RESEARCH ARTICLE



Polypores and genus concepts in Phanerochaetaceae (Polyporales, Basidiomycota)

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Abstract

We explored whether DNA-phylogeny-based and morphology-based genus concepts can be reconciled in the basidiomycete family Phanerochaetaceae. Our results show that macromorphology of fruiting bodies and hymenophore construction do not reflect monophyletic groups. However, by integrating micromorphology and re-defining genera, harmonization of DNA phylogeny and morphological genus concepts is possible in most cases. In the case of one genus (*Phlebiopsis*), our genetic markers could not resolve genus limits satisfactorily and a clear morphological definition could not be identified.

We combine extended species sampling, microscopic studies of fruiting bodies and phylogenetic analyses of ITS, nLSU and *rpb1* to revise genus concepts. Three new polypore genera are ascribed to the Phanerochaetaceae: Oxychaete gen. nov. (type Oxyporus cervinogilvus), Phanerina gen. nov. (type Ceriporia mellea), and Riopa (including Ceriporia metamorphosa and Riopa pudens sp. nov.). Phlebiopsis is extended to include Dentocorticium pilatii, further species of Hjortstamia and the monotypic polypore genus Castanoporus. The polypore Ceriporia inflata is combined into Phanerochaete.

The identity of the type species of the genus *Riopa*, *R. davidii*, has been misinterpreted in the current literature. The species has been included in *Ceriporia* as a species of its own or placed in synonymy with *Ceriporia camaresiana*. The effort to properly define *R. davidii* forced us to study *Ceriporia* more widely. In the process we identified five closely related *Ceriporia* species that belong to the true *Ceriporia* clade (Irpicaceae). We describe those species here, and introduce the *Ceriporia pierii* group. We also select a lectotype and an epitype for *Riopa metamorphosa* and neotypes for *Sporotrichum aurantiacum* and *S. aurantium*, the type species of the anamorphic genus *Sporotrichum*, and recommend that teleomorphic *Riopa* is conserved against it.

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Key words

Systematics, taxonomy, morphology, anamorphic fungi

Introduction

Fruiting bodies are the most visible and easily studied element of the life cycle of macrofungi. Fruiting body morphology, including overall shape and construction of the spore-producing surface (hymenophore in basidiomycetes), was adopted early on as the guiding principle of fungal classification. This practical, but artificial, system has been largely replaced by a more natural, phylogenetic classification based on molecular characters (Hibbett et al. 2007, McLaughlin and Spatafora 2014, 2015).

At higher levels, there is rampant convergence and parallelism in the evolution of fruiting body and hymenophore types, possibly with a general trend towards evolution of more complex types. For instance, some orders of basidiomycetes only contain simple, effused fruiting bodies (e.g. Atheliales, Corticiales), while others are dominated by more complex forms (e.g. Agaricales, Gloeophyllales). Nevertheless, fruiting body morphology and hymenophore type remain significant for classification of fungi, particularly at very low taxonomic levels (e.g. within genera). The separate research traditions of specialists on morphological groups such as agarics, corticioid fungi and polypores have hindered comparisons of morphologically distinct yet closely related taxa. Otherwise well implemented studies for instance in polypore systematics sometimes neglect closely related corticioid fungi (Li and Cui 2013, Jia et al. 2014, Chen et al. 2015).

A number of studies have shown that hymenophore types classified separately may actually belong to the same genus. Examples include *HyphodontialXylodon* (Langer 1994, Larsson et al. 2007), *Resupinatus* (Thorn et al. 2005), *Schizophyllum* (Nakasone 1996), *Sidera* (Miettinen and Larsson 2011), *Steccherinum* (Miettinen et al. 2012), and *Trechispora* (Larsson 1994, Larsson et al. 2011, Birkebak et al. 2013). In the present study we explore whether phylogenetic genus-level classification and hymenophore type based classification can be united into a coherent system in the family Phanerochaetaceae.

Larsson (2007) suggested the adoption of Phanerochaetaceae for a clade of corticioid fungi around the genus *Phanerochaete*. A more comprehensive sampling of the Polyporales by Binder et al. (2013) suggests that Phanerochaetaceae is indeed a wellsupported subclade of the large phlebioid clade, with the polypore genus *Bjerkandera* as the sister clade to the rest of the family. The family, as well as others mentioned in this paper, will also be adopted in the forthcoming treatment of Polyporales systematics by Justo et al. (in preparation). Aside from *Bjerkandera*, all the members of the Phanerochaetaceae identified in previous analyses have been corticioid or hydnoid fungi, most of them simple septate and monomitic, with the exception of *Hapalopilus*, a polypore genus with clamped hyphae. Here we describe two new polypore genera for the family (Figure 1).



Figure I. Fruiting body diversity in Phanerochaetaceae. **a** *Phlebiopsis castanea* (=*Castanoporus castaneus*), Russia, Spirin 5704 **b** effused polypore *Phanerina mellea*, Indonesia, Miettinen 11393 **c** corticioid *Phlebiopsis pilatii*, Russia, Spirin 6268 **d** polypore *Riopa metamorphosa* intermixed with its anamorphic stage *Sporotrichum aurantiacum*, Czech Republic, Vlasák 0511/15. Photos taken in the field.

The corticioid members of the Phanerochaetaceae have been popular subjects of phylogenetic research, which has resulted in revision of genus concepts within the family. Greslebin et al. (2004) created the new genus *Rhizochaete* for pigmented *Phanerochaete*like taxa in a separate clade within the Phanerochaetaceae. Wu et al. (2010) produced an extended phylogeny of the Phanerochaetaceae, extending the genera *Hjortstamia* and *Phlebiopsis*. The most comprehensive phylogenetic treatment until now, produced by Floudas and Hibbett (2015), resulted in creation of *Phaeophlebiopsis* for *Phlebia*-like taxa that are phylogenetically separated from the similar *Phlebiopsis* species, and moved a species of *Hjortstamia* to *Phlebiopsis*. Chikowski et al. (2016) extended the genus *Rhizochaete* further, including species with inconspicuous, poorly differentiated cystidia.

As a result of these and other (De Koker et al. 2003, Hallenberg et al. 2008) studies, Phanerochaetaceae contained 8–9 genera of corticioid fungi at the onset of this study (*Donkia, Hyphodermella, Phaeophlebiopsis, Phanerochaete, Phlebiopsis, Pirex, Rhizochaete, Terana* and probably *Porostereum*). Looking at species numbers, Phanerochaetaceae is heavily dominated by corticioid fruiting body types. The polypore genera *Bjerkandera* and *Hapalopilus* are neatly separated from corticioid species.

To better understand the morphological variation and evolution within the Phanerochaetaceae, we have incorporated new species — polypores and corticioid fungi to the datasets published by earlier authors. With this new data we provide an updated phylogeny of the family, and revise species concepts therein.

Methods

DNA and phylogenetics

We produced 36 new nuclear ribosomal DNA internal transcribed spacer (ITS) sequences, 20 large subunit (nLSU, 28S) sequences, and 4 RNA Polymerase II Largest Subunit (*rpb1*) sequences. They have been deposited in the INSDC (Cochrane et al. 2016) under the accession numbers KX752590–KX752629. We also used ITS, nLSU and *rpb1* sequences of 99 specimens retrieved from the INSDC (Suppl. material 1 – INSDC accession numbers), chosen based mainly on previous studies (Wu et al. 2010, Binder et al. 2013, Floudas and Hibbett 2015, Volobuev et al. 2015).

Various DNA extraction methods were used: standard chloroform extraction (Murray and Thompson 1980), E.Z.N.A. forensic DNA kit (Omega Bio-Tek, Norcross, GA, USA), and DNeasy plant mini kit (Qiagen, Hilden, Germany). PCR primers included ITS1F, ITS5, ITS1, ITS4 and LR22 for the ITS; CTB6, LR0R and LR7 for the partial nLSU (http://biology.duke.edu/fungi/mycolab/primers.htm); and RPB1-Af and RPB1-Cr for *rpb1* (Matheny et al. 2002). Sequencing primers were the same with the addition of primers LR5 and LR3R for nLSU and RPB1-Int2.2f (Binder et al. 2009) for *rpb1*.

We compiled three datasets for phylogenetic analyses:

- LSU-dataset of the phlebioid clade (Irpicaceae, Meruliaceae, Phanerochaetaceae) based on nuclear ITS and LSU sequences, with 122 specimens. Of these, 100 had ITS and 118 nLSU sequence available. Total alignment length after manually removing unalignable characters was 1799 bp with 474 (26%) parsimony informative characters. The tree was rooted with *Phlebia radiata* (Meruliaceae).
- *Rpb1*-dataset for Phanerochaetaceae based on *rpb1*, ITS and nLSU sequences with 34 species, all containing all three genetic markers. Total alignment length after re-

moving unalignable characters was 3064 bp with 672 (22%) parsimony informative characters. The tree was rooted with *Bjerkandera adusta*.

3. *Hapalopilus* dataset with 16 ITS sequences, with a total alignment length 593 bp and 20 (3%) parsimony informative characters. The tree was rooted with *H. percoctus* (described in this paper).

Sequences were aligned using MAFFT online versions 7.233-7.244 with strategy E-INS-I (http://mafft.cbrc.jp, Katoh and Standley 2013) and adjusted manually using PhyDE 0.9971 (Müller et al. 2010). Numbers of informative characters were calculated in MEGA6 (Tamura et al. 2013).

We used MrBayes 3.2 (Ronquist et al. 2012) for inferring Bayesian consensus trees for the three datasets. The LSU and *rpb1* datasets were partitioned as follows: ITS1 and ITS2 in one partition, 5.8S and LSU in another, and *rpb1* separately. The nucleotide substitution model GTR+I+G was used for all partitions except *Hapalopilus* ITS, for which GTR was used. Models were chosen based on AIC scoring produced in jmodeltest (Darriba et al. 2012). Bayesian analyses were run with eight chains in three parallel runs, temp=0.1. LSU dataset was run for 10 (LSU dataset), 2 (*rpb1*) and 4 (*Hapalopilus*) million generations sampling every 2000 generations. All runs converged to below 0.01 average standard deviation of split frequencies. A burn-in of 25% was used before computing the consensus tree.

In parallel with the Bayesian analyses, we used RAxML 8.1.3 (Stamatakis 2014) for maximum likelihood inference and bootstrapping, partitioned similarly as in Bayesian analysis but using the GTR+G substitution model for all datasets. The tree with the highest likelihood from 100 individual runs was selected, and bootstrap values were calculated from 1000 repetitions. All the phylogenetic analyses were done at the CSC – IT Center for Science (https://www.csc.fi) multi-core computing environment. The resulting phylograms were pre-edited in FigTree 1.4.2 (Rambaut 2014) and processed further in CorelDRAW X6. Since the Bayesian and maximum likelihood analyses had similar topologies in all well-supported and relevant nodes, we report here only the Bayesian results amended with bootstrap support values from the maximum likelihood analyses. The alignments and phylograms are available in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S19710).

Microscopy

We used a Leica DMLB microscope with optional phase contrast illumination for microscopic observations. Basic mountant was Cotton Blue (CB, Merck 1275) made in lactic acid, but we also used Melzer's reagent (IKI), 5% KOH, and Cresyl Blue (CRB, Merck 1280). Sketches were made using a drawing tube with the exception of spores that were drawn with free hand after a real measured spore. The sketches were then imported to CorelDRAW X6 and converted to vector graphics. Spore statistics were produced with R version 3.0.2 (R Core Team 2013).

In microscopic descriptions, the following abbreviations are used: L – mean spore length, W – mean spore width, Q – L/W ratio. Entry CB+ means cyanophily, CB– acyanophily; IKI– means neither amyloid nor dextrinoid reaction. While reporting pore and spore measurements, the whole range is given in parentheses; 90% range excluding 5% extreme values from both ends of variation is given without parentheses; in case the values are identical, parentheses are omitted. For basidial and hyphal width measurements, the 20% tails are in parentheses.

Results

Our phylogenetic analyses support the division of the phlebioid clade into three lineages in line with previous research (Binder et al. 2013, Floudas and Hibbett 2015): Meruliaceae, Irpicaceae (*Byssomerulius* clade in the sense of Larsson 2007) and Phanerochaetaceae (Figure 2). In the analyses of our LSU dataset (ITS+nLSU), the Phanerochaetaceae receives excellent support (posterior probability=1, bootstrap support=98%) and the Irpicaceae good to moderate support (pp=0.97, bs=59%), while the tree was rooted within the Meruliaceae (*Phlebia radiata*).

The Phanerochaetaceae can further be divided into several clades: *Bjerkandera* clade (pp=0.71, bs=57%), *Phanerochaete* clade (pp=1, bs=87%), *Donkia* clade (pp=1, bs=85%), and *Phlebiopsis* clade (pp=1, bs=0.98%) (Figure 2). Support values are similar for the *rpb1*-dataset (ITS+nLSU+*rpb1*, Figure 3). We report polypores in all of these clades except the *Donkia* clade.

The *Bjerkandera* clade contains three genera: pileate polypores in the genus *Bjerkandera*, the effused corticioid genus *Terana*, and *Porostereum* spp. with smooth hymenophore and caps. All known species in these genera have clamped septa.

The *Phanerochaete* clade contains numerous corticioid species as well as five species of polypores: *Ceriporia inflata, Oxychaete cervinogilva* (=*Oxyporus cervinogilvus*), *Phanerina mellea* (=*Ceriporia mellea*), *Riopa metamorphosa* (=*Ceriporia metamorphosa*), and *Riopa pudens*. This clade contains only simple-septate species with one exception (*Phanerochaete krikophora* nom. prov.), whereas clamped and simple-septate species are intermixed in other parts of the Phanerochaetaeae. To create monophyletic genera, we have two options: a wide, morphologically heterogeneous *Phanerochaete* that includes a number of different-looking polypores, or three polypore genera in addition to a more homogenous *Phanerochaete*. We have opted to use three polypore genera: *Oxychaete, Phanerina* and *Riopa*. Even after this, a polypore species, *Ceriporia inflata* with incomplete pores, is nested within *Phanerochaete*, where it is closely related and microscopically very similar to spiny species. Nevertheless, this arrangements allows us to stick largely with morphologically identifiable genera (Tables 1 and 2).

Even though somewhat different from *Phanerochaete*, the polypore species in the *Phanerochaete* clade have an uncharacteristically simple hyphal structure for a polypore. They have no hyphal pegs or cystidioles. The subhymenial structure is loose, reminding a cymoid corymb in botanical terms (see Figs 7–9). In contrast, a typical



Figure 2. Phylogeny of the phlebioid clade of the Polyporales with emphasis on *Ceriporia* clade and Phanerochaetaceae. Bayesian consensus tree based on ITS and nLSU sequences. Figures denote posterior probabilities (figures between 0 and 1) and bootstrap support values of the maximum likelihood analysis (figures between 50 and 100).

polypore subhymenium is more difficult to study, hyphae are tightly interwoven, less clearly oriented and more irregular. Pores of *Phanerochaete* clade polypores are shallow and in many species irregular. Basidiocarps are relatively thin. All cystidia are hymenial, and no cystidia of tramal origin typical for many cystidioid polypores (such as *Rigidoporus*) are present.

The **Donkia clade** is a sister to the *Phanerochaete* clade, and contains the genera *Donkia, Hyphodermella* and *Pirex* as well as some species ascribed to *Phlebia* sensu lato. It includes smooth to hydnoid, pileate to effused species, many of which have clamped septa and are also otherwise morphologically quite different from *Phanerochaete*.

The *Phlebiopsis* clade contains a wide variety of different fruiting body types: pileate polypores with clamped septa (*Hapalopilus*), a resupinate polypore with simple septa (*Phlebiopsis castanea* or *Castanoporus castaneus*), phlebioid taxa with tight, simple-



Figure 2. Continued.

septate fruiting bodies and encrusted cystidia (*Phlebiopsis*), and loose rhizomorphic fruiting bodies (*Rhizochaete*). The internal structure of the clade is poorly resolved in the LSU dataset (Figure 2). The *rpb1* dataset (Figure 3) includes too few species to be of much help either at this point. Three clades are well supported — *Hapalopilus*, *Phaeophlebiopsis* and *Phlebiopsis* — but *Rhizochaete* is poly- or paraphyletic. Further species sampling and genes may help the situation, but in our experience poor resolution of nrDNA markers in Polyporales often persists in expanded datasets.

| | Phanerochaete | Phlebiopsis | Phaeophlebiopsis | Rhizochaete | Hyphodermella |
|---------------------------|-------------------------|------------------------|------------------------|------------------------------|--------------------|
| number of known species | many | >10 | 3 | 6 | 6 |
| spore shape | cylindrical, ellipsoid | cylindrical, ellipsoid | cylindrical, ellipsoid | cylindrical, ellipsoid | ellipsoid |
| hymenophore | smooth, hydnoid, poroid | smooth, poroid | smooth | smooth | hydnoid |
| clamps | *1 | I | I | -/+ | I |
| subhymenium | loose, corymb like | interwoven | interwoven | interwoven | loose, corymb type |
| lamprocystidia | I | + | + | -/+ | I |
| basal layer / cap context | not agglutinated | agglutinated/tight | agglutinated/tight | not agglutinated | not agglutinated |
| colors | pale | pale to brown | pale | many bright-colored or brown | pale to brown |
| KOH reaction | red or green if present | purple if present | absent | purple if present | absent |
| rhizomorphs | many species | absent | absent | always present | absent |

Table 1. Morphological comparison of simple septate corticioid genera of the Phanerochaetaceae.

