Allophlebia, a new genus to accommodate Phlebia ludoviciana (Agaricomycetes, Polyporales)

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Abstract

Allophlebia is proposed as a new genus in Meruliaceae based on morphological characters and molecular data. The genus, so far monotypic, is typified by Peniophora ludoviciana and the new combination A. ludoviciana is proposed. The type species is characterized by a resupinate basidioma, a monomitic hyphal system with clamp connections, two types of cystidia (leptocystidia and metuloids), clavate basidia, and hyaline, thin-walled and ellipsoid basidiospores. A phylogeny for Allophlebia and related taxa was inferred from ITS and nLSU rDNA sequences and new information on the geographic distribution of A. ludoviciana is provided.

Keywords Atlantic Rainforest - Caatinga - Brazil - Basidiomycota - Corticioid fungi - New taxon

Introduction

Phlebia Fr. (Polyporales, Meruliaceae) was described by Fries in 1821 and intended for species with a hymenium composed of irregular veins and ridges. Fries (1828) pointed to P. radiata as the most typical member of his new genus and this species is now generally accepted as the type (Donk 1957). Species in Phlebia sensu lato usually have resupinate basidiomata that are ceraceous to subgelatinous in fresh specimens, and with a membranous, firm ceraceous, corneous, or coriaceous consistency when dried. The hymenial surface varies from smooth, tuberculate, odontioid, merulioid to poroid. The hyphal system is monomitic, rarely dimitic, with hyphae clamped and embedded in a more or less evident gelatinous matrix. Cystidia can be present or absent; basidia are clavate, narrow, with a basal clamp and disposed in a dense palisade; and basidiospores are allantoid to ellipsoid, smooth, thin-walled, IKI−, and CB− (Eriksson et al. 1981; Bernicchia and Gorjón 2010). All species analyzed are saprobes on decaying wood (Nakasone 1990).

The original concept for Phlebia was considerably broadened along the years (Donk 1931, 1957, Nakasone 1991, 1996, 1997, 2002, Nakasone and Burdsall 1984). However, this wide concept for Phlebia proved to be polyphyletic (Larsson et al. 2004, Binder et al. 2013, Floudas and Hibbett 2015, Justo et al. 2017). Several genera have been introduced or resurrected to accommodate different species of Phlebia, e.g., Cabalodontia Piątek, Crustodontia Hjortstam & Ryvarden, Cytidiella Pouzar, Hermanssonia Zmitr., Jacksonomyces Jülich, Mycoacia Donk, Mycoaciella J. Erikss. & Ryvarden, Phlebiopsis Jülich, Scopuloides Hjortstam & Ryvarden, and Stereophlebia Zmitr. Other Phlebia species have been moved to other genera, most notably to Crustoderma Parmasto and Skvortzovia Bononi & Hjortstam. After such removal and transfer of species and after adjustments for synonyms, the genus still holds around 100 species, many of which are based on names for which there are no modern interpretation (www.mycobank.org). According to molecular data, P. radiata together with many other Phlebia species belong in Meruliaceae in Polyporales (Justo et al. 2017), while a few are recovered in Hymenochaetales (Larsson et al. 2006).
During studies of corticioid fungi from northeast Brazil, specimens of Phlebia ludoviciana (Burt) Nakasone & Burds. were collected. Molecular phylogenetic analyses showed that this species could not be placed in any of the corticioid genera already described. Thus, the aims of this paper were to describe a new genus for P. ludoviciana and to discuss the geographical distribution of this species.

Material and methods

Studied area and morphological analysis

Field trips were undertaken in northeast Brazil in the Atlantic Rainforest (Reserva Biológica de Pedra Talhada, (09°14′40″S, 36°25′35″W); Reserva Biológica de Guaribas (06°33′12″S, 35°10′55″W); Refúgio Ecológico Charles Darwin (07°49′42″S, 34°52′29″W), Reserva Particular do Patrimônio Natural (RPPN) Frei Caneca (08°42′41″S, 35°50′30″W), Reserva Biológica de Saltinho (8°44′16.9″S, 35°10′22.6″W) and in montane forest (Brejos Nordestinos) in Caatinga: Reserva Ecológica Estadual Mata do Pau-Ferro (06°58′12″S, 35°42′15″W).

