New data in *Porotheleaceae* and *Cyphellaceae*: epitypification of *Prunulus scabripes* Murrill, the status of *Mycopan* Redhead, Moncalvo & Vilgalys and a new combination in *Pleurella* Horak emend.

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Abstract

*Mycopan* is a genus established for *Hydropus scabripes* by Redhead, Moncalvo & Vilgalys (in Redhead 2013). They considered the genus to be distinct based on morphology and the phylogenetic analysis by Moncalvo et al. (2002) which included a sequence of *Hydropus scabripes* (AF042635, DAOM 192847) unrelated to the type species of *Hydropus* (*H. fuliginarius*). Subsequent sequences of material identified as *Hydropus scabripes* are not conspecific with the sequence of DAOM 192847. We consider this sequence (obtained from a mycelium culture) to be misidentified. We investigated the true phylogenetic position of authentic *Mycopan* including genera previously included in *Cyphellaceae* and *Porotheleaceae*. Sixteen collections of *M. scabripes* from Europe and North America were studied on morphological and molecular basis (nrITS and nrLSU sequences). No sequences were obtained from the holotype of *Mycopan scabripes*, and we designate an epitype to fix the interpretation of this species and the genus *Mycopan*. *Mycopan* is maintained as a good genus nested within *Cyphellaceae* as sister to the mycenoid genus *Atheniella*. The misidentified *Hydropus scabripes* AF042635 (DAOM 192847) represents a different species that is closely related to the holotype (and a new Italian collection) of *Hebelomina microspora* and the monospecific genus *Pleurella* described from New Zealand. Consequently, *Hebelomina microspora* is transferred to the emended genus *Pleurella*, which is sister to *Baeospora* within the *Cyphellaceae*. Additionally, based on these phylogenetic results, an updated taxonomic arrangement of *Cyphellaceae* and *Porotheleaceae* is proposed, emphasizing once again the polyphyletic nature of *Hydropus* and *Gerronema*.

Keywords  
Basidiomycota · Agaricomycetes · Agaricales · Hydropoid clade · Marasmiineae · Mycena · Mycopan scabripes · nrITS · nrLSU · TEF1 · RPB2 · Taxonomy

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Introduction

The genus *Hydropus* Kühner ex Singer, based on *Agaricus plexipes* b. *fuliginaria* Batsch (1783), traditionally contains pileostipitate saprotrophic species with mycenoid, omphalinoïd to collybioid habit, non- or weakly amyloid trama, non-diverticulate cystidia, amyloid or inamyloid spores, and a pileipellis without diverticulate elements, generally at least in part subhymeniform and/or with ventricose/swollen pileocystidia (Singer 1982, 1986; Hausknecht et al. 1997; Contu and Robich 1998; Bas 1999; Estève-Raventós et al. 2002). It was described originally by Kühner (1938) as an informal group/subsection of the genus *Mycena* (Pers.) Roussel, within the subgenus *Eu-Mycena* section *Spuriae* which encompasses puzzling species with non- or weakly amyloid trama and non-diverticulate cystidia and pileipellis elements. *Hydropus* was then raised to the genus level by Singer (invalidly 1942, validly 1948). It was enlarged by Kühner (1980) to encompass *Megacollybia* Kotl. & Pouzar (as subgenus). Species of *Hydropus* are widespread especially in tropical areas (e.g., Singer and Grinling 1967; Singer 1973, 1982; Pinheiro et al. 2013; Cooper et al. 2018), but they also occur in the temperate zone (e.g., Kotlaba and Pouzar 1962; Moser 1968; Bas 1983, 1999; Bas and Weholt 1984; Robich 1986, 1990, 1992; Maas Geesteranus and Hausknecht 1993; Contu and Robich 1998; Estève-Raventós et al. 2002; Moreau and Courtecuissie 2004; Holec 2008a, b; Læsøe 2008, 2012; Deceuninck 2012, 2019). There has been no detailed molecular phylogenetic study of the genus, but it is recovered as strongly polyphyletic (Moncalvo et al. 2002; Bodenstein et al. 2004; Matheny et al. 2006; Eberhardt et al. 2018; Antonín et al. 2019; Varga et al. 2019; Vizzini et al. 2019; Kaygusuz et al. 2020; Matheny et al. 2020; Sánchez-García et al. 2020). Species placed in the genus are spread over numerous independent evolutionary lines (hydropod fungi) in the *Porotheleaceae* Murrill and *Cyphellaceae* Lotsy (Eberhardt et al. 2018), families which are part of the sub-order *Marasmiineae* Aime, Dentinger & Gaya as circumscribed on a phylogenomic basis by Dentinger et al. (2016) (= Marasmioid clade s. Matheny et al. 2006; Binder et al. 2010). The first evolutionary line of hydropod fungi to be recognized as an independent genus from *Hydropus* was the monospecific *Mycopan* Redhead, Moncalvo, Viögaly (in Redhead 2013). *Mycopan* is based on *Prunulus scabripes* Murrill [= *Hydropus scabripes* (Murrill) Singer]. It was established as independent using a reference (nLSU) sequence present in the phylogenetic analyses by Moncalvo et al. (2000, 2002) (AF042635, DAOM 192847) where the sequence, labelled *H. scabripes*, is sister to *Baeospora* Singer and unrelated to the type of *Hydropus* (*H. fuliginarius* (Batsch) Singer). *Prunulus scabripes* was originally described based on material from New York state (USA) (Murrill 1916a). It has been found subsequently in other parts of North America and Europe (e.g., Kühner 1938; Smith 1947; Hausknecht et al. 1997; Bas 1999; Læsøe 2008, 2012) and North Africa (Morocco, Malençon and Bertault 1975). Only a few sequences attributed to *Hydropus/Mycopan scabripes* have been deposited in public databases (GenBank) after the work by Moncalvo et al. (2002) and these unexpectedly do not match the AF042635 sequence (see the phylogenetic analysis in Eberhardt et al. 2018). The aim of the present paper is to i) morphologically study and sequence European and North American collections of *Hydropus scabripes* (holotype included); ii) establish their placement within *Cyphellaceae/Porotheleaceae*; iii) select a North American newly sequenced collection as an epitype; and iv) provide a modern morphological description of *Hydropus scabripes* and comment on the discrepancy between the sequences of *H. scabripes* present in GenBank.

Materials and methods

Collections studied

Samples studied are identified by the code of the public fungaria (Thiers, continuously updated) where they are stored: AMB, BRNM, MCVE, NY, PDD and TENN-F. Sample collection data are presented in the Taxonomy part and supplementary materials.

Morphological studies

Macroscopic morphological features were studied in fresh specimens. Colour abbreviations follow Munsell (1988). The following abbreviations are employed: L = number of lamellae reaching the stipe, l = number of lamellulae between each pair of lamellae. Microscopic structures were examined in dried material or fresh material (*Pleurella microspora*) using different mounting media: water, L4 (Clémonçon 1972), Melzer’s reagent, ammoniacal Congo red, phloxine, Cresyl blue and Cotton blue. Dried pieces of the samples were rehydrated in water and mounted in L4. Microscopic measurements were carried out with a Nikon Eclipse 80i, Olympus BX-50 and Zeiss Primostar light microscopes, using immersion oil at ×1000. Spore measurements were made by capturing images of a single visual field with multiple spores (taken from lamellar squashes of exsiccate material of mature specimens) which were then measured using the DS-L1 Nikon camera control unit. Spore dimensions do not include the hilar appendix, and are reported as follows: average minus standard deviation of length – average plus standard deviation of length × average minus standard deviation of width – average plus standard deviation of width; Q = average minus standard deviation.
Table 1  Taxa, vouchers, locations, and GenBank accession numbers of the DNA sequences used in the phylogenetic analyses. Newly sequenced collections are bold-faced

| Family | Revised name | Label | Voucher | State | nrITS | nrLSU | Reference |
|--------|--------------|-------|---------|-------|-------|-------|-----------|
| CYPH   | Acanthocorticium brueggaemnnii | JMB2621 | ICN (holotype) | Brazil | KT275194 | KT275196 | Baltazar et al. 2015 |
| CYPH   | Actiniceps lasiis | ATCC 20629 | | Singapore | — | DQ284917 | Dentinger and McLaughlin 2006 |
| CYPH   | Athelia bombacina | DAOM 174885 | | not indicated | — | AF279377 | Bhattacharya et al. 2000 |
| CYPH   | Atheniella adonis | Mycena adonis | AFTOL-ID 1686 | USA (Washington) | DQ490644 | DQ457691 | Matheny et al. 2006 |
| CYPH   | Atheniella amabilissima | Mycena aurantiidiscsa | F15202 UBC | Canada (British Columbia) | DQ384585 | DQ384585 | Berbee ML et al. unpublished |
| CYPH   | Atheniella aurantiidiscsa | Mycena aurantiidiscsa | AFTOL-ID 1685 | USA (Washington) | DQ490646 | DQ470811 | Matheny et al. 2006 |
| CYPH   | Atheniella flaxida | Atheniella sp. | FAAAS0350 | China | MW969653 | MW969665 | Ge et al. 2021 |
| CYPH   | Atheniella xuyao | Atheniella sp. | FAAAS0354 | China | MW969658 | MW969668 | Ge et al. 2021 |
| CYPH   | Baeospora myosura | Baeospora myosura | AFTOL-ID 1799 | USA (Massachusetts) | DQ484063 | DQ457648 | Matheny et al. 2006 |
| CYPH   | Baeospora myosura | Baeospora myosura | CBS 129,47 | France | MH856182 | MH867708 | Vu et al. 2019 |
| CYPH   | Baeospora myriadophylla | myriadophylla | 14-10-98-3/DAOM 188774 | not indicated | DQ868346 | AF042634 | Hutchison LJ and Kropp BR, unpublished; Matheny et al. 2000 |
| CYPH   | Baeospora occidentalis | Baeospora occidentalis | Mushroom Observer 420460 | USA | — | MZ354638 | Clements TA, unpublished |
| CYPH   | Calypella capula | Calypella capula | AMB 18736 | Italy | OL393159 | — | This study |
| CYPH   | Calypella capula | Calypella capula | PB315 | Norway | AY571031 | AY570995 | Bodenstein et al. 2004 |
| CYPH   | Calypella capula | Calypella capula | CBS 485,86 | Netherlands | AY571030 | — | Bodenstein et al. 2004 |
| CYPH   | Calypella capula | Calypella capula | 7110217 | Japan | ABS12316 | ABS12346 | Osono T and Hirose D, unpublished |
| CYPH   | Campanophyllum proboscidaeum | Campanophyllum proboscidaeum | TENNS6402 | Mexico | AY230866 | AY230866 | Cifuentes et al. 2003 |
| CYPH   | Chaetothyphula hyalina | Chaetothyphula hyalina | DJM1348 | Singapore | — | DQ284912 | Dentinger and McLaughlin 2006 |
| CYPH   | Chelmonophyllum candidissimum | Chelmonophyllum candidissimum | AFTOL-ID 1765 | USA (Washington) | DQ486687 | DQ457654 | Matheny et al. 2006 |
| CYPH   | Chondrostereum purpureum | Chondrostereum purpureum | CBS 350,53 | France | MH857241 | MH867775 | Vu et al. 2019 |
| CYPH   | Cyphella digitalis | Cyphella digitalis | GEL5348 | not indicated | — | AJ406563 | Langer E, unpublished |
| CYPH   | Cyphella digitalis | Cyphella digitalis | AFTOL-ID 663 | Austria | DQ486698 | AY635771 | Matheny et al. 2006; Matheny PB and Hibbett DS, unpublished |
| CYPH   | Gloeostereum cinri | Gloeostereum cinri | SA-2019a/CBS 145006 | USA | — | MN266884 | Ahmed et al. 2020 |
| Family | Revised name | Label | Voucher | State | nrITS | nrLSU | Reference |
|--------|--------------|-------|---------|-------|-------|-------|-----------|
| CYPH   | *Gloeostereum* incarnatum | *Gloeostereum* incarnatum | 3332 | not indicated | AF141637 | AF141637 | Hallenberg N and Parmasto E, unpublished |
| CYPH   | *Granulobasidium vellereum* | *Granulobasidium vellereum* | AFTOL-ID 887 | not indicated | — | AY745729 | Matheny PB and Hibbett DS, unpublished |
| CYPH   | *Hemimycena gracilis* | *Hemimycena gracilis* | AFTOL-ID 1732 | USA (Colorado) | DQ490623 | DQ457671 | Matheny et al. 2006 |
| CYPH   | *Hemimycenomyces candidus* | *Hemimycenomyces candidus* | PB338 | France | AY571044 | AY571008 | Bodensteiner et al. 2004 |
| CYPH   | *Hemimycenomyces puber* | *Hemimycenomyces puber* | GUA-307 | Guyana | AY571045 | AY571009 | Bodensteiner et al. 2004 |
| CYPH   | *Lignomphalia lignicola* | *Lignomphalia lignicola* | LE262727 | Russia | — | — | Malysheva et al. 2010 |
| CYPH   | *Mycochaeta quiniaulensis* | *Mycochaeta quiniaulensis* | MICH 11521 | USA | MNR09552 | — | Gordon M, unpublished |
| CYPH   | *Mycochaeta quiniaulensis* | *Mycochaeta quiniaulensis* | OSC 67121 isolate p182i | USA | EU669310 | EU681183 | Gordon M and Zych P, unpublished; Gordon M, unpublished |
| CYPH   | *Mycenella bryophila* | *Mycenella bryophila* | 15730/NL-3570 | Italy/Hungary | JF908500 | MK278407 | Garbelotto et al., unpublished; Varga et al. 2019 |
| CYPH   | *Mycenella salicina* | *Mycenella salicina* | 843KR 7435 | France/not indicated | JF908497 | DQ071720 | Garbelotto et al., unpublished; Gamica et al. 2007 |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | AMB 18737 | Italy | OL839161 | OL839176 | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | AMB 18738 | Italy | OL839160 | — | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | 507a | Italy (incorrectly referred to as Sweden in GenBank) | JF908448 | — | Osmundson et al. 2013 |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | BRNM 793297 | Czech Republic | OL839169 | OL839183 | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | F26474 | USA | MZ345002 | — | Aime MC, unpublished |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | TENN-F-076400 | Canada | OL839163 | OL839178 | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | TENN-F-076401 | Canada | OL839164 | OL839179 | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | BRNM 829033 | Czech Republic | OL839166 | OL839180 | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | BRNM 829032 | Czech Republic | OL839167 | OL839181 | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | NY01983317 | USA | OL839170 | — | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | NY02763988 | USA | OL839165 | — | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | BRNM 788135 | Czech Republic | OL839168 | OL839182 | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | BRNM 829032 | Czech Republic | OL801354 | — | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | MCVE 507 | Czech Republic | OL801355 | — | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | NY 02763989 | USA | OL801356 | — | This study |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | iNAT 16782378 | USA | MZ241313 | — | Taylor GM, unpublished |
| CYPH   | *Mycopan scabripes* | *Mycopan scabripes* | AFTOL-ID 535/PBM2513 | not indicated | DQ404389 | DQ411536 | Matheny PB, Wang Z and Hibbett DS, unpublished; Matheny et al. 2006 |
| CYPH   | *Mycopan scabripes* | *Hydropus scabripes* | GG355_86 | Norway (Svalbard) | GU234149 | — | Geml et al. 2012 |
Table 1 (continued)

