

A history of the taxonomy and systematics of arbuscular mycorrhizal fungi belonging to the phylum Glomeromycota

Sidney Luiz Stürmer

Received: 24 August 2011 / Accepted: 14 February 2012 / Published online: 6 March 2012
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Abstract Arbuscular mycorrhizal fungi (AMF) are grouped in a monophyletic group, the phylum Glomeromycota. In this review, the history and complexity of the taxonomy and systematics of these obligate biotrophs is addressed by recognizing four periods. The initial discovery period (1845–1974) is characterized by description mainly of sporocarp-forming species and the proposal of a classification for these fungi. The following alpha taxonomy period (1975–1989) established a solid morphological basis for species identification and classification, resulting in a profuse description of new species and a need to standardize the nomenclature of spore subcellular structures. The cladistics period from 1990 to 2000 saw the first cladistic classification of AMF based on phenotypic characters only. At the end of this period, genetic characters played a role in defining taxa and elucidating evolutionary relationships within the group. The most recent phylogenetic synthesis period (2001 to present) started with the proposal of a new classification based on genetic characters using sequences of the multicopy rRNA genes.

Keywords Historical analysis · Discovery · Nomenclature · Species description · Alpha taxonomy

Introduction

The Glomeromycota, the fungal phylum that contains all known arbuscular mycorrhizal fungi (AMF), have co-

evolved with their hosts since plants conquered the terrestrial environment during the Ordovician Period more than 430 millions years ago (Simon et al. 1993; Redecker et al. 2000a). Evidences from the Rhynie Chert formation demonstrated that subterranean organs developed by fossil plants like *Aglaophyton* contained structures that resemble arbuscules formed by extant AMF species (Remy et al. 1994). Taylor et al. (1995) described a fossil species based on the morphology of structures resembling spores and mycelium from the early Devonian. Stubblefield et al. (1987) observed hyphae, vesicles, and spores in well-preserved roots from the Triassic resembling extant mycorrhizal structures. Later molecular data from Simon et al. (1993) corroborated these findings, setting the origin of AMF at a time between the Ordovician and the Devonian. Interestingly, the mycorrhizal (Gr. *mykes*=fungi+*rhiza*=roots) association appeared before plants had evolved true roots (Dotzler et al. 2009; Bonfante and Selosse 2010), in subterranean absorbing structures that were horizontal extensions of the aerial stem.

Considering the long evolutionary history of AMF and their seeming lack of host specificity (Bever et al. 1996; Helgason et al. 2007), it is not surprising that the mycorrhizal association is found in 80% of all vascular plant families (Brundrett 1991; Wang and Qiu 2006) and virtually all terrestrial ecosystems, including tropical to temperate forests, sand dunes, deserts, and grasslands as well agroecosystems (Brundrett 1991). AMF are considered to be obligate biotrophs in that they are unable to grow and complete their life cycle in the absence of an association with a living root (Smith and Read 2008), although spores of one AMF were reported to germinate, support mycelium growth, and produce new spores when grown with *Paenibacillus validus* in the absence of any plant host (Hildebrandt et al. 2002; Hildebrandt et al. 2006). In establishing mycorrhizal association with host roots, the somatic body of AMF differentiates discrete structures

Electronic supplementary material The online version of this article (doi:10.1007/s00572-012-0432-4) contains supplementary material, which is available to authorized users.

S. L. Stürmer (✉)
Departamento de Ciências Naturais,
Universidade Regional de Blumenau,
Cx.P. 1507, 89012-900, Blumenau, SC, Brazil
e-mail: sturmer@furb.br

(arbuscules, vesicles, auxiliary cells, internal/external mycelia) and asexual spores which contain most of the morphological diversity used to group disparate geographical populations into species (Morton 1990).

Taxonomy and systematics of the AMF, which have been the subject of intensive investigation, have experienced controversy and radical transformations in recent years. Schüßler and Walker (2011) recently discussed the history of AMF research in the context of evolution, taxonomy, and phylogeny of these asexual organisms. In the present review, the progress and complexity of taxonomy and systematics of the Glomeromycota are presented by defining and characterizing periods in a historical timeline frame in order to provide a concise reference for specialists and non-specialists to apprehend the changes that have happened and are happening in this area of arbuscular mycorrhizal research. Each period focuses on the taxonomic position of AMF within the kingdom Fungi and the proposal of classifications, the erection of new taxa, and aspects related to nomenclature of the morphological subcellular characters found in AMF spores. Also, the significant role of molecular biology in elucidating evolutionary relationships within the Glomeromycota and in proposing taxa is considered.

The discovery period (1845–1974)

During this initial period, much of the discovery and description of new species focused on sporocarp-forming species that could be recognized macroscopically. It is characterized by three main events: (1) the description of first species, especially those forming their spores in well-organized sporocarps, (2) the discovery of the link between large soil-borne spores and sporocarps with the formation of an arbuscular mycorrhizal association, and (3) the first classification of AMF. The time span of 130 years begins with erection of the genus *Glomus*, starting with the description of two species by the Tulasne brothers (Tulasne and Tulasne 1845) and ending with the classification published by Gerdemann and Trappe (1974).

