# A revised genus-level classification for *Cerrenaceae* (*Polyporales, Agaricomycetes*)

O. Miettinen[1*], J. Vlasák[2], E. Larsson[3], J. Vlasák Jr.[4], J.S.S. Seelan[5], Hernawati[6], Q. Levicky[7], K.-H. Larsson[8], V. Spirin[1]

[1]Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland
[2]Biology Centre, Academy of Sciences of the Czech Republic, Branišovská 31, CZ 37005, České Budějovice, Czech Republic
[3]Biological and Environmental Sciences, University of Gothenburg, and Gothenburg Global Biodiversity Centre, Box 461, 40530 Gothenburg, Sweden
[4]207 Silverbrook Dr., Schwenksville, PA, USA
[5]Mycology and Pathology Laboratory, Institute for Tropical Biology and Conservation (ITBC), Universiti Malaysia Sabah, 88400 Kota Kinabalu, Sabah, Malaysia
[6]Fakultas Kehutanan (Faculty of Forestry), Universitas Muhammadiyah Sumatera Barat, Padang, Sumatera Barat 25172, Indonesia
[7]The Royal Botanic Gardens, Kew, Richmond, TW9 3AB, UK
[8]Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway

*Corresponding author: otto.miettinen@helsinki.fi

**Abstract:** *Cerrenaceae* is a small family of polypores and hydnoid fungi in the order *Polyporales* (*Basidiomycota*). The family consists of white-rot fungi, some of which are serious tree pathogens. Combining morphological evidence with a phylogenetic dataset of six genetic markers, we revise generic concepts in the family and propose a seven-genus classification system for the family. Two genera are introduced as new: the monotypic *Acanthodontia* for *Radulodon cirrhatinus*, and *Lividopora* for the *Rigidoporus vinctus* complex. We re-introduce the name *Somion* for the *Spongipellis delectans* complex. Other recognized genera in the family are *Cerrena, Irpiciporus, Pseudolagarobasidium*, and *Radulodon*. New species introduced are *Irpiciporus branchiformis* from Tanzania, *Lividopora armeniaca*, and *L. facilis* from Southeast Asia, and *Somion strenuum* from East Asia. We provide nomenclatural comments on all the names combined to the above *Cerrenaceae* genera and typify *Cerrena unicolor*, *C. zonata*, *Polyporus carneopallens* (= *L. vincta*), *Somion occarium*, and *S. unicolor*. The genus *Hyphoradulum* belongs to *Cystostereaceae* (*Agaricales*), and we transfer the type species *H. conspicuum* to *Crustomyces*. Our study highlights the importance of integrating different basidiocarp types in analyses when revising genus classification in macrofungi.

## INTRODUCTION

A phylogenetic framework became available to mycologists in the 1990s with the onset of easy and low-cost DNA sequencing. Its impact has step by step penetrated fungal systematics and classification. Hibbett *et al.* (2007) established a classification system at the order level and above. Justo *et al.* (2017) extended the phylogeny-based classification to the family level in the order *Polyporales*, which is dominated by macrofungal basidiocarp types, polypores and crusts (corticioid fungi). Family concepts in this scheme are monophyletic groups defined by their genetic similarity; morphology was not – and one could argue cannot be – a leading principle when designing fungal classification at the higher levels.

Yet DNA-based phylogenetics does not liberate us from considering morphological or ecological characters in taxonomy. Most species can be and are being defined by morphological or ecological traits. Some of the families might be characterized morphologically, others not; but between the family and species level there is a space, genus-level and intermediary ranks, where

morphology and phylogenetics both can and should define classification. The question how to define monophyletic genera so that they would be morphologically identifiable whenever possible is an important consideration when revising classification. Each family is likely to represent a unique dilemma in this sense, and it is becoming evident that only suboptimal solutions exist in some cases, thus is the level of morphological plasticity in fungi.

The subject of our paper is one of the families Justo *et al.* (2017) established, the *Cerrenaceae*. This small family includes wood decomposers and tree pathogens. Basidiocarp morphology varies from polypores such as *Antrodiella p.p.*, *Cerrena*, *Rigidoporus p.p.*, and *Spongipellis p.p.* (Fig. 1) to hydnoid fungi such as *Pseudolagarobasidium* and *Radulodon* (Fig. 2). When establishing the genus, Justo *et al.* did not elaborate on how the family might be delimited morphologically or how to classify species diversity within it. Here we have studied most of the species complexes and all the genera in the *Cerrenaceae*, and propose a genus classification for the family. This task exemplifies the problem of balancing morphological signal with phylogenetics – in essence between the extremes of many small

**Fig. 1.** Poroid members of the *Cerrenaceae*. **A.** *Cerrena albocinnamomea* (*Niemelä 6372*). **B.** *Cerrena unicolor* (*Miettinen 16901*). **C.** *Cerrena zonata* (*Miettinen 13798*). **D.** *Lividopora benetosta* (*Miettinen 18135*). **E.** *Somion occarium* (*Overall*, K(M) 159049). **F.** *Somion strenuum* (holotype). **G.** *Somion tomsovskyi* (*Vlasák Jr.*, JV 1307/8). Scale bars = 1 cm.

**Fig. 2.** Hydnoid and irpicoid representatives of *Cerrenaceae*. **A.** *Acanthodontia cirrhatina* (*Miettinen 13717*). **B.** *Irpiciporus pachyodon* (*Spirin 13785*). **C.** *Radulodon erikssonii* (*Miettinen 10977*). **D.** *Pseudolagarobasidium subvinosum* in herbarium (*Wu 8609*). Scale bars = 1 cm.

genera or a few larger ones. As we will show below, neither solution is perfect. Both solutions would create a situation where morphological genus definition is difficult, and yet one of them has to be implemented to avoid non-phylogenetic genera.

If polypores and hydnoid fungi would be viewed in isolation, one could arrive at two classification systems that do a good job creating monophyletic, morphologically easy-to-recognize genera within the *Cerrenaceae*. However, these two schemes would not be mutually compatible (phylogenetically logical). We

argue that genus taxonomy should be revised in overview papers such as Justo & Hibbett (2011), Miettinen *et al.* (2012), Chen *et al.* (2021), Savchenko *et al.* (2021) and Li *et al.* (2022) to mention a few good examples from corticioid fungi and polypores. These papers are based on large, multi-marker, and taxonomically inclusive datasets. In contrast, many current taxonomic papers treat each case in isolation and routinely erect new genera for newly-discovered clades in the most recent phylogram without the benefit of a wider perspective.

Following is a short introduction to currently recognized genera in the *Cerrenaceae*.

*Antrodiella* is a polypore genus that historically included dimitic white-rot species with small pores and spores. Miettinen *et al.* (2012) suggested a narrower, monophyletic concept for the genus, a concept that was adopted by some subsequent authors (Yuan 2014, Westphalen *et al.* 2019) but not all (Ryvarden 2018, 2020a). *Antrodiella sensu stricto* belongs to the *Steccherinaceae*. In his paper on Chinese *Antrodiella*, Yuan (2014) showed that *A. albocinnamomea* and *A. zonata* are related to *Cerrena* and transferred them to *Cerrena*, though without wider consideration of genus classification in the *Cerrena* clade (*Cerrenaceae*). We show in this paper that *A. multipileata* also belongs to the *Cerrenaceae*.

*Cerrena*, as currently recognized, is a small polypore genus perhaps best known for *Cerrena unicolor*, a wide-spread temperate species in the northern hemisphere. *Cerrena unicolor* has two relatives (*C. cystidiata* and *C. 'gilbertsonii'*). As mentioned, Yuan (2014) also included two former *Antrodiella* species in the genus as *C. albocinnamomea* and *C. zonata*. In our experience, *Cerrena unicolor* is a phytopathogen, and Dai *et al.* (2007) list *C. zonata* as a heartwood rotter of living trees. *Cerrena unicolor* has been studied for its enzymatic capabilities (Janusz *et al.* 2007, Elisashvili *et al.* 2010, Lisova *et al.* 2010, Hartikainen *et al.* 2016, Janusz *et al.* 2018), as has *C. albocinnamomea* (Yuan *et al.* 2012).

*Pseudolagarobasidium* contains nine temperate to tropical species with thin, hydnoid basidiocarps. The current genus concept derives from Hallenberg *et al.* (2008) and Nakasone & Lindner (2012). Two species are known to be tree pathogens, causing root rot (Jang & Chen 1985, Wood & Ginns 2006), while others have been reported as endophytes and saprotrophs (Hallenberg *et al.* 2008).

*Radulodon* contains several light-coloured hydnoid species. Nakasone & Lindner (2012) narrowed the genus concept by excluding a set of species, and we continue here, leaving two temperate species and a recently described species from the Eastern Himalayas (Wang & Dai 2022). *Radulodon* spp. are apparently saprotrophs of angiosperms.

*Rigidoporus* in the traditional sense is a highly polyphyletic genus. Species placed under it are found in two orders (*Hymenochaetales* and *Polyporales*) and within the *Polyporales* in several families, the largest of which is the *Meripilaceae* (Justo *et al.* 2017, Wu *et al.* 2018). Justo *et al.* (2017) showed that the *Rigidoporus vinctus* complex belongs to the *Cerrenaceae*. It is clear that *Rigidoporus* in the strict sense is not related, and consequently a better-fitting genus has to be found for the *R. vinctus* complex. This species group includes effused polypores mostly found in the tropics. Several species (previously called varieties) are known as tree pathogens in the tropics and New Zealand ("red root-rot", Setliff & Mesner 1971, Setliff 1972b, Hood & Dick 1988). They have also been detected as endophytes of rubber (Martin *et al.* 2015). We revise this species complex here.

*Spongipellis* is a small genus of polypores comprising about 10 species. Its current concept was introduced by Bondartsev & Singer (1941), but their concept has been shown to be polyphyletic and their species concepts outdated (Tomšovský

2012, Dvořák *et al.* 2014). *Spongipellis* in the strict sense is related to *Meripilaceae*, whereas the species complexes *S. delectans* and *S. pachyodon* are in the *Cerrenaceae* (Justo *et al.* 2017, Kotiranta *et al.* 2017). The genus name *Irpiciporus* is available for the *S. pachyodon* species complex and has been put in use recently (Wang & Dai 2022). Species of the *S. delectans* complex have been reported to be serious tree pathogens of oaks (Ljubarsky 1934, Černý 1979, Dai *et al.* 2007). Wang & Dai (2022) recently described the genus *Pseudospongipellis* for the *S. delectans* complex. We re-introduce here the older genus name *Somion* for this clade. Nakasone & Ortiz-Santana (2022) added several species.

In this paper, we comment on all names combined to *Cerrena*, *Irpiciporus*, *Pseudolagarobasidium*, and *Radulodon*. For *Spongipellis* nomenclature, see Spirin *et al.* (2022), who focused on *Spongipellis sensu stricto*. We comment further on *Spongipellis* names here, including all names we know are associated with the *Cerrenaceae*, but provide no exhaustive checklist for this genus.

## MATERIALS AND METHODS

We studied 152 specimens from the following fungaria: H, O, BPI, CFMR, DAOM, FH, FLOR, GB, K, NY, PC, PRM, and W (Thiers 2023). JV refers to the personal fungarium of Josef Vlasák. The basic mountant used in microscopic descriptions is Cotton Blue (CB). We measured 30 basidiospores per specimen and 20 hyphae for each hyphal type for each specimen used in making the descriptions. When presenting measurements of basidiospores, 5 % extreme values from both ends of variation are given in parentheses. For hyphal measurements, the 20 % tails are placed in parentheses. The following abbreviations are used in descriptions below: L – mean spore length, W – mean spore width, Q – L/W ratio, n – number of measurements per specimens. For more details on microscopic routine, consult Miettinen *et al.* (2018).

DNA extractions were performed as described in Miettinen *et al.* (2012), Spirin *et al.* (2013), and Gutaker *et al.* (2017). The nuclear ribosomal internal transcribed spacer (ITS) region was amplified by PCR and sequenced using primers ITS1, ITS2, ITS5, ITS4, and LR22; nuclear large subunit or 28S (LSU) with CTB6, LR5 and LR7; and mitochondrial small subunit or 16S (mtSSU) with MS1 and MS2 (White *et al.* 1990, Vilgalys lab 1992 https://sites.duke.edu/vilgalyslab/rdna_primers_for_fungi, Garbelotto *et al.* 1997); mitochondrially encoded ATP synthase membrane subunit 6 (*ATP6*) with ATP6-1, -3, and -4 (Kretzer & Bruns 1999); DNA-directed RNA polymerase II largest subunit RPB1 encoding gene (*RPB1*) with rpb1-gAf and rpb1-fCr (Matheny *et al.* 2002); and translation elongation factor 1-alpha (*TEF1*) with EF1-983F (Rehner & Buckley 2005) and EFgr (Rehner, GCAATGTGGGCRGTRTGRCARTC). Sanger sequencing was mostly conducted at Macrogen (Korea and Netherlands) and the Academy of Sciences of the Czech Republic (České Budějovice, Czech Republic). Also, Illumina NextSeq data were used to retrieve markers from partial genome sequences for a few specimens as described in Viner *et al.* (2021). Newly created sequences were submitted to GenBank (Sayers *et al.* 2022, Table 1).

**Table 1.** List of specimens with DNA sequences used in this study. Codes refer to INSDC or UNITE accession numbers. Newly produced sequences are printed in **bold**. Asterisk (*) denotes cultures as the origin of the sequences. Abbreviation of provinces/states follows ISO 3166-2.

| Species | Specimen / culture* | Country (province/state) | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
| *Acanthodontia cirrhatina* | **holotype** | **Malaysia** | **OR262205** | — | — | — | — | — |
| *Cerrena albocinnamomea* | **Miettinen 13717** | **Indonesia (SB)** | **OR262179** | **OR262179** | — | **OR296385** | **OR296392** | **OR296407** |
| | **Miettinen 10511** | **China (JL)** | **OR262168** | **OR262168** | **OR295446** | **OR296382** | — | **OR296402** |
| | holotype of *C. aurantiopora* | South Korea | FJ821532 | — | — | — | — | — |
| | | — | KC485522 | KC485539 | — | — | — | — |
| *Cerrena cystidiata* | | Brazil | MZ649034 | MZ649034 | — | — | — | — |
| *Cerrena 'gilbertsonii'* | **D. Vlasák (JV 1609/29)** | **Guadeloupe** | **OR262202** | — | — | — | **OR296399** | — |
| *Cerrena multipileata* | **Vandevender 94-144** | **Mexico** | **OR262171** | **OR262171** | **OR295447** | — | — | — |
| | **J. Vlasák (JV 1407/63)** | **Costa Rica** | **OR262201** | **OR262201** | — | — | **OR296398** | — |
| | **Ryvarden 43881** | **Costa Rica** | **OR262155** | **OR262155** | **OR295442** | — | — | — |
| | **Kout (JV 0611/A36)** | **Guatemala** | **OR262203** | — | — | — | — | — |
| *Cerrena* sp1 | | China | KX527879 | — | — | — | — | — |
| | | China | MK247953 | — | — | — | — | — |
| | | China | MT908560 | — | — | — | — | — |
| *Cerrena* sp2 | | Vietnam | MT269762 | — | — | — | — | — |
| | | Vietnam | MT269763 | — | — | — | — | — |
| | | China | OP022000 | — | — | — | — | — |
| *Cerrena unicolor* | | Indonesia | KJ654531 | — | — | — | — | — |
| | | Taiwan | MN592928 | — | — | — | — | — |
| | | Antarctica | HM589361 | — | — | — | — | — |
| | | Argentina (TF) | MH019790 | — | — | — | — | — |
| | | Canada (ON) | MH855029 | — | — | — | — | — |
| | | China (XJ) | OM100740 | OM083972 | ON417068 | — | ON424672 | ON424825 |
| | | China | JQ798288 | — | — | — | — | — |
| | | China | MW467890 | — | — | — | — | — |
| | | Czech Republic | FJ821536 | — | — | — | — | — |
| | | Finland | FN907915 | FN907915 | — | — | — | — |
| | | Italy | MK581063 | — | — | — | — | — |
| | | Japan | LC415531 | — | — | — | — | — |
| | **Uotila 47558** | **Kyrgyzstan** | **OR262167** | — | — | — | — | — |
| | | Serbia | MW485440 | — | — | — | — | — |
| | | South Korea | MN294859 | — | — | — | — | — |
| | | Sweden | JN710525 | JN710525 | JN710663 | JN710614 | — | JX109891 |

**Table 1.** (Continued).

| Species | Specimen / culture* | Country (province/state) | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
|---|---|---|---|---|---|---|---|---|
| | | | | | GenBank accession numbers | | | |
| | | Turkey | MK120293 | – | – | – | – | – |
| | | United Kingdom | MZ159683 | – | – | – | – | – |
| | | USA (MA) | KP135304 | KP135209 | – | – | KP134874 | – |
| | | Uzbekistan | MT526291 | – | – | – | – | – |
| *Cerrena zonata* | **Genevieve Gates 39555** | **Australia (TAS)** | **OR262160** | **OR262160** | – | – | – | – |
| | | Bhutan | UDB0780153 | – | – | – | – | – |
| | **Miettinen 9773** | **China (YN)** | **OR262157** | **OR262157** | – | – | – | – |
| | **Miettinen 9889/OMC 13*** | **China (YN)** | **OR262158** | **OR262158** | **OR295443** | **OR296380** | **OR296390** | **OR296401** |
| | **Miettinen 13798** | **Indonesia (SB)** | **OR262166** | **OR262166** | – | – | – | – |
| | | Japan | LC631683 | – | – | – | – | – |
| | | New Zealand | HQ533016 | – | – | – | – | – |
| | | South Korea | MN294861 | – | – | – | – | – |
| | | Vietnam | OP985107 | – | – | – | – | – |
| *Crustomyces albidus* | holotype | China (YN) | ON117191 | ON117175 | – | – | – | – |
| *Crustomyces isabellinus* | | Vietnam | ON117185 | ON117170 | – | – | – | – |
| *Crustomyces laminiferus* | | Costa Rica | EU118622 | – | – | – | – | – |
| *Crustomyces* sp. | | China | ON117190 | ON117174 | – | – | – | – |
| *Crustomyces subabruptus* | | France | MF183941 | – | – | – | – | – |
| *Crustomyces tephroleucus* | **Spirin 4826** | **Russia (LEN)** | **OR262177** | – | – | – | – | – |
| | holotype | China (HI) | MF290417 | MF290415 | – | – | – | – |
| *Cymatoderma* sp. | | USA (FL) | KY948826 | KY948872 | – | – | KY948971 | – |
| *Cymatoderma africanum* | **Niemelä 8803** | **Mozambique** | **OR236211** | **OR236211** | **OR295457** | **OR296389** | – | **OR296425** |
| *Cymatoderma caperatum* | | Venezuela | JN710529 | JN710529 | JN710666 | JN710617 | – | – |
| *Cystostereum crassisporum* | holotype | China (GX) | ON117193 | ON117179 | – | – | – | – |
| *Cystostereum murrayi* | | Germany | MH855588 | MH867098 | – | – | – | – |
| *Cystostereum submurrayi* | holotype | China (JX) | ON117192 | ON117177 | – | – | – | – |
| *Effusomyces thailandicus* | | Thailand | ON117194 | ON117180 | – | – | – | – |
| *Hyphoradulum conspicuum* | **holotype** | **Czech Republic** | **OR262206** | – | – | – | – | – |
| *Irpiciporus branchiformis* | **holotype** | **Tanzania** | **OR262193** | **OR262193** | – | – | – | **OR296421** |
| *Irpiciporus mollis* | **Dollinger 770** | **USA (FL)** | **OR262192** | – | – | – | – | **OR296420** |
| | | USA (MA) | KP135302 | KP135288 | – | – | KP134875 | – |
| | **J. Vlasák (JV 0709/174)** | **USA (VA)** | **OR359379** | **OR359379** | – | – | – | **OR387174** |

**Table 1.** (Continued).

| Species | Specimen / culture* | Country (province/state) | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | | GenBank accession numbers | | | |
| *Irpiciporus pachyodon* | Heilmann-Clausen 07-286 | USA | DQ249277 | AY629322 | AFTOL705 | EU339271 | — | DQ028599 |
| | **J. Vlasák (JV 9311/1)** | **Bulgaria** | **OR262165** | **OR262165** | — | — | — | — |
| | **Kotlaba (JV 1611/1)** | **Czech Republic** | **OR262191** | **OR262191** | — | — | — | **OR296419** |
| | | **Czech Republic** | **OR253988** | **OR253988** | **OR295456** | **OR296388** | **OR296395** | **OR296422** |
| | | Czech Republic | HQ728293 | HQ729003 | — | — | — | — |
| | | Italy | AY849307 | — | — | — | — | — |
| *Irpiciporus sinuosus* | holotype | China (YN) | KX161649 | KX161658 | — | — | — | OM982699 |
| | | Thailand | MK589288 | — | — | — | — | — |
| *Irpiciporus* sp. | | Ecuador | KX161650 | KX161659 | — | — | — | — |
| *Lividopora armeniaca* | **isotype** | **Malaysia** | **KY953211** | KY953211 | **OR291311** | **OR296404** | KY953212 | **OR296384** |
| *Lividopora benetosta* | | Cameroon | KJ831816 | — | — | — | — | — |
| | | Cameroon | KJ831817 | — | — | — | — | — |
| | | Cameroon | KJ831819 | — | — | — | — | — |
| | | Cameroon | KJ831837 | — | — | — | — | — |
| | | Cameroon | KJ831838 | — | — | — | — | — |
| | | China (GD) | KU904221 | — | — | — | — | — |
| | | China (HI) | KX013197 | — | — | — | — | — |
| | | China (HK) | KU194316 | — | — | — | — | — |
| | **Härkönen K778** | **China (HN)** | **OR262204** | — | — | — | — | — |
| | **Härkönen K8** | **China (HN)** | **OR262170** | — | — | — | — | — |
| | **Miettinen 10225** | **China (YN)** | **OR262178** | — | — | — | — | — |
| | | French Polynesia | MZ996950 | — | — | — | — | — |
| | | French Polynesia | MZ996951 | — | — | — | — | — |
| | | French Polynesia | MZ996952 | — | — | — | — | — |
| | | India | OM033590 | — | — | — | — | — |
| | **Miettinen 8823.2** | **Indonesia (RI)** | **OR262156** | — | — | — | — | — |
| | | Indonesia (RI) | KJ654526 | — | — | — | — | — |
| | | Indonesia (RI) | KJ654534 | — | — | — | — | — |
| | **Miettinen 9166.5** | **Indonesia (PA)** | **OR262162** | OR262162 | OR295445 | OR296381 | — | — |
| | **Miettinen 9176.2** | **Indonesia (PA)** | **OR262163** | — | — | — | — | — |
| | | Malaysia | HQ400710 | — | — | — | — | — |
| | **Hallenberg 15301** | **New Zealand** | **OR262161** | — | — | — | — | — |

