin at the 5′ starting motif 5′-ATCATTA-3′ and to end at the 5′ start of the 28S at 5′-TGACCT-3′. The ITS maximum likelihood analysis used RAxML (Stamatakis 2014) as implemented in Geneious v. 10, with the GTR GAMMA model.

RESULTS AND DISCUSSION

A summary of the DNA sequence data available for each of the genera listed as *Leotiomycetes* in Hyde *et al.* (2024) is provided in Table S4. For each genus the type is listed, and an indication whether ITS, multigene or genome data are available for that species, along with whether that data was derived from the type specimen. Where data is not available for the type species, but other species from the same genus were included, the species treated are listed.

Table 2 summarises the number of genera treated in the multigene and ITS phylogenies and provides a comparison with the numbers treated in the earlier Johnston *et al.* (2019) study. The number of genomes is important because these allow a full complement of 15 genes to be treated for a specimen (see Introduction). A version of the multigene phylogeny is provided as Fig. S1 as an Adobe PDF file with gene coverage included in the specimen label for each specimen.

Several new *Leotiomycetes* genomes are reported in this paper (bold in Table S1), 13 from New Zealand and one from Argentina, accessioned as NCBI Bioproject PRJNA1270366. Most of these genome assemblies had BUSCO scores > 99 % (Manni *et al.* 2021). All 15 target loci were successfully extracted from 13 of the assemblies; one was missing from one of the assemblies. In total, data extracted from 144 genomes were included in the multigene analysis (Table S1).

Multi-locus phylogeny (Figs 1–6)

Most families are resolved as monophyletic clades and most of these clades have 100 % bootstrap support. The large order *Helotiales* is consistently strongly supported. Johnston *et al.* (2019) discussed whether *Helotiales* could be divided into several smaller order-level taxa. These were discussed as informal clades (e.g., sclerotinioid clade, helotioid clade, etc). The broader taxon coverage included in this paper challenges those earlier concepts and here we conclude that there is no obvious sensible or useful scheme that could be used to break apart *Helotiales* above the family level.

Taxa outside *Helotiales* include several orders that are monotypic, containing a single family – e.g. *Marthamycetales* for *Marthamycetaceae*, *Chaetomellales* for *Chaetomellaceae*, etc. *Thelebolales* sensu Quijada *et al.* (2022) is strongly supported and contains three strongly supported, monophyletic families. *Rhytismatales* is strongly

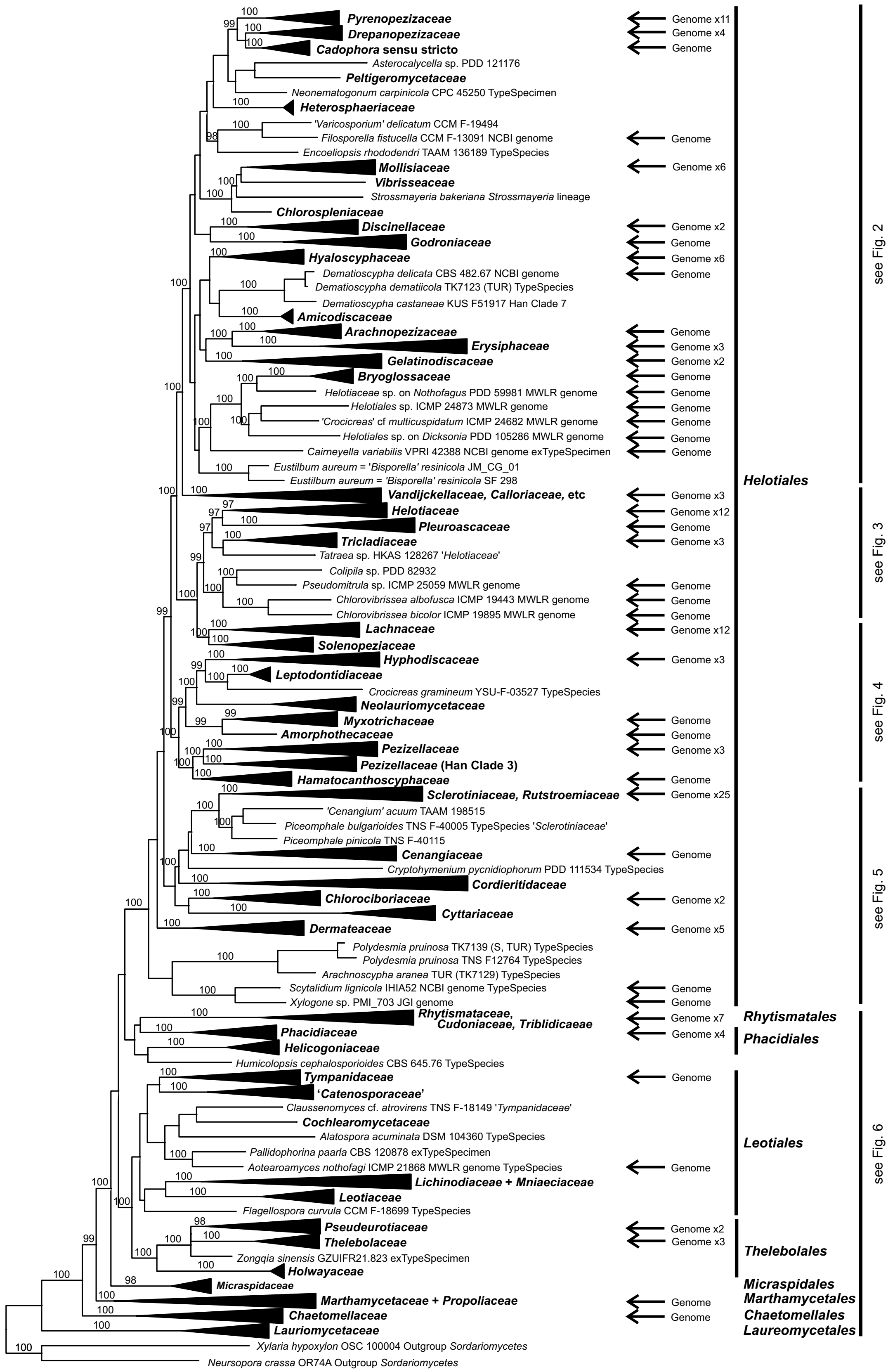

Fig. 1. Summary tree from the ML analysis based on up to 15 concatenated loci. Names for the collapsed family level clades are those accepted in this paper and generally the clades follow Hyde *et al.* (2024). Order-level taxa are indicated on the right, together with references to expanded trees, Figs 2–6. Taxa with available genome-scale data are indicated. These data are especially valuable because they generally provide sequences for all 15 loci included in the multigene analysis. Bootstrap values 95 % or greater indicated. Figs 2–6 provide details of the genera and species treated in each clade.

supported, but the family *Rhytismataceae* is paraphyletic, the families *Cudoniaceae* and *Triblidiaceae* forming subclades within *Rhytismatales*. However, two of the orders outside *Helotiales*, *Leotiales* and *Phacidiales*, each comprising several families plus additional incertae sedis genera, are accepted here mainly for historical reasons. They have poor bootstrap support and *Phacidiales* is not monophyletic. The often-poor support for a higher classification in this part of the phylogeny could reflect lower levels of genome-scale coverage, hence missing several of the loci that are highly informative at deep levels in the phylogeny.

ITS phylogeny (Fig. S2)

Although *Leotiomycetes*-wide phylogenies based on ITS or ITS + LSU sequences have many poorly supported branches and can generate misleading phylogenetic relationships, the ITS-based tree presented here often groups taxa within the same family together within the phylogeny. This is despite the MAFFT generated alignment appearing visually to be very messy to the human eye. Bootstrap support values are generally low throughout the phylogeny and deeper relationships, such as those between family-level clades or at the level of order, are poorly supported. Long branch attraction should always be kept in mind for taxa with no close relatives in the ITS analysis and because of the low levels of support for many branches, branching patterns can change depending on taxon sampling, especially for taxa with no close relatives. Examples in the ITS analysis provided here include the genera *Arboricolonus* and *Medeolaria* falling amongst *Dermateaceae*, and the families *Amicodiscaceae*, *Bryoglossaceae* and *Godroniaceae* as subclades amongst *Hyaloscyphaceae*. The positions of these taxa are unstable between analyses with slightly different sets of taxa, but always on long branches.

Several families are split across several clades in the ITS phylogeny, these may cluster together with no bootstrap support, or they are often just in the same part of the tree, in several adjacent clades. Depending on taxon selection, these adjacent clades sometimes split apart. Often the different clades in the ITS phylogeny reflect phylogenetic structure within the family in the multigene analysis.

The value of the ITS tree is that it enables more than twice as many genera to be treated compared to the multigene analysis (Table 2). Assuming those genera are represented by reliable DNA sequences from accurately identified specimens, it allows some of them to be placed phylogenetically within a family. For example, the ITS sequence from the epitype of the type of *Miricatena*, *M. prunicola*, places this genus in *Drepanopezizaceae* for the first time (Fig. S2). Reasonable confidence can be given to the placement of *Brachyalara*, a monotypic genus with type *Brachyalara straminea*, in *Hamatocanthoscyphaceae* for the first time, based on isolate AKA2 from Görke & Apel (2016). Although no ITS sequence is available from the type specimen of *B. straminea*, there is a 485 bp overlap between the 5' end of the sequence deposited for AKA2 (MK533015) and the 3' end of the SSU sequences deposited from the type specimen of *B. straminea* (HQ609482) and this overlapping region is identical. This, together with the shared *Bulgaria inquinans* host, suggest that isolate AKA2 has been correctly identified.

An example with less confidence is *Geniculospora*, belonging in *Discinellaceae* rather than *Tricladiaceae* in Fig. S2 based on an ITS sequence from a specimen identified as the type, *G. inflata* (isolate VG79-1, Franco-Duarte *et al.* 2022), but the basis of the morphological identification of this isolate is not clear.

Tatraea is placed in *Helotiaceae* in Hyde *et al.* (2024). The genus is represented here by a specimen identified as the type *T. dumbirensis* along with a specimen identified as *Tatraea* sp. (HKAS 128267). These specimens are congeneric within the ITS phylogeny but separate from other *Helotiaceae*. The *Tatraea* sp. specimen is also in the multigene phylogeny and this also places it in *Helotiales* but outside *Helotiaceae*. The genus is accepted here as *Helotiales* incertae sedis.

Myxocephala and *Malbranchea* were included in Johnston *et al.* (2019) in error — *Myxocephala* is *Sodariomycetidae*; the type of *Malbranchea*, *M. pulchella*, is *Onygenales* [although the specimen that was used to represent the genus in Johnston *et al.* (2019), identified as *M. flavorosea* in GenBank (MH037296), is *Myxotricaceae*]. In the ITS phylogeny in the 2019 paper *Myxocephala* was close to a specimen identified in GenBank as the type of *Gloeotinia*, *G. temulenta* (GenBank DQ235697) and a specimen identified as *Lauriomyces sakaeratensis* (GenBank KX649976), but BLAST searches shows that both GenBank accessions were based on *Hypocreales* contaminants. This 'clade' containing these diverse specimens in the Johnston *et al.* (2019) ITS phylogeny was surely the result of long branch attraction.

Comments on the taxa treated

Brief comments are provided for each of the families treated, these notes are presented alphabetically. The comments include a comparison of phylogenetic support and taxon coverage for the family in the multigene and ITS phylogenies.

Table 2. DNA sequence data available for *Leotiomycetes* families and genera listed in 2024 Outline of Fungi (Hyde *et al.* 2024). There are two families with no DNA sequence data, *Ascodichaenaceae* and *Lahmiaceae*; *Lichinodiaceae* has no ITS data. The multigene values include data where genes have been extracted from genomes. The values in parentheses are those from Johnston *et al.* (2019).

	Families	Genera	Generic types	Generic type specimens
Total	60	720	715*	715
Genomes	31 (21)	84 (38)	42 (11)	9 (2)
Multigenes	50 (31)	231 (165)	162 (77)	49 (22)
ITS	58 (39)	565 (316)	376 (151)	150 (78)

* Based on data in Index Fungorum.

