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TAXONOMY OF AM FUNGI - AN UPDATE

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Introduction

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 also 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 200 described species distributed among 14 genera. With the exception of genus *Geosiphon*, remaining all are exclusively mycorrhizal. According to Morton *et al.* (1994), the number of species of this group of fungi may come upto 2700.

Morphological characters used for identification of AM 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 3)** and described below:

Table 3: Various morphological characters of spores used for identification of AM fungi.

Morphological characters	
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 caracaces 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 Otospora, *Entrophospora, Gigaspora, Rancocetra, Cetraspora, Dentiscutata, Fuscutata*, *Quatunica* and

Scutellospora (Ames and Schneider, 1979; Berch, 1985; Walker and Sanders, 1986; Oehl *et al*., 2006; Oehl *et al.*, 2008). 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 10-12µm, while in contrast, *Gigaspora gigantea* is the largest spore with dimensions ranging from 183-500 x 291-812µm. 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 or constricted at the point of attachment to the spore in *Glomus* species. The sporophore in *Gigaspora, Scutellospora, Rancocetra, Cetraspora, Dentiscutata, Fuscutata and Quatunica* is bulbous and bears one or more peg like hypha. During extractions from the soil, sporophore may detach from the spore, leaving the bulbous structure attached to the spore (Walker, 1992). 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* and *Entrophospora* or a distinct pedicel as in *Otospora*. 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

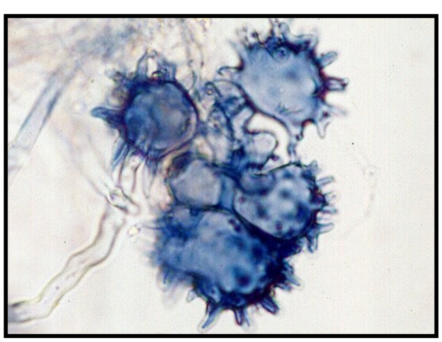

Plate 2f: Auxiliary cells of Gigaspora

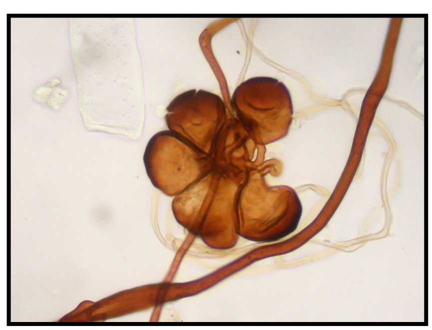

Plate 3a. Auxiliary cells in Scutellospora sp

The auxiliary cells are encountered in both roots **(Plate 2 f)** and soil **(Plate 3 a)**. The size and the shape of the auxiliary cells have been found to be important in differentiating species of *Gigaspora* from

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 knobby and highly variable in shape and size (Morton, 1995).

5. Mycorrhizal anatomy

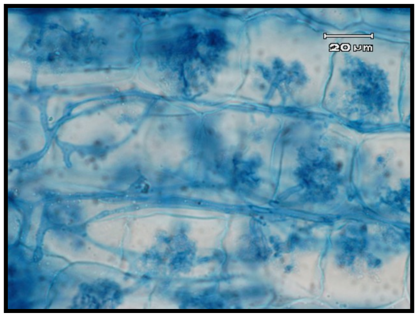

Plate 1c. Arum type of arbuscules

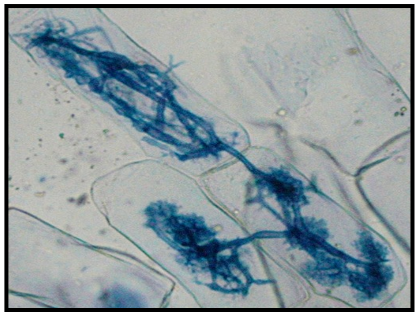

Plate 1d. Paris type of arbuscules

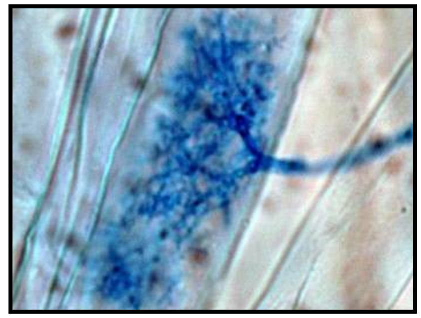

Plate 1e. Closer view of arbuscule

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 **(Plate 1 c, d & e)**, 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 **(Plate 1 f & Plate 2 a, b & c)**. 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 **(Plate 2 d & e)**.

