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Revision of *Glomeromycetes* with entrophosporoid and glomoid spore formation with three new genera

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Abstract — New ribosomal gene analyses reveal that *Entrophospora* is non-monophyletic and its type species *E. infrequens* closely related to *Claroideoglomus* species, which supports transfer of the *Entrophosporaceae* from *Diversisporales* to *Glomerales* as well as the 'ancestral' *Claroideoglomus* spp. to *Albahypha* gen. nov. *Entrophospora baltica,* supported as a separate clade within *Diversisporales,* is designated as type species for the new monospecific *Sacculosporaceae*. *Entrophospora nevadensis,* phylogenetically close to *Diversipora* spp. and *Otospora bareae,* is transferred to *Tricispora* gen. nov. (*Diversiporaceae*). *Entrophospora*, *Sacculospora,* and *Tricispora* are morphologically distinguished by spore wall structure, pattern of the two spore pore closures proximal and distal to the sporiferous saccule, and relative spore and sporiferous saccule sizes. The shape of the white hyphae subtending the spore base separates *Albahypha* spp. from *Claroideoglomus* spp.

Key words — otosporoid, tricisporoid, evolution, molecular phylogeny, rDNA

Introduction

The genus *Entrophospora* was initially characterized according to intrahyphal spore formation within the neck of a sporiferous saccule (e.g. Ames & Schneider 1979, Błaszkowski et al. 1998, Palenzuela et al. 2010). Sieverding & Oehl (2006)

have transferred three species originally placed in *Entrophospora* (Schenck et al. 1984, Sieverding & Toro 1985, 1987, Wu et al. 1995) to new genera as *Intraspora schenckii* (Sieverd. & S. Toro) Oehl & Sieverd., *Kuklospora colombiana* (Spain & N.C. Schenck) Oehl & Sieverd., and *K. kentinensis* (C.G. Wu & Y.S. Liu) Oehl & Sieverd. Support for the re-classification included i) clear morphological differences from the type species, *Entrophospora infrequens* (Hall 1977; Ames & Schneider 1979; Sieverding & Oehl 2006); ii) morphological aspects placing the three species unequivocally in the *Acaulosporaceae* and *Archaeosporaceae*; and iii) neither spore morphology nor genetic analysis of *E. infrequens* support that species in *Acaulosporaceae*, where *Kuklospora* species phylogenetically belong (Sieverding & Oehl 2006).

Phylogenetic analyses showed that the recently described *E. nevadensis* belonged in *Diversisporaceae* (Palenzuela et al. 2010). To date *Diversisporaceae* includes 13 *Diversispora* and six *Redeckera* species that form diversisporoid spores on subtending hyphae (Oehl et al. 2011b) and one species with otosporoid spores formed laterally on the neck of sporiferous saccules (Palenzuela et al. 2008). Another newly described species, *Acaulospora colliculosa* Kaonongbua et al., was also believed to form its spores within the neck of sporiferous saccules (Kaonongbua et al. 2010) but the illustrations rather indicate a mixture of specimens of different species, isolated directly from field soil samples. Since no saccule was presented in the latter study, further observations are needed to confirm the existence of this species, which is assumed to form pacisporoid spores instead of kuklosporoid spores as indicated by the images.

Recent morphological and molecular analyses suggest that the genus *Entrophospora*, currently comprising three species, is not monophyletic, since *E. infrequens* and *E. nevadensis* phylogenetically belong to different orders, according to the recently revised *Glomeromycetes* (Oehl et al. 2011d). This means that of the original species in the genus, only *E. infrequens* and *E. baltica* (Błaszkowski et al. 1998) might remain in *Entrophospora*. Thus, one objective of the current study was to analyze and re-classify *Entrophospora* species based on combined morphological and phylogenetic analyses. In particular, we hoped to resolve the confusion regarding the sequence variabilities for *E. infrequens* noted by Millner et al. (2001) and Rodriguez et al. (2001). Another objective was to confirm the phylogenetic position of *Otospora bareae* (Palenzuela et al. 2008) within the *Diversisporaceae*.

Material & methods

Specimens analyzed by morphological means

Type and non-type material representing 30 arbuscular mycorrhizal (AM) fungal species currently placed in *Entrophosporaceae*, *Claroideoglomeraceae* and *Diversisporaceae* (Sieverding & Oehl 2006, Schüßler & Walker 2010, Oehl et al. 2011b) were analyzed (Table 1). Source material of *Entrophospora infrequens* was originated

from field samples and from trap and pure cultures obtained from several countries, with the pure cultures established in three different laboratories —EEZ, Granada, Spain; CIAT, Cali, Colombia; and Swiss Collection of Arbuscular mycorrhizal fungi (SAF) at Agroscope ART, Zurich, Switzerland (see Sieverding & Toro 1985, Palenzuela et al. 2010, Oehl et al. 2010a, 2011a). *Entrophospora baltica* was obtained from the type location in Poland and from several montane and alpine locations in Switzerland and Spain. *Entrophospora nevadensis* and *O. bareae* have so far been reported only from their type locations in the Sierra Nevada National Park and Sierra de Baza Natural Park in Andalucia (Spain), respectively (Palenzuela et al. 2008, 2010).

Table 1. Collections analysed for reorganizing *Entrophosporaceae*, *Claroideoglomeraceae,* and *Diversisporaceae*.

