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Advances in *Glomeromycota* taxonomy and classification

Fritz Oehl[1], Ewald Sieverding[2], Javier Palenzuela[3], Kurt Ineichen[4], and Gladstone Alves da Silva[5]

[1]Agroscope Reckenholz-Tänikon Research Station (ART), Ecological Farming Systems, Reckenholzstrasse 191, CH-8046 Zürich, Switzerland; corresponding author e-mail: fritz.oehl@art.admin.ch

[2]Institute of Plant Production and Agroecology in the Tropics and Subtropics, University of Hohenheim, Garbenstrasse 13, D-70593 Stuttgart, Germany

[3]Departamento de Microbiología del Suelo y Sistemas Simbióticos, Estación Experimental del Zaidín, CSIC, Profesor Albareda 1, 18008 Granada, Spain

[4]Basel-Zürich Plant Science Center, Institute of Botany, University of Basel, Hebelstrasse 1, CH-4056 Basel, Switzerland

[5]Departamento de Micologia, CCB, Universidade Federal de Pernambuco, Av. Prof. Nelson Chaves s/n, Cidade Universitaria, 50670-420, Recife, PE, Brazil

Abstract: Concomitant morphological and molecular analyses have led to major breakthroughs in the taxonomic organization of the phylum *Glomeromycota*. Fungi in this phylum are known to form arbuscular mycorrhiza, and so far three classes, five orders, 14 families and 29 genera have been described. *Sensu lato*, spore formation in 10 of the arbuscular mycorrhiza-forming genera is exclusively glomoid, one is gigasporoid, seven are scutellosporoid, four are entrophosporoid, two are acaulosporoid, and one is pacisporoid. Spore bimorphism is found in three genera, and one genus is associated with cyanobacteria. Here we present the current classification developed in several recent publications and provide a summary to facilitate the identification of taxa from genus to class level.

Key words:
Archaeosporomycetes
endomycorrhizas
evolution
Gigasporales
Glomerales
Glomeromycetes
Paraglomeromycetes
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INTRODUCTION

Glomeromycota taxonomy was largely morphologically driven up to the end of the last millennium. All glomeromycotean fungi, except one genus, are known to form arbuscular mycorrhiza. Their identification was based on spore morphology, spore formation, and spore wall structure (e.g. Gerdemann & Trappe 1974, Walker & Sanders 1986, Morton & Benny 1990, Schenck & Pérez 1990). However, as soon as molecular phylogenetic tools became available, they were included in taxonomic analyses (e.g. Simon *et al*. 1992) and soon became the drivers of the establishment of a new taxonomy (Morton & Redecker 2001, Schüßler *et al*. 2001). In 1990, without the benefit of molecular aspects, the arbuscular mycorrhiza-forming fungi were organized in three families (*Acaulosporaceae, Gigasporaceae,* and *Glomeraceae*) and six genera (*Acaulospora*, *Entrophospora*, *Gigaspora, Glomus*, *Sclerocystis,* and *Scutellospora*) within one order, *Glomerales* (Morton & Benny 1990) of the fungal phylum *Zygomycota*. That classification was based on spore morphology and spore formation characteristics (acaulosporoid, entrophosporoid, gigasporoid, glomoid, radial-glomoid, and scutellosporoid). Differences in spore wall structure were used at the species level.

Today, we accept three classes (*Archaeosporomycetes*, *Glomeromycetes*, and *Paraglomeromycetes*), five orders (*Archaeosporales, Diversisporales*, *Gigasporales*, *Glomerales* and *Paraglomerales*), 14 families, 29 genera and approximately 230 species (e.g. Morton & Redecker 2001, Schüßler *et al*. 2001, Oehl & Sieverding 2004, Walker & Schüßler 2004, Sieverding & Oehl 2006, Spain *et al*. 2006, Oehl *et al*. 2008, 2011a–d, Palenzuela *et al*. 2008).

Until recently, it was unclear whether glomoid and gigasporoid species could be further divided into different morphological groups congruent with the major phylogenetic clades obtained by molecular analyses. A first revision of the sporogenous cell forming (gigasporoid and scutellosporoid) *Glomeromycetes* according to concomitant morphological and phylogenetic features (Oehl et *al*. 2008) was not accepted by all mycologists (Morton & Msiska 2010). However, later studies with a broader database (e.g. Goto *et al*. 2010, 2011, Oehl *et al*. 2010, 2011b) confirmed that the revised genus *Scutellospora*, as well as the new *Racocetra*, *Cetraspora*, *Dentiscutata,* and *Orbispora,* are monophyletic.

