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# Rise up, *Rhizoctonia*: moving to one fungus, one name in the *Ceratobasidiaceae* (*Agaricomycetes*, *Cantharellales*)

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**Abstract:** *Ceratobasidiaceae* is a family of cryptic basidiomycetous fungi, most notable for the plant pathogens known under generic names such as *Rhizoctonia*, *Thanatephorus*, *Ceratorhiza,* and *Ceratobasidium*. While responsible for billions of dollars in crop losses annually, members of these genera also serve important ecological functions as orchid mycorrhizal symbionts and saprotrophs. While asexually-typified (*Rhizoctonia* and *Ceratorhiza*) and sexually-typified (*Thanatephorus* and *Ceratobasidium*) names have been utilised, molecular studies have repeatedly demonstrated these genera to be paraphyletic. In addition, the type of *Ceratobasidium* is not congeneric with the many other species introduced in the genus. Despite previous attempts to synonymise various names under a broadly-defined *Rhizoctonia*, authors have continued to describe new species using outdated generic names. Using publicly-available ITS, LSU, *ATP6, RPB2*, and *TEF1* sequences generated from holotype specimens or from isolates obtained from permanently preserved cultures of type collections (ex-type specimens), we recovered a phylogeny of the *Ceratobasidiaceae* that reiterates the paraphyly of various genera within a well-supported clade to which we apply the name *Rhizoctonia*. We review the placements of names introduced in the genera *Ceratobasidium*, *Ceratorhiza*, and *Thanatephorus*, and formalise 32 new combinations in *Rhizoctonia*. While it is accepted that the type of *Ceratobasidium* does not belong in *Rhizoctonia*, we advocate continued use of the family name *Ceratobasidiaceae* and discuss a nomenclatural solution to formally cement this usage. Using *Rhizoctonia* as a case study, we argue that continued use of names that are evident synonyms is out of step with contemporary fungal taxonomic practice and precludes a holistic understanding of the classification and biology of this group.

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## INTRODUCTION

*Ceratobasidiaceae* (*Agaricomycetes*, *Cantharellales*) is a family of cryptic basidiomycetous fungi which encompasses several genera of major economic and ecological significance (Mosquera-Espinosa *et al.* 2013, Oberwinkler *et al.* 2013, Veldre *et al.* 2013). Taking its name from the genus *Ceratobasidium* (henceforth abbreviated as *Cb.*) (asexual morph: *Ceratorhiza*, henceforth abbreviated as *Cr.*), members of the family span multiple trophic modes including plant pathogens, saprotrophs, and orchid mycorrhizal symbionts (Oberwinkler *et al.* 2013, Veldre *et al.* 2013). Most notably, the family currently includes the genus *Rhizoctonia* (sexual morph: *Thanatephorus*); a necrotrophic plant pathogen responsible for billions of dollars of crop losses annually (Okubara *et al.* 2014). *Ceratobasidiaceae* is one of the three major families that form mycorrhizas with orchids, alongside *Tulasnellaceae* and *Serendipitaceae* (Dearnaley *et al.* 2012). Together, the orchid-mycorrhizal fungi within these three families have been, for convenience, referred to in the literature as 'rhizoctonias', a term not to be confused with the genus *Rhizoctonia*. *Ceratobasidiaceae* is hypothesised to be the ancestral orchid mycorrhizal symbiont family, highlighting the family's importance in the orchid-mycorrhizal interaction (Yukawa *et al.* 2009). Jülich's (1982) treatment of the *Ceratobasidiaceae* also included the genera *Koleroga*, *Oliveonia*, *Scotomyces*, *Uthatobasidium*, and *Ypsilonidium*. Roberts (1999) subsequently placed *Koleroga* under *Ceratobasidium* and several other genera under *Thanatephorus* including *Uthatobasidium*, *Ypsilonidium*, *Aquathanatephorus*, *Cejpomyces*, *Oncobasidium*, and *Tofispora*. *Oliveonia* has since been treated in a separate family – *Oliveoniaceae* – placed within the *Auriculariales* (Roberts 1998b, Cao *et al.* 2021, Olariaga 2021).

*Ceratobasidium* and *Thanatephorus* were separated on morphology by the latter having wider hyphae and comparatively more elongate basidia, along with subtle differences in sporophore thickness, the arrangement of hyphae and the layering of basidia (Stalpers & Andersen 1996, Roberts 1999). However, it was recognised that intermediate forms existed (Roberts 1999) and that there was "a continuum of species displaying various combinations of characteristics", making the separation of *Ceratobasidium* and *Thanatephorus* "vague" (Stalpers & Andersen 1996). Nuclear number was also used to separate *Ceratobasidium* (binucleate) and *Thanatephorus* (multinucleate), although again there were exceptions, such as binucleate species of *Thanatephorus* (Roberts 1999).

Molecular phylogenies of the group over the past two decades have repeatedly demonstrated the major genera of the *Ceratobasidiaceae* – *Ceratobasidium*, *Ceratorhiza*, *Rhizoctonia*, and *Thanatephorus* – to be a paraphyletic assemblage with poorly defined generic boundaries and a lack of consistent synapomorphies (Gónzalez *et al.* 2001, González *et al.* 2002, Otero *et al.* 2004, 2011, Bougoure *et al.* 2009, Shefferson *et al.* 2010, Xu *et al.* 2010, Mosquera-Espinosa *et al.* 2013, Oberwinkler *et al.* 2013, Diederich *et al.* 2014, Gónzalez *et al.* 2016, Blanco *et al.* 2018, de Melo *et al.* 2018, Ferreira *et al.* 2021, Freestone *et al.* 2021, Cruz *et al.* 2022). The majority of molecular studies to date have predominantly used only the internal transcribed spacer (ITS) and large-subunit rRNA (LSU) regions for phylogenetic inference. In addition to the ITS and LSU regions, Gónzalez *et al.* (2016) also incorporated sequences of two nuclear genes – second largest subunit of RNA polymerase II (*RPB2*), translation elongation factor 1 alpha (*TEF1*) – and one mitochondrial gene, ATP synthase subunit 6 (*ATP6*) in their phylogenetic analyses. Despite the addition of these additional gene regions, Gónzalez *et al.* (2016) still recovered the genera of the *Ceratobasidiaceae* as paraphyletic. There has been little systematic work to date at the genomic scale incorporating multiple genera of the *Ceratobasidiaceae*. However, a study which generated a draft genome assembly of *Cb. theobromae* (Ali *et al.* 2019) found that the vast majority of genome assembly contigs they generated clustered most closely with contigs from *R. solani* (Kühn 1858).

Oberwinkler *et al.* (2013) began the process of transitioning towards a unified nomenclature by transferring the majority of accepted *Ceratobasidium* species to *Rhizoctonia* (which they preferenced over *Thanatephorus*), with the exception of the type for the name *Ceratobasidium*; *Cb. calosporum*. Re-examination of the holotype of *Cb. calosporum* revealed several aberrant micromorphological and ultrastructural characters which separated *Cb. calosporum* from all other described species of *Ceratobasidium* (Oberwinkler 1982, Oberwinkler *et al.* 2013). For example, *Cb. calosporum* exhibits vermiform basidiospores, dolipores with continuous parenthesomes, and partially to completely longitudinally septate basidia. In contrast, all other species described as *Ceratobasidium*, *Ceratorhiza, Rhizoctonia*, and *Thanatephorus* share globose to ellipsoid or cylindrical basidiospores, dolipores with discontinuous parenthesomes, and aseptate basidia (Roberts 1999, Oberwinkler *et al.* 2013). On this basis, Oberwinkler *et al.* (2013) concluded that the generic name *Ceratobasidium* should be applied only to *Cb. calosporum* to the exclusion of all other species described under that generic name. The choice between *Rhizoctonia* (asexually-typified) over *Thanatephorus* (sexually-typified) was confirmed when Stalpers *et al.* (2021) chose to let priority rule and adopted the former name.

Despite the delimitation by Oberwinkler *et al.* (2013) of a broadly circumscribed *Rhizoctonia* (inclusive of *Ceratobasidium*), several studies have since published new species using the name *Ceratobasidium* (Diederich *et al.* 2014, de Melo *et al.* 2018, Ferreira *et al.* 2021, Cruz *et al.* 2022, Tan & Adhikari 2024, Tan & Shivas 2024). Each of these studies incorporated molecular phylogenetic analyses which placed sequences from the types of new species described as *Ceratobasidium* within a large clade also containing species of *Rhizoctonia*. This continued use of evidently synonymous names is not reflective of biology, or contemporary mycological understanding and practice. This is especially problematic in the case of economically significant pathogens, as the use of multiple names for the one lineage fractures attempts to have a holistic understanding of organisms which are fundamentally united in their biology (Wingfield *et al.* 2012).

To address generic limits in *Ceratobasidiaceae*, we sourced publicly available ex-type and representative ITS, LSU, *ATP6*, *RPB2*, and *TEF1* sequences to infer a phylogeny of described species of *Ceratobasidiaceae*, incorporating recently described species of *Ceratobasidium* and *Ceratorhiza*. Echoing previous studies, we recovered a single well-supported clade that contained species assigned to *Ceratobasidium*, *Ceratorhiza*, *Rhizoctonia*, and *Thanatephorus*, and failed to recover any well-supported internal clades to which any of these names could be applied as separate genera. Then, to demonstrate the variable use of different generic names within the *Ceratobasidiaceae* across the scientific literature, we conducted a Scopus database search for various combinations of the main generic names encompassed within the family. Searches revealed an overwhelming use of the name *Rhizoctonia*, along with differences in the use of certain names between pathogen and orchid mycorrhizal research. We consequently formalise the transfer of 32 species of *Ceratobasidium*, *Ceratorhiza*, and *Thanatephorus* to *Rhizoctonia* to continue the push towards a unified taxonomy. Furthermore, we review the validity of all epithets within the group and provide a summary of all valid and invalid names. Following this revision, we accept a total of 52 species of *Rhizoctonia*. We discuss several nomenclatural issues within *Ceratobasidiaceae* and provide recommendations for their resolution. Using the *Ceratobasidiaceae* as a case study, we show that the continued recognition of synonymous generic names precludes a holistic understanding of an organism's fundamental biology and ecology.

## MATERIALS AND METHODS

### Tree inference

To recover a phylogeny of described species of *Ceratobasidiaceae*, publicly-available ITS, LSU, *ATP6*, *RPB2*, and *TEF1* sequences were sourced from GenBank (Sayers *et al.* 2022). Where possible, sequences derived from type material or from ex-type cultures were identified from either GenBank accession type citations, or by searching for holotype voucher numbers/culture collection numbers. If sequences from type material were unavailable, representative sequences were sourced from published studies which were thus considered as the contemporary concept of the taxon in question. Where available, ex-type sequences are indicated in subsequent text with (T), while representative sequences are indicated with (R). All accessions used for named taxa within *Ceratobasidiaceae* are outlined in Table 1.

To place sequences from named taxa within a broader *Ceratobasidiaceae*, a second tree was inferred using the

ITS sequences from described taxa, along with all UNITE (Nilsson *et al.* 2019) species hypotheses (SHs) identified as "*Ceratobasidiaceae*" sourced from the UNITE general FASTA release for Fungi v.10.0 (Abarenkov *et al.* 2024) (Supporting Information Table S1). The UNITE general FASTA release adopts dynamic (i.e. lineage-specific) clustering thresholds. Sequences identified as "*Ceratobasidiaceae*" were extracted from the UNITE FASTA using SeqKit v.2.8.2 (Shen *et al.* 2016) with the command "seqkit grep -r -n -p '.*Ceratobasidiaceae.*'" which collates all sequences with the string "*Ceratobasidiaceae*" in the FASTA header line. Examination of selected *Ceratobasidiaceae* UNITE SHs showed that they were all clustered at the 1.5 % level. Because some UNITE SHs belonging to members of the *Ceratobasidiaceae* were identified only to higher taxa (e.g. "*Agaricomycetes* sp."), to ensure all species hypotheses corresponding with named taxa were included for analysis, a local BLAST database was created using the UNITE general FASTA release and all ITS sequences from named taxa were then queried against this database using blastn v. 2.12.0 (Camacho *et al.* 2009). Sequences for species hypotheses matching named taxa that were not captured by the initial string matching filter (but that were identified by the BLAST match against UNITE locally) were subsequently retrieved manually from the UNITE general release FASTA file. A preliminary tree was inferred to ascertain whether all retained SHs were recovered within a congruent *Ceratobasidiaceae* clade based on named species. All SHs not falling within this clade were BLASTed using the BLAST web application (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to determine whether they represented misclassified accessions. There were nine misclassified SHs; four belonging to *Waitea* (*Corticiaceae*), one representing *Rhizoctonia rubi* i.e. '*Monilinia rubi*' nom. inval. (Table 3) (an ascomycete), along with one *Sarcoscyphaceae* sp. (1968), one "uncultured *Cantharellales*" and two "uncultured basidiomycete" (Supporting Information Table S2). These nine SHs were removed from the initial raw FASTA before repeating all alignment, trimming, and tree inference steps to produce a final tree. Misclassified SHs excluded from subsequent analyses are outlined in Supporting Information Table S2.

To examine the phylogenetic structure of trophic modes/lifestyles within the *Ceratobasidiaceae* (e.g. orchid mycorrhizal, pathogenic, saprotrophic, lichenicolous), a third phylogeny was inferred using ITS sequences (Supporting Information Table S3) including all named species included in the first and second analyses, along with 149 additional representative sequences from undescribed orchid mycorrhizal operational taxonomic units (OTUs) and pathogenic anastomosis group (AG) OTUs without formal names, also sourced from GenBank. Classification of anastomosis group sequences as pathogens or orchid symbionts follows Roberts (1999) and González *et al.* (2006). Orchid mycorrhizal OTUs were sourced from studies incorporating germination experiments with orchid collections spanning Africa (Waterman *et al.* 2011), Asia (Suetsugu *et al.* 2019), Australia (Otero *et al.* 2011, Freestone *et al.* 2021), Europe (Calevo *et al.* 2020), North America (Kaur *et al.* 2019), and South America (Otero *et al.* 2004, Fracchia *et al.* 2014).

Final inferred trees were rooted using *Tremella mesenterica* (*Tremellaceae*, *Tremellales*) as the outgroup taxon using pxrr v. 1.3 in the Newick utilities suite of tools (Junier & Zdobnov 2010). Additional outgroup representatives were selected from the *Cantharellales* (*Clavulina livida*, *Hydnaceae*; *Tulasnella violea*, *T. pruinosa*, *Tulasnellaceae*).

ITSx v. 1.1.3 (Bengtsson-Palme *et al.* 2013) was used to extract the LSU region from ITS sequences sourced from GenBank which contained both regions. The ITS, LSU, *ATP6, RPB2*, and *TEF1* regions were each aligned separately using MAFFT v. 7.453 (Katoh & Standley 2013) on a local computing cluster with the arguments "--localpair --maxiterate 1000 --leavegappyregion --adjustdirectionaccurately". Terminal ends were trimmed from each alignment using trimAl v. 1.4.rev22 (Capella-Gutiérrez *et al.* 2009) using the arguments "-gapthreshold 0.12 -terminalonly -gw 1". For the main analysis incorporating multiple regions, input alignments were concatenated and analysed as separate partitions using IQ-TREE 2 v. 2.2.2.7 (Minh *et al.* 2020) on a local computing cluster with the argument "iqtree2 -p" which automatically loads all alignments within a given input directory, concatenates them into a supermatrix, and subsequently treats each alignment as a separate partition. Substitution models for each separate partition were identified using ModelFinder Plus (Kalyaanamoorthy *et al.* 2017) in IQ-TREE 2 by using the -m MFP flag. Branch support was quantified by calculating 1000 replicates using both the SH-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al.* 2010) and ultrafast bootstrap approximation (UFBoot) (Minh *et al.* 2013, Hoang *et al.* 2018) as implemented in IQ-TREE 2. Nodes were considered well-supported if they were recovered with SH-aLRT scores ≥ 85 (Guindon *et al.* 2010) and UFBoot scores ≥ 95 (Minh *et al.* 2013). Trees were visualised with the *R package ggtree* v. 3.13.0 (Yu *et al.* 2017). All input alignments used for phylogenetic inference and all resulting tree files are available at https://doi.org/10.5281/zenodo.15043254.

## Literature database searches

To interrogate how the various generic names circumscribed within the *Ceratobasidiaceae* are represented across the scientific literature, we conducted several term searches using the Scopus abstract and citation database (www.scopus.com). Scopus searches were performed on 8 November 2023. The terms '*Rhizoctonia', 'Thanatephorus', 'Ceratobasidium',* and *'Ceratorhiza'* were first queried individually, and the number of search hits was recorded. Following this, additional generic names were sequentially added to the search query using the operator 'AND' for each possible permutation of the original four search terms (e.g. '*Rhizoctonia* AND *Thanatephorus*'; '*Rhizoctonia* AND *Thanatephorus* AND *Ceratobasidium*'; '*Rhizoctonia* AND *Thanatephorus* AND *Ceratobasidium* AND *Ceratorhiza*'). To determine whether there are quantitative differences in search term usage between orchid mycorrhizal and plant pathogen research fields, searches were repeated to include the terms 'AND pathogen', 'AND orchid', and 'AND orchid AND pathogen'. To test whether any differences observed between 'pathogen' and 'orchid' searches were statistically significant, a Pearson's Chi-squared test was completed using the chisq.test() function in the *stats R package* (R Core Team 2017). To identify which search terms contributed to significant differences between 'pathogen' and 'orchid' searches, relative contribution percentages were calculated using the formula $\frac{r^2}{\chi^2}$, where *r* represents the Pearson residual value, and $\chi^2$ represents the chi-squared test statistic. The number of search hits between search terms was visualised as an euler diagram with the *R package eulerr* (Larsson & Gustafsson 2018).

## RESULTS

### Tree inference

The final concatenated ITS + LSU + *ATP6* + *RPB2* + *TEF1* alignment included 45 named taxa (41 within *Ceratobasidiaceae* and four outgroup taxa) with a combined total of 5488 sites (1248 parsimony-informative; 2725 invariant; Table 2). Of the 45 named taxa included, 27 of these were represented by sequences generated from ex-type material, while 18 taxa used representative sequences (Table 1). All accessions considered to fall within the *Ceratobasidiaceae* were recovered as a well-supported clade (SH-aLRT = 91.8; UFBoot = 97). Sequences variously identified as *Rhizoctonia*, *Thanatephorus*, *Ceratobasidium*, *Ceratorhiza* and *Moniliopsis* were placed within the *Ceratobasidiaceae* clade with no monophyletic groups clearly corresponding with generic boundaries (Fig. 1). Furthermore, apart from the high support for the clade of the entire *Ceratobasidiaceae*, many deeper branches had poor support and the pattern of branching and support does not allow for recognition of subtaxa within the overall *Ceratobasidiaceae* clade at the generic level. This pattern was repeated in the analysis which incorporated sequences from an additional 559 UNITE species hypotheses (Fig. 2). Finally, this pattern was again repeated in analysis of the dataset containing 149 representative orchid mycorrhizal OTUs and pathogenic AG sequences. In addition, analysis of this third dataset showed no clear phylogenetic structure with respect to lifestyle mode, indicating that lifestyle mode does not segregate in distinct phylogenetic lineages. This is especially clear deeper in the tree, at the level where any segregate genera would be recognised. Therefore, lifestyle mode is a poor character on which to base generic circumscription in the *Ceratobasidiaceae*, from a phylogenetic approach (Fig. 3).

### Literature database searches

Scopus searches (Fig. 4) found *Rhizoctonia* to be the most commonly used generic name (41771 hits), followed by *Thanatephorus* (4150 hits), *Ceratobasidium* (1010 hits) and *Ceratorhiza* (223 hits). A chi-squared test found a significant difference in the usage of different search terms between 'pathogen' and 'orchid' searches ($\chi^2$ = 6726.4; $p$ = < 0.001). Significant differences between 'pathogen' and 'orchid' searches were driven primarily by searches incorporating *Ceratobasidium* and *Ceratorhiza* as search terms, with the main search terms contributing to significant differences identified as 'orchid AND *Ceratobasidium*' (18.3 %), 'orchid AND *Rhizoctonia* AND *Ceratobasidium*' (13.5 %), 'orchid AND *Ceratorhiza*' (12.6 %) and 'orchid AND *Rhizoctonia* AND *Ceratorhiza'* (11.8 %).

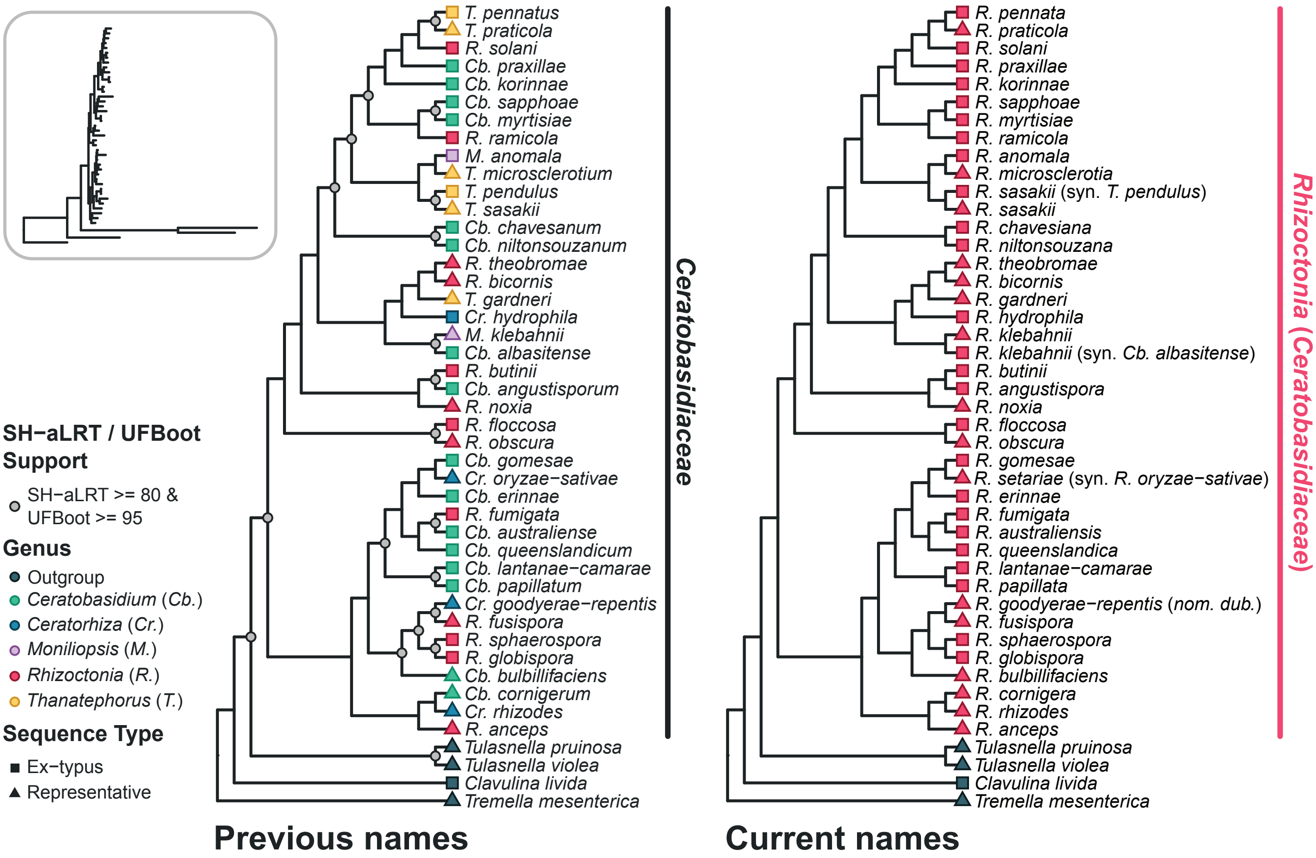


**Fig. 1.** Cladograms of named taxa within *Ceratobasidiaceae* inferred from ITS, LSU, *ATP6*, *RPB2*, and *TEF1* sequence data using IQ-TREE 2. A phylogram of the same tree with unscaled branch lengths is provided as an inset. Previously used names (as applied to the sequences listed in Table 1) are shown on the left, while revised names formalised in this manuscript are shown on the right. Well-supported nodes (i.e. nodes with SH-aLRT ≥ 80 and UFBoot ≥ 95) are indicated with grey circles. Node support is only provided on the tree that uses previous names. Tip shapes indicate whether sequences are ex-type or regarded as representative sequences. Tip shapes are coloured by genus names.