Basionym (species)	Type material (examiner)	Non-type material (examiner; coll. date or publication)
Entrophosporaceae		
Glomus infrequens	Type OSC (Oehl)	Specimen from USA, Brazil, Chile (Castillo et al. 2006), Colombia, Spain (Palenzuela; July 2004; pure culture established in 2006), Bolivia, Switzerland (Oehl et al. 2004, 2011a; August 2005)
Entrophospora baltica	Type (Oehl)	Specimen from Chile (Castillo et al. 2006), Spain (Palenzuela & Oehl; July 2007), Switzerland (Sieverding & Oehl 2006; July 2004)
E. nevadensis	Type (Oehl & Palenzuela; Palenzuela et al. 2010)	
Claroideoglomeraceae		
Glomus candidum	No access	
G. claroideum	Type OSC #40252 (Oehl)	Specimen from Brazil, Europe (Oehl et al. 2010b); cultures from Benin (Oehl; Tchabi et al. 2010)
G. drummondii	Type (Oehl), ex type (Goto)	
G. etunicatum	Holotype OSC (Oehl)	Specimen from Benin, Bolivia, Paraguay, Europe, Mexico (Oehl; Bashan et al. 2007)
G. lamellosum	Isotype OSC #50183 (Oehl)	Specimen from Poland, Germany (Oehl & Sieverding; Oehl et al. 2003, 2005)
G. luteum	Type OSC, ex type INVAM (Oehl)	
G. viscosum	Ex type (Oehl)	
G. walkeri	Type (Oehl), ex type (Goto)	
Diversisporaceae		
Diversispora celata	Ex type, inclusive pure cultures (Oehl; April 2009; deposited at SAF)	Specimen from Switzerland (Oehl; April 2009)
Glomus arenarium	Type at OSC (Oehl), ex type (Goto)	Specimen from Chile and UAE (Sieverding; Castillo et al. 2006)
G. aurantium	Type (Oehl)	Specimen from Germany (Oehl)
G. eburneum	Ex type at INVAM (Oehl)	Specimen from Bolivia & Oman (Oehl; Al-Yahya'ei et al. 2011)
G. epigaeum	Holotype OSC #39475 (Oehl)	
G. gibbosum	Type (Błaszkowski online pages)	Specimen from UAE (Sieverding, unpublished)

Table 1, concluded.

Basionym (species)	Type material (examiner)	Non-type material (examiner; coll. date or publication)
G. insculptum	Type (Oehl)	
G. przelewicense	No access	Specimen and pure pot cultures from Switzerland (Oehl & Sieverding; Oehl et al. 2009, published as *Glomus* sp. BR12)
G. pustulatum	Holotype OSC #46721 (Oehl)	Błaszkowski collection (Oehl)
G. spurcum	Ex type at INVAM (Oehl)	Specimen from Bolivia (Oehl; Nov. 2000)
G. avelingiae	No access	
G. canadense		Thaxter collection, Trappe collection (Oehl)
G. fragile		Trappe collection (Oehl)
G. fulvum		Trappe collection (Oehl), specimen from Brazil (Goto)
G. megalocarpum	Ex type (Oehl)	
G. pulvinatum		Trappe collection (Oehl)
G. tenerum		Specimen from Australia (Oehl; McGee & Trappe 2002)
G. trimurales	Holotype OSC #49584 (Oehl)	
Endogone versiformis		Specimen at INVAM; specimen from Central Europe (Oehl & Sieverding; Oehl et al. 2003)
Otospora bareae	Type (Oehl & Palenzuela; Palenzuela et al. 2008)	

Morphological analyses

Morphological observations of spores (including sporiferous saccules and subcellular structures), were based on freshly prepared specimens mounted in polyvinyl alcohol-lactic acid-glycerol (PVLG), in a mixture of PVLG and Melzer's reagent (Brundrett et al. 1994), in a 1:1 (v/v) mixture of lactic acid and water, in Melzer's reagent, or in water. Spore structure terminology for species with acaulosporoid, entrophosporoid, or glomoid spore formation follows Goto & Maia (2006), Sieverding & Oehl (2006), Oehl et al. (2006, 2011b), Spain et al. (2006), and Palenzuela et al. (2008, 2011). Photographs were taken using an Olympus digital camera (model DP70-CU) mounted on a Zeiss Axioplan compound microscope.

Molecular and phylogenetic analyses

Materials selected for molecular analyses included: *E. infrequens*— spores from trap and pure culture material maintained at EEZ (Granada, Spain) and SAF (Zurich, Switzerland); *E. baltica*— trap cultures and field samples from Mulhacen in Sierra Nevada (Southern Spain, 3200 m asl) and Piz Corvo (Passo del Lugmagno, Swiss Central Alps, 2700 m asl); *E. nevadensis*— EEZ pure culture (Palenzuela et al. 2010); *O. bareae*— EEZ maintained trap cultures (Palenzuela et al. 2008).

DNA extraction, amplification and sequencing from Spanish isolates were performed at EEZ (Palenzuela et al. 2011) and from non-Spanish isolates at UFPE (Recife; see Goto et al. 2011, Oehl et al. 2011c).

For sequence alignment we first verified the National Center for Biotechnology Information (NCBI) databases using the BLASTn program to ensure that the *E. infrequens* sequences were affiliated to *Claroideoglomeraceae* (*Glomerales*), and that the sequences

from *E. baltica, E. nevadensis* and *O. bareae* correctly aligned with *Diversisporales*. AM fungal rRNA sequences (SSU = ~1770 bp; LSU = 733 bp) obtained in our laboratories were then aligned with GenBank glomeromycotean sequences using ClustalX (Larkin et al. 2007) and edited with BioEdit (Hall 1999) to obtain a final alignment. The sequences were deposited at GenBank under the accession numbers FR865452–FR865456 and JN113035-JN113037 for *E. infrequens*, FR865457–FR865462 and FR865449–FR865451 for *E. baltica*, FR865465–FR865467 and FR865446–FR865448 for *E. nevadensis,* and FR8655463–FR865464 and FR865444–FR865445 for *O. barea*.

