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## **TAXONOMY OF PHYLUM GLOMEROMYCOTA: HISTORICAL PERSPECTIVE AND RECENT ADVANCES**

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### **Abstract**

Arbuscular mycorrhizal (AM) fungi, a major component of soil microbial community, forms symbiotic association with the roots of more than 90% of terrestrial plants. Arbuscular mycorrhizal colonization has also been reported in hepatics and hornworts. Fossil records indicate that the AM fungi may have played an important role in the success of early terrestrial plants. Arbuscular mycorrhizal fungi play a very important role in the improvement of plant growth. They are vital for the uptake and accumulation of ions from the soil and their translocation to the hosts because of their high metabolic rate and strategically diffuse distribution in the upper layers.

Since molecular methods have been used to elucidate the phylogenetic relationships among these fungi, their classification has been in a rapid transition. Molecular field studies have also revealed a large number of putative new species. Presently, the AM fungi are placed in the phylum Glomeromycota, which currently comprises of approximately 150 described species distributed among 10 genera. With the exception of genus *Geosiphon*, remaining all are exclusively mycorrhizal.

### **Introduction**

Arbuscular mycorrhizae (AM) are the most common type of mycorrhizae present in nearly 90% of all plant families. Only in the last few decades have botanists and mycologists realized that most terrestrial plants live in symbiosis with soil fungi (Mosse, 1956). Arbuscular mycorrhizas may have been described as early as 1842 (Nageli, 1842), but most of Nageli's drawings only remotely resemble the arbuscular mycorrhiza.

Frank (1887) was fairly certain that these symbiotic plant-fungus associations were required for the nutrition of both partners. Studies carried out by Schlicht (1889), Dangeard (1896), Janse (1897), Petri (1903), Gallaud (1905), Peyronel (1924), Jones (1924) and Lohman (1927) provided detailed description of endomycorrhizal fungi other than those found in Ericales and orchids (now known as arbuscular mycorrhizal fungi). As early as 1889, Schlicht had already observed the basic anatomical relationships between host and fungal tissues. Janse (1897) called the intramatrical spores "v\_sicules" and determined that other structures, named "arbuscules" by Gallaud (1905), were located in the inner cortex. Gallaud (1905) made very accurate observations of the arbuscule and concluded that it is entirely surrounded by a host membrane. He also noted that partial digestion of the arbuscule resulted in a structure called

the “sporangiole” by Janse (1897). These observations were later confirmed (Cox and Sanders 1974). Gallaud (1905) further distinguished between *Arum* and *Paris* types of arbuscules. Many herbaceous plants exhibit the *Arum* type of colonization, which involves extensive intercellular growth of the fungus as it penetrates the root cortex, followed later in the colonization by formation of arbuscules. In *Paris* type of colonization growth into the root is slow, being primarily intra-cellular, and the fungus coils inside each cell with rare or minimally structured arbuscules (Gallaud, 1905). Jones (1924) described the appressorium, which are hyphal swellings between two adjacent root epidermal cells. These are sites where hyphae first penetrate root cells by exerting pressure and/or enzymatic activity.

More recently, mycorrhizas have been defined as associations between fungal hyphae and organs of higher plants concerned with absorption of substances from the soil (Harley and Smith, 1983). Most mycorrhizal associations occur in roots, which evolved to house fungi (Brundrett, 2002), but they also occur in the subterranean stems of certain plants and the thallus of bryophytes (Rodrigues, 1995 & 1996; Smith and Read, 1997; Read *et al.*, 2000). A new, broader definition of mycorrhizas that embraces the full diversity of mycorrhizas (while excluding all other plant-fungus associations) has been put forth recently by Brundrett (2004). He defines mycorrhizas as a symbiotic association essential for one or both partners, between a fungus (specialized for life in soils and plants) and a root (or other substrate-contacting organ) of a living plant that is primarily responsible for nutrient transfer. Mycorrhizas occur in a specialized plant organ where intimate contact results from synchronized plant-fungus development.

It is now evident that the AM fungi originated more than 460 million years ago (Redecker *et al.*, 2000). These fungi may have played a crucial role in facilitating the colonization of land by plants. These fossilized fungal hyphae and spores strongly resembled modern AM fungi. This evidence indicates that AM fungi represent an ancient phylogenetic clade within the fungi. Until recently there was confusion about their monophyly (Morton, 2000). However, the later studies have clearly indicated that they belong to a distinct monophyletic group quite separate from other fungi (Schüßler *et al.*, 2001).

Taxonomy is an essential subdivision of the biological sciences. The AM fungal taxonomy has advanced greatly during the last three decades. This paper gives an overview of the taxonomic advances in Arbuscular mycorrhizal (AM) fungi over the years. It also gives an account of the various characters, which aid in the identification of these fungi.