*present in one species

| Table 2. M | lorphological comp | arison of simple | e-septate polypores o | f the Phaneroch | aetaceae with similar | r genera. | | |
|--------------------------|---|--|--|--|--|--|---|--|
| | Phlebiopsis | Oxychaete | Phanerina | Riopa | Oxyporus | Emmia | Ceriporia | Phanerochaete (core) |
| number of polypores | 1 | 1 | 1 | 2 | >10 | 2 | many | 1 |
| dry basidi- ocarp | resupinate, thin | pileate, light board-like | resupinate, rather fragile | resupinate, fragile | tough | resupinate, not particularly fragile | resupinate, fragile | resupinate, rather fragile |
| color | yellowish brown | yellow-brown | yellow | white-orange | white-cream | white-cream | white-red-purple | light-colored |
| pores | shallow, large | shallow, large, regular | shallow, large | shallow, me- dium to large | deep, small to large | deep, medium seized | small to medium | absent/irpicoid |
| cystidia | thick-walled subu- late, encrusted | thick-walled subulate, encrusted | thin-walled subulate, naked | tubular thin- walled, naked | thin- to thick-walled subulate, encrusted; gloeocystidia | cylindrical, thin- walled, encrusted | no (cystidioles) | thin-walled cylindrical (polypore) to thick-walled subulate, often encrusted |
| encrustation | abundant | only in cystidia | large crystals | large crystals & sticky resin | variable, large crystals, cystidia | scarce, coarse | often abundant, also sticky resin | large crystals, sometimes on cystidia |
| hyphae | thick-walled throughout, wide | thick-walled throughout, wide | thin- to thick-walled, slightly wider in subiculum | thin- to slightly thick-walled, narrow | narrow, thick-walled | narrow, thin- walled | often wide and in- flated in subiculum, thin- to thick-walled | often wide in subiculum, thin- to thick-walled |
| hyphal consistency | rather dense, subiculum may be loose, basal layer agglutinated | very loose, hy- phae straight | trama rather dense, subiculum loose | rather loose | rather dense | rather loose | loose | subiculum loose, subhy- menium often dense |
| hyphal H- connections | ou | ои | по | ou | ои | оп | yes | yes |

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ellipsoid, mid-sized, thin-

walled

cylindrical to narrow

curved cylindrical to mid-sized, thin-

narrow ellipsoid,

mid-sized

globose, mid-sized to large, slightly thick-

(5-5.5×2-2.5 μm), curved

cylindrical to narrow ellipsoid, walls rather

large (6.5×3 μm),

mid-sized (5.5×2.8 $| \text{large } (7 \times 3 \ \mu\text{m}), \ \mu\text{m})$, cylindrical, cylindrical, slightly curved, thin- slightly curved,

μm), cylindrical,

spores

mid-sized

broad ellipsoid to

basidia long interwoven,

cells

branching corymb

dense but still cor-

distinct corymb branching, long

condensed, basidia

hymenium

subhymenium mid-sized

ymb branching

basidia

to ellipsoid, small

walled

(4-6×2.5-3 μm),

thin-walled

walled

cylindrical

thin but distinct

thin-walled

walled

corymb branching

subhymenium very woven, cells often

short-celled, inter-

very short-celled,

tight interwoven to looser with inflated

subhymenium

inflated, basidia short



Figure 3. Phanerochaetaceae phylogeny, Bayesian consensus tree based on ITS, nLSU and *rpb1* sequences. Figures denote posterior probabilities (figures between 0 and 1) and bootstrap support values of the maximum likelihood analysis (figures between 50 and 100).



3.0E-6

Figure 4. Relations of *Hapalopilus* spp. Bayesian consensus tree based on ITS sequences. Figures denote posterior probabilities.

No intuitively pleasing genus arrangement seems to be in reach for the *Phlebiopsis* clade. Based on our LSU dataset, the only well supported options for including all species in monophyletic genera would be either one genus for the whole clade (for which *Hapalopilus* has priority), or 10–13 separate genera, most of them new and monotypic. Neither is a satisfactory solution, and we have therefore taken a pragmatic stand and chosen a strict concept of *Hapalopilus* as a polypore genus and expanded the genus *Phlebiopsis* to include *Castanoporus*, leaving classification for the rest of the clade unresolved.

Thus defined, *Hapalopilus* is a small genus, currently with four polypore species (Figure 4). The rest of the species currently accepted in *Hapalopilus* (11 species), with different pigmentation and denser fruiting body consistency (cf. *Aurantiporus croceus*), do not belong to Phanerochaetaceae but rather to Meruliaceae (Figure 2) and probably also other families. The expanded concept makes *Phlebiopsis* variable in terms of fruiting body morphology: smooth and effused (*Phlebiopsis*), poroid effused (*Castanoporus*), and stereoid, pileate species with smooth hymenophore (*Hjortstamia*). Microscopically the genus is rather uniform but not distinguishable from *Phaeophlebiopsis*, so for now we have had to abandon a strictly morphological genus concept for this species group.

The genus *Riopa* described by Reid (1969) has been considered a taxonomic synonym of *Ceriporia*, typified by *C. viridans* (Irpicaceae, Figure 2). This conclusion arises from an incorrect interpretation of the identity of the type species of the genus, *R. davidii*, as *Ceriporia camaresiana* (Ryvarden 1991, Bernicchia 2005). Our study of the type specimen shows that *R. davidii* is instead a synonym of *Ceriporia metamorphosa* (*=Riopa metamorphosa*, Phanerochaetaceae). The species called *Ceriporia davidii* (*=Riopa davidii*) by Pieri and Rivoire (1997) turns out to be an undescribed member of the *Ceriporia* clade in the Irpicaceae. The new species, named here as *C. pierii*, and four other newly described species form a well-supported group within the *Ceriporia* clade (Figure 2).

Riopa metamorphosa has been placed previously also in the genus *Emmia*, typified by *Emmia latemarginata* (=*Rigidoporus latemarginatus*) (Zmitrovich et al. 2006). That species is a close relative of *Irpex lacteus* (Irpicaceae), and thus *Riopa* and *Emmia*, though morphologically quite similar, are widely separate phylogenetically (Figure 2, Binder et al. 2013, Zmitrovich and Malysheva 2014).

Discussion

In our treatment, Phanerochaetaceae contains 14 genera, half of them with poroid species. We expect further sampling to result in more polypores and polypore genera for the family. Even so, corticioid species and genera will likely dominate Phanerochaetaceae.

Our taxonomic revision has managed to retain morphological genus concepts within Phanerochaetaceae, although this has required creation of three new genera for polypores. We show that natural genera (*Phanerochaete*, *Phlebiopsis*) contain a wide

variety of hymenophore types — poroid, hydnoid and smooth — and can be best defined with a combination of microscopic characters of fruiting bodies. However, in one case (the *Phlebiopsis* clade, genus *Rhizochaete* in particular) no morphologically unique, phylogenetically justified genera could be defined, and we have felt the need to adopt an interim, partial classification arrangement.

Our results mirror those of Miettinen et al. (2012), whose similar treatment of Steccherinaceae identified genera (*Antrodiella, Metuloidea, Steccherinum*) each with variable hymenophore types (poroid, hydnoid or smooth). Like us, they found it generally possible to integrate phylogenetic information and morphological genera, but also identified one clade (*Steccherinum*), for which no morphologically satisfactory genus arrangement was in reach.

These studies reinforce the view that genera of macrofungi may contain species with widely variable fruiting body morphology. It seems that morphological genus concepts do have a future, but in many cases only when based on a wide set of microscopic characters. Finally, in a small minority of cases, it appears that morphologically unique genera of macrofungi may not be feasible.

Any taxonomist working with DNA sequences has the advantage of comparing their taxa with publically available sequences regardless of morphology of the source. We encourage a broad-minded approach outside traditional morphological conventions in taxonomic studies. When studying genus limits in particular, sampling and taxonomic treatment should be extended to include all the taxa with similar micromorphology and DNA sequences.

What factors gave rise to the diversity of fruiting body types in Phanerochaetaceae? We believe that ecological specialization is the major factor in driving fruiting body evolution within the family. For instance, rhizomorphic species with pellicular, simple fruiting bodies in *Phanerochaete* and *Rhizochaete* prefer decaying wood in advanced stages of decomposition and seem to colonize suitable substrates by growing through soil vegetatively. Their closest relatives in *Phanerochaete* and *Phlebiopsis* with denser fruiting bodies occur more frequently on recently fallen logs or even still attached branches. Most poroid, hydnoid and stereoid Phanerochaetaceae with relatively complex fruiting bodies produce them in earlier stages of wood decomposition, living trees or drier microclimatic conditions (*Bjerkandera*, *Donkia*, *Oxychaete*, *Phlebiopsis castanea*, *Pirex*, *Porostereum*, *Riopa metamorphosa*, *Terana*).

We see here a pattern where simple, ephemeral, rhizomorphic fruiting bodies belong mainly to species growing in soil and very decayed wood, whereas more persistent, complex and denser fruiting bodies tend to belong to species inhabiting living or recently dead trees. Species specialized in colonizing quickly consumed substrates such as rotten pieces of wood in soil are probably better off producing short-lived, simple fruiting bodies. Species using more concentrated and longer-term energy sources, such as recently fallen logs, can invest in more complex or longer-living fruiting bodies. Yet Phanerochaetaceae includes no species with long-lived perennial fruiting bodies, and it might be that the genetic make-up of species in the family sets limits to evolution of fruiting body forms.

Taxonomy

Castanoporus Ryvarden

Synopsis Fungorum 5: 121 (1991).

Type species. Castanoporus castaneus (Lloyd) Ryvarden

Remarks. This monotypic genus contains one conifer-dwelling resupinate polypore species from East Asia. With its simple-septate hyphae, monomitic and dense structure (in basal layer) with thick-walled hyphae, middle-sized spores and subulate, encrusted cystidia the species brings into mind *Phlebiopsis* under the microscope. For a more detailed description see Nuñez and Ryvarden (2000).

Phylogenetically the species comes close to *Phlebiopsis flavidoalba* and *P. pilatii*. Together those three species form a sister clade to core *Phlebiopsis*, typified by *P. gigantea* (Figures 2 and 3). For now the most practical solution is to include *Castanoporus* in *Phlebiopsis* (see discussion under *Phlebiopsis*). Hjortstam (1987) listed *Castanoporus castaneus* under *Phlebiopsis* in his check-list of corticioid fungi, but made no formal combination. If *Phlebiopsis* would be defined more strictly, then *Castanoporus* could be put in use.

The genus *Cystidiophorus* has been described for *Castanoporus castaneus*, but for nomenclatural reasons described below we think *Castanoporus* should prevail against *Cystidiophorus*. Bondartsev and Ljubarsky (1963) described the monotypic genus *Cystidiophorus* with the species *C. merulioideus* as the type. Unfortunately, they did not indicate a type specimen for the species, which makes the species name invalid, and also rendered the genus invalid (Melbourne Code Art. 40; the cut-off year for type indication is 1958). Later, Imazeki (Imazeki and Hongo 1965) made the combination *Cystidiophorus castaneus* based on *Merulius castaneus* Lloyd, mentioning *C. castaneus* and *C. merulioideus* as synonyms. This combination does not qualify as a validation of Bondartsev and Ljubarsky's genus name, because Imazeki did not provide reference to the genus description, which is clearly separate from the species description in the original paper (Art. 38.1). In such a case, the genus could be considered valid with the condition that no previously described species is mentioned (Art. 38.5a), but this is not the case as Imazeki mentions Lloyd's species. Thus, we follow Ryvarden (1991) and regard *Castanoporus* as the correct name for this genus.

Ginns (1969) lectotypified *C. castaneus* and gave a description of the type, which agrees well with our concept of the species as well as that of Imazeki's and Bond-artsev's. Also Maas Geesteranus (1974) studied the lectotype from BPI.

Zmitrovich et al. (2006) combined *C. castaneus* in *Australohydnum*. We do not have material of *Australohydnum* from Australia (the type locality of the type species) or any sequences, but judging from the type of cystidia and hyphal structure we think it is unlikely (but possible) that *Australohydnum* belongs to *Phlebiopsis* as delineated here (see *Oxychaete* for further notes on *Australohydnum*). If *Phlebiopsis* were to be split, *Castanoporus* and *Australohydnum* would probably both persist being morphologically quite distinct.

Hapalopilus P. Karst.

Revue Mycologique Toulouse 3(9): 18 (1881).

Type species. Hapalopilus nidulans (Fr.) P. Karst. (= H. rutilans (Pers.) Murrill)

Description. Pileate to resupinate polypores with soft to cottony corky, ochre to pink basidiocarps. Hyphal structure monomitic, clamps always present, generative hyphae slightly thick-walled, $2-5.5 \mu m$ in diameter, CB-, IKI-, KOH-, covered with granular, golden yellow pigment that dissolves in KOH turning purple. Cystidia absent. Hymenial cells relatively long, $12-25\times4.2-5.5 \mu m$. Spores ellipsoid to subcy-lindrical, thin-walled, $3-5\times2-3.2 \mu m$.

Remarks. Altogether 36 species have been combined to *Hapalopilus*, most of them bright-colored, soft polypores with a monomitic, clamped hyphal system. The genus type *H. nidulans* belongs to the Phanerochaetaceae as shown by us (Figure 2) and previous work (Binder et al. 2005, Binder et al. 2013, Floudas and Hibbett 2015). Other species traditionally referred to this genus (*H. alborubescens, H. croceus, H. ochraceolateritius* etc.) belong to other lineages of the *Polyporales* (Niemelä et al. 2012, Dvořák et al. 2014), and their phylogeny and taxonomy will be revisited on further occasion.

Here we include four species in *Hapalopilus* in the strict sense, three of which are new to the genus. According to our data, *Hapalopilus rutilans* is a holarctic species, *H. eupatorii* and *H. ribicola* are found in Europe, and *H. percoctus* is so far only known from the type locality in Botswana. These species are morphologically very similar, and thus *Hapalopilus* as a genus is morphologically easy to characterize. The purple KOH reaction of *Hapalopilus* is shared by its pigmented, corticioid relatives in *Rhizochaete* (Wu et al. 2010, Chikowski et al. 2016).

Unlike other Phanerochaetaceae polypore genera recognized here, *Hapalopilus* has a typical polypore subhymenium of sinuous, tightly packed, interwoven hyphae instead of the loose corymb type seen in *Oxychaete*, *Phanerina*, *Phanerochaete* and *Riopa*. Also *Phlebiopsis* species (including *Castanoporus*) have an interwoven subhymenium.

Morphological, ecological and geographic data of *Hapalopilus* species are summarized in Table 3.

Hapalopilus eupatorii (P. Karst.) Spirin & Miettinen, comb. nov.

MycoBank 817920 Figures 5b and 6e

≡Physisporus eupatorii P. Karst., Revue Mycol. 6: 214 (1884). *=Ceriporiopsis herbicola* Fortey & Ryvarden.

Remarks. *H. eupatorii* has completely resupinate, thin basidiocarps on dead herbaceous stems (*Arctium, Eupatorium,* and *Reynoutria*). It has been recorded once on thin fallen branches of *Robinia* in a thicket of *Reynoutria*. Karsten (1884) described the species from

| Species | Distribution | Hosts | Basidiocarp | Pores per mm | Tramal hyphae diameter | Basidiospores |
|--------------|------------------|---|---|--------------|---|--|
| H. eupatorii | temperate Europe | dead herbaceous stems, one record on <i>Robinia</i> | effused, small-sized | 2-4 | 2.0–3.2(4.2) μm, me- dian=3.0 μm, n=30/1 | ellipsoid, (3.3)3.4–4.5(5.2)×(2.2)2.4– 3.1(3.2) μm, L=3.96 μm, W=2.75 μm, Q=1.44, n=91/2 |
| H. percoctus | Botswana | dicot log, savanna/park | pileate, projecting several cm | 3-4 | (2.0)3.0–4.8(5.6) μm, median=4.3 μm, n=21/1 | ellipsoid, (3.7)3.8–4.6×(2.7)2.8–3.3 µm, L=4.11 µm, W=2.98 µm, Q=1.38, n=30 |
| H. ribicola | North Europe | dead, still attached branches of <i>Ribes</i> | effused-reflexed or resupinate, pilei poorly developed, project- ing up to 0.5 cm | 3-4 | 3.0-4.0(4.3) μm, me- dian=3.7 μm, n=30/2 | narrowly ellipsoid to ellipsoid, (3.9)4.0– 5.0(5.2)×(2.2)2.3–3.0(3.3) μm, L=4.36 μm, W=2.66 μm, Q=1.64, n=90/3 |
| H. rutilans | holarctic | twigs and logs of deciduous trees, rarely also conifers | sessile or effused reflexed, pilei projecting up to 1–5 cm | 3-4 | (2.0)3.0–3.7(4.6) μm, median=3.3 μm, n=121/8 | cylindrical to narrowly ellipsoid, (3.1)3.2–5.1(5.8)×(1.9)2.0–2.7(3.1) µm, L=4 µm, W=2.3 µm, Q=1.74, n=400/13 |

Table 3. Comparison of Hapalopilus species. Spore statistics of H. rutilans include only European specimens.