In 1845, Tulasne and Tulasne published a brief description of the species *Glomus microcarpus* and *Glomus macrocarpus* in a manuscript written in Latin. The description of *G. macrocarpus* is rather uninformative as compared with recent species description:

Subamorphus, sordide griseus, peridio tenuissimo vel obsoleto; sporangiis crassissimis. Cum praecedente sed frequentior prope Parisios, Aestate Autumno

In this work, Tulasne and Tulasne (1845) considered the genus *Glomus* phylogenetically close to *Endogone*, a genus erected by Link in 1809 (Link 1809), because of the formation of sporocarps. Later, Tulasne and Tulasne (1851) transferred

both species of *Glomus* to *Endogone* because chlamydospores of the former were perceived to be similar to zygospores of the latter (Schüßler and Walker 2011). The genus *Sclerocystis* was proposed by Berkeley and Broome (1873) to encompass species forming spores in small sporocarps. Both genera were classified in the family Endogonaceae, order Mucorales. The family Endogonaceae was initially proposed by Fries in 1849 as pertaining to the Tuberales, but later further transferred to the Mucorales by Bucholtz in 1912 (cited in Koide and Mosse 2004). Interestingly, *Glomus* and *Sclerocystis* were described before the term “mycorrhiza” was coined by Frank in 1885.

One of the key publications during this period was the revision of the Endogonaceae by Thaxter (1922) to include the genera *Endogone*, *Glaziella*, *Sclerocystis*, and *Sphaeroceas*. Thaxter illustrated his work with drawings made under the dissecting and compound microscope of some chlamydospore-forming *Endogone* species which are currently placed in *Glomus*. Species forming chlamydospores and zygospores were included in a single genus based on the similarity of both types of spores. Thaxter (1922) also considered *Sclerocystis* as a valid genus within the Endogonaceae, as this genus had been synonymized with *Sphaeroceas* by von Höhnelt (1910).

Researchers then attempted to establish a link between sporocarps and a mycorrhizal association. Peyronel (1923) was the first to suggest that so called “vesicular–arbuscular mycorrhizae” were formed by fungi in the genus *Endogone*, which Butler in 1939 (cited in Koide and Mosse 2004) considered as probably representing anamorphic stages of members of the Endogonaceae. However, it was Mosse (1953) who first demonstrated that a sporocarpic *Endogone* species was attached to mycorrhizal strawberry roots and that adding these sporocarps to sterile soils with strawberry seedlings resulted in a typical mycorrhizal colonization. The fungal species was later described in her honor as *Endogone mosseae* (= *Glomus mosseae*, = *Funneliformis mosseae*). The use of the genus name *Endogone* was consistent with knowledge at the time, though it is completely inconsistent with current phylogenetic classification. For example, none of the spore types described by Mosse and Bowen (1968) would now be considered to be in *Endogone*. Some papers in this period referred to spores types by letter codes. For example, Gerdemann (1955) described spores of types A, B, and C, where type A clearly would have been placed in *Glomus* at the time, while type B referred to a species in a yet to be named family Gigasporaceae because of the presence of a bulbous base, and type C described auxiliary cells that were considered spores and also unique to species in Gigasporaceae.

During this period, the widely used method of wet sieving to extract sporocarps and non-sporocarpic spores from soils was developed by Gerdemann and Nicolson (1963), which led to an increase in taxonomic activity. This started with the

cooperation between Gerdemann and Nicolson and was continued by further cooperation between Gerdemann and Trappe, resulting in the classical publication by Gerdemann and Trappe in 1974. In a seminal paper entitled “The Endogonaceae in the Pacific Northwest”, the authors proposed a classification for fungal taxa including 30 species which form arbuscular mycorrhiza. They recognized *Glomus* as a valid genus distinct from *Endogone*, as previously proposed by the Tulasne brothers, and erected two new genera, *Acaulospora* and *Gigaspora*, which had also been shown to form arbuscular mycorrhizal associations. In this classification (Table 1), the genera *Glomus*, *Sclerocystis*, *Acaulospora*, and *Gigaspora* were placed in the family Endogonaceae, order Mucorales, phylum Zygomycota, together with *Endogone* and two other genera, *Glaziella* and *Modicella*, which were not known to form arbuscular mycorrhizal associations. Later, *Modicella* was transferred to the family Mortierellaceae by Trappe (1982) and *Glaziella* was transferred to the Ascomycota by Gibson et al. (1986). The classification by Gerdemann and Trappe (1974) was important for the taxonomy of these organisms, and it provided a sound basis for systematic knowledge during several years to follow.

The alpha taxonomy period (1975–1989)

This period contributed to the establishment of a solid morphological basis for identification and classification of glomeromycotan fungi. The 15 years are characterized by: (1) the proposal of several new genera and families, (2) a profuse description of new species, and (3) the proposal for standardization of phenotypic characters of AMF spores to describe new species.

New taxa forming arbuscular mycorrhizal associations were proposed based on living and fossil evidence. A new genus, *Entrophospora*, was erected by Ames and Schneider (1979) based on the observation that the formation of a “sacule” prior to spore development in the former *Glomus infrequens* was similar to that observed in *Acaulospora* species, but that its position was sufficiently different to merit the new genus, *Entrophospora*. Walker and Sanders (1986) differentiated between species of *Gigaspora* proposed by Gerdemann and Trappe (1974) based on whether spore germination occurred through a flexible “shield” on an inner flexible wall or directly through the spore wall, and they used the former character to define a new genus, *Scutellospora*. At the suprageneric level, Pirozynski and Dalpé (1989) proposed the family Glomeraceae (published as Glomaceae) to group the genera *Glomus* and *Sclerocystis*, because of the similarity between living spores of these genera and fossil spores.

