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

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Abstract: A reappraisal of the phylogenetic integrity of bitunicate ascomycete fungi belonging to or previously affiliated with the *Hysteriaceae*, *Mytilinidiaceae*, *Gloniaceae* and *Patellariaceae* is presented, based on an analysis of 121 isolates and four nuclear genes, the ribosomal large and small subunits, transcription elongation factor 1 and the second largest RNA polymerase II subunit. A geographically diverse and high density taxon sampling strategy was employed, including multiple isolates/species from the following genera: *Anteaglonium* (6/4), *Encephalographa* (1/1), *Farlowiella* (3/1), *Gloniopsis* (8/4), *Glonium* (4/2), *Hysterium* (12/5), *Hysterobrevium* (14/3), *Hysterographium* (2/1), *Hysteropatella* (2/2), *Lophium* (4/2), *Mytilinidion* (13/10), *Oedohysterium* (5/3), *Ostreichnion* (2/2), *Patellaria* (1/1), *Psiloglonium* (11/3), *Quasiconcha* (1/1), *Rhytidhysteron* (8/3), and 24 outgroup taxa. Sequence data indicate that although the *Hysteriales* are closely related to the *Pleosporales*, sufficient branch support exists for their separation into separate orders within the *Pleosporomycetidae*. The *Mytilinidiales* are more distantly related within the subclass and show a close association with the *Gloniaceae*. Although there are examples of concordance between morphological and molecular data, these are few. Molecular data instead support the premise of a large number of convergent evolutionary lineages, which do not correspond to previously held assumptions of synapomorphy relating to spore morphology. Thus, within the *Hysteriaceae*, the genera *Gloniopsis*, *Glonium*, *Hysterium* and *Hysterographium* are highly polyphyletic. This necessitated the transfer of two species of *Hysterium* to *Oedohysterium gen. nov.* (*Od. insidens comb. nov.* and *Od. sinense comb. nov.*), the description of a new species, *Hysterium barrianum sp. nov.*, and the transfer of two species of *Gloniopsis* to *Hysterobrevium gen. nov.* (*Hb. smilacis comb. nov.* and *Hb. constrictum comb. nov.*). While *Hysterographium*, with the type *Hg. fraxini*, is removed from the *Hysteriaceae*, some of its species remain within the family, transferred here to *Oedohysterium* (*Od. pulchrum comb. nov.*), *Hysterobrevium* (*Hb. mori comb. nov.*) and *Gloniopsis* (*Gp. subrugosa comb. nov.*); the latter genus, in addition to the type, *Gp. praelonga*, with two new species, *Gp. arciformis sp. nov.* and *Gp. kenyensis sp. nov*. The genus *Glonium* is now divided into *Anteaglonium* (*Pleosporales*), *Glonium* (*Gloniaceae*), and *Psiloglonium* (*Hysteriaceae*). The hysterothecium has evolved convergently no less than five times within the *Pleosporomycetidae* (e.g., *Anteaglonium*, *Farlowiella*, *Glonium*, *Hysterographium* and the *Hysteriaceae*). Similarly, thin-walled mytilinidioid (e.g., *Ostreichnion*) and patellarioid (e.g., *Rhytidhysteron*) genera, previously in the *Mytilinidiaceae* and *Patellariaceae*, respectively, transferred here to the *Hysteriaceae*, have also evolved at least twice within the subclass. As such, character states traditionally considered to represent synapomorphies among these fungi, whether they relate to spore septation or the ascomata, in fact, represent symplesiomorphies, and most likely have arisen multiple times through convergent evolutionary processes in response to common selective pressures.

Key words: Evolution, fungi, *Hysteriales*, *Mytilinidiales*, *Patellariales*, phylogeny, speciation, taxonomy.
Taxonomic novelties: New species: *Gloniopsis arciformis* E.W.A. Boehm, G.K. Mugambi, S.M. Huhndorf & C.L. Schoch, *Gp. kenyensis* E.W.A. Boehm, G.K. Mugambi, S.M. Huhndorf & C.L. Schoch, *Hysterium barrianum* E.W.A. Boehm, A.N. Miller, G.K. Mugambi, S.M. Huhndorf & C.L. Schoch. **New genera:** *Hysterobrevium* E.W.A. Boehm & C.L. Schoch, *Oedohysterium* E.W.A. Boehm & C.L. Schoch. **New combinations:** *Gloniopsis subrugosa* (Cooke & Ellis) E.W.A. Boehm & C.L. Schoch, *Hysterobrevium constrictum* (N. Amano) E.W.A. Boehm & C.L. Schoch, *Hb. mori* (Schwein.) E.W.A. Boehm & C.L. Schoch, *Hb. smilacis* (Schwein.) E.W.A. Boehm & C.L. Schoch, *Oedohysterium insidens* (Schwein.) E.W.A. Boehm & C.L. Schoch, *Od. pulchrum* (Checa, Shoemaker & Umaña) E.W.A. Boehm & C.L. Schoch, *Od. sinense* (Teng) E.W.A. Boehm & C.L. Schoch, *Psiloglonium araucanum* (Speg.) E.W.A. Boehm, S. Marincowitz & C.L. Schoch, *P. chambianum* (Guyot) E.W.A. Boehm & C.L. Schoch, *P. colihuae* (Lorenzo & Messuti) E.W.A. Boehm & C.L. Schoch, *P. ephedrae* (Henn.) E.W.A. Boehm & C.L. Schoch, *P. hysterinum* (Rehm) E.W.A. Boehm & C.L. Schoch, *P. pusillum* (H. Zogg) E.W.A. Boehm & C.L. Schoch, *P. sasicola* (N. Amano) E.W.A. Boehm & C.L. Schoch, and *P. uspallatense* (Speg.) E.W.A. Boehm & C.L. Schoch.

INTRODUCTION

Class *Dothideomycetes*, subphylum *Pezizomycotina* (*Ascomycota*), is currently classified into two subclasses, based on centrum type (Schoch *et al.* 2006, 2009b, Spatafora *et al.* 2006). The *Dothideomycetidae* is characterised by the absence of sterile centrum elements (*e.g.*, pseudoparaphyses). This subclass includes the *Dothideales*, *Capnodiales*, and *Myriangiales*. The *Microthyriales*, and *Trypetheliales*, while within the *Dothideomycetes*, lie outside of the *Dothideomycetidae* (Schoch *et al.* 2009a). The second subclass recognised within the *Dothideomycetes* is the *Pleosporomycetidae*, characterised by a hamathecium of wide to narrow cellular to trabeculate pseudoparaphyses, which may or may not persist at maturity. This subclass currently comprises the *Pleosporales*, *Hysteriales*, and *Mytilinidiales*, and tentatively the *Jahnulales*. The *Botryosphaeriales*, and *Patellariales*, possess pseudoparaphyses, and would be expected to fall into the *Pleosporomycetidae*, however, at present, statistical support is weak. 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* (*Hysteriales*), *Mytilinidiaceae* (*Mytilinidiales*), and *Gloniaceae* (*Pleosporomycetidae fam. incertae sedis*), possess persistent, carbonaceous ascomata that characteristically dehisce by a longitudinal suture. Recent molecular data support the inclusion of all three families within

the *Pleosporomycetidae* (Schoch *et al.* 2006, Boehm *et al.* 2009, Mugami & Huhndorf 2009). In the *Hysteriaceae* ascomata are thick-walled, navicular, characteristically dehiscing by an invaginated slit or sulcus (Zogg 1962). Fungi in the *Mytilinidiaceae*, on the other hand, possess strongly laterally compressed, connivent, thin-walled conchate ascomata, reminiscent of miniature bivalve molluscs. These mytilinidioid 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 *Phacidiacei*, but later (Fries 1835) placed them in his new class *Discomycetes*, stating: "*Transitum sistunt ad Discomycetes, sed discum verum non monstrant*." Chevallier (1826) recognised the unique nature of the hysterothecium and established the *Hysteriineae*, which he considered as pyrenomycetes distinct from Fries' *Phacidiei*. Corda (1842), on the other hand, retained the *Phacidiei* 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.

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

Duby (1862) was the first to propose that hysteriaceous fungi be divided into two sections, the *Hystériées* and the *Lophiées*, the latter to accommodate mytilinidioid forms. One hundred years later, Zogg (1962) proposed two families: the *Hysteriaceae s. str.* to accommodate thick-walled hysteriaceous forms, and the *Lophiaceae* (Zogg 1962, von Arx & Müller 1975) to accommodate thin-walled, mytilinidioid fungi. Barr (1990a) made the argument for retention of the earlier name *Mytilinidiaceae* over the *Lophiaceae*, despite the proposal to conserve the latter (Hawksworth & Eriksson 1988). Luttrell (1953) studied ascomatal ontogeny and hamathecial development in *Glonium stellatum*. 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 recognise 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 *Mytilinidiaceae* was placed in the *Melanommatales* 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 *Mytilinidiaceae* 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 (*TEF1*) 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 *Mytilinidiaceae*, 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*, *Gloniopsis*, and *Hysterographium* were demonstrated to be polyphyletic, with affinities not premised on spore septation and pigmentation. (3) The genus *Glonium* was also shown to be polyphyletic, but along two highly divergent lines. *Glonium* lies outside of the *Hysteriaceae*, and instead finds close affinities with the family *Mytilinidiaceae*, for which was proposed the *Gloniaceae* (Boehm *et al.* 2009), to accommodate the type, *G. stellatum*, and related forms. (4) The genus *Psiloglonium* was reinstated within the *Hysteriaceae*, with *P. lineare* as type, to accommodate

didymospored species segregated from *Glonium*. (5) The genera *Mytilinidion* and *Lophium* formed a strongly supported clade within the *Pleosporomycetidae*, thus defining the monophyletic *Mytilinidiaceae*, adjacent to the *Gloniaceae*, for which was proposed the *Mytilinidiales* (Boehm *et al.* 2009). (6) The genus *Farlowiella*, previously in the *Hysteriaceae*, was placed as *Pleosporomycetidae gen. incertae sedis.* (7) The genus *Ostreichnion*, previously in the *Mytilinidiaceae*, was transferred to the *Hysteriaceae*. (8) The genus *Rhytidhysteron*, previously in the *Patellariaceae*, was transferred to the *Hysteriaceae*.

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

In an effort to facilitate species identification, a number of dichotomous keys are presented in the current study. These keys take into consideration taxonomic changes brought about by DNA and amino acid sequencing studies (Schoch *et al.* 2006, Boehm *et al.* 2009, Mugambi & Huhndorf 2009), and attempt to provide a morphological basis for the many new relationships revealed by molecular data. Although the keys are based on those first presented by Zogg (1962), they considerably expand upon them to include a number of new species and genera described since the original publication (*e.g.*, Darker 1963, Tilak & Kale 1968, Barr 1975, 1990a, Barr & Blackwell 1980, Amano 1983, Speer 1986, Pande & Rao 1991, van der Linde 1992, Kantvilas & Coppins 1997, Lorenzo & Messuti 1998, Messuti & Lorenzo 1997, 2003, 2007, Vasilyeva 2000, 2001, Chlebicki & Knudsen 2001, Checa *et al.* 2007). In addition to incorporating new species and genera, the revised keys also take into consideration variation in ascospore measurements as presented by different authors, and include widened distribution reports as well. Additional information can be found at www.eboehm.com/.

MATERIALS AND METHODS

Taxon sampling

Fungal cultures, collection data and DNA GenBank accession numbers are listed in Table 1 - see online Supplementary Information. Fungal cultures initiated for this study were based on the isolation of individual ascospores, employing a method whereby individual ascomata were affixed to Petri plate lids suspended over potato-dextrose agar. Every 12 h the lids were rotated 45 degrees, such that after 96 h, 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 and deposits with the CBS; Centraalbureau voor Schimmelcultures). 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 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.

An attempt was made to include a broad range of fungal isolates, belonging to or previously affiliated with the *Hysteriaceae*, *Mytilinidiaceae*, *Gloniaceae* and *Patellariaceae* (Table 1). A geographically diverse (Cuba, Europe, Ghana, Kenya, New Zealand, South Africa, Tasmania, North and South America) and high density taxon sampling strategy was employed. This included multiple isolates/species from the genera: *Anteaglonium* (6/4), *Encephalographa* (1/1), *Farlowiella* (3/1), *Gloniopsis* (8/4), *Glonium* (4/2), *Hysterium* (12/5), *Hysterobrevium* (14/3), *Hysterographium* (2/1), *Hysteropatella* (2/2), *Lophium* (4/2), *Mytilinidion* (13/10), *Oedohysterium* (5/3), *Ostreichnion* (2/2), *Patellaria* (1/1), *Psiloglonium* (11/3), *Quasiconcha* (1/1), *Rhytidhysteron* (8/3), and 24 outgroup taxa, for a total of 121 taxa. All cultures and the herbarium specimens from which they were derived, have been deposited and are permanently conserved in the certified public institutions given in Table 1.

Within the *Pleosporales*, we sampled *Anteaglonium abbreviatum*, *A. globosum*, *A. latirostrum* and *A. parvulum*, *Byssothecium circinans*, *Cochliobolus heterostrophus*, *Delitschia winteri*, *Herpotrichia diffusa*, *Leptosphaeria maculans*, *Phoma herbarum*, and *Pleospora herbarum*. Eight representatives from the *Dothideomycetidae* were included as outgroups to the *Pleosporomycetidae*, namely *Elsinoë veneta* and *Myriangium duriaei* (*Myriangiales*), *Dothidea sambuci* and *D. insculpta* (*Dothideales*), *Mycosphaerella punctiformis* and *Scorias spongiosa* (*Capnodiales*). *Botryosphaeria dothidea*, and *Guignardia gaultheriae* (*Botryosphaeriales*). *Jahnula aquatica* and *Aliquandostipite khaoyaiensis* (*Jahnulales*), were also included. Four taxa in the *Arthoniomycetes*, were used as outgroups to the *Dothideomycetes*, namely *Opegrapha dolomitica*, *Simonyella variegata*, *Roccella fuciformis*, and *Arthonia caesia*. These are not presented in Fig. 1, due to space limitations, but are presented as a full tree available on TreeBASE, as well as in Table 1.

DNA extraction, amplification and sequencing

Genomic DNA was recovered using the DNeasy® Plant Mini Kit (Qiagen Inc., Valencia, CA, U.S.A.), 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 µM of each forward and reverse primer, 2 mM $MgCl_2$, 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.* (2006). 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

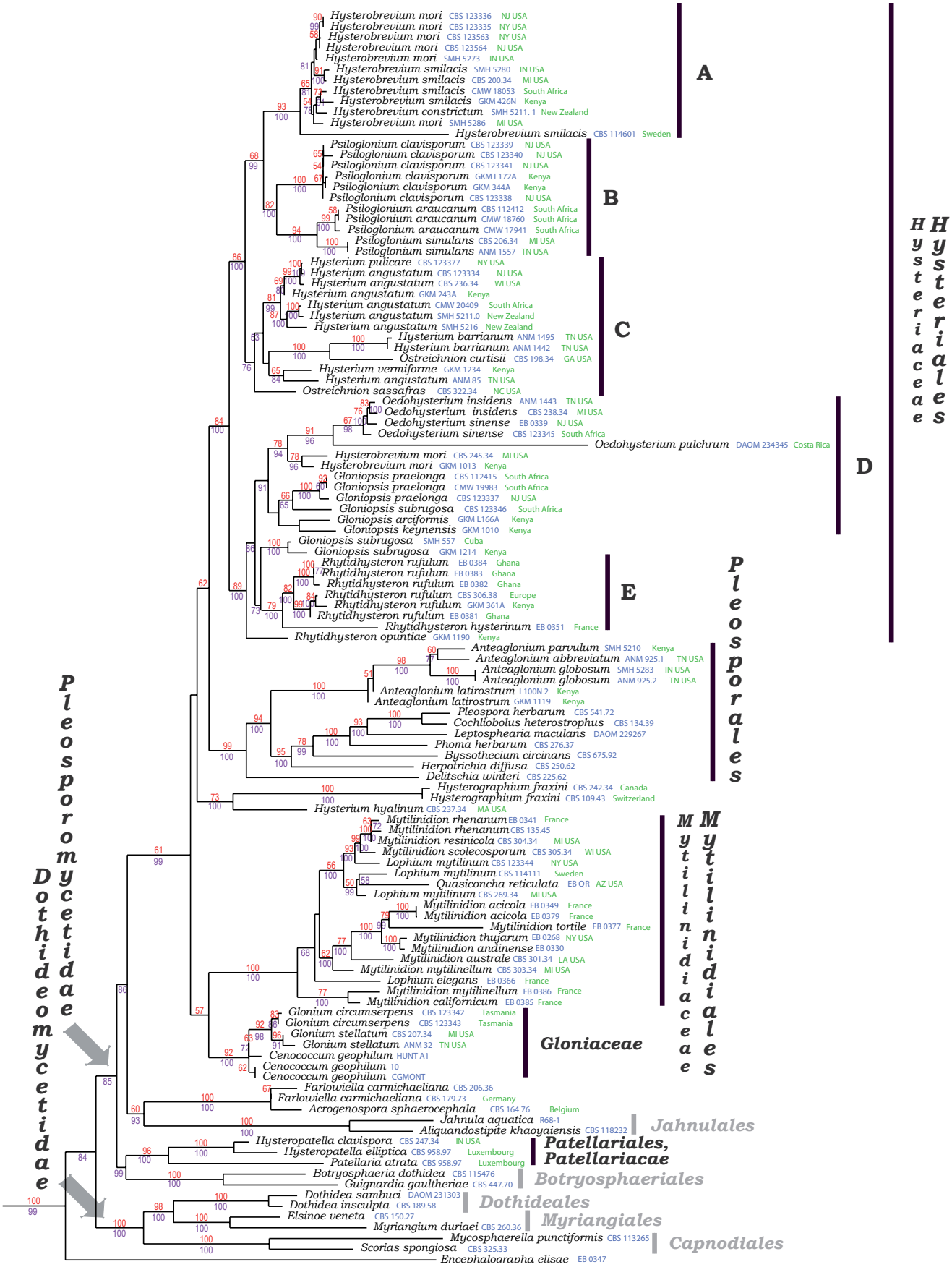

Fig. 1. Combined ribosomal (nuSSU & nuLSU) and protein coding gene (*TEF1* & *RPB2*) DNA phylogeny for bitunicate ascomycetes belonging to or previously affiliated with the *Hysteriaceae*, *Mytilinidiaceae*, *Gloniaceae* and *Patellariaceae*. Also included are representatives from allied groups such as the *Pleosporales*, *Jahnulales*, *Patellariales*, and *Botryosphaeriales*, as well as representatives from the *Dothideales*, *Myriangiales* and *Capnodiales* in the *Dothideomycetidae*. The *Arthoniomycetes*, chosen as outgroup, are not presented here due to space limitations, but are available in the full tree on TreeBASE. The tree is the highest scoring tree obtained by maximum likelihood in RAxML. Nodal values, given as percentages, are as follows: Bayesian posterior probability / maximum likelihood bootstrap. Only values above 50 % are shown.

Corporation (Fitchburg, Wisconsin, U.S.A.) and run on an iCycler® from Biorad (Hercules, California, U.S.A.). 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 utilised 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 U.S.A., Inc.).

Phylogenetic analysis

DNA sequences were derived from previous studies (Schoch *et al.* 2006, Boehm *et al.* 2009, Mugambi & Huhndorf 2009), as well as from a number of new accessions generated in this study (Table 1). Sequences were aligned using default options for a simultaneous method of estimating alignments and tree phylogenies, SATé (Liu *et al.* 2009). Protein coding fragments were translated using BioEdit v. 7.0.1 (Hall 2004), and aligned within SATé as amino acid sequence data. These were then aligned with their respective DNA sequences using the RevTrans v. 1.4 Server (Wernersson & Pedersen 2003). Newly generated sequences were subsequently added to the core alignment with MAFFT v. 6.713 (Katoh *et al.* 2009). A supermatrix of four genes (nuLSU, nuSSU *TEF1*, *RPB2*) consisting of 56 % gaps and undetermined characters, across 121 taxa was obtained.

The matrix was analysed using maximum likelihood in RAxML v. 7.0.4 (Stamatakis 2006). Data was partitioned by individual gene and, where applicable, by codon, as in Schoch *et al.* (2009). A most likely tree was obtained after 100 successive searches in RAxML under the GTR model with gamma rate distribution across 11 partitions and starting each search from a randomised tree with a rapid hill climbing option and joint branch length optimisation. Five hundred fast bootstrap pseudoreplicates (Stamatakis *et al.* 2008) were run under the same conditions and these values are given above each node. The matrix analysed in this study produced 4174 distinct alignment patterns and the most likely tree had a log likelihood of -72114.22899. The average log likelihood over 100 trees was -72117.730727. Three independent Bayesian phylogenetic analyses were performed in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) using a uniform [GTR+I+G] model. The Metropolis-coupled Markov chain Monte Carlo (MCMC) sampling approach was used to calculate posterior probabilities (PP). For each Bayesian run four Markov chains were run from a random starting tree for 5 000 000 generations and trees sampled every 100 generations. The first 50 000 generation trees were discarded as burn-in prior to convergence of four of the chains. All three runs reached a plateau that converged. One run was chosen to construct a 50 % majority rule consensus tree of all trees remaining after the burn in was discarded. Bayesian Posterior Probabilities with those equal or greater than 50 % are given below each node (Fig. 1).