Specimens were identified based on macro- (measures, texture, consistency, shape, and color of the basidiomata) and micro-morphology and sections of the basidiomata were checked with 3% potassium hydroxide solution (KOH), stained with 1% aqueous phloxine. Melzer’s reagent and Cotton Blue were used to analyze, respectively, dextrinoid and amyloid (IKI+/IKI−), and cyanophilous (CB+/CB−) reactions of the microstructures. Presence/absence of sterile structures and basidiospores was noted and measurements of at least 20 of them were taken, when possible (Hjortstam et al. 1987; Watling 1969). The material was deposited in the Herbarium Pe. Camille Torrend (URM), Departamento de Micologia (UFPE), and in the Herbarium of the University of Oslo (O).

DNA extraction, PCR amplification, and sequencing

Basidiomata fragments (30–50 mg) were removed, placed in tubes of 1.5 ml, and stored at -20 °C until DNA extraction. The method of DNA extraction followed Goés-Neto et al. (2005) and the reaction mix and parameters for PCR reactions of the ITS and LSU regions followed Smith and Sivasithamparam (2000), using the primer pairs ITS4-ITS5 and LR0R-LR5, respectively (White et al. 1990; Moncalvo et al. 2000; Lima-Júnior et al. 2014). The purification of PCR products was done with ExoSAP-IT™ PCR Product Cleanup Reagent (Thermo Fisher Scientific, USA), following the manufacturer’s recommendations. The samples were sequenced at the Plataforma Tecnológica de Genômica e Expressão Gênica do Centro de Biociências (CB), UFPE, Brazil, or sent to Stab Vida Lda (Madan Parque, Caparica, Portugal). The cycle sequencing was carried out with the same primers used for PCR reactions (Moncalvo et al. 2000). All new sequences were deposited in GenBank (National Center for Biotechnology Information, Bethesda, MD, USA).

Phylogenetic analyses

The 2.0 Staden Package software was used for analyses and edition of electropherograms (Bonfield et al. 1995). These sequences were subjected to BLASTn search in NCBI to recover similar sequences from GenBank and used in the dataset to establish phylogenetic relationships (Table 1). Each gene region was aligned with the MAFFT v.7 online server using default settings (http://mafft.cbrc.jp/alignment/server/), then improved manually using MEGA 7.0 and combined to form the concatenated dataset (Kumar et al. 2016).

The ITS and LSU regions were first analyzed independently (data not shown). Since no important topological differences were detected, the regions were combined into a single matrix for the final analyses. The models of evolution were obtained from MEGA 7.0 (Kumar et al. 2016) and confirmed in TOPALi v2.5 (Milne et al. 2008) for each dataset. Phylogenetic analyses and tree construction were performed using maximum likelihood (ML) and confirmed in Bayesian algorithm (BA). ML analysis was performed using MEGA 7.0 (Kumar et al. 2016) with 5000 bootstrap replications and based on GTR + G + I model. BA analyses were run in TOPALi v2.5 (Milne et al. 2008) with 5×10⁶ generations, also based on GTR+G + I model. Statistical support for branches was considered informative with Bayesian posterior probabilities (BPP) ≥0.95 and bootstrap (BS) values ≥70%. The trees were visualized with FigTree (Rambaut 2014) and the final layout was made in Adobe Illustrator CS6.

Results

Five specimens were sequenced (URM 93082, URM 93251, URM 93329, O-F-110340, O-F-110341), generating five ITS and four LSU sequences (Table 1). These were combined with ITS and LSU sequences selected through BLAST searches against GenBank.

No strongly supported topological conflict was detected among the datasets analyzed (ITS, LSU, and ITS+LSU). Thus, only the combined analysis is presented here, performed mainly with ITS sequences since only that region is available for some key specimens. The combined dataset included 174 sequences (116 ITS and 58 LSU) and comprised 2138 characters including gaps. Climacocystis borealis (Fr.) Kotl. & Pouzar and Junghuhnia nitida (Pers.) Ryvarden were selected...
Table 1 Sequences of *Meruliaceae* used in this study with vouchers, locality, and GenBank accession numbers for the ITS and LSU regions. The sequences in bold were generated in this study.

