

## Article

# Four New Families of Arbuscular Mycorrhizal Fungi Within the Order Glomerales

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**Abstract:** Based on molecular phylogenetic analyses, and also considering morphological characters, four new families are separated from the family Glomeraceae within the order Glomerales and the class Glomeromycetes. The revised family Glomeraceae comprises only four genera: the type genus *Glomus*, *Complexispora*, *Sclerocarpum* and *Simiglomus*. Septoglomeraceae fam. nov. comprises, besides *Septoglomus*, *Funneliformis*, *Funneliglomus*, *Blaszkowskia* and *Viscospora*. Sclerocystaceae fam. nov. is represented by the type genus *Sclerocystis* but also by *Halonatospora*, *Oehlia*, *Parvocarpum*, *Rhizoglomus* and *Silvaspora*. Kamienskiaceae fam. nov. encompasses *Kamienskia*, *Microkamienskia* and *Epigeocarpum*. Finally, Dominikiaceae fam. nov. includes the genera *Dominikia*, *Macrodominikia* gen. nov. *Microdominikia*, *Nanoglomus* and *Orientoglomus*. The genera *Oehlia* and *Halonatospora* form two other clades well separated from *Silvaspora*, *Sclerocystis* and *Rhizoglomus* and might represent two further families within Glomerales. This deeper separation is, in our opinion, fully supported by molecular phylogeny, but in view of the low numbers of taxa, the separation is not yet proposed at this stage of research progress.

**Keywords:** classification; systematics; taxonomy; arbuscular mycorrhizal fungi



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## 1. Introduction

The fungal phylum Glomeromycota (arbuscular mycorrhizal fungi, AMF) currently comprises three classes, six orders, sixteen families and >50 genera [1–6]. In the class Glomeromycetes, four orders were described, which are called Diversisporales, Entrophosporales, Gigasporales and Glomerales [4,7–10]. Within Glomerales and Entrophosporales, there has been just one family for each, Glomeraceae and Entrophosporaceae [9,11], while Diversisporales comprises the type family (Diversisporaceae) and three other families: Acaulosporaceae, Pacisporaceae and Sacculosporaceae [9,12–14]. The order Gigasporales comprises the five families Gigasporaceae, Scutellosporaceae, Racocetraceae, Dentiscutataceae and Intraornatosporaceae [2,3,15,16]. Finally, in the most ancient clades of AM fungi, there are Archaeosporales, including the families Archaeosporaceae, Ambisporaceae, Geosiphonaceae and Polonosporaceae, and Paraglomerales, comprising Paraglomeraceae and Pervetustaceae [2,3].

Within the last few years, new genera were separated within Glomerales due to concomitant morphological and molecular analyses and especially phylogenetic progresses [5,6,17–21]. The DNA differences for specific markers also can be used in some cases. According to Silva et al. [5], the genera in Glomerales present a difference about 10% in the maximum identity (MI) of the partial nrDNA gene. Glomeraceae is the family with highest species richness in Glomeromycota (>150), and the latest phylogenetic trees for Glomeraceae species revealed at least four or five major clades [4,6,17,19–21].

*Glomus macrocarpum*, *Septoglomus constrictum*, *Sclerocystis coremioides*, *Kamienskia bistrata* and *Dominikia minuta* might be the most representative species of these five major clades. The family Glomeraceae also includes two genera of outstanding importance, which are counted among the 50 most cited fungal genera within the last decades, *Funneliformis* and *Rhizoglomus*, due to the species *F. mosseae* and *R. irregulare*. These species have often been used in basic research, applied sciences and commercial applications, e.g., to enhance soil fertility and improve plant nutrition and root health [22]. Two complexes of genera were already reported in previous works, the *Dominikia* and *Septoglomus* complexes [5,19]. Based on our observations (phylogenetic and morphological analyses), our hypothesis is that at least five major clades/complexes exist in Glomeraceae, and thus the family could be divided into five different families based on these five major clades/complexes. Thus, the objectives of this study were to perform a thorough phylogenetic analysis on the described Glomerales species and to re-organize all the families and genera justified within the order. At the end, a revision of the family Glomeraceae will be needed, and new families will have to be described based on significative type species.

## 2. Materials and Methods

### 2.1. Phylogenetic Analyses

To reconstruct the phylogeny, three alignments (datasets) were generated with AM fungal sequences from the genera of Glomeromycetes (Supplementary Material, Spreadsheet S1). The first dataset was used to reconstruct the Glomeromycetes phylogeny based on partial SSU, ITS region and LSU nrDNA (Glomeromycetes SSU-ITS-LSU). The second dataset was used to reconstruct the Glomerales phylogeny based on partial SSU, ITS region and partial LSU nrDNA (Glomerales SSU-ITS-LSU). The third dataset was used to reconstruct the Glomerales phylogeny based on partial SSU, 5.8S and partial LSU nrDNA (Glomerales SSU-5.8S-LSU). *Paraglomus brasilianum* (Spain & J. Miranda) J.B. Morton & D. Redecker was included as an outgroup in the first dataset analyses, and *Entrophospora etunicata* (W.N. Becker & Gerd.) Błaszk., Niezgodna, B.T. Goto & Magurno was included as the outgroup in the second and third dataset analyses. For the first dataset, sequences with at least the ITS region and partial LSU nrDNA were used. For the second and third datasets, some isolates with only sequences from the partial LSU nrDNA were used, which are indicated in the phylogenetic trees generated. Sequences from *Septoglomus titan* were not used in the phylogenetic analyses because we decided to not include sequences in the alignment with less than 500 bp (sequences from *S. titan* have 457 bp). According to Silva et al. [5], it is not possible to be sure about the phylogenetic position of this species due to the short LSU nrDNA fragment and unavailability of its ITS sequences. The datasets were aligned in Mafft [23] using the default parameters. Prior to phylogenetic analyses, the model of nucleotide substitution was estimated using Topali 2.5 [24]. Bayesian [two runs over  $5 \times 10^6$  generations ( $1 \times 10^7$  generations for the first dataset), with a sample frequency of 500 (1000 for the first dataset) and a burnin value of 25%] and maximum likelihood (1000 bootstrap) analyses were performed, respectively, in MrBayes 3.1.2 [25] and PhyML [26], launched from Topali 2.5, using the GTR + I + G model for the first dataset and GTR + G for the second and third datasets.

