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Ambispora reticulata, a new species in the Glomeromycota from mountainous areas in Switzerland and Chile

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Summary

A new glomeromycotean fungus, *Ambispora reticulata*, was found in the Swiss Alps and in the Chilean Andes. Only acaulo-ambisporoid spores were detected so far, 87-131 x 125-150 µm in diameter and having a three-layered, yellow-brown to brown outer wall, a bi-layered, hyaline middle wall and a generally three-layered, hyaline inner wall. The middle wall has a characteristic reticulate outer surface with irregular triagonal to octagonal (usually tetra- to hexagonal) pits that are surrounded by ridges. As known for all *Ambispora* species with acaulo-ambisporoid spore formation, the middle wall is a substantial part of the pedicel which connects the spore with the mycelium. The new species is a frequent member of arbuscular mycorrhizal fungal communities in mountainous and subalpine grasslands of the Swiss Alps at 1000-2100 m above sea level. It occurred less frequent in high alpine grasslands and at altitudes below 1000 m, where the fungus was found in a conservation tillage and a low-input tillage system. It was also detected in evergreen and in deciduous forests in the Andes of Southern Chile at elevations of 550-1600 m.

Introduction

In the last two decades, biodiversity studies have worldwide been intensified. This is especially true for arbuscular mycorrhizal fungi (AMF) of the Glomeromycota (e.g. Błaszkowski, 1993; Vestberg, 1995; Castillo et al., 2006, 2010; Sánchez-Castro et al., 2011; Bezerra et al., 2011; Souza et al., 2012). While until 1990, only ca. 130 glomeromycotean species were described (Schenck and Pérez, 1990), today we count approximately 250 species. Also remarkably, the more recently published new AMF species (e.g. Gamper et al., 2009; Furrazola et al., 2011; Rodriguez et al., 2011) have been described by an steadily increasing number of research groups (Stürmer, 2012).

High AMF species and genus diversities were for instance revealed in Central Europe (Jansa et al., 2002, 2003; Gamper et al., 2004; Oehl et al., 2005a, 2010) even up to the highest altitudes and harshest environments in the Swiss Alps where higher plants live (Oehl et al., 2011a; Körner, 2011). While several species were found in all habitats investigated, others were characteristic for specific soils (Oehl et al., 2003, 2005b), soil depths (Oehl et al., 2005a), land use practices (Oehl et al., 2009) or altitudes (Oehl et al., 2006, 2011e, 2012).

One unknown AMF species was mainly found in mountainous to subalpine grasslands of the Swiss Alps at 1000-2100 m above sea level (a.s.l.). It was simultaneously found also in mountainous forests in the Andes of Southern Chile (Castillo et al., 2006). It is here published under the epithet *Ambispora reticulata*. The new species did not reproduce in single spore bait cultures. It is described from spore morphological characters as these are clearly indicating that the species belong to *Ambispora* in the Archaeosporales, Archaeosporomycetes (Spain et al., 2006; Walker et al., 2008; Oehl et al., 2011c).

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Materials and methods

Study sites and soil sampling

Soil samples were taken between March 2000 and April 2009 all over Switzerland from about 100 tillage and conservation tillage farming sites in the lowlands, and from in total > 400 grassland sites in the lowlands, mountainous and alpine areas from altitudes between 300 and 3000 m a.s.l. The soils have developed on different geological bedrocks from nutrient poor Jurassic sandstones over granite and gneiss rocks to carbonatic Loess sediments, limestones and ultrabasic serpentinites (e.g. Oehl et al., 2005b, 2010, 2011a). Undisturbed soil cores from 0-10 cm depth were collected at study sites. Spores of Glomeromycota were separated from the soil samples by the wet sieving, decanting and subsequent sugar gradient centrifugation technique (Sieverding, 1991). In Chile, soil samples were taken from replicated plots of a nutrient recycling experiment in an evergreen natural rainforest and a deciduous secondary forest in the Experimental Station San Pablo de Tregua of the University Austral de Chile (Valdivia, Chile, 39°30-39°38'S and 72°02-72°09'W) at an elevation between 550 and 1600 m a.s.l. (Castillo et al., 2006). Spores were separated as given above.

