Reclassification of Pterulaceae Corner (Basidiomycota: Agaricales) introducing the ant-associated genus *Myrmecopterula* gen. nov., *Phaeopterula* Henn. and the corticioid Radulomycetaceae fam. nov.

Caio A. Leal-Dutra[1,5], Gareth W. Griffith[1], Maria Alice Neves[2], David J. McLaughlin[3], Esther G. McLaughlin[3], Lina A. Clasen[1] & Bryn T. M. Dentinger[4]

[1] Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth, Ceredigion SY23 3DD WALES

[2] Micolab, Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil

[3] Department of Plant and Microbial Biology, University of Minnesota, 1445 Gortner Avenue, St. Paul, Minnesota 55108, USA

[4] Natural History Museum of Utah & Biology Department, University of Utah, 301 Wakara Way, Salt Lake City, Utah 84108, USA

[5] CAPES Foundation, Ministry of Education of Brazil, P.O. Box 250, Brasília – DF 70040-020, Brazil

Author's e-mails in order :

caioboss@gmail.com

gwg@aber.ac.uk **(*Corresponding author)**

maliceneves@gmail.com

davem@umn.edu

pterula@yahoo.com

linaclasen@gmail.com

bryn.dentinger@gmail.com

ABSTRACT

Pterulaceae was formally proposed to group six coralloid and dimitic genera [*Actiniceps* (=*Dimorphocystis)*, *Allantula*, *Deflexula*, *Parapterulicium*, *Pterula* and *Pterulicium*]. Recent molecular studies have shown that some of the characters currently used in Pterulaceae Corner do not distinguish the genera. *Actiniceps* and *Parapterulicium* have been removed and a few other resupinate genera were added to the family. However, none of these studies intended to investigate the relationship between Pterulaceae genera. In this study, we generated 278 sequences from both newly collected and fungarium samples. Phylogenetic analyses support by morphological data allowed a reclassification of Pterulaceae where we propose the introduction of *Myrmecopterula* gen. nov. and Radulomycetaceae fam. nov., the reintroduction of *Phaeopterula*, the synonymisation of *Deflexula* in *Pterulicium* and 51 new combinations. *Pterula* is rendered polyphyletic requiring a reclassification; thus, it is split into *Pterula*, *Myrmecopterula* gen. nov., *Pterulicium* and *Phaeopterula*. *Deflexula* is recovered as paraphyletic alongside several *Pterula* species and *Pterulicium*, and is sunk into the latter genus. *Phaeopterula* is reintroduced to accommodate species with darker basidiomes. The neotropical *Myrmecopterula* gen. nov. forms a distinct clade adjacent to *Pterula*, and most members of this clade are associated with active or inactive attine ant nests. The resupinate genera *Coronicium* and *Merulicium* are recovered in a strongly supported clade close to *Pterulicium*. The other resupinate genera previously included in Pterulaceae, and which form basidiomes lacking cystidia and with monomitic hyphal structure (*Radulomyces*, *Radulotubus* and *Aphanobasidium*), are reclassified into Radulomycetaceae fam. nov.. *Allantula* is still an enigmatic piece in this puzzle known only from the type specimen that requires molecular investigation. A key for the genera of Pterulaceae and Radulomycetaceae fam. nov. is provided here.

KEYWORDS

Molecular phylogeny; fungal taxonomy; Pleurotineae; corticioid fungi; coralloid fungi; clavarioid fungi; coral mushroom; Aphyllophorales; fungal diversity; neotropical fungi; attine ants; fungus-farming ants; Attini; Attina

INTRODUCTION

The history of Pterulaceae Corner begins with the hesitant proposal of the genus *Pterula* Fr. (hereinafter abbreviated as *Pt*.) in the 1820s and 1830s by Elias Magnus Fries (Fries 1821, 1825, 1830). The typification of this genus was the subject of discussion by Lloyd (1919) and finally enlightened by Corner (1952c) in a thorough discussion on the timeline of Fries' decisions.

The number of species in *Pterula* grew during the late 19th and early 20th centuries, with J.H. Léveille, N.T Patouillard, P. C. Hennings, P. A. Saccardo, C. G. Lloyd, C. L. Spegazzini and M. J. Berkeley being the most active in the naming of taxonomic novelties of *Pterula* in this period (Corner 1950, 1970). Lloyd (1919) devoted an entire chapter to discuss the taxonomy of the genus.

However, the major contribution to the genus was made by E. J. H. Corner who added at least 45 new taxa (Corner 1950, 1952b, 1970, 1966, 1967). Corner (1950) created the Pteruloid series in Clavariaceae Chevall. to group, besides *Pterula*, other genera with coralloid basidiome and dimitic hyphal system. The Pteruloid series was raised by Donk (1964) to Pteruloideae, a subfamily of Clavariaceae.

Pterulaceae was formally proposed by Corner (1970) including the genera from the original Pteruloideae: *Allantula* Corner, *Deflexula* Corner, *Dimorphocystis* Corner (=*Actiniceps* Berk. & Broome), *Parapterulicium* Corner, *Pterula* and *Pterulicium* Corner (hereinafter abbreviated as *Pm*.) (Corner 1950, 1952a, b, 1970) (Fig. 1).

Fig. 1 Diversity of coralloid genera of Pterulaceae. A-F: *Myrmecopterula* (A: *Apterostigma sp*. nest with *M. velohortorum* with *Myrmecopterula sp.* SAPV1 growing atop of the garden veil; B, C, F: *Myrmecopterula sp.* D: *Apterostigma sp*. nest with *M. nudihortorum*; E: *M. moniliformis*). G-H: *Pterula* (G: *P. cf. loretensis*; H: *P. cf. verticillata*). I-L: *Pterulicium* (I: *P. secundirameum*; J: *P. aff fluminensis*; K: *P. lilaceobrunneum*. L: *P. sprucei*). M-O: *Phaeopterula* (M: *Phaeopterula sp.*; N: *P. stipata*; O: *P. juruensis*). Close observation on photos B and C reveal the basidiomes growing from granular substrate resembling substrate of ants' fungus garden. Photos D and G kindly provided by Ted Schultz and Michael Wherley respectively. Scale bars: 1 cm.

Following Corner's reclassifications, the major changes in Pterulaceae have resulted from molecular phylogenetic analyses. *Actiniceps* Berk. & Broome was shown within Agaricales to be distantly related to

Pterulaceae and *Parapterulicium* was removed to Russulales (Dentinger and McLaughlin 2006; Leal-Dutra et al. 2018). Four resupinate genera were transferred to Pterulaceae: *Aphanobasidium* Jülich, *Coronicium* J. Erikss. & Ryvarden, *Merulicium* J. Erikss. & Ryvarden, and *Radulomyces* M.P. Christ. (Larsson 2007; Larsson et al. 2004) and, finally, the new poroid genus *Radulotubus* Y.C. Dai, S.H. He & C.L. Zhao was proposed in the family (Zhao et al. 2016) (Fig. 2).

Fig. 2 Corticioid genera of Pterulaceae (A-C) and Radulomycetaceae (D-F). A: *Coronicium alboglaucum*. B-C: *Merulicium fusisporum.* D: *Radulomyces confluens.* E: *Radulotubus resupinatus*. F: *Aphanobasidium cf. pseudotsugae*. Photos kindly provided by L. Zíbarová (A and F), S. Blaser (B and C), D.J. Harries (D) and C.L. Zhao (E). Scale bars: 1 cm.

Pterulaceae has attracted more attention recently following the discovery of two distinct symbionts of fungus-farming ants in the genus *Apterostigma* Mayr. Despite the absence (hitherto) of any teleomorph, phylogenetic analyses placed both species [*Pterula nudihortorum* Dentinger and *Pterula velohortorum* Dentinger, previously known as G2 and G4 (Dentinger 2014)] in a strongly supported clade within Pterulaceae (Munkacsi et al. 2004; Villesen et al. 2004).

Whilst these earlier phylogenetic studies did not focus on resolving evolutionary relationships of the genera, they did demonstrate that the coralloid genera of Pterulaceae are clearly polyphyletic. Amongst the morphological characters previously used to separate the genera, but now known to be phylogenetically unreliable, is the orientation of basidiome growth that differentiates *Pterula* from *Deflexula* and the presence of a corticioid patch at the base of the basidiome in *Pterulicium*. Therefore, the reclassification of Pterulaceae is required to restore the monophyly of the genera.

Our recent fieldwork in Brazil and sampling of fungarium material has yielded sequence data from many specimens not previously included in phylogenetic analysis, permitting a comprehensive reappraisal of the phylogeny of Pterulaceae. Here we present a proposal for a new classification based on the phylogeny inferred from three nuclear loci (nrITS, nrLSU and RPB2), including representatives of all genera currently accepted in Pterulaceae except *Allantula*. Despite several attempts for recollecting *Allantula* in its type locality, the monotypic genus is still only known from the type specimen collected by Corner (1952a).

METHODS

Collections and morphological observations

Several field campaigns between 2011-2017 have obtained new specimens from >15 locations in nine states across Brazil (Amazonas, Espírito Santo, Minas Gerais, Pará, Paraíba, Paraná, Rio de Janeiro, Rio Grande do Sul and Santa Catarina).

The samples were dried in a low-heat food dehydrator and deposited at FLOR, HSTM, INPA, K and RB. Herbarium acronyms follow Index Herbariorum (Thiers continuously updated). Morphological identification and taxonomy of Pterulaceae are treated *sensu* Corner. Microscopic observations followed the methods described in Leal-Dutra (2015) and Leal-Dutra et al. (2018).

DNA extraction, amplification, cloning and sequencing

DNA was extracted from dried basidiomes or freeze-dried culture first grinding with liquid nitrogen followed by lysis with CTAB buffer (100 mM Tris-HCl pH 8.0, 1.4 M NaCl, 20 mM EDTA, 2% CTAB), clean-up with chloroform:isoamyl alcohol (24:1), wash with isopropanol (0.6 vol.) and a final wash with 70% ethanol.

Partial sequences of the nrITS, nrLSU and RPB2 were amplified by PCR using the primer pairs listed on Table 1 and following the cycling conditions in the original publications. PCR products were purified using 2 U of Exonuclease I (Thermo Fisher Scientifics) and 1 U FastAP Thermosensitive Alkaline Phosphatase (Thermo Fisher Scientifics) per 1 µl of PCR product, incubated at 37 °C for 15 min, followed by heat inactivation at 85 °C for 15 min. The samples were then sent for Sanger sequencing at the FIOCRUZ-MG sequencing platform (Belo Horizonte, Brazil; through the FungiBrBOL project), the IBERS Translational Genomics Facility (Aberystwyth University) or Jodrell Laboratory (Royal Botanic Gardens, Kew). The same PCR primers were used for sequencing; additional primers were used to sequence the nrLSU and RPB2 (Table 1).

Table 1 Primers used in this study for PCR and sequencing.

Primer	Region	Application	Sequence	Reference
ITS8F	nrITS	PCR and sequencing	AGTCGTAACAAGGTTTCCGTAGGTG	(Dentinger et al. 2010)
ITS6R	nrITS	PCR and sequencing	TTCCCGCTTCACTCGCAGT	(Dentinger et al. 2010)
LR0R	nrLSU	PCR and sequencing	ACCCGCTGAACTTAAGC	(Vilgalys and Hester 1990)
LR7	nrLSU	PCR and sequencing	TACTACCACCAAGATCT	(Vilgalys and Hester 1990)
LR5	nrLSU	Sequencing	TCCTGAGGGAAACTTCG	(Vilgalys and Hester 1990)
fRPB2-5F	RPB2	PCR and sequencing	GAYGAYMGWGATCAYTTYGG	(Liu et al. 1999)
bRPB2-7.1R	RPB2	PCR and sequencing	CCCATRGCYTGYTTMCCCATDGC	(Matheny 2005)
bRPB2-6F	RPB2	Sequencing	TGGGGYATGGTNTGYCCYGC	(Matheny 2005)

Chromatograms were checked and sequences assembled and edited using GENEIOUS 10.0.2 (Kearse et al. 2012). Samples presenting indels were cloned using pGEM-T Easy Vector Systems (Promega) into Subcloning Efficiency DH5α Competent Cells (Invitrogen). Up to five clones from each sample were amplified and sequenced as above. The clones sequences were treated as in Leal-Dutra et al. (2018).

