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Glomeromycota: three new genera and glomoid species reorganized

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Abstract —Species in the orders *Glomerales* and *Diversisporales* (*Glomeromycetes*) with glomoid spore formation are reorganized based on combined ribosomal sequence and morphological analyses. Within the *Glomerales* two genera in the *Glomeraceae* (*Septoglomus, Simiglomus*) and one genus in the *Claroideoglomeraceae* (*Viscospora*) are proposed as new. *Paraglomerales* species (thus far monogeneric) also form glomoid spores that may all germinate directly through the spore wall instead through subtending hyphae as in *Glomerales*.

Key words — *Glomus* group A, *Glomus* group B, molecular phylogeny, rDNA

Introduction

Molecular biological studies have dramatically improved the understanding of phylogenetic relationships across a broad swathe of organisms. Arbuscular mycorrhizal (AM) fungi are no exception, as molecular analyses have expanded our knowledge of this group (e.g. Simon et al. 1992, Redecker et al. 2000a, b, Morton & Redecker 2001, Schwarzott et al. 2001, Schüßler et al. 2001, Souza et al. 2005, Palenzuela et al. 2008, 2010). This has led to taxonomic re-organization and the description of several new genera and families (e.g. Morton & Redecker 2001, Walker et al. 2007, Oehl et al. 2008). Schüßler et al. (2001) established the phylum *Glomeromycota* with four orders (*Archaeosporales*, *Diversisporales*, *Glomerales*, *Paraglomerales*) within one class (*Glomeromycetes*) described earlier by Cavalier-Smith (1998).

Within the *Glomeromycota*, species with glomoid spore formation represent the largest group. These species had previously been included within the *Glomeraceae* (Pirozynski & Dalpé 1989) of the suborder *Glomerineae* of the *Glomerales* (Morton & Benny 1990). However, after this large group of *Glomus* species was found to be polyphyletic (e.g. Redecker et al. 2000b, Schwarzott et al. 2001), several glomoid spore-forming species were separated from the *Glomerales* sensu Morton & Benny. Based on DNA sequence analyses, *Gl. occultum* was declared type species of the new genus *Paraglomus* (*Paraglomeraceae;* Morton & Redecker 2001) in the new order *Paraglomerales* (Schüßler et al. 2001). *Glomus spurcum* was moved as type species to a new genus *Diversispora* (Walker & Schüßler 2004) in the *Diversisporaceae* (*Diversisporales*) (Schüßler et al. 2001). More recently Oehl & Sieverding (2004) established *Pacispora* (*Pacisporaceae*, Walker & Schüßler 2004) with *Glomus scintillans* S.L. Rose & Trappe (Rose & Trappe 1980) as type species for all glomoid species possessing two spore walls and specific germination characteristics. Moreover, some glomoid species were recently transferred into the *Ambisporaceae* of the *Archaeosporales* (e.g. *Gl. callosum*, *Gl. fecundisporum, Gl. leptotichum*; Walker et al. 2007, Walker 2008). However, the remaining large group of *Glomus* spp. is considered particularly difficult to differentiate morphologically (Morton & Redecker 2001, Schwarzott et al. 2001, Walker & Schüßler 2004).

Phylogenetic reconstructions within AM fungi over the last 10 years indicate that this large group of *Glomus* species likely originated from a single ancestor, from which (according to Schwarzott et al. 2001) descend the *Glomus* groups Aa (related to *Gl. mosseae* and *Gl. geosporum*), Ab (related to *Gl. intraradices* and *Gl. irregulare*), Ac (related to *Glomus* sp. W3347, now *Gl. hoi*; see Daniell et al. 2001, Öpik et al. 2006), and B (related to *Gl. etunicatum*). Schüßler et al. (2001) also showed that the clades of groups Aa, Ab and B divide further. Adapting and slightly modifying the numbering system of Schwarzott et al. (2001), we differentiate the clades into group Aa1 (lead sp. *Gl. mosseae*), Aa2 (lead sp. *Gl. hoi*), Aa3 (lead sp. *Gl. constrictum*), Ab1 (lead spp. *Gl. microcarpum, Gl. macrocarpum*), Ab2 (lead spp. *Gl. intraradices*, *Gl. irregulare, Gl. aggregatum*), Ab3 (lead spp. *Gl. sinuosum, Gl. coremioides*), B1 (lead sp. *Gl. etunicatum*), and B2 (lead sp. *Gl. viscosum*). In the present study, "lead species" are those with typical morphological characters and not necessarily type species. Under "Results & discussion" we present the supporting phylogenetic clades and detail the major morphological spore characteristics for each of our groups — Aa1, Aa2, Aa3, Ab1, Ab2, Ab3, B1, B2. In those cases where morphological and molecular data are congruent, species of the same group and number can be classified together at the genus level (e.g., group Aa1 represents one genus, while Aa2 represents another genus), while the major groups A and B are suggested to be family levels. In the case of clades Ab1, Ab2, Ab3, however, the molecular database remains under-represented with regard to the known species and the results are contradictory, as some sequences are derived from species that have been only poorly characterized. Although the morphological data indicate a division of Ab into at least three subgroups (genera), we currently lack sufficient genetic data to support new genera. Thus, clades Ab1, Ab2, Ab3 will be considered in one single genus (group Ab) at this time.

Previous phylogenetic analyses indicated that several *Glomus* spp. (e.g. *Gl. versiforme*) belong to clade '*Glomus* group' 'C' (e.g. Schwarzott et al. 2001, Schüßler et al. 2001, Redecker et al. 2007), currently *Diversispora* (*Diversisporaceae*). Only six glomoid spore-forming species have so far been included in this genus (Walker & Schüßler 2004, Gamper et al. 2009, Schüßler & Walker 2010). The morphology of *Diversispora* spores differs, however, from spores of groups A and B. We call this group of species "group Ca" and will transfer them to the genus *Diversispora.*

Recently, Redecker et al. (2007) identified another *Glomus* group (including *Gl. fulvum* and *Gl. pulvinatum*) that was genetically related to group C but phylogenetically and morphologically clearly distinct from group Ca (*Diversispora*). The authors did not separate this group from the other species of group C (*Diversispora*), possibly due to lack of recognition of the morphologically distinct features of spores. Recently, Schüßler & Walker (2010) erected the genus *Redeckera* ("group Cb") with three species (*Gl. fulvum*, *Gl. megalocarpum,* and *Gl. pulvinatum*) within the *Diversisporaceae.*

When Schüßler et al. (2001) proposed a new phylum for the AM fungi, although they initiated a principal re-organization of species with the four orders, they did not propose families and genera that were clearly separated genetically from each other. For example, *Diversisporales* and *Diversisporaceae,* lacking either type genus or type species, were at that time invalidly described, while the same authors mentioned only that some *Glomus* groups in the *Glomerales* and *Glomeraceae* were clearly genetically different. This had the unfortunate result that other taxonomists or ecological mycorrhizologists continued to refer to *Glomus* group A, group B, and 'the like' as Schüßler et al. (2001) had called them. Even new taxa were being justified on the basis of small differences in partial rDNA sequences within such *Glomus* groups as A, B or C (e.g. Błaszkowski et al. 2004, 2006, 2008, Oehl et al. 2005). Furthermore, in a recent study (Gamper et al. 2009) species of *Glomus*, *Diversispora* and others, e.g. *Glomus versiforme* and *D. celata,* were shown to be phylogenetically strongly related, although no attempts were made to reorganize *Gl. versiforme* and related '*Glomus*' spp. into *Diversispora*. In ecological studies, so-called 'environmental sequences' (DNA sequences from AM species as yet unrecorded in databases, often directly recovered from mycorrhizal root or soil analyses instead of from identified spores) are named and referred to as '*Glomus* sp. uncultured' or

‘*Glomus* unknown,’ not particularly helpful to someone who wishes to know whether the species so named represents *Diversispora*, *Glomus* group A or B sensu Schüßler et al., or a different group that might have completely different spore formation.

It is clear that an improved phylogeny of *Glomus* is urgently needed (see also Krüger et al. 2009, Stockinger et al. 2009). Currently, new or unknown species that are related to ‘groups of genetically related fungi’ but belong to clearly distinct phylogenetic groups continue to be called ‘*Glomus*’ and thus remain incorrectly classified. One motivation for this paper was the feeling that because *Gl. versiforme* has been supported as belonging to *Diversispora*, it should officially be included within that genus. From that it followed that if group A could phylogenetically be separated from groups B and C (*Diversispora*), a new organization of the known and described species is both justified and necessary. A first attempt was tried only recently by Schüßler & Walker (2010); however, these authors based their conclusions almost exclusively on molecular analyses and did not correlate their phylogenetic results with the morphological characters of the different phylogenetic clades that our analyses indicate.

The objectives of the present study were therefore to: 1) identify and describe morphological differences or similarities of species in the various ‘*Glomus* groups,’ and 2) reorganize the species into existing or new genera as accurately as possible according to currently available information. Thus, we aim here at re-organizing the AM fungal species with glomoid spore formation using existing genetic information combined with existing or new morphological spore characteristics within the *Glomerales* and *Diversisporales.*

Material & methods

Specimen analyses

We analyzed specimens representing 101 of a total 117 described *Glomus* and *Diversispora* spp. (TABLE 1). Holotype, isotype, paratype and ex-type materials were examined along with representatives from institutional herbaria — OSC, FH, Z+ZT, URM (Recife, Brazil), Embrapa Agrobiologia (Seropédica, Brazil), DCS-UFLA (Lavras, Brazil), International Culture Collection of Vesicular-Arbuscular Mycorrhizal Fungi (INVAM), Swiss collection of Arbuscular Mycorrhizal Fungi (SAF, Agroscope ART Zurich) — and private AM fungal collections curated by Sieverding, Oehl, Trappe, Błaszkowski, McGee, and Goto. The Hall & Abbott (1979) photographic slide collection was also reviewed. For this paper, all original species descriptions and published species emendations were also considered.

Older specimens (mounted on microscopic slides prior to 1990) were mostly mounted in lactophenol, while others were fixed with polyvinyl alcohol-lactic acid-glycerol (PVLG) or in a mixture of PVLG + Melzer’s reagent, which post-1990 are the principal fixing media (Brundrett et al. 1994). Newly mounted spores and sporocarps from collections or from cultures were fixed using the latter two fixing media, or occasionally also in a mixture of 1:1 lactic acid to water, in Melzer’s reagent, and in water.

When available, spores freshly isolated from soils or bait cultures were also mounted and analyzed. Spore wall terminology follows the nomenclature of Walker (1983) and Stürmer & Morton (1997). Analyses of the spore walls, the germination structures and all other mycorrhizal structures were performed using compound microscopes at 100–1000×. Most photographs were taken with a digital camera (Olympus model DP70-CU) mounted on a Zeiss Axioplan compound microscope, although a few were taken at OSC, URM or INVAM during short-term visits. Legends and scales were inserted with Adobe Photoshop CS2 9.0.

All spore observations and all information on spore characteristics are based on spores extracted from soil, from trap cultures or from single or multiple spore-derived pure cultures. No information is provided from in-vitro-cultured materials.

Molecular and phylogenetic analyses

Genes analyzed: Partial sequences of β-tubulin and rRNA (SSU and LSU) genes were used to reconstruct, by independent analyses, the phylogeny of the *Glomeromycota*. Intron sequences from the β-tubulin gene were excluded and only exon regions were considered within analyses. ITS sequences were also used to clarify relationships among members of the *Diversisporales*.

Sequence alignment: The sequences (all obtained from the National Center for Biotechnology Information-NCBI) were aligned using the program ClustalX (Larkin et al. 2007) and edited with the BioEdit program (Hall 1999) to obtain a final alignment.

Table 1. Type and non-type specimens from 115 *Glomus* and 2 *Diversispora* species analyzed for reorganization of the *Glomerales*.

Species name	Type material (observer)	Non type material (observer)
Diversispora spurca	Ex type at INVAM (Oehl)	Specimen from Bolivia & Oman (Oehl)
Di. celata	Ex type, inclusive pure cultures (Oehl)	Specimen from Switzerland (Oehl)
Glomus achrum	Type (Oehl), ex type (Goto)	
Gl. africanum	No access	
Gl. aggregatum	Type OSC #40254 (Oehl)	OSC #45840 (Oehl)
Gl. albidum	Holotype OSC #40400 (Oehl)	
Gl. ambisporum	Holotype OSC #44289 (Oehl)	Specimen from Bolivia, Benin (Oehl)
Gl. antarcticum	No access	
Gl. arborense	No access	
Gl. arenarium	Type at OSC (Oehl), ex type (Goto)	Specimen from Chile and UAE (Sieverding)
Gl. atrouva	Ex type (Oehl, Goto)	
Gl. aurantium	Type (Oehl)	Specimen from Germany (Oehl)
Gl. aureum	Holotype Z+ZT, isotypes OSC #; FB; Pure culture (Oehl)	Specimen & pure cultures from Central Europe (Oehl)
Gl. australe	No access	(Trappe, McGee, Oehl)
Gl. avelingiae	No access	
Gl. badium	Holotype Z+ZT, isotypes deposited at OSC (Sieverding, Oehl)	Specimen from Central Europe (Oehl, Sieverding)
Gl. bagyarajii	No access	
Gl. bistratum	Type (Oehl), ex type (Goto)	
Gl. boreale	Photographic slide collection of Hall & Abbott (1979)	
Gl. botryoides		Trappe collection (Oehl)
Gl. brohultii	Ex type (Sieverding)	Specimen from Benin (Oehl), and Costa Rica (Sieverding)
Gl. caesaris	Holotype Z+ZT, isotypes OSC #; FB; Pure culture (Oehl)	Specimen and pure cultures from Germany (Oehl)

