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A Complete Review on Ericoid Mycorrhiza: An Understudied Fungus in the Ericaceae Family

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ABSTRACT

Ericoid mycorrhiza (ErM) is an unexplored and understudied member of the mycorrhizal world, surprisingly belonging to Ascomycota and Basidiomycota instead of Glomeromycota (the phylum comprising fungi forming associations with higher plants). ErM obtained its etymology due to its symbiotic relationship with members of the *Ericaceae* Family. Just like any other mycorrhiza, ErM also helps its hosts through nitrogen uptake and phosphorus bioavailability and provides defense to host plants against various phytopathogens. It also takes part in the decomposition of organic matter and depolymerization of complex substances. These mycorrhizae are distributed across all continents except Antarctica. The majority of culturable ErM is spread across England, Australia, Canada, the United States etc. This review focuses on the literature survey on ErM, its taxonomy, and diversity alongside its functions. Our review also sheds light on the host range of the ericoid fungi, wherein, out of all the hosts, Salal (*Gautheria shallon*) has been identified as one of the most promising ones.

INTRODUCTION

'Mycorrhiza' is a symbiotic association between fungus and root system. Etymologically, "Mycorrhiza" is made up of two Greek words, *viz.*, '*mykes*' (fungus) and '*rhiza*' (roots). This association is known to be one of the ancient relationships between plants and microbes, having its fossils dating back to the Paleozoic era. However, recent molecular data insinuated that this fungus root system may have arisen during the Proterozoic era (Brundrett 2002). Members of the kingdom Plantae, Monera, and Protista are known to have essential mutualistic relationships, e.g., interactions between soil mycoflora and plants in contemporary terrestrial ecosystems. Interestingly, according to the hypothesis put forth by Pirozynski & Malloch (1975), The evolution of plants themselves is said to be possible through such "mutualistic relationships," and the terrestrial plants that we have today are the result of an old and continuous association among an aquatic fungus and primordial semi-aquatic green alga. The fungi involved in the mutualistic associations are known to absorb the essential nutrients (both available and non-available forms) such as phosphate and nitrogen (N) more effectively than plant roots alone. In return, the plants give carbohydrates to the fungus that was made through photosynthesis.

Discovered in 1988 by Becard & Fortin, mycorrhiza, apart from enhancing nutrient absorption (phosphorus uptake), also produces auxins, boosts disease resistance, and improves the rhizosphere habitat. There are two types of mycorrhizas most frequently found, *viz.*, endomycorrhizas (penetrating cortical cells) and ectomycorrhizas (not deeply penetrating). There is another category, ecto-endo mycorrhizas (arbutoids), comprising properties of both types, while

arbuscular, orchid, and ericoid mycorrhizas are categorized as endomycorrhiza (Van der Heijden et al. 2015).

Ectomycorrhiza, also abbreviated as EcM, often forms linkages between fungi from Phyla - Zygomycota, Basidiomycota, and Ascomycota woody plants (For example Willow, pine, oak, spruce, beech, fir, and birch). Ectomycorrhizal connections exist in approximately 10 percent of plant families. Although EcM mainly consists of around 8000 primarily woody plants, they have a significant presence in a variety of biomes (Plett & Martin 2011). In ectomycorrhiza, the hyphal mantle is present and forms a Hartig net, whereas, arbuscules and vesicles both are absent.

The endomycorrhiza is further categorized into three types, *viz.,* Vesicular Arbuscular mycorrhiza (VAM), Ericoid mycorrhiza (ErM), and Orchid mycorrhiza (OM). VAM is the most abundant symbiotic association between certain fungi and the roots of the majority of plants. In the plant's root system, the fungus creates a network of small filaments called hyphae that branch out to form an arbuscule (a highly branched structure). These fungi are a vital part of healthy soil and can be found in a variety of environments, including forests and agricultural fields. They are essential for maintaining thriving and productive ecosystems because they increase nutrient uptake and boost plant development. Although arbuscular mycorrhizas were first reported in 1842 by Nageli, however, the majority of his illustrations hardly resembled arbuscular mycorrhiza. Further early reports of the symbiosis from the years 1875-1895 are cited by Trappe & Berch (1985). Arbuscules, vesicles, and colonization from adjacent cells or root surface mycelia are all present in arbuscular mycorrhiza as these are required for survival by reducing competition, therefore providing protection and nutrition.

Members of the Orchidaceae family are known to be myco-heterotrophic, wherein the Orchid mycorrhizae form symbiotic interactions with the orchid plants during seed germination. In this mutualistic connection, orchids depend upon the OM for food rather than on photosynthesis. In return, the fungi get the organic carbon compounds from the orchids that they require to develop. The link is quite specialized and may only apply to specific orchid species or groupings. The roots of the orchids and the fungi develop a specific structure called the peloton that enables communication and the flow of nutrients between the two organisms. The life and development of orchids depend on this symbiotic interaction, which is also vital to the ecology of many habitats where orchids are found**.**

'Ericoid mycorrhiza' is a particular kind of mycorrhiza in which fungus and plants create a symbiotic relationship with plants growing in acidic soils, such as Heath and Moorland species. Heathers, blueberries, and rhododendrons are just a few examples of the plants in the *Ericaceae* family, which are most frequently associated with this form of mycorrhiza, which is why it is called "Ericoid". The majority of terrestrial plant species have mycorrhizal fungi colonizing their roots, which enhance nutrient uptake in exchange for sugars produced during photosynthetic activities and make them significant players in the carbon and nutrient cycling in many ecosystems (Van der Heijden et al. 2008).

Ericoid mycorrhiza is said to be one of a kind in the world of fungal associations due to its ability to survive in extreme conditions (acidic soils), along with its high specificity towards choosing its host plants. All the studies done on ErM fungi revealed that they have developed mycorrhizal association only with the members belonging to the order *Ericales*. It is also reported that certain ascomycetous fungi also participate in their symbiotic relationships (Harley & Smith1983, Leopold 2016).

In Ericoid mycorrhiza, the fungi's hyphae enter the plant's roots and create a network of small, branching structures inside the root cortex cells that are termed Hartig nets. The plant provides the fungus with carbohydrates, while the fungi provide the plant with all nutrients from the soil, including phosphate and nitrogen, which they're able to absorb and transport. In addition to being able to accept and thrive in acidic soils, ericoid mycorrhizal fungi are also capable of creating enzymes that disintegrate complicated organic material so that the plant may use them. Many heathland and moorland plants require this form of mycorrhiza for their development and survival, and it can be essential to nutrient cycling in these habitats.

