



A new genus and three new species of hysteriaceous ascomycetes from the semiarid region of Brazil

DAVI AUGUSTO CARNEIRO DE ALMEIDA¹, LUÍS FERNANDO PASCHOLATI GUSMÃO¹ & ANDREW NICHOLAS MILLER²

¹ Universidade Estadual de Feira de Santana, Av. Transnordestina, S/N – Novo Horizonte, 44036-900. Feira de Santana, BA, Brazil.

² Illinois Natural History Survey, University of Illinois, 1816 S. Oak St., Champaign, IL 61820

* email: daviaugusto@gmail.com

Abstract

During an inventory of ascomycetes in the semi-arid region of Brazil, one new genus and three new species of hysteriaceous ascomycetes were found. Maximum likelihood and Bayesian phylogenetic analyses of the nuclear ribosomal 28S large subunit were performed to investigate the placement of the new taxa within the class Dothideomycetes. *Anteaglonium brasiliense* is described as a new species within the order Pleosporales, and *Graphyllum caracolinense* is described as a new species nested inside Hysteriales. Morphological and molecular data support *Hysterodifractum* as a new monotypic genus in the Hysteriaceae. The type species, *H. partisporum*, is characterized by navicular, carbonaceous, gregarious hysterothecia and pigmented, fusiform ascospores that disarticulate into 16 ovoid or obovoid, septate, part-spores. This is the first report of a hysteriaceous fungus producing part-spores.

Key words: Dothideomycetes, LSU, phylogeny, Pleosporomycetidae, taxonomy, tropical microfungi

Introduction

Hysteriaceous ascoloculares ascomycetes produce navicular, carbonaceous, persistent ascomata that are superficial or erumpent and dehisce through a longitudinal slit (Boehm *et al.* 2009a, Mugambi & Huhndorf 2009), traditionally referred to as hysterothecia (Clements 1909). The classification of hysterothecia has been debated since the 19th century, due to the transitional nature of the ascoma in which they sometimes resemble perithecia or appear as apothecium. Fries (1823), for instance, included *Actidium*, *Glonium*, *Hysterium* and *Lophium* in Phacidiacei in the Pyrenomycetes. Thereafter, Fries (1835) changed his classification and transferred Phacidiacei to Discomycetes, while keeping *Lophium* in the Pyrenomycetes. In 1842, Corda included *Actidium*, *Glonium*, *Hysterium*, *Hysterographium*, and *Lophium* in Hysteriaceae (Corda 1842a,b) in the Myelomycetes. Later authors did not agree with this classification of the Hysteriaceae (Bisby 1923), since some included it in the Pyrenomycetes (De Notaris 1847, Duby 1862, Saccardo 1874), while others placed it in the Discomycetes (Fuckel 1869, Saccardo 1873, Schroeter 1908, Seaver 1909). Classifications proposed from the 20th century onwards placed the hysteriaceous fungi in the Loculoascomycetes (Luttrell 1955), which was subsequently replaced in part by the Dothideomycetes (Eriksson & Winka 1997). At the ordinal level, the Hysteriaceae was classified in Pseudosphaeriales (Gäumann 1949), Dothiorales (Müller & von Arx 1950), Dothideales (von Arx & Ma 1975), Pleosporales (M. E. Barr 1987) or in its own order, the Hysteriales (Kirk *et al.* 2001, 2008, Luttrell 1955). Hysteriaceous fungi producing conchate or dolabrate, thin-walled, laterally compressed ascomata with an evaginated slit, were segregated from Hysteriaceae and placed in Mytiliniaceae, under Melanommatales (Barr 1990a), Pleosporales (Kirk *et al.* 2008) or Mytiliniales (Boehm *et al.* 2009a, Lumbsch & Huhndorf 2010).

Phylogenetic studies based on molecular data have shown that the hysteriaceous fungi do not form a monophyletic group (Boehm *et al.* 2009a,b, Mugambi & Huhndorf 2009). These studies indicated that the navicular, thick-walled hysterothecium with a prominent longitudinal slit evolved at least five times, while the conchate or dolabrate, thin-walled, laterally compressed hysterothecium has evolved at least two times within

Pleosporomycetidae (Boehm *et al.* 2009a). These studies resulted in several changes in the classification of the group, such as the description of a new order, Mytilinidiales, two new families, Anteagloniaceae (Pleosporales) and Gloniaceae *incertae sedis*, along with several new genera and combinations (Boehm *et al.* 2009a,b, Hyde *et al.* 2013, Mugambi & Huhndorf 2009). Hysteriales and Mytilinidiales are separate monophyletic groups that include polyphyletic genera such as *Gloniopsis*, *Hysterium*, *Hysterographium*, and *Lophium*, while *Anteaglonium*, *Farlowiella* and *Glonium* occur outside these two orders (Boehm *et al.* 2009b). Several genera, however, have yet to be included in phylogenetic analyses such as *Actidiographium*, *Actidium*, *Gloniella*, *Glyphium*, *Graphyllum*, *Hysterocarina*, *Ostreola* and *Zoggium*.

