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

E.W.A. Boehm¹, G.K. Mugambi², A.N. Miller³, S.M. Huhndorf⁴, S.L. Marinowitz⁵, and C.L. Schoch⁶

¹ Department of Biological Sciences, Kean University, 1000 Morris Ave., Union, New Jersey 07083; ² National Museum of Kenya, Botany Department, PO Box 40658, 00100, Nairobi, Kenya; ³ Illinois Natural History Survey, Section for Biodiversity, 1816 South Oak Street, Champaign, IL 6182; ⁴ The Chicago Field Museum, 1400 S. Lake Shore Dr, Chicago, IL 60605; ⁵ Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria 0002, South Africa; ⁶ National Institute of Health (NIH), National Library of Medicine, National Center for Biotechnology Information (NCBI), GenBank, 45 Center Drive, MSC 6510, Building 45, Room 6a.18, Bethesda, MD, 20892.

* Correspondence: E.W.A. Boehm, eboehm@kean.edu

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 102 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 (United States, Europe, Ghana, Kenya, South Africa, New Zealand, Tasmania, Cuba) and high density taxon sampling strategy was employed, including multiple isolates/species from the following genera: *Hysterium* (16/7), *Hysterographium* (15/4), *Gloniopsis* (8/2), *Psiloglonium* (11/3), *Anteaglonium* (10/4), *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). 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 *Mytilinidiales* are more distantly related within the subclass and show instead a close association with the *Gloniaceae*. Speciation patterns within these families are complex, and not premised on classical taxonomic assumptions relating to ascoma and spore morphology. Thus, within the *Hysteriaceae*, the genera *Hysterium*, *Hysterographium*, and *Gloniopsis* are highly polyphyletic, necessitating the transfer of some species to new genera, namely *Hystumidium* and *Hysterobrevium* *gen. nov.* In contrast, the genera *Psiloglonium* and *Rhytidhysterion* form monophyletic clades within the family. While the *Mytiliniaceae* forms a highly monophyletic family, based on *Mytilinidion*, *Lophium* and *Quasiconcha*, molecular data indicate that speciation events in this family also do not correspond to previously held assumptions based on spore morphology. The genus *Glyphium* originally classified within the *Mytiliniaceae*, but recently transferred to the *Chaetothyriales* in the *Eurotiomycetes*, is here retained within the *Dothideomycetes*, as *Pleosporomycetidae* *gen. incertae sedis*, but with close association to the genera *Hysteropatella* and *Patellaria* in the *Patellariaceae*. The hysterothecium, traditionally considered a synapomorphic character state for the *Hysteriaceae*, defines no fewer than four separate lineages outside of the family, as represented by *Hysterographium fraxini*, *Farlowiella*, *Glonium* in the *Gloniaceae*, and the genus *Anteaglonium* in the *Pleosporales*. It can therefore be concluded that the gain and loss of the hysterothecium occurred multiple times within the *Pleosporomycetidae*. In contrast, the conchate, thin-walled, connivent ascomata of the *Mytilinidiales* seems to have evolved only once within the subclass, but then radiated into a number of different spore lineages within the order.

Taxonomic novelties: New species: *Hysterium barrianum*, *Gloniopsis arciformis*. New genera: *Hystumidium*, *Hysterobrevium*. New combinations: *Psiloglonium pusillum*, *P. chambianum*, *P. uspatallense*, *P. sasicola*, *P. ephedrae*, *P. hysterinum*, *P. colihuiae*, *P. araucanum*, *Hystumidium insidens*, *Hst. sinense*, *Hst. pulchrum*, *Hysterobrevium mori*, *Hsb. smilacis*, *Hsb. constrictum*, *Gloniopsis subrugosa*.

Keywords: Hysteriales, Mytilinidiales, 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

and *Myriangiiales* Starbäck 1899 (Schoch *et al.* 2007a). 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, the *Hysteriales* Lindau, the *Mytilinidiales* Boehm, Schoch & Spatafora, the *Botryosphaeriales* Schoch, Crous & Shoemaker, and the *Jahnulales* Pang, Abdel-Wahab, El-Sharouney, E.B.G. Jones & Sivichai. 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. (*Hysteriales*), the *Mytiliniaceae* Kirschst. (*Mytilinidiales*), and within the reinstated family *Gloniaceae* (Corda) Boehm, Schoch & Spatafora (*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, hysteriaceous 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 hysteriaceous 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 hysteriaceous fungi into the Phaeosporii and the Hyalosporii. Saccardo (1873) initially followed Fries, but later (1874) placed hysteriaceous 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 Hönel 1918; Massee 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* Lindau 1897, closely related to the *Pleosporales* Luttrell ex M.E. Barr (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 hysteriaceous fungi be divided into two sections, the *Hystériées* and the *Lophiées*, the latter to accommodate mytilinioid 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, mytilinioid fungi. Barr (1990a) made the argument for retention of the earlier name *Mytiliniaceae* Kirschst. 1924 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 *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). 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., previously in the *Hysteriaceae*, 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 &

Spatofora 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 a highly monophyletic *Mytiliniaceae*, adjacent to the *Gloniaceae*, for which was proposed the *Mytiliniales* 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. First and foremost is the inclusion of *Ostreichnion* within the *Hysteriaceae*. Unlike the most members of the family, the peridium in *Ostreichnion* is sclerenchymatoid and thin-walled, defining a fragile mytilinidioid 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 mytilinidioid 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*.

Furthermore, recent molecular data (Boehm *et al.* 2009; Mugambi & Huhndorf 2010) indicate that the hysterothecium defines no fewer than four separate evolutionary lineages outside of the family, as represented by: (1) the type species of the genus *Hysterographium*, *Hg. fraxini* (Pers. : Fr.) De Not., (2) *Farlowiella*, (3) *Glodium* in the *Gloniaceae*, and (4) the new genus *Anteaglonium* Mugambi & Huhndorf in the *Pleosporales*. These studies were based on a high taxon sampling, including multiple isolates from diverse geographical sources. It can therefore be concluded that the gain and loss of the hysterothecium has occurred multiple times within the *Pleosporomycetidae*. As such, character states relating to the hysterothecium (e.g., ascotal type, peridial wall thickness, cellular pseudoparaphyses *versus* trabeculae, etc.), previously considered to represent synapomorphies among these fungi, in fact, represent symplesiomorphies, and most likely have arisen multiple times through convergent evolutionary processes in response to common selective pressures (Boehm *et al.* 2009). The taxonomy of the *Hysteriaceae* is therefore currently in a state of flux, as molecular data have

only recently been obtained for a handful of species (Boehm *et al.* 2009; Mugambi & Huhndorf 2010; Schoch *et al.* 2007a).

In an effort to facilitate species identification, a number of dichotomous keys are presented in the current study. These build on the original keys first outlined by Zogg (1962), expanding on 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 taxonomic changes brought about by DNA and amino acid sequencing studies (Boehm *et al.* 2009; Mugambi & Huhndorf 2010; Schoch *et al.* 2007a), as well as take into account variation in ascospore measurements as presented by different authors, including 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 ascospores 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, totaling 102, 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 following classical genera: *Hysterium* (16/7), *Hysterographium* (15/4), *Gloniopsis* (8/2), *Psilogonium* (11/3), *Anteaglonium* (10/4), *Rhytidhysterium* (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). 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 & fRPB2-7cR. 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*, molecular data presented here (Fig. 1) and elsewhere (Boehm *et al.* 2009), indicate that the *Mytiliniaceae* forms a highly monophyletic assemblage of species within the *Pleosporomycetidae*, distant from the *Hysteriales*, for which was proposed the *Mytiliniales* (Boehm *et al.* 2009). We conclude that the conchate fruitbody configuration which characterizes the order has only evolved once within the *Pleosporomycetidae*, but subsequently radiated into a number of different lineages as defined by divergent spore morphologies.

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 *Hysteroglyphium 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* E.W.A. Boehm & C.L. Schoch, *gen. nov.*, with the new combinations *Hsb. mori* (Schwein.) Boehm & Schoch (Fig. 3C-F), *Hsb. constrictum* (N. Amano) Boehm & Schoch (Fig. 3A), and *Hsb. smilacis* (Schwein. : Fr.) Boehm & Schoch (Fig. 3B).