A large group of species forms glomoid spores, and it had been believed that there were too few morphological characters of significance to differentiate them. Taxonomists have consequently started basing groupings of the glomoid species almost exclusively on molecular phylogenetic characters. A recent revision of these glomoid species has, however, shown that molecular phylogeny is actually congruent with the morphological characteristics of these fungi (Oehl *et al.* 2011c). Fungal species with entrophosporoid spore formation were also revised (Oehl *et al.* 2011d). The objective of this paper is to present the current overall classification system of *Glomeromycota* that has emerged from these recent studies, and to summarize the major morphological features in the phylum down to genus level.

MATERIALS AND METHODS

The morphological, molecular, and phylogenetic analyses performed are presented in a series of recent publications dealing with different species groups of *Glomeromycota* (e.g. Oehl *et al*. 2006, 2010, 2011a, b, d, f, Sieverding & Oehl 2006, Silva *et al.* 2006, Spain *et al.* 2006, Palenzuela *et al.* 2008, 2010, 2011).

RESULTS AND DISCUSSION

Figure 1 is a schematic tree for *Glomeromycota* based on molecular phylogenetic analyses of the SSU, ITS region, partial LSU of the rRNA gene, and partial β-tubulin gene (e.g. Oehl *et al*. 2008, 2010, 2011a–d). In Table 1, the major morphological features of all higher level taxa are presented, with the taxa arranged according to their taxonomic rank down to genus. Three glomeromycotean classes, five orders, 14 families, and 29 genera have been recognized to date (Table 1). *Sensu lato*, spore formation in 10 of the arbuscular mycorrhiza-forming genera have exclusively glomoid, one has gigasporoid, seven have scutellosporoid, four have entrophosporoid, two genera have acaulosporoid, and one has pacisporoid spore formation, while three genera show spore bimorphism, and one genus is associated with cyanobacteria (the only one not forming arbuscular mycorrhizas).

Hitherto, *Paraglomeromycetes* are monogeneric (Table 1), are characterized by mono-walled spores formed terminally on hyphae (i.e. glomoid spores *sensu lato*), and germinate directly through the spore wall. Their arbuscular mycorrhizal structures do not or only faintly stain in trypan blue. *Archaeosporomycetes* includes organisms that are exclusively bimorphic since they form either acaulosporoid or entrophosporoid spores simultaneously with glomoid spores, or are associated with cyanobacteria. The mycorrhizal structures of *Archaeosporaceae* are similar to those of *Paraglomeraceae*, while *Ambisporaceae* form vesicular-arbuscular mycorrhizal structures staining pale blue in trypan blue. In contrast, mycorrhizal structures in *Glomeromycetes* stain blue to dark blue in trypan blue. In *Glomeromycetes*, *Gigasporales* species do not form intraradical vesicles but auxiliary cells in soils, which clearly distinguish them from *Glomerales* and *Diversisporales*.

Gigasporales exhibit gigasporoid or scutellosporoid spore formation (Oehl *et al.* 2011b), i.e. spores formed terminally on sporogenous cells and with either germ warts on the inner surface of the mono-walled spore wall (gigasporoid; *Gigasporaceae*), or a discrete germination shield on the innermost (= 'germinal wall') of 2–4 walls (scutellosporoid). There are three families with scutellosporoid spore formation (*sensu lato*): *Dentiscutataceae, Racocetraceae* and *Scutellosporaceae* (Oehl *et al*. 2008). *Scutellosporaceae* form mono-lobed (*Orbispora*) or bi-lobed (*Scutellospora*), hyaline germination shields (Figs 2–4). *Racocetraceae* species form wavy-like, multiply lobed, hyaline germination shields and have either two (*Racocetra*) or three (*Cetraspora*) spore walls (Figs 5–8). *Dentiscutataceae* species form yellow-brown to brown germ shields that are bi-lobed (*Fuscutata*; Fig. 9) or with multiple compartments (*Dentiscutata*, triple-walled; *Quatunica* four-walled; Figs 10–11).

In *Archaeosporales* and *Diversisporales,* four genera have spore formation laterally on the neck of terminal or intercalary sporiferous saccules (= acaulosporoid *sensu lato*; Table 1): *Acaulospora*, *Otospora*, and the bi-morphic *Ambispora* and *Archaeospora*. These genera can easily be separated on spore wall number and spore wall structure (Palenzuela *et al.* 2008). Triple-walled *Acaulospora* species have a characteristic granular, 'beaded' inner wall surface (Morton & Benny 1990), which is absent in acaulo-ambisporoid spores of triple-walled *Ambispora* species (Spain *et al*. 2006, Palenzuela *et al*. 2011). The wall structure of the bi-walled *Otospora* is more complex than that of bi-walled *Archaeospora* species (Palenzuela *et al*. 2008).