### **Characters used for identification of arbuscular mycorrhizal fungi:**

Various morphological characters play an important role in establishing the taxonomic identity and relationships of AM species and thus aids in the construction of a workable system of classification. Hence, undoubtedly, certain characters will be of greater importance than others. Various morphological characteristics used for the identification of AM fungi are listed (**Table 1**) and described below:

**Table 1: Various morphological characters of spores used for identification of AM fungi.**

<b>Morphological characters</b>	
Sporocarp morphology	Size, Shape, Peridium.
Spore morphology	Colour, Shape, Size, Content.
Subtending hyphae	Shape, Width, Pore Occlusion.
Auxiliary Cells	Ornamentation.
Mycorrhizal Anatomy	Hyphal characters, Intraradical spores.
Spore wall structure	Colour, Dimension, Number, Type, Ornamentation, Reaction.
Spore Germination	Direct, Indirect.

**1. Sporocarp morphology**– The sporocarpic species produce spores in a loose arrangement or in a highly ordered arrangement around a hyphal plexus (Gerdemann and Trappe, 1974). The sporocarps may be formed in soil, root, empty seed coats, insect carapaces or rhizomes. *Glomus* species form single spores 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 loosely or compact interwoven hyphae, a patchy covering over the sporocarps or as 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. Sporocarps are not known in *Entrophospora*, *Gigaspora* and *Scutellospora* (Ames and Schneider, 1979; Berch, 1985; Walker and Sanders, 1986). Sporocarps are also typically absent in *Acaulospora* with the exception of *Acaulospora myriocarpa* wherein the spores are in a cluster (Schenck *et al.*, 1986) and *A. sporocarpa* that has an aggregation of spores in a network of hyphae (Berch, 1985). External sporocarp colour range from white to brown, while the internal sporocarp colour range from white to black and brown.

**2. Spore morphology** – Spores in the soil may be produced terminally, laterally on subtending hyphae or on a single suspensor-like cell. Characters such as spore colour, shape and size may vary considerably depending on the developmental stage and environmental conditions. Spore colour varies from hyaline to white to yellow, red, brown and black with all intermediate shades. The difference in colour may be due to pigmentation in spore wall or in the spore content (Morton, 1988).

Morton (1988) suggested that variation in spore shape might be due to the result of environmental stress. 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 the

extraradical spores may be globose, sub globose, ellipsoidal, oblong 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  $\mu\text{m}$ , while in contrast, *Gigaspora gigantea* is the largest spore with dimensions ranging from 183-500 x 291-812 $\mu\text{m}$ . Spore size varies considerably within the same species and hence both immature and mature spores are taken into account while describing the species.

**3. Subtending hyphae** – At generic level of classification, the shape of the subtending hyphae or the sporophore assumes great importance. The subtending hyphae may be simple to recurved or sometimes swollen in *Glomus* species. The sporophore in *Gigaspora* and *Scutellospora* is bulbous and bears one or more peg like hypha. During extractions from the soil, sporophore may get detached from the spore, but the bulbous structure continues with the wall of the spore (Walker, 1992) and usually remains attached to the spore. In *Entrophospora*, the sporophore is swollen and straight but at times may be totally absent due to a detachment close to the spore. Sometimes, the spores are sessile or may bear small pedicel as in *Acaulospora*. The width of the hyphae varies considerably within different genera and species of AM fungi.

The mechanism of pore 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.

**4. Auxiliary cells** – The size and the shape of the auxiliary cells have been found to be of little importance in differentiating species of *Gigaspora* or *Scutellospora*. In *Gigaspora*, the auxiliary cells are echinulate with spines that are forked dichotomously (Bentivenga and Morton, 1995), whereas in *Scutellospora*, the projections on the surface of the auxiliary cells are highly variable in shape and size (Morton, 1995).

**5. Mycorrhizal anatomy** – Generally, fungal anatomy in roots is not used in taxonomic descriptions to separate taxa below the generic level. Colonization of the root with AM fungi initiates a series of developmental processes culminating in a morphologically and functionally unique symbiosis. Arbuscular mycorrhizal fungal hyphae penetrate host roots through the epidermis. The hyphae grow inter- and intra-cellularly in the cortical cells (Mosse, 1973). The hyphae from intercellular lateral branches penetrate the cell walls and form a branching, tree-like structure termed as ‘arbuscule’ inside the cell lumen, and the plant invaginates the plasma membrane, matching the branching pattern of the fungus. The resulting dendritic structure has a large membrane surface area, and these membrane interfaces are where nutrient transfer between plant and fungus occurs. It is possible to differentiate among certain AM fungi, using visual

differences in morphology of fungal hyphae and vesicles within roots (Abbott and Gazey, 1994). Harley and Smith (1983) suggested that vesicles might perform the function of storage because lipids and glycolipids are the most abundant substances in them. Biermann and Linderman (1983) thought that intraradical vesicles in some species of AM fungi act as propagules and contribute significantly to the colonization of other roots.