| Species                     | Voucher            | GenBank Access Number       | Locality | References                                      |
|-----------------------------|--------------------|------------------------------|----------|------------------------------------------------|
| *Allophlebia ludoviciana*   | URM 93082          | MN044657                     | Brazil   | This study                                     |
| *A. ludoviciana*            | URM 93251          | MN044659 MN044661            | Brazil   | This study                                     |
| *A. ludoviciana*            | URM 93329          | MN044658 MN044660            | Brazil   | This study                                     |
| *A. ludoviciana*            | O-F-110340         | MT974604 MT982121            | Ecuador  | This study                                     |
| *Climacocystis borealis*    | KHL13318           | JQ031126                     | Estonia  | Sjökvist et al. 2012                          |
| *Climacodon septentrionalis*| RLG-6890           | KP135344                     | USA      | Floudas and Hibbett 2015                      |
| *Crustodontia chrysocreas*  | HHHB-3946          | KP135357                     | USA      | Floudas and Hibbett 2015                      |
| *Hjortstam & Ryvarden*      |                    |                              |          |                                                 |
| *C. chrysocreas*            | FCUG2827           | HQL35411                     | USA      | Ghabad-Nejad and Hallenberg 2012               |
| *Geesterania carnea*        | KUC20121123-24     | KJ668482 KJ668335            | Korea    | Jang et al. 2016                              |
| *G. gorgonea*               | MA-Fungi 86622     |KF528013 KF528013             | Spain    | Telleria et al. 2017                          |
| *H. canariensis*            | MA-Fungi 86623     |KF483013 KF528014             | Spain    | Telleria et al. 2017                          |
| *H. gorgonea*               | MA-Fungi 86659     |KF483049 KF528139             | Cape Verde | Telleria et al. 2017                          |
| *H. meloi*                  | MA-Fungi 86654     |KF483044 KF528135             | Cape Verde | Telleria et al. 2017                          |
| *H. omnivora*               | ME-497             |KP135332 KP135218             | USA      | Floudas and Hibbett 2015                      |
| *H. omnivora*               | KKK-112            |KP135334 KP135216             | USA      | Floudas and Hibbett 2015                      |
| *H. subchrysochilus*        | Cui 16185          |MK860722 MK860739             | China    | Unpublished                                   |
| *Junghuhnia nitida*         | KHL11903           |EU118638 EU118639             | Sweden   | Larsson 2007                                  |
| *Luteoporia albomarginata*  | Dai 15229          |NR154126 NG060338             | China    | Wu et al. 2016                                |
| *L. albomarginata*          | Dai 15240          |KU598874 KU598879             | China    | Wu et al. 2016                                |
| *Mycoacia fusca*            | KHL13275           |JN649352 JN649353             | Estonia  | Sjökvist et al. 2012                          |
| *M. fuscoatra*              | MA-Fungi 86659     |KF483049 KF528140             | Cape Verde | Telleria et al. 2017                          |
| *M. nothofagi*              | MA-Fungi 86654     |KF483048 KF528139             | Cape Verde | Telleria et al. 2017                          |
| *M. notophagi*              | KHL13750           |GU480000 GU480001             | France   | Moreno et al. 2010                            |
| *M. notophagi*              | AH31887            |GQ59416                       | Spain    | Moreno et al. 2010                            |
| *Mycoacia uda*              | Kropp1             |KY948764                      | USA      | Justo et al. 2017                             |
| *M. tida*                   | CBS 224.56         |MH857593 MH869142             | France   | Vu et al. 2019                                |
| *Phelebia acanthocystis*    | KUC20131001        |KJ668484 KJ668337             | South Korea | Jang et al. 2016                             |
| *P. acanthocystis*          | CLZhao 1582        |KH14855 -                     | China    | Unpublished                                   |
| *P. acerina*                | CLZhao 3879        |MH784918 MH784928             | China    | Shen et al. 2018                              |
| *P. acerina*                | CLZhao 3882        |MH784919 MH784929             | China    | Shen et al. 2018                              |
| *P. aff. argentina*         | CBS 125860         |MH863815 MH875278             | Australia | Vu et al. 2018                                |
| *P. aff. argentina*         | CBS 125860         |MH863815 MH875278             | Australia | Vu et al. 2018                                |
| *P. ailaoshanensis*         | CLZhao 3879        |MH784918 MH784928             | China    | Shen et al. 2018                              |
| *P. ailaoshanensis*         | CLZhao 3882        |MH784919 MH784929             | China    | Shen et al. 2018                              |
| *P. albida*                 | GB 1833            |KY948748 KY948889             | Spain    | Justo et al. 2017                             |
| *P. albida*                 | CBS 214.67         |MH785951 MH7870641            | USA      | Vu et al. 2019                                |
| *P. albomellea*             | FP-101843          |AY219369 -                    | USA      | De Koker et al. 2003                          |
| *P. albomellea*             | no voucher         |L43378 -                      | USA      | Nakasone 1996                                 |
| *P. aurea*                  | FCUG2767           |HQ153409 -                    | Turkey   | Ghabad-Nejad and Hallenberg 2012               |
| *P. brevispora*             | BM-298030          |M130854 MH875278             | Argentina | Fonseca et al. 2015                          |
Table 1 (continued)