Moreover, 27 sequences of nrITS (4), nrLSU (10) and RPB2 (13) were mined from 13 previously assembled and unpublished genomes using NCBI BLAST+ package v2.7.1 (Camacho et al. 2009). Two sequences of each Pterulaceae genus were used as query and the best hit based on the combination of e-value and bit score was selected; the same hit should usually appear for all query sequences. In one case (sample KM190547), more than one optimal hit was found; the subject sequences were compared for occurrence of indels and treated as virtual clones (VC). These sequences are included in the dataset (Table 2).

The sequences generated in this study have been submitted to GenBank (Table 2).

Table 2: Details of new sequences generated in this study used in the tree of Fig. 3. (a full version is presented as excel file in Additional file 1).

Phylogenetic analyses

A preliminary maximum-likelihood (ML) analysis was conducted with the sequences generated in this study alongside GenBank sequences to find the best outgroup for Pterulaceae based on previous studies (Dentinger et al. 2016; Zhao et al. 2016; Matheny et al. 2006; Larsson 2007) and to assess the similarities between the cloned sequences (Additional file 1; Additional file 2).

Additional file 1: Full details of all samples studied here (simplified in Table2; as excel file)

Additional file 2: Additional phylogenetic reconstructions, including detailed analyses relating to Figure 3

A reduced version of the previous dataset with only one sequence from each cloned sample was created. After removing nearly identical sequences with no phylogenetic resolution. The final dataset was comprised of 119 sequences, including 32 sequences from GenBank and using four sequences of *Stephanospora* Pat. as outgroups, and was divided into five partitions for further analyses: ITS1, 5.8S, ITS2, LSU and RPB2.

Each partition was aligned separately with MAFFT v7.311 (Katoh and Standley 2013) using the E-INS-i algorithm for ITS1 and ITS2, and L-INS-i for 5.8S, LSU and RPB2. The alignments were examined and corrected manually in AliView v1.5 (Larsson 2014) and trimmed to remove uneven ends.

Maximum-likelihood tree reconstruction was performed with IQ-TREE v1.6.7.1 (Nguyen et al. 2015). The best-fit evolutionary models and partitioning scheme for this analysis were estimated by the built-in ModelFinder (option -m MF+MERGE) allowing the partitions to share the same set of branch lengths but with their own evolution rate (-spp option) (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017). Branch support was assessed with 1000 replicates of ultrafast bootstrapping (UFBoot) (Hoang et al. 2018) and allowing resampling partitions and then sites within these partitions to reduce the likelihood of false positives on branch support (option -bspec GENESITE).

Bayesian Inference (BI) was implemented using MRBAYES v3.2 (Ronquist et al. 2012) with two independent runs, each one with four chains and starting from random trees. The best-fit evolutionary models and partitioning scheme for these analyses were estimated as for the ML analysis but restricting the search to models implemented on MRBAYES (options -m TESTMERGEONLY -mset mrbayes). Chains were run for 10^7 generations with tree sampling every 1000 generations. The burn-in was set to 25% and the remaining trees were used to calculate a 50% majority consensus tree and Bayesian Posterior Probability (BPP). The convergence of the runs was assessed on TRACER v1.7 (Rambaut et al. 2018) to ensure the potential scale reduction factors (PSRF) neared 1.0 and the effective sample size values (ESS) were sufficiently large (>200).

Nodes with BPP ≥0.95 and/or UFBoot ≥95 were considered strongly supported.

Alignment and phylogenetic trees are deposited in Treebase (ID: 24428).

RESULTS

From this section, all taxa are treated by the nomenclatural treatment proposed in this study.

Field data

Fieldwork resulted in the discovery of approximately 100 new specimens, now placed within Pterulaceae (Table 2). Axenic culture isolation was also possible from several of these specimens.

Phylogenetic analyses

A total of 278 sequences from 123 samples were generated in this study: 153 nrITS, 74 nrLSU and 51 RPB2; 61 from cloning and 40 from genome mining. The final alignment consisted of 113 sequences with 2737 characters and 1050 parsimony-informative sites. The BI analysis converged both runs as indicated by the effective sample sizes (ESS) of all parameters above 2800 and the potential scale reduction factors (PSRF) equal 1.000 for all the parameters according to the 95% HPD Interval.

The new classification proposed in this study (Fig. 3), highlights six main clades containing nine genera are highlighted: Radulomycetaceae (containing *Aphanobasidium*, *Radulotubus* and *Radulomyces*), *Phaeopterula* (hereinafter abbreviated as *Ph*.; previously *Pterula* spp.), *Coronicium* superclade (grouping *Merulicium* and *Coronicium*), *Pterulicium* (previously *Pterulicium*, *Pterula* spp. and *Deflexula* spp,), *Pterula* and *Myrmecopterula* (*Myrmecopterula* gen. nov., previously *Pterula* spp.).

Fig. 3 Maximum-likelihood tree of Pterulaceae and Radulomycetaceae. Support values on the branches are UFBoot/BPP and showed only for UFBoot≥70 and BPP≥0.70 and branch length ≥ 0.003 substitutions per site.

Details for the complete tree can be found in Additional file 2 and TreeBase (ID: 24428). Scale bar: nucleotide substitutions per site.

Radulomycetaceae (UFBoot=99; BPP=1)

This clade groups with strong support three of the five resupinate genera recognized in Pterulaceae, namely *Aphanobasidium (UFBoot=100; BPP=1), Radulotubus (UFBoot=100; BPP=1) and Radulomyces (UFBoot=100; BPP=0.86)*. The placement of *Aphanobasidium* and *Radulomyces* into Pterulaceae was previously shown by phylogenetic reconstructions of corticioid taxa (Larsson et al. 2004; Larsson 2007). *Radulotubus* was proposed by Zhao et al. (2016) as sister clade of *Radulomyces* to accommodate one species bearing poroid hymenophore. In our analyses, *Radulotubus* was recovered in the same position as in the original publication. This is the only poroid species within Pterulaceae.

No members of the three genera within this superclade are pteruloid (i.e. coralloid basidiomes with dimitic hyphal system) in their morphology and consequently we propose the creation of Radulomycetaceae fam. nov. to accommodate them, as discussed in greater detail below. The current sister clade to Pterulaceae in our analyses is Stephanosporaceae Oberw. & E.Horak, from which members of the Radulomycetaceae clade are clearly distinct phylogenetically and morphologically.

Phaeopterula (UFBoot=100; BPP=1)

Phaeopterula received maximum support in both analyses. It includes *Pterula stipata* Corner, *Pterula anomala* P. Roberts, *Pterula juruensis* (Henn.) Corner and other species which all have dark brown basidiomes. This clade is the first coralloid lineage to diverge within Pterulaceae. As these species render *Pterula* paraphyletic, a reclassification is needed. The generic name *Phaeopterula* (Henn.) Sacc. & D. Sacc was originally proposed as a subgenus of *Pterula* to accommodate *Ph. hirsuta* Henn. and *Ph. juruensis* (Hennings 1904; Hennings 1899). We propose its reintroduction to distinguish these brown-pigmented taxa from *Pterula* s.s.

Coronicium superclade (UFBoot=98; BPP=1)

This clade groups the remaining two resupinate genera of Pterulaceae, the monospecific *Merulicium* and *Coronicium (UFBoot=100; BPP=1)*. Both genera form resupinate basidiomes but differ in the hyphal system present (dimitic in *Merulicium*, monomitic in *Coronicium*). Some *Pterulicium* species also show transitions in their morphology to a resupinate state. Corner (1950) showed that *Pm. xylogenum* (Berk. & Broome) Corner could form monomitic corticioid patches independent of the coralloid state and even in its absence, thus appearing to be truly corticioid. Furthermore, experimental studies on *Pm. echo* D.J. McLaughlin & E.G. McLaughlin show a dimitic, resupinate, fertile corticioid phase both on agar and when cultured on cocoa twigs (McLaughlin and McLaughlin 1980; McLaughlin et al. 1978; McLaughlin and McLaughlin 1972). Despite the morphological distinctiveness from the rest of Pterulaceae, there is a trend in the morphology and strong phylogeny support for the placement of the *Coronicium* superclade among *Pterula*/*Myrmecopterula* and *Pterulicium* clades within Pterulaceae.

Pterulicium (UFBoot=99; BPP=1)

Two type species, *Pterulicium xylogenum* and *Deflexula fascicularis*, are nested within this clade alongside several species currently assigned to *Pterula* but which all have simple basidiomes (unbranched or limited branching). The *Pterula* species are interspersed with some *Deflexula*, rendering both genera polyphyletic. *Pterulicium xylogenum* forms a well-supported subclade with *Pterula secundiramea* (Lév.) Corner (=*Pm. palmicola* Corner). *Deflexula fascicularis* forms a subclade with other *Deflexula* species that share globose spores, an unusual feature within Pterulaceae, most of which form ellipsoid to subamygdaliform spores.

Pterula (UFBoot=100; BPP=1)

This clade groups the true *Pterula* spp. that are represented by very bushy coralloid basidiomes, usually robust and taller than those of *Pterulicium*, stipe concolorous with hymenophore and lacking a cottony subiculum.

Pterula has a mainly pantropical and pan-subtropical distribution, with occurrence reported to all continents except Antarctica (Corner 1970).

Myrmecopterula (UFBoot=97; BPP=1)

This sister clade of *Pterula* represents the newly proposed genus (see below). It groups the two species cultivated by attine ants in the *Apterostigma pilosum* group with *M. moniliformis* and several unidentified free-living species. The species in this clade are only known from the Neotropics. *Myrmecopterula* is divided in seven subclades (Fig. 3) representing the two mutualists (MUT 1-2), three closely related to *M. velohortorum* (SAPV 1-3), one closely related to *M. nudihortorum* (SAPN1) and one of unknown relationship (SAPX1).

Taxonomy

Radulomycetaceae Leal-Dutra, Dentinger, G.W. Griff., **fam. nov.**

MycoBank MB831047 **(Fig. 2D-F)**

Etymology

From the type genus *Radulomyces*.

Diagnosis

Basidiome resupinate, effused, mostly adnate, ceraceous, hymenophore smooth, tuberculate, odontioid, raduloid or poroid. Hyphal system monomitic, generative hyphae with clamps, hyaline, thin- to slightly thick-walled. Cystidia absent. Basidia terminal clavate or other form if pleural, usually with 4-sterigmata and a basal clamp. Basidiospores ellipsoid to globose, hyaline, mostly smooth, thin- to slightly thick-walled, acyanophilous, inamyloid and non-dextrinoid.

Type genus

Radulomyces M.P. Christ.

Notes

Radulomyces, *Aphanobasidium* and *Radulotubus* are placed in Radulomycetaceae fam. nov. Larsson (2007) suggested that *Lepidomyces* Jülich has affinities to *Aphanobasidium* and could possibly be placed in Pterulaceae. However, no sequence data for the genus are available. *Lepidomyces* is described as bearing pleurobasidia as in *Aphanobasidium*, but also leptocystidia as in *Coronicium* and *Merulicium*. Given its morphological similarities to the *Aphanobasidium* and the *Coronicium* superclade, we suggest to keep *Lepidomyces* as *incertae sedis* until molecular data are available to confirm its phylogenetic position.

Phaeopterula (Henn.) Sacc. & D. Sacc., *Syll. fung*. **17**: 201 (1905)

(Fig. 1M-O)

Basionym

Pterula subgen. *Phaeopterula* Henn., in Warburg, *Monsunia* **1**: 9 (1899) [1900].

Type Species

Phaeopterula hirsuta (Henn.) Sacc. & D. Sacc.

Updated description:

Basidiomes Pteruloid solitary or gregarious, scarcely branched to almost bushy, monopodial and slightly symmetric, branches from light brownish pink or greyish to pale brown and stipe dark reddish to rusty brown. Stipe surface glabrous with agglutinated hyphae (not sclerotioid) to villose-tomentose. Dark brown mycelial cords usually present. Hyphal system dimitic with thick-walled skeletal hyphae, generative hyphae thin-walled and often clamped. Hymenial cystidia absent, caulocystidia sometimes present. Basidia terminal, clavate to suburniform. Basidiospores less than 9 µm varying between pip-shaped, subamygdaliform and ellipsoid. Growing on dead twigs or dead wood.