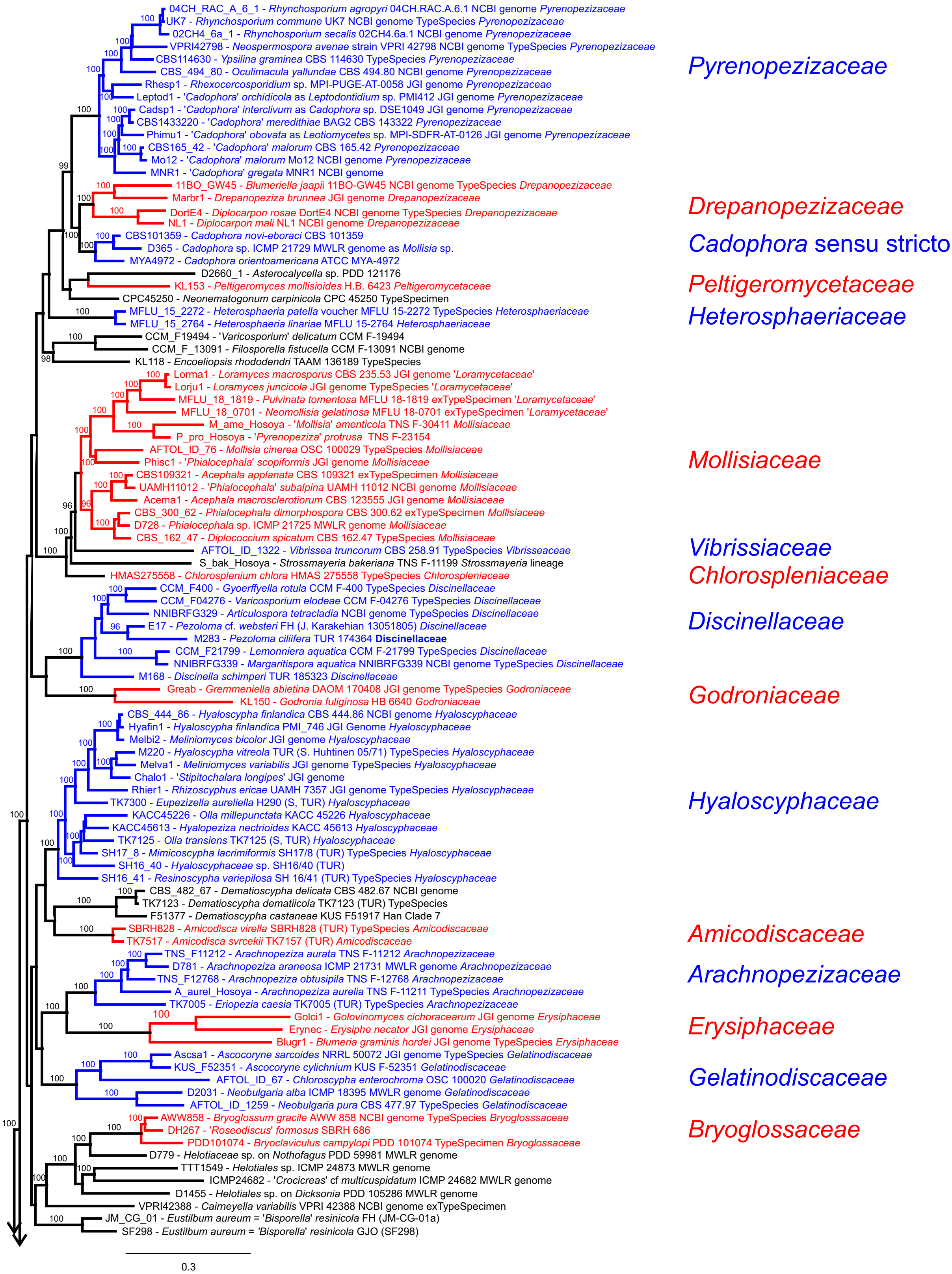

Fig. 2. Detail from Fig. 1. ML tree based on 15 concatenated sequences for specimens from the families *Pyrenopezizaceae*, *Drepanopezizaceae*, *Heterosphaeriaceae*, *Mollisiaceae*, *Vibrisseaceae*, *Chlorospleniaceae*, *Discinellaceae*, *Godroniaceae*, *Hyaloscyphaceae*, *Amicodiscaceae*, *Arachnopezizaceae*, *Erysiphaceae*, *Gelatinodiscaceae* and *Bryoglossaceae* from *Helotiales*. The labels for taxa include the voucher specimen from which the sequences were obtained, the type status of the specimen (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus) and the source of the genome data for those that have had their genome sequenced. Family level clades are coloured blue or red as a visual cue, taxa in black are *Helotiales* incertae sedis. Bootstrap values 95 % or greater indicated. The loci available for each specimen, and the sources of the sequence data, are provided in Table S1.

Amicodiscaceae (Figs 2, S2)

Amicodiscaceae is well resolved in the multigene phylogeny, with a poorly supported sister relationship to another strongly supported monophyletic clade containing *Dematioscypha* species.

Amicodisca was placed in *Hyaloscyphaceae* in Hyde *et al.* (2024), with *Amicodiscaceae* presumably treated as a synonym of *Hyaloscyphaceae*. Although sister to *Hyaloscyphaceae* in the ITS phylogeny, there is no support for that position in the multigene phylogeny and we accept *Amicodiscaceae*.

Amorphothecaceae and *Myxotrichaceae* (Figs 4, S2)

A clade *Amorphothecaceae* + *Myxotrichaceae* is well resolved in both the multigene and ITS phylogenies. The ITS phylogeny includes an additional two genera, both represented by the type specimen of their respective types, as well as the type specimen of the type of *Oidiodendron*, *O. fuscum*.

In the multigene phylogeny these families are represented by the type of *Amorphotheca*, a species of *Oidiodendron* that is close to type of the genus (based on ITS), and the type of *Myxotrichum*. Although phylogenetically there is a case for placing these two families in synonymy, *Amorphotheca* is sister to a monophyletic *Myxotrichaceae*, and differences in lifestyle perhaps warrant two families being retained.

Arachnopezizaceae (Figs 2, S2)

Arachnopezizaceae forms well-resolved clades in both the multigene and ITS phylogenies. The ITS phylogeny treats an additional two genera, both represented by their type specimens.

The multigene analysis places *Arachnopezizaceae* sister to *Erysiphaceae* with strong support.

Bryoglossaceae (Figs 2, S2)

Bryoglossaceae forms a well-resolved clade of moss-inhabiting fungi in both the multigene and ITS phylogenies. The multigene phylogeny includes a specimen identified as ‘*Roseodiscus*’ *formosus*, but this is not congeneric with a specimen identified as the type of the genus, *Roseodiscus rhodoleucus*. The ‘*R*’. *formosus* specimen was noted as moss-inhabiting (Baral & Haelewaters 2015).

The ITS phylogeny includes the type specimen of *Neocudoniella radicella* (UAMH 5794), a fungus isolated as a possible mycorrhiza from fine *Picea* roots amongst moss (https://www.uamh.ca/details.php?id=5794) but DNA sequence data is not available for the type of the genus, *N. jezoensis*.

In the multigene phylogeny, *Bryoglossaceae* has a strongly supported sister relationship with several unnamed litter-inhabiting species from New Zealand, along with the Australian, root-inhabiting *Cairneyella variabilis*. Perhaps *Bryoglossaceae* could be expanded to include this wider group of taxa but whether there are morphological features that could be used to diagnose this larger clade is not known.

‘*Catenosporaceae’* (Figs 6, S2)

An informal family name for a group of fern-inhabiting fungi in the informal genus ‘*Catenospora*’ from the Younginger (2018) PhD thesis. The sequences are in GenBank, the informal names in the thesis. These taxa have been included here as these data help resolve relationships in this part of the *Leotiomycetes* phylogeny.

Amongst ‘*Catenospora*’ in the ITS phylogeny is another fern-inhabiting fungus, the type of *Scolecoleotia*, *S. eriocamporesi*, represented here by its type specimen. If there is morphological support for these taxa being congeneric, *Scolecoleotia* will provide a formal generic name for ‘*Catenospora*’ sensu Younginger (2018).

Chaetomellaceae (Figs 6, S2)

Chaetomellaceae forms a well resolved clade in both the multigene and ITS phylogenies. The ITS phylogeny includes an additional two genera but neither is represented by their types. Sister to *Chaetomellaceae* in the ITS phylogeny is *Neosatchmopsis*, represented by the type specimen. Whether it belongs in *Chaetomellaceae* needs to be confirmed using additional genes.

Chlorociboriaceae (Fig. 5 S2)

Chlorociboriaceae is well resolved in the multigene phylogeny but *Brahmaculus*, sister to two *Chlorociboria* species in a monophyletic clade in the multigene phylogeny, makes *Chlorociboria* paraphyletic. The family breaks apart to some extent in the ITS analysis, reflecting the phylogenetic structure within *Chlorociboriaceae* in the multigene phylogeny.

Cenangiaceae (Figs 5, S2)

Cenangiaceae forms a well resolved clade in the multigene phylogeny but breaks into two clades in the ITS phylogeny. The ITS phylogeny treats an additional seven genera, six represented by specimens identified as types of the genera. In the ITS phylogeny, the divergent clade includes *Meria laricis* (*Cenangiaceae* in the multigene phylogeny), one of the *Sarcotrochila* species treated, and *Rhabdocline*. The two putative *Sarcotrochila* species in the ITS phylogeny are in different *Cenangiaceae* clades. As shown by Koukol *et al.* (2024) specimens identified as the type, *Sarcotrochila alpina*, match *Meria laricis*, which is now placed in *Rhabdocline*. The type of this genus, *Rhabdocline pseudotsugae*, is sister to *M. laricis* in our ITS phylogeny. *Sarcotrochila macrospora* needs a new genus.

The type of *Calycellinopsis, C. xishuangbanna*, has been placed in *Trochila* (Gómez-Zapata *et al.* 2021), but the multigene analysis shows the two genera to be phylogenetically distinct. The New Zealand species *Cenangium colensoi* (= ‘*Trochila*’ *colensoi*) seems to be congeneric with *Calycellinopsis*. *Trochila* sensu Gómez-Zapata *et al.* (2021) is not supported in the multigene analysis.

Cochlearomycetaceae (Figs 6, S2)

Cochlearomycetaceae is represented by a single specimen of *Satchmopsis metrosideri* in the multigene phylogeny. In the ITS phylogeny, *S. metrosideri* is clearly congeneric with a specimen identified as the type of *Satchmopsis*, *S.*

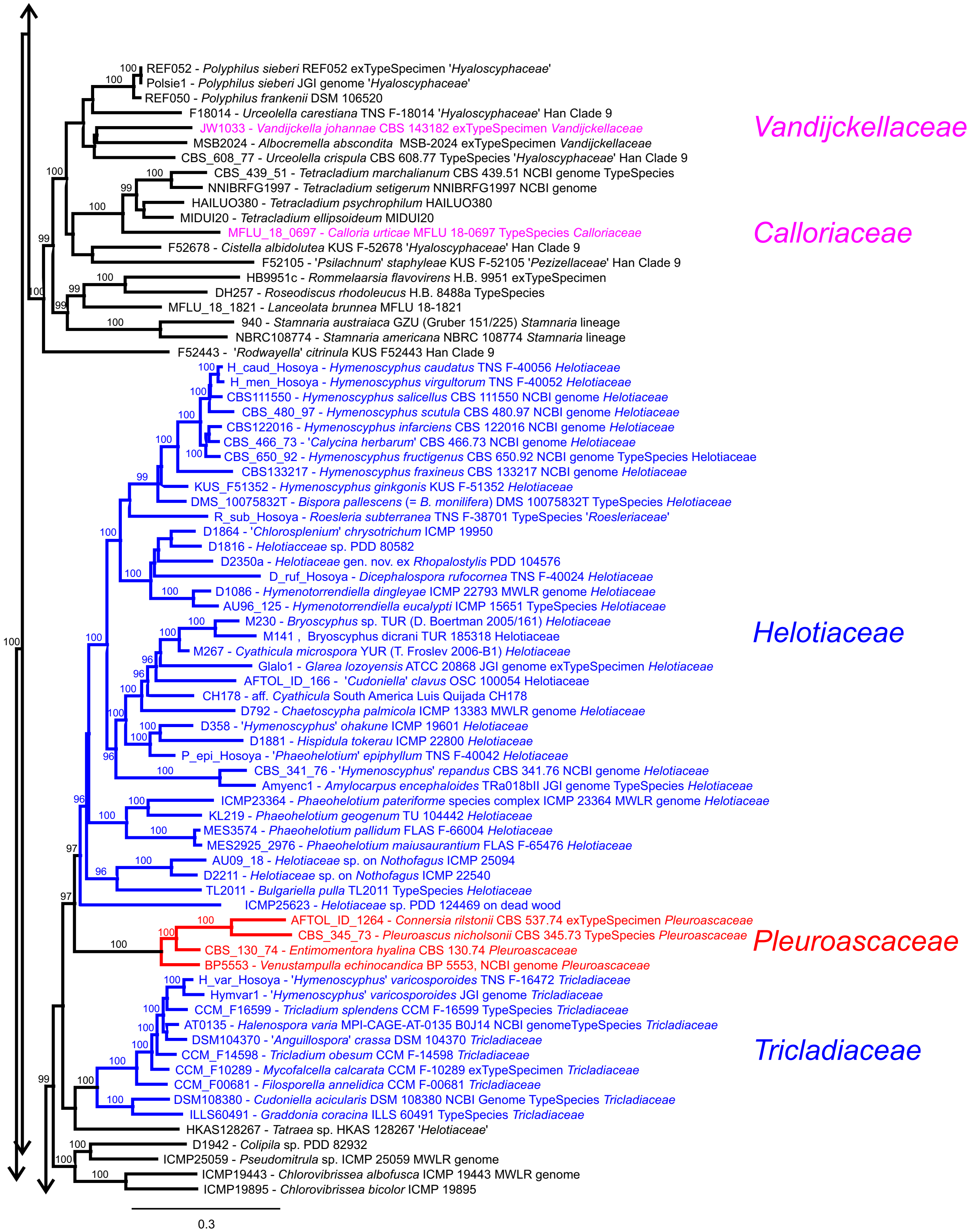

Fig. 3. Detail from Fig. 1. ML tree based on 15 concatenated sequences for specimens from the families *Vandijckellaceae*, *Calloriaceae*, *Helotiaceae*, *Pleuroascaceae* and *Tricladiaceae* from *Helotiales*. The labels for taxa include the voucher specimen from which the sequences were obtained, the type status of the specimen (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus) and the source of the genome data for those that have had their genome sequenced. Family level clades are coloured blue or red as a visual cue, taxa in black are *Helotiales* incertae sedis, taxa in purple have unresolved taxonomic issues that are treated in more detail in the text. Bootstrap values 95 % or greater indicated. The loci available for each specimen, and the sources of the sequence data, are provided in Table S1.

brasiliensis, however the concept of *Cochlearomycetaceae* containing *Satchmopsis* plus *Cochlearomyces* is not well supported in our ITS phylogeny. The relationship between *Satchmopsis* and *Cochlearomyces* is strongly supported by LSU sequences from GenBank (unpubl. data) but clarification of the phylogenetic limits of these taxa requires additional genes.

Cordieritidaceae (Figs 5, S2)

Cordieritidaceae forms a monophyletic clade in the multigene phylogeny, although the clade contains numerous long branches, and it clusters together in a poorly supported clade in the ITS phylogeny. The ITS phylogeny includes an additional five genera, three represented by their type specimens and two with specimens identified as the generic types.

The ITS phylogeny includes the type specimen of *Unguiculella globosa*. *Unguiculella* (type *U. falcipila*) has been placed traditionally in *Hyaloscyphaceae* but the only species with a DNA sequence available is *U. globosa* (GenBank NR_163778). However, based on the description in Ekanayaka *et al.* (2019), the morphology of *U. globosa* appears to be a good match for *Unguiculariopsis*, and Yu *et al.* (2025) recently recombined *U. globosa* in *Unguiculariopsis*. Yu *et al.* (2025) also reported a morphologically distinctive asexual morph for *Cordierites*.

