
A molecular phylogenetic reappraisal of the *Hysteriaceae*, *Mytiliniaceae* and *Gloniaceae* (*Pleosporomycetidae*, *Dothideomycetes*) with keys to world species

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Abstract: A reappraisal of the phylogenetic integrity of bitunicate ascomycete fungi belonging to or previously affiliated with the *Hysteriaceae*, *Mytiliniaceae*, *Gloniaceae* and *Patellariaceae* is presented, based on an analysis of 124 isolates and four nuclear genes, the ribosomal large and small subunits, transcription elongation factor 1 α and the second largest RNA polymerase II subunit. A geographically diverse and high density taxon sampling strategy was employed, including multiple isolates/species from the following genera: *Hysterium* (12/5), *Oedohysterium* (5/3), *Hysterobrevium* (14/3), *Gloniopsis* (8/4), *Hysterographium* (2/1), *Psiloglonium* (11/3), *Anteaglonium* (6/4), *Rhytidhysterion* (8/3), *Ostreichnion* (2/2), *Farlowiella* (3/1), *Glonium* (4/2), *Mytilinidion* (13/10), *Lophium* (4/2), *Quasiconcha* (1/1), *Encephalographa* (1/1), *Glyphium* (3/1), *Hysteropatella* (2/2) and *Patellaria* (1/1), and 21 outgroup taxa. Sequence data indicate that although the *Hysteriales* are closely related to the *Pleosporales*, sufficient branch support exists for their separation into separate orders within the *Pleosporomycetidae*. The *Mytiliniales* are more distantly related within the subclass and show a close association with the *Gloniaceae*. The genus *Glyphium* originally classified within the *Mytiliniaceae*, but recently transferred to the *Chaetothyriales* in the *Eurotiomycetes*, is retained here within the *Dothideomycetes*, as *Pleosporomycetidae* gen. incertae sedis, but in close association with the genera *Hysteropatella* and *Patellaria* in the *Patellariaceae*. Although there are examples of concordance between morphological and molecular data, these are few. Molecular data instead support the premise of a large number of convergent evolutionary lineages, which do not correspond to previously held assumptions of synapomorphy relating to spore morphology. Thus, within the *Hysteriaceae*, the genera *Hysterium*, *Hysterographium*, *Gloniopsis* and *Glonium* are highly polyphyletic. This necessitated the transfer of two species of *Hysterium* to *Oedohysterium* gen. nov. (*Oedo. insidens* and *Oedo. sinense*) and two species of *Gloniopsis* to *Hysterobrevium* gen. nov. (*Hsb. smilacis* and *Hsb. constrictum*). While *Hysterographium*, with the type *Hg. fraxini*, is removed from the *Hysteriaceae*, some of its species remain within the family, transferred here to *Oedohysterium* (*Oedo. pulchrum*), *Hysterobrevium* (*Hsb. mori*) and *Gloniopsis* (*Glp. subrugosa*); the latter genus, in addition to the type, *Glp. praelonga*, with two new species, *Glp. arciformis* and *Glp. kenyensis* sp. nov. The genus *Glonium* is now divided into *Psiloglonium* (*Hysteriaceae*), *Glonium* (*Gloniaceae*), and *Anteaglonium* (*Pleosporales*). The hysterothecium has evolved convergently no less than five times within the *Pleosporomycetidae* (e.g., *Farlowiella*, *Glonium*, *Anteaglonium*, *Hysterographium* and the *Hysteriaceae*). Similarly, thin-walled mytilinidioid (e.g., *Ostreichnion*) and patellarioid (e.g., *Rhytidhysterion*) genera, previously in the *Mytiliniaceae* and *Patellariaceae*, respectively, transferred here to the *Hysteriaceae*, have also evolved at least twice within the subclass. As such, character states traditionally considered to represent synapomorphies among these fungi, whether they relate to spore septation or the ascomata, in fact, represent sympleiomorphies, and most likely have arisen multiple times through convergent evolutionary processes in response to common selective pressures.

Taxonomic novelties: New species: *Hysterium barrianum*, *Gloniopsis arciformis*, *Glp. kenyensis*. New genera: *Oedohysterium*, *Hysterobrevium*. New combinations: *Psiloglonium pusillum*, *P. chambianum*, *P. uspallatense*, *P. sasicola*, *P. ephedrae*, *P. hysterinum*, *P. colihuae*, *P. araucanum*, *Oedohysterium insidens*, *Oedo. sinense*, *Oedo. pulchrum*, *Hysterobrevium mori*, *Hsb. smilacis*, *Hsb. constrictum*, *Gloniopsis subrugosa*.

Keywords: Hysteriales, Mytiliniales, Patellariales, Eumycota, fungi, taxonomy, phylogeny, speciation, evolution.

INTRODUCTION

Class *Dothideomycetes*, subphylum *Pezizomycotina* (*Ascomycota*), is currently classified into two subclasses, based on centrum type (Schoch *et al.* 2007a; Spatafora *et al.* 2007). The *Dothideomycetidae* P.M. Kirk, P.F. Cannon, J.C. David & J.A. Stalpers, *ex* Schoch, Spatafora, Crous & Shoemaker 2007 is characterized by the absence of sterile centrum elements (e.g., pseudoparaphyses), and includes the *Dothideales* Lindau 1897, *Capnodiales* Woron. 1925 *Myriangiales* Starbäck 1899, and *Patellariales* D. Hawks. & O.E. Erikss. 1986 (Lumbsch & Huhndorf 2007). The second subclass currently recognized within the *Dothideomycetes* is the *Pleosporomycetidae* Schoch, Spatafora, Crous & Shoemaker 2007, characterized by a hamathecium of wide to narrow cellular to trabeculate pseudoparaphyses, which may or may not persist at maturity. This subclass currently comprises five recognized orders, namely the *Pleosporales* Luttrell *ex* M.E. Barr 1987, *Hysteriales* Lindau 1897, *Mytilinidiales* Boehm, Schoch & Spatafora 2009, *Botryosphaeriales* Schoch, Crous & Shoemaker 2007, and the *Jahnulales* Pang, Abdel-Wahab, El-Sharouney, E.B.G. Jones & Sivichai 2002. However, a greater number of orders, families, and genera still await placement, and are currently designated as *incertae sedis* within the *Dothideomycetes* (Lumbsch & Huhndorf 2007).

Fungi classified in the *Hysteriaceae* Chevall. 1826 (*Hysteriales*), *Mytiliniaceae* KirscoOedo. 1924 (*Mytilinidiales*), and within the reinstated family *Gloniaceae* (Corda) Boehm, Schoch & Spatafora 2009 (*fam. incertae sedis*), all possess persistent, carbonaceous ascomata, that characteristically dehisce by a longitudinal suture. Recent molecular data support the inclusion of all three families within the *Pleosporomycetidae* (Boehm *et al.* 2009; Mugami & Huhndorf 2010; Schoch *et al.* 2007a). In the *Hysteriaceae* ascomata are thick-walled, navicular, characteristically dehiscing by an invaginated slit or sulcus (Zogg 1962). Fungi in the *Mytiliniaceae*, on the other hand, possess strongly laterally compressed, connivent, thin-walled conchate ascomata, reminiscent of miniature bivalve mollusks. These mytilinioid ascomata typically dehisce by an evaginated slit, in some species forming a longitudinal keel or cristate apex (Barr 1990a). Fungi belonging to the *Gloniaceae*, have dichotomously branched, laterally anastomosed pseudothecia, that form radiating pseudo-stellate composites and dehisce by an inconspicuous, longitudinal, but evaginated slit (Boehm *et al.* 2009).

We are broadly interested in the evolution of character states traditionally used to define higher taxa within each family. Essentially, we wish to address whether morphological features historically used in the classification of these fungi are phylogenetically informative in the context of sequence-based phylogenies. This would have bearing on which morphological features are phylogenetically significant, and therefore useful for a

natural delineation of higher taxa. Morphological character states traditionally used to classify these fungi have related primarily to features associated with (1) the pseudothecium, (2) the peridium, (3) the hamathecium, and (4) differences in ascospore symmetry (Barr 1987, 1990a). Character states within each family relate primarily to ascospore septation and pigmentation (Zogg 1962).

Due to the seemingly transitional nature of the ascoma, neither fully open nor closed, hysterothecium fungi have been placed in the discomycetes and pyrenomycetes about equally by various mycologists throughout the 19th Century (Bisby 1923). In his *Systema Mycologicum*, Fries (1823) initially considered hysterothecium fungi to belong to the pyrenomycetes and placed them in the Phacidieae, but later (1835) placed them in his new class Discomycetes, stating: "*Transitum sistunt ad Discomycetes, sed discum verum non monstrant.*" Chevallier (1826) recognized the unique nature of the hysterothecium and established the Hysteriineae, which he considered as pyrenomycetes distinct from Fries' Phacidieae. Corda (1842), on the other hand, retained the Phacidieae within the *Hysteriaceae*, and divided the family into a number of subfamilies. De Notaris (1847) considered the *Hysteriaceae* to belong to the pyrenomycetes and used spore pigmentation to classify hysterothecium fungi into the Phaeosporii and the Hyalosporii. Saccardo (1873) initially followed Fries, but later (1874) placed hysterothecium fungi in the pyrenomycetes, and carried de Notaris' (1847) spore classification scheme further by dividing the *Hysteriaceae* into nine sections based on pigmentation and the morphology of spore septation (Saccardo 1883). Ellis & Everhart (1892), in their *North American Pyrenomycetes*, tentatively included the *Hysteriaceae*, but stated that they had not at first intended to do so due to the transitional nature of the hysterothecium. In Rabenhorst's *Kryptogamen-Flora, Die Pilze*, Rehm (1896) compromised and placed the *Hysteriales* as an order intermediate between the pyrenomycetes and the discomycetes.

Mytilinioid fungi have also historically been classified within the family *Hysteriaceae*, due to perceived similarities in ascocarp morphology, specifically its means of longitudinal dehiscence (Bisby 1923; De Notaris 1847; Ellis & Everhart 1892; Fries 1823; von Höhnell 1918; Masee 1895; Rehm 1896; Saccardo 1875, 1883). Modern authors have likewise included mytilinioid fungi within the *Hysteriaceae*, placing the family in the *Pseudosphaeriales* (Nannfeldt 1932; Gäumann 1949), the *Dothiorales* (Müller & von Arx 1950; von Arx & Müller, 1954), the *Dothideales* (von Arx & Müller 1975), and in a separate order *Hysteriales*, closely related to the *Pleosporales* (Miller 1949; Luttrell 1955). The *Hysteriales* were placed in the subclass *Loculoascomycetes* by Luttrell (1955), due to the presence of bitunicate asci, corresponding to the *Ascoloculares* first proposed by Nannfeldt (1932).

Duby (1862), however, was the first to propose that hysterothecium fungi be divided into two sections, the

Hysteriées and the Lophiées, the latter to accommodate mytilinidioid forms. One hundred years later, Zogg (1962) proposed two families: the *Hysteriaceae* s. str. to accommodate thick-walled hysteriaceous forms, and the *Lophiaceae* H. Zogg ex Arx & E. Müller (Zogg 1962; von Arx & Müller 1975) to accommodate thin-walled, mytilinidioid fungi. Barr (1990a) made the argument for retention of the earlier name *Mytiliniaceae* over the *Lophiaceae*, despite the proposal to conserve the latter (Hawksworth & Eriksson 1988). Luttrell (1953) studied ascotal ontogeny and hamathical development in *Glonium stellatum* Muhl. : Fr. and concluded that the *Hysteriaceae* possess the pseudoparaphysate *Pleosporaceae* type centrum, in which cellular, septate pseudoparaphyses grow downwards from the cavity roof, initially anchored at both ends, and occupy the locule prior to the formation of asci (Luttrell 1951). Luttrell (1973) held a wide concept of the *Hysteriales*, but did not recognize the family *Lophiaceae*, instead proposing a subfamily, the *Lophioideae*, within the *Hysteriaceae* to accommodate mytilinidioid forms. Barr (1979) however maintained the two-family distinction. The *Mytiliniaceae* was placed in the *Melanommatales* Barr 1983 based on a thin-walled peridium of scleroparenchymatous cells enclosing a hamathecium of narrow trabeculate pseudoparaphyses, asci borne in a peripheral layer and with ascospores typically showing bipolar symmetry (Barr 1987, 1990a). Later, Barr & Huhndorf (2001) noted that the family was somewhat atypical of the *Melanommatales*, in that, as a consequence of reduced locule space attributed to lateral compression, they possess a basal, rather than peripheral, layer of asci and a reduced hamathecium at maturity. More recently, the *Melanommatales* have been included within the *Pleosporales* (Lumbsch & Huhndorf 2007). Barr (1983) eventually abandoned the *Hysteriales* and placed the *Hysteriaceae* within the *Pleosporales* due to the presence of cellular pseudoparaphyses, asci borne in a basal rather than peripheral layer and ascospores typically showing bipolar asymmetry. Eriksson (2006) removed the *Mytiliniaceae* from the *Hysteriales* and considered it as *Dothideomycetes et Chaetothyriomycetes incertae sedis*, leaving the *Hysteriaceae* as the sole family in the *Hysteriales*.

More recently, Boehm *et al.* (2009) presented the first combined use of DNA and amino acid sequence data to reconstruct the phylogeny of hysteriaceous fungi. This study was based on a wide taxon sampling strategy, and employed four nuclear genes, namely the nuSSU and nuLSU, Transcription Elongation Factor 1 α (TEF1 α) and the second largest RNA polymerase II subunit (RPB2). A number of specific conclusions were reached: (1) Multigene phylogenies provided strong support for the monophyly of the *Hysteriaceae* and of the *Mytiliniaceae*, both within the *Pleosporomycetidae*. However, sequence data also indicated that both families were not closely related within the subclass. (2) Although core groups for

many of the genera in the *Hysteriaceae* were defined, the genera *Hysterium* Tode : Fr., *Gloniopsis* De Notaris, and *Hysterographium* Corda were demonstrated to be polyphyletic, with affinities not premised on spore septation and pigmentation. (3) The genus *Glodium* Muhl. : Fr. was also shown to be polyphyletic, but along two highly divergent lines. The genus lies outside of the *Hysteriaceae*, and instead finds close affinities with the family *Mytiliniaceae*, for which was proposed the *Gloniaceae* (Corda) Boehm, Schoch & Spatafora *fam. nov.*, to accommodate the type, *G. stellatum* Muhl. : Fr. and related forms. (4) The genus *Psilogonium* Höhn. was reinstated within the *Hysteriaceae*, with *P. lineare* (Fr.) Petr., as type, to accommodate didymospored species segregated from *Glodium*. (5) The genera *Mytilinidion* Duby and *Lophium* Fr. formed a strongly supported clade within the *Pleosporomycetidae*, thus defining the monophyletic *Mytiliniaceae*, adjacent to the *Gloniaceae*, for which was proposed the *Mytilinidiales* Boehm, Schoch & Spatafora *ord nov.* (6) The genus *Farlowiella* Sacc., previously in the *Hysteriaceae*, was placed as *Pleosporomycetidae gen. incertae sedis*. (7) The genus *Ostreichnion* Duby, previously in the *Mytiliniaceae*, was transferred to the *Hysteriaceae*. (8) The genus *Rhytidhysterion* Speg., previously in the *Patellariaceae* Corda (*Patellariales* D. Hawksw. & O.E. Erikss. 1986), was transferred to the *Hysteriaceae*.

These taxonomic changes present a number of challenges for understanding evolution within this group of fungi. The lack of agreement between traditional morphological character states, previously considered synapomorphic (e.g., Zogg 1962), and recent molecular data based on the nuSSU, nuLSU, TEF1 α and RPB2, had resulted in a highly polyphyletic core set of genera (e.g., *Hysterium*, *Hysterographium*, *Gloniopsis*, and *Glodium*) for the *Hysteriaceae* (Boehm *et al.* 2009). This presented us with a complicated picture of past speciation events for the family, and necessitated the current reappraisal. As a result, a number of taxonomic changes are proposed in the current study, resulting in two new genera and three new species for the *Hysteriaceae*, as well as a number of new combinations. The challenge was to reconcile discrepancies between morphological and molecular data, to more accurately reflect natural phylogenetic relationships with the family. As a result, the revised *Hysteriaceae* bears little resemblance to original concept of the family (Zogg 1962).

In an effort to facilitate species identification, a number of dichotomous keys are presented in the current study. These keys take into consideration taxonomic changes brought about by DNA and amino acid sequencing studies (Boehm *et al.* 2009; Mugambi & Huhndorf 2010; Schoch *et al.* 2007a), and attempt to provide a morphological basis for the new relationships discerned by molecular data. Although the keys are based on those first presented by Zogg (1962), they considerably expand upon them to

accommodate a number of new species described since the original publication (e.g., Amano 1983; Barr 1975, 1990a; Barr & Blackwell 1980; Checa *et al.* 2007; Chlebicki & Knudsen 2001; Darker 1963; Goree 1974; Kantvilas & Coppins 1997; Lorenzo & Messuti 1998; Mathiassen 1993; Messuti & Lorenzo 1997, 2003, 2007; Pande & Rao 1991; Speer 1986; Sutton 1970; Tilak & Kale 1968; van der Linde 1992; Vasilyeva 2000, 2001). In addition to incorporating new species, the revised keys also take into consideration variation in ascospore measurements as presented by different authors, and include widened distribution reports. Additional information can be found at <http://www.eboehm.com/>.

MATERIALS AND METHODS

Taxon sampling

Fungal cultures, collection data and DNA GenBank accession numbers are listed in Table 1. All fungal cultures initiated for this study were based on the isolation of individual ascospores, employing a method whereby individual ascomata were affixed to Petri plate lids suspended over potato dextrose agar. Every twelve hours the lids were rotated 45 degrees, such that, by 96 hrs., confirmation of spore deposits could be made under a stereomicroscope using transmitted light. Discharged spores were observed microscopically to confirm identity, transferring a single ascospore to initiate an axenic culture (e.g., EB cultures). In some cases, spore discharge was not obtained, necessitating DNA extraction from individual fruitbodies (e.g., all GKM, SMH, ANM and some EB accessions). Lastly, a number of original cultures, from the Centraalbureau voor Schimmelcultures (CBS) were employed in this study, the provenance of which could not be ascertained beforehand. Confirmation of taxonomic identity was based on whether different isolates of the same species co-segregated in the final tree. In all cases possible, taxonomic identification was based on the original herbarium specimens.

An attempt was made to include a broad range of fungal isolates, belonging to or previously affiliated with the *Hysteriaceae*, *Mytiliniaceae*, *Gloniaceae* and *Patellariaceae* (Table 1). A geographically diverse (United States, Europe, Ghana, Kenya, South Africa, New Zealand, Tasmania, Cuba) and high density taxon sampling strategy was employed. This included multiple isolates/species from the genera: *Hysterium* (12/5), *Oedohysterium* (5/3), *Hysterobrevium* (14/3), *Gloniopsis* (8/4), *Hysterographium* (2/1), *Psilogonium* (11/3), *Anteaglonium* (6/4), *Rhytidhysterion* (8/3), *Ostreichnion* (2/2), *Farlowiella* (3/1), *Glonium* (4/2), *Mytilinidion* (13/10), *Lophium* (4/2), *Quasiconcha* (1/1), *Encephalographa* (1/1), *Glyphium* (3/1), *Hysteropatella* (2/2) and *Patellaria* (1/1), and 21 outgroup taxa, for a total of 124 taxa. All cultures and the herbarium specimens from which they were derived, have been

deposited and are permanently conserved in the certified public institutions as given in Table 1.

DNA extraction, amplification and sequencing

Genomic DNA was recovered using the DNeasy® Plant Mini Kit (Qiagen Inc.), following the instructions of the manufacturer, but using sterile white quartz sand and a Kontes® battery-powered pestle grinder in 1.5 mL microfuge tubes. The nuSSU was amplified and double-strand sequenced using the primers NS1 and NS4 (White *et al.* 1990), while amplification of the nuLSU utilised the primers LROR (Rehner & Samuels 1994) and LR7 (Vilgalys & Hester 1990), in addition to the internal sequencing primers LR3R and LR16 (Moncalvo *et al.* 1993). Final concentrations for 50 µL PCR amplification reactions were as follows: 1.0 µM of each forward and reverse primer, 2.0 mM MgCl₂, 200 µM dNTP, 1X Promega GoTaq® Flexi Reaction Buffer, 1.25 U of Promega GoTaq® Polymerase, and 2 µL template DNA diluted tenfold. For the nuSSU and nuLSU, PCR reaction parameters were as follows: a 95°C pre-melt for 3 min, and 35 cycles of 95°C for 20 s, 54°C for 30 s and 72°C for 60 s, followed by a final extension at 72°C for 10 min. For TEF1 and RPB2, PCR amplification conditions followed those in Schoch *et al.* (2007b). Primers used for the amplifications and sequencing of these protein coding genes were for TEF1: 983 & 2218R; and for RPB2: fRPB2-5F & rRPB2-7cR. PCR reactions were performed using PCR Master Mix Polymerase from Promega Corporation (Fitchburg, Wisconsin, USA) and run on an iCycler from Biorad (Hercules, California, USA). For the amplification of DNA fragments used to infer the TEF1 amino acid sequence, the following conditions were used: (1) 94°C for 2 min; (2) five cycles of 94°C for 40 s, 55°C for 45 s lowering by 0.8°C per cycle and 72°C for 90 s; (3) 30 cycles of 94°C for 30 s, 52°C for 45 s and 72°C for 120 s and (4) a cycle for 10 min at 72°C. Amplifications of DNA fragments used to infer the RPB2 amino acid sequence utilized the same cycle parameters, except for changes in steps (2) and (3) where the annealing temperatures of 55°C and 52°C were changed to 50°C and 45°C, respectively. Amplified PCR products were cleaned using the QIAquick® PCR Purification Kit (Qiagen Inc.) and resuspended in water prior to outsourcing for sequencing (Macrogen USA, Inc.).

Phylogenetic analysis

RESULTS AND DISCUSSION

Phylogenetic analysis – ordinal level

At the ordinal level in the *Pleosporomycetidae*, molecular data indicate that the *Hysteriales* are closely related to the *Pleosporales* (Fig. 1), as was indicated in earlier studies

(Boehm *et al.* 2009; Schoch *et al.* 2007a). This is also confirmed by morphological evidence related to the centrum. Thus, the *Hysteriales* share a very similar hamathecium with the *Pleosporales*, that is, defined by the *Pleospora*-type centrum, in which cellular, septate pseudoparaphyses grow downwards from the cavity roof, initially anchored at both ends, and occupy the locule prior to the formation of asci (Luttrell 1951). However, there is also strong branch support for its separation from the *Pleosporales* (Boehm *et al.* 2009). The *Hysteriales* are therefore retained as defined by Luttrell (1955), to emphasize the elongated hysteriaceous locule, capable of relatively indeterminate linear growth, as distinct from the strict *Pleospora*-type centrum, defined as it is by constrained concentric growth. In contrast to the close association between the *Hysteriales* and the *Pleosporales*, the *Mytilinidiaceae* forms a highly monophyletic assemblage of species within the *Pleosporomycetidae*, distant from the *Hysteriales*, for which was proposed the *Mytilinidiales* (Boehm *et al.* 2009).

