

Occurrence of *Glomeromycota* species in aquatic habitats: a global overview

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ABSTRACT — Arbuscular mycorrhizal fungi (AMF) are recognized in terrestrial and aquatic ecosystems. The latter, however, have received little attention from the scientific community and, consequently, are poorly known in terms of occurrence and distribution of this group of fungi. This paper provides a global list on AMF species inhabiting aquatic ecosystems reported so far by scientific community (lotic and lentic freshwater, mangroves, and wetlands). A total of 82 species belonging to 5 orders, 11 families, and 22 genera were reported in 8 countries. Lentic ecosystems have greater species richness. Most studies of the occurrence of AMF in aquatic ecosystems were conducted in the United States and India, which constitute 45% and 78% reports coming from temperate and tropical regions, respectively.

KEY WORDS — checklist, flooded areas, mycorrhiza, taxonomy

Introduction

Aquatic ecosystems comprise about 77% of the planet surface (Rebouças 2006) and encompass a diversity of habitats favorable to many species from marine (ocean), transitional estuaries to continental (wetlands, lentic and lotic) environments (Reddy et al. 2018). Despite this territorial representativeness and biodiversity already recorded, there are gaps when considering certain types of organisms, e.g. fungi.

Fungi are considered a common and important component of almost all trophic levels. Their diversity is estimated as reaching 2.2 to 3.8 million species (Wurzbacher et al. 2011; Grossart & Rojas-Jimenez 2016; Hawksworth & Lücking 2016). Fungi that inhabit aquatic ecosystems can be classified as “truly aquatic fungi” and “transient fungi”. Truly aquatic fungi have life cycle strongly dependent on these habitats, while transient fungi prefer terrestrial habitats, although they also establish in submerged sites (Park 1972). An example of transient fungi are the Arbuscular Mycorrhizal Fungi (AMF), organisms commonly not considered in studies about global aquatic biodiversity (Shearer et al. 2007; Grossart et al. 2019).

AMF of the phylum *Glomeromycota* are classified in three classes, five orders, 16 families, 50 genera and approximately 322 species (Goto & Jobim 2020; Schüssler et al. 2001; Tedersoo et al. 2018; Wijayawardene et al. 2020). These fungi form a symbiotic association with roots of approximately 80% of plant families and have a widespread occurrence in different ecosystems (Read 1991; Smith & Read 2008).

Since the first report of the association of endomycorrhizae with aquatic macrophytes (Sondergaard & Laegaard 1977), efforts were applied to understand the functional role played by such symbiosis, taking into account environmental variables obtained from different aquatic ecosystems (Chaubal 1982; Clayton & Bagyaraj 1984; Stevens & Peterson 1996; Baar et al. 2011). Although interest in AMF existing in aquatic ecosystems was low, the potential of these ecosystems to harbor such fungi was highlighted (Ragupathy et al. 1990; Kennedy et al. 2002; Rodrigues & Anuradha 2009; Marins et al. 2009; D’Souza & Rodrigues 2013). The advent of the molecular approach allowed to recognize a high number of AMF species, including new virtual taxa (Moora et al. 2016) and a newly described species, *Rhizoglomus melanum* Sudová, Sykorová & Oehl (Sudová et al. 2015).

Some reviews on AMF in aquatic conditions have been published in the last 40 years, providing data on: i) the occurrence and ecological significance of these fungi for aquatic plants (Khan & Belik 1995); ii) the role of arbuscular mycorrhiza in these habitats (Shah 2014) and iii) the occurrence of this symbiosis in aquatic macrophytes, depending on the hydrological conditions of their existence, taxonomy and life forms of these hosts and their colonization by Dark Septate Fungi (DSF) (Xu et al. 2016; Marins et al. 2017; Fusconi & Mucciarelli 2018). However, none of the published papers on this topic informed of species of AMF occurring in sampled sites, except for that by Radhika et al. (2012) coming from India.

Taking into account the gap in knowledge on the occurrence and geographical distribution of AMF in aquatic ecosystems worldwide, this paper proposes the first global checklist for these ecosystems. An analysis of the distribution and representativeness pattern was also provided.

Material & methods

A bibliographic review of AMF studies in aquatic environments was performed taking into account the main databases used by scientific community (eg. Scopus, Scielo, Web of Science) and combining keywords (eg. arbuscular mycorrhizal fungi, aquatic habitats, flooded areas, hydrophytes, macrophytes, wetlands and others synonyms). A total of 110 papers published from 1965 to 2020 were detected. Of these, 20 were selected to compose the list of species, using as a criterion the presence of morphological/ molecular identification of AMF at the species level. The latter approach included species presented in descriptions and those identified in molecular environmental studies.

The classification system used here is that proposed by Oehl et al. (2011) and Błaszkowski (2012) with subsequent additions and modifications proposed by Goto et al. (2012), Marinho et al. (2014), Sieverding et al. (2014), Błaszkowski et al. (2018a, 2018b), Symanczik et al. (2018) and Wijayawardene et al. (2020). The taxonomic nomenclature follows that used in the Mycobank database (<http://www.mycobank.org/>). We follow the arguments presented by Sieverding et al. (2014) and use the generic name *Rhizogloous* Sieverd., G.A. Silva & Oehl instead of *Rhizophagus* C. Walker & A. Schüßler.

Results & Discussion

A total of 82 AMF species were recorded in aquatic environments worldwide. The fungi belonged to five orders: *Archaeosporales* (6), *Diversisporales* (22), *Glomerales* (33), *Gigasporales* (19) and *Paraglomerales* (2); 11 families: *Acaulosporaceae* (16), *Ambisporaceae* (3), *Archaeosporaceae* (3), *Dentiscutataceae* (3), *Diversisporaceae* (6), *Entrophosporaceae* (6), *Gigasporaceae* (4), *Glomeraceae* (27), *Paraglomeraceae* (2), *Racocetraceae* (8) and *Scutellosporaceae* (4) and 22 genera: *Acaulospore* (16), *Ambispora* (3), *Archaeospore* (2), *Cetraspora* (1), *Claroideoglomus* (4), *Dentiscutata* (2), *Diversispora* (5), *Entrophospora* (1), *Fuscotata* (1), *Funneliformis* (4), *Gigaspora* (4), *Glomus* (9), *Intraspora* (1), *Paraglomus* (2), *Racocetra* (7), *Rhizogloous* (10), *Sclerocystis* (2), *Scutellospora* (4), *Septogloous* (1), *Simigloous* (1) and *Viscospora* (1).

The checklist corresponds to 69% of the families, 45% of the genera and 25% of the species known for the *Glomeromycota* phylum. The highest AMF representativeness belong to *Glomerales* (40%) and *Diversisporales* (27%) orders; to the families *Glomeraceae* (33%) and *Acaulosporaceae* (19%), and to the genera *Acaulospore* (20%), *Rhizogloous* (12%) and *Glomus* (11%). This pattern is similar to that of terrestrial ecosystems. Monospecific genera such as *Entrophospora*, *Simigloous*, *Tricispore* and *Viscospora* have also been reported but we did not find records of *Dominikia*, *Halonatospora*, *Kamienskia*, *Microdominikia*, *Pervetustus*, *Sclerocarpum* and *Sieverdingia* in flooded systems.