Notes

Hennings (1899) created the subgenus *Phaeopterula* to accommodate *Pterula hirsuta* that was distinguished from other *Pterula* spp. by its reportedly brown spores. Hennings (1904) later described a second species in the subgenus, *Ph. juruensis*, but noted that it was morphologically quite distinct from *Ph. hirsuta*. *Phaeopterula* was raised to genus level by Saccardo and Saccardo (1905) who cited only *Ph. juruensis*. *Pterula hirsuta* was recombined in *Dendrocladium* by Lloyd (1919) but later put back in *Pterula* by Corner (1950), even though Corner did not confirm the presence of brown spores in the samples he examined. Although we also have not observed pigmented spores in any of these taxa, dark brown pigments in the stipe hyphae are a consistent and diagnostic feature in this group, so we resurrect the name *Phaeopterula* and reassign the reference to brown in the name (phaeo-) to the brown hyphal pigments rather than brown-pigmented basidiospores.

Pterulicium Corner, *Monograph of Clavaria and allied Genera*: 689, 699 (1950)

(Fig. 1I-L)

Type Species

Pterulicium xylogenum (Berk. & Broome) Corner

Updated description

Basidiomes pteruloid rarely corticioid, solitary or gregarious, simple or scarcely branched, occasionally exhibiting abundant unilateral branching (Fig. 1I and 1L), with colour varying from creamy white to brown on the stipe and creamy white on the tips or creamy white or pale lilaceous to pale brown on uniformly coloured basidiomes. Stipe surface sometimes sclerotioid [see Corner, (1950)]. Hyphal system dimitic with slightly thick-walled skeletal hyphae, generative hyphae thin-walled and often clamped. Hymenial cystidia usually present, caulocystidia sometimes present. Basidia terminal, clavate to suburniform. Basidiospores shape varying between globose to subglobose, pip-shaped, amygdaliform to subamygdaliform, ellipsoid. Growing on dead leaves, dead twigs or dead wood, rarely as a pathogen or endophyte of living plants.

Notes

Deflexula is synonymised with *Pterulicium* in this study. In addition, several species previously placed in *Pterula* are transferred to *Pterulicium* (see the new combinations below). Other *Pterula* species that might need to be recombined in *Pterulicium*, require further investigation since their original descriptions do not provide enough information to confidently assign them here.

Myrmecopterula Leal-Dutra, Dentinger & G.W. Griff., **gen. nov.**

MycoBank MB831048 **(Fig. 1A-F)**

Etymology

From the ancient Greek word μύρμηκος (=mýrmēkos), genitive form of μύρμηξ (=mýrmēx), ants. Thus, *Pterula* of the ants, due to the observed relationship of most taxa in this genus with nests of fungus-growing ants.

Type Species

Myrmecopterula moniliformis (Henn.) Leal-Dutra, Dentinger & G.W. Griff.

Diagnosis

Usually associated with the nests of ants, growing on top or from living or dead nest or being cultivated by the ants. Bushy pteruloid basidiome, white-cream to light-brown and greyish surface, normally concolorous or stipe with a darker tone than the hymenophore, arising from cottony subiculum with mycelial cords, stipe surface sterile, dimitic hyphal system, relatively small spores (usually less than 7µm wide), or no basidiome. Differs from *Pterula* by the presence of the cottony subiculum.

Notes

Basidiomes of *Myrmecopterula* species are very similar to *Pterula* in habit, shape and colour, but they differ in the presence of mycelial cords and of a cottony subiculum from which basidiomes emerge. Some species of *Myrmecopterula* arise from soil, while others superficially appear to grow on wood. Closer observation of wood-dwelling basidiomes revealed that rather than being lignicolous, instead they grow from a loose, granular substrate within a cavity inside the wood. This substrate in some cases resembles the substrate in the fungus gardens of *Apterostigma pilosum* group ants. In addition, *M. moniliformis*, which arises from soil, has been found emerging from active and inactive attine nests, (S. Sourell, pers. comm.; M.C. Aime, pers. comm.). Thus, all but one of the *Myrmecopterula* taxa found to date are associated with attine ants, of which the two farmed mutualist species (*M. nudihortorum* and *M. velohortorum*) are best known (REF). The five other species (of which only *M. moniliformis* is named) are less well studied and may play a role in decomposition of residual substrates in abandoned fungus garden, or potentially even as mycoparasites of the ant cultivar. In contrast, no *Pterula* spp. have any reported association with ants, but instead are found growing directly from wood and leaf litter.

Myrmecopterula moniliformis (Henn.) Leal-Dutra, Dentinger & G.W. Griff., **comb. nov.**

MycoBank MB831049 **(Fig. 1E)**

Basionym: *Lachnocladium moniliforme* Henn., *Hedwigia* **43**(3): 198 (1904).

Synonym: *Pterula moniliformis* (Henn.) Corner, *Ann. Bot.*, Lond., n.s. **16**: 569 (1952). *Thelephora clavarioides* Torrend, *Brotéria*, sér. bot. **12**(1): 61 (1914).

Description in (Corner 1952b).

Myrmecopterula nudihortorum (Dentinger) Leal-Dutra, Dentinger & G.W. Griff., **comb. nov**

MycoBank MB831050 **(Fig. 1D)**

Basionym: *Pterula nudihortorum* Dentinger [as *'nudihortus'*, later referred to as '*nudihorta*'], *Index Fungorum* **98**: 1 (2014).

Updated Description

In the field, it is recognized by the absence of any veil on the fungus garden in the *Apterostigma* nests, usually inside decomposing trunks or underground. In culture, it forms very little aerial mycelium and exhibits very slow growth (2-3 mm/week radial growth rate on PDA at 25C). Hyphal clamps abundant.

Notes

This species was formerly known as the ant cultivar G4. It is only known from the nest of fungus-growing ants in the *Apterostigma pilosum* group in the *A. manni* subclade (Schultz 2007).

Myrmecopterula velohortorum (Dentinger) Leal-Dutra, Dentinger & G.W. Griff., **comb. nov.**

MycoBank MB831051 **(Fig. 1A)**

Basionym: *Pterula velohortorum* Dentinger [as *'velohortus'*, later referred to as '*velohorta*'], *Index Fungorum* **98**: 1 (2014).

Updated description.

In the field, it is recognized by the *Apterostigma* garden covered by a mycelial veil, usually inside decomposing trunks, below the leaf litter or hanging on exposed surfaces aboveground. In culture, it forms very cottony aerial mycelia with presence of racquet hyphae (Fig. 5 in Additional file 3). Large and abundant hyphal clamps. Slow growth rate, but faster than *M. nudihortorum*.

Additional file 3: Additional images of coralloid Pterulaceae and micrographs of *Myrmecopterula velohortorum*.

Notes

This species was formerly known as the ant cultivar G2. It is only known from the nest of fungus-growing ants in the *Apterostigma pilosum* group in the *A. dentigerum* subclade (Schultz 2007).

Discussion

Introduction of Radulomycetaceae

We consider that it is better to erect a new family for these three genera than to leave them in Pterulaceae where they are clearly phylogenetically and morphologically distinct from nearly all the other member of Pterulaceae. In contrast, *Merulicium* (Fig. 2B-C) and *Coronicium* (Fig. 2A) form corticioid basidiomes but our phylogenetic analyses place them clearly within Pterulaceae. Two *Pterulicium* species, *Pm. echo* and *Pm. xylogenum*, also form both pteruloid and corticioid basidiomes, either independently or together (McLaughlin and McLaughlin 1980; Corner 1950).

Whilst the corticioid basidiomes of *Merulicium* and *Pm. echo* contain a dimitic hyphal system, typical of Pterulaceae, those of *Coronicium* spp. and *Pterulicium xylogenum* form a monomitic hyphal system, like all members of Radulomycetaceae. However, no members of Radulomycetaceae form cystidia, whereas these cells are found in most Pterulaceae (McLaughlin and McLaughlin 1980; Corner 1970, 1967, 1952a, b, 1950; Bernicchia and Gorjón 2010), including *Coronicium* spp.

Thus, Radulomycetaceae fam. nov. is morphologically characterized by the combination of resupinate basidiomes, monomitic hyphal system and lack of cystidia. Moreover, our phylogenetic analyses strongly support the segregation of Radulomycetaceae fam. nov. from Pterulaceae.

Reintroduction of *Phaeopterula*

Phaeopterula spp. are distinct from other pterulaceous genera due to the distinctive brown colour of the main axis of the basidiome and monopodial/symmetric branching of these structures. This contrasts with other Pterulaceae which are either highly branched (bushy) and of uniform colour (*Pterula* and *Myrmecopterula*) or pigmented only at the stipe base, and (mostly) unbranched (*Pterulicium*). Hennings (1899) originally defined *Phaeopterula* by its brown spores. Corner (1950) cast doubt on the significance of this trait but our results show that, despite an apparently misguided justification, Hennings was correct to group *Ph. juruensis* with *Ph. hirsuta*.

All *Phaeopterula* spp. are exclusively found on decaying wood, whereas members of other genera of Pterulaceae inhabit more diverse lignocellulosic substrates. Given the basal position of *Phaeopterula* in Pterulaceae, and the fact that all members of the sister family Radulomycetaceae are also lignicolous on wood, this habit is parsimoniously the ancestral condition. The reintroduction of *Phaeopterula* aims to pay tribute to Paul Hennings' work and his contribution to the taxonomy of Pterulaceae.

Synonymy of *Deflexula* with *Pterulicium*

Besides the paraphyly represented by *Phaeopterula*, the *Pterulicium* clade shows the clear polyphyly of *Pterula* and *Deflexula*. Several species in the two latter genera are intermixed in a strongly supported subclade (Fig. 3). The presence of the type species of both *Deflexula* and *Pterulicium* within this clade requires that only one name be kept. Both genera were proposed by Corner (1950), to accommodate the dimitic and coralloid (but non-bushy) species, not fitting the description of *Pterula*. The name *Pterulicium* was based on a 'portmanteau' combination of *Pterula* and *Corticium* to reflect the presence of a corticioid patch at the stipe base (Corner 1950). However, this patch has only been reported in two species, *Pterulicium xylogenum* (Corner 1950) and *Pm. echo* (McLaughlin and McLaughlin 1980). *Deflexula* was named for the downward-oriented (positively geotropic) basidiomes (Corner 1950). Corner (1950) stated that the resupinate patch in *Pterulicium xylogenum* is monomitic, can exist independently of the coralloid basidiome and is fertile when facing downward; he suggested that there was a close similarity between *Deflexula* and *Pterulicium* in the way the resupinate patch develops from the base of the basidiome. He also made a case for the formation of a fertile hymenium when facing downward in the two genera as supporting this similarity. Nonetheless, experimental studies on *Pm. echo* show that orientation of the hymenium does not affect the ability to produce spores, i.e., the hymenium is ageotropic (McLaughlin et al. 1978) and raised doubts about the validity of the genus *Deflexula*. This morphological distinction is not supported by phylogenetic analysis (Dentinger et al. 2009, Fig. 3) and its emphasis through taxonomic preservation would perpetuate misunderstanding. Accordingly, we propose to retain *Pterulicium* for this clade to avoid major misinterpretations of the species morphology.

Introduction of *Myrmecopterula* gen. nov.

Two species of Pterulaceae are cultivated by fungus-farming ants of the *Apterostigma pilosum* group in South and Central America (Dentinger et al. 2009; Munkacsi et al. 2004; Villesen et al. 2004; Mueller et al. 2018).

Despite intensive investigation, neither has been observed to form basidiomes, but *M. velohortorum* is characterised by the formation of a veil of mycelium around the fungus garden, whilst *M. nudihortorum* lacks this veil. We recovered both species in a strongly supported clade, as a sister clade of *Pterula*, alongside five other subclades containing fertile, apparently free-living species.

All the samples in this clade were collected from neotropical habitats (Fig. 1A-F), mostly as part of our recent fieldwork. During sampling campaigns by ourselves and others, it was observed that many of the 'free-living' specimens were associated in some way with living ant colonies or abandoned attine nests. Two *Myrmecopterula* samples belonging to subclade SAPV1 (CALD170307-02 and CALD170307-03; Fig. 1A) were found forming basidiomes atop two distinct but adjacent (1 m apart) living *Apterostigma* nests in Amazonian Rainforest. The cultivated mutualists from both nests were also analysed and found to belong to *M. velohortorum* confirming that the basidiomes were not linked to the cultivated mycelia in these nests. The third member of subclade SAPV1 was also reported forming a nascent basidiome on a living *Apterostigma* nest in Panama (Munkacsi et al. 2004). *M. moniliformis* (SAPN1; Fig. 1E) has been reported to be found outside both active and apparently inactive (see *Myrmecopterula*: Notes on Taxonomy section above) attine nests (S. Sourell, pers. comm.; M.C. Aime, pers.comm.) as was CALD170315-04 (SAPV2; Fig. 1B) and CALD170122-04 (SAPV3; Fig. 1C). Lastly, the mycelium of one sample (JSP 07-03 B 5.1; SAPV3) was isolated from a living *Atta capiguara* nest by Pereira et al. (2016).