**Table 1.** (Continued).

| Species | Specimen / culture* | Country (province/state) | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
|---|---|---|---|---|---|---|---|---|
| | | | | | | GenBank accession numbers | | |
| | **ICMP 18224*** | **New Zealand** | **OR262169** | – | – | – | – | – |
| | | New Zealand | MN007016 | – | – | – | – | – |
| | | Papua New Guinea | KR015166 | – | – | – | – | – |
| | | Papua New Guinea | KR015237 | – | – | – | – | – |
| | | Papua New Guinea | KR016181 | – | – | – | – | – |
| | | Philippines | MK817568 | – | – | – | – | – |
| | | Philippines | MT597859 | – | – | – | – | – |
| | **Miettinen 18035** | **Puerto Rico** | **OR262175** | **OR262175** | – | – | – | – |
| | **Miettinen 18135** | **Puerto Rico** | OR262176 | – | – | – | – | OR296406 |
| | | Taiwan | MZ423082 | – | – | – | – | – |
| | | Thailand | LC269928 | – | – | – | – | – |
| | | Thailand | MG545057 | – | – | – | – | – |
| *Lividopora facilis* | isotype | **Indonesia (RI)** | OR262154 | OR262154 | OR295441 | OR296379 | – | OR296400 |
| *Lividopora subvincta* | holotype | **Zimbabwe** | OR262197 | – | – | – | – | – |
| | Savchenko 171129/1309A | **Kenya** | OR262196 | – | – | – | – | – |
| | **CFMR ECS-194-R*** | **Tanzania** | KY948734 | KY948873 | OR295449 | – | KY948953 | – |
| *Lividopora vincta* | **Gazis *et al*. NHB39*** | **Brazil (PA)** | OR262173 | – | – | – | – | – |
| | J. Vlasák (JV 1704/102) | Costa Rica | OM669884 | – | – | – | – | – |
| | | Mexico | KU747939 | – | – | – | – | – |
| | **Gazis *et al*. MS512*** | **Peru** | OR262172 | OR262172 | – | – | – | – |
| | | Peru | KJ831895 | – | – | – | – | – |
| | | Peru | KJ831906 | – | – | – | – | – |
| | | Peru | KJ831912 | – | – | – | – | – |
| | | Peru | KJ831915 | – | – | – | – | – |
| | | Peru | KJ831927 | – | – | – | – | – |
| | | Peru | KJ831935 | – | – | – | – | – |
| | | Peru | KJ831950 | – | – | – | – | – |
| | | Peru | KJ832036 | – | – | – | – | – |
| *Panus conchatus* | **Miettinen 17916/OMC 1567*** | **USA (FL)** | KY948735 | KY948874 | – | – | KY948954 | OR296405 |
| | | Finland | JN710579 | JN710579 | JN710695 | JN710643 | – | – |
| | | Puerto Rico | OM337524 | OM337524 | – | – | JACDTX010000312 | JACDTX010000141 |
| *Panus lecomtei* | | USA (AZ) | KP135328 | KP135233 | – | – | KP134877 | – |

**Table 1.** (Continued).

| Species | Specimen / culture* | Country (province/state) | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
| *Parvodontia austrosinensis* | | China (GX) | ON117195 | ON117183 | – | – | – | – |
| *Pseudolagarobasidium acaciicola* | | China | MK247443 | – | – | – | – | – |
| | | China | MT814716 | – | – | – | – | – |
| | | India (AP) | KR149461 | – | – | – | – | – |
| | | India | HQ323693 | – | – | – | – | – |
| | | India | JX886000 | – | – | – | – | – |
| | | India | KP297894 | – | – | – | – | – |
| | | India | MK163558 | – | – | – | – | – |
| | | South Africa | DQ517882 | EU569321 | – | – | – | – |
| | | South Africa | DQ517883 | – | – | – | – | – |
| | | Thailand | KF673346 | – | – | – | – | – |
| *Pseudolagarobasidium baiyunshanensis* | | China (GD) | MT428549 | MT428547 | – | – | – | – |
| | | China (GD) | MT428550 | MT428548 | – | – | – | – |
| *Pseudolagarobasidium belizense* | isotype | Belize | JQ070173 | – | – | – | – | – |
| | **Gazis *et al.* VPB197*** | **Brazil (PA)** | **OR262174** | **OR262174** | **OR295448** | **OR296383** | **OR296391** | **OR296403** |
| | | China (GD) | KM278016 | – | – | – | – | – |
| *Pseudolagarobasidium* sp. | | China | MK790683 | – | – | – | – | – |
| | | China | MK790684 | – | – | – | – | – |
| | | China | MK790685 | – | – | – | – | – |
| | | India | KM053237 | – | – | – | – | – |
| | | Thailand | MK589289 | – | – | – | – | – |
| | | Vietnam | KM234009 | – | – | – | – | – |
| *Pseudolagarobasidium venustum* | holotype of *P. pallens* | Brazil (RS) | MZ649030 | MZ649030 | – | – | – | – |
| | | Brazil (RS) | MZ649031 | MZ649031 | – | – | – | – |
| | | Brazil (SP) | MZ649033 | – | – | – | – | – |
| | **Carranza 120929** | **Costa Rica** | **OR262150** | **OR262150** | – | – | – | – |
| | **K.H. Larsson 11363** | **Costa Rica** | **OR262151** | **OR262151** | – | – | – | – |
| | **K.H. Larsson 10040** | **Puerto Rico** | **OR262152** | **OR262152** | – | – | – | – |
| *Radulodon americanus* | | USA (MN) | JQ070174 | – | – | – | – | – |
| | | USA (MT) | JQ070175 | – | – | – | – | – |
| | | China (YN) | MK404494 | – | – | – | – | – |
| *Radulodon casearius* | | USA (FL) | KY948752 | KY948871 | – | – | KY948943 | – |

**Table 1.** (Continued).

| Species | Specimen / culture* | Country (province/state) | GenBank accession numbers | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
| *Radulodon erikssonii* | **Pennanen 3794** | **Finland** | **OR262200** | – | – | – | – | **OR296426** |
| | **Pennanen 3886** | **Finland** | **OR262199** | – | – | – | – | – |
| | | Norway | KY415963 | KY415963 | KY415964 | KY415971 | – | – |
| | | Sweden | MH864059 | – | – | – | – | – |
| | **Martini (GB 0181279)** | **Switzerland** | **OR359377** | **OR359377** | – | – | – | – |
| *Radulodon yunnanensis* | holotype | China (YN) | OM971916 | OM971936 | – | – | – | OM982705 |
| | | China (YN) | OM971915 | OM971897 | – | – | – | OM982704 |
| | | China (YN) | OM971917 | OM971898 | – | – | – | OM982706 |
| *Somion delectans* | | India | MG719295 | – | – | – | – | – |
| | | India | MT126488 | – | – | – | – | – |
| | | USA | MH856070 | – | – | – | – | – |
| | | USA (KY) | MN430947 | – | – | – | – | – |
| | | USA (MD) | HQ728301 | – | – | – | – | – |
| | | USA (MD) | KY948750 | – | – | – | – | – |
| | **CFMR FP-101579-Sp\*** | **USA (MD)** | **OR262198** | – | – | – | – | – |
| | | USA (MI) | KP135301 | KP135287 | – | – | KP134876 | – |
| | | USA (MS) | HQ728299 | – | – | – | – | – |
| | **J. Vlasák (JV 0809/62)** | **USA (NH)** | **OR262183** | **OR262183** | – | – | – | **OR296411** |
| | **J. Vlasák Jr (JV 1507/22)** | **USA (PA)** | **OR262182** | **OR262182** | – | – | – | **OR296410** |
| | | USA (PA) | HQ728297 | – | – | – | – | – |
| | | USA (PA) | HQ728298 | – | – | – | – | – |
| | | USA (PA) | HQ728300 | HQ729007 | – | – | – | – |
| *Somion formosanum* | **ATCC MYA-262\*, ex-holotype** | **Taiwan** | JQ070094 | JQ070165 | – | – | **OR296396** | **OR296423** |
| *Somion litschaueri* | | Austria | HQ728304 | – | – | – | – | – |
| | | Austria | HQ728306 | HQ729009 | – | – | – | – |
| | | Austria | UDB0802574 | – | – | – | – | – |
| | | China (BJ) | FJ789779 | – | – | – | – | – |
| | | China | MH425279 | – | – | – | – | – |
| | | China | OM971907 | – | – | – | – | – |
| | | China | OM971912 | – | – | – | – | – |
| | **J. Vlasák (JV 1309/1)** | **Czech Republic** | **OR262189** | **OR262189** | – | – | – | **OR296417** |
| | | Czech Republic | HQ728303 | – | – | – | – | – |

Table 1. (Continued).

| Species | Specimen / culture* | Country (province/state) | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
| | | Czech Republic | HQ728305 | — | — | — | — | — |
| | | Czech republic | HQ728307 | — | — | — | — | — |
| | | Czech Republic | HQ729014 | HQ729014 | — | — | — | — |
| | | Russia (PRI) | UDB0780498 | — | — | — | — | — |
| | **J. Vlasák (JV 1309/7)** | **Slovakia** | **OR262190** | **OR262190** | — | — | — | **OR296418** |
| | | — | MH860539 | — | — | — | — | — |
| *Somion occarium* | **epitype** | **Czech Republic** | **OR262180** | **OR262180** | — | — | — | **OR296408** |
| | **J. Vlasák (JV 1310/23)** | **Czech Republic** | **OR262181** | **OR262181** | — | — | — | **OR296409** |
| | | Czech Republic | HQ728294 | HQ729004 | — | — | — | — |
| | | Czech Republic | HQ728295 | HQ729005 | — | — | — | — |
| | | Czech republic | HQ728296 | — | — | — | — | — |
| | **K.H. Larsson 14261** | **Sweden** | **OR262194** | — | — | — | — | — |
| | | — | AJ006670 | — | — | — | — | — |
| *Somion strenuum* | **holotype** | **Russia (KHA)** | **OR262186** | **OR262186** | **OR295451** | — | **OR296394** | **OR296414** |
| | Dai 3041 | China (LN) | KY415961 | KY415961 | KY415966 | KY415969 | — | — |
| | **Miettinen 10546** | **China (LN)** | **OR262164** | **OR262164** | — | — | — | — |
| | | China (LN) | KY415961 | — | — | — | — | — |
| | **Spirin 6112** | **Russia (KHA)** | **OR262187** | **OR262187** | — | — | — | **OR296415** |
| *Somion tomsovskyi* | **J. Vlasák Jr (JV 1209/55)** | **USA (AZ)** | **OR236210** | **OR236210** | **OR295455** | **OR296387** | — | **OR296413** |
| | **J. Vlasák Jr (JV 1307/8)** | **USA (AZ)** | **OR262184** | **OR262184** | — | **OR296386** | **OR296393** | **OR296412** |
| | | USA (AZ) | KY948751 | — | — | — | KY948942 | — |
| *Somion unicolor* | | France | FJ349625 | — | — | — | — | — |
| | | USA (AZ) | HQ728302 | — | — | — | — | — |
| | | USA (GA) | OL142241 | — | — | — | — | — |
| | | USA (LA) | HQ728312 | — | — | — | — | — |
| | | USA (MI) | HQ728311 | — | — | — | — | — |
| | | USA (MO) | HQ728310 | — | — | — | — | — |
| | **J. Vlasák Jr (JV 1304/1)** | **USA (NJ)** | **OR262188** | **OR262188** | — | — | — | **OR296416** |
| | **J. Vlasák Jr (JV 1708/10)** | **USA (NJ)** | **OR262195** | **OR262195** | — | — | **OR296397** | **OR296424** |
| | | USA (VA) | HQ729011 | HQ729011 | — | — | — | — |
| | | USA (WI) | HQ728308 | — | — | — | — | — |
| | | USA (WI) | HQ728309 | — | — | — | — | — |

**Table 1.** (Continued).

| Species | Specimen / culture* | Country (province/state) | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | ITS | LSU | mtSSU | ATP6 | RPB1 | TEF1 |
| | | — | HQ728313 | — | — | — | — | — |
| | | — | MH854650 | — | — | — | — | — |
| *Somion cf. unicolor* | | USA (AZ) | OP297810 | — | — | — | — | — |
| *Somion* sp. | | China | MW554292 | — | — | — | — | — |
| | | — | AY089734 | — | — | — | — | — |

We compiled eight sequence datasets for phylogenetic analysis. Selection was based on ITS and LSU sequence similarity searches for each *Cerrenaceae* species in GenBank (using BLAST; Altschul *et al.* 1997) and UNITE (Nilsson *et al.* 2018) implemented in PlutoF (using BLAST and species hypothesis annotation; Abarenkov *et al.* 2010). We referred to Justo *et al.* (2017) when selecting the outgroup (the closest relative *Panaceae*) for the family-level dataset. For the other datasets (genus-level trees), which were compiled mainly for species delimitation, we used mid-point rooting without an outgroup. Since genetic distances between genera are generally large, including outgroup sequence with a divergent ITS sequence would have decreased the number of homologous (alignable) characters significantly, reducing species resolution.

We aligned the sequences with PRANK v. 170427 (Löytynoja 2021) or the MAFFT online service with E-INS-I (Katoh *et al.* 2017), each marker individually, and adjusted them manually in PhyDE v. 0.9.7.1 (Müller *et al.* 2010). We excluded characters from the 6-marker dataset manually when judged as non-homologous. The datasets, with the final alignment length and the number of parsimony informative sites calculated in MEGA v. 7 (Kumar *et al.* 2016) are as follow: i) a 6-marker dataset of *Cerrenaceae* (1 091 parsimony informatic characters/5 228 total characters), ii) *Cerrena* ITS (72/618), iii) *Irpiciporus* ITS (32/588), iv) *Irpiciporus* ITS+*TEF1* (63/1 604), v) *Lividopora* ITS (39/604), vi) *Pseudolagarobasidium* ITS (61/564), vii) *Radulodon* ITS (11/597), viii) *Somion* ITS (32/542), ix) *Somion* ITS+*TEF1* (138/1 684), and x) *Cystostereaceae* ITS (93/708).

The 6-marker dataset of the *Cerrenaceae* contained nrDNA ITS and LSU, mtSSU, *ATP6*, *TEF1* and *RPB1*. Two of the markers are mitochondrial (mtSSU and *ATP6*), and all, except for ITS and LSU, independently evolving. To reduce gaps in the alignment, data within five species were fused so that for *Cerrena 'gilbertsonii'*, GenBank OR296399 was used for *RPB1* while the rest of the markers were from *Vandevender 94-144* (GenBank OR262171, *etc.*); GenBank KP134874 was used for *RPB1* of *Cerrena unicolor* while the rest were from the collection *Larsson* (GenBank JN710525, *etc.*); GenBank KP134876 for *RPB1* of *Somion delectans* while the rest of the markers were from the collection *Vlasák Jr.* JV 1507/22 (GenBank OR262182, *etc.*); GenBank KY948942 for *RPB1* of *Somion tomsovskyi* while the rest of the markers were from *Vlasak* JV 1209-55 (GenBank OR236210, *etc.*); and GenBank OR296426 for *TEF1* of *Radulodon erikssonii* while the rest were from *Hofton 09820* (GenBank KY415963, *etc.*). In all these cases, the ITS similarity was > 99.5 %. Thus compiled, marker data were missing for 27 % of the maximum 180 marker sequences. At the level of genera, only one marker sequence out of 54 (mtSSU of *Acanthodontia*) was missing.

Models for the phylogenetic analyses were selected for each marker and dataset by AICc ModelTest-NG v. 0.2.0 (Darriba *et al.* 2020). We inferred phylogenies with MrBayes v. 3.2.7a (Ronquist *et al.* 2012) and RAxML-NG v. 1.1.0 (Kozlov *et al.* 2019). Bootstrap support values for the RAxML maximum likelihood analyses were calculated from 1 000 replicas. MrBayes v. 3.2.7a was run with three parallel runs of 8 chains each for 2–4 million generations, sampling every 10 000 generations. Good convergence (standard deviation of split frequencies < 0.01) was reached in all cases and the standard 25 % burnin was used when compiling the consensus tree. All computations were run at the CSC – IT Centre for Science (Espoo, Finland) computing environment. The alignments, with model information included in their nexus blocks, are available at PlutoF (doi: 10.15156/BIO/2938061).
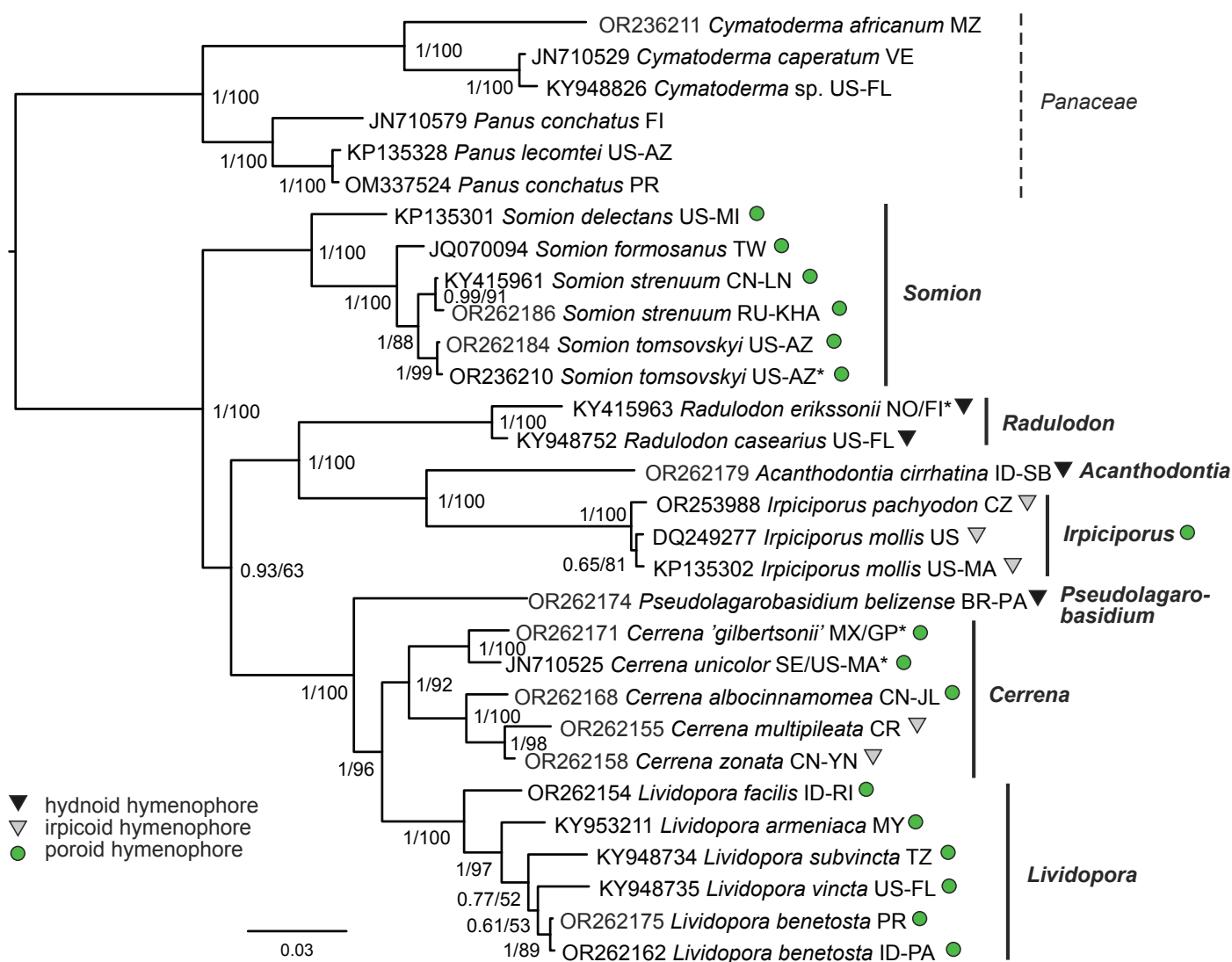
**Fig. 3.** Bayesian consensus phylogram of the *Cerrenaceae* based on four nuclear (ITS, nLSU, *RPB1, TEF1*) and two mitochondrial (mtSSU, *ATP6*) genetic markers. Decimal support values denote posterior probabilities, while values over 50 % denote bootstrap support. The INSDC accession numbers for each leaf refer to ITS. Leaves with asterisk (*) contain data of several specimens (see Material and Methods). Countries (and states) of origin are denoted with ISO 3166 codes.

## RESULTS

The 6-marker phylogenetic estimate confirms the *Cerrenaceae* as a well-supported family (Fig. 3). It resolves three main clades within the family: *Somion* containing *Spongipellis delectans* and relatives, *Irpiciporus-Radulodon* and *Cerrena-Pseudolagarobasidium*. Individual marker phylogenies mostly confirm this, but *TEF1* and *RPB1* do not support monophyly of the *Irpiciporus-Radulodon* clade (Supplementary Figs S1–S5).

How should genera in the family be delimited in the light of this information? Our analysis provides several possible solutions in balancing morphology with phylogenetic information. We have assumed here that phylogenetic distance must be reflected in genus limits. Thus, we consider all clades of equal phylogenetic distance consistently as genera within the family, requiring all clades above a threshold be treated equally when deciding on their generic status. Under this condition, and by maximizing morphological distinctiveness and minimizing nomenclatural change, we have divided the family into seven genera, two of them newly described: *Acanthodontia gen. nov.*, *Cerrena*, *Irpiciporus*,

*Lividopora gen. nov.*, *Pseudolagarobasidium*, *Radulodon*, and *Somion* (Table 2). ITS-based trees of all the genera (except the monotypic *Acanthodontia*) are provided in the taxonomy section.

### *Cerrena-Pseudolagarobasidium* clade

The 6-marker phylogeny supports dividing the *Cerrena-Pseudolagarobasidium* clade into three to four parts: *Cerrena unicolor* and relatives, *Cerrena zonata* and relatives, *Rigidoporus vinctus* and relatives, and *Pseudolagarobasidium* (Fig. 3). When analyzed individually (Supplementary Figs S1–S5), only *RPB1* (Supplementary Fig. S4) produces a similar topology as the 6-marker dataset (supporting a clade containing *C. unicolor* and *C. zonata*). However, also the ITS+LSU and *ATP6* datasets support division into the above-mentioned four subclades, albeit with a different branching order (Supplementary Figs S1, S3). The rest of the markers, mtSSU and *TEF1*, fail to recover the four clades (Supplementary Figs S2, S5). None of the individual marker phylogenies contradicts the 6-marker phylogeny, and differences are due to the lack of support for most nodes.

**Table 2.** Morphological comparison of accepted genera in the *Cerrenaceae*.

| Genus | Basidiocarp | Hymenial surface | Hyphal system | Cystidia | Spores | Other |
|---|---|---|---|---|---|---|
| *Acanthodontia* | Effused-reflexed, whitish | **Regular long spines** | **Dimitic** but dominated by generatives, gen. hyphae slightly thick-walled, uniform, neatly arranged | **Tramal cystidia** slightly thick-walled, bend into hymenium | Slightly thick-walled, with guttula | Subhymenium well developed |
| *Cerrena* | Effused to reflexed, whitish to brown-gray | Regularly **poroid** to irpicoid | **Dimitic** | Hymenial thin-walled, staining cystidia | Thin-walled, no guttula | — |
| *Lividopora* | Effused, red to brown to gray | Regularly **poroid**, **small-pored** | **Dimitic** | 1) **Encrusted skeletocystidia**, 2) hymenial thin-walled stained cystidia | Thin-walled, no guttula | **Clamps absent** |
| *Pseudolagarobasidium* | **Effused**, whitish tobrownish-grayish, thin | **Hydnoid** with short blunt teeth to irpicoid | Monomitic & microbinding hyphae | 1) **Tramal cystidia** slightly thin-walled, bend into hymenium, 2) hymenial thin-walled, staining cystidia | **Thin-walled, no guttula** | — |
| *Radulodon* | **Effused**, whitish | **Regular spines** | Monomitic, **messy**, hyphae thin- to slightly thick-walled | **Hymenial cystidia**, thin-walled | **Slightly thick-walled**, **with guttula** | — |
| *Irpiciporus* | Effused-reflexed to reflexed, relatively **thin**, whitish | **Irpicoid** to sinuous pores | **Monomitic**, **neat**, hyphae slightly thick-walled, uniform | **None** | **Slightly thick-walled**, with guttula | Subhymenium almost nonexistent; **basidia long** (> 20 µm) |
| *Somion* | Reflexed, **thick**, context duplex, whitish | **Pores regular to sinuous** | **Monomitic**, **neat**, with a mix of thin- and **thick-walled hyphae** | **None** | **Thick-walled**, with guttula | Subhymenial cells differentiated; basidia short (mostly < 20 µm) |

The resulting phylogeny leaves us with four well-supported options in delimiting genera in the *Cerrena-Pseudolagarobasidium* clade. First, phylogenetically perhaps the simplest solution would be to include all species in this clade in one genus (*Cerrena*). All the species in this clade share some morphological characters: dimitic hyphal structure, thin-walled, ellipsoid, middle-sized spores, and thin-walled hymenial cystidia ("gloeocystidia"). They are all aggressive wood-rotters, and there are tree pathogens in all the subclades. Species in the clade grow fast on malt agar and are enzymatically active (Nobles 1948, Westhuizen 1963, Setliff 1972a, Maekawa 2002, Wood & Ginns 2006). However, morphological differences of basidiocarps between the extremes are still quite significant (see below), and one large genus would be at odds with the current traditions of defining polypore and corticioid genera morphologically.