| Family | Revised name | Label | Voucher | State       | nrITS      | nrLSU      | Reference                  |
|--------|--------------|-------|---------|-------------|------------|------------|----------------------------|
| CYPH   | Mycopan scabripes | Hydropus trichoderma | AMB 18739 | Italy       | OL839162   | OL839177   | This study                 |
| CYPH   | Mycopan scabripes | Hydropus trichoderma | 855      | Italy       | JF908049   | —           | Osmundson et al. 2013     |
| CYPH   | "Mycopan paradoxus" | Hydropus paradoxus | AMB 18772 | Italy       | OL839172   | OL839185   | This study                 |
| CYPH   | Mycopansp. | Hydropussp. | TENN-F-076402 | Canada     | OL839171   | OL839184   | This study                 |
| CYPH   | Phloeomana clavata | Mycena clavata | PRM 935560 | Czech Republic | LT671447   | LT671447   | Holec and Kolarík 2017     |
| CYPH   | Phloeomana minutula | Mycena olida | S.D. Russell (Naturalist # 857453) | USA (Indiana) | MN06080    | —           | Russell SD, unpublished   |
| CYPH   | Phloeomana speirea | Mycena speirea | AMB 18773 | Italy       | OL839158   | —           | This study                 |
| CYPH   | Phloeomana speirea | Marasmiellus omphaliformis | WU 17815 | —           | OL990024   | —           | This study                 |
| CYPH   | Phloeomana speirea | Mycena speirea | PRM 860810 | Czech Republic | LT671446   | LT671446   | Holec and Kolarík 2017     |
| CYPH   | Phloeomana speirea | Mycena ardeziaca | ICMP 20518 | New Zealand | MH380192   | MH380192   | Weir BS and Park D, unpublished |
| CYPH   | Pleurotopsis longinquus | Pleurotopsis longinquus | PRM 922296 | New Zealand | JQ694106   | —           | Cooper JA, Park D and Johnston P, unpublished |
| CYPH   | Pleurotopsis sp. | Pleurotopsis sp. | NZFS 216C | —           | —           | —           | —                          |
| CYPH   | Pleurotopsis sp. | Pleurotopsis sp. | AMB 18917 | Italy       | OL839173   | OL839186   | This study                 |
| CYPH   | Pleurotopsis sp. | Pleurotopsis sp. | DAOM 192847 | Canada (Ontario) | —           | AF042635   | Moncalvo et al. 2000, 2002 |
| CYPH   | Rectipilus fasciculatus | Rectipilus fasciculatus | RV95/473 | not indicated | —           | AF042604   | Moncalvo et al. 2000, 2002 |
| CYPH   | Rectipilus idahoensis | Rectipilus idahoensis | PB3/30/17 | not indicated | —           | AJ06539    | Langer E, unpublished      |
| CYPH   | Scytinotus ringens | Panellus ringens | Marson 30-Sep-2014 | Luxembourg | KY007610   | KY007610   | Garnier-Delcourt et al. 2016 |
| CYPH   | Setigeroclavula afflae ascendens | Setigeroclavula afflae ascendens | JAC9241/PDD 80716 | New Zealand | OL998338   | —           | This study                 |
| PORO   | Chrysomyces dunicola | Agaricales sp. | FD-2019a | Italy       | —           | MN496428   | Vizzini et al. 2019        |
| PORO   | Clitocybula abundans | Clitocybula abundans | PRM 899168 | Slovakia    | —           | LT854016   | Antonín et al. 2019        |
| PORO   | Clitocybula familia | Clitocybula familia | BRNM 736053 | Slovakia    | —           | JF730323   | Antonín et al. 2011        |
| PORO   | Clitocybula intervensa | Clitocybula sp. | AC-2015a | Sao Tome    | —           | MH85335    | Cooper et al. 2018         |
| PORO   | Clitocybula lacerata | Clitocybula lacerata | PRM 915404 | —           | LT854054   | —           | Antonín et al. 2019        |
| PORO   | Clitocybula oculata | Clitocybula oculata | AFTOL-ID 1554 | —           | —           | —           | Matheny et al. 2006        |
| PORO   | Clitocybula sp. | Clitocybula sp. | WU 20008 | Austria     | —           | LT854018   | Antonín et al. 2019        |
| Family | Revised name | Label | Voucher | State | nrITS | nrLSU | Reference |
|--------|--------------|-------|---------|-------|-------|-------|------------|
| PORO   | Clitocybula sp. | Halling 4598 NY | USA | — | JF730324 | Antonín et al., unpublished |
| PORO   | Clitocybula sp. | CORT 5690 | USA | — | LT854024 | Antonín et al. 2019 |
| PORO   | Delicatula integrella | NL-5062 | USA | — | MK27924 | Varga et al. 2019 |
| PORO   | Delicatula sp. | DED 823 SFSU | São Tomé | — | MH385341 | Cooper et al. 2018 |
| PORO   | Gerronema atrialbum | AFTOL-ID 1529 | USA | — | DQ457659 | Matheny et al. 2006 |
| PORO   | Gerronema indigisticum | HMJAU47636 (holotype) | China | — | MK693732 | Liu et al. 2019 |
| PORO   | Gerronema keralense | CAL 1666 (holotype) | India | — | NG_064531 | Latha et al. 2018 |
| PORO   | Gerronema karvense | CAL 1665 (holotype) | India | — | NG_064530 | Latha et al. 2018 |
| PORO   | Gerronema sp. | TU112037 | Gabon | — | JQ657793 | Tedersoo et al. 2012 |
| PORO   | Gerronema sp. | OKM27143 | not indicated | — | AF261365 | Moncalvo et al. 2002 |
| PORO   | Gerronema strombodes | JEJ.580 | not indicated | — | AF261364 | Moncalvo et al. 2002 |
| PORO   | Gerronema subclavatum | Redhead 5175 DAOM | not indicated | — | U66434 | Lutzoni 1997 |
| PORO   | Gerronema wildpretii | BRNM 788347 | Portugal | — | LT854045 | Antonín et al. 2019 |
| PORO   | Gerronema xanthophyllum | PRM 924657 | Czech Republic | — | LT854023 | Antonín et al. 2019 |
| PORO   | Hydropus atramentosus | WU0016972 | France | — | MK278153 | Varga et al. 2019 |
| PORO   | Hydropus fuliginarius | DAOM 196062 | not indicated | — | AF261368 | Moncalvo et al. 2002 |
| PORO   | Hydropus globocephalus | BAP 661 (holotype SFSU) | São Tomé | — | MH385340 | Cooper et al. 2018 |
| PORO   | Hydropus marginellus | AFTOL-ID 1720 | USA | — | DQ457674 | Matheny et al. 2006 |
| PORO   | Hydropus marginellus | OSC 112834 | Turkey | — | EU852808 | Gordon M, unpublished |
| PORO   | Hydropus marginellus | PBM 2780 (CUW) | USA | — | EF537890 | Matheny PB and Hibbett DS, unpublished |
| PORO   | Hydropus sp. | TENN 063881 | USA | — | MT241839 | Matheny PB, unpublished |
| PORO   | Hydropus subalpinus | C JV06499 | Denmark | — | FN394645 | Harder et al. 2010 |
| PORO   | Hydropus subalpinus | OKA-TR-K364 | Turkey | — | MN700170 | Kaygusuz et al. 2020 |
| PORO   | Hydropus subalpinus | OKA-TR-K380 | Turkey | — | MN700171 | Kaygusuz et al. 2020 |
| PORO   | Hydropus subalpinus | OKA-TR-B400 | Turkey | — | MN700172 | Kaygusuz et al. 2020 |
| PORO   | Hydropus subalpinus | NL-2623 | Hungary | — | MK278157 | Varga et al. 2019 |
| PORO   | Leucoconocybe auricoma | AFTOL-ID 1341 | China | — | DQ470812 | Matheny et al. 2006 |
| Family | Revised name | Label | Voucher | State  | nrITS | nrLSU | Reference          |
|--------|--------------|-------|---------|--------|-------|-------|--------------------|
| PORO   | *Leucoinocybe lenta* | herb. F. Bellu 85/110 (31 Oct 1985) (epitype) | Italy | —     | LT854032 | Antonín et al. 2019 |
| PORO   | *Leucoinocybe sulcata* | CAL 1246 (holotype) | India | —     | KR029721 | Latha et al. 2015   |
| PORO   | *Leucoinocybe taniae* | IB (Contu 18 Sept 2002) | Italy | —     | LT854029 | Antonín et al. 2019 |
| PORO   | *Megalocyllia marginata* | PRM 859785 | Czech Republic | —     | LT854046 | Antonín et al. 2019 |
| PORO   | *Megalocyllia platyphylla* | PRM 924408 | Czech Republic | —     | LT854019 | Antonín et al. 2019 |
| PORO   | *Megalocyllia rodmanii* | AFTOL-ID 560 | not indicated | —     | AY635778 | Matheny et al. 2006 |
| PORO   | *Megalocyllia sp.* | BRNM 747514 | South Korea | —     | LT854055 | Antonín et al. 2019 |
| PORO   | *Porotheleum fimbriatum* | KUC20131022 | South Korea | —     | KJ668472 | Jang et al. 2016   |
| PORO   | *Porotheleum fimbriatum* | TUF115493 | Estonia | —     | UDB016348 | Saar I, unpublished |
| PORO   | *Porotheleum fimbriatum* | TUF115522 | Estonia | —     | UDB016379 | Saar I, unpublished |
| PORO   | *Porotheleum fimbriatum* | TUF124001 | Estonia | —     | UDB027971 | Saitta A, unpublished |
| PORO   | *Porotheleum sp.* | NL-5174 | USA | —     | MK278580 | Varga et al. 2019   |
| PORO   | *Pulverulina ulmicola* | TENN 065567 | USA | —     | MT237456 | Matheny et al. 2020 |
| PORO   | *Pulverulina ulmicola* | TENN 029208 (holotype) | USA | —     | HQ179668 | Matheny et al. 2020 |
| PORO   | *Trogia infundibuliformis* | KUN_HKAS6709 | China | —     | JQ031781 | Yang et al. 2012   |
| PORO   | *Trogia venenata* | KUN_HKAS6799 (holotype) | China | —     | JQ031779 | Yang et al. 2012   |
| Physalacriaceae (OUTGROUP) | *Flammulina velutipes* | AFTOL-ID 558 | Not indicated | AY854073 | AY639883 | Matheny PB, Hughes KW, Petersen RH and Hibbett DS, unpublished |

**Table 1 (continued)**
DNA extraction, amplification, and sequencing

Total DNA was extracted from dry specimens (Table 1) employing a modified protocol based on Murray and Thompson (1980). PCR amplification (Mullis and Faloona 1987) included 35 cycles with an annealing temperature of 54 °C. Primers ITS1F and ITS4 or ITS4B (White et al. 1990; Gardes and Bruns 1993) were used to amplify the LSU/28S DNA extraction, amplification, and sequencing

(Porotheleaceae) + (Cyphellaceae) found in previous phylogenetic studies (Moncalvo et al. 2002; Matheny et al. 2006; Eberhardt et al. 2018; Antonin et al. 2019; Varga et al. 2019; Vizzini et al. 2020; Matheny et al. 2020; Sánchez-García et al. 2020) and obtained in the present work. (2) Second, a combined alignment of nrITS and 28S rDNA (nrLSU) focused on Porotheleaceae, including new sequences and those obtained by Cooper (2016a, b), Eberhardt et al. (2018), Antonin et al. (2019), Vizzini et al. (2019), Kaygusuz et al. (2020) and Matheny et al. (2020).

