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What's in a name? The case for standardised nomenclature for mutualistic Mucoromycotina 'fine root endophytes'.

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Highlight statement

Multiple names are currently used to describe same group of root-associated fungi. Following the International Conference for Mycorrhizas 12 (4-9th August 2024, Manchester, UK), we propose unifying them as "MFRE" to improve clarity, consistency, and distinguish them from similar fungal groups.

Introduction

Arbuscular mycorrhizal (AM) fungi are a near-ubiquitous group of plant symbiotic fungi and have been the focus of much mycorrhizal research over the last 60 years (Koide & Mosse, 2004). However, a lesser-known group of mycorrhizal fungi, the Mucoromycotina 'fine root endophytes' (MFRE), have garnered increasing research interest in recent years. This early branching lineage of fungi (Bidartondo *et al.*, 2011; Field *et al.*, 2015) was recently reclassified as belonging to the subphylum Mucoromycotina (Orchard *et al.*, 2017a) rather than the Glomeromycotina which encompasses the AM fungi (or 'coarse-root endophytes'). Considering the rapidly growing interest

in fine root endophytes, the use of a consistent nomenclature has become an important issue for research community. Here, we summarise the background literature and recent discussion at the 12th International Conference on Mycorrhiza (ICOM12; 4-9th August, 2024, Manchester, UK), proposing a standardised and cohesive terminology for this group of enigmatic, though widespread, endomycorrhizal fungi.

Main text

Mucoromycotina 'fine root endophytes' have a somewhat obscure and limited recorded history because, until recently, they have been difficult to observe, identify, isolate, and culture. Endophytic fungi likely to have been Mucoromycotina 'fine root endophytes' were probably first identified in association with the evergreen tree species *Griselinia littoralis* (Kapuka, New Zealand broadleaf, or Pāpāuma, family - Griseliniaceae) by Greenall (1963) and named *Rhizophagus tenuis* owing to their morphological similarity to the AM fungal species *Rhizophagus populinus.* This similarity was based on the presence of arbuscule-like structures, though it was noted that the vesicles and hyphal diameters were both smaller than those of *R. populinus*. This endophyte also resisted attempts at axenic culture at the time of the study.

In the following decade, *R. tenuis* was mostly portrayed as being a type of AM fungus. References to fine root endophytes ("FRE") in the mycorrhizal literature simply indicated its likely presence in a sample (Baylis, 1967; Mosse & Hayman, 1971; Crush, 1973a). In 1973, Crush (1973b) reported the effects of *R. tenuis* colonisation on the growth of three grass species under low phosphorus (P) conditions, where *R. tenuis* was shown to improve plant biomass, an effect that was reversed on fertile soils. This effect was confirmed by Johnson (1976), with fine root endophyte colonisation of *Griselinia littoralis* (Kapuka, New Zealand broadleaf or Pāpāuma) and *Leptospermum scoparium* (Mānuka or tea tree, family - Myrtaceae) resulting in higher P concentration in plant dry matter produced on low-P soils compared to asymbiotic plants.

Since the early studies in the 1960s and 70s, fine root endophytes have featured only occasionally in the mycorrhizal literature, with both field and laboratory studies focusing on their effects on plant hosts in terms of biomass. However, none of these studies measured carbon-for-nutrient exchange between symbiotic partners, merely recording presence or absence of the fungus in samples based on morphology determined through optical light microscopy (Daft & Nicholson, 1974; Sainz *et al.,* 1990; Postma *et al.,* 2007). The occurrence of such nutrient exchange has now

been confirmed to occur between Mucoromycotina 'fine root endophytes' and diverse vascular and non-vascular plant species (Field *et al*., 2016; Hoysted *et al*., 2023; Howard *et al*., 2024; Figure 1)

R. *tenuis* was reclassified as *Glomus tenue* by Hall (1977), based on morphological features distinctive from other species of *Rhizophagus,* albeit noting some physical differences also between *G*. *tenue* and other members of the genus. This morphological distinction (Figure 1), coupled with DNA analysis, allowed Orchard *et al*. (2017a) and Desirò *et al*. (2017) to conclude that *G. tenue* (or *tenuis*) belongs within the fungal subphylum Mucoromycotina, rather than Glomeromycotina which contains AM-forming species. Subsequently, a new genus, *Planticonsortium,* has been suggested for Mucoromycotina fine root endophytes (Walker *et al*., 2018) with the combination *P*. *tenue*. It remains unclear whether these fine root endophytes (formerly *G. tenue*), might represent more than one species as suggested by Thippayarugs *et al*. (1999).

