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REVIEW

An evidence-based consensus for the classification of arbuscular mycorrhizal fungi (*Glomeromycota*)

Dirk Redecker · Arthur Schüßler · Herbert Stockinger · Sidney L. Stürmer · Joseph B. Morton · Christopher Walker

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Abstract The publication of a large number of taxon names at all levels within the arbuscular mycorrhizal fungi (*Glomeromycota*) has resulted in conflicting systematic schemes and generated considerable confusion among biologists working with these important plant symbionts. A group of biologists with more than a century of collective experience in the systematics of *Glomeromycota* examined all available molecular–phylogenetic evidence within the framework of phylogenetic hypotheses, incorporating morphological characters when they were congruent. This study is the outcome, wherein the classification of *Glomeromycota* is revised by rejecting some new names on the grounds that they are founded in error and by synonymizing others that, while validly published, are not evidence-based. The proposed "consensus" will provide a framework for additional original research aimed at clarifying the evolutionary history of this important group of symbiotic fungi.

Keywords *Glomeromycota* · Classification · Taxonomy · Phylogenetics

D. Redecker (✉) · H. Stockinger
Université de Bourgogne/INRA, UMR 1347 Agroécologie,
17 rue Sully, BP 86510, 21000 Dijon, France
e-mail: dirk.redecker@dijon.inra.fr

A. Schüßler
Department Biology I, Genetics, Ludwig-Maximilians-University of Munich, Großhaderner Straße 4,
82152 Planegg-Martinsried, Germany

S. L. Stürmer
Departamento de Ciências Naturais,
Universidade Regional de Blumenau, Cx.P. 1507,
89012-900 Blumenau, SC, Brazil

J. B. Morton
West Virginia University, 1090 Agricultural Sciences Building,
Morgantown, WV 26506, USA

C. Walker
Royal Botanic Garden Edinburgh, 20A Inverleith Row,
Edinburgh EH3 5LR, UK

C. Walker
School of Earth Sciences and Environment,
University of Western Australia, 35 Stirling Highway,
Crawley, WA 6009, Australia

Introduction

The publication of new scientific and formal names and taxonomic classifications should be undertaken with great care because of its considerable impact on a scientific community that extends well beyond the circles of taxonomists and phylogeneticists. The recent publication of numerous new taxa at all levels within the *Glomeromycota* has created confusion and operational difficulties for those working with arbuscular mycorrhizal fungi (AMF). We have examined these changes and found that some were based on selective analysis (bias) or erroneous interpretation of poor quality data. Therefore, we conclude that many of the recent taxonomic revisions do not reflect a robust phylogenetic framework and thus will not provide the strong foundation needed to conduct good science in the field of AMF taxonomy and systematics.

The most widely usable taxonomy is one founded on a scientifically sound phylogenetic classification which, by definition, must infer evolutionary changes that have resulted in speciation. Taxonomy is a comparative science and requires intensive and long-term study of many specimens and developmental stages of an organism rather than a casual and short-term examination of a few scraps. The requirements for good scientific practice and communication are of particular importance in the *Glomeromycota*. The

fungi in this phylum are exclusively obligate symbionts and thereby pose problems not encountered for many other groups of organisms. Only if the classification of AMF reflects universal evolutionary patterns and processes will it provide an operational framework for research into understanding these complex and ecologically vital organisms.

Concerned systematists with long and extensive experience studying the biology and taxonomy of AMF formed a working group with the goal of reevaluating all of the evidence available in the current literature and incorporating new data essential to the analysis. This work represents interpretations and conclusions that, in general, are shared among all authors. Some differences in viewpoints existed, but they were discussed and adjusted to achieve compromise and share a vision of a conceptual framework that was based on all available evidence and hence acceptable to all. To achieve this goal, four tasks were undertaken. First, fundamental and essential points that should be considered in any systematic analysis were summarized. Second, taxa in *Glomeromycota* recognized as problematic because of conflicts of scientific importance were reanalyzed from existing or new evidence. Third, nomenclature was revised to resolve these conflicts where possible. Last, the group's discussions and analyses were incorporated into a consensus classification (Fig. 1) intended to be meaningful to the broader scientific community.

The role of the Code

Naming fungi is covered by rules and recommendations, published in the past as the *International Code of Botanical Nomenclature* (*ICBN*) (McNeill et al. 2006). The most recent revision, the *International Code of Nomenclature for Algae, Fungi, and Plants* (*ICN*) (Miller et al. 2011; McNeill et al. 2012) is applicable from 1 January 2012. These regulations (known collectively as "the Code") are intended to "provide clear, fair rules that provide stability to the fundamental process of naming organisms and reflect changes in technology and in the science underpinning this process" (Miller et al. 2011). Nomenclature (the application of names) and taxonomy (arranging these names in a hierarchical classification system) are different but still closely related. The Code strictly regulates the former, but merely provides a nomenclatural framework for the latter. Consequently, names published within the rules may be validly published, but have no relation to a "natural," phylogeny-based classification. This can create difficulties when the classification is intended to reflect evolutionary relationships. Most importantly, there is nothing to prevent the creation of nonmonophyletic taxa that eventually must be resolved either by synonymization or by creating additional taxa. In general, it should be noted that the erection of new taxa that are not supported by concrete evidence is against the spirit of the Code because such efforts disrupt rather than clarify a classification.

Before molecular biological tools were available, species in the *Glomeromycota* were named solely from morphological evidence. For many of these fungi, nothing was known about their nutritional associations, whereas others were proven to be arbuscular mycorrhizal symbionts. In a revision of the ordinal, familial, and generic relationships (Schüßler and Walker 2010), such species of unclear phylogeny retained their current generic name because of uncertainty in their taxonomic positions. In contrast, species whose relationships were defined by well-supported molecular evidence were placed in the corresponding existing, new, or based on priority, resurrected taxa. Recently, in what can only be considered a seriously retrograde move, Oehl et al. (2011b) moved those species, together with several of the formally defined new combinations, back into the genus *Glomus* in its former nonmonophyletic state. At the same time, these authors applied a contrary "strategy" and split other well-established taxa into new ones, erecting a larger number of new taxa including some that consisted of only monogeneric or even monospecific families. Such proliferation of taxa establishes nomenclatural priority, but much of the work did not follow an appropriate rationale because it lacked evidentiary foundations. As a consequence, the Code's aim of establishing a stable and scientifically based nomenclature not only was not achieved, but was seriously compromised.

General principles and recommendations

Formal nomenclatural changes should be based fundamentally on patterns and processes that reflect biological significance

Formal recognition of the research and evidence that justifies nomenclatural changes is outside the purview of the Code, but nomenclatural changes are not scientifically sound unless compelling and justifiable evidence exists to warrant them. Only then can stability in an evolving classification be preserved as much as possible.

Morphological data are meaningful when representing evolution of a broad range of genes

Morphological data can be easily misinterpreted without careful study and well-defined comparative analyses. Characters distributed among taxa of distant clades, as defined by other datasets, should not be used because they probably are homoplastic (analogous, convergent