Porotheleaceae + Cyphellaceae

The LSU alignment (890 bp), which included 108 sequences, was analysed using Bayesian Inference (BI) and the Maximum Likelihood (ML) methods implemented on the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). The Bayesian analysis was performed using MrBayes 3.2.7a (Zhang et al. 2019) with the parameters of 2 simultaneous runs, 6 chains, temperature set at 0.2, sampling every 1000 generations, until reaching convergence (standard deviation less than 0.01) and PSRF (Potential Scale Reduction Factor) (Gelman and Rubin 1992) equal to 1 (after 2730000 generations). The 25% of sampled trees were discarded as burn-in. RAxML was run (Stamatakis 2014) using the standard search algorithm with 1000 bootstrap cycles. We estimated the best fit substitution model for each single alignment using the Bayesian information criterion (BIC) with jModelTest 2 (Darriba et al. 2012) and therefore selected the GTR+G+I model for all alignments. Flammulina velutipes (Physalacriaceae Corner) was used as the outgroup. The resulting trees were read with the SEA VIEW version 4 (Gouy et al. 2010) and saved in a vector format for printing. Both BI and ML analyses produced the same topology.

Fig. 1 50% majority rule 28S rDNA consensus phylogram of the families Porotheleaceae and Cyphellaceae (with Flammulina velutipes as outgroup) obtained in MrBayes. Nodes were annotated if supported by ≥ 0.95 Bayesian BPP (left) or ≥ 70% MLB (right). Non-significant support values are exceptionally represented inside parentheses ().
Figure 1 shows the BI tree with the bootstrap values (MLB) combined with those of the posterior probabilities (BPP). Significance thresholds was set ≥ 0.95 for posterior probability (BPP) and ≥ 70% for bootstrap values (MLB). The lengths of the branches are estimated as average values on the sampled trees.

Cyphellaceae

The data matrices of ITS (572 bp) and LSU (911 bp), which covered a total of 66 sequences and 56 sequences, respectively, were combined into a single multilocus matrix. This matrix (1483 BP), which covered a total of 78 sequences, was analyzed by using the Bayesian Inference (BI) and the maximum likelihood (ML) criteria as above and using the same parameters (Fig. 2).

Results of the phylogenetic analysis

Sequences analyzed grouped in two main clades (Fig. 1): (i) a well-supported one (BPP = 1.0, MLB = 90%) corresponding to the family Porotheleaceae (partially corresponding to the Hydropoid clade sensu Moncalvo et al. 2002; Antonín et al. 2019; Kaygusuz et al. 2020; Matheny et al. 2006, 2020), and (ii) another partially supported clade (BPP = 0.99, MLB = 29%) corresponding to the family Cyphellaceae.

Fig. 2 50% majority rule ITS rDNA-28S rDNA consensus phylogram of the family Cyphellaceae (with Flammulina velutipes as outgroup) obtained in MrBayes. Nodes were annotated if supported by ≥ 0.95 Bayesian BPP (left) or ≥ 70% MLB (right). Non-significant support values are exceptionally represented inside parentheses (). Newly sequenced collections are boldfaced. Hydropus scabripes DAOM 192847 is delimited by a red rectangle.

Fig. 3 Mycopen scabripes basidiomes. a Prunulus scabripes (NY, Murrill 864, NY00775141, holotype) b TENN-F-076401 (epitype) c-e TENN-F-076400 d BRNM 829033 e AMB 18737 f AMB 18739 g AMB 18854 h AMB 18738. Photos: a, d by H. Ševčíková; b, c, e by R. Lebeuf; f by E. Campo; g-h by G. Consiglio.
Porotheleaceae is composed of five different lineages: 1) (BPP = 1.0, MLB = 87%) Chrysomyces dunicola, Gerronema 1, 2, 3, Megaglobia, Trogia; 2) (BPP = 0.93, MLB = 64%) Haprosus s.s. (containing the type species H. fuliginosus) and Ciliocybula; 3) (BPP = 1.0, MLB = 95%) Delicatula; 4) (BPP = 0.92, MLB = 62%) Haprosus subalpinus, Porotheleum fimbiatum, Pulverulina umilicola, and two Haprosus sp.; and 5) (BPP = 1.0, MLB = 94%) Luecoinocybe.

Within Cyphellaceae at least five different lineages are recognized: 1) (BPP = 1.0, MLB = 54%) Actiniceps, Athelia, Chaetophylla, Calyptrula, a Mycopan clade (including all sequences named M. scabripes except one), Phloeomana, Pleurotopsis/Scytinotus; 2) (BPP = 1.0, MLB = 77%) Baeospora, Pleurella clade (BPP = 1.0, MLB = 99%) composed of Pleurella ardesiaca, Heloboma microsporum (including also the holotype) and ‘Mycopan scabripes’ DAOM 192847, GB AF042635; 3) (BPP = 1.0, MLB = 100%) Mycenella; 4) (BPP = 0.97, MLB = 48%) Athelia bombacina, Granulobasidium vellereum, Campanophilum proboscideum, Cheimonophyllum candidissimum, Porotheleum riparium, Scytinotus, and two Hydrospus sp.; and 5) (BPP = 0.92, MLB = 64%) Hydropus subalpinus, Porotheleum fimbiatum, Pulverulina umilicola, and two Hydrospus sp.; and 5) (BPP = 1.0, MLB = 94%) Luecoinocybe.

Within Cyphellaceae at least five different lineages are recognized: 1) (BPP = 1.0, MLB = 54%) Actiniceps, Athelia, Chaetophylla, Calyptrula, a Mycopan clade (including all sequences named M. scabripes except one), Phloeomana, Pleurotopsis/Scytinotus; 2) (BPP = 1.0, MLB = 77%) Baeospora, Pleurella clade (BPP = 1.0, MLB = 99%) composed of Pleurella ardesiaca, Heloboma microsporum (including also the holotype) and ‘Mycopan scabripes’ DAOM 192847, GB AF042635; 3) (BPP = 1.0, MLB = 100%) Mycenella; 4) (BPP = 0.97, MLB = 48%) Athelia bombacina, Granulobasidium vellereum, Campanophilum proboscideum, Cheimonophyllum candidissimum, Porotheleum riparium, Scytinotus, and two Hydrospus sp.; and 5) (BPP = 1.0, MLB = 100%) Acanthocorticium brueggemannii, Henningsomyces and Rectipilus.

In our combined ITS/LSU analysis focused on Cyphellaceae (Fig. 2), nine different lineages are recovered: 1) (BPP = 1.0, MLB = 98%) a Mycopan clade and Atheniella, Artsactica, Cymatotrichum, and Glyptotinaria (BPP = 1.0, MLB = 100%) Athelia, Chaetophylla, Calyptrula and Seigeroclowula aff. adscendens; 4) (BPP = 1.0, MLB = 99%) Phloeomana and Hemimycena gracilis; 5) (BPP = 1.0, MLB = 100%) Pleurotopsis/Scytinotus; 6) (BPP = 0.98, MLB = 62%) Athelia, Chondrostereum, Cyphella digitalis, Campanophilum, Cheimonophyllum, Gloeostereum, Granulobasidium; 7) (BPP = 1.0, MLB = 98%) Baeospora, Pleurella clade (BPP = 1.0, MLB = 100%) composed of Pleurella ardesiaca, Heloboma microsporum (including also the holotype) and ‘Mycopan scabripes’ DAOM 192847, GB AF042635; 8) (BPP = 1.0, MLB = 100%) Mycenella; and 9) Lignomphalaria lignicola.

Focusing on the sequences named as M. scabripes, these fall within the Cyphellaceae in two distinct clades (Figs. 1–2): a strongly supported Mycopan clade, sister to Atheniella, which contains all but one of the sequences named as such; and the strongly supported Pleurella clade, sister to Baeospora, which encompasses the sequence of Hydrospus scabripes DAOM 192847 (Redhead 2013).

**Taxonomy**

*Mycopan scabripes* (Murrill) Redhead, Moncalvo & Vilgalys, in Redhead, Index Fungorum 15: 1 (2013) Figs. 3, 4a–b, 5–6

*Basionym: Prunulus scabripes* Murrill, N. Amer. Fl. (New York) 9(5): 331 (1916)
≡ *Mycena scabripes* (Murrill) Murrill, Mycologia 8(4): 221 (1916)
≡ *Hydropus scabripes* (Murrill) Singer, Sydowia 15(1–6): 66 (1962)
≡ *Hydropus var. quadrisporus* Baeospora, Persoonia 17(1): 140 (1998)
≡ *Mycena trichoderma* Joss., in Kühner, Encyclop. Mycol. 10: 689 (1938)
≡ *Hydropus trichoderma* (Joss.) Singer, Agrar. mod. Tax., Edn 2 (Weinheim): 389 (1962) [1961]

Holotype: Murrill 864 NY, NY00775141

Epitype here designated: TENN-F-076401, MycoBank MBT10004920

*Basidiome mycenoid. Pileus* 16–46(–55) mm, conico-convex to convex or almost campanulate, later plano-convex with distinct broad umbo, distinctly sulcate-striate at the margin up to 1/2–2/3 of pileus, rarely non-striate, slightly or not hygrophanous, with or without lobed, slightly crenulate margin, dark brown, dark yellowish brown, to very dark greyish brown (10YR3/2–3/6), rarely almost black (5YR2/5/1), with slightly paler margin (10YR4/3–4/6) when young, glabrous to slightly rugulose to tomentose. *Lamellae* moderately crowded, L = 18–26, L = 0–3, narrowly adnate to slightly emarginate or subfree, moderately broad to almost ventricose, whitish to very pale greyish, with concolorous or slightly paler minutely fimbriate edge. *Stipe* 30–70 × 2–6(–7) mm, cylindrical or slightly thickening downwards, straight or curved, white to very pale greyish, fibrillos, flocculose (mainly at apex) by distinct concolorous or brown to grey-brown squamules, hollow or not, with or without distinct white tomentum at the base. *Context* whitish in pileus, slightly more yellowish grey in the stipe. *Smell* and *taste* indistinct. *Spore print* white.