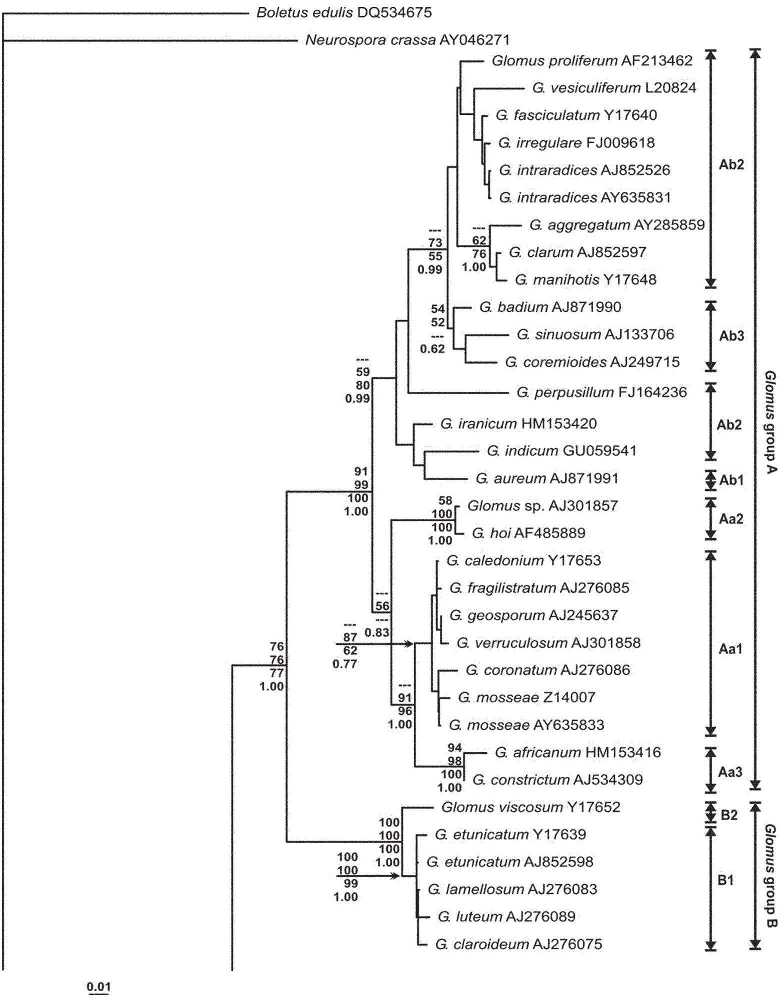
Table 1, continued

Gl. caledonium	Type FH (Oehl)	Specimen and pure cultures from Central Europe (Oehl)
Gl. canadense		Thaxter collection, Trappe collection (Oehl)
Gl. candidum	No access	
Gl. canum	Ex type (Oehl, Goto)	
Gl. cerebriforme	Ex type (Oehl)	
Gl. citricola	No access	
Gl. claroideum	Type OSC #40252 (Oehl)	Specimen from Brazil, Europe (Oehl), cultures from Benin (Oehl)
Gl. clarum	Ex type specimen (Sieverding)	INVAM; specimen from Colombia (Sieverding)
Gl. clavisporum	Ex type (Oehl))	Specimen from Benin (Oehl)
Gl. constrictum	Paratypes OSC #38850 (Oehl, Sieverding)	Specimen and pure cultures from Central Europe (Oehl)
Gl. convolutum	Paratype OSC #30986, ex isotype (Oehl)	
Gl. coremioides		Specimen from Brasil (Goto); Trappe collection (Oehl)
Gl. coronatum	Ex type (Oehl)	Specimen from India, Mexico, Spain (Oehl)
Gl. corymbiforme	Type OSC # 53909 (Oehl)	
Gl. cuneatum	Ex type (Goto)	
Gl. delhiense	No access	
Gl. diaphanum	Ex type (Oehl)	Specimen from Central Europe, Bolivia (Oehl)
Gl. dimorphicum	No access	
Gl. deserticola	Holotype 44474, Paratype OSC #47834 (Oehl)	Colombia (Sieverding)
Gl. dolichosporum	No access	
Gl. drummondii	Type (Oehl), ex type (Goto)	
Gl. eburneum	Ex type at INVAM (Oehl)	Specimen from Bolivia & Oman (Oehl)
Gl. epigaeum	Holotype OSC #39475 (Oehl)	
Gl. etunicatum	Holotype OSC (Oehl)	Specimen from Benin, Bolivia, Paraguay, Europe, Mexico (Oehl)
Gl. fasciculatum	Type *sensu* (Walker & Koske 1987)	Specimen from Central Europe (Oehl, Sieverding)
Gl. flavisporum		Trappe collection (Oehl)
Gl. formosanum		Specimen from UAE (Sieverding)
Gl. fragile		Trappe collection (Oehl)
Gl. fragilistratum	Ex type at INVAM (Oehl)	Specimen from Switzerland (Oehl)
Gl. fuegianum		Trappe collection (Oehl)
Gl. fulvum		Trappe collection (Oehl)
Gl. geosporum	Type OSC #29419 (Oehl)	Specimen and pure culture and from Central Europe (Oehl)
Gl. gibbosum	Type: Błaszkowski online pages	Specimen from UAE (Sieverding)
Gl. globiferum	Holotype OSC #46718 (Oehl)	Specimen at INVAM (Oehl)
Gl. glomerulatum	Isotype OSC #46674, ex type (Sieverding)	Specimen from Brazil (Goto)
Gl. goaense	No access	
Gl. halonatum	Paratype Trappe 3594 (Oehl)	Specimen from Brazil (Goto)
Gl. heterosporum	Holotype 44288 (Oehl)	Specimen from Germany (Oehl)
Gl. hoi	Paratype Trappe 3058 (Oehl)	Specimen from Germany (Oehl), cultures from Benin (Oehl, IITA)
Gl. hyderabadense		Specimen from Benin (Oehl) and from Colombia (Sieverding)
Gl. indicum	No access	
Gl. insculptum	Type (Oehl)	
Gl. intraradices		Specimen and cultures from Europe &, specimen from INVAM (Oehl)
Gl. invermaium	Isotype OSC #43941 (Oehl)	Specimen from UAE (Sieverding)
Gl. iranicum	No access	
Gl. irregulare	Type (Oehl)	Specimen from Switzerland (Oehl)

Table 1, concluded.

Gl. kerguelense		Specimen from UAE (Sieverding)
Gl. lacteum	Type OSC (Oehl)	
Gl. lamellosum	Isotype OSC #50183 (Oehl)	Specimen from Poland, Germany (Oehl, Sieverding)
Gl. liquidambaris		Specimen from Brazil (Oehl, Goto)
Gl. luteum	Type OSC, ex type INVAM (Oehl)	
Gl. macrocarpum		INVAM; specimen from Central Europe, Benin, Mexico (Oehl)
Gl. magnicaule	Ex type, photographic slide collection by Hall & Abbott (1979) (Oehl)	
Gl. manihotis	Holotype OSC #41498 (Oehl)	
Gl. megalocarpum	Holotype OSC #28739, ex type (Oehl)	
Gl. melanosporum	Holotype OSC #, ex type (Oehl)	
Gl. microaggregatum	Holotype OSC #46719 (Oehl)	Specimen from Mexico (Oehl)
Gl. microcarpum	Ex type (Oehl)	Specimen from Central Europe (Oehl)
Gl. minutum	Ex type (Oehl)	
Gl. monosporum	Type OSC (Oehl)	Specimen from Switzerland (Oehl)
Gl. mortonii	Holotype OSC #49460 (Oehl)	Specimen from Germany (Oehl, Sieverding)
Gl. mosseae	Holotype FH (Oehl)	Specimen and pure cultures from Germany (Oehl)
Gl. multicaule	Holotype OSC #35386 (Oehl)	
Gl. multiforum	Type (Oehl)	Specimen from Switzerland &India (Oehl)
Gl. nanolumen	Isotype OSC #49585	
Gl. pachycaule		Specimen from India and Benin (Oehl)
Gl. pallidum	Type at PDD (Oehl)	
Gl. pansihalos	Holotype OSC (Oehl)	Specimen at INVAM (Oehl)
Gl. pellucidum	Ex type (Oehl, Goto)	
Gl. perpusillum	Type (Oehl), Ex type (Goto)	
Gl. proliferum	Ex type (Oehl)	
Gl. przelewicense	No access	Specimen and pure pot cultures from Switzerland (Oehl, Sieverding)
Gl. pubescens		OSC #30990 (Oehl)
Gl. pulvinatum		Trappe collection (Oehl)
Gl. pustulatum	Holotype OSC #46721 (Oehl)	Błaszkowski collection (Oehl)
Gl. radiatum		Trappe collection (Oehl)
Gl. rubiforme	Type OSC #30931, paratypes (Oehl)	Specimen from Switzerland (Oehl)
Gl. segmentatum	Type , ex type (Oehl)	
Gl. sinuosum		Specimen and cultures from Central Europe, India, Oman, Benin, Bolivia (Oehl, Sieverding)
Gl. spinosum	Ex type (Sieverding)	
Gl. spinuliferum	Holotype Z+ZT, isotopes at OSC & FB (Oehl, Sieverding)	Specimen from Switzerland (Oehl)
Gl. taiwanense		Specimen from Benin (Oehl), Thailand (Sieverding), Brasil (Goto)
Gl. tenebrosum		Specimen from Switzerland (Oehl)
Gl. tenerum		Specimen from Australia (Oehl)
Gl. tenue		Specimen from alpine areas (Oehl)
Gl. tortuosum	Type OSC #40‘251 (Oehl)	OSC #32894
Gl. trimurales	Holotype OSC #49584 (Oehl)	
Gl. verruculosum	Ex type, INVAM (Oehl)	
Gl. versiforme		Specimen at INVAM; specimen from Central Europe (Oehl, Sieverding)
Gl. vesiculiferum		OSC #28727 (Oehl)
Gl. viscosum	Ex type (Oehl)	Specimen at INVAM
Gl. walkeri	Type (Oehl), ex type (Goto)	
Gl. warcupii	Ex type (Oehl)	
Gl. xanthium	Type (Oehl) ex type (Goto)	
Gl. zaozhangianum	No access	

Phylogenetic analyses: The main tree was constructed by a heuristic search using the maximum likelihood (ML) method with the Phylogenetic Analysis Using Parsimony (PAUP) program version 4 (Swofford 2003). Maximum parsimony (MP) and neighbor joining (NJ) analyses with 1000 bootstrap replications also were performed by PAUP. Bayesian (two runs over 1 x 10^6 generations with a burnin value of 2500) and maximum likelihood (1000 bootstrap) analyses were executed, respectively, in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) and PhyML (Guindon & Gascuel 2003), launched from Topali 2.5. The model of nucleotide substitution was estimated using Topali 2.5 (Milne et al. 2004). Sequences from *Neurospora crassa, Boletus edulis, Rhizophydium sphaerotheca* were used as outgroups for *Glomeromycota*, and *Glomus intraradices* and *G. xanthium* for *Diversisporales* (ITS analysis).



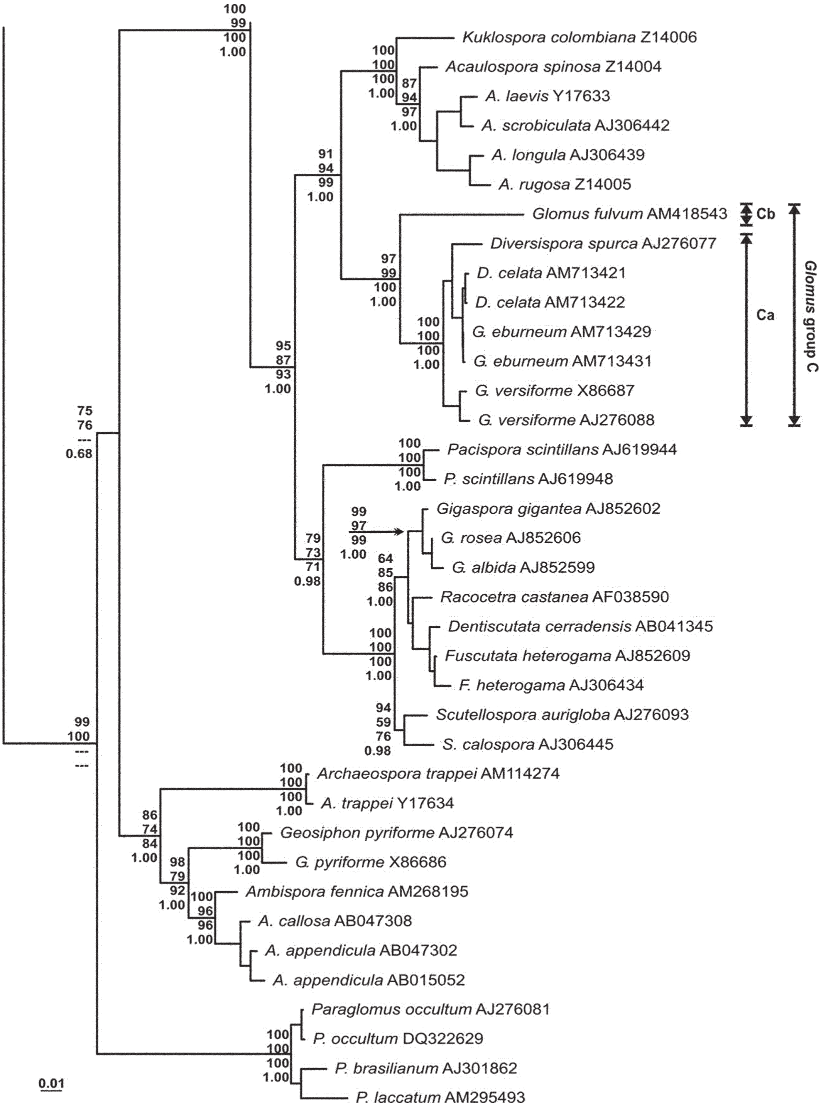
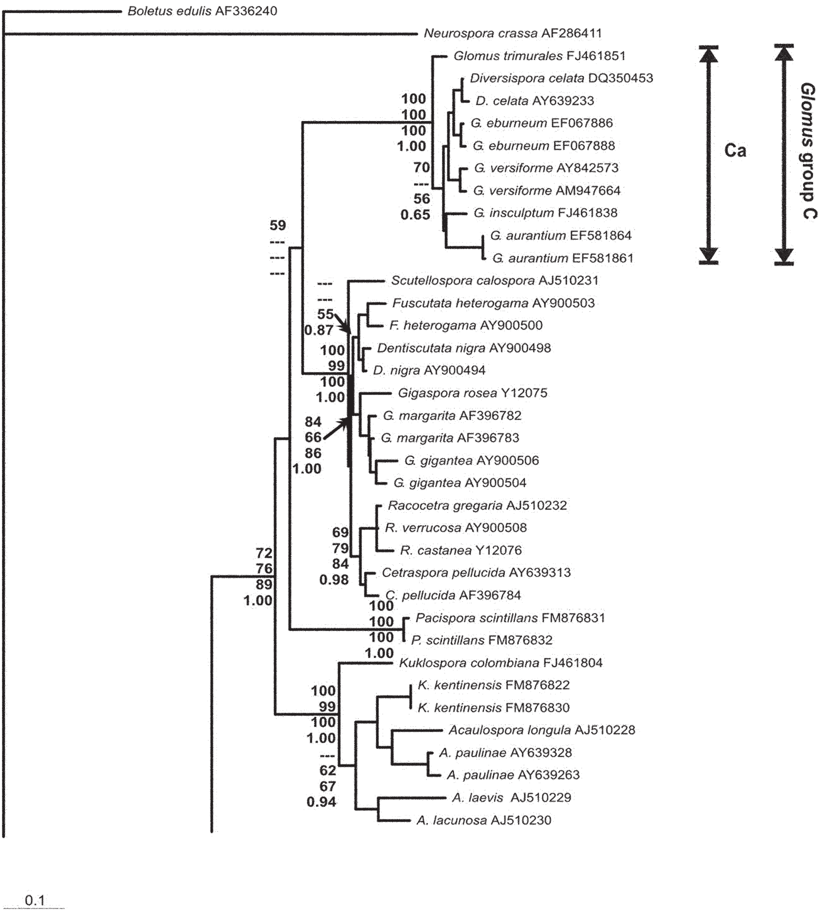


Fig. 1a–b. Phylogenetic reconstruction of the *Glomeromycota* obtained from partial SSU rDNA sequences (~1800 bp). Group C are *Diversisporaceae*. The neighbor-joining (NJ), maximum likelihood (ML) and bayesian analyses were performed with GTR+G+I substitution model. Sequences are labeled with their database accession numbers. Bootstrap values (in %) are from NJ, maximum parsimony (MP) and ML analyses (1000 bootstraps), respectively. The lasting numbers below each branch line denotes the credibility value from the bayesian analysis. Only topologies with bootstrap values of at least 50% are shown (Consistency Index = 0.4701; Retention Index = 0.8241). (Fig. 1A left on p. 82; Fig. 1B above)

Results & discussion

Relationships between general phylogenetics and morphological features

All four orders of the *Glomeromycota* have species that form glomoid spores. *Paraglomerales* and *Archaeosporales* have low phylogenetic relationship with *Glomerales* and *Diversisporales* (e.g. Redecker et al. 2007, Palenzuela et al. 2008; Figs. 1–2, 4). Representatives of *Ambispora, Archaeospora, Intraspora,* and *Paraglomus* form extraradical mycelia and mycorrhizal structures that stain faintly to not at all in trypan blue (Spain & Miranda 1996, Spain 2003, Spain et al. 2006, Sieverding & Oehl 2006). (The reasons for this are unclear: vesicle formation is rarely reported or might have been misinterpreted in *Archaeospora, Intraspora* and *Paraglomus*.) This differs from the current glomeralean and diversisporalean species, which have fungal structures that stain blue to deep



blue with trypan blue. They are also reported to form vesicular arbuscular mycorrhiza (Schüßler et al. 2001), except for *Gigasporaceae, Scutellosporaceae, Racocetraceae* and *Dentiscutataceae,* which form arbuscular mycorrhiza but not intraradical vesicles, or at least vesicles have never been observed (Bentivenga & Morton 1995, Oehl et al. 2008). To date *Paraglomerales* species are monogeneric and form glomoid spores that may all germinate directly through the spore wall instead of through the subtending hyphae as in *Glomus* and *Diversispora* (Spain and Miranda 1996; Oehl pers. obs. on *P. occultum*).