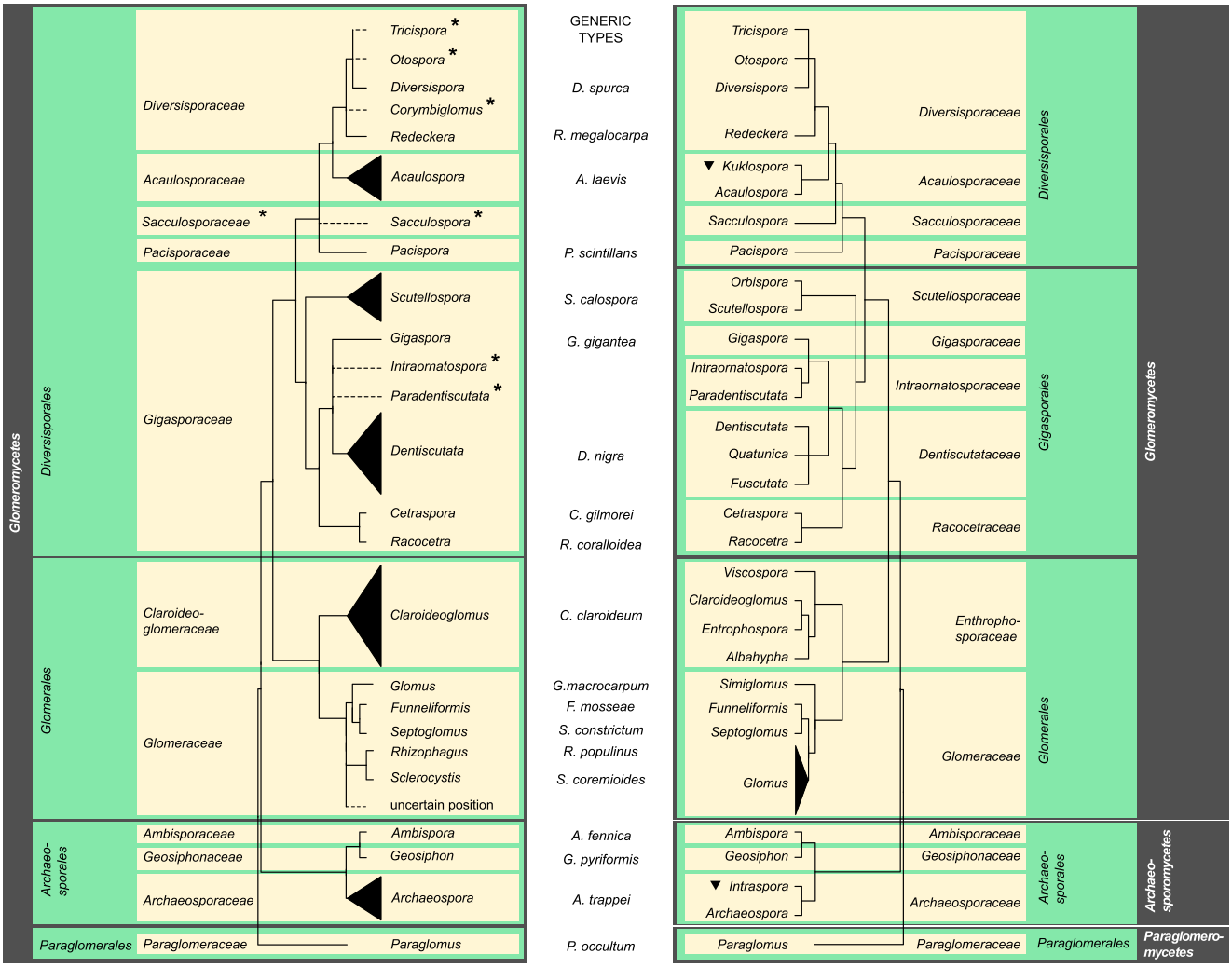

Fig. 1 Consensus classification of the *Glomeromycota* (*left panel*) in comparison to the system summarized by Oehl et al. (2011f) (*right panel*), including additional taxa proposed by Goto et al. (2012a). *Dashed lines* indicate genera of uncertain position, *asterisks* indicate insufficient evidence, but no formal action taken, *inverted triangles* indicate taxa already rejected in previous publications

characters) and thus are not phylogenetically significant. Robust tests of homology are available and should always be implemented. Characters with a broad range of phenotypic variation may not be sufficiently discrete to function as apomorphies (derived characters) and thus may reflect only population-level evolution rather than speciation events. Discrete and stable differences do not necessarily reflect speciation events because AMF are, as far as is known, asexual and mutations can be expressed within populations and become rapidly fixed and maintained indefinitely if they are not deleterious. An example is an albino mutant of *Scutellospora heterogama* (Morton and Msiska 2010a). Given the lack of complexity in many of the characters available, these should be interpreted as most informative when they are congruent with one (or preferably more) gene phylogenies. For these reasons, we recommend that morphological and molecular data should be collected together as much as possible to provide independent tests of species evolution. Exclusive use of morphological data should be limited to exceptional cases where supporting data are unambiguous.

DNA sequence data should be linked to material that can be verified independently and have clear provenance

The use of third-party DNA sequence data without consideration of its veracity to erect new taxa is dangerous because it may be error-prone or subject to misinterpretation. The pitfalls of the annotations in public sequence databases have been known for many years. These databases explicitly serve as repositories of sequence data, with validation dependent on the vigilance of the scientific community and the commitment of depositors to making necessary corrections.

Short DNA sequences of low resolving power or hypervariable regions that cannot be evaluated for homology should not be used to define taxa higher than species

Short sequences cause ambiguity because phylogenetic signal is so low there is little statistical support for topologies in phylogenetic trees. This leads to severe problems in the comparability of taxa and the interpretations that emerge. Short partial SSU sequences do not resolve species of AMF, and even full-length SSU sequences fail to resolve closely related species (Walker et al. 2007). Higher-level taxa can also not be defined satisfactorily from short sequence data alone. Multilocus phylogenies are widely recognized as providing more robust evidence of taxon evolution than single-locus phylogenies, although the outcome depends on the quality (e.g., sequence variability, existence of paralogs) of the loci chosen and often limited taxon sampling is a major problem.

A taxon at any rank must be defined by the criterion of monophyly

To fit within a systematic scheme based on a phylogenetic species concept, in particular for asexually reproducing species where a biological species concept is difficult to apply, a taxon at any rank must be defined by the criterion of monophyly. Erection of paraphyletic taxa violates this principle because phylogenetically relevant relationships become obscured. Disregarding phylogenetic principles creates taxonomic instability and confusion that can be corrected only by new analyses and even more nomenclatural changes. Monotypic genera, families, or higher-level taxa should only be erected in cases of very strong evidence for separation. Even then, any revision is tenuous because such taxa are being defined in the absence of sufficient comparative data. The topology of phylogenetic trees is sensitive to the taxa being sampled, so subsequent discovery of additional taxa could significantly alter patterns of weakly supported relationships. Extensive "taxon splitting" abuses the rules of nomenclature by establishing priority for names that are not based on sound phylogenetic principles, and the result is a confusing proliferation of taxa in tenuous or erroneously determined relationships.

Ranking decisions for monophyletic groups should be consistent within and among clades of a phylogenetic scheme, as much as possible

For a classification of AMF to be broadly representative of evolutionary patterns throughout phylogenetic trees, genetic distances should be reasonably comparable. Moreover, assignment of taxonomic rank should at least roughly conform to equivalent divergence of clades throughout the tree to reflect inferences when and where evolutionary splits occurred.

Taxonomists should discuss their concepts with colleagues to achieve the broadest consensus

Conflicting hypotheses or ideas are important to motivate progress in science, but only if they are based on legitimate conflicts in data or analyses. The Code does not formally require peer review for the publication of valid names, but the inevitable criticisms and temporal delays generally inherent in peer review systems should be seen as an opportunity to refine taxonomic concepts. If taxonomy is perceived by the scientific community as an endeavor in which even those specializing in the field will not communicate and for which standards of scientific proof and presentation of evidence are rejected or compromised, its impact will suffer.

However, there appears to be a trend of an increasing reluctance of peer-reviewed journals to accept purely taxonomic works, which may be an additional reason for taxonomists to avoid them. This situation calls for action by the peer-reviewed mycological journals to reserve some space for taxonomy papers because they often provide basic information for studies such as those in molecular ecology. At the same time, journals specialized in taxonomic matters need to tighten their standards. A particular case is the journal *Mycotaxon*, whose subject matter includes a strong focus on fungal taxonomy. Some of the recent papers on AMF published in *Mycotaxon* have resulted in very confusing taxonomies that have required modification very soon after publication. It should be noted that this journal has a somewhat unusual reviewing policy, where authors are requested to obtain their own reviewers from outside the senior author's home institution. This policy may satisfy peer-reviewing standards if these reviewers are independent of the authors, but conflicts of interest may arise depending on whom authors select. Effective publication of a taxonomic work automatically establishes the nomenclature as valid and can be overturned only by extensive revisionary efforts such as those being proposed in this paper. The policies of some journals can raise questions of autonomy in the review process, such as allowing frequent coauthors to serve as reviewers (e.g., Goto et al. 2012b) or turnaround times of only 8 days for a major taxonomic synthesis (Oehl et al. 2011f).

The articles (rules) of the Code must be followed

The Code contains rules, some of which are mandatory (called Articles) and some advisory (called Recommendations). The

former must be followed for taxa to be accepted. The recommendations are for guidance only. While it is best to follow the recommendations, there may be occasions where they can be ignored.

Nomenclatural changes must be accompanied by reference to a valid type

Names of taxa below the rank of family must be linked to a specimen designating a species, known as the "type." The Code nowadays specifies that the type must be a single collection, which means that it cannot be derived from collections taken from different locations or at different sampling dates. It recommends that the type should be deposited in a herbarium or other public collection with a policy of giving bona fide researchers access to deposited material and that the type be scrupulously conserved. Unfortunately, this is not always followed and some types of glomeromycotan taxa are not readily available.

If type material is not available or in poor condition, as is the case with many of the older species placed in the *Glomeromycota* and particularly in the genus *Glomus* in its broad sense, those species or taxa should be considered to be of uncertain taxonomic position. A recent case in which the type is almost uninterpretable is that of *Otospora bareae*. It was examined on loan from the herbarium in Zurich where it had been lodged. The spores were in such poor condition that wall structure was impossible to interpret and any reference to ontogeny could not be inferred. Almost all spores were empty of contents or they were invaded by non-AMF. From the condition of these specimens, it is not easy to see how good quality DNA could be assigned to this organism with any degree of confidence. Assigning these specimens to a species, let alone a genus or suprageneric taxon, communicates a false sense of certainty regarding its phylogenetic validity. The Code in fact makes provision for such a situation by placing such organisms incertae sedis: using the literal translation, "of uncertain position," is nowadays preferable.