Most contemporary literature continues to use variations of the term 'Fine Endophyte' including 'Fine Root Endophyte' (FRE), 'Mucoromycotina Fine Root Endophyte' (MFRE), or 'MucFRE'. These nomenclatures avoid ambiguity and maintain a clear distinction from Glomeromycotina AM-forming fungi. More recently, however, this group of fungi has been referred to as 'Mucoromycotinian arbuscular mycorrhizal fungi' ("M-AM" fungi, or "M-AMF"; Albornoz *et al*., 2022; Kowal *et al*., 2022). By conflating the fine root endophytes with AM fungi, the distinctiveness of the two groups of fungi is obscured in three critical ways. First, it departs from the conventions of all previous common names which included some reference to the morphology ('fine endophytic') of these fungi. If the term "M-AM" fungi, or "M-AMF", were adopted, all subsequent research on and reference to these fungi would be nominatively detached from the preceding work, hindering literature searches and concealing current knowledge from future research, further complicating an already complex history. Secondly, the use of the 'AM fungi' as part of this new term adds unnecessary taxonomic confusion as all AM fungal species (excluding FRE/MFRE/MucFRE) belong to the Glomeromycotina subphylum (Orchard *et al*., 2017b). Referring to the fungi in question with a term already in use for species within a different taxonomic group adds unnecessary confusion and conflates the distinction between these separate fungal groups. Additionally, while arbuscule-like structures are sometimes observed in host plants colonised by Mucoromycotina 'fine root endophyte' fungi (Sinanaj *et al*., 2021; Hoysted *et al*., 2023), they are by no means ubiquitous or diagnostic of colonisation by these fungi, and their function remains unconfirmed. It is clear that arbuscules are not required for bi-directional

exchange of resources between plant hosts and Mucoromycotina fine root endophytes (e.g. Hoysted *et al*., 2023, Howard *et al*., 2024). Finally, the use of the term M-AM fungi (M-AMF) would necessitate the renaming of all other AM fungi species as Glomeromycotinian AM fungi (G-AMF) (Albornoz *et al*., 2022), the wide adoption of which is extremely unlikely to occur consistently in an already large and rapidly growing body of literature.

Therefore, based on phylogenetic evidence (Bidartondo *et al*., 2011; Rimington *et al*., 2015, 2018; Desiró *et al*., 2017; Orchard *et al*., 2017a), we propose the more accurate term Mucoromycotina 'fine root endophyte' ("MFRE") is used to refer to the endosymbiotic fungi within the Mucoromycotina clade. This name is consistent with both the historical nomenclature and the currently known genetic identity of these fungi. "MFRE" retains the historically used morphological description of "fine root endophyte", showing a clear connection between early and more modern literature while further reducing possible conflation with AM fungi by the inclusion of "Mucoromycotina". This term also avoids both the need to rename AM fungi in all future publications, and any reference to arbuscular structures that are not consistently present in these symbioses.

Concluding remarks

Currently, several names are used to refer to the same group of mycorrhiza-forming soil fungi in the subphylum Mucoromycotina. We believe this should be streamlined for consistency, clarity and ease of understanding for the wider scientific community. We propose that the term Mucoromycotina 'fine root endophytes', "MFRE", be adopted as representing a phylogenetically and morphologically accurate term that pays reference to the classic literature and minimises confusion or conflation with the other common group of endosymbiotic mycorrhiza-forming fungi, AM fungi, which belong to the single fungal subphylum, Glomeromycotina.