Second, the genus could be divided into hydnoid and near-monomitic *Pseudolagarobasidium* on one hand, and dimitic polypores of *Cerrena* and *Rigidoporus vinctus* on the other. Thus delimited, *Cerrena* would be better morphologically defined, but still quite heterogenous. This option would induce minimal name changes.

The third option is to divide the clade into three genera: hydnoid, effused, nearly monomitic *Pseudolagarobasidium*, dimitic *Cerrena* with clamped hyphae and irregular/dentate pores (including *C. unicolor* and *C. zonata* subclades), and dimitic but simple septate *Rigidoporus vinctus* coll. with encrusted skeletocystidia and regular, small pores. Thus defined, the three groups are distinct and easy to separate from each other. We consider this the best solution currently and describe here the genus *Lividopora* for the *R. vinctus* subclade.

Lastly, the fourth option would be to divide the clade into four genera: *Cerrena sensu stricto* (*C. unicolor* and relatives), a new genus for *C. zonata* and relatives, *Lividopora*, and *Pseudolagarobasidium*. This option, too, has merits. Morphologically, there are some differences between the *C. unicolor* and *C. zonata* clades: more pronounced pigmentation in *Cerrena sensu stricto*, duplex context, more distinct gloeocystidia in the *C. zonata* subclade, and subtle differences in hyphal structure. However, these characters (except duplex context) are subject to gradation. In our experience, they are not as informative phylogenetically as, for instance, the presence of skeletocystidia or type of septation, which are more reliable and easier to interpret among polypores. Furthermore, as shown under taxonomy part of *Cerrena*, diversity in the *C. zonata* clade exceeds the currently described species and our material. Hence, a genus description for this clade would be outdated from the start – a clear argument for sticking to larger

genera. Finally, if the *Cerrena-Pseudolagarobasidium* clade would be divided into four genera, and we would define all similarly distant clades in the family as separate genera, the *Somion* clade (*Spongipellis delectans* and relatives) would also be split into two, morphologically very similar sister genera, which we think is unnecessary.

### *Radulodon-Irpiciporus* clade

The *Radulodon-Irpiciporus* clade is divided phylogenetically into three subclades: *Radulodon sensu typi*, *R. cirrhatinus*, and *Irpiciporus*. This clade is morphologically fairly homogenous: basidiocarps are light-coloured, hydnoid or irpicoid, (nearly) monomitic with clamps, hymenial cells relatively large, and spores slightly thick-walled. Placing these species in one genus would be a good option from this perspective. Phylogenetically the three parts are distant, however. Considering our genus concepts in the *Cerrena-Pseudolagarobasidium* clade, *i.e.*, division of that clade into several genera, the three parts of the *Radulodon-Irpiciporus* clade must be considered separate genera. We describe here a monotypic genus *Acanthodontia* for *Radulodon cirrhatinus*. Despite similarities, there are some differences between the genera: *Acanthodontia* and *Radulodon* are fully hydnoid whereas *Irpiciporus* are irpicoid to poroid; cystidia and rare skeletal hyphae are found in *Acanthodontia* and *Radulodon*. The latter two differ for instance in their hyphal structure and nature of skeletal hyphae (Table 2).

### *Somion* clade

*Spongipellis delectans* and its relatives form a distinct clade and clearly merit recognition at the genus level. They are monomitic polypores with clamps and loose structure, thick-walled spores and big, light-coloured caps, somewhat similar to *Spongipellis sensu stricto*, which belongs to a different family, *Meripilaceae* (Spirin *et al.* 2022). Wang & Dai (2022) reached similar conclusion about this clade's generic status and described *Pseudospongipellis*. We adopt the genus name *Somion* as the correct name for this clade. *Somion delectans* and its European sibling *S. occarium* are phylogenetically distinct from the rest of the species, but since morphological differences are small, we see no reason to split this genus further.

### Taxonomy

***Acanthodontia*** Miettinen & Spirin*, gen. nov.* MycoBank MB 849641.

*Type species*: *Acanthodontia cirrhatina* (Hjortstam & Spooner) Miettinen & Spirin

*Etymology*: Derived from ἄκανθος (Greek, noun), thorn, and -odon derived from the Greek word for sharp teeth, ὀδοντιάω.

Pileate, sessile, white to cream *basidiocarps* with long spines underneath. *Hyphal system* dimitic with clamps in all septa of generative hyphae, but skeletal hyphae found in context and subiculum only, otherwise monomitic and dominated by slightly thick-walled generative hyphae, in trama subparallel. Long, slightly thick-walled sack-like *cystidia* embedded in trama and hymenium. *Basidiospores* ellipsoid, mid-sized, smooth, slightly thick-walled, with a large guttule, cyanophilous.

***Acanthodontia cirrhatina*** (Hjortstam & Spooner) Miettinen & Spirin, ***comb. nov.*** MycoBank MB 849642. Figs 2, 4.
*Basionym*: *Radulodon cirrhatinus* Hjortstam & Spooner, Kew Bull. 45: 312, 1990.

*Typus*: **Malaysia**, Sabah, Danum Valley, on a fallen log, 30 Nov. 1985, *Spooner 295\** (**holotype** K(M) 62575, studied).

*Basidiocarp* resupinate to half-resupinate, caps white, with a rough but hairless upper surface, projecting up to 2 cm; resupinate patches up to 10 cm wide. Hymenophore consists of regular conical spines, 4–15 mm long and 2 per mm, white to cream when fresh with reddish brownish tints upon drying. Subiculum white, uniform, 0.5–1 mm thick, cap context 1–2 mm thick, up to 7 mm at the base. Margin distinct, often with a 1–2 mm wide zone of sterile subiculum visible.

*Hyphal system* dimitic, but skeletal hyphae rare and concentrated in cap context, clamps present. Generative hyphae homogenous, slightly thick-walled, (2.2–)2.8–4.4(–5.8) µm diam in subiculum, (2.4–)3.0–4.2(–5.3) µm in trama. Subiculum structure similar to context, but skeletal hyphae fewer. Context a loose, interwoven structure with segments of skeletal hyphae here and there, (2.0–)2.4–3.1(–3.9) µm diam. Tramal hyphae subparallel, structure rather loose; a distinct subhymenial layer consisting of strongly interwoven hyphae, 20–50 µm thick. *Cystidia* clavate, tramal or rarely subhymenial in origin, bending into hymenium, projecting up to 10 µm, slightly thick-walled basally when young, thick-walled and cyanophilous when old, often with constrictions when old, occasionally tapering but always blunt, sometimes with a deep root, 38–135 × 9–17 µm (up to 70 µm long without the root). Similar, swollen cells embedded in context. *Basidia* clavate, some constricted, (14–) 16–26 × 5.5–6.8 µm, with 4 sterigmata. *Basidiospores* ellipsoid, slightly thick-walled (walls 0.2–0.3 µm), uniguttulate, slightly to distinctly cyanophilous, 4.0–5.1(–5.2) × (3.4–)3.5–4.2(–4.3) µm, L = 4.69 µm, W = 3.79 µm, Q = 1.21–1.26.

*Distribution and ecology:* The two known finds are from lowland rainforests in insular Southeast Asia, *viz*. Borneo and Sumatra.

*Notes*: *Acanthodontia cirrhatina* is easy to identify by its long spines, effused-reflexed basidiocarps and tramal cystidia that penetrate the hymenium. This monotypic genus is morphologically quite similar to its sister taxon, *Irpiciporus*. The phylogenetic distance to *Irpiciporus* is sufficiently large and consistent throughout genetic markers that *A. cirrhatina* should warrant its own genus. They share very similar cyanophilous spores, hymenium, and the tramal construction of loosely arranged, subparallel hyphae. Basidiocarp habit is also quite similar, but the *A. cirrhatina* hymenophore consists of regular, slender, conical spines, whereas *Irpiciporus* spp. have poroid to irpicoid hymenophore. Microscopically, skeletal hyphae and cystidia of *Acanthodontia* are lacking in basidiocarps of *Irpiciporus*. Subhymenial layer appears more visible and thicker than in *Irpiciporus* spp.

The next closest kin, *Radulodon* spp., form fully effused, thinner basidiocarps. Microscopically, the interwoven, messy-looking hyphal structure is different, and skeletal hyphae are much narrower. Cystidia are a shared character between the two genera, and along with the hydnoid hymenophore the reason why *A. cirrhatina* was described in *Radulodon*.
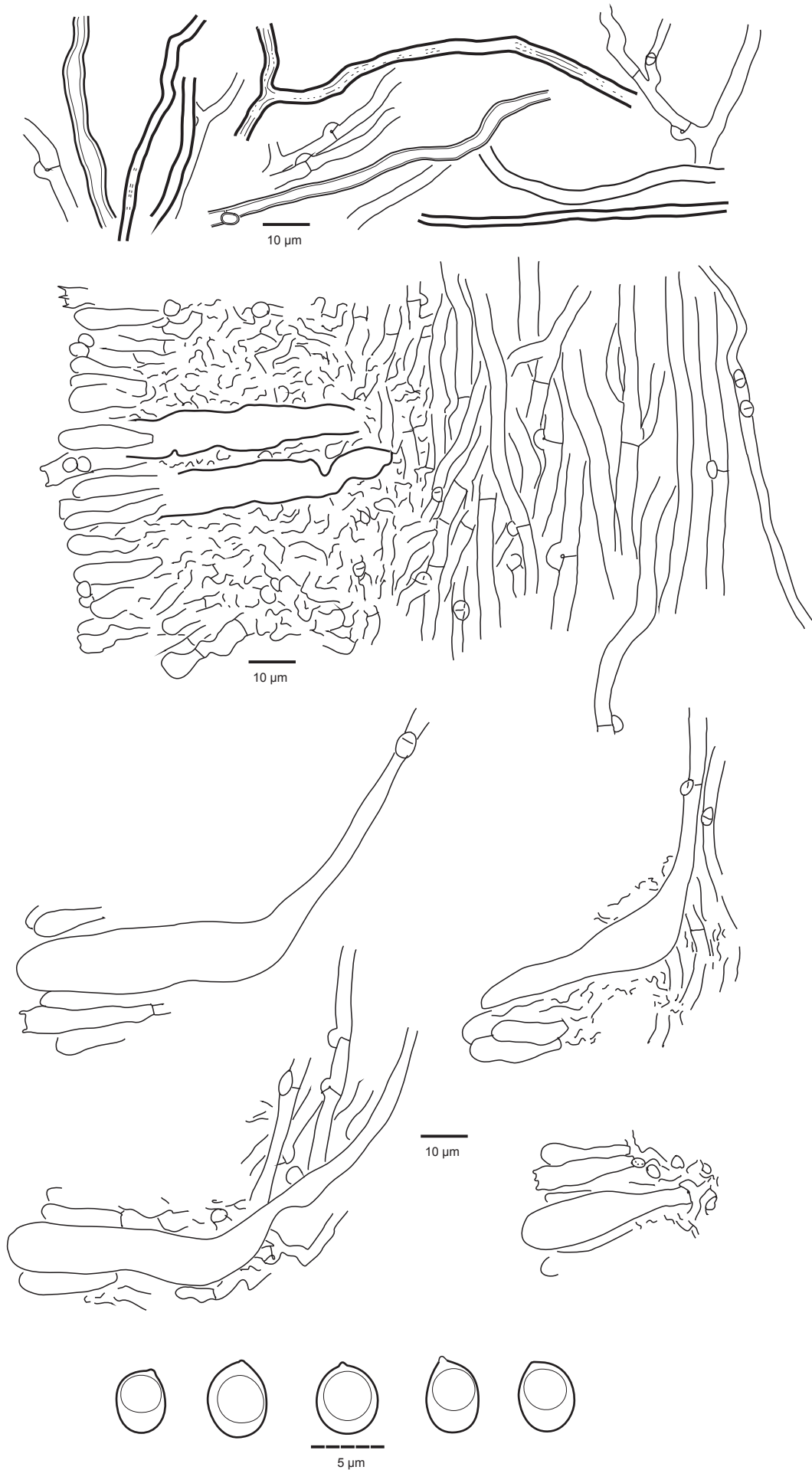
**Fig. 4.** Microscopic structures of *Acanthodontia cirrhatina* (*Miettinen 13717*). Subicular skeletal and generative hyphae, trama and hymenium, cystidia, and spores.

Nakasone (2001) studied the type specimen and accurately described skeletal hyphae; later she considered the species monomitic with sclerified segments of generative hyphae (Nakasone & Ortiz-Santana 2022). In our view, those segments and hyphae should be called skeletal hyphae. They are found in old cap context, and do not dominate structure anywhere. Another slightly younger specimen (*Miettinen 13717*) has so few skeletal hyphae that we found them only after specifically looking for them in context. Vegetative mycelial mats associated with the latter specimen are dominated by narrow skeletal hyphae with occasional thin-walled branches that branch at right angles, reminiscent of (but not fully similar to) the microbinding hyphae documented by David (1969) in *Irpiciporus pachyodon*.

***Cerrena*** Gray, *A natural arrangement of British plants* 1: 649. 1821.

*Type species*: *Boletus unicolor* Bull.

Pileate to resupinate polypores with cream, brownish to grey *basidiocarps* with a cottony context. *Pores* mid-sized, irregular in old specimens, in some species irregular already when young. *Hyphal system* dimitic with clamps; intermediary hyphae and branching skeletal hyphae may be present. Hyphae CB(+), IKI-, KOH-, CRB lilac. Hymenial, thin-walled cystidia with a stained inclusion ("gloeocystidia") present, though may be absent in young specimens. *Basidiospores* ellipsoid, mid-sized, with thin or distinct walls. Aggressive white rotters.

*Notes*: *Cerrena* can remind of other polypore genera with pilei and dimitic hyphal structure, such as *Antrodiella*, *Funalia*, and *Trametes*. However, thin-walled hymenial cystidia are not present in *Funalia* or *Trametes*, and the latter genus is distinctly trimitic. Furthermore, ellipsoid spores are rare in *Trametes* and not known from *Funalia*. In *Antrodiella sensu stricto*, thin-walled hymenial cystidia ("gloeocystidia") may be present in older basidiocarps, but spore and basidial size is consistently smaller and so is mostly pore size.

Two subclades can be distinguished in *Cerrena* as we define it (Fig. 3): the *Cerrena unicolor* complex (incl. *C. cystidiata* and *C. 'gilbertsonii'*) with brownish-greyish basidiocarps, and the *C. zonata* complex (incl. *C. albocinnamomea* and *C. multipileata*) with light-colored basidiocarps. The latter complex was placed in *Antrodiella* (Dai & Niemelä 1997, Nuñez & Ryvarden 2001, Ryvarden 2015), until Yuan (2014) moved some of them to *Cerrena* solely on phylogenetic grounds. We considered two separate genera for these clades, but we decided against splitting. Microscopically, the larger *Cerrena* is quite homogenous. Irregular pores are also shared by all species. Colour difference of basidiocarps is also not a clear separating character: *C. albocinnamomea*, as the name implies, turns brownish when old, and young specimens of *C. unicolor* are white. ITS data (Fig. 5) show that more species than described here are present, forming a third clade, but we have no information about their morphology. All these arguments support a larger genus. Duplex context is a unique character for the *C. unicolor* clade within the genus.

When Gray (1821: 649) described *Cerrena*, he accepted only one species, *Cerrena cinerea* (Pers.) Gray. He mentioned *Sistotrema cinereum* Pers. and *Boletus unicolor* Sowerby (= *B. unicolor* Bull.) as synonyms of the aforementioned species. Both are available for typification of the genus (ICN Shenzhen art.

10.2). The lectotypification is traditionally assigned to Murrill (1903: 91), who chose *Daedalea unicolor* (Bull.) Fr. as the genus type. Later he mentioned *S. cinereum* as the type (Murrill 1908). Recent changes in the International Code of Nomenclature suppress typifications by Murrill (art. 10.5, 10.7). The next oldest typification we could trace is by Bondartsev (1953: 45), who selected "*Cerrena unicolor* (Bull.) Murrill" as the type species.

Fries (1821, 1828) considered *Sistotrema cinereum* Pers. a synonym of *Daedalea unicolor* (Bull.) Fr. The latter name is thus sanctioned. Fries also accepted *Daedalea cinerea* as a separate species, but with a different identity than *S. cinereum*, even though he considers part of Persoon's concept of *S. cinereum* to belong to his *D. cinerea*. Formally, the identity of *D. cinerea* Fr. is not relevant for the typification of *Cerrena*. To conclude, the correct, sanctioned name for the type species of *Cerrena* is *C. unicolor* (Bull.) Murrill.

The relationship of *Cerrena* and *Trametes* has been a subject of discussion due to their morphological similarity (Ryvarden 1991). The two genera are not closely related as DNA phylogenies reveal. Bipolar mating system (Westhuizen 1963, Nobles 1965), broad ellipsoid spore shape (rare in *Trametes*), and less clearly trimitic hyphal system are some of the characters that separate *Cerrena* from *Trametes*.

The hyphal system in *Cerrena unicolor* does not readily fit into terminology of hyphal system types. Gilbertson & Ryvarden (1986) and Bernicchia (2005), for instance, call it trimitic and Niemelä (2005) di-trimitic. The context and lower trama consist of long, straight, wide skeletal hyphae intermixed with generative and narrower, winding, and occasionally branching skeletal hyphae ("binding hyphae"). The structure appears trimitic initially, but it is not as distinct as in *Trametes*, where skeletal and binding hyphae can usually be separated with ease. In the case of *Cerrena*, the distinction between the two "types" is not clear-cut, and intermediary hyphae occur – sometimes a single hypha may turn from skeletal to "binding". In his detailed study Westhuizen (1963) finds two types of hyphae but points out that clamps are found on the thick-walled hyphae. He goes on to define this species monomitic. We have also observed that thick-walled clamps at the start/end of skeletal segments are rather common (not so in *Trametes*). In our view, the hyphal structure in *C. unicolor* is best described as dimitic, with some intermediary hyphae and branching of skeletal hyphae.

***Cerrena albocinnamomea*** (Y.C. Dai & Niemelä) H.S. Yuan, *Mycol. Progr*. **13**: 362. 2013. [2014]. Fig. 1.
*Basionym*: *Antrodiella albocinnamomea* Y.C. Dai & Niemelä, *Mycotaxon* **64**: 70. 1997.
*Synonym*: *Cerrena aurantiopora* J.S. Lee & Y.W. Lim. *Mycologia* **102**: 212. 2010.

*Typus*: **China**, Jilin, Antu, Changbaishan, on stump of *Acer*, 5 Sep. 1993, *Dai 1063* (**holotype** of *Antrodiella albocinnamomea* H).

*Notes*: For description, see Dai & Niemelä (1997). This temperate East Asian species with resupinate basidiomes can be mistaken for *Antrodiella*. The cottony subiculum and sterile, even fimbriate margin, relatively large size of basidiomes and a bit larger spore size separate it from *Antrodiella sensu stricto*. The hymenial cystidia, although present, can be rare and difficult to find.

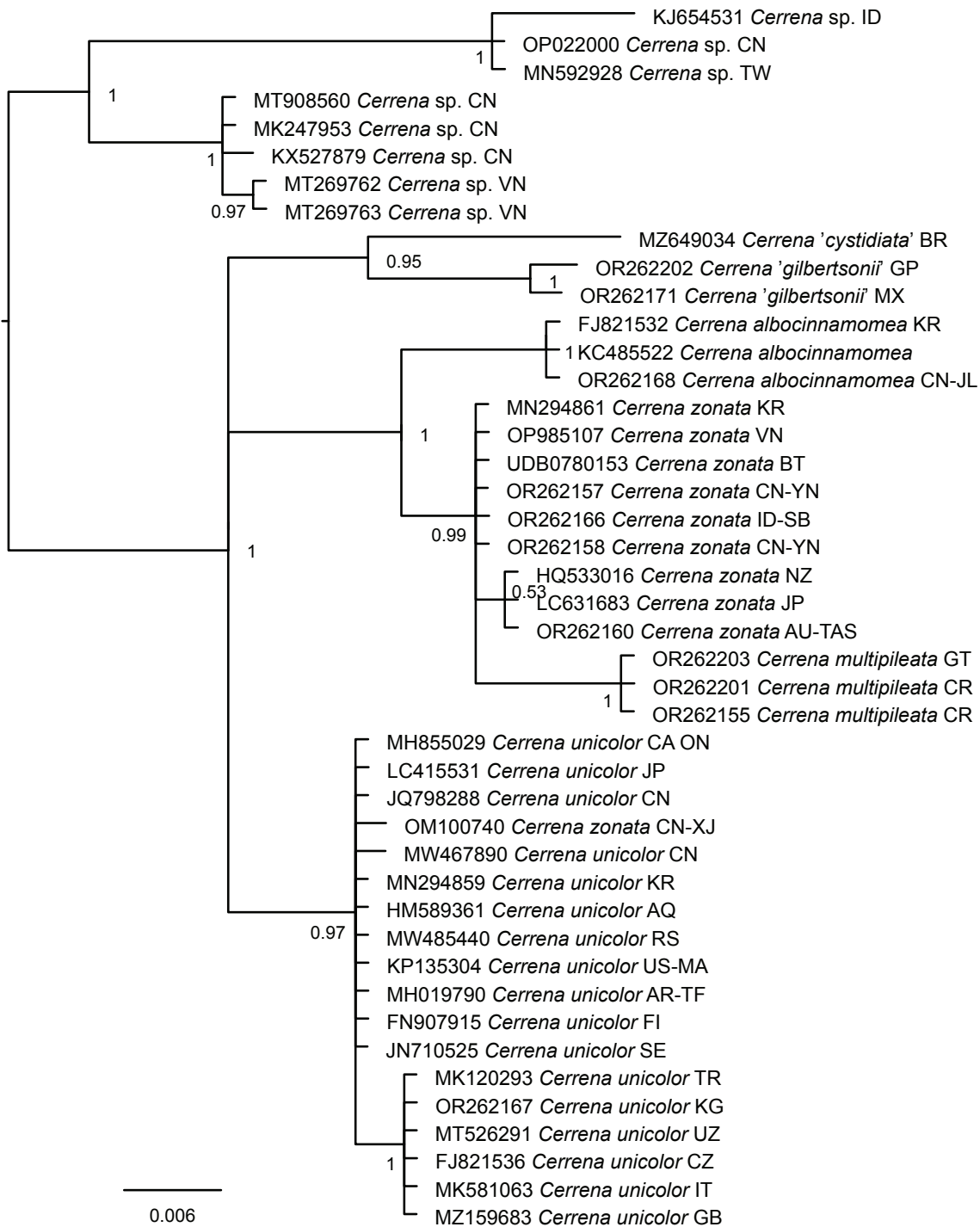***Cerrena cystidiata*** Rajchenb. & Meijer, *Mycotaxon* **38**: 176. 1990.

**Fig. 5.** Bayesian consensus phylogram of *Cerrena* spp. based on ITS sequences. For each leaf, the GenBank accession number, the species name (as available), and the ISO 3166 country code of the country of origin are shown.

*Typus*: **Brazil**, Paraná, São José dos Pinhais, Reserva Biológica Cambuí, dead and standing *Sebastia connersoniana*, 22 May 1988, *de Meijer 1169* (**holotype** BAFC 31626).