Despite the limited numbers of studies, different types of submerged habitats were inventoried, especially lotic and lentic freshwater, mangroves and wetlands (FIG. 1), under eutrophic and oligotrophic conditions. Some studies have investigated more than one type of habitat. Of the total species, 55 occurred in lentic ecosystems, 46 in wetlands, 36 in mangroves and 28 in lotic conditions,

with 14 species shared by all ecosystems. The number of species in lentic ecosystems and wetlands is a consequence of the number of studies (9) compared to lotic environments (5) and mangroves (4).

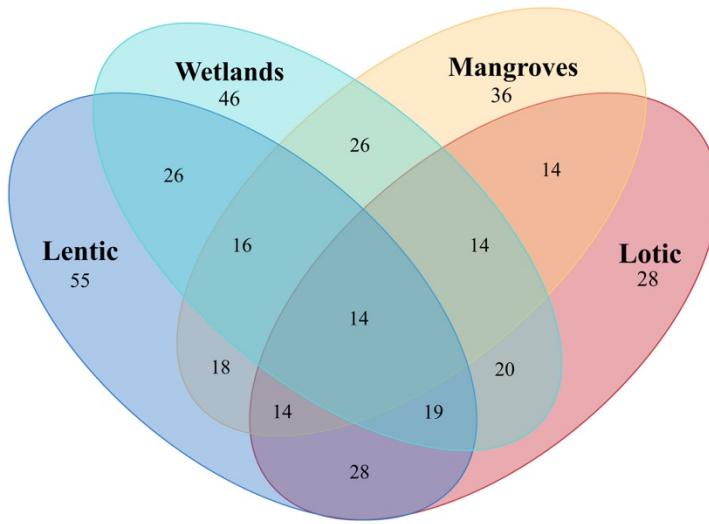


FIG. 1. Venn diagram of AMF richness in different aquatic habitats.

Lentic ecosystems (lakes, ponds, seasonal pools), especially oligotrophic, are identified as potential shelters for AMF diversity. Endomycorrhizal colonization can act as an important component for the survival and growth of aquatic macrophytes that face the low availability of soil nutrients (Moora et al. 2016).

Wetlands represent a generic term used to define a heterogeneous set of natural or artificial ecosystems (e.g. marshes, swamps, fens, peatlands, shallow open waters and other similar areas) that experience periodic or permanent flooding with a maximum depth of 6 meters at low tide (Ramsar 2013). Although considered stressful environments, present high plant biodiversity and have shown promise for AMF species, with high richness as well as positive colonization in many hydrophytes (Turner et al. 2000; Bohrer et al. 2004).

The low availability of phosphorus and nitrogen in the soil, and saline stress in mangroves suggests that the AMF symbioses can also be an important adaptation (Sengupta & Chauduri 2002). D'Souza & Rodrigues (2013) showed colonization in most hosts and high AMF richness (28 species), alerting to consider these ecosystems in mycorrhizal inventories.

Some species records evaluated have no specific information about habitats available in the original publications. We reiterate the need for characterization of habitats to better understand the occurrence of species in aquatic condition.

Acaulosporaceae, *Archaeosporaceae*, *Entrophosporaceae*, *Gigasporaceae*, and *Glomeraceae* were present in all conditions (FIG. 2A), such as the genera *Acaulospora*, *Archaeospora*, *Claroideoglomus*, *Funneliformis*, *Gigaspora*, *Glomus* and *Rhizoglomus* (FIG. 2B). However, the genera *Dentiscutata*, *Cetraspora*, *Simiglomus*, *Tricispora* and *Viscospora*, were restricted to the lentic condition.

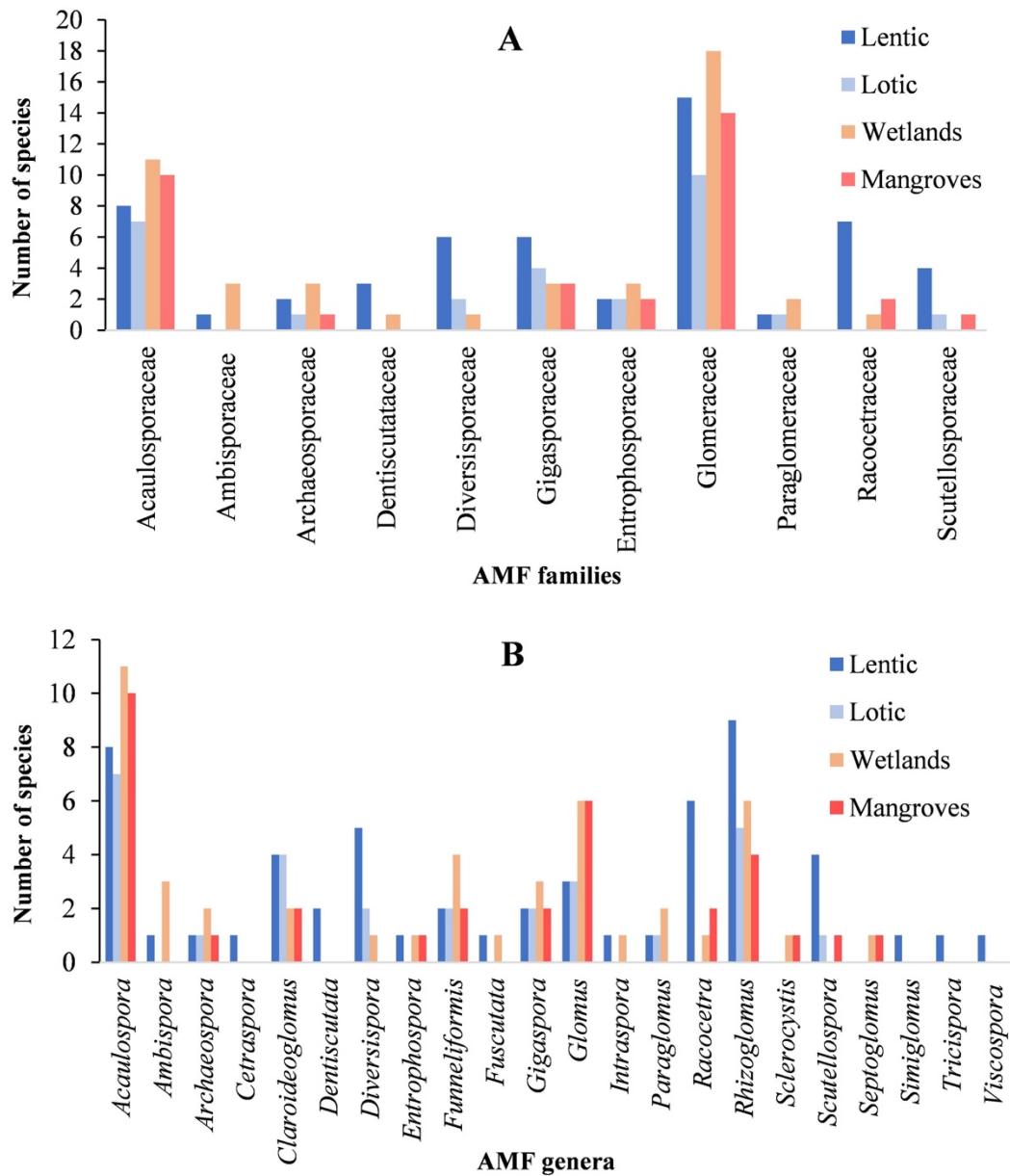


FIG. 2. AMF families (A) and genera (B) in different aquatic habitats.