### 2.2. Specimen Analyses

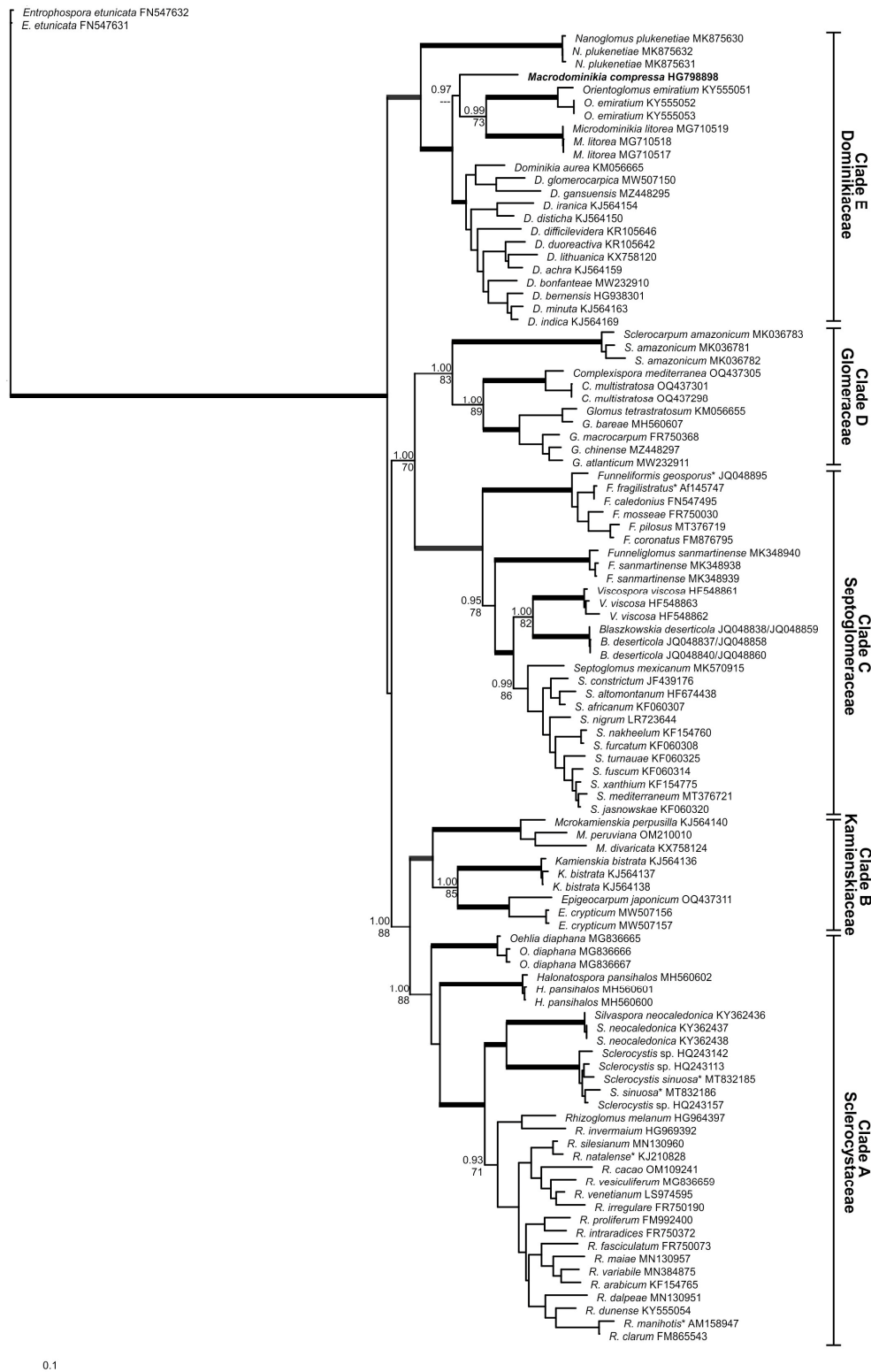
We morphologically analyzed all species belonging to Glomerales and analyzed specimens representing >120 taxa in detail. Holotype, isotype, paratype and ex-type materials were examined along with representatives from institutional herbaria—OSC, FH, Z + ZT, URM (Recife, Brazil); Embrapa Agrobiologia (Seropédica, Brazil); DCS-UFLA (Lavras, Brazil); International Culture Collection of Vesicular-Arbuscular Mycorrhizal Fungi (IN-VAM); and the Swiss collection of Arbuscular Mycorrhizal Fungi (SAF, Agroscope ART, Zurich, Switzerland)—and private AM fungal collections curated by Sieverding, Oehl, Trappe, Błaszkowski and McGee; see also Oehl et al. [9]. The Hall and Abbott [27] photographic slide collection was also reviewed. Older specimens (mounted on microscopic

slides prior to 1990) were mostly mounted in lactophenol, while others were fixed with polyvinyl alcohol–lactic acid–glycerol (PVLG) or in a mixture of PVLG + Melzer’s reagent, which after 1990 are the principal fixing media [28]. Newly mounted spores and sporocarps from collections or from cultures were fixed using the latter two fixing media or occasionally also in a mixture of 1:1 lactic acid to water, in Melzer’s reagent and in water. When available, spores freshly isolated from soils or bait cultures were also mounted and analyzed. All spore observations and all information on spore characteristics are based on spores extracted from soil, from trap cultures or from single or multiple spore-derived pure cultures. No information is provided from in vitro cultured materials. Spore wall terminology follows the nomenclature of Walker [29] and Stürmer and Morton [30]. Analyses of the spore walls, germination structures and all other mycorrhizal structures were performed using compound microscopes at 100–1000× magnification. For this paper, all original species descriptions and published species emendations were also considered and thoroughly studied.