Figure 5. *Hapalopilus* fruiting bodies, a *Hapalopilus rutilans*, Vlasák Jr. 0407/34-J b *Hapalopilus eupatorii*, Rivoire 5333.

France as *Physisporus eupatorii*, but it long remained an enigma for mycologists (Lowe 1956, Donk 1974). Recently it was reported from England as *Ceriporiopsis herbicola* (Fortey and Ryvarden 2007) and Germany as *H. nidulans* f. *resupinata* (Dämmrich 2014).

Hapalopilus percoctus Miettinen, sp. nov.

MycoBank 817921 Figure 6

Holotype. Botswana. Gaborone, Golf course, -24.652°: 25.936°, strip of natural bush, felled log or tree stump (40 cm in diameter), 28 May 2008, Reijo Miettinen (H 7008581).

Etymology. *Percoctus*, parched, scorched; refers to the sun-exposed habitat of the species.

Remarks. Similar to *Hapalopilus rutilans* with pileate basidiocarps. Microscopically otherwise identical, but *H. percoctus* has clearly wider spores and tramal hyphae (Table 3). The spore dimensions come close to *H. eupatorii*, which has larger pores, effused basidiocarps and grows usually on woody herbs. Its tramal hyphae are also narrower. *Hapalopilus percoctus* is the only species in the genus known to us from the Southern Hemisphere.

Hapalopilus ribicola (P. Karst.) Spirin & Miettinen, comb. nov.

MycoBank 817922 Figure 6g

≡Trametes ribicola P. Karst., Hedwigia 20: 178 (1881).

Remarks. This species was described by Karsten (1881) based on the sole collection from Finland. It had usually been regarded as a form of *H. rutilans* (Lowe 1956). However, our data show that specimens growing on *Ribes* spp. in North Europe are



Figure 6. Microscopic characters of *Hapalopilus. Hapalopilus percoctus*, holotype, **a** subicular hyphae **b** tramal hyphae **c** hymenium and subhymenium **d** hymenial cells. Spores of **e** *Hapalopilus eupatorii*, lectotype **f** *Hapalopilus percoctus*, holotype **g** *Hapalopilus ribicola*, lectotype **h** *Hapalopilus rutilans*, Niemelä 7134.

distinct from *H. rutilans* and phylogenetically closer to *H. eupatorii*. All specimens of *H. ribicola* studied by us are from Finland, from branches of both wild and cultivated *Ribes* spp. The species is evidently widely distributed and just overlooked.

Hapalopilus rutilans (Pers.) Murrill

Figures 5a and 6h

- *≡Boletus rutilans* Pers., Icones et Descriptiones Fungorum Minus Cognitorum 1: 19, t. 6:3 (1798).
- =Hapalopilus nidulans (Fr.) P. Karst.

Remarks. This common species has gone under two names, *H. rutilans* and *H. nidulans*. Many authors have chosen to use *H. nidulans* over *H. rutilans*, (Bondartsev 1953, Gilbertson and Ryvarden 1986, Bernicchia 2005, Ryvarden and Melo 2014), but also the latter name has been in use (Murrill 1904, Donk 1974, Niemelä 2005). *Hapalopilus rutilans* is an older name than *H. nidulans*, and since both were sanctioned by Fries, the former has priority (ICBN Melbourne code art. 15.4).

Neither of the names has been typified. Persoon's original publication includes a rather uninformative painting of the fungus, probably *Hapalopilus rutilans* or *Inonotus*

sensu lato. The original description of *H. nidulans* is similarly scanty. No material suitable for lectotypification remains of either species, so we have chosen to designate neotypes for both species to fix the nomenclature: *H. rutilans* based on a French specimen from oak in accordance to the protologue (Persoon 1798) as Persoon got material mainly from Germany and France, and *H. nidulans* based on a Finnish specimen, since Fries (1821) based his description on his own collection from neighboring Sweden.

Ryvarden (1991) attempted to designate a lectotype for *H. nidulans*. We dispute his typification, since he used an illustration in Bulliard's publication from 1791 as the type, whereas Fries's original work does not refer to Bulliard. The fact that Fries later (1836-1838) referred to Bulliard doesn't make the drawing available for lectotypification: only the original material is valid under the code (ICBN Melbourne art. 9.2, 9.12).

Oxychaete Miettinen, gen. nov.

MycoBank 811534

Type species. Oxychaete cervinogilva (Jungh.) Miettinen

Etymology. Constructed from *Oxyporus* and *Phanerochaete*, but can be interpreted as "bearing sharp setae".

Description. Effused-reflexed polypores with yellow-brown colors, light cardboard-like consistency and large, shallow pores. Monomitic, simple-septate, with slightly thick-walled hyphae and abundant subulate, naked, thick-walled cystidia of subhymenial origin. Hymenial branching corymb-like. Spores curved cylindrical, large ($6-8\times3-3.5 \mu m$).

Remarks. Other hydnoid and poroid genera with simple-septate hyphae and encrusted, thick-walled cystidia include *Australohydnum*, *Phlebiopsis*, *Flavodon* and *Irpex*. The latter two are phylogenetically distantly related to *Oxychaete*, and they possess dimitic hyphal structure quite different from the loose monomitic structure of *Oxychaete*. *Phlebiopsis* is phylogenetically distinct from *Oxychaete* (Figure 2), and its hyphal structure is more compact, even agglutinated (basal layer). Hyphae are also winding and covered with abundant brownish encrustation, which is lacking in *Oxychaete*. Cystidia are tramal in origin (as opposed to hymenial in *Oxychaete*). Due to the hyphal structure the basidiocarp is tougher and not board-like when cut as in *Oxychaete*.

Australohydnum is a more difficult case to decide on since there are no good references on the microscopic characters of the type species, *Hydnum griseofuscescens* Reichardt from Australia. Descriptions vary so much that it is possible that many species and even genera have been recognized as *Australohydnum dregeanum* (Berk.) Hjortstam & Ryvarden and its supposed synonyms (Jülich 1978, Hjortstam and Ryvarden 1989, Gilbertson and Adaskaveg 1993, Melo and Hjortstam 2002, Zmitrovich et al. 2006). Sometimes the structure is monomitic, sometimes dimitic; cystidia may be subulate or obtuse; basidiocarps may be resupinate with smooth hymenophore or hydnoid with caps.

Reid (1955, 1963) refers directly to Australian material and the type, and provides an illustration (under *Irpex vellereus*). His *A. griseofuscescens* is a pileate, hydnoid species with violaceous brownish basidiocarps, very thick-walled, simple-septate hyphae 4–9 µm in diameter, and abundant long, obtuse, poorly differentiated cystidia with tramal origin and fine apical encrustation. Reid states that the hyphal structure is monomitic, but has also drawn long aseptate hyphae. Spores are ellipsoid, medium-sized. The description and illustrations provided by Melo and Hjortstam (2002) from Portugal are very similar to those of Reid, and agree largely with an Indian specimen we have studied.

Morphology suggests that *A. griseofuscescens* is not congeneric with *Oxychaete cervinogilva*, the latter being a polypore with regular pores, much looser hyphal structure without wide-spread encrustation, more regular and less-thick-walled hyphae, different type of cystidia with hymenial origin, differently shaped spores and lighter color of the basidiocarp.

Oxychaete cervinogilva (Jungh.) Miettinen, comb. nov.

MycoBank 811535 Figure 7

≡Polyporus cervinogilvus Jungh., Praemissa in floram cryptogamicam Javae insulae: 45 (1838).

Description. Basidiocarp half-resupinate to pileate, annual, upper surface felt-like, yellowish brown with a lighter margin, lower surface brownish yellow or light ochraceous, 1–2 mm thick, caps projecting up to 3 cm, can fuse to form wide fruiting bodies. Consistency light cardboard-like when dry, somewhat flexible but easy to break apart. Pores regular, thin-walled, mouths rather smooth, (1)2–3 per mm. Cap context and subiculum yellowish brown, homogenous, upper surface not differentiated, up to 1 mm thick. Cap with a sharp, 1 mm wide sterile margin.

Hyphal system monomitic, clamps absent. Hyphae homogenous throughout, mostly thick-walled, always with a wide lumen, rather stiff and straight, CB– to CB(+), IKI–, KOH–, CRB lilac. Encrustation absent except on cystidia. Subicular hyphae interwoven, loosely arranged, (3.2)4–5.4(7.5) µm in diameter, walls up to 1.5 µm thick, mostly ≤ 1 µm. Contextual hyphae mostly horizontally arranged but not strictly parallel, (3.8)4–5.1(5.5) µm in diameter. Tramal tissue loose and easy to study, hyphae rather straight, parallel in lower trama, subparallel and interwoven towards subiculum, (3)3.5–4.8(6.2) µm in diameter, walls mostly 0.8–1.2 µm thick. Subhymenial hyphae thin- to slightly thick-walled, richly branching mostly like a corymb, not much winding.

Cystidia abundant, hymenial, thick-walled, often with an apical crystal cap, $(15)20-40(55)\times4.5-9$, projecting 5–25 µm above hymenium.

Hymenium dominated by basidioles and cystidia, cells with constrictions especially in older basidiocarps. Basidia cylindrical to narrowly clavate, collapsing upon spore release and difficult to spot, with 4 sterigmata. Cystidioles absent.

Basidiospores cylindrical, curved, thin-walled, smooth, $(5.9)6-8.4(8.9)\times2.8-3.7(3.8)$ µm, L=6.93 µm, W=3.17 µm, Q'=(1.8)1.9-2.5(2.6), Q=2.19, CB-, IKI-, plasma stains in CB.



Figure 7. Microscopic characters of Oxychaete cervinogilvus, Schigel 5216, a subicular hyphae b tube trama and hymenium **c** hymenial cells **d** hymenial cystidia **e** spores.

Distribution. Tropical Asia and Australia (Ryvarden and Johansen 1980). Not common in Indonesia although described from there.

Ecology. Apparently prefers small-diameter dead wood of angiosperms. According to the description, the type was collected in a wet, shady forest in Javanese mountains. Australian collections we have seen are from drier localities (monsoon forest and city park).

Remarks. Junghuhn (1838) provides a good painting of the species (Tab. IX), available through Google books (https://books.google.fi/books?id=AFJUAAAAcAAJ).

Phanerina Miettinen, gen. nov. MycoBank 811536

Type species. Phanerina mellea (Berk. & Broome) Miettinen.

Description. Basidiocarps resupinate, yellow, fragile, pores shallow and large (1–4 per mm). Hyphal structure monomitic, simple-septate, loose, hyphae not swollen, wider (4–5 μ m in diameter) in subiculum, a bit narrower in trama (3–4 μ m). Hymenial branching corymb-like, subulate thin-walled cystidia present. Spores rather large (6–7×3 μ m), cylindrical to narrowly ellipsoid.

Remarks. This monotypic genus comes close to *Riopa* both morphologically and phylogenetically, though the two do not seem to form a monophyletic group (Figure 2). Morphological differences are summarized in Table 2.

Phanerina mellea (Berk. & Broome) Miettinen, comb. nov.

MycoBank 811537 Figures 1b and 8

≡Polyporus melleus Berk. & Broome, J. Linn. Soc., Bot. 14: 53 (1873).

Description. Basidiocarp resupinate, yellow, ranging from yellowish cream to brownish yellow, $1-10\times1-5$ cm patches, 1(2) mm thick. Consistency fragile when dry. Pores shallow, somewhat irregular, splitting and eventually may turn dentate, 2-4 per mm, larger when split. Subiculum cream-colored, a bit lighter than pore surface, pellicular, cottony under the lens, 0.1-0.3 mm. Margin thinning out, smooth areas of several millimeters similar to tube bottoms may be present.

Hyphal system monomitic, clamps absent. Hyphae cylindrical, not much swollen, branching in sharp angles, rather similar throughout the basidiocarp, CB– to CB(+), IKI–, KOH–, CRB lilac. Large crystal clumps mostly of rhomboidal shape present in trama. Subiculum loose, hyphae interwoven, slightly thick-walled to thick-walled when old, $(2)3-5(6.4) \mu m$ in diameter, walls mostly <0.5 μm thick, up to 1.2 μm in old basidiocarps. Tramal hyphae subparallel, thin- to slightly thick-walled, $(2)3-3.8(4.8) \mu m$ in diameter. Subhymenium branching corymb-like, cells not sinuous, relatively easy to study.

Cystidia present but often rare, hymenial, thin-walled, subulate, rarely septate, naked, $40-80\times5.8-9.2 \ \mu m$, projecting $20-50 \ \mu m$.

Hymenium relatively loose. Basidia clavate, $15-26\times5.2-6.8$ µm, with 4 wide, spindle-shaped sterigmata, $4-4.8\times1.8$ µm.

Basidiospores cylindrical to narrowly ellipsoid, usually abundant, with thin but distinct walls, smooth, $(5.2)5.8-7.5(7.8)\times(2.8)2.9-3.8(4.4) \ \mu m$, L=6.55 μm , W=3.26 μm , Q'= (1.6)1.8-2.3(2.4), Q=2.01. Spore shape variation is rather large and abnormally broad ellipsoid spores can be present.

Distribution. Described from Sri Lanka. We can confirm it from East Africa (Tanzania, Kenya), Japan (Okinawa), and Indonesia (New Guinea). Sequences of Chinese specimens are also available in the INSDC.

Ecology. Grows on dead dicot trees, both standing and fallen, often in sun-exposed habitats.

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Figure 8. Microscopic characters of *Phanerina mellea*. **a** Subicular hyphae **b** tube trama **c** basidia, Miettinen 9134. Hymenial cystidia **d** Nuñez 503 **e** Ryvarden 10132. Spores **f** lectotype **g** Miettinen 9134 **h** Nuñez 503.

Remarks. East Asian, East African and New Guinean specimens have neither ITS sequence differences nor morphological differences, so we feel it is safe to assume that the type from Sri Lanka belongs to the same species. Morphologically the type specimen agrees very well with other material. Its spores are a little larger on average than in other specimens studied, but considering the large variability in size and shape of spores this is best interpreted as normal variance within species.

Phanerochaete P. Karst.

Bidrag till Kännedom av Finlands Natur och Folk 48: 426 (1889).

Type species. Phanerochaete alnea (Fr.) P. Karst.

Phanerochaete inflata (B.S. Jia & B.K. Cui) Miettinen, comb. nov. MycoBank 818689

≡Ceriporia inflata B.S. Jia & B.K. Cui, Mycotaxon 121: 306 (2012).

Remarks. We have chosen to apply the genus name *Phanerochaete* for most of the *Phanerochaete* clade, excluding the three polypore genera *Oxychaete*, *Phanerina* and *Riopa* (Figure 2). Morphologically, species in the *Phanerochaete* clade share microscopic characters such as simple-septate, relatively simple, loose hyphal structure, mid-sized hymenial cells, mid-sized straight cylindrical to narrow ellipsoid spores, and cystidia of subhymenial origin (Table 1 and 2). However, cystidia are rare and poorly differentiated or absent in three of the polypores (in the genera *Phanerina* and *Riopa*), and spores are distinctly curved in two species (*Riopa*). The third newly introduced polypore genus *Oxychaete* with its encrusted cystidia and large spores produces pileate and poroid basidiocarps. With the inclusion of these species, the genus *Phanerochaete* would become difficult to define morphologically.

Ceriporia inflata described by Jia and Cui (2012) belongs to Phanerochaetaceae with *P. raduloides* as the closest relative (Figure 2). The hymenophore of *C. inflata* is composed of irregular pores with lacerate mouths, and that of *P. raduloides* of irregular teeth. Also *Ceriporia jianxiensis* (no sequence available) described in the same paper as *Ceriporia inflata* may be closely related. Their identity against *P. capitata* and *P. aculeata* along with other species in the *P. raduloides* group should be checked.

For now we consider *Ceriporia inflata* a species of *Phanerochaete*. Splitting the hydnoidporoid *Phanerochaete* of this group into a separate genus (possibly *Phanerodontia* Hjortstam) would make it necessary to split *Phanerochaete* into many small genera and would place morphologically very similar corticioid species into separate genera. For this reason we strongly prefer a wide concept of *Phanerochaete* that includes the hydnoid and poroid members, which are microscopically very similar to *Phanerochaete* sensu typi. See Tables 1 and 2 for characterization of the genus against similar genera in the Phanerochaetaceae.

Hjortstam and Ryvarden (2010) described *Phanericium* and *Phanerodontia* for a few species placed traditionally in *Phanerochaete*. Their *Phanerodontia* includes four taxa with smooth to hydnoid hymenophores. *Phanerodontia* is probably a taxonomic synonym of *Phanerochaete*. Although the type, *P. dentata*, has not been sequenced, two other members of the genus have (*P. chrysosporium* and *P. magnoliae*). They clearly belong to *Phanerochaete*, and according to the *rpb1* dataset to the same subclade within the genus with smooth to poroid members (Figure 3). *Phanerodontia dentata* does not closely resemble any polypore genus discussed here (except *Phanerochaete*) with its combination of thin-walled tubular cystidia, long basidia, thick-walled subicular hyphae and ellipsoid spores.

