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REVISED CLASSIFICATION OF ARBUSCULAR MYCORRHIZAL FUNGI (ZYGOMYCETES): A NEW ORDER, GLOMALES, TWO NEW SUBORDERS, GLOMINEAE AND GIGASPORINEAE, AND TWO NEW FAMILIES, ACAULOSPORACEAE AND GIGASPORACEAE, WITH AN EMENDATION OF GLOMACEAE.

JOSEPH B. MORTON

Division of Plant & Soil Sciences, West Virginia University, 401 Brooks Hall,
Morgantown, WV 26506-6057

and

GERALD L. BENNY

Plant Pathology Department, 1453 Fifield Hall, University of Florida,
Gainesville, FL 32611

ABSTRACT

A new order, Glomales, is proposed to include all soil-borne fungi which form arbuscules in obligate mutualistic associations with terrestrial plants. The proposed suborder, Glomineae, consists of the type family Glomaceae and Acaulosporaceae fam. nov. *Glomus* and *Sclerocystis* are genera in the Glomaceae characterized by "chlamydospores" borne singly, in aggregates, or in compact sporocarps on one or more cylindrical to flared subtending hyphae. *Acaulospora* and *Entrophospora* in the Acaulosporaceae are historically equivalent sister groups. Species in these genera are distinguished by "chlamydospores" formed laterally from or within a hypha terminating in a sporiferous saccule. Intermediate species in Acaulosporaceae show a progressive transformation from spores resembling *Glomus* to those which are uniquely sessile. Gigasporineae subord. nov. is proposed to include Gigasporaceae fam. nov. Both genera in this family, *Gigaspora* and *Scutellispora*, produce "azygospores" borne terminally on a sporogenous cell. Taxa in Gigasporineae produce extraradical auxiliary cells and no intraradical vesicles, whereas taxa in Glomineae form intraradical vesicles. The Endogonales was emended to contain only one family, Endogonaceae, with a single genus, *Endogone*. A key to supraspecific taxa in Glomales is provided.

Key words: Endogonales, Endogonaceae, vesicular-arbuscular mycorrhizal fungi, VAM fungi.

INTRODUCTION

Until recently, the order Endogonales (Zygomycotina) has consisted of only one family, the Endogonaceae (Benjamin, 1979; Morton, 1988). Six genera (*Acaulospora* Gerdemann & Trappe emend. Berch, *Entrophospora* Ames & Schneider, *Gigaspora* Gerdemann & Trappe, *Glomus* Tulasne & Tulasne, *Sclerocystis* Berkeley & Broome, and *Scutellispora* Walker & Sanders) were included whose members formed an arbuscular mutualistic symbiosis with many terrestrial plant families (Trappe, 1987) and one genus (*Endogone* Link:Fr.) whose members were saprobic (Gerdemann and Trappe, 1974) or formed putative ectomycorrhizal associations (Chu-Chou and Grace, 1979; Fassi et al., 1969). The historical reasons for combining this heterogeneous assemblage in the same order have been documented by Berch (1986b), Gerdemann and Trappe (1974; 1975), Morton (1988) and Walker (1987) and they will not be reviewed again here. These and other workers have recognized the artificiality of this classification, but the taxonomic relationships within and between levels of the geneological hierarchy were too nebulous to make significant changes.

Pirozynski and Dalpé (1989) separated *Glomus* and *Sclerocystis* into a separate family, the Glomaceae. Their rationale appeared to rest on paleontological evidence spanning 400 million years of fossilized intraradical spores resembling extant analogues in *Glomus* and *Sclerocystis* (Pirozynski and Dalpé, 1989; Stubblefield and Taylor, 1988). The move was valid, but it did not provide neontological arguments of hierarchial relationships among extant taxa. Important taxonomic comparisons not discussed were: (i) the extent of morphological diversity within extant taxa, (ii) phylogenetic relationships between fossilized and extant taxa, and (iii) phylogenetic affinities between Glomaceae and other arbuscular fungal taxa.

The fossil record has been invaluable in establishing early origin of a putative symbiosis (Stubblefield et al., 1987) and a measure of evolutionary rate of change in some members of the Glomaceae (Pirozynski and Dalpé, 1989; Stubblefield and Taylor, 1988). Described fossils, however, represent less than 5% of total morphological diversity in the Glomaceae and show nothing of other arbuscular genera. Revision of the present classification to make hierarchial groupings more "natural", then, must be predicated on character analyses of extant species.

A natural classification can be organized along different guidelines. Cain (1962), for example, considers that characters which have the greatest physiological importance in an organism's life cycle reflect hierarchial processes in nature. Others deem that classification should be interpretable within an evolutionary context (Cronquist, 1988; Eldredge and Cracraft, 1980). Often, this means grouping taxa which are related by descent from a common ancestor (e.g. monophyly). Both criteria are met in this revision.

Morton (1990a) used all available data on selected morphological characters of somatic (hyphae, arbuscules, vesicles) and reproductive (resting spores) stages of known arbuscular species to hypothesize explicit geneological trends. Cladistic analysis and a phylogenetic reconstruction were based on an evolutionary species definition (Wiley, 1978): clonal populations which together maintained a distinct morphological identity from other clonal assemblages and which had the same evolutionary role and tendencies. A revised species concept to accommodate phenotypic variability as well as historical and contemporary evolutionary processes is elaborated by Morton (1990b).

In this paper, classification of the Endogonales (*sensu lato*) is revised to more accurately arrange groups of arbuscular fungi according to patterns of common descent. It is based in part on results of Morton (1990a), with additional considerations of spore ontogeny and modes of spore germination. Interpretations of putative mechanisms of speciation and macro- and microevolutionary processes for the revised classification are examined in greater detail by Morton (1990b). Spelling of scientific names in this paper are in accordance with recommendations of Almeida (1989).

NEW TAXA AND EMENDATIONS

Endogonales Moreau, 1953 (*Encycl. Mycol.* **23**: 1231) ex R. K. Benjamin, 1979 (*in* Kendrick, *The Whole Fungus*, p. 599) emend Morton & Benny

Fungi mostly hypogeous or rarely epigeous; saprobic and free-living, sometimes forming associations resembling those of ectomycorrhizae. Somatic hyphae coenocytic; septa sometimes produced which contain micropores. Sexual reproduction by nearly globose or ovoid zygospores most often formed in sporocarps. Zygospores formed on apposed suspensors which are nearly equal or unequal. Sexual and somatic hyphae similar.

Endogonaceae Paoletti, 1889 (*in* Saccardo, *Sylloge Fungorum* **8**: 905) emend Morton et Benny

A single family, with the characteristics of the order, is recognized.

Type genus: *Endogone* Link:Fr.

The sporocarpic habit appears to be a convergent character among many disparate taxa in the Zygomycetes. Three Zygomycete orders contain sporocarpic taxa: Mucorales [*Modicella* Kanouse (Mortierellaceae--Trappe and Schenck, 1982; Benny et al., 1987)]; Endogonales [*Endogone* (Endogonaceae--Gerdemann and Trappe, 1974; Benjamin, 1979)], and Glomales [*Glomus, Sclerocystis* (Glomaceae--Pirozynski and Dalpé, 1989)]. However, the sporocarps of *Endogone* species bear only superficial morphological similarity to those of arbuscular fungi. Zygospores most often develop in *Endogone* sporocarps whereas only putative asexual chlamydospores form in *Glomus* and *Sclerocystis* sporocarps (Gerdemann and Trappe, 1974; Morton, 1988). Similarity between the pre-germination chamber formed in the zygospore wall of *E. pisiformis* and "germination chambers" or "germination shields" in *Acaulospora* and *Scutellispora*, respectively, also has been used to suggest phylogenetic relatedness among taxa (Berch and Fortin, 1982), but these characters are not homologous (Morton, 1990a). Cladistic analysis (Morton, 1990a) clearly indicates that sporocarp development was a convergent character state in *Endogone*. No other characters unite members of this genus with arbuscular mycorrhizal fungi.

Phylogenetic affinities are too obscure to confidently place *Endogone* in another family within the Zygomycetes. The only taxonomic solution at this time is to maintain *Endogone* as the sole genus in the Endogonaceae (Endogonales). Berch (1986b) suggests that enough heterogeneity exists to warrant possible generic distinctions. This problem is beyond the scope of this paper, and it will need to be addressed by other workers.

Glomales Morton et Benny, **ord. nov.**

Fungi plerumque hypogaei, raro epigaei; endomycorrhizas arbusculis in radicibus formantes et in symbiose cum plantis viventes. Hyphae somaticae coenocyticae. Reproductio sexualis raro. Reproductio asexualis a sporis chlamydosporis vel azygosporis simulantibus. Sporae plerumque singulatim efformatae; alterne, sporae gregatum vel in sporocarpiae compactae efformatae.

Fungi mostly hypogeous, sometimes epigeous; forming arbuscular endomycorrhizae in mutualistic symbiosis with living plants. Somatic hyphae generally coenocytic. Sexual reproduction rare. Asexual reproduction by spores resembling chlamydospores and azygospores. Spores formed singly, but also in aggregates or in sporocarps.

Familia typica: Glomaceae Pirozynski & Dalpé

All fungi in this order grow and reproduce in an "adaptive zone" (Van Valen, 1976), or collective niche (Simpson, 1961), where carbon is acquired obligately from their host plants via intraradical dichotomously-branched arbuscules. In return, the fungus aids in uptake of water and essential nutrients for benefit to the host (Harley and Smith, 1983). In the physical and physiological interaction between host and fungal partners, the arbuscule is central to nutrient interchange (Bonfante-Fasolo, 1984; Bowen, 1987). The importance of the endomycorrhizal association in both plant and fungal evolution is discussed by Pirozynski and Malloch (1975), Malloch (1987); Malloch et al. (1980), Pirozynski (1981) and Morton (1990b). Structure and function of the arbuscule clearly unites members of the Glomales into a monophyletic group (Morton, 1990a) (Fig. 1).

