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CONTRIBUIÇÕES À TAXONOMIA E FILOGENIA DE PHALLALES E. FISCH. (BASIDIOMYCOTA, AGARICOMYCETES)

Recife
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Tese apresentada ao Programa de Pós-Graduação em Biologia de Fungos do Departamento de Micologia do Centro de Biociências da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutora em Biologia de Fungos.
Área de concentração: Micologia básica.

Orientador: Prof. Dr. Iuri Goulart Baseia

Coorientadora: Profª. Dra. María P. Martín

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Dedico ao meu marido e aos meus pais, meus maiores incentivadores.

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“A experiência nunca falha, apenas as nossas opiniões falham, ao esperar da experiência aquilo que ela não é capaz de oferecer.” (Leonardo da Vinci).

RESUMO

Fungos da ordem Phallales são conhecidos como chifres fedorentos que exalam odor e atraem insetos, responsáveis pela dispersão dos basidiosporos. Estudos aplicados foram desenvolvidos com Phallales destacando-se a descoberta de ações antitumorais, antifúngicas e inseticidas, além de serem utilizados como alimento. Em 2006 foi publicado o primeiro trabalho com filogenia molecular que representou a ordem dividida em seis famílias: Clatraceae, Claustulaceae, Lysuraceae, Phallaceae, Protophallaceae e Trappeaceae. Gastrosporiaceae foi incorporada à ordem em 2014, mas tal filogenia não representou todas as sete famílias, o que trouxe dúvidas em relação ao real posicionamento das famílias em Phallales. Além disso, alguns gêneros da ordem careciam de revisão taxonômica e ainda não tinham seus dados moleculares incluídos em estudados filogenéticos, como *Staheliomyces* E. Fisch. Diante do exposto, o objetivo geral desta tese foi reavaliar as relações filogenéticas das famílias de Phallales e contribuir para a sistemática do grupo. Para isso, foram realizadas análises morfológicas e moleculares, com materiais oriundos de empréstimos de herbários e coletados por parceiros. Foram identificadas a nível de espécie 163 exsicatas, totalizando 28 espécies de 13 gêneros, destacando-se onze tipos. Como resultado foram desenvolvidos cinco artigos: 1. A filogenia com as sete famílias de Phallales foi representada por meio da análise filogenética de ITS, nuc-LSU, mt-SSU, *ATP*6, *RPB*2 e *TEF*1-α, depositadas em bases de dados. Foi discutido o posicionamento dos gêneros nas famílias; determinadas 118 hipóteses de espécies em Phallales baseadas em ITS; demonstrada a distribuição geográfica mundial dos gêneros; o estilo de vida, saprotrófico e ectomicorrízico; e a comestibilidade, comestíveis e venenosos. 2. Foram estabelecidas quatro novas espécies de *Staheliomyces* com base em morfologia e filogenia de ITS, nuc-LSU e *ATP*6: *S. candeliformis* N.M. Assis, Melanda & T.S. Cabral, *S. costariquensis* Ovrebo, Melanda, N.M. Assis & T.S. Cabral, *S. cylindricus* Melanda, N.M. Assis & T.S. Cabral e *S. quadratus* N.M. Assis, Melanda, T.S. Cabral, com chave de identificação. A emenda na descrição do gênero, a designação do lectótipo de *S. cinctus* E. Fisch. e um mapa de distribuição foram apresentados. 3. Foi elaborado um *checklist* de Phallales para o nordeste brasileiro juntamente e a descrição de novos registros: primeiro registro para o país de *Mutinus bambusinus* (Zoll.) E. Fisch.; segundo de *Phallus atrovolvatus* Kreisel & Calonge; e segundo registro para a ciência de *Clathrus natalensis* G.S. Medeiros, Melanda, T.S. Cabral, B.D.B. Silva & Baseia. 4. O primeiro registro de *Blumenavia rhacodes* Möller para o bioma Pampa foi publicado, ampliando a distribuição da espécie para além da

Mata Atlântica. 5. Por fim, foi desenvolvida uma revisão morfológica do tipo de *Colus schellenbergiae* Sumst., confirmando sua sinonimização com *Pseudocolus schellenbergiae* (Sumst.) Johnson e demonstrando as diferenças desta espécie com *P. fusiformis* (E. Fisch.) Lloyd, que eram aceitas como sononímias. Além disso, foram analisados materiais da localidade tipo de *Clathrus columnatus* Bosc, espécie publicada em 1811, mundialmente distribuída, mas ainda sem uma revisão taxonômica atual. Nesta tese foi possível constatar que a diversidade de Phallales está subestimada e ressaltar a importância de trabalhos de base para a construção do conhecimento do grupo.

Palavras-chave: Fungos gasteroides; Chifres fedorentos; Clathraceae; Diversidade; Phallaceae; Sistemática.

ABSTRACT

Fungi of the order Phallales are known as stinkhorns that exude odor and attract insects, responsible for the dispersion of basidiospores. Applied studies were developed with Phallales, highlighting the discovery of antitumor, antifungal and insecticide actions, in addition to being used as food. The first work with molecular phylogeny was published in 2006 and represented the order divided into six families: Clatraceae, Claustulaceae, Lysuraceae, Phallaceae, Protophallaceae and Trappeaceae. Gastrosporiaceae was incorporated into the order in 2014, but such phylogeny did not represent all seven families, which raised doubts regarding the real placement of families in Phallales. Furthermore, some genera of the order lacked a taxonomic review and their molecular data had not yet been included in phylogenetic studies, such as *Staheliomyces* E. Fisch. In view of the above, the general objective of this thesis was to reassess the phylogenetic relationships of the families of Phallales and contribute to the systematics of the group. For this, morphological and molecular analyses were carried out, with borrowed materials from herbaria, and collected by partners. In total, 163 specimens were identified at the species level, totaling 28 species of 13 genera, emphasizing eleven types. As a result, five articles were developed: 1. The phylogeny with the seven families of Phallales was represented through the phylogenetic analysis of ITS, nuc-LSU, mt-SSU, *ATP*6, *RPB*2 e *TEF*1-α, deposited in databases. The positioning of genera in families was discussed; determined 118 species hypotheses in Phallales based on ITS; demonstrated the worldwide geographic distribution of the genera; lifestyle, saprotrophic and ectomycorrhizal; and edibility, edible and poisonous. 2. Four new species of *Staheliomyces* were established based on the morphology and phylogeny of ITS, nuc-LSU e *ATP*6: *S. candeliformis* N.M. Assis, Melanda & T.S. Cabral, *S. costariquensis* Ovrebo, Melanda, N.M. Assis & T.S. Cabral, *S. cylindricus* Melanda, N.M. Assis & T.S. Cabral e *S. quadratus* N.M. Assis, Melanda, T.S. Cabral, with identification key. The proposal to emend the genus, the lectotype designation of *S. cinctus* E. Fisch. and a distribution map was presented. 3. A checklist of Phallales for Northeastern Brazil was prepared together with the description of new records: the first record for the country of *Mutinus bambusinus* (Zoll.) E. Fisch.; second from *Phallus atrovolvatus* Kreisel & Calonge; and second record for science of *Clathrus natalensis* G.S. Medeiros, Melanda, T.S. Cabral, B.D.B. Silva & Baseia. 4. The first record of *Blumenavia rhacodes* Möller for the Pampa biome was published, expanding the species' distribution beyond the Atlantic Forest. 5. Finally, a morphological revision of the type of

Colus schellenbergiae Sumst. was developed, confirming its synonymization with *Pseudocolus schellenbergiae* (Sumst.) Johnson, and demonstrating the differences between this species with *P. fusiformis* (E. Fisch.) Lloyd, which were accepted as synonyms. In addition, materials from the type locality of *Clathrus columnatus* Bosc, a species published in 1811, widely distributed, but still without a current taxonomic revision, were analyzed. In this thesis, it was possible to verify that the diversity of Phalllales is underestimated and to emphasize the importance of basic work for the construction of the group's knowledge.

Keywords: Diversity; Clathraceae; Gasteroid fungi; Phallaceae; Systematic; Stinkhorns.

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SUMÁRIO

1 INTRODUÇÃO

A ordem Phallales E. Fisch. agrupa os fungos gasteroides que apresentam mecanismo adesivo de dispersão, nos quais os basidiosporos encontram-se misturados com uma mucilagem que exala um odor para atração dos agentes dispersores (MILLER; MILLER, 1988). Possuem o hábito saprotrófico e ectomicorrízico (PÕLME et al., 2020) e têm sido estudados em relação às ações antitumorais, antifúngicas e inseticidas (LIN et al., 2020; LIN et al., 2021; LU; LUO, 2010; ZHANG et al., 2019). Apresentam valor econômico pois são utilizados como alimento em vários países, entretanto algumas espécies possuem propriedades tóxicas (LI, H. et al., 2021).

Linnaeus (1753) nomeou os primeiros gêneros de Phallales: *Clathrus* P. Micheli ex L. e *Phallus* Junius ex L. Mais de cem anos depois a ordem Phallales foi proposta (FISCHER, 1898) para agrupar as famílias Clathraceae Chevall. (tipo *Clathrus*) e Phallaceae Corda (tipo *Phallus*) com basidiomas que se ramificam, ou não, em braços, ou formam um pseudoestipe alongado, respectivamente. Apesar da família Lysuraceae Corda já ter sido proposta à época (CORDA, 1842), para abrigar os gêneros *Lysurus* Fr. e *Aseroë* Labill., que possuem pseudoestipe alongado e ramificação no ápice – caracteres que unem as duas formas de *Phallus* e *Clathrus* – esta família não foi aceita por Fischer (1898), e os gêneros de Lysuraceae foram colocados em Clathraceae. Outros autores utilizando estudos morfológicos também concordaram com essa classificação (CUNNINGHAM, 1944; HIBBETT; THORN, 2001; KIRK et al., 2008; PEGLER; GOMEZ, 1994), enquanto publicações com dados moleculares (HE et al., 2019; WIJAYAWARDENE et al., 2020) e bases de dados (INDEX FUNGORUM, 2020; MYCOBANK, 2020; NILSSON et al., 2019; SCHOCH et al., 2020) agrupam os gêneros de Lysuraceae em Phallaceae. O primeiro representante de Phallales em uma filogenia molecular foi *Pseudocolus fusiformis* (E. Fisch.) Lloyd, por Hibbett et al. (1997), cujo trabalho demonstrou a polifilia dos fungos gasteroides. Após esse estudo muitos outros foram realizados, mas ainda sem consenso em relação ao quantitativo de famílias na ordem.

Cunningham (1931), ao observar que alguns caracteres morfológicos do gênero sequestrado (com basidiomas indeiscentes, ou seja, que não expandem) *Claustula* K.M. Curtis correspondiam a ordem Phallales, incluiu o mesmo em uma nova família desta ordem: Claustulaceae G. Cunn. Após isso, novas famílias de gêneros sequestrados foram propostas: Gelopellaceae Zeller, Protophallaceae Zeller, Trappeaceae P.M. Kirk, porém foram

consideradas parte de Hysterangiales, a qual possui somente representantes sequestrados (KIRK et al., 2008; ZELLER, 1939).

Estudos filogenéticos confirmaram que Phallales era representada por basidiomas sequestrados e expandidos (que expandem o receptáculo/pseudoestipe do ovo), passando a considerar seis famílias: Claustulaceae, Clathraceae, Lysuraceae, Phallaceae, Protophallaceae e Trappeaceae (HOSAKA et al., 2006). Neste mesmo trabalho a família de fungos sequestrados Gastrosporiaceae Pilát foi citada como possível representante de Phallales, porém não foi incluída na filogenia, e o grupo de fungos gasteroides antes denominado *gomphoid-phalloid* foi proposto como a subclasse Phallomycetidae K. Hosaka, Castellano & Spatafora.

Em 2014 um artigo focado na filogenia de Phallales (TRIERVEILER-PEREIRA; DA SILVEIRA; HOSAKA, 2014) concordou com a divisão da ordem em sete famílias, incluindo então Gastrosporiaceae, fato também aceito nessa tese. Porém, na filogenia deste trabalho de 2014 foram representadas somente seis famílias, sem a inclusão de Trappeaceae. Além do mais, alguns trabalhos recentes (HE et al., 2019; WIJAYAWARDENE et al., 2020) com filogenia molecular consideraram apenas três famílias em Phallales: Claustulaceae, Gastrosporiaceae e Phallaceae (com os representantes de Clathraceae e Lysuraceae); e a família Trappeaceae e Phallogastraceae (com os representantes de Protophallaceae) como integrantes da ordem Hysterangiales.

Alguns gêneros de Phallales, por exemplo: *Staheliomyces* E. Fisch. e *Neolysurus* O.K. Mill., Ovrebo & Burk, ainda não foram representados por análises filogenéticas, uma ferramenta muito importante nas análises taxonômicas. Especialmente para os representantes de Phallales que possuem basidioma efêmeros, ou seja, que perdem muitas características morfológicas após a coleta (MAGNAGO; TRIERVEILER-PEREIRA; NEVES, 2013). Além disso, muitos gêneros carecem de revisão sistemática, já que foram publicados há muitos anos, e em muitos casos não há registro do local de tombamento do tipo, dificultando as revisões taxonômicas. A revisão de materiais de localidade tipo pode ser uma das soluções para esse problema, e a comparação desses com materiais de diferentes regiões, de morfotipos distintos identificados com um mesmo nome, pode revelar a existência de mais de uma espécie. Diante disso a hipótese geral da tese é que a diversidade de Phallales está subestimada, principalmente porque as análises são escassas e as filogenias não estão utilizando tipos em sua maioria.

1.1 OBJETIVOS

1.1.1 Objetivo Geral

- Reavaliar as relações filogenéticas das famílias da ordem Phallales e contribuir para a sistemática do grupo.

1.1.2 Objetivos Específicos

- Avaliar as relações filogenéticas entre as sete famílias de Phallales (Claustulaceae, Clathraceae, Gastrosporiaceae, Lysuraceae, Phallaceae, Protophallaceae e Trappeaceae) [APÊNDICE D];
- Identificar caracteres morfológicos diagnósticos das espécies, baseado na integração de dados morfológicos, moleculares e distribuição geográfica [APÊNDICE E];
- Revisar a identidade de espécies descritas na literatura e descrever possíveis espécies novas [APÊNDICE E, F, G, H].

2 FUNDAMENTAÇÃO TEÓRICA

2.1 FUNGOS GASTEROIDES: DA CLASSE AO GRUPO POLIFILÉTICO

Os fungos gasteroides (*gaster* = estômago; *mycetes* = fungo) são macrofungos do filo Basidiomycota reconhecidos por possuírem a maturação dos basidiosporos dentro do basidioma, denominada desenvolvimento angiocárpico, e subsequente dispersão passiva desses basidiosporos, denominada estatimospórica (MILLER; MILLER, 1988). O início da classificação dos fungos gasteroides se deu em um estudo de Persoon (1801), na qual distinguiu os fungos Basidiomycota em duas classes (Angiocarpi e Gymnocarpi), em função da formação dos basidiosporos no basidioma fechado ou aberto, alocando os fungos gasteroides na classe Angiocarpi. Tal classificação foi adotada por Fries (1821) ao estabelecer a classe Gasteromycetes Fr., o que representou um marco no estudo destes fungos. Fries continuou estudando os gasteroides como classe (FRIES, 1823), citando como característica básica: '*uterus*', referente ao desenvolvimento angiocárpico. Vinte e seis anos depois o mesmo autor reclassificou a classe como uma família (FRIES, 1849). Esta reclassificação foi considerada nome inválido de acordo com o código de nomenclatura (Art. 33.4, Art. 32,1(b); ver Art. 18.1), por ter sido declarado por Fries como uma família em uma posição supra-ordem, já que a terminação *-mycetes* indica uma classe e usar essa terminação para família seria incorreto.

Os fungos gasteroides apresentam uma gama de morfologias dos basidiomas e de mecanismos de dispersão, sendo conhecidos popularmente por tais características, por exemplo: os *puffballs* (bufas-de-lobo) possuem basidiomas globosos com gleba geralmente pulverulenta; *earthstars* (estrelas-da-terra) são fungos em forma de estrela também com gleba pulverulenta; *stinkhorns* (chifres fedorentos) possuem gleba geralmente gelatinosa que atrai insetos através de um odor característico; os *cannonballs fungus* (fungo bala de canhão) disparam os basidiosporos em um mecanismo de catapulta; já os *bird's nest fungi* (fungos ninho de passarinho) possuem basidioma em forma de ninho de pássaro, com os basidiosporos em peridíolos em seu interior (MILLER; MILLER, 1988).

Hibbett et al. (1997) realizaram a análise filogenética de Máxima Parcimônia, inferida a partir das sequências das subunidades menores do DNA ribossômico nuclear (nuc-SSU) e mitocondrial (mt-SSU), de cogumelos que possuem dispersão ativa dos basidiosporos (com himênio formado por lamelas e não-lamelados) e os com dispersão passiva (gasteroides). Os resultados mostraram a polifilia dos fungos gasteroides, os quais apareceram em quatro linhagens evolutivas independentes (ramos em azul na Figura 1) juntamente com

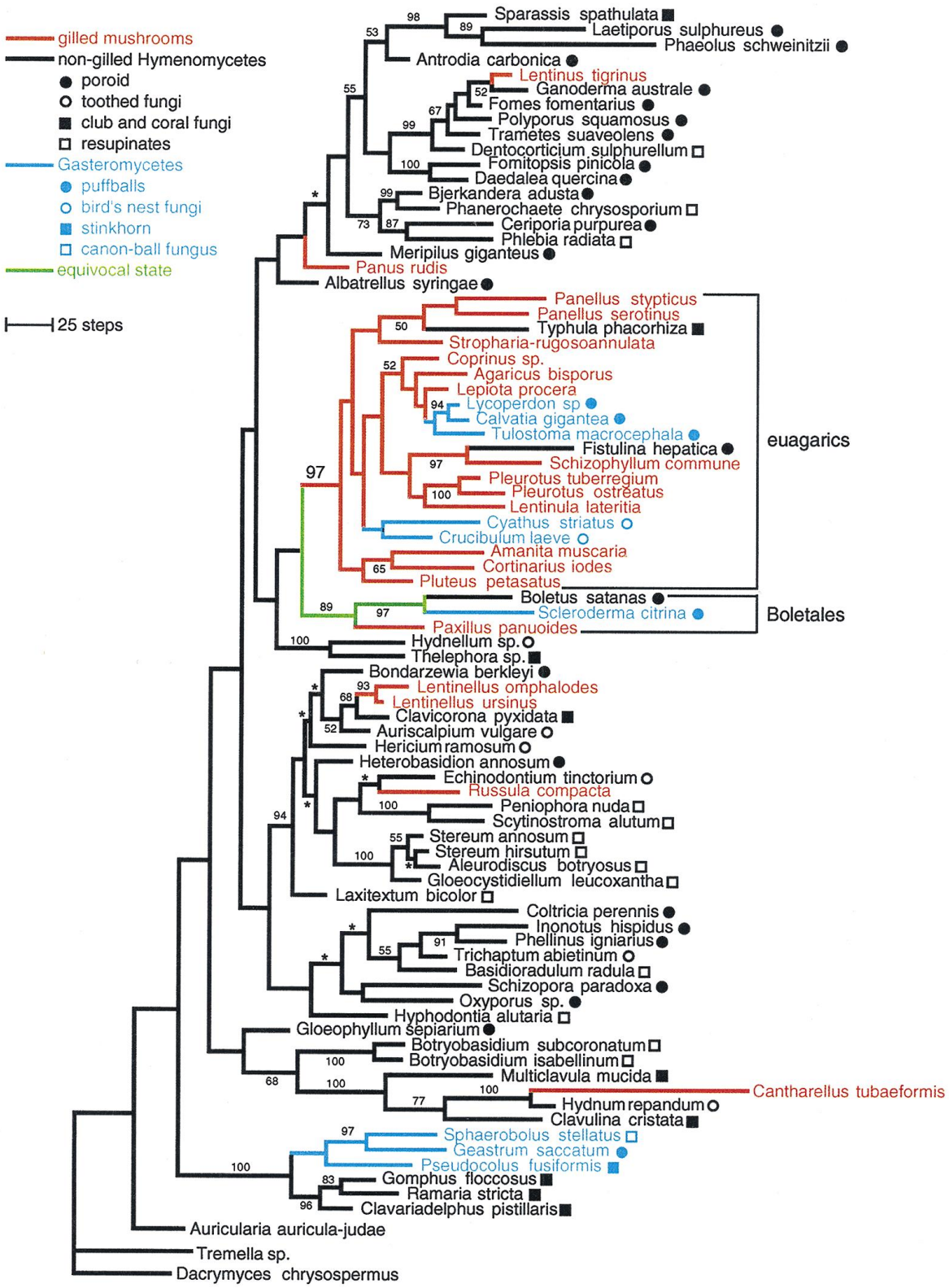
cogumelos de dispersão ativa. Após essa análise inicial, a classe Gasteromycetes passa a ser desprovida de valor taxonômico.

No estudo de Hibbett et al. (1997), os *pufballs* agruparam-se em duas linhagens distintas, nos clados chamados de euagaricos – representados por *Lycoperdon* sp., *Calvatia gigantea* (Batsch) Lloyd e *Tulostoma macrocephalum* Long (escrito como uma variante ortográfica no artigo: *T. macrocephala*) – e boletales – *Scleroderma citrinum* Pers. (escrito como uma variante ortográfica no artigo: *S. citrina*). Os *bird's nest fungi – Cyathus striatus* (Huds.) Willd. e *Crucibulum laeve* (Huds.) Kambly– aparecem também no clado euagaricos, compartilhando um ancestral comum com os *puffballs* e com cogumelos lamelados e não-lamelados. *Earthstars* – *Geastrum saccatum* Fr.– (considerados como *puffballs* no artigo) se agruparam em um clado separado dos anteriores, juntamente com *cannonballs fungus* – *Sphaerobolus stellatus* Tode – ambos compartilhando um ancestral comum com *stinkhorns* – *Pseudocolus fusiformis* – os três últimos compartilhando um ancestral comum com fungos corais (HIBBETT et al., 1997). Este último clado (*earthstars*, *cannonballs fungus*, *stinkhorns* e fungos corais) foi chamado de *gomphoid-phalloid* (BINDER; HIBBETT, 2002; HIBBETT; BINDER, 2001; HIBBETT; THORN, 2001; PINE; HIBBETT; DONOGHUE, 1999), e posteriormente de subclasse Phallomycetidae por Hosaka et al. (2006).

Hibbett et al. (2007) trouxeram a primeira classificação filogenética de consenso básica do reino Fungi, a qual mostram mais uma vez a polifilia dos fungos gasteroides distribuídos no subfilo Agaricomycotina Doweld, classe Agaricomycetes Doweld, nas subclasses Agaricomycetidae Locq. e Phallomycetidae (Figura 2). Na subclasse Agaricomycetidae, estão as ordens Agaricales Underw. e Boletales E.-J. Gilbert, mencionadas anteriormente como os clados euagaricos e boletales, respectivamente, e em Phallomycetidae as ordens Geastrales K. Hosaka & Castellano, Gomphales Jülich, Hysterangiales K. Hosaka & Castellano e Phallales.

Hibbett et al. (2014) apresentaram uma nova filogenia de Basidiomycota com foco em Agaricomycotina, revelando um incremento de clados dentro de Agaricomycetidae e uma melhor resolução filogenética das ordens de Phallomycetidae (Figura 2).

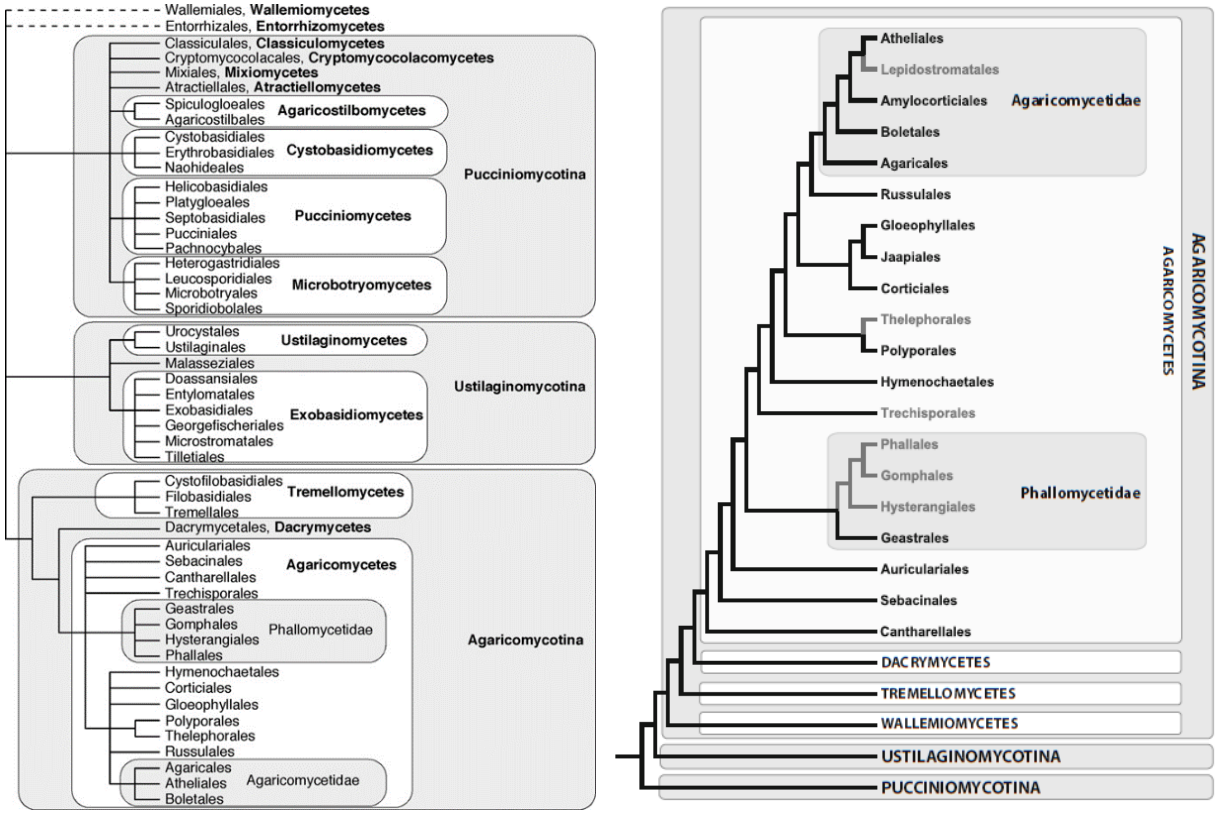
Figura 1 – Análise filogenética de cogumelos lamelados, não-lamelados e gasteroides



Fonte: Retirado de Hibbett et al. (1997), pág. 12004, como Fig.1.

Legenda: Uma das 52 árvores igualmente parcimoniosas. Ramos com asteriscos entram em colapso na árvore de consenso estrito. Os números por nós são frequências de bootstrap (valores menores que 50% não mostrados). As cores das ramificações representam otimizações morfológicas do estado dos caracteres. Os símbolos dos nomes dos táxons indicam tipos específicos de corpos frutíferos de Gasteromycetes e Hymenomycetes não lamelados.

Figura 2 – Relações filogenéticas de Agaricomycetes e outros Basidiomycota



Fonte: Imagem da esquerda retirada de Hibbett et al. (2007), pág. 538, como Fig. 3; imagem da direita retirada de Hibbett et al. (2014), pág. 375, como Fig. 14.1.

2.2 SUBCLASSE PHALLOMYCETIDAE: ORDEM PHALLALES

Os primeiros gêneros de Phallales foram publicados por Linnaeus em *Species Plantarum* (1753), são eles: *Clathrus* e *Phallus*. Utilizando-se das obras de Junius (1552) e Micheli (1729), Linnaeus modifica os nomes dos gêneros para a forma lineana de nomenclatura, por esse motivo o nome desses autores é também citado no nome dos gêneros. A ordem Phallales ainda não havia sido proposta, Linnaeus (1753) faz as descrições das espécies novas na seção nomeada "Fungi". Em Dring (1980) a autoria do gênero *Clathrus* está citada erroneamente como: *Clathrus* Micheli ex Persoon, Synopsis Methodica Fungorum 2: 241 (1801).

Phallus foi caracterizado por Linnaeus (1753) por possuir pseudoestipe com receptáculo ovalado (descrição em latim: *pileo ovato, stipe nudo rugofo*) descrevendo a espécie tipo do gênero *Phallus impudicus* L. O gênero *Clathrus*, por sua vez, foi dividido em acauleado (sem pseudoestipe) e estipitado. A espécie "acauleada" é caracterizada por possuir basidioma arredondado (descrição em latim: *caulis fubrotundus*). Neste grupo, o autor descreveu *Clathrus cancellatus* L., como uma combinação nova com as sinonímias *C. ruber*

P. Micheli ex Pers. e *Boletus cancellatus purpureus* Tournefort. As espécies estipitadas são caracterizadas por possuírem um pseudoestipe e receptáculo oval (descrição em latim: *stipitatus, capitolo ablongo volvato*) descrevendo neste grupo *Clathrus denudatus* L. e *C. nudus* L.

Fries (1823) estabeleceu o gênero *Lysurus*, com o tipo *Lysurus mokusin* (L.) Fr. tendo como sinonímia homotípica *Phallus mokusin* L. Para Fries o novo gênero é um intermédio entre *Phallus* e *Clathrus*. Nesta publicação o autor faz a classificação dos gêneros *Phallus, Aseroë, Lysurus* e *Clathrus* como pertencentes à subordem Phalloideae, ordem Angiogastres, classe Gasteromycetes. Fries (1823) faz a separação dos gêneros principalmente de acordo com as a forma do receptáculo e divide *Phallus* e *Clathrus* em tribos:

- *Phallus*: receptáculo estipitado, campanulado (em latim: *Receptaculum stipite suffultum, capituliforme, integrum*). Tribos: *Hymenophallus* (com *Phallus indusiatus* Vent., *P. daemonum* Rumph. ex Fr., *P. duplicatus* Bosc), *Ithyphallus* (com *P. impudicus* L.), *Lejophallus* (com *P. hadriani* Vent., *P. rubicundus* (Bosc) Fr.), *Cynophallus* (com *P. caninus*. Huds.).
- *Aseroë:* receptáculo estipitado, dividido em raios bifurcados (em latim: *Receptaculum stipite suffultum, in radios bifidos expansum*). Espécie *A. rubra* Labill.
- *Lysurus:* receptáculo estipitado, dividido em partes inteiras (em latim: *Receptaculum stipite suffultum, in lacinias integras liberas divisum*). Espécie *L. mokusin.*
- *Clathrus:* receptáculo séssil, com vários ramos se juntando (em latim: *Receptaculum sessile, e ramis pluribus conjunctis cancellatum*). Tribos: *Laternea* Turpin (com *Clathrus triscapus* (Turpin) Fr. = *Laternea triscapa* Turp., *C. columnatus* Bosc.), *Clethria* Brown. (com *Clathus cancellatus* Tourn. ex Fr. e *Clathus crispus* Turpin).

A família Clathraceae foi proposta em 1826 (CHEVALLIER, 1826) com os gêneros *Clathrus* e *Laternea*, caracterizados, principalmente, pelo receptáculo redondo com ramos anastomosados. Os basidiomas desta família são denominados fungos gaiola (*cage-fungi*) (PEGLER; GOMEZ, 1994) ou chifres fedorentos em forma de rede (*lattice stinkhorns*) (HOSAKA et al., 2006). Várias formas de classificar os gêneros desta família foram adotadas, como a divisão em tribos: Columnateæ, Stellateæ e Clathrateæ (CUNNINGHAM, 1944); ou em séries: Clathroid, Lysuroid e Laternoid (PEGLER; GOMEZ, 1994) ou Anthuroid, Blumenavioid, Clathrelloid, Laternoid, Lysuroid e Treubii (DRING, 1980), observando-se

grande divergências no agrupamento dos gêneros dependendo dos caracteres considerados pelos taxonomistas dos estudos.

Corda (1842) descreveu as famílias Lysuraceae (como Lysuroideae) e Phallaceae (como Phalloideae). Os gêneros *Lysurus* e *Aseroë* compunham Lysuraceae e *Cynophallus* Pers., *Hymenophallus* Nees, *Phallus* e *Simblum* Klotzsch ex Hook, Phallaceae. Nesta publicação, o autor concorda com Chevallier (1826) onde a família Clathraceae abrange os gêneros *Clathrus* e *Laternea* e inclui nessa família o gênero *Colus* Cavalier & Séchier (escrito por Corda como *Coleus*).

Fries (1849) faz um novo trabalho de classificação dos fungos falóides agrupando-os como Phalloidei, e concordou em partes com as divisões dos gêneros nas três famílias de acordo com Corda (1842), mas não cita os nomes das famílias e sim as denominações Phallei, Lysurei e Clathrei. A característica geral citada por Fries para Phallodei é: perídio em forma de volva, duplo, com camada gelatinosa. Receptáculo expandido, basidiosporos em extrato mucoso (em latim: *Peridium volvaceum, discretum, duplex, gelatina distentum, receptaculum liberum, sporis in strato mucoso*). As características gerais de cada grupo são:

- Phallei: campanulado, estipe único (em latim: *mitrati, l. capitati, stipe discreto*). Considerou os gêneros *Phallus*, *Simblum*, *Satyrinus* Bosc., e estabeleceu o gênero *Mutinus* Fr., com o tipo *M. caninus* (Huds.) Fr., antes em *Cynophallus*.
- Lysurei: estipitado, receptáculo repartido (em latim: *stipitati, rec. laciniato-partito*). Incluiu aqui o gênero *Aseroë*, antes em um agrupamento separado (FRIES, 1823), juntamente com *Lysurus*, *Aserophallus* Lepr. & Mont. e *Calathiscus* Mont.
- Clathrei: séssil, grade (em latim: *sessiles, cancellati*). Gêneros *Clathrus* e *Ileodictyon* Tul.

Fischer (1898) descreveu a ordem Phallales com as famílias Clathraceae – basidioma ramificado, ou não, em braços – e Phallaceae – basidioma formando um pseudoestipe alongado. Lysuraceae proposta juntamente com Phallaceae (CORDA, 1842), não foi reconhecida por Fischer (1898) como uma família independente, que incluiu os representantes de Lysuraceae na família Clathraceae. Essa classificação de Fisher (1898) foi adotada por autores subsequentes como Dring (1980), em seu trabalho de revisão de Clathraceae, em Miller e Miller (1988), no livro sobre a classe gasteromycetes, e por outros autores (CUNNINGHAM, 1944; DRING, 1980; HIBBETT; THORN, 2001; KIRK et al., 2008; MILLER; MILLER, 1988; PEGLER; GOMEZ, 1994).

Cunningham (1931) fez uma emenda na ordem Phallales ao propor uma terceira família monogenérica, Claustulaceae, abrigando o gênero *Claustula*, que inclui representantes

com basidiomas sequestrados. Cunningham (1931) apresentou diversas características em comum da família Claustulaceae com outros falóides (fungos da ordem Phallales), como perídio gelatinoso, receptáculo imaturo dividido em câmaras e basidiosporos lisos e elípticos. Esse tratamento taxonômico foi aceito por diversos outros estudos, tais como Bottomley (1948), Dring (1973), Jülich (1981) e Kirk et al. (2001, 2008).

Zeller (1939), também ao estudar a morfologia de macrofungos com basidiomas sequestrados, estabeleceu as famílias Protophallaceae e Gelopellaceae, que juntamente com Hysterangiaceae E. Fisch., compuseram a ordem Hysterangiales. Posteriormente, as três famílias foram acomodadas em Phallales por Miller e Miller (1988), que nesse livro nomearam Gelopellaceae erroneamente como Gelopellidaceae. A ordem Hysterangiales acomoda somente basidiomas sequestrados, tal ordem publicada em Zeller (1939) e Locquin (1974) foi considerada como *nomen nudum*, por não apresentar descrição ou diagnóstico, sendo somente validada após 67 anos por Hosaka et al. (2006). Para Hosaka et al. (2006) (Figura 3): Hysterangiaceae é uma família de Hysterangiales; Protophallaceae é uma família de Phallales; o gênero de Gelopellaceae, *Gelopellis* Zeller, foi incluído em Claustulaceae; e uma nova família é sugerida como um nome provisório, Trappeaceae P.M. Kirk, que foi proposta formalmente dois anos depois por Kirk et al. (2008).

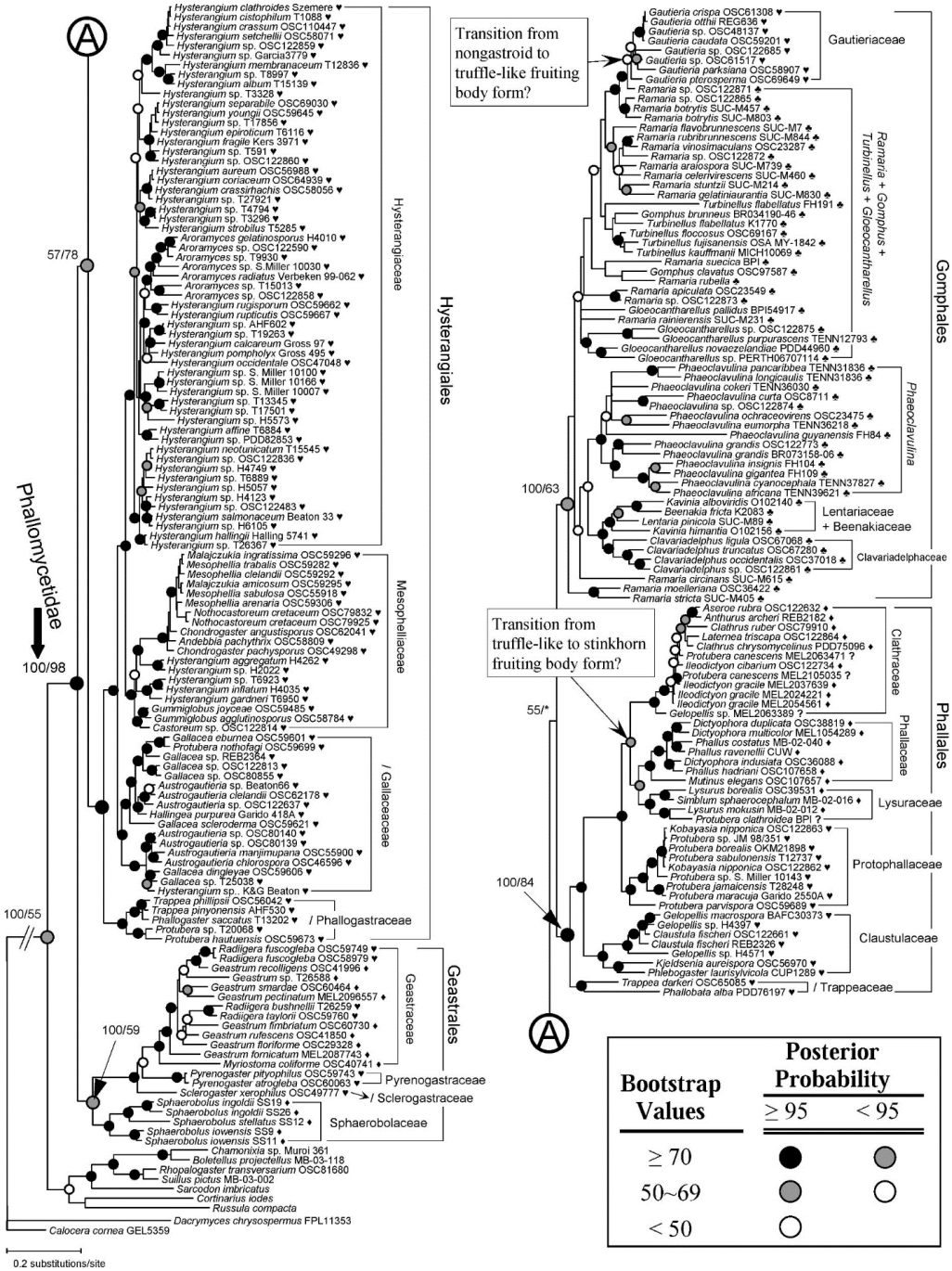
Hosaka et al. (2006) estabeleceram a subclasse Phallomycetidae e duas novas ordens, Hysterangiales e Geastrales, para compor a subclasse juntamente com as ordens já descritas Gomphalles e Phallales. Os resultados deste trabalho foram baseados em análises filogenéticas de parcimônia e bayesiana (Figura 3), conduzidas com a matriz concatenada de cinco marcadores moleculares, incluindo: subunidade maior do DNA ribossomal nuclear (nuc-LSU); mt-SSU; subunidade 6 da ATPase (*ATP*6); segunda maior subunidade da RNA polimerase (*RPB*2); região da subunidade 1α do fator de alongamento da tradução (*TEF*-1α).

Hosaka et al. (2006) concordam com Cunningham (1931) na definição da ordem Phallales por incluir basidiomas expandidos e sequestrados, ao contrário de Fischer (1898) que estabeleceu a ordem Phallales para acomodar apenas espécies epígeas (desenvolvimento do basidioma sobre o substrato) com basidioma expandido. Portanto, em Hosaka et al. (2006) Phallales é composta pelas famílias:

1- Clathraceae, tipo *Clathrus*;
2- Claustulaceae (= Gelopellaceae), tipo *Claustula*;
3- Lysuraceae, tipo *Lysurus*;
4- Protophallaceae, tipo *Protophallus* Murrill;
5- Phallaceae, tipo *Phallus*;

6- Trappeaceae, tipo *Trappea* Castellano.

Figura 3 – Filogenia de Phallomycetidae

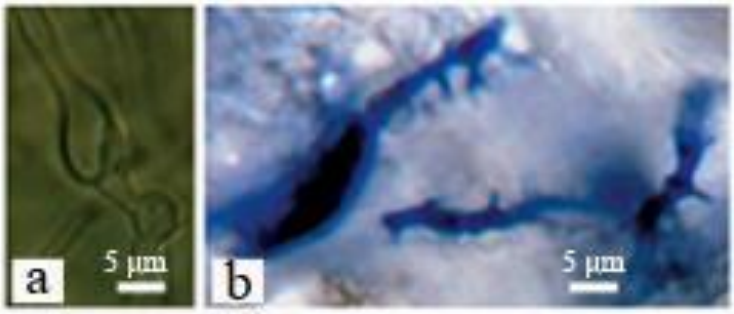


Fonte: Topologia da árvore com análise bayesiana retirada de Hosaka et al. (2006), pág. 952, como Fig. 2.
Legenda: Números nos ramos são valores de bootstrap de probabilidade posterior bayesiana / máxima parcimônia (mostrados como porcentagem). Os nomes provisórios dos táxons são indicados com uma barra (/). Os nomes dos táxons são seguidos por símbolos que indicam as formas do corpo de frutificação: ♥ = gasteroide sequestrado (semelhante a trufas), ♦ = gasteroide não sequestrado (incluindo *stinkhorns*, *earthstars* e *cannonball fungi*), ♣ = não gasteroide.

Apesar de Hosaka et al. (2006) não citarem sinapomorfias definitivas para Phallomycetidae, os autores sugerem potenciais caracteres sinapomórficos, como a

morfologia da rizomorfa pela presença de hifas ampuliformes - "*ampullate hyphae*" (Figura 4a) e acantohifas - "*acanthohypha*" (Figura 4b), bem como, já proposto por Hibbett e Thorn (2001), o conteúdo de pistilarina e ultraestrutura do parentosoma do poro septal – "*septal pore cap*". Hibbett e Thorn (2001) definem a pistilarina como um composto a base de nitrogênio que gera reações incolores a verde escuro com cloreto férrico nos corpos frutíferos, já encontrados nos gêneros *Ramaria* Fr. ex Bonord., *Clavariadelphus* Donk e *Gomphus* Pers.

Figura 4 – Possível micromorfologia sinapomórfica em Phallomycetidae



Fonte: Adaptação de Hosaka et al. (2006), pág. 950, como Fig. 1.
Legenda: a. hifas ampuliformes de *Ramaria eumorpha* (T25800, foto de Efren Cazares). b. acantohifas de *R. cystidiophora* (Giachini 03) corada com azul de algodão (foto de Efren Cazares).

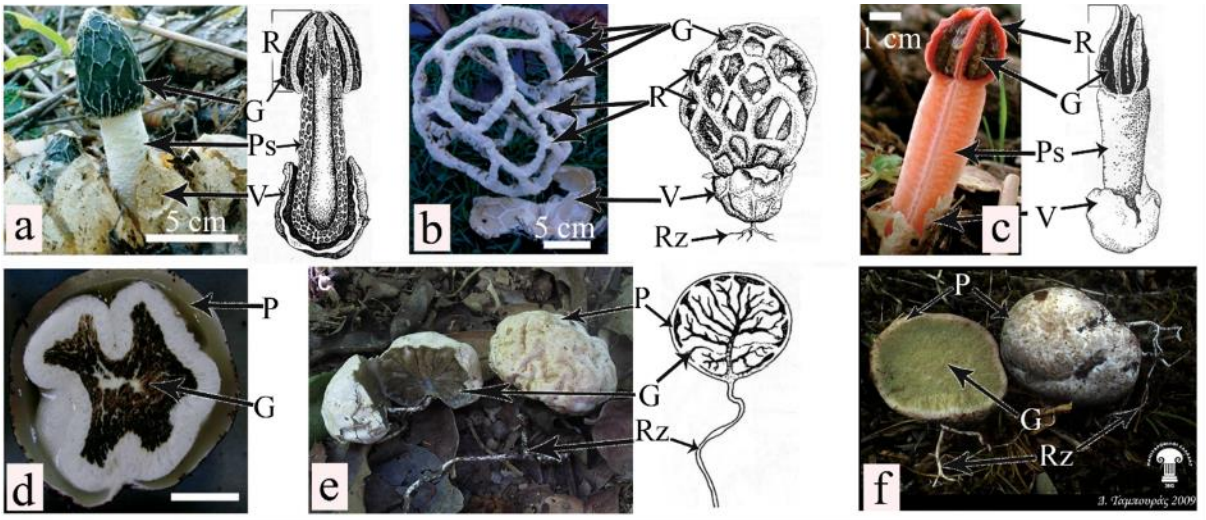
Portanto, os basidiomas de Phallales são caracterizados por possuírem (HOSAKA et al., 2006; MILLER; MILLER, 1988):

- receptáculo imaturo dividido em câmaras;
- basidiomas epígeos e expandidos: *stinkhorns* - Phallaceae (Figura 5a); *lattice stinkhorns* - Clathraceae (Figura 5b) e Lysuraceae (Figura 5c); ou basidiomas sequestrados tipo falsas trufas, alguns podendo ser hipógeos (desenvolvimento total abaixo do substrato, imerso neste): Claustulaceae (Figura 5d), Protophallaceae (Figura 5e) e Trappeaceae (Figura 5f), algumas falsas trufas também foram observadas (Figura 3) no clado de Clathraceae (como *Protubera canescens* G.W. Beaton & Malajczuk e *Gelopellis* sp.) e em Lysuraceae (como *Protubera clathroidea* Dring);
- perídio com duas ou três camadas (Figura 6d), sendo uma delas gelatinosa;
- gleba em sua maioria gelatinosa a mucilaginosa (ver itens G nas Figuras 5 e 6), podendo ser pulverulenta na maturidade, como em *Gastrosporium* Mattir.;
- basidiosporos em sua maioria elipsoides e lisos, com apenas alguns gêneros com ornamentação na parede, como em *Kjeldsenia* W. Colgan, Castellano & Bougher e *Gastrosporium*;

- hábito maioritariamente sapróbio.

