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Novel Root-Fungus Symbiosis in *Ericaceae*

Ericaceae (the heath family) are widely distributed calcifuges inhabiting soils with inherently poor nutrient status. *Ericaceae* overcome nutrient limitation through symbiosis with ericoid mycorrhizal (ErM) fungi that mobilize nutrients complexed in recalcitrant organic matter. At present, recognized ErM fungi include a narrow taxonomic range within the Ascomycota, and the *Sebacinales*, basal Hymenomycetes with unclamped hyphae and imperforate parenthesomes. Here we describe a novel type of basidiomycetous ErM symbiosis, termed 'sheathed ericoid mycorrhiza', discovered in two habitats in mid-Norway as a co-dominant mycorrhizal symbiosis in *Vaccinium* spp.

The basidiomycete forming sheathed ErM possesses clamped hyphae with perforate parenthesomes, produces 1- to 3-layer sheaths around terminal parts of hair roots and colonizes their rhizodermis intracellularly forming hyphal coils typical for ErM symbiosis. Two basidiomycetous isolates were obtained from sheathed ErM and molecular and phylogenetic tools were used to determine their identity; they were also examined for the ability to form sheathed ErM and lignocellulolytic potential. Surprisingly, ITS rDNA of both conspecific isolates failed to amplify with the most commonly used primer pairs, including ITS1 and ITS1F + ITS4. Phylogenetic analysis of nuclear LSU, SSU and 5.8S rDNA indicates that the basidiomycete occupies a long branch residing in the proximity of *Trechisporales* and *Hymenochaetales*, but lacks a clear sequence relationship (.90% similarity) to fungi currently placed in these orders. The basidiomycete formed the characteristic sheathed ErM symbiosis and enhanced growth of *Vaccinium* spp. in vitro, and degraded a recalcitrant aromatic substrate that was left unaltered by common ErM ascomycetes. Our findings provide coherent evidence that this hitherto undescribed basidiomycete forms a morphologically distinct ErM symbiosis that may occur at significant levels under natural conditions, yet remain undetected when subject to amplification by 'universal' primers. The lignocellulolytic assay suggests the basidiomycete may confer host adaptations distinct from those provisioned by the so far investigated ascomycetous ErM fungi.

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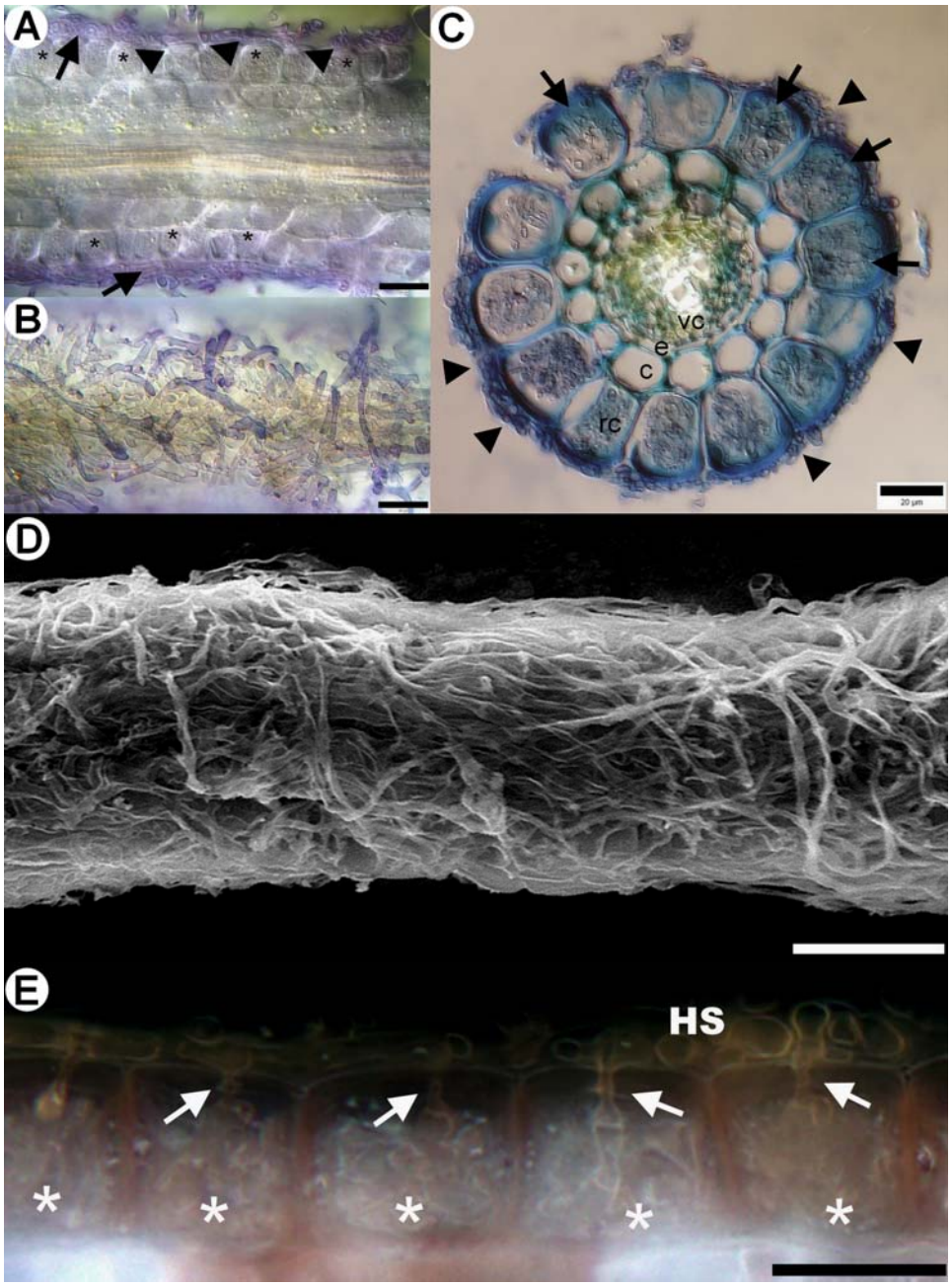

Morphological and anatomical characteristics of sheathed ericoid mycorrhiza from field-collected European blueberry (*Vaccinium myrtillus*) roots. A) Longitudinal section through sheathed ericoid mycorrhiza. The hyphae forming the sheath (arrows) penetrate rhizodermal cell walls (arrowheads) and form dense coils typical for ericoid mycorrhiza (asterisks); bar = 20 mm. B) Surface view of the same sheathed ericoid mycorrhiza displaying the structure of a dense hyphal sheath covering the hair root; bar = 20 mm. C) Cross section of sheathed ericoid mycorrhiza. The hair root is covered by a hyphal sheath (arrowheads), its rhizodermal cells (rc) are filled with dense hyphal coils (arrows). The mycobiont never advances to the cortex/exodermis (c), the endodermis (e) or the vascular cylinder (vc); bar = 20 mm. D) Surface view of sheathed ericoid mycorrhiza showing a dense hyphal sheath; bar = 50 mm. E) Detail of a longitudinal section of sheathed ericoid mycorrhiza. Hyphae forming the hyphal sheath (HS) penetrate rhizodermal cells (arrows) and form coils typical of ericoid mycorrhizal symbiosis (asterisks); bar = 20 mm.