Maximum parsimony (MP) and neighbor joining (NJ) analyses with 1000 bootstrap replications were performed using the Phylogenetic Analysis Using Parsimony (PAUP) vers. 4 (Swofford 2003). Bayesian (two runs over 1 x 10^6 generations with a burnin value of 2500) and maximum likelihood (1000 bootstrap) analyses were performed, respectively, in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) and PhyML (Guindon & Gascuel 2003), launched from Topali 2.5. The nucleotide substitution model was estimated using Topali 2.5 (Milne et al. 2004). Sequences from *Neurospora crassa* Shear & B.O. Dodge and *Boletus edulis* Bull. were used as outgroups for *Glomeromycota*.

Results

Molecular phylogenetic analyses

The phylogenetic analyses on the nearly complete SSU of the ribosomal gene and on partial sequences of the LSU show that *E. infrequens*, type species of the *Entrophosporaceae* (Sieverding & Oehl 2006), is related to *Claroideoglomus* species in the *Glomerales* (Figs 1–2). However, *E. infrequens* is phylogenetically unrelated to the two other *Entrophospora* species that form two monophyletic clades in the *Diversisporales* (Figs 1–2). *Entrophospora nevadensis* groups next to *O. bareae* and several *Diversispora* species, while *E. baltica* groups in its own clade, well distant from the other major clades representing families within the *Diversisporales*. The phylogenetic analyses also render the genus *Diversispora* paraphyletic (Figs 1–2).

Morphological comparisons

For the *E. infrequens*, *E. baltica*, *E. nevadensis*, and *Otospora bareae* clades and the two *Claroideoglomus* clades, some morphological characters are congruent with the phylogenetic findings. These characters are principally the sporiferous saccule characteristics, pore closure patterns at the spore bases for species forming spores within/on the saccule necks (Figs 3–19), and spore base and subtending hyphae characteristics for species forming spores terminally on hyphae (Figs 20–31).

Entrophospora infrequens forms saccules that are regularly larger than the spores formed beneath, and the pore formed by the subtending hypha distal to the saccules is closed by hyaline evanescent outer spore wall layers; the next-inner structural pigmented persistent layer does not continue into the distal part of the hyphal neck and never forms a pore distally to the saccule

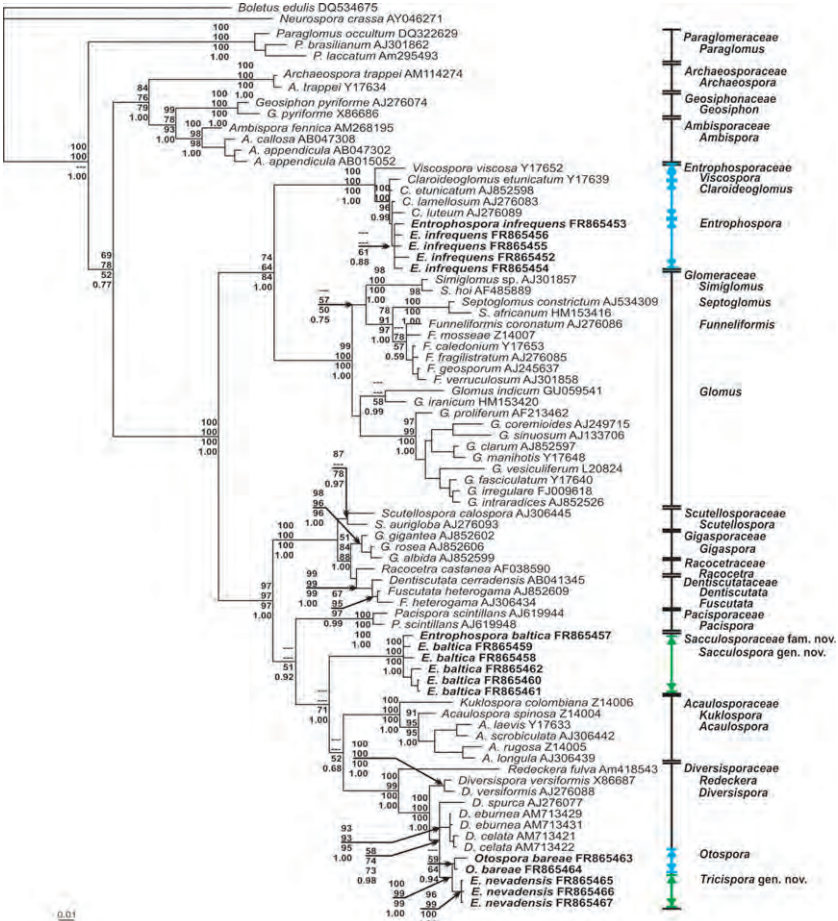


FIG. 1. A phylogeny of the *Glomeromycota* based on partial SSU rDNA sequences (~1800 bp). NJ (neighbor joining), ML (maximum likelihood), and Bayesian analyses were performed with GTR+G+I substitution model. Sequence labels correspond to their database accession numbers. Support values are from NJ, MP (maximum parsimony), ML, and Bayesian analyses. New sequences obtained in this study are indicated in bold. Only topologies with bootstrap values ≥ 50% are shown. Consistency Index = 0.47; Retention Index = 0.84.