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Conflicts of interest

The authors declare no conflicts of interest

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References

Albornoz FE, Ryan MH, Bending GD, Hilton S, Dickie IA, Gleeson DB, Standish RJ 2022. Agricultural land-use favours Mucoromycotinian, but not Glomeromycotinian, arbuscular mycorrhizal fungi across ten biomes. *New Phytologist*, 233(3), 1369–1382. https://doi.org/10.1111/nph.17780

Baylis GTS. 1967. Experiments on the ecological significance of phycomycetous mycorrhizas. *New Phytologist*, 66(2), 231–243. https://doi.org/10.1111/j.1469-8137.1967.tb06001.x

Bidartondo MI, Read DJ, Trappe JM, Merckx V, Ligrone R, Duckett JG. 2011. The dawn of symbiosis between plants and fungi. *Biology Letters* 7(4), 574–577. https://doi.org/10.1098/rsbl.2010.1203

Crush JR. 1973a. Significance of endomycorrhizas in tussock grassland in Otago, New Zealand. *New Zealand Journal of Botany*, 11(4), 645-660. https://doi.org/10.1080/0028825X.1973.10430306

Crush JR. 1973b. The effect of *Rhizophagus tenuis* mycorrhizas on ryegrass, cocksfoot and sweet vernal. *New Phytologist*, 72(5), 965-973. https://doi.org/10.1111/j.1469-8137.1973.tb02073.x

Daft MJ, Nicolson TH. 1974. Arbuscular mycorrhizas in plants colonizing coal wastes in Scotland. *New Phytologist*, 73(6), 1129–1138. https://doi.org/10.1111/j.1469-8137.1974.tb02142.x

Desirò A, Rimington WR, Jacob A, Pol NV, Smith ME, Trappe JM, Bidartondo MI, Bonito G. 2017. Multigene phylogeny of Endogonales, an early diverging lineage of fungi associated with plants. *IMA fungus*, 8, 245-257. https://doi:10.5598/imafungus.2017.08.02.03

Field KJ, Pressel S, Duckett JG, Rimington WR, Bidartondo MI. 2015. Symbiotic options for the conquest of land. *Trends in Ecology & Evolution*, 30(8), 477–486. https://doi.org/10.1016/j.tree.2015.05.007

Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Pressel S. 2016. Functional analysis of liverworts in dual symbiosis with Glomeromycota and Mucoromycotina fungi under a simulated Palaeozoic CO_2 decline. *ISME Journal* 10, 1514–1526.

Gerdemann JW, Trappe JM. 1974. The endogonaceae in the Pacific Northwest. Publisher: New York Botanical Garden in collaboration with the Mycological Society of America

Greenall JM. 1963. The mycorrhizal endophytes of *Griselinia littoralis* (Cornaceae). *New Zealand Journal of Botany*, 1(4), 389–400. https://doi.org/10.1080/0028825X.1963.10428694

Hall IR. 1977. Species and mycorrhizal infections of New Zealand endogonaceae. *Transactions of the British Mycological Society*, 68(3), 341–356. https://doi.org/10.1016/S0007-1536(77)80186-1

Howard NOA, Williams A, Durant E, Pressel S, Daniell TJ, Field KJ. 2024. Preferential nitrogen and carbon exchange dynamics in Mucoromycotina "fine root endophyte"-plant symbiosis. *Current Biology*, 34(23), 5484-5493.e3. https://doi.org/10.1016/j.cub.2024.10.028

Howard N, Pressel S, Kaye RS, Daniell TJ, Field KJ. 2022. The potential role of Mucoromycotina 'fine root endophytes' in plant nitrogen nutrition. *Physiologia Plantarum*, 174(3), e13715.

Hoysted GA, Field KJ, Sinanaj B, Bell CA, Bidartondo MI, Pressel S. 2023. Direct nitrogen, phosphorus and carbon exchanges between Mucoromycotina 'fine root endophyte' fungi and a flowering plant in novel monoxenic cultures. *New Phytologist*, 238(1), 70–79. https://doi.org/10.1111/nph.18630

Johnson PN. 1976. Effects of soil phosphate level and shade on plant growth and mycorrhizas. *New Zealand Journal of Botany*. 14(4), 333-340. https://doi.org/10.1080/0028825X.1976.10428906

Koide, R. T., Mosse, B. 2004. History of research on arbuscular mycorrhiza. *Mycorrhiza*, 14(3), 145–163. https://doi.org/10.1007/s00572-004-0307-4

