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Abstract: *Poriella subacida* gen. & comb. nov., previously known as *Perenniporia subacida*, which causes white rot, has been documented in temperate and tropical forests. Specimens from Asia, North America, and Europe were examined, including the type specimen of *Polylorus subacidus*. Sequences of the ITS1-5.8S-ITS2 region, the 28S rDNA, the mitochondrial rDNA small subunit (mtSSU), and the gene encoding the translation elongation factor 1-α (EF1) were generated. In multigene phylogenies (maximum parsimony, maximum likelihood, Bayesian inferences), “*Perenniporia subacida*” formed a well-supported lineage, distinct from the core “*Perenniporia*” clade (type species: “*P. medulla-panis*”), and sister to the “*Yuchengia narymica*” lineage. We therefore conclude that “*P. subacida*” should be placed in the new genus “*Poriella*” gen. nov. Morphologically, “*Poriella*” is characterized by a di- to trimitic hyphal system, non-truncate basidiospores, and strongly dextrinoid, cyanophilic skeletal hyphae.

Keywords: polypore; systematics; taxonomy; white rot fungus; wood-inhabiting fungi

1. Introduction

Polyporales is one of the most intensively studied clades of fungi, being of interest to both fungal ecologists and applied scientists [1,2]. The family Polyporaceae accommodates 92 genera [3], and recently many new genera of polypores have been described, such as *Amylosporia* (B.K. Cui, C.L. Zhao & Y.C. Dai), *Crystallicutis* (El-Gharabawy and Griffith), *Hirticrusta* Matozaki (T. Hatt. and Sotome), and *Murinicarpus* (B.K. Cui and Y.C. Dai) [4–7]. The family is typified by *Polyporus* P. Micheli ex Adans. (1763) and many taxa have been separated from *Polyporus* as new genera over time [1,4,6].

*Perenniporia subacida* (Peck) Donk (basionym *Polyporus subacidus* Peck, 1885) is a widespread species of wood-decaying polypores with perennial, resupinate to effused-reflex basidiomes and thick-walled, non-truncate basidiospores. The species has been reported to occur in many forest ecosystems, in boreal, temperate, subtropical, and tropical regions [8–15]. This species was described by Peck (1885) as *Polyporus subacidus*, but its taxonomic position has long been debated. It has been treated in several genera, but none of these placements have been fully satisfactory [16–20]. Currently, the species is widely accepted in *Perenniporia* Murrill, which is typed by *P. medulla-panis* (Jacq.) Donk [8–13]. However, Decock and Stalpers argued for a different placement [13].

Molecular studies involving Polyporaceae, mainly based on ITS and/or nLSU sequences, have been carried out [21–27]. Further studies employing a six-gene dataset have helped to clarify the generic relationships of polyporoid fungi for 373 taxa. The latter study showed that *Perenniporia subacida* clustered in the core polyporoid clade in which it was related to *P. medulla-panis* (Jacq.) Donk [23]. Further studies of *Perenniporia* inferred...
from nuclear ribosomal 28S and ITS sequence data revealed that *P. subacid*a formed a monophyletic lineage distant from the *Perenniporia* s.s. [15,16,28].

To resolve the placement of this species, phylogenetic research was carried out employing the ITS, 28S, TEF1 and mtSSU and a comparative morphological study of the type specimen was conducted. We conclude that *Perenniporia subacid*a should be treated as a distinct, new genus as described below.

### 2. Materials and Methods

#### 2.1. Morphological Studies

Specimens studied are deposited at the Farlow Herbarium of Harvard University (FH), MA, USA, Beijing Forestry University (BJFC), Beijing, China and United States National Fungus Collections (BPI), New York, NY, USA. Macromorphological descriptions were on the basis of field notes and study of specimens. Color terms followed previous studies [29]. Microscopic measurements were made from slide preparations of dried specimens stained with Cotton Blue and Melzer’s reagent by light microscopy [30,31]. Sections were studied using an Olympus BX40 compound microscope (Tokyo, Japan). In presenting spore size variation, 5% of measurements were excluded from each end of the range. The following abbreviations are used: KOH = 5% potassium hydroxide, CB = Cotton Blue, CB+ = cyanophilous; IKI = Melzer’s reagent, IKI− = both non-amyloid and non-dextrinoid, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = mean each spore length/width ratio, n (a/b) = number of spores (a) measured from given number of specimens (b).