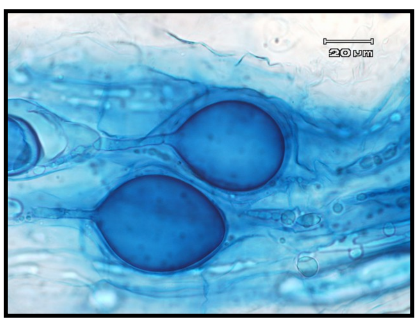

Plate 1f. Vesicular colonization

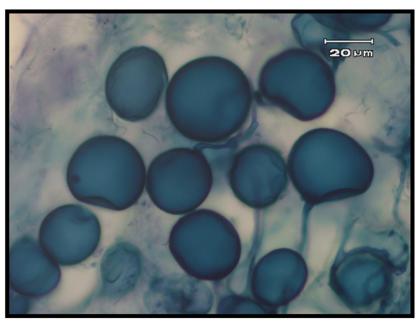

Plate 2a. Vesicular colonization

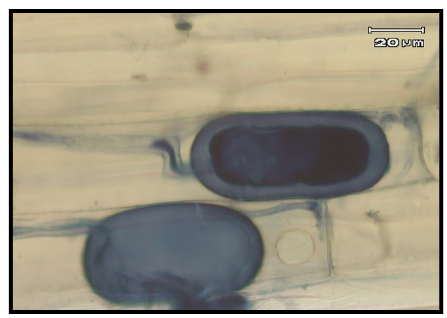

Plate 2b. Vesicular colonization

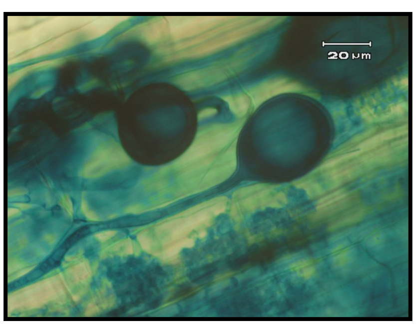

Plate 2c. Arbuscular & vesicular colonization

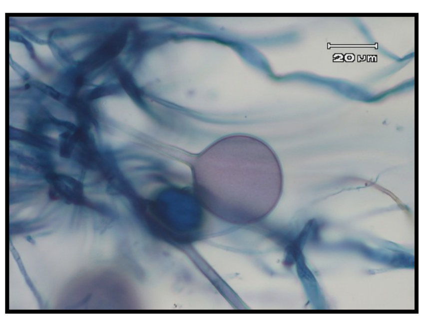

Plate 2d. Intra radical spores

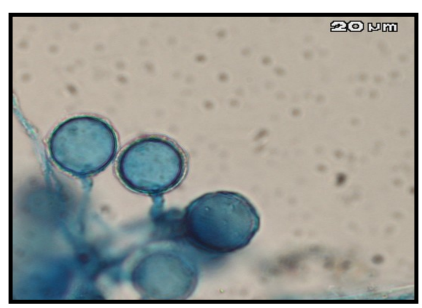

Plate 2e. Extra radical spores

It has been suggested that certain hyphal characters such as long infection units with 'H' connections between parallel strands of hyphae in *Glomus* **(Plate 1 a)** (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) **(Plate 1 b)**. 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 mycorrhiza 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.

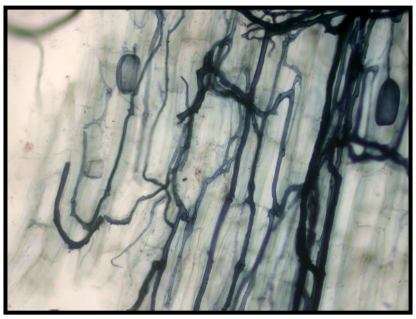

Plate 1a. Hyphal & vesicular colonization

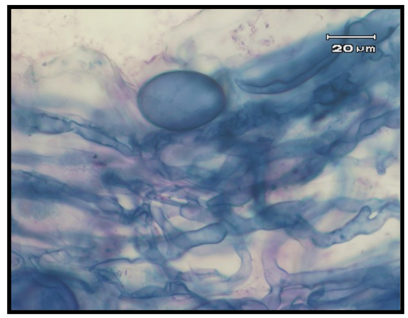

Plate 1b. Hyphal swelling & vesicle

6. Spore wall structure

The spore wall of AM fungi exhibit a unique array of wall layers which are taxonomically important as they are highly conserved and phenotypically stable in almost any environment. 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).

Every spore, irrespective of species, forms a spore wall (Morton, 2002). Besides the spore wall, all species of the genera *Acaulospora, Ambispora, Archaeospora, Centraspora, Dentiscutata*, *Entrophospora, Fuscutata*, *Gigaspora, Intraspora, Kuklospora, Pacispora, Quatunica*, *Racocetra,* and *Scutellospora* produce spores with 1-3 inner walls terms as "germinal walls". Exclusively in *Gigaspora* species, the germinal wall is physically associated with their spore wall. In rest of the genera, the germinal walls originate and functions independently of their spore wall.

In most juvenile spores, the spore wall may be 1 to 2 layered. However, the spore wall of most AM fungal species usually consist of at least two wall layers, while some species the spore wall differentiates upto 4 wall layers. In all AM fungal species, the spore wall layers originates successively towards the spore interior except in *Ambispora gerdimannii*, the inner spore wall layer is formed prior to the outer wall layer which originates *de novo* (Morton and Redecker 2001).

Walker (1983) organized the various discrete phenotypes of spore sub-cellular structures into wall classes and then depicted each wall in murograph form for standardization and ease of comparison. The muronym encodes the wall structure of a spore. This has been widely accepted and the terminology was expanded as new wall phenotypes were discovered (Walker, 1986). Walker (1983) defined a wall group was defined as "*an aggregation of walls that are either adherent, or that remain close together when a spore is crushed*". This concept of wall group proved to be subject to much variation and interpretation because the degree of wall separation is often influenced greatly by factors like: (a) spore condition (fresh, fixed, parasitized, aged), (b) amount of pressure applied during crushing (light, heavy, super-squashes), and (c) the type of mountant used.

The different wall types and the muronym codes (given in brackets) encountered in AM fungal spores are as follows.

1. **Amorphous (A)**: A formless, flexible wall whose elasticity is affected by the mountant. It appears rigid in water or glycerol; in acidic mountants (< pH 2) it is plastic and tends to collapse partially. The shape is maintained when attached to a more rigid wall.

2. **Coriaceous (C)** – a robust, tough but flexible inner walls which turns leathery in appearance in hypertonic solutions.

3. **Germinal (G)** - Innermost layer of *Gigaspora* species from which germ tube arises. Frequently bears papillae which project distally from innermost surface.

4. **Evanescent (E)** – An outermost ephemeral one to multilayered wall, which is sloughed off as spore matures. Seen only in pot culture and rarely in field.

5. **Laminated (L)** – Generally outer many layered wall, layers increasing as spore ages.