In *Archaeosporales*, *Diversisporales,* and *Glomerales,* there are five genera with spore formation within the neck of terminal or intercalary sporiferous saccules (i.e. entrophosporoid *sensu lato*; Table 1): *Entrophospora*, *Kuklospora*, *Sacculospora*, *Tricispora,* and bimorphic *Intraspora* (Oehl *et al.* 2011d). Triple-walled *Kuklospora* has the characteristic granular, 'beaded' inner wall surface of *Acaulosporaceae* (Sieverding & Oehl 2006), which is absent in spores of triple-walled *Sacculospora* (Oehl *et al*. 2011d). The wall structure of bi-walled *Entrophospora* and *Tricispora* is more complex than that of bi-walled, bimorphic *Intraspora* species (Sieverding & Oehl 2006, Oehl *et al*. 2011d). *Entrophospora* and *Tricispora* can be distinguished through the two cicatrices (scars) and pore structures proximal and distal to the sporiferous saccule: the proximal pore is wide in *Tricispora* and closed by a septum, while it is narrow and closed by a plug in *Entrophospora*. The distal pore and scar is absent in *Entrophospora* from the structural layer, and formed only on the overlying, hyaline, evanescent layer, while, in light microscopy, the distal pore with a distal scar is obvious in *Tricispora* (Sieverding & Oehl 2006, Palenzuela *et al*. 2010, Oehl *et al.* 2011d).

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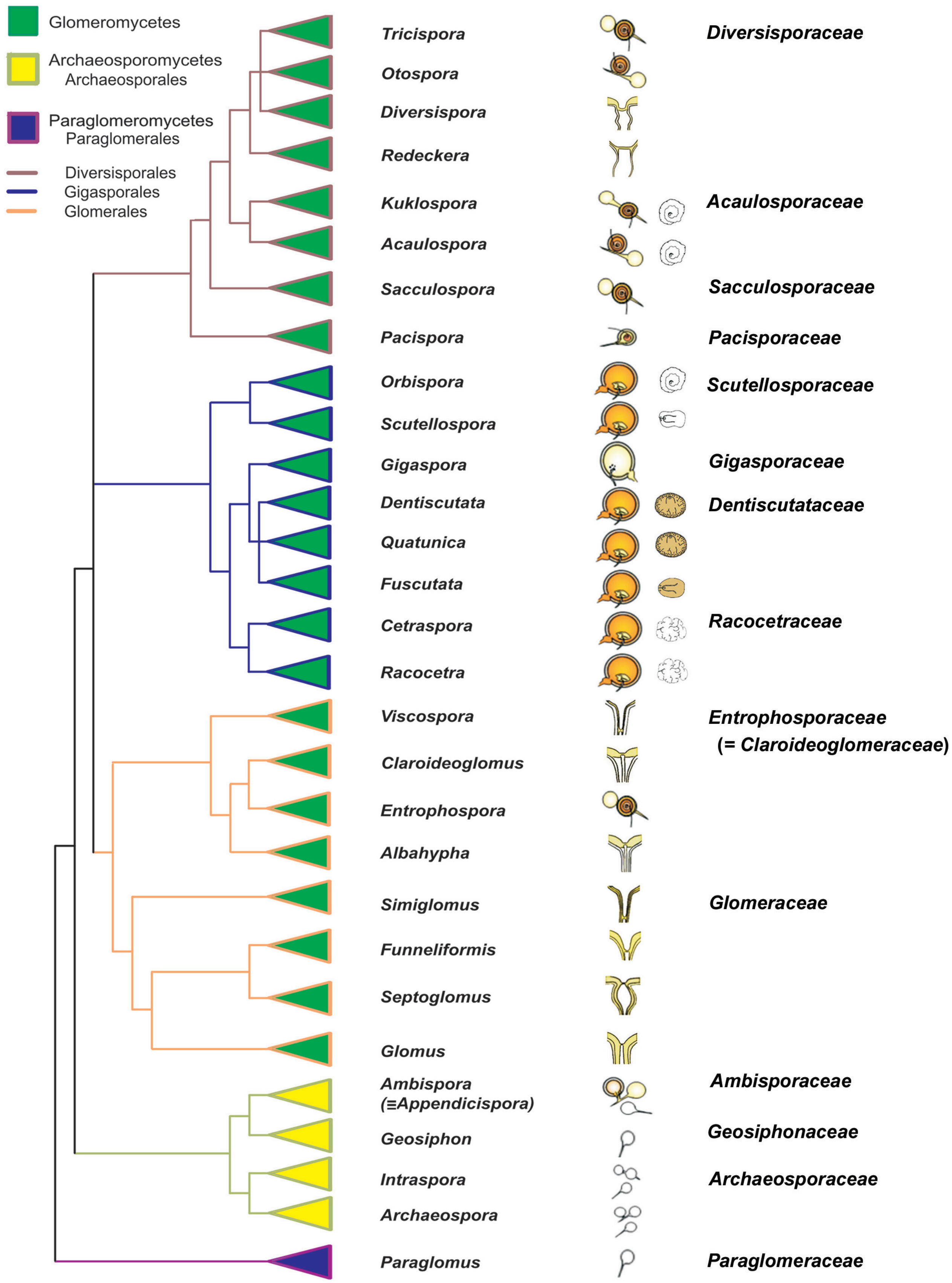