Kowal J, Arrigoni E, Jarvis S, Zappala S, Forbes E, Bidartondo MI, Suz LM. 2022. Atmospheric pollution, soil nutrients and climate effects on Mucoromycota arbuscular mycorrhizal fungi. *Environmental Microbiology*, 24(8), 3390–3404. https://doi.org/10.1111/1462-2920.16040

Liu Z, Fang J, He Y, Bending GD, Song B, Guo Y, Wang X, Fang Z, Adams JM. 2024. Distinct biogeographic patterns in Glomeromycotinian and Mucoromycotinian arbuscular mycorrhizal fungi across China: A meta-analysis. *Science of The Total Environment*, 912, 168907.

Mansfield TM, Albornoz FE, Ryan MH, Bending GD, Standish RJ. 2023. Niche differentiation of Mucoromycotinian and Glomeromycotinian arbuscular mycorrhizal fungi along a 2-million-year soil chronosequence. *Mycorrhiza*, 33(3),139-152.

Mosse B, Hayman DS. 1971. Plant growth responses to vesicular-arbuscular mycorrhiza. *New Phytologist,* 70(1), 29–34. https://doi.org/10.1111/j.1469-8137.1971.tb02505.x

Orchard S, Hilton S, Bending GD, Dickie IA, Standish RJ, Gleeson DB, Jeffery RP, Powell JR, Walker C, Bass D, Monk J, Simonin A, Ryan MH. 2017a. Fine endophytes (*Glomus tenue*) are related to Mucoromycotina, not Glomeromycota. *New Phytologist*, 213(2), 481–486. https://doi.org/10.1111/nph.14268

Orchard S, Standish RJ, Dickie IA, Renton M, Walker C, Moot D, Ryan MH. 2017b. Fine root endophytes under scrutiny: a review of the literature on arbuscule-producing fungi recently suggested to belong to the Mucoromycotina. *Mycorrhiza*, 27, 619-638. https://doi.org/10.1007/s00572-017-0782-z

Postma JWM, Olsson PA, Falkengren-Grerup U. 2007. Root colonisation by arbuscular mycorrhizal, fine endophytic and dark septate fungi across a pH gradient in acid beech forests. *Soil Biology & Biochemistry*, 39(2), 400–408. https://doi.org/10.1016/j.soilbio.2006.08.007

Prout JN, Williams A, Wanke A, Schornack S, Ton J, Field KJ. 2024. Mucoromycotina 'fine root endophytes': a new molecular model for plant–fungal mutualisms?. *Trends in Plant Science*, 29(6),650-661.

Rimington WR, Pressel S, Duckett JG, Bidartondo MI. 2015. Fungal associations of basal vascular plants: reopening a closed book?. *New Phytologist*, 205(4), 1394-1398.

Rimington WR, Pressel S, Duckett JG, Field KJ, Read DJ, Bidartondo MI. 2018. Ancient plants with ancient fungi: liverworts associate with early-diverging arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B*, 285(1888), 20181600.

Rosling A, Eshghi Sahraei S, Kalsoom Khan F, Desirò A, Bryson AE, Mondo SJ, Grigoriev IV, Bonito G, Sánchez-García M, 2024. Evolutionary history of arbuscular mycorrhizal fungi and genomic signatures of obligate symbiosis. *BMC genomics*, 25(1), 529.

Sainz MJ, Vilariño A, Arines J. 1990. Competition between *Glomus tenue* and some coarse fungi for colonizing red clover roots in acid soils. *Agriculture, Ecosystems & Environment*. 29(1-4), 337-340. https://doi.org/10.1016/0167-8809(90)90297-Q

Seeliger M, Hilton S, Muscatt G, Walker C, Bass D, Albornoz F, Standish RJ, Gray ND, Mercy L, Rempelos L, Schneider C. 2024. New fungal primers reveal the diversity of Mucoromycotinian arbuscular mycorrhizal fungi and their response to nitrogen application. *Environmental Microbiome*, 19(1), 71.