Reference to the type material must be factually correct. For example, in the list of material examined in Oehl et al. (2011b), *Glomus convolutum* is claimed to have been examined from "ex-isotype (Oehl)" specimens. According to Article 8B.2, the term ex-type is specified as to be used for living material derived from metabolically inactive culture type material, though the term has also been used to describe specimens directly descended from a living "type culture" (Schüßler et al. 2011). Such material, by definition, is not actually the nomenclatural type. Thus, the term "ex-isotype" would be interpreted to mean that the specimens were derived from a living descendant culture of isotype material, which by definition must be the same as that giving rise to the type (an isotype is part of the type). This cannot be the case, as the type of *G. convolutum* is from a field collection of J.M. Trappe, Oregon, USA (Trappe 2778; Gerdemann and Trappe 1974), and the species, as far as is known, has never been established in culture. We, therefore, assume that the authors probably studied isotype specimens.

Similar statements have been made for other species, including *Glomus canum*, *Glomus cerebriforme*, *Glomus cuneatum*, *Glomus glomerulatum*, and *Glomus macrocarpum*, for which ex-type cultures could not have existed. It would be beneficial if such species, where possible, were epitypified with specimens derived from living cultures that can be made available for future study.

For species descriptions, it is essential (indeed, mandatory) that type material be lodged. A recent species, *Dentiscutata nigerita*, was described, and although it is written that the holotype was deposited in the Department of Botany, Goa University, India (Khade 2010), enquiries have revealed that no such specimens were deposited or exist (S.W. Khade, personal communication; P.K. Sharma, Professor and Head, Department of Botany, Goa University, personal communication). Moreover, when type materials are lodged, all details that will allow access by independent investigators should be communicated in the pertinent publication.

Living cultures should ideally be available so taxa can be studied further

Although there is no requirement in the Code that a name must be attached to a living organism, it is highly desirable that cultures of *Glomeromycota*, particularly those used for derivation of type material, are available. These cultures then can be scrupulously conserved in more than one culture collection so that future workers can continue to work on them. Indeed, recommendation 8B.1 of the Code states that, whenever practicable, a living culture from the holotype material of the name of a newly described taxon should be deposited in at least two institutional culture or genetic resource collections. With new species, restraint should be exercised when apparently undescribed species are found in field collections or even in trap pot cultures. Every effort should be made to establish pure cultures, and only after such efforts have failed should erection of new species even be considered, and then only for organisms with some major characteristic that is very different from anything known in existing species. For new genera that are segregated from existing ones by using the type of an already named species, it is important to check for available cultures and to use only species that are available as such cultures for types. As one example where such practice has not been followed, *Cetraspora* and *Dentiscutata* were new genera typified by Oehl et al. (2008) using species in *Gigasporaceae* not

known to be in culture in any public collection, even though both the proposed genera contained fungi readily available from culture collections. Erection of *Fuscutata* was based on a culture available in the International Culture Collection of Arbuscular Mycorrhizal Fungi (INVAM) originating from Brazil, but no accession number was specified in their publication and, therefore, the material could not be traced directly to its source culture. Only by inference and by testing all available INVAM cultures was it possible to obtain important additional information. In another example, the genus *Intraornatospora* was defined from a fungus known only from field collections and, therefore, is not available for corroboration or further study by the scientific community (Goto et al. 2012a).

It is desirable that, for any taxonomic treatment to be thorough, it should encompass all relevant taxonomic analyses previously published and logically justify all changes from documented evidence

Cases exist where published references were selectively omitted, with the result that taxonomic changes are based on incomplete data that undermine the classification until further revisions are made. One example is the description of three new genera within the context of a classification (Oehl et al. 2011b) that resurrected family names rejected by Morton and Msiska (2010b) and Schüßler and Walker (2010), without any reference or discussion of these works. Oehl et al. (2011a) further erected two new classes and a new order in the *Glomeromycota* without correcting earlier errors, despite published evidence to the contrary. In a second example, the new species *Entrophospora nevadensis* was described from spores from a soil trap culture, along with partial DNA sequences. Attention was drawn to the unexpected phylogenetic position of this fungus when morphology was considered (Schüßler et al. 2011). However, instead of considering factors that account for such unusual placement, Oehl et al. (2011e) just placed the species in a new monospecific genus, *Tricispora*. A third example was incorrect generic placement of *Ambispora brasiliensis* (Goto et al. 2008). Examination of the type material and new collections from Scotland showed that the species had to be transferred to *Acaulospora* (Krüger et al. 2012). In a brief comment, without examining the Scottish specimens and lacking reference to any further evidence, Oehl et al. (2011c) wrote that this synonymy "… cannot be accepted …" because the "… spore morphology of the Scottish fungus … does not match the morphology of *Am. brasiliensis* …." More to the point, the actual spore morphology of the holotype of *Ambispora brasiliensis*, which is of relatively poor quality, does not match its species description, but matches the phenotype of the Scottish fungus (Fig. 2).

Taxonomic errors should be corrected as soon as possible

An error was made when the former *Glomus vesiculiferum* was transferred to the genus *Funneliformis* (Schüßler and Walker 2010). The error was "flagged" shortly afterwards on the website amf-phylogeny.com and in a corrigendum, but had not been formalized, despite the passage of almost 2 years. The species should be in the genus *Rhizophagus*, and the correction is made here.

Rhizophagus vesiculiferus (Thaxt.) C. Walker & A. Schüßler comb. nov. IF550088

≡ *Funneliformis vesiculiferum* (Thaxt.) C. Walker & A. Schüßler, *The Glomeromycota*, a species list with new families and new genera (Gloucester): 14 (2010).
≡ *Endogone vesiculifera* Thaxt., Proc. Amer. Acad. Arts & Sci. 57: 309 (1922).
≡ *Glomus vesiculiferum* (Thaxt.) Gerd. & Trappe [as '*vesiculifer*'], Mycol. Mem. 5: 49 (1974).

Similarly, the species *Glomus iranicum* was erroneously transferred to *Rhizophagus*, though it belongs, as a species, to a basal lineage in the *Glomeraceae* that has as yet unknown taxonomic affiliation. Its original name, *G. iranicum*, should, therefore, be retained.

Glomus iranicum Błaszk., Kovács & Balázs Mycologia 102: 1457 (2010)

≡ *Rhizophagus iranicus* (Błaszk., Kovács & Balázs) C. Walker & A. Schüßler, *The Glomeromycota*, a species list with new families and new genera (Gloucester): 19 (2010).

Discussion of taxa requiring formal changes

Taxa at the class level

The Code stipulates that, for any given circumscription of taxa from the ranks of species to family, there can be only one correct name. *Index Fungorum* (http://www.indexfungorum.org/) endeavors to list the "current name" of fungi, though it may not always be completely up to date. In contrast, for taxa above the rank of family, the scientific community decides which validly described higher taxon systematics it will accept. Thus, different systems may exist in parallel for higher taxa, but of course the use of only one such system is most advantageous. Moreover, any nomenclatural change at these levels should have strong biological justification.

While no universal criteria exist for ranking of taxa higher than family, any nomenclatural change at these levels should take into account the evolutionary history of the included taxa. Our understanding of life history and other

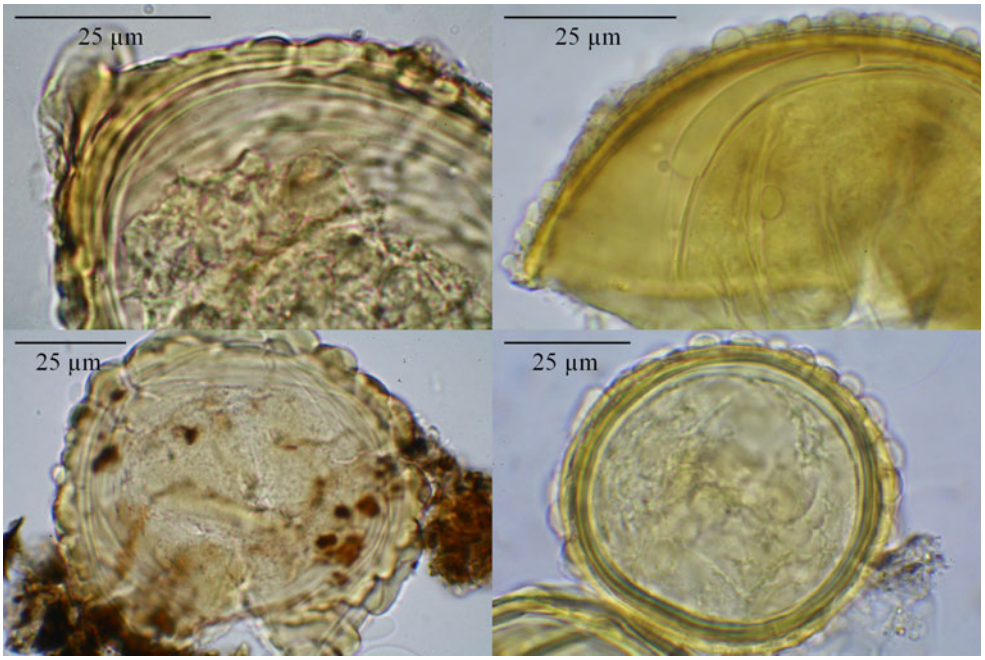

Fig. 2 Type material of *Ambispora brasiliensis* (*left*) and specimens of *Acaulospora brasiliensis* from Scotland (*right*) showing similar morphological characteristics