Phylogenetic analysis – family level

Hysteriaceae

Although the *Hysteriales* receives high branch support as a monophyletic entity, distinct from the closely related *Pleosporales*, two major groups can be defined within the *Hysteriaceae* (Fig. 1), with high branch support.

Group I: The first group defines three separate well supported clades within the *Hysteriaceae*:

Clade A: This first clade (Fig. 1) is characterized by *Hysterographium mori* (Schwein.) Rehm, with short pigmented dictyospores, *Gloniopsis constrictum* N. Amano, and *Glp. smilacis* (Schwein. : Fr.) Underwood & Earl, the latter two with hyaline dictyospores. The *Glp. smilacis* isolates originate from highly divergent geographical sources (e.g., the United States, Sweden, and South Africa; Table 1), thus strongly supporting its phylogenetic placement. As these taxa are far removed from the types for their respective genera, we propose here to unite them in *Hysterobrevium* Boehm & Schoch, *gen. nov.*, as *Hsb. mori* (Schwein.) Boehm & Schoch *comb. nov.* (Fig. 2C-F), *Hsb. constrictum* (N. Amano) Boehm & Schoch *comb. nov.* (Fig. 2A), and *Hsb. smilacis* (Schwein. : Fr.) Boehm & Schoch (Fig. 2B) *comb. nov.*

Clade B: This clade (Fig. 1) appears monophyletic for the newly reinstated genus *Psiloglonium* (Boehm *et al.* 2009), with hyaline didymospores. It includes the following species: *P. simulans* (W.R. Gerard) Boehm, Schoch & Spatafora (Fig. 3A), *P. clavisorum* (Seaver) Boehm, Schoch & Spatafora (Fig. 3B), and *P. araucanum* (Speg.) Boehm, Marinowitz & Schoch *comb. nov.* (Fig. 3D). In this

study, we propose a number of new combinations for the genus *Psiloglonium*, with *P. lineare* (Fr.) Petrak (Fig. 3C) as the type (Boehm *et al.* 2009), to accommodate species previously classified under the genus *Glonium*, now in the *Gloniaceae*.

Clade C: This clade (Fig. 1) is characterized by pigmented phragmospores belonging to four species of the genus *Hysterium*, namely *H. pulicare* (Lightf. : Fr.) Pers. (Fig. 4A), *H. angustatum* Alb. & Schwein. (Fig. 4B), *H. vermiforme* Masee (Fig. 4C), which have three-septate spores, and *H. barrianum* Boehm, Miller, Huhndorf & Schoch *sp. nov.* (Fig. 4D), which has nine-septate spores. Again, a geographically diverse set of isolates were surveyed (Table 1). For instance, taxon sampling for *H. angustatum* included isolates originating from the United States, South Africa, Kenya and New Zealand. Also within this clade, but with weak branch support, is *Ostreichnion sassafras* (Schwein.) M.E. Barr, and *Ostreichnion curtisii* (Duby) M.E. Barr, previously transferred from the *Mytilinidiaceae* to the *Hysteriaceae* (Boehm *et al.* 2009).

Group II: The second identified group within the *Hysteriaceae* defines an additional three clades, also with high branch support:

Clade D: This clade (Fig. 1) is heterogeneous, but can be divided into two sub-clades. The first sub-clade includes two species formerly in the genus *Hysterium*, namely *H. insidens* Schwein. and *H. sinense* Teng. Molecular data indicate that these species are not related to the type species, *H. pulicare*, nor to related species within Clade C (Group I). Morphology also supports this separation, as *H. insidens* and *H. sinense* both possess phragmospores with a swollen or tumid supra-median cell. We therefore propose *Oedohysterium* Boehm & Schoch *gen. nov.*, to accommodate *Oedo. insidens* (Schwein.) Boehm & Schoch *comb. nov.* (Fig. 4E) and *Oedo. sinense* (Teng) Boehm & Schoch *comb. nov.* (Fig. 4F). Also grouping in Clade D is *Hysterographium pulchrum* Checa, Shoemaker & Umaña. Despite the fact that *Hg. pulchrum* possesses dictyospores, we propose to unite it within *Oedohysterium*, as *Oedo. pulchrum* (Checa, Shoemaker & Umaña) Boehm & Schoch *comb. nov.*, on account that it too possesses a swollen supra-median cell. The second sub-clade in Clade D defines the type species for the genus *Gloniopsis*, namely *Glp. praelonga* (Schwein.) Zogg (Fig. 5A-B). Closely associated with *Glp. praelonga* is *Hg. subrugosa* (Cooke & Ellis) Sacc. Dictyospores of both species are of similar shape, size and degree of septation, differing only in the lack of pigmentation and a gelatinous sheath. We thus propose that *Glp. praelonga* and *Hg. subrugosa* be united within the same genus, proposing *Gloniopsis subrugosa* (Cooke & Ellis) Boehm & Schoch *comb. nov.* (Fig. 5C-E). An additional two species are described in this sub-clade, namely *Gloniopsis arciformis* Boehm, Mugambi, Huhndorf

& Schoch *sp. nov.* (Fig. 6A) and *Glp. kenyensis* Boehm, Mugambi, Huhndorf & Schoch *sp. nov.* (Fig. 6B).

Clade E: This clade is well-supported and highly homogeneous. It defines three species in the genus *Rhytidhysterion* Speg., namely *R. rufulum* (Spreng.) Speg. (Fig. 6D-G), *R. hysterinum* (Duf.) Samuels & E. Müll., and *R. opuntiae* (J.G. Brown) M.E. Barr (Fig. 6C). Taxon sampling included isolates originating from France, Ghana, Kenya and the United States. This clade supports the transference of the genus *Rhytidhysterion* from the *Patellariaceae* to the *Hysteriaceae* (Boehm *et al.* 2009).

It is apparent that members of the classical genera *Hysterium*, *Gloniopsis* and *Hysterographium* span both Groups I & II (Fig. 1), and, as such, are highly polyphyletic. Since the data set is based on multiple isolates with diverse geographic origins and four nuclear genes (Table 1), we feel justified in proposing new genera (e.g., *Oedohysterium* and *Hysterobrevium*) and new combinations, to more accurately reflect past speciation events within the *Hysteriaceae*.

Mytilinidiaceae

In contrast to the *Hysteriales*, the family *Mytilinidiaceae* represents a highly monophyletic entity, defining the order *Mytilinidiales* (Boehm *et al.* 2009). The conchate nature of the fruitbody and the thin-walled peridium, seem to unite what at first may seem a disparate group of fungi into a single family (Fig. 1). In this study, we have sampled 10 of the 15 species of *Mytilinidion* Duby (Fig. 8D-F), characterized by phragmospores and scolecospores, two of the four species of *Lophium* Fr. (Fig. 8G), with filiform spores, as well as the monotypic *Quasiconcha* M.E. Barr & M. Blackw., with reticulated 1-septate spores (Table 1). Although monophyletic, sequence data also indicate a complex pattern of speciation within the family, one that is not premised on past assumptions based on spore morphology (Fig. 1). The genus *Glyphium* Nitschke *ex* Lehmann, originally classified within the *Mytilinidiaceae*, but recently transferred to the *Chaetothyriales* in the *Eurotiomycetes*, based on a mis-identified culture (CBS 268.34), is here retained within the *Dothideomycetes*, as *Pleosporomycetidae gen. incertae sedis*, but with close affinities to the genera *Hysteropatella* Rehm and *Patellaria* Fr. in the *Patellariaceae* (Fig. 1).

Gloniaceae

As for the monotypic family *Gloniaceae* (Boehm *et al.* 2009), based on the genus *Glonium* Muhl. : Fr., previously classified within the *Hysteriaceae* (Zogg 1962), surprisingly, sequence data indicate that it finds close affinity with the *Mytilinidiaceae* (Fig. 1). This is based on four isolates, representing two species, *Glonium stellatum*

Muhl. : Fr. (Fig. 8A) and *G. circumserpens* (Nyl.) Kantvilas & Coppins (Fig. 8B-C). However, the *Gloniaceae* is not included within the *Mytilinidiales*, due to the highly divergent morphology associated with the genus *Glonium*. These include character states related to the hamathecium (persistent cellular pseudoparaphyses *versus* narrow trabeculate pseudoparaphyses) and to the fruitbody (dichotomously branched *versus* conchate), for the *Gloniaceae* and *Mytilinidiaceae*, respectively. Thus, for the present, we propose that the family *Gloniaceae* be considered *Pleosporomycetidae incertae sedis*.

TAXONOMY

Hysteriaceae Chevall. 1826, **Hysteriales** Lindau 1897, **Pleosporomycetidae** Schoch *et al.* 2007

Fungi classified in the *Hysteriaceae* Chevall. (Chevallier 1826) have been traditionally defined by a specialized ascocarp termed the hysterothecium (Clements 1909). Hysterothecia are dense, persistent carbonaceous structures, distinctly navicular in outline, and bear a pronounced longitudinal slit running the length of the long axis of the fruitbody. They can be immersed to erumpent to entirely superficial, solitary to gregarious, ellipsoid to greatly elongated, sometimes branched or triradiate. In vertical section, hysterothecia are globose to obovoid, typically with a thick three-layered peridium, composed of small pseudoparenchymatous cells, the outer layer heavily encrusted with pigment and often longitudinally striated on the surface, the middle layer lighter in pigmentation and the inner layer distinctly thin-walled, pallid and compressed (Barr 1987). The hamathecium is composed of persistent, narrow cellular pseudoparaphyses, often borne in a gel matrix, with tips darkened or branched at maturity above the asci. Bitunicate asci are borne in a basal layer and at maturity are typically clavate to cylindrical, bearing eight ascospores, overlapping biserially, ranging from hyaline to dark brown, obovoid, clavate, ellipsoid or fusoid. Ascospores are highly diverse in septation and range from didymospores to phragmospores to dictyospores, at times surrounded by a gel coating, and often show bipolar asymmetry (Barr 1987). Zogg (1962) accepted the following seven genera within the *Hysteriaceae*: *Hysterium* Tode : Fr., *Gloniella* Sacc., *Hysterographium* Corda, *Gloniopsis* De Not., *Farloweilla* Sacc., *Glonium* Muhl. : Fr., and *Hysterocarina* Zogg.

The traditional circumscription of the *Hysteriaceae* (Zogg 1962) was based on character states related to the hysterothecium and spore morphology (e.g., septation and pigmentation), character states previously considered synapomorphic. Although morphology has served well to define the classical genera, it is now called into question in light of molecular data presented here and elsewhere (Boehm *et al.* 2009; Mugambi & Huhndorf 2010; Schoch *et al.* 2007a). Thus, a number of examples of convergent

evolution are presented in the current study, which relate not only to the fruitbody, but to spore morphology as well. As a result, a number of genera have been shown not to be related to the *Hysteriaceae*, and have been removed from the family (e.g., *Glonium*, *Hysterographium*, and *Farlowiella*). This implies that morphological character states associated with the hysterothecium are not confined to the family, and instead represent sympleisiomorphies (Boehm *et al.* 2009). Additionally, several genera (e.g., *Hysterium*, *Hystereographium* and *Gloniopsis*), have their members spanning both Groups I and II (Fig. 1), thus necessitating a radical reappraisal of the phylogenetic integrity of the family. Thus, in the current study, two new genera are proposed (e.g., *Oedohysterium* and *Hysterobrevium* *gen. nov.* as well as three new species, one in *Hysterium* and two in *Gloniopsis*, in addition to a number of new combinations involving *Psilogonium*, *Oedohysterium*, *Hysterobrevium* and *Gloniopsis*.

Molecular data have also necessitated that we expand the concept of the *Hysteriaceae* to also include thin-walled mytilinioid forms previously in the *Mytiliniaceae* (e.g., *Ostreichnion*), as well as patellarioid forms previously in the *Patellariaceae* (e.g., *Rhytidhysterion*). The inclusion of *Ostreichnion* within the *Hysteriaceae* was unexpected. Unlike most members of the family, the peridium in *Ostreichnion* is sclerenchymatoid and thin-walled, defining a fragile mytilinioid ascoma, that is conchate with a cristate apex, and with a hamathecium typified by trabeculate pseudoparaphyses (Barr 1975, 1990a). Including the genus *Ostreichnion* in the *Hysteriaceae* implies that, either morphological features within the genus need to be re-evaluated, or that the family *Hysteriaceae* must also encompass mytilinioid forms. More difficult to understand perhaps is the inclusion of the genus *Rhytidhysterion* within the *Hysteriaceae*. Although included within the *Patellariaceae* (Kutorga & Hawksworth 1997), phylogenetic data presented here and elsewhere (Boehm *et al.* 2009), clearly indicate that this genus lies quite distant from other members of the *Patellariaceae*.

Some authors have included a number of additional genera within the *Hysteriaceae*. For instance, the genera *Hysteropatella* Rehm, *Hysteroglonium* Rehm *ex* Lindau, and *Pseudoscypha* J. Reid & Piroz., were included in the *Hysteriaceae* by Eriksson (2006). In addition, the genera *Hemigrapha* (Müll. Arg.) R. Sant. *ex* D. Hawksw., *Graphyllum* Clem. (Shoemaker & Babcock 1992), and *Encephalographa* Massal., were included in the family by Kirk *et al.* (2001). In Boehm *et al.* (2009), two species belonging to *Hysteropatella*, namely *Hp. clavisporea* (Peck) Seaver (CBS 247.34) and *Hp. elliptica* Fr. (CBS 935.97), did not cluster with any of the hysteriaceous taxa surveyed. Instead, they formed a distant clade within the *Pleosporomycetidae*; the authors suggested this to represent the emergence of the *Patellariales*. Therefore, we do not include the genus *Hysteropatella* within the *Hysteriaceae*. In the present study, these two species of

Hysteropatella continue to be distant from the *Hysteriaceae*, and also cluster now with *Patellaria atrata* (Hedw.) Fr. (CBS 958.97), thus reinforcing the clade supporting the *Patellariaceae*.

Reid & Pirozynski (1966) in describing *Pseudoscypha* on the needles of *Abies balsamea* did not mention the *Hysteriaceae*, and in fact stated that the fungus cannot be assigned to any presently known order. In their illustrations, no sterile tissue or excipulum is presented, and the bitunicate asci and pseudoparaphyses arise directly from an erumpent orange basal stromatic cushion. As such, we do not include *Pseudoscypha* as a member of the *Hysteriaceae*. As for the genus *Hemigrapha*, Diederich & Wedin (2000) make the argument for the inclusion of the genus in the *Microthyriaceae*, not the *Hysteriaceae*. The genus *Graphyllum* possesses applanate, clathrate ascospores borne in thin-walled membranous hysterothecia, at first subcuticular, later erumpent, often associated with aquatic poaceous hosts. The genus was included in the *Hysteriaceae* by Shoemaker & Babcock (1992) and Kirk *et al.* (2001), but was classified in the *Phaeosphaeriaceae* by Barr (1987). A new species was recently described from Costa Rica (Checa *et al.* 2007). The unique ascospore and the lack of carbonization or peridial wall thickness argue against the inclusion in the *Hysteriaceae*, but molecular data are lacking.

The genus *Encephalographa* was originally placed in the *Hysteriaceae* by Renobales & Aguirre (1990) who thought it to be lichenicolous. Tretiach & Modenesi (1999) demonstrated it to be lichenized, and maintained its placement within the *Hysteriaceae*. The latter authors illustrate endolithic, saxicolous, dichotomously branched, laterally anastomosed, lirelliform pseudothecia with a longitudinal sulcus, and clavate bitunicate asci bearing pigmented didymospores, highly reminiscent of the saxicolous forms of *G. circumserpens*, in the *Gloniaceae*. We recently were able to obtain fresh material of *Encephalographa elisae* A. Massal. from Mauro Tretiach (Dipartimento di Biologia, Università di Trieste, Trieste, Italy), and, although cultures failed, we were able to isolate DNA directly from the ascomata (EB 0347). Sequence data presented here indicate that *E. elisae* does not reside within the *Hysteriaceae*, nor within the *Gloniaceae*. Instead, *E. elisae* lies outside of the *Pleosporomycetidae* and *Dothideomycetidae* (Fig. 1).

Thus, to summarize, currently accepted genera in the *Hysteriaceae* include: *Hysterium*, *Hystumidum*, *Gloniella*, *Hysterobrevium*, *Gloniopsis*, *Hysterocarina*, *Psilogonium*, *Actidiographium*, *Ostreichnion*, and *Rhytidhysterion*. Dichotomous keys are presented here for hysteriaceous fungi, with the caveat that phylogenetically unrelated taxa share the same key. Thus, despite their transference from the *Hysteriaceae* (Boehm *et al.* 2009), the genera *Hysterographium*, *Farlowiella*, *Glodium* and *Anteaglonium* (Mugambi & Huhndorf 2010), are nevertheless included in

the key. This is because they typically possess ascospores that have traditionally been referred to as hysterothecia.

Key to the genera and allied genera of the *Hysteriaceae*

1. Acomata apothecioid, opening widely when hydrated, fully exposing the hymenium, which may be red or black (i.e., patellarioid) **Rhytidhysterion**
- 1'. Hysterothecia usually remaining closed, or only opening slightly through a longitudinal fissure or sulcus to reveal a lenticular, disk-like hymenium when hydrated and mature 2
2. Ascospores pedicellate asexual spores, the upper cell pigmented and much larger than the lower, which remains unpigmented; anamorph *Acrogenospora* **Farlowiella**
 Note: The genus *Farlowiella* is currently removed from the *Hysteriaceae* and listed as *Pleosporomycetidae incertae sedis* (Boehm *et al.* 2009).
- 2'. Ascospores not as above, didymospores, phragmospores or dictyospores, sometimes pigmented 3
3. Didymospores small, the two cells more or less equal in size 4
- 3'. Ascospores not as above, phragmospores, dictyospores, +/- pigmentation, or very large didymospores (*O. curtisii*) 7
4. Ascospores hyaline 5
- 4'. Ascospores pigmented **Actidiographium**
5. Didymospores less than 8 µm long **Anteaglonium**
 Note: The genus *Anteaglonium* Mugambi & Huhndorf is not a member of the *Hysteriaceae*, but lies within the *Pleosporales* (Mugambi & Huhndorf 2010). The four species of *Anteaglonium* are keyed out in the *Psiloglonium* key.
- 5'. Didymospores longer than 8 µm 6
6. Didymospores hyaline, borne in solitary or gregarious hysterothecia, rarely associated with a subiculum, not laterally anastomosed to form radiating stellate composites **Psiloglonium**
 Note: One species of *Anteaglonium*, *A. latirostrum* Mugambi & Huhndorf, will key out here, but belongs in the *Pleosporales* (Mugambi & Huhndorf 2010) and is keyed out in the *Psiloglonium* key.
- 6'. Didymospores hyaline, borne in modified hysterothecia, usually associated with a subiculum, strongly laterally anastomosed along their length to form radiating stellate composites **Glonium**
 Note: The genus *Glonium* has been transferred from the *Hysteriaceae* to the *Gloniaceae*, currently listed as *fam. incertae sedis* within the *Pleosporomycetidae* (Boehm *et al.* 2009).
7. Ascospores transversely septate phragmospores, or if with dictyospores then also with red pigmentation 8
- 7'. Ascospores transversely and longitudinally septate dictyospores, or very large didymospores (*O. curtisii*) 10
8. Ascospores hyaline phragmospores **Gloniella**
- 8'. Ascospores pigmented phragmospores or in one case (*Oedo. pulchrum*) with pigmented dictyospores and red pigmentation in the hamothecium 9
9. Phragmospores three-septate or rarely more, but without swollen supra-median cell(s) **Hysterium**
- 9'. Phragmospores with swollen supra-median cell, usually more than 3-septate, in one case with pigmented dictyospores and red centrum pigmentation (*Oedo. pulchrum*) **Oedohysterium**
10. Dictyospores hyaline, +/- gelatinous sheath, or pigmented, but short, less than 25 µm in length **Hysterobrevium**

- 10'. Dictyospores hyaline, +/- gelatinous sheath, or pigmented, but longer than 25 µm, or very large didymospores (*Ostreichnion curtisii*) 11
11. Dictyospores, if hyaline, then longer than 25 µm, or if pigmented, then measuring (22-)25-34(-45) x (6-)8-12(-17) µm, with 7-11 transverse and 1-2 vertical septa, and no red pigment associated with the hamathecium (*Glp. subrugosa*) **Gloniopsis**
- 11'. Dictyospores pigmented, of different length, or if similar in length to *Glp. subrugosa*, then tropical with red pigment associated with the hamathecium, or very large didymospores (*O. curtisii*) 12
12. Dictyospores pigmented, borne in typical hysterothecia, that are erumpent or sessile on the substrate **Hysterographium**
 Note: The genus *Hysterographium*, with the type species *Hg. fraxini*, has been transferred out of the *Hysteriaceae* and is considered as *Pleosporomycetidae* gen. *incertae sedis* (Boehm *et al.* 2009). Residual species classified as *Hysterographium*, remaining within the *Hysteriaceae*, for which sequence data are lacking, are provisionally retained within the genus.
- 12'. Hysterothecia borne within the substrate, hardly erumpent, with cristate longitudinal apex instead of a sulcus; neotropical (Brazil), on *Eucalyptus* **Hysterocharina**
- 12''. Ascomata thin-walled, globoid to conchate, mytilinioid, without sunken longitudinal slit; pigmented dictyospores or very large didymospores **Ostreichnion**
 Note: The genus *Ostreichnion*, previously in the *Mytiliniaceae*, was transferred to the *Hysteriaceae* (Boehm *et al.* 2009).

1. The genus *Hysterium* Tode : Fr.

Schrift. Berlin. Ges. Naturf. Freunde 5: 53 (1784).
 Syst. mycol. 2, 579 (1823).

The genus *Hysterium* is characterized by pigmented versicolorous or concolorous asymmetric phragmospores, three- or more transversely-septate, borne in hysterothecia. A historical overview of the nomenclature of the genus was presented in Boehm *et al.* (2009). Zogg (1962) recognized two morphological types within the genus *Hysterium*. Type I is characterized by three-septate phragmospores, and includes the versicolorous type species *H. pulicare* (Lightf. : Fr.) Pers. (Fig. 4A), and its closely related concolorous counterpart, *H. angustatum* Alb. & Schwein. (Fig. 4B), both extremely common in the temperate zones of both hemispheres. These are followed by *H. vermiforme* Masee (Fig. 4C), from Africa, and the much larger-spored *H. macrosporum* Teng, reported from the United States and China (Teng 1933). Although Zogg (1962) did not accept *H. hyalinum* Cooke & Peck, Lohman (1934) provided legitimacy to the epithet, noting that pigmentation is delayed in the maturation of the three-septate ascospores (Boehm *et al.* 2009). The species is temporarily retained in this genus.

Type II corresponds to a different phragmospore, one in which, typically, there are five or more septa, and in which there exists a swollen cell, either just above the median septum (i.e., supramedian) or, rarely, some distance up from the median septum. Type II includes, by increasing spore length, the cosmopolitan *H. insidens* Schwein. (Fig. 4E), the larger-spored counterpart *H. sinense* Teng (Fig. 4F), and the unusual *H. magnisporum* W.R. Gerard, seven-septate, with three of the septa

crowded to each end, the two central cells much larger. The latter two species are reported from the United States and China (Teng 1933). *Hysterium velloziae* P. Henn., provisionally included by Zogg (1962), with up to 21 septa at maturity, has only been reported from Africa (van der Linde 1992).