Phanericium is a monotypic genus, and the type *P. subquercinum* is characterized by hydnoid, effused fruiting bodies, absence of cystidia, hyphae of even width throughout the fruiting body and broad ellipsoid spores. This set of characters does not closely match taxa discussed in detail in this paper, and more detailed study is needed to conclude whether the genus belongs to Phaerochaetaceae.

Phlebiopsis Jülich

Persoonia 10: 137 (1978).

Type species. Phlebiopsis gigantea (Fr.) Jülich.

Phlebiopsis brunneocystidiata (Sheng H. Wu) Miettinen, comb. nov. MycoBank 817923

≡Phanerochaete brunneocystidiata Sheng H. Wu, Mycotaxon 90: 423 (2004)

Phlebiopsis castanea (Lloyd) Miettinen & Spirin, comb. nov. MycoBank 817928

≡Irpex castaneus Lloyd, Mycological Writings 6 (65): 1060 (1920)

Phlebiopsis friesii (Lév.) Spirin & Miettinen, comb. nov.

MycoBank 817924

≡ Thelephora friesii Lév., Systematisches Verzeichnis der im indischen Archipel in den Jahren 1842–1848 gesammelten sowie aus Japan empfangenen Pflanzen (1854)

Phlebiopsis laxa (Sheng H. Wu) Miettinen, comb. nov.

MycoBank 817925

≡Phanerochaete laxa Sheng H. Wu, Botanical Bulletin of the Academia Sinica (Taipei) 41: 169 (2000)

Phlebiopsis papyrina (Mont.) Miettinen & Spirin, comb. nov.

MycoBank 817926

≡Stereum papyrinum Mont., Annales des Sciences Naturelles Botanique 17: 125 (1842)

Phlebiopsis pilatii (Parmasto) Spirin & Miettinen, comb. nov.

MycoBank 817927

≡Laeticorticium pilatii Parmasto, Eesti NSV Teaduste Akadeemia Toimetised 14(2): 228 (1965)

Remarks. *Phlebiopsis* is typified by *P. gigantea*, a phlebioid species with agglutinated lower subiculum, well-developed basal layer/upper subiculum, thick-walled, simple-septate hyphae and thick-walled, conical, encrusted cystidia (lamprocystidia). Our wider concept of *Phlebiopsis* dilutes this set of characters, but lamprocystidia, inter-woven subhymenium and tightly built subiculum remain as important characters for genus delimitation against similar genera of the Phanerochaetaceae (Table 1).

Hjortstamia crassa has been shown to be a close relative of *Phlebiopsis*, and has been included in that genus (Floudas and Hibbett 2015). We agree with this conclusion. The type species of *Hjortstamia* (*H. friesii*) has not been sequenced, but it is very similar to *H. crassa*. Thus *Hjortstamia* should for now be considered as a taxonomic synonym of *Phlebiopsis*. In addition to the above-mentioned *Hjortstamia* spp., a third similar species, *H. papyrina*, is combined to *Phlebiopsis* on morphological grounds.

The two main differences that have been emphasized to separate *Hjortstamia* from *Phlebiopsis* are reflexed basidiocarps and the loose subiculum of the former as opposed to the dense, agglutinated subiculum and totally effused basidiocarps of the latter. A closer look reveals that the difference is not as striking as often described. Whereas the genus type of *Hjortstamia* — *H. friesii* — and its close relative *H. papyrina* are distinctly pileate, basidiocarps of *Hjortstamia crassa* are much of the time fully resupinate or caps are small. *Hjortstamia crassa* also has an agglutinated upper subiculum or basal layer similar to agglutinated *Phlebiopsis* structures, as depicted by Wu and Chen (1992). *Hjortstamia friesii* has a tight (though not agglutinated) subicular layer composed of parallel hyphae as well (Hjortstam and Ryvarden 1989, Boidin and Gilles 2002). Subicular/cystidial hyphae of the above-mentioned species are strikingly similar, thick-walled, straight, stiff and sparsely septate.

A loose subiculum or pileate fruiting bodies do not seem to be useful characters separating *Hjortstamia* from *Phlebiopsis*, since loose and agglutinated species are widely intermixed phylogenetically within *Phlebiopsis* sensu lato (Figure 2). *Hjortstamia crassa* for instance is more closely related to the type species of *Phlebiopsis* than is *Phlebiopsis* flavidoalba with a very dense structure and effused fruiting bodies.

Sequences made available by Wu et al. (2010) include *Phanerochaete brunneocystidiata* and *Phanerochaete laxa*. The former is based on a paratype and the latter on the holotype. Wu combined the species in *Hjortstamia* due to sequence similarity to *H. crassa*. We haven't seen authentic material, but according to original descriptions, they seem to share basic *Phlebiopsis* characters except that no agglutinated layer was described (Wu 2000, 2004).

Some *Phlebiopsis* species may turn out to belong to the *Hapalopilus-Rhizochaete* subclade instead of the *Phlebiopsis* subclade. For instance *Phlebiopsis* roumeguerei is nested within *Phaeophlebiopsis* as defined by Floudas and Hibbett (2015). More indepth research is needed to settle genus classification for *Rhizochaete* and *Phaeophlebiopsis*-like taxa.

Riopa D. A. Reid

Revue Mycol., Paris 33: 244 (1969).

Type species. *Riopa davidii* D. A. Reid (*=Riopa metamorphosa* (Fuckel) Miettinen & Spirin).

Description. White, resupinate polypores with shallow pores, 2–5 per mm. Hyphal structure monomitic, clamps absent. Hyphae thin- to slightly thick-walled, similar throughout the basidiocarp, hyphae not swollen, wider (3–5 μ m in diameter) in subiculum, a bit narrower in trama (2.8–3.5 μ m). Hymenial branching corymb-like. Thin-walled, poorly differentiated hymenial cystidia and conidia in one species. Spores curved cylindrical, sausage-like, thin-walled, mid-sized (4.5–6.5×2–3 μ m).

Remarks. Reid (1969) described *Riopa* as a monotypic genus with *Riopa davidii* D. A. Reid from Corsica as the sole species. Ryvarden (1991) considered *R. davidii* as a synonym of *Ceriporia camaresiana* (Bourdot & Galzin) Bondartsev & Singer, in effect making *Riopa* a synonym of *Ceriporia*. Pieri and Rivoire (1997) regarded *Riopa davidii* and *Ceriporia camaresiana* as separate species, and made the combination *Ceriporia davidii*. Their concept of the species was mixed, as can be seen already from the spore variation they report. Their specimens from mainland France did seem to represent a species of *Ceriporia* separate from *C. camaresiana*, and consequently *Ceriporia davidii* was adopted by Bernicchia (2005) and Ryvarden and Melo (2014).

We studied the type of *Riopa davidii*, and it turned out to be a more recent synonym for *Ceriporia metamorphosa* (Fuckel) Ryvarden & Gilb. After studying the French material of *Ceriporia davidii* collected by B. Rivoire, we could also conclude that *Ceriporia davidii* sensu Pieri and Rivoire (1997) needs to be described with a new name (*Ceriporia pierii*). *Ceriporia pierii* and also *C. camaresiana* belong to the *Ceriporia* clade and are only distantly related to *Riopa* (Figure 2).

Riopa metamorphosa (Fuckel) Miettinen & Spirin, comb. nov. MycoBank 811538 Figures 1d and 9

≡Polyporus metamorphosus Fuckel, Jb. Nassau Ver. Naturk. 27–28: 87 (1874) ['1873–74'].

Lectotype. Germany. Oestrich (Nassau): Mittelheimer Vorderwald, rotten trunk of *Quercus*, "Herbier Fuckel 1894, Herbier Barbey-Boissier", no. 2008 (S F43290, designated here).

Epitype. Czech Republic. Moravia: Lanžhot, Ranšpurk virgin forest, rotten trunk of *Quercus robur*, 5 Oct 1988 Pouzar (PRM871894, designated here, duplicate H 7008579).

Description. Basidiocarp resupinate, white, cream or straw-colored, consistency fragile when dry. Forms patches of a few cm that can fuse to extensive basidiocarps, up to 2(-3) mm thick. Pores rounded angular, soon splitting and then irregular and sinuous, mouths smooth, 2–3(4) per mm, up to 2 mm wide when split. Subiculum very thin, arachnoid to



Figure 9. Microscopic characters of *Riopa. Riopa metamorphosa*, epitype: **a** subicular hyphae **b** tube trama and hymenium **c** anamorph (*Sporotrichum aurantiacum*) **d** basidioles and basidia showing the characteristic corymb branching **e** hymenial cystidia. Spores of **f** *Riopa metamorphosa* drawn from the holotype of *R. davidii* **g** epitype of *R. metamorphosa* **h** holotype of *R. pudens*.

pellicular, white to cream, often lighter than pores. Margin thinning out, usually no sterile margin.

Hyphal system monomitic, simple septate, hyphae rather homogenous throughout. Subicular hyphae interwoven, tissue loose, hyphae thin-walled to slightly thick-walled, $(2.8)3.2-4.4(6.4) \mu m$, walls rarely up to 1 μm in diameter. Tramal hyphae thin- to slightly thick-walled, interwoven but mostly vertically arranged, $(2.2)2.9-3.5(4.0) \mu m$ in diameter. Subhymenium relatively loose, structure uncharacteristically simple for a polypore, composed of branching corymb-like, straight hyphae similar to those in trama. Crystals present as irregular aggregates of rhomboidal plates of various sizes, also fine encrustation present in subiculum. Shiny, hyaline, amorphous droplets floating around in CB.

Cystidia thin-walled, cylindrical, projecting above hymenial layer $5-20 \mu m$, often covered with spores, $(15)20-50\times4-6.2 \mu m$, born in subhymenium, poorly differentiated, appear as elongated basidioles, rare.

Hymenium loosely arranged, cells thin-walled. Basidia clavate, often projecting slightly above the rest of the hymenium, $15-28(35)\times4-5.5(6.2)$ µm, with 4 sterigmata.

Basidiospores curved cylindrical, thin-walled, $(4.2)5-6.6(8.2)\times(2)2.2-3.1(3.5)$ µm, L=5.69 µm, W=2.59 µm, Q=2.19.

Anamorph known as *Sporotrichum aurantiacum* Link present or absent. Most but not all basidiocarps produce at least conidia in subiculum. When the anamorphic stage is well developed, it appears as an orange mass of conidia similar in shape to *Haplotrichum aureum*, in conjunction with basidiocarps or separately. Microscopically composed of thick-walled, ellipsoid to constricted conidia (8.2–12.2×5.2–7.8 µm, n=36/3) born singly as apical parts of slightly to clearly thick-walled, partly encrusted hyphae, (3.2)3.6–4.5(7.2) µm in diameter, walls ≤1.5 µm. The conidia and hyphae are yellow, the plasma of the conidia stains in CB, and the walls are CB– to CB(+) and slightly dextrinoid. In KOH the conidia stain pinkish red in masses. Wakefield (1952) proved in the lab that the polypore and conidial stages belong to the same organism.

Distribution. Temperate Europe: Germany, Poland, Slovakia, Czech Republic, Russia (Nizhny Novgorod), France (mainland, Corsica) (Vampola and Pouzar 1996, Pieri and Rivoire 1997). Northernmost records from Southern Norway (Ryvarden and Melo 2014) and Stockholm, Sweden (Romell 1926).

Ecology. Grows preferably on rotten oak trunks. We have seen it on *Eucalyptus* and *Salix caprea*, also reported on *Castanea*, *Juglands* and *Malus* (Bourdot and Galzin 1928, Ryvarden and Gilbertson 1993, Pieri and Rivoire 1997).

Remarks. Fuckel's herbarium is in Wiesbaden (WIES), but its material is not available for loan. A duplicate of an original Fuckel specimen in Stockholm is chosen as the lectotype here. It represents an almost completely destroyed anamorphic stage. For practical reasons we also select an epitype from the Czech Republic.

Conidia have been reported from few other members of the Phanerochaetaceae: *Phanerochaete chrysosporium* (Burdsall and Eslyn 1974) and *Hyphodermella rosae* (Rahimlou et al. 2015). *Riopa metamorphosa* conidia are similar to the conidia of these species, particularly *Hyphodermella rosae*.

Riopa pudens Miettinen, sp. nov.

MycoBank 811539 Figure 9h

Holotype. Indonesia. Riau: Indragiri Hulu, Bukit Aluran Babi, -0.838: 102.226, selectively logged forest slope, piece of a dicot log (15 cm in diameter, decay stage 2–4/5), 1 Jul 2004, Miettinen 8772 (ANDA, isotype H 7008582).

Etymology. Pudens (adj., L), shy, modest, refers to the scarcity of distinct characters.

Description. Basidiocarp resupinate, annual, cream, young parts white, up to half a meter wide, up to 4 mm thick. Consistency resistant to breaking but not tough. Pores thin-walled, mouths finely dentate, splitting when older, angular, 4–5 mm, 2–3 per mm when split/fused, 0.5–1.2 mm long. Subiculum white, 0.1–0.4 mm thick. Margin thinning out.

Hyphal system monomitic, clamps absent. Hyphae not swollen, rather similar in all parts. Subicular tissue loose, hyphae interwoven, thin- to thick-walled, mostly slightly thick-walled, (2.8)3.4-4.8(6.2) µm in diameter, walls rarely up to 1 µm thick. Tramal hyphae vertical, subparallel to interwoven, only moderately winding, thin-walled or slightly

thick-walled, (2.4)2.8-3.2(4.2) µm in diameter. Shiny hyaline resin droplets floating around, fine-grained crystalline-amorphous substance glued on tramal hyphae in CB.

Cystidia not seen.

Hymenium relatively loosely arranged, basidia very thin-walled, collapsing soon, basidioles $10-14\times3-4.2 \ \mu m$.

Basidiospores curved cylindrical, thin-walled, $(4.2)4.3-5.6(6.2)\times(1.8)1.9-2.2(2.3) \ \mu\text{m}$, L=5.01 μm , W=2.08 μm , Q=2.41.

Distribution. Southeast Asia. Known from Riau, Sumatra and Fujian, China (the INSDC sequence JX623931, Cui 3238, '*Ceriporia camaresiana*').

Ecology. Grows on fairly rotten angiosperm wood. The type comes from low-land rainforest.

Remarks. The species lacks any distinct characters. Cream-colored basidiocarp with non-inflated hyphae and corymb-subhymenium help to distinguish this species from *Ceriporia* spp. It is similar to *Phanerochaete inflata* and *Ceriporia jianxiensis*, but differs in having long-celled, narrower subicular hyphae (mostly <5 µm in diameter). The relatively small cylindrical curved spores exclude *Oxyporus* spp. and *Emmia* spp. Except for the smaller pores and the lack of cystidia and a conidial stage it is very similar to *Riopa metamorphosa*.

Sporotrichum Link

Magazin der Gesellschaft Naturforschenden Freunde Berlin 3(1): 12 (1809).

Type species. *Sporotrichum aureum* Link (= *Riopa metamorphosa* (Fuckel) Miettinen & Spirin)

Remarks. Hughes (1958) lectotypified the genus with *S. aureum*. The original description of *S. aureum* does not permit accurate identification of the fungus in question, and no type seems to exist (Stalpers 1984). Fries (1932) considered *S. aureum* a synonym of *Trichoderma aurantiacum* Pers. 1796 (*=Sporotrichum aurantiacum* (Pers.) Fr). In his monograph of *Sporotrichum* Stalpers (1984) chose to follow Fries. He also considered *S. aureum* as an anamorphic stage of *Riopa metamorphosa*.

To formally settle the names *Sporotrichum*, *S. aureus* and *S. aurantiacum* we need to designate neotypes for the two species in question. In line with Stalper's interpretation, we designate here the collection Vlasák 0511/15 (H 7008577) as the neotype of *S. aureum* Link, and collection Spirin 2456 (H 7029505) as the neotype of *S. aurantiacum*.

This makes *Sporotrichum* an older name available for *Riopa* under the ICBN Melbourne code article 59.1. However, adoption of *Sporotrichum*, traditionally a very heterogeneous set of anamorphs, for a small genus of polypores would only create confusion. Stalpers (1984) described the genus as a "litterbag" of conidiogenous fungi, and accepted only three species. According to him the teleomorphs of those three species are in separate genera (*Laetiporus*, *Phanerochaete* and *Pycnoporellus*/*Riopa*) that we now know are phylogenetically distinct. Although the type species *Riopa* produces an anamorph, we have seen no conidia in the other species of the genus (*R. pudens*). In this situation it is better to coin *Riopa*, a name without identity problems, for this polypore genus. We suggest conservation of the teleomorphic name *Riopa* D. A. Reid 1968 over the anamorphic *Sporotrichum* Link 1809.