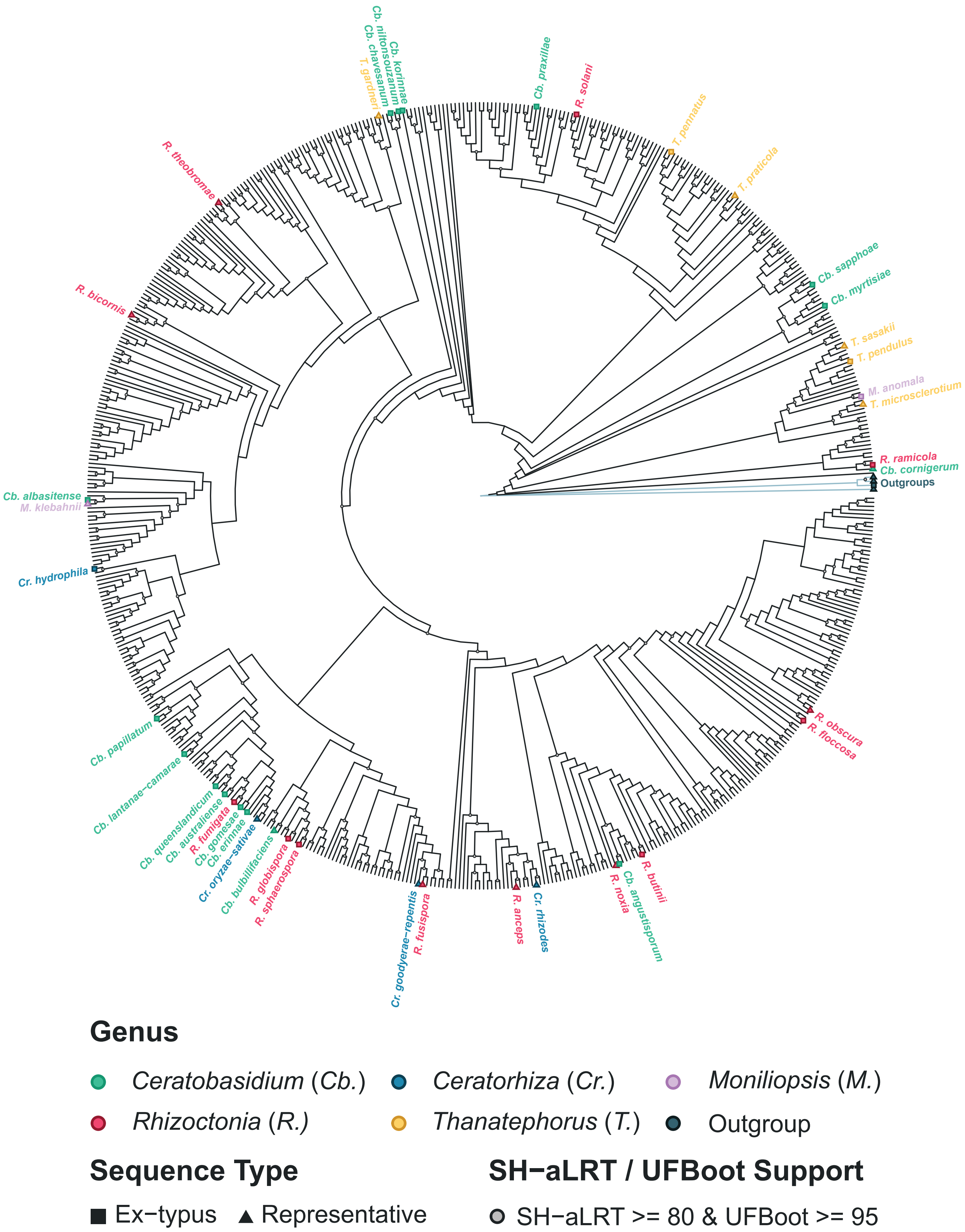


**Fig. 2.** Cladogram of 41 named taxa within *Ceratobasidiaceae*, along with 559 additional UNITE 1.5 % species hypotheses, inferred from ITS sequence data using IQ-TREE 2. Outgroup branches are in grey, while all branches within the *Ceratobasidiaceae* clade are coloured black. Named taxa are indicated by their previously used names. Well-supported nodes (i.e. nodes with SH-aLRT ≥ 80 and UFBoot ≥ 95) are indicated with grey circles. Tip shapes indicate whether sequences are ex-type or regarded as representative sequences. Tip shapes are coloured by genus names. All tips lacking a label and tip shape represent a UNITE species hypothesis.

**Table 1.** GenBank accessions for named taxa within *Ceratobasidiaceae* and outgroup representatives used in analysis of the concatenated ITS + LSU + *ATP6* + *RPB2* + *TEF1* dataset. R = representative sequence; T = ex-type sequence.

| **Current name** | **Previous name** | **Seq. type** | **ITS** | **LSU** | ***ATP6*** | ***RPB2*** | ***TEF1*** |
|---|---|---|---|---|---|---|---|
| *Clavulina livida* | — | T | KU219604 | KU219602 | KU143687 | — | — |
| *Rhizoctonia anceps* | — | R | MH855251 | MH866704 | DQ301583 | — | DQ301652 |
| *Rhizoctonia angustispora* | *Ceratobasidium angustisporum* | T | AJ427403 | MH873364 | DQ301591 | DQ301722 | — |
| *Rhizoctonia anomala* | *Moniliopsis anomala* | T | ITS1: KF267003;<br>ITS2: KF267040 | KF267077 | — | — | — |
| *Rhizoctonia australiensis* | *Ceratobasidium australiense* | T | PP794647 | — | — | — | — |
| *Rhizoctonia bicornis* | — | R | AF200514 | — | — | — | — |
| *Rhizoctonia bulbillifaciens* | *Ceratobasidium bulbillifaciens* | R | KC336072 | KC336071 | — | OR473843 | OR490360 |
| *Rhizoctonia butinii* | — | T | KF386035$^{*}$ | KF386035$^{*}$ | — | — | — |
| *Rhizoctonia chavesiana* | *Ceratobasidium chavesanum* | T | KX870113 | — | — | — | — |
| *Rhizoctonia cornigera* | *Ceratobasidium cornigerum* | R | AJ301903 | — | DQ301576 | DQ301707 | DQ301645 |
| *Rhizoctonia erinnae* | *Ceratobasidium erinnae* | T | PQ061104 | — | — | — | — |
| *Rhizoctonia floccosa* | — | R | MH855816 | MH867319 | — | — | — |
| *Rhizoctonia fumigata* | — | T | FJ231392 | FJ212353 | — | — | — |
| *Rhizoctonia fusispora* | — | R | DQ398957 | AF518664 | — | — | — |
| *Rhizoctonia gardneri* | *Thanatephorus gardneri* | R | GQ175295 | GQ200563 | — | — | — |
| *Rhizoctonia globispora* | — | T | DQ278942 | MH873365 | DQ301592 | DQ301723 | DQ301644 |
| *Rhizoctonia gomesae* | *Ceratobasidium gomesae* | T | MT796443 | — | — | — | — |
| *Rhizoctonia goodyerae-repentis* | *Ceratorhiza goodyerae-repentis* | R | EU218895 | AY243523 | — | DQ381842 | — |
| *Rhizoctonia hydrophila* | *Ceratorhiza hydrophila* | T | FJ231396 | FJ212349 | — | — | — |
| *Rhizoctonia klebahnii* | *Ceratobasidium albasitensis* | T | AJ242875 | — | — | — | — |
| *Rhizoctonia klebahnii* | *Moniliopsis klebahnii* | R | MH854971 | — | — | — | — |
| *Rhizoctonia korinnae* | *Ceratobasidium korinnae* | T | PQ061105 | — | — | — | — |
| *Rhizoctonia lantanae-camarae* | *Ceratobasidium lantanae-camarae* | T | MW361943 | — | — | — | — |
| *Rhizoctonia microsclerotia* | *Thanatephorus microsclerotium* | R | DQ279038 | KP171642 | DQ301616 | DQ301730 | DQ301677 |
| *Rhizoctonia myrtisiae* | *Ceratobasidium myrtisiae* | T | PQ061106 | — | — | — | — |
| *Rhizoctonia niltonsouzana* | *Ceratobasidium niltonsouzanum* | T | KU175888 | — | — | — | — |
| *Rhizoctonia noxia* | — | R | EU810056 | — | DQ301584 | DQ301715 | DQ301653 |
| *Rhizoctonia obscura* | — | R | EU218894 | KF267087 | — | — | — |
| *Rhizoctonia papillata* | *Ceratobasidium papillatum* | T | AJ427401 | KF267084 | DQ301593 | DQ301724 | — |
| *Rhizoctonia pennata* | *Thanatephorus pennatus* | T | EU218892 | — | — | — | — |
| *Rhizoctonia praticola* | *Thanatephorus praticola* | R | AY154307 | AF354118 | DQ301604 | DQ301736 | DQ301668 |
| *Rhizoctonia praxillae* | *Ceratobasidium praxillae* | T | PQ061107 | — | — | — | — |
| *Rhizoctonia queenslandica* | *Ceratobasidium queenslandicum* | T | PP794648 | — | — | — | — |

**Table 1.** (Continued).

| Current name | Previous name | Seq. type | ITS | LSU | *ATP6* | *RPB2* | *TEF1* |
|---|---|---|---|---|---|---|---|
| *Rhizoctonia ramicola* | — | T | DQ278931 | — | DQ301577 | DQ301708 | DQ301646 |
| *Rhizoctonia rhizodes* | *Ceratorhiza rhizodes* | R | MH859145 | MH870857 | — | — | — |
| *Rhizoctonia sapphoae* | *Ceratobasidium sapphoae* | T | PQ061108 | — | — | — | — |
| *Rhizoctonia sasakii* | *Thanatephorus pendulus* | T | KP171634 | MH873283 | DQ301596 | DQ301727 | DQ301660 |
| *Rhizoctonia sasakii* | *Thanatephorus sasakii* | R | AF354060 | — | — | — | — |
| *Rhizoctonia setariae* | *Ceratorhiza oryzae-sativae*; *Ceratobasidium oryzae-sativae* | R | AF354087* | AF354087* | — | — | — |
| *Rhizoctonia solani* | — | T | MH862557 | — | — | — | — |
| *Rhizoctonia sphaerospora* | — | T | DQ278943 | — | DQ301594 | DQ301725 | DQ301658 |
| *Rhizoctonia theobromae* | — | R | HQ424246 | HQ424242 | — | — | — |
| *Tremella mesenterica* | — | R | KY105690 | FJ534914 | KF147745 | FJ534945 | FJ534868 |
| *Tulasnella violea* | — | R | OR471237 | — | — | OR473855 | OR490353 |
| *Tulasnella pruinosa* | — | R | DQ457642 | AY243522 | — | DQ381839 | DQ061274 |

* Accession includes both ITS and LSU.

**Table 2.** Alignment statistics for datasets used for phylogenetic inference.

| Region | No. of seqs | Total sites | Informative sites | Singleton sites | Invariant sites |
|---|---|---|---|---|---|
| Named taxa dataset (ITS + LSU + *ATP6* + *RPB2* + *TEF1*) | | | | | |
| ITS | 45 | 957 | 421 | 240 | 296 |
| LSU | 25 | 1105 | 142 | 354 | 609 |
| *ATP6* | 12 | 713 | 190 | 204 | 319 |
| *RPB2* | 15 | 1651 | 332 | 495 | 824 |
| *TEF1* | 13 | 1062 | 163 | 222 | 677 |
| Total | | 5488 | 1248 | 1515 | 2725 |
| Named taxa + UNITE species hypotheses (ITS only) | | | | | |
| ITS | 604 | 1078 | 768 | 189 | 121 |
| Named taxa + representative orchid mycorrhizal OTUs and pathogenic AG groups (ITS only) | | | | | |
| ITS | 194 | 1006 | 566 | 243 | 197 |

## TAXONOMY

We provide here a summary of all valid names published within *Rhizoctonia*, and propose the transfer of 32 names to *Rhizoctonia*. Names transferred here to *Rhizoctonia* include species formerly circumscribed within *Ceratobasidium*, *Ceratorhiza*, *Moniliopsis*, *Thanatephorus*, *Tofispora*, and *Ypsilonidium*. We propose the recognition of 52 accepted species within *Rhizoctonia*. Several species were considered to be conspecific with *R. solani* on the basis of morphology by Andersen & Stalpers (1994) and Roberts (1999); however, we do not automatically accept them as synonyms. Instead, we list them in the notes under *R. solani* as pending examination of type material (and typification where necessary) in order to establish their correct application. Some names treated as synonyms by Roberts (1999) are accepted as separate species based on phylogenetic analyses (see notes under individual species). We also summarise 66 invalid/illegitimate names (Table 3) and 34 names of uncertain application (nomina dubia) (Table 4). Epithets previously placed within generic synonyms of *Rhizoctonia* which are now placed elsewhere are summarised in Table 5. UNITE ITS 1.5 % SHs for accepted species are cited in the treatment below under each species and summarised in Table 6, with n/a indicating that sequences of the species are not included in the latest UNITE release (usually because the species is recently

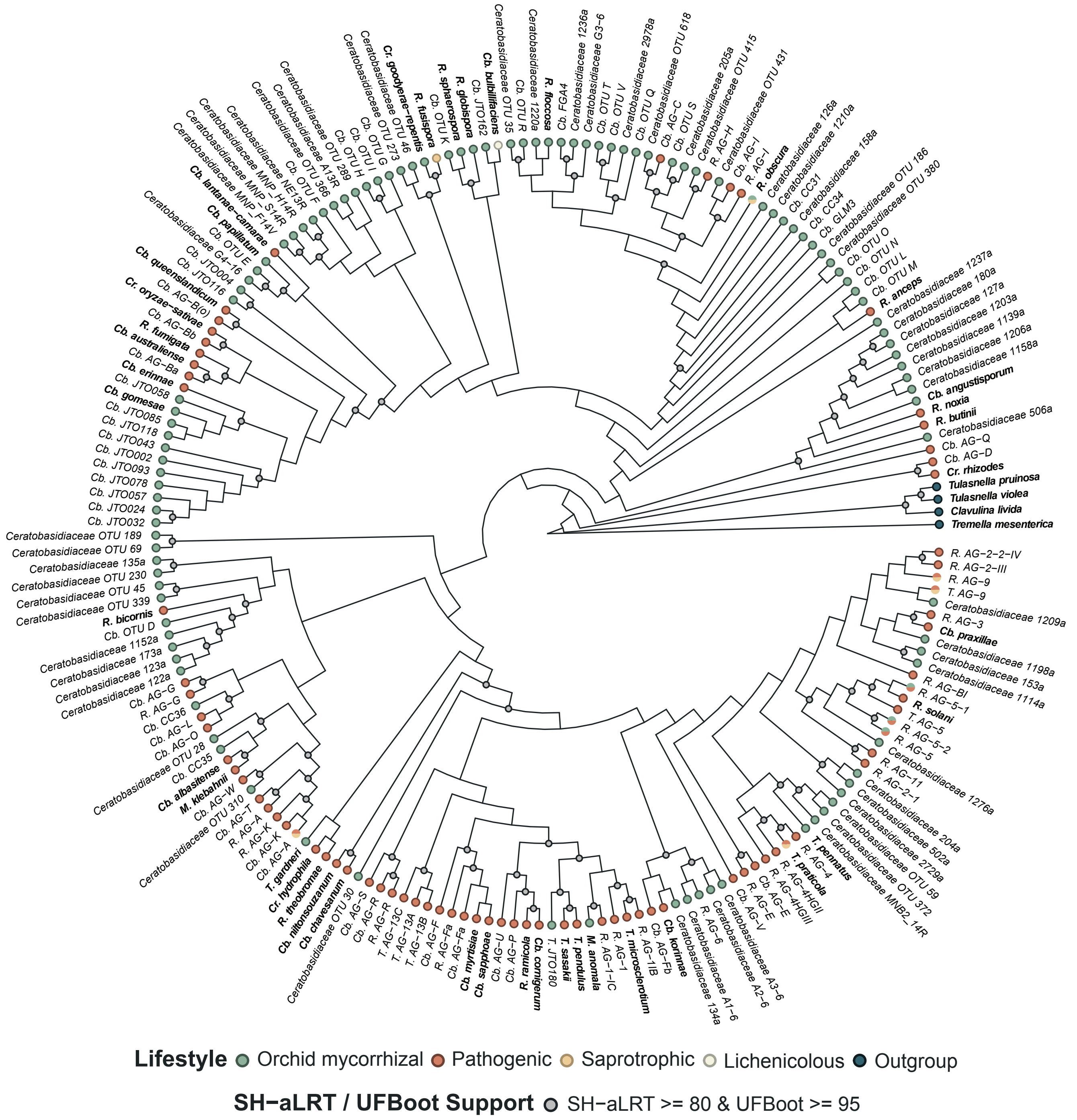


**Fig. 3.** Cladogram of 41 named taxa along with 149 representative orchid mycorrhizal OTUs and pathogenic AGs within *Ceratobasidiaceae* and four outgroup taxa inferred from ITS sequence data using IQ-TREE. Named taxa are indicated as their previously used names, in bold. Well-supported nodes (i.e. nodes with SH-aLRT ≥ 80 and UFBoot ≥ 95) are indicated with grey circles. Tip shapes are coloured by lifestyle mode.

**Table 3.** Invalid and illegitimate names introduced within *Rhizoctonia* or its generic synonyms.

| **Name** | **Article (Shenzhen Code)** | **Reason invalid/illegitimate** |
|---|---|---|
| *Ceratobasidium fibulatum* C.C. Tu & Kimbr. | Art. 40.1 | No holotype designated |
| *Ceratobasidium filamentosum* (Pat.) L.S. Olive | Art. 41.1 | Basionym not indicated/omitted |
| *Ceratobasidium flavecens* (Bonord.) L.S. Olive | Art. 41.1 | Basionym not indicated/omitted |
| *Ceratobasidium fragariae* Kohmoto, N. Maek., Ogihara & S. Nishim. | Art. 39.1 | No Latin description or diagnosis |
| *Ceratobasidium incrustans* Rick | Art. 40.1 | No holotype designated |
| *Ceratobasidium praticola* (Kotila) L.S. Olive | Art. 41.1 | Basionym not indicated/omitted |
| *Ceratobasidium stevensii* (Burt) Venkatar. | Art. 41.1 | Basionym not indicated/omitted |
| *Ceratorhiza cerealis* (E.P. Hoeven) R.T. Moore | Art. 41.2 | Combination based on the invalid basionym *R. cerealis* |
| *Ceratorhiza fragariae* (S.S. Husain & W.E. McKeen) R.T. Moore | Art. 40.1, Art. 41.2 | Combination based on the invalid basionym *R. fragariae* |
| *Corticium fusisporum* (J. Schröt.) Brinkmann | Art. 53.1 | Later homonym of *Corticium fusisporum* Cooke & Ellis 1879 |
| *Hydrabasidium terrigenum* (Bres.) Park.-Rhodes | Art. 41.2 | Combination made using invalid genus name (*Hydrabasidium*) |
| *Rhizoctonia alpina* E. Castell. | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia anomala* Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia apocynacearum* K.J. Demet. | Art. 36.1 | Provisional name |
| *Rhizoctonia asclerotica* Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia asparagi* Fuckel | Art. 38.1(a) | No description or diagnosis provided |
| *Rhizoctonia bicolor* Ellis | Art. 36.1 | Provisional name |
| *Rhizoctonia borealis* J.T. Curtis | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia callae* E.Castell. | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia candida* W. Yamam. | Art. 40.1 | No holotype designated |
| *Rhizoctonia cavendishiana* Burgeff | Art. 36.1 | Provisional name |
| *Rhizoctonia cerealis* E.P. Hoeven | Art. 40.1 | No holotype designated |
| *Rhizoctonia dauci* Rabenh. | Art. 38.1(a) | No description or diagnosis provided |
| *Rhizoctonia dichotoma* H.K. Saksena & Vaartaja | Art. 40.1 | No holotype designated |
| *Rhizoctonia endophytica* H.K. Saksena & Vaartaja | Art. 40.1 | No holotype designated |
| *Rhizoctonia endophytica* var. *filicata* H.K. Saksena & Vaartaja | Art. 40.1 | No holotype designated |
| *Rhizoctonia fragariae* S.S. Husain & W.E. McKeen | Art. 40.1 | No holotype designated |
| *Rhizoctonia fraxini* E. Castell. | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia globularis* H.K. Saksena & Vaartaja | Art. 40.1 | No holotype designated |
| *Rhizoctonia gossypinum* Speg. | Art 29–31 | Never validly published |
| *Rhizoctonia gracilis* Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia hiemalis* H.K. Saksena & Vaartaja | Art. 40.1 | No holotype designated |
| *Rhizoctonia juniperi* Lihnell | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia lupini* E. Castell. | Art. 39.1 | No Latin description or diagnosis |

**Table 3.** (Continued).

| Name | Article (Shenzhen Code) | Reason invalid/illegitimate |
|---|---|---|
| *Rhizoctonia monilioides* J.T. Curtis | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia monteithiana* F.T. Benn. | Art. 36.1, 39.1 | Provisional name; no Latin description or diagnosis |
| *Rhizoctonia muneratii* E. Castell. | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia nandorii* Biradar & Bonde | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia neottiae* (H. Wolff) Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia oryzae* Ryker & Gooch | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia papayae* Cifferi. | Art. 36.1 | Provisional name |
| *Rhizoctonia pini-insignis* E. Castell. | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia praticola* H.K. Saksena & Vaartaja | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia psycodis* K.S. Thomas | Art. 36.1 | Provisional name |
| *Rhizoctonia quercus* E. Castell. | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia rapae* Oudem. | Art. 36.1 | Provisional name |
| *Rhizoctonia robusta* Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia rubi* McKeen | Art. 40.1 | No holotype designated. Weldon *et al*. (2022) transferred *R. rubi* to the genus *Monilinia* Honey (Ascomycota) with the combination '*Monilinia rubi*' Weldon and Stockwell based on the phylogenetic placement of sequences generated from an authentic (but not ex-type) culture (CBS 382.59). However, as the basionym *R. rubi* is invalid, the combination *M. rubi* is also invalid. |
| *Rhizoctonia sclerotica* Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia solani* var. *brassicae* Sneh, Burpee & Ogoshi | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia solani* var. *cedri-deodarae* E.Castell. | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia solani* var. *cichorii-endiviae* E.S. Schultz | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia solani* var. *fuchsiae* E.S. Schultz | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia solani* var. *graminis* Bunschoten | Art 29–31 | Never validly published |
| *Rhizoctonia solani* var. *hortensis* Schulz | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia solani* var. *lycopersicae* E.S. Schultz | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia solani* var. *typica* Sneh, Burpee & Ogoshi | Art. 24.3 | Infraspecific name “typicus” is not the same final epithet as the name of the corresponding higher-ranked taxon |
| *Rhizoctonia sphacelati* Burgeff | Art. 36.1 | Provisional name |
| *Rhizoctonia stahlii* Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia suavis* K.S. Thomas | Art. 36.1 | Provisional name |
| *Rhizoctonia subtilis* Burgeff | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia subtilis* var. *nigra* J.T. Curtis | Art. 39.1 | No Latin description or diagnosis |
| *Rhizoctonia tomato* Bahariev | Art. 39.1, 40.1 | No Latin description or diagnosis; no holotype specified |
| *Rhizoctonia tricolor* Ellis & Everh. | Art. 36.1 | Provisional name |
| *Rhizoctonia versicolor* E. Müll. & Nüesch | Art. 40.1 | No holotype designated |
| *Thanatephorus anomalus* (P.H.B. Talbot) Stalpers & T.F. Andersen | Art. 41.1 | Basionym not indicated/omitted |

**Table 4.** Names of uncertain application (nomina dubia) placed at some time under Rhizoctonia or its generic synonyms.