An additional two species have been recently described. *Hysterium asymmetricum* Checa, Shoemaker & Umaña (Checa *et al.* 2007) from Costa Rica, has outer centrum tissues pigmented red, and three-septate phragmospores, showing an extended basal cell. *Hysterium andinense* Messuti & Lorenzo has been recently described from the conifer *Austrocedrus chilensis* in Argentina (Messuti & Lorenzo 1997). However, molecular data (Boehm *et al.* 2009) has placed this taxon in the *Mytiliniaceae*, as *Mytilinidion andinense* (Messuti & Lorenzo) Boehm, Schoch & Spatafora, based on CBS 123562 (EB 0330 / BPI 878737). This brings the total number of species within the genus *Hysterium* to ten. An additional new species is described here.

Hysterium barrianum Boehm, Miller, Mugambi, Huhndorf & Schoch, *sp. nov.*, MycoBank MB 515330, Fig. 4D.

Ascomata inconspicue hysterothecioidea, modice compressa e latere in parte superiore, paulo conniventia, sulco inconspicuo angusto, latera paucis striis profundis praedita; ascomata recta vel flexuosa, sessilia, raro furcata, matura altiora quam lata, 1-2.5 µm longa, 250-450 µm alta, 200-300 µm lata. Pseudoparaphyses hyalinae, cellulares, 1-2 µm latae, supra ascos ramosae epithecium formantes. Asci bitunicati, cylindrici, breviter stipitati, (110-)125-135 x 15-20 µm. Phragmosporeae fusiformes,

angustae, rectae vel paulo curvatae, primum hyalinae, maturae pallide luteae, quaque cellula guttulis magnis refringentibus repleta, (7–)9(–11)-septatae, (35–)40–45(–55) x (7–)9–10(–12) μm .

Etymology: Named after the late Dr. Margaret E. Barr, preeminent American mycologist.

Ascomata atypically hysterithecioid, somewhat laterally compressed in the upper region, slightly connivent, sulcus very shallow, existing as a narrow rim, sides laterally striate, striae few and deep, straight to flexuous, sessile on the substrate, rarely bifurcating, taller than wide at maturity: 1–2.5 mm long x 250–450 μm high, 200–300 μm wide. Pseudoparaphyses hyaline, cellular, 1–2 μm wide, branched above the ascus layer to form an epithecium. Ascii bitunicate, cylindrical, short-stipitate, (110–)125–135 x 15–20 μm (n=9). Phragmospores fusiform, narrow, hyaline and straight when young, becoming pale-yellow to lightly clear-brown, and curved when mature, highly guttulate, with guttulae large, highly refractive, present in every cell, with (7–)9(–11) septa, measuring (35–)40–45(–55) x (7–)9–10(–12) μm when mature (n=27).

Holotype: **United States**, Tennessee, Sevier Co., Great Smoky Mountains National Park, Chimney Tops Picnic Area, Cove Hardwood Loop Trail, 35° 38' 10.7" N, 83° 29' 32.1" W, 4 Nov 2007, A. N. Miller, S. M. Huhndorf, J. L. Crane, T.J. Atkinson, I. Promputtha, M. Grief, G. K. Mugambi & P. Chaudhary (ANM 1442, deposited as ILLS 59907).

Additional specimen examined: **United States**, Tennessee, Sevier Co., Great Smoky Mountains National Park, Elkmont, Little River Trail, 35° 39' 13.4" N, 83° 34' 44.7" W, 686 m elev., 5 Nov 2007, A. N. Miller, S. M. Huhndorf, J. L. Crane, T.J. Atkinson, I. Promputtha, M. Grief, G. K. Mugambi, & P. Chaudhary (ANM 1495; ILLS 59908).

Notes: A superficial resemblance exists between *Hysterium barrianum* in Group I (Clade C), with *H. sinense* in Group II (Clade D, see below). The phragmospores of *H. barrianum* (Fig. 4D) have a similar number of septa, (7–)9(–11), as those of *H. sinense* (Fig. 4F), the latter with (3–)5–9(–11) septa. The two species also have spores of similar length. However, the width measurements of *H. barrianum*, (35–)40–45(–55) x (7–)9–10(–12) μm , serve to separate it from *H. sinense*, (34–)38–50 x 11–15 μm . Most importantly, *H. barrianum* does not possess a swollen or tumid supra-median cell, as does *H. sinense* and the closely related *H. insidens*. Furthermore, *H. barrianum* is highly guttulate, and lightly pigmented at maturity, whereas *H. sinense* and *H. insidens* possess few if any guttulae, and are much darker in pigmentation at maturity. Lastly, molecular data place the species in different groups within the *Hysteriaceae*.

In this study, we were able to secure a fairly wide taxon sampling strategy for the genus *Hysterium* (Table 1),

including multiple isolates for seven of the eleven currently recognized species, namely: *H. pulicare* (1), *H. angustatum* (7), *H. vermiforme* (1), *H. insidens* (2), *H. sinense* (2), *H. barrianum* (2) and *H. hyalinum* (1). Multiple gene phylogenies indicate that the genus *Hysterium* is polyphyletic, along three separate lines, two within the *Hysteriaceae* and one, *H. hyalinum*, outside of the family (Fig. 1). This implies that the evolution of pigmented phragmospores borne in hysterothecia has occurred at least three times within the *Pleosporomycetidae*.

Sequence data indicate that Clade C (Group I) contains the type species, *Hysterium pulicare*, as well as the closely related *H. angustatum*, and *H. vermiforme* (Fig. 1). All three taxa have 3-septate, pigmented phragmospores, corresponding to Type I. Also, within Clade C resides the newly described *H. barrianum*, with 9-septate spores. None of these species has a swollen supra-median cell. Isolates of *H. angustatum* (Fig. 4B), originating from South Africa (CMW 20409 / PREM 57585), Kenya (GKM 243A), New Zealand (SMH 5211, SMH 5216) and the United States, from New Jersey (CBS 123334 / EB 0324 / BPI 878724), Wisconsin (CBS 236.34) and Tennessee (ANM 85) form a highly supported monophyletic clade with *H. pulicare* (Fig. 4A), collected from New York, USA (CBS 123377 / EB 0238 / BPI 878723). Both species possess similar pigmented three-septate phragmospores, versicolorous in *H. pulicare* and concolorous in *H. angustatum*. Interestingly, ~10% of the ascospores within a given hysterothecium of *H. pulicare* are typically found to be concolorous (Bisby 1941). Likewise, versicolorous ascospores have also been observed in *H. angustatum*, stated at less than ~5% for a given hysterothecium (Lee & Crous 2003). Although ascospore size in *H. pulicare* may be twice that found in *H. angustatum* (Zogg 1962), a certain degree of overlap in spore length measurements exists between the two, and molecular data presented here and elsewhere (Boehm *et al.* 2009) indicate that they are closely related.

In this study, one of the *H. angustatum* accessions from Tennessee (ANM 85), the United States, did not cluster with the other surveyed *H. angustatum* in Clade C. Instead, ANM 85 clustered with *H. vermiforme* from Kenya (GKM 1234). Spore measurements of ANM 85 were compared to the other *H. angustatum* accessions, from the United States (CBS 123334 / BPI 878724), Kenya (GKM 243A), and New Zealand (SMH 5211.0) which formed the other sub-clade within Clade C. All of these specimens showed remarkably little variability in their spore morphology. Additionally, no obvious differences were noted in their fruitbody morphology. This may indicate early stages of speciation within the taxon, with sequence variation preceding morphologic change.

Grouping with the anomalous *H. angustatum* ANM 85, was *H. vermiforme* (Fig. 4C), a taxon known only from the original description by Masee in 1901 from West Africa (Ghana). The isolate included here (GKM 1234) originated

from Mt. Kenya, Kenya, and possesses smaller spore measurements, (20–)25–28 x (4–)5–6 µm, than those given by Masee (1901), and reiterated by Zogg (1962), as (30–)35–40 x 12–14 µm. In other respects, however, GKM 1234 matches closely Masee's (1901) original description, and we choose here to simply expand the spore measurements for *H. vermiforme* to (20–)25–40 x (4–)5–14 µm, rather than describe a new species.

The three-septate *H. hyalinum* (CBS 237.34) lies outside of the *Hysteriaceae* altogether. It falls in a small, isolated, but well-supported clade along with the type species of *Hysterographium*, namely *Hg. fraxini*. Since only one isolate is represented, it is premature to draw conclusions. Molecular data indicate that the remaining two species of *Hysterium* in our survey, namely *H. sinense* and *H. insidens*, are not related to the type *H. pulicare* and associated species within Clade C (Group I). Rather, data indicate that they belong to Clade D (Group II). As such, we propose the following new genus to accommodate these taxa.

2. The genus *Oedohysterium* Boehm & Schoch

Oedohysterium Boehm & Schoch, *gen. nov.*, MycoBank MB 515328.

Typus: *Oedohysterium insidens* (Schwein.) Boehm & Schoch, *comb. nov.*

Hysterothecia solitaria vel gregaria, iuvenia erumpentia, deinde superficialia, navicularia, nonnumquam linearia, plus minusve parallela, neque confluentia, nonnumquam angulo inserta, raro flexuosa vel furcata, plerumque utrinque obtuse, et fissura longitudinali prominente praedita. Latitudo altitudine minor vel major. Peridium crassum, carbonaceum, maturum fragile, per longitudinem striatum, basim versus incrassatum, sursum attenuatum, bistratosum. Pseudoparaphyses cellulares, 1–2.5 µm latae, hyalinae, septatae, sursum ramosae, vulgo epithecium pigmentatum ascos obtegens formantes. Asci cylindrici vel clavati, bitunicati. Ascospores irregulariter biseriatae, phragmoseptatae (dictyoseptatae), fusiformes, curvatae, utrinque angustatae, ad septum medium constrictae, (4–)6–8 (raro –11) septis divisae, primum pallide luteae, deinde brunnescentes. Cellula (raro duo cellulae) ascosporarum supramediana conspicue inflata. Anamorphe ad *Septonema* pertinens.

Etymology: Greek, *Oedo-* meaning swollen, referring to the swollen central cells of the ascospores and *Hys-* from *Hysterium*.

Hysterothecia isolated to gregarious, erumpent when young, superficial when mature, navicular, sometimes linear in more or less parallel rows, but non confluent laterally, or sometimes situated at angles, rarely flexuous or bifurcating, usually with obtuse ends, and with a prominent longitudinal slit. Sometimes taller than wide

(e.g., *Oedo. insidens*), othertimes wider than tall (e.g. *Oedo. sinense*). Peridium thick, carbonaceous, brittle with age, longitudinally striated on the margins, thickened towards base, less thick apically, composed of two to three distinct layers, the inner compressed and pallid, the outer thickened and pigmented. Pseudoparaphyses cellular, 1–2.5 µm wide, hyaline, septate, branched above, forming a usually pigmented epithecium above the asci. Asci cylindrical to clavate, bitunicate. Ascospores irregularly biseriatae in ascus, typically phragmospores, in one case dictyospores, curved, fusiform, with tapering apices, constricted at the median septum, with (4–)6–8(–11[rarely]) septa, at first hyaline-yellow, then pigmented sepia to brown at maturity. Genus characterized by a swollen or tumid supra-median cell, rarely with two cells swollen.

Oedohysterium insidens (Schwein.) Boehm & Schoch, *comb. nov.*, MycoBank MB 515332, Fig. 4E.

Basionym: *Hysterium insidens* Schwein., *Trans. Amer. philos. Soc., New Series* 4(2): 244 (1832).

- = *Hysterographium insidens* (Schwein.) Sacc., *Syll. Fung.* 2: 778 (1883).
- = *Hysterium complanatum* Duby, *Mém. Soc. Phys. Hist. nat. Genève* 16(1): 38 (1862).
- = *Hysterium depressum* Berk. & M.A. Curtis, *Grevillea* 4(29): 10 (1875).
- = *Hysterium fusigerum* Berk. & M.A. Curtis, *Grevillea* 4(29): 11 (1875) (as '*fusiger*').
- = *Hysterium berengeri* Sacc., *Syll. Fung.* 2: 751 (1883).
- = *Hysterium janusiae* Rehm, *Hedwigia* 37: 299 (1898).
- = *Hysterium apiculatum* Starbäck, *Bih. K. Svensk. Vet.-Akad. Handl.* 25(1): 19 (1899).
- = *Hysterium batucense* Speg., *Revista Fac. Agron. Univ. Nac. La Plata* 6(1): 116 (1910).
- = *Hysterium andicola* Speg., *Anal. Mus. nac. Hist. nat. B. Aires* 23: 85 (1912).
- = *Hysterium atlantis* Maire, *Mém. Soc. Sci. Nat. Maroc.* 45: 35 (1937).
- = *Hysterium lavandulae* Urries, *Anal. Jard. Bot. Madrof* 1: 64 (1941).

Hysterothecia isolated to gregarious, variably erumpent to sessile, 0.5–2.5 mm long, 0.2–0.5 mm high, lying parallel, but not confluent laterally, generally in line with the grain of the wood, and striated laterally with age. Pseudoparaphyses hyaline, cellular, 1–2.5 µm wide, walls thickend at apices, forming an epithecium above the ascal layer. Asci cylindrical, 8-spored, irregularly biseriatae, 130–150 x 15–24 µm. Phragmospores transversely (4–)6–8 (–11[rarely]) septate, constricted at the median septum, inequilateral, slightly curved, at first hyaline-yellow, then brown at maturity, with a prominent swollen supra-median cell. If 5-septate, then swollen cell located at the second position; if 6-septate, then often the third from the top, measuring (20–)23–28(–38) x (5–)7–10(–13) µm. Anamorph: *Septonema spilomeum* Berk. (Lohman 1933a). Principally North- and South-America, and Europe (Italy). Bark and old wood of *Pinus*, *Larix*, *Castanea*, *Quercus*, *Eucalyptus*, *Fraxinus*, *Aspidosperma*, *Lavandula* (Zogg

1962). Also reported from South Africa (van der Linde, 1992). Anamorph: *Septonema spilomeum* Berk.

Oedohysterium sinense (Teng) Boehm & Schoch, *comb. nov.*, MycoBank MB 515333, Fig. 4F.

Basionym: *Hysterium sinense* Teng, *Sinensia* 4: 134 (1933).

≡ *Hysterium macrosporum* Teng, *Sinensia* 4: 134 (1933), *non* Peck, *Rep. N.Y. St. Mus. nat. Hist.* 26: 83 (1874) [1873].

Hysterothecia very similar to *Oedo. insidens*, that is, scattered to subgregarious, linear, parallel but non-confluent laterally, and striated in age, of a similar size. Pseudoparaphyses as in *Oedo. insidens*. Asci 140–170 x 26–30 µm, short-stipitate, spores biseriate to subsperate in ascus. Phragmospores large, fusiform, asymmetric and curved, at first hyaline, then pale-yellow to -brown, finally deep brown, with (3–)5–9(–11) septa, and with a prominent median septal constriction, measuring (34–)38–50 x 11–15 µm. Spores with a prominent swollen supra-median cell, usually located just above the median septum. From North America, Europe (Zogg 1962), China (Teng 1933), and South Africa (van der Linde 1992). From decorticated hardwood trees and structures (e.g., fence posts).

Notes: Species of *Oedohysterium* belonging to Clade D (Group II) are characterized by elongate asymmetric spores with more than three septa, typically showing a swollen or tumid supra-median cell (Type II). In this study, two single-ascospore isolates of *Oedo. sinense* (Fig. 4F), one from South Africa (CBS 123345 / EB 0333 / BPI 878730), and one from the United States, New Jersey (EB 0339), cluster with two isolates of *Oedo. insidens* (Fig. 4E), both from the United States, Massachusetts (CBS 238.34) and Tennessee (ANM 1443). Both species have remarkably similar phragmospores. As these two taxa belong to Group II and are far removed from the type species, *H. pulicare*, we propose that they be accommodated in the new genus *Oedohysterium*. An additional new combination is proposed below.

Oedohysterium pulchrum (Checa, Shoemaker & Umaña) Boehm & Schoch, *comb. nov.*, MycoBank MB 515334.

Basionym: *Hysterographium pulchrum* Checa, Shoemaker & Umaña, *Mycologia* 99: 289 (2007).

Notes: The newly described *Hysterographium pulchrum* Checa, Shoemaker & Umaña from Costa Rica (Checa *et al.* 2007) also falls within Clade D (Fig. 1) and is here transferred to *Oedohysterium*, as *Oedo. pulchrum*. This is because molecular data indicate a close association with the two species of *Oedohysterium*, *Oedo. insidens* and *Oedo. sinense*. At first surprising, on further consideration, this sub-clade forms a natural assemblage premised on morphological features. The spores of all three taxa show a remarkable degree of similarity in morphology, which includes being similarly pigmented, slightly curved and fusiform, with a common number of transverse septa. The sole difference is the presence of one or two vertical septa in *Oedo. pulchrum*, a feature noted by the authors to be absent in some spores (Checa *et al.* 2007). Most importantly, like *Oedo. insidens* and *Oedo. sinense*, *Oedo. pulchrum* also possesses a swollen supra-median cell. Interestingly, a striking resemblance to the phragmospores of *Oedo. insidens* can be seen for those spores of *Oedo. pulchrum* that do not possess vertical septa (Checa *et al.* 2007). This is based on similarities in shape (e.g., curved and fusiform), size [(20–)23–28(–38) x (5–)7–10(–13) µm versus 22–25(–27) x 5–6 µm], and in the number of transverse septa [(4–) 6 to 8 (–11[rarely]) versus (5–) 6], for *Oedo. insidens* and *Oedo. pulchrum*, respectively. As molecular data indicate that the presence or absence of vertical septa should be considered a sympleisiomorphic character state within the *Hysteriaceae* (Boehm *et al.* 2009), we feel justified in including both phragmospores and dictyospores within the genus *Oedohysterium*.

We choose to provide the following dichotomous key whereby all hysteriaceous fungi, bearing transversely septate pigmented phragmospores (including *Oedo. pulchrum* with dictyospores) are identified together, with the caveat that unrelated taxa appear in the same key.

Key to the species of *Hysterium* and *Oedohysterium*

1. Phragmospores mainly three-septate 2
 - 1'. Phragmospores concolorous, more than three-septate, in one instance pigmented dictyospores with 1-2 vertical septa (*Oedo. pulchrum*) 7
 2. Phragmospores either versicolorous or delayed concolorous 3
 - 2'. Phragmospores truly concolorous (sepia to dark brown in colour) 4
 3. Terminal cell mainly remaining hyaline with inner spore cells pigmented brown (versicolorous); ascospores 20–40 x 6–12 µm ***H. pulicare***

- 3'. Phragmospores tardily pigmented, often remaining hyaline for quite some time after discharge, but eventually becoming uniformly concolorous; 20–26(–28) x 6–8.5 µm **H. hyalinum**
 Note: Currently recognized as *Pleosporomycetidae* sp. *incertae sedis* (Boehm *et al.* 2009).
4. Phragmospores three-septate, 28 µm or less in length 5
- 4'. Phragmospores three-septate, longer than 28 µm 6
5. Phragmospores (12–)14–21(–28) x (3–)4–8(–10) µm, firmly three-septate, no septal constrictions; end-cells obtuse **H. angustatum**
- 5'. Phragmospores (14–)15–18(–20) x 5–7 µm; three- (rarely two- or four-)septate; prominently constricted at first-formed septum; basal cell extended; red hamathecial pigment; neotropical **H. asymmetricum**
6. Phragmospores fusoid, slightly curved, guttulate; (20–)25–40 x (4–)5–14 µm; West and East Africa **H. vermiforme**
- 6'. Phragmospores fusoid, curved, highly guttulate; 40–57 x 11–15 µm; on *Pinus*, NY, USA and China **H. macrosporum**
7. Phragmospores or dictyospores (four-) six- to eight- (eleven-) celled, fusiform in outline, with +/- swollen supra-median cell(s) 8
- 7'. Phragmospores with more than 11 septa, fusiform, light brown, (13–)14–15(–21)-septate, (35–)45–50(–60) x (10–)12–13(–14) µm; Africa **H. velloziae**
8. Swollen supra-median cell(s) present, either phragmospores or dictyospores (*Oedohysterium*) 9
- 8'. Phragmospores only, no swollen supra-median cells(s) present 11
9. Dictyospores lightly pigmented, 22–25(–27) x 5–6 µm, with (5–)6 transverse and 1 vertical septum in either cell or both cells adjacent to the primary septum, absent in some spores, with a swollen supra-median cell; typically with red pigment in the hamathecium; neotropical (Costa Rica) **Oedo. pulchrum**
- 9'. With no red pigment present 10
10. Phragmospores with (4–)6–8(–11[rarely]) septa, slightly curved, fusiform, at first hyaline-yellow then reddish brown at maturity, if 5-septate, showing a swollen cell at the second position, if 6-septate, often the third from the top, +/- median septal constriction, (20–)23–28(–38) x (5–)7–10(–13) µm; cosmopolitan **Oedo. insidens**
- 10'. Phragmospores larger, fusiform, straight to curved, at first hyaline, then yellow or pale brown, finally deep brown; swollen supra-median cell(s) present, (3–)5–9(–11) septa, with median septal constriction; (34–)38–50 x 11–15 µm **Oedo. sinense**
11. Phragmospores fusiform, narrow, straight to very slightly curved, pale hyaline at first, then pale-yellow at maturity, with highly refractive guttules, in every cell, with (7–)9(–11) septa, no supra-median swollen cell(s), (35–)40–45(–55) x (7–)9–10(–12) µm; TN, USA **H. barrianum**
- 11'. Phragmospores oblong, wide, slightly curved, bulging on one side, nearly hyaline and 1-septate at first, becoming clear brown and 7-septate, septa highly asymmetric, (2–)3 of the septa close to each end, the two central cells much larger; 48–67 x 15–20 µm; NJ, NY, USA **H. magnisporum**

3. The genus *Gloniella* Sacc.
 Syll. Fung. 2: 765 (1883).

The genus *Gloniella* was established by Saccardo (1883) to accommodate hysteriaceous fungi that possess hyaline phragmospores, from three- to nine-septate. As such, most

authors have considered the genus to be closely related to *Hysterium*, showing a similar relationship as does *Gloniopsis* to *Hysterographium*. Molecular data have confirmed the latter relationship (Boehm *et al.* 2009), but are presently lacking for *Gloniella*. Zogg (1962) recognized six species: three collected on ferns from Europe and the

Mediterranean, namely *Gl. adianti* (Kunze) Petrak on *Adiantum*, and *Gl. graphidoidea* Rehm and *Gl. normandina* Rehm, both on *Pteridium*. Zogg also accepted *Gl. sardoa* Sacc. & Trav. from *Populus* in Europe, *Gl. typhae* (Fuckel) Sacc. on *Typha*, the latter described from Europe (Zogg 1962) and Chile (Lorenzo & Messuti 1998), and *Gl. bambusae* Zogg on *Bambusa* from Brazil. Since then, an additional three species have been described: *Gl. gracilis* Checa, Shoemaker & Umaña from Costa Rica (Checa *et al.* 2007), *Gl. corticola* Pande & Rao from India (Pande & Rao 1991), and *Gl. clavatispora* T.D. Steinke & K.D. Hyde from South Africa (Steinke & Hyde 1997). Data presented

in Chapter 1 of this volume indicate that *Gl. clavatispora* finds association with members of the *Patellariaceae*. As this is based on only a single isolate, it may be premature to draw conclusions; however, both *Gloniella* and several genera within the *Patellariaceae* possess remarkably similar hyaline phragmospores. More recently, Barr (2009) recognized *Gl. abietina* Syd. on *Abies* from Idaho, and *Gl. lapponica* (P. Karst.) Sacc. on *Arctostaphylos* from Washington, thus bringing the total number of species in the genus to eleven. A number of species in the key may be conspecific, since reported spore measurements may be identical or nearly so.