*Basidiospores* 7.5–10.5 × 4.9–6.8 μm [816/18/15] (on average 9.0 × 5.9 μm), Q = 1.37–1.72 (Q = 1.55), V = 86–259 μ3 (V = 173 μ3), ellipsoid to oblong, with broadly rounded apex, rarely slightly subamygdaliform, slightly tapering towards apiculus or not, thin-walled, often with granular contents, without or with 1–2 guttules, weakly to rather strongly amyloid, cyanophilous, conglutinous. *Basidia* 26–45 × (6.0–)7.0–10.0(–12.0) μm, narrowly clavate to subcylindrical, thin-walled, colourless, sometimes slightly amyloid at apex (Fig. 6d), mono- to tetrasporic, the number of sterigmata varying according to the collection studied and the portion of lamella within the single basidiome, 6–9(–11.5) μm long. *Subhymenium* consisting of short-celled, often intertwined, 3–5 μm wide elements. *Hymenophoral trama* regular of parallel, 4–12 μm wide, cylindrical hyphae, thin-walled to moderately thick-walled (0.5–1 μm thick), smooth, colourless.
slightly dextrinoid to dextrinoid after 3 min of reaction in Melzer. Lamellar edge heterogenous, fertile. Cheilocystidia 50–90(–120) × 10–20(–25) μm, scattered to moderately abundant, lageniform, sub fusiform to subcylindrical with long cylindrical and broadly rounded apex and short neck, often with a narrow pedicel up to 20(–25) μm long and inflated in the middle part (and then up to 25 μm wide), thin-walled or with slightly thickened wall up to 1 μm in the middle part, colourless, often with granular contents and sometimes covered with mucous material incorporating spores or crystalline deposits. Pleurocystidia quite abundant, 50–110(–130) × 12–20 μm, similar in shape and size to cheilocystidia. Pileipellis as a radially arranged cutis composed of (3.0–)5.0–7.0(–8.0) μm wide cylindrical hyphae, thin-walled, colourless or with pale brown vacuolar pigment and minutely to heavily encrusting pigment, very weakly dextrinoid in Melzer, with rare to quite abundant clavate to subcylindrical, broadly fusiform or vesiculose to almost rounded ascending terminal elements (pilocystidia), 20–50 × 7–12 μm, colourless or with pale brown vacuolar pigment. Subcutis of broad-celled, fusoid-ventricose elements (subcellular), 15–40 μm wide, thin-walled, colourless. Caulocystidia rare to abundant, single, or clustered, (sub)fasciculate, (25–)35–70(–85) × 5–15(–20) μm, similar to the hymenial cystidia but shorter, sinuous, sometimes septate, thin-walled, colourless or with brown contents. Stipitpellis a cutis composed of 3.0–7.0(–10) μm wide parallel hyphae with light brownish contents. Stipititrama sarcodimitic (sensu Redhead 1987), with walls of sarcoskeletons strongly metachromatic in Cresyl blue, not or very weakly dextrinoid, colourless or with yellowish contents; thinner hyphae, 4–12 μm wide, larger hyphae, 6–25 μm wide. Clamp-connections present, rare to moderately abundant.

Habitat and distribution Solitary or gregarious on or associated with well decayed wood or forest litter, often near or on...
the base of stems or stumps of deciduous trees, with a preference for Fagus (in Europe). Autumn. Rare but widespread in Europe (Kühner 1938; Hausknecht et al. 1997; Bas 1999; Læssøe 2008, 2012), North America (Canada and USA, Smith 1947) and North Africa (Malençon & Bertault 1975). It is probably also present in Asia because an environmental ITS sequence (GB KP238192) obtained from the roots of the mycoheterotrophic (achlorophyllic) orchid Gastrodia
flabilabella from Taiwan (Lee et al. 2015) clusters with Hydropus cf. scabripes (GB DQ411536) (Lee et al. 2015) or with Hydropus scabripes (GB GU234149) (Ogura-Tsujita et al. 2021, suppl. mat.).

Examined material: **Mycopan scabripes. CANADA:** Québec, Terrebonne, on soil, under *Pinus strobus*, 19 October 2011, R. Lebeuf (TENN-F-076400); Québec, Saint-Casimir, chemin de l’Île Grandbois/rang de la Rivière Noire, on the remains of a large, decayed trunk of unknown nature, 28 September 2014, R. Lebeuf (TENN-F-076401, epitype). **CZECH REPUBLIC:** Bory, Rasuveř, Fagetum, on soil under *Fagus*, 15 October 2015, H. Ševčíková (BRNM 829032); Kladeruby nad Oslavou, Údolí Oslavy a Chvojnice Nature Reserve, Vlčí kopec, Fagetum, under fallen *Fagus*, 30 October 2015, H. Ševčíková (BRNM 829033); Březník, Údolí Oslavy a Chvojnice Nature Reserve, on soil under *Carpinus, Quercus, Acer, Tilia*, 25 November 2016, H. Ševčíková and D. Dvořák (BRNM 788135); Březník, on soil under ruin Lamberk, under *Carpinus, Pinus, Picea, Quercus*, 1 October 2017, H. Ševčíková (BRNM 793297). **ITALY:** Emilia-Romagna, Bologna, Via Bezzecca, in a public garden under broad-leaved trees, 17 November 1999, G. Consiglio (AMB 18738); Sardegna, Tempio Pausania (SS), in a flowerbed of a public garden, 31 October 2003, G. Consiglio (AMB 18854); Friuli-Venezia Giulia, Udine, Codroipo, Parco di Villa Manin, on litter of *Cedrus atlantica*.
and *Cupressus sempervirens*, 12 December 2020, E. Campo (AMB 18739); Pordenone, Castelnuovo del Friuli, Celante, on a trunk of *Populus nigra* covered with moss about 2 m from the ground, 7 November 2020, E. Campo (AMB 18737); **Trentino Alto-Adige**, Trento, S. Orsola, Dos dei Fungi, at the base of a rotting stump in a mixed forest (*Fagus sylvatica*, *Larix decidua*, *Picea abies*), 4 October 1996, B. Oss Emer (MCVE 507a), USA: New York, Essex Co., Lake Placid, Adirondacks, by roadside (?) in coniferous or mixed forest at 2000 ft elevation, 3-14 October 1912, W.A. and Edna Murrill, NY00775141 (holotype of *Prunulus scabripes*); Tompkins Co., near Dryden, Ringwood Preserve, gregarious on woodchips around stump, 13 September 1984, R. E. Halling (NY 02763989, no. 3806) (as *Mycena scabripes*); **Maine**, South of Carrabassett Village near old rail roadbed, Franklin County, 11 October 1971, H. E. Bigelow (NY 02763988, Bigelow 16847) (as *Mycena scabripes*); **California**, Coast Red woods, 0.5 mile E on Freshwater Rd., stand on S side of highway across from College Forest, Humboldt Co., 22 November 1986, O. K. & H. H. Miller, D. Largent (NY 01983317, OKM22785).

Notes- *Prunulus scabripes* was established by Murrill (1916a) for a mycenoid species with an avellaneous slightly striate pileus, minutely and densely scabrous stipe, oblong-ellipsoid, 8–9 × 4–5 μm spores, growing among grasses (*Poaceae*), in Lake Placid, NY. Murrill (1916b) then combined it in *Mycena*. Smith (1936) found in the holotype collection bisporic basidia, amyloid spores 8.5–11 × 6–7 μm, and cylindrical to subfusoid, 77–95 × 8–10 μm, smooth, scattered hymenial cystidia with obtuse apex. He additionally described new records of the species from Ann Arbor (Michigan, in oak groves) and Orick (California, under redwoods), with darker pileus colours than those of the protologue ("mummy brown" to "clove brown", "olive-brown" to "buffy brown"), broadly ellipsoid and faintly amyloid spores 7–9(–10) × 5–6 μm, tetrasporic basidia, abundant smooth hymenial cystidia, 60–100 × 8–14 μm with an inflated base and a long narrow neck, occasional cystidia on pileus surface, and a subcutis of inflated elements. In his monographic work on *Mycena*, Kühner (1938) included *Mycena scabripes*, together with *M. trichoderma*, within subg. *Eu-Mycena* (amyloid spores), sect. *Spuriae* (non-amyloid to faintly amyloid trama elements and non-diverticulate hymenial cystidia and pileipellis elements), subsect. *Subtypicae* (large spores and hymenial cystidia and non-hymeniform pileipellis); he accurately described both (tri-)tetrasporic and (rare) bisporic collections from France and first pointed out the metachromatic reaction (purple-violet) of tissue trama in Cresyl blue. Following an exchange of letters and material with A.H. Smith, Kühner considered the North American and European collections as conspecific. In his monograph on North American species of *Mycena*, Smith (1947) included *M. scabripes* in the genus *Mycena* section *Typicae* (sic!), close to some well-known species such as *M. alcalina* or *M. leptocephala* and described further tetrasporic and (rare) bisporic collections from USA (California, Michigan, Montana, New York, Oregon, Tennessee, Washington) and Canada (Ontario). Singer (1962) combined it in *Hydropus* and later (Singer 1982, 1986) placed it in sect. *Floccepides* Kühner ex Singer (spores amyloid or not; pileipellis usually non hymeniform, without or with rare pileocystidia; pseudocystidia absent or present; pigment vacuolar, not parietal or extracellular/encrusting), subsect. *Spurii* Kühner ex Singer (spores amyloid, without pseudocystidia). Bas (1998) established *H. scabripes* var. *quadrisporus* (typed with a collection from Belgium) distinguished by tetrasporic basidia and presence of clamp connections. Prompted by the molecular phylogenetic output of Moncalvo et al. (2002), in which the unique *H. scabripes* sequence GenBank AF042635 (DAOM 192847) was not related to that of *H. fuliginarius* (GB AF261368, DAOM 196062, type species of the genus), Redhead, Moncalvo & Vilgalys (in Redhead 2013) erected the monospecific genus *Myconop for Prunulus scabripes*, with AF042635 as "reference" sequence.

As all attempts (also including Illumia MiSeq technology) made to produce molecular data from the *Prunulus scabripes* holotype failed, a North American collection whose morphological characteristics fit well the protologue, the morphological data of the holotype and the descriptions of most of the authors was selected as epitype. As previously pointed out by Kühner (1938) and Smith (1947) (only on a morphological basis), the North American and European collections are conspecific (Fig. 2 and Table 2).

A morphologically closely related species, *Mycena trichoderma* Joss., was described from France (in Kühner 1938) and later also combined in *Hydropus* (Singer 1962). After the original description, this species has been found in several European areas (Josserand 1965; Enderle 1985; Robich 1986, 1990; Dâémon 1995; Hauskncheht et al. 1997; Watling and Turnbull 1998; Hühner 2004; Lassoe 2008, 2012; Pérez-de-Gregorio and Picón 2011) and in the USA (Michigan, Smith 1947). Hauskncheht et al. (1997) described *H. trichoderma* var. *lobaenesis* from Austria, as a taxon with bisporic basidia and absence of clamp connections, taxon found also in Italy by Robich (2004). The main characters differentiating *Hydropus trichoderma* from *M. scabripes* seem to be the greater abundance of larger pileocystidia and the presence of heavily encrusting pigment on the hypheae of the pileipellis and subcutis. However, these incrustations can be rather inconspicuous and scarce.

Our molecular analysis (Fig. 2) pointed out that all the collections named *H. scabripes*, *H. cf. scabripes* or *H. trichoderma* from Europe and North America (except for *H. scabripes* INAT 16782378 and DAOM 192847) are conspecific and form a subclade, together with *Mycena dura* (MCVE 507a, GB JF908448, from Italy), within the strongly
supported Mycopan clade (BPP = 1.0, MLB = 98%). The Mycopan clade is sister (BPP = 1.0, MLB = 98%) to Atheniella within the Cyphellaceae. The second subclade (/quiniaultensis) consists of Mycena quiniaultensis (MICH 11521, GB MN809552, from the USA), M. cf. quiniaultensis (OSC 67121 isolate p182i, from the USA), Mycopan scabripes (iNAT 16782378, GB MZ241313, from the USA), and Mycopan sp. (TENN-F-076402, from Canada, Fig. 7). The third subclade consists of a newly sequenced collection of Hydropus paradoxus Moser from Italy (AMB 18772). These subclades are not completely resolved using ribosomal markers, but some differential morphological characters (see below) and TEF1/RPB2 sequences indicate that they are independent entities (Table 2). As “Hydropus scabripes” DAOM 192847 falls within the Pleurella clade, it is a misidentified collection.

The above mentioned Italian Mycena dura collection (incorrectly referred to as Swedish in GenBank) represents a misidentification because the real M. dura Maas Geest. & Hauskn. is a member of Mycena sect. Calodontes (M. pura complex), as stated by Harder et al. (2010, 2013) and Olariaga et al. (2015). The close molecular affinity of Mycena dura MCVE 507a with H. scabripes was already highlighted by Cooper (2016a) and Eberhardt et al. (2018), but without providing any comment. Original microscopical observations by HS indicate the collection as conspecific with M. scabripes.

In the /quiniaultensis subclade, Mycena quiniaultensis Kauffman is characterized by a glutinous pileus and stipe surface and narrowly ellipsoid spores (6.5–8 × 3–3.5 μm) (Smith 1947). The closely related Mycopan sp. (TENN-F-076402) has a quite smooth stipe surface and also small and narrow spores (5.5–8.5 × 3.5–4.5(–5) μm; Fig. 7b).

Hydropus paradoxus Moser (1968) is characterized by a peculiar structure of pileipellis and stipitipellis almost forming a trichodermic/hymeniform layer (terminal elements 60–140(–180) × 10–17 μm) (which is reflected in a very velvety-tomentose pileus surface), and subcutis elements heavily covered with encrusting pigment (Fig. 8).