During this period, a large number of new species were described (Fig. 1). Walker in the UK established an interest in this group of fungi, initially publishing with Trappe

(USA), but later also establishing cooperation with several other researchers, principally Koske (USA). After initial work with Nicolson (UK), Schenck (USA) also established a group describing new species, and partly stemming from work with Schenk, Spain and Sieverding published new species from their work in Colombia. Toward the end of this period, Blaszkowski (Poland) and Morton (USA) began to publish new species based on morphological characteristics. Only 12 years after the monograph by Gerdemann and Trappe (1974), the number of described glomeromycotan species had jumped to 77 (Trappe 1982), and 6 years later, Schenck and Perez (1988) listed 126 species. In parallel, different keys for AMF species identification developed, such as the synoptic key of Trappe (1982), the dichotomous key of Hall and Fish (1979), and Hall (1984), and keys for groups of species (e.g., Koske and Walker 1985). A significant step forward for those interested on AMF taxonomy and identification at the time was publication of the “Manual for the Identification of VA Mycorrhizal Fungi” (Schenck and Pérez 1988) which compiled all summary species descriptions. Although this manual has been controversial and is out of print, it is still being used in some laboratories as an aid to identify AMF species.

All descriptions during this time were based on morphological features of spores. Spore subcellular structures, which are diverse and largely accounted for most differences between species, lacked a standardized terminology which tended to impair attempts to identify species. In an effort to overcome this difficulty, Walker (1983) proposed a new terminology for the description of species based on the distinct types of “walls” formed by glomeromycotan spores and which can be grouped into “wall groups”. Wall types are identified solely by their phenotype in intact or broken spores and the wall groups represent aggregations of different wall types that are evident in most cases when a spore is broken. Walker also proposed a “murograph” that consists of a graphic representation to depict the different wall types and groups found in a spore. In the original article by Walker (1983), unit, laminated, evanescent and membranous walls are described. As new species were described, additional wall types were introduced: expanding (Berch and Koske 1986), amorphous (Morton 1986), coriaceous (Walker 1986), notched (Koske and Gemma 1995), and germinal (Spain et al. 1989). This terminology was criticized by Berch (1986) in her treatise on the Endogonaceae arguing that “wall layers” instead of “wall” used as differences among the wall types should be based on the knowledge of the origin of each structure. At that time, this argument had no solid experimental basis and was not accepted, although it pointed to the need of elucidating spore development to better define spore subcellular structures. The terminology proposed by Walker (1983) is still used in species description, although sometimes it is embedded within an ontogenetic framework, and this work represents one of the

Table 1 Proposals of classification of glomeromycotan fungi within the kingdom Fungi

Phylum	Class	Order	Family	Genera
Gerdemann and Trappe (1974)				
Zygomycota	Zygomycetes	Endogonales	Endogonaceae	<i>Glomus</i> <i>Sclerocystis</i> <i>Acaulospora</i> <i>Gigaspora</i>
Morton and Benny (1990)				
Zygomycota	Zygomycetes	Glomerales	Glomeraceae	<i>Glomus</i> <i>Sclerocystis</i>
			Acaulosporaceae	<i>Acaulospora</i> <i>Entrophospora</i>
			Gigasporaceae	<i>Gigaspora</i> <i>Scutellospora</i>
Schüßler et al. (2001)				
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	<i>Glomus</i>
		Diversisporales	Gigasporaceae	<i>Gigaspora</i> <i>Scutellospora</i>
			Acaulosporaceae	<i>Acaulospora</i> <i>Entrophospora</i>
			Diversisporaceae	<i>Diversispora</i>
		Paraglomerales	Paraglomeraceae	<i>Paraglomus</i>
		Archaeosporales	Archaeosporaceae	<i>Archaeospora</i>
			Geosiphonaceae	<i>Geosiphon</i>
Walker and Schüßler (2010)				
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	<i>Glomus</i> <i>Funneliformis</i> <i>Sclerocystis</i> <i>Rhizophagus</i>
		Diversisporales	Claroideoglomeraceae	<i>Claroideoglomus</i>
			Gigasporaceae	<i>Gigaspora</i> <i>Racocetra</i> <i>Scutellospora</i>
			Acaulosporaceae	<i>Acaulospora</i>
			Entrophosporaceae	<i>Entrophospora</i>
			Pacisporaceae	<i>Pacispora</i>
			Diversisporaceae	<i>Diversispora</i> <i>Otopora</i> <i>Redeckera</i>
		Paraglomerales	Paraglomeraceae	<i>Paraglomus</i>
		Archaeosporales	Archaeosporaceae	<i>Archaeospora</i>
			Ambisporaceae	<i>Ambispora</i>
			Geosiphonaceae	<i>Geosiphon</i>
Oehl et al. (2011a)				
Glomeromycota	Glomeromycetes	Glomerales	Glomeraceae	<i>Glomus</i> <i>Funneliformis</i> <i>Simiglomus</i> <i>Septoglomus</i>
			Claroideoglomeraceae	<i>Claroideoglomus</i> <i>Viscospora</i>
		Diversisporales	Diversisporaceae	<i>Diversispora</i>

Table 1 (continued)

Phylum	Class	Order	Family	Genera
				<i>Redeckera</i>
				<i>Otospora</i>
			Entrophosporaceae	<i>Entrophospora</i>
			Acaulosporaceae	<i>Acaulospora</i>
				<i>Kuklospora</i>
			Pacisporaceae	<i>Pacispora</i>
		Gigasporales	Gigasporaceae	<i>Gigaspora</i>
			Scutellosporaceae	<i>Scutellospora</i>
				<i>Orbispora</i>
			Racocetraceae	<i>Racocetra</i>
				<i>Cetraspera</i>
			Dentiscutataceae	<i>Dentiscutata</i>
				<i>Fuscutata</i>
				<i>Quatunica</i>
	Archaeosporomycetes	Archaeosporales	Archaeosporaceae	<i>Archaeospora</i>
				<i>Intraspora</i>
			Ambisporaceae	<i>Ambispora</i>
			Geosiphonaceae	<i>Geosiphon</i>
	Paraglomeromycetes	Paraglomerales	Paraglomeraceae	<i>Paraglomus</i>

most important advances for the taxonomy of glomeromycotan fungi in this period. Towards the end of this period, Morton (1988) critically evaluated all morphological criteria used to classify and identify AMF species and suggested some approaches to clarify taxonomy concepts.