Most of the studies to date focus on the other mycorrhizal associations known since their arrival, dating back to 400 million years. Therefore, in this review, we have attempted to summarize the functions and diversity of this younger mycorrhizal symbiont known as Ericoid Mycorrhiza.

Bibliometric Survey

The systemic literature survey using keywords "Ericoid Mycorrhiza", "Ericoid Mycorrhiza Functions," and "Ericoid Mycorrhiza and diversity" was performed using 3 databases, i.e., Scopus, Science Direct, and PubMed (Fig. 1a & b). The literature search for "Ericoid Mycorrhiza" using the Scopus database revealed 615 papers from 1973 to 2024; the same search on Science Direct (1990-2024) gave 856 results comprising Reviews, research articles, and Book chapters. There are 436 research papers wherein 12 were published in 2024. Out of 96 reviews, not even a single hit showed these two words, i.e., "Ericoid" and "Mycorrhiza," together, indicating a lack of complete review on this mycorrhiza.

These two words, when searched together on PubMed (1980-2024), gave 234 results.

The next search was done for the combination of the words "Ericoid Mycorrhiza and diversity," for which PubMed revealed 63 articles from 2000 till date, Science Direct gave 329 articles from 2000 onwards, and 127 documents were searched on the Scopus database. Similarly, the keywords "Ericoid Mycorrhiza Functions" revealed only 79 documents on Scopus, 638 articles on Science Direct, and 164 articles on PubMed from 1980-2024.

Ericoid Mycorrhizal Biology

The *Ericale*s are a large group of plants that are found all over the world. They are frequently found as ground cover species in parts of the Mediterranean and boreal forests. They are dominant in some frigid locations, frequently establishing practically pure plant communities. The mycorrhizal relationship with ericoid fungi, a kind of soil fungus, is a characteristic feature shared by most of the plant species in the *Ericaceae* family. These fungal classes are widely distributed in ericaceous plants' characteristic fine-haired

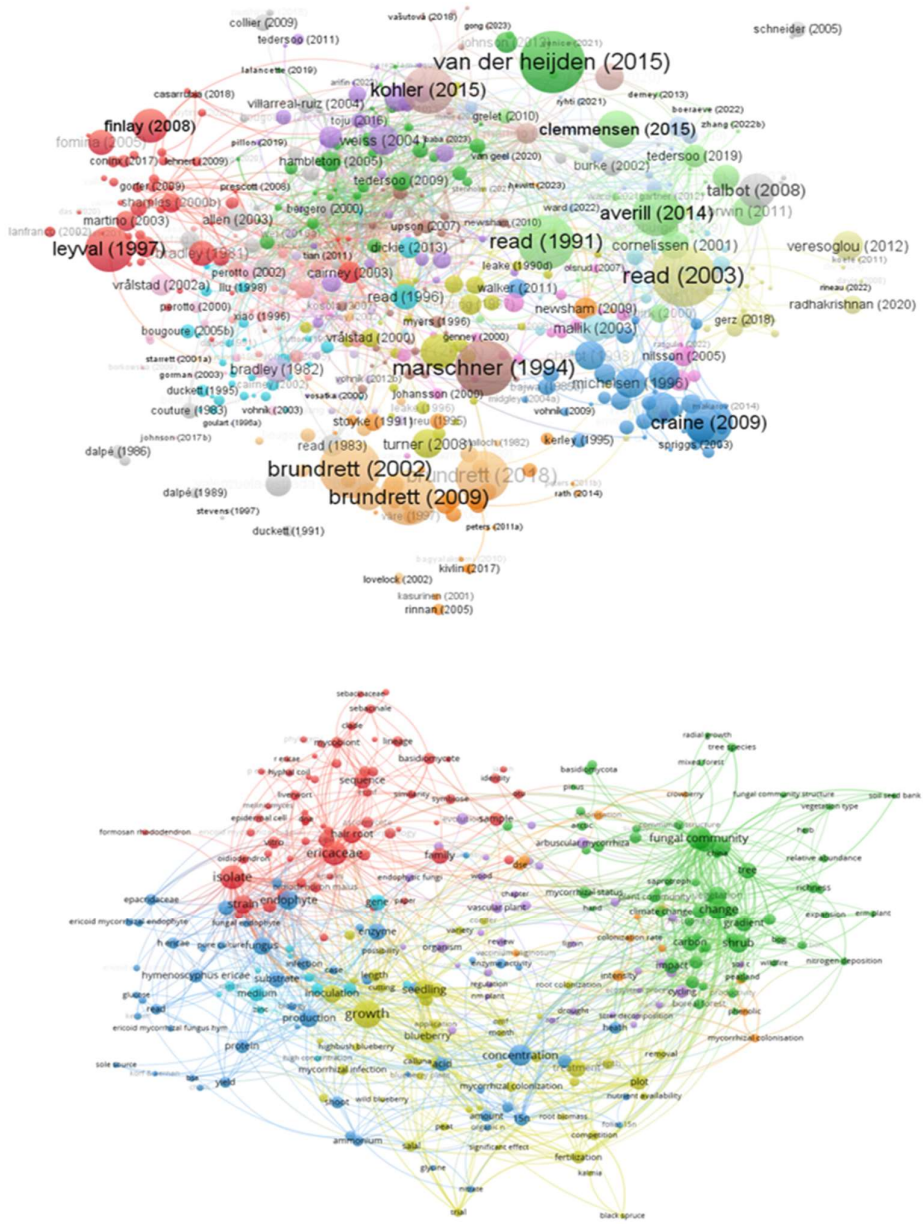

Fig. 1a: Literature survey based on "Author" search and keyword "Ericoid Mycorrhiza" from 1980 and 2024.