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 (Schoch *et al.* 2006, Boehm *et al.* 2009). This is also confirmed by morphological evidence related to the centrum. Thus, the *Hysteriales* share a very similar centrum with the *Pleosporales*, that is, one defined by the *Pleospora*-type, 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 emphasise the elongated hysteriaceous locule, capable of relatively indeterminate linear growth, as distinct from the strict *Pleospora*-type centrum, defined as it is by constrained concentric growth. In contrast to the close association between the *Hysteriales* and the *Pleosporales*, the *Mytilinidiales* forms a more distant clade within the *Pleosporomycetidae* (Boehm *et al.* 2009).

Phylogenetic analysis – family level

Hysteriaceae

Although the *Hysteriales* receives high branch support as a monophyletic entity, distinct from the closely related *Pleosporales*, two major groups can be defined within the family. The first supports Clades A–C, whereas the second supports Clades D and E (Fig. 1).

Clade A: This first clade is characterised by *Hysterographium mori*, with short pigmented dictyospores, *Gloniopsis constricta*, and *Gp. smilacis*, the latter two with short hyaline dictyospores. The *Gp. smilacis* isolates originate from highly diverse geographical sources (*e.g.*, Sweden, South Africa, North America; 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 gen. nov.*, as *Hb. mori comb. nov.*, *Hb. constrictum comb. nov.*, and *Hb. smilacis comb. nov.*

Clade B: This clade (Fig. 1) appears monophyletic for the newly reinstated genus *Psiloglonium* (Boehm *et al.* 2009), with hyaline didymospores. It includes the following species: *P. simulans*, *P. clavisporum,* and *P. araucanum comb. nov.* In this study, we propose a number of new combinations for the genus *Psiloglonium*, with *P. lineare* as the type (Boehm *et al.* 2009), to accommodate species previously classified under the genus *Glonium*, now in the *Gloniaceae*.

Clade C: This clade is characterised by pigmented phragmospores belonging to four species of the genus *Hysterium*, namely *H. pulicare*, *H. angustatum*, *H. vermiforme*, which have 3-septate spores, and *H. barrianum sp. nov.*, which has 9-septate spores. Again, a geographically diverse set of isolates were surveyed (Table 1). For instance, taxon sampling for *H. angustatum* included isolates originating from Kenya, New Zealand, South Africa, and North America (Fig. 1). Also within this clade, but with weak bootstrap support, is *Ostreichnion sassafras*, and *O. curtisii*, previously transferred from the *Mytilinidiaceae* to the *Hysteriaceae* (Boehm *et al.* 2009).

Clade D: This clade 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* and *H. sinense*. Molecular data indicate that these species are not related to the type species, *H. pulicare*, nor to related species within Clade C. Morphology also supports this separation, as *H. insidens* and *H. sinense* both possess phragmospores with a swollen supra-median cell. We therefore propose *Oedohysterium gen. nov.*, to accommodate *Od. insidens comb. nov.* and *Od. sinense comb. nov.* Also grouping in Clade D is *Hysterographium pulchrum*. Despite the fact that *Hg. pulchrum* possesses dictyospores, we propose to unite it within *Oedohysterium*, as *Od. pulchrum comb. nov.*, on account that it too possesses a swollen supra-median cell. Also present in this subclade are two isolates of *Hb. mori*, distant from the other *Hb. mori* accessions in Clade A; this anomaly will be discussed later. A separate subclade is evident in Clade D, and defines the type species for the genus *Gloniopsis*, namely *Gp. praelonga*. Closely associated with *Gp. praelonga* is one representative of *Hg. subrugosum*. 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 *Gp. praelonga* and *Hg. subrugosum* be united within the same genus, proposing *Gloniopsis subrugosa comb. nov*. The other two representatives of *Gp. subrugosa* do not fall into Clade D, but lie adjacent. Lastly, an additional two species are described in Clade D, namely *Gloniopsis arciformis sp. nov.* and *Gp. kenyensis sp. nov.*, both from East Africa (Table 1).

Clade E: This clade is well-supported and defines two species in the genus *Rhytidhysteron*, namely *R. rufulum*, and *R. hysterinum*. Taxon sampling included isolates originating from France, Ghana, Kenya and North America. This clade therefore supports the transference of the genus *Rhytidhysteron* from the *Patellariaceae* to the *Hysteriaceae*, as initially proposed by Boehm *et al.* (2009). The third species of *Rhytidhysteron*, *R. opuntiae*, is distant to the first two species, but remains adjacent to Clade E.

Mytilinidiaceae

In contrast to the *Hysteriales*, the family *Mytilinidiaceae* represents a highly monophyletic entity, defining the order *Mytilinidiales* (Boehm *et al.* 2009). The conchate nature of the fruitbody and the thin-walled peridium, seem to unite what at first may seem a disparate group of fungi into a single family (Fig. 1). In this study, we have sampled 10 of the 15 species of *Mytilinidion*, characterised by phragmospores and scolecospores, two of the four species of *Lophium*, with filiform spores, as well as the monotypic *Quasiconcha*, 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).

Gloniaceae

As for the monotypic family *Gloniaceae* (Boehm *et al.* 2009), based on the genus *Glonium*, previously classified within the *Hysteriaceae* (Zogg 1962), surprisingly, sequence data indicate that it finds close affinity with the *Mytilinidiaceae* (Fig. 1). This is based on four isolates, representing two species, *Glonium stellatum* and *G. circumserpens*. However, the *Gloniaceae* is not included within the *Mytilinidiales*, due to the highly divergent morphology associated with the genus *Glonium*. These include character states related to the hamathecium (persistent cellular pseudoparaphyses *versus* narrow trabeculate pseudoparaphyses) and to the fruitbody (dichotomously branched *versus* conchate), for the *Gloniaceae* and *Mytilinidiaceae*, respectively. Thus, for the present, we propose that the family *Gloniaceae* be considered *Pleosporomycetidae fam. incertae sedis*.

TAXONOMY

Hysteriaceae Chevall. 1826, ***Hysteriales*** Lindau 1897.

Fungi classified in the *Hysteriaceae* (Chevallier 1826) have been traditionally defined by a specialised 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 cylindric, bearing 8 ascospores, overlapping biseriate, ranging from hyaline to dark brown, obovoid, clavate, ellipsoid or fusoid. Ascospores are highly diverse in septation and range from didymospores to phragmospores to dictyospores, at times surrounded by a gel coating, and often show bipolar asymmetry (Barr 1987). Zogg (1962) accepted the following seven genera within the *Hysteriaceae*: *Farlowiella*, *Gloniella*, *Gloniopsis*, *Glonium*, *Hysterium*, *Hysterocarina*, and *Hysterographium*.

The traditional circumspection of the *Hysteriaceae* was based on character states related to the hysterothecium and spore morphology (*e.g.*, septation and pigmentation), character states previously considered synapomorphic (Zogg 1962). However, recent molecular data underscore the potential for morphology to be difficult to interpret, and even unhelpful in phylogenetic inference and reconstruction for this group of fungi (Schoch *et al.* 2006, Boehm *et al.* 2009, Mugambi & Huhndorf 2009). Thus, a number of examples of convergent evolution are presented in the current study, which relate not only to the fruitbody, but to spore morphology as well. As a result, three genera have been removed from the family (*Glonium*, *Hysterographium* and *Farlowiella*), based on convergence associated with the fruitbody. Additionally, within the family, several genera have their members spanning different clades (Fig. 1). This necessitated the description of two new genera (*Oedohysterium* and *Hysterobrevium*), as well as three new species, one in *Hysterium* and two in *Gloniopsis*, in addition to a number of new combinations involving *Psiloglonium*, *Oedohysterium*, *Hysterobrevium* and *Gloniopsis*. These taxonomic changes have de-emphasised both spore septation and spore pigmentation as reliable character states for deducing phylogenetic relationships within the family. Nevertheless, in the keys that follow, we have endeavoured to provide a morphological basis for the new phylogenies revealed by molecular data.

Data have also necessitated that we expand the concept of the *Hysteriaceae* to include thin-walled mytilinidioid forms previously in the *Mytilinidiaceae* (*e.g.*, *Ostreichnion*), as well as patellarioid forms previously in the *Patellariaceae* (*e.g.*, *Rhytidhysteron*). The inclusion of *Ostreichnion* within the *Hysteriaceae* was unexpected. Unlike most members of the family, the peridium in *Ostreichnion* is sclerenchymatoid and thin-walled, defining a fragile mytilinidioid ascoma, 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 *Rhytidhysteron* within the *Hysteriaceae*. Although included within the *Patellariaceae* (Kutorga & Hawksworth 1997), phylogenetic data presented here and elsewhere (Boehm e*t al.* 2009), clearly indicate that this genus lies quite distant from other members of the *Patellariaceae*.

Some authors have included a number of additional genera within the *Hysteriaceae*. For instance, the genera *Hysteropatella*, *Hysteroglonium*, and *Pseudoscypha* were included in the *Hysteriaceae* by Eriksson (2006). In addition, the genera *Hemigrapha*, *Graphyllium*, and *Encephalographa* were included in the family by Kirk *et al.* (2001). In Boehm *et al.* (2009), two species belonging to *Hysteropatella*, namely *Hp. clavispora* (CBS 247.34) and *Hp. elliptica* (CBS 935.97), did not cluster with any of the hysteriaceous taxa surveyed. Instead, they formed a distant clade within the *Pleosporomycetidae*, postulated to represent the emergence of the *Patellariales*. In the present study, these two species of *Hysteropatella* continue to be distant from the *Hysteriaceae*, and also cluster now with *Patellaria atrata* (CBS 958.97). Therefore, we do not include the genus *Hysteropatella* within the *Hysteriaceae*.

Reid & Pirozynski (1966) in describing *Pseudoscypha abietis* 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 *Graphyllium* possesses applanate, clathrate ascospores borne in thin-walled membranous hysterothecia, at first subcuticular, later erumpent, often associated with aquatic poaceous hosts. The genus was included in the *Hysteriaceae* by Shoemaker & Babcock (1992) and Kirk *et al.* (2001), but was earlier classified in the *Phaeosphaeriaceae* (Barr 1987). A new species was recently described from Costa Rica (Checa *et al.* 2007). The unique ascospore and the lack of carbonisation 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 lichenised, 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*, in the *Gloniaceae*. We recently were able to obtain fresh material of *Encephalographa elisae* 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 / BPI 879773). 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).

To summarise, we accept the following genera in the *Hysteriaceae*: *Actidiographium*, *Gloniella*, *Gloniopsis, Hysterium*, *Hysterobrevium*, *Hysterocarina*, *Oedohysterium*, *Ostreichnion*, *Psiloglonium*, and *Rhytidhysteron*. Dichotomous keys are presented here for hysteriaceous fungi, with the caveat that phylogenetically unrelated taxa share the same key. Thus, despite their transference from the *Hysteriaceae* (Boehm *et al.* 2009), the genera *Hysterographium*, *Farlowiella*, *Glonium* and *Anteaglonium* (Mugambi & Huhndorf 2009), are nevertheless included in the key. This is because they typically possess ascomata that have traditionally been referred to as hysterothecia.

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

1. Ascomata apothecioid, opening widely when hydrated, fully exposing the hymenium, which may be red or black (*i.e.*, patellarioid) ..... ***Rhytidhysteron***
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 amerospores, the upper cell pigmented and much larger than the lower, which remains un- or less-pigmented; anamorph *Acrogenospora* ..... ***Farlowiella***
   Note: The genus *Farlowiella* has been removed from the *Hysteriaceae* and is currently listed as *Pleosporomycetidae gen. incertae sedis* (Boehm *et al.* 2009).
2. Ascospores not as above, didymospores, phragmospores or dictyospores, sometimes pigmented 3

3. Didymospores small, the two cells more or less equal in size 4
3. Ascospores not as above, phragmospores, dictyospores, +/- pigmentation, or very large didymospores (*O. curtisii*) 7

4. Ascospores hyaline 5
4. Ascospores pigmented ..... ***Actidiographium***

5. Didymospores less than 8 µm long ..... ***Anteaglonium***
   Note: The genus *Anteaglonium* lies within the *Pleosporales* (Mugambi & Huhndorf 2009), but is keyed out here with *Psiloglonium*.
5. Didymospores longer than 8 µm 6

6. Didymospores hyaline, borne in solitary or gregarious hysterothecia, rarely associated with a subiculum, not laterally anastomosed to form radiating stellate composites ..... ***Psiloglonium***
   Note: One species of *Anteaglonium*, *A. latirostrum*, will key out here, but belongs in the *Pleosporales* (Mugambi & Huhndorf 2009) and is also keyed out in the *Psiloglonium* key.
6. Didymospores hyaline, borne in modified hysterothecia, usually associated with a subiculum, strongly laterally anastomosed along their length to form radiating stellate composites ..... ***Glonium***
   Note: The genus *Glonium* has been transferred from the *Hysteriaceae* to the *Gloniaceae*, currently listed as *fam. incertae sedis* within the *Pleosporomycetidae* (Boehm *et al.* 2009).

7. Ascospores transversely septate phragmospores, or if with dictyospores then also with red pigmentation 8
7. Ascospores transversely and longitudinally septate dictyospores, or very large didymospores (*O. curtisii*) 10

8. Ascospores hyaline phragmospores ..... ***Gloniella***
8. Ascospores pigmented phragmospores or in one case (*Od. pulchrum*) with pigmented dictyospores and red pigmentation in the hamathecium 9

9. Phragmospores 3-septate or rarely more, but without swollen supra-median cell(s) ..... ***Hysterium***
9. Phragmospores with swollen supra-median cell, usually more than 3-septate, in one case with pigmented dictyospores and red centrum pigmentation (*Od. pulchrum*) ..... ***Oedohysterium***

10. Dictyospores hyaline, +/- gelatinous sheath, or pigmented, but short, less than 25 µm in length ..... ***Hysterobrevium***
10. Dictyospores hyaline, +/- gelatinous sheath, or pigmented, but longer than 25 µm, or very large didymospores (*O. curtisii*) 11

11. Dictyospores, if hyaline, then longer than 25 µm, or if pigmented, then measuring (22–)25–34(–45) x (6–)8–12(–17) µm, with 7–11 transverse and 1–2 vertical septa, and no red pigment associated with the hamathecium (*Gp. subrugosa*) ..... ***Gloniopsis***
11. Dictyospores pigmented, of different length, or if similar in length to *Gp. subrugosa*, then tropical with red pigment associated with the hamathecium, or very large didymospores (*O. curtisii*) 12

12. Dictyospores or large didymospores borne in conchate, mytilinidioid, thin-walled, slerenchymatous, fragile fruitbodies ..... ***Ostreichnion***
    Note: The genus *Ostreichnion*, previously in the *Mytilinidiaceae*, was transferred to the *Hysteriaceae* (Boehm *et al.* 2009).
12. Dictyospores borne in thick-walled, navicular hysterothecia **13**

13. Dictyospores pigmented, borne in typical hysterothecia, that are erumpent or sessile on the substrate ..... ***Hysterographium***
    Note: The genus *Hysterographium*, with the type species *Hg. fraxini*, has been transferred out of the *Hysteriaceae* as *Pleosporomycetidae gen. incertae sedis* (Boehm *et al.* 2009). Residual species classified as *Hysterographium*, for which sequence data are lacking, are provisionally retained within the genus.
13. Hysterothecia borne within the substrate, hardly erumpent, with cristate longitudinal apex instead of a sulcus; neotropical ..... ***Hysterocarina***

Hysterium Tode, Schriften Berlin. Ges. Naturf. Freunde 5: 53 (1784).

The genus *Hysterium* is characterised 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) recognised two morphological types within the genus. Type I is characterised by 3-septate phragmospores, and includes the versicolorous type species *H. pulicare* (Fig. 2A–B), and its closely related concolorous counterpart, *H. angustatum* (Fig. 2C–F), both extremely common in the temperate zones of both hemispheres. These are followed by *H. vermiforme* (Fig. 2G–K), from Africa, and the much larger-spored *H. macrosporum*, reported from North America and China (Teng 1933). Although Zogg (1962) did not accept *H. hyalinum*, Lohman (1934) provided legitimacy to the epithet, noting that pigmentation is delayed in the maturation of the 3-septate ascospores (Boehm *et al.* 2009).

Type II corresponds to a different phragmospore, one in which, typically, there are five or more septa, and in which there exists a swollen cell, either just above the median septum (*i.e.*, supramedian) or, rarely, some distance up from the median septum. Type II includes, by increasing spore length, the cosmopolitan *H. insidens* (Fig. 3A–D), the larger-spored counterpart *H. sinense* (Fig. 3E–H), and the unusual *H. magnisporum*, 7-septate, with three of the septa crowded to each end, the two central cells much larger. The latter two species are reported from China (Teng 1933) and North America (Boehm, unpubl. data). *Hysterium velloziae*, provisionally included by Zogg (1962), with up to 21 septa at maturity, has only been reported from Africa (van der Linde 1992).

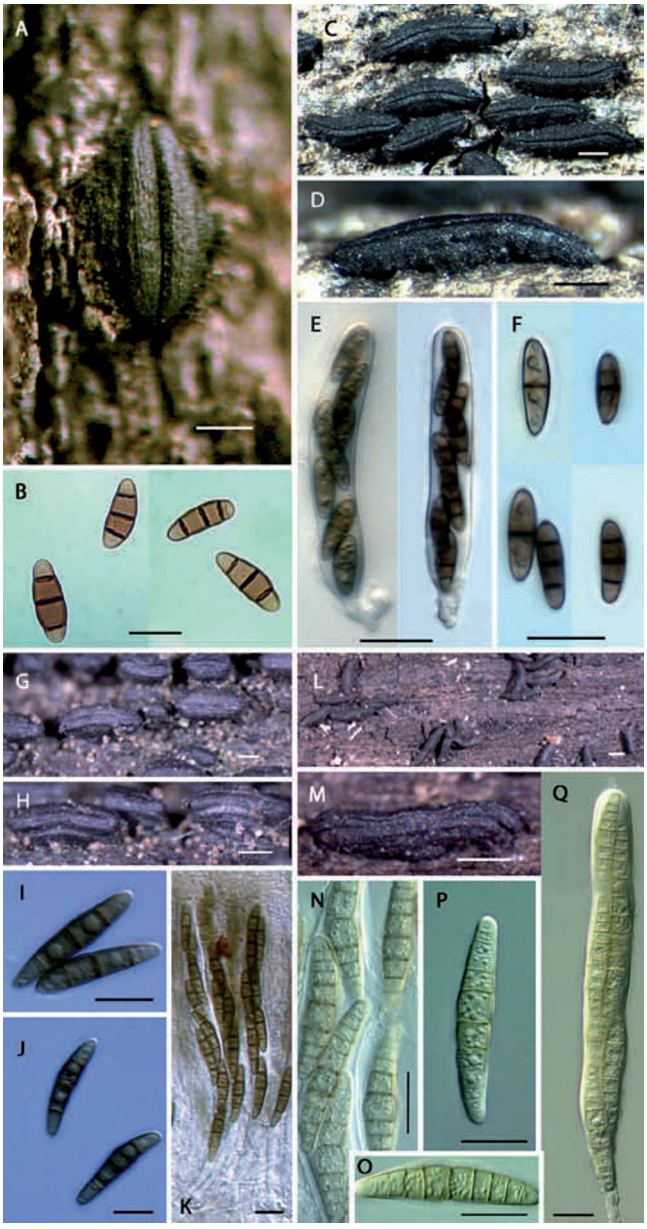

Fig. 2. The genus *Hysterium* (Clade C). A–B. *Hysterium pulicare* [CBS 123377 (BPI 878723), U.S.A.]; C–F. *Hysterium angustatum* [ANM 120 (ILLS), U.S.A.; not incl.]; G–K. *Hysterium vermiforme* [GKM 1234 (BPI 879785), Kenya]; L–Q. *Hysterium barrianum sp. nov.* [ANM 1495 (ILLS 59908 = holotype), U.S.A.]. Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 20 µm.

An additional two species have been recently described. *Hysterium asymmetricum* (Checa *et al.* 2007) from Costa Rica, has outer centrum tissues pigmented red, and 3-septate phragmospores, showing an extended basal cell. *Hysterium andinense* has been recently described from the conifer *Austrocedrus chilensis* in Argentina (Messuti & Lorenzo 1997). However, molecular and morphological data (Boehm *et al.* 2009) has placed this taxon in the *Mytilinidiaceae*, as *Mytilinidion andinense*, based on CBS 123562 (BPI 878737). This brings the total number of species within the genus *Hysterium* to 10. An additional new species is described here.

Hysterium barrianum E.W.A. Boehm, A.N. Miller, G.K. Mugambi, S.M. Huhndorf & C.L. Schoch, **sp. nov.** MycoBank MB515330. Fig. 2L–Q.

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

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 mm longa, 250–450 µm alta, 200–300 µm lata. Pseudoparaphyses hyalinae, cellulares, 1–2 µm latae, supra ascos ramosae epithecium formantes. Asci bitunicati, cylindrici, breviter stipitati, (110–)125–135 x 15–20 µm. Phragmosporae fusiformes, angustae, rectae vel paulo curvatae, primum hyalinae, maturae pallide luteae, quaque cellula guttulis magnis refringentibus repleta, (7–)9(–11)-septatae, (35–)40–45(–55) x (7–)9–10(–12) µm.

