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Taxonomy of Arbuscular Mycorrhizal Fungi

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ABSTRACT

Taxonomy of arbuscular mycorrhizal fungi (AMF) created problems mainly being obligate symbionts. In this review, the history and development of taxonomy of AMF is addressed. In the initial discovery period (1845-1974) the sporocarp-forming species were described and a classification for these fungi was proposed. This was followed by alpha taxonomy period (1975-1989) in which time solid morphological basis for species identification was developed resulting in description of several new species. The next cladistic period (1990-2000) resulted in the first cladistic classification of AMF based on phenotypic characters. The present phylogenetic synthesis period (2001- till date) proposed a new classification based on genetic characters using sequences of multicopy rRNA genes. In conclusion it can be said that the taxonomy of AMF belonging to the phylum *Glomeromycota* has generated considerable confusion and controversy among mycologists working with this important plant symbionts.

KEYWORDS: AM fungi, Classification, *Glomeromycota*, Taxonomy

INTRODUCTION

Arbuscular mycorrhiza (AM) is a symbiosis between fungus and the root, in which the fungus supplies the root with nutrient and the root supplies the fungus with carbon (Harley and Smith, 1983). Intensive research has been carried out throughout the world on the role of these fungi in improving growth and yield in plants. It is now well-demonstrated that these fungi can substantially increase the uptake of mineral nutrients, particularly P, drought tolerance and resistance to soil-borne plant pathogens (Bagyaraj, 2011). Formerly, all fungi forming arbuscular mycorrhizal associations were placed under the genus *Endogone*. The genus *Endogone* (Gr. Endo=inside; gone=seed) was first described by Link in 1809 which form mycorrhizal associations with higher plants and also produce hypogeous sporocarps in soil. The history of AMF taxonomy can be grouped under different periods as suggested by Stürmer (2012).

THE DISCOVERY PERIOD (1845-1974)

In 1845, Tulasne and Tulasne published a brief description of the species *Glomus microcarpus* and *Glomus macrocarpus* in a manuscript written in Latin and later transferred the two species to the genus *Endogone* (Tulasne and Tulasne, 1851). The genus *Sclerocystis* was proposed by Berkeley and Broome (1873) to encompass species forming spores in small sporocarps. Both genera were classified in the family *Endogonaceae*, order *Mucorales*. Interestingly, *Glomus* and *Sclerocystis* were described before the term "mycorrhiza" was coined by Frank in 1885. The first monograph of the family *Endogonaceae* treated in the order *Mucorales* (*Zygomycetes*) has been prepared by Thaxter (1922). Fungi of this family were located in four genera producing spores in sporocarps: *Endogone* Link: Fries, *Glaziella* Berk., *Sclerocystis* Berk. & Br., and *Sphaerocreas* Sacc. & Ellis. In 1935, Zycha transferred the one species of *Sphaerocreas* to *Endogone*. The existing genera included both chlamydosporic and zygosporic species. Thaxter (1922) and Godfrey (1957) considered chlamydosporic species to be anamorphs of those producing zygospores, following the finding of both types of spores in sporocarps of *Glomus fasciculatum* (at that time known as *Endogone fasciculata* and *E. microcarpa*).

During this period, the widely used method of wet sieving to extract sporocarps and non-sporocarpic spores from soils was developed by Gerdemann and Nicolson (1963), which led to an increase in taxonomic activity. Collaboration between Gerdemann and Trappe resulted in the classical publication "The *Endogonaceae* in the Pacific Northwest" by Gerdemann and Trappe in 1974. The authors in this publication proposed a classification for fungal taxa including 30 species forming arbuscular mycorrhiza. They recognized *Glomus* as a valid genus distinct from *Endogone*, as previously proposed by the Tulasne brothers, and erected two new genera, *Acaulospora* and *Gigaspora*, which had also been shown to form arbuscular mycorrhizal associations. In this classification (**Table 1**), the genera *Glomus*, *Sclerocystis*, *Acaulospora*, and *Gigaspora* were placed in the family *Endogonaceae*, order *Mucorales*, phylum *Zygomycota*, together with *Endogone* and two other genera, *Glaziella* and *Modicella*, which were not known to form arbuscular mycorrhizal associations. Later, *Modicella* was transferred to the family *Mortierellaceae* by Trappe (1982) and *Glaziella* was transferred to the *Ascomycota* by Gibson *et al*. (1986). A new genus, *Complexipes*, erected by Walker (1979) and tentatively placed in *Endogonaceae* was later transferred to *Discomycetes* (Trappe, 1982). The classification by Gerdemann and Trappe (1974) was important for the taxonomy of these organisms, and it provided a sound basis for systematic knowledge during several years to follow.

