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Phylogenetic origins and family classification of typhuloid fungi, with emphasis on *Ceratellopsis, Macrotyphula* and *Typhula* (Basidiomycota)

I. Olariaga, S. Huhtinen, T. Læssøe, J.H. Petersen, and K. Hansen

INTRODUCTION

Clavarioid fungi have club- or coral-shaped basidiomata with the hymenium fully exposed and include at least 540 species (Corner 1950, Kirk et al. 2008). Phylogenetic studies have demonstrated that clavarioid basidiomata have arisen multiple times from ancestors with agaricoid or corticioid basidiomata in several lineages of Basidiomycota (Pine et al. 1999, Dentinger & McLaughlin 2006), but molecular phylogenies of clavarioid fungi and allied taxa are far from being complete. Clavarioid lineages are known to have evolved in the Agaricales, Cantharellales, Gomphales, Hymenochaetales, Russulales, Thelephorales and Trechisporales among the Agaricomycetes (Pine et al. 1999, Hibbett & Binder 2002, Hibbett 2004, Dentinger & McLaughlin 2006, Birkebak et al. 2013), but fully supported multigene phylogenies are lacking in most cases and details as to how transitions to a clavarioid basidioma type have occurred are vague. A more comprehensive taxon sampling and addition of more molecular markers is still needed in many groups, including clavarioid fungi, to better understand the evolution of basidioma configuration.

In this study, we target a group of clavarioid fungi with tiny basidiomata (Fig. 1A–K), here referred to as “typhuloid” following e.g. Corner (1950), Petersen (1974), Petersen et al. (2014), and Olariaga et al. (2016). Corner (1950: 145) characterised typhuloid fungi by: i) small basidiomata and limited growth, ii) distinct stipe and fertile head, iii) simple hymenium, iv) epiphyllic habitat on wood, stems or leaves, rather than being tericolous, v) smooth, white ellipsoid spores, vi) monomitic, generally clamped hyphae, and vii) agglutination of the hyphae on the surface of the stem. Three genera were regarded as typhuloid, *Typhula, Phyllotopsis* and *Pterula* with a dimitic hyphal system and from *Ceratellopsis* with highly reduced
clavarioid basidiomata with generally sterile apices. Berthier (1976), in his monograph "Typhula and allied genera", treated typhuloid fungi in a broader sense and considered Ceratellopsis, Macrotyphula, Pterula and Typhula to represent a natural group without proposing any family classification. Hirticlavula elegans, a member of Clavariaceae producing minute, hairy basidiomata, has also been considered somewhat typhuloid (Petersen et al. 2014), and limits between typhuloid fungi and other reduced clavarioid fungi are not always clear. Typhuloid fungi represent one of the most overlooked, poorly known and enigmatic groups of homobasidiomycetes. The family classification of these fungi is uncertain or based on weakly supported phylogenies with a very limited taxon sampling. Macrotyphula and Typhula were previously placed in Clavariadellaceae (Corner 1970, Hawksworth et al. 1995), but recent classifications place both genera in Typhulaceae together with Sclerotium (Kirk et al. 2008, Knudsen & Vesterholt 2012). The family classification of Ceratellopsis is even more controversial. Initially included by Corner (1970) in Clavariadellaceae, Jülich (1982) accommodated it in Typhulaceae. Hawksworth et al. (1995) and Begerow et al. (2018), probably following Corner, included it in Gomphaceae, although Ceratellopsis lacks the synapomorphic characters of this family, such as pistillarin, ampullate septa and cyanophilous, ornamented spores (Hosaka et al. 2006). As no

Fig. 1. Diversity of typhuloid and pleurotoid fungi suggested to be closely related to Typhula. A. Macrotyphula fistulosa s.l. (IO.14.214, ARAN-Fungi). B. Macrotyphula juncea (IO.16.53, S). C. Typhula phacorrhiza, current type of Typhula (ARAN-Fungi 7446), here combined in Macrotyphula. D. Compressed sclerotium of T. phacorrhiza (ARAN-Fungi 7446). E. Typhula incarnata, showing scleridia at the base (IO.14.92, S), proposed conserved type of Typhula. F. Typhula uncialis (IO.14.94, S, UPS), type of Gliocoryne. G. Typhula crassipes (IO.14.83, S, UPS). H. Typhula subhyalina (IO.15.06, S), type of Pistillina and Dacryopsella. I. Typhula erythropus (IO.16.83, ARAN-Fungi). J. Ceratellopsis aff. aculeata (ARAN-Fungi 11746). K. Pterulicium gracile (IO.14.142, S, UPS). L. Phyllotopsis nidulans (ARAN-Fungi). M. Pleurocybella porrigens (BIO-Fungi 13431). N. Sarcomyxa serotina (IO.14.130, S, UPS). Photographs I. Olariaga, except L by J.I. Iturrioz.
molecular data of Ceratellopsis has been available, its phylogenetic relationships and classification have remained doubtful. Besides the above-mentioned genera treated by Berthier (1976), Mucronella and Horticiavula, both producing tiny clavarioid basidiomata, have been assigned to the Clavariaceae based on molecular data (Birkebak et al. 2013, Petersen et al. 2014). Regardless of their phylogenetic origin, all typhuloid fungi share similar taxonomic problems. For many species of those genera only the type specimen or very few collections are known, species limits are unclear and distribution data are meagre. Molecular data of only a handful of species are available in public sequence repositories and the high morphological diversity of the group remains poorly sampled.

**Typhula and segregated genera, Macrotyphula, and phylogenetic position of Typhulaceae**

The phylogenetic position of Typhulaceae has been inferred from only two species, Typhula phacorrhiza and Macrotyphula fistulosus, type of Typhula and Macrotyphula, respectively. Through analyses of a 5-locus dataset, Matheny et al. (2006) recovered Typhulaceae in the hygrophoroid clade (Agaricales) with phylogenetic confidence, as sister to the Hygrophoraceae in a supported clade encompassing Pterulaceae and members of two pleurotoid agaric genera (Sarcomyxa serotina and Phyllopatris spp.) (Fig. 1L–N). Binder et al. (2010), employing a broader taxon sampling of the Agaricomycetes, recovered also Typhulaceae as sister to Hygrophoraceae but without support, while Pterulaceae was supported as closely related to Stephanosporaceae instead (Binder et al. 2010). Other studies have not been able to confirm or reject the inclusion of Typhulaceae in the hygrophoroid clade, but recovered agaric or pleurotoid genera, such as Phyllopatris, Pleurocybella, Tricholomopsis, as sister taxa of Typhulaceae with phylogenetic confidence (Dentinger & McLaughlin 2006, Lodge et al. 2014). Dentinger et al. (2016) resolved for the first time several deep nodes of the Agaricales through a 208-locus dataset containing 35 taxa of Agaricales, and found that the hygrophoroid clade, as defined by Matheny et al. (2006), was paraphyletic. Also, Hygrocybe conica (Hygrophoraceae) was recovered as sister to the Clavariaceae, while Pterulaeae (Pterula multifida; recovered in the hygrophoroid clade by Matheny et al. (2006)), appeared in a branch with Pleurotus ostreatus. Thus, the results by Dentinger et al. (2016) question the inclusion of the Typhulaceae in the hygrophoroid clade. In addition to its uncertain phylogenetic position, the monophyly of Typhulaceae has not been tested appropriately.

Two genera, Typhula and Macrotyphula, are currently accepted in Typhulaceae (e.g. Berthier 1976, Knudsen & Vesterholt 2012). Macrotyphula differs from Typhula in having large, yellow-brown basidiomata (30–300 mm) that never arise from sclerotia and non-amyloid spores (Berthier 1976). In contrast, Typhula includes species with smaller basidiomata (generally under 10 mm long) that often arise from sclerotia and usually have amyloid spores. Some Typhula species are important plant pathogens that cause economic loss in cereal crops (e.g. Ekstrand 1955). These are popularly known as “snow moulds”, producing symptoms known as “Typhula blight” (Matsumoto et al. 2001, Hoshino et al. 2008). Several economically important species like T. incarnata and T. ishikariensis have been subjected to extensive research on their ecology, physiology and genetics (e.g. Matsumoto 1992, Vergara et al. 2004, Blunt et al. 2015, Chang 2015, Koch 2016). Generics limits of Typhula are not fully delineated and lack a complete consensus. Probably due to the fact that its species show diverse basidioma morphologies, sclerotal anatomy and asexual morph states (Berthier 1976), a number of genera have been segregated from Typhula, such as Cnazonaria, Dacryopsella, Gliocoryne, Phacorhiza, Pistillaria, Pistillina, Scleromitra and Sphaerula. These genera have been used to a certain extent. Of these, Corner (1950) recognised Pistillaria (with Cnazonaria, Gliocoryne, Scleromitra and Sphaerula in synonymy), Pistillina and Typhula (with Phacorhiza in synonymy). Donk (1954) adopted also Pistillaria, Typhula and Pistillina, and further synonymised Dacryopsella under Pistillina. Pistillaria has been recognised generally based on a ceraceous consistency of the fresh fruitbodies, horny when dried, and the absence of sclerotia (Corner 1950, 1970, Pilát 1958), but generic limits between Pistillaria and Typhula have been long debated (Corner 1950, Bourdot & Galzin 1928, Donk 1954, Berthier 1976). Pistillina has been distinguished by basidiomata with a globose fertile part (Corner 1950). Berthier (1976), after examining extensive material and type specimens available, merged all these genera under Typhula (Sphaerula, Scleromitra and Dacryopsella were not treated in the monograph), but recognised Cnazonaria, Gliocoryne, Pistillaria and Pistillina as subgenera. After the publication of Berthier’s monograph, a few authors have continued to use Pistillaria and Pistillina at the generic level (Shiryaev & Kotiranta 2007, Kaygusuz & Čolak 2017, Begerow et al. 2018, Petersen & Læssøe 2019). Recently, the new monotypic genus Tygervalleyomyces was described in Typhulaceae based on analyses of the 28S region (Crous et al. 2017). The asexual morph of Tygervalleyomyces podocarpi, the only known morph, is similar to the asexual morph of Typhula crassipes (Berthier 1976, as Typhula corallina) in the cylindrical conidia with a truncate base, and in fact these two species have highly similar 28S sequences (98 %) and nested within a larger highly supported clade containing other Typhula species (Crous et al. 2017). In view of this, the status of Tygervalleyomyces needs to be re-evaluated in the light of a phylogeny with a broader sampling of Typhula species. Oliariaga & Salcedo (2013) synonymised Typhula and Macrotyphula due to the fact that T. phacorrhiza formed a monophyletic group with Macrotyphula in previous analyses (Pine et al. 1999, Hibbett 2007), as well as morphological similarities. The designation of T. phacorrhiza as lectotype of Typhula by Donk (1933) has been considered unfortunate (Berthier 1976, Oliariaga 2009, Oliariaga & Salcedo 2013), because T. phacorrhiza, with long filiform basidiomata and unique compressed sclerotia, is an atypical species in Typhula (Remsberg 1940, Corner 1950, Berthier 1976). In fact, T. phacorrhiza shares many features with M. fistulosus, i.e. the pale brown, large basidiomata, the stipe surface with thin hyphae and caitlocrichomes, the basal tomentum formed by thick-walled, scarcely septate hyphae and the presence of a hyaline, striped encrustation on the medulla hyphae (Oliariaga & Salcedo 2013). Molecular phylogenetic analyses show that these species are closely related and nested in the Agaricales (Binder et al. 2010). Nevertheless, taxon sampling in phylogenetic studies of Typhulaceae is extremely poor and the synonymy of Typhula and Macrotyphula needs to be further explored.
The type of Sclerotium is conspecific with the type of Typhula

The genus Sclerotium, also included in Typhulaceae (Kirk et al. 2008), is currently treated as an artificial genus that accommodates fungi producing sclerotia but not, or rarely, a sexual morph (Xu et al. 2010). Tode (1790) included originally eight species in Sclerotium, of which Fries (1821) treated S. complanatum in the first place and Clements & Shear (1931: 411) thus selected this species as the type of Sclerotium. A number of authors, especially during the XIXth century, described numerous species in Sclerotium, including ascomycetous and basidiomycetous fungi (e.g. Fries 1822, Léveillé 1843, Duby 1830, Desmazières 1848, Rostrup 1866), and numerous plant pathogens (Xu et al. 2010). Until now, 464 names have been described or combined in Sclerotium (Index Fungorum, viewed on 11 June 2019) and it is evident that species assigned to Sclerotium have multiple evolutionary origins, but very few attempts to disassemble it have been made (Xu et al. 2010). With the end of the asexual-sexual morph dual nomenclature, many names in Sclerotium may turn out to have priority over species names in use. Several early authors observed that some Sclerotium species appeared in connection or directly attached to basidiomata of Typhula species (e.g. Berkeley 1837, Léveillé 1843 (as Clavania), Rostrup 1866). Sclerotium complanatum, type of Sclerotium, is characterised by producing compressed sclerotia attached to the substrate by a small stalk (Tode 1790) which conform to those produced by T. phacorrhiza (Berkeley 1837, Rostrup 1866, Schröter 1889). Thus, it is generally accepted that S. complanatum is a synonym of T. phacorrhiza (Xu et al. 2010, Kaygusuz & Çolak 2017), although only Remsberg (1940) has proposed this synonymy according to our search. Other authors attributed S. complanatum to the sclerotial morph of T. gyrans (Fries 1874, Corner 1950, Donk 1962), but this view appears to have been abandoned. In the meantime, the taxonomic identity of S. complanatum has not been reassessed and the name remains untypified. As currently asexual names compete with sexual names for priority, the possible synonymy of S. complanatum and T. phacorrhiza would make Sclerotium and Typhula taxonomic synonyms, and all Typhula names in use, including those being applied to economically important plant pathogens, would have to be transferred to the older and equally sanctioned genus Sclerotium. Examining in depth the taxonomic concept of S. complanatum and proposing a typification is thus of paramount importance to deal with a possible scenario of undesirable nomenclatural changes.

The poorly known genus Ceratellopsis, a possible earlier synonym of Pterulicium

Ceratellopsis differs from Typhula in having minute filiform basidiomata with a sterile apex and a non-corticulate stipe (Corner 1950, Berthier 1976). Short basidia up to 20 μm have also been suggested to be a diagnostic character (Jülich 1982). Pterulicium gracile, called Pterula gracilis until very recently (Leal-Dutra et al. 2020), strongly resembles species of Ceratellopsis because of its minute white basidiomata with a sterile apex, at least at early stages of development (Corner 1950, Berthier 1976), but it differs microscopically in having skeletal hyphae, typical for Pterulaceae, 2-spored basidia and no stipe (Corner 1950, Olariaga 2009). Furthermore, we have made collections with very minute basidiomata with a clearly delimited stipe suggesting Ceratellopsis, but having skeletal hyphae as typical in Pterulaceae. Limits between Ceratellopsis and Pterulaceae, thus, are not always clear-cut.

As pointed out by Donk (1954), Konrad & Maublanc (1937) introduced Ceratellopsis based on the validly published but illegitimate Cerateila Pat. (Patoüillard 1887; later homonym of Cerateila Hook. f. 1844) and explicitly indicated Ceratellopsis queletii as the type of Ceratellopsis. While Donk (1954) followed this typification, Corner (1950), noted that C. queletii might represent a rudimentary Pterula, and he selected instead Ceratellopsis aculeata as type so that Ceratellopsis could be used with certainty and not reduced to a synonym of Pterula. This choice, nevertheless, is not permissible (Turland et al. 2018; Art. 7.8) since the original type indication of Ceratellopsis by Konrad & Maublanc (1937) is unequivocal and irrevocable. Also, Olariaga (2009) proposed tentatively that C. queletii might be a synonym of Pterulicium gracile, but up to present, no consistent and stable interpretation of C. queletii has been provided and the taxonomic status of Ceratellopsis remains unresolved. Twenty-four names have been described or combined in Ceratellopsis, but several of them represent P. gracile (Berthier 1976) or Typhula species.