*Notes*: Westphalen & Motato-Vásquez (2022) provide a sequence they have labelled as *C. cystidiata* from the south of Brazil, where the type was collected. They do not mention if they have compared it with the type, nor do they provide a description. The sequence is unique and closely related to *C. 'gilbertsonii'* and *C. unicolor* (Fig. 5). It is not out of the question that *C. 'gilbertsonii' sensu* Ryvarden could be found in Brazil as well, so comparison

with the type is needed to confirm if the Brazilian specimen or *C. 'gilberstonii'* actually belong to this species. Looking at the protologue, we cannot readily point to any clear differences to separate *C. cystidiata* from *C. 'gilbertsonii'*.

***Cerrena 'gilbertsonii'* Ryvarden, *nom. prov.* Fig. 6.**

*Typus*: **Mexico**, Sonora, Alamos area, Rio Cuchujaqui, El Guyabo crossing, on *Croton cf. niveus*, 14 Mar. 1994, *Vandevender 94-144* (**holotype** ARIZ, **isotype** O* studied).

*Notes*: When Ryvarden (2012) first described this species, he omitted holotype herbarium information, making the description invalid from a nomenclatural perspective (ICN Art. 40.7). In Ryvarden (2015) he amended his description with the holotype information to validate the name, but without supplying a digital identifier, which is required since 2013 (ICN Art. F.5.1). Thus, the name remains invalid. Since the identity of *C. cystidiata* vs. *C. 'gilberstonii'* is unclear, we refrain from validating the name, but use it as *nomen provisorum* to denote a good species separate from *C. unicolor*.

*Cerrena 'gilbertsonii'* is very close to *C. unicolor* phylogenetically and morphologically. As Ryvarden (2012) describes, usually its basidiocarps are smaller and thinner and more hydnoid than those of *C. unicolor*. However, variation in *C. unicolor* is considerable and equally hydnoid specimens are found in the latter species as well. Its basidiocarps may also be small and thin. Judging by the few samples we have seen, the upper surface is consistently brown and hairs shorter than in *C. unicolor*, whose caps are initially much lighter in colour and never as evenly brown. Ryvarden (2015) mentions the presence of gloeocystidia as a separating character. Gloeocystidia are also found in *C. unicolor*, and they are notoriously unreliable as a character for identification, being sometimes absent and highly dependent on basidiocarp age. Spore shape and size, however, seem to be reliable microscopic characters: spores in *C. unicolor* are narrower (on average about 3 µm, Q > 1.5) than in *C. 'gilbertsonii'* (width about 3.5 µm, Q < 1.5; Table 3, Fig. 6).

*Cerrena multipileata* (C.L. Leite & J.E. Wright) Miettinen, *comb. nov.* MycoBank MB 849643.
*Basionym*: *Antrodiella multipileata* C.L. Leite & J.E. Wright, *Mycotaxon* **41**: 167. 1991.

*Typus*: **Brazil**, Santa Catarina, Florianópolis, Morro da Lagoa da Conceição, 27 Jul. 1998, *Leite & Furlani 251* (**holotype** FLOR 10633, studied).

*Notes*: This species is an American counterpart of *C. zonata* from Asia. We have not been able to find morphological differences between the two species, but it should be said we have limited material of *C. multipileata* at hand. Our sequenced specimens of *A. multipileata* are not from the type area in South Brazil but rather from Central America. ITS sequences differ slightly (7 bp, 1.3 %) between the two species. For the time being, we retain *C. multipileata* as a distinct, geographically defined species.

*Cerrena unicolor* (Bull.) Murrill, *North American Flora* **9**(2): 124. 1908. Figs 1, 6.
*Basionym*: *Boletus unicolor* Bull., *Herbier de la France* **9**: t. 408. 1789; sanctioned as *Daedalea unicolor* (Bull.) Fr., *Syst. Mycol.* **1**: 336. 1821.
*Synonyms*: *Polystictus prosector* Lloyd, *Mycological Writings* **7**(67): 1147. 1922. See MycoBank for additional synonyms.

*Typus*: **Lectotype** of *Daedalea unicolor* designated here, plate 408 of Bulliard (1789) cited in the sanctioning work (Fries 1821), MBT 10014555.

*Notes*: *Cerrena unicolor* is a variable species, abundant in the boreal zone and rather frequent in the temperate zone. For a description, see Ryvarden & Melo (2016).

It would appear that the northern specimens are on average more robust and less irpicoid than the southern ones. ITS variation (Fig. 5) does not suggest more than one species in Eurasia. The same species is also found in North America. Nuñez & Ryvarden (2001) list *C. cystidiata* for East Asia, though it is unclear if their description is based on Asian material (the species was described from South America). Our sequenced specimen from Kyrgyzstan fits their description yet it represents *C. unicolor*. As mentioned under *'C. gilbertsonii'*, gloeocystidia are not a reliable character for separating species in this complex. The type of *Polystictus prosector* from China is a similar, thin, small-pored specimen with many gloeocystidia, and for the time being we consider it a synonym of *C. unicolor*.

We have not been able to locate a proper typification for the species *Daedalea unicolor*. Ryvarden (1991) selected a neotype (his "lectotype" from 1850 must be considered a neotype), but a neotype should only be selected if no original material is in existence (ICN art. 9.8). The illustrations cited in the protologue and the sanctioning work are part of such original material and, in the absences of specimens, must be used for lectotypification (art. 9.4). Thus, we select here the plate 408 of Bulliard (1789) cited in the sanctioning work (Fries 1821) as the lectotype of *D. unicolor* (Bull.) Fr. The current species concept of *C. unicolor* in Europe and the lectotype illustrations are clear enough that we see no need for an epitype.

Murrill (1903) did not accept *Cerrena* as a good genus, and therefore his 1903 combination of *C. unicolor* is invalid (ICN art. 33.1). In Murrill (1908: 124) he does accept *Cerrena* and this should be considered the correct publication for the valid combination.

*Cerrena zonata* (Berk) H.S. Yuan, *Mycol. Progr.* **13**: 363. 2013. [2014]. Figs 1, 7.
*Basionym*: *Irpex zonatus* Berk., *Hook. J. Bot.* **6**: 168, 1854.
*Synonyms*: *Irpex consors* Berk., *J. Linn. Soc. Bot.* **16**: 51. 1877.
*Cerrena consors* (Berk.) K.S. Ko & H.S. Jung, *FEMS Microbiol. Lett.* **170**: 185. 1999.
*Irpiciporus consors* (Berk.) Murrill, *Mycologia* **1**: 166. 1909.
*Irpiciporus japonicus* Murrill, *Mycologia* **1**: 166. 1909.

*Typus*: **Nepal**, Ilam district, 8 Nov. 1848, *Hooker* (**lectotype** of *Irpex zonatus* designated here K(M) 147643, MBT 10014532, studied).

*Notes*: This species is easy to recognize by its pilei with an irpicoid hymenophore combined with dimitic structure with clamps and cystidia. Ryvarden (1992) provided a description and compiled a comprehensive treatise on the nomenclature. He studied types of *I. zonatus* and eight other species described from Australia, Indian Himalayas, Japan, and New Zealand. He found them to represent the same taxon, for which the oldest name is *I. zonatus*. Ryvarden gives a good description of the species, and we trust his concept of the species. Our ITS dataset (Fig. 5) contains sequences of this species among others from New Zealand, Australia, Sumatra, Vietnam, Bhutan, Japan, and Chinese Himalayas, and these specimens show little ITS variation, supporting the conclusion about one wide-spread species, excluding Neotropics, where the sister species *C. multizonata* is found.

In his otherwise comprehensive paper, Ryvarden (1992) did not lectotypify *I. zonatus*. Also Maas Geesteranus (1974: 503) left the matter open, and in his type studies Ryvarden (1977) does not deal with the species. Berkeley's species description
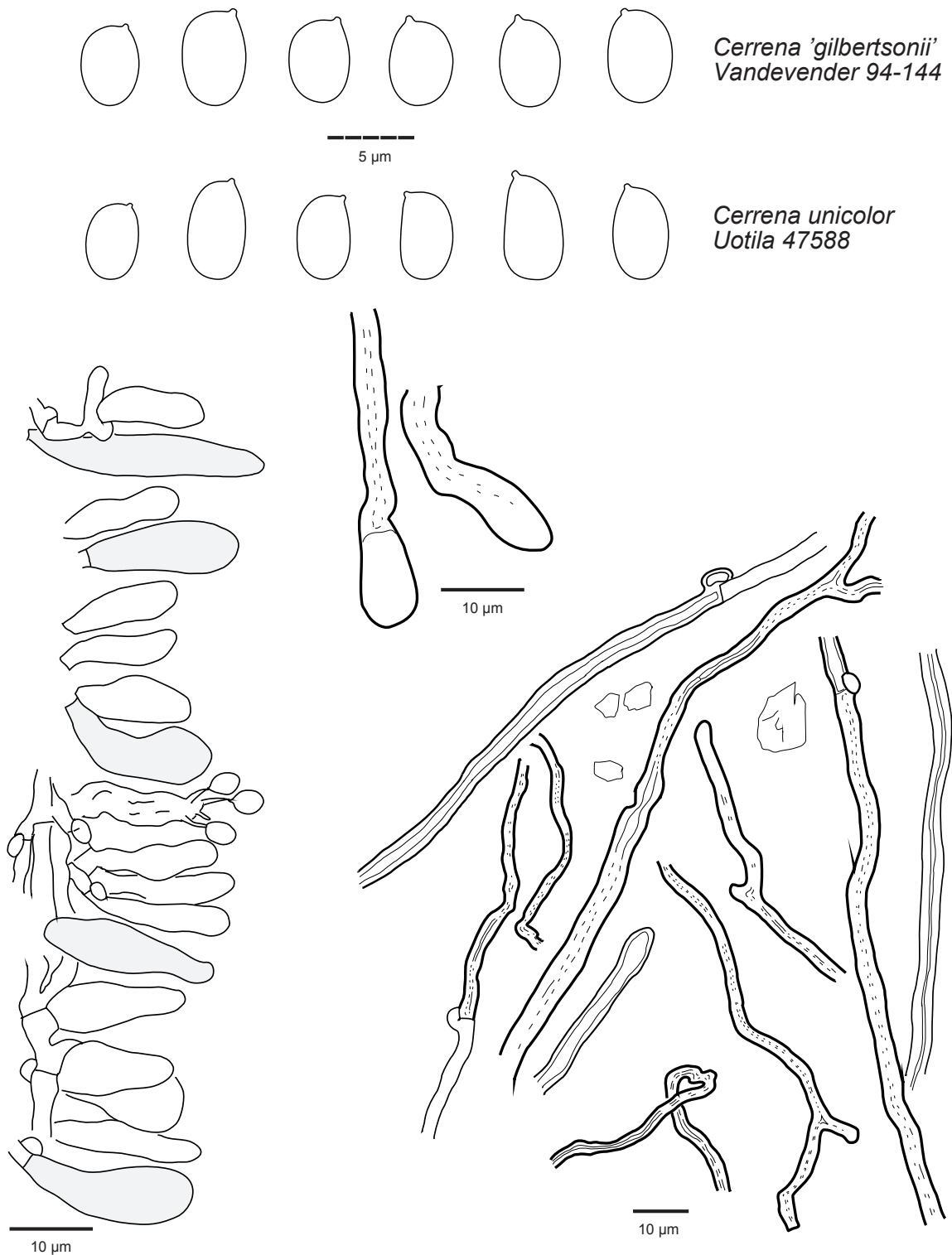
**Fig. 6.** Spores of *Cerrena gilbertsonii* and *C. unicolor*. Other hyphal structures, gloeocystidia, swollen skeletal hyphal ends, context skeletal hyphae, belong to *Cerrena unicolor* (*Uotila 47588*).

seems to mention two specimens, one from Sikkim and another from East Nepal collected by Hooker: "Sikkim; East Nepal. November 8. (Dr. Hooker.)" (Berkeley 1854). There are two specimens marked as syntypes in Kew, one from Sikkim, another from East Nepal, collected on 8 November. The envelope from Sikkim contains only remnants of context glued to paper, but the latter is a good-sized specimen. We designate here the specimen "East Nepal, November 8", K(M) 147643 as the lectotype of *Irpex zonatus*. The lectotype is sterile and mouldy, but recognizable. According to Hooker's travel journal, it was collected between

"Jummanoo" [Jamuna?] and "Sakkiazung" [Sakhejung?] villages, in today's Ilam district of Nepal (Hooker 1854).

*Irpiciporus* Murrill, *Bull. Torrey Bot. Club* **32**: 471. 1905.

*Basidiocarps* annual or biennial, sessile, effused-reflexed or completely resupinate, light-coloured, watery in fresh condition, rather tough after drying. Context duplex, with softer upper and more compact lower layer. *Pores* range from regular angular when young, splitting to irregular pores in some species, to

**Table 3.** Spore measurements of studied specimens of the *Cerrenaceae*.

| Species / specimen | Length | L | Width | W | Q | n |
|---|---|---|---|---|---|---|
| ***Acanthodontia cirrhatina*** | **4.0–5.1(–5.2)** | **4.69** | **(3.4–)3.5–4.2(–4.3)** | **3.79** | **1.24** | **65/2** |
| holotype | (4.0–)4.2–4.9(–5.0) | 4.48 | (3.4–)3.5–4.1 | 3.71 | 1.21 | 30 |
| Miettinen 13717 | (4.2–)4.6–5.2 | 4.86 | 3.4–4.2(–4.3) | 3.87 | 1.26 | 35 |
| ***Cerrena gilbertsonii*** | **(4.5–)4.7–5.4(–5.6)** | **5,00** | **(3.2–)3.3–4.0(–4.7)** | **3.68** | **1.36** | **64/2** |
| isotype | 4.5–5.4 | 4.94 | 3.2–3.8(–3.9) | 3.52 | 1.40 | 34 |
| Vlasák (JV 1609/29) | (4.6–)4.7–5.6 | 5.05 | (3.5–)3.6–4.1(–4.7) | 3.87 | 1.31 | 30 |
| ***Cerrena multipileata*** | **(3.5–)3.7–5.0(–5.4)** | **4.16** | **(2.4–)2.5–3.1(–4.4)** | **2.79** | **1.49** | **93/3** |
| de Meijer 2623 | (3.9–)4.0–5.2(–5.4) | 4.49 | (2.5–)2.7–3.2 | 2.88 | 1.56 | 30 |
| Ryvarden 43881 | (3.6–)3.7–4.7 | 4.11 | 2.4–3.1(–4.4) | 2.76 | 1.49 | 32 |
| Vlasák (JV 1407/63) | 3.5–4.5(–5.0) | 3.90 | 2.4–3.0 | 2.73 | 1.43 | 31 |
| ***Cerrena unicolor*** | **(3.9–)4.2–5.6(–6.2)** | **4.86** | **(2.5–)2.6–3.3(–3.8)** | **2.93** | **1.66** | **150/5** |
| Miettinen 16729 | (4.4–)4.6–5.2(–5.5) | 4.83 | (2.6–)2.7–3.2 | 2.97 | 1.63 | 30 |
| Niemelä 30 Jun. 1970 | 4.0–5.3(–5.4) | 4.83 | 2.5–3.1(–3.2) | 2.84 | 1.70 | 30 |
| Niemelä 5352 | (3.9–)4.2–5.3(–5.5) | 4.80 | 2.5–3.0 | 2.74 | 1.75 | 30 |
| Niemelä 6098 | 4.1–6.0(–6.2) | 4.82 | 2.6–3.3(–3.4) | 2.90 | 1.66 | 30 |
| Uotila 47588 | (4.2–)4.4–5.8(–6.2) | 5.03 | (2.8–)2.9–3.7(–3.8) | 3.19 | 1.58 | 30 |
| ***Cerrena zonata*** | **(3.7–)4.0–5.5(–6.4)** | **4.66** | **(2.5–)2.6–3.4(–3.6)** | **2.95** | **1.58** | **103/3** |
| Gates *s.n.* | (4.0–)4.2–5.2(–5.5) | 4.62 | 2.6–3.6 | 2.93 | 1.58 | 30 |
| Miettinen 13798 | 3.7–4.7(–4.8) | 4.24 | (2.5–)2.6–3.2 | 2.86 | 1.48 | 33 |
| Miettinen 9773 | 4.3–5.7(–6.4) | 5.04 | 2.8–3.4(–3.5) | 3.05 | 1.65 | 40 |
| ***Irpiciporus branchiformis*** | **(4.4–)4.7–6.0(–6.2)** | **5.30** | **4.0–5.2(–5.3)** | **4.67** | **1.14** | **62/2** |
| holotype | (4.4–)4.6–5.7(–5.8) | 5.17 | 4.0–5.1(–5.2) | 4.65 | 1.11 | 32 |
| Niemelä 5937 | (4.6–)4.8–6.1(–6.2) | 5.43 | (4.0–)4.1–5.2(–5.3) | 4.69 | 1.16 | 30 |
| ***Irpiciporus mollis*** | **(4.8–)5.1–6.2(–6.3)** | **5.45** | **(4.0–)4.3–5.3(–6.0)** | **4.84** | **1.13** | **121/4** |
| lectotype | 5.1–6.2(–6.3) | 5.60 | (4.2–)4.3–5.6(–6.0) | 4.97 | 1.13 | 30 |
| Vlasák (JV 0108/115) | (5.0–)5.2–6.0(–6.2) | 5.54 | (4.3–)4.4–5.2 | 4.87 | 1.14 | 30 |
| Vlasák (JV 0709/174) | (4.8–)5.0–5.9(–6.1) | 5.34 | (4.2–)4.3–5.2(–5.3) | 4.72 | 1.13 | 30 |
| Vlasák (JV 0808/45) | (5.0–)5.1–5.8(–5.9) | 5.34 | (4.0–)4.2–5.3(–5.5) | 4.80 | 1.11 | 31 |
| ***Irpiciporus pachyodon*** | **(5.2–)5.5–6.5(–7.4)** | **6.02** | **(4.2–)4.5–5.6(–6.4)** | **5.09** | **1.18** | **122/4** |
| Heilmann-Clausen 07–286 | (5.4–)5.5–6.3(–6.5) | 5.87 | (4.3–)4.4–5.3(–5.6) | 4.94 | 1.19 | 30 |
| Melo 327 | 5.4–6.8(–6.9) | 6.02 | (4.7–)4.8–5.6(–6.1) | 5.21 | 1.15 | 30 |
| Spirin 13785 | (5.2–)5.3–6.3(–6.8) | 6,00 | (4.2–)4.4–5.4(–5.6) | 4.94 | 1.22 | 30 |
| Vlasák (JV 9311/1) | (5.6–)5.8–7.2(–7.4) | 6.17 | (4.6–)4.8–5.7(–6.4) | 5.25 | 1.18 | 32 |
| ***Lividopora armeniaca*** | **(3.7–)3.8–4.6(–4.8)** | **4.10** | **3.3–4.0(–4.2)** | **3.61** | **1.14** | **38** |
| ***Lividopora benetosta*** | **(3.2–)3.4–4.6(–4.9)** | **3.94** | **(2.9–)3.0–3.9(–4.3)** | **3.46** | **1.14** | **220/8** |
| Hallenberg 15301 | 3.7–4.4 | 4.10 | 3.2–3.8(–3.9) | 3.48 | 1.18 | 30 |
| Härkönen K778 | 4.0–4.8(–4.9) | 4.43 | 3.0–3.9(–4.1) | 3.62 | 1.22 | 20 |
| Lloyd 5042 | 3.6–4.3 | 4.02 | 3.1–3.8 | 3.44 | 1.17 | 10 |
| Miettinen 10394,1 | 3.8–4.6 | 4.14 | 3.3–3.9 | 3.60 | 1.15 | 5 |
| Miettinen 13647,1 | (3.3–)3.5–4.8(–4.9) | 4.03 | (3.0–)3.1–4.2(–4.3) | 3.63 | 1.11 | 32 |
| Miettinen 13891 | 3.7–4.6 | 4.08 | 3.3–3.8 | 3.59 | 1.14 | 20 |
| Miettinen 18035 | 3.2–3.8(–3.9) | 3.52 | (2.9–)3.0–3.5 | 3.21 | 1.10 | 34 |
| Miettinen 18135 | (3.4–)3.5–4.1(–4.2) | 3.82 | (3.1–)3.2–3.8(–4.0) | 3.48 | 1.10 | 30 |
| Miettinen 8823,2 | 3.5–4.2 | 4.04 | 3.0–3.5 | 3.24 | 1.25 | 5 |
| Miettinen 9023,2 | 3.7–4.3 | 3.91 | 3.2–3.8 | 3.46 | 1.13 | 24 |
| Miettinen 9166,5 | 3.6–4.2(–4.6) | 3.90 | 2.9–3.7 | 3.34 | 1.17 | 30 |
| Miettinen 9978,2 | 3.6–3.9 | 3.70 | 3.3–3.6 | 3.48 | 1.06 | 8 |
| ***Lividopora facilis*** | **3.2–4.0** | **3.50** | **2.5–3.0** | **2.69** | **1.30** | **33** |

**Table 3.** (Continued).

| Species / specimen | Length | L | Width | W | Q | n |
|---|---|---|---|---|---|---|
| *Lividopora subvincta* | **(3.4–)3.6–4.6(–5.2)** | **4.02** | **(2.6–)2.9–3.4(–3.5)** | **3.13** | **1.28** | **90/3** |
| holotype | (3.6–)3.7–4.6 | 4.02 | (2.8–)2.9–3.3 | 3.10 | 1.30 | 30 |
| Savchenko 171124/1505 | (3.4–)3.5–4.2 | 3.87 | 2.9–3.5 | 3.17 | 1.22 | 30 |
| Savchenko 171129/1309X | (3.5–)3.6–5.1(–5.2) | 4.18 | (2.6–)2.8–3.4(–3.5) | 3.14 | 1.33 | 30 |
| *Lividopora vincta* | **(3.2–)3.3–4.2(–4.5)** | **3.80** | **(2.8–)2.9–3.4(–3.5)** | **3.13** | **1.21** | **62/2** |
| Lowe (CFMR L-13218-Sp) | (3.6–)3.7–4.2(–4.5) | 3.95 | 2.9–3.4(–3.5) | 3.22 | 1.23 | 30 |
| Miettinen 17916,1 | (3.2–)3.3–4.0(–4.3) | 3.65 | 2.8–3.3(–3.5) | 3.06 | 1.20 | 32 |
| *Somion delectans* | **(5.8–)6.0–7.3(–7.6)** | **6.60** | **(5.0–)5.1–6.6(–6.8)** | **5.64** | **1.17** | **90/3** |
| isotype | (5.8–)6.0–7.4(–7.6) | 6.59 | (5.0–)5.1–6.7(–6.8) | 5.66 | 1.16 | 30 |
| Thaxter 799 | 6.0–7.2(–7.3) | 6.61 | (5.1–)5.2–6.7 | 5.72 | 1.16 | 30 |
| Vlasák 1507/22 | (6.0–)6.1–7.2(–7.3) | 6.61 | (5.0–)5.1–6.5(–6.6) | 5.55 | 1.19 | 30 |
| *Somion litschaueri* | **(6.6–)6.8–8.6(–9.1)** | **7.71** | **(4.9–)5.2–7.0(–7.7)** | **6.00** | **1.28** | **120/4** |
| holotype | (6.8–)6.9–8.6(–9.1) | 7.77 | (4.9–)5.0–7.2(–7.7) | 6.14 | 1.27 | 30 |
| Vampola 198 | 6.6–8.1(–8.2) | 7.28 | (5.4–)5.5–6.3(–6.4) | 5.94 | 1.23 | 30 |
| Vlasák (JV 1309/1) | (6.7–)7.0–8.8(–8.9) | 7.69 | (5.0–)5.1–6.3(–6.6) | 5.79 | 1.33 | 30 |
| Vlasák (JV 1309/7) | (6.8–)7.3–8.8(–9.1) | 8.08 | (5.3–)5.4–7.0(–7.1) | 6.16 | 1.31 | 30 |
| *Somion occarium* | **(5.3–)6.0–7.2(–7.6)** | **6.60** | **(3.9–)4.3–5.5(–6.2)** | **5.02** | **1.31** | **120/4** |
| holotype | (5.3–)5.8–7.1(–7.5) | 6.47 | (4.2–)4.3–5.6(–6.2) | 5.06 | 1.28 | 60 |
| Vampola 149 | 6.0–7.5(–7.6) | 6.78 | (3.9–)4.0–5.5(–5.6) | 4.94 | 1.37 | 30 |
| Vlasák 0511/8 | (5.9–)6.0–7.2(–7.3) | 6.68 | (4.4–)4.6–5.3(–5.6) | 5.03 | 1.33 | 30 |
| *Somion strenuum* | **(5.0–)5.2–6.4(–7.2)** | **5.90** | **(4.1–)4.2–5.3(–6.0)** | **4.80** | **1.23** | **120/4** |
| Miettinen 10456 | (5.1–)5.2–6.3(–7.1) | 5.89 | (4.1–)4.2–5.2(–5.7) | 4.69 | 1.26 | 30 |
| Spirin 10989 | (5.0–)5.1–6.8(–7.2) | 5.75 | (4.1–)4.2–5.6(–6.0) | 4.82 | 1.19 | 30 |
| Spirin 6112 | (5.2–)5.4–6.3(–6.4) | 6.03 | (4.1–)4.2–5.5(–5.7) | 4.90 | 1.23 | 30 |
| Spirin 7330 | (5.2–)5.3–6.5(–6.8) | 5.94 | (4.1–)4.2–5.3(–5.4) | 4.77 | 1.25 | 30 |
| *Somion tomsovskyi* | **(6.4–)6.8–8.3(–8.7)** | **7.50** | **(5.1–)5.5–6.8(–7.1)** | **6.11** | **1.23** | **60/2** |
| Vlasák Jr. (JV 1209/55) | (6.4–)6.8–8.2(–8.7) | 7.47 | (5.2–)5.4–6.9(–7.1) | 6.05 | 1.23 | 30 |
| Vlasák Jr. (JV 1307/8) | 6.8–8.3(–8.6) | 7.55 | (5.1–)5.5–6.8(–7.1) | 6.18 | 1.22 | 30 |
| *Somion unicolor* | **(5.2–)5.3–7.1(–7.3)** | **6.13** | **(4.0–)4.2–5.4(–5.9)** | **4.78** | **1.28** | **90/3** |
| Lewis DAOM 9080 | (5.3–)5.8–7.2(–7.3) | 6.38 | (4.1–)4.2–5.5(–5.6) | 4.77 | 1.34 | 30 |
| Vlasák (JV 1708/10) | 5.2–6.7(–6.8) | 5.88 | (4.0–)4.1–5.4(–5.9) | 4.82 | 1.22 | 30 |
| Vlasák Jr. (JV 1304/1) | (5.4–)5.5–6.9(–7.0) | 6.11 | (4.1–)4.2–5.3(–5.8) | 4.74 | 1.29 | 30 |

incomplete, becoming dentate or spathulate in others. *Hyphal structure* monomitic, loose, homogenous, hyphae clamped and slightly cyanophilous, thin- to thick-walled, subparallel in trama. *Basidia* long-clavate, 20–45 × 5–8 µm, four-spored, with guttulate contents. *Basidiospores* broadly ellipsoid to subglobose, slightly thick-walled (wall 0.2–0.3 µm thick), with a central oil-drop, slightly to distinctly cyanophilous. Causes a white rot of living and dead dicot trees.