O perídio (parede externa do basidioma) no início do desenvolvimento envolve completamente o receptáculo e a gleba, formando um ovo (ver itens P nas Figuras 5 e 6), e na maturidade pode se romper a partir do ápice, onde ocorrerá a expansão do receptáculo nas espécies com basidiomas expandidos (Figura 5a-c), e a não expansão nos sequestrados (Figura 5d-f); após a expansão o perídio restante na base do basidioma é chamado de volva (ver itens V na Figura 5) (CUNNINGHAM, 1931; MILLER; MILLER, 1988).

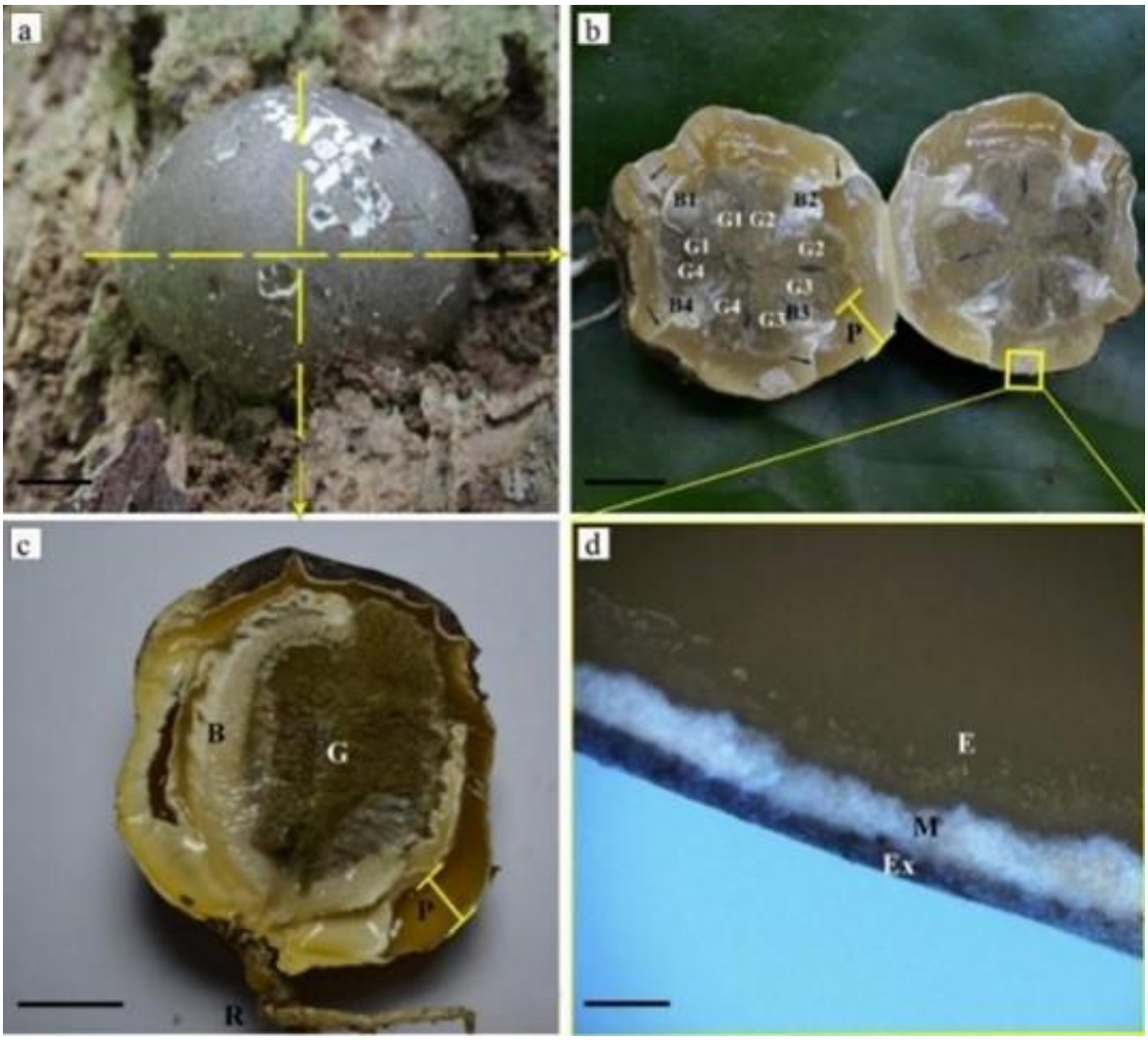
Figura 5 – Macromorfologia de Phallales



Fonte: Ilustrações em preto e branco retiradas de Miller e Miller (1988). Fotos coloridas: a-d. adaptação de Hosaka et al. (2006), pág. 950, como Fig. 1; e. adaptação de Trierveiler-Pereira, da Silveira e Hosaka (2014) pág. 39, como Fig. 2c; f. retirado de http://www.mycohellas.gr/mc/viewarticle.asp?a=161 em 31/12/2020.
Legenda: a. *Phallus* sp. basidioma em campo e ilustração de um corte longitudinal. b. *Clathrus* sp. basidioma em campo e ilustração. c. *Lysurus* sp. basidioma em campo e ilustração. d. *Claustula fischeri* em corte transversal. e. *Protubera* sp. basidioma em campo em corte longitudinal e inteiro e ilustração. f. *Trappea* sp. basidioma em campo em corte longitudinal e inteiro. G = gleba; P = perídio; Ps = pseudoestipe; R = receptáculo; Rz = rizomorfa; V = volva.

O gênero *Gastrosporium* não foi incluído nas análises filogenéticas de Hosaka et al. (2006) pela falta de um marcador molecular, mas foi considerado possível integrante da ordem Phallales, sendo incluído na descrição geral da morfologia do grupo, como apresentado anteriormente. Onze anos mais tarde a inclusão de sequências de *Gastrosporium* em uma revisão molecular somente de Phallales levam a uma emenda na ordem para incluir a família Gastrosporiaceae e as características de gleba pulverulenta na maturidade, bem como os basidiosporos verrucosos dourados a marrons (TRIERVEILER-PEREIRA; DA SILVEIRA; HOSAKA, 2014). Uma nova espécie do gênero *Gastrosporium*, *G. gossypinum* T. Kasuya, S. Hanawa & K. Hosaka (KASUYA; HANAWA; HOSAKA, 2020), confirma as características mencionadas anteriormente e a aceitação da família Gastrosporiaceae em Phallales.

Figura 6 – Ovo e camadas do perídio de *Blumenavia baturitensis* Melanda, M.P. Martín & Baseia



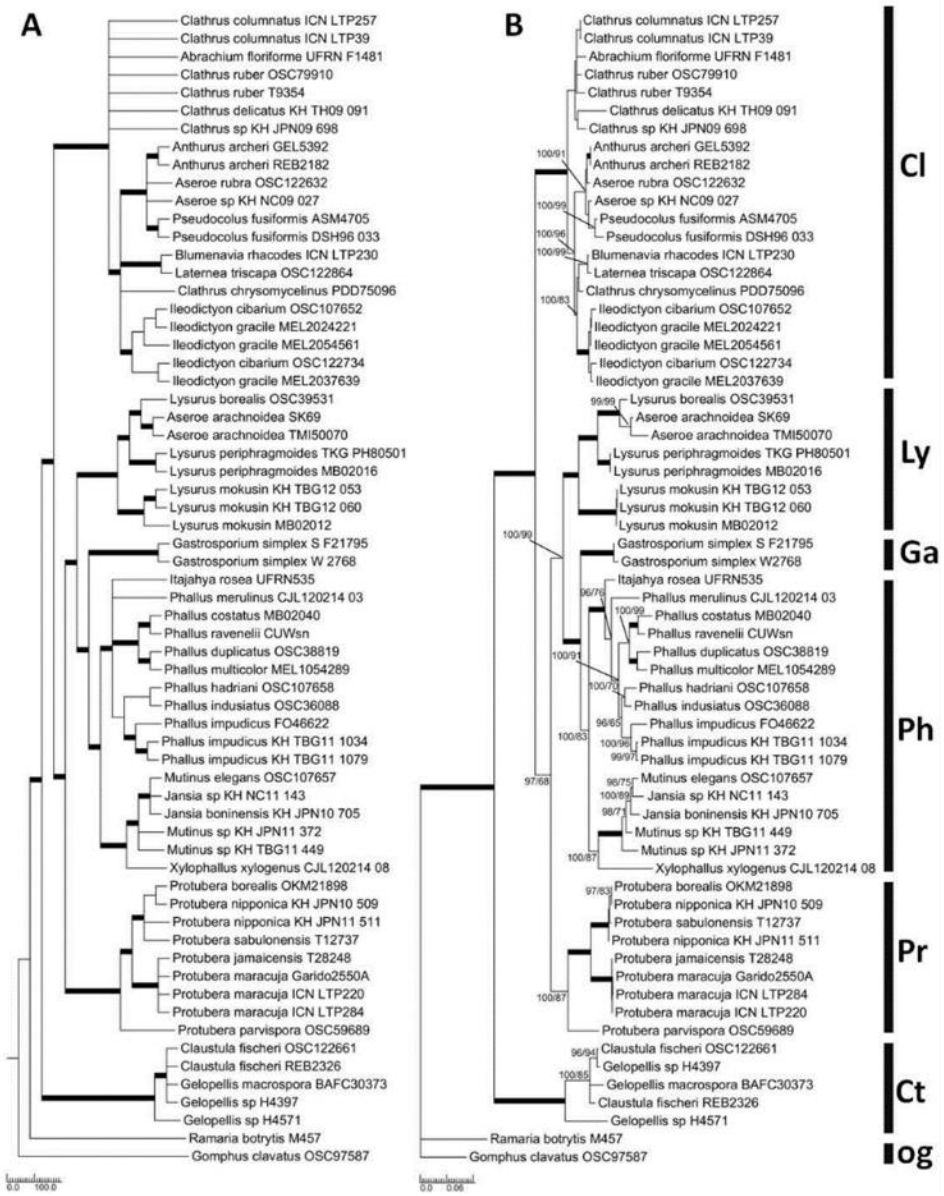
Fonte: Retirado de Melanda (2018) pág. 46, como Fig. 13.

Legenda: a. Ovo de *Blumenavia* sobre tronco em decomposição, no campo, traços e setas amarelas representam a direção dos cortes. b. Corte transversal do ovo fresco, mostrando desenvolvimento multipileado; na parte do ovo da esquerda: setas pretas representam as suturas peridiais; Bn = braço número n; Gn = gleba e tecidos de glebíferos imaturos que ficarão aderido ao braço n após a expansão; na parte da direita: quadrado amarelo representa a parte do ovo de b que está ampliada em d. c. Corte longitudinal do ovo; B = Braço; G = gleba e tecido de glebífero imaturos; R = rizomorfa. Em b e c: linhas amarelas delimitam a camada do perídio (P). d: Camadas do perídio no ovo (aumento de 3x); E = endoperídio, Ex = exoperídio, M = mesoperídio (fotos da autora). Barras a-c = 1 cm, d = 0,5 mm.

A reconstrução de caráter ancestral em Hosaka et al. (2006) revelou inicialmente que basidiomas expandidos são restritos aos clados derivados, com apenas uma transição de formas sequestradas para basidiomas expandidos (Figura 3), mas a incorporação da nova família com basidiomas sequestrados, Gastrosporiaceae, sugere que houve ao menos uma reversão de basidiomas expandidos para sequestrados na ordem (TRIERVEILER-PEREIRA; DA SILVEIRA; HOSAKA, 2014). Trierveiler-Pereira, da Silveira e Hosaka (2014) fizeram análises de Máxima Parcimônia, Bayesiana e Máxima Verossimilhança, com base nas

sequências combinadas dos marcadores nuc-LSU, *ATP*6 e *RPB*2, para propor a relação filogenética da ordem Phallales (Figura 7), sendo esta a mais recente até o resultado desta tese.

Figura 7 – Filogenia de Phallales



Fonte: Filogenia retirada de Trierveiler-Pereira, da Silveira e Hosaka (2014), como Fig. 2.
Legenda: A. Árvore de consenso da regra da maioria das 5475 árvores mais parcimoniosas obtidas após 1000 repetições de pesquisa heurística. Ramos espessos em negrito indicam nós totalmente ou fortemente suportados (≥ 80). B. Árvore de consenso bayesiana. Os valores de suporte para os nós internos são probabilidade posterior/bootstrap de máxima verossimilhança. Ramificações espessas em negrito indicam nós totalmente suportados. Cl = Clathraceae; Ly = Lysuraceae; Ga = Gastrosporiaceae; Ph = Phallaceae; Pr = Protophallaceae; Ct = Claustulaceae; og = grupos externos.

Após a emenda em Phallales, para incorporação da família Gastrosporiaceae, os representantes da ordem caracterizam-se por (TRIERVEILER-PEREIRA; DA SILVEIRA; HOSAKA, 2014):

- basidioma imaturo hipógeo ou epígeo;
- perídio composto por 2 ou 3 camadas;
- geralmente com rizomorfas brancas e espessas na base (ver itens Rz na Figura 5 e item R na Figura 6);
- basidioma maduro geralmente epígeo ou parcialmente hipógeo, expandido ou sequestrado;
- receptáculo pseudoestipitado (Figura 5a, 5c) ou séssil (Figura 5b);
- pseudoestipe pseudoparenquimatoso;
- receptáculo contendo a gleba; gleba verde, olivácea a castanha, mucilaginosa quando imatura, mucilaginosa ou pulverulenta quando madura;
- basidiosporos hialinos, verdes, dourados a marrons, bacilaroides, cilíndricos a oblongos, lisos a ornamentados.

Trierveiler-Pereira, da Silveira e Hosaka (2014) aceitaram em Phallales sete famílias, as seis apresentadas em Hosaka et al. (2006), adicionando-se Gastrosporiaceae, e apesar de citarem Trappeaceae como pertencente à Phallales tal família não é apresentada na filogenia. Sulzbacher et al. (2016) propuseram um novo gênero com hábito sequestrado na família Trappeaceae, *Restingomyces* Sulzbacher, Grebenc & Baseia, e elaboraram uma emenda nesta família. O gênero *Restingomyces* é caracterizado pelos basidiosporos ornamentados e gleba de cor verde, olivácea para marrom, com abundantes lóculos estéreis contidos em uma camada gelatinizada ou cartilaginosa localizada dentro do perídio verdadeiro. Este trabalho apresenta a filogenia de Phallales com seis famílias, sem incluir representantes de *Gastrosporium*. De la Fuente et al. (2021) revisaram o gênero *Restingomyces* e propuseram duas novas espécies, confirmando tal gênero em Phallales.

Segundo Trierveiler-Pereira, da Silveira e Hosaka (2014) os gêneros *Calvarula* Zeller e *Protubera* Möller (= *Kobayasia* S. Imai & A. Kawam., = *Protophallus* Murril) pertenceriam à Protophallaceae em Phallales, no entanto, essa família não é suportada em nenhuma reconstrução filogenética recente (HE et al., 2019; WIJAYAWARDENE et al., 2020). He et al. (2019) e Wijayawardene et al. (2020) estabeleceram três famílias em Phallales: Claustulaceae, Gastrosporiaceae e Phallaceae, com representantes de Lysuraceae e Clathraceae em Phallaceae. Segundo tais trabalhos: a família Trappeaceae e o gênero

Protubera (na família Phallogastraceae) estariam alocados em Hysterangiales; e os gêneros, também sequestrados, *Kobayasia* e *Calvarula* pertenceriam à família Phallaceae na ordem Phallales.

2.3 ECOLOGIA E IMPORTÂNCIA DE PHALLALES

De acordo com a base de dados FungalTraits, que fornece informações ecológicas gerais sobre fungos (PÕLME et al., 2020), todos os gêneros de Phallales estão classificados com o estilo de vida primário como saprotróficos – *soil saprotroph* – (decompositores de matéria orgânica). Alguns gêneros sequestrados que já foram considerados Phallales, como *Phallobata* G. Cunn., *Phlebogaster* Fogel, *Restingomyces* e *Trappea* (HOSAKA et al., 2006; SULZBACHER et al., 2016; TRIERVEILER-PEREIRA; DA SILVEIRA; HOSAKA, 2014), foram classificados no FungalTraits como parte de Hysterangiales, sendo todos saprotróficos com exceção de *Phlebogaster*, que é ectomicorrízico. Ao considerar esses gêneros na avaliação do estilo de vida de Phallales amplia-se para saprotróficos ou ectomicorrízicos.

Espécies de *Phallus* têm sido cultivadas e consumidas, principalmente em países asiáticos, como por exemplo *P. echinovolvatus* (M. Zang, D.R. Zheng & Z.X. Hu) Kreisel, *P. dongsun* T.H. Li, T. Li, Chun Y. Deng, W.Q. Deng & Zhu L. Yang e *P. rubrovolvatus* (M. Zang, D.G. Ji & X.X. Liu) Kreisel, sendo observado alto teor de proteína na volva e píleo deste último (DAI et al., 2010; LI, H. et al., 2021; LI, T. et al., 2020; ZHUANG; SUN, 2011). Além disso, espécies venenosas também são encontradas na ordem, como *Phallus tenuis* (E. Fisch.) Kuntze e *Mutinus bambusinus* (Zoll.) E. Fisch. (LI, H. et al., 2021). Em 2014 foi reportado para o sul do Brasil um caso de envenenamento de um cachorro, causado pela ingestão de *Lysurus cruciatus* (Lepr. & Mont.) Henn. (CORTEZ; ROSSINI, 2014).

Na área medicinal *Phallus impudicus* L. é indicado como um cogumelo que além de comestível, estimula a circulação e tem propriedades antitumorais (LU; LUO, 2010). Já na área de bioprodutos para agricultura a espécie *Lysurus mokusin* tem sido estudada em relação à sua ação antifúngica contra patógenos de plantas, foi verificada a sua ação contra *Botrytis cinerea* Pers. (causador da podridão cinzenta) (ZHANG et al., 2019) e *Pestalotiopsis neglecta* (Thuem.) Steyaert (LIN et al., 2021), bem como sua ação inseticida (LIN et al., 2020).

3 METODOLOGIA

3.1 SELEÇÃO DOS MATERIAIS PARA ANÁLISE

Exsicatas de Phallales de diversas localidades foram localizadas nos artigos científicos com registros de espécies e por meio das bases de dados: *Mycoportal Search collections* (https://mycoportal.org/portal/collections/index.php), *SpeciesLink* (http://www.splink.org.br/), GBIF (https://www.gbif.org/), *National Museum of Nature and Science* - TNS (http://db.kahaku.go.jp/webmuseum_en/). Para busca nas bases de dados foram utilizadas como palavras-chave os gêneros estudados e seus sinônimos reconhecidos na literatura. A seleção das exsicatas se deu por meio dos critérios: amostragem de diferentes locais e espécimes de localidade tipo. Do total encontrado foram selecionadas 867 exsicatas alocadas em 52 herbários para solicitação de empréstimos, conforme observado no APÊNDICE A (os códigos de herbário estão de acordo com o *Index Herbariorum* - http://sweetgum.nybg.org/science/ih/). As solicitações de empréstimos foram enviadas por meio do Herbário UFRN-Fungos.

Foram obtidas por empréstimo 179 exsicatas (APÊNDICE A). No Herbário UFRN-Fungos as exsicatas de *Laternea triscapa* (UFRN-Fungos 194) e *Clathrus columnatus* (UFRN-Fungos 1986) não foram encontradas, portanto, não foi possível a análise.

Além destes, foram analisados 21 materiais coletados por parceiros (APÊNDICE C), que após análise foram depositados em herbários nacionais: um no Herbário Bruno Edgar Irgang (HBI); dois no Instituto Nacional de Pesquisas da Amazônia no Brasil (INPA); um no Museu de Biologia prof. Mello Leitão (MBML); 16 no Herbário de Fungos da Universidade Federal do Rio Grande do Norte (UFRN-Fungos) e; um no Herbário Luis A. Fournier Origgi (USJ) da Costa Rica.

3.2 ANÁLISES MORFOLÓGICAS

As análises morfológicas foram realizadas no Laboratório de Biologia de Fungos, Departamento de Botânica e Zoologia – Centro de Biociências da Universidade Federal do Rio Grande do Norte (DBZ – CB – UFRN). Os basidiomas viáveis para análise (APÊNDICE B, C) foram analisados macro e microscopicamente. Artigos base para cada gênero/espécie foram utilizados como referência para análise dos caracteres chave para identificação dos espécimes.

Para as análises macroscópicas os caracteres: formato do basidioma, tamanho (com paquímetro) e cor (KÜPPERS, 2002) foram observados por meio de observações a olho nu e com auxílio de lupa (microscópio estereoscópico Leica EZ4 e para fotografias o NikonSMZ15000 com câmera Nikon DS-Ri1 acoplada).

Todos basidiomas analisados foram fotografados para confecção de pranchas, com uma régua ao lado, que serve para escala da foto e também para conferência posterior das medidas, caso necessário, se o material já tiver sido devolvido.

Todas as partes dos basidiomas (pseudoestipe, se tiver; receptáculo; gleba; volva; rizomorfa) foram analisados microscopicamente montando lâminas em seções à mão livre com auxílio de lupa e lâminas de corte em KOH a 5% (hidróxido de potássio) e Vermelho Congo a 1%. As estruturas foram visualizadas no microscópio óptico (Modelo Nikon Eclipse *Ni*) com captura (câmera Nikon DS-Ri1), e 30 hifas de cada estrutura, bem como 30 basidiosporos por espécime, foram medidos no software do microscópio instalado no computador, e analisados posteriormente em Excel quanto à forma por meio do valor de Q (razão entre comprimento e largura, c/l) e Q_m (média dos valores de Q: 1,0–1,05 = globoso; 1,05–1,15 = subgloboso; 1,15–1,3 = amplamente elipsoide; 1,3–1,6 = elipsoide; 1,6–2,0 = alongado; 2,0–3,0 = cilíndrico; > 3,0 = baciliforme) de acordo com Bas (1969).

Todos os caracteres analisados foram escritos nas descrições de cada material, e por meio da comparação desses caracteres com a literatura de cada grupo, foi possível fazer a identificação de cada material, verificando se a identificação na exsicata estava correta ou se o material pode ser considerado uma espécie nova. Para alguns materiais, além da morfologia foram imprescindíveis para a identificação os dados de filogenia.

Todas categorias taxonômicas foram destacadas em itálico nos artigos dos APÊNDICES D e E, resultados da tese, seguindo a recomendação de Thines et al. (2020) para facilitar o rápido reconhecimento dessas categorias em artigos científicos.

3.3 ANÁLISES MOLECULARES

As análises moleculares, desde a extração até o depósito de novas sequências no GenBank e a análise filogenética, foram realizadas pela coorientadora Dra. Tiara S. Cabral, com espécimes do gênero *Staheliomyces* (APÊNDICES B e C: espécies marcadas como sequências novas geradas). Essas análises compuseram o artigo do APÊNDICE E. Foram amplificadas as regiões: ITS – espaçador interno transcrito do DNA ribossômico nuclear; nuc-LSU e *ATP*6. Sendo utilizados para cada região, respectivamente, os *primers*: ITS1/ITS4 (WHITE et al., 1990), LR0R/LR5 (VILGALYS; HESTER, 1990), ATP6-1/ATP6-2

(KRETZER; BRUNS, 1999). Todas amplificações foram purificadas com ExoProStar (GE Healthcare, Chicago, EUA) e sequenciadas usando o Big Dye Terminator Cycle Sequencing Kit (Applied Biosystems, Waltham, EUA) com o mesmo grupo de *primers* na Universidade Federal do Amazonas (UFAM).

Além destas, foram realizadas análises filogenéticas de sequências de Phallales já depositadas nas bases de dados públicas, GenBank e UNITE, que resultaram no artigo do APÊNDICE D. Foram selecionadas sequências de ITS, nuc-LSU, nuc-SSU, mt-SSU, *ATP*6, *RPB*2 e *TEF*1-α. Foram utilizadas *query strings* (códigos de consulta) para baixar as sequências de forma automática. Foi utilizado um código geral para selecionar as sequências identificadas como Phallales, com o tamanho de 300 - 10000 pares de bases: txid68804[Organism] AND 300:10000[SLEN], e adicionais para cada marcador:

- *ATP*6: ATP6[Title] OR ATPase6[Title] OR ATP synthase F0 subunit 6[Title] OR ATP synthase subunit 6[Title] OR MTATP synthase F0 subunit 6[Title] OR MT-ATP6[Title] OR MTATP6[Title] OR ATP-6[Title]
- *RPB*2: rpb2[Title] OR rpbII[Title] OR RNA polymerase II second largest subunit[Title] OR RNA polymerase II second large subunit[Title] NOT rpb1
- *TEF*1- α: TEF1[Title] OR EF1[Title] OR EF-1[Title] OR TEF-1[Title] OR TEF[Title] OR tef1a[Title] OR EF[Title] OR translation elongation factor 1[Title] OR EF1alpha[Title] OR EF1a[Title] OR EF1-alpha[Title] OR TEF1-alpha[Title]
- - Os genes ribossomais (ITS; nuc-LSU; nuc-SSU; mt-SSU) foram baixados em uma mesma *query strings*: rRNA[Title] OR ribosomal RNA[Title] e separados manualmente.

Os resultados das buscas foram baixados no formato TinySeq_XML e aditados no Excel para montar uma planilha única com cada linha representando um voucher seguido de todas as sequências disponíveis para este. As sequências do UNITE de Phallales, que não haviam sido recuperadas pelo GenBank foram baixadas manualmente e incorporadas nesta planilha geral. Para as análises filogenéticas o marcador nuc-SSU foi desconsiderado observando a pequena quantidade de sequências disponíveis.

Todas as sequências de ITS baixadas para este artigo foram submetidas à busca no Nucleotide BLAST do NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi) com o objetivo de

selecionar sequências de Phallales que não estavam identificadas nesta ordem, e portanto não haviam sido baixadas com as *query strings*, tendo como parâmetros: *query cover* > 80%, *identity* > 70%, e *e-value* < e-1,000. De acordo com Tedersoo et al. (2014) 80% é o nível de similaridade para identificação a nível de ordem.

Para os dois artigos (APÊNDICES D, E), os arquivos com as sequências foram alinhados no AliView v. 1.26 (LARSSON, 2014) usando alinhamento muscle ou MAFFT v.7 (KATOH; STANDLEY, 2013) sob o critério E-INS-i e conferidos manualmente. Os modelos de substituição foram determinados no MrModelTest (NYLANDER, 2004) ou jModelTest 2v.1.6 (DARRIBA et al., 2012). Os alinhamentos foram depositados no TreeBASE.

Foram realizadas análises filogenéticas de Bayesiana e Máxima Verossimilhança, por meio dos programas MrBayes 3.2.6 (RONQUIST et al., 2012) e RAxML v8.2.X (STAMATAKIS, 2014) respectivamente, por meio da plataforma CIPRES (MILLER; PFEIFFER; SCHWARTZ, 2010). As Inferências Bayesianas foram realizadas com duas corridas independentes, cada uma começando a partir de árvores aleatórias com quatro cadeias independentes simultâneas, com 3 e 20 milhões de gerações, com amostragem de árvores a cada mil gerações. As análises de Máxima Verossimilhança foram realizadas combinadas com o algoritmo de bootstrapping rápido com 1.000 réplicas com modelo de substituição nucleotídica GTRGAMMA+I e GTRGAMMA. O detalhamento das análises pode ser consultado diretamente nos artigos.

Além das análises de Bayesiana e Máxima Verossimilhança, foi realizado um método de delimitação de espécies baseado em sequências: Bayesian Posterior Tree Poisson (bPTP), indicado para pequenos conjuntos de dados e especialmente para espécies representadas por singletons para o artigo de *Staheliomyces* (APÊNDICE E). E no artigo geral de Phallales (APÊNDICE D) as sequências de ITS também foram utilizadas para determinar o número de hipótese de espécies, por meio da submissão das sequências no CD-HIT-EST (HUANG et al., 2010) à 98% de similaridade, de acordo com o nível de similaridade estabelecido para reconhecimento a nível de espécie segundo Tedersoo et al. (2014). Além disso, os dados gerais que acompanham cada sequência, como a localidade e data de coleta, também foram baixados e avaliados.

4 RESULTADOS E DISCUSSÃO

4.1 MATERIAIS ANALISADOS

Os APÊNDICES B e C apresentam a relação dos materiais analisados nesta tese, informando a identificação antes e depois da revisão, o país/estado de coleta de cada material e a indicação se o material identificado é do país e/ou estado tipo (ver nos apêndices a informação em: local[1]). Sobre o local de coleta, uma exceção foi feita para *Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral, que por apresentar um elevado número de exsicatas do estado tipo (Rio Grande do Norte), foram também subdivididos por município, e os seus números de herbário foram agrupados. Além disso, foram indicados os materiais identificados por morfologia, mas que os dados moleculares seriam importantes para a confirmação da espécie (ver nos apêndices a informação em: espécie[2]), bem como os materiais com novas sequências geradas (APÊNDICE B: espécie[8]; APÊNDICE C: espécie[3]).

Das 200 exsicatas disponíveis para análise (APÊNDICE B, C), 163 foram revisadas a identificação (totalizando 13 gêneros divididos em 28 espécies – Tabela 1), duas foram possíveis identificar a nível de gênero e 35 não foram possíveis identificar, destas últimas 24 estavam mal preservadas (APÊNDICE B: Não identificado[3]), muitas delas foram totalmente desintegradas, sobrando somente um pó; quatro eram compostas de basidiomas não expandidos (APÊNDICE B: Não identificado[4]); três estavam com o envelope/caixa sem material (APÊNDICE B: Não identificado[5]); duas continham somente parte do material (APÊNDICE B: Não identificado[6]); e duas eram compostas por cultura desidratada em papel (APÊNDICE B: Não identificado[7]).

Tabela 1 – Gêneros e espécies identificadas

Família	**Gênero**	**Espécie**
Clathraceae	*Abrachium* Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral
	Aseroë Labill.	*Aseroë rubra* Labill.
	Blumenavia Möller	*Blumenavia baturitensis* Melanda, M.P. Martín & Baseia *Blumenavia rhacodes* Möller
	Clathrus P. Micheli ex L.	*Clathrus columnatus* Bosc *Clathrus crispus* Turpin *Clathrus natalensis* G.S. Medeiros, Melanda, T.S. Cabral, B.D.B. Silva & Baseia *Clathrus ruber* P. Micheli ex Pers.
	Colus Cavalier & Séchier	*Colus hirudinosus* Cavalier & Séchier
	Ileodictyon Tul.	*Ileodictyon cibarium* Tul.

(continua)

(conclusão)

Família	Gênero	Espécie
Clathraceae	*Laternea* Turpin	*Laternea dringii* A. López, D. Martínez & J. García
		Laternea pusilla Berk. & M.A. Curtis
		Laternea triscapa Turpin
	Ligiella J.A. Sáenz	*Ligiella rodrigueziana* J.A. Sáenz
	Pseudocolus Lloyd	*Pseudocolus fusiformis* (E. Fisch.) Lloyd
		Pseudocolus schellenbergiae (Sumst.) Johnson
Lysuraceae	*Lysurus* Fr.	*Lysurus borealis* (Burt) Henn.
		Lysurus mokusin (L.) Fr.
		Lysurus pusillus Coker
		Lysurus sphaerocephalum (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez
	Neolysurus O.K. Mill., Ovrebo & Burk	*Neolysurus arcipulvinus* O.K. Mill., Ovrebo & Burk
Phallaceae	*Mutinus* Fr.	*Mutinus argentinus* Speg.
		Mutinus bambusinus (Zoll.) E. Fisch.
	Phallus Junius ex L.	*Phallus atrovolvatus* Kreisel & Calonge
	Staheliomyces E. Fisch.	*Staheliomyces candeliformis* N.M. Assis, Melanda & T.S. Cabral
		Staheliomyces costariquensis Ovrebo, Melanda, N.M. Assis & T.S. Cabral
		Staheliomyces cylindricus Melanda, N.M. Assis & T.S. Cabral
		Staheliomyces quadratus N.M. Assis, Melanda, T.S. Cabral

Fonte: A autora (2022).

Dentre os materiais analisados destacam-se onze exsicatas de tipos (APÊNDICE B e C: em negrito), dentre as quais cinco já estavam identificadas como tipos quando emprestadas:

- *Colus schellenbergiae* Sumst. (isótipo: NCU-F-0006887);
- *Lysurus borealis* var. *serotinus* Peck (holótipo: NYSf 2769);
- *Lysurus pusillus* Coker (holótipo: NCU-F-0017338);
- *Neolysurus arcipulvinus* O.K. Mill., Ovrebo & Burk (parátipo: F: C0374489F);
- *Simblum rubescens* W.R. Gerard (tipo: NYSf 4442).

E seis foram designadas como tipos como resultado desta tese (APÊNDICE E):

- *Staheliomyces candeliformis* N.M. Assis, Melanda & T.S. Cabral (holótipo: INPA 25583; parátipo: UFRN-Fungos 2748);
- *Staheliomyces costariquensis* Ovrebo, Melanda, N.M. Assis & T.S. Cabral (holótipo: USJ 109573);
- *Staheliomyces cylindricus* Melanda, N.M. Assis & T.S. Cabral (holótipo: UFRN-Fungos 2177; parátipo: UFRN-Fungos 1222);

- *Staheliomyces quadratus* N.M. Assis, Melanda, T.S. Cabral (holótipo: UFRN-Fungos 2746).

Não foi possível fazer a revisão morfológica total das exsicatas dos tipos de *Lysurus borealis* var. *serotinus* e *Simblum rubescens* porque o herbário onde estão depositadas faz empréstimo somente de parte de materiais que são tipo, então, com isso foram obtidos apenas pedaços dos basidiomas para análise (APÊNDICE B: Não identificado[6]).

Parte do material analisado foi utilizado na elaboração de artigos: foram descritas quatro novas espécies de *Staheliomyces* (APÊNDICE E); registros de Phallales para o Brasil com *checklist* para o nordeste (APÊNDICE F); *Blumenavia rhacodes* como registro novo para o Bioma Pampa (APÊNDICE G); e revisão de materiais coletados nos Estados Unidos, incluindo o tipo de *Colus schellenbergiae*, e de localidade tipo *Clathrus columnatus* (APÊNDICE H). Tais artigos serão detalhados na seção seguinte.

Os materiais que ainda não estão como resultado da tese em artigos serão incluídos em futuras publicações, especialmente após a finalização das análises com dados moleculares de DNA.

4.2 SÍNTESE DOS ARTIGOS PRODUZIDOS

- Como primeiro resultado da tese foram analisados dados já disponíveis com o objetivo de apresentar a diversidade de Phallales representada por dados moleculares ao longo dos 24 anos de estudos com a ordem, desde a primeira sequência de Phallales depositada em 1997 (HIBBETT et al., 1997) até 2021, ano da publicação deste artigo. Esse trabalho foi publicado com o nome: *An Overview of 24 Years of Molecular Phylogenetic Studies in Phallales (Basidiomycota) With Notes on Systematics, Geographic Distribution, Lifestyle, and Edibility* [Uma visão geral de 24 anos de estudos filogenéticos moleculares em Phallales (Basidiomycota) com notas sobre sistemática, distribuição geográfica, estilo de vida e comestibilidade] (APÊNDICE D).

O artigo apresentou a diversidade de Phallales por meio da análise filogenética de sequências de representantes da ordem depositadas em bases de dados públicas, fazendo também a discussão do posicionamento dos gêneros dentro de cada família e a confirmação do número de famílias na ordem. Além disso, no artigo foi apresentado o posicionamento filogenético de sequências não nomeadas como Phallales, mas que pertencem ao grupo, por terem sido resgatadas pelo BLAST com sequências de Phallales como busca; o número de

hipótese de espécies em Phallales baseado em ITS; a distribuição geográfica mundial dos gêneros, seu estilo de vida e comestibilidade.

Foram baixadas 1149 sequências de DNA de Phallales, divididas em 492 ITS, 303 nuc-LSU, 11 nuc-SSU, 75 mt-SSU, 129 *ATP*6, 88 *RPB*2 e 51 *TEF*1-α. Destas, 122 sequências representam 41 coleções tipo.

A primeira sequência de Phallales depositada foi de nuc-SSU de *Pseudocolus fusiformis* (E. Fisch.) Lloyd (HIBBETT et al., 1997), e a sequência obtida do voucher mais antigo foi de nuc-LSU de *Colus hirudinosus* Cavalier and Séchier (voucher UC 955042) coletado em 1 de fevereiro de 1952, sequência ainda não publicada sendo o autor da sequência Kuo, M.

Foi observado que os picos de depósito das sequências estão relacionados com a crescente utilização da ferramenta molecular nos artigos chave que ampliaram o número de sequências de Phallales, como em 2006 (HOSAKA et al., 2006) e o aumento no número de trabalhos com diversidade de Phallales a partir de 2013.

Foram incluídas na filogenia 41 sequências que não haviam sido depositadas como Phallales, que representaram cinco famílias: Clathraceae, Gastrosporiaceae, Lysuraceae, Phallaceae e Trappeaceae. Deste total: 13 foram identificadas a nível de gênero; 15 a nível de espécie; 11 a nível de família e duas a nível de ordem.

Com os dados obtidos foi possível determinar a quantidade de indivíduos que possuem sequência de DNA em Phallales, baseando-se em vouchers, cada indivíduo foi representado por um número de voucher ou número de coleta que o identificasse, estes resultaram em 664 indivíduos e 58,7% destes estavam representados somente por um marcador molecular.

Baseando-se nas sequências de ITS foram reveladas 118 hipóteses de espécies. Ao comparar esse valor com os 576 nomes científicos legítimos de espécies depositados no MycoBank, com base em dados baixados em 2020 (MYCOBANK, 2020), observa-se que quase 20% das espécies reconhecidas em Phallales possuem sequência de DNA, mostrando ainda muito trabalho a ser feito nessa área.

Foi confirmada a existência de sete famílias em Phallales: com basidiomas expandidos – Clathraceae, Lysuraceae e Phallaceae – e basidiomas sequestrados – Claustulaceae, Gastrosporiaceae, Protophallaceae e Trappeaceae. Esta foi a primeira filogenia publicada com a representação das sete famílias em Phallales. Foram reconhecidos 22 gêneros na ordem, com *Dictyophora* Desv. e *Jansia* Penz. confirmadas como sinônimos de *Phallus* e *Mutinus*, respectivamente. *Phallus* foi o gênero mais representativo com 313 indivíduos e 471

sequências. A representação das famílias e dos gêneros está na figura da árvore concatenada no artigo. Análises filogenéticas de cada marcador também foram realizadas e adicionadas nos arquivos suplementares. O artigo apresenta o resultado e a discussão das sete famílias separadamente.

Algumas inconsistências foram observadas nos gêneros *Abrachium* Baseia & T.S. Cabral, *Aseroë*, *Blumenavia* Möller, *Clathrus*, *Claustula*, *Gelopellis*, *Laternea*, *Protubera*, *Pseudocolus* Lloyd, e *Trappea*, além disso ainda não haviam sido representados por dados moleculares os gêneros: *Aporophallus* Möller (Phallaceae), *Floccomutinus* (F.M. Bailey) Lloyd (Phallaceae), *Kalchbrennera* Berk. (Lysuraceae), *Ligiella* J.A. Sáenz (Clathraceae), *Linderia* G. Cunn. (Clathraceae), *Linderiella* G. Cunn. (Clathraceae), *Neolysurus* (Lysuraceae) e *Staheliomyces* (Phallaceae).

Foram observadas nesse artigo a distribuição geográfica da ordem no geral e por gêneros, representadas em mapas. Há a distribuição da ordem em 46 países, concentrando-se nas áreas tropicais e subtropicais, com baixa ocorrência nos círculos polares.

Amostras ambientais representaram 168 indivíduos: 148 de solo, oito de raízes de *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (grama azul), dois de filtros de ar, três de caule de mudas [dois de *Hevea nitida* Mart. Ex Müll. Arg e um de *Micrandra spruceana* (Baill.) R. E. Schult.], um de solo contaminado com metal pesado, um de sedimentos marinhos subterrâneos e um da poeira da casa. De acordo com o banco de dados FungalTraits (PÕLME et al., 2020) 21 gêneros reconhecidos em nosso trabalho são saprotróficos, e apenas um, *Phlebogaster*, é mencionado como ectomicorrízico.

Por fim, das espécies com sequências baixadas para este artigo 11 são comestíveis, três são comestíveis com condições, seis não são confirmadas a comestibilidade e três são venenosas: *Lysurus arachnoideus* (E. Fisch.) Trierv.-Per. & Hosaka, *Mutinus bambusinus* e *M. caninus*. Os dados de comestibilidade foram consultados em Li et al. (2021).

Este trabalho mostrou a possibilidade de investigação, neste caso de uma ordem de fungos, com dados já disponíveis em bases de dados, resultando em zero custo laboratorial. Vários resultados foram extraídos desde a ecologia, distribuição geográfica, filogenia e taxonomia, com muitas dúvidas taxonômicas sendo sanadas, além de mostrar as lacunas ainda existentes na área.

- Intitulado *Loosening the belt: unknown diversity of the strangled stinkhorn genus Staheliomyces* (*Phallales*, *Basidiomycota*) [Afrouxando o cinto: diversidade desconhecida do gênero *stinkhorn* estrangulado *Staheliomyces* (Phallales, Basidiomycota)] (APÊNDICE E), este artigo sana uma das lacunas observadas no artigo anterior: a falta de

sequências moleculares do gênero *Staheliomyces*. Este gênero descrito em 1921 (FISCHER, 1921), além de não ter sido representado por nenhuma sequência ou análise filogenética, era considerado monoespecífico, com a espécie tipo *Staheliomyces cinctus* E. Fisch. O epíteto "cinctus", que significa cinto, foi dado justamente pela morfologia da região glebal do basidioma, um pouco abaixo do ápice fazendo uma constrição no mesmo, dando a impressão de ser um cinto apertado, o que também justifica o nome *stinkhorn* estrangulado.

Neste artigo foi investigada a história nomenclatural do gênero, sua diversidade morfológica e molecular bem como seu posicionamento filogenético em Phallales.

Foram geradas 37 novas sequências distribuídas em 8 ITS, 17 nuc-LSU e 12 *ATP*6. O gênero foi confirmado como pertencente à família Phallaceae, por meio das análises filogenéticas, compartilhando ancestral comum mais próximo com *Xylophallus* (Schltdl.) E. Fisch. Este clado, composto por estes dois gêneros, possui espécies exclusivamente neotropicais. Ambos gêneros, assim como *Mutinus*, não apresentam diferenciação entre o receptáculo e o pseudoestipe como ocorre em *Phallus* e *Itajahya* Möller.

Foi proposta uma emenda na descrição do gênero para inclusão da variação dos caracteres diagnósticos determinados com as análises das exsicatas deste trabalho: cor da volva, largura do pseudoestipe ao longo do comprimento, quantidade e tamanho das perfurações no pseudoestipe, tamanho da constrição para formar a região glebal, forma e textura da região glebal, forma da região apical estéril e presença ou ausência de abertura apical. Tais caracteres foram utilizados nas descrições de todas espécies além da descrição da rizomorfa e dos caracteres microscópicos. No artigo a região glebal também foi mencionada como cinto, e foram usados os nomes pseudoestipe para a parte que sai da volva até a constrição que forma o cinto, e região apical estéril, porção acima da região glebal.

O material tipo do gênero foi localizado no herbário BERN (Botanical Garden of the University of Bern), não mencionado na descrição original, sendo possível a confirmação das características do protólogo, bem como a comparação com as novas espécies. A partir desse material tipo foi designado o lectótipo de *Staheliomyces cinctus*.

Quatro novas espécies foram estabelecidas em *Staheliomyces* baseando-se em materiais do Brasil e Costa Rica, são elas: *S. candeliformis*, *S. costariquensis*, *S. cylindricus* e *S. quadratus*.

Staheliomyces candeliformis é caracterizado por sua porção apical estéril em forma de lágrima/gota, uma constrição pronunciada no pseudostipe que forma a região glebal, superfície reticulada do cinto sob a gleba e volva marrom avermelhada.

Staheliomyces cinctus, tipo do gênero, se caracteriza pelo espessamento do pseudoestipe do meio para a parte superior, várias perfurações laterais no pseudoestipe, menores na metade inferior e maiores no meio até próximo à constrição, região glebal doliforme (forma de tonel), porção apical estéril triangular e volva esbranquiçada.

Staheliomyces costariquensis tem como caracteres principais a porção apical estéril triangular com ponta ligeiramente quadrada, região glebal alongada e doliforme com superfície rugosa sob a gleba e a superfície esbranquiçada a laranja-ferrugem da volva.

Staheliomyces cylindricus se caracteriza por sua largura constante ao longo de todo o pseudoestipe, pela porção apical estéril alongada com ápice arredondado, pelo estreitamento mínimo do pseudostipe na constrição que forma o cinto, superfície rugosa da região glebal e volva branca.

Staheliomyces quadratus é caracterizado pela ponta quadrada da porção apical estéril que possui um poro apical, lados arredondados do cinto com superfície reticulada sob a gleba e pela volva marrom avermelhada.

Além destas foi descrita uma espécie como ‘sp.’ (INPA 264932) que possui principalmente a morfologia da porção apical estéril distinta das demais, menor que a região glebal. Foi coletado um basidioma com essa morfologia e a distinção dessa característica com as demais não foi possível ser confirmada como uma variação na espécie ou uma falha no desenvolvimento da porção apical. Além disso, esse espécime se agrupa no clado de *Staheliomyces quadratus*, porém, com baixo suporte. No entanto, mais materiais são necessários para a confirmação da espécie como distinta ou não.

A espécie tipo do gênero não está representada por molecular, por não ser possível o empréstimo para extração já que estava preservada em álcool. A filogenia apresentou cinco clados representando as espécies: 1. *S. candeliformis*, 2. *S. cylindricus*, 3. *S. costariquensis*, 4. *Staheliomyces* sp. INPA 264932 e 5. *S. quadratus* com *Staheliomyces* sp. INPA 272311. A espécie *Staheliomyces* sp. INPA 272311 foi possível a análise molecular por ter sido separada uma parte do basidioma na hora da coleta, mas não foi analisada por morfologia no artigo por não ter sido encontrada no herbário. Como resultado final a análise de bPTP estimou a média de 5 espécies no gênero, concordando com a filogenia.

Foi apresentada uma chave de identificação das espécies, pranchas com as macro e microestruturas, uma tabela comparativa dos caracteres diagnósticos, a distribuição geográfica mundial do gênero, e também foi demonstrada em uma prancha a variação de formas em *Staheliomyces* com imagens recuperadas do GBIF de registros de coletas. Concluiu-se que os

caracteres mais distinguíveis para espécies em *Staheliomyce*s são a forma e o tamanho da porção apical estéril, a forma e a superfície da região glebal e a cor da volva.

Este trabalho mostrou a importância de trabalhos de revisão sistemática e como a análise filogenética contribui para o estudo da diversidade de fungos, sanando dúvidas que podem ficar somente com a análise morfológica.

- No artigo *Phallales (Agaricomycetes, Basidiomycota) from northeastern Brazil: occurrences, new records with an updated distribution map and checklist* [Phallales (Agaricomycetes, Basidiomycota) do nordeste do Brasil: ocorrências, novos registros com mapa de distribuição atualizado e *checklist*] (APÊNDICE F) foi apresentada a descrições de espécies de Phallales, com novos registros, uma prancha com as espécies descritas, um *checklist* para o nordeste e um mapa de distribuição delimitando a região nordeste e os biomas que nela se encontram.