Fig. 1. Representative tree of the phylum *Glomeromycota* based on molecular (SSU, ITS region, partial LSU of the rRNA gene, and partial β-tubuline gene) and morphological analyses (spore wall structures, structures of the spore bases and subtending hyphae, germination, and germination shield structures). Adapted from (Oehl *et al.* 2008, 2011a–d). The drawings in the central columns show the spore formation types of the genera, and the typical germination shields for those genera which form persistent shields already during spore formation.

Table 1. Major morphological characters for higher level taxa of *Glomeromycota* from class to genus level.

Class Order	Family	Genus	Spore formation	Number of spore walls	Germination; specific germination structure	Mycorrhizal structures; staining in Trypan blue
Glomeromycetes					Germ tube (gt)	Vesicles, Arbuscles, Hyphae
Glomerales	*Glomeraceae*	*Glomus*	 Glomoid (terminally on hyphae)	1	gt through hypha	V, A, H
		Funneliformis	 Glomoid Funneliformoid sensu stricto	1	gt through hypha	V, A, H
		Septoglomus	 Glomoid Septoglomoid sensu stricto	1	gt through hyphae	V, A, H
		Simiglomus	 Glomoid Simiglomoid sensu stricto	1	gt through hypha?	V, A, H
	Entrophosporaceae	*Claroideoglomus*	 Glomoid sensu lato Claroideoglomoid sensu stricto	1	gt through hypha	V, A, H
		Albahypha	 Glomoid Claroideoglomoid sensu lato	1	gt through hypha?	V, A, H
		Viscospora	 Glomoid Claroideoglomoid sensu lato	1	gt through hypha	V, A, H
		Entrophospora	 Entrophosporoid (in the neck of a saccule)	2	gt through wall?	V, A, H
Diversisporales	*Diversisporaceae*	*Diversispora*	 Glomoid Diversisporoid sensu stricto	1	gt through hypha	V, A, H
		Redeckera	 Glomoid (Diversisporo-)Redeckeroid sensu stricto	1	gt through hypha?	V, A, H
		Otospora	 Acaulosporoid (on the neck of sporiferous saccule): otosporoid sensu stricto	2	Unknown?	V, A, H
		Tricispora	 Entrophosporoid Tricisporoid sensu stricto	2	Unknown?	V, A, H
	Sacculosporaceae	*Sacculospora*	 Entrophosporoid Sacculosporoid sensu stricto	3	Unknown?	V, A, H
	Pacisporaceae	*Pacispora*	 Pacisporoid	2	gt through wall; multiply lobed germ structure	V, A, H
	Acaulosporaceae	*Kuklospora*	 Entrophosporoid Kuklosporoid sensu stricto	3	gt through wall; mono-lobed, hyaline germ shield (=orb)	V, A, H
		Acaulospora	 Acaulosporoid	3	gt through wall; mono-(to multiply) lobed, hyaline germ shield (=orb)	V, A, H