The confirmation that C. queletii, type of Ceratellopsis, is a synonym of P. gracile would have important consequences in the classification of Pterulaceae. The family, centered on the genus Pterula, has included several clavarioid genera with a dimitic hyphal system (Corner 1970). Based on molecular studies, four resupinate genera (Aphanobasidium, Coronicium, Merulicium, Radulomyces; Larsson 2007, Larsson et al. 2004) and the polyporoid Radulotubus (Zhao et al. 2016) were later transferred to Pterulaceae. In light of analyses of the ITS, 28S and RPB2 regions, employing a rich taxon sampling of the Pterulaceae, Leal-Dutra et al. (2020) elucidated generic limits in the family. This study discovered Pterula to be polyphylectic and splits its species into the new genus Myrmepterula, Phaeotepetula and Pterulicium, leaving in Pterula sensu stricto a handful of species around Pterula plumosa. Deflexula was shown to be paraphyletic because some species nest in the Pterula clade, while the type D. fascicularis is in the Pterulicium clade. In total, 46 names earlier treated in Pterula and Deflexula were combined in Pterulicium, a genus up to then monospecific. Pterula gracilis was found to belong to the Pterulicium clade and accordingly combined as Pterulicium gracile. In this framework, the synonymy between C. queletii and P. gracile be confirmed, the name Ceratellopsis (1937) would have priority over Pterulicium (1950). Thus, the identity of C. queletii needs urgent clarification.

In the present study, we expand the taxon sampling of typhuloid fungi based on the multigene datasets used by Matheny et al. (2006) and Binder et al. (2010). With these data, our main goals were to: 1) provide a robust phylogenetic hypothesis for typhuloid fungi, especially for T. phacorrhiza (type of Typhula), types of genera segregated from Typhula, Sclerotium complanatum (type of Sclerotium) and Ceratellopsis species; 2) test the monophyly of Typhula; 3) assign typhuloid fungi to appropriate families; and 4) propose an updated nomenclature in the light of a robust multigene phylogeny.
MATERIAL AND METHODS

Molecular techniques

DNA was extracted from fresh (stored in 1 % SDS extraction buffer) basidiomata, using a DNeasy Plant Mini Kit (Qiagen) according to the manufacturer’s instructions. The following six gene regions were amplified: 1) nu5.8S rDNA, the 5’ end of the nuclear 28S rDNA (spans domains D1–D2), part of the nuSSU rDNA (ca. 1 600 bp), RPB1 (900 bp; A–C), RPB2 (5–7 region, ca. 1 100 bp) and EF-1α (1 100 bp). The ITS (ITS1-5.8S-ITS2) and 28S regions were amplified in one piece using the primers ITS5-LR7, or otherwise as separate pieces: ITS using ITS5-ITS4, (White et al. 1990); and 28S using LR0R-LR5 (or LR3) and LR3-LR7 (Vilgalys & Hester 1990). The same primers were used for sequencing. The ITS was sequenced using the primers ITS1-ITS4 and/or in a few instances ITS5, 5.8S and ITS3. The SSU region was amplified in one piece employing primers NS1-NS8 or in two pieces using NS1-NS4 and NS3-NS8 (White et al. 1990). PCR products of the RPB1 region were obtained using gRPB1-A (Stillier & Hall 1997) and gRPB1-C rev primers (Matheny et al. 2002). The sequence spanning RPB2 regions 5–7 was amplified in one piece, using RPB2-5F and bRPB2-7R, or if required, in two pieces with primers RPB2-5F-grRPB2-6R and bRPB2-6F-bRPB2-7R (Liu et al. 1999, Matheny 2005). For samples that did not successfully amplify or for sequencing, Typhula-specific primers were designed for the RPB2 region and used in different combinations (Table 1). The EF-1α region was PCR amplified and sequenced employing 983F and 2218R primers (Rehner & Buckley 2005). Typhula-specific primers of the EF-1α region were designed and used for PCR amplification and sequencing of problematic samples (Table 1). PCR amplifications were performed using Illustra™ Hot Start Mix RTG PCR beads (GE Healthcare, UK) in a 25 μL volume, containing 3 μL of genomic DNA, 10 μM of each primer and distilled water. PCRs were conducted in Applied Biosystems GeneAmp® PCR System 9700 and 2720 Thermal Cyclers. Amplifications were performed using the following program: initial denaturation at 95 °C for 5 min, followed by 35–40 cycles of 95 °C for 45–60 s, 52–58 °C for 50 s, 72 °C for 1 min, followed by a final extension at 72 °C for 10 min. PCR amplifications of protein-coding genes follow O’Donnell et al. (2011, RPB1) and Hansen et al. (2013, RPB2, EF-1α). PCR products were purified using the enzymatic method Exo-sap-IT (USB Corporation, Santa Clara, California, USA). When multiple bands were amplified in the RPB1 and RPB2 regions, PCR products were size-fractionated in a 1 % agarose gel, stained with GelRed™ (Biotium Inc.), visualised over a UV trans-illuminator, excised and purified using QIAquick spin columns (Qiagen). Purified PCR products were sequenced at Macrogen Europe service (www.macrogen.com).

Type specimens, taxon and molecular sampling

Type specimens of small typhuloid fungi available at E, FH, M, PC, S and UPS herbaria were examined: Ceratella ferryi, Ceratellopsis carestiae, C. nickii, C. acuminate, C. equisetiocola, Clavaria aculina, C. microscopica, Pistillaria attenuata, P. juncicola, Pterulicium gracile, Typhula brunnaudii, T. cressipes, T. sclerotioides, T. sphaeroidea, T. subhyalina and T. uncialis. Material deposited in G (customs blocked the loan), PAD (not available on loan) and SAPA (several contact attempts unsuccessful) could not be examined. The notation “*” indicates that type or other original material was examined by us. Cultures of the taxa collected and described in this study were deposited in the CBS-KNAW culture collection at the Westerdijk Fungal Biodiversity Institute.

For molecular analyses, types and other species of genera considered to be typhuloid or assigned to Typhulaceae were sampled, namely Ceratellopsis, Macrotyphula, Pterulicium gracile, Typhula s.l. and Sclerotium. A collection identified as C. acuminate, with skeletal hyphae, was included to test the limits between Ceratellopsis and Pterula. Nucleotide sequences were aligned in the six-genome dataset (nu5.8S rDNA, nu28S rDNA, nu18S rDNA, RPB1, RPB2 and EF-1α) assembled by Binder et al. (2010; TreeBASE no. S10185), in order to preliminarily explore their phylogenetic affinities. Nucleotide sequences were aligned in Allview (Larsson 2014). This alignment was subjected to a maximum likelihood (ML) analysis using the “RAxML HPC2 on XSEDE” tool (Stamatakis 2014) in the CIPRES Science Gateway (Miller et al. 2010), starting from a random tree. A GTR-Gamma model with four rate categories was selected for tree inference. For branch confidence, 1 000 ML bootstrap replicates were conducted with a GTRCAT model (ML-BP). Targeted typhuloid taxa nested in Agaricales (ML-BP 92 %), except for Ceratellopsis sagittiforins that was placed in Hymenochaetales. Based on this analysis, a first 6-locus (5.8S, 28S, 18S, RPB1, RPB2, EF-1α) dataset (the Agaricales matrix) was prepared to phylogenetically place typhuloid fungi among the Agaricales. Three taxa, Amylocorticium cebernense, Plicatopus crispa and Serpulomyces borealis, were included as outgroup for rooting purposes based on previous studies (Binder et al. 2010). A second dataset with the same molecular markers (the Pleurotineae matrix) included Typhulaceae

Table 1. Newly designed Typhula-specific primers for the RPB2 and EF-1α (5’–3’) regions.

| Locus    | Primer          | Sequence                  | PCR | Sequencing |
|----------|-----------------|----------------------------|-----|------------|
| EF-1α    | 1007F-Typ       | SGAGAGAYCGTCTAACGAG       | X   |            |
| EF-1α    | 1447F-Typ       | GCATGCCTGGTWCACAGG       | X   | X          |
| EF-1α    | 1825F-Typ       | GACAGTVTCCGYAAGGAYA      | X   | X          |
| EF-1α    | 2100R-Typ       | ATGKGGCTTGGARAGGRACRA    | X   |            |
| RPB2     | RPB2-5Fint-Typ  | AARARCGDYYNGAYYTSGC     | X   |            |
| RPB2     | RPB2-6F-Typ     | TGGGGGYTGGACCTGTGAGA     | X   | X          |
| RPB2     | RPB2-6R-Typ     | TCCACGACTTCCARCCTCCA    | X   |            |
| RPB2     | RPB2-7Rint-Typ  | TASSGTGGTACAGGAGRCAT    | X   | X          |
Table 2. Sequenced specimens used in this study, with GenBank accession numbers for 5.8S, 28S, 18S, RPB1, RPB2 and EF-1α regions. Numbers in parentheses following the species names indicate multiple collections of a species. The GenBank accessions of sequences generated in this study are in bold. Asterisks indicate sequences obtained from genome data through the JGI portal (https://jgi.doe.gov/). Abbreviations of datasets are: ag = Agaricales, cl = Clavariineae; hy = Hymenochaetales, pl = Pleurotineae.

| Original name                        | Updated name | Voucher specimen | Dataset   | GenBank accession numbers |
|--------------------------------------|--------------|-----------------|-----------|--------------------------|
|                                      |              |                 | 5.8S      | 28S                      | 18S | RPB1 | RPB2 | EF-1α |
| Agaricus bisporus*                   | —            | H97             | Genome    | Genome                   | Genome | genome | Genome | genome |
| Alloclavaria purpurea                | —            | PBM 2731 (CUW)  | hy        | DQ48690                  | DQ457657 | DQ437679 | —       | —       |
| Anomoporia bombycina                 | —            | CFMR-L-6240     | cl        | —                        | GU187564 | —       | —       | —       |
| A. kamtschatica                      | —            | GB/M Edman K426 | cl        | —                        | DQ144615 | —       | —       | —       |
| Anthracophyllum archeri              | —            | PBM 2201 (WTU)  | ag        | DQ444308                 | AY745709 | DQ092915 | DQ435799 | DQ385877 | DQ028566 |
| Amanita brunnescens                  | —            | PBM 2429 (CUW)  | ag        | AY789079                 | AY631902 | AY707096 | AY788847 | AY780936 | AY881021 |
| Aphanobasidium pseudotsugae         | —            | HHB-822 (CFMR)  | ag, pl    | GU187509                 | GU187567 | GU187620 | GU187695 | GU187781 | GU187695 |
| Armillaria mellea                    | —            | PBM 2470 (CUW)  | ag        | AY789081                 | AY700194 | AY787217 | AY788849 | AY780938 | AY881023 |
| Basidioradulum radula                | —            | GEL 2493 (KASSEL) | hy        | DQ234537                 | AY700184 | AY771611 | —       | —       |
| Blasiphalia pseudogrisea             | —            | P. Högner 4933  | (H7031951)/ IO.14.231 (S) | hy | MF319048 | MF318999 | MF318900 | MT24239 |
| Bolbitius vitellinus                 | —            | MTS 5020 (WTU)  | ag        | DQ200920                 | AY691807 | AY705955 | DQ435802 | DQ385878 | DQ408148 |
| Camarophytopsis schulzeri           | —            | S. Jacobsson 3453 | (H) | cl | —                      | AM946415 | —       | —       |
| Cantharellopsis prescotii            | —            | I. Kybvuori 08-0808/ H6059300 | hy | MF319050 | MF318901 | MF318992 | MF288855 | —       |
| Cantharocybe gruberi                 | —            | PBM 510 (WTU)   | ag, pl    | DQ200927                 | DQ234540 | DQ234546 | DQ435808 | DQ385879 | DQ059045 |
| Ceratophytopsis acuminatae           | —            | CBS 146691      | ag, cl    | MT232347                 | MT232298 | MT232493 | MT24236  | MT24230  |
| C. aculeata                          | —            | ARAN-Fung 13729 | cl        | —                        | MT232300 | —       | —       |
| C. aff. acuminata                    | —            | ARAN-Fung 11746 | cl        | —                        | MT232348 | MT232299 | —       | —       |
| C. sagittiformis(1)                  | Bryopistiella sagittiformis | IO.15.41 (S) | hy | —                        | MT232301 | —       | MT24231 |
| C. sagittiformis(2)                  | B. sagittiformis | IO.15.85 (S) | hy | —                        | MT232302 | —       | MT24232 |
| C. sagittiformis(3)                  | B. sagittiformis | IO.14.164 (S) | hy | —                        | MT232349 | MT232303 | —       |
| Cheimophytopsis candidissimum        | —            | PBM 2411 (WTU)  | ag        | DQ486687                 | DQ457654 | DQ435812 | DQ447888 | DQ470831 | GU187760 |
| Calocera cornea                      | —            | GEL 5359 (KASSEL) | hy | AY789083 | AY701526 | AY771610 | AY536286 | —       |
| Clavaria acuta(1)                    | —            | RHP55840 (TENN043602) | cl | — | HQ877681 | —       | —       |
| C. acuta(2)                          | —            | MT54577 (WTU)   | cl        | —                        | HQ877679 | —       | —       |
| C. acuta(3)                          | —            | JFA10440 (WTU)  | cl        | —                        | HQ877680 | —       | —       |
| C. alboglobospora                    | —            | TENN042295      | cl        | —                        | HQ877682 | —       | —       |
| C. argilacea                         | —            | TFB10720 (TENN058804) | cl | — | HQ877683 | —       | —       |
| C. australiana                       | —            | ADM1311 (TENN051311) | cl | — | HQ877685 | —       | —       |
| Original name                  | Updated name | Voucher specimen | Dataset  | GenBank accession numbers |
|-------------------------------|-------------|------------------|---------|--------------------------|
| C. aff. fragilis              | —           | SAT96-349-01 (WTU) | cl      | HQ877688                |
| C. fumosa                     | —           | GG_151003        | cl      | EF535286                |
| C. fusca                      | —           | RHP5840 (TENN043602) | cl      | HQ877681                |
| C. inaequalis                 | —           | MB 04-016 (WTU) | cl      | AY745693                |
| C. pullei                     | —           | KGN98            | cl      | AY586646                |
| C. cf. rubicundula            | —           | TENN043695       | cl      | HQ877697                |
| Clavaria sp.(1)               | —           | TFB11835         | cl      | HQ877692                |
| Clavaria sp.(2)               | —           | JMB10061001 (TENN065665) | cl      | HQ877684                |
| C. stegasaurioides            | —           | PBM3337          | cl      | HQ877698                |
| C. zollingeri                 | —           | JMB08040912 (TENN064095) | cl      | HQ877700                |
| Clavicularia taxophila        | —           | 9186             | cl      | AF115333                |
| Clavulinopsis amoena          | —           | PBM3381          | cl      | HQ877702                |
| C. corallinorosacea           | —           | PBM3380          | cl      | HQ877707                |
| C. fusiformis                 | —           | MGW672 (TENN064110) | cl      | HQ877717                |
| C. sulcata                    | —           | PBM3379          | cl      | HQ877709                |
| Clitocella mundula            | —           | TJB 7599 (CORT)  | ag      | DQ494694 AY700182       |
| C. candidans                  | —           | WUT              | ag      | DQ202268 AY645055       |
| C. subditopoda                | —           | WUT              | ag      | DQ202269 AY691889       |
| Coltricia perennis            | —           | P. Salo 11024 (H) | hy      | MF318907 MF319056       |
| Collybia tuberosa             | —           | TENN 35340       | ag      | AY854072 AY639884       |
| Conocybe lactea               | —           | PBM 2411 (WTU)   | ag      | DQ486693 DQ457660       |
| Coprinus comatus              | —           | ECV 3198 (UC)    | ag      | AY854066 AY635772       |
| Coprinopsis cinerea*          | —           | AmutBmut #326    | ag      | Genome Genome Genome     |
| Coronicium alboglaucum        | —           | NH4208           | pl      | AY463400 AY586650       |
| Cortinarius iodes             | —           | WUT              | ag      | AF389133 AY702013       |
| Colytia sp.                   | —           | WUT              | hy      | AY854079 AY629317       |
| C. undulatea                  | —           | IO.15.126 (S)    | hy      | MT232350 MT232304       |
| Crepidotus cf. asplanatus     | —           | PBM 717 (WTU)    | ag      | DQ202273 AY380406       |
| Cristinia sp.                 | —           | FP-100305 (CFMR) | pl      | GU187526 GU187585       |
| Entoloma prunuloide           | —           | TJB 4765 (CORT)  | ag      | DQ206983 AY700180       |