The cladistics period (1990–2000)

This period is marked by a new classification and the entry of molecular biology into systematics of glomeromycotan

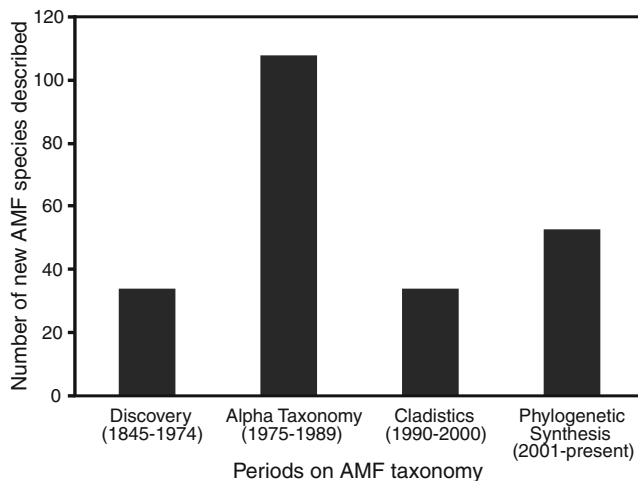


Fig. 1 Number of new species of Glomeromycota described in each period

fungi. It is characterized mainly by: (1) proposal of a cladistic classification for AMF based on phenotypic characters, (2) description of new taxa based on fossil records, (3) proposal of a spore development model with re-evaluation of terminology for spore subcellular characters, and (4) use of genetic characters to define taxa and elucidate evolutionary relationships.

One of the important landmarks in these 11 years was the first cladistic analysis of glomeromycotan fungi and the proposal of a new classification. Morton (1990) analyzed 57 AMF species using 27 phenotypic characters of spores and mycorrhiza and hypothesized that glomeromycotan fungi comprised a monophyletic group defined by the establishment of a mutualistic symbiosis with plant roots and the formation of intraradical arbuscules. He also proposed two main clades, one consisting of *Gigaspora* and *Scutellospora* species and the other harboring *Glomus*, *Sclerocystis*, *Acaulospora*, and *Entrophospora*. This cladistic analysis, together with additional information from spore ontogeny and mode of spore germination, formed the basis for a radical change in classification (Morton and Benny 1990) (Table 1). Genera of AMF were removed from the order Endogonales and placed in the newly erected order Glomerales (published as Glomales) in the families Glomeraceae (*Glomus* and *Sclerocystis*), Acaulosporaceae (*Acaulospora* and *Entrophospora*), and Gigasporaceae (*Gigaspora* and *Scutellospora*). Glomeraceae and Acaulosporaceae were hypothesized to be closely related and placed in the sub-order Glomineae and the family Gigasporaceae in the sub-order Gigasporineae. This was the first

new classification proposed since Gerdemann and Trappe (1974) had considered that AMF should remain in the phylum Zygomycota some 25 years earlier. Although one of the authors considered that AMF have evolved independently from zygomycetes (see discussion in Morton 2000), phenotypic characters were not homologous between the two groups, and so, there was no concrete evidence to place AMF in a separate phylum. This classification established an important and theoretical framework for future hypotheses to be tested concerning the biology of the fungal species or other aspects of the mycorrhizal symbiosis.

The classification by Morton and Benny (1990) was first contested by Walker (1992), who suggested that *Glomus* was possibly polyphyletic, and by Simon et al. (1993) regarding the phylogenetic relationships among the three families within the order Glomerales (see below). Later in this period, Morton (2000) also questioned the monophyly of the entire order Glomerales. Considering several aspects of the AMF life cycle, he proposed that the arbuscular mycorrhizal symbiosis had arisen during two distinct periods rendering the order Glomerales polyphyletic: Glomineae and Gigasporineae would represent two evolutionary branches. Evidence to support this hypothesis is related to the mode of spore formation (Franke and Morton 1994), morphology of fungal mycelium (Brundrett and Kendrick 1990), types of infective propagules (Biermann and Linderman 1983; Jasper et al. 1989), and cell wall composition (Gianinazzi-Pearson et al. 1994).

The classifications of Gerdemann and Trappe (1974) and Morton and Benny (1990) did not state clearly into which class the AMF species should be included: Endogonales in the former and Glomerales in the latter were left in the class Zygomycetes. Cavalier-Smith (1998) later proposed that fungal species establishing (vesicular)–arbuscular mycorrhizas with plants could be grouped in a new class, the Glomomycetes, within a new phylum, Archemycota.