AM fungal bait cultures

Bait cultures were established in Switzerland directly after soil sampling as described in Oehl et al. (2005b, 2011a) using a sterilised substrate (Terragreen (American aluminium oxide, Oil Dry US special, type III R, >0.125 mm; Lobbe Umwelttechnik Iserlohn, Germany) -Loess mixture 3:1; pH-KCl 6.2; organic carbon 0.3 %; available P (Na-acetate) 2.6 mg kg^{-1}; available K (Na-acetate) 350 mg kg^{-1}) in pots of different sizes (1 L in 2003-2005; Oehl et al., 2011a, 3.5 L in 2009-2010, and 9 L in 2000-2002; Oehl et al., 2005b). Sub-samples of the field samples represented natural field inocula and were placed as a thin sandwich layer between two substrate layers, about 5 cm below the surface. Above the soil inocula, about 5-7 seeds of each of the four bait plants, *Plantago lanceolata* L., *Lolium perenne* L., *Trifolium pratense* L., and in some experiments also *Hieracium pilosella* L. were sown. Two weeks-old *Trifolium pratense* plants received 1 mL of a 1:5 with water diluted 12 h old culture of *Rhizobium trifolii* (DSM 30138, from DSMZ-Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany), grown in liquid DSMZ 98 medium at 27 C. An automated watering system (Tropf-Blumat, Weninger GmbH, A-6410 Telfs) was installed and the cultures were kept in the greenhouse under ambient light and temperature conditions for 16-32 months. The spore formation was monitored in the bait cultures in bi- or four-monthly intervals as described in Oehl et al. (2009, 2011a). The new fungus reproduced spores only in two of approximately 650 bait cultures established. All trials to

reproduce the new fungus in so-called AMF mono-species cultures so far failed.

Morphological analyses
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 basically is that suggested by Spain et al. (2006) for *Ambispora* species, and by Oehl et al. (2011b) for all glomeromycotean taxa. Photographs in Fig. 1-9 were taken with a digital camera (Olympus model DP70-CU) on a compound microscope (Zeiss Axioplan). Specimens mounted in PVLG and the mixture of PVLG and Melzer's reagent were deposited at the mycological herbarium of the ETH Zürich (Z+ZT, Zurich, Switzerland).

Latin diagnosis
Ambispora reticulata Oehl & Sieverd. sp. nov. (**Fig. 1-9**)
Mycobank MB 800269
Sporae acaulo-ambisporoideae flavo-fuscae vel fuscae, 87-131 x 125-150 µm, formatae appendice, tunicis tribus; tunica media duobus stratis hyalinis reticulum tetragonale at hexagonale formans, depressionibus 3-7.5(-10) µm in diametro et 0.5-2.5 µm profundis. Typus hic designatus # 57-5701 (ZT Myc 24171).

Etymology. Latin, *reticulata* referring to the reticulate ornamentation of the middle wall.

Holotype
Holotype (here designated: Slide Nr. 57-5701; accession number ZT Myc 24171) and isotypes (ZT Myc 24172) were isolated from soil samples taken from the rhizosphere of an high mountainous pasture characterized by *Nardus stricta*, at Cuolms dil Run Alp (46°42'57''N; 8°57'54''E), Surrein-Sumvitg, Surselva, Kanton Graubünden, Switzerland, at about 1600 m a.s.l. Paratypes isolated from several locations in the Swiss Alps and central lowlands of Switzerland (see below) were also deposited at Z+ZT (ZT Myc 24173-24175).

Description
Acaulo-ambisporoid spores are formed by the fungus, but so far sporiferous saccules and glomo-ambisporoid spores were not detected. The acaulo-ambisporoid spores are yellow brown to brown, globose to oval to fig-like, 87-131 x125-150 µm in diameter (Fig. 1-2) consisting of three walls: outer wall (OW), middle wall (MW) and inner wall (IW; Fig. 3).

Outer spore wall consists of three layers (OWL1-OWL3) and is in total 4-9 µm thick (Fig. 2-3). OWL1 is hyaline, unit, 0.5-1.0 µm thick (Fig. 1), evanescent (Fig. 2) and thus, usually difficult or not to observe in mature spores. Second layer (OWL2) is yellow-brown to brown, laminated, 3-8 µm thick. It sometimes swells up to 10-20 µm in PVLG (plus Melzer reagent) under pressure applied on the cover slide (Fig. 4). OWL3 is hyaline, 0.5-1.5 µm thick, often tightly adherent to OWL2, but can be separated under pressure. Swelling laminae of OWL2 stain pinkish, and OWL3 stains pinkish purple to purple in Melzer's reagent (Fig. 4). With age, OW shows many fissures, a feature that becomes more obvious when pressure is applied on the cover slide (Fig. 3).