The genus *Dactylaria* (*Helotiales* incertae sedis in Hyde *et al.* 2024), is currently being used in many senses. Based on BLAST search results, GenBank accessions identified as this genus are scattered amongst a range or orders in *Orbiliomycetes*, *Sordariomycetes* and *Dothideomycetes*. An accession referred to as the type, *D. purpurella*, is *Venturiales* (*Dothideomycetes*). A GenBank accession identified as *Dactylaria acicularis* (GenBank MH860548, voucher CBS 511.72), the only *Leotiomycetes* amongst the GenBank accessions placed in this genus, is in *Cordieritidaceae* and is sister to *Sabahriopsis* in our ITS phylogeny.

Llimoniella is represented by *L. terricola* in the multigene analysis, where it is *Cordieritidaceae*. The only ITS data available for the genus is from *L. gregorellae*, which sits apart from *Cordieritidacdeae* in the ITS phylogeny. The type, *L. scabrida*, has no DNA sequence data available.

Cyttariaceae (Figs 5, S2)

As accepted in Haelewaters *et al.* (2021), *Cyttariaceae* belongs in *Helotiales*. Although represented by different sets of species in the multigene and ITS phylogenies respectively, the genus forms a monophyletic clade in both.

Dermateaceae (Figs 5, S2)

Dermateaceae is well resolved in the multigene phylogeny. The ITS phylogeny includes an additional five genera placed in *Dermateaceae* in Hyde *et al.* (2024), three represented by their type specimens, one by a specimen identified as the type of the genus.

Parafabraea is treated as synonym of *Coleophoma* in Hyde *et al.* (2024) but based on the genome identified as *Coleophoma crateriformis*, the type of *Coleophoma*, and the type specimen of *Parafabraea eucalypti*, the multigene analysis shows that the two genera are phylogenetically distinct.

The ITS phylogeny includes *Medeolaria* (*Medeolariaceae* in Hyde *et al.* 2024) and *Arboricolonus* (*Rutstroemiaceae* in Hyde *et al.* 2024) on long branches amongst *Dermateaceae*, however, these genera have unstable positions across different ITS-based analyses, dependent in part on taxon selection (unpubl. data). The LSU from the type specimen of the type of *Arboricolonus, A. simplex* (GenBank NG_073755), places the genus in the *Vandijckellaceae* + *Calloriaceae* clade (unpubl. data). The *Arboricolonus* placement in Hyde *et al.* (2024) seems to be a mistake, there is no suggestion in Bien & Damm (2020) that this is *Rutstroemiaceae* and it is accepted here as *Helotiales* incertae sedis.

Pseudotryblidium (*Helotiales* incertae sedis in Hyde *et al.* 2024), sits amongst *Dermateaceae* in the ITS phylogeny, a relationship shown earlier by Suija *et al.* (2020).

Discinellaceae (Figs 2, S2)

Discinellaceae forms a well resolved clade in both the multigene and ITS phylogenies. The ITS phylogeny includes an additional seven genera, three represented by the type specimens of the generic types, the other four by specimens identified as the type of the genus.

The phylogenies include two specimens identified as *Pezoloma* spp., but the type of this genus, *P. griseum*, has no DNA sequence data available.

A specimen identified as the type of *Geniculospora*, *G. inflata* (VG79-1, GenBank OM907735, Franco-Duarte *et al.*, 2022), is *Discinellaceae* in our ITS phylogeny. This genus was placed in *Tricladiaceae* by Hyde *et al.* (2024), following Johnston & Baschien (2020), based on DNA sequences from specimens identified as '*Geniculospora' grandis*, but Johnston & Baschien (2020) did not have access to sequence data for the type of the genus.

Erysiphaceae (Figs 2, S2)

Erysiphaceae forms a well-resolved clade in both the multigene and ITS phylogenies. Several additional genera are included in the ITS phylogeny but not all genera with DNA sequence data are treated here.

Gelatinodiscaceae, *Helicodendron* (Figs 2, S2)

Although represented by few taxa, *Gelatinodiscaceae* is well resolved in the multigene phylogeny, however it splits apart in the ITS phylogeny. The split in the ITS phylogeny between the clade containing *Ascocoryne* + *Chloroscypha* versus *Neobulgaria* + *Ascotremella*, reflects phylogenetic structure within *Gelatinodiscaceae* in the multigene phylogeny. The ITS phylogeny includes an additional four genera, one represented by the type specimen, three by specimens identified as types of the genus.

Helicodendron is placed in *Helotiaceae* in Hyde *et al.* (2024) but assuming the specimen representing the type, *H. paradoxum*, in the ITS phylogeny is correctly identified, then the genus should be placed in *Gelatinodiscaceae*. ITS from specimens identified as *Helicodendron paradoxum*, *H. triglitziense* and *H. microsporum* are in *Gelatinodiscaceae* but other *Helicodendron* specimens and

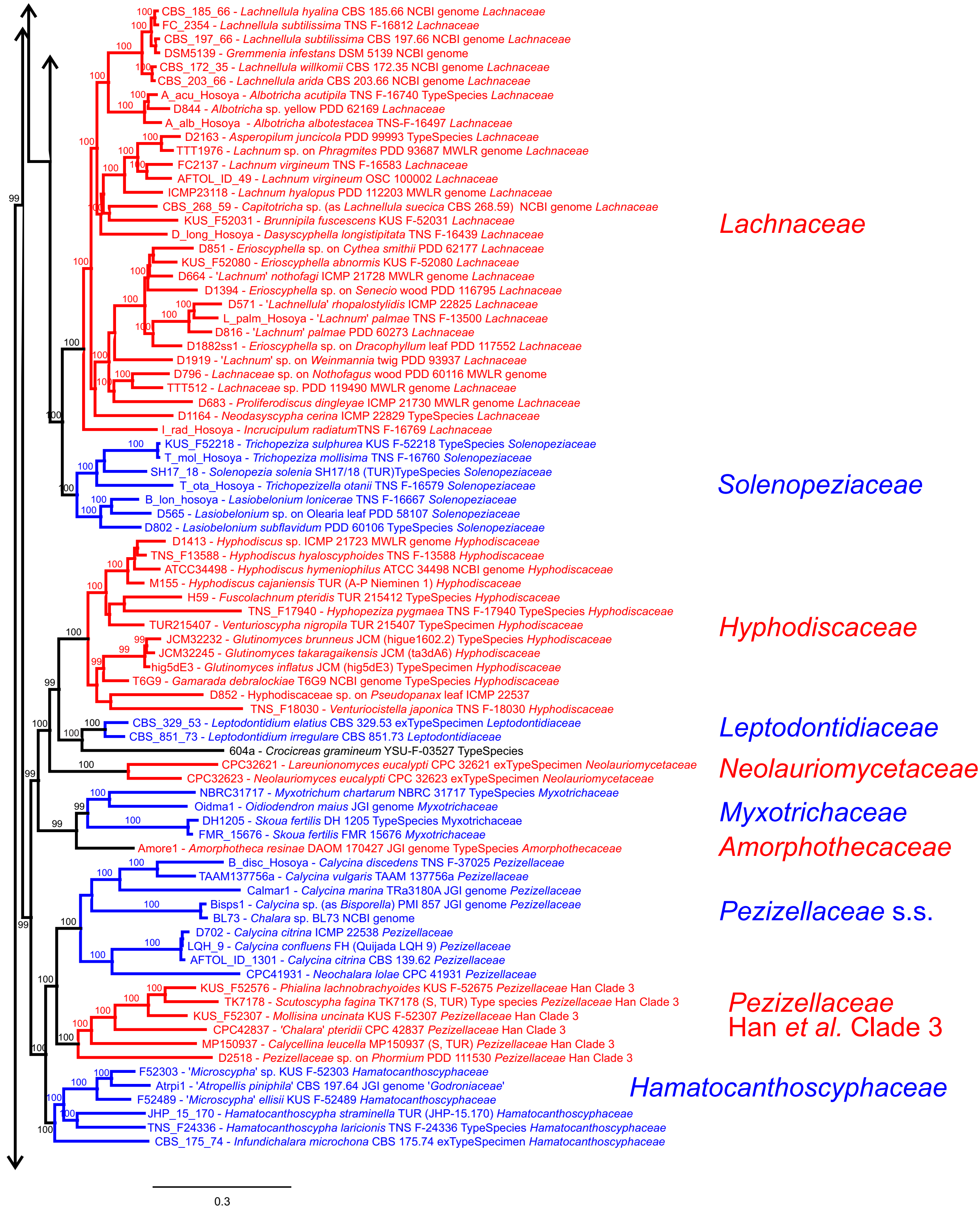

Fig. 4. Detail from Fig. 1. ML tree based on 15 concatenated sequences for specimens from the families *Lachnaceae*, *Solenopeziaceae*, *Hyphodiscaceae*, *Leptodontidiaceae*, *Neolauriomycetaceae*, *Myxotrichaceae*, *Amorphothecaceae*, *Pezizellaceae* and *Hamatocanthoscyphaceae* from *Helotiales*. The labels for taxa include the voucher specimen from which the sequences were obtained, the type status of the specimen (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus) and the source of the genome data for those that have had their genome sequenced. Family level clades are coloured blue or red as a visual cue, taxa in black are *Helotiales* incertae sedis. Bootstrap values 95 % or greater indicated. The loci available for each specimen, and the sources of the sequence data, are provided in Table S1.

species are scattered widely across the *Helotiales* (including *Vandijckellaceae*, *Phacidiales*, *Pezizellaceae*, *Tricladiaceae*, *Hamatocanthoscyphaceae*, and near *Mollisiaceae* (PRJ, unpubl. data; Ma *et al.* 2024). Ma *et al.* (2024) noted that Fisher and Webster (1983) described *Hymenoscyphus paradoxus*, a fungus they considered the sexual morph of *Helicodendron paradoxum*, based on a morphological comparison of the asexual morphs. Based on this, Ma *et al.* (2024) suggested that the type of *Helicodendron* should be *H. fuscum*, but apparently without a formal proposal to change the type of *Helicodendron*. However, neither *Helicodendron fuscum* or *Hymenoscyphus paradoxus* have DNA sequences available, so the link of *Hymenoscyphus paradoxus* to *Helicodendron paradoxum* and the link of *Helicodendron fuscum* to *Gelatinodiscaceae* cannot be confirmed genetically. Species placed in both *Hymenoscyphus* and *Helicodendron* are scattered throughout *Helotiales*, an indication that morphology is a poor predictor of relationships amongst these fungi. Although the two putative *Helicodendron paradoxum* isolates in GenBank (CBS 300.50, CBS 299.50) have an ITS sequence identical to the type specimens of *Helicodendron websteri* (CBS 745.96) and *Helicodendron microsporum* (CBS 100149), for now we see no reason not to retain *Helicodendron paradoxum* as the type of the genus.

The limits of the *Gelatinodiscaceae* clade containing *Ascocoryne* and *Chloroscypha* in the ITS phylogeny are not clear. Within this *Gelatinodiscaceae* clade is a well-supported subclade with the type specimen of *Hydrocina*, a specimen identified as the type of *Clathrosporium*, *C. intricatum*, and a specimen identified as *Filosporella fistucella*. The *Filosporella* specimen is also in the multigene analysis where it is distant to *Gelatinodiscaceae*, suggesting the apparent relationships in the ITS tree are misleading. Both *Hydrocina* and *Clathrosporium* are *Helotiales* incertae sedis in Hyde *et al.* (2024).

Asterocalycella falls within *Gelatinodoscaceae* in the ITS phylogeny, but it is on a long branch and its position within the ITS phylogeny is unstable depending on taxon selection. The multigene phylogeny clearly placed it as *Helotiales* incertae sedis.

Godroniaceae (Figs 2, S2)

Well resolved in both multigene and ITS phylogenies, but with few taxa and limited data. The *Godroniaceae* clade falls as a subclade amongst *Helotiaceae* in the ITS analysis used here, but its position is inconsistent between analyses with slightly different sets of taxa, usually separate from other families in *Helotiales*. The ITS phylogeny treats one additional genus. The type of *Godronia, G. muehlenbeckii,* has no DNA sequence data.

Hamatocanthoscyphaceae (Figs 4, S2)

Hamatocanthoscyphaceae is well resolved in both the multigene and ITS phylogenies. The ITS phylogeny includes an additional 12 genera, seven of these from type specimens, four from specimens identified as types of the genera. Amongst these is *Brachyalara straminea*, the type of *Brachyalara*, placed as *Helotiales* incertae sedis in Hyde *et al.* (2024). Note however that the limits of *Hamatocanthoscyphaceae* are not strongly resolved in the ITS phylogeny, with three genera, *Brachyalara*, *Gemmina* and *Kukwaea*, in a poorly supported sister clade.

In some preliminary multigene analyses carried out as part of this study, *Kukwaea* (genes available SSU, mtSSU, *RPB2*, LSU) falls within *Hamatocanthoscyphaceae* but when *Kukwaea* is included in the multigene analysis, the *Hamatocanthoscyphaceae* clade becomes poorly supported. Checking the genes individually, in the SSU and mtSSU gene trees *Kukwaea* clusters with the other *Hamatocanthoscyphaceae* specimens, but in the *RPB2* and LSU gene trees *Kukwaea* is distant to the other *Hamatocanthoscyphaceae* (which otherwise all cluster together). Uncertainty around the accuracy of these DNA sequences means that *Kukwaea* was excluded from the multigene analysis.

The putative *Gremmenia infestans* specimen with GenBank accession KM216393, in *Hamatocanthoscyphaceae*, is probably misidentified; see discussion of GenBank accessions with this name under *Lachnaceae*.

The JGI genome Atrpi1, cited as *Atropellis piniphila* from CBS 197.64, is *Hamatocanthoscyphaceae* in the multigene phylogeny, a family morphologically atypical of *Atropellis* (cf. Reid & Funk 1966). The specimen from which the genome was extracted is assumed to have been misidentified. There is no DNA data available for the type, *A. pinicola* (placed in synonymy with *Godronia zelleri* in Species Fungorum).