| Name | Notes |
|---|---|
| *Ceratobasidium album* Rick | Type not extant (Roberts 1999). |
| *Ceratobasidium gramineum* (Ikata & Matsuura) Oniki, Ogoshi & T. Araki | Considered a nom. dub. by Roberts (1999). |
| *Ceratobasidium ochroleucum* (F. Noack) Ginns & M.N.L. Lefebvre [as '*ochroleuca*'] | Type not extant. Considered either a nom. dub. or syn. *Cb. cornigerum* by Roberts (1999). |
| *Ceratorhiza goodyerae-repentis* (Costantin & L.M. Dufour) R.T. Moore | Type not extant, no illustration, no authentic strain available (Andersen & Stalpers 1994); see notes under *R. fusispora*. |
| *Moniliopsis fagi* Konopacka | Konopacka (1926) states that *M. fagi* is similar to *M. foliicola* based on morphology. Illustrations in the protologue do not show characters that are consistent with *Rhizoctonia*. As *M. foliicola* is considered below to be synonymous with *Mycopappus alni* (Dearn. & Barthol.) Redhead & G.P. White, it is unlikely that *M. fagi* is placed within *Rhizoctonia*. |
| *Moniliopsis foliicola* (Woron.) Siemaszko | The sequence MH854875 (CBS 161.26) which is stated to represent a collection of *M. foliicola* identified by Siemaszko is a 99.37 % match with *Mycopappus alni* when BLASTed. Therefore, at least sensu Siemaszko, *M. foliicola* is synonymous with *M. alni*. |
| *Moniliopsis rigida* Petch | Characters not consistent with *Rhizoctonia* based on description. |
| *Rhizoctonia aerea* Burgeff | Type not extant, no illustration (Andersen & Stalpers 1994). |
| *Rhizoctonia alba* Matz | Type not extant, description lacking sufficient detail (Andersen & Stalpers 1994). |
| *Rhizoctonia arachnion* Burgeff | Type not extant, no illustration. Description lacking sufficient detail (Andersen & Stalpers 1994). |
| *Rhizoctonia aurantiaca* Ellis & Everh. | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia batatas* Schwein. ex Fr. | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia brassicarum* Lib. | Type lost (Andersen & Stalpers 1994). |
| *Rhizoctonia carnea* Ellis & Everh. | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia coniothecioides* Sappa & Mosca | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia destruens* Tassii | Type not extant. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia fuliginea* Sappa & Mosca | Type not extant. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia goodyerae-repentis* Costantin & L.M. Dufour | Type not extant, no illustration, no authentic strain available (Andersen & Stalpers 1994); see notes under *R. fusispora*. |
| *Rhizoctonia himantia* Schwein. | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia lanuginosa* G.E. Bernard | Type not extant, description lacking sufficient detail (Andersen & Stalpers 1994). |
| *Rhizoctonia lilacina* Sappa & Mosca | Type not extant. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia mali* DC | Type not extant, no illustration, description lacking sufficient detail (Andersen & Stalpers 1994). |
| *Rhizoctonia moniliformis* Ellis & Everh. | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia muscorum* Fr. | Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia pallida* | Type not extant. Considered by Parmeter & Whitney (1970) to not be *Rhizoctonia*. Andersen & Stalpers (1994) suggest based on colony descriptions that this taxon is more likely to be a species of *Athelia*. Considered *Athelia* sp. by Roberts (1999). |
| *Rhizoctonia placenta* Schwein. | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia radiciformis* Schwein. | Type not extant, no illustration. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia rubiginosa* Sappa & Mosca | Type not extant. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |

**Table 4.** (Continued).

| Name | Notes |
|---|---|
| *Rhizoctonia silvestris* Melin | Type not extant. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). CBS 300.37 and 299.37 are identified as *Rhizoctonia silvestris* but they do not appear to be authentic strains. CBS 299.37 is from Germany, but other notes are scant, only the collector “BIHM”. CBS 300.37 is from the UK, which does not match the type locality. Neither culture clusters with *Rhizoctonia* when BLASTed. The LSU sequence from CBS 299.37 (MH867417) is a 99.77 % percent identity match with the holotype of *Leptodophora echinata* (Koukol & Maciá-Vicente) Koukol & Maciá-Vicente, while the ITS sequence for the same CBS number (MH855913) is a 99.47 % match with *L. orchidicola* (Sigler & Currah) Koukol & Maciá-Vicente. The LSU sequence from CBS 300.37 (MH867418) is a 99.77 % match with the type specimen of *Acephala macrosclerotiorum* Münzenb. & Bubner. |
| *Rhizoctonia solani* var. *ambigua* Baldacci & Cabrini | Type not extant. Description lacking sufficient detail (Andersen & Stalpers 1994). |
| *Rhizoctonia strobi* E. Scholz | Type not extant. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Rhizoctonia strobilina* Link | Type not extant, no illustration, description lacking sufficient detail (Andersen & Stalpers 1994). |
| *Rhizoctonia subepigaea* Bertoni bis | Type not extant. Characters not consistent with *Rhizoctonia* based on description (Andersen & Stalpers 1994). |
| *Ypsilonidium bananisporum* N. Maek. | Listed by Roberts (1999) as a “probable” synonym of *Thanatephorus sterigmaticus*. However, the type of *Y. bananisporum* is from Japan, whereas the type of *T. sterigmaticus* is from France. Similar spores suggest synonymy, but needs confirmation from molecular data. |

**Table 5.** Names previously placed within *Rhizoctonia* or its generic synonyms hat are now placed in other genera.

| Previous name | Accepted name | Citation/notes |
|---|---|---|
| *Cejpomyces globosisporus* Boidin & Gilles | *Botryobasidium globisporum* (Boidin & Gilles) G. Langer. | Roberts (1999) |
| *Ceratobasidium atratum* (Bres.) D.P. Rogers | *Scotomyces subviolaceus* (Peck) Jülich | Roberts (1999) |
| *Ceratobasidium fibrillosum* (Burt) D.P. Rogers & H.S. Jacks. | *Oliveonia fibrillosa* (Burt) Donk | Donk (1958) |
| *Ceratobasidium mycophagum* M.P. Christ. | *Syzygospora mycophaga* (M.P. Christ.) Hauerslev | Knudsen & Hansen (1996) |
| *Ceratobasidium pearsonii* (Bourdot) M.P. Christ. | *Paullicorticium pearsonii* (Bourdot) J. Erikss. | Roberts (1999) |
| *Ceratobasidium plumbeum* G.W. Martin | *Scotomyces subviolaceus* (Peck) Jülich | Roberts (1999) |
| *Ceratobasidium striisporum* Rick | *Xenasma pulverulentum* (H.S. Jacks.) Donk | Roberts (1999) |
| *Ceratobasidium subatratum* S.S. Rattan | *Scotomyces subviolaceus* (Peck) Jülich | Roberts (1999) |
| *Ceratobasidium vagum* (Berk. & M.A. Curtis) Pilát | *Botryobasidium vagum* (Berk. & M.A. Curtis) D.P. Rogers | Roberts (1999) |
| *Rhizoctonia allii* L. Graves ex Duby | *Helicobasidium purpureum* (Tul.) Pat. | Andersen & Stalpers (1994) note that ‘no publication or type from Graves could be traced.’ There is, however, a description/diagnosis in the publication by Duby [Bot. Gall., Edn 2 (Paris) 2: 867 (1830)], who mentions ‘Graves in litt.’) - what cannot be traced is any previous mention by Graves. Andersen & Stalpers (1994) considered *R. allii* as conspecific with *R. crocorum* and this placement was accepted by Roberts (1999) who considered it as a synonym for *Thanatophytum crocorum* (=*Helicobasidium purpureum*). |
| *Rhizoctonia anaticula* Currah | *Tulasnella anaticula* (Currah) S. Fujimori, J.P. Abe, I. Okane & Y. Yamaoka | Transferred to *Epulorhiza* by Currah *et al.* (1990) and then transferred to *Tulasnella* by Fujimori *et al.* (2018) |
| *Rhizoctonia asparagi* Fuckel ex Erikss. | *Helicobasidium purpureum* (Tul.) Pat. | Andersen & Stalpers (1994) |
| *Rhizoctonia bataticola* (Taubenh.) E.J. Butler | *Macrophomina phaseolina* (Tassi) Goid. | Andersen & Stalpers (1994) |

**Table 5.** (Continued).

| Previous name | Accepted name | Citation/notes |
|---|---|---|
| *Rhizoctonia carotae* Rader | *Athelia arachnoidea* (Berk.) Jülich | Adams & Kropp (1996) |
| *Rhizoctonia centrifuga* Lév., | *Athelia epiphylla* Pers. | Adams & Kropp (1996) |
| *Rhizoctonia crocorum* (Pers.) DC. | *Helicobasidium purpureum* (Tul.) Pat. | Andersen & Stalpers (1994); Stalpers *et al.* (1998) |
| *Rhizoctonia lamellifera* W. Small | *Macrophomina phaseolina* (Tassi) Goid. | Andersen & Stalpers (1994) |
| *Rhizoctonia leguminicola* Gough & E.S. Elliott | *Slafractonia leguminicola* (Gough & E.S. Elliott) Alhawatema, Baucom, Sanogo & Creamer | Alhawatema *et al.* (2015) |
| *Rhizoctonia medicaginis* DC | *Helicobasidium purpureum* (Tul.) Pat. | Andersen & Stalpers (1994); Roberts (1999) |
| *Rhizoctonia menthae* Berk. & Broome | *Puccinia menthae* Pers. | Buddin & Wakefield (1927) identified *R. menthae* as the *Tuberculina* state of *Puccinia menthae*. Roberts (1999) accepted *R. menthae* as a synonym of *P. menthae*. |
| *Rhizoctonia orobanches* Mérat | *Urocystis orobanches* (Mérat) A.A. Fisch. Waldh. | Fischer von Waldheim (1877) |
| *Rhizoctonia quercina* R. Hartig | *Rosellinia quercina* R. Hartig | Hartig (1880) |
| *Rhizoctonia repens* N. Bernard | *Tulasnella deliquescens* (Juel) Juel | Moore (1987) |
| *Rhizoctonia rubiae* M.J. Decne. | *Helicobasidium purpureum* (Tul.) Pat. | Andersen & Stalpers (1994) |
| *Rhizoctonia solani* f. *paroketea* Cif. | *Agroathelia rolfsii* (Sacc.) Redhead & Mullineux | Andersen & Stalpers (1994) |
| *Rhizoctonia tabifica* Hallier | *Colletotrichum coccodes* (Wallr.) S. Hughes | Dickson (1926) |
| *Rhizoctonia zeae* Voorhees | *Waitea zeae (Voorhees)* J.A. Crouch & Cubeta | Stalpers *et al.* (2021) |
| *Uthatobasidium citriforme* M.P. Christ. | *Sistotrema citriforme* (M.P. Christ.) K.H. Larss. & Hjortstam | Hjortstam & Larsson (1987) |

**Table 6.** UNITE 1.5 % SHs for accepted species of *Rhizoctonia*. Seq. type (Sequence type, as designated herein): R = representative sequence; T = ex-type sequence. UNITE RepS/RefS: RepS = representative sequence; RefS = reference sequence, as designated in UNITE. ITS sequence identifiers are all from GenBank except those with UDB prefixes, which are from UNITE. n/a: the type or reference sequences for this species chosen by us are not present in UNITE SHs.

| Current name | Seq. type | ITS | UNITE SH (1.5 %) | UNITE RepS/RefS | UNITE ITS Sequence | UNITE ID | No. seqs. in SH |
|---|---|---|---|---|---|---|---|
| *Rhizoctonia anceps* | R | MH855251 | SH0961344.10FU | RepS | MH855251 | *Ceratobasidium anceps* | 2 |
| *Rhizoctonia angustispora* | T | AJ427403 | SH0987490.10FU | RefS | AJ427403 | *Ceratobasidium angustisporum* | 7 |
| *Rhizoctonia anomala* | T | ITS1: KF267003;<br>ITS2: KF267040 | n/a | — | — | — | — |
| *Rhizoctonia australiensis* | T | PP794647 | n/a | — | — | — | — |
| *Rhizoctonia bicornis* | R | AF200514 | SH0897788.10FU | RepS | AF200515 | *Ceratobasidiaceae* | 13 |
| *Rhizoctonia bulbillifaciens* | R | KC336072 | SH0961369.10FU | RepS | OR471312 | *Ceratobasidium bulbillifaciens* | 9 |
| *Rhizoctonia butinii* | T | KF386035[*] | SH0897760.10FU | RepS | KF386035 | *Ceratobasidiaceae* | 17 |
| *Rhizoctonia chavesiana* | T | KX870113 | SH0814273.10FU | RefS | KX870113 | *Ceratobasidium chavesanum* | 15 |

**Table 6.** (Continued).

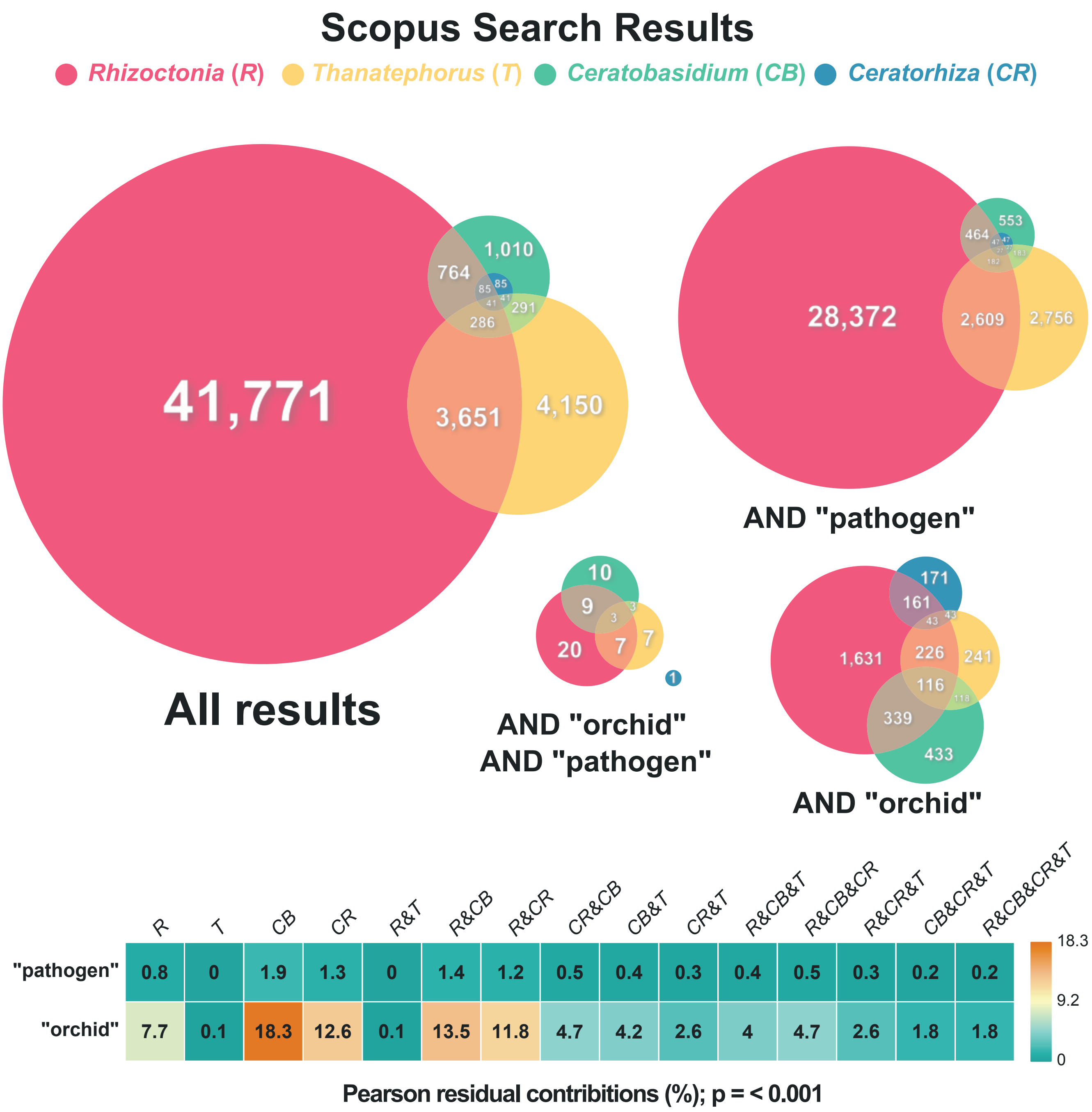
| Current name | Seq. type | ITS | UNITE SH (1.5 %) | UNITE RepS/RefS | UNITE ITS Sequence | UNITE ID | No. seqs. in SH |
|---|---|---|---|---|---|---|---|
| *Rhizoctonia cornigera* | R | AJ301903 | n/a | — | — | — | — |
| *Rhizoctonia erinnae* | T | PQ061104 | n/a | — | — | — | — |
| *Rhizoctonia floccosa* | R | MH855816 | SH0987472.10FU | RepS | UDB01689715 | *Ceratobasidiaceae* | 7 |
| *Rhizoctonia fumigata* | T | FJ231392 | SH0961366.10FU | RepS | AB196641 | *Ceratobasidiaceae* | 7 |
| *Rhizoctonia fusispora* | R | DQ398957 | SH0961356.10FU | RefS | DQ398957 | *Rhizoctonia fusispora* | 5 |
| *Rhizoctonia gardneri* | R | GQ175295 | SH0897913.10FU | RepS | GQ175302 | *Ceratobasidiaceae* | 3 |
| *Rhizoctonia globispora* | T | DQ278942 | n/a | — | — | — | — |
| *Rhizoctonia gomesae* | T | MT796443 | SH0961466.10FU | RepS | HQ630980 | *Ceratobasidium* | 114 |
| *Rhizoctonia hydrophila* | T | FJ231396 | SH0916688.10FU | RepS | FJ231396 | *Ceratorhiza hydrophila* | 6 |
| *Rhizoctonia klebahnii* | R | MH854971 | SH0897862.10FU | RepS | JX649076 | *Agaricomycotina* | 156 |
| *Rhizoctonia korinnae* | T | PQ061105 | n/a | — | — | — | — |
| *Rhizoctonia lantanae-camarae* | T | MW361943 | SH0970519.10FU | RepS | MW361942 | *Ceratobasidium cornigerum* | 2 |
| *Rhizoctonia microsclerotia* | R | DQ279038 | SH0814404.10FU | RepS | MK583629 | *Ceratobasidiaceae* | 317 |
| *Rhizoctonia myrtisiae* | T | PQ061106 | n/a | — | — | — | — |
| *Rhizoctonia niltonsouzana* | T | KU175888 | SH0814308.10FU | RepS | EU810053 | *Ceratobasidium niltonsouzanum* | 33 |
| *Rhizoctonia noxia* | R | EU810056 | SH0987559.10FU | RepS | EU810056 | *Rhizoctonia noxia* | 1 |
| *Rhizoctonia obscura* | R | EU218894 | SH0987497.10FU | RepS | JQ972076 | *Ceratobasidium* | 52 |
| *Rhizoctonia papillata* | T | AJ427401 | n/a | — | — | — | — |
| *Rhizoctonia pennata* | T | EU218892 | SH0814614.10FU | RepS | FJ688118 | *Thanatephorus ochraceus* | 17 |
| *Rhizoctonia praticola* | R | AY154307 | SH0814616.10FU | RefS | UDB035102 | *Rhizoctonia solani* | 1968 |
| *Rhizoctonia praxillae* | T | PQ061107 | n/a | — | — | — | — |
| *Rhizoctonia queenslandica* | T | PP794648 | n/a | — | — | — | — |
| *Rhizoctonia ramicola* | T | DQ278931 | SH0814574.10FU | RefS | DQ278931 | *Ceratobasidium ramicola* | 40 |
| *Rhizoctonia rhizodes* | R | MH859145 | SH0987670.10FU | RepS | FJ231395 | *Ceratorhiza rhizodes* | 4 |
| *Rhizoctonia sapphoae* | T | PQ061108 | n/a | — | — | — | — |
| *Rhizoctonia sasakii* | R | AF354060 | n/a | — | — | — | — |
| *Rhizoctonia setariae* | R | AF354087* | n/a | — | — | — | — |
| *Rhizoctonia solani* | T | MH862557 | SH0814567.10FU | RepS | KU245690 | *Ceratobasidiaceae* | 438 |
| *Rhizoctonia sphaerospora* | T | DQ278943 | SH1013385.10FU | RepS | DQ278943 | *Ceratobasidium sphaerosporum* | 2 |
| *Rhizoctonia theobromae* | R | HQ424246 | SH1006168.10FU | RefS | FJ763577 | *Ceratobasidium theobromae* | 41 |

* Accession includes both ITS and LSU.

described). UNITE assigns to each SH either a representative sequence (RepS), chosen automatically by the program, or a reference sequence (RefS) when that choice is overridden (or confirmed) by "users with expert knowledge of the taxon at hand" (https://unite.ut.ee/repository.php#general). Note that we denote ITS sequences for each species as either derived from Type (T) material or as representative (R) for the species. In some cases, sequences from types are not included in UNITE due to being considered as poor quality (e.g. because of inclusion of ambiguous bases). Hence, our type or representative sequences do not necessarily match up to the UNITE reference or representative sequences, although in all cases they are highly similar, due to falling within the same SH at only 1.5 % divergence.

***Ceratobasidiaceae*** G.W. Martin, *Lloydia* **11**: 114. 1948.
*Type*: *Ceratobasidium* D.P. Rogers, *State Stud. Nat. Hist. Iowa Univ.* **17**(5): 4. 1935. [To be conserved with conserved type, see below].
*Synonym*: *Cejpomycetaceae* Jülich, *Biblioth. Mycol.* **85**: 359. 1982. [1981].
*Type*: *Cejpomyces* Svrček & Pouzar, *Česká Mykol.* **24**(1): 5. 1970.

***Ceratobasidium*** D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(5): 4. 1935.
*Type*: *Ceratobasidium sphaerosporum* Warcup & P.H.B. Talbot [to be proposed, as conserved type, to replace *Cb. calosporum* D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(1): 5. 1935].



| | R | T | CB | CR | R&T | R&CB | R&CR | CR&CB | CB&T | CR&T | R&CB&T | R&CB&CR | R&CR&T | CB&CR&T | R&CB&CR&T |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| "pathogen" | 0.8 | 0 | 1.9 | 1.3 | 0 | 1.4 | 1.2 | 0.5 | 0.4 | 0.3 | 0.4 | 0.5 | 0.3 | 0.2 | 0.2 |
| "orchid" | 7.7 | 0.1 | 18.3 | 12.6 | 0.1 | 13.5 | 11.8 | 4.7 | 4.2 | 2.6 | 4 | 4.7 | 2.6 | 1.8 | 1.8 |

**Fig. 4.** Euler diagrams of Scopus database search results for various combinations of *Rhizoctonia*, *Thanatephorus*, *Ceratobasidium* and *Ceratorhiza*. Separate plots are provided for all results, along with additional searches where the additional search terms 'AND pathogen', 'AND orchid', or 'AND orchid AND pathogen' were added. A correlation plot of Pearson residual contribution values in percentages outlining significant differences between 'pathogen' and 'orchid' searches is presented below.

***Ceratobasidium calosporum*** D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(1): 5. 1935.
*Synonym*: *Ceratorhiza anacalospora* P. Roberts, *Rhizoctonia-Forming Fungi* (Richmond): 38. 1999.
*Type citation*: 'On bark of a dead branch of *Ulmus* sp., Linder's Woods, Iowa City, V. 7. 1932, D. P. R. 224, type.'.

*Notes*: *Ceratobasidium calosporum* is not conspecific with the majority of species subsequently introduced in or placed in the genus *Ceratobasidium.* Therefore, a nomenclatural solution is suggested for the re-typification of *Ceratobasidium* in order to prevent disadvantageous name changes (see the section *Problems with the name* Ceratobasidium in the Discussion, below). Roberts (1999) described *Cr. anacalospora* as the anamorph of *Cb. calosporum* and the pair are treated here as synonymous.