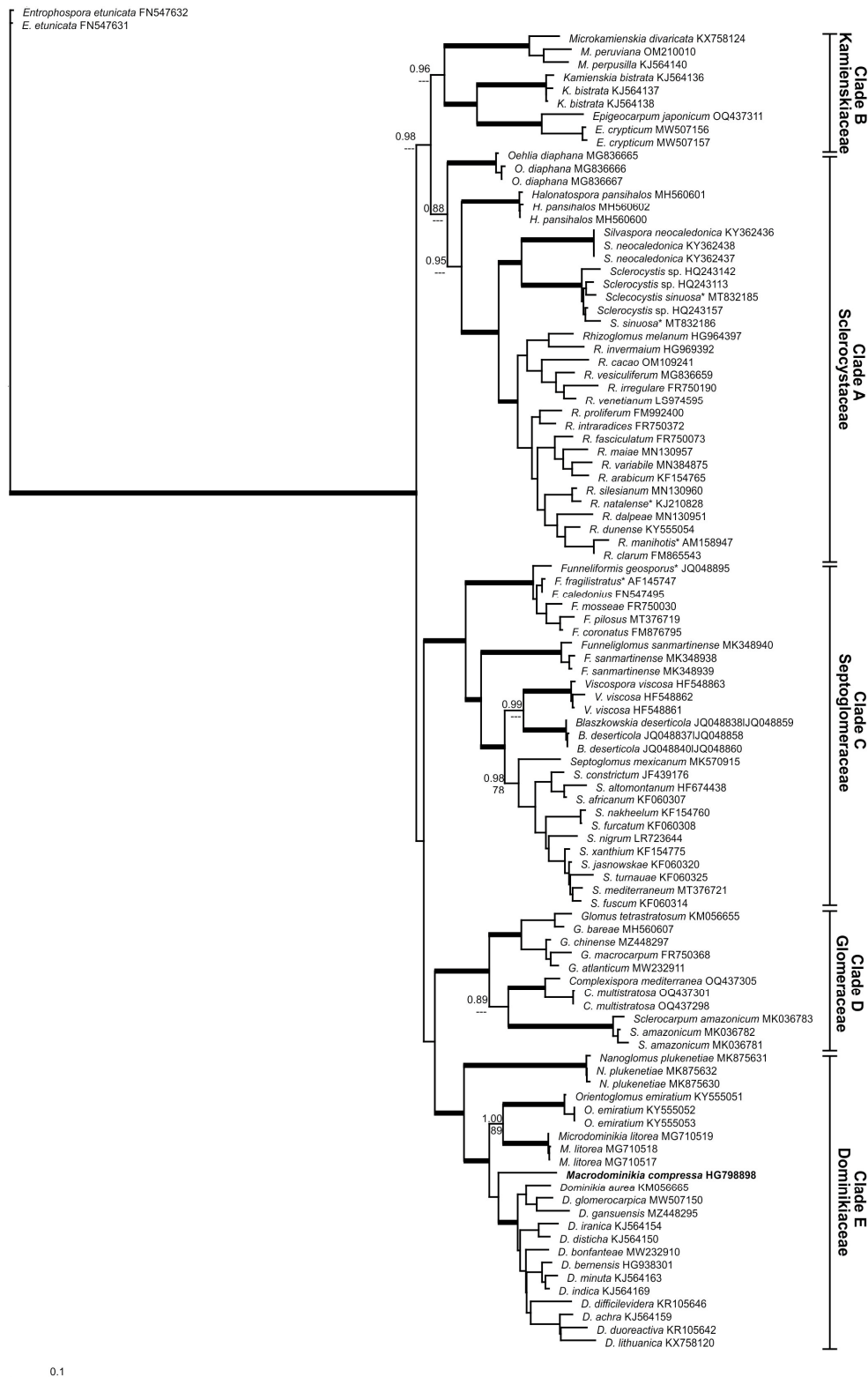
### 3. Results

#### 3.1. Molecular Phylogeny

The Glomeromycetes tree (Supplementary Material, Figure S1) showed the different orders and already-described families of the class with full support for ML and Bayesian inference (BI) analyses (except Diversisporales and Scutellosporaceae with 75% and 99% of support for ML, respectively). Five different clades were separated within Glomerales in all trees generated (Figure S1, Figures 1 and 2). Clade “A”, composed of the genera *Halonatospora*, *Oehlia*, *Rhizoglosum*, *Sclerocystis* and *Silvaspora*, had strong support from BI and ML analyses (1.00/88%) in the Glomerales SSU-ITS-LSU tree obtained (Figure 1). However, this clade was not supported by ML analyses and presented a low support of 0.88 for BI in the Glomerales SSU-5.8s-LSU tree (Figure 2). In the Glomeromycetes SSU-ITS-LSU tree (Figure S1), clade “A” had full support from BI and low support (67%) from ML analysis. Clade “B” was strongly supported by ML and BI in two of the three trees obtained; however in the Glomerales SSU-5.8s-LSU tree, there was no support by ML. This clade comprises the genera *Epigeocarpum*, *Kamienskia* and *Microkamienskia*. Clades “C”, “D” and “E” received strong support in all analyses of the three trees. Clade “C” is represented by *Blaszkowskia*, *Funneliformis*, *Funneliglosum*, *Septoglosum* and *Viscospora*; clade “D” by *Complexispora*, *Glomus* and *Sclerocarpum*; and clade “E” by *Dominikia*, *Macrodominikia* gen. nov., *Microdominikia*, *Nanoglosum* and *Orientoglosum*, respectively. Our findings indicate that each clade represents a different family in Glomerales with a total of 23 AMF genera.



**Figure 1.** Phylogenetic tree from partial SSU, ITS region and partial LSU nrDNA sequences of Glomerales. Sequences are labeled with their database accession numbers. Support values from Bayesian inference (BI) and maximum likelihood (ML) are shown only at the genera level or above. Only support values of at least 70% are shown. Thick branches represent clades with more than 90% support in all analyses. The new genus is in bold. The tree was rooted by *Entrophospora etunicata*. Sequences with only the partial LSU nrDNA are indicated by \*.



**Figure 2.** Phylogenetic tree from partial SSU, 5.8S and partial LSU nrDNA sequences of Glomerales. Sequences are labeled with their database accession numbers. Support values from Bayesian inference (BI) and maximum likelihood (ML) are shown only for the genera level or above. Only support values of at least 70% are shown. Thick branches represent clades with more than 90% support in all analyses. The new genus is in bold. The tree was rooted by *Entrophospora etunicata*. Sequences with only the partial LSU nrDNA are indicated by \*.

### 3.2. Morphological Analyses

All 23 currently known AMF genera in Glomerales have in common that they form their spores terminally at the end of so-called subtending hyphae or intercalarily. In pigmented and unpigmented spores, these subtending hyphae generally have the same or sometimes slightly lighter or darker pigmentation as the spores when observed under a compound microscope. The 23 genera can morphologically be separated only by a combination of several principal characters (Supplementary Material, Table S1). These characters refer mainly to the sporocarps, cluster formation and spores (e.g., sizes and pigmentation) but also to the features of their pore closure and subtending hyphae, including intra-clustural, intra- or extra-sporocarpic hyphae; specific spore formation features (e.g., radial organization of spores within sporocarps); frequent sporocarp formation in roots; preferably in clusters or singly; and preferably to exclusively in soils. The position and type of pore closure at the spore base or within the subtending hyphae is an outstanding morphological feature in Glomerales (e.g., [9]), from large, strong septa, as known for *Funneliformis* and *Septoglosum*, to introverted wall thickening (in *Sclerocarpum* and *Epigeocarpum*); small but long, irregular pore channels, as known for *Macrodominikia*; or just relatively wide, open pores in *Rhizoglosum*, *Kamienskia* and *Microkamienskia* (Corazon-Guivin et al. [21,31]. Ornamentation or viscose structures on spore surfaces (as in *Funneliglosum* or *Viscospora*) and the number of spore wall layers (e.g., *Complexispora*) are rarely characters used to differentiate at the genus level, but the spore wall composition is always helpful for AMF species identification (e.g., [19,20,32,33]).

### 3.3. Taxonomy

**Glomerales** J.B. Morton and Benny, emend. Błaszk., B.T. Goto, and Magurno, Mycotaxon 37: 473. 1990.

MycoBank MB 90425

Description: Spores formed in soils or in roots, terminally on or intercalarily in hyphae, either singly, in loose spore clusters or in multiple-spored loose to compact sporocarps, when compact spores are randomly distributed or organized around a central plexus of hyphae. Compact sporocarps with or without a peridium and with or without an intrasporocarpic hyphal gleba. Spores with one mono- to multiple-layered wall. Wall of the subtending hyphae (SH) conspicuously continuous and concolorous with the spore wall (SW) or slightly lighter in color than the SW; SH funnel-shaped, cylindrical or constricted; straight, curved or flared; pore at spore base open or closed by a bridging, straight or curved septum or by introverted wall thickening, or SH closed at some distance from the spore base by a septum or plug-like structure forming typical vesicular–arbuscular mycorrhizae, with vesicular–arbuscular mycorrhizal structures that stain blue to dark blue in trypan blue.

Type family: Glomeraceae Piroz. & Dalpé

Other families: Septoglomeraceae Oehl et al., Sclerocystaceae Oehl et al., Dominikiaceae G.A. Silva et al., Kamienskiaceae G.A. Silva et al.

Type genus: *Glomus* Tul. & C. Tul.

Other genera: *Sclerocarpum* B.T. Goto et al., *Complexispora* Błaszk. et al., *Simiglosum* Sieverd. et al., *Błaszkowskia* G.A. Silva & Oehl, *Septoglosum* Sieverd. et al., *Funneliformis* C. Walker & A. Schüssler, *Funneliglosum* Corazon-Guivin et al., *Viscospora* Sieverd. et al., *Rhizoglosum* Sieverd. et al., *Oehlia* Błaszk. et al., *Sclerocystis* Berk. & Broome, *Halonatospora* Błaszk. et al., *Kamienskia* et al. Błaszk. et al., *Microkamienskia* G.A. Silva et al., *Dominikia* Błaszk. et al., *Macrodominikia* Oehl et al., *Microdominikia* Oehl et al., *Nanoglosum* Corazon-Guivin et al., *Orientoglosum* G.A. Silva et al., *Epigeocarpum* Błaszk. et al., *Silvaspora* Błaszk. et al., *Parvocarpum* Magurno.