(continued on next page)
| Original name          | Updated name          | Voucher specimen | Dataset                  | GenBank accession numbers          |
|-----------------------|-----------------------|------------------|--------------------------|-------------------------------------|
|                       |                       |                  |                          | 5.8S | 28S | 18S | RPB1 | RPB2 | EF-1α |
| Globulicium hiemale   |                       |                  |                          | DQ873595 | DQ873595 | DQ873594 | —   | —   | —   |
| Gymnopus contrarius   |                       |                  |                          | DQ486708 | DQ457670 | DQ440643 | DQ447902 | DQ472716 | GU187700 |
| Gyroflexis breviasiadi |                       |                  |                          | MT232351 | MT232305 | —   | —   | MT24235 | —   |
| Fibricium rude        |                       |                  |                          | AY700202 | AY654888 | —   | —   | —   | —   |
| Fistulina Antarctica  |                       | —                | (AFTOL-ID 1335)         | DQ486702 | AY293181 | AY283131 | DQ447899 | DQ472713 | GU187698 |
| Flammulina velutipes  |                       | TENN 52002       |                           | AY854073 | AY639883 | AY665781 | AY858966 | AY786055 | AY883423 |
| Hemimycena gracilis   |                       |                  |                          | DQ490623 | DQ457671 | DQ440644 | DQ447905 | DQ472719 | GU187709 |
| Hirticlavula elegans  |                       | JHP-13.364 (O)   | cl                       | KJ939349 | —   | —   | —   | —   | —   |
| Hodophilus aff. foetens |                  | ECV4175 (TENN065670) | cl                       | HQ787687 | —   | —   | —   | —   | —   |
| Hodophilus hymenocephalus(1) |               |                  |                          | —     | —   | DQ457679 | —   | —   | —   |
| H. hymenocephalus(2)  |                       |                 |                           | —     | —   | —   | —   | —   | —   |
| Hoehnbeuhelia tremula |                       |                  |                          | DQ182504 | KU355405 | DQ440645 | —   | KU355434 | KU355465 |
| Hydropus cf. scabripes |                       | WTU              |                           | DQ404389 | DQ411536 | DQ444855 | DQ447908 | DQ457634 | —   |
| Hygrocybe coccinea    |                       |                  |                          | DQ490629 | DQ457676 | DQ444858 | DQ447910 | DQ472723 | GU187705 |
| H. aff. conica        |                       |                  |                          | —     | DQ534589 | —   | —   | —   | —   |
| Hygrophorus pudorinus |                       |                  |                          | DQ490631 | DQ457678 | DQ444861 | DQ447912 | DQ472725 | GU187710 |
| Hyphodontia alutaria  |                       |                  |                          | DQ873603 | DQ873603 | DQ873602 | —   | —   | —   |
| Hyphodontiella multisepatata |            |                  |                          | —     | —   | —   | —   | —   | —   |
| Inocybe myriadophylla |                       |                  |                          | DQ221106 | AY700196 | AY657016 | DQ447916 | AY803751 | DQ435791 |
| Inonotus griseus      |                       |                  |                          | KX674583 | KX364623 | —   | —   | KX364919 | —   |
| Infundibulicybe gibba |                       |                  |                          | DQ490635 | DQ457682 | DQ411537 | DQ447913 | DQ472727 | GU187759 |
| Kuehneromyces subalutacea |              |                  |                          | DQ873630 | DQ873631 | DQ873629 | —   | —   | —   |
| Kuehneromyces rostratus |                     |                  |                          | DQ490638 | DQ457684 | DQ457624 | DQ447918 | DQ472730 | GU187712 |
| Laccaria bicolor*     |                       |                  |                          | genome | genome | genome | genome | genome | —   |
| Lacthena villosa      |                       |                  |                          | DQ097362 | DQ097347 | AY705969 | —   | —   | —   |
| Leifia flavelladilata |                       |                  |                          | DQ873635 | DQ873635 | —   | —   | —   | —   |
| Lepista inina         |                       |                  |                          | DQ221109 | DQ234538 | AY705948 | DQ447919 | DQ385885 | DQ289591 |
| Lycoperdon pyriforme  |                       |                  |                          | AY854075 | AF287873 | AF026619 | AY860523 | AY218495 | AY883426 |
| Macrolepiota dolichola |                       |                  |                          | DQ221111 | DQ11537 | AY771602 | DQ447920 | DQ385886 | DQ435785 |
| Macrothlypa fistulosa(1) |                    |                  |                          | —     | DQ071735 | —   | MT232494 | MT24236 | MT242353 |

|                      |                       |                  |                          | DQ071735 | DQ068002 | MT24236 | —   | —   | —   |

Table 2. (Continued).
| Original name                  | Updated name                  | Voucher specimen   | Dataset            | GenBank accession numbers |
|-------------------------------|-------------------------------|-------------------|--------------------|--------------------------|
| *M. fistulosa* (2)            | —                             | IO.14.214 (ARAN-Fungi, S) ag |                    | MT232352 KY224086 MT232495 MT242373 MT242373 MT242354 |
| *M. juncea* s.l.             | —                             | IO.14.177 (S) ag    |                    | MT232353 MT232306 MT241267 MT242373 MT242354 |
| *Megaloclybia platyphylla*   | —                             | TENN 59432 ag      |                    | DQ249275 AY702016 AY786053 DQ447923 DQ385887 DQ435786 |
| *Mucronella calva* (1)       | —                             | JS16142 cl         |                    | — AYS86869 AYS86869 — — — — |
| *M. calva* (2)               | —                             | GEL4458 cl         |                    | — AJ406588 — — — — — — |
| *M. aff. calva*              | —                             | KHL10317 cl        |                    | — AYS868690 — — — — — — |
| *M. flavo*                   | —                             | IO.16.84 (S) ag, cl |                    | MT232354 MT232307 MT232496 MT242373 MT242354 |
| *M. fusiformis*              | —                             | DJM 1309 ag, cl    |                    | — DQ284905 — — — — — — |
| *M. pendula*                 | —                             | PBM 3437 ag, cl    |                    | — HQ229921 — — — — — — |
| *Muscinupta laevis*          | —                             | V. Haikonan 19745 (H6059292) hy | MF319066 MF318921 MF319004 — MF288861 — |
| *Mycetinopsis alliiceps*     | —                             | TENN 55620 ag      |                    | AY854076 AY635776 AY787214 AY860526 AY786060 AY883431 |
| *Odoniophylla ronellii*      | —                             | KHL s. n. (GB) hy  |                    | DQ873639 DQ873639 DQ873599 DQ873598 — — — — — — |
| *Onnia scuria*               | —                             | P53A hy            |                    | genome Genome genome genome Genome — |
| *Oxyporus populinus*         | —                             | Dai 12793/ DSH 93-188 hy | KF110109 KF110201 AF026616 — KT210380 — |
| *Peniophorale praeterrrmissa*| —                             | GEL 2182 (KASSEL) hy |                    | AY854081 AY700185 AY770904 AY8787221 — — — — — — |
| *P. pubera*                  | —                             | KHL 13154 (GB) hy  |                    | DQ873599 DQ873599 DQ873598 — — — — — — |
| *Pluteus ronellii*           | —                             | ECV 3201 (UC) ag   |                    | AY854065 AY634279 AY657014 AY862187 AY880633 AY883433 |
| *Phaeomarasmius proximans*   | —                             | PBM 1951 (WTU) ag  |                    | DQ404381 AY752970 AY752970 — — AY333414 DQ028592 |
| *Phellinum ferrugineofuscum* | —                             | Spk3Phefer14 Genome Genome genome — — — — — — |
| *Phellinus tremulae*          | —                             | KCTC 6569/ NIB2011-P2-F hy | AY189703 KU39202 KU39277 KU39227 — — — — — — |
| *Phyllostrophium nidulans*   | —                             | IO.14.196 (S) ag, pl |                    | — MT232308 MT232497 MT24239 MT24238 MT242357 MT242357 |
| *Phyllophora* sp.            | —                             | MB 35 (WTU) ag, pl |                    | DQ404382 AY684161 AY707090 AY447933 AY786031 DQ59047 MT201380 |
| *Porotheleum fimbriatum*     | —                             | CBS 788.86 ag      |                    | DQ490686 DQ475767 DQ448454 DQ447907 DQ472721 — — — — — — |
| *Pleurocybella porrigens*    | —                             | JFA 12544 (WTU)/ TUB012154/ UPS F-611822 ag, pl | MT232309 MT232309 | GU187760 GU187760 DQ067994 MT24239 GU177740 |
| *Pleurotus eryngii*          | —                             | X102 ag, pl        |                    | KX977448 FJ379286 — — — — — — |
| *P. ostreatus*               | —                             | TENN 53662 ag      |                    | NG_027634 AY645052 AY657015 AY682186 AY786062 AY883432 |
| *Plicaturotus crispis*       | —                             | FD-325 SS-3 ag, pl |                    | genome genome genome genome genome — — — — — — |
| *Podoserpula pusio*          | —                             | Hlepp-329 ag       |                    | — EF535271 — — — — — — |
| *Porodaedalea pini*          | —                             | No-6170-T hy       |                    | JX110037 JX110081 — — — — JX109561 — — — — — — |

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| Original name | Updated name | Voucher specimen | Dataset |
|--------------|--------------|-----------------|---------|
| Pseudoclitocybe cyathiformis | — | JFA 12811 (WTU)/GLM 46020 (GB) | ag | GU187553 EF551313 GU187659 DQ067939 GU187815 GU187742 |
| Pterulicium echo(1) | — | DJM 302558 (MINN) | ag, pl | DQ494693 AY458123 DQ092911 — GU187805 GU187743 |
| *P. echo*(2) | cf. *Pterula* | ZRL20151311 | pl | LT716065 KY418881 KY418947 KY418979 KY419026 KY419076 |
| *P. gracile*(1) | — | CBS 309.79 | ag, pl | genome genome genome genome genome genome |
| *P. gracile*(2) | — | IO.14.142 (S) | pl | MT232356 MT232310 MT232498 — — MT242358 |
| Radulomyces confluens* | — | OMC1631 | ag, pl | genome genome genome genome genome genome |
| R. molaris | — | ARAN-Fungi 2003 | ag, pl | — MT232311 MT232499 MT24230 MT24230 MT242359 |
| Ramariospora biforis | — | JMB10061006 (TENN056660) | cl | — — — — |
| R. crocea | — | JMB10071001 (TENN056661) | cl | — — — — |
| R. aff. kunzei | — | Mann5064 (WTU) | cl | — — — — |
| R. pseudosubtilis | — | RHP27722 (TENN027722) | cl | — — — — |
| R. tenariumosa | — | GG_0611104 | cl | — EF535269 — — — — |
| Repetobasidium conicum | — | KHL 12338 (GB) | hy | DQ873647 DQ873647 DQ873646 — — — |
| *R. mlnficum* | — | FP-13558-sp | hy | — AT292308 AT293155 — — — |
| Resinicium bicolor | — | GEL 2071 (KASSEL) | hy | DQ218310 AY700183 — — DQ457635 |
| Rickennella fibula | — | PBM 2503 (WTU) | hy | DQ241782 AY700195 AY771599 — DQ408115 — |
| Rhodocollybia maculate | — | WTU | ag | DQ404383 AY639980 AY752966 DQ447936 AY787220 DQ061279 |
| Sarcomyxa serotina | — | WTU/ DSH 93-218 | ag, pl | genome genome genome genome genome genome |
| Schizopodermal radiatum | — | FH | ag | AY571060 AY571023 AY705952 DQ447939 DQ484052 — |
| Schizopora radula | — | Dai 12631 | hy | KT203307 KT203328 — — KT210382 |
| Solerotium complanatum Macrotephytha phaconthiza | — | Microf. Exs. No. 49 (UPS) | pl | — MT234400 — — — |
| Sistotrema confuens | — | FCUG 298 | hy | DQ267125 AY647214 AY757260 — DQ381837 |
| Stephanospora caroticolor | — | TUB019072/ IOC 137-97/ R44008 | ag, pl | KM086827 AFS18652 AFS18591 KF211335 — GU187747 |
| Trichaptum abietinum* | — | R44008 | hy | genome genome genome genome — |
| Tubulicrinis globosporus | — | KHL 12133 (GB) | hy | DQ873655 DQ873655 DQ873654 — — |
| T. nornatus | — | KHL 11763 (GB) | hy | DQ873659 DQ873659 DQ873658 — — |
| Tygervalleyomyces podocarpi Typhula podocarpis | — | CPC 29979 | CPG | NR_156661 NG_059851 — — — |
| Typhula capitata | — | IO.15.122 (S, UPS)/ CBS 143727 | ag, pl | MT232357 MT232312 MT232500 MT24231 MT24231 MT242360 |
| T. crassipes | — | IO.14.83 (S, UPS) | ag, pl | MT232358 KY224094 — — — MT24232 MT242361 |
| T. erythropus | — | IO.14.123 (S, UPS)/ CBS 143797 | ag, pl | MT232359 KY224096 MT232501 MT24232 MT24233 MT242362 |
| T. grisar | — | IO.14.103 (S)/ CBS 143796 | ag, pl | MT232360 KY224097 MT232502 MT24233 MT24234 MT242363 |
| Original name | Updated name | Voucher specimen | Dataset | GenBank accession numbers |
|---------------|--------------|------------------|---------|--------------------------|
| *T. micans*   | —            | IO.14.165 (S)    | ag, pl  | MT232361, KY224102, MT232503, MT24234, MT24235, MT242364 |
| *T. incarnata*| —            | IO. 14. 92 (S)/ CBS 143742/ CBS 350.79 | ag, pl  | MT232362, MT232313, MT232504, MT24235, MT24236, MT242365 |
| *T. phacorrhiza*(1) | *Macrothyphula phacorrhiza* | IO.14.200 (S) | ag, pl  | MT232363, MT232314, MT232505, —, MT24237, MT242366 |
| *T. phacorrhiza*(2) | *M. phacorrhiza* | IO.14.167 (S) | ag, pl  | MT232364, MT232315, MT232506, MT24236, MT24238, MT24237 |
| *T. phacorrhiza*(3) | *M. juncea s.l.* | DSH 96-059 | pl | —, AF393079, AF026630, —, —, —, — |
| *T. phacorrhiza*(4) | *M. phacorrhiza* | ARAN-Fungi 7446 | pl | —, MT232316, —, —, —, — |
| *T. sclerotioides* | —            | IO.14.22 (S) | ag, pl  | MT232365, MT232317, MT232507, MT24237, MT24239, MT242369 |
| *T. subhyalina* | —            | IO.15.06 (S)/ CBS 143735 | ag, pl  | MT232366, MT232318, MT232508, —, MT24230, MT242370 |
| *T. uncialis* | —            | IO.14.74 (S) | ag, pl  | MT232367, MT232319, MT232509, MT24238, MT24231, MT242371 |
| Uncultured Basidiomycota(5) | *Ceratellopsis sp.* | Soil sample | cl | DQ341741, DQ341741, —, —, —, — |
| Uncultured Basidiomycota(1) | *Ceratellopsis sp.* | Soil sample | cl | HQ433218, HQ433218, —, —, —, — |
| Uncultured Basidiomycota(2) | *Ceratellopsis sp.* | Soil sample | cl | GQ159941, GQ159941, —, —, —, — |
| Uncultured Basidiomycota(3) | *Ceratellopsis sp.* | Soil sample | cl | EU691875, EU691875, —, —, —, — |
| Uncultured Basidiomycota(4) | *Ceratellopsis sp.* | Soil sample | cl | EU861817, EU861817, —, —, —, — |
| Uncultured Basidiomycota(5) | *Ceratellopsis sp.* | Soil sample | cl | DQ341741, DQ341741, —, —, —, — |
| Uncultured Basidiomycota(6) | *Ceratellopsis sp.* | Soil sample | cl | EF434117, EF434117, —, —, —, — |
| Uncultured Basidiomycota(7) | *Ceratellopsis sp.* | Soil sample | cl | GQ159939, GQ159939, —, —, —, — |
| *Xerula radicata* | —            | TENN 59235       | ag     | DQ241780, AY645051, AY654884, DQ447946, AY786067, DQ029194 |
| *Xylodon rimosissimus* | —            | CBS 105.045/ Ryberg 02/1031 (GB) | hy     | DQ873627, DQ873628, DQ873626, —, —, LNT14662, — |
and closely related families, with a more species-inclusive sampling than in the Agaricales matrix. Cantharocybe gruberi was used as an outgroup based on analyses of the Agaricales matrix. A third 28S alignment (the Clavariaceae matrix) was constructed based on Birkebak et al. (2013) to infer phylogenetic relationships of Ceratellopsis within the Clavariaceae, and employed Anomoporia bombycina, A. kantschatica and Podoserpula pusio as outgroup taxa. A fourth 4-locus (5.8S, 28S, 18S, RPB2) dataset (the...
Hymenochaetales matrix) was assembled to further explore phylogenetic relationships of C. sagittiformis within the Hymenochaetales. Sequences of Calocera cornea were set as outgroup.