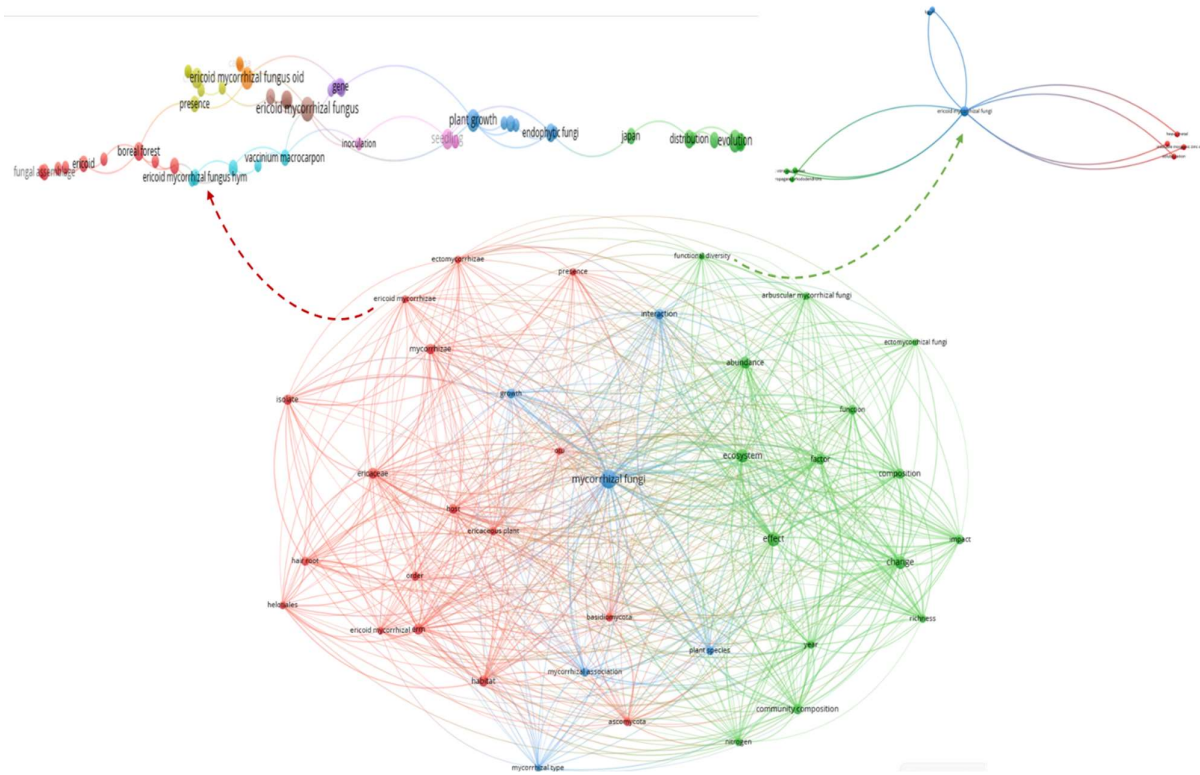

Fig. 1b: Literature survey on different aspects (ericoid diversity & functions) of Ericoid Mycorrhiza from 1980 and 2024.

roots, and they are very crucial for the nutrition and mineral cycling of plants (Read 1996).

Morphometric Analysis

The majority of ericoid isolates have walls made up of an exterior layer and an inner layer that is transparent to electrons, which are both dense in electrons, but others simply have an amorphous electron-dense wall. Using immunocytochemical methods, the septa and innermost layer have been found to include skeletal components. The symbiotic strains are characterized by a fibrillar sheath projecting from the wall, which is only sometimes formed by strains with a lesser capacity for symbiosis. This coating is more prevalent on the fungus that is traveling along the surface of the root than it is on the hyphae that are coiling up inside the infected root cell. Moreover, it appears that the type of substrate affects how it is produced. Mannose and glucose residues have been found in the fiber-like sheath in situ by utilizing the Concanavalin A lectin compound (Bonfante et al. 1987). Current reports about the existence of immunogenic (Bonfante et al. 1987) and enzymatic glycoproteins (Straker et al. 1989) suggest that ericoid mycorrhizal cell surface is a compound molecular structure with a mosaic appearance that may have significant roles during the primary stages of host plant interaction.

The delicate and fragile structure present on roots, known as hair roots, is a characteristic of ericoid plants (Read 1996). Root hairs are composed of a stele on the inner side that is encircled by two-layered cortical cells, an outermost layer with massive epidermal cells, and a relatively small diameter typically less than 100 mm. The only root hair cells that have been captured by ErM fungi are these epidermal cells, which serve as the contact with the soil (Smith & read 2010). Here, the plant plasma membrane-invading ErM fungus produces hyphal coils that often take up the majority of the cell volume (Bonfante-Fasolo & Gianinazzi-Pearson 1979, Peterson et al. 2004).

The majority of cells represent individual colonization units since fungi often colonize epidermal cells straight from the soil through the thicker tangential wall outside (Massicotte et al. 2005). In the older regions of the hair roots, epidermal cells slough off, exposing the cortical layer. Ericoid Mycorrhizal cells are. Therefore, transient and symbiotic nutrition interchange is probably only possible in the young parts of the root, where both partners are still alive. Ericoid hyphae that are viable have been seen in cells of plants that exhibit cytoplasm and organelle degradation, in contrast to other endomycorrhizal partnerships such as arbuscular and orchid mycorrhiza (Bonfante-Fasolo &

Gianinazzi-Pearson 1979, Read 1982). All of the ericoid mycorrhiza studied to date by various researchers reported that they created the same kind of intracellular loops when they colonized the roots of their host.

Biochemical Nature of Ericoid Mycorrhizal Fungi

Ericoid fungus makes a variety of enzymes that are extracellular into the medium, enabling them to break down and use organic soil matrix, increasing their competitive capacity in the soil. Several of these enzymes, such as *Carboxyproteinases* (Leake & Read 1991) and *Acid phosphatases* (Straker & Mitchell 1986), are probably crucial for the nutrition in mycorrhizal plants that acquire entry to nutrients that would not be available otherwise (Leake & Read 1991). Moreover, compound organic polymers, which are characteristic parts of fungal and plant cell walls, can be broken down by ericoid mycorrhizal fungus. It has been observed that ericoid fungi can attack tannins, chitin, and lignins (Leake & Read 1991). The culture-rich filtrates of ericoid growing *in vitro* have also been found to produce other enzymes that degrade cell walls, such as β-1,3-*glucanase* β-1,4-*glucanase* (Varma & Bonfante 1994) and *polygalacturonase* (PG) (Peretto et al. 1993) (Fig. 2).