Key to the species of *Gloniella*

1. Ascospores 3-septate, shorter than 15 µm 2
- 1'. Ascospores 3- or more-septate, and longer 3
2. Ascospores 10–15 x 5–6 µm; on wood, India ***Gl. corticola***
- 2'. Ascospores 12–14 x 4–5 µm; on *Typha*, Europe ***Gl. typhae***
3. On ferns in Europe 4
- 3'. Not on ferns 6
4. Ascospores (2–)3(–4) septate, (11–)15–20(–23) x 3–5 µm; on *Adiantum*, Europe ***Gl. adianti***
- 4'. Ascospores (3–)5(–7)-septate, slightly longer 5
5. Ascospores (3–)5-septate, (15–)18–20(–22) x 4–5 µm; on *Pteridium*, Europe ***Gl. graphidoidea***
- 5'. Ascospores 5–7-septate, (22–)25–27(–30) x 3–4 µm; on *Pteridium*, Europe ***Gl. normandina***
6. Ascospores 1–3-septate, 36–39 x 10 µm; on *Arctostaphylos*, Washington, USA ***Gl. lapponica***
- 6'. Ascospores with more septa 7
7. Ascospores (6–)7(–8)-septate, (16–)18–21(–26) x 6–7(–8) µm; on *Populus*, Europe ***Gl. sardoa***
- 7'. Ascospores larger 8
8. Ascospores (5–)6(–8)-septate, (18–)37(–41) x 10–11.5 µm, hyaline, smooth; on *Avicennia marina*, South Africa ***Gl. clavatispora***
- 8'. Ascospores 6–7-septate, 32–37(–40) x 4–6 µm; on wood, Costa Rica ***Gl. gracilis***
- 8". Ascospores (5–)6–7-septate, (28–)32–38(–44) x (3–)4–8(–9) µm; on *Bambusa*, Brazil ***Gl. bambusae***

The genus *Hysteroglyphium* Corda

Icon. Fung. 5: 34 (1842).

Hysteriopsis Speg. 1906

Polhysterium Speg. 1912

Fragosoa Cif., in Ciferri & Fragoso 1926

Although the genus *Hysteroglyphium* has been removed from the *Hysteriaceae* (Boehm *et al.* 2009), and is currently recognized as *Pleosporomycetidae gen. incertae sedis*, it is included here. This is because it forms the basis for a number of new combinations within the family. The genus

is characterized by pigmented dictyospores, with one to several longitudinal septa, ovoid to ellipsoid-fusoid, relatively broad, usually constricted at the first-formed septum. Zogg (1962) extensively revised the synonymy of the genus and accepted four species: *Hg. fraxini* (Pers. : Fr.) De Not. (Fig. 7B and D), the type species, and *Hg. flexuosum* (Schwein. : Fr.) Sacc. (Fig. 7A and C), with large, relatively wide dictyospores, constricted primarily at the median septum, and *Hg. mori* (Schwein.) Rehm and *Hg. subrugosa* (Cooke & Ellis) Sacc., with smaller, fewer-celled dictyospores, short and squat in the former, longer and more slender in the latter, both constricted at the median septum.

Since then, an additional three species have been described: *Hg. minus* N. Amano from Japan (Amano 1983), *Hg. spinicola* Doidge from South Africa, recollected from the thorns of *Acacia* and validated by van der Linde (1992), with a brick-red epithecium and spores only slightly longer than those of *Hg. mori*, and, lastly, *Hg. pulchrum* Checa, Shoemaker & Umaña from Costa Rica, also with a red pigment in the hamathecium (Checa *et al.* 2007), here transferred to *Oedohysterium*, as *Oedo. pulchrum*.

Four of the seven species were surveyed in the present study, with multiple isolates (Table 1): *Hg. mori* (8), *Hg. subrugosa* (4), *Hg. fraxini* (2) and *Oedo. pulchrum* (1), falling into no fewer than three separate clades, two within the *Hysteriaceae* (Clades A and D) and one far removed from the family (Fig. 1). The latter clade includes the type species for the genus *Hysterographium*, namely *Hg. fraxini* (Fig. 7B and D), represented by isolates from Switzerland (CBS 109.43), deposited by Zogg in 1943, and from Canada (CBS 242.34), deposited by M.L. Lohman in 1934. *Hysterographium fraxini* forms a well-supported clade distant from the *Hysteriaceae*, but remains within the *Pleosporomycetidae* (Fig. 1). As this is substantiated by two geographically disparate isolates from two different continents, deposited by two reputable workers, it is significant. The implication is that the genus *Hysterographium* Corda must follow the type species and be removed from the *Hysteriaceae* (Boehm *et al.* 2009). Species with pigmented dictyospores remaining within the *Hysteriaceae*, previously classified in *Hysterographium*, must therefore be accommodated in other genera. In this study, these would include the following species, for which we have sequence data: *Hg. mori*, *Hg. subrugosa*, and *Hg. pulchrum* (= *Oedo. pulchrum*). The remaining species for which we do not have sequence data, namely *Hg. minus*, *Hg. spinicola* and *Hg. flexuosum*, must remain as species of *Hysterographium*, until such time that sequence data are available. We therefore propose the following new genus.

4. The genus *Hysterobrevium* Boehm & Schoch

Hysterobrevium Boehm & Schoch, *gen. nov.*, MycoBank MB 515329.

Typus: *Hysterobrevium mori* (Schwein.) Boehm & Schoch 2010, *comb. nov.*

Hysterothecia navicularia, fissura longitudinali prominente praedita, utrinque acuminata vel obtusa, linearia vel flexuosa, solitaria vel gregaria, vulgo per longitudinem striata, nonnumquam erecta, quasi stipitata, superficialia vel partim in substrato immersa. Asci bitunicati, cylindrici vel clavati. Dictyosporae pigmentatae vel hyalinae, plerumque breviores quam 25 µm, ad septum medium constrictae; ascosporae hyalinae vel luteae iuvenes vulgo strato mucido circumdatae; pigmentatae pallide brunneae, pariete levi; ascosporae ovoideae vel obovoideae, apice obtuso vel acuminato, 3–4(–6) septis transversalibus et 1–2 longitudinalibus divisae.

Etymology: *Hystero-* from *Hysterographium*, Latin *brevis*, short, referring to the spores of the type, *Hsb. mori*.

Hysterothecia navicular, with a prominent longitudinal slit, variable with acuminate to obtuse ends, linear to flexuous, solitary to densely gregarious, surface usually longitudinally striate, sometimes erect, superficial, almost stipitate, to erumpent and partially embedded in substrate, the latter especially when gregarious. Asci bitunicate, cylindrical to clavate. Spores pigmented or hyaline dictyospores, usually less than 25 µm long, constricted at least at the median septum. If hyaline to pale-yellow, then typically associated with a gelatinous sheath when young, dissipating with age. If pigmented then lightly so, transparent clear brown, walls smooth. Spores generally ovoid to obovoid, with either obtuse or acuminate ends, 3–4(–6) transverse septa, and 1–2 longitudinal septa, these mostly associated with the two central cells, but highly variable and sometimes at oblique angles in the end cells.

Hysterobrevium mori (Schwein.) Boehm & Schoch, *comb. nov.*, MycoBank MB 515335, Fig. 2C-F.

Basionym: *Hysterium mori* Schwein., Trans. Amer. Philosoph. Soc. 4(2): 244 (1832).

Synonym: *Hysterographium mori* (Schwein.) Rehm, Ascomyceten no. 363 (1876).

= *Hysterium grammodes* De Not., Giom. Bot. Ital. 2 (7-8): 55 (1847).

= *Hysterium rousseii* De Not., Piren. Ister. 2(7-8): 19 (1847).

≡ *Hysterographium rousseii* (De Not.) Sacc., Syll. Fung. 2: 779 (1883).

= *Hysterium vulgare* De Not., Piren. Ister. 2(7-8): 18 (1847).

= *Hysterium australe* Duby, Mém. Soc. Phys. Hist. nat.

Genève 16(1): 44 (1862).

= *Hysterium lesquereuxii* Duby, Mém. Soc. Phys. Hist. nat.

Genève 16(1): 41 (1862).

≡ *Hysterographium lesquereuxii* (Duby) Sacc., Syll. Fung. 2: 779 (1883).

= *Hysterium gerardi* Cooke & Peck, Bull. Buffalo Soc. Nat. Sci. 3: 33 (1875).

≡ *Hysterographium gerardi* (Cooke & Peck) Sacc., Syll. Fung.

2: 783 (1883).

= *Hysterium viticolum* Cooke & Peck, Bull. Buffalo Soc. Nat. Sci. 3: 33 (1875).

- ≡ *Hysterographium viticola* (Cooke & Peck) Rehm, Ascomyc. No. 316; in Sacc., Syll. Fung. 2: 782 (1883).
- = *Hysterium variabile* Cooke & Peck, Bull. Buffalo Soc. Nat. Sci. 3: 33 (1875).
- ≡ *Hysterographium variabile* (Cooke & Peck) Sacc., Syll. Fung. 2: 780 (1883).
- = *Hysterium formosum* Cooke, Grevillea 7(no. 41): 3 (1878).
- ≡ *Hysterographium formosum* (Cooke) Sacc., Syll. Fung. 2: 783 (1883).
- = *Hysterium putaminum* Cooke Grevillea 7: 48 (1878).
- ≡ *Hysterographium putaminum* (Cooke) Sacc. Syll. Fung. 2: 783 (1883).
- = *Hysterographium portenum* Speg., Anal. Soc. cient. Argent. 9(4): 185 (1880).
- = *Hysterographium grammodes* var. *minus* Sacc., Syll. Fung. 2: 783 (1883).
- = *Hysterographium pumilionis* Rehm, Discom. 1(3): 21 (1887).
- = *Hysterographium guaraniticum* Speg., Anal. Soc. cient. Argent. 26(1): 56 (1888).
- = *Hysterographium punctiforme* Pat., Bull. Soc. Mycol. France 4: 120 (1888).
- = *Hysterographium ruborum* Cooke, in Rehm, Ascom., No. 918 (1888).
- = *Hysterium insulare* P. Karst. & Har., Rev. Mycol. Toulouse No. 47: (1890).
- = *Hysterographium incisum* Ellis & Everh., Bull. Torrey Bot. Club 24: 462 (1897).
- = *Hysterographium ziziphi* Pat., Cat. Rais. Pl. Cell. Tunisie: 112 (1897) (as 'zizyphi').
- = *Hysterographium rousseii* var. *piri* Feltg., Vorst. Pilz. Luxemb. Nachtr. 3: 111 (1903).

Hysterothecia erumpent-superficial, ellipsoidal, oblong, linear or cylindrical, 1–2(–3) mm long, 220–275(–440) µm wide, by 190–330 µm high, mostly straight and lying parallel, but not confluent laterally, often gregarious and crowded so as to cover the substrate, longitudinally striate in age, navicular with tapering ends. Peridium 30–60 µm thick, to 100 µm at the base. Pseudoparaphyses 1–2 µm wide, hyaline, thickened apically, septate, branched, and forming an epithecium. Asci (50–)80–110 x 10–18 µm. Ascospores pigmented, thin-walled dictyospores, obovoid, ends obtuse, 3–(5–7) septate, with with 1–2(–3) vertical septa usually associated with mid-cells, but on occasion also present obliquely in end cells, constricted at the median septum, sometimes, when hydrated, at additional septa, (12–)14–22(–26) x (5–)7–10(–11) µm. Anamorph coelomycetous, *Aposphaeria*-like in nature, in culture conidiomata as irregular locules, with conidiogenous cells 8–10 x 1.5–2 µm; conidia (2–)2.5–3.5(–4) x 1–2 µm (Lohman 1932). Cosmopolitan, on aged wood of *Pinus*, *Juniperus*, *Salix*, *Ostrya*, *Castanea*, *Quercus*, *Ulmus*, *Morus*, *Pyrus*, *Amelanchier*, *Crataegus*, *Rubus*, *Cercocarpus*, *Prunus*, *Gleditsia*, various *Fabaceae*, *Melia*, *Pistacia*, *Cotinus*, *Rhus*, *Acer*, *Ziziphus*, *Vitis*, *Fraxinus*, *Olea*, and *Aspidosperma* (Zogg 1962).

Hysterobrevium smilacis (Schwein. : Fr.) Boehm & Schoch, *comb. nov.*, MycoBank MB 515336, Fig. 2B.

Basionym: ≡ *Hysterium smilacis* Schwein. *Schr. naturf. Ges. Leipzig* 1: 49 (1822).

- Synonym: *Gloniopsis smilacis* (Schwein. : Fr.) Underw. & Earle, Bull. Alabama Agric. Exp. Sta. 80: 196 (1897).
- ≡ *Hysterographium smilacis* (Schwein. : Fr.) Ellis & Everh., N. Amer. Pyrenomyc. 709 (1892).
- = *Hysterium bifforme* Fr., Observ. mycol. (Havniae) 2: 354 (1818).
- ≡ *Gloniopsis biformis* (Fr.) Sacc., Syll. Fung. 2: 773 (1883).
- = *Hysterium elongatum* β *curvatum* Fr., Elench. Fung. (Greifswald) 2: 138 (1828).
- = *Hysterium curvatum* Fr., Elench. Fung. 2: 139 (1828).
- ≡ *Gloniopsis curvata* (Fries) Sacc., Syll. Fung. 2: 775 (1883).
- = *Hysterium rocheanum* Duby, Mém. Soc. Phys. Hist. nat. Genève 16: 51 (1862).
- ≡ *Gloniopsis rocheana* (Duby) Sacc., Syll. Fung. 2: 773 (1883).
- = *Hysterographium naviculare* P. Karst. Symb. Mycol. Fenn. 6: 37 (1877).
- = *Hysterium gloniopsis* Gerard in Peck, Rep. New York St. Mus. 32: 49 ([for 1877] 1879).
- ≡ *Hysterographium gloniopsis* (W.R. Gerard) Ellis & Everh., N. Amer. Pyrenomyc. 708 (1892).
- ≡ *Gloniopsis gloniopsis* (W.R. Gerard) House, Bull. New York State Mus. 219-220: 235 (1920).
- = *Gloniella scortechiniana* Sacc. & Roum., Rev. Mycol. Toulouse 5: tab. 41, fig. 17 (1883).
- = *Gloniopsis gerardiana* Sacc., Syll. Fung. 2: 774 (1883).
- = *Gloniopsis decipiens* var. *cisti* Rehm, Hedwigia 25: 13 (1886).
- = *Gloniopsis cisti* Rehm, Hedwigia 25: 13 (1896).
- = *Gloniopsis ambigua* Sacc., Ann. Mycol. 10(3): 317 (1912).
- = *Gloniopsis ellisii* Cash, Mycologia 31: 294 (1939).

Barr (1990b) discussed the nomenclatural history of the taxon. *Hysterothecia* erumpent, many times surrounded at the base by ruptured epidermis or periderm (especially when borne in herbaceous stems, much less so on wood, then completely superficial), 0.5–1.5 mm long, 300–400 µm wide, 200–250 µm high, longitudinally striated. The periderm is 25–50 µm wide, narrower at base within the substrate, widest at mid-point, carbonaceous. Asci are 70–120 x 15–25 µm, cylindrical clavate. Dictyospores are completely hyaline to pale yellow at maturity, with a gelatinous sheath, usually dissipating at maturity. Zogg (1962) gives the spore measurements and septation as (12–)14–18(–24) x (4–)6–8(–10) µm, with 3–5(–9) transverse and 1(–3) vertical septa that pass through one to three cells; whereas Barr (1990b) gives the spores as 15–26(–31) x 5–9 µm, 3–5(–7)-septate and with one longitudinal septum in mid cells. Both state that the spores are constricted at the first-formed septum. Barr (1990b) notes that the spores of *Hsb. smilacis* (as *Glp. smilacis*) possess acuminate ends, whereas those of *Glp. praelonga* possess obtuse ends, with additional differences in size and septation. The hyaline dictyospores of *Hsb. smilacis*, like the pigmented dictyospores of similar size found in *Hsb. mori*, are highly variable in size and septation, often with one specimen favouring one or the other extremes in length measurement (Boehm, unpubl.). Cosmopolitan on old bark & wood of *Pinus*, *Chamaerops*, *Smilax*, *Populus*, *Salix*, *Juglans*, *Betula*, *Fagus*, *Quercus*, *Ficus*, *Pyrus*, *Crataegus*, *Rubus*, *Rosa*, *Prunus*, *Robinia*, *Butea*, *Pistacia*, *Cotinus*, *Acer*, *Cistus*, *Erica*, and *Lavandula* (Zogg 1962).

Notes: *Hysterobrevium mori* (Fig. 2C-F) while falling within the *Hysteriaceae*, finds itself in two separate clades in the family (Fig. 1). In Clade A (Group I), one set of isolates originating from diverse locals within the United States, associates with six highly geographically diverse isolates of *Hsb. smilacis*. The *Hsb. mori* isolates originate from New Jersey (CBS 123336 / EB 0304 / BPI 878733 and CBS 123564 / EB 0315 / BPI 878732), New York (CBS 123335 / EB 0243 / BPI 878734 and CBS 123563 / EB 0249 / BPI 878731), Indiana (SMH 5273; Fig. 2C) and Michigan (SMH 5286). The *Hsb. smilacis* isolates originate from the United States, Indiana (SMH 5280) and Michigan (CBS 200.34), New Zealand (SMH 5211), South Africa (CMW 18053 / PREM 57546), Sweden (CBS 114601), and Kenya (GKM 426N, Fig. 2B). Dictyospores of both species are of similar shape, size and degree of septation: (12–)15–23(–25) x (5–)7–10(–11) μm , with 3–(5–7) transverse and 1–2 vertical septa, versus (12–)14–18(–24) x (4–)6–8(–10) μm , with 3–4 transverse and 1(–2) vertical septa, for *Hsb. mori* and *Hsb. smilacis*, respectively. They differ in the absence of pigmentation and the presence of a gelatinous sheath in the latter. Thus, these two species, previously classified in two separate genera, *Gloniopsis* and *Hysterographium*, are in fact closely related, with each species far removed from the type species of their respective genera. Further support for this argument, can be found in Lohman (1933a), who found a similar *Aposphaeria* anamorph for both *Hsb. mori* (as *Hg. mori*) and *Hsb. smilacis* (as *Glp. gerardiana*) and stated that they were indistinguishable in culture. The implication is that both taxa should be united within the same genus, for which we propose *Hysterobrevium*.

In addition to the association with *Hsb. smilacis* in Clade A (Group I), *Hsb. mori* also finds itself in Clade D (Group II). As this is validated by two geographically diverse isolates, one from the United States, Michigan (CBS 245.34), and one from Kenya (GKM 1013; Fig. 5F), it is significant. Spore measurements of the Kenyan accession GKM 1013 in Clade D (Fig. 5F) versus those of other *Hsb. mori* accessions in Clade A, represented by specimens from the United States, namely Indiana (SMH 5273 [Fig. 2C]), New York (CBS 123335 / BPI 878734), and New Jersey (CBS 123336 / BPI 878733), failed to detect any significant morphological differences; nor were there any appreciable differences detected in their hysterothecia. The association of *Hsb. mori* with unrelated taxa within the *Hysteriaceae* in Clade A and D may be significant in that *Hsb. mori* has long been regarded as a highly variable taxon (Ellis & Everhart 1892; Lohman 1933a), resulting in the synonymy of no fewer than 28 names since its inception by Schweinitz in 1834 (Zogg 1962). Future studies may well reveal that *Hsb. mori* contains a number of cryptic species, morphologically similar, but genetically unrelated, evidence, perhaps, of speciation in progress. We propose an additional new combination below.

Hysterobrevium constrictum (N. Amano) Boehm & Schoch, *comb. nov.*, MycoBank MB 515337, Fig. 2A.

Basionym: *Gloniopsis constricta* N. Amano, *Trans. Mycol. Soc. Japan* 24: 289 (1983).

Notes: Amano (1983) described a small-spored species of *Gloniopsis* from Japan, *Glp. constrictum* N. Amano, noting a prominent median septal constriction. The measurements of the dictyospores were given as 10.4–13.2 x 4.4–5.8 μm , usually with 3–4 transverse and one vertical septum that passes through one to three cells. Although not mentioned (Amano 1983), the illustrations depict a very thick wall and dictyospores highly symmetric in outline and septation. Amano (1983) stated of the spores "...hyaline, later becoming brown...", but did not mention the presence of a gelatinous sheath. He also noted that the closest resemblance is with *Hsb. smilacis* (as *Glp. curvata* (Fr.) Sacc.), the latter however with slightly larger spores. In this study, we were fortunate to obtain a specimen from New Zealand (SMH 5211.1; Fig. 2A) that corresponds to the published description given by Amano (1983), but differs on several counts. Like *Hsb. constrictum*, the hyaline dictyospores in SMH 5211.1, are thick-walled, (1–)3(–4)-septate, with 1(–2) vertical septa, but the constriction at the median septum in SMH 5211.1, while present, is not prominent. Also unlike *Hsb. constrictum*, the spores in SMH 5211.1 have an obvious gelatinous sheath when young, but this quickly dissipates with age, and may be completely absent in mature specimens. In SMH 5211.1, the spores measure (18–)20(–23) x 10–12 μm , which is considerably larger than those of *Hsb. constrictum*. Nevertheless, these differences, in our opinion, are not sufficient to warrant a new species, and we choose here to simply expand the spore measurements for *Hsb. constrictum* to (11–)13–20(–23) x 5–12 μm , rather than describe a new species.

5. The genus *Gloniopsis* De Not.

Giorn. Bot. Ital. 2(2): 23 (1847).