The observations above and the phylogenetic analyses suggests that association with attine ants is a widespread trait amongst members of this clade, hence its naming as *Myrmecopterula*.

The ecological roles of Pterulaceae are not well understood, most being classified from superficial observations as saprotrophs, growing on wood or leaf litter, with wood decay potentially being the ancestral state as discussed above. Whilst many species are found inhabiting soil or litter, two species are reported to associate with living plants, namely *Pterula* cf. *tenuissima*, endophytic in asymptomatic leaves of *Magnolia grandiflora*, and *Pterulicium xylogenum*, causal agent of culm rot disease of bamboo (Munkacsi et al. 2004; Villesen et al. 2004; Harsh et al. 2005) and possibly also a pathogen of sugarcane [see Corner (1952b)].

Most recent attention on Pterulaceae has been lavished on the ant-cultivated mutualists *M. nudihortorum* and *M. velohortorum*. These were once thought to be sister clades (Munkacsi et al. 2004; Villesen et al. 2004) but are now known to be only distantly related within the *Myrmecopterula* clade (Dentinger et al. 2009, Fig. 3). This suggests two possibilities for the evolution of the *Myrmecopterula*-*Apterostigma* mutualism: 1) that it evolved independently on two occasions or, 2) that it is an ancestral condition of all *Myrmecopterula*. However, it is at present unclear whether the extant mutualistic association found for *M. nudihortorum* and *M. velohortorum* is ancestral, implying that the other taxa escaped the mutualism, or whether the looser association with ant nests widespread amongst members of *Myrmecopterula* was more recently elevated to a higher level of interdependence for these two species, as suggested by Dentinger et al. (2009).

The basis of the association of 'free-living' species with attine ants and/or their abandoned nests is unclear. Given the apparent preference of some for abandoned nests, they may be specialised early stage colonisers of ant nest debris. A further possibility is that they are cheaters, deriving nutrition from the ant-collected biomass but not reciprocating by producing hyphae palatable to ants. This would represent a novel form of fungal mimicry, perhaps achieved by the ants' inability to differentiate hyphae of closely related species. Lastly, they may be mycoparasitic, including on ant cultivars, although there is currently no direct evidence supporting this hypothesis.

<u>Re-delimitation of Pterulaceae</u>

All the accepted genera in Pterulaceae were sampled in this study except for the monotypic *Allantula*. One specimen, with morphology consistent with Corner's description of *Allantula diffusa*, with pteruloid basidiomes borne on slender mycelial cords as curved intercalary swellings, was collected during our fieldwork (Fig. 1M). Phylogenetic reconstruction placed this specimen firmly within *Phaeopterula*. However, we have been unable to obtain the type specimen (no other collections authenticated exist) for more detailed analysis.

Thus, we re-delimit Pterulaceae containing six genera: *Allantula*, *Coronicium*, *Merulicium*, *Myrmecopterula*, *Phaeopterula*, *Pterula* and *Pterulicium*.

Conclusion

In this study, we presented a reclassification of Pterulaceae based on morphological and phylogenetic analyses with samples from six out of seven genera previously accepted in the family. Three early diverging resupinate genera were placed in Radulomycetaceae fam. nov. (*Aphanobasidium*, *Radulomyces* and *Radulotubus*), *Myrmecopterula* gen. nov. was erected to accommodate ant associated species previously classified in *Pterula*; several species from the latter were also recombined in the reintroduced *Phaeopterula* and in *Pterulicium*, and finally *Deflexula* was synonymised with *Pterulicium*. Pterulaceae was thus re-delimited to accommodate seven genera *Allantula*, *Coronicium*, *Merulicium*, *Myrmecopterula*, *Phaeopterula*, *Pterula* and *Pterulicium*.

Some species kept in *Pterula* might also need to be recombined since the original description was not enough to make these changes. Type specimens should be analysed considering the delimitations proposed in this study.

Key to genera of Pterulaceae and Radulomycetaceae fam. nov.

1.1 Cultivated by ants on *Apterostigma pilosum* group, basidiomes absent .... *Myrmecopterula**

1.2 Growing free-living, basidiomes present 2

2.1 Basidiomes resupinate to effused 3

2.2 Basidiomes coralloid, thread like or allantoid** 10

3.1 Hymenophore surface poroid .... *Radulotubus*

3.2 Hymenophore surface smooth, tuberculate, odontioid to raduloid or merulioid 4

4.1 Cystidia present 5

4.2 Cystidia absent 8

5.1 Hyphal system monomitic 6

5.2 Hyphal system dimitic 7

6.1 Spores ellipsoid to navicular, thin-walled, cystidia with incrustation .... *Coronicium*

6.2 Spores amygdaliform, slightly thick-walled, cystidia smooth .... *Pterulicium xylogenum****

7.1 Hymenophore surface merulioid, presence of cystidia with resinous excretion .... *Merulicium*

7.2 Hymenophore surface smooth, cystidia smooth .... *Pterulicium echo****

8.1 Basidia pleural .... *Aphanobasidium*

8.2 Basidia terminal 9

9.1 Spores ellipsoid to globose .... *Radulomyces*

9.2 Spores amygdaliform .... *Pterulicium xylogenum****

10.1 Basidiome allantoid with swollen fertile regions intercalating with mycelial chords .... *Allantula*

10.2 Basidiome coralloid or thread like 11

11.1 Stipe and base of branches very dark brown fading towards the tips .... *Phaeopterula*

11.2 Basidiomes uniformly coloured or only the stipe light brown coloured 12

12.1 Basidiomes simple or scarcely branched, growing up- or downwards .... *Pterulicium*

12.2 Basidiomes densely ramified, always ageotropic 13

13.1 Cottony subiculum present, associated with attine ants .... *Myrmecopterula*

13.2 Cottony subiculum absent, without association with attine ants .... *Pterula*

* *Myrmecopterula* cultivated by *Apterostigma* was never reported forming basidiomes.

** Allantoid = sausage-shaped, in this case with inflated portions of hymenium intercalating with rhizomorph [see *Allantula* in Corner (1952a)]

*** *Pterulicium xylogenum* and *Pm. echo* can have corticioid growth independently of coralloid basidiomes. The cystidia in the former may be either present or absent.

ACKNOWLEDGEMENTS

The authors are grateful to the managers of Parque Nacional da Tijuca (ICMBio), Floresta Nacional do Tapajós, Parque Nacional do Iguaçú, Parque Nacional da Serra dos Orgãos and Reserva Biológica Augusto Ruschi, for logistical support and collection permits. Biological Dynamics of Forest Fragmentation Project (BDFFP) for providing logistical and field support. This is publication XXX of the BDFFP - INPA/STRI Technical Series (field reserve; location of specimen used here). We thank Supercomputing Wales for computing support. We are also thankful for the kind support and loan from the following herbaria: FLOR (Universidade Federal de Santa Catarina), K (Royal Botanical Gardens, Kew), INPA (Instituto Nacional de Pesquisas da Amazônia), HSTM (Universidade Federal do Oeste do Pará), CGE (Cambridge University). We thank the FungiBrBOL project for use of the FIOCRUZ-MG sequencing platform. The researchers who kindly collect and provide samples or photos, or helped in other way to this study: Ted Schultz, M. Cathie Aime, Dennis Desjardin, D. Jean Lodge, Bitty Roy, Michael Wherley, Tobias Policha, Jesse McAlpine, Tommy Jenkinson, Rocío Manobanda, Celeste Heisecke, Altielys C. Magnago, Eduardo P. Fazolino, Ariadne N. M. Furtado, Emerson L. Gumboski, Elisandro R. Drechsler-Santos, Julia Simon, Cauê Oliveira, Stefan Blaser, David J. Harries, Genivaldo Alves da Silva, Susanne Sourell, Lucie Zíbarová and André Rodrigues, Quimi Vidaurre Montoya, Louro Lima, Ocírio Juruna de Souza Pereira, Laura Martínez-Suz, Shaun Pennycook, Phillip Camarota Moura and Rafael Trevisan.

DECLARATION

Ethics approval and consent to participate

Not applicable

Adherence to national and international regulations

For samples obtained from fungarium collections, appropriate permissions were granted. Field sampling was undertaken with appropriate permissions from Brazilian authorities.

Consent for publication

All authors have approved the manuscript for submission

Availability of data and material

All the sequences generated in this study are deposited in GenBank (accession numbers can be found in Additional file 1). Alignments used to generate the phylogenies are deposited on TreeBase (ID: 24428). Samples are deposited in the fungaria indicated on Aditional file 1, some might be available from the authors via request.

Competing interests

The authors declare no competing interests

Funding

This article is part of the PhD thesis of CALD. CALD scholarship was provided by Coordination for the Improvement of Higher Education Personnel - Brazil, BEX 2145/15-4. Funding was provided in part from a Systematics and Taxonomy (SynTax) grant (Biotechnology and Biological Sciences Research Council, Natural Environment Research Council) to BTMD. Funding was provided in part by the National Geographic Society (No. 8317-07 to B.A. Roy and B.T.M. Dentinger) and the National Science Foundation (DEB-0841613 to B.A. Roy and B.T.M. Dentinger). The Institute of Biological, Environmental and Rural Sciences receives strategic funding from the Biotechnology and Biological Sciences Research Council (BBSRC; BBS/OS/GC/000011B).

Authors' contributions

CALD, BTMD, MAN, DJM, EGM and LAC conducted field sampling; CALD and LAC conducted the sequencing and phylogenetic analyses; CALD, GWG and BTMD wrote the manuscript with input from DJM, EGM, LAC and MAN

REFERENCES

Bernicchia A, Gorjón SP (2010) Corticiaceae s.l. Fungi Europaei, vol 12. Candusso, Italia

Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K, Madden TL (2009) BLAST+: architecture and applications. BMC Bioinformatics 10 (1):421. doi:10.1186/1471-2105-10-421

Chernomor O, von Haeseler A, Minh BQ (2016) Terrace Aware Data Structure for Phylogenomic Inference from Supermatrices. Systematic Biology 65 (6):997-1008. doi:10.1093/sysbio/syw037

Corner EJH (1950) A monograph of Clavaria and allied genera, vol 1. Annals of Botany memoirs. Dawsons, London

Corner EJH (1952a) Addenda Clavariacea I. Two new Pteruloid genera and Deflexula. Annals of Botany 16 (2):269-291

Corner EJH (1952b) Addenda Clavariacea II. Pterula and Pterulicium. Annals of Botany 16 (4):531-569

Corner EJH (1952c) Generic names in Clavariaceae. Transactions of the British Mycological Society 35 (4):285-298

Corner EJH (1957) Some clavarias from Argentina. Darwiniana 11 (2):193-206

Corner EJH (1966) Clavarioid genera and Thelephora from the Congo. Bulletin du Jardin botanique de l'État a Bruxelles 36 (Fasc. 3):257-279

Corner EJH Clavarioid fungi of the Solomon Islands. In: Proceedings of the Linnean Society of London, 1967. vol 2. Oxford University Press, pp 91-106

Corner EJH (1970) Supplement to "A Monograph of Clavaria and Allied Genera". Beihefte zur Nova Hedwigia 33:1-299

Dentinger BTM (2014) Nomenclatural novelties. Index Fungorum (98):1

Dentinger BTM, Gaya E, O'Brien H, Suz LM, Lachlan R, Díaz-Valderrama JR, Koch RA, Aime MC (2016) Tales from the crypt: genome mining from fungarium specimens improves resolution of the mushroom tree of life. Biological Journal of the Linnean Society 117 (1):11-32. doi:10.1111/bij.12553

Dentinger BTM, Lodge DJ, Munkacsi AB, Desjardin DE, McLaughlin DJ (2009) Phylogenetic Placement of an Unusual Coral Mushroom Challenges the Classic Hypothesis of Strict Coevolution in the Apterostigma Pilosum Group Ant-Fungus Mutualism. Evolution 63 (8):2172-2178. doi:10.1111/j.1558-5646.2009.00697.x

Dentinger BTM, Margaritescu S, Moncalvo J-M (2010) Rapid and reliable high-throughput methods of DNA extraction for use in barcoding and molecular systematics of mushrooms. Molecular Ecology Resources 10 (4):628-633. doi:10.1111/j.1755-0998.2009.02825.x