***Rhizoctonia*** DC., *Fl. franç.,* Edn **3** (Paris) 5/6: 110. 1815.
*Sanctioning citation*: Fr., *Syst. mycol.* **2**(1): 265. 1822.
*Type*: *Rhizoctonia solani* J.G. Kühn, Die Krankheiten der Kulturgewächse, ihre Ursachen und Verbreitung (Berlin): 224. 1858. (Typ. cons.).
*Synonyms*: *Moniliopsis* Ruhland, *Arbeiten Kaiserl. Biol. Anst. Land- Forstw.* **6**: 76. 1908.
*Type*: *Moniliopsis aderholdii* Ruhland, *Arbeiten Kaiserl. Biol. Anst. Land- Forstw.* **6**: 76. 1908.
*Ceratobasidium* D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(5): 4. 1935.
*Type*: *Ceratobasidium sphaerosporum* Warcup & P.H.B. Talbot [to be proposed, as conserved type, to replace *Cb. calosporum* D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(1): 5. 1935].
*Thanatephorus* Donk, *Reinwardtia* **3**: 376. 1956.
*Type*: *Thanatephorus cucumeris* (A.B. Frank) Donk, *Reinwardtia* **3**: 376. 1956.
*Uthatobasidium* Donk, *Reinwardtia* **3**: 376. 1956.
*Type*: *Hypochnus fusisporus* J. Schröt., in Cohn, *Krypt.-Fl. Schlesien* (Breslau) **3.1**(25–32): 416. 1988. [1889].
*Koleroga* Donk, *Fungus*, Wageningen **28**: 35. 1958.
*Type*: *Koleroga noxia* Donk, *Fungus*, Wageningen **28**: 35. 1958.
*Cejpomyces* Svrček & Pouzar, *Česká Mykol*. **24**(1): 5. 1970.
*Type*: *Cejpomyces terrigenus* (Bres.) Svrček & Pouzar, *Česká Mykol*. **24**(1): 6. 1970.
*Oncobasidium* P.H.B. Talbot & Keane, *Austral. J. Bot.* **19**: 203. 1971.
*Type*: *Oncobasidium theobromae* P.H.B. Talbot & Keane, *Austral. J. Bot.* **19**: 203. 1971.
*Ypsilonidium* Donk, *Proc. Kon. Ned. Akad. Wetensch. C.* **75**: 371. 1972.
*Type*: *Ypsilonidium sterigmaticum* (Bourdot) Donk, *Proc. Kon. Ned. Akad. Wetensch. C.* **75**: 371. 1972.
*Aquathanatephorus* C.C. Tu & Kimbr., *Bot. Gaz*. **139**(4): 459. 1978.
*Type*: *Aquathanatephorus pendulus* C.C. Tu & Kimbr., *Bot. Gaz*. **39**(4): 459. 1978.
? *Ceratorhiza* R.T. Moore, *Mycotaxon* **29**: 94. 1987.
*Type*: *Ceratorhiza goodyerae-repentis* (Costantin & L.M. Dufour) R.T. Moore, *Mycotaxon* **29**: 94. 1987.
*Tofispora* G. Langer, *Biblioth. Mycol.* **158**: 32. 1994.
*Type*: *Tofispora repetospora* G. Langer & Ryvarden, in Langer, *Biblioth. Mycol.* **158**: 338. 1994.

*Ceratorhiza* is listed above as a probable synonym. Certainly, a number of species placed in this genus introduced for asexual morphs of *Ceratobasidium* now belong in *Rhizoctonia*, but confirmation of the generic synonymy requires identification of the type of the name *Ceratorhiza*, *Cr. goodyerae-repentis*, here listed as a name of uncertain application.

*Accepted species*: ***Rhizoctonia amygdalispora*** (Hauerslev *et al.*) Oberw. *et al.*, ***R. anceps*** (Bres. *et al.*) Oberw. *et al.*, ***R. angustispora*** (Warcup & P.H.B. Talbot) R.P. O'Donnell *et al.*, ***R. anomala*** (Currah) R.P. O'Donnell *et al.*, ***R. australiensis*** (Y.P. Tan & P. Adhikari) R.P. O'Donnell *et al.*, ***R. biapiculata*** (D.P. Rogers) R.P. O'Donnell *et al.*, ***R. bicornis*** (J. Erikss. & Ryvarden) Oberw *et al.*, ***R. brevispora*** (Pouzar) R.P. O'Donnell *et al.*, ***R. bulbillifaciens*** (Diederich & Lawrey) R.P. O'Donnell *et al.*, ***R. butinii*** Oberw. *et al.*, ***R. chavesiana*** (M.P. Melo *et al.*) R.P. O'Donnell *et al.*, ***R. cornigera*** (Bourdot), Zmitr., ***R. erinnae*** (Y.P. Tan) R.P. O'Donnell *et al.*, ***R. floccosa*** Burgeff, ***R. fumigata*** (N. Nakata ex Hara) P.S. Gunnell & R.K. Webster, ***R. fusispora*** (J. Schröt.) Oberw. *et al.*, ***R. gardneri*** (Warcup) R.P. O'Donnell *et al.*, ***R. globispora*** (Warcup & P.H.B. Talbot) Oberw. *et al.*, ***R. gomesae*** (E.S. Cruz *et al.*) R.P. O'Donnell *et al.*, ***R. hebelomatospora*** (Boidin & Gilles) R.P. O'Donnell *et al.*, ***R. hydrophila*** (Sacc.) R.P. O'Donnell *et al.*, ***R. klebahnii*** (G. Burchard) R.P. O'Donnell *et al.*, ***R. korinnae*** (Y.P. Tan) R.P. O'Donnell *et al.*, ***R. lantanae-camarae*** (H.C. Evans *et al.*) R.P. O'Donnell *et al.*, ***R. microsclerotia*** Matz, ***R. myrtisiae*** (Y.P. Tan) R.P. O'Donnell *et al.*, ***R. niltonsouzana*** (M.P. Melo *et al.*) R.P. O'Donnell *et al.*, ***R. noxia*** (Donk) Oberw. *et al.*, ***R. obscura*** (D.P. Rogers) Oberw. *et al.*, ***R. ochracea*** (Massee) Oberw. *et al.*, ***R. papillata*** (Warcup & P.H.B. Talbot) R.P. O'Donnell *et al.*, ***R. pennata*** (Currah) R.P. O'Donnell *et al.*, ***R. pernacatena*** (Zelmer & Currah) R.P. O'Donnell *et al.*, ***R. praticola*** (Kotila) R.P. O'Donnell *et al.*, ***R. praxillae*** (Y.P. Tan) R.P. O'Donnell *et al.*, ***R. pseudocornigera*** (M.P. Christ.) Oberw. *et al.*, ***R. queenslandica*** (Y.P. Tan & P. Adhikari) R.P. O'Donnell *et al.*, ***R. ramicola*** W.A. Weber & D.A. Roberts, ***R. repetospora*** (G. Langer & Ryvarden) R.P. O'Donnell *et al.*, ***R. rhizodes*** (Auersw.) R.P. O'Donnell *et al.*, ***R. robertsii*** R.P. O'Donnell *et al.*, ***R. sapphoae*** (Y.P. Tan) R.P. O'Donnell *et al.*, ***R. sasakii*** (Shirai) R.P. O'Donnell *et al.*, ***R. scaberula*** (Hjortstam & Ryvarden) R.P. O'Donnell *et al.*, ***R. setariae*** (Sawada) R.P. O'Donnell *et al.*, ***R. solani*** J.G. Kühn, ***R. sphaerospora*** (Warcup & P.H.B. Talbot) Oberw. *et al.*, ***R. sterigmatica*** (Bourdot) Oberw. *et al.*, ***R. stridii*** (J. Erikss. & Ryvarden) Oberw. *et al.*, ***R. terrigena*** (Bres.) Oberw. *et al.*, ***R. theobromae*** (P.H.B. Talbot & Keane) Oberw. *et al.*, ***R. tradescantiae*** (D.M. Macedo *et al.*) R.P. O'Donnell *et al.*

***Rhizoctonia amygdalispora*** (Hauerslev *et al.*) Oberw. *et al.*, *Mycol. Progr.* **12**(4): 774. 2013.
*Basionym*: *Thanatephorus amygdalisporus* Hauerslev *et al.*, *Nordic J. Bot.* **16**(2): 217. 1996.

*Type citation*: 'Type: Sweden, Berthlga, Svinskinnshagen, on wood, 12.10.1947, J.A. Nannfeldt 9652 (K).' Roberts (1999) cites 'J.A. Nannfeldt 9652, K(M) 30010' as holotype.

***Rhizoctonia anceps*** (Bres. *et al.*) Oberw. *et al.*, *Mycol. Progr.* **12**(4): 774. 2013.
*Basionym*: *Tulasnella anceps* Bres. *et al.*, *Ann. Mycol.* **8**(5): 490. 1910.

*Synonyms*: *Corticium anceps* (Bres. *et al.*) Gregor, *Ann. Mycol.* **30**(5-6): 464. 1932.
*Ceratobasidium anceps* (Bres. *et al.*) H.S. Jacks., *Canad. J. Res., Sec. C.* **27**: 242. 1949.
*Thanatephorus anceps* (Bres. *et al.*) Parmasto, *Eesti N. S. V. Tead. Akad. Toimet., Biol.* **17**(2): 225. 1968.
*Sclerotium deciduum* Davis, *Trans. Wisconsin Acad. Sci.* **19**: 689. 1919.
*Ceratorhiza decidua* (Davis) P. Roberts, *Rhizoctonia-Forming Fungi* (Richmond): 32. 1999.

*Type citation*: 'in frondibus *Pteridis aquilinae* quas enecat, pr. Graal, Mecklenburg, 8. 1908, leg. H. Sydow.' ['in the leaves of *Pteridium aquilinum* which it kills, pr. Graal, Mecklenburg, 8. 1908, leg. H. Sydow.'(i.e. Sydow, Myc. Germ. 858)]. Roberts (1999) cites '(Myc. Germ. 858), K(M) 35724' as isotype.

*ITS barcode*: MH855251 (R).
*UNITE 1.5 % SH*: SH0961344.10FU.
*Alternative markers*: *ATP6* = DQ301583 (R); LSU = MH866704 (R); *TEF1* = DQ301652.

*Notes*: The type of *R. anceps* has not been sequenced. A sequence from a culture identified as *Cb. anceps* (CBS 152.32) which was isolated from the same host species cited in the protologue (*Pteridium aquilinum*) generated by Vu *et al.* (2019) was selected as a representative sequence for this study. The treatment of *Sclerotium deciduum* as a synonym follows Roberts (1999).

***Rhizoctonia angustispora*** (Warcup & P.H.B. Talbot) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852035.
*Basionym*: *Ceratobasidium angustisporum* Warcup & P.H.B. Talbot, *New Phytol.* **86**(3): 267. 1980.

*Type citation*: 'Holotypus: Herb. ADW No. 16594, J. H. Warcup (0507) (described 1971 as *C.* sp.) … Host: *Pterostylis mutica* R. Br., Hincks, Eyre Peninsula, South Australia.' According to Roberts (1999) the type 'cannot now be found'.

*ITS barcode*: AJ427403 (T).
*UNITE 1.5 % SH*: SH0987490.10FU.
*Alternative markers*: *ATP6* = DQ301591 (T); LSU = MH873364 (T); *RPB2* = DQ301722 (T).

*Ex-type culture*: CBS 568.83.

*Notes*: Roberts (1999) treated this taxon as conspecific with *R. pseudocornigera*, despite the highly disjunct distribution between the type of *Ceratobasidium angustisporum* (Australia) and the type of *R. pseudocornigera* (Denmark). The type specimen of *R. pseudocornigera* has to date not been sequenced; however, the ex-type culture of *Cb. angustisporum* has been sequenced. Sequences of *Cb. angustisporum* are curated in the UNITE database as species hypothesis SH0987490.10. Sequences corresponding with this species hypothesis from global soil samples appear to have only been identified in Australia and South Africa, supporting the proposition that this taxon is distinct from the northern hemisphere *R. pseudocornigera*.

***Rhizoctonia anomala*** (Currah) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852043.
*Basionym*: *Moniliopsis anomala* Currah, *Canad. J. Bot.* **68**(6): 1180. 1990.
*Synonym*: '*Rhizoctonia anomala*' Burgeff, *Samenkeim. Orch.*: 132. 1936. nom. inval. (Table 3)

*Type citation*: 'Neotype a dried colony of UAMH 6451 on CMA, ex *C. viride*, Cardinal River Divide.' Given that the name was being newly described by Currah, the designation as "neotype" should be corrected to "holotype".

*ITS barcode*: ITS1 = KF267003 (T); ITS2 = KF267040 (T).
*UNITE 1.5 % SH*: n/a.
*Alternative marker*: LSU = KF267077 (T).

*Ex-type culture*: CBS 193.90.

*Notes*: Currah *et al.* (1990) introduced the name '*Moniliopsis anomala* Burgeff ex Currah, *sp. nov.*' accompanied by a description and citation of a 'neotype'. According to Art. 46.4, the name should be attributed to Currah alone, even though it was an attempt to validate '*Rhizoctonia anomala* Burgeff', because Burgeff's name was introduced in a different genus. Even though the name *R. anomala* has been used in the literature, it is not valid. Therefore, we here create the valid combination *R. anomala* by formalising the transfer of *M. anomala* to *Rhizoctonia*.

***Rhizoctonia australiensis*** (Y.P. Tan & P. Adhikari) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 856690.
*Basionym*: *Ceratobasidium australiense* Y.P. Tan & P. Adhikari, *Index of Australian Fungi* **37**: 1 2024, as *'australiensis'*.

*Type citation*: 'Australia, Queensland, Bundaberg, from root lesion of *Saccharum officinarum* (*Poaceae*), 2019, *P. Adhikari* (holotype BRIP 73022a permanently preserved in a metabolically inactive state).'

*ITS barcode*: PP794647 (T).
*UNITE 1.5 % SH*: n/a.

*Notes*: A BLAST search of the type accession of *R. australiensis* found that it is similar to accessions identified as *Rhizoctonia* AG-Ba, identified here as *R. fumigata.* However, the type sequence for *R. australiensis* was found to be only 94.29 % identical with the type sequence of *R. fumigata* (GenBank FJ231392). As there appears to be substantial divergence between these two accessions, *R. australiensis* and *R. fumigata* are best treated as distinct entities.

***Rhizoctonia biapiculata*** (D.P. Rogers) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852036.
*Basionym*: *Pellicularia biapiculata* D.P. Rogers 1944, *Lloydia* **7**(1): 71. 1944.
*Synonyms*: *Tofispora biapiculata* (D.P. Rogers) G. Langer, *Biblioth. Mycol.* **158**: 328. 1994.
*Thanatephorus biapiculatus* (D.P. Rogers) P. Roberts, *Mycotaxon* **69**: 38. 1998.

*Type citation*: 'BRAZIL: Estado do São Paulo. São Leopoldo, December 1939. Rev. J. Rick, Type. In herb. Univ. Iowa 1555.' Roberts (1999) cites 'J. Rick, IA 371814' as holotype.

***Rhizoctonia bicornis*** (J. Erikss. & Ryvarden) Oberw. *et al.*, *Mycol. Progr.* **12**(4): 774. 2013.
*Basionym*: *Ceratobasidium bicorne* J. Erikss. & Ryvarden 1973, *Corticiaceae of North Europe*, 2 Aleurodiscus-Confertobasidium (Oslo): 221. 1973.
*Synonym*: *Thanatephorus ovalisporus* Číźek & Pouzar, *Česká Mykol.* **46**(1–2): 62. 1992.

*Type citation*: 'Holotypus: Eriksson & Nannfeldt no. 14236 (herb. Eriksson). Type locality: Denmark, Sjælland, Grib Skov, on living specimens of *Polytrichum attenuatum* 2.10.1955.' Roberts (1999) cites 'J. Eriksson & J.A. Nannfeldt 14236, K(M) 35666' as isotype.

*ITS barcode*: AF200514 (R).
*UNITE 1.5 % SH*: SH0897788.10FU.

*Notes*: The type for *R. bicornis* has not been sequenced. A sequence identified as *Cb. bicorne* (GenBank AF200514) generated by Hietala *et al.* (2001) from a specimen of *Polytrichum* in their study linking *Cb. bicorne* to a uninucleate *Rhizoctonia* pine pathogen was selected for use as a representative sequence here.

***Rhizoctonia brevispora*** (Pouzar) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852037.
*Basionym*: *Thanatephorus brevisporus* Pouzar, *Czech Mycol*. **53**(2): 122. 2001.

*Type citation*: 'Holotypus: Bohemia, Voškov apud Karlštejn, *Carpinus betulus* - ad truncum iacentem, 7. V. 2001, leg. Z. Pouzar, PRM 895056, in Museo Nationale Pragae asservatur.' ['Holotype: Bohemia, Voškov near Karlštejn, on a trunk of *Carpinus betulus*, 7.V.2001., collected by Z. Pouzar, PRM 895056, preserved in the National Museum in Prague.']

***Rhizoctonia bulbillifaciens*** (Diederich & Lawrey) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852038.
*Basionym*: *Ceratobasidium bulbillifaciens* Diederich & Lawrey, *Lichenologist* **46**(3): 345. 2014.

*Type citation*: 'Type: Germany, Hessen, Gießen, Parkplatz bei Sporthalle im süden von Heuchelheim, alt. 155 m, on *Acer platanoides*, on unidentified, dying lichenized crust, also on young thalli of *Physcia tenella*, 6 September 2010, R. Cezanne & M. Eichler 8193 (BR–holotype; hb. Diederich–isotype). Ex-type culture: CBS 129339. '['Type: Germany, Hessen, Gießen. Parking lot at the sport hall in the south of Heuchelheim...'].

*ITS barcode*: OR471309 (T); KC336072 (R).
*UNITE 1.5 % SH*: SH0961369.10FU.
*Alternative markers*: LSU = KC336071 (R); *RPB2* = OR473843 (R); *TEF1* = OR490360 (R).

*Ex-type culture*: CBS 129339.

*Notes*: In the protologue for *Cb. bulbillifaciens,* CBS 129339 is cited as the ex-type culture for the collection "Eichler-Cezanne 8193"; however, there was no ITS sequence from this culture generated by the authors in their published phylogeny as "another sequence (Eichler-Cezanne 8193) proved to be too short to be reliably placed phylogenetically" (p. 338). Instead, the authors incorporated a single ITS sequence from CBS 132236 which represents the collection "Eichler-Cezanne 8067", listed as an additional specimen examined. Diederich *et al.* (2014) inferred a separate LSU tree which did incorporate sequences from both CBS 129339 and CBS 132236, which were clustered together. Sequences of the ITS region from the ex-type culture (CBS 129339) were later generated by Swenie *et al.* (2024). When BLASTed, the ITS sequence from CBS 132236 published by Diederich *et al.* (2014) was found to share > 99 % similarity to ITS sequences generated from the ex-type culture by Swenie *et al.* (2024). Sequences from both accessions are clustered within the UNITE 1.5 % SH SH0961369.10FU. On this basis, CBS 129339 and CBS 132236 should indeed be considered conspecific. There are sequences of the *RPB2* and *TEF1* regions for *Cb. bulbillifaciens* available on GenBank; however, they have been sequenced from CBS 132236. As sequences for the ITS, LSU, *RPB2*, and *TEF1* regions were available for CBS 132236 and not CBS 129339, sequences representing CBS 132236 were selected for phylogenetic analyses in this study to ensure all regions incorporated were from the same collection. These sequences are cited here as representative sequences in addition to the type ITS barcode.

***Rhizoctonia butinii*** Oberw., R. Bauer *et al.*, *Mycol. Progr*. **12**(4): 770. 2013.

*Type citation*: 'Type: Bavaria, Aufichtenwald/ Spiegelau, Bavarian Forest, 760 m, N 48.91418, E 13.357186, 10.9.2009, H. Butin (M, holotype).'

*ITS barcode*: KF386035 (T).
*UNITE 1.5 % SH*: SH0897760.10FU.
*Alternative marker*: LSU = KF386035 (sequence contains both ITS and LSU regions - T).

***Rhizoctonia chavesiana*** (M.P. Melo *et al.*) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852044.
*Basionym*: *Ceratobasidium chavesianum* M.P. Melo *et al.*, *Trop. Pl. Pathol.* **43**(6): 569. 2018, as '*chavesanum*'.

*Type citation*: 'Brazil, State of Espírito Santo, Conceição do Castelo (41° 17 '45 "W, 20° 22' 08" S), in *Coffea arabica*, May 2010, Hélcio Costa and José Aires Ventura (Holotype VIC 44207, Ex-type CML 3474).'

*ITS barcode*: KX870113 (T).
*UNITE 1.5 % SH*: SH0814273.10FU.

*Ex-type culture*: CML 3474.

*Note*: The epithet *chavesanum* is erroneously terminated as per Art. 60.8(d) (Shenzhen) and is here corrected to *chavesianum*.

***Rhizoctonia cornigera*** (Bourdot) Zmitr. *Biol. Bull. Rev*. **14** (Suppl. 1): S33. 2024.
*Basionym*: *Corticium cornigerum* Bourdot, *Rev. Sci. Bourbonnais Centr. France.* **35**(1): 15. 1922.
*Synonyms*: *Ceratobasidium cornigerum* (Bourdot) D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(1): 5. 1935.
*Rhizoctonia cerealis* E.P. Hoeven, *Netherlands J. Pl. Pathol.* **83**(5): 191. 1977*,* nom. inval. (Table 3).
*Ceratorhiza cerealis* (E.P. Hoeven) R.T. Moore, *Mycotaxon* **29**: 94. 1987, nom. inval. (Table 3).
*Ceratobasidium cereale* D.I. Murray & Burpee, *Trans. Brit. Mycol. Soc.* **82**(1): 172. 1984.

*Type citation*: 'Vere et aestate, ad caules putrescentes *Helianthi tuberosi*, Saint-Priest-en-Murat. '['Spring and summer, on putrescent stems of *Helianthus tuberosus*, Saint-Priest-en-Murat']. Roberts cites the collection 'Allier, St. Priest, on rotting stalks of *Helianthus tubersosus*, 13 May 1913, H. Bourdot 9355 PC' as holotype.

*ITS barcode*: AJ301903 (R).
*UNITE 1.5 % SH*: n/a.
*Alternative markers*: *ATP6* = DQ301576; *RPB2* = DQ301707; *TEF1* = DQ301645.

*Notes*: Refer to notes for *R. ramicola* and *R. lantanae-camarae.* The type of *R. cornigera* has not been sequenced. Oberwinkler *et al.* (2013) note that *Cb. cornigerum* is a broadly circumscribed taxon with no clear preference with respect to host or nutritional mode. The taxon is likely a species complex which contains several distinct taxa. Sequences from a CBS culture (CBS 132.82) identified as *Cb. cornigerum* in the analyses of Oberwinkler *et al.* (2013) generated by Gónzalez *et al.* (2001) were selected as representative sequences in this study. The synonymy of *R. cerealis* with *R. cornigera* follows Roberts (1999). Bondartseva & Zmitrovich (2024) transferred *Cb. cornigerum* to *Rhizoctonia* and noted (p. S33) that "If synonymy of *Ceratobasidium cornigerum* with *Rhizoctonia goodyerae-repentis* or *Rh. fragariae* is confirmed by modern methods for assessing taxonomic distance, one of these names should be used in the application to this species. If all three names are synonyms, the priority should be given to *Rh. goodyerae-repentis*." However, we note that *R. fragariae* is an invalid name (Table 3), and *R. goodyerae-repentis* is considered a name of uncertain application (see notes under *R. fusispora*; Table 4).

***Rhizoctonia erinnae*** (Y.P. Tan) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 856693.
*Basionym*: *Ceratobasidium erinnae* Y.P. Tan, *Index of Australian Fungi* **41**: 1. 2024.

*Type citation*: 'Australia, Queensland, Jimbour, from root of *Cicer arietinum* (*Fabaceae*), 16 Sep. 2014, *S.M. Thompson* (holotype BRIP 61614a permanently preserved in a metabolically inactive state).'

*ITS barcode*: PQ061104 (T).
*UNITE 1.5 % SH*: n/a.

***Rhizoctonia floccosa*** Burgeff, *Saprophyt. Symb.*: 152. 1932.

*Type citation*: 'M. R. [Mycelium radicis] (*Myrmechis*) *glabrae* (Pangerango, Java)...M.R. (*Myrmechis*) *gracilis* (Pangerango, Java).'

*ITS barcode*: MH855816 (R).
*UNITE 1.5 % SH*: SH0987472.10FU.
*Alternative marker*: LSU = MH867319 (R).

*Authentic strain culture*: CBS 336.36.

*Notes*: Considered a nomen dubium by Andersen & Stalpers (1994) and Roberts (1999), as no holotype specimen was designated. However, an authentic strain (CBS 336.36) isolated by Burgeff from the host orchid (*Myrmechis glabrae*) mentioned in the protologue and collected from the type locality ('Tjibodas'[Cibodas], 'Pangerango'[Pangrango]) is extant and has been sequenced. In the present study, phylogenetic analysis recovered this representative sequence as separate from sequences from named *Rhizoctonia* species but closely related to unnamed orchid mycorrhizal OTUs. Andersen & Stalpers (1994) note in their discussion of *R. floccosa* that "the very small monilioid cells are quite distinct" (p. 442). This morphological distinction, coupled with molecular results in this study suggest that recognition of *R. floccosa* at the species level is indeed warranted.

***Rhizoctonia fumigata*** (N. Nakata ex Hara) P.S. Gunnell & R.K. Webster, *Mycologia* **79**(5): 735. 1987.
*Basionym*: *Sclerotium fumigatum* N. Nakata ex Hara, *Pathologia Agriculturalis Plantarum*: 168. 1930.