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. 6A), *P. clavispurum* (Seaver) Boehm, Schoch & Spatafora (Fig. 6B), and *P. araucanum* (Speg.) Boehm & Schoch (Fig. 6D). In this study, we propose a number of new combinations for the genus *Psiloglonium*, with *P. lineare* (Fr.) Petrak (Fig. 6C) as the type, 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. 2A), *H. angustatum* Alb. & Schwein. (Fig. 2B), *H. vermiforme* Masee (Fig. 2C), which have three-septate spores, and *H. barrianum* Boehm, Miller, Huhndorf & Schoch *sp. nov.* (Fig. 2F), 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, are *Ostreichnion sassafras* (Schwein.) M.E. Barr, and *Ostreichnion curtisii* (Duby) M.E. Barr, previously transferred from the *Mytiliniaceae* 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 *Hystumidium* E.W.A. Boehm & C.L. Schoch *gen. nov.*, to accommodate *Hst. insidens* (Schwein.) Boehm & Schoch *comb. nov.* (Fig. 2D) and *Hst. sinense* (Teng) Boehm & Schoch *comb. nov.* (Fig. 2E). Also grouping in Clade D is *Hysteroglyphium pulchrum* Checa, Shoemaker & Umaña. Despite the fact that *Hg. pulchrum* possesses dictyospores, we propose to unite it within *Hystumidium*, as

Hst. 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 also defines the type species for the genus *Gloniopsis*, namely *Glp. praelonga* (Schwein.) Zogg (Fig. 4A-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. 4C-E). An additional species is described in this sub-clade as *Gloniopsis arciformis* Boehm, Mugambi, Huhndorf & Schoch *sp. nov.* (Fig. 4F).

Clade E: This clade is well-supported and highly homogeneous. It defines three species in the genus *Rhytidhysterium* Speg., namely *R. rufulum* (Spreng.) Speg. (Fig. 5D-G), *R. hysterinum* (Duf.) Samuels & E. Müll., and *R. opuntiae* (J.G. Brown) M.E. Barr (Fig. 5C). Taxon sampling included isolates originating from France, Ghana, Kenya and the United States. This clade supports the transference of the genus *Rhytidhysterium* 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., *Hystumidium* and *Hysterobrevium*) and new combinations, to more accurately reflect past speciation events within the *Hysteriaceae*.

Mytiliniaceae

In contrast to the *Hysteriales*, the family *Mytiliniaceae* 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. 7D-F), characterized by phragmospores and scolecospores, two of the four species of *Lophium* Fr. (Fig. 7G), 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 *Mytiliniaceae*, but recently transferred to the *Chaetothiales* 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*.

Gloniaceae

As for the monotypic family *Gloniaceae* (Boehm *et al.* 2009), based on the genus *Glonium*, previously classified within the *Hysteriaceae*, surprisingly, sequence data indicate that it finds close affinity with the *Mytiliniaceae* (Fig. 1). However, the *Gloniaceae* is not included within the *Mytilinidiales*, due to the highly divergent morphology associated with the genus *Glonium* (Fig. 7A-C). 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 *Mytiliniaceae*, 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 biserial, 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).

These character states have served well to define the classical genera, but now are called into question in light of

molecular data presented here and elsewhere (Boehm *et al.* 2009; Mugambi & Huhndorf 2010; Schoch *et al.* 2007a). This requires a radical reappraisal of the phylogenetic integrity of the family, since several genera (e.g., *Hysterium*, *Hystereographium* and *Gloniopsis*), have their members spanning both Groups I and II (Fig. 1). This has necessitated the transference of a number of species previously classified in these genera to two new genera, *Hystumidium* and *Hysterobrevium*. Furthermore, molecular data necessitate that we expand the concept of the family 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*). Lastly, as mentioned previously, a number of genera have been removed from the family (e.g., *Farlowiella*, *Anteaglonium* and *Glonium*), thus indicating that these morphological character states are not confined to the family, and instead represent sympleisiomorphies.

Some authors have included a number of additional genera within the *Hysteriaceae*. For instance, the genera *Hysteropatella* Rehm, *Hysterglonium* Rehm ex Lindau, and *Pseudoscypha* J. Reid & Piroz., were tentatively 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. clavispora* (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 membraneous 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 *Glonium circumserpens* (Nyl.) Kantvilas & Coppins, 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).

Despite the fact that a great deal of polyphyly surrounds *Hysterium*, *Hystereographium*, and *Gloniopsis*, taxa belonging to these three genera must still be identified based on morphological grounds. Thus, dichotomous keys are presented here for the *Hysteriaceae*, with the caveat that phylogenetically unrelated taxa share the same key. Likewise, despite their transference from the *Hysteriaceae*, the genera *Farlowiella* and *Glonium* (Boehm *et al.* 2009) and *Anteaglonium* (Mugambi & Huhndorf 2010), are nevertheless included in the key. This is because they typically possess ascomata that have traditionally been referred to as hysterothecia. Conversely, morphologically dissimilar fungi, shown to be phylogenetically related, also share the same key (e.g., *Ostreichnion* and *Rhytidhysterion*).

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 amero-spores, the upper cell pigmented and much larger than the lower, which remains un- or less-pigmented; 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*) 6
4. Ascospores hyaline 5
- 4'. Ascospores pigmented..... **Actidiographium**
5. Didymospores hyaline, borne in solitary or gregarious hysterothecia, rarely associated with a subiculum, not laterally anastomosed to form radiating stellate composites **Psilogonium, Anteaglonium**
 Note: The genus *Anteaglonium* Mugambi & Huhndorf is not a member of the *Hysteriaceae*, but lies within the *Pleosporales* (Mugambi & Huhndorf 2010). **Please try to key out these 2 genera!**
- 5'. 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).
6. Ascospores transversely septate phragmospores, or if with dictyospores then also with red pigmentation 7
- 6'. Ascospores transversely and longitudinally septate dictyospores, or very large didymospores (*O. curtisii*) 9
7. Ascospores hyaline phragmospores **Gloniella**
- 7'. Ascospores pigmented phragmospores or in one case (*Hst. pulchrum*) with pigmented dictyospores and red pigmentation in the hamathecium 8
8. Phragmospores three-septate or rarely more, but without swollen supra-median cell(s) **Hysterium**
- 8'. Phragmospores with swollen supra-median cell, usually more than 3-septate, in one case with pigmented dictyospores and red centrum pigmentation (*Hst. pulchrum*) **Hystumidium**
9. Dictyospores hyaline, +/- gelatinous sheath, or pigmented, but short, less than 25 µm in length **Hystero brevium**
- 9'. Dictyospores hyaline, +/- gelatinous sheath, or pigmented, but longer than 25 µm, or very large didymospores (*Ostreichnion curtisii*) 10
10. 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**
- 10'. 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*) 11
11. Dictyospores pigmented, borne in typical hysterothecia, that are erumpent or sessile on the substrate **Hystero graphium**
 Note: The genus *Hystero graphium*, 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 *Hystero graphium*, remaining within the *Hysteriaceae*, for which sequence data are lacking, are provisionally retained within the genus.

11'. *Hysterothecia* borne within the substrate, hardly erumpent, with cristate longitudinal apex instead of a sulcus; neotropical (Brazil), on *Eucalyptus* ***Hysteroarina***

11". 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. 2A), and its closely related concolorous counterpart, *H. angustatum* Alb. & Schwein. (Fig. 2B), both extremely common in the temperate zones of both hemispheres. These are followed by *H. vermiforme* Masee (Fig. 2C), 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., suprmedian) or, rarely, some distance up from the median septum. Type II includes, by increasing spore length, the cosmopolitan *H. insidens* Schwein. (Fig. 2D), the larger-spored counterpart *H. sinense* Teng (Fig. 2E), 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 has placed this taxon in the *Mytiliniaceae*, as

Mytilinidion andinense (Messuti & Lorenzo) Boehm, Schoch & Spatafora (Boehm *et al.* 2009). 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 MBXXXX, Fig. 2F.

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 μ m longa, 250-450 μ m alta, 200-300 μ m lata. Pseudoparaphyses hyalinae, cellulares, 1-2 μ m latae, supra ascos ramosae epithecium formantes. Asci bitunicati, cylindrici, breviter stipitati, (110-)125-135 x 15-20 μ m. 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) μ m.