Key to genera of Phanerochaetaceae

| 1 | Hyphae always with clamps2 |
|---|--|
| _ | Hyphae mostly with simple septa11 |
| 2 | Hymenophore with regular pores |
| _ | Hymenophore smooth, hydnoid or dentate4 |
| 3 | Basidiocarps ochre yellow in color throughout, with abundant granular, |
| | golden pigment when under microscope, purple in KOH Hapalopilus |
| _ | Basidiocarps whitish to grey, no granular pigment |
| 4 | Distinctly hydnoid or dentate hymenophore |
| _ | Smooth hymenophore, more or less |
| 5 | Basidiocarps pileate, spines regular conicalDonkia |
| _ | Basidiocarps resupinate, spines irregular, dentate Pirex |
| 6 | Dendrohyphidia, blue colors |
| _ | No dendrohyphidia7 |
| 7 | Thick-walled, encrusted cystidia present |
| _ | Cystidia absent or thin-walled10 |
| 8 | Basidiocarps pileate, encrusted cystidia deep-rooted, brownPorostereum |
| _ | Basidiocarps resupinate, cystidia more or less hyaline, not deep rooted9 |
| 9 | Tissue dense throughout, no rhizomorphs Phlebia unica |
| _ | Tissue loose thizomorphs present Rhizochaete |
| _ | 1 issue ioose, imzonioipiis present |
| 10 | Tissue dense throughout |
| 10 | Tissue loose, inizoniorphis presenter Tissue dense throughout |
| 10 - 11 | Tissue dense throughout |
| 10 11 | Tissue loose, inizoniorphis presentation Phlebia spp. Tissue loose Phlebia spp. Tissue loose Rhizochaete (incl. Ceraceomyces spp.) Poroid species 12 Smooth or hydnoid species 17 |
| 10 11 12 | Tissue loose, inizoniorphis presentation Tissue dense throughout |
| 10 - 11 - 12 - | Tissue loose, mizorinorphis presentation Phlebia spp. Tissue loose Phlebia spp. Tissue loose 12 Smooth or hydnoid species 12 Sasidiocarps with encrusted, thick-walled subulate cystidia. 13 Cystidia thin-walled and naked or lacking 14 |
| 10 11 12 13 | Tissue loose, mizorinorphis presentation Philebia spp. Tissue loose throughout |
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| 10 - 11 - 12 - 13 - 14 - 15 - | Tissue loose, fillboniorphs presentation Phlebia spp. Tissue loose Phizochaete (incl. Ceraceomyces spp.) Poroid species 12 Smooth or hydnoid species 17 Basidiocarps with encrusted, thick-walled subulate cystidia 13 Cystidia thin-walled and naked or lacking 14 Hyphal structure loose, basidiocarps pileate Oxychaete Hyphal structure dense, basidiocarps resupinate Phlebiopsis Basidiocarp with thick-walled conidia and often orange, anamorphic regions 15 Basidiocarp yellow, tramal tissue relatively dense Phanerina Basidiocarps whitish to buff, tramal tissue loose 16 |
| $ \begin{array}{c} - \\ 10 \\ - \\ 11 \\ - \\ 12 \\ - \\ 13 \\ - \\ 14 \\ - \\ 15 \\ - \\ 16 \\ \end{array} $ | Tissue loose, mizorinorphs presentation Tissue dense throughout |
| $ \begin{array}{c} - \\ 10 \\ - \\ 11 \\ - \\ 12 \\ - \\ 13 \\ - \\ 14 \\ - \\ 15 \\ - \\ 16 \\ \end{array} $ | Tissue loose, fillbolioppis presentation Philebia spp. Tissue loose Philebia spp. Tissue loose 12 Smooth or hydnoid species 17 Basidiocarps with encrusted, thick-walled subulate cystidia. 13 Cystidia thin-walled and naked or lacking 14 Hyphal structure loose, basidiocarps pileate Oxychaete Hyphal structure dense, basidiocarps resupinate Philebiopsis Basidiocarp with thick-walled conidia and often orange, anamorphic regions 15 Basidiocarp yellow, tramal tissue relatively dense Phanerina Basidiocarps whitish to buff, tramal tissue loose 16 Subicular hyphae regularly >5 µm in diameter, looking slightly inflated Phanerochaete |
| $ \begin{array}{c} 10 \\ - \\ 11 \\ - \\ 12 \\ - \\ 13 \\ - \\ 14 \\ - \\ 15 \\ - \\ 16 \\ - \\ - \\ - \\ - \\ 16 \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ -$ | Tissue loose, innompris presentation Phlebia spp. Tissue loose Phlebia spp. Tissue loose 12 Smooth or hydnoid species 12 Smooth or hydnoid species 17 Basidiocarps with encrusted, thick-walled subulate cystidia 13 Cystidia thin-walled and naked or lacking 14 Hyphal structure loose, basidiocarps pileate Oxychaete Hyphal structure dense, basidiocarps resupinate Phlebiopsis Basidiocarp with thick-walled conidia and often orange, anamorphic regions 15 Basidiocarp yellow, tramal tissue relatively dense Phanerophosa No conidia attached to basidiocarps, no separate anamorphic stage 16 Subicular hyphae regularly >5 µm in diameter, looking slightly inflated Phanerochaete Subicular hyphae mostly <5 µm in diameter, cylindrical |
| $ \begin{array}{c} 10 \\ - \\ 11 \\ - \\ 12 \\ - \\ 13 \\ - \\ 14 \\ - \\ 15 \\ - \\ 16 \\ - \\ 17 \\ \end{array} $ | Tissue loose, fillboliophis presentation Phlebia spp. Tissue loose Phizochaete (incl. Ceraceomyces spp.) Poroid species 12 Smooth or hydnoid species 17 Basidiocarps with encrusted, thick-walled subulate cystidia 13 Cystidia thin-walled and naked or lacking 14 Hyphal structure loose, basidiocarps pileate Oxychaete Hyphal structure dense, basidiocarps resupinate Phlebiopsis Basidiocarp with thick-walled conidia and often orange, anamorphic regions |

| 18 | Spines small, their apices composed of heavily encrusted, cystidia-like hyphal |
|----|--|
| | endings |
| _ | Spines not apically heavily encrusted Phanerochaete |
| 19 | Tissue dense at least basally, subhymenium dense with no corymb-type |
| | branching, no rhizomorphs, cystidia very thick-walled, heavily encrusted |
| | (lamprocystidia) Phlebiopsis or Phaeophlebiopsis |
| _ | Subicular tissue loose, subhymenium dense or loose corymb-type, rhizo- |
| | morphs often present, thick-walled encrusted cystidia present or absent 20 |
| 20 | Subhymenium of the corymb-type, loose, rhizomorphs present or absent, no |
| | species with very thick-walled, heavily encrusted cystidia Phanerochaete |
| _ | Subhymenial hyphae irregularly interwoven, basidiocarps pellicular, rhizo- |
| | morphs always present, cystidia if present thick-walled, heavily encrusted, |
| | conical Rhizochaete (see also Phlebiopsis brunneocystidiata, P. laxa) |
| | |

Ceriporia pierii –group (Irpicaceae)

Ceriporia pierii and four closely related species described below seem to form a subclade of the large *Ceriporia – Leptoporus* clade (Figure 2). In morphological terms, the *C. pierii* group encompasses species with pale colored (white, pale pink or pale ochraceous), minutely rhizomorphic basidiocarps (Figure 10), and cylindrical to ellipsoid basidiospores normally exceeding 2 μ m in width. In addition, fan-like crystal aggregations occur among hyphae (Figure 11g), and subicular hyphae are considerably wider than tramal and subhymenial ones. The latter feature is not unique for the *C. pierii* group but is found for instance in the genus type *C. viridans* and its closest relatives.

The *C. viridans* group is not very closely related to *C. pierii* and its sibling species (Figure 2), although morphological differences are very subtle. In the *Ceriporia viridans* complex the basidiospores are curved and mostly cylindrical, less than 2 μ m in width (except *C. excelsa*), and hyphae possess more or less thickened walls (hyphal walls are thin in the *C. pierii* group). The *C. purpurea* and *C. spissa* species complexes have much brighter, red-colored basidiocarps, cylindrical spores, and hyphae of more or less equal diameter throughout the basidiocarp.

Morphologically species in the *C. pierii* group are very similar to each other, pore and spore characters being the most useful for identification (Table 4). ITS sequence differences are clear, 3.2–10.6% between species. Below is a general description for species in this group.

Description. Basidiocarps annual, resupinate, very thin (below 1 mm), 1–20 cm wide. Sterile margin byssoid, white to cream-colored, producing thin, white rhizomorphs (in all species but not all specimens). Pore surface pale-colored (white-yellow-pale ochraceous), pores shallow, uneven, angular, partly fusing together and even irpicoid, 2–6 per mm. Dissepiments mostly thin, wavy to dentate. Subiculum byssoid, white, very thin (up to 0.1 mm). **Hyphal system** monomitic, simple-septate. Subicular hyphae thin- to moderately thick-walled, branched at sharp angles, producing abundant H-like connections, always wider than

| Species | Distribution | Color of dry basidiocarps | Pores per mm | Basidiospores L×W |
|---------------|------------------------------------|-------------------------------------|-----------------|---|
| C. humilis | temperate Eurasia | white to cream-colored | 5–6 | narrowly ellipsoid to cylindrical 3.8×2.1 μm |
| C. mpurii | New Guinea | cream-colored to pale gray | 5–6 | ellipsoid to narrowly ellipsoid 3.4×2.2 μm |
| C. pierii | temperate Europe | cream-colored to rosy | 2–3 | ellipsoid to narrowly ellipsoid 4.7×2.8 μm |
| C. sericea | temperate East Asia | cream-colored to pale ochraceous | 3–5 | thick cylindrical 4.3×2.4 μm |
| C. sordescens | temperate Eastern North America | yellowish to dirty ochraceous | 3-4 | ellipsoid to narrowly ellipsoid 3.6×2.2 μm |

Table 4. Comparison of species in the *Ceriporia pierii* group.

tramal hyphae, 4–14 μ m in diameter, with rare clamps. Tramal hyphae parallel, with thin or a bit thickened walls, some with H-connections, 2.6–5.3 μ m in diameter. Crystals abundant among or on subicular/tramal hyphae, fan- or star-shaped, up to 20–30 μ m in the widest dimension. Resinous, hyaline or yellowish matter present as small droplets among tramal hyphae. Subhymenial hyphae vertically arranged, short-celled, thin-walled, branched at sharp angles, 2.5–4.5 in diameter. Dissepiment edges sterile, consisting of tramal hyphal ends.

Cystidia absent.

Hymenium. Basidia clavate, 4-spored, 8.5–19×3.5–5.5 μm.

Basidiospores thin-walled, hyaline, thick-cylindrical to ellipsoid, about $3-5.5\times2-3$ µm. **Ecology.** All the species produce basidiocarps on rotten, white-rot angiosperm wood.

Ceriporia humilis Spirin & Miettinen, sp. nov.

MycoBank 811540 Figures 10b and 11a

Holotype. Russia. Nizhny Novgorod: Lukoyanov Dist., Sanki, *Quercus robur*, 14 Jul 2012, Spirin 4706 (H).

Etymology. *Humilis* (Lat.), simple, shy; refers to basidiocarps devoid of good characters.

Description. Basidiocarp 0.1–0.2 mm thick. Pore surface white to cream-colored, pores 5–6 per mm. Sterile margin narrow (up to 0.5 mm wide). Subicular hyphae irregularly arranged to subparallel, 4–8.3 μ m in diameter. Tramal hyphae 4.1–5.3 μ m in diameter. Subhymenial hyphae 3–4.7 μ m in diameter. Basidia 9.2–13.3×4.2–5.1 μ m. Basidiospores narrowly ellipsoid to cylindrical, ventral side flat, rarely concave, (3.1)3.2–4.2(5.0)×(1.8)1.9–2.2(2.3) μ m, L=3.78 μ m, W=2.09 μ m, Q=1.81.

Remarks. *Ceriporia humilis* produces rather large basidiocarps with rhizomorphs at the marginal area or in the substrate. The type specimen was collected from a fallen oak log in Nizhny Novgorod Region, European part of Russia. Another, much older collection derives from Helsinki, Finland (HFR009978, a fallen log of *Acer*)



Figure 10. Fruiting bodies of species in the *Ceriporia pierii* group. **a** *Ceriporia mpurii*, holotype **b** *Ceriporia humilis*, holotype **c** *Ceriporia sordescens*, holotype. Photos taken in the field.



Figure 11. Microscopic characters in the *Ceriporia pierii* group. Spores of **a** *C. humilis*, holotype **b** *C. mpurii*, holotype **c** *C. pierii*, holotype **d** *C. pierii*, Rivoire 2378 **e** *C. sericea*, holotype **f** *C. sordescens*, holotype **g** Fan-shaped and rhomboidal crystals characteristic for the *C. pierii* group in *C. mpurii*, holotype. Hyphal structures of *C. pierii*, holotype: **h** subicular hyphae **i** tramal hypha **j** hymenial cells.

platanoides). One sequence of *C. viridans* in the INSDC from Shanxi, China belongs to *C. humilis* (KC182775, Dai 7642) showing that the species is present in East Asia, too. *Ceriporia humilis* has the narrowest spores in the whole species complex.

Ceriporia mpurii Miettinen & Spirin, sp. nov.

MycoBank 811541 Figures 10a and 11b, g

Holotype. Indonesia. Papua Barat: Saukorem, Minjanbiat, -0.5755°: 133.1447°, lowland primary forest, fallen trunk of *Spondias* (40 cm in diameter, decay stage 4/5), 3 Nov 2010, Miettinen 14381 (H, ANDA, MKW).

Etymology. Named after mpur, the people and language spoken around the type locality.

Description. Basidiocarp 0.1–0.2 mm thick, up to 10 cm in the widest dimension. Pore surface cream-colored, in older parts with light gray hues, pores 5–6 per mm. Sterile margin narrow (up to 0.5 mm wide). Subicular hyphae irregularly arranged, 4.8–12.7 μ m in diameter. Tramal hyphae 3.2–4.8 μ m in diameter, in older parts glued together. Subhymenial hyphae 3–4 μ m in diameter. Basidia 8.7–11.2×3.9–5.3 μ m. Basidiospores ellipsoid to narrowly ellipsoid, ventral side mostly flat, very rarely slightly convex, (2.7)2.8–3.9(4.2)×2–2.3(2.4) μ m, L=3.35 μ m, W=2.15 μ m, Q=1.55.

Remarks. *Ceriporia mpurii* is very similar to *C. humilis* (see above), differing in slightly darker color of the basidiocarps and a bit rounder spores. Moreover, hyphae in older parts of tubes are densely arranged and glued together, while they are loosely arranged in *C. humilis. Ceriporia mpurii* is known so far from its type locality in New Guinea.

Ceriporia pierii Rivoire, Miettinen & Spirin, sp. nov.

MycoBank 811542 Figure 11

Holotype. France. Rhône-Alpes: Vernaison, *Populus nigra*, 24 Sep 1995, Rivoire 1161 (H, LY).

Etymology. Named after Max Pieri, who with Bernard Rivoire first discovered this species.

Description. Basidiocarp 0.2–1 mm thick, 1–4 cm in the widest dimension. Sterile margin narrow (up to 1 mm wide). Pore surface cream-colored to rosy, in well-developed basidiocarps with apricot tints, pores 2–3(4) per mm, dissepiments mostly entire. Subicular hyphae more or less parallel to substrate, (5)5.1–8.2(9.1) μ m in diameter; a few hyphae bearing incomplete clamps or inflated portions. Tramal hyphae 4–5.2 μ m in diameter. Subhymenial hyphae 2.9–4 μ m in diameter. Basidia 13.8–19.3×4.4–5.2 μ m. Basidiospores ellipsoid to rarely cylindrical, ventral side flat or slightly concave, (3.9)4.1–5.4(6.1)×2.4–3.1(3.2) μ m, L=4.72 μ m, W=2.77 μ m, Q=1.70.

