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Paraglomus pernambucanum sp. nov. and *Paraglomus bolivianum* comb. nov., and biogeographic distribution of *Paraglomus* and *Pacispora*

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Summary

Paraglomus pernambucanum sp. nov. (Paraglomeromycetes) was found in a tropical dry forest in the semi-arid Caatinga biome of Pernambuco State (NE Brazil), in a cowpea and in two maize production sites. It was characterized by combined morphological and molecular analyses on the spores isolated from field soil samples. Another species, *Pacispora boliviana* (Glomeromycetes), first described only by spore morphology, had been known from another semi-arid biome in Southern America, the Gran Chaco in Bolivia. We detected this fungus now also at different locations in semi-arid to semi-humid NE Brazil. As for *P. pernambucanum* phylogenetic analyses were performed on nuclear ribosomal RNA gene sequences of the LSU region. For *P. boliviana*, the spores for these analyses originated from a trap culture inoculated with soils from the type location. The results now revealed that also *P. boliviana* belongs to *Paraglomus*. It grouped in a separate monophyletic cluster adjacent to *P. pernambucanum*, to *P. brasilianum*, *P. laccatum* and the type species *P. occultum*. Thus, *P. boliviana* is transferred to *Paraglomus*, as *Paraglomus bolivianum* comb. nov. Remarkably, it is the first species known in the Paraglomeromycetes with pigmented spores. *Paraglomus pernambucanum* and *P. bolivianum* have several features in common: e.g. bi-walled spores, and densely pitted surface ornamentations on the structural layer of the outer wall. Spores of the two species can be distinguished by color and the diagnostic nature of their pitted ornamentation. The current knowledge about the global distribution of *Paraglomus* and *Pacispora* species is summarized and discussed.

Introduction

Arbuscular mycorrhizal (AM) fungi play an important role in ecosystem functioning since they are associated with the majority of plant species, deliver essential nutrients to their symbiotic partners, and are for instance also able to suppress harmful soil-borne pathogens and pests, and may protect soils against erosion through stabilization of soil aggregates (SMITH and READ 2008). They can also serve as bio-, soil and land use indicators (e.g. OEHL et al. 2005a, 2011a, 2012). We assume that especially *Pacispora* species might be characteristic for specific soils, land use intensity and different climates since they were found to be characteristic for soils with pH > 6.0, either in alpine areas (e.g. *P. robigina*; OEHL and SIEVERDING 2004, BŁASZKOWSKI et al. 2008), in cultivated soils of temperate areas with lower phosphorus levels (e.g. *P. dominikii*; BŁASZKOWSKI, 1993; OEHL et al., 2005b; OEHL et al., 2010), or in Mediterranean and subtropical areas under semi-arid conditions subjected to naturally elevated soil pH (e.g. *P. scintillans* and *P. franciscana*; e.g. ROSE and TRAPPE, 1980; BASHAN et al., 2007; PALENZUELA et al., 2008).

One fungus, *P. boliviana*, was never found in alpine, temperate, Mediterranean or subtropical areas of higher soil pH despite of extensive AMF diversity studies performed in Europe and Northern America during the last decades (e.g. BŁASZKOWSKI, 1993; KOSKE and TEWS, 1987; DANIELL et al., 2001; JANSA et al., 2002; LANDIS et al., 2004), but so far only in the tropical, semi-arid Gran Chaco of Bolivia (pH 6.3; OEHL and SIEVERDING, 2004), and recently also from a tropical Atlantic rainforest in NE Brazil (SILVA et al., 2012). We have lastly detected it several times in the semi-arid Caatinga biome of NE Brazil, which focused again our attention to this fungus. In tropical areas, however, other *Pacispora* species were so far never reported, neither by morphological spore identifications from field soils, long-term trap culture propagations (e.g. GOTO et al., 2010; STÜRMER and SIQUEIRA, 2011; TCHABI et al., 2009) nor through molecular root analyses (e.g. HUSBAND et al., 2002; ÖPIK et al., 2010), although species of this genus could be expected in the Tropics at least in semi-arid regions and soils with increased pH.

Pacispora boliviana has a distinct pitted ornamentation on its spore surface (SIEVERDING and OEHL, 2004). The fungus was preliminary attributed to this genus, since it forms, like all *Pacispora*, bi-walled spores terminally on subtending hyphae. However, it was obvious from the beginning that its spore structure, and above all the structure of the subtending hyphae and the staining reaction of the wall layers in Melzer's reagent, does not fit with those characters typical for *Pacispora* species (OEHL and SIEVERDING, 2004). However, at that time, molecular analyses of the fungus were not available, and morphologically its spores could not be attributed to any other genus within the Glomeromycota, such as *Glomus* or *Paraglomus* (OEHL et al., 2011b). *Glomus* has only mono-walled spores, while the spore wall structure of *Paraglomus* has not yet been fully resolved, and the genus has so far had only species without substantial spore pigmentation. When morphological analyses cannot (or not yet) resolve the relationship between different taxa, molecular analyses are urgently needed to elucidate their phylogeny (GAMPER et al., 2009; PALENZUELA et al., 2010; OEHL et al., 2011d; GOTO et al., 2012). In the present study, we performed first molecular analyses on *P. boliviana* in order to clarify its phylogenetic position in relation to the other glomeromycotan fungi.

More recently, an undescribed fungus, with congruent overall spore and subtending hyphae morphology as *P. boliviana*, was found in another tropical, semi-arid biome of Southern America, i.e. in the Caatinga biome of NE Brazil. Thus, the second objective of the present study was to carefully elaborate both the spore morphology and the phylogenetic position of this new fungus. Based on the results obtained from concomitant morphological and molecular phylogenetic analyses, the new fungus is formally described hereafter. Another objective was to discuss the biogeographic distribution of the two fungi, as far as this was possible at this early stage of species identification. Finally, we aimed at comprehensively presenting the biogeography of the two genera, *Paraglomus* and *Pacispora*, in general.

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Materials and methods

Study sites

The new AM fungus was found in Caruaru and Serra Talhada, Pernambuco State (NE Brazil), in maize (*Zea mays* L.) fields in the semi-arid tropical Caatinga biome. The sampling sites are located at 08º08'00"S and 36º02'00"W (550 m a.s.l.) and 7º59'00''S and 38º19'16''W (650 m a.s.l.), respectively. The climate is tropical-(semi-)arid (type Bs of Köppen-Geiger; KOTTEK et al., 2006) with six to eight months of dry season. Mean annual temperature is 24-26°C, and annual rainfall is 650 and 550 mm, respectively. The maize variety sown was BR 5026 'São José' (LEMOS et al., 1995). At these two sites, the pasture plant species sudan grass (*Sorghum sudanense* (Piper) Stapf) and onion had previously been grown, respectively. More recently, the fungus was also found in a tropical Caatinga dry forest where *Mimosa tenuifolia* was the most dominant plant species and in an adjacent cowpea (*Vigna unguiculata*) field. Both locations are near Petrolina, in Pernambuco State (6°28'20''-6°30'00''S; 34°55'50-34°57'10''W, 380 m a.s.l., mean annual temperature 26°, mean annual rainfall 550 mm). At the natural Caatinga site *Mimosa tenuifolia* was the most dominant plant species.