Middle wall is hyaline, bi-layered (MWL1-MWL2) and 1.5-3.5 µm thick (Fig. 5-6). Both layers are tightly adherent to each other. MWL1 is semi-flexible, 0.8-2.5 µm thick and has a reticulate surface ornamentation (Fig. 6-7). The pits are irregular triagonal to octagonal (usually tetra- to hexagonal) and are 3-7.5(-10) µm wide and 0.5-2.5 µm deep (Fig. 6, 7). Pits are surrounded by ridges that are 0.5-1.2 µm wide. Inner MWL2 is unit, smooth and 0.8-2.1 µm thick. None of the layers reacts to Melzer's reagent.

Inner wall is hyaline, with (two to) generally three layers (IWL1-IWL3) that are 1.2-3.0 µm thick in total (Fig. 8). IWL1 is < 0.5 µm thick, and often appears to be missing (Fig. 5-6). IWL2 is 1.2-2.5 µm thick and rigid, and IWL3 is very thin and usually very difficult to detect since tightly adherent to IWL2. None of the layers reacts to Melzer's reagent, but in old spores IWL3 sometimes becomes yellow (Fig. 8).

Pedicel at spore base is formed by the outer wall and the outer layer of the middle wall (Fig. 2, 9). It is 7-14 µm broad and 4-16 µm long, respectively, at the spore base. The pedicel OW layers are 3-6 µm thick at spore base and taper to 1.2-2.2 µm within a few µm distances from the base. On the spore surface, they may form a wide pore (=collar), which is 5-13 µm in diameter. The continuation of MWL1 is reticulate to undulate at the pedicel (Fig. 9). MWL1 wall layer regularly is only 0.5-1.5 µm thick at pedicel.

Distribution. In all regions of the Swiss Alps and in Southern Chile, where the fungus was found, spores of *Am. reticulata* were common, but they were rarely found in numbers > 1 g^{-1} soil. In Switzerland, they were frequently isolated from the rhizosphere of mountainous to subalpine grasslands at 1000-2100 m a.s.l. up to the tree line with vegetation characterized by the dominance of *Nardus stricta* or *Trisetum flavescens*, in soils of pH 3.6-5.9. Spores were rarely found in alpine *Nardus stricta* grasslands and generally absent in (high) alpine grasslands characterized by *Carex ferruginea* or *Sesleria caerulea*. They were also less frequently found in lower mountainous and lowland grasslands. In detail, *Am. reticulata* was found in Eastern Switzerland at Piz Nadels (Trun and Surrein-Sumvitg, Surselva, Chantun Grischun) between 1500-2000 m a.s.l.in *Nardus stricta* grasslands, in Southeastern Switzerland at Spadla Alp (Sent, Engiadina, Chantun Grischun) at 2300 m a.s.l. in a *Nardus stricta* grassland, in Central Switzerland in the Gotthard-Furka region between 1500-1900 m a.s.l. (Hospental and Realp, Kanton Uri; Airollo, Cantone Ticino) in *Nardus stricta* and *Trisetum flavescens* grasslands, at Axalp (Brienzer See) between 1000-1800 m a.s.l., and at Grindelwald (Grosse Scheidegg) between 1200-2000 m a.s.l. (Berner Oberland, Kanton Bern) in *Nardus stricta* and *Trisetum flavescens* grasslands, and in Southwestern Switzerland at 1000-1800 m a.s.l. (La Valette, Champex d'en Bas, Bourg-St.-Pierre, all Canton Valais) in *Trisetum flavescens* grasslands. Recently, they were also detected in the Canton Berne in an extensively managed conventional crop rotation system in Niederösch (three years of temporary grassland and one year of potatoes production) and in a conservation tillage system in Rubigen (7 year crop rotation with winter wheat, sugar beet, winter wheat, maize, winter barley and one year of grass/clover). The soil types were a broad range of Eutric to Dystric Cambisols in the Swiss Alps, and a Luvisol and Calcaric Cambisol in the lowlands of Berne, that had developed on a broad range of bedrocks: acidic sandstones, siliceous gneiss and granite