Taxonomy, Diversity and Phylogeny

Ericoid mycorrhiza, being a diverse group, is largely associated with a wide range of plant species like *Ericaceae* and *Epacridaceae*. It can be seen in countries such as Europe, Canada, Australia, the United States, and so forth. Although there are many *Ericaceae* plant species in India, such as rhododendrons, azaleas, and blueberries, there have been no studies or research on ericoid relationships thus far. Not just in India but also globally, there are very few findings on ericoid mycorrhizal association (Leopold et al. 2021).

As per early research findings, the *Ericaceae* family is classified into nine distinct subfamilies. The foundational evolutionary branches of *Ericaceae*, especially *Arbutoideae, Monotropoideae, Enkianthoideae*, and *Pyroloideae*, do not possess the ability to establish Ericoid Mycorrhizal (ErM) associations. Contrastingly, species within the *Monotropoideae* subfamily engage in what's known as monotropoid mycorrhizal symbiosis, featuring ectendomycorrhizal anatomical structures. This symbiosis involves particular groups of Ectomycorrhizal (EcM) fungi from the phylum Basidiomycota (Hynson & Bruns 2009). On the other hand, plants belonging to the Pyroloideae and Arbutoideae subfamilies accommodate a wide variety of EcM fungi in their root systems (Krpata et al. 2007).

The majority of Ericoid Mycorrhizal (ErM) fungi consist mainly of Ascomycetes found within the Leotiomycetes, along with a few Basidiomycetes, notably those in the family Serendipitaceae (Weiß et al. 2016). The first fungal species isolated from ErM roots was *Rhizoscyphus ericae*, belonging to the Leotiomycetes. Initially categorized under the genus *Pezizella*, it was subsequently reclassified into *Hymenoscyphus* and later into *Rhizoscyphus* (Zhang & Zhuang 2004). Until the development of molecular tools for assessing phylogenetic relationships, the majority of slowly growing mycelia isolated from Ericoid Mycorrhizal (ErM) roots remained unidentified. To address various fungal taxa isolated from ErM roots that were closely related to *R. ericae*, an aggregate was established within the order *Helotiales* (Perotto et al. 2018,1993). This aggregate, referred to as the '*R. ericae* aggregate' by Vrålstad et al. (2000), due to its inclusion of *R. ericae*, comprised four primary clades (Fig. 3). Hambleton & Sigler (2005) later enhanced the definition of these clades, simultaneously suggesting three novel species within the anamorphic genus Meliniomyces as part of the "*R. ericae* aggregate" (Vrålstad et al. 2000,

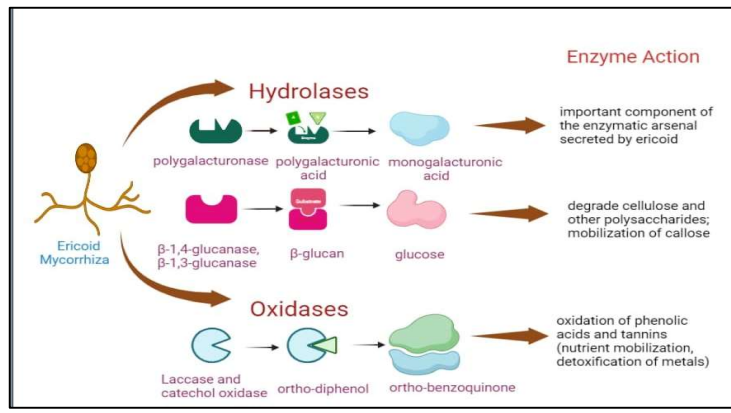

Fig. 2: Illustration of various enzymes released by ErM along with their functions.

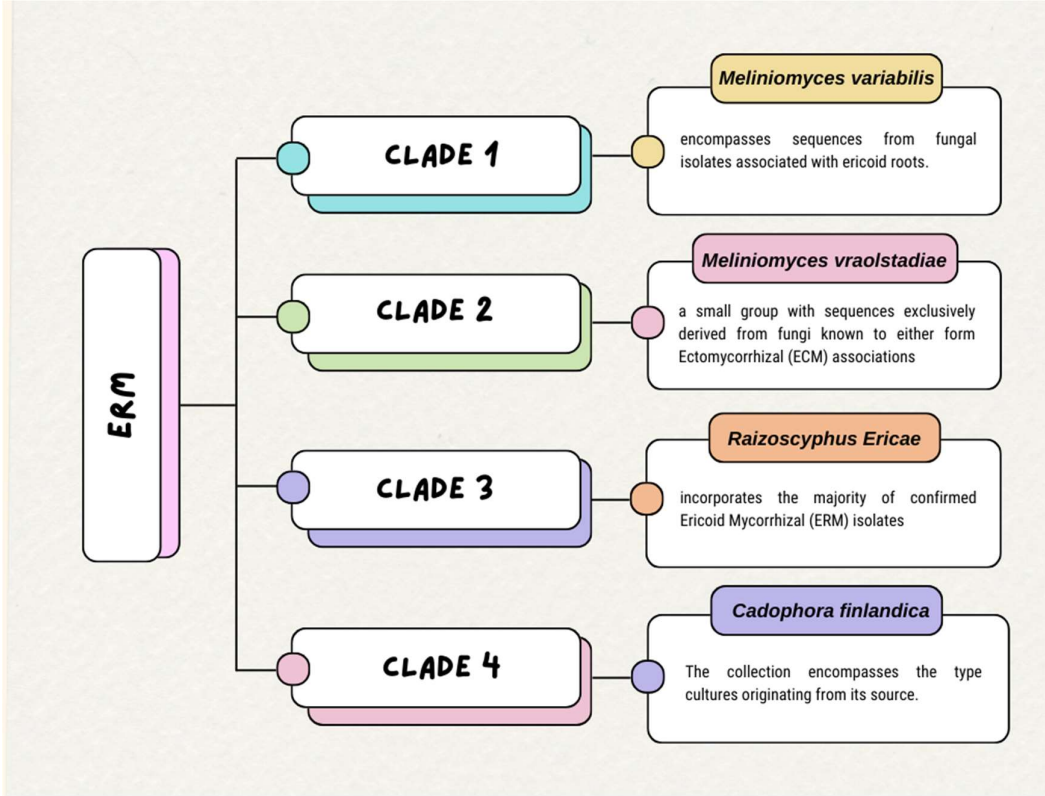

Fig. 3: The four major clades of Ericoid mycorrhizae under the order *Helotiales*.