Speciation most likely occurred as an adaptive shift from a saprobic to mutualistic association (Morton, 1990b). Many of the characteristics of spore development, spore phenotype, and spore germination are unique to the Glomales and not readily interpretable within classification systems of other zygomycetous groups. If the Glomales is perceived as an evolutionary cul-de-sac (Malloch, 1987) bounded by a unique adaptive zone, then these complications are a source of enlightenment rather than frustration.

Glomineae Morton et Benny, **subord. nov.**

Arbuscules vesicaeque solum in mycorrhizarum radices efformatae. Chlamydosporae terminales, intercalares, vel laterales ex hyphis fertilis. Cellulae auxiliares nihil efformatae.

Arbuscules and vesicles formed in mycorrhizal roots. "Chlamydospores" produced terminally, intercalarily, and laterally from the fertile hyphae. Auxiliary cells not formed.

The magnitude of the morphological differences in spore development and organization, as well as mycorrhizal anatomy, is large enough between Glomineae and Gigasporineae to justify their status as suborders (Fig. 1). Taxa in Glomineae form intraradical vesicles in addition to arbuscules in mycorrhizal roots. Hence, they may fit the acronym "VAM" in describing mycorrhizal morphology. Spores resemble "chlamydospores" in the Glomaceae. Those in the Acaulosporaceae traditionally have been called "azygospores" (Gerdemann and Trappe, 1974). However, morphological divergence in spore development progresses step-wise from Glomaceae to Acaulosporaceae via transition species. *Acaulospora appendicula* Spain, Sieverding & Schenck is the most obvious of these species (Morton, 1990a). This dimorphic fungus has many characters in common with species in Glomaceae (Fig. 13): (i) "chlamydospores" formed on a subtending hypha (although it branches from the neck of a sporiferous saccule); (ii) an outer wall evanescent on older spores that is discontinous with the subtending hyphal wall; (iii) more than one structural wall (two ornamented unit walls), one of which is continuous with the hyphal wall; and (iv) separate and morphologically distinct "chlamydospores" formed singly (Schenck et. al., 1984; Morton, unpubl.).

Glomaceae Pirozynski & Dalpé, 1989 (*Symbiosis* **7**: 19)

Type genus: *Glomus* Tul. & Tul., 1845 (*Giorn. Bot. Ital.* **2** (Pt. 1): 63)
Other taxon: *Sclerocystis* Berk. & Broome, 1875 (*J. Linn. Soc. London* **14**: 137)

The fossil record links a putative ancestor for the Glomales with modern species in *Glomus* and *Sclerocystis* (Pirozynski and Dalpé, 1989). Most stages of spore development, from those formed singly on a subtending hypha to those formed in compact sporocarps, are represented at least minimally in fossilized remains of plant roots (Stubblefield and Taylor, 1988). Chronologically, these fossil specimens indicate that glomuslike spores were formed as early as the Devonian (Pirozynski and Dalpé, 1989, Stubblefield and Taylor, 1988) and that arbuscular development occurred in plants at least by the Triassic Period (Stubblefield et al., 1987). Extant species (*G. aggregatum* Schenck & Smith emend. Koske, *G. intraradix* Schenck & Smith) whose spores are similar morphologically to those of fossil specimens have a propensity to form numerous spores within mycorrhizal roots, and it is these intraradical propagules which appear to have been preserved. The majority of species in *Glomus* and *Sclerocystis* do not form intraradical spores (Morton, 1988), so their absence in the fossil record is not a surprise. Spores outside the protected environment of plant roots are less likely to resist microbial decomposition long enough to become fossilized, particularly in oxygenated soils or those with high organic matter. Sporocarpic forms in the fossil record superficially resemble taxa currently placed in *Sclerocystis*. Many of these species are being transferred to *Glomus*, with the exception of *Sclerocystis coremioides* Berk. & Broome (Almeida and Schenck, pers. commun.).

A number of characters (Table 1) distinguish extant members of the Glomaceae from those in other proposed families of arbuscular fungi. The term "chlamydospore" still is retained to describe resting asexual spores in the Glomaceae, although their similarities to analagous structures in non-arbuscular zygomycetous fungi is equivocal (Morton, 1988).

The sporocarpic habit, defined here as spores embedded within compact intertwining hyphae or around a central hyphal plexus (Fig. 2), is found only in the Glomaceae. Berch (1986a) emended the description of *Acaulospora* to include the sporocarpic habit, but the dense aggregates of spores formed by several species (*A. myriocarpa* Schenck, Sieverding & Schenck and *A. sporocarpia* Berch) are indicative of a more plesiomorphic stage in an evolutionary transition to sporocarp development (Morton, 1990a). The sporocarpic habit is a highly variable character in some *Glomus* species (Morton, 1988) and hence must be interpreted with caution. Indications are that species forming highly organized sporocarps may be more stable in pot culture, but more experimental studies are needed for verification.

Spore wall structure in the Glomaceae has a number of unique characteristics (Table 1). Inner walls are few in number (rarely more than one is present), and they usually are membranous. One interpretational problem is that the membranous phenotype is not always consistent. It ranges from very thin (membranous) to thick (appearing coriaceous) to semi-rigid (breaking sharply with only slight pressure to the spore) in spores of some species (Koske and Walker, 1986; Morton, 1985). Spores of most members of Glomaceae have only one wall group (Figs. 2-10) when they are broken *gently* in mountants such as lactophenol or polyvinyl alcohol-lactic

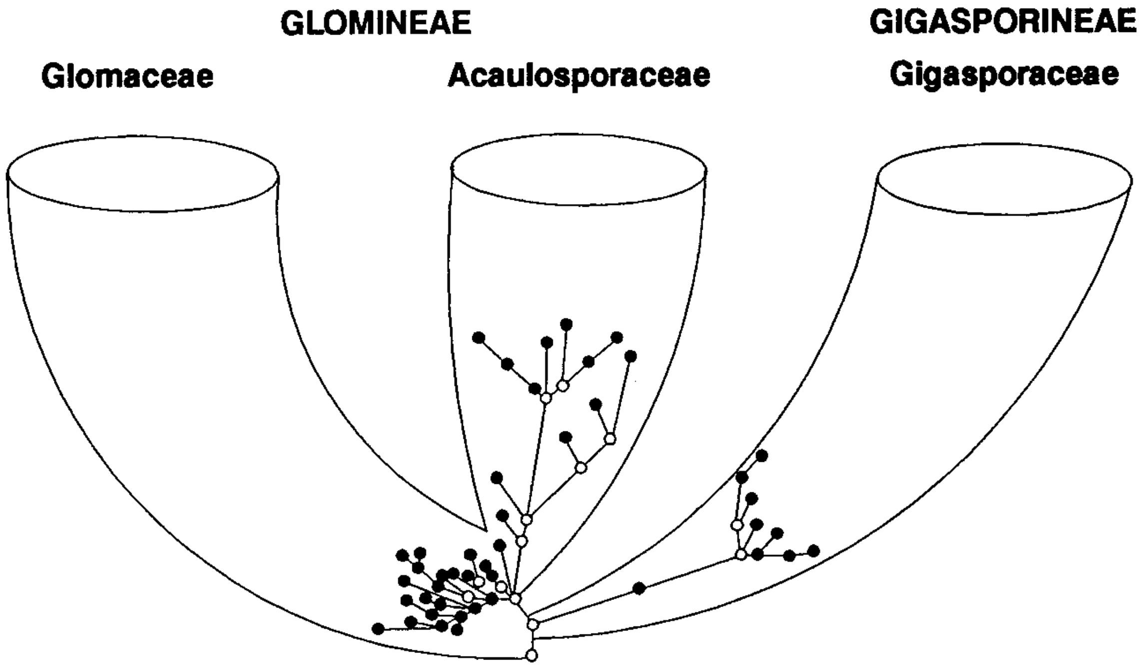


Fig. 1. Phylogenetic patterns of taxa confirmed as arbuscular mycorrhizal symbionts (from Morton, 1990a) which distinguish suborders (Glomineae and Gigasporineae) and families (Glomaceae, Acaulosporaceae, and Gigasporaceae) of the Glomales. Solid circles = extant species; hollow circles = hypothetical ancestors. The length of each line connecting circles indicates extent of morphological change.

acid-glycerin (PVLG) (Hall, 1984). Two wall groups may be present in spores of *Glomus* species having one or more flexible inner walls, but such distinctions are equivocal (Fig. 8). The extent to which wall groups reflect temporally distinct stages in spore wall development, as observed in the Acaulosporaceae and Gigasporaceae, has yet to be determined.

Ontogeny of spores in the Glomaceae has received little study. In species with a single structural laminated wall, spores form by expansion of the sporophore tip and then gradual thickening of the structural spore wall (Morton, unpubl.). In spores of *G. intaradix*, which have a more complex wall structure (Fig. 29), temporal progression of the two outer walls could not be separated (Fig. 9). The inner laminated wall formed last (Fig. 10), but no chemical markers (such as a reaction in Melzer's reagent) specified when spores were fully mature. Considerable more work is needed to clarify ontogenetic sequences in *Glomus* species with more diverse spore wall structures.

Most taxa in Glomaceae appear to have the potential to form vesicles (Figs. 30-31), although the rate and pattern of vesicle development in mycorrhizal roots appears to vary among host species and with changing environmental conditions (Morton, 1985; Tommerup, 1984). In some *Glomus* species, vesicles appear to be transformed into thick-walled spores (Fig. 31) indistinguishable from extraradical spores (Morton, 1985). In other species, neither arbuscules or vesicles have been confirmed because intraradical structures do not stain easily (Morton, 1988).