Sequence alignment and phylogenetic analyses

Sequences were edited and assembled using Sequencher v. 4.10.1 (Gene Codes Corp., Ann Arbor, MI) and deposited in GenBank (Table 2). Additional sequences were downloaded

**Phylogenetic origins of typhuloid fungi**

Fig. 3. Bayesian inference 50 % majority rule consensus phylogram of the Pleurotineae from 5.8S-18S-28S-RPB1-RPB2-EF-1α sequence data. Bayesian posterior probabilities (PP) and Maximum Likelihood bootstrap values (ML-BP) are shown on branches, ordered as PP/ML-BP. Thickened branches received support at least in one of the analyses (ML-BP ≥ 70 % and/or PP ≥ 95 %). Family names recognised within the Pleurotineae are marked with colour boxes. Basidioma types are indicated with different colours for ingroup taxa.

**Basidioma types-colour legend**

- Agaricoid (pleurotoid)
- Clavarioid
- Reduced clavarioid/typhuloid
- Corticioid
- Gasteroid

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**Phylogenetic origns of typhuloid fungi**

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from GenBank and from the following genomes through the MycoCosm portal (Grigoriev et al. 2014): Agaricus bisporus, Coprinopsis cinerea (Murat et al. 2015), Laccaria bicolor (Martin et al. 2008), Onnia scabra, Phellinus ferrugineofuscus, Plicatiporus crispa (Kohler et al. 2015), Pterulicium gracile (Varga et al. 2019, deposited as Pterula gracilis), Radulomyces confluens and Trichaptum abietinum (Table 2). Nucleotide sequences were aligned manually using Aliview (Larsson 2014). Protein-coding genes were translated to amino acids to determine intron positions. In order to check gene-tree congruence, each individual gene-region was analysed using a ML approach, as explained above. Gene congruence was assessed manually by comparing supported clades among single-gene genealogies (Mason-Gamer & Kellogg 1996). Clades were considered in conflict if a supported clade (ML-BP >70 %) for one marker was contradicted with significant support by another one. Since no conflict was detected, markers were concatenated in the Agaricales, Typhulaceae and Hymenochaetales alignments. Introns were excluded and the third codon position was partitioned in the protein-coding genes (RPB1, RPB2 and EF-1α). Each matrix was subjected to ML and Bayesian analyses. ML analyses were conducted as explained above. Bayesian analyses were implemented in MrBayes v. 3.2.6 (Ronquist et al. 2012), using two parallel runs of eight Metropolis-coupled Markov chain Monte Carlo (MCMC) chains for 30 M generations, starting from a random tree, and sampling one tree every 1 000th generation from the posterior distribution. Substitution models were sampled across the GTR space during the MCMC simulation (Ronquist et al. 2012). Stationarity was assumed when average standard deviation of split frequencies fell below 0.01. A burn-in sample of 30 000 trees was discarded. To assess branch confidence, a 50 % majority rule consensus tree was computed with the remaining 30 002 trees using the SUMT command of MrBayes. Bayesian posterior probability (PP) values 0.95 were considered to be significant. The alignments and respective phylogenetic trees were deposited in TreeBASE, study number S25967.

RESULTS

Origins of typhuloid fungi within Agaricales and Pleurotinae

A total of 118 (21 5.8S, 23 28S, 18 18S, 13 RPB1, 23 RPB2, 20 EF-1α) sequences were generated for this study (Table 2). The Agaricales matrix comprised 81 taxa and contained 6 292 unambiguously aligned nucleotide positions (161 nu5.8S, 1 480 nu28S, 1 745 nu18S, 861 RPB1, 1 056 RPB2 and 989 EF-1α), with all genes available for 86.4 % of taxa. The Pleurotinae matrix had 39 taxa and contained 6 215 unambiguously aligned nucleotide positions (159 nu5.8S, 1 418 nu28S, 1 732 nu18S, 863 RPB1, 1 056 RPB2 and 987 EF-1α), with all genes available for 72.2 % of taxa. The Bayesian analysis of the Agaricales and Pleurotinae datasets reached average standard deviations of split frequencies > 0.01 after 12 195 000 and 425 000 generations, respectively. The Bayesian majority rule consensus tree of the Agaricales was fully resolved and many deeper branches received high support by Bayesian PP (Fig. 2). The majority of these branches were, however, not supported by ML-BP (< 70 %). Typhuloid fungi do not form a monophyletic group.

Species with skeletal hyphae nest in Pleurotinae (Pterulicium gracile) and in Clavariinae (C. acuminata). Sequences of the specimen of P. gracile collected by us (IO.14.142) were identical to those obtained from the available genome of P. gracile (CBS 309.79) (Fig. 3), employed also by Leal-Dutra et al. (2020). Clavariinae forms a strongly supported clade (PP 1, ML-BP 86) that is resolved as an early diverging lineage within Agaricales (PP 1). Ceratellopsis acuminata forms a highly supported clade with Ramariopsis kunzei (PP 1, ML-BP 100). The remaining Agaricales form a strongly supported monophyletic group (PP 1), within which Ampullolitocybe clavipes, Cantharocybe gruberi, Hygrocybe coccinea, Hygrocybe pudorinus and Pseudomariellaria ectypoides, corresponding to the Hygrophoraceae, constitute a strongly supported lineage in the Bayesian analysis (PP 0.98), as a sister group to the rest of the Agaricales (PP 1). The suborders Agaricinatae (PP 0.96), the Tricholomatinae (PP 1), the Marasmiineae (PP 0.99) and the Pluteineae (PP 0.95) also received high support in the Bayesian analysis. Xeromphalina campanella, previously assigned to the hygrophorid clade, is supported as an early diverging sister lineage to the Marasmiineae (PP 0.98). Species of Typhula and Macrotyphula form a well-supported clade together with other pleurotoid, clavarioid, corticioid and gastrodiscoid species (PP 0.95) that is referred to the Pleurotinae. The Agaricales (ag) and Pleurotinae (pl) phylogenies (Figs 2, 3) show similar supported nodes in the Pleurotinae, except that the Pleurotaceae formed a sister group to the rest of the Pleurotinae in both Bayesian and ML analyses of the Pleurotinae matrix (PP 1, ML-BP 99). In all analyses T. phacorrhiza is nested within a monophyletic Macrotyphula (ag PP 1, ML-BP 100; pl PP 1, ML-BP 100). A specimen identified as Sclerotium complanatum is nested within a clade of three T. phacorrhiza collections in the analyses of the Pleurotinae matrix. The Macrotyphula clade is encompassed in a larger supported clade together with Phylotopsis and Pleurocybella porrigens (pl PP 1). Stephanospora caroticolor, Cristina rhena, Pterulaceae and Radulomycetaceae (Aphanobasidium, Radulomyces) form a strongly supported clade (pl PP 1, ML-BP 73) sister to the Macrotyphula clade, Phylotopsis and Pleurocybella porrigens. All Typhula species but its type T. phacorrhiza, form a distinct separate lineage (pl PP 1, ML-BP 100). It includes the types of Cnazonaria, Dacyropsella, Gliocoremy, Phacorrhiza, Pilillaria, Pilillaria, Scleromitra, Sphaerula and Tygervalleyomyces. Typhula is a sistergroup to the clade formed by Macrotyphula, Phylotopsis, Pleurocybella porrigens, Pterulaceae and Stephanosporaceae in the Pleurotinae phylogeny (Fig. 3), albeit without support (pl PP 0.94). Pleurotus and Hohenbuehelia tremula are supported as a sistergroup to the rest of the Pleurotinae in the Pleurotinae phylogeny (Fig. 3, PP 1, ML-BP 99).

The Clavariaceae phylogeny

The Clavariaceae matrix comprised 53 taxa and contained 1 505 unambiguously aligned nucleotide positions (28S rDNA). Bayesian and ML analyses produced very similar topologies (Fig. 4). Species of Mucronella form a highly supported sister group to the rest of the Clavariaceae (PP 1, ML-BP 100). Clavaria, Camarophyllopsis, Hodophilus and Hirticlavula elegans form a highly supported monophyletic group (PP 1, ML-BP 84), characterised by lacking clamp connections on context hyphae in all species but Clavicorona taxophila. Three species of
Ceratellopsis form a distinct clade with several environmental sequences (uncultured Basidiomycota in GenBank). The relationships of the Ceratellopsis clade to the other genera with clamp connections, Ramariopsis and Clavulinopsis, are not resolved with support.

The Hymenochaetales phylogeny

The Hymenochaetales matrix contained 37 taxa and 4,239 unambiguously aligned characters. The majority rule consensus tree of the Bayesian analysis is provided in Fig. 5. The Hymenochaetales is recovered as monophyletic with
high support in the Bayesian analysis (PP 1, ML-BP 62). It comprises two larger clades: a) a clade containing \textit{Coltricia}, \textit{Kneiffiella}, \textit{Xylodon} and \textit{Hymenochaetaceae}, corresponding to clades C–F in Larsson \textit{et al.} (2006), along with two species of \textit{Repetobasidium} (PP 0.91, ML-BP 26); and b) a clade corresponding to the \textit{Rickenella} clade (clade B in Larsson \textit{et al.} 2006) (PP 1, ML-BP 57). Within the \textit{Rickenella} clade, the three \textit{Ceratellopsis sagittiformis} specimens are encompassed in a well-supported clade (PP 1, ML-BP 65) with species of agaricoid (\textit{Blasphalia}, \textit{Cantharellopsis}, \textit{Gyroflexus}, \textit{Rickenella}), clavarioid (\textit{Alloclavaria}), corticioid (\textit{Globulicium}, \textit{Hyphodontia}, \textit{Peniophorella}, \textit{Resinicium}), cyphelloid (\textit{Muscinupta}) and thelephoroid (\textit{Cotylidia}) basidiomata. The position of \textit{Hyphodontia alutaria} and \textit{Resinicium bicolor} is in conflict; both species form a supported monophyletic group with \textit{Rickenella fibula} and \textit{C. sagittiformis} in the Bayesian analysis (PP 99), as opposed to a monophyletic group with \textit{Cotylidia} spp. in the ML analysis (ML-BP 75).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig5.png}
\caption{Bayesian inference 50\% majority rule consensus phylogram of the hymenochaetoid clade from 5.8S-18S-28S-RPB2 sequence data. Bayesian posterior probabilities (PP) and Maximum Likelihood bootstrap values (ML-BP) are shown on branches, ordered as PP/ML-BP. Thickened branches received support at least in one analysis (ML-BP $\geq$ 70\% and/or PP $\geq$ 95\%). Basidioma types are indicated with different colours for ingroup taxa.}
\end{figure}
Taxonomy

Clavariineae Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, subord. nov. MycoBank MB831365.

Basidiomata clavarioid, more rarely agaricoid with waxy decurrent gills, or corticioid. Hyphal system monomitic, or more rarely dimitic. Basidiospores hyaline, usually thin-walled, smooth or ornamented, usually with multiguttulate contents, sometimes with amyloid or dextrinoid reactions, usually with a cubic apiculus. Basidia claviform, with up to 4 sterigmata, chiastic, sometimes characteristically long (< 50 μm) or short (> 20 μm), occasionally sometimes with a loop-like basal clamp (Clavaria subgen. Holocoryne). Cystidia usually absent. Pileipellis either a hymeniderm or a trichoderm with rounded terminal elements in genera with agaricoid basidiomata. Basal tomentum composed of narrow, usually < 2 μm broad thick-walled hyphae in clavarioid genera (Ceratellopsis, Clavaria, Clavulinopsis, Ramariopsis), possibly also in other stipitate genera. Clamp connections present or absent, sometimes restricted to basidia. Saprotrophic on dead wood, herbaceous plants or leaves, or biotrophic with grasses and bryophytes. Presence of EF-1α intron 21 (numbering according to Matheny et al. 2007) in some genera (absent in Ceratellopsis).

Type family: Clavariaceae Chevall.

Notes: This suborder contains a single family. Similar isotopic ratios to those found in the Hygrophoraceae suggest that at least non-lignicolous members of Clavariaceae have some kind of biotrophic association with plants (Birkebak et al. 2013), whereas genera occurring on dead plant remnants are probably saprotrophic (Ceratellopsis, Mucronella, Hirticlavula). Very narrow and slightly thick-walled hyphae in the basal tomentum and mycelium

Fig. 6. Ceratellopsis acuminata (epitype, Huhtinen 15/07, S). A–C. Dried basidiomata. D. Basidioma observed using a light microscope. E. Close-up of basidium apex. F. Basidiospores. G. Basidia. H. Medullar hyphae resembling skeletal hyphae. I. One-year-old culture in MEA, kept at 5 °C (culture ex-epitype, CBS 146691). J. Hyphae from cultured mycelium (culture ex-epitype, CBS 146691). Mounting media were Melzer’s reagent (D), Congo Red in ammonia (E–H) and water (I). Scale bars: D = 100 μm, E–H = 10 μm; I = 10mm. Photographs I. Olariaga.
are characteristic for many species of Clavariaceae, including species in Clavaria, Clavulinopsis, Ramariopsis (Olariaga 2009) and Ceratellopsis (Fig. 6) and it might be a synapomorphic character of the Clavariaceae. The presence of EF-1α intron 21, absent in the rest of the Agaricales (Matheny et al. 2007) seems so far unique to some Clavariaceae (Clavaria, Clavulinopsis, Camarophyllum). Clavariaceae Chevall., Fl. Gen. Env. Paris 1: 102. 1826. [“Clavariæ”; “ordre”; considered family according to Art. 18.2].