Clearly the systematics of the hysteriaceous fungi requires further study with the inclusion of additional species and genera in phylogenetic analyses so that an improved classification can be established for this group. The goal of this study was to include members of this group from Brazil, including one new putative genus and three new species, in phylogenetic analyses to determine their evolutionary relationships within the Dothideomycetes.

Materials and methods

Study area and morphological characterization

Samples of dead twigs and decaying wood were collected from November 2011 to May 2013 at Mata do Pau-Ferro State Ecological Reserve (6°58'14"S, 35°44'55"W), Ubajara National Park (3°50'24"S, 40°54'17"W), Serra da Jibóia (12°50'57"S, 39°28'31"W) and Serra das Confusões National Park (9°13'22"S, 43°29'39"W), in northeastern Brazil. The former three areas are enclaves of Atlantic Forest located on mountain tops in the Caatinga bioma with an area of approximately 600 ha, 6,288 ha and 5,928 ha, respectively (Barbosa *et al.* 2004, Brasil 2002, Marques *et al.* 2008). Serra das Confusões National Park is characterized by caatinga vegetation and has an approximate area of 823,435 ha (Brasil 2010). All four areas are located in the Brazilian semi-arid region.

Digital images of the ascomata were taken with a Canon G5 digital camera mounted on a MZ7.5 Leica dissecting microscope. Ascomata were sectioned with a razor blade and the centrum placed in a drop of water on a glass slide and covered with a cover slip. Digital images and measurements ($n = 30$) of the pseudoparaphyses, asci and ascospores were made using a BX51 Olympus microscope equipped with brightfield and Nomarski interference optics and a DP25 Olympus digital camera. Images were processed using Adobe Photoshop CS6 and ImageJ. Holotypes were deposited in the Herbarium of the State University of Feira de Santana (HUEFS) and isotypes were deposited in the Fungarium of the Illinois Natural History Survey (ILLS).

Multispore isolates were obtained by transferring the centrum onto Petri plates (60 mm diam.) containing antibiotic water agar (agar 15g, chloramphenicol 100 mg, distilled water 1L) and spreading the asci and ascospores on the agar surface. After 24–48 h of incubation at room temperature, germinated ascospores were transferred to Petri plates (60 mm diam) containing potato dextrose agar (PDA, Difco). Fungal cultures were deposited at the Bahia Culture Collection of Microorganisms (CCMB).

Molecular study

DNA was extracted from either fungal mycelia grown in potato dextrose broth (Difco) or from air-dried ascomata ($n = 30–50$) using a DNeasy Plant Mini Kit (QIAGEN Inc., Valencia, California). Ascomata were rehydrated in 50 μ L AP1 buffer for 3 h, followed by freezing at -80°C for 7 days before DNA extraction. The primer pair LROR-LR3 (Rehner & Samuels 1995) was used to PCR amplify partial 28S large subunit (LSU) nrDNA using puReTaq™ Ready-To-Go PCR Beads (Amersham Biosciences Corp., Piscataway, New York) according to the manufacturer's instructions. To increase efficiency, 2.5 μ L of 10 ng/ μ L BSA (bovine serum albumin) and 2.5 μ L of 50% DMSO (dimethyl sulfoxide) were added to the 25 μ L PCR reactions. The thermocycling parameters were as follows: initial denaturation at 95°C for 5 min; 40 cycles of denaturation at 95°C for 30 sec; annealing at 47°C for 15 sec, extension at 72°C for 1 min with a final extension step of 72°C for 10 min. PCR products were purified using a Wizard® SV Gel and PCR Clean-Up System (Promega). Purified PCR products were used in 11 μ L sequencing reactions with BigDye® Terminator v3.1 (Applied Biosystems, Foster City, California) and primers LROR and LR3 (Rehner & Samuels 1995). Sequences were generated on an Applied Biosystems 3730XL high-throughput capillary sequencer at the Keck Center at the University of Illinois Urbana-Champaign. Each sequence fragment was subjected to an individual blast search to verify its identity. Sequences

were assembled using Sequencher 5.0.1 (Gene Codes Corp., Ann Arbor, Michigan). Newly generated DNA sequences are listed in Table I.

TABLE 1. New sequences obtained in this study.

Species	Voucher info ^a	Provenance	GenBank accession numbers
<i>Anteaglonium brasiliense</i>	CCMB 256/2013	Serra da Jibóia - Brazil	KF906410
<i>Graphyllum caracolinense</i>	HUEFS 42838	Serra das Confusões National Park - Brazil	KF914914
<i>Hysterodifractum partisporum</i>	CCMB 252/2012	Mata do Pau-Ferro State Ecological Reserve - Brazil	KF914916
<i>Rhytidhysterium rufulum</i>	HUEFS 192194	Mata do Pau-Ferro State Ecological Reserve - Brazil	KF914915

^aHUEFS, Herbarium of the State University of Feira de Santana; CCMB, Bahia Culture Collection of Microorganisms.