traits among glomeromycotan higher taxa is almost nonexistent at the present time, and so we rely on congruent topology of as many gene trees as possible to resolve relationships at these levels. All four clades corresponding to orders (*Glomerales*, *Diversisporales*, *Paraglomerales*, and *Archaeosporales*) are congruent and represent the next level of dichotomy in all trees above the rank of family and, therefore, are justified by current evidence (Schüßler and Walker 2010; Msiska and Morton 2009; Walker and Schüßler 2004; Schüßler et al. 2001). There is no need to elevate these clades to class rank except perhaps to enlarge the "container" within which more taxa at lower ranks can be erected. The lack of morphological evidence is emphasized when considering that the range of analogous characters used to rank classes in other groups of fungi are homoplasies in *Glomeromycota*. One example where a character is used at the wrong level of resolution is "spore dimorphism," which served as the basis for erection of the *Archaeosporomycetes*. This character is neither unique to this clade nor is it conserved in all of the taxa comprising this clade. The outcome, then, has been a proliferation of new classes devoid of any information that contribute meaningfully to the phylotaxonomy of the *Glomeromycota*. Erection of such "empty taxa" at these higher ranks has a destabilizing effect of not only magnifying difficulties in making corrections but also of inhibiting objective integration of new data.

Therefore, we consider that current data do not support splitting the phylum *Glomeromycota* into three classes *Glomeromycetes*, *Archaeosporomycetes*, and *Paraglomeromycetes* (Oehl et al. 2011a) and thus conclude that all glomeromycotan orders group into only one class, the *Glomeromycetes* (Fig. 1).

Taxa at the order level

Oehl et al. (2011b) divided *Diversisporales* to erect *Gigasporales* as a group of equivalent rank. No published molecular phylogeny supports this ranking decision because *Gigasporales* sensu Oehl et al. (2011f) is not a clade positioned equivalently to other clades designated as orders. Rather, it is nested within the clade classified as *Diversisporales*. The ranking criterion of principle equivalency in clade topology thus is violated. As a result, *Gigasporales* is also rejected here as being unsupportable.

Retained in place are the four orders *Glomerales*, *Diversisporales*, *Archaeosporales*, and *Paraglomerales*, as proposed by Schüßler et al. (2001) and Walker and Schüßler (2004), because available sequence data indicate they are near-equivalent sister groups (Fig. 1).

Taxa at the family and genus levels

Glomeraceae

Glomus, Sclerocystis, Rhizophagus, and Funneliformis are valid genera Oehl et al. (2011b) rejected the concept of genera in the *Glomeraceae* as proposed by Schüßler and Walker (2010), stating they were unable to recover *Rhizophagus* as a monophyletic group. This rejection is a contradiction in that these same authors erected a proliferation of new taxa based partly on conflicting tree topologies used as evidence in the same paper. Strikingly, their analyses did not take *G. macrocarpum* into consideration, which is the type species of the genus *Glomus* and thus of the

Glomeromycota. Any classification which fails to consider the type species of the discussed genera ignores essential evidence and greatly weakens its validity. *Glomus* (defined by *G. macrocarpum*) clearly separates from the clade containing *Rhizophagus* and *Sclerocystis* species at the generic level. Therefore, the circumscription of the genus *Glomus* as proposed by Oehl et al. (2011b) is both unsupported and unacceptable. For that reason, we recognize *Glomus*, *Rhizophagus*, *Sclerocystis*, and *Funneliformis* as distinct monophyletic clades and genera. As a nomenclatural matter, the names assigned at the time of their erection in published descriptions to the genera *Glomus*, *Rhizophagus*, and *Sclerocystis* have to be applied again to the corresponding groups to satisfy the principle of priority. We consider the monophyly of *Sclerocystis* and its relationship with *Rhizophagus* to require further clarification through the collection of new data from additional well-documented and verified sporocarpic species. Pending such work, these existing genera have nomenclatural priority and cannot simply be ignored, as was done in Oehl et al. (2011b). To clarify again the nomenclature of the widespread model fungus MUCL43194 or DAOM197198, this organism, previously considered to be *Glomus intraradices*, corresponds to a different species, described with the basionym (the original, validly published name) *Glomus irregulare*, and its current valid name is *Rhizophagus irregularis*.

Septoglomus is accepted as a genus We accept the argument for the separation of *Septoglomus* (Oehl et al. 2011b) from *Funneliformis*, though we would have preferred a more conservative approach because the rigor of evidence to justify the separation does not match that applied to *Glomus* sensu stricto and *Funneliformis*. The morphological characters used to define *Septoglomus* are symplesiomorphies (shared ancestral characters; color and shape and degree of wall thickening of the subtending hypha, lack of spore wall thickening, occlusion by a proximal or distal septum in the subtending hypha), and thus cannot define monophyletic groups. Moreover, these characters are neither sufficiently conserved nor are they inherited by all of the transferred species, so they are not phylogenetically informative. Nevertheless, we recommend that the genus be retained pending further investigation, based on the rDNA phylogenies and also from analysis of partial rpb1 sequence data (H. Stockinger et al., in preparation).

Glomus constrictum is the species used as the basionym of the genus *Septoglomus*. The original description of this species was based entirely on field-collected material preserved in lactophenol and so type specimens cannot be tested by molecular analysis. Oehl et al. (2011b) based their analysis on examination of paratype rather than holotype specimens. Paratypes do not have any status in typifying a species name when the type exists. To verify the phylogenetic position of this species by independent molecular characters, the only realistic option was to define an epitype from a living strain with similar morphological traits (herein defined from Attempt 756-1). Material from this culture was used by Krüger et al. (2012) in a molecular–phylogenetic analysis of the SSU rRNA gene.

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

Basionym: *Glomus constrictum* Trappe Mycotaxon 6: 361 (1977). **Holotype**: Trappe 3574 (OSC; isotype ENCB).

≡ *Funneliformis constrictus* (Trappe) C. Walker & A. Schüßler, *The Glomeromycota*, a species list with new families and new genera (Gloucester): 14 (2010).

Epitype: W3809, 11 Dec. 2001, in the C. Walker collection at E, **here designated**. Derived from the culture isolated from soil beneath *Centaurea stoebe*, in a sandy heathland, Germany, Darmstadt, Truppenübungsplatz, with the designator Attempt 756-1, a single spore isolate established by C. Walker & A. Schüßler, in its ancestry (representative nucleotide sequence of SSU rRNA gene: FR750212).

Simiglomus is rejected as a genus The establishment of *Simiglomus* as a new genus (Oehl et al. 2011b) was based on two SSU rDNA sequences obtained from a pot culture designated UY110. This culture produced both a sporocarpic *G. macrocarpum*-like fungus (W3344) and morphologically distinct ectocarpic spores. The ectocarpic spores were identified first as *Glomus hoi* by Helgason et al. (2002), which was the provenance for sequence AF485889. Schwarzott et al. (2001) later reinterpreted these spores as an undetermined *Glomus* species, which was the provenance for sequence AJ301857. DNA was not analyzed from the sporocarp. Recent collections from descendants of UY110 have produced only ectocarpic spores, so it is impossible to know whether the cultures consisted of one species producing two spore morphotypes or of two different species. However, a culture named as *G. hoi* from Finland (BEG104, accession number AM743188) yielded SSU sequences that cluster with those from UY110 (Sýkorová et al. 2007).