THE ALPHA TAXONOMY PERIOD (1975-1989)

This period contributed to the establishment of a solid morphological basis for identification and classification of glomeromycotan fungi. The 15 years are characterized by: (1) the proposal of several new genera and families, (2) a profuse description of new species, and (3) the proposal for standardization of phenotypic characters of arbuscular mycorrhizal fungal (AMF) spores to describe new species. New taxa forming arbuscular mycorrhizal associations were proposed based on living and fossil evidence. A new genus, *Entrophospora*, was erected by Ames and Schneider (1979) based on the observation that the formation of a "saccule" prior to spore development. Walker and Sanders (1986) differentiated between species of *Gigaspora* proposed by Gerdemann and Trappe (1974) based on whether spore

germination occurred through a flexible "shield" on an inner flexible wall or directly through the spore wall, and they used the former character to define a new genus, *Scutellospora*. During this period, a large number of new species were described. Walker in the UK established an interest in this group of fungi, initially publishing with Trappe (USA), but later also establishing collaboration with several other researchers, principally Koske (USA). After initial work with Nicolson (UK), Schenck (USA) also established a group describing new species, and partly stemming from work with Schenk, Spain and Sieverding published new species from their work in Colombia. Towards the end of this period, Blaszkowski (Poland) and Morton (USA) began to publish new species based on morphological characteristics.

Only 12 years after the monograph by Gerdemann and Trappe (1974), the number of described glomeromycotan species had jumped to 77 (Trappe, 1982), and 6 years later, Schenck and Pérez (1988) listed 126 species. In parallel, different keys for AMF species identification developed, such as the synoptic key of Trappe (1982), the dichotomous key of Hall and Fish (1979), and Hall (1984), and keys for groups of species (e.g., Koske and Walker, 1985). A significant step forward for those interested on AMF taxonomy and identification at the time was publication of the "Manual for the Identification of VA Mycorrhizal Fungi" (Schenck and Pérez, 1988) which compiled all summary species descriptions. All descriptions during this time were based on morphological features of spores. Spore subcellular structures, which are diverse, largely accounted for most differences between species. Walker also proposed a "murograph" that consists of a graphic representation to depict the different wall types and groups found in a spore. Berch (1986) in her treatise on the *Endogonaceae* suggested the use of the word "wall layers" instead of "wall". The different wall layers described were laminated, evanescent, membranous, amorphous, coriaceous and germinal. Towards the end of this period, Morton (1988) critically evaluated all morphological criteria used to classify and identify AMF species and suggested some approaches to clarify taxonomy concepts.

THE CLADISTICS PERIOD (1990-2000)

This period is marked by a new classification and the entry of molecular biology into systematics of glomeromycotan fungi. It is characterized mainly by: (1) proposal of a cladistic classification for AMF based on phenotypic characters, (2) description of new taxa based on fossil records, (3) proposal of a spore development model with re-evaluation of terminology for spore subcellular characters, and (4) use of genetic characters to define taxa and elucidate evolutionary relationships. One of the important landmarks in these 11 years was the first cladistic analysis of glomeromycotan fungi and the proposal of a new classification. Morton (1990) proposed two main clades, one consisting of *Gigaspora* and *Scutellospora* species and the other harboring *Glomus*, *Sclerocystis*, *Acaulospora*, and *Entrophospora*. This cladistic analysis, together with additional information from spore ontogeny and mode of spore germination, formed the basis for a radical change in classification (Morton and Benny, 1990) (**Table 1**). Genera of AMF were removed from the order *Endogonales* and placed in the newly erected order *Glomerales* (published as *Glomales*) in the families *Glomeraceae* (*Glomus* and *Sclerocystis*), *Acaulosporaceae* (*Acaulospora* and *Entrophospora*), and *Gigasporaceae* (*Gigaspora* and *Scutellospora*). *Glomeraceae* and *Acaulosporaceae* were hypothesized to be closely related and placed in the sub-order *Glomineae* and the family *Gigasporaceae* in the sub-order *Gigasporineae*. This was the first new classification proposed since Gerdemann and Trappe (1974) had considered that AMF should remain in the phylum *Zygomycota* some 25 years earlier.