The type location of *Pacispora boliviana* was described in OEHL and SIEVERDING (2004). Briefly, it was isolated from a degraded pasture in the semi-arid Gran Chaco of tropical Bolivia (Departamento de Santa Cruz de la Sierra; 18°05'S; 63°20'W, 550 m a.s.l., mean annual temperature 24°, mean annual rainfall approximately 800 mm), and from trap cultures inoculated with soils from that pasture. The trap cultures were maintained under tropical temperatures in the greenhouse at the University of Basel (Switzerland) for eight months in 2001.

In recent years, we found *P. boliviana* also in the semi-arid Caatinga of NE Brazil, e.g. in Triunfo (7°50'17''S; 38°06'06''W), Belém do São Francisco (8°45'28''S; 38°57'52''W) and, together with the herein described new fungus, also in Serra Talhada (7º59'00''S; 38º19'16''W). All these sites are also in Pernambuco State. Mean annual temperature in Belém do São Francisco (400 m a.s.l.) is 26°C, and the mean annual rainfall is 450 mm. These values are 22°C and approximately 1200 mm, respectively, in Triunfo. This isolation site has a more humid climate than it is common in the Caatinga biome, with typical vegetation of an Atlantic rainforest. This site profits from more frequent rainfalls due to its exposed higher altitude (650 m a.s.l.), when compared to the typical Caatinga dry forest in its surrounding.

Soil sampling and chemical soil analyses

Soil samples in Caruaru, Serra Talhada and Petrolina (NE Brazil) were taken in March 2011 as described by MELLO et al. (2012). The soils in Belém do São Francisco and Triunfo were already taken in September and October 2008, respectively. Soil samples in the Gran Chaco (Bolivia) were taken in November 2000 as described in OEHL and SIEVERDING (2004). The soil in Caruaru had a pH (H_2O) of 6.4, 1.1 g kg^{-1} organic C and 49.4 mg kg^{-1} available P extracted according to NELSON et al. (1953). In Serra Talhada, the soil had a pH (H_2O) of 6.2, 0.7 g kg^{-1} organic C and 58.0 mg kg^{-1} available P, and in Petrolina, pH was 5.2-6.0, organic C was 16.1 g kg^{-1}, and available P was 22.0 mg kg^{-1}. In Belém do São Francisco, pH was 6.8, organic C was 23.8 g kg^{-1}, and available P was 16.8 mg kg^{-1}, while pH was 6.8, organic C 39.4 g kg^{-1}, and available P 195.0 mg kg^{-1} in Triunfo. The Bolivian soil had a pH (H_2O) of 6.5; organic carbon was 26 mg kg^{-1}, and available P (here extracted with Na-acetate, see OEHL et al., 2005b) was 2.3 mg kg^{-1}.

AM fungal trap cultures

Trap cultures were established directly after sampling as described in OEHL et al. (2003), TCHABI et al. (2009) and MELLO et al. (2012). *Pacispora boliviana* produced abundantly spores only in one of 64 trap cultures, in the rhizosphere of *Stylosanthes guianensis*, *Bracharia humicicola* and *Chromolaena odorata*. The new fungus from Pernambuco did not form spores in the trap cultures. Using *Sorghum bicolor* as host plant, single species cultures were initiated, that were inoculated with single or multiple (10-20) spores isolated directly from the field for the new fungus, or obtained from the trap cultures for *Pacispora boliviana*. All these mono- or multiple spore cultures failed so far.

Morphological analyses

Spores of the two fungi were separated from the soil samples by wet sieving as described by SIEVERDING (1991). The described morphological characteristics of spores and their subcellular structures are based on observations of specimens mounted in polyvinyl alcohol-lactic acid-glycerol (PVLG; KOSKE and TESSIER, 1983), in a mixture of PVLG and Melzer's reagent (BRUNDRETT et al., 1994), a mixture of lactic acid to water at 1:1, Melzer's reagent, and in water (SPAIN, 1990). The terminology of the spore structure follows OEHL and SIEVERDING (2004) and OEHL et al. (2011b, c) for species with glomoid (sensu lato and sensu stricto), paraglomoid and pacisporoid spore formation. Specimens mounted in PVLG and the mixture of PVLG and Melzer's reagent were deposited at Z+ZT (Zurich, Switzerland) and URM (Recife, Brazil) herbaria.

Molecular analyses

Before DNA extraction all spores isolated were first washed in ultrapure water and sonicated three to four times. For *P. boliviana* (culture code: BOL 35), crude DNA extracts were obtained from three single isotype spores, extracted from the trap culture that had been inoculated with field soil samples from the type location in the Gran Chaco. For the new fungus from Pernambuco, the DNA extracts were obtained from two single spores that were directly separated from the field samples of the type location in Caruaru. The spores were singly placed on a slide in a drop (5-10 µl) of ultrapure water, crushed with a sterile needle. Crude DNA extract was used as template for a semi-nested PCR using the primers ITS3 (WHITE et al., 1990) 28G2 (SILVA et al., 2006) and LR1 (VAN TUINEN et al., 1998) 28G2, consecutively. PCR reactions were carried out in a volume of 50 µl, containing 75 mM Tris-HCl pH 8.8, 200 mM $(NH_4)_2SO_4$, 0.01% Tween 20, 2 mM $MgCl_2$, 200 µM each dNTPs, 1 µM of each primer and 2 units of Taq™ DNA polymerase (Fermentas, Maryland, USA); cycling parameters were 5 min at 95°C (1 cycle), 45s at 94°C, 1 min at 55°C, 1 min at 72°C (40 cycles), and a final elongation of 7 min at 72°C followed the last cycle. The final amplicons (~690bp) were purified with the PureLink PCR Purification Kit (Invitrogen), sequenced directly or cloned with a CloneJET™ PCR Cloning kit (Fermentas; Carlsbad, USA) following the manufacturer's instructions and sequenced. Sequencing was provided by the Human Genome Research Center (São Paulo, Brazil). Sequence data were compared to gene libraries (EMBL and Gen Bank) using BLASTn (ALTSCHUL et al., 1990). The new sequences deriving from the AM fungi from Bolivia and Pernambuco were deposited in the NCBI database under the accession numbers JX122769-JX122777.