#### 2.2. Molecular Techniques and Phylogenetic Analyses

CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to extract DNA from dried specimens from China and other regions, and 2xTaq PCR Mix (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to perform PCR products [30]. The primer pair ITS5 and ITS4 were amplified for the ITS region [32]. The primer pair LR0R and LR7 were for the nuclear r28S region [33]. The primer pair MS1 and MS2 were for the mitochondrial SSU region [32]. The primer pair EF1-983F and EF1-2218R were for Tef1 [34]. The PCR cycling program for ITS, mtSSU, 28S and TEF1 followed previous studies [27]. The Beijing Genomics Institute (Beijing, China) was in charge of purifying and direct sequencing of the PCR products. All sequences used in the phylogeny were downloaded from GenBank (Table 1) with references. The sequence alignment was deposited in TreeBase (submission ID 23826).

| Species Name          | Sample No. | ITS Accessions | LSU Accessions | mtSSU Accessions | TEF1 Accessions | References |
|-----------------------|------------|----------------|----------------|------------------|-----------------|------------|
| Aboriporus biennis    | TFRI 274   | EU232187       | EU232235       |                  |                 | [21]       |
| A. biennis            | EL65-03    | JN649325       | JN649325       |                  |                 | [21]       |
| Abundisporus roseolbus| Dai 12269  | KC415908       | KC415910       | KF051037         | KF181131        | [5]        |
| A. pubertatis         | Cui 5776   | KC787565       | KC787572       | KF051029         | KF181129        | [5]        |
| A. sclerosetosus      | MUC 41438  | FJ411101       | FJ393868       |                  |                 | [28]       |
| A. violaceus          | Ryvarden 10775 | KF051085         | KF181152        |                  |                 | [5]        |
| Amylocystis lapponica | KHL 11755  | EU118603       | EU118603       |                  |                 | [21]       |
| Antrodia albida       | CBS 308.82 | DQ91414        |                |                  |                 | [35]       |
| A. allida             | FP 105979  | EU232272       | EU232272       |                  |                 | [36]       |
| A. heteromorpha       | CBS 200.91 | DQ91415        |                |                  |                 | [35]       |
| A. macra              | MUAF 887   | EU340898       |                |                  |                 | [23]       |
| Bjerkandera adusta    | NBRC 4983  | AB733156       | AB733333       |                  |                 | [23]       |
| Cineromyces lindbladii| FBCC 177   | HQ659223       | HQ659223       |                  |                 | [23]       |
| Climacocystis borealis| KH 13318   | JQ031126       | JQ031126       |                  |                 | [23]       |
| Coriolopsis caperata  | LE(BIN)-0677 | AB158316        | AB158316       |                  |                 | [37]       |
| Donkioporia expansa   | MUCU 35116 | FJ411104       | FJ393872       |                  |                 | [28]       |
| Earliella scabrosa    | PR1209     | JN165009       | JN164793       |                  |                 | [38]       |