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 μ m high, 200-300 μ m wide. Pseudoparaphyses hyaline, cellular, 1-2 μ m wide, branched above the ascal layer to form an epithecium. Asci bitunicate, cylindrical, short-stipitate, (110-)125-135 x 15-20 μ m (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) μ m 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. Promptutha, M. Grief, G. K. Mugambi & P. Chaudhary (ANM 1442, deposited in **BPI XXXX**).

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 November 2007, A. N. Miller, S. M. Huhndorf, J. L. Crane, T.J. Atkinson, I. Promputtha, M. Grief, G. K. Mugambi, & P. Chaudhary (ANM 1495; **BPI XXXX**).

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. 2F) have a similar number of septa, (7–)9(–11), as those of *H. sinense* (Fig. 2E), 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. 2B), originating from South Africa (CMW 20409), Kenya (GKM 243A), New Zealand (SMH 5211, SMH 5216) and the United States (CBS 123334, CBS 236.34, ANM 85) form a highly supported monophyletic clade with *H. pulicare* (Fig. 2A), collected from New York, USA (CBS 123377). 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.

Grouping with the anomalous *H. angustatum* ANM 85, was *H. vermiforme* (Fig. 2C), 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 *Hystumidium* E.W.A. Boehm & C.L. Schoch

Hystumidium E.W.A. Boehm & C.L. Schoch, *gen. nov.*, MycoBank **MBXXXX**.

Typus: *Hystumidium insidens* (Schwein.) Boehm & Schoch, *comb. nov.*
Basionym: *Hysterium insidens* Schwein., *Trans. Amer. philos. Soc.*, New Series 4(2): 244 (1832).

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. Ascosporae 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: *Hys-* from *Hysterium*, Latin *tumidus* swollen, referring to the swollen central cells of the ascospores.

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., *Hst. insidens*), othertimes wider than tall (e.g. *Hst. 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 biseriate in ascus, typically phragmospores, in one case dictyospores, asymmetric, 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.

Hystumidium insidens (Schwein.) Boehm & Schoch, *comb. nov.*, MycoBank MBXXXX, Fig. 2D.

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 ascus layer. Asci cylindrical, 8-spored, irregularly biseriate, 130–150 x 15–24 μm . Phragmospores transversely (4–)6–8 (–11[rarely]) septate, constricted at the median septum, asymmetric, 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.

Hystumidium sinense (Teng) Boehm & Schoch, *comb. nov.*, MycoBank MBXXXX, Fig. 2E.

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 *Hst. insidens*, that is, scattered to subgregarious, linear, parallel but non-confluent laterally, and striated in age, of a similar size. Pseudoparaphyses as in *Hst. insidens*. Asci 140–170 x 26–30 μm , short-stipitate, spores biseriate to subseriate 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 *Hystumidium* 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 *Hst. sinense* (Fig. 2E), one from South Africa (CBS 123345), and one from the United

States, New Jersey (EB 0339), cluster with two isolates of *Hst. insidens* (Fig. 2D), 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 *Hystumidium*. An additional new combination is proposed below.

Hystumidium pulchrum (Checa, Shoemaker & Umaña) Boehm & Schoch, *comb. nov.*, MycoBank MBXXXX.

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 *Hystumidium*, as *Hst. pulchrum*. This is because molecular data indicate a close association with the two species of *Hystumidium*, *Hst. insidens* and *Hst. 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, asymmetric, slightly

curved and fusiform, with a common number of transverse septa. The sole difference is the presence of one or two vertical septa in *Hst. pulchrum*, a feature noted by the authors to be absent in some spores (Checa *et al.* 2007). Most importantly, like *Hst. insidens* and *Hst. sinense*, *Hst. pulchrum* also possesses a swollen supra-median cell. Interestingly, a striking resemblance to the phragmospores of *Hst. insidens* can be seen for those spores of *Hst. pulchrum* that do not possess vertical septa (Checa *et al.* 2007). This is based on similarities in shape (e.g., asymmetric, 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 cross septa [(4–) 6 to 8 (–11[rarely]) *versus* (5–) 6], for *Hst. insidens* and *Hst. pulchrum*, respectively. As molecular data indicate that the presence or absence of vertical septa should be considered a sympleiomorphic character state within the *Hysteriaceae* (Boehm *et al.* 2009), we feel justified in including both phragmospores and dictyospores within the genus *Hystumidium*.

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

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

1. Phragmospores mainly three-septate 2
 - 1'. Phragmospores concolorous, more than three-septate, in one instance pigmented dictyospores with 1-2 vertical septa (*Hst. 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 (*Hystumidium*) 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) *Hst. 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 *Hst. 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 *Hst. 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	<i>Gl. corticola</i>
2'. Ascospores 12–14 x 4–5 µm; on <i>Typha</i> , Europe	<i>Gl. typhae</i>
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 <i>Adiantum</i> , Europe	<i>Gl. adianti</i>
4'. Ascospores (3–)5(–7)-septate, slightly longer	5
5. Ascospores (3–)5-septate, (15–)18–20(–22) x 4–5 µm; on <i>Pteridium</i> , Europe	<i>Gl. graphidoidea</i>
5'. Ascospores 5–7-septate, (22–)25–27(–30) x 3–4 µm; on <i>Pteridium</i> , Europe	<i>Gl. normandina</i>
6. Ascospores 1–3-septate, 36–39 x 10 µm; on <i>Arctostaphylos</i> , Washington, USA	<i>Gl. lapponica</i>
6'. Ascospores with more septa	7
7. Ascospores (6–)7(–8)-septate, (16–)18–21(–26) x 6–7(–8) µm; on <i>Populus</i> , Europe	<i>Gl. sardoa</i>
7'. Ascospores larger	8
8. Ascospores (5–)6(–8)-septate, (18–)37(–41) x 10–11.5 µm, hyaline, smooth; on <i>Avicennia marina</i> , South Africa	<i>Gl. clavatispora</i>
8'. Ascospores 6–7-septate, 32–37(–40) x 4–6 µm; on wood, Costa Rica	<i>Gl. gracilis</i>
8". Ascospores (5–)6–7-septate, (28–)32–38(–44) x (3–)4–8(–9) µm; on <i>Bambusa</i> , Brazil	<i>Gl. bambusae</i>

4. The genus *Hysterographium* Corda Icon. Fung. 5: 34 (1842).

Hysterobrevium Speg. 1906

Polhysterium Speg. 1912

Fragosoa Cif., in Ciferri & Fragoso 1926

The nomenclatural history of the genus *Hysterographium* was presented in Boehm *et al.* (2009). The genus is characterized by pigmented asymmetric 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. 5B), the type species, and *Hg. flexuosum* (Schwein. : Fr.) Sacc. (Fig. 5A), 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, possessing the smallest spores in the genus (Amano 1983), *Hg. spinicola* Doidge from S. 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 *Hystumidium*, as *Hst. 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 *Hst. 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. 5B), 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), currently recognized as *gen. incertae sedis* (Boehm *et al.* 2009). 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*. 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* (= *Hst. 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.

5. The genus *Hysterobrevium* E.W.A. Boehm & C.L. Schoch

Hysterobrevium E.W.A. Boehm & C.L. Schoch, *gen. nov.*, MycoBank MBXXXX.

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

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

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

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) cross 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 MBXXXX, Fig. 3C-F.

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

Synonym: *Hysterographium mori* (Schwein.) Rehm, Ascomyc. Faslcl. 7, no. 26; Ber. Nat. Hist. Verein Augsburg 26: 76 (1881).

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

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

≡ *Hysterographium roussellii* (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 zizyphi* Pat., Cat. Rais. Pl. Cell. Tunisie: 112 (1897) (as *'zizyphi'*).

= *Hysterographium roussellii* 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, asymmetric dictyospores, obovoid, ends obtuse, 3–(5–7) septate, with one to two vertical septa, usually associated with mid-cells, but on occasion also present obliquely in end cells, constricted at the median septum, (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 MBXXXX, Fig. 3B.