Gigasporales	*Scutellosporaceae*	*Orbispora*	Scutellosporoid (on sporogenous cells, and forming germ shields); Orbisporoid *sensu stricto*	3	gt through wall; mono-lobed, hyaline germ shield (=orb)	A, H
		Scutellospora	Scutellosporoid	3	gt through wall; bi-lobed, hyaline, violin-shaped germ shield	A, H
	Dentiscutataceae	*Fuscutata*	Scutellosporoid Fuscutatoid sensu stricto	3	gt through wall; bi-lobed, brown, oval shield	A, H
		Dentiscutata	Scutellosporoid Dentiscutatoid sensu stricto	3	gt through wall; brown germ shield with multiple small compartments	A, H
		Quatunica	Scutellosporoid Dentiscutatoid sensu stricto	4	gt through wall; brown germ shield with multiple compartments	A, H
	Racocetraceae	*Cetraspora*	Scutellosporoid Racocetroid sensu stricto	3	gt through wall; multiply lobed, hyaline germ shield	A, H
		Racocetra	Scutellosporoid Racocetroid sensu stricto	2	gt through wall; multiply lobed, hyaline germ shield	A, H
	Gigasporaceae	*Gigaspora*	Gigasporoid (on sporogenous cells, and forming germ warts)	1	gt through wall; germ warts on inner spore wall layer	A, H
Archaeosporomycetes						
Archaeosporales	*Ambisporaceae*	*Ambispora*	Bimorph: Acaulo- & Glomo-ambisporoid	3 (Ac) 1 (Gl)	Multiply-lobed germ structure (Ac) & gt through hypha (Gl)	V, A, H
	Archaeosporaceae	*Archaeospora*	Bimorph: Acaulo- & Glomo-archaeosporoid	2 (Ac) 1 (Gl)	gt through wall; germ trunk (Ac), & gt through hypha (Gl)?	A, H
		Intraspora	Bimorph: Entropho-& Glomo-intrasporoid	2 (Ac) 1 (Gl)	Unknown?	A, H
	Geosiphonaceae	*Geosiphon*	Glomoid sensu lato	1	gt through hypha?	Associated with cyanobacteria
Paraglomeromycetes						
Paraglomerales	*Paraglomeraceae*	*Paraglomus*	Glomoid sensu lato	1	gt through wall	A, H