It has been suggested that certain hyphal characters such as long infection units with 'H' connections between parallel strands of hyphae in *Glomus* (Abbott and Robson, 1979), pale staining of intraradical hyphae by trypan blue in *Acaulospora* (Bentivenga and Morton, 1995), constrictions near branch points in hyphae of *Acaulospora* and *Entrophospora*, and coiled, irregularly swollen hyphae with lateral projections or knots in *Gigaspora* or *Scutellospora* may be utilized as diagnostic features to identify genera in mycorrhizal roots (Morton and Bentivenga, 1994). Intraradical spores in Glomaceae usually are globose, subglobose to elliptical, whereas those in *Acaulospora* are pleomorphic, knobby and stain lightly in trypan blue. Morton (1988) hypothesized that either the host or environmental factors may cause variations in morphological structures. Abbott and Robson (1978) concluded that the anatomy of AM fungi formed by a particular endophyte species grown under a range of conditions may not be as variable as has been generally assumed. Abbott (1982) developed a key for 10 AM fungal species using 20 characteristics (based entirely on the morphological anatomy of hyphal development) such as hyphal diameter, mode of branching, vesicles, arbuscules, staining reactions, *etc.* and concluded that these characteristics are stable in different hosts and soil environments.

**6. Spore wall structure** – Spore wall characteristics have been universally accepted as more stable and reliable criteria than other spore features (Mehrotra, 1997). A spore wall has been defined as the first individual structure formed, originating from the wall of sporogenous hypha and differentiating into phenotypically distinctive layers (Morton *et al.*, 1995). Spore wall characteristics became the important morphological characteristic after Walker (1983) developed the concept of "wall groups" He defined a wall group as "an aggregation of walls that are either adherent, or that remain close together when a spore is crushed" and suggested the use of standard terminology and wall micrographs. This concept proved to be a subject of much variation and interpretation because the degree of separation was often influenced greatly by condition of the spores (fresh, fixed, parasitized, aged), amount of pressure applied to a spore when it is crushed on a slide, and the type of mounting media used. In all, eight-wall layer types *viz.*, evanescent, laminated, membranous, unit (Walker, 1983), expanding (Berch and Koske, 1986), coriaceous (Walker, 1986), amorphous (Morton, 1986) and germinal (Spain *et al.*, 1989) have been described so far. They are distinguished mainly on the basis of their morphological features and their reaction to certain chemicals such as lactophenol and Melzer's reagent.

The number, width and position of wall layers differ among species and they have been increasingly relied upon for identification purposes. Differentiation of sub-cellular morphological characters in spores of *Gigaspora* (Bentivenga and Morton, 1995) and *Scutellospora* species (Morton, 1995) are used for identification. Ornamentation on the spore wall layer appears to be an important taxonomic criterion in identification of species, especially when other morphological characters are overlapping.

**7. Spore germination** – Ultrastructural studies of spore germination processes may play a role in the identification of AM fungal species. Spores of glomalean fungi have all the necessary metabolic constituents and genetic information to germinate and produce new hyphae (Sequeira *et al.*, 1985), although they cannot continue to grow without a host. However, spore germination in AM fungi has been studied in only a few species. Two methods of spore germination is known to exist in the Glomales *viz.*, a. Direct germination takes place when 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. This type of germination has been observed in *Glomus* and *Gigaspora*. b. Indirect germination takes place by the development of “germination shield” prior to emergence of germ tube. This type of germination is known to occur in *Acaulospora*, *Entrophospora* and *Scutellospora*. In *Acaulospora leavis* the germination shields are difficult to see and many a times are not observed because of the kinds of mountants used to prepare permanent slides (Spain, 1992). Even though in *Acaulospora* and *Scutellospora*, the germination shields are formed in the same way, the wall types associated with germination differ. In Acaulosporaceae, the germination shield is formed on an innermost flexible wall that has beaded layer while in *Scutellospora*, it is formed on the innermost flexible wall with a coriaceous layer (Spain, 1992; Frank and Morton, 1994).

#### **Taxonomy of Arbuscular Mycorrhizal (AM) Fungi:**

The term mycorrhiza, created to reflect this reality, comes to us, moreover, from the combination of two words, one Greek “mikes” (fungus) and the other Latin “rhiza” (roots). Traditionally, Albert Bernhard Frank (1885), a German botanist introduced the word “Mycorrhiza”. It was Kelley (1931, 1950) who incorporated the second ‘r’ to the word “mycorrhiza”. Later Frank (1887) distinguished between ectomycorrhiza and endomycorrhiza on the basis of his studies carried out on Cupuliferae for the former on Ericales and orchids for the later.