Evidence so far suggests that emergence of the germ tube through the subtending hypha is the most common mode of spore germination. Direct germination through the spore wall has been documented for several species (Hall, 1977; Walker and

Table 1. Morphological characters or character complexes unique to each family in Glomales [see Morton (1988) for a more complete explanation of each feature, except where noted otherwise].

Glomaceae

Chlamydospore-like resting structures are borne terminally on one or more subtending hyphae (Figs. 2-10).

Compact sporocarps with spores embedded in an unorganized (Fig. 3) to highly organized hyphal matrix (Fig. 2) are formed by some species.

Different types of multiple outer walls (Figs. 5-6) account for most diversity in spore wall structure. Distinct outer walls include the expanding wall, a mucilagenous evanescent outer wall (Figs. 7, 10) which stains dextrinoid in Melzer's reagent (Morton, 1989), and tortuose hyphae over the spore surface (Figs. 9-10).

At least one structural wall of the spore wall is continuous with a wall of the subtending hypha (Figs. 2-10)

Inner flexible spore walls rarely react with Melzer's reagent (Fig. 8); those that do are atypically slow and diffuse.

Spore contents are isolated from the sporophore by a variety of mechanisms: an amorphous plug, a curved septum (Fig. 7), an inner flexible wall (Fig. 8), or thickening of the structural wall (Fig. 10).

Spores of most species germinate by emergence of the germ tube through the subtending hypha (Fig. 4).

Mycorrhizal vesicles are intraradical mostly, with the potential to become thick-walled spores in some species (Figs. 30-31).

Acaulosporaceae

Spores develop from (Fig. 11) or within (Fig. 12) the neck of a sporiferous saccule.

Sporiferous saccules and attached spores usually are borne singly (Figs. 11-12), but occasionally they form aggregates.

Spores rarely have more than one structural wall, the surface of which ranges from smooth (Figs. 14-15) to highly ornamented (Figs. 16-18).

Spores have a minimum of one flexible wall (Fig. 13), but usually two or more are present (Figs. 14-19).

Number and type of inner flexible walls account for most diversity in spore wall structure. Distinct wall types include the semi-rigid unit wall and the "beaded" membranous wall (Figs. 14-15); the latter complexing with either an innermost membranous (Figs. 18-19) or amorphous wall (Figs. 14-15).

Spore wall material appears to seal the opening to the neck of the sporiferous saccule (Fig. 18).

Spore germination occurs with a germ tube emerging from ephemeral "germination compartments" (Mosse, 1970) between a semi-rigid unit wall and a beaded membranous wall (Fig. 19).

Mycorrhizal vesicles are intraradical (Figs. 32-33); they do not appear to have the potential to become thick-walled spores.

Gigasporaceae

Spores are borne terminally on a sporogenous cell (Spain et al., 1989) (Figs. 20-26).

Spores generally are large, usually exceeding 300 μm in diameter.

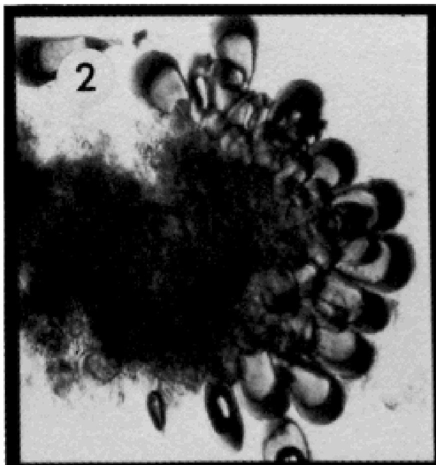
Spores have, as a minimum, a thin outer unit wall tightly adherent with a laminated structural wall (Figs. 20, 22); both walls appear to be continuous with the walls of the sporogenous cell (Gibson et al., 1987).

Flexible inner walls form an "endospore"; with number and type of walls accounting for most structural diversity (Figs. 24-25). Distinct wall types include the coriaceous wall alone or complexed with either a membranous (Fig. 28) or amorphous innermost wall (Figs. 23, 25).

Spore contents are isolated from the sporogenous cell by what appears to be a thin septum (Fig. 26) not discernible in all spores.

Germ tubes arise from a warty germinal wall (Spain et al., 1989) (Fig. 27) or a complex germination shield (Figs. 25, 28).

Mycorrhizae is arbuscular (Figs. 34-35) with thin-walled auxiliary cells (Fig. 35) produced in soil; cell surfaces range from smooth to highly ornamented.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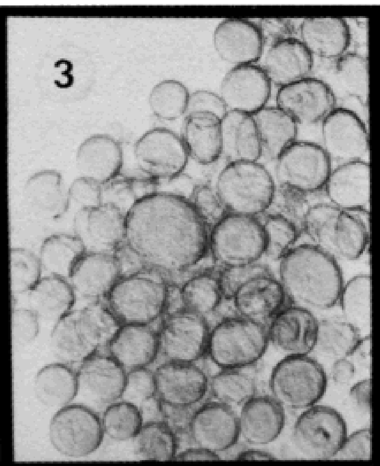
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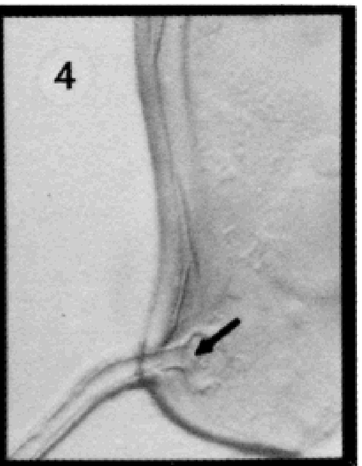
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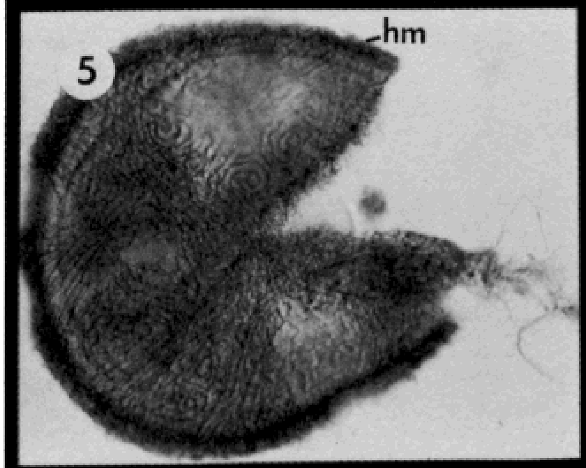
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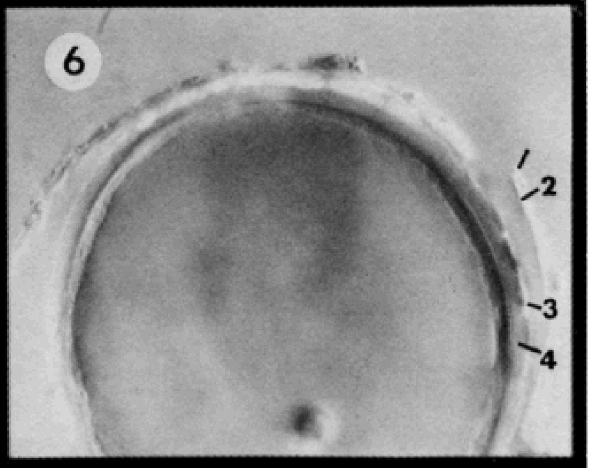
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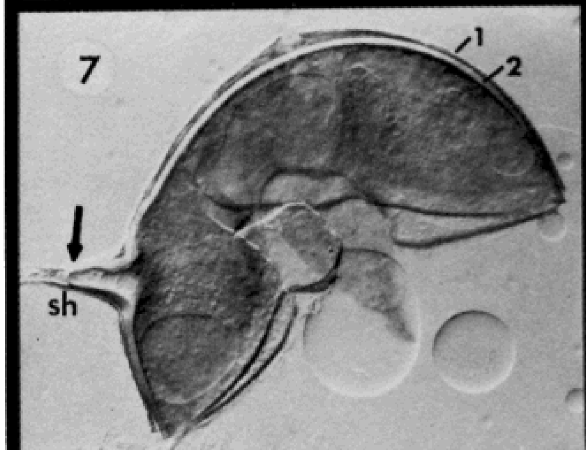
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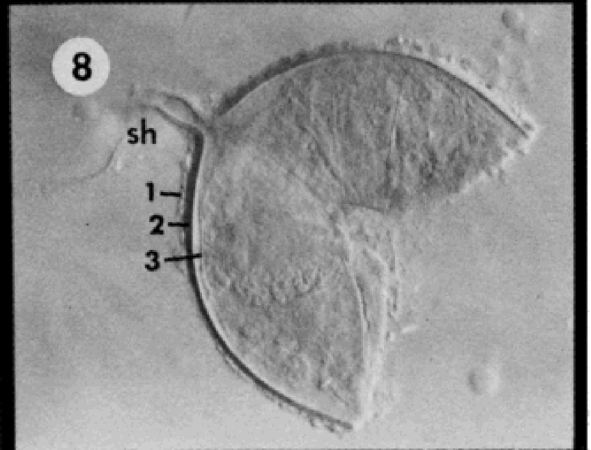
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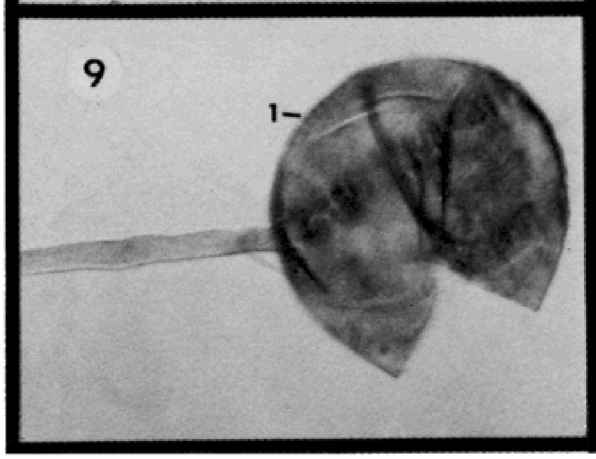
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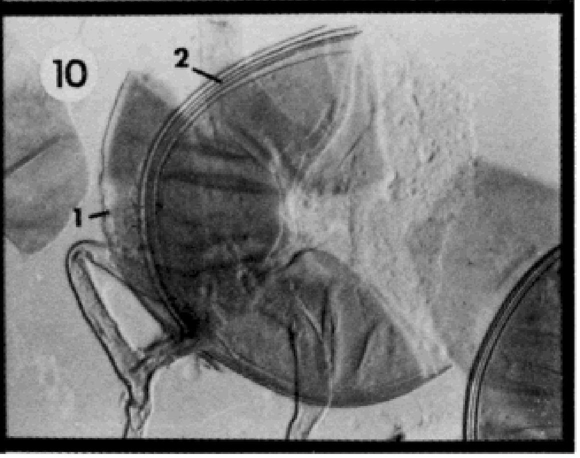
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Rhodes, 1981), but greater documentation is needed because of its putative evolutionary significance in defining divergent lineages.