At issue is evidence that spores from neither UY110 nor BEG104 cultures share the morphology of *G. hoi*, which was described from specimens of a pot culture established from roots of *Fragaria chiloensis* collected at Tombstone Pass, Oregon (Berch and Trappe 1985). Spores of the ectocarpic fungus in UY110 and BEG104 do not possess the "membranous inner wall layer" or the "sloughing outer wall surface" used to define the species (Fig. 3). As a consequence, the two published sequences derived from these cultures cannot be linked to the physical description of *G. hoi*, and they probably represent the genotype of a different AMF species. In fact, the holotype cited as the basionym of the genus was not included in the deliberations

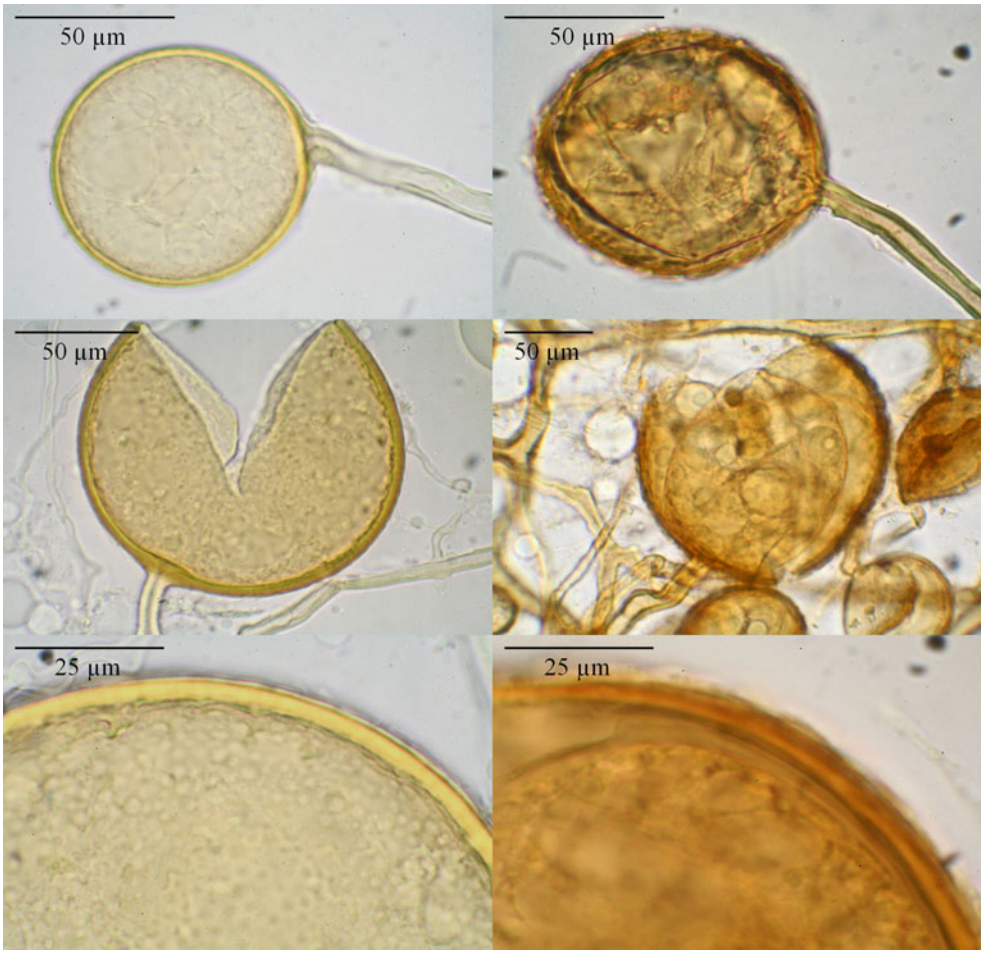

Fig. 3 Details of spores from UY110 (*left*) and the type of *Glomus hoi* (*right*) showing different morphological characteristics

of Oehl et al. (2011b), even though the requirements of the Code make it abundantly clear that the type must be respected as the foundation of the taxon name. The nomenclatural type of *Simiglomus* (*G. hoi*) must be returned to "species of uncertain position in *Glomus* sensu lato," the sequences from UY110 (accession numbers KC182044 and KC182045) and BEG104 (KC182046–KC182048) cluster within the *G. macrocarpum* clade, and *Simiglomus* must be rejected as a genus. This is an example where the basionym of a supposedly new genus represents one organism, but the molecular evidence, upon which the generic status is based, originates from a different species.

Glomus hoi S.M. Berch & Trappe, Mycologia 77: 654 (1985). **Holotype** Trappe 2116 (= OSC29177).

≡ *Simiglomus hoi* (S.M. Berch & Trappe) G.A. Silva, Oehl & Sieverd. in Oehl, Silva, Goto & Sieverding, Mycotaxon 116: 104 (2011).

Claroideoglomeraceae (sensu Schüßler and Walker 2010)

The placement of Entrophospora is unsure (of uncertain position) and Clariodeoglomeraceae is a valid family The erection of *Entrophosporaceae* (Oehl et al. 2011e) as a family that includes *Claroideoglomus* as a member genus is not supported by any evidence, and therefore, was a purely speculative decision. *Entrophospora infrequens* forms spores that are morphologically and developmentally quite distinct from all other species within *Claroideoglomus*. Yet both SSU and LSU rDNA sequences embed this species in the *Claroideoglomus* clade. The incongruence between morphological and molecular characters cannot be explained from either dataset. It is not even certain that *E. infrequens* represents a distinct monophyletic species equivalent to other species within *Claroideoglomus*, and consequently, its recognition as a taxon of equivalent rank is unsupportable. There are aspects of the *Claroideoglomus* clade which suggest atypical evolutionary patterns compared to that in other glomeromycotan clades. Sequences from several closely related but morphologically distinct species intergrade possibly as the result of retention of ancestral polymorphisms (VanKuren et al. 2012). Given the ambiguity in patterns of speciation within *Claroideoglomus*, erection of a new family, *Entrophosporaceae*, is not only premature but also unjustified. Therefore, we do not recognize the *Entrophosporaceae* and return the genus *Entrophospora* to "as of uncertain position"

until evidence is discovered that clarifies the yet unclear relationship of *E. infrequens* with other species in the *Glomeromycota*.

Viscospora is rejected as a genus *Viscospora* (Oehl et al. 2011b) is another example of a genus erected based on uncritical use of third-party data. The single SSU rDNA sequence from *Glomus viscosum* used in their analysis not only places the species in *Claroideoglomeraceae*, but fails to provide sufficient evidence to define a clade that warrants rank as a new genus. The clustering of this SSU rDNA sequence from an ex-type culture of *G. viscosum* in *Claroideoglomus* seemed problematic and Schüßler and Walker (2010) suggested the possibility that the sequence may have originated from a contaminant AMF in the ex-type culture. Reexamination of this culture revealed that it was contaminated by a *Claroideoglomus* species, so the most parsimonious conclusion was that this sequence belonged to the contaminant fungus rather than *G. viscosum* (Krüger et al. 2012). We tested rDNA sequences from other cultures determined to be *G. viscosum* (BEG50, INVAM MD215) and they grouped within the *Septoglomus* clade (accession numbers KC182036, KC182037, KC161976–KC161978). To answer the question about the affiliation of the species, the ex-type culture was purified resulting in Attempt 179-15 of *G. viscosum* (corresponding to BEG27). New rDNA sequences (accession numbers HF548853–HF548863) were obtained from two individual spores of this culture and grouped in the *Septoglomus* clade, together with sequences from other putative *G. viscosum* cultures (accession numbers KC182038–KC182040). These data provide conclusive evidence that *G. viscosum* is a member of *Septoglomus* rather than a unique monophyletic clade warranting erection as a new genus.

Septoglomus viscosum shares few morphological characters with other species in the genus, so these traits do not appear to be phylogenetically informative in defining the clade at the genus level. Like *Paraglomus*, which was initially found to have distinct fatty acid profiles (Graham et al. 1995) and later separated based on DNA sequences (Morton and Redecker 2001), *Septoglomus* currently must be considered largely a morphologically cryptic genus that is dependent on molecular analyses for its classification.

Septoglomus viscosum (T.H. Nicolson) C. Walker, D. Redecker, D. Stille & A. Schüßler comb. nov. **IF550089**.

≡ *Viscospora viscosa* (T.H. Nicolson) Sieverd., Oehl & G.A. Silva in Oehl, Silva, Goto & Sieverding, Mycotaxon 116: 108 (2011).
≡ *Glomus viscosum* Glomus T.H. Nicolson in Walker, Giovannetti, Avio, Citernesi & Nicolson, Mycol. Res. 99: 1502 (1995).

Albahypha is rejected as a genus Sequences of *Albahypha walkeri* and *Albahypha drummondii*, the only species transferred to this genus by Oehl et al. (2011e), cluster within the *Claroideoglomus* clade (Krüger et al. 2012). Not only was there no significant support in the LSU tree to support the genus *Albahypha* (Oehl et al. 2011e) but this move also creates the untenable situation where *Claroideoglomus* is rendered paraphyletic. Therefore, the two species in *Albahypha* are returned to the genus *Claroideoglomus*.

Claroideoglomus walkeri (Blaszk. & C. Renker) C. Walker & A. Schüßler in Schüßler & Walker, *The Glomeromycota*, a species list with new families and new genera (Gloucester): 22 (2010).

≡ *Glomus walkeri* Blaszk. & C. Renker, Mycol. Res. 110: 563 (2006).
≡ *Albahypha walkeri* (Błaszk. & Renker) Sieverd., Oehl, B.T. Goto & G.A. Silva, Mycotaxon 117: 309 (2011).

Claroideoglomus drummondii (Blaszk. & C. Renker) C. Walker & A. Schüßler in Schüßler & Walker, *The Glomeromycota*, a species list with new families and new genera (Gloucester): 22 (2010).