Dentinger BTM, McLaughlin DJ (2006) Reconstructing the Clavariaceae using nuclear large subunit rDNA sequences and a new genus segregated from Clavaria. Mycologia 98 (5):746-762. doi:DOI 10.3852/mycologia.98.5.746

Dogma IJ (1966) Philippine Clavariaceae. I. The pteruloid series. Philippine Agriculturist 49 (10):18

Donk MA (1964) A conspectus of the families of Aphyllophorales. Persoonia 3 (2):199-324

Fries EM (1821) Systema Mycologicum volumen I, vol 1. Ex Officina Berlingiana. Lund & Greifswald

Fries EM (1825) Systema Orbis Vegetabilis Typographia Academia. Lundae, Sweden

Fries EM (1830) Eclogae fungorum, praecipue ex herbariis germanorum de scriptorum. Linnaea

Harsh SNK, Singh YP, Gupta HK, Mushra BM, McLaughlin DJ, Dentinger B (2005) A new culm rot disease of bamboo in India and its management. J Bamboo Rattan 4:387-398

Hennings P (1899) Fungi monsunenses. Monsunia 1:38

Hennings P (1904) Fungi amazonici II, a cl. Ernesto Ule collecti. Hedwigia 43:242-273

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. Molecular biology and evolution 35 (2):518-522. doi:10.1093/molbev/msx281

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14:587. doi:10.1038/nmeth.4285

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular biology and evolution 30 (4):772-780. doi:10.1093/molbev/mst010

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28 (12):1647-1649. doi:10.1093/bioinformatics/bts199

Larsson A (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30 (22):3276-3278. doi:10.1093/bioinformatics/btu531

Larsson K-H (2007) Re-thinking the classification of corticioid fungi. Mycological research 111 (9):1040-1063

Larsson K-H, Larsson E, Kõljalg U (2004) High phylogenetic diversity among corticioid homobasidiomycetes. Mycological research 108 (09):983-1002

Leal-Dutra CA (2015) Contribuições Taxonômicas e Filogenéticas ao Estudo de Pterulaceae (Agaricales) Coraloides. Universidade Federal de Santa Catarina, Florianópolis

Leal-Dutra CA, Neves MA, Griffith GW, Reck MA, Clasen LA, Dentinger BTM (2018) Reclassification of Parapterulicium Corner (Pterulaceae, Agaricales), contributions to Lachnocladiaceae and Peniophoraceae (Russulales) and introduction of Baltazaria gen. nov. MycoKeys 37. doi:10.3897/mycokeys.37.26303

Liu YJ, Whelen S, Hall BD (1999) Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. Molecular biology and evolution 16 (12):1799-1808

Lloyd CG (1919) Mycological notes. Mycological Writings 5 (60):15

Maas Geesteranus R (1964) Notes on Hydnums—II. Persoonia-Molecular Phylogeny and Evolution of Fungi 3 (2):155-192

Matheny PB (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (Inocybe; Agaricales). Molecular phylogenetics and evolution 35 (1):1-20

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge Z-W, Yang Z-L, Slot JC, Ammirati JF, Baroni TJ (2006) Major clades of Agaricales: a multilocus phylogenetic overview. Mycologia 98 (6):982-995

McLaughlin DJ, McLaughlin EG (1972) Pure Culture Studies of Fruiting and Sporulation in a Clavarioid Fungus, Pterula sp. Mycologia 64 (3):599-608. doi:10.2307/3757875

McLaughlin DJ, McLaughlin EG (1980) A new species of Pterula (Aphyllophorales) with corticioid characteristics. Canadian Journal of Botany 58 (12):1327-1333. doi:10.1139/b80-163

McLaughlin EG, McLaughlin DJ, Adson DE (1978) Developmental anatomy of a dimitic basidiomycete, Pterula sp. Canadian Journal of Botany 56 (3):288-296. doi:10.1139/b78-036

Mueller UG, Kardish MR, Ishak HD, Wright AM, Solomon SE, Bruschi SM, Carlson AL, Bacci M (2018) Phylogenetic patterns of ant-fungus associations indicate that farming strategies, not only a superior fungal cultivar, explain the ecological success of leafcutter ants. Molecular Ecology 27 (10):2414-2434. doi:10.1111/mec.14588

Munkacsi A, Pan J, Villesen P, Mueller U, Blackwell M, McLaughlin D (2004) Convergent coevolution in the domestication of coral mushrooms by fungus–growing ants. Proceedings of the Royal Society of London B: Biological Sciences 271 (1550):1777-1782

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. Molecular biology and evolution 32 (1):268-274. doi:10.1093/molbev/msu300

Pereira JS, Costa RR, Nagamoto NS, Forti LC, Pagnocca FC, Rodrigues A (2016) Comparative analysis of fungal communities in colonies of two leaf-cutting ant species with different substratum preferences. Fungal Ecology 21:68-75. doi:https://doi.org/10.1016/j.funeco.2016.03.004

Remsberg RE (1940) A New Species of *Pistillaria* on Rice Straw. Mycologia 32 (5):4. doi:10.1080/00275514.1940.12017444

Roberts P (1999) Clavarioid fungi from Korup National Park, Cameroon. Kew Bulletin:517-539

Saccardo PA, Saccardo D (1905) Sylloge Fungorum, vol XVII. Patavii, Italy

Schultz TR (2007) The fungus-growing ant genus Apterostigma in Dominican amber. In: Snelling R, BL Fisher, PS Ward (ed) Advances in ant systematics (Hymenoptera: Formicidae): homage to E. O. Wilson – 50 years of contributions., vol 80. Memoirs of the American Entomological Institute. American Entomological Institute, Gainesville, FL, pp 425-436

Spegazzini C (1921) Mycetes chilenses. Boletín de la Academia Nacional de Ciencias en Córdoba 25:124

Index Herbariorum: A global directory of public herbaria and associated staff. (continuously updated) http://sweetgum.nybg.org/science/ih/.

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172 (8):4238-4246

Villesen P, Mueller UG, Schultz TR, Adams RM, Bouck AC (2004) Evolution of ant‐cultivar specialization and cultivar switching in Apterostigma fungus‐growing ants. Evolution 58 (10):2252-2265

Zhao C-L, Chen H, He S-H, Dai Y-C (2016) Radulotubus resupinatus gen. et sp. nov. with a poroid hymenophore in Pterulaceae (Agaricales, Basidiomycota). Nova Hedwigia 102 (3-4):3-4

ADDITIONAL NOMENCLATURAL NOVELTIES

Phaeopterula anomala (P. Roberts) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB830999

Basionym: *Pterula anomala* P. Roberts, *Kew Bull*. **54**(3): 528 (1999).

Description in Roberts (1999).

Phaeopterula hirsuta (Henn.) Sacc. & D. Sacc., *Syll. fung.* (Abellini) **17**: 201 (1905)

MycoBank MB469044

Basionym: *Pterula hirsuta* Henn., in Warburg, *Monsunia* **1**: 9 (1899) [1900].

Synonym: *Dendrocladium hirsutum* (Henn.) Lloyd, *Mycol. Writ*. **5**: 870 (1919).

Description in Corner (1950).

Phaeopterula juruensis Henn. ex Sacc. & D. Sacc., *Syll. fung.* (Abellini) **17**: 201 (1905)

MycoBank MB634235 **(Fig. 1O)**

Basionym: *Pterula juruensis* Henn. [as '*Phaeopterula juruensis*'], *Hedwigia* **43**(3): 175 (1904).

Synonym: *Dendrocladium juruense* (Henn.) Lloyd, *Mycol. Writ*. **5**: 870 (1919).

Descriptions in Corner (1950, 1952b).

Phaeopterula stipata (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831000 **(Fig. 1N)**

Basionym: *Pterula stipata* Corner, *Ann. Bot*., Lond., n.s. **16**: 568 (1952).

Description in Corner (1952b).

Phaeopterula taxiformis (Mont.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831001

Basionym: *Pterula taxiformis* Mont., *Syll. gen. sp. crypt*. (Paris): 181 (1856).

Synonyms: *Lachnocladium taxiforme* (Mont.) Sacc., *Syll. fung.* (Abellini) **6**: 740 (1888). *Pterula humilis* Speg., *Revista Argent. Hist. Nat*. **1**(2): 110 (1891). *Pterula humilis* var. *tucumanensis* Speg., *Anal. Mus. nac. B. Aires*, Ser. 3 **12**: 280 (1909).

Descriptions in Corner (1950, 1952b).

Phaeopterula taxiformis* var. *gracilis (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831002

Basionym: *Pterula taxiformis* var. *gracilis* Corner, *Ann. Bot.*, Lond., n.s. 16: 568 (1952).

Description in Corner (1952b).

Pterulicium argentinum (Speg.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831003

Basionym: *Mucronella argentina* Speg., *Anal. Mus. nac. Hist. nat. B. Aires* **6**: 178 (1898) [1899].

Synonyms: *Deflexula argentina* (Speg.) Corner, *Ann. Bot.*, Lond., n.s. **16**: 276 (1952). *Deflexula lilaceobrunnea* var. *elongata* Corner, *Ann. Bot*., Lond., n.s. **16**: 276 (1952).

Description in Corner (1952a, 1970)

Pterulicium argentinum* var. *ramosum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831004

Basionym: *Deflexula argentina* (Speg.) Corner, *Ann. Bot*., Lond., n.s. **16**: 276 (1952).

Description in Corner (1970).

Pterulicium bambusae (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831005

Basionym: *Pterula bambusae* Corner, *Beih. Nova Hedwigia* **33**: 209 (1970).

Description in Corner (1970).

Pterulicium bromeliphilum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831006

Basionym: *Pterula bromeliphil*a Corner, *Beih. Nova Hedwigia* **33**: 210 (1970).

Description in Corner (1970).

Pterulicium brunneosetosum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831007

Basionym: *Pterula brunneosetosa* Corner, *Ann. Bot*., Lond., n.s. **16**: 566 (1952)

Descriptions in Corner (1952b, 1957, 1970).

Pterulicium campoi (Speg.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831008

Basionym: *Pterula campoi* Speg., *Bol. Acad. nac. Cienc. Córdoba* **25**: 29 (1921).

Descriptions in Corner (1970) and Spegazzini (1921).

Pterulicium caricis-pendulae (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831009

Basionym: *Pterula caricis-pendulae* Corner, *Beih. Nova Hedwigia* **33**: 211 (1970).

Description in Corner (1970).

Pterulicium crassisporum (P. Roberts) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831010

Basionym: *Pterula crassispora* P. Roberts, *Kew Bull*. **54**(3): 531 (1999).

Description in Roberts (1999).

Pterulicium cystidiatum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831011

Basionym: *Pterula cystidiata* Corner, *Ann. Bot*., Lond., n.s. **16**: 567 (1952).

Description in Corner (1952b).

Pterulicium debile (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831012

Basionym: *Pterula bromeliphil*a Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 698 (1950).

Description in (Corner 1950).

Pterulicium echo (D.J. McLaughlin & E.G. McLaughlin) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831013

Basionym: *Pterula echo* D.J. McLaughlin & E.G. McLaughlin, *Can. J. Bot*. **58**: 1328 (1980).

Description in McLaughlin and McLaughlin (1980).

Pterulicium epiphylloides (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831014

Basionym: *Pterula epiphylloides* Corner, *Ann. Bot*., Lond., n.s. **16**: 567 (1952).

Description in Corner (1952b).

Pterulicium epiphyllum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831015

Basionym: *Pterula epiphylla* Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 698 (1950).

Description in (Corner 1950).

Pterulicium fasciculare (Bres. & Pat.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831016

Basionym: *Pterula fascicularis* Bres. & Pat., *Mycol. Writ*. **1**: 50 (1901).

Synonym: *Deflexula fascicularis* (Bres. & Pat.) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 395 (1950).

Description in Corner (1950).

Pterulicium fluminense (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831017

Basionym: *Pterula fluminensis* Corner, *Ann. Bot.*, Lond., n.s. **16**: 567 (1952).

Descriptions in Corner (1952b, 1970).

Pterulicium gordium (Speg.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831018

Basionym: *Clavaria gordius* Speg., *Anal. Soc. cient. argent*. **17**(2): 83 (1884).

Synonym: *Pterula gordius* (Speg.) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 513 (1950).

Description in (Corner 1950).

Pterulicium gordium* var. *macrosporum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831019

Basionym: *Pterula gordius* var. *macrospora* Corner, *Proc. Linn. Soc.* London **178**: 100 (1967).