Phylogenetic analyses

The phylogeny was reconstructed by partial sequences of the LSU rRNA gene. The AM fungal sequences were aligned in ClustalX (LARKIN et al., 2007) and edited with the BioEdit program (HALL, 1999). *Boletus edulis* Bull. and *Neurospora crassa* Shear & B.O. Dodge were included as outgroup. Prior to phylogenetic analysis,

the model of nucleotide substitution was estimated using Topali 2.5 (MILNE et al., 2004). Bayesian (two runs over 1 x 10^6 generations with a burnin value of 2500) and maximum likelihood (1,000 bootstrap) analyses were performed, respectively, in MrBayes 3.1.2 (RONQUIST and HUELSENBECK, 2003) and PhyML (GUINDON and GASCUEL, 2003), launched from Topali 2.5, using the GTR + G model. Neighbor-joining (established with the model cited above) and maximum parsimony analyses were performed using PAUP*-4b10 (SWOFFORD, 2003) with 1,000 bootstrap replications.

Biogeographic analyses

A comprehensive literature and sequence data bank research was performed in order to study the biogeographic distribution of the genera *Paraglomus* and *Pacispora* on global scale. We included identifications performed either on the genus or on the species level, and considered for studies that were either based on spore morphology, or on the generation of species and environmental sequences.

Results

Molecular phylogeny

Phylogenetic analyses on the partial sequences of the LSU rRNA gene place the two fungi from Bolivia and Pernambuco firmly, with high support values, in a monophyletic clade within the order Paraglomerales next to *Paraglomus occultum*, *P. laccatum* and *P. brasilianum* (Fig. 1).

Taxonomy

Paraglomus pernambucanum Oehl, C.M. Mello, Magna & G.A. Silva sp. nov. (Figs. 2-9)
Mycobank MB 800575

Diagnosis: Sporae albae ad flavo-albae, 66-95 × 62-75 mm in diametro, tunicis duabus. Stratum laminatum tunicae exterioris, album ad flavo-album, 2.9-4.2 mm crassum, cum depressionibus subtilibus, 0.5-1.1 mm latis et 0.5-1.0 mm profundis ornatum, 1.3-2.4 mm in distancia. Tunica interior hyalina; 1.9-3.0(-3.9) mm crassa, de novo formans et porum basae sporarum occudens. Tunica hyphae confluentis cum stratis exterioribus tunicae externae, raro porum hyphae affixae occludens. In solutione Melzeri tunica interior non colorans. Holotypus # 37-3701: ZT Myc 24205.

Etymology: Latin, *pernambucanum*, referring to the NE Brazilian State where the species was found first.

Holotype: Brazil, Pernambuco State, Caruaru (37/3701, ZT Myc 24205). Isotypes (37-3702–37-3705 at ZT Myc 24206; 37-3711–37-3713 at URM). Paratypes: Brazil, Pernambuco State, in the municipalities of Serra Talhada and Petrolina (37-3751, 37-3752, 37-3761; as ZT Myc 24207, 24208, 24209 at Z+ZT).

Spores are formed singly in soil. They are white to yellowish white, globose to subglobose to ovoid, 66-95 × 62-75 mm in diameter (Figs. 1-4) and have an outer and an inner wall (Figs. 2-3).

Outer wall with three layers (Figs. 5-7): outer layer (OWL1) evanescent to semi-persistent, subhyaline to light yellow, 0.5-0.9 mm thick, and usually tightly adherent to second layer (OWL2); OWL2 finely laminated, brilliant white in young mature spores to yellowish white in older spores, 2.0-2.6 mm thick, with regular, round but shallow and inconspicuous pits that are 0.5-1.1 µm in diameter and 0.5-1.0 µm deep and 1.3-2.4 µm apart; inner layer (OWL3) hyaline and thin, 0.4-0.7 mm, separable under pressure but usually adherent to OWL2 and then extremely difficult to observe. OWL2 stains yellow in Melzer's reagent.

Inner wall is hyaline and three-layered (Figs. 6-8). Outer layer (IWL1) is 0.5-0.8 mm thick. In crushed spores it sometimes separates under light pressure from the central layer (IWL2); the central layer (IWL2) is 1.0-2.4 mm thick and the inner layer (IWL3) is very thin, 0.4-0.7 mm, flexible and may show several folds in broken spores; IWL3 is usually adherent to IWL2 and thus very difficult to observe. None of the layers stains in Melzer's reagent (Fig. 9).

Subtending hypha (sh) is straight or recurved, 4.0-5.5 mm in diam at the spore base tapering to 3.5-4.5 mm within 6-15 mm distance from the base. It is generally slightly funnel-shaped to cylindrical (Figs. 2-6), or rarely slightly constricted (Fig. 9). The wall of the subtending hypha is of the same color as, and continuous with the spore wall layers OWL1 and OWL2, and of the same thickness, tapering to 0.5-1.1 mm within 25-90 mm distance. The length of the subtending hypha persistently remaining at the spore is often shorter (10-15 mm from the spore base), or sh is completely broken away. Pore of the subtending hypha usually is open at spore base, and IW generally functions as pore closure at spore base.

Distribution: The new fungus was detected in maize production sites in Caruaru and Serra Talhada, and in a tropical dry forest and a cowpea field in Petrolina. All these sites are located in the semi-arid Caatinga biome of Pernambuco State, NE Brazil.

Specimens examined: Brazil, Pernambuco, Caruaru (37-3701–37-3750). Brazil, Pernambuco, Serra Talhada (37-3751–37-3760); Brazil, Pernambuco, Petrolina (37-3761–37-3770).

Paraglomus bolivianum (Sieverd. & Oehl) Oehl & G.A. Silva comb. nov.
BASIONYM: ***Pacispora boliviana*** Sieverd. & Oehl. J. Appl. Bot. Food Qual. 78:79. 2004.
Mycobank MB 800596

Emendation: The species was well described in OEHL and SIEVERDING (2004). Here it might be mentioned that the subtending hyphae sometimes have a constricted appearance when OWL2 (hw2 in Fig. 6A of OEHL and SIEVERDING, 2004) is constricted and OWL1 already degraded. However, overall subtending hyphae shape, including OWL1 respective hw1, is cylindrical to slightly funnel-shaped since sh is regularly broader at spore base than at some distance from the spore (Fig. 6A of OEHL and SIEVERDING, 2004).