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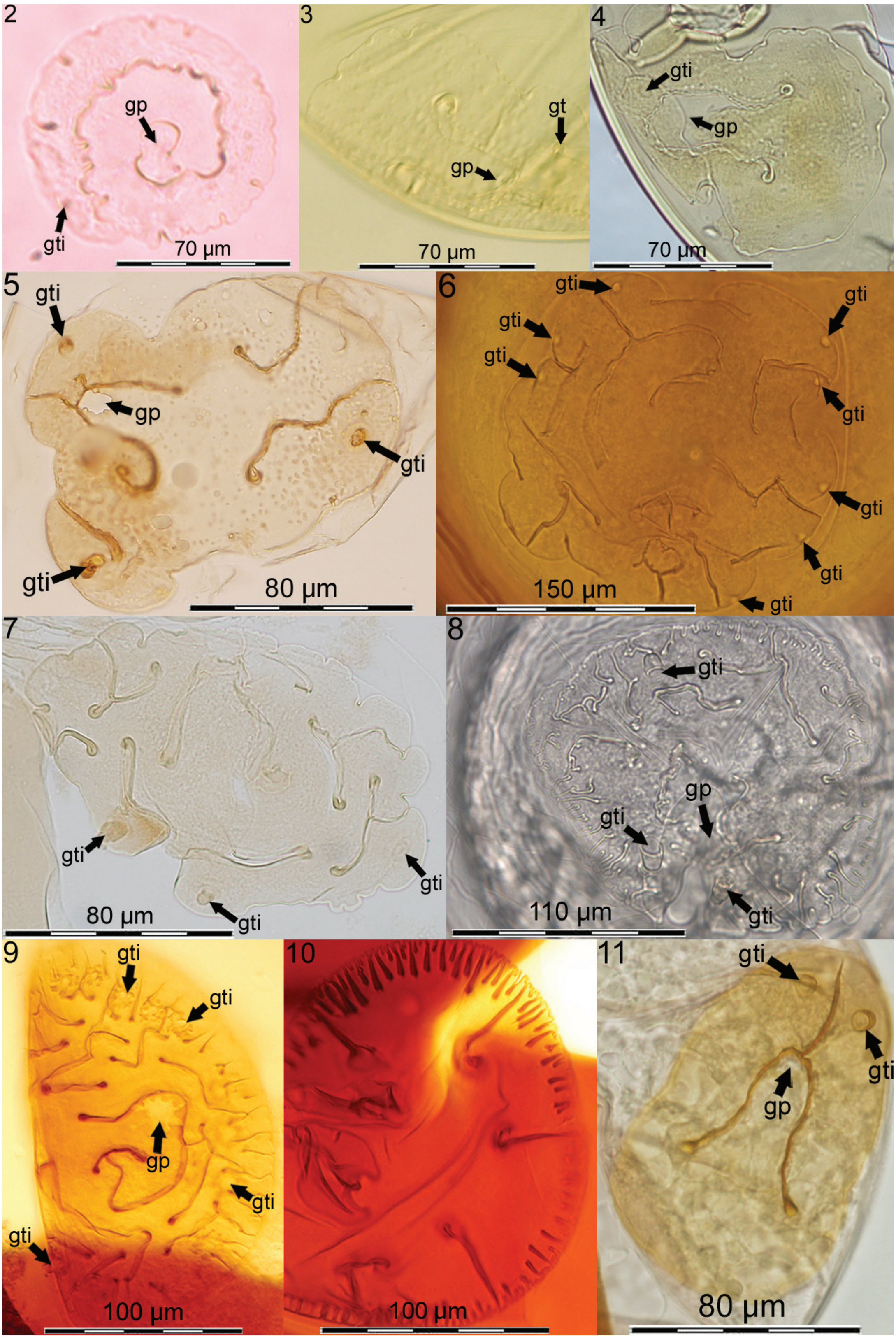
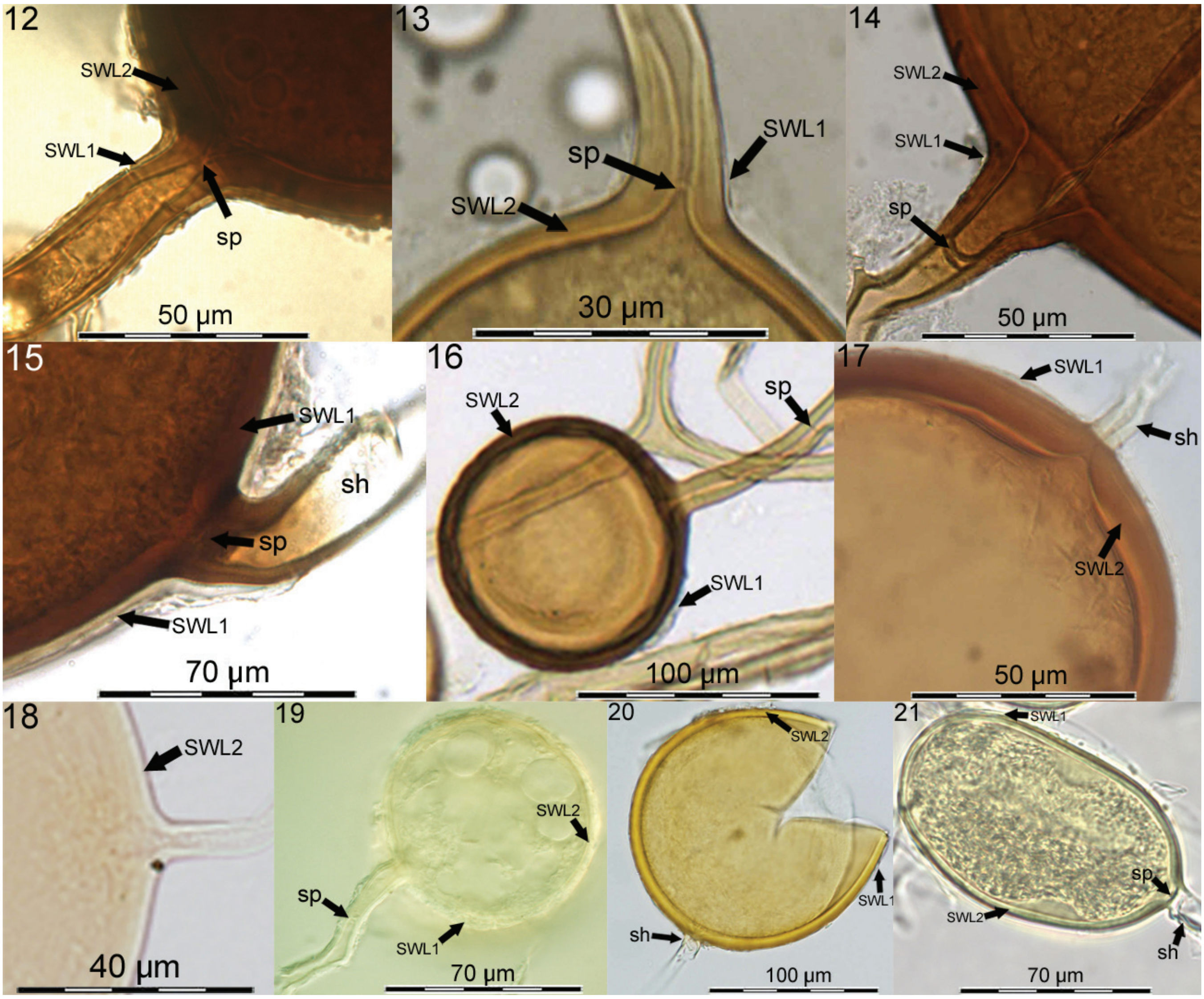