A review of the nomenclatural history of the genus *Gloniopsis* was given in Boehm *et al.* (2009). The genus is characterized by hyaline to yellow dictyospores, often inequilateral, curved, in outline obovoid, ends obtuse to sub- to acuminate, multi-septate, with one or more longitudinal septa, constricted at the first-formed septum, sometimes constricted at additional septa, and usually surrounded by a gelatinous sheath, which may dissipate with age. Zogg (1962) synonymized a number of names under the type species, *Glp. praelonga* (Schwein.) Zogg (Fig. 5A-B), and accepted only one additional species, namely *Glp. curvata* (Fr.) Sacc. with smaller ascospores. Barr (1990a) proposed to include this latter species under the earlier name *Glp. smilacis* (Schwein. : Fr.) Underwood & Earle, following Cash (1939). In this study, we have

transferred *Glp. smilacis* to *Hysterobrevium*, closely related to *Hsb. mori* in Clade A. Recently, *Glp. argentinensis* Speg., previously considered by Zogg (1962) as a doubtful species, was reinstated by Lorenzo & Messuti (1998). The authors state that the ascospores are 7-septate, with 1–3(–4) longitudinal septa, some passing through multiple cells, in outline widely ellipsoid, measuring 20–26 x 9–12 µm. The septation and spore measurements are nearly identical to those of *Glp. praelonga*, the latter 5–7(–10)-septate, with 2–3 longitudinal septa, (16–)20–32(–34) x (6–)9–12(–15) µm. We therefore synonymize *Glp. argentinensis* under *Glp. praelonga*. Lastly, Amano (1983) described an additional two species of *Gloniopsis* from Japan, namely *Glp. macrospora* N. Amano and *Glp. constrictum* N. Amano (Fig. 2A), the latter transferred here to *Hysterobrevium* (Clade A, Group I).

Molecular data indicate that the genus *Gloniopsis* is polyphyletic, with the type, *Glp. praelonga*, belonging to Clade D in Group II (Fig. 1). Closely associated with the type, are a number of species possessing pigmented dictyospores, which would previously have been classified in the genus *Hysterographium* [e.g., *Hysterographium subrugosa* (Cooke & Ellis) Sacc.]. Based on molecular data presented here, we therefore propose to redefine the genus *Gloniopsis*, to include both hyaline and pigmented dictyospores. The following new combination is proposed, as well as two new species from Africa.

Gloniopsis subrugosa (Cooke & Ellis) Boehm & Schoch, *comb. nov.*, MycoBank MB 515338, Fig. 5C-E.

Basionym: *Hysterium subrugosum* Cooke & Ellis, *Grevillea* 5: 54 (1876).
 Synonym: *Hysterographium subrugosum* (Cooke & Ellis) Sacc., *Syll. Fung.* 2: 780 (1883).

= *Hysterographium hiascens* Rehm, *Ber. Nat. Hist. Ver. Augsburg* 26: 780 (1881).
 = *Hysterographium kansense* Ellis & Everh., *Erythea* 2: 22 (1894).
 = *Hysterographium cylindrosporium* Rehm, *Bih. Kongl. Svenska Vetensk.-Akad. Handl.* 25(6): 11 (1899).
 = *Hysterographium minutum* M.L. Lohman, *Pap. Michigan Acad.* 17: 267 (1933).

Hysterothecia scattered to densely crowded, navicular, straight to flexuous, with tapered ends, surface not striated in age, but smooth to sub-rugose in texture, 1 mm long, 250–350 µm diam. Asci 80–150 µm long. Dictyospores (22–)25–34(–45) x (6–)8–12(–17) µm, mostly with 7–11 transverse and 1–2 vertical septa; not constricted at septa, clear brown, ends paler at times. Anamorph coelomycetous, *Aposphaeria*-like, conidiogenous cells 5–8 x 1 µm; conidia 2–2.5 x 0.7 µm (Lohman 1933a, as *Hysterographium minutum* M.L. Lohman). Less frequently collected, but reported from North America, Europe (Southern France), Argentina (Messuti & Lorenzo 2003) and South Africa (van der Linde 1992). Old wood and bark of *Populus*, *Quercus*, *Celtis*, *Crataegus*, *Rosa*, and *Cotinus* (Zogg 1962), as well as fence posts and old planks.

Notes: In the current study, we were able to include three geographically diverse isolates of *Glp. praelonga* (Table 1), two from South Africa (CBS 112415 and CMW 19983, PREM 57539), and one from New Jersey, USA (CBS 123337 / EB 0154 / BPI 878725; Fig. 5A-B). These isolates belong to Clade D in Group II and are closely associated with one isolate of *Glp. subrugosa* from South Africa (CBS 123346 / EB 0334 / BPI 878735; Fig. 5C). An additional two isolates of *Glp. subrugosa*, from Kenya (GKM 1214; Fig. 5D) and Cuba (SMH 557; Fig. 5E), are more distantly related within the same clade. However, no discernable morphological differences were noted between these two more distantly associated isolates of *Glp. subrugosa* and CBS 123346 (EB 0334 / BPI 878735). Both *Glp. subrugosa* and *Glp. praelonga* are similar in the shape, size and septation of their dictyospores, pigmented in the former, hyaline in the latter. The spores of *Glp. subrugosa* measure (22–)25–34(–45) x (6–)8–12(–17) µm, whereas those of *Glp. praelonga* are (16–)20–32(–34) x (6–)9–12(–15) µm. Septation is also similar, with 7–11 transverse and 1–2 vertical septa in *Glp. subrugosa*, versus 5–11 transverse and 1–3 vertical septa in *Glp. praelonga*. They differ in the absence of pigmentation and the presence of a gelatinous sheath in the latter. Molecular data indicate that they are closely related.

Although spore morphology dictates that CBS 123346 (South Africa), GKM 1214 (Kenya) and SMH 557 (Cuba) are all *Glp. subrugosa*, molecular data point to genetic heterogeneity in the taxon. This is analogous to the situation in *Hsb. mori*, mentioned earlier, which, despite identical morphologies, finds affinities in both Clade A (Group I) and D (Group II). It can be concluded that both *Hsb. mori* and *Glp. subrugosa* are in the process of speciating, the latter more recently, and with genetic variation preceding morphological change. These examples of intraspecific variation are the exceptions however, as most of the species surveyed in this study display remarkably little morphological or molecular variation, despite originating from widely divergent geographic sources (e.g., *Hysterium angustatum*, *Psilogonium claviformis*, *Oedohysterium sinense*) (Fig. 1). Also associating with this clade are two new species, described below.

Gloniopsis arciformis Boehm, Mugambi, Huhndorf & Schoch, *sp. nov.*, MycoBank MB 515331, Fig. 6A.

Hysterothecia solitaria vel pauca aggregata, recta vel flexuosa, carbonacea, plerumque erecta, conspicue appanata et altiora quam lata, (0.5–)1–2.5 mm longa, 250–350 µm lata, 400–600 µm alta, per longitudinem striata, sulco inconspicuo maturitate clauso. Peridium 40–75 µm crassum in medio, basim versus crassius, sursum tenuius, bistratosum. Pseudoparaphyses cellulares 1–1.5 µm latae, ramosae, sursum magis crassitunicatae, epithecium

pigmentatum ascos obtegens formantes. Asci cylindrici vel clavati, stipite sinuoso, bitunicati, 50–75 × 14–18 µm; ascosporae irregulariter biseriatae, dictyosporae, pigmentatae, tenuitunicatae, fragiles, facile dilabentes, conspicue arcuatae, 3–5(–7)-septatae, 1–2(–3) septis verticalibus divisae; cellulis centralibus multo maioribus quam distales, ad septa haud constrictae, (10–)12–18(–22) × 6–10 µm.

Etymology: Latin *arcus*, a bow or arch, referring to the arcuate or arciform dictyosporae.

Hysterothecia solitary to sparsely aggregated, straight to flexuous, carbonaceous, mainly erect, distinctly flattened and taller than wide, (0.5–)1–2.5 mm long, 250–350 µm wide, by 400–600 µm high, longitudinally striated, with an inconspicuous sulcus remaining closed at maturity. Peridium 40–75 µm thick medially, thicker towards the base, thinner towards the sulcus, composed of two layers, the inner thin, compressed and hyaline, the outer denser, and darkly pigmented. Cellular pseudoparaphyses 1–1.5 µm wide, branched and thicker-walled distally towards the top, forming a pigmented epithecium above the asci. Asci cylindrical to clavate, with a sinuous stalk, bitunicate, 50–75 × 14–18 µm (n=7), ascospores irregularly biseriate. Pigmented dictyosporae thin-walled, fragile, easily breaking under the slightest pressure, pronouncedly arcuate or bent (arciform), and thus highly asymmetric, 3–5(–7)-septate, with 1–2(–3) vertical septa, these mostly associated with the mid cells, which are much larger and swollen than the end-cells, no septal constrictions, measuring (10–)12–18(–22) × 6–10 µm (n=17). Known from only one collection, Malindi Province, Kenya, East Africa.

Holotype: **Kenya**, Coast Province, Malindi District, Arabuko-Sokoke National Park, 6 Nov 2006, G.K. Mugambi (GKM L166A, deposited as XXXX).

Notes: *Gloniopsis arciformis* is represented by a single specimen (GKM L166A; Fig. 6A) of only ~30 fruitbodies in the protected crevice of a small piece of decorticated hardwood, collected in Arabuko-Sokoke National Park, Malindi Province, Kenya. Although the material is sparse, it does permit the description of a new species on account of the highly unusual arcuate dictyosporae. *Glp. arciformis* resides in Clade D, Group II, and is phylogenetically closely associated with two other species of *Gloniopsis* (*Glp. praelonga* and *Glp. subrugosa*), as well as with an additional new species described below. Interestingly, the arcuate spores of *Glp. arciformis* (Fig. 6A) closely resemble those found in *R. rufulum* in outline (Fig. 6C), the genus *Rhytidhysterion* being adjacent in Clade E.

Gloniopsis kenyensis Boehm, Mugambi, Huhndorf & Schoch, *sp. nov.*, MycoBank MB 515359, Fig. 6B.

Hysterothecia navicularia, carbonacea, recta vel flexuosa, utrinque obtusa, dense aggregata, erumpentia, ad latera inconspicue striata vel levia, (0.5–)1–3 µm longa, 250–350 µm lata, 250–350 µm alta. Peridium prope basim ad 100 µm crassum, bi- vel tristratosum, stratum internum compressum, hyalinum, strata exteriora densiora et fusca. Pseudoparaphyses cellulares, septatae, 1–1.5 µm latae, sursum ramosae et anastomosantes, epithecium pigmentatum ascos obtegens formantes. Asci cylindrici vel clavati, stipite sinuoso, bitunicati, 60–80 × 12–16 µm, ascosporas irregulariter biseriatas continentes. Ascosporae dictyoseptatae, pigmentatae, obovoideae, tenuitunicatae, fragiles, polis asymmetricis: apice obtuso, ad basim acuminatae vel nonnumquam protrudentes, 3(–4)-septatae, 1–2 septis verticalibus, utrinque saepe septis obliquis divisae, ad septa vix constrictae, iuvenes guttulis repletatae, (12–)15–18(–19) × 5–7(–8) µm.

Etymology: From the Latin *-ensis* to denote origin, from Kenya.

Hysterothecia navicular, carbonaceous, straight to flexuous, with obtuse ends, densely aggregated, erumpent, slightly striated laterally to smooth, (0.5–)1–3 mm long, 250–350 µm wide, by 250–350 µm high. Peridium to 100 µm thick at base, composed of composed of two to three layers, the inner thin, compressed and hyaline, the outer two progressively denser, and darkly pigmented. Pseudoparaphyses cellular, septate, 1–1.5 µm wide, branched, anastomosed distally, forming a pigmented epithecium above the asci. Asci cylindrical to clavate, with a sinuous stalk, bitunicate, 60–80 × 12–16 µm (n=5), ascospores irregularly biseriate. Ascospores pigmented dictyosporae, in outline obovoid, thin-walled, very fragile, spore apices asymmetric, the upper obtuse, the lower acuminate and sometimes drawn out, 3(–4[rarely])-septate, with 1–2 vertical septa, often with oblique septa in end cell, hardly constricted at the septa, highly guttulate when young, measuring (12–)15–18(–19) × 5–7(–8) µm (n=14). Known from only one collection, Malindi Province, Kenya, East Africa.

Holotype: **Kenya**, Coast Province, Malindi District, Arabuko-Sokoke National Park, 6 April 2005, G.K. Mugambi (GKM 1010, deposited as XXXX).

Notes: Molecular data indicate that both *Glp. kenyensis* and *Glp. arciformis* are closely associated, adjacent to *Glp. praelonga* and *Glp. subrugosa* in Clade D (Group II). The spores of all four taxa, however, are different, and thus their association would not have been predicted based on spore morphology. The spores of *Glp. kenyensis* do bear a close resemblance, however, to those of *Hsb. mori*. Both have predominantly 3-septate, thin-walled, pigmented dictyosporae, with 1–2 vertical septa, often with oblique septa in the end cell. They can be differentiated on spore

size: (12–)14–22(–26) x (5–)7–10(–11) µm for *Hsb. mori* versus (12–)15–18(–19) x 5–7(–8) µm for *Glp. kenyensis*. The spores of *Hsb. mori* are usually longer and wider, and also show prominent septal constrictions, especially when fresh and hydrated. Additionally, *Glp. kenyensis* is highly guttulate when young, where this is rarely observed in *Hsb. mori*. Molecular data indicate that they are not related.

To summarize, molecular data have necessitated the break up of the genus *Hysterographium*, because the type, *Hg. fraxini*, no longer resides within the *Hysteriaceae* (Boehm *et al.* 2009). This break up has resulted in: (1) the new genus *Hysterobrevium*, which includes both species with hyaline dictyospores, previously classified as *Gloniopsis* (*Hsb. constrictum* and *Hsb. smilacis*), and species with pigmented dictyospores, previously classified as

Hysterographium (*Hsb. mori*) in Clade A; (2) the inclusion in *Gloniopsis* of both hyaline (*Glp. praelonga*) and pigmented (*Glp. subrugosa*, *Glp. arciformis*, *Glp. kenyensis*) dictyospores in Clade D; (3) the inclusion in *Oedohysterium* of pigmented dictyospored species previously classified in *Hysterographium* (*Oedo. pulchrum*), also in Clade D; and, lastly, (4) the removal of *Hysterographium*, with the type *Hg. fraxini*, from the *Hysteriaceae*, currently placed as *Pleosporomycetidae*, *gen. incertae sedis*. As the taxonomy of *Hysterographium*, *Hysterobrevium* and *Gloniopsis* is currently in flux, we chose to provide the following dichotomous key, whereby all hysteriaceous fungi, bearing transversely and longitudinally septate dictyospores, whether pigmented or hyaline, are identified together, with the caveat that unrelated taxa share the same key.

Key to the species of *Hysterographium*, *Hysterobrevium* and *Gloniopsis*

1. Dictyospores, usually shorter than 25 µm 2
- 1'. Dictyospores mostly longer than 25 µm 6
2. Dictyospores pigmented, thin-walled, fragile, pronouncedly arcuate or bent, 3–5(–7)-septate, with 1–2(–3) vertical septa, which are mostly associated with the mid-cells, these much larger and swollen than the end-cells, no septal constrictions, (10–)12–18(–22) x 6–10 µm; Kenya ***Glp. arciformis***
- 2'. Not with the above combination of characters 3
3. Dictyospores hyaline at maturity 4
- 3'. Dictyospores pigmented at maturity 5
4. Dictyospores highly symmetric in outline and septation, with thickened walls, gelatinous sheath present when young, absent at maturity, (1–)3(–4)-septate, with 1(–2) vertical septa, that may pass through one to two cells; (11–)13–20(–23) x 5–12 µm; Japan, New Zealand ***Hsb. constrictum***
- 4'. Dictyospores asymmetric, with acuminate ends, with a gelatinous sheath when young, mostly 3–5(–9)-septate and with 1(–3) vertical septa passing through multiple mid-cells, prominently constricted at the median septum, sometimes constricted at multiple septa, (13–)15–26(–31) x (4–)5–9(–10) µm; highly variable and cosmopolitan ***Hsb. smilacis***
5. Dictyospores thin-walled, obovoid, with obtuse ends, 3–(5–7)-septate, with 1–2(–3) vertical septa, usually associated with mid-cells, but occasionally present obliquely in end-cells, constricted at the median septum, sometimes at additional septa, (12–)14–22(–26) x (5–)7–10(–11) µm; highly variable and cosmopolitan ***Hsb. mori***
- 5'. Dictyospores thin-walled, very fragile, obovoid, 3(–4[rarely])-septate, highly guttulate when young, spore apices asymmetric, the upper obtuse, the lower acuminate and sometimes drawn out, often with oblique septa in end cell(s), hardly constricted at the septa, measuring (12–)15–18(–19) x 5–7(–8) µm ***Glp. kenyensis***
6. Red pigment present in hamathecium and/or centrum; dictyospores pigmented 7
- 6'. No red pigment present, spores pigmented or hyaline 8
7. Dictyospores, 22–25(–27) x 5–6 µm, with (5–)6 transverse and 1 vertical septum in either cell or both cells adjacent to the primary septum; typically with red pigment in the hamathecium; neotropical (Costa Rica) ***Oedo. pulchrum***

Note: *Oedo. pulchrum* is accommodated in the genus *Oedohysterium* and is present in both keys.

- 7'. Dictyospores 25–28 x 11–13 µm, with 5–6 transverse and mostly one longitudinal septum; hamathecium brick-red; on *Acacia* thorns, S. Africa **Hg. spinicola**
8. Dictyospores hyaline or turning brown tardily 9
- 8'. Dictyospores pigmented in the ascus 10
9. Dictyospores hyaline turning yellow in age, obovoid, ends usually obtuse, 5–7(–10)-septate, with 2–3 longitudinal septa, constricted at the median and often other septa, gelatinous sheath when young, (16–)20–32(–34) x (6–)9–12(–15) µm; cosmopolitan **Glp. praelonga**
- 9'. Ascospores irregularly biserial, ellipsoid, hyaline but becoming brown tardily, with the upper half generally wider than the lower half, sometimes surrounded by a gelatinous sheath, with 7–13 transverse and 1–3 longitudinal septa, constricted at the median transverse septum; 25–49 x 8–17 µm; Japan **Glp. macrospora**
10. Dictyospores usually less than 38 µm long 11
- 10'. Dictyospores 30–80 µm long 12
11. Dictyospores (22–)25–34(–45) x (6–)8–12(–17) µm, mostly with 7–11 transverse and 1–2 vertical septa; cosmopolitan **Glp. subrugosa**
- 11'. Dictyospores 26–38 x 10–15 µm, with 6–13 transverse and 1–3 vertical septa, obovoid, ends obtuse; Japan **Hg. minus**
12. Dictyospores (25–)30–45(–51) x (10–)12–15(–22) µm, with 7–9 transverse and 2–3 vertical septa, obovoid, ends obtuse; cosmopolitan **Hg. fraxini**
 Note: *Hysterographium faxini*, the type species for the genus *Hysterographium*, lies outside of the *Hysteriaceae*, and is currently recognized as *Pleosporomycetidae sp. incertae sedis* (Boehm *et al.* 2009).
- 12'. Ascospore outline ellipsoid, fusoid, ends slightly acuminate, (30–)40–65(–80) x (8–)10–18(–19) µm, with 7–15 transverse and 1–3 vertical septa; cosmopolitan **Hg. flexuosum**

6. The genus *Psiloglonium* Höhn.

Ann. Mycol. 16: 145 (1918)

A discussion of the genus *Psiloglonium* (von Höhn 1918; Petrak 1923 a, b) by necessity must begin with the genus *Glonium* Muhl. : Fr. This is because Zogg (1962) synonymized a number of species under the genus *Glonium* that were originally classified in *Psiloglonium* by von Höhn (1918) and Petrak (1923a, b). Both *Psiloglonium* and *Glonium* possess hyaline to yellow didymospores, somewhat constricted at the septum, with obtuse or acuminate ends, typically with cells unequal in size, borne in hysterothecia.

Von Höhn (1918) was the first to view the genus *Glonium* as comprised of two distinct morphological types, and stressed the importance of subicula, using it to divide the genus, at first, into two subgenera, *Glonium* and *Psiloglonium*, and, further in the same article, into two separate genera, with or without subicula, respectively. Petrak (1923a) recognized that von Höhn (1918) had established the genus *Psiloglonium*, both at sub-generic and generic rank, but it was Petrak (1923a) who explicitly

designated the type species for *Psiloglonium* as *P. lineare* (Fr.) Petrak, retaining *G. stellatum* Muhl. : Fr. as the type species for the genus *Glonium sensu* von Höhn (1918). Petrak (1923a, b) eventually placed a number of species in *Psiloglonium*, all subsequently transferred to *Glonium* by Zogg (1962). Müller & von Arx (1950) originally accepted the genus *Psiloglonium*, but later reduced it to a synonym of *Glonium* (von Arx & Müller 1975). Lohman (1933a, 1937) also did not support *Psiloglonium*, based on the observation that similar anamorphs were shared between species of the two subgenera. Barr (1987), was the only modern author to retain the genus *Psiloglonium*, as distinct from the subiculate *Glonium*.

Although von Höhn (1918) and Petrak (1923a, b) both stressed the importance of subicula as a major morphological distinction between *Psiloglonium* and *Glonium*, Zogg (1962) noted that some species previously classified as *Psiloglonium* by Petrak (1923a) (e.g., *P. lineare*) do in fact possess subicula on occasion. Zogg (1962) further noted an additional two species that were occasionally associated with subicula, namely *Glonium pusillum* Zogg and *Glonium graphicum* (Fries) Duby

stating: "...ohne Subiculum oder auf ziemlich deutlichem Subiculum sitzend..." Hence, Zogg (1962) considered subicula not to be a synapomorphic character state, and transferred those species previously classified by Petrak in *Psiloglonium* (e.g., *P. lineare*, *P. microspermum* Höhn., *P. ruthenicum* Petrak, and *P. finkii* Petrak) to *Glonium*.

Although Zogg (1962) did not support the genus *Psiloglonium*, he did in fact recognize three distinct morphological forms within his concept of *Glonium*, two of which (Types I and II) we incorporate in *Psiloglonium*, the third (Type III) forming the basis for the *Gloniaceae*. Zogg (1962) arranged the species of *Glonium* based on (1) didymospore shape: spore apices obovoid to rounded (Type I) versus spores fusiform with acuminate apices (Type II and III); and (2) the degree of complexity surrounding the architecture of the hysterothecia, simple, linear, solitary to gregarious (Types I, II) versus complex bifurcating, laterally anastomosing to form flabelliform pseudostellate composites, or associated with a thin stromal crust (Type III). This, then, de-emphasized the presence or absence of subicula. Nevertheless, Zogg (1962) maintained all three types within the genus *Glonium*.

Type I: This type is characterized by hysterothecia that may be solitary to gregarious, erumpent to entirely superficial, navicular to linear to highly flexuous, even triradiate, sometimes arranged in parallel orientation and confluent linearly to some degree, but never dichotomously branched, or associated with a stromal crust, as found in the *Gloniaceae* (Type III). These species correspond to *Psiloglonium sensu* von Höhnel (1918). Here, the didymospores are relatively small, hyaline, and have at least one, if not both ends, obovoid to obtuse (Type I), rather than acuminate (Types II and III). Zogg (1962) recognized five species, listed here by increasing ascospore length: *G. abbreviatum* (Schwein.) Lohman, *G. pusillum* Zogg, *G. lineare* (Fr.) De Not., *G. chambianum* Guyot, and *G. curtisii* (Duby) Lohman. Barr (1975) transferred the last species to *Ostreichnion* Duby, as *O. curtisii* (Duby) M.E. Barr, in the *Mytiliniaceae*, since transferred to the *Hysteriaceae* (Boehm *et al.* 2009). A sixth species, *G. finkii* (Petrak) Lohman, was included by Zogg (1962), based on ascospore shape, but placed apart in the key due to the unusual arrangement of the ascospores within the upper part of the ascus (Lohman 1937).