AMF are able to tolerate different flood conditions, with several families and genera occurring in more than one condition. The 20 papers analyzed included eight countries only: Australia, Brazil, China, the United States, India, Mexico, Norway and Sweden (FIG. 3).

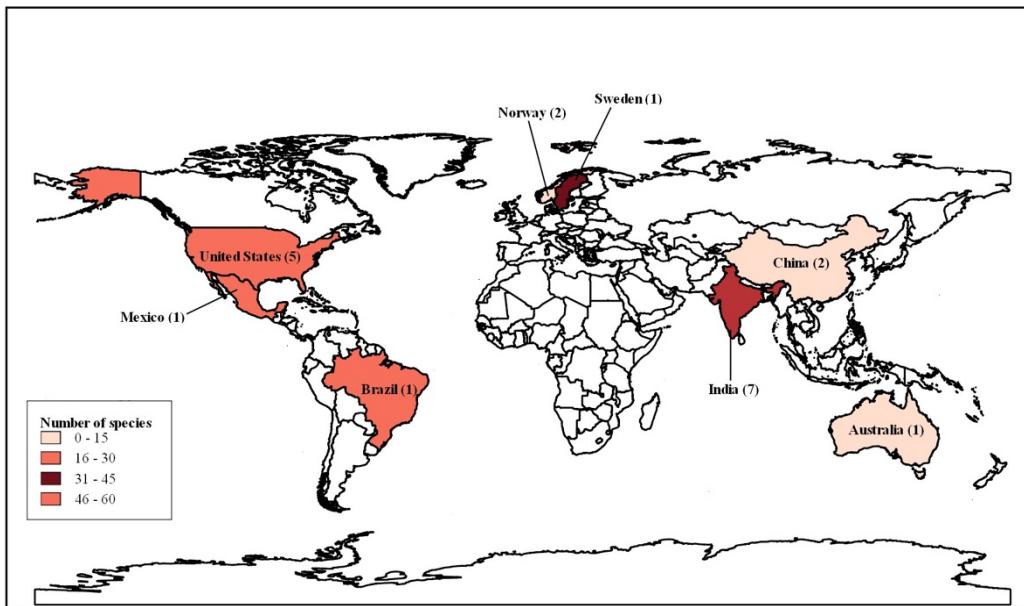


FIG. 3. Studies on occurrence and diversity of AMF in aquatic ecosystems reported for the world.

There is a notable difference in the number of AMF diversity inventories and countries studied when compared to terrestrial conditions, where these organisms are recorded on all continents (Davison et al. 2015). Differences in morpho-climatic domains can also be observed, since most of the countries belong to temperate areas. The United States is the most representative country with 45% of inventories. The tropical regions present studies conducted in three countries, Brazil, Mexico and India, the latter constituting 78% of papers.

In our analysis, we detected 59 species occurring in temperate regions, 54 species in tropical regions and 31 common to both climatic domains (FIG. 4). However, the numbers probably do not express the real occurrence of AMF in these regions because the numbers of studies, countries in which such studies were performed, and publications from these countries differ significantly, being highest in tropical areas.

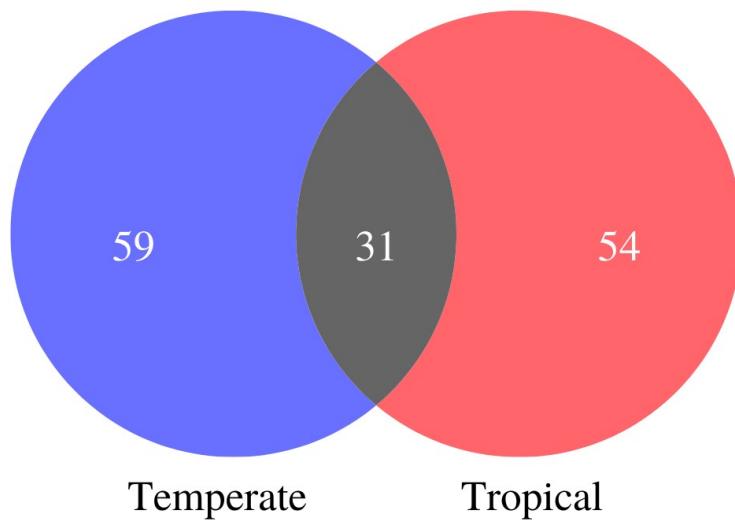


FIG. 4. Venn diagram of AMF species in temperate and tropical aquatic ecosystems around the world.

Most species were recorded for Sweden and India, 57 and 44, respectively. Also, most papers on the topic came from India, whereas only one came from Sweden. However, the Swedish records were based on molecular environmental studies (Moora et al. 2016), which allow finding AMF much faster, on a larger scale, and previously not described morphologically.

Acaulosporaceae (*Acaulospora*) and *Glomeraceae* (*Glomus*) are more representative in the tropic. *Diversisporaceae* and *Racocetraceae* predominated in the temperate condition (FIG. 5A), as such genera *Diversispora*, *Racocetra* and *Rhizoglonius*. Species of *Cetraspora*, *Dentiscutata*, *Simiglomus*, *Tricispore* and *Viscospora* were documented only in the temperate condition, while *Intraspora* and *Septoglonius* only in the tropical condition (FIG. 5B).