*Type citation*: 'NEOTYPE: In herb. Univ. of California, Berkeley, UC 1475045 … CULTURE EXAMINED: CBS 577.81 from Japan … A dried specimen of *S. fumigatum* CBS 577.81 has been deposited at UC to serve as a neotype.' designated by Gunnell & Webster (1987).

*ITS barcode*: FJ231392 (T).
*UNITE 1.5 % SH*: SH0961366.10FU.
*Alternative marker*: LSU = FJ212353 (T).

*Ex-type culture*: CBS 577.81.

*Notes*: See also notes under *R. setariae*. *Rhizoctonia fumigata* is considered to represent *Rhizoctonia* AG-Ba (Ogoshi *et al.* 1983, Oniki *et al.* 1986, Roberts 1999). No holotype was designated by Nakata for the basionym *Sclerotium fumigatum* but Gunnell & Webster (1987) have designated a neotype.

***Rhizoctonia fusispora*** (J. Schröt.) Oberw. *et al.*, *Mycol. Progr*. **12**(4): 774. 2013.
*Basionym*: *Hypochnus fusisporus* J. Schröt., in Cohn, *Krypt.-Fl. Schlesien* (Breslau) **3.1**(25–32): 416. 1888. [1889].
*Synonyms*: *Corticium fusisporum* (J. Schröt.) Brinkmann, *Westf. Pilze* **2**: no. 53. 1906, *nom. illeg.* (Table 3).
*Peniophora fusispora* (J. Schröt.) Höhn. & Litsch., *Ann. Mycol.* **4**(3): 289. 1906.

*Uthatobasidium fusisporum* (J. Schröt.) Donk, *Fungus*, Wageningen **26**(1–4): 22. 1958.
*Thanatephorus fusisporus* (J. Schröt.) Hauerslev & P. Roberts, *Nordic J. Bot.* **16**(2): 218. 1996.

*Type citation*: ‘Auf Holz und Rinden. Moos u. dergl. überziehend. Oktober–Dezember. — Neumarkt: Lissa.’ [‘on wood and bark, covered with moss etc. October–December. — Neumarkt: Lissa.’]. Roberts (1999) indicated that ‘the species lacks a type collection’.

*ITS barcode*: DQ398957 (R).
*UNITE 1.5 % SH*: SH0961356.10FU.
*Alternative marker*: LSU = AF518664 (R).

*Notes*: Roberts (1999) stated that ‘this species lacks a type collection and should be suitably neotypified.’ (p. 79). A neotype has not yet been designated. Representative sequences for this taxon have been selected from Hibbett & Binder (2002). A BLAST search found that representative sequences for *R. fusispora* used in this study are identical with sequences considered by Currah *et al.* (1990) and Taylor & McCormick (2008) to represent *Cr. goodyerae-repentis*. Phylogenetic analyses in this study similarly clustered the purported sequences of *Cr. goodyerae-repentis* together with sequences of *R. fusispora.* It is possible that *R. fusispora* and *Cr. goodyerae-repentis/R. goodyerae-repentis* are conspecific; however, Andersen & Stalpers (1994) noted that no type was designated for *Cr. goodyerae-repentis/R. goodyerae-repentis*, and that no illustration or authentic strain exists. Additionally, Moore’s (1987) treatment of *Cr. goodyerae-repentis* considered it the teleomorph of *Cb. cornigerum*. Andersen & Stalpers (1994) considered *Cr. goodyerae-repentis* and *R. goodyerae-repentis* as nomina dubia which is followed in this treatment, pending typification of the names.

***Rhizoctonia gardneri*** (Warcup) R.P. O’Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852057.
*Basionym*: *Thanatephorus gardneri* Warcup, *Mycol. Res.* **95**(6): 658. 1991.

*Type citation*: ‘Holotypus: Herb ADW 17023, J.H. Warcup, ex *Rhizanthella gardneri*, Corrigin, W. A., 11 February 1986.’ [MEL 2146230]

*ITS barcode*: GQ175295 (R).
*UNITE 1.5 % SH*: SH0897913.10FU.
*Alternative marker*: LSU = GQ200563 (R).

*Notes*: Considered a nomen dubium by Roberts (1999) on the basis that the herbarium specimen had been lost. However, the herbarium specimen has since been located at the National Herbarium of Victoria (MEL) and digitised (MEL 2146230). The specimen is a dried agar culture and sequencing of this specimen was attempted by us but failed. Bougoure *et al.* (2009) isolated and sequenced a species of *Ceratobasidiaceae* from the orchid *Rhizanthella gardneri* from the type locality of *Thanatephorus gardneri* (Sorensons Reserve, Corrigin, W.A.), which was later designated as ‘OTU C’ sensu Freestone *et al.* (2021). Based on the specificity of the mycorrhizal associations of *R. gardneri* (Warcup 1985, 1991, Bougoure *et al.* 2009, 2010), the taxon identified by Bougoure *et al.* (2009) is almost certainly conspecific with *Th. gardneri*. A sequence from Bougoure *et al.* (2009) isolated from *R. gardneri* from the type locality (which was recovered within the *Rhizoctonia* clade in our analysis) is taken as a representative sequence here.

***Rhizoctonia globispora*** (Warcup & P.H.B. Talbot) Oberw. *et al.*, *Mycol. Progr.* **12**(4): 774. 2013.
*Basionym*: *Ceratobasidium globisporum* Warcup & P.H.B. Talbot, *New Phytol.* **86**(3): 267. 1980.

*Type citation*: ‘Holotypus: Herb. ADW No. 16595, J.H. Warcup (0792) … Hosts: *Trichoglottis australiensis* Dockr., Northern Queensland (isolate 0792)’. According to Roberts (1999) the type ‘cannot now be found’.

*ITS barcode*: DQ278942 (T) [MH873365 is also derived from the same ex-type culture].
*UNITE 1.5 % SH*: n/a.
*Alternative markers*: *ATP6* = DQ301592 (T); LSU = MH873365 (T); *RPB2* = DQ301723 (T); *TEF1* = DQ301644 (T).

*Ex-type culture*: CBS 569.83.

***Rhizoctonia gomesae*** (E.S. Cruz *et al.*) R.P. O’Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852058.
*Basionym*: *Ceratobasidium gomesae* E.S. Cruz *et al.*, *Phytotaxa* **550**(3): 227. 2022.

*Type citation*: ‘Type: – BRAZIL. Minas Gerais: Parque Estadual Serra do Brigadeiro, from roots of *Gomesa recurva* R.Br. (Orchidaceae), September 2019, Cruz, E.S. (Holotype VIC 47413, ex-type living culture COAD 3147).’

*ITS barcode*: MT796443 (T).
*UNITE 1.5 % SH*: SH0961466.10FU.

*Ex-type culture*: COAD 3147.

***Rhizoctonia hebelomatospora*** (Boidin & Gilles) R.P. O’Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852059.
*Basionym*: *Botryohypochnus hebelomatosporus* Boidin & Gilles, *Mycotaxon* **14**: 287. 1982.
*Synonyms*: *Tofispora hebelomatospora* (Boidin & Gilles) G. Langer, *Biblioth. Mycol.* **158**: 334. 1994.
*Thanatephorus hebelomatosporus* (Boidin & Gilles) P. Roberts, *Mycotaxon* **69**: 36. 1998.

*Type citation*: ‘LY 9022, sous un tronc abattu, même lieu [en lisière du fourré littoral à 14 km au N. de Libreville], 7 décembre 1978, G. Gilles 1326.’ [‘LY 9022, under a felled trunk, same place (on the edge of the coastal thicket 14 km. N. of Libreville), 7 December 1978, G. Gilles 1326.’]

*Notes*: The epithet *hebelomatosporus* is based on the generic name *Hebeloma*, formed from words with an origin in Ancient Greek, with a termination based on the Greek noun σπορα, treated in Botanical Latin as *spora*. According to Art. 60.10 “adjectival epithets that combine elements derived from two or more Greek or Latin words are to be compounded … [by] adding a connecting vowel (-i- for Latin elements, -o- for

Greek elements)". Some sources, such as Index Fungorum, amend the spelling to *hebelomatisporus* but given that the word elements are both ultimately derived from Greek, the original spelling is best maintained.

***Rhizoctonia hydrophila*** (Sacc.) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852068.
*Basionym*: *Sclerotium hydrophilum* Sacc. *Syll. fung.* (Abellini) **14**(2): 1141. 1899.
*Synonym*: *Ceratorhiza hydrophila* (Sacc.) Z.H. Xu *et al.*, *Mycologia* **102**(2): 340. 2010.

*Type citation*: 'ap. Rothert Ueb. *Sclerotium hydroph.* Leipzig. 1892 (Bot. Zeit.)…Hab. in caulibus, quos vexat v. necat, *Myriophylli* et *Hydrocharidis* in horto bot. Strasbourg et Kazan, ubi legit cl. ROTHERT, qui inde coluit in compluribus aliis plantis.' ['In the writings of Rothert about *Sclerotium hydroph.* Leipzig. 1892 (Bot. Zeit.) ... Living in the stems, where it plagues or kills, *Myriophyllum* and *Hydrocharis* in the botanic gardens of Strasbourg and Kazan, where it was collected by ROTHERT, who later cultivated it in several other plants.']. **Lectotype** (here designated, MBT 10018477), illustration in Rothert, W. (1892) Botanische Zeitung 50, Taf. VII (reproduced here as Fig. 5a and 5b). **Epitype** (here designated, MBT 10018479): **The Netherlands**, isolated from *Victoria regia*,1927, *C.J. Buisman* (CBS 201.27, culture stored in a metabolically inactive state).

*ITS barcode*: FJ231396 (T).
*UNITE 1.5 % SH*: SH0916688.10FU.
*Alternative marker*: LSU = FJ212349 (T).

*Ex-epitype culture*: CBS 201.27.

*Notes*: In their molecular analyses to determine the phylogenetic placement of *Sclerotium hydrophilum*, Xu *et al.* (2010) used sequences from CBS cultures CBS 201.27 (isolated from the water lily *Victoria regia* in The Netherlands) and CBS 385.63 (from a "submerged leaf in garden pond" in Italy). Both CBS-derived sequences were recovered in a clade closely related to sequences variously identified as *Ceratorhiza,* and *S. hydrophylum* was consequently transferred to *Ceratorhiza*. The name *Ceratorhiza hydrophila* has subsequently been used to identify further isolates from aquatic plants, including *Myriophyllum spicatum* (Elsaba *et al.* 2022). The name *S. hydrophilum* was originally introduced by Rothert (1892) in an extensive discussion of a sclerotium-forming fungus found in association with water plants. Rothert (1892) indicated that P.A. Saccardo examined material and provided the comment 'Nous pouvez, je pense, le decrire sous un nom provisoire, p. e. *Sclerotium hydrophilum*' ['We can, I think, describe it under a provisional name *Sclerotium hydrophilum*'.] Due to the provisional nature of the name, as introduced by Rothert (1892), it is invalid according to Art. 36.1. Saccardo & Sydow (1899) later validly published the name, attributed there to P.A. Saccardo alone, and provided a description which cited Rothert (1892). Gola (1930) in his catalogue of the Saccardo Herbarium (now at PAD) does not list any material of *S. hydrophilum*. Hence, we designate as lectotype the illustration in Rothert (1892) because it can be considered part of the original material under Art. 9.4, being published illustrations that Saccardo (in Saccardo & Sydow, 1899) associated with the taxon via his citation of Rothert (1892). The illustration in Rothert (1892) depicts the internal structure of the sclerotium (as globose to irregularly subglobose to ellipsoid elements) along with cylindrical, septate hyphae, lacking clamp connections, some with right angled branching. These characters are consistent with *Rhizoctonia* but are not characteristic enough at species level because a number of species of *Rhizoctonia* form sclerotia (Sumner 1996). Because of this ambiguity, we therefore epitypify the name as above. A separate phylogenetic analysis of GenBank ITS sequences identified as *Ceratorhiza hydrophila/Sclerotium hydrophilum* and sequences that BLAST to GenBank FJ231390 (Supporting Information Fig. S1; Table S4) recovered two sister clades; one containing CBS 201.27 (GenBank FJ231396) from the Netherlands [one of the sequences utilised by Xu *et al.* (2010)] along with sequences from China, and the other containing GenBank EU152867 (Hu *et al.* 2010) and other sequences from China, as well as sequences from Egypt, Myanmar, Philippines and USA. Interestingly, the sequence representing CBS 385.63 was recovered as sister to the clade containing CBS 201.27. When BLASTed, the ITS sequence of CBS 385.63 shares only 91.19 % identity with CBS 201.27. However, BLAST results for LSU sequences of the same two CBS cultures found 97.99 % identity. Given the existence of two or more clades in our analysis, it is possible that there are multiple taxa represented among sequences in GenBank currently identified as *Cr. hydrophila*. We chose as epitype one of the sequences utilised by Xu *et al.* (2010), from the Netherlands (CBS 201.27) as it was recovered within a distinct clade with several other accessions (and thus more representative of this particular taxon), rather than CBS 385.63 which was recovered as a single branch. On the basis of the sequence information, *S. hydrophilum* clearly belongs in *Rhizoctonia*.

***Rhizoctonia klebahnii*** (G. Burchard) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852069.
*Basionym*: *Moniliopsis klebahnii* G. Burchard *Phytopathol. Z.* **1**: 277. 1929, as '*klebahni*'.
*Synonym*: *Ceratobasidium albasitensis* V. González & V. Rubio, *Persoonia* **17**(4): 603. 2002.

*Type citation*: 'Ich möchte dem Pilz, im Hinblick auf die Verdienste Herrn Prof. Klebahns um die Erforschung der Kiefernschädlinge überhaupt, und da er den Pilz zuerst in Kultur zog, den Namen *Moniliopsis klebahni* geben.' [I would like to give to the fungus, in view of Prof. Klebahn's achievements in researching pine pests in general, and since he was the first to grow the fungus in culture, the name *Moniliopsis klebahni*.']

*ITS barcode*: MH854971 (R).
*UNITE 1.5 % SH*: SH0897862.10FU.

*Notes*: BLAST results show that the sequence of *M. klebahnii* used in this study (GenBank MH854971) generated by Vu *et al.* (2019) which is cited as being sequenced from an authentic isolate produced by G. Burchard – the author of *M. klebahnii* – is 99–100 % identical with several accessions of *Cb. albasitensis* published by González *et al.* (2002), including the ex-type sequence of *Cb. albasitensis* used in this study (GenBank AJ242875). These two accessions are

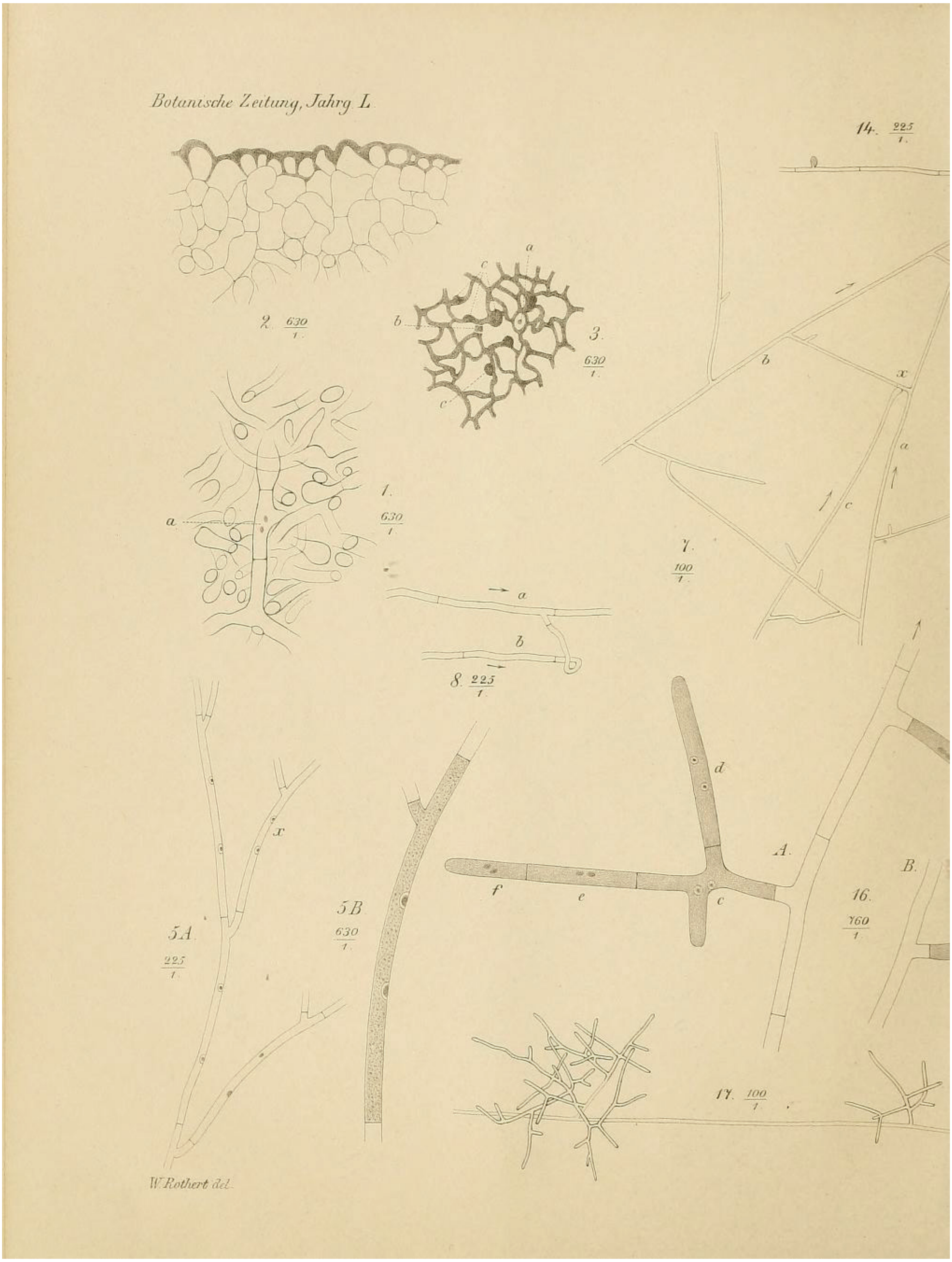


**Fig. 5.** Reproduction of Rothert's (1892) illustrations of R. *hydrophila* (Botanische Zeitung 50, Taf. VII). Taf. VII is spread across two pages in the source publication and each page is reproduced here.

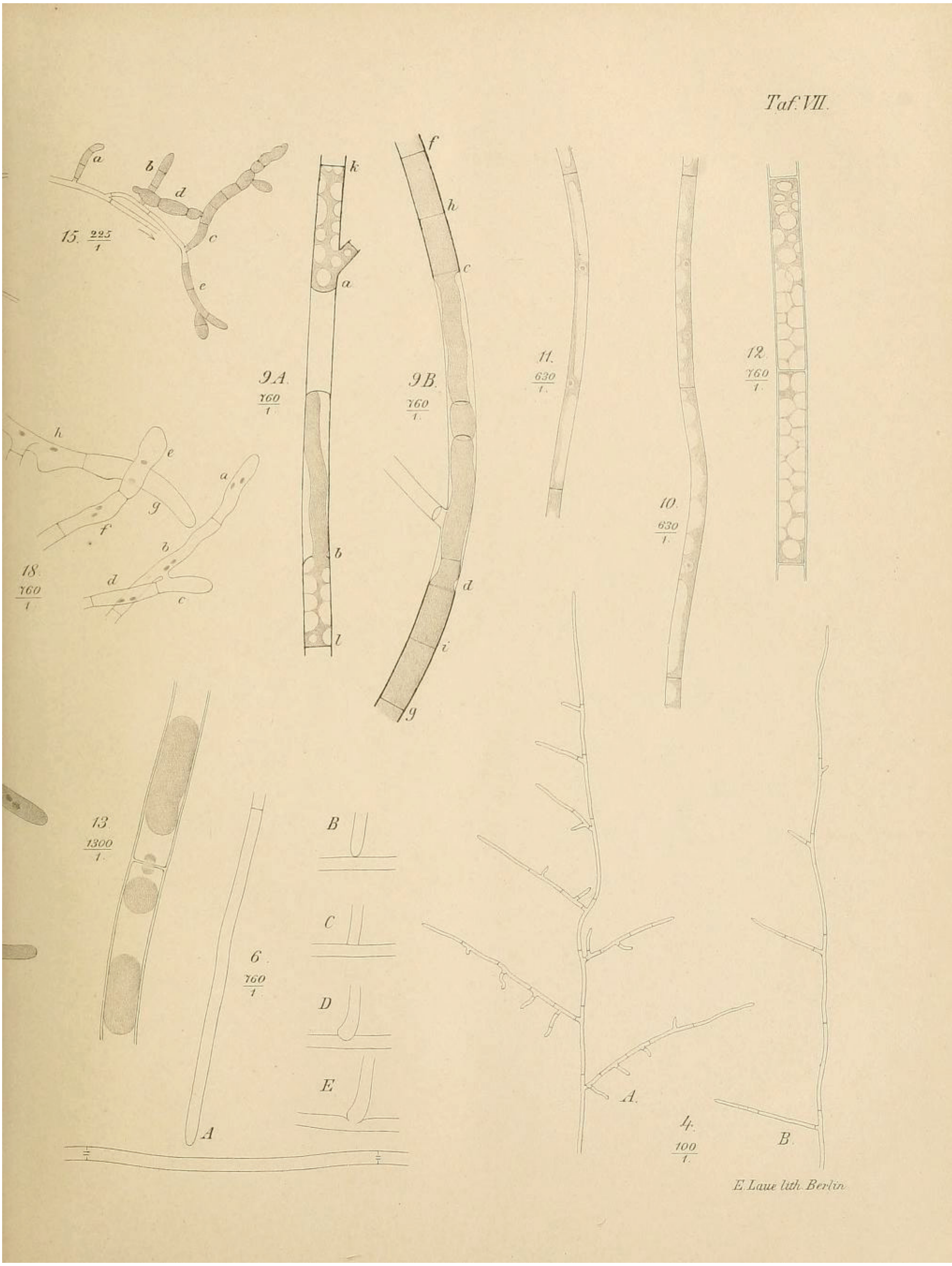


**Fig. 5.** (Continued).

placed together in the UNITE 1.5 % SH SH0897862.10FU. Sequences from the 1.5 % SH come from a wide geographic range and from a wide variety of hosts, but we note that *M. klebahnii* and *Cb. albasitensis* are both stated to be pine pathogens in their respective protologues. Due to the high identity between reference sequences of both *Moniliopsis klebahnii* and *Cb. albasitensis*, they should be considered synonymous. As *M. klebahnii* (1929) predates the publication of *Cb. albasitensis* (2002), the epithet *klebahnii* takes priority.

***Rhizoctonia korinnae*** (Y.P. Tan) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 856691.
*Basionym*: *Ceratobasidium korinnae* Y.P. Tan, *Index of Australian Fungi* **41**: 2. 2024.

*Type citation*: 'Australia, Queensland, Biloela, from root canker of *Medicago sativa* (*Fabaceae*), 24 Apr. 1997, *J. Mackie* (holotype BRIP 27717a permanently preserved in a metabolically inactive state).'

*ITS barcode*: PQ061105 (T).
*UNITE 1.5 % SH*: n/a.

***Rhizoctonia lantanae-camarae*** (H.C. Evans *et al.*) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852070.
*Basionym*: *Ceratobasidium lantanae-camarae* H.C. Evans *et al.*, *Mycol. Res.* **99**(7): 770. 1995.

*Type citation*: '*Holotype:* IMI 360868, on *Lantana camara,* Rio Ariaú–Rio Negro, Manacaparu, Amazonas, Brazil, 31 July 1991, R. W. Barreto & H. C. Evans.'. An epitype was designated by Ferreira *et al.* (2021): 'Brazil: Amazonas, Presidente Fiqueiredo, Iracema Falls, on *Lantana camara*, 28 Jun 2019, R.W. Barreto (VIC 47,338– epitype designated here; epitype culture – COAD 2919, MBT 395235)'.

*ITS barcode*: MW361943 (T).
*UNITE 1.5 % SH*: SH0970519.10FU.

*Ex-type culture*: COAD 2919.

*Notes*: Roberts (1999) placed *Cb. lantanae-camarae* as synonymous with *Cb. cornigerum*; however, molecular phylogenies recovered by Ferreira *et al.* (2021) placed accessions of *Cb. lantanae-camarae* in a distinct clade, separate to all sampled accessions identified as *Cb. cornigerum*. Ferreira *et al.* (2021) consequently reinstated *Cb. lantanae-camarae* at the species level and designated an epitype.