Morton (2000) proposed that the arbuscular mycorrhizal symbiosis had arisen during two distinct periods rendering the order *Glomerales* polyphyletic: *Glomineae* and *Gigasporineae* would represent two evolutionary branches. Evidence to support this hypothesis is related to the mode of spore formation (Franke and Morton, 1994), morphology of fungal mycelium (Brundrett and Kendrick, 1990), types of infective propagules (Biermann and Linderman, 1983; Jasper *et al*., 1989), and cell wall composition (Gianinazzi-Pearson et al., 1994). The classifications of Gerdemann and Trappe (1974) and Morton and Benny (1990) did not state clearly into which class the AMF species should be included: *Endogonales* in the former and *Glomerales* in the latter were left in the class *Zygomycetes*. Cavalier-Smith (1998) later proposed that fungal species establishing (vesicular) arbuscular mycorrhizas with plants could be grouped in a new class, the *Glomomycetes*, within a new phylum, *Archemycota*. The number of new species described in this "cladistics period" totaled one third of that described in the previous "alpha-taxonomy" period. One of the main events during these 11 years was the use of SSU gene sequences to elucidate evolutionary relationships among taxa within the order *Glomerales*. This period ends with the identification of two ancestral clades based on rDNA sequences (Redecker *et al*., 2000).

THE PHYLOGENETIC SYNTHESIS PERIOD (2001 TO TILL TODAY)

This ultimate period is characterized by: (1) the proposal of a new classification based solely on genetic characters (SSU rRNA gene), (2) description of new taxa based on the fossil record, and (3) the creation of new taxa and a new classification based on a combination of phenotypic and genetic characters. The most important event in this period has been the naming by Schüßler *et al*. (2001) of a new phylum within the kingdom Fungi to group all AMF species. The proposed phylum *Glomeromycota* is based on a phylogenetic analysis of SSU rRNA gene sequences. Four new orders (*Paraglomerales*, *Archaeosporales*, *Diversisporales*, and *Glomerales*) and new families were proposed (**Table 1**). The term "glomerospores" was coined by Goto and Maia (2006) to denominate spores formed by fungi in the *Glomeromycota*. After the new classification by Schüßler *et al*. (2001), the last 10 years have been characterized by descriptions and proposals of new families and genera for both ancient and extant AMF, with some of the taxa proposed still in debate among taxonomists. A more radical expansion of genera and families in the