The nomenclature of arbuscular mycorrhizae has changed over the last three decades. Currently, many researchers refer to them as arbuscular mycorrhizae (AM) as not all these fungi form vesicles. However, in some of the associations involving these fungi may not even produce proper arbuscules (Smith and Smith, 1997). They are also commonly referred to as vesicular arbuscular mycorrhizae (VAM), and in the older literature, they may be referred to as endomycorrhizae.

#### a. History of the group:

The history of members of Glomales is long and convoluted. German mycologist, Link (1809) established the genus *Endogone*. Tulasne and Tulasne (1845) were the first to describe the genus *Glomus* then comprising of two species viz., *Glomus microcarpum* and *G. macrocarpum* known only from spore clusters found in the soil. They considered *Glomus* to be closely related to *Endogone*. Dangeard (1896) for the first time described arbuscular mycorrhiza formed from popular roots. He regarded this as a disease and named the fungus as *Rhizophagus populinus* and placed it in Chytridales.

Fries (1849) established the family Endogonaceae and placed it in the Tuberales, which as later transferred to the Mucorales by Bucholtz (1912) due to the affinities of *Endogone* with members of the Mortierellaceae. The genus *Sclerocystis* was first described by Berkeley and Broome (1875). Thaxter (1922) revised the family Endogonaceae and placed all members of *Glomus* in the genus *Endogone*, while maintaining the genus *Sclerocystis*. The family Endogonaceae was placed in its own order, Endogonales by Moreau (1953), which was later, validated to class Zygomycetes (Benjamin, 1979). The characteristic features of AM fungi that prompted mycorrhizologists to place them in the class Zygomycetes include:

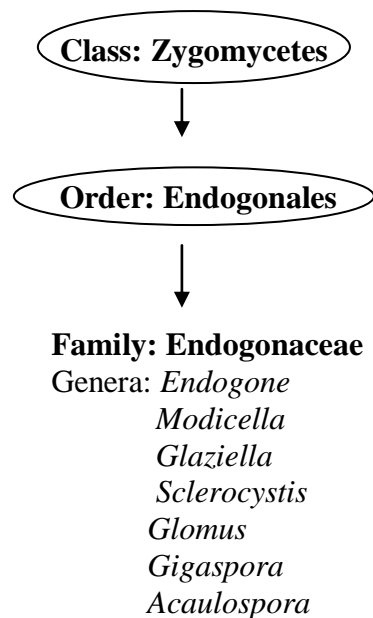
- a. The presence of chitin in the cell wall (Weijman and Meuzelaar, 1979; Bonfante-Fasolo *et al.*, 1990).
- b. Presence of nonseptate and coenocytic mycelium.
- c. Formation of non-motile spores, the chlamydospores.
- d. Formation of putative zygospores in *Gigaspora decipiens* (Tommerup and Sivasithamparam, 1990).
- e. Features of nuclei in spores similar to the spores of other Zygomycetous fungi (Maia, 1991).

Mosse and Bowen (1968) did not use the production of sporocarps as a major characteristic, instead considered the developmental stages of spores as major characteristics. Nicolson and Gerdeman (1968) divided the fungi into two groups of *Endogone* viz., one forming extrametrical azygospores/zygospores arising from the tip of a swollen hyphal suspensor but producing number of intramatrical vesicles, and the other forming extrametrical chlamydospores and intramatrical vesicles.

Gerdemann and Trappe (1974) suggested a division of *Endogone*, the largest and most heterogenous genus in the family Endogonaceae, into seven genera (**Table 2**). Of these, three genera do not form mycorrhizal associations. These include the genus *Endogone* that is known to form putative ectomycorrhizal associations (Chu-Chou and Grace, 1979). It produces zygospores and have saprobic mode of nutrition and is retained in the order Endogonales with the sole family Endogonaceae. Mehrotra and Bajjal (1994) suggested that Endogonales need not be retained as a separate order and the only genus *Endogone* be transferred to the order Mucorales as the formation of zygospores in *Endogone* is somewhat similar to that formed by the members of the order Mucorales. The phylogenetic analysis of the nuclear small subunit ribosomal