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

Specimens examined: **U.S.A.**, Tennessee, Sevier Co., Great Smoky Mountains National Park, Elkmont, Little River Trail, 35˚ 39' 13.4" N, 83˚ 34' 44.7" W, 686 m elev., 5 Nov. 2007, A.N. Miller, S.M. Huhndorf, J.L. Crane, T.J. Atkinson, I. Promputtha, M. Grief, G.K. Mugambi, & P. Chaudhary, deposited as ILLS 59908 (ANM 1495) = **holotype**; BPI 879783 = **paratype**; Tennessee, Sevier Co., Great Smoky Mountains National Park, Chimney Tops Picnic Area, Cove Hardwood Loop Trail, 35˚ 38' 10.7" N, 83˚ 29' 32.1" W, 4 Nov. 2007, A.N. Miller, S.M. Huhndorf, J.L. Crane, T.J. Atkinson, I. Promputtha, M. Grief, G.K. Mugambi & P. Chaudhary, deposited as ILLS 59907 (ANM 1442), and BPI 879784.

Notes: A superficial resemblance exists between *Hysterium barrianum* in Clade C, with *H. sinense* in Clade D. The phragmospores of *H. barrianum* (Fig. 2N–Q) have a similar number of septa, (7–)9(–11), as those of *H. sinense* (Fig. 3H), 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 wide taxon sampling strategy for the genus *Hysterium* (Table 1), including multiple isolates for seven of the eleven currently recognised 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 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-sepate spores. None of these species has a swollen supra-median cell. Accessions of *H. angustatum*, originating from South Africa (CMW

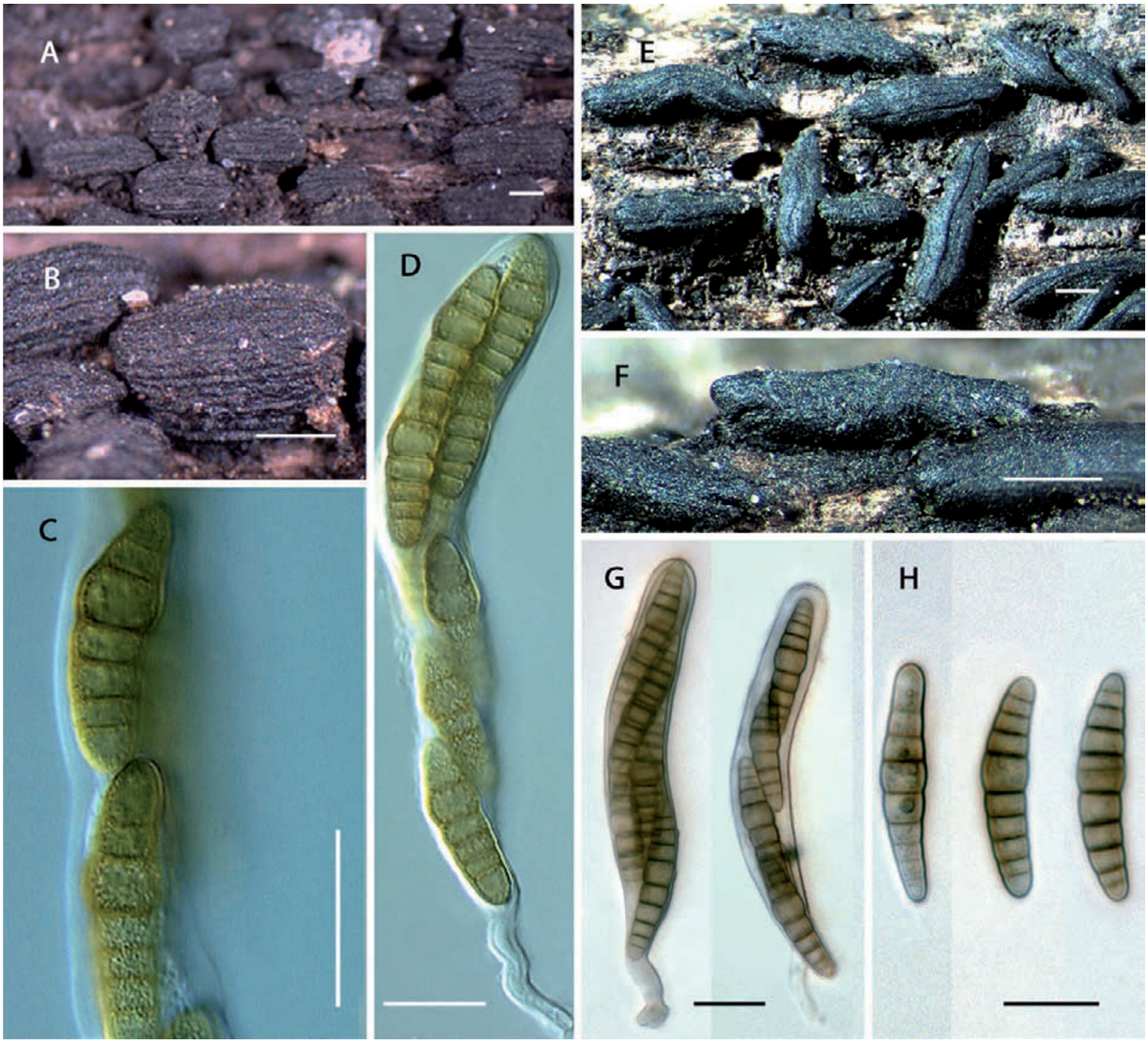

Fig. 3. The genus *Oedohysterium* (Clade D). A–D. *Oedohysterium insidens* [ANM 1443 (BPI 879799), U.S.A.]; E–H. *Oedohysterium sinense* [ANM 119 (ILLS), U.S.A.; not incl.]. Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 20 µm.

20409), Kenya (GKM 243A), New Zealand (SMH 5211.0, SMH 5216) and the United States, New Jersey (CBS 123334) and Wisconsin (CBS 236.34), form a highly supported monophyletic clade with *H. pulicare*, collected from the United States, New York (CBS 123377). Both species possess similar pigmented 3-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), 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 (ILLS) were compared to the other *H. angustatum* accessions from the United States (CBS 123334 / BPI 878724), Kenya (GKM 243A, EA), and New Zealand (SMH 5211.0, F) which formed the other sub-clade within Clade C. All of these specimens showed remarkably little variability in their spore morphology. Additionally, no obvious differences were noted in their fruitbody morphology. This may indicate early stages of speciation within the taxon, with sequence variation preceding morphologic change.

Grouping with the anomalous *H. angustatum* ANM 85, was *H. vermiforme*, a taxon known only from the original description by Massee in 1901 from West Africa (Ghana). The isolate included here (GKM 1234 / BPI 879785; Fig. G–K) originated from Mt. Kenya, Kenya, and possesses smaller spore measurements, (20–)25–28 x (4–)5–6 µm, than those given by Massee (1901), and reiterated by Zogg (1962), as (30–)35–40 x 12–14 µm. In other respects, however, BPI 879785 matches closely Massee'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 3-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. Rather, data indicate that they belong to Clade D. As such, we propose the following new genus to accommodate these taxa.

Oedohysterium E.W.A. Boehm & C.L. Schoch, **gen. nov.** MycoBank MB515421.

Etymology: Greek, *Oedo-* meaning swollen, referring to the swollen supra-median cell of the ascospores and *Hys-* from *Hysterium.*

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(–11) septis divisae, primum pallide luteae, deinde brunnescentes. Cellula (raro duo cellulae) ascosporarum supramediana conspicue inflata. Anamorphe ad *Septonema* pertinens.

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, other times wider than tall. *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, usually short stipitate, and bitunicate. *Ascospores* irregularly biseriate in ascus, typically phragmospores, in one case dictyospores, curved, fusiform, with tapering apices, constricted at the median septum, with (4–)6–8(–11) septa, at first hyaline-yellow, then pigmented sepia to brown at maturity. Genus characterised by a swollen or tumid supra-median cell, rarely with two cells swollen. *Anamorph*: *Septonema*.

Type species: *Oedohysterium insidens* (Schwein.) E.W.A. Boehm & C.L. Schoch, comb. nov.

Oedohysterium insidens (Schwein.) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515422. Fig. 3A–D.

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. 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, Bidrag Kungl. Svenska Vetensk.-Akad. Hist. 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, Ann. Jard. Bot. Madrid 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, 1–2.0 µm wide, walls thickened at apices, forming an epithecium, borne in mucilage, above the ascal layer, often encrusted with dark, pigmented crystals. *Asci* bitunicate, cylindrical, 8-spored, irregularly biseriate, 130–150 x 15–24 µm, short stipitate, and with a prominent apical nasse, especially when young. *Ascospores* phragmospores transversely (4–)6–8(–11)-septate, constricted at the median septum, inequilateral, slightly curved, at first hyaline-yellow, then brown at maturity, with a prominent swollen supra-median cell. If 5-septate, then swollen cell located at the second position; if 6-septate, then often the third from the top, measuring (20–)23–28(–38) x (5–)7–10(–13) µm. Principally North- and South-America, and Europe (Italy), from bark and old wood of *Pinus, Larix, Castanea, Quercus, Eucalyptus, Fraxinus, Aspidosperma,* and *Lavandula* (Zogg 1962). Also reported from South Africa (van der Linde, 1992). Anamorph: *Septonema spilomeum*.

Oedohysterium sinense (Teng) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515423. Fig. 3E–H.

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

= *Hysterium macrosporum* Teng, Sinensia 4: 134. 1933, non Peck, Rep. (Annual) New York State Mus. Nat. Hist. 26: 83. 1874 (1873).

Hysterothecia scattered to subgregarious, linear, sometimes parallel but non-confluent laterally, more often lying at irregular angles, depending on the grain of the substrate, striated in age, usually of a similar size (2–3.5 mm in length), that is, maturing synchronously in a given colony. *Pseudoparaphyses* hyaline to pale-yellow, cellular, 2–2.5 µm wide, apically branched, walls of even thickness along length, forming a darkened gelatinous epithecium above the ascal layer, +/- encrusted with pigmented crystals. *Asci* bitunicate, cylindrical, 8-spored, irregularly biseriate, 140–170 x 26–30 µm, short-stipitate, ascospores biseriate to subseriate in ascus, with a prominent apical nasse, especially when young, but sometimes persisting through maturity. *Ascospores* large, fusiform, asymmetric, curved phragmospores, at first hyaline, then pale-yellow to -brown, finally deep brown at maturity, with (3–)5–9(–11) septa, with a medial septal constriction, measuring (34–)38–50 x 11–15 µm, and, like *Od. insidens*, with a prominent swollen or tumid supra-median cell, usually located just above the median septum. From North America (Boehm, unpubl. data), Europe (Zogg 1962), China (Teng 1933), and South Africa (van der Linde 1992), on decorticated hardwood trees and structures (*e.g.*, aged fence posts).

Notes: Species of *Oedohysterium* belonging to Clade D are characterised by elongate asymmetric spores with more than 3 septa, typically showing a swollen or tumid supra-median cell. In this study, two single-ascospore isolates of *Od. sinense*, one from South Africa (CBS 123345 / BPI 878730), and one from the United States, New Jersey (EB 0339 / BPI 879800), cluster with two isolates of *Od. insidens*, both from the United States, Massachusetts (CBS 238.34) and Tennessee (ANM 1443 / BPI 879799). Both species have remarkably similar phragmospores (*e.g.*, Fig. 3D *versus* Fig. 3H). As these two taxa belong to Clade D and are far removed from the type species, *H. pulicare*, in Clade C, we propose that they be accommodated in the new genus *Oedohysterium*. An additional new combination is proposed below.

Oedohysterium pulchrum (Checa, Shoemaker & Umaña) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515424.

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

Notes: The newly described *Hg. pulchrum* from Costa Rica (Checa *et al.* 2007) also falls within Clade D (Fig. 1) and is here transferred to *Oedohysterium*, as *Od. pulchrum* (DQ 402184 / DAOM 234345). This is because molecular data indicate a close association with the two species of *Oedohysterium*, *Od. insidens* and *Od. sinense*. At first surprising, on further consideration, this sub-clade forms a natural assemblage premised on morphological features. The spores of all three taxa show a remarkable degree of similarity in morphology, which includes being similarly pigmented, slightly curved and fusiform, with a common number of transverse septa. The sole difference is the presence of one or two vertical septa in *Od. pulchrum*, a feature noted by the authors to be absent in some spores (Checa *et al.* 2007). Most importantly, like *Od. insidens* and *Od. sinense*, *Od. pulchrum* also possesses a swollen supra-median cell. Interestingly, a striking resemblance to the phragmospores of *Od. insidens* can be seen for those spores of *Od. pulchrum* that do not possess vertical septa (Checa *et al.* 2007). This is based on similarities in shape (*e.g.*, curved and fusiform), size [(20–)23–28(–38) x (5–)7–10(–13) µm *versus* 22–25(–27) x 5–6 µm], and in the number of transverse septa (4–)6–8(–11) *versus* (5–)6, for *Od. insidens* and *Od. pulchrum*, respectively. As molecular data indicate that the presence or absence of vertical septa should be considered a sympleisiomorphic character state within the *Hysteriaceae* (Boehm *et al.* 2009), we feel justified in including both phragmospores and dictyospores within the genus *Oedohysterium*.

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

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

1. Phragmospores mainly 3-septate 2
1. Phragmospores concolorous, more than 3-septate, in one instance pigmented dictyospores with 1-2 vertical septa (*Od. 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; cosmopolitan ..... ***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; North America ..... ***H. hyalinum***
Note: Currently recognised as *Pleosporomycetidae sp. incertae sedis* (Boehm *et al.* 2009).

4. Phragmospores 3-septate, 28 µm or less in length 5
4. Phragmospores 3-septate, longer than 28 µm 6

5. Phragmospores (12–)14–21(–28) x (3–)4–8(–10) µm, firmly 3-septate, no septal constrictions; end-cells obtuse; cosmopolitan ..... ***H. angustatum***
5. Phragmospores (14–)15–18(–20) x 5–7 µm; 3- (rarely 2- or 4)-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*, North America and China ..... ***H. macrosporum* Peck**

7. Phragmospores or dictyospores (4-) 6- to 8- (11-) celled, fusiform in outline, with +/- swollen supra-median cell(s) 8
7. Phragmospores with more than 11 septa, fusiform, pale brown, (13–)14–15(–21)-septate, (35–)45–50(–60) x (10–)12–13(–14) µm; Africa ..... ***H. velloziae***

8. Swollen supra-median cell(s) present, either phragmospores or dictyospores (*Oedohysterium*) 9
8. Phragmospores only, no swollen supra-median cells(s) present 11

9. Dictyospores lightly pigmented, 22–25(–27) x 5–6 µm, with (5–)6 transverse and 1 vertical septum in either cell or both cells adjacent to the primary septum, absent in some spores, with a swollen supra-median cell; typically with red pigment in the hamathecium; neotropical (Costa Rica) ..... ***Od. pulchrum***
9. With no red pigment present 10

10. Phragmospores with (4–)6–8(–11) 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 ..... ***Od. 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; cosmopolitan ..... ***Od. 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; North America ..... ***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; China and North America ..... ***H. magnisporum***

Gloniella Sacc., Syll. Fung. 2: 765 (1883).

The genus *Gloniella* was established by Saccardo (1883) to accommodate hysteriaceous fungi that possess hyaline phragmospores, from 3- to 9-septate. Zogg (1962) recognised six species: three collected on ferns from Europe and the Mediterranean, namely *Gl. adianti* on *Adiantum*, and *Gl. graphidioidea* and *Gl. normandina*, both on *Pteridium*. Zogg also accepted *Gl. sardoa* from *Populus* in Europe, *Gl. typhae* on *Typha*, the latter described from Europe (Zogg 1962) and Chile (Lorenzo & Messuti 1998), and *Gl. bambusae* on *Bambusa* from Brazil. Since then, an additional three species have been described: *Gl. gracilis* from Costa Rica (Checa *et al.* 2007), *Gl. corticola* from India (Pande & Rao 1991), and *Gl. clavatispora* from South Africa (Steinke & Hyde 1997). More recently, Barr (2009) recognised *Gl. abietina* on *Abies* from Idaho, and *Gl. lapponica* on *Arctostaphylos* from Washington. A number of species in the key may be conspecific, since reported spore measurements are 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; India ..... ***Gl. corticola***
2. Ascospores 12–14 x 4–5 µm; on *Typha*, Europe ..... ***Gl. typhae***

3. On ferns in Europe 4
3. Not on ferns 6

4. Ascospores (2–)3(–4)-septate, (11–)15–20(–23) x 3–5 µm; on *Adiantum*, Europe ..... ***Gl. adianti***
4. Ascospores (3–)5(–7)-septate, slightly longer 5

5. Ascospores (3–)5-septate, (15–)18–20(–22) x 4–5 µm; on *Pteridium*, Europe ..... ***Gl. graphidoidea***
5. Ascospores 5–7-septate, (22–)25–27(–30) x 3–4 µm; on *Pteridium*, Europe ..... ***Gl. normandina***

6. Ascospores 1–3-septate, 36–39 x 10 µm; on *Arctostaphylos*, Western North America ..... ***Gl. lapponica***
6. Ascospores with more septa 7

7. Ascospores 3(–5) septate, 20–27 um x 7–8 µm; on *Abies grandis*, Western North America ..... ***Gl. abietina***
7. Ascospores with more septa 8

8. Ascospores (6–)7(–8)-septate, (16–)18–21(–26) x 6–7(–8) µm; on *Populus*, Europe ..... ***Gl. sardoa***
8. Ascospores larger 9

9. Ascospores (5–)6(–8)-septate, (18–)37(–41) x 10–11.5 µm, hyaline, smooth; on *Avicennia marina*, South Africa ..... ***Gl. clavatispora***
9. Ascospores smaller, neotropical 10

10. Ascospores 6–7-septate, 32–37(–40) x 4–6 µm; Costa Rica ..... ***Gl. gracilis***
10. Ascospores (5–)6–7-septate, (28–)32–38(–44) x (3–)4–8(–9) µm; on *Bambusa*, Brazil ..... ***Gl. bambusae***

Hysterographium Corda, Icon. Fung. 5: 34. 1842.

= *Hysteriopsis* Speg., Revista Fac. Agron. Univ. Nac. La Plata 2: 308. 1907.
= *Polhysterium* Speg., Anales Mus. Nac. Buenos Aires 23: 87. 1912.
= *Fragosoa* Cif., in Ciferri & Fragoso, Bol. Real Soc. Esp. Hist. Nat., Secc. Biol. 26(3-4): 194. 1926.

Although the genus *Hysterographium* has been removed from the *Hysteriaceae* (Boehm *et al.* 2009), and is currently recognised as *Pleosporomycetidae gen. incertae sedis*, it is included here. This is because it forms the basis for a number of new combinations within the family. The genus is characterised by pigmented dictyospores, with one to several longitudinal septa, ovoid to ellipsoid-fusoid, relatively broad, usually constricted at the first-formed septum. Zogg (1962) extensively revised the synonymy of the genus and accepted four species: *Hysterographium flexuosum* (Fig. 4A–B) and *Hg. fraxini* (Fig. 4C–D), the type, both with large dictyospores, prominently constricted at the median septum, the former with slightly longer, narrower spores. Zogg (1962) also accepted *Hg. mori* and *Hg. subrugosum*, with smaller, fewer-celled dictyospores, short and squat in the former, longer and more slender in the latter, both also constricted at the median septum.

Since then, an additional three species have been described: *Hysterographium minus* from Japan (Amano 1983), *Hg. spinicola*

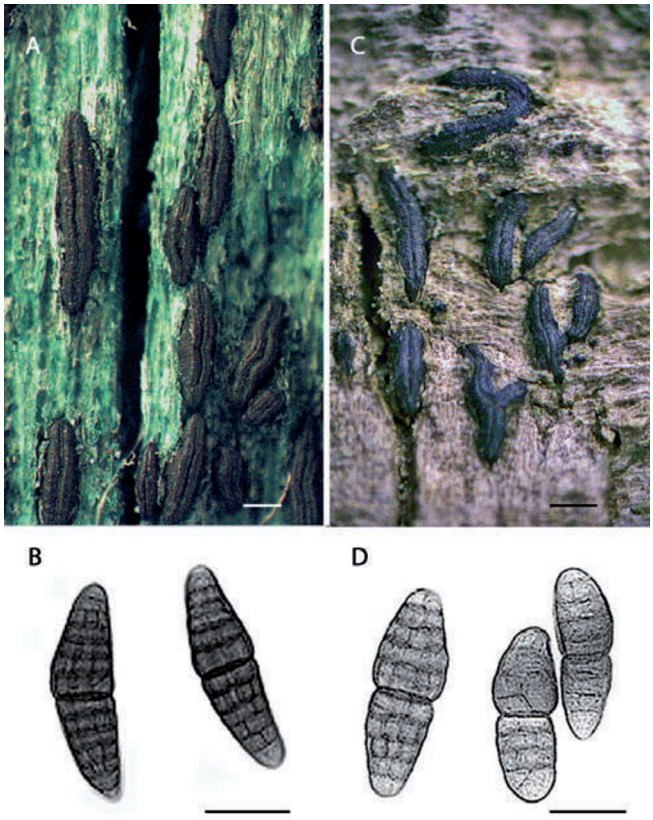

Fig. 4. The genus *Hysterographium*. A–B. *Hysterographium flexuosum* (EB 0098, U.S.A.; not incl.); C–D. *Hysterographium fraxini* (EB 0100, U.S.A.; not incl.). Scale bar (habitat) = 1 mm; Scale bar (spores) = 20 µm.

from South Africa, recollected from the thorns of *Acacia* and validated by van der Linde (1992), with a brick-red epithecium and spores only slightly longer than those of *Hg. mori*, and, lastly, *Hg. pulchrum* from Costa Rica, also with a red pigment in the hamathecium (Checa *et al.* 2007), here transferred to *Oedohysterium*, as *Od. pulchrum*.