6. **Membranous (M)** – Generally inner, very thin, frequently wrinkled, flexible walls that frequently collapse in hypertonic solutions.

7. **Hyphal peridium (P)** – Tightly adherent hyphal layers around the spore or spores.

8. **Unit (U)** – Outer, single, rigid non-layered walls sheathing like brittle plastic on crushing.

9. **Expanding (X)** – A unit wall which expands when placed in lactic acid or polyvinyl alcohol.

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 Gigasporaceae (Bentivenga and Morton, 1995) and Scutellosporaceae species (Morton, 1995; Oehl *et al*., 2008) 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 though 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 **(Plate 13 d & e)**. This type of germination is known to occur in *Acaulospora, Entrophospora, Centraspora, Dentiscutata*, *Fuscutata*, *Intraspora, Kuklospora, Quatunica*, *Racocetra* and *Scutellospora*. In

Plate 13d. In vivo spore germination

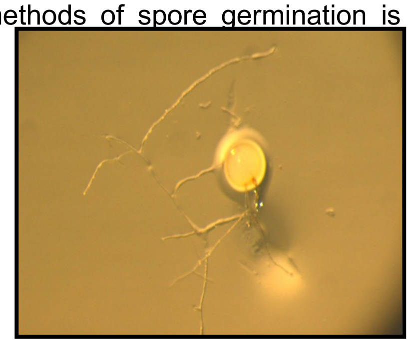

Plate 13e. In vitro spore germination

Acaulospora laevis 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). Although 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 AM fungi – over the years

Link (1809), a German mycologist erected an order *Endogone* and placed the members of Glomales in it. Later Tulasne and Tulasne (1845) described the genus *Glomus*, then comprising of two species *viz. G. microcarpum* and *G. macrocarpum*. They considered *Glomu*s to be closely related to *Endogone*, which was earlier placed in the Tuberaceae by Fries (1849).

Berkeley and Broome (1875) described the genus *Sclerocystis*. Thaxter (1922) revised the family Endogoneae which comprised of four genera that produced spores in sporocarps *viz. Endogone* Link (included all species of *Glomus*), *Glaziella* Berk., *Sclerocysti*s Berk., & Br., and *Sphaerocreas* Sacc. & Ellis. 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* (then described as *Endogone fasciculata* and *E. microcarpa*).

Bucholtz (1922) placed the Endogonaceae in the order Mucorales, due to the affinities of Endogone with the members of Mortierellaceae. Zycha (1935) transferred one species of *Sphaerocreas* to *Endogone*. Moreau (1953) placed the Endogonaceae in the order Endogonales, which was later validated by Benjamin (1979).

The first key to recognition of the types of the endogonaceous spores isolated was prepared by Mosse and Bowen (1968). Gerdemann and Trappe (1974) revised the Endogonaceae. They resurrected *Glomus* in the Endogonaceae and moved several species from *Endogon*e to *Glomu*s. They also described two new genera *Acaulospora* and *Gigaspora*. The chlamydospores produced in the members of genus *Glomus* occurred mainly in loose aggregates or singly in the soil. However, it also included species that formed compact sporocarps with or without a peridium. The members of the genus *Sclerocystis* also produced chlamydospores within the sporocarps. However, the main difference between them was that the members of *Sclerocystis* produced chlamydospores arranged in a single layer around a central, spore-free plexus.

The members of *Acaulospora* species produced spores laterally on the neck of a sporiferous saccule while members of *Gigaspora* formed spores terminally at the tip of an inflated, bulbous sporogenous hypha (bulbous suspensor). The genus *Endogon*e was left with 11 species which were either ectomycorrhizal or saprophytic. Similarly, the genus *Glaziella* include chlamydosporic species while *Modicella* were represented by sporangial forms.

Ames and Schneider (1979) described a new genus in the Endogonaceae, *Entrophospora* with *E*. *infrequen*s, a species earlier described *Gl*. *infrequen*s (Hall 1977) and included in the genus *Glomus*.

Walker (1979) proposed to establish a new genus *Complexipes* in the Endogonaceae (with a single species *C. moniliformis* C. Walker). He isolated ornamented spores of *C. moniliformis* that resembled spores of the genus *Glomus*. Danielson (1982) suggested that *C. moniliformis* belong to Ascomycota.

The presence of septa in the fragments of sporocarps of *Glaziella aurantiaca* (Berk & Centis) Cook prompted Gibson (1984) to transfer *Glaziella* to Deuteromycotina. Later to a new order Glaziellales under family Glaziellaceae (Gibson *et al*., 1986). Similarly, the genus *Modicella* was transferred to the Mortierellaceae (Trappe and Schenck 1982).

Morton and Benny (1990) placed the soil borne fungi forming arbuscules in a new order, Glomales (orthographically corrected to Glomerales by Schuβler *et al.,* 2001). The Glomerales consisted of two suborders, Glomineae and Gigasporineae. The suborder Glomineae comprised of type family Glomaceae with the genera *Glomus* and *Sclerocystis*, and Acaulosporaceae with the genera *Acaulospora* and *Enthrophospora*. The suborder Gigasporineae included the family Gigasporaceae with the genera *Gigaspora* and *Scutellospora*. Besides, the differences in the mode of formation of spores and their subcellular structures, the members of suborder Glomineae showed the ability to form vesicles, a feature that lacked in the members of suborder Gigasporineae.

Almeida and Schenck (1990) suggested that, except for a single species of *Sclerocystis* i.e. *S. coremioides* as continuum of morphological properties exists between sporocarpic species of *Glomus* and other members of *Sclerocystis*. Thus, the genus *Sclerocystis* was combined with *Glomus*. Later, Redecker *et al.* (2000) based on molecular evidence, transferred *S. coremioides* to the genus *Glomus*, thereby eliminating the genus *Sclerocystis* from the Kingdom Fungi.