Psiloglonium lineare (Fr.) Petrak (Fig. 3C) was previously reinstated within the *Hysteriaceae*, listing *G. lineare* as a synonym (Boehm *et al.* 2009). Here we also reinstate *Psiloglonium finkii* Petrak. An additional two species are included in Type I, namely *G. clavispurum* Seaver and *G. simulans* W.R. Gerard, synonymized by Zogg (1962) under *G. lineare*, but earlier recognized by Lohman (1932a, 1937) to be distinct from *G. lineare*. Boehm *et al.* (2009) proposed new combinations for these

taxa, based on morphological as well as molecular data, as *Psiloglonium clavispurum* (Seaver) Boehm, Schoch & Spatafora (Fig. 3B) and *P. simulans* (W.R. Gerard) Boehm, Schoch & Spatafora (Fig. 3A).

To these species can also be added *G. sasicola* N. Amano, from Japan, the first report of a gelatinous sheath in the genus (Amano 1983). In this same publication Amano (1983) proposed an additional new species, *G. macrosporum* N. Amano, also from Japan. The spore measurements were given as 13.1–16.8 x 4.0–5.6 μm , nearly identical to those of *P. simulans* at (10–)14–16(–18) x (4.5–)5–6 μm (Lohman 1937). Moreover, the illustrations given by Amano (1983) match closely those given by Lohman (1932a) for *P. simulans*. We therefore synonymize *G. macrosporum* under *P. simulans*.

More recently, Lorenzo & Messuti (1998), in a reappraisal of the type specimens collected by Spegazzini and Hennings from Argentina and Chile, have reinstated *G. costesi* Speg. (1918). In a later publication, Messuti & Lorenzo (2007) synonymized *G. costesi* under the earlier epithet *G. ephedrae* Henn. (1900). With spore measurements of 26–35 x 8–15 μm , *G. ephedrae* possesses the largest spores in Type I. In the same publication, Messuti & Lorenzo (2007) also accepted two additional species: *G. chilense* Speg. and *G. uspallatense* Speg., previously considered by Zogg (1962) to be doubtful species. The spores of *G. chilense* measure 15–16 x (5–)7–8 μm , which places it very close to *P. lineare*, the latter with slightly smaller spores, (10–)12–14(–18) x (4–)5–7(–8) μm (Zogg 1962). However, *G. chilense* has almost identical ascotal and spore measurements as *P. simulans*, given above. We therefore synonymize *G. chilense* with the earlier name *G. simulans*, as *P. simulans*. For *G. uspallatense*, Messuti & Lorenzo (2007) gave spore measurements of 18–24 x 10–12 μm , intermediate between *G. chambianum*, (14–)16–18(–21) x (6–)8–9(–10) μm (Zogg 1962), and *G. sasicola*, 25–32 x 5–8 μm (Amano 1983).

Recently, Mugambi & Huhndorf (2010) proposed a new genus, *Anteaglonium* Mugambi & Huhndorf, outside of the *Hysteriales* and within the *Pleosporales*, to accommodate *G. abbreviatum* as *A. abbreviatum* (Schwein.) Mugambi & Huhndorf (Fig. 3F) and the related species *A. globosum* Mugambi & Huhndorf (Fig. 3G), *A. parvulum* (W.R. Gerard) Mugambi & Huhndorf (Fig. 3H), and *A. latirostrum* Mugambi & Huhndorf (Fig. 6I). The first three species are characterized by hyaline didymospores that belong to Type I, as defined by Zogg (1962), and are less than 8 μm in length. The fourth species, *A. latirostrum*, belongs to Type II (see below), with longer spores. Although genetically unrelated to *Psiloglonium*, these species share a similar morphology and thus are included in the key below.

Type II: This type is characterized by relatively large didymospores, distinctly fusoid in outline, prominently constricted at the septum, and with acuminate apices.

Zogg (1962) recognized two species, namely *G. caucasicum* (Rehm) Zogg, and the much larger-spored, neotropical *G. hysterinum* Rehm, to which can be added the newly described *G. colihuae* Lorenzo & Messuti, on *Chusquea culeou* from Argentina (Lorenzo & Messuti 1998). *G. caucasicum* has recently been synonymized under the earlier name *G. araucanum* Speg. by Messuti & Lorenzo (2007), based on a comparison of the type specimen of *G. caucasicum* to Spegazini's earlier type of *G. araucanum* from Chile.

Type III: This type corresponds to von Höhnel's (1918) and Petrak's (1923 a,b) circumscription of the genus *Glonium*, and includes species with fusiform spores, with acuminate apices, typically producing complex laterally anastomosing hysterothecia, forming stellate composites, usually with prominent subicula, with or without stroma. Zogg (1962) included the type, *G. stellatum* Muhl. : Fr. (Fig. 8A), *G. compactum* Kern, and *G. graphicum* (Fries) Duby, the later sometimes variably associated with subicula. Zogg (1962) also stated that *G. compactum* possesses a subiculum, much like *G. stellatum*, and with similar spore size, but whereas hysterothecia in *G. stellatum* are merely seated on the subiculum, in *G. compactum* the hysterothecia are embedded in and arise from a thin stromal crust, which is itself seated on subicula. Recently, a fourth species was added, based on molecular evidence (Boehm *et al.* 2009), namely *G. circumserpens* (Nyl.) Kantvilas & Coppins (Fig. 8B–C) from Tasmania (Kantvilas & Coppins 1997).

Sequence data presented here (Fig. 1) and elsewhere (Boehm *et al.* 2009, Mugambi & Huhndorf 2010), clearly indicate that the genus *Glonium sensu* Zogg (1962) actually comprises three entirely unrelated lineages within the *Pleosporomycetidae*, one within the *Hysteriaceae* and two forming clades outside of the family. The first lineage corresponds to *Psiloglonium sensu* von Höhnel (1918), and forms a highly supported monophyletic clade in this study (Clade B, Group I) (Fig. 1). These include *P. clavisorum* (Fig. 3B), with isolates from the United States (CBS 123340 / EB 0312 / BPI 878728, CBS 123339 / EB 0311 / BPI 878727, CBS 123341 / EB 0313 / BPI 878729, CBS 123338 / EB 0309 / BPI 878726), and Kenya (GKM 344A, GKM L172A), *P. simulans* (Fig. 3A), from the United States (CBS 206.34, ANM 1557), and *P. araucanum* (Fig. 3D), from South Africa (CBS 112412 / PREM 57570, CMW 18760 / PREM 57569, CMW 17941 / PREM 57566). A second lineage has recently been shown to be associated with the *Pleosporales*, now accommodated in *Anteaglonium* (Fig. 3F–I) (Mugambi & Huhndorf 2010). In this study we have included six accessions for the genus *Anteaglonium* (Fig. 1; Table 1). The third lineage corresponds to *Glonium* (Fig. 8A–C), in the *Gloniaceae* (Boehm *et al.* 2009), for which we have included four isolates representing two species.

We treat here all species of *Glonium sensu* Zogg (1962), belonging to Types I and II, outside of *Anteaglonium*, as species belonging to *Psiloglonium*. Since the generic name *Glonium* is reserved for species in the *Gloniaceae*, we propose eight new combinations for the genus *Psiloglonium*:

New combinations

Psiloglonium pusillum (Zogg) Boehm & Schoch, *comb. nov.*, MycoBank MB 515327.

Basionym: *Glonium pusillum* Zogg, Beitr. Kryptfl. Schweiz 11(3): 62 (1962).

Notes: Zogg (1962) described this species as *G. pusillum* from *Juniperus phoenicea* and *Pinus sylvestris* from Southern France, noting that it was quite rare. Zogg (1962) stated that this species may or may not be associated with a subiculum, and hence was one of the factors behind his transfer of Petrak's (1923a, b) *Psiloglonium* species to *Glonium*. *P. pusillum* has ascospores only slightly larger than those of *P. abbreviatum*, measuring (9–)10–12(–13) x 4–5(–6) μm . Lee & Crous (2003) also identified this fungus from *Proteaceae* and *Restionaceae* in South Africa, and Sivanesan & Hsieh (1989) reported it from Taiwan.

Psiloglonium chambianum (Guyot) Boehm & Schoch, *comb. nov.*, MycoBank MB 515320, Fig. 3E.

Basionym: *Glonium chambianum* Guyot, Ann. Serv. Bot. Agric. Tunisie 28: 90 (1955).

Notes: Originally collected from *Lonicera implexa* (*Caprifoliaceae*) in North Africa, the fungus has since been reported from the *Proteaceae* in South Africa (Lee & Crous 2003). Zogg (1962) gave the spore measurements for *P. chambianum* as (14–)16–18(–21) x (6–)8–9(–10) μm , whereas Lee & Crous (2003) gave slightly larger measurements, (18–)20–21(–23) x (4–)5–6(–7) μm . Spores ellipsoid to oblong, with upper cell broader than the lower, and with an obvoid, obtuse apex. *P. chambianum* (Fig. 3E) possesses larger spores than *P. lineare* (Fig. 3C), *P. simulans* (Fig. 3A), and *P. clavisorum* (Fig. 3B), but smaller than *P. uspallatense*.

Psiloglonium uspallatense (Speg.) Boehm & Schoch, *comb. nov.*, MycoBank MB 515321.

Basionym: *Glonium uspallatense* Speg., Anal. Mus. Nac. Buenos Aires, Ser 3, v. 12, 19: 436 (1909).

Notes: Zogg (1962) listed the species a “doubtful”, but Messuti & Lorenzo (2007) reinstated *Glonium uspallatense* after locating the original holotype material. They gave the spore measurements as 18–24 x 10–12 μm , placing the taxon as intermediate between *P. chambianum* and *P.*

sasicola. (The epithet *uspallatense* is misspelled in Messuti & Lorenzo (2007) as “uspatalense”, but refers to Uspallata, Mendoza, Argentina).

Psiloglonium sasicola (N. Amano) Boehm & Schoch, *comb. nov.*, MycoBank MB 515322.

Basionym: *Glonium sasicola* N. Amano, Trans. mycol. Soc. Japan 24: 287 (1983).

Notes: Amano (1983) described this species from dead culms of *Sasa* sp. (*Bambusaceae*). The ascospore measurements were given as 25–32 x 5–8 µm, with a rounded apical cell, placing it between *P. uspallatense* and *P. ephedrae*. Amano (1983) further reported that ascospores of this species are associated with a gelatinous sheath, previously not known among these didymosporous fungi.

Psiloglonium ephedrae (Henn.) Boehm & Schoch, *comb. nov.*, MycoBank MB 515323.

Basionym: *Glonium ephedrae* Henn., Öfvers. K. Vet. Akad. Förhandl. 2: 328 (1900).

= *Glonium costesi* Speg., Bol., Acad. Nci. Ci., Córdoba 25: 78-79 (1921).

Notes: Messuti & Lorenzo (2007) reinstated *Glonium ephedrae* Henn. (1900) with the synonym *Glonium costesi* Speg. (1921), after locating and comparing original type materials. *P. ephedrae* possesses very large didymospores, measuring 26–35 x 8–15 µm, the upper cells broadly ovate. It has been collected from *Ephedra andicola*, and, as *G. costesi*, from *Proustia pyrifolia* from Chile.

Psiloglonium hysterinum (Rehm) Boehm & Schoch, *comb. nov.*, MycoBank MB 515324.

Basionym: *Glonium hysterinum* Rehm, Hedwigia 37: 298 (1898).

Notes: Rehm (1898) originally described a species of *Glonium* from Southern Brazil with large fusiform didymospores, prominently constricted at the septum, and with acuminate spore apices (“*Enden zugespitzt*”). The spore measurements were given as 45 x 9 µm.

Psiloglonium colihuae (Lorenzo & Messuti) Boehm & Schoch, *comb. nov.*, MycoBank MB 515325.

Basionym: *Glonium colihuae* Lorenzo & Messuti, Mycol. Res. 102: 1104 (1998).

Notes: Lorenzo & Messuti (1998) described a new species on culms of *Chusquea culeou* from the Argentine rainforests of *Nothofagus dombeyi*. They gave the spore measurements as 30–43 x 4–9.8 µm, and, although the spores are fusiform in outline, they possess moderately

acuminate apices. In comparing this species to other acuminate-spored species of *Glonium*, the authors noted that the greatest degree of similarity resides with the slightly smaller-spored *G. caucasicum* (Rehm) Zogg (= *P. araucanum* (Speg.) Boehm & Schoch, see below).

Psiloglonium araucanum (Speg.) Boehm, Marinowitz & Schoch, *comb. nov.*, MycoBank MB 515326, Fig. 3D.

Basionym: *Glonium araucanum* Speg., Rev. Fac. Agron. Veter. La Plata 6: 110 (1910).

= *Gloniella caucasicum* Rehm, Vestn. Tiflissk. Bot. Sada 25:12 (1912).

≡ *Glonium caucasicum* (Rehm) H. Zogg, Beitr. Kryptfl. Schweiz 11(3): 67 (1962).

Notes: Messuti & Lorenzo (2007) transferred *G. caucasicum* to *G. araucanum*, after examining the types for both species. Previously, Zogg (1962) had transferred *Gloniella caucasicum* Rehm to *Glonium*. Here we transfer *G. araucanum* to *Psiloglonium* (Fig. 3D). This taxon possesses fusiform spores with highly acuminate apices. Messuti & Lorenzo gave the spore measurements as 22–28 x 8–10 µm, whereas Zogg (1962) gives them as (19–)22–25(–27) x (6–)7–9(–10) µm. Although originally European in distribution (Zogg 1962), the taxon has subsequently been collected from South (Messuti & Lorenzo 2007) and North America (Boehm unpubl.), and from South Africa as well (Lee & Crous 2003).

Lee & Crous (2003) identified a series of isolates from South Africa on the *Restionaceae* as *Glonium compactum* Kern (CBS 112412, CMW 18760, CMW 17941). However, in their study they did not state the presence of subicula, nor even of a stromal crust, as being present. These features were stressed for this taxon by Zogg (1962). These same isolates were used in Boehm *et al.* (2009), and were shown to associate, with high branch support, with two species of *Psiloglonium*, *P. clavisporum* and *P. simulans*, distant from the other species of *Glonium* surveyed (i.e., *G. stellatum* and *G. circumserpens*). Thus, a new combination was proposed, *Psiloglonium compactum* (Kern) Boehm, Schoch & Spatafora. However, it is now realized that this new combination was made in error and is hereby retracted. It must be concluded that the South African isolates (Lee & Crous 2003) were not *G. compactum*, due to the absence of subicula and stroma, but rather, we suspect, the cosmopolitan *P. araucanum*, which has similar, but slightly smaller, fusiform acuminate didymospores. Lee & Crous (2003) give the ascospore measurements for the South African “*G. compactum*” as (24 –)26–27(–30) x (4–)5–6(–7) µm, which matches closely those given above for *P. araucanum*. Furthermore, the illustrations in Lee & Crous (2003) closely match *P. araucanum*, and not those of *G. compactum*, as given by Zogg (1962). If we are correct in assuming that the South African isolates used in Boehm *et al.* (2009) are in fact *P. araucanum*, and not *G. compactum*, then this would

provide a high degree of support for the inclusion of species with acuminate spore apices, belonging to Type II, in the genus *Psiloglonium*, with species with obtuse spore apices, belonging to Type I (e.g., *P. simulans* and *P. clavisporum*). A reanalysis of the original herbarium specimens from which the isolates (CBS 112412, CMW 18760, CMW 17941) were derived, by SL Marinowitz, has

confirmed that they do indeed correspond to *P. araucanum* and not to *G. compactum*.

In addition to the 12 currently recognized species in *Psiloglonium*, the following key also includes entries for the unrelated *Gloniaceae*, *Anteaglonium* and *O. curtisii*.

Key to the species of *Psiloglonium* and *Anteaglonium*

- 1'. Asci ovoid, +/- cylindrical; ascospores borne in the upper portion of the ascus, not evenly distributed; ascospores (12–)13–15 x 6–7 μm ; Puerto Rico ***P. finkii***
1. Asci typically cylindrical to club-shaped; ascospores in one row or distichous in the asci, but always regularly arranged for its full length 2
2. Ascospores obovoid, with at least one, often both, ends obtuse, typically with upper cell larger, +/- constricted at the septum 3
- 2'. Ascospores fusiform (i.e., spindle-shaped), with both ends acuminate, usually constricted at the septum 13
3. Ascospores small, 8 μm or less in length 4
- 3'. Ascospores longer than 8 μm 5
4. Ascospores (5–)6–7(–8) x 2–3(–3.5) μm ; hysterothecia acuminate with flattened apices, seated on a dark crust; +/- soluble pigment in KOH; cosmopolitan ***A. abbreviatum***
Note: *A. abbreviatum* (Schwein.) Mugambi & Huhndorf lies within the *Pleosporales* (Mugambi & Huhndorf 2010).
- 4'. Ascospores as in *A. abbreviatum*, but hysterothecia with rounded ends, with pointed apices, and not associated with a dark crust; no KOH-soluble pigments ***A. parvulum***
Note: *A. parvulum* (W.R. Gerard) Mugambi & Huhndorf lies within the *Pleosporales* (Mugambi & Huhndorf 2010).
- 4". Ascospores as in *A. abbreviatum* and *A. parvulum*, 6–7 x 2–3 μm long; hysterothecia globose with roughened walls and indistinct slit, associated with a dark crust, and sparse, short subicula, also with short tomentum on the walls of the ascomata; producing green soluble pigments in KOH ***A. globosum***
Note: *A. globosum* Mugambi & Huhndorf lies within the *Pleosporales* (Mugambi & Huhndorf 2010).
5. Ascospores (9–)10–12(–13) x 4–5(–6) μm ; Europe, Africa ***P. pusillum***
- 5'. Ascospores slightly larger 6
6. Ascospores (10–)12–14(–18) x (4–)5–7(–8) μm ; ascomata +/- confluent laterally, in parallel rows, semi-immersed to erumpent; cosmopolitan ***P. lineare***
- 6'. Ascospores similar in length; ascomata not confluent laterally, usually entirely superficial 7
7. Ascospores (10–)14–16(–18) x (4.5–)5–6 μm ; cosmopolitan ***P. simulans***
- 7'. Ascospores slightly larger 8
8. Ascospores (15–)16–18(–20) x 5–6(–7) μm ; *Sporidesmium stygium* anamorph usually present; N. and S. America ***P. clavisporum***
- 8'. Ascospores slightly larger in length and breadth 9

9. Ascospores (14–)16–18(–21) x (6–)8–9(–10) μm ; Europe and N. Africa ***P. chambianum***
- 9'. Ascospores slightly larger 10
10. Ascospores 18–24 x 10–12 μm ; Argentina ***P. uspallatense***
- 10'. Ascospores slightly larger 11
11. Ascospores 25–32 x 5–8 μm , with a gelatinous sheath; Japan ***P. sasicola***
- 11'. Ascospores slightly larger 12
12. Ascospores 30–35 x 8–15 μm ; Chile ***P. ephedrae***
- 12'. Ascospores (59–)62–68(–76) x 13–15 μm ; SE USA ***Ostreichnion curtisii***
 Note: The genus *Ostreichnion*, previously placed in the *Mytiliniaceae*, has been transferred to the *Hysteriaceae* (Boehm *et al.* 2009).
13. Hysterothecia usually borne in/on subicula, typically bifurcated, forming radiating flabelliform or pseudo-stellate composites, with or without a stroma ***Gloniaceae***
 Note: In this study, a key to the species of the *Gloniaceae* is provided under that family.
- 13'. Hysterothecia not bifurcated, forming radiating flabelliform or pseudo-stellate composites, nor with a stroma 14
14. Ascospores less than 30 μm long 15
14. Ascospores more than 30 μm long 16
15. Ascospores (19–)22–25(–27) x (6–)7–9(–10) μm , both ends acuminate, with a prominent septal constriction; cosmopolitan ***P. araucanum***
- 15'. Ascospores 22–28 x 4–6 μm , acuminate, 1-septate, hyaline and with a mucilaginous sheath when young, but acquiring additional septa and pigmentation with age, to become 3–5-septate and pale brown at maturity ***A. latirostrum***
 Note: *A. latirostrum* Mugambi & Huhndorf lies within the *Pleosporales* (Mugambi & Huhndorf 2010).
16. Ascospores 30–43 x 4–9.8 μm ; Argentina ***P. colihuae***
- 16'. Ascospores about 45 x 9 μm ; neotropical (Brazil) ***P. hysterinum***

7. The genus *Actidiographium* L.N. Vasilyeva
 Mikol. Fitopatol. 34 (6): 4 (2000).

Vasilyeva (2000) established the monotypic genus *Actidiographium* to accommodate a hysteriaceous fungus with pigmented 1-septate ascospores, reminiscent of those found in *Actidium* Fr. in the *Mytiliniaceae*. In *Actidiographium orientale* L.N. Vasilyeva, the didymospores are borne in a typical thick-walled hysterothecium. The pigmented didymospores measure 13.2–16.5 x 3–4 μm . As molecular data do not exist for this taxon, it is not clear at present whether the genus *Psilogonium* should include pigmented didymosporous members, or whether the genus *Actidium* should include hysterothecioid members.

8. The genus *Hysterocarina* Zogg
 Ber. Schweiz. Bot. Ges. 59: 39 (1949).

Zogg (1949) erected this monotypic genus for *Hysterocarina paulistae* Zogg, with pigmented dictyospores as in *Hysterographium*, but the hysterothecia are borne within the substrate, barely erumpent at maturity, and with a cristate, slightly evaginated longitudinal keel, instead of the invaginated sulcus typical of most members of the *Hysteriaceae*. Described from old wood of *Eucalyptus* in Brazil, the pigmented dictyospores measure 20–25 x 8–10 μm . The presence of an evaginated keel-like fissure in *Hysterocarina* is intriguing, as it seems to belong to an evolutionary trend that culminates in the *Mytiliniaceae* and *Gloniaceae*. Clearly, molecular data are needed to resolve these issues.

9. The genus *Ostreichnion* Duby

Mém. Soc. Phys. Hist. nat. Genève 16: 22 (1862).

Ostreion Sacc. 1883

The nomenclatural history of the genus *Ostreichnion*, previously in the *Mytiliniaceae* (Barr 1975, 1990a), and its transference to the *Hysteriaceae*, has been presented in Boehm *et al.* (2009). Since its reappraisal (Barr 1975), the genus has been heterogeneous, due to the inclusion of *Ostreichnion curtisii* (Duby) M.E. Barr, an unusual taxon, from the southeastern United States to Louisiana (Lohman 1937) and Brazil (Zogg 1962). It is very different from the other two species of this genus, namely the type *O. sassafras* (Schwein.) M.E. Barr and *O. nova-caesariense* (Ellis) M.E. Barr. Whereas the latter two species possess pigmented dictyospores, in *O. curtisii* the ascospores are one-septate below the middle, with walls greatly thickened towards the spore apices. When mounted with different stains, the spore cytoplasm appears subdivided into numerous compartments, giving the impression of a potentially muriform structure. Lohman (1937) provided details as to the highly unusual spore germination process in this fungus, which involves a distended apical plug and numerous median germ tubes, differing from that found in other species of *Psiloglonium*, that send out apical germ

tubes (Lohman 1931, 1932a). *O. sassafras* occurs on both sides of the Atlantic, as well as in China, and has been recovered from *Sassafras*, *Quercus*, *Liriodendron*, and *Liquidambar* (Barr 1975; Bisby 1932; Teng 1933). It is unusual in having very large dictyospores, measuring (65–)76–100(–135) x 20–32 µm, with up to 27 septa, borne four to an ascus. *O. nova-caesariense* is known only from the type locality in New Jersey on *Pinus*, and has similar, but smaller, ascospores (Barr 1975).