Description in Corner (1967).

Pterulicium gracile (Desm. & Berk.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831020

Basionym: *Typhula gracilis* Desm. & Berk., Ann. nat. Hist., Mag. Zool. Bot. Geol. 1: 202 (1838).

Synonyms: *Pistillaria gracilis* (Desm. & Berk.) Pat., *Tab. analyt. Fung*. (Paris)(6): 30 (1886). *Hirsutella gracilis* (Desm. & Berk.) Pat., *Revue mycol.*, Toulouse **14**(no. 54): 69 (1892). *Pterula gracilis* (Desm. & Berk.) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 514 (1950). *Clavaria aculina* Quél., *C. r. Assoc. Franç. Avancem. Sci*. **9**: 670 (1881) [1880]. *Pistillaria aculina* (Quél.) Pat., *Tab. analyt. Fung*. (Paris)(6): 29 (fig. 570) (1886). *Ceratella aculina* (Quél.) Pat., *Hyménomyc. Eur*. (Paris): 157

(1887). *Cnazonaria aculina* (Quél.) Donk, *Meded. Bot. Mus. Herb. Rijks Univ*. Utrecht **9**: 97 (1933). *Pistillaria aculina* subsp. *juncicola* Bourdot & Galzin, *Hyménomyc. de France* (Sceaux): 138 (1928) [1927]. *Pistillaria aculina* subsp. *graminicola* Bourdot & Galzin, *Hyménomyc. de France* (Sceaux): 139 (1928) [1927]. *Pistillaria aculina* subsp. *acicula* Bourdot & Galzin, *Hyménomyc. de France* (Sceaux): 139 (1928) [1927]. *Typhula brunaudii* Quél., *C. r. Assoc. Franç. Avancem. Sci*. **13**: 283 (1885) [1884]. *Clavaria brunaudii* (Quél.) Sacc., *Syll. fung*. (Abellini) **6**: 730 (1888). *Ceratella ferryi* Quél. & Fautrey, *Revue mycol*., Toulouse **15**(no. 57): 15 (1893). *Pistillaria ferryi* (Quél. & Fautrey) Sacc., *Syll. fung*. (Abellini) **11**: 141 (1895). *Pistillaria ferryi* subsp. *tremula* Sacc., *Syll. fung*. (Abellini) **17**: 202 (1905). *Mucronella rickii* Oudem., *Ned. kruidk. Archf*, 3 sér. **2**(3): 667 (1902). *Cnazonaria rickii* (Oudem.) Donk, *Meded. Bot. Mus. Herb. Rijks Univ*. Utrecht **9**: 99 (1933). *Ceratellopsis rickii* (Oudem.) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 205 (1950).

Description in (Corner 1950).

Pterulicium incarnatum (Pat.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831021

Basionym: *Pterula incarnata* Pat., in Patouillard & Lagerheim, *Bull. Herb. Boissier* **3**(1): 58 (1895)

Description in (Corner 1950, 1970)

Pterulicium intermedium (Dogma) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831022

Basionym: *Pterula intermedia* Dogma, *Philipp. Agric*. **49**: 852 (1966)

Descriptions in (Corner 1970) and Dogma (1966)

Pterulicium laxum (Pat.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831023

Basionym: *Pterula laxa* Pat., *Bull. Soc. mycol. Fr*. **18**(2): 175 (1902).

Description in (Corner 1950, 1970) Pat. 1902

Pterulicium lilaceobrunneum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.** **(Fig. 1K)**

MycoBank MB831024

Basionym: *Deflexula lilaceobrunnea* Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 695 (1950).

Description in Corner (1952a).

Pterulicium lilaceobrunneum* var. *evolutius (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831025

Basionym: *Deflexula lilaceobrunnea* var. *evolutior* Corner, *Beih. Nova Hedwigia* **33**: 197 (1970).

Description in Corner (1970).

Pterulicium longisporum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831026

Basionym: *Pterula longispora* Corner, *Ann. Bot*., Lond., n.s. **16**: 567 (1952)

Description in (Corner 1952b).

Pterulicium macrosporum (Pat.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831027

Basionym: *Ceratella macrospora* Pat., in Patouillard & Lagerheim, *Bull. Soc. mycol. Fr*. **8**(3): 119 (1892).

Synonyms: *Pistillaria macrospora* (Pat.) Sacc., *Syll. fung*. (Abellini) **11**: 142 (1895). *Pterula macrospora* (Pat.) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 518 (1950).

Description in (Corner 1950, 1970). Pat 1892

Pterulicium majus (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831028

Basionym: *Deflexula major* Corner, *Ann. Bot*., Lond., n.s. **16**: 277 (1952).

Description in Corner (1952a).

Pterulicium mangiforme (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831029

Basionym: *Deflexula mangiformis* Corner, *Ann. Bot*., Lond., n.s. **16**: 278 (1952).

Description in Corner (1952a).

Pterulicium microsporum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831030

Basionym: *Deflexula microspora* Corner, *Bull. Jard. bot. État Brux*. **36**: 264 (1966).

Description in Corner (1966).

Pterulicium nanum (Pat.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831031

Basionym: *Pterula nana* Pat., Bull. *Soc. mycol. Fr*. **18**(2): 175 (1902).

Synonyms: *Deflexula nana* (Pat.) Corner, *Bull. Jard. bot. État Brux*. **36**: 264 (1966). *Pterula vanderystii* Henn. [as *'vanderysti'*], *Ann. Mus. Congo Belge*, Bot., Sér. 5 **2**(2): 96 (1907). *Deflexula vanderystii* (Henn.) Corner, *Ann. Bot*., Lond., n.s. **16**: 284 (1952).

Description in Corner (1966).

Pterulicium naviculum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831032

Basionym: *Pterula navicula* Corner, *Ann. Bot*., Lond., n.s. **16**: 568 (1952).

Description in (Corner 1952b).

Pterulicium oryzae (Remsberg) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831033

Basionym: *Pistillaria oryzae* Remsberg, *Mycologia* **32**(5): 668 (1940).

Synonym: *Pterula oryzae* (Remsberg) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 519 (1950).

Descriptions in (Corner 1950) and Remsberg (1940)

Pterulicium phyllodicola (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831034

Basionym: *Pterula phyllodicola* Corner, *Beih. Nova Hedwigia* **33**: 220 (1970).

Description in Corner (1970)

Pterulicium phyllophilum (McAlpine) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831035

Basionym: *Clavaria phyllophila* McAlpine, *Agric. Gaz. N.S.W.*, Sydney **7**: 86 (1896).

Synonym: *Pterula phyllophila* (McAlpine) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 520 (1950).

Description in (Corner 1950).

Pterulicium rigidum (Donk) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831036

Basionym: *Pterula rigida* Donk, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 698 (1950).

Description in Corner (1950)

Pterulicium sclerotiicola (Berthier) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831037

Basionym: *Pterula sclerotiicola* Berthier, *Bull. trimest. Soc. mycol. Fr.* **83**: 731 (1968) [1967]

Description in Corner (1970)

Pterulicium secundirameum (Lév) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov. (Fig. 1I)**

MycoBank MB831038

Basionym: *Clavaria secundiramea* Lév., *Annls Sci. Nat., Bot*., sér. 3 **2**: 216 (1844).

Synonyms: *Pterula secundiramea* (Lév.) Speg., *Bol. Acad. nac. Cienc. Córdoba* **11**(4): 466 (1889). *Deflexula secundiramea* (Lév.) Corner, *Beih. Nova Hedwigia* **33**: 199 (1970). *Pterula palmicola* Corner, *Ann. Bot.*, Lond., n.s. **16**: 568 (1952) **syn. nov.**

Descriptions in Corner (1950, 1952b).

Notes

The synonymisation of *Pm. palmicola* (samples M50 and M83) in *Pm. secundirameum* (samples M70 and genome5) is based on our phylogenetic results and morphological comparisons. The only morphological difference between the two species is the shape of the basidiome, however, the other characters are similar and both species are nested together within our tree (Additional file 2).

Pterulicium sprucei (Mont.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov. (Fig. 1L)**

MycoBank MB831039

Basionym: *Hydnum sprucei* Mont., *Syll. gen. sp. crypt.* (Paris): 173 (1856).

Synonyms: *Pterula sprucei* (Mont.) Lloyd, *Mycol. Writ.* **5**: 865 (1919). *Deflexula sprucei* (Mont.) Maas Geest., *Persoonia* **3**(2): 179 (1964). *Pterula pennata* Henn., *Hedwigia* **43**(3): 174 (1904). *Deflexula pennata* (Henn.) Corner, *Ann. Bot.*, Lond., n.s. **16**: 278 (1952).

Description in Corner (1952a) as *D. pennata*, Corner (1970) and Maas Geesteranus (1964).

Pterulicium subsimplex (Henn.) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831040

Basionym: *Pterula subsimplex* Henn., *Hedwigia* **36**(4): 197 (1897).

Synonyms: *Deflexula subsimplex* (Henn.) Corner, *Ann. Bot.*, Lond., n.s. **16**: 279 (1952). *Pterula nivea* Pat., *Bull. Soc. mycol. Fr.* **18**(2): 174 (1902). *Deflexula nivea* (Pat.) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 398 (1950). *Mucronella pacifica* Kobayasi, *Bot. Mag.*, Tokyo **53**: 160 (1939). *Deflexula pacifica* (Kobayasi) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 399 (1950).

Descriptions in Corner (1952a) and Corner (1950) as D. pacifica.

Pterulicium subsimplex* var. *multifidum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831041

Basionym: *Deflexula subsimplex* var. *multifida* Corner, *Ann. Bot.*, Lond., n.s. **16**: 282 (1952).

Description in Corner (1952a).

Pterulicium subtyphuloides (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831042

Basionym: *Pterula subtyphuloides* Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 698 (1950).

Description in Corner (1950).

Pterulicium sulcisporum (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831043

Basionym: *Deflexula sulcispora* Corner, *Ann. Bot.*, Lond., n.s. **16**: 283 (1952).

Description in Corner (1952a).

Pterulicium tenuissimum (M.A. Curtis) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831044

Basionym: *Typhula tenuissima* M.A. Curtis, *Am. Journ. Art. Scienc*. **6**: 351 (1848).

Synonym: *Pterula tenuissima* (M.A. Curtis) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 524 (1950).

Description in Corner (1950).

Pterulicium ulmi (Peck) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831045

Basionym: *Mucronella ulmi* Peck, *Ann. Rep. Reg. N.Y. St. Mus*. **54**: 154 (1902) [1901].

Synonym: *Deflexula ulmi* (Peck) Corner, *Monograph of Clavaria and allied Genera*, (Annals of Botany Memoirs No. 1): 400 (1950).

Description in Corner (1950, 1970).

Pterulicium velutipes (Corner) Leal-Dutra, Dentinger, G.W. Griff., **comb. nov.**

MycoBank MB831046

Basionym: *Pterula velutipes* Corner, *Ann. Bot.*, Lond., n.s. **16**: 569 (1952).

Description in Corner (1952b).

Captions for Figures and Additional files:

Fig. 1 Diversity of coralloid genera of Pterulaceae. A-F: *Myrmecopterula* (A: *Apterostigma sp*. nest with *M. velohortorum* with *Myrmecopterula sp.* SAPV1 growing atop of the garden veil; B, C, F: *Myrmecopterula sp.* D: *Apterostigma sp*. nest with *M. nudihortorum*; E: *M. moniliformis*). G-H: *Pterula* (G: *P. cf. loretensis*; H: *P. cf. verticillata*). I-L: *Pterulicium* (I: *P. secundirameum*; J: *P. aff fluminensis*; K: *P. lilaceobrunneum*. L: *P. sprucei*). M-O: *Phaeopterula* (M: *Phaeopterula sp*.; N: *P. stipata*; O: *P. juruensis*). Close observation on photos B and C reveal the basidiomes growing from granular substrate resembling substrate of ants' fungus garden. Photos D and G kindly provided by Ted Schultz and Michael Wherley respectively. Scale bars: 1 cm.

Fig. 2 Corticioid genera of Pterulaceae (A-C) and Radulomycetaceae (D-F). A: *Coronicium alboglaucum*. B-C: *Merulicium fusisporum.* D: *Radulomyces confluens*. E: *Radulotubus resupinatus*. F: *Aphanobasidium cf. pseudotsugae*. Photos kindly provided by L. Zíbarová (A and F), S. Blaser (B and C), D.J. Harries (D) and C.L. Zhao (E). Scale bars: 1 cm.