(FIGS 3–7). Thus, on the spores (particularly once the outer wall layers have become degraded) just one single opening/pore forming a 'cicatrix' is visible proximal to the saccules; the pore is closed by a plug-like wall material derived apparently from the structural wall layer (OWL3; FIGS 3–4). The structural wall layer extends into the saccule over 10–30 µm, with the spore wall layer

FIG. 2. A phylogeny of the *Glomeromycota* based on partial LSU rDNA sequences (~600 bp). NJ (neighbor joining), ML (maximum likelihood), and Bayesian analyses were performed with GTR + G substitution model. Sequence labels correspond to their database accession numbers. Support values are from NJ, MP (maximum parsimony), ML, and Bayesian analyses. New sequences obtained in this study are indicated in bold. Only topologies with bootstrap values ≥ 50% are shown. Consistency Index = 0.41; Retention Index = 0.79.

ornamentation apparently continuing to the pore closure area, although not within the saccule.

Entrophospora baltica and *E. nevadensis* (FIGS 8–19) have smooth proximal cicatrices; here the ornamentation does not continue at the area of the generally wide pore proximal to the sporiferous saccule. Both the distal and proximal

spore pores are closed by a smooth, rather thin septum of the structural, laminate wall layer, and the structural wall layer continues for a small distance into the distal hypha of the saccule neck (Figs 8, 12, 16). In both species the saccules are often slightly (*E. baltica*) or substantially (*E. nevadensis*) smaller than spores formed beneath since they sometimes equal half or a quarter of the spore diameter, respectively. Remarkably, detailed spore wall structure analyses revealed that *E. baltica* has three walls (Figs 17–19), while spores of *E. nevadensis* (and *Otospora bareae*) are clearly bi-layered (Fig. 13, and Palenzuela et al. 2010).

Typical *Claroideoglomus* species (e.g., *C. etunicatum*, *C. claroideum*, *C. lamellosum* (Figs 20–25), *C. luteum*) form hyaline subtending hyphae, which are 'funnel-shaped' — their width at the spore base is regularly > 2.5 times wider than 10–50 µm distant from the spore. However, two species that are basal within the *Claroideoglomeraceae — C. drummondii*, *C. walkeri* (Fig. 2, Oehl el al. 2011b)— have only slightly funnel-shaped to sometimes cylindrical subtending hyphae that are regularly < 2.0 times broader at spore base than the supporting hypha (Figs 26–31).

Based on our phylogenetic analyses, we propose to include the *Entrophosporaceae* and its type species *E. infrequens* in the *Glomerales*. The LSU rRNA sequence analyses indicate that *Claroideoglomus* should be further divided into two genera, which is supported by the morphological differences between the two recognized clades.

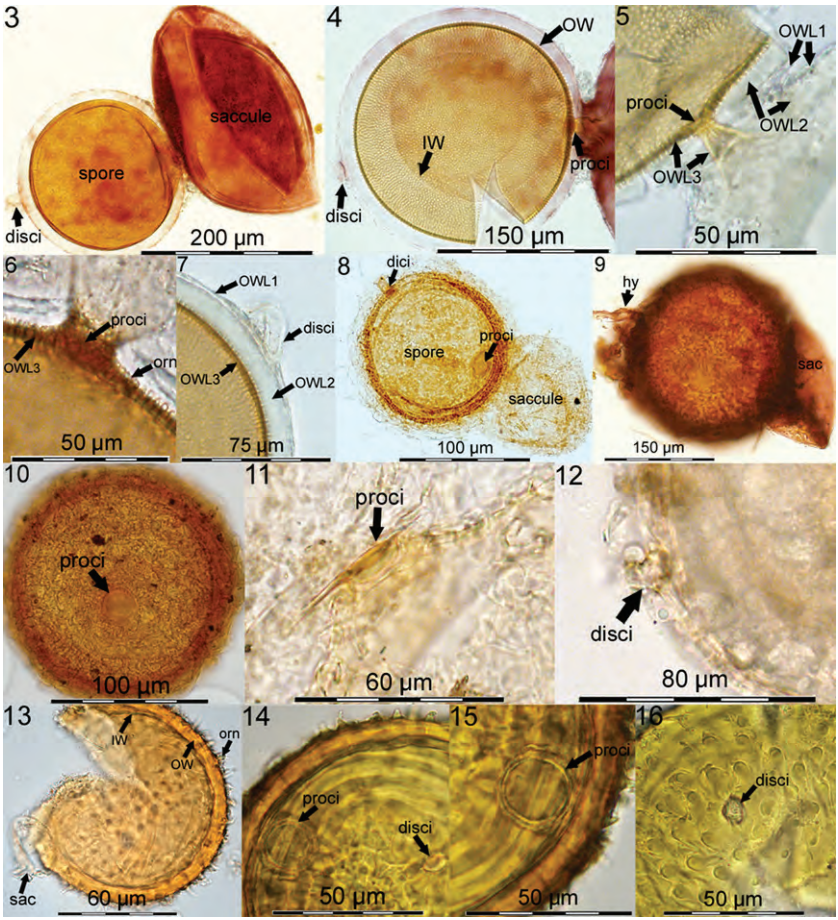
Since *E. nevadensis* forms a clade within the *Diversisporaceae,* a new genus is indicated with it serving as type species. *Entrophospora baltica*, which forms a monophyletic major clade within the *Diversisporales,* should serve as the type species of a new family in the order.

Sequence analyses further imply that *Diversispora* is paraphyletic. However, here the molecular and morphological databases do not yet provide sufficient information to reclassify accurately the *Diversispora* species.

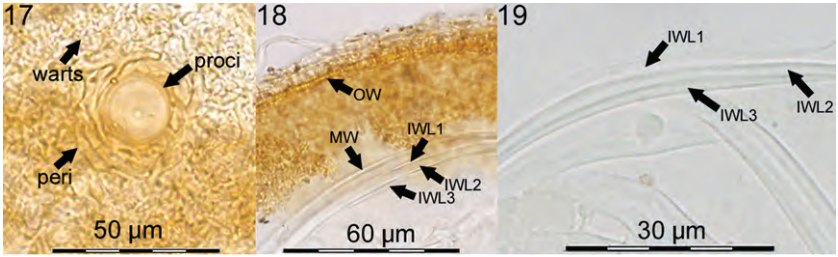
Taxonomic revision

Glomerales J.B. Morton & Benny, emend. Oehl, Palenz., G.A. Silva & Sieverd.