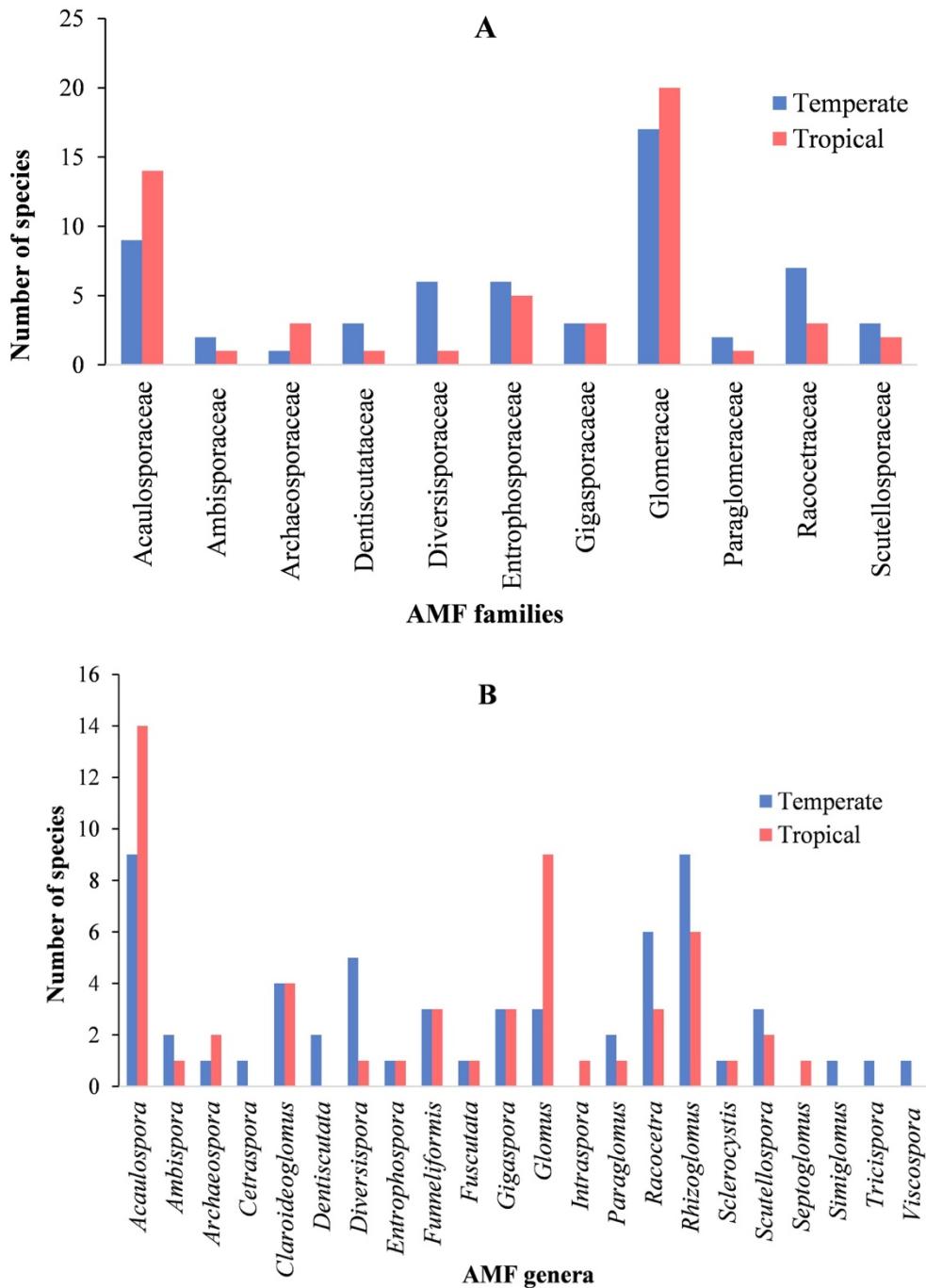


FIG. 5. AMF families (A) and genera (B) in temperate and tropical aquatic ecosystems.

All reported families, however, were present in temperate and tropical aquatic environments. Biogeographic analyzes have shown a high share of AMF taxa across the globe (Davison et al. 2015) and the majority of AMF families occurring in all climate zones (Stürmer et al. 2018).

Importantly, the difficulties in finding AMF in aquatic ecosystems certainly result from the low sporulation of these fungi due to low availability of O₂ (Turner & Friese 1998) and difficulties in collecting soil and root samples in such ecosystems (Shah 2014).

The data compiled in this paper significantly increase the knowledge about the global occurrence and distribution of AMF. The large number of aquatic macrophytes found to be colonized by AMF (Xu et al. 2016; Marins et al. 2017) and molecular sequences of many AMF species identified in environmental analyses performed in different regions of the world (Baar et al. 2011; Moora et al. 2016; Ortiz-Vera et al. 2018; Perkins et al. 2019) clearly demonstrate a high potential of these ecosystems to harbor a wide AMF diversity. To better recognize this diversity and its determinants, further studies in different regions of the world are needed, which will consider the occurrence, distribution, and sporulation of these fungi, depending on physical, chemical, and biological properties of the sampled sites.

Checklist of species

Archaeosporales

Ambisporaceae

Ambispora gerdemannii (S.L. Rose, B.A. Daniels & Trappe) C. Walker, Vestberg & A. Schüssler.

Mycological Research 111: 148. 2006.

≡ *Glomus gerdemannii* S.L. Rose, B.A. Daniels & Trappe. Mycotaxon 8: 297. 1979.

≡ *Appendicispora gerdemannii* (S.L. Rose, B.A. Daniels & Trappe) Spain, Oehl & Sieverd. Mycotaxon 97: 174. 2006.

≡ *Archaeospora gerdemannii* (S.L. Rose, B.A. Daniels & Trappe) J.B. Morton & D. Redecker. Mycologia 93: 186. 2001.

HABITAT: freshwater wetlands, United States (Miller & Bever 1999).

Ambispora leptoticha (N.C. Schenck & T.H. Nicolson) Walker, Vestberg & A. Schüssler.

Mycological Research 111: 148. 2006.

≡ *Glomus leptotichum* Schenck, N. C. & Smith, G. S. Mycologia 77: 4. 1982.

≡ *Archaeospora leptoticha* (N.C. Schenck & G.S. Sm.) J.B. Morton & D. Redecker. Mycologia 93: 184. 2001.

≡ *Pseudoglomus leptotichum* (N.C. Schenck & G.S. Sm.) S.P. Gautam & U.S. Patel. The Mycorrhizae: Diversity, Ecology and Applications 10. 2007.

≡ *Appendicispora leptoticha* (N.C. Schenck & G.S. Sm.) C. Walker, Vestberg & A. Schüssler. Mycological Research 111: 255. 2007.

HABITAT: freshwater wetlands, United States (Miller & Bever 1999).

Ambispora nicolsonii (C. Walker, L.E. Reed & F.E. Sanders) Oehl, G.A. Silva, B.T. Goto & Sieverd.

Mycotaxon 117: 431. 2012.

≡ *Acaulospora nicolsonii* C. Walker, L.E. Reed & F.E. Sanders, Transactions of the British Mycological Society 83: 360. 1984.

HABITAT: river–floodplain system, Brazil (Marins et al. 2009); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009).

Archaeosporaceae

Archaeospora myriocarpa (Spain, Sieverd. & N.C. Schenck) Oehl, G.A. Silva, B.T. Goto & Sieverd.

Mycotaxon 117: 430. 2011.

≡ *Acaulospora myriocarpa* Spain, Sieverd. & N.C. Schenck. Mycotaxon 25: 112. 1986.

HABITAT: mangrove and coastal wetland, India (Rodrigues & Anuradha 2009).

Archaeospora trappei (R.N. Ames & Linderman) J.B. Morton & D. Redecker.

Mycologia 93: 183. 2001.

≡ *Acaulospora trappei* R.N. Ames & Linderman, Mycotaxon 3: 566. 1976.

HABITAT: freshwater wetlands, United States (Miller & Bever 1999); riparian sites, United States (Kennedy et al. 2002); river–floodplain system, Brazil (Marins et al. 2009); oligotrophic lakes, Sweden (Moora et al. 2016).

Intraspora schenckii (Sieverd. & S. Toro) Oehl & Sieverd. Journal of Applied Botany 80: 77. 2006.

≡ *Entrophospora schenckii* Sieverd. & S. Toro. Proceedings of the 1st European Symposium on Mycorrhizae 1985: 624. 1986.

≡ *Entrophospora schenckii* Sieverd. & S. Toro. Mycotaxon 28: 210. 1987.

≡ *Archaeospora schenckii* (Sieverd. & S. Toro) C. Walker & A. Schüssler. The *Glomeromycota*: a species list with new families and new genera. 53. 2010.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990).

Diversisporales

Acaulosporaceae

Acaulospora bireticulata F.M. Rothwell & Trappe. Mycotaxon 8: 472. 1979.