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 bifformis* (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. 3C–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, CBS 123564), New York (CBS 123335, CBS 123563), Indiana (SMH 5273; Fig. 3C) 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), Sweden (CBS 114601), and Kenya (GKM 426N, Fig. 3B). 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, *Hsb. smilacis* appears to be the hyaline counterpart to the pigmented *Hsb. mori* and is itself far removed from the type species of *Gloniopsis*, namely *Glp. praelonga* (Schwein.) Zogg (Fig. 4A–B), in Clade D. 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. 3F), it is significant. Spore measurements of the Kenyan accession GKM 1013 in Clade D (Fig. 3F) *versus* those of other *Hsb. mori* accessions in Clade A, represented by specimens from the United States, namely Indiana (SMH 5273 [Fig. 3C]), 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 additional cryptic species within the taxon. We propose an additional new combination below.

Hysterobrevium constrictum (N. Amano) Boehm & Schoch, *comb. nov.*, MycoBank MBXXXX, Fig. 3A.

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. 3A) 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. constricta* to (11–)13–20(–23) x 5–12 µm, rather than describe a new species.

6. 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 yellowish dictyospores, often inequilateral or curved, in outline obovoid, ends obtuse to sub-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. 4A-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*. Recently, *Glp. argentinensis* Speg., previously considered by Zogg (1962) as a doubtful species, was reinstated by Lorenzo & Messuti (1998). Lastly, Amano (1983) described an additional two species of *Gloniopsis* from Japan, namely *Glp. macrospora* N. Amano and *Glp. constrictum* N. Amano (Fig. 3A), the latter is here transferred to *Hysterobrevium*.

Molecular data indicate that the genus *Gloniopsis* is polyphyletic, with the type, *Glp. praelonga*, belonging to Clade D in Group II. This is based on a number of isolates from South Africa and the United States (Table 1). Closely associated with the type are multiple isolates of *Hysterographium subrugosa* (Cooke & Ellis) Sacc. Thus, based on molecular data presented here, we propose to redefine the genus *Gloniopsis*, to include both hyaline and pigmented dictyospores. The following new combination is proposed, as well as a new species.

Gloniopsis subrugosa (Cooke & Ellis) Boehm & Schoch, *comb. nov.*, MycoBank MBXXXX, Fig. 4C-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 cylindrosporum* 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) × (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 × 1 µm; conidia 2–2.5 × 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, CMW 19983), and one from New Jersey, USA (CBS 123337; Fig. 4A-B). These isolates belong to Clade D in Group II and are closely associated with *Glp. subrugosa*, based on isolates from South Africa (CBS 123346; Fig. 4C), Kenya (GKM 1214; Fig. 4D), and Cuba (SMH 557; Fig. 4E). Both *Glp. subrugosa* and *Glp. praelonga* are similar in the shape, size and septation of the dictyospores, pigmented in the former, hyaline in the latter. The spores of *Glp. subrugosa* measure (22–)25–34(–45) × (6–)8–12(–17) µm, whereas those of *Glp. praelonga* are (16–)20–32(–34) × (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. Thus, *Glp. praelonga* (Fig. 4A-B) is considered to be the hyaline counterpart to *Glp. subrugosa* (Fig. 4C-E), analogous to the situation in Clade A (Group I), where *Hsb. smilacis* (Fig. 3B) was associated with *Hsb. mori* (Fig. C-F). An additional new species of *Gloniopsis* is described below.

Gloniopsis arciformis Boehm, Mugambi, Huhndorf & Schoch, *sp. nov.*, MycoBank MBXXXX, Fig. 4F.

Hysterothecia solitaria vel pauca aggregata, recta vel flexuosa, carbonacea, plerumque erecta, conspicue applanata 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 dictyospores.

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 dictyospores 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.

Notes: *Gloniopsis arciformis* is represented by a single specimen (GKM L166A; Fig. 4F) 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 dictyospores. *Glp. arciformis* resides in Clade D, Group II, within the *Hysteriaceae*, and is phylogenetically closely associated with multiple isolates of *Glp. subrugosa* and *Glp. praelonga*. These three taxa form a sub-clade within Clade D, adjacent to the other subclade containing *Hystumidium* (Fig. 1). Interestingly, the arcuate spores of *Glp. arciformis* (Fig. 4F) closely resemble those found in *R. rufulum* in outline (Fig. 5D), the genus *Rhytidhysterion* being adjacent in Clade E, a feature not found among other members of the *Hysteriaceae*.

Holotype: Kenya, Coast Province, Malindi District, Arabuko-Sokoke National Park, 4 January 2008, G.K. Mugambi (GKM L166A, deposited as BPI XXXX).

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 restructuring of *Gloniopsis* to now include both hyaline (*Glp. praelonga*) and pigmented (*Glp. subrugosa* and *Glp. arciformis*) dictyospores, in Clade D; (3) the inclusion of a pigmented dictyospored species previously classified in *Hysterographium* in the new genus *Hystumidium*, as *Hst. pulchrum*, 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 5
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, 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***
- 3'. Dictyospores longer, much more asymmetric in outline and septation, thinner-walled, pigmented or hyaline 4
4. Dictyospores hyaline, 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***
- 4'. Dictyospores pigmented, thin-walled, asymmetrical, obovoid, with obtuse ends, 3–(5–7)-septate, with one to two vertical septa, usually associated with the mid-cells, but on occasion also present obliquely in the end-cells, constricted at the median septum, (12–)14–22(–26) x (5–)7–10(–11) µm; highly variable and cosmopolitan ***Hsb. mori***
5. Red pigment present in hamathecium and/or centrum; dictyospores pigmented 6
- 5'. No red pigment present 7
6. 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) ***Hst. pulchrum***
Note: *Hst. pulchrum* is accommodated in the genus *Hystumidium* and is present in both keys.
- 6'. 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***
7. Dictyospores hyaline or tardily pigmented 8
- 7'. Dictyospores pigmented in the ascus 9
8. Dictyospores hyaline, yellowish in age, obovoid, ends obtuse, 5–7(–10)-septate, with 2–3 longitudinal septa, constricted at the median and often other septa, (16–)20–32(–34) x (6–)9–12(–15) µm; cosmopolitan ***Glp. praelonga***
- 8'. Ascospores 7-septate, with 1–3(–4) longitudinal septa, some passing through multiple cells, outline widely ellipsoid; 20–26 x 9–12 µm; Argentina ***Glp. argentinensis***

- 8". 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***
9. Dictyospores pigmented, 25–38 μm long 10
- 8'. Dictyospores pigmented 30–45 long or more 11
10. Dictyospores (22–)25–34(–45) x (6–)8–12(–17) μm , mostly with 7–11 transverse and 1–2 vertical septa; cosmopolitan ***Glp. subrugosa***
- 10'. Dictyospores 26–38 x 10–15 μm , with 6–13 transverse and 1–3 vertical septa, obovoid, ends obtuse; Japan ***Hg. minus***
11. 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 fraxini*, 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).
- 11'. 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***

5. The genus *Psiloglonium* Höhn.

Ann. Mycol. 16: 145 (1918)

A discussion of the genus *Psiloglonium* (von Höhnel 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 Höhnel (1918) and Petrak (1923 a, b), a position accepted by most modern authors (e.g., Lohman 1932a, 1937; Lorenzo & Messuti 1998; Luttrell 1973; Messuti & Lorenzo 2007; von Arx & Müller 1975). Both *Psiloglonium* and *Glonium* possess hyaline to yellowish 1-septate, asymmetric didymospores, +/- constricted at the septum, with obtuse or acuminate ends, typically with cells unequal in size, borne in hysterothecia.

Von Höhnel (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 Höhnel (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* as the type species for the genus *Glonium sensu* von Höhnel (1918). Petrak (1923a, b) eventually placed a number of non-subiculate 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), however, was the only modern author to retain the genus *Psiloglonium*, as distinct from the subiculate *Glonium*.

The presence or absence of subicula is complicated. Although von Höhnel (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 on occasion 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 the genus *Glonium*.