Remarks. Ceriporia pierii is introduced here to encompass C. davidii sensu Pieri and Rivoire (1997). Pieri and Rivoire identified C. camaresiana (Bourdot & Galzin) Bondartsev & Singer as the most similar species to C. pierii, but our data show that the two are not closely related (Figure 2). Basidiospores of C. camaresiana are clearly curved, mostly bean-shaped and longer, $5.26 \times 2.74 \mu m$ (Table 5). Moreover, the hy-

| C | Turral | т | W7: 1.1 | W/ | O' | 0 | |
|---|-------------------|-----------|-------------------|------|---------------------|------|------------|
| Species | Length | L F OC | | W | Q | | n 20 |
| Ceriporia camaresiana | (4.6)4./-6.2 | 5.20 | 2.4-3.0(3.1) | 2./4 | 1./-2.2(2.4) | 1.92 | 30 (0/2 |
| Ceriporia numuis | (3.1)3.2-4.2(3.0) | 3./8 | (1.8)1.9-2.2(2.3) | 2.09 | 1.5-2.1(2.5) | 1.01 | 20 |
| | (3.4)3.3-4.2 | 3.92 | (1.8)1.9-2.2(2.3) | 2.05 | (1.6)1./-2.1(2.3) | 1.91 | 30 |
| Kujala HFR009978 | (3.1)3.2-4.2(3.0) | 3.05 | 2.0-2.5 | 2.15 | 1.5-2.0(2.5) | 1./1 | 50 |
| Ceriporia mpurii | (2./)2.8-3.9(4.2) | 3.35 | 2.0-2.3(2.4) | 2.15 | (1.3)1.4-1.8 | 1.55 | 50 |
| Ceriporia pierii | (3.9)4.1-5.4(0.1) | 4./Z | 2.4-3.1(3.2) | 2.// | (1.4)1.5-2.0(2.3) | 1./0 | 90/3 |
| holotype | (3.9)4.1-5.2(5.3) | 4.65 | 2.6-3.1(3.2) | 2.83 | (1.4)1.5 - 1.8(1.9) | 1.64 | 30 |
| Rivoire 1822 | 4.1-5.2(5.3) | 4.56 | 2.4-3.1(3.2) | 2./3 | 1.5-1.8(1.9) | 1.6/ | 30 |
| Rivoire 23/8 | (4.0)4.2-5./(6.1) | 4.94 | 2.4-3.1(3.2) | 2./4 | (1.5)1.6-2.3 | 1.81 | 30 |
| Ceriporia sericea | (3.8)3.9-4.8(5.2) | 4.32 | (2.1)2.2–2.7 | 2.38 | (1.5)1.6-2.1 | 1.82 | 30 |
| Ceriporia sordescens | (3.2)3.3-4.2(4.6) | 3.61 | (2.0)2.1-2.5(2.6) | 2.24 | 1.4-1.8 | 1.61 | 30 |
| Hapalopilus eupatorii | (3.3)3.4-4.5(5.2) | 3.96 | (2.2)2.4-3.1(3.2) | 2.75 | (1.2)1.3–1.6(1.9) | 1.44 | 91/2 |
| holotype | 3.3-4.5(4.8) | 4.00 | (2.2)2.3–3.1(3.2) | 2.80 | (1.2)1.3–1.6(1.7) | 1.43 | 60 |
| holotype of <i>Ceriporiopsis</i> herbicola | (3.5)3.6-4.5(5.2) | 3.89 | 2.4–2.9 | 2.65 | 1.4-1.7(1.9) | 1.47 | 31 |
| Hapalopilus percoctus | (3.7)3.8-4.6 | 4.11 | (2.7)2.8-3.3 | 2.98 | 1.3-1.5(1.6) | 1.38 | 30 |
| Hapalopilus ribicola | (3.9)4.0-5.0(5.2) | 4.36 | (2.2)2.3-3.0(3.3) | 2.66 | (1.4)1.5-1.9(2.0) | 1.64 | 90/3 |
| lectotype | (4.0)4.1–5.0(5.1) | 4.37 | 2.2–3.0 | 2.55 | 1.5-1.9(2.0) | 1.71 | 30 |
| Alanko 145112 | 4.0-5.1(5.2) | 4.43 | (2.3)2.4-3.1(3.3) | 2.76 | (1.4)1.5-1.8(1.9) | 1.60 | 30 |
| Eriksson 1201 | (3.9)4.0-4.8(5.0) | 4.29 | (2.3)2.4-3.0(3.1) | 2.67 | 1.5–1.7 | 1.61 | 30 |
| Hapalopilus rutilans | (3.1)3.2–5.1(5.8) | 4.00 | (1.9)2.0-2.7(3.1) | 2.30 | (1.3)1.5-2.1(2.4) | 1.74 | 400/13 |
| neotype | 3.4-4.6(4.9) | 4.00 | (2.1)2.2–2.6(2.7) | 2.37 | 1.4-1.9(2.0) | 1.69 | 40 |
| Haikonen 19509 | (3.4)3.5-4.6(4.8) | 4.00 | 1.9-2.4(2.6) | 2.14 | (1.6)1.7-2.1(2.2) | 1.87 | 30 |
| Haikonen 26561 | 3.1-4.2(4.3) | 3.59 | 1.9-2.4(2.5) | 2.18 | 1.4-2.0(2.1) | 1.65 | 30 |
| Kotiranta 18819 | (3.4)3.5-4.2(4.3) | 3.79 | 1.9-2.2(2.3) | 2.09 | 1.6-2.1 | 1.81 | 30 |
| Miettinen 14427 | (3.8)3.9–5.3 | 4.50 | 2.0-2.4 | 2.20 | (1.6)1.7–2.4 | 2.05 | 30 |
| Miettinen 15793 | (3.2)3.3-4.2(4.8) | 3.72 | 1.9–2.3 | 2.12 | 1.5-2.2 | 1.76 | 30 |
| Niemelä 6749 | (3.8)3.9-4.6(5.7) | 4.29 | 2.3-2.7(2.8) | 2.52 | 1.5-1.9(2.2) | 1.70 | 30 |
| Niemelä 7134 | (3.1)3.2-4.2(4.3) | 3.52 | 2.0-2.4(2.5) | 2.20 | 1.4-1.8 | 1.60 | 30 |
| Niemelä 8896 | (3.8)3.9–5.1 | 4.32 | (2.2)2.3–2.8(2.9) | 2.50 | (1.5)1.6–2.0 | 1.73 | 30 |
| Saarenoksa 28283 | (4.0)4.1–5.0(5.3) | 4.45 | (2.2)2.3–2.8 | 2.47 | 1.6-2.1 | 1.80 | 30 |
| Spirin 5968 | 3.2-3.9(4.1) | 3.49 | (2.0)2.1-2.4 | 2.22 | 1.4-1.7(1.8) | 1.57 | 30 |
| Oxychaete cervinogilva | (5.9)6.0-8.4(8.9) | 6.93 | 2.8-3.7(3.8) | 3.17 | (1.8)1.9–2.5(2.6) | 2.19 | 60/2 |
| Curnow 3772 | (5.9)6.0-8.0 | 6.66 | 2.8-3.7 | 3.07 | 1.9-2.5(2.6) | 2.17 | 30 |
| Schigel 5216 | 6.0-8.8(8.9) | 7.20 | (2.9)3.0–3.8 | 3.27 | (1.8)1.9–2.5(2.6) | 2.20 | 30 |
| Phanerina mellea | (5.2)5.8–7.2(7.8) | 6.43 | 2.8-3.7(4.1) | 3.19 | (1.6)1.8-2.3(2.4) | 2.02 | 100/4 |
| Miettinen 9134 | (6.0)6.1–7.2(7.8) | 6.48 | (2.9)3.0-3.7(3.8) | 3.20 | 1.7-2.3(2.4) | 2.03 | 30 |
| Miettinen 11393 | (5.2)5.4-6.9(7.0) | 6.20 | 2.8-3.2 | 2.98 | (1.8)1.9-2.3(2.4) | 2.08 | 30 |
| Nuñez 503 | (5.7)5.8–7.5(7.7) | 6.49 | (2.9)3.0-4.0(4.1) | 3.33 | (1.6)1.7-2.3(2.4) | 1.95 | 30 |
| Ryvarden 10519B | 5.9–7.4 | 6.81 | 3.2–3.7 | 3.38 | 1.8–2.2 | 2.01 | 10 |
| Riopa metamorphosa | (4.2)5.0-6.6(8.2) | 5.69 | (2.0)2.2-3.1(3.5) | 2.59 | (1.7)1.9–2.6(2.8) | 2.19 | 168/4 |
| epitype | 5.2-6.6(6.8) | 5.84 | (2,1)2,3-3,0(3,1) | 2.59 | 1.9-2.7 | 2.25 | 50 |

Table 5. Spore measurement statistics of polypores. Bold-face values are composite statistics for species. L = average of spore length, W = average of spore width, Q = L/W, and n = number of spores measured. The whole range is given in parentheses; 90% range excluding 5% extreme values from both ends of variation is given without parentheses; in case the values are identical, parentheses are omitted.

| Species | Length | L | Width | W | Q' | Q | n |
|---|-------------------|------|-------------------|------|-------------------|------|----|
| holotype of <i>Ceriporia</i> davidii | 4.9-6.2(6.3) | 5.51 | 2.3–3.0 | 2.68 | 1.9–2.3 | 2.05 | 30 |
| Spirin 2395 | 5.0-7.6(8.2) | 5.82 | (2.0)2.1-3.3(3.5) | 2.55 | (1.8)1.9-2.7(2.8) | 2.29 | 58 |
| Spirin 2686 | (4.2)4.6-6.2(6.5) | 5.35 | 2.3–2.9(3.1) | 2.59 | (1.7)1.8–2.3(2.4) | 2.07 | 30 |
| Riopa pudens | (4.2)4.3–5.6(6.2) | 5.01 | (1.8)1.9-2.2(2.3) | 2.08 | 2.1-2.7(2.8) | 2.41 | 40 |

phal structure is different: in *C. camaresiana* hyphae are mostly long-celled and not inflated, covered with small resinous droplets, and their diameter is approximately the same in all parts of the basidiocarp $(3-4 \ \mu m$ in trama and $4-5 \ \mu m$ in subiculum).

Ceriporia sericea Spirin & Vlasák, sp. nov.

MycoBank 811543 Figure 11e

Holotype. Russia. Khabarovsk: Khabarovsk Dist., Malyi Niran, *Tilia amurensis*, 6 Aug 2012, Spirin 4944 (H).

Etymology. Sericeus (Lat.), silky, refers to the soft consistency of basidiocarp

Description. Basidiocarps 0.3–0.5 mm thick, up to 4 cm in the widest dimension. Margin narrow (up to 1 mm wide). Pore surface cream-colored to pale ochraceous, pores 3–5 per mm. Subicular hyphae subparallel, 4.4–9.4 μ m in diameter, some inflated. Tramal hyphae 3.2–4.8 μ m in diameter. Subhymenial hyphae 2.9–3.7 μ m in diameter. Basidia 10.4–13.8×3.4–5 μ m. Basidiospores thin-walled, hyaline, thick cylindrical, ventral side concave (bean-shaped), (3.8)3.9–4.8(5.2)×(2.1)2.2–2.7 μ m, L=4.32 μ m, W=2.38 μ m, Q=1.82.

Remarks. *Ceriporia sericea* is characterized by soft, pale-colored, rhizomorphic basidiocarps and medium-sized, bean-shaped spores.

Ceriporia sordescens Miettinen & Spirin, sp. nov.

MycoBank 811544 Figures 10c and 11f

Holotype. United States. New York: Essex Co., Huntington Wildlife Forest, Arbutus Lake, 43.9856° : -74.2469°, fallen dicot trunk (*Acer saccharum*?, 50 cm in diameter, decay stage 3/5), 18 Aug 2012, Miettinen 15492.2 (H).

Etymology. *Sordescens* (Lat.), becoming dirty-colored, refers to color change upon drying.

Description. Basidiocarps 0.2–0.5 mm thick, up to 20 cm in the widest dimension. Sterile margin up to 3 mm wide. Pore surface yellowish, in dry specimens pale to dirty ochraceous, in a few portions with pinkish hues, pores 3–4 per mm. Subicular hyphae subparallel, 5–13.6 μ m in diameter, some inflated. Tramal hyphae 2.6–4 μ m

in diameter. Subhymenial hyphae 2.5–4.6 μ m in diameter. Basidia 10.1–18.4×4.1– 5.2 μ m. Basidiospores ellipsoid to narrowly ellipsoid, ventral side flat or slightly convex, very rarely slightly concave, (3.2)3.3–4.2(4.6)×(2.0)2.1–2.5(2.6) μ m, L=3.61 μ m, W=2.24 μ m, Q=1.61.

Remarks. *Ceriporia sordescens* is a close relative of *C. pierii* differing by its ochraceous colors and smaller spores. We have studied one morphologically very similar specimen to *C. sordescens* from Ontario, Canada identified (incorrectly in our view) as *Poria griseoalba* by R.F. Cain (H ex TRTC 33465). It may represent yet another species in the *C. pierii* group, differing from *C. sordescens* mainly by its smaller pores 4–5 per mm, and longer, thick cylindrical spores 4.2–5.1×2–2.3 μ m (n=30), L=4.54, W=2.15, Q=2.12. *Poria griseoalba* (Peck) Saccardo was described from Osceola, New York (Peck 1885) as having small-pored, grayish white basidiocarps, and Lowe (1966) placed it among the synonyms of *Poria rhodella* Fr. (= *Ceriporia viridans* s. lato). Even if Lowe's species concept was probably wider than today, *Poria griseoalba* belongs in the vicinity of *C. viridans* and is clearly not conspecific with *C. sordescens*.

Specimens examined

We studied specimens from herbaria H, O, K and LY, as well as specimens from the personal herbarium of Josef Vlasák (JV). Type specimens of species described here are omitted since their specimen information is found in the descriptions. Sequenced specimens are marked with an asterisk (*).

- Australohydnum dregeanum. INDIA. Madhya Pradesh: Dhuma, Boswellia serrata, 6 Sep 1990, March & Tiwari IDF 223 (O, H).
- *Ceriporia camaresiana*. FRANCE. Bouches-du-Rhône: Eygalières, *Viburnum tinus*, 26 Oct 1995, Rivoire 1233 (H*, LY).
- *Ceriporia humilis*. FINLAND. Uusimaa: Helsinki, Laajasalo, *Acer platanoides*, 20 Oct 1963, Kujala (H, HFR9978).
- Ceriporia pierii. FRANCE. Rhône-Alpes: Vernaison, Populus nigra, 14 Oct 2000, Rivoire 1822 (H, LY); Orlienas, hardwood, 18 Apr 2004, Rivoire 2378 (H, LY), dead Funalia gallica on Fraxinus excelsior, 3 Jan 2007, Rivoire 3052 (H, LY).
- *Ceriporia viridans.* NETHERLANDS. Noord-Holland: Amsterdam, Sloterdijk, dicot, 23 Jun 2007, Miettinen 11701 (H*).
- *Emmia latemarginata.* POLAND. Małopolska: Tarnów, Krzyskie Forest, *Quercus robur*, 4 Sep 1997, Piątek (H*).
- Hapalopilus eupatorii. FRANCE. Seine-Maritime: Petit-Couronne, Eupatorium cannabinum, 1882 Letendre 19 (H 7008580, Karsten's herbarium 5927, lectotype of *Physisporus eupatorii* selected by Lowe 1956). Rhône: Vourles, *Robinia pseudoacacia* in *Renynoutria japonica* thicket, 3 Mar 2014, Rivoire 5333 (LY*). GERMANY. Nordrhein-Westfalen: Mönchengladbach, Volksgarten, *Reynoutria japonica* 04 Nov 2013, Bender (LY BR-5305*). UNITED KINGDOM. Oxfordshire: Henley

on Thames, *Arctium* sp., 10 Dec 2006, Fortey (holotype of *Ceriporiopsis herbicola* in K, isotype in O* studied).

- Hapalopilus rutilans. CROATIA. Zagreb: Maksimir, Quercus, 21 Sep 1979, Tortič (H). FINLAND. Ahvenanmaa: Lemland, Nåtö, deciduous tree, V.1996 Kinnunen (H). Uusimaa: Helsinki, Käpylä, Sorbus aucuparia, 23 Sep 2001, Kotiranta 18819 (H), Veräjämäki, Betula, 17 Jan 2011, Miettinen 14427 (H*); Inkoo, Fagervik, Corylus avellana, 3 Sep 1983, Saarenoksa 28283 (H); Kirkkonummi, Sundsberg, Betula, 20 Oct 2012, Miettinen 15793 (H*). Kittilän Lappi: Kittilä, Kolvakero, Betula pubescens, 22 Sep 2001, Niemelä 7134* (H 7008578*, neotype for Polyporus nidulans designated here). RUSSIA. Buryatia: Baikal, Svyatoi Peninsula, Betula platyphylla, 25 Aug 2000, Kotiranta 17180 (H). Khabarovsk Reg.: Khabarovsk Dist., Malyi Niran, Tilia amurensis, 6 Aug 2012, Spirin 4967 (H), Bolshoi Khekhtsir Nat. Res., Abies nephrolepis, 2 Sep 2013, Spirin 6516 (H*); Solnechnyi Dist., Suluk-Makit, A. nephrolepis, 17 Aug 2011, Spirin 4168 (H). Primorie Reg.: Krasnoarmeiskii Dist., Mel'nichnoe, A. nephrolepis, 23 Aug 2013, Spirin 6299 (H). Nizhny Novgorod Reg.: Bogorodsk Dist., Chudinovo, Tilia cordata, 4 Aug 2013, Spirin 5968 (H*). FRANCE. Rhône: Rontalon, Bois des rivoires, N45.64575:E4.61808, alt. 622 m, Quercus petraea, 15 Aug 2008, Rivoire 3429 (LY*, neotype of Boletus rutilans designated here). SWEDEN. Uppland: Stockholm, Betula, 11 Jun 2002, Vlasák 0206/2* (JV). Vlasák SWIT-ZERLAND. Glarus: Filzbach, Corylus avellana, 21 Apr 1999, Haikonen 19509 (H); Obstalden, Fagus sylvatica, 20 Sep 2008, Haikonen 26561 (H). UNITED STATES. Pennsylvania: Hatfield, Pinus, 31 Jul 2004, Vlasák Jr. 0407/34-J (JV*).
- Hapalopilus ribicola. FINLAND. Uusimaa: Helsinki, Viikki, Ribes nigrum, 25 May 2010, Alanko 145112 (H*). Etelä-Häme: Tammela, Mustiala, Ribes sp., 10 Oct 1881, Karsten (H 6016987, Karsten's herbarium 3795, lectotype of Trametes ribicola selected by (Lowe 1956)); Kangasala, Suinula, Ribes spicatum, 30 May 2003, Eriksson 1201 (H*); Lahti, Mukkulankatu, Ribes alpinum, 31 Dec 1989, Haikonen 11175 (H).
- *Irpex lacteus.* FINLAND. Etelä-Häme: Lammi, Biological Station, *Laburnum alpinum*, 23 Sep 2004, Niemelä 7932 (H*).
- Oxychaete cervinogilva. AUSTRALIA. Queensland: Cape Tribulation NP, 4 Dec 1990, Curnow 3772 (H, ex CBG). Cairns, 22 Aug 2006, Schigel 5216 (H*). IN-DIA. Tamil Nadu: Salem, Kolli Hills, 17 Dec 1978, Kolandavelu (H, O). INDO-NESIA. Java. Junghuhn (L6053180, lectotype by Ryvarden (Ryvarden 1981)).
- Phanerina mellea. INDONESIA. Papua: Jayapura reg., Sentani, Mt Cycloop foothills, secondary forest, *Mimosoidae*? log, 26 Aug 2004, Miettinen 9134.2 (H*, ANDA, MAN); Abepura, roadside, standing *Cassia*, 26 Jan 2007, Miettinen 11393 (H*). Japan. Okinawa: Iriomote island, Nakama river, 22 Jun 1994, Nuñez 503 (O, H). Kenya. Coast Prov: Kwale dist., Diani Beach Forest, alt. 10 m, 15 Feb 1973, Ryvarden 10519*B* (O, H). SRI LANKA. CENTRAL PROVINCE: Feb 1869, no. 535 (K(M) 203382, lectotype by Ryvarden 1984). Tanzania. Arusha Prov: Arusha NP, Meru E slope rd to crater, 8 Feb 1973, Ryvarden 10132 (O, H*).