Mutinus bambusinus foi registrado pela primeira vez para o país, *Phallus atrovolvatus* Kreisel & Calonge como segundo registro e *Clathrus natalensis* G.S. Medeiros, Melanda, T.S. Cabral, B.D.B. Silva & Baseia como segundo registro para a ciência. Além disso, *Mutinus argentinus* Speg. foi registrado pela primeira vez para o Rio Grande do Norte e as exsicatas de *Abrachium floriforme* depositadas do UFRN-Fungos foram revisadas e novas ocorrências dessas espécies foram registradas para o Ceará e Rio Grande do Norte.

Uma tabela comparativa de caracteres entre *Mutinus argentinus* e *M. bambusinus* foi apresentada, ressaltando a forma do basidioma imaturo: subgloboso em *M. bambusinus* e elipsoide em *M. argentinus*; a superfície da porção fértil e seu ápice: granulosa com ponta estéril em *M. bambusinus* e rugosa sem ponta estéril em *M. argentinus*; e a superfície da porção estéril: com câmaras abertas (perfurações) em *M. bambusinus* e sem essas aberturas em *M. argentinus*.

O *checklist* apresentou todos os registros de representantes de Phallales para o nordeste brasileiro publicados em artigos científicos até 1º de maio de 2020. Foram computados dez gêneros e 22 espécies (spp.), totalizando 61 ocorrências (occ.). Destes, um gênero e oito espécies são novos para a ciência. *Mutinus* é o gênero com maior número de registros de espécies (6 spp.), seguido por *Phallus* e *Clathrus* (4 spp. ambos) e *Laternea* (2 spp.). As espécies com maior número de ocorrências são *Abrachium floriforme* (16 occ.) e *Phallus indusiatus* (7 occ.). Todas as espécies citadas foram coletadas na Mata Atlântica, exceto *Itajahya rosea* (Delile) E. Fisch. e *Clathrus cristatus* Fazolino, Calonge & Baseia na Caatinga. O Rio Grande do Norte é o estado com maior número de ocorrências de Phallales

na região nordeste (28 occ.), seguido por Ceará (14 occ.), Paraíba (10 occ.), Pernambuco (7 occ.) e Bahia (2 occ.).

Este trabalho mostrou que o nordeste do Brasil é favorável ao desenvolvimento de fungos falóides, mas ainda está longe de mostrar sua real diversidade. Existe uma assimetria de conhecimento, por isso vários estudos são necessários, principalmente em áreas pouco exploradas.

- O artigo: Primeira ocorrência de *Blumenavia rhacodes* Möller (Basidiomycota, Fungi) na porção do bioma Pampa (APÊNDICE G), traz a contribuição de expansão da área de ocorrência de *Blumenavia rhacodes* além das áreas de Mata Atlântica. Poucos trabalhos registraram esse gênero no Brasil, com localidade tipo a região sul do país. Como resultado da minha dissertação fez-se uma publicação com a revisão morfológica e molecular das espécies do gênero (MELANDA et al., 2020).

Este trabalho, apresentado na tese, traz uma grande relevância para os estudos do gênero *Blumenavia* ao ampliar a sua distribuição e confirmar os caracteres apresentados na revisão taxonômica proposta.

- O último artigo que compõe a tese é intitulado: Taxonomic review of *Colus schellenbergiae* and *Clathrus columnatus* (Phallales, Basidiomycota) from North America [Revisão taxonômica de *Colus schellenbergiae* e *Clathrus columnatus* (Phallales, Basidiomycota) da América do Norte] (APÊNDICE H). Este artigo está apresentado como um primeiro rascunho e seu objetivo principal é reavaliar a identidade de *Colus schellenbergiae* e *Clathrus columnatus* por meio de análises morfológicas.

Clathrus columnatus é citado com ampla distribuição geográfica (DRING, 1980), com a localidade tipo: Carolina do Norte - Estados Unidos. Foi realizada uma revisão de materiais de *C. columnatus* coletados dos Estados Unidos, incluindo a localidade tipo, e apresentada uma descrição completa dos exemplares, incluindo caracteres não apresentados no protólogo.

Colus schellenbergiae Sumst. foi descrito na Pensilvânia, Pittsburgh, também nos Estados Unidos, com base em materiais coletados no quintal da Sra. F. F. Schellenberg, o que justifica o nome da espécie (SUMSTINE, 1916). Segundo Sumstine (1916) os espécimes tipo foram depositados no Museu Carnegie (Pittsburgh, Pensilvânia), e no Jardim Botânico de Nova York. Nenhum número de catálogo foi citado e nenhuma figura foi representada. Johnson (1929) transferiu a espécie para *Pseudocolus*, propondo a combinação *Pseudocolus schellenbergiae* (Sumst.) Johnson.

O gênero *Colus* é caracterizado por possuir um basidioma composto por um conjunto de braços com aparência colunar perto da volva mas formando uma rede no topo do basidioma, e *Pseudocolus* por um conjunto de braços que emergem da volva, unidos na base formando uma pequena estrutura em forma de estipe; (LLOYD, 1907a, b; RIBEIRO et al., 2022). Ao aceitar essa definição aceitamos também que a espécie *Colus schellenbergiae* faz parte do gênero *Pseudocolus*, com o nome *Pseudocolus schellenbergiae*.

Dring (1980) considerou *Pseudocolus javanicus*, *P. rothae* (E. Fisch.) Lloyd, *P. rugulosus* Lloyd e *P. schellenbergiae* sinonímias heterotípicas de *P. fusiformis*. Ao analisar espécimes dos Estados Unidos sob os nomes: *Colus schellenbergiae* (incluindo o isótipo), *Pseudocolus schellenbergiae*, *P. fusiformis*, *P. javanicus*, *Clathrus* sp. e *Clathrus columnatus* foi possível delimitar a existência duas espécies, *Pseudocolus schellenbergiae* e *P. fusiformis*, observando como caractere principal de diferenciação a variação no tamanho dos basidiosporos e foi observado que *Pseudocolus schellenbergiae* e *P. fusiformis* têm distribuição na região nordeste e sudeste dos Estados Unidos, respectivamente, sendo estas delimitadas geograficamente.

Visto isso, no artigo foi apresentada a descrição de *Pseudocolus schellenbergiae* e *P. fusiformis*, com a menção do código de herbário do isótipo de *Pseudocolus schellenbergiae*: NCU-F-0006887. As duas espécies são muito próximas na morfologia macroscópica e essa variação dos basidiosporos e regionalização pode apresentar um indício de especiação. O protólogo de *P. fusiformis* é uma ilustração depositada no herbário PC com a localidade tipo Ilha de Reunião, portanto a espécie dos EUA poderia ser até uma espécie distinta de *P. fusiformis*.

Este trabalho ressalta mais uma vez a importância das revisões taxonômicas, principalmente baseando-se em espécimes tipo e de localidade tipo, e como a acurada análise dos materiais pode revelar informações ainda não mencionadas que são importantes na delimitação das espécies.

5 CONSIDERAÇÕES FINAIS

A tese apresentada atingiu o objetivo geral proposto ao reavaliar o posicionamento filogenético das famílias em Phallales, e ampliar o conhecimento sistemático do grupo por meio de cinco artigos: quatro já publicados e um ainda a ser submetido.

O estudo a partir de dados depositados em ferramentas moleculares de DNA com o uso de marcadores combinados permitiu uma visão mais clara de delimitação e posicionamento das famílias e gêneros em Phallales. As sete famílias de Phallales foram apresentadas pela primeira vez na filogenia e o posicionamento dos 22 gêneros reconhecidos foram avaliados e discutidos dentro de cada família. Ainda é necessário um esforço extra em estudos taxonômicos dos gêneros *Abrachium*, *Aseroë*, *Blumenavia*, *Clathrus*, *Claustula*, *Gelopellis*, *Laternea*, *Protubera*, *Pseudocolus* e Trappea, porque algumas inconsistências na identificação de espécies e o posicionamento de seus representantes devem ser esclarecidos. Também é necessário incluir sequências dos gêneros *Aporophallus*, *Floccomutinus*, *Kalchbrennera*, *Ligiella*, *Linderia*, *Linderella* e *Neolysurus*. O gênero *Staheliomyces*, que ainda não havia sido representado com sequência de DNA neste primeiro artigo, foi revisado por taxonomia e filogenia e também fez parte dos resultados da tese.

Os dados moleculares combinados com dados morfológicos permitiram demonstrar que a diversidade de Phallales está subestimada, confirmando a hipótese da tese. Tal afirmação foi confirmada ao fazer a revisão do gênero monoespecífico *Staheliomyces* e verificar a existência de mais quatro espécies para o gênero. Além disso foi determinado um lectótipo para o gênero e uma emenda na descrição do mesmo. Estes dados são relevantes para melhor delimitação das espécies em futuras coletas, já que até este trabalho todos exemplares coletados eram identificados como uma única espécie.

Dados de levantamento de diversidade e de revisão de espécimes de herbário, com identificação morfológica, também ampliaram as ocorrências de espécies em Phallales. Observou-se que a região nordeste brasileira tem alto potencial para ocorrência de espécies da ordem, e ainda é necessário grande esforço de coleta para esclarecer sobre essa diversidade, principalmente aumentando as delimitações geográficas já estudadas. A ampliação da área de ocorrência de *Blumenavia rhacodes* no bioma Pampa, para além da Mata Atlântica, confirma que os estudos em áreas inexploradas têm grande possibilidade de aumentar os dados de ocorrências das espécies, e também podem até revelar espécies novas.

Ainda com esta tese foi possível através da acurada revisão taxonômica delimitar os caracteres de *Pseudocolus schellenbergiae*, analisando o isótipo, e *P. fusiformis*, não

aceitando a sinonimização das duas espécies como aceito por alguns taxonomistas, e também delimitar a espécie *Clathrus columnatus* com o estudo de novos caracteres, principalmente microscópicos, por meio da análise de materiais da localidade tipo, já que o tipo não foi encontrado.

Tais trabalhos apresentados aqui são de extrema importância para a sistemática de Phallales e dão suporte para futuros trabalhos, como ecológicos, de delimitação de espécies, trabalhos aplicados de bioquímica, entre outros. Amplia-se o conhecimento do grupo, ao mesmo tempo que se incentiva novas pesquisas que ainda precisam ser feitas na área da taxonomia.

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APÊNDICE A – TOTAL DE EXSICATAS SOLICITADAS PARA EMPRÉSTIMOS E SEUS RESPECTIVOS HERBÁRIOS

Acrônimo do herbário	nome por extenso	País	Total de exsicatas
			179 recebidas
CUP	Plant Pathology Herbarium	EUA	11
DBG	Denver Botanic Gardens	EUA	2
F	Field Museum of Natural History	EUA	22
FLOR	Universidade Federal de Santa Catarina	Brasil	5
JPB	Herbário Lauro Pires Xavier	Brasil	3
MIN	University of Minnesota	EUA	2
NCU-F	University of North Carolina at Chapel Hill	EUA	25
NY	New York Botanic Garden	EUA	1
NYSf	New York State Museum	EUA	2
OSC	Oregon State University	EUA	9
SP-Fungi	Instituto de Botânica	Brasil	5
TENN-F	University of Tennessee	EUA	21
UFRN-Fungos	Herbário de Fungos da Universidade Federal do Rio Grande do Norte	Brasil	68
URM	Herbário Pe. Camille Torrend	Brasil	3
			688 não recebidas
BAFC-H	Universidad de Buenos Aires	Argentina	3
BISH	Bishop Museum	EUA	5
BO	Herbarium Bogoriense	Indonésia	6
BPI	U.S. National Fungus Collections, USDA-ARS	EUA	43
BRI	Queensland Herbarium	Austrália	19
C-F	Natural History Museum of Denmark	Dinamarca	5
CORT	State University of New York College at Cortland	EUA	7
CR	Museo Nacional de Costa Rica	Costa Rica	10
DUKE	Duke University	EUA	3
FH	Farlow Reference Library and Herbarium of Cryptogamic Botany	EUA	44
FR	Herbarium Senckenbergianum Frankfurt	Alemanha	10
IBUG	Universidad de Guadalajara	México	11
IBUNAM/ MEXU	Universidad Nacional Autónoma de México	México	1
ICN	Herbário da Universidade do Rio Grande do Sul	Brasil	14
ILL	University of Illinois at Urbana-Champaign	EUA	6
INB	Instituto Nacional de Biodiversidad	Costa Rica	7
ISC	Iowa State University	EUA	13
K	Royal Botanic Gardens	EUA	18
LSUM Fungi	Louisiana State University	EUA	9
MA Fungi	Real Jardín Botánico de Madrid	Espanha	50
MCVE	Museo di Storia Naturale di Venezia	Itália	25
MEL	Royal Botanic Gardens Victoria	Austrália	30
MICH	University of Michigan	EUA	24
MU	Miami University	EUA	4
NEB	University of Nebraska State Museum, Lincoln NE	EUA	6
NY	The New York Botanical Garden	EUA	80

(continua)

(conclusão)

Acrônimo do herbário/nome por extenso		País	Total de exsicatas não recebidas
PACA	Instituto Anchietano de Pesquisas/UNISINOS	Brasil	48
PC	Muséum National d'Histoire Naturelle	França	11
PDD	New Zealand Fungarium	Nova Zelândia	30
PERTH	Western Australian Herbarium	Austrália	28
PH	Academy of Natural Sciences	EUA	5
PH	Botany Department Academy of Natural Sciences	EUA	5
PREM	Plant Protection Research Institute	África do Sul	48
QCAM	Fungario Pontificia Universidad Catolica del Ecuador	Equador	1
RMS	University of Wyoming	EUA	2
TNS-F	National Museum of Nature and Science	Japão	21
UC	University of California	EUA	29
USJ	Herbario Luis A. Fournier Origgi	Costa Rica	5
WIS	University of Wisconsin	EUA	2

APÊNDICE B – LISTA DE ESPÉCIMES REVISADOS

Legenda: Em negrito espécime tipo.[1]País ou estado tipo da espécie identificada. [2]Confirmar identificação por análise molecular. [3]Material danificado. [4]Basidioma não expandido (imaturo). [5]Envelope vazio. [6]Parte do material disponível para análise. [7]Cultura desidratada. [8]Com sequência nova gerada.

Identificação na exsicata	Identificação pós revisão	Local de coleta	Número de tombo
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral (APÊNDICE F)	Brasil[1], Ceará	UFRN–Fungos 2093
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral	Brasil[1], Espírito Santo	FLOR 42358
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral	Brasil[1], Rio de Janeiro	FLOR 64599
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral (APÊNDICE F)	Brasil[1], Rio Grande do Norte[1], Baía Formosa	UFRN–Fungos 130, 202, 203, 341, 1429, 3195
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral (APÊNDICE F)	Brasil[1], Rio Grande do Norte[1], Extremoz	UFRN–Fungos 1254
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral (APÊNDICE F)	Brasil[1], Rio Grande do Norte[1], Natal[1]	UFRN–Fungos 131, 133, 134, 135, 137–140, 142, 201, 203, 204, 208, 209, 341, 448, 449, 452, 453, 467, 497, 838, 1162, 1219, 1390, 1430, 1484, 3194, 3271,3272
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral	Brasil[1], Rio Grande do Norte[1], Natal[1]	UFRN–Fungos 136; 193
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Phallus* sp.	Brasil, Rio Grande do Norte, Natal	UFRN–Fungos 1430
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral (APÊNDICE F)	Brasil[1], Rio Grande do Norte[1], Tibau do Sul	UFRN–Fungos 3273; 3274

(continua)

(continuação)

Identificação na exsicata	Identificação pós revisão	Local de coleta	Número de tombo
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral	Brasil[1], Rio Grande do Norte[1], Natal[1]	UFRN–Fungos 136, 193
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Phallus* sp.[2]	Brasil, Rio Grande do Norte, Natal	UFRN–Fungos 1430
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral (APÊNDICE F)	Brasil[1], Rio Grande do Norte[1], Tibau do Sul	UFRN–Fungos 3273, 3274
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral	Brasil[1], Rio Grande do Norte[1], Tibau do Sul	UFRN–Fungos 2917
Anthurus borealis Burt	*Lysurus borealis* (Burt) Henn.	EUA, Pensilvânia	NCU-F-0000781
Anthurus borealis Burt	*Lysurus borealis* (Burt) Henn.	EUA, Nova York	NCU-F-0000782
Aseroë rubra Labill.	*Aseroë rubra* Labill.[2]	Honduras, Francisco Morazán	F: C0235400F
Aseroë rubra Labill.	*Aseroë rubra* Labill.[2]	EUA, Hawai	TENN-F-059478
Aseroë rubra Labill.	*Aseroë rubra* Labill.	Nova Zelândia, Waikato	TENN-F-044409
Aseroë sp.	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral	Brasil[1], Bahia	F: C0235401F
Blumenavia rhacodes Möller	*Blumenavia baturitensis* Melanda, M.P. Martín & Baseia[2]	Venezuela, Aragua	NY1938679
Clathrus cancellatus L.	*Clathrus ruber* P. Micheli ex Pers.[2]	EUA, Flórida	F: C0226318F
Clathrus cancellatus L.	*Clathrus ruber* P. Micheli ex Pers.[2]	Chile	F: C0235403F
Clathrus cancellatus L.	*Clathrus ruber* P. Micheli ex Pers.[2]	República Dominicana	NCU-F-0003255
Clathrus cibarius (Tul.) E. Fisch.	*Ileodictyon cibarium* Tul.	Nova Zelândia[1], Wellington	NCU-F-0003260
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Pernambuco	UFRN-Fungos 151
Clathrus columnatus Bosc	Não identificado[5]	Brasil	UFRN-Fungos 2396
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Ceará	UFRN-Fungos 2419
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Ceará	UFRN-Fungos 2424

(continuação)

Identificação na exsicata	Identificação pós revisão	Local de coleta	Número de tombo
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Ceará	UFRN-Fungos 2434
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Rio Grande do Norte	UFRN-Fungos 2912
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Rio Grande do Norte	UFRN-Fungos 2918
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Rio Grande do Norte	UFRN-Fungos 2919
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, São Paulo	SP-FUNGI 466706
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, São Paulo	SP-FUNGI 466707
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, São Paulo	SP-FUNGI 466708
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, São Paulo	SP-FUNGI 466709
Clathrus columnatus Bosc	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Tennessee	TENN-F-063250
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA, Flórida	TENN-F-020278
Clathrus columnatus Bosc	Não identificado[4]	EUA, Louisiana	F: C0226320F
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Texas	F: C0349805F
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Paraíba	JPB 47313
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Paraíba	JPB 65666
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Santa Catarina	FLOR 10127
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Flórida	NCU-F-0003224
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Carolina do Norte	NCU-F-0003225
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Carolina do Sul[1]	NCU-F-0003256
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Carolina do Sul[1]	NCU-F-0003257
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Carolina do Norte	NCU-F-0003258
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Flórida	NCU-F-0003259
Clathrus crispus Turpin	*Clathrus crispus* Turpin	EUA, Tennessee	TENN-F-070823

(continuação)

Identificação na exsicata	Identificação pós revisão	Local de coleta	Número de tombo
Clathrus crispus Turpin	Não identificado[3]	Porto Rico	CUP-PR-001143
Clathrus sp.	Não identificado[3]	Porto Rico	CUP-PR-001273
Clathrus sp.	Não identificado[3]	Porto Rico	CUP-PR-003416
Clathrus sp.	Não identificado[3]	Porto Rico	CUP-PR-003417
Clathrus sp.	*Clathrus columnatus* Bosc (APÊNDICE H)	EUA[1], Flórida	F: C0226317F
Clathrus sp.	*Pseudocolus schellenbergiae* (Sumst.) Johnson[2]	Honduras, Olancho	F: C0235402F
Clathrus sp.	*Ligiella rodrigueziana* J.A. Sáenz	Costa Rica[1], Guanacaste	F: C0370366F
Clathrus sp.	*Blumenavia rhacodes* Möller	Argentina	F: C0349803F
Clathrus sp.	*Blumenavia rhacodes* Möller	Argentina	F: C0349802F
Clathrus sp.	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Carolina do Norte	NCU-F-0003254
Clathrus sp.	Não identificado[3]	Jamaica	OSC 30176
Clathrus sp.	Não identificado[4]	EUA	OSC 29130
Clathrus sp.	Não identificado[3]	EUA, Carolina do Norte	TENN-F-040668
Clathrus sp.	*Ileodictyon cibarium* Tul.	Nova Zelândia[1], Wellington	TENN-F-045385
Clathrus sp.	Não identificado[4]	Brasil, Pernambuco	URM 75657
Clathrus sp.	*Clathrus natalensis* G.S. Medeiros, Melanda, T.S. Cabral, B.D.B. Silva & Baseia	Brasil[1], Rio Grande do Norte[1]	UFRN-Fungos 933
Clathrus sp.	*Clathrus columnatus* Bosc.[2]	Brasil, Ceará	UFRN-Fungos 1737
Clathrus ruber Turpin	*Clathrus ruber* Turpin	EUA, Califórnia	OSC 79910
Clathrus ruber Turpin	Não identificado[3]	EUA, Califórnia	OSC 79914
Clathrus ruber Turpin	*Clathrus ruber* Turpin	Bélgica	TENN-F-036911
Colus hirudinosus Cavalier & Séchier	*Colus hirudinosus* Cavalier & Séchier	Portugal	F: C0239492F

(continuação)

Identificação na exsicata	**Identificação pós revisão**	**Local de coleta**	**Número de tombo**
Colus sp.	*Lysurus mokusin* (L.) Fr.[2]	EUA, Carolina do Norte	NCU-F-0006888
Colus sp.	*Colus hirudinosus* Cavalier & Séchier[2]	Brasil, Alagoas	UFRN-Fungos 3347
Colus schellenbergiae Sumst.	*Pseudocolus schellenbergiae* (Sumst.) Johnson (APÊNDICE H)	EUA[1], Nova York	NCU-F-0006885
Colus schellenbergiae Sumst.	*Pseudocolus schellenbergiae* (Sumst.) Johnson (APÊNDICE H)	EUA[1], Nova Jersey	NCU-F-0006886
***Colus schellenbergiae* Sumst.**	***Pseudocolus schellenbergiae* (Sumst.) Johnson** (APÊNDICE H)	**EUA[1], Pensilvânia[1]**	**NCU-F-0006887 (isótipo)**
Laternea columnata (Bosc) Nees	*Clathrus columnatus* Bosc[2]	Brasil, Santa Catarina	FLOR 47630
Laternea dringii A. López, D. Martínez & J. García	*Laternea dringii* A. López, D. Martínez & J. García[2]	Brasil, Ceará	UFRN-Fungos 2984
Laternea pusilla Berk. & M.A. Curtis	*Laternea pusilla* Berk. & M.A. Curtis	Brasil, Santa Catarina	FLOR 47616
Laternea sp.	*Laternea triscapa* Turpin[2]	Costa Rica, Puntarenas	F: C0371592F
Laternea sp.	*Laternea triscapa* Turpin[2]	Brasil, Paraíba	JPB 65670
Laternea triscapa Turpin	*Laternea triscapa* Turpin[2]	Brasil, São Paulo	SP-FUNGI 178024
Laternea triscapa Turpin	*Clathrus columnatus* Bosc[2]	Brasil, Rio Grande do Norte	UFRN-Fungos 200
Laternea triscapa Turpin	Não identificado[3]	Brasil, Rio Grande do Norte	UFRN-Fungos 795
Lysurus sp.	Não identificado[3]	EUA, Nova York	CUP-061467
Lysurus sp.	Não identificado[3]	EUA, Colorado	DBG-F-029605
Lysurus sp.	Não identificado[3]	EUA, Tennessee	TENN-F-043660
Lysurus borealis (Burt) Henn.	*Lysurus borealis* (Burt) Henn.	EUA, Missouri	OSC 6045
Lysurus borealis (Burt) Henn.	*Lysurus borealis* (Burt) Henn.	EUA, Oregon	OSC 39089
Lysurus borealis (Burt) Henn.	*Lysurus borealis* (Burt) Henn.	EUA, Oregon	OSC 39531
Lysurus borealis (Burt) Henn.	*Lysurus borealis* (Burt) Henn.	EUA, Oregon	OSC 40045

(continuação)

Identificação na exsicata	**Identificação pós revisão**	**Local de coleta**	**Número de tombo**
Lysurus borealis (Burt) Henn.	Não identificado[3]	Canadá, Columbia Britânica	TENN-F-016849
***Lysurus borealis* var. *serotinus* Peck**	**Não identificado[6]**	**EUA[1], Massachusetts[1]**	**NYSf 2769 (holótipo)**
Lysurus cruciatus (Lepr. & Mont.) Henn.	*Lysurus borealis* (Burt) Henn.[2]	EUA, Illinois	F: C0226324F
Lysurus cruciatus (Lepr. & Mont.) Henn.	*Lysurus borealis* (Burt) Henn.[2]	EUA, Colorado	DBG-F-025304
Lysurus cruciatus (Lepr. & Mont.) Henn.	*Lysurus borealis* (Burt) Henn.[2]	EUA, Minnesota	MIN 814144
Lysurus cruciatus (Lepr. & Mont.) Henn.	Não identificado[3]	EUA, Minnesota	MIN 814145
Lysurus mokusin (Lepr. & Mont.) Henn.	Não identificado[5] (dois pequenos pedaços e uma lâmina de basidiosporos)	China, Yunnan	NCU-F-0031529
Lysurus mokusin (Lepr. & Mont.) Henn.	*Lysurus* sp.[2]	EUA, California	OSC 35381
Lysurus periphragmoides (Klotzsch) Dring	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Illinois	F: C0226322F
Lysurus periphragmoides (Klotzsch) Dring	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Texas	F: C0226325F
Lysurus periphragmoides (Klotzsch) Dring	Não identificado[3]	EUA, Illinois	F: C0226326F
Lysurus periphragmoides (Klotzsch) Dring	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Tennessee	TENN-F-073590
***Lysurus pusillus* Coker**	***Lysurus pusillus***	**EUA[1], Carolina do Sul[1]**	**NCU-F-0017338 (holótipo)**
Lysurus texensis Ellis ex Sacc.	Não identificado[3]	EUA, Texas	F: C0226323F
***Neolysurus arcipulvinus* O.K. Mill., Ovrebo & Burk**	***Neolysurus arcipulvinus* O.K. Mill., Ovrebo & Burk**	**Costa Rica[1], Heredia[1]**	**F: C0374489F (parátipo)**
Pseudocolus sp.	*Pseudocolus schellenbergiae* (Sumst.) Johnson [2]	Turquia, Trabzon	TENN-F-055659
Pseudocolus fusiformis (E. Fisch.) Lloyd	Não identificado[3]	EUA, Nova York	CUP-067953
Pseudocolus fusiformis (E. Fisch.) Lloyd	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Carolina do Norte	F: C0295891F
Pseudocolus fusiformis (E. Fisch.) Lloyd	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Carolina do Norte	F: C0295893F

(continuação)

Identificação na exsicata	Identificação pós revisão	Local de coleta	Número de tombo
Pseudocolus fusiformis (E. Fisch.) Lloyd	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Carolina do Norte	NCU-F-0017607
Pseudocolus fusiformis (E. Fisch.) Lloyd	Não identificado[4]	EUA, Carolina do Norte	NCU-F-0026676
Pseudocolus fusiformis (E. Fisch.) Lloyd	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Carolina do Norte	NCU-F-0026674
Pseudocolus fusiformis (E. Fisch.) Lloyd	*Pseudocolus schellenbergiae* (Sumst.) Johnson (APÊNDICE H)	EUA[1], Connecticut	TENN-F-066866
Pseudocolus garciae (Möller) Lloyd	Não identificado[3]	Brasil[1], RS	UFRN-Fungos 1522
Pseudocolus javanicus (Penz.) Lloyd	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Tennessee	TENN-F-023098
Pseudocolus schellenbergiae (Sumst.) Johnson	Não identificado[3]	Sem informação	CUP-062549
Pseudocolus schellenbergiae (Sumst.) Johnson	*Pseudocolus schellenbergiae* (Sumst.) Johnson (APÊNDICE H)	EUA[1], Nova York	TENN-F-027643
Pseudocolus schellenbergiae (Sumst.) Johnson	*Pseudocolus fusiformis* (E. Fisch.) Lloyd (APÊNDICE H)	EUA, Carolina do Norte	TENN-F-041965
Simblum sp.	Não identificado[3]	Sem informação	CUP-034876
Simblum sp.	Não identificado[3]	Índia	NCU-F-0030100
Simblum sp.	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Tennessee	TENN-F-040646
Simblum rubescens W.R. Gerard	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Carolina do Norte	F: C0226327F
Simblum rubescens W.R. Gerard	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	Sem informação	NCU-F-0030093
***Simblum rubescens* W.R. Gerard**	**Não identificado[6]**	**EUA, Nova York**	**NYSf 4442 (tipo)**
Simblum sphaerocephalum Schltdl.	Não identificado[3]	Ilha Bermudas	CUP-034598
Simblum sphaerocephalum Schltdl.	Não identificado[5]	Venezuela, Aragua	CUP-VZ-4059
Simblum sphaerocephalum Schltdl.	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Carolina do Norte	NCU-F-0030094

(conclusão)

Identificação na exsicata	**Identificação pós revisão**	**Local de coleta**	**Número de tombo**
Simblum sphaerocephalum Schltdl.	Não identificado[3]	Sem informação	NCU-F-0030096
Simblum sphaerocephalum Schltdl.	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	Sem informação	NCU-F-0030098
Simblum sphaerocephalum Schltdl.	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Tennessee	TENN-F-009705
Simblum sphaerocephalum Schltdl.	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Tennessee	TENN-F-022658
Simblum sphaerocephalum Schltdl.	Não identificado[3]	EUA, Tennessee	TENN-F-041510
Simblum sphaerocephalum Schltdl.	*Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka & L.S. Domínguez	EUA, Tennessee	TENN-F-044142
Simblum texense (G.F. Atk. & Long) Long	Não identificado[3]	EUA, Texas	CUP-053234
Simblum texense (G.F. Atk. & Long) Long	Não identificado[7]	EUA	URM 10114
Simblum texense (G.F. Atk. & Long) Long	Não identificado[7]	Sem informação	URM 12159
***Staheliomyces cinctus* E. Fisch.**	***Staheliomyces cylindricus* Melanda, N.M. Assis & T.S. Cabral (APÊNDICE E)[8]**	**Brasil, Rio Grande do Norte**	**UFRN-Fungos 1222 (parátipo)**
***Staheliomyces cinctus* E. Fisch.**	***Staheliomyces cylindricus* Melanda, N.M. Assis & T.S. Cabral (APÊNDICE E)[8]**	**Brasil, Paraíba**	**UFRN-Fungos 2177 (holótipo)**

APÊNDICE C – MATERIAIS RESULTANTE DE COLETAS POR PARCEIROS

Legenda: Em negrito espécime tipo.[1]País ou estado tipo da espécie identificada.[2]Confirmar identificação por análise molecular. [3]Com sequência nova gerada.

Identificação na coleta	Identificação pós revisão	Local de coleta	Coletor	Número de tombo
Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral	*Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral (APÊNDICE F)	Brasil[1], Rio Grande do Norte[1], Goianinha	Alexandro A. Lima	UFRN-Fungos 3214
Blumenavia rhacodes Möller	*Blumenavia rhacodes* Möller	Brasil[1], Rio Grande do Sul	Gilberto Coelho	UFRN-Fungos 3500
Blumenavia sp.	*Blumenavia baturitensis* Melanda, M.P. Martín & Baseia[2]	Brasil[1], Espírito Santo	Samela S. Recla	MBML 54484
Blumenavia sp.	*Blumenavia rhacodes* Möller (APÊNDICE G)	Brasil, Rio Grande do Sul	Jorge R. P. Velloso	HBEI 047
Clathrus columnatus Bosc	*Clathrus columnatus* Bosc[2]	Brasil, Paraíba, Cabedelo	Wartchow, F.	UFRN-Fungos 3505
Clathrus natalensis G.S. Medeiros, Melanda, T.S. Cabral, B.D.B. Silva & Baseia	*Clathrus natalensis* G.S. Medeiros, Melanda, T.S. Cabral, B.D.B. Silva & Baseia (APÊNDICE F)	Brasil[1], Rio Grande do Norte[1]	Alexandro A. Lima	UFRN-Fungos 3215
Laternea triscapa Turpin	*Laternea triscapa* Turpin[2]	Brasil, Paraíba	Marcelo A. Sulzbacher & Bruno T. Goto	UFRN-Fungos 3506
Laternea triscapa Turpin	*Laternea triscapa* Turpin[2]	Costa Rica, Heredia	Clark L. Ovrebo	UFRN-Fungos 3501
Laternea triscapa Turpin	*Laternea triscapa* Turpin[2]	Brasil, Rio Grande do Norte	Alexandro A. Lima	UFRN-Fungos 3503
Laternea triscapa Turpin	*Laternea triscapa* Turpin[2]	Brasil, Rio Grande do Norte	Alexandro A. Lima	UFRN-Fungos 3504
Mutinus argentinus Speg.	*Mutinus argentinus* Speg. (APÊNDICE F)	Brasil, Rio Grande do Norte	Alexandro A. Lima	UFRN-Fungos 3220
Mutinus argentinus Speg.	*Mutinus argentinus* Speg. (APÊNDICE F)	Brasil, Rio Grande do Norte	Alexandro A. Lima	UFRN-Fungos 3221
Mutinus bambusinus (Zoll.) E. Fisch.	*Mutinus bambusinus* (Zoll.) E. Fisch. (APÊNDICE F)	Brasil, Rio Grande do Norte	Alexandro A. Lima	UFRN-Fungos 3218

(continua)

(conclusão)

Identificação na coleta	**Identificação pós revisão**	**Local de coleta**	**Coletor**	**Número de tombo**
Mutinus bambusinus (Zoll.) E. Fisch.	*Mutinus bambusinus* (Zoll.) E. Fisch. (APÊNDICE F)	Brasil, Rio Grande do Norte	Alexandro A. Lima	UFRN-Fungos 3219
Mutinus bambusinus (Zoll.) E. Fisch.	*Mutinus bambusinus* (Zoll.) E. Fisch. (APÊNDICE F)	Brasil, Rio Grande do Norte	Alexandro A. Lima	UFRN-Fungos 3222
Phallus sp. Kreisel & Calonge	*Phallus atrovolvatus* Kreisel & Calonge (APÊNDICE F)	Brasil, Pernambuco	Alexandro A. Lima	UFRN-Fungos 3216
***Staheliomyces cinctus* E. Fisch.**	***Staheliomyces candeliformis* N.M. Assis, Melanda & T.S. Cabral (APÊNDICE E)[3]**	**Brasil, Amazonas**	**Tiara S. Cabral**	**INPA 25583 (holótipo)**
***Staheliomyces cinctus* E. Fisch.**	***Staheliomyces candeliformis* N.M. Assis, Melanda & T.S. Cabral (APÊNDICE E)[3]**	**Brasil, Amazonas**	**Tiara S. Cabral**	**UFRN-Fungos 2748 (parátipo)**
***Staheliomyces cinctus* E. Fisch.**	***Staheliomyces costariquensis* Ovrebo, Melanda, N.M. Assis & T.S. Cabral (APÊNDICE E)[3]**	**Costa Rica, Heredia**	**Clark Ovrebo**	**USJ 109573 (holótipo)**
***Staheliomyces cinctus* E. Fisch.**	***Staheliomyces quadratus* N.M. Assis, Melanda, T.S. Cabral (APÊNDICE E)[3]**	**Brasil, Amazonas**	**Tiara S. Cabral**	**UFRN-Fungos 2746 (holótipo)**
Staheliomyces cinctus E. Fisch.	*Staheliomyces* sp. (APÊNDICE E)[3]	Brasil, Pará	Tiara S. Cabral	INPA 264932

APÊNDICE D – AN OVERVIEW OF 24 YEARS OF MOLECULAR PHYLOGENETIC STUDIES IN PHALLALES (BASIDIOMYCOTA) WITH NOTES ON SYSTEMATICS, GEOGRAPHIC DISTRIBUTION, LIFESTYLE, AND EDIBILITY

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An Overview of 24 Years of Molecular Phylogenetic Studies in *Phallales* (*Basidiomycota*) With Notes on Systematics, Geographic Distribution, Lifestyle, and Edibility

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The order *Phallales* (*Basidiomycota*) is represented by gasteroid fungi with expanded and sequestrate basidiomata, known as stinkhorns and false truffles. In phalloids, the first DNA sequence was published in 1997, and after that, some studies aimed to resolve phylogenetic conflicts and propose new species based on DNA markers; however, the number of families and genera in the order still generates controversies among researchers. Thus, this work aims to provide an overview of *Phallales* diversity represented by selected DNA markers available in public databases. We retrieved *Phallales* sequences from DNA databases (GenBank and UNITE) of seven markers: ITS (internal transcribed spacer), nuc-LSU (nuclear large subunit rDNA), nuc-SSU (nuclear small subunit rDNA), mt-SSU (mitochondrial small subunit rDNA), *ATP*6 (ATPase subunit 6), *RPB2* (nuclear protein-coding second largest subunit of RNA polymerase), and *TEF*1-α (translation elongation factor subunit 1α). To compose our final dataset, all ITS sequences retrieved were subjected to BLASTn searches to identify additional ITS sequences not classified as *Phallales*. Phylogenetic analyses based on Bayesian and maximum likelihood approaches using single and combined markers were conducted. All ITS sequences were clustered with a cutoff of 98% in order to maximize the number of species hypotheses. The geographic origin of sequences was retrieved, as well as additional information on species lifestyle and edibility. We obtained a total of 1,149 sequences, representing 664 individuals. Sequences of 41 individuals were unidentified at genus level and were assigned to five distinct families. We recognize seven families

and 22 genera in *Phallales*, although the delimitation of some genera must be further revisited in order to recognize only monophyletic groups. Many inconsistencies in species identification are discussed, and the positioning of genera in each family is shown. The clustering revealed 118 species hypotheses, meaning that approximately 20% of all described species in *Phallales* have DNA sequences available. Information related to geographic distribution represents 462 individuals distributed in 46 countries on all continents, except Antarctica. Most genera are saprotrophic with only one putative ectomycorrhizal genus, and 2.1% of the legitimate specific names recognized in *Phallales* are confirmed edible species. Great progress in the molecular analyses of phalloids has already been made over these years, but it is still necessary to solve some taxonomic inconsistencies, mainly at genus level, and generate new data to expand knowledge of the group.

Keywords: gasteroid fungi, GenBank, phylogeny, stinkhorns, UNITE

INTRODUCTION

The first molecular analyses including gasteroid fungi (Hibbett et al., 1997) showed that they represent a polyphyletic and artificial grouping of taxa that share a common ancestor with gilled and nongilled mushrooms that have active dispersion of the basidiospores. Hibbett et al. (1997) showed the gasteroid–phalloid fungi to group in a clade with other forms of gasteroid fungi, the *Geastraceae* Corda (earthstars) and *Sphaerobolaceae* J. Schröt. (cannonballs), all sharing a common ancestor with coralloid fungi. After that, Pine et al. (1999) confirmed the phylogenetic relationship between some cantharelloid, clavarioid, and phalloid fungi, naming all of them the gomphoid–phalloid clade, which was later confirmed as monophyletic (Hibbett and Thorn, 2001; Krüger et al., 2001; Binder and Hibbett, 2002; Hibbett and Binder, 2002) and designated as a subclass of *Agaricomycetes*: *Phallomycetidae* K. Hosaka, Castellano and Spatafora (Hosaka et al., 2006).

Phallales E. Fisch (*Agaricomycetes*, *Phallomycetidae*) includes representatives of gasteroid fungi with basidiospores that are passively dispersed mainly by insects and commonly named phalloid fungi, alien fungi, stinkhorns, and lattice or cage stinkhorns (Fischer, 1898; Cunningham, 1931; Miller and Miller, 1988; Pegler and Gomez, 1994). The phalloid fungi are mostly saprobic and characterized by hypogeous or epigeous immature basidiomata that are divided into chambers; thick white rhizomorphs are usually present; peridium with two or three layers, one of which is gelatinous; mature basidiomata that are usually epigeous or partially hypogeous, expanded, or sequestrate; pseudostipitate or sessile receptacle; receptacle carrying the green, olive to brown gleba; the usual presence of gelatinous to mucilaginous gleba that may be powdery at maturity, as in *Gastrosporium* Mattir.; and basidiospores mostly ellipsoid and smooth, with only a few genera with ornamentation on the basidiospore wall, as in *Gastrosporium*, *Kjeldsenia* Colgan, Castellano and Bougher, and *Phlebogaster* Fogel (Hosaka et al., 2006; Trierveiler-Pereira et al., 2014a).

Fischer (1898) grouped in *Phallales* the families *Clathraceae* Chevall. and *Phallaceae* Corda, which include specimens with expanded branched and unbranched basidiomata, respectively. *Lysuraceae* Corda was established in the same article as the establishment of *Phallaceae* (Corda, 1842); both families are characterized by basal pseudostipitate basidiomata, but unlike the morphology in *Phallaceae*, the apical part of the basidiomata in *Lysuraceae* is branched. *Lysuraceae* was not accepted by Fischer (1898) as an independent family in *Phallales*, and their species were considered by this author within *Clathraceae*, a view also adopted by a number of subsequent authors such as Cunningham (1944), Dring (1980), Jülich (1981), Miller and Miller (1988), Pegler and Gomez (1994), Hibbett and Thorn (2001), and Kirk et al. (2008). On the other hand, some authors (He et al., 2019; Wijayawardene et al., 2020) and well-known databases (Nilsson et al., 2019; Index Fungorum, 2020; MycoBank., 2020; Schoch et al., 2020) have placed in *Phallaceae* all the species traditionally classified as *Lysuraceae*. However, Hosaka et al. (2006), Degreef et al. (2013), Trierveiler-Pereira et al. (2014a), and Sulzbacher et al. (2016) consider these three families to be independent (**Table 1**).

Cunningham (1931) accepted in *Phallales* sequestrate (truffle-like) basidiomata classified in the genus *Claustula* K.M. Curtis and established this genus as a type of the new monogeneric family *Claustulaceae* G. Cunn. As mentioned by Cunningham (1931), this family shares with other phalloid fungi the gelatinous peridium, immature basidiomata divided into chambers, and elliptical smooth basidiospores. Zeller (1939) also studied sequestrate fungi and proposed two new families: *Gelopellaceae* Zeller and *Protophallaceae* Zeller. However, these two families, as well as *Hysterangiaceae* E. Fisch., have been consolidated within the order *Hysterangiales* K. Hosaka and Castellano, according to Zeller (1939). *Hysterangiales* was first proposed by Zeller (1939), but it was considered a *nomen nudum* because it was published without a description or diagnosis; it was later formally established in Hosaka et al. (2006).

Moreover, Hosaka et al. (2006) established the subclass *Phallomycetidae*, including the new order *Hysterangiales*

TABLE 1 | Family classification of *Phallales* and related orders according to published molecular studies and taxonomic and molecular databases.

Work	Families accepted in *Phallales*	Families accepted in *Hysterangiales*	Families accepted in *Boletales*
Hosaka et al. (2006), Degreef et al. (2013)	*Clathraceae*, *Claustulaceae* (=*Gelopellaceae*), *Lysuraceae*, *Phallaceae*, *Protophallaceae*, *Trappeaceae*		
Trierveiler-Pereira et al. (2014a)	*Clathraceae*, *Claustulaceae* (=*Gelopellaceae*), *Gastrosporiaceae*, *Lysuraceae*, *Phallaceae*, *Protophallaceae*, *Trappeaceae*		
Sulzbacher et al. (2016)	*Clathraceae*, *Claustulaceae* (=*Gelopellaceae*), *Lysuraceae*, *Phallaceae*, *Protophallaceae*, *Trappeaceae*		
He et al. (2019), Wijayawardene et al. (2020)	*Claustulaceae*, *Gastrosporiaceae*, *Phallaceae* (=*Clathraceae*; *Lysuraceae*)	*Trappeaceae*, *Phallogastraceae* (=*Protophallaceae*)	
Schoch et al. (2020)	*Clathraceae*, *Phallaceae* (=*Lysuraceae*; =*Protophallaceae*)	*Hysterangiaceae* (=*Trappeaceae*)	*Gastrosporiaceae*
Nilsson et al. (2019)	*Clathraceae*, *Claustulaceae*, *Gastrosporiaceae*, *Phallaceae* (=*Lysuraceae*)	*Hysterangiaceae* (=*Trappeaceae*)	
Index Fungorum (2020)	*Claustulaceae* (=*Gelopellaceae*), *Phallaceae* (=*Clathraceae*; =*Lysuraceae*)	*Phallogastraceae* (=*Protophallaceae*), *Trappeaceae*	*Gastrosporiaceae*
MycoBank. (2020)	*Claustulaceae* (=*Gelopellaceae*), *Gastrosporiaceae*, *Phallaceae* (=*Clathraceae*; =*Lysuraceae*), *Protophallaceae*	*Trappeaceae*	

mentioned previously and the new *Geastrales* K. Hosaka and Castellano. Thus, in the study by Hosaka et al. (2006), *Phallomycetidae* comprises *Geastrales*, *Gomphalles* Jülich., *Hysterangiales*, and *Phallales*, a classification that is also accepted in He et al. (2019). In this way, Hosaka et al. (2006) agreed with Cunningham (1931) in the definition of *Phallales* including families with expanded basidiomata (*Clathraceae*, *Lysuraceae*, *Phallaceae*), as well as with sequestrate ones (*Claustulaceae*, *Trappeaceae* P.M. Kirk, and *Protophallaceae*). Although *Trappeaceae* was provisionally proposed in *Phallales* by Hosaka et al. (2006) with the genera *Phallobata* G. Cunn. and *Trappea* Castellano, the family was formally proposed two years later by Kirk et al. (2008), who classified it as part of *Hysterangiales*. Later, Sulzbacher et al. (2016) proposed a new genus in *Trappeaceae* (*Restingomyces* Sulzbacher, T. Grebenc and Baseia) and also considered the family in *Phallales* as previously pointed out by Hosaka et al. (2006).

After these 24 years of molecular studies, the sampling of some genera and families within molecular phylogenies of *Phallales* is incomplete. For example, *Gastrosporium*, which is part of the monogeneric family *Gastrosporiaceae* Pilát, was first incorporated in a molecular phylogenetic work by Hibbett and Binder (2002), who considered it as a sequestrate member of *Phallales*. This was later confirmed by Trierveiler-Pereira et al. (2014a), He et al. (2019), Kasuya et al. (2020), and Wijayawardene et al. (2020). However, Hosaka et al. (2006) did not include *Gastrosporium* in their phylogeny because of the lack of a protein code gene in their dataset. In the study by Trierveiler-Pereira et al. (2014a), *Trappeaceae* representatives were not included, and they recognized seven families in *Phallales*, which include *Gastrosporiaceae* plus the six families recognized by Hosaka et al. (2006).

On the other hand, the acceptance in *Phallales* of families composed of species characterized by sequestrate basidiomata (*Claustulaceae*, *Gastrosporiaceae*, *Gelopellaceae*, *Trappeaceae*, and *Protophallaceae*) has also generated controversies. For instance, morphological studies conducted by Zeller (1939, 1948) and Jülich (1981) considered *Gelopellaceae* and *Protophallaceae* in *Hysterangiales*, whereas Miller and Miller (1988) considered these families and *Claustulaceae* in *Phallales*. The last edition of Dictionary of the Fungi (Kirk et al., 2008) recognized three families in *Phallales*: *Claustulaceae* (=*Gelopellaceae*), *Gastrosporiaceae*, and *Phallaceae* (=*Clathraceae*; =*Lysuraceae*; =*Protophallaceae*), with *Trappeaceae* placed in *Hysterangiales*. Additionally, recent works based on *Basidiomycota* and general fungal classification (He et al., 2019; Wijayawardene et al., 2020) also considered *Trappeaceae* in *Hysterangiales* and only three families in *Phallales*: *Claustulaceae*, *Gastrosporiaceae*, and *Phallaceae* (**Table 1**). Representatives of some families of *Phallales* are shown in **Figure 1**.