Sinanaj B, Hoysted GA, Pressel S, Bidartondo MI, Field KJ. 2021. Critical research challenges facing Mucoromycotina 'fine root endophytes'. *New Phytologist*, 232(4), 1528-1534. https://doi.org/10.1111/nph.17684

Sinanaj B, Pressel S, Bidartondo MI, Field KJ 2024. Fungal symbiont diversity drives growth of *Holcus lanatus* depending on soil nutrient availability. *Functional Ecology* 38(4), 984-997.

Thippayarugs S, Bansal M, Abbott LK 1999. Morphology and infectivity of fine endophyte in a mediterranean environment. *Mycological Research*, 103(11), 1369–1379. https://doi.org/10.1017/S0953756299001094

Yang H, Berckx F, Fransson P, Weih M, 2024. Harnessing plant–microbe interactions to promote nitrogen use efficiency in cereal crops. *Plant and Soil*, 494(1), pp.75-83.

Walker C, Gollotte A, Redecker D. 2018. A new genus, *Planticonsortium* (Mucoromycotina), and new combination (*P. tenue*), for the fine root endophyte, *Glomus tenue* (basionym *Rhizophagus tenuis*). *Mycorrhiza*, 28, 213-219. https://doi.org/10.1007/s00572-017-0815-7

Figures and Tables

Figure 1. Trypan blue stained light micrographs **(A & B)** and scanning electron micrographs (SEM; **C-F**) showing fungal structures produced by MFRE isolates (A, C-E) vs. those formed by the AM fungus *Rhizophagus irregularis* MUCL 41833 (**B & F**) in roots of white clover (*Trifolium repens* L.) (**B-F**) and Ri T-DNA transformed carrot (*Daucus carota* L.) roots established under *in vitro* culture conditions (**A**). **A**) MFRE highly branching fine hyphae and vesicle-like structure (arrowed) in cells. **B**) *R. irregularis* coarse hyphae (arrowed)) next to vesicle and arbuscules (*) in cells. **C**) *T. repens* root heavily colonised by MFRE fungus, note the 'hyphal mantle' enveloping the root (arrowed). **D**) Cells packed with tightly wound hyphal coils (*). Abundant MFRE mycelium is tightly appressed to the root surface (arrowed) forming a 'mantle-like' structure. **E**) MFRE fine branching hyphae and vesicle-like spherical structure (arrowed) inside a root cell. **F**) *R. irregularis* coarse hypha (arrowed) and arbuscules (*) in root cells. Scale bars: (C) 100µm; (A, B, D-F) 20µm. Image credits: original micrographs produced by Victor H. RodriguezMorelos and Silvia Pressel.

Table 1. Summary of terminologies used to refer to endosymbiotic Mucoromycotina fungi.

Name / Abbreviation	Also known as	Key sources	Notes
Rhizophagus tenuis	Fine root endophytes (FRE) Fine endophytes (FE)	Greenall (1963)	Original description and naming of "fine endophyte" in *Griselinia littoralis* roots. Classification conflates FRE with AM fungi.
Glomus tenuis		Gerdemann & Trappe (1974) Hall (1977)	*Rhizophagus tenuis* revised taxonomically and reclassified under *Glomus,* alongside AM fungi.
Mucoromycotina fungi		Bidartondo *et al.* (2011) Field *et al*. (2015, 2016) Rimington *et al*. (2017)	Identified as mutualistic endosymbionts in non-vascular plants. Evidence of diversity within Mucoromycotina fungi reflected in broad naming convention.
MFRE / MucFRE	Mucoromycotina fine root endophyte	Orchard *et al.* (2017a,b) Hoysted *et al*. (2018, 2021, 2023) Kowal *et al*. (2020) Sinanaj *et al.* (2021, 2024) Howard *et al*. (2022, 2024) Yang e*t al*. (2024) Prout *et al*. (2024) Rosling et al. (2024)	Link between Mucoromycotina fungi and FRE confirmed. MFRE established as widely distributed nutritional mutualists in a variety of vascular plant species. Term effectively delineates MFRE from AM fungi and makes link between Mucoromycotina fungi and fine root endophytes explicit.
Plantiscortium tenue		Walker *et al*. (2018)	Taxonomic reclassification from *Glomus tenuis* to *Plantiscortium tenue.* Term does not reflect diversity of MFRE which remains largely unknown.
M-AMF / M-AM	Mucoromycotinian arbuscular mycorrhizal fungi	Albornoz *et al*. (2022) Kowal *et al*. (2022) Mansfield *et al*. (2023) Seeliger et al. (2023) Liu *et al*. (2024)	Reversion to arbuscular mycorrhizal (AM) terminology to describe fine endophytes. Conflates the distinctions between fungal groups; adoption would require renaming of AM fungi.