Table 1. Information of the sequences used in this study.
| Species Name               | Sample No. | ITS Accession | LSU Accession | mtSSU Accession | TEF1 Accession | References |
|---------------------------|------------|---------------|---------------|-----------------|----------------|------------|
| *Fragiliporia fragilis*   | Dai 1308   | KJ734260      | KJ734264      | KJ734268        | KJ790245       | [5]        |
| *F. fragilis*             | Dai 13559  | KJ734261      | KJ734265      | KJ734269        | KJ790246       | [5]        |
| *F. fragilis*             | Dai 13561  | KJ734262      | KJ734266      | KJ734270        | KJ790247       | [5]        |
| *Ganoderma sichuanense*   | Wu 1006-38 | JQ781858      | JQ781864      | JX029989        | JX029997       | [5]        |
| *G. australis*            | Cui 9511   | JN048773      | JN048792      |                 |                | [39]       |
| *G. sinense*              | Wei 5327   | KF494998      | KF495008      |                 | KF494976       | [5]        |
| *G. applanatum*           | Dai 12483  | KF494999      | KF495009      |                 | KF494977       | [5]        |
| *Gelatoporia subvermispora*| BRNU 592909| FJ496694      | FJ496706      |                 |                | [37]       |
| *Grammethiopsis subtropica*| Cui 9041   | JQ845096      | JQ845099      |                 | KF051039       | [39]       |
| *Heterobasidion annosum*  | PFC 5252   | KC492906      | KC492906      |                 |                | [23]       |
| *Hornodermoporus latissima*| Cui 6625   | HQ876604      | JF706340      | KF051040        | KF181134       | [5]        |
| *H. martius*              | Cui 7992   | HQ876603      | HQ654114      | KF051041        | KF181135       | [5]        |
| *H. martius*              | MUCL 41677 | FJ411092      | FJ393859      |                 |                | [28]       |
| *H. martius*              | MUCL 41678 | FJ411093      | FJ393860      |                 |                | [28]       |
| *Hydnaporpus fimbriatus*  | LR 4055    | JN649347      | JN649347      |                 |                | [23]       |
| *Hypococnium lyndoniae*   | NL 041031  | JX124704      | JX124704      |                 |                | [23]       |
| *Lentinus tigrinus*       | DSH93-181  | AF518627      | U27050        |                 |                | [38]       |
| *Microphellus violaceocinerascens* | MULC 45229  | FJ411106      | FJ393874      |                 |                | [28]       |
| *M. violaceocinerascens*  | Cui 8459   | HQ876606      | HQ654113      | KF051042        | KF181136       | [5]        |
| *Obba riculosa*           | KCTC 6892  | FJ496693      | FJ496710      |                 |                | [4]        |
| *Perenniporia hainaniana* | Cui 6364   | JQ61743       | JQ61759       | KF051044        | KF181138       | [5]        |
| *P. hainaniana*           | Cui 6365   | JQ61744       | JQ61760       | KF051045        | KF181139       | [5]        |
| *P. hainaniana*           | Cui 6366   | JQ61745       | JQ61761       | KF494996        | KF494981       | [5]        |
| *P. medulla-panis*        | MUCL 49581 | FJ411088      | FJ393876      |                 |                | [28]       |
| *P. medulla-panis*        | MUCL 43250 | FJ411087      | FJ393875      |                 |                | [28]       |
| *P. medulla-panis*        | Cui 3274   | JN112792      | JN112793      | KF051043        | KF181137       | [5]        |
| *P. substraminea*         | Cui 10177  | JQ001852      | JQ001844      | KF051046        | KF181140       | [5]        |
| *P. substraminea*         | Cui 10191  | JQ001853      | JQ001845      | KF051047        | KF181141       | [5]        |
| *P. substraminea*         | Dai 10781  | KF495007      | KF495018      | KF494995        | KF494983       | [5]        |
| *Perenniporiella chaquenia*| MUCL 47647 | FJ411083      | FJ393855      | HM467609        |                | [28]       |
| *P. chaquenia*            | MUCL 47648 | FJ411084      | FJ393856      | HM467610        |                | [28]       |
| *P. micropora*            | MUCL43581  | FJ411086      | FJ393858      | HM467608        |                | [28]       |
| *P. neofulva*             | MUCL 45091 | FJ411080      | FJ393852      | HM467599        |                | [28]       |
| *P. pendula*              | MUCL 46034 | FJ411082      | FJ393853      | HM467601        |                | [28]       |
| *Phanerochaete chrysosporium* | BKM-F-1767 | HQI88436      | GQ470643      |                 |                | [37]       |
| *Phlebia unica*           | KHL 11786  | EU118657      | EU118657      |                 |                | [37]       |
| *Physioporus sanguinolentus* | BRNM 699576| FJ496671      | FJ496725      |                 |                | [37]       |
| *Piloporia sajaniensis*   | Mannine 2733a | H659239       | H659239       |                 |                | [37]       |
| *Podocospora venustula*   | CBS 65684  | JN649367      | JN649367      |                 |                | [23]       |
| *Polyporus tuberaster*    | CulTENN 8976| AF516898      | AF488136      |                 |                | [40]       |
| *Poria subacida*          | Dai 8224   | HQB76605      | JF13024       | KF218322        | KF286328       | [15]       |
| *P. subacida*             | Cui 3643   | FJ631655      | AY336753      | KF286320        | KF286326       | [15]       |
| *P. subacida*             | Cui 10053  | KF495006      | KF495017      | KF286321        | KF286327       | [15]       |
| *P. subacida*             | MUCL 31402 | FJ411103      | FJ393880      |                 |                | [28]       |
| *P. subacida*             | CBS 463.30 | FJ805245      |                | Direct submission |                |          |
| *P. subacida*             | DLL 2009-125 | JQ673136   |                | Direct submission |                |          |
| *P. subacida*             | DLL 2009-150 | JQ673014   |                | Direct submission |                |          |
| *P. subacida*             | DLL 2009-154 | JQ673015   |                | Direct submission |                |          |
| *P. subacida*             | Dai 8859   | FJ613656      |                |                |                | [42]       |

Table 1. Cont.
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| Species Name          | Sample No. | GenBank Accessions | References |
|-----------------------|------------|--------------------|------------|
| Postia alni           | X 1400     | KC595932 KC595932  | [23]       |
| P. caesia             | CIEFAP 174 | JX090109 JX090129  | [23]       |
| P. guttulata          | KHL 11739  | EU11865 EU11865    | [43]       |
| P. venata             | CIEFAP 346 | JX090113 JX090133  | [43]       |
| P. lactea             | X 1391     | KC595939 KC595939  | [23]       |
| Pyrofomes denisioffii | MUCL 41034 | FJ411105 FJ393873  | [28]       |
| Sebipora aquosa       | Miettinen 8680 | HQ659240 HQ659240 | [22]       |
| Skeletocutis amorphia | Miettinen 11038 | FN907913 FN907913 | [37]       |
| Stereum hirsutum      | NBRC 6520  | AB733150 AB733325  | [23]       |
| Trametes elegans      | FP105679  | JN048766 JN048785  | [15]       |
| T. hirsuta            | Cui 7784   | JN048768 JN048787  | [15]       |
| T. pubescens          | PRM 900586 | AY684173 AY855906  | [27]       |
| Truncospora ochroleuca | Dai 11486  | HQ654105 JF706349  | [5]        |
| T. ochroleuca         | MUCL 39726 | FJ411098 FJ393865  | [28]       |
| T. ochroleuca         | Cui 5671   | JX941584 JX941602  | [5]        |
| T. ochroleuca         | Cui 5673   | JX941585 JX941603  | [5]        |
| T. ornata             | Cui 5714   | HQ654103 HQ654116  | [5]        |
| T. ochiisn           | MUCL 41036 | FJ411096 FJ393863  | [28]       |
| Tyromyces chionaeus   | Cui 10225  | KF698745 KF698756  | [5]        |
| T. knetii             | Penttila 13474 | KF705040 KF705041 | [5]        |
| Vanderbyeia delavayi | Dai 6891   | JQ661738 KF495019  | [5]        |
| V. fraxinea           | DP 83      | AM269789 AM269853  | [28]       |
| V. fraxinea           | Cui 7154   | HQ654095 HQ654110  | [5]        |
| V. fraxinea           | Cui 8885   | HQ863611 JF706344  | [5]        |
| V. fraxinea           | Cui 8871   | JF706329 JF706345  | [5]        |
| V. robindophila       | Cui 5644   | HQ876609 JF706342  | [5]        |
| V. vicina             | MUCL 44779 | FJ411095 AF518666  | [28]       |
| Yuchengia narymica    | Dai 7050   | JN048776 JN048795  | [39]       |
| Y. narnyica           | Dai 10510  | HQ654101 JF706346  | [39]       |
| Y. narnyica           | Dai 6998   | JN048775 JN048794  | [39]       |
| Y. narnyica           | 0709/42    | JN641258 JN641265  | [39]       |
| Y. narnyica           | 0709/157   | JN641259 JN641266  | [39]       |
| Y. narnyica           | 0809/3     | JN641261 JN641268  | [39]       |