Phylogenetic analyses

To investigate the phylogenetic placement of the new species, LSU sequences were manually aligned with those from two previously published studies on the Hysteriales, Mytilinidiales and Gloniaceae (Boehm *et al.* 2009a, Mugambi & Huhndorf 2009) using MacClade v. 4.0 (Maddison & Maddison 2000). This dataset included sequences of numerous genera currently circumscribed within the Dothideomycetes (Boehm *et al.* 2009a,b, Mugambi & Huhndorf 2009). Ambiguous regions and introns were excluded from the final alignment using Gblocks (Talavera & Castresana 2007). jModeltest (Posada 2008) was used to obtain the best-fit model of nucleotide evolution, which was TrN+I+G. The final aligned dataset was subjected to maximum likelihood (ML) analyses using PHYML (Guindon & Gascuel 2003) under the GTR model (Rodríguez *et al.* 1990) with 1000 ML bootstrap (BS) replicates and a combined Nearest Neighbor Interchange (NNI) and Subtree Pruning and Regrafting (SPR) tree search option.

Bayesian analyses were performed using MrBayes v 3.12 (Huelsenbeck & Ronquist 2001, 2005) under the TrN+I+G model on the CIPRES Portal v. 2.0 (Miller *et al.* 2010). Constant characters were included and 100 million generations with trees sampled every 1000th generation were ran resulting in 100,000 total trees. The first 10,000 trees were discarded as burn-in and Bayesian posterior probabilities (BPP) were determined from a consensus tree generated from the remaining 90,000 trees using PAUP* 4.0b10 (Swofford 2002).

Results

Taxonomy

Anteaglonium brasiliense D.A.C. Almeida, Gusmão & A.N. Mill., *sp. nov.* MycoBank MB 807154 (Fig. 1)

Anteaglonium brasiliense is similar to *A. latirostrum* Mugambi & Huhndorf (2009: 462), but differs in having smaller ascospores with fewer septa.

Type:—BRAZIL. Bahia: Santa Terezinha, Serra da Jibóia (12°50'57"S, 39°28'31"W), on twig of unidentified plant, 10 May 2013, D.A.C. Almeida *s.n.* (holotype HUEFS 192250; isotype ILLS 71161).

Etymology:—Referring to the country (Brazil) in which it was collected.

Hysterothecia erumpent to superficial with base immersed, black, carbonaceous, subglobose to ellipsoid, straight or flexuous, with a longitudinal slit, sulcus deep, smooth or slightly striated laterally, gregarious, lying at irregular angles, 170–820 µm long × 110–160 µm high × 110–220 µm wide. *Pseudoparaphyses* hyaline, septate, apically branched, 1–1.5 µm wide. *Asci* bitunicate, clavate, 8-spored, irregularly biseriate, short-stalked, 34.5–47 × 4–5.5 µm. *Ascospores* hyaline, fusiform, smooth, straight to slightly flexuous, 1-septate, constricted at the septa, guttulate, 9–13(–15) × 2–4 µm. *Anamorph* unknown.

Notes:—Previously, only four species were accepted in *Anteaglonium*. *Anteaglonium abbreviatum* (Schweinitz 1832: 245) Mugambi & Huhndorf (2009: 460), *A. globosum* Mugambi & Huhndorf (2009: 460) and *A. parvulum* (Gerard 1874: 40) Mugambi & Huhndorf (2009: 462) can be easily differentiated from *A. brasiliense* by their obovoid ascospores. The fourth species, *A. latirostrum*, has ascospores with a similar shape to those in *A. brasiliense* but differs in having larger ascospores ($22\text{--}28 \times 4\text{--}6 \mu\text{m}$) with more septa (1–4).