*Genus type*: Irpex mollis Berk. & M.A. Curtis

*Notes*: *Irpiciporus* spp. have completely monomitic basidiocarps, but David (1969) has shown that when cultured *I. pachyodon* produces microbinding hyphae similar to *Pseudolagarobasidium* and *Radulodon*. She does not report similar hyphae for *Somion occarium* (as "*Spongipellis delectans*").

We accept here five *Irpiciporus* species, but from available DNA data it is evident that at least one additional species also belongs to the core *Irpiciporus* (Fig. 8). Zhao *et al.* (2017) published a sequence under the name *Tyromyces xuchilensis* from Ecuador (*Ryvarden 44669*, studied, GenBank KX161650). This sequence belongs to *Irpiciporus* in the close vicinity of *I. sinuosus* – but not to *T. xuchilensis* (see Excluded taxa). It might belong to *Tyromyces irpiceus*, which is possibly a species of *Irpiciporus* as indicated by Corner (1989) himself. *Irpiciporus sinuosus* and the Ecuadorian material have regularly poroid hymenophore unlike the other species, which are truer to the genus name in having an irpicoid hymenophore of splitting pores. Otherwise, basidiocarp configuration, colouration, and micromorphology are very similar among all the species in the genus.

Nakasone & Ortiz-Santana (2022) combined three hydnoid species in the genus. We accept one of those species (*Irpiciporus revolubilis*) in *Irpiciporus*, but we show here that *Irpiciporus africanus* (Ipulet & Ryvarden) Nakasone belongs to *Hypochnicium* rather than to the *Cerrenaceae*. We treat the third species (*I. decolorans*) as insufficiently known (see Excluded taxa).
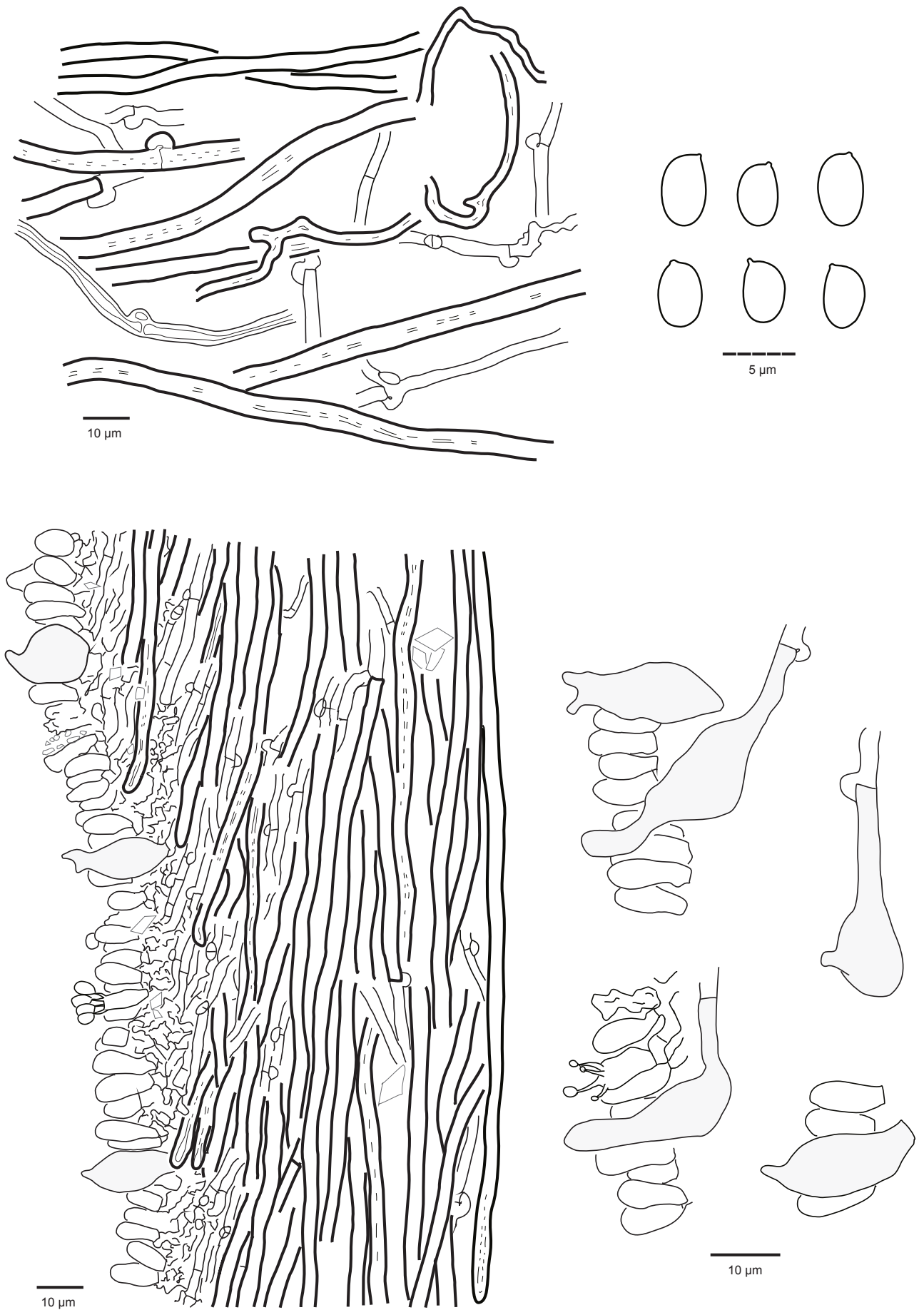
**Fig. 7.** *Cerrena zonata* (*Miettinen 9773*). Context hyphae, tube trama and hymenium, hymenial cystidia and spores.
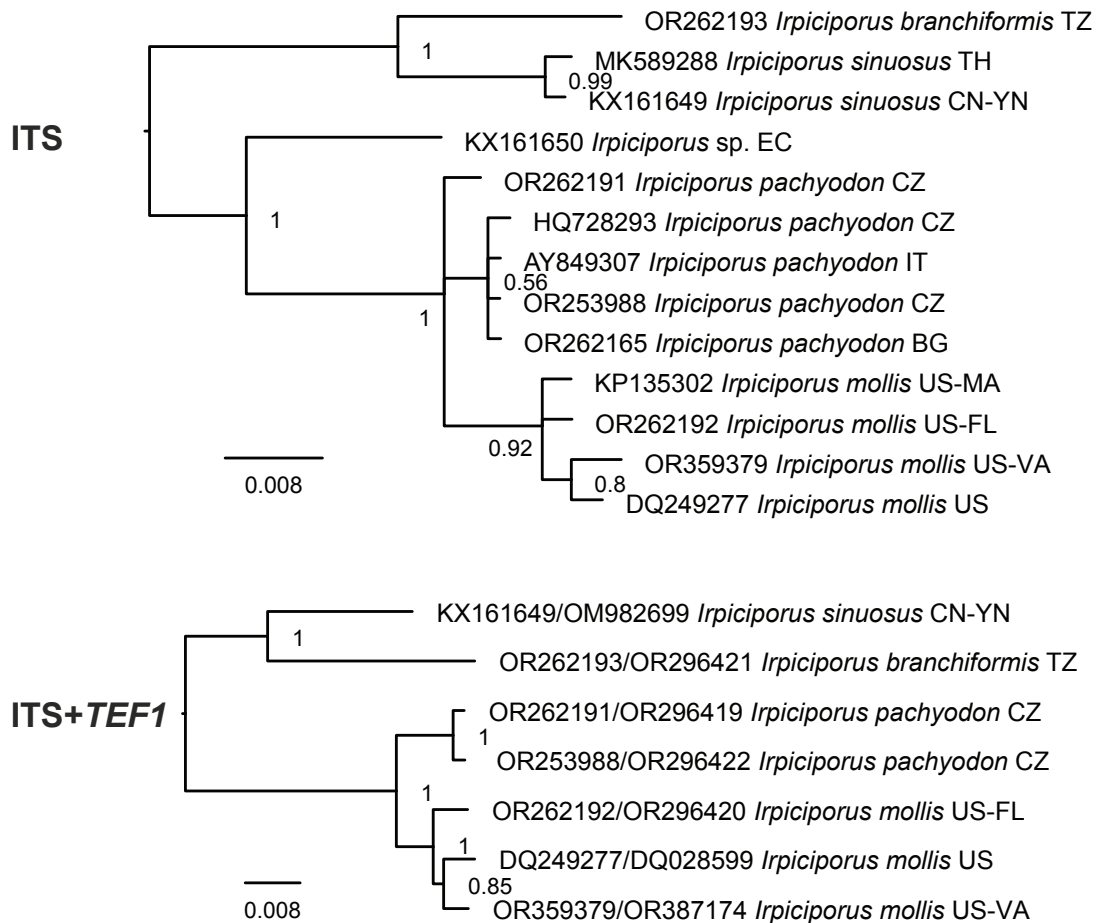
**Fig. 8.** Bayesian consensus phylograms of *Irpiciporus* spp. based on ITS and ITS+ *TEF1* datasets. Countries (and states) of origin are denoted with ISO 3166 codes.

After describing the genus, Murrill used *Irpiciporus* as a replacement for *Irpex*. From *Irpiciporus sensu* Murrill, only the type species is in the *Cerrenaceae*, and the rest of the species are a variable set of unrelated irpicoid polypores (Donk 1974). All names combined to *Irpiciporus* are commented either as recognized species or synonyms or under Excluded taxa.

***Irpiciporus branchiformis*** Miettinen & Spirin, ***sp. nov.*** MycoBank MB 849644. Fig. 9.

*Typus*: **Tanzania**, Tanga, Lushoto, Mazumbai Forest Res., -4.8075° : 38.5032° ± 300 m, alt. 1 500–1 600 m, lower montane rainforest, fallen log of *Ocotea usambarensis*, 17 Apr. 1991, *Saarimäki 869* (**holotype** H 7200355).

*Etymology*: *Branchiformis* (Lat., adj.), reminiscent of fish gills, in reference to the irpicoid caps of the species.

*Basidiocarps* annual or biennial, sessile, pilei projecting up to 3 cm. Upper surface pubescent, azonate, cream coloured. Edge of pileus sharp, fertile, concolourous with pileal surface. Hymenial surface more or less concave, cream coloured to pale ochraceous; pores incomplete, shallow, present only in marginal areas, 2–3 per mm, quickly becoming dentate to spathulate and finally transforming to flattened, sharp-pointed spines, 2–3 per mm. Section: context cream coloured, soft, indistinctly fibrillose, up to 0.5 mm thick; hymenial layer soft, concolourous or slightly paler than hymenial surface, up to 0.7

cm thick.

*Hyphal structure* monomitic, all septa with clamp connections. Context hyphae slightly thick-walled, interwoven to subparallel, (3.0–)3.8–4.4(–5.3) μm diam. Tramal hyphae thin- to slightly thick-walled, subparallel, (2.9–)3.1–4.1(–4.6) μm diam. Subhymenial hyphae not differentiated from tramal ones. *Basidiospores* slightly thick-walled, subglobose to more rarely broadly ellipsoid, (4.4–)4.7–6.0(–6.2) × 4.0–5.2(–5.3) μm, L = 5.3 μm, W = 4.67 μm, Q = 1.11–1.16.

*Distribution and ecology*: The species is so far known only from two localities in East Africa (Tanzania), inhabiting decorticated wood of angiosperms.

*Notes*: *Irpiciporus branchiformis* differs from two other irpicoid species of the genus (*I. mollis* and *I. pachyodon*) in having fragile, thinner basidiocarps, more densely arranged pores/spines, and smaller basidiospores (Table 3).

***Irpiciporus mollis*** (Berk. & M.A. Curtis) Murrill, Bull. Torrey Bot. Club 32: 471, 1905. Fig. 9.
*Basionym*: *Irpex mollis* Berk. & M.A. Curtis, Hooker's J. Bot. 1: 236, 1849.

*Typus*: **USA**, South Carolina, Santee River, unknown collection date, leg. *Ravenel*, herb. *Curtis 1729* (**lectotype** K(M) 64592, studied – selected by Murrill 1905: 471).
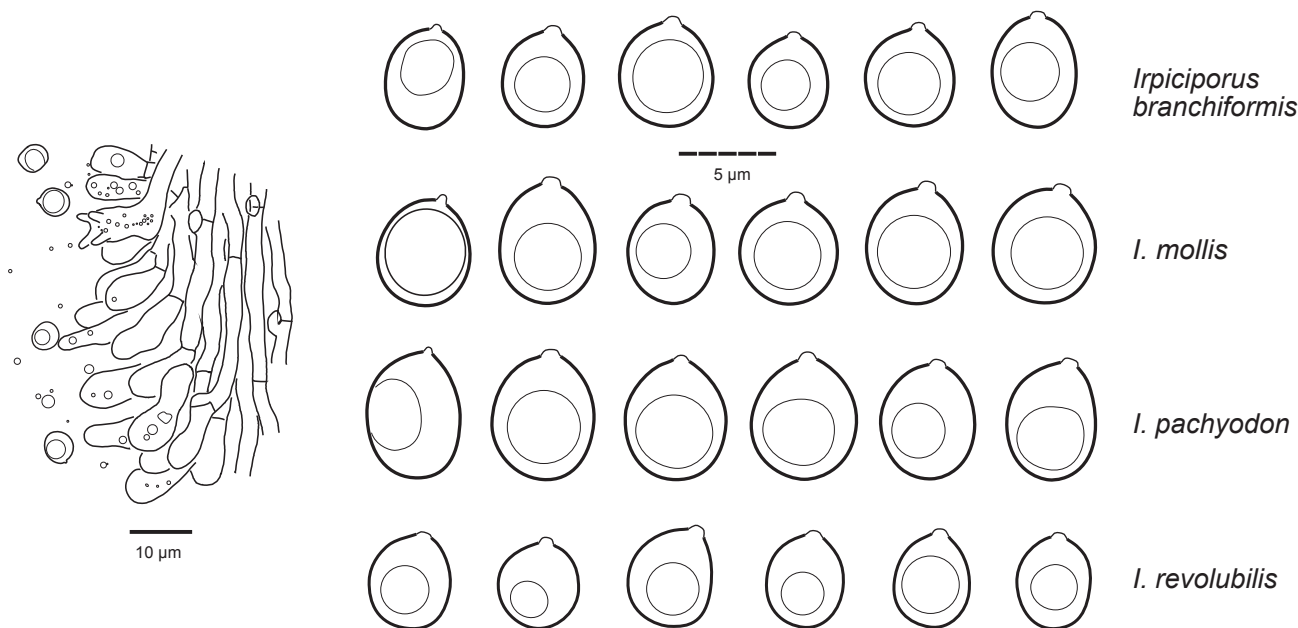
**Fig. 9.** *Irpiciporus* microscopic structures. Tube trama, hymenium and spores of *I. branchiformis* (holotype), and spores of *I. mollis* (*Vlasák*, JV 0808/45), *I. pachyodon* (*Vlasák*, JV 9311/1) and *I. revolubilis* (holotype).

*Basidiocarps* annual or biennial, sessile or effused-reflexed, rarely completely resupinate, pilei projecting up to 3 cm. Upper surface pubescent, azonate, cream coloured to pale ochraceous, in oldest parts almost smooth. Edge of pileus sharp, fertile, concolourous with pileal surface. Hymenial surface more or less concave, cream coloured to pale ochraceous, in very old basidiocarps brownish; pores incomplete, shallow, present only in marginal areas, 1–2 per mm, quickly becoming dentate to spathulate and finally transforming to flattened, sharp-pointed spines, about 1 per mm. Section: context cream coloured, in old herbarium specimens pale ochraceous, watery in fresh condition, firm, distinctly fibrillose and sometimes indistinctly zonate when dry, up to 2 cm thick; hymenial layer tough, concolourous with or slightly paler than hymenial surface, up to 1.5 cm thick.

*Hyphal structure* monomitic; all septa with clamp connections. Context hyphae very thick-walled, interwoven to subparallel, (4.3–)5.2–6.2(–6.7) μm diam. Tramal hyphae slightly to distinctly thick-walled (lumen wide to capillary), subparallel, (2.8–)3.4–4.3(–5.2) μm diam. Subhymenial hyphae thin- to slightly thick-walled, some short-celled and inflated, 3–5 μm diam. *Basidiospores* slightly thick-walled, broadly ellipsoid to subglobose, (4.8–)5.1–6.2(–6.3) × (4.0–)4.3–5.3(–6.0) μm, L = 5.45 μm, W = 4.84 μm, Q = 1.11–1.14.

*Distribution and ecology*: Widely distributed in the eastern part of North America, reaching Florida at the southernmost limit of its distribution. Occurs on many angiosperm tree species, and Gilbertson & Ryvarden (1987) report it from living trees, but we have not been able to find any reference that it would be pathogenic. It also grows on dead trees.

*Notes*: This species was originally described from South Carolina (Berkeley & Curtis 1849) and recognized as such until Kotlaba & Pouzar (1957) placed it among the synonyms of the European species *I. pachyodon*. However, both morphological and DNA data confirm that they are different species, whose distribution

areas do not seem to overlap. *Irpiciporus mollis* is distributed in the eastern part of USA and Canada (Gilbertson & Ryvarden 1987, as S. pachyodon). According to Murrill (1905) and Maas Geesteranus (1974), *Irpex crassus* Berk. & Curtis and *Irpex crassitatus* Lloyd are conspecific with *I. mollis*. Ryvarden (2020b) lists further junior synonyms.

***Irpiciporus pachyodon*** (Pers.) Kotl. & Pouzar, *Česká Mykol*. **11**: 156. 1957. Figs 2, 9.
*Basionym*: *Hydnum pachyodon* Pers., *Mycol. Europaea* **2**: 174. 1825.
*Synonym*: *Hydnum schestunovii* Nikol., *Notulae Syst. Sect. Cryptogam. Inst. Bot*. **6**: 38. 1949 (*fide* Nikolaeva 1964).

*Typus*: **France**, *Delastre* (**lectotype** of *Hydnum pachyodon* L 910.263–1321 – selected and studied by Maas Geesteranus 1974: 491).

*Basidiocarps* annual or biennial, effused-reflexed to completely resupinate, pilei projecting up to 5 cm. Upper surface pubescent, azonate, cream coloured to pale ochraceous, in oldest parts almost smooth. Edge of pileus sharp to rather blunt, fertile, concolourous with pileal surface. Hymenial surface more or less concave, cream coloured or yellowish, in very old basidiocarps pale ochraceous; pores incomplete, shallow, present only in marginal areas, 0.5–1 per mm, quickly becoming dentate to lamellate and finally transforming to flattened, sharp-pointed spines, 0.5–1 per mm. Section: context almost white to cream coloured, tough in fresh condition, compact when dry, up to 3 cm thick; hymenial layer tough, concolourous with or slightly paler than hymenial surface, up to 2 cm thick.

*Hyphal structure* monomitic; all hyphae with clamp connections. Context hyphae thin- or only slightly thick-walled, easily collapsing, interwoven to subparallel, (4.7–)4.9–6.0(–6.8) μm diam. Tramal hyphae thin- or slightly thick-walled, subparallel, (3.0–)3.3–4.1(–4.5) μm diam. Subhymenial hyphae thin-walled, some short-celled and slightly inflated, 3.0–4.5 μm diam. *Basidiospores* slightly thick-walled, broadly ellipsoid to

subglobose, (5.2–)5.5–6.5(–7.4) × (4.2–)4.5–5.6(–6.4) μm, L = 6.02 μm, W = 5.09 μm, Q = 1.15–1.22.

*Distribution and ecology*: *Irpiciporus pachyodon* is a temperate European species inhabiting mostly living oak trees (Ryvarden & Melo 2014). It has also been reported from Caucasus (Nikolaeva 1964).

*Notes*: *Irpiciporus pachyodon* is the European counterpart of North American *I. mollis*. Morphological differences between these species are subtle: tramal hyphae of *I. pachyodon* are slightly narrower than in *I. mollis* and not so thick-walled, and its basidiospores are slightly larger.

**Irpiciporus revolubilis** (Hjortstam & Ryvarden) Nakasone, *Lilloa* **59** (Suppl.): 97. 2022. Fig. 9.
*Basionym*: *Radulodon revolubilis* Hjortstam & Ryvarden, *Syn. Fungorum* **23**: 88. 2007.

*Typus*: **Venezuela**, Aragua, Parque National Henri Pittier, Rancho Grande Research Station, on decayed hardwood, 14 Apr. 1999, *Ryvarden 41417* (**holotype** O, studied).

