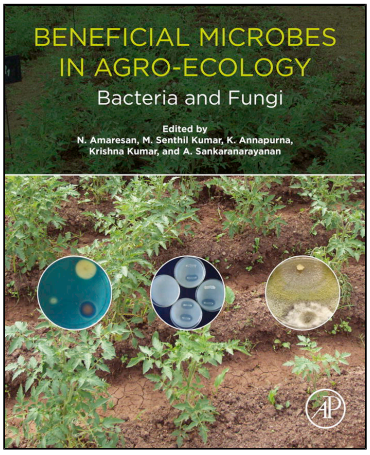

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CHAPTER

27

Glomus

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1. Introduction

Arbuscular mycorrhizal (AM) fungi are a group of ever-present obligate symbionts having a prerequisite to develop close mutualistic association with plant roots to grow and complete their life cycle (Parniske, 2008). They are found in almost all ecosystems (Read, 1991; Brundrett, 2009). AM fungi form a monophyletic group in the phylum Glomeromycota (Schüßler et al., 2001). About 288 taxonomically described species are currently included in this group (Öpik and Davison, 2016). Molecular studies have significantly improved our understanding of AM fungi (Redecker et al., 2000a,b; Morton and Redecker, 2001, Schwarzott et al., 2001; Schüßler et al., 2001; de Souza et al., 2005; Palenzuela et al., 2008, 2010). The nuclear-encoded rDNA phylogenies have revealed a considerable polyphyly of some genera, which has been used to reassess taxonomic concepts (Morton and Redecker, 2001; Redecker and Raab, 2006; Walker et al., 2007; Oehl et al., 2008).

2. Phylogenetic relationships

Species forming glomoid spores represent the largest group within the phylum Glomeromycota. These species were formerly placed within the family Glomeraceae (Pirozynski and Dalpé, 1989) of the suborder Glomerineae in order Glomerales (Morton and Benny, 1990). rDNA phylogenies revealed that the genus *Glomus* is several times polyphyletic (Redecker et al., 2000b; Schwarzott et al., 2001). AM species, which form *Glomus*-like spores, can be found in six different lineages within the Glomeromycota. Genus *Paraglomus* emerges to be the most primitive diverging glomeromycotan lineage as revealed in rDNA phylogenies. The separation of *Pacispora* and *Diversispora* clades from other "*Glomus* lineages" is well-supported by rDNA phylogenies (http://tolweb.org/Glomeromycota). *Glomus* groups A and B represented by the species *Glomus mosseae* and *Glomus claroideum*, respectively, are genetically rather distant but still form a monophyletic group in rDNA phylogenies (Schwarzott et al., 2001). The formation of "sporiferous saccule" was thought to be a characteristic

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feature solely of the Acaulosporaceae (*Acaulospora* and *Entrophospora*), but now it is known to occur in the *Archaeospora*. The Gigasporaceae (*Scutellospora* and *Gigaspora*) members are well distinguished by the formation of "bulbous suspensor," which is exemplified by molecular data (http://tolweb.org/Glomeromycota). Gigasporaceae and Acaulosporaceae representatives form a clade in most rDNA phylogenies, which is in conflict with previous investigations based on cladistic analysis of morphological features that placed *Glomus* and Acaulosporaceae together (Morton and Benny, 1990). Phylogenetic reorganization within AM fungi over the last 10 years indicates that the large group of *Glomus* species likely originated from a single ancestor (Schwarzott et al., 2001). With approximately 70 species, the genus *Glomus* remains morphologically heterogeneous and the largest genus in the phylum Glomeromycota (Oehl et al., 2011a,b).

In an attempt to redefine the genus more naturally, Schüßler and Walker (2010) reassigned several *Glomus* species characterized by the frequent formation of intraradical spores to *Rhizophagus* (type: *R. populinus*) a pathogenic genus that does not belong in the Glomeromycota. Sieverding et al. (2014) proposed *Rhizoglomus* gen. nov. (Glomeraceae, Glomeromycetes) typified by *Glomus intraradices* [≡ *Rhizoglomus intraradices*]. The taxonomy and identification of AM fungi is still undergoing a radical reform and remains challenging.

3. Isolation of AM fungal spores

The isolation of spores from rhizosphere soil samples reveals spore abundance and species diversity. It is extremely important to conduct seasonal sampling or to initiate trap cultures, as many AM fungal species sporulate seasonally. Routine extraction from soil samples is made possible by the wet sieving and decanting technique, a method commonly used to extract nematodes from soil and adapted to AM fungi by Gerdemann (1955), (Gerdemann and Nicolson, 1963).