There is still no consensus in family level systematics of *Phallales*, based on a compilation of sources (**Table 1**), such as works of fungal classification (He et al., 2019; Wijayawardene et al., 2020), taxonomic (Index Fungorum, 2020; MycoBank., 2020) and molecular databases (Nilsson et al., 2019; Schoch et al., 2020), and phylogenetic studies focused on *Phallales* (Hosaka et al., 2006; Degreef et al., 2013; Trierveiler-Pereira et al., 2014a; Sulzbacher et al., 2016). Thus, based on the importance of molecular data for systematics and phylogenetic studies and the fact that DNA databases can be a good tool to assess the history behind the sequences generated over the years, as well as the geographic distribution of certain taxa, we have undertaken this study using *Phallales* as a target group to retrieve sequences in molecular databases and to provide an overview of *Phallales* diversity represented by selected DNA markers available in public databases. Moreover, we aim to test

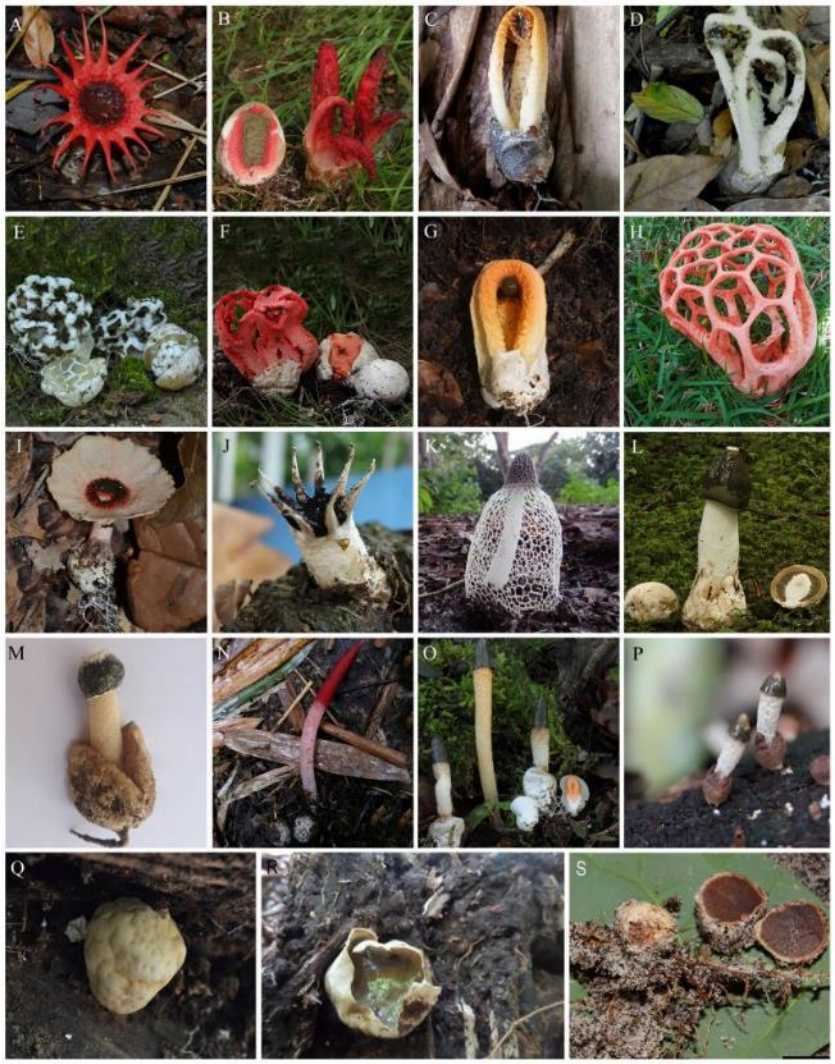

FIGURE 1 | Basidiomata of *Phallales*. *Clathraceae*: **(A)** *Aseroë rubra*; **(B)** *Clathrus archeri* MT13072101B (personal herbarium); **(C)** *Laternea dringii* (coll. AAL94); **(D)** *Blumenavia baturitensis* UFRN-Fungos 2868, holotype (coll. GCSM15); **(E)** *Ileodictyon gracile* MT141003001B (personal herbarium); **(F)** *Clathrus ruber* MT15100406B (personal herbarium); **(G)** *Clathrus columnatus* UFRN-Fungos 2912 (coll. AAL42); **(H)** *Clathrus natalensis* (coll. GSCM30); **(I)** *Abrachium floriforme* UFRN-Fungos 3271. *Lysuraceae*: **(J)** *Lysurus arachnoideus* INPA-Fungos 256537 (coll. TSC41). *Phallaceae*: **(K)** *Phallus indusiatus* INPA-Fungos 264931, neotype (coll. TSC148); **(L)** *Phallus impudicus*; **(M)** *Itajahya* sp. UFRN-Fungos 3342 (coll. AAL106); **(N)** *Mutinus bambusinus* UFRN-Fungos 3222 (coll. AAL100); **(O)** *Mutinus caninus*; **(P)** *Xylophallus clavatus* INPA-Fungos 271637 (coll. TSC237). *Protophallaceae*: **(Q,R)** *Protubera maracuja* (coll. GCSM18). *Trappeaceae*: **(S)** *Restingomyces reticulatus* UFRN-Fungos 1890, holotype (coll. MAS335). Photographs: **(A)** Clark L. Ovrebo; **(B,E,F,L,O)** Manuel Tabarés; **(C,G,M,N)** Alexandro de A. de Lima; **(D,H,Q,R)** Gislaine C. S. Melanda; **(I)** Alexandre G. S. Silva-Filho; **(J,K,P)** Tiara S. Cabral; **(S)** Marcelo A. Sulzbacher.

the phylogenetic positioning of named and unnamed sequences; to assess phylogenetic hypotheses using combined markers to recognize families and genera and to compare these data with the extant classification; to recognize the total number of species hypothesis (SH) represented in *Phallales* based on internal transcribed spacer (ITS) sequence clustering; and, finally, to record the global geographic distribution of their representative genera, their lifestyle, and edibility.

MATERIALS AND METHODS

Sequence Metadata

Our work used two databases to obtain *Phallales* sequences: NCBI GenBank[1] and UNITE[2]. All sequences were downloaded on August 7 to 9, 2020, from both databases. GenBank is part of the International Nucleotide Sequence Database Collaboration and contains the vast majority of phalloid sequences from published articles. The UNITE database automatically clusters ITS sequences of eukaryotic organisms to approximately the species level (called SHs), and to facilitate unambiguous scientific communication, a DOI is given to each SH.

According to the revised bibliography already mentioned (Hibbett et al., 1997; Hosaka et al., 2006; Trierveiler-Pereira et al., 2014a; Sulzbacher et al., 2016; Kasuya et al., 2020), seven markers were selected to retrieve sequences in GenBank using query strings (**Table 2**): nuclear ribosomal ITS, nuclear large subunit rDNA (nuc-LSU), nuclear small subunit rDNA (nuc-SSU); mitochondrial small subunit rDNA (mt-SSU), mitochondrial protein-coding ATPase subunit 6 (*ATP*6), and nuclear protein-coding second largest subunit of RNA polymerase (*RPB*2); and nuclear protein-coding translation elongation factor subunit 1α (*TEF*1-α). GenBank query results were downloaded in TinySeq_XML format, and single datasets of nucleotide sequences were created for each marker. One single dataset of all ribosomal markers from GenBank was downloaded, and in order to identify each marker, this single dataset was separated manually, based on the marker name in each sequence title. From the UNITE database, the sequences under *Phallales* (DOI: TH005985) not placed in GenBank were retrieved manually. Furthermore, manual checking was done for some genera, as they are not classified in *Phallales* in GenBank (*Gastrosporium*, *Kjeldsenia*, *Phallobata*, *Phlebogaster*, and *Trappea*) and UNITE (*Phlebogaster* and *Trappea*).

Sequence metadata were retrieved from GenBank qualifiers and UNITE annotations. GenBank qualifiers include[3]: *country*, *collection_date*, *culture_collection*, *environmental_sample*, *clone*, *isolate*, *isolation_source*, *lat_lon*, *organism*, *specimen_voucher*, *strain*, *tissue_type*, *type_material*, and *PCR_primers*, as well as information about authors, reference, title, and journal. UNITE annotations were obtained directly from the online database for each sequence; UNITE metadata include *sampling_area* (*country*), *sample_type* [Linked to (source)], and *collection_date*.

All ITS sequences obtained from GenBank and UNITE were used for additional Nucleotide BLAST searches in their respective database (NCBI BLAST, 2020; UNITE BLAST, 2020). These searches aimed to find ITS sequences of *Phallales* members that were deposited without being classified in this order. We retrieved unclassified sequences using the following cutoffs: query cover > 80%, identity > 70%, and e-value < e-1,000. The 80% sequence similarity represents the criterion to recognize the identity of sequences approximately at the order level (Tedersoo et al., 2014).

[1]http://www.ncbi.nlm.nih.gov/

[2]https://unite.ut.ee/index.php

[3]http://www.insdc.org/documents/feature_table.html#7.3

TABLE 2 | Query strings used to search for DNA sequences from phalloid fungi in GenBank.

Query	Query strings
Main query	txid68804[Organism] AND 300:10000[SLEN]
ITS; nuc-LSU; nuc-SSU; mt-SSU	rRNA[Title] OR ribosomal RNA[Title]
*ATP*6	ATP6[Title] OR ATPase6[Title] OR ATP synthase F0 subunit 6[Title] OR ATP synthase subunit 6[Title] OR MTATP synthase F0 subunit 6[Title] OR MT-ATP6[Title] OR MTATP6[Title] OR ATP-6[Title]
*RPB*2	rpb2[Title] OR rpbII[Title] OR RNA polymerase II second largest subunit[Title] OR RNA polymerase II second large subunit[Title] NOT rpb1
*TEF*1-α	TEF1[Title] OR EF1[Title] OR EF-1[Title] OR TEF-1[Title] OR TEF[Title] OR tef1a[Title] OR EF[Title] OR translation elongation factor 1[Title] OR EF1alpha[Title] OR EF1a[Title] OR EF1-alpha[Title] OR TEF1-alpha[Title]

All information from the sequences retrieved from both databases and the BLAST searches was merged manually and organized in **Supplementary Table 1** to better identify all markers of each individual based on their herbarium/culture accession number and/or other code given by whoever generated the sequences. An individual was considered repeated when it had more than one sequence of the same marker under different accession numbers or when it was indicated as a clone in the databases (individuals with "R" in the columns "R = repeated or duplicated voucher" of **Supplementary Table 1**). In these cases, two lines were created in **Supplementary Table 1** for the same individual. The names of genera and species present in our **Supplementary Table 1** are based on the qualifier *organism* in GenBank for each individual. In UNITE, the names adopted were according to the UNITE taxon name.

Phylogenetic Positioning of Sequences and Recognition of Families and Genera

Phylogenetic analyses were performed using seven datasets, the combined one and the other six with each individual marker: ITS, nuc-LSU, mt-SSU, *ATP*6, *RPB*2, and *TEF*1-α. The marker nuc-SSU was not considered in the analyses because of the few (1%) sequences available (**Supplementary Table 1**). Sequences of *Hysterangiales* species were used as outgroup for individual marker analyses, as seen in **Supplementary Table 2**. The combined dataset (ITS + nuc-LSU + mt-SSU + *ATP*6 + *RPB*2 + *TEF*1-α) was constructed to confirm the organization in families, and this also used members of *Hysterangiales* as outgroup (**Supplementary Table 3**). Specimens from almost all genera retrieved in *Phallales* and that had most markers sequenced were chosen for the combined dataset (**Supplementary Table 3**), which includes 139 sequences: 69 ITS, 114 nuc-LSU, 26 mt-SSU, 76 *ATP*6, 65 *RPB*2, and 41 *TEF*1-α.

All datasets were aligned using MAFFT v.7 (Katoh and Standley, 2013) under the E-INS-i criteria. Seaview v.4

(Gouy et al., 2010) was used to visualize and adjust the alignments. The *RPB2* alignment was partitioned into intron and exon, and *TEF*1-α alignment into intron 1/2/3 and exon 1/2 according to GenBank coding sequence notation. The best nucleotide substitution model was selected with BIC (Bayesian information criterion) using jModelTest 2v.1.6 (Darriba et al., 2012) for each individual dataset. Two strategies were used for phylogenetic reconstructions of each alignment: maximum likelihood and Bayesian inference. Maximum likelihood analyses were performed in RAxML v8.2.X (Stamatakis, 2006), combined with the rapid bootstrapping algorithm with 1,000 replicates under the GTRGAMMA option to obtain the maximum likelihood bootstrap (MLbs). Bayesian inferences were performed using MrBayes 3.2.6 (Ronquist et al., 2012) with two independent runs, each one beginning from random trees with four simultaneous independent chains, performing 2×10^7 Markov chain Monte Carlo (MCMC) generations, sampling one tree every 1×10^3 generation. The first 5×10^3 sampled trees were discarded as burn-in, whereas the remaining ones (all sampled after the average standard deviation of split frequencies reached < 0.01) were used to reconstruct a 50% majority-rule consensus tree and to calculate Bayesian posterior probabilities (PP) of the clades. The jModelTest 2v.1.6, RAxML v8.2.X, and MrBayes 3.2.6 were run from the CIPRES Science Gateway 176 3.1 (Miller et al., 2010). All final alignments and the resulting topologies were deposited in TreeBASE under the number 28016.

Species Hypotheses Recognition

The ITS sequences of *Phallales* retrieved were clustered using CD-HIT-EST (Huang et al., 2010) at 98.0% sequence similarity threshold (Tedersoo et al., 2014) to assess species hypotheses in *Phallales*.

Geographic Distribution, Lifestyle, and Edibility

The qualifiers *country* and *lat_lon* from GenBank and *sampling_area* from UNITE were used to organize the global geographic distribution map of *Phallales* and each genus. To construct the maps based on this global distribution, the locality of each individual identified at genus level was retrieved from the databases (**Supplementary Table 4**). When possible, the missing localities in DNA databases were double searched in their original article or in secondary articles that give this information (**Supplementary Table 4**). When the geographic coordinate information was missing, we made an effort to establish it through Google Maps[4] to complete the table. In the case of individuals for which the only origin information was the country, the geographic coordinates suggested by Google Maps were used based on the name of the respective country as a search keyword. One general map with all *Phallales* distribution was made, as well as separate maps according to genera.

To record the information related to lifestyle of each genus, we followed the FungalTraits database (Põlme et al., 2021) and additional data obtained from the qualifiers *environmental_sample* (GenBank), *isolation_source* (GenBank), and *sample_type* (UNITE). To complement and better explore the use of the phalloid species sampled with molecular data, the edibility status of the species was considered based on Li et al. (2021) and complementarily searched in the main text of the articles in which the sequences were generated.

[4]https://www.google.com.br/maps

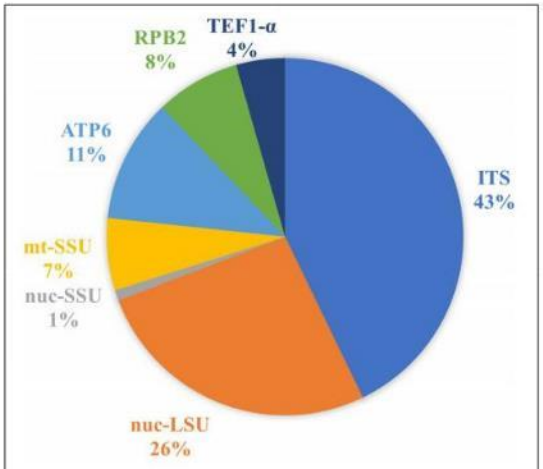

FIGURE 2 | Relative proportion of phalloid DNA sequences deposited in DNA databases (GenBank and UNITE) according to the molecular marker.

RESULTS

Sequence Metadata

Our final dataset led to a total of 1,149 DNA sequences of *Phallales* divided into 492 ITS, 303 nuc-LSU, 11 nuc-SSU, 75 mt-SSU, 129 *ATP*6, 88 *RPB*2, and 51 *TEF*1-α (**Figure 2**).

Based on the available records of collection date (**Figure 3**), the first uploaded sequences of *Phallales* individuals were the nuc-SSU sequences of *Pseudocolus fusiformis* (E. Fisch.) Lloyd, dated October 31, 1997 (AF026623), and November 5 of the same year (AF026666), both part of the work published by Hibbett et al. (1997). In 2006, there was a peak of deposited sequences, including new markers such as *ATP*6, *RPB*2, and *TEF*1-α (**Figure 3**), and in 2012, there was a higher constancy of deposited sequences, in which ITS and nuc-LSU are the most represented markers (**Figure 3**). Interestingly, the sequence obtained from the oldest phalloid individual belongs to *Colus hirudinosus* Cavalier and Séchier (voucher UC 955042, dated February 1, 1952) and was uploaded in GenBank on April 4, 2020 (nuc-LSU accession code MK607412, author of sequence: Kuo, M.).

The 1,149 sequences comprise 664 individuals, with 19 of them comprising repeated sequences for the same maker. A total of 58.7% of all individuals have only one sequenced marker, 23.9% have two sequenced markers, and 17.4% have three to five sequenced markers. There are 122 sequences representing 41 type collections (**Supplementary Table 5**).

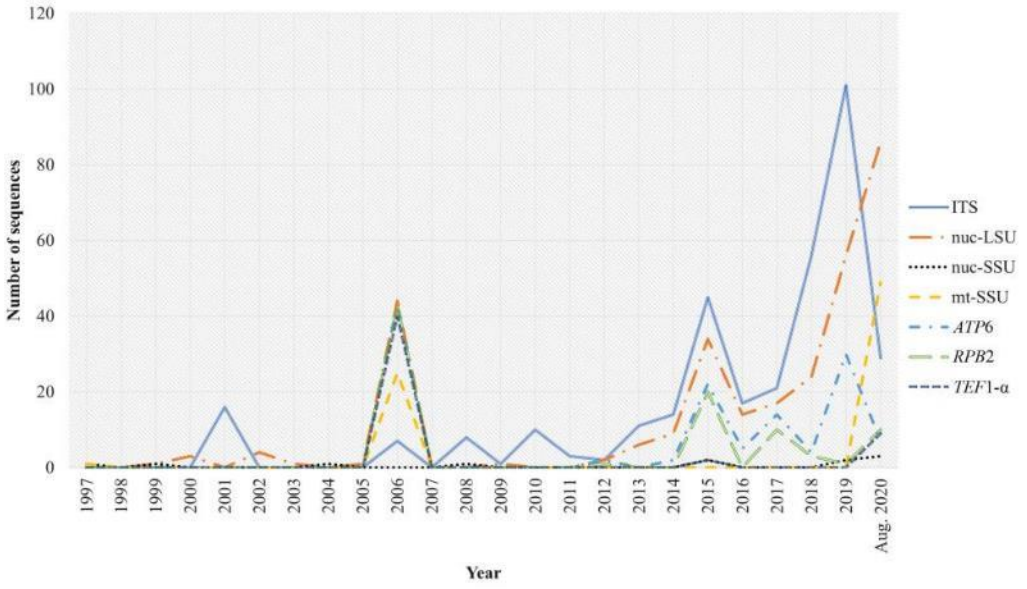

FIGURE 3 | Number of *Phallales* DNA sequences uploaded in DNA databases (GenBank and UNITE) along the years.

Sequences of 22 recognized genera were retrieved: *Abrachium* Baseia and T.S. Cabral, *Aseroë* Labill., *Blumenavia* Möller, *Clathrus* P. Micheli ex L., *Claustula*, *Colus* Cavalier and Séchier, *Gastrosporium*, *Gelopellis* Zeller, *Ileodictyon* Tul. and C. Tul., *Itajahya* Möller, *Kjeldsenia*, *Laternea* Turpin, *Lysurus* Fr., *Mutinus* Fr. (=*Jansia* Penz.), *Phallobata*, *Phallus* Junius ex L. (=*Dictyophora* Desv.), *Phlebogaster*, *Protubera* Möller, *Pseudocolus* Lloyd, *Restingomyces* (as *Phallales* sp.), *Trappea*, and *Xylophallus* (Schltdl.) E. Fisch. (**Table 3**). Sequences named *Gymnotelium* Syd. were retrieved as *Phallales*, but they are excluded from the present study because of their doubtful quality and because it is a genus classified in *Pucciniaceae* Chevall., *Pucciniales* Clem. and Shear (He et al., 2019). The genus *Calvarula* Zeller was not included in the combined analyses, because only one *TEF*1-α sequence is available and its placement at family level is questionable (see *Phylogenetic analyses*).

Phallus is the most highly represented genus, with 313 individuals and 471 sequences (**Table 3**). Forty-three unidentified *Phallales* individuals were not classified at genus level (see individuals with "NO" in genus columns in **Supplementary Table 1**); they are specified in **Table 3**. The possible classification of these individuals is discussed in *Phylogenetic analyses*.

Phylogenetic Analyses

The final aligned matrices for the analyses of each independent marker contain 481 sequences of ITS (1,210 positions), 306 nuc-LSU (1,245 positions), 77 mt-SSU (600 positions), 131 *ATP6* (743 positions), 90 *RPB2* (822 positions), and 53 *TEF*1-α (849 positions), and 139 of the combined matrix (4637 positions). The evolutionary models selected for the final dataset were as follows: ITS: TIM1 + I + G; nuc-LSU: TrN + I + G; mt-SSU: TPM3uf + G; *ATP6*: TVM + I + G; *RPB2* Intron: TIM3 + I + G, *RPB2* exon: TIM3 + I + G; *TEF*1-α intron 1: TrNef + G, *TEF*1-α exon 1: TrN + I + G, *TEF*1-α intron 2: TPM1 + G; *TEF*1-α exon 2: TPM1 + G, and *TEF*1-α intron 3: K80 + G.

The concatenated tree is shown in **Figure 4**, in which some names were changed according to the current name recognized by their phylogenetic positioning. The trees that resulted from the independent analyses of each marker are available in **Supplementary Figures 1–3**.

Phylogenetic Positioning of Unnamed and Doubtfully Named Sequences

Two ITS sequences of environmental samples retrieved from GenBank (EF218792 and MF487330) did not match any phalloid sequence in BLAST, and thus, they were eliminated from our data and not included in **Supplementary Tables 1**, **3**. Thirteen ITS sequences (MK518965, UDB015101 (JQ657782), MT644888, UDB018620, UDB0673787, UDB0317538, UDB0321542, UDB0215586, UDB0196057, UDB089976, MT512648, UDB0180761, and MH930315) and five nuc-LSU (MK518662, MH532563, MH532564, MH532565, and MH532566) were excluded from the dataset because they had many ambiguous bases and long gaps, possibly the result of poorly edited sequences. These sequences were also checked on NCBI BLAST, and they do not correspond to any species of *Phallales*. Six sequences were divided into ITS and nuc-LSU and incorporated

TABLE 3 | Total of individuals and number of sequences of each molecular marker for each taxon retrieved from GenBank and UNITE databases from phalloid fungi searches.

Genus or name in sequence	N° unrepeated individuals	N° sequences	ITS	nuc-LSU	nuc-SSU	mt-SSU	*ATP6*	*RPB2*	*TEF1-α*
Abrachium	1	4	0	2	0	0	1	1	0
Aseroë	9	17	3	6	2	1	1	3	1
Blumenavia	17	51	11	12	0	1	8	10	9
Calvarula ?	1	1	0	0	0	0	0	0	1
Clathrus	42	83	24	34	0	6	9	8	2
Claustula	2	5	0	0	0	1	0	2	2
Colus	1	1	0	1	0	0	0	0	0
"Dictyophora"	43	52	41	3	0	2	2	2	2
Gastrosporium	6	14	7	7	0	0	0	0	0
Gelopellis	5	16	0	4	0	2	4	3	3
Gymnotelium ?	1	3	1	1	1	0	0	0	0
Ileodictyon	8	25	1	8	0	4	5	4	3
Itajahya	10	13	9	2	0	0	2	0	0
"Jansia"	14	17	14	1	0	0	1	1	0
Kjeldsenia	1	3	0	1	0	0	0	1	1
Laternea	1	5	0	1	0	1	1	1	1
Lysurus	38	98	17	31	0	12	20	16	2
Mutinus	59	89	37	31	1	9	7	4	0
Phallobata	1	4	0	1	0	0	1	1	1
Phallus	313	471	274	115	4	27	40	6	5
Phlebogaster	1	2	1	1	0	0	0	0	1
Protubera	28	88	6	22	0	6	21	20	13
Pseudocolus	8	15	5	7	1	2	0	0	0
Trappea	5	15	2	4	0	1	3	3	2
Xylophallus	3	4	0	3	0	0	0	1	0
Basidiomycota sp.	3	3	3	0	0	0	0	0	0
Clathraceae sp.	2	4	2	0	2	0	0	0	2
Hysterangiales sp.	1	1	1	0	0	0	0	0	0
Phallaceae sp.	3	3	1	2	0	0	0	0	0
Phallales sp.	2	3	2	1	0	0	0	0	0
Phallales sp. (*Restingomyces*)	2	5	1	2	0	0	2	0	0
uncultured *Agaricomycetes*	1	1	1	0	0	0	0	0	0
uncultured fungus	25	25	25	0	0	0	0	0	0
uncultured *Phallaceae*	3	2	3	0	0	0	0	0	0
uncultured *Pleosporales*	1	1	1	5	2	0	2	0	0
Total	**664**	**1109**	**492**	**303**	**11**	**75**	**129**	**88**	**55**

Genus names followed by a question mark represent doubtful identification, and between quotes represent synonyms.

in both ITS and nuc-LSU alignments (see individuals with "YES" in the column "nuc-LSU sequence incorporated in phylogenetic analyses. . ." in **Supplementary Table 1**).

Among the sequences that need revision because of possible misidentification or doubtful positioning are those of the monospecific genus *Calvarula*, as *Calvarula excavata* Zeller (*TEF*1-α, DQ219293), which is positioned in *Lysuraceae* (**Supplementary Figure 1A**), although its classification was in *Protophallaceae* (Zeller, 1939). Sequences named *Protubera* sp. (T20068), *Protubera hautuensis* Castellano and Beever (OSC59673), *Protubera nothofagi* Castellano and Beever (OSC59699), *Trappea phillipsii* (Harkn.) Castellano (OSC56042), and *Trappea pinyonensis* States (AHF530) are grouped outside the *Phallales* core, in the outgroup of *Hysterangiales*. Thus, these sequences, as well as *Hysterangium* sequences, were used to root the trees as representative of *Hysterangiales*, and their identification must be further investigated. Sequences named *Protubera* sp. (vouchers FLAS-F60616 and FLAS-F 61859), *Protubera canescens* G.W. Beaton and Malajczuk, and *Protubera clathroidea* Dring also need to be investigated because they clustered in *Clathraceae* or *Lysuraceae* (**Supplementary Figures 1–3**), despite the classification of the genus in *Protophallaceae* (Hosaka et al., 2006; Trierveiler-Pereira et al., 2014a,b). Finally, some sequences of *Gelopellis* need further studies because they clustered out of the expected *Claustulaceae* (Hosaka et al., 2006; Trierveiler-Pereira et al., 2014a); *Gelopellis purpurascens* G.W. Beaton and Malajczuk (voucher H292) is grouped in *Phallaceae*

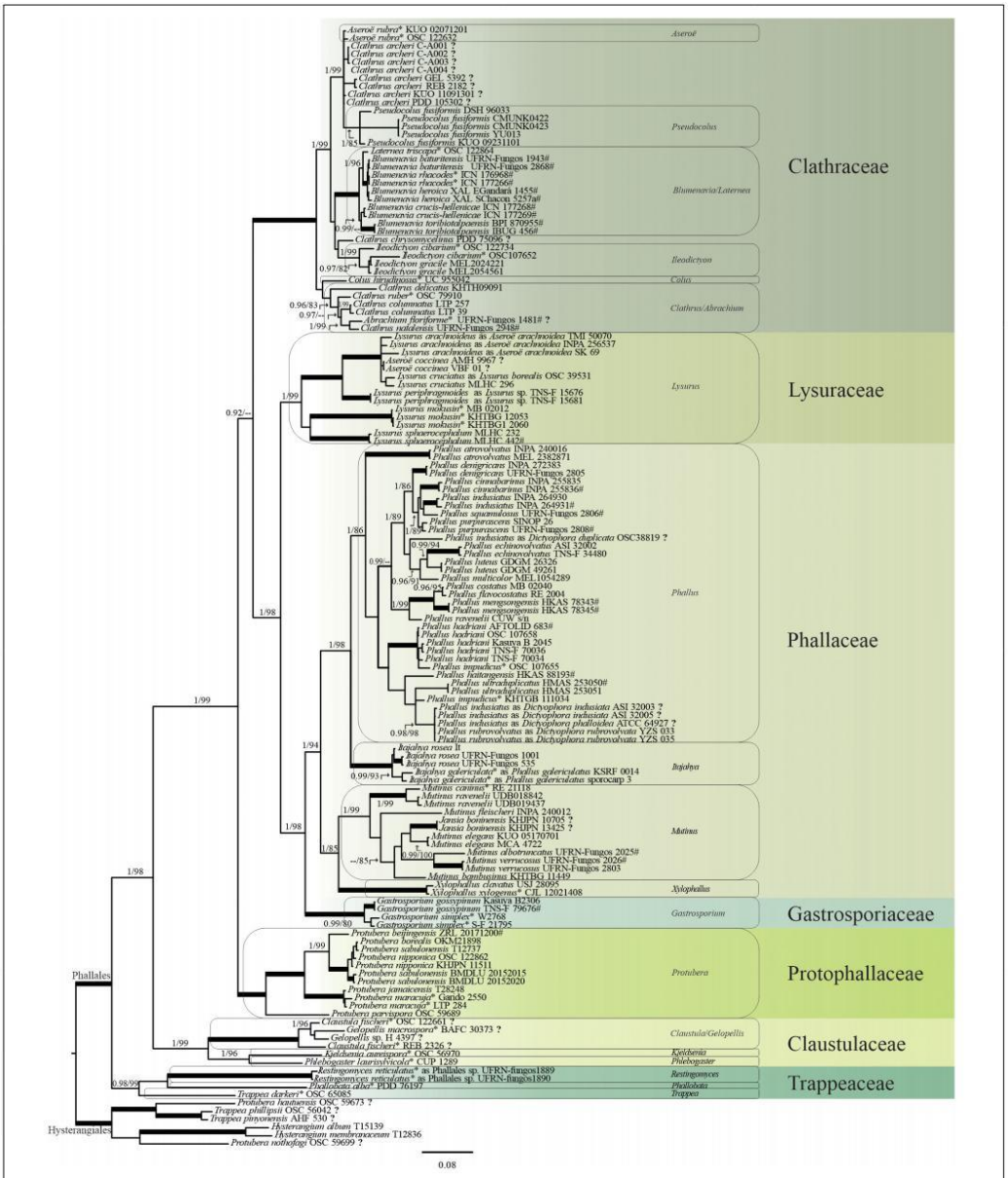

FIGURE 4 | Phylogenetic tree of the *Phallales* based on a combined dataset (ITS/nuc-LSU/mt-SSU/*ATP6*/*RPB2*/TEF1-α). Family clades are colored in green shades and named on the right. Names of recognized genera are highlighted in the boxes. (*) Type species. (?) Sequences that need review of their identity or generic status. (#) Type specimens. Tree topology is based on the Bayesian analyses. Numbers on branches are posterior probabilities (PP, before slash) and maximum likelihood bootstrap values (MLbs, after slash). Thickened branches in boldface indicate fully supported nodes (PP = 1, MLbs = 100). Scale bar indicates expected changes per site.

(**Supplementary Figure 3B**); *Gelopellis* sp. (voucher MEL 2063389) is in *Clathraceae* (**Supplementary Figures 2B**, **3A**) or external to *Phallaceae* (**Supplementary Figure 3B**).

For the total of 43 unidentified individuals not classified at genus level (**Table 3**), 39 were placed in five distinct families, two did not group with any family in *Phallales* (**Figure 5** and **Supplementary Table 6**), and the last two (*Hysterangiales* sp. UDB015101, and *Phallales* sp. UDB018620), as mentioned previously, were excluded from analyses. A total of 13 individuals were assigned to a specific genus: *Ileodictyon*, *Gastrosporium*, *Mutinus*, and *Phallus* (**Supplementary Table 6**). Fifteen individuals were identified to species level: *Blumenavia crucis-hellenicae* G. Coelho, Sulzbacher, Grebenc and Cortez, *Phallus impudicus* L., *Phallus hadriani* Vent., *Restingomyces reticulatus* Sulzbacher, B.T. Goto and Baseia (**Supplementary Table 6**). The identification of the sequences of *R. reticulatus* was possible by consulting the original article that proposed the new taxon (Sulzbacher et al., 2016). **Supplementary Figures 1A**, **2A,B**, **3B** show the phylogenetic positioning and the possible identification of some of the 41 unidentified individuals retrieved according to *TEF*1-α, ITS, nuc-LSU, and *ATP*6, respectively.

Recognition of Families and Genera

Based on the phylogenetic inferences using the concatenated data matrix (ITS + nuc-LSU + mt-SSU + *ATP*6 + *RPB*2 + *TEF*1-α), our results show *Phallales* as a strongly supported monophyletic order (PP = 1, MLbs = 100) and composed of seven families (**Figure 4**). We recognized 22 genera in *Phallales*, with *Dictyophora* and *Jansia* confirmed as synonyms of *Phallus* and *Mutinus*, respectively, although the recognition of some genera and the placement of their representatives deserve attention: *Abrachium*, *Aseroë*, *Blumenavia*, *Clathrus*, *Claustula*, *Gelopellis*, *Laternea*, *Protubera*, *Pseudocolus*, and *Trappea*.

The composition of each family based on our analyses is presented below.

Clathraceae

This family grouped the genera *Abrachium*, *Aseroë*, *Blumenavia*, *Clathrus*, *Ileodictyon*, *Laternea*, and *Pseudocolus* (**Figure 4**). In the combined analyses, *Aseroë* in the *Clathraceae* clade is represented by the type species *Aseroë rubra* Labill. but is not recognized as monophyletic and forms a paraphyletic group with other sequences named *Clathrus archeri* (Berk.) Dring. These sequences warrant further examination. *Pseudocolus*, represented by *P. fusiformis*, is within the well-supported clade formed by *A. rubra* and *C. archeri*.

Laternea, based on the type species *Laternea triscapa* Turpin, forms a monophyletic clade together with sequences of *Blumenavia*, which includes the epitype specimen *Blumenavia rhacodes* Möller (voucher ICN 177266).

Ileodictyon is recognized as monophyletic (PP = 1, MLbs = 99), including seven sequences of two individuals of the type species *Ileodictyon cibarium* Tul. and C. Tul and another eight sequences of two individuals of *I. gracile* Berk. The specific identity of OSC107652, named as *I. cibarium*, must be investigated because it is positioned closer to sequences identified as *I. gracile*. Although with no support, *Clathrus chrysomycelinus* Möller is external to *Ileodictyon*, and the identity or generic status of the individual PDD75096 must be investigated.

Colus is represented by one nuc-LSU sequence of the type species *C. hirudinosus* Cavalier and Séchier, and it is closer to *Clathrus*, although this relationship is not supported.

Clathrus is recovered as polyphyletic with representatives clustered in at least three clades (**Figure 4**). Its core is represented by the type species *Clathrus ruber* P. Micheli ex Pers. plus *Clathrus delicatus* Berk. and Broome, *Clathrus columnatus* Bosc, *Clathrus natalensis* G.S. Medeiros, Melanda, T.S. Cabral, B.D.B Silva and Baseia, and *Abrachium floriforme* (Baseia and Calonge) Baseia and T.S. Cabral. *Abrachium* is represented here by only one collection (holotype of the type species). Sequences of *C. archeri* and *C. chrysomycelinus* are related to species of *Aseroë* and *Ileodictyon*, respectively; as mentioned previously, these should be further investigated for a possible reannotation or recombination.

Lysuraceae

In the family *Lysuraceae*, sequences named under *Lysurus* and *Aseroë* are included, although the latter has been formally classified in *Clathraceae*. Sequences are distributed in four well-supported clades (**Figure 4**). The most well-sampled clade includes sequences of *Lysurus arachnoideus* (E. Fischer) Trierv.-Per. and Hosaka (=*Aseroë aracnoidea* E. Fisch.), *Aseroë coccinea* Imazeki and Yoshimi, and *Lysurus borealis* (Burt) Henn. (=*Lysurus cruciatus* Henn.). Our results confirm the synonymizing of *A. aracnoidea* in *Lysurus* (Trierveiler-Pereira et al., 2014a), and based on the individuals retrieved, *L. borealis* is the confirmed synonym of *L. cruciatus* (Dring, 1980). The other three clades represent the following three taxa: *Lysurus periphragmoides* (Klotzsch) Dring from Japan (Caffot et al., 2018), the type species *Lysurus mokusin* (L.) Fr., and *Lysurus sphaerocephalum* (Schltdl.) Hern. Caff., Urcelay, Hosaka and L.S. Domínguez., with the latter considered an invalid name (Index Fungorum, 2020; MycoBank., 2020) according to Art. F.5.1 (Shenzhen), due to the absence of an identifier-issued citation in a recognized repository.

Phallaceae

This family is composed of *Itajahya*, *Phallus* (=*Dictyophora*), *Mutinus* (=*Jansia*), and *Xylophallus* (**Figure 4**). The type species *P. impudicus* is represented by two individuals that are positioned in two different clades, although the collection OSC107655 is closer to other sequences of *P. hadriani* Vent. and most likely is misidentified as *P. impudicus*. Anyway, the identity and positioning of *P. impudicus* deserve further investigations. Sequences of *Phallus indusiatus* Vent. closer to *Phallus rubrovolvatus* (M. Zang, D.G. Ji and X.X. Liu) Kreisel also most likely represent misidentification.

Itajahya, recognized as monophyletic and sister to *Phallus*, is represented by sequences of *Itajahya rosea* (Delile) E. Fisch. and *Itajahya galericulata* Möller. Sister to *Itajahya* and *Phallus* is the clade formed by *Mutinus* and *Xylophallus*. *Mutinus* is represented by eight species, including the type species *Mutinus caninus* (Huds.) Fr. and *Jansia boninensis* Lloyd. *Xylophallus* is represented by

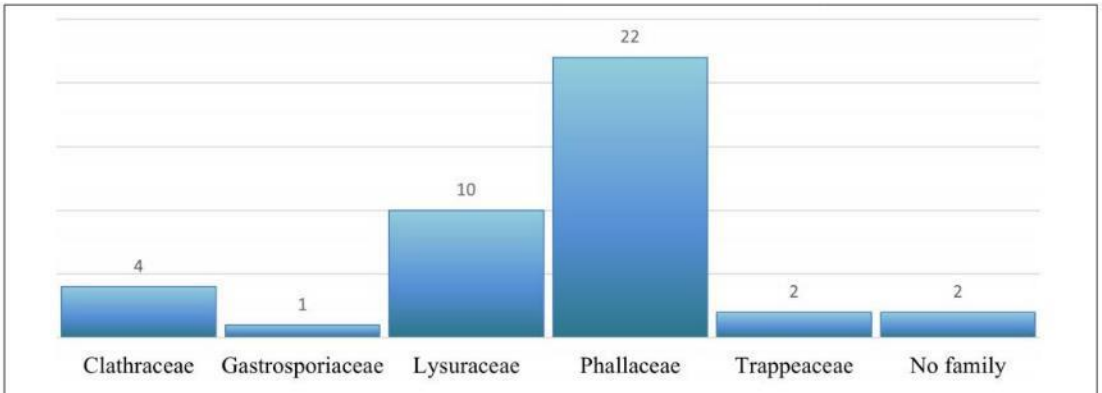

FIGURE 5 | Number of undetermined *Phallales* individuals and their putative family level classification according to the phylogenetic position of the sequences recovered.

Xylophallus clavatus T.S. Cabral, M.P. Martín, C.R. Clement, K. Hosaka and Baseia and the type species *Xylophallus xylogenus* (Mont.) E. Fisch.

Gastrosporiaceae

Gastrosporiaceae is delimited in our analysis with high support (PP = 0.98, MLbs = 80) and sharing a common ancestor with *Phallaceae*, with both families (*Gastrosporiaceae* and *Phallaceae*) as sister of *Lysuraceae* (**Figure 4**). This monogeneric family is here represented by sequences of *Gastrosporium gossypinum* T. Kasuya, S. Hanawa and K. Hosaka, and the type species *Gastrosporium simplex* Mattir.

Protophallaceae

Protophallaceae is represented by the genus *Protubera* with the type species *Protubera maracuja* Möller plus *Protubera beijingensis* G.J. Li and R.L. Zhao, *Protubera borealis* S. Imai, *Protubera jamaicensis* (Murrill) Zeller, *Protubera nipponica* Kobayasi, *Protubera sabulonensis* Malloch, and *Protubera parvispora* Castellano and Beever (**Figure 4**). *Protubera parvispora* (OSC59689) was not placed in the *Protophallaceae* clade in the *ATP6* tree (**Supplementary Figure 3B**), but it was in *Protophallaceae* in the other analyses (combined, nuc-LSU, *RPB2*, and *TEF1*-α).

Claustulaceae

In the *Claustulaceae*, clustered sequences were named *Claustula*, *Gelopellis*, *Kjeldsenia*, and *Phlebogaster* (**Figure 4**). *Claustula* and *Gelopellis* formed a monophyletic clade represented by four individuals including their type species: *Claustula fischeri* K.M. Curtis (type country New Zealand) and *Gelopellis macrospora* Zeller (type country Chile). *Gelopellis macrospora* is represented by a sample from Argentina, whereas *C. fischeri* is represented by two individuals from New Zealand, but these did not cluster together in our analyses, which puts into doubt the identification of one or more of these individuals as *C. fischeri*. The other clade in *Claustulaceae* is formed by *Kjeldsenia* and *Phlebogaster* represented by their type species: *Kjeldsenia aureispora* W. Colgan, Castellano and Bougher and *Phlebogaster laurisylvicola* Fogel, respectively. We retrieved two sequences (nuc-LSU and *TEF1*-α) of one individual of *P. laurisylvicola* (CUP 1289), which appears close to *Hysterangium* species in the nuc-LSU analyses (**Supplementary Figure 2B**) but is in *Claustulaceae* in the *TEF1*-α (**Supplementary Figure 1A**) and the concatenated analyses (**Figure 4**), which support our classification of *Phlebogaster* in *Claustulaceae* (*Phallales*).

Trappeaceae

This family is represented as monophyletic (PP = 0.98, MLbs = 99) in the combined analyses by *Restingomyces*, *Phallobata*, and *Trappea* with their respective type species *R. reticulatus*, *Phallobata alba* G. Cunn., and *Trappea darkeri* (Zeller) Castellano, respectively (**Figure 4**). However, the sequences of these genera were not recovered as a single-family clade in some of the unique marker analyses: in *TEF1*-α (**Supplementary Figure 1A**) and *RPB2* (**Supplementary Figure 3A**), *P. alba* and *T. darkeri* are recovered separately; in ITS (**Supplementary Figure 2A**), *R. reticulatus* and *T. darkeri* do not form a clade (although the individuals of *T. darkeri* in the ITS analyses are not the same as all the other analyses); in nuc-LSU (**Supplementary Figure 2B**) *T. darkeri* is external (PP = 0.96) to all *Phallales*, whereas *R. reticulatus* and *P. alba* clustered together but with no support.

Species Hypotheses Recognition

The clustering of the 479 sequences of ITS revealed 118 species hypotheses in *Phallales*, based on a sequence similarity threshold of 98.0%. In MycoBank. (2020), 576 legitimate specific names have already been deposited in *Phallales*. Our clustering shows that almost 20% of the total recognized species of *Phallales* have DNA sequences available, revealing that a lot of work remains to be done in this area.

Notes on Geographic Distribution, Lifestyle, and Edibility

Information on the country of origin included in DNA databases is available for 462 individuals (69.8%), from which 191 contain detailed information of the location but only 36 with the exact geographic coordinates. These individuals were distributed in 46 countries, which are concentrated in tropical and subtropical areas, with lower occurrence closer to the polar circles. Estonia is the source of the highest number of sequences (131) and individuals (131) deposited, all ITS. The United States is the second most sampled country, with 121 sequences of 79 individuals, and China is the third, with 108 sequences of 72 individuals. A map of global distribution of all phalloid individuals segregated by genera can be observed in **Figure 6**. For all 22 recognized genera, only *Phallobata* is not represented on the map, because there is no location information for the voucher. Individuals named under *Jansia* are represented as *Mutinus*, and those under *Dictyophora* as *Phallus* (**Supplementary Table 4**).

A total of 168 individuals (25.3%) are from environmental samples, including 148 individuals from soil, eight from roots of *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama), two from air filters, three from seedling stem [two from *Hevea nitida* Mart. ex Müll. Arg and one from *Micrandra spruceana* (Baill.) R. E. Schult.], one from heavy metal–contaminated soil, one from marine subsurface sediments, and one from house dust. According to the FungalTraits database (Põlme et al., 2021), a total of 21 phalloid genera recognized in our work are soil saprotrophic, and only *Phlebogaster* is mentioned as ectomycorrhizal.

Among the *Phallales* sequences sampled in our work and their respective published references, only *Phallus dongsun* T.H. Li, T. Li, Chun Y. Deng, W.Q. Deng and Zhu L. Yang is reported by Li et al. (2020) as an edible species commercially cultivated in China. To complement the list of edible species of *Phallales* with molecular data available, according to edibility categories proposed Li et al. (2021), our study includes 11 confirmed edible species (E1): *Ileodictyon cibarium*, *Phallus echinovolvatus* (M. Zang, D.R. Zheng and Z.X. Hu) Kreisel, *Phallus fuscoechinovolvatus* T.H. Li, B. Song and T. Li, *P. hadriani*, *P. indusiatus*, *Phallus luteus* (Liou and L. Hwang) T. Kasuya, *Phallus merulinus* (Berk.) Cooke (as *Dictyophora merulina* Berk.), *P. rubrovolvatus*, *Phallus ultraduplicatus* X.D. Yu, W. Lv, S.X. Lv, Xu H. Chen and Qin Wang, *Protubera nipponica* [as *Kobayasia nipponica* (Kobayasi) S. Imai and A. Kawam.], and *Pseudocolus fusiformis*; three confirmed edible species, but with conditions (E2): *Clathrus archeri*, *Phallus impudicus*, and *Phallus multicolor* (Berk. and Broome) Cooke (as *Dictyophora multicolor* Berk. and Broome); six unconfirmed edible species (E3): *Clathrus columnatus*, *Ileodictyon gracile*, *Jansia boninensis*, *Lysurus mokusin*, *L. periphragmoides*, *Phallus rugulosus* (E. Fisch.) Lloyd; and three poisonous species (P): *Lysurus arachnoideus*, *Mutinus bambusinus* (Zoll.) E. Fisch., and *M. caninus*.