Acaulosporaceae Morton et Benny, **fam. nov.**

Chlamydosporae gestae a lateribus in vel intra hypha infundibuliformis vel cylindracea in sacculo sporangifere globoso prope terminatae. Chlamydosporae singulatim gregatimve in terra efformatae; post dehiscentia ab collo sacculi sessiles; globosae a irregulare. Chlamydosporae parietibus saltem triformibus: pariete exteriore evanida; pariete lammellata vel monas; parieteque interiore flexile e hyaline. Endomycorrhizae cum vesicules et arbuscules in radicibus; vesiculae ellipsoidae vel irregulares vel lobatae.

"Chlamydospores" formed laterally on or within a cylindrical or funnel-shaped hypha terminating in a sporiferous saccule. Chlamydospores borne singly or occasionally in loose aggregates in soil; sessile after detachment from the saccule neck. Chlamydospores with at least three wall types: an evanescent outer wall, a unit or laminated structural wall, and an inner hyaline flexible wall. Endomycorrhizae with intraradical arbuscules and vesicles; vesicles ellipsoid to irregular to lobed.

Type genus: *Acaulospora* Gerd. & Trappe, 1974 (*Mycologia Mem.* **5**: 31) emend.
Berch, 1986 (*Mycotaxon* **23**: 31).

Other taxon: *Entrophospora* Ames & Schneider, 1979 (*Mycotaxon* **8**:347).

The fossil record holds no clues of the temporal origin or rate of evolutionary change in Acaulosporaceae. This blank geological slate may be attributed more to the absence of sporulation by these fungi in plant roots and poor preservation rather than to recent ancestry.

In *Acaulospora*, species follow a progressive transformation of spores with many *Glomus* characters (e.g. *A. appendicula*) to spores with characters unique to the Acaulosporaceae (Table 1). The branching subtending hypha (of *A. appendicula*) (Fig. 13) appears to be reduced in an evolutionary transition series (Morton, 1990a) from a short "pedicel" in *A. myriocarpa* Spain, Sieverding & Schenck and *A. sporocarpia* Berch to a "collar" in *A. nicolsonii* Walker, Reed & Sanders and *A. spinosa* Walker & Trappe (Fig. 18) and finally to slight thickening between spore and saccule neck. The outer spore wall also is modified from an origin independent of the saccule neck in *A. appendicula* (Fig. 13) to one where it is continuous with the saccule neck (Fig. 11). The formation of spores within the saccule neck (Fig. 12) appears to be a discrete evolutionary advancement canalized in all *Entrophospora* species.

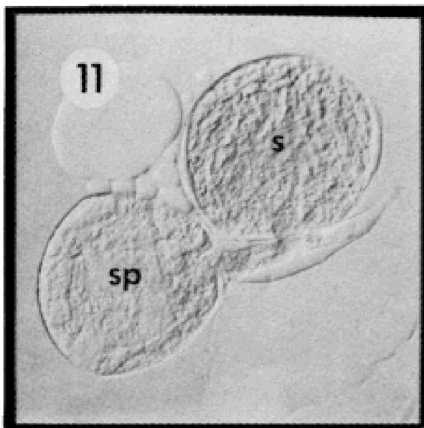
Figs. 2-10. "Chlamydospores" of species in the Glomaceae, mounted in polyvinyl-lactic acid-glycerin (PVLG) and photographed using Nomarski interference optics. Wall numbers correspond to those on murographs depicted in Fig. 29. **2.** *Sclerocystis clavispora* Trappe sporocarp (in transfer to *Glomus* by Almeida & Schenck) (OSC #38,846), x 150. **3.** Loose sporocarp of *Glomus intraradix* Schenck & Smith, (Morton #513), x 66. **4.** Germination of a *G. intraradix* spore (Morton #783), arrow points to germ tube, x 420. **5.** A spore resembling *G. tortuosum* Schenck & Smith (Olexia #156), with a sinuous outer hyphal mantle (hm) covering the laminated wall, x 140. **6.** Complex outer wall structure of *G. fragilistratum* Skou & Jakobsen (Skou #33), x 335. **7.** Spore of *G. mosseae* (Nicol. & Gerd.) Gerd. & Trappe (Morton #787) in Melzer's reagent, arrow points to curved septum in subtending hypha (sh), x 215. **8.** A spore resembling *G. claroideum* Schenck & Smith (Morton #785) in Melzer's reagent, x 242. **9.** A young spore of *G. intraradix* from a 6-week-old sudangrass pot culture (Morton #832), in Melzer's reagent, x 350. **10.** A mature spore of *G. intraradix* from the same culture after 4 months growth, in Melzer's reagent, x 300.

Cladogenesis of *Acaulospora* and *Entrophospora* from a common (hypothetical) ancestor (Morton, 1990a) and subsequent radiation into "sister groups" discloses "historical equivalence" (Wiley, 1980). Emergence of the sporiferous saccule (Figs. 11-12) pinpoints divergence of Acaulosporaceae from Glomaceae. The causal source of this evolutionary novelty is a matter of conjecture since the fossil record is unhelpful. Either some form of parasexual recombination led to the incorporation of new structural and regulatory genes or the sporiferous saccule emerged *de novo* from macromutations in a *Glomus* genotype. Other unique characters emerged (Table 1) during evolution of species initially constrained by this exclusive mode of spore development. Parallel sequences in spore ontogeny and organization are evident in *Acaulospora* and *Entrophospora*. It is so dramatic that species in both genera cannot be distinguished easily without knowledge of hyphal attachment(s). This is exemplified by *A. dilatata* Morton and *E. colombiana* Spain & Schenck (Figs. 14-15), which have indistinguishable spore wall structure (Fig. 29). The large number of character states common to both genera could be the result of common extrinsic selection pressures in ancestral species which led to similar epigenetic constraints in spore development (Morton, 1990b).

Parallelisms signify commonality in genetic background and kindred "evolutionary potentiality" (Cronquist, 1963). Parallelisms common to both Glomaceae and Acaulosporaceae corroborate their close phylogenetic affinities. These characters include: (i) an inner flexible wall which can range in appearance from membranous to semi-rigid, (ii) loose to compact aggregation of spores, (iii) vesicle development in mycorrhizal roots (Figs. 32-33), and (iv) mycorrhizae of some species which stain faintly or not at all in trypan blue (Morton, 1988).

Ontogenetic events in *Acaulospora* and *Entrophospora* appear to be similar at the light microscope level, although only two species of the former and one of the latter have been examined (Morton, unpubl.). Wall groupings originally proposed by Walker (1983) now appear to be highly significant in delineating developmental stages in spore maturation. They explicitly pinpoint temporal breaks in the synthesis of different wall types of the mature spore. In *A. spinosa*, the ornamented structural wall formed first (Fig. 16), a semi-rigid unit wall developed next (Fig. 17), and flexible inner walls formed last (Fig. 18). The synthesis of flexible walls of the inner wall group could not be separated temporally, although a change in Melzer's reaction of the innermost membranous wall from neutral to red-brown indicated that it was the last to mature (Fig. 18). This ontogenetic sequence sets Acaulosporaceae apart from other families in the Glomales.