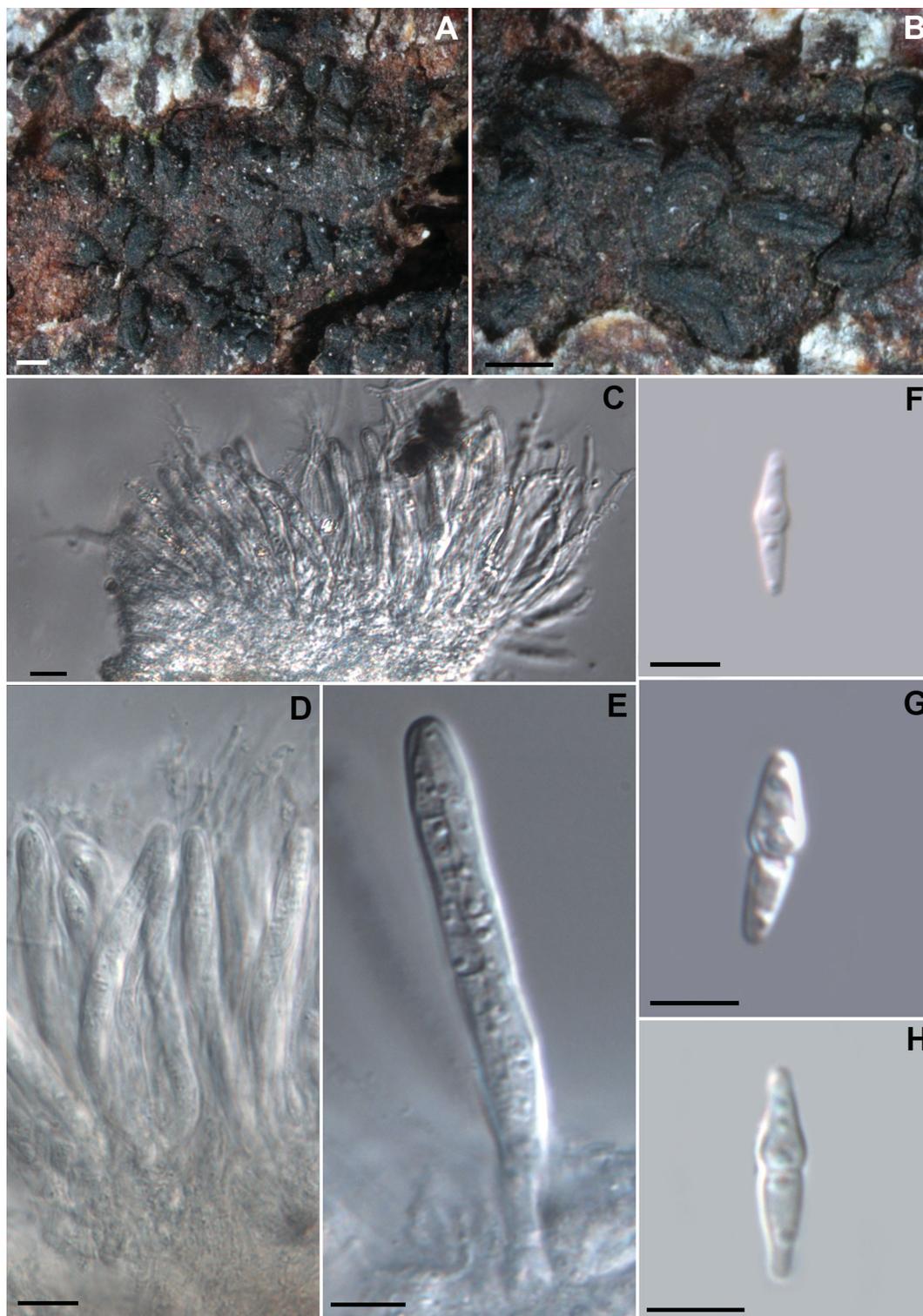


FIGURE 1. *Anteaglonium brasiliense*. A–B. Ascomata. C–D. Asci with ascospores and pseudoparaphyses. E. Ascus with ascospores. F–H. Ascospores. Scale bars: A–B = 0.5 mm, C–E = 10 μm , F–H = 5 μm .

Graphyllum caracolinense D.A.C. Almeida, Gusmão & A.N. Mill., *sp. nov.* MycoBank MB 807156 (Fig. 2)

Graphyllum caracolinense is similar to *Graphyllum panduratum* Checa *et al.* (2007: 288), but differs by having non-applanate ascospores with 1–3 longitudinal septa in the central cells and sometimes surrounded by a gelatinous sheath.

Type:—BRAZIL. Piauí: Caracol, Serra das Confusões National Park (9°13'22"S, 43°29'39"W), on twig of unidentified plant, 8 November 2011, *D.A.C. Almeida s.n.* (holotype HUEFS 42838; isotype ILLS 71162).

Etymology:—Referring to the county (Caracol) in which it was collected.