Molecular data are available for 81.5% of the *Phallales* species mentioned by Li et al. (2021) as having a known edibility status. Only *Mutinus borneensis* Ces., *Phallus armeniacus* Pat., *Phallus fragrans* M. Zang, and *Phallus tenuis* (E. Fisch.) Kuntze lack public sequence data. *Mutinus borneensis* and *P. armeniacus* are categorized by the authors as E3 (unconfirmed edible species), *P. fragrans* as E1 (confirmed edible species), and *P. tenuis* as P (poisonous species).

DISCUSSION

Phallales Molecular Data From the Past 24 Years

The year 2006 can be marked as a huge advance in *Phallales* taxonomy with the work of Hosaka et al. (2006), a study aided by the Deep Hypha initiative (Blackwell et al., 2006). Hosaka et al. (2006) were responsible for 68 phalloid sequences deposited in GenBank (**Figure 3**), as well as the introduction of new markers (*ATP*6, *RPB*2, and *TEF*1-α). Another important turning point observed in **Figure 3** is the increased use of molecular data in many works focused on *Phallales* diversity since 2013: nuc-LSU sequences – Degreef et al. (2013); ITS sequences – Moreno et al. (2013), Lu et al. (2014), Cabral et al. (2015), Kim et al. (2015), Elwess and Latourelle (2016), Patel et al. (2018), and Bobade and Dahanukar (2020); nuc-LSU and *ATP*6 sequences – Marincowitz et al. (2015); ITS and nuc-LSU sequences – Pietras et al. (2016); ITS, nuc-LSU, *RPB*1 and *ATP*6 sequences – Garnica et al. (2016). Trierveiler-Pereira et al. (2014a) also merit a spotlight because of their phylogenetic review of *Phallales* using nuc-LSU, *ATP*6, and *RPB*2 markers and by generating 53 sequences.

Recognition of Families and Genera

Clathraceae

Clathraceae is characterized by fungi with clathrate (branched) or pseudostipitate and clathrate basidiomata that are named cage or lattice stinkhorns (Pegler and Gomez, 1994; Melanda et al., 2020). Individuals with clathrate format belong to *Blumenavia*, *Clathrus*, *Ileodictyon*, and *Laternea*, whereas those with prominent pseudostipe and a clathrate part composed of arms, armless, or lattice belong to *Abrachium*, *Aseroë*, *Colus*, and *Pseudocolus*. Cabral et al. (2012) accepted in *Clathraceae* the genera *Abrachium*, *Aseroë*, *Blumenavia*, *Clathrus*, *Pseudocolus*, *Lysurus*, and *Ileodictyon*. Our phylogenetic analyses, in agreement with Hosaka et al. (2006) and Trierveiler-Pereira et al. (2014a), show *Lysurus* as part of *Lysuraceae*. Based on morphological taxonomy using as the main diagnostic feature the disposition of the gleba in the receptacle, Pegler and Gomez (1994) classified the following genera in the *Clathraceae* series Lysuroid: *Aseroë*, *Colus*, *Lysurus*, *Kalchbrennera* Berk., *Neolysurus* O.K. Mill., *Pseudocolus*, and *Simblum* Klotzsch ex Hook. According to Pegler and Gomez (1994), these genera share the receptacle composed of a tubular and sterile pseudostipe, with the gleba attached to the upper portion of the receptacle. For Dring (1980), *Kalchbrennera* and *Simblum* were considered synonyms of *Lysurus*. However, our phylogeny (**Figure 4**) does not confirm this morphological approach as a natural character, with representatives of *Clathraceae* series Lysuroid sensu Pegler and Gomez (1994) in both *Clathraceae* (*Aseroë* and *Colus*) and *Lysuraceae* (*Lysurus*).

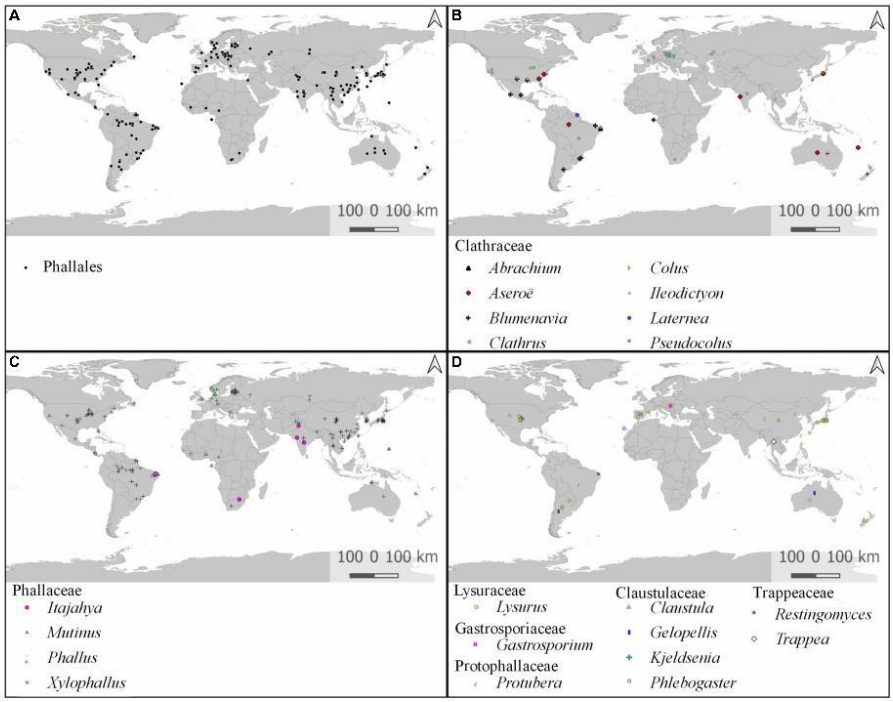

FIGURE 6 | Global geographic distribution of *Phallales* based on samples with molecular sequences available and locality information. **(A)** Global distribution of all *Phallales* samples. Global distribution of **(B)** *Clathraceae* genera; **(C)** *Phallaceae* genera; **(D)** *Lysuraceae*, *Gastrosporiaceae*, *Protophallaceae*, *Claustulaceae*, and *Trappeaceae* genera.

The relationship of the type species of *Aseroë*, *A. rubra* from Australia (type country), and *C. archeri* (**Figure 4**) has been previously shown by Hosaka et al. (2006), Degreef et al. (2013), and Trierveiler-Pereira et al. (2014a). The name *C. archeri* is a result of the combination of *Lysurus archeri* Berk. (Dring, 1980), which also has *Anthurus archeri* (Berk.) E. Fisch. as a synonym. The morphological research into *Clathraceae* performed by Dring (1980) considered *Anthurus* as a synonym of *Clathrus*. No other sequences of any other name previously treated as *Anthurus* are available. Considering that the type species of *Clathrus* is found in another clade, another generic name must be investigated for *C. archeri*, with *Anthurus* and *Aseroë* being two putative names, considering this taxonomic history and the relationship shown in our analyses.

The positions of *Laternea* and *Blumenavia* indicate that they may belong to the same genus, in which *Laternea* would have nomenclatural priority. *Blumenavia* and *Laternea* are also grouped in a monophyletic clade, as previously observed by Degreef et al. (2013) and Trierveiler-Pereira et al. (2014a), although both of these works performed their phylogenetic analyses with only one individual of each genus. Melanda et al. (2020) reviewed *Blumenavia* but did not present any *Laternea* species in the phylogeny. Considering that the molecular global sampling of *Laternea* is represented by only one representative, new molecular studies involving *Laternea* are encouraged, so as to better understand the relationship between *Laternea* and *Blumenavia*.

The genus *Colus* was considered as a member of the family *Clathraceae*, based on a morphological approach by Cunningham (1944), Dring (1980), and Pegler and Gomez (1994); here, we confirm this classification and also encourage the generation of more sequences of this genus.

Clathrus was shown to be polyphyletic by Hosaka et al. (2006) and Trierveiler-Pereira et al. (2014a). The relationship between *Abrachium* and *Clathrus* was observed by Trierveiler-Pereira et al. (2014a), who showed *A. floriforme* in an unsupported clade with *C. ruber* (type species) and *C. columnatus*. *Abrachium* is a monospecific genus proposed by Cabral et al. (2012), with the type species *A. floriforme* being a combination from *Aseroë floriformis* Baseia and Calonge. Cabral et al. (2012) emended the family *Clathraceae* to include the armless sunflower-shaped receptacle characteristic of *Abrachium*. Based

on the high morphological variation between *Abrachium* and *Clathrus*, we have to wait for more sequences of abrachinoid individuals to infer any synonymy among the two genera, with *Clathrus* having nomenclatural priority. *Abrachium* appears to be widely distributed in the Atlantic Forest and Caatinga Biomes[5], and additional studies may show unknown diversity.

Linderia G. Cunn, *Linderiella* G. Cunn., *Ligiella* J.A. Sáenz, and other possible representatives of *Clathraceae* do not have any sequences available and need to be included in further molecular phylogenetic studies. MycoBank. (2020) and Index Fungorum (2020) consider *Linderiella* and *Linderia* as synonyms of *Clathrus*, whereas He et al. (2019) consider only *Linderiella* as a synonym of *Clathrus*, but the inclusion of sequences of these genera in phylogenetic studies can confirm their relationships.

Lysuraceae

The positioning of the type species of *Lysurus* (*L. mokusin*, type country: China) from the United States and Japan has been previously shown by Trierveiler-Pereira et al. (2014a). *Simblum*, *Kalchbrennera*, and *Neolysurus*, other possible representatives of *Lysuraceae*, do not have any sequences available and need to be included in further studies. *Simblum* and *Kalchbrennera* are considered synonyms of *Lysurus* by Dring (1980), He et al. (2019), and in Index Fungorum (2020), whereas MycoBank. (2020) considers only *Kalchbrennera* to be a synonym of *Lysurus*, but the inclusion of sequences of these genera in phylogenetic studies can clarify their relationships. *Lysurus periphragmoides* and *L. sphaerocephalum* (nom. inval.) are names that have been previously placed in *Simblum*, and the phylogenetic placement of sequences under these names in our analyses could confirm the synonymizing between *Lysurus* and *Simblum*. *Simblum periphragmoides* Klotzsch and *S. sphaerocephalum* Schltdl. were considered as heterotypic synonyms by Dring (1980), who proposed the combination *L. periphragmoides*, but this synonymizing was not accepted by Caffot et al. (2018), and based on our analyses (**Figure 4**) it is also not confirmed. Considering the positioning of sequences named *A. coccinea* in the *Lysuraceae*, we encourage further studies to investigate the generic status of this taxon and the identity of the individuals under this name.

Phallaceae

Li et al. (2014, 2016) provided phylogenetic data to show that *Dictyophora* and *Phallus* should be treated as a single genus, *Phallus*. Cabral et al. (2019) described a high diversity in *Phallus indusiatus*, a species complex well-known for the presence of an indusium; however, *P. indusiatus* actually represents at least four phylogenetic species. Li et al. (2020) published the new species *P. dongsun*, which is not included in our concatenated tree, and mentioned that samples named *P. impudicus* from China represent *P. dongsun*, as *P. impudicus* is a species described from Europe (the type locality of *P. impudicus*). As previously mentioned, the identity of the sequences named *P. impudicus* recovered in our analyses needs further examination in order to obtain a robust view of the phylogenetic position of the species.

Kreisel (1996) accepted the genus *Itajahya* as *Phallus* subgenus *Itajahya*. In the same work, the type species of *Itajahya*, *I. galericulata*, originally described from South Brazil (Möller, 1895), was combined in *Phallus galericulatus* (Möller) Kreisel (Kreisel, 1996). However, based on our analyses (**Figure 4**), *I. galericulata* is clustered in a clade separate from *Phallus* and together with other *Itajahya* species, which does not justify the classification and the synonymizing proposed by Kreisel (1996). For *Mutinus* and *Jansia*, however, they are considered synonymous as previously pointed out by Crous et al. (2017). The positioning of *Xylophallus* as sister to *Mutinus* has been previously shown by Trierveiler-Pereira et al. (2014a) and Crous et al. (2018).

There are no molecular data for *Aporophallus* Möller, *Floccomutinus* Henn., and *Staheliomyces* E. Fisch., all genera also accepted in *Phallaceae* (Index Fungorum, 2020; MycoBank., 2020), although *Floccomutinus* is considered a synonym of *Mutinus* by He et al. (2019) and in MycoBank. (2020). *Aporophallus* and *Staheliomyces* are monospecific genera, and their revision will be highly relevant. Sequences of taxa dealt under *Floccomutinus* could be useful to better assess their relationships with *Mutinus*.

Gastrosporiaceae

The monogeneric family *Gastrosporiaceae* was confirmed as part of *Phallales* in our study and also by previous authors: Kirk et al. (2008), Trierveiler-Pereira et al. (2014a), He et al. (2019), Kasuya et al. (2020), and Wijayawardene et al. (2020). The genus *Gastrosporium* contains three described species: *G. simplex* (type species) from Italy, *G. asiaticum* Dörfelt and Bumžaa from Mongolia, and *G. gossypinum* from Japan (Honshu). The positioning of the family *Gastrosporiaceae* external to *Phallaceae* in our phylogeny (**Figure 4**) rejects the suggestion by Hosaka et al. (2006), who did not include *Gastrosporium* in their analyses and thus suggested that the ancestor of *Clathraceae*, *Phallaceae*, and *Lysuraceae* could be the point of transition from sequestrated to expanded basidiomata in *Phallales*.

Protophallaceae

Protophallaceae is represented in our analyses only by *Protubera* species, as also shown by Trierveiler-Pereira et al. (2014a,b). *Protophallaceae* was proposed by Zeller (1939) with species of *Calvarula*, *Protophallus* Murril, and *Protubera*. *Calvarula* is not included in our combined analyses (**Figure 4**), and the identity of the individual EF5-1 as *C. excavata* needs to be investigated. Additional individuals and sequences of *Calvarula* are needed to clarify its family level positioning. *Protophallus* is considered a synonym of *Protubera* (Malloch, 1989; He et al., 2019), and the positioning of *Protubera jamaicensis* (=*Protophallus jamaicensis* Murrill) in our analyses (**Figure 4**) confirms this synonymization.

Sanshi and Kawamura (1958) analyzed specimens of *Protubera* from Japan and proposed a new genus named *Kobayasia* S. Imai and A. Kawam. to accommodate *Protubera nipponica*. However, Hosaka et al. (2006) and Trierveiler-Pereira et al. (2014a,b) have shown sequences of

[5]https://www.gbif.org/occurrence/map?taxon_key=7812817

P. nipponica within the clade formed by other *Protubera*, as also shown in our analyses (**Figure 4**), which does not justify *Kobayasia* as a separate genus and confirms its synonymization under *Protubera*. *Kobayasia kunmingica* M. Zang, K. Tao and X.X. Liu is the only other species described in *Kobayasia*, and its phylogenetic positioning should be investigated to better understand the relationship between *Protubera* and *Kobayasia*.

The relationship of *Protubera borealis* (voucher OKM21898) and *P. sabulonensis* has been shown by Hosaka et al. (2006) and Cabral et al. (2012). Sanshi and Kawamura (1958) considered *Protubera borealis* under the genus *Protuberella* S. Imai and A. Kawam. as *Protuberella borealis* (S. Imai) S. Imai and A. Kawam. However, the recognition of *Protuberella* as a separate genus was not accepted by Hosaka et al. (2006), Cabral et al. (2012), and Li et al. (2018), and it is also not confirmed here (**Figure 4**), although it is still considered as a distinct genus by He et al. (2019) and in Index Fungorum (2020).

Besides the sequences of *Protubera* clustered in *Phallales*, some individuals (T20068, OSC59673, and OSC59699) named under *Protubera* (including *P. nothofagi* and *P. hautuensis*) clustered in *Hysterangiales* (our outgroup), in agreement with Hosaka et al. (2006) and Trierveiler-Pereira et al. (2014b), who classified *P. nothofagi* in *Gallaceae* and *P. hautuensis* in *Phallogastraceae*. However, based on the positioning of the type species *P. maracuja* in *Phallales*, this must be the best classification for *Protubera* and *Protophallaceae*. The positioning of the individuals named *Protubera canescens* and *P. clathroidea* in *Clathraceae* and *Lysuraceae*, respectively (**Supplementary Figures 1–3**), has been shown also by Hosaka et al. (2006), Degreef et al. (2013), and Trierveiler-Pereira et al. (2014b). According to May et al. (2010), *P. canescens* is an egg (immature) form of *Ileodictyon*, and for Trierveiler-Pereira et al. (2014b), these *Protubera* species out of *Protophallaceae* may be egg forms of expanded phalloid taxa or misidentification.

Claustulaceae

In this family clade, the four genera *Claustula*, *Gelopellis*, *Kjeldsenia*, and *Phlebogaster* clustered together as in Hosaka et al. (2006). In Trierveiler-Pereira et al. (2014a), the family clade was represented only by *Gelopellis* and *Claustula*. Although *Claustula* and *Gelopellis* clustered together, it would be important to have sequences of nondoubtful identification and more representatives of both genera to confirm whether they could be considered synonyms, of which *Claustula* has nomenclatural priority. Individuals of *Gelopellis* clustered out of *Claustulaceae*, in *Clathraceae* (**Supplementary Figures 2B, 3A**), or external to *Phallaceae* (**Supplementary Figure 3B**), and they also need revision to confirm their identity or generic status, mainly because immature basidiomata can lead to misidentification of some expanded phalloids, as seen in individuals of *Protubera*.

Trappeaceae

The composition of *Trappeaceae* in our study by the three genera *Restingomyces*, *Phallobata*, and *Trappea* is in agreement with Sulzbacher et al. (2016). *Trappea* is the type genus of the family as established by Castellano (1990), in a study that mentioned that the genus represents a transition between *Clathraceae* and *Hysterangium*, and proposed the type species of *Trappea* based on *Hysterangium darkeri* Zeller. The positioning of *Trappea* in *Phallales* as a member of *Trappeaceae* is based on an individual of *T. darkeri* without information on the location, as also previously shown by Hosaka et al. (2006) and Sulzbacher et al. (2016). As in *Protubera*, some species of *Trappea* are also placed in *Hysterangiales*, but considering the positioning of its type species in *Phallales*, we confirm the classification of *Trappea* in *Phallales*. The positioning of some *Trappea* in *Hysterangiales* has also been observed by Hosaka et al. (2006) and Trierveiler-Pereira et al. (2014b), and both authors showed *T. phillipsii* and *T. pinyonensis* positioned in the *Phallogastraceae* (*Hysterangiales*) family. The identity or the generic status of these individuals of *Trappea* in *Hysterangiales* needs further revision.

Distribution, Lifestyle, and Edibility

The DNA databases contain many sequences of *Phallales* representatives without precise information on the collection location or even without any metadata. In addition, the sequences have a low representation across continents, which makes it impossible to draw any robust inferences about the biogeographical distribution of families, genera, species, and clades. Thus, we encourage the inclusion of DNA sequences from representatives of *Phallales* from underexplored locations, such as Africa and maritime Southeast Asia, as well as the sequencing of collections already deposited in herbaria around the world and of taxa not yet sequenced. These further data will contribute to a better understanding of the evolutionary processes and distribution patterns in *Phallales*.

The explanation for the high number of sequences from Estonia is the increase of studies of ITS using environmental samples and the high number of these sequences deposited in UNITE (see **Supplementary Table 1**). Other locations with a large number of *Phallales* records and DNA sequences are partly due to the proximity of the research centers and specialists in the group.

Studies of environmental biodiversity or other ecological approaches including phalloid species started in 2003 (Bidartondo et al., 2003) and has continued in a few works (Sato et al., 2012; Kellner et al., 2014; Skaltsas et al., 2019; Vu et al., 2019).

In the FungalTraits database (Põlme et al., 2021), all their genera in *Phallales* are classified as saprotrophic. The genera *Phallobata*, *Phlebogaster*, *Restingomyces*, and *Trappea* are classified as part of *Hysterangiales*, but we recognize them in *Phallales*. *Phlebogaster* is considered an ectomycorrhizal genus in FungalTraits. Thus, considering *Phlebogaster* in *Phallales*, as supported by our analyses, the *Phallales* lifestyle must be expanded to include both saprotrophic and ectomycorrhizal genera. The ectomycorrhizal habit of *Phlebogaster* is most likely based on Fogel (1980), who described *P. laurisylvicola* as a hypogeous taxon under the plant species *Laurus azorica* (Seub.) Franco (*Lauraceae* Lindley). Kreisel (2001), in a checklist of gasteroid fungi, also mentioned *P. laurisylvicola* in association with *L. azorica*. However, we did not find any confirmation and description of these associations as an ectomycorrhizal symbiosis.

We regard this species as putatively ectomycorrhizal, but further investigation is needed.

Hosaka et al. (2006) cited *Protubera canescens* as the only *Phallales* ectomycorrhizal, but according to May et al. (2010), this species is an immature form of *Ileodictyon*, as mentioned previously. In addition, Trierveiler-Pereira et al. (2014b) affirmed that all *Protubera* species are saprotrophic as reported in FungalTraits (Põlme et al., 2021). Therefore, we suggest further investigation to clarify the ectomycorrhizal association in this phalloid species.

Wild edible fungi are an important renewable natural resource in some regions, constituting important sources of income and nutrition. Despite their unpleasant odor, many representatives of *Phallales* are edible but are considered mushrooms with little culinary value. Stinkhorns are the most popular edible *Phallales* (Boa, 1988). The stinkhorn *Phallus* is the genus with the largest number of species with edible status (14: nine E1, two E2, two E3, and one P), followed by *Lysurus* (three E3 and one P) and *Mutinus* (one E3 and two P) that include only poisonous and unconfirmed edible species (Li et al., 2021). *Phallus* was reported by Li et al. (2021) as a genus with 43 described species, whereas He et al. (2019) reported 34 known species. Based on these numbers, the percentage of confirmed edible species in the genus represents 20.9 to 26.5%; however, the number of known species is probably underestimated because MycoBank. (2020) lists approximately 125 legitimate specific names for the genus. For *Phallales*, considering the 576 legitimate specific names recognized in MycoBank. (2020), the number of confirmed edible species in the order represents only 2.1%, whereas the number of poisonous species represents only 0.7%. The proportion of the number of confirmed edible and poisonous species in *Phallales* in relation to the 118 SHs that we found is 10.2 and 3.4%, respectively. This confirms that the edibility of *Phallales* species is poorly explored.

Many stinkhorns are consumed in the egg stage because of their tasty flavor (Phillips et al., 2018). In Germany and North America, the egg stage of *Phallus* is sold canned or fresh (Læssøe and Spooner, 1994). In China, *L. mokusin* and *P. rubrovolvatus* (as *Dictyophora rubrovolvata* M. Zang, D.G. Ji and X.X. Liu) are considered edible (Læssøe and Spooner, 1994). In addition, *P. indusiatus* and *P. dongsun* stand out in China for their flavor, where they are commercially cultivated (Boa, 1988; Li et al., 2020) and represent an important economic product. Despite the nutritional and commercial importance, the consumption of wild stinkhorns is not recommended unless their taxonomic affiliation is known with certainty because some of them are poisonous, such as species of *Lysurus* and *Mutinus*. Additionally, some species of the same genus are confirmed edible, whereas others are controversial, such as *P. tenuis*, which is considered poisonous (Li et al., 2021).

CONCLUSION

This work presents a summary of studies using molecular tools in *Phallales*. In general, as in other groups of fungi, these tools clarify results of previous studies based on morphology; also, the use of combined markers has allowed a clearer delimitation and positioning of the families and genera. Although we recognized seven families and 22 genera in *Phallales*, an extra effort is needed in taxonomic studies of the genera *Abrachium*, *Aseroë*, *Blumenavia*, *Clathrus*, *Claustula*, *Gelopellis*, *Laternea*, *Protubera*, *Pseudocolus*, and *Trappea*, because some inconsistencies in species identification and positioning of their representatives should be clarified. It is also necessary to include sequences of the genera *Aporophallus* (*Phallaceae*), *Floccomutinus* (*Phallaceae*), *Kalchbrennera* (*Lysuraceae*), *Ligiella* (*Clathraceae*), *Linderia* (*Clathraceae*), *Linderiella* (*Clathraceae*), *Neolysurus* (*Lysuraceae*), and *Staheliomyces* (*Phallaceae*). The DNA databases are an excellent source of molecular data, both when searching for sequences and in helping to understand the evolution of traits shown in previous studies, but missing metadata can be a stalemate for that. Therefore, it is vital to fill in the records in DNA databases correctly and accurately.

Since the inclusion of molecular tools for systematics studies, considerable progress has been achieved in the taxonomic and evolutionary study of fungi. Sequences of different markers deposited in databases represent a valuable repository that is still poorly exploited. The data we utilized have been shown to be a good, no-cost tool to clarify taxonomic and systematics problems, test phylogenetic position of misidentified sequences, examine the geographic distribution of groups, explore the ecology and use of phalloid species, and to visualize where our knowledge gaps are. We therefore encourage all mycologists to conduct extensive reviews of molecular data available for their particular fungal taxa of expertise.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

GM and NM designed the project. ALe, GM, and NM extracted the data. GM organized the metadata. ALi, AS-F, ALe, GM, NA, and RF analyzed the data. ALi and GM performed quantitative analyses. AS-F performed BLAST and phylogenetic analyses. ALe performed species hypothesis recognition. GM, MM, AS-F, ALi, ALe, TC, NM, and RF wrote the draft. IB, MM, and NM supervised the project. All authors reviewed and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmicb.2021.689374/full#supplementary-material

Supplementary Figure 1 | Phylogenetic trees of the *Phallales* order obtained with *TEF*1-α **(A)** and mt-SSU **(B)**. Names in blue and question marks indicate individuals with uncertain position or that represent a misidentification. Individuals retrieved without a genus name are represented in red with the possible species name based on our analyses given first. Family clades are colored in green shades and named on the right. Tree topology is based on the Bayesian analyses. Numbers on branches are posterior probabilities (PP, before slash) and maximum likelihood bootstrap values (MLbs, after slash). Thickened branches in boldface indicate fully supported nodes (PP = 1, MLbs = 100). Scale bar indicates expected changes per site.

Supplementary Figure 2 | Phylogenetic trees of the *Phallales* order obtained with ITS **(A)** and nuc-LSU **(B)**. Names in blue and question marks indicate individuals with uncertain position or that represent a misidentification. Individuals retrieved without a genus name are represented in red with the possible species name based on our analyses given first. Family clades are colored in green shades and named on the right. Tree topology is based on the Bayesian analyses. Numbers on branches are posterior probabilities (PP, before slash) and maximum likelihood bootstrap values (MLbs, after slash). Thickened branches in boldface indicate fully supported nodes (PP = 1, MLbs = 100). Scale bar indicates expected changes per site.

Supplementary Figure 3 | Phylogenetic tree of the *Phallales* order obtained with *RPB2* **(A)** and *ATP6* **(B)**. Names in blue and question marks indicate individuals with uncertain position or that represent a misidentification. Individuals retrieved without a genus name are represented in red with the possible species name based on our analyses given first. Family clades are colored in green shades and named on the right. Tree topology is based on the Bayesian analyses. Numbers on branches are posterior probabilities (PP, before slash) and maximum likelihood bootstrap values (MLbs, after slash). Thickened branches in boldface indicate fully supported nodes (PP = 1, MLbs = 100). Scale bar indicates expected changes per site.

Supplementary Table 1 | General data compilation of all *Phallales* sequences recovered.

Supplementary Table 2 | GenBank accession numbers for the outgroup used in phylogenetic analyses for individual markers.

Supplementary Table 3 | Taxa, individuals, and accession numbers of sequences used in phylogenetic analyses from the combined dataset.

Supplementary Table 4 | Taxa, individuals, and their respective geographic location used for the global distribution map.

Supplementary Table 5 | Type collections and collections of reference (REF.) in *Phallales* with the respective GenBank accession numbers. When the status of the type is unknown, only "type" is indicated.

Supplementary Table 6 | Putative identification for the undetermined *Phallales* individuals recovered.

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APÊNDICE E – LOOSENING THE BELT: UNKNOWN DIVERSITY OF THE STRANGLED STINKHORN GENUS *Staheliomyces* (*PHALLALES*, *BASIDIOMYCOTA*)

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Abstract
Known to date only from the Neotropics, the genus Staheliomyces E. Fisch. (*Phallaceae*, *Phallales*) was described from Suriname with only a single species, *S. cinctus* E. Fisch. Nearly 100 years have passed since the original description, and its systematic position and species diversity have not been investigated. Collections from Brazil and Costa Rica were studied, and four new species are described based on morphology, molecular phylogenetic analyses, and nomenclatural review. We provide morphological descriptions together with a key to species, and a proposal to emend the genus. We review the type material of *S. cinctus* located in herbarium of Botanischer Garten der Universität Bern (BERN), and establish the phylogenetic position of the genus which clusters with *Xylophallus* (Schltdl.) E. Fisch. in an exclusively neotropical clade. Our results highlight the importance of studying neglected taxa that impacts knowledge of biodiversity especially for localities that have been poorly collected. The study of herbarium collections can reveal data on forgotten type materials and shed light on the work of pioneering mycologists. This study also brings insights into biogeographical diversity of the phalloid fungi.
Keywords Biodiversity . Gasteroid fungi . Molecular phylogeny . Morphology . Neotropics . 4 new taxa

Introduction

Staheliomyces E. Fisch. was first described in 1921, based on a specimen from Suriname (FISCHER, 1921). The genus is considered monotypic with the species type *S. cinctus* E. Fisch., also known as strangled stinkhorn. Although described from Suriname, Fischer mentioned a first record from Guiana, as a photograph cited as “jungle fungus” on page 74 of Beebe et al. (1917), though there is no taxonomic information associated with the picture. Fischer described the species based on a collection from Gerold Stahel, a botanist who worked for c. 30 years in Paramaribo, Suriname (Reyne 1955). He collected the specimen in 1918 near Coppename River and sent it to E. Fischer (Fischer 1921). *Staheliomyces cinctus* is

mainly characterized by the glebal region forming a constricted part of the basidioma above pseudostipe that forms a "belt", which is the reason for the epithet "*cinctus*". Fischer presented a very detailed description of the species, but there was little information on the type specimen such as the collection number and herbarium deposition. The lack of a type specimen prevents the development of further comparative taxonomic studies.

Apparently, *S. cinctus* distribution is restricted to the Neotropics, on ombrophilous forests, with formal records for Bolivia (Rocabado et al. 2007), Brazil, specifically in Brazilian Atlantic and Amazon forests (Baseia et al. 2006; Leite et al. 2007; Magnago et al. 2013; Cabral et al. 2014; Trierveiler-Pereira et al. 2019), Costa Rica (Saénz and Nassar 1982), Ecuador (Burr et al. 1996), French Guyana (Cheype 2010), Panama (Gube and Piepenbring 2009), South Mexico (Coates et al. 2017), and Suriname (Fischer 1921). In addition, there are 79 occurrences from the neotropics in GBIF (Global Biodiversity Information Facility) that expands the distribution also to Honduras and Colombia (GBIF 2021).

Besides its relatively simple morphology and geographical distribution, as compared to other phalloid fungi, little is known about the ecology of *Staheliomyces*. Facts like the interaction with other species and the usage by humans are yet to be studied. As for phalloids in general, it is well known that insects play major role in spore dispersal. Burr et al. (1996) were able to register this interaction for *S. cinctus* in a specific case of melittophily – dispersion of spores by bees – where they observed the visitation of social bees of the genus *Trigona* on *S. cinctus* basidiomata. In regard to the human usage of species, Trujillo (2009) reported several medicinal, mythological and ritualistic uses of *S. cinctus* by some indigenous and traditional communities. This species along with other phalloid fungi are also used for medicinal purposes by the Yanomami indigenous people in Brazil, who use it for treatment of leishmaniasis and malaria (Yanomami et al. 2014).

Since the original publication of *S. cinctus*, no other species have been described in the genus. According to Index Fungorum (www.indexfungorum.org) and Flora do Brasil (Cabral 2020), the genus belongs to the family *Phallaceae* (*Phallales*, *Phallomycetidae*) and this systematic position has not been questioned over the years. Several molecular phylogenies for the order *Phallales* have been published (Hosaka et al. 2006; Trierveiler-Pereira et al. 2014; Melanda et al. 2021), but none has included this species, so the phylogenetic position of Staheliomyces has not yet been confirmed by DNA analyses. Given the geographical distribution range of the species, it is predicted that some degree of morphological/molecular variation should exist among collections of *S. cinctus*. This type of variation can be seen in the neotropical genus *Xylophallus* (Schltdl.) E. Fisch. (Crous et al. 2018), which is evident when comparing its published descriptions. Collections of Staheliomyces have been reported as a single species because no detailed study of the genus has been made. In this study, we have investigated the genus nomenclatural history, morphological/molecular diversity, and phylogenetic placement

Materials and Methods

Morphological analyses and Nomenclature

Field trips were made to several areas of Brazilian Amazon rainforest to collect phalloid specimens, especially *Staheliomyces*, following methodologies of Vargas-Isla et al. (2014). Specimens from Brazilian Atlantic Rainforest deposited at the herbarium of Universidade Federal do Rio Grande do Norte (UFRN-Fungos) were also included for analyses, as well as specimens from a Tropical Wet Forest, Costa Rica (University of Costa Rica Herbarium, USJ). GBIF, which covers data from iNaturalist (https://www.inaturalist.org.), was consulted to access geographical occurrences of species identified as *Staheliomyces.* Photos from GBIF were downloaded to illustrate the morphological diversity within the genus from South and

Central American countries. We followed the Creative Commons (https://creativecommons.org/) licenses for each downloaded photo, from which we only used the six different licenses that allow the usage of photos for scientific purposes (CC-BY, CC-BY-NC, CC-BY-SA, CC-BY-ND, CC-BY-NC-ND, CC-BY-NC-SA – for licenses' attributions, please check https://creativecommons.org/licenses/?lang=en).

Morphological analyses were carried out on fresh and dried material. Macroscopic characters were recorded from field notes and photographs of both collected and herbaria specimens. Fischer named the region where the gleba is located as "belt", while other authors consider it as "ring" (Saénz and Nassar 1982; Calonge et al. 2005); here, we refer to both glebal region and belt. We considered the portion above the belt as "apical sterile portion", and the portion below as "pseudostipe". The constriction – where both pseudostipe and apical sterile portion narrows to the glebal region – measurement was calculated by subtracting the upper part width of pseudostipe from the basal part width of glebal region. The glebal region surface (underneath the gleba) was also described. These measurements were taken using Leica EZ4 stereomicroscope. Color designations follow Küppers (1979). Microscopic details were obtained by mounting slides with dried fragments from different layers and structures of dried basidiomata: apical sterile portion and pseudostipe, belt (glebal region), gleba, volva and rhizomorphs. Mounts were prepared in 5% potassium hydroxide (KOH) and/or stained with Congo Red dye. Optical Nikon Eclipse Ni (LM) microscope with Nikon DS–Ri1 camera attached, with NIS–Elements AR v.4.51.00 software, was used to make microscopic observations. All illustrations were edited on at GNU Image Manipulation Program (GIMP) version 2.10.24 (https://www.gimp.org/).

In order to understand the nomenclatural history, we contacted several herbaria to identify where E. Fischer's collections could have been deposited. After this, we requested information on the existence and conditions of possible type specimens, as well as other collections that could be the original material used to describe *S. cinctus*. We also located the place where several of Fischer's original illustrations are deposited. *Staheliomyces cinctus* is described here based on Fischer's original descriptions, notes, and on the photos of collections deposited at Botanischer Garten der Universität Bern (BERN).

Molecular Phylogenetic Analyses

Genomic DNA was extracted from a fragment of a basidioma following Hosaka (HOSAKA, 2009). Three DNA regions were amplified, internal transcribed spacer (ITS), ribosomal large subunit (nc LSU rDNA) and mitochondrial ATPase subunit 6 (*ATP*6), with the primer pairs ITS1/ITS4 (WHITE et al., 1990), LR0R/LR5 (VILGALYS; HESTER, 1990), and ATP6-1/ATP6-2 (KRETZER; BRUNS, 1999), respectively. The amplified regions were visualized on a 1.5% agarose gel stained with GelRed™ (Biotium, Fremont, USA) under UV light. All amplicons were purified with Ilustra ExoProStar (GE Healthcare, Chicago, USA) and then sequenced using the Big Dye Terminator Cycle Sequencing Kit (Applied Biosystems, Waltham, USA) with the same primer pairs, at Federal University of Amazonas (UFAM).

Sequences were visualized and assembled on Geneious R6.1 (Biomatters Ltd.), and then submitted to a BLAST search to check for their integrity and for the closest sequences deposited at GenBank (Benson et al. 2015). We retrieved sequences belonging to *Phallales*, mainly from Hosaka et al. (2006), Trierveiler-Pereira et al. (2014), Marincowitz et al. (2015), Melanda et al. (2020). The alignments and manual edition of aligned matrices were done in AliView v. 1.26 (LARSSON, 2014) using Muscle alignment. For molecular phylogenetic analyses, two datasets were prepared: (A) one with all available sequences from *Phallales*, in order to place the genus Staheliomyces, using ATP6+nc LSU rDNA concatenated; and (B) a second one composed of sequences of *Mutinus* Fr., *Xylophallus*, and *Staheliomyces*, using an ITS+nc LSU rDNA+ATP6 concatenated matrix, aiming to understand the possible

relationships within the genus Staheliomyces. The outgroup was chosen based on previous work (TRIERVEILER-PEREIRA et al. 2014). To the dataset A, *Hysterangium album* Zeller & C.W. Dodge and H. cistophilum (Tul. & C. Tul.) Zeller & C.W. Dodge were chosen as outgroup, and to dataset B, *Mutinus albotruncatus* B.D.B. Silva & Baseia and *Mutinus verrucosus* T.S. Cabral, B.D.B. Silva, K. Hosaka, M.P. Martín & Baseia were used as outgroup. For both datasets, two different approaches were used, Bayesian and maximum likelihood analyses, each using partitioned dataset. The substitution model for each partition (ITS1, 5.8S, ITS2, nc LSU rDNA, *ATP6*) was chosen MrModelTest (Nylander 2004). MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) was used to run Bayesian analysis (BA), on two parallel runs executed with four incrementally heated simultaneous MCMC simulations over 3 million generations for both datasets, with trees sampled every 1000 generations for both datasets. Maximum likelihood analyses were run in RAxML (Stamatakis 2014) using partitioned dataset, with estimated proportion of invariable sites (GTRGAMMA + I), at CIPRES Science Gateway (MILLER, et al. 2010). Trees were visualized and edited in FigTree version 1.4.2. All analyses were submitted to TreeBASE under ID 27667.

Additionally, we explored DNA sequences diversity in order to better understand how species are structured. We performed a sequence-based method of species delimitation, the Bayesian Posterior Tree Poisson (bPTP) analysis, which is indicated to small datasets and especially for species represented by singletons (Zhang et al. 2013). This method infers species boundaries based on a phylogenetic tree. Thus, an unrooted input tree was generated in MrBayes from a concatenated dataset composed only of Staheliomyces DNA sequences, and following the parameters: HKY+I +G for ITS partition and GTR+I+G for nc LSU rDNA and ATP6 partitions; and 2 million generations with tree sampled every 1000 generations. The bPTP analysis was run in a web server (http://species.h-its.org/ptp/) with 500,000 MCMC generations and the remaining default settings. Distances matrices were generated based on ITS sequences, calculated both between all specimens, and between one representative of each species defined by bPTP, using dist.dna function of the ape package (Paradis and Schliep 2019), with default values; the distances were plotted in a heatmap using heatmapSpp function of spider package (Brown et al. 2012) for R environment.

Results

Phylogenetic analysis

In total, we generated 37 new sequences of phalloid fungi in this study (8 ITS, 17 nc LSU rDNA, and 12 ATP6). After DNA sequencing and retrieving sequences from GenBank, in the dataset A, 86 taxa were included (including *Hysterangium album* and *H. cistophilum* as outgroup), with 156 sequences, from which 75 were ATP6 and 81 were nc LSU rDNA (Online Resource 1 – table). The final aligned matrix had 1444 characters (631 for ATP6 and 813 for nc LSU rDNA). For the two matrices (nc LSU rDNA and *ATP6*), the GTR+I+G model was selected by MrModelTest. In the phylogenetic trees of *Phallales* obtained either with Bayesian or with maximum likelihood, the genus *Staheliomyces* was placed in family *Phallaceae*, grouping with genus *Xylophallus* (Fig. 1), with high support values (posterior probability, pp = 1; maximum likelihood bootstrap, MLbs = 98).

The dataset B had 13 taxa and 29 sequences, of which 13 were ITS, 12 were nc LSU rDNA and 4 were *ATP6* (Online Resource 1 – table). The final aligned matrix had 2055 positions (276 ITS1, 166 5.8S, 237 ITS2, 815 nc LSU rDNA, and 727 ATP6). The following models were chosen for each partition: HKY for ITS1; JC for 5.8S; HKY+I for ITS2; GTR+G for nc LSU rDNA; and F81+I for ATP6. This dataset resulted in a phylogeny with three different genera of *Phallaceae* (Fig. 2). In *Staheliomyces*, it is possible to delimit 5 species-

level clades, of which four correspond to new species, described and discussed in the next section. We were able to get material for phylogenetic analyses from the specimen INPA 272311 during field trip, but unfortunately, it was not found at herbarium by the time of morphological analyses. Even so, we have decided to include it in the phylogenetic tree because it provides a better node support value, although we could not morphologically describe it.

The bPTP method estimated a mean number of 5 species for the dataset, with acceptance rate of 0.72 (see Online Resource 2), in accordance with phylogenetic tree and morphological analyses, although bPTP clustered some species with relatively low support value (*S. cylindricus* = 0.316 and *S. candeliformis* = 0.368). The pairwise distances of ITS sequences between the 5 species defined by bPTP is shown on Fig. 2b, where distances ranged from 1 to 3%, while between specimens of the same species the minimum genetic distance was 0.2% (Online Resource 3). These analyses also indicate *Staheliomyces* sp. INPA 272311 as part of *S. quadratus* species; however, we prefer to not maintain it as such, since we do not have enough morphological evidence.

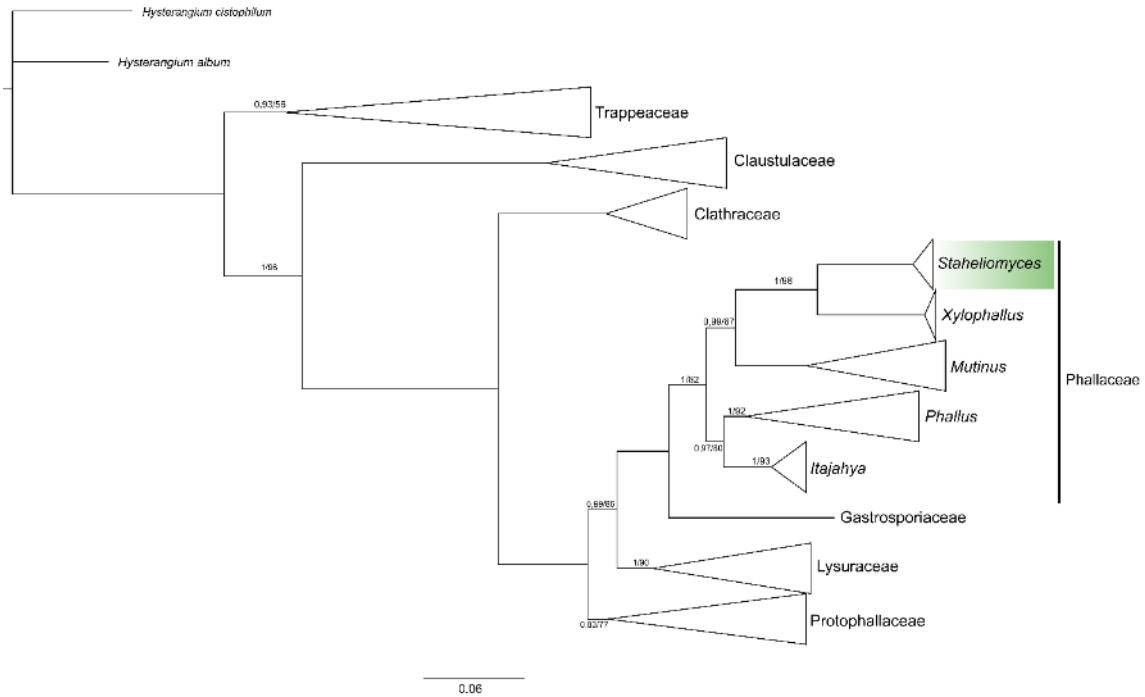

Fig. 1 Consensus phylogenetic tree of order *Phallales*, obtained by Bayesian inference with dataset A (*ATP*6 + nc LSU rDNA). Families clades are collapsed, except for *Phallaceae*, where genera clades are collapsed. In green, the phylogenetic placement of *Staheliomyces* genus. Numbers on nodes indicate posterior probabilities (pp, before slash) and Maximum Likelihood bootstrap values (MLbs, after slash).

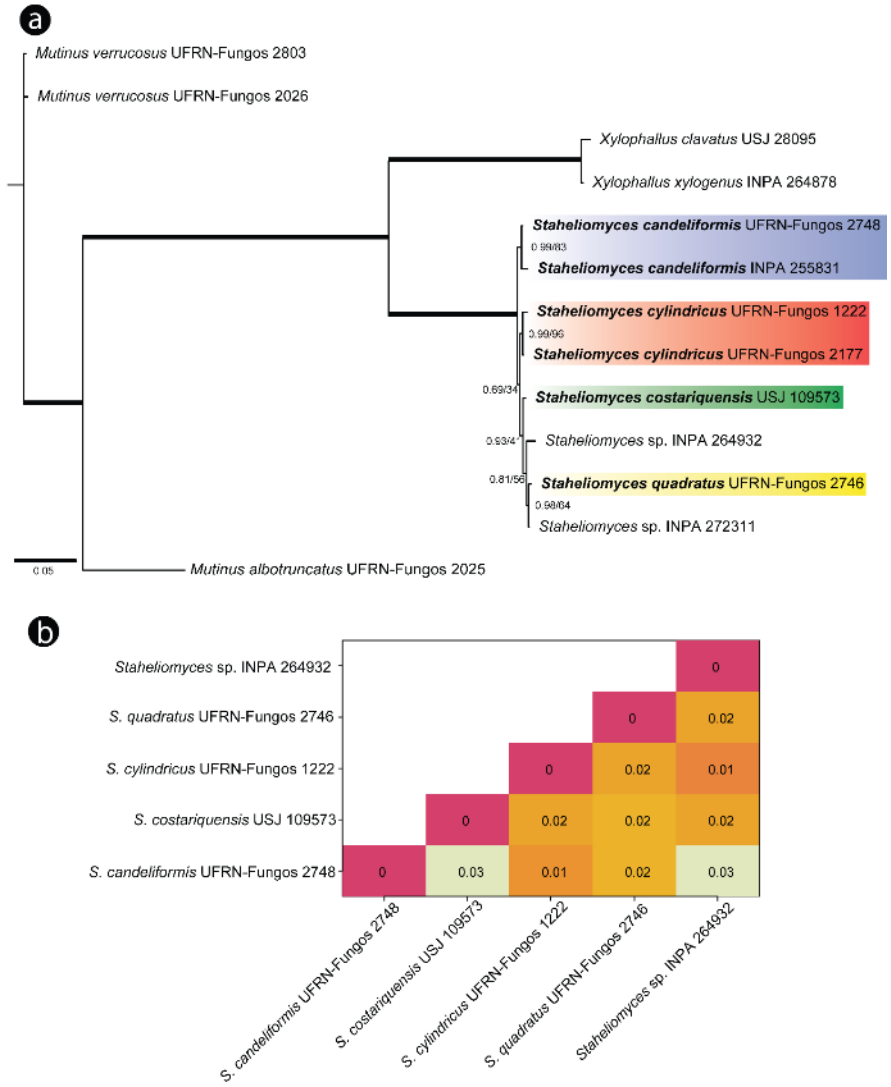

Fig. 2 a. Consensus phylogenetic tree of family *Phallaceae*, obtained by Bayesian inference with dataset B (ITS + nc LSU rDNA + *ATP*6), showing the infrageneric phylogenetic relationships in *Staheliomyces*. Colored clades correspond to new species: *S. candeliformis* (blue), *S. costariquensis* (green), *S. quadratus* (yellow), *S. cylindricus* (red). Posterior probabilities values and Maximum Likelihood (ML) bootstrap values are indicated on nodes (pp/ MLbs). Nodes fully supported are indicated by thicker branches. **b.** Heat map representing the distance matrix between species and specimens of *Staheliomyces*, based on pairwise distances from the ITS alignment.