Comments: The intra-specific variation between the LSU rRNA gene sequences for *P. pernambucanum* and for *P. bolivianum* was around 1-2%. The sequences from *P. bolivianum* presented 95% of identity with those from *P. pernambucanum*. In the BLASTn analysis, the closest related species to *P. bolivianum* and *P. pernambucanum* was *P. brasilianum* with 93% and 92% of identity, respectively

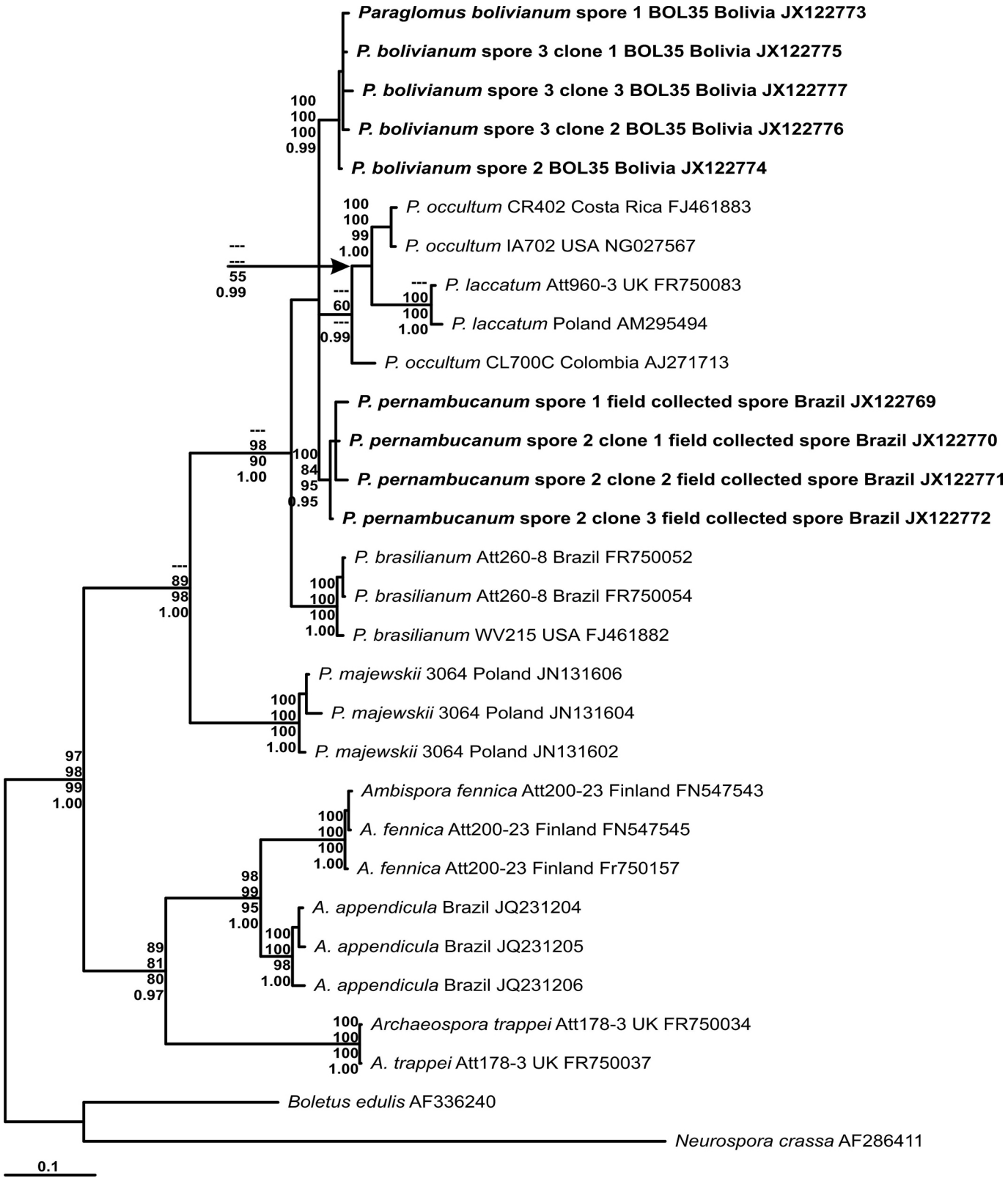
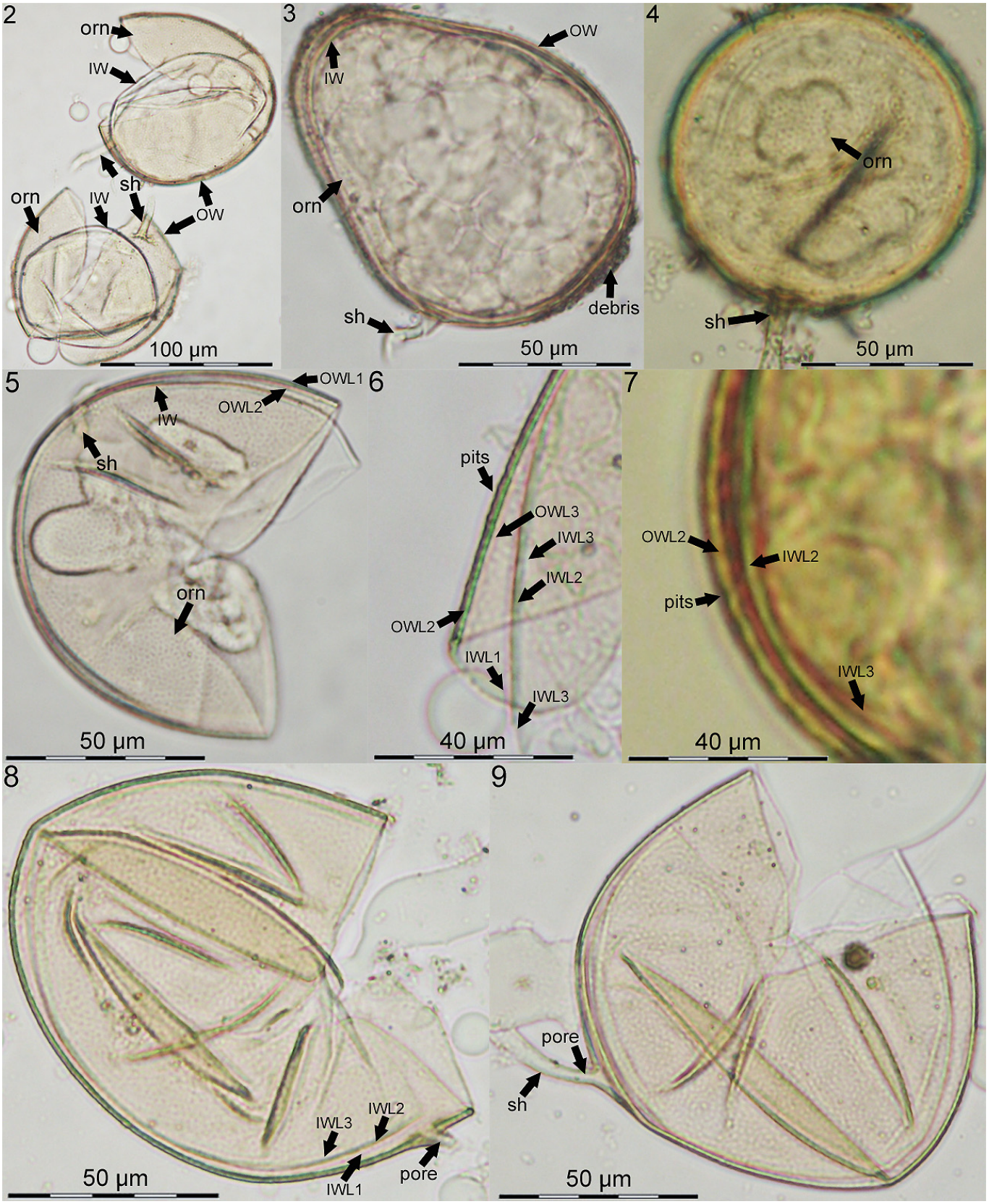