Type genus: Clavaria Vaill. ex L. : Fr.

Genera: Camarophyllum, Ceratellopsis, Clavaria, Clavulinopsis, Hirticlavula, Hodophilus, Hyphodontiella, Mucronella, Ramariopsis.

Ceratellopsis Konrad & Maubl., Icon. Select. Fung. 6: 502. 1937.

Basionym: Ceratella Pat., Hymenomyc. Eur.: 137. 1887. [nom. illeg. Art. 53.1, later homonym of Ceratella Hook f. 1844].

Presumed presaprobic on bark, dead wood or culms. Basidiomata gregarious, clavarioid, 0.2–1(–2) mm high, lanceolate with a sterile pointed apex, white. Stipe usually present, short, glabrous or pubescent. Hypgal system monomitic or dimitic. Basidiospores without iodine reactions. Basidia claviform, short, 10–16 μm long. Generative hyphae present in the medulla, unidirectional, cylindrical, septate, thick-walled, 1–2.5 μm broad, sometimes dextrinoid. Skeletal hyphae present in the medulla of C. acuminata and further undescribed species known by us. Clamp connections scattered.

Type: Ceratellopsis acuminata (Fuckel) Corner, typ. cons. prop.

Notes: The background of the name Ceratellopsis requires, however, further clarification as its type has been a matter of controversy. According to our nomenclatural study, Ceratellopsis is a validly published replacement name based on Ceratella Pat. and typified by Pistillaria queletii. The final epithet Ceratella was first employed by Quellet (1886) for an unranked infrageneric name. Later, although Patouillard (1887) referred to Ceratella as “CERATELLA (Quel.)“ he did not have in mind Clavaria [un-ranked] Ceratella as the basionym of a new combination. As explained in the introduction of the Hymenomycètes (Patouillard 1887: VII), authors of generic names were cited between round brackets only when Patouillard’s circumscriptions were absolutely different from the original ones. Therefore, we consider Ceratella as the name of a new taxon to be cited as “Ceratella Pat.” (J. McNeill, pers. comm.) in agreement with Donk (1954) and the ING (Farr & Zijlstra 2020). Nevertheless, Ceratella Pat. (1887) is illegitimate as a later homonym of Ceratella Hook f. (1846). When Ceratellopsis was introduced, Konrad & Maublanc (1937) referred to it as a new name for “Ceratella (Quel. p.p.), Patouillard (1887)” and proposed Ceratellopsis queletii as the type, without providing a Latin description. Since Ceratellopsis was a replacement name for Ceratella Pat., and not a new taxon, Ceratellopsis is a validly published generic name even though it lacked a Latin description and was published later than 1935 (Art. 39.1), because such is not required for a replacement name. The type proposed for Ceratellopsis by Konrad & Maublanc is also in order, since Ceratella queletii was one of the three species listed under Ceratella Pat. (1887). A relevant fact that might have affected the typification of Ceratellopsis is whether the combination Ceratella queletii was validly published when Patouillard erected Ceratella Pat. Patouillard (1887) listed C. queletii as “C. Queletii” without explicitly citing its basionym Pistillaria queletii. However, we interpret that Patouillard (1887: VI) gave an indirect reference to the basionym that fulfills conditions for valid publication of C. queletii (Art. 41.3 and 38.14) by explicitly stating that Tabulae Analyticae Fungorum, the place of publication of Pistillaria queletii, basionym C. queletii, was one of the main works on which he based his Hyménomycètes (Art. 41.4, Ex. 9), and because Patouillard himself was author of the basionym.

For details on our choice to suggest C. acuminata as the conserved type for Ceratellopsis see notes under Pterulicum and the Discussion.

Ceratellopsis acuminata (Fuckel) Corner, Ann. Bot. Mem. 1: 202. 1950. Fig. 6. 
Basionym: Pistillaria acuminata Fuckel, Fungi Rhen. Exs. (suppl.) 4: no 1888. 1867. Synonym: Ceratella acuminata (Fuckel) Pat., Essai Tax. Hyménomyc.: 49. 1900.

Basidiomata gregarious, 0.2–0.4 mm high, simple, with a short stipe and a sterile apex. Fertile part cylindrical to oblong, sharply delimited from the stipe and the apex, white, 0.1–0.3 × 0.02–0.04 mm. Stipe short, cylindrical, glabrous, hyaline white, 0.04–0.12 × 0.01–0.02 mm. Apex pointed, acute, hyaline white, 0.04–0.1 mm long. Basidiospores ellipsoid to pip-shaped, sometimes in tetrads, hyaline, without iodine reactions, (3–) 4–6 × (1.5–)2–3 μm. Basidia claviform, 2–4-spored, 10–16 × 3.5–4.5 μm, clamped. Generative hyphae cylindrical, hyaline, thin-walled, clamped, sometimes with scarce septa at the stipe base, 1.2–2.2 μm broad. Skeletal hyphae present in the medulla, cylindrical, refractive, slightly dextrinoid, 1.2–2.8 μm broad. Colonies on MEA 30–40 mm diam after 1 yr at 5 °C, superficial, effuse, convex, tomentose, hard-textured, with erect white tufts and strong smell reminiscent of Soloroderma. Reverse white. Margin regular and distinct. Vegetative hyphae cylindrical, closely septate, very slightly thick-walled, hyaline, 2.5–4 μm broad, with scattered clamp connections. Asexual morh not observed in culture.

Typus: Germany, Nassau, Johannisberger Schlosswald, ad pini Sylv. folia putrida fales humus, Fuckel, Fungi Rhen. Exs. no 1888 (S-F128455 !, lectotype of Pistillaria acuminata designated here, MycoBank MBT387677). Isolotyptes: S-F267533 (!), S-F267533 (!), FH00068504 (!), K(M) 159801, M. Sweden, Härjedalen, Tännadal, Hamrafjallet Nature Protection Area, on dead leaves of Dryas octopetala, 4 Aug. 2015, S. Hultinen 15/07 (S, epitype of Pistillaria acuminata designated here, MycoBank MBT389356). Culture ex-epitype: CBS 146691.

Known distribution: Denmark, Finland, France, Germany, Norway, Spain and Sweden.

Additional materials examined: Denmark, Sjælland, Bognes skov, on leaves of Leymus on exposed beach, 26 Oct. 2019, T. Løvæs, DMS-10058526 (C). Finland, Pera-Pohjarnaa, Rovaniemii, Lovevaa Nature Protection area, brooksides herb-rich forest, on leaf litter under alders, 7 Sep. 2012, S. Hultinen 12/15 (TUR 197690). France, Val-d’Oise, Montmorency, ad cortices, 1889, Boudier herbarium (PC). Norway, Finnmark, Nord Varanger, Varanger Peninsula, Fosefjellet (ca. 3 km NW of Valdø), on hare dung (Lepus timidus) in moist chamber, 27 Jul. 1966, N. Lundquist 4965g (UPS F-152857), Sweden, Gärskirkan, Gäve, Lövudden, Satix viminal, fola dejecta, 25 Jun. 1953, J.A. Nannfeldt 12800 (UPS F-152650, as Ceratellopsis sp.); Lycksele Lappmark, Saxnäs, Satsfjälad, on dead fern stems, 28 Jul. 2010, K. Hansen, K. Gillen & I. Olariaga, IO.10.01 (S); Västergötland, Häkantorp, Aspås hållplats, on Quercus robur leaves, 2 Oct. 1955, S. Kiland (UPS F-152830).
Notes: Ceratellopsis acuminata differs from C. aculeata in having skeletal hyphae in the basidioma core. Another collection identified as C. aff. acuminata by us (ARAN-Fungi 11746) possessed also skeletal hyphae, but had longer and shorter basidiomata and nested in a different clade than the epitype of C. acuminata (Fig. 4). This substantiates the idea that an additional species of Ceratellopsis exists and when more specimens become available the species limits should be studied further.

Corner (1950: 203) mentioned a type collection of Pistillaria acuminata (that Donk had examined in ms) without providing a collection number or a herbarium. Since we believe that Corner’s type indication did not fulfil requirements for achieving a valid typification (Art. 7.11), we propose here a lectotypification of C. acuminata. The four syntypes examined are very meagre. Therefore, we select as epitype a recent collection from which a living culture and several gene regions have been obtained. We found C. acuminata to have a very broad host range and distribution, and feel justified in selecting Swedish material collected on Dryas leaves as epitype.

Ceratellopsis aculeata (Pat.) Corner, Ann. Bot. Mem. 1: 200. 1950.

Basionym: Pistillaria aculeata Pat., Tab. anal. Fung. 1: 26. 1883.
Synonyms: Ceratella aculeata Pat., Essai Tax. Hyménomyc.: 49. 1900.
(?) Pistillaria mucedinea Boud., Bull. Soc. bot. Fr. 24: 308. 1878.
(?) Ceratellopsis mucedinea (Boud.) Corner, Ann. Bot. Mem. 1: 204. 1950.

Type: No type specimen in the Patouillard herbarium (FH, PC).

Lectotype of Pistillaria aculeata designated here: Patouillard, Tab. Anal. Fung. 1: fig. 58. 1883. MycoBank MBT387467.

Specimens examined: Denmark, Lolland, Maribo Søndersee, on stems of Cladium mariscus, 9 Oct. 2000, T. Lolland, Maribo Søndersee, DMS-376001 (C). Denmark, Lolland, Maribo Søndersee, on Cladium mariscus, 12 Aug. 1926, E.J.H. Corner (PC).

Notes: Medulla hyphae in Ceratellopsis aculeata are thick-walled and have scarce septa, as noted by Corner (1950). Originally described as occurring on fallen leaves, C. aculeata has been considered to typically occur on dead leaves of Cladium mariscus (Corner 1950, Hansen & Knudsen 1997). Specimens collected on bark or dead wood share a similar basidioma configuration, hyphae and spores.

As Corner (1950) suggested Pistillaria mucedinea is very close to C. aculeata. The small size of basidiomata (0.5–0.75 mm) and the 4-spored basidia described in the protologue support this view. Furthermore, our study of an authentic specimen kept at PC, collected on bark as described in the protologue, has scarcely septeate thick-walled hyphae as observed in the material on Cladium mariscus. We agree with Corner (1950) and even suggest P. mucedinea might be conspecific with C. aculeata and list it as a possible earlier synonym. However, a better insight on species limits in Ceratellopsis needs to be acquired to further test this.

Names formerly placed in Ceratellopsis and imperfectly known, excluded here or illegitimate

Ceratellopsis aciculata (Durieu & Lév. ex Sacc.) Corner, Ann. Bot. Mem. 1: 200. 1950.

Basionym: Pistillaria aciculata Durieu & Lév. ex Sacc., Syll. Fung. 6: 759. 1887.

Type: Lectotype designated here: Bory de Saint-Vincent & Durieu de Maisonneuve, Explic. Sci. Algèr. 1(5): tab. 32, fig. 4. 1846. MycoBank MBT387461.

Notes: Pistillaria aciculata, published as a nomen nudum (Bory de Saint-Vincent & Durieu de Maisonneuve 1846), was invalid until Saccardo provided a description. The illustration provided by Bory de Saint-Vincent & Durieu de Maisonneuve (1846) shows brown, pointed acute structures that do not look like a fertile fungus but rather incipient basidiomata of a marasmioid fungus. This figure, to our knowledge, the only original element and it is accordingly proposed as lectotype.

Ceratellopsis asphodeli (Pat.) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: Ceratella microscopica var. asphodeli Pat., Cat. Pl. Cell. Tunisie: 66. 1897.

Type: No type specimen in the Patouillard herbarium (FH, PC). No original illustration.

Notes: The 2-spored basidia and the presence of cystidia described in Patouillard (1897) suggest that C. asphodeli is a synonym of Pterulicium gracile. The pink tones can be present in P. gracile (Olariaga 2009).

Ceratellopsis biforis Khurana in Berthier, Bull. Soc. Linn. Lyon. 45: 190. 1976 [nom. illeg., Art. 39, 40].

Notes: The description provided by Berthier (1976) based on Corner’s notes of a fungus on Quercus leaves from India suggests that C. biforis may belong to Ceratellopsis as conceived here due to its narrow, 1.5–2 μm broad, medulla hyphae. Nevertheless, C. biforis was never validly published since neither a Latin diagnosis nor a type specimen were provided for it.

Ceratellopsis brondaei (Quél.) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: Clavaria brondaei Quél., Revue mycol. (Toulouse) 14(54): 65. 1892.

Type: No type specimen in PC and TL.

Notes: Quélé (1892) described C. brondaei apparently based only on the Brondeau plate no. 165 (“Alb. 165”). The illustration provided in the protologue (plate 126, fig. 3), probably a reproduction of plate no. 165, shows a small white clavarioid fungus, said to grow in forest on soil among tiny mosses. The description, except the ecology, tallies with a species of Ceratellopsis as treated here, but in the absence of microscopic information and a type specimen, a reliable interpretation cannot be provided, as Corner (1950) stated.

Ceratellopsis caespitulosa (Sacc.) Corner, Ann. Bot. Mem. 1: 203. 1950.

Basionym: Pistillaria caespitulosa Sacc., Atti del Congr. bot. di Palermo. 1902.

Type: [from Saccardo, Syll. Fung. 17: 202. 1905] France, Côte d’Or, in cortice emortuo Loniceræ periclymeni [Loniceræ periclymenum], PAD.

Notes: The denticulate “basidia” and the 1-septate biguttulate spores suggest that C. caespitulosa is an asexual morph fungus,
probably conspecific with *Isaria friesii* (Leotiomycetes, Ascomycota).

**Ceratellopsis carestiae** (Ces.) Corner, Ann. Bot. Mem. 1: 203. 1950.

**Basionym**: *Pistillaria carestiae* Ces. in Bres. & Sacc., Malpighia 11: 255. 1897.

**Typus**: *Italy*, Piemonte, Alagna Valsesia, *sur ramis secchi Syringa vulgaris*, 13 Oct. 1857, Ab. Carestia no 27 (S-F15983 !, ex Bresadola herbarium; *lectotype* designated here, MycoBank MBT387464).

*Notes*: The material constitutes an asexual fungal state growing on bark, very probably conspecific with *Isaria friesii*. The spore content, described as divided in two ("plasma bipartito") is due, in fact, to the 1-septate spores, as in *C. caespitulosa* (see above).

**Ceratellopsis corneri** Berthier, Bull. mens. Soc. linn. Lyon 43: 188. 1974.

**Typus**: *France*, Lyon, Soucieu-en-Jarrest, sur liècocur pourrissant d’un arbre abattu (Gymnosperme?), Bussy, 11 Apr. 1970 (*holotype* G).

*Notes*: Due to the 4–6 μm broad medulla hyphae and the amyloid spores, *C. corneri* does not conform to *Ceratellopsis*. We consider it that *C. corneri* should be examined and compared to *Mucronella* instead.

**Ceratellopsis dryopteridis** (S. Imai) Corner, Ann. Bot. Mem. 1: 203. 1950.

**Basionym**: *Pistillaria dryopteridis* S. Imai, Sapporo Trans. Soc. Sci. 13(4): 386. 1934.

**Typus**: *Japan*, Ishikari province, Nov. probably at SAPA.

*Notes*: The filiform 1–5 mm long basidiomata and 9–12.5 μm long spores suggest that *C. dryopteridis* should not be excluded from *Ceratellopsis*. The spores of *C. dryopteridis* are asperulate and therefore a relationship with *Pterula* is suggested here, but the type specimen, if it exists, should be examined to confirm this.