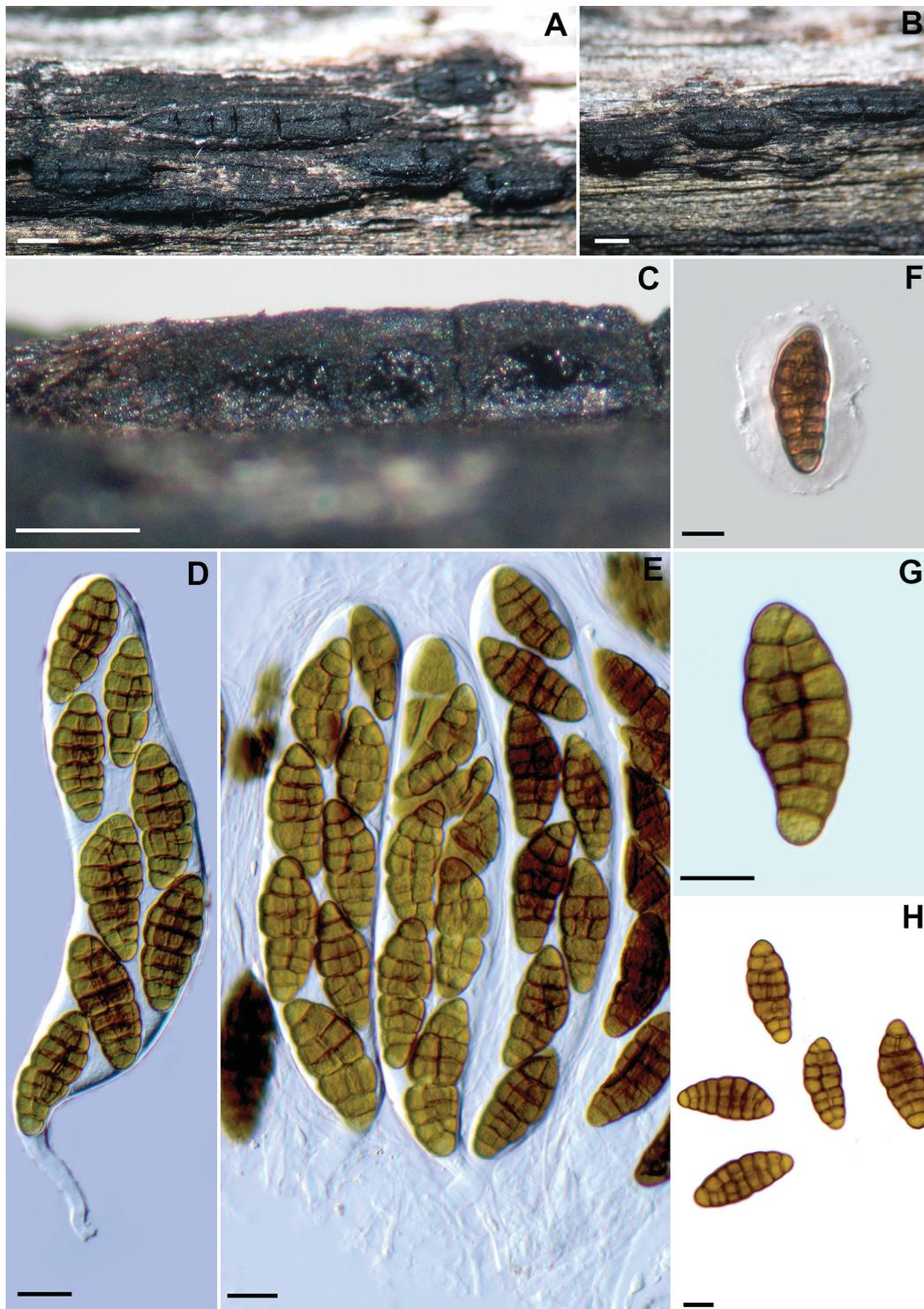


FIGURE 2. *Graphyllum caracolinense*. A–B. Ascomata. C. Longitudinal section of ascomata. D–E. Asci with ascospores. F–H. Ascospores. Scale bars: A–C = 0.5 mm, D–H = 10 μ m.