Fig. 1: Phylogenetic tree of the Paraglomeromycetes and Archaeosporomycetes based on analysis from partial sequences of the LSU rRNA gene. *Boletus edulis* and *Neurospora crassa* were used as outgroup. Sequences are labeled with database accession numbers. Support values (from top) are from neighbor-joining (NJ), maximum parsimony (MP), maximum likelihood (ML) and Bayesian analyses, respectively. Sequences obtained in this study are in bold. (Consistency Index = 0.70; Retention Index = 0.86).



Figs. 2-9: *Paraglomus pernambucanum*: Figs. 2-3. Crushed and uncrushed spores with outer and inner wall (OW, IW), cylindric to funnel-shaped subtending hyphae (sh) and minute pit ornamentation on OW surface. Fig. 4. Outer wall staining yellow in Melzer's reagent. Figs. 5-6. OW and IW triple-layered (OWL1-3; IWL1-3); outer surface of OWL2 with minute pits. Fig. 7. OWL2 staining yellow in Melzer's. Figs. 8-9. Pore at spore base regularly open but closed by IW.

Tab. 1: Detection sites of *Paraglomus* and *Pacispora* species around the globe

AMF isolate	Ecosystem/plant species/(Isolate) [1]	State/region, Country	pH[1]	Detected by[2]	Reference
***Paraglomus* spp.**					
Paraglomus occultum	Poplar plantations	Iowa, USA	NA	M	Walker et al. (1982)
P. occultum	Ornamental plants in greenhouse	Oregon, USA	NA	M	Walker et al. (1982)
P. occultum	NA	Illinois, USA	NA	M	Walker et al. (1982)
P. occultum	NA	The Netherlands	NA	M	Walker et al. (1982)
P. occultum	Agro-ecosystems; temperate	Pennsylvania, USA North America	NA	M	Franke-Snyder et al. (2001)
P. occultum	Sonoran desert	Texas & Arizona, USA	7.7-7.9	M	Stutz and Morton (1996)
P. occultum	Boojum tree in a desert reserve	Baja California, Mexico	7.0-8.0	M	(Bashan et al. 2007)
P. occultum	Evergreen forests & pastures	Nicaragua & Costa Rica	3.9-5.6	M	Picone (2000)
P. occultum	Natural ecosystems; crops like	Carimagua, Colombia cassava, maize	5.0-7.0	M	Sieverding (1989)
P. occultum	Maize	Pernambuco, Brazil	5.5-5.7	M	Maia and Trufem (1990)
P. occultum	Semi-arid copper mining area	Bahia, Brazil	6.2-7.8	M	Silva et al. (2005)
P. occultum	Evergreen and deciduous forests	Araucanía Region, Chile	4.6-5.4	M	Castillo et al. (2006)
P. occultum	Horticultural systems	Araucanía Region, Chile	5.5-6.1	M	Castillo et al. (2010)
P. occultum	Highest elevation of plant occurrence	Valais, Switzerland in Europe, 4505 m asl!	ca. 5.0	M	Oehl, in Körner (2011)
P. occultum	Subnival siliceous scree, 2700 m asl	Valais, Switzerland	5.0-5.4	M	Oehl, unpublished
P. occultum		Poland		M	Błaszkowski (1989, 1993)
P. occultum	Grasslands and crop rotation systems	Alsace, France; Baden, Germany; Basel, Switzerland	4.0-8.0, 5.3-7.7	M	Oehl et al. (2005b, 2010)
P. occultum	Tropical forests and yam field sites	Benin	6.1-6.9	M	Tchabi et al. (2009)
P. occultum	Namib Desert	Namibia	7.0-8.0	M	Stutz et al. (1999)
P. occultum	Forest and grassland	India	7.8	M	Muthukumar and Udaiyan (2000)
P. occultum	Wheat	Golestan, Iran	NA	M	Sadravi (2006)
P. occultum	Natural habitats: date palm (oasis) and native *Prosopis cineraria* (undisturbed desert habitat)	Sultanate of Oman	8.2-8.4	M	Al-Yahya'ei et al. (2011)
P. occultum	Desert ephemerals	Xinjiang, China	8.2	M	Shi et al. (2006)
P. occultum	(Isolates from INVAM; IA702, FL703, HA771)	Iowa/Florida/Hawaii, USA	NA	SpSeq	Millner et al. (2001), James et al. (2006), Msiska and Morton (2009)
P. occultum (JX301683-4)	Cultivated Soils of the Canadian Prairies	Saskatchewan, Canada	NA	SpSeq	Unpublished
P. occultum (FJ461883)	(Isolate from INVAM, CR402)	Costa Rica	NA	SpSeq	Unpublished
P. occultum	(Isolates from INVAM; CL700, CL700C, CL383)	Colombia	NA	SpSeq	Millner et al. (2001), Turnau et al. (2001)
P. occultum	(Isolate from INVAM, GR582)	Germany	NA	SpSeq	Millner et al.(2001)
P. occultum	(Isolate from BEG, BEG120)	Alicante, Spain	NA	SpSeq	Ferrol et al. (2004)
P. albidum	Winter wheat	Ohio, USA	NA	M	Walker and Rhodes (1981)
P. albidum	Poplar plantations	Iowa, USA	NA	M	Walker et al. (1982)
P. albidum	'Caatinga' dry forest	Bahia, Brazil	6.2	M	Silva et al. (2005)
P. albidum	Maize mono-cropping, crop rotations, grasslands	France, Germany, Switzerland	5.3-7.7	M	Oehl et al. (2009, 2010)
P. bolivianum	Gran Chaco grasslands	Santa Cruz, Bolivia	6.5	M&SpSeq	Oehl and Sieverding (2004), present study
P. bolivianum	'Caatinga' dry forest	Pernambuco, Brazil	5.2-6.8	M	Present study
P. bolivianum	coastal 'restinga' forest vegetation	Pernambuco, Brazil	5.1	M	Silva et al. (2012)
P. brasilianum	Greenhouse cultures on *Allium porrum*	D.F., Brasilia, Brazil	NA	M	Spain and Miranda (1996)
P. brasilianum	Desert ephemerals	Xinjiang, China	8.2	M	Shi et al. (2006)
P. brasilianum	(Isolate from INVAM; BR 105)	D.F., Brasilia, Brazil	NA	SpSeq	Krüger et al. (2012),
P. brasilianum	(Isolates from INVAM; WV224, WV219, WV215, WV215A)	West Virginia, USA	NA	SpSeq	Millner et al. (2001), Msiska and Morton (2009)