Figs. 11-19. "Chlamydospores" of species in Acaulosporaceae, mounted in polyvinyl-lactic acid-glycerin (PVLG) and photographed using Nomarski interference optics. Wall numbers correspond to those on murographs depicted in Fig. 29. **11.** Young spore of *A. laevis* Gerd. & Trappe (Morton #579), s = spore, sp = sporiferous saccule, x 120. **12.** Mature spore of *E. colombiana* Spain & Schenck (INVAM #356), broken to show the inner flexible walls still intact as an "endospore", x 165. **13.** Spore of *A. appendicula* Spain, Sieverding & Schenck, (Morton #674) with subtending hypha (sh), x 125. **14.** Spore of *A. dilatata* Morton (Morton #469) in Melzer's reagent, x 250. **15.** Spore of *E. colombiana* (Morton #859) in Melzer's reagent, arrows point to hyphal attachment sites, x 350. **16-18.** Stages in ontogeny of *A. spinosa* Walker & Trappe spores (Morton #745) in Melzer's reagent. **16.** Young spore with only three walls present, x 250. **17.** More mature spore with four walls, x 280. **18.** Fully mature spore with 6 walls, the innermost wall staining red, arrow points to "collar" connecting spore to saccule neck, x 280. **19.** Germination compartments (large arrow) between the semi-rigid wall 3 and the beaded membranous wall 4 of *A. delicata* Walker, Pfeiffer & Bloss (Morton, #793), small arrow points to germ tube, x 330.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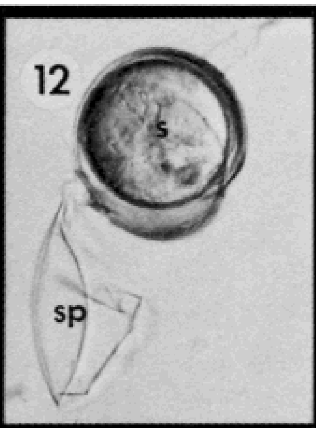
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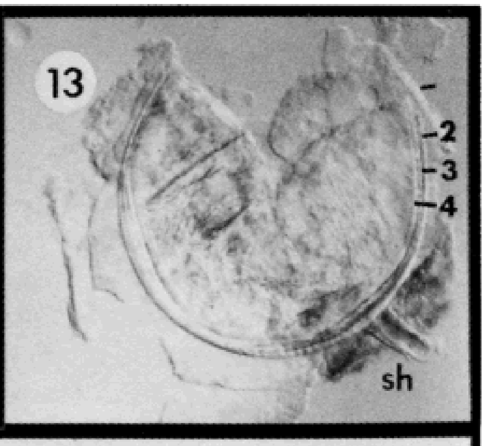
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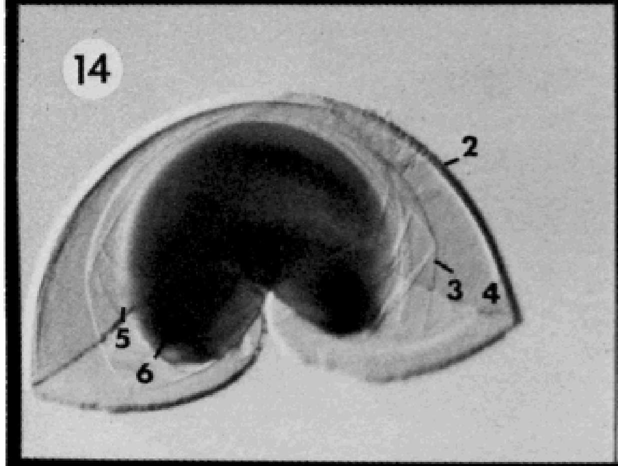
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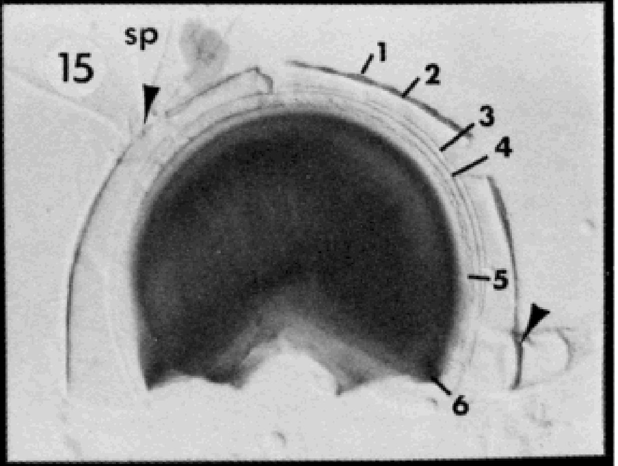
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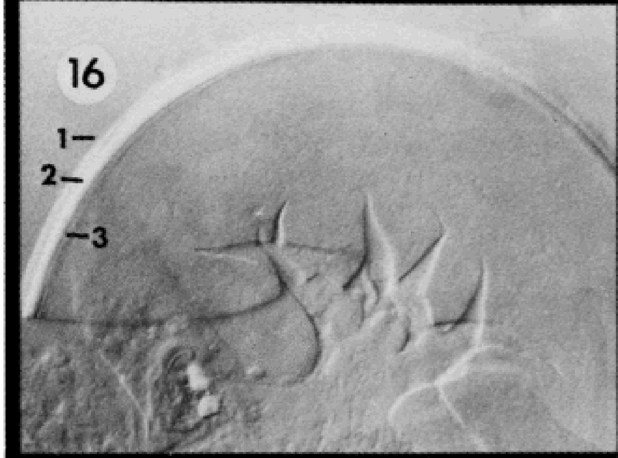
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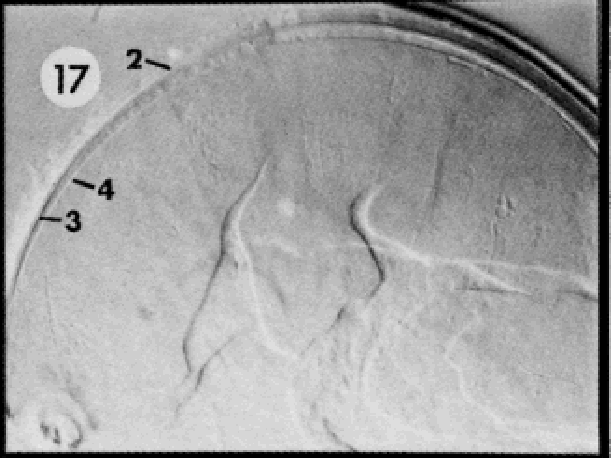
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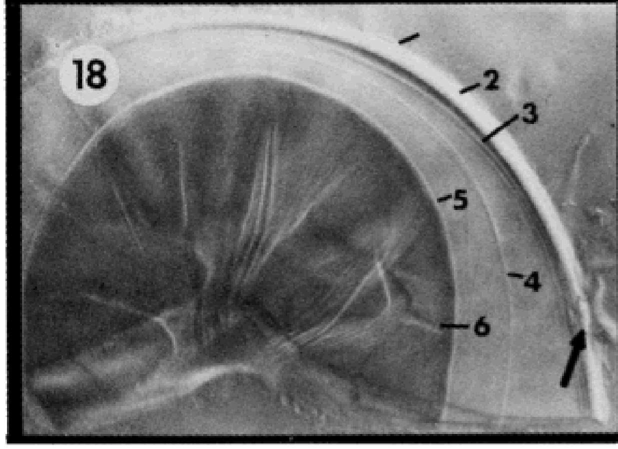
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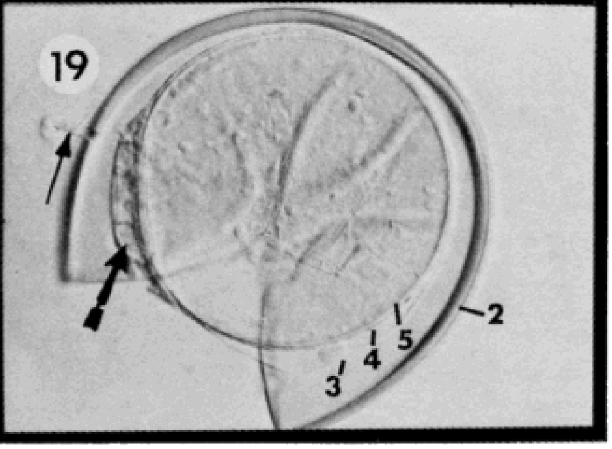
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Mosse (1970) accurately described the "germination compartments" formed in *A. laevis* Gerd. & Trappe, but the absence of observations at the light microscope level failed to expose the ephemeral nature of this structure. In separate observations of germinating spores of *A. laevis* (contributed by C. Gazey and L. Abbott) and *A. delicata* Walker, Pfeiffer & Bloss (from WVU pot cultures), germination compartments were detected between the semi-rigid unit wall and the beaded membranous wall (Fig. 19). These compartments retained structural integrity only when they remained firmly bounded by both walls. When these walls were fractured in crushed spores, the compartments became completely disrupted and were no longer recognizable. Even in intact spores, these compartments still cannot be seen except in transverse views. Thus, this pre-germination structure is morphologically distinct from that in *Scutellispora* spores (Walker and Sanders, 1986). We infer similar germination in *Entrophospora* species, although it has yet to be verified. Germination has not been described for the more primitive transitional species (e.g. *A. appendicula* and *E. infrequens* Ames & Schneider). Knowledge of these events will be important in further documenting relationships between Glomaceae and Acaulosporaceae.

In mycorrhizal roots, intraradical vesicles of both *Acaulospora* and *Entrophospora* are highly variable in shape (Figs. 32-33). They appear to be more more irregularly shaped than those in the Glomaceae, ranging from sausage-shaped (McGee, 1986) to highly lobed (Gerdemann and Trappe, 1974).

Gigasporineae Morton et Benny, **subord. nov.**

Solum arbuscules in mycorrhizarum radices efformatae. Azygosporae in in terra singulares productae; formatur in apice cellulae sporogenae. Cellulae auxiliares efformatae.

Only arbuscules formed in mycorrhizal roots (Figs. 34-35). "Azygospores" formed on the apex of a sporogenous cell. Auxiliary cells formed.

The Gigasporaceae are not vesicular-arbuscular mycorrhizal (or VAM) fungi. They do not form intraradical vesicles in mycorrhizal roots. There is no evidence that auxiliary cells (Fig. 35) are a substitute for the vesicles found in mycorrhizae of Glomaceae and Acaulosporaceae (Figs. 30-33). These extraradical structures are more reminiscent of relict reproductive spores. They do not germinate readily, they show no evidence of being capable of initiating mycorrhizal infection, and morphological complexity of the cell wall is being reversed from highly ornamented cells in *Gigaspora* to smooth in some species of *Scutellispora*. Their persistence in extant taxa may be due to the stabilizing effects of the symbiosis. Strong directional selection pressures against synthesis of auxiliary cell would not develop as long as fitness was not reduced substantially.