A previous study [30] was followed for maximum parsimony analysis. The combined multiple genes dataset was analyzed under heuristic search and 1000 homogeneity replicates, giving a P value of 1.000, which is much greater than the 0.01 used in PAUP* version 4.0b10, which means there is no discrepancy among the four loci in reconstructing phylogenetic trees. Trees were constructed in PAUP* version 4.0b10 [44]. All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 bootstraps. Max-trees were set to 5000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates [45]. DNA sequence data was also analyzed using Maximum Likelihood (ML) with RAxML-HPC2 on Abe through the Cipres Science Gateway [46], with default settings except that branch support was obtained with 1000 rapid bootstrap replicates. Mr Modeltest 2.3 was used to estimate the best-fit evolution model for each data set for Bayesian inference (BI). The best fit models were general time reversible (GTR)+G for ITS, and general time reversible (GTR)+I+G for nr28S, mtSSU, the exons of Tef1, and the combined dataset. The partitioned mixed model, which allows for model parameters to be estimated separately for each genetic marker, was used in the Bayesian analysis. BI
was performed using MrBayes 3.1.2 [47–49]. Two runs of four Markov chains were run from random starting trees for two datasets: (ITS+28S) dataset for 5 million generations and (ITS+28S+mtSSU+Tef1) dataset for 10 million generations. Trees were sampled every 100 generations. The first quarter of the generations was by default discarded as burn-in. A majority rule consensus tree of all remaining trees was calculated. Branches that received bootstrap support for maximum likelihood (ML-BS), maximum parsimony (MP-BT), and Bayesian posterior probabilities (BPP) greater than or equal to 75% (ML-BS and MP-BS) and 0.95 (BPP) were considered significantly supported.

3. Results

3.1. Molecular Phylogeny

The ITS+28S dataset included sequences from 63 fungal specimens representing 56 taxa. The dataset had an aligned length of 2112 characters, of which 1216 characters are constant, 256 are variable and parsimony-uninformative, and 640 are parsimony-informative. Maximum parsimony analysis yielded 12 equally parsimonious trees (TL = 4377, CI = 0.337, HI = 0.664, RI = 0.525, RC = 0.177). The best model for the ITS+28S dataset estimated and applied in the Bayesian analysis is general time reversible (GTR)+I+G, lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). Bayesian analysis and ML analysis resulted in a similar topology to the MP analysis, with an average standard deviation of split frequencies = 0.005569 (BI).

The phylogeny (Figure 1) inferred from ITS+28S sequences resolves seven major clades for 56 species of the Polyporales. Collections of *Perenniporia subacida* formed a lineage distinct from the *Perenniporia s.s.* lineage, within the core polyporoid clade. The *P. subacida* lineage is closely related to the *Yuchengia* lineage based on *Y. narymica* (Pilát) (B.K. Cui, C.L. Zhao, and Steffen) with good support (100% BS, 100% BP, 1.00 BPP).

The four gene (ITS+28S+mtSSU+Tef1) sequence dataset did not show any conflicts in tree topology for the reciprocal bootstrap trees, which allowed us to combine them. The combined dataset included sequences from 61 specimens representing 29 species. The dataset had an aligned length of 3515 characters, of which 2489 characters are constant, 219 are variable and parsimony-uninformative, and 807 are parsimony-informative. Maximum parsimony analysis yielded 10 equally parsimonious trees (TL = 3075, CI = 0.498, HI = 0.502, RI = 0.747, RC = 0.372). Best model for the combined ITS+28S+mtSSU+Tef1 estimated and applied in the Bayesian analysis: general time reversible (GTR)+I+G, lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). Bayesian analysis and ML analyses resulted in a topology similar to the MP analysis, with an average standard deviation of split frequencies = 0.003420.