The specimens in *Hamatocanthoscyphaceae* identified as *Microscypha* in the multigene phylogeny have been misidentified, see notes under *Hyphodiscaceae*.

Helicogoniaceae (Figs 6, S2)

Although there are no sequences in GenBank identified as *Helicogonium*, other genera placed in *Helicogoniaceae* form a well resolved clade in both the multigene and ITS phylogenies. There is one additional genus treated in the ITS phylogeny.

Also in *Helicogoniaceae* in the ITS phylogeny is a specimen identified as *Gelatinopsis fungicola* (GenBank LC425051, voucher TNS F44003). In Hyde *et al.* (2024) *Gelatinopsis* is *Leotiomycetes* genera incertae sedis but, with no DNA data from the type*, G. geoglossi*, the correct placement of this genus cannot be confirmed.

Calloriopsis is *Helicogoniaceae* in Hyde *et al.* (2024). The type, *C. gelatinosa*, has no DNA sequence data but other putative *Calloriopsis* sp. sequences in GenBank (e.g. MF322776, OR243608) do not align well across *Leotiomycetes* and are nowhere near other *Helicogoniaceae*; BLAST matches are poor but perhaps place them closer to *Lecanorales* or *Ostropales*).

Helotiaceae (Figs 3, S2)

Johnston *et al.* (2019) had a broad concept for *Helotiaceae*, including in the family two strongly supported, monophyletic subclades, one of these later treated by Untereiner *et al.* (2019) as *Pleuroascaceae* and the other by Johnston & Baschien (2020) as *Tricladiaceae*. The multigene phylogeny presented here shows strong support for the three monophyletic family level clades, *Helotiaceae*, *Pleuroascaceae* and *Tricladiaceae*. There remains significant phylogenetic structure within the *Helotiaceae* clade with several subclades on long branches.

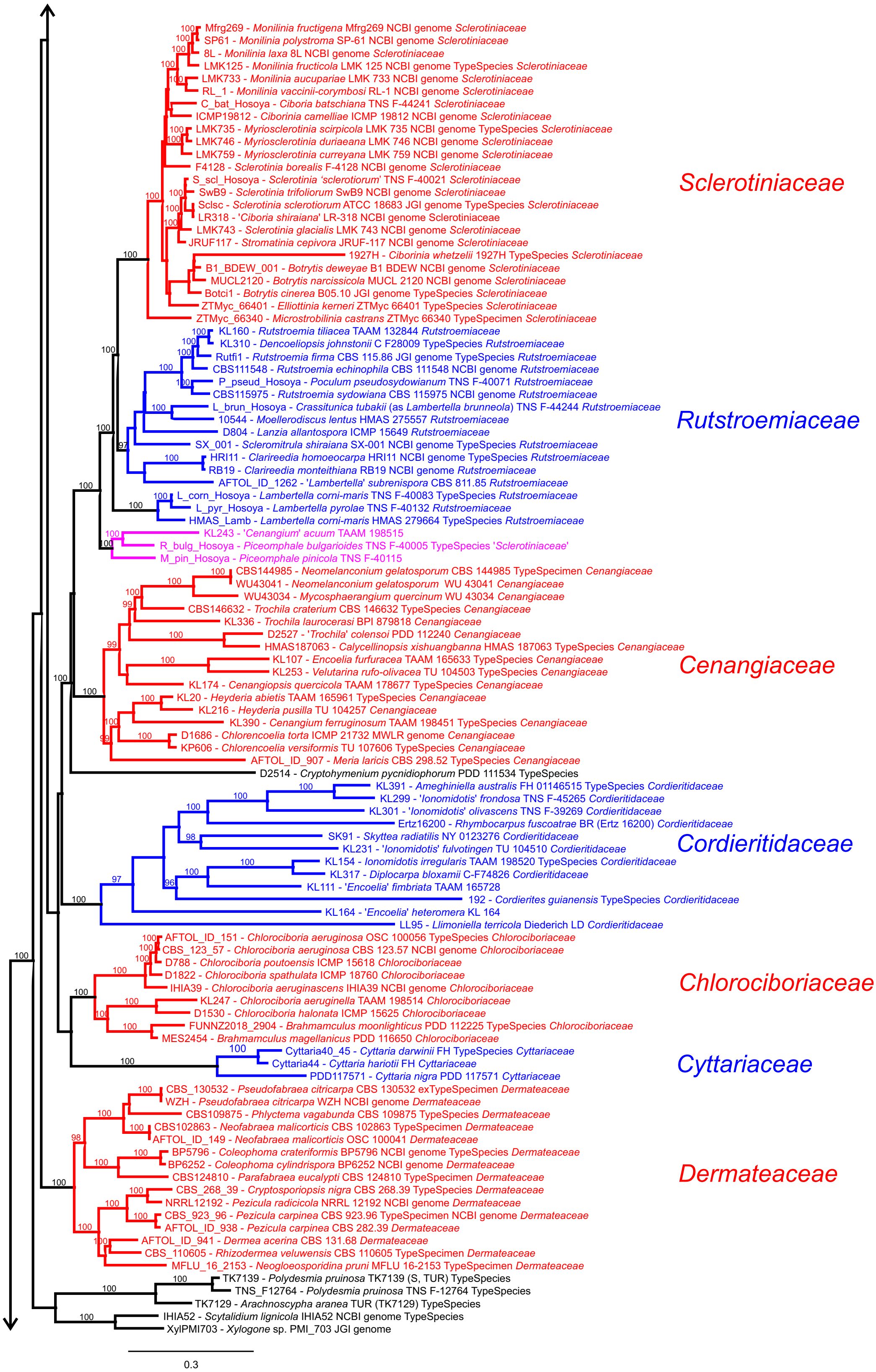

Fig. 5. Detail from Fig. 1. ML tree based on 15 concatenated sequences for specimens from the families *Sclerotiniaceae*, *Rutstroemiaceae*, *Cenangiaceae*, *Cordieritidaceae*, *Chlorociboriaceae*, *Cyttariaceae* and *Dermateaceae* from *Helotiales*. The labels for taxa include the voucher specimen from which the sequences were obtained, the type status of the specimen (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus) and the source of the genome data for those that have had their genome sequenced. Family level clades are coloured blue or red as a visual cue, taxa in black are *Helotiales* incertae sedis, taxa in purple have unresolved taxonomic issues that are treated in more detail in the text. Bootstrap values 95 % or greater indicated. The loci available for each specimen, and the sources of the sequence data, are provided in Table S1.

This structure is reflected in the ITS phylogeny, where the *Phaeohelotium* subclade is separate from the remainder of *Helotiaceae*. Earlier, Mitchell *et al.* (2022) treated the '*Bulgariella* clade' as separate from the clade they labelled as *Helotiaceae*.

The ITS phylogeny includes an additional six genera, five represented by specimens identified as generic types. In addition, a specimen identified as the type of *Cyathicula, C. coronata,* is included.

Tatraea is placed in *Helotiaceae* in Hyde *et al.* (2024). The genus is represented here by a specimen identified as the type, *T. dumbirensis*, along with a specimen identified as *Tatraea* sp. (HKAS 128267). These specimens are congeneric within the ITS phylogeny but separate from other *Helotiaceae*. The *Tatraea* sp. specimen is also present in the multigene phylogeny, and this also places it in *Helotiales* but outside *Helotiaceae*. The genus is accepted here as *Helotiales* incertae sedis.

Note that there is a nomenclatural issue around the current use of the name *Helotiaceae*. The type of the genus *Helotium* is *Helotium aciculare* (Dennis 1956), today widely accepted as *Cudoniella acicularis*. Unfortunately, *C. acicularis* belongs in *Tricladiaceae* as accepted in this paper (Fig. 3), based on DNA sequences from the specimens CBS 100273 and DSM 108380. To be nomenclaturally correct, for *Helotiaceae* to be retained in its present sense the rules of nomenclature require selection and conservation of a new type for *Helotium*.

Holwayaceae, *Pseudeurotiaceae* and *Thelebolaceae* (Figs 6, S2)

In the multigene phylogeny *Thelebolales* contains three strongly supported monophyletic clades representing *Holwayaceae*, *Pseudeurotiaceae* and *Thelebolaceae*. Jointly, *Pseudeurotiaceae* + *Thelebolaceae* form a well-supported monophyletic clade in the multigene phylogeny, together with the type specimen of the type of *Zongqia*. The family level clades are similar in the ITS phylogeny but they do not cluster at the order level. Also, in the ITS phylogeny the type specimen of the type of *Pseudeurotium*, *P. zonatum*, is phylogenetically distinct from other genera currently regarded as *Pseudeurotiaceae*. Although *Pseudeurotiaceae* is strongly supported in the multigene phylogeny, *P. zonatum* is sister to all other taxa treated. Quijada *et al.* (2022) discussed differences in asexual morphology between *P. zonatum* and other genera in *Pseudeurotiaceae*; *Pseudogymnoascus*, *Leuconeurospora*, *Solomyces* and *Geomyces*.

The ITS phylogeny treats and additional four genera of *Thelebolaceae*: three represented by the type specimen of their types, one by a specimen identified as the type of the genus. An additional two genera of *Pseudeurotiaceae* are treated in the ITS phylogeny, both represented by specimen identified as the types of the genera. The ITS phylogeny includes two additional genera of *Holwayaceae*, one represented by a specimen identified as the type of the genus.

Zongqia is a monotypic genus known only from its asexual morph. The type is *Z. sinensis*, a soil saprobe. It is distinguished morphologically from *Pseudeurotium* by the presence of chains of conidia, forming on clavate conidiogenous cells (Zhang *et al.* 2021). It is accepted here as incertae sedis within *Thelebolales*.

Hyaloscyphaceae (Figs 2, S2)

Hyaloscyphaceae forms a well-resolved clade in the multigene phylogeny, but in the ITS phylogeny presented here the *Hyaloscyphaceae* clade contains several subclades on long branches, representing *Godroniaceae*, *Amicodiscaceae* and *Bryoglossaceae*. In other analyses, with slightly different taxon selection, these other families are separate from *Hyaloscyphaceae* within *Helotiales*, with a monophyletic *Hyaloscyphaceae* being well resolved.

Hyaloscyphaceae as accepted here includes five additional genera in the ITS phylogeny, two represented by the type specimens of their types, two others by specimens identified as the types of their genus.

Other genera placed in *Hyaloscyphaceae* in Hyde *et al.* (2024) that fall elsewhere in the ITS phylogeny include species representing *Crucellisporiopsis*, *Incrupila* and *Unguiculella*. The type specimen of *Crucellisporiopsis marquesiae* is *Lachnaceae* in the ITS phylogeny, but no other species in the genus, including the type, *C. gelatinosa*, have DNA sequence data available. A specimen identified as the type of *Incrupila*, *I. aspidii* (GenBank MT040757, voucher SBRH909, on *Polystichum* leaves, Spain), is incertae sedis close to *Vandijckellaceae* in the ITS tree. See notes on *Unguiculella* under *Cordieritidaceae*.

Specimens used in this paper that were originally identified as the type of *Stipitochalara*, *S. longipes*, represent two different fungi. The specimen used to generate the genome used in the multigene analysis (Barbi *et al.* 2020, strain BDJ) is *Hyaloscyphaceae*, whereas the CBS culture from Finland (CBS 264.94) used to represent this species in the ITS phylogeny is *Hamatocanthoscyphaceae*, a position also reported by Wu & Diao (2023). The ITS from CBS 264.94 matches all other GenBank accessions identified as *S. longipes*, except for strain BDJ, and the CBS culture is assumed to have been correctly identified, with *Stipitochalara* accepted as *Hamatocanthoscyphaceae*. Epitypification would formally establish this taxonomic concept of *Stipitochalara*.

Hyphodiscaceae (Figs 4, S2)

Well resolved in the multigene analysis, most *Hyphodiscaceae* genera cluster close by each other in the ITS phylogeny, but the type specimen of *Scolecolachnum* is separate from the other genera treated. The only other data available for *Scolecolachnum* is LSU (GenBank KU597765) and this also places the genus outside *Hyphodiscaceae* (unpubl. data); multigene data is needed to confirm the position of *Scolecolachnum*. The ITS phylogeny includes an additional four genera: two are represented by type specimens, two by specimens identified as types of the genera.

The specimen used to represent *Microscypha* by Han *et al.* (2014) was identified as *M. ellisii* (voucher KUS 52489) and is *Hamatocanthoscyphaceae* in both the multigene and ITS phylogenies. However, based on the ITS phylogeny, this specimen is not congeneric with the type of the genus, *M. grisella* (GenBank OM203546, Quijada *et al.* 2022, *Hyphodiscaceae*).