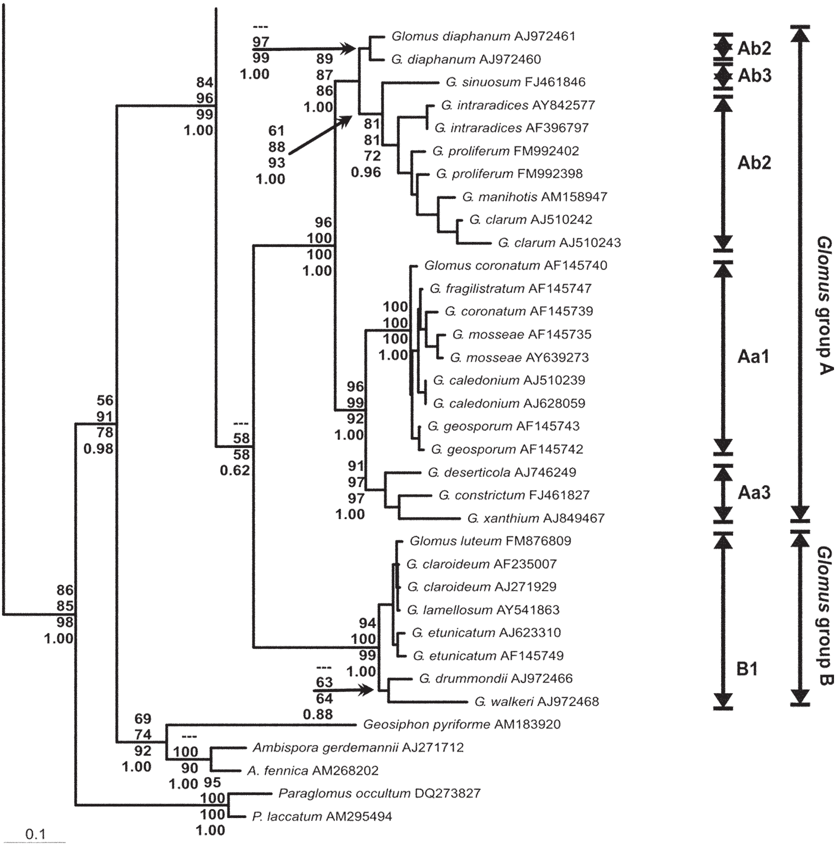


Fig. 2. Phylogenetic reconstruction of the *Glomeromycota* obtained from partial LSU rDNA sequences (~600 bp). The neighbor-joining (NJ), maximum likelihood (ML) and bayesian analyses were performed with GTR+G+I substitution model. Sequences are labeled with their database accession numbers. Bootstrap values (in %) are from NJ, maximum parsimony (MP) and ML analyses (1000 bootstraps), respectively. The lasting numbers below each branch line denotes the credibility value from the bayesian analysis. Only topologies with bootstrap values of at least 50% are shown (Consistency Index = 0.4207; Retention Index = 0.7818). (Fig. 2A left on p. 84; Fig. 2B above.)

Phylogenetic reconstructions for glomeromycotan species based on analyses of the 18S, 28S, and ITS regions of the ribosomal gene, and of the β-tubulin gene

The major clades for groups Aa, Ab, B and C were monophyletically obtained in the phylogenetic trees constructed for the genome regions analyzed (Figs. 1–4). Clade group Aa was divided into three subclades with *Gl. mosseae*, *Gl. hoi,* and *Gl. constrictum* as lead species of Aa1, Aa2 and Aa3, respectively. Further separation of clade Ab is not clear, although former *Sclerocystis* spp. (group Ab3) and *Gl. badium* (morphologically also in group Ab3) are monophyletic (Fig. 1). Clades Ab1 and Ab2, which differ consistently in glomoid spore morphology (see below) and contain the largest number of species, were not re-organized because the genetic database is not yet complete. Of the species analyzed, only *Gl. aureum* represents clade Ab1, which should have *Gl. macrocarpum* as type species according to Clements & Shear (1931). However, the 18S rDNA region (Fig. 1) does not provide sufficient support by itself for creating a new genus. The two lead species of group Ab2 are *Gl. intraradices* and *Gl. irregulare*, but this group also is not yet recognized at the genus level. The group B clade clearly stands apart from the others and splits into *Glomus* groups B1 and B2. *Glomus viscosum* is hereafter attributed as a single species to group B2, while *Gl. etunicatum* was recognized as the lead species for the group B1 (Fig. 1). The ITS regions from clade groups Ca and Cb were analyzed because other sequence data were either unavailable for group Cb species or (for the 18S) available only for the lead species, *Gl. fulvum*. ITS analyses showed the Ca and Cb clades well separated from each other (Fig. 3).

Morphology of glomoid, diversisporoid, and pacisporoid spores

All glomoid spores of the present *Glomeraceae* and *Diversisporaceae* have one single spore wall with several layers. In many species the structural wall layer is the inner layer, although other species possess additional innermost (semi-)flexible layers. Because these additional layers are generally thin (often <1μm), closely adhere to the structural layer, and can be separated from the latter only through hard pressure on the cover slides, they are not considered separate walls. The presence or absence of innermost flexible layers is not sufficient to distinguish morphologically between *Glomus* groups since the majority of groups have some species with and some species without innermost flexible layers. Such characters as mycelial/ mycorrhizal infection features, spore size, spore wall color, wall ornamentation, and layer numbers or their staining features could rarely be attributed to all species within a specific clade.

Spores of groups A and B have a structural layer that forms a continuum from attached hyphal to spore wall layers (Figs. 5–17). We refer to such spore types as GLOMOID.

Because Ca and Cb group spores have a structural layer that appears to be inserted into the wall of the terminal element of the attached hypha, the

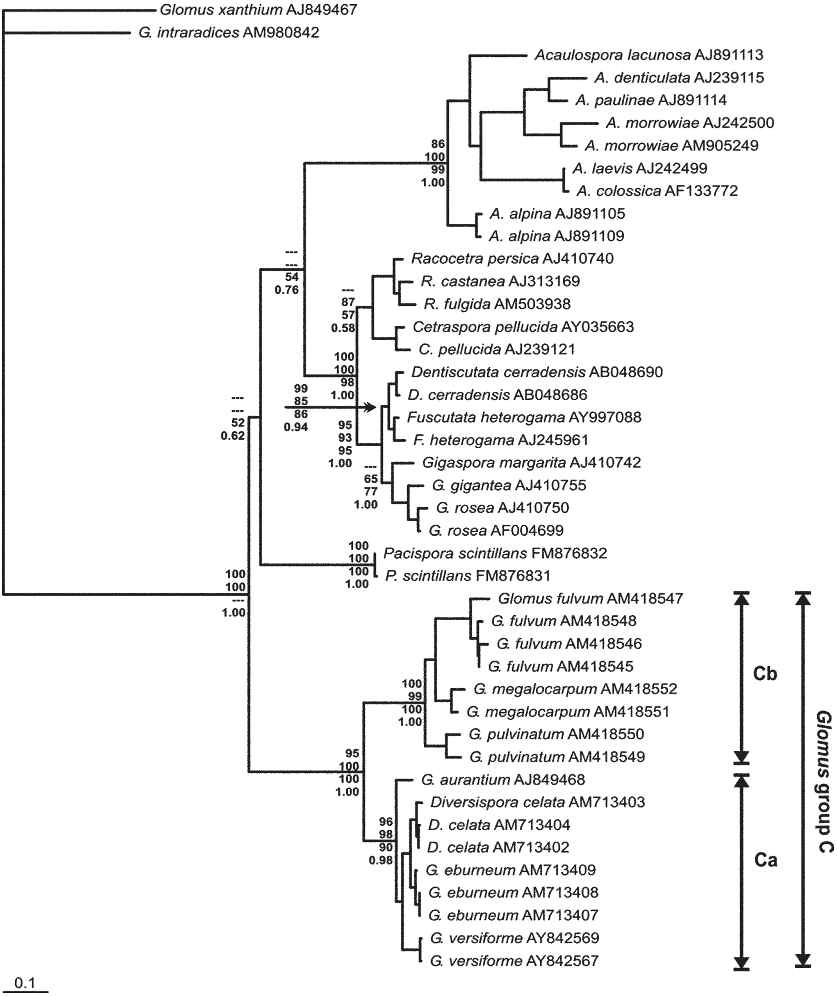


Fig. 3. Phylogenetic reconstruction of the *Diversisporales* obtained from ITS sequences (~500 bp). The neighbor-joining (NJ), maximum likelihood (ML) and bayesian analyses were performed with GTR+G+I substitution model. Sequences are labeled with their database accession numbers. Bootstrap values (in %) are from NJ, maximum parsimony (MP) and ML analyses (1000 bootstraps), respectively. The lasting numbers below each branch line denotes the credibility value from the bayesian analysis. Only topologies with bootstrap values of at least 50% are shown (Consistency Index = 0.5539; Retention Index = 0.8092).

structural spore wall layers may not form a continuum with the hyphal wall layers (Figs. 18–21). The inner wall layer appears to differentiate de novo, similar (but not equal) to inner walls in *Acaulosporaceae* or *Entrophosporaceae*

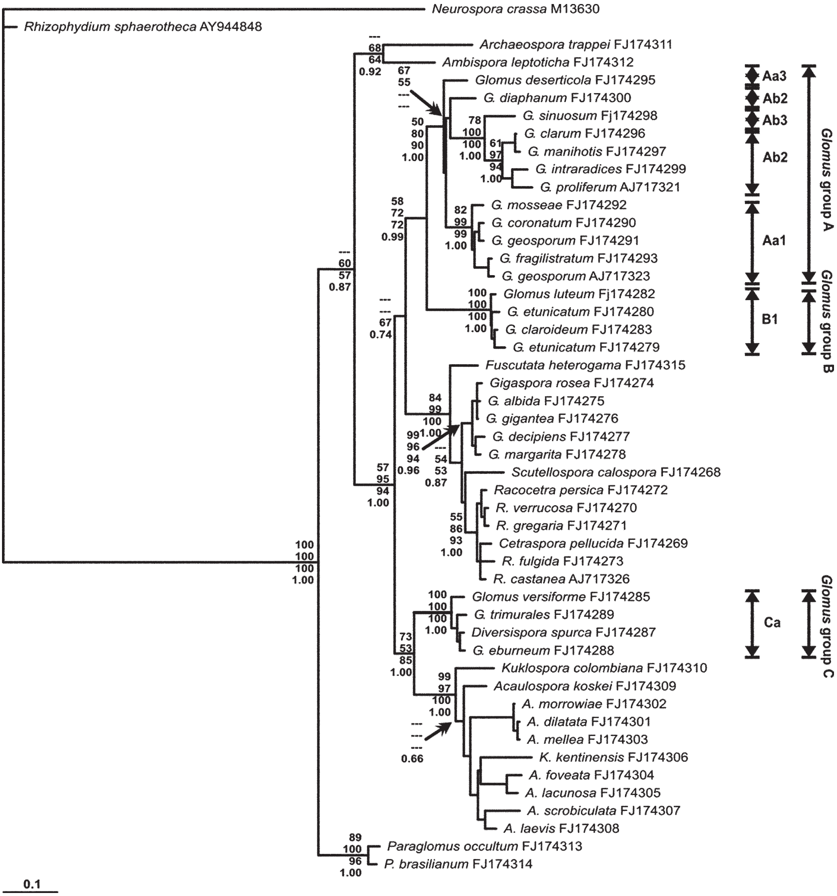


Fig. 4. Phylogenetic reconstruction of the *Glomeromycota* obtained from partial β-tubulin sequences (~600 bp). The neighbor-joining (NJ), maximum likelihood (ML) and bayesian analyses were performed with GTR+G+I substitution model. Sequences are labeled with their database accession numbers. Bootstrap values (in %) are from NJ, maximum parsimony (MP) and ML analyses (1000 bootstraps), respectively. The lasting numbers below each branch line denotes the credibility value from the bayesian analysis. Only topologies with bootstrap values of at least 50% are shown. (Consistency Index = 0.3709; Retention Index = 0.6969).

(Oehl et al. 2006, Sieverding & Oehl 2006). In Ca the structural and (if present) inner flexible spore wall layers form a septum at the base or at a short distance from the base of the spore within the subtending hypha. In Cb the inner lamina of the structural wall layer always forms a septum at the spore base and the outer lamina may continue for 1–10 µm into the subtending hypha. We refer to this spore type as DIVERSISPOROID.

Pacispora spores superficially resemble glomoid spores, as the spore wall structural layer forms a continuum with the hyphal wall layers. However, *Pacispora* spores strongly differ from glomoid spores: i) in possessing an additional thick inner germinal wall that forms de novo and is clearly separate from the outer wall; ii) by species-specific germination structures resembling a germ shield; and iii) by germ tubes that arise from the 'shields' on the inner wall and penetrate directly the adjacent outer wall. We refer to this spore type as pacisporoid.

Morphology of the subtending hypha, spore base, and spore pore closure

A combination of two major morphological features and one secondary feature are congruent with the major molecular phylogenetic groups of the glomoid, diversisporoid, and pacisporoid species (Table 2): i) the morphology of the spore base including the pore closure and position of the septum (Figs. 5–23, 24–114); ii) the morphology of the subtending hypha (SH) (Figs. 5–23, 24–114); and iii) secondarily, the prevailing formation and spore organization level within either sporocarps or spore clusters or singly in soil.

Spores of *Glomus* groups Aa(1,2,3) and Ab(1,2,3) all have SH that are concolorous with (or slightly lighter in color than) the structural spore wall, and the spore wall differentiation extends completely into the SH (Table 2, Figs. 5–14, 24–89). In group B1 and B2 spores the structural spore wall differentiation also extends into the SH, but the SH colour changes abruptly to hyaline or white at the spore base, even when the spore wall layers are distinctly pigmented (Table 2, Figs. 15–17, 90–98).

Table 2. Morphology of subtending hyphae (SH) and spore formation in glomoid spored species in *Glomerales* and *Diversisporales*

Group	Aa1	Aa2	Aa3	Ab1	Ab2
Lead species	*Gl. mosseae*	*Gl. hoi*	*Gl. constrictum*	*Gl. macrocarpum* *Gl. microcarpum*	*Gl. intraradices* *Gl. irregulare*
Recent or New genus	*Funneliformis*	*Simiglomus*	*Septoglomus*	*Glomus*	*Glomus*
SH characters					
Color	Same as spore wall	Same as spore wall	Same as spore wall	Same as spore wall	Same as spore wall
Shape &	Funnel-shape to cylindric,	Cylindric/sl. funnel-shape,	Cylindric to constricted, rarely sl. funnel-shape,	Cylindric to slightly funnel-shape,	Cylindric,
thickness	thick walled	thick walled	+/- thick walled	thick walled	thick walled
Pore closure	Conspicuous septum under / at spore base	Sev. conspic. septa distant to spore base	Septum under / at spore base	Introverted sw thickening; +/- bridging septum	Open or septum distant to spore base; introverted sw thickening rudimentary
Spore formation	Singly or in few-spored sporocarps	Singly or open spore clusters	Singly or open spore clusters	Compact, unorganized multi-spored sporocarps, clusters or singly	Loose or compacted, unorganized clusters; also singly

Table 2, concluded.