***Rhizoctonia microsclerotia*** Matz, *Phytopathology* **7**: 116. 1917. MB 271074.
*Synonym*: *Thanatephorus microsclerotium* (Matz) Boidin *et al.* [as '*microsclerotius*'], *Mycotaxon* **66**: 482. 1998.

*Type citation*: 'Hab. On living leaves, branches and fruit of the cultivated fig, *Ficus carica*, Gainesville, Florida, U. S. A.' Roberts (1999) cites 'G.F. Weber 7850, FLAS' as holotype.

*ITS barcode*: DQ279038 (R).
*UNITE 1.5 % SH*: SH0814404.10FU.
*Alternative markers*: *ATP6* = DQ301616 (R); LSU = KP171642 (R); *RPB2* = DQ301730 (R); *TEF1* = DQ301677 (R).

*Notes*: *Thanatephorus microsclerotium* is considered to represent *Rhizoctonia* AG-1-IB (Boidin *et al.* 1998, Roberts 1999, Gónzalez *et al.* 2001). While Roberts (1999) treated *R. microsclerotia* as synonymous with *Th. cucumeris* (the anamorph name for *R. solani*) molecular analyses by Boidin (1998), Gónzalez *et al.* (2001), and this study indicate that *R. microsclerotia* is genetically distinct from *R. solani* s. s. and that species-level recognition is warranted. Representative sequences for this taxon were selected from sequences available on GenBank generated from the CBS culture CBS 206.84 identified as *R.* AG-1-IB by Gónzalez *et al.* (2016).

***Rhizoctonia myrtisiae*** (Y.P. Tan) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 856694.
*Basionym*: *Ceratobasidium myrtisiae* Y.P. Tan, *Index of Australian Fungi* **41**: 3. 2024.

*Type citation*: 'Australia, Queensland, Moura, from root rot of *Arachis hypogaea* (*Fabaceae*), Feb. 2004, *J.R. Tatnell* (holotype BRIP 44989a permanently preserved in a metabolically inactive state).'

*ITS barcode*: PQ061106 (T).
*UNITE 1.5 % SH*: n/a.

*Notes*: A BLAST search of the type accession of *R. myrtisiae* found that it shares more than 99 % identity with a number of accessions identified as *Rhizoctonia/Ceratobasidium* AG-Fa in studies such as Gónzalez *et al.* (2016: GenBank DQ279014 at 99.20 % identity), Sharon *et al.* (2008: e.g. GenBank AB219144 at 99.52 %) and Muzhinji & Lekota (2024: e.g. GenBank JX913819 at 99.08 %). Thus, *R. myrtisiae* should be considered the epithet associated with this AG group. See also comments under *R. sapphoae*.

***Rhizoctonia niltonsouzana*** (M.P. Melo *et al.*) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852071.
*Basionym*: *Ceratobasidium niltonsouzanum* M.P. Melo *et al.*, *Trop. Pl. Pathol.* **43**(6): 568. 2018.

*Type citation*: 'Brazil, State of Piauí, Teresina, Centro de Ciências Agrárias, Campus da Universidade Federal do Piauí (42 ° 46 '57 "W; 05 ° 02' 45 "S), in *Eugenia uniflora*, April 2015, Maruzanete Pereira de Melo (Holotype VIC 44275, Ex-type CML 3598).'

*ITS barcode*: KU175888 (T).
*UNITE 1.5 % SH*: SH0814308.10FU.

*Ex-type culture*: CML 3598.

***Rhizoctonia noxia*** (Donk) Oberw. *et al.*, *Mycol. Progr*. **12**(4): 774. 2013.
*Basionym*: *Koleroga noxia* Donk, *Fungus*, Wageningen 28: 35. 1958.
*Synonym*: *Ceratobasidium noxium* (Donk) P. Roberts, *Rhizoctonia-Forming Fungi* (Richmond): 48. 1999.

*Type citation*: 'that portion of the type of *Pellicularia Koleroga* Cooke (K) represented by the hyphae giving rise to basidia and spores illustrated by Burt (*in* Ann. Missouri bot. Gdn 5: 124 *f. Ia.* 1918; 13: 293 *f. Ia.* 1926).' Roberts (1999) selected a lectotype: 'INDIA: Mysore, on living leaf of *Coffea*, 1875, ex herb, M.C. Cooke, ex herb. M.J. Berkeley, K(M) 29396, lectotype (!).' (Roberts, 1999).

*ITS barcode*: EU810056 (R).
*UNITE 1.5 % SH*: SH0987559.10FU.
*Alternative markers*: *ATP6* = DQ301584 (R); *RPB2* = DQ301715 (R); *TEF1* = DQ301653 (R).

*Notes*: Representative sequences listed here for *R. noxia* were generated from a culture isolated by the Indian phytopathologist M.J. Narasimhan (1891–1970) from black rot of a *Coffea* sp. from India (CBS 154.35). Ceresini *et al.* (2012) cite CBS 154.35 as the 'type strain' for *Cb. noxium*, but we have been unable to locate any further literature which designates it as such. It does not appear to represent type material, but given the identical geographic location and host, we associate the culture with this name.

*Pellicularia koleroga* was introduced for a fungus growing on leaves of *Coffea* with a gelatinous sporophore. Because some mycologists who examined authentic material of *P. koleroga* found a mixture of hyphae from one fungus (consistent with *Ceratobasidium*) with spores from another unrelated fungus, Donk (1954) considered the name *P. koleroga* to be a "nomen confusum" (and therefore to be rejected) and specified the portion of the original material with basidia as the type of his newly introduced name *Koleroga noxia*. The term "nomen confusum" was referred to in the *International Code of Botanical Nomenclature* in editions up to the *Amsterdam Rules* of 1950 in connection with taxa whose "characters were derived from two or more entirely discordant elements". In subsequent editions the term nomen confusum did not appear, but the provision about discordant elements was retained (such as in the *Montreal Code* of 1961). In such circumstances, a name could be rejected. However, Article 70, dealing with discordant elements, was deleted by the Leningrad Congress and does not appear in the 1978 *Leningrad Code*. Under the current *Code*, the interpretation of names is via types and a name cannot simply be rejected because the type material is thought to contain discordant elements. Rogers (1951) typified *Pellicularia koleroga* on the portion of the type specimen that gives rise to and includes the basidia, as illustrated by Burt (1918). Donk (1954) considered that if a typification was to be carried out (which he argued was not necessary) it should have been done by reference to the spores. The *Coffea* leaf among Cooke's original material of *Pellicularia koleroga*, from which Burt prepared the illustration, appears not to have survived, with Roberts (1999) stating: "A leaf-shaped stain was all that was left of what was possibly the specimen illustrated by Burt and noted as in unusable condition" (p 50). Consequently, Roberts (1999) selected a lectotype for *K. noxia* from among other leaves of *Coffea* at K. However, these leaves are not strictly original material of Donk's name, as the name was not a *nomen novum*, replacing *Pellicularia koleroga*, but a new name introduced because Donk considered *P. koleroga* to be illegitimate. Strictly speaking, *K. noxia* was typified only by the illustrated material and the lectotype chosen by Roberts (1999) and it is not *Code*-compliant. Typification of *P. koleroga* also remains to be settled in terms of whether or not to accept the choice of type by Rogers (1951). Thus, *Pellicularia koleroga* remains a potential earlier name for *K. noxia* (which is typified by material, at least in part, that is intimately related to original material of *P. koleroga*). Given that there is still usage of the "*koleroga*" epithet for the coffee web-blight, albeit under older generic names, such as in *Corticium koleroga* [for example by Gidisa *et al.* (2024)], should *Pellicularia koleroga* be shown to be an available name that must displace *K. noxia*, there is not necessarily a clear case for proposing conservation of *K. noxia* over *P. koleroga*. Re-examination of remaining original material at K is required, along with an analysis of the phytopathological literature on the prevalence of the competing names for the coffee disease caused by *P. koleroga* / *Koleroga noxia*, before finalising the nomenclature of the species. For the moment, we follow Roberts' (1999) choice to take up the epithet "*noxia*" in his monograph of *Rhizoctonia*-forming fungi and make the necessary new combination in *Rhizoctonia*.

***Rhizoctonia obscura*** (D.P. Rogers) Oberw. *et al.*, *Mycol. Progr*. **12**(4): 775. 2013.
*Basionym*: *Ceratobasidium obscurum* D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(1): 6. 1935.
*Synonym*: *Thanatephorus obscurus* (D.P. Rogers) P. Roberts, *Mycol. Res.* **102**(9): 1074. 1998a.

*Type citation*: 'On lower side of a much rotted prostrate log of *Ulmus* sp., in woods along the Iowa River east of North Liberty, Iowa, June 11, 1934, D. P. R. 291, type.' Roberts (1999) cites 'D.P. Rogers 291, K(M) 53178' as an isotype.

*ITS barcode*: EU218894 (R). *UNITE 1.5 % SH*: SH0987497.10FU.
*Alternative marker*: LSU = KF267087 (R).

*Note*: Representative sequences for *R. obscura* listed here were generated by Taylor & McCormick (2008) from a culture isolated from the orchid *Amerorchis rotundifolia* identified by Currah *et al.* (1987) as *Cb. obscurum* (UAMH 5443).

***Rhizoctonia ochracea*** (Massee) Oberw. *et al.*, *Mycol. Progr*. **12**(4): 775. 2013.
*Basionym*: *Coniophora ochracea* Massee, *J. Linn. Soc., Bot*. **25**(no. 170): 137. 1889.
*Synonyms*: *Uthatobasidium ochraceum* (Massee) Donk, *Fungus*, Wageningen **28**: 23. 1958.
*Thanatephorus orchidicola* Warcup & P.H.B. Talbot, *Trans. Brit. Mycol. Soc.* **49**(3): 432. 1966.

*Type citation*: '(Pl. XLVII. f.13.) (Type in Herb. Kew.) Spreading continuously over the inside of elm-bark which had become slightly separated from the wood of a prostrate trunk. England (Kew).' Roberts (1999) cites 'G. Massee, K' as holotype, but notes that, according to Donk (1958), the specimen is missing.

*Notes*: The synonymy of *Th. orchidicola*, described from England from roots of *Orchis mascula*, follows Roberts (1999). Given that another of the species listed by Roberts (1999) under *Thanatephorus ochraceus* (i.e. *Th. pennatus*) appears to be distinct, it would be of interest to revisit the placement of *Th. orchidicola* by attempting to generate sequences from type material.

***Rhizoctonia papillata*** (Warcup & P.H.B. Talbot) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852072.
*Basionym*: *Ceratobasidium papillatum* Warcup & P.H.B. Talbot, *New Phytol*. **86**(3): 268. 1980.

*Type citation.* 'Holotypus: Herb. ADW No. 16596, J.H. Warcup (0808)...Hosts: *Sarcochilus dilatatus* F. Muell., Toowoomba, Queensland (isolate 0808)'.

*ITS barcode*: AJ427401 (T).
*UNITE 1.5 % SH*: n/a.
*Alternative markers*: LSU = KF267084 (T); *RPB2* = DQ301724 (T).

*Ex-type culture*: CBS 570.83.

*Notes*: Roberts (1999) considered *Cb. papillatum* as synonymous with *Cb. cornigerum* and stated that the type specimen was lost. However, an ex-type culture (CBS 570.83) is extant, and corresponds with Warcup's original isolate number (0808). Sequences from this ex-type culture used in our analyses place *Cb. papillatum* in a different clade altogether to *Cb. cornigerum* and *R. ramicola* which it was previously considered synonymous with. *Ceratobasidium papillatum* is therefore treated here as a distinct species and transferred to *Rhizoctonia*. A sequence for the ATP6 mitochondrial region from the ex-type culture of *Cb. papillatum* (CBS 570.83) has been deposited in GenBank (DQ301593); however, when BLASTed, the only result returned is a single accession matching the original search query (i.e. itself). Additionally, this sequence was unable to be aligned confidently with any other *ATP6* sequences retrieved here. This sequence appears to be an aberration that cannot be matched with any other existing *ATP6* sequence on GenBank, and it is unlikely that it is representative of this taxon. For these reasons, we have excluded it from our analyses here and do not include it among sequenced markers listed above.

***Rhizoctonia pennata*** (Currah) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852073.
*Basionym*: *Thanatephorus pennatus* Currah, *Canad. J. Bot*. **65**(9): 1958. 1987.

*Type citation*: 'TYPUS: cultura exsiccata "UAMH 5405," ex radicis *Calypso bulbosa*, Albertiensis.' ['TYPE: dried culture "UAMH 5405," from the roots of *Calypso bulbosa*, from Alberta.'].

*ITS barcode*: EU218892 (T).
*UNITE 1.5 % SH*: SH0814614.10FU.

*Ex-type culture*: ATCC 64683 (=UAMH 5405).

*Notes*: Roberts (1999) considered *Thanatephorus pennatus* a synonym of *Th. ochraceus*; however, the publicly-available 'type' sequence attributed to *Th. ochraceous* by Taylor & McCormick (2008) was actually sequenced from the holotype of *Th. pennatus. Coniophora ochracea* (the basionym of *Th. ochraceus*) was described from decaying elm bark in England, while *Th. pennatus* was isolated from roots of the orchid *Calypso bulbosa* collected from Alberta, Canada. Donk (1958) and Roberts (1999) also note that the type specimen for *Coniophora ochracea* is apparently lost. Given the differences in type locality and host substrate between *Th. pennatus* and *Th. ochraceus*, along with the fact that the true type specimen for *Th. ochraceus* is lost, it would appear prudent to treat *Th. pennatus* and *Th. ochraceus* as separate from one another. Consequently, we have here chosen to resurrect the name *Th. pennatus* as *Rhizoctonia pennata*.

***Rhizoctonia pernacatena*** (Zelmer & Currah) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852074.
*Basionym*: *Ceratorhiza pernacatena* Zelmer & Currah, *Canad. J. Bot.* **73**(12): 1982. 1995.

*Type citation*: 'HOLOTYPE: Dried colony of UAMH 7790 (=Z137-or-c) on CMA, ex *Platanthera praeclara,* Tolstoi—Vita, Manitoba, isolated in 1991.'

***Rhizoctonia praticola*** (Kotila) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852075.
*Basionym*: *Corticium praticola* Kotila, *Phytopathology* **19**: 1065. 1929.
*Synonyms*: '*Ceratobasidium praticola*' (Kotila) L.S. Olive, *Amer. J. Bot.* **44**(5): 431. 1957, nom. inval. (Table 3).
*Thanatephorus praticola* (Kotila) Flentje, *Austral. J. Biol. Sci.* **16**: 451. 1963, as '*praticolus*'.
'*Rhizoctonia praticola*' H.K. Saksena & Vaartaja, *Canad. J. Bot*. **39**: 637. 1961, nom. inval. (Table 3).

*Type citation*: 'Type cultivated in the laboratory; obtained in Michigan. Saprophytic in soil and parasitic on *Medicago sativa* L. in cultivated fields, collected by J. E. Kotila, October, 1924.'

*ITS barcode*: AY154307 (R).
*UNITE 1.5 % SH*: SH0814616.10FU.
*Alternative markers*: *ATP6* = DQ301604; LSU = AF354118 (R); *RPB2* = DQ301736; *TEF1* = DQ301668.

*Notes*: Roberts' (1999) treatment noted that *Thanatephorus praticola* represented *Rhizoctonia* AG-4, while also considering *Th. praticola* as synonymous with *Th. cucumeris* (=*R. solani*). The results of Gónzalez *et al.* (2001), Gónzalez *et al.* (2016) and this study support *Rhizoctonia* AG-4 as a lineage distinct from *R. solani* s. s. and for this reason we treat *R. praticola* as separate from *R. solani*. Representative sequences for this taxon were selected from sequences of *Rhizoctonia* AG-4 generated by Gónzalez *et al.* (2001) and Gónzalez *et al.* (2016).

***Rhizoctonia praxillae*** (Y.P. Tan) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 856692.
*Basionym*: *Ceratobasidium praxillae* Y.P. Tan*, Index of Australian Fungi* **41**: 4. 2024.

*Type citation*: 'Australia, New South Wales, Grafton, from root of *Lolium* sp. (*Poaceae*), 2 May 2014, *S.M. Thompson* (holotype BRIP 61490b permanently preserved in a metabolically inactive state).'

*ITS barcode*: PQ061107 (T).
*UNITE 1.5 % SH*: n/a.

***Rhizoctonia pseudocornigera*** (M.P. Christ.) Oberw. *et al*., *Mycol. Progr*. **12**(4): 775. 2013.
*Basionym*: *Ceratobasidium pseudocornigerum* M.P. Christ., *Dansk Bot. Ark*. **19**(no. 2): 46. 1959.
*Synonym*: *Ceratobasidium cornigerum* var. *pseudocornigerum* (M.P. Christ.) Krieglst*., Beitr. Kenntn. Pilze Mitteleurop*. **12**: 36. 1999.

*Type citation*: ‘MPC 251, on *Fraxinus*, Ermelunden, May 22, 1949 (type)’. Roberts (1999) cites ‘M.P. Christiansen 251, C’ as holotype.

***Rhizoctonia queenslandica*** (Y.P. Tan & P. Adhikari) R.P. O’Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 856695.
*Basionym*: *Ceratobasidium queenslandicum* Y.P. Tan & P. Adhikari, *Index of Australian Fungi* **37**: 2. 2024.

*Type citation*: ‘Australia, Queensland, Jimbour, from root lesion of *Saccharum officinarum* (*Poaceae*), 2019, P. Adhikari (holotype BRIP 73024a permanently preserved in a metabolically inactive state).’

*ITS barcode*: PP794648 (T).
*UNITE 1.5 % SH*: n/a.

*Notes*: BLAST searches of the ITS type accession found that *R. queenslandica* is more than 97.8 % identical with some accessions identified as *Ceratobasidium* AG-B(o) as identified by Sharon *et al.* (2008: e.g. GenBank AB219143 at 98.4 %). For this reason, *R. queenslandica* should be considered the epithet associated with this AG group. Note that according to Sharon *et al.* (2008) some isolates originally identified as AG-B(o), for example SIR-2 (ITS sequence GenBank AF354091) as included in Gónzalez *et al.* (2001), belong instead to other AG groups. SIR-2 was placed in AG-A by Gónzalez *et al.* (2016).

***Rhizoctonia ramicola*** W.A. Weber & D.A. Roberts, *Phytopathology* **41**: 618. 1951.
*Synonyms*: *Ceratorhiza ramicola* (W.A. Weber & D.A. Roberts) R.T. Moore, *Mycotaxon* **29**: 94. 1987.
*Ceratobasidium ramicola* C.C. Tu *et al*., *Mycologia* **61**: 781. 1969.

*Type citation*: ‘On living twigs, petioles, and leaf blades of *Elaeagnus pungens,* Thun., Gainesville, Florida, U. S. A. Dried specimen deposited in the University of Florida Agricultural Experiment Station Herbarium, number F-41694.’

*ITS barcode*: DQ278931 (T).
*UNITE 1.5 % SH*: SH0814574.10FU.
*Alternative markers*: *ATP6* = DQ301577; *RPB2* = DQ301708; *TEF1* = DQ301646.

*Ex-type culture*: CBS 133.82.

*Notes*: Roberts (1999) considered *R. ramicola* to be synonymous with a broadly circumscribed *Cb. cornigerum*. No type has been designated for *Cb. cornigerum*; however, it was described from a locality in France from rotting stems of *Helianthus tuberosus.* In contrast, *R. ramicola* was described from living twigs, petioles, and leaf blades of *Pittosporum tobira* and *Elaeagnus pungens* in the United States. The ex-type sequence of *R. ramicola* used in this study is placed in the UNITE database as SH0814574.10FU, and sequences from this species hypothesis occur in the Americas, Indonesia, and several localities in Europe. With this considered, given the distinctions between *R. ramicola* and *Cb. cornigerum* in host plants, the differences in their pathology (leaf blight vs root rot), and the geographical distance between their type localities, it would be prudent at this stage to consider the two as distinct entities and we recognise them here as such with the resurrection of the name *R. ramicola* and the transfer of the name *Cb. cornigerum* to *Rhizoctonia*.

***Rhizoctonia repetospora*** (G. Langer & Ryvarden) R.P. O’Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852076.
*Basionym*: *Tofispora repetospora* G. Langer & Ryvarden, *Biblioth. Mycol.* **158**: 338. 1994.
*Synonym*: *Thanatephorus repetosporus* (G. Langer & Ryvarden) P. Roberts, *Mycotaxon* **69**: 38. 1998, as ‘*repetospora*’.

*Type citation*: ‘Holotypus: Ethiopia, provincia Shoa, Chilomo silva, Ginchu, ca. 2400 alt., leg. L. Ryvarden, 20.9.1992. In herbario O, LR 24060.’ [‘Holotype: Ethiopia, Shoa province, Chilomo forest, Ginchu, ca. 2400 alt., leg. L. Ryvarden, 20.9.1992. In herbarium O, LR 24060.’]. Roberts (1999) cites ‘L. Ryvarden 28060, K(M)’ as an isotype.

***Rhizoctonia rhizodes*** (Auersw.) R.P. O’Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852077.
*Basionym*: *Sclerotium rhizodes* Auersw., *Bot. Zeitung (Berlin)* **7**: 294. 1849.
*Synonym*: *Ceratorhiza rhizodes* (Auersw.) Z.H. Xu *et al.*, *Mycologia* **102**(2): 340. 2010.

*Type citation*: ‘Auf Blättern von *Calagrostis epigeios* schon vor deren Entwicklung.’ [‘On leaves of *Calagrostis epigeios* before their development.’].

*ITS barcode*: MH859145 (R).
*UNITE 1.5 % SH*: SH0987670.10FU.
*Alternative marker*: LSU = MH870857 (R).

*Notes*: No type specimen has been designated for this taxon. Xu *et al.* (2010) used sequences from CBS cultures CBS 321.68, CBS 276.69, and CBS 126.13 identified as *Sclerotium rhizodes* to determine their phylogenetic placement. All three CBS-derived sequences were recovered in a clade closely related to sequences variously identified as *Ceratobasidium* and *Rhizoctonia*. Xu *et al.* (2010) then transferred *S. rhizodes* to *Ceratorhiza* with no neotype designated. The transfer of *S. rhizodes* to *Ceratorhiza* demonstrates that these cultures and sequences represent a contemporary concept of *S. rhizodes/ Cr. rhizodes* and that transfer of this epithet to *Rhizoctonia* is justified based on this understanding. Sequences from CBS 321.68 were selected as representative sequences for our analysis.

***Rhizoctonia robertsii*** R.P. O'Donnell, C.C. Linde & T.W. May, ***nom. nov.*** MB 852078.

*Etymology*: In honour of Dr Peter Roberts who worked extensively on the taxonomy of the *Ceratobasidiaceae* and other rhizoctonia-forming fungi.

*Replaced synonym*: *Ypsilonidium anomalum* P.H.B. Talbot, *New Phytol.* **86**(3): 270. 1980.

*Type citation*: 'Holotypus: Herb. ADW No. 16598, J. H. Warcup (0708) ... Host: *Prasophyllum macrostachyum* R. Br. var. *ringens* (Reichb. f.) A. S. George, near Perth, Western Australia (two isolates).'

*Notes*: Roberts (1999) previously considered this species to be conspecific with *R. bicornis* but considering the specificity of mycorrhizal associations in *Prasophyllum* (Warcup 1981, Burns-Balogh 1984, Freestone *et al.* 2021, 2022, O'Donnell *et al.* 2024) – the orchid genus from which this species was isolated and typified from – and the disjunct distribution of this species and the type of *R. bicornis*, we have chosen to resurrect this species. The name *Ypsilonidium anomalum* was published before *Moniliopsis anomala* However, we have chosen to retain the epithet *anomala* for the latter species (which we here formally transfer to *Rhizoctonia*) in order to retain continuity with the earlier invalid use of the binomial "*Rhizoctonia anomala*" by Burgeff (1936) which was the basis for the introduction of *Moniliopsis anomala* by Currah *et al.* (1990) (see notes for *R. anomala*).

***Rhizoctonia sapphoae*** (Y.P. Tan) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 856696
*Basionym*: *Ceratobasidium sapphoae* Y.P. Tan, *Index of Australian Fungi* **41**: 5. 2024.

*Type citation*: 'Australia, Queensland, Gatton, from stem rot of *Trifolium repens* (*Fabaceae*), 7 Jun. 1996, *J. Mackie* (holotype BRIP 27716a permanently preserved in a metabolically inactive state).'

*ITS barcode.* PQ061108 (T).
*UNITE 1.5 % SH*: n/a.