Fig. 3 Maximum-likelihood tree of Pterulaceae and Radulomycetaceae. Support values on the branches are UFBoot/BPP and showed only for UFBoot$\geq$70 and BPP$\geq$0.70 and branch length $\geq$ 0.003 substitutions per site. Details for the complete tree can be found in Additional file 2 and TreeBase (ID: 24428). Scale bar: nucleotide substitutions per site.

Additional file 1: Full details of all samples studied here (simplified in Table2; as excel file)

Additional file 2: Additional phylogenetic reconstructions, including detailed analyses relating to Figure 3

Additional file 3: Additional images of coralloid Pterulaceae and micrographs of *Myrmecopterula velohortorum*.

Table 2: Details of new sequences generated in this study used in the tree of Fig. 3. (a full version is presented as excel file in Additional file 1).

Taxon (former genus in brackets)	**DNA sample ID**	**Herbarium voucher**	**Country**	**Region**	**ITS**	**LSU**	**RPB2**
Coronicium alboglaucum	K15	K(M) 170129	UK	England	MK953245	–	–
Coronicium gemmiferum	K13	K(M) 133847	UK	England	MK953246	–	–
Coronicium gemmiferum	K14	K(M) 68853	UK	England	MK953247	MK953403	–
Merulicium fusisporum	K16	K(M) 45181	UK	England	MK953248	–	–
Myrmecopterula (Pterula) moniliformis	F92 Consensus 1	INPA 280127	Brazil	Amazonas	MK953251	MK953405	MK944362
Myrmecopterula (Pterula) moniliformis	M39	FLOR 56397	Brazil	Paraíba	MK953253	MK953406	–
Myrmecopterula (Pterula) moniliformis	MCA	not deposited	–	–	MK953239	MK953392	MK944363
Myrmecopterula (Pterula) nudihortorum	F144 Consensus 1	not deposited	Brazil	Amazonas	MK953257	MK953393	MK944364
Myrmecopterula (Pterula) nudihortorum	KM190547_VC1	K(M) 190547	Panama	–	MK953240	MK953394	MK944365
Myrmecopterula (Pterula) sp.	F103	HSTM-Fungos 9931	Brazil	Pará	MK953260	MK953407	MK944325
Myrmecopterula (Pterula) sp.	F138	FLOR 63724	Brazil	Paraná	MK953262	MK953409	–
Myrmecopterula (Pterula) sp.	F40	FLOR 63725	Brazil	Paraná	MK953264	MK953410	MK944327
Myrmecopterula (Pterula) sp.	F82 Consensus 1	not deposited	Brazil	Amazonas	MK953269	MK953412	MK944366
Myrmecopterula (Pterula) sp.	F94	HSTM-Fungos 9928	Brazil	Pará	MK953274	MK953414	MK944329
Myrmecopterula (Pterula) sp.	F99	HSTM-Fungos 9930	Brazil	Pará	MK953276	MK953415	MK944330
Myrmecopterula (Pterula) sp.	M111	FLOR 56451	Brazil	Santa Catarina	MK953277	–	–
Myrmecopterula (Pterula) sp.	M40 Consensus 1	FLOR 56398; K(M)	Brazil	Paraíba	MK953280	MK953416	MK944367

		205347					
Myrmecopterula (Pterula) sp.	M69	FLOR 56418	Brazil	Rio Grande do Sul	MK953281	MK953395	MK944368
Myrmecopterula (Pterula) velohortorum	F114	not deposited	Brazil	Espírito Santo	MK953282	MK953396	MK944369
Myrmecopterula (Pterula) velohortorum	F117	not deposited	Brazil	Santa Catarina	MK953283	–	–
Myrmecopterula (Pterula) velohortorum	F135	not deposited	Brazil	Pará	MK953285	–	–
Myrmecopterula (Pterula) velohortorum	F136	not deposited	Brazil	Pará	MK953286	–	–
Myrmecopterula (Pterula) velohortorum	F137	not deposited	Brazil	Pará	MK953287	–	–
Myrmecopterula (Pterula) velohortorum	F140 Clone 1	not deposited	Brazil	Amazonas	MK953288	–	–
Myrmecopterula (Pterula) velohortorum	F152	not deposited	Brazil	Santa Catarina	MK953290	–	–
Myrmecopterula (Pterula) velohortorum	KM190546	K(M) 190546	Panama	–	MK953242	MK953397	MK944370
Myrmecopterula (Pterula) velohortorum	RC12 Consensus 1	not deposited	Brazil	Amazonas	MK953291	–	–
Phaeopterula (Pterula) anomala	KM38182	K(M) 38182	Cameroon	–	MK953295	–	–
Phaeopterula (Pterula) cf. juruensis	F45 Consensus 1	FLOR 63732	Brazil	Paraná	MK953296	MK953417	MK944331
Phaeopterula (Pterula) cf. juruensis	F79 Consensus 1	FLOR 63717	Brazil	Paraná	MK953299	MK953418	–
Phaeopterula (Pterula) cf. stipata	F66 Consensus 1	HSTM-Fungos 9938	Brazil	Pará	MK953301	–	–
Phaeopterula (Pterula) cf. stipata	F98 Consensus 1	HSTM-Fungos 9929	Brazil	Pará	MK953302	–	–
Phaeopterula (Pterula) cf. taxiformis	M4	FLOR 56367	Brazil	Santa Catarina	MK953303	MK953419	–
Phaeopterula (Pterula) juruensis	F41	FLOR 63728	Brazil	Paraná	MK953304	MK953420	MK944332
Phaeopterula (Pterula) juruensis	M21	FLOR 56381	Brazil	Minas Gerais	MK953305	–	–

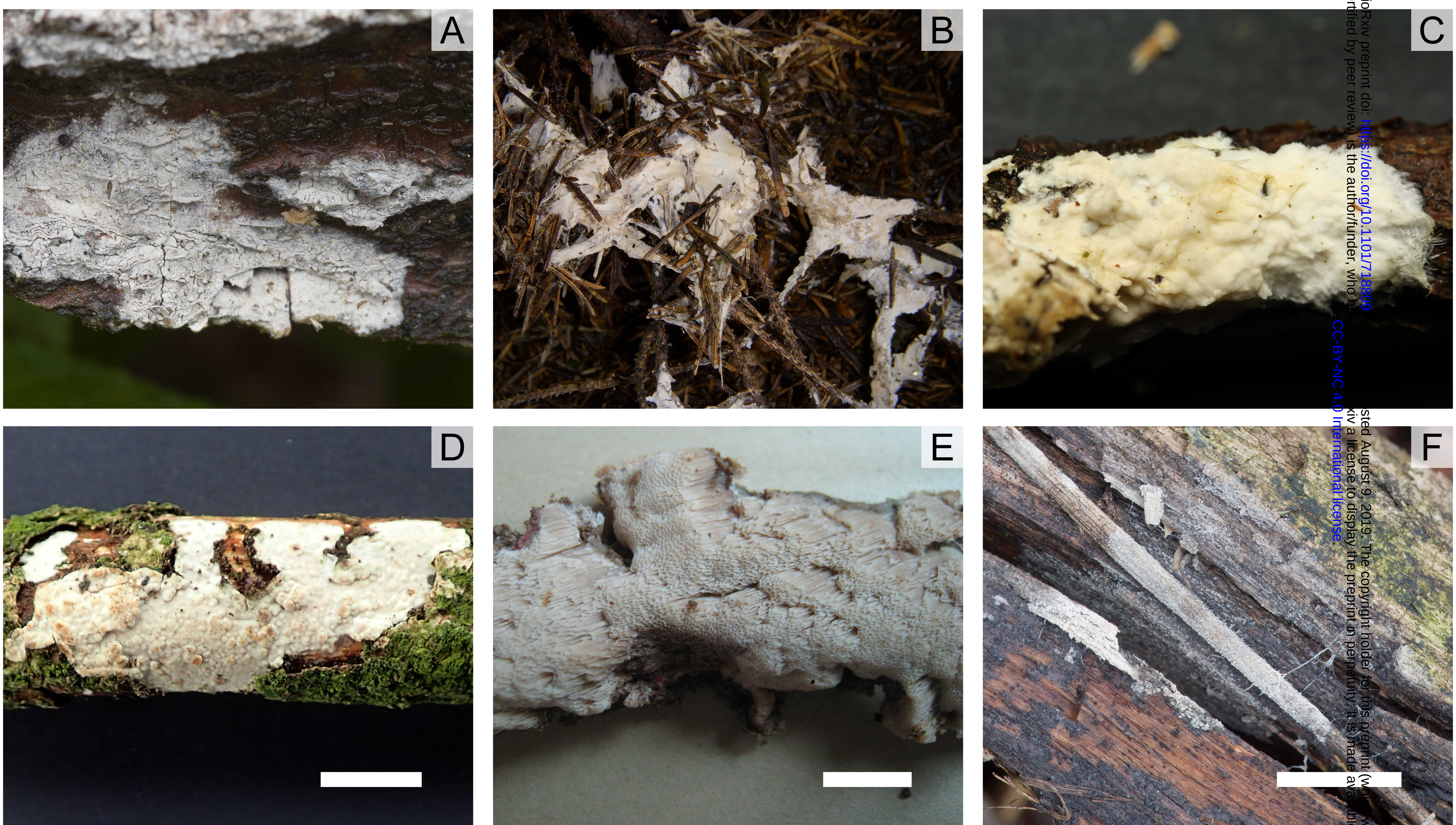
Phaeopterula (Pterula) juruensis	M36	FLOR 56396	Brazil	Santa Catarina	MK953307	MK953422	–
Phaeopterula (Pterula) sp.	F63 Consensus 1	HSTM-Fungos 9935	Brazil	Pará	MK953316	MK953425	MK944335
Phaeopterula (Pterula) sp.	F78 Clone 1	FLOR 63716	Brazil	Paraná	MK953321	MK953428	MK944338
Phaeopterula (Pterula) sp.	KM135954	K(M) 135954	Belize	–	MK953326	–	–
Phaeopterula (Pterula) sp.	KM137475	K(M) 137475	Puerto Rico	–	MK953327	–	–
Phaeopterula (Pterula) stipata	M15 Consensus 1	FLOR 56375	Brazil	Minas Gerais	MK953330	MK953431	–
Phaeopterula sp. (Allantula?)	F7 Consensus 1	HSTM-Fungos 9944	Brazil	Pará	MK953331	MK953432	MK944339
Pterula cf plumosa	KM167176	K(M) 167176	Ethiopia	–	MK953333	–	–
Pterula cf. loretensis	RLC273	K(M) 205553	Ecuador	Imbabura	MK953334	MK953398	MK944371
Pterula multifida	KM195746	K(M) 195746	UK	England	MK953335	MK953399	MK944372
Pterula sp.	F42	FLOR 63729	Brazil	Paraná	MK953336	MK953433	–
Pterula sp.	F48	FLOR 63735	Brazil	Paraná	–	MK953434	–
Pterula sp.	M112 Consensus 1	FLOR 56452	Brazil	Santa Catarina	MK953337	MK953435	MK944340
Pterula sp.	M153	FLOR 57849	Brazil	Santa Catarina	MK953339	MK953436	MK944341
Pterula sp.	M54	FLOR 56407	Brazil	Santa Catarina	MK953341	MK953438	–
Pterula sp.	M71 Consensus 1	FLOR 56424	Brazil	Santa Catarina	MK953342	MK953439	MK944342
Pterula sp.	KM141379	K(M) 141379	Puerto Rico	–	MK953344	–	–
Pterula sp.	KM167221	K(M) 167221	Australia	Queensland	MK953345	–	–
Pterula subulata	KM145950	K(M) 145950	Italy	–	MK953346	–	–