Although Zogg (1962) did not support the genus *Psiloglonium*, he did in fact recognize three distinct morphological types within his concept of *Glonium*, two of which (Types I and II) we incorporate to *Psiloglonium*, the third (Type III) comprising the type species and 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 hysterothecia 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 members of 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 *Mytilinidiaceae*, now in the *Hysteriaceae* (Boehm *et al.* 2009). A sixth species, *G. finkii* (Petra) Lohman, was considered in Type I 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.) Petra (Fig. 6C) was previously reinstated within the *Hysteriaceae*, listing *G. lineare* as a synonym (Boehm *et al.* 2009). Here we also reinstate *Psiloglonium finkii* Petra. An additional two species are included in Type I, namely *G. clavisorum* 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 clavisorum* (Seaver) Boehm, Schoch & Spatafora (Fig. 6B) and *P. simulans* (W.R. Gerard) Boehm, Schoch & Spatafora (Fig. 6A).

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 for *G. macrosporum* are 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 *G. simulans* W.R. Gerard (1876), as *P. simulans* (W.R. Gerard) Boehm, Schoch & Spatafora.

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. uspatallense* Speg., species previously considered by Zogg (1962) to represent doubtful species. *G. chilense* is described as having hyaline didymospores measuring 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 ascomatal and spore measurements as *P. simulans*, the latter with spores measuring (10–)14–16(–18) x (4.5–)5–6 μm (Lohman 1937). We therefore synonymize *G. chilense* with the earlier name *G. simulans*, as *P. simulans* (W.R. Gerard) Boehm, Schoch & Spatafora. For *G. uspatallense*, 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. 6F) and the related species *A. globosum* Mugambi & Huhndorf (Fig. 6G), *A. parvulum* (W.R. Gerard) Mugambi & Huhndorf (Fig. 6H), 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 asymmetric 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 Spegazzini's earlier type of *G. araucanum* from Chile.

Type III: This type corresponds to von Höhnel's (1918) and Petra'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. 7A), *G. compactum* Kern, and *G. graphicum* (Fries) Duby. Zogg (1962) 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. *Glonium graphicum* (Fries) Duby, was noted as variably associated with subicula. Recently, a fourth species was added, based on molecular evidence (Boehm *et al.* 2009), namely *G. circumserpens* (Nyl.) Kantvilas & Coppins (Fig. 7B–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 (Clade B, Group I) within the *Hysteriaceae* (Fig. 1). These include *P. clavisporum* (Fig. 6B), with isolates from the United States (CBS 123340, CBS 123339, CBS 123341, CBS 123338), and Kenya (GKM 344A, GKM L172A), *P. simulans* (Fig. 6A), from the United States (CBS 206.34, ANM 1557), and *P. araucanum* (Fig. 6D), from South Africa (CMW 18760, CBS 112412, CMW 17941). A second lineage has recently been shown to be associated with the *Pleosporales*, now accommodated in *Anteaglonium* (Fig. 6F–I) by Mugambi & Huhndorf (2010). The third clade corresponds to *Glonium* (Fig. 7A–C), in the *Gloniaceae* (Boehm *et al.* 2009).

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 MBXXXX.

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 MBXXXX, Fig. 6E.

Basionym: *Gonium 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. 6E) possesses larger spores than *P. lineare* (Fig. 6C), *P. simulans* (Fig. 6A), and *P. clavisporum* (Fig. 6B), but smaller than *P. uspatallense*.

Psiloglonium uspatallense (Speg.) Boehm & Schoch, *comb. nov.*, MycoBank MBXXXX.

Basionym: *Glonium uspatallense* 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 uspatallense* 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*.

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

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. uspatallense* and *P. ephedrae*. Amano (1983) further reported that ascospores of this species are associated with a gelatinous sheath, previously not known among these didymospored fungi.

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

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 MBXXXX.

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 MBXXXX.

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 MBXXXX, Fig. 6D.

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

= *Gloniella caucasica* 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 caucasica* Rehm to *Glonium*. Here we transfer *G.*

araucanum to *Psiloglonium* (Fig. 6D). 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. clavisorum* 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. clavisorum*). 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: <i>A. abbreviatum</i> (Schwein.) Mugambi & Huhndorf lies within the <i>Pleosporales</i> (Mugambi & Huhndorf 2010).	
4'. Ascospores as in <i>A. abbreviatum</i> , but hysterothecia with rounded ends, with pointed apices, and not associated with a dark crust; no KOH-soluble pigments	A. parvulum
Note: <i>A. parvulum</i> (W.R. Gerard) Mugambi & Huhndorf lies within the <i>Pleosporales</i> (Mugambi & Huhndorf 2010).	
4". Ascospores as in <i>A. abbreviatum</i> and <i>A. parvulum</i> , 6-7 x 2-3 µm long; hysterothecia globose with roughened walls and indistinct slit, associated with a dark crust on the substratum and sparse, short subicula, also with short tomentum on the walls of the ascomata; producing green soluble pigments in KOH	A. globosum
Note: <i>A. globosum</i> Mugambi & Huhndorf lies within the <i>Pleosporales</i> (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; <i>Sporidesmium stygium</i> 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. uspatallense
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**

6. 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.

7. 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 *Hysterothecium*, 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.

8. 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 *Hysterographium 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***

9. 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. 5E), somewhat resembling those found in the *Hysteriaceae*, then later opening by a longitudinal sulcus to become irregularly apothecoid at maturity, often with incurved margins (Fig. 5F-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. 5E), 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. 5D-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. 5C) and *Hsb. mori* (Fig. 3C-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. 5C). 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 *Rhytidhysteron* 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 *Rhytidhysteron* 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 clavispota* (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 Kirschst. 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* Kirschst. (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*, 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*, *Camaroglobulus*, *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, cylindric, 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 *Mytilinidiales*, 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, slightly asymmetric 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. baccharinii* (Paoli) Zogg and *A. pulchrum* (Teng) Zogg, all on *Pinaceae*. Due to similarities in ascospore morphology, the genus *Actidium* may have affinities with other didymospored 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. baccharinii***
- 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 closely resemble. Again, this suggests that the evolution of the conchate fruitbody configuration evolved only once within the *Pleosporomycetidae*, but then radiated fairly rapidly into a number of different spore morphologies within the *Mytilinidiales*.

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 globose 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. resiniae* Speer, *M. decipiens* (P. Karst.) Sacc., *M. tortile* (Schwein.) Ellis & Everhart (Fig. 7D), 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. 7E), *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. 7F). These last three scolecosporous species were postulated to form a transitional series to connect *Mytilinidion* with the heretofore somewhat isolated genus *Lophium* (Fig. 7G), 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 *Mytilinidiaceae*. 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. Ascospores 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'. Ascospores 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, unconstricted, 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. 7G), 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) 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 *Zoggiium 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).

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 ascumata, 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 ascumata, 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.

6. The genus *Ostreola* Darker

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

Barr (1975, 1990a) recognized two genera with muriform ascospores in the *Mytilinidiaceae*, namely *Ostrechnion* 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 *Ostrechnion* 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.

Key to the species of *Ostreola*

1. Ascumata on coniferous hosts; North America, Europe 2
- 1'. Ascumata on non-coniferous hosts; India 3
2. Base of ascumata 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 ascumata 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**

Gloniaceae (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 *Gloniaceae* 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 Höhnelt (1918) and then by Petrak (1923a). We feel justified in reinstating the *Gloniaceae* 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

Psilogonium (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. 7A), 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 biseriate; 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

Gloniaceae. These are the type species *G. stellatum* Muhl. : Fr. (Fig. 7A), *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. 7B-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***

Pleosporomycetidae genera incertae sedis

The genus *Farlowiella* Sacc.

Syll. Fung. 9: 1101 (1891).