*Notes*: The ITS sequence from the type of *Rhizoctonia sapphoae* is 96.7 % similar to that of *R. myrtisiae*, which we equate with AG-Fa. No morphological information was provided with the description of *R. sapphoae* and it and *R. myrtisiae* were described on the basis of single collections. The accompanying phylogenetic tree (Tan & Shivas 2024) did not include any other closely related sequences, making it impossible to assess where the cut-off for species delimitation lies in this lineage. We note that the ITS sequence from the type of *R. sapphoae* also has high BLAST matches against sequences identified as AG-F in various studies, as for example the 98–100 % matches against sequences assigned to AG-F by Muzhinji & Lekota (2024: e.g. GenBank MK442087 at 100 %), but specifically against AG-F when treated as a separate but sister clade to Ag-Fa. Combining subgroups of AG-F, Sharon *et al.* (2008), tabulated 90–100 % within group variation, indicating that further species-level taxa are likely to be found among isolates assigned to AG-F. A phylogenetic study of a wide range of isolates assigned to AG-F – including sequences from types of names such as *R. sapphoae* – would be instructive.

***Rhizoctonia sasakii*** (Shirai) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852079.
*Basionym*: *Hypochnus sasakii* Shirai, *Bot. Mag. (Tokyo)* **20**: 319. 1906.
*Synonyms*: *Thanatephorus sasakii* (Shirai) C.C. Tu & Kimbr., *Bot. Gaz*. **139**(4): 457. 1978.
*Aquathanatephorus pendulus* C.C. Tu & Kimbr., *Bot. Gaz.* **139**(4): 459. 1978.
*Thanatephorus pendulus* (C.C. Tu & Kimbr.) Stalpers & T.F. Andersen, *Rhizoctonia Species, Taxonomy, Molecular Biology, Ecology, Pathology and Disease Control* (Dordrecht): 57. 1996.

*Type citation*: '樟苗ノ白絹病菌 (Hypochnus Sasakii n.sp.)' ['Camphorinae white silk disease fungus (*Hypochnus sasakii* n. sp.)'].

*ITS barcode*: AF354060 (R).
UNITE 1.5 % SH: n/a.

*Notes*: Roberts (1999) listed *H. sasakii* and *A. pendulus* under *Thanatephorus cucumeris*. BLAST results show that the ex-type sequence of *Th. pendulus* used in this study (GenBank KP171634) is 99–100 % identical with accessions identified as *Rhizoctonia* AG-1-IA. *Rhizoctonia* AG-1-IA is considered to be *Th. sasakii* (Boidin *et al.* 1998; Roberts 1999; Gónzalez *et al.* 2001). Because the basionym for *Th. sasakii* (*Hypochnus sasakii,* 1906) predates the basionym for *Th. pendulus* (*Aquathanatephorus pendulus*, 1978), the epithet *sasakii* takes priority. A representative sequence for *R. sasakii* was selected from sequences of *Rhizoctonia* AG-1-IA generated by Gónzalez *et al.* (2001).

***Rhizoctonia scaberula*** (Hjortstam & Ryvarden) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852067.
*Basionym*: *Botryohypochnus scaberulus* Hjortstam & Ryvarden, *Mycotaxon* **64**: 230. 1997.
*Synonym*: *Tofispora scaberula* (Hjortstam & Ryvarden) Hjortstam & Ryvarden, *Syn. Fungorum* (Oslo) 23: 93. 2007.

*Type citation*: 'HOLOTYPUS: Colombia, Cundinamarcha, 6.VI.1978, Ryvarden No. 15500 (GB)'.

***Rhizoctonia setariae*** (Sawada) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852080.
*Basionym*: *Hypochnus setariae* Sawada, *Bot. Mag. (Tokyo)* **26**: 191. 1912.
*Synonyms*: *Ceratobasidium setariae* (Sawada) Oniki *et al.*, *Trans. Mycol. Soc. Japan* **27**(2): 153. 1986.
*Sclerotium oryzae-sativae* Sawada, *Trans. Nat. Hist. Soc. Formosa* **9**: 138. 1919.
*Rhizoctonia oryzae-sativae* (Sawada) Mordue, *CMI Descriptions of Pathogenic Fungi and Bacteria* **41**: no. 409. 1974.
*Ceratorhiza oryzae-sativae* (Sawada) R.T. Moore, *Antonie van Leeuwenhoek* **55**(4): 394. 1989.
*Ceratobasidium oryzae-sativae* P.S. Gunnell & R.K. Webster, *Mycologia* **79**(5): 731. 1987.

*Type citation*: 'TYPE: No type was designated and no specimens were available for study. Sawada's illustration of *H. setariae* (1912) is therefore selected as a lectotype.', as designated by Gunnell & Webster (1987). The illustration is on p. (192) and shows basidia, spores, hyphae, and a section of a sclerotium. Note that the volume of *Botanical Magazine, Tokyo* where the protologue appears, volume 26, has two series of pages, one for text in English and one for text in Japanese, with the latter pages given in parentheses.

*ITS barcode*: AF354087 (R).
*UNITE 1.5 % SH*: n/a.
*Alternative marker*: LSU = AF354087 (sequence contains both ITS and LSU regions - R).

*Notes*: A type specimen for *H. setariae* is not extant, and the original illustration by Sawada (1912) was designated as a lectotype by Gunnell & Webster (1987). Roberts (1999) considered *Cb. setariae* as synonymous with *R. oryzae-sativae,* and *R. fumigata.* Roberts' treatment also noted that *Cb. setariae* and *Cr. oryzae-sativae* were considered to represent *Rhizoctonia* AG-Bb, while *R. fumigata* represented *Rhizoctonia* AG-Ba. *Rhizoctonia* AG-Ba and AG-Bb have previously been shown to be genetically distinct entities (Gónzalez *et al.* 2001), and this distinction is supported by the results of this study (Fig. 1). *Rhizoctonia* AG-Ba (*R. fumigata*) and *Rhizoctonia* AG-Bb (*Cb. setariae/Cr. oryzae-sativae*) should therefore be retained as separate taxa. As the epithet *setariae* precedes the publication of the epithet *oryzae-sativae* (1912 vs 1919), the epithet *setariae* takes priority. Sequences identified as *Ceratobasidium* AG-Bb by Gónzalez *et al.* 2001 are selected here as representative sequences.

***Rhizoctonia solani*** J.G. Kühn, *Die Krankheiten der Kulturgewächse, ihre Ursachen und Verbreitung* (Berlin): 224. 1858.
*Synonyms*: *Hypochnus cucumeris* A.B. Frank, *Ber. Deutsch. Bot. Ges.* **1**: 62. 1883.
*Thanatephorus cucumeris* (A.B. Frank) Donk, *Reinwardtia* **3**: 376. 1956.
*Ceratobasidium solani* (Prill. & Delacr.) Pilát, *Česká Mykol*. **11**(2): 81. 1957.
*Moniliopsis solani* (J.G. Kühn) R.T. Moore, *Mycotaxon* **29**: 95. 1987.

*Type citation*: The citation in the protologue is: 'Der von mir beobachtete Pilz ist ein, wie ich glaube, noch nicht beschriebene Gebilde, *Rhizoctonia solani* mihi … Man sieht der Pilz hier auf der Oberflache in Form einzelner, nicht sehr reich verzweigter, aber vielfach oft scharfeckig gebogener, dunkelbraunen Fäden, von Denen man bei verschiedener Einstellung nicht selten deutlich wahrnehmen kann, dass sie an ihren Ausgangspunkte aus der Rinde der Kartoffeln hervorkommen.' ['The fungus which I observed is one, which I believe, whose structures have not yet been described, is named by me *Rhizoctonia solani …* One observes the fungus on the surface in the individual form, not very richly branched, but often many sharply curved, dark brown threads, from which one can clearly observe from different angles, that they emerge from the rind of the potatoes.']. The name is conserved with a conserved type: 'Netherlands, Aug 1995, *Boogaert* ([dried culture ex] CBS No. 739.95 "239.95")' (Typ. cons.).

*ITS barcode*: MH862557 (T).
*UNITE 1.5 % SH*: SH0814567.10FU.

*Ex-type culture*: CBS 739.95.

*Notes*: *Rhizoctonia solani* is considered the asexual morph name of *Th. cucumeris*, and the two names are treated as synonymous (Stalpers *et al.* 2021). Andersen & Stalpers (1994) and Roberts (1999) include many further synonyms under *R. solani*, but this would have been under a morphological concept. Given the few morphological characters available for the asexual morph, all synonyms need to be re-examined in the light of the phylogenetic species delimitation adopted herein. Names which require re-examination of type material to ascertain placement under current phylogenetically-defined species include *R. napae* Westend. & Wallays, [as '*napaeae*'], *R. betae* Eidam., *R. fusca* Rostr., *R. mucoroides* G.E. Bernard, *R. potomacensis* Wollenw., *R. grisea* (J.A. Stev.) Matz, *R. dimorpha* Matz, *R. ferruginea* Matz, *R. macrosclerotia* Matz, *R. melongenae* Matz, *R. gossypii* var. *anatolica* Forsten., *R. gossypii* var. *egyptiaca* Forsten., *R. gossypii* Forsten. var. *gossypii*., *R. aderholdii* (Ruhland) Marchion., *R. chousii* Crand. & Arill., and *Th. corchori* C.C. Tu *et al.*

In their proposal to conserve the names *Rhizoctonia* and *R. solani*, Stalpers *et al.* (1998) cite the CBS culture CBS 239.95 as a proposed conserved type. The culture CBS 239.95 is currently identified as *Amoenomyces catenosporus*. However, the entry for *R. solani* in Appendix III of the Shenzhen Code indicates that the accession number should be corrected to CBS 739.95 (Wiersema *et al*. 2018).

Among the four major AG groups delimited by Boidin *et al.* (1998), the following set were placed under *R. solani* (as *Th. cucumeris*): AG-2, AG-3, AG-5, AG-6, AG-8 and AG-BI. Among these, Andersen & Stalpers (1994) and Roberts (1999) considered that AG-3 is "associated" with the names *R. solani* and *Th. cucumeris*. However, the ITS sequence generated from the conserved type culture for *R. solani* (CBS 739.95; GenBank MH862557) is clustered with sequences of AG-5 in this study (Fig. 3). Indeed, when BLASTed, the majority of close matches for this sequence are identified as AG-5. While Stalpers *et al.* (1998) may have intended to use an isolate of AG-3 to anchor the name *R. solani*, molecular data suggest that they may have instead selected an isolate of AG-5. With this considered, AG-5 should consequently be the AG name associated with the name *R. solani*. Careful examination of the types of the numerous un-assigned names in *Rhizoctonia*, in concert with generation of ex-type or reference sequences, is necessary to match up potential names to as yet un-named AG groups formerly placed under *R. solani* that can be shown to be phylogenetically distinct.

***Rhizoctonia sphaerospora*** (Warcup & P.H.B. Talbot) Oberw. *et al.*, *Mycol. Progr*. **12**(4): 775. 2013.
*Basionym*: *Ceratobasidium sphaerosporum* Warcup & P.H.B. Talbot, *New Phytol.* **70**: 38. 1971.

*Type citation*: 'Typus: Herb. ADW. No. 16219, J.H. Warcup (0122) … Hosts: *Pomatocalpa macphersonii* (F. Muell.) T.E.

Hunt, Coen, N. Queensland (I); *Robiquetia wassellii* Dockr., Coen, N. Queensland (I).' According to Roberts (1999) the type 'cannot now be found'.

*ITS barcode*: DQ278943 (T).
*UNITE 1.5 % SH*: SH1013385.10FU.
*Alternative markers*: *ATP6* = DQ301594 (T); *RPB2* = DQ301725 (T); *TEF1* = DQ301658 (T).

*Ex-type culture*: CBS 571.83.

***Rhizoctonia sterigmatica*** (Bourdot) Oberw. *et al.*, *Mycol. Progr*. **12**(4): 775. 2013.
*Basionym*: *Corticium sterigmaticum* Bourdot, *Rev. Sci. Bourbonnais Centr. France.* **35**(1): 15. 1922.
*Synonyms*: *Ceratobasidium sterigmaticum* (Bourdot) D.P. Rogers, *Stud. Nat. Hist. Iowa Univ.* **17**(1): 7. 1935.
*Thanatephorus sterigmaticus* (Bourdot) P.H.B. Talbot, *Persoonia* **3**(4): 39. 1965.
*Thanatephorus langlei-regis* D.A. Reid, *Trans. Brit. Mycol. Soc.* **52**(1): 22. 1969.

*Type citation*: 'Æstate, ad terram nudam, in sepibus; Saint-Priest-en-Murat.' ['Summer, on bare earth, in hedges; Saint-Priest-en-Murat.']. Roberts (1999) cites "H. Bourdot 17697, PC" as holotype.

*Note*: The synonymy of *Th. langlei-regis* with *Corticium sterigmaticum* follows Roberts (1999).

***Rhizoctonia stridii*** (J. Erikss. & Ryvarden) Oberw. *et al.*, *Mycol. Progr*. **12**(4): 775. 2013.
*Basionym*: *Ceratobasidium stridii* J. Erikss. & Ryvarden, *Corticiaceae of North Europe, 2 Aleurodiscus-Confertobasidium* (Oslo): 227. 1973.

*Type citation*: 'Typus: Å. Strid. 10383 (herb. Strid and herb. Eriksson). Type locality: Sweden, Norrbotten, Råneå parish, Yttre Aborrviken, on bark of fallen *Sorbus aucuparia,* 3.9.1972, Å. Strid.' Roberts (1999) cites 'Å. Strid. 10383, S" as 'holotype', but because duplicates in both herb. Strid and herb. Eriksson were mentioned in the protologue, the type indication by Roberts (1999) should be corrected to a lectotypification, as allowed under Art. 9.10. The database of S (https://herbarium.nrm.se/search/specimens/) gives the accession number of Å. Strid. 10383 as F20002.

***Rhizoctonia terrigena*** (Bres.) Oberw. *et al.*, *Mycol. Progr.* **12**(4): 775. 2013.
*Basionym*: *Corticium terrigenum* Bres., *Ann. Mycol.* **1**(2): 99. 1903.
*Synonyms*: *Ceratobasidium terrigenum* (Bres.) Wakef., *Trans. Brit. Mycol. Soc.* **35**(1): 64. 1952.
*Hydrabasidium terrigenum* (Bres.) Park.-Rhodes, *Trans. Brit. Mycol. Soc.* **37**(4): 325. 1954*, nom. inval*. (Table 3).
*Cejpomyces terrigenus* (Bres.) Svrček & Pouzar, *Česká Mykol*. **24**(1): 6. 1970.
*Thanatephorus terrigenus* (Bres.) G. Langer, *Biblioth. Mycol.* **158**: 324. 1994.

*Type citation*: 'Hab. ad terram, augusto.' ['On soil, August.']. Roberts (1999) cites 'B. Eichler, S' as holotype.

*Notes*: Parker-Rhodes (1954) believed that *R. terrigena* (or *Cb. terrigenum* at the time) was best placed outside of *Ceratobasidium* based on morphological differences from the type of the name *Ceratobasidium*, *Cb. calosporum*. Consequently, Parker-Rhodes attempted to erect the genus *Hydrabasidium* to accommodate this taxon; however, due to a lack of description or diagnosis for this proposed genus name, the name is invalid (Art. 38.1) (Eriksson *et al.* 1978). Thus, the intended combination "*Hydrabasidium terrigenum* (Bres.) Park.-Rhodes" is also invalid (Art. 35.1). Eriksson *et al.* (1978) later validated the name *Hydrabasidium* as *Hydrabasidium* Parker-Rhodes ex Eriks. & Ryv., albeit with *Hypochnus subviolaceus* Peck designated as the type for this name [as *Hydrabasidium subviolaceum* (Peck) Erikss. & Ryv], without mention of *Hydrabasidium terrigenum*. *Hydrabasidium subviolaceum* was transferred to *Scotomyces* by Jülich (1979), making *Hydrabasidium* a synonym of *Scotomyces*. Notably, *Hydrabasidium* and *Scotomyces* share the exact same date of publication, December 28, 1978, and therefore the choice by Jülich (1979) to adopt *Scotomyces* over *Hydrabasidium* establishes the priority of the former name (Art. 11.5.).

***Rhizoctonia theobromae*** (P.H.B. Talbot & Keane) Oberw. *et al.*, *Mycol. Progr.* **12**(4): 775. 2013.
*Basionym*: *Oncobasidium theobromae* P.H.B. Talbot & Keane, *Austral. J. Bot.* **19**: 203. 1971.
*Synonyms*: *Thanatephorus theobromae* (P.H.B. Talbot & Keane) P. Roberts, *Rhizoctonia-Forming Fungi* (Richmond): 101. 1999.
*Ceratobasidium theobromae* (P.H.B. Talbot & Keane) Samuels & Keane, *Fungal Biol.* **116**(1): 19. 2012.

*Type citation*: 'Holotype. – Herb. ADW 16221, P. J. Keane, on *Theobroma cacao*, Keravat, New Guinea.'

*ITS barcode*: HQ424253 (R).
*UNITE 1.5 % SH:* SH1006168.10FU.

*Notes*: The ITS and LSU sequences identified as *Cb. theobromae* from pure cultures generated by Samuels **et al.** (2012) (including Keane – one of the authors of the basionym *Oncobasidium theobromae*) were selected as representative sequences for our analyses.

***Rhizoctonia tradescantiae*** (D.M. Macedo *et al.*) R.P. O'Donnell, C.C. Linde & T.W. May, ***comb. nov.*** MB 852081.
*Basionym*: *Ceratobasidium tradescantiae* D.M. Macedo *et al.*, *Australas. Pl. Pathol.* **45**(1): 49. 2016.

*Type citation*: 'BRAZIL: Rio Grande do Sul, Vale dos Vinhedos – entrance of Santa Tereza, living leaves of *Tradescantia fluminensis* Vell, 23 Apr. 2004, O. L. Pereira, HOLOTYPE: VIC 31342'.

## DISCUSSION

### Genera of the *Ceratobasidiaceae* are paraphyletic

In this study, we inferred phylogenies using multi-gene sequence data for almost 75 % of accepted species of

*Ceratobasidiaceae* (38 out of 52), along with two additional named taxa identified as synonyms here, and one taxon with a name identified as a nomen dubium. Additional ITS-only analyses that included either the 559 UNITE *Ceratobasidiaceae* species hypotheses or the sequences from un-named AGs and orchid-derived OTUs demonstrate that the taxon sampling, as far as the named taxa are concerned, is scattered throughout the larger groups of *Ceratobasidiaceae* sequences. Hence, we are not missing significant diverse lineages in the analysis of named species upon which the taxonomic conclusions are being made.

The results of this study reinforce what has been repeatedly demonstrated over the past two decades – *Rhizoctonia*, *Thanatephorus*, *Ceratobasidium*, and *Ceratorhiza* are paraphyletic (Gónzalez *et al.* 2001, González *et al.* 2002, Otero *et al.* 2004, 2011, Taylor & McCormick 2008, Bougoure *et al.* 2009, Shefferson *et al.* 2010, Xu *et al.* 2010, Mosquera-Espinosa *et al.* 2013, Oberwinkler *et al.* 2013, Diederich *et al.* 2014, Gónzalez *et al.* 2016, Blanco *et al.* 2018, de Melo *et al.* 2018, Ferreira *et al.* 2021, Freestone *et al.* 2021, Cruz *et al.* 2022). As these data and our analyses indicate that these genera are not monophyletic and instead represent a single lineage that cannot be split into evolutionarily meaningful components (on current information), there is no case to support their continued recognition. Recognition of a single genus was accepted by Stalpers *et al.* (2021), with *Rhizoctonia* being the earliest recognised name. Stalpers *et al.* (2021) discussed the synonymy of *Rhizoctonia* and *Thanatephorus*; however, no mention was made of *Ceratobasidium* or *Ceratorhiza*, which has no doubt contributed to the continued but inappropriate use of these latter names.

## Problems with the name *Ceratobasidium*

Doubt has surrounded the genus name *Ceratobasidium* since the mid-20th Century, when Parker-Rhodes (1954) noted (p. 315): "The genus *Ceratobasidium* Rogers was regrettably founded on *Cb. calosporum* Rog. as type, and this appears to be only a form of *Prototremella calospora* Boud. with aseptate basidia, the name *Ceratobasidium* cannot stand, though it is certainly a good genus." Re-examination by Oberwinkler *et al.* (1982, 2013) of the holotype of *Cb. calosporum* (i.e. the type of the genus name *Ceratobasidium*) revealed morphological incongruencies which distinguish it from all other species within the *Ceratobasidiaceae. Ceratobasidium calosporum* is characterised by dolipores with continuous/imperforate parenthesomes, partially to completely longitudinally septate basidia [although the presence of septate basidia was not noted by Parker-Rhodes (1954) and Roberts (1999)], and long vermiform basidiospores. Contrastingly, all other described species within the *Ceratobasidiaceae* share dolipores with discontinuous/perforate parenthesomes, non-septate basidia, and globose to ellipsoid basidiospores (Roberts 1999; Oberwinkler *et al.* 2013). Based on this combination of morphological characters, Chen *et al.* (2002) proposed that *Cb. calosporum* is best placed within the *Auriculariales*. Oberwinkler *et al.* (2013), however, believed that *Cb. calosporum* likely belonged in the *Sebacinales,* within *Sebacinaceae* on the basis of morphological similarities with *Sebacina calospora* (= *Exidiopsis calospora*).

The placement of *Cb. calosporum* is currently uncertain as sequence data has to date not been recovered from the holotype, which was originally collected in 1932 (Rogers 1935). Roberts (1999) produced an early molecular phylogeny of the *Ceratobasidiaceae* using ITS sequences which purportedly included sequence data for *Cb. calosporum* which placed it close to other members of the *Ceratobasidiaceae*. These sequence data were not deposited in any public repository, and were later found to be a misidentified/mislabelled sequence (P. Roberts, pers. comm. 2023). Based on the age and paucity of remaining type material for *Cb. calosporum* (KM 35733, isotype, as examined by us), it is unlikely that reliable, non-contaminated DNA will be able to be extracted from this material using available technology. While sequence data for *Cb. calosporum* is not currently available, it is clear from morphology alone that this taxon is best placed outside of the *Ceratobasidiaceae*.

As *Cb. calosporum* – the type of the name *Ceratobasidium*, which is the type of the name *Ceratobasidiaceae* – does not fall within *Rhizoctonia* s. s., the correct family name for the *Ceratobasidiaceae* as currently understood should technically be *Cejpomycetaceae* Jülich (1982). *Cejpomycetaceae* was created to accommodate the genus *Cejpomyces* Svrček & Pouzar (1970), later synonymised with *Rhizoctonia* (Langer 1994, Roberts 1999, Oberwinkler *et al.* 2013). The name *Cejpomycetaceae;* however, is scarcely known or used – a Google Scholar search for *Cejpomycetaceae* retrieved only two hits compared to more than 5000 for *Ceratobasidiaceae*. Moreover, with acceptance of the placement of *Cb. calosporum* within *Sebacinaceae* (Begerow *et al.* 2018), the correct name for *Sebacinaceae* should technically be *Ceratobasidiaceae*, as the name *Ceratobasidiaceae* predates the name *Sebacinaceae* (1948 vs 1982).

Replacing the widely-used family name *Sebacinaceae* with *Ceratobasidiaceae* – a family name that has until now been used to refer to what is now technically *Cejpomycetaceae* – would be a highly confusing and disadvantageous nomenclatural change. To avoid replacement of the name *Sebacinaceae*, and to retain the use of the name *Ceratobasidiaceae* for species currently described within it, a formal proposal to conserve *Ceratobasidium* with a conserved type will be submitted separately. *Ceratobasidium sphaerosporum* (now *R. sphaerospora*) would be an appropriate conserved type for *Ceratobasidium*, as there is an ex-type sequence available that confirms its position inside *Rhizoctonia* s. s. (Fig. 1). *Ceratobasidium calosporum* will need to be placed in another genus, should a proposal to conserve *Ceratobasidium* with *Cb. sphaerosporum* as the type be successful. We advocate continued use of the name *Ceratobasidiaceae* (exclusive of *Cb. calosporum*) as the most nomenclaturally stable approach, pending assessment of the future conservation proposal.