The ITS sequence of the Mycena pseudotenax holotype (MK169371, MICH 7168; not included in the present

| Sequence | GenBank Acc. n. | Subclade | Voucher and State | Coverage | Identity | Mismatches | Gaps |
|----------|----------------|----------|------------------|----------|----------|------------|------|
| TEF1     | OM100068       | M. scabripes | TENN-F-076401 (epitype), Canada | 95.8% | 99.4% | 3 | 0 |
| versus OM100066 | M. scabripes | AMB 18739, Italy | 81.5% | 99.6% | 2 | 0 |
| versus OM100067 | M. scabripes | TENN-F-076400, Canada | 77.4% | 95.3% | 20 | 1 |
| versus OM100065 | H. paradoxus | AMB 18772, Italy | 93.5% | 90.3% | 50 | 3 |
| versus OM100069 | quiniaultensis clade | TENN-F-076402, Canada | 97.3% | 90.9% | 56 | 0 |
| RPB2     | OM100063       | M. scabripes | TENN-F-076401 (epitype), Canada | 100% | 98.7% | 8 | 0 |
| versus DQ457634 | M. scabripes | PBM 2513 AFTOL-ID 535, USA | 97.9% | 98.5% | 9 | 0 |
| versus OM100062 | M. scabripes | TENN-F-076400, Canada | 100% | 98.3% | 11 | 0 |
| versus OM100061 | M. scabripes | AMB 18739, Italy | 98.6% | 93.6% | 40 | 0 |
| versus OM100060 | H. paradoxus | AMB 18772, Italy | 97.3% | 90.9% | 56 | 0 |
| versus OM100064 | quiniaultensis clade | TENN-F-076402, Canada | 97.3% | 90.9% | 56 | 0 |
analysis) shows a homology of 97.9%, 98.3% and 97.7% with those of *M. scabripes* epitype, *Mycopan* sp. (TENN-F-076402) and *Hydropus paradoxus* (AMB 18772), respectively. *Mycena pseudotenax* A.H. Sm. (≡ *M. scabripes* f. *safranopes* Mañé & Bertault fide Esteve-Raventós and Ortega 1995) differs from *H. scabripes* by smaller spores, 6.5–8.2 × 3.5–4.2 μm, smaller hymenial cystidia, 55–80 × 8–14 μm, and presence of a saffron-yellow mycelium at the
Table 3  Microscopic features (basidia and spore measurements, presence/absence of clamp connections and number of spores per basidium) of *Mycopan scabripes* collections as reported in literature and in this study (*boldfaced*, *Hydropus trichoderma* included)

| Reference                        | Taxon                             | Spore range (μm) | Number of spores per basidium | Clamp connections | Basidia dimensions (μm) |
|----------------------------------|-----------------------------------|------------------|-------------------------------|-------------------|-------------------------|
| Kühner 1938                      | *Mycena scabripes*               | (8–)8.5–11.5(–15.2) × 4.5–5.7(–6.2) | (3-sp.4-sp. +) | 27–45 × 7–9.5 |
| Kühner 1938                      | *Mycena scabripes*               | (8–)8.5–10(–11) × (5–)5.5–6.5 | 2-sp. | Not indicated |
| Josserand, in Kühner 1938        | *Mycena trichoderma*             | 7.5–9.4 × 5–5.5  | 4-sp. | Not indicated |
| Smith 1937                       | *Mycena scabripes*               | 7–9(–10) × 5–6  | 4-sp. | Not indicated |
| Smith 1947                       | *Mycena scabripes*               | 7–8 × 5–6       | 4-sp. | Not indicated |
| Josserand 1965                   | *Mycena trichoderma*             | 8–10 × 6–4 × 7  | 4-sp. | Not indicated |
| Einhellinger 1973                | *Hydropus trichoderma*           | (7–)8–9×(5–10) × (4.5–)5–6 | Not indicated | Not indicated |
| Malençon and Bertault 1975       | *Mycena scabripes*               | 8–10 × 5–5.5    | 4-sp. | + |
| Enderle 1985                     | *Hydropus trichoderma*           | 7.5–10 × 4.9–5.8 | 4-sp. | – |
| Lonati 1986                      | *Hydropus scabripes*             | 8–10 × 4–5      | 4-sp. | + |
| Robich 1986                      | *Hydropus scabripes*             | 9–10.5 × 4–5.5  | 4-sp. | + |
| Seni-Irlet 1987                  | *Hydropus scabripes*             | 8–9 × 5–6       | 4-sp. | Not indicated |
| Robich 1990                      | *Hydropus trichoderma*           | 9–10 × 5.5–6    | (2-sp.)4-sp. + | 37–44 × 7–8 |
| Krisai-Greilhuber 1992           | *Hydropus trichoderma*           | 7.5–8.7 × 5.6   | 4-sp. | + |
| Bas in Maas Geesteranus and Hausknecht 1993 | *Prunulus scabripes holotype*     | 9.8–11.2(–12.9) × 5.5–6.8 | 2-sp. | Not indicated |
| Bon 1995                         | *Hydropus scabripes*             | (7.5–)9–11 × 5–6(–7) | 2-sp. | – |
| Dämon 1995                       | *Hydropus trichoderma*           | (6–)7.5–9(–9.5) × 4.5–6(–6.5) | (2-sp.)4-sp. + | 25–35 × 8–9 |
| Hausknecht et al. 1997           | *Hydropus scabripes*             | 6.8–11 × 4.4–7.2 | 2-sp. 4-sp. | + |
| Hausknecht et al. 1997           | *Hydropus trichoderma*           | 7.2–10.7 × 4.4–6.4 | 4-sp. | + |
| Hausknecht et al. 1997           | *Hydropus trichoderma var. lobanensis* | 7.9–12.3 × 5.2–6.6 | 2-sp. | – |
| Watling and Turnbull 1998        | *Hydropus scabripes*             | 8.5–10 × 4.5–5 | (2-sp.)4-sp. + | 27–45 × 7–9.5 |
| Watling and Turnbull 1998        | *Hydropus trichoderma*           | 7.5–9(–10) × 5–6 | 4-sp. | + |
| Bas 1999                         | *Hydropus scabripes*             | 8.5–11 × 5.5–7 | 2-sp. | – |
| Bas 1999                         | *Hydropus scabripes var. quadrisporus* | 7–10 × 4.5–6 | 4-sp. | + |
| Migliozzi and Camboni 2000        | *Hydropus scabripes*             | (7.3–)7.9–9.5(–10) × 5(–)5.3–6.3 | 4-sp. | + |
| Hübner 2004                      | *Hydropus trichoderma*           | 7.5–10 × 5–6    | 4-sp. | + |
| Robich 2004                      | *Hydropus trichoderma var. lobanensis* | 9–11 × (6–)7.5–9 | 2-sp. | – |
| Læssøe 2008, 2012                | *Hydropus scabripes var. quadrisporus* | 7–10 × 4.5–7.5 | (2-sp.)4-sp. | + |
| Læssøe 2008, 2012                | *Hydropus scabripes var. scabripes* | 8.5–11(–13) × 5.5–7 | 2-sp. | – |
| Læssøe 2008, 2012                | *Hydropus trichoderma*           | (7.5–)8.5–10 × (5–)6–7 | (2-sp.)4-sp. | + |
| Pérez-de-Gregorio and Pícon 2011 | *Hydropus trichoderma*           | 7–11 × 5–7.6   | 4-sp. | + |
| Rubio Domínguez 2013              | *Hydropus scabripes*             | 7.2–9.3 × 5.3–6.1 | 4-sp. | + |
| Wölfl und Tertlutter 2016         | *Mycopan scabripes*              | 7–9.5(–10) × 5–6.5 | 4-sp. | + |
| Deceuninck 2019                   | *Mycopan scabripes var. scabripes* | 8.5–10(–11.0) × (5.5–)6–6.5 (7.0) | 2-sp.(4-sp.) | – |
| Robinson and Hausknecht 1993     | *Hydropus scabripes*             | 8.5–10(–11.0) × (5.5–)6–6.5 (7.0) | 2-sp.(4-sp.) | – |
| Robinson and Hausknecht 1993     | *Hydropus scabripes*             | 8.5–10(–11.0) × (5.5–)6–6.5 (7.0) | 2-sp.(4-sp.) | – |
| Robinson and Hausknecht 1993     | *Hydropus scabripes*             | 8.5–10(–11.0) × (5.5–)6–6.5 (7.0) | 2-sp.(4-sp.) | – |
This study

Mycopan scabripes

This study

Hydropus trichoderma

This study

(continued)

Table 3 (continued)

| Reference       | Taxon                               | Spore range (μm) | Number of spores per basidium | Clamp connections | Basidia dimensions (μm) |
|-----------------|-------------------------------------|------------------|-------------------------------|-------------------|-------------------------|
| AA VV 2020      | Mycopan scabripes                   | 8.5–9.9(–10.5) × 5.5–6.5(–6.7) | 4-sp.                         | +                 | Not indicated           |
| This study      | Prunulus scabripes NY00775141       | 10–12 × 6.0–7.5 (n = 49) | 2-sp., 4-sp.                  | +                 | 30–42 × 8–10(–11)      |
| This study      | “Mycena dura” MCVE 507a             | 7.0–9.0(10) × 4.9–6.2 (n = 60) | (1-3-sp.)4-sp.                | + (rare)          | 27–43 × 6.5–9.5(–10)   |
| This study      | Mycopan scabripes AMB 18737         | 10.2–12 × 6.4–7.4 (n = 83) | 2-sp., 4-sp.                  | +                 | 28–42 × 8–9.5           |
| This study      | Hydropus trichoderma AMB 18739      | 9.9–12 × 6.8–8.4 (n = 50) | 2-sp., 1-sp.                  | +                 | 30–40 × 7.5–9.5         |
| This study      | Mycopan scabripes NY02763989        | 7–9.5(–11) × (4.8–5)5–6 (n = 63) | 4-sp.                         | +                 | 26–42 × (5.5–6)10.5(–11.5) |
| This study      | Mycopan scabripes NY02763988        | 7.8–9.3 × 5.4–6.4 (n = 40) | 4-sp.                         | + (rare)          | 24–36 × 8–10            |
| This study      | Mycopan scabripes NY01983317        | 7.8–8.8 × 4.8–5.4 (n = 45) | 2-sp., 4-sp.                  | + (rare)          | 25–35(40) × 6.5–9(–10) |
| This study      | Mycopan scabripes TENN-F-076400     | 7.2–8.5 × 5.1–5.8 (n = 58) | 2-sp., 4-sp.                  | + (rare)          | 26–35 × 7–9             |
| This study      | Mycopan scabripes epitype TENN-F-076401 | 8.5–10.3 × 5.2–5.9 (n = 86) | 2-sp., 4-sp.                  | +                 | 25–42 × 7–10            |
| This study      | Mycopan scabripes BRNM 829033       | 7.8–9.2 × 5.2–5.9 (n = 45) | 2-sp., 4-sp.                  | + (rare)          | 26–35 × 8–9             |
| This study      | Mycopan scabripes BRNM 829032       | 8.0–9.7 × 4.9–5.6 (n = 57) | (2-sp.)4-sp.                  | +                 | 28–46 × 7.5–9.5         |
| This study      | Mycopan scabripes BRNM 788135       | 7.0–8.0 × 4.7–5.4 (n = 48) | (2-sp.)4-sp.                  | +                 | 23–40 × 7–10            |
| This study      | Mycopan scabripes BRNM 793297       | 6.6–8.1 × 5.1–6.0 (n = 50) | 4-sp., 2-sp.                  | + (rare)          | 25–45 × 7–9             |
| This study      | Mycopan scabripes AMB 18738         | 9.5–10.9 × 6.2–7.1 (n = 32) | 2-sp., 1-sp.                  | –                 | 25–38 × 7–9.5           |
| This study      | Mycopan scabripes AMB 18854         | 7.8–9.3 × 5.0–5.7 (n = 50) | 2-sp., 4-sp.                  | –                 | 25–40 × 8–10.5          |

stipe base (Smith 1947; Lonati 1986; Esteve-Raventós and Ortega 1995; Esteve-Raventós et al. 2002).