HABITAT: mangroves, India (D'Souza & Rodrigues 2013).

Acaulospora colombiana (Spain & N.C. Schenck) Kaonongbua, J.B. Morton & Bever.

Mycologia 102: 1501. 2010.

≡ *Entrophospora colombiana* Spain & N.C. Schenck Mycologia 76: 693. 1984.

≡ *Kuklospora colombiana* (Spain & N.C. Schenck) Oehl & Sieverd., Journal of Applied Botany 80: 74. 2006.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); freshwater wetlands, United States (Miller & Bever 1999); river–floodplain system, Brazil (Marins et al. 2009); wetlands, México (Fabián et al. 2018).

Acaulospora delicata Walker, C.M. Pfeiff. & Bloss. Mycotaxon 25: 622. 1986.

HABITAT: riparian sites, United States (Kennedy et al. 2002); river–floodplain system, Brazil (Marins et al. 2009); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013).

Acaulospora dilatata J.B. Morton. Mycologia 78: 641. 1986.

HABITAT: mangrove and coastal wetland, India (Rodrigues & Anuradha 2009).

Acaulospora foveata Trappe & Janos. Mycotaxon 15: 516. 1982.

HABITAT: mangroves, India (D'Souza & Rodrigues 2013).

Acaulospora kentinensis C.G. Wu & Y.S. Liu ex Kaonongbua, J.B. Morton & Bever,

Mycologia 102: 1501. 2010.

≡ *Entrophospora kentinensis* C.G. Wu & Y.S. Liu, Mycotaxon 53: 287. 1995.

≡ *Kuklospora kentinensis* C.G. Wu & Y.S. Liu ex Oehl & Sieverd., Journal of Applied Botany 80: 74. 2006.

HABITAT: wetlands, México (Fabián et al. 2018).

Acaulospora koskei Błaszk. Mycological Research 99: 237. 1995.

HABITAT: freshwater wetlands, United States (Miller & Bever 1999).

Acaulospora laevis Gerd. & Trappe. Mycologia Memoirs 5: 33. 1974.

HABITAT: freshwater wetlands, United States (Miller & Bever 1999); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013); rivers and lakes, India (Seerangan & Thangavelu 2014); oligotrophic lakes, Sweden (Moora et al. 2016).

Acaulospora longula Spain & N.C. Schenck. Mycologia 76: 689. 1984.

HABITAT: river–floodplain system, Brazil (Marins et al. 2009); oligotrophic lakes, Sweden (Moora et al. 2016).

Acaulospora mellea Spain & N.C. Schenck. Mycologia 76: 689. 1984.

HABITAT: river estuary, India (Sengupta & Chaudhuri 2002); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013).

Acaulospora morrowiae Spain & N.C. Schenck. Mycologia 76: 692. 1984.

HABITAT: riparian sites, United States (Kennedy et al. 2002); river–floodplain system, Brazil (Marins et al. 2009); wetlands, México (Fabián et al. 2018).

Acaulospora rhemii Sieverd. & S. Toro. Angewandte Botanik 61: 219. 1987.

HABITAT: mangrove and coastal wetland, India (Rodrigues & Anuradha 2009).

Acaulospora rugosa J.B. Morton. Mycologia 78: 645. 1986.

HABITAT: river–floodplain system, Brazil (Marins et al. 2009); oligotrophic lakes, Sweden (Moora et al. 2016); lake, Norway (Pereira et al. 2016).

Acaulospora scrobiculata Trappe. Mycotaxon 6: 363. 1977.

HABITAT: riparian sites, United States (Kennedy et al. 2002); lakes and streams, China (Kai & Zhiwei 2006); river–floodplain system, Brazil (Marins et al. 2009); mangrove swamps, China (Wang et al. 2010); mangroves, India (D'Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Acaulospora spinosa C. Walker & Trappe, Mycotaxon 12: 515. 1981.

HABITAT: mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013).

Acaulospora tuberculata Janos & Trappe. Mycotaxon 15: 519. 1982.

HABITAT: lakes and streams, China (Kai & Zhiwei 2006).

Diversisporaceae

Diversispora aurantia (Błaszk., Blanke, Renker & Buscot) C. Walker & Schüssler.

The Glomeromycota: a species list with new families and new genera 43. 2010.

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

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Diversispora celata C. Walker, Gamper & A. Schüüssler. New Phytologist 182: 497. 2009.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Diversispora eburnea (L.J. Kenn., J.C. Stutz & J.B. Morton) C. Walker & Schüssler.

The Glomeromycota: a species list with new families and new genera 43. 2010.

≡ *Glomus eburneum* L.J. Kenn., J.C. Stutz & J.B. Morton. Mycologia 91: 1084. 1999.

HABITAT: riparian sites, United States (Kennedy et al. 2002); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Diversispora epigaea (B.A. Daniels & Trappe) C. Walker & A. Schüüssler.

The Glomeromycota: a species list with new families and new genera 43. 2010.

≡ *Glomus epigaeum* B.A. Daniels & Trappe, Canadian Journal of Botany 57: 540. 1979.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Diversispora spurca (C.M. Pfeifer, C. Walker & Bloss) C. Walker & Schüssler.

Mycological Research 108: 982. 2004.

≡ *Glomus spurcum* C.M. Pfeiff., C. Walker & Bloss. Mycotaxon 59: 374. 1996.

HABITAT: riparian sites, United States (Kennedy et al. 2002); oligotrophic lakes, Sweden (Moora et al. 2016).

Tricispora nevadensis (Palenzuela, Ferrol, Azcón-Aguilar & Oehl) Oehl, Palenzuela, G.A. Silva & Sieverd. Mycotaxon 117: 310. 2012.

≡ *Entrophospora nevadensis* Palenzuela, Ferrol, Azcón-Aguilar & Oehl. Mycologia 102: 627. 2009.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Glomerales

Entrophosporaceae

Claroideoglomus claroideum (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüssler.

The *Glomeromycota*: a species list with new families and new genera 21. 2010.

≡ *Glomus claroideum* N.C. Schenck & G.S. Sm. Mycologia 74: 84. 1982.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); freshwater wetlands, United States (Wetzel & van der Valk 1996); freshwater wetlands, United States (Miller & Bever 1999); riparian sites, United States (Kennedy et al. 2002); lakes and streams, China (Kai & Zhiwei 2006); marsh environment and aquatic habitats, India (Radhika & Rodrigues 2007); river–floodplain system, Brazil (Marins et al. 2009); mangrove and coastal wetland, India (Rodrigues & Anuradha, 2009); mangroves, India (D’Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Claroideoglomus etunicatum (W.N. Becker & Gerd.) C. Walker & A. Schüssler.

The *Glomeromycota*: a species list with new families and new genera 22. 2010.

≡ *Glomus etunicatum* W.N. Becker & Gerd. Mycotaxon 6: 29. 1977.

HABITAT: floating wetland, United States (Stenlund & Charvat 1994); freshwater lotic environment, United States (Miller & Bever 1999); riparian sites, United States (Kennedy et al. 2002); mangroves, India (D’Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Claroideoglomus lamellosum (Dalpé, Koske & Tews) C. Walker & A. Schüssler.