| Species | Voucher | GenBank Access Number | Locality | References |
|---------|---------|-----------------------|----------|------------|
|         |         | ITS | LSU |       |                   |
| P. brevispora | FBCC1463 | LN611135 | LN611136 | USA | Kuuskeri et al. 2015 |
| P. centrifuga (Bourdot & Galzin) | CBS 125890 | MH864088 | MH875547 | Sweden | Vu et al. 2019 |
| P. cf. martiana | OMC1242 | KY948765 | - | USA | Justo et al. 2017 |
| P. cf. subserialis | HBB-8715 | KY948770 | KY948846 | USA | Justo et al. 2017 |
| P. cf. subserialis | MS42b | KJ831936 | - | USA | Martin et al. 2015 |
| P. coccineofulva | HBB-1146sp | KY948766 | KY948851 | USA | Justo et al. 2017 |
| P. floridensis | HHB-7175 | KP135384 | - | USA | Floudas and Hibbett 2015 |
| P. floridensis | FP-102562 | KP135386 | - | USA | Floudas and Hibbett 2015 |
| P. leptospermi (G. Cunn.) Stalpers | CBS 126031 | MH863894 | MH875535 | New Zealand | Vu et al. 2019 |
| P. livida (Pers.) Bres. | GB501 | KY948772 | KY948847 | Norway | Justo et al. 2017 |
| P. livida subsp. tuberculata Hallenb. & E. Larss. | FCUG2716 | HQ153417 | - | Russia | Ghoobad-Nejad and Hallenberg 2012 |
| P. livida subsp. tuberculata | TTT1418 | HQ153419 | - | New Zealand | Ghoobad-Nejad and Hallenberg 2012 |
| P. livida | HB-4160 | KY948755 | KY948849 | USA | Justo et al. 2017 |
| P. radiata | Champ-81 | KX449485 | - | France | Pérez-Izquierdo et al. 2017 |
| P. subserialis | GB-240 | KY949227 | KY949300 | USA | Justo et al. 2017 |
| P. subserialis | V2EF16a | KX065955 | KX065989 | USA | Maynard et al. 2017 |
| P. subserialis | G1085 | MF061328 | - | French Guiana | Jaoen et al. 2019 |
| P. subserialis | JSP 01-10 | KR093857 | - | Brazil | Pereira et al. 2016 |
| P. subserialis | CY997 | HQ609794 | - | USA | Rodrigues et al. 2011 |
| P. subserialis | UFMCGB 2216 | HM997135 | - | Brazil | Vieira et al. 2012 |
| P. subserialis | UFMCGB 1883 | HQ377286 | - | Brazil | Vieira et al. 2012 |
| P. subserialis | KRT 1021 | MN430941 | - | USA | Rogers et al. 2020 |
| P. subserialis | HBB-9768 | KP135343 | - | USA | Floudas and Hibbett 2015 |
| P. subserialis | CBS 211.54 | MH857296 | MH868828 | France | Vu et al. 2019 |
| P. subserialis | CK463 | MH474313 | MH483585 | USA | Ndinga-Muniania et al. 2021 |
| P. subserialis | CBS 211.54 | MH857296 | MH868828 | France | Vu et al. 2019 |
| P. subserialis | CB-240 | KY949735 | - | Brazil | Pereira et al. 2016 |
| P. subserialis | UFMCGB 2216 | HM997135 | - | Brazil | Vieira et al. 2012 |
| P. subserialis | UFMCGB 1883 | HQ377286 | - | Brazil | Vieira et al. 2012 |
| P. subserialis | KRT 1021 | MN430941 | - | USA | Rogers et al. 2020 |
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| P. subserialis | UFMCGB 2216 | HM997135 | - | Brazil | Vieira et al. 2012 |
| P. subserialis | UFMCGB 1883 | HQ377286 | - | Brazil | Vieira et al. 2012 |
| P. subserialis | KRT 1021 | MN430941 | - | USA | Rogers et al. 2020 |
| P. subserialis | HBB-9768 | KP135343 | - | USA | Floudas and Hibbett 2015 |
| P. subserialis | CBS 211.54 | MH857296 | MH868828 | France | Vu et al. 2019 |
| P. subserialis | CB-240 | KY949735 | - | Brazil | Pereira et al. 2016 |
| P. subserialis | UFMCGB 2216 | HM997135 | - | Brazil | Vieira et al. 2012 |
| P. subserialis | UFMCGB 1883 | HQ377286 | - | Brazil | Vieira et al. 2012 |
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| P. subserialis | KRT 1021 | MN430941 | - | USA | Rogers et al. 2020 |
as outgroup in accordance with the phylogenetic structure of Polyporales recovered in Justo et al. (2017).