Taxonomy

In this section we provide a proposal to emend the genus *Staheliomyces*, the translated description from Fischer (1921) and type specimens for *Staheliomyces cinctus* (Fig. 3), as well as descriptions and illustrations (Figs. 4 and 5) for four new species. The main morphological differences among *Staheliomyces* species can be found in Table 1, and the species geographical distribution is in Fig. 6.

Emended description of the genus *Staheliomyces* E. Fisch., Mitt. naturf. Ges. Bern: 142 (1921) [1920] (Fischer 1921) emend. Melanda, N.M. Assis & T.S. Cabral.

Expanded basidioma epigeous, pseudostipitate, pseudostipe white, hollow with lateral perforations, divided in pseudostipe and apical sterile portion. Hypogeous *volva* reddish brown, whitish to white, remaining attached to pseudostipe, with white *rhizomorph* attached to the volva base. Pseudostipe cylindrical, constrict to form a belt where the glebal mass is found. *Glebal region* short-cylindrical, doliiform, elongate-doliiform, cylindrical or almost squared with rounded sides; with rugulose or reticulate texture. *Apical sterile portion* tear-drop, triangular or elongate, with apical aperture present or absent. *Gleba* olive brown, mucilaginous. *Basidiospores* cylindrical to very narrowly elliptic, hyaline, smooth.
The type species: ***Staheliomyces cinctus*** E. Fisch. (Fischer 1921).

Staheliomyces candeliformis **N.M. Assis, Melanda & T.S. Cabral, sp. nov.** Fig. 4a–d, 5a–c

MycoBank: 838513

Typification: Brazil, Amazonas, Codajás, 3°47'08.9" S, 62°01'08.8" W, 12 December 2012, leg. Cabral TS 30, holotype (INPA 255831). GenBank accessions: MW546289 (ITS), MW546304 (nc LSU rDNA). Brazil, Amazonas, Parintins, Açai Community, 2°37'42.7" S, 56°32'49.9" W, 5 November 2015, leg. Cabral TS 234, paratype (UFRN-Fungos 2748). GenBank accessions: MW546288 (ITS), MW546303 (nc LSU rDNA).

Etymology: From the Latin *candela* (candle) referring to the basidiomata shape resembling a lighted candle.

Diagnosis: This species is characterized by its tear-drop shaped apical sterile portion, a pronounced constriction in the pseudostipe that forms the glebal region, reticulate belt surface under the gleba, and reddish brown volva. The reddish brown volva and the reticulate surface under the gleba is also found in *S. quadratus*; however, they differ by the apical sterile portion shape (tear-drop in *S. candeliformis* and elongate with a square tip in *S. quadratus*).

Macromorphological description: *Unexpanded basidiomata* not observed. *Expanded basidioma* epigeous, 60–130 mm long. Hypogeous *volva* remaining attached to pseudostipe, 25 mm high × 27 mm diam. (from dried volva), reddish brown when dried (Y_{70}, M_{70}, C_{40}). White *rhizomorph* (N_{00}, M_{00}, C_{00}) attached to the volva base. *Pseudostipe* 35–87 mm long, widening from the middle to the upper part (8–25 mm diam. basal, 10–27 mm diam. mid-pseudostipe, and 31 mm diam. on upper part), hollow, spongy, cylindrical, with several lateral perforations, smallest (0.5–1–3 mm diam.) near the base, larger (4–7 mm diam.) in the middle part, becoming smaller (1–2 mm diam.) near to the constriction, white (N_{00}, M_{00}, C_{00}), upper part of pseudostipe narrowing to 3–11 mm in diam. at the constriction of belt where the glebal mass is spread. *Glebal region* short-cylindrical, 9–11 mm long, basal part of belt widest (7–19 mm diam. basal, 9–17 mm diam. middle, 6–14 mm diam. upper part), belt surface reticulate under gleba. *Apical sterile portion* tear-drop shaped, 14.5–30 mm long, 14 mm diam. base, 22 mm diam. widest part, 7 mm upper part, apex thin, white (N_{00}, M_{00}, C_{00}), hollow, spongy, with several lateral perforations (1–5 mm diam.), apical aperture present. *Gleba* olive brown (N_{99}, A_{50}, M_{10}), mucilaginous; odor neutral.

Micromorphological description: Volva formed by filamentous hyphae 2.7–5.4 µm (x = 3.9 ± 0.5) diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm), with crystal deposits in globose cells widely distributed amongst the hyphae. *Rhizomorph* composed of filamentous hyphae 2.3–5.8 µm (x = 3.9 ± 0.9) diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm), with crystal deposits in globose cells widely distributed amongst the hyphae. *Pseudostipe* pseudoparenchymatous, composed of globose to broadly ellipsoid cells, 27.9 – 68.7× 24.6–56.5 µm (x = 47.6 ± 9.0 × 41.1 ± 7.8, Qm = 1.16 ± 0.07), hyaline, walls thin (<2.8 µm). *Glebal region* tissue pseudoparenchymatous, composed of globose to broadly ellipsoid cells, 15.6–44.7 × 14.1–32.9 µm (x = 27.5 ± 5.4 × 22.9 ± 4.9, Qm = 1.20 ± 0.10), hyaline, walls thin (<2.5 µm). *Apical sterile portion* pseudoparenchymatous, composed of globose to ellipsoid cells, 22.0–66.8 × 18.8–55.1 µm (x = 42.3 ± 9.4 × 36.9 ± 9.0, Qm = 1.15 ± 0.07), hyaline, walls thin (<2.5 µm). *Basidiospores* 3.0–3.5 × 1.5–2.0µm (x = 3.3 ± 0.1 × 1.7 ± 0.1, (Qm = 1.88 ± 0.12, n = 30), cylindric to very narrowly elliptic, hyaline, smooth.

Habitat and distribution: On decaying wood in Brazilian Amazon Rainforest domain.

Notes: The tear-drop shaped apical sterile portion, the pronounced constriction of the pseudostipe that forms the belt, reticulate texture of the belt surface beneath the gleba, and reddish brown volva are distinguishing features of *S. candeliformis*. This species differs from *S. cinctus* by the belt shape, apical sterile portion shape, as well as by the volva color. The reddish brown volva and the reticulate texture below the gleba are also found in *S. quadratus*;

however, the latter differs by having an elongate apical sterile portion with a square apex. *S. costariquensis* differs by having a triangular-shaped apical sterile portion with a slightly square apex, rugulose surface texture of the belt, and by the rusty orange outer volval surface (Table 1). Phylogenetically, it is the most distinctive clade, formed by specimens from Amazonia, and a sister group of all other *Staheliomyces* species proposed here.

Staheliomyces cinctus E. Fisch., Mitt. naturf. Ges. Bern: 142, Figure 1, p. 138. (1921) [1920]. Fig. 3

MycoBank: 219534

Typification: Suriname, Paramaribo: near Coppename river, in a forest behind a "Caraib" village, 12 June 1918, leg. G. Stahel, lectotype (designated here), deposited at the Wet collection of the Botanical Garden of the University of Bern (BERN), temporarily without voucher or deposit number (!).

Description (loosely translated from Fisher (1921)): "The total height of the basidiome reaches c. 12 cm, the largest diameter reaches 2 cm. Pseudostipe (*basal*) 8.5 cm long, the color was pure white. The spore mass (*gleba*) covers a conspicuously constricted, belt-shaped zone, c. 1 cm high, about 2 cm below the tip, forming a compact greenish mass. The spores are c. 3.5 µm long and have a diameter of 1.5 µm. Above the spore mass follows the approximately 2 cm high spore-free apex (*apical sterile portion*) of the receptaculum. This suddenly widens quite strongly immediately above the spore-covered belt and then tapers conically towards the tip ("mitraeformis", i.e., in shape of a miter). The wall of this spore-free part (*apical sterile portion*) of the head is essentially the same as the wall of the stem below (*pseudostipe*) the spore-covered belt, only it is extremely delicate and thin and has therefore become quite slack in alcohol. Its chambers are for the most part open to the outside, and one notices several larger openings running through the whole wall. It is also perforated at the top of the head by an opening that appears to have been made in advance. The stem initially expands immediately below the spore-bearing part just like the cap above it, then it gradually decreases in diameter further downwards. Almost all of its chambers are open to the outside in the upper part; In addition, quite a number of large openings penetrating the entire thickness of the wall are striking in the thicker upper part of the stem."

Habitat and distribution: Suriname.

Specimens examined: Suriname, Calebar creek, on the lower Coppename River, June 1920, leg. G. Stahel. Forest next to the Raleigh Falls on the upper Coppename River (65 km from Paramaribo), 21 August 1920, leg. G. Stahel. "Jodensavanne" at Suriname River, 1921, leg. Junker. Sipaliwini disctrict, "between Tockoemoetoe and Hendrikstop", 22 March 1922, leg. G. Stahel. Sipaliwini, Mombabasoe, on the Saramacca River, 27 March 1922, leg. G. Stahel. Brokopondo, Brownsberg Nature Park, 4°56'51.6" N 55°10'09.5"W), July 1924, leg. G. Stahel (determined as "cotypus" by Fischer), and 30 January 1925, leg. G. Stahel. All deposited at the wet collection of the Botanical Garden of the University of Bern (BERN), temporarily without voucher or deposit number (!).

Notes: *Staheliomyces cinctus,* the type species of *Staheliomyces*, is characterized by its pseudostipe thickening from the middle to the upper part; several lateral perforations in pseudostipe, smaller in the inferior half of pseudostipe, larger in the middle until near to the constriction; glebal region doliiform; apical sterile portion triangular; volva whitish. The thickened pseudostipe of *S. cinctus* differs from *S. cylindricus*, which has constant width until the belt. The lateral perforations of the pseudostipe of S. cinctus differ from *S. costariquensis* and *S. quadratus* in that these two species have several lateral perforations over most of the pseudostipe. The doliiform shape of the glebal region of *S. cinctus* is slightly similar to that of *S. costariquensis*, but the latter differs by having a more elongate upper part to its belt. The triangular apical sterile portion of *S. cinctus* is very different from *S. cylindricus* which has a

wider rounded tip; from *S. candeliformis* which has a tear-drop like tip; and from *S. quadratus* which has an elongate, squared tip. The triangular slightly squared tip of *S. costariquensis* is somewhat similar to *S. cinctus*, with the tip of the latter not being squared-off.

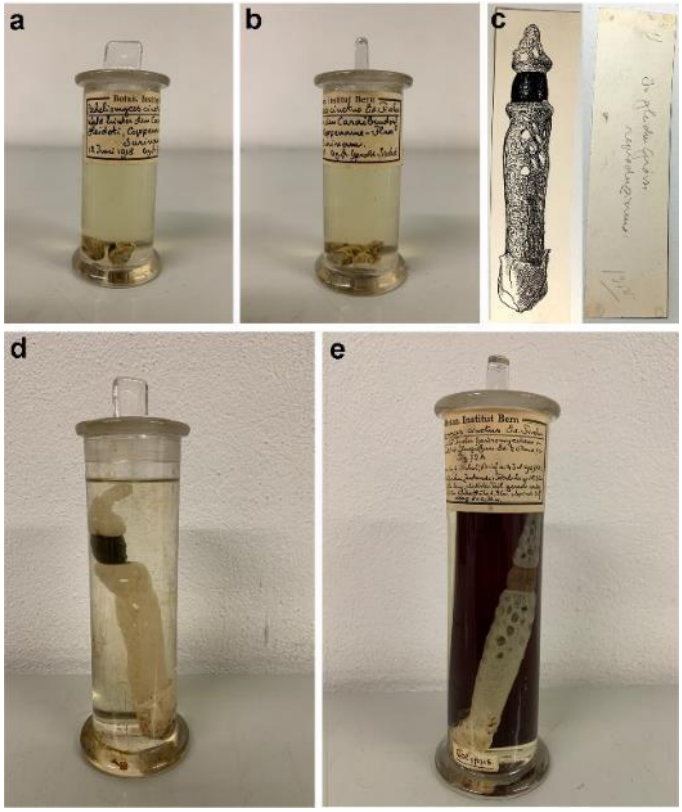

Fig. 3 *Staheliomyces cinctus* type **a, b, c;** basidiome without identification tag **d**; and "cotypus" e determined by E. Fischer (Photos: Katja Rembold)

Staheliomyces costariquensis **Ovrebo, Melanda, N.M. Assis & T.S. Cabral, sp. nov.** Fig. 4e–h, 5 d–f

MycoBank: 838516

Typification: Costa Rica, Heredia Prov., Lindero Occidental, La Selva Biological Station and Reserve, near Puerto Viejo, 17 July 1986, leg. C. Ovrebo 2213, holotype (USJ 109573). GenBank accessions: MW546290 (ITS), MW546305 (nc LSU rDNA), MW543438 (*ATP*6).

Etymology: With reference to the locality of the collection, Costa Rica.

Diagnosis: This species is characterized by the whitish to rusty orange volval surface, triangular apical sterile portion with a slightly square tip, glebal region elongate and doliiform, with a rugulose belt surface rugulose under gleba. It differs from other species mostly in that *S. candeliformis* has a tear-drop shaped apical sterile portion; *S. quadratus* has a reddish brown volva; and *S. cinctus* has a doliiform glebal region.

Macromorphological description: *Unexpanded basidiomata* globose to subglobose 20–30 mm diam., whitish (N_{00}, C_{00}, Y_{00}) to rusty orange (Y_{70}, M_{40}, C_{00}). *Expanded basidiomata* epigeous, 150–160 mm long. *Volva* 21–30 mm high × 26–28 mm diam., whitish (N_{00}, C_{00}, Y_{00}) to rusty orange (Y_{70}, M_{40}, C_{00}), ovoid in fresh material. White *rhizomorph* (N_{00}, M_{00}, C_{00}) attached to the volva base. *Pseudostipe* 70–90 mm long, widening from the middle to the upper part (17–20 mm diam. basal, 26–23 mm diam. mid-pseudostipe, and 25–27 mm diam. on upper part), white (N_{00}, M_{00}, C_{00}), hollow, spongy, cylindrical, with several lateral perforations, smallest (3 mm diam.) near the base, becoming larger (6–8 mm diam.) toward the constriction at the belt, upper part of pseudostipe narrowing to 5–7 mm diam. at the

constriction of belt where the glebal mass is spread. *Glebal region* doliiform elongate, 21–29 mm long, thickest in the middle part (20 mm diam. basal, 22.5–23 mm diam. middle, 13 mm upper part), belt surface (under gleba) white (N_{00}, M_{00}, C_{00}), rugulose. *Apical sterile portion* 28 mm long, triangular shape with slightly square tip, 15 mm base, 14 mm medium and 8 mm upper part, white (N_{00}, M_{00}, C_{00}), hollow, spongy, with several lateral perforations (5–8 mm diam.), apical aperture present. *Gleba* olive brown (N_{99}, A_{50}, M_{10}), mucilaginous.

Micromorphological description: *Volva* formed of filamentous hyphae 3–8.6 (x = 4.5 ± 1.0) µm diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm). *Rhizomorph* formed of filamentous hyphae 1.5–6.3 (x = 3.5 ± 0.8) µm diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm), with crystal deposits in globose cells widely distributed amongst the hyphae. *Pseudostipe* pseudoparenchymatous, composed of globose to elongate cells, 35–70 × 35–61 µm (x = 53.5 ± 6.5 × 45 ± 5.4, Qm = 1.18 ± 0.10), hyaline, walls thin (<2.5 µm). *Glebal region* tissue pseudoparenchymatous, composed of globose to subglobose cells,13–36 × 12–35 µm (x = 26 ± 4.8 × 25 ± 4.1, Qm = 1.06 ± 0.06), hyaline, walls thin (<2.5 µm). *Apical sterile portion* pseudoparenchymatous, composed of globose to elongate cells, 27–58 × 25–44µm (x = 39 ± 5.8 × 35 ± 4.2, Qm = 1.15 ± 0.13), hyaline, walls thin (<2 µm). *Basidiospores* 3–3.6 × 1.5–2 µm (x = 3.37 ± 0.1 × 1.8 ± 0.1, Qm = 1.84 ± 0.1, n=30), cylindric to very narrowly elliptic, hyaline, smooth.

Habitat and distribution: On decaying wood. Known from Atlantic Lowland tropical rainforest of Costa Rica.

Notes: *Staheliomyces costariquensis* is mainly characterized by the short triangular apical sterile portion pseudostipe with a slightly square tip, relatively long belt with a rugulose surface texture beneath the gleba and a whitish to rusty orange volval surface. This species is comparable to *S. cinctus*, *S. candeliformis* and *S. quadratum* by the widening of the pseudostipe from the middle to the upper part, and with *S. cylindricus* by the rugulose belt surface. However, these three species differ from *S. costariquensis* by the following: *S. candeliformis* has a tear-drop shaped apical sterile portion; *S. quadratus* has a reddish brown volva; and *S. cinctus* has a doliiform belt. Another morphological characteristic that differentiates *S. cinctus* from *S. costariquensis* is the perforation pattern along the pseudostipe. In *S. cinctus*, perforations are bigger in the central region of the pseudostipe until near to the belt, whereas *S. costariquensis* presents bigger perforations along the entire pseudostipe. Regarding *S. cylindricus,* it has a cylindrical belt shape and elongate apical sterile portion. Other specimens from Costa Rica, according to GBIF data, show morphological variations especially in relation to the apical sterile portion (Figure 7 c, d). *Staheliomyces costariquensis* has been found, so far, only in the northeastern region of the country, in a lowland tropical rainforest (Ovrebo and Baroni 1988; Hartshorn and Himmel 1994).

***Staheliomyces cylindricus* Melanda, N.M. Assis & T.S. Cabral, sp. nov.** Fig. 4i–l, 5g–h

MycoBank: 838514

Typification: Brazil, Paraíba, Mamanguape, REBIO Guaribas, 7°10'36.7" S, 35°18'03.3" W, 11 July 2013, leg. Sousa JO, Silva BDB, Rodrigues ACM and Cruz RHFS, holotype (UFRN-Fungos 2177). GenBank accessions: MW546292 (ITS), MW546307 (nc LSU rDNA), MW543439 (*ATP*6). Brazil, Rio Grande do Norte, Parnamirin, Mata do Jiqui, 6°30'13.3" S, 35°52'56.7" W, 28 August 2008, leg. Fazolino EP and Ali M, paratype (UFRN-Fungos 1222). GenBank accessions: MW546291 (ITS), MW546306 (nc LSU rDNA).

Etymology: From Latin "*cylindricus"* meaning cylindrical, with reference to elongate cylindrical basidiomata.

Diagnosis: This species is characterized by its constant width over the entire length of the pseudostipe, the elongate apical sterile portion with rounded apex, the minimal narrowing of the pseudostipe at the cylindrical belt, rugulose belt surface under gleba, and the white volva. *Staheliomyces cinctus, S. costariquensis* and *S. candeliformis* differ from *S. cylindricus* by their shorter apical sterile portion, while *S. quadratus* differs by the square apex.

Macromorphological description: *Unexpanded basidiomata* not observed. *Expanded basidiomata* epigeous, 120–140 mm long. Hypogeous *volva* remaining attached to pseudostipe 26–30 mm high × 17–26 mm diam., white (N_{00}, M_{00}, C_{00}). White *rhizomorph* (N_{00}, M_{00}, C_{00}) attached to the volva base. *Pseudostipe* 60–85 mm long × 11–13 mm diam., constant width over the entire length of the pseudostipe, hollow, spongy, cylindrical, with several perforations smallest (1–3 mm diam.) near the base, larger (3–8 mm diam.) in the middle part, becoming smaller (1–2 mm diam.) until close to the constriction, white (N_{00}, M_{00}, C_{00}), upper part of pseudostipe narrowing to 1 mm in diam. at the constriction of belt where the glebal mass is spread. *Glebal region* cylindrical, 11–25 mm high, slightly tapering at upper part (9–13 mm diam. base, 9–11 mm diam. medium and 6–9 mm diam. upper part), belt surface rugulose under gleba. *Apical sterile portion* elongate, 24–27 mm high, approximate width over the entire length 5–9 mm diam., with wide rounded tip, white (N_{00}, M_{00}, C_{00}), hollow, spongy, with several lateral perforations (1–4 mm diam.), apical aperture absent. *Gleba* olive brown (N_{99}, A_{50}, M_{10}), mucilaginous; odor neutral.

Micromorphological description: *Volva* composed of filamentous hyphae 1.7–3.9 µm (x = 2.7 ± 0.4) diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm), with crystal deposits in globose cells widely distributed amongst the hyphae. *Rhizomorph* composed of filamentous hyphae 2.6–5 µm (x = 3.6 ± 0.6) diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm), with crystal deposits in globose cells widely distributed amongst the hyphae. *Pseudostipe* pseudoparenchymatous, composed of globose to broadly ellipsoid cells, 27–64 × 24–60 µm (x = 45.4 ± 8.5 × 40.1 ± 6.9, Qm = 1.13 ± 0.07), hyaline, walls thin (<2.0 µm). *Glebal region* pseudoparenchymatous, composed of globose to ellipsoid cells, 18–43 × 13–34 µm (x = 28.5 ± 5.9 × 22.5 ± 4.3, Qm = 1.27 ± 0.08), hyaline, walls thin (<1.5 µm). *Apical sterile portion e* pseudoparenchymatous, composed of globose to broadly ellipsoid cells, 17.5–45 × 16–42 µm (x = 30.6 ± 6.1 × 26.3 ± 5.3, Qm = 1.17 ± 0.08), hyaline, walls thin (<2.0 µm). *Basidiospores* 2.9–3.8 × 1.7–2.3 µm (x = 3.4 ± 0.1 × 1.9 ± 0.08, Qm = 1.84 ± 0.09, n=30), cylindrical to very narrowly elliptic, hyaline, smooth.

Habitat and distribution: On the soil on litter in Atlantic Rainforest domain.

Notes: *Staheliomyces cylindricus* is the most distinctive species amongst our collections because of its elongate, rounded, apical sterile portion, cylindrical-shaped belt, and white volva. The upward narrowing of the pseudostipe toward the belt is less in comparison to all species (Table 1) so is also a diagnostic feature. This species shares with *S. costariquensis* the rugulose belt surface, rather than reticulated as in *S. quadratus* and *S. candeliformis*. *Staheliomyces cylindricus* has an elongate apical sterile portion while those of *S. cinctus, S. costariquensis* and *S. candeliformis* have a shorter apical sterile portion. The elongate pseudostipe is also found in *S. quadratus* but the apex is square compared to the rounded apex in *S. cylindricus*. Phylogenetically, *S. cylindricus* is in a well-supported group (pp = 0.99, MLbs = 96), and a sister clade of a group formed by *S. costariquensis*, *S. quadratus* and *Staheliomyces* sp. INPA264932 and INPA 272311.

***Staheliomyces quadratus* N.M. Assis, Melanda, T.S. Cabral, sp. nov.** Fig. 4m–p, 5 j–l

MycoBank: 838515

Typification: Brazil, Amazonas, Manaus, Reserva Ducke, 2°54'53.3" S, 59°58'39.9" W, 14 January 2014, leg. Cabral TS 84, holotype (UFRN-Fungos 2746). GenBank accessions: MW546286 (ITS), MW546301 (nc LSU rDNA).

Etymology: With reference to square tip apical sterile portion.

Diagnosis: This species is characterized by the square tip of the apical sterile portion that possesses an apical pore, belt having rounded sides, belt surface reticulate under gleba, and by the reddish brown volva. *Staheliomyces cinctus* and *S. costariquensis* differ from *S. quadratus* by the shape and texture of belt; while the color of the volva is different in *S. cylindricus* (whitish) and *S. costariquensis* (rusty orange).

Macromorphological description: *Unexpanded basidiomata* not observed. *Expanded basidiomata* epigeous, 116 mm high. Hypogeous *volva* remaining attached to pseudostipe, 22 mm high × 20 mm diam. (from dried volva), subglobose, reddish brown (Y_{70}, M_{70}, C_{40}) when dry. White *rhizomorph* (N_{00}, M_{00}, C_{00}) attached to the volva base. *Pseudostipe* 60 mm long, widening from the middle to the upper part (17 mm diam. basal, 20 mm diam. mid-pseudostipe, and 25 mm diam. on upper part), hollow, spongy, cylindrical, with several lateral perforations, 5–8 mm diam. to the fullest extent, white (N_{00}, M_{00}, C_{00}), upper part of pseudostipe narrowing to 10 mm in diam. at the constriction of belt where the glebal mass is found. *Glebal region* almost squared with rounded sides, 15 mm high, wider in the middle part (15 mm diam. basal and upper parts, 17 mm diam. middle part), with belt surface reticulate under gleba. *Apical sterile portion* 40 mm high, tapered to apex (20 mm diam. basal, 17 mm middle, 14 mm diam. upper part), square at the tip, white (N_{00}, M_{00}, C_{00}), hollow, spongy, with several lateral perforations (1–7 mm diam.), apical aperture present. *Gleba* olive brown (N_{99}, A_{50}, M_{10}), mucilaginous; odor neutral.

Micromorphological description: *Volva* formed of filamentous hyphae 2.8–6.3 (x = 4.4 ± 0.7) µm diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm). *Rhizomorph* formed of filamentous hyphae 2.2–4.6 µm (x = 3.2 ± 0.6) diam., regularly septate, branched, tips inflated, clamp connections absent, hyaline, walls thin (<1 µm), with crystal deposits in globose cells widely distributed amongst the hyphae. *Pseudostipe* pseudoparenchymatous, composed of globose to ellipsoid cells, 20–62 × 18–49 µm (x = 40.9 ± 11.3 × 32.9 ± 5.9, Qm = 1.22 ± 0.14), hyaline, walls thin (<2.5 µm). *Glebal region* pseudoparenchymatous, composed of globose to broadly ellipsoid cells, 17–40 × 15–42 µm (x = 26.9 ± 4.3 × 23.9 ± 4.1, Qm = 1.15 ± 0.05), hyaline, walls thin (<1.5 µm). *Apical sterile portion* pseudoparenchymatous, composed of globose to ellipsoid cells, 25–50 × 20–40.5 µm (x = 37.3 ± 5.6 × 31.4 ± 4.9, Qm = 1.19 ± 0.09), hyaline, walls thin (<2.5 µm). *Basidiospores* 2.9–3.8 × 1.5–2 µm (x = 3.4 ± 0.1 × 1.8 ± 0.1, Qm =1.83 ± 0.14, n=30), cylindric to very narrowly elliptic hyaline, smooth.

Habitat and distribution: On the soil on litter in Brazilian Amazon Rainforest domain.

Notes: *Staheliomyces quadratus* is comparable to *S. cinctus*, *S. costariquensis* and *S. candeliformis* by the pseudostipe that widens from the middle to the upper part, and by the middle part with big lateral perforations (4–8 mm diam.); however, *S. cinctus* and *S. costariquensis* have a triangular apical sterile portion, and *S. candeliformis* has a tear-drop shaped apical sterile portion. *Staheliomyces quadratus* has a squared tip apical sterile portion. The belt shape differs in these species: *S. cinctus*, *S. costariquensis*, *S. candeliformis* and *S. quadratus*: doliiform elongate; short-cylindrical; and almost squared with rounded sides, respectively. The reticulate texture of belt beneath the gleba in *S. quadratus* is the same of *S. candeliformis*, but *S. cylindricus* and *S. costariquensis* have a rugulose texture. *Staheliomyces quadratus* and *S. candeliformis* also share the same reddish brown volva color, while the volva is whitish in *S. cylindricus* and *S. cinctus*, and rusty orange in *S. costariquensis.*

***Staheliomyces* sp.** Fig. 4q–t, 5m–o

Macromorphological description: *Unexpanded basidiomata* not observed. *Expanded basidiomata* epigeous, 127 mm long. Hypogeous *volva* remaining attached to pseudostipe, 27 mm high × 22 mm diam., white (N_{00}, M_{00}, C_{00}). White *rhizomorph* (N_{00}, M_{00}, C_{00}) attached to the volva base. *Pseudostipe* 79 mm long, widening from the middle to the upper part (18 mm upper part and 15 mm diam. base), dehydrated material measuring 74 mm long × 9 mm diam., hollow, spongy, cylindrical, with several lateral perforations, smaller (2 mm diam.) in the lower half, becoming larger (5 mm) from the middle to the constriction with an abrupt increase in size, white (N_{00}, M_{00}, C_{00}), upper part of pseudostipe narrowing to 7 mm in diam. at the constriction of belt where the glebal mass is spread. *Glebal region* 13 mm high (7 mm diam. upper part, 11 mm diam. middle, 11 mm diam. base), with reticulate surface texture beneath the gleba. *Apical sterile portion* 8 mm long (5 mm diam. upper part, 8 mm diam. middle,8 mm diam. base), white (N_{00}, M_{00}, C_{00}), hollow, spongy, with several lateral perforations. *Gleba* olive brown (N_{99}, A_{50}, M_{10}), mucilaginous.

Micromorphological description: *Volva* and *rhizomorph* lacking on dried material. *Pseudostipe* pseudoparenchymatous, composed of globose to broadly ellipsoid cells, 26–64 × 22–56 µm (x = 40.2 ± 8.2 × 35.2 ± 7.8, Qm = 1.14 ± 0.05), hyaline, walls thing (<2.6 µm). *Glebal region* pseudoparenchymatous, composed of globose to elongate cells,16.5–30 × 13–26 µm (x = 23.7 ± 3.0 × 20.0 ± 2.4, Qm = 1.18 ± 0.07), hyaline, walls thin (<2.0 µm). *Apical sterile portion* pseudoparenchymatous, composed of globose to elongate cells, 27–71 × 24–62 µm (x = 50.0 ± 7.6 × 41.3 ± 6.6, Qm = 1.21 ± 0.07), hyaline, walls thin (<2.0 µm). *Basidiospores* 2.9–3.7 × 1.3–2.2 µm (x = 3.16 ± 0.2 × 1.68 ± 0.2, Qm = 1.89 ± 0.19, n=30), cylindric to very narrowly elliptic, hyaline, smooth.

Habitat and distribution: In soil on litter in Brazilian Amazon Rainforest domain.

Specimen examined: Brazil, Pará, Belterra, Flona Tapajós, Comunidade Maguary, 2°48'12.0"S, 55°00'01.0" W, 30 March 2014, leg. Cabral TS 176 (INPA 264932). GenBank accessions: MW546287 (ITS), MW546302 (nc LSU rDNA), MW543437 (*ATP*6).

Notes: In *Staheliomyces* sp., distinctive characteristics are the variation in the perforation pattern along the pseudostipe as well as the apical sterile portion that is shorter than the glebal region (8 mm high, 5 mm diam. upper part, 8 mm diam. medium, 8 mm diam. base) compared to the other specimens discussed here. Compared to *S. cinctus*, this species has different format of belt (doliiform in *S. cinctus* and tuned a little in the center in *Staheliomyces* sp.) and larger expanded basidioma (150–160 mm high in *S. cinctus*; 127 mm high in *Staheliomyces* sp.). In the materials observed in this study, the shape of the apical sterile portion has been shown to be an important morphological characteristic in species differentiation. However, only one basidioma was collected of *Staheliomyces* sp. and as we have not observed this characteristic (apical sterile portion smaller than belt) in other species analyzed in this work. It is not possible to verify whether it is an individual characteristic of the species or just a failure in the formation of this structure. Therefore, as it was not possible to confirm the authenticity of all morphological characteristics, we add this specimen here as *Staheliomyces* sp. Also, this specimen groups in the clade with *S. quadratus* and *Staheliomyces* sp. (INPA 272311), but with low support value (pp = 0.81; MLbs = 56). Thus, more collections of this fungus are necessary to confirm whether it is a new species.

Key to *Staheliomyces* species

1. Volva white/whitish……..……...…..2

1'. Volva not white/whitish ……...……..……...……3

2. Apical sterile portion triangular; belt shape doliiform…….…...……. ***S. cinctus***

2'. Apical sterile portion elongate with wide rounded apex; belt shape cylindrical……..***S. cylindricus***

3. Volva rusty brown with white areas; belt surface (under gleba) rugulose; apical sterile portion with triangular, slightly squared apex; belt shape elongate-doliiform.....***S. costariquensis***

3'. Volva reddish brown; belt surface (under gleba) reticulate; apical sterile portion and belt shape different…….……...…..4

4. Apical sterile portion tear-drop shaped; belt shape short-cylindric.....***S. candeliformis***

4'. Apical sterile portion elongate with a square apex; belt shape nearly square with rounded sides…….……***S. quadratus***

Fig. 4 *Staheliomyces* spp. macro-morphology.
a, e, i, m, q Basidiomata in field.
b, f, j, n, r Close-up in belt and apical sterile portion.
c, g, k, o, s Belt texture of dehydrated basidiomata.
d, h, l, p, t Volva close-up.
a, b, d *S. candeliformis* (UFRN-Fungos 2748, paratype):
(d) Part of dehydrated volva.
c *S. candeliformis* (INPA 255831, holotype).
e, f, g, h *S. costariquensis* (USJ 109573, holotype).
i, j, l *S. cylindricus* (UFRNFungos 2177, holotype),
(Photo: Julieth Souza).
k *S. cylindricus* (UFRN-Fungos 1222, paratype).
m, n, o, p *S. quadratus* (UFRN-Fungos 2746, holotype).
q, r, s, t *Staheliomyces* sp. (INPA 264932). Scale bars:
(**a, b, e, f, h, i, j, l, m, n, p, q, r, t**) = 10 mm, (**k**) = 2mm, (**c, d, g, o, s**) = 1 mm

Table 1. Comparative morphological table with *Staheliomyces* species

Character	*S. candeliformis*	*S. cinctus*	*S. costariquensis*	*S. cylindricus*	*S. quadratus*
Volva color	Reddish brown	Whitish*	Rust orange with white areas	White	Reddish brown
Pseudostipe width (shape)	Widening from the middle to the upper part	Widening from the middle to the upper part	Widening from the middle to the upper part	Constant width over the entire length	Widening from the middle to the upper part
Constriction in diam. (mm)	3–11	5	5–7	1	10
Glebal region shape	Short-cylindrical	Doliiform	Doliiform elongate	Cylindrical	Almost squared with rounded sides
Belt texture under gleba	Reticulate	**	Rugulose	Rugulose	Reticulate
Apical sterile portion shape	Tear-drop	Triangular	Triangular, slightly square tip	Elongate, rounded tip	Elongate, square tip

* Data analyzed in Figure 3d (basidiomata in alcohol). ** Not analyzed in original description.

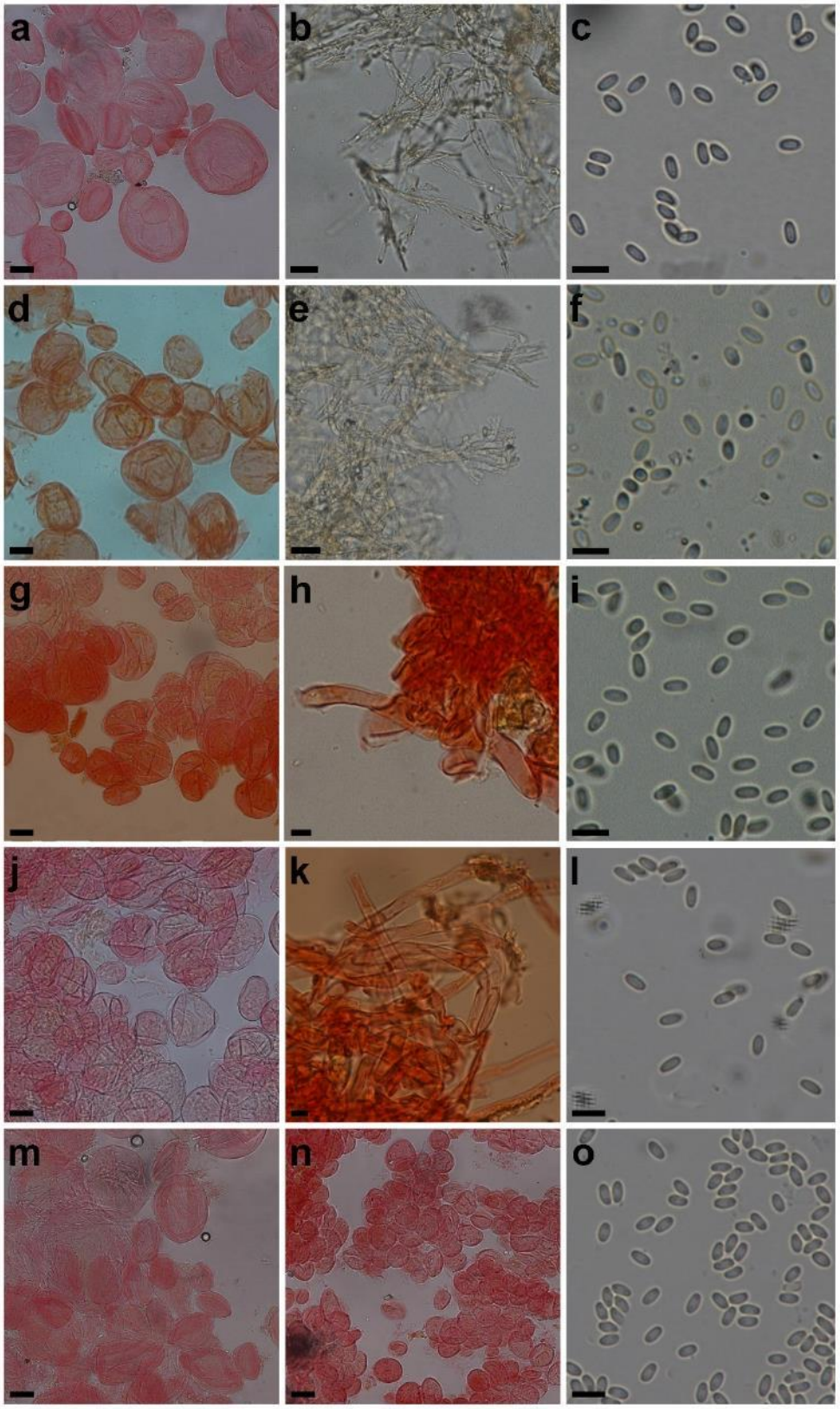

Fig. 5 *Staheliomyces* spp. micro-morphology. **a, d, g, j, m** Pseudoparenchymatous hyphae of apical sterile portion. **b, e, h, k** Hyphae from volva. **n** Hyphae from belt. **c, f, i, l, o** Basidiospores. **a, b, c** *S. candeliformis* (INPA 255831, holotype). **d, e, f** *S. costariquensis* (USJ 109573, holotype). **g, h** *S. cylindricus* (UFRN-Fungos 1222, paratype). **i** *S. cylindricus* (UFRN Fungos 2177, holotype). **j, k, l** *S. quadratus* (UFRN-Fungos 2746, holotype). **m, n, o** *Staheliomyces* sp. (INPA 264932). Scale bars: **(a, b, d, e, g, j, m, n)** = 20 μm, **(c, f, h, i, k, l, o)** = 5 μm.

Discussion

It has been a hundred years since the publication of the genus *Staheliomyces*, and so far, only one species has been de- scribed, namely *S. cinctus* (Fischer 1921). The only informa- tion about the type specimen in the protologue is that Gerold Stahel collected it in 1918, in Paramaribo, Suriname. Stahel made great contribution to the knowledge of neotropical fun- gi, by sending several collections to known mycologists. Eduard Fischer was a Swiss botanist and mycologist, from University of Bern, and later from Botanic Garden and Botanical Institute in Bern, who described several species of gasteroid fungi, from which many were sent by G. Stahel (Fischer 1933a).

Originally, Eduard Fischer's collection was deposited at the Botanical Garden of University of BERN, but part of his collection was moved to ETH Zurich (Eidgenössische Technische Hochschule) fungal collec- tion. We contacted both curators of fungal collections and Dr. Katja Rembold, curator of the herbarium BERN, found Fischer' *Staheliomyces* collection, collected and sent by Stahel during the years of 1918–1925. She kindly provided pictures and information about this collection, which allowed us to define type material for *S. cinctus*. Several collections of *Staheliomyces* were found at BERN, also numerous original illustrations made by Fischer for different species are currently stored in the archive of the Library Plant Sciences (a sub-section of the University Library of Bern).

The type material found at BERN (Fig. 3a and b) is now apparently composed only of an immature basidiome, but Fischer's illustration of the expanded basidiome cited in protologue is represented here in Fig. 3c. Among Fischer's collection there is also an expanded basidiome without an identification tag (Fig. 3d). Since Fischer mentions that the original material sent by Stahel is composed of both mature and immature basidiome, we believe this unidentified material can be part of the original material, and therefore a possible syntype. We designate here as lectotype the material com- posed of immature basidiome, since it has the original identification tag with information on date and locality of collection, as well as the collector, indicated by Fischer in his publication—all in accordance to the International Code of Nomenclature for algae, fungi, and plants (Section 2, Art. 9.12) (Turland et al. 2018). We also found a material designated by Fischer himself as "cotypus" on the herbarium tag (Fig. 3e), which corre- sponds to the illustration on Fischer (1933b), page 98 figure 72A. All these findings are especially outstanding, since it is very difficult to find well-preserved specimens of phalloid fungi from such a long period of time since the original description (c. 100 years), specifically the original material.

Morphological and phylogenetic molecular analyses from the collected material showed some expected diver- sity within *Staheliomyces*. We expected that there would be some degree of infrageneric diversity because this ge- nus has never been analyzed in detail. Recently, several examples of hidden diversity have been found in mono- specific genera that have been published, especially when studying Neotropical species, as in *Myriostoma* Desv. and *Xylophallus* (Sousa et al. 2017; Crous et al. 2018). This highlights the importance of studying neglected taxa es- pecially in geographic regions that are underexplored or hard to reach.

In the phylogenetic analysis A (Fig. 1), *Staheliomyces* belongs to *Phallaceae* in an exclusively Neotropical clade that includes *Staheliomyces* and *Xylophallus*. This is par-

ticularly interesting and brings insights into future biogeo- graphical studies of phalloid fungi, since the species from this clade appear to have diversified both recently and rapidly, as it is reflected by the short branch lengths in phylogenies. Morphologically, these two genera are very distinct, but they do share a common character, which is also found in *Mutinus*. These three genera do not have a differentiation between the receptacle and the pseudostipe, as it is in *Phallus* Junius and *Itajahya* Möller species— where the receptacle forms a bell-like structure at the apex of basidioma. Studies aiming to reconstruct ancestral character states would be necessary to understand the dy- namic of character evolution in phalloid fungi.

In South America, *Staheliomyces* and *Xylophallus* current- ly have a disjunct distribution in Amazonia and Brazilian Atlantic rainforest, which is a pattern also found in several groups of Neotropical plant and animal species. For plants and animals, this pattern is usually related to the last glacial cycle (21 Mya), which together with Andean uplift in Neogene, led to climate and geographical changes that drasti- cally modified the landscape (Hoorn et al. 2010; Sobral-Souza et al. 2015; Ledo and Colli 2017). There has been an expan- sion of dry forests and retraction of humid forests, where the dry forests functioned as a corridor between these biomes— now called the South American dry diagonal (Sobral-Souza et al. 2015). The same disjunct distribution pattern is also found in several groups of gasteroid fungi including phalloid species (da Silva et al. 2013; Accioly et al. 2019; Cabral et al. 2019), which might also indicate a signature of possible con- nections between the two forests in the past. Similarly, Sánchez-Ramírez et al. (2015) evaluated the effects of past glaciation in diversification of *Amanita caesarea* (Scop.) Pers. species complex in North America, and revealed a cryp- tic diversity and high speciation rates in refugia. In spite of suggestions on the emergence of the order *Phallales* to 77 Mya (He et al. 2019), it is still not known when phalloid species colonized Neotropical areas. For this reason, biogeo-graphical and dating studies need to be developed in order to better understand the past processes that influenced the speci- ation in this group. Additionally, a better sampling effort is needed in specific Neotropical areas, as between Amazonia and Atlantic Rainforest or Central America, to confirm the current geographical distribution of Neotropical species.

By comparing our material to published descriptions, we noticed that *S. cinctus* is not represented in the collec- tions that we have made in this study, although we do believe that Fig. 7j from GBIF data may well represent that species. It is a specimen from French Guyana, macro- morphologically very similar to Fischer's description, and geographically very close to the type locality (Suriname)— found specifically on the border with Suriname. It is also similar to some of the material found at BERN, described by Fischer (data not shown). On the other hand, based on the phylogenetic analysis (Fig. 2a) which is allied to the morphological analysis, at least four new species could be identified and described here. There is a clear morphological delimitation of species, even though some phylogenetic clades do not have high support values.

Staheliomyces cylindricus is the most distinct species in our study and the most phylogenetic consistent clade, characterized by the elongate apical sterile portion, and known only by specimens from Brazilian Atlantic Rainforest. *Staheliomyces costariquensis* is an intriguing species characterized mainly by its long belt and very short apical sterile portion, consistently different from other specimens. Apparently, at least two morphospecies can be identified in Costa Rica (Fig. 7c and d) accord- ing to our data and

the data obtained in GBIF (GBIF 2021). *Staheliomyces costariquensis* occurs in the North portion, while the other one is found mainly on South Costa Rica, showing differences mainly in the shape of apical sterile portion (Fig. 7c–e). *Staheliomyces candeliformis*, in turn, grouped in an Amazonian clade, and has a tear-drop apical sterile portion, while

S. quadratus has a square apical sterile portion. We conclude that the most distinguishable characters for species in *Staheliomyces* are the shape and size of api- cal sterile portion, shape and surface of the belt, and the color of the volva. This is clearly shown in Fig. 7 where it is possible to see different shapes for the apical sterile portion which are different from those described in this study; for example, the cup shape seen in some of the Ecuadorian specimens (Fig. 7f–h).

The expansion of basidiomata sampling in the known geographical occurrence range of *Staheliomyces*, togeth- er with the detailed study of species morphology and phylogenetic or phylogenomics analyses, will ameliorate our understanding of the diversity found within the ge- nus. These further studies may also indicate the biogeographical drivers of such a diversity as well as may clarify the speciation events in the order *Phallales*.