Analysis of extant species of AMF and the examination of fossil records led to the proposition of new taxa and the transfer of species to other genera. Taylor et al. (1995) proposed the genus *Glomites* and described *Glomites rhytiensis* from aerial stems and rhizomes of the 400-million-year-old fossil Devonian plant *Aglaophyton major*, based on extraradical and intraradical hyphae, chlamydospore-resembling spores, and arbuscule-resembling structures in the fossil plant. Phipps and Taylor (1996) proposed the genus *Gigasporites* and the species *Gigasporites myriamyces* and *Glomites cycestris* from the Triassic plant *Antarcticycas* from a siliceous chert. *Glomites* and *Gigasporites* were hypothesized to be related to the extant genera *Glomus* and *Gigaspora*, respectively. The number of new species described in this “cladistics period” totaled one third of that described in the previous “alpha-taxonomy” period (Fig. 1).

The wall terminology previously proposed by Walker (1983), and complemented by other authors, was useful to standardize the description of new AMF species. However, definition of the distinct wall types was strictly typological, and it needed to be changed to accommodate new variations when new species were described or new wall types had to be proposed. Furthermore, no connection was established between the wall types proposed and a biological process. Considering these aspects, a research program to elucidate AMF spore ontogeny was launched by Morton and co-workers. Results of these studies were a spore developmental model and reinterpretation of phenotypic characters of spores (Morton et al. 1995). The model depicts that the phenotypic characters of spores are hierarchically organized (primary, secondary, and tertiary characters) with primary characters being defined by the spore wall, germinal walls (=inner flexible walls), and germination structure and species-level variation being mostly confined to variation in spore wall layers (Morton et al. 1995). Spore development was elucidated for a few species of *Scutellospora* (Franke and Morton 1994; Morton 1995), of *Gigaspora* (Bentivenga and Morton 1995), of *Glomus* (Morton 1996; Stürmer and Morton 1997), and of *Acaulospora*, as well as for the species *Entrophospora colombiana* (Stürmer and Morton 1999), now considered to be a member of the genus *Acaulospora* (Kaonongbua et al. 2010). In the arena of spore wall structure terminology, Walker and Vestberg (1998) used the term “component” to describe the elements of wall structure and retained the term “wall group” to identify an assemblage of these components that separate in slide-mounted crushed spores.

Particular attention was paid to the sporocarpic genus *Sclerocystis* during this period. Almeida and Schenck (1990) first transferred all species of *Sclerocystis* except *Sclerocystis coremioides* to the genus *Glomus*. However, Wu (1993) disagreed and argued in favor of the maintenance of the genus *Sclerocystis* based on spore arrangement and mode of sporocarp formation. Later, Redecker et al. (2000b) used small subunit rRNA (SSU) gene sequencing to demonstrate that *S. coremioides* and *Glomus sinuosum* form a clade that is phylogenetically close to other species of *Glomus*, such as *Glomus intraradices* and *Glomus vesiculiferum*. As a consequence, the last species of *Sclerocystis* was transferred to *Glomus*.

In fact, one of the main events during these 11 years was the use of SSU gene sequences to elucidate evolutionary relationships among taxa within the order Glomerales. Simon et al. (1993) first demonstrated the ancient origin of AMF based on a molecular clock approach measuring the rate of SSU gene evolution calibrated against the fossil record. A family-level molecular phylogeny also hypothesized that the Acaulosporaceae family was closely related to Gigasporaceae and not a sister group of the Glomeraceae as hypothesized by the morphologically based cladistic analysis of Morton

(1990). This period ends with the identification of two ancestral clades based on rDNA sequences (Redecker et al. 2000c). This analysis showed that some species included in the genus *Acaulospora*, such as *Acaulospora trapei* and *Acaulospora gerdemannii*, and in *Glomus*, including *Glomus occultum* and *Glomus brasilianum*, were positioned outside the families Acaulosporaceae and Glomeraceae and diverged early in the evolution of what were then still known as the Glomerales.

The phylogenetic synthesis period (2001 to present)

This ultimate period is characterized by: (1) the proposal of a new classification based solely on genetic characters (SSU rRNA gene), (2) description of new taxa based on the fossil record, and (3) the creation of new taxa and a new classification based on a combination of phenotypic and genetic characters.

Morton and Redecker in 2001 proposed new taxa, based on the congruence of phenotypic and genetic traits, to harbor species corresponding to the ancestral clades identified by Redecker et al. (2000c). Mycorrhizal morphology combined with rDNA sequences, fatty acid profiles, and immunological reactions provided the basis for recognition of two families and two genera: the genus *Archaeospora* in the family Archaeosporaceae including species forming monomorphic spores (acaulosporoid) or dimorphic spores (acaulosporoid and glomoid), and the genus *Paraglomus* in the family Paraglomeraceae encompassing species forming glomoid spores indistinguishable from those formed in *Glomus*. Mycorrhizal structures formed by either genus stain weakly or sometimes not at all in trypan blue and they share the fatty acid C16:1 ω 7 cis. Schwarzott et al. (2001) provided a phylogenetic analysis based on the nearly full-length SSU rRNA gene sequences from 30 isolates of *Glomus* species. Their results indicated that *Glomus* is not monophyletic but can be separated into three clades, two of which are phylogenetically distant enough to warrant a family level distinction (*Glomus* group A and B—although no formal classification was proposed at the family level) and one of which is closely related to the families Acaulosporaceae and Gigasporaceae. This phylogeny conflicts topologically with that erected by Morton and Benny in 1990.