According to the literature and our observations, M. scabripes is a macro- and microscopically quite variable species depending on the collection examined. The pileus can be grey, dark grey-brown, dark olivaceous grey-brown to nearly blackish (Fig. 3–4a, b); the surface can be glabrous or slightly rugulose to tomentose. There are variants with an almost glabrous, or a white-pruinose or brownish pruinose stipe. Some collections show very rare and short pileocystidia, while in others pileocystidia are rather large and more abundant. The pigment in the elements of the pileipellis is always vacuolar, accompanied or not by scarce or abundant encrusting extracellular pigment. A great range of variation in spore size is observed (Table 3), as already noted by Kühner (1938), Smith (1947), Josserand (1965) and Bas (1999), and this variability is related to the number of basidial sterigmata. As previously highlighted by Smith (1936), Bas (in Maas Geesteranus and Hausknecht 1993) and Bas (1998, 1999), the holotype collection turned out to be bisporic. In our observations on the holotype (MM, HS), we found spores measuring 10–12 × 6–7.5 μm (n = 49), a mixture of bi- and tetrasporic basidia and clamp connections, as observed in the selected epitype. Most collections we have studied display clamp connections, irrespective of being tetrasporic, bi/tetrasporic or mono/bisporic (Table 3). The number of sterigmata varies not only according to the collection studied but also to the portion of lamella examined within the single basidiome. Our collections AMB 18738 (mono-bisporic) and AMB 18854 (bi-tetrasporic) exhibit no clamp connections. A possibility remains also of rare completely bisporic collections without clamp connections (Hausknecht et al. 1997 and Robich 2004 as H. trichoderma var. lobauensis; Enderle 1985; Bon 1995; Bas 1999; Læsøe 2008, 2012; Deceuninck 2019 and AA VV 2020 as H. scabripes var. scabripes).

Pleurella E. Horak, N. Z. J. Bot. 9(3): 477 (1971) here emended

Basidiome gymnocarpic. Pileus convex or conical-campanulate, later becoming applanate or depressed, dry, smooth
or densely covered with minute squamules. Lamellae adnate or subdecurrent, emarginate, crowded. Stipe excentric to lateral, or centrally inserted, cylindrical, with darker dots (caulocystidia) near the apex to fibrillose or longitudinally striate, dry, without veil remnants. Spore-print white. Basidiospores ellipsoid to subcylindrical, smooth, thin-walled, strongly amyloid, without germ pore. Cheilocystidia present, thin-walled, colourless; pleurocystidia absent or rare to scattered, thin-walled, colourless. Caulocystidia present, clustered, thin-walled to moderately thick-walled (wall up to 1 μm thick). Pileipellis trichodermic/hymeniform or as a radially arranged cutis with elements strongly encrusted with a brown pigment. Stipititrama saccodimitic. Clamp connections present. On rotten wood and bark (rarely on living trees) of Phyllocladus alpinus, rarely on Dacrydium cupressinum or Nothofagus spp. (New Zealand); on litter or buried wood fragments (Italy).

Type species: Leucopaxillus ardesiacus G. Stev. & G.M. Taylor

Pleurella ardesiaca (G. Stev. & G.M. Taylor) E. Horak, N.Z. J. Bot. 9(3): 477 (1971) Fig. 4e
≡ Hydropus ardesiacus (G. Stev. & G.M. Taylor) Singer, Fl. Neotrop., Monogr. 32: 38 (1982)
≡ Leucopaxillus ardesiacus G. Stev. & G.M. Taylor, in Stevenson, Kew Bull. 19(1): 20 (1964)

Selected descriptions: Stevenson (1964: pl 3.5, as Leucopaxillus ardesiacus). Selected iconography: Stevenson (1964: as Leucopaxillus ardesiacus), Horak (1971: 477–478).

Notes- The genus Pleurella was erected by Horak (1971) for Leucopaxillus ardesiacus, a lignicolous pleuropodal species from the North Island of New Zealand, characterized by smooth, amyloid spores [4.5–6–(6.5) × 2–3 μm], presence of cheilocystidia, abundance of extracellular brown encrusting pigment in the pileipellis elements, and clamp connections (Stevenson 1964; Horak 1971). Horak believed that the genus might have an affinity with Melanoleuca Pat. and Leucopaxillus Bourier due to its habit and amyloid spores. Pleurella was synonymized with Hydropus by Singer (1982).

The earliest molecular-based inferences about the phylogenetic position of this genus are those of Sánchez-García et al. (2014): they first recognized a close relationship with Dennisiomyces Singer or Porpoloma Singer s. str. based on morphological similarities, but recovered, after a BLASTn search, the nearest alliance between the ITS sequence (JQ694106) publicly available from a collection (PDD 87446) referred to as Pleurella ardesiaca from New Zealand to Baeospora in the Marasmioid clade (Matheny et al. 2006; Binder et al. 2010; = Marasminiae Dentinger et al. 2016) or to Hypsizygus (Gillet) Singer in the Lyophyllaceae. Cooper (2016a, b) considered Pleurella a member of Cyphellaceae Lortsy together with Cyphella, Cheimonomophyllum, Baeospora, + “Mycopan”’s. Redhead, without providing molecular evidence, but probably based on previous results which indicated, on a BLASTn basis, an affinity of Pleurella with Baeospora, the latter genus having been shown to belong to the Cyphellaceae by Moncalvo et al. (2000, 2002) and Matheny et al. (2006).

Eberhardt et al. (2018) recovered a well-supported Cyphellaceae clade consisting of Cyphella digitalis (type species of the genus), Baeospora myosora. Pleurella ardesiaca, Hebeloma microsporum holotype MF039240, and ‘Hydropus scabripes’ DAOM 192847 (indicated as “Mycopan?””).

He et al. (2019) and Kalichman et al. (2020) still considered it as an incertae sedis genus at a family level within the Agaricales (Marasmiineae).

Our analyses (Figs. 1–2) indicate that Pleurella is part of Cyphellaceae, sister to Baeospora.

Pleurella microspora (Alessio & Nonis) Vizzini, Consiglio & E. Campo, comb. nov. MycoBank MB842382 Fig. 9

Basionym: Hebeloma microsporum Alessio & Nonis, Micol. Ital. 6(3): 19 (1977)

Non Hebeloma microspora Huijsman, Persoonia 9(4): 485 (1978), nom. illegit., Art. 53.1, Gymnopus neerlandicus (Huijsman) Contu, Boll. Assoc. Micol. Ecol. Romana 24(73-74): 16 (2008), Hebeloma neerlandica Huijsman, Persoonia 9(4): 490 (1978).
≡ Hebeloma microsporum (Alessio & Nonis) Contu, Boll. Assoc. Micol. Ecol. Romana 24(73-74): 16 (2008)

Basidiome mycenoid. Pileus 25–65 mm diam., conical-campanulate then planate but with persistent conical umbo; surface smooth and strongly hygrophanous, tawny-orange with darker spots, then paling to light hazelnut (7.5YR 6/4–6/6). Lamellae crowded, L = 30–40, l = 0–3, deeply emarginate or subfree, sinuous, cream-pink with apricot hues (5YR 8/2–8/3), with a concolorous minutely eroded edge. Stipe 40–90 × 4–9 mm, central, cylindrical, or slightly widened at the base, sometimes flared at the apex; longitudinally striate or smooth (appears minutely velvety when observed with a magnifying glass), base with whitish strigosity; the colour is ± uniform hazelnut (7.5YR between 7/2–7/4). Context thin, fibrous, uniformly whitish. Smell pleasant, aromatic, reminiscent of Leucocybe connata (Schumach.) Vizzini, P. Alvarado, G. Moreno & Consiglio. Taste herbaceous, bitterish. Spore print white.

Basidiospores 6.0–7.1 × 3.1–3.7 μm [44/2/1] (on average 6.5 × 3.4 μm), Q = 1.81–2.07 (Qm = 1.94), V = 30–49 μm³ (Vm = 39 μm³), ellipsoid to subcylindrical, smooth, thin-walled, strongly amyloid, acyanophilous, often with granulose contents. Basidia 26–31(–35) × 4–7.5(–8) μm, clavate, thin-walled, tetrasporic with 4–5 μm long sterigmata, with

Comparisons- Compared to the type species, Pleurella microspora dif
basal clamp connection. **Hymenophoral trama** regular, consisting of subparallel, slightly metachromatic but non-dextrinoid 5–15 μm wide cylindrical hyphae, the more voluminous constricted at septa. **Cheilocystidia** 60–90(–100) × 7–12(–17) μm, mainly lageniform to subcylindrical, rarely utriform, faintly metachromatic, without clamp connection at the base, wall up to 1 μm thick, apex attenuated, fusiform or capitulate, often covered with mucous matter; the latter is clearly evident on fresh material, but almost completely disappears in the dried and then rehydrated material, the traces being visible only after treatment with Cresyl blue. **Pleurocystidia** very rare, scattered, similar to cheilocystidia. **Pileipellis** as a radially arranged cutis composed of 5–10 μm wide hyphae with obtuse (rounded) or attenuated (sometimes cystidioid) terminal elements, non-dextrinoid and non-metachromatic; brown encrusting pigment abundant.

*Fig. 9* **Pleurella microspora** (AMB 18917, Italy). a Basidiomes b–c Elements of the pileipellis (in water) d–g Cheilocystidia (d–f in ammoniacal Congo red; g in Cresyl blue) h Pleurocystidia (in ammoniacal Congo red) i Caulocystidia (in ammoniacal Congo red) j Basidiospores (in Melzer’s reagent). Bars = 10 μm. Photos by E. Campo
Subcutis formed by 8–20 μm wide, cylindrical to allantoid (sausage-shaped) hyphae, non-dextrinoid and non-metachromatic, with minute yellowish parietal pigment. Pileitrama consisting of an intricate interweaving of hyphae of variable shape and size, cylindrical, allantoid, lobed, abruptly inflated, weakly metachromatic, non-dextrinoid. Caulocystidia 45–75(–82) × 4–10(–12) μm, clustered, subcylindrical to lageniform, often sinuous with irregular enlargements along the length, weakly metachromatic, non-dextrinoid, wall up to 1 μm thick, with obtuse or attenuated apex and usually with a basal clamp connection. Stipititrama saccodimitic, consisting of weakly metachromatic, non-dextrinoid cylindrical hyphae, the thinnest 3–6 μm wide and strongly tuberculate, diverticulate or branched, the largest 10–25 μm wide, smooth but with thickened wall (1 μm). Thromboplerous hyphae absent. Clamp connections present, quite abundant.

Habitat and distribution: Solitary or gregarious on or associated with well decayed wood or forest litter. So far known only from Italy. Very rare.

Examined material: ITALY: Friuli-Venezia Giulia, Casel della Guardia, Caneva (PN), on beech litter, in a mixed forest with Fagus sylvatica and Picea abies, 1 June 2020, E. Campo (AMB 18917).

Notes- Hebeloma microspora Alessio & Nonis (belonging to the genus Hebeloma which is artificial according to Cittadini et al. 2008; Vizzini et al. 2014; and Eberhardt et al. 2018) was originally established (Alessio and Nonis 1977) to replace Hebeloma microspora Huijsman (Huijsman 1946), invalidly published without a Latin diagnosis (Art. 39.1; Turland et al. 2018). Later, Huijsman (1978) validated it unaware of Alessio & Nonis’ proposal, but as unfortunately that species seems to be quite different from the H. microspora described in his paper, he erected, in a note added in proof, Hebeloma neerlandica Huijsman as a nomen novum for Hebeloma microspora. Hebeloma neerlandica was later transferred to Gymnopilus (Cittadini et al. 2008; Eberhardt et al. 2018). Contu (in Cittadini et al. 2008) combined the species of Alessio & Nonis in Hebeloma, without providing any justification and above all without having seen the holotype.

Hebeloma microspora was described by Alessio and Nonis (1977) and Alessio (1981) as characterized by an hemispheric-convex pileus with an obtuse umbo, surface dry, at first whitish-cream, soon ochre-brown and clay to pale orange spotted; emarginate lamellae, whitish cream, then with strong orange hues, ochre-brown when old; a cylindrical stipe, central, concolorous to the pileus, floculose at apex; a white spore print; strongly amyloid spores, 6–8(–9) × 4–4.5 μm; abundant colourless cheilocystidia; a smell at first of elderberry flowers then rancid floury, taste bitter; and growth on buried and decayed conifer wood (Pinus strobus) in May, in a city park (Turin, Italy).

The species, no longer found after the original description, remained of dubious generic attribution until Eberhardt et al. (2018) examined and sequenced the holotype. They found it in bad condition and without spores, but cheilocystidia and pleurocystidia, the latter being numerous and not reported in the original diagnosis, were detected. In the molecular analysis published in their work, the ITS/partial LSU sequence of the holotype clustered within Cyphellaceae as sister (MLB 100%) to Hydropus scabripes DAOM 192847 whose sequence was considered a reference for the establishment of the genus Mycopan by Redhead (2013). This couple is sister (MLB 92%) to Pleurella ardesiaca PDD87446, GB JQ694106. The clad Mycopan + Hebeloma microspora + Pleurella is sister (MLB 97%) to Baeospora myosura AFTOL-ID 1799.