Farlowia Sacc. 1883

The genus *Farlowiella* 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 *Mytilinidiaceae* (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

Synapomorphic character states traditionally used to delineate higher taxa within the *Hysteriaceae* have relied primarily on spore septation and pigmentation (Zogg 1962). However, data presented here clearly demonstrate that spore morphology is homoplasious, and therefore a poor indicator of genetic relatedness. 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. To achieve a natural phylogeny, one based on molecular data, required that we break-up what were once thought of as stable genera. Thus, two species of *Hysterium* were transferred to *Hystumidium* (*Hst. insidens* and *Hst. 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 in the family, here transferred to *Hystumidium* (*Hst. pulchrum*), *Hysterobrevium* (*Hsb. mori*) and *Gloniopsis* (*Glp. subrugosa*). 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, to *Anteaglonium* in the *Pleosporales* (Mugambi & Huhndorf 2010). Lastly, the genera *Rhytidhysterion* and *Ostreichion* were included in the *Hysteriaceae* (Boehm *et al.* 2009). These taxonomic changes were unexpected, as they were not premised on past assumptions of synapomorphy based on spore morphology, or, in the case of the last two genera, of fruitbody morphology. Although we have included here a total of 58 isolates, representing 20 species in seven genera, for the *Hysteriaceae*, and another 69 isolates 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 also long been considered a synapomorphic character state. However, data indicate that this type of ascromata has evolved convergently no less than five times within the *Pleosporomycetidae*: *Farlowiella*, *Glonium*, *Anteaglonium*, and *Hysterographium* all reside outside of the *Hysteriaceae*. The hysterothecium must confer some degree of selective advantage, as evidenced by its repeated evolution. One advantage 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 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.

ACKNOWLEDGMENTS

The first author wishes to acknowledge early encouragement for this study from the late Dr Margaret Barr, to whom this manuscript is dedicated. The authors also wish to thank Eunice Nkansah (Kean University, Union NJ), Guy Marson (Division of Mycology, Museum of Natural History, Luxembourg), Geir Mathiassen (Tromsø Museum, Universitetsmuseet Fagenhet for Botanikk, Tromsø, Norway), Alain Gardiennet (Veronnes, France), Gintaras Kantvilas (Tasmanian Herbarium, Hobart, Tasmania), Marieka Gryzenhout (Dept. Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, South Africa), Maria Inéz Messuti and Laura Emma Lorenzo (Departamento de Botanica, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Quintral, Bariloche, Rio Negro, Argentina), and Meredith Blackwell (Dept. Biological Sciences, Louisiana State University, Baton

Rouge, Louisiana) for kindly supplying some of the isolates used in this study. The authors also wish to thank Walter Gams (Baarn, the Netherlands) for the Latin translations, and for his numerous helpful insights into the taxonomic and nomenclatural issues raised by this work. We also wish to acknowledge Gary Samuels (USDA, Agriculture Research Service, Systematic Mycology and Microbiology Lab, Beltsville, MD), and Scott Redhead (National Mycological Herbarium, Agriculture and Agri-Food Canada, Ottawa, Canada) who both provided thorough pre-reviews of the manuscript prior to submission. The first author wishes to acknowledge support from the Kean University Faculty Foundation Research Awards, and the National Science Foundation (NSF) Major Research Instrumentation (MRI) Grant DBI 0922603 issued to the first author. The last author (CLS) also acknowledges funding support from the NSF through a grant DEB 0717476.

REFERENCES

- Amano N (1983). Saprobic loculoascomycetous fungi from Japan 1. Hysteriaceous fungi. *Transactions of the Mycological Society of Japan* **24**: 283-297.
- Arx JA von, Müller E (1954). Die Gattungen der amerosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* **11**(1): 1-434.
- Arx JA von, Müller E (1975). A re-evaluation of the bitunicate Ascomycetes with keys to families and genera. *Studies in Mycology* **9**: 1-159.
- Barr ME (1975). The genus *Ostreichnion*. *Mycotaxon* **3**: 81-88.
- Barr ME (1979). A classification of loculoascomycetes. *Mycologia* **71**: 935-957.
- Barr ME (1983). The ascomycete connection. *Mycologia* **75**: 1-13.
- Barr ME (1987). *Prodromus to class Loculoascomycetes*. Hamilton I. Newell, Inc., Amherst, Massachusetts: M.E. Barr Bigelow. 168 p.
- Barr ME (1990a). *Melanommatales* (Loculoascomycetes). *North American Flora*, Series II, Part **13**: 1-129.
- Barr ME (1990b). Some dictyosporous genera and species of Pleosporales in North America. *Memoirs of the New York Botanical Garden* **62**: 1-92.
- Barr ME (2009). A Nomenclator of Loculoascomycetous Fungi from the Pacific Northwest. *North American Fungi* **4**(1): 1-94.
- Barr ME, Blackwell M (1980). A new genus in the *Lophiaceae*. *Mycologia* **72**: 1224-1227.
- Barr ME, Huhndorf SM (2001). *Loculoascomycetes*. Chapter 13, In: *The Mycota, Systematics and Evolution, Part A. VII*. McLaughlin, McLaughlin, Lemke Eds. Springer. pp. **need chapter pages!**
- Bezerra JL, Kimbrough JW (1981). Culture and cytological development of *Rhynchostyrium rufulum* on citrus. *Canadian Journal of Botany* **60**: 568-579.
- Bisby GR (1923). The literature on the classification of the *Hysteriales*. *Transactions of the British Mycological Society* **8**: 176-189.
- Bisby GR (1932). Type specimens of certain *Hysteriales*. *Mycologia* **24**: 304-329.
- Blackwell M, Gilbertson RL (1985). *Quasiconcha reticulata* and its anamorph from conifer roots. *Mycologia* **77**: 50-54.
- Boehm EWA, Schoch CL, Spatafora JW (2009). On the evolution of the *Hysteriaceae* and *Mytiliniaceae* (*Pleosporomycetidae*, *Dothideomycetes*, *Ascomycota*) using four nuclear genes. *Mycological Research* **113**: 461-479.
- Cappitelli F, Nosanchuk JD, Casadevall A, Toniolo L, Brusetti L, Florio S, Principi P, Borin S, Sorlini C (2007). Synthetic consolidants attacked by melanin-producing fungi: Case study of the biodeterioration of Milan (Italy) cathedral marble treated with acrylics. *Applied Environmental Microbiology* **73**: 271-277.
- Cash E (1939). Two species of *Hysteriales* on *Smilax*. *Mycologia* **31**: 289-296.
- Checa J, Shoemaker RA, Umaña L (2007). Some new hysteriaceous fungi from Costa Rica. *Mycologia* **99**: 285-290.
- Chevallier FF (1826). *Flore générale des environs de Paris*, Vol I.
- Chlebicki A, Knudsen H (2001). Dryadicolous microfungi from Greenland. I. List of species. *Acta Societatis Botanicorum Poloniae* **70**: 291-301.
- Clements FE (1909). *The Genera of Fungi*. HW Wilson Co., Minneapolis, MN. 227 p.
- Clements FE, Shear CL (1931). *The Genera of Fungi*. HW Wilson Co., NY. 496 p.