≡ *Glomus drummondii* Błaszk. & Renker, Mycol. Res. 110: 559 (2006).
≡ *Albahypha drummondii* (Błaszk. & Renker) Sieverd., Oehl, B.T. Goto & G.A. Silva, Mycotaxon 117: 308 (2011).

Acaulosporaceae

Kuklospora is rejected again as a genus The synonymization of *Kuklospora* with *Acaulospora* by Kaonongbua et al. (2010) was substantiated by the phylogenetic analysis of Krüger et al. (2012). Placement of *Acaulospora kentinensis* and *Acaulospora colombiana* in a separate genus, *Kuklospora*, infers that they evolved from an ancestor separate from the most recent common ancestor of other species in *Acaulospora*. There is no evidence to support such a conclusion. Instead, Oehl et al. (2011a, f) completely disregarded the analysis of Kaonongbua et al. (2010) and retained a genus phylogenetically unsupportable by all available evidence. Mode of spore formation within the neck of a sporiferous saccule is a convergent trait because it also arose in other highly divergent clades (see the "*Archaeosporaceae*" section). Such strong congruence of both developmental and molecular evidence cannot just be ignored.

Diversisporaceae

Redeckera and Diversispora For both *Redeckera* and *Diversispora*, no action is needed at this time, although it

has to be mentioned that no molecular data are available for several *Redeckera* species listed by Oehl et al. (2011b).

Otospora and Tricispora are questionable genera For the genus *Otospora* (Palenzuela et al. 2008), evidence is insufficient to support a connection between rDNA sequences and the spores from which they were putatively extracted. *O. bareae* is the basionym of this genus and the condition of the source material of this species warrants discussion. First, the type material deposited at the herbarium Z + ZT consists of degraded or parasitized spores. Second, these spores appear to have been obtained from trap cultures, few of which are ever monospecific. Even if only one spore type is produced from a trap culture, this still does not guarantee a pure culture, as nonsporulating species may be present at the time of sampling. No pure cultures were successfully established, which is not surprising considering the condition of the type spores. Given that any impure material used for DNA extraction is easily subject to contamination and that the source specimens in this case likely were degraded, the two published SSU sequences of the species are of questionable provenance. Of equal concern is that these two sequences are short and non-overlapping, so that information content is inadequate to support resolution at the rank of species. The SSU sequences published from two spores were identical. The morphology of *O. bareae* spores and that of other species placed in the same clade differ widely and the phenotype places *O. bareae* spores close to, or conspecific with, *Acaulospora nicolsonii* (= *Ambispora nicolsonii*). There is no unequivocal evidence that the sequences do not come from these two spores. However, huge divergence between morphology and expected phylogenetic position, possible contaminants in pot cultures, possible DNA contamination, poor condition of specimens, and lack of strong evidence that they form an AM symbiosis together cast doubt on the validity of this classification. Further analyses are needed to resolve these ambiguities.

For *Tricispora*, Figs. 17 and 18 in Palenzuela et al. (2010) are described as showing evidence of mycorrhiza formation for *Tricispora nevadensis* (= *E. nevadensis*), but these show glomoid spores clearly attached to each other by common mycelium. These spores are similar to those produced by, for example, members of *Rhizophagus*. Since the cultures were apparently produced in open pots, their association with the spores produced from saccules is not proven, and they could have come from contaminant AMF. According to the protologue (Oehl et al. 2011e), *Tricispora* appears to group with taxa in *Diversispora*, which is not congruent with described morphological characters. The type species of *Tricispora* was described originally as *E. nevadensis* (Palenzuela et al. 2010), but diagnostic characters are not defined clearly because the type material is in such bad condition. No physical specimens directly linked to the type are available from which DNA could be extracted to confirm or determine the taxonomic or phylogenetic position of this species. If the reported sequences were correct, then the most parsimonious solution would simply be to place the fungus in *Diversispora*.

Without more data to clarify monophyly and phylogenetic position, *Otospora* and *Tricispora* can be retained only as "mystery" or "orphan" genera. Zoological nomenclature rules allow the designation of "nomina dubia" for such taxa. While no similar provision exists in the ICN, this designation can be used informally, especially pending an application for the rejection of a name. The names *Otospora* and *Tricispora* are perfect candidates for this treatment because it clarifies their classification status.

Corymbiglomus is retained as a genus but requires verification Błaszkowski (2012) used an LSU rDNA phylogeny to justify the transfer of *Glomus corymbiforme* into a new, yet monospecific genus, *Corymbiglomus*, within the *Diversisporaceae*. We consider this move to be premature, but we accept the genus in the absence of conflicting evidence. *Corymbiglomus corymbiforme* is basal to *Diversispora* species. However, as mentioned earlier in this paper, tree topology is sensitive to taxon sampling and sequence quality and length. In this context, it should be mentioned that the closest potential relative of this clade, *Redeckera*, was not included in the phylogenetic analysis and the sequences used to produce the tree shown in the protologue cannot be reanalyzed as they are not yet publicly available. Moreover, no clearly identified synapomorphy was identified in the protologue. The evidence, as presented, neither provides clear resolution of this taxon as an equivalent sister clade to *Diversispora* warranting genus status nor as a basis for grouping in *Diversispora*. Additional data and analyses clearly are needed to better resolve the relationship between *Corymbiglomus* and putative sister taxa.

Pacisporaceae

No action needed.

Sacculosporaceae

Sacculospora is retained, but its phylogenetic position is unclear The family *Sacculosporaceae* was erected by Oehl et al. (2011e), containing the sole member, *Sacculospora baltica* (former synonym *Entrophospora baltica*) in the new genus *Sacculospora*. The species is distant from other species in the *Glomeromycota*, but it remains completely unclear from the analyses of Oehl et al. (2011e) to which higher taxon it is related. Clearly, a better taxon sampling and more sequences

are needed before these relationships can be satisfactorily understood. As the species clearly does not belong to any other known clade, we accept family and genus pending further study. However, incongruence between molecular and morphological data due to convergent evolution in other entrophosporoid taxa (see section on *Entrophospora*) indicates that interpretation of evolutionary relationships in this genus is ambiguous at this time and requires more data.

Gigasporaceae

Scutellosporaceae, Dentiscutataceae, Racocetraceae, and Intraornatosporaceae are rejected as families It has been known for many years that the genus *Scutellospora* in its original conception is not monophyletic (e.g., Kramadibrata et al. 2000). The split of the *Gigasporaceae* into several families by Oehl et al. (2008) was rejected and the family *Gigasporaceae* was defined comprising the genera *Gigaspora*, *Scutellospora*, and *Racocetra* (Morton and Msiska 2010b). The phylogenetic analyses of rRNA genes indicated the evolution of at least one additional clade, but as the branching order in the *Gigasporaceae* was yet unclear, it was concluded that more robust evidence should be awaited before any further taxonomic change was made (Schüßler and Walker 2010). However, the recently published nomenclatures (Oehl et al. 2011f; Goto et al. 2012a) not only use the seven genera (*Scutellospora*, *Gigaspora*, *Dentiscutata*, *Quatunica*, *Fuscutata*, *Cetraspora*, and *Racocetra*) considered by Oehl et al. (2008), but also add three additional genera (*Orbispora*, *Intraornatospora*, and *Paradentiscutata*), with the genera distributed among five different families (Fig. 1).

As already pointed out by Morton and Msiska (2010b), the revised classification of *Scutellospora* by Oehl et al. (2008) was based to a large extent on "… faulty premises, circular reasoning, and imposition of phylogenetic significance to selective characters in the absence of appropriate methodology…." The molecular phylogenies proposed in their analyses suffered from serious undersampling, with some of the new genera—and even families—represented by only a single species. Notably, one species, *S. heterogama*, was interpreted as belonging to two different genera, an unprecedented controversial move that is not supported by either comparative morphological or molecular evidence (see succeeding paragraphs).

Morton and Msiska (2010b) undertook a rigorous approach to incorporate molecular and morphological characters in a consensus classification of this clade. They show that the germination shield is not phylogenetically informative as a criterion for genus delimitation in *Gigasporaceae* as circumscribed by Schüßler et al. (2001). Neither was it possible to bring molecular-based and morphology-based phylogenies into concordance. Morton and Msiska (2010b) were very conservative in their taxonomic conclusions, leaving all taxa of uncertain position in the genus *Scutellospora*. This approach also was followed by Schüßler and Walker (2010), with the only exception of *Racocetra weresubiae*, for which rRNA sequence data were prioritized to establish generic placement despite differences in organization of inner germinal walls. In the light of new molecular data and careful consideration of all available evidence for the erection of newly proposed genera and higher taxa (Oehl et al. 2011f; Goto et al. 2012a), we revise this classification to recognize only those genera that form clearly supported monophyletic clades. Species without sequence information are left as of uncertain position in *Scutellospora* until living specimens are available for further analyses. We recognize only one family, the *Gigasporaceae*, and agree with the recommendation of Morton and Msiska (2010b) to reject a split of this clade into several families.

Because of problems associated with phylogenetic interpretation of gains and losses of morphological characters such as "germinal" walls or variation in germination shield organization, our working concept of the *Gigasporaceae* at this time is based mainly on gene sequence data.