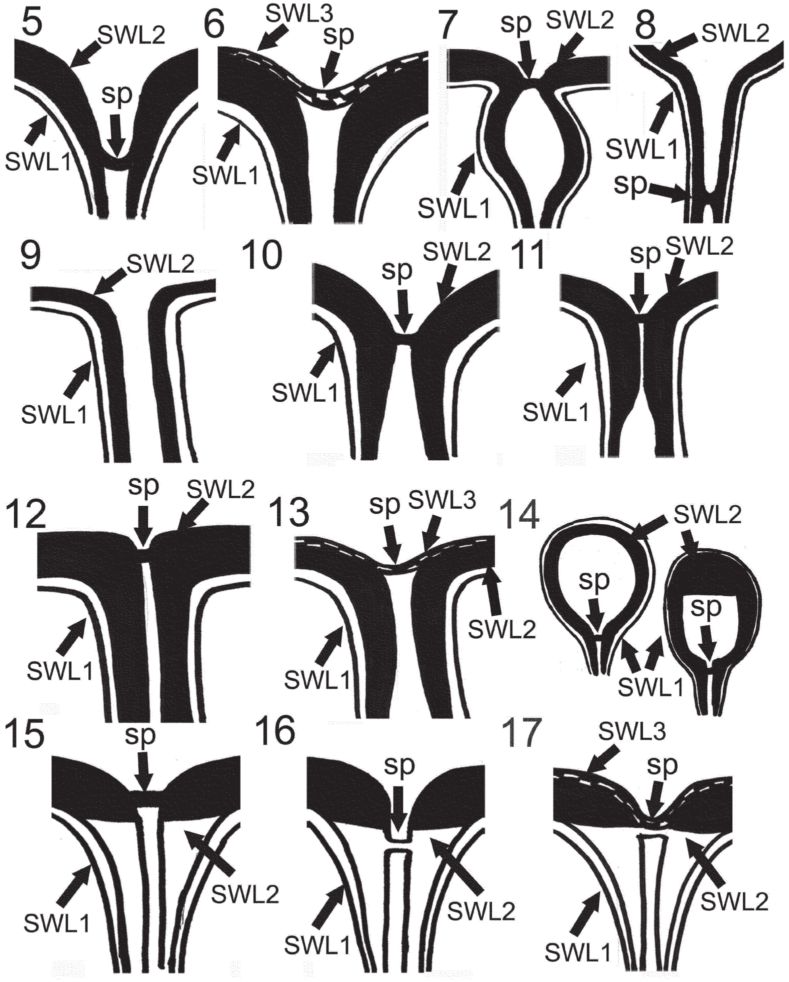
Group	Ab3	B1	B2	Ca	Cb
Lead species	*Gl. coremioides*	*Gl. etunicatum*	*Gl.viscosum*	*Gl. versiforme*	*Gl. fulvum*
Recent or New genus	*Glomus*	*Claroideoglomus*	*Viscospora*	*Diversispora*	*Redeckera*
SH characters					
Color	Same as spore wall	White to hyaline, abrupt color change at spore base if spore wall pigmented	White to hyaline	Hyaline distant to septum that is concolorous with structural SWL	Hyaline distant to septum that is concolorous with structural SWL
Shape; &	Cylindric, funnel-, or bill-shaped,;	Conspicuously bill-shaped;	Cylindric;	Generally fragile, cylindric distant to septum, or constricted;	Generally fragile and inflated ;
Thickness	thick-walled	+/- thick-walled	thick-walled	thin-walled	thin-walled
Pore closure	Introverted sw thickening	Septum at spore base	Constricted wall or open	Septum at or beneath spore base, or open	Broad septum at spore base
Spore formation	In compact, organized sporocarps, around hyphal center; initially also singly	Singly	Singly or in loose clusters	In large, compact sporocarps, or cluster aggregates, or singly	In large, compact sporocarps/ clusters, open aggregates, or singly

In contrast, the spore wall differentiation generally does not extend into the SH in group Ca and Cb spores (TABLE 2, Figs. 14–19, 99–114), as lamination and differentiation of the structural spore wall layer either does not extend into the SH or extends only a short distance from the base. Within these Ca and Cb, therefore, the SH are usually quite fragile (Figs. 99–107) and hyaline to white, distal to the pore closure at the spore base (*Gl. spurcum* = *Di. spurca*) or in the SH (*Gl. eburneum*). The hyaline to white color of the SH behind the septum changes conspicuously when spores are pigmented. Cb species have broad SH and broad septa at the spore bases (Figs. 108–114). Their SH are inflated (*Gl. pulvinatum*) or (sometimes) very short within compact sporocarps (e.g. *Gl. fulvum* and *Gl. canadense*).

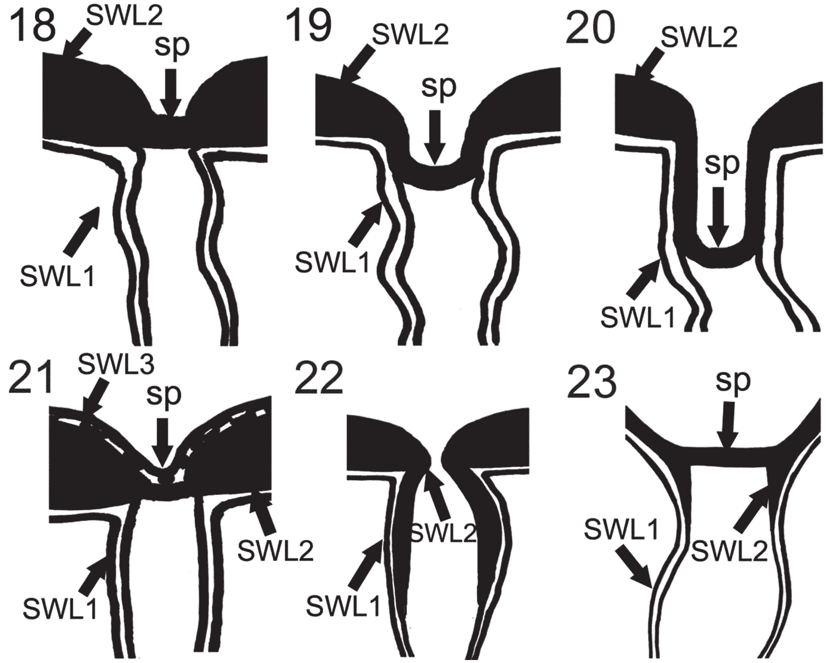
Type of spore formation

Glomus group spore formation is intercalary or terminal on SH, both for spores formed either singly in soil (e.g. *Gl. arborense, Gl. etunicatum*) or in loose/dense spore clusters or sporocarps (e.g. *Gl. fasciculatum*, *Gl. pallidum, Gl. glomerulatum*).

Figs 5–17. Examples of spore bases (with 1–3 spore wall layers; SWL1–3) and subtending hyphae (SH) of species assigned to phylogenetic clades Aa1, Aa2, Aa3, Ab1, Ab2, Ab3, B1 and B2; structural spore wall layers are continuous with the SH wall. **5–14.** SH of A clade spores are concolorous with or slightly lighter than the spore wall. **5–8.** Clade Aa species never have an introverted wall thickening at the base; spore pores are generally closed by a conspicuous septum (sp) arising



from the structural layer and/or the (semi-)flexible layer beneath. **5–6.** Aa1. **5.** Lead species *Glomus mosseae*. **6.** *Gl. geosporum*. **7.** Aa3: lead species *Gl. constrictum*. **8.** Aa2: so far single lead species *Gl. hoi*. **9.** Ab2: without introverted wall thickening; spore base pore regularly open; lead species *Gl. intraradices*. **10–13.** Ab1: typical *Glomus* species with an introverted wall thickening at the spore base; sometimes a short bridging septum arising from the structural wall layer or innermost flexible lamina closes the spore base pore. **10.** Lead species *Gl. microcarpum*. **11.** *Gl. aureum*. **12.** Lead species *Gl. macrocarpum*. **13.** *Gl. pellucidum*. **14.** Ab3; also with a slight introverted wall thickening but pores generally closed by a short septum arising from the structural layer and/or the (semi-)flexible layers beneath. In some clade Ab3 species the spore head sometimes is also thickened towards the sporocarp surface; lead species *Gl. coremioides* and *Gl. sinuosum*. **15–17.** B1: spore SH bill-shaped and hyaline to white, even when the spore wall is pigmented. **15–16.** lead species *Gl. etunicatum*. **17.** *Gl. claroideum*.



Figs 18–23. Clades Ca (*Diversispora*) and Cb (*Redeckera)* spore bases (with 1–3 spore wall layers; SWL1–3) and subtending hyphae (SH): structural spore wall layer seemingly extends only a very short distance into the subtending hyphae, soon becoming hyaline to white and undetectable; often only the adherent outer spore wall layer(s) appears continuous with the mycelial hyphal wall to connect the two neighboring spores in compact sporocarps. The structural layer often appears inserted into the 'swollen hyphal tips'. **18–22**. Ca: spore SH generally white and cylindrical at the spore base, soon fragile. Septum (sp) arises from the structural spore wall layer and either closes the pore immediately or at some distance from the spore base (**18–21**) or the spore pore appears open (**22**). **23**. Cb: spore SH generally inflated a very short distance from the spore base with the structural layer extending an equally short distance in the subtending hypha. At base, spores are 'endospore-like,' with a broad, thick septum formed by the structural layer.

Aa1 species generally form spores singly (e.g. *Gl. geosporum, Gl. caledonium*) or occasionally in sporocarps containing just a few (2–20) spores (e.g. *Gl. mosseae*, *Gl. monosporum, Gl. coronatum*). Aa2 and Aa3 species form spores preferably singly in soil or roots, or in very loose spore clusters (*Gl. hoi*, *Gl. constrictum*, *Gl. deserticola, Gl. xanthium*). Ab1 and Ab2 species generally form spores in multi-spored loose/dense variably sized spore clusters. During initial spore formation they may also form spores singly, although some isolates appear never to form clusters in single species cultures on certain hosts. Ab3 species form spores strictly in sporocarps but may initially form single spores on their mycelia (*Gl. sinuosum*).

B1 species generally form spores either singly in soil (e.g. *Gl. etunicatum*, *Gl. claroideum, Gl. walkeri*) or in variably sized loose spore clusters (*Gl. viscosum*). Sporocarp formation is extremely rare, if ever. The solitary B2 species — *Gl. viscosum* — forms spores in clusters of highly variable size. Ca species form spores singly in soils (e.g. *Gl. spurcum = Di. spurca; Gl. eburneum*) or in small to large and irregular shaped compacted clusters with numerous spores (e.g. *Gl. versiforme, Gl. epigaeum*) depending on culture and site conditions. Finally, Cb species generally form spores in large, compact sporocarps (e.g. *Gl. fulvum, Gl. fragile*) that are among the largest known within the *Glomeromycota* (especially *Gl. megalocarpum*). As the formation of a peridium around the sporocarps or single spores does occur in groups Aa1, Ab1, Ab3, and Cb, it is not a consistent morphological indicator at the family or genus level. Peridium formation has not yet been observed for B1, B2, and Ca species.

Organization level of sporocarps

Except for group Ab3, spores of other *Glomus* groups have (with some exceptions) limited to no organization in sporocarps or compacted spore clusters. As spores in sporocarps appear to be randomly distributed, SH are variably long (e.g. *Gl. mosseae*, *Gl. coronatum*, *Gl. macrocarpum*, *Gl. ambisporum*, *Gl. versiforme*, *Gl. fulvum, Gl. pulvinatum*). In contrast, Ab3 sporocarps are highly organized with spores forming around a central hyphal plexus. Variation in SH length is much lower (e.g. *Gl. sinuosum, Gl. rubiforme*). Sporocarp size variability of Ab3 species is low, largely dependent on the diameter of the central hyphal plexus and spore size in individual species. In unorganized sporocarps of the other '*Glomus* groups' sporocarp size is much more variable due to a lack of symmetry, greater SH length variability, and greater variability of numbers of spores formed per sporocarp. According to our analyses, species that form dense, highly compact sporocarps (e.g., *Gl. radiatum, Gl. vesiculiferum, Gl. segmentatum, Gl. convolutum, Gl. fuegianum*) do not form spores around a central hyphal plexus arising from a single hypha but sporocarps appear to have several hyphal attachments. They thus probably belong to group Ab1 and so are not attributed to group Ab3.

Taxonomic revision

Glomeraceae Piroz. & Dalpé emend. Oehl, G.A. Silva & Sieverd. (*Glomus* group A)

EMENDED DESCRIPTION: Spores formed terminally on or intercalary in hyphae, in soil and sometimes in roots, either singly, in spore clusters, or in multiple-spored loose to compact sporocarps when compact spores are randomly distributed or organized around a central plexus of hyphae. Compact sporocarps with or without peridium. Spores with one mono-to-multiple layered wall. Wall of the SH conspicuously continuous and concolorous with the spore wall, or slightly lighter in color than the spore wall; SH funnel-shaped, cylindrical or constricted; forming typical vesicular-arbuscular mycorrhiza, with mycorrhizal structures that stain blue to dark blue in trypan blue.

TYPE GENUS: *Glomus* Tul. & C. Tul.

OTHER GENERA: *Funneliformis* C. Walker & A. Schüssler, *Septoglomus* Sieverd. et al., *Simiglomus* Sieverd. et al.

Glomus Tul. & C. Tul. emend. Oehl, G.A. Silva & Sieverd. FIGS. 25–74
(*Glomus* groups Ab1, Ab2 & Ab3)

EMENDED DESCRIPTION: Spores formed singly within soil or sometimes roots, in disorganized, multiple-spored loose spore clusters or in compact sporocarps; compact sporocarps without or with peridium, spores are either not organized in sporocarp, or organized around a central hyphal plexus. Spores with a mono-to-multiple layered wall. Wall of the SH conspicuously continuous and concolorous with the spore wall, or slightly lighter in color than the spore wall. Spore pore closure often by introverted wall thickening, sometimes supported by a short bridging septum, rarely open. Forming typical vesicular-arbuscular mycorrhiza, with mycorrhizal structures that stain blue to dark blue in trypan blue.

TYPE SPECIES: *Glomus macrocarpum* Tul. & C. Tul.

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≡ *Sclerocystis dussii* (Pat.) Höhn., Sitzungsber. K. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 119: 399. 1910.

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FIGS 24–46. *Glomus* clade Ab1 forms spores in unorganized clusters/sporocarps or (sometimes) singly in soil; subtending hyphae (SH) are concolorous with (or slightly lighter than) the spore wall, normally with introverted, species-specific basal wall thickenings; SH often cylindrical (very short if formed in compact sporocarps). Species-specific SH wall thickening may continue over rather long distances (≤ 200–500 µm) even in sporocarps. Spores with 1–4 wall layers (SWL1–SWL4); pore at spore base pores often closed by introverted wall thickenings or with an additional septum (sp) that arises from the structural layer, from an adherent innermost (semi-)flexible layer, or from both layers. Individual layers might be species-specifically ornamented (ORN). **24–25**. *Gl. microcarpum.* **26**. *Gl. macrocarpum.* **27**. *Gl. spinuliferum.* **28**. *Gl. magnicaule.* **29**. *Gl. multicaule.* **30**. *Gl. heterosporum.* **31**. *Gl. aureum.* **32**. *Gl. invermaium.* **33**. *Gl. glomerulatum.* **34**. *Gl. ambisporum.* **35**. *Gl. warcupii.* **36**. *Gl. melanosporum.* **37**. *Gl. atrouva.* **38**. *Gl. botryoides.* **39**. *Gl. spinosum.* **40**. *Gl. mortonii.* **41**. *Gl. australe.* **42**. *Gl. fuegianum.* **43**. *Gl. tenerum.* **44**. *Gl. pellucidum.* **45**. *Gl. segmentatum.* **46**. *Gl. convolutum*: spore peridium was removed by strong pressure on the cover slide.