Glomeromycota was proposed by Oehl *et al*. (2008) based on interpretation of the previous works of Walker *et al*. (2004), De Souza *et al.* (2005), Ahulu *et al*. (2006), and Redecker *et al.* (2007). In the past few years, two distinct classifications have been further proposed for the *Glomeromycota* (**Table 1**), both of which are characterized by a rearrangement of the genus *Glomus sensu lato* shown previously to be polyphyletic by Schwarzott *et al*. (2001). Schüßler and Walker (2010) performed a phylogenetic analysis of glomeromycotan fungi, based on near-full-length SSU rRNA gene sequences and proposed a new family and three new genera. They separated *Glomus* into the genera *Funneliformis*, *Sclerocystis*, and *Rhizophagus* in the family *Glomeraceae* with the remaining species of *Glomus* and *Claroideoglomus* in the family *Claroideoglomeraceae*. *Rhizophagus* was first proposed by Dangeard (1900) and synonymized with *Glomus* by Gerdemann and Trappe (1974). Inspection of the protologue of *Rhizophagus populinus* revealed that this fungus is an AMF species, and it was resurrected by Schüßler and Walker (2010) to harbour AMF species that form large numbers of spores in the roots. Schüßler and Walker (2010) recognized that their phylogeny is incomplete because no living material is available for molecular analyses of many previously described glomeromycotan species. Therefore, some species were retained in their original genus but referred to as "species of uncertain position." Oehl *et al*. (2011) proposed a rearrangement of species in the genus *Glomus sensu lato* and erected the genera *Simiglomus* and *Septoglomus* in the *Glomeraceae*, and *Viscospora* in the *Claroideoglomeraceae*. An evidence-based consensus for the classification of AMF (*Glomeromycota*) was published by Redecker *et al*. (2013). The authors point out that recent publication of numerous new taxa at all level within *Glomeromycota* has created confusion and operational difficulties for those working with AMF. The fungi being obligate symbionts pose problems not encountered for many other groups of organisms. The taxonomy of AM fungi thus has undergone intensive investigation and has experienced lots of controversy and radical transformations. However the characteristics of some of the commonly occurring AM fungi used by majority of mycorrhiza workers to identify them are given below.

Glomus: Spores formed blastically on subtending hyphae, singly, in loose aggregates or in a sporocarp. Vesicles are thin walled and ellipsoid. Intraradical hyphae rarely coiled, with cross-connecting branched hyphae. Mycorrhiza stains darkly. Arbuscules with flared or cylindrical trunks with incremental narrowing of branch hyphae. Spores with spore wall formed by a variable number of layers all originating from the subtending hyphae, no germinal walls differentiated. Germination through the lumen of the subtending hyphae or through the spore wall.

Acaulospora: Spores formed laterally from the neck of a sporiferous saccule which leaves one scar on the spore surface. Vesicles vary in shape with knobs and concavities. Intraradical hyphae straight or coiled near the entry points. Mycorrhiza stains weakly. Arbuscules with flared or cylindrical trunks with incremental narrowing of branch hyphae. Spores with spore wall formed by three layers and two inner germinal walls each with two thin layers that can be adherent. The innermost germinal wall has a beaded surface. Germination through a flexible, plate like germination orb.

Entrophospora: Spores formed within the neck of a sporiferous saccule which leaves two scars on the spore surface. Vesicles, arbuscules, intraradical hyphae and mycorrhizae staining as in *Acaulospora*. Spores with spore wall formed by two layers. Other spore subcellular structures and germination identical to that in *Acaulospora*.

Gigaspora: Spores formed terminally on a bulbous sporogenous cell; auxiliary cells finely papillate or echinulate. No vesicles produced. Intraradical hyphae frequently coiled, especially near entry points, often knobby or with projections. Arbuscules with swollen trunks with abrupt narrowing of branch hyphae. Spores with spore wall formed by two permanent layers, no inner germinal walls differentiated. At germination, a thin layer interspersed with warts differentiate and germ tube grows throughout the spore wall.

Scutellospora: Spores formed terminally on a bulbous sporogenous cell; auxiliary cells almost smooth to knobby. No vesicles produced. Arbuscules and intraradical hyphae similar in morphology to *Gigaspora*. Spores with spore wall formed by two permanent layers and 1-3 inner germinal walls, each with two layers. Germ tube grows from flexible, plate- like germination shield that differentiates on the surface of the last germinal wall.