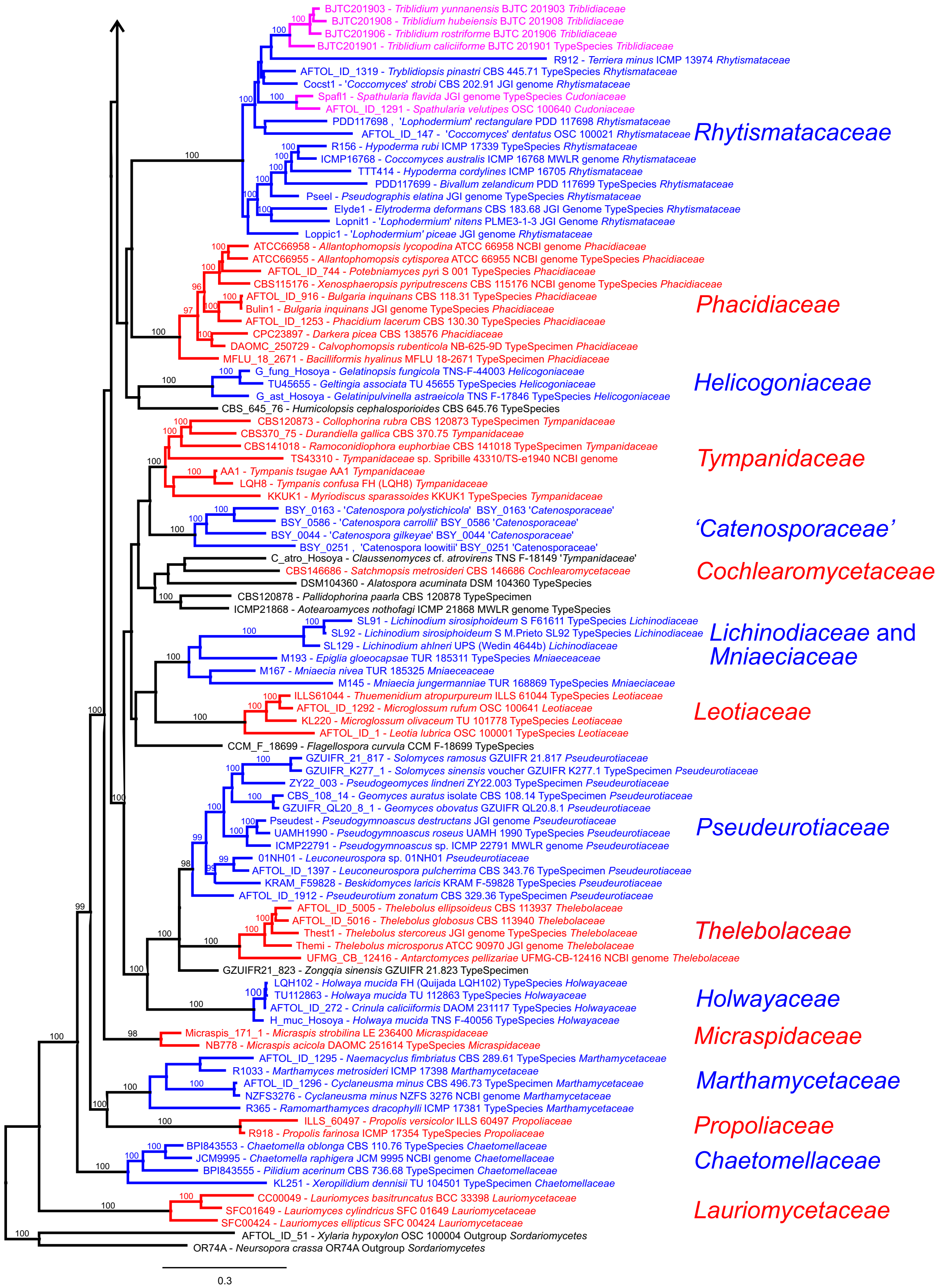

Fig. 6. Detail from Fig. 1. ML tree based on 15 concatenated sequences for specimens from the families *Rhytismataceae*, *Triblidiaceae* and *Cudoniaceae* (*Rhytismatales*), *Phacidiaceae* and *Helicogoniaceae* (*Phacidiales*), *Tympanidaceae*, 'Catenosporaceae', *Cochlearomycetaceae*, *Lichinodiaceae*, *Mniaeceae* and *Leotiaceae* (*Leotiales*), *Pseudeurotiaceae*, *Thelebolaceae* and *Holwayaceae* (*Thelebolales*), *Micraspidaceae* (*Micraspidales*), *Marthamycetaceae* (*Marthamycetales*), *Chaetomellaceae* (*Chaetomellales*), and *Lauriomycetaceae* (*Lauriomycetales*). The labels for taxa include the voucher specimen from which the sequences were obtained, the type status of the specimen (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus) and the source of the genome data for those that have had their genome sequenced. Family level clades are coloured blue or red as a visual cue, taxa in black are *Helotiales* incertae sedis, taxa in purple have unresolved taxonomic issues that are treated in more detail in the text. Bootstrap values 95 % or greater indicated. The loci available for each specimen, and the sources of the sequence data, are provided in Table S1.

Lachnaceae (Figs 4, S2)

Lachnaceae forms well-resolved clades in both the multigene and ITS phylogenies. The ITS phylogeny treats an additional four genera, one represented by the type specimen and three by specimens identified as the types of their genera.

The specimen identified as *Gremmenia infestans* with a genome (DSM 5139, on *Pinus* needles, Austria, Zerouki *et al.* 2023), has an ITS sequence matching GenBank accession U92035 (voucher P431, *Pinus* needles, Germany, Gernandt *et al.* 1997) (unpubl. data). The two specimens appear to have been independently identified based on morphology and ecology. The multigene analysis places this fungus in *Lachnaceae*, based on DSM 5139. A second fungus, represented in the ITS phylogeny by GenBank KM216393 (CBS 396.48, from Sweden, no substrate indicated, Crous *et al.* 2014), is also identified in GenBank as *Gremmenia infestans*, but this fungus is *Hamatocanthoscyphaceae* (Fig. S2). Several other GenBank accessions labelled with the same name match CBS 396.48, but these are all isolates from leaf endophytes of various hosts (none *Pinaceae*) or from samples from marine sediments or sponges. They are assumed to have been identified using an ITS match to CBS 396.48. For now, we accept specimens DSM 5139 and P431 as *Gremmenia infestans*. Morphologically this placement seems unlikely, however, another fungus in *Lachnaceae* in the multigene phylogeny (*Lachnaceae* sp., PDD 119490) also has an unlikely macromorphology for *Lachnaceae*, the Cudoniella-like apothecium having short scales rather than hairs on the receptacle surface (e.g. see images https://scd.landcareresearch.co.nz/Specimen/PDD_116706, https://scd.landcareresearch.co.nz/Specimen/PDD_108691).

Based on the multigene phylogeny, several genomes for species identified as *Lachnellula*, including *L. hyalina* (CBS 185.66), *L. subtilissima* (CBS 197.66), *L. willkommii* (CBS 172.35) and *L. arida* (CBS 203.66), appear to represent the same genus, while another genome for a specimen identified as *L. suecica* (BioSample SAMN08873675 ex CBS 268.59) represents a different genus in *Lachnaceae* but with no clear generic relationship in the multigene analysis. As well as the genome, CBS 268.59 has a GenBank ITS accession (MH857859); however a comparison of the MH857859 sequence with the ITS extracted from the genome, shows that they come from two different species. The MH857859 sequence clusters with the other *Lachnellula* specimens with sequences in GenBank, whereas the ITS extracted from the SAMN08873675 genome is close to several *Capitotricha* specimens (e.g. LT904861, LT904864, LT904862). The SAMN08873675 genome is treated here as representing *Capitotricha*, a genus otherwise not treated in the multigene phylogeny.

Based on the ITS phylogeny, *Crucellisporiopsis marquesiae* and *Crucellisporium umtamvunae* (neither are the types of these genera) are both in *Lachnaceae*, but because these are morphologically cryptic fungi and the generic types have no DNA sequence data, the two genera are tentatively treated here as *Helotiales* incertae sedis.

Lauriomycetaceae (Figs 6, S2)

Lauriomycetaceae forms a well-resolved clade in both the multigene and ITS phylogenies. The ITS phylogeny treats one additional genus, represented by its type specimen.

Leotiaceae (Figs 6, S2)

Leotiaceae is well resolved in the multigene phylogeny but breaks apart in the ITS phylogeny. *Miniancora*, represented by the type specimen, is *Leotiaceae* in Hyde *et al.* (2024) but based on the ITS phylogeny, appears to be *Leotiales* incertae sedis. Additional genes are needed to confirm this placement.

Lichinodiaceae and *Mniaeciaceae* (Figs 6, S2)

Mniaeciaceae + *Lichinodiaceae* form a well-supported monophyletic clade in the multigene phylogeny, but within this clade the two genera of *Mniaeciaceae*, *Epiglia* and *Mniaecia* do not form a monophyletic clade. Phylogenetically *Epiglia* and *Mniaecia* (both represented by specimens identified as their types) seem to be separate genera, although they were treated as synonyms by Baral (in Johnston *et al.* 2019).

The two families *Mniaeciaceae* and *Lichinodiaceae* could be placed in synonymy (*Lichinodiaceae* is the older name), to include the lichenicolous *Lichinodium* spp. and the broyphyte-inhabiting *Epiglia* and *Mniaecia*. Morphologically all these fungi are very simple.

The only two species of *Mniaeciaceae* treated in the ITS phylogeny are widely scattered in the phylogeny. There are no ITS data is available for *Lichinodium*; addition of these data might settle the position of *Mniaeciaceae* in the ITS phylogeny.

Marthamycetaceae and *Propoliaceae* (Figs 6, S2)

Marthamycetales forms a strongly supported clade in the multigene analysis with two internal subclades, these recently accepted as separate families, *Marthamycetaceae* and *Propoliaceae* (Karakehian *et al.* 2025). The two families are widely separated in the ITS phylogeny. One additional genus of *Marthamycetaceae* is treated in the ITS phylogeny.

Medeolariaceae (Fig. S1)

The only species of *Medeolaria*, *M. farlowii*, is a pathogen of *Medeola virginiana*. This fungus has highly reduced ascomata, historically making its phylogenetic and taxonomic position within *Ascomycota* uncertain. Based on the first DNA sequences generated for the genus it was recognised by LoBuglio & Pfister (2010) as *Leotiomycetes*. They retained it in its own family and order. Hyde *et al.* (2024) retained *Medeolariaceae* but placed *Medeolariales* in synonymy with *Helotiales*.

Mollisiaceae, *Loramycetaceae*, *Vibrisseaceae* and *Chlorospleniaceae* (Figs 2, S2)

Mollisiaceae and sister families are treated here in the sense of Tanney & Seifert (2020). In our multigene phylogeny *Mollisiaceae* is not strongly supported as phylogenetically distinct from *Vibrisseaceae* and *Chlorospleniaceae*, but these latter two families are represented by single taxa on long branches. Additional taxa, closely related to *Vibrisseaceae* and *Chlorospleniaceae* respectively may help better resolve relationships between these families.

In the multigene phylogeny, the morphologically distinctive *Loramycetaceae* forms a clade within *Mollisiaceae*; following

Tanney & Seifert (2020) the two families are treated here as synonyms. Our analyses include a specimen identified as the type of *Diplococcium*, *D. spicatum*, a fungus known only from its asexual morph (Tanney & Seifert 2020). This genus was accepted as *Mollisiaceae* by Tanney & Seifert (2020) but is not listed in Hyde *et al.* (2024).

In the ITS phylogeny *Mollisiaceae* breaks into two separate clades, one of which includes *Loramyces* and related genera. Several additional genera are treated in the ITS phylogeny that fall amongst the *Mollisiaceae* clades, including ex-type specimens of three genera and specimens identified as the types of three more genera.

Hysteronaevia is *Helotiales* incertae sedis in Hyde *et al.* (2024); one species, *H. scirpina*, was sampled in the ITS phylogeny and this is placed in one of the *Mollisiaceae* clades, however the position of the genus needs confirming with additional genes and DNA sequences from the type, *H. holoschoeni*.

Neodictyocheirosporaceae **(Fig. S2)**

Neodictyocheirosporaceae is a monotypic family in *Helotiales*, with just two species in the genus *Neodictyocheirospora*. Only ITS and LSU sequences are available and based on these, *Neonematogonum* (*Helotiales* incertae sedis in Hyde *et al.* (2024)) may belong in the same family.

Neolauriomycetaceae **(Figs 4, S2)**

Neolauriomycetaceae is well resolved in both the multigene and ITS phylogenies. The ITS phylogeny incudes an additional genus, represented by its type specimen.

Peltigeromycetaceae **(Fig. 2)**

Not included in Hyde *et al.* (2024), *Peltigeromycetaceae* was newly named by Baral *et al.* (2025), is represented in the multigene phylogeny by *Peltigeromyces mollisioides*. Its position is similar to that reported by Baral *et al.* (2025) based on an ITS + LSU phylogeny.

Pezizellaceae **(Figs 4, S2)**

Pezizellaceae sensu Johnston *et al.* (2019) comprised three monophyletic subclades. These were treated by Han *et al.* (2014) as Clade 1, Clade 2 and Clade 3. Subsequently, Clade 1 was named *Hamatocanthoscyphaceae* by Ekanayaka *et al.* (2019), and this family is consistently strongly supported in multigene phylogenetic analyses. In the multigene analysis, Clades 2 and 3 jointly form a monophyletic clade sister to *Hamatocanthoscyphaceae*. Han Clade 2 contains *Calycina* (= *Pezizella*) and is treated here as *Pezizellaceae* s. str. Han Clade 3 remains unnamed, typically treated as part of *Pezizellaceae* but is morphologically somewhat distinct (and distinctive) in most species having ascomata associated with a subiculum (sometimes well developed, sometimes poorly developed) or being covered with a dark clypeus that splits irregularly to reveal the mature apothecia. Spooner (1987) in his discussion on *Austropezia* and *Eriopezia*, compared the subiculum of some species with a loosely constructed stroma; perhaps a similar explanation could apply to the macro-morphological variation of the sterile tissue around the apothecia of these fungi. Clade 3 deserves a name of its own. See also Johnston (2020).

The two subclades treated here as *Pezizellaceae* have a sister relationship in the multigene and ITS phylogenies. Of those taxa treated in both analyses, all consistently fall into either Han *et al.* Clade 2 or Han *et al.* Clade 3 in both phylogenies. The ITS phylogeny treats an additional seven genera from Han *et al.* Clade 2 (*Pezizellaceae* s. str.): two represented by their type specimens, five by specimens identified as the types of the genera. In Han *et al.* Clade 3, the ITS phylogeny treats an additional 11 genera: six represented by their type specimens, two by species identified as the types of the genera.