**Ceratellopsis equiseticola** (Boud.) Corner, Ann. Bot. Mem. 1: 204. 1950.

**Basionym**: *Pistillaria equiseticola* Boud., Bull. Trimestr. Soc. Mycol. France 33(1): 13. 1917.

**Typus**: *France*, Saône-et-Loire, Clovey (?), *ad caules Equiseti uviatile* [Equisetum fluviatile], May 1915, Boudier herbarium (PC !, as *P. equisetina*; *lectotype* designated here, MycoBank MBT387465).

*Notes*: As earlier suggested by Berthier (1976), we conclude that *C. equiseticola* is a synonym of *P. gracile* after examining type material.

**Ceratellopsis graminicola** (Bourd. & Galzin) Corner, Ann. Bot. Mem. 1: 204. 1950.

**Basionym**: *Pistillaria graminicola* Bourdot & Galzin, Hymenomyc. France: 139. 1928.

**Typus**: No type specimen in the Bourdot & Galzin herbarium (PC). No original illustration.

*Notes*: The 12–18 μm long, 2–4-spored basidia, small spores (6–7 × 4 μm) and narrow, 1.5–2.5 μm broad hyphae given in the original description would indicate that *C. graminicola* should be retained in *Ceratellopsis*, rather than being conspecific with *P. gracile*. It might be conspecific with *C. aculeata* or *C. acuminata*, but details on its hyphal structure are necessary to provide a solid interpretation.

**Ceratellopsis helenaee** (Pat.) Corner, Ann. Bot. Mem. 1: 204. 1950.

**Basionym**: *Pistillaria helenaee* Pat., Tab. Anal. Fung. 1: 26. 1883.

**Typus**: No type specimen in the Patouillard herbarium (FH, PC).

**Lectotype** designated here: Patouillard, Tab. Anal. Fung. 1: fig. no. 57. 1883. MycoBank MBT387466.

*Notes*: The forked or sparsely branched basidiomata, with a tendency to be caespitose, and the presence of a distinct stipe, suggest that *C. helenaee* is a synonym of *Typhula crassipes*. Although basidiomata of *T. crassipes* are usually simple, we have observed branched basidiomata as those depicted in the lectotype figure. Also, 2-spored basidia and incarnate tones are sometimes present in *T. crassipes* (Olariaga 2009). Corner (1950) compared *C. helenaee* to *P. gracile*, but the latter lacks a stipe.

**Ceratellopsis kubickae** Plát., Česká Mykol. 12(4): 217. 1958.

**Typus**: *Czech Republic*, prope Tieboň, *ad folium putridum Salisic aunitae* [Salix aunita], 15 May 1958, Kubička (PRM 655767).

*Notes*: Plát (1958) described *C. kubickae* as monomitic and compared it with *P. gracile*. Berthier (1976) investigated the type material and proposed that *C. kubickae* is a synonym of *P. gracile*, and that Plát (1958) overlooked skeletal hyphae. In our opinion, the 2-spored basidia and the absence of a stipe in *C. kubickae* support it is a synonym of *P. gracile*.

**Ceratellopsis mucosa** (Berk. & M.A. Curtis) Corner, Ann. Bot. Mem. 1: 205. 1950.

**Basionym**: *Typhula mucosa* Berk. & M.A. Curtis, Grevillea 2(14): 18. 1873.

**Typus**: *USA*, South Carolina, Society Hill, in herb. mort., 1852, Carolina inf. No. 3832 (*syntypes* FH 596847, K).

*Notes*: The original description is very meagre, and we are unable to propose a reliable interpretation without checking type material. Corner (1950) failed also to provide a specific interpretation and stated that *C. mucosa* "may be *Ceratellopsis, Pterula*, or a rudimentary *Pistillaria*".

**Ceratellopsis rickii** (Oudem.) Corner, Ann. Bot. Mem. 1: 205. 1950.

**Basionym**: *Mucronella rickii* Oudem., Ned. kruikd. Archf., 3 sér. 2(3): 667. 1902.

**Synonym**: *Cnaezonaria rickii* (Oudem.) Donk, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 9: 99. 1933.

**Typus**: *The Netherlands*, Limburg, Valkenburg, *in caulibus herbarum praesertim Asparagi officinalis*. [Asparagus officinalis], May 1901, J. Rick, herb. Oudemans (*holotype* L). *Isotype*: Bourdot & Galzin herbarium (PC !).

*Notes*: Jūlich (1980) reduced *C. rickii* to a synonym of *P. gracile* after examining type material. We confirm this synonymy based on characters seen on the cited isotype.

**Ceratellopsis rosella** (Fr.) Corner, Ann. Bot. Mem. 1: 206. 1950.
Basionym: Pistillaria rosella Fr., Epicr. syst. mycol.: 587. 1838. [1836–1838].

Typus: No type specimen in the Fries herbarium (UPS). No original illustration.

Notes: The pink colour described in the protologue is almost unique to T. micans among typhuloid fungi and we thus agree with Berthier (1976) in considering C. rosella a synonym of T. micans.

Ceratellopsis sydowi (Bres.) Corner, Ann. Bot. Mem. 1: 206. 1950.

Basionym: Clavaria sydowi Bres. in Sydow, Hedwigia 35: (61). 1896.

Typus: Germany, Saxony, Muskau, O.L. Bergpark, ad ramulos Robiniae pseudoacacieae, Jul. 1895, P. Sydow, Mycoth. March. 4405 (syntypes CHRBR, MIN, NCU).

Notes: The caespitose growth habit on dicot. bark, pale pink colour (“dilute carnei”), long basidia (24–26 μm) and spore size mentioned in the protologue (9–10 × 5–5.5 μm) suggest that C. sydowi is a synonym of T. crassipes.

Ceratellopsis terrigena Berthier, Bull. Soc. Linn. Lyon 43(6): 188. 1974.

Typus: France, Rhone, Lyon, Izeron, sur terre nü d’un talus en sous-bois, 7 Aug. 1966, CL 29 (holotype G).

Notes: Due to its 1.5–3.5 μm broad medulla hyphae C. terrigena does not conform to Ceratellopsis as here defined. Also, the presence of striking protruding cystidia is unknown for any other species of Ceratellopsis. The shape of cystidia and the absence of clamp connections may suggest C. terrigena to be allied with Alloclavaria in the Rickenella clade (Hymenochaetales).

Ceratellopsis thujicola (Kauffman) Corner, Ann. Bot. Mem. 1: 206. 1950.

Basionym: Pistillaria thujicola Kauffman, Pap. Mich. Acad. Sci. 9: 207. 1929 [1928].

Typus: USA, Michigan, Alger: Rock River, on inner side of Thuya occidentalis on loose bark, 8 Sep. 1927, C.H. Kauffman (holotype MICH11745).

Notes: The up to 10 mm long branched basidiomata do not conform clearly to Ceratellopsis as here defined, and we thus exclude it from this genus. The type material should be examined to propose a more precise interpretation.

Ceratellopsis tremula (Sacc.) Corner, Ann. Bot. Mem. 1: 207. 1950.

Basionym: Pistillaria ferryci subsp. tremula Sacc. in Sacc. & D. Sacc., Syll. Fung. 17: 202. 1905.

Typus: Italy, Padova, horto botanico Patavino, ad fructum putrem Trichosanthis anguineae [Trichosanthes sanguinea], ubi Botrytis vulgaris et Acremoniella atra, Feb. 1904 (syntype PAD).

Notes: The 3–5 mm long basidiomata, 2-spored basidia and 8–11 μm long spores conform to P. gracile, but the type specimen needs to be examined to confirm the synonymy. Although this synonymy is listed in Index Funorum (2019, viewed on 11 June 2019), it has not been otherwise proposed to our knowledge.

Pleurotineae Aime, Dentlinger & Gaya, Biol. J. Linn. Soc.: 10.1111/bij.12553, 16. 2015.

Phyllotopsisidae Locquin ex Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, fam. nov. MycoBank MB831374.

Basidiomata pleurotoid or clavarioid and sometimes arising from a sclerotium. Spore deposit white to salmon pink. Hymenial system monomitic. Basidiospores hyaline, cylindrical, allantoid or sub-globose, smooth, without iodine reactions. Cheilocystidia sometimes present in pleurotoid genera. Clamp connections present, rarely absent. Saprotrophic.

Type genus: Phyllotopsis E.-J. Gilbert & Donk ex Singer

Representative genera: Macrotypha, Phyllotopsis and Pleurocybella.

Notes: Macrotypha, Phyllotopsis and Pleurocybella were suggested to be closely related by Dentlinger & McLaughlin (2006) and our analyses confirm that they form a monophyletic group. Despite this, no obvious synapomorphic characters support the relationship between the typhuloid Macrotypha and the pleurotoid Phyllotopsis and Pleurocybella (Moncalvo et al. 2002). All three genera contain saprotrophic species, mostly lignicolous, and possess clamp connections.

Macrotypha R.H. Petersen, Mycologia 64: 140. 1972. nom. cons. prop.

Type: Clavaria fistulosa Holmsk.: Fr. (synonym: Macrotypha fistulosa (Holmsk.: Fr.) R.H. Petersen).

Synonyms: Sclerotium Tode, Fung. mecklenb. sel. 1: 2. 1790 : Fr., Syst. Mycol. 2: 246. 1822. nom. rej. prop. Type: Sclerotium complanatum Tode : Fr. (synonym: Typhula phacorrhiza (Reichard : Fr.) Fr.). Clavariadelphus subgen. Typhulus Corner, Ann. Bot. Mem. 1: 692. 1950 [nom. inval. Art. 40.3, two species were indicated as type].

Macrotypha megasperma (Berthier) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, comb. nov. MycoBank MB831762.

Basionym: Typhula megasperma Berthier, Bull. Soc. Linn. Lyon 45: 78. 1976.

Macrotypha phacorrhiza (Reichard : Fr.) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, comb. nov. MycoBank MB831761.

Basionym: Clavaria phacorrhiza Reichard, Schriffen Berlin. Ges. Naturf. Freunde 1: 315. 1780. [Clavaria phacorrhiza] : Fr., Syst. mycol. 1: 495. 1821.

Synonyms: Sclerotium complanatum Tode, Fung. Mecklenb. Sel. 1: 5. 1790.

Typhula phacorrhiza (Reichard : Fr.) Fr., Observ. Mycol. 2: 298. 1818. [*Typhula*].

Phacorrhiza filiformis Grev., Scott. Crypt. Fl. 2: 93. 1824 [nom. nov. based on Clavaria phacorrhiza Reichard]

Typhula phacorrhiza var. complanata (Tode) Sacc., Syll. Fung. 6: 745. 1888. [*complanata*].

Typus: Lectotype of Clavaria phacorrhiza: Sowerby, Col. Fig. Eng. Fung. 2: tab. 233. 1798, as “phacorrhiza”, designated by Olariaga & Salcedo (2013: 42).

Lectotype of Sclerotium complanatum designated here: Tode, Fung. Mecklenb. 1: tab. 1, fig.
9. 1790. MycoBank MBT387906. Germany. Bayern, Oberbayern, Landkreis Miesbach, valley Kleinhall near Miesbach, in a garden under Ribes nigrum and Ribes rubrum, on wet litter of various plants, mostly of Ribes, 2 Mar. 1992, F. Brand, Microf. Exs. No. 49 (UPS, as Sclerotium complanatum; epitype of Sclerotium complanatum designated here; Isoetitypes in B, BPI, CANB, DAOM, FH, GZU, H, HAL, HMAS, LE, M, MA, NMW, PRM, TNS). MycoBank MBT389352.

Specimens examined: Austria, prope Tullnerbach, in silva ‘Wiener Wald, ad petiolos Fraxinex excelsioris L., C. de Keissly, Krypt. Exs. 1840 (PC, as Sclerotium complanatum). France, Pyrénées atlantiques, Borde, Le Gave d’Aspe, on the ground, among Rubus idaeus and Myrrhis odora, 12 Oct. 2014, J.C. Zamora & I. Olariaga, IO.14.200 (S); without locality, dans les bois, parmi les tas de feuilles pourrées, Desmazières, Pl. Crypt. N. France, Ed. 1536 (PC, as Sclerotium complanatum). Spain, Navarra, Basaburua, Orokietza, Loxandi, on the ground among needles under Picea abies, 27 Oct. 2017, I. Olariaga, J. Martin, J. Teres & J.M. Riezu, ARAN-Fungi 7446. Sweden, Skåne, Eriksdal, Vitabackskällan Nature Reserve, on wet ground under Alnus, 3 Oct. 2014, N.-O. Nilsson & I. Olariaga, IO.14.167 (S); Uppland, Uppsala-Näs, Vreta, in a compost-heap, 18 Oct. 1975, L. Jonsell, Fung. Exs. Suec. 3249 (PC).

**Typhula phacorrhiza var. heterogenea** Berthier, Bull. Soc. Linn. Lyon 45: 197. 1976.

**Type genus:** Pterula Fr.: Fr.

**Representative genera:** Allantula, Coronicium, Dimorphocystis, Merulicium, Pterula, Pterulicum.

**Pterula** Fr.: Fr., Syst. Orb. Veg. 1: 90. 1825.

**Basionym:** Anthina [unranked] Pterula (Fr.) Fr., Syst. Mycol. 3: 285. 1832: Fr., idem.

**Type:** Pterula plumosa (Schwein. : Fr.) Fr., selected by Donk (1954: 472).

**Pterulicum** Corner, Ann. Bot. Mem. 1: 699. 1950. Type: Pterulicum xylogenum Corner

**Synonyms:** Ceratellopsis Konrad & Maubl., Icon. Select. Fung. 6: 502. 1937. Type: Ceratellopsis queletii (Pat.) Konrad & Maubl. (synonym Pterulicum gracile (Desm. & Berk.), Leal-Dutra, Denlinger, G.W. Griff., typ. rej. prop. Defflexula Corner, Ann. Bot. Mem. 1: 695. 1950. Type: Defflexula fascicularis (Bres. & Pat.) Corner

**Notes:** Since the type of Ceratellopsis nests in Pterulicum (Fig. 3), the correct name for Pterulicum is Ceratellopsis under the current nomenclatural rules. A proposal to preserve the current usage of Ceratellopsis and Pterulicum is, however, in preparation (see Discussion).

**Pterulicum gracile** (Desm. & Berk.) Leal-Dutra, Denlinger & G.W. Griff. in Leal-Dutra, Griffith, Neves, McLaughlin, McLaughlin, Clasen & Denlinger, IMA Fungus 11(2): 15. 2020. Basionym: Typhula gracilis Desm. & Berk. in Berk, Ann. Nat. Hist., Ser. 1, 1: 202. 1838. ["Typhula? gracilis."]

**Synonyms:** Clavaria gracilis (Desm. & Berk.) P. Karst., Bidrag Könnedom Finlands Natur Folk 37: 181. 1882. [Cl? gracilis; nom. illeg., later homonym of Clavaria gracilis Bolton and C. gracilis Pers. : Fr., Art. 53.]

**Pistillaria gracilis** (Desm. & Berk.) Pat., Tab. Anal. Fung. 6: 30. 1887. Ceratella gracilis (Desm. & Berk.) Pat., J. Bot. (Morot) 3: 36. 1889.