Four of the seven species were surveyed in the present study, with multiple isolates (Table 1): *Hysterographium mori* (8), *Hg. subrugosum* (3), *Hg. fraxini* (2) and *Od. 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*, represented by isolates from Switzerland (CBS 109.43), deposited by Zogg in 1943, and from Canada (CBS 242.34), deposited by Lohman in 1934. *Hysterographium fraxini* forms a well-supported clade distant from the *Hysteriaceae,* but remains within the *Pleosporomycetidae* (Fig. 1). As this is substantiated by two geographically disparate isolates from two different continents, deposited by two reputable workers, it is significant. The implication is that the genus *Hysterographium* must follow the type species and be removed from the *Hysteriaceae* (Boehm *et al.* 2009). Species with pigmented dictyospores remaining within the *Hysteriaceae*, previously classified in *Hysterographium*, must therefore be accommodated in other genera. In this study, these would include the following species, for which we have sequence data: *Hysterographium mori*, *Hg. subrugosum*, and *Hg. pulchrum* (= *Od. 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.

Hysterobrevium E.W.A. Boehm & C.L. Schoch, **gen. nov.** MycoBank MB515329.

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

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, cyindrici 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.

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. *Ascospores* 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; ascospores generally ovoid to obovoid, with either obtuse or acuminate ends, 3–4(–6) transverse septa, and 1–2 longitudinal septa, these mostly associated with the two central cells, but highly variable and sometimes at oblique angles in the end cells.

Type species: *Hysterobrevium mori* (Schwein.) E.W.A. Boehm & C.L. Schoch, comb. nov.

Hysterobrevium mori (Schwein.) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515335. Fig. 5J–R.

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

≡ *Hysterographium mori* (Schwein.) Rehm, Ascomyceten No. 363. 1876.
= *Hysterium grammodes* De Not., Giorn. Bot. Ital. 2 (7–8): 55. 1847.
≡ *Hysterographium grammodes* (De Not.) Sacc., Syll. Fung. 2: 782. 1883.
= *Hysterium rousselii* De Not., Piren. Ister. 2(7–8): 19. 1847.
≡ *Hysterographium rousselii* (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. Genève 16(1): 44. 1862.
= *Hysterium lesquereuxii* Duby, Mém. Soc. Phys. 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, in Harkness & Cooke, Grevillea 7: 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., Anales Soc. Ci. Argent., Secc. Santa Fe. 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., Anales Soc. Ci. Argent., Secc. Santa Fe. 26(1): 56. 1888.
= *Hysterographium punctiforme* Pat., Bull. Soc. Mycol. France 4: 120. 1888.
= *Hysterographium ruborum* Cooke, in Rehm, Ascom., No. 918. 1888.
= *Hysterium insulare* P. Karst. & Har., Rev. Mycol. Toulouse No. 47: 1890.
= *Hysterographium incisum* Ellis & Everh., Bull. Torrey Bot. Club 24: 462. 1897.

= *Hysterographium ziziphi* Pat., Cat. Rais. Pl. Cell. Tunisie: 112. 1897 (as *"zizyphi"*).
= *Hysterographium rousselii* (De Not.) Sacc. var. *piri* Feltgen, Vorst. Pilz. Luxemb. Nachtr. 3: 111. 1903.

Hysterothecia erumpent-superficial, ellipsoidal, oblong, linear or cylindrical, 1–2(–3.5) 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. Two types of hysterothecial aggregations regularly observed, depending on substrate: (1) Colonies on weathered, whitened decorticated hardwood often forming large oval colonies, with acuminate ends, measuring 5–15 cm in length, with hysterothecia gregarious in the center, densely packed in longitudinal formations, showing multiple stages of development, and darkening the adjacent substrate; when young, prior to emergence of hysterothecia, smaller colonies are seen, but still presenting darkened oval patches, often with coelomycetous anamorph present. (2) Colonies on bark (*i.e.*, corticolous) less gregarious, not darkening the substrate, hysterothecia often situated at angles, rather than in parallel orientation. *Peridium* 30–60 µm thick medially, to 100+ µm at the base, distinctly three-layered in cross-section, the outer layer darkly pigmented, the middle less so, and the inner layer, thin-walled, pallid and compressed. *Pseudoparaphyses* cellular, septate, persistent, 1–2 µm wide, hyaline, thickened apically, branched and forming an epithecium in a gelatinous matrix above the ascal layer. *Asci* cylindrical to clavate, bitunicate, short-stipitate, (50–)80–110 x 10–18 µm. *Ascospores* pigmented, thin-walled dictyospores, obovoid, ends obtuse, 3–(5–7)-septate, with 1–2(–3) vertical septa usually associated with mid-cells, but on occasion also present obliquely in end cells, constricted at the median septum, sometimes, when fully hydrated, at additional, more distal septa, measuring (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, usually decorticated, weathered wood or bark 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).

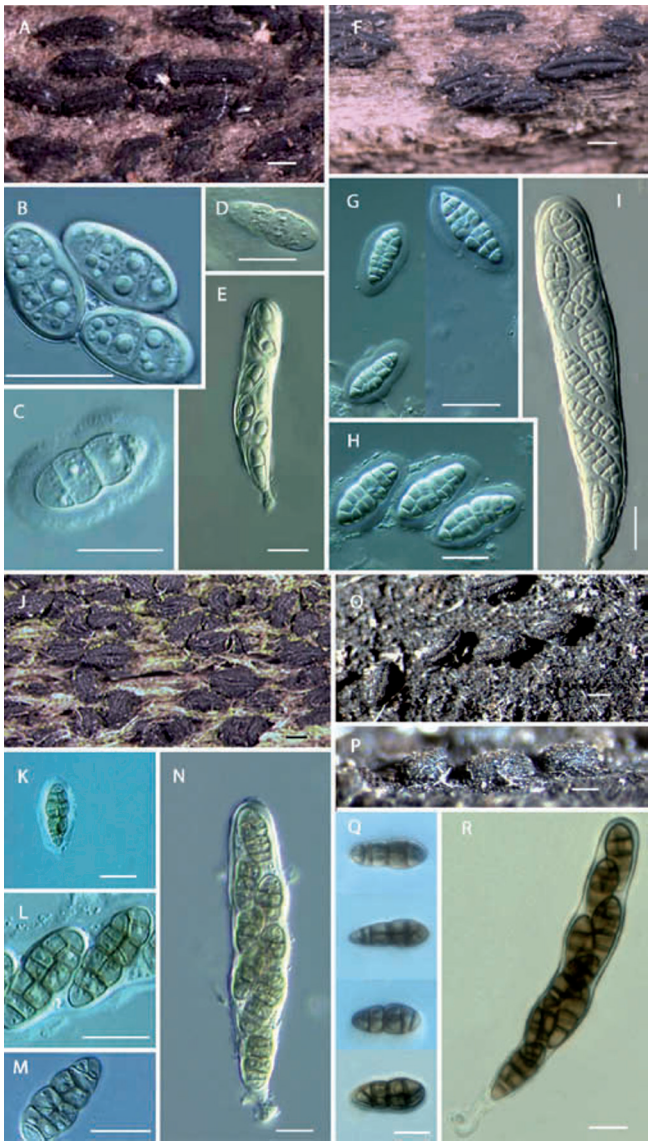

Fig. 5. The genus *Hysterobrevium* (Clade A). A–E. *Hysterobrevium constrictum* [SMH 5211.1 (F), New Zealand]; F–I. *Hysterobrevium smilacis* [GKM 426N (EA), Kenya]; L–N. *Hysterobrevium mori* [SMH 5273 (BPI 879787), U.S.A.]; O–R. *Hysterobrevium mori* [ANM 43 (ILLS), U.S.A.; not incl]. Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 10 µm.

Hysterobrevium smilacis (Schwein.) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515336. Fig. 5F–I.

Basionym: *Hysterium smilacis* Schwein., Schriften Naturf. Ges. Leipzig 1: 49. 1822.

≡ *Gloniopsis smilacis* (Schwein.) Underw. & Earle, Bull. Alabama Agric. Exp. Sta. 80: 196. 1897.
≡ *Hysterographium smilacis* (Schwein.) Ellis & Everh., N. Amer. Pyrenomyc. 709. 1892.
= *Hysterium biforme* Fr., Observ. Mycol. (Havniae) 2: 354. 1818.
≡ *Gloniopsis biformis* (Fr.) Sacc., Syll. Fung. 2: 773. 1883.
= *Hysterium elongatum β curvatum* Fr., Elench. Fung. (Greifswald) 2: 138. 1828.
= *Hysterium curvatum* Fr., Elench. Fung. 2: 139. 1828.
≡ *Gloniopsis curvata* (Fr.) Sacc., Syll. Fung. 2: 775. 1883.
= *Hysterium rocheanum* Duby, Mém. Soc. Phys. 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* W.R. Gerard in Peck, Rep. New York State Mus. 32: 49. 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.

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. *Peridium* 25–50 µm wide, narrower at base within the substrate, widest at mid-point, carbonaceous and brittle when dry. *Pseudoparaphyses* cellular, septate, persistent, 1–1.5 µm wide, hyaline to pale yellow in mass, branched above, forming an epithecium, but not darkly pigmented, exposed surface yellow-brown. *Asci* cylindrical to clavate, bitunicate, short-stipitate, 70–120 x 15–25 µm at maturity. *Ascospores* asymmetric, hyaline to pale yellow dictyospores, with acuminate ends, and a gelatinous sheath that usually dissipates at maturity, measuring (13–)15–26(–

31) x (4–)5–9(–10) µm. Spore septation highly variable, usually 3–5(–9)-septate and with 1(–3) vertical septa, passing through multiple mid-cells, and usually prominently constricted at the median septum, when fresh and hydrated, sometimes constriced along multiple transverse septa. *Anamorph* coelomycetous, *Aposphaeria*-like. Cosmopolitan on *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*, while falling within the *Hysteriaceae*, finds itself in two separate clades (Fig. 1). In Clade A, one set of North American *Hb. mori* isolates associates with six highly geographically diverse isolates of *Hb. smilacis*. The *Hb. mori* isolates originate from the United States, from New Jersey (CBS 123336, CBS 123564), New York (CBS 123335, CBS 123563), Indiana (SMH 5273) and Michigan (SMH 5286). The *Hb. smilacis* isolates originate from the United States, from Indiana (SMH 5280) and Michigan (CBS 200.34), as well as from South Africa (CMW 18053), Sweden (CBS 114601) and Kenya (GKM 426N). Dictyospores of both species are of similar shape, size and degree of septation: (12–)14–22(–26) x (5–)7–10(–11) µm, 3–(5–7)-septate, with 1–2(–3) vertical septa, for *Hb. mori versus* (13–)15–26(–31) x (4–)5–9(–10) µm, 3–5(–9)-septate, with 1(–3) vertical septa, for *Hb. smilacis*. They differ in the absence of pigmentation and the presence of a gelatinous sheath in the latter. Thus, these two species, previously classified in two separate genera, *Hysterographium* and *Gloniopsis*, are in fact closely related, with each species far removed from the type species of their respective genera. Further support for this argument, can be found in Lohman (1933a), who found a similar *Aposphaeria* anamorph for both *Hb. mori* (as *Hg. mori*) and *Hb. smilacis* (as *Gp. 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 *Hb. smilacis* in Clade A, *Hb. mori* also finds itself in Clade D. As this is validated by two geographically diverse isolates, one from the United States, Michigan (CBS 245.34) and one from Kenya (GKM 1013 / BPI 879788), it is significant. Spore measurements of the Kenyan accession GKM 1013 (BPI 879788) in Clade D *versus* those of other *Hb. mori* accessions in Clade A, represented by SMH 5273 / BPI 879787, CBS 123335 / BPI 878734, and CBS 123336 / BPI 878733, failed to detect any significant morphological differences; nor were there any appreciable differences detected in their hysterothecia. The association of *Hb. mori* with unrelated taxa within the *Hysteriaceae* in Clade A and D may be significant in that *Hb. mori* has long been regarded as a highly variable taxon (Ellis & Everhart 1892, Lohman 1933a), resulting in the synonymy of no fewer than 30 names since its inception by Schweinitz in 1832 (Zogg 1962). Future studies may well reveal that *Hb. mori* contains a number of cryptic species, morphologically similar, but genetically unrelated. We propose an additional new combination below.

Hysterobrevium constrictum (N. Amano) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515337. Fig. 5A–E.
Basionym: *Gloniopsis constricta* N. Amano, Trans. Mycol. Soc. Japan 24: 289. 1983.

Notes: Amano (1983) described a small-spored species of *Gloniopsis* from Japan, *Gp. constricta*, 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 *Hb. smilacis* (as *Gp. curvata*), the latter however with slightly larger spores. In this study, we were fortunate to obtain a specimen from New Zealand (SMH 5211.1, deposited in F; Fig. 5A–E) that corresponds to the published description given by Amano (1983), but differs on several counts. Like *Gp. constricta*, the hyaline dictyospores in SMH 5211.1, are highly symmetric and 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 *Gp. constricta*, 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 *Gp. constricta*. Nevertheless, these differences, in our opinion, are not sufficient to warrant a new species, and we choose here to simply expand the spore measurements to (11–)13–20(–23) x 5–12 µm, rather than describe a new species, proposing instead the new combination *Hb. constrictum*.

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 characterised by hyaline to yellow dictyospores, often inequilateral, curved, in outline obovoid, ends obtuse to sub- to acuminate, multi-septate, with one or more longitudinal septa, constricted at the first-formed septum, sometimes constricted at additional septa, and usually surrounded by a gelatinous sheath, which may dissipate with age. Zogg (1962) synonymised a number of names under the type species, *Gp. praelonga* (Fig. 6A–B), and accepted only one additional species, namely *Gp. curvata* with smaller ascospores. Barr (1990a) proposed to include this latter species under the earlier name *Gp. smilacis*, following Cash (1939). In this study, we have transferred *Gp. smilacis* to *Hysterobrevium*, closely related to *Hb. mori* in Clade A. Recently, *Gp. argentinensis*, previously considered by Zogg (1962) as a doubtful species, was reinstated by Lorenzo & Messuti (1998). The authors state that the ascospores are 7-septate, with 1–3(–4) longitudinal septa, some passing through multiple cells, in outline widely ellipsoid, measuring 20–26 x 9–12 µm. The septation and spore measurements are nearly identical to those of *Gp. praelonga*, the latter 5–7(–10)-septate, with 2–3 longitudinal septa, (16–)20–32(–34) x (6–)9–12(–15) µm. We therefore synonymise *Gp. argentinensis* under *Gp. praelonga*. Lastly, Amano (1983) described an additional two species of *Gloniopsis* from Japan, namely *Gp. macrospora* and *Gp. constricta*, the latter transferred here to *Hysterobrevium* (Clade A).

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

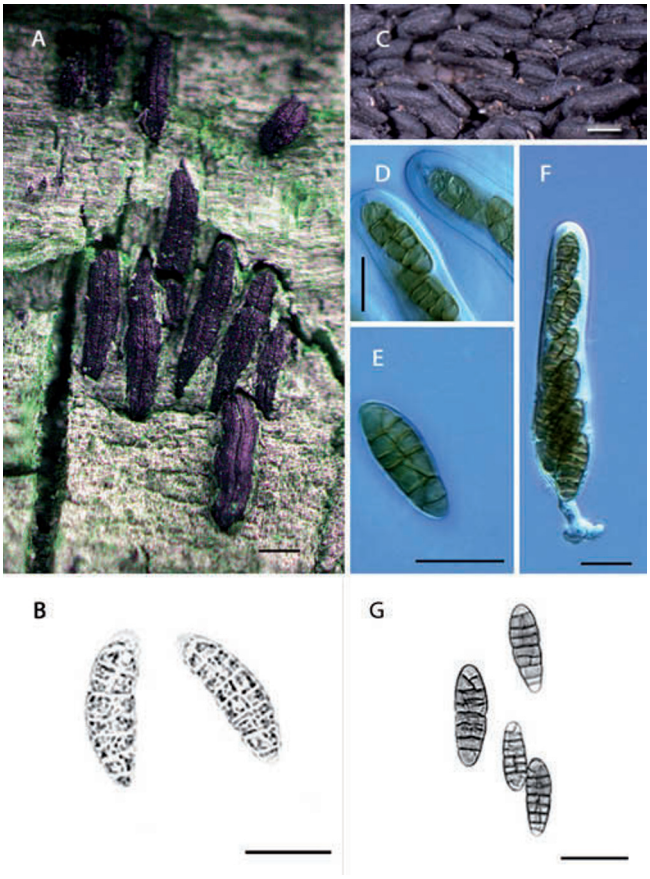

Fig. 6. The genus *Gloniopsis* (Clade D). A–B. *Gloniopsis praelonga* [CBS 123337 (BPI 878725), U.S.A.]; C–F. *Gloniopsis subrugosa* [GKM 1214 (BPI 879776), Kenya]; G. *Gloniopsis subrugosa* (CBS 123346, BPI 878735; South Africa). Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 20 µm.

Gloniopsis subrugosa (Cooke & Ellis) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515338. Fig. 6C–G. *Basionym*: *Hysterium subrugosum* Cooke & Ellis, Grevillea 5: 54. 1876.

≡ *Hysterographium subrugosum* (Cooke & Ellis) Sacc., Syll. Fung. 2: 780. 1883.

= *Hysterographium hiascens* Rehm, Ber. Naturhist. Vereins. 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. Sci. 17: 267. 1933.

Hysterothecia erumpent to superficial, scattered to densely crowded, navicular, straight to flexuous, with tapered ends, surface not striated in age, but smooth to sub-rugose in texture, 1–2 mm long, 250–350 µm diam. *Peridium* composed of small pseudoparenchymatous cells, heavily pigmented at the surface, not showing a distinct number of layers, relatively smooth on outer surface. *Pseudoparaphyses* narrowly cellular, septate, 1–1.5 µm in diam., hyaline, branched above the asci, borne in a gelatinous matrix. *Asci* cylindrical to clavate, bitunicate, short-stipitate, 80–150 x 18–25 µm, with a prominent apical nasse, especially when young. *Ascospores* pigmented thin-walled, dictyospores (22–)25–34(–45) x (6–)8–12(–17) µm, mostly with 7–11 transverse and 1–2 vertical septa, hardly constricted at septa, clear brown, ends paler at times, slightly asymmetric in outline. *Anamorph* coelomycetous, *Aposphaeria*-like (Lohman 1933a). Less frequently collected, but reported from North America (Barr 1990b), Europe (Zogg 1962), Argentina (Messuti & Lorenzo 2003) and from South Africa (van der Linde 1992) as well. Old wood and bark of *Populus, Quercus, Celtis, Crataegus, Rosa,* and *Cotinus* (Zogg 1962), as well as on weathered fence posts and old planks (Boehm, unpubl. data).

Notes: In the current study, we were able to include three geographically diverse isolates of *Gp. praelonga* (Table 1), two from South Africa (CBS 112415 and CMW 19983 / PREM 57539), and one from the United States, New Jersey (CBS 123337 / BPI 878725). These isolates cluster together in Clade D and associate with one isolate of *Gp. subrugosa* from South Africa (CBS 123346 / BPI 878735). Both *Gp. praelonga* and *Gp. subrugosa* are somewhat similar in the shape, size and septation of their dictyospores, hyaline in the former (Fig. 6B), pigmented in the latter (Fig. 6G). The spores of *Gp. praelonga* are (16–)20–32(–34) x (6–)9–12(–15) µm, and those of *Gp. subrugosa* are (22–)25–34(–45) x (6–)8–12(–17) µm. Septation is also similar in both species, with 5–7(–10) transverse and 2–3 vertical septa in *Gp. praelonga* and 7–11 transverse and 1–2 vertical septa in *Gp. subrugosa*. They differ in pigmentation and the presence of a gelatinous sheath in the type. Molecular data indicate that they are closely related.

An additional two isolates of *Gp. subrugosa*, from Kenya (GKM 1214 / BPI 879776) and Cuba (SMH 557 / BPI 879777), are more distantly related and do not fall in Clade D. Moreover, no morphological differences were noted between these two more distantly associated isolates of *Gp. subrugosa* and CBS 123346 (BPI 878735) from South Africa in Clade D. Although spore morphology dictates that all three specimens of *Gp. subrugosa* should be classified as the same species, molecular data point to genetic heterogeneity within the taxon. This is similar to the situation in *Hb. mori*, mentioned earlier, which, despite identical morphologies, finds affinities in both Clades A and D. *Hysterobrevium mori* and, to a lesser extent, *Gp. subrugosa*, may represent ancestral lineages that have maintained stable morphologies, while simultaneously incurring sufficient genetic change to, in the case of *Hb. mori*, fall into different clades within the family. Alternatively, these isolates may represent examples of convergent evolution among genetically unrelated lineages, which produce remarkably similar ascospores and hysterothecia. Also associating with *Gp. praelonga* and *Gp. subrugosa* in Clade D are two new species from East Africa, described below.