2002a). Clade 1, represented by *Meliniomyces variabilis*, encompasses sequences from fungal isolates associated with ericoid roots, previously identified as the "variable white taxon" (Hambleton & Currah 1997). Additionally, it includes sequences from root endophytes found in various host plants in cold-temperate Northern Hemisphere soils. Clade 2, featuring *Meliniomyces vraolstadiae*, this small cluster comprises sequences exclusively sourced from fungi recognized for either forming Ectomycorrhizal (ECM) associations or displaying non-mycorrhizal behavior (Vrålstad et al. 2002b). Clade 3 incorporates the majority of confirmed Ericoid Mycorrhizal (ERM) isolates, including the type cultures of *S. vaccinii* and *R. ericae*. Clade 4 includes the type cultures of *Meliniomyces bicolor* and *Cadophora finlandica* (Perotto et al. 2012).

Usually, mycorrhiza has been grouped under "Glomeromycota" (Redecker & Raab 2006). However, ErM fungi exhibit a distinctive clustering pattern, aligning themselves under the higher dikaryotic sister clades of "Ascomycota" and "Basidiomycota".

"Ascomycota," characterized by their leisurely developing mycelia obtained from Ericoid Mycorrhiza (ErM), remained elusive until the advent of molecular tools capable of investigating their phylogenetic affinities (Perotto et al. 2012). Up to this point, ericoid fungal endophytes that have been isolated predominantly belong to ascomycetes. However, it's worth noting that basidiomycetes have been detected through an electron microscope within locally colonized roots, as reported by Perotto & Bonfante (1998). This observation underscores the complexity of the ErM fungal community and highlights the significance of advanced molecular techniques in unraveling the intricate taxonomic relationships within this fungal group. Over the past few years, our knowledge of the biodiversity of ericoid mycorrhizal fungi has seen a swift growth (Stoyke et al. 1992, Perotto et al. 1996). Initially, the sole ericoid fungal endophyte known for approximately a decade was identified as an ascomycete featuring a dark, sluggish sterile mycelium, subsequently recognized as *Hymenoscyphus ericae* (formerly *Pezizella ericae*) (Perotto & Bonfante 1998). Subsequently, additional ericoid mycorrhizal (ErM) fungi have been successfully cultured and identified as ascomycetes within the genus *Oidiodendron* (Perotto et al. 2012). Notably, the initial recognition of symbionts associated with ericaceous hosts highlighted the prevalence of Ascomycetes, specifically *Hymenoscyphus ericae* (62-92% endophyte isolates) and *Oidiodendron spp*., both in their anamorphic stage (Smith & Read 1997, Sharples et al. 2000c, Perotto et al. 2002).

In addition to Ascomycota, various lineages of Ericoid Mycorrhizal (ErM) fungi are also identified within the phylum "Basidiomycota" (Kohout 2017). Among the basidiomycetes, the majority of recognized mycorrhizal species belong to homobasidiomycetes. Distinguishing homobasidiomycetes, as presently defined, from other hymenomycetous taxa such as Tulasnellales and Ceratobasidiales poses a challenge (Hibbett & Thorn, 2001, Weiß et al. 2004).

Several decades back, Seviour et al. (1973) proposed the possibility of an Ericoid Mycorrhizal (ErM) habit for *Clavaria sp*. Nevertheless, the evidence supporting nutrient exchange in both directions between the host plant *Clavaria sp*. and *Rhododendron sp*. remained uncertain, as reported by Mueller et al. (1986). Early indirect indications of basidiomycete fungi engaging in ericoid mycorrhiza formation in the roots of *Calluna, Vaccinium,* and *Rhododendron* were noted (Bonfante- 1980, Peterson et al. 1980, Englander & Hull 1980). These early observations were aligned with recent findings in Italy, where hyphae featuring dolipore septa and clamp connections were observed as characteristic typical mycorrhizal coils in the roots of *E. arborea* (Perotto et al. 2002). Due to the lack of evidence of ericoid mycorrhizal association on a broad scale, its diversity needs to be examined on a genetic basis.

1. **Genetic diversity of ericoid mycorrhizal fungi:** The first and most important step in studying mycorrhizal association at the genetic level is to understand the number of taxa and the phylogeny of mycorrhizal fungus (Berch et al. 2002). The majority of mycorrhizal fungus species are secluded or confined to a specific region. *Rhizoscyphus ericae*, on the other hand, is widely dispersed (Kohout et al. 2017). According to the data gathered so far, the understudied and undetected group of mycorrhizal fungus, the information on critical portions of this issue is expanding day by day. The fundamental cause for this expansion is molecular characterization, which uses numerous target genes and particular approaches to develop and intensify the effects of symbiotic interaction between mycorrhiza and the roots of higher fungi. (Pearson & Read 1973) isolated the first taxonomically identifiable ErM fungus from *Calluna vulgaris* roots, which was eventually encouraged to grow.

A significant level of genetic variation has been detected among diverse parts of various roots, the majority of which are even from the same plant. Perotto et al. (1996) used random amplified polymorphism DNA (RAPD) analysis to conduct the first systematic assessment of the variety of mycorrhizal endophytes associated with *C. vulgaris*. Molecular characterization benefits substantially from PCR techniques such as PCR-RFLP analysis. *O. maius and S. vaccinii* were reliably isolated from 19 *Ericaceae* species collected in three different North American settings by Hambleton & Currah (1997). Additionally, *O. grisem* was isolated from a variety of plants, demonstrating that one plant's root systems can be colonized by two or more endophytes at once.

Fig. 4: Global geographic distribution of Ericoid Mycorrhiza. Most of the ErM are confined to North America, Europe, Vancouver, Northern California, British Columbia, Northern Europe, China, England, Canada, United States, British Columbia coast, Arctic Tundra, Australia, and are associated with *Gautheria shallon, Calluna vulgaris, Epacris impressa, Astroloma pinifofolium* and so on.

Table 1: List of ErM Diversity characterized and studied.