A further phylogeny (Figure 2) inferred from the combined ITS+28S+mtSSU+Tef1 sequences was obtained for ten genera in *Perenniporia* s.l. and demonstrated that this taxon formed a clade together with *Y. narymica*, with strong support (100% BS, 100% BP, 1.00 BPP). The clade is distinct from *P. medulla-panis* (Jacq.) We, along with Donk, conclude that it belongs to a distinct, new genus, hereafter called *Poriella*.

3.2. Taxonomy

*Poriella* C.L. Zhao, gen. nov.

Mycobank: 840061.

It is characterized by producing resupinate to effused-reflex basidiomata with dingy-yellowish to pale tan to ochraceous surface and a di-trimitic hyphal system with unbranched and strongly dextrinoid skeletal hyphae, and thick-walled, non-dextrinoid, cyanophilous basidiospores.

Type species: *Poriella subacida* (Peck) C.L. Zhao.

Etymology: *Poriella* (Lat.): referring to its similar appearance to the genus *Perenniporia*.

Basidiomata perennial, resupinate to effused-reflex. Pore surface is dingy-yellowish to pale tan to ochraceous. Pores round to angular. Subiculum cream to buff, thin. Tubes concolorous with pore surface, corky. Hyphal system di-trimitic, generative hyphae hyaline,
thin-walled, with clamp connections; skeletal hyphae predominant, unbranched, strongly dextrinoid, cyanophilous, rarely dissolving in KOH. Basidiospores ellipsoid, non-truncate, hyaline, thick-walled, smooth, non-dextrinoid, CB+.

**Poriella subacida** (Peck) C.L. Zhao, comb. nov. Figures 3 and 4.

MycoBank: 840062.

Basionym: *Polyporus subacidus* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 38: 92, 1885.

=Poria subacida* (Peck) Sacc., Syll. fung. (Abellini) 6: 325 (1888).

=**Chaetoporus subacidus** (Peck) Bondartsev & Singer, Annls mycol. 39(1): 51 (1941).

=**Oxyporus subacidus** (Peck) Komarova, Mycoth. Eston. 3: 13 (1961).

=**Perenniporia subacida** (Peck) Donk, Persoonia 5(1): 76 (1967).

=**Porina colorea** Overh. & Englerth, Bull. Yale Univ. School For. 50: 21 (1942).

=**Poria fuscomarginata** Berk. ex Cooke, Grevillea 15(no. 73): 24 (1886).

=**Poria subaurantia** Berk. ex Cooke, Grevillea 15(no. 73): 27 (1886).

![Maximum parsimony strict consensus tree illustrating the phylogeny of *Poriella subacida* and related species in Polyporales based on ITS+28S sequences. Branches are labeled with maximum likelihood bootstrap higher than 70%, parsimony bootstrap proportions higher than 50% and Bayesian posterior probabilities more than 0.95, respectively. Clade names [23].](image-url)
Figure 2. Maximum Parsimony strict consensus tree illustrating the phylogeny of *Poriella subacida*, and related species in *Perenniporia* s.l. based on the combined ITS+28S+mtSSU+TEF1 sequence datasets. Branches are labeled with maximum likelihood bootstrap higher than 70%, parsimony bootstrap proportions higher than 50% and Bayesian posterior probabilities more than 0.95, respectively. Clade names follow [15].

Fruiting body: Perennial, resupinate to effused-reflex, becomes corky when dried, about 22 cm or more at the longest dimension, 15 cm or more at the widest dimension, and up to 17 mm thick at the center. Pore surface pale yellowish to dingy-yellowish when fresh, dingy-yellowish to pale tan to ochraceous when dry; pores round to angular, 4–6 per mm; dissepsiments thin, entire. Subiculum thin, cream to buff, up to 1 mm thick. Tubes concolorous with pore surface, up to 16 mm thick.
skeletal hyphae dominant, thick-walled, with a wide lumen, unbranched, subparallel, 3–5 µm in diameter; 2.5–3.5 µm in diameter; 4.5 µm in diameter; 5 µm in diameter; skeletal -binding hyphae hyaline, thick-walled, smooth, non-walled, 2–5 µm in diameter; 2–9 µm in diameter; 3–5 µm in diameter; skeletal hyphae strongly dextrinoid, CB+; dissolving in KOH.

Figure 3. Basidiomata of *Poriella subacida* (Holotype, BPI 844697). Scale bar = 1 cm.

Figure 4. Microscopic structures of *Poriella subacida* (Holotype). (a) Basidiospores. (b) Basidia and basidioles. (c) Cystidioles. (d) Hyphae from trama. (e) Hyphae from context. Bars: A = 5 µm; B–E = 10 µm.

Hyphal structure: Hyphal system di-trimitic; generative hyphae with clamp connections; skeletal hyphae strongly dextrinoid, CB+; dissolving in KOH.
Context: Generative hyphae infrequent, hyaline, thin-walled, 2.5–4 µm in diameter; skeletal hyphae dominant, thick-walled with a wide lumen, unbranched, subparallel, 3–5.5 µm in diameter; skeletal-binding hyphae hyaline, thick-walled, frequently branched, flexuous, interwoven, 1–2 µm in diameter.