Gloniopsis arciformis E.W.A. Boehm, G.K. Mugambi, S.M. Huhndorf & C.L. Schoch, **sp. nov.** MycoBank MB515331. Fig. 7A–H.

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

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) x 6–10 µm.

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

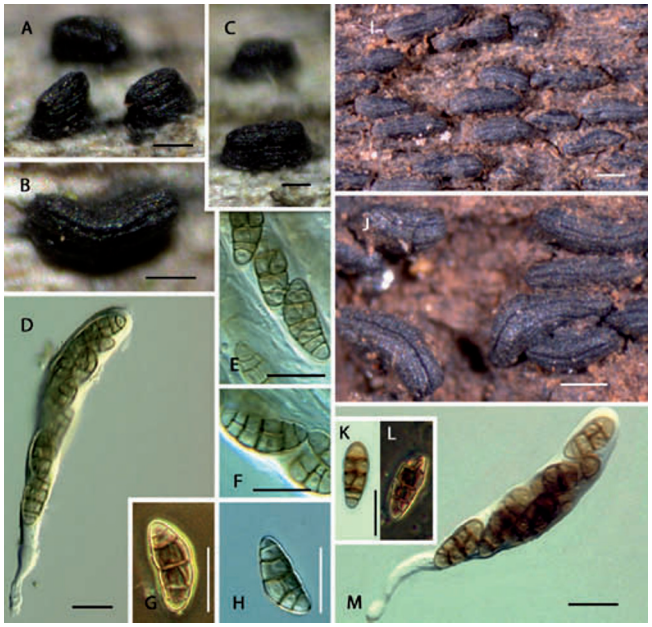

Fig. 7. The genus *Gloniopsis* (Clade D). A–H. *Gloniopsis arciformis sp. nov.* [GKM L166A (BPI 879774 = holotype), Kenya]; I–M. *Gloniopsis kenyensis sp. nov.* [GKM 1010 (BPI 879775 = holotype), Kenya]. Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 10 µm.

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. *Pseudoparaphyses* cellular 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 x 14–18 µm (n = 7), ascospores irregularly biseriate. *Ascospores* pigmented, thin-walled, dictyospores, 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) x 6–10 µm (n = 17).

Specimen examined: **Kenya**, Coast Province, Malindi District, Arabuko-Sokoke National Park, 6 Nov. 2006, G.K. Mugambi. Deposited as BPI 879774, **holotype** [formerly, GKM L166A (EA)].

Notes: *Gloniopsis arciformis* is represented by a single specimen (BPI 879774) of only ~30 fruitbodies in the protected crevice of a small piece of decorticated hardwood, collected in Arabuko-Sokoke National Park, Malindi District, Kenya. Although the material is sparse, it does permit the description of a new species on account of the highly unusual arcuate dictyospores. *Gloniopsis arciformis* resides in Clade D, and is phylogenetically closely associated with two other species of *Gloniopsis* (*Gp. praelonga* and *Gp. subrugosa*), as well as with an additional new species described below.

Gloniopsis kenyensis E.W.A. Boehm, G.K. Mugambi, S.M. Huhndorf & C.L. Schoch, **sp. nov.** MycoBank MB515359. Fig. 7I–M.

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

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

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

Specimen examined: **Kenya**, Coast Province, Malindi District, Arabuko-Sokoke National Park, 6 Apr. 2005, G.K. Mugambi. Deposited as BPI 879775, **holotype**; GKM 1010 (EA), **paratype**.

Notes: Molecular data indicate that both *Gp. kenyensis* and *Gp. arciformis* are closely associated, adjacent to *Gp. praelonga* and *Gp. subrugosa* in Clade D. The spores of all four taxa, however, are different, and thus their association would not have been predicted based on traditional morphology. The spores of *Gp. kenyensis* do bear a close resemblance, however, to those of *Hb. mori*. Both have predominantly 3-septate, thin-walled, pigmented dictyospores, with 1–2 vertical septa, often with oblique septa in the end cell. They can be differentiated on spore size: (12–)14–22(–26) x (5–)7–10(–11) µm for *Hb. mori, versus* (12–)15–18(–19) x 5–7(–8) µm for *Gp. kenyensis*. The spores of *Hb. mori* are usually longer and wider, and also show prominent septal constrictions, especially when fresh and hydrated. Additionally, *Gp. kenyensis* is highly guttulate when young, where this is rarely observed in *Hb. mori*. Molecular data indicate that they are not related.

To summarise, 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* (*Hb. constrictum* and *Hb. smilacis*), and species with pigmented dictyospores, previously classified as *Hysterographium* (*Hb. mori*) in Clade A; (2) the inclusion in *Gloniopsis* of both hyaline (*Gp. praelonga*) and pigmented (*Gp. subrugosa*, *Gp. arciformis*, *Gp. kenyensis*) dictyospores in Clade

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

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

1. Dictyospores, usually shorter than 25 µm 2
1. Dictyospores mostly longer than 25 µm 6

2. Dictyospores pigmented, thin-walled, fragile, pronouncedly arcuate or bent, 3–5(–7)-septate, with 1–2(–3) vertical septa, which are mostly associated with the mid-cells, these much larger and swollen than the end-cells, no septal constrictions, (10–)12–18(–22) x 6–10 µm; Kenya ..... ***Gp. arciformis***
2. Not with the above combination of characters 3

3. Dictyospores hyaline at maturity 4
3. Dictyospores pigmented at maturity 5

4. Dictyospores highly symmetric in outline and septation, with thickened walls, gelatinous sheath present when young, absent at maturity, (1–)3(–4)-septate, with 1(–2) vertical septa, that may pass through one to two cells; (11–)13–20(–23) x 5–12 µm; Japan, New Zealand ..... ***Hb. constrictum***
4. Dictyospores asymmetric, with acuminate ends, with a gelatinous sheath when young, mostly 3–5(–9)-septate and with 1(–3) vertical septa, passing through multiple mid-cells, prominently constricted at the median septum, sometimes constriced at multiple septa, (13–)15–26(–31) x (4–)5–9(–10) µm; cosmopolitan ..... ***Hb. smilacis***

5. Dictyospores thin-walled, obovoid, with obtuse ends, 3–(5–7)-septate, with 1–2(–3) vertical septa, usually associated with mid-cells, but occasionally present obliquely in end-cells, constricted at the median septum, sometimes at additional septa, (12–)14–22(–26) x (5–)7–10(–11) µm; cosmopolitan ..... ***Hb. mori***
5. Dictyospores thin-walled, very fragile, obovoid, 3[–4(rarely)]-septate, with 1–2 vertical septa, highly gutulate when young, spore apices asymmetric, the upper obtuse, the lower acuminate and sometimes drawn out, often with oblique septa in end cell(s), hardly constricted at the septa, measuring (12–)15–18(–19) x 5–7(–8) µm; Kenya ..... ***Gp. kenyensis***

6. Red pigment present in hamathecium and/or centrum; dictyospores pigmented 7
6. No red pigment present, spores pigmented or hyaline 8

7. Dictyospores, 22–25(–27) x 5–6 µm, with (5–)6 transverse and 1 vertical septum in either cell or both cells adjacent to the primary septum; typically with red pigment in the hamathecium; neotropical (Costa Rica) ..... ***Od. pulchrum***
Note: *Od. pulchrum* is accommodated in the genus *Oedohysterium* and is present in both keys.
7. Dictyospores 25–28 x 11–13 µm, with 5–6 transverse and mostly one longitudinal septum; hamathecium brick-red; on *Acacia* thorns, South Africa ..... ***Hg. spinicola***

8. Dictyospores hyaline or turning brown tardily 9
8. Dictyospores pigmented in the ascus 10

9. Dictyospores hyaline turning yellow in age, obovoid, ends usually obtuse, 5–7(–10)-septate, with 2–3 longitudinal septa, constricted at the median and often other septa, gelatinous sheath when young, (16–)20–32(–34) x (6–)9–12(–15) µm; cosmopolitan ..... ***Gp. praelonga***
9. Ascospores irregularly biseriate, 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 ..... ***Gp. macrospora***

10. Dictyospores usually less than 38 µm long 11
10. Dictyospores 30–80 µm long 12

11. Dictyospores (22–)25–34(–45) x (6–)8–12(–17) µm, mostly with 7–11 transverse and 1–2 vertical septa; cosmopolitan ..... ***Gp. subrugosa***
11. Dictyospores 26–38 x 10–15 µm, with 6–13 transverse and 1–3 vertical septa, obovoid, ends obtuse; Japan ..... ***Hg. minus***

12. Dictyospores (25–)30–45(–51) x (10–)12–15(–22) µm, with 7–9 transverse and 2–3 vertical septa, obovoid, ends obtuse; cosmopolitan ..... ***Hg. fraxini***
Note: *Hysterographium fraxini*, the type species for the genus *Hysterographium*, lies outside of the *Hysteriaceae*, as *Pleosporomycetidae incertae sedis* (Boehm *et al.* 2009).
12. Ascospore outline ellipsoid, fusoid, ends slightly acuminate, (30–)40–65(–80) x (8–)10–18(–19) µm, with 7–15 transverse and 1–3 vertical septa; cosmopolitan ..... ***Hg. flexuosum***

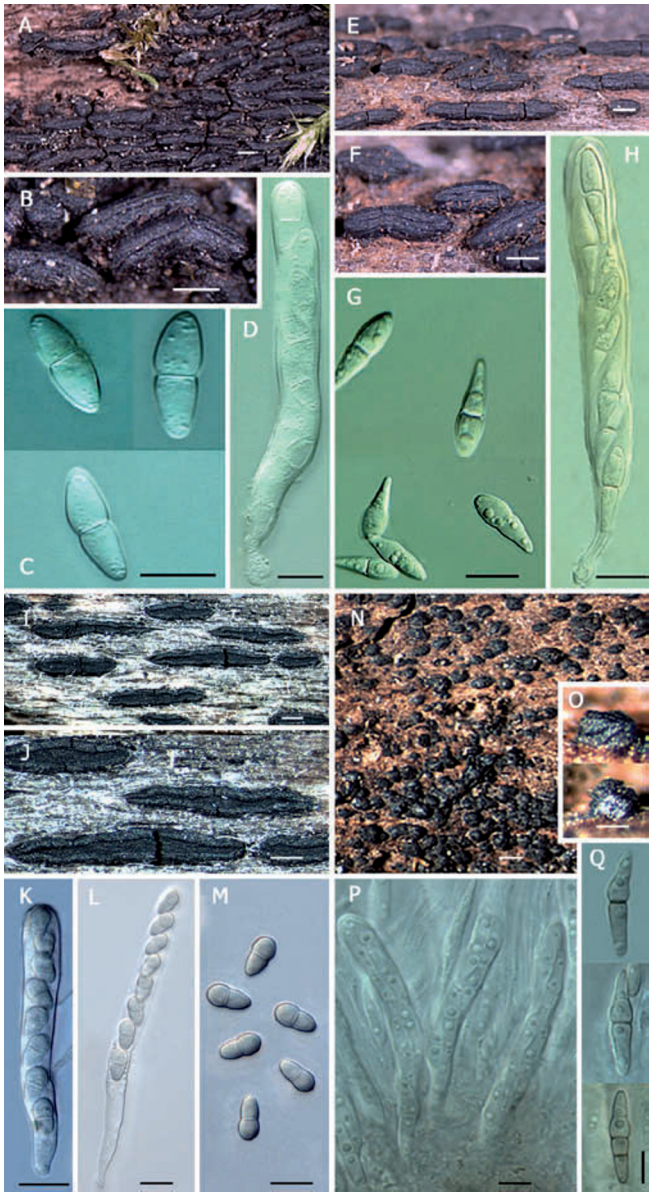

Fig. 8. The genus *Psiloglonium* (Clade B). A–D. *Psiloglonium simulans* [ANM 1557 (BPI 879803), U.S.A.]; E–H. *Psiloglonium clavisporum* [GKM 344A (BPI 879801), Kenya]; I–M. *Psiloglonium lineare* [ANM 117 (ILLS), U.S.A.; not incl.]; N–Q. *Psiloglonium araucanum* [ANM 42 (ILLS), U.S.A.; not incl.]. Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 10 µm.

Psiloglonium Höhn., Ann. Mycol. 16: 145. 1918.

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

Von 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) recognised 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* (Fig. 8I–M), retaining *G. stellatum* as the type species for the genus *Glonium sensu* von Höhnel (1918). Petrak (1923a, b) eventually placed a number of species in *Psiloglonium*, all subsequently transferred to *Glonium* by Zogg (1962). Müller & von Arx (1950) originally accepted the genus *Psiloglonium*, but later reduced it to a synonym of *Glonium* (von Arx & Müller 1975). Lohman (1933a, 1937) also did not support *Psiloglonium*, based on the observation that similar anamorphs were shared between species of the two subgenera. Barr (1987), was the only modern author to retain the genus *Psiloglonium*, as distinct from the subiculate *Glonium*.

Although von 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) do in fact possess subicula on occasion (*e.g.*, *P. lineare*). Zogg (1962) further noted an additional two species that were occasionally associated with subicula, namely *G. pusillum* and *G. graphicum*, 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 (1923a, b) in *Psiloglonium* (*e.g.*, *P. lineare*, *P. microspermum*, *P. ruthenicum*, and *P. finkii*) to the genus *Glonium*.

Although Zogg (1962) did not support *Psiloglonium*, he did in fact recognise three distinct morphological forms within his concept of *Glonium*, two of which (Types I and II) we incorporate in *Psiloglonium*, the third (Type III) forming the basis for the *Gloniaceae* (Boehm *et al.* 2009). Zogg (1962) arranged the species of *Glonium* based on (1) didymospore shape: spore apices obovoid to rounded (Type I) *versus* spores fusiform with acuminate apices (Type II and III); and (2) the degree of complexity surrounding the architecture of the hysterothecia, simple, linear, solitary to gregarious (Types I, II) *versus* complex bifurcating, laterally anastomosing to form flabelliform pseudostellate composites, sometimes associated with a thin stromal crust (Type III). Thus, the genus *Glonium sensu* Zogg (1962) was comprised of two groups of species, one with obovoid to rounded spores apices borne in regular hysterothecia (Type I) *versus* those with acuminate spore apices borne in complex bifurcating or modified hysterothecia (Type III). Species belonging to Type II possess fruitbodies of Type I, but spores of Type III; the assumption was that they constituted an intermediate, perhaps transitional, morphological group. This, then, de-emphasised the presence or absence of subicula *per se*, as stressed by von Höhnel (1918) and Petrak (1923a, b). Nevertheless, Zogg (1962) maintained all three types within the genus *Glonium*. Molecular data

presented here (see below), indicate that Types I & II are closely related, with Type III forming a distant clade in the *Gloniaceae* (Boehm *et al.* 2009).

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

Psiloglonium lineare was previously reinstated within the *Hysteriaceae*, listing *G. lineare* as a synonym (Boehm *et al.* 2009). Here we also reinstate *Psiloglonium finkii*. An additional two species are included in Type I, namely *G. simulans* and *G. clavisporum*, synonymised by Zogg (1962) under *G. lineare*, but earlier recognised 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 *P. simulans* (Fig. 8A–D) and *P. clavisporum* (Fig. 8E–H). To these species can also be added *G. sasicola* 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*, also from Japan. The spore measurements were given as 13.1–16.8 x 4–5.6 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 synonymise *G. macrosporum* under *P. simulans*.

More recently, Lorenzo & Messuti (1998), in a reappraisal of the type specimens collected by Spegazzini and Hennings from Argentina and Chile, have reinstated *Glonium costesii*. In a later publication, Messuti & Lorenzo (2007) synonymised *G. costesii* under the earlier epithet *G. ephedrae*. 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* and *G. uspallatense*, previously considered by Zogg (1962) to be doubtful species. The spores of *G. chilense* measure 15–16 x (5–)7–8 µm, which places it very close to *P. lineare*, the latter with slightly smaller spores, (10–)12–14(–18) x (4–)5–7(–8) µm (Zogg 1962). However, *G. chilense* has almost identical ascomatal and spore measurements as *P. simulans*, given above. We therefore synonymise *G. chilense* with the earlier name *G. simulans*, as *P. simulans*. For *G. uspallatense*, Messuti & Lorenzo (2007) gave spore measurements of 18–24 x 10–12 µm, intermediate between *G. chambianum*, (14–)16–18(–21) x (6–)8–9(–10) µm (Zogg 1962), and *G. sasicola*, 25–32 x 5–8 µm (Amano 1983).

Recently, Mugambi & Huhndorf (2009) proposed a new genus, *Anteaglonium*, outside of the *Hysteriales* but within the *Pleosporales*, to accommodate *A. abbreviatum* (Fig. 9A–E), *A. globosum* (Fig. 9F–I), *A. parvulum* (Fig. 9J–M), and *A. latirostrum* (Fig. 9N–R). The

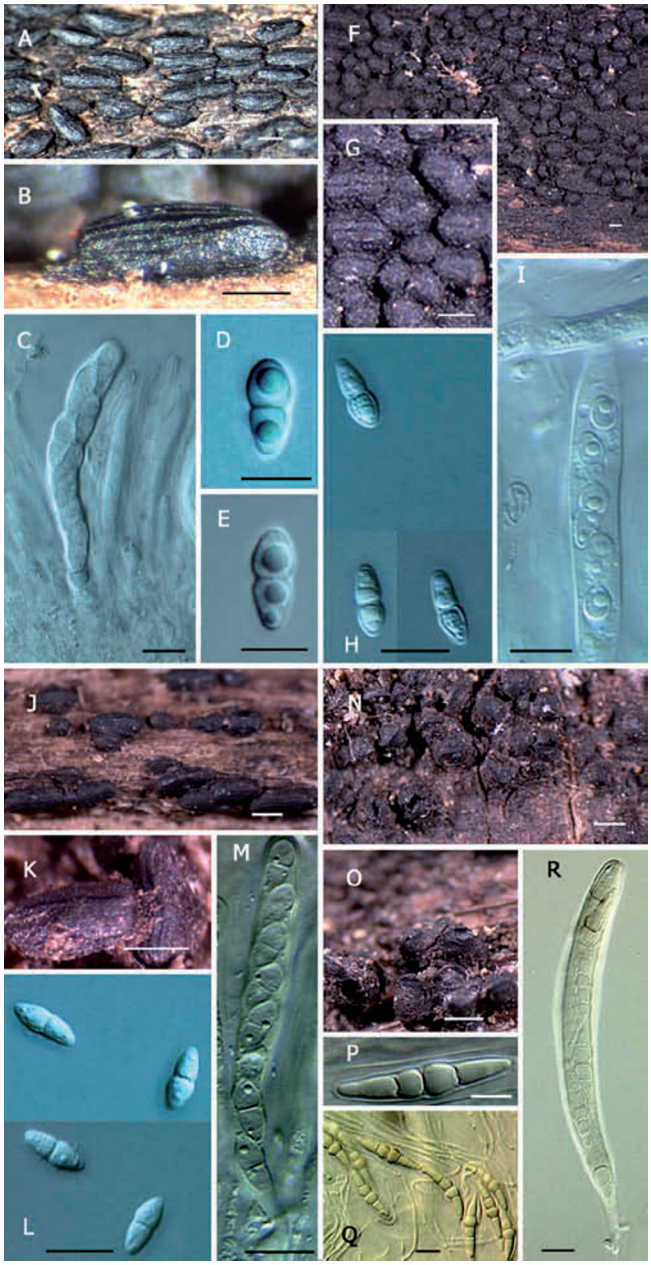

Fig. 9. The genus *Anteaglonium* (*Pleosporales*). A–E. *Anteaglonium abbreviatum* [ANM 37 (ILLS), U.S.A.; not incl.]; F–I. *Anteaglonium globosum* [ANM 925.2 (ILLS), U.S.A.]; J–M. *Anteaglonium parvulum* [GKM 219N (EA), Kenya; not incl.]; N–R. *Anteaglonium latirostrum* [GKM L100N.2 (EA), Kenya]. Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 5 µm.

first three species are characterised 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 phylogenetically unrelated to *Psiloglonium*, these species share a similar morphology and thus are included in the key below.

Type II: This type is characterised by relatively large didymospores, distinctly fusoid in outline, prominently constricted at the septum, and with acuminate apices. Zogg (1962) recognised two species, namely *Glonium caucasicum* and the much larger-spored, neotropical *G. hysterinum*, to which can be added the newly described *G. colihuae*, on *Chusquea culeou* from Argentina (Lorenzo & Messuti 1998). *Glonium caucasicum* has recently been synonymised under the earlier name *G. araucanum* by Messuti & Lorenzo (2007), based on a comparison of the type specimen of *G. caucasicum* to Spegazini's earlier type of *G. araucanum* from Chile.