RNA strongly suggests that *Endogone* (Endogonales) and the Glomeromycota do not form a clade (Gehrig *et al.*, 1996). The genus *Modicella* produces thin-walled sporangia and, the genus *Glaziella*. Trappe and Schenck (1982) transferred the genus *Modicella* to the family Mortierellaceae in the order Mucorales of the Zygomycetes. Similarly, the teleomorphic stage of *Glaziella* was found to be an Ascomycete and hence the entire genus *Glaziella* was transferred to the Ascomycetes in a new family, Glaziellaceae and a new order, Glaziellales (Gibson *et al.*, 1986). The remaining four genera form mycorrhizal associations. These include *Glomus*, *Gigaspora*, *Acaulospora* and *Entrophospora*. The genus *Glomus* produces sporocarpic and non-sporocarpic chlamydospores. They also described the genera *Acaulospora* and *Gigaspora*. The genus *Gigaspora*, is nonsporocarpic, and produce azygospores while *Acaulospora* is characterized by non-sporocarpic producing spores that were borne singly and laterally on a hypha, which terminates in a large thin-walled vesicles and formed mycorrhizal associations. Ames and Schneider (1979) described the genus *Entrophospora*. They transferred *Glomus infrequens* into the new genus *Entrophospora* and called it *E. infrequens*, as the fungal spores were unlike any other described species in the Endogonaceae.

**Table 2: Classification of endomycorrhizal fungi (Gerdemann and Trappe, 1974).**

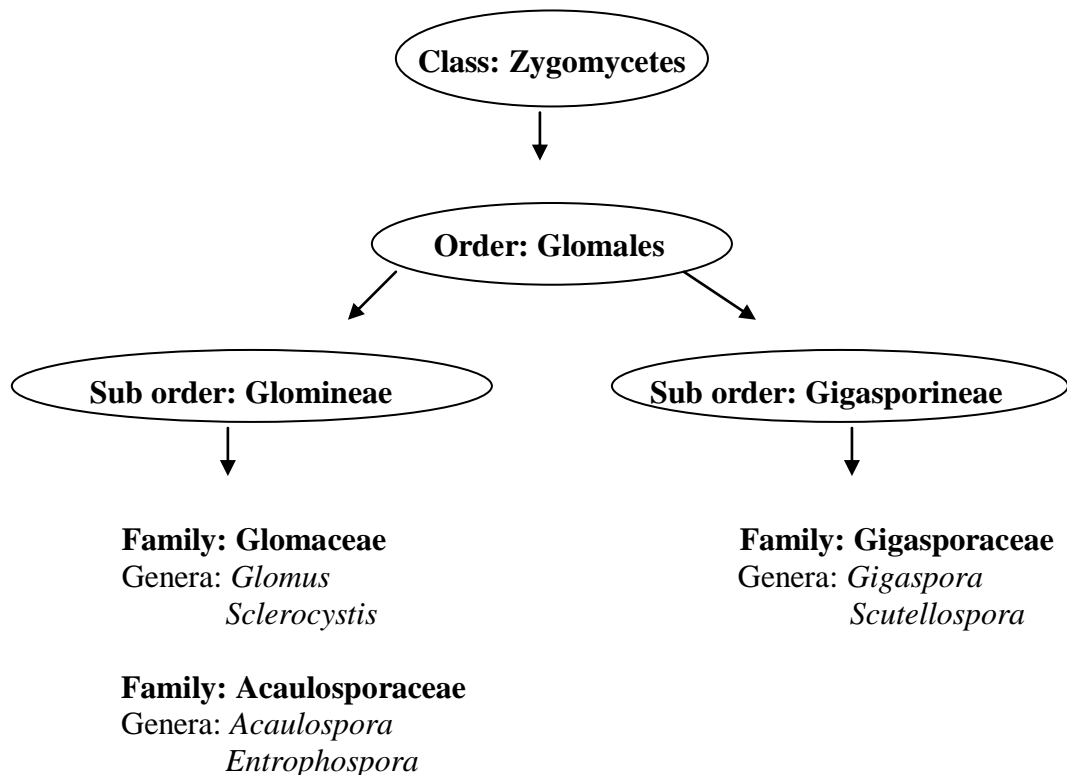


The genus *Gigaspora* was split into two genera *viz.*, *Gigaspora* and *Scutellospora* (Walker and Sanders, 1986). The creation of new genus *Scutellospora* was based on details of spore germination, spore wall structures and morphology of auxiliary cells. Morton and Benny (1990) erected the order Glomales that is characterized by the unique ability of its members to form



arbuscular mycorrhizae in mutualistic symbiosis with living plants. The order Glomales, includes two suborders *viz.*, the Glomineae, which is characterized by the presence of arbuscules and vesicles in the roots and formation of chlamydospores (thick wall, asexual spores) borne from subtending hyphae and, Gigasporineae, which is characterized by the absence of vesicles in the roots and formation of auxiliary cells and azygospores (spores resembling a zygospore but developing asexually from a subtending hypha resulting in a distinct bulbous attachment) in the soil. The suborder Glomineae was separated into two families *viz.*, the Glomaceae (Pirozynski and Dalpe, 1989) and Acaulosporaceae (Morton and Benny, 1990), while the suborder Gigasporineae contains the sole family Gigasporaceae (**Table 3**). All these families were characterized by the mode of spore formation and were initially supported by molecular data (Simon *et al.*, 1993).