Taxa in Gigasporineae have few spore or mycorrhizal characters homologous with those in other families, except for intraradical arbuscular development (Morton, 1990a). The "azygospores" are so distinct developmentally that relatedness to other arbuscular or non-arbuscular zygomycetous fungi is difficult to establish. Structures such as the sporogenous cell and the ever-present hyphal peg branching from this cell (Figs. 11-16) are features suggestive of a development unique from that of sporangia or azygospores in other zygomyceteous fungi. Tommerup (1988) reports separate "azygospores" during zygosporogenesis in *Gigaspora decipiens* Hall & Abbott, but their true identity remains equivocal in the absence of complete descriptions. Walker (1987) suggests that resting spores may be unispored sporangia, a conclusion based on continuity between the outermost unit spore wall and the wall of the sporogenous cell (Gibson et al., 1987). Much more needs to be done examining nuclear condition and hormonal interactions to pin down spore properties.

The absence of a fossil record for Gigasporineae is unfortunate, because the origin of this suborder cannot be resolved cladistically (Morton, 1990a). Evidence of a putative sexual stage in *Gigaspora* (Tommerup, 1988) as well as substantive morphological divergence from a presumed glomuslike ancestor (Morton, 1990a) suggests an independent origin, possibly later in plant evolution.

Rapid morphological divergence of a primitive *Gigaspora* from a glomuslike ancestor cannot be ruled out. But why are there no intermediate species between Glomaceae and Gigasporaceae like those found in the Acaulosporaceae? Assessment of the extent of molecular relatedness relative to morphological divergence (Bruns et al., 1989) in arbuscular families will help to resolve this question. Aldwell et al. (1985) found greater immunological relatedness between hyphal antigens of Acaulosporaceae and Gigasporaceae than those from Glomaceae. These results support the common ancestor hypothesis, but morphological evidence provides strong evidence that the antigens indicated convergence.

Gigasporaceae Morton et Benny, **fam. nov.**

Azygosporae in terra singulares productae, plerumque magnae, globosae vel subglobosae, formantur in apice cellulae sporogenae, cum hypha angusta ad sporam extensa. Azygosporae minimis parietibus duobus; paries externus tenuis; paries interiore lamellatus. Tubuli germinativi parietem prope basim azygosporae directe penetrantes vel ex germinationis clipeo producti. Cellulae auxiliares prietibus tenuis plerumque in terra a hyphis circinatis in greges confertae; superficies spinosa ad laevis. Endomycorrhizae arbusculis in radicibus efferentes.

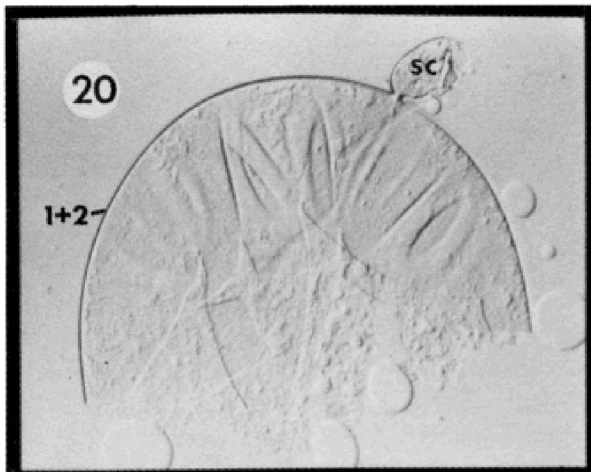
"Azygospores" generally large, globose to subglobose, borne singly in soil on a sporogenous cell with a lateral peg often protruding toward the spore. Azygospores with a minimum of two walls; a thin outer unit wall enclosing a structural laminated wall. Germ tubes produced directly through the wall or from a germination shield. Thin-walled auxiliary cells produced usually in clusters on coiled hyphae in soil; surface ranging from echinulate to smooth. Mycorrhizae forming arbuscules in roots.

Spores generally large, globose to subglobose, borne singly in soil on a sporogenous cell with a lateral peg often protruding toward the spore. Sporangia-like spores with a minimum of two walls: a thin outer unit wall enclosing a structural laminated wall. Germ tubes produced directly through the wall or from a germination shield. Thin-walled auxiliary cells produced usually in clusters on coiled hyphae in soil; surface ranging from echinulate to smooth. Mycorrhizae forming arbuscules in roots.

Type genus: *Gigaspora*, Gerd. & Trappe, 1974 (*Mycologia Mem.* **5**: 25).

Other taxon: *Scutellispora* Walker & Sanders, 1986 (*Mycotaxon* **27**: 179).

Members of *Gigaspora* have no uniquely derived characters (autapomorphies) that distinguish them from species in *Scutellispora* (Morton, 1990a). This pattern in character distribution indicates that the former genus is ancestral to the latter. Ontogeny of spores in *Scutellispora* also corroborates *Gigaspora* as a primitive ancestor [see Nelson (1978) for discussion of Haeckel's biogenetic law of ontogeny recapitulating phylogeny]. Young spores of *Scutellispora* (Fig. 22) are identical in wall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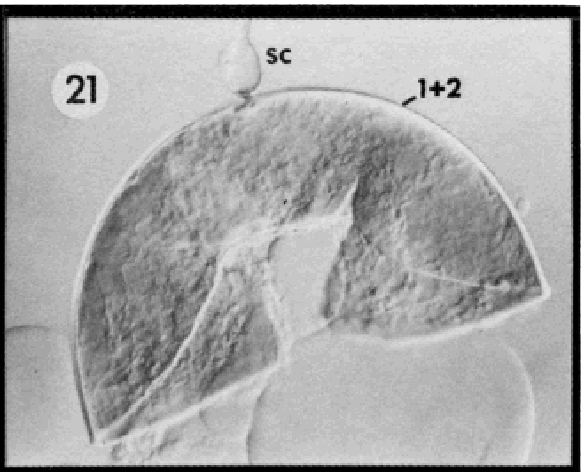
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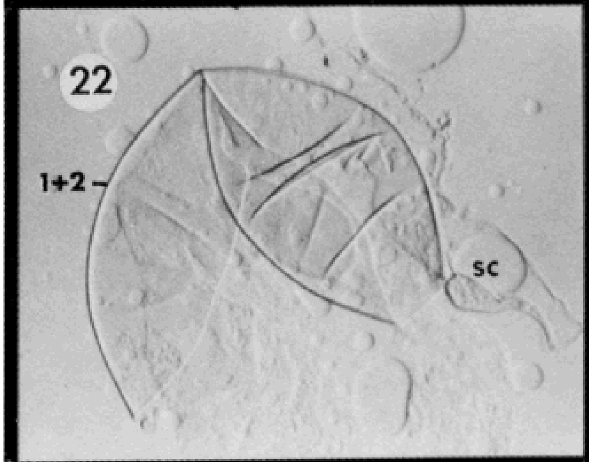
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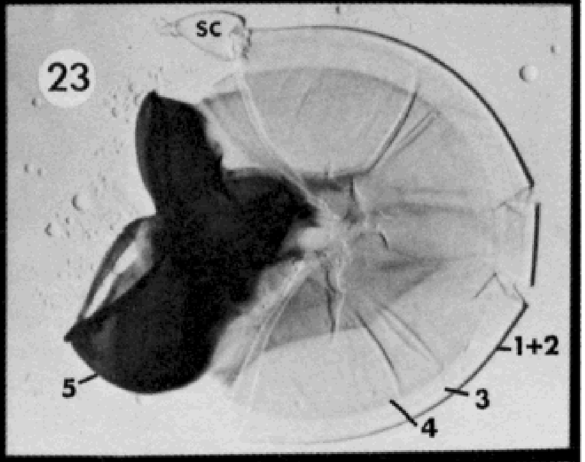
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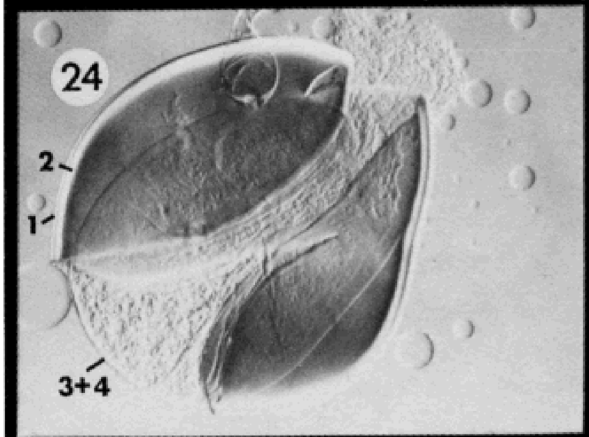
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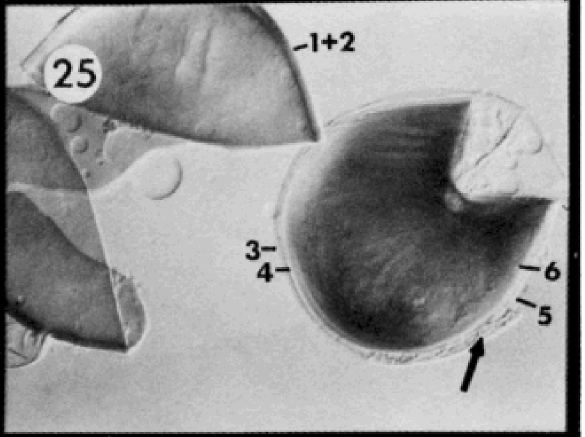
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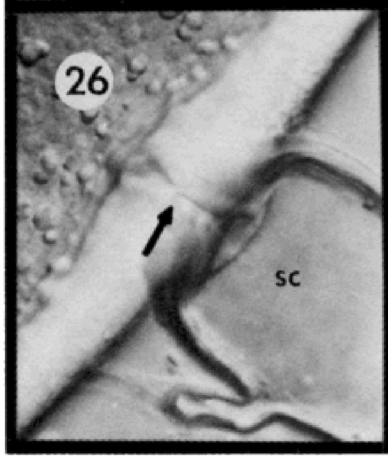
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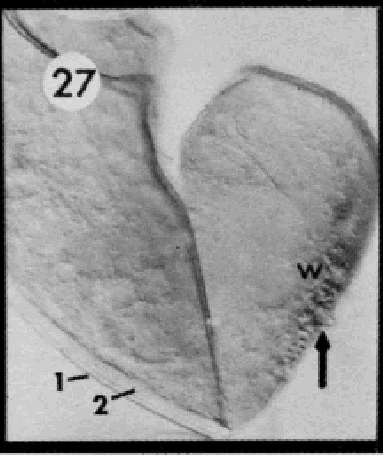
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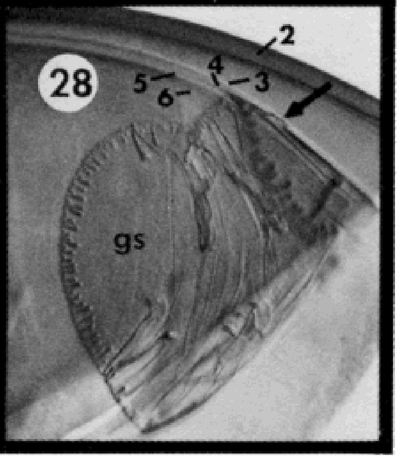
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structure to those of *Gigaspora* young or old (Figs. 20-21). The two outer (structural) walls of *Scutellispora* spores are temporally uncoupled from development of the inner flexible walls (Figs. 22-23).