The results of the phylogenetic analyses generated from ML and BA showed similar tree topologies and small or insignificant differences in statistical support values. Thus, the ML tree with bootstrap support values (BS) and posterior probabilities (PP) from the BA analysis was used to show the results of this study (Fig. 1).

The newly generated sequences were placed in a strongly supported clade (BS 99%, PP 0.99) with several samples of A. ludoviciana previously deposited in GenBank. Other sequences at GenBank identified differently also grouped in the same clade. The A. ludoviciana clade was phylogenetically separated from the clade representing Phlebia s.s., and from other described genera (Fig. 1).

### Taxonomy

**Allophlebia** C.R.S. de Lira, Gibertoni & K.H. Larss., gen. nov.

Mycobank: MB 838839

**Type species:** *Peniophora ludovicia* Burt

**Allophlebia ludoviciana** (Burt) C.R.S. de Lira & K.H. Larss., comb. nov., Fig. 2a–f

Mycobank: MB 838839

Basionym: *Peniophora ludoviciana* Burt, Annals of the Missouri Botanical Garden 12: 244 (1926)

Description: Nakasone et al. (1982).

Synonym: *Peniophora flammea* Burt, Annals of the Missouri Botanical Garden 12: 252 (1926)

Remarks: *Allophlebia* is so far monotypic. *Allophlebia ludoviciana* is characterized by an effused, resupinate, ceraceous, pale yellow to golden yellow or deep orange basidioma (Fig. 2a–b), a smooth to minutely warty hymenophore without or with a weak reddish reaction in 3% KOH, and a monomitic hyphal system. Two types of cystidia can be observed: 1) leptocystidia, narrowly obclavate to ventricose, hyaline and projecting above the hymenium, (35)45–70 × 5.5–7 μm (Fig. 2e), and 2) cylindrical metuloids, heavily encrusted with hyaline crystals, with obtuse to slightly conical apex, mostly immersed in the hymenium, 35–70 × 6–9 μm (Fig. 2f). The basidia are narrowly clavate and the basidiospores are ellipsoid, (4.5)5.5–6.5 × 2–2.5 μm, smooth, thin-walled, hyaline (Fig. 2f) and IKI- and CB-. *Allophlebia ludoviciana* and *Phlebia subochracea* are both bright yellow-orange when fresh and tan to light brown when dry. However, *P. subochracea* has wider basidiospores (5–7 × 2.5–3.5 μm) and lacks the metuloids found in *A. ludoviciana* (Nakasone et al. 1982).

Distribution: Confirmed *A. ludoviciana* basidiomata have been collected from USA (Nakasone et al. 1982), Cuba (Burt as outgroup in accordance with the phylogenetic structure of Polyporales recovered in Justo et al. (2017).

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Distribution: Confirmed *A. ludoviciana* basidiomata have been collected from USA (Nakasone et al. 1982), Cuba (Burt...
Here, the presence of basidiomata in Brazil, Colombia, and Ecuador is reported (Fig. 1, Table 1). Additional observations of environmental DNA, including misidentified ones, indicate a presence in Mexico, Peru, and China (Fig. 1, Table 1). The Brazilian specimens studied by us were collected on decaying wood in Atlantic Rainforest (Southeast and Northeast Brazil) and montane forests in Caatinga (Brejos Nordestinos).