Emended description: Spores form terminally on or intercalary in hyphae or within the necks of sporiferous saccules in soil (or sometimes roots) singly or (when glomoid) also in spore clusters or multi-spored loose to compact sporocarps; when in compact sporocarps (with or without peridium), spores randomly distributed or organized around a central hyphal plexus. Glomoid spores with one single or multiple-layered wall. Entrophosporoid spores with two walls: outer structural wall and inner (germinal) wall. In glomoid spores, wall of the subtending hyphae (sh) conspicuously continuous with the spore wall, sh funnel-shaped, cylindrical, or constricted and concolorous with



Figs 3–16. Examples of intra-hyphal spore formation within the neck of a sporiferous saccule. Figs 3–7. *Entrophospora infrequens*: Spores have two walls (OW & IW); saccule generally larger than attached spore. OW is triple-layered (OWL1–3) and has a characteristic ornamentation ('orn') on structural layer OWL3. At spore bases two cicatrices are formed: proximal and distal to the saccule. The persistent proximal cicatrix ('proci') formed by the persistent OWL3 (Figs 5–6) wall material resembles a plug. The evanescent distal cicatrix ('disci') is formed by evanescent OWL2 (Fig. 7) material. Figs 8–12. *Sacculospora baltica*: spores with two cicatrices; saccule (sac) substantially smaller than attached spore. The proximal cicatrix (proci) is persistent and formed by the structural OW layer (Figs 10–11); the corresponding spore pore is closed by a septum that does not resemble a plug. The distal cicatrix ('dici') is also persistent and formed by the same layer (Fig. 12). Figs 13–16. *Tricispora nevadensis*: spores have two walls (OW & IW) and two cicatrices; saccule (sac) substantially smaller than the attached spore. The proximal cicatrix (proci) is persistent and formed by the structural OW layer (Figs 14–15); the corresponding spore pore is closed by a septum that does not resemble a plug. The distal cicatrix (dici) is also persistent and formed by the same layer (Fig. 16).



Figs 17–19. *Sacculospora baltica* spore wall structure showing peridial hyphal mantle (peri), conspicuous proximal cicatrix (proxy), and warts on the outer wall (ow) surface; middle wall (mw) is 1(–2)-layered and inner wall is triple-layered (iwl1–3). The three iw layers generally tightly adhere, making iwl1 and iwl3 difficult to observe (Fig. 18); the separation of the three layers in Fig. 19 is an artifact of cover-slip pressure.

spore, slightly paler, or (sub-)hyaline. In entrophosporoid spores, structural pigmented outer wall layer discontinuous with the hyphal wall distal to the saccule; forming typical vesicular-arbuscular mycorrhiza with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type family: *Glomeraceae* Piroz. & Dalpé

Other family: *Entrophosporaceae* Oehl & Sieverd.

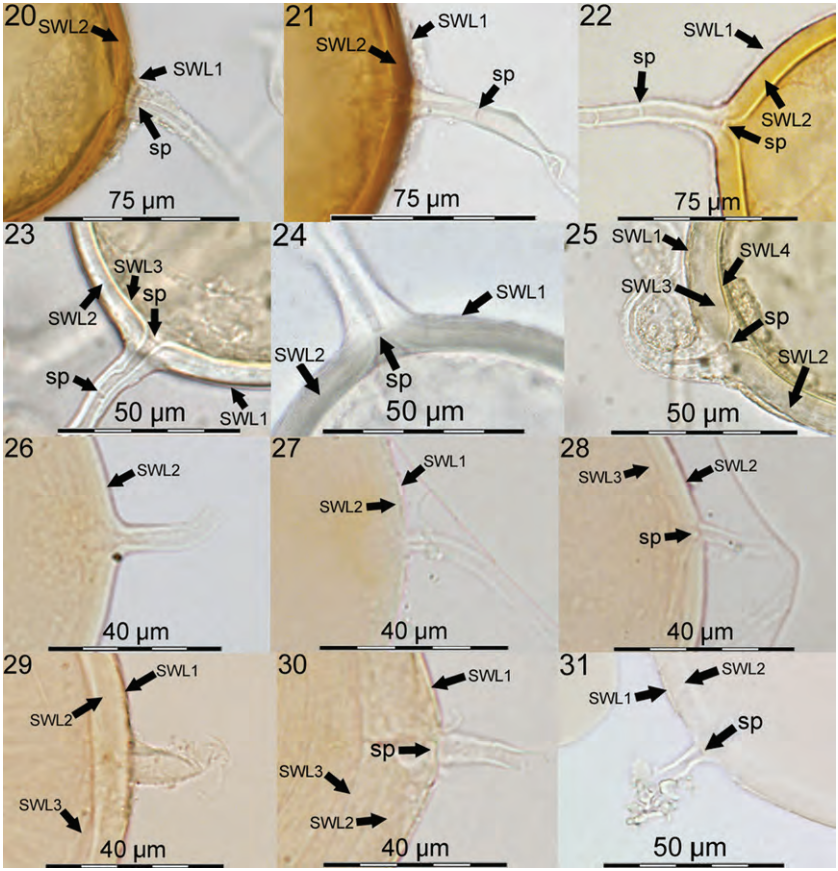
Entrophosporaceae Oehl & Sieverd., emend. Oehl, Sieverd., Palenz. & G.A. Silva

= *Claroideoglomeraceae* C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 21. 2010.