**Table 3: Classification of AM fungi (Morton and Benny, 1990).**



The family Glomaceae consisted of two genera *viz.*, *Glomus* and *Sclerocystis*. In *Glomus*, spores are globose to ellipsoidal, thick walled hyaline to black, usually attached to single subtending hypha. Spores germinate by germ tube through subtending hypha. While in *Sclerocystis*, spores are similar to *Glomus* except they are clavate in shape and are arranged in a sporocarp.

The members of family Acaulosporaceae develop spores from or within neck of sporiferous saccule while the members of the family Gigasporaceae produce large azygospores with bulbous base. Germination of the spores is either through the production of germ tube through the cell wall or from the germination shield. They do not produce vesicles but produce auxiliary cells in the soil.

The family Acaulosporaceae consisted of two genera viz., *Acaulospora* and *Entrophospora*. In both the genera spores are large (up to 600 µm) with a typical bulbous base with characteristic lateral projections. The genus *Acaulospora* is characterized by spores that are formed laterally on the neck of a small thin walled saccule. Whereas the genus *Entrophospora* differs from *Acaulospora* as in the former the spores are formed inside the parent hypha just below the sporiferous saccule. The family Gigasporaceae consisted of two genera viz., *Gigaspora* and *Scutellospora*. Species of *Gigaspora* and *Scutellospora* form large spores in the soil. Spores are produced terminally on a single, bulbous-shaped subtending hypha, termed as bulbous suspensor (Morton, 1988). The subtending hypha has one or more small lateral projections pointing towards and sometimes in contact with the outer surface of the spore wall. The function of these small lateral projections is not known. Gerdemann and Trappe (1968) used the term azygospore to describe spores in *Gigaspora* because of the similarity of the single subtending hypha to a gametangium in *Endogone*. There is no evidence that spore development in *Gigaspora* or *Scutellospora* is parthenogenic or that development evolved from zygosporangia via the reduction of one of a pair of gametangia (Powell and Bagyaraj, 1984). In *Gigaspora*, germ tube develops directly from the spores while in *Scutellospora* the germ tube emerges from germination shields formed in between outer and inner cell walls (Morton and Benny, 1990).

*Acaulospora* and *Entrophospora* tend to form spores associated with a small hyphal chamber. Spores in *Acaulospora* are formed laterally on the stalk in a large terminal and thin walled hyphal chamber (Berch, 1985). The spores are hyaline, yellow to reddish brown, globose to ellipsoid with spore wall ornamentation. However, in *Entrophospora*, spores are produced completely within the neck of the hyphal chamber (Ames and Schneider, 1979). The small chamber in *Acaulospora* and *Entrophospora* has been variedly named such as a mother spore (Mosse, 1970), a vesicle (Gerdemann and Trappe, 1974), a hyphal terminus (Schenck *et al.*, 1984), a sporiferous saccule (Walker *et al.*, 1984), a sporogenous saccule (Berch, 1985) or a swollen sac (Morton, 1988). Microscopic examination indicates that spores in *Acaulospora* species may not develop from the side of the chamber neck. Spores develop within a lateral swelling of the chamber neck since the outer wall of the spore may be continuous with the wall of the chamber itself (Walker *et al.*, 1984). Berch (1986) first used the term “sporogenous vesicle” to describe the hyphal swelling associated with spores of *Entrophospora*. Walker (1987) suggested that the so-called azygospores in *Acaulospora* are sporangiospores and the saccule is a sporangium.

**a. Recent advances in taxonomy:**

The genus, *Glomites* was erected by Taylor *et al.*, (1995) to describe fossil fungi that closely resemble modern day *Glomus* species. The genus *Gigaspora* was re-described by Bentivenga and Morton (1995) incorporating developmental patterns of morphological characters.

The separation between *Glomus* and *Sclerocystis* became controversial in the early 1990's. Almeida and Schenck (1990) placed all *Sclerocystis* species in *Glomus* with the exception of *S. coremioides*. They were of the opinion that an unbroken continuum of morphological characters existed between sporocarpic *Glomus* species and all the *Sclerocystis* species except one (*S. coremioides*). Almeida and Schenck (1990) considered *S. coremioides* unique and therefore separated from the *Glomus* clade based on following four morphological traits:

- a. Spore formation on separate subtending hyphae rather than from branching sporophores.
- b. A well-defined septum at the same position near the spore base.
- c. Arrangement of spores in hemispherical layer.
- d. New sporocarps formed from older sporocarps to often fuse into columns.