The most important event in this period has been the naming by Schüßler et al. (2001) of a new phylum within the kingdom Fungi to group all AMF species, along with a little-known fungus, *Geosiphon pyriforme* that forms a symbiosis with *Nostoc* (Schüßler and Kluge 2001). The proposed phylum Glomeromycota is based on a phylogenetic analysis of SSU rRNA gene sequences. With this classification, AMF were removed from the polyphyletic phylum Zygomycota and placed in their own phylum that is

hypothesized to share a common ancestry with the phyla Ascomycota and Basidiomycota. Four new orders (Paraglomerales, Archaeosporales, Diversisporales, and Glomerales) and new families were proposed (Table 1). Within the kingdom Fungi, asexual spores have a vast number of names and the term “glomerospores” was coined by Goto and Maia (2006) to denominate spores formed by fungi in the Glomeromycota. The term applies to different kinds of asexual spores produced by these fungi (acaulosporoid, glomoid, and gigasporoid spores), and these types are probably not homologous (Krüger et al. 2011a).

After the new classification by Schüßler et al. (2001), the last 10 years have been characterized by descriptions and proposals of new families and genera for both ancient and extant AMF, with some of the taxa proposed still in debate among taxonomists. Redecker et al. (2002) erected the genus *Palaeoglomus* from fossil records and described the species *Palaeoglomus grayi* from the Ordovician based on the morphology of hyphae and spores. The presence of germination shields in fossil glomeromycotan spores suggests that diversification within the Glomeromycota occurred before the Early Devonian. Dotzler et al. (2006) reported for the first time the existence of a germination shield in glomeromycotan spores from the Lower Devonian Rhynie chert (at least 400 million years old). These authors erected the genus *Scutellosporites* within the family Gigasporaceae and described the species *Scutellosporites devonicus* based on the presence of a round or oval germination shield in fossil spores. Fossil acaulosporoid spores later described by Dotzler et al. (2009) had a plate-like to tongue-shaped germination shield and clearly formed laterally at the neck of a sporiferous saccule, suggesting a relationship with extant genera such as *Acaulospora*, *Archaeospora*, *Ambispora*, or *Otopora*.

Some species that were originally placed in *Glomus* (e.g., *Glomus scintillans*, *Glomus chimonobambusae*, and *Glomus dominikii*) were transferred to two new genera based on the fact that type species differentiate an inner wall composed of three layers, suggesting that they are distinct enough to be in a different genus. Oehl and Sieverding (2004) erected *Pacispora* while Walker et al. (2004) proposed *Gerdemannia* to contain these species. Following the principle of priority laid down in the International Code of Botanical Nomenclature, the genus *Pacispora* is current and has priority because the hard copy paper describing *Pacispora* was published before that describing *Gerdemannia*.

In 2006, Sieverding and Oehl revised all five species of *Entrophospora* and erected the genera *Kuklospora* and *Intraspora*. The authors recognized only the type species *Entrophospora infrequens* and *Entrophospora baltica* as belonging in *Entrophospora* and placed these species in the newly erected family Entrophosporaceae. *Kuklospora* included the species *Kuklospora colombiana* and

Kuklospora kentinensis, both of which share a spore subcellular organization with some members of the genus *Acaulospora* (presence of two germinal walls formed by two layers with a beaded layer in the second germinal wall). Finally, *Intraspora* was created as a monospecific genus containing *Intraspora schenckii* characterized by a spore wall with three hyaline layers and the absence of germinal walls. On the same occasion, they proposed a new terminology for spore wall structures (outer spore wall, middle wall, inner wall), adapted from INVAM and Stürmer and Morton (1999). Walker et al. (2007) emended the family Archaeosporaceae and included *Intraspora* in this family. *Intraspora schenckii* and *Archaeospora trappei* are very similar morphologically and differ only in the position that the spore is formed in the saccule neck. Kaonongbua et al. (2010) synonymized *Kuklospora* with *Acaulospora*, considering that the entrophosporoid mode of spore formation evolved several times, and therefore it is a convergent character. These authors then transferred the species *K. colombiana* and *K. kentinensis* to *Acaulospora*.

Among the glomeromycotan fungi, *Archaeospora* is possibly the genus with the most complicated history from a nomenclature standpoint, mainly due to the dimorphic nature of member species which form acaulosporoid and glomoid spores in the same fungal mycelium. Acaulosporoid morphotypes of this genus were originally included in *Acaulospora* (e.g., *Acaulospora appendicula*) while glomoid morphotypes were described as *Glomus* (e.g., *Glomus leptotichum*). Morton et al. (1997) synonymized *A. appendicula* with *A. gerdemannii*, and *Glomus fecundisporum* with *G. leptotichum* and provided strong evidence from living cultures that *A. gerdemannii* and *G. leptotichum* are synanamorphs (two anamorphic states of the same organism). Morton and Redecker (2001) then transferred these dimorphic species to *Archaeospora* together with *A. trappei*. In a subsequent revision of the genus *Archaeospora*, Spain et al. (2006) observed that most species in this genus share some characters, like spore wall structure, mycorrhizal morphology, and spore formation on an appendix formed laterally from the neck of a sporiferous saccule that differed from *A. trappei*. As a result, the authors proposed the genus *Appendicispora* to include *Appendicispora appendicula*, *Appendicispora gerdemannii*, and *Appendicispora jimgerdemannii*, retaining the genus *Archaeospora* as a monospecific genus containing *Archaeospora trappei*. Walker et al. (2007), examining the same group of organisms named *Appendicispora* by Spain et al. (2006), proposed the genus *Ambispora* and the family Ambisporaceae. Later, Walker (2008) pointed out that the name *Appendicispora* was not valid for AMF as it is an illegitimate homonym of a fungus in the Xylariaceae (based on the Art. 53.3 of the International Code), rendering the genus *Ambispora* as that valid to contain the above group of AMF species.