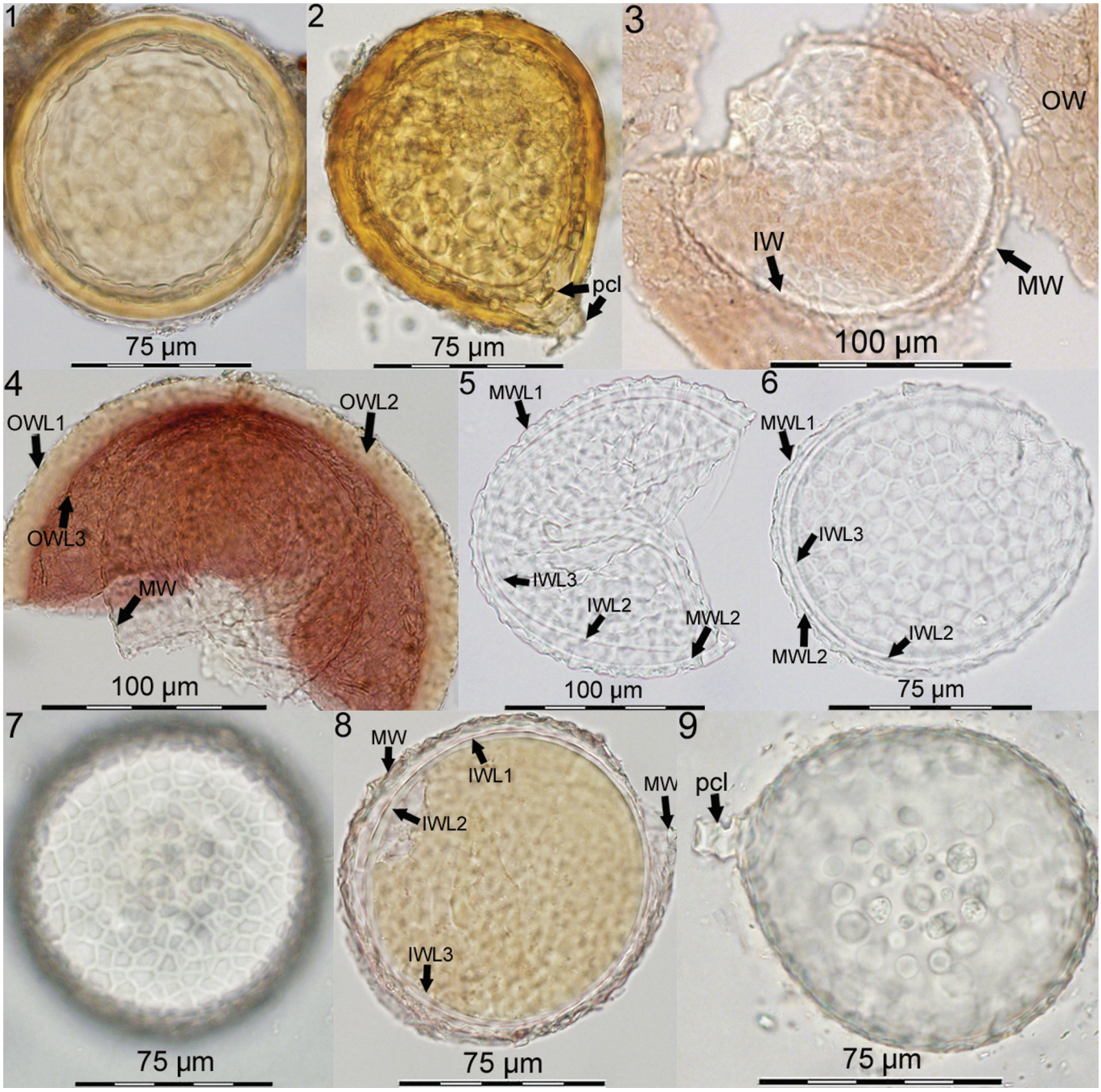

Fig. 1-9: *Ambispora reticulata* – all acaulo-ambisporoid morphs. 1-2. Uncrushed spores isolated from field soils with a pedicel (pcl) formed by the outer and the middle wall. 3. Crushed spores with outer, middle and inner wall: OW, MW and IW; OW showing multiple fissures which are especially seen in aged spores. 4. Crushed spore in PVLG & Melzer's reagent, with slight pinkish staining reaction on layer OWL2 and purple reaction of layer OWL3. 5-8. Bi-layered MW (MWL1-MWL2) and triple layered IW (IWL1-IWL3). Middle wall has a diagnostic tetragonal to hexagonal reticulate ornamentation on the outer surface. Rarely depressions have three or more than six sides. 9. Wall of the pedicel (pcl) is a continuation of MWL1 having flexible to semi-flexible appearance.

rocks, calcareous 'Bündner Schiefer' schists, moraine sediments and carbonatic limestones. The soil pH was always < 6.0 in the mountainous areas, while it was 6.0 and 7.1 in the two lowland sites. Available P (Na-acetate, see OEHL et al., 2011a) was between 3.2-15.2 mg kg^{-1} in the mountainous to low alpine areas and 17.2 and 42.8 mg kg^{-1} in the two lowland soils.