CONCLUSIONS

Taxonomic and systematic studies of AMF can be traced back to the early works of the Tulasne brothers (1845) and the Thaxter (1922) revision of *Endogonaceae*. In the last 45 years, the classification of this group of fungi has undergone considerable transformations, from being merely descriptive and based solely on spore morphology (Gerdemann and Trappe, 1974) to being based on cladistic analysis of genetic and phenotypic characters. Morton and Benny's (1990) classification is based on the analysis of phenotypic characters (spore morphology and mycorrhizal characters), classifications of Schüßler *et al*. (2001), that of Schüßler and Walker (2010) on genetic characters (sequence variation of the SSU rDNA), and that of Oehl *et al.* (2011) on combined genetic and phenotypic characters. Up to 2001, these fungi were included in one class, one order, three families, and six genera; 10 years later, with the use of genetic characters, they are distributed into one to three classes, four to five orders, 11-14 families, and 18-29 genera depending on the classification scheme followed (**Table 1**). Though some emendations to the classification of AMF (Redecker *et al*., 2013) has come from time to time; Schüßler et al. (2001) classification has been generally accepted by mycorrhiza researchers and mycologists. This classification is valid till today as evidenced by Hibbett *et al*. (2007) in their comprehensive phylogenetic classification of the kingdom Fungi. Identification of AMF can be done by referring to the "Manual for the Identification of VAM Fungi" by Schenck and Perez (1990) and the INVAM website by Joe Morton. http://invam.caf.wvu.edu.

Table 1: Proposals of classification of glomeromycotan fungi within the kingdom Fungi

Phylum	Class	Order	Family	Genera
Gerdemann and Trappe (1974)				
Zygomycota	*Zygomycetes*	*Endogonales*	*Endogonaceae*	*Glomus* *Sclerocystis* *Acaulospora* *Gigaspora*
Morton and Benny (1990)				
Zygomycota	*Zygomycetes*	*Glomerales*	*Glomeraceae*	*Glomus* *Sclerocystis*
			Acaulosporaceae	*Acaulospora* *Entrophospora*
			Gigasporaceae	*Gigaspora* *Scutellospora*
Schüßler *et al.* (2001)				
Glomeromycota	*Glomeromycetes*	*Glomerales*	*Glomeraceae*	*Glomus*
		Diversisporales	*Gigasporaceae*	*Gigaspora* *Scutellospora*
			Acaulosporaceae	*Acaulospora* *Entrophospora*
			Diversisporaceae	*Diversispora*
		Paraglomerales	*Paraglomeraceae*	*Paraglomus*
		Archaeosporales	*Archaeosporaceae*	*Archaeospora*
			Geosiphonaceae	*Geosiphon*
Schüßler and Walker (2010)				
Glomeromycota	*Glomeromycetes*	*Glomerales*	*Glomeraceae*	*Glomus* *Funneliformis* *Sclerocystis* *Rhizophagus*
			Claroideoglomeraceae	*Claroideoglomus*
		Diversisporales	*Gigasporaceae*	*Gigaspora* *Racocetra* *Scutellospora*
			Acaulosporaceae	*Acaulospora*
			Entrophosporaceae	*Entrophospora*
			Pacisporaceae	*Pacispora*
			Diversisporaceae	*Diversispora* *Otospora* *Redeckera*
		Paraglomerales	*Paraglomeraceae*	*Paraglomus*
		Archaeosporales	*Archaeosporaceae*	*Archaeospora*
			Ambisporaceae	*Ambispora*
			Geosiphonaceae	*Geosiphon*
Oehl *et al*. (2011)				
Glomeromycota	*Glomeromycetes*	*Glomerales*	*Glomeraceae*	*Glomus* *Funneliformis* *Simiglomus* *Septoglomus*
			Claroideoglomeraceae	*Claroideoglomus* *Viscospora*
		Diversisporales	*Diversisporaceae*	*Diversispora* *Redeckera* *Otospora*
			Entrophosporaceae	*Entrophospora*
			Acaulosporaceae	*Acaulospora* *Kuklospora*
			Pacisporaceae	*Pacispora*
		Gigasporales	*Gigasporaceae*	*Gigaspora*
			Scutellosporaceae	*Scutellospora* *Orbispora*
			Racocetraceae	*Racocetra* *Cetraspora*
			Dentiscutataceae	*Dentiscutata* *Fuscutata* *Quatunica*
	Archaeosporomycetes	*Archaeosporales*	*Archaeosporaceae*	*Archaeospora* *Intraspora*
			Ambisporaceae	*Ambispora*
			Geosiphonaceae	*Geosiphon*
	Paraglomeromycetes	*Paraglomerales*	*Paraglomeraceae*	*Paraglomus*

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