The *Glomeromycota*: a species list with new families and new genera 22. 2010.

≡ *Glomus lamellosum*. Dalpé, Koske & Tews. Mycotaxon 43: 289. 1992.

HABITAT: river–floodplain system, Brazil (Marins et al. 2009); oligotrophic lakes, Sweden (Moora et al. 2016).

Claroideoglomus luteum (L.J. Kenn., J.C. Stutz & J.B. Morton) C. Walker & A. Schüssler.

The *Glomeromycota*: a species list with new families and new genera 22. 2010.

≡ *Glomus luteum* L.J. Kenn., J.C. Stutz & J.B. Morton. Mycologia 91: 1090. 1999.

HABITAT: riparian sites, United States (Kennedy et al. 2002); river–floodplain system, Brazil (Marins et al. 2009); oligotrophic lakes, Sweden (Moora et al. 2016).

Entrophospora infrequens (I.R. Hall) R.N. Ames & R.W. Schneid. Mycotaxon 8: 348. 1979.

≡ *Glomus infrequens* I.R. Hall. Transactions of the British Mycological Society 68: 345. 1977.

HABITAT: mangroves, India (D’Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Viscospora viscosa (T.H. Nicolson) Sieverd., Oehl & G.A. Silva. Mycotaxon 116: 108. 2011.

≡ *Glomus viscosum* T.H. Nicolson, Mycological Research 99: 1502. 1995.

≡ *Septoglomus viscosum* (T.H. Nicolson) C. Walker, D. Redecker, D. Stiller & A. Schüssler: [10] (2013)

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Glomeraceae

Funneliformis caledonium T.H. Nicolson & Gerd.) C. Walker & A. Schüssler.

The *Glomeromycota*: a species list with new families and new genera: 13. 2010.

≡ *Endogone macrocarpa* var. *caledonia* T.H. Nicolson & Gerd. Mycologia 60: 322. (1968).

≡ *Glomus caledonium* (T.H. Nicolson & Gerd.) Trappe & Gerd. (1974).

HABITAT: floating wetland, United States (Stenlund & Charvat 1994).

Funneliformis geosporum (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler.

The *Glomeromycota*: a species list with new families and new genera 14: 2010.

≡ *Endogone macrocarpa* var. *geospora* T.H. Nicolson & Gerd. *Mycologia* 60: 318. 1968.

≡ *Glomus geosporum* (T.H. Nicolson & Gerd.) C. Walker. *Mycotaxon* 15: 56. 1982.

≡ *Glomus macrocarpum* var. *geosporum* (T.H. Nicolson & Gerd.) Gerd. & Trappe. *Mycologia Memoirs* 5: 55. 1974.

HABITAT: lakes and streams, China (Kai & Zhiwei 2006); mangrove and coastal wetland, India (Rodrigues & Anuradha, 2009); mangrove swamps, China (Wang et al. 2010); mangroves, India (D'Souza & Rodrigues 2013); wetlands, México (Fabián et al. 2018).

Funneliformis mosseae (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler.

The *Glomeromycota*: a species list with new families and new genera 13: 2010.

≡ *Endogone mosseae* T.H. Nicolson & Gerd. *Mycologia* 60: 314. 1968.

≡ *Glomus mosseae* (T.H. Nicolson & Gerd.) Gerd. & Trappe, *Mycologia Memoirs* 5: 40. 1974.

HABITAT: salt marsh, India (Sengupta & Chaudhuri 1990); lakes, lotic environments and shallow swamps, Australia (Khan 1993); riparian sites, United States (Kennedy et al. 2002); river estuary, India (Sengupta & Chaudhuri 2002); lakes and streams, China (Kai & Zhiwei 2006); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangrove swamps, China (Wang et al. 2010); mangroves, India (D'Souza & Rodrigues 2013).

Funneliformis verruculosum (Blaszk.) C. Walker & A. Schüßler,

The *Glomeromycota*: a species list with new families and new genera 14: 2010.

≡ *Glomus verruculosum* Blaszk., *Mycologia* 89: 809. 1997.

HABITAT: wetlands, México (Fabián et al. 2018).

Glomus ambisporum G.S. Sm. & N.C. Schenck. *Mycologia* 77: 566. 1985.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); rivers and lakes, India (Seerangan & Thangavelu 2014); wetlands, México (Fabián et al. 2018).

Glomus formosanum C.G. Wu & Z.C. Chen. *Taiwania* 31: 71. 1986.

HABITAT: mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013).

Glomus hyderabadensis Swarupa, Kunwar, G.S. Prasad & Manohar. *Mycotaxon* 89: 247. 2004.

HABITAT: mangroves, India (D'Souza & Rodrigues 2013).

Glomus macrocarpum Tul. & C. Tul. *Giornale Botanico Italiano* 2: 63. 1845.

≡ *Endogone macrocarpa* (Tul. & Tul.) Tul. & C. Tul. *Fungi Hypogaei: Histoire et Monographie des Champignons Hypogés* 20:1. 1851.

HABITAT: marsh and lagoon, United States (Liberta et al. 1983); salt marsh, India (Sengupta & Chaudhuri 1990); river estuary, India (Sengupta & Chaudhuri 2002); riparian sites, United States (Kennedy et al. 2002); river-floodplain system, Brazil (Marins et al. 2009); rivers and lakes, India (Seerangan & Thangavelu 2014); oligotrophic lakes, Sweden (Moora et al. 2016).

Glomus microcarpum Tul. & C. Tul. *Giornale Botanico Italiano* 2: 63. 1845.

≡ *Endogone microcarpa* (Tul. & Tul.) Tul. & C. Tul. *Fungi Hypogaei: Histoire et Monographie des Champignons Hypogés* 20: 2. 1851.

HABITAT: floating wetland, United States (Stenlund & Charvat 1994); wetlands, México (Fabián et al. 2018).

Glomus multicaule Gerd. & B.K. Bakshi. *Transactions of the British Mycological Society* 66: 340. 1976.

≡ *Glomus multicaulis* Gerd. & B.K. Bakshi (1976).

HABITAT: salt marsh, India (Sengupta & Chaudhuri 1990); river estuary, India (Sengupta & Chaudhuri 2002); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013).

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

HABITAT: mangroves, India (D'Souza & Rodrigues 2013).

Glomus pachycaule (C.G. Wu & Z.C. Chen) Sieverd. & Oehl. Mycotaxon 116: 99. 2011.

≡ *Sclerocystis pachycaulis* C.G. Wu & Z.C. Chen. Taiwania 31: 74. 1986.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990).

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

≡ *Sclerocystis rubiformis* Gerd. & Trappe. Mycologia Memoirs 5: 60. 1974.

≡ *Sclerocystis indica* Bhattacharjee & Mukerji. Acta Botanica Indica 8: 99. 1980.

HABITAT: lakes, lotic environments and shallow swamps, Australia (Khan 1993); lakes and streams, China (Kai & Zhiwei 2006); mangrove swamps, China (Wang et al. 2010); mangroves, India (D'Souza & Rodrigues 2013); wetlands, México (Fabián et al. 2018).

Rhizoglomus aggregatum (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl.

Mycotaxon 129: 378. 2015.

≡ *Glomus aggregatum* N.C. Schenck & G.S. Sm. Mycologia 74: 80. 1982.