Tubes: Generative hyphae infrequent, hyaline, thin-walled, 2.5–3.5 µm in diameter; skeletal hyphae dominant, thick-walled with a wide lumen, unbranched, subparallel, 3–4.5 µm in diameter; skeletal-binding hyphae hyaline, thick-walled, frequently branched, flexuous, interwoven, 0.7–1.7 µm in diameter. Cystidia absent, but fusoid cystidioles present, hyaline, thin-walled, 13–16 × 3–4.5 µm. Basidia barrel-shaped, with four sterigmata and a basal clamp connection, 20–22.5 × 7–8 µm; basidioles similar in shape to basidia, but slightly smaller.

Basidiospores: Ellipsoid, not truncate, hyaline, thick-walled, smooth, non-dextrinoid, CB+, (4.2–)4.5–6.2(–6.4) × (3.2–)3.6–4.6(–4.9) µm, L = 5.25 µm, W = 3.92 µm, Q = 1.13–1.42 (n = 450/15).

Associated wood-rot: White.

Substrates and distribution: Mainly on conifers, but also on hardwood, causes white rot in *Abies* Mill and *Tsuga* Carr. and common on dead fallen trees in many areas. A boreal eastern species in Europe, widely distributed in forest regions of Asia and North America [8,10,11].

Additional specimen examined: CANADA, Ontario, Gull lake, on *Thuja occidentalis* L., July 25 1919, J.H. Faull (5088) (FH 00605379); Lake Timagami, Timagami Is., on fallen trunk of *Abies balsamea* (L.) Mill., September 10 1918, J.H. Faull (3365) (FH 00605372); Lake Rosseau, on *Tsuga* Carr., September 1902, Harper (587) (FH 00605380); Lake Rosseau, on *Pinus* Linn log, October 1903, S.A. Haper (832) (FH); Lake Rosseau, on fallen log of *Abies balsamea* (L.) Mill., 18 August 1921, J.H. Faull (6013) (FH 00605381); Humber Valley, on roots of *Thuja occidentalis* L., September 1914, J.H. Faull (169) (FH 00605373); Humber Valley, on dead hardwood, September 1914, J.H. Faull (156) (FH 00605375); Sudbury District, Cleland Tp., on dead coniferous wood, 15 September 1918, J.H. Faull (3502) (FH 00605377). CHINA, Fujian Province, Wuyishan Nature Reserve, on fallen angiosperm trunk, 21 October 2005, Dai 7316 (IFP); Guizhou Province, Jiangkou County, Fanjingshan Nature Reserve, on fallen angiosperm trunk, 21 August 2010, Yuan 5511 (IFP); Heilongjiang Province, Yichun, Fenglin Nature Reserve, on fallen trunk of *Picea balsamea* (L.) Mill., September 10 1918, J.H. Faull (3365) (FH 00605372); Lake Rosseau, on *Tsuga* Carr., September 1902, Harper (587) (FH 00605380); Lake Rosseau, on *Pinus* Linn log, October 1903, S.A. Haper (832) (FH); Lake Rosseau, on fallen log of *Abies balsamea* (L.) Mill., 18 August 1921, J.H. Faull (6013) (FH 00605381); Humber Valley, on roots of *Thuja occidentalis* L., September 1914, J.H. Faull (169) (FH 00605373); Humber Valley, on dead hardwood, September 1914, J.H. Faull (156) (FH 00605375); Sudbury District, Cleland Tp., on dead coniferous wood, 15 September 1918, J.H. Faull (3502) (FH 00605377). USA, Arizona, Coronado National Forest, on conifer, 28 August 1958, Lowe (9407) (FH 00605393); Connecticut, New Haven, Sleeping Giant State Park, on fallen trunk of *Betula* L., 22 July 2012, Dai 12773 (BJFC); as above, on fallen trunk of *Tsuga* Carr., 22 July 2012, Dai 12785 (BJFC); as above, 24 July 2012, Dai 10287 (BJFC); as above, on fallen trunk of *Picea* Engelm., 24 July 2012, Dai 10285 (BJFC); Idaho, Bovill County, on dead fallen trunk of *Pinus* Linn, 2 October 1920, A.S. Rhoads (15891) (FH 00605391); Priest River, on *Picea engelmannii*, September 1915, J.R. Weir (9551) (FH 00605392); Priest River, on *Abies grandis* (Doug l ex D Don) Lindl, September 1915, J.R. Weir (8152) (FH 00605394); Kansas, Rooks County, Rockport, on underside of old log, 9 December 1893, (1315) (FH 00605389); Maine, Norcross, on fallen *Populus* L. log, 20 August 1940, D.H. Linder s.n. (FH 00605344), Kittery Point, on log of *Quercus* L., 28 July 1922, J.R. Weir (897) (FH 00605347); Linekin, on *Picea* Dier., September 1899, Burt (2125B) (FH); as above, 16 August 1899, Burt 2127 (FH); Massachusetts, Norfolk County, Sharon, 28 June 1946, A.P.D.Figueur (54) (FH 00605353); Michigan, Neebish, September 1911, E.T.Harper & S.A.Harper s.n. (FH 00605383); Isle Royal, Rock Harbor, August 1904, E.T.Harper & S.A.Harper s.n. (FH 00605384); Pleasant Ridge, on fallen *Tsuga* Carr., 25 September 1915, P.Spaulding & J.F.Collins s.n. (FH 00605345); New York, Osceola, on *Tsuga* Carr., August 1885, C.H. Peck, BPI 844697 (Holotype, BPI); as above, on *Picea* Dietr. log, FH 0053717 (FH);
Dryden, Ringwood Preserve, on old wood, 9 June 1952, W.B. Cooke & V.G. Cooke (29105) (FH 00605356); Ithaca, on Betula lutea F. Michx., nom. illeg. 21 March 1935, W.L. White (1568) (FH 00605360); Floodwood, on conifer, August 1900, Burt 2122B (FH); Floodwood, on Picea Dietr. log, 20 August 1900, 2123B (FH); Pennsylvania: Bedford County, New Paris, on fallen Quercus L., 1 September 1916, J.H. Faull (1490) (FH 00605366); Lackawanna County, Carbondale, on Tsuga Carr. log, 13 December 1898, Burt 2124 (FH); Tennessee, Knox County, Ball Camp Pike, on Pinus Linn log, 18 December 1938, L.R. Hesler (11907) (FH 00605387); Vermont: Addison County, Ripton, on hardwood log, 31 October 1896 (FH 00605346); Addison County, Ripton, on Picea Dietr., 4 November 1896, Burt 2126A (FH); Addison County, Ripton, on Picea Dietr., 31 October 1896, Burt 2126B (FH); Abby, on Tsuga Carr. log, 31 October 1896, Burt 2123A (FH); Underhill, on hardwood, 18 May 1880, Pringle (1025) (FH 00605350); as above, on dead conifer, August 1897, Burt 2121A, B, C (FH); as above, on fallen trunk of Tsuga Carr., September 1902, Harper 625 (FH); Dunamase, on Tsuga Carr. log, 14 September 1896, Burt 2121E (FH); Dunamase, on Tsuga Carr., October 1896, Burt 2122A (FH); Snake Mountain, January 1896, 2124A (FH); as above, September 1902, Harper 746 (FH); Washington: Marymere Falls, Olympic National Park, on Pseudotsuga taxifolia (Lamb.) Britton, WB (27590) (FH 00605395); Clallam County, Sol Duc Hot Springs, on fallen Tsuga heterophylla (Raf.) Sarg., 4 July 1920, J.R. Weir (650) (FH 00605396); as above, on fallen trunk of Picea sitchensis (Bong.) Carr., 14 July 1920, J.R. Weir (609) (FH 00605397); Wisconsin, June 21 1946, Neuman (162) (FH 00605386).