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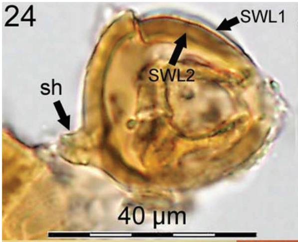

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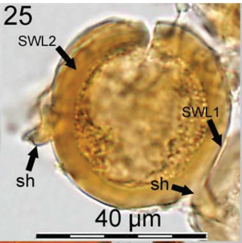

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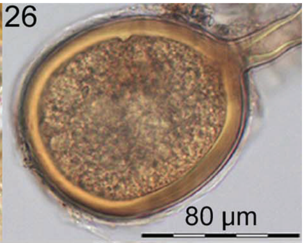

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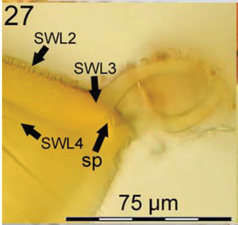

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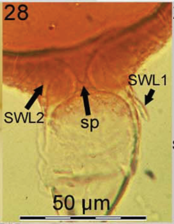

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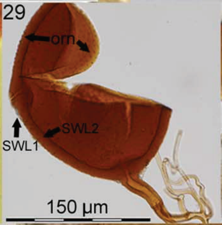

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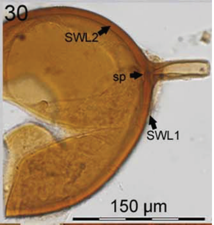

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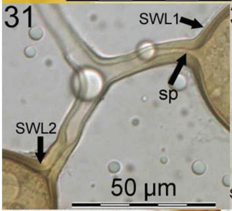

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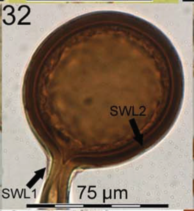

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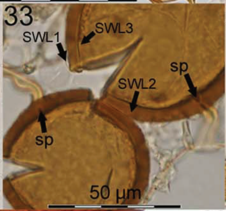

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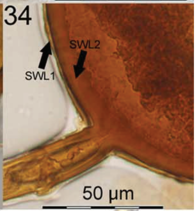

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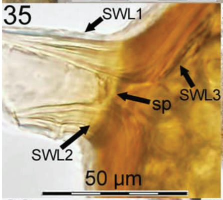

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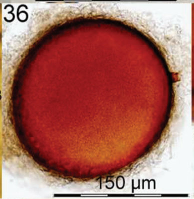

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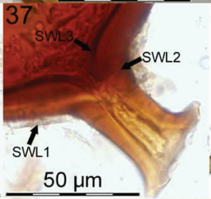

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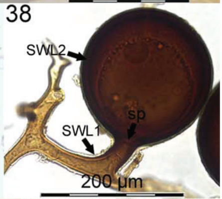

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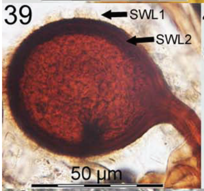

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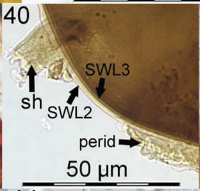

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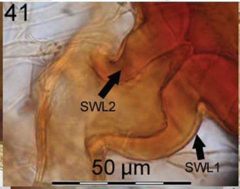

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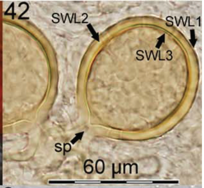

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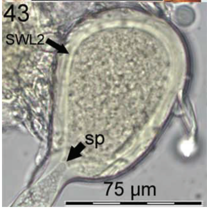

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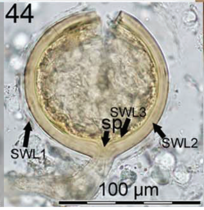

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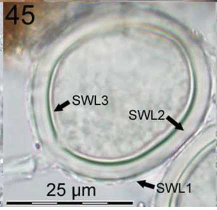

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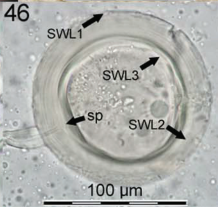
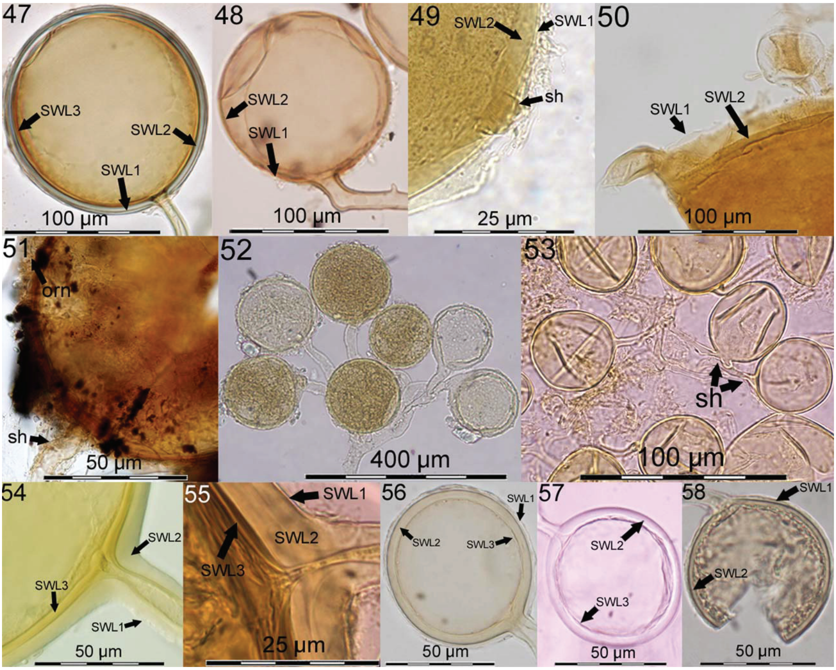




Figs 47–58. *Glomus* clade Ab2 form spores in disorganized loose/dense clusters/sporocarps (sometimes singly in soil); subtending hyphae (sh) concolorous with (or slightly lighter than) the spore wall. sh generally openly cylindric; introverted wall thickenings rudimentary, but usually not existent; spore base pore diagnostic: open or (rather rarely) with a septum arising from innermost adherent (semi-)flexible layer. Spores with 1–4 wall layers (swl1–swl4). **47**. *Gl. intraradices.* **48**. *Gl. aggregatum.* **49**. *Gl. vesiculiferum.* **50**. *Gl. globiferum.* **51**. *Gl. tortuosum.* **52**. *Gl. corymbiforme.* **53**. *Gl. microaggregatum.* **54**. *Gl. clarum.* **55**. *Gl. manihotis.* **56**. *Gl. fasciculatum.* **57**. *Gl. diaphanum.* **58**. *Gl. pallidum.*

Glomus iranicum Błaszk., Kovács & Balázs, Mycologia 102: 1457. 2010.

≡ *Rhizophagus iranicus* (Błaszk., Kovács & Balázs) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 19. 2010.

Glomus irregulare Błaszk., Wubet, Renker & Buscot, Mycotaxon 106: 252. 2008.

≡ *Rhizophagus irregularis* (Błaszk., Wubet, Renker & Buscot) C. Walker & A. Schüssler, The *Glomeromycota* – species list: 19. 2010.

Glomus liquidambaris (C.G. Wu & Z.C. Chen) Y.J. Yao, Kew Bull. 50: 306. 1995.

≡ *Sclerocystis liquidambaris* C.G. Wu & Z.C. Chen, Trans. Mycol. Soc. Rep. China, 2: 74. 1987.

= *Sclerocystis cunninghamia* H.T. Hu, Quart. J. Chinese For. 21: 52. 1988.

Glomus macrocarpum Tul & C. Tul., Giorn. Bot. Ital., Anno 1, 2(7–8): 63. 1845.

≡ *Endogone macrocarpa* (Tul. & C. Tul.) Tul. & C. Tul., Fungi Hypog.: 182. 1851.

= *Endogone guttulata* E. Fisch., Ber. Schweiz. Bot. Ges. 32: 13. 1923.
= *Endogone nuda* Petch., Ann. R. Bot. Gdns Peradeniya 9: 322. 1925.
= *Endogone pampaloniana* Bacc., Nuovo Giorn. Bot. Ital., n.s. 10: 90. 1903.
= *Paurocotylis fulva* var. *zelandica* Cooke, Grevillea 8: 59. 1879.

Glomus magnicaule I.R. Hall, Trans. Br. Mycol. Soc. 68: 345. 1977.

Glomus manihotis R.H. Howeler, Sieverd. & N.C. Schenck, Mycologia 76: 695. 1984.
≡ *Rhizophagus manihotis* (R.H. Howeler, Sieverd. & N.C. Schenck) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 19. 2010.

Glomus melanosporum Gerd. & Trappe, Mycol. Mem. 5: 46. 1974.

Glomus microaggregatum Koske, Gemma & P.D. Olexia, Mycotaxon 26: 125. 1986.

Glomus microcarpum Tul. & C. Tul., Giorn. Bot. Ital., Anno 1, 2(7–8): 63. 1845.
≡ *Endogone microcarpa* (Tul. & C. Tul.) Tul. & C. Tul., Fungi Hypog.: 182. 1851.
= *Endogone neglecta* Rodway, Proc. Roy. Soc. Tasmania 1917: 107. 1918.

Glomus minutum Błaszk., Tadych & Madej, Mycologia 76: 189. 2000.

Glomus mortonii Bentiv. & Hetrick, Mycotaxon 42: 10. 1991.

Glomus multicaule Gerd. & B.K. Bakshi, Trans. Br. Mycol. Soc. 66: 340. 1976.

Glomus nanolumen Koske & Gemma, Mycologia 81: 935. 1990.

Glomus pachycaule (C.G. Wu & Z.C. Chen) Sieverd. & Oehl, **comb. nov.**
MycoBank MB 519622
≡ *Sclerocystis pachycaulis* C.G. Wu & Z.C. Chen, Taiwania 31: 74. 1986.

Glomus pallidum I.R. Hall, Trans. Br. Mycol. Soc. 68: 343. 1977.

Glomus pansihalos S.M. Berch & Koske, Mycologia 78: 832. 1986.

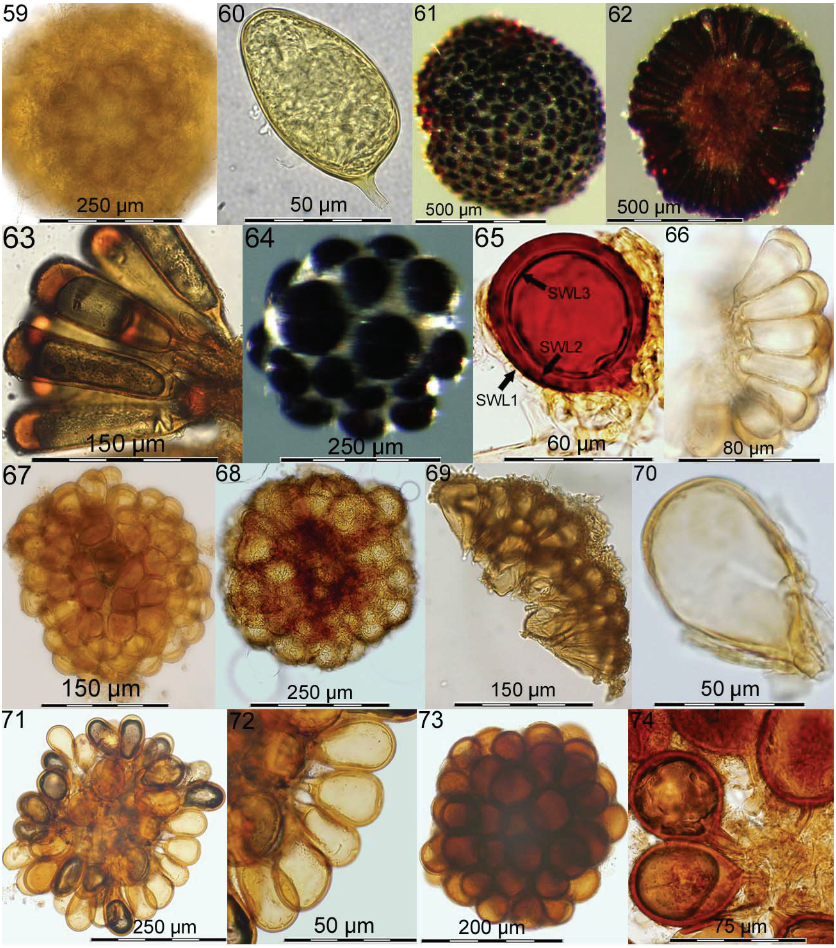
Glomus pellucidum McGee & Pattinson, Austral. Syst. Bot. 15: 120. 2002.

Glomus perpusillum Błaszk. & Kovács, Mycologia 101: 249. 2009.

Glomus proliferum Dalpé & Declerck, Mycologia 92: 1180. 2000.
≡ *Rhizophagus prolifer* (Dalpé & Declerck) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 19. 2010.

Glomus pubescens (Sacc. & Ellis) Trappe & Gerd., Mycol. Mem. 5: 57. 1974.
≡ *Sphaerocreas pubescens* Sacc. & Ellis, Michelia 2: 582. 1882.
≡ *Stigmatella pubescens* (Sacc. & Ellis) Sacc., Syll. Fung. 4: 680. 1886.
≡ *Sclerocystis pubescens* (Sacc. & Ellis) Höhn., Sitzungsber. K. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 119: 399. 1910.
≡ *Endogone pubescens* (Sacc. & Ellis) Zycha, Krypt.-Fl. Brandenburg 6a: 214. 1935.

Glomus radiatum (Thaxt.) Trappe & Gerd., Mycol. Mem. 5: 46. 1974.
≡ *Endogone radiata* Thaxt., Proc. Am. Acad. Arts & Sci. 57: 316. 1922.



Figs 59–74. *Glomus* clade Ab3, with species virtually all belonging to the former genus *Sclerocystis*; form spores in highly organized, compact sporocarps, generally with > 50 spores per sporocarp; subtending hyphae (sh) generally short, bill-shaped or cylindrical, and concolorous with (or slightly lighter than) the spore wall. Spores species-specifically with (1–)2 wall layers (SWL1–SWL2) and wall thickening at spore base, but pore generally closed by a septum that regularly arises from the structural wall layer. **59–60**. *Gl. coremioides*. **61–63**. *Gl. clavisporum*. **64–65**. *Gl. badium*. **66–67**. *Gl. taiwanense*. **68–70**. *Gl. sinuosum*. **71–72**. *Gl. pachycaule*. **73–74**. *Gl. rubiforme*.

Glomus rubiforme (Gerd. & Trappe) R.T. Almeida & N.C. Schenck, Mycologia 82: 709. 1990.

≡ *Sclerocystis rubiformis* Gerd. & Trappe, Mycol. Mem. 5: 60. 1974.

= *Sclerocystis indica* Bhattacharjee & Mukerji, Acta Bot. Indica 8: 99. 1980.

Glomus segmentatum Trappe, Spooner & Ivory, Trans. Br. Mycol. Soc. 73: 362. 1979.

Glomus sinuosum (Gerd. & B.K. Bakshi) R.T. Almeida & N.C. Schenck, Mycologia 82: 710. 1990

≡ *Sclerocystis sinuosa* Gerd. & B.K. Bakshi, Trans. Br. Mycol. Soc. 66: 343. 1976.