Molecular data exist for two of the three species (Table 1), namely *O. curtisii* (CBS 198.34) and *O. sassafras* (CBS 322.34). Although both species find residency within Clade C (Group I), their association with the genus *Hysterium* (Fig. 1) could not have been predicted. Given the unique nature of the ascospore in *O. curtisii*, considered potentially muriform, one would assume affinities with the genus *Hysteroglyphium sensu* Zogg (1962), or, given its 1-septate ascospores at maturity, with *Psiloglonium*, where it was originally treated by Lohman (1937) as *Glonium curtisii* (Duby) Lohman. However, molecular data suggest neither. Instead, *O. curtisii* shares a subclade with *Hysterium barrianum*, with 9-septate phragmospores (Fig. 1). *O. sassafras* is more distant within Clade C. Although we recognize the genus as artificial, we present the following key, adapted from Barr (1975), to facilitate species identification.

Key to the species of *Ostreichnion*

1. Ascospores mostly one-septate, ends greatly thickened, (45–)62–80 x (10–)12–15 µm ***O. curtisii***
- 1'. Ascospores with both transverse and longitudinal septa 2
2. Ascospores measuring 35–45(–50) x 11–13 µm, with 7–13 septa, borne eight to an ascus ***O. nova-caesariense***
- 2'. Ascospores measuring (65–)76–100(–135) x 20–32 µm, with up to 27 septa, borne four to an ascus ***O. sassafras***

10. The genus *Rhytidhysteron* Speg.

An. Soc. Ci. Argent. 12: 188 (1881).

The genus *Rhytidhysteron* is characterized by ascomata that are at first closed and navicular (Fig. 6E), somewhat resembling those found in the *Hysteriaceae*, then later opening by a longitudinal sulcus to become irregularly apothecioid at maturity, often with incurved margins (Fig. 6F-G). The peridium is much thinner than that found in the *Hysteriaceae*, gelatinous when wet, as opposed to carbonaceous, and may possess striations, but in *Rhytidhysteron* these are often perpendicular to the long axis (Fig. 6E), rather than parallel, as in other genera of the *Hysteriaceae*. The ascospores tend to be heavily pigmented and thick-walled, as opposed to lightly pigmented and thin-walled in other members of the *Hysteriaceae*. Kutorga & Hawksworth (1997) have reviewed the nomenclatural history of the genus. Samuels & Müller (1980) revised the genus, providing a number of

synonyms, and accepted only two species, namely the type, *R. rufulum* (Spreng.) Speg. (Fig. 6D-G), with three-septate phragmospores, and *R. hysterinum* (Duf.) Samuels & E. Müll., with one-septate spores, both darkly pigmented and thick-walled. Anamorphs have been characterized as *Diplodia*- and *Aposphaeria*-like (Samuels & Müller 1980). Subsequently, another two species have been accepted in the genus, namely *R. dissimile* (P. Karst.) Magnes (Magnes 1997), with five-septate phragmospores, and *R. opuntiae* (J.G. Brown) M.E. Barr (1990b), from the American South West, with short pigmented dictyospores, reminiscent of those found in *Hsb. mori*.

Dictyospores of both *R. opuntiae* (Fig. 6C) and *Hsb. mori* (Fig. 2D-F) are similar in shape, obovoid, with obtuse ends, and are also similar in size and septation: 19–24(–33) x (8–)9–13 µm and (1–)3–(4–5)-septate, with one vertical septum, for *R. opuntiae*, versus (12–)15–23(–25) x (5–)7–10(–11) µm, and with 3–(5–7) transverse and 1–2 vertical septa, for *Hsb. mori*. In both, the longitudinal

septum is usually associated with the mid-cells, but on occasion it can be found obliquely in the end cells. However, unlike *Hsb. mori*, the spores of *R. opuntiae* are thick-walled, verruculose and darkly pigmented. The most surprising morphological feature of *R. opuntiae* is that the spores are not borne within patellarioid "apothecia", as in other members of the genus. Rather, the ascomata are hysterothecoid, that is, carbonaceous and navicular, with a longitudinal sulcus (Fig. 6C). In this study we were fortunate to acquire an isolate of *R. opuntiae* from Kenya (GKM 1190), and were able to compare the molecular phylogeny of this taxon to multiple isolates of *Hsb. mori*, as well as to two other *Rhytidhysterion* species, namely *R. rufulum*, with six isolates, from Kenya (GKM 361A), Ghana (EB 0382, EB 0383, EB 0384, EB 0381), and Europe (CBS 306.38), and *R. hysterinum* from France (EB 0351).

Boehm *et al.* (2009) were the first to provide sequence data indicating that the genus *Rhytidhysterion* does not lie within the *Patellariaceae*. Although based on only a single isolate of *R. rufulum* (CBS 306.38), the genus was tentatively noted to be associated with the *Hysteriaceae*. In the current study, a total of eight isolates, representing three species, clearly indicates that the genus *Rhytidhysterion* belongs to the family *Hysteriaceae*, and not

to the *Patellariaceae*, the latter defined in this study to include *Hysteropatella clavispora* (CBS 247.34), *Hp. elliptica* (CBS 935.97), and *Patellaria atrata* (CBS 958.97). In hindsight, it is quite remarkable that Barr (1990) recognized *R. opuntiae* as a member of *Rhytidhysterion*, transferring it from *Hysterographium opuntiae* J.G. Brown, despite the presence of atypical ascomata. Earlier, Barr (1987) had noted the differences between *Rhytidhysterion* and other members of the *Patellariaceae*, stating: "*Rhytidhysterion rufulum* illustrates the problem: paraphysoids and a well-developed pseudoepithecium are conspicuous, but the structure of the peridium, thickened base of ascoma, cylindrical asci, are all features attributed to members of the *Hysteriaceae*. When the heterogeneous family *Patellariaceae* is revised, *Rhytidhysterion* should be segregated in its own family". Samuels & Müller (1980) also noted that "The genus does not have any close relatives in the heterogeneous *Patellariaceae*". However, other authors (Bezerra & Kimbrough 1982) presented arguments against the inclusion of *Rhytidhysterion* within the *Hysteriaceae*, based on patterns of centrum development. Nevertheless, molecular data presented here, necessitate a radical reappraisal of the *Hysteriaceae* to include patellarioid forms.

Key to the species of *Rhytidhysterion*

- 1. Ascospores mainly one-septate ***R. hysterinum***
- 1'. Ascospores with more than one septum 2
- 2. Ascospores mainly three-septate 3
- 2'. Ascospores with five or more septa ***R. dissimile***
- 3. Ascospores with three transverse, but also one or more longitudinal septa ***R. opuntiae***
- 3'. Ascospores transversely three-septate, with no longitudinal septa ***R. rufulum***

Mytiliniaceae KirscOedo. 1924, ***Mytilinidiales*** Boehm, Schoch & Spatafora 2009, ***Pleosporomycetidae*** Schoch *et al.* 2007a

Lophiaceae Zogg ex Arx & E. Müll., Stud. Mycol. Baarn 9: 60 (1975).

Lophiaceae Zogg, Beitr. Kryptogamenfl. Schweiz 11(3): 90. (1962). *nom. inval.* ICBN Art. 36.

Fungi classified in the *Mytiliniaceae* KirscOedo. (Kirschstein 1924) are characterized by fragile yet persistent carbonaceous ascomata, which range from globoid to obovoid to strongly laterally compressed erect, bivalve shell-shaped structures, standing on edge, with lateral walls more or less connivent, and extended vertically to a prominent longitudinal keel or cristate apex. Mytilinioid fungi possess a thin-walled,

scleroparenchymatous peridium enclosing a hamathecium of narrow trabeculate pseudoparaphyses, borne in a gel matrix, which are often sparse to lacking at maturity. Bitunicate asci are borne in a basal, rarely lateral, orientation within the centrum, and contain eight, rarely four, ascospores, overlapping uniseriate, biseriate or in one or two fascicles. Ascospores are diverse, ranging from scoleospores to didymospores to phragmospores or dictyospores, hyaline, soon yellow to dark brown, and generally showing bipolar symmetry (Barr 1987, 1990a; Zogg 1962).

Currently accepted genera in the *Mytiliniaceae* include: *Actidium* Fr., *Lophium* Fr., *Mytilinidion* Duby, *Ostreola* Darker, and *Quasiconcha* M.E. Barr & M. Blackw., to which has recently been added *Zoggium* Vasilyeva (Barr 1975, 1990a; Barr & Blackwell 1980; Darker 1963; Lohman 1932b; Vasilyeva 2001; Zogg 1962). The genus

Ostreichnion Duby, previously classified within the *Mytiliniaceae*, has been removed to the *Hysteriaceae* (Boehm *et al.* 2009). Anamorphs in the *Mytiliniaceae* are primarily coelomycetous (e.g., *Aposphaeria*, *Pyrenochaeta*, *Camarglobulus*, *Dothiorella*, and *Sclerochaeta*) and less frequently hyphomycetous (e.g., *Chalara*-like, *Papulaspora*, *Peyronelia*, and *Septonema*) (Blackwell & Gilbertson 1985; Lohman 1932b, 1933a and b; Speer 1986; Sutton 1970). Typically temperate in distribution, mytilinioid fungi are found in association with the wood, bark, resin, cones, scales, needles, seeds, and roots of gymnosperms.

The genus *Glyphium* Nitschke ex Lehmann. was originally included by Zogg (1962), Barr (1987, 1990a) and others (e.g., Goree 1974; Lorenzo & Messuti 2005; Sutton 1970) in the *Mytiliniaceae*. Molecular evidence (Lindemuth *et al.* 2001; Lumbsch *et al.* 2005) has recently led to moving *Glyphium* to the *Chaetothyriales* in the *Eurotiomycetes*. This unusual placement has been restated in a number of subsequent publications (Geiser *et al.* 2006; Kodsueb *et al.* 2006; Lücking *et al.* 2004; Schmitt *et al.* 2005), including the Assembling the Fungal Tree of Life (AFTOL) Project (Lutzoni *et al.* 2004). These studies, however, were based on sequences derived from a single isolate (CBS 268.34; AFTOL 1145) labeled as *Gly. elatum*, but identified by Sutton (1970) as belonging to *Gly. leptothecium* (Earle) B. Sutton, later designated as *Gly. corrugatum* (Ellis) Goree (Goree 1974).

In this study, we have been able to obtain fresh material of *Gly. elatum* from France on *Salix caprea* (EB 0388) from Aliain Gardiennet (Veronnes, France) (Table 1). We were also able to secure samples from a different species, *Gly. grisonense* G. Mathiassen (Mathiassen 1993) from Norway on *Salix myrsinifolia* subsp. *myrsinifolia* (EB 0375) and on *S. myrsinifolia* subsp. *borealis* (EB 0376) from Geir Mathiassen (Tromsø Museum, Universitetsmuseet Fagenhet for Botanikk, Tromsø, Norway). Molecular data presented here do not support the placement of *Glyphium* in the *Chaetothyriales* in the *Eurotiomycetes*, but rather retain the genus within the *Dothideomycetes*, surprisingly closely associated with the genera *Hysteropatella* and *Patellaria*, in the *Patellariaceae* (Fig. 1). We presently consider the genus *Glyphium* as *Pleosporomycetidae* gen. *incertae sedis* and must conclude that the isolate CBS 268.34, used in a number of previous studies, does not represent *Gly. elatum*. A study is currently in preparation (Boehm, Marson, Mathiassen, Gardiennet & Schoch unpubl.) to further address issues related to the phylogenetic placement of the genus *Glyphium*. Despite their transference out of the *Mytiliniaceae*, both *Ostreichnion* and *Glyphium* are included in the current key to effectuate identification of morphologically similar fungi, regardless of whether close phylogeny is implied or not.

Key to the genera of the *Mytiliniaceae*

1. Ascospores one-septate, small, shorter than 30 µm 2
 - 1'. Ascospores not didymospores, or if one-septate, then longer than 30 µm 3
 2. Didymospores brown, ellipsoid, symmetric, with coarsely reticulate wall; 6–8 x 5–5.5 µm **Quasiconcha**
 - 2'. Didymospores olive- to reddish brown, walls thin, smooth or delicately longitudinally striate, but not reticulated; longer than 10 µm **Actidium**
 3. Ascospores filiform, multiseptate, about equal in length to the ascus, in some case, at maturity longer than the ascus, often spirally arranged 4
 - 3'. Ascospores ellipsoid, fusoid, cylindrical, if scolecospores then shorter than the ascus and not spirally arranged 6
 4. Ascomata conchate, solitary to gregarious, but never forming fused, ridge-like assemblages **Lophium**
 - 4'. Ascomata either forming rigid, fused band- or ridge-like structures or solitary, erect, dolabrate to ligulate 5
 5. Ascomata conchate, densely gregarious, forming band- or ridge-like assemblages **Zoggium**
 - 5'. Ascomata erect, dolabrate to ligulate in outline; often with subtending hyphal strands; cosmopolitan **Glyphium**
- Note: Sequence data presented here indicate that *Glyphium* does not belong to the *Mytiliniales*, but remains as *Pleosporomycetidae* gen. *incertae sedis*. A key to the species is not presented here.

6. Ascospores transversely septate; if scolecospores and more than 50 µm long, then only 2–4 µm wide **Mytilinidion**
- 6'. Ascospores dictyospores, or large and remaining 1-septate 7
7. Ascomata conchate; ascospores ellipsoid, not over 30 x 10 µm, with single longitudinal septum in mid-cell **Ostreola**
- 7'. Ascomata conchate; ascospores ellipsoid or cylindric, longer than 30 µm, with several longitudinal septa in cells or large and remaining one-septate **Ostreichnion**
- Note: The genus *Ostreichnion* previously classified within the *Mytiliniaceae* (Barr 1975, 1987, 1990a) has been transferred to the family *Hysteriaceae* (Boehm *et al.* 2009).

1. The genus *Actidium* Fr. : Fr.
Syst. Myc. 2: 595 (1823).

Mytilidion Duby, subgen. *Bulliardella* Saccardo 1883
≡ *Bulliardella* (Sacc.) Paoli 1905
Ostreionella Seaver 1926

The genus *Actidium* was established by Fries (1823) to accommodate *A. hysterooides* Fr., a stellate mytilinioid fungus found on *Pinus* and *Picea* in Europe, with two-celled, symmetric ascospores, light olive- to reddish brown, faintly longitudinally striate in age (Barr 1990a). Fries (1823) was the first to note its similarity with *Glonium* in the

Hysteriaceae, with hyaline to yellow didymospores (Zogg 1962). One species, *A. nitidum* (Ellis) Zogg, is known from the *Cupressaceae* in temperate North America (Barr 1990a). Zogg (1962) recognized an additional three species from Europe, namely *A. hysterooides*, *A. baccarinii* (Paoli) Zogg and *A. pulchrum* (Teng) Zogg, all on *Pinaceae*. Due to similarities in ascospore morphology, the genus *Actidium* may have affinities with other didymosporous hysteroaceous genera (e.g., *Psilogonium*, *Actidiographium* and *Glonium*), although molecular data are presently lacking.

Key to the species of *Actidium*

1. Fruitbodies star-shaped; spores 11–14 x (1.5–)2–3 µm; Europe on *Pinus*, *Picea* ***A. hysterooides***
- 1'. Fruitbodies shell-shaped (conchate), not star-shaped 2
2. Ascospores (9–)11–14(–16) x (1.5–)2–3 µm; Europe, N. America (USA), on *Pinus*, *Picea*, *Juniperus* ***A. nitidum***
- 2'. Ascospores larger 3
3. Ascospores (16–)18–22(–24) x (3–)4–5(–6) µm; Europe, on *Pinus*, *Picea*, *Thuja* ***A. baccarinii***
- 3'. Ascospores 23–28 x 6–7.5 µm; China, on *Pinaceae* ***A. pulchra***

2. The genus *Quasiconcha* M.E. Barr & M. Blackw.
Mycologia 72: 1224 (1980).

The genus *Quasiconcha* was established by Barr & Blackwell (1980) to accommodate *Q. reticulata* M.E. Barr & M. Blackw., an unusual mytilinioid fungus, with one-septate, highly reticulated ascospores, borne in conchate, thin-walled ascomata, found in association with *Juniperus* seeds excreted in dung and the roots of two conifers in the southwestern United States (Barr & Blackwell 1980; Blackwell & Gilbertson 1985). In the present study, we were fortunate to obtain original material of *Q. reticulata* (Table 1) from Meredith Blackwell (Louisiana State University, Baton Rouge, LA), from which we isolated DNA (EB QR). Sequence data (Fig. 1) clearly indicate that the genus *Quasiconcha* belongs to the *Mytiliniaceae*, in close

association with *Lophium*, to which its fruitbodies most closely resemble.

3. The genus *Mytilinidion* Duby
Mém. Soc. Phys. Hist. nat. Genève 16: 34 (1862).

Mytilidion Sacc. 1875
Hypodermopsis Earle 1902 (non Kuntze 1898)
Murashkinskija Petrak 1928

The genus *Mytilinidion*, the type for the family *Mytiliniaceae*, was established by Duby (1862) with an etymology from *Mytilus*, a genus of mussels. Boehm *et al.* (2009) reviewed the nomenclatural history of the genus. Species of *Mytilinidion* are characterized by yellow- to reddish-brown, ellipsoid, fusoid, obovoid to elongate, transversely septate ascospores, borne in thin-walled

globoid to conchate pseudothecia, with lateral walls more or less connivent and extended vertically to a cristate apex. There are currently fifteen recognized species, occurring on members of *Pinaceae*, *Cupressaceae*, and *Taxodiaceae* (Barr 1990a; Zogg 1962).

Ascospore morphology can be used to discern four morphological types within the genus, listed here by increasing ascospore length: (1) Short squat phragmospores: *M. californicum* Ellis & Harkness, *M. acicola* G. Winter, *M. resinae* Speer, *M. decipiens* (P. Karst.) Sacc., *M. tortile* (Schwein.) Ellis & Everhart (Fig. 8D), and *M. resinicola* M.L. Lohman; (2) Elongate phragmospores, with a spore length to width ratio of 10:1 or less: *M. mytilinellum* (Fr.) Zogg (Fig. 8E), *M. rhenanum* Fuckel, and *M. gemmigenum* Fuckel; (3) Fusoid or spindle-shaped spores: *M. thujarum* (Cooke & Peck) M.L. Lohman, *M. oblongisporum* Teng, and *M. andinense* (Lorenzo & Messuti) Boehm, Schoch & Spatafora; and (4) Highly elongated phragmospores, or rather scolecospores, with a ratio of approximately 20:1, defining subgenus *Lophiopsis sensu* Lohman (1932b): *M. scolecosporum* M.L. Lohman, *M. parvulum* M.L. Lohman and *M. australe* M.L. Lohman (Fig. 8F). These last three scolecosporous species were postulated to form a transitional series to connect *Mytilinidion* with the heretofore somewhat isolated genus *Lophium* (Fig. 8G), and formed the basis for the subgenus

Lophiopsis M.L. Lohman (Lohman 1932b), accepted by Zogg (1962).

Sequence data presented here (Fig. 1), based on an analysis of 11 of the 15 currently recognized species (Table 1), support the association of fusoid or spindle-shaped spores belonging to *M. thujarum* (EB 0268) and to *M. andinense* (CBS 123562), thus defining a clear lineage for this type of spore within the genus. On the other hand, molecular data do not support subgenus *Lophiopsis sensu* Lohman (1932b): *Mytilinidion scolecosporum* (CBS 305.34) does not belong to the same clade as *M. australe* (CBS 301.34) (Fig. 1). This implies that the scolecospore has independently evolved at least twice within the family. Furthermore, species possessing short, squat phragmospores, namely *M. acicola* (EB 0349, EB 0379), *M. californicum* (EB 0385), *M. tortile* (EB 0377), and *M. resinicola* (CBS 304.34) display complex relationships with species possessing elongate phragmospores, such as *M. mytilinellum* (EB 0386, CBS 303.34) and *M. rhenanum* (EB 0341, CBS 135.45). This indicates that phragmospores with different length to width ratios have evolved multiple times within the genus (Fig. 1). A manuscript currently in preparation (Boehm, Gardiennet & Schoch unpubl.) will address speciation events within the *Mytiliniaceae*. Despite the lack of support from molecular data for the subgenus *Lophiopsis*, it is included in the key below to facilitate species identification.

Key to the species of *Mytilinidion*

1. Spore length to width ratio = 10:1 or less (phragmospores): Subgenus *Eu-Mytilinidion sensu* Lohman (1932b) 2
- 1'. Spore length to width ratio = approx. 20:1 (scolecospores): Subgenus *Lophiopsis sensu* Lohman (1932b) 13
2. Ascomata not conchate, erect, low and spreading at the base (scutate), seated on a shield-like process fused to the substrate; ascospores 3–5(–6)-septate, 3
- 2'. Ascomata conchate, shell-shaped, standing on edge, with a clearly defined longitudinal cristate apex 4
3. Ascospores 13–15 x 4–4.5(–6) µm; California, on *Sequoia* ***M. californicum***
- 3'. Ascospores 14–22(–28) x (4.5–)6–8(–10) µm; Europe, on *Juniperus*, *Thuja* ***M. acicola***
4. Ascospores elongate phragmospores, usually not constricted at the septa 5
- 4'. Ascospores shorter, squat, or longer, but not narrowly elongated, usually constricted at more than the median septum 7
5. Ascospores (2–)3(–5)-septate, measuring (14–)16–22(–24) x (2.5–)3–4(–5) µm ***M. mytilinellum***
- 5'. Ascospores longer, with more septa 6
6. Ascospores 3–5(–7)-septate, measuring (24–)30–42(–50) x 3–5 µm ***M. rhenanum***
- 6'. Ascospores slightly curved, (3–)7–9(–11)-septate, measuring (27–)32–38(–48) x (4–)5–6(–8) µm ***M. gemmigenum***

7. Ascospores (2-)3-septate, small, 10-13 x 4-6 µm; neotropical, on resin of *Araucaria* ***M. resiniae***
- 7'. Ascospores 3(-5)-septate, longer 8
8. Ascospores 3-septate, slightly curved, oblong-elliptic, with obtuse ends, unstricted, measuring (11-)13-15(-21) x 3-4(-6) µm ***M. decipiens***
- 8'. Ascospores longer, or similar in length but then slightly wider 9
9. Ascospores 3-septate, slightly curved, but oblong, fusiform, with slight constrictions, measuring (11-)14-17(-21) x 5-7(-8) µm ***M. tortile***
- 9'. Ascospores longer 10
10. Ascospores 3-septate, elliptic-oblong, deeply constricted at the septa, measuring 24-26 x 8-9 µm ***M. resinicola***
- 10'. Ascospores longer, fusoid 11
11. Ascospores 3-septate, constricted at the median septum, measuring 27-33 x 7-8.5 µm; China and W. USA ***M. oblongisporum***
- 11'. Ascospores longer 12
12. Ascospores 3-(4-5-) septate, measuring (26-)30-34(-40) x (10-)12-13(-15) µm ***M. thujarum***
- 12'. Ascospores wider, 3-7(-9)-septate, with swollen middle cells, 32-44 x 10-15 µm ***M. andinense***
13. Ascospores 5-7-septate, measuring 40-50 x 2-2.5 µm, slightly constricted at central septa ***M. scolecosporum***
- 13'. Ascospores longer, with more septa, less constricted 14
14. Ascospores 7-9(-11)-septate, measuring (48-)54-62(-65) x 2.7-3 µm ***M. parvulum***
- 14'. Ascospores (10-)11-14-septate, measuring (54-)58-70(-75) x 3-4 µm ***M. australe***

4. The genus *Lophium* Fr. : Fr.
Syst. Mycol. 2: 534 (1823).

Lophidium P. Karsten 1873.