- *Phanerochaete raduloides.* FINLAND. Pohjois-Karjala: Ilomantsi, *Betula pubescens*, 6 Sep 2003, Penttilä 14355 (H*).
- *Phlebiopsis castanea*. RUSSIA. Khabarovsk: Ulika, *Pinus koraiensis*, 15 Aug 2012, Spirin 5295 (H*). Povorotnaya, *Pinus koraiensis*, 27 Aug 2012, Spirin 5704 (H).
- *Phlebiopsis crassa.* JAPAN. Ibraki: Kasama, 5 Nov 1991, Ryvarden 30366 (O, H). NEPAL. Gandaki: Pokhara, 27 Oct 1979, Ryvarden 18502 (O, H).
- *Phlebiopsis friesii*. INDONESIA. Sulawesi Utara: Dumoga-Bone NP, 6–8 Oct 1985, Samuels 2068 (O, H).
- *Phlebiopsis flavidoalba.* UNITED STATES. Florida: Gainesville, 24 Nov 2013, Miettinen 17896 (H*).
- Phlebiopsis gigantea. FINLAND. Uusimaa: Helsinki, 5 May 2012, Miettinen 15354 (H 6012967*). Kainuu: Puolanka, 25 Sep 2010, Miettinen 14181 (H).
- *Phlebiopsis papyrina.* UNITED STATES. Florida: Sarasota, 10 Mar 2016, Dollinger 677 (H).
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- Riopa metamorphosa. CZECH REPUBLIC. Moravia: Lanžhot, Ranšpurk virgin forest, Quercus robur, 19 Nov 2005,, Vlasák 0511/15 (H 7008577, neotype of Sporotrichum aureum, JV*), 5 Oct 1988, Pouzar (PRM871894 epitype, H 7008579).
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Supplementary material I

S1 Table - INSDC accession numbers

Authors: Otto Miettinen, Viacheslav Spirin, Josef Vlasák, Bernard Rivoire, Soili Stenroos, David Hibbett

Data type: DNA sequence identifiers

- Explanation note: INSDC accession numbers for DNA sequences used in this study. Specimens provided with collector and collection number information have been sequenced for this study, the rest retrieved from the INSDC database.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

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RESEARCH ARTICLE



Five new species of Graphidaceae (Ascomycota, Ostropales) from Thailand

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Abstract

Five new species of Graphidaceae are described from Thailand. Molecular evidence and phenotypical characters support their independent status from related and similar species. *Glaucotrema thailandicum* Naksuwankul, Lücking & Lumbsch is unique within the genus in having submuriform ascospores. *Ocellularia klinhomii* Naksuwankul, Lücking & Lumbsch is characterized by having a whitish gray, rimose thallus with ascomata in verrucae and surrounded by a black ring and lack of secondary metabolites. *Ocellularia phatamensis* Naksuwankul, Parnmen & Lumbsch has a grayish, thick and rimose thallus, differing from *O. klinhomii* in lacking a dark apothecial rim and having ascomata that are not immersed in verrucae. *Ocellularia thailandica* Naksuwankul, Kraichak & Lumbsch differs from *O. albocincta* in lacking a columella. *Ocellularia rotundifumosa* Naksuwankul, Lücking & Lumbsch differs from *O. fumosa* in having ascospores with rounded ends. An epitype for *O. krathingensis* is selected.

Key words

East Asia, lichens, taxonomy, thelotremoid lichens, tropical diversity

Introduction

Phenotypical characters, such as morphology of the thallus and ascomata and anatomy of the ascomata as well as secondary chemistry have traditionally guided species delimitation in lichenized ascomycetes. However, especially crustose lichens often exhibit only few traits and without independent markers, such as DNA sequence data, it is often difficult to assess whether variation is due to genetic differences or plasticity. Indeed, recent phylogenetic studies suggest high amounts of homoplasy in phenotypical characters used to delimit taxa in lichenized fungi (Grube et al. 2004; Tehler and Irestedt 2007; Schmitt et al. 2009; Rivas Plata and Lumbsch 2011; Lumbsch et al. 2014a). Hence, molecular data have greatly increased our ability to identify distinct lineages, including the detection of numerous cryptic lineages (Crespo and Lumbsch 2010; Lumbsch and Leavitt 2011; Leavitt et al. 2015). While numerous foliose and fruticose lichen groups have been studied in some detail, especially in the diverse Parmeliaceae, our knowledge on species delimitation in crustose lichens is still in its infancy. However, among predominantly crustose families, Graphidaceae is now relatively well known.

Graphidaceae constitutes the largest family of crustose tropical lichens with about 2100 accepted species (Rivas Plata et al. 2012; Lücking et al. 2013; Cáceres et al. 2014; Van den Broeck et al. 2014; Lumbsch et al. 2014b; Kraichak et al. 2014). The family has its center of distribution in the tropics, but also occurs in temperate regions with a smaller number of species, in some cases even extending towards the Sub-Antarctic region. The family is most common, however, in the tropics where its species occur often on bark, but can also be found on rocks, wood or soil and sometimes on leaves. Recently, the first author started a project on the diversity of thelotremoid Graphidaceae in East Asia (Papong et al. 2014). Thelotremoid Graphidaceae have rounded ascomata (formerly placed in Thelotremataceae), in contrast to species with lirellate ascomata. The group is still relatively poorly known in Thailand and generally in south-east Asia, but preliminary studies have provided important baseline data for the distribution of species and have indicated that numerous additional species can be expected in Thailand (Homchantara and Coppins 2002; Papong et al. 2010; Sutjaritturakan and Kalb 2015). Molecular data have been used to identify distinct lineages in this group of lichenized fungi and subsequent re-analysis of phenotypical characters often allowed identification of morphological or chemical traits to separate those species (Lumbsch et al. 2008; Mangold et al. 2014; Poengsungnoen et al. 2014; Medeiros et al. 2016). This paper employs molecular, morphological and chemical data to identify six distinct lineages of thelotremoid lichens from Thailand and to describe them as species new to science. Based on our limited sampling of thelotremoid Graphidaceae from other regions of southeast Asia, we expect the new species described here from Thailand to occur in other countries of the region.

This study is mainly based on new collections made by the first two authors deposited in F and MSUT. Sections of thalli and apothecia were cut using a razor blade and examined in water, a solution of KOH, and Lugol's solution using a ZEISS Axioscope 2 plus compound microscope. Chromatography (HPTLC) was performed with standard solvent systems A and C (Culberson 1972; Arup et al. 1993).

We performed two different phylogenetic analyses: 1) sequences of six samples of the genus *Glaucotrema* were aligned with two outgroup taxa (*Leptotrema wightii*, *Reimnitzia santensis*) and 2) sequences of 35 samples of *Ocellularia* s. str. were aligned with *O. cavata* as outgroup. Selection of samples was done using Blast searches and included best hits to ensure that all similar sequences were included. In addition sequences of morphologically similar species were added to the data set. Sequences of mtSSU rDNA, nuLSU rDNA, and the protein-coding RPB2 gene were used for this study. Voucher information and Genbank numbers are listed in Table 1. DNA isolation, PCR, and direct cycle sequencing conditions were described previously (Kraichak et al. 2014).

For the phylogenetic analyses, the alignment of the nucleotide sequences for each dataset was performed separately using Geneious version 8.0.3 (Drummond et al. 2014) and manually inspected for removal of any ambiguous characters. We then performed a maximum likelihood analysis, using RAxML-HPC Blackbox version 8.2.8 (Stamatakis 2006) with the default rapid hill-climbing algorithm and the GTRGAM-MA model of nucleotide substitution. The analysis was carried out on the online server CIPRES science Gateway version 3.3 (Miller et al. 2010) with a total of 1,000 pseudoreplicates to assess the rapid bootstrap value support. A bootstrap support value of 70 and above was considered a strong support for a clade. The resulting bipartitioned trees were visualized with the program FigTree version 1.4.2 (Rambaut 2012).

Results and discussion

Phylogenetic analysis

The final alignment of the combined data set for the Glaucotrema analysis consisted of 802 unambiguously aligned nucleotide positions for mtSSU, 865 for nuLSU, and for 985 RPB2. The final alignment of the dataset for the *Ocellularia* taxa consisted of 787 unambiguously aligned nucleotide positions for mtSSU, 879 for nuLSU, and for 913 RPB2. As the topologies of the single locus phylogenies for these two datasets did not show any conflicts, they were analyzed in a concatenated matrix.

In the *Glaucotrema* tree (Fig. 1), the Thai material formed an unsupported sistergroup relationship with *G. glaucophaenum*, and *G. stegoboloides*. The latter two species were not separated in our analysis but were supported as different species in a broader

| Species | Country | Collector | Number | mtSSU | nuLSU | RPB2 |
|-----------------------------|---------------|-------------|-----------|----------|----------|----------|
| Glaucotrema glaucophaenum | Philippines | Rivas Plata | 1099 | JX421061 | JX421501 | JX420862 |
| Glaucotrema glaucophaenum | Thailand | Lumbsch | 19751g | [] | JX421502 | [—] |
| Glaucotrema glaucophaenum | Australia | Lumbsch | 19127eA | JX421060 | [] | [] |
| Glaucotrema stegoboloides | Brazil | Cáceres | 11817 | KJ435228 | [] | [] |
| Glaucotrema subcostaricense | Tanzania | Frisch | 99Tz866 | DQ384899 | [] | [] |
| Glaucotrema thailandicum | Thailand | Papong | 8560 | [] | KJ435152 | [—] |
| Leptotrema wightii | Costa Rica | Nelsen | 2034A | JX421074 | EU075622 | [—] |
| Ocellularia albocincta | Thailand | Kalb | 38891 | JX421114 | [—] | [—] |
| Ocellularia albocincta | Australia | Mangold | 430 | EU075585 | EU075633 | [—] |
| Ocellularia albocincta | Australia | Mangold | 34a | JX421112 | [—] | [—] |
| Ocellularia ascidioidea | New Caledonia | Papong | 7511 | KJ435201 | KJ435125 | KJ435267 |
| Ocellularia cavata | Cameroon | Frisch | 99Ka403 | DQ384879 | DQ431935 | [—] |
| Ocellularia diacida | Australia | Lumbsch | 19120jB | EU075583 | EU075630 | [—] |
| Ocellularia diacida | Australia | Lumbsch | 19120jD | JF828965 | [—] | [—] |
| Ocellularia exigua | Thailand | Papong | 8434 | KJ435244 | [—] | [—] |
| Ocellularia fumosa | Thailand | Lumbsch | 19756n | [] | JX421539 | [—] |
| Ocellularia halei | Brazil | Cáceres | 11071 | KJ435218 | [—] | [—] |
| Ocellularia klinhomii | Thailand | Papong | 8574 | KJ435252 | [—] | [—] |
| Ocellularia krathingensis | Thailand | Papong | 8478 | KJ435248 | KJ435153 | [—] |
| Ocellularia krathingensis | Thailand | Papong | 8479 | KJ435246 | [—] | [—] |
| Ocellularia krathingensis | Thailand | Papong | 8483 | KJ435241 | [—] | [—] |
| Ocellularia krathingensis | Thailand | Papong | 8496 | KJ435232 | KJ435143 | [—] |
| Ocellularia mauritiana | Peru | Rivas Plata | 803D | JX421170 | [—] | [—] |
| Ocellularia natashae | Peru | Rivas Plata | 1 canopy | JX421175 | [—] | JX420877 |
| Ocellularia percolumellata | Brazil | Cáceres | 6002a | JX421180 | [—] | JX420888 |
| Ocellularia polydiscus | Brazil | Lücking | 27966 | DQ384876 | [—] | [—] |
| Ocellularia portoricensis | Puerto Rico | Mercado | F19 | KJ435178 | [—] | KJ435256 |
| Ocellularia phatamensis | Thailand | Papong | 8541 | KJ435239 | KJ435150 | [—] |
| Ocellularia phatamensis | Thailand | Papong | 8542 | KJ435249 | KJ435154 | [—] |
| Ocellularia phatamensis | Thailand | Papong | 8552 | KJ435236 | KJ435147 | [—] |
| Ocellularia phatamensis | Thailand | Papong | 8557 | KJ435238 | KJ435149 | [—] |
| Ocellularia phatamensis | Thailand | Papong | 8566 | KJ435233 | KJ435144 | [—] |
| Ocellularia phatamensis | Thailand | Papong | 8567 | KJ435245 | [—] | [] |
| Ocellularia phatamensis | Thailand | Papong | 8568 | KJ435237 | KJ435148 | [] |
| Ocellularia phatamensis | Thailand | Papong | 8570 | KJ435250 | KJ435155 | [—] |
| Ocellularia phatamensis | Thailand | Papong | 8573 | KJ435251 | KJ435156 | [—] |
| Ocellularia rhabdospora | Puerto Rico | Mercado | F74 | KJ435172 | KJ435108 | KJ435254 |
| Ocellularia rotundifumosa | Thailand | Papong | 8576 | KJ435231 | [—] | [—] |
| Ocellularia thailandica | Thailand | Papong | 8439 | KJ435235 | KJ435146 | [—] |
| Ocellularia thailandica | Thailand | Papong | 8458 | KJ435247 | [—] | [—] |
| Ocellularia thryptica | Peru | Rivas Plata | 103D | JX421222 | [—] | [—] |
| Ocellularia violacea | Brazil | Cáceres | sn | JX421225 | [—] | [—] |
| Ocellularia xanthostromiza | Peru | Rivas Plata | 809canopy | JX421171 | [—] | [—] |
| Reimnitzia santensis | El Salvador | Lücking | 28015 | HQ639622 | [—] | JF828952 |

Table 1. Genbank numbers and voucher information of specimens used in this study. For author names see *Index Fungorum* (http://www.indexfungorum.org). Missing data are indicated by [–].



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0.02 substitution/site
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Figure 1. Phenogram depicting phylogenetic relationships of *Glaucotrema* species. Only bootstrap support values above 70 are displayed on the nodes.

analysis in Kraichak et al. (2014) with more samples, in which the Thai material was also included and supported as distinct species. In the *Ocellularia* tree (Fig. 2), *O.* aff. *ascidioidea* from Thailand did not form a monophyletic group with *O. ascidioidea* from New Caledonia but an unsupported sister-group relationship with Thai material of *O. exigua*, similar to the analysis by Kraichak et al. (2014). Subsequent morphological re-analysis revealed that the Thai samples previously identified as *O.* aff. *ascidioidea* are identical to *O. krathingensis* described from Thailand (Homchantara and Coppins 2002). As already indicated by Kraichak et al. (2014), *Ocellularia* aff. *fumosa* from Thailand did not cluster with *O. fumosa* but appeared closely related to *O. natashae* and *O. thryptica*. The latter differs in having a clear hymenium and containing protoce-traric acid, whereas *O. natashae* has longer ascospores and contains the hirtifructic acid chemosyndrome (Hale 1973; Rivas Plata and Lücking 2013). The close phylogenetic



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0.0070 substituion/site
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Figure 2. Phenogram depicting phylogenetic relationships of *Ocellularia* species. Only bootstrap support values above 70 are displayed on the nodes.

relationship of these three taxa, which are not only phenotypically disparate but also have distinct geographic distributions, suggests that the loci here used may be of limited use for species delimitation in recently evolved complexes, which has already been discussed for mtSSU by Kraichak et al. (2014). Two samples, included as spec. nov. 8 in Kraichak et al. (2014), formed an unsupported sister-group relationship with *O. albocincta*, a species that differs morphologically (see below) and so the Thai material is described as a new species (*O. siamensis*) below. Nine samples included as spec. nov. 6 in Kraichak et al. (2014) from Thailand clustered together, related to *O. diacida*, which is readily distinguished by the presence of the hirtifructic acid chemosyndrome. The species is described new to science below as *O. phatamensis*. A single specimen, included as spec. nov. 7 in Kraichak et al. (2014), is also related to *O. diacida* but differs – among other characters – by the absence of secondary metabolites.