AMF isolate	Ecosystem/plant species/(Isolate) [1]	State/region, Country	pH[1]	Detected by[2]	Reference
P. laccatum	*Festuca* sp.	Jastrzębia Góra, Poland.	NA	M&SpSeq	Błaszkowski (1988b), Renker et al. (2007)
P. laccatum	*Ammophila arenaria*, *Helictotrichon pubescens*	Slowinski National Park, Poland	NA	M&SpSeq	Tadych and Błaszkowski (2000), Renker et al. (2007)
P. laccatum	Grassland	Thuringia, Germany	7.0-7.5	EnSeq	König et al. (2010)
P. laccatum	(Isolate Att960-3)	UK	NA	SpSeq	Krüger et al. (2012)
P. lacteum	Central Oregon desert	Oregon, USA	7.0-8.0	M	Rose and Trappe (1980)
P. majewskii	Zea mays	Algarve, Portugal	NA	M	Błaszkowski et al. (2012)
P. majewskii	*Ammophila. arenaria*	Mallorca, Spain	NA	M	Błaszkowski et al. (2012)
P. majewskii	*Ammophila. arenaria*	Karabucak-Tuzla, Turkey	NA	M&SpSeq	Błaszkowski et al. (2012)
P. majewskii	'Cultivated and uncultivated plants'	Lubuskie, Poland	NA	M	Błaszkowski et al. (2012)
P. majewskii	*Ammophila. arenaria*	Near Bornholm, Denmark	NA	M	Błaszkowski et al. (2012)
P. majewskii	Weeds	Asmara, Eritrea	NA	M	Błaszkowski et al. (2012)
P. majewskii	*Plantago lanceolata*	West Pomerian, Poland	NA	M&SpSeq	Błaszkowski et al. (2012)
P. pernambucanum	Natural Caatinga, maize and cowpea	Pernambuco, Brazil	5.2-6.4	M&SpSeq	Present study
Paraglomus sp.	Isolated from *Miscanthus sinensis*	Jeonbuk, South Korea	NA	EnSeq	Lee et al. (2008)
Paraglomus sp.	Roots of *Panax japonicus*	Chungbuk, South Korea	NA	EnSeq	Lee et al. (2008)
Paraglomus sp. (FJ461884)	Isolate from INVAM - NI116B	Nicaragua	NA	SpSeq	Unpublished
Paraglomus sp.	Pioneer grass species *Miscanthus sinensis* in acid sulfate soils	Hokkaido/Aichi/Okinawa, Japan	2.7-6.8	EnSeq	An et al. (2008)
Paraglomus sp.	Seminatural grasslands - Roots of *Lolium multiforum*	Thuringia, Germany	6.2	EnSeq	Renker et al. (2003), Börstler et al. (2006)
Paraglomus sp.	Wetland, Roots of *Dactylis glomerata*	Thuringia, Germany	NA	EnSeq	Wirsel et al. (2004)
Paraglomus sp.	Semi-natural grasslands – Roots of *Plantago major*	Thuringia, Germany	6.2	EnSeq	Börstler et al. (2006)
Paraglomus sp.	Semi-natural grasslands	Thuringia, Germany	6.2	EnSeq	Börstler et al. (2006), Hempel et al. (2007)
Paraglomus sp. (AJ854100)	Roots of *Ajuga reptans*	Yorkshire, UK	NA	EnSeq	Unpublished
Paraglomus sp. (FN555262-92)	Onion (trap plant roots)	England-UK	NA	EnSeq	Unpublished
Paraglomus sp.	Arable soils – Roots of *Zea mays*	Basel, Switzerland	4.8-5.4	EnSeq	Hijri et al. (2006)
Paraglomus sp.	Arable soils – Roots of *Triticum aestivum*	Basel, Switzerland	5.4	EnSeq	Hijri et al. (2006)
Paraglomus sp.	Arable soils – colonized roots	Basel, Switzerland	4.8	EnSeq	Hijri et al. (2006)
Paraglomus sp.	Aquatic macrophytes in oligotrophic and ultra-oligotrophic lakes	The Netherlands	NA	EnSeq	Baar et al. (2011)
Paraglomus sp.	Organic and conventional farming systems – Roots of *Allium cepa*	The Netherlands	7.4	EnSeq	Galván et al. (2009)
Paraglomus sp.	Geothermal soils – Roots of *Agrostis stolonifera*	Iceland	4.0-4.5	EnSeq	Appoloni et al. (2008)
Paraglomus sp.	Geothermal soils – colonized roots	Yellowstone, USA	3.4-4.8	EnSeq	Appoloni et al. (2008)
Paraglomus sp.	Geothermal soils– Roots from *Dichanthelium lanuginosum*	Yellowstone,USA	4.8	EnSeq	Bunn et al. (2009)
Paraglomus sp.	Colonized roots	Yellowstone,USA	4.8-6.5	EnSeq	Lekberg et al. (2011)
Paraglomus sp. (GQ890654, GQ890656)	Grasslands dominated by exotic plant species	California, USA	NA	EnSeq	Unpublished
Paraglomus sp.	Reforestation plots on degraded pastures- Roots of *Setaria sphacelata* and *Heliocarpus americanus*	South of Ecuador	4.0-5.0	EnSeq	Haug et al. (2010)
Paraglomus sp.	Roots of *Retama sphaerocarpa*, *Psoralea bituminosa* and *Lolium perenne*	Murcia, Spain	NA	EnSeq	Alguacil et al. (2011a)
Paraglomus sp.	Seedlings grown in a heavy metal polluted soil	Murcia, Spain	NA	EnSeq	Alguacil et al. (2011b)
Paraglomus sp.	Roots of *Herniaria fruticosa* and *Senecio auricula*	Murcia, Spain	NA	EnSeq	Alguacil et al. (2012b)