= *Sclerocystis pakistanica* S.H. Iqbal & Perveen, Trans. Mycol. Soc. Japan 21: 59. 1980.

Glomus spinosum H.T. Hu, Mycotaxon 83: 160. 2002.

Glomus spinuliferum Sieverd. & Oehl, Mycotaxon 86: 158. 2003.

Glomus taiwanense (C.G. Wu & Z.C. Chen) R.T. Almeida & N.C. Schenck ex Y.J. Yao, Kew Bull. 50: 306. 1995.

≡ *Sclerocystis taiwanensis* C.G. Wu & Z.C. Chen, Trans. Mycol. Soc. Rep. China 2: 78. 1987.

Glomus tenebrosum (Thaxt.) S.M. Berch. Can. J. Bot. 60: 2615. 1983.

≡ *Endogone tenebrosa* Thaxt., Proc. Am. Acad. Arts Sci. 57: 314. 1922.

Glomus tenue (Greenall) I.R. Hall, Trans. Br. Mycol. Soc. 68: 350. 1977.

≡ *Rhizophagus tenuis* Greenall, New Zealand J. Bot. 1: 398. 1963.

Glomus tortuosum N.C. Schenck & G.S. Sm., Mycologia 74: 83. 1982.

Glomus vesiculiferum (Thaxt.) Gerd. & Trappe, Mycol. Mem. 5: 49. 1974.

≡ *Endogone vesiculifera* Thaxt., Proc. Am. Acad. Arts Sci. 57: 309. 1922.

≡ *Funneliformis vesiculifer* (Thaxt.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 14. 2010.

Glomus warcupii McGee, Trans. Br. Mycol. Soc. 87: 125. 1986.

Glomus zaozhuangianum F.Y. Wang & R.J. Liu, Mycosystema 21: 522. 2002.

Funneliformis C. Walker & A. Schüssler, emend. Oehl, G.A. Silva & Sieverd.
(*Glomus* group Aa1) FIGS. 75–84

EMENDED DESCRIPTION: Spores formed within soil or rarely roots, singly or sometimes in sporocarps with a few to several spores per sporocarp only; the conspicuous SH is concolorous with spore wall color (or slightly lighter in color), SH is species-specific and generally funnel-shaped to cylindrical. Wall differentiation and pigmentation may continue over long distances from the spore base (often > 50–250 µm), then mycelium may become hyaline. Pore regularly closed by a conspicuous septum that species-specifically arises from the structural wall layer, from an additional adherent innermost, (semi-)flexible lamina, or from both but not by introverted wall thickening, which is lacking. Forming typical vesicular-arbuscular mycorrhiza, with mycorrhizal structures that stain blue to dark blue in trypan blue.

GENDER: *Funneliformis* is a compound Latin adjective with a masculine/feminine termination. Although under ICBN [Vienna Code] Article 62.3, the authors had the prerogative to choose either of these genders, their actual choice of neuter gender was not an available option. We therefore choose to treat this genus as masculine (Article 62.3) and have made the appropriate corrections to all adjectival epithets.

Type species: *Funneliformis mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler

Funneliformis caesaris (Sieverd. & Oehl) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518445

≡ *Glomus caesaris* Sieverd. & Oehl, Mycotaxon 84: 381. 2002.

Funneliformis caledonius (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 13. 2010.

≡ *Endogone macrocarpa* var. *caledonia* T.H. Nicolson & Gerd., Mycologia 60: 318. 1968.
≡ *Glomus caledonium* (T.H. Nicolson & Gerd.) Trappe & Gerd., Mycol. Mem. 5: 56. 1974.

Funneliformis coronatus (Giovann.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 13. 2010.

≡ *Glomus coronatum* Giovann., Can. J. Bot. 69: 162. 1990.

Funneliformis dimorphicus (Boyetchko & J.P. Tewari) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518447

≡ *Glomus dimorphicum* Boyetchko & J.P. Tewari, Can J. Bot. 64: 90. 1986.

Funneliformis fragilistratus (Skou & I. Jakobsen) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 13. 2010.

≡ *Glomus fragilistratum* Skou & I. Jakobsen, Mycotaxon 36: 276. 1989.

Funneliformis geosporus (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 14. 2010.

≡ *Endogone macrocarpa* var. *geospora* T.H. Nicolson & Gerd. Mycologia 60: 318. 1968.
≡ *Glomus macrocarpum* var. *geosporum* (T.H. Nicolson & Gerd.) Gerd. & Trappe, Mycol. Mem. 5: 55. 1974.
≡ *Glomus geosporum* (T.H. Nicolson & Gerd.) C. Walker, Mycotaxon 15: 56. 1982.

Funneliformis halonatus (S.L. Rose & Trappe) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518453

≡ *Glomus halonatum* S.L. Rose & Trappe, Mycotaxon 10: 413. 1980.

Funneliformis kerguelensis (Dalpé & Strullu) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518454

≡ *Glomus kerguelense* Dalpé & Strullu, Mycotaxon 84: 53. 2002.

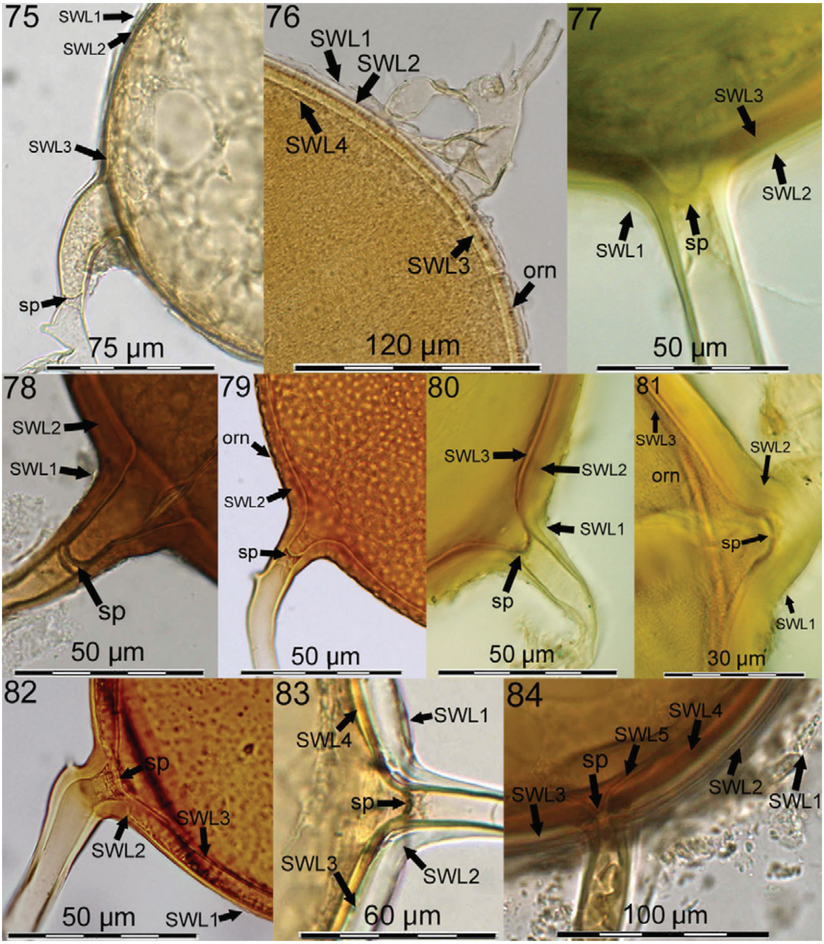
Funneliformis monosporus (Gerd. & Trappe) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518456

≡ *Glomus monosporum* Gerd. & Trappe, Mycol. Mem. 5: 41. 1974.

Funneliformis mosseae (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 13. 2010.

≡ *Endogone mosseae* T.H. Nicolson & Gerd., Mycologia 60: 314. 1968.
≡ *Glomus mosseae* (T.H. Nicolson & Gerd.) Gerd. & Trappe, Mycol. Mem. 5: 40. 1974.



Figs 75–84. *Funneliformis* species (clade Aa1) generally form big (150–400 µm) spores, singly and (species-specifically) also in 'small' sporocarps with only a few to several spores per sporocarp; subtending hyphae (SH) are concolorous with (or slightly lighter than) the spore wall without introverted wall thickening at the spore base and are species-specifically cylindrical, funnel-shaped, or (rarely) slightly constricted. SH wall thickening may extend over long distances (> 100–300 µm). Spores with 1–5 wall layers (SWL1–SWL5); pore regularly closed by a conspicuous septum (sp) that species-specifically arises from the structural layer, from an adherent innermost, (semi-)flexible layer, or from both layers. **75**. *Fu. mosseae*. **76**. *Fu. monosporus*. **77**. *Fu. fragilistratus*. **78**. *Fu. coronatus*. **79**. *Fu. multiforus*. **80**. *Fu. geosporus*. **81**. *Fu. verruculosus*. **82**. *Fu. kerguelensis*. **83**. *Fu. caledonius*. **84**. *Fu. caesaris*.

Funneliformis multiforus (Tadych & Błaszk.) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518459

≡ *Glomus multiforum* Tadych & Błaszk., Mycologia 89: 805. 1997.

Funneliformis verruculosus (Błaszk.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 14. 2010.
≡ *Glomus verruculosum* Błaszk., Mycologia 89: 809. 1997.

Simiglomus Sieverd., G.A. Silva & Oehl, **gen. nov.** FIGS. 85–86
MYCOBANK MB 518435 (*Glomus* group Aa2)

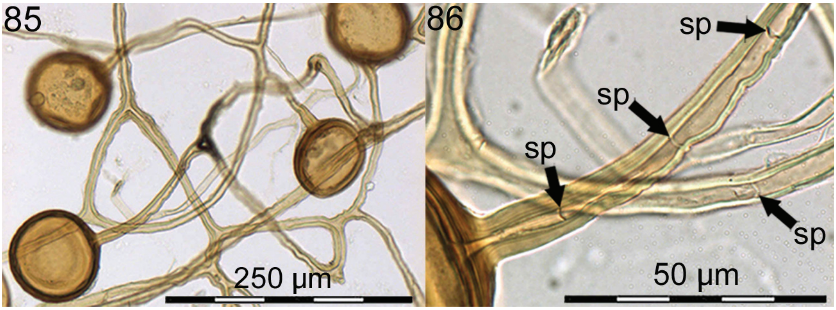
Sporae singulariter vel in congregatos apertos cum sporis pauciaribus efformatae; tunica sporarum cum tunica hypharum coniuncta; porum sporarum apertum; hyphae cylindricae vel infundiles pori sporarum aperti, pauciores septa in distanica ex tunicae hyphalis in hypha; mycorrhizas vesicular-arbusculares formans caeruleas colorantes cum 'trypan blue'.

ETYMOLOGY: from the Latin: *simi(laris)* = similar; *glomus* = cluster; referring to the relation with *Glomus,* to which species of the new genus previously belonged.

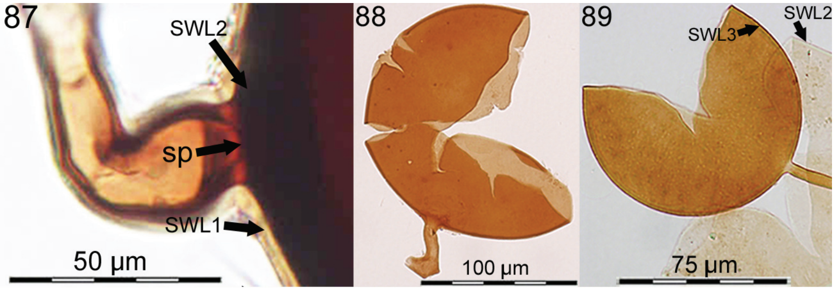
KEY CHARACTERS: Spores formed singly or in very loose, small clusters. Spores with a mono-to-multiple layered spore wall. Wall of the SH conspicuously continuous and concolorous with the spore wall, or slightly lighter in color than the spore wall. SH are funnel-shaped to cylindrical. Wall at spore attachment not with introverted wall thickening. Pore at spore base open but several septa in hyphae in some distance from spore base can separate spore contents from mycelia contents. Walls of SH thickened over very long distances from the spore base (up to > 1000 µm). Forming typical vesicular-arbuscular mycorrhiza, with mycorrhizal structures that stain blue to dark blue in trypan blue.

TYPE SPECIES: *Simiglomus hoi* (S.M. Berch & Trappe) G.A. Silva et al.

Simiglomus hoi (S.M. Berch & Trappe) G.A. Silva, Oehl & Sieverd., **comb. nov.**
MYCOBANK MB 518461
≡ *Glomus hoi* S.M. Berch & Trappe, Mycologia 77: 654. 1985.



FIGS 85–86. *Simiglomus hoi* (clade Aa2). Spores formed singly or in very loose small clusters; the subtending hyphae (SH) are concolorous with (or slightly lighter than) the spore wall without introverted wall thickening at the spore base and generally cylindrical to slightly funnel-shaped or slightly constricted. SH wall thickening may extend over very long distances. The spore pore is generally closed by conspicuously recurved septa at varying distances from the spore base. Often several recurved septa (sp) visible that arise from the structural layer in the subtending hyphae.



Figs 87–89. *Septoglomus* (clade Aa3) species form spores singly in soil or in very loose small clusters; subtending hyphae (sh) are concolorous with (or slightly lighter than) the spore wall without introverted wall thickening at the spore base and generally cylindrical to constricted. sh wall thickening may extend over long distances. Spores with 1–3 wall layers (swl1–swl3); if closed, pore often with one to several septa (sp) that species-specifically arise from the structural layer in the subtending hyphae. **87**. *Se. constrictum*. **88**. *Se. deserticola*. **89**. *Se. xanthium*.

Septoglomus Sieverd., G.A. Silva & Oehl, **gen. nov.** Figs. 87–89

MycoBank MB 518436 (*Glomus* group Aa3)

Sporae singulariter vel in congregatos apertos efformatae; tunica sporarum cum tunica hypharum coniuncta; hyphae cylindricae vel infundiles pori sporarum occlusi septo. Mycorrhizas vesicular-arbusculares formans caeruleas colorantes cum 'trypan blue'.

Etymology: from the Latin: *septum* = septum; *glomus* = cluster; referring to the relation with *Glomus*, to which species of the new genus previously belonged.

Key characters: Spores formed singly or in very loose, small clusters. Spores with a mono-to-multiple layered spore wall. Wall of the sh conspicuously continuous and concolorous with the spore wall, or slightly lighter in color than the spore wall. sh are cylindrical to constricted or slightly funnel shaped at spore base. Pore at spore base or in some distance from spore based closed by a septum. Forming typical vesicular-arbuscular mycorrhiza, with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type species: *Septoglomus constrictum* (Trappe) Sieverd. et al.

Septoglomus africanum (Błaszk. & Kovács) Sieverd., G.A. Silva & Oehl, **comb. nov.**

MycoBank MB 519466

≡ *Glomus africanum* Błaszk. & Kovács, Mycologia 102: 1452. 2010.
≡ *Funneliformis africanus* (Błaszk. & Kovács) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 13. 2010.

Septoglomus constrictum (Trappe) Sieverd., G.A. Silva & Oehl, **comb. nov.**

MycoBank MB 518462

≡ *Glomus constrictum* Trappe, Mycotaxon 6: 361. 1977.
≡ *Funneliformis constrictus* (Trappe) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 14. 2010.

Septoglomus deserticola (Trappe, Bloss & J.A. Menge) G.A. Silva, Oehl & Sieverd., **comb. nov.**

MycoBank MB 518463

≡ *Glomus deserticola* Trappe, Bloss & J.A. Menge, Mycotaxon 20: 123. 1984.