Based on molecular, morphological and biochemical data, Morton and Redecker (2001) erected two new families *viz.*, Archaeosporaceae and Paraglomaceae (now Paraglomeraceae) in the order Glomales (now Glomerales). The family Archaeosporaceae consists of a single genus, *Archaeospora* with three species forming *Acaulospora*–like spores from the neck of a sporiferous saccule. Two of these species *viz., Ar. gerdemannii* and *Ar. leptotica* were considered dimorphic, and also formed *Glomus*-like spores. The genus *Paraglomus* consisted of two species producing spores different from *Glomus* species. The classification of AM fungi given below is that of Schuβler *et al.,*(2001) with emendations of Oehl and Sieverding (2004), Walker and Schuβler (2004), Sieverding and Oehl (2006), Spain *et al.,* (2006), Walker *et al.* (2007 a, b), Palenzuela *et al*. (2008) and Oehl *et al*. (2008).

GLOMEROMYCOTA C. Walker & Schuβler
- **Glomeromycetes** Cavalier-Smith
  - **Archaeosporales** C. Walker & Schuβler
    - **Ambisporaceae** C. Walker, Vestberg & Schuβler
      - *Ambispora* Spain, Oehl & Sieverd.
    - **Archaeosporaceae** J.B. Morton & D. Redecker emend. Oehl & Sieverd.
      - *Archaeospora* J.B. Morton & D. Redecker
      - *Intraspora* Oehl & Sieverd.
    - **Geosiphonaceae** Engler. & E. Gilg emend. Schuβler
      - *Geosiphon* (Kütz.) F. Wettst.
  - **Diversisporales** C. Walker & Schuβler
    - **Acaulosporaceae** J.B. Morton & Benny
      - *Acaulospora* Gerd. & Trappe emend. S.M. Berch
      - *Kuklospora* Oehl & Sieverd.
      - *Acaulospora* Gerd. & Trappe emend. S.M. Berch
    - **Diversisporaceae** C. Walker & Schuβler
      - *Diversispora* C. Walker & Schuβler
      - *Otospora* Oehl, J. Palenzuela & N. Ferrol
    - **Entrophosporaceae** Oehl & Sieverd.
      - *Entrophospora* R.N. Ames & R.W. Schneid. emend. Oehl & Sieverd.
    - **Gigasporaceae** J.B. Morton & Benny emend. Sieverd., F.A. Souza & Oehl
      - *Gigaspora* Gerd. & Trappe emend. C. Walker & F.E. Sanders
    - **Scutellosporaceae** Sieverd., F.A. Souza & Oehl
      - *Scutellospora* C. Walker & F.E. Sanders. emend. Oehl, F.A. Souza & Sieverd.
    - ***Racocetraceae*** Oehl, Sieverd. & F.A. Souza
      - *Racocetra* Oehl, F.A. Souza & Sieverd.
      - *Cetraspora* Oehl, F.A. Souza & Sieverd.
    - ***Dentiscutataceae*** F.A. Souza, Oehl & Sieverd.
      - *Dentiscutata* Sieverd., F.A. Souza & Oehl
      - *Fuscutata* Oehl, F.A. Souza & Sieverd.
      - *Quatunica* F.A. Souza, Sieverd. & Oehl
    - **Pacisporaceae** C. Walker, Blaszk., Schuβler & Schwarzott
      - *Pacispora* Oehl & Sieverd.
  - **Glomerales** J.B. Morton & Benny
    - **Glomeraceae** Piroz. & Dalpé
      - *Glomus* Tul. & C. Tul.
  - **Paraglomerales** C. Walker & Schuβler
    - **Paraglomaceae** J.B. Morton & D. Redecker
      - *Paraglomus* J.B. Morton & D. Redecker

In this system of classification, all the AM fungal species are placed in four orders *i.e.* Archaeosporales, Diversisporales, Glomerales and Paraglomerales which, comprise of thirteen families and 20 genera that belong to class Glomeromycetes of the phylum Glomeromycota. The family Geosiphonaceae with a single species *viz., Geosiphon pyriformis* is placed under the order Archaeosporales and does not form arbuscular mycorrhizae. It forms endocytosymbiosis with cyanobacteria (*Nostoc* sp.) and is placed under the phylum Glomeromycota due to its close molecular relationship.

Characteristic features of Orders

1. Archaeosporales

The members of the order Archaeosporales form endocytosymbioses with photoautotrophic prokaryotes or produce mycorrhizae with arbuscules, with or without vesicles. The members produce colourless spores which do not react in Melzer's reagent. They produce both glomoid and acaulosporoid spores.

The distinct feature of the members belonging to this order is the possession of the rRNA SSU gene signature YCT**AT**CYKYCTGGTGAKRCG, corresponding to homologous position 691 of *Saccharomyces cerevisiae* SSU rRNA sequence J01353, with the nucleotides in bold being specific for the taxon.

The order Archaeosporales contains two families, Archaeosporaceae with the genera *Appendicispora*, *Archaeospora* and *Intraspora* and Geosiphonaceae with the genus *Geosiphon*.

2. Diversisporales

The members of the order Diversisporales form mycorrhizae with arbuscules, frequently failing to produce vesicles, may or may not produce auxiliary cells. They produce spores which develop either inside (entrophosporioid) or laterally on the neck of a sporiferous saccule (acaulosporioid), from a bulbous base (gigasporioid) or blastically at the tip of a sporogenous hypha (glomoid).