Gigaspora is unchanged This genus is monophyletic and requires no further discussion.

Scutellospora is redefined as a valid genus This genus is defined by *Scutellospora calospora*, for which a sample from a culture of BEG32 was designated as the epitype (Schüßler and Walker 2010) so that living material would be available to facilitate future research. Species in *Scutellospora* sensu stricto usually tended to group unresolved at the base of the *Gigasporaceae* and only recently produced rRNA gene sequences of sufficient length support this clade as monophyletic. Species sufficiently well-characterized at the molecular level are *S. calospora*, *Scutellospora projecturata*, *Scutellospora dipurpurescens*, and *Scutellospora aurigloba*.

Orbispora is rejected as a genus *Orbispora* was erected as a distinct clade populated by only two species transferred from *Scutellospora*, namely, *Orbispora projecturata* and *Orbispora pernambucana* (Oehl et al. 2011d). The rDNA evidence used to justify this change was weak. *O. pernambucana* was resolved in an LSU rRNA gene phylogeny as being basal to the clade containing other species of the *Scutellospora* sensu stricto clade, with all sequences apparently originating from spores from the same location. *O. projecturata* was the only representative in an SSU tree, in which no substantial support for separation of this species from other species of *Scutellospora* sensu stricto was shown (60 % for distance-based analysis and none for maximum

likelihood analysis). Performing phylogenetic analyses of two species using two different gene regions is clearly insufficient to conclude the monophyly of the genus. Neither of these two species can be separated at the genus level from *Scutellospora*, and *Orbispora* is reabsorbed within *Scutellospora*.

Scutellospora projecturata Kramad. & C. Walker, in Kramadibrata, Walker, Schwarzott & Schüßler, Ann. Bot., Lond., N.S. 86: 22 (2000).

≡ *Orbispora projecturata* (Kramad. & C. Walker) Oehl, G. A. Silva & D. K. Silva in Oehl, Silva, Maia, Sousa, Vieira & Silva, Mycotaxon 116: 166 (2011).

Scutellospora pernambucana Oehl, D.K. Silva, N. Freitas & L.C. Maia, Mycotaxon 106: 363. 2009 [‘2008’].

≡ *Orbispora pernambucana* (Oehl, D.K. Silva, N. Freitas & L.C. Maia) Oehl, G. A. Silva & D. K. Silva in Oehl, Silva, Maia, Sousa, Vieira & Silva, Mycotaxon 116: 166 (2011).

Cetraspora is retained pending further study Combined rDNA region analyses separate *Racocetra* and *Cetraspora* into supported clades (Krüger et al. 2012), but near-complete SSU gene-based phylogenies do not show support for such a separation (Fig. 2 in Krüger et al. 2012; Fig. 1 in Oehl et al. 2011d). As discussed previously, Morton and Msiska (2010b) clearly demonstrate that germination shield characters used to define these genera are homoplastic and, therefore, phylogenetically uninformative. The collective rDNA data do not provide the same level of resolution afforded other clades recognized as genera, which raises doubt that available evidence is providing a clear picture of the relationship between these two clades. Ambiguity in resolution of monophyletic clades in molecular analyses can have many causes, including undersampling of relevant taxa. When all of the available evidence is considered, although it is overall rather weak and ambiguous, we decided to retain *Cetraspora* pending further study.

Two species of uncertain position (*Cetraspora armeniaca* and *Cetraspora striata*) are retained within *Scutellospora*, as recommended by Schüßler and Walker (2010). *Scutellospora spinosissima* was placed in *Cetraspora* by Oehl et al. (2008) based on misannotated sequences (*Scutellospora nodosa* and *S. spinosissima* sequences were accidentally labeled vice versa, see Krüger et al. 2012), and so it also should remain in *Scutellospora* (Schüßler and Walker 2010). The three species thus retained in *Cetraspora* are *Cetraspora nodosa*, *Cetraspora gilmorei*, and *Cetraspora pellucida*.

Scutellospora spinosissima C. Walker & Cuenca, Ann. Bot., Lond., N.S. 82: 723 (1998).

≡ *Cetraspora spinosissima* (C. Walker & Cuenca) Oehl, F.A. Souza & Sieverd. Mycotaxon 106: 340 (2008).

Racocetra is accepted as a genus The genus was recognized by Morton and Miska (2010b) and Schüßler and Walker (2010). rDNA sequence data indicate that two other species, *R. tropicana* and *R. undulata* are members of *Racocetra*. A third new species, *R. beninensis*, was published exclusively from morphological evidence and so its phylogenetic position in this genus is tentative pending verification from molecular data. We, therefore, retain it as a species in *Racocetra* but of uncertain phylogenetic position.

Fuscutata is superfluous and its members are synonymized with Dentiscutata The type species of this genus is *Fuscutata heterogama*, with the type described as being from at least two collections, some from the field and others from pot cultures in Brazil and Florida (Oehl et al. 2008). The authors indicated that they included other description based on specimens collected from Brazil, including strains cultured in INVAM, some of which were used in an ontogenetic study by Franke and Morton (1994). Oehl et al. (2008) interpreted these specimens as representing a *Scutellospora* species different from the one originally described as *Endogone heterogama* by Nicolson and Gerdemann (1968) (later moved to *Gigaspora* and then *Scutellospora*), which they had transferred to the genus *Dentiscutata*. No sequence evidence was presented to support this separation, and the morphological characters used were not phylogenetically informative. Oehl et al. (2008) separate *Dentiscutata heterogama* from *F. heterogama* solely by “…spore color and especially by morphology of the shield…” [p. 346]. However, spore color is highly variable in *S. heterogama*, ranging from pale orange–brown to dark red–brown. More importantly, these variations overlap among all INVAM and BEG accessions classified as *S. heterogama*, including all of those originating from Brazil (J.B. Morton, unpublished). Although the problems with interpretation of germination shield characteristics within a phylogenetic context have been addressed exhaustively by Morton and Msiska (2010b), they were ignored by Oehl et al. (2011f) in their determination to retain this taxon.

Oehl et al. (2008) do not explicitly identify the provenance of the type material used to erect *Fuscutata* except to state that it was composed of field samples collected in Pernambuco, Brazil, in 1997 and maintained in pure culture at Recife and INVAM (p. 346). Other specimens grouped in this genus included other unspecified INVAM accessions from Florida and Illinois studied during a visit in 2002 and the two strains used by Franke and Morton (1994) for an ontogenetic study. Currently, unresolvable ambiguity fails to establish an essential link between type material and living cultures with which to collect other data. The only available course of action to resolve the relationship between *D.*

heterogama and *F. heterogama* was to sequence additional strains encompassed within the range of those used to erect the genus and not yet reported by Morton and Msiska (2010b). The only three INVAM cultures that fit this criterion were IL203, BR154, and BR155. IL203 came from the type locality of *S. heterogama* and thus was treated as the morphological reference strain for the species in INVAM. BR154 and BR155 were the Brazilian cultures used in the Franke and Morton (1994) study. In an analysis of a 750-bp fragment of an LSU rRNA fragment, sequences from spores of all these cultures grouped into a highly supported monophyletic clade with all other known *S. heterogama* sequences (accession numbers KC161973–KC161975). Moreover, strain BEG 35, which is thought to be the ex-type culture of *Gigaspora heterogama* (and, if so, is linked genotypically with the fungus defined as the type of *D. heterogama*), also clusters within this group based on analyses of a 1,500-bp SSU-ITS-LSU rDNA fragment (Krüger et al. 2012). Oehl et al. (2008) state that most strains assigned to *S. heterogama* should be in *F. heterogama*, and only the original type of *E. heterogama* should be retained in *D. heterogama*. This conclusion cannot be substantiated because the overwhelming molecular evidence clearly indicates conspecificity. These results also affirm the conclusion of Morton and Msiska (2010b) that neither the morphological characters used to erect *Fuscutata* nor those used to distinguish *Dentiscutata* are sufficiently informative (either taxonomically or phylogenetically) to merit separation into two genera.

The focus of this discussion has been exclusively on the resolution of the relationship between all relevant cultures of *S. heterogama* because Oehl et al. (2008) did not provide any additional data to justify grouping *Scutellospora savannicola*, *Scutellospora trirubiginopa*, and *Scutellospora rubra* in this clade. *S. heterogama* clearly belongs to a clade divergent from that containing *S. calospora*, and so it cannot remain in *Scutellospora*. The clade populated by members of the three newly published genera, *Fuscutata*, *Dentiscutata*, and *Quatunica*, is robustly supported in rRNA gene phylogenies. We thus transfer all species in this clade for which sequence data are available, into the single genus, *Dentiscutata*.

In this context, it may be mentioned that, even the tree used as evidence in Oehl et al. (2011d; Fig. 1) demonstrates that the proposed genera *Dentiscutata* and *Racocetra* are paraphyletic in the sense used by these authors. Thus, even their own phylogenetic analyses conflicts with their proposed classification scheme.