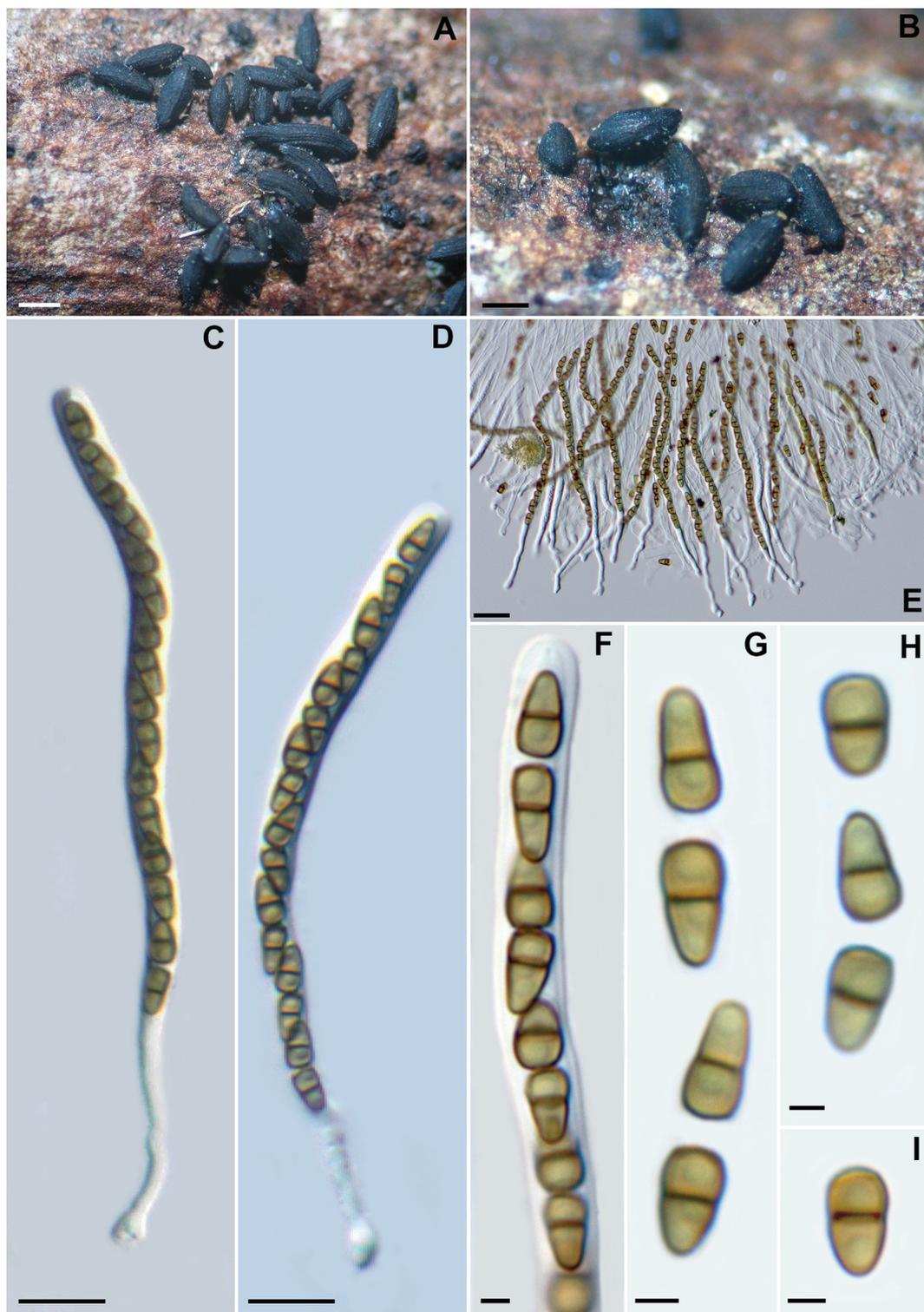


FIGURE 3. *Hysterodiffractum partisporum*. A–B. Ascomata. C–D. Ascus with ascospores. E. Asci with ascospores and pseudoparaphyses. F. Apex of the ascus with ascospores. G–I. Ascospores. Scale bars: A–B = 0.5 mm, C–D = 10 μ m, E = 20 μ m, F–I = 2 μ m.

Hysterothecia erumpent, black, carbonaceous, navicular, straight, often transversely segmented, with a longitudinal slit, sulcus deep, smooth laterally, gregarious, linear, 0.9–6.5 mm long \times 0.2–0.5 mm high \times 0.3–0.7 mm wide. *Pseudoparaphyses* hyaline, septate, apically branched, 1.5–2.5 μ m wide. *Asci* bitunicate, clavate, 8-spored, irregularly biseriate, short-stalked, 130–223 \times 22.5–25 μ m. *Ascospores* pale brown, broadly ellipsoidal, narrowing at the ends, smooth, straight to slightly flexuous, transversally 7(–8)-septate, strongly constricted at the median septa, with 1–3 longitudinal septa in central cells, sometimes surrounded by a gelatinous sheath, 31–40 \times 10–15 μ m. *Anamorph* unknown.

Notes:—The morphology and measurements of the hysterothecia of *G. caracolinense* are similar to *Graphyllum panduratum*, both being erumpent and transversely segmented. The measurements of the ascospores also are similar between these two species (30–38 × 10–13 µm versus 31–40 × 10–15 µm), but *G. panduratum* differs in having applanate and obpyriform ascospores that are longitudinally 3-septate and lack a sheath.

Hysterodifractum D.A.C. Almeida, Gusmão & A.N. Mill., *gen. nov.* MycoBank MB 807155

Hysterodifractum differs from all other genera in the Hysteriaceae in having ascospores that disarticulate into part-spores when mature.

Type species:—*Hysterodifractum partisorum* D.A.C. Almeida, Gusmão & A.N. Mill.

Etymology:—From Latin *Hystero-* referring to the hysterothecium type of ascomata, and *difractum*, referring to the ascospores disarticulating into part-spores.

Hysterothecia superficial, black, carbonaceous, navicular, straight or sometimes flexuous, with a longitudinal slit, smooth or slightly striated laterally, gregarious, lying at irregular angles. *Pseudoparaphyses* hyaline, apically branched, forming an epithecium above the asci. *Asci* bitunicate, cylindrical, 8-spored, uniseriate to irregularly biseriata. *Ascospores* pale brown, fusiform, smooth, disarticulating into part-spores.

Hysterodifractum partisorum D.A.C. Almeida, Gusmão & A.N. Mill., *sp. nov.* MycoBank MB 807161 (Fig. 3)

Hysterodifractum partisorum is comparable to *Actidiographium orientale* (Vasilyeva 2000: 5), but differs by unbranched hysterothecia that are not densely aggregated and by ascospores disarticulating into part-spores.

Etymology:—Referring to the ascospores disarticulating into part-spores.

Type:—BRAZIL. Paraíba: Areia, Mata do Pau-Ferro State Ecological Reserve (6°58'14"S, 5°44'55"W), on twig of unidentified plant, 8 November 2011, D.A.C. Almeida *s.n.* (holotype HUEFS 42865, isotype ILLS 71163).