AMF isolate	Ecosystem/plant species/(Isolate) [1]	State/region, Country	pH[1]	Detected by[2]	Reference
Paraglomus sp.	Galls and Roots of *Prunus persica*	Aragua, Venezuela	5.18	EnSeq	Alguacil et al. (2011c)
Paraglomus sp.	*Ricinus communis* soil	Guantanamo, Cuba	8.7	EnSeq	Alguacil et al. (2012a)
Paraglomus sp.	Roots of *Dichanthium aristatum*	Guadeloupe, French Antilles	7.8	EnSeq	Jalonen et al. (2012)
Paraglomus sp.	Roots of *Zea mays*	Martonvasar, Hungary	5.8-6.2	EnSeq	Sasvári et al. (2011)
Paraglomus sp. (HE775341-50)	Roots of *Tanacetum vulgare*, *Brachypodium pinnatum*, and *Knautia arvensis*	Bohemia, Czech Republic	NA	EnSeq	Unpublished
Paraglomus sp.	Roots of *Trifolium repens*	Lombardy, Italy	5.7-6.4	EnSeq	Lumini et al. (2011)
Paraglomus sp.	Roots of *Zea mays*	Marche, Italy	8.3-8.5	EnSeq	Borriello et al. (2012)
Paraglomus sp. (HM044471)	Roots of *Larix decidua*	South Tyrol, Italy	NA	EnSeq	Unpublished
Paraglomus sp. (JQ315319-36)	Roots of *Camellia japonica*	Piedmont, Italy	5.8	EnSeq	Unpublished
Paraglomus sp.	Pasture soil	Sardinia, Italy	5.4-6.2	EnSeq	Orgiazzi et al. (2012)
Paraglomus sp.	Pasture soil	Sardinia, Italy	5-6.5	EnSeq	Lumini et al. (2009)
Paraglomus sp. (HQ108153-9)	NA	Cameroon	NA	EnSeq	Unpublished
Paraglomus sp. (JF340036-39)	Chickpea rooting soil	Canada	NA	EnSeq	Unpublished
Paraglomus sp. (JQ864337)	Rhizosphere of *Tectona grandis*	Chiang Mai, Thailand	NA	EnSeq	Unpublished
Paraglomus sp.	Semiarid Mediterranean prairies	Murcia, Spain	NA	EnSeq	Torrecillas et al. (2012)
***Pacispora* spp.**					
Pacispora scintillans	High Mediterranean dessert	Oregon, USA	NA	M	Rose and Trappe (1980)
P. scintillans	Pot culture with *Plantago lanceolata* inoculated with field soil from beneath *Triticum aestivum*	Pomerania, Poland	NA	SpSeq	Walker et al. (2004)
P. scintillans	Sandy heathland, beneath *Dactylis glomerata*, *Anthericum liliago* and associated plants	Hessen, Germany	NA	SpSeq	Walker et al. (2004), Krüger et al. (2009)
P. scintillans	Ancient meadow, beneath *Lolium perenne* and associated plants	Dorset, UK	NA	SpSeq	Walker et al. (2004)
P. chimonobambusae	Bamboo garden	Nan-Tou, Taiwan	NA	M	Wu et al. (1995)
P. chimonobambusae	*Trisetum* grassland on serpentinite	Grisons, Switzerland	6.1	M	Oehl, unpublished
P. coralloidea	Subnival siliceous scree	Valais, Switzerland	6.5	M	Oehl and Sieverding (2004)
P. dominikii	*Trifolium pratense*	NW Poland	NA	M	Błaszkowski (1988a)
P. dominikii	*Trisetum* grasslands	Grisons, Switzerland	7.8	M	Oehl, unpublished
P. dominikii	Organic farming systems	Basel, Switzerland	6.4-7.5	M	Oehl et al. (2005b, 2010)
P. dominikii	*Pterocephalus spathulatus*, *Thymus granatensis*	Andalusía, Spain	8.1	M&SpSeq	Palenzuela et al. (2008)
P. franciscana	Olive tree-grasslands	Umbria, Italy	7.0-7.5	M	Oehl and Sieverding (2004)
P. franciscana	Subnival calcareous screes	Grisons, Switzerland	7.5	M	Oehl and Sieverding (2004)
P. franciscana	NA	Pomerania, Poland	NA	SpSeq	Krüger et al. (2012)
P. franciscana	NA	Lower Saxony, Germany	NA	SpSeq	Krüger et al. (2012)
P. patagonica	*Nothofagus* forest	Santa Cruz, Argentina	5.5	M	Novas et al. (2005)
P. robigina	Subnival calcareous and serpentinite screes	Grisons, Switzerland	7.0-7.8	M	Oehl and Sieverding (2004)
P. robigina	Subnival screes	Valais Switzerland	6.5	M	Oehl and Sieverding (2004)
P. robigina	*Soldanella carpatica*	Tatra Mountains, Poland	NA	M	Oehl and Sieverding (2004)
Pacispora sp.	McLaughlin Reserve on serpetinite	California, USA	NA	EnSeq	Schechter and Bruns (2008)
Pacispora sp.	Alpine plant species (4500 m asl)	Tibet, China	NA	EnSeq	Liu et al. (2011)
Pacispora sp. (JQ182767)	Tibet Plateau	China	NA	EnSeq	Unpublished

Accession numbers are given in the left column for available sequences that so far have not yet been published in peer-reviewed journals. [1] No information Available. [2] M = Identified by morphological analyses, SpSeq identified by molecular analyses, M&SpSeq identified by both approaches, EnSeq = environmental sequences deposited in public data bases.

(Fig. 1). Environmental sequences that were closely related to the two fungi were not found in the public data bases.

Distribution: *Paraglomus bolivianum* was found in a degraded pasture of the semi-arid Gran Chaco (Bolivia, OEHL and SIEVERDING, 2004). In recent years, it was also found in the semi-arid Caatinga of NE Brazil, e.g. in Triunfo, Belém do São Francisco and Serra Talhada, all in Pernambuco State. Finally, *P. bolivianum* was also found in a coastal 'restinga' forest vegetation in Mataraca (Paraíba State; 6°28'20''-6°30'00''S; 34°55'50-34°57'10''W (SILVA et al., 2012).

Biogeography of *Paraglomus* and *Pacispora* spp.

In Tab. 1, a comprehensive summary of the biogeography of the genus *Paraglomus* and *Pacispora*, and their conclusively and non-conclusively identified species, is given. The identifications have been based on spore morphology, molecular analyses on formerly morphologically identified species, and on so-called environmental sequences deposited in the public data bases. It can be deduced from these results that the genus *Paraglomus* has a worldwide distribution and occurs in many terrestrial ecosystems throughout the globe. It has been recorded from high alpine to nival areas, temperate to Mediterranean up to sub- to inner tropic, arid to humid areas, in different soil types covering a wide spectrum of soil pH and land use intensities (Tab. 1). There have been > 300 *Paraglomus* sequences from the ribosomal gene deposited in the public data bases, from 36 countries and from many quite different ecosystems. The most widespread fungus of this genus so far might be *P. occultum*, followed by *P. albidum*, since these two species were most often identified. However, the phylogenetic tree shows at least two species identified as *P. occultum*, revealing current problems in the species identification of this small-spored genus. Only one *P. occultum* clade, fixed by the isolate from the type area in Iowa, can be *P. occultum*, while the sequence AJ271713 obviously belongs to another *Paraglomus* species (Fig. 1).