**Hirsutella gracilis** (Desm. & Berk.) Pat., Essai tax. Hyménomyc.: 50. 1990.

**Pterula gracilis** (Desm. & Berk.) Corner, Ann. Bot. Mem. 1: 514. 1950.

**Clavaria microscopica** Malbr. & Sacc., Michelia 2(6): 42. 1880.

**Clavaria aculina** Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 9: 670. 1881. ["1880"]

**Pistillaria aculina** (Quél.) Pat., Tab. Anal. Fung. 6: 29. 1887.

**Ceratella aculina** (Quél.) Pat., Hymenomyc. Eur.: 137. 1887.

**Clavaria aculina** (Quél.) Donk., Meded. Ned. Mycol. Ver. 22: 97. 1933.

**Pistillaria queletii** Pat., Tab. Anal. Fung. 1: 22. 1882.

**Ceratella queletii** (Pat.) Pat., Hymenomyc. Eur.: 137. 1887. [valid combination following Arts. 41.3 and 38.14.]

**Ceratellopsis queletii** (Pat.) Konrad & Maubl., Icon. Sel. Fung. 6: 502. 1937.

**Typhula brunaudii** Quél., Compt. Rend. Assoc. Franç. Avancem. Sci 13: 283. 1885. [1884].

**Clavaria brunaudii** (Quél.) Sacc., Syll. fung. 11: 730. 1888.

**Ceratella ferryi** Quél. & Fautrey, Revue. Mycol. (Toulouse) 15(57): 15. 1893.

**Pistillaria ferryi** (Quél. & Fautrey) Sacc., Syll. Fung. 11: 141. 1895.

**Ceratella microscopica var. asphodeli** Pat., Cat. Pl. Cell. Tunisie: 66. 1897.

**Ceratellopsis asphodeli** (Pat.) Corner, Ann. Bot. Mem. 1: 203. 1950.

**Pistillaria attenuata** SYD. & P. SYD., Hedwigia 39: (1). 1900.

**Clavaria aculina** Bourdot & Galzin, Hymenomyc. France: 139. 1928. ["1927"].

**Pistillaria juncicola** Bourdot & Galzin, Hymenomyc. France: 138. 1928. ["1927"].

**Typus:** UK, without locality, ex Desmazières herbarium (PC, not found, lectotype designated in Corner (1950: 515) by type indication). **Isolectotype:** UPS (!).

**Additional materials examined: France, Charente-Maritime, Saintonge, maïs [Zea mays], P. Brunaud, Quellet herbarium (PC !, lectotype of Typhula brunaudii designated here, MycoBank MBT387470); Côte-d’Or, Nodan, sur tiges séches de Coix lacryma-jobi, Fautrey, Jun. 1892, Fungi Sel. Gall. Exs. no 6203 (PC, lectotype of Ceratella ferryi designated here, isolectotypes: BR, ILL, MIPS, MycoBank MBT38491); Rhône, Saint Priest, les Bouys, vers le Souey, "sur joncs [Juncus] pursifolians", H. Bourdot, 27 Sep. 1918, Bourdot 24978 (PC !, lectotype of Pterulicum juncicola designated here, MycoBank MBT38771); Seine-Maritime, environs de Rouen, sur jonc [Juncus], Apr. 1880, A. Le Breton, Quellet herbarium (PC !, lectotype of Clavaria aculina designated here, MycoBank MBT387469); Seine-Maritime, Rouen, sur les joncs [Juncus] morts et humides, forêt de Noumare (?), A. Malbranche, (PC !, lectotype of Clavaria microscopica designated here, MycoBank MBT387468). Germany, Brandenburg, Finkenkrug pr. Nauen, ad folia culmosque graminum, Calamagrostis epigej ad folia culmosque graminum, Calamagrostis epigejos (Calamagrostis epigejos), Agrostis alba [Agrostis alba] etc., Mycoth. Mar. no. 4803 (S F15411 !, lectotype of Pistillaria attenuata designated here, isollectotypes: FH00608505 (!, MICH, MycoBank MBT387678). Lectotype of Pistillaria queletii designated here: Patouillard, Tab. Anal. Fung. 1: fig. 45. 1883. MycoBank MBT389354. Sweden, Skåne, Kristianstads kommun, Balsberget Nature Reserve, on dead standing Juncus effusus stalks, at damp place, N.-O.
Typhula

Type

Typhula podocarpi (Crous) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, gen. nov. MycoBank MB831377. Basionym: Tygervalleyomyce podocarpi Crous, Persoonia 39: 387. 2017. Type: Tygervalleyomyce podocarpi Crous.

New combinations in Typhula

Typhula podocarpi (Crous) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, comb. nov. MycoBank MB831376. Basionym: Tygervalleyomyce podocarpi Crous, Persoonia 39: 387. 2017.

Notes: The asexual and only known morph of T. podocarpi, described from South Africa, conforms to that of Typhula crassipes, described from Germany (Berthier 1976). The ITS region of T. podocarpi differs in 23 positions from that of European specimens of T. crassipes and we thus consider T. podocarpi to be a separate species.

Rickenellaceae

Vizzini, Mic. Veg. Medit. 25(2): 144. 2010.

Type genus: Rickenella Raitheh.

Representative genera: Alloclavaria, Athloderma, Blasiphalia, Bryopistillaria, Cantharellopsis, Contumyces, Cotylidia, Ginnisia, Globulicium, Gyrolyxus, Loreitia, Muscinupta, Odonticum, Peniophorea, Resinicum, Rickenella, Sidera, Skvortzovia and Taugacorticium. Excluded from Rickenellaceae: Repetobasidium.

Notes: Genera in the Rickenella clade have been assigned to the Repetobasidiaceae (Zhang et al. 2018), often left without family assignment (Kirk et al. 2008, Knudsen & Vesterholt 2012), or included in the family Rickenellaceae (Begerow et al. 2018). Our analyses suggest that Repetobasidium does not nest in the Rickenella clade, and Repetobasidiaceae cannot therefore be used to accommodate genera in the Rickenella clade. Consequently, we adopt Rickenellaceae as the correct placement for genera in this clade, excluding Repetobasidium so that Rickenellaceae is not superfluous as when erected by Vizzini (2010).

Bryopistillaria

Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, gen. nov. MycoBank MB831377.

Etyymology: From ancient Greek ("bryon", moss), referring to its habitat on bryophytes, and from Pistillaria, referring to its similarity with several species placed in that genus.

Biotrophic on mosses, and maybe in addition saprobic on dead leaves and culms. Basidiomata gregarious or fasciculate (2–5 basidiomata), simple clavidioid, 0.6–1 mm high, initially lanceolate and with sterile apex, then cylindrical or claviform, with rounded fertile apex, white. Stipe short or absent, cylindrical, glabrous or pubescent. Hyphal system monomitic. Basidiomata differ in 23 positions from that of European specimens of T. crassipes and we thus consider T. podocarpi to be a separate species.

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Bryopistillaria

Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, gen. nov. MycoBank MB831377.

Etyymology: From ancient Greek ("bryon", moss), referring to its habitat on bryophytes, and from Pistillaria, referring to its similarity with several species placed in that genus.

Biotrophic on mosses, and maybe in addition saprobic on dead leaves and culms. Basidiomata gregarious or fasciculate (2–5 basidiomata), simple clavidioid, 0.6–1 mm high, initially lanceolate and with sterile apex, then cylindrical or claviform, with rounded fertile apex, white. Stipe short or absent, cylindrical, glabrous or pubescent. Hyphal system monomitic. Basidiomata differ in 23 positions from that of European specimens of T. crassipes and we thus consider T. podocarpi to be a separate species.
**Basionym:** Pistillaria sagittiformis Pat., Tab. Anal. Fung. 1: 26. 1883 ['sagittæformis']

**Synonym:** Ceratellopsis sagittiformis (Pat.) Corner, Ann. Bot. Mem. 1: 206. 1950. ['sagittæformis']

**Basidiomata** gregarious or caespitose in groups of 2–5 basidiomata, 0.7–1.2 mm high, simple, with a short stipe. Fertile part narrowly claviform, sharply delimited from the stipe, white, 0.6–0.1 × 0.15–0.3 mm. Stipe short, cylindrical, glabrous or with sparse hairs, hyaline white, 0.1–0.4 × 0.1–0.2 mm. Subiculum spreading out on the substratum among basidiomata. Apex pointed and sterile in very young basidiomata, hyaline white, then obtuse and fertile. 

**Basidiospores** ellipsoid, sometimes in tetrads, hyaline, smooth, without iodine reactions, 4.5–6.5(–8) × 3–3.5(–4) μm. **Basidia** claviform, (1–2)–4-spored, 16–23 × 4.5–7 μm, clampless. **Subhymenium** composed of globose to subglobose hyphae, thin-walled, hyaline, 4–10(–12) μm broad. **Generative hyphae** cylindrical to fusiform, hyaline, thin-walled, clampless, 2.5–6(–9) μm broad, without iodine reactions. Hyphae on the stipe surface cylindrical, thin-walled, clampless, 3–3.5 μm broad. **Caulinar hairs** sparse, cylindrical, thin-walled, up to 50 × 3 μm. Subiculum formed by cylindrical hyphae, thin-walled, straight, branching at right angles, clampless, 3–4 μm broad. Skeletal hyphae absent. Crystals sometimes present among the medulla hyphae, bipyr- amidal or spheraoid. Attempts to obtain cultures from shed spores on MEA unsuccessful.

**Typus:** Lectotype designated here: Patouillard, Tab. Anal. Fung. 1: fig. 56. 1883. MycoBank MBT389355. **Estonia,** Otepää, Karula National Park, Peräjärve forest trail, on living Pleurozium schreberi, 13 Sep. 2015, I. Olariaga, IO.15.85 (S, epitype designated here; isoepitype in UPS). MycoBank MBT387918.

**Known distribution:** Denmark, Estonia, Finland, France, Sweden.

**Additional materials examined:** Denmark, Lolland, Biowide plot 120, Hejrede Sø, 5 Nov. 2014, T. Læssøe & T. Smidt, DMS-695059 (C); Sjælland, Allindølløvre Fredskov, on dead stem of Alnus, 20 Oct. 1977, H. Knudsen, C-F-124736; Amager Strandpark, on moss, 17 Nov. 2014, T. Læssøe, C-F-113951; Asserbo Plantage, on damp Juniperus bark and living mosses, 28 Feb. 2019, O. Martin, DMS-10005573 (C); Vestskoven, on damp Juniperus bark and mosses, 14 Feb. 2018, T. Kehlet, DMS-9242450 (C); Biowide Plot 079, Melby Hede, 6 Nov. 2014, T. Læssøe, DMS-695405 (C); Biowide Plot 070, Gjessøvej, on moss, 31 Aug.
2015, T. Borgen & T. Lassøe, C-F-114679; Biowide plot 120, Hejreda Sø, base of Poaceae plant, 5 Nov. 2014, T. Lassøe & T. Smith, C-F-114417; Stredam Reservatet, on mosses, rotten leaves and bark, 8 Nov. 2003, T. Lassøe, DMS-398331(C); Jagersborg Dyrehave, on moss and algae, 20 Jun. 1996, T. Lassøe, DMS-384562 (C-F-38168); Mans Klínetskoy, v. Nizkerenden, on moss on branch in damp hole, 23 Oct. 1971, H. Knudsen, C-F-94572; Stabjerggård, on Tortula, 14 Nov. 1976, H. Knudsen, C-F-94573. Finland, Pohjois-Hame, Laukka, Hallaalinde, on water dripping hillside west of the spring, on stock covered with moss, abundant on Pikurozium schreberi, 14 Sep. 2004, T. Rami (TUR 178089).

France, Pyrénées atlantiques, Escot, Le Barescou, on living mosses, 8 Oct. 2016, I. Olariaga (ARAN-Fungi 4625). Sweden, Dalarna, Särna, ca. 1.5 km W from Kryptiamen, on living Thuidium tamariscinum and Plagiomnium, spreading on a dead herbaceous culm, 31 Aug. 2015, I. Olariaga, IO.15.41 (S); Skåne, Erikstad, Vitabacksskallen Nature Reserve, on living leaves of Scorpidium cosmonti, 3 Oct. 2014, N.-O. Nilsson & I. Olariaga, IO.14.164 (S); Skåne, Tomelilla, Ånpkäret Nature Reserve, on living Scorpidium cosmonti, i.a fen, 3 Oct. 2014, N.-O. Nilsson & I. Olariaga, IO.14.163 (S); Uppland, Uppsala, the cemetery wall, southeast corner adjacent to Carolinaparken, on low mosses (Tortula ruralis), 12 Sep. 1932, S. Lundell (UPS F-152985, as Ceratellopsis cf. sagitiformis).

### Key to genera that contain species that can be considered typhuloid

| Key | Description |
|-----|-------------|
| 1   | Lichenised; growing on a thallus containing green algae. | Multiclavula |
| 2   | Non-lichenised; not associated with green algae. |  |
| 3   | Basidia with transverse septa; on living bryophytes. | Eocronartium muscicola |
| 4   | Basidia without septa; on various substrates incl. bryophytes. |  |
| 5   | Clamp connections verticillate on context hyphae. | Lutyspa sclerotiphila |
| 6   | Clamp connections absent or simple when present. |  |
| 7   | With a sclerotium. |  |
| 8   | Without a sclerotium. |  |
| 9   | With skeletal hyphae; smell phenolic when fresh. | unbranched forms of Pterula sclerotica |
| 10  | Without skeletal hyphae; smell not phenolic (living basidiomata). |  |
| 11  | Sclerotium compressed; sclerotial rind normal (i.e. with cells rooting in the medulla) with medulla gelatinised; basidiomata brown; fertile part cylindrical. | Macrotypyula phacorhiza and M. megasperma |
| 12  | Sclerotium usually not compressed, sclerotial rind inverse (i.e. with cells not rooting in the medulla), if normal, with medulla rarely gelatinised; basidiomata brown or with other colours, fertile part cylindrical to convex. | Typhula p.p. |
| 13  | With skeletal hyphae. |  |
| 14  | Without skeletal hyphae. |  |
| 15  | Stipe absent; protruding hymenial cystidia producing conidia; basidia 2-spored; spores 9–16 × 3.5–7 μm; smell phenolic when fresh. | Pterulicium gracile |
| 16  | Stipe short; hymenial cystidia absent; basidia 1–4-spored; spores smaller; smell not phenolic. | Ceratellopsis p.p. |
| 17  | Spores ornamented. | Ramariopsis p.p. |
| 18  | Spores smooth. |  |
| 19  | With hymenial cystidia. |  |
| 20  | Without hymenial cystidia. |  |
| 21  | Fertile part more or less cylindrical; terricolous; clamps absent; caulocystidia absent. | “Ceratellopsis” terrigena |
| 22  | Fertile part globose to spathulate; on dead plant remnants; clamp connections sometimes present; caulocystidia sometimes present. |  |
| 23  | Spores ellipsoid, fusiform or sigmoid. | Physalacria |
| 24  | Spores broadly ellipsoid to subglobose. | Actiniceps (= Chaetothyphula) |
| 25  | Basidiomata < 2 mm high; apex sterile and pointed at least in young basidiomata. |  |
| 26  | Basidiomata higher, if < 2 mm high then apex fertile even in young basidiomata. |  |
| 27  | Medulla hyphae < 2.5 μm broad; subhymenial hyphae not swollen, < 2.5 μm broad; on dead plant remnants; clamps (always?) present. | Ceratellopsis p.p. |
| 28  | Medulla hyphae 2.5–6(–9) μm broad; subhymenial hyphae globose to subglobose, 4–10(–12) μm broad; often on living mosses; clamps absent. | Bryopistillaria sagitiformis |
| 29  | Basidiomata pale brown; usually > 10 mm high; spores inamyloid. | Macrotyphula p.p. |
| 30  | Basidiomata if > 10 mm high then colour not brown; spores amyloid or not. |  |
| 31  | Clamps present and abundant on hyphae in the context. |  |

Notes: The original plate of *B. sagitiformis* shows a fungus with a fertile apex, 2-spored basidia and aseptate medulla hyphae reminiscent of skeletal hyphae. Corner (1950) suggested this plate might correspond to a *Pterula* species, but this view cannot be verified, as no type specimen appears to exist in the Patouillard herbarium (FH, PC). Instead, we interpret *B. sagitiformis*, as a species with obtuse fertile basidiomata at least when not extremely young, medulla hyphae 3–4 μm broad, lacking clamp connections and occurring usually, though apparently not strictly, on living mosses (Hansen & Knudsen 1997). It is possible that mosses are always present but not necessarily act directly as substrate for the basidiomata. Accordingly, we propose an epitype specimen to stabilise its current interpretation (Corner 1950, Hansen & Knudsen 1997).
DISCUSSION

Evolution of typhuloid fungi and family delimitation in the Agaricales and the Pleurotinae

This study provides the most robust phylogenetic hypothesis for typhuloid fungi to date, and it resolves for the first-time relationships with other genera in the Agaricales. Terminal nodes recovered in our Agaricales analyses using ML and Bayesian approaches are consistent to a great extent with those obtained by Matheny et al. (2006). In addition, several more basal nodes received support when analysed using a Bayesian method (Figs 2, 3), while ML bootstrap values were low for most of those. As RAxML does not allow for a free model-choice, the same dataset was analysed using IQ-TREE (Nguyen et al. 2015) and Garli (Zwickl 2006), but the supported topology was identical and bootstrap values were similar to those obtained in RAxML. It has long been known that Bayesian PP tend to be higher than ML bootstrap values (e.g. Susko 2009), and have been claimed to refer to different properties of phylogenetic confidence (García-Sandoval 2014). Although our dataset is the most comprehensive ever assembled for typhuloid fungi, it might still contain too little molecular characters to reconstruct the comparatively deep divergences among clades. In any case, it was highly expected that novel supported topologies would be recovered for the first time when more taxa were added to the analyses, even if many nodes so far only received support in the Bayesian analyses.