Material examined: Brazil: Alagoas, Quebrangulo, Reserva Biológica Pedra Talhada, leg. R.L.M. Alvarenga & A. Meiras-Ottoni, A., 6 June 2017, RC38 (URM93082); Ibid, leg. V. Xavier de Lima, 19 Sep. 2018, VXL550 (URM93250); Ibid, 20 Sep. 2018 VXL591 (URM93251); Paraíba, Areia, Reserva Ecológica Estadual Mata do Pau-Ferro, 29 April 2013, C.R.S. Lira 583 (URM 93329); Ibid, Jaqueira, RPPN Natural Frei Caneca, 30 March 2013, R.S. Chikowski 548 (URM85875); São Paulo: São Paulo, Santos, Cananeia, Ilha do Cardoso, 2-5 Feb. 1987, L. Ryvarden 44743 (O-F-110340); Ibid, 9 Sep. 2012 R.S. Chikowski 381 (URM92972), Ibid, 9 March 2013, R.S. Chikowski 548 (URM85875); São Paulo: Santos, Cananeia, Ilha do Cardoso, 2-5 Feb. 1987, L. Ryvarden 24695 (O-F-110338); São Paulo: São Paulo, Parque Estadual Fontes do Ipiranga, 16-24 Jan. 1987, K. Hjortstam 16335 (SP213701); Ibid L. Ryvarden 24141 (O-F-110339). Colombia: Magdalena, Parque Nacional Tayrona, Estacion de Gaira, 12 June 1978, L. Ryvarden 15780 (O-F-918462). Ecuador: Orellana, Yasuni Nat. Park, Yasuni Research St., 9-12 Mar. 2002, L. Ryvarden 44743 (O-F-110340). USA: Iowa, Iowa City, 8 July 1934, D.P. Rogers 104 (O-F-504275); Louisiana, Plaquemines Parish, F. Edward Hebert Center, 26 July 1972, W.B. & V.G. Cooke 45633 (O-F-985538); Wisconsin, La Crosse Co, Goose Island County Park, 21 Sep. 1979, K.K. Nakasone (GB-0161253).

### Table 1

| **Species**                        | **Locality**                      | **Year** | **References**            |
|------------------------------------|-----------------------------------|----------|---------------------------|
| Phlebia subserialis                | Brazil: Alagoas, Quebrangulo      | 2017     | R.L.M. Alvarenga & A. Meiras-Ottoni, A. |
|                                    | São Paulo, Santos, Cananeia        | 1987     | L. Ryvarden 44743         |
|                                    | São Paulo, Parque Estadual Fontes do Ipiranga | 1987 | K. Hjortstam 16335       |
|                                    | Magdalena, Parque Nacional Tayrona | 1978     | L. Ryvarden 15780          |
|                                    | Orellana, Yasuni Nat. Park, Yasuni Research St. | 2002 | L. Ryvarden 44743          |
|                                    | Iowa, Iowa City                   | 1934     | D.P. Rogers 104            |
|                                    | Louisiana, Plaquemines Parish      | 1972     | W.B. & V.G. Cooke 45633    |
|                                    | Wisconsin, La Crosse Co            | 1979     | G504275                   |
|                                    | Goose Island County Park          | 1979     | G504275                   |

**Discussion**

When combining *Peniophora ludoviciana* to *Phlebia*, Nakasone et al. (1982) grouped this species with *P. brevispora*, *P. subochracea*, and *P. subserialis* in section Leptocystidiophlebia Parmasto based on morphology and culture characteristics. Our results show that *P. ludoviciana* is phylogenetically close to *P. subochracea*, while *P. brevispora* and *P. subserialis* are distantly related, both from each other and from *P. ludoviciana* and *P. subochracea* (Fig. 1). Floudas and Hibbett (2015) included *P. brevispora*, *P. subochracea*, and several samples identified as *P. subserialis* in their analyses. They recovered *Phlebia brevispora* in the *Phlebia s.s.* clade, while the samples posterior probabilities (higher than 0.92) are showed along the branches, respectively, except for within-species variation. The sequences in bold were generated in this study.