Species	Host	Target Gene	Technique	Reference
Mortierella sp. *Oidiodendron spp.*	*Calluna vulgaris and Vaccinium myrtillus*	NA	Direct Planting, Maceration	Pearson and Read (1973)
Oidiodendron griseum	*Gaultheria shallon*	NA	NA	Xiao and Berch (1992)
Hymenoscyphus ericae *O. maius* *Scytalidium vaccinii* *Pseudogymnorcus roseum* *Pseudogymnoarcus roseus* *Oidiodendron flavum*	*Gaultheria shallon*	NA	NA	Xiao and Berch (1995)
O. maius *Acremonium strictum* *Unknown 1* *Unknown 2*	*Gaultheria shallon*	NA	NA	Xiao and Berch (1996)
O. maius *O. periconioides* *O. pilicola* *O. cerealis* *O. griseum*	*Epacris impressa, Astroloma pinifofolium*	ITS5 and ITS4	NA	Mclean et al. (1999)
Acremonium strictum *Hyaloscypha aureliella* *Hymenoscyphus ericae*	*Gaultheria shallon, Vaccinium angustifolium, V. corymbosum*	ITS 2	RFLP, PCR	Monreal et al. (2000)
Phialocephala dimorphospora *P. forinii* *P. Finlandia*	*Cassiope mertensiana, Pinus sylvestris*	ITS 2	RFLP, PCR	Monreal et al. (2000)
Oidiodendron maius *O. griseum* *O. tenuissimum* *Paecillium spp.* *Torulomyces lagena*	*Quercus ilex and Erica arborea*	ITS1 & ITS4	PCR, RFLP, RAPD	Bergero et al. (2000)
Capronia villosa *O. maisus* *Hymenosyphus ericae* *Unknown 1* *Unknown 2*	*Gaultheria shallon*	ITS 1 & ITS 2	RFLP	Berch et al. (2002)
Sebacina vermifera *Capronia villosa* *Hymenoscyphus ericae* *Trechispora spp.* *Oidiodendron maius*	*Gaultheria shallon*	ITS 2	RFLP, PCR	Allen et al. (2003)
Meliniomyces variabilis *Meliniomyces vraolstadiae* *Rhizoscyphus ericae* *Neocudonicella radicella* *Scytalidium lignicola*	*Orchidaeae, Pinaceae, Betulaceae, Saliaceae*	ITS, SSU, SSU-ITS	RFLP, PCR	Hambleton and Sigler (2005)
OIdiodendron maisus *O. citrinum* *O. spp. (others)*	*Chamaedaphne calyculata, Oxycocus quadripetalus, Pseudotsuga menziesii*	ITS1, ITS2, ITS4	PCR	Sigler and Gibas (2005)
Cryptosporiopsis ericae *Hymeoscyphus monotropae* *Lachnum pygmaeum* *Meliniomyces variabilis* *Mollisia minutella* *Phialocephala fortinii* *Hypocrea pachybasioides* *Irpen lacteus*	*Empetrum nigrum, Vaccinium vitis-idaea, Cassiope tetragona*	ITS1F, ITS4	PCR	Walker et al. (2011)

Table Cont....

Species	Host	Target Gene	Technique	Reference
Pochonia bulbillosa *Mycena galopus* *Nectriaceae spp.* *Galerina spp.* *Pleosporales spp.*	*Caccinium myrtillus L.*	ITS1F, ITS4	PCR	Vohnik et al. (2012)
Rhizoscyphus *Oidiodendron* *Lachnum* *Phialocephala* *Clavaria* *Acephala* *Meliniomyces*	*Vaccinium uliginosum*	ITS1 and ITS4	PCR	Yang et al. (2018)
Cryphtosporiopsis ericae *Sordariomycetes spp.*	*Vaccinium uliginosum*	ITS1 and ITS4; gfp gene	In situ PCR and Green Fluorescent Protein	Yang et al. (2020)
Helotiales *Rhizodermea veluwensis* *Glutinomyces* *Clavulinopsis*	*Cinium calycium*	ITS1, ITS2	PCR	Leopold et al. (2021)

Most recently, these molecular techniques have had a significant impact on the genetic diversity of ericoid mycorrhiza, allowing us to learn more about some groups that had been kept dormant. It should be feasible to gain more exact taxonomic information by using such approaches on the mycorrhizal endophytes of *Epacridaceae* plants, enabling in-depth research of population and community dynamics. In our review, an attempt was made to compile the majority of the ErM fungi that have been studied and characterized so far (Table 1).

2. **Host plant species associated with ericoid mycorrhiza:** Ericoid mycorrhiza is known to have a specific mutualistic association with the members of the *Ericaceae* family. Their association is considered to have evolved since the first appearance of *Ericaceae*. The *Ericaceae* family consists of 9 subfamilies, 4 of which do not have ErM. Recently, it was found that *Enkianthus campanulatus* had a symbiotic relationship with ErM. From this study, we can infer that ErM is still undergoing evolution, and this proves the very fact that ErM remains understudied in comparison with other mycorrhizae. The diversity of ErM remains unknown at the global level, although its culturable nature serves as a vital tool. Due to a lack of study on this fungus, its complete lineage remains unexplored. Reports have shown that the majority of diversity work done was using internal transcribed spacer (ITS) regions; although ITS is a universal barcode marker for fungi, it has been seen that it was not useful in the estimation of this Ericeae root mycobiont (Kohout 2017, Vohnik 2020).

Salal (*Gautheria shallon*): The authors mentioned in Table 1 discovered several potential fungi that form ericoid mycorrhiza in *Gaultheria shallon* using traditional culturing and genetic characterization. The identification of ericoid mycorrhizal fungi as well as their geographical distribution (Fig. 4), can be determined with the help of molecular characterization and phylogenetic analysis of the ITS sequence of gene bank.

Others: Many other potential host plant species of Ericaceae and Epacridaceae are selected for identifying the mycorrhizal association with different fungi. Some of them are *Calluna vulgaris, Vaccinium myrtillus, Epacris impressa, Astroloma pinifofolium, Cassiope mertensiana, Pinus sylvestris, Quercus ilex, Erica arborea* and so forth.