Wu (1993) resisted this change on the basis of comparative studies of spore ontogeny and sporocarps morphology of the *Sclerocystis* species carried out to show that the above mentioned traits were shared to varying degrees by other *Sclerocystis* species. Wu (1993) hypothesized a model of a smooth evolutionary transition between relatively unorganized, *Glomus*-like sporocarps of *S. rubiformis* and intermediate forms like *S. clavisporea*, *S. liquidambaris* and *S. sinuosa* to *S. coremioides*. He concluded that *S. coremioides* was not unique. These series of transformations led Wu (1993) to reject the changes of Almeida and Schenck (1990) and revert to Gerdemann and Trappe's (1974) classification scheme. Wu's rationale for genus-level separation, based on ontogeny of sporogenesis and sporocarp formation, was not convincing. Later Redecker *et al.*, (2000a) carried out phylogenetic analysis of the 18S ribosomal subunit of *Glomus sinuosum* (= *S. sinuosa*) and *S. coremioides* which revealed that both species are each other's closest relatives and fall within a monophyletic clade comprising the well characterized species, *Glomus mosseae*, *G. intraradices* and *G. versiculiferum*, to the exclusion of several other *Glomus* species. Their study indicated that formation of complex sporocarps is an advanced character of some *Glomus* species, but the sporocarpic trait is not sufficiently unique to group these species into a separate genus *Sclerocystis*.

Later it was clear that the mode of spore formation is not a useful diagnostic feature for some genera. A number of AM fungal species in *Glomus* (Glomaceae) and *Acaulospora* (Acaulosporaceae) have not fit easily into family or genus definitions (Morton and Benny, 1990). Spores of *Glomus* and *Acaulospora* types were reported to be produced by several distinct, deeply divergent lineages (Redecker *et al.*, 2000a). Subsequently, Morton and Redecker (2001) erected two new families *viz.*, Archaeosporaceae and Paraglomaceae. This work was based on combination of 18S rDNA sequences, fatty acid profiles, immunological reactions against specific antibodies, and mycorrhizal

morphology. On the basis of type specimens, culture manipulations (Morton *et al.*, 1997) and rDNA sequence data (Redecker *et al.*, 2000a, Sawaki *et al.*, 1998), the two AM species *viz.*, *Acaulospora gerdemannii* and *Glomus leptotichum* were found to be synanamorphs of the same organism. Similarly, *Glomus gerdemannii* also proved to be dimorphic in monospecific pot cultures and both spore morphotypes bore striking resemblance to synanamorph of *Acaulospora gerdemannii*/*Glomus leptotichum* (Morton and Redecker, 2001). Root colonization by *Glomus occultum* is so faint that roots often appear to be nonmycorrhizal, despite of abundant sporulation (Morton, 1985). Similarly, root colonization by *Glomus brasilianum* and *Acaulospora trappei* also show faint staining, but both show abundant sporulation. *Glomus brasilianum* is almost indistinguishable from *Glomus occultum* when observed under a dissecting microscope, while *Acaulospora trappei* forms spores with a subcellular structure more like that of *Acaulospora gerdemannii* than other species of Acaulosporaceae. Nucleotide sequence data sets from ITS, 5.8S and 18S rDNA regions established that these species are more closely related to the dimorphic species than species in either Acaulosporaceae or Glomaceae and are grouped in two distinct clades (Redecker *et al.*, 2000a). One clade of species forming acaulosporoid spores *viz.*, *Acaulospora gerdemannii* (= *Glomus leptotichum*)/*Glomus gerdemannii* along with *Acaulospora trappei* defines the genus *Archaeospora* of the new family Archaeosporaceae, while the other clade of species forming only glomoid spores *viz.*, *Glomus occultum* and *Glomus brasilianum* is placed in the genus, *Paraglomus*, of the new family Paraglomaceae (Morton and Redecker, 2001).

Schüßler *et al.*, (2001) using molecular data elevated the group of arbuscular mycorrhizal fungi to the level of phylum (Glomeromycota), which was shown to have monophyletic origin. The endocytobiotic fungus *Geosiphon pyriformis* analysed phylogenetically by their small subunit (SSU) rRNA gene sequences was added to the Glomeromycota. They reported that Glomeromycota probably diverged from the same common ancestor as the Ascomycota and Basidiomycota. They also erected new orders *viz.*, Archaeosporales (Archaeosporaceae, Geosiphonaceae), Paraglomerales (Paraglomaceae) and Diversisporales (Acaulosporaceae, Diversisporaceae, Gigasporaceae), and Glomerales (Glomeraceae) with their respective families given in parenthesis. The most recent classification of AM fungi is given in **Table 4**.

*Geosiphon pyriforme* inhabiting the surface of humid soils in German fields represents the only known example of endocytobiosis between a fungus and cyanobacteria (Nostoc). Except for the genus *Geosiphon*, all the species included in the phylum Glomeromycota are exclusively mycorrhizal (Morton and Redecker, 2001, Redecker *et al.*, 2000). The cyanobacterium provides carbon and nitrogen to the fungus, as in a lichen (Gehrig *et al.*, 1996). Oddly, current molecular phylogenetic studies place *Geosiphon* inside the Glomalean clade, not in the outlying position that its wildly divergent anatomy and physiology would seem to indicate (Redecker *et al.*, 2000).