4. Identification of AM fungal spores

The identification techniques employed by taxonomists have become increasingly sophisticated. Primarily, taxonomies were based upon morphological and anatomical characteristics of the fungi. Later on, methods based on serology (Aldwell and Hall, 1987), isozyme variation through gel electrophoresis (Hepper, 1987), and fatty acid variation (Bentivenga and Morton, 1994) were introduced. Presently, systematists have come to rely increasingly on DNA-based methods (Cummings, 1990; Davidson and Geringer, 1990; Simon et al., 1990, 1992, 1993; Redecker, 2000), which are considered to be the best measure of genealogical relationships among organisms (Koide and Mosse, 2004). DNA target regions mostly used for AM fungal identification are located on the ribosomal genes (small and large ribosomal subunits [SSU and LSU] and the internal transcribed spacers [ITS1 and ITS2]) as they show variation that is sufficient to distinguish between AM species or isolates (Krüger et al., 2012). All this has led to the modern era of molecular identification of AM species (Redecker et al., 2013). Next-generation sequencing (NGS) tools represent a further step forward for biodiversity surveys of all organisms (Shokralla et al., 2012), including AM fungi. Over the last few years, the number of NGS-based AM fungal biodiversity studies has increased while the spectrum

of the target environments has broadened (Öpik et al., 2013a,b). Furthermore, new sets of primer pair for the specific amplification of AM fungal DNA sequences, capable of providing higher accuracy and a broad coverage of the whole phylum Glomeromycota have been developed (Krüger et al., 2009). Nowadays, AM fungal assemblages are no longer studied only in plant roots, but also in the bulk rhizosphere soil (Lumini et al., 2010; Borriello et al., 2012; Davison et al., 2012). The main result obtained from the application of NGS to the study of AM biodiversity has been the discovery of an unpredictable diversity within the phylum Glomeromycota (Öpik et al., 2013a,b). However, this series of novel molecular tools has introduced a new issue, i.e., the continuously increasing number of unidentified AM fungal DNA sequences from environmental samples with no correspondence whatsoever to sequences of known species (Öpik et al., 2010). This has naturally made scientists aware of the fact that the number of AM species could be larger than expected. However, it is not reliable to have new species described just on the basis of short DNA sequences obtained by using NGS tools. Instead, for each new suggested taxon, a series of steps needs to be followed to characterize the morphotype, the functional traits, and the ecological role offered when present in combination with other organisms in a given environment. Therefore, NGS tools cannot be considered as complete replacements of the traditional methods of identification and description of new species (Berruti et al., 2014). Routine identification of AM fungi will probably continue to be based primarily on morphological characters and thus an increased acceptance of the combined approach between anatomy and DNA will be important. The ability to properly name the fungi, avoid duplication of names, and relate the species to one another also depends heavily on international culture collection center's such as the International Culture Collection of Arbuscular and Vesicular-arbuscular Mycorrhizal Fungi (INVAM), and the International Bank for the Glomeromycota (BEG/IBG) (Koide and Mosse, 2004).

5. General morphological characters used for identification of AM fungal spores

The AM fungal spores have unique morphological and biochemical features. Several morphological features play a key role in establishing the taxonomic identity and relationships of AM species, which help in the construction of a system of classification (Rodrigues and Muthukumar, 2009). General morphological characters used for the identification of AM fungi are given as

Sr. No.		Morphological characters
1.	Sporocarp	Size, shape, peridium
2.	Spore	Color, shape, size, content
3.	Subtending hyphae	Shape, width, pore occlusion
4.	Auxiliary cells	Ornamentation
5.	Mycorrhizal anatomy	Hyphal characters, intra-radical spores
6.	Spore wall	Color, dimension, number, type, ornamentation, reaction
7.	Spore germination	Direct, indirect

Morphological characters used for identification of *Glomus* species:

- **Sporocarp morphology**

Glomus species form a single spore or spores in sporocarps, where the spores are arranged randomly in the matrix hyphae. Peridium may be present around the sporocarps in the form of loose or compact interwoven hyphae, a patchy covering over the sporocarps or as a hyphal network covering single or small clusters of spores. The presence or absence of peridium accounts for much of the variation observed in size of sporocarps (Rodrigues and Muthukumar, 2009).

- **Spore morphology**

Characters such as spore color, shape, and size may vary considerably depending on the developmental stage and environmental conditions. Spore color varies from hyaline to white to yellow, red, brown, and black with all intermediate shades. The difference in color may be due to pigmentation in the spore wall or in the spore content (Morton, 1988). The shape of spores is mainly governed by the genotype of the fungus and the substrate in which the spores are formed. Intraradical spores are mainly globose, subglobose to ellipsoidal while extraradical spores may be globose, subglobose, ellipsoidal, oblong, or ovate to highly irregular-shaped. Of all the known species of AM fungi, *Glomus tenue* is the smallest with an average diameter of 10–12 μm. Spore size varies considerably within the same species and hence both immature and mature spores are taken into consideration while describing the species (Rodrigues and Muthukumar, 2009).

- **Subtending hyphae**

In *Glomus* species, the subtending hypha may be simple to recurved or sometimes swollen or constricted at the point of attachment to the spore. The width of the hyphae varies considerably within the species. The mechanism of spore occlusion at the point of attachment of the subtending hypha to the spore has some taxonomic significance. Walker (1992) suggested three distinct lines with regard to the occlusion of the spore content in *Glomus* viz., spores possessing a complete endospore formed by more or less flexible inner-wall group, spores sealed by the ingrowths and thickening of the wall layer of the subtending hypha and occlusion by the septum usually somewhat distal to the spore base (Rodrigues and Muthukumar, 2009).