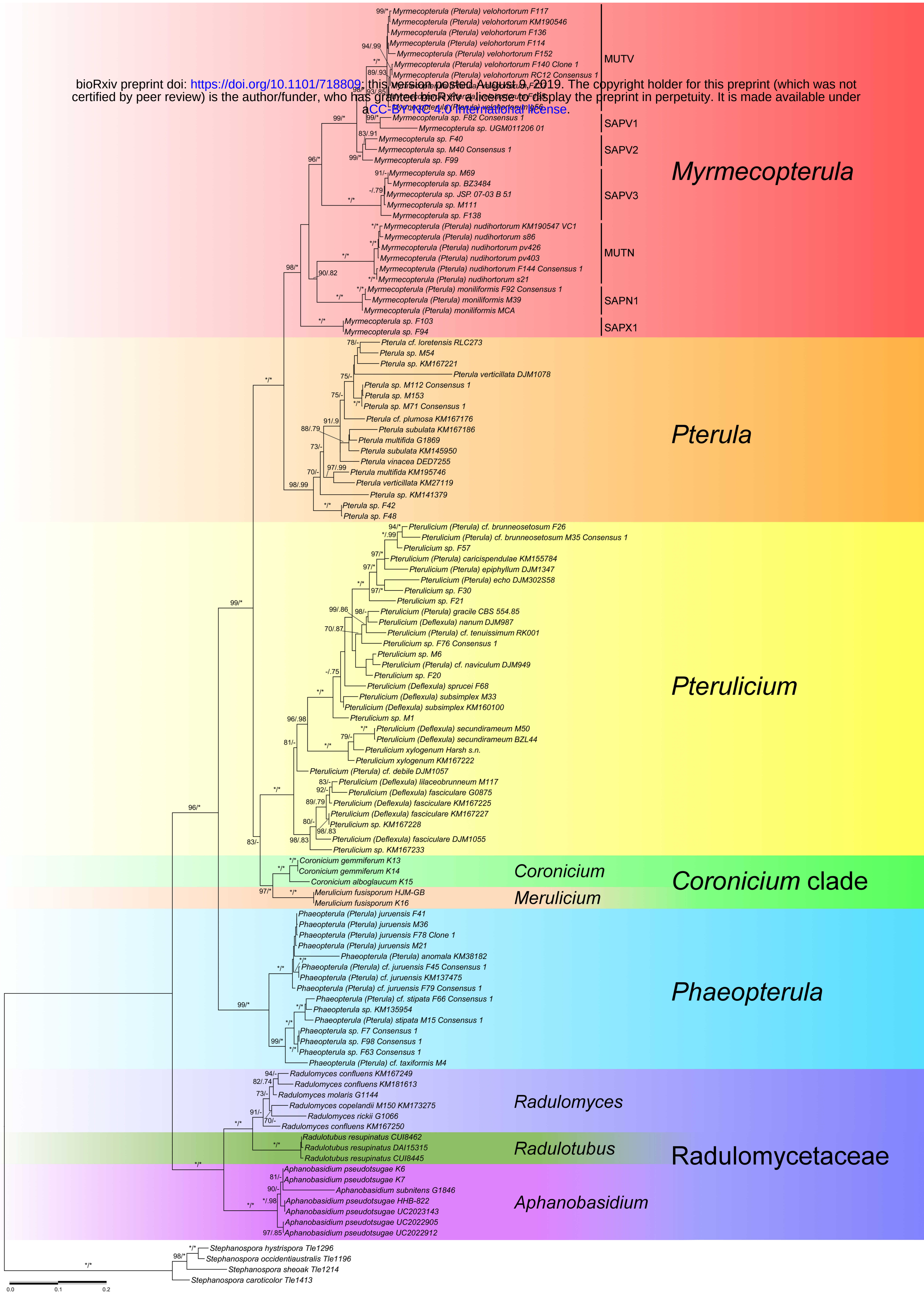
Pterula subulata	KM167186	K(M) 167186	Sweden	–	MK953347	–	–
Pterula verticillata	KM27119	K(M) 27119	Brunei	–	MK953348	–	–
Pterulicium (Deflexula) fasciculare	KM167225	K(M) 167225	Australia	–	MK953349	–	–
Pterulicium (Deflexula) fasciculare	KM167227	K(M) 167227	Malaysia	–	MK953350	–	–
Pterulicium (Deflexula) lilaceobrunneum	M117	FLOR 56455	Brazil	Rio de Janeiro	MK953351	MK953440	MK944343
Pterulicium (Deflexula) secundirameum	BZL44	RB 575791	Brazil	Rio de Janeiro	MK953353	MK953400	MK944373
Pterulicium (Deflexula) secundirameum	M50	FLOR 56403	Brazil	Santa Catarina	MK953354	MK953442	MK944344
Pterulicium (Deflexula) sp.	KM167228	K(M) 167228	Malaysia	–	MK953357	–	–
Pterulicium (Deflexula) sp.	KM167233	K(M) 167233	Sierra Leone	–	MK953358	–	–
Pterulicium (Deflexula) sprucei	F68	HSTM-Fungos 9940	Brazil	Pará	MK953361	MK953447	MK944349
Pterulicium (Deflexula) subsimplex	KM160100	K(M) 160100	Ecuador	–	–	MK953449	–
Pterulicium (Deflexula) subsimplex	M33	FLOR 56393	Brazil	Santa Catarina	MK953363	MK953450	MK944351
Pterulicium (Pterula) brunneosetosum	M35 Consensus 1	FLOR 56395	Brazil	Santa Catarina	MK953366	MK953452	MK944353
Pterulicium (Pterula) caricispendulae	KM155784	K(M) 155784	UK	England	MK953367	–	–
Pterulicium (Pterula) sp.	F20	INPA 280129	Brazil	Amazonas	MK953370	MK953454	–
Pterulicium (Pterula) sp.	F21	INPA 280132	Brazil	Amazonas	MK953371	MK953455	MK944355
Pterulicium (Pterula) sp.	F26	not deposited	Brazil	Espírito Santo	MK953372	MK953456	MK944356
Pterulicium (Pterula) sp.	F30	not deposited	Brazil	Espírito Santo	MK953373	MK953457	MK944357
Pterulicium (Pterula) sp.	F57	HSTM-Fungos 9925	Brazil	Pará	MK953376	MK953460	MK944359

Pterulicium (Pterula) sp.	F76 Consensus 1	HSTM-Fungos 9950	Brazil	Pará	MK953382	MK953461	MK944360
Pterulicium (Pterula) sp.	M1	FLOR 56364	Brazil	Santa Catarina	MK953383	MK953462	MK944361
Pterulicium (Pterula) sp.	M6	FLOR 56369	Brazil	Santa Catarina	MK953384	MK953463	–
Pterulicium (Pterulicium) xylogenum	KM167222	K(M) 167222	Bangladesh	–	MK953387	–	–
Aphanobasidium pseudotsugae	K6	K(M) 170662	UK	England	MK953243	MK953402	–
Aphanobasidium pseudotsugae	K7	K(M) 180787	UK	Scotland	MK953244	–	–
Radulomyces confluens	KM167249	K(M) 167249	Brazil	–	MK953388	–	–
Radulomyces confluens	KM167250	K(M) 167250	Argentina	–	MK953389	–	–
Radulomyces confluens	KM181613	K(M) 181613	UK	England	MK953390	MK953401	MK944374
Radulomyces copelandii	M150	K(M) 173275	USA	–	MK953391	MK953465	–

1107


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O


A
B
C
D
E
F


Myrmecopterula
MUTV
SAPV1
SAPV2
SAPV3
MUTN
SAPN1
SAPX1
Myrmecopterula (Pterula) velohortorum F117
Myrmecopterula (Pterula) velohortorum KM190546
Myrmecopterula (Pterula) velohortorum F136
Myrmecopterula (Pterula) velohortorum F114
Myrmecopterula (Pterula) velohortorum F152
Myrmecopterula (Pterula) velohortorum F140 Clone 1
Myrmecopterula (Pterula) velohortorum RC12 Consensus 1
Myrmecopterula sp. F82 Consensus 1
Myrmecopterula sp. UGM011206 01
Myrmecopterula sp. F40
Myrmecopterula sp. M40 Consensus 1
Myrmecopterula sp. F99
Myrmecopterula sp. M69
Myrmecopterula sp. BZ3484
Myrmecopterula sp. JSP 07-03 B 5.1
Myrmecopterula sp. M111
Myrmecopterula sp. F138
Myrmecopterula (Pterula) nudihortorum KM190547 VC1
Myrmecopterula (Pterula) nudihortorum s86
Myrmecopterula (Pterula) nudihortorum pv426
Myrmecopterula (Pterula) nudihortorum pv403
Myrmecopterula (Pterula) nudihortorum F144 Consensus 1
Myrmecopterula (Pterula) nudihortorum s21
Myrmecopterula (Pterula) moniliformis F92 Consensus 1
Myrmecopterula (Pterula) moniliformis M39
Myrmecopterula (Pterula) moniliformis MCA
Myrmecopterula sp. F103
Myrmecopterula sp. F94
Pterula
Pterula cf. loretensis RLC273
Pterula sp. M54
Pterula sp. KM167221
Pterula verticillata DJM1078
Pterula sp. M112 Consensus 1
Pterula sp. M153
Pterula sp. M71 Consensus 1
Pterula cf. plumosa KM167176
Pterula subulata KM167186
Pterula multifida G1869
Pterula subulata KM145950
Pterula vinacea DED7255
Pterula multifida KM195746
Pterula verticillata KM27119
Pterula sp. KM141379
Pterula sp. F42
Pterula sp. F48
Pterulicium
Pterulicium (Pterula) cf. brunneosetosum F26
Pterulicium (Pterula) cf. brunneosetosum M35 Consensus 1
Pterulicium sp. F57
Pterulicium (Pterula) caricispendulae KM155784
Pterulicium (Pterula) epiphyllum DJM1347
Pterulicium (Pterula) echo DJM302S58
Pterulicium sp. F30
Pterulicium sp. F21
Pterulicium (Pterula) gracile CBS 554.85
Pterulicium (Deflexula) nanum DJM987
Pterulicium (Pterula) cf. tenuissimum RK001
Pterulicium sp. F76 Consensus 1
Pterulicium sp. M6
Pterulicium (Pterula) cf. naviculum DJM949
Pterulicium sp. F20
Pterulicium (Deflexula) sprucei F68
Pterulicium (Deflexula) subsimplex M33
Pterulicium (Deflexula) subsimplex KM160100
Pterulicium sp. M1
Pterulicium (Deflexula) secundirameum M50
Pterulicium (Deflexula) secundirameum BZL44
Pterulicium xylogenum Harsh s.n.
Pterulicium xylogenum KM167222
Pterulicium (Pterula) cf. debile DJM1057
Pterulicium (Deflexula) lilaceobrunneum M117
Pterulicium (Deflexula) fasciculare G0875
Pterulicium (Deflexula) fasciculare KM167225
Pterulicium (Deflexula) fasciculare KM167227
Pterulicium sp. KM167228
Pterulicium (Deflexula) fasciculare DJM1055
Pterulicium sp. KM167233
Coronicium clade
Coronicium
Coronicium gemmiferum K13
Coronicium gemmiferum K14
Coronicium alboglaucum K15
Merulicium
Merulicium fusisporum HJM-GB
Merulicium fusisporum K16
Phaeopterula
Phaeopterula (Pterula) juruensis F41
Phaeopterula (Pterula) juruensis M36
Phaeopterula (Pterula) juruensis F78 Clone 1
Phaeopterula (Pterula) juruensis M21
Phaeopterula (Pterula) anomala KM38182
Phaeopterula (Pterula) cf. juruensis F45 Consensus 1
Phaeopterula (Pterula) cf. juruensis KM137475
Phaeopterula (Pterula) cf. juruensis F79 Consensus 1
Phaeopterula (Pterula) cf. stipata F66 Consensus 1
Phaeopterula sp. KM135954
Phaeopterula (Pterula) stipata M15 Consensus 1
Phaeopterula sp. F7 Consensus 1
Phaeopterula sp. F98 Consensus 1
Phaeopterula sp. F63 Consensus 1
Phaeopterula (Pterula) cf. taxiformis M4
Radulomycetaceae
Radulomyces
Radulomyces confluens KM167249
Radulomyces confluens KM181613
Radulomyces molaris G1144
Radulomyces copelandii M150 KM173275
Radulomyces rickii G1066
Radulomyces confluens KM167250
Radulotubus
Radulotubus resupinatus CUI8462
Radulotubus resupinatus DAI15315
Radulotubus resupinatus CUI8445
Aphanobasidium
Aphanobasidium pseudotsugae K6
Aphanobasidium pseudotsugae K7
Aphanobasidium subnitens G1846
Aphanobasidium pseudotsugae HHB-822
Aphanobasidium pseudotsugae UC2023143
Aphanobasidium pseudotsugae UC2022905
Aphanobasidium pseudotsugae UC2022912
Stephanospora hystrispora Tle1296
Stephanospora occidentiaustralis Tle1196
Stephanospora sheoak Tle1214
Stephanospora caroticolor Tle1413
0.0
0.1
0.2