A more radical expansion of genera and families in the Glomeromycota was proposed by Oehl et al. (2008) based on interpretation of the previous works of Walker et al. (2004), de Souza et al. (2005), Ahlu et al. (2006), and Redecker et al. (2007). Oehl et al. (2008) viewed the genus *Scutellospora* to be polyphyletic based on selective characters associated with the germination shield and combined tree of partial SSU and partial LSU rRNA gene. They subsequently reorganized *Scutellospora sensu lato* into three new families and five new genera, erecting the families Scutellosporaceae for *Scutellospora*, Racocetraceae for *Racocetra* and *Cetraspora*, and Dentiscutataceae for *Dentiscutata*, *Fuscutata*, and *Quatunica*. The emphasis on the morphology of the germination shield to delimit genera had some operational as well as theoretical difficulties. From a practical standpoint, identification of a species in these genera requires presence of a differentiated and visible shield, which is not a common occurrence for some species, and germination shield types are shared by various genera proposed. This proposal to reorganize *Scutellospora* was contested by Morton and Msiska (2010), who carried out a phylogenetic analysis based on morphological and molecular characters for 71% and 35% of *Scutellospora* species, respectively. Results from this more thorough analysis suggested that only the genus *Racocetra* could be supported. However, some clades proposed by Oehl et al. (2008) based on 25S rDNA sequences do appear in the tree of concatenated sequences of 25S rRNA and β -tubulin published by Morton and Msiska (2010), but with low bootstrap support probably due to taxa undersampling. Palenzuela et al. (2008) proposed the genus *Otospora* for an organism with a similar mode of spore formation as *Acaulospora*, although SSU sequence data groups it closely to *Diversispora*.

In the past 2 years, two distinct classifications have been further proposed for the Glomeromycota (Table 1), both of which are characterized by a rearrangement of the genus *Glomus sensu lato* shown previously to be polyphyletic by Schwarzott et al. (2001). Schüßler and Walker (2010) performed a phylogenetic analysis of glomeromycotan fungi, based on near-full-length SSU rRNA gene sequences and proposed a new family and three new genera. They separated *Glomus* into the genera *Funneliformis*, *Sclerocystis*, and *Rhizophagus* in the family Glomeraceae with the remaining species of *Glomus* and *Claroideoglomus* in the family Claroideoglomeraceae. *Rhizophagus* was first proposed by Dangeard (1900) and synonymized with *Glomus* by Gerdemann and Trappe (1974). Inspection of the protologue of *Rhizophagus populinus* revealed that this fungus is an AMF species, and it was resurrected by Schüßler and Walker (2010) to harbor AMF species that form large numbers of spores in the roots. They also erected the genus *Redeckera* in the Diversisporaceae to harbor a clade formed by three sporocarpic species (*Redeckera megalocarpum*, *Redeckera pulvinatum*, and *Redeckera fulvum*) based on the

analysis of 18S and 5.8S rDNA subunits and the ITS regions 1 and 2. Schüßler and Walker (2010) recognize that their phylogeny is incomplete because no living material is available for molecular analyses of many previously described glomeromycotan species. Therefore, some species were retained in their original genus but referred to as “species of uncertain position.” In this classification, some taxa have been defined based on characteristics that are not proved to be stable and therefore not phylogenetic informative. For example, *Rhizophagus* is characterized by abundant spore formation in roots, despite sporulation rates being influenced by host (Bever et al. 1996), seasonal periodicity (Gemma and Koske 1988), and nutrient regimes (Douds and Schenck 1990). Oehl et al. (2011a) proposed a rearrangement of species in the genus *Glomus sensu lato* and erected the genera *Simiglomus* and *Septoglomus* in the Glomeraceae, and *Viscospora* in the Claroideoglomeraceae, and transferred back to *Glomus* all species of *Sclerocystis* and *Rhizophagus* as proposed by Schüßler and Walker (2010) (Table 1). Their classification was based on combined genetic (partial sequences of β -tubulin, and SSU and LSU rRNA) and phenotypic (traits associated with subtending hypha, e.g., color, shape and thickness, pore closure) characters, although some of the phenotypic characters used are found across several of their proposed genera. Some of the genera rejected by Kaonongbua et al. (2010) and Morton and Msiska (2010) were still considered current by Oehl et al. (2011a) and are included in their classification scheme.

New classes and orders have been proposed by Oehl et al. (2011b) at higher levels of the taxonomic hierarchy in the phylum Glomeromycota. These authors erected the classes Archaeosporomycetes and Paraglomeromycetes to contain the orders Archaeosporales and Paraglomerales, respectively. They also proposed the order Gigasporales to be placed within the class Glomeromycetes. In the same year, new genera and families were proposed by Oehl and co-workers. *Scutellospora pernambucana* and *S. projecturata* were transferred to the newly erected genus *Orbispora*, hypothesized to be ancestral to species of glomeromycotan fungi forming spores with a bulbous base (Oehl et al. 2011c). In the same period, *Entrophospora* was found to be non-monophyletic and *E. infrequens* to be closely related to *Claroideoglomus* species, based on ribosomal gene analyses (Oehl et al. 2011d). These authors then transferred the family Entrophosporaceae from the order Diversisporales to the Glomerales, synonymized Entrophosporaceae with Claroideoglomeraceae, and proposed the new genus *Albahypha*. In the same paper, they erected the monospecific genera *Tricispora* (= *Entrophospora nevadensis*) within the family Diversisporaceae and *Sacculospora* (= *Sacculospora baltica*) within a newly proposed family Sacculosporaceae.