*Basidiocarps* annual, effused, up to 5 cm in longest dimension. Margin sharply compact, delimited, up to 1 mm, detaching and rolling in dry basidiocarps. Hymenial surface cream coloured to pale ochraceous; hymenophore irpicoid, spines sharp to rather blunt, 3–5 per mm, partly fusing together and forming dentate or spathulate projections. Section: context cream-colored, soft, up to 0.5 mm thick; hymenial layer soft, concolourous with or slightly paler than hymenial surface, up to 0.3 cm thick.

*Hyphal structure* monomitic, all septa with clamp connections. Context hyphae slightly to distinctly thick-walled, interwoven to subparallel, (3.4–)4.1–5.0(–5.6) μm diam. Tramal hyphae slightly to distinctly thick-walled, predominantly subparallel, (2.5–)2.7–4.1(–5.1) μm diam. Subhymenial hyphae not differentiated from tramal ones. *Basidiospores* slightly thick-walled, ellipsoid to broadly ellipsoid, more rarely subglobose, (4.2–)4.3–5.0(–5.1) × (3.3–)3.5–4.3(–4.4) μm, L = 4.63 μm, W = 3.98, Q = 1.17.

*Notes*: We agree with Nakasone & Ortiz-Santana (2022) that this species belongs to *Irpiciporus*. It has the smallest spores among the species in the genus and reminds closely of the African *I. branchiformis*.

**Irpiciporus sinuosus** Y.C. Dai & Chao G. Wang, *Mycol. Progr.* **21**(73): 8. 2022.

*Typus*: **China**, Yunnan, Puer, Laiyanghe Forest Park, angiosperm, 6 Jun. 2011, *Dai 12234* (**holotype** BJFC 010517).

*Notes*: This species has well-developed pores, even though they start to split soon (Zhao *et al.* 2017). It is the first truly poroid species confirmed to belong to *Irpiciporus*.

**Lividopora** Miettinen, **gen. nov.** MycoBank MB 849645.

*Type species*: *Lividopora facilis* Miettinen

*Etymology*: Derived from *lividum* (Lat., adjective), livid, refers to the greyish (dull) tint of the basidiocarps.

Resupinate annual to short-lived perennial *polypores* with reddish to grey colours, leathery tough when fresh, drying hard, with a distinct margin. *Pores* regular, mid-sized to small (5–15 per mm) thin-walled and entire. Brown, black or red basal layer present. *Hyphal system* dimitic, clamps absent, weakly to moderately cyanophilous, IKI-, KOH-, CRB lilac. Skeletal hyphae interwoven but not agglutinated, with a visible narrow lumen, generative hyphae slightly thick-walled, dominating in lower tube trama. The overall impression of hyphal structure is messy. Two main types of *cystidia*: tramal encrusted skeletocystidia are clavate, abundant and conspicuous, embedded or penetrating hymenium; thin-walled, often mamillate, slightly projecting, sack-like hymenial cystidia also present, often with a stained plasma and could be called gloeocystidia. In addition to these, encrusted and naked hyphidia in hymenium. *Basidia* with four sterigmata, barrel-like to clavate. *Basidiospores* ellipsoid to subglobose, smooth, mid-sized, thin-walled or with distinct walls, devoid of guttulae.

*Notes*: Incorporation of ITS sequences from public nucleotide databases in our analyses (Fig. 10) shows that two *Lividopora* species are widespread, *L. benetosta* in the Paleotropics and Caribbean, and *L. vincta* in the Neotropics. We could not find public sequences of the other three species. Both *L. benetosta* and *L. vincta* show some ITS variation, but differences are small, giving no reason to recognize more species in the genus.

Species of *Lividopora* are similar microscopically, and in many cases macroscopic characters of the basidiocarp such as colour (Fig. 11) and pore size are more useful for identification. Geographic origin too is of help, since all but one species seem to be restricted to some part of the tropics. However, young specimens, for instance in the Caribbean where both *L. benetosta* and *L. vincta* occur, can be very difficult or even impossible to identify with certainty by their morphology.

Table 4 provides key identification characters. For cultural characters and further morphological characters of the group, we recommend Setliff (1972a, b). He notes that *L. vincta* coll. produce clamps in culture.

Skeletocystidia (Figs 12, 13) appear first as thin-walled, swollen hyphal ends with sparse encrustation, often in hymenium, though rooted in trama. At this stage, they may appear similar to the permanently thin-walled hymenial cystidia ("gloeocystidia"). Later in development the skeletocystidia become thick-walled and obtain a coarse and thick crystal cover that finally obscures view to the hyphae inside the cystidia. The two types are easy to distinguish in slides, even though, pending on developmental stage, the thin-walled "gloeocystidia" may be rare or only found in some parts of the basidiocarp. Cystidial encrustation is very persistent, visible even in otherwise destroyed (old, mouldy, or sterile) specimens.

*Lividopora* spp. have been included in *Rigidoporus* by Ryvarden (1972b) and Corner (1987) as *R. vinctus* and *R. hypobrunneus* (= *L. benetosta* below). Even though not closely related, the two genera share morphological characters such as cyanophilous simple-septate hyphae in basidiocarps, ellipsoid to subglobose spores, short and broad, barrel-like hymenial cells, and heavily encrusted, thick-walled club-like tramal cystidia. Their main difference is in the hyphal structure, which is distinctly dimitic in *Lividopora* spp. and monomitic or indistinctly dimitic in *Rigidoporus* spp. The structure of trama is different: hyphae are parallel in most *Rigidoporus* spp. and related *Physisporinus* spp. but interwoven in *Lividopora*. Spores of *Rigidoporus* are
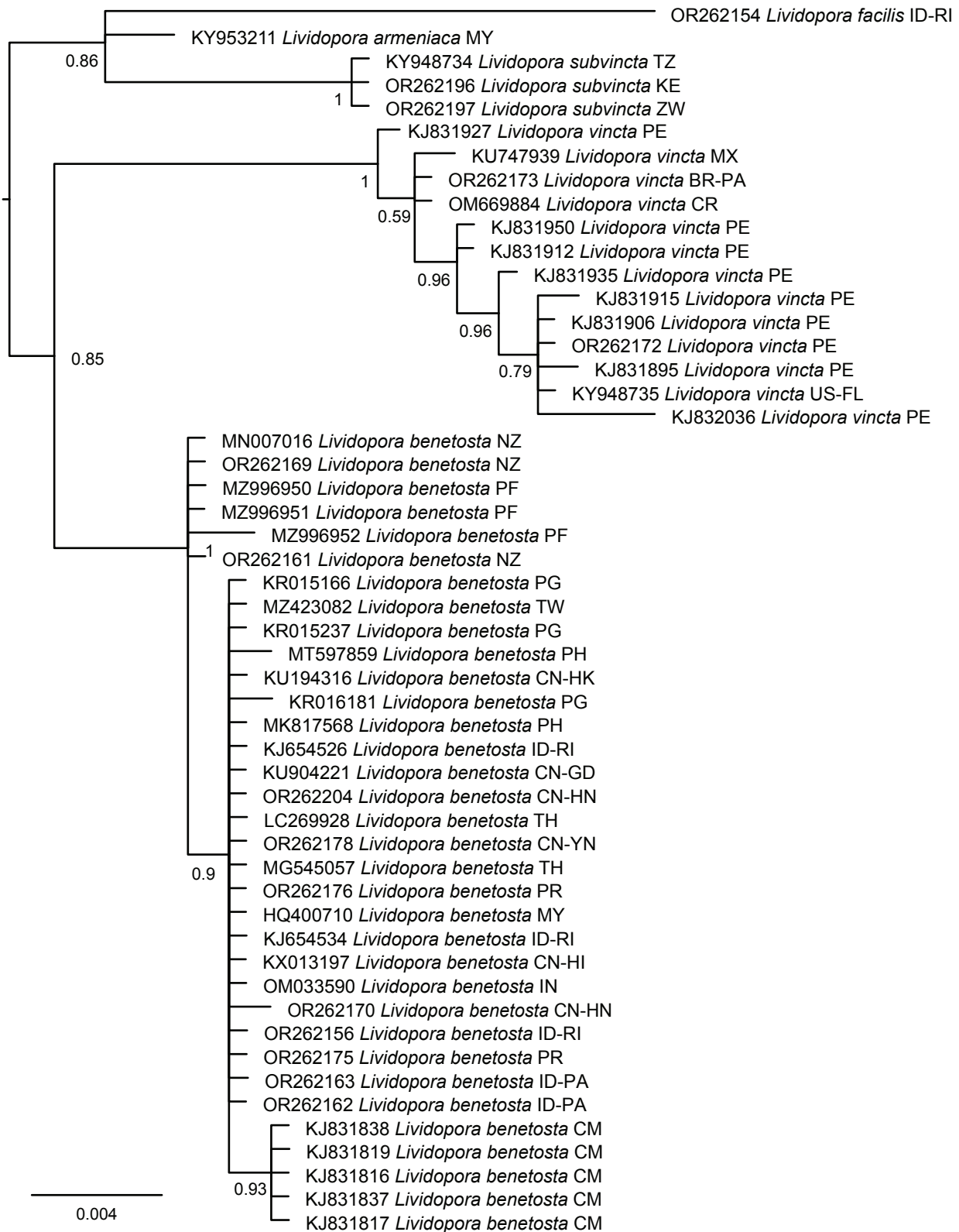
**Fig. 10.** Bayesian consensus phylogram of *Lividopora* spp. based on ITS sequences. Countries (and states) of origin are denoted with ISO 3166 codes.

cyanophilous and usually slightly thick-walled, whereas in *Lividopora* spp. they are thin-walled and acyanophilous.

Ryvarden (1972b) considered the hyphal system of *L. vincta* monomitic, consisting of apparent skeletal hyphae or their segments, but with transitions to generative hyphae. He softened his stand later, settling for "apparently dimitic" (Gilbertson & Ryvarden 1987). Intermediary hyphae are not a rare phenomenon in dimitic polypores. In our view, the intermediary hyphae are not prevalent in *Lividopora*, and for all practical purposes (normal morphological examination and functionality for the fungus), the structure may be called dimitic.

***Lividopora armeniaca*** Miettinen & J. S. Seelan, ***sp. nov.*** MycoBank MB 849646. Figs 11–13.

**Table 4.** Comparison of morphological characters of *Lividopora* spp.

| Species | Encrusted cystidia (L and W in µm) | Pore size (60 % mid range) | Spores (L and W in µm) | Color | Tramal skeletal hyphae (µm in diameter, 60 % mid range) | Other |
|---|---|---|---|---|---|---|
| *L. armeniaca* | **Narrow, L = 23, W = 7.2** | 10–12 | **Subglobose, L = 4.10, W = 3.61, Q = 1.14** | Orange when fresh, dries brick | Yellowish, **narrow**, 2.5–3.0 | – |
| *L. benetosta* | Most very broad and short (Q < 2), L = 34, W = 14.9 | 8–13 | **Subglobose, L = 3.94, W = 3.46, Q = 1.14** | Faded reddish when young, **brownish-grayish** when old | Yellow to brown, wide, 3.0–4.0 | Gloeocystidia commonly > 10 µm wide |
| *L. facilis* | **Narrow, L = 21, W = 9.7** | **5–6** | **Ellipsoid, L = 3.5 µm, W = 2.69 µm, Q = 1.30** | Faded reddish, dries brown | Almost hyaline, narrow, 2.8–3.3 | – |
| *L. subvincta* | Broad and long, L = 32, W = 11 | 9–11 | **Ellipsoid, L = 4.02 µm, W = 3.13 µm, Q = 1.28** | Dark gray | Brown, wide, 3.2–4.2 | – |
| *L. vincta* | Broad and long, L = 47, W = 14.6 | 9–11 | **Ellipsoid, L = 3.80, W = 3.13, Q = 1.21** | Reddish | Yellowish, wide, 3.7–4.5 | – |

*Typus*: **Malaysia**, Sabah, Ranau. Kinabalu Park, Timpohon peak trail, 6.02775° 116.54527°, alt. 1 880 m, upper montane rainforest, on a fallen crown of a dicot (24 cm diam, decay stage 3/5), 14 Jun. 2013, *Miettinen 16136 & Seelan* (**holotype** SNP33533, **isotype** H 7200338\*).

*Etymology*: *Armeniacus* (Lat., adj.), apricot-coloured, refers to basidiocarp colour.

*Basidiocarps* resupinate, apricot-coloured when fresh, drying dull reddish brown, patches up to 7 × 3 cm and 2 mm thick. Consistency hard woody when dry, curving inwards upon drying, detaching from wood. Pores thin-walled, regular, angular, mouths smooth, (10–)11–12(–13) per mm, up to 1.2 mm long. Subiculum cream-colored, in contrast to darker tubes, 0.2–0.6 mm thick. Basal layer in dry state a dark, reddish waxy film, orange when fresh.

   *Hyphal structure* dimitic, clamps absent. Generative hyphae thin- to slightly thick-walled, frequently septate, uniform except in basal layer, 2.0–3.0(–3.6) µm diam. Subiculum dominated by skeletal hyphae, interwoven, winding, yellowish to hyaline, tissue rather loose; basal layer about 20 µm, strongly agglutinated, brown, (2.7–)3.3–4.2(–4.5) µm diam, with a distinct lumen third to sixth of the total cell width. Tramal tissue dense, hyphae interwoven to subparallel, dominated equally by slightly thick-walled generative hyphae and slightly yellowish skeletal hyphae (2.1–)2.5–3.0(–3.5) µm diam, towards tube mouths by generative hyphae. *Cystidia*: Tramal skeletocystidia abundant, often bending into hymenium, (7–)15–30(–47) × (5.3–)6.3–8(–12) µm, L = 23.0 µm, W = 7.2 µm (n = 37). Thin-walled hymenial cystidia rather narrow, clavate, few mamillate, heavily but finely encrusted, 11–40 × 4.7–8.8 µm, W = 6.1 µm (n = 13). Basidia barrel-like, 8–10 × 4.2–5.5 µm. *Basidiospores* broadly ellipsoid, thin-walled, (3.7–)3.8–4.6(–4.8) × 3.3–4.0(–4.2) µm, L = 4.10 µm, W = 3.61 µm, Q = 1.14.

*Distribution and ecology*: Known from dead wood from a montane rainforest in Sabah, North Borneo.

*Notes*: The type specimen reminded of a thin *Rigidoporus microporus* specimen when fresh. *Lividopora benetosta* may look similar, for differences see Table 4. The type is well developed but does not contain any old parts. This should be taken into account when interpreting cystidial characters, which are age-dependent in *Lividopora*.

***Lividopora benetosta*** (Berk.) Miettinen*, **comb. nov.** MycoBank MB 849647. Figs 1, 11–13.
*Basionym*: *Polyporus benetostus* Berk., *Bot. J. Linn. Soc.* **16**: 52. 1877.
*Synonyms*: *Poria fulvobadia* Pat., *J. Bot. (Morot)* **11**: 340. 1897.
*Poria fumosa* Bres. & Pat., *Mycological Writings* **1**(6): 49. 1901.
*Poria porphyrophaea* Bres., *Hedwigia* **56**: 296. 1915.
*Poria hypobrunnea* Petch, *Ann. Roy. Bot. Gard.* (Peradeniya) **6**: 137, 1916.
*Poria vincta* var. *cinerea* (Bres.) Setliff, *Mycologia* **64**: 695. 1972, *pro parte*.

*Typus*: **French Polynesia**, Tahiti, on bark, 24 Sep. 1875, *Challenger Expedition* (**holotype** of *Polyporus benetostus* K(M) 192246, ex herb. Berkeley, studied). **Vietnam**, Thanh Hóa, 20 Apr. 1892, *Bon 5294* (**lectotype** of *Poria fulvobadia* FH 290623 – selected by Ryvarden (1983), studied). **Samoa**, *Lloyd 5042* (**lectotype** of *Poria fumosa* BPI US0318515 – selected by Stevenson & Cash 1936: 1940, **isotype** FH

**Fig. 11.** Species of *Lividopora*. **A.** *L. armeniaca* (holotype). **B.** *L. benetosta*, young basidiocarp (*Miettinen 18133*). **C.** *L. benetosta*, old basidiocarp (*Miettinen 13011.3*). **D.** *L. facilis* (holotype). **E.** *L. subvincta* (*Savchenko 171124/1505*). **F.** *L. vincta* (*Vlasák 1704/102*). Scale bars = 1 cm.

290621 studied). **Philippines**, Mindanao. Zamboanga, San Ramon, 12 May 1904, *Copeland 743* (**lectotype** of *Poria porphyrophaea* NY 00742723 – selected by Ryvarden 1988). **Sri Lanka**, Gangaruwa, Dec. 1913, *Petch 3930* (**lectotype** of *Poria hypobrunnea* K(M) 56199 – selected by Setliff (1972b), studied).

*Basidiocarps* resupinate, annual or more rarely lasting for 2–3 growth seasons, juvenile fruiting bodies nearly white, quickly attaining reddish-greyish colour ranging from nearly orange, purplish or pinkish to brick-colour with a grey overlay, later dark brown or grey; colours fade after drying, patches from a few cm to a couple of dm, 0.5–2(–4) mm thick. Old basidiocarps curving and bone-hard when dry, tough leathery when fresh. Pores regular, rounded, thin-walled, (7–)9–13(–16) per mm, median 8–15 so quite variable between specimens. Subiculum cream coloured when young, brown when old, cottony, topped by a brown, agglutinated basal layer, which is also visible between annual layers, 0.2–0.5 mm. Margin abrupt, very narrow, if any sterile part at all, sometimes a narrow beige or cream-colored band of younger growth in contrast to darker old pores.

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*Hyphal structure* dimitic, clamps absent. Generative hyphae slightly thick-walled, yellowish, (1.5–)2.0–3.4(–4.2) µm diam. Subiculum dominated by interwoven brownish skeletal hyphae, (2.4–)3.0–4.3(–5.4) µm diam with a usually distinct lumen, 1/4 to 1/6 of total width. Tramal tissue dense, interwoven, difficult to study but not agglutinated, lower trama dominated by generative hyphae or equally by skeletal hyphae, (2.0–)3.0–4.0(–4.8) µm diam. *Cystidia:* Skeletocystidia abundant and persistent, embedded in trama, heavily encrusted, encrustation commonly short but wide, (12–)20–45(–155) × (8–)11.5–18(–26), L = 33.6 µm, W = 14.9 µm (n = 134/15), width up to 17 µm when naked; in slides it is typical to see only large ellipsoid crystal clumps and not the root of the cystidia. Hymenial gloeocystidia mamillate, varying in number but often numerous, broad and conspicuous, (10–)14–19.5(–31) × (5–)9–11.2(–16), W = 10.1 µm (n = 44/11). *Basidia* clavate to barrel-shaped, 7.5–17 × 4.6–6.5 µm. *Basidiospores* broad ellipsoid to subglobose, (3.2–)3.4–4.6(–4.9) × (2.9–)3.0–3.9(–4.3) µm, L = 3.94 µm, W = 3.46 µm, Q = 1.10–1.22.

*Distribution and ecology*: Widely distributed in tropical and subtropical areas in the Old World and Pacific, in the southern hemisphere reaching Australia and New Zealand. In the Neotropics known from the Caribbean. Basidiocarps develop on dead wood of various angiosperms but known also for attacking living trees.

*Notes*: Hymenophore colour changes drastically with age from light-coloured to brown or grey. Specimens have a pink or purple tinge combined with dull greyness, except in senescent specimens that lose all reddish colour. Microscopically, subglobose spores and wide but short cystidial encrustation are characteristic. Young specimens, where cystidial characters and grey colour are not well developed, might be difficult to tell apart from *L. vincta*.

*Lividopora benetosta* is a very common species in old world tropics. *Poria vincta* var. *cinerea* of Setliff (1972a, b) is largely based on *L. benetosta*, but also on *L. subvincta* and possibly other species as well. Corner (1987) adopted *Poria hypobrunnea* for this species. Corner's description and the type of this species fit well our concept of *L. benetosta*. However, *Poria hypobrunnea* is just one name in a long list of synonyms of *Lividopora benetosta*, and one of the most recent ones.

The reports on *Acacia* heartwood rot caused by *Rigidoporus hypobrunneus* (Lee & Noraini Sikin 1999) probably refer to *L. benetosta* as defined here. Data by Martin *et al.* (2015) on endophytic fungi shows that *L. benetosta* is rather common on living rubber trees (*Hevea brasiliensis*) in Cameroon, and we speculate that it could be a pest of rubber plantations.

***Lividopora facilis*** Miettinen, ***sp. nov.*** MycoBank MB 849648. Figs 11, 12.

*Typus*: **Indonesia**, Riau, Indragiri Hulu, Bukit Aluran Babi, -0.83541° : 102.2278° ± 140 m, alt. 150 m, secondary, half-open forest on moist, level ground, fallen branch on the ground (*Anthocephalus*?, 3 cm diam, decay stage 2/5), 29 Jun. 2004, *Miettinen 8742*\* (**holotype** BO, **isotype** H 7200351).

*Etymology*: *Facilis* (Lat., adj.), easy, referring to easy identification of this species.

*Basidiocarps* resupinate, greyish pinkish or faded brick colour, like a dull version of *Steccherinum collabens*, in senescent parts light ochraceous brown, patches of 2–5 × 1–2 cm, 0.4–1 mm thick. Consistency tough, woody when dry. Pores rather regular in size, thin-walled, rounded angular; mouths whitish pruinose due to projecting hyphal ends, 5–6(–7) per mm. Subiculum very thin, white, lighter in colour than pores, ≤ 0.1 mm thick. A thin basal layer with a reddish-brownish colour present.

*Hyphal structure* dimitic, clamps absent. Generative hyphae uniform, thin- to slightly thick-walled, (1.5–)1.8–2.8(–3.2) µm diam. Subiculum dominated by interwoven, faintly yellowish to hyaline skeletal hyphae, (2.5–)2.6–3.3(–5.0) µm diam, their lumen visible and 1/6–1/3 of total width, tissue rather loose. A very tightly packed basal layer of 20–40 µm composed of slightly thick-walled generative hyphae is found next to the substrate. Tramal hyphae interwoven to subparallel, skeletal hyphae (2.4–)2.8–3.3(–3.9) µm diam, tissue rather dense but not agglutinated. Dominance of skeletal hyphae fades towards tube mouths, which are nearly monomitic. *Cystidia:* Encrusted hyphal ends in trama, occasionally bending into hymenium, when young slightly thick-walled generative hyphal ends that later develop into larger thick-walled skeletocystidia, (7–)12.5–27.6(–55) × (6–)8.7–10.8(–14) µm, L = 20.8 µm, W = 9.7 µm (n = 24), up to at least 10 µm wide without encrustation. The second type of cystidia ("gloeocystidia") often mamillate, 9.4–20 × 5–8, µm W = 6.3 µm (n = 18), projecting up to 10 µm beyond hymenium. *Basidia* clavate to cylindrical, 8.5–14 × 4.3–5.5 µm. *Basidiospores* thin-walled, ellipsoid, 3.2–4.0 × 2.5–3.0 µm, L = 3.5 µm, W = 2.69 µm, Q = 1.3.

*Distribution and ecology*: Known from dead dicot wood from a secondary lowland rainforest in Sumatra.

*Notes*: Larger pores and clearly narrower spores separate *L. facilis* from other *Lividopora* species.

***Lividopora subvincta*** (Ryvarden) Miettinen, ***comb. nov.*** MycoBank MB 849649. Figs 11–13.
*Basionym*: *Rigidoporus subvinctus* Ryvarden, *Syn. Fungorum* **40**: 105. 2020.
*Synonym*: *Poria vincta* var. *cinerea* (Bres.) Setliff, *Mycologia* **64**: 695. 1972. *pro parte*.

*Typus*: **Zimbabwe**, Manicaland, Vumba, Leopard rock, angiosperm, 14 Mar. 1995, *Ryvarden 37098*\* (**holotype** of *Rigidoporus subvinctus* O-F-76331, studied).