The distinct feature of the members belonging to this order is the possession of the rRNA SSU gene sequence signature YV**R**RYW/1-5/NGY**Y**YGB, corresponding to homologous position 658 of *S. cerevisiae* SSU rRNA sequence J01353 SSU rRNA, GTYARDYH**M**HYY/2-4/GRADRKKYGWCRAC, corresponding to homologous position of *S. cerevisiae* SSU rRNA sequence position 1346 of *S. cerevisiae* SSU rRNA sequence J01353, TTATCGGTTR**A**ATC, corresponding to homologous position 650 of *S. cerevisiae* rRNA SSU sequence J01353, and A**CT**GAGTTMATYT, corresponding to homologous position 1481 of *S. cerevisiae* rRNA SSU sequence J01353 with the nucleotides in bold being specific for the taxon.

The order Diversisporales is represented by eight families, Diversisporaceae with the genera *Diversispora* and Otospora, Acaulosporaceae with the genera *Acaulospora* and *Kuklospora,* Entrophosporaceae with the genus *Entrophospora*, Gigasporaceae with the genera *Gigaspora,* Scutellosporaceae with the genus *Scutellospora,* Dentiscutaceae with genera *Fuscutata, Dentiscutata and Quatunica,* Racocetraceae with genera *Racocetra and Cetraspora*, and Pacisporaceae with the genus *Pacispora*.

3. Glomerales

The members of the order Glomerales form mycorrhizae with arbuscules, vesicles and spores. Spores form either blastically at the tip of a sporogenous hypha or intercalarously inside them. Spores occur singly, in clusters or as sporocarps having a peridium.

The distinct feature of the members belonging to this order is the possession of the rRNA SSU gene sequence signature **YTRRY**/2-5/R**YYA**RGTYGNCARCTTCTTAGAGGGACTATCGG**T**GTYTA**A**CCGRTGG, corresponding to homologous position 1353 of *S. cerevisiae* SSU rRNA sequence J J01353, with the nucleotides in bold being specific for the taxon.

The order Glomerales is represented by single family Glomeraceae that includes one genus, *Glomus*.

4. Paraglomerales

The members of the order Paraglomerales form arbuscular mycorrhizae, rarely with vesicles. Spores are glomoid and colourless.

The distinct feature of the members belonging to this order is the possession of rRNA SSU gene sequence signature G**C**GAA**G**CGTCATG**G**CCTTAAC**C**GG**C**CGT, corresponding to homologous position 703 of *S. cerevisiae* SSU rRNA sequence J01353, with the nucleotides in bold being specific for the taxon.

The order Paraglomerales is represented by one family Paraglomeraceae containing one genus, *Paraglomus*.

Characteristic features of Genera

Ambispora Walker Vestberg & Schüβler

Entymology: Latin: '*ambispora'* referring to the capability to produce two kinds of propagules, acaulosporoid and glomoid.

- Species of the genus *Ambispora* are dimorphic producing both acaulosporoid and glomoid spores i.e. spores originating similarly to those of *Acaulospora* and *Glomus* species (Morton and Redecker, 2001; Spain *et al*., 2006).
- The acaulosporoid spores occur singly in the soil and the glomoid ones are formed singly or in loose clusters in the soil and develop terminally from the thin walled hyphae grown from either the wall of a pedicel or branched germ tubes (Spain *et al*., 2006). In contrast to the sessile acaulosporoid spores of the genus *Acaulospora* and *Archaeospora,* those of *Ambispora* species develop blastically at the tip of a short branch formed at the distal end of the neck of a sporiferous saccule. This branch is called the appendix or pedicel.
- The sporiferous saccule orginates terminally from mycorrhizal extraradical hyphae by their swelling.
- The spores are globose to subglobose and coloured.
- The sub cellular structure consists of three layered, coloured spore wall with two inner colourless germination walls. The outer spore wall completes development subsequent to the formation of the outer layer of the first inner germination wall. The spore wall and the outer layer of the first inner germination of the spores of *Ambispora* species are continuous with the pedicel wall layer.
- The mycorrhiza of the species *Ambispora* consists of arbuscules, vesicles as well as intra- and extra-radical hyphae. All these structures stain faintly in trypan blue (Spain *et al*., 2006).

Archaeospora Morton & Redecker

Etyomology: Greek, *archaios* (ancient), referring to the ancient position of this genus in Glomales.

- *Archaeospora* is dimorphic, forming both acaulosporioid and glomoid spores (Morton and Redecker, 2001; Sieverding and Oehl, 2006; Spain *et al*., 2006).
- Acaulosporioid spores develop laterally, directly on the neck of a sporiferous saccule and are sessile.
- Two-layered glomoid spores originate blastically at the tip of or intercalarously in fertile hyphae, as spores of *Glomus* species.
- Spores germinate by a germ tube emerging from an irregular germination structure.
- Mycorrhizae of *Archaeospora* (1) do not contain intraradical vesicles or they form rarely, (2) have intraradical hyphae with many coils located within and between cortical cells, (3) stain lightly or not at all in trypan blue and other stains, and (4) are patchily distributed along roots (Morton, 2002).

Intraspora Oehl & Sieverd.

Etymology: Latin: *intra* (inside, within), *spora* (seed) referring to the spore formation with in the hyphal stock of the sporiferrous saccule.

- Spores occur singly in the soil or in roots.
- The spores develop within the neck of a sporiferous saccule at some distance from the saccule.
- The sporiferous saccule originates terminally or intercalarously in extra- and intra-radical hyphae.
- The spores are globose to subglobose and frequently pyriform.
- Their sub cellular structure consists of two walls, a spore wall and an inner germination wall. The spore wall is composed of two layers, of which the outer layer sloughs with age and is continuous

with the wall of the neck of the sporiferous saccule. The inner layer of this wall is persistent, semi-flexible
and closes two opposite pores of spores. The inner germination wall is semi-flexible and laminate.