Typhulaceae, Pleurotaceae, Pterulaceae, Stephanosporaceae, Sarcomyxa, Pleurocybella and Phylloptosis are resolved as a monophyletic group for the first time (Figs 2, 3), corresponding to the Pleurotinae (Dentinger et al. 2016). Our results confirm that Sarcomyxa and the Typhulaceae belong to Pleurotinae as anticipated by Dentinger et al. (2016). The back-bone of the Pleurotinae phylogeny is fully resolved (Fig. 3) and suggest that Macrotyphula and Typhula, with a typhuloid basidioi configuration, might have evolved from a pleurotoid ancestor. The phylogenetic relationships of Phylloptosis, Pleurocybella and Sarcomyxa, of debated family placement, are also resolved in our Bayesian Pleurotinae phylogeny (Fig. 3). These three pleurotoid genera have been placed, not always together, in families containing white-spored agarics, such as Marasmiaceae, Mycenaceae, Pleurotaceae and Tricholomataceae (e.g. Jülich 1982, Moncalvo et al. 2000, Kirk et al. 2008, Begerow et al. 2018), or even Pterulaceae (Begerow et al. 2018), but previous phylogenies did not support any of these family placements (e.g. Matheny et al. 2006, Binder et al. 2010). Based on our phylogenies and the high Bayesian PP (Figs 2, 3), we propose the new family Sarcomyxaceae to encompass Sarcomyxa and validate the family Phylloptosidaceae to accommodate Macrotyphula, Phylloptosis and Pleurocybella. On the other hand, Pterulaceae and Radulomyctaceae, recently split sister families (Leal-Dutra et al. 2020), contains an assemblage of fungi with clavarioïd, corticioid and polyporoid basidiomata types (Zhao et al. 2016), monomitic or dimitic, defined as “morpho-anatomically a very diverse family with colourless spores” (Begerow et al. 2018), but well-supported in molecular phylogenies (Fig. 3; Matheny et al. 2006, Binder et al. 2010). All members of Pterulaceae and Radulomyctaceae studied when fresh (Aphanobasidium filicinum, Pterula subulata, Pterulicium gracile, P. sclerotica, Radulomyces confluens, R. molaris, and R. richii had a distinct phenolic or naphthalene odour, as sometimes described for P. multiformis (e.g. Petersen 1999). It is thus suggested here that such an odour, produced by a probably unidentified fungal metabolite, may be a synapomorphic character of Pterulaceae, but further species must be tested to draw a final conclusion.

According to our results, the hygrocyboid clade as recovered by Matheny et al. (2006), is not monophyletic, because the Hygrophoraceae, the Pleurotinae and Xerophilina campanella, all previously assigned to the hygrophoroid clade (Matheny et al. 2006), are encompassed in three independent lineages within the Agaricales (Fig. 2). The position of the Hygrophoraceae inferred from our analyses is not consistent with the 208-locus phylogeny by Dentinger et al. (2016), which placed Hygrocybe conica (Hygrophoraceae) and Clavaria fumosa (Clavariaceae) in a monophyletic group described as the Hygrophorineae. The dataset employed by Dentinger et al. (2016) contained 36 taxa of the highly diverse Agaricales and only a single taxon of the Hygrophoraceae. Phylogenetic analyses of a matrix with few taxa, even when the number of overall characters is large, can be subject to strong systematic biases and can be susceptible to long-branch attraction (Heath et al. 2008). In our preliminary analyses, H. coccinea nested in Clavariaceae when no other Hygrophoraceae were included in the matrix. With the addition of a few taxa of the Hygrophoraceae (Fig. 2), Clavariaceae and Hygrophoraceae do not form a monophyletic group, but are suggested to be successive sister taxa to the rest of the Agaricales. Our data indicates that Dentinger et al. (2016) recovered H. conica and C. fumosa in a monophyletic clade due to a long-branch attraction artifact and we anticipate that this clade will no longer be resolved when more species of Hygrophoraceae are included in phylogenomic
analyses of large multigene datasets. Following our phylogenetic hypothesis, we propose the new suborder Clavariineae to accommodate the Clavariaceae.

**Typhula phacorrhiza** is a synonym of Sclerotium complanatum that nests in Macrotyphula

Earlier hypotheses on the phylogenetic position of Typhula and Typhulaceae relied on a misidentified specimen of *T. phacorrhiza* (DSH96-059; Pine et al. 1999) that belongs to the Macrotyphula juncea species complex (Olariaga et al. in prep.). Therefore, this is the first time that *T. phacorrhiza* is included in a multigene phylogenetic study. As previously suggested, based on morphology (Olariaga & Salcedo 2013), *T. phacorrhiza* and Sclerotium complanatum belong to Macrotyphula. The bulk of species of Typhula form a distinct separate clade (referred to as the Typhula-core clade). Thus, our analyses confirm that the selection of *T. phacorrhiza* as type of *Typhula* is unfortunate (Berthier 1976, Olariaga & Salcedo 2013), also for the sake of nomenclatural stability. The examination of material deposited in herbaria under *S. complanatum* showed that this name is usually applied to sclerotia of *T. phacorrhiza* (e.g. Pl. Crypt. N. France, ed. 1, no 536; Microf. Exs. no 49; Krypt. Exs. no 1840; see material examined under *T. phacorrhiza*) and that *S. complanatum* is a synonym of *T. phacorrhiza* as proposed long ago (Remsberg 1940). Furthermore, the Typhula-core clade contains the types of all genera segregated from *Typhula* at some point. Based on analyses of more inclusive species sampling of *Typhula* (Olariaga et al., in prep), we consider it more appropriate to merge all those genera, as done by some authors (Berthier 1976, Knudsen & Vesterholt 2012), rather than splitting *Typhula* into several genera that could be recognised only with great difficulty.

A strict application of nomenclatural rules in the light of our phylogenetic hypothesis (Figs 2, 3) would result in a high number of undesirable name changes. The correct generic name for species of Macrotyphula and *T. phacorrhiza* would be Sclerotium. However, the adoption of *Sclerotium* for Macrotyphula species would be misleading, because nearly all Macrotyphula species lack sclerotia and *Macrotyphula* is a well-established name. At the same time, species in the *Typhula-*core clade would need to be transferred to *Pistillaria*, the oldest alternative genus name for the group. Pathogenic species of *Typhula*, such as *T. idahoensis*, *T. incarnata* or *T. ishikariensis*, on which extensive literature has been published, would undergo name changes. Also, the epithet of *T. incarnata* would need to be changed to avoid creating a later illegitimate homonym of *Pistillaria incarnata* Desm. In order to preserve nomenclatural stability, two proposals are in preparation to conserve: 1) *Typhula* with *T. incarnata* as conserved type, and 2) *Macrotyphula* against *Sclerotium* (Olariaga et al. unpubl.). In accordance with our proposals, we combine in *Macrotyphula* two closely related taxa treated by Berthier in *Typhula* subgen. *Typhula*: *T. phacorrhiza* and *T. megasperma*.

**Ceratellopsis s. auct.** is polyphyletic and misapplied

Despite our efforts to find good material, very few specimens of *Ceratellopsis* were available for this study. Besides those types examined by Berthier (1976), only a few more type specimens of *Ceratellopsis* could be located and examined. The type specimens of most names placed in *Ceratellopsis* appear to be lost and can only be interpreted through their protologues. Most non-type specimens of *Ceratellopsis* were characterised by having a central medulla of narrow, thick-walled hyphae, a poorly differentiated subhymenium of cylindrical < 2 μm broad hyphae, a sterile basidioma apex, a well-delimited stipe, basidia < 20 μm long and spores < 8 μm long. Some of these collections had skeletal hyphae in the medulla, as also observed in the type specimens of *C. acuminate*, while other specimens assigned to *C. aculeata* and *C. mucedinea* had scarcely septate hyphae with thinner walls. Specimens identified as *C. sagittiformis* differed in having broader (up 3–4(–8) μm), more often septate medulla hyphae, a well differentiated subhymenium with swollen, globose to subglobose hyphae (4–10(–12) μm) and a basidioma apex becoming fertile. Three type specimens (*C. attenuata*, *C. equisetotica* and *C. rickii*) and several other specimens filed under the names *C. aculeata* and *C. acuminate* represent *P. gracile*, because they possessed skeletal hyphae, 2-spored basidia, acuminate cystidia and lacked a stipe. As earlier suggested (Corner 1950, Berthier 1976), several names originally described or combined in *Ceratellopsis* represent in fact *P. gracile*.

This study provides the first molecular data of *Ceratellopsis*. It resolves the genus as polyphyletic, with species belonging to both the *Clavariaceae* and the *Hymenochaetales*. Among the specimens sampled for the molecular phylogenetic study, those with a sterile pointed apex and narrow thick-walled medulla hyphae nest in the *Clavariaceae*. This position is supported by the fact that tiny clavarioid basidiomata are also known in other *Clavariaceae*, such as in *Hirticlavula* (Petersen et al. 2014) and *Murconella* (Birkebak et al. 2013). Narrow hyphae on the base of the stipe, typical in *Clavariaceae* (Olariaga 2009), have also been observed in species of *Ceratellopsis*. For the first time, we demonstrate that skeletal hyphae are present in some species of *Ceratellopsis* and that it is not a unique character for *Pterulaceae* among typhuloid fungi. The species of *Ceratellopsis* placed in *Clavariaceae* differ from *P. gracile* in having basidia < 20 μm long, a well-delimited stipe and in lacking protruding acuminate cystidia. This lineage of *Ceratellopsis* conforms to Corner’s (1950) concept of *Ceratellopsis*, i.e. “*Ceratellopsis aculeata* and the species which appear to resemble it”, except for the presence of skeletal hyphae in some species. The examination of a specimen identified as *C. aculeata* by Corner (PC), with very narrow, scarcely septate medulla hyphae, confirms this view. In accordance with this, we conclude that *C. corneri* and *C. terrigena*, having medullar hyphae 4–6 μm and 1.5–3.5 μm broad, respectively, do not belong to this lineage and must be placed elsewhere (see Taxonomy).

The inclusion of *C. sagittiformis* in the *Rickenella* clade of the hymenochaetoid clade is a novel and unexpected finding although material identified as *C. sagittiformis* is often associated with living bryophytes, as several members of the clade are (Korotkin et al. 2018). The *Rickenella* clade encompasses fungi with a diverse basidioma configuration (agaricoid, clavarioid, cypheloid, thelephoroid, corticioid, etc.) that often are associated with mosses (Larsson et al. 2006). Within the *Rickenella* clade, *C. sagittiformis* resembles *Muscinupta laevis* in having white basidiomata, in growing on living bryophytes and in lacking clamp connections (Eriksson & Ryvarden 1975, as *Cyphelostereum laeve*), but our phylogenetic analyses lack support to confirm a close relationship. Phylogenetic relationships within the *Rickenella* clade were previously explored using only ribosomal nuclear markers (5.8S and 28S: Larsson et al. 2006), and only recently using also the RPB2 region. Even with the addition of
the 18S and the RP2B regions and more taxa to the analyses of the hymenochaetoid clade, relationships within the *Rickenella* clade remain largely unresolved (Korotkin et al. 2018, Fig. 5). The three specimens of *C. sagittiformis* have identical sequences and formed a distinct lineage. Based on this and the fact that *C. sagittiformis* is the only bryophilous, reduced clavarioid species known to belong to the *Rickenella* clade, we propose the new genus *Bryopistillaria* to accommodate it (see Taxonomy).

Proposing a reliable and stable interpretation of *C. queletii*, type of *Ceratellopsis*, is necessary to be able to provide a solid interpretation of *Ceratellopsis*. The name *Ceratellopsis queletii* appears not to have been employed since its original description (Patoïillard 1883). Regrettably, no type specimen exists in PC and FH (G. E. Tocci pers. comm.) and no original specimen is likely to be present in any other fungarium. The absence of a type, the sterile apex, the 2-spored basidia and the presence of protruding acuminate cystidia, clearly depicted in the original illustration of *C. queletii* selected here as lectotype, are characteristic of *P. gracile* (Corner 1950, Berthier 1976, Jülich 1980).

The spore size estimated by Corner from the original Patoïillard plate of *C. queletii* is smaller (6 × 3 μm) than the range we have estimated (8–8.5 × 4.5–5 μm) and the size reported by Qu (8μm′, 1884) for *C. queletii*. Spores in *P. gracile* are generally reported as slightly larger than our measure estimates from the Patoïillard plate, but those are almost within the ranges published for *P. gracile*: 9–16 × 4–7 μm (Corner 1950), 10.5–12.5 × 5.5–5.6 μm (Berthier 1976), 10–14 × 5.5–6.5 μm (Jülich 1980) and 8–11 × 5–7 μm (Daniels & Moreno-Arroyo 2007). Based on this, we consider *C. queletii* a synonym of *P. gracile*, as already Corner (1950) suggested.

Leal-Dutra et al. (2020), using one of the specimens of *P. gracile* employed in our analyses (CBS 309.759), showed that it belongs to the *Pterulicum* clade. This taxonomic conclusion reduces *Pterulicum*, as recently circumscribed, to a later synonym of *Ceratellopsis* and the forty-six names combined in *Pterulicum* (Leal-Dutra et al. 2020), besides its type *Pterulicum xyloogenum*, would have to be combined again in *Ceratellopsis*. In addition, a new genus name would be required for *C. acuminata* and *C. aculeata*. In order to avoid nomenclatural changes that may cause confusion, a proposal to conserve *Ceratellopsis* with *C. acuminata* as conserved type is in preparation. The acceptance of this proposal would preserve the current usage of *Ceratellopsis* and *Pterulicum*, typified by *P. xyloogenum*, a presumed causal agent of culm rot disease of bamboo (Harsh et al. 2005) and possibly also of sugarcane (Corner 1952).

**CONCLUSIONS**

This study reveals that typhuloid fungi appeared several times among the *Agaricomycetes* and contributes to the understanding of fungal evolution and shifts of basidiomata configuration. Novel phylogenetic hypotheses are provided for several groups of typhuloid fungi and pleurotoid agarics, and pertinent family and generic classifications are proposed. Future phylogenomic analyses will hopefully incorporate more taxa, including typhuloid fungi, and will serve to further test our phylogenetic hypotheses.

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