4. Discussion

The taxonomic position of this taxon has been long debated [16–20]. It was transferred to Perenniporia by Donk [20], and this placement has been generally accepted [8–12]. Due to a combination of characteristics (completely unbranched skeletal hyphae and ellipsoid and non-truncate basidiospores), Decock and Staplers [13] mentioned that the species did not belong to Perenniporia. Based on phylogenetic and morphological grounds, Robledo et al. confirmed that this taxon should be separated from Perenniporia, and could be recognized as a distinct genus morphologically as well [28]. Previous studies also confirmed that this species formed a clade distinct from the P. medulla-panis clade [5,6,28]. The present study confirms these results from previous studies and formally describes the new genus, Poriella with P. subacida as type species.

Other species of Perenniporia and Poriella subacida share the morphological features of unbranched skeletal hyphae and non-truncate basidiospores, such as Perenniporia africana (Ipulet and Ryvarden) in Uganda [50,51], P. contraria (Berk. and M.A. Curtis) Ryvarden in Cuba, and P. ellipsospora (Ryvarden and Gilb.) in North America [10]. A comparison of Poriella and related genera is presented in Table 2.

Table 2. A comparison of Poriella subacida and related genera and species.

| Genera            | Hyphal System | Basidiospore Morphology | Chemical Reactions                                                                 | Reference |
|-------------------|---------------|-------------------------|-----------------------------------------------------------------------------------|-----------|
| Perenniporia s.s. | dimitic        | ellipsoid, truncate or not | dextrinoid or not, CB+ dextrinoid, CB+ in the context, CB+ in the trama            | [13]      |
| Perenniporiopsis  | trimitic       | oblong-ellipsoid, truncate | non-dextrinoid to strongly dextrinoid, slightly to distinctly cyanophilous         | [6]       |
| Perenniporia      | dimitic        | globose to subglobose, non-truncate | strongly dextrinoid, CB+ amyloid, CB+                                             | [51]      |
| Poriella subacida | di-trimitic    | ellipsoid, non-truncate | variable dextrinoid, CB+ dextrinoid, CB+                                           | This study|
| Yuchengia narymica| dimitic        | ellipsoid, non-truncate | non-dextrinoid, CB+ amyloid, CB+                                                  | [38]      |

CB+ = cyanophilous, CB– = acyanophilous.