In our phylogenetic analyses (Figs. 1–2) a well-supported Pleurella clade is recovered, containing Pleurella collections, the holotype and the novel Italian collection of H. microspora (AMB 18917) and the reference collection of M. scabripes.

The novel collection of H. microspora fits quite well the original description (Alessio and Nonis 1977) and its characteristics are such that it can be mistaken for Hydropus scabripes apart from the lamellae with apricot tones, and the strongly amyloid subcylindrical spores. There is no reasonable doubt that the two collections of H. microspora are congeneric with Mycopan scabripes DAOM 192847. The phylogenetic analysis also suggests that H. microspora can be considered to belong to the genus Pleurella. Pleurella ardesiaca and H. microspora share a whole range of characters such as emarginate crowded lamellae, white spore print, ellipsoid to subcylindrical strongly amyloid spores, presence of cheilocystidia and caulocystidia, elements of the pileipellis with abundant extracellular encrusting pigment, a saccodimitic stipe trama and growth on dead wood. Pleurella ardesiaca differs by having usually pleuropodal basidiomes (stipe excentric or lateral, Fig. 4e), but some collections may show a nearly central stipe (Horak 1971), a trichodermic/hymenidermic pileipellis, and an absence of pleurocystidia (Horak 1971 and Cooper, https://scd.landcareresearch.co.nz/specimen/PDD_87446), even though facial cystidia may be rare and scattered in H. microspora (the novel collection) and can easily go unnoticed. Since these differences appear to be of minimal importance, we decided to transfer H. microspora to Pleurella and we propose the emendation of this genus (see above). Cooper (2016b) had previously suggested a possible congenericity between Hydropus scabripes DAOM 192847 (GB AF042635) and Pleurella ardesiaca.

Baeospora Singer (typified with Agaricus myosurus Fr.) is sister, in our analysis (Fig. 1), to Pleurella emend., as already highlighted by Eberhardt et al. (2018). As originally circumscribed by Singer (1938), the genus Baeospora contained four species, B. familia (Peck) Singer, B. myosura (Fr.) Singer, B. myriadophylla (Peck) Singer, and
B. oligophylla Singer], but Singer (1943, 1961) later excluded a species with dextrinoid spores and tissues [combined as Pseudobaeospora oligophylla (Singer) Singer] and another species with well-developed and long pileocystidia [combined as Clitocybula famila (Peck) Singer]. In this narrow sense, the genus corresponds to Mycena section Xeromyces Kühner (1938). To date, of the 13 known species of Baeospora, three show a temperate distribution (Hutchison et al. 2012), and ten are tropical (Singer 1961, 1986, 1989; Pegler 1983; Corner 1994; Maas Geesteranus and Horak 1995). Taken together, species within this genus are characterized by their collybioid basidiomes, small, colourless and smooth, amyloid basidiospores, hyphae with clamp connections, and their saprotrophic nature on woody debris. The three temperate species, B. myosura (type), B. myriadophylla, and B. occidentalis L.J. Hutchison & Kropp, the only ones for which DNA sequences are available, are widely distributed (known from the temperate zones of Europe, Asia and America) and were extensively studied from a morphological point of view (e.g., Kühner 1938; Singer 1938, 1986; Redhead 1974; Lennox 1979; Desjardin 1987; Watling and Turnbull 1998; Vellinga 1999; Clémençon 2004; Hutchison et al. 2012; Siegel et al. 2019). In particular, these latter species and Pleurella species have very crowded, narrow lamellae, amyloid basidiospores, hymenial cystidia, pileocystidioid elements, caulocystidia, encrusting brown pigment, and the frequent presence of long tapering pseudorhizae (Lennox 1979; Desjardin 1987; Breitenbach and Kränzlin 1991; Watling and Turnbull 1998; Vellinga 1999; Hutchison et al. 2012). Furthermore, these representative Baeospora species are known to produce masses of simple Sporothrix-like conidia (arthroconidia) in culture (Redhead 1974; Petersen 1995; Hutchison et al. 2012), and a similar conidial state is also present in H. scabripes DAOM 192847 (Redhead, pers. comm., in Moncalvo et al. 2002). However, Baeospora differs by strictly Collybioid-like (versus mycenoid to hydropoid) basidiomes, small-sized (10–25 mm) and thin-fleshed pileus, thin stipe (0.5–3(–4) mm), even smaller faintly amyloid basidiospores (on average hardly exceeding 5 μm in length and 3 μm in width), smaller hymenial cystidia (rarely exceeding 35–40 μm), and the frequent presence of long tapering pseudorhizae (Lennox 1979; Desjardin 1987; Breitenbach and Kränzlin 1991; Watling and Turnbull 1998; Vellinga 1999; Hutchison et al. 2012).

Pending future studies on the tropical species of Baeospora, for whom we consider Pleurella and Baeospora as two distinct sister genera. In case of synonymization of both taxa by future authors, Baeospora would have priority, on a temporal basis, over Pleurella.

### Discussion

#### The current state of knowledge of the Porotheleaceae and Cyphellaceae and polyphyly of the genus Hydropus

The first molecular phylogenetic analysis including a member of the genus Hydropus is that by Moncalvo et al. (2000), where “H. scabripes” (DAOM 192847; GB AF042635, sequenced from a culture) formed a clade (named Clade E) together with Baeospora myriadophylla.

Moncalvo et al. (2002), in their pioneering nrLSU-based molecular analysis of Agaricales, first highlighted the polyphyletic nature of Hydropus as it was morphologically circumscribed by Singer (1982, 1986). Indeed, they recovered /Baeosporoid (16) formed by Baeospora myosura, B. myriadophylla and Hydropus scabripes (DAOM 192847; GB AF042635) as sister to /Gloeostereae (14) (Gloeostereum incarnatum and Cheimonophyllum candidissimum) and phylogenetically unrelated to the morphologically look-alike /Hydropod (27) consisting of other species of Hydropus (including the type, H. fuliginarius), Gerronema Singer, Megacollybia Kotl. & Pouzar, Clitocybula (Singer) Singer ex Métrod and Porotheleum fimbriatum (Pers.) Fr.

The same configuration of the /Hydropod clade was recovered by Bodenstein et al. (2004). Thorn et al. (2005) recognized in the clade also Henningomyces candidus (Pers.) Kurtz. In the multigene study of Matheny (2006), the Hydropod clade (as part of the larger Marasmioid clade), in addition to the aforementioned taxa, also included Hydropus cf. scabripes (PBM2513 isolate AFTOL-ID 535), some Mycena (M. auricomae Har. Takah., M. amabilissima (Peck) Sacc., M. aurantiidiscia (Murrill) Murrill); in their phylotree, P. fimbriatum is incorrectly indicated (labelled as Hydnopolyporus fimbriatum ( Cooke) DA Reid; it is sister (with no support) to Cyphellaceae (Cheimonophyllum candidissimum, Cyphella digitalis, Chondrostereum purpureum, Athelia bombacina ATCC 20629, Granulobasidium vellereum, Baeospora myosura). The collection named Athelia bombacina ATCC 20629 represents an erroneous identification, as A. bombacina is recognized as a member of Atheliales, an order phylogenetically very distant from Agaricales (Sulistyö et al. 2021). The analyses by Binder et al. (2010) produced results comparable to those of Matheny et al. (2006) but with Hemimycena gracilis sister to B. myosura. Calypella capula (Holm.) Quél. and two species of Trogia Fr. (viz. Trogia infundibuliformis Berk. & Broome and T. venenata Zhu L. Yang) also clustered within the Hydropod clade in the study of Yang et al. (2012). Redhead (2012, 2013, 2016a, b) included in the Hydropod clade the species of the mycenoid genera Atheniella Redhead, Moncalvo, Vilgalys, Desjardin, B.A. Perry and Phloeomana.
Redhead. Redhead (2013) established the genus Mycopan for Pruunlus scabripes using AF042635 (DAOM 192847) as reference sequence which clustered close to Baeospora in Moncalvo et al. (2000, 2002).

In the phylogenomic study by Dentinger et al. (2016), Hydropoid clade (Megacollybia platyphylla) and Cyphellaceae (Baeospora myosura) are sister (MLB 100%) and part of the suborder Marasmiineae Aime, Dentinger & Gaya (= Marasmioid clade s. Binder et al. 2010). Based on the phylogenomic analysis by Wang et al. (2019), the Cyphellaceae diverged ~174 million years ago.

Cooper (2016 a, b) first used the family name Porotheleaceae Murrill for the Hydropoid clade (while "Trogiaceae" Loq. is nom. inval., Art. 39.1, Melbourne) and added Inflatostratum aff. glabrum, Rectitopus ssp., Clavomphalia yumanensis, Delicatula integrella, Clitocybe ulmícola H.E. Bigelow and Setigeroclaudula sp. He incorrectly recognized Mycopan as being represented by the misidentified sequence labelled Hydropus scabripes DAOM 192847 (GB AF042635) and noted the relationship of the sequence to Baeospora. Eberhardt et al. (2018) confirmed the polyphyly of Hydropus, split into at least three clades, and the dual nature of Mycopan, with Hydropus cf. scabripes PBMA2513 sister to Atheniella species and Hydropus scabripes DAOM 192847 sister to the holotype of Hebéloma microspondá and nested within Cyphellaceae together with Baeospora myosura, Pleurérella ardesiaca and Cyphella digitalis. Oliveira et al. (2019) recovered Cyphellaceae as close (but without statistical support) to Porotheleaceae.

Antonín et al. (2019) assigned to the Hydropoid clade the new genera Leucoinocybe Singer ex Antonín, Borovička, Holec & Kolářík (segregated from Clitocybula) and Lignomphalia Antonín, Borovička, Holec & Kolářík (for Pseudoomphalinna lignicola Lj. N. Vassílijeva), and Mycena olida Bres. (= Phleomana minutula (Sacc.) Redhead); a clade formed by Hydropus trichoderma, Hydropus aff. scabripes and Geronisma viridílucens Desjardin, Capelari & Stevani (a Brazilian bioluminescent species) was also recovered.

Varga et al. (2019) added Flavophlebia sulphuríosabellina to the Porotheleaceae (suppl. mat.), and a clade consisting of Baeospora myosura, B. myriadiophylla, Mycopan scabripes (DAOM), Pleurotus longínqua, Panelíus (Scytínutos) ríngens, Mycénella bryophila, and M. salicina was found.

Vizzini et al. (2019) described within Porotheleaceae the new nonspecific genus Chrysomyaca (= Mycena section Dunicolae Esteve-Rav., M. Villarreal, Barrasa & A. Ortega).

Kaygusuz et al. (2020) found a Mycopan clade (H. scabripes, H. aff. scabripes, H. trichoderma, H. moserianus, Mycena pseudotenax).

Matheny et al. (2020) established the new genus Pulverulina for Clitocybe ulmícola, Hydropus rugosidiscus comb. nov., and Leucoinocybe aurícima comb. nov. and also recognized in Porotheleaceae s. lato (Porotheleaceae + Cyphellaceae partim) Troíga delicata, Rectitopus fasciculátus, Acanthorchitícum brueggemannii, Actiníces laevis, Chaetotyphla hyalína and Hemyíncena gracílis. A conspec- tus of the so far known Porotheleaceae can be found in Kalichman et al. (2020).

Sánchez-García et al. (2020) found, in their general phlytotype, the same situation as Matheny et al. (2020) additionally with Mycénella salícina sister to a clade formed by B. myriadiophylla and M. scabripes (DAOM 192847), and Mycena cf. quiníaultensis (OSC 67121 1) sister to Hydropus cf. scabripes (PBM 2513). Finally, Villarreal et al. (2021), in a study on Chrysomycena, recovered in Porotheleaceae the same clade as Vizzini et al. (2019) and Matheny et al. (2020).

In the phylogenetic analysis by Ahmed et al. (2020), Cyphellaceae is limited to Baeospora myosura, B. myriadiophylla, Campanophyllum protoxideum, Cyphella digitalis, Cheimonophyllum candisíssimum, Granulobasidium velléreum, Athélia bombacína (see above), Chondrostereum purpureum, Gloeostereum incarnátum and G. ciníri.

Olariaga et al. (2020) highlighted an unsupported clade consisting of Perothóleum fimbriátum, Megacollybia platyphylla, Hydropus cf. scabripes, Cheimonophyllum candisíssimum, Hemyíncena gracílis and Baeospora myosura, within Marasmiineae + Schizophyllíneae.

Two major clades are recovered in our analysis (Fig. 1), Porotheleaceae and Cyphellaceae. The Porotheleaceae appears to have no characters which uniquely define it, although the core group Gernéena/Hydropus/Clytocebula/Mégacollíbya is recognisable by form, lignicolous habit and sarcodimitic tissue.