Based on multigene and ITS analyses, Han Clade 3 includes:

- *Scutoscypha fagina* – described by Raitviir (2004) as having apothecia developing beneath a dark brown shield of radiating, brown-walled hyphae.
- *Mollisina uncinata* – although a clypeus or subiculum is not reported, Raitviir (2004) mentions that the apothecia arise from a black ring at the base (possibly a highly reduced clypeus), he also mentions a brown basal ring for *Phialina*. Note that the type *Mollisina rubi* is *Pezizellaceae* s. str.
- *Phialina lachnobrachyoides* – no mention of clypeus or subiculum in the protologue.
- *Scleropezicula alnicola* – groups of more or less sessile apothecia developing on a basal stroma (possibly a poorly developed subiculum) (Verkley 1999).
- *Calycellina punctata* – sessile, gregarious, at first globose, black basal cells, often covering most of the excipulum (Lowen & Dumont 1984). Resembles the clypeus found on several of the unnamed New Zealand species (Johnston 2020).
- *Rodwayella sessilis* – small sessile discs surrounded by subiculum-like hyphae (Spooner 1987). Note that '*Rodwayella*' *citrinula*, included in the multigene phylogeny, is a different genus, either the specimen is misidentified or the genus polyphyletic.
- *Rubropezicula thailandica* – small, sessile, gregarious discs. The image in Ekanayaka *et al.* (2019) looks like there could be some subiculum-like tissue.
- PDD 111530 is the only one of the New Zealand taxa included in the multigene tree, but an ITS analysis includes several closely related species, almost all with well-developed subiculum or clypeus (Johnston 2020), except for PDD 81741 which has small, sessile, gregarious discs, yellow discs sitting amongst poorly developed, subiculum-like hyphae.
- *Austropezia* – well developed subiculum (Spooner 1987).
- Genera known only from an asexual morph include *Nagrajchalara*, *Parachalara*, *Triposporium deviatum* and *Zymochalara*.

Wu & Diao (2023) revised the taxonomy of *Leotiomycetes* with chalara-like asexual morphs. It has long been known that *Chalara* is polyphyletic, but a lack of reliable DNA sequences from the type, *C. fusidioides*, has hampered efforts to clearly define the genus phylogenetically. Wu & Diao (2023) accepted *Chalara* sensu stricto to accommodate eight chalara-like fungi (represented in the ITS phylogeny by *Chalara bambusicola*, *C. clidemiae*, and *C. longiphora*) based on phylogenetic and morphological data. These species are in *Pezizellaceae* s. str. in the ITS phylogeny. However, because *C. fusidioides* has no reliable DNA sequence data available, the conclusions of Wu & Diao (2023) need confirming following epitypification of *C. fusidioides*. *Neochalara* is separate from *Pezizellaceae* in our ITS phylogeny, however this is an artifact of our ITS analysis, the multigene phylogeny places the genus in *Pezizellaceae* s. str.

Pezizellaceae is polyphyletic in Wu & Diao (2023), the genera *Bloxamiella*, *Nagrajchalara*, *Parachalara* and *Zymochalara* are separate from the rest of *Pezizellaceae* in their phylogeny; all these genera are in *Pezizellaceae* Han Clade 3 in our ITS phylogeny.

Phacidiaceae (Figs 6, S2)

Phacidiaceae is well resolved in both the multigene and ITS phylogenies. The ITS phylogeny treats an additional five genera, two represented by their type specimens and two by specimens identified as the types of their genera.

Pleuroascaceae (Figs 3, S2)

Pleuroascaceae is strongly supported in both the multigene and ITS phylogenies. The ITS phylogeny includes also the type specimen of the type of *Venustampulla*, *V. parva*. *Connersia* (*Pleuroascaceae*), represented by the type specimen of the type, *C. rilstonii*, was mistakenly placed in *Pseudeurotiaceae* in Hyde *et al.* (2024).

Pyrenopezizaceae, *Drepanopezizaceae* and *Cadophora* sensu stricto (Figs 2, Fig. S2)

In the multigene analysis *Drepanopezizaceae* forms a well-supported clade sister to *Cadophora* s. str. and collectively these two clades form a monophyletic clade that is sister to *Pyrenopezizaceae*. The *Cadophora* s. str. clade is present in both the multigene and ITS phylogenies, and in the ITS phylogeny includes a specimen identified as the type of *Cadophora*, *C. fastigiata*.

Most species currently placed in *Cadophora* are in the *Pyrenopezizaceae* clade, phylogenetically distinct from *Cadophora* s. str. The *Cadophora* species in these two clades have largely distinct lifestyles, *Cadophora* s. str. being mostly vascular staining pathogens, those ‘*Cadophora’* species in *Pyrenopezizaceae* mostly associated with healthy roots (Maciá-Vicente *et al.* 2020). The *Cadophora* s. str. clade differs in lifestyle from leaf-spotting species in *Drepanopezizaceae*. The *Cadophora* s. str. clade needs a family name.

The ITS phylogeny shows the same sister relationships between these three clades, but treats 14 more genera in both *Drepanopezizaceae* and *Pyrenopezizaceae*, seven represented by the type specimen of the type, another five by specimens identified as the types of their genera. The epitype specimen of *Miricatena prunicola*, the type species of *Miricatena*, belongs in *Drepanopezizaceae* in the ITS phylogeny, although it was placed in *Helotiales* incertae sedis in Hyde *et al.* (2024). *Miricatena prunicola* is a leaf-spotting fungus known only from its asexual morph. A specimen identified as *Pseudopeziza trifolii* is close to *Drepanopezizaceae* in the ITS phylogeny but not within the *Drepanopezizaceae* clade. Its position shifts in different ITS analyses, depending in part on taxon selection, and is sometimes within the *Drepanopezizaceae* clade.

Dennisiodiscus was placed in *Pyrenopezizaceae* in Hyde *et al.* (2024) but based on the DNA sequence from specimen K(M) 57466 (GenBank MZ159325) is unstable in the ITS phylogeny depending on taxon selection, sometimes amongst *Pyrenopezizaceae*, but sometimes distant from the other members of the family.

Cylindrosporium was treated as a synonym of *Pyrenopeziza* in Hyde *et al.* (2024). This followed Johnston *et al.* (2014) who proposed protection of the name *Pyrenopeziza* 1870 over *Cylindrosporium* 1823, despite no clear evidence that the types of these genera are congeneric. Based on GenBank accessions of ITS sequences, specimens identified as *Pyrenopeziza brassicae* (mentioned in Johnston *et al.* 2014 paper as support for a link with *Cylindrosporium*) and the type of *Cylindrosporium*, *C. concentricum*, is indeed well supported. However, *P. brassicae* is phylogenetically distant from a specimen identified as the type of *Pyrenopeziza*, *P. chailletii* (data for this species was not available to Johnston *et al.* 2014). There is no genetic evidence that the type species of *Pyrenopeziza* and *Cylindrosporium* are congeneric, although both belong in *Pyrenopezizaceae*.

Rhytismataceae, *Cudoniaceae* and *Triblidiaceae* (Figs 6, S2)

Collectively, a clade containing *Rhytismataceae*, *Cudoniaceae* and *Triblidiaceae* is well resolved in both the multigene and ITS phylogenies. The ITS phylogeny includes an additional 27 genera, nine represented by their type specimens, eleven by specimens identified as the types of their genera.

Relationships at both the family and genus level within this clade are poorly understood, barely reflecting the morphologically based taxonomy still widely used for these fungi. There are three putative *Lophodermium* spp. included in the multigene phylogeny, but none are congeneric with *Lophodermium* s. str., the clade with the grass-inhabiting species, represented *by L. actinothyrium* in the ITS phylogeny.

The new genome for *Coccomyces australis* may represent *Coccomyces* s. str. *Coccomyces australis* is morphologically very similar to the type of *Coccomyces*, *C. tumidus* (Johnston 2001, Johnston & Park 2007). Note that the surprising relationship between *C. australis*, *Hypoderma rubi* and *H. cordylines* in the multigene phylogeny is likely to be an artifact of uneven gene coverage between the *C. australis* genome and *H. rubi*, and the *C. australis* genome and *H. cordylines* respectively. Apart from the 5.8S, there are no loci in common between the two sets of taxa (Fig. S1). Some consideration needs to be given to gene coverage when interpreting the significance of relationships represented in the multigene phylogeny, especially where they do not seem to reflect other sets of data, such as morphology.

Canavirgella (type *C. banfieldii*) is represented by GenBank KF889713, accessioned into GenBank as *Lophophacidium dooksii*. Laflamme *et al.* (2015) showed that these two species are synonyms, and they used the earlier name *L. dooksii* for this fungus. However, *Lophophacidium* is placed in *Phacidiaceae* in Hyde *et al.* (2024), placing doubt on whether *L. dooksii* is congeneric with the type of the genus, *L. hyperboreum*. DNA sequences are not available for *L. hyperboreum*.

Sclerotiniaceae and *Rutstroemiaceae* (Figs 5, S2)

Jointly, *Sclerotiniaceae* + *Rutstroemiaceae* form a well-supported monophyletic clade in the multigene phylogeny. However, the monophyletic *Sclerotiniaceae* subclade makes *Rutstroemiaceae* paraphyletic. *Rutstroemiaceae* in the sense that it is currently applied, comprises at least two monophyletic subclades in the multigene phylogeny.

Multigene data from several *Monilinia* genomes show that these form two monophyletic sister clades representing 'Disjunctoriae' (*M. aucupariae*, *M. vaccinii-corymbosi*) and 'Junctoriae' (*M. fructicola*, *M. fructigena*, *M. laxa*, *M. polystroma*) sensu Honey (1936), Holst-Jensen *et al.* (1997) and van Leeuwen *et al.* (2002); the larger inclusive clade is also monophyletic (Fig. 6).

The clade containing *Piceomphale* and '*Cenangium*' *acuum* is sister to *Sclerotiniaceae* + *Rutstroemiaceae* in the multigene analysis. It was treated by Johnston *et al.* (2019) as *Rutstroemiaceae*, but here we follow Pärtel *et al.* (2017) and Hyde *et al.* (2024) in placing it as *Helotiales* incertae sedis. However, note that the asci of *Piceomphale* have a typical sclerotiniaceous apical ring, characteristic of *Sclerotiniaceae* and *Rutstroemiaceae* (Jaklitsch *et al.* 2016, Hans-Otto Baral, pers. comm.).

The ITS phylogeny treats an additional 13 genera of *Sclerotiniaceae*, one represented by the type specimen, and ten specimens identified as types of the genera. *Rutstroemiaceae* has an additional eight genera in the ITS phylogeny, three represented by type specimens, four by specimens identified as types of the genera. One of these genera is *Amphobotrys*, *Sclerotiniaceae* in Hyde *et al.* (2024), but the type, *Amphobotrys ricini*, is on a very long branch within *Rutstroemiaceae* in the ITS phylogeny. LSU sequences are available for *A. ricini*, these place it sister to *Sclerotiniaceae* but again on a very long branch (unpubl. data). *Martininia*, *Sclerotiniaceae* in Hyde *et al.* (2024) has an unstable position within ITS phylogenies, often distant from the *Sclerotiniaceae* + *Rutstroemiaceae* clade, but the LSU sequence (GenBank MH872212) place it in *Rutstroemiaceae* (unpubl. data).

Staheliella, represented by the type specimen of the type, *S. nodosa*, is *Rutstroemiaceae* based on the ITS sequence (MH860777 ex CBS 589.73), but was listed in Hyde *et al.* (2024) as *Ascomycota* incertae sedis. This fungus is known only from tropical America, from its asexual morph from soil.

Two genera placed in *Rutstroemiaceae* in Hyde *et al.* (2024) are distant to *Rutstroemiaceae* in the ITS phylogeny, *Pseudolanzia* and *Arboricolonus*. Their positions within *Helotiales* are unstable, dependent in part of taxon selection in the analysis. The ITS sequence from *Pseudolanzia* has several large introns within the ITS region and the ITS2 region has no clear BLAST match. It is excluded from the ITS phylogeny presented here, although the LSU sequence from *Pseudolanzia* does cluster with *Rutstroemiaceae*, but on a long branch (unpubl. data). The *Arboricolonus* placement in Hyde *et al.* (2024) seems to be a mistake; there is no suggestion in Bien & Damm (2020) that this is *Rutstroemiaceae*; see notes under *Hyphodiscaceae*. An accurate phylogenetic position for these two genera requires additional genes.

Sclerotium was placed in *Sclerotiniaceae* in Hyde *et al.* (2024) but the epitype specimen selected as the type, *S. complanatum*, is a basidiomycete, *Typhulaceae* (Olariaga *et al.* 2020).

Solenopeziaceae (Figs 4, S2)

Solenopeziaceae is well resolved in both the multigene and ITS phylogenies, and in both it is sister to *Lachnaceae*.

A specimen morphologically typical of *Colipila* (PDD 82932, GenBank OQ466382) is *Solenopeziaceae* in the ITS phylogeny, but this position is not supported in multigene phylogeny where the *Colipila* specimen is incertae sedis within *Helotiales*, supporting Hyde *et al.* (2024). The LSU sequence from the PDD 82932 specimen (GenBank OQ466394) is a close match to that from the type of *Colipila*, *C. masduguana* (CBS 128287, GenBank HQ69450, Baral *et al.* 2012).

Tricladiaceae (Figs 3, S2)

Tricladiaceae is well resolved in both the multigene and ITS phylogenies. The ITS phylogeny includes one additional genus, *Spirosphaera*, represented by the type specimen of the type, *S. floriformis*.

A specimen identified as '*Anguillospora' crassa* is included in the multigene analysis. Although this specimen is *Tricladiaceae*, the type of *Anguillospora*, *A. longissima*, is *Dothideomycetes* (Baschien *et al.* 2006).

Tympanidaceae (Figs 6, S2)

Tympanidaceae is well resolved phylogenetically in the multigene phylogeny. In the ITS phylogeny most genera cluster together but the family is not well resolved, with genera spread across several separate clades. The ITS phylogeny treats an additional four genera, three represented by type specimens, another by a specimen identified as the type of the genus.

Vandijckellaceae, *Calloriaceae* etc. (Figs 3, S2)

The big unnamed clade in the middle of *Helotiales* that includes the type of *Vandijckellaceae* (*Vandijckella johannae*) and *Calloriaceae* (*Calloria urticae*), some Han Clade 9 (Han *et al.* 2014) specimens, and the *Stamnaria* lineage sensu Baral in Jaklitsch *et al.* (2016). A similar clade was reported in Johnston *et al.* (2019) and as in this earlier work there is little support for internal branches amongst these taxa that have a diverse set of morphologies.

In the ITS phylogeny, this clade is reasonably well resolved. The types of *Basingstokeomyces* and *Mycoarthris* are very closely related to *Vandijckella* and here are accepted as *Vandijckellaceae*. These two genera are not treated in the multigene phylogeny. The type specimens of *Blastosporium* and *Populomyces* form sister relationships with *Calloria* and *Tricellula*, both *Calloriaceae*, and are tentatively accepted here as *Calloriaceae*.