![Fig. 1 Phylogenetic reconstruction of sequences of Meruliaceae specimens inferred from a combined dataset of ITS and nLSU. Parsimony bootstrap generated by ML (higher than 80%) and BA posterior probabilities (higher than 0.92) are showed along the branches, respectively, except for within-species variation. The sequences in bold were generated in this study.](image-url)
Fig. 1 continued.
identified as *P. subseralis* were placed in three different clades, one corresponding to *A. ludoviciana* and sister to *P. subochracea*, one close to *P. nothofagi* and *P. fuscoatra*, currently belonging to Mycoacia, and the last one belonging to the Phanerochaete clade and provisionally identified as *Phanerochaete krikophora*. Justo et al. (2017) recovered *P. ludoviciana* (FD-427, reported as *Phlebia* sp. in GenBank) in a clade with *P. subochracea* I (HHB8715) reported as *Phlebia* *cf.* *subseralis* in GenBank), both representing *A. ludoviciana* and sister to *P. subochracea* II.

In our study, the Allophlebia clade is phylogenetically separated from the *Phlebia* s.s. clade (BS=87/PP=0.96) as well as from other genera in Meruliaceae and from other sequenced species of *Phlebia* recovered outside Meruliaceae. It is strongly supported as a monophyletic group (99) (Fig. 1), and in accordance with the recommendations by Vellinga et al. (2015). The new genus may also include *Fungal* sp. (TP2) from Thailand (Klomklieng et al. 2014) and *P. ochraceofulva* (FBCC295) from Sweden (Kuuskeri et al. 2015), but they represent isolates without vouchers, which prevents morphological studies.

The five sequences of *A. ludoviciana* generated in our study clustered with two sequences from the USA and French Guiana and 22 other sequences also representing *A. ludoviciana*, but identified differently: *P. aff. argentina* from French Guiana; *P. subseralis* from Brazil, China, Colombia, Ecuador; *P. cf. subseralis* from Peru and the USA; *Grammothelopsis puiggarii* from Brazil and China, as well as unidentified fungal samples from the USA and Mexico (Table 1). *Phlebia argentina* (Speg.) Rajchenb. & J.E. Wright,
originally collected on Salix humboldtiana in Argentina, is characterized by membranous basidiomata and one kind of cystidia, viz. strongly encrusted metuloids projecting beyond the hymenium (Rajchenberg and Wright 1987). The type of P. subserialis is from France and sequences from there and other European countries, as well as one sequenced specimen from India (Table 1), are distantly placed in the phylogenetic tree (Fig. 1). Phlebia subserialis has narrower leptocystidia (3–4 μm), lacks encrusted cystidia, and has longer, subballantoid basidiospores [6–7(–8) × 2–2.5 μm] (Bernicchia and Gorjón 2010). It is unclear why this species has been confused with A. ludoviciana. One reason could be that some early mycologists established an opinion that the two cystidia types in A. ludoviciana are just a single type in different stages of development (Rogers and Jackson 1943). Specimens of P. subserialis reported in the Americas should be reevaluated (Nakasone et al. 1982). Grammothelopsis puiggarii is a species characterized by large, angular pores (1–2 per mm), large, dextrinoid, thick-walled basidiospores and dextrinoid skeletal hyphae (Rajchenberg and Wright 1987). This species is currently placed in Polyporaceae and cannot possibly be confused with A. ludoviciana. The sequences named G. puiggarii are most likely the result of contamination or sequencing mistakes.

The specimens of A. ludoviciana studied by Nakasone et al. (1982) were all collected on dead wood of various angiosperm tree species. The specimens sequenced by us and by earlier studies were also all collected on decaying angiosperm wood. The environmental sequences of A. ludoviciana in GenBank were mostly generated from living tissue of angiosperm plants representing the genera Elaeis (oil palm), Hevea, Polylepis, Phragmites, Rubia, and Solanum. Sequences were also generated from the rhizosphere of Broussonetia, from Nyssa root ties, dry grassland soil, air, and from nests of Atta and Cyphomyrmex ants (Fig. 1). This information adds to the growing body of evidence indicating that basidiomycetes with a saprophytic lifestyle may serve also other ecological functions (Pinruan et al. 2010; Martin et al. 2015).

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Data availability All material is deposited in Herbarium URM and O. The sequences are deposited in GenBank. Data will be available online after the acceptance of the manuscript in http://www.splink.org.br/ and https://www.ncbi.nlm.nih.gov/genbank/.

Code availability Not applicable

Declarations

Ethics approval Not applicable

Consent to participate Not applicable

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