The genus *Pacispora* is biogeographically more restricted to specific habitats and specific climatic zones than *Paraglomus* (Tab. 1), which confirms our assumption in the introduction. Based on morphological spore identification, the genus is characteristic for higher pH soils (> 6.0) and a more restricted to specific ecosystems when compared to *Paraglomus*. One exception might be *P. patagonica* which was found in soil with pH 5.5, but it was not given in NOVAS et al. (2005) in which medium the soil pH was measured. Also in the public data bases, sequences of *Pacispora* spp. have so far been rarely deposited: from the ribosomal gene, only nine environmental sequences and 23 sequences from formerly morphologically identified species have been found. They are from USA, Poland, Germany, UK, Spain and China, all detected from soils with pH > 6.0 (Tab. 1). Nevertheless, our investigation shows that the genus occurs worldwide, but none of the *Pacispora* species appear to have a similar wide distribution as *P. occultum*.

Discussion

Paraglomus pernambucanum and *P. bolivianum* can easily be distinguished by their spore wall ornamentations, and by spore color and size. The spores of *P. bolivianum* are yellow brown to brown and their pits are substantially larger and deeper (OEHL and SIEVERDING, 2004) than those of *P. pernambucanum*, whose spores are hyaline to subhyaline. In *Paraglomus*, there is one other species known with ornamentation on the spore wall. This is *P. brasilianum* whose ornamentation is labyrinthiform (SPAIN and MIRANDA, 1996; MORTON and REDECKER, 2001).

Within *Paraglomus*, six to seven of the eight species might have two spore walls. These are *P. occultum* (WALKER, 1982), *P. brasilianum* (SPAIN and MIRANDA, 1996), *P. bolivianum* (OEHL and SIEVERDING, 2004), *P. pernambucanum*, and, according to our analyses (OEHL, own observations), also *P. lacteum* (ROSE and TRAPPE, 1980) and *P. laccatum* (RENKER et al., 2007). Beneath its multi-laminated spore wall layer, *P. laccatum* has a separate inner wall which is difficult to observe (RENKER et al., 2007; OEHL et al., 2011c). This might be also true for *P. albidum* (WALKER and RHODES, 1981; OEHL et al., 2011c) but this need to be checked on newly isolated spores. Thus, only *P. majewskii* might have solely one, triple-layered spore wall with a relatively thin innermost layer, which is substantially thinner than those in the other *Paraglomus* species like *P. occultum*, *P. brasilianum*, and *P. bolivianum*. Interestingly, *P. majewskii* was reported as forming a relatively distant lineage within *Paraglomus* (BŁASZKOWSKI et al., 2012), which is confirmed by our analyses.

Beside *P. pernambucanum*, there has been only one other recently described *Paraglomus* species, with phylogenetic analyses in the original description (*P. majewskii*, BŁASZKOWSKI et al., 2012). Like *P. bolivianum*, *P. laccatum* was transferred to the genus *Paraglomus* due to new phylogenetic analyses (RENKER et al., 2007) on type specimens of the former *Glomus laccatum* (BŁASZKOWSKI, 1988b). Sequences on the ribosomal gene of *P. occultum* and *P. brasilianum* (formerly *G. occultum* and *G. brasilianum*) were the base for the transfer of the later two species (WALKER, 1982; SPAIN and MIRANDA, 1996) from the Glomerales and Glomeraceae to the Paraglomerales and Paraglomeraceae, respectively (MORTON and REDECKER, 2001; SCHÜSSLER et al., 2001). Up to date, six *Paraglomus* species have been sequenced on the rRNA or other genes (Fig. 9), while for *P. albidum* and *P. lacteum* molecular phylogenetic evidence is still missing (OEHL et al., 2011c). Remarkably, *P. bolivianum* is the first species known in the Paraglomeromycetes with pigmented spores.

In the Glomeromycota, there are currently two genera with bi-walled spores formed on subtending hyphae. This is true for all *Pacispora* species (OEHL and SIEVERDING, 2004; OEHL et al., 2001b) and for most of the *Paraglomus* species. *Pacispora* species form characteristic constricted to cylindrical subtending hyphae that may bear one to a few hyphal pegs, and the outermost spore wall layer is semi-persistent, while the inner wall regularly stains purple to deep purple in Melzer's reagent. In contrast, bi-walled *Paraglomus* spores generally have slightly funnel-shaped to cylindrical subtending hyphae without hyphal pegs, and the outermost spore wall layer is rapidly degrading ('short-lived') and thus, can be called evanescent, while the inner wall never stains in Melzer's. Remarkably, species of *Pacispora* with ornamented spore surfaces regularly have projections on OWL1 (*P. scintillans*, *P. dominikii*, *P. coralloidea*, *P. chimonobambusae*, *P. patagonia*) (OEHL and SIEVERDING, 2004; WALKER, 2008), while the *Paraglomus* species with ornamented spore surfaces have a pitted OWL2 (*P. brasilianum*, *P. bolivianum* and *P. pernambucanum*).

Our literature and data bank research strongly suggests that *Paraglomus* species have a wider distribution than *Pacispora* species, since they were found in many different ecosystems from the warm to very cold climates and in soils of very different soil pH (Tab. 1). *Pacispora* species are characteristic for soils with pH > 6.0, either in high alpine areas (e.g. *P. robigina*, OEHL and SIEVERDING, 2004; BŁASZKOWSKI et al., 2008), in cultivated soils of temperate areas (e.g. *P. dominikii*, BŁASZKOWSKI, 1993; OEHL et al., 2005b; OEHL et al., 2010) or in Mediterranean and subtropical areas un-

der semi-arid conditions subjected to naturally elevated soil pH (e.g. *P. scintillans* and *P. franciscana*, Rose and Trappe, 1980; Błaszkowski, 1993; Oehl and Sieverding, 2004; Bashan et al., 2007). However, so far they were, to our knowledge, never found in tropical areas (e.g. Sieverding, 1989; Stürmer and Siqueira, 2011; Tchabi et al., 2008). In contrast, *Paraglomus bolivianum* and *P. pernambucanum* were so far only found from tropical regions in South America, beside a single isolation site of *P. bolivianum* reported from southeast Tibet (Wang and Shi, 2008). It has to be taken into account that many *Paraglomus* species, and especially *P. pernambucanum*, form rather small, rapidly degrading spores that in the past might have often been difficult to identify from field samples. Thus, we do not exclude that both species have, like *P. occultum*, a much larger distribution than known so far.

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