≡ *Rhizophagus aggregatum* (N.C. Schenck & G.S. Sm.) C. Walker, Index Fungorum 286: 1. 2016.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); freshwater wetlands, United States (Wetzel & van der Valk 1996); lakes and streams, China (Kai & Zhiwei 2006); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013).

Rhizoglomus clarum (T.H. Nicolson & N.C. Schenck) Sieverd., G.A. Silva & Oehl.

Mycotaxon 129: 380. 2015.

≡ *Glomus clarum* T.H. Nicolson & N.C. Schenck. Mycologia 71: 182. 1979.

≡ *Rhizophagus clarum* (T.H. Nicolson & N.C. Schenck) C. Walker & A. Schüssler. The *Glomeromycota*: a species list with new genera families and new genera 19. 2010.

HABITAT: marsh and lagoon, United States (Liberta et al. 1983); freshwater wetlands, United States (Miller & Bever 1999); lakes and streams, China (Kai & Zhiwei 2006); mangroves, India (designed as *Glomus maculosum*) (D'Souza & Rodrigues 2013); wetlands, México (Fabián et al. 2018).

Rhizoglomus fasciculatum (Thaxt.) Sieverd., G.A. Silva & Oehl. Mycotaxon 129: 380. 2015.

≡ *Endogone fasciculata* Thaxt. Proceedings of the American Academy of Arts and Science 57: 308. 1922.

≡ *Glomus fasciculatum* (Thaxt.) Gerd. & Trappe. Mycologia Memoirs 5: 51. 1974.

≡ *Rhizophagus fasciculatum* (Thaxt.) C. Walker & A. Schüssler. The *Glomeromycota*: a species list with new families and new genera 19. 2010.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); salt marsh, India (Sengupta & Chaudhuri, 1990); lakes, lotic environments and shallow swamps, Australia (Khan 1993); river estuary, India (Sengupta & Chaudhuri 2002); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangroves, India (D'Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Rhizoglomus intraradices (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl.

Mycotaxon 129: 378. 2015.

≡ *Glomus intraradices* N.C. Schenck & G.S. Sm. Mycologia 74: 78. 1982.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); freshwater wetlands, United States (Wetzel & van der Valk 1996); riparian sites, United States (Kennedy et al. 2002); mangrove and coastal wetland, India (Rodrigues & Anuradha 2009); mangrove swamps, China (Wang et al. 2010); mangroves, India (D'Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Rhizoglomus invermaium (I.R. Hall) Sieverd., G.A. Silva & Oehl, Mycotaxon 129: 381. 2015.

≡ *Glomus invermaium* I.R. Hall, Transactions of the British Mycological Society 68: 345. 1977.

HABITAT: rivers and lakes, India (Seerangan & Thangavelu 2014).

Rhizoglomus irregularare (Błaszk., Wubet, Renker & Buscot) Sieverd., G.A. Silva & Oehl. Mycotaxon 129: 381. 2015.
 ≡ *Glomus irregularare* Błaszk., Wubet, Renker & Buscot, Mycotaxon 106: 252. 2009.
 ≡ *Rhizophagus irregularis* (Błaszk., Wubet, Renker & Buscot) C. Walker & A. Schüssler. The *Glomeromycota*: a species list with new families and new genera: 19. 2010.
 HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Rhizoglomus manihotis (R.H. Howeler, Sieverd. & N.C. Schenck) Sieverd., G.A. Silva & Oehl. Mycotaxon 129: 381. 2015.
 ≡ *Glomus manihotis* R.H. Howeler, Sieverd. & N.C. Schenck. Mycologia 76: 695. 1984.
 ≡ *Rhizophagus manihotis* (R.H. Howeler, Sieverd. & N.C. Schenck) C. Walker & A. Schüssler. The *Glomeromycota*: a species list with new families and new genera 19. 2010.
 HABITAT: freshwater wetlands, United States (Wetzel & van der Valk 1996).

Rhizoglomus melanum Sudová, Sykorová & Oehl. Mycological Progress 14: 5. 2015.
 HABITAT: freshwater lake, Norway (Sudová et al. 2015).

Rhizoglomus microaggregatum (Koske, Gemma & P.D. Olexia) Sieverd., G.A. Silva & Oehl, Mycotaxon 129: 381. 2015.
 ≡ *Glomus microaggregatum* Koske, Gemma & P.D. Olexia. Mycotaxon 26: 125. 1986.
 HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); riparian sites, United States (Kennedy et al. 2002); wetlands, México (Fabián et al. 2018).

Rhizoglomus vesiculiferum (Thaxt.) Błaszk., Kozłowska, Niezgoda, B.T. Goto & Dalpé, Nova Hedwigia 107: 509. 2018.
 ≡ *Endogone vesiculifera* Thaxt. Proceedings of the American Academy of Arts and Sciences 57: 309. 1922.
 ≡ *Glomus vesiculiferum* (Thaxt.) Gerd. & Trappe. Mycologia Memoirs 5: 49. 1974.
 ≡ *Funneliformis vesiculiferum* (Thaxt.) C. Walker & A. Schüssler. The *Glomeromycota*: a species list with new families and new genera 14. 2010.
 HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Sclerocystis sinuosa Gerd. & B.K. Bakshi, Transactions of the British Mycological Society 66: 343. 1976.
 ≡ *Glomus sinuosum* (Gerd. & B.K. Bakshi) R.T. Almeida & N.C. Schenck, Mycologia 82: 710. 1990.
 ≡ *Sclerocystis pakistanica* S.H. Iqbal & Perveen, Transactions of the Mycological Society of Japan 21: 59. 1980.
 HABITAT: wetlands, México (Fabián et al. 2018).

Sclerocystis taiwanensis C.G. Wu & Z.C. Chen. Transactions of the Mycological Society of the Republic of China 2: 78. 1987.
 ≡ *Glomus taiwanense* (C.G. Wu & Z.C. Chen) R.T. Almeida & N.C. Schenck ex Y.J. Yao. Kew Bulletin 50: 306. 1995.
 HABITAT: mangroves, India (D'Souza & Rodrigues 2013).

Septoglomus constrictum (Trappe) Sieverd., G.A. Silva & Oehl. Mycotaxon 116: 105. 2011.
 ≡ *Glomus constrictum* Trappe. Mycotaxon 6: 361. 1977.
 ≡ *Funneliformis constrictum* (Trappe) C. Walker & A. Schüssler. The *Glomeromycota*: a species list with new families and new genera 14. 2010.
 HABITAT: mangroves, India (D'Souza & Rodrigues 2013); wetlands, México (Fabián et al. 2018).

Simiglomus hoi (S.M. Berch & Trappe) G.A. Silva, Oehl & Sieverd. Mycotaxon 116: 104. 2011.
 ≡ *Glomus hoi* S.M. Berch & Trappe. Mycologia 77: 654. 1985.
 HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Gigasporales

Dentiscutataceae

Dentiscutata colliculosa B.T. Goto & Oehl. Nova Hedwigia 90: 385. 2010.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Dentiscutata reticulata (Koske, D.D. Miller & C. Walker) Sieverd., F.A. de Souza & Oehl.

Mycotaxon 106: 342. 2009.