- Corda ACJ (1842). Abbildungen der Pilze und Schwaemme. *Icones Fungorum, Hucusque Cognitorum* **5**: 34.
- Darker GD (1963). A new genus of the *Lophiaceae*. *Canadian Journal of Botany* **41**: 1383-1388.
- De Notaris CG (1847). Prime linee di una nuova disposizione dei Pirenomiceti Isterini. *Giornale Botanico Italiano* **2**, part I, fasc. **7-8**: 5-52.
- Dennis RWG (1955). Ascomycetes from Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha (1937-1938)* **36-38**: 1-10.
- Diederich P, Wedin M (2000). The species of *Hemigrapha* (lichenicolous Ascomycetes, Dothideales) on *Peltigerales*. *Nordic Journal of Botany* **20**: 203-214.
- Duby JE (1862). Mémoire sur la tribu des Hystérinées de la famille des Hypoxylées (Pyrénomycètes). *Mémoires de la Société de Physique et Histoire Naturelle de Genève* **16**: 15-70.
- Ellis JB, Everhart BM (1892). *The North American Pyrenomycetes*. Newfield NJ. 793 p.
- Eriksson OE (2006). Outline of Ascomycota. *Myconet* **12**: 1-88.
- Eriksson OE, Hawksworth DL (1991). Notes on ascomycete systematics - Nos 1252-1293. - *Systema Ascomycetum* **10**: 135-149.
- Fries EM (1823). *Systema Mycologicum, sistens fungorum ordines, genera et species hucusque cognitae, II, pars II*: 276-620.
- Fries EM (1835). *Corpus florum provincialium Sueciae. I. Floram scanicam scripsit Elias Fries*. pp. 1-192. Uppsala.
- Gäumann EA (1949). *Die Pilze, Grundzüge ihrer Entwicklungsgeschichte und Morphologie*. Birkhäuser. Basel. 382 pp.
- Geiser DM, Gueidan C, Miadlikowska J, Lutzoni F, Kauff F, Hofstetter V, Fraker E, Schoch CL, Tibell L, Untereiner WA, Aptroot A (2007). *Eurotiomycetes: Eurotiomycetidae and Chaetothyriomycetidae*. *Mycologia* **98** (2006): 1053-1064.
- Goh TK, Hyde KD, Tsui KM (1998). The hyphomycete genus *Acrogenospora*, with two new species and two new combinations. *Mycological Research* **102**: 1309-1315.
- Goree H (1974). *Glyphium* in western Canada and United States. *Canadian Journal of Botany* **52**: 1265-1269.
- Hawksworth DL, Eriksson OE (1988). Proposals to conserve 11 family names in the *Ascomycotina* (Fungi). *Taxon* **37**: 190-193.
- Hönel F. von (1918). Mycologische Fragmente, 272. Über die Hysteriaceen. *Annales Mycologici* **16**: 145-154.
- Inderbitzin P, Landvik S, Abdel-Wahab MA, Berbee ML (2001). *Aliquandostipitaceae*, a new family for two new tropical ascomycetes with unusually wide hyphae and dimorphic ascospores. *American Journal of Botany* **88**: 52-61.
- Kantvilas G, Coppins BJ (1997). *Melaspilea circumserpens* Nyl. rediscovered and referred to *Glonium*, with discussion on the provenance of some of Robert Brown's lichen specimens. *Lichenologist* **29**: 525-531.
- Kirk PM, Cannon PF, David JC, Stalpers JA (2001). *Dictionary of the Fungi. 9th Ed.* CAB International. **Use the 2008 Edition!**
- Kirschstein W (1924). Beiträge zur Kenntnis der Ascomyceten. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* **66**: 23-29.
- Kodsueb R, Dhanasekaran V, Aptroot A, Lumyong S, McKenzie EHC, Hyde KD, Jeewon R (2006). The family *Pleosporeaceae*: intergeneric relationships and phylogenetic perspectives based on sequence analyses of partial 28S rDNA. *Mycologia* **98**: 571-583.
- Kutorga E, Hawksworth DL (1997). A reassessment of the genera referred to the family *Patellariaceae* (Ascomycota). *Systema Ascomycetum* **15**: 1-110.
- Lee S, Crous PW (2003). Taxonomy and biodiversity of hysteriaceous ascomycetes in fynbos. *South African Journal of Botany* **69**: 480-488.
- Lindemuth R, Wirtz N, Lumbsch HT (2001). Phylogenetic analysis of nuclear and mitochondrial rDNA sequences supports the view that loculoascomycetes (Ascomycota) are not monophyletic. *Mycological Research* **105**: 1176-1181.
- LoBuglio KF, Berbee ML, Taylor JW (1996). Phylogenetic origins of the asexual mycorrhizal symbiont *Cenococcum geophilum* Fr. and other mycorrhizal fungi among the ascomycetes. *Molecular Phylogenetics and Evolution* **6**: 287-94.
- Lohman ML (1931). A study of *Glonium parvulum* in culture. *Papers of the Michigan Academy of Science Arts & Letters* **13**: 141-156.

- Lohman ML (1932a). The comparative morphology of germinating ascospores in certain species of the *Hysteriaceae*. *Papers of the Michigan Academy of Science Arts & Letters* **15**: 97-111.
- Lohman ML (1932b). Three new species of *Mytilidion* in the proposed subgenus *Lophiopsis*. *Mycologia* **24**: 477-484.
- Lohman ML (1933a). *Hysteriaceae*: Life histories of certain species. *Papers of the Michigan Academy of Science Arts & Letters* **17**: 229-288.
- Lohman ML (1933b). *Septonema toruloideum*: A stage of *Mytilidion scolecosporum*. *Mycologia* **25**: 34-43.
- Lohman ML (1934). A cultural and taxonomic study of *Hysterium hyalinum*. *Papers of the Michigan Academy of Science Arts & Letters* **19**: 133-140.
- Lohman ML (1937). Studies in the genus *Glonium* as represented in the Southeast. *Bulletin of the Torrey Botanical Club* **64**: 57-73.
- Lorenzo LE, Messuti MI (1998). Noteworthy *Hysteriaceae* from southern South America. *Mycological Research* **102**: 1101-1107.
- Lorenzo LE, Messuti MI (2005). *Glyphium elatum* (Ascomycota) in Patagonia (Argentina). *Boletín de la Sociedad Argentina de Botánica* **40**(1-2): 13-16.
- Lücking R, Stuart BL, Lumbsch HT (2004). Phylogenetic relationships of *Gomphillaceae* and *Asterothyriaceae*: evidence from a combined Bayesian analysis of nuclear and mitochondrial sequences. *Mycologia* **96**: 283-294.
- Lumbsch HT, Huhndorf SM (2007). Outline of the Ascomycota. *Myconet* **13**: 1-58.
- Lumbsch HT, Schmitt I, Lindemuth R, Miller A, Mangold A, Fernando F, Huhndorf S (2005). Performance of four ribosomal DNA regions to infer higher-level phylogenetic relationships of inoperculate euascomycetes (*Leotiomyceta*). *Molecular Phylogenetics and Evolution* **34**: 512-524.
- Luttrell ES (1951). Taxonomy of the Pyrenomycetes. *University of Missouri Studies in Science* **24**: 1-120.
- Luttrell ES (1953). Development of the ascocarp in *Glonium stellatum*. *American Journal of Botany* **40**: 626-633.
- Luttrell ES (1955). The ascostromatic ascomycetes. *Mycologia* **47**: 511-532.
- Luttrell ES (1973). Loculoascomycetes. In: *The Fungi: an advanced treatise*. IVA. Ainsworth GC, Sparrow FK, Sussman AS, eds. London, Academic Press.
- Lutzoni F, Kauff F, Cox CJ, McLaughlin DJ, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung GH, Lücking R, Lumbsch, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosaka K, Lim YW, Batheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyana J, Yahr R, Vilgalys R (2004). Assembling the fungal tree of life: Progress, classification, and evolution of subcellular traits. *American Journal of Botany* **91**:1446-1480.
- Magnes M (1997). Weltmonographie der *Tribliaceae*. *Bibliotheca Mycologica* **165**: 127-130.
- Massee G (1895). *British Fungus Flora, A Classified Textbook of Mycology, Vol IV*. George Bell & Sons, London & New York. 520 pp.
- Massee G (1901). Fungi exotici III. *Royal Botanic Gardens, Kew, Bulletin No.* **175-177**: 150-169.
- Mathiassen G (1993). Corticolous and lignicolous Pyrenomycetes s. lat. (Ascomycetes) on *Salix* along a mid-Scandinavian transect. *Sommerfeltia* **20**: 1-180.
- Messuti MI, Lorenzo LE (1997). A new species of *Hysterium* from Patagonia, Argentina. *Mycological Research* **101**: 302-304.
- Messuti MI, Lorenzo LE (2003). Notes on the genus *Hysterographium* (Ascomycota, *Hysteriaceae*) in southern South America. *Nova Hedwigia* **76**: 451-458.
- Messuti MI, Lorenzo LE (2007). Taxonomy of *Glonium* (*Hysteriales*, Ascomycota) in southern Argentina and Chile. *Nova Hedwigia* **84**: 521-528.
- Miller JH (1949). A revision of the classification of the Ascomycetes with special emphasis on the Pyrenomycetes. *Mycologia* **41**: 99-127.
- Moncalvo JM, Rehner SA, Vilgalys R (1993). Systematics of *Lyophyllum* section *Difformia* based on evidence from culture studies and ribosomal DNA sequences. *Mycologia* **85**: 788-794.
- Mugambi GK, SM Huhndorf (2010). Parallel evolution of hysterothecial ascomata in ascolocularous fungi. *Systematics and Biodiversity* **XX**: xx-xx.