Functions of ericoid mycorrhizal cells: *Ericaceae* plants generally thrive on acidic as well as nutrient-poor soils where most of the essential nutrients are present in fixed forms. Studies have shown that the presence of ErM in such an environment plays a major role in the survival of the *Ericaceae* members as these mycobionts help to convert fixed nutrients into accessible forms that are then mobilized by plants (Fig. 5). Major functions of ErM are therefore summarized below:

1) Nitrogen Uptake

Due to the sluggish breakdown rates, acid-heathland (shrubland) soils only have trace levels of accessible inorganic nitrogen (Straker 1996, Haselwandter 1997). *Ericaceae* plants depend upon ericoid mycorrhizal fungus to retain the wide variety of various nitrogen compounds present in the soil. The findings of various experiments showed that plants with mycorrhizal association have accessibility to additional sources of nitrogen in the soil in addition to ammonium, while non-mycorrhizal plants used ammonium-nitrogen. The availability of carbon in the growing media affects the capacity of mycorrhizal fungi that are ericoid to consume nitrate, ammonium, or glutamine

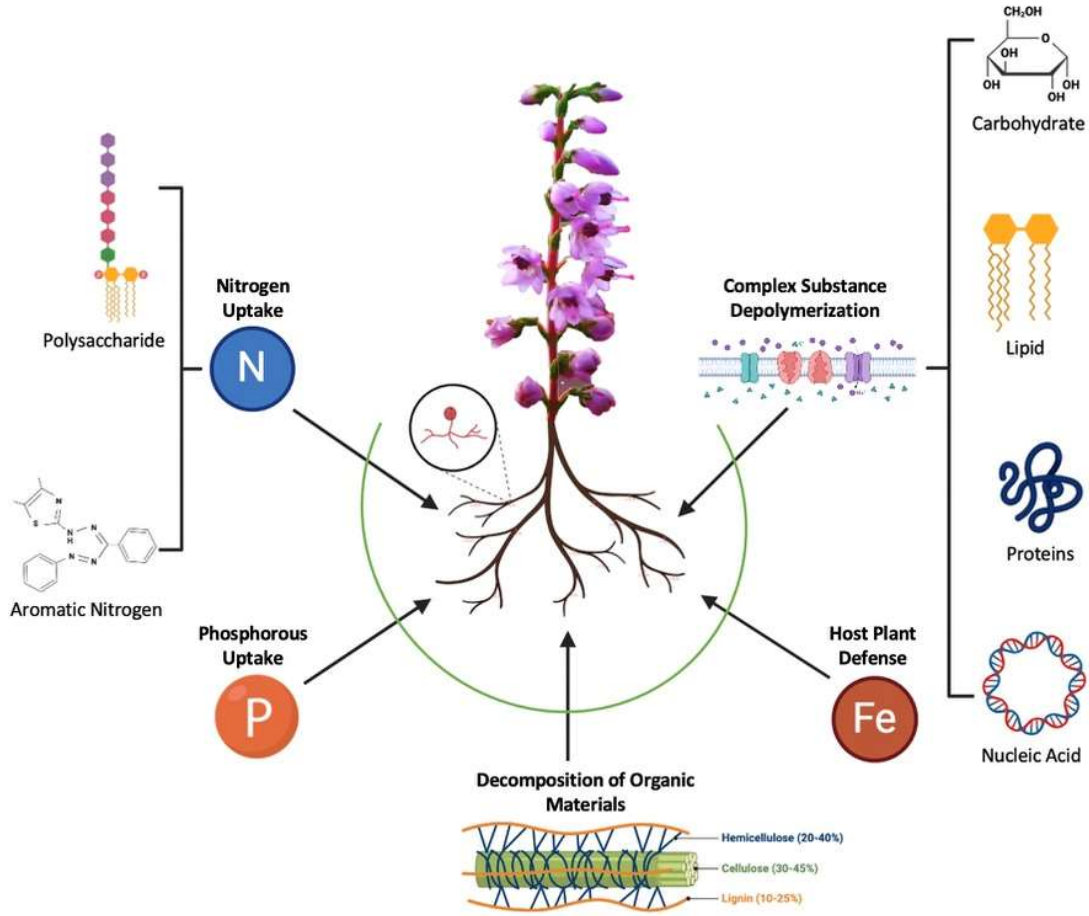

Fig. 5: Various roles of Ericoid Mycorrhiza (ErM) in the symbiotic relationship between ErM and host plant from *Ericaceae*.

(Grelet et al. 2005). Variations in absorption kinetics may be the cause of the growth disparities across strains under conditions of high carbon supply (Grelet et al. 2005).

Compared to plants without mycorrhizal associations, mycorrhizal plants are widely accessible to organic nitrogen (Schimel & Bennett 2004). Several processes are necessary for the direct intake of monomers- and oligomers by mycorrhizal fungi, intrinsic modification of organic nitrogen, and translocation throughout the fungus—host plant interaction for organic nitrogen to be taken up by ErM fungi and then transferred to the plant (Talbot & Treseder 2010). Aliphatic-N, which includes aromatic-nitrogen, and polysaccharide-nitrogen, which includes the substances found in humus, are the two main types of organic nitrogen compounds that are available in the soil (Roberts & Jones 2008). Depending upon how much organic nitrogen is present in the soil, it is possible for mycorrhizal roots to be exposed to as much or more organic nitrogen than inorganic nitrogen in most soils (Talbot & Treseder 2010). Depending on the fungus and plant species, different kinds of organic nitrogen may be given to the plant; asparagine, glutamine, and alanine are the three most common types (Chalot & Brun 1998). ErM fungi like *Rhizoscyphus ericae*, which can produce a wide range of extracellular enzymes, are dominant in systems with high efficiency of organic nitrogen uptake (Cairney & Meharg 2003, et al. 2006).

2) Phosphorus Nutrition

As evidenced by the consistent finding that mycorrhizal plants pile up so much phosphorus than non-mycorrhizal plants, the formation of symbiotic frameworks of mycorrhizal fungi is thought to be the most common approach to enhance plant Phosphorus uptake to get around the limitation of phosphorus within the rhizosphere (Smith et al. 2000, Burleigh et al. 2002, Tibbett & Sanders 2002, Smith & Read 2010). The major process is the expansion of added hyphae's capacity to penetrate through the phosphorus depletion layer surrounding the roots and acquire new locations with accessible P. This results in an increase in phosphorus absorption *via* fungal phosphorus carriers located at the fungal-soil interface.

The capacity of ErM fungi to utilize phosphorus bonded to soluble metal phosphates that are not organic has not been extensively studied. Numerous ericoid mycorrhizal fungi were examined by Van Leerdam et al. (2001) for their capacity for solubilizing phosphate. The majority of isolates could dissolve the rock phosphate hydroxyapatite when ammonium was added. None of the isolates were able to dissolve fluorapatite when a nitrogen source was used.