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Authors contribution Material preparation and data collection and anal- yses were performed by Tiara S. Cabral, Gislaine C.S. Melanda, and Nathalia M. de Assis. The first draft of the manuscript was written by T.S.C., G.C.S.M, and N.M.A, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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APÊNDICE F – PHALLALES (AGARICOMYCETES, BASIDIOMYCOTA) FROM NORTHEASTERN BRAZIL: OCCURRENCES, NEW RECORDS WITH AN UPDATED DISTRIBUTION MAP AND CHECKLIST

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With 2 figures and 2 tables

Abstract: With its peculiar climate and wide range of ecosystems, Northeast Brazil is one of the richest regions in terms of biodiversity. The Phallales order, commonly known as stinkhorns, com- prises morphologically distinct organisms with a great variability in shape and color patterns. Based on morphological data, five phalloid fungi taxa are described and illustrated. An updated checklist and map of Phallales in the Northeastern Region is provided. Additionally, with new exsiccates, a review of the *Abrachium floriforme* samples deposited in the UFRN-Fungos collection was per- formed. *Clathrus natalensis* is the second record for science. *Mutinus bambusinus* is the first record for Brazil and *Phallus atrovolvatus* is the second record for this country. *Mutinus argentinus* is the first record for Rio Grande do Norte state. *Abrachium floriforme* is a new occurrence for Ceará and Rio Grande do Norte state.

Keywords: Biodiversity; phalloid fungi; stinkhorns; neotropics; taxonomy

Introduction

Phallales E. Fisch. is an order of Phallomycetidae K. Hosaka, Castellano & Spatafora subclass (Hosaka et al. 2006). These fungi present a zoochoric mode of dispersion, in which they exhale unpleasant odor of gelatinous gleba (basidiospore masses) that attracts insects (Fulton 1889, Arora 1986). Because of this dispersion they are called stinkhorns (Miller & Miller 1988). The non-sequestrate species form and mature their basidiospores in a mycoegg, surrounded by the peridium (with two or three layers) with a rhizomorph in the base, who support and fix it in the substrate (Miller & Miller 1988, Pegler & Gomez 1994). After complete maturation the basidiomata expand and are composed basically of: rhizomorph, volva (the mycoegg after expansion), pseudostipe (may divided into sterile and fertile portion), receptacle and gleba mass (with basidiospores) (Miller & Miller 1988). Other parts like the indusium and glebifer may appear in some genera.

The Brazilian Northeast has an area of approximately 1.6 million km² (Araújo 2011). Due to its location in the extreme east of tropical South America, it is subject to the influence of meteorological phenomena, allowing it peculiar and unique characteristics in the world (Molion & Bernardo 2002). Moreover, it is formed by several biomes such as the Ama- zon, Atlantic rainforest, Caatinga and Cerrado (IBGE 2019a). As a tropical

region, north- eastern Brazil has the potential to be a center of diversity for many species of stinkhorns (Dring 1980). Northeast Brazil has proven to be an interesting environment for phalloid fungi, including the discovery of new species (Lima et al. 2019).

The purpose of this paper is to describe new Phallales records from northeastern Brazil and to organize a list and distributional map with all records of studies on Phallales fungi in this region.

Material and methods

Samples, collection sites and methods

Fresh basidiomata were collected in areas originally from the Atlantic rainforest, in the municipalities of Arez, Goianinha (Rio Grande do Norte State) and Recife (Pernambuco State) during the rainy season in 2018 and 2019. The collection methods followed Baseia et al. (2014). The specimens were deposited in the Fungi Collection of the Federal University of Rio Grande do Norte (UFRN-Fungos), Natal, Brazil. Other materials from the collection have been added to our analyses.

Morphological analyses

Macroscopic characteristics such as measurement, color and texture were performed with the basidiomata still fresh. The measurement of these structures followed $height_{(Min.)}$ – $height_{(Max.)}$ × $width_{(Min.)}$ – $width_{(Max.)}$ mm, or $diameter_{(Min.)}$ – $diameter_{(Max.)}$ mm, in the last case noted in the description. The colors were coded following Küppers et al. (2002).

Microscopic analysis was carried out in the Laboratório de Biologia de Fungos (Lab-Fungi-UFRN). As mounting medium 5% KOH was used. The observations and measurements of the microstructures were done using NIS - Elements AR v.4.51.00 software associated with a Nikon Eclipse Ni (LM) optical microscope with a Nikon DS-Ri1 camera attached

For microscopic structures, 30 measurements (for basidiospores) and 20 (for other hyphal structures) were performed and represented as follows: $height_{(Min.)}$ – $height_{(Max.)}$ × $width_{(Min.)}$ – $width_{(Max.)}$ µm; for basidiospores: $height_{(Min.)}$ – $height_{(Max.)}$ × $width_{(Min.)}$ – $width_{(Max.)}$ µm (x = $height_{(mean)}$ ± standard deviation × $width_{(mean)}$ ± standard deviation, Qm = mean of height/width quotient). The outlier values are identified by "[ ]". Macro- and micro-structures are highlighted in bold in the descriptions.

Checklist and distribution map

A checklist of Phallales fungi collected in the Northeast region of Brazil was made after searching records in publications up to May 1st, 2020. The scientific names and their status name follow Mycobank (http://www.mycobank.org/quicksearch.aspx).

A distribution map was constructed using QGis 3.4.14 software, Geographic Coordinate Systems: Datum SIRGAS, 2000. Cartographic bases of federation units downloaded from IBGE (2017), for Biomes from IBGE (2019b) and for the Northeast region of Brazil from Codegeo (2013).

Results and Discussion

Taxonomy

Abrachium floriforme (Baseia & Calonge) Baseia & TS Cabral (2012) (Fig. 1, A–C)

Description: Immature basidiomata 10–20 × 5–16 mm, globose to subglobose, epigeous, papery, white ($N_{00}Y_{00}M_{00}$), smooth base, cracked in yellowish grey scales above ($N_{50}C_{20}Y_{40}$). **Expanded basidiomata** 30–60 mm high. **Receptacle** 40–55 mm diameter, flat to concave, orange rose ($N_{00}Y_{40}M_{20}$), sunflower-shaped with slightly serrated edge, without arms or any vestiges of them, with **central disc** perforated, 10–20 mm diam, 3–7 mm width (difference between hole and disc diameter), hollow (in some basidiomata), reddish pink ($N_{00}Y_{60}M_{99}$), reticulate surface, covered by **gleba** gelatinous, olive brown ($N_{90}C_{00}Y_{50}$), fetid. **Pseudostipe** 20–30 × 7–10 mm, orange pink ($N_{00}Y_{40}M_{20}$), cylindrical, spongy, hollow. **Volva** 10–20 × 7–16 mm, subglobose, tree layers: gelatinous endoperidium, yellow ($N_{00}Y_{40}M_{00}$); spongy mesoperidium, white ($N_{00}Y_{00}M_{00}$); papery exoperidium, white ($N_{00}Y_{00}M_{00}$) smooth base, cracked in yellowish grey scales above ($N_{50}C_{20}Y_{40}$). **Rhizomorph** up to 25 × 0.5–1 mm, white ($N_{00}Y_{00}M_{00}$), with ramifications, adhered to the base of the volva and immature basidiomata. **Basidiospores** 3.9–5.6[–6.1] × 1.4–2.4 μm (x = 4.8 ± 0.2 × 1.9 ± 0.1, Qm = 2.57), cylindrical, smooth, with an inner gutule at each end of the length, hyaline in 5% KOH. **Receptacle** composed of pseudoparenchymatous hyphae, 15.7–35[–40] × 12.5–34.1 μm, hyaline, globose, subglobose and broadly ellipsoid, straight and regular walls, 0.5–1 μm thick. **Central disc** composed of pseudoparenchymatous hyphae, 14.7–41.7 × 13–37.4 μm, hyaline, globose, subglobose and broadly ellipsoid, straight and regular walls, 0.6–1.6 μm thick. **Pseudostipe** composed of pseudoparenchymatous hyphae, 18.6–33.7[–45.4] × 17.2–31.2[–38.6] μm, hyaline, globose to subglobose, straight and regular walls, 0.6–1.2 μm thick. **Endoperidium** composed of filamentous and branched hyphae, swollen towards the septa and at the end of some hyphae, regularly septate, 2.2–3 μm, hyaline, straight and regular walls, 0.2–0.5 μm thick. **Mesoperidium** composed of filamentous and branched hyphae, not swollen, regularly septate, septa slightly apart from each other, [2.5–]3.2–6.6[–7.1] μm, hyaline, straight and regular walls, 0.3–0.7 μm thick. **Exoperidium** composed of pseudoparenchymatous hyphae, 3.2–8.5 × 2.4–7.7 μm, hyaline with dark brown lumen, globose, subglobose and irregular, straight and regular walls, 0.2–0.5 μm thick. **Rhizomorph** composed of filamentous and branched hyphae, swollen towards some hyphae end, regularly septate,

septa with thick middle part, 1.8–4.6 µm, hyaline, with connection clamps, straight and regular walls, 0.3–0.6 µm thick.

Material examined: Brazil, Ceará, **Ubajara,** Parque Nacional de Ubajara, Trilha Ubajara-Araticum (3°46'0"S, 40°54'0"W), 24 Jun 2013, A.C.M. Rodrigues, Sá M.C.A., F. Wartchow (UFRN–Fungos 2093); **Rio Grande do Norte**, **Baía Formosa**, Reserva Particular do Patrimônio Natural Mata da Estrela – RPPN Mata Estrela (6°24'33"S, 34°59'25"W), on sandy soil, 29 May 2004, M.M.B. Barbosa, I.G. Baseia, P.P.T. Lacerda, (UFRN–Fungos 203); *ibid*. 03 Jun 2004, I.G. Baseia (UFRN–Fungos 202, UFRN–Fungos 341); *ibid*. 01 Jul 2004, I.G. Baseia, P.P.T. Lacerda (UFRN–Fungos 130); *ibid*. 21 Apr 2010, M.M.B. Barbosa, T. Lockwood, I.G. Baseia (UFRN–Fungos 1429); *ibid*. on Trilha Principal 26 Jul 2019, P.M.G. Nascimento, J.F. Freitas-Neto, J.S. Góis, L.D.S. Eugênio, I.L.S.F. Freitas (UFRN–Fungos 3195); **Extremoz**, Praia de Pitangui (5°37'20.4"S, ”35°13'33.3"W), on sandy soil, 03 May 2008, B.D.B. Silva (UFRN–Fungos 1254); **Goianinha**, Limoal (6°14'56.9"S, 35°13'58.7"W), on sandy soil with litter, 05 May 2018, A.A. Lima, AAL 077 (UFRN-Fungos 3214); **Natal**, Parque Estadual Dunas de Natal (5°49'12"S, 35°11'16”W), on sandy soil covered by litter, 29 May 2004, I.G. Baseia, P.P.T. Lacerda, M.M.B Barbosa (UFRN–Fungos 203, UFRN–Fungos 204); *ibid*. in the Bosque 10 Jul 2004, I.G. Baseia, P.P.T. Lacerda (UFRN–Fungos 131; UFRN–Fungos 132; UFRN–Fungos 135, UFRN–Fungos 138; UFRN–Fungos 139, UFRN–Fungos 140); *ibid*. 16 Jul 2004, I.G. Baseia, P.P.T. Lacerda (UFRN–Fungos 133, UFRN–Fungos 134, UFRN–Fungos 137, UFRN–Fungos 142); *ibid*. 29 Apr 2005, Baseia, I.G.; Lacerda, P.P.T; Barbosa, M.M.B. (UFRN–Fungos 201); *ibid*. 17 Jul 2005, I.G. Baseia, P.P.T. Lacerda, M.M.B Barbosa (UFRN–Fungos 208); *ibid*. 20 Jul 2005, I.G. Baseia, P.P.T. Lacerda, M.M.B Barbosa (UFRN–Fungos 209); *ibid*. 18 Jun 2006, B.D.B. Silva, P.P.T. Lacerda A.G. Leite (UFRN–Fungos 448, UFRN–Fungos 449, UFRN–Fungos 467, UFRN–Fun- gos 497); *ibid*. 18 Jun 2006, E. P. Fazolino, B.D.B. Silva, A.G. Leite (UFRN–Fungos 453, UFRN–Fungos 467, UFRN–Fungos 497); *ibid*. 08 Jul 2006, E. P. Fazolino, B.D.B. Silva, A.G. Leite (UFRN–Fungos 452); *ibid*. in Centro de Pesquisa 23 Jun 2007, B.D.B. Silva; E. P. Fazolino (UFRN–Fungos 1219); *ibid*. on Trilha do Urubu 30 Aug 2008, M.I.M. Cocentino, E. P. Fazolino (UFRN–Fungos 838); *ibid*. 24 Jun 2010, I.G. Baseia, B.D.B. Silva, D.S. Alfredo, H.K.F. Assis, (UFRN–Fungos 1162); *ibid*. 28 Jun 2010, M.M.B. Barbosa (UFRN–Fungos 1430); *ibid*. on Trilha Perobinha 17 Jul 2010, B.D.B. Silva, A.G. Leite, N. Menoli, R.H.S.F. Cruz (UFRN–Fungos 1390); *ibid*. on Trilha da Peroba 11 May 2011, A.G. Leite, J.O. Sousa, E. Jalles,. B.D.B. Silva (UFRN–Fungos 1484); *ibid*. on Trilha da Geologia 07 Jul 2014, E.J. Sousa, Sulzbacher M.A., J.S. Góis, J.F. Freitas-Neto; *ibid*. on Trilha da Geologia 09 Aug 2019, P.M.G. Nascimento, J.F. Freitas-Neto, J.S. Góis, L.D.S. Eugênio, I.L.S.F. Freitas (UFRN–Fungos 3194); *ibid*. on Trilha da Geologia 15 Aug 2019, M.D. Xavier (16: UFRN–Fungos 3271; 17: UFRN–Fungos 3272); **Tibau do Sul**, Pipa, (6°11'23"S, 35°5'29"W), on sandy soil covered with litter, 17 Jun 2010, Silva, B.D.B.; Leite, A.G. (51: UFRN–Fungos 3273, 54: UFRN–Fungos 3274).

Habitat: Solitary habit, found on sandy soil covered by litter.

Geographic distribution in Brazil: Bahia (Bezerra et al. 2009), Ceará (Leite et al. 2007, Baseia et al. 2014), Espírito Santo (Magnago et al. 2013), Paraíba (Trierveiler-Pereira & Baseia 2011), Santa Catarina (Trierveiler-Pereira et al. 2019), Rio Grande do Norte (Baseia & Calonge 2005, Baseia et al. 2006, Leite et al. 2007, Cabral et al. 2012, Lima & Baseia 2018, present study).

Notes: *Abrachium floriforme* was reported for the first time in Brazil under *Aseroë floriformis* (Baseia & Calonge 2005). With the molecular biology, Cabral et al. (2012) recognized *Abrachium* as a new genus and proposed an amendment in the Clathraceae family, because although this genus has multipileate development, it does not present arms or any vestige of them. We made a review of all exsiccates deposited under UFRN-Fungos Her- barium and those not published were listed here. Most of the records are for Rio Grande do Norte State. In our review, we checked variations between sizes and colors of the ba- sidiomata. When comparing with other publications (Magnago et al. 2013, Trierveiler- Pereira et al. 2019), it is possible to see variations in the forms of pseudostipe, receptacle and central disc too. Some revision and more molecular data are important to understand if the genus is monospecific or not.

Clathrus natalensis GS Medeiros, Melanda, TS Cabral, BDB Silva & Baseia (2018) (Fig. 1, D–G)

Description: Immature basidiomata 21 × 24 mm, subglobose, epigeous, yellowish white ($N_{00}Y_{10}M_{00}$), glabrous surface, encrusted with sand. **Expanded basidiomata** 71–90 × 63–70 mm, subglobose to obovate. **Arms** meshes pentagonal to hexagonal, white ($N_{00}Y_{00}M_{00}$) to pinkish white ($N_{00}Y_{20}M_{10}$), smooth, becoming rugose after drying, transverse section of an arm shows 4–5 tubes subglobose to elongated. **Pseudostipe** absent. **Gleba** mucilaginous, in all inner part of arms, olive brown ($N_{90}C_{00}Y_{90}$), fetid. **Volva** 26–32 × 24–28 mm, two layers: gelatinous endoperidium, yellow ($N_{00}Y_{40}M_{00}$); papery exoperidium, yellowish white ($N_{00}Y_{10}M_{00}$), subglobose, glabrous surface. **Rhizomorph** up to 31 mm high, yellowish white ($N_{00}Y_{10}M_{00}$) adhered to the base of the volva and immature basidiomata. **Basidiospores** 4.2–5.5 × 1.5–2.1 µm (x = 4.7 ± 0.3 × 1.8 ± 0.1; Qm = 2.66), cylindrical, smooth, hyaline in 5% KOH. **Arms** exhibiting pseudoparenchymatous hyphae, 18.7–29.7 × 12–25 µm, hyaline, globose, subglobose to ellipsoid, wall <1µm. **Endoperidium** composed of filamentous hyphae, 2.4–4.9 µm, straight, hyaline, wall <1µm, septate and branched. **Exoperidium** composed of filamentous hyphae, 2,3–8,5 µm, straight, with irregular parts, hyaline, thin wall <1µm, septate and branched. **Rhizomorph** composed of filamentous hyphae, 1.7–4.7 µm, hyaline, wall <1µm.

Material examined: Brazil, Rio Grande do Norte, Goianinha, Limoal (6°14'45.3"S, 35°13'26.9"W), on sandy soil, 09 May 2018, A.A. Lima, AAL 078 (UFRN-Fungos 3215).

Habitat: Gregarious habit, found on sandy soil with sugarcane litter.

Geographic distribution in Brazil: Rio Grande do Norte (Crous et al. 2018, present study).

Notes: *Clathrus natalensis* highlighted with the color of the arms as well as the gleba mass in all inner part of arms. There are still some doubts about the color to separate species in Phallales in general, a species with similar color to *C. natalensis* is *C. cristatus* but this differs from the former by the crests along the arm edges (Fazolino et al. 2010). *C. crysomycelinus*. *C. delicatus*, *C. preussi* (groove and fringe) and *C. oahuensis* have whitish basidiomata, somewhat similar to *C. natalensis*. *C. crysomycelinus* differs in presenting a gleba restricted to small droplets seated on the glebifers at the junction of the arms. *C. preussi* and *C. oahuensis* presents short setae like arm extensions, in the first as a neat fringe along the out-lateral edge of the arms, and in the second scattered irregularly; *C. preussi* also differs by smaller (up to 60 mm high) basidiomata with a

longitudinal groove down the outer face of the arms. *C. delicatus* also presents a deep groove on the outer face of the arms but is smaller than *C. preussi*, reaching up to 25 mm high and no setae. *C. ruber*, in contrast, presents a vivid red color and differs from *C. natalensis* in having smaller meshes, wider arms and the immature basidiome marked by reticulations (Dring 1980). For northeastern Brazil, in addition to *C. natalensis* described from a collection carried out in Natal-RN and now collected at Goianinha-RN in the present study, only *Clathrus chrysomycelinus*, *C. cristatus* and *C. columnatus* were recorded, the last of these does not present meshes in the arms.

Mutinus argentinus Speg. (1887) (Fig. 1, H–K)

Description: Immature basidiomata 12–16 × 6–10 mm, ellipsoid, semi-hypogeous, white ($N_{00}Y_{00}M_{00}$) to yellowish brown ($N_{60}Y_{90}M_{60}$). **Expanded basidiomata** 77–95 × 7 mm. **Pseudostipe** cylindrical, apically not perforate, hollow, spongy; **sterile portion** whitish ($N_{00}Y_{00}M_{00}$) to light pink ($Y_{30}M_{40}C_{00}$), slightly curved, not chambered; **fertile portion** reddish pink ($Y_{60}M_{99}C_{40}$), well-defined, subulate, slightly rugulose to rugulose, covering about 1/3 of the total length of pseudostipe. **Volva** 13–17 × 7–10 mm, white ($N_{00}Y_{00}M_{00}$) to yellowish brown ($N_{60}Y_{90}M_{60}$). **Rhizomorph** white ($N_{00}Y_{00}M_{00}$) adhered to the base of the volva and immature basidiomata. **Gleba** spread in the fertile region of the pseudostipe, olive brown ($N_{90}C_{00}Y_{40}$), mucilaginous, fetid. **Basidiospores** 3.7–5 × 0.8–
1.8 μm (x = 4.3 ± 0.2 × 1.2 ± 0.2, Qm = 3.65), cylindrical to bacilliform, smooth, hyaline in 5% KOH. **Pseudostipe** composed of pseudoparenchymatous hyphae, 25–89.5 × 18.6–

70.4 μm, hyaline, globose, subglobose to irregular shaped, thick walls (>1 μm). **Volva** composed of filamentous hyphae, 2.3–7 μm, hyaline, septate, branched. **Rhizomorphs** composed of filamentous hyphae, 2.8–7.5 μm, hyaline, septate, branched.

Material examined: Brazil, Rio Grande do Norte, Arez, BR 101 highway (6°14'1.3"S, 35°12'51.9"W), on bamboo litter, 22 Jul 2019, A.A. Lima, AAL 096 (UFRN-Fungos 3220); **Goianinha**, BR 101 highway (6°14'33.9"S, 35°12'56.7"W), on bamboo litter, 22 Jul 2019, A.A. Lima, AAL 99 (UFRN-Fungos 3221).

Habitat: Solitary habit, found on bamboo litter.

Geographic distribution in Brazil: Paraná (Meijer 2006, Alves & Cortez 2016, Alves et al. 2018, Trierveiler-Pereira et al. 2019), Paraíba (Magnago et al. 2013), Santa Catarina (Möller 1895 – as *M. bambusinus*, Alves et al. 2018, Trierveiler-Pereira et al. 2019), Ceará (Lima et al. 2019), Rio Grande do Norte (present study).

Notes: This species is recognized by its pseudostipe with fertile portion reddish-pink and well-defined, rugulose surface and sterile portion white to light pink without chambers. *Mutinus argentinus* resembles *M. elegans* (Mont.) E. Fisch. However, *M. elegans* differs by the orange pseudostipe and not markedly defined fertile portion, presenting the same texture throughout its surface (Trierveiler-Pereira et al. 2019). *M. argentinus* and *M. bambusinus* (Zoll.) E. Fisch are also similar (see note below about *M. bambusinus*). This is the first record for Rio Grande do Norte State.

Mutinus bambusinus (Zoll.) E. Fisch. (1887) (Fig. 1, L–O)

Description: Immature basidiomata 23–25 × 18–20 mm, subglobose, semi-hypogeous, white ($N_{00}Y_{00}M_{00}$), encrusted, with rhizomorph adhered at the base. **Expanded basidiomata** 89–148 × 9–12 mm. **Pseudostipe** cylindrical, apically not perforate, hollow, spongy; **sterile portion** light pink ($N_{00}Y_{10}M_{00}$), slightly curved, with open chamber; **fertile portion** reddish pink ($Y_{60}M_{99}C_{00\text{-}50}$), well-defined, conical, slightly granulose, covering more than 1/3 of the total length of pseudostipe, with a sterile tip on the apex. **Volva** 21–23 × 15–19 mm, two layers: gelatinous endoperidium, yellow ($N_{00}Y_{40}M_{00}$); papery exoperidium, white ($N_{00}Y_{00}M_{00}$), encrusted. **Rhizomorph** white ($N_{00}Y_{00}M_{00}$) adhered to the base of the volva and immature basidiomata. **Gleba** spreaded in the fertile region of the pseudostipe, olive brown ($Y_{70}M_{50}C_{50}$), mucilaginous, fetid. **Basidiospores** 3.5–4.4 [–5] × 1.1–1.7 µm (x = 4.0 ± 0.2 × 1.3 ± 0.1, Qm = 2.96), cylindrical to bacilliform, smooth, hyaline in 5% KOH. **Pseudostipe** composed of pseudoparenchymatous hyphae, 24–51.4 × 18.5–47.7 µm hyaline, globose, subglobose to slightly elliptical shaped, thin walls (<1 µm). **Endoperidium** composed of filamentous hyphae, 1.4–3 µm, straight, hyaline, thin walls (<1µm), septate. **Exoperidium** composed of filamentous hyphae, 2–9.2[–10.4] µm, straight, with irregular parts, hyaline, thin walls (<1 µm), septate and branched. **Rhizomorph** composed of filamentous hyphae, 2.3–4.2 µm, hyaline, septate.

Material examined: Brazil, Rio Grande do Norte, **Arez**, BR 101 highway (6°14'01.0"S, 35°12'53.9"W), on bamboo litter, 09 Jul 2019, A.A. Lima, H.P. Lima, AAL 092 (UFRN- Fungos 3218), AAL 093 (UFRN-Fungos 3219); **Goianinha,** BR 101 highway (6°14'33.9"S, 35°12'56.7"W), on bamboo litter, 22 Jul 2019, A.A. Lima, H.P. Lima, AAL 100 (UFRN-Fungos 3222).

Habitat: Solitary or gregarious habit, found on bamboo litter.

Geographic distribution in Brazil: Rio Grande do Norte (present study).

Notes: *Mutinus bambusinus* is recognized for its pseudostipe with a reddish-pink, well-defined fertile portion, granulose surface, with a sterile tip on the apex and light pink sterile portion with open chambers. *Mutinus bambusinus* and *M. argentinus* have been treated as synonyms by different authors (Kobayasi 1938, Cunningham 1944, Liu 1984). Dring & Rose (1977) distinguished the two species. Below, Table 1 shows the morphological differences between the two species, noted in our collections.

In addition, the volva in *M. bambusinus* remains white, while in *M. argentinus* it becomes brownish at the apex at maturity. After drying, the gelatinous layer becomes collapsed or indistinct in *M. argentinus*. In neotropics, many records of *M. bambusinus* may correspond to *M. argentinus* (Reid 1977, Gube & Piepenbring 2009). In a review of Phallales for Southern Brazil, Trierveiler-Pereira et al. (2019) verified that the record of *M. bambusinus* from Möller (1985) corresponds to *M. argentinus* and the record from Rick (1961) corresponds to *M. elegans*. Based on these misidentifications, the present record of *M. bambusinus* is the first for Brazil.

Table 1. Morphological differences between *M. bambusinus* and *M. argentinus.*

		Mutinus bambusinus	*Mutinus argentinus*
Immature basidioma		subglobose	ellipsoid
Fertile portion	surface	granulose	rugulose
	apex	with a sterile tip	without a sterile tip
Sterile portion	surface	with open chamber	without open chamber

Phallus atrovolvatus Kreisel & Calonge (2005) (Fig. 1, P–T)

Description: Immature basidiomata 20–32 × 22–30 mm, globose to subglobose, epigeous, dark grey ($N_{80}Y_{00}M_{30}$), white ($N_{00}M_{00}C_{00}$) in some basidiomata. **Expanded basidiomata** 102–160 mm high. **Receptacle** 20–30 × 24–33 mm, white ($N_{00}M_{00}C_{00}$), campanulate, asperulate to rugulose surface with rudimentary apical pore. **Pseudostipe** 90–132 × 20–30 mm, white ($N_{00}M_{00}C_{00}$), cylindrical, spongy, hollow. **Indusium** covering 1/3 to 1/2 of the basidiome, white ($N_{00}M_{00}C_{00}$), polygonal meshes, joined to the apex of the pseudostipe. **Volva** 25–35 × 30–36 mm, two layers: gelatinous endoperidium, yellow ($N_{00}Y_{40}M_{00}$); papery exoperidium, dark grey ($N_{80}Y_{00}M_{30}$), globose, smooth surface. **Rhizomorph** white ($N_{00}M_{00}C_{00}$), adhered to the base of volva and immature basidiomata. **Gleba** spreaded in the receptacle, olive green ($Y_{70}M_{50}C_{40}$) to olive brown ($Y_{70}M_{90}C_{70}$), mucilaginous, pleasant and sweet odor. **Basidiospores** 3.1–4.6 × 1.3–2 µm (x = 3.7 ± 0.3 × 1.5 ± 0.1, Qm = 2.40), cylindrical, smooth, hyaline in 5% KOH. **Pseudostipe** composed of pseudoparenchymatous hyphae, 26.7–55.5 × 25.5–48.5 µm, hyaline, subglobose to slightly elliptical, thin walls (<1 µm). **Indusium** composed of pseudoparenchymatous hyphae, 28.6–56.2 × 27–50.7 µm, hyaline, subglobose to slightly elliptical, thin walls (<1 µm). **Endoperidium** composed of filamentous hyphae, 1.8–4.1 µm, straight, hyaline, thin walls (<1 µm), branched, septate, with connection clamps. **Exoperidium** composed of filamentous hyphae, 2.9–6.8[–8.4] µm, straight, with inflated parts, hyaline, thin walls (<1 µm), branched, septate, with connection clamps. **Rhizomorph** composed of filamentous hyphae, 1.76–6.8 µm, hyaline, thin walls (<1 µm), with inflated tips.

Material examined: Brazil, Pernambuco, Recife, Sistema Agroflorestal (SAf)–UFPE (8°03'01.1"S, 34°56'57.3"W), on clay soil and wood decaying, 08 May 2019, A.A. Lima, G.G. Barreto, AAL 083 (UFRN-Fungos 3216).

Habitat: Solitary or gregarious habit, found on clay soil and decaying wood.

Geographic distribution in Brazil: Amazonas (Cabral et al. 2014) and Pernambuco (present study).

Notes: *Phallus atrovolvatus* is characterized by a well-developed white indusium, receptacle with rugulose to merulioid surface, gleba with a sweet, non-repellent odor and a black volva (Calonge; Kreisel & Mata 2005). It can be confused with *P. merulinus*, but the latter differs in that it has a pale volva, fetid gleba and bacilliform spores up to 3.2 × 1.2 µm (Cheype 2010). *Phallus denigricans*, a new neotropical species, also has a white indusium and blackish volva, but differs by a reticulate receptacle and elongated spores up to 4.6 × 2.5 µm (Cabral et al. 2019). In our samples, the volva showed a white to blackish color variation in some basidiomata. A species of *Phallus* with white indusium has been treated in the literature many times as *Phallus indusiatus*. In their analysis, Trierveiler-Pereira et al. (2017) indicated that this morphological species probably corresponds to a complex. Cabral et al. (2019) reviewed *Phallus indusiatus* and confirmed a hidden diversity within the complex. We agree with Calonge, Kreisel & Mata (2005) concerning the need and urgency for a worldwide monograph. This is the second record for Brazil and the first for Northeast Brazil.

Fig 1. *Abrachium floriforme*. A, B. Expanded basidioma. C. Basidiospores. *Clathrus natalensis*. D. Expanded basidioma. E. Immature basidioma. F. Sectioned arm. G. Basidiospores. *Mutinus argentinus.* H. Expanded basidioma. I. Sectioned immature basidioma. J. Fertile portion rugulose, without a sterile tip. K. Basidiospores. *Mutinus bambusinus*. L. Expanded basidioma. M. Sectioned immature basidioma. N. Fertile portion granulose, with a sterile tip. O. Basidiospores. *Phallus atrovolvatus*. P. Expanded basidioma. Q. Sectioned immature basidioma. R. Receptacle asperulate with rudimentary apical pore. S. Volva. T. Basidiospores. – Bars: A, B, D, E, H, I, J, L, M, N, P, Q, R, S = 10 mm, F = 2 mm, C, G, K, O, T = 10 µm.

Checklist of Phallales with distribution map from northeastern Brazil

Ten genera and 22 species (spp.) of phalloid fungi from northeastern Brazil had already been recorded by May 1st, 2020, totaling 61 occurrences (occ.). Of these, one genus and eight species are new to science (Table 2).

Table 2. Checklist of Phallales collected in northeastern Brazil up to 2019. * species collected from northeastern Brazil described as new to science. **: equivalent analyzed material from another publication. State: Bahia (BA), Ceará (CE), Paraíba (PB), Pernambuco (PE), Rio Grande do Norte (RN). Biome: Atlantic rainforest (Atl.), Caatinga (Caa.)

Species	State	City	Biome	Published in
Abrachium Baseia & TS Cabral				
*Abrachium floriforme**	BA	Jussari	Atl.	Bezerra et al. 2009 (as *Aseroë floriformis*)
	BA	Ilhéus	Atl.	Bezerra et al. 2009 (as *Aseroë floriformis*)
	CE	Tianguá	Atl.	Baseia et al. 2014
	CE	Crato	Atl.	Baseia et al. 2014
	CE	Viçosa do Ceará	Atl.	Leite et al. 2007 (as *Aseroë floriformis*)
	CE	Ubajara	Atl.	Present study
	PB	Mataraca	Atl.	Trierveiler-Pereira & Baseia 2011 (as *Aseroë floriformis*)
	RN	Extremoz	Atl.	Present study
	RN	Natal	Atl.	Baseia & Calonge 2005 (as *Aseroë floriformis*), Baseia et al. 2006, Leite et al. 2007** (as *Aseroë floriformis*); Cabral et al. 2012, Present study
	RN	Baia Formosa	Atl.	Baseia & Calonge 2005, Leite et al. 2007** (as *Aseroë floriformis*)
	RN	Tibau do Sul	Atl.	Lima & Baseia 2018, Present study
	RN	Goianinha	Atl.	Present study
Blumenavia Möller				
*Blumenavia baturitensis**	CE	Guaramiranga	Atl.	Rodrigues & Baseia 2013 (as *B. angolensis*), Melanda et al. 2020
Clathrus P. Micheli ex L.				
Clathrus chrysomycelinus	PE	Caruaru	Atl.	Fazolino et al. 2010
Clathrus columnatus	CE	Crato	Atl.	Baseia et al. 2014, Lima et al. 2019
	PB	Mamanguape	Atl.	Magnago et al. 2013
	RN	Tibau do Sul	Atl.	Lima & Baseia 2018
*Clathrus cristatus**	PB	Santa Terezinha	Caa.	Fazolino et al. 2010
*Clathrus natalensis**	RN	Natal	Atl.	Crous et al. 2018
	RN	Goianinha	Atl.	Present study

Table 2. cont.

Species	State	City	Biome	Published in
Ileodictyon Tul.				
Ileodictyon cibarium	PE	–	–	Lloyd 1906 (as *Clathrus cibarius*)
	RN	Natal	Atl.	Baseia et al. 2006, Leite et al. 2007**
Itajahya Möller				
Itajahya rosea	RN	Serra Negra do Norte	Caa.	Ottoni et al. 2010 (as *Phallus roseus*), Cabral et al. 2012**
Laternea Turpin				
Laternea dringii	CE	Crato	Atl.	Lima et al. 2019
	PB	Mamanguape	Atl.	Magnago et al. 2013
Laternea triscapa	RN	Natal	Atl.	Baseia et al. 2006, Leite et al. 2007**
Mutinus Fr.				
*Mutinus albotruncatus**	CE	Crato	Atl.	Silva et al. 2015; Lima et al. 2019
Mutinus argentinus	PB	João Pessoa	Atl.	Magnago et al. 2013
	CE	Crato	Atl.	Lima et al. 2019
	RN	Arez	Atl.	Present study
	RN	Goianinha	Atl.	Present study
Mutinus bambusinus	RN	Arez	Atl.	Present study
	RN	Goianinha	Atl.	Present study
Mutinus caninus	PB	Areia	Atl.	Baseia et al. 2014
	PB	Mamanguape	Atl.	Magnago et al. 2013
	RN	Natal	Atl.	Baseia et al. 2006
Mutinus elegans	CE	Ubajara	Atl.	Baseia et al. 2014
*Mutinus verrucosus**	RN	Baía Formosa	Atl.	Crous et al. 2017
Phallus Junius ex L				
Phallus atrovolvatus	PE	Recife	Atl.	Present study
*Phallus denigricans**	RN	Natal	Atl.	Cabral et al. 2019
Phallus indusiatus	CE	Crato	Atl.	Lima et al. 2019
	PB	Mamanguape	Atl.	Magnago et al. 2013
	PB	Mataraca	Atl.	Trierveiler-Pereira & Baseia 2011
	RN	Baia Formosa	Atl.	Baseia et al. 2006
	RN	Goianinha	Atl.	Lima & Baseia 2018
	RN	Natal	Atl.	Baseia et al. 2006
	RN	Tibau do Sul	Atl.	Lima & Baseia 2018
*Phallus squamulosus**	RN	Baia Formosa	Atl.	Cabral et al. 2019

Table 2. cont.

Species	State	City	Biome	Published in
Staheliomyces E. Fisch.				
Staheliomyces cinctus	RN	Natal	Atl.	Baseia et al. 2006, Leite et al. 2007**
	PB	João Pessoa	Atl.	Magnago et al. 2013
Xylophallus (Schltdl.)				
Xylophallus xylogenus	PE	Cabo de Santo Agostinho	Atl.	Baseia et al. 2003 (as *Phallus pygmaeus*), Baseia et al. 2006, Leite et al. 2007** (as *Phallus pygmaeus*)
	PE	Moreno	Atl.	Trierveiler & Silveira 2012
	PE	Recife	Atl.	Trierveiler & Silveira 2012

In the Northeast, *Abrachium floriforme* (as *Aseroë floriformis*) was the first Phallales species registered as new to science. In addition, seven other new species were proposed: *Blumenavia baturitensis* Melanda, M.P. Martín & Baseia, two *Clathrus* spp. (*C. cristatus* Fazolino, Calonge & Baseia and *C. natalensis*), two *Mutinus* spp. (*M. albotruncatus* B.D.B. Silva & Baseia and *M. verrucosus* T.S. Cabral, B.D.B. Silva, K. Hosaka, M.P. Martín & Baseia) and two *Phallus* spp. (*P. denigricans* T.S.Cabral, B.D.B.Silva & Baseia and *P. squamulosus* T.S. Cabral, B.D.B. Silva & Baseia). Another new species recorded was *Phallus pygmaeus* Baseia (Baseia et al. 2003) but this is actually a synonym of *Xylophallus xylogenus* (Mont.) E. Fisch. (Trierveiler-Pereira & Silveira 2012). Of these only *C. cristatus* was reported in the Caatinga, while the others were collected in the Atlantic rainforest.

Mutinus is the genus with the highest number of species records (6 spp.), followed by *Phallus* and *Clathrus* (4 spp. both) and *Laternea* (2 spp.). For *Abrachium*, *Blumenavia*, *Ileodictyon*, *Itajahya*, *Staheliomyces* and *Xylophallus* one species of each was recorded. All these cited species were collected in Atlantic rainforest except *Itajahya rosea* and *C. cristatus* in Caatinga. The species with the highest number of occurrences are *A. floriforme* (16 occ.) and *P. indusiatus* (7 occ.). *Abrachium* is a monospecific genus (Cabral et al. 2012) and *P. indusiatus* a species complex (Cabral et al. 2019). A review with molecular data may modify this statistic.

Rio Grande do Norte is the state with the highest number of occurrences of Phallales in the Northeast Region (28 occ.) (Fig. 2). Of these, nine occurrences are of *Abrachium floriforme*. Next, there is Ceará (14 occ.), Paraíba (10 occ.), Pernambuco (7 occ.) and Bahia (2 occ.). The other northeastern states still do not have registers of phalloid fungi. Regarding biomes, 95.1% of the occurrences were in Atlantic rainforest, 3.3% in Caat- inga and 1.6% are doubtful occurrences. One of the main explanations for this asymmetry of records is the proximity of the Atlantic rainforest to Brazilian capitals and academic centers, which leads to more visits and exploration by researchers. Another factor is that expanded basidiomata of Phallales are ephemeral and lose their characters easily after a while (Magnago et al. 2013), so that they may not be possible to identify, and one-off collections may not result in records of these fungi. The data showed that Northeast Brazil is favorable for the development of phalloid fungi. However, it is still far from showing its real diversity. There is an asymmetry of knowledge, so several studies are needed, especially in unexplored areas.

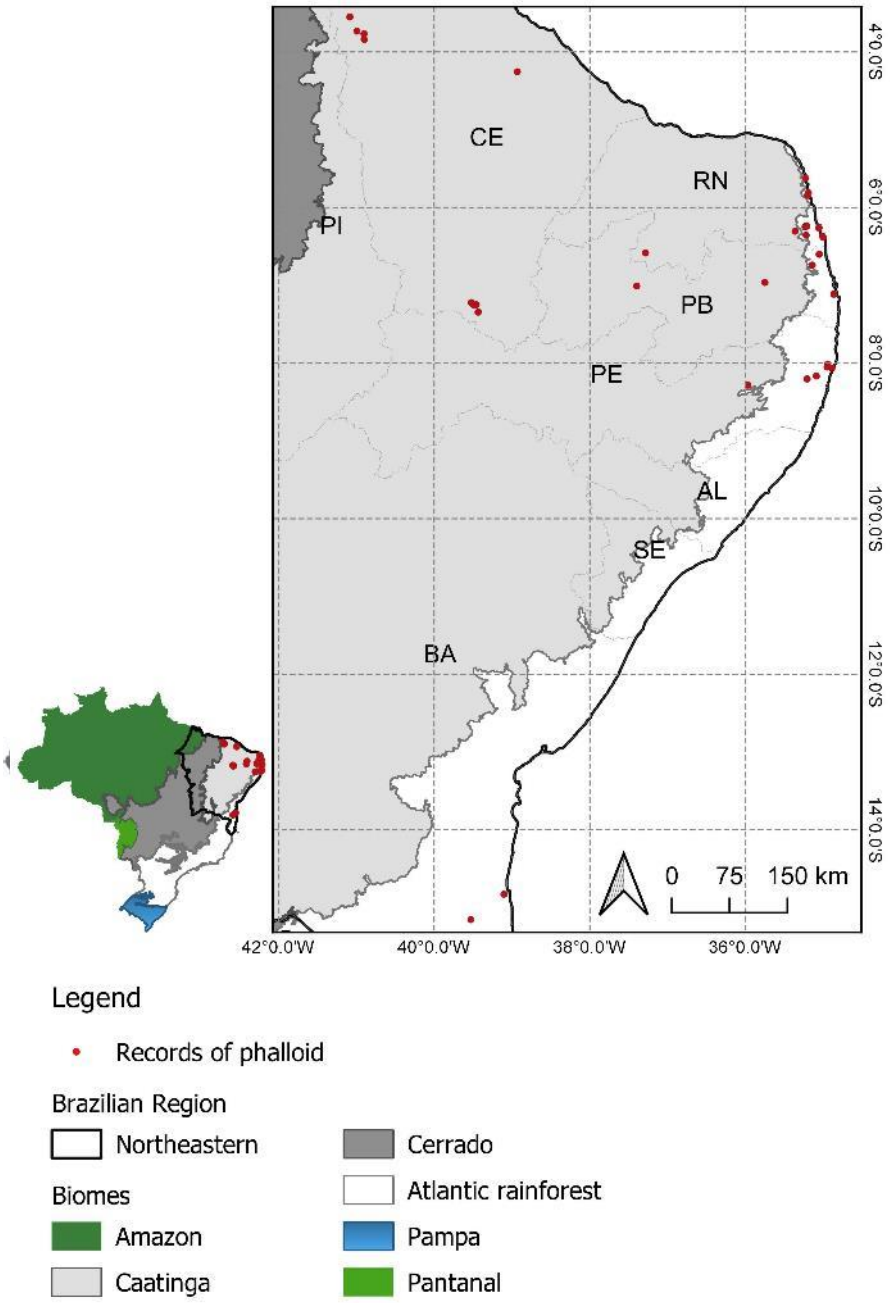

Fig. 2. Distribution map of phalloid fungi in northeastern Brazil.

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APÊNDICE G – PRIMEIRA OCORRÊNCIA DE *Blumenavia rhacodes* MÖLLER (BASIDIOMYCOTA, FUNGI) NA PORÇÃO BRASILEIRA DO BIOMA PAMPA

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Arrudea
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Primeira ocorrência de *Blumenavia rhacodes* Möller (Basidiomycota, Fungi) na porção brasileira do bioma Pampa

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Abstract

The genus *Blumenavia* Möller is mentioned for the first time to the Brazilian Pampa, with *B. rhacodes* Möller, increasing the known distribution area of the species in Brazil, reporting its occurrence for the first time outside Atlantic Rain Forest areas.

Keywords

Biodiversity, Clathraceae, Phallales

Resumo

O gênero *Blumenavia* Möller é citado pela primeira vez para o Pampa brasileiro, com *B. rhacodes* Möller, aumentando a área de distribuição conhecida da espécie no Brasil e relatando sua ocorrência pela primeira vez fora de áreas de Mata Atlântica.

Palavras-chave

Biodiversidade, Clathraceae, Phallales

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Introdução

O bioma Pampa abrange todo o território do Uruguai, parte do território da Argentina e, no Brasil, é restrito ao estado do Rio Grande do Sul, ocupando sua metade sul, cobrindo mais de 60% do território gaúcho e cerca de 2% do território nacional (IBGE 2019). Apesar de sua grande importância ecológica, o Pampa rio grandense só foi reconhecido como um bioma brasileiro em 2004, o que ajudou a valorizar sua riqueza e a ressaltar a necessidade de conservação de sua área. Talvez, seja este reconhecimento tardio, um dos motivos para que haja nele tão poucas áreas protegidas. Neste bioma apenas 17 áreas, distribuídas por 6.494 hectares e representativas de somente 3,6 % da sua área total (Schnadelbach & Picoli 2007).

O Pampa rio grandense possui grande predominância de gramíneas, abrigando uma das mais ricas diversidades do planeta (Boldrini 2009). No entanto, juntamente com o Pantanal, é um dos biomas cuja funga é menos estudada no Brasil, com apenas 84 espécies citadas (Maia et al. 2015), sendo apenas dois representantes da ordem Phalales: *Clathrus columnatus* Bosc e *Lysurus cruciatus* (Leor. & Mont.) Henn. (Trierveller-Pereira 2014).

Na ordem Phalales encontra-se o gênero *Blumenavia* Möller, proposto por Möller (1895), baseado em material coletado no sul do Brasil, estado de Santa Catarina, no município de Blumenau, de onde provém o seu nome. Este gênero tem como espécie tipo, *Blumenavia rhacodes* Möller, proposta por Möller (1895). Posteriormente Hennings (1902) descreveu uma nova espécie, *B. usambarensis* Henn., para a África oriental, a qual foi considerada por Dring (1980) como sinonímia de *B. angolensis* (Welw. & Curr.) Dring. Vargas-Rodríguez & Vasquez-Garcia (2005) descreveram uma terceira espécie, *B. toribiotalpaensis* Vargas-Rodr., para o México, porém, Calonge et al. (2007) e López & Garcia (2012), consideram-na como sinonímia de *B. rhacodes*.

A existência de apenas duas espécies para o gênero, *B. rhacodes* e *B. angolensis*, foi aceita em todos os trabalhos com o grupo até então. No entanto, Melanda et al. (2020), com base em caracteres morfológicos e dados moleculares, propõem a revalidação de *B. usambarensis* e *B. toribiotalpaensis*, além de três novas espécies, a saber: *B. heroica* Melanda, Baseia & M.P. Martín, *B. baturitensis* Melanda, M.P. Martín & Baseia e *B. crucis-hellenicae* G. Coelho, Sulzbacher, Grebenc & Cortez. Ainda de acordo com Melanda et al. (2020), as duas últimas ocorrem apenas no Brasil, nas regiões Nordeste (Ceará) e Sul (Paraná e Rio Grande do Sul), respectivamente, e *B. rhacodes*, ocorre somente no sul do país, em Santa Catarina e Rio Grande do Sul, existindo ainda citações de ocorrência para a Argentina (Domínguez de Toledo 1995) e Colômbia, depositado no Herbario Nacional Colombiano (COL) e Venezuela, depositado no New York Botanical Garden (NY).

No Brasil, *Blumenavia rhacodes*, que ocorre apenas na região Sul, é restrita às áreas de Mata Atlântica, não havendo relatos de sua ocorrência em outro local no país (Trierveiler-

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Pereira et al. 2014; Melanda et al. 2020). Diante disso, visando contribuir com o conhecimento e distribuição da funga do Rio Grande do Sul, este trabalho traz o primeiro relato de ocorrência de *Blumenavia rhacodes* para a porção brasileira do bioma Pampa.