Figs 2–11. Characteristic germination shields in *Gigasporales* with germ pore (*gp*) as connection between spore cell contents and shields that are positioned on the surface of the germinal wall; germ tubes emerge from germ tube initiations (*gti*). **Fig. 2.** *Orbispora pernambucana* (isotype, ZT Myc 641) with mono-lobed, hyaline germ shield (*orb*). **Figs 3–4.** *Scutellospora calospora* (photo taken at INVAM) and *S. dipurpurescens* (holotype OSC #83343) have bi-lobed, violin-shaped, hyaline shields. **Figs 5–8.** *Racocetra coralloidea* (type, OSC #31026), *R. castanea* (ex type, ZT Myc 4377), *Cetraspora nodosa* (isotype, DPP, Szczecin, Poland) and *C. helvetica* (isotype, ZT Myc 3038) have wavy-like, multiply lobed, hyaline shields. **Figs 9–11.** *Dentiscutataceae* shields are yellow brown to brown. **Fig. 9.** *Dentiscutata reticulata* (photo taken at INVAM) shields with multiple small compartments. **Fig. 10.** *Quatunica erythropa* (photo taken at INVAM) is assumed to be the only known species in *Glomeromycota* with four spore walls. **Fig. 11.** *Fuscutata heterogama* (ex type, ZT Myc 642) has a bi-lobed, oval to ovoid shield.



Figs 12–21. Characteristic spore bases (*sb*) and subtending hyphae (*sh*) in *Glomeromycetes* genera with glomoid spore formation. **Figs 12–13.** *Glomus ambisporum* (Oehl collection, from Bolivia) and *G. aureum* (type, ZT Myc 822) with two wall layers (SWL1 and SWL2), marked introverted wall thickening at *sb* and in *sh*, and a small, bridging septum (*sp*). **Fig. 14.** *Funneliformis coronatus* (ex type, Oehl collection) with funnel-shaped *sh* and conspicuous *sp*; introverted wall thickening is lacking. **Fig. 15.** *Septoglomus constrictum* (Oehl collection, from Switzerland) with conspicuous septum that sometimes resembles a plug. **Fig. 16.** *Simiglomus hoi* (Oehl collection, specimen mounted at York university) with cylindrical *sh*; *sh* wall thickened over long distances; several septae are regularly observed within the hyphae; no introverted wall thickening at *sb*, pore at *sb* generally opened. **Fig. 17.** *Claroideoglomus etunicatum* (Oehl collection, from Bolivia) with funnel/bill-shaped, white *sh*; all *Entrophosporaceae* (syn. *Claroideoglomeraceae*) with characteristic color change of structural wall layer at *sb*, if spores are pigmented. **Fig. 18.** *Albahypha drummondii* (type, DPP) with slightly funnel-shaped, white *sh*. **Fig. 19.** *Viscospora viscosa* (ex type, photo taken at INVAM) with cylindrical, white hypha; *sp* within *sh* in some distance of *sb*; introverted wall thickening of *sh* at *sp* position, here not that obvious as usually found for this species; viscose spore surface. **Fig. 20.** *Diversispora versiformis* with short, fragile *sh* that is principally continuous with semi-persistent outermost spore wall layer (SWL1) but not with structural layer SWL2 (Oehl collection, from Tibet). **Fig. 21.** *Redeckera fulva* (Oehl ex Trappe collection) with inflating *sh* and conspicuous broad *sp* exactly at spore base.