Septoglomus xanthium (Błaszk., Blanke, Renker & Buscot) G.A. Silva, Oehl & Sieverd., **comb. nov.**

MycoBank MB 518464

≡ *Glomus xanthium* Błaszk., Blanke, Renker & Buscot, Mycotaxon 90: 459. 2004.

≡ *Funneliformis xanthius* (Błaszk.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 14. 2010.

Claroideoglomeraceae C. Walker & A. Schüssler, emend. Oehl, G.A. Silva & Sieverd. (*Glomus* group B)

Emended Description: Spores formed singly or in clusters with low spore numbers, extremely rarely in sporocarps; in soils or rarely in roots; sh hyaline to white, rarely subhyaline, often conspicuously bill-shaped. Spores with 1–4 wall layers (swl1–swl4); pore closure at spore base often with a septum that species-specifically may arise from the structural layer, from an adherent inner, (semi-)flexible layer, or from both layers.

Type genus: *Claroideoglomus* C. Walker & A. Schüssler

Other genus: *Viscospora* Sieverd. et al.

Claroideoglomus C. Walker & A. Schüssler, emend. Oehl, G.A. Silva & Sieverd. (*Glomus* group B1) Figs. 90–98

Emended Description: Spores generally formed singly in soil or rarely in roots; sh hyaline to white, rarely subhyaline, conspicuously bill-shaped. Spores with 1–4 wall layers (swl1–swl4); pore closure at spore base often with a septum that species-specifically may arise from the structural layer, from an adherent innermost, (semi-)flexible layer, or from both layers.

Type species: *Claroideoglomus claroideum* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüssler

Claroideoglomus candidum (Furrazola, Kaonongbua & Bever), Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 519459

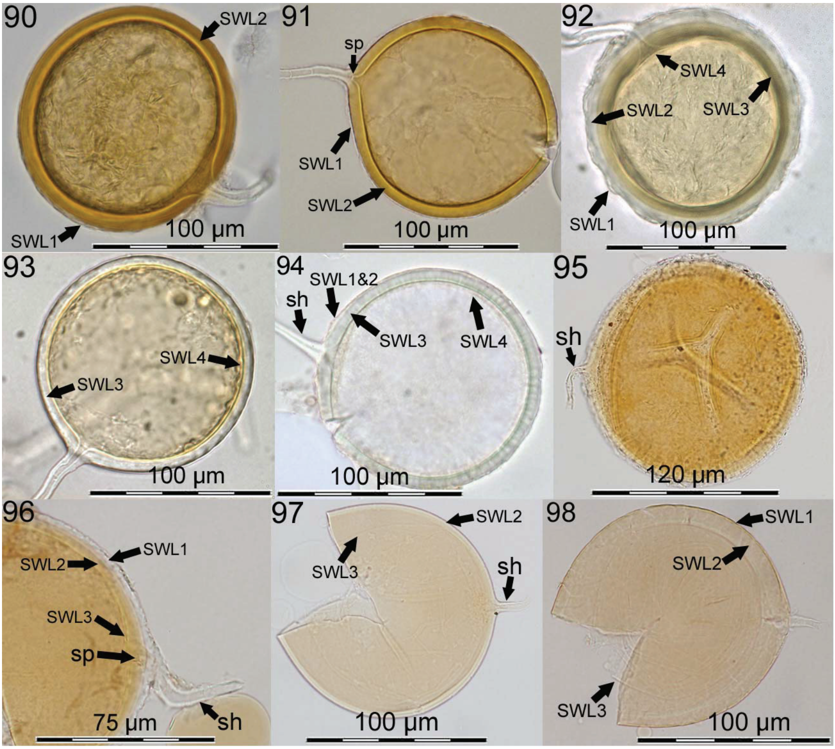
≡ *Glomus candidum* Furrazola, Kaonongbua & Bever, Mycotaxon 113: 103. 2010.

Claroideoglomus claroideum (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 21. 2010.

≡ *Glomus claroideum* N.C. Schenck & G.S. Sm., Mycologia 74: 84. 1982 (emend. Walker & Vestberg 1998).

Claroideoglomus drummondii (Błaszk. & Renker) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 22. 2010.

≡ *Glomus drummondii* Błaszk. & Renker, Mycol. Res. 110: 559. 2006.



Figs 90–98. *Claroideoglomus* (clade B1) species generally form spores singly in soils or (rarely) in roots; rarely also in very loose spore clusters; subtending hyphae (sh) conspicuously bill-shaped but hyaline to white, rarely subhyaline. Spores with 1–4 wall layers (swl1–swl4); pore closure at spore base generally with a septum (sp) that species-specifically may arise from structural wall layer, an adherent inner (semi-)flexible layer, or both layers. **90–91**. *Cl. etunicatum*. **92**. *Cl. lamellosum*. **93–94**. *Cl. claroideum*. **95–96**. *Cl. luteum*. **97**. *Cl. drummondii*. **98**. *Cl. walkeri*.

Claroideoglomus etunicatum (W.N. Becker & Gerd.) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 22. 2010.
≡ *Glomus etunicatum* W.N. Becker & Gerd., Mycotaxon 6: 29. 1977.

Claroideoglomus lamellosum (Dalpé, Koske & Tews) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 22. 2010.
≡ *Glomus lamellosum* Dalpé, Koske & Tews, Mycotaxon 43: 289. 1992.

Claroideoglomus luteum (L.J. Kenn., J.C. Stutz & J.B. Morton) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 22. 2010.
≡ *Glomus luteum* L.J. Kenn., J.C. Stutz & J.B. Morton, Mycologia 91: 1090. 1999.

Claroideoglomus walkeri (Błaszk. & Renker) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 22. 2010.
≡ *Glomus walkeri* Błaszk. & Renker. Mycol. Res. 110: 563. 2006.

Viscospora Sieverd., Oehl & G.A. Silva, **gen. nov.** (*Glomus* group B2)

MycoBank MB 518439

> *Sporae in congregatos apertos efformatae; tunica sporarum cum tunica hypharum coniuncta; hyphae hyalinae vel albae; stratum exterior hyphae et sporarum cum materia mucilagina; porum sporarum non occlusum vel occlusum hyphae crassae. Mycorrhizas vesicular-arbusculares formans caeruleas colorantes cum 'trypan blue'.*
>
> Etymology: from the Latin: *viscosus* = sticky; *spora* = spore; referring to the adhesive nature of the spore surface of the type species of the genus.

Key characters: Spores generally formed in loose clusters; sh hyaline to white, rarely subhyaline, often thick-walled. Spores with 1–4 wall layers (swl1–swl4); outer wall layer exuding a mucigel-like substance. Pore closure at spore base often open, or semi-closed by wall thickening.

Type species: *Viscospora viscosa* (T.H Nicolson) Sieverd. et al.

Viscospora viscosa (T.H Nicolson) Sieverd., Oehl & G.A. Silva, **comb. nov.**

MycoBank MB 518471

≡ *Glomus viscosum* T.H. Nicolson, Mycol. Res. 99: 1502. 1995.

Diversisporaceae C. Walker & A. Schüssler, emend. Oehl, G.A. Silva & Sieverd.
(*Glomus* group C)

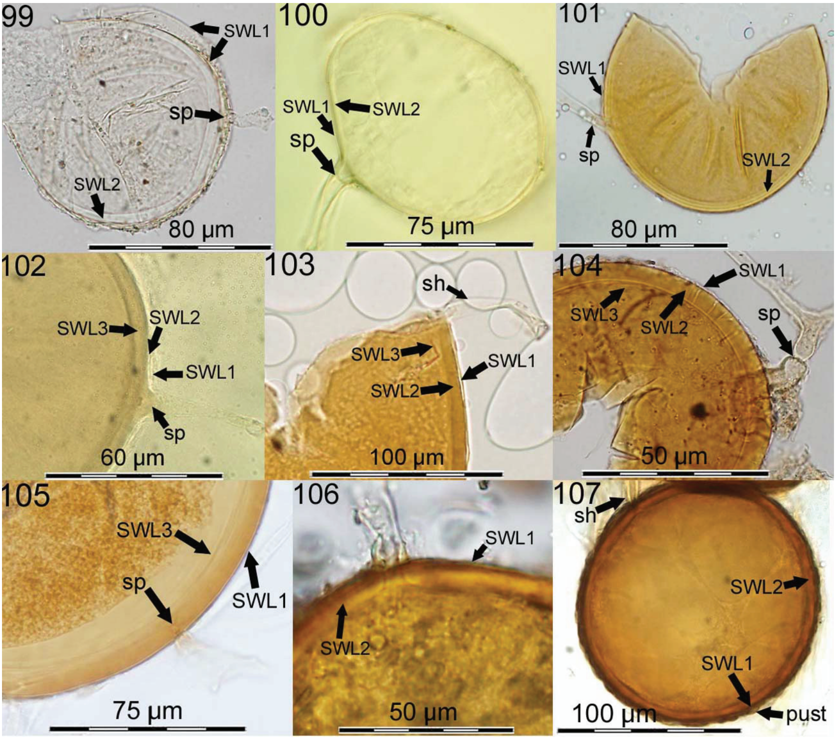
Emended description: Spore formation either diversisporoid or otosporoid. Diversisporoid spores either formed singularly, in clusters or in large sporocarps with high spores numbers, not organized; in pigmented spores sh conspicuously change color, becoming hyaline to white behind the septum, i.e. immediately or in a minimal distance to this septum; sh generally straight, cylindrical, sometimes species-specifically constricted or inflated. Spores with 1–3 wall layers (swl1–swl3); pore closure often with a septum that may species-specifically arise from innermost wall lamina or overlaying laminate layer, or from both; pore of hyphal attachment rarely (species-specifically) open. Otosporoid spores with two multiple-layered walls, spore attachment generally closed by a septum.

Type genus: *Diversispora* C. Walker & A. Schüssler

Other genera: *Otospora* Oehl et al., *Redeckera* C. Walker & A. Schüssler

Diversispora C. Walker & A. Schüssler, emend. G.A. Silva, Oehl & Sieverd.
(*Glomus* group Ca) Figs. 99–107

Emended description: Spores either formed singularly, in small open clusters or in large multi-spored clusters or sporocarps where spores are not organized. In pigmented spores sh conspicuously change color, becoming hyaline to white behind the septum; sh generally straight, cylindrical, sometimes species-specifically constricted, often hyphal attachment looks like inserted in spore wall. Spores with 1–3 wall layers (swl1–swl3); pore closure often with a



Figs 99–107. *Diversispora* (clade Ca) species form spores singly or in unorganized clusters or sporocarps; in pigmented spores subtending hyphae (sh) with a conspicuous color change distant to the first septum at or near the spore base; sh generally cylindrical, species-specifically sometimes constricted. Spores species-specifically with 1–3 wall layers (swl1–swl3); pore closure at spore base often with a septum (sp) that species-specifically may arise from a structural wall layer, an adherent inner (semi-)flexible layer, or both layers; rarely (species-specifically) pore open. **99**. *Di. spurca*. **100**. *Di. eburnea*. **101**. *Di. insculpta*. **102**. *Di. arenaria*. **103–104**. *Di. aurantia*. **105**. *Di. epigaea*. **106**. *Di. tenera*. **107**. *Di. pustulata*.

septum that may species-specifically arise from the innermost wall layer; rarely (species-specifically) pore of attachment open.

Type species: *Diversispora spurca* (C.M. Peiff. et al.) C. Walker & A. Schüssler

Diversispora arenaria (Błaszk., Tadych & Madej) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518472

≡ *Glomus arenarium* Błaszk., Tadych & Madej, Acta Soc. Bot. Pol. 70: 97. 2001.

Diversispora aurantia (Błaszk., Blanke, Renker & Buscot) C. Walker & A. Schüssler, – a species list: 43. 2010.

≡ *Glomus aurantium* Błaszk., Blanke, Renker & Buscot, Mycotaxon 90: 450. 2004.

Diversispora celata C. Walker, Gamper & A. Schuessler, New Phytol. 182: 497. 2009.

Diversispora eburnea (L.J. Kenn., J.C. Stutz & J.B. Morton) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 43. 2010.
≡ *Glomus eburneum* L.J. Kenn., J.C. Stutz & J.B. Morton, Mycologia 91: 1084. 1999.

Diversispora epigaea (B.A. Daniels & Trappe) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 43. 2010.
≡ *Glomus epigaeum* B.A. Daniels & Trappe, Can. J. Bot. 57: 540. 1979.

Diversispora gibbosa (Błaszk.) Błaszk. & Kovács, **comb. nov.**
MycoBank MB 518475
≡ *Glomus gibbosum* Błaszk., Mycologia 89: 339. 1997.

Diversispora insculpta (Błaszk.) Oehl, G.A. Silva & Sieverd., **comb. nov.**
MycoBank MB 519546
≡ *Glomus insculptum* Błaszk., Mycotaxon 89: 227. 2004.

Diversispora przelewicensis (Błaszk.) Oehl, G.A. Silva & Sieverd., **comb. nov.**
MycoBank MB 518477
≡ *Glomus przelewicense* Błaszk., Bull. Pol. Acad. Sci., Biol. Sci. 36: 272. 1988.

Diversispora pustulata (Koske, Friese, C. Walker & Dalpé) Oehl, G.A. Silva & Sieverd., **comb. nov.**
MycoBank MB 518478
≡ *Glomus pustulatum* Koske, Friese, C. Walker & Dalpé, Mycotaxon 26: 143. 1986.

Diversispora spurca (C.M. Pfeiff., C. Walker & Bloss) C. Walker & A. Schüssler, Mycol. Res. 108: 982. 2004.
≡ *Glomus spurcum* C.M. Pfeiff., C. Walker & Bloss, Mycotaxon 59: 374. 1996.

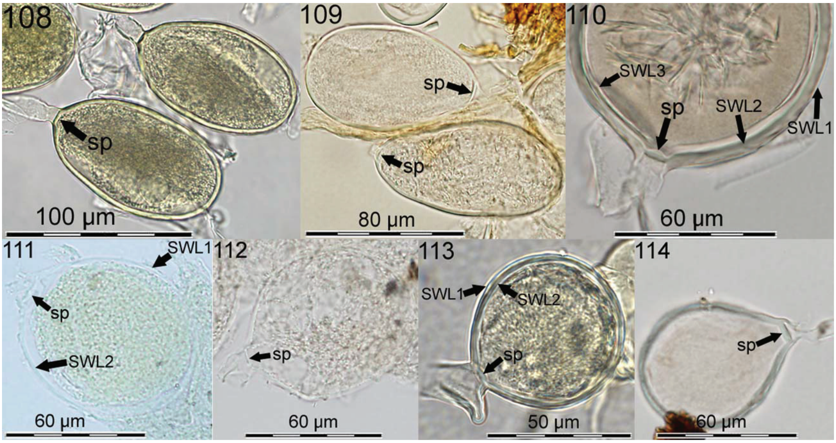
Diversispora tenera (P.A. Tandy) Oehl, G.A. Silva & Sieverd., **comb. nov.**
MycoBank MB 518479
≡ *Glomus tenerum* P.A. Tandy, Austral. J. Bot. 23: 864. 1975.

Diversispora trimurales (Koske & Halvorson) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 43. 2010.
≡ *Glomus trimurales* Koske & Halvorson, Mycologia 81: 930. 1990.

Diversispora versiformis (P. Karst.) Oehl, G.A. Silva & Sieverd., **comb. nov.**
MycoBank MB 518481
≡ *Endogone versiformis* P. Karst., Hedwigia 23: 39. 1884.
= *Glomus versiforme* (P. Karst.) S.M. Berch, Can. J. Bot. 61: 2614. 1983.