Emended description: Spore formation is of glomoid or entrophosporoid type. Glomoid spores form in soil or (rarely) in roots singly, in clusters with few spores, or (extremely rarely) in sporocarps; sh hyaline to white, rarely subhyaline, often conspicuously funnel- or bill-shaped. Spores with one wall of 1–4 layers; spore base pore closure often with a septum that arises from the structural layer, an adherent thin inner layer, or both layers. Entrophosporoid spores form singly in soils or rarely in roots, subterminally or intercalary within the neck of a tightly attached sporiferous saccule that generally is larger in size than the underlying spore; they have two walls: outer and inner. Outer, hyaline, semi-persistent to evanescent layers of the outer spore wall are the hyphal neck and sporiferous saccule wall layers. The pigmented structural layer does not continue within the hyphal wall but only within the saccule terminus for some distance. Pore closed by a plug towards the saccule. The inner wall is generally thick, finely laminated and forms de novo. No inner wall layer has a beaded appearance or stains in Melzer's reagent. Fungal structures in roots stain blue with trypan blue; forming vesicular-arbuscular mycorrhizae.

Type genus: *Entrophospora* R.N. Ames & R.W. Schneid.

Other genera: *Claroideoglomus* C. Walker & A. Schüssler, *Albahypha* Oehl et al., *Viscospora* Sieverd. et al.



Figs 20–31. Examples of terminal spore formation on subtending, hyaline to white hyphae (SH); spores with 2–4 layers (SWL1–4); spore pores regularly closed by a septum (sp) at the spore base. Figs 20–25. *Claroideoglomus* (Figs 20–22: *C. etunicatum,* Figs 23–24: *C. claroideum,* Fig. 25: *C. lamellosum*) — *Claroideoglomus* spores have a significantly funnel-shaped hypha with structural wall layer (generally SWL2 or SWL3) that is >2.5 times thicker at spore base than 10–25 µm distant at transition between SH and mycelia hypha. Figs 26–31. *Albahypha* (Figs 26–28: *A. drummondii,* Figs 29–31: *A. walkeri*) — *Albahypha* spores have a slightly funnel-shaped to cylindrical hypha with structural wall layer (generally SWL2) that is <2.0 times thicker at spore base than 10–25 µm distant.

Entrophospora R.N. Ames & R.W. Schneid., emend. Oehl, Sieverd., Palenz. & G.A. Silva Figs 1–5

Emended description: Sporocarps unknown. Entrophosporoid spores form within the hyphal neck of tightly attached terminal or intercalary sporiferous saccules, singly in soils, or (rarely) in roots. Sporiferous saccules generally are

larger in size than the underlying spores. Entrophosporoid spores are globose to subglobose and have two walls: an outer and an inner. Outer, semi-persistent to evanescent layers of the outer spore wall are the wall layers of the hyphal stalk and the sporiferous saccule. The structural, pigmented layer beneath does not continue within the hyphal wall but only for a short distance within the saccule terminus. Thus, spores have only one persistent cicatrix, which is proximal to the globose saccule terminus. A plug closes the pore towards the saccule. The inner wall is thick, finely laminated wall and forms de novo. No inner wall layers have a beaded appearance. Fungal structures in roots stain blue with trypan blue; forming vesicular-arbuscular mycorrhizae.

Type species: *Entrophospora infrequens* (I.R. Hall) R.N. Ames & R.W. Schneid.

Claroideoglomus C. Walker & A. Schüssler, emend. Oehl, Sieverd., B.T. Goto & G.A. Silva Figs 20–25

Emended description: Spores formed on subtending hyphae (sh), generally singly in soil or rarely in roots; sh are hyaline to white, rarely subhyaline, and funnel- or bill-shaped with widths > 2.5 times greater at the spore base than at 10–20 µm from the spore. Spores with one wall of 1–4 layers; pore closure at spore base often with a septum that arises species-specifically from the structural layer, an adherent thin innermost layer, or both innermost layers.

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

Albahypha Oehl, G.A. Silva, B.T. Goto & Sieverd., **gen. nov.** Figs 26–31

MycoBank MB 561639

Sporae singulariter efformatae; tunica sporarum cum tunica hypharum coniuncta; hyphae albae, tunica hyphae 1.2–2.0 maior ad basem sporarum quam in 10-20 µm distantia basae sporarum; porum sporarum occlusum septa tunicae sporarum, rarum apertum. Mycorrhizas vesiculares-arbusculares formans caeruleas colorantes cum 'trypan blue'.

Type species: *Albahypha drummondii* (Błaszk. & Renker) Sieverd. et al.

Etymology: derived from the Latin: *alba* = white; *hypha* = hypha; referring to the white, slightly funnel-shaped subtending hypha which is characteristic for species of this genus.

Key characters: Spores formed generally singly in soil or rarely in roots; sh white, rarely subhyaline, 1.2–2.0 times wider at spore base than their width 10–20 µm distance from the spore, giving a slightly funnel-shaped or cylindrical appearance. Spores with one wall of 1–4 layers; spore base pore closure often with a septum that may arise from the structural layer, an adherent innermost, (semi-)flexible layer, or both innermost layers.

Albahypha drummondii (Błaszk. & Renker) Sieverd., Oehl, B.T. Goto & G.A. Silva, **comb. nov.**

MycoBank MB 561640

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

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

Albahypha walkeri (Błaszk. & Renker) Sieverd., Oehl, B.T. Goto & G.A. Silva, **comb. nov.**

MycoBank MB 561641

≡ *Glomus walkeri* Błaszk. & Renker. Mycol. Res. 110: 563. 2006.

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

Viscospora Sieverd., Oehl & G.A. Silva, Mycotaxon 116: 108. 2011.