In *Diversisporales* and *Glomerales,* 10 genera exclusively differentiate mono-walled, glomoid (9) or bi-walled pacisporoid (1) spores, all formed on subtending hyphae (Oehl & Sieverding 2004, Oehl *et al.* 2011a). The morphological differentiation of the glomoid species is mainly based on the morphology of the subtending hyphae of the spores, and spore wall structure. Spores of *Funneliformis*, *Glomus*, *Septoglomus,* and *Simiglomus* species have subtending hyphae that are concolorous or slightly lighter in colour than the spore wall (Table 1, Figs 12–16). *Albahypha, Claroideoglomus*, and *Viscospora* form spores in which the structural wall layer is continuous with the subtending hyphal wall layer, but the subtending hyphae are hyaline (Figs 17–19). In contrast, *Diversispora* and *Redeckera* form spores whose structural wall layer is not obviously continuous with the hyphal wall layer (Figs 20–21); consequently, such spores appear to have included 'endospores'.

Funneliformis, *Glomus*, *Septoglomus,* and *Simiglomus* can be separated by the structure of the spore base and subtending hyphae (*sh*). *Glomus* species often have an introverted wall thickening (Oehl *et al*. 2011a; Figs 12–13) which is only otherwise seen in *Viscospora*. *Funneliformis* species generally have an easily visible septum in the area of the spore base, and their *sh* are regularly funnel-shaped to cylindrical (Fig. 14). *Septoglomus* species have constricted to cylindrical *sh*, and usually there is a septum at the spore base (Fig. 15). In *Simiglomus*, *sh* are cylindrical and thick-walled, and they have several septa some distance from the spore base (Fig. 16). *Claroideoglomus* has funnel- to bird-bill-shaped *sh*, with *sh* and *sh* walls that are > 2.5 times wider at the spore base than some distance from the base (Fig. 17). *Albahypha* has slightly funnel to bill-shaped *sh* and *sh* walls that are < 2.0 times wider at the spore base than at some distance from the base (Fig. 18), and *Viscospora* has cylindrical *sh* (Fig. 19) with an *sh* wall that may be thickened over large distances and may bear septa in the hyphae with introverted wall thickenings in the area of the septum. In *Diversispora*, the *sh* are usually quite fragile and hyaline, distal to the pore closure at the spore base or in the *sh* (Fig. 20). *Redeckera* species have a broad septum at the spore base (Fig. 21), and the structural wall layer does not continue more than 5–15 µm into the subtending hypha, and thus, the *sh* may inflate at this distance from the spore base.

There are three bi-morphic genera with glomoid spore formation. Glomo-ambisporoid spores have a subhyaline to ochraceous, evanescent outer wall layer continuous with the outer acaulo-ambisporoid spore wall, while the second, structural layer is hyaline and continuous with the middle wall of acaulo-ambisporoid spores (Spain *et al*. 2006, Palenzuela *et al.* 2011). Glomo-archaeosporoid and Glomo-intrasporoid spores are among the smallest within *Glomeromycota* (*ca*. 30 µm), and thus difficult to observe.

PERSPECTIVES

Further separations of genera and families can be expected in the near future since many species and several species groups have not yet been analyzed by molecular phylogenetic methods (e.g. *Glomus* group Ab1, *sensu* Oehl *et al*. 2011a). Major efforts are needed to properly describe the morphology of, in particular, small-spored *Glomus* species (Błaszkowski *et al.* 2009a, b, 2010a, b), and it is difficult to predict how morphological identification will develop in those fungi. Other recent progress has been made on *Acaulospora* species with pitted surface ornamentation, where several species, that superficially all resembled *A. scrobiculata*, have been separated through extensive morphological and molecular spore analyses (e.g. Oehl *et al.* 2006, 2011e, f). The establishment of international and national collections of arbuscular mycorrhizal fungi, such as INVAM in Morgantown (International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi, West Virginia State University, USA), CICG in Blumenau (International Collection of *Glomeromycota* at FURB, Santa Catarina State, Brazil), GINCO-BEL in Louvain-La-Neuve (*Glomeromycota* In Vitro Collection at the Catholic University of Louvain, Belgium), or SAF in Zurich (Swiss Collection of Arbsucular Mycorrhizal Fungi at Agroscope ART, Switzerland) will facilitate further progresses in the taxonomy of glomeromycotean fungi that were thought to have not enough criteria to morphologically separate them unequivocally into the higher level taxa they phylogenetically belong to. Currently, several arbuscular mycorrhizal fungi are being described as new to science each year by an increasing numbers of research groups. A simple, but well justified conclusion is that, as a result of future concomitant morphological and molecular analyses, yet more higher level taxa will be proposed in this ancient fungal phylum, at all levels from class down to genus.

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