*Basidiocarps* resupinate, annual to biennial, dark grey, patches of a few cm to dm, 0.5–2 mm thick. Consistency hard when dry, curving inwards upon drying. Pores regular, round, (7–)9–12(–14) per mm. Subiculum brown, in younger parts cream coloured, basal layer a thin, waxy black line, visible between annual layers, 0.2 mm. Margin abrupt or an up to 1 mm wide light-coloured sterile zone.

*Hyphal structure* dimitic, clamps absent. Generative hyphae slightly thick-walled, (1.9–)2.2–2.8(–3.4) µm diam. Subiculum dominated by interwoven, brown skeletal hyphae, basal layer with partly parenchymatic tissue, apparently consisting of both skeletal and generative hyphae, skeletal hyphae (3.4–)3.7–4.8(–5.6) µm diam, with a distinct lumen 1/3–1/6 of total width. In trama skeletal hyphae similar to subicular hyphae, interwoven,

*Lividopora armeniaca*

*L. benetosta*

*L. facilis*

*L. subvincta*
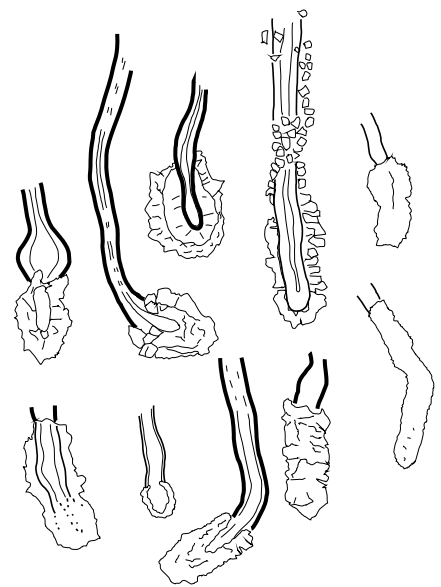
*L. vincta*

5 µm

10 µm

10 µm

10 µm

**Fig. 12.** *Lividopora facilis* basidiome hyphal structures (subiculum, trama, and encrusted cystidia) and spores of the five *Lividopora* species treated here.
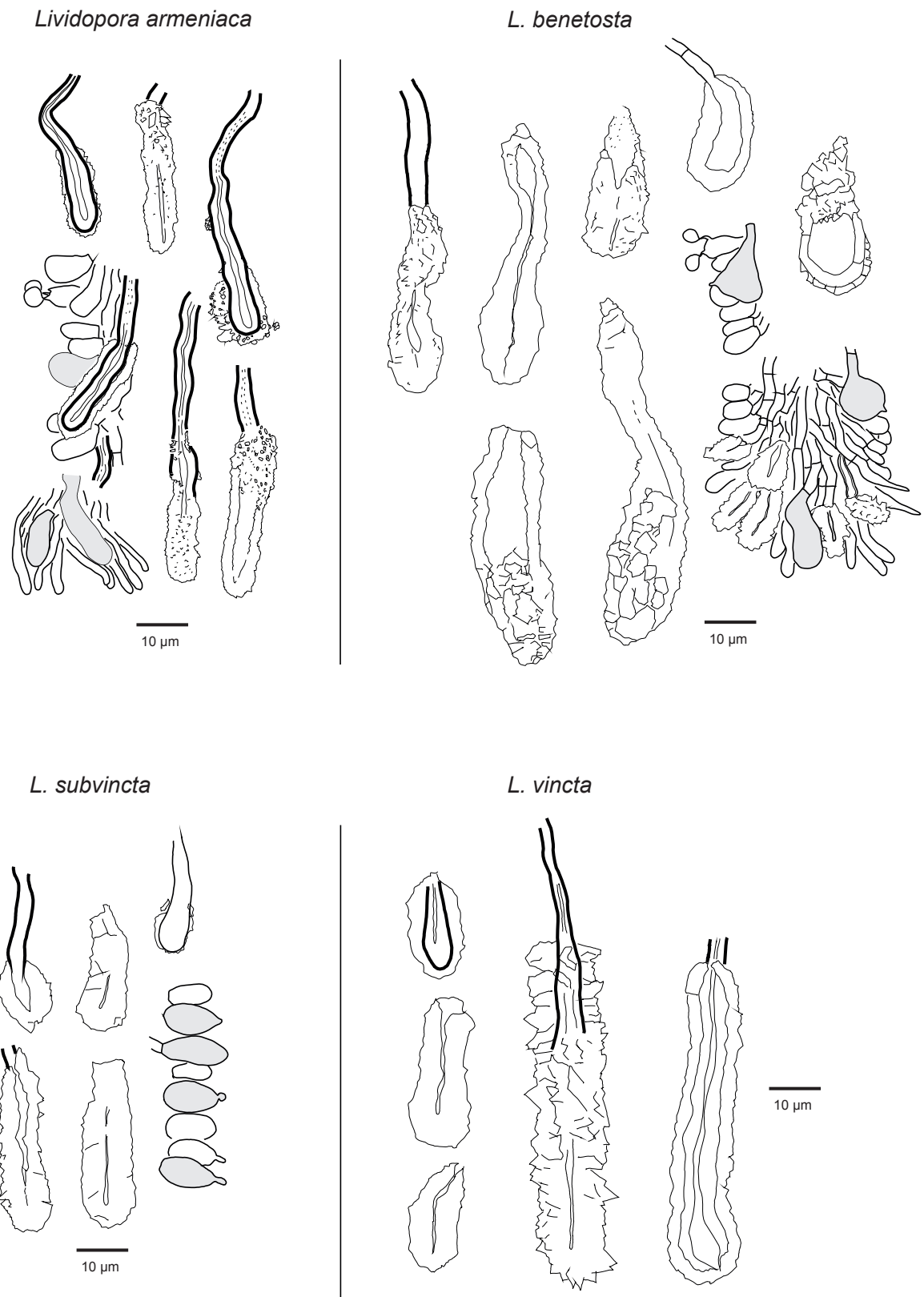
*Lividopora armeniaca*

*L. benetosta*

10 µm

10 µm

*L. subvincta*

*L. vincta*

10 µm

10 µm

10 µm

**Fig. 13.** Cystidia of *Lividopora* spp.

dominant in upper trama, (2.4–)3.2–4.2(–5.0) µm diam; generative hyphae dominate close to tube mouths. *Cystidia:* Skeletocystidia abundant, encrusted heavily, ranging from mid-sized to broad, usually encrustation long, (9.5–)23–42(–58) × (6.8–)9.4–12(–17) µm, L = 31.6 µm, W = 11.0 µm, (n = 75/3), up to at least 9.5 µm in width without encrustation. Stained thin-walled hymenial cystidia variable in numbers, may be

locally abundant close to tube mouths, round, partly mamillate, (13–)14–18.3(–40) × (5.5–)6.8–8.2(–8.8) µm, W = 7.4 µm (n = 27/3). Basidia clavate to barrel-shaped, 8.8–10 × 5.4–6 µm. *Basidiospores* broad ellipsoid to subglobose, with distinct walls and no guttulae, (3.4–)3.6–4.6(–5.2) × (2.6–)2.9–3.4(–3.5) µm, L = 4.02 µm, W = 3.13 µm, Q = 1.22–1.30.

*Distribution and ecology*: Known from Kenya, Tanzania, and Zimbabwe from *Cupressus* and dicot wood; tree pathogen causing root rot.

*Notes*: This species is dark already when young unlike the other African species of *Lividopora*, *L. benetosta*. Basidiocarps are darker than in *L. benetosta* also when older. According to Ryvarden (2020a), this species is different from "*Rigidoporus vinctus*" by having two types of cystidia, while the latter has only one type. This is incorrect, as we have shown here that all *Lividopora*, including *L. vincta*, have two types of cystidia. His concept of *R. vinctus* may be mixed (including some *Meripilaceae*), but he quite correctly likened the two species when describing *L. subvincta*. Microscopic differences include slightly narrower spores in *L. subvincta* (Q > 1.2) and shortly but widely encrusted skeletocystidia in *L. benetosta* as opposed to long encrustation in *L. subvincta*.

Setliff & Mesner (1971) report this species as *Poria vincta* var. *cinerea* as a tree plantation pest from Mt. Meru, Tanzania. We sequenced a Tanzanian strain of Setliff (ECS-194-R) very likely associated with this study. Later their concept of the aforementioned variety included also *L. benetosta*, as can be deduced from their list of studied specimens (Setliff 1972b).

*Lividopora vincta* (Berk.) Miettinen, **comb. nov.** MycoBank MB 849650. Figs 11–13.
*Basionym*: *Polyporus vinctus* Berk., *Ann. Mag. Nat. Hist.* **9**: 196. 1852.
*Synonym*: *Polyporus carneopallens* Berk., *Hooker's J. Bot. Kew Gard. Misc*. **8**: 235, 1856.

*Typus*: **Dominican Republic**, Santo Domingo, unknown collection date, *Sallé 34* (**holotype** of *Polyporus vinctus* K(M) 167866, studied). **Brazil**, Amazon, Rio Uaupés, Ipanoré ("Panuré"), on dead trees, Feb. 1853, *Spruce 178* (**lectotype** of *Polyporus carneopallens* designated here K(M) 192248, MBT 10014556, studied; **isolectotype** FH 00290615, studied).

*Basidiocarps* resupinate, orange reddish or pinkish when fresh, drying duller reddish ochraceous, 1–2.5 mm thick. Consistency hard when dry. Pores regular, rounded, (7–)8–10(–12). Subiculum ochraceous, 0.2–1 mm thick, basal waxy, red to black layer present, 20–100 µm thick. Margin cream coloured.
*Hyphal structure* dimitic, clamps absent. Generative hyphae slightly thick-walled, CB(+), (1.7–)2.2–3.0(–3.8) µm diam. Subiculum dominated by interwoven, yellowish skeletal hyphae, loose to rather tight, (2.3–)3.1–4.6(–5.4) µm diam, with a distinct lumen of 1/3–1/6 total width. Basal layer monomitic, composed of agglutinated, thick-walled generative hyphae, (3.2–)3.7–4.7(–5.0) µm diam. Tramal skeletal hyphae interwoven, (2.0–)3.7–4.6(–5.9) µm diam, dominate in upper trama, less so towards tube mouths where hyphae are subparallel, tissue dense but not agglutinated. *Cystidia:* Skeletocystidia clavate, large and heavily encrusted, (17–)31–60(–105) × (7–)9.8–20(–23) µm, L = 46.1 µm, W = 14.8 µm (n = 94/5), up to 12.5 µm in width when naked. Thin-walled hymenial cystidia clavate to mamillate, (10–)14–40(–46) × (4.6–)7.0–9.5(–12.4) µm, W = 8.2 µm (n = 34/5). *Basidia* not seen, basidioles 7.5–10.5 × 4.5–5.3. *Basidiospores* broad ellipsoid, with thin to distinct walls, (3.2–)3.3–4.2(–4.5) × (2.8–)2.9–3.4(–3.5) µm, L = 3.80 µm, W = 3.13 µm, Q = 1.20–1.23.

*Distribution and ecology*: Found in tropical and warm temperate Americas. Endophyte DNA data of Martin et al. (2015) show that

*L. vincta* appears to be common on living *Hevea brasiliensis* in natural forests in Brazil and Peru.

*Notes*: The name *Rigidoporus vinctus* has been interpreted confusingly in the literature and herbaria, and we know from our own experience that it covers many species. Part of the material under this name belongs to *Meripilaceae*, and part of it to *Lividopora*.

The distributions of *L. benetosta* and *L. vincta* overlap at least in the Caribbean. *Lividopora vincta* is lighter in colour than *L. benetosta*, its spores are narrower and its cystidia are long, not short and wide as often seen in *L. benetosta* (Table 4).

There is some ITS variation in *L. vincta* (Fig. 10), and it would be interesting to see a more in-depth study of this species with more specimens and several markers. It may yet turn out to be a species complex, but ITS variation is small and gradual enough to be the result of geographic spread of sequenced specimens or quality issues.

*Pseudolagarobasidium* J.C. Jang & T. Chen, *Trans. Brit. Mycol. Soc.* **85**: 374. 1985.

*Type species*: *Pseudolagarobasidium subvinosum* (Berk. & Broome) Sheng H. Wu

*Notes*: Hallenberg et al. (2008) showed that *Pseudolagarobasidium*, a genus of hydnoid wood-inhabiting resupinate fungi, is related to *Cerrena*. Nakasone & Lindner (2012) gave a taxonomic treatment of the genus recently, and good illustrations of *Pseudolagarobasidium* species can be found in Maekawa & Hasebe (2002) and Wood & Ginns (2006). Nakasone & Ortiz-Santana (2022) expanded the genus so that in their view it includes 11 species. We have shown here that *Acanthodontia cirrhatina* does not belong to *Pseudolagarobasidium*, as they suggested, and we exclude *Hyphoradulum conspicuum* from the genus.

The genus would require a revision with properly sequenced material to ascertain the real species number. In particular, the paleotropical *Pseudolagarobasidium* species should be revised, and historical names should be checked against newly described species. It would appear there are several closely related species parasitic on *Fabaceae*. Currently, the six species listed below have been sequenced and described reliably enough that we conclude that they belong to the genus. They are listed below. For two of them, only LSU data is available, making integrative species-level comparison within the genus problematic at present. We consider the remaining names as insufficiently known taxa.

Our ITS-based tree of all publicly available sequences (Fig. 14) represents nominally four species (*P. acaciicola*, *P. baiyunshanensis*, *P. belizense*, and *P. pallens*). We find it difficult to interpret these results. Species number may vary between three and seven. We suggest future papers utilize another marker beside ITS to delimit species.

Thin-walled hymenial cystidia just like those shared by other genera of the *Cerrena* clade are found in the genus. *Pseudolagarobasidium* species are also dimitic and their blunt, raduloid ("subporoid") hymenophore reminds of old, irpicoid *Cerrena* a lot. However, hyphal structure in *Pseudolagarobasidium* is mostly monomitic and skeletal hyphae are found only in the basal part of the basidiocarp. These skeletal hyphae are furthermore peculiar "microbinding hyphae", *i.e.* narrow and regularly branching, quite unlike the regular, rarely branching skeletal hyphae in *Cerrena*.
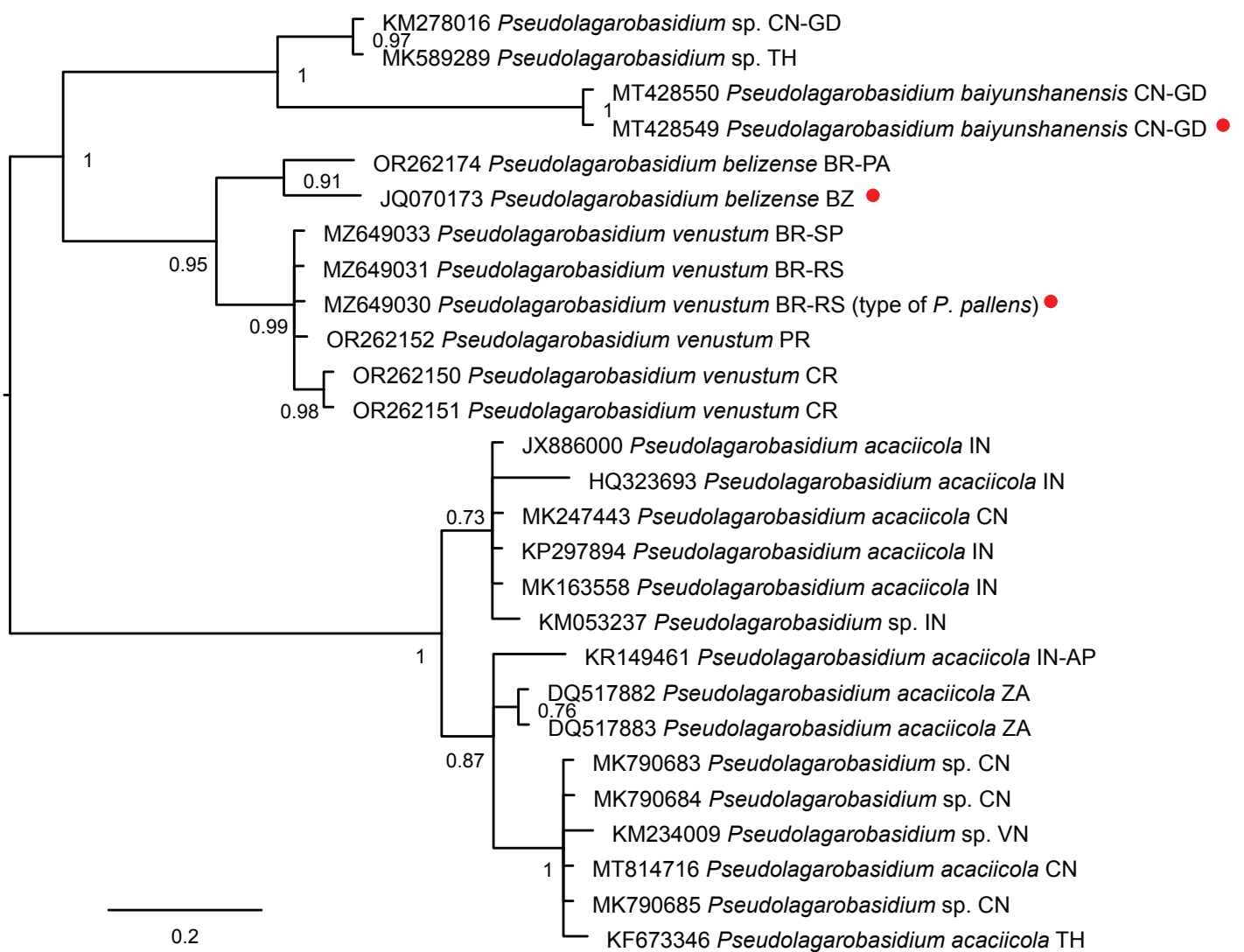
**Fig. 14.** Bayesian consensus phylogram of *Pseudolagarobasidium* spp. based on ITS sequences. Red circles denote type specimens. Countries (and states) of origin are denoted with ISO 3166 codes.

## Accepted species with DNA sequences available

*Pseudolagarobasidium acaciicola* Ginns, *Canad. J. Bot*. **84**: 752. 2006.

*Note*: Even though Wood & Ginns (2006) do not mention sequence accession numbers, they published ITS sequences of two paratypes (GenBank DQ517882, DQ517883), complemented with a LSU (GenBank EU569321) by Hallenberg *et al*. (2008).

*Pseudolagarobasidium baiyunshanense* M.L. Han, L.S. Bian & Q. An, *Phytotaxa* **483**: 171. 2021.

*Pseudolagarobasidium belizense* Nakasone & D.L. Lindner, *Fungal Diversity* **55**: 158. 2012.

*Pseudolagarobasidium subvinosum* (Berk. & Broome) Sheng H. Wu, *Acta Bot. Fenn*. **142**: 113. 1990. Fig. 2.
*Basionym*: *Hydnum subvinosum* Berk. & Broome, *J. Linn. Soc., Bot*. **14**(73): 60. 1873 [1875].
*Synonym*: *Pseudolagarobasidium leguminicola* J.C. Jang & T. Chen, *Trans. Brit. Mycol. Soc*. **85**: 374. 1985.

*Typus*: **Sri Lanka**, Peradeniya, Nov. 1867, no. 180 (**holotype** of *Hydnum subvinosum* K). **Taiwan**, Hua-Ling, Fung-Ping, *Leucaena leucocephala*, Feb. 1983, *Jang & Chen* (**holotype** of *Pseudolagarobasidium leguminicola* TAI 9020).

*Notes*: This species is distinctive enough that we trust the conclusion of Nakasone & Lindner (2012) that the generic type *P. leguminicola* and *P. subvinosum* belong to the same species, or at least are closely related. An LSU sequence (GenBank EU569319) was published by Hallenberg et al. (2008).

*Pseudolagarobasidium pronum* (Berk. & Broome) Nakasone & D.L. Lindner, *Fungal Diversity* **55**: 162. 2012.

*Notes*: Hallenberg *et al*. (2008) provide an LSU sequence (GenBank EU569320) based on a Taiwanese specimen of Wu identified as *P. calcareum*, a species described from the southern part of Australia. This LSU sequence clearly belongs to *Pseudolagarobasidium*. We have studied Wu's Taiwanese collection of *P. calcareum*, the same one studied by Nakasone & Lindner (2012), and it is very similar to *P. belizense* and thus a true *Pseudolagarobasidium*. Nakasone & Lindner (2012) concluded that this species is a synonym of *P. pronum*, which was described

from Sri Lanka. Now that species diversity in the genus has increased, also the identity of *P. calcareum* against *P. pronum* should be re-assessed. We have not studied the types involved. If they belong to separate species of *Pseudolagarobasidium*, an affinity of Taiwanese material to Sri Lankan *P. pronum* appears more likely than to the South Australian *P. calcareum*.

***Pseudolagarobasidium venustum*** (Hjortstam & Ryvarden) Nakasone & D.L. Lindner, *Fungal Diversity* **55**: 165. 2012.
*Basionym*: *Radulodon venustus* Hjortstam & Ryvarden, *Mycotaxon* **74**: 250, 2000.
*Synonym*: *Pseudolagarobasidium pallens* Motato-Vazq. & Westphalen, *Phytotaxa* **555**: 163. 2022.

*Typus*: **Brazil**, São Paulo, Reg. Santos, Cananeia, Ilha do Cardoso, on bark of palm, 2 Feb. 1987, *Hjortstam 16838* (**holotype** of of *Radulodon venustus* K(M) 77909, studied).

*Notes*: Our sequenced material from Costa Rica and Puerto Rico agrees well with the type. The sequences are near identical with the Brazilian material that Westphalen & Motato-Vásquez (2022) described as *P. pallens*. They cited as main differences yellow to orange colour and smaller spores of *P. venustum*, though apparently without studying the type of *P. venustum*. The protologue of *P. venustum* states that the colour is at first whitish and later straw-coloured. Their statement about colour probably refers to Nakasone & Lindner (2012), who studied the type but also included other specimens in their description, none of which was sequenced, and whose identity we cannot confirm. Spores are of equal width and a bit longer in *P. pallens* than reported for the type of *P. venustum*. Spore length can vary, and we think it is highly likely *P. pallens* is conspecific with *P. venustum*. Both were described from the same area in southern Brazil.

***Radulodon*** Ryvarden, *Canad. J. Bot.* **50**: 2073. 1972.

*Genus type*: *Radulodon americanus* Ryvarden

*Notes*: Nakasone & Lindner (2012) showed that most species of *Radulodon sensu lato* belong to *Pseudolagarobasidium* instead. As currently recognized, the genus contains 3–4 boreal to temperate species, depending on whether *R. americanus* is recognized as a separate species. The differences in ITS sequences within the genus are small (Fig. 15).

Phylogenetically, *Radulodon* is a sister genus to *Irpiciporus* (Fig. 3). We have retained the genus here, though alternatively it would be possible to include it in *Irpiciporus*. Our reasons relate to the overall generic arrangement of the *Cerrenaceae* – even though sister taxa, the two are genera are genetically distant (see Results). We suspect our dataset is lacking a lot of species diversity around *Radulodon*, and hence minimal nomenclatural change is justified until wider genetic and morphological datasets may indicate otherwise.

As defined here, *Radulodon* is characterized by rather thin, hydnoid basidiocarps as opposed to larger, effused-reflexed found in *Acanthodontia* and *Irpiciporus*. Microscopically, cystidia and dense, interwoven subhymenial structure are characteristic. Cystidia are found in *Acanthodontia* also, but its hyphal structure is consistently looser and more regular as in *Irpiciporus*, which lacks cystidia. The differences are small, however.

***Radulodon casearius*** (Morgan) Ryvarden, *Canad. J. Bot.* **50**: 2075. 1972.
*Basionym*: *Hydnum casearium* Morgan, *J. Cincinnati Soc. Nat. Hist.* **10**: 11, 1887.

*Typus*: **USA**, Ohio, Cincinnati, *Carya*, unknown collection date, *A. P. Morgan* (**holotype** BPI US0324642, C. G. Lloyd herb. 16737 – selected by Stevenson & Cash 1936: 74).