- The mycorrhizae comprise of arbuscules, vesicles as well as intra- and extra-radical hyphae. Vesicles form rarely and all the mycorrhizal structures stain faintly in trypan blue.

Acaulospora Gerdemann & Trappe emend. Berch
Etyomolgy: Greek, *a* (without), *caulos* (stem), and *spora* (spore) - referring to the sessile spores.

- Spores of fungi of the genus *Acaulospora* develop laterally from the neck of a sporiferous saccule (Morton and Benny, 1990; Morton 2000).
- The spores are sessile, i. e. no pedicel (a short branch of the sporiferous saccule neck) is formed. The wall of the most juvenile spores consists of only one layer continuous with the wall of a sporiferous saccule hypha.
- Spores produced singly in soil, generally globose to subglobose with oily contents. Spore composed of two distinct, separable wall groups; outer wall is continuous laminated; variously ornamented, inner wall composed of one or more walls that are membranous, hyaline, laminated and ornamented.
- Spore walls are continuous except for a small-occluded pore.
- Spores of the genus *Acaulospora* germinate by germ tubes emerging from a plate-like germination orb formed by centrifugally rolled hyphae. The germ tubes penetrate through the spore wall.

- The mycorrhizae of *Acaulospora* species consist of (a) arbuscules with cylindrical or slightly flared trunks (b) irregular and knobby vesicles, and (c) straight and coiled intraradical hyphae with coils mostly concentrated at entry points (Morton, 2000).

Kuklospora Oehl & Sieverd.
Etymology: Greek: *kuklo* (ring) and *spora* (seed) refers to the two cicatrices, which resemble circular depressions and the borders of them wedding ring on the spore surface when the hyphal connection have detached from the young spore.

- The spores develop inside the neck of a sporiferous saccule at some distance from this saccule and originate from the neck and saccule contents.
- The sporiferous saccules originate terminally or intercalarously inside mycorrhizal extraradical hyphae by their swelling and are globose to subglobose.
- The sub cellular structure consists of a 3-layered, coloured spore wall and two inner colourless germination walls. The outermost spore wall layer is colourless, and is continuous with the wall of the sporiferous saccule neck. The second structural layer of this wall consists of coloured, tightly adherent, thin sub layers (laminae). This layer occasionally develops towards the saccule, forming a stalk supporting the wall of the sporiferous saccule neck. The first inner germination wall consists of two adherent flexible to semi-flexible layers. The second germination wall is composed of three layers, of which the outermost one is ornamented with small granules.
- The spores form typical mycorrhizae intensively stained in trypan blue.

Diversispora Walker & Schüßler
Entymolgy: Referring to the diverse nature of the spores found within the order the genus lends its name.

- Spores of *Diversispora* develop blastically at the tip of cylindrical to slightly flared sporogenous hyphae continuous with extraradical hyphae of AM fungi.
- The mycorrhizae of most *Glomus* species consist of arbuscules, vesicles and hyphae staining intensively in trypan blue whereas those of *D*. *spurca* lack vesicles and stain variably, from almost no staining to intensive staining (Morton, 2002).

Otospora Oehl, J. Palenzuela & N. Ferrol
Etymology: Greek: *oto* (ear) and *spora* (seed) referring to the persistent lateral ear-like stalk at the spore base after the detachment of sporiferrous saccule.

- Sporocarps unknown.

- Spores formed at a short distance to a terminal or intercalary formed sporiferous saccule by swelling laterally on the hyphal stalk of the saccule with outer and an inner wall. Layers of the outer wall are continuous with the wall of the sporiferous saccule. The inner layers of the outer wall are persistent.
- One to several septa formed in the hyphal stalk during spore formation.
- During initial stages of sporogenesis, the content of the sporiferous saccule separated from the hypha by septa at some distance of the terminus and the not yet developed spore. Later developmental stages additional septa in the stalk, positioned between the saccule terminus and the developing spore, may separate the collapsing saccule terminus from the spore. A final plug-like septum usually closes the pore at the spore base. The inner wall forms *de novo* during spore formation and consists of a thick, finely laminate layer that might have each one thin layer adherent on its outer and its inner surface. None of the layers of the inner wall has a beaded appearance.
- Formation of vesicular arbuscular mycorrhizae unknown.

Entrophospora Ames & Schneid. emend. Oehl & Sieverd.
Entymolgy: Greek: *en* (within), *trophos* (nourshied) and *spora* (seed), referring to the spores reared within the vesicular stalk.

- Spores occur singly in the soil or inside roots (Sieverding and Oehl, 2006).
- Spores develop inside the neck of a sporiferous saccule directly at or at a short distance from the saccule originating from the neck. The sporiferous saccule originate terminally or intercalarously inside extra- and intra-radical hyphae by their swelling.
- The spores are globose to subglobose and coloured; their sub cellular structure consists of a multilayered, coloured spore wall and one inner 3-layered, colourless germination wall. In spores lacking the sporiferous saccules, two opposite cicatrices resembling small rings with a slightly raised border are visible.
- The cicatrices are frequently accompanied by stalks developed from the permanent spore wall layers.
- The mycorrhizae of *Entrophospora* show intense staining in trypan blue (Sieverding and Oehl, 2006).

Gigaspora Gerdemann & Trappe emend. Walker & Sanders
Etymology: Greek, *giga* (giant) and *spora* (spore). Referring to the exceptionally large spores typically produced by the members of the genus.