**Glomeraceae** Piroz. & Dalpé emend. Oehl, G.A. Silva & Sieverd.

MycoBank 82026

Emended description: Spores formed in soil and sometimes in roots, terminally on or intercalarily in hyphae, either singly, in loose spore clusters or in multiple-spored

loose to compact sporocarps, when compact, then spores are randomly distributed, but not organized around a central plexus of hyphae. Compact sporocarps with or without a peridium and with or without an intrasporocarpic hyphal gleba. Spores with one (mono-)bi- to multiple-layered wall. SH wall conspicuously continuous and concolorous with the SW, or slightly lighter in color than the SW; SH cylindrical or slightly funnel-shaped or slightly constricted; straight, curved or flared; pore at spore base open or closed at spore base by a straight or curved septum or by introverted wall thickening or at some distance from the spore base by a bridging septum arising from the SH wall; forming typical vesicular-arbuscular mycorrhiza staining blue to dark blue in trypan blue.

Type genus: *Glomus* Tul. & C. Tul.

Other genera: *Sclerocarpum* B.T. Goto et al., *Simiglomus* Sieverd. et al., *Complexispora* Błaszk. et al.

*Glomus* Tul. & C. Tul., G. bot. ital. 2(1): 63. 1845. [1844].

MycoBank 20244

Emended description: Spores formed singly within soil or sometimes roots, in disorganized, multiple-spored, loose spore clusters or in compact sporocarps; compact, but not radially organized around a central hyphal plexus, without or with a peridium; spores are either in the sporocarp or organized. Spores with a mono- to multiple-layered wall. SH wall conspicuously continuous and concolorous with the SW or slightly lighter in color than the SW. Spore pore closure often by introverted wall thickening, sometimes supported by a short bridging septum, rarely open. Forming typical vesicular-arbuscular mycorrhizae, with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type species: *Glomus macrocarpum* Tul & C. Tul., G. bot. ital. 2(1): 63. 1845. [1844].

MycoBank MB 240247

≡ *Endogone macrocarpa* (Tul. & C. Tul.) Tul. & C. Tul., Fungi Hypog.: 182. 1851.

MycoBank MB 218537

≡ *Endogone guttulata* E. Fisch., Ber. Schweiz. Bot. Ges. 32: 13. 1923.

≡ *Endogone nuda* Petch., Ann. R. Bot. Gdns Peradeniya 9: 322. 1925.

≡ *Endogone pampalonia* Bacc., Nuovo Giorn. Bot. Ital., n.s. 10: 90. 1903.

≡ *Paurocotylis fulva* var. *zelandica* Cooke, Grevillea 8: 59. 1879.

*Simiglomus* Sieverd., G.A. Silva & Oehl, Mycotaxon 116: 104. 2011.

MycoBank MB 518435

Description: Spores formed in soil or in roots, terminally on or intercalarily in hyphae, in small to multiple-spored loose clusters, randomly distributed, but not organized around a central plexus of hyphae. Loose sporocarps generally without a peridium and without an intrasporocarpic hyphal gleba. Spores with one mono- to multiple-layered wall. SH wall conspicuously continuous and concolorous with the SW or slightly lighter in color than the SW; SH cylindrical or rarely slightly funnel-shaped or slightly constricted; straight, curved or flared; pore open at spore base, but often at some distance by one to multiple bridging, straight to curved septa, not supported by introverted wall thickening; forming typical vesicular-arbuscular mycorrhizae, with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type species: *Simiglomus hoi* (S.M. Berch & Trappe) G.A. Silva, Oehl & Sieverd., Mycotaxon 116: 104 (2011).

MycoBank MB 518461

Basionym: *Glomus hoi* S.M. Berch & Trappe, Mycologia 77: 654. 1985.

*Sclerocarpum* B.T. Goto, Błaszk., Niezgodna, Kozłowska & Jobim, Mycol. Progr. 18(3): 375. 2019.

MycoBank MB 828316

Description: Producing spores in scleroid, epigeous and sub-hypogeous, light- to dark-colored, unorganized sporocarps, very hard to break, with a peridium and a gleba comprising hyphae and glomoid glomerospores (=spores) with a single SH; spores hyaline; globose to subglobose; small, <100 µm diam; frequently ovoid; SW composed of a few smooth layers, of which one layer laminate and much thicker than the outermost layer,

forming the spore surface. SH funnel-shaped with a wall continuous with the SW; pore narrow, open or occluded by thickening of the SH wall or (rarely) occluded by a straight or slightly invaginated septum continuous with some innermost laminae of the laminated SW layer; septum positioned at the spore base.

Type species: *Sclerocarpum amazonicum* B.T. Goto, Błaszcz., Niezgoda, Kozłowska & Jobim, Mycol. Progr. 18: 377. 2019.

Mycobank MB 828317

Specific morphological observation of *Sclerocarpum*

Especially *Sclerocarpum* shows well-defined, outstanding morphological characteristics of hard sporocarps, their spores, which are exclusively formed within these sporocarps, and of their funnel-shaped subtending hyphae, including a pronounced wall thickening at the spore base at the point of pore closure. Three *Glomus* species described in the past clearly exhibit all these characteristics. These are *G. convolutum*, *G. pellucidum* and *G. segmentatum* [34–36]. Consequently, these species are hereafter transferred to the genus *Sclerocarpum*.

*Sclerocarpum convolutum* (Gerd. & Trappe) Oehl, Sieverd. & G.A. Silva, comb. nov.

Mycobank MB 855472

Basionym: *Glomus convolutum* Gerd. & Trappe, Mycol. Mem. 5: 42. 1974.

Mycobank MB 314590

*Sclerocarpum segmentatum* (Trappe, Spooner & Ivory) Oehl, Sieverd. & G.A. Silva, comb. nov.

Mycobank MB 855473

Basionym: *Glomus segmentatum* Trappe, Spooner & Ivory, Trans. Br. Mycol. Soc. 73: 362. 1979.

Mycobank MB 314610

*Sclerocarpum pellucidum* (McGee & Pattinson) Oehl, Sieverd. & G.A. Silva, comb. nov.

Mycobank MB 855474

Basionym: *Glomus pellucidum* McGee & Pattinson, Austral. Syst. Bot. 15: 120. 2002.

Mycobank MB 374910

*Complexispora* Błaszcz., B.T. Goto, Niezgoda & Magurno, Mycol. Progr. 22(5, no. 34): 7. 2023.

Mycobank MB 847607

Description: Producing hypogeous glomoid spores singly and in clusters. Spores four to six layers, of which two consist of tightly adherent sublayers (laminae). SH cylindrical to funnel-shaped, concolorous with the SW layer, with a wall composed of layers continuous with all SW layers, except for the innermost layer. Pore closed by a septum continuous with the innermost SW layer, occasionally also by a septum connecting the inner surfaces of the main structural laminate SW layer. Forming mycorrhiza with vesicles and arbuscules staining dark in trypan blue.

Type species: *Complexispora multistratosa* Błaszcz., B.T. Goto, Niezgoda & Magurno, Mycol. Progr. 22(5, no. 34): 6. 2023.

Mycobank MB 847608

**Septoglomeraceae** Oehl, G.A. Silva, Sieverd. fam. nov.

Mycobank MB 855466

Description: Spores formed in soil and sometimes in roots, terminally on or intercalarily in hyphae, either singly, in loose spore clusters or in sporocarps. Compact sporocarps with or without a peridium, without an intrasporocarpic hyphal gleba. Spores with one mono- to multiple-layered wall. SH wall conspicuously continuous and concolorous with the SW or slightly lighter in color than the SW; SH pronounced, funnel-shaped, slightly funnel-shaped, cylindrical or constricted, rarely inflated; straight, curved or flared; forming typical vesicular–arbuscular mycorrhiza with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type genus: *Septoglomus* Sieverd., G.A. Silva & Oehl



Other genera: *Funneliformis* C. Walker & A. Schüssler, *Funneliglomus* Corazon-Guivin et al., *Viscospora* Sieverd. et al., *Blaszkowskia* G.A. Silva & Oehl

Type species: *Septoglomus constrictum* (Trappe) Sieverd., G.A. Silva & Oehl

*Septoglomus* Sieverd., G.A. Silva & Oehl, Mycotaxon 116: 105. 2011.