Our analyses (Fig. 1) suggest that the traditional concept of Gernéena Singer (omphalinoid-to-clitocyboid habit, central or slightly eccentric long stipe, growth on rotting wood, irregular/confused lamellar trama, absence of cystidia, non-amylloid spores, intracellular pigment, present or absent clamp connections) (Singer 1951, 1964, 1970, 1986), even when limited only to species with lignicolous habit, thin-walled spores, pileipellis in the form of cutis and sarcodimitic structure (Redhead 1986, 1987; Norvell et al. 1994), is artificial and polyphyletic. The species of Gernéena are distributed in several clades in the Porotheleaceae, as previously highlighted by Latha et al. (2018), Vizzini et al. (2019) and Matheny et al. (2020). Gernéena s. stricto may in the future be delimited only when the type species of the genus (G. melánonphax Singer from Tucumán, tropical Argentina) is sequenced. Gernéena is monophyletic in the studies of Moncalvo et al. (2002), Antonín et al. (2008, 2019), Yang et al. (2012), Liu et al. (2019), and Kaygusuz et al. (2020), but their analyses are based on an extremely limited number of species and collections of Gernéena and/or closely related genera.
Similarly, *Hydropus* (Fig. 1) was found to be polyphyletic, several species being spread over numerous independent evolutionary lines (as previously highlighted by Moncalvo et al. 2002, Bodensteiner et al. 2004, Matheny et al. 2006, Eberhardt et al. 2018, Antonin et al. 2019, Varga et al. 2019, Vizzini et al. 2019, Kaygusuz et al. 2020, Matheny et al. 2020, Sánchez-Garcia et al. 2020). *Hydropus* s. stricto must be limited to the clade encompassing the type species, *H. fuliginarius* (Batsch) Singer. This clade is, in our analysis, sister (BP = 0.93, MLB = 64%) to *Clitocybula*, a genus with species differing by a radially fibrillose to squamulose pileus surface, and an absence of pleurocystidia and of cellular hypoderm (Bigelow 1973; Singer 1978, 1986; Bon 1997; Barrasa et al. 2006; Antonin et al. 2011; Deepna Latha et al. 2015; Antonin et al. 2019).

In our sense (Figs. 1–2), *Cyphellaceae* includes many more genera than in Matheny et al. (2006), Eberhardt et al. (2018), Ahmed et al. (2020) and Kalichman et al. (2020), where a problem of poor taxon sampling is evident. *Porotheleaceae* s. lato Kalichman et al. (2020) and Matheny et al. (2020) also incorporates some taxa, viz. *Acanthocorticium brueggemannii*, *Actiniceps laevis*, *Atheniella*, *Calyptella*, *Chaetotyphula hyla*ina, *Hemimycena gracilis*, *Henningsomyces candidus*, *Lignomphalia*, *Phloeomana*, *Rectipilus fasciculatus*, *Scytinotus ringens*, that are part of the *Cyphellaceae* in our analysis. In Kaygusuz et al. (2020), *Porotheleaceae* (as Hydrodropoid clade) includes also *Lignomphalia* and *Hydropus* (*Mycopan* in our sense). Cooper (2016a) highlighted that *Mycopan* and *Atheniella* were not part of the core Hydrodropoid clade.

*Cyphellaceae*, as outlined in the present paper, consists of a heterogeneous assembly of lignicolous fungi with different types of basidiomes: reduced cyphelloid morphology (*Calyptella*, *Cyllella*, *Henningsomyces*, *Rectipilus*), clavarioid/typophiloid basidiomes (*Actiniceps*, *Chaetotyphula*, *Setigeroclavula*), pleurotoid (*Campanophyllum*, *Cheimonophyllum*, *Scytinotus*/*Pleurotopsis*, *Pleurella partim*), corticioid (*Acanthocorticium*, “*Athelia bombacina*”, *Granulobasidium vellereum*), corticioid (*Hendrostroma*), corticioid (*Chondrostereum*, *Gloeostereum*, *Cheironomycina*), agaricoid-collybioid (*Baesopora*), agaricoid-*mycenoid* (*Atheniella*, *Hemimycena*, *Mycenella*, *Mycopan*, *Phloeomana*, *Pleurella partim*), and agaricoid-omphaloid (Lignomphalia).

*Hemimycena gracilis* (AFTOL-ID 1732 PBM 2715, GB DQ490623 DQ457671) is nested within *Phloeomana*, a genus established by Redhead (2013) (type species *Agaricus speireus* Fr. 1815) and corresponding to species in *Mycena*, section *Hiemales* Konrad & Maubl., characterized by greyish-brownish mycenoid to omphaloid basidiomes, non-amyloid spores, cheilocystidia of shape slightly different from that of basidia, hyphae of pileipellis with ramified digitations, usually smooth stipel hyphae with scattered caulocystidia, growing on bark and dead wood (Maas Geesteranus 1992a, b; Roniker and Aronsen 2007; Redhead 2013; Aronsen and Læsøe 2016; Robich 2016; Holec and Kolárík 2017; Lehmann and Lüderitz 2018). In the ITS-based molecular analysis by Dima (in Lehmann and Lüderitz 2018) the genus *Hemimycena* is polyphyletic; most species cluster together with *Phloeomana*, but the core *Hemimycena* clade (= *Hemimycena* s. stricto, where the type species, *H. lactea* is included) occupies an isolated position and is distant related to *Cyphellaceae*. In the study by Bau et al. (2021), *Hemimycena* was resolved into two clades, *Hemimycena* clade 1 (encompassing *H. lactea*) and *Hemimycena* clade 2, within a polyphyletic *Mycenaceae* clade. To better understand the status of *Hemimycena* versus *Phloeomana*, the taxon sampling will have to be expanded in the future, and additional non-ribosomal markers will have to be used.

*Mycenella* (J.E. Lange) Singer is still considered as an incertae sedis genus in recent publications (He et al. 2019; Kalichman et al. 2020). However, Garnica et al. (2007, LSU based analysis) found *M. bryophila* to be close to *Megacollybia platyphylla*; Cooper (2016b) recovered a clade formed by *M. salicina*, *M. bryophila*, *M. variispora*, *M. minima* and M. sp. sister to *Hemimycena lactea* (ITS-based analysis); in Holec & Kolárík (2017), *M. salicina*, *M. bryophila* and *M. variispora* form a highly supported clade sister (with no support) to *Henningsomyces candidus* (ITS-based analysis). Finally, Varga et al. (2019) highlighted a clade consisting of *Baesopora myosura*, *B. myriadophylla*, “*Mycopan scabripes*”, *Pleurotopsis longingua*, *Panellus ringens*, *Mycenella bryophila* and *M. salicina*.

Our analysis (Fig. 2) supports the existence of nine distinct genetic lineages within *Cyphellaceae*: 1) *Mycopan + Atheniella*; 2) a clade consisting of the two cyphelloid genera *Henningsomyces* and *Rectipilus* and the corticioid *Acanthocorticium*; 3) a clade including the three clavarioid/typophiloid genera *Actiniceps*, *Chaetotyphula* and *Setigeroclavula* and the cyphelloid *Campanophyllum*; 4) *Phloeomana + Hemimycena gracilis*; 5) a clade encompassing the two stereoid *Chondrostereum* and *Gloeostereum*, the corticioid “*Athelia*” and *Granulobasidium*, the pleurotoid *Cheimonophyllum* and *Campanophyllum* and the cyphelloid *Cyphella digitalis* (type species); 6) a clade including the collybioid *Baesopora* and the mycenoid/pleurotoid *Pleurella*; 7) a *Mycenella* clade (mycenoid); 8) a clade containing the pleurotoid *Scytinotus*/*Pleurotopsis*; and 9) a lineage consisting of only the omphaloid *Lignomphalia liniicola*.

**Solving the Mycopan mystery**

In their pioneering work on the phylogeny of *Agaricales*, Matheny et al. (2006) included in their multi-gene analysis a collection labelled *Hydropus* cf. *scabripes* (PBM 2513, isolate AFTOL-ID 535) probably because they could obtain additional
gene sequences and because the LSU did not match GB AF042635 (DAOM 192847), which however was not incorporated. The first authors to have noticed the non-correspondence of sequences in GenBank named Hydropus scabripes were Cooper (2016a, b) and Eberhardt et al. (2018). Cooper (2016a, b) noted the close relationship of AF042635 to Baeospora and suggested that ‘Hydropus scabripes’ (AF042635) was congeneric with Pleurella ardesiaca. Eberhardt et al. (2018) included three groups identified as Hydropus scabripes in an analysis of ITS/LSU sequences. Their ‘H. scabripes’ (STU HKr0681/91, GB MF039247) is closely related to Hydropus fuliginarius DAOM 196062 and represents a further misidentification. They also included Hydopus cf. scabripes (PBM 2513) and the original ‘H. scabripes’ (DAOM 192847), showing the close relationship of PBM 2513 to Atheniella species, and of DAOM 192847 to Pleurella ardesiaca and the holotype of Hebeloma microsporum (MF039240). In noting the various sequences of H. scabripes and in particular referring to Hydopus cf. scabripes (PBM 2513) they concluded: “Based on the available data and in the absence of molecular data from the type of M. scabripes, we suspect the majority opinion is that, if the type of M. scabripes was sequenced, it would fall into this group”.

In our analysis (Fig. 2), 14 newly sequenced collections of H. scabripes from Canada, the Czech Republic, Italy, and the USA clustered into a strongly supported Mycopan clade (BPP = 1.0, MLB = 98%) which is divided into three subclades not USA clustered into a strongly supported Mycopan clade (BPP from Canada, the Czech Republic, Italy, and the Mycopan (DAOM 192847, MB), the second clade consists of M. quiniaultensis, M. cf. quiniaultensis, Mycopan scabripes iNAT 16782378 MZ241313, from the USA, and Mycopan sp. (TENN-F-076402) from Canada; the third subclade is represented by a H. paradoxus collection (AMB 18772) from Italy. All the newly sequenced collections of H. scabripes, which have also been studied microscopically, show morphological characters compatible with those of the holotype. Among these collections, one was chosen as epitype because, after many unsuccessful attempts, it was not possible to obtain any sequence from the holotype. It is reasonable to conclude that the real (true) Mycopan is represented by the aforementioned multisequence clade containing also the epitype of Prunulus scabripes. This clade is here considered to represent the original concept of Prunulus scabripes.

The sequence of M. scabripes AF042635 (DAOM 192847, Canada), which was obtained from a mycelial culture (Moncalvo et al. 2000, 2002), falls into Pleurella (as previously noted by Cooper 2016a, b) and Eberhardt et al. (2018), and is putatively conspecific with (or very close to) Hebeloma microspora (see above), which morphologically differs from Hydropus scabripes mainly by its lamellae with apricot orange tinges, strongly amyloid smaller subcylindrical spores, and scattered pleurocystidia.

Mycopan in our phylogenies (Figs. 1–2) occupies a sister position (BPP = 0.97, MLB 58%; BPP = 1.00, MLB 98%, respectively) to the clade encompassing the Atheniella species (as previously pointed out by Matheny et al. 2006), Binder et al. (2010), Cooper (2016b), Eberhardt et al. (2018), and Vizzini et al. (2019). The genus Atheniella Redhead, Moncalvo, Vilgalys, Desjardin & B.A. Perry (= Adonis clade sensu Moncalvo et al. 2002), typified with Agaricus adonis Bull., is a small lignonicolous to leaf-litter mycenoid genus, formerly treated as Mycena sect. Adonideae (Fr.) Quél., that was elevated to genus rank by Redhead, Moncalvo, Vilgalys, Desjardin & B.A. Perry (in Redhead 2012) based on the brightly coloured pileus (e.g., yellow, orange, cream, pink, red or white) and the absence of reaction of all tissues (spores included) in Melzer’s reagent. Species of Atheniella are widespread in temperate regions, but also distributed in the tropical zone (Smith 1935a, b, 1937, 1939; Maas Geesteranus 1980, 1990, 1992a, b; Redhead 1984; Perry 2002; Grgrurinovic 2003; Robich 2003; Aravindakshan and Manimohan 2015; Aronsen and Læssøe 2016; Ge et al. 2021). It is distinguished from Mycopan by the brightly coloured pileus surface, inamyloid spores, and pileipellis hyphae covered with simple to branched excrescences (Kühner 1938; Smith 1947; Maas Geesteranus 1992a, b; Robich 2003, as Mycena; Redhead 2012; Aronsen and Læssøe 2016; Lehmann and Lüderitz 2018; Ge et al. 2021).

In the light of these results, the genus Pleurella is emended above, to accommodate the non-pleurotoid Hebeloma microspora.

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Declarations

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