≡ *Gigaspora reticulata* Koske, D.D. Mill. & C. Walker. Mycotaxon 16: 429. 1983.

≡ *Scutellospora reticulata* (Koske, D.D. Mill. & C. Walker) C. Walker & F.E. Sanders. Mycotaxon 27: 181. 1986.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Fuscotata heterogama Oehl, F.A. Souza, L.C. Maia & Sieverd., Mycotaxon 106: 344. 2009.

HABITAT: freshwater wetlands, United States (Miller & Bever 1999); oligotrophic lakes, Sweden (Moora et al. 2016); wetlands, México (Fabián et al. 2018).

Gigasporaceae

Gigaspora albida N.C. Schenck & G.S. Sm. Mycologia 74: 85. 1982.

HABITAT: freshwater wetlands, United States (Wetzel & van der Valk 1996); mangroves, India (D'Souza & Rodrigues 2013).

Gigaspora decipiens I.R. Hall & L.K. Abbott, Transactions of the British Mycological Society 83: 204. 1984.

HABITAT: wetlands, México (Fabián et al. 2018).

Gigaspora gigantea (T.H. Nicholson & Gerd.) Gerd. & Trappe. Mycologia Memoirs 5: 29. 1974.

≡ *Endogone gigantea* T.H. Nicolson & Gerd. Mycologia 60: 321. 1968.

HABITAT: lakes and streams, China (Kai & Zhiwei 2006).

Gigaspora margarita W.N. Becker & I.R. Hall. Mycotaxon 4: 155. 1976.

HABITAT: salt marsh, India (Sengupta & Chaudhuri, 1990); lakes, lotic environments and shallow swamps, Australia (Khan 1993); river estuary, India (Sengupta & Chaudhuri 2002).

Racocetraceae

Cetraspora gilmorei (Trappe & Gerd.) Oehl, F.A. de Souza & Sieverd. Mycotaxon 106: 338. 2009.

≡ *Gigaspora gilmorei* Trappe & Gerd. Mycologia Memoirs 5: 27. 1974.

≡ *Scutellospora gilmorei* (Trappe & Gerd.) C. Walker & F.E. Sanders. 1986.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Racocetra castanea (C. Walker) Oehl, F.A. de Souza & Sieverd. Mycotaxon 106: 336. 2009.

≡ *Scutellospora castanea* C. Walker. Cryptogamie Mycologie 14: 280. 1993.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Racocetra fulgida (Koske & C. Walker) Oehl, F.A. de Souza & Sieverd. Mycotaxon 106: 336. 2009.

≡ *Scutellospora fulgida* Koske & C. Walker. Mycotaxon 27: 221. 1986.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Racocetra gregaria (N.C. Schenck & T.H. Nicolson) Oehl, F.A. de Souza & Sieverd.

Mycotaxon 106: 337. 2009.

≡ *Gigaspora gregaria* N.C. Schenck & T.H. Nicolson. Mycologia 71: 185. 1979.

≡ *Scutellospora gregaria* (N.C. Schenck & T.H. Nicolson) C. Walker & F.E. Sanders. Mycotaxon 27: 181. 1986.

HABITAT: mangroves, India (D'Souza & Rodrigues 2013), oligotrophic lakes, Sweden (Moora et al. 2016).

Racocetra persica (Koske & C. Walker) Oehl, F.A. de Souza & Sieverd. Mycotaxon 106: 337. 2009.

≡ *Gigaspora persica* Koske & C. Walker. Mycologia 77: 708. 1985.

≡ *Scutellospora persica* (Koske & C. Walker) C. Walker & F.E. Sanders. Mycotaxon 27: 181. 1986.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Racocetra tropicana Oehl, B.T. Goto & G.A. Silva. Nova Hedwigia 92: 72. 2011.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Racocetra verrucosa (Koske & C. Walker) Oehl, F.A. de Souza & Sieverd. Mycotaxon 106: 337. 2009.

≡ *Gigaspora verrucosa* Koske & C. Walker. Mycologia 77: 705. 1985.

≡ *Scutellospora verrucosa* (Koske & C. Walker) C. Walker & F.E. Sanders. Mycotaxon 27: 181. 1986.

HABITAT: aquatic habitat, India (Radhika & Rodrigues 2007).

Racocetra weresubiae (Koske & C. Walker) Oehl, F.A. de Souza & Sieverd.

Mycotaxon 106: 337. 2009.

≡ *Scutellospora weresubiae* Koske & C. Walker. Mycotaxon 27: 224. 1986.

HABITAT: mangrove and coastal wetland, India (Rodrigues & Anuradha, 2009); mangroves, India (D'Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016).

Scutellosporaceae

Scutellospora aurigloba (I.R. Hall) C.Walker & F.E. Sanders. Mycotaxon 27: 180. 1986.

≡ *Gigaspora aurigloba* I.R. Hall. Transactions of the British Mycological Society 68: 35. 1977.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Scutellospora calospora (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders.

Mycotaxon 27: 180. 1986.

≡ *Endogone calospora* T.H. Nicolson & Gerd. Mycologia 60: 322. 1968.

≡ *Gigaspora calospora* (T.H. Nicolson & Gerd.) Gerd. & Trappe, Mycologia Memoirs 5: 28. 1974.

HABITAT: lakes and streams, China (Kai & Zhiwei 2006); oligotrophic lakes, Sweden (Moora et al. 2016).

Scutellospora dipapillosa (C. Walker & Koske) C. Walker & F.E. Sanders. Mycotaxon 27: 181. 1986.

≡ *Gigaspora dipapillosa* C. Walker & Koske, Mycologia 77: 709. 1985.

HABITAT: oligotrophic lakes, Sweden (Moora et al. 2016).

Scutellospora dipurpurescens J.B. Morton & Koske. Mycologia 80: 520. 1988.

HABITAT: mangroves, India (D'Souza & Rodrigues 2013); oligotrophic lakes, Sweden (Moora et al. 2016).

Paraglomerales

Paraglomeraceae

Paraglomus albidum (C. Walker & L.H. Rhodes) Oehl, F.A. Souza, G.A. Silva & Sieverd. Mycotaxon 116:

112. 2011.

≡ *Glomus albidum* C. Walker & L.H. Rhodes, Mycotaxon 12: 509. 1981.

HABITAT: floating wetland, United States (Stenlund & Charvat 1994).

Paraglomus occultum (C. Walker) J.B. Morton & D. Redecker. Mycologia 93: 190. 2001.

≡ *Glomus occultum* C. Walker, Mycotaxon 15: 50. 1982.

HABITAT: eutrophic lakes and wetland areas, India (Ragupathy et al. 1990); riparian sites, United States (Kennedy et al. 2002); wetlands, México (Fabián et al. 2018).

Acknowledgments

The authors thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for research grant awarded to BT Goto. We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the doctoral scholarship granted to K Jobim and Leroy JAS and to the Consejo Nacional de Ciencia y Tecnología (CONACYT-México) for the doctoral scholarship of XM Vista in Brazil. The authors greatly appreciate the scientific reviews by Janusz Błaszkowski (West Pomeranian University of Technology, Szczecin, Poland), Eduardo Furrazola Gómez (Institute of Ecology and Systematics, Cuba), and Danielle Karla Alves da Silva (Universidade Federal da Paraíba, Brazil).

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