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

Diversisporaceae C. Walker & A. Schüssler, emend. Oehl, Palenz., I.C. Sánchez, G.A. Silva, B.T. Goto & Sieverd.

Emended description: Spore formation diversisporoid, otosporoid, or entrophosporoid sensu lato ('tricisporoid' sensu stricto). Diversisporoid spores formed singly, in clusters, or in large disorganized sporocarps with high spore numbers. In pigmented spores, subtending hyphae (sh) conspicuously change color, becoming hyaline to white behind the septum, (immediately or at a very short distance from this septum); sh generally straight, cylindrical, in some species constricted or inflated. Spores with 1–3 wall layers; pore often closed with a septum that may arise from innermost wall lamina, an overlaying laminate layer, or from both; sh pore rarely open. Otosporoid and tricisporoid spores with two multiple-layered walls; otosporoid spores formed laterally on the persistent neck of a terminal or intercalary sporiferous saccule at some distance from the saccule terminus; spore pore generally closed by a septum at spore base. Tricisporoid spores formed within the evanescent neck of a tightly attached terminal or intercalary sporiferous saccule, closely attached to the saccule terminus which is often smaller in size than the mature spores attached, rarely equal in size; tricisporoid spores with two cicatrices formed by the outer wall pigmented structural layer.

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

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

Diversispora C. Walker & A. Schüssler, Mycol. Res. 108: 982. 2004.

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

Otospora Oehl, Palenz. & N. Ferrol, Mycologia 100: 297. 2008.

Type species: *Otospora bareae* Palenz. et al.

Redeckera C. Walker & A. Schüssler, The *Glomeromycota* – a species list: 44. 2010.

Type species: *Redeckera fulva* (Berk. & Broome) C. Walker & A. Schüssler

Tricispora Oehl, Sieverd., G.A. Silva & Palenz., **gen. nov.** Figs 13–16

MycoBank MB 561642

Sporocarpia ignota. Sporae singulatim efformatae subterminaliter vel intercalariter in hypha inflata anguste adiacetum ad sacculum sporiferum terminalem vel intercalarem. Sacculus sporiferus frequenter minor quam sporae globosae vel subglobosae; sporae duabus tunicis stratis pluribus. Stratum exterior tunicae exterioris coniunctum tunica hyphae et sacculi. Stratum interiorem tunicae exterioris laminatum, duas poras sporae occludens. Stratum exterior tunicae interioris non granulatum. Formans mycorrhizas vesicular-arbusculares. Structurae fungorum colorantes caeruleae cum 'trypan blue'.

Type species: *Tricispora nevadensis* (Palenz. et al.) Oehl et al.

Etymology: derived from the Latin: *(cica-)trix* = cicatrix: and *spora* = spore; referring to the two conspicuous cicatrices left on the structural wall layer of the spores, even when the sporiferous saccules and the hyphal neck distal to the saccule have detached completely from the spores.

Key characters: Sporocarps unknown. Spores formed within the hyphal neck of closely adherent terminal or intercalary sporiferous saccules. The globose saccule terminus generally is substantially smaller than the attached mature spore. Spores have an outer and an inner wall. At least two layers (including the outer wall structural layer) are continuous with the sporiferous saccule wall. The outer layer of the outer wall is evanescent, the inner layers are permanent. After the hyphal neck connections break off, spores show two, often opposite, cicatrices that are closed by the permanent sublayers of the outer wall structural layer. The inner wall forms de novo, consists of several layers without granular ('beaded') appearance and does not stain with Melzer's reagent. The fungal structures in the roots stain blue to dark blue with trypan blue; forming vesicular-arbuscular mycorrhiza.

Tricispora nevadensis (Palenz., N. Ferrol, Azcón-Aguilar & Oehl) Oehl, Palenz., G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 561644

≡ *Entrophospora nevadensis* Palenz., N. Ferrol, Azcón-Aguilar & Oehl, Mycologia 102(3): 627. 2010.

Sacculosporaceae Oehl, Sieverd., G.A. Silva, B.T. Goto, I.C. Sánchez & Palenz., **fam. nov.**

MycoBank MB 561645

Sporae singulatim efformatae in hypha inflata anguste adiacetum ad sacculum sporiferum terminalem vel intercalarem. Sporae tribus tunicis stratis pluribus. Stratum interiorem tunicae exterioris laminatum, duas poras sporae occludens. Stratum exterior tunicae interioris non granulatum.

Key characters: Sporocarps unknown. Spores formed within the hyphal neck of closely adherent terminal or intercalary sporiferous saccules. Spores have three walls: outer, middle and inner. At least two layers (including the outer wall structural layer) are continuous with the sporiferous saccule wall. After the

hyphal neck connections break off, spores show two, often opposite, cicatrices that are closed by the permanent sublayers of the outer wall structural layer. Middle and inner wall form de novo. Middle wall is 1–2-layered. Inner wall consists of several layers, none of which has a granular ('beaded') appearance, and does not stain in Melzer's reagent.

Type genus: *Sacculospora* Oehl et al.

Sacculospora Oehl, Sieverd., G.A. Silva, B.T. Goto, I.C. Sánchez & Palenz., **gen. nov.**

MycoBank MB 561646 Figs 8–12, 17–19

Sporocarpia ignota. Sporae singulatim efformatae subterminaliter vel intercalariter in hypha inflata anguste adiacetum ad sacculum sporiferum terminalem vel intercalarem. Sporae globosae vel subglobosae, tribus tunicis stratis pluribus. Stratum exterior tunicae exterioris coniunctum tunica hyphae et sacculi. Stratum interiorem tunicae exterioris laminatum, duas poras sporae occludens. Stratum exterior tunicae interioris non granulatum.