Type III: This type corresponds to von Höhnel's (1918) and Petrak's (1923a, 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* (Fig. 12A–E), *G. compactum*, and *G. graphicum*, the later sometimes variably associated with subicula. Zogg (1962) also stated that *G. compactum* possesses a subiculum, much like *G. stellatum*, and with similar spore size, but whereas hysterothecia in *G. stellatum* are merely seated on the subiculum, in *G. compactum* the hysterothecia are embedded in and arise from a thin stromal crust, which is itself seated on subicula. Recently, a fourth species was added, based on molecular evidence (Boehm *et al.* 2009), namely *G. circumserpens* (Fig. 12F–H), from Tasmania (Kantvilas & Coppins 1997).

Sequence data presented here (Fig. 1) and elsewhere (Boehm *et al.* 2009, Mugambi & Huhndorf 2009), clearly indicate that the genus *Glonium sensu* Zogg (1962) actually comprises three entirely unrelated lineages within the *Pleosporomycetidae*, one within the *Hysteriaceae* and two forming clades outside of the family. The first lineage corresponds to *Psiloglonium sensu* von Höhnel (1918), and forms a highly supported monophyletic clade in this study (Clade B in Fig. 1). This clade includes: *Psiloglonium clavisporum*, with four single-ascospore isolates from New Jersey, the United States (CBS 123338 / BPI 878726, CBS 123339 / BPI 878727, CBS 123340 / BPI 878728 and CBS 123341 / BPI 878729), and two from Kenya (GKM 344A / BPI 879801, GKM L172A in EA), *P. simulans*, with two isolates from the United States, one from Michigan (CBS 206.34), deposited in 1934 by Lohman, and a more recent collection from Tennessee (ANM 1557 / BPI 879803), and, lastly, *P. araucanum*, with three isolates from South Africa, two from Kirstenbosch (CBS 112412 / PREM 57570, CMW 18760/ PREM 57569) and one from Jonkershoek (CMW 17941 / PREM 575566). *Psiloglonium clavisporum* and *P. simulans* belong to Type I, whereas *P. araucanum* belongs to Type II. Both are phylogenetically related and reside in Clade B (Fig. 1). Recently, a second lineage has been shown to be associated with the *Pleosporales*, now accommodated in the new genus *Anteaglonium* (Mugambi & Huhndorf 2009), for which we include six accessions representing four species (Table 1). The third lineage corresponds to *Glonium* (Type III), in the *Gloniaceae* (Boehm *et al.* 2009), for which we have included four isolates, representing two species (Table 1). We treat here all species of *Glonium sensu* Zogg (1962), belonging to Types I and II, outside of *Anteaglonium*, as belonging to *Psiloglonium*. Since the generic name *Glonium* is reserved for species in the *Gloniaceae* (Boehm *et al.* 2009), we propose eight new combinations for the genus *Psiloglonium*.

Psiloglonium pusillum (H. Zogg) E.W.A. Boehm & C.L. Schoch, ***comb. nov.*** MycoBank MB515327.
Basionym: *Glonium pusillum* H. Zogg, Beitr. Kryptogamenfl. 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*. *Psiloglonium 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. It has also been found in North America (Boehm, unpubl. data).

Psiloglonium chambianum (Guyot) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515320.
Basionym: *Glonium chambianum* Guyot, Ann. Serv. Bot. Tunisie 28: 90. 1955.

Notes: Originally from North Africa, on *Lonicera implexa* (*Caprifoliaceae*), the fungus has since been reported from the *Proteaceae* in South Africa (Lee & Crous 2003) and Europe. Zogg (1962) gave the spore measurements for *G. 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 obovoid, obtuse apex. *Psiloglonium chambianum* possesses larger spores than *P. lineare*, *P. simulans*, and *P. clavisporum*, but smaller than *P. uspallatense*.

Psiloglonium uspallatense (Speg.) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515321.
Basionym: *Glonium uspallatense* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires. 19: 436. 1909.

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

Psiloglonium sasicola (N. Amano) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515322.
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*) in Japan. The ascospore measurements were given as 25–32 x 5–8 µm, with a rounded apical cell, placing it between *P. uspallatense* and *P. ephedrae*. Amano (1983) further reported that ascospores of this species are associated with a gelatinous sheath, previously not known among these didymospored fungi.

Psiloglonium ephedrae (Henn.) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515323.
Basionym: *Glonium ephedrae* Henn., Öfvers. K. Vet. Akad. Förhandl. 2: 328. 1900.
= *Glonium costesi* Speg., Bol., Acad. Ci., Córdoba 25: 78. 1921.

Notes: Messuti & Lorenzo (2007) reinstated *G. ephedrae* with the synonym *G. costesi*, after locating and comparing original type materials. *Psiloglonium 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* in Chile.

Psiloglonium hysterinum (Rehm) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515324.
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) E.W.A. Boehm & C.L. Schoch, **comb. nov.** MycoBank MB515325.
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 *Nothofagus* rainforests. The spore measurements were given 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 was with the slightly smaller-spored *G. caucasicum*.

Psiloglonium araucanum (Speg.) E.W.A. Boehm, S. Marincowitz & C.L. Schoch, **comb. nov.** MycoBank MB515326. Fig. 8N–Q.
Basionym: *Glonium araucanum* Speg., Revista Fac. Agron. Univ. Nac. La Plata 6: 110. 1910.
= *Gloniella caucasica* Rehm, Vestn. Tiflissk. Bot. Sada 25:12. 1912.
≡ *Glonium caucasicum* (Rehm) H. Zogg, Beitr. Kryptogamenfl. Schweiz. 11(3): 67. 1962.

Notes: Messuti & Lorenzo (2007) transferred *Glonium caucasicum* to *G. araucanum*, after examining the types for both species. Previously, Zogg (1962) had transferred *Gloniella caucasica* to *Glonium*. Here we transfer *G. araucanum* to *Psiloglonium*. 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. data), and from South Africa (Lee & Crous 2003).

Lee & Crous (2003) identified a series of isolates from South Africa on the *Restionaceae* as *Glonium compactum* (CBS 112412, CMW 18760, CMW 17941). However, in their study they did not note the presence of subicula, nor a stromal crust. These features were stressed for this taxon by Zogg (1962). These same isolates were used in Boehm *et al.* (2009), and were shown to associate, with high branch support, with two species of *Psiloglonium*, *P. clavisporum* and *P. simulans*, distant from the other species of *Glonium* surveyed (*e.g.*, *G. stellatum* and *G. circumserpens*). Thus, a new combination was proposed, *Psiloglonium compactum*. However, it is now realised 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* (Type II) and not *G. compactum* (Type III), 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*, along with species with obtuse spore apices, belonging to Type I (*e.g.*, *P. simulans* and *P. clavisporum*). A reanalysis of the original South African herbarium specimens from which the sequences were derived (PREM 57570, PREM 57569, PREM 57566), by S. Marincowitz, has confirmed that they do indeed correspond to *P. araucanum* and not to *G. compactum*. Molecular data thus supports the association of Types I and II within the genus *Psiloglonium*.

In addition to the 12 currently recognised species in *Psiloglonium*, the following key also includes entries for the unrelated *Gloniaceae*, *Anteaglonium* and *Ostreichnion 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 (Type I) 3
2. Ascospores fusiform (*i.e.*, spindle-shaped), with both ends acuminate, usually constricted at the septum (Types II and III) 14

3. Ascospores small, 8 µm or less in length (*Anteaglonium*, in part) 4
3. Ascospores longer than 8 µm (*Psiloglonium* Type I) 6

4. Ascospores 6–8 x 2.5–3 µm; hysterothecia with apices acuminate, but not associated with a darkened crust; no KOH-soluble pigments; New Zealand, East Africa, North America ..... ***A. parvulum***
Note: *A. parvulum* lies within the *Pleosporales* (Mugambi & Huhndorf 2009).
4. Not with the above combination of characters 5

5. Ascospores (5–)6–7(–8) x 2–3(–3.5) µm (as in *A. parvulum*); but hysterothecia with apices truncated, and associated with a darkened crust (tending to darken the substratum); minute amounts of soluble pigment in KOH (easily missed); Europe, East Africa, North America ..... ***A. abbreviatum***
Note: *A. abbreviatum* lies within the *Pleosporales* (Mugambi & Huhndorf 2009)

5. Ascospores 6–7 x 2–3 µm (as in *A. parvulum* and *A. abbreviatum*); but hysterothecia globose with roughened walls, an indistinct slit, and associated with sparse, short subicula, and also with short tomentum on the walls of the ascomata; like *A. abbreviatum* also associated with a darkened crust on substrate; producing a strong green soluble pigment in KOH; eastern and mid-western North America ..... ***A. globosum***
Note: *A. globosum* lies within the *Pleosporales* (Mugambi & Huhndorf 2009).

6. Ascospores (9–)10–12(–13) x 4–5(–6) µm; cosmopolitan ..... ***P. pusillum***
6. Ascospores slightly larger 7

7. Ascospores (10–)12–14(–18) x (4–)5–7(–8) µm; ascomata +/- confluent laterally, in parallel rows, semi-immersed to erumpent; cosmopolitan ..... ***P. lineare***
7. Ascospores similar in length; ascomata not confluent laterally, usually entirely superficial 8

8. Ascospores (10–)14–16(–18) x (4.5–)5–6 µm; cosmopolitan ..... ***P. simulans***
8. Ascospores slightly larger 9

9. Ascospores (15–)16–18(–20) x 5–6(–7) um; *Sporidesmium stygium* anamorph usually present; North and South America, Africa ..... ***P. clavisporum***
9. Ascospores slightly larger in length and breadth 10

10. Ascospores (14–)16–18(–21) x (6–)8–9(–10) µm; Europe, North Africa ..... ***P. chambianum***
10. Ascospores slightly larger 10

11. Ascospores 18–24 x 10–12 µm; Argentina ..... ***P. uspallatense***
11. Ascospores slightly larger 12

12. Ascospores 25–32 x 5–8 µm, with a gelatinous sheath; Japan ..... ***P. sasicola***
12. Ascospores slightly larger 13

13. Ascospores 26–35 x 8–15 µm; Chile ..... ***P. ephedrae***
13. Ascospores (59–)62–68(–76) x 13–15 µm; North and South America ..... ***O. curtisii***
Note: The genus *Ostreichnion*, previously placed in the *Mytilinidiaceae*, has been transferred to the *Hysteriaceae* (Boehm *et al*. 2009).

14. Hysterothecia usually borne in/on subicula, typically bifurcated, forming radiating flabelliform or pseudo-stellate composites, with or without a stroma (Type III) ..... ***Gloniaceae***
Note: In this study, a key to the species of the *Gloniaceae* is provided under that family.
14. Hysterothecia not bifurcated, forming radiating flabelliform or pseudo-stellate composites, nor with a stroma 15

15. Ascospores less than 30 µm long 16
15. Ascospores more than 30 µm long 17

16. Ascospores (19–)22–25(–27) x (6–)7–9(–10) µm, both ends acuminate, with a prominent septal constriction; cosmopolitan (Type II) ..... ***P. araucanum***
16. 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; Kenya ..... ***A. latirostrum***
Note: *A. latirostrum* lies within the *Pleosporales* (Mugambi & Huhndorf 2009).

17. Ascospores 30–43 x 4–9.8 µm; Argentina (Type II) ..... ***P. colihuae***
17. Ascospores about 45 x 9 µm; Brazil (Type II) ..... ***P. hysterinum***

Actidiographium Lar.N. Vassiljeva**,** Mikol. Fitopatol. 34 (6): 4. 2000.

Vasilyeva (2000) established the monotypic genus *Actidiographium* to accommodate a hysteriaceous fungus with pigmented one-septate ascospores, reminiscent of those found in *Actidium* in the *Mytilinidiaceae*. However, in *Actidiographium orientale*, the two-celled spores are borne in a typical thick-walled hysterothecium. The pigmented didymospores measure 13.2–16.5 x 3–4 µm. Molecular data are lacking for this taxon.

Hysterocarina H. Zogg, Ber. Schweiz. Bot. Ges. 59: 39. 1949.

Zogg (1949) erected this monotypic genus for *Hysterocarina paulistae*, with pigmented dictyospores as in *Hysterographium*, but the hysterothecia are borne within the substrate, barely erumpent at maturity, and with a cristate, slightly evaginated longitudinal keel, instead of the invaginated sulcus typical of most members of the *Hysteriaceae*. Described from old wood of *Eucalyptus* sp. 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 *Mytilinidiaceae* and *Gloniaceae*. Clearly, molecular data are needed to resolve these issues.

Ostreichnion Duby, Mém. Soc. Phys. Genève 16: 22. 1862.
= *Ostreion* Sacc., Syll. Fung. 2: 765. 1883.

Since its reappraisal (Barr 1975), the genus *Ostreichnion* has been heterogeneous, due to the inclusion of *O. curtisii* an unusual taxon, from the southeastern United States (Lohman 1937) and Brazil (Zogg 1962). It is very different from the other two species of this genus, namely the type *O. sassafras* and *O. nova-caesariense*. Whereas the latter two species possess pigmented dictyospores, in *O. curtisii* the ascospores are 1-septate below the middle, with walls greatly thickened towards the spore apices. When mounted under 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 species of *Psiloglonium* and *Glonium*, which send out apical germ tubes (Lohman 1931, 1932a). *Ostreichnion sassafras* occurs on both sides of the Atlantic, as well as in China, and has been recovered from *Sassafras*, *Quercus*, *Liriodendron*, and *Liquidambar* (Bisby 1932, Teng 1933, Barr 1975). 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. *Ostreichnion nova-caesariense* is known only from the type locality in New Jersey on *Pinus*, and has similar, but smaller, ascospores (Barr 1975).

Based on a recent four-gene analysis (Boehm *et al.* 2009), the genus *Ostreichnion*, previously in the *Mytilinidiaceae* (Barr 1975, 1990a), was transferred to the *Hysteriaceae*. This was based on sequence data derived from two of the three species (Table 1), namely *O. curtisii* (CBS 198.34) and *O. sassafras* (CBS 322.34), deposited by Lohman in 1934. Although both species find residency within Clade C (Fig. 1), their association with the genus *Hysterium* 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*. However, molecular data suggest neither. Instead, *O. curtisii* shares a subclade with *Hysterium barrianum*, with 9-septate phragmospores (Fig. 1). *Ostreichnion sassafras* is more distant within Clade C. Although we recognise 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 1-septate, ends greatly thickened, (45–)62–80 x (10–)12–15 µm; North & South America ..... ***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; North America ..... ***O. nova-caesariense***
2. Ascospores measuring (65–)76–100(–135) x 20–32 µm, with up to 27 septa, borne four to an ascus; cosmopolitan ..... ***O. sassafras***

Rhytidhysteron Speg., Anales Soc. Ci. Argent. 12: 188. 1881.

The genus *Rhytidhysteron* is characterised by ascomata that are at first closed and navicular (*e.g.*, Fig. 10K), somewhat resembling those found in the *Hysteriaceae*, but then later opening by a longitudinal sulcus to become irregularly apothecioid at maturity, often with incurved margins (*e.g.*, Fig. 10M) – a feature never observed in the *Hysteriaceae*. The peridium in *Rhytidhysteron* is somewhat gelatinous when wet, as compared to the hard, carbonaceous peridium found in the *Hysteriaceae*. Although ascomata may possess striations, in *Rhytidhysteron* these are perpendicular to the long axis (Fig. 10K), rather than parallel, as in the *Hysteriaceae* (*e.g.*, Figs 1A, 2B, and 6A). The ascospores in *Rhytidhysteron* tend to be heavily pigmented and thick-walled, as opposed to lightly pigmented and thin-walled in the *Hysteriaceae.* These features, among others, have been used to place *Rhytidhysteron* within the *Patellariaceae* (*e.g.*, Kutorga & Hawksworth 1997). Samuels & Müller (1979) revised the genus, providing a number of synonyms, and accepted only two species, namely the type, *R. rufulum* (Fig. 10E–K), with 3-septate phragmospores, and *R. hysterinum* (Fig. 10M), with 1-septate spores, both darkly pigmented and thick-walled. Anamorphs have been characterised as *Diplodia*- and *Aposphaeria*-like (Samuels & Müller 1979). Subsequently, another two species have been accepted in the genus, namely *R. dissimile* (Magnes 1997), with 5-septate phragmospores, and *R. opuntiae* (1990b), from the American South West, with short pigmented dictyospores (Fig. 10A–D), reminiscent of those found in *Hb. mori*.

Dictyospores of both *R. opuntiae* and *Hb. mori* are similar in shape, obovoid, with obtuse ends, and are also similar in size and septation. 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 *Hb. 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 ascomata, as in other members of the genus. Rather, the ascomata are hysterithecioid, that is, carbonaceous, navicular, with an invaginated longitudinal sulcus (Fig. 10A–B). In hindsight, it is remarkable that Barr (1990) recognised *R. opuntiae* as a member of *Rhytidhysteron*, transferring it from *Hysterographium opuntiae,* despite the presence of hysterithecioid ascomata. In this study we were fortunate to acquire an isolate of *R. opuntiae* from Kenya (GKM 1190 / BPI 879805). *Rhytidhysteron opuntiae* falls distant from *R. rufulum* and *R. hysterinum,* lying outside of Clade E altogether (Fig. 1). Although both morphological and molecular data suggest that *R. opuntiae* should be removed from the genus *Rhytidhysteron*, this is based only on a single specimen, and clearly needs to be substantiated with other isolates.

The six isolates of *R. rufulum* included one from Kenya (GKM 361A / BPI 879806; Fig. 10E–J), four from Ghana (EB 0381 / BPI 879807, Fig. 10L; EB 0382 / BPI 879808, Fig. 10K; EB 0383 / 879809; EB 0384 / BPI 879810), and one from Europe (CBS 306.38). Also included was one isolate of *R. hysterinum* from

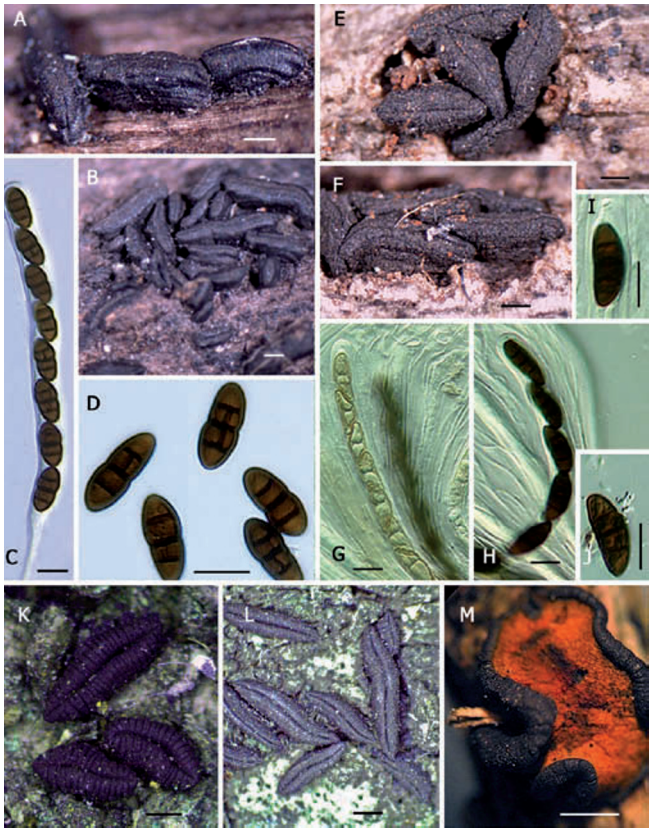

Fig. 10. The genus *Rhytidhysteron* (Clade E). A–D. *Rhytidhysteron opuntiae* [GKM 1190 (BPI 879805), Kenya]; E–J. *Rhytidhysteron rufulum* [GKM 361A (BPI 879806), Kenya]; K. *Rhytidhysteron rufulum* [EB 0382 (BPI 879808), Ghana]; L. *Rhytidhysteron rufulum* [EB 0381 (BPI 879807), Ghana]; M. *Rhytidhysteron hysterinum* [EB 0351 (BPI 879804) France, photo by Alain Gardiennet]. Scale bar (habitat) = 1 mm; Scale bar (spores and asci) = 10 µm.

France (EB 0351 / BPI 879804). Three of the Ghanian isolates clustered together in Clade E (Fig. 1), but one (EB 0381 / BPI 879807) associated in another subclade, along with the Kenyan (GKM 361A) and European (CBS 306.38) accessions of *R. rufulum*. The morphology of the ascomata (Fig. 10L) of *R. rufulum* EB 0381 (BPI 879807) differs from other more typical specimens of *R. rufulum* (*e.g.*, Fig. 10 K), although the 3-septate spores in both are identical. Finally, molecular data indicate that *R. hysterinum*, with 1-septate spores, falls outside of the *R. rufulum* subclades, while still within Clade E (Fig. 1).

Boehm *et al.* (2009) were the first to provide sequence data indicating that *Rhytidhysteron* does not lie within the *Patellariaceae*. Although initially 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 that the genus *Rhytidhysteron* belongs to the family *Hysteriaceae*, and not to the *Patellariaceae*, the latter defined in this study to include *Hysteropatella clavispora* (CBS 247.34), *Hp. elliptica* (CBS 935.97), and *Patellaria atrata* (CBS 958.97).