Maintaining *Gigaspora* and *Scutellispora* as separate genera is misleading for biologists who interpret classification as a direct representation of cladogenesis (Eldredge and Cracraft, 1980). For example, *Acaulospora* and *Entrophospora* are sister groups in the Acaulosporaceae and hence they have approximate equivalence historically. *Gigaspora* is clearly ancestral to *Scutellispora*, and both genera technically should be grouped together (similar to the glomuslike and sessile spore forms of *Acaulospora*). Otherwise, it is interpreted cladistically as a paraphyletic group (Donoghue and Cantino, 1988). We have chosen to sustain this imperfect phenetic separation of *Gigaspora* and *Scutellispora* for the time being until transitional stages between the germinal wall (in *Gigaspora*) and the germination shield (in *Scutellispora*) are more thoroughly investigated. As it stands, origin of *Scutellispora* is marked by major evolutionary advances in organization or "grade" (Mayr, 1963) of spore phenotypes. Virtually all morphological divergence in Gigasporaceae is manifested in *Scutellispora*, where a number of unique morphological characters evolved (Table 1). The sexual stage found only in *Gi. decipiens* could have provided the genetic diversity to ameliorate origin and adaptive radiation (and speciation) in *Scutellispora* from a *Gigaspora* ancestor persisting to the present day. Certainly, evolutionary novelties arose and spread from rather than within *Gigaspora*. The development of an inner flexible wall complex in *Scutellispora* may have had considerable adaptive significance at the time of speciation by providing an additional barrier (as an endospore) against parasitism or some other disruptive extrinsic biotic or abiotic factors. The development of at least one flexible inner wall is directly correlated with origin of the germination shield (Walker and Sanders, 1986). The emergence of additional inner walls, so that the germination shield is positioned between them (Figs. 25, 28), may have had additional adaptive value.

Interspecific morphological divergence in *Gigaspora* is nominal, being limited to quantitative and qualitative characters of questionable heritability (phenotypically too variable). The number of species is low and the distinctions between them are highly equivocal (Morton, 1988). We predict that many species will be combined, so that their number will decrease with time rather than increase. Some continuous characters (e.g. spore size, color, wall thickness, etc.) now used to delimit species may eventually have evolutionary significance [and hence taxonomic value--see Morton (1990b)] once discriminant analyses (Sneath and Sokal, 1973) are applied to sorting

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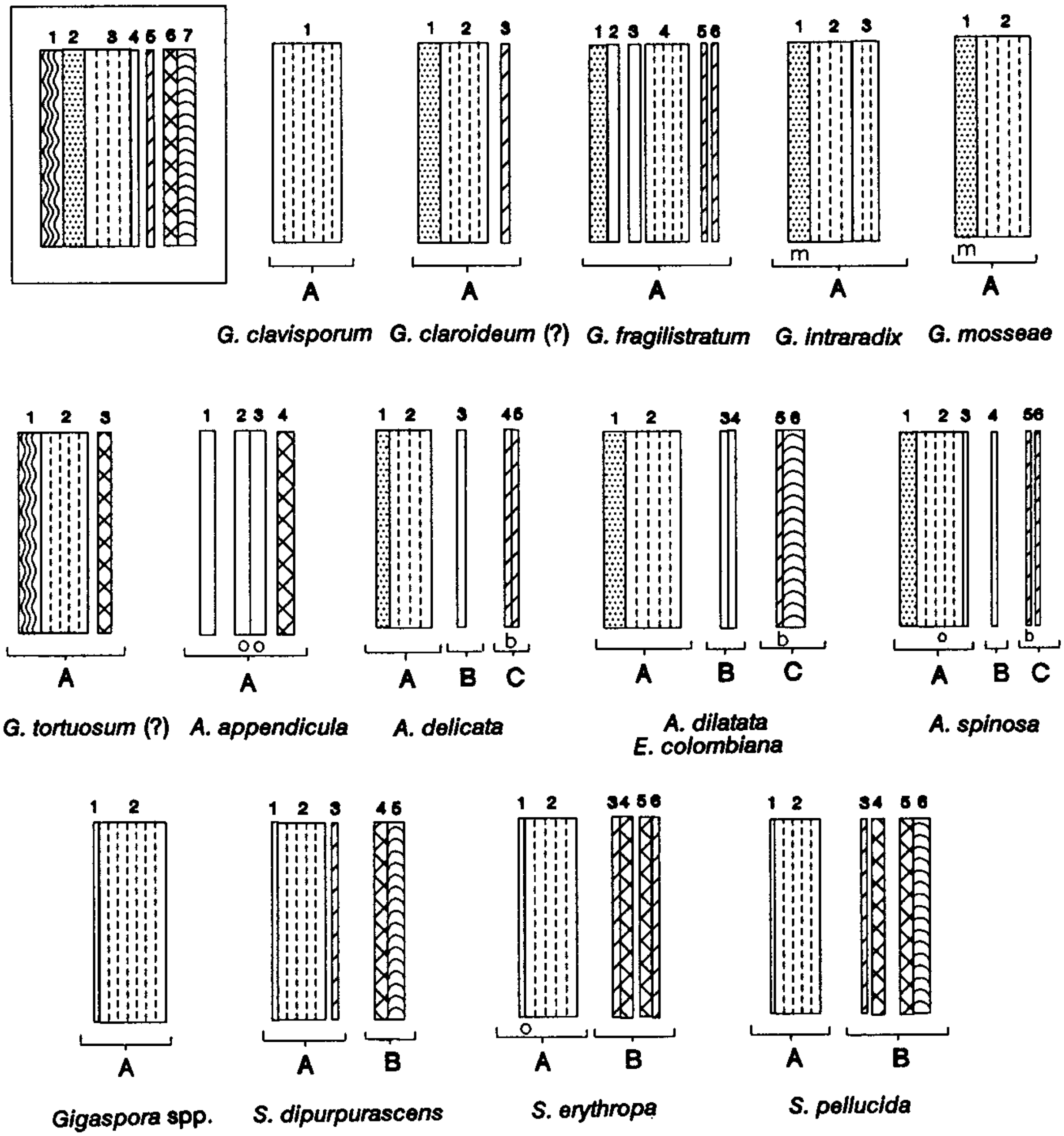
Figs. 20-28. "Azygospores" of species in Gigasporaceae, mounted in polyvinyl-lactic acid-glycerin (PVLG) and photographed using Nomarski interference optics. Wall numbers correspond to those on murographs depicted in Fig. 29. **20.** Immature spore of *Gigaspora margarita* Becker & Hall (Morton #836), sc = sporogenous cell, x 176. **21.** Mature spore of *Gi. margarita* from same culture, x 115. **22.** Immature spore of *S. dipurpurascens* Morton & Koske (Morton #666) in Melzer's reagent, x 100. **23.** Mature spore of *S. dipurpurascens* in Melzer's reagent (Morton #666) x 140. **24.** Immature spore of *S. pellucida* (Nicol. & Schenck) Walker & Sanders (Morton #611) in Melzer's reagent, only four walls present; x 140. **25.** Mature spore of *S. pellucida* in Melzer's reagent, all 6 walls present, arrow pointing to germination shield between walls 4 and 5; (Morton #611) x 120. **26.** Spore of *Gi. gigantea* (Nicol. & Gerd.) Gerd. & Trappe (Morton #550), showing membranous septum (arrow) partitioning spore contents from cytoplasm of the sporogenous cell (sc); x 736. **27.** Germinating spore of *Gi. decipiens* Hall & Abbott (Morton #890), arrow points to the germ tube surrounded by warts of the germinal wall, x 200. **28.** Spore of *S. dipapillosa* (Walker and Koske) Walker & Sanders (Morton #602) in Melzer's reagent, arrow points to the hole left by the germ tube that grew from the germination shield (gs); x 250.