MycoBank MB 518436

Emended description: Spores formed in soil and sometimes in roots, terminally on or intercalarily in hyphae, either singly or in loose spore clusters. Spores with one mono- to multiple-layered wall. SH wall conspicuously continuous and concolorous with the SW or slightly lighter in color than the SW; SH constricted to cylindrical, rarely slightly funnel-shaped or inflated at some distance to the spore base; straight, curved or flared; pore closed by a broad, pronounced septum or a plug at spore base or at some distance from spore; forming typical vesicular–arbuscular mycorrhizae, with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type species: *Septoglomus constrictum* (Trappe) Sieverd., G.A. Silva & Oehl. Mycotaxon 116: 105. 2011.

MycoBank MB 518462

Basionym: *Glomus constrictum* Trappe, Mycotaxon 6: 361. 1977.

MycoBank MB 314589

≡ *Funneliformis constrictus* (Trappe) C. Walker & A. Schüssler, The Glomeromycota—a species list: 14. 2010.

MycoBank MB 542904

*Blaszkowskia* G.A. Silva & Oehl, Mycol. Progr. 22(11, no. 74): 5. 2023.

MycoBank MB 847414

Description: Spores light yellow to yellow brown to dark brown or dark red–brown, generally 20–200 µm, with >1 SW layer; SH funnel-shaped, rarely constricted, thick walled; spore pores might be open at the spore base but often closed by one to several thin septa within the SH at some distance from the spore base. SH thicker walled than mycelium hyphae and pigmented over long distances and within the whole spore clusters, including intraradical spore formations (>100 µm).

Type species: *Blaszkowskia deserticola* (Trappe, Bloss & J.A. Menge) Oehl & G.A. Silva. Mycol. Progr. 22(11, no. 74): 5. 2023.

MycoBank MB 847415

Basionym: *Glomus deserticola* Trappe, Bloss & J.A. Menge, Mycotaxon 20: 123. 1984.

MycoBank MB 106847

≡ *Septoglomus deserticola* (Trappe, Bloss & J.A. Menge) G.A. Silva, Oehl & Sieverd. Mycotaxon 116: 106. 2011.

MycoBank MB 518463

*Funneliglomus* Corazon-Guivin, G.A. Silva & Oehl, Sydowia 71: 19. 2019.

MycoBank MB 829266

Description: Spores formed in soil or rarely in roots, terminally on or intercalarily in hyphae, singly or in small clusters; the conspicuous SH is concolorous with the SW (or slightly lighter in color); SH is species specific and funnel-shaped to slightly funnel-shaped, rarely cylindrical or slightly constricted, or inflated at some distance to the spore base; straight, curved or flared. Pore regularly closed by a conspicuous septum that species specifically may arise from the structural wall layer; from an additional adherent, innermost, (semi-)flexible lamina; or from both but not by introverted wall thickening, which is lacking. Forming typical vesicular–arbuscular mycorrhizae, with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type species: *Funneliglomus sanmartinense* Corazon-Guivin, G.A. Silva & Oehl. Sydowia 71: 21. 2019

MycoBank MB 829267 (*Funneliglomus sanmartinensis*), MycoBank MB 830216 (corrected to *Funneliglomus sanmartinense* by Mycobank after publication)

*Funneliformis* C. Walker & A. Schüssler, emend. Oehl, G.A. Silva & Sieverd [9], The Glomeromycota—a species list with new families and genera: 13. 2010.

MycoBank MB 542894

Description: Spores formed within soil or rarely in roots, singly or sometimes in sporocarps with a few to several spores per sporocarp only; the conspicuous SH is concolorous with the SW (or slightly lighter in color); the SH is species specific and generally pronounced funnel-shaped to slightly funnel-shaped or rarely cylindrical. Wall differentiation and pigmentation may continue over long distances from the spore base (often >50–250 µm), and then the mycelium may become hyaline. Pore regularly closed by a conspicuous septum that species specifically arises from the structural wall layer; from an additional adherent, innermost, (semi-)flexible lamina; or from both but not by introverted wall thickening, which is lacking. Forming typical vesicular–arbuscular mycorrhizae, with mycorrhizal structures that stain blue to dark blue in trypan blue.

Type species: *Funneliformis mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler, *The Glomeromycota—a species list with new families and genera*: 13. 2010.

MycoBank MB 542895

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

MycoBank MB 330367

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

MycoBank MB 314604

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

MycoBank MB 518439

Emended description: Spores hyaline to white or subhyaline, terminally or intercalarily on pronounced funnel-shaped to slightly funnel-shaped to cylindrical or inflated subtending hyphae, hyaline, singly or in loose clusters with up to 100 spores per cluster. Outer layer is evanescent, viscose, gathering large amounts of debris during degradation. SWL2 is persistent, unite to laminate, and might stain whitish yellow to yellowish when exposed to Melzer's reagent. SH straight or recurved, sometimes folded to rarely flared. Regularly, one to several straight to curved septa are formed in the SH close to the spore base or at a distance of up to 10–100 µm from the spore base. The SW layers continue in the SH, with similar to slightly lower thickness toward the mycelium hyphae.

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

MycoBank MB 518471

Basionym *Glomus viscosum* T.H. Nicolson, *Mycol. Res.* 99: 1502. 1995.

MycoBank MB 413125

≡ *Septoglomus viscosum* (T.H. Nicolson) C. Walker, D. Redecker, D. Stiller & A. Schüßler: *Mycorrhiza* 23: 524. 2013

MycoBank MB 550089

**Sclerocystaceae** Oehl, G.A. Silva, & Sieverd. fam. nov.

MycoBank MB 855467

Description: Spores formed in loose sporocarps, in clusters or singly in soil and frequently in roots. When formed in compact sporocarps, spores can be randomly distributed on SH of different lengths or well-organized around a central plexus of hyphae. SH wall continuous with the SW and for a certain distance concolorous with the SW or slightly lighter in color. SH cylindrical or seldom slightly funnel-shaped at spore base. Pore at spore base open or closed by a septum. SW shows rarely one, generally two to three (and up to five) distinct layers, of which one or several of the outermost may separate when pressure is applied to spores. Forming vesicular–arbuscular mycorrhizae, the fungal structures of which stain blue to dark blue in trypan blue.

Type genus: *Sclerocystis* Berk. & Broome

Other genera: *Oehlia* Błaszk. et al., *Rhizoglomus* Sieverd. et al., *Halonatospora* Błaszk. et al., *Silvaspora* Błaszk. et al., *Parvocarpum* Magurno

*Sclerocystis* Berk. & Broome, *J. Linn. Soc., Bot.* 14(no. 74): 137. 1873. [1875].

MycoBank MB20512

Emended description: Spores formed in compact sporocarps, in soils or roots, in culture, sometimes also singly or in loose clusters. When formed in compact sporocarps, then spores are regularly organized, arising radially around a central plexus of hyphae. SH wall continuous with the SW and for a certain distance concolorous with the SW or slightly lighter in color. SH funnel-shaped to cylindrical at spore base. Pore at spore base regularly closed by a fine septum, which is formed within the small pore channel within the spore base. SW shows more than one and generally two or rarely more than two distinct layers. Forming vesicular–arbuscular mycorrhizae, the fungal structures of which stain blue to dark blue in trypan blue.

Type species: *Sclerocystis coremioides* Berk. & Broome, J. Linn. Soc., Bot. 14(no. 74): 137. 1873. [1875].