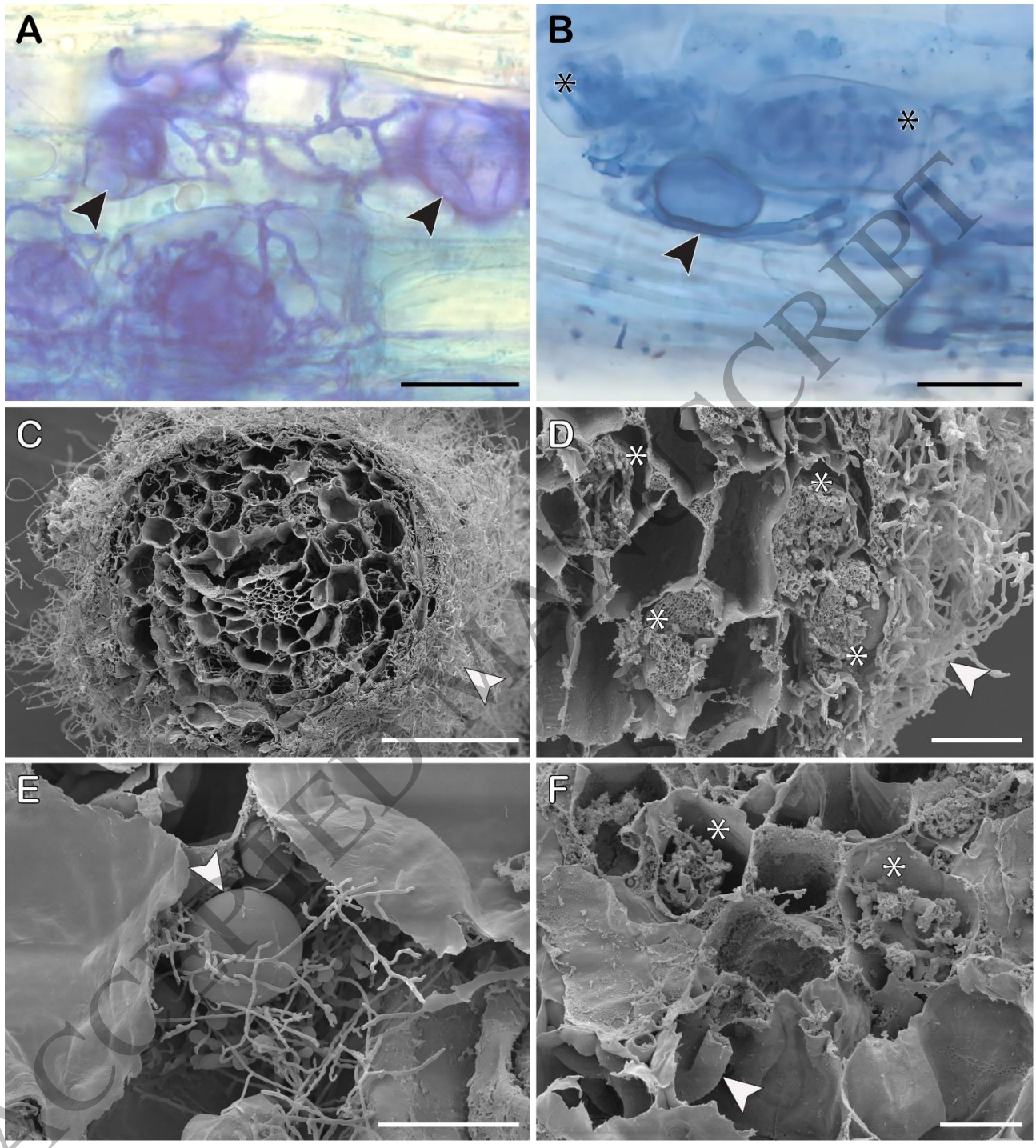

Figure 1
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