Type species: *Sacculospora baltica* (Błaszk. et al.) Oehl et al.

Etymology: derived from the Latin: *sacculus* = saccule: and *spora* = spore; referring to the spore formation within the neck of sporiferous saccules.

Key characters: Sporocarps unknown. Spores formed within the hyphal neck of closely adherent, terminal or intercalary sporiferous saccules. Spores have three walls: outer, middle and inner. At least two layers (including the outer wall structural layer) are continuous with the sporiferous saccule wall. Inner layers of the outer spore wall are permanent. After the hyphal neck connections break off, spores show two, often opposite, cicatrices that are closed by the permanent sublayers of the outer wall structural layer. Middle and inner wall form de novo. Middle wall is 1–2-layered. Inner wall consists of several layers, none of which have a granular ('beaded') appearance (Fig. 18–19), and does not stain in Melzer's reagent. The inner wall may be germinal in function, but a germination structure has not yet been found.

Sacculospora baltica (Błaszk., Madej & Tadych) Oehl, Palenz., I.C. Sánchez, B.T. Goto, G.A. Silva & Sieverd., **comb. nov.**

MycoBank MB 561647

≡ *Entrophospora baltica* Błaszk., Madej & Tadych, Mycotaxon 68: 167. 1998.

Discussion

New molecular and morphological analyses elucidated the molecular phylogenetic and morphological congruencies within a group of species that have long been considered heterogeneous (e.g. Morton & Benny 1990, Sieverding & Oehl 2006). Species with entrophosporoid (sensu lato) spore formation are now found within *Entrophosporaceae* (*E. infrequens*), *Acaulosporaceae* (*K. colombiana, K. kentinensis*), *Diversisporaceae* (*T. nevadensis*), *Sacculosporaceae* (*S. baltica*), and *Archaeosporaceae* (*Intraspora schenckii*).

Sequence analyses of *E. infrequens*, with a unique entrophosporoid spore formation, place this species so close to *Claroideoglomus* that we regard

the recently described *Claroideoglomeraceae* as a heterotypic synonym of *Entrophosporaceae*. Morphological congruencies were found to support the phylogeny and helped identify a fourth genus, *Albahypha*, to include with the type genus *Entrophospora*, *Claroideoglomus,* and *Viscospora* within the revised *Entrophosporaceae*.

The *Diversisporaceae* now comprise four genera: two with diversisporoid spore formation (*Diversispora* and *Redeckera*; Oehl et al. 2011b) and one each with otosporoid (*Otospora*) and tricisporoid (*Tricispora*) spore formation.

There are now several phylogenetic clades that form spores terminally on hyphae as well as on or within sporiferous saccules (spore formation type glomoid s.l., acaulosporoid s.l., entrophosporoid s.l.). These are represented in the *Entrophosporaceae* (*Glomerales*), *Diversisporaceae* (*Diversisporales*), and *Archaeosporaceae* and *Ambisporaceae* (*Archaeosporales*) clades but only *Diversisporaceae*, *Archaeosporaceae* and *Ambisporaceae* are represented by all three major spore formation types.

Further studies are still needed to determine whether the entrophosporoid (sensu lato) genus *Kuklospora* is monophyletic. Most phylogenetic analyses split the type species, *K. colombiana*, off at the base of *Acaulosporaceae* (Schüßler et al. 2001, Palenzuela et al. 2008, 2010, Oehl et al. 2011d). Thus, we conclude that the synonymization of *Kuklospora* with *Acaulospora* (Kaonongbua et al. 2010) is not justified and needs to be substantiated (Oehl et al. 2011e). Moreover, a revision of the phylogenetically and morphologically heterogeneous *Acaulosporaceae* is urgently needed (Spain 1992, Oehl et al. 2011e).

Our analyses supports *Tricispora nevadensis* (≡ *E. nevadensis*) and *Otospora bareae* as sister taxa within the *Diversisporaceae* (Figs 1–2). Both *Entrophospora* and *Otospora* can readily be distinguished by spore formation type, distance between the saccule terminus and the differentiated spore within (*Entrophospora*) or laterally (*Otospora*) on the saccule neck, and the relative size differences between saccule and spore. Morphologically, these genera have little in common with the type genus of their family, *Diversispora*, whose species form spores simply on subtending hyphae. We emphasize that there have never been genera in *Glomeromycetes* (sensu Oehl et al. 2011d) that encompass species with both glomoid and entrophosporoid or acaulosporoid spore formation. This strongly supports the proposition of *Otospora* and *Tricispora*. However, phylogenetically, both *T. nevadensis* and *O. bareae* render the genus *Diversispora* polyphyletic.

We regard the *Diversispora* molecular database as still rudimentary, as the genus comprises several species that yet to be molecularly analyzed (Oehl et al. 2011b). Additionally, the morphological differences among *Diversispora* clades (Figs 1–2) are not yet clear. Before the genus *Diversispora* can confidently be reclassified, additional molecular and morphological studies are needed to

determine relationships accurately within this heterogeneous family.

Glomus hyderabadense Swarupa et al. also deserves mention, for it regularly forms a small terminal spore and an adjacent, subterminal large spore on subtending hyphae. Since the terminal spore is generally much smaller than the subterminal spore (Swarupa et al. 2004), its spore formation superficially resembles that of *T. nevadensis*. Although the *G. hyderabadense* sequence (AY211274) aligns adjacent to *G. clarum* (Swarupa et al. 2004), the deposited sequence does not represent a glomeromycotan fungus. *Glomus hyderabadense* possibly forms its own clade within the *Glomeromycetes* and thus may represent an undescribed fungal genus with a unique, diagnostic spore formation and morphology.

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