MycoBank MB 213141

≡ *Glomus coremioides* (Berk. & Broome) D. Redecker & J.B. Morton, Mycologia 92: 284. 2000.

MycoBank MB 464612

*Rhizoglomus* Sieverd., G.A. Silva & Oehl, Mycotaxon 129: 377. 2015.

MycoBank MB 803191

Description: Spores formed in loose sporocarps, in clusters or singly in soil and frequently also in roots. When formed in compact sporocarps, they are not organized around a central plexus of hyphae. SH wall continuous with the SW and for a certain distance concolorous with the SW or slightly lighter in color. SH cylindrical or seldom slightly funnel-shaped at spore base. Pore at spore base regularly open, rarely closed by a septum. SW shows more than one, generally two to three (and up to five) distinct layers, of which one or several of the outermost layers may separate when pressure is applied to spores. Forming vesicular–arbuscular mycorrhizae, the fungal structures of which stain blue to dark blue in trypan blue.

Type species: *Rhizoglomus intraradices* (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl, Mycotaxon 129(2): 378. 2015 [2014].

MycoBank MB 803192

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

MycoBank MB 110704

≡ *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schussler, The Glomeromycota: 19. 2010.

MycoBank MB 542910

*Oehlia* Błaszk., Kozłowska, Niezgodna, B.T. Goto & Dalpe, Nova Hedwigia 107: 507. 2018.

MycoBank MB 824689

Emended description: Spores formed in loose sporocarps, in clusters or singly, in soil and frequently also in roots. When formed in compact sporocarps, they are not organized around a central plexus of hyphae. SH wall continuous with the SW and for a certain distance concolorous with the SW or slightly lighter in color. SH cylindrical or seldom slightly funnel-shaped at spore base. Pore at spore base regularly closed by a septum. SW shows more than one, generally two to three (and up to five) distinct layers. Forming vesicular–arbuscular mycorrhizae, the fungal structures of which stain blue to dark blue in trypan blue.

Type species: *Oehlia diaphana* (J.B. Morton & C. Walker) Błaszk., Kozłowska & Dalpe, Nova Hedwigia 107(3–4): 507. 2018.

MycoBank MB 824693

Basionym: *Glomus diaphanum* J.B. Morton & C. Walker. Mycotaxon 21: 433, 1984.

MycoBank MB 106161

*Parvocarpum* Magurno, MycoKeys 107: 283. 2024.

MycoBank MB 853558

Description: Producing glomoid spores mainly in small sporocarps, irregularly around a small central plexus of interwoven, intrasporocarpic hyphae or singly in soils. SH gener-

ally short and cylindrical, often breaking at the spore base during sporocarp degradation. Pore closed by introverted wall thickening at the spore base and additionally by a septum arising from the laminated wall layer and/or an additional flexible inner layer.

Type species: *Parvocarpum badium* (Oehl, Redecker & Sieverd.) Magurno, MycoKeys 107: 284. 2024.

MycoBank MB 853560

Basionym: *Glomus badium* Oehl, D. Redecker & Sieverd., J. Appl. Bot. Food Qual. 79: 39. 2005.

MycoBank MB 341387

≡ *Funneliformis badius* (Oehl, D. Redecker & Sieverd.) C. Walker & A. Schüssler, The Glomeromycota—a species list: 13. 2010.

MycoBank MB 541897

*Silvaspora* Błaszk., Niezgoda, B.T. Goto, Crossay & Magurno, Frontiers in Microbiology 12(no. 655910): 14. 2021.

MycoBank 838881

Description: Forming pigmented spores with 2–3 wall layers, of which only layer 1, forming the spore surface, is impermanent and hyaline to brightly colored. SH colored similarly to the SW, cylindrical, slightly funnel-shaped or constricted at the spore base, with a pore occluded due to thickening of the SH wall layer continuous with the laminate SW layer, rarely slightly open. Forming mycorrhizae with arbuscules, vesicles and hyphae staining dark in trypan blue.

Type species: *Silvaspora neocaledonica* (D. Redecker, Crossay & Cilia) Błaszk., Niezgoda, B.T. Goto, Crossay & Magurno, Frontiers in Microbiology 12(no. 655910): 14 (2021)

MycoBank MB 838882

≡ *Rhizoglomus neocaledonicum* (D. Redecker, Crossay & Cilia) Oehl, A. Turrini & Giovann., Mycol. Progr. 17: 1216 (2018).

MycoBank MB 827095

Basionym: *Rhizophagus neocaledonicus* D. Redecker, Crossay & Cilia, Mycol. Progr. 17: 739. 2018.

MycoBank MB 820537

*Halonatospora* Błaszk., Niezgoda, B.T. Goto & Kozłowska, Botany 96(11): 743. 2018.

MycoBank MB 826963

Description: Spores formed in loose clusters or singly in soil and frequently in roots. When formed in sporocarps, they are not organized around a central plexus of hyphae. SH wall continuous with the SW and for a certain distance concolorous with the SW or slightly lighter in color. Outer SW layer strongly swells in PVLG, forming a halo with radiate columns. SH cylindrical or slightly flared, sometimes slightly constricted at spore base, straight or slightly curved. Pore open or closed by a septum at spore base. SW shows more than one, generally two to three (and up to five) distinct layers. Forming vesicular–arbuscular mycorrhizae, the fungal structures of which stain blue to dark blue in trypan blue.

Type species: *Halonatospora pansihalos* (S.M. Berch & Koske) Błaszk., Niezgoda, B.T. Goto & Kozłowska, Can. J. Bot. 96(11): 743 (2018)

MycoBank MB 826964

Basionym: *Glomus pansihalos* S.M. Berch & Koske. Mycologia 78: 832, 1986.

MycoBank MB 358213

**Kamienskiaceae** G.A. Silva, Sieverd. & Oehl fam. nov.

MycoBank MB 855468

Description: Spores hypogeous and/or intraradical, produced in loose clusters to compact sporocarps and never organized around a central plexus of hyphae. Spores hyaline, small, up to 50 µm diam. when globose. SW with two permanent, smooth layers, of which one may stain in Melzer's reagent. The structural laminate layer is layer 1 or 2. SH cylindrical to funnel-shaped with an open pore. Forming vesicular–arbuscular mycorrhizae staining dark in trypan blue.

Type genus: *Kamienskia* Błaszk., Chwat & Kovács

Other genera: *Microkamienskia* Corazon-Guivin, G.A. Silva & Oehl, *Epigeocarpum* Błaszk., B.T. Goto, Jobim, Niezgoda & Marguno

*Kamienskia* Błaszk., Chwat & Kovács, Nova Hedwigia 100(1–2): 230. 2014 [2015].

MycoBank MB 808260

Emended description: Spores hypogeous and/or intraradical, produced in loose clusters to compact, but fast-degrading sporocarps, never organized around a central plexus of hyphae. Spores hyaline, small, up to 50 µm diam. when globose. SW with two permanent, smooth layers. The structural laminate layer might be layer 1 or 2. SH regularly funnel-shaped with an open pore. Forming vesicular–arbuscular mycorrhizae staining dark in trypan blue.

Type species: *Kamienskia bistrata* (Błaszk., D. Redecker, Koegel, Symanczik, Oehl & Kovács) Błaszk., Chwat & Kovács, Nova Hedwigia 100(1–2): 230. 2014 [2015].

MycoBank MB 808261

Basionym: *Glomus bistratum* Błaszk., D. Redecker, Koegel, Symanczik, Oehl & Kovács, Botany 87: 267. 2009.

MycoBank MB 512540

*Microkamienskia* Corazon-Guivin, G.A. Silva & Oehl, Nova Hedwigia 109: 359. 2019.