Dentiscutata heterogama (T. H. Nicolson & Gerd.) Sieverd., F. A. Souza & Oehl, Mycotaxon 106: 342 (2008).

= *Fuscutata heterogama* Oehl, F.A. Souza, L.C. Maia & Sieverd., Mycotaxon 106: 344 (2009).

Epitype: INVAM specimen number 2670, 29 Oct. 1994, **here designated** collected from the third propagation cycle of INVAM culture with designator IL203A derived from a multispore culture established 20 Sep. 1991 from soil sampled from Field 1011 of the Morrow Plots (the type locality of *Endogone heterogama* Nicol. & Gerd.) on the University of Illinois South Farm, continuously cropped with *Zea mays* since 1879 (representative nucleotide sequence KC161975). Descendants of this culture are available from INVAM upon request.

Dentiscutata is accepted as a genus Oehl et al. (2008) erected the new genus *Dentiscutata* and designated it as the type genus of a new family *Dentiscutataceae* based on morphological characters so exceedingly broad that not a single relevant synapomorphy could be defined. The focus on germination shield structure fails utterly in this group (Fig. 4). *S. heterogama* (as *D. heterogama*) has a simple bilobed germination shield. However, spores of the type species of the new genus, *Dentiscutata nigra*, possess a very complex germination shield (Walker and Sanders 1986). Combined ITS-LSU sequence data resolve a clade corresponding to *Dentiscutata* but neither SSU rDNA nor beta-tubulin sequence data support monophyly of this genus as it is published (see also Fig. 1 of Oehl et al. 2011d).

A sample of the fungus annotated in the public sequence database as *Scutellospora nigra* was kindly provided to C. Walker by Jan Jansa, Switzerland. This fungus proved to be *Scutellospora reticulata*, rather than *S. nigra*. The sequences (AY900495, AY900497, and AY400498) used to erect *Dentiscutata* were therefore from a species different from that used as the generic type. The type of *S. nigra*, collected in Florida, was equated by Oehl et al. (2008) with specimens from a Kenyan culture of *S. reticulata* used for sequence analysis (Mathimaran et al. 2007) to support the erection of *Dentiscutata*. A genus cannot have two type species and the nominated type for the genus name is *D. nigra*. Thus, the molecular evidence cannot be used to show that *D. nigra* belongs to the same clade as *D. reticulata*, even though it seems possible from morphological comparison (remark: sequences AY900494, AY900495, AY900496, AY900497, AY900498, DQ122384, DQ122385, and FN252820 should be reannotated in the public databases). The preponderance of evidence does not provide support for a taxonomic division sufficiently distinct to warrant the erection of a genus separate from the other two proposed genera (*Quatunica* and *Fuscutata*), and especially not a new family to accommodate that genus.

Quatunica is rejected and combined with Dentiscutata Oehl et al. (2008) erected *Quatunica* within the new family *Dentiscutataceae* to accommodate one species, *Quatunica erythropus*. There is no molecular evidence that justifies placing this one species (*Scutellospora erythropus*) in its own

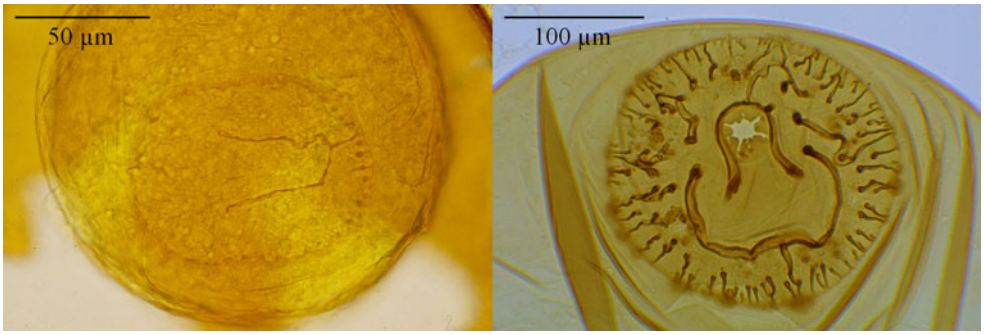

Fig. 4 Germination shields from type material of both *Dentiscutata heterogama* (*left*) and *D. nigra* (*right*) showing contrasting morphological characteristics

genus (for further discussion, see Morton and Msiska 2010b). Any morphological distinctions are apomorphies and, therefore, do not provide any valid grouping criterion that warrants the erection of a new genus. We, therefore, place *Q. erythropus*, together with all species of *Fuscutata* for which robust DNA sequence data is known, in an expanded *Dentiscutata*.

Dentiscutata erythropus (Koske & C. Walker) C. Walker & D. Redecker **comb. nov. IF550090**.

≡ *Gigaspora erythropus* Koske & C. Walker, Mycologia 76: 250 (1984).
≡ *Scutellospora erythropus* (Koske & C. Walker) C. Walker & F. E. Sanders, Mycotaxon 27: 181 (1986).
≡ *Quatunica erythropus* (Koske & C. Walker) F. A. Souza, Sieverd. & Oehl in Oehl, Souza & Sieverd. Mycotaxon 106: 348 (2008).

Intraornatospora and Paradentiscutata are orphan taxa The molecular and morphological data used to erect the genera *Intraornatospora* and *Paradentiscutata* as well as the family *Intraornatosporaceae* are clearly insufficient to support these taxa. Neither the individual morphological characters listed in the protologue (Goto et al. 2012a) nor their combination set these two new genera apart from other taxa in *Gigasporaceae*. *Intraornatospora* may be the only genus in the *Glomeromycota* defined by rDNA sequences from a single field-collected spore of an uncultured fungus. Bootstrap support and posterior probability for the family *Intraornatosporaceae* are insignificant. Statistical support for a sister group relationship with *Gigaspora* is equally unconvincing. Based on the scarce data available, the relationships involving these two genera cannot be either verified or falsified. As a result, both genera are considered to be irrelevant "orphan" lineages. There is no advantage to publishing such names, except perhaps the establishment of a name that, because of the principle of priority, may be used later if new evidence is produced that provides more convincing support for the taxon.

Archaeosporaceae

Intraspora cannot be sustained Intraspora already has been synonymized with *Archaeospora* (Schüßler and Walker 2010). Nevertheless, the name was again used by Oehl et al. (2011e, f) without mention of published comparative evidence. We reiterate that *Intraspora schenckii* is a synonym of a species in *Archaeospora*, and that its current phylogenetically coherent name is *Archaeospora schenckii*. Two other species (*Ac. myriocarpa* and *Ac. undulata*) have been moved into *Archaeospora* by Oehl et al. (2011c) although no confirmatory molecular evidence was provided.

Geosiphonaceae

No action is needed. This family contains a single organism in the genus, *Geosiphon*, which has not been shown to be mycorrhizal but does form a symbiosis with *Nostoc*, and rDNA evidence clearly places it in a clade within *Archaeosporales* (Schüßler et al. 2001).

Ambisporaceae

No action is needed.

Paraglomeraceae

No action is needed. There is general agreement that this family currently contains a single genus, *Paraglomus*. This is fully supported by molecular and morphological evidence (Błaszkowski et al. 2011).

Conclusions

In nomenclatural terms, both the schemes of Oehl et al. (2011f) and of Schüßler and Walker (2010) were validly published. We offer here an updated synopsis to resolve much of the confusion caused by several recent publications.

For taxa higher than family, it is up to the individual to decide which of these schemes to follow. For families and below, the system published here best fits a natural phylogeny and should be followed as the most recent revision. In the future, authors should be conservative when erecting new taxonomic names in the *Glomeromycota* because of the confusion that can result and because the corrections of

problematic data that later have to be made become increasingly complicated. Also, the reputation of journals may be weakened, if nonevidence-based manuscripts and concepts are not critically reviewed. In this context, we would like to address some comments to the editors of journals and to those referees who accept the onerous duty of reviewing manuscripts in which new taxa are proposed. The phylum *Glomeromycota* contains many species that are of uncertain phylogeny. Publication of names or deposition of molecular data (including DNA barcodes; Schoch et al. 2012) in public databases for such organisms or taxa without availability and documentation of high quality type or otherwise authenticated material does a disservice to AM research in particular and biology in general. In view of the importance of molecular evidence in modern taxonomy, ecology, and applied biology, it would also be helpful if authors made suitable specimens available for independent molecular analysis, as well as for other kinds of research. Nobody wishes to prevent the valid publication of biologically significant evidence, but as with all other science, taxonomy requires a high standard of evidence and proof. It is a responsibility of editors and reviewers to ensure that such proof has been presented so that biologists can have confidence in the quality of the work presented.

In this paper, we propose a taxonomic revision that is based on the consensus of leading experts for use as a framework when considering new taxa and their phylogenetic relationships. It is aimed at providing a stable and robust systematics of the *Glomeromycota* as a solid base for the many scientists working on these extremely important plant symbionts.

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