Taxonomic novelties

Glaucotrema thailandicum Naksuwankul, Lücking & Lumbsch, sp. nov. Mycobank # 818194

Figure 3A–E

Type. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, Sang Chan waterfall, 15°30'N, 105°35'E, 124 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8560* (holotype: MSUT; isotype: F).

Diagnosis. Characterized within the genus by having submuriform ascospores.

Etymology. The specific epithet refers to the country where the type specimen was collected.

Description. Thallus endophloeodal to epiphloeodal, up to c. 120 µm thick, pale green to yellowish green, smooth. True cortex ±continuous, to c. 25 µm thick. Algal layer poorly to well developed, ±continuous; calcium oxalate crystals sparse to abundant, large and clustered; medulla usually distinct. Vegetative propagules not seen. Ascomata conspicuous, to c. 0.8-1.2 mm diam., often larger when fused, ±rounded to irregular, apothecioid to somewhat chroodiscoid, solitary to more often fused, becoming slightly to distinctly emergent, mostly irregularly or regularly urceolate. Disc usually partly visible from above, rarely completely exposed, pale yellowish to whitish green. Pores broad to gaping, to c. 0.6–08 mm wide, ±rounded to irregular, entire to slightly ragged; thalline exciple often becoming apically visible, rarely completely visible from above, ±free, whitish. Thalline rim margin broad to gaping, ±rounded, more commonly irregular, thick, entire, concolorous to whitish. Thalline exciple fused to partly or entirely free, thick, hyaline internally, pale yellowish or greenish marginally, with calcium oxalate crystals. Hymenium to c. 120 µm thick, clear, strongly conglutinated; paraphyses thick, irregular and often distoseptate, ±interwoven, with thickened irregular tips; lateral paraphyses absent; columella whitish and reticulate. Epihymenium hyaline, with fine crystals. Asci 8-spored; tholus initially thick, thin when mature, $100-110 \times 10-12$ µm. Ascospores submuriform with $3 \times 0-1$ septa, hyaline, slightly amyloid, $15-20 \times 7.5$ µm. Pycnidia not seen.

Secondary chemistry. Thallus K+ yellowish, C–, P+ yellow; containing psoromic acid.

Distribution and ecology. The new species was found in northeastern Thailand, growing on bark in a dry evergreen forest. It is known only from the type locality.

Remarks. This new species is unique within the genus in having submuriform ascospores, whereas all other described species have transversely septate ascospores. In addition, the ascospores in *G. bahianum*, *G. costaricense* and *G. stegoboloides* are smaller than in the new species. Molecular data support the distinction of the new taxon. In morphology it resembles *G. bahianum* and *G. stegoboloides*.



Figure 3. Morphology and anatomy of *Glaucotrema thailandicum* (**A–E**) **A–B** habitat of ascoma **C** crosssection of ascoma show whitish and reticulate columella **D** asci with spores and **E** submuriform ascospores (holotype), *Ocellularia klinhomii* (**F–K**) **F–G** ascomata immersed in verrucae and surrounded by a black ring **H** cross-section of ascoma with carbonized columella and apically carbonized exiple **I–K** ascus and ascospores (holotype). Scale bar **A–B**, **F–G** = 1 mm, **H** = 100 μm, **C–D**, **I** = 50 μm, **E**, **J–K** = 20 μm.

Ocellularia klinhomii Naksuwankul, Lücking & Lumbsch, sp. nov. Mycobank # 818195

Figure 3F–K

Type. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, Sang Chan waterfall, 15°30'N, 105°35'E, 124 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8566* (holotype: MSUT; isotype: F).

Diagnosis. Differing from the similar *O. krathingensis* in having a whitish grey, rimose thallus.

Etymology. The specific epithet refers to the collector Mr. Winia Klinhom, my-cologist from Thailand.

Description. Thallus corticolous, epiperidermal, up to c. 5 cm diam., continuous; surface rimose, whitish grey, medulla white; prothallus absent. Thallus in section 30-40 µm thick, with prosoplectenchymatous cortex, 5-10 µm thick, photobiont layer 15-20 μm thick, and medulla 20–25 μm thick, with scattered clusters of calcium oxalate crystals. Photobiont Trentepohlia; cells rounded to irregular in outline, in irregular groups, green, $7-9 \times 6-8$ µm. Ascomata rounded, vertucae and surrounded by a black ring, erumpent to immersed, with complete thalline margin, 0.4–0.7 mm diam., 0.15–0.2 mm high; disc covered by 0.05-0.1 mm wide pore more or less filled with black-tipped columella but columella often immersed; proper margin indistinct, entire to slightly fissured, visible as whitish rim around the pore; thalline margin entire to slightly fissured, smooth, yellowish green. Excipulum entire, prosoplectenchymatous, brown with apically carbonized, 15–20 μm wide, fused with thalline margin and difficult to separate from the bordering periderm; laterally covered by algiferous, corticate thallus containing periderm layers; columella present, finger-like, carbonized, up to 100 µm broad and 120-140 µm high; hypothecium prosoplectenchymatous, 5–10 µm high, light brown; hymenium 125–150 µm high, hyaline, clear; epithecium indistinct, $5-7 \mu m$ high, hyaline. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical to narrowly clavate, $110-115 \times 12-15 \mu m$. Ascospores 8 per ascus, ellipsoid, 6–9-septate, $25-38 \times 7-8 \mu m$, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue. Pycnidia not seen.

Secondary chemistry. No substances detected by TLC.

Distribution and ecology. The new species was collected in northeastern Thailand, growing on bark in a dry evergreen forest. It is known only from the type locality.

Remarks. Similar in ascospore size, lack of secondary metabolites and only apically carbonized exciple to *O. krathingensis* but differing in having a whitish gray, rimose thallus with ascomata in verrucae and surrounded by a black ring, reminiscent of *O. wirthii* (Mangold et al. 2008). The latter species is readily distinguished by having a broader, carbonized columella and the presence of the psoromic acid chemosyndrome. The species would key out at alternative 60 in the *Ocellularia* key for Thailand (Sutjaritturakan & Kalb 2015).

Additional specimen examined. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, Sang Chan waterfall, 15°30'N, 105°35'E, 124 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8568*, *8552*, *8567*, *8570*, *8542*, *8541*, *8573*, *8574* (MSUT), K. Papong *8557* (RAMK).

Ocellularia phatamensis Naksuwankul, Parnmen & Lumbsch, sp. nov. Mycobank # 818196 Figure 4A–B

Type. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, Sang Chan waterfall, 15°30'N, 105°35'E, 124 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8574* (holotype: MSUT; isotype: F).

Diagnosis. Differing from the similar *O. krathingensis* in having an a grayish, thick and rimose thallus.

Etymology. The specific epithet refers to the name of the Pha Tam National Park in Ubon Ratchathani Province, Thailand.

Description. Thallus corticolous, epiperidermal, up to c. 5 cm diam., continuous; surface uneven-verrucose to rimose, grayish, medulla white; prothallus absent. Thallus in section 60-75 µm thick, with prosoplectenchymatous cortex, 5-8 µm thick, photobiont layer 20-25 µm thick, and medulla 35-40 µm thick, with scattered clusters of calcium oxalate crystals. Photobiont Trentepohlia; cells rounded to irregular in outline, in irregular groups, green, $8-10 \times 6-7$ µm. Ascomata rounded, erumpent, with complete thalline margin, 0.4-0.7 mm diam., 0.15-0.2 mm high; disc covered by 0.07–0.1 mm wide pore more or less filled with black-tipped columella but columella often immersed; proper margin indistinct; thalline margin entire to slightly fissured, smooth, light yellowish green. Excipulum entire, prosoplectenchymatous, apically carbonized, 15-20 µm wide, fused with thalline margin and difficult to separate from the bordering periderm; laterally covered by algiferous, corticate thallus containing periderm layers; columella present, finger-like, carbonized, up to 110 µm broad and $120-135 \,\mu\text{m}$ high; hypothecium prosoplectenchymatous, $5-10 \,\mu\text{m}$ high, light brown; hymenium 120-150 µm high, hyaline, clear; epithecium indistinct, 5-10 µm high, hyaline. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical to narrowly clavate, $100-110 \times 12-15 \mu m$. Ascospores 8 per ascus, ellipsoid, 7–8-septate, $25-30 \times 7.5-8 \mu m$, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue. Pycnidia not seen.

Secondary chemistry. No substances detected by TLC.

Distribution and ecology. The new species was collected in northeastern Thailand, growing on bark in a dry evergreen forest. It is known only from the type locality.

Remarks. The new species is similar to *O. krathingensis* in having an apically carbonized exciple and columella, transversely septate, amyloid ascospores, and lacking secondary metabolites, but differs in having a grayish and thicker thallus (Homchantara and Coppins 2002). Another similar species is *O. klinhomii*, but differs in lacking a dark apothecial rim and the ascomata are not immersed in verrucae. Molecular data support the distinction of these two species (Fig. 2). Another similar and related species is *O. diacida*, which is readily distinguished by the presence of the hirtifructic acid chemosyndrome. The species would key out at alternative 60 in the *Ocellularia* key for Thailand (Sutjaritturakan and Kalb 2015).



Figure 4. Morphology and anatomy of *Ocellularia phatamensis* (**A–B**) **A** habitat of ascomata **B** ascospores (K. Papong 8574, holotype MSUT!), *O. rotundifumosa* (**C–E**) **C** ascomata **D** hymenium with ascus and **E** ascospores (holotype MSUT), *O. thailandica* (**F–H**) **F** habitat of ascomata **G** ascus with ascospores and **H** ascospores (holotype). Scale bar **A**, **C**, **F** = 1 mm, **D**, **G** = 50 μm, **B**, **E**, **H** = 20 μm.

Ocellularia rotundifumosa Naksukankul, Lücking & Lumbsch, sp. nov. Mycobank # 818197 Figure 4C–E

Type. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, Sang Chan waterfall, 15°30'N, 105°35'E, 124 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8576* (holotype: MSUT; isotype: F).

Diagnosis. Differing from *O. fumosa* in having ascospores with rounded ends.

Etymology. The specific epithet refers to the ascospore shape with rounded ends and to the similarity with *O. fumosa*.

Description. Thallus corticolous, endophloeodal to epiphloeodal, up to c. 200 µm thick, greenish gray to olive, slightly glossy, smooth, rarely continuous to usually ±verrucose. True cortex discontinuous, to c. 15 µm thick, formed by irregular hyphae. Algal layer well developed, continuous; calcium oxalate crystals moderately large, scattered. Photobiont Trentepohlia; cells rounded to irregular in outline, in irregular groups, green, $7-9 \times 6-9 \mu m$. Vegetative propagules not seen. Ascomata rounded with complete thalline margin, 0.4-0.9 mm diam., solitary to marginally fused, immersed to rather emergent, then verrucose-hemispherical to urceolate. Disc with the columella visible from above, entire, free, slightly pruinose, dark gray. Pores formed by the thalline rim margin, c. 0.5 mm diam., the apex of the proper exciple becoming visible from above as a brownish to dark gray line, moderately thick, concolorous with the thallus or brighter; thalline rim incurved. Proper exciple fused, dark brown to carbonized marginally and towards the tips, usually distinctly amyloid at the base. Hymenium to c. 150 µm thick, densely inspersed, distinctly conglutinated; paraphyses slightly bent, ±interwoven, unbranched, with moderately thickened tips; columellar structures moderately well developed, to 150 µm wide, entire, the upper parts brownish to carbonized. Epihymenium brownish, with grayish or brownish granules. Asci 8-spored; tholus initially thick, thin when mature. Ascospores 7-9-septate, fusiform to oblong-fusiform, rarely clavate, with rounded ends, $24-35 \times 7-10 \mu m$, hyaline, distoseptate with lens-shaped lumina, I+ violetblue. Pycnidia not seen.

Secondary chemistry. No compounds detectable by TLC.

Distribution and ecology. The new species was collected in northeastern Thailand, growing on bark in a dry evergreen forest. It is known only from the type locality.

Remarks. Similar to *O. fumosa*, but differing in having rounded ends of the ascospores instead of acute ones in *O. fumosa*. Molecular data support the distinction of the species (Fig. 2). Characters to separate the related *O. natashae* and *O. thryptica* are discussed above. The species would key out at alternative 23 in the *Ocellularia* key for Thailand (Sutjaritturakan and Kalb 2015).

Ocellularia thailandica Naksuwankul, Kraichak & Lumbsch, sp. nov.

Mycobank # 818198 Figure 4F–H

Type. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, trail to Huai Sanom, 15°27'N, 105°34'E, 245 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8458* (holotype: MSUT; isotype: F).

Diagnosis. Differing from the similar *O. viridipallens* in having broader ascospores with up to 7 septa.

Etymology. The specific epithet refers to the country where the type specimen was collected.

Description. Thallus corticolous, epiperidermal, up to c. 5 cm diam., continuous; surface uneven-verrucose to rimose, light yellowish green, medulla white; prothallus absent. Thallus in section 40-60 µm thick, with prosoplectenchymatous cortex, 5-7 μ m thick, photobiont layer 15–25 μ m thick, and medulla 20–30 μ m thick, with scattered clusters of calcium oxalate crystals. Photobiont Trentepohlia; cells rounded to irregular in outline, in irregular groups, green, $7-8 \times 5-9$ µm. Ascomata rounded, erumpent, with complete thalline margin, 0.3–0.5 mm diam., 0.12–0.2 mm high; disc covered by 0.05–0.1 mm wide pore; proper margin indistinct, entire to slightly fissured, visible as whitish rim around the pore; thalline margin entire to slightly fissured, smooth, light yellowish green. Excipulum entire, prosoplectenchymatous, brown to dark brown, 15–20 µm wide, fused with thalline margin and difficult to separate from the bordering periderm; laterally covered by algiferous, corticate thallus containing periderm layers; columella present, finger-like, carbonized, up to 100 µm broad and 120-135 µm high; hypothecium prosoplectenchymatous, 5-10 µm high, hyaline; hymenium 125-140 µm high, hyaline, clear; epithecium indistinct, 5-10 µm high, hyaline. Paraphyses unbranched, apically smooth; periphysoids absent; asci cylindrical to narrowly clavate, $87-100 \times 12-15 \mu m$. Ascospores 8 per ascus, ellipsoid, 5–7-septate, $20-23 \times 7-8 \mu m$, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue. Pycnidia not seen.

Secondary chemistry. No substances detected by TLC.

Distribution and ecology. The new species was collected in northeastern Thailand, growing on bark in a dry evergreen forest. It is known only from the type locality.

Remarks. This new species is closely related to *O. albocincta* (Fig. 2). However, this species differs in lacking a columella (Papong et al. 2010). Morphologically it resembles *O. viridipallens*, which differs in having narrower ascospores. The species would key out at alternative 60 in the *Ocellularia* key for Thailand (Sutjaritturakan & Kalb 2015).

Additional specimen examined. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, trail to Huai Sanom, 15°27'N, 105°34'E, 245 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8439* (MSUT).

Epitypification of *Ocellularia krathingensis* **Homchant. & Coppins** Figure 5D–F

Epitype. THAILAND. Ubon Ratchathani Province: Pha Tam National Park, trail to Huai Sanom, 15° 27' 620" N, 105° 34' 615" E, 245 m, dry evergreen forest, on bark; 12 Apr. 2013, *K. Papong 8479* (epitype MSUT!).

In order to clarify the application of the name *Ocellularia krathingensis*, we propose an epitype for this species that agrees morphologically well with the holotype (RAMK!) and has been sequenced.



Figure 5. Morphology and anatomy of *O. krathingensis* (**A–F**); **A** habitat of ascomata **B** hymenium with ascus and **C** ascospores. (**D–F**) **D** erumpent ascomata **E** ascus and **F** ascospores **A–C** K. Papong *8483* **D–F** K. Papong *8479* (epitype). Scale bar **A**, **D** = 1 mm, **B**, **E** = 50 μm, **C**, **F** = 20 μm.

Additional specimens examined. THAILAND, Ubon Ratchathani Province, Pha Tam National Park, trail to Huai Sanom, 15°27'N, 105°34'E, 245 m, dry evergreen forest, on bark; 12 April 2013, K. Papong *8496*, *8478*, *8483* (F, MSUT) (Figure 5A–C).

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