Hysterothecia superficial, black, carbonaceous, navicular, straight or sometimes flexuous, with a longitudinal slit, sulcus shallow, slightly striated laterally to smooth, gregarious, lying at irregular angles, 0.3–1.5 mm long × 0.2–0.3 mm high × 0.2–0.4 mm wide. *Pseudoparaphyses* hyaline, aseptate, apically branched, forming an epithecium above the asci, 1–2 µm wide. *Asci* bitunicate, cylindrical to clavate, 8-spored, uniseriate to partially biseriata, 77–115 × 4.5–8.5 µm. *Ascospores* pale brown, fusiform, smooth, straight, disarticulating into 16 part-spores; part-spores ovoid or obovoid, 1-septate, 5–7.5 × 2.5–4 µm. *Anamorph* unknown.

Notes:—*Hysterodifractum* has the typical thick-walled, carbonaceous, navicular hysterothecium found in Hysteriaceae, but can be distinguished from all accepted genera in this family by the ascospores disarticulating into part-spores when mature. This is the first report of part-spores occurring in a hysteriaceous fungus.

Molecular analysis

The original LSU alignment comprised 123 taxa and 1,393 bp positions. After using Gblocks to remove ambiguous regions from the sequence alignment the final dataset consisted of 1,253 bp. PHYML analyses produced a single most likely tree (Fig. 4). Molecular analyses based on LSU sequence data indicate that these species found in the Brazilian semi-arid region occur in two distinct orders, Hysteriales and Pleosporales. *Anteaglonium brasiliense* occurred in a strongly supported clade with all other species of *Anteaglonium* in the Pleosporales (≥ 95% BPP, 97% BS). *Graphyllum caracolinense* occurred as a well-supported sister clade to *Oedohysterium* (≥ 95% BPP, 88% BS) in the Hysteriaceae. *Hysterodifractum partisorum* grouped within Hysteriaceae with high Bayesian PP value (≥ 95%) but without significant BS support. The Brazilian isolate of *Rhytidhysterium rufulum* clustered in a highly supported clade (≥ 95% BPP, 79% BS) with all other isolates of *R. rufulum* from Europe, Ghana and Kenya.