MycoBank MB 830814

Description: Spores hypogeous and/or intraradical, produced in loose clusters to compact, but fast-degrading sporocarps, never organized around a central plexus of hyphae. Spores hyaline, small, up to 50 µm diam. when globose. SW with two permanent, smooth layers, of which one may stain in Melzer’s reagent. The structural laminate layer might be layer 1 or 2. SH cylindrical to rarely slightly funnel-shaped with an open pore. Forming vesicular–arbuscular mycorrhizae staining dark in trypan blue.

Type species: *Microkamienskia perpusilla* (Błaszk. & Kovács) Corazon-Guivin, G.A. Silva & Oehl. Nova Hedwigia 109: 361. 2019.

MycoBank MB 830815

Basionym: *Glomus perpusillum* Błaszk. & Kovács. Mycologia 101: 249. 2009.

MycoBank MB 512346

≡ *Kamienskia perpusilla* (Błaszk. & Kovács) Błaszk., Chwat & Kovács. Nova Hedwigia 100: 231. 2015.

MycoBank MB 808264

*Epigeocarpum* Błaszk., B.T. Goto, Jobim, Niezgoda & Marguno, Frontiers in Microbiology 12(no. 655910): 10. 2021.

MycoBank MB 838879

Description: Spores hyaline to light yellow, formed in compact, unorganized sporocarps. Spores have 2–3 wall layers, laminate layer usually transferring into a crown-like structure due to contracting in spores crushed in PVLG and PVLG + Melzer’s reagent. The channel connecting the lumen of the SH with the interior of the spores is closed by a septum usually positioned at half the thickness of the laminate layer; SH funnel-shaped, SH lumen gradually narrowing in maturing spores due to internal thickening of the laminate wall layer.

Type species: *Epigeocarpum crypticum* Jobim, Błaszk., Niezgoda, Magurno & B.T. Goto, Frontiers Microbiol. 12(no. 655910): 14. 2021.

MycoBank MB 838880

**Dominikiaceae** G.A. Silva, Sieverd. & Oehl fam. nov

MycoBank MB 855469

Description: Spores hypogeous and/or intraradical, produced in loose clusters to compact sporocarps, but never organized around a central plexus of hyphae. Spores hyaline to creamy or yellow to yellow brown; SW with one to regularly two or more than two layers. SH wall continuous with the SW and for a certain distance concolorous with the SW or slightly lighter in color. Spore pore often closed at spore base by a thin bridging septum, sometimes supported by a certain degree of introverted wall thickening,

rarely continuing in the SH for a short distance (2–10  $\mu\text{m}$ ). Forming vesicular–arbuscular mycorrhizae staining dark in trypan blue.

Type genus: *Dominikia* Błaszk., Chwat & Kovács

Other genera: *Macrodominikia* Oehl et al., *Microdominikia* Oehl et al., *Nanoglomus* Corazon-Guivin et al., *Orientoglomus* G.A. Silva et al.

*Dominikia* Błaszk., Chwat & Kovács, *Nova Hedwigia* 100(1–2): 228. 2014 [2015].

MycoBank MB 808255

Emended description: Spores hypogeous and/or intraradical, produced in loose clusters to compact sporocarps but never organized around a central plexus of hyphae. Spores hyaline to creamy or yellow to yellow brown, small, up to 70  $\mu\text{m}$  diam; SW with one to regularly two or more than two layers. SW wall continuous with the SH and for a certain distance concolorous with the SW or slightly lighter in color. Spore pore often closed at spore base by a thin bridging septum, sometimes supported by a certain degree of introverted wall thickening, rarely continuing in the SH for a short distance. Forming vesicular–arbuscular mycorrhizae staining dark in trypan blue.

Type species: *Dominikia minuta* (Błaszk., Tadych & Madej) Błaszk., Chwat & Kovács, *Nova Hedwigia* 100: 230. 2014 [2015].

MycoBank MB 808256

Basionym: *Glomus minutum* Błaszk., Tadych & Madej. *Mycotaxon* 76: 189. 2000.

*Macrodominikia* Oehl, Sieverd. & G.A. Silva, gen. nov.

MycoBank 855470

Description: Spores hypogeous and/or intraradical, produced singly or in loose clusters to loose sporocarps but never organized around a central plexus of hyphae. Spores creamy to yellow to yellow brown, generally 70–110  $\mu\text{m}$  diam; SW with one to regularly two or more than two layers. SH wall continuous with the SW and for a certain distance concolorous with the SW or slightly lighter in color. Spore pore often closed at spore base by a thin bridging septum, supported by a large degree of introverted wall thickening, continuing in the SH for 10–50  $\mu\text{m}$  distance, forming an irregular, tortuous pore channel. Forming vesicular–arbuscular mycorrhizae staining dark in trypan blue.

Etymology: Macro-, -dominikia, referencing to the spores, which are larger than known hitherto for other genera in the Dominikiaceae

Type species: *Macrodominikia compressa* (Sieverd., Oehl, Palenz., Sánchez-Castro & G.A. Silva) Oehl, Siev. & G.A. Silva. comb. nov.

MycoBank MB 855471

Basionym: *Glomus compressum* Błaszk., Tadych & Mad Sieverd., Oehl, Palenz., Sánchez-Castro & G.A. Silva. *Nova Hedwigia* 99: 433. 2014.

MycoBank MB 807530

$\equiv$  *Dominikia compressa* (Sieverd., Oehl, Palenz., Sánchez-Castro & G.A. Silva) Oehl, Palenz., Sánchez-Castro & G.A. Silva. *Nova Hedwigia*. 101: 71. 2014 [2015].

MycoBank MB 809861

*Microdominikia* Oehl, Corazon-Guivin & G.A. Silva, *Mycol. Progr.* 18(12): 1400. 2019.

MycoBank MB 831098

Description: Spores formed singly or in clusters in soils or rarely in roots, terminally or intercalarily on SH, globose to subglobose, generally hyaline to subhyaline, 10–45  $\mu\text{m}$  in diameter, rarely egg-shaped or irregular, 25–50  $\times$  20–35  $\mu\text{m}$ , with a permanent outer SW layer. SH straight or recurved, usually funnel-shaped, more rarely cylindrical, rarely slightly constricted at the spore base. Spore pores open at the spore base but closed within SH at some distance.

Type species: *Microdominikia litorea* (Błaszk. & Kozłowska) Oehl, Corazon-Guivin & G.A. Silva, *Mycol. Progr.* 18(12): 1400. 2019.

MycoBank MB 831099

Basionym: *Dominikia litorea* Błaszk. & Kozłowska, *Phytotaxa* 338(3): 246. 2018.

MycoBank MB 823832

*Nanoglomus* Corazon-Guivin, G.A. Silva & Oehl, *Mycol. Progr.* 18(12): 1398. 2019.

MycoBank MB 831096

Description: *Nanoglomus* species differentiate small spores, generally <40 µm in diameter when globose, singly or in loose clusters, terminally or intercalarily on cylindrical to slightly funnel-shaped, rarely inflating SH, which are concolorous with the spores and have a fine, straight or rarely curved septum closing the pore at the spore base. So far, they can be differentiated from *Dominikia* spp. by the generally smaller and thinner-walled spores and by molecular phylogeny on the partial SSU, ITS region and partial LSU rDNA.

Type species: *Nanoglomus plukenetiae* Corazon-Guivin, G.A. Silva & Oehl, Mycol. Progr. 18(12): 1398. 2019.

MycoBank MB 831097

*Orientoglomus* G.A. Silva, Oehl & Corazon-Guivin, Mycol. Progr. 18(12): 1400. 2019.