Earlier, Barr (1987) had noted the differences between *Rhytidhysteron* and other members of the *Patellariaceae*, stating: "*Rhytidhysteron rufulum* illustrates the problem: paraphysoids and a well-developed pseudoepithecium are conspicuous, but the structure of the peridium, thickened base of ascoma, cylindric asci, are all features attributed to members of the *Hysteriaceae*. When the heterogeneous family *Patellariaceae* is revised, *Rhytidhysteron* should be segregated in its own family". Samuels & Müller (1979) 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 *Rhytidhysteron* 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 *Rhytidhysteron*

1. Ascospores mainly 1-septate; Europe ..... ***R. hysterinum***
1. Ascospores with more than one septum 2

2. Ascospores mainly 3-septate 3
2. Ascospores with five or more septa; Europe ..... ***R. dissimile***

3. Ascospores with three transverse, but also one or more longitudinal septa; Southwestern United States, East Africa ..... ***R. opuntiae***
3. Ascospores transversely 3-septate, with no longitudinal septa; cosmopolitan ..... ***R. rufulum***

Mytilinidiaceae Kirschst. 1924, ***Mytilinidiales*** E.W.A. Boehm, C.L. Schoch & J.W. Spatafora 2009.

= *Lophiaceae* H. Zogg *ex* Arx & E. Müll., Stud. Mycol. 9: 60. 1975.

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

Fungi classified in the *Mytilinidiaceae* (Kirschstein 1924) are characterised by fragile yet persistent carbonaceous ascomata, which range from globoid to obovoid to strongly laterally compressed erect, bivalve shell-shaped (*i.e.*, conchate) structures, standing on edge, with lateral walls more or less connivent, and extended vertically, in some species, to a prominent longitudinal keel or cristate apex. Mytilinidioid 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 scolecospores to didymospores to phragmospores or dictyospores, hyaline, soon yellow to dark brown, and generally showing bipolar symmetry (Zogg 1962, Barr 1987, 1990a). Anamorphs in the *Mytilinidiaceae* are primarily coelomycetous (*e.g.*, *Aposphaeria*, *Pyrenochaeta*, *Camaroglobulus*, *Dothiorella*-like, and *Sclerochaeta*) and less frequently hyphomycetous (*e.g.*, *Chalara*-like, *Papulaspora*, and *Septonema*) (Lohman 1932b, 1933a, b, Blackwell & Gilbertson 1985, Speer 1986). Typically temperate in distribution, mytilinidioid fungi are found in association with the wood, bark, resin, cones, scales, needles, seeds, and roots of gymnosperms.

Currently accepted genera in the *Mytilinidiaceae* include: *Actidium*, *Lophium*, *Mytilinidion*, *Ostreola*, and *Quasiconcha*, to

which has recently been added *Zoggium* (Lohman 1932b, Zogg 1962, Darker 1963, Barr 1975, 1990a, Barr & Blackwell 1980, Vasilyeva 2001). The genus *Ostreichnion*, previously classified within the *Mytilinidiaceae*, has been removed to the *Hysteriaceae* (Boehm *et al.* 2009). The genus *Glyphium*, originally classified within the *Mytilinidiaceae*, has recently been transferred to the *Chaetothyriales* in the *Eurotiomycetes* (Lindemuth *et al.* 2001, Lumbsch *et al.* 2005). This has been restated in a number of subsequent publications (Lücking *et al.* 2004, Schmitt *et al.* 2005, Geiser *et al.* 2006, Kodsueb *et al.* 2006), including the Assembling the Fungal Tree of Life (AFTOL) Project (Lutzoni *et al.* 2004). A study currently in preparation (Boehm *et al*.) will address issues related to the phylogenetic placement of the genus *Glyphium*. Despite their transference out of the *Mytilinidiaceae*, 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 *Mytilinidiaceae*

1. Ascospores 1-septate, small, shorter than 30 µm 2
1. Ascospores not didymospores, or if 1-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, multi-septate, about equal in length to the ascus, in some case, at maturity longer than the ascus, often spirally arranged 4
3. Ascospores ellipsoid, fusoid, cylindrical, if scolecospores, then shorter than the ascus and not spirally arranged 6

4. Ascomata conchate, solitary to gregarious, but never forming fused, ridge-like assemblages ..... ***Lophium***
4. Ascomata either forming rigid, fused band- or ridge-like structures or solitary, erect, dolabrate to ligulate 5

5. Ascomata 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: A key to the species is not presented here.

6. Ascospores transversely septate phragmospores, or scolecospores ..... ***Mytilinidion***
6. Ascospores dictyospores, or large and remaining 1-septate 7

7. Ascospores ellipsoid, less than 30 µm long, with a single longitudinal septum, usually passing through the mid-cells, or spanning the entire length of the ascospore ..... ***Ostreola***
7. Ascospores ellipsoid or cylindric, longer than 30 µm, with several longitudinal septa in cells or large and remaining 1-septate ..... ***Ostreichnion***
Note: The genus *Ostreichnion* previously classified within the *Mytilinidiaceae* (Barr 1990a) has been transferred to the *Hysteriaceae* (Boehm *et al.* 2009).

Actidium Fr., Observ. Mycol. 1: 190. 1815.
= *Mytilinidion* subgen. *Bulliardella* Sacc., Syll. Fung. 2: 764. 1883.
= *Bulliardella* (Sacc.) Paoli, Nuovo Giorn. Bot. Ital. 12:101. 1905.
= *Ostreionella* Seaver, Sci. Surv. Porto Rico & Virgin Islands 8(1): 77. 1926.

The genus *Actidium* was established by Fries (1823) to accommodate *A. hysterioides*, a stellate mytilinidioid fungus found on *Pinus* and *Picea* in Europe, with two-celled, symmetric ascospores, light olive- to reddish-brown, later noted to be faintly longitudinally striate (Barr 1990a). Fries (1823) noted its similarity with the genus *Glonium*. Zogg (1962) recognised a total of four species, namely *A. hysterioides*, *A. baccarinii*, both from Europe, *A. pulchra*, from China, and *A. nitidum*, from Europe and North America, on *Pinus*, *Picea, Juniperus*, and *Thuja* (Zogg 1962, Barr 1990a). Due to similarities in ascospore morphology, the genus *Actidium* may have affinities with other didymospored hysteriaceous genera (*e.g.*, *Actidiographium, Glonium* and *Psiloglonium*), although molecular data are presently lacking.

Key to the species of *Actidium*

1. Ascomata stellate; spores 11–14 x (1.5–)2–3 µm; on *Pinus*, *Picea*, Europe ..... ***A. hysterioides***
1. Ascomata shell-shaped (conchate), not star-shaped 2

2. Ascospores (9–)11–14(–16) x (1.5–)2–3 µm; on *Pinus*, *Picea, Juniperus*, Europe, North America ..... ***A. nitidum***
2. Ascospores larger 3

3. Ascospores (16–)18–22(–24) x (3–)4–5(–6) µm; on *Pinus*, *Picea*, *Thuja,* Europe ..... ***A. baccarinii***
3. Ascospores 23–28 x 6–7.5 µm; China ..... ***A. pulchra***

Quasiconcha M.E. Barr & M. Blackw., Mycologia 72: 1224. 1980.

The genus *Quasiconcha* was established by Barr & Blackwell (1980) to accommodate *Q. reticulata*, an unusual mytilinidioid fungus, with 1-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 from the southwestern United States (Barr & Blackwell 1980, Blackwell & Gilbertson 1985). In the present study, we were fortunate to obtain original material (RLG 141189) 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 *Mytilinidiaceae*, in close association with *Lophium*, to which its fruitbodies most closely resemble.

Mytilinidion Duby, Mém. Soc. Phys. Genève 16: 34. 1862.
= *Mytilidion* Sacc., Atti Soc. Veneto-Trentino Sci. Nat. Padova 4: 99. 1875.
= *Hypodermopsis* Earle, Bull. New York Bot. Gard. 2: 345. 1902.
= *Murashkinskija* Petr., Hedwigia 68: 203. 1928.

The genus *Mytilinidion*, the type for the family *Mytilinidiaceae*, was established by Duby (1862) with an etymology from *Mytilus*, a genus of mussels. Saccardo (1883, p. 760) considered the name *Mytilinidion* to be linguistically incorrect and replaced it with *Mytilidion*. It remained for Barr (1975) to note that the name *Mytilinidion* had historical precedence (Rogers 1953), and therefore should replace the later name *Mytilidion*. Species of *Mytilinidion* are characterised by yellow- to reddish-brown, ellipsoid, fusoid, obovoid to elongate, transversely septate, usually symmetric, ascospores, or scolecospores, borne in thin-walled globoid to conchate pseudothecia, with lateral walls more or less connivent and extended vertically to a cristate apex. There are currently 15 recognised species, occurring on the *Pinaceae*, *Cupressaceae*, and *Taxodiaceae* (Lohman 1932b, Zogg 1962, Speer 1986, Barr 1990a).

Ascospore morphology can be used to discern four morphological types within the genus, listed here by increasing ascospore length: (1) Short squat phragmospores: *M. acicola*, *M. resinae*, *M. decipiens*, *M. tortile* (Fig. 11A–B), and *M. resinicola*; (2) Elongate phragmospores, with a spore length to width ratio of 10 : 1 or less: *M. californicum*, *M. mytilinellum* (Fig. 11C–D), *M. rhenanum*, and *M. gemmigenum*; (3) Fusoid or spindle-shaped spores: *M. thujarum*, *M. oblongisporum*, and *M. andinense*; and (4) Highly elongated phragmospores, termed scolecospores, with a length to width ratio of 20 : 1: *M. scolecosporum*, *M. parvulum* and *M. australe* (Fig. 11E–I). These last three scolecosporous species were postulated to form a transitional series to connect *Mytilinidion* with the heretofore somewhat isolated genus *Lophium* (Fig. 11J–K), and formed the basis for subgenus *Lophiopsis*, distinct from subgenus *Eu-Mytilinidion sensu* Lohman (Lohman 1932b), a concept accepted by Zogg (1962).

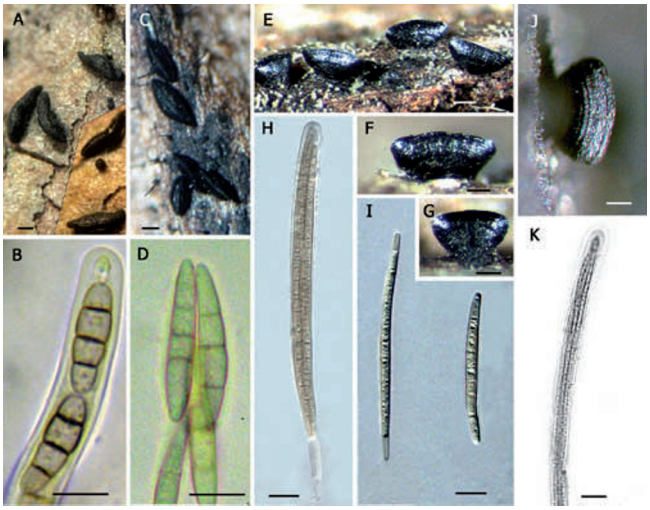

Fig. 11. The *Mytilinidiaceae*. A–B. *Mytilinidion tortile* [EB 0377 (BPI 879798), France]; C–D. *Mytilinidion mytilinellum* [EB 0386 (BPI 879796), France]; E–I. *Mytilinidion australe* [ANM 1524 (ILLS), U.S.A.; not incl.]; J–K. *Lophium mytilinum* [CBS 123344 (BPI 878736), U.S.A.]. Photo credits Alain Gardiennet, Figs. A–D. Scale bar (habitat) = 500 µm; Scale bar (spores and asci) = 10 µm.

Sequence data presented here (Fig. 1), based on an analysis of 10 of the 15 currently recognised species (Table 1), 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. Data do however support the association of fusoid or spindle-shaped spores belonging to *M. thujarum* (EB 0268 / BPI 879797) and to *M. andinense* (CBS 123562 / BPI 878737), thus defining a lineage for this type of spore within the genus. On the other hand, species possessing short, squat phragmospores, namely *M. acicola* (EB 0349 / BPI 879794, EB 0379 / BPI 879793), *M. tortile* (EB 0377 / BPI 879798), and *M. resinicola* (CBS 304.34) display complex relationships with species possessing elongate phragmospores, such as *M. californicum* (EB 0385 / BPI 879795), *M. mytilinellum* (EB 0386 / BPI 879796, CBS 303.34) and *M. rhenanum* (EB 0341, CBS 135.45). This indicates that phragmospores with different length to width ratios have also evolved multiple times within the genus (Fig. 1). A manuscript currently in preparation (Boehm *et al.*) will address speciation events within the *Mytilinidiaceae*. Despite the lack of molecular support for the subgenus *Lophiopsis*, it is included in the key below to facilitate species identification.

Key to the species of *Mytilinidion*

1. Spore length to width ratio = 10 : 1 or less (phragmospores): Subgenus *Eu-Mytilinidion sensu* Lohman (1932b) 2
1. Spore length to width ratio = approx. 20 : 1 (scolecospores): Subgenus *Lophiopsis sensu* Lohman (1932b) 13

2. Ascomata not conchate, but erect, low and spreading at the base (scutate), seated on a shield-like process fused to the substrate, apical portion slightly connivent; ascospores 3–5(–6)-septate 3
2. Ascomata conchate, standing on edge, usually with a clearly defined longitudinal cristate apex 4

3. Ascospores 23–25 x 4–4.5(–5) µm, 3-septate; California on *Sequoia* ..... ***M. californicum***
3. Ascospores 14–22(–28) x (4.5–)6–8(–10) µm, 3–4–5–(–6) septate; on *Juniperus*, *Thuja*, Europe and North America ..... ***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 median septum 7

5. Ascospores (2–)3(–5)-septate, measuring (14–)16–22(–24) x (2.5–)3–4(–5) µm; cosmopolitan ..... ***M. mytilinellum***
5. Ascospores longer, with more septa 6

6. Ascospores 3–5(–7)-septate, measuring (24–)30–42(–50) x 3–5 µm; Europe ..... ***M. rhenanum***
6. Ascospores slightly curved, asymmetric, (3–)7–9(–11)-septate, measuring (27–)32–38(–48) x (4–)5–6(–8) µm; cosmopolitan ..... ***M. gemmigenum***

7. Ascospores (2–)3-septate, small, 10–13 x 4–6 µm; resinicolous on *Araucaria*, Brazil ..... ***M. resinae***
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; on *Larix*, *Juniperus*, Europe ..... ***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; cosmopolitan ..... ***M. tortile***
9. Ascospores longer 10

10. Ascospores 3-septate, elliptic-oblong, deeply constricted at the septa, measuring 24–26 x 8–9 µm; North America ..... ***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 northwestern North America ..... ***M. oblongisporum***
11. Ascospores longer 12

12. Ascospores 3-(4–5)-septate, measuring (26–)30–34(–40) x (10–)12–13(–15) µm; on *Thuja*, cosmopolitan ..... ***M. thujarum***
12. Ascospores wider, 3–7(–9)-septate, with swollen middle cells, 32–44 x 10–15 µm; on *Austrocedrus chilensis*, Argentina ..... ***M. andinense***

13. Ascospores 5–7-septate, measuring 40–50 x 2–2.5 µm, slightly constricted at central septa; North America and Europe ..... ***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; North America ..... ***M. parvulum***
14. Ascospores (10–)11–14-septate, measuring (54–)58–70(–75) x 3–4 µm; North America ..... ***M. australe***

Lophium Fr., Syst. Mycol. 2: 534. 1823.

= *Lophidium* P. Karst., Bidrag. Kännedom Finlands Natur Folk. 23: 33, 247. 1873.

The genus *Lophium* is characterised 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* (Fig. 11J–K), is cosmopolitan in the temperate zones and has been recorded from both sides of the Atlantic (Zogg 1962, Barr 1990a). Zogg (1962) described two additional species, namely *L. elegans* on *Juniperus* from alpine regions of France, Italy and Switzerland, and *L. mayorii* on *Pinus* and *Larix* from the European Alps. Like *Mytilinidion*, most species of *Lophium* have only been recovered from coniferous substrates. The exception being the recently described *L. igoschinae*, recovered on *Dryas octopetala* and *D. crenulata* (*Rosaceae*) from Russia and Greenland (Chlebicki & Knudsen 2001).

Three isolates of the type species, *L. mytilinum*, were surveyed (Table 1), two from the United States, one from Michigan (CBS 269.34) and one from New York (CBS 123344 / BPI 878736), and one from Sweden (CBS 114111). An additional species of *Lophium*, namely a single-spored isolate of *L. elegans* from France (EB 0366 / BPI 879792), was included as well (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 however to the genus *Quasiconcha* (EB QR), with reticulated didymospores (Fig. 1). 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; Europe, Russian Far East ..... ***L. mayorii***
   Note: Transferred to the genus *Zoggium* (Vasilyeva 2001).

2. Ascospores filiform, 12–15-septate, measuring 78–86 x 2.6–3 µm; on *Dryas*, Greenland, Russia ..... ***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; cosmopolitan ..... ***L. mytilinum***
3. Ascospores spirally arranged in the ascus; measuring (200–)260–280(–300) x 2 µm; Europe ..... ***L. elegans***

Zoggium Lar.N. Vassiljeva, Mikol. Fitopatol. 35: 17. 2001.

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

Ostreola Darker, Canad. J. Bot. 41: 1383. 1963.

Barr (1975, 1990a) recognised two genera with muriform ascospores in the *Mytilinidiaceae*, namely *Ostreichnion* and *Ostreola*. Darker (1963) originally established the genus *Ostreola* for dictyospored forms that otherwise resembled species of *Mytilinidion* – that is, mytilinidioid counterparts to *Hysterographium sensu* Zogg (1962). Barr (1990a) differentiated *Ostreola* from *Ostreichnion* by smaller ascospores in the former, and recognised two species from North America, *Ot. consociata* from northeastern North America, and *Ot. formosa*, the latter common on conifers in western North America and Europe, with spores similar to those of *Hysterobrevium mori*. Tilak & Kale (1968) added another two species from India, namely *Ot. indica* and *Ot. ziziphi*, surprisingly both from non-coniferous substrates. Molecular data are presently lacking for this genus.

Key to the species of *Ostreola*

1. Ascomata on coniferous hosts; North America, Europe 2
1. Ascomata on non-coniferous hosts; India 3

2. Base of ascoma foot-like, 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 North America ..... ***Ot. consociata***
2. Base of ascoma tapered or applanate on surface of substrate; ascospores (3–)5(–6)-septate, wider than in *O. consociata*, 15–21 x 6.5–9.5 µm; alpine, on *Abies*, Europe and Western North America ..... ***Ot. 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 ..... ***Ot. indica***
3. Ascospores as above but smaller, 19–23 x 6–7.5 µm; on culms of *Ziziphus*, India ..... ***Ot. ziziphi***

Gloniaceae (Corda) E.W.A. Boehm, C.L. Schoch & J.W. Spatafora 2009, *Pleosporomycetidae fam. incertae sedis.*
= *Gloniaceae* Corda, Icon. Fung. (Abellini) 5: 34. 1842.

Corda (1842) originally proposed the *Gloniaceae* as an intrafamilial taxonomic rank under the family *Hysteriaceae*, to comprise *Hysterographium* and *Glonium*. Boehm *et al.* (2009) emended and restricted the circumscription and elevated the taxon to family rank. The genus *Glonium* was retained as circumscribed first by von Höhnel (1918) and then by Petrak (1923a). We feel justified in reinstating the *Gloniaceae* and, more importantly, recognising 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.

Glonium Muhl., Cont. Lab. Plant Disease Sci. Fac. Agric. Gifu Univ. 101. 1813.
= *Solenarium* Spreng., Syst. Veg. 4(1): 376, 414. 1827.
= *Psiloglonium* Höhn., Ann. Mycol. 16(1): 149. 1918.

The genus *Glonium* is characterised by modified hysterothecia, progressively dichotomously branched, laterally anastomosed along their length to form radiating flabelliform or pseudo-stellate composites, usually seated upon a conspicuous brown felt-like subiculum, sometimes borne in a stroma (Zogg 1962). Hysterothecia in vertical section globose to obovoid, typically with a thick, three-layered peridium, but fragile, unlike the robust peridium of the *Hysteriaceae*. Luttrell (1953) described the development of the ascocarp in the type species, *G. stellatum* as 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 consisted 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 cylindric, bearing eight ascospores, overlapping biseriate; ascospores ranging from hyaline to pale 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) listed three species that he grouped together in his key, that later formed the basis for the *Gloniaceae* (Boehm *et al.* 2009). These are the type species, *G. stellatum* (Fig. 12A–E), *G. graphicum*, and *G. compactum*, the latter associated with both subicula and stroma. To these three species, we can add the recently described saxicolous, terricolous and lignicolous *G. circumserpens* (Fig. 12F–H) from Tasmania (Kantvilas & Coppins 1997). Although von Höhnel (1918) and Petrak (1923a) stressed the importance of subiculum as a synapomorphic character state, Zogg (1962) noted that *G. graphicum* may or may not be associated with a subiculum. This, combined with the observation that *P. lineare* may also on occasion be associated with subiculum, led Zogg not to accept the genus *Psiloglonium*. Data presented here and elsewhere (Boehm *et al.* 2009), however, indicate that the synapomorphic character state is not subicula *per se*, but the ascomata, which are modified hysterothecia that are progressively dichotomously branched, to form radiating pseudostellate composites. This is most pronounced in *G. stellatum* and *G. circumserpens*, but may also be found to a lesser extent in *G. graphicum* (Zogg 1962). One distinguishing feature that separates *G. stellatum* from *G. circumserpens* is that, although both are associated with subicula, in the former this extends as a wide margin in front of the developing hysterothecia (Fig. 12A–C), whereas in *G. circumserpens* (Fig. 12F–G) the subicula is only associated with the under surface of the hysterothecia, closely appressed to the substrate, with only minor deviations from the long axis of the fruitbody.