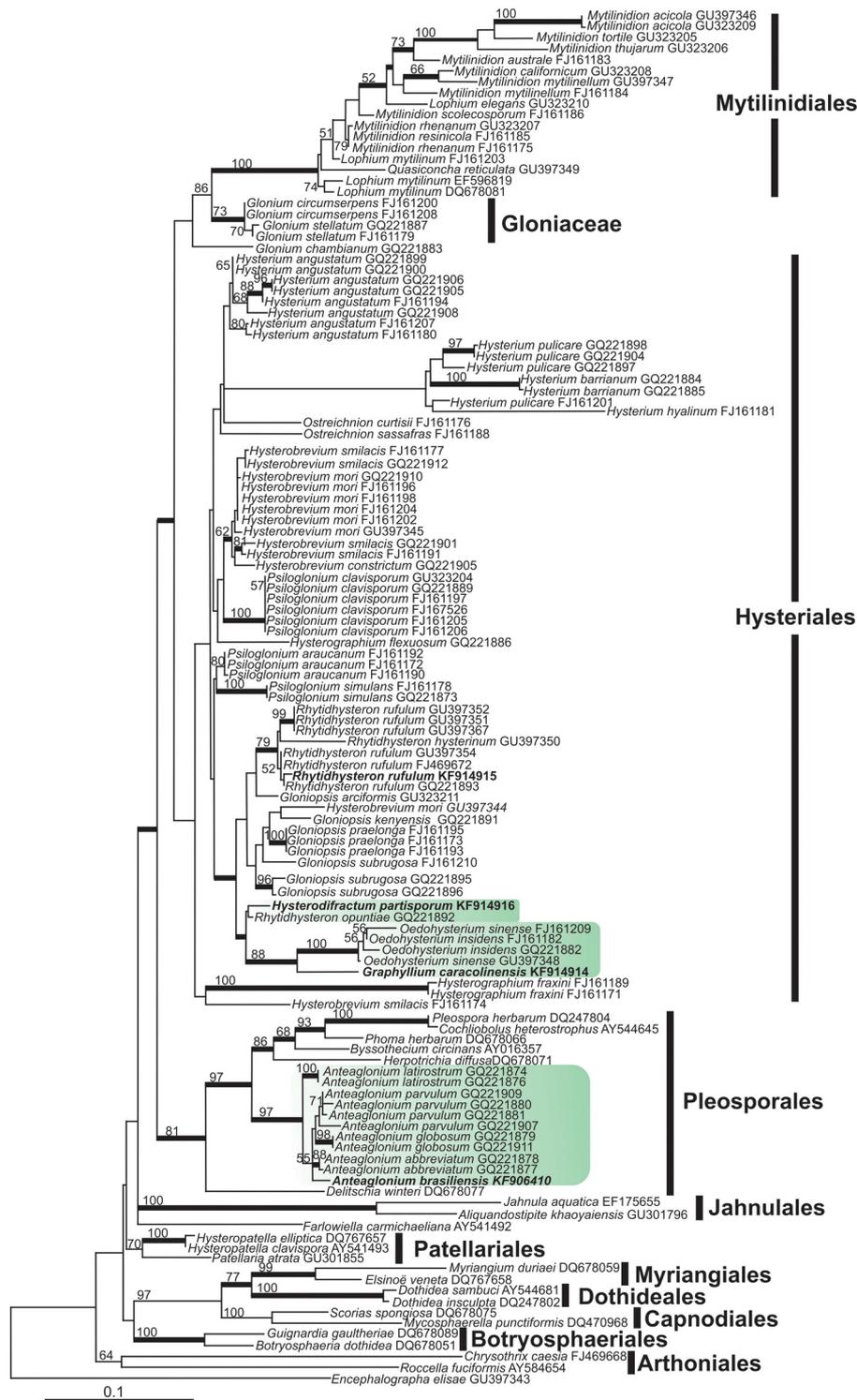


FIGURE 4. Phylogram of the most likely tree obtained from a maximum likelihood analysis of 123 taxa based on LSU nrDNA. Thickened branches indicate significant Bayesian posterior probabilities $\geq 95\%$; numbers refer to PhyML bootstrap support values $\geq 50\%$. *Encephalographa elisae* was used as the outgroup taxon. Newly sequenced taxa are in bold. Clades that contain the three new species are shaded.

Discussion

The phylogenetic analyses based on LSU generated similar results to those found in Boehm *et al.* (2009a), Mugambi & Huhndorf (2009) and Hyde *et al.* (2013). Gloniaceae and Mytilinidiales, for example, formed a moderately-supported monophyletic clade and *Anteaglonium* formed a well-supported monophyletic clade within Pleosporales. In our analyses the Hysteriales lacked significant support and occurred as a sister group to the Gloniaceae and Mytilinidiales as found by Mugambi & Huhndorf (2009) and Hyde *et al.* (2013) rather than the Pleosporales as reported by Boehm *et al.* (2009a).

Anteaglonium was proposed by Mugambi & Huhndorf (2009) for four species that formed a strongly supported clade within Pleosporales. The genus was recently placed in a new family, the Anteagloniaceae by Hyde *et al.* (2013). Three species (*A. abbreviatum*, *A. globosum* and *A. parvulum*) produce obovoid didymospores with one or both ends obtuse (Type I), while the fourth species (*A. latirostrum*) produces fusiform didymospores with acuminate apices (Type II). Although *A. brasiliense* has type II ascospores, our analyses indicate that it is more closely related to the species having type I ascospores (Fig 4).

Graphyllum was placed in the Hysteriaceae by Shoemaker & Babcock (1992) and recently reported to be in the Diademaceae (Pleosporales) by Lumbsch & Huhndorf (2010). Zhang *et al.* (2011, 2012) suggested that *Graphyllum* belonged in the Hysteriales or another higher-level taxa containing hysteriaceous fungi due to its hysterothecium-like ascomata. Our analysis supports the placement of *Graphyllum* in the Hysteriales, where it occurs close to *Oedohysterium* with strong support (Fig. 4). This result, however, must be interpreted with caution since molecular data are presently lacking for other species in this genus, including the type species, *G. chloes* Clements (1901: 6). *Graphyllum caracolinense* does not have aplanate ascospores as in other species in the genus and may represent a different genus. The affinity of *G. caracolinense* with *Oedohysterium* was not expected due to their differences in ascospore morphology, dictyospores in the former and phragmospores in the later.

Hysterodifractum partisporum occurred as a sister taxon to *Rhytidhysterion opuntiae* (Brown 1953: 967) Barr (1990b: 72) without support in the Hysteriales. These species, however, are morphologically very different. *Rhytidhysterion opuntiae* has ellipsoid, 3-septate dictyosporous ascospores usually with one longitudinal septum in the middle cell, whereas *H. partisporum* has didymospores. Furthermore, as shown by Boehm *et al.* (2009a) and by our analyses, the genus *Rhytidhysterion* is polyphyletic with *R. opuntiae* distantly related to *R. hysterinum* (Dufour in De Notaris 1847: 15) Samuels & Müller (1986: 286) and the type species of the genus, *R. rufulum* (Sprengel 1820: 50) Spegazzini (1921: 79) (Fig. 4). Thus, *R. opuntiae* should be accommodated in a new genus after additional study. Due to the morphological differences between *Hysterodifractum* and *R. opuntiae* and lack of support for the clade formed by these two species, *Hysterodifractum* is not an appropriate genus for *R. opuntiae*. *Hysterodifractum partisporum* was frequently collected during this survey, being found in all three collecting expeditions to Mata do Pau-Ferro State Ecological Reserve (29 samples) and during one expedition to Ubajara National Park (one sample). These results suggest that the semi-arid region is poorly sampled and further study may reveal additional new species and records for improving the knowledge of the diversity and distribution of ascomycetes in this region.

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