The genus *Lophium* is characterized by fragile, conchate ascocarps, sometimes seated on a foot-like base or sessile directly on the substrate. The thin-walled scleroparenchymatous peridium encloses a basal hamathecium of narrow trabeculate pseudoparaphyses, with very elongate asci, each bearing one fascicle of transversely septate filiform ascospores, often spirally arranged. The type species, *Lophium mytilinum* (Pers. : Fr.) Fr. (Fig. 8G), is cosmopolitan in the temperate zones and has been recorded from both sides of the Atlantic (Barr 1990a; Zogg 1962). Zogg (1962) described two additional species, *L. elegans* Zogg on *Juniperus* from alpine regions of France, Italy and Switzerland, and *L. mayorii* Zogg on *Pinus* and *Larix* from the Swiss and French Alps. Like *Mytilinidion*, species of *Lophium* have only been recovered from coniferous substrates. The sole exception is the

recently described *Lophium igoschinae* Chlebicki recently recovered from *Dryas octopetala* and *D. crenulata* (*Rosaceae*) from Russia and Greenland (Chlebicki & Knudsen 2001).

Three isolates of the type species, *L. mytilinum* Pers. : Fr. were surveyed (Table 1), originating from the United States (CBS 269.34, CBS 123344 / BPI 878736) and Sweden (CBS 114111). An additional species of *Lophium*, namely a single-spored isolated of *L. elegans* from France (EB 0366) was included in the analysis (Table 1). Both species are morphologically similar, with *L. elegans* having spirally arranged spores in the ascus and *L. mytilinum* having them in parallel orientation (Zogg 1962). Molecular data indicate that the two species are not closely related within the family. *Lophium mytilinum*, with filiform ascospores, shows a close phylogenetic relationship to *Quasiconcha reticulata* M.E. Barr & M. Blackw. (EB QR), with reticulated didymospores. Although having dissimilar spores, the fruitbodies of both taxa are remarkably similar in their shape, size and fragility.

Key to the species of *Lophium*

1. Fruitbody erect, conchate, with thin-walled sclerenchymatoid peridium 2
- 1'. Fruitbody conchate, but crowded, band- or ridge-like, horizontal to recumbent and elongated; ascospores arranged parallel in the ascus, measuring (60–)80–100(–110) x 3–4(–5) μm ***L. mayorii***
 Note: *L. mayorii* was recently transferred to *Zoggium mayorii* (Zogg) L.N. Vasilyeva (Vasilyeva 2001).
2. Ascospores filiform, 12–15 septate, measuring 78–86 x 2.6–3 μm ; Greenland, on *Dryas* ***L. igoschinae***
- 2'. Ascospores filiform, but longer; on conifers 3
3. Ascospores arranged parallel in the ascus; measuring (130–)170–250(–300) x 1–2(–2.5) μm ***L. mytilinum***
- 3'. Ascospores spirally arranged in the ascus; measuring (200–)260–280(–300) x 2 μm ***L. elegans***

5. The genus *Zoggium* L. Vasilyeva Mikol. Fitopatol. 35: 17 (2001).

Canad. J. Bot. 41: 1383 (1963).

Zogg described *Lophium mayorii* Zogg on *Pinus* and *Larix* from the Swiss and French Alps, but noted that it differed from other species of *Lophium* in having rigid, band-forming ascomata, with a less fragile peridium as compared to *Lophium* and *Mytilinidion*. Vasilyeva (2001) found the same fungus in the Russian Far East and stated that it differed sufficiently from other species of *Lophium* in having gross, erumpent crowded ascomata, band- or ridge-like in appearance, as compared to the smaller, fragile, and entirely superficial fruitbodies typical of species of *Lophium* and made the transfer to *Zoggium mayorii* (Zogg) Vasilyeva (Vasilyeva 2001). Molecular data are presently lacking.

Barr (1975, 1990a) recognized two genera with muriform ascospores in the *Mytilinidiaceae*, namely *Ostreichnion* and *Ostreola*. Darker (1963) established the genus *Ostreola* for dictyosporous forms that otherwise resembled species of *Mytilinidion* – that is, mytilinidioid counterparts to *Hysterographium*. Barr (1987, 1990a) differentiated *Ostreola* from *Ostreichnion* by smaller ascospores in the former. Barr (1990a) recognized two species from North America, *O. consociata* Darker from the Northeast and *O. formosa* (Cooke) M.E. Barr, the latter common on conifers in western North America and Europe, with spores similar to those of *Hysterographium mori*. Tilak & Kale (1968) added another two species from India, namely *O. indica* Tilak & Kale and *O. ziziphi* Tilak & Kale, surprisingly both from non-coniferous substrates. Molecular data are presently lacking for this genus.

6. The genus *Ostreola* Darker

Key to the species of *Ostreola*

1. Ascomata on coniferous hosts; North America, Europe 2
- 1'. Ascomata on non-coniferous hosts; India 3
2. Base of ascoma footlike, immersed in substrate; ascospores 3–5(–7)-septate, with a longitudinal septum in the mid-cells, 14–18(–22) x 5–7 μm ; on *Picea*, Northeastern America ***O. consociata***
- 2'. Base of ascoma tapered or applanate on surface of substrate; ascospores (3–)5(–6)-septate, wider than in *O. consociata*, 15–21 x 6.5–9.5 μm ; on *Abies*, Western North America, Europe, alpine ***O. formosa***
3. Ascospores transversely 3–7-septate, with 2–3 longitudinal septa, slightly constricted in the middle; 24–30 x 8–9.6 μm ; on culms of *Maduca*, India ***O. indica***
- 3'. Ascospores as above but smaller, 19–23 x 6–7.5 μm ; in culms of *Ziziphus*, India ***O. ziziphi***

Glioniaceae (Corda) Boehm, Schoch & Spatafora 2009
fam. incertae sedis, **Pleosporomycetidae** Schoch *et al.*
 2007a

The nomenclatural history of the genus *Glonium* was presented in Boehm *et al.* (2009). Corda (1842) originally proposed the *Glioniaceae* Corda as an infrafamilial taxonomic rank under the family *Hysteriaceae*, to comprise *Hysterographium* and *Glonium*. Boehm *et al.* (2009) emended the circumscription and elevated the taxon to family rank. The genus *Glonium* was retained as circumscribed first by von Höhnel (1918) and then by Petrak (1923a). We feel justified in reinstating the *Glioniaceae* and, more importantly, recognizing it at family rank for a single genus, because of the high support the group receives in a recent four-gene analysis (Boehm *et al.* 2009), and corroborated here with additional isolates.

The genus *Glonium* Muhl. : Fr.
 Syst. Mycol. 2: 594 (1823).

Solenarium Sprengel 1827

Psiloglonium (Höhn. 1918) Petrak 1923b

The genus *Glonium* is characterized by modified hysterothecia, progressively dichotomously branched, laterally anastomosed along their length to form radiating flabelliform or pseudo-stellate composites, seated upon a conspicuous brown felt-like subiculum (arrows in Fig. 8A), sometimes borne in a stroma. Hysterothecia in vertical section globose to obovoid, typically with a thick three-layered peridium, but fragile, unlike the robust peridium of the *Hysteriaceae*, composed of small pseudoparenchymatous cells, the outer layer heavily encrusted with pigment and often longitudinally striate on the surface, the middle layer lighter in pigmentation and the inner layer distinctly thin-walled, pallid and compressed. The hamathecium consists of persistent narrow cellular

pseudoparaphyses, often borne in a gel matrix, with tips darkened or branched at maturity. Bitunicate asci are borne in a basal layer and at maturity are typically clavate to cylindrical, bearing eight ascospores, overlapping biseriately; ascospores ranging from hyaline to light yellow, 1-septate, conspicuously constricted at the septum, fusoid in outline, with at least one end, often both, acuminate, and showing bipolar asymmetry.

Zogg (1962) accepted three species that he grouped together in his key under Type III that form the basis for the *Glioniaceae*. These are the type species *G. stellatum* Muhl. : Fr. (Fig. 8A), *G. graphicum* (Fr.) Duby, and *G. compactum* Kern, to which we can add the recently described saxicolous / terricolous species *G. circumserpens* (Nyl.) Kantvilas & Coppins (Fig. 8B-C) from Tasmania (Kantvilas & Coppins 1997). Although von Höhnel (1918) and Petrak (1923a) stressed the importance of a subiculum as a synapomorphic character state separating the two genera, Zogg (1962) noted that *G. graphicum* may or may not be associated with a subiculum. Thus, the synapomorphic character state here is not subicula *per se*, but the ascomata, which are modified hysterothecia that are progressively dichotomously branched, laterally anastomosing to form radiating pseudo-stellate composites (e.g., *G. stellatum*, *G. graphicum* and *G. circumserpens*), or are associated with a thin stromal crust, that is itself seated on a subiculum (e.g., *G. compactum*).

Four isolates, two of *G. stellatum*, from Michigan (CBS 207.34) and Tennessee (ANM32), the United States, share the same clade with two isolates of *G. circumserpens*, recently isolated from wood (CBS 123342) and dolerite stone (CBS 123343) from Tasmania (Fig. 1). Surprisingly, this clade also includes multiple isolates of *Cenococcum geophilum* Fr., an ecologically important ectomycorrhizal fungus with a global distribution and a wide host range, but with no known teleomorph (LoBuglio *et al.* 1996).

Key to the species of *Glonium*

1. Hysterothecia associated and seated upon a thin crust-like stroma, or arising from within a stromal crust; stroma itself seated on subiculum; didymospores spindle-shaped with the upper cell slightly swollen and larger than the lower cell, measuring 24–28 x 5–6 µm; Ivory Coast, West Africa ***G. compactum***
- 1'. Hysterothecia not associated with stroma 2
2. Hysterothecia somewhat branched, irregular, “graphoid”; without well-developed subiculum (Zogg 1962); didymospores oblong to spindle-shaped; upper cell pear-shaped, constricted at septum; both ends acuminate, measuring (13–)15–18(–21) x (3–)5–6 µm; on *Pinus*, *Juniperus*, Europe ***G. graphicum***
- 2'. Hysterothecia in mature specimens highly bifurcated, closely appressed to the substrate, dichotomously branched to form irregular creeping masses; usually seated upon or sitting behind a front of well-developed brown to black subiculum 3

3. Didymospores hyaline, constricted at the septum, apices pointed, measuring (15–)16–17 x 6–7 µm; on soil (terricolous) or rock (saxicolous), or lignicolous; Tasmania **G. circumserpens**

3'. Didymospores oblong to spindle-shaped; upper cell pear-shaped, constricted at septum; both ends acuminate, measuring (18–)21–26(–28) x (4–)5–6(–7) µm; cosmopolitan **G. stellatum**

The genus *Farlowiella* Sacc.

Syll. Fung. 9: 1101 (1891).

Farlowia Sacc. 1883

The genus *Farlowiella* has been transferred out of the *Hysteriaceae* (Boehm *et al.* 2009), and is currently designated as *Pleosporomycetidae genera incertae sedis*. It is characterized by one-celled pedicellate slightly laterally compressed amerospores, the upper cell pigmented and much larger than the lower, which remains hyaline or moderately pigmented, and can be considered as an associated papilla. The carbonaceous hysterothecia are somewhat laterally compressed, but nonetheless thick-walled and with a prominent sunken slit. They can be solitary to gregarious, but remain erect, and elevated, presenting an almost stipitate appearance. Anamorphs

have been described in the genus *Acrogenospora* (Goh *et al.* 1998). Two species are recognized, namely *F. carmichaeliana* (Berk.) Sacc. from Europe (England, Belgium, Germany, Switzerland), from the bark and wood of *Fagus*, *Quercus*, *Sorbus* and *Prunus*, and *F. australis* Dennis, known only from the original collection on *Phyllica arborea* from Tristan da Cunha in the South Atlantic (Dennis 1955). Sequence data from two isolates of *F. carmichaeliana* (CBS 206.36 and CBS 179.73) indicate that this taxon lies quite distant from both the *Hysteriaceae* and the *Mytiliniaceae* (Fig. 1), but remains within the *Pleosporomycetidae* as *gen. incertae sedis* (Boehm *et al.* 2009; Schoch *et al.* 2007a). An additional isolate of the anamorph, *Acrogenospora sphaerocephala* (Berk. & Broome) M.B. Ellis (CBS 164.76), further supports the current placement of the genus *Farlowiella*.

Key to the species of *Farlowiella*

1. Ascospores unequally 2-celled; upper cell pigmented, much larger than the lower cell, which is smaller and hyaline, together measuring 18–21 x 7–12 µm **F. carmichaeliana**

1'. Ascospores as above, but smaller, 13–15 x 6–7.5 µm; Tristan da Cunha **F. australis**

Conclusions

Hysteriaceae fungi are an ancient and ecologically successful group of organisms, as attested by their wide geographic distribution on a multitude of gymnosperm and angiosperm host species (Zogg 1962). Presumably they underwent rapid speciation in response to the angiosperm radiation of the mid- to late-Cretaceous, 65–100 mya. However, this must have occurred prior to the complete loss of continental contiguity, which occurred during the same time period. This is because we see today a remarkable degree of intraspecific stability, in both morphology and sequence data, among geographically divergent collections (Fig. 1). For example, little morphological or sequence variation was detected in *Hysterium angustatum*, from the United States (CBS 123334), Kenya (GKM 243A), New Zealand (SMH 5211.0), and South Africa (CMW 20409; Lee & Crous 2003). Similarly, little variation was detected in *Psilogonium claviforme*, from Kenya (GKM L172A, GKM 344A) and the United States (e.g., CBS 123338), or in *Oedohysterium sinense*, from South Africa (CBS 123345) and the United States (EB 0339). As we are presumably sampling remnants of once contiguous sexual populations, their similarity today must imply that speciation occurred prior to

complete genetic isolation. The break-up of Pangea during the Triassic 200 mya, and the formation of the nascent central Atlantic Ocean, separating Gondwana from Laurasia, during the Jurassic, 150 mya, effectively disrupted once contiguous populations. Although most flowering plant families were established by the end of the Cretaceous, 65–70 mya, it is now believed that they diversified into their present lineages (e.g., eudicots, Magnoliids and monocots) much earlier, around 140 mya (Davies *et al.* 2004; Moore *et al.* 2007; Palmer *et al.* 2004). This may have allowed for remnants of once contiguous populations to colonize early angiosperm lineages, prior to the complete dissolution of continental integrity during the Cretaceous. Whatever the timing, hysteriaceous fungi incurred little appreciable intraspecific morphological or genetic (e.g., nuLSU, nuSSU, TEF1 and RPB2) change over significant periods of geologic time. Thus, with the exception of *Hsb. mori*, and perhaps, *Glp. subrugosa*, most members of the *Hysteriaceae* appear to be stable species.

Although there are examples of concordance between morphological and molecular data in this study (e.g., *Rhytidhysterium*, *Glomium*, and the *Mytiliniaceae*), these are few. For the most part, molecular data support the premise of a large number of convergent evolutionary lineages, sharing similar spore morphologies, but that are

not closely related. This resulted in a polyphyletic core set of genera for the *Hysteriaceae* (Boehm *et al.* 2009), and presented us with a complicated picture of past speciation events within the family. To achieve a natural phylogeny, that is, one based on the congruence of morphological and molecular data, required that we break-up what were once thought to be stable genera. Thus, two species of *Hysterium* were transferred to *Oedohysterium* (*Oedo. insidens* and *Oedo. sinense*) and two species of *Gloniopsis* to *Hysterobrevium* (*Hsb. smilacis* and *Hsb. constrictum*). While *Hysterographium*, with the type *Hg. fraxini*, was removed from the *Hysteriaceae*, some of its species remained within the family, transferred here to *Oedohysterium* (*Oedo. pulchrum*), *Hysterobrevium* (*Hsb. mori*) and *Gloniopsis* (*Glp. subrugosa*). New species were described (e.g., *Glp. arciformis* and *Glp. kenyensis*) that would previously have been classified in *Hysterographium*, but are now accommodated in *Gloniopsis*. Thus, the genera *Gloniopsis* and *Hysterobrevium* now include both hyaline and pigmented dictyospores, and the genus *Oedohysterium* includes both phragmospores and dictyospores. The genus *Glonium sensu* Zogg (1962) was divided into *Psiloglonium* in the *Hysteriaceae* and *Glonium* in the *Gloniaceae* (Boehm *et al.* 2009), and, more recently, *Anteaglonium* in the *Pleosporales* (Mugambi & Huhndorf 2010). These taxonomic changes were unexpected, as they were not premised on past assumptions of synapomorphy related to spore morphology (Zogg 1962). Although we have included here a total of 59 accessions, representing 22 species in seven genera, for the *Hysteriaceae*, and another 65 outside of the family (Table 1), taxon sampling may still be insufficient. Clearly, additional species and genera need to be sampled before a complete picture emerges for the family.

The hysterothecium, thick-walled, navicular, and with a prominent longitudinal slit, has long been considered synapomorphic, defining the *Hysteriales*. However, this type of fruitbody has evolved convergently no less than five times within the *Pleosporomycetidae* (e.g., *Farlowiella*, *Glonium*, *Anteaglonium*, *Hysterographium* and the *Hysteriaceae*). Similarly, thin-walled mytilinioid (e.g., *Ostreichnion*) and patellarioid (e.g., *Rhytidhysterion*) ascomata have also evolved at least twice within the subclass, having been transferred from the *Mytiliniaceae* and *Patellariaceae*, respectively, to the *Hysteriaceae*. As such, character states relating not only to the external features of the ascoma, but to the centrum as well (e.g., cellular pseudoparaphyses *versus* trabeculae, etc.), previously considered to represent synapomorphies among these fungi (e.g., Barr 1987, 1990a), in fact, represent symplesiomorphies, and most likely have arisen multiple times through convergent evolutionary processes in response to common selective pressures. One advantage of the hysterothecium may be spore discharge over prolonged periods of time, since some, if not most, species may be perennial (Lohman 1931, 1933a). The thick-walled

peridium further contributes to xerotolerance, as many of these fungi persist on decorticated, weathered woody substrates prone to prolonged periods of desiccation. Thus, the ability to perennate, and time spore discharge with environmental conditions suitable for germination, spanning multiple seasons, may be the driving force behind the repeated evolution of the hysterothecium.

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Fig. 1. Combined ribosomal (nuSSU & nuLSU) and protein (TEF1 & RPB2) phylogeny for the Dothideomycetes, with extensive representation of the Pleosporomycetidae, containing the *Hysteriaceae* (*Hysteriales*), *Pleosporales*, *Mytilinidiales*...

Fig. 2. The genus *Hysterobrevium* (Clade A). A. *Hysterobrevium constrictum* (SMH 5211.1; Clade A; New Zealand). B. *Hsb. smilacis* (GKM 426N; Clade A; Kenya). C. *Hsb. mori* (SMH 5273; Clade A; USA). D. *Hsb. mori* (ANM 43; USA; not incl). E-F. *Hsb. mori* (CBS 123563, BPI 878731). Scale: habitat bar = 500 µm; spore bar = 20 µm.

Fig. 3. The genera *Psiloglonium* (Clade B, *Hysteriaceae*) and *Anteaglonium* (*Pleosporales*). A. *Psiloglonium simulans* (ANM 1557; USA). B. *P. clavisorum* (GKM 344A; Kenya). C. *P. lineare* (ANM 117; USA). D. *P. araucanum* (ANM 42; USA). E. *P. chambianum* (ANM 1484; USA). F. *Anteaglonium abbreviatum* (ANM 37; USA). G. *A. globosum* (ANM 925b; USA). H. *A. parvulum* (GKM 219N; Kenya). I. *A. latirostrum* (GKM L100Nb; Kenya). Scale: spore bar = 10 µm.

Fig. 4. The genus *Hysterium* (Clade C) and *Oedohysterium* (Clade D). A. *Hysterium pulicare* (CBS 123377, USA; BPI 878723). B. *H. angustatum* (ANM 120; USA). C. *H. vermiforme* (GKM 1234; Kenya). D. *H. barrianum* sp. nov. (ANM 1495; USA). E. *Oedohysterium insidens* (ANM 1443; USA). F. *Oedo. sinensis* (ANM 119; USA). Scale: habitat bar = 500 µm; spore bar = 20 µm.

Fig. 5. The genus *Gloniopsis* (Clade D). A-B. *Gloniopsis praelonga* (CBS 123337, BPI 878725, USA). C. *Glp. subrugosa* (CBS 123346, BPI 878735; South Africa). D. *Glp. subrugosa* (GKM 1214; Kenya). E. *Glp. subrugosa* (SMH 557; Cuba). F. *Hsb. mori* (GKM 1013; Clade D; Kenya). Scale: habitat bar = 500 µm; spore bar = 20 µm.

Fig. 6. The genera *Gloniopsis* (Clade D) and *Rhytidhysterion* (Clade E). A. *Gloniopsis arciformis* sp. nov. (GKM L166A; Kenya). B. *Glp. kenyensis* (GKM 1010; Kenya). C. *Rhytidhysterion opuntiae* (GKM 1190; Kenya). D. *R. rufulum* (GKM 361A; Kenya). E-G. *R. rufulum* (EB 0382; Ghana). Scale: habitat bar = 500 µm; spore bar = 20 µm.

Fig. 7. The genus *Hysteroglyphium*. A-B. *Hysteroglyphium flexuosum* (EB 0098; USA). C-D. *Hg. fraxini* (EB 0100; USA). Scale: habitat bar = 500 µm; spore bar = 20 µm.

Fig. 8. The *Gloniaceae* and *Mytiliniaceae*. A. *Glonium stellatum* (ANM 41; USA). B-C. *G. circumserpens* (CBS 123343, BPI 878739; Tasmania). D. *Mytilinidion tortile* (EB 0377; France). E. *M. mytilinellum* (EB 0386; France). F. *M. australe* (ANM 1524; USA). G. *Lophium mytilinum* (CBS 123344, BPI 878736; USA). Scale: habitat bar = 500 µm; spore bar = 10 µm.