Error in Fig. 28: *S. erythropa* (Walker & Koske) Walker & Sanders (Morton #813)

Fig. 29. Murographs of spore wall structure of species photographed in Figs. 2-28. Walls are numbered consecutively from outer to inner surface of spore. Each wall group is bracketed in parentheses with consecutive capital letters from outer to inner surface of spore. "o" = ornamented, "b" = beaded, "m" = mucilagenous. Numbers above fill patterns in upper left corner bounded box correspond to the following wall types: 1 = peridium (mantle), 2 = evanescent, 3 = laminated, 4 = unit, 5 = membranous, 6 = coriaceous, 7 = amorphous.



Figs. 30-35. Endomycorrhizal roots of red clover (*Trifolium pratense* L.) grown in greenhouse pot cultures; mounted in polyvinyl-lactic acid-glycerin (PVLG). **30.** Vesicular (ve) and arbuscular (ar) colonization by *G. etunicatum* Becker & Gerd. (Morton #579), with extraradical hyphae (hy) growing along outside of root, x 130. **31.** Vesicle (ve) and intraradical sporulation (sp) by *Glomus intraradix* Schenck & Smith (Morton #832), x 195. **32.** Vesicular-arbuscular colonization by *A. spinosa* Walker and Trappe (Morton #745), x 250. **33.** Lobed vesicles (ve) produced by *E. colombiana* Spain & Schenck (INVAM #356), x 325. **34.** Arbuscular colonization (ar) by *Gi. margarita* Becker & Hall (Morton #836), x 300. **35.** Auxiliary cells (au) produced by *S. dipurpurascens* Morton & Koske (Morton #666), x 60.

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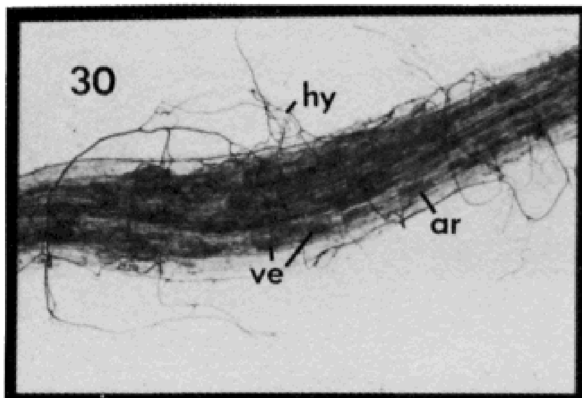
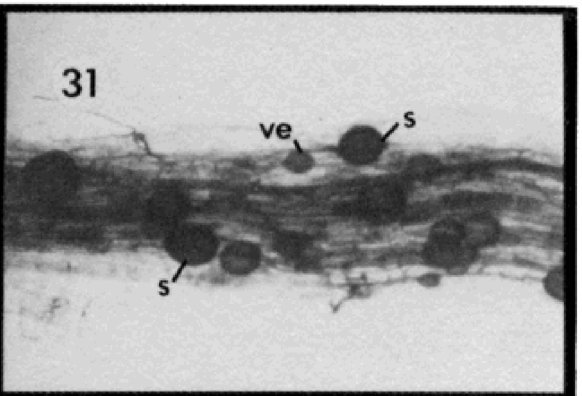
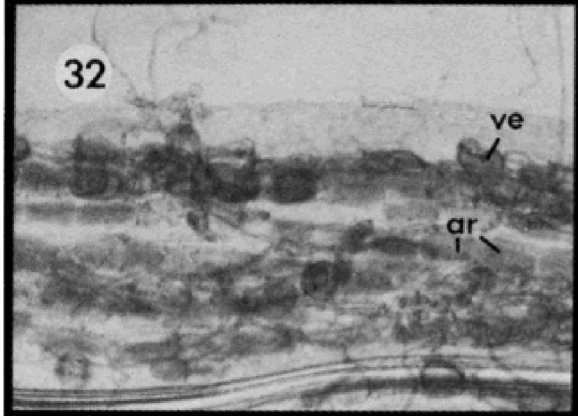
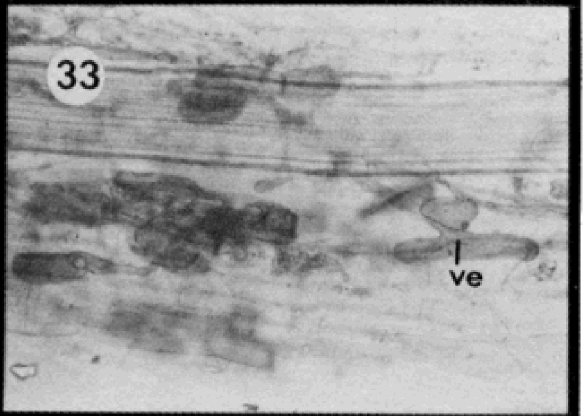
phenetic discontinuities. By most measurable parameters, *Gigaspora* appears to be composed of species which, *historically*, were precariously adapted to the environment in which they originated and that emergence of *Scutellispora* was a natural consequence. The fact that *Gigaspora* is not extinct is indicative of evolutionary stasis and persistence not paralleled in too many other groups of living organisms (Morton, 1990b).

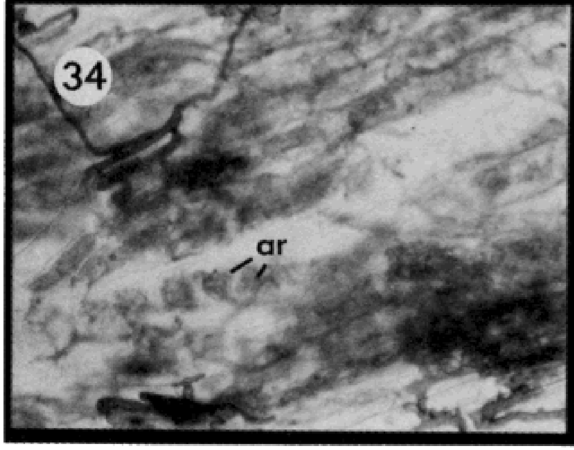
Ontogeny has been followed in spores of several *Scutellispora* species, with *S. pellucida* serving as the representative species in this paper. In young spores, the outer unit and second laminated walls appear to be synthesized almost simultaneously. Spores resemble those seen in Figs. 20 and 22. A dextrinoid reaction in the laminated wall (Fig. 25) sometimes occurs even before the inner flexible wall group forms. This indicates that the temporal gap between structural wall development and flexible wall development is protracted relative to that *within* each group. The inner flexible walls

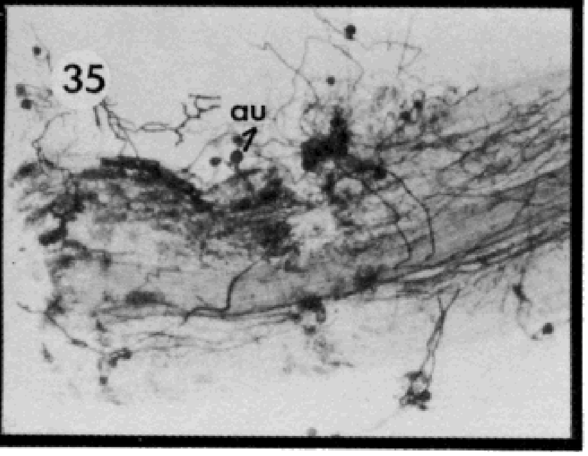












form sequentially from outer to innermost wall, but a temporal break can be detected between flexible walls formed "above" (membranous + coriaceous) (Fig. 24) and "below" (coriaceous + amorphous) the germination shield (Fig. 25). All inner walls appear membranous initially, after which they take on the appearance of mature wall types. The germination shield never is synthesized before all spore walls are fully mature (based on dark red-purple reaction of the innermost amorphous wall in Melzer's reagent) (Fig. 25).

Temporal discontinuities in spore wall development are grossly correlated with number of wall groups. The exception are those species with a germination shield *between* flexible walls, because walls on each side of the germination shield develop discretely. They still appear as one wall group (or "endospore") because of their elasticity [see Fig. 11 in Morton (1988)].

KEY TO TAXA IN GLOMALES

A. Only arbuscules formed in mycorrhizal roots; "Azygospores" produced on the apex of a sporogenous cell of a fertile hypha; auxiliary cells formed	GIGASPORINEAE
With a single family	Gigasporaceae (B)
B. Germ tubes produced directly through spore wall; inner flexible wall group absent; auxiliary cells finely papillate or echinulate	*Gigaspora*
BB. Germ tubes from germination shield; inner flexible wall group always present; auxiliary cells knobby, broadly papillate, or smooth	*Scutellispora*
AA. Arbuscules and vesicles formed in mycorrhizal roots. "Chlamydospores" produced terminally or laterally on or within fertile hyphae; auxiliary cells not produced	GLOMINEAE (C)
C. "Chlamydospores" formed apically from fertile hyphae	Glomaceae (D)
D. Fruiting body of a sporocarp composed of spores will lateral walls adherent to one another; connecting hyphae embedded in a central hyphal plexus; chlamydospores in a single layer except at the base; base composed of sterile hyphae	*Sclerocystis*
DD. Fruiting structure a sporocarp not formed as in "D" above; spores also produced singly or in loose to tight aggregates in soil, less commonly in roots	*Glomus*
CC. "Chlamydospores" formed from or within the "neck" of a sporiferous saccule	Acaulosporaceae (E)
E. Spores arise laterally from the neck of a sporiferous saccule	*Acaulospora*
EE. Spores formed in the neck of the sporiferous saccule	*Entrophospora*

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