- Müller E, von Arx JA (1950). Einige Aspekte zur Systematik pseudosphäraler Ascomyceten. *Berichte der Schweizerischen Botanischen Gesellschaft* **60**: 329-397.
- Nannfeldt JA (1932). Studien über die Morphologie und Systematik der nicht-lichenisierten, inoperkulaten Discomyceten. *Nova Acta Regiae Societatis Scientiarum Uppsaliensis* **IV**, **8(2)**: 1-368.
- Ott SJ, El Mokhtari NE, Rehman A, Rosenstiel P, Hellmig S, Kühbacher T, Lins M, Simon R, Schreiber S (2007). Fungal rDNA signatures in coronary atherosclerotic plaques. *Environmental Microbiology* **9**: 3035-3045.
- Pande A, Rao VG (1991). On three hysteriaceous fungi from peninsular India. *Geobios new Reports* **10**: 62-64.
- Petrak F (1923a). Mykologische Notizen VI. No. 226. Über die Gattung *Glonium* Muhl. *Annales Mycologici* **21**: 225-227.
- Petrak F (1923b). Mykologische Notizen VI, Nr. 284. *Psilogonium Finkii* n.sp. *Annales Mycologici* **21**: 308-309.
- Rehm H (1896). Ascomyceten: Hysteriaceen und Discomyceten, In: L. Rabenhorst's *Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz*. 2nd Ed, Eduard Kummer, Leipzig **3**: 1-56.
- Rehm H (1898). Beiträge zur Pilzflora von Südamerika. V. *Hysteriaceae*. *Hedwigia* **37**: 296-302.
- Rehner SA, Samuels GJ (1994). Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. *Mycological Research* **98**: 625-634.
- Reid J, Pirozynski KA (1966). A new loculoascomycete on *Abies balsamea* (L.) Mill. *Canadian Journal of Botany* **44**: 351-354.
- Renobales G, Aguirre B (1990). The nomenclature and systematic position of the genus *Encephalographa*. *Systema Ascomycetum* **8**: 87-92.
- Rogers DP (1953). Disposition of nomina generica conservanda for fungi. *Taxon* **2**: 29-32.
- Saccardo PA (1873). Mycologiae Venetae Specimen. *Atti della Società Veneto-Trentina di Scienze Naturali Padova* **2**: 53-264.
- Saccardo, P.A. (1875). Conspectus generum pyrenomycetum italicorum additis speciebus fungorum Venetorum novis vel criticis, systemate carpologico dispositorum. *Atti della Società Veneto-Trentina di Scienze Naturali Padova* **4**: 77-100.
- Saccardo PA (1883). *Sylloge Fungorum*. **2**: 1-815. Patavii, Italy.
- Samuels GJ, Müller E (1980). Life-history studies of Brazilian Ascomycetes. 7. *Rhytidhysteron rufulum* and the genus *Eutrybliella*. *Sydowia* **32**: 277-292 [1979].
- Schmitt I, Mueller G, Lumbsch HT (2005). Ascoma morphology is homoplaseous and phylogenetically misleading in some pyrenocarpous lichens. *Mycologia* **97**: 362-374.
- Schoch CL, Shoemaker RA, Seifert KA, Hambleton S, Spatafora JW, Crous PW (2007a). A multigene phylogeny of the *Dothideomycetes* using four nuclear loci. *Mycologia* **98** (2006): 1041-1052.
- Schoch CL, Sung GH, Volkmann-Kohlmeyer B, Kohlmeyer J, Spatafora JW (2007b). Marine fungal lineages in the *Hypocreomycetidae*. *Mycological Research* **111**: 154-162.
- Shoemaker RA, Babcock CE (1992). Applanodictyosporus *Pleosporales*: *Clathrospora*, *Comoclathris*, *Graphillium*, *Macrospora*, and *Platysporoides*. *Canadian Journal of Botany* **70**: 1617-1658.
- Sivanesan A, Hsieh WH (1989). New species and new records of ascomycetes from Taiwan. *Mycological Research* **93**: 340-351.
- Spatafora JW, Johnson D, Sung G-H, Hosaka K, O'Rourke B, Serdani M, Spotts R, Lutzoni F, Hofstetter V, Fraker E, Gueidan C, Miadlikowska J, Reeb V, Lumbsch T, Lücking R, Schmitt I, Aptroot A, Roux C, Miller A, Geiser D, Hestmark G, Arnold AE, Büdel B, Rauhut A, Hewitt D, Untereiner W A, Cole MS, Scheidegger C, Schultz M, Sipman H, Schoch CL (2007). A five-gene phylogenetic analysis of the *Pezizomycotina*. *Mycologia* **98** (2006): 1018-1028.
- Speer EO (1986). A propos de champignons du Brésil III. *Mytilidion resinae* sp. nov. (*Hysteriales*) et sa forme conidienne, *Camaroglobulus resinae* gen. et spec. nov. (*Sphaeropsidales*). *Bulletin Trimestriel de la Société de Mycologie de France* **102**: 97-100.
- Spegazzini C (1906). Algunos micromicetes de los cacaoyeros. *Rev. Fac. La Plata* **2**: 303-311.
- Steinke TD, Hyde KD (1997). *Gloniella clavatispora*, sp. nov. from *Avicennia marina* in South Africa. *Mycoscience* **38**: 7-9.

- Sutton BC (1970). *Glyphium leptothecium* (Earle) comb. nov., *G. schizosporum* (Maire) Zogg, and their imperfect states. *Transactions of the British Mycological Society* **54**: 255-264.
- Teng SC (1933). Notes on *Hysteriales* from China. *Sinensia* **4**: 129-144.
- Tilak ST, Kale SB (1968). Contribution to the genus *Ostreola*. *Indian Phytopathology* **21**: 289-293.
- Tretiach M, Modenesi P (1999). Critical notes on the lichen genus *Encephalographa* A. Massal. (?*Hysteriaceae*). *Nova Hedwigia* **68**: 527-544.
- van der Linde EJ (1992). Notes on the South African *Hysteriaceae* (Ascomycetes: Mycotina). *South African Journal of Botany* **58**: 491-499.
- Vasilyeva LN (1999a). Hysteriaceous fungi in the Russian Far East I. *Hysterium*. *Mikologiya i Fitopatologiya* **33**: 225-227.
- Vasilyeva LN (1999b). Hysteriaceous fungi in the Russian Far East II. The genus *Hysterographium*. *Mikologiya i Fitopatologiya* **33**: 297-301.
- Vasilyeva LN (2000). Hysteriaceous fungi in the Russian Far East III. *Glonium* and *Actidiographium*. *Mikologiya i Fitopatologiya* **34**: 3-5.
- Vasilyeva LN (2001). Hysteriaceous fungi in the Russian Far East IV. *Glyphium*, *Lophium* and *Mytilinidion*. *Mikologiya i Fitopatologiya* **35**: 15-18.
- Vilgalys R, Hester M (1990). Rapid identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238-4246.
- White TJ, Bruns T, Lee S, Taylor J (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315-322. In: *PCR Protocols: A guide to methods and applications*. Eds., Innis MA, Gelfand DH, Sninsky JJ, White TJ. Academic Press, New York.
- Zogg H (1949). Beiträge zur Kenntnis der brasilianischen *Hysteriaceen*. *Berichte der Schweizerischen botanischen Gesellschaft* **59**: 39-42.
- Zogg H (1962). Die *Hysteriaceae* s. str. und *Lophiaceae*, unter besonderer Berücksichtigung der mitteleuropäischen Formen. *Beiträge zur Kryptogamenflora der Schweiz*, Band **11(3)**: 1-190.

Figure Legends:

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

Fig. 3. The genus *Hysterobrevium* (Clade A & D). 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* (GKM 1010; Kenya; not incl.). E. *Hsb. mori* (ANM 43; USA; not incl.). F. *Hsb. mori* (GKM 1013; Clade D; Kenya). Scale: habitat bar = 500 µm; spore bar = 20 µm.

Fig. 4. 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. *Glp. arciformis* sp. nov. (GKM L166A; Kenya). Scale: habitat bar = 500 µm; spore bar = 20 µm.

Fig. 5. The genera *Hysterographium* and *Rhytidhysterion*. A. *Hysterographium flexuosum* (EB 0098; USA). B. *Hg. fraxini* (EB 0100; USA). 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. 6. The genera *Psiloglonium* (Clade B, *Hysteriaceae*) and *Anteaglonium* (*Pleosporales*). A. *Psiloglonium simulans* (ANM 1557; USA). B. *P. clavisporum* (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. 7. 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.