Schüßler *et al.*, (2003) corrected the formerly orthographically incorrect term Glomales to Glomerales, which represents one of the four orders within the

phylum Glomeromycota. *Glomus* groups A and B (as defined by Schwarzott *et al.*, 2001) are exemplified by the well-known species of *Glomus mosseae* and *Glomus claroideum*, respectively. These two groups are genetically relatively distant but still form a monophyletic group in rDNA phylogenetic trees.

**Table 4: Most recent classification of AM fungi (with *Glomus* subgroups as defined by Schwarzott *et al.*, 2001).**

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<b>Phylum: Glomeromycota</b>
<b>Class: Glomeromycetes</b>
<b>Order: Glomerales</b>
Family: Glomeraceae
Genus: <i>Glomus</i> (group A and B)
<b>Order: Diversisporales</b>
Family: Gigasporaceae
Genus: <i>Gigaspora</i>
<i>Scutellospora</i>
Family: Acaulosporaceae
Genus: <i>Acaulospora</i>
<i>Entrophospora</i>
Family: Pacisporaceae
Genus: <i>Pacispora</i>
Family: Diversisporaceae
Genus: <i>Diversispora</i>
<i>Glomus</i> (group C)
<b>Order: Paraglomales</b>
Family: Paraglomaceae
Genus: <i>Paraglomus</i>
<b>Order: Archaeosporales</b>
Family: Geosiphonaceae
Genus: <i>Geosiphon</i>
Family: Archaeosporaceae
Genus: <i>Archaeospora</i>

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rDNA phylogenies have shown that the genus *Glomus* is several times polyphyletic (Redecker *et al.*, 2000a; Schwarzott *et al.*, 2001). Oehl and Siverding (2004), erected a new genus *Pacispora*. According to them, it comprised of *Pacispora scintillans* (the type species) and *P. dominikii* (as a separate species) and *P. chimonobambusae*, all formerly placed in the genus *Glomus* of the Glomeraceae along with four newly identified species *viz.*, *P. franciscana*, *P. robigina*, *P. coralloidea* and *P. boliviana*. However, the morphological and molecular data presented by Walker *et al.*, (2004) show that the two names *viz.*, *Pacispora scintillans* and *P. dominikii* are synonyms. The

genus *Gerdemannia* published by Walker *et al.*, (2004) is a synonym of *Pacispora*, and is an illegitimate name based on the publication date.

The spores of the genus *Pacispora* are formed terminally on hyphae, a feature they share only with *Glomus* and *Paraglomus*. An inner, usually three-layered wall is present inside the spores, from which the spores germinate directly through the outer spore wall, which usually is also three-layered. This germination characteristic is shared with *Scutellospora*, *Acaulospora* and *Entrophospora* but not with *Glomus* and *Paraglomus*. The staining characteristics of the root internal fungal structures and the features of the subtending hyphae of the spores are most similar to species of the genus *Glomus*. All the *Pacispora* species can morphologically be differentiated by the spore surface structure, the characteristics of the spore wall ornamentation, and by the spore colour and spore size (Oehl and Siverding, 2004).

Similarly, another genus erected as a result of split off from *Glomus* is named *Diversispora*, which at present comprises of only one species *viz.*, *Diversispora spurcum* and its erection is mainly based on ribosomal small subunit sequence signatures (Walker and Schüßler, 2004).

Earlier, the ‘sporiferous saccule’ was thought to be characteristic feature of the family Acaulosporaceae (*Acaulospora* and *Entrophospora*), but now it is known to occur in at least one additional lineage *viz.*, *Archaeospora*.

The characteristic feature of the family Gigasporaceae (*Gigaspora* and *Scutellospora*) is the formation of spores on a “bulbous suspensor” which is well supported by molecular data. However, based on most rDNA sequence analysis, the families Gigasporaceae and Acaulosporaceae form a clade, which is conflicting with the earlier morphology that placed *Glomus* and Acaulosporaceae together in the sub order Glomineae (Morton and Benny, 1990). This amounts to not only just complete divergence in the process of spore formation and traits of inner wall development, but also in mycorrhizal structures, timing of their formation, infectivity of those structures, fatty acid profiles, cell wall chemistry, and even timing and abundance of transcript synthesis during spore germination. To resolve this conflict, besides the relationship from rDNA data, would also require congruence with other genes. Although additional genes have begun to be sequenced from some taxa (Helgason *et al.*, 2003; Corradi *et al.*, 2004), phylogenetic hypothesis based on multilocus DNA sequence data is yet to be incorporated in the classification.

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