- **Mycorrhizal anatomy**

Hyphal character such as long infection units with "H" connections between parallel strands of hyphae in *Glomus* (Abbott and Robson, 1979) can be utilized as a diagnostic feature to identify the genus in mycorrhizal roots (Morton and Bentivenga, 1994). Intraradical spores in Glomaceae are usually globose, subglobose to elliptical (Rodrigues and Muthukumar, 2009).

- **Spore wall**

In *Glomus* species, the spore wall forms at the tip of the sporogenous hypha. Changes in the spore wall occur as the spore size increases, i.e., it grows, thickens, and differentiates. Once the spore ceases to expand small changes in color, thickness, and rigidity appear in the spore wall. The spore wall layers can be either permanent or impermanent structures (Błaszkowski, 2012). In most juvenile spores, the spore wall may be one to two layered. However, the spore wall of most *Glomus* species usually consists of at least two wall layers and can differentiate up to four wall layers. The spore wall layers originate successively toward the spore interior. The number, width, and position of wall layers differ among species (Rodrigues and Muthukumar, 2009).

- **Spore germination**

In the genus *Glomus*, spore germination is direct wherein the inner-wall layers protrude through a weakened area of the outer wall layer as a germ tube initially, later elongating into a typical hypha (Rodrigues and Muthukumar, 2009).

Characteristic features of the genus Glomus Tulasne and Tulasne.

The genus *Glomus* is based on the type species *Glomus macrocarpum* Tulasne and C. Tulasne (1845), later lectotypified by Berch and Fortin (1983).

Etymology: Latin, *Glomus* (a ball of yarn), possibly in reference to sometimes rounded and cottony appearance of the species.

- Spores of *Glomus* species develop blastically at the end of sporogenous hyphae, although intercalary spore formation has also been reported.
- The spores are produced singly (most species) or in disorganized loose multiple-spored clusters or in compact sporocarps (spores enveloped in a hyphal mantle "gleba") in the soil or substrate. The compact sporocarps are usually without or with peridium, where spores are either not organized in sporocarp or organized around a central hyphal plexus.
- The spore surface may be smooth (in most species) or ornamented.
- The spores have a mono-to-multiple layered wall.
- The wall of the subtending hypha is conspicuously continuous and concolorous with the spore wall layers or slightly lighter in color than the spore wall.
- At the end of spore development, the lumen of the subtending hypha usually becomes closed by either (a) a curved septum continuous with the innermost lamina of the laminate spore wall layer, (b) an invaginated flexible innermost layer, (c) an amorphous plug, or (d) thickening subtending hyphal wall.
- Spore germination by emergence of the germ tube through the lumen of the subtending hypha (most species) or the spore wall.
- The mycorrhizae of *Glomus* species consist of arbuscules, vesicles, and intra- and extraradical hyphae.
- Arbuscules have cylindrical or slightly flared trunks with branches progressively tapering in width toward tips.
- Vesicles usually are thin-walled and ellipsoid.
- Intraradical hyphae usually spread along roots and frequently form Y-shaped branches, H-shaped connections, and coils, mainly occurring at entry points.
- The genus *Glomus* forms typical vesicular-arbuscular mycorrhizae consisting of arbuscules, vesicles and hyphae that stain intensively blue to dark blue in Trypan blue (Rodrigues and Muthukumar, 2009; Schüßler and Walker, 2010; Oehl et al., 2011a,b).

6. Beneficial role

Coexistence of various AM fungal isolates in the soil results in

(a) Improved plant nutrient acquisition: AM fungi primarily improve uptake of immobile nutrients mainly phosphorus (P) (Bell et al., 1989; Jakobsen et al., 2005; Bucher, 2007), and also contribute in uptake of calcium (Ca) (Azcón and Barea, 1992), iron (Fe) (Treeby, 1992), manganese (Mn) (Kothari et al., 1991), zinc (Zn) (Bell et al., 1989), and nitrogen (N) (Nasholm et al., 2009);

(b) Enhanced plant tolerance to biotic and abiotic stress (Augé, 2004; Al-Karaki, 2006; Bennett and Bever, 2007);
(c) Healthy plant growth and development, and help in seedling establishment (Strullu, 1985);
(d) Nutrient cycling (Tiwari and Sati, 2008);
(e) Conservation of soil structure (Rillig et al., 2002; Rillig and Mummey, 2006; Bedini et al., 2009);
(f) Enhanced diversity of plant community (Smith et al., 1997; Bonfante and Genre, 2010); and
(g) Bioremediation of heavy metal contaminated soils (Leyval et al., 1997; Liao et al., 2003).

7. Conclusion

Species belonging to the genus *Glomus* are usually generalist symbionts found in diverse habitats, suggesting tolerance to various stressful environmental factors, and also have considerable functional heterogeneity (presence of different isolates), causing larger variations in plant growth response (Corkidi et al., 2004; Öpik et al., 2006; Oehl et al., 2010; Berruti et al., 2015).

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