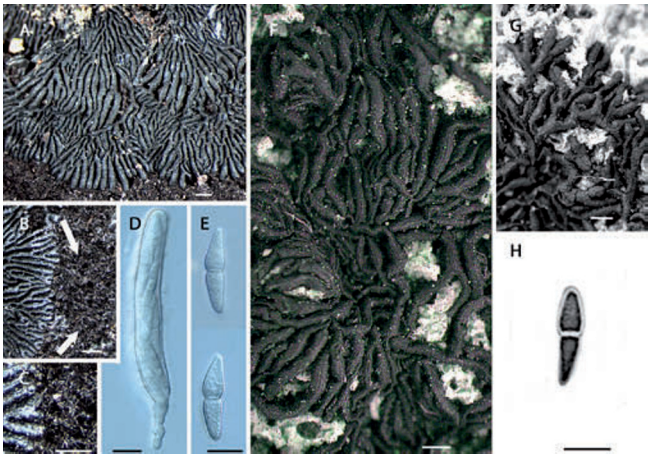

Fig. 12. The *Gloniaceae*. A–E. *Glonium stellatum* [ANM 41 (ILLS), U.S.A.; not incl.], arrows in 12B, subiculum. F–H. *Glonium circumserpens* [CBS 123343 (BPI 878739), Tasmania]. Scale bar (habitat) = 1 mm; Scale bar (spores and asci) = 10 µm.

Four isolates were surveyed for the *Gloniaceae*. Two of *G. stellatum*, from Michigan (CBS 207.34) and Tennessee (ANM 32), the United States, and two of *G. circumserpens*, recently isolated from wood (CBS 123342 / BPI 878738) and dolerite stone (CBS 123343 / BPI 878739) from Tasmania (Table 1). Molecular data indicate that all four isolates are closely related. Surprisingly, this clade also includes multiple isolates of *Cenococcum geophilum*, 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; Africa ..... ***G. compactum***
1. Hysterothecia not associated with stroma 2

2. Hysterothecia somewhat branched, irregular, "graphoid"; without well-developed subiculum; 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***

Farlowiella Sacc., Syll. Fung. 9: 1101. 1891.
= *Farlowia* Sacc., Syll. Fung. 2: 727. 1883.

Recent molecular data (Schoch *et al.* 2006; Boehm *et al.* 2009) support the transference of the genus *Farlowiella* from the *Hysteriaceae*, and its current placement as *Pleosporomycetidae gen. incertae sedis*. The genus is characterised by 1-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 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 recognised, namely *Farlowiella carmichaeliana* from Europe (Belgium, England, Germany, Switzerland), from the bark and wood of *Fagus, Quercus, Sorbus* and *Prunus*, and *F. australis*

known only from the original collection on *Phylica 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 the *Hysteriaceae* (Fig. 1). An additional isolate of the anamorph, *Acrogenospora sphaerocephala* (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; Europe ..... ***F. carmichaeliana***
1. Ascospores as above, but smaller, 13–15 x 6–7.5 µm; Tristan da Cunha ..... ***F. australis***

CONCLUSIONS

Hysteriaceous fungi are an ancient and ecologically successful group of organisms, as attested by their wide geographic distribution on a multitude of gymnosperm and angiosperm host species. Whereas the *Mytilinidiaceae* are found almost exclusively on conifers, the *Hysteriaceae* occur primarily on angiosperms (Zogg 1962). Presumably, the *Hysteriaceae* underwent rapid speciation in response to the angiosperm radiation of the mid- to late-Cretaceous, 65–100 mya (Palmer *et al.* 2004). However, this must have occurred prior to the complete loss of continental contiguity, which occurred during the same time period. This is because we see today a remarkable degree of intraspecific stability, in both morphology and sequence data, among geographically disparate accessions (Fig. 1). For example, little morphological or sequence variation was detected in *Hysterium angustatum*, from North America (CBS 123334), Kenya (GKM 243A), New Zealand (SMH 5211.0), and South Africa (CMW 20409; Lee & Crous 2003). Similarly, little variation was detected in *Psiloglonium clavisporum*, from Kenya (GKM L172A, GKM 344A) and North America (*e.g.*, CBS 123338), or in *Oedohysterium sinense*, from South Africa (CBS 123345) and North America (EB 0339). As we are presumably sampling remnants of once contiguous sexual populations, their similarity today must imply that speciation occurred prior to complete genetic isolation. The break-up of Pangea during the Triassic 200 mya, and the formation of the nascent central Atlantic Ocean, separating Gondwana from Laurasia, during the Jurassic, 150 mya, must have effectively disrupted once contiguous populations. Although most flowering plant families were established by the end of the Cretaceous, 65–70 mya, it is now believed that they diversified into their present lineages (*e.g.*, eudicots, Magnoliids and monocots) much earlier, around 140 mya (Davies *et al.* 2004, Palmer *et al.* 2004, Moore *et al.* 2007). This may have allowed for remnants of once contiguous populations to colonise early angiosperm lineages, prior to the complete dissolution of continental integrity during the mid- to late-Cretaceous. Recent studies (Lücking *et al.* 2009), based on a recalibration of published molecular clock trees, using internally unconstrained, uniform calibration points, have suggested an origin for the fungi between 760 mya to 1.0 bya, with the origin of the *Ascomycota* set at 500-650 mya. Whatever the timing, hysteriaceous fungi incurred little appreciable intraspecific morphological or genetic (*e.g.*, nuLSU, nuSSU, *TEF1* and *RPB2*) change over significant periods of geologic time, on different continents. Thus, with the exception of *Hb. mori*, and perhaps, *Gp. subrugosa* (see below), most members of the *Hysteriaceae* appear to be stable species.

Sequence data indicate that *Hb. mori* occurs in both Clades A and D. However, analysis of *Hb. mori* specimens originating from each clade (*e.g.*, CBS 123563 / BPI 878731, and others, in Clade A *versus* GKM 1013 / BPI 879788 in Clade D), failed to find any appreciable difference in either spore morphology (*e.g.*, septation, pigmentation, symmetry, or measurement), substrate-choice, or features associated with the hysterothecium. Likewise, no morphological difference could be detected among genetically unrelated accessions of *Gp. subrugosa*, from South Africa (CBS 123346 / BPI 878735), in Clade D, *versus* those from Kenya (GKM 1214 / BPI 879776) and Cuba (SMH 557 / BPI 879777), outside of Clade D. These two examples illustrate a lack of correspondence between the morphospecies concept (Burnett 2003) and the genealogical concordance phylogenetic species recognition concept (Taylor *et al.* 2000), the latter indicating here the presence of cryptic species within the two morphospecies. *Hysterobrevium mori* and, to a lesser extent, *Gp. subrugosa*, may represent examples of convergent evolution, whereby similar ascospores borne in hysterothecia have evolved multiple times within the family. This is supported by the polyphyly inherent in the circumspection of the classical genera of the *Hysteriaceae* (*e.g.*, *Gloniopsis*, *Glonium*, *Hysterium*, and *Hysterographium*), revealed by recent studies (Schoch *et al.* 2006, Boehm *et al.* 2009, Mugambi & Huhndorf 2009). Alternatively, *Hb. mori* and *Gp. subrugosa* may have retained ancestral character states, and thus may represent evolutionary lineages that did not incur appreciable morphological change, while at the same time accumulating sufficient genetic change to fall, in the case of *Hb. mori*, into distant clades within the family. If this is the case, then these two taxa may represent examples of speciation in progress, with genetic change preceding morphological change, thus differing from independent convergent character states. Whatever the mechanism, it is difficult to see how *Hb. mori*, for example, may be classified into different species, in different genera (*e.g.*, *Hysterobrevium* and *Oedohysterium*), without a sound morphological basis. We conclude that both *Hb. mori* and *Gp. subrugosa* contain genetically unrelated, cryptic, and potentially different biological species, that can not at present be morphologically differentiated.

Although there are examples of concordance between morphological and molecular data in this study (see below), these are few. For the most part, molecular data support the premise of a large number of convergent evolutionary lineages, sharing similar spore morphologies, but that are not closely related. This resulted in a polyphyletic core set of genera for the *Hysteriaceae*, and presented us with a complicated picture of past speciation events within the family (Boehm *et al.* 2009). To achieve a natural phylogeny, that is, one based on the concordance of morphological and molecular data, required that we break-up what were once thought to be stable genera. Thus, two species of *Hysterium* were transferred to *Oedohysterium* (*Od. insidens* and *Od. sinense*), and two species of *Gloniopsis* to *Hysterobrevium* (*Hb. smilacis* and *Hb. constrictum*). While *Hysterographium*, with the type *Hg. fraxini*, was removed from the *Hysteriaceae* (Boehm *et al.* 2009), some of its species remained within the family, transferred here

to *Oedohysterium* (*Od. pulchrum*), *Hysterobrevium* (*Hb. mori*) and *Gloniopsis* (*Gp. subrugosa*). New species were described (*e.g.*, *Gp. arciformis* and *Gp. kenyensis*) which would previously have been classified in *Hysterographium*, but are now accommodated in *Gloniopsis*. Molecular data necessitated that both *Gloniopsis* and *Hysterobrevium* include hyaline and pigmented dictyospores, and the genus *Oedohysterium*, both phragmospores and dictyospores. This, then, de-emphasised spore morphology as a synapomorphic character state. Likewise, the genus *Glonium sensu* Zogg (1962) was divided into *Psiloglonium* in the *Hysteriaceae* and *Glonium* in the *Gloniaceae* (Boehm *et al.* 2009), and, more recently, *Anteaglonium* in the *Pleosporales* (Mugambi & Huhndorf 2009). These taxonomic changes were unexpected, as they were not premised on past assumptions of synapomorphy related to spore morphology (Zogg 1962). Although we have included here a total of 59 accessions, representing 22 species in seven genera, for the *Hysteriaceae*, and another 62 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 quest for synapomorphic character states that correlate with molecular data was one of the goals of this study. If traditional character states associated with spore septation/pigmentation or the fruitbody (Zogg 1962) can not be relied upon to deduce phylogeny, are there other character states that can be emphasised instead? Two examples are discussed below, the first relating to spore morphology, the second to characters associated with the fruitbody. Although both *Oedohysterium* and *Hysterium* possess similar pigmented asymmetric phragmospores, species of *Oedohysterium* can be morphologically differentiated by the possession of an enlarged supra-median cell. Molecular data also revealed that a species previously classified as *Hysterographium*, namely *Hg. pulchrum*, belonged to *Oedohysterium*, despite the presence of dictyospores. Closer inspection, however, reveals that the dictyospores of *Od. pulchrum* also possess a swollen supra-median cell. Additionally, a certain number of spores remain as transversely septate phragmospores (Checa *et al.* 2007), thus reinforcing its placement within *Oedohysterium*, and perhaps underscoring the plasticity of spore septation configurations for this group of fungi.

The second example relates to character states associated with the fruitbody. Fruitbody morphology clearly supports the transfer of the genus *Glonium* out of the *Hysteriaceae* to its own family, the *Gloniaceae*, closely allied with the *Mytilinidiales*. The *Gloniaceae* possess a modified hysterothecium, one in which the frutibodies frequently bifurcate to a greater (*e.g.*, *G. stellatum* and *G. circumserpens*) or lesser (*e.g.*, *G. graphicum*) degree, the former two species with radiating stellate composites, usually seated on subicula. This is in contrast to hysterothecia found in the *Hysteriaceae* which may be gregarious, but are never laterally anastomosed to form radiating composites. Additionally, the morphology of the dehiscence slit found in the *Gloniaceae* is unlike that found in the *Hysteriaceae*. In the *Gloniaceae*, the aperture is in most cases evaginated, forming a miniscule crest, similar to the more extended version found in some species in the *Mytilinidiaceae*; whereas, in the *Hysteriaceae*, hysterothecia have deeply invaginated slits. Also, hysterothecia found in the *Gloniaceae*, like those in the *Mytilinidiaceae*, are considerably more fragile, as compared to those found within the *Hysteriaceae*. These character states were either not noted before (*e.g.*, swollen supra-median cell in *Oedohysterium* and evaginated slit in *Glonium*), or were noticed, but given less taxonomic weight (*e.g.*, modified hysterothecium in *Glonium*; Zogg 1962). These examples illustrate that morphological features can be found that correlate with molecular data, despite the anomalies presented by *Hb. mori* and *Gp. subrugosa*, mentioned earlier.

The hysterothecium, thick-walled, navicular, and with a prominent longitudinal slit, has long been considered synapomorphic, defining the *Hysteriales*. However, this type of fruitbody has evolved convergently no less than five times within the *Pleosporomycetidae* (*e.g.*, *Farlowiella*, *Glonium*, *Anteaglonium*, *Hysterographium* and the *Hysteriaceae*). Similarly, thin-walled mytilinidioid (*e.g.*, *Ostreichnion*) and patellarioid (*e.g.*, *Rhytidhysteron*) ascomata have also evolved at least twice within the subclass, the genera having been transferred from the *Mytilinidiaceae* and *Patellariaceae*, respectively, to the *Hysteriaceae*. As such, character states relating not only to the external features of the ascoma, but to the centrum as well (*e.g.*, cellular pseudoparaphyses *versus* trabeculae, etc.), previously considered to represent synapomorphies among these fungi, in fact, represent symplesiomorphies, and most likely have arisen multiple times through convergent evolutionary processes in response to common selective pressures. Similar findings have emerged for a number of other ascomycete lineages within the *Pezizomycotina* (*e.g.*, Schoch *et al.* 2009b). One selective advantage of the hysterothecium may be spore discharge over prolonged periods of time, since some, if not most, species may be perennial (Lohman 1931, 1933a). The thick-walled peridium further contributes to xerotolerance, as many of these fungi persist on decorticated, weathered woody substrates prone to prolonged periods of desiccation. Thus, the ability to perennate, and time spore discharge with environmental conditions suitable for germination, spanning multiple seasons, may be the driving force behind the repeated evolution of the hysterothecium.

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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**: 1–434.

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: published by the author.
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**: 1–94.
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 DJ, McLaughlin EG, Lemke PA, eds). Springer: 283–305.
Bezerra JL, Kimbrough JW (1982). Culture and cytological development of *Rhytidhysterium 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.
Bisby GR (1941). British species of *Hysterium*, *Gloniopsis*, *Dichaena* and *Mytilidion*. *Transactions of the British Mycological Society* **25**: 127–140.
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 *Mytilinidiaceae* (*Pleosporomycetidae*, *Dothideomycetes*, *Ascomycota*) using four nuclear genes. *Mycological Research* **113**: 461–479.
Burnett J (2003). *Fungal Populations and Species*. Oxford University Press, Oxford, U.K.
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.* Ferra Librairie-Editeur, Paris, France.
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. Publ., Minneapolis, MN, U.S.A.
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.
Davies JT, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V (2004). Darwin's abominable mystery: Insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences* **101**: 1904–1909.
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, U.S.A.
Eriksson OE (2006). Outline of *Ascomycota*. *Myconet* **12**: 1–88.
Fries EM (1823). *Systema Mycologicum, sistens fungorum ordines, genera et species hucusque cognitas, II, pars II*: 276–620.
Fries EM (1835). *Corpus florarum provincialium Sueciae. I. Floram scanicam scripsit Elias Fries.* Uppsala.
Gäumann EA (1949). *Die Pilze, Grundzüge ihrer Entwicklungsgeschichte und Morphologie.* Birkhäuser. Basel.
Geiser DM, Gueidan C, Miadlikowska J, Lutzoni F, Kauff F, *et al.* (2006). *Eurotiomycetes*: *Eurotiomycetidae* and *Chaetothyriomycetidae*. *Mycologia* **98**: 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.
Hall, T. 2004. Bioedit v7.0.1. Isis Pharmaceuticals, U.S.A.
Hawksworth DL, Eriksson OE (1988). Proposals to conserve 11 family names in the *Ascomycotina* (Fungi). *Taxon* **37**: 190–193.
Höhnel F. von (1918). Mycologische Fragmente, 272. Über die Hysteriaceen. *Annales Mycologici* **16**: 145–154.
Huelsenbeck JP, Ronquist F (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.
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.
Katoh K, Asimenos G, Toh H (2009). Multiple alignment of DNA sequences with MAFFT. *Methods in Molecular Biology* **537**: 39–64.
Kirk PM, Canon PF, David JC, Stalpers JA (2001). *Dictionary of the Fungi. 9th Ed.* CAB International, U.K.
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, *et al.* (2006). The family *Pleosporaceae*: 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.
Lindau G (1897). *Hysteriineae*. In: *Engler & Prantl, Naturliche Pflanzenfamilien. I. Teil, I. Abteilung*. **1**: 265-278.
Linde EJ van der (1992). Notes on the South African *Hysteriaceae* (*Ascomyctes*: Mycotina). *South African Journal of Botany* **58**: 491–499.
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.
Liu K, Raghavan S, Nelesen S, Linder CR, Warnow T (2009). Rapid and accurate large-scale coestimation of sequence alignments and phylogenetic trees. *Science* **324**: 1561–1564.
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.
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.
Lücking R, Huhndorf S, Pfister DH, Plata ER, Lumbsch HT (2009). Fungi evolved right on track. *Mycologia* **101**: 810–822.
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: 135–219.
Lutzoni F, Kauff F, Cox CJ, McLaughlin DJ, Celio G, *et al.* (2004). Assembling the fungal tree of life: Progress, classification, and evlutiion of subcellular traits. *American Journal of Botany* **91**: 1446–1480.
Magnes M (1997). Weltmonographie der *Triblidiaceae*. *Bibliotheca Mycologica* **165**: 127–130.
Massee G (1895). *British Fungus Flora, A Classified Textbook of Mycology, Vol IV.* George Bell & Sons, London & New York, U.S.A.
Massee G (1901). Fungi exotici III. *Royal Botanic Gardens, Kew, Bulletin No.* **175–177**: 150–169.
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.

Moore MJ, Bell CD, Soltis PS, Soltis DE. 2007. Using plastid genome-scale data to resolve enigmatic relationships among basal angiosperms. *Proceedings of the National Academy of Sciences, U.S.A.* **104**: 19363–19368.

Mugambi, G.K. and S.M. Huhndorf. 2009. Parallel evolution of hysterothecial ascomata in ascolocularous fungi (*Ascomycota*, Fungi). *Systematics and Biodiversity* **7**: 453–464.

Müller E, von Arx JA (1950). Einige Aspekte zur Systematik pseudosphärialer 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**: 1–368.

Palmer JD, Soltis DE, Chase MW. 2004. The plant tree of life: An overview and some points of view. *American Journal of Botany* **91**: 1437–1445.

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. *Psiloglonium finkii nov. 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 PA (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 (1979). Life-history studies of Brazilian Ascomycetes. 7. *Rhytidhysteron rufulum* and the genus *Eutryblidiella*. *Sydowia* **32**: 277–292.

Schmitt I, Mueller G, Lumbsch HT (2005). Ascoma morphology is homoplaseous and phylogenetically misleading in some pyrenocarpous lichens. *Mycologia* **97**: 362–374.

Schoch CL, Crous PW, Groenewald JZ, Boehm EWA, Burgess TI, *et al*. (2009a). A class-wide phylogenetic assessment of *Dothideomycetes*. *Studies in Mycology* **64**: 1–15.

Schoch CL, Shoemaker RA, Seifert KA, Hambleton S, Spatafora JW, Crous PW (2006). A multigene phylogeny of the *Dothideomycetes* using four nuclear loci. *Mycologia* **98**: 1041–1052.

Schoch CL, Sung G-H, López-Giráldez F, Townsend JP, Miadlikowska J, *et al.* (2009b). The *Ascomycota* Tree of Life: A phylum wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. *Systematic Biology* **58**: 224–239.

Schoch CL, Sung GH, Volkmann-Kohlmeyer B, Kohlmeyer J, Spatafora JW (2007). 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, *et al.* (2006). A five-gene phylogenetic analysis of the *Pezizomycotina*. *Mycologia* **98**: 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.

Stamatakis A (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–90.

Stamatakis A, Hoover P, Rougemont J (2008). A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology* **57**: 758–771.

Steinke TD, Hyde KD (1997). *Gloniella clavatispora*, sp. nov. from *Avicennia marina* in South Africa. *Mycoscience* **38**: 7–9.

Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, *et al.* (2000). Phylogenetic species recognition and species concepts in fungi. *Fungal Genetics and Biology* **31**: 21–32.

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.

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.

Wernersson R, Pedersen AG (2003). RevTrans: Multiple alignment of coding DNA from aligned amino acid sequences. *Nucleic Acids Research* **31**: 3537–3539.

WhiteTJ, Bruns T, Lee S, Taylor J (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR Protocols: A guide to methods and applications*. (Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds.). Academic Press, New York: 315–322.

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**: 1–190.