In Chile, *Am. reticulata* was found in an evergreen forest dominated by *Nothofagus dombeyi* and *Laureliopsis philippiana* tree species and a deciduous forest dominated by *Nothofagus alpina* at mountainous altitudes between 550-1600 m a.s.l. (CASTILLO et al., 2006). Soil pH was 4.6 and 5.4, and available P was 6.1 and 3.6 mg kg^{-1}, respectively.

Discussion

Ambispora reticulata can be easily distinguished from all other glomeromycotean fungi by its spore wall structure since the reticulate ornamentation on the middle spore wall is hitherto unique

and thus, diagnostic. In the genus *Ambispora* there are only two other fungi with ornamentation on the middle wall. These are *Am. appendicula* and *Am. jimgerdemannii* that both have an alveolate middle wall, in which both middle wall layers are ornamented on their interface (Rose et al., 1979; Schenck et al., 1984; Spain et al., 2006), while in *Am. reticulata* the reticulum is only on the outer surface of the middle wall.

The outer wall (OW) of aging spores of *Am. reticulata* regularly shows many fissures. This is a feature that becomes more obvious when pressure is applied to the cover slide of permanent specimens in PVLG, and is also known for the acaulo-ambisporoid morph of most of the other *Ambispora* species. These are *Am. appendicula*, *Am. gerdemannii*, *Am. fennica*, *Am. nicolsonii*, and *Am. brasiliensis* (Spain et al., 2006; Goto et al., 2008; Oehl et al., 2011d), while this is not observed with *Am. granatensis* which has a shorter-lived, since substantially thinner OW (Palenzuela et al., 2011).

Remarkably, spores of *Am. reticulata* were never found with sporiferous saccules attached, although in addition of field sampled spores, also bait cultured spores were analyzed. The reason of not detecting sporiferous saccules in these bait cultures might be that the intervals between single sampling periods were four months in these pots instead of two months. In the shorter intervals we usually found sporiferous saccules attached with e.g. *Acaulospora nivalis*, *Ac. alpina*, *Am. fennica*, *Am. appendicula*, *Otospora bareae* (e.g. Oehl et al., 2006, 2009, 2012; Palenzuela et al., 2008). Hence, the mode of spore formation of *Am. reticulata* still has to be discovered. Also the glomoid morph of *Am. reticulata*, if existent, still has to be identified. In the genus *Ambispora*, glomoid morphs are known only for some species but not for all (Spain et al., 2006; Walker et al., 2007).

In Switzerland, the new species was frequently found in mountainous to subalpine regions between 1000 and 2100 m a.s.l., whereas it was regularly absent in higher alpine areas and only sporadically found in lowland areas. In the Chilean Andes, *Am. reticulata* was hitherto revealed solely from mountainous areas between 550 and 1600 m a.s.l. indicating that the preferential occurrence of this fungus may be in medium altitudes within such colder climates. Distinct altitude respective climatic preferences in the Swiss Alps and in Sierra Nevada (Spain) were recently described also for other *Ambispora* species, as well as for several other glomeromycotean fungi like *Acaulospora alpina*, *Ac. nivalis*, *Ac. punctata*, *Glomus badium*, *Pacispora robigina* and *Tricispora nevadensis* (Oehl and Sieverding, 2004; Spain et al., 2006; Oehl et al., 2005a, 2006, 2011e, f, 2012; Palenzuela et al., 2010). By studying different ecosystems on global scales, we will gradually get a clearer picture about the biogeography of the Glomeromycota, that are counted among the most important soil micro-organisms, since they deliver a series of ecosystem services like soil aggregation, soil erosion protection, plant growth promotion, plant health and pathogen suppression, and seedling survival at sites as for example stressed by Rillig and Mummey (2006), Smith and Read (2008) and van der Heijden and Horton (2009).

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