Krüger et al. (2011b) recognized that phylotaxonomically reliable sequence data were limited or absent for most

glomeromycotan species and provided a reference data set for further molecular systematic studies and analysis of environmental sequences. They provided phylogenetic trees based on three rDNA markers (ribosomal SSU, LSU, and ITS) from 109 named AMF species and 27 cultures representing non-described species. Their SSU full-5.8S-LSU phylogeny of 35 species is congruent with previously published rDNA trees and supports the monophyly of Glomeromycota, with Paraglomerales and Archaeosporales as basal lineages within the phylum. An SSU phylogeny from available sequences of 76 species shows a 100% bootstrap support for Gigasporaceae and Acaulosporaceae, the former being a sister group with Pacisporaceae, as well as the families Glomeraceae and Claroideoglomeraceae. Finally, an SSU-ITS-LSU phylogeny is provided for all four orders in the Glomeromycota, with important implications for the systematics of the group: (a) Paraglomerales represents the most ancient lineage within the phylum, (b) Entrophosporaceae is a phylogenetically undefined family, (c) *Intraspora* is congeneric with *Archaeospora*, (d) some genera proposed by Oehl et al. (2008) and rejected by Morton and Msiska (2010) are supported, (e) the transfer of *Kuklospora* species to *Acaulospora* is supported, and (f) *Glomus* is polyphyletic and currently comprises several genera. Most important, Krüger et al. (2011b) established a solid phylogenetic backbone based on rDNA sequences that can be used in new species descriptions.

Conclusions

Taxonomic and systematic studies of AMF can be traced back to the early works of the Tulasne brothers (1845) and the Thaxter (1922) revision of Endogonaceae. In the last 40 years, the classification of this group of fungi has undergone considerable transformations, from being merely descriptive and based solely on spore morphology (Gerdemann and Trappe 1974) to being based on cladistic analysis of genetic and phenotypic characters. Morton and Benny's (1990) classification is based on the analysis of phenotypic characters (spore morphology and mycorrhizal characters), classifications of Schüßler et al. (2001), that of Schüßler and Walker (2010) on genetic characters (sequence variation of the SSU rDNA), and that of Oehl et al. (2011a) on combined genetic and phenotypic characters. Schüßler et al.'s (2001) classification has been generally accepted by mycorrhiza researchers and mycologists. It demonstrates the importance of genetic characters to elucidate phylogenetic relationships within a group of fungi where evolutionary convergence of phenotypic characters is common (Morton 1990). Where phylogenetic trees generated using genetic and phenotypic characters are congruent, it can probably be assumed that a true phylogeny is being depicted;

conversely, divergent phylogenies implies that different processes are acting in different levels of organization (Morton 2009).

The use of genetic characters in glomeromycotan systematics has revealed the same trend observed in other groups of organisms: the proliferation of new taxa in all levels of the taxonomic hierarchy. Up to 2001, these fungi were included in one class, one order, three families, and six genera; 10 years later, with the use of genetic characters, they are distributed into one to three classes, four to five orders, 11–14 families, and 18–29 genera depending on the classification scheme followed (Table 1). A timeline of genera proposed for glomeromycotan fungi since 1845 up to 2011 is found in Electronic supplementary materials Table 2. On the other hand, genetic characters usually reveal clades not resolvable by phenotypic characters, so resulting in new taxa at any level of the taxonomic hierarchy. Nevertheless, each taxon proposed should be clearly embedded in a proper classification in order to provide powerful tools for comparative biology at all levels (e.g., physiological, ecological, biochemical), otherwise, we might find ourselves with a hodgepodge of names (Carvalho et al. 2008). For glomeromycotan fungi, it is desirable that each taxa proposed be linked to living cultures, a laudable aim that is probably unachievable for some species in a short to medium term.

The congruence of phenotypic and genetic characters has been attempted by taxonomists to erect new taxa in the Glomeromycota. In some cases, this approach was accepted (Morton and Redecker 2001) while, in others, it has been questioned (Oehl et al. 2008). Regardless of which dataset is chosen, systematists working with these organisms must first identify conserved characters that are phylogenetically informative and can be used to provide an evolutionary tree (Patterson et al. 1993). Failure to identify conserved traits in a phylogenetic analysis and the creation of ranks provoke instability in a classification scheme (Hibbett and Donoghue 1998).

In conclusion, any phylogenetic classification to depict evolutionary relationships between groups within the Glomeromycota represents a hypothesis that can be tested throughout observation and experimentation. In this respect and considering the hypothetic–deductive method of science advocated by Karl Popper (Popper 1972), the proposal of distinct phylogenies as hypotheses and attempts to falsify them is an acceptable way for systematists to progress in this branch of science within mycorrhizology. These hypotheses, however, must be both based on solid biological grounds and rigorous character analyses during phylogeny reconstruction, in order to avoid the risk of further confusion in glomeromycotan systematics.

Acknowledgments The author would like to thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a

Research Assistantship (Process 302667/2009-1). I am indebted to Joseph B. Morton, Francisco Adriano de Souza, Dirk Redecker, and Christopher Walker for critically reading the manuscript and/or providing important insights and suggestions. This paper resulted after a lecture given by the author at the VI Brazilian Conference of Mycology, in Brasília, Brazil. I thank Dr. José Carmine Dianese and the Conference organizing committee for the opportunity to present that lecture. I am indebted to James Trappe and Dirk Redecker for providing hard and electronic copies of some of the old sources referenced here and to two anonymous reviewers for their helpful comments and constructive suggestions to strength this manuscript. I dedicate this paper to Prof. Margarida Matos de Mendonça, who guided my steps as an undergraduate student into the world of mycorrhiza research.

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