Redeckera C. Walker & A. Schüssler, emend. Oehl, G.A. Silva & Sieverd.
(*Glomus* group Cb) Figs. 108–114

Emended description: Spore formation disorganized in large and compact sporocarps, containing hundreds to thousands of spores per sporocarp; spores



Figs 108–114. *Redeckera* (clade Cb) with spore formation in unorganized but large and compact sporocarps (usually with hundreds to thousands spores per sporocarp); spores species-specifically with 2(–3) wall layers (SWL1–SWL3); subtending hyphae (SH) generally broad at spore base and with a conspicuous thick, broad septum (sp) arising from the inner lamina of the generally bi-laminated spore wall layer (SWL2); structural SWL2 generally extend over very short (2–10 µm) distances into SH; SWL1 fragile and usually inflating where SWL2 becomes invisible in the SH. **108**. *Re. fulva.* **109**. *Re. megalocarpa.* **110**. *Re. pulvinata.* **111–112**. *Re. canadensis.* **113–114**. *Re. fragilis.*

with 2 to rarely 3 wall layers (SWL1–SWL3); SH generally broad at spore base and with a conspicuous, thick and broad septum that arises from the inner lamina (SWL2) of the generally bi-laminated, structural wall layer; structural SWL2 generally continue over very short distances (2–10 µm) into SH; SWL1 fragile, usually inflating in a short distance to the spore base where SWL2 becomes invisible in the SH.

Gender: *Redeckera* is a Latin feminine noun, formed according to ICBN [Vienna Code] Recommendation 60B.1(b). Because the feminine gender is clearly apparent (and reinforced by the implication of Recommendation 20A.1(i)), Article 62.3 does not apply, and the authors did not have the prerogative to choose any other gender. We therefore correct all adjectival epithets to feminine.

Type species: *Redeckera megalocarpa* (D. Redecker) C. Walker & A. Schüssler

Redeckera avelingiae (R.C. Sinclair) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518482

≡ *Glomus avelingiae* R.C. Sinclair, Mycotaxon 74: 338. 2000.

Redeckera canadensis (Thaxt.) Oehl, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 518483

≡ *Endogone canadensis* Thaxt., Proc. Am. Acad. Arts Sci. 57: 317. 1922.

≡ *Glomus canadense* (Thaxt.) Trappe & Gerd., Mycol. Mem. 5: 59. 1974.

Redeckera fragilis (Berk. & Broome) Oehl, G.A. Silva & Sieverd., **comb. nov.**
MycoBank MB 518484
≡ *Paurocotylis fragilis* Berk. & Broome, J. Linn. Soc. Bot. 14: 137. 1873.
≡ *Glomus fragile* (Berk. & Broome) Trappe & Gerd., Mycol. Mem. 5: 59. 1974.

Redeckera fulva (Berk. & Broome) C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 44. 2010.
≡ *Paurocotylis fulva* Berk. & Broome, J. Linn. Soc. Bot. 14: 137. 1873.
≡ *Glomus fulvum* (Berk. & Broome) Trappe & Gerd., Mycol. Mem. 5: 59. 1974.

Redeckera megalocarpa (D. Redecker) C. Walker & A. Schüssler, The *Glomeromycota*: 44. 2010.
≡ *Glomus megalocarpum* D. Redecker, Mycol. Progress 6: 38. 2007.

Redeckera pulvinata (Henn.) C. Walker & A. Schüssler, The *Glomeromycota*: 44. 2010.
≡ *Endogone pulvinata* Henn., Hedwigia 36: 212. 1897.
≡ *Glomus pulvinatum* (Henn.) Trappe & Gerd., Mycol. Mem. 5: 59. 1974.

Otospora Oehl, Palenz. & N. Ferrol
Type species: *Otospora bareae* Palenz. et al.

Otospora bareae Palenz., N. Ferrol & Oehl, Mycologia 100: 298. 2008.

Paraglomeraceae J.B. Morton & D. Redecker

Paraglomus J.B. Morton & D. Redecker
Type species: *Paraglomus occultum* (C. Walker) J.B. Morton & D. Redecker

Paraglomus albidum (C. Walker & L.H. Rhodes) Oehl, G.A. Silva & Sieverd., **comb. nov.**
MycoBank MB 518488
≡ *Glomus albidum* C. Walker & L.H. Rhodes, Mycotaxon 12: 509. 1981.

Paraglomus brasilianum (Spain & J. Miranda) J.B. Morton & D. Redecker, Mycologia 93: 190. 2001.
≡ *Glomus brasilianum* Spain & J. Miranda, Mycotaxon 60: 139. 1996.

Paraglomus laccatum (Błaszk.) Renker, Błaszk. & Buscot, Nova Hedwigia 84: 400. 2007.
≡ *Glomus laccatum* Błaszk., Bull. Pol. Acad. Sci., Biol. Sci. 36: 271. 1988.

Paraglomus lacteum (S.L. Rose & Trappe) Oehl, G.A. Silva & Sieverd. **comb. nov.**
MycoBank MB 518489
≡ *Glomus lacteum* S.L. Rose & Trappe, Mycotaxon 10: 415. 1980.

Paraglomus occultum (C. Walker) J.B. Morton & D. Redecker, Mycol. Res. 93:190. 2001.
≡ *Glomus occultum* C. Walker, Mycotaxon 15: 50. 1982.

Taxonomic problems

We were unsure whether we had attributed *Gl. dolichosporum* and *Gl. citricola* to the correct genus, as the available descriptions were either short or in Chinese, images were missing or relatively poor, or the type specimen was not accessible. Moreover, in several species descriptions (some even very recent), the focus on the spore base and SH features was minimal to absent. For such cases, we decided to retain these species within *Glomus*, pending future revision. Placement of *Gl. pubescens* was similarly difficult: Already transferred to four different genera other than its basionym genus, this particular species may not even represent an AM fungus (e.g. Trappe, pers. comm.). Of all clades discussed here and fungal genera known, this species appears to fit best in *Glomus* group Ab1.

During our spore analyses, it was apparent that several genetic groups (clades) possess species with spores so similar that either the species are difficult to differentiate morphologically or may be conspecific. Examples include Aa3—*Se. deserticola*, *Se. xanthium;* Ab2—*Gl. clarum*, *Gl. manihotis, Gl. zaozhuangianum;* and Ca—*Di. versiformis, Di. przelewicensis, Di. epigaea.* As it was beyond the scope of this study to clarify all vagaries and possible taxonomic uncertainties at the species level, we have placed them into genera based on morphological characteristics, especially as many type specimens were unavailable (see TABLE 1). In some cases confusion may have resulted from misidentification or incorrect re-naming prior to genetic analysis. For example, the *Gl. clarum* isolate BR147B (supplied by Bioplanta) that grouped with *Gl. manihotis* in the initial phylogenetic study by Schüßler et al. (2001) was an ex-type of *Gl. manihotis* when sent in 1987 to Bioplanta (Sieverding pers. com.) but which some time later was relabeled as *Gl. clarum* by someone else. Not surprisingly, this particular '*Gl. clarum*' isolate grouped with other *Gl. manihotis* ex-type material in the study by Schüßler et al. (2001). Consequently, genetic information provided for some species as well as the conclusion that other species are conspecific may be based on erroneous information.

Until recently, both germination and germination structures were regarded as important features to distinguish between AM fungal genera and families (e.g., *Pacisporaceae* vs. *Glomeraceae* by Oehl & Sieverding 2004, Walker & Schüßler 2004; among *Gigasporaceae*, *Scutellosporaceae*, *Racocetraceae,* and *Dentiscutataceae* by Oehl et al. 2008, 2011a; and *Archaeospora* vs. *Ambispora* by Spain et al. 2006). There are clear indications that *Paraglomus* species germinate directly through the spore wall as observed for *Pa. occultum*, *Pa. brasilianum* and *Pa. lacteum* (Spain & Miranda 1996, Rose & Trappe 1980, Oehl pers. obs.) in contrast to all other species forming single-walled glomoid or diversisporoid spores where a germ tube emerges apparently through the SH (e.g. *Glomus*, *Diversispora*). There are uncertainties surrounding germ tube formation in some *Glomus* spp., such as *Gl. pallidum*, which Hall (1977) reported as germinating directly through the spore wall, although his description and photos suggest instead either intercalary spore formation or two hyphal attachments on the same spore. Intercalary spore formation (= two attachments) is a frequent feature for many *Glomus* sporocarpic (Ab) species.

Molecular difficulties

The major problem encountered during the current study revolved around the limited molecular database, especially for species of the former *Glomus* groups Ab1, Ab3, and Cb. Moreover, only a limited number of *Glomeromycota* species in the public databases have been sequenced for all currently available markers (LSU rDNA, SSU rDNA, ITS region, β-tubulin). Some individual clades were supported in just one dataset. Another major difficulty was that either many cultures of glomoid or diversisporoid spore-forming species are lost or yet to be cultured successfully in single species cultures or the species were not culturable. This renders analyses difficult or impossible. During the study, DNA extraction was attempted from several species using field spores or sporocarps but they largely failed (e.g., *Gl. invermaium, Gl. taiwanense*). These obstacles have left the database incomplete and slowed progress in complete molecular AM fungal identification.

Discussion

In this paper, we have revised the taxonomic organization of AM fungal species with glomoid spore formation, based largely on newly available molecular data retrieved from the literature and public databases. This organization is also based upon morphological spore characteristics, which were either already well established or newly established during this study. Phylogenetic trees support all genera proposed in this paper and some genera proposed by Walker & Schüßer (2010), with bootstrap support > 80% (except *Septoglomus* in the beta-tubulin phylogeny) in at least one analysis (NJ, ML, Bayesian or MP). However, *Rhizophagus* (Ab2) and *Sclerocystis* (Ab3) were not supported by our phylogenetic analyses and thus, the resurrection of these genera Walker & Schüßer (2010) cannot be accepted. The genera proposed or confirmed in the present study are shown as clusters in the trees: *Glomus* (Ab1, Ab2, Ab3), *Funneliformis* (Aa1), *Simiglomus* (Aa2), *Septoglomus* (Aa3), *Claroideoglomus* (B1), *Viscospora* (B2), *Diversispora* (Ca) and *Redeckera* (Cb). In Table 3, we summarize the new taxonomic organization of AM fungal species within the *Glomeromycota*.

There is no doubt that glomoid and diversisporoid spores in *Glomeraceae*, *Claroideoglomeraceae* and *Diversisporaceae* can clearly be differentiated by molecular phylogeny (Figs. 1–4), as shown earlier (Schüßler et al. 2001, Silva

Table 3. New classification of the *Glomeromycota*

Class	Order	Family	Genus
Glomeromycetes	*Glomerales*	*Glomeraceae*	*Glomus*
			Funneliformis
			Simiglomus
			Septoglomus
		Claroideoglomeraceae	*Claroideoglomus*
			Viscospora
	Diversisporales	*Diversisporaceae*	*Diversispora* *Redeckera* *Otospora*
		Entrophosporaceae	*Entrophospora*
		Acaulosporaceae	*Acaulospora*
			Kuklospora
		Pacisporaceae	*Pacispora*
	Gigasporales	*Gigasporaceae*	*Gigaspora*
		Scutellosporaceae	*Scutellospora* *Orbispora*
		Racocetraceae	*Racocetra*
			Cetraspora
		Dentiscutataceae	*Dentiscutata*
			Fuscutata
			Quatunica
Archaeosporomycetes	*Archaeosporales*	*Archaeosporaceae*	*Archaeospora* *Intraspora*
		Ambisporaceae	*Ambispora*
		Geosiphonaceae	*Geosiphon*
Paraglomeromycetes	*Paraglomerales*	*Paraglomeraceae*	*Paraglomus*

The taxa *Archaeosporomycetes*, *Paraglomeromycetes*, *Gigasporales* and *Orbispora* are presented in this volume (Oehl et al. 2011a, 2011b).

et al. 2006, Stockinger et al. 2010). *Glomeraceae* and *Claroideoglomeraceae* differ morphologically in the hyphal attachments at the spore base and in spore clustering/aggregation or sporococarp formation. The phylogenetic trees also show *Glomeraceae* and *Claroideoglomeraceae* as separate clades with high bootstrap values in SSU, LSU, and beta-tubulin analyses.

Differences in hyphal connections at the spore base are also basic morphological indicators for other related but clearly genetically separate families of the *Glomeromycota* (e.g., *Acaulosporaceae*, *Pacisporaceae, Scutellosporaceae*). It has been argued earlier that unequivocal assignment of glomoid and diversisporoid spore-forming species to the correct major phylogenetic clade through morphological spore analyses alone would be impossible (e.g. Schüßler et al. 2001, Morton & Redecker 2001, Walker et al. 2007), primarily because glomoid and diversisporoid spores have but few differentiating morphological characters (which may yet hold true). Features other than hyphal connections (such as spore size and color) overlap between many glomoid and diversisporoid species, and intraspecific variation might be considerable. Spore aggregation and cluster/sporocarp formation in glomoid and diversisporoid species are not well investigated and have thus far received only limited attention. However, sporocarp formation and organization may be stable characteristics, as found in the former genus *Sclerocycstis*, which at some point may need to be raised again to genus level within the *Glomeraceae.* Other species of *Glomeraceae* are also always formed in sporocarps (e.g. *Gl. glomerulatum, Gl. formosanum*) but as yet there are insufficient molecular data to support their placement within their own genus. Other glomoid spores form in clusters or sporocarps occurring in relatively small to sometimes huge spore numbers (*Gl. macrocarpum, Gl. microcarpum, Gl. aureum*) as well as form singly in soil or in roots, so that spore aggregation alone cannot be used to diagnose the taxonomic order. We acknowledge that the large genus *Glomus* currently has morphologically heterogeneous spores, and recent findings by Błaszkowski et al. (2009a, b) show that several clades with small-spored species also belong to this group. To date, there are insufficient sequence sets available for more detailed analyses, although new genera could result from such analyses. This applies also for *Gl. intraradices* versus *Gl. macrocarpum* and *Gl. microcarpum* and *Glomus* Ab1 species in general. Recent research has also shown that genetic information generated years ago may actually be derived from another species, *Gl. irregulare* (Stockinger et al. 2009). Based on morphology alone, species such as *Gl. intraradices* should be excluded from *Glomus*.

Within *Diversispora* (respective former *Glomus* group C, our clade Ca) and *Redeckera* (our clade Cb), there has been no previous attempt to explain how these species differ morphologically from the former *Glomeraceae* groups A and B (Schüßler et al. 2001, Walker & Schüßler 2004). While morphological differentiation between *Diversispora* and *Redeckera* is possible, the morphology of *Diversispora* spores that differentiates them from spores of some *Claroideoglomus* spp. may be difficult to recognize, even for taxonomic specialists.

To conclude, our paper reports on the congruence of morphological groups (genera and family) with molecular phylogeny that has shown the need for a substantial reorganization of taxa in *Glomeromycota*.

Unsolved obstacles in the *Glomeraceae*

With approximately 70 species, the revised *Glomus* remains morphologically heterogeneous and the largest genus in the *Glomeromycota*. Species such as

Gl. intraradices, *Gl. aggregatum,* and *Gl. proliferum* are atypical in the genus regarding spore base closure by wall thickening and/or septum. These are normally quite stable features and not highly variable within species: a septum not readily seen at the spore base is either species specific or indicates the spore development stage. Mature spores have septa more frequently formed by the innermost lamina of the inner spore wall layer. Morphologically speaking, species like *Gl. intraradices, Gl. aggregatum,* and *Gl. proliferum* should be included in a separate genus, but the absence of sufficient genetic information (in particular of the other *Glomus* spp.) does not support this hypothesis. Additionally, we include several small-spored, cluster-forming species within the revised *Glomus* (e.g. *Gl. perpusillum*, *Gl. indicum, G. iranicum*) whose spores quickly decompose, suggesting that some earlier may have erroneously been designated 'non-sporulating AM fungi' (Błaszkowski et al. 2009b). Verification is still needed to establish whether there are indeed species of 'non-sporulating' fungi within the *Glomus* clade.

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