3) To Defend the Host Plant Against Harmful Circumstances

The majority of research on ericoid mycorrhizal nutrition has been phosphorus and nitrogen-centric. However, few have also discussed the increased consumption of essential and non-essential nutrients, for example, regulating the amount of iron taken up by host plants having a mutualistic relationship with *Hymenoscyphus* ericae (Shaw & Read 1989). Even in the presence of relatively small external amounts of iron, this fungus displays a strong attraction for it (Smith & Read 2010). The discharge of siderophores specific to iron (Fe) may control iron intake (Schuler & Haselwandter 1988). A decrease in metal concentration within host shoots is related to mycorrhizal protection of the host. These metal ions are utilized by many pathogenic microbes. However, sequestration of these metals, like Fe by ErM indirectly provides the host plant protection. According to Bradley et al. (1982), the mycorrhizal root system's ability to sequester metals or process of selectivity at the mycorrhizal root may be a cause of the decrease in shoot copper accumulation (Gibson & Mitchell 2004, 2005(a), 2005(b)). Both the plant and the fungus would be safeguarded by the mechanism of exclusion working on the mycorrhiza root. By preventing the flow of metal ions, the development of hyphae covered in mucilaginous slime may function as a mechanism of exclusion (Denny & Ridge 1995). Ultra-structural studies (Duddridge & Read 1982) show that the binding of metals inside the mycorrhizal root system has been confirmed by pectin in the interfacial layer dividing fungus and plant plasma membranes inside the invaded cells.

The defense against positively charged metals has been discussed in the majority of studies. However, the use of now-banned pesticides has caused a lot of soils to become contaminated with organic arsenic compounds (Meharg & Hartley, Whitaker 2002). It has been experimented that the *C. vulgaris*/*H. ericae* combination may thrive on arsenate-rich sites (Sharples et al. 2000(a)) and is protected by fungi that are tolerant to arsenic (Sharples et al. 2000(b)). Because arsenate metal is a phosphate counterpart, the phosphorus co-transporter system carries it across the plasma membrane (Meharg & Macnair 1992). Ericoid mycorrhizal fungi that are resistant to arsenate are ejected from mycelium without competing with the `transport of phosphate, changing arsenate to arsenite (Sharples et al. 2000a, 2000b, 2001).

Therefore, under selective pressure, new or altered phenotypic features may result in increased metal tolerance in ErM fungus. Given that each cell's genetic makeup determines its phenotype, alterations in genetic sequences and arrangement may have emerged in ErM fungi that have evolved to external metal toxicity. Many environmental conditions are known to produce mutations either through direct or indirect means by forming reactive oxygen compounds, which is one of the main drivers of genetic variation (Hartwig et al. 2002).

4) Decomposition of Organic Materials

According to Lindahl & Tunlid (2015) and Zak et al. (2019), Mycorrhizal fungi differ from saprotrophs, which are free-living and primarily get carbon through plant photosynthetic pigments rather than through the breakdown of organic components. It is possible to assess and contrast the inherent saprotrophic capacity of various species and functional groupings using the variety and richness of such genes. However, some mycorrhizal fungi have genes that produce extracellular enzymes needed in the breakdown of the organic materials. Kohler et al. (2015), Op De Beeck et al. (2018), and Nicolás et al. (2019) claim that some mycorrhizal fungi employ oxidative and non-enzymatic mechanisms to extract nitrogen from organic substances by partial degradation of lignocellulose.

It has been proven that ErMFs have the capacity to speed up the degradation of organic materials. Two distinct enzyme types can be secreted by ErMFs. The first kind has the ability to break down hemicellulose, cellulose, tannic acid, polyphenols, and lignin, which can hasten the dissolution of essential nutrient compounds. The other form encourages direct uptake of nutrients (Cairney & Burke 1998, Read & Perez-Moreno 2003).

5) Complex Substrates Depolymerization

A variety of extracellular enzymes produced by ericoid fungi catalyze the breakdown of numerous organic macromolecules and provide plants with the ability to cut down the bi-products of complex polymers that plant leaves or roots cannot digest (Read & Perez-Moreno 2003). This capability seems to be especially crucial in systems with little nitrogen since there is not enough mineralization to meet plant demand for nitrogen (Schimel & Bennett 2004. Enzymes that degrade polymers can be distinguished into two (Read et al. 2004). The primary class contains numerous 'hydrolases' that cleave the molecules containing nutrients themselves. These enzymes include *polyphenol oxidases* and *lignases*, which are anticipated to contribute significantly to both plant nutrition

and the decomposition of litter. The other class improves the uptake of nutrients by destroying biological compounds, including tannins, polyphenols, and lignins, which could precipitate vital elements. In addition to this, *chitinases* and *proteases* conduct phenol oxidase activities that may make it easier for hosts to access phosphorus and nitrogen from dormant plant parts or complexes of polyphenols in the soil. These hydrolytic enzymes break down cell wall polysaccharides like cellulose, hemicelluloses, and pectin.

It is understood that the ErM fungus produces *polyphenol oxidases* (Burke & Cairney 2002). This enzyme, which exhibits a significant amount of overlap in substrate affinities, includes laccase, catechol oxidase, and tyrosinase (Burke & Cairney 2002). *R. ericae* generates *laccase* with a variety of phenol-associated-oxidizing activity (Burke & Cairney 2002). It is hypothesized that *laccases,* which are produced by ErM fungi, might be involved in numerous varieties of symbiotic functions. The nutrition of plants in phenol-rich contexts is greatly influenced by ErM fungi's capacity to utilize a variety of monomeric phenol-rich compounds as their carbon source (Leake & Read 1991) and the ability to release the enzymes *catechol oxidase* and *laccase*. (Bending & Read 1996 a,b), that are associated with the degradation of hydrolyzable polyphenols.

CONCLUSION AND FUTURE PROSPECTS

The literature survey sheds light on the fact that ErM is understudied. ErM is known to help its host in Nitrogen and phosphorus uptake, decomposition of organic material, complex substrates depolymerization, and to defend host plants against harmful substances. Most of the molecular studies done to date are based on ITS region (found in all the Eukaryotes). However, it does not shed light on the molecular diversity of the ErM. To explore the genetic diversity, we should start targeting the variable regions, conserved only for ericoid mycorrhizae. The incorporation of genomics tools can be useful to study the functionality of various ErM genes. The phylogeny of ErM needs to be studied in depth, which can help to understand its evolutionary path and further trace its distribution. The cultural nature of ErM provides a huge advantage in carrying out various studies that remain unexplored in the world of ErM symbionts.

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