## Characters previously used to delimit genera in the *Ceratobasidiaceae* are unsupported by genetic data

Cytological, morphological, and ecological characters that have previously been used to delimit generic boundaries in the *Ceratobasidiaceae* assemblage do not appear to hold up to scrutiny. Given that many species now placed in the broadly circumscribed *Rhizoctonia* are not known to produce sexual spores, the basidial characters are of limited value in defining groupings, and in any case, species formerly assigned to *Ceratobasidium* or *Thanatephorus* are scattered throughout the phylogeny of *Rhizoctonia*. The morphological variation now encompassed by *Rhizoctonia* is no more than shown by other genera of Agaricomycetes, once a molecular phylogenetic delimitation is applied. Large variations in sporophore form are now well-known, such as between resupinate and coralloid, as in *Trechispora* inclusive of *Scytinopogon* (Liu *et al.* 2022). Most species of *Rhizoctonia* have smooth spores (when present) but there are also a few species with ornamented spores (formerly placed in *Tofispora*), although sequence data are so far lacking from this group. *Coprinopsis* is one example of a genus of mostly smooth-spored species with occasional species with ornamented spores, whose generic placement is confirmed by molecular phylogenetic analysis (Gierczyk *et al.* 2017).

Regarding cytology, *Rhizoctonia* was distinguished by a uninucleate state (vs binucleate *Ceratobasidium* and multinucleate *Thanatephorus*); although as Roberts (1999) notes, this character is highly variable. Flentje *et al.* (1963) and Julian *et al.* (1997) observed a wide range of variation with respect to the number of nuclei found per cell across isolates of *Rhizoctonia*, *Thanatephorus* and *Ceratobasidium*. While a binucleate state was apparently characteristic of *Ceratobasidium*, Flentje *et al.* (1963) noted that isolates of *Thanatephorus* were occasionally binucleate. Julian *et al.* (1997) observed multinucleate vegetative hyphal cells in *R. solani* which later became binucleate, along with binucleate cells in isolates of *Th. cucumeris*. Using molecular data, Hietala *et al.* (2001) later found uninucleate isolates of *Rhizoctonia* to be conspecific with binucleate isolates identified as *Ceratobasidium*. Molecular phylogenies estimated by Gónzalez *et al.* (2001) and Veldre *et al.* (2013) similarly found binucleate isolates clustered with multinucleate isolates. These results highlight that cytological states are a poor character upon which to base generic limits in the *Ceratobasidiaceae.*

Ecological characters such as trophic modes in *Ceratobasidiaceae* similarly do not appear to serve as an accurate means of generic distinction. Previous phylogenetic studies of the *Ceratobasidiaceae* have found that symbiotic mycorrhizal or saprotrophic species of *Ceratobasidiaceae* are closely related (or in some cases sister) to pathogenic species (Mosquera-Espinosa *et al.* 2013, Veldre *et al.* 2013, Freestone *et al.* 2021). Orchid mycorrhizal taxa of *Ceratobasidiaceae* were interspersed with pathogenic taxa in phylogenetic analyses in this study (Fig. 3), agreeing with previous work. Diederich *et al.* (2014) identified and described a lichenicolous species of *Ceratobasidiaceae* (*Cb. bulbillifaciens* treated here as *R. bulbillifaciens*), which was here recovered as closely related to orchid mycorrhizal OTUs. It is unclear at this stage whether the lack of clear phylogenetic structure with respect to trophic modes in *Ceratobasidiaceae* indicates that fungi within this family are facultatively symbiotic/pathogenic, or whether several trophic mode shifts have occurred over the course of the family's evolutionary history (Mosquera-Espinosa *et al.* 2013, Veldre *et al.* 2013, Freestone *et al.* 2021). Indeed, as several lineages within *Ceratobasidiaceae* appear to have the capacity to be both mycorrhizal and pathogenic (Fig. 3), it is possible that the ecological niches of other lineages within this family have been underestimated, as has been demonstrated in other fungal groups (Selosse *et al.* 2018). Future studies of the family would benefit from close examination of trophic mode shifts between closely related pathogenic and symbiotic species in parallel with examination of genome-wide data to detect signals of trophic mode.

## *Rhizoctonia* anastomosis groups (AGs) are distinct lineages that require species-level recognition

Species delimitation in the *Ceratobasidiaceae* to date has principally relied on the criterion of the 'anastomosis group' i.e. the ability of hyphae from conspecific isolates to recognise and fuse with one another ('anastomose'), independent of their capacity to mate (Burpee *et al.* 1980, Ogoshi *et al.* 1983, Roberts 1999, Gónzalez *et al.* 2016). In addition to anastomosis as a core criterion, additional criteria such as host association, nuclear condition (i.e. uninucleate vs binucleate vs multinucleate), or biochemistry have also been used to characterise these groups (Gónzalez *et al.* 2016). At least 16 AG designations are currently in use, although several more have been identified and characterised across *Rhizoctonia*, *Thanatephorus*, *Ceratobasidium*, and *Ceratorhiza* (Sharon *et al.* 2008). Andersen & Stalpers (1994) and Roberts (1999) treated the majority of AGs under a broad concept of *R. solani* on the basis of morphological characteristics. However, molecular phylogenetic analyses in recent decades have shown that most AGs do indeed represent monophyletic groups representing genetically and evolutionarily distinct lineages that warrant species-level recognition (Boidin *et al.* 1998, Gónzalez *et al.* 2001, Pope & Carter 2001, González *et al.* 2006, Sharon *et al.* 2006, 2008, Veldre *et al.* 2013, Gónzalez *et al.* 2016, Francis *et al.* 2023). While in this study we have been able to match a number of AGs to named taxa (AG-Ba = *R. fumigata*; AG-Bb = *R. setariae*; AG-B(o) = *R. queenslandica*; AG-Fa = *R. myrtisiae*; AG-1-IA = *R. sasakii*; AG-1-IB = *R. microsclerotia*; AG-4 = *R. praticola;* AG-5 = *R. solani*), there are still numerous AGs that lack a formal name. It is possible that some of the numerous names introduced in *Rhizoctonia* currently lumped as *R. solani* under a broad morphological concept are potential names for unnamed AGs, but careful typification and designation of ex-type or reference sequences will be required before associating such names with AG groups. Alternatively, given the difficulty of effectively typifying names often introduced with minimal information, AGs that lack formal names could be newly named, and the set of species in the genus that has names connected to reference sequences could be proposed for protection under Art. F.2.1 (May *et al.* 2019). This would confer protection against un-listed synonyms, preventing the accepted names being overturned by long-overlooked prior names, should they turn out to be synonyms.

## There is much un-named diversity within *Ceratobasidiaceae*

Many published phylogenies include only named taxa and ignore un-named sequences. Of course, inclusion of sequences from the types of named species are essential for any taxonomic study. However, there is value in hyper-diverse lineages in integrating UNITE SHs and as wide a sample of un-named sequences as possible, in order to reveal the true scale of species-level diversity and to delimit the range of variation within species.

In this study, the inclusion of the UNITE SHs provides a salutary perspective on the prospects for a complete formal inventory of species in *Ceratobasidiaceae*. If the 1.5 % level of the UNITE SHs approximates species, upwards of 500 species remain to be formally named, based on existing sequences. For example, in the lineage that contains *R. pennata*, *R. praticola*, *R. praxillae,* and *R. solani*, there are dozens of un-named UNITE SH at the 1.5 % level interspersed between the named species (Fig. 2). Some of these putative species are already represented by specimens or cultures, such as the sources of the ca 150 unnamed orchid derived OTUs and unnamed AGs. However, many of the unnamed UNITE SHs are known only from soil samples.

The primary purpose of our analysis was to delimit generic level-lineages in *Ceratobasidiaceae*. Further analyses are required to accurately delimit the species of *Rhizoctonia*. The UNITE general FASTA release, which incorporates dynamic lineage-specific thresholds appears to utilise a 1.5 % threshold for all SH within the *Ceratobasidiaceae*. Certainly, a 3 % threshold is too high as it lumps together well-established species, such as for the case of *R. pennata*, *R. praticola* and *R. solani*, where the reference sequence of each (as chosen by us) fall into separate SH at 1.5 % but at 3 % fall within the one large SH (SH0052871.10FU) containing almost 6000 sequences. However, the exact threshold for species delimitation needs to be confirmed. For accurate species delimitation, confirmation of the effectiveness of ITS (or alternative regions) as species-level barcodes is an essential first step, which requires analyses of multi-gene or genome-wide data for densely sampled lineages that contain sister taxa (Linde *et al.* 2014, Stefani *et al.* 2014, Widhelm *et al.* 2023). Such analyses will then assist to set the tolerances for within and between species divergence and the appropriate threshold for SHs, if indeed a single threshold is appropriate across the whole family. Future reliance on ITS alone for species delimitation in the genus must be based on rigorous confirmation of this region as an appropriate barcode.

There are already many thousands of ITS sequences available for the family and some individual 1.5 % UNITE SHs within *Ceratobasidiaceae* have hundreds, or in some cases more than a thousand, sequences assigned to them (Table 6), many of which are environmental sequences from soil or plant roots, rather than specimens. There is no indication that UNITE *Ceratobasidiaceae* SHs known only from soil or plant roots are unculturable. Hence, the family is suitable as a testing ground for the development of novel methodologies for robot-assisted selection of cultures associated with large scale sequencing as a means of screening for novel taxa. Robotic handling for imaging and sequencing, integrating machine-learning, is already being developed for invertebrates in an effort to create step change in the rate of species description (Wührl *et al.* 2021).

UNITE SHs are useful as indications of un-named diversity but also for linking environmental sequences to named species. The representative sequences we chose, such as on the basis of coming from ex-type cultures, were not necessarily the same sequences already chosen as “representative sequences” for UNITE SHs. In addition, some UNITE SHs were not yet labelled with appropriate species names (even when they contained sequences from types). As a follow on to this study, we will annotate the UNITE SH names and representative sequences to as far as possible align with the taxonomy presented herein. Annotation of UNITE SHs for recently described species will be carried out once the next release of UNITE is available.

## Use of different generic names impacts how we frame our research

Our examination of how various generic names within the *Ceratobasidiaceae* are represented in the literature (Fig. 5) revealed that *Rhizoctonia* is the dominant name in use, followed by *Thanatephorus*, *Ceratobasidium*, and *Ceratorhiza* in that order. Unsurprisingly, our results show that the number of studies mentioning two or more alternate generic names diminishes sharply as more search terms are added. Moreover, our search also revealed significant differences in how certain generic names are used between orchid mycorrhizal literature and pathogen literature. While *Rhizoctonia* is still the dominant name cited in orchid mycorrhizal research, the use of the names *Thanatephorus*, *Ceratobasidium* and *Ceratorhiza* is more evenly spread compared to the pathogen literature. Additionally, use of the name *Ceratobasidium* is proportionally higher in the orchid mycorrhizal literature than use of the name *Thanatephorus.* In contrast, the name *Thanatephorus* is used more widely across the pathogen literature, while the name *Ceratorhiza* is scarcely used. In short, *Rhizoctonia* and *Thanatephorus* are the dominant terms used across the collected pathogen and orchid mycorrhizal literature; however, the terms *Ceratobasidium* and *Ceratorhiza* are used more frequently in the orchid mycorrhizal literature than they are in the pathogen literature. Out of more than 40000 papers mentioning *Rhizoctonia*, only 20 of these mention the terms ‘orchid’ and ‘pathogen’ together. From our results, it is evident that much scientific literature is potentially being overlooked when mycologists with different interests focus on one or other generic name as a result of the continuing legacy of fungal dual nomenclatural systems.

As the *Ceratobasidiaceae* encompasses taxa displaying a variety of trophic modes ranging from saprotrophy, to symbiosis, to pathogenicity (Mosquera-Espinosa *et al.* 2013, Veldre *et al.* 2013, Freestone *et al.* 2021), the family presents an ideal system through which the evolution of plant-fungal host interactions can be studied comparatively. However, it is evident from our results that the fields of orchid mycorrhizal research and plant pathogen research appear to be operating in silos. Transcriptomic and proteomic studies interrogating the molecular mechanisms mediating the orchid-mycorrhizal interface have identified several upregulated plant immune response genes that are believed to be somehow implicated in this interaction (Valadares *et al.* 2014, Zhao *et al.* 2014, Chen *et al.* 2017). On this basis, there are likely to be commonalities between symbiotic and pathogenic plant-fungal interactions. It is clear that in order to deepen our understanding of both symbiotic and pathogenic relationships, we must consider both interactions simultaneously. By considering the various genera of the *Ceratobasidiaceae* as a unified *Rhizoctonia*, it will be possible to gain a more holistic understanding of the mechanisms involved in governing plant-fungal interactions and trophic mode shifts, and their evolution.

### Conclusions

In this study we aimed to build on the work of Oberwinkler *et al.* (2013), by unifying the various generic names of the *Ceratobasidiaceae* under an expanded *Rhizoctonia*. Using publicly available ex-type and representative taxon sequences we recovered a phylogeny which once again showed that *Rhizoctonia*, *Thanatephorus*, *Ceratobasidium*, and *Ceratorhiza* are a paraphyletic assemblage comprising in total a single well-supported clade that should be known as *Rhizoctonia*. We transferred to *Rhizoctonia* several species formerly placed in generic synonyms of *Rhizoctonia* and in *Ceratobasidium*, and stress that use of the name *Ceratobasidium* is not recommended. Furthermore, using literature database searches, we demonstrated that there are distinct differences between research fields with respect to how they engage with various generic names used up until now within the *Ceratobasidiaceae*. The continued use of names that are evidently synonyms potentially blinds us to large sections of the scientific literature, and precludes a holistic understanding of the organisms that we study.

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### DATA AVAILABILITY STATEMENT

Sequence alignments used for phylogenetic analyses along with raw output trees with support values and branch lengths are available on Zenodo at doi.org/10.5281/zenodo.15043254.

**Declaration on conflict of interest:** The authors declare that there is no conflict of interest.

## INDEX

This index includes all species described in *Rhizoctonia* (*R.*) and its generic synonyms, i.e. *Aquathanatephorus* (*A.*), *Cejpomyces* (*Cj.*), *Ceratobasidium* (*Cb.*), *Ceratorhiza* (*Cr.*), *Koleroga* (*K.*), *Moniliopsis* (*M.*), *Oncobasidium* (*O.*), *Thanatephorus* (*Th.*), *Tofispora* (*To.*), *Uthatobasidium* (*U.*) and *Ypsilonidium* (*Y.*). Accepted names in **bold**. Spelling of epithets is according to the form in the genus of the accepted name. Most names indicated below as synonyms of *R. solani* are not accepted herein; see discussion under *R. solani*.

*aderholdii, R.* = *R. solani*
*aerea, R.* = nom. dub.
*alba, R.* = nom. dub.
*albasitensis, Cb.* = *R. klebahnii*
*album, Cb.* = nom. dub.
*allii, R.* = *Helicobasidium purpureum*
*alpina, R.* = nom. inval.
***amygdalispora, R.***, *Th.*
*anacalospora, Cr.* = *Cb. calosporum*
*anaticula, R.* = *Tulasnella anaticula*
***anceps, R.***, *Cb., Corticium, Th., Tulasnella*
***angustispora, R.***, *Cb.*
***anomala, R.***, *M.*
*anomalus, Th.* = nom. inval.
*apocynacearum, R.* = nom. inval.
*arachnion, R.* = nom. dub.
*asclerotica, R.* = nom. inval.
*asparagi, R.* = nom. inval.
*asparagi, R.* = *Helicobasidium purpureum*
*atratum, Cb.* = *Scotomyces subviolaceus*
*aurantiaca, R.* = nom. dub.
***australiensis, R.***, *Cb.*
*bananisporum, Y.* = nom. dub.
*batatas, R.* = nom. dub.
*bataticola, R.* = *Macrophomina phaseolina*
*betae, R.* = *R. solani*
***biapiculata, R.***, *Pellicularia, To., Th.*
*bicolor, R.* = nom. inval.
***bicornis, R.***, *Cb.*
*borealis, R.* = nom. inval.
*brassicarum, R.* = nom. dub.
***brevispora, R.***, *Th.*
***bulbillifaciens, R.***, *Cb.*
***butinii, R.***
***calosporum, Cb.***
*callae, R.* = nom. inval.
*candida, R.* = nom. inval.
*carnea, R.* = nom. dub.
*carotae, R.* = *Athelia arachnoidea*
*cavendishiana, R.* = nom. inval.
*centrifuga, R.* = *Athelia epiphylla*
*cerealis, R.* = nom. inval.
***chavesiana, R.***, *Cb.*
*chousii, R.* = *R. solani*
*citriforme, U.* = *Sistotrema citriforme*
*coniothecioides, R.* = nom. dub.
*corchori, Th.* = *R. solani*
***cornigera, R.***, *Corticium, Cb.*
*crocorum, R.* = *Helicobasidium purpureum*
*cucumeris, Hypochnus, Th.* = *R. solani*
*dauci, R.* = nom. inval.
*decidua, Cr., Sclerotium* = *R. anceps*
*destruens, R.* = nom. dub.
*dichotoma, R.* = nom. inval.
*dimorpha, R.* = *R. solani*
*endophytica, R.* = nom. inval.
*endophytica, R.* = nom. inval.
***erinnae, R.***, *Cb.*
*ferruginea, R.* = *R. solani*
*fibrillosum, Cb.* = *Oliveonia fibrillosa*
*fibulatum, Cb.* = nom. inval.
*filamentosum, Cb.* = nom. inval.
*flavecens, Cb.* = nom. inval.
***floccosa, R.***
*foliicola, M.* = nom. dub.
*fragariae, Cb., Cr., R.* = nom. inval.

*fragariae, R.* = nom. inval.
*fraxini, R.* = nom. inval.
*fuliginea, R.* = nom. dub.
***fumigata, R.***, *Sclerotium*
*fusca, R.* = *R. solani*
***fusispora, R.***, *Corticium, Hypochnus, Peniophora, Th., U.*
***gardneri, R.***, *Th.*
***globispora, R.***, *Cb.*
*globosisporus, Cj.* = *Botryobasidium globisporum*
*globularis, R.* = nom. inval.
***gomesae, R.***, *Cb.*
*goodyerae-repentis, Cr., R.* = nom. dub.
*gossypii* var. *anatolica, R.* = *R. solani*
*gossypii* var. *egyptiaca, R.* = *R. solani*
*gossypii* var. *gossypii, R.* = *R. solani*
*gossypinum, R.* = nom. inval.
*gracilis, R.* = nom. inval.
*gramineum, Cb., Corticium* = nom. dub.
*grisea, R.* = *R. solani*
***hebelomatospora, R.***, *Botryohypochnus, Th., To.*
*hiemalis, R.* = nom. inval.
*himantia, R.* = nom. dub.
***hydrophila, R.***, *Cr., Sclerotium*
*incrustans, Cb.* = nom. inval.
*juniperi, R.* = nom. inval.
***klebahnii, R.***, *M.*
***korinnae, R.***, *Cb.*
*lamellifera, R.* = *Macrophomina phaseolina*
*langlei-regis, Th.* = *R. sterigmatica*
***lantanae-camarae, R.***, *Cb.*
*lanuginosa, R.* = nom. dub.
*leguminicola, R.* = *Slafractonia leguminicola*
*lilacina, R.* = nom. dub.
*lupini, R.* = nom. inval.
*macrosclerotia, R.* = *R. solani*
*mali, R.* = nom. dub.
*medicaginis, R.* = *Helicobasidium purpureum*
*melongenae, R.* = *R. solani*
*menthae, R.* = *Puccinia menthae*
***microsclerotia, R.***, *Th.*
*moniliformis, R.* = nom. dub.
*monilioides, R.* = nom. inval.
*monteithiana, R.* = nom. inval.
*mucoroides, R.* = *R. solani*
*muneratii, R.* = nom. inval.
*muscorum, R.* = nom. dub.
*mycophagum, Cb.* = *Syzygospora mycophaga*
***myrtisiae, R.***, *Cb.*
*nandorii, R.* = nom. inval.
*napae, R.* = *R. solani*
*neottiae, R.* = nom. inval.
***niltonsouzana, R.***, *Cb.*
***noxia, R.***, *Cb., K.*
***obscura, R.***, *Cb., Th.*
***ochracea, R.***, *Coniophora, Th., U.*
*ochroleucum, Cb.* = nom. dub.
*orchidicola, Th.* = *R. ochracea*
*orobanches, R.* = *Urocystis orobanches*
*oryzae, M.* = *Waitea circinata*
*oryzae, R.* = nom. inval.
*oryzae-sativae, Cr., Cb., R., Sclerotium* = *R. setariae*
*ovalisporus, Th.* = *R. bicornis*
*pallida, R.* = nom. dub.
*papayae, R.* = nom. inval.
***papillata, R.***, *Cb.*
*pendulus, A., Th.* = *R. sasakii*
*pearsonii, Cb.* = *Paullicorticium pearsonii*
***pennata, R.***, *Th.*
***pernacatena, R.***, *Cr.*
*pini-insignis, R.* = nom. inval.
*placenta, R.* = nom. dub.
*plumbeum, Cb.* = *Scotomyces subviolaceus*
*potomacensis, R.* = *R. solani*
***praticola, R.***, *Cb., Corticium, Th.*
***praxillae, R.***, *Cb.*
***pseudocornigera, R.***, *Cb.*
*psycodis, R.* = nom. inval.
***queenslandica, R.***, *Cb.*
*quercina, R.* = *Rosellinia quercina*
*quercus, R.* = nom. inval.
*radiciformis, R.* = nom. dub.
***ramicola, R.***, *Cb., Cr.*
*rapae, R.* = nom. inval.
*repens, R.* = *Tulasnella deliquescens*
***repetospora, R.***, *Th., To.*
***rhizodes, R.***, *Cr., Sclerotium*
*rigida, M.* = nom. dub.
***robertsii, R.***
*robusta, R.* = nom. inval.
*rubi, R.* = nom. inval.
*rubiae, R.* = *Helicobasidium purpureum*
*rubiginosa, R.* = nom. dub.
***sapphoae, R.***, *Cb.*
***sasakii, R.***, *Hypochnus, Th.*
***scaberula, R.***, *Botryohypochnus, To.*
*sclerotica, R.* = nom. inval.
***setariae, R.***, *Cb., Hypochnus,*
*silvestris, R.* = nom. dub.
***solani, R.***, *Cb., M.*
*solani f. paroketea, R.* = *Agroathelia rolfsii*
*solani* var. *ambigua, R.* = nom. dub.
*solani* var. *brassicae, R.* = nom. inval.
*solani* var. *cedri-deodarae, R.* = nom. inval.
*solani* var. *cichorii-endiviae, R.* = nom. inval.
*solani* var. *fuchsiae, R.* = nom. inval.
*solani* var. *graminis, R.* = nom. inval.
*solani* var. *hortensis, R.* = nom. inval.
*solani* var. *lycopersicae, R.* = nom. inval.
*solani* var. *typica, R.* = nom. inval.
*sphacelati, R.* = nom. inval.
***sphaerospora, R.***, *Cb.*
*stahlii, R.* = nom. inval.
***sterigmatica, R.***, *Cb., Corticium, Th.*
*stevensii, Cb.* = nom. inval.
***stridii, R.***, *Cb.*
*striisporum, Cb.* = *Xenasma pulverulentum*
*strobi, R.* = nom. dub.
*strobilina, R.* = nom. dub.
*suavis, R.* = nom. inval.
*subatratum, Cb.* = *Scotomyces subviolaceus*
*subepigaea, R.* = nom. dub.
*subtilis, R.* = nom. inval.
*subtilis, R.* = nom. inval.

*tabifica, R. = Colletotrichum coccodes*
***terrigena, R.**, Cb., Cj., Corticium, Hydrabasidium, Th.*
***theobromae, R.**, Cb., O., Th.*
*tomato, R.* = nom. inval.
***tradescantiae, R.**, Cb.*
*tricolor, R.* = nom. inval.
*vagum, Cb. = Botryobasidium vagum*
*versicolor, R.* = nom. inval.
*zeae, M., R. = Waitea zeae*

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## Supplementary material

**Fig. S1.** Phylogram of accessions identified as *Sclerotium hydrophilum* and their placement with named taxa within *Ceratobasidiaceae* inferred from ITS sequence data using IQ-TREE 2. SH-aLRT and UFBoot support values are presented as node labels. The epitype sequence for *Ceratorhiza hydrophila/Rhizoctonia hydrophila* is highlighted with bold text.

**Table S1.** UNITE species hypotheses (SHs) identified as "*Ceratobasidiaceae*" sourced from the UNITE general FASTA release for Fungi v.10.0.

**Table S2.** Misclassified UNITE SHs excluded from phylogenetic analyses.

**Table S3.** GenBank ITS accessions of representative orchid mycorrhizal OTUs and pathogenic AGs used in phylogenetic analyses.

**Table S4.** GenBank ITS accessions identified as *Ceratorhiza hydrophila/Sclerotium hydrophilum* used to generate Supporting Information Fig. S1.