- Azygospores produced singly in soil, generally globose to subglobose, with oily contents, usually with a narrow hypha extending from the suspensor cell to the pore.
- Spores of *Gigaspora* develop blastically from a bulbous sporogenous cell formed at the end of a fertile hypha connected with mycorrhizal roots (Bentivenga and Morton, 1995; Walker and Sanders, 1986).
- The wall of the most juvenile, expanding spores consists of two layers of equal thickness. The inner layer thickens due to the synthesis of new sub layers (laminae). At the end of ontogeny, a warty or knobby one-layered germination wall is formed, from which germ tubes arise. This wall tightly adheres to the inner surface of the laminate spore wall layer. The outermost spore wall layer of all the *Gigaspora* species is smooth. Apart from spores, *Gigaspora* species also form clusters of auxiliary cells. They are echinulate with spines.
- The mycorrhizae of *Gigaspora* species consist of only arbuscules and hyphae staining darkly in trypan blue; no vesicles are produced (Bentivenga and Morton, 1995). Arbuscules generally form fine branches directly from a swollen basal hypha. Intraradical hyphae are straight to coiled and vary in diameter because of the presence of knob-like projections and inflated areas.

Scutellospora C. Walker & F.E. Sanders. emend. Oehl, F.A. Souza & Sieverd.
Etymology: Latin *scutellum* (small shield) and *spora,* (spore) referring to the production of germination shield in spores of members of the genus.

- Spores formed singly on sporogenous cells formed terminally on an extraradical hypha.

- Outer spore wall is 3 layered and continuous with the wall of the sporogenous cell. Outer layer of the outer spore wall generally rigid, second layer laminate and third layer thin, often membranous, tightly adherent to the laminate layer and thus, often difficult to observe.
- Pore between the spore and sporogenous cell is narrow and usually closed by a plug formed by spore wall material.
- Two hyaline walls (‘mw’ and ‘iw’) having 1–2 and 2–3 layers, respectively are formed *de novo* during sporogenesis. The iw forms a germination shield on its outer surface or between the outer and the subsequent layer of iw (Oehl *et al*., 2008).
- Germination shield transparent, or hyaline to subhyaline, seldom light yellow, bi- to mono-lobed; often violin-shaped to oval to ovoid to more rarely cardioids or coiled and then, either circulr or apparently broad ellipsoid to irregular; only a few folds cover the shield surface where 1–2 rounded germ tube initiations (~2–4 μm in diam.).
- Mycelia hyphae form one to several septa in some distance to the sporogenous cells.
- Auxiliary cells are knobby without spines on the surface.
- Forming typical arbuscular mycorrhizae without intraradical vesicles.

Racocetra Oehl, F.A. Souza & Sieverd.
Etymology: Greek, *ρακος*, *racos* (cloth, lobe), and Latin, *cetra* (light shield), referring to the wavy-lobed surface of the germination shield in planar view.

- Spores formed singly in soil and rarely in roots, on bulbous sporogenous cells arising terminally on mycelia hyphae (Oehl *et al*., 2008).
- Outer spore wall 3 layered and continuous with the wall of the sporogenous cell. Outer layer of the outer spore wall generally semi-persistent to persistent, rigid; second layer laminated; third layer thin, often membranous, tightly adherent to the laminate layer.
- Pore between spore and sporogenous cell is narrow and usually closed by a plug formed by spore wall material.
- A single inner wall forms *de novo* during spore formation and has 2-3 layers. A germination shield arises on the outer surface or beneath a thin outer layer of the inner wall.
- Germination shield: hyaline to subhyaline seldom light yellow, generally oval to ellipsoid or subglobose, with several (4–12) wave-like lobed projections forming the outer surface of the shield; folds separate the lobes on the shield, and each lobe have a germ tube initiation (2–5 μm in diam.).
- In the subtending hypha of the sporogenous cell one to several septa formed in some distance to the sporogenous cells.
- Auxiliary cells knobby.
- Forming typical arbuscular mycorrhizae without vesicle formation in roots.

Cetraspora Oehl, F.A. Souza & Sieverd.
Etymology: Latin, *cetra* (light shield) and spora (spore), refers to the light colored germination shield which often is difficult to observe.

- Spores formed singly in soil and rarely in roots on bulbous sporogenous cells arising terminally on a subtending hypha (Oehl *et al*., 2008).
- Outer spore wall 3 layered and continuous with the wall of the sporogenous cell.
- Outer layer of the outer spore wall generally semi-persistent to persistent, rigid; second layer laminate; third layer thin, often membranous, tightly adherent to the laminate layer and thus, often difficult to observe.
- Pore between spore and sporogenous cell is narrow and usually closed by a plug formed by spore wall material.
- Two hyaline walls (‘mw’ and ‘iw’) form *de novo* during spore formation and have 1–2 and 2–3 layers, respectively.
- A germination shield arises on the outer surface of the iw or beneath a thin outer layer of the iw.
- Germination shield: hyaline to subhyaline seldom light yellow, generally oval to ellipsoid or subglobose, with several (4–12) wave-like lobed projections forming the outer surface of the shield; large folds separate the lobes on the shield, and each lobe may have an germ tube initiation (~ 2–5 μm in diam.).

- Subtending hyphae form one to several septa in some distance to the sporogenous cells.
- Auxiliary cells knobby.
- Forming typical arbuscular mycorrhizae but lacking vesicles in roots.

Dentiscutata Sieverd., F.A. Souza & Oehl
Etymology: Latin *denti* (*culata*) (dentate) and *scutata* (shielded) referring to the dentate nature of the brown germination shield periphery.