Duebenia, *Calloriaceae* in Hyde *et al.* (2024), is represented by two species in the ITS phylogeny. *Duebenia compta* (GenBank KY462820) is in the clade with *Calloriaceae* and *Vandijckellaceae* and *Duebenia subcompta* (GenBank NR_163784) is phylogenetically distant with no clear family relationship. No DNA data is available for the type, *D. rufa*.

ORDERS, FAMILIES AND GENERA ACCEPTED IN *LEOTIOMYCETES*

* = notes in Table S4; # = genera published after Hyde *et al.* (2024), classification based on the opinion provided in the publishing article.

Chaetomellales Crous & Denman, *Persoonia* **39**: 423. 2017.
Chaetomellaceae Baral, P.R. Johnst. & Rossman, *Index Fungorum* **225**: 1. 2015. — Type: *Chaetomella*.
Chaetomella Fuckel, *Jahrb. Nassauischen Vereins Naturk.* **23–24**: 401. 1870. — Type: *Chaetomella oblonga* Fuckel
Pilidium Kunze, *Mykol. Hefte* **2**: 92. 1823. — Type: *Pilidium acerinum* (Alb. & Schwein.) Kunze
Sphaerographium Sacc., *Syll. fung.* **3**: 596. 1884. — Type: *Sphaerographium squarrosum* (Riess) Sacc.
Synchaetomella Decock & Seifert, *Antonie van Leeuwenhoek J. Microbiol. Serol.* **88**: 234. 2005. — Type: *Synchaetomella lunatospora* Decock, G. Delgado & Seifert.
Xeropilidium Baral & Pärtel, *Fungal Diversity* **82**: 210. 2016. — Type: *Xeropilidium dennisii* Baral, Pärtel & G. Marson

Helotiales Nannf., *Nova Acta Regiae Soc. Sci. Upsal.* **8(2)**: 68. 1932.
Amicodiscaceae Ekanayaka & K.D. Hyde, *Mycosphere* **10**: 376. 2019. — Type: *Amicodisca*.
Amicodisca Svrček, *Česká Mykol.* **41**: 16. 1987. — Type: *Amicodisca virella* (P. Karst.) Huhtinen *
Amorphothecaceae Parbery, *Austral. J. Bot.* **17**: 345. 1969. — Type: *Amorphotheca* Parbery.
Amorphotheca Parbery, *Austral. J. Bot.* **17**: 340. 1969. — Type: *Amorphotheca resinae* Parbery

Arachnopezizaceae Hosoya, J.G. Han & Baral, *Index Fungorum* **225**: 1. 2015. — Type: *Arachnopeziza* Fuckel
Arachnopeziza Fuckel, *Jahrb. Nassauischen Vereins Naturk.* **23–24**: 303. 1870. — Type: *Arachnopeziza aurelia* (Pers.) Fuckel
Eriopezia (Sacc.) Rehm, *Rabenh. Krypt.-Fl. ed* 2 **1(3)**: 695. 1892. — Type: *Eriopezia caesia* (Pers.) Rehm
Gelida M.M. Wang [nom. illegit.] = *Natara* Kovalova, Yurkov & Baschien #
Phragmiticola Sherwood, *Mycotaxon* **28**: 168. 1987. — Type: *Phragmiticola phragmitis* (Dearn. & House) Magnes
Leochalara W.P. Wu, *Fungal Diversity* **119**: 436. 2023. — Type: *Leochalara danxiashanensis* W.P Wu & Y. Z. Diao
Parachnopeziza Korf, *Mycotaxon* **7**: 468. 1978. — Type: *Parachnopeziza miniopsis* (Ellis) Korf
Thamnochortomyces Crous, *Fungal Syst. Evol.* **13**: 409. 2024. — Type: *Thamnochortomyces kirstenboschensis* Crous

Ascocorticiaceae J. Schröt., *Pilze Schles.* **3(1–2)**: 15. 1893. — Type: *Ascocorticium* Bref.
Ascocorticiellum Julich & B. de Vries, *Persoonia* **11**: 410. 1982. — Type: *Ascocorticiellum vermisporum* (Hauerslev) Jülich & B. de Vries
Ascocorticium Bref., *Untersuch. Gesammtgeb. Mykol.* **9**: 145. 1891. — Type: *Ascocorticium albidum* Bref. & Tavel [current name *Ascocorticium anomalum* (Ellis & Harkn.) J. Schröt.]
Ascosorus Henn. & Ruhland, *Bot. Jahrb. Syst.* **28(3)**: 276. 1900. — Type: *Ascosorus floridanus* (Ellis & Everh.) Henn. & Ruhland
Ascodichaenaceae D. Hawksw. & Sherwood, *Mycotaxon* **16**: 262. 1982. — Type: *Ascodichaena* Butin
Ascodichaena Butin, *Trans. Brit. Mycol. Soc.* **69**: 249. 1977. — Type: *Ascodichaena rugosa* Butin
Delpinoina Kuntze, *Revis. gen. pl.* **2**: 851. 1891. — Type: *Delpinoina lusitanica* (Pass. & Thüm.) Kuntze

Bryoglossaceae Ekanayaka & K.D. Hyde, *Mycosphere* **10**: 375. 2019. — Type: *Bryoglossum* Redhead
Bryoclaviculus L. Ludw., P.R. Johnst. & Steel, *New Zealand J. Bot.* **51**: 322. 2013. — Type: *Bryoclaviculus campylopi* L. Ludw., P.R. Johnst. & Steel
Bryoglossum Redhead, *Canad. J. Bot.* **55**: 323. . 1977.. — Type: *Bryoglossum gracile* (P. Karst.) Redhead
Neocudoniella S. Imai, *J. Fac. Sci. Hokkaido Imp. Univ.* **45**: 233. 1941. — Type: *Neocudoniella jezoensis* (S. Imai) S. Imai

Calloriaceae Baral & G. Marson, *Index Fungorum* **407**: 1. 2019. — Type: *Calloria* Fr.
Aivenia Svrček, *Česká Mykol.* **31**: 132. . 1977.. — Type: *Aivenia tantula* Svrček
Blastosporium Z.F. Yu & H. Zheng, *MycoKeys* **51**: 60. 2019. — Type: *Blastosporium persicolor* Z.F. Yu & Hua Zheng *
Calloria Fr., *Fl. Scan.* p. 343. 1836. — Type: *Calloria urticae* (Pers.) J. Schröt. ex Rehm (=*C. fusarioides*)
Chaetonaevia Arx, *Antonie van Leeuwenhoek J. Microbiol. Serol.* **17**: 85. 1951. — Type: *Chaetonaevia nannfeldtii* Arx
Diplonaevia Sacc., *Syll. fung.* **8**: 666. 1889. — Type: *Diplonaevia caricum* (Auersw.) Sacc.
Duebenia Fr., *Summa veg. Scand.* **2**: 356. 1849. — Type: *Duebenia rufa* Fr. *
Eupropolella Höhn., *Ann. Mycol.* **15**: 311. 1917. — Type: *Eupropolella vaccinii* (Rehm) Höhn.
Hyalacrotes (Korf & L.M. Kohn) Raitv., *Nizshie Rasteniya, Griby i Mokhoobraznye Sovetskogo Dal'nego Vostoka* **2**: 337. 1991. — Type: *Hyalacrotes hamulata* (Rehm) Raitv.
Iridinea Velen., *Monogr. Discomyc. Bohem.*: 299. 1934. — Type: [no type designated]
Laetinaevia Nannf., *Nova Acta Regiae Soc. Sci. Upsal.* **8(2)**: 190. 1932. — Type: *Laetinaevia lapponica* (Nannf.) Nannf. *
Loricella Velen., *Monogr. Discomyc. Bohem.*: 383 — Type: [none designated]
Micropodia Boud., *Bull. Soc. Mycol. France* **1**: 118.

1885. — Type: *Micropodia pteridina* (Nyl.) Boud.
Naeviella Clem., *Gen. fung.* p. 63. 1909. — Type: *Naeviella paradoxa* (Rehm) Clem.
Naeviopsis B. Hein, *Willdenowia*, Beih. **9**: 60. 1976. — Type: *Naeviopsis epilobii* (P. Karst.) B. Hein
Ploettnera Henn., *Verh. Bot. Vereins Prov. Brandenburg* **41**: 94. 1900. — Type: *Ploettnera caeruleoviridis* (Rehm) Henn.
Populomyces Hern.-Restr., *Fungal Syst. Evol.* **7**: 319. 2021. — Type: *Populomyces zwinianus* Hern.-Restr. *
Pseudopopulomyces D.F. Bao, K.D. Hyde & Y.Z. Lu, in Bao, *Mycosphere* **16**: 2324. 2025. — Type: *Pseudopopulomyces dicranopteridis* J.Y. Zhang, D.F. Bao, K.D. Hyde & Y.Z. Lu #
Tricellula Beverw., *Antonie van Leeuwenhoek J. Microbiol. Serol.* **20**: 15. 1954. — Type: *Tricellula inaequalis* Beverw.

Cenangiaceae Rehm, *Rabenh. Krypt.-Fl. ed 2* **1(3)**: 213. 1889. — Type: *Cenangium* Fr.
Calycellinopsis W.Y. Zhuang, *Mycotaxon* **38**: 121. 1990. — Type: *Calycellinopsis xishuangbanna* W.Y. Zhuang *
Cenangiopsis Rehm, *Ber. bayer. bot. Ges.* **13**: 189. 1912. — Type: *Cenangiopsis quercicola* (Romell) Rehm
Cenangium Fr., *Kongl. Vetensk. Acad. Handl.*, ser. 3 **39**: 360. 1818. — Type: *Cenangium ferruginosum* Fr.
Chlorencoelia J.R. Dixon, *Mycotaxon* **1**: 223. 1975. — Type: *Chlorencoelia versiformis* (Pers.) J.R. Dixon
Crumenulopsis J.W. Groves, *Canad. J. Bot.* **47**: 48. 1969. — Type: *Crumenulopsis pinicola* (Rebent.) J.W. Groves
Encoelia (Fr.) P. Karst., *Bidrag Kännedom Finlands Natur Folk* **19**: 217. 1871. — Type: *Ecoelia furfuracea* Roth.
Fabrella Kirschst., *Hedwigia* **80**: 131. 1941. — Type: *Fabrella tsugae* (Farl.) Kirschst.
Heyderia Link, *Handbuch.* **3**: 311. 1833. — Type: *Heyderia abietis* (Fr.) Link
Hymenobolus Durieu & Mont., *Ann. Sci. Nat., Bot.*, sér. 3 **4**: 359. 1845. — Type: *Hymenobolus agaves* Durieu & Mont.
Hysterostegiella Höhn., *Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss, Kl.*, Abt. 1 **126(4–5)**: 313. 1917. — Type: *Hysterostegiella fenestrata* (Roberge ex Desm.) Höhn.
Mycosphaerangium Verkley, *Stud. Mycol.* **44**: 156. 1999. — Type: *Mycosphaerangium tetrasporum* (Ellis) Verkley
Neomelanconium Petr., *Ann. Mycol.* **38**: 208. 1940. — Type: *Neomelanconium gelatosporum* (H. Zimm.) Petr.
Rhabdocline Syd., *Ann. Mycol.* **20**: 194. 1922. — Type: *Rhabdocline pseudotsugae* Syd.
Sarcotrochila Höhn., *Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss, Kl.,* Abt. 1 **126(4–5)**: 309. 1917. — Type: *Sarcotrochila alpina* (Fuckel) Höhn. *
Trochila Fr., *Summa veg. Scand.* **2**: 367. 1849. — Type: *Trochila craterium* (DC.) Fr.
Velutarina Korf, *Phytologia* **21**: 201. 1971. — Type: *Velutarina rufo-olivacea* (Alb. & Schwein.) Korf
Vestigium Piroz. & Shoemaker, *Canad. J. Bot.* **50**: 1163. 1972. — Type: *Vestigium felicis* Piroz. & Shoemaker

Chlorociboriaceae Baral & P.R. Johnst., *Index Fungorum* **225**: 1. 2015. — Type: *Chlorociboria* Seaver ex C.S. Ramamurthi, Korf & L.R. Batra
Brahmaculus P.R. Johnst., *MycoKeys* **80**: 23. 2021. — Type: *Brahmaculus moonlighticus* P.R. Johnst.
Chlorociboria Seaver ex C.S. Ramamurthi, Korf & L.R. Batra, *Mycologia* **49**: 857. 1958. — Type: *Chlorociboria aeruginosa* (Oeder) Seaver ex C.S. Ramamurthi, Korf & L.R. Batra

Chlorospleniaceae Ekanayaka & K.D. Hyde, *Mycosphere* **10**: 373. 2019. — Type: *Chlorosplenium* Fr.
Chlorosplenium Fr., *Summa veg. Scand.* **2**: 356. 1849. — Type: *Chlorosplenium chlora* (Schwein.) M.A. Curtis

Chrysodiscaceae Baral & Haelew., *Mycol. Montenegr.* **20**: 81. 2019. — Type: *Chrysodisca* Baral, Polhorský & G. Marson
Chrysodisca Baral, Polhorský & G. Marson, *Mycol. Montenegr.* **20**: 81. 2019. — Type: *Chrysodisca peziculoides* Baral, Polhorský & G. Marson