MycoBank MB 831100

Description: Glomeraceae spores formed singly or in clusters in soil or rarely in roots, terminally on SH, globose to subglobose, 40–90 µm in diameter, rarely egg-shaped, 50–100 × 40–85 µm; SH wall with significant and regular thickening, resulting in a cylindrical pore channel. Outermost SW layer permanent, smooth; at least one SW layer laminate. Pore open or closed by a straight to curved to septum.

Type species: *Orientoglomus emiratium* (Błaszk., Kozłowska, Mullath, AlDhaheri & Al-Yahya'ei) G.A. Silva, Oehl & Corazon-Guivin, Mycol. Progr. 18(12): 1403. 2019.

MycoBank MB 831101

Basionym: *Dominikia emiratia* Błaszk., Kozłowska, Mullath, AlDhaheri & Al-Yahya'ei, Botany 95(7): 632. 2017.

MycoBank MB 819815

#### 4. Discussion

In the present study, the family Glomeraceae of the order Glomerales was divided into five different families based on five phylogenetically different major clades, well known and increasingly elaborated within the last fifteen years of research on the ribosomal gene. To observe the phylogenetic relationship among the different orders and families within Glomeromycetes, a tree was also constructed for the entire class (Figure S1). Glomerales is a sister clade from two groups including all other orders in the class (Entrophosporales as one related clade: Gigasporales and Diversisporales (forming the other clade)). In the tree, it is possible to see these three well-supported separate clades (Entrophosporales; Gigasporales and Diversisporales; Glomerales). All these clades have a relation as sister groups with each other, considering the low support from BI (0.83) and no support from ML separating Entrophosporales from other orders. In general, the orders and families within the Glomeromycetes were separated with strong phylogenetic support. Glomerales is the order with almost 50% of the species and genera described in the phylum Glomeromycota. When the relations of the families in the different orders of Glomeromycetes were compared, it was clear that the old family Glomeraceae needed to be divided into at least five families.

Clades “B”, “C”, “D” and “E” were very well supported by BI and ML analyses using different datasets (except, clade “B”, not supported by ML in the Glomerales SSU-5.8S-LSU tree) to generate the trees and indicate very stable taxa. Clade “A” was supported with good values only for BI of the Glomeromycetes SSU-ITS-LSU tree (Figure S1) and both analyses of Glomerales SSU-ITS-LSU tree (Figure 1). These same clades were found in the tree generated by Corazon-Guivin et al. [21] and Tedersoo et al. [6]. The families Glomeraceae, Dominikiaceae, Septoglomeraceae and Sclerocystaceae are also supported by Corazon-Guivin et al. [19,20].

Clade “A” represents the most heterogeneous clade within the Glomerales, and we are sure that in the future, this group will be divided in further families based first on phylogeny but also on morphology. The genera *Oehlia* and *Halonatospora* form two clades within clade “A” that are well separated from *Silvaspora*, *Sclerocystis* and *Rhizoglomus* and might represent the type genera for such further families within Glomerales. In our trees, *Halonatospora* was placed near *Oehlia*, *Silvaspora*, *Sclerocystis* and *Rhizoglomus*. However, according to the tree

from Tedersoo et al. [6], *Halonatospora* is near *Kamienskia*, *Microkamienskia* and *Epigeocarpum*, which also confirms the lower degree of relationship between *Halonatospora* and the other genera clustering together within Sclerocystaceae. A deeper separation is, in our opinion, fully supported by molecular phylogeny, but in view of the low numbers of taxa, this separation is not yet proposed at this stage of research progress.

Morphologically, all genera listed within Glomerales can clearly be identified based on the combination of their major morphological characteristics: formation of the sporocarp, spore, pore closure and subtending hyphae (see also Silva et al. [5], including an identification key for almost all genera within Glomerales). However, attribution to a distinct family is not unequivocally possible at this stage of research progress, since none of the major morphological characteristics are unique to one of the five families separated here. Some simple indications, however, might at least offer hints for the family attribution, which is the genus identification itself. Otherwise, our simplified Supplementary Material (Table S1) shall help to differentiate and quickly attribute a specific morphotype to a specific genus and thus to the correct family, to which the morphotype and the genus belongs. In this study, we accordingly transferred three *Glomus* species to the genus *Sclerocarpum* based on their unique morphological characteristics, fitting exactly to the latter genus. For other Glomeraceae species, new combinations would also be justified, either based on molecular phylogeny or morphology of the “fruit bodies”, including sporocarps, spores and their subtending hyphae, but at this stage, we do not propose to do so.

The genus *Parvocarpum* [6] was not placed in our phylogenetic analyses because the only sequence available for *P. badium* (the type genus) represents 564 bp of the SSU fragment and 53 bp of ITS1. We conclude that this genus was described mainly based on the high quantity of environmental sequences, which could be attributed to this short SSU-ITS fragment [6]. Solely for morphological reasons, there were already sufficient arguments to describe this genus when the species *P. badium* was originally described, but at that time, the phylogenetic resolution was not provided [37], and the related genus *Sclerocystis* had been synonymized with *Glomus* just a few years before instead of being clearly separated from *Glomus*.

In our trees (Figure S1, 1 and 2), *Macrodominikia compressa* is not grouped with other *Dominikia* spp. According to Tedersoo et al. [6], this species represents a new genus, which is confirmed here and also supported by its distinct spore morphology [5,38], and it was thus described within the present study. By including environmental sequences for reliable spore and sequence identifications [39], more genera and even families can probably be found, since the phylogenetic resolution will further increase. *Rhizoglomus* spp., for instance might then be separated from Sclerocystaceae. This separation is already suggested by our phylogenetic trees.

*Blaszkowskia* was synonymized with *Viscospora* by Tedersoo et al. [6]. The tree generated by these authors present two different major clades for *Viscospora* sensu Tedersoo et al. [6]; one clade is divided in two subclades, the first with one sequence from *B. deserticola* and one environmental sequence and the second with one sequence from *V. viscosa* and six environmental sequences. The second clade has only environmental sequences (28 sequences) and for us could be a new, different genus represented by these sequences. Thus, in our opinion, *Blaszkowskia* continues to be a genus. For morphological reasons, the genera *Viscospora* and *Blaszkowskia* can be easily separated and continued [5].

In the past, and especially during the first stages of molecular phylogenetic classifications, there were several major synonymizations of AMF genera within Glomeraceae, even for genera with distinct spore morphologies. A time of doubts followed, and, for example, *Sclerocystis* was resurrected. In the meantime, molecular phylogeny has become the driving force to identify and separate new taxa, especially at the genus and species levels. With the expected inclusion of environmental sequences directly into taxonomy research, morphological identification might lose its importance and significance, and taxon numbers might strongly increase in Glomeromycota, especially in Glomerales. However, researchers should never stop trying to identify the morphological characteristics of new



taxa that currently are only known from environmental sequences and the identification of which is exclusively molecularly based.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/taxonomy4040041/s1>, Spreadsheet S1: GenBank accession numbers for the sequences used in this study; Table S1: Principal morphological characters of the families and genera within the order Glomerales; Figure S1: Phylogenetic tree from partial SSU, ITS region and partial LSU nrDNA sequences of Glomeromycetes. Sequences are labeled with their database accession numbers. Support values from Bayesian inference (BI) and maximum likelihood (ML) are shown only for the genera level or above. Only support values of at least 65% are shown. Thick branches represent clades with more than 90% of support in all analyses. The new genus is in bold. The tree was rooted by *Paraglomus brasilianum*.

**Author Contributions:** All authors contributed to the study's conception and design. Phylogenetic analyses were performed by G.A.d.S. and morphological analyses by E.S. and F.O. The manuscript was written and revised by all authors. All authors have read and agreed to the published version of the manuscript.

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