- Spores formed singly formed on bulbous sporogenous cells that are formed terminally on subtending hypha (Oehl *et al*., 2008).
- Outer spore wall 3-5 layered and continuous with the wall of the sporogenous cell.
- Pore between the spore and sporogenous cell is narrow and usually closed by a plug formed by outer spore wall material.
- A hyaline middle wall (mw) and a hyaline inner wall (iw) form *de novo* during spore formation; mw 1-2 layered; iw 2-3 layered.
- Germination shield formed on the outer surface of the iw or beneath a thin outer layer of the iw, yellow-brown to brown, generally ellipsoid (to oval), or rarely reniforme to cardioforme, with many (8–30) large folds separating the shield into 8–30 'small compartments'. Each small compartment has one circular germ tube initiation.
- The periphery of the germination shield generally appears dentate in planar view.
- Septa often formed in subtending hypha in some distance to the sporogenous cells.
- Auxiliary cells knobby.
- Forming typical arbuscular mycorrhizae without vesicle formation in roots.

Fuscutata Oehl, F.A. Souza & Sieverd.
Etymology: Latin *fu*(*scus*) (brown) and *scutata* (shielded), referring to the brown colour of the germination shield.

- Spores formed singly on bulbous sporogenous cells which arise terminally on the subtending hypha (Oehl *et al*., 2008).
- Outer spore wall 3-4 layered.
- Pore between the spore and sporogenous cell is narrow and usually closed by a plug formed by spore wall material.
- Two hyaline walls (middle wall and inner wall) form *de novo* during spore formation and have 1–2 and 2–3 layers, respectively.
- Germination shield generally formed on the outer surface of the innermost wall or beneath a thin outer layer of the inner wall, yellow-brown to brown, ovoid to violin-shaped to heart-shaped, consisting of 2 lobes and folds; both lobes with a germ tube initiation ('gti', about 3-6 μm in diam).
- Spore germination generally from one gti.
- In the subtending hypha one to several septa are formed in some distance to the sporogenous cell.
- Auxiliary cells knobby.
- Forming typical arbuscular mycorrhizae without vesicles in roots.

Quatunica F.A. Souza, Sieverd. & Oehl
Etymology: Latin *qua* [abbr. from *quartuor*] (four) and *tunica* (wall) referring to the four spore walls.

- Spores singly formed on bulbous sporogenous cells that are formed terminally on a subtending hypha (Oehl *et al*., 2008).
- Spores have 4 walls.
- Outer spore wall 3-4 layered and continuous at least in part with the wall of the sporogenous cell.
- Pore between the spore and sporogenous cell is narrow and usually closed by a plug formed by outer spore wall material.
- Two hyaline middle walls and a hyaline inner wall form *de novo* during spore formation.
- Germination shield generally arising on the outer surface of the inner wall or beneath a thin outer layer of the inner wall, yellow-brown to brown, generally ellipsoid to oval, or rarely reniforme to cardioforme, usually with a many (8–30) large folds separating the shield into 8–30 small compartments. Each small compartment generally with one germ tube initiation ('gti). From one or

few gti germ tubes may arise penetrating the middle walls and the outer wall; periphery of shield wall conspicuously dentate in planar view.

- One to several septa often formed in the subtending hypha in some distance to the sporogenous cell.
- Auxiliary cells knobby.
- Typical arbuscular mycorrhizal formation without vesicles is seen in roots.

Pacispora Oehl & Sieverd.
Etymology: Latin, *paci* (peace or peaceful), and *spora* (seed). Dedicated to the peace in the world.

- Spores of fungi of the genus *Pacispora* develop blastically at the end of cylindrical sporogenous hyphae (subtending hyphae) continuous with extraradical hyphae of AM fungi.
- Spore wall consist of three layers.
- Spore development is by the formation of a uniform, plate-like germination shield on the surface layer of the inner germination wall.
- A germ tube grows from this shield and penetrates through the spore wall.
- The mycorrhizae consist of arbuscules, vesicles, intra- and extra-radical hyphae, as well as of auxiliary cells.

The arbuscules, vesicles and hyphae morphologically resembled those of *Glomus* species and stained intensively in trypan blue. Auxiliary cells occur both outside and inside roots and are knobby.

Glomus Tulasne & Tulasne
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 surface of spores of *Glomus* species may be smooth (in most species) or ornamented.
- Some species produce spores enveloped in a hyphal mantle 'Gleba' consisting of interwoven 'Peridium'.
- The wall layers of a subtending hypha are continuous with spore wall layers.
- 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 and (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.
- Most species of the genus *Glomus* produce spores singly in the soil. Other taxa form more or less compact spore aggregates consisting of spores and a peridium.
- The mycorrhizae of *Glomus* species consist of arbuscules, vesicles (not always formed), and intra- and extra-radical 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 occur at entry points.

The mycorrhizae of most *Glomus* species consist of arbuscules, vesicles and hyphae staining intensively in trypan blue.

Paraglomus Morton & Redecker
Etymology: Resembling "*Glomus*" with identical spore morphotypes.

- Spores develop blastically at the tip of extraradical hyphae.
- Spores occur singly in the soil, globose to irregular and colourless to pale-coloured.

- Spores sub cellular structure consists of a spore wall comprising 2-3 layers continuous with those of their subtending hyphae. Spore of germinates by germ tubes emerging from both the lumen of the subtending hypha and the spore wall (Morton and Redecker, 2001).
- Arbuscules of are cylindrical or slightly flared trunks with branches progressively tapering in width towards the tips (Morton, 2002; Morton and Redecker, 2001).
- The mycorrhizae of do not contain vesicles and their intraradical hyphae are frequently coiled within and between cortical cells.
- The main visible evidence of mycorrhizae is their light staining or the lack of any staining reaction in trypan blue or other stains.

Plate 13c. Spore in spore syndrome

Spore in spore syndrome

Various studies have reported the presence of AM fungal spores inside the dead spores of other AM fungal species (Koske *et al.,* 1986; Muthukumar and Udaiyan, 1999) **(Plate 13 c)**. This suggests that spores of AM fungi act as a microhabitat when they are dead, apart from their normal role as propagules. This also suggests the ability of different AM fungal species to sporulate in close proximity with each other.

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