Cordieritidaceae Sacc., *Syll. fung.* **8**: 810. 1889. — Type: *Cordierites* Mont.
Ameghiniella Speg., *Bol. Acad. Nac. Ci. Córdoba* **11**: 270. 1887. — Type: *Ameghiniella australis* Speg.
Annabella Fryar, Haelew. & D.E.A. Catches., *Mycol. Progr.* **18**: 975. 2019. — Type: *Annabella australiensis* Fryar, Haelew. & D.E.A. Catches.
Austrocenangium Gamundí, *Mycotaxon* **63**: 262. 1997. — Type: *Austrocenangium australe* (Speg.) Gamundí
Cordierites Mont., *Ann. Sci. Nat., Bot.*, sér. 2 **14**: 330. 1840. — Type: *Cordierites guianensis* Mont.
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Lasiostictella Sherwood, *Sydowia* **38**: 32. 1986. — Type: *Lasiostictella bambusae* Sherwood
Lirula Darker, *Canad. J. Bot.* **45**: 1420. 1967. — Type: *Lirula nervisequa* (DC.) Darker *
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Neotherrya Lan Zhuo & C.L. Hou, *IMA Fungus* **16** (no. e138790): 32. 2025. — Type: *Neotherrya circinata* Lan Zhuo & C.L. Hou #
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Nothorhytisma Minter, P.F. Cannon, A.I. Romero & Peredo, *Syst. Ascomycetum* **16**: 34. 1998. — Type: *Nothorhytisma nahuelitae* Minter, P.F. Cannon, A.I. Romero & Peredo
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Pseudococcomyces Lan Zhuo & C.L. Hou, *IMA Fungus* **16** (no. e138790): 41. 2025. — Type: *Pseudococcomyces yunnanensis* Lan Zhuo & C.L. Hou #
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Pseudorhytisma Juel, *Öfvers. Kongl. Vetensk.-Akad. Förh.* **51**: 498. 1894. — Type: *Pseudorhytisma bistortae* (DC.) Juel
Pureke P.R. Johnst., *New Zealand J. Bot.* **29**: 395. 1991. — Type: *Pureke zelandicum* P.R. Johnst.
Rhodohypoderma M.J. Guo, M. Piepenbr. & C.L. Hou, *Mycosphere* **15**: 812. 2024. — Type: *Rhodohypoderma rhododendri* M.J. Guo & C.L. Hou
Rhytisma Fr., *Kongl. Vetensk. Acad. Handl.*, ser. 3 **40**: 104. 1819. — Type: *Rhytisma acerinum* (Pers.) Fr.
Septofusella M.J. Guo & C.L. Hou, *Mycosphere* **15**: 818. 2024. — Type: *Septofusella triseptata* M.J. Guo & C.L. Hou
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Shiqia C.L. Hou, Q.T. Wang & P.F. Cannon, *Fungal Diversity* **120**: 104. 2023. — Type: *Shiqia yuexiensis* (C.L. Hou & M. Piepenbr.) C.L. Hou, Q.T. Wang & P.F. Cannon
Shuqunia M.J. Guo, M. Piepenbr. & C.L. Hou, *Mycosphere* **15**: 823. 2024. — Type: *Shuqunia longa* M.J. Guo, M. Piepenbr. & C.L. Hou
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Sporomega Corda, *Icon. fung.* **5**: 34. 1842. — Type: *Sporomega degenerans* (Kunze) Corda *
Stipamyces Lan Zhuo & C.L. Hou, *IMA Fungus* **16** (no. e138790): 43. 2025. — Type: *Stipamyces pinicola* (R.H. Lei & C.L. Hou) Lan Zhuo & C.L. Hou #
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Therrya Sacc., *Michelia* **2**: 604. 1882. — Type: *Therrya gallica* Sacc. & Penz. *

Truncomyces M.J. Guo & C.L. Hou, *Mycology*: 10.1080/21501203.2025.2461211: 35. 2025. — Type: *Truncomyces vaginatus* M.J. Guo & C.L. Hou #

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Yingrenia M.J. Guo, M. Piepenbr. & C.L. Hou, *Mycosphere* **15**: 846. 2024. — Type: *Yingrenia erumpens* (C.L. Hou & M. Piepenbr.) M.J. Guo, M. Piepenbr. & C.L. Hou

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Holwaya Sacc., *Syll. fung.* **8**: 646. 1889. — Type: *Holwaya ophiobolus* (Ellis) Sacc. [current name *Holwaya mucida* (Schulzer) Korf & Abawi]

Patinella Sacc., *Grevillea* **4**: 22. 1875. — Type: *Patinella hyalophaea* Sacc.

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Kimbr.

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Thelebolus Tode, *Fung. mecklenb. sel.* **1**: 41. 1790. — Type: *Thelebolus stercoreus* Tode

Thelebolales **genera incertae sedis**

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Umbellidion B. Sutton & Hodges, *Nova Hedwigia* **26**: 529. 1975. — Type: *Umbellidion radulans* B. Sutton & Hodges

Leotiomycetes **order incertae sedis**

Cochlearomycetaceae Crous, *Persoonia* **39**: 351. 2017. — Type: *Cochlearomyces* Crous

Cochlearomyces Crous, *Persoonia* **39**: 351. 2017. — Type: *Cochlearomyces eucalypti* Crous

Satchmopsis B. Sutton & Hodges, *Nova Hedwigia* **26**: 1. 1975. — Type: *Satchmopsis brasiliensis* B. Sutton & Hodges *

Neocrinulaceae Crous, *Persoonia* **39**: 393. 2017. — Type: *Neocrinula* Crous

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Leotiomycetes **genera incertae sedis**

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Callerascus Whitton, K.D. Hyde & McKenzie, *Fungal Diversity Res. Ser.* **21**: 45. 2012. — Type: *Callerascus caerulitunicatus* Whitton, K.D. Hyde & McKenzie

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Fig. 7. Comparison of the macroscopic appearance of sister taxa *Colipila* and *Pseudomitrula*. **A.** *Colipila* sp. (PDD 82932, dried specimen). **B.** *Pseudomitrula* sp. (PDD 121212, fresh specimen). Scale bars = 0.5 mm.

Gelatinopsis Rambold & Triebe, *Notes Roy. Bot. Gard. Edinburgh* **46**: 375. 1990. — Type: *Gelatinopsis geoglossi* (Ellis & Everh.) Rambold & Triebel *

Helotiella Sacc., *Botan. Zbl.* **18**: 218. 1884. — Type: *Helotiella citri* (Penz.) Sacc.

Humicolopsis Cabral & S. Marchand, *Boln Soc. Argent. Bot.* **17**: 69. 1976. — Type: *Humicolopsis cephalosporioides* Cabral & S. Marchand

Melanormia Körb., *Parerga lichenol.* **5**: 437. 1865. — Type: *Melanormia velutina* Körb.

Metapezizella Petr., *Sydowia* **20**: 207. 1968. — Type: *Metapezizella phyllachorivora* Petr.

Nannfeldtia Petr., *Sydowia* **1**: 18. 1947. — Type: *Nannfeldtia atra* Petr.

Ocotomyces H.C. Evans & Minter, *Trans. Brit. Mycol. Soc.* **84**: 68. 1985. — Type: *Ocotomyces parasiticus* H.C. Evans & Minter

Phyllopezis Petr., *Sydowia* **3**: 238. 1949. — Type: *Phyllopezis andina* Petr.

Physmatomyces Rehm, *Hedwigia* **39**: 216. 1900. — Type: *Physmatomyces compacti* Rehm

Polydiscina Syd., *Ann. Mycol.* **28**: 439. 1930. — Type: *Polydiscina boliviana* Syd.

Psilothecium Clem., *Bull. Torrey bot. Club* **30**: 85. 1903. [nom. illegit.] — Type: *Psilothecium incurvum* Clem.

CONCLUSIONS

Although many additional genera, families and orders are included in this paper in addition to those treated in Johnston *et al.* (2019), the overall structure of the phylogeny is very similar. The large order *Helotiales* is strongly supported and there is still no useful scheme that could be used to break apart *Helotiales* above the family level. The situation with respect to resolving stable relationships between genera and families in the taxa outside of *Helotiales* remains uncertain, despite the increase in the number of taxa treated. A concerted effort to generate additional genomes from taxa in this part of the phylogeny may help better resolve a sensible and stable higher-level classification for *Leotiomycetes* outside of *Helotiales*, towards the root of the trees presented here.

The taxonomic conclusions and changes suggested in this paper are based almost solely on phylogenetic relationships supported by analysis of DNA sequences. In some cases, apparent incongruence with morphology or ecology has helped tease out DNA sequence data that appears to be derived from misidentified specimens, a real problem with accessions into international DNA sequence databases (Nilsson *et al.* 2006). This can become a serious issue when incorrectly annotated DNA sequence data are used in subsequent identifications based solely on DNA sequence comparisons, one example discussed in this paper being *Gremmenia infestans* (see comments in *Lachnaceae* section above).

However, some surprising relationships reported here, strongly supported in the multigene phylogeny and based on reliably identified specimens, are difficult to understand based on macromorphology. One example is the macroscopically cudoniella-like species of *Lachnaceae* discussed under the *Lachnaceae* section above. Another example is that of a sister relationship between *Colipila* and *Pseudomitrula* (Fig. 7). *Colipila* recalls *Lachnum* and *Dasyscyphella* macroscopically, but differs in its smooth, spindle shaped hairs and paraphyses (Baral *et al.* 2012). The specimen representing *Colipila* in the multigene phylogeny matches the description in Baral *et al.* (2012) microscopically and has an LSU sequence very close to that from a specimen identified as the type *Colipila masduguana* (GenBank MH876292, voucher CBS 128287). The specimen representing *Pseudomitrula* is macromorphologically typical of the genus as described by Gamundí (1980) and the LSU is very close to a GenBank accession from Chile identified as *Pseudomitrula* (GenBank OR075121, voucher FLAS-F-65145). It is possible that the apparent relationship in Fig. 3 reflects a lack of taxon sampling in this part of the phylogeny, rather than a recently shared ancestry.

Johnston *et al.* (2019) briefly discussed the impact that uneven gene coverage may have on the phylogenies. Based on an ad hoc examination of their data, they concluded that missing genes had minimal impact on the topology of their multigene phylogenetic tree. However, some consideration should be given to gene coverage when interpreting the significance of relationships represented in the multigene phylogeny, especially where they do not seem to reflect other sets of data, such as morphology. An apparent relationship between *Coccomyces australis* and two *Hypoderma* species may provide an example in this paper, see comments in the *Rhytismataceae* section above.

Some paraphyletic taxa are retained here, even though classifications that include paraphyletic taxa have the potential to mislead rather than to inform (Johnston *et al.* 2019). For example, a good case can be made for accepting a broader concept of *Sclerotiniaceae*, to include both *Sclerotiniaceae* and *Rutstroemiaceae*. A specialised ascus morphology supports such a scheme (Baral in Jaklitsch *et al.* 2016), and it would avoid having to establish additional families and resolve limits of *Rutstroemiaceae* s. str. However, retaining *Sclerotiniaceae* in its current sense restricts it to a clade of genetically similar, economically important necrotrophic pathogens, an extremely useful taxonomic concept for plant pathologists. Because of its value to users, there are strong reasons for *Sclerotiniaceae*, excluding *Rutstroemiaceae*, to be retained. A paraphyletic *Rhytismataceae* is retained in a provisional sense as taxonomic limits of genera with *Rhytismataceae* are as poorly resolved as are the limits of *Rhytismataceae*, *Triblidiaceae* and *Cudoniaceae*. For example, no multigene data is available for the large genus *Lophodermium*, *Lophodermium* s. str. being represented by the grass-inhabiting species *L. actinothyrium* in Fig. S2, a species phylogenetically distant from important species such as the pine pathogen *L. pinastri* (Ortiz-García *et al.* 2003). A paraphyletic *Chlorociboria* is also retained. *Brahmaculus*, sister to two *Chlorociboria* species in a monophyletic clade in the multigene phylogeny, makes *Chlorociboria* paraphyletic, but it is not clear how these two Brahmaculus-like *Chlorociboria* spp. can be distinguished morphologically from the other *Chlorociboria* species.

Quandt & Haelewaters (2021) discussed issues around geographic bias in existing phylogenetic data for *Leotiomycetes*. This is reflected in our analyses with respect to the strong phylogenetic structure within *Helotiaceae*, most of which is associated with species known from only the Southern Hemisphere. This diversity may be reflected taxonomically in the future but would be unrecognised without the southern focus of some of the sampling reported here.

Availability of data and materials
The datasets generated and analysed during the current study are available in the Manaaki Whenua — Landcare Research Datastore, https://doi.org/10.7931/e59n-b194.

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Supplementary Material: http://fuse-journal.org

Supplementary materials are also available through the Manaaki Whenua – Landcare Research Datastore, https://doi.org/10.7931/e59n-b194.

Fig. S1. ML tree expanded from Fig. 1. The labels for taxa include the voucher specimen from which the sequences were obtained, the type status of the specimen (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus), and the source of the genome data for those that have had their genome sequenced, together with the sequenced loci available for each specimen. Family level clades are coloured blue or red as a visual cue, taxa coloured purple have taxonomic issues discussed in the text, the taxa in black are incertae sedis within an order or *Leotiomycetes*.

Fig. S2. RAxML tree based on ITS sequences. The labels for taxa include GenBank accession number, species name, type status of the specimen (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus), and family accepted for the taxon. Labels with # indicate taxa not treated in the multigene analysis. Family level clades are coloured blue or red as a visual cue, taxa coloured purple have taxonomic issues discussed in the text, the taxa in black are incertae sedis within an order or *Leotiomycetes*. Details of the specimens included are provided in suppl. data Table S3. Although many of the family-level clades that were strongly supported in the multigene phylogeny are resolved in this tree, bootstrap values are mostly very low; whether the inferred relationships suggested by the ITS phylogeny are meaningful needs to be assessed by comparisons back to the multigene phylogeny.

File S1. Fasta format alignment used for multigene analysis. Partitions are provided in Suppl. Data Table S2.

Table S1. Sequences used for the multigene phylogeny. Newly published genomes deposited as NCBI Bioproject PRJNA1270366 are in bold.

Table S2. Partitions and models used for the multigene analysis.

Table S3. GenBank accession numbers, vouchers and type status (TypeSpecies = a specimen identified as the type for that genus; exTypeSpecimen = the type specimen of the type for that genus) of the taxa included in the ITS phylogeny (Suppl. Data Fig S2).

Table S4. DNA sequence data available for each of the genera listed as *Leotiomycetes* in Outline of Fungi 2024 (Hyde *et al.* 2024). For each genus the generic type is listed, and an indication whether ITS, multigene or genome data are available for that species, along with whether that data was derived from the type specimen. Where data is not available for the generic type, but other species from the same genus were included, the species treated are listed.