Three species have been mentioned as possible synonyms of this highly variable species. Poria colorea Overh. & Englerth, described from Western Tsuga Carr. and has generally been considered to be conspecific with Polyporus subacidus. Poria fuscomarginata Berk. ex Cooke was commented on by Murrill [52] who found the type material to be badly
preserved and scanty. He concluded that “it was suggested little.” Poria subaurantia Berk. ex Cooke was considered a synonym of Polyporus subacidus by Murrill [53]. Judging by their descriptions, these fungi show a range of variation that is acceptable for P. subacidus.

Our molecular phylogenetic analyses revealed that the genus Poriella is closely related to Yuchengia narymica and then grouped with Vanderbylia based on the ITS+28S gene regions and the combined ITS+28S+mtSSU+Tef1 sequences (Figures 1 and 2). Morphologically, two species share the same hyphal system and basidiospores. However, Y. narymica differs markedly from the acyanophilous, amyloid skeletal hyphae [38,53–55]. Vanderbylia mainly differs in its pileate basidiomata, a dimitic hyphal system with distinctly arboriform vegetative hyphae in the hymenophoral trama and obovoid basidiospores [10,56].

Poriella subacida is primarily a boreal taxon and is widely distributed in forest regions of northern Asia, North America and Europe [8,10,11]. It mainly grows on conifers, especially Picea Dietr., but also on Larix and Pinus Linn. In Europe, it has also been found occasionally on hardwoods like Populus L. and Prunus L. [8], and other hardwoods in North America and Asia [10,11]. The species is also present in tropical areas (e.g., in Africa) [57], but these records should be treated with caution. Ipulet and Ryvarden [50] recently described Perenniporia africana Ipulet and Ryvarden, from Uganda, with seemingly the same combination of characteristics, i.e., unbranched skeletal hyphae and non-truncate basidiospores [57,58]. A list of characteristics of Poriella subacida comb. nov. from different regions is presented in Table 3.

### Table 3. A list of characteristics of Poriella subacida comb. nov. from different regions.

| Specimens | Locality        | Basidiospores (μm) | Average Q Pores/mm Substrate | Substrate |
|-----------|-----------------|--------------------|------------------------------|-----------|
| BPI 844697 (Type) | USA, NY | (4.2–)4.4–5.6(–4.1) | 5.4 1.3 4–5 on beetle盘点 | on the log of Poria asperata Mast. |
| BPI 844698 | USA, NY | (4.7–)4.9–5.6(–5.1) | 5.3 1.3 4–5 on beetle盘点 | on the log of Poria asperata Mast. |
| BPI 844699 | USA, NY | (4.3–)4.5–5.6(–5.1) | 5.2 1.3 4–5 on beetle盘点 | on the log of Poria asperata Mast. |
| BPI 885858 | USA, NY | (3.7–)3.9–4.6(–4.4) | 5.2 1.3 4–5 on beetle盘点 | on the log of Poria asperata Mast. |
| FH0053717 | USA, NY | (4.8–)5.2–5.6(–4.6) | 5.1 1.3 4–5 on beetle盘点 | on the log of Poria asperata Mast. |
| Hesler 19007 | USA, TN | (4.4–)4.6–5.6(–5.1) | 4.9 1.2 4–5 on beetle盘点 | on the log of Poria asperata Mast. |
| 00605389 | USA, KS | (4.1–)4.5–5.1(–4.3) | 4.8 1.3 4–6 on the log of Poria asperata Mast. |
| Lowe 9407 | USA, AZ | (4.6–)4.9–5.6(–5.1) | 4.9 1.2 4–6 on the log of Poria asperata Mast. |
| 00605344 | USA, ME | (4.3–)4.6–5.8(–5.1) | 4.9 1.3 4–6 on the log of Poria asperata Mast. |
| 00605372 | Canada, Ontario | (4.4–)4.6–5.8(–5.1) | 4.9 1.2 4–6 on the log of Poria asperata Mast. |
| Cui 9849 | China, Hainan | (4.9–)5.1–5.6(–5.1) | 4.9 1.3 4–6 on the log of Poria asperata Mast. |
| Yuan 3854 | China, Yunnan | (5–)5.2–5.8(–5.1) | 4.9 1.3 4–6 on the log of Poria asperata Mast. |
| Cui 2712 | China, Zhejiang | (4.9–)5.1–5.6(–5.1) | 4.9 1.3 4–6 on the log of Poria asperata Mast. |
| Dai 2648 | Finland, Pohjanmaa | (4.3–)4.7–5.8(–5.1) | 4.9 1.3 4–6 on the log of Poria asperata Mast. |
| Dai 12619 | Finland, Pohjanmaa | (4.5–)4.6–5.6(–5.1) | 4.9 1.3 4–6 on the log of Poria asperata Mast. |

Poriella subacida causes white rot of conifers and hardwoods and also butt and root rots of living conifers. Due to the cream to golden yellow mycelia felts that develop in the decayed wood, this rot is commonly called “feather rot” [10].

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