Material e Métodos

O material foi coletado na Reserva Ecológica da Sanga da Bica (Figura 1), no município de São Gabriel – RS, em abril de 2019. O município está inserido no bioma Pampa, na porção oriental da região fisiográfica da Campanha, localizado a 320 km de distância de Porto Alegre, com clima do tipo Cfa (clima temperado úmido com verão quente), conforme a classificação de Köeppen (Moreno 1961).

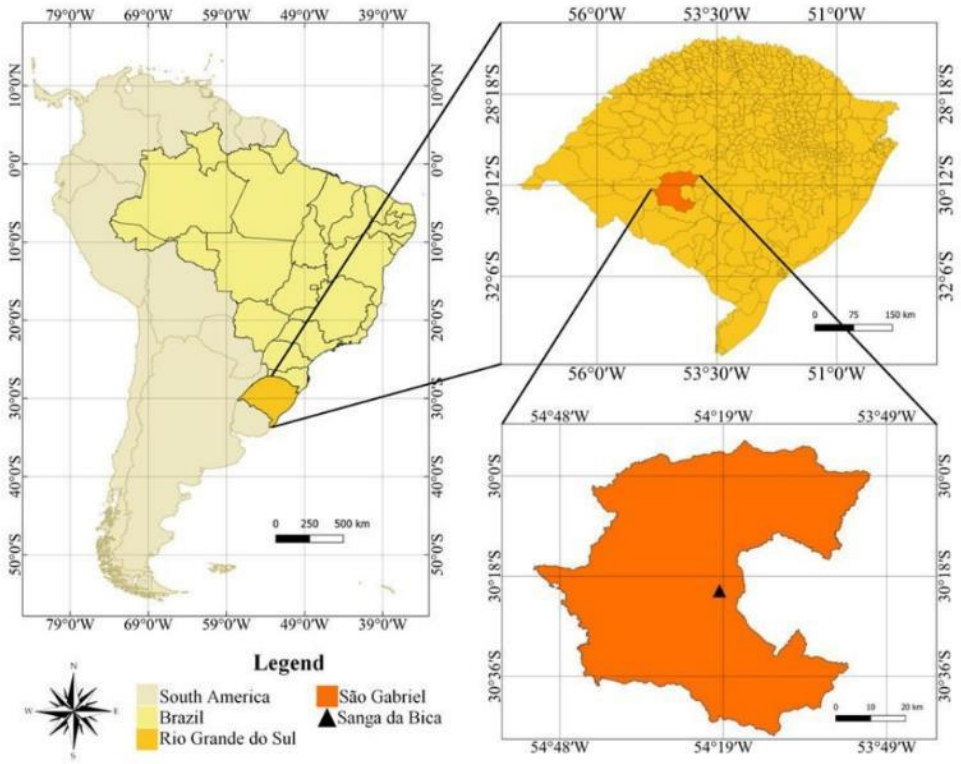

Figura 1. Localização da coleta do novo registro de *Blumenavia rhacodes* para a porção brasileira do bioma Pampa

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Após a coleta, o espécime foi levado ao laboratório Núcleo de Estudos da Vegetação Antártica – N.E.V.A., na Universidade Federal do Pampa – UNIPAMPA, onde foram feitas análises macromorfológicas e micromorfológicas para determinação da espécie, utilizando-se literatura especializada para o grupo (Trierveiler-Pereira et al. 2014; Melanda et al. 2020). Os códigos das cores seguiram a carta de cores de Küppers (2002). O material passou pelo processo de herborização, desidratando em estufa, por aproximadamente 72 horas, a 40 graus. Após desidratado, o material foi adicionado ao acervo do Herbário Bruno Edgar Irgang – HBEI.

Resultados

Taxonomia

***Blumenavia rhacodes* Möller 1895** (Figura 2)

Receptáculo com 142 mm de alt. total, coloração amarelado-esbranquiçado a laranja-claro (Y70M10C00 – Y99M40C20), textura esponjosa, formado por 4 colunas trapezionais, tendo a parte externa mais larga que a parte interna, livres na base e unidas no ápice; presença de um sulco mediano ao longo de todo o comprimento externo de cada uma das colunas. Parte interna das colunas dentada e lacerada, tornando-se mais acentuado na região meso-apical. A região meso-abaxial apresenta crateras ao redor do sulco. Gleba com odor de frutas fermentadas, distribuindo-se internamente nas colunas, em glebíferos de forma triangular. Exoperídio branco (N00Y00M00) com a superfície externa quebrando em escamas irregulares cinzas (N70Y00M00). Rizomorfa com 24 mm de comprimento. Hifas do exoperídio apical hialinas em KOH 5%, filamentosas e com septos regularmente distribuídos. Esporos cilíndricos hialinos em KOH 5% lisos, com um sulco longitudinal, (3,1-) 3,2–4(-4,4) x (1) 1,2–1,4(1,6) µm.

Habitat: Solo de mata de galeria, em local parcialmente sombreado.

Material Examinado: BRASIL. Rio Grande do Sul: São Gabriel, Reserva Ecológica Sanga da Bica, 13.IV.2019, (30°20'37"S 54°19'14"O), J.R.P.Velloso 114 (HBEI 047).

Discussão

O material examinado é fiel aos caracteres típicos de *Blumenavia rhacodes*, citados por Melanda et al. (2020), como um leve sulco na face externa das colunas, glebíferos triangulares dispostos de maneira uniforme, hifas do exoperídio apical filamentosas, com septos uniformemente dispostos. Além da sua coloração amarelo-alaranjado claro, que a difere de *B. angolensis, B.usambarensis* e *B. crucis-hellenicae*, que apresentam coloração mais esbranquiçada. De *B. heroica*, *B. rhacodes* diferencia-se pelo basidioma maior, além de diferenças nas hifas do exoperídio apical. Já *Blumenavia baturitensis* não possui um sulco na face externa das colunas e seu glebífero apresenta projeções tentaculares enrugadas, diferente de *B. rhacodes* que apresenta sulco e glebíferos formados por projeções triangulares. Os glebíferos de *B. toribiotalpaensis* também se diferenciam de *B. rhacodes,* por serem retorcidos, com morfologia diferente ao longo do braço.

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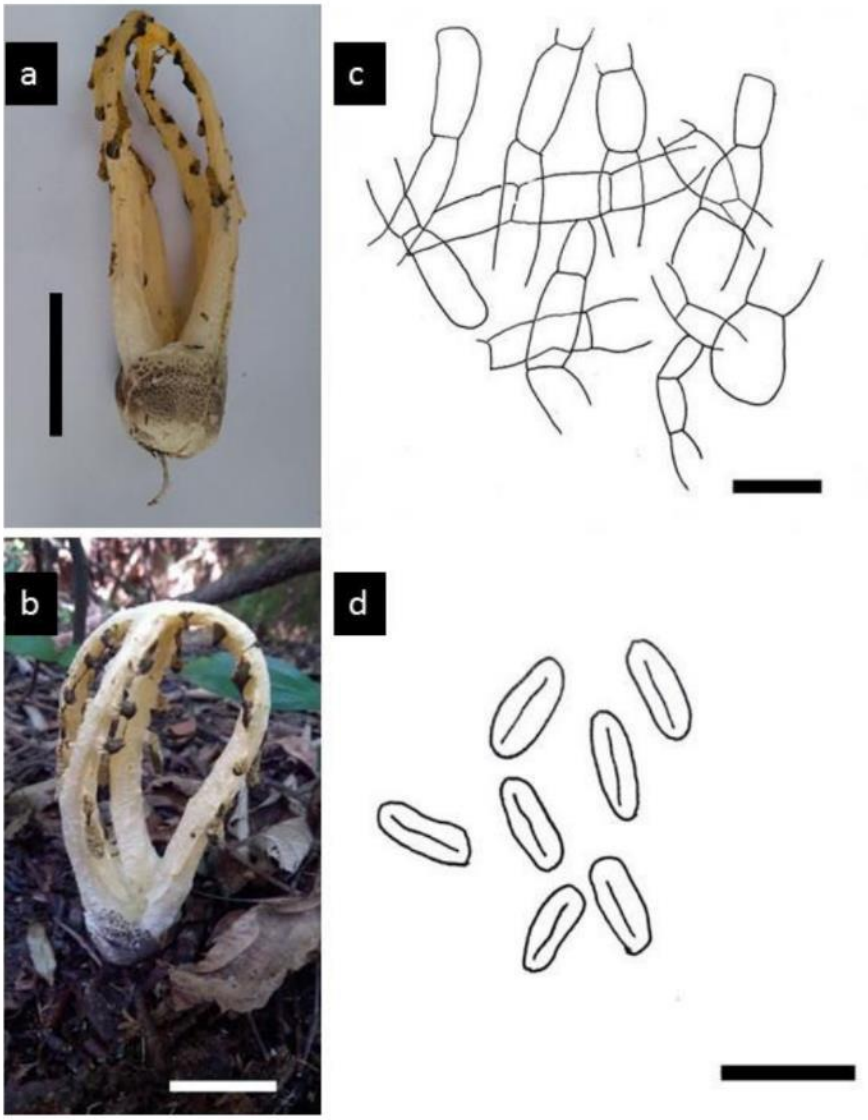

Figura 2. Morfologia de *Blumenavia rhacodes*. a – b: basidioma de *Blumenavia rhacodes*; c: hifas do exoperídio apical; d: esporos. Escalas: (a) 5 cm; (b) 5 cm; (c) 5 µm (d) 10 µm.

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A ocorrência de *B. rhacodes* no bioma Pampa já é conhecida para a Argentina, na Província de Santa Fé (Domínguez de Toledo 1995), a 760 km do município de São Gabriel – RS, onde o espécime deste trabalho foi coletado. Porém o único estudo realizado com fungos da ordem Phallales na porção brasileira do bioma menciona a ocorrência de apenas duas espécies: *Clathrus columnatus* e *Lysurus cruciatus* (Trierveiler-Pereira et al. 2014) ficando a grande maioria do conhecimento acerca do grupo, no Rio Grande do Sul, concentrada nas áreas de Mata Atlântica. Do mesmo modo, *B. rhacodes* é uma espécie cuja ocorrência limitava-se a apenas esse bioma, o que, de acordo com a literatura, pode ser explicado pela aproximação dessas áreas com os centros de pesquisa, sendo essa a primeira vez em que a espécie é citada para outro bioma no Brasil.

A citação de *B. rhacodes* para a porção brasileira do bioma Pampa aumenta a área de distribuição conhecida para a espécie, contribuindo com o conhecimento acerca da funga do Rio Grande do Sul, sobretudo na porção do Pampa. Essa nova ocorrência também prova que conhecer a diversidade dos diferentes grupos de fungos ocorrentes nesse bioma é de grande importância tanto para compreensão da ecologia desses organismos nos ecossistemas, quanto para a elaboração de políticas de conservação das espécies desse bioma. Isso deixa evidente a necessidade de mais trabalhos voltados à ecologia e taxonomia básica de fungos.

Agradecimentos

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APÊNDICE H – TAXONOMIC REVIEW OF *Colus schellenbergiae* AND *Clathrus columnatus* (PHALLALES, BASIDIOMYCOTA) FROM NORTH AMERICA

Primeiro *draft* do artigo a ser submetido possivelmente na *Journal of the Torrey Botanical Society*

RESUMO

Os fungos da ordem Phallales são macrofungos comumente conhecidos como chifres-fedorentos, devido aparência e odor que exalam para atração de agentes dispersores. A ordem é dividida em sete famílias com representantes expandidos e sequestrados, sendo os expandidos representados pelas famílias *Clathraceae*, *Lysuraceae* e *Phallaceae*. Estudos taxonômicos com estes fungos coletados no Estados Unidos resultaram na publicação de novas espécies, e posteriores revisões taxonômicas sinonimizaram algumas delas. *Clathrus columnatus* coletado na Carolina do Sul não apresenta indicação do voucher tipo em seu protólogo, e se considera que têm uma distribuição mundial. *Colus schellenbergiae* coletado na Pensilvânia, foi transferido para o gênero *Pseudocolus* e posteriormente alocado na espécie *P. fusiformis* como um sinônimo heterotípico. A revisão de materiais tipo ou materiais de localidade tipo, quando o tipo não existe ou não foi encontrado, são de extrema importância para a reavaliação da identificação e confirmação das sinonimizações. Visto isso, o objetivo do presente artigo é reavaliar a identidade de *Clathrus columnatus* e *Colus schellenbergiae* por meio de análises morfológicas de materiais tipo ou localidade tipo. Foi analisado o isótipo de *Colus schellenbergiae* e materiais da localidade tipo de *Clathrus columnatus*, além de espécimes de *Pseudocolus fusiformis* coletados nos EUA. A identificação de *Clathrus columnatus* foi mantida e *Colus schellenbergiae* foi aceito como pertencente ao gênero *Pseudocolus*, embora não como sinônimo de *P. fusiformis*. A principal diferença entre *P. schellenbergiae* e *P. fusiformis* está no tamanho dos basidiosporos.
Palavras-chave:, chifres-fedorentos, diversidade, Pensilvânia, *Pseudocolus fusiformis*.

ABSTRACT

The fungi of the Phallales order are macrofungal commonly known as stinkhorns, due to the appearance and odor they exude to attract dispersing agents. The order is divided into seven families with expanded and sequestered representatives, the expanded ones being represented by the *Clathraceae*, *Lysuraceae* and *Phallaceae* families. Taxonomic studies with these fungi collected in the United States resulted in the publication of new species, and later taxonomic revisions synonymized some of them. *Clathrus columnatus* collected in South Carolina has no

indication of the voucher type in its protologue, and is considered to have a worldwide distribution. *Colus schellenbergiae* collected in Pennsylvania, was transferred to the genus *Pseudocolus* and later allocated to the species *P. fusiformis* as a heterotypic synonym. The review of type materials or type locality materials, when the type does not exist or has not been found, is extremely important for the re-evaluation of the identification and confirmation of synonymities. Given this, the objective of this article is to reassess the identity of *Clathrus columnatus* and *Colus schellenbergiae* through morphological analyzes of type materials or type locality. The isotype of *Colus schellenbergiae* and materials from the type locality of *Clathrus columnatus* were analyzed, as well as specimens of *Pseudocolus fusiformis* collected in the USA. The identification of *Clathrus columnatus* was maintained and *Colus schellenbergiae* was accepted as belonging to the genus *Pseudocolus*, although not as a synonym of *P. fusiformis*. The main difference between *P. schellenbergiae* and *P. fusiformis* is in the size of the basidiospores.

Keywords: Diversity, Pennsylvania, *Pseudocolus fusiformis*, South Carolina, stinkhorns.

INTRODUCTION

The Phallales order comprise a huge gasteroid mushroom morphologies (stinkhorns, cage fungi, flower-fungi and false truffles) with mostly zoochoric passive dispersion of basidiospores, through the attraction of insects by the unpleasant odoriferous gleba (Miller and Miller 1988; Pegler and Gomez 1994; Hibbett et al. 1997; Hosaka et al. 2006; Cabral et al. 2012). The families with expanded basidiomata belong to *Clathraceae* Chevall., *Lysuraceae* Corda and *Phallaceae* Corda, with the types genera: *Clathrus* P. Micheli ex L., *Lysurus* Fr. and *Phallus* Junius ex L., respectively (Chevallier 1826; Corda 1842; Hosaka et al. 2006; Trierveiler-Pereira et al. 2014; Melanda et al. 2021). *Clathraceae* comprise the cage and flower-fungi, with sessile receptacle, and several branches connected or not (Chevallier 1826; Cabral et al. 2012). North American collections result in new species of *Clathraceae*, as *Clathrus columnatus* Bosc (Bosc 1811) and *Colus schellenbergiae* Sumst. (Sumstine 1916). *Clathrus columnatus* was described from South Carolina. This specie has four red quadrangular arms which are united above and free bellow, and differs from the clathrate *Clathrus* by the shape (Bosc 1811). In the protologue plate 5/figure 5 is represented the species with the natural size, and Bosc (1811) did not cite the local of the type deposit. Dring (1980) made a revision with specimens from North, South and Central America, Ethiopia and Australasia, expanding the *C. columnatus* distribution.

Colus schellenbergiae was described from Pennsylvania, Pittsburgh, based on materials collected in the yard of Mrs. F. F. Schellenberg, which justifies the species name. This species has a stipitate receptacle divided in three arms united in the apex, attenuate upward, 3–6 cm height; and the stipe portion is white below, orange-colored above and the arms are orange (Sumstine 1916). According Sumstine (1916) the type specimens have been deposited in the Carnegie Museum (Pittsburgh, Pennsylvania), and in the New York Botanical Garden. No catalog numbers were cited and no figures were represented; according to Coker and Couch (1928), this was the first collection of the genus in United States. Tirteen years later, Johnson (1929) transferred the species to *Pseudocolus*, proposing the combination *Pseudocolus schellenbergiae* (Sumst.) Johnson. However, Seaver (1931) did not agree with the combination *Pseudocolus schellenbergiae*, and identified New York collections as *Colus schellenbergiae*.

The genus *Pseudocolus* proposed by Lloyd is characterized by a receptacle composed of columnar arms united at the apex and in the base supported by one pseudostipe (Lloyd 1907a, b). According to Lloyd the genus *Colus* is characterized by a clathrate receptacle supported by arms which are united below in a pseudostipe; these arms are part of the pseudostipe and not part of the receptacle such as in *Pseudocolus* (Lloyd 1907a, b, 1909). The type species is *Pseudocolus rothae* (E. Fisch.) Lloyd, with the basonym *Colus rothae* E. Fisch (Lloyd 1907a). Besides *Colus rothae*, Lloyd also transferred to *Pseudocolus* the following species: *Colus fusiformis* E. Fisch. (Lloyd 1909), *Colus javanicus* Penz. (Lloyd 1907b, 1909) and *Colus garciae* Möller (Lloyd 1907b). Dring (1980) agreed with Lloyd and considered all pseudostipited with united columnar arms species in *Pseudocolus*, and the ones pseudostipited with arms and a clathrate part as *Colus*, and he considered *Pseudocolus javanicus*, *P. rothae* and *P. schellenbergiae*, heterotypic synonymies of *P. fusiformis*. On the other hand, Cunningham (1931) emended *Anthurus* Kalhbr. & McOwan ex Kalchr. & Cooke to include the genus *Pseudocolus*; although, some authors maintained the distinction of the two genera (Dring 1973, 1980; Blanton 1976).

The review of type materials and type locality materials can be important to clarify these taxonomic doubts that have arisen over time; such as the classification of species in certain genera and the acceptance of synonyms. Thus, the objective of this work is to verify the identity of *Clathrus columnatus* and *Colus schellenbergiae*, species with type locality in the USA, through morphological analysis and nomenclatural review.

MATERIAL AND METHODS

Collection data

The material analyzed were loaned from the following USA Herbaria: Field Museum of Natural History (F), University of North Carolina at Chapel Hill Herbarium- Fungi collection (NCU-F) and University of Tennessee Herbarium – Fungi collection (TENN-F).

Morphologic analyses

The basidiomata were analyzed macro and microscopically. To evaluate the macromorphology basidiomata size, shape and color were observed by naked eye or with the aid of a stereoscopic microscope; the colors code are according Küppers (2002). The micromorphology was carried out with optical microscope; the measurement and photos were done with 100X magnification. Slides were mounted, in freehand sections, with all parts of the basidiomata in 5% KOH and 1% Congo Red. Thirty hyphae of each structure, as well as 30 basidiospores per specimen were measured. For filamentous hyphae, the diameter and wall thickness were measured; for globose hyphae, the height and width plus wall thickness were measured. To basidiospores, the main values were described, as well as their respective standard deviation; the Qm value (length-to-width ratio) described in Bas (1969) was used to determine the shape of the basidiospores and globose hyphae.

RESULTS AND DISCUSSION

Three species in *Clathraceae* family were identified. The analyses of materials from the type locality of *Clathrus columnatus,* as well as others from North America, confirmed *C. columnatus* as a unique species. The isotype of *Colus schellenbergiae* was compared with other North American specimens and ratifed as belonged to the genus *Pseudocolus*. Moreover, *P. schellenbergiae* was verified as a distinct species of *Pseudocolus fusiformis*.

Taxonomy

Clathraceae

Clathrus columnatus Bosc, Magazin der Gesellschaft Naturforschenden Freunde Berlin 5: 85 (1811) [MB#200050] Figures 1A-F; 2A

Homotypic synonyms:

Clathrus colonnarius Leman, in Dict. Sci. Nat. 9: 360 (1817) [MB#202614]

Laternea columnata (Bosc) Nees, in Nees von Esenbeck & Henry, Das System der Pilze 2: 96 (1858) [MB#239159]

Clathrus cancellatus c. *columnatus* E. Fisch., Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss 32: 54 (1890)

Linderia columnata (Bosc) G. Cunn., Proceedings of the Linnean Society of New South Wales 56: 193 (1931) [MB#261377]

Colonnaria columnata (Bosc) E. Fisch., in Engler & Prantl, Die Natürl. Pflanzenf. 7a: 85 (1933) [MB#251522]

Linderiella columnata (Bosc) G. Cunn., New Zealand J. Sci. Technol., 23: 171B (1942) [MB#287791]

Heterotypic synonyms:

Colonnaria truncata Raf., Med. Repos. Hexade ser. 2, vol. 3: 423 (1806) [MB#151127] - *nomen nudum*

Colonnaria urceolata Raf., Med. Repos. Hexade ser. 2, vol. 3: 423 (1806) [MB#150836] - *nomen nudum*

Macroscopic characters— *Expanded basidiomata* including volva 40–70 mm long, about 15–25 mm between opposite arms where widest, receptacle with 4 columnar arms joined at apex, in some specimens united by a transversal arm at the top (Fig. 1C), free at base, smooth, light yellow to yellowish brown when dry ($Y_{99}M_{10}C_{10}$ – $Y_{99}M_{30}C_{30}$), arms even thickness throughout its length about 3–10 mm wide, outer face with a marked longitudinal groove. *Gleba* olive brown ($N_{99}A_{50}M_{10}$), attached of the inner face of the arms, most concentrated in the apical part. *Volva* 15–41 × 10–30 mm, subglobose to elongate; *peridium* composed of two layers: when dry exoperidium light brown ($N_{30}Y_{90}M_{30}$), encrusted by sand, and endoperidium dark yellow ($N_{10}Y_{80}M_{20}$). *Rhizomorph* single branched, white ($N_{00}M_{00}C_{00}$) extending from base.

Microscopic characters— *Rhizomorphs* consisting of septate filamentous hyphae, irregularly spaced septa, with inflated tips, and without clamp connections, 1.7–6.2 [$\bar{x}$= 3.6 ± 1.2] µm broad, straight, and regular walls 0.1–0.6 [$\bar{x}$ = 0.4 ± 0.1] µm thick, hyaline in 5% KOH, reddish with Congo red; with irregularly shaped cyan crystals. *Apical exoperidium* consisting of filamentous and elongated hyphae, hyaline in 5% KOH, some with brown lumen, reddish with Congo red, with irregularly shaped cyan crystals; filamentous hyphae branched, regularly septate, with inflated tips, and without clamp connections, (1.9) 3–9.4 (15.9) [$\bar{x}$ = 5.1 ± 1.6] µm broad, straight, and regular walls 0.3–1 [$\bar{x}$ = 0.6 ± 0.2] µm thick; elongated hyphae look like the filamentous hyphae separated in the septa. *Endoperidium* consisting of

branched filamentous hyphae, irregularly septate, with inflated tips, and without clamp connections, 1.5–5(7.2) [$\bar{x}$ = 3.5 ± 0.8] µm broad, straight, and regular walls 0.3–0.8 [$\bar{x}$ = 0.4 ± 0.1] µm thick, hyaline in 5% KOH, reddish with Congo red; with irregularly shaped cyan crystals. *Arms* exhibiting globose, subglobose to elongate cells, 11–52.5 × 9.4–39.1 [$\bar{x}$ = 25.9± 6.4 × 20.4 ± 5.0, Q = 1.00–1.70, Qm =1.29 ± 0.14] µm, straight and regular walls 0.4–1.4 [$\bar{x}$ = 0.8 ± 0.2] µm thick, hyaline in 5% KOH, reddish with Congo red. *Basidiospores* elongate to cylindrical 3.6–5.6 × 1.8–2.7 [$\bar{x}$ = 4.7 ± 0.2 × 2.3 ± 0.1, Q = 1.63–2.61, Qm = 2.05 ± 0.15] µm, smooth, with one inner guttule at each end of the length, hyaline in 5% KOH.

Distribution— USA: Florida, North Carolina,South Carolina (type locality), Texas.
Studied material— USA: FLORIDA, Alachua, Gainesville, 24.II.1928, Loucks & West s/nº (NCU-F-0003224); Franklin, On the west side of Eastpoint, southwest of Eastpoint, on a sand dune, 31.I.1949, F.E. Drouet & C.S. Nielsen s/nº (F: C0226317F, as *Clathrus* sp.); Leon, Tallahassee, 27.XII.1951, L.R. Hesler LRH20278 (TENN-F-020278); Polk, Babson Park, 17.II.1940, C.A. Reneger s/nº (NCU-F-0003259). NORTH CAROLINA, Forsyth, 806 South Hawthorn Rd, Winston Salem, in backyard, 1.XII.1948, A. Mordecai s/nº (NCU-F-0003225); Orange, Chapel Hill, 21.II.1937, M.S. Hamer 10410 (NCU-F-0003258). SOUTH CAROLINA, Three miles from Georgetown, in sandy soil, 29.XII.1922, W.C. Coker 6013 (NCU-F-0003256); Twelve miles from Georgetown, springwood, XI.1929, W.C. Coker 8432 (NCU-F-0003257). TEXAS, Hardin, Big Thicket National Preserve, Turkey Creek Unit; Kirby Nature Trail, in mixed woods with pine and hardwoods, 27.X.1984, D.P. Lewis 3790 (F: C0349805F).

Remarks— *Clathrus columnatus*, by the singular morphology of the basidiomata comprised by arms, was described as new in the genus, although the color is the same (red, *vermilion*), as the type species of the genus, *Clathrus ruber* P. Micheli ex Pers. (Bosc 1811).
Linderia columnata is the species type of the genus *Linderia* G. Cunn. (Cunningham 1931). The same author eleven years later changed the name of the genus to *Linderiella* G. Cunn. (Cunningham 1942). Cunningham (1944) accepted as synonyms of *Linderiella* the genera *Linderia* and *Colonnaria*, with three species: *Linderiella columnata*, *L. bicolumnata* (Lloyd) G. Cunn. and *L. pusilla* (Berk & Curt) G. Cunn., the last two as new combinations with basionyms of *Laternea*; and, as synonyms of *Linderiella columnata*: *Clathrus columnatus*, *C. collonarius*, *Laternea columnata*, *Clathrus cancellatus* f. *columnatus*, *C. trilobatus* Cobb., *Linderia columnata* and *Colonnaria columnata*. According Cunningham (1944) *Linderiella*

columnata shows variations in color, number and shape of columns, and the arms free in the base justified the not placement in the genus *Clathrus*.

Rafinesque mentioned the names *Colonnaria truncata* and *Colonnaria urceolata* as new names in 1806 and proposed the new genus in 1808 (Rafinesque 1806, 1808). These two names are considered invalids as *nomen nudum* in Mycobank (2022).

Leman (1817) when writing the definition of *Clathrus* in the *Dictionnaire des sciences naturelles* divided the genus into: *cancellé* (lattice, reticulated) and *colonnaire* (columnated). The *collonnaire* comprised *Clathrus colonnarius*, as a new species formed by four straight branches united at the apex with spores at the edge. This author mentioned that also participates in this group the species described by Bosc (1811), *Clathrus columnatus*, collected in South Carolina and by Rafinesque(1806), *Colonnaria truncata* and *C. urceolata*, collected in Pennsylvania. According Dring (1980) the name *Clathrus colonnarius* is a redundant name proposed by Leman based on Bosc's material.

Fischer assumed *Clathrus columnatus*, *C. collonarius* and *C. angolensis*, as well as, *Colonnaria truncata*, *C. urceolata*, *Laternea columnata* and *L. angolensis* as synonyms of *Clathrus cancellatus* f. *columnatus* (Fischer 1890). In the other hand, the author considered in the genus *Colonnaria* as sinonyms of *Colonnaria columnata*: *Collonaria urceolata* et. *truncate* (nomina nuda), *Clathrus columnatus*, *Laternea columnata*, *Clathrus trilobatus*, and *Laternea bicolumnata* Lloyd (Fischer 1933).

For Dring (1980) all species cited in Fischer (1890, 1933) as synonyms of *Clathrus cancellatus* f. *columnatus* and *Colonnaria columnata*, including these species are synonyms of *Clathrus columnatus*, except *Clathrus angolensis*, *Laternea angolensis* and *Laternea bicolumnata*. Dring (1980) accepted *Laternea bicolumnata* as a basonym of *Clathrus bicolumnatus* (Lloyd) Sacc. & Trotter, and *Clathrus angolensis*, *Laternea angolensis* as *Blumenavia angolensis* (Welw. & Curr.) Dring. *Clathrus angolensis* and *Laternea Angolensis*, they were confirmed in *Blumenavia* genus based on molecular evidences (Melanda et al. 2020). Also included in *Clathrus columnatus* the synonyms: *Clathrus australis* Speg.; *Clathrus brasiliensis* E. Fisch.; *Clathrus cancellatus* f. *australis* (Speg.) E. Fisch.; *Clathrus cancellatus* f. *brasiliensis* E. Fisch.; *Clathrus cancellatus* f. *fayodi* E. Fisch. (as *fayodii* in Dring's publication); *Laternea brasiliensis* (E. Fisch.) Long & Stouffer; *Linderia columnata* and *Linderiella columnata*. According Dring the description to *Clathrus australis*, *Clathrus brasiliensis* and *C. trilobatus* correspond to *Clathrus columnatus*.

To Fischer (1890) *Clathrus cancellatus* f. *brasiliensis* has the synonyms: *Clathrus brasiliensis*, *Clathrus triscapus* and *Laternea triscapa*. The main difference between *Clathrus*

cancellatus f. *brasiliensis*; *Clathrus cancellatus* f. *columnatus* and *Clathrus cancellatus* f. *australis* is the number of columns: three, four and five respectively.

Here we considered as synonyms of *Clathrus columnatus* the homotypic synonymies and the species of *Colonnaria.* So far, the positioning of the species in *Clathrus* is supported by molecular analyses, which present *C. columnatus* in a clade with *C. ruber*, the type species of the genus. Therefore, neither of the two sequenced materials are types, or of type locality.

The distribution of the species according to Dring (1980) is wide, encompassing America, Africa, Ethiopia and Australasia, however it indicates a number of regional variants of the species. Here we considered the distribution only based on our review, North America. Coker and Couch (1928) like in our work cited to USA the distribution in Florida, North and South Carolina, and added to Mississippi, Louisiana and Porto Rico. Therefore, the morphologic and molecular worldwide review will be important to confirm the identity of the species along the world.

Pseudocolus fusiformis (E. Fisch.) Lloyd, Mycol. Writ. Vol. III: Synopsis of the known phalloids: 53 (1909) [MB#297422] Figures 1G-K; 2B

Basonym: *Colus fusiformis* E. Fisch., Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss 32: 64 (1890) [MB#201219]

Macroscopic characters— *Expanded basidiomata* including volva 25–45 mm long, receptacle with 3-5 columnar arms joined at apex and at base by a hollow pseudostipe 3–8 × 2–6 mm, light yellow to yellowish brown when dry ($Y_{99}M_{10}C_{00}$ – $Y_{99}M_{40}C_{30}$), arms thinner in the upper fifth about 2–3 mm wide base and 0.9–1.5 mm wide in thinner part, outer face with a marked longitudinal groove. *Gleba* olive brown ($N_{99}A_{50}M_{10}$), attached of the inner face of the arms. *Volva* 12–15 × 6–8 mm, subglobose to elongate; *peridium* composed of three layers: when dry exoperidium cracked into dark gray ($N_{90}C_{00}Y_{10}$) scales above, and white ($N_{00}M_{00}C_{00}$) in the base; mesoperidium white ($N_{00}M_{00}C_{00}$), and endoperidium dark yellow ($N_{10}Y_{80}M_{20}$). *Rhizomorphs* single, branched, white ($N_{00}M_{00}C_{00}$), extending from base.

Macroscopic characters— *Rhizomorphs* consisting of septate filamentous hyphae, with inflated tips and with some septa connecting inflated tips, without clamp connections, 2.2–6.8 [$\bar{x}$= 4.1 ± 1] µm broad, straight, and regular walls 0.2–0.8 [$\bar{x}$ = 0.3 ± 0.1] µm thick, hyaline in 5% KOH, reddish with Congo red; with crystals arranged in globose structures, and irregularly shaped cyan crystals separated from each other. *Apical exoperidium* consisting of

filamentous and elongated hyphae, hyaline in 5% KOH, reddish with Congo red, with brown crystals arranged in radius and with irregularly shaped cyan crystals; filamentous hyphae branched, regularly septate, with inflated tips, and without clamp connections, 4.1–9.2 [$\bar{x}$ = 6.7 ± 1.1] µm broad, straight, and regular walls 0.2–0.8 [$\bar{x}$ = 0.4 ± 0.1] µm thick; elongated hyphae look like the filamentous hyphae separated in the septa. *Mesoperidium* consisting of branched filamentous hyphae, regularly septate, without inflated tips and clamp connections, 2.3–4.8 [$\bar{x}$ = 3.2 ± 0.7] µm broad, straight, and regular walls 0.1–0.5 [$\bar{x}$ = 0.3 ± 0.1] µm thick, hyaline in 5% KOH, reddish with Congo red; with irregularly shaped cyan crystals. *Endoperidium* consisting of branched filamentous hyphae, irregularly septate, with inflated tips, and without clamp connections, 1.9–3.3 [$\bar{x}$ = 2.7 ± 0.3] µm broad, straight, and regular walls 0.2–0.5 [$\bar{x}$ = 0.3 ± 0.1] µm thick, hyaline in 5% KOH, reddish with Congo red; with irregularly shaped cyan crystals. *Pseudostipe* exhibiting globose, subglobose to broadly ellipsoid cells, 21.9–42.9 × 19.4–42.3 [$\bar{x}$ = 31.5 ± 6.8 × 28.8 ± 7.0, Q = 1.01–1.28, Qm =1.10 ± 0.08] µm, straight and regular walls 0.3–1.3 [$\bar{x}$ = 0.7 ± 0.2] µm thick, hyaline in 5% KOH, reddish with Congo red. *Arms* exhibiting globose, subglobose to ellipsoid cells, 16–38.1 × 13.6–31.7 [$\bar{x}$ = 26.6± 3.9 × 18.8 ± 3.6, Q = 1.01–1.60, Qm =1.22 ± 0.16] µm, straight and regular walls 0.4–1 [$\bar{x}$ = 0.6 ± 0.2] µm thick, hyaline in 5% KOH, reddish with Congo red. *Basidiospores* elongate to cylindrical 3.1–4.6 × 1.5–2.2 [$\bar{x}$ = 4.0 ± 0.2 × 1.9 ± 0.1, Q = 1.74–2.57, Qm = 2.16 ± 0.15] µm, smooth, with one inner guttule at each end of the length, hyaline in 5% KOH.

Distribution— Island of Reunion (type locality). USA: North Carolina; Tennessee.
Studied material— USA: NORTH CAROLINA, s/d (NCU-F-0003254, as *Clathrus* sp.); Buncombe, Blue Ridge Parkway, Mile 391, 16.VII.2004, Nathan Wilson North American Mycological Association (NAMA) 2004-250 (F: C0295891F); Buncombe, Swannanoa, Warren Wilson College, 26.IX.2015, M. Brenner North American Mycological Association (NAMA) 2015-196 (F: C0295893F); Henderson, Tuxedo, Green River Gorge, 16.IX.1980, A. Stanley 55508 (TENN-F-041965, as *Pseudocolus schellenbergiae*); Orange, Battle Park, 1975, R. L. Blanton & J. C. Kennedy s/nº (NCU-F-0026674); Wake, Holly Springs near Middle Creek, 35°39'50.4"N 78°48'46.8"W, 17.V.2019, D.J. Meyers DJM 54 (NCU-F-0017607). TENNESSEE, Knox, Knoxville, 2.VIII.1958, W.W. Wyatt LRH23098 (TENN-F-023098, as *Pseudocolus javanicus*); Shelby, Memphis, Goldsmith Botanic Gardens, 18.x.1977, A.H. Smith & H.D. Black HDB 21 (TENN-F-063250, as *Clathrus columnatus*).

Remarks— Fischer (1890) proposed the new species *Colus fusiformis* based on an illustration deposited in the Muséum National d'Histoire Naturelle (PC) in Paris. This species was collected in Bélouve, Réunion, March 1875. The epithet '*fusiformis*' referred to the shape of the receptacle. Regarding the color, Blanton (1976) described *Pseudocolus fusiformis* from North America with white to grayish white pseudostipe and volva, but Fischer (1890) mention the color of the receptacle is red with brownish-white mottled volva.

Since the specimens studied are from herbaria, and were preserved after dehydration, the receptacle and pseudostipe have yellow tons. However, looking the image of fresh collection from North Carolina (F: C0295893F), it was possible to determine the color pinkish orange of arms with white base and pseudostipe, and brownish white volva. Also, one specimen from North Carolina (NCU-F0017607) shows in the collector information orange receptacle fading to a white base with brown volva. These color data were not represented in our description because the lack of the fresh color of the other specimens. In Phallales the basidiomata color can be one diagnostic character for some species, like *Blumenavia* (Melanda et al. 2020).

Lloyd (1909) proposed the combination *Pseudocolus fusiformis* and accepted this species as different to *Pseudocolus javanicus*, from Indonesia, Java, which according with Lloyd himself is more similar to *Pseudocolus garciae* (Möller) Lloyd from Brazil, but differ in the color and the arms texture. Here we agreed with this definition. Blanton (1976) considered in the review of North Carolina specimens, besides the basonym of *Pseudocolus fusiformis* the heterotypic synonymies: *Colus rothae* Berk. ex Fisch.; *Pseudocolus rothae* (Berk. ex Fisch.) Lloyd; *Anthurus rothae* (Berk. ex Fisch.) Cunn.; *C. javanicus* Penz.; *P. javanicus* (Penz.) Llloyd; *A. javanicus* (Penz.) Cunn.; *P. rugulosus* Lloyd; *Colus schellenbergiae*; *P. schellenbergiae*. The basidiospores according Blanton (1976) have 3.75–5 × 1.75–2.25 μm and is slightly larger than our specimens: 3.1–4.6 × 1.5–2.2 μm, and both are smaller than *Colus schellenbergiae*: 4.5–5.5 × 2–2.5 μm (Sumstine 1916). Dring (1980) agree of all synonymies cited in Blanton (1976) and presented a description of the species based on *Pseudocolus javanicus*, the author showed the distribution of the species to: Reunion, Australia, New Zealand, Indonesia, Japan, Hawaii and Eastern USA. To Dring (1980) the USA specimens can be introductions. Blanton (1976) made the first record of *P. fusiformis* from North Carolina, confirmed here in our work. Burk (1976) besides Tennessee, which also we made revision, listed Connecticut, Georgia, Hawaii, Massachusetts, New Jersey, New York, Pennsylvania and Rhode Island, as sites of occurrence in the United States, also considering *Colus schellenbergiae* as synonymy of *P. fusiformis*. Here we do not agree with this sinonimization and did not list the other heterotypic synonyms as *P. javanicus*, *P. rothae* and *P. rugulosus* because this confirmation

need to be made analyzing the type materials, or from type locality. And molecular studies can confirm if this USA specimens are authentic *Pseudocolus fusiformis* or no.

Pseudocolus schellenbergiae (Sumst.) Johnson, Ohio Biol. Survey Bull. 22: 338 (1929) [MB#277601] Figures 1L-O; 2C

Basonym: *Colus schellenbergiae* Sumst., Mycologia 8 (3): 183 (1916) [MB#224413]

Macroscopic characters— *Expanded basidiomata* including volva 26–60 mm long, receptacle with 3, rarely 4 columnar arms joined at apex and at base by a pseudostipe 2–10 × 2–6 mm, white below ($N_{00}M_{00}C_{00}$) orange above when fresh, light yellow to yellowish brown when dry ($Y_{99}M_{10}C_{00}$ – $Y_{99}M_{40}C_{30}$), arms thinner in the upper quarter about 1.5–3.5 mm wide base and 0.5–2 mm wide in thinner part, outer face with a marked longitudinal groove. *Gleba* olive brown ($N_{99}A_{50}M_{10}$), attached of the inner face of the arms. *Volva* 8–12 × 8–10 mm, globose to subglobose; *peridium* composed of three layers: when dry exoperidium dark gray ($N_{90}C_{00}Y_{10}$); mesoperidium white ($N_{00}M_{00}C_{00}$), and endoperidium dark yellow ($N_{10}Y_{80}M_{20}$), smooth. Single, branched, white ($N_{00}M_{00}C_{00}$) rhizomorph extending from base.

Microscopic characters— *Rhizomorphs* consisting of septate filamentous hyphae, with inflated tips and with some septa connecting inflated tips, without clamp connections, 2.9–6.9 [$\bar{x}$= 4.1 ± 0.8] µm broad, straight, and regular walls 0.2–0.6 [$\bar{x}$ = 0.4 ± 0.1] µm thick, hyaline in 5% KOH, reddish with Congo red; with spindle hyaline crystals arranged in radius, and irregularly shaped cyan crystals separated from each other. *Pseudostipe* exhibiting globose, subglobose to ellipsoid cells, 16.4–48.4 × 13.1–40.8 [$\bar{x}$ = 28.9 ± 5.5 × 24.2 ± 4.6, Q = 1.02–1.59, Qm =1.23 ± 0.12] µm, straight and regular walls 0.3–1.3 [$\bar{x}$ = 0.7 ± 0.2] µm thick, hyaline in 5% KOH, reddish with Congo red. *Arms* exhibiting globose, subglobose to ellipsoid cells, 12–43.1 × 8.3–33.5 [$\bar{x}$ = 24.1± 6.5 × 19.6 ± 5.2, Q = 1.00–1.59, Qm =1.24 ± 0.16] µm, straight and regular walls 0.2–1.6 [$\bar{x}$ = 0.6 ± 0.2] µm thick, hyaline in 5% KOH, reddish with Congo red. *Basidiospores* elongate to cylindrical 4.3–5.5(5.9) × 1.9–2.7 [$\bar{x}$ = 5.0 ± 0.3 × 2.3 ± 0.1, Q = 1.88–2.75, Qm = 2.18 ± 0.17] µm, smooth, with one inner guttule at each end of the length, hyaline in 5% KOH.

Distribution— USA: Connecticut, New Jersey, New York, Pennsylvania (type locality).

Studied material— USA: CONNECTICUT, Tolland, Union, Bigelow Hollow State Park, s/d, Seizman & Morgenstern s/nº (TENN-F-066866, as *Pseudocolus fusiformis*). NEW JERSEY,

Union, Summit, 1938, J. Miller 10972 (NCU-F-0006886, as *Colus schellenbergiae*). NEW YORK, New York, Bronx, New York Botanical Garden, near the Museum Blg., 20.IX.1928, F. J. Seaver s/nº (NCU-F-0006885, as *Colus schellenbergiae*); *ibid.* 17.VIII.1960, R. H. Petersen RHP27643 (TENN-F-027643, as *Pseudocolus schellenbergiae*). PENNSYLVANIA, Pittsburgh, Yard of Mrs. F. F. Schellenberg, VII.1915, D.R. Sumstine s/nº (NCU-F-0006887, isotype of *Colus schellenbergiae*).

Remarks— *Pseudocolus schellenbergiae* differs from *Pseudocolus fusiformis* by the receptacle color, orange and red respectively. The species was described as *Colus* (Sumstine 1916) and was combined to *Pseudocolus* (Johnson 1929), here we agreed with the species belongs to *Pseudocolus* according to Lloyd definition of the genera. According Sumstine (1916) who described the basonym this species is similar to *Colus javanicus*, although the author was not able to compare the colors between them. In Dring (1980)'s description of *P. fusiformis*, that was based in *P. javanicus*, the color is white at the base and flushing pink to red upwards. Regarding the two species of *Pseudocolus* presented here the main difference is the basidiospores measurement, in which *P. schellenbergiae* present a larger height and slightly wider width: 4.3–5.5 × 1.9–2.7 μm, against 3.1–4.6 × 1.5–2.2 μm of *P. fusiformis*. Besides Pennsylvania, the type locality, the species was recorded to New York by Seaver (1931). Here we expand the distribution to Connecticut and New Jersey. It was possible to define an imaginary line between the two *Pseudocolus* species distribution in USA: *P. schellenbergiae* was restricted to the Northeast and *P. fusiformis* to the Southeast.

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Figure 1. Exsiccates of the species. A-F. *Clathrus columnatus*: A-B. Basidiomata (NCU-F-0003224), B. arms joined at apex, with groove in one arm; C. Flattened specimen with arms joined at apex united by a transversal arm (NCU-F-0003225); D-F. Basidiomata from type locality (D. NCU-F-0003256, E-F. NCU-F-0003257). G-K. *Pseudocolus fusiformis*: G. Basidiomata without volva: arms and pseudostipe (left), only arms (right) (NCU-F-0003254); H. Basidiomata without (two left) and with (right) volva (NCU-F-0026674); I-J. TENN-F-023098, I. Arms and pseudostipe, J. Hollow pseudostipe; K. Basidiomata with three (left) and four (right) arms (TENN-F-063250). L-O. *Pseudocolus schellenbergiae*: L-M. TENN-F-066866, L. Basidiomata without volva, M. Two volvas (one broken) and rhizomorphs; N. Basidiomata without volva (NCU-F-0006885). O. Isotype (NCU-F-0006887). Scale bars = 5mm.

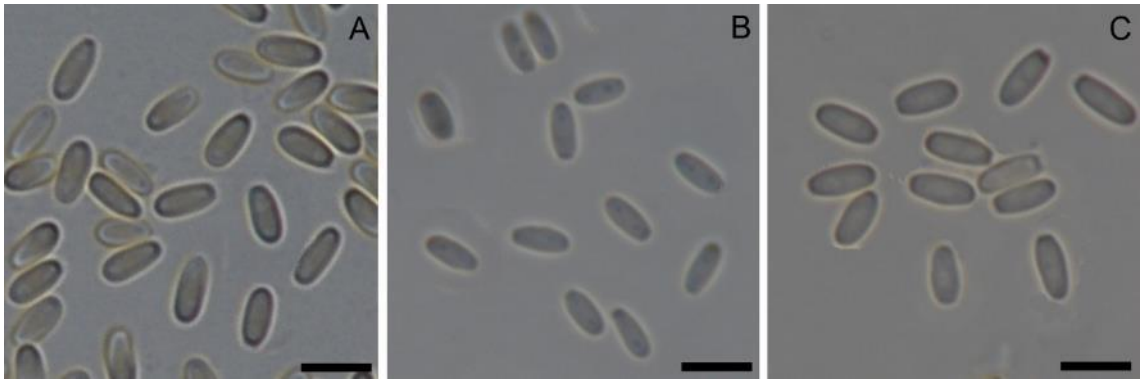

Figure 2. Basidiospores. A. *Clathrus columnatus* (NCU-F-0003257). B. *Pseudocolus fusiformis* (NCU-F-0026674). C. *Pseudocolus schellenbergiae* (isotype NCU-F-0006887). Scale bars = 5μm.