*Notes*: See Nakasone (2001) for a description. Smaller spores separate it from the other species of the genus. This species is known from south temperate United States so far.

***Radulodon erikssonii*** Ryvarden, *Canad. J. Bot.* **50**: 2075. 1972. Fig. 2.

*Typus*: **Norway**, Oslo, Sørkedalen, *Populus tremula*, 24 Oct. 1968, *Ryvarden* (**lectotype** O – selected by Nakasone (2001), studied; **isotypes** in DAOM, L).

*Notes*: See Eriksson *et al.* (1981) for a description. ITS sequences of *Radulodon americanus* and *R. erikssonii* are nearly identical (2 bp difference in our set of seven sequences). Morphologically, material from North America and Eurasia are indistinguishable; the characters outlined by Ryvarden (1972a) do not separate these species (presence of cystidia, basidiocarp thickness). North temperate to boreal distribution with a continental preference and *Populus tremula/tremuloides* as a host also join the two. Hence, we consider it likely that *R. americanus* and *R. erikssonii* are synonyms, but we would like to see this confirmed with more extensive sampling and several genetic markers. The two species were described in the same paper, but *R. erikssonii* has been used more widely than *R. americanus*, and it is included in red lists of several European countries. We recommend therefore maintaining *R. erikssonii* over *R. americanus*, if the two are synonymized.

***Radulodon yunnanensis*** Y.C. Dai & Chao G. Wang, *Mycol. Progr.* **21**(73): 11. 2022.

*Typus*: **China**, Yunnan, Pingbian, Daweishan Forest Park, *Castanea*, 5 Jun. 2011, *Dai 12204* (**holotype** BJFC 010487).

*Notes*: Wang & Dai (2022) described this species from the mountains of Yunnan, China, *i.e*. eastern Himalayas. It is genetically distinct, but the morphological characters (fimbriate margin, spine density) that the authors list do not separate it from *R. erikssonii*. Notably, the authors cite one collection from *Pinus*, while the rest are from angiosperms. This is the only collection of conifer-dwelling *Radulodon* known to us.

***Somion*** Adans., *Familles des plantes* **2**: 5. 1763.

*Genus type*: *Hydnum occarium* Batsch, chosen by Donk (1974: 175).

*Etymology*: σῶμα (Gr., noun) derives from body, torso, flesh, evidently referring to fleshy basidiocarps.

*Basidiocarps* annual or biennial, sessile to effused-reflexed, light-colored, watery in fresh condition, rather tough after drying. *Context* duplex, with softer upper and more compact lower
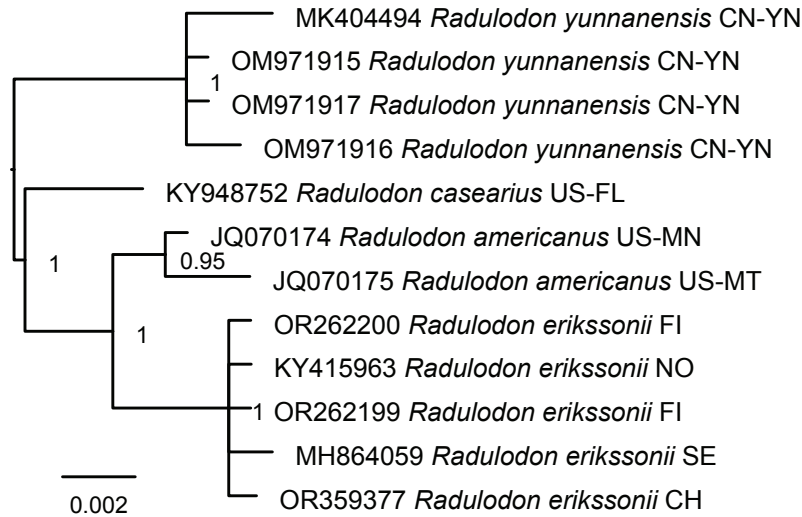
**Fig. 15.** Bayesian consensus tree of *Radulodon* spp. based on ITS sequences. Countries (and states) of origin are denoted with ISO 3166 codes.

layers. *Pores* angular to sinuous, 1–4 per mm. *Hyphal structure* monomitic, hyphae clamped and slightly cyanophilous, distinctly thick-walled in both context and trama. *Basidia* short-clavate, 13–25 × 5–8 µm, four-spored, with guttulate contents, quickly collapsing. *Basidiospores* ellipsoid or ovoid to subglobose, thick-walled (spore wall up to 1 µm thick), with a large central oil-drop, cyanophilous. Causes a white rot of living and dead deciduous trees.

*Notes*: *Somion* is a sister clade to the rest of the *Cerrenaceae* (Fig. 3). Being so distinct phylogenetically if not morphologically, this clade clearly requires its own genus, whose nomenclature is discussed below. Phylogenetically, the genus is divided in two groups: *S. delectans* and *S. occarium* form a clade distinct from the rest. ITS sequences alone are not sufficient to separate all species in the genus, in particular *S. formosanum*, *S. litschaueri,* and *S. strenuum* (Fig. 16). However, *TEF1* and the joint *TEF1*-ITS dataset show clear support for dividing this complex into seven species overall (Fig. 17). For identification of species within the genus, see Table 5.

Dismantling traditional, morphology-based genera requires not only a re-consideration of their younger synonyms (*e.g. Irpiciporus* in the case of *Spongipellis sensu lato*) but also a careful revision of suppressed older names. Recent DNA-based revisions of the corticioid genera *Hyphodontia* and *Tomentella*, both conserved *versus* their older synonyms, made it necessary to restore some suppressed generic names (*e.g., Kneiffiella, Odontia*, and *Xylodon*). This restoration is allowed if the type species of the conserved and the suppressed genus cannot be anymore considered congeneric (ICN Shenzhen code art. 14.6). In the case of *Spongipellis*, the older name which requires further examination is *Somion* Adans. against which *Spongipellis* has been conserved (ICN Appendix III). We show below that the type species of *Somion* cannot belong to *Spongipellis sensu stricto* (*Meripilaceae*), and thus the name is available for use and must be considered when *Spongipellis sensu lato* is being divided into several genera.

The genus *Somion* was described by Adanson (1763: 5) based on three illustrations published by Micheli (1729: Tabula 64, figs 3–5). No binomial species names were addressed to the genus in the protologue; nevertheless, *Somion* meets the requirements for a validly published generic name (see Donk

1960: 283). The name may have gone unnoticed because Ryvarden's index to generic names does not contain it (Ryvarden 1991). The three aforementioned Micheli's figures were the basis for the subsequent introduction of four species names: *Hydnum occarium* Batsch (fig. 3 – Batsch (1783: 113), sanctioned by (Fries 1821: 412), *H. orbiculatum* Pers. (fig. 5 – Persoon 1801: 559), sanctioned by Fries (1821: 412) and *H. pectinatum* Fr. (fig. 4 – Fries 1821: 412). Batch's *H. pectiniforme* is based on figs 4 and 5, but Fries considers it as a synonym of *H. orbiculatum*, so the latter as a conserved name has priority over the former and *H. pectiniforme* is obsolete.

Donk (1974: 175) selected *H. occarium* as a lectotype of *Somion* (at that time a devalidated generic name) and treated it as a synonym of *Spongipellis* – he had suggested earlier that *H. occarium* might be a synonym of *Spongipellis pachyodon* (Donk 1960: 176). Changing the starting point for validly published fungal genera from 1821 to 1753 (ICBN Sydney code 1981) made *Somion* available for use although under the aforementioned condition only. The identity of *H. occarium* decides whether *Somion* is going to be kept as a suppressed synonym of *Spongipellis* or whether it should be put in use as an independent genus.

The protologue by Batsch (1783) and the subsequent redescription of *H. occarium* by Fries (1821) introduced it as a white, large fungus with hairy upper surface and flat, thick and blunt "aculei"; additionally, Fries describes the consistence of *H. occarium* as "probably fleshy" ('substantia … forsan carnosa'), and size being 3 inches wide and projecting 1–1.5 inches. The generic name *Somion* refers to a fleshy fungus, which may be the origin of Fries's statement. The measurements probably derive from Persoon (1801). Micheli's drawing, which may serve as a lectotype of the species (ICN art. 9.3, 9.4), shows three pileate, mid-sized caps with something like irpicoid or blunt hydnoid hymenophore viewed from the side.

There are not many non-stipitate pileate, light-coloured hydnoid-irpicoid fungi in Europe. *Climacodon septentrionalis*, *Donkia pulcherrima*, and *Hericium cirrhatum* have sharp, rather small teeth in contrast to descriptions of Batsch (1783) and Fries (1821). Old caps of *Cerrena unicolor* may be irpicoid but then also grey, not light-coloured, and caps are rather thin. *Irpex lacteus*, *Irpicodon pendulus*, and *Steccherinum oreophilum* fruiting bodies are much too small to fit the description. *Trametopsis cervina* has daedaleoid pores that may turn irpicoid, but its caps
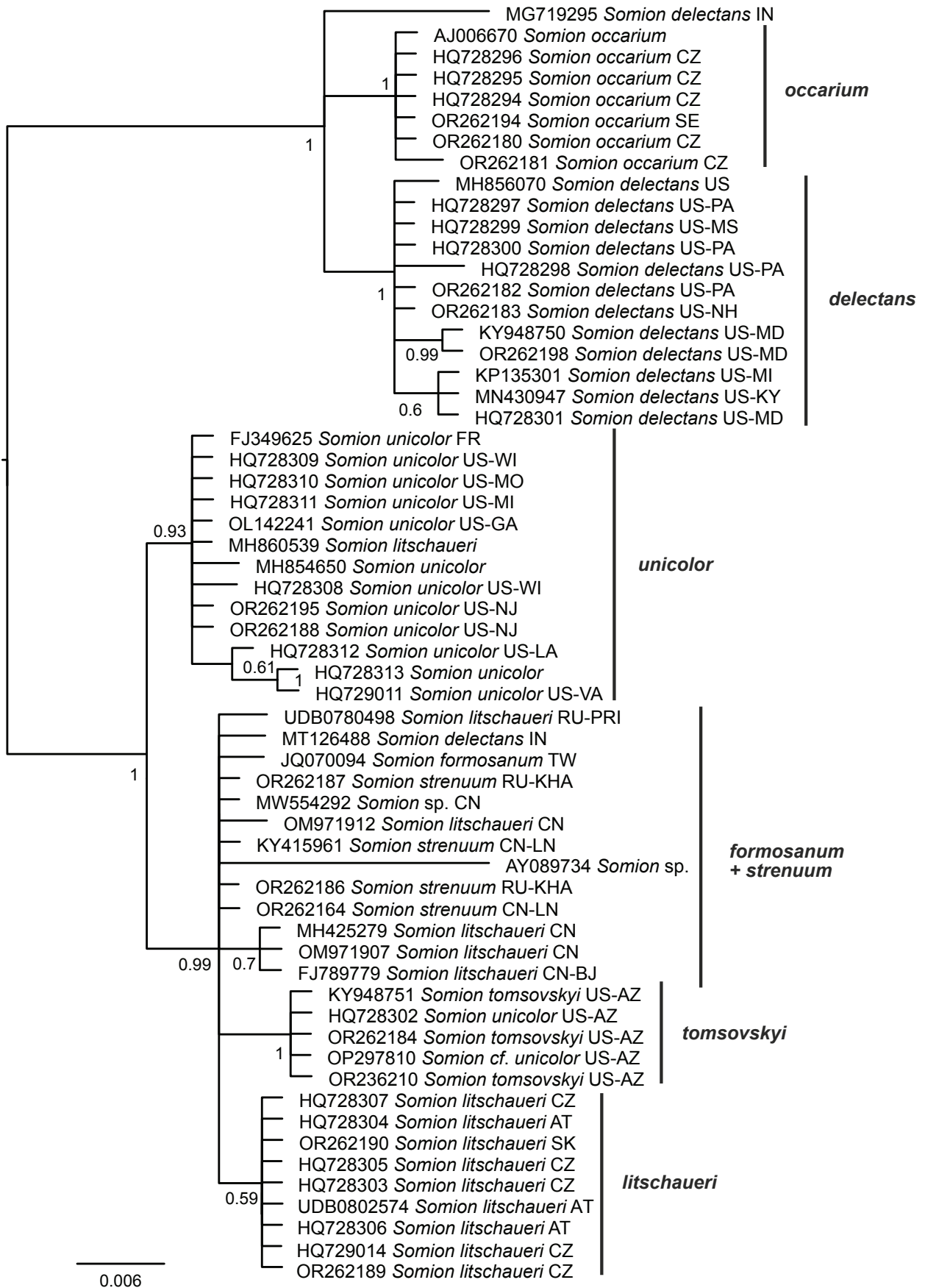
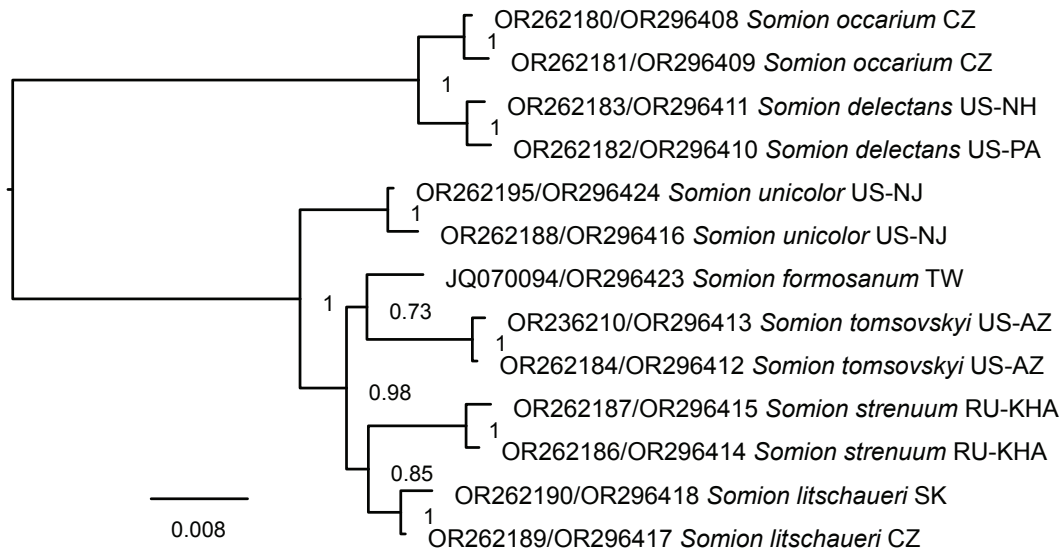**Fig. 16.** Bayesian consensus phylogram of *Somion* spp. based on ITS sequences. Countries (and states) of origin are denoted with ISO 3166 codes.

are usually quite thin, projecting less than described, and not fleshy, so this species is not the most likely candidate either.

Turning to *Spongipellis*, the hymenophore construction precludes the two European species of *Spongipellis sensu stricto*,

*S. profissilis* and *S. spumea* (Spirin *et al.* 2022). They both possess normal poroid hymenophore, which cannot be interpreted as having tooth-like appearance, and thus synonymy of *Somion* and *Spongipellis* is excluded. The illustration and description

**Fig. 17.** Bayesian consensus phylogram of *Somion* spp. based on ITS and *TEF1* sequences. Countries (and states) of origin are denoted with ISO 3166 codes.

of the hymenophore would fit well to *Spongipellis* (*Irpiciporus*) *pachyodon*. However, all the specimens we have seen have smooth (or near so) pileal surface, and this seems to be the case in the literature as well: Bernicchia (2005) describes the upper surface as tomentose to smooth, and Rivoire (2020) as cottony to felt-like. The relatively small size of caps in *S. pachyodon* does not fit the descriptions of *H. occarium* either.

The European taxon so far called *S. delectans* but proven to represent a good species in this study, is yet another option. It has nearly white, substantial basidiocarps with often strigose pileal surface (Fig. 1E) and large, irregular pores that may become dentate (described as irpicoid by Bernicchia 2005 and Rivoire 2020). Micheli, Batsch, and Fries (who apparently never saw specimens) might have described such a hymenophore as consisting of blunt teeth. We find the European *S. delectans* as the most credible option for typifying *H. occarium* in that it does not contradict any element of the protologue and agrees well in many. Consequently, we designate here an epitype to supplement the lectotype illustration among the European material of *S. delectans.*

As a result, *Somion* becomes the oldest name available for the *S. delectans* complex, which requires its own genus. The correct species name of European *S. delectans* is then *Somion occarium* (Batsch) Spirin & Miettinen.

**Somion delectans** (Peck) Vlasák & Spirin, **comb. nov.** MycoBank MB 849651. Fig. 18.
*Basionym*: *Polyporus delectans* Peck, *Bull. Torrey Bot. Club* **11**: 26. 1884.

*Typus*: **USA**, Ohio, Cincinnati, fallen log, unknown collection date, *Morgan 106* (**holotype** NYS, **isotype** BPI US 0207202, studied).

*Basidiocarps* annual, sessile or effused-reflexed, up to 15 cm in widest dimension. Upper surface finely pubescent, later almost smooth, azonate, cream coloured to pale ochraceous. Edge of pileus sharp to rather blunt, sterile, concolourous with pileal surface. Hymenial surface even to more-or-less concave or rarely convex, cream coloured to pale ochraceous; pores angular to somewhat elongated, 2–3 per mm, dissepiments rather

thin, first even, later serrate. Section: context white to cream coloured or pale ochraceous (old herbarium specimens only), watery in fresh condition, firm, indistinctly fibrillose and azonate when dry, up to 1 cm thick; tube layer soft, concolourous with pore surface, up to 1 cm thick.

*Hyphal structure* monomitic; all hyphae with clamp connections. Context hyphae very thick-walled, arranged in subparallel bundles, a few thin-walled, (4.1–)4.7–6.2(–7.7) µm diam. Tramal hyphae thick-walled (lumen capillary to indistinct), subparallel, (3.2–)3.8–4.7(–5.2) µm diam. Subhymenial hyphae more or less thin-walled, 2.7–4.0 µm diam. *Basidiospores* thick-walled, broadly ellipsoid to subglobose, (5.8–)6.0–7.3(–7.6) × (5.0–)5.1–6.6(–6.8) µm, L = 6.6 µm, W = 5.64 µm, Q = 1.16–1.19.

*Distribution and ecology:* Found in temperate forests in the eastern part of North America, uncommon. Occurs on still standing trees and fallen logs of various angiosperms.

*Notes*: Morphologically, *S. delectans* is the most similar to the European *S. occarium*. Both species share sessile or effused-reflexed, rather thin and pale coloured (compared with other *Somion* species) basidiocarps. However, pores of *S. delectans* are not as irregular in size and shape as in *S. occarium*, and on average smaller, 2–3 per mm. Moreover, basidiospores of the first species are slightly wider than in *S. occarium* although these differences are merely statistical.

*Polyporus delectans* was described from Ohio (Peck 1884) and later reported from the US Northeast and adjacent parts of Canada (Lowe 1975, as *Tyromyces delectans*). It inhabits living and fallen deciduous trees from many genera (Gilbertson & Ryvarden 1987). Its earlier records from the Pacific Northwest and Alaska should be confirmed.

**Somion formosanum** (T.T. Chang & W.N. Chou) Miettinen & Vlasák, **comb. nov.** MycoBank MB 849652.
*Basionym*: *Tyromyces formosanus* T.T. Chang & W.N. Chou, *Mycol. Res*. **103**: 675. 1999.

*Typus*: **Taiwan**, Nantou, Meifeng, hardwood, Dec. 1997, *Chou TFRI c2873* (**holotype** "TAIF").

**Table 5.** Identification table for *Spongipellis s.l.* All species have slightly thick-walled tramal hyphae and grow on a variety of dicots unless otherwise indicated. Excludes *Somion formosanum*, which we only know from a sequence from Taiwan. Information for *Irpiciporus sinensis* from Wang & Dai (2022).

| Species | Distribution | Hosts | Caps | Pores (per mm) | Basidia | Basidiospores (L and W in µm) | Other |
|---|---|---|---|---|---|---|---|
| *Aurantiporus s.l.* | temperate to tropical | — | Thick, often reddish | Regular, 2–4 | Short | Thin-walled, mid-sized | Tramal hyphae thin-walled, oil abundant |
| *Irpiciporus branchiformis* | East Africa, tropical | — | Thin, effused | Irpicoid, 2–3 | Long | Slightly thick-walled, L = 5.19, W = 4.69, Q = 1.11 | — |
| *Irpiciporus mollis* | American Northeast, temperate to subtropical | Preferably *Fagaceae* | Thin, effused | Irpicoid, 1 | Long | Slightly thick-walled, L = 5.46, W = 4.84, Q = 1.14 | Tramal hyphae thick-walled |
| *Irpiciporus pachyodon* | Europe and Caucasus, temperate | Preferably *Fagaceae* | Thin, effused | Irpicoid, 0.5–1 | Long | Slightly thick-walled, L = 6.00, W = 5.14, Q = 1.17 | — |
| *Irpiciporus sinuosus* | Southeast Asia, subtropical to tropical | — | Thin, reflexed | Sinuous, 4–5 | Long | Slightly thick-walled, L = 5.31, W = 4.42, Q = 1.20 | — |
| *Somion delectans* | American Northeast, temperate | — | Thick, context duplex | Regular to elongated, 2–3 | Short | Slightly thick-walled, L = 6.61, W = 5.64, Q = 1.18 | Tramal hyphae thick-walled |
| *Somion litschaueri* | Central Europe, Caucasus, temperate | *Quercus* | Thick, context duplex, hirsute | Regular to elongated, 1–3 | Short | Thick-walled, L = 7.68, W = 5.96, Q = 1.29 | Tramal hyphae thick-walled |
| *Somion occarium* | Europe, North Africa, temperate to subtropical | Preferably *Fagaceae* | Thick, context duplex | Regular to sinuous, 1–3 | Short | Thick-walled, L = 6.60, W = 5.02, Q = 1.32 | Tramal hyphae thick-walled |
| *Somion strenuum* | East Asia, temperate | *Quercus* | Thick, context duplex, hirsute | Regular, 3–4 | Short | Thick-walled, L = 5.90, W = 4.80, Q = 1.23 | Tramal hyphae thick-walled |
| *Somion tomsovskyi* | American Southwest, temperate to subtropical | *Quercus* | Thick, context duplex, hirsute | Regular, 1–2 | Short | Thick-walled, L = 7.51, W = 6.12, Q = 1.24 | Tramal hyphae thick-walled, interwoven |
| *Somion unicolor* | American Northeast, temperate | *Quercus* | Thick, context duplex, hirsute | Regular to sinuous, 1–2 | Short | Thick-walled, L = 6.12, W = 4.78, Q = 1.29 | Tramal hyphae thick-walled |
| *Spongipellis ambiens* | East Asia, boreal to temperate | Preferably *Populus* | Rather thick, hirsute | Regular, 4–6 | Rather long | Slightly thick-walled, L = 5.18, W = 4.31, Q = 1.20 | — |
| *Spongipellis occidentalis* | North America, temperate | Type from *Fagus* | Thick, hirsute | Regular, 4–6 | Rather long | Slightly thick-walled, L = 6.24, W = 5.00, Q = 1.25 | — |
| *Spongipellis profissilis* | East Asia, boreal to temperate | Preferably *Populus* | Thick | Regular, 3–4 | Rather long | Slightly thick-walled, often ovoid, L = 7.31, W = 5.24, Q = 1.41 | — |
| *Spongipellis spumea* | Europe, temperate | — | Thick, hirsute | Regular, 3–4 | Rather long | Slightly thick-walled, L = 6.14, W = 5.02, Q = 1.23 | — |
| *Spongipellis variispora* | East Asia, temperate | Preferably *Ulmus* | Thick, hirsute | Regular, 4–6 | Rather long | Slightly thick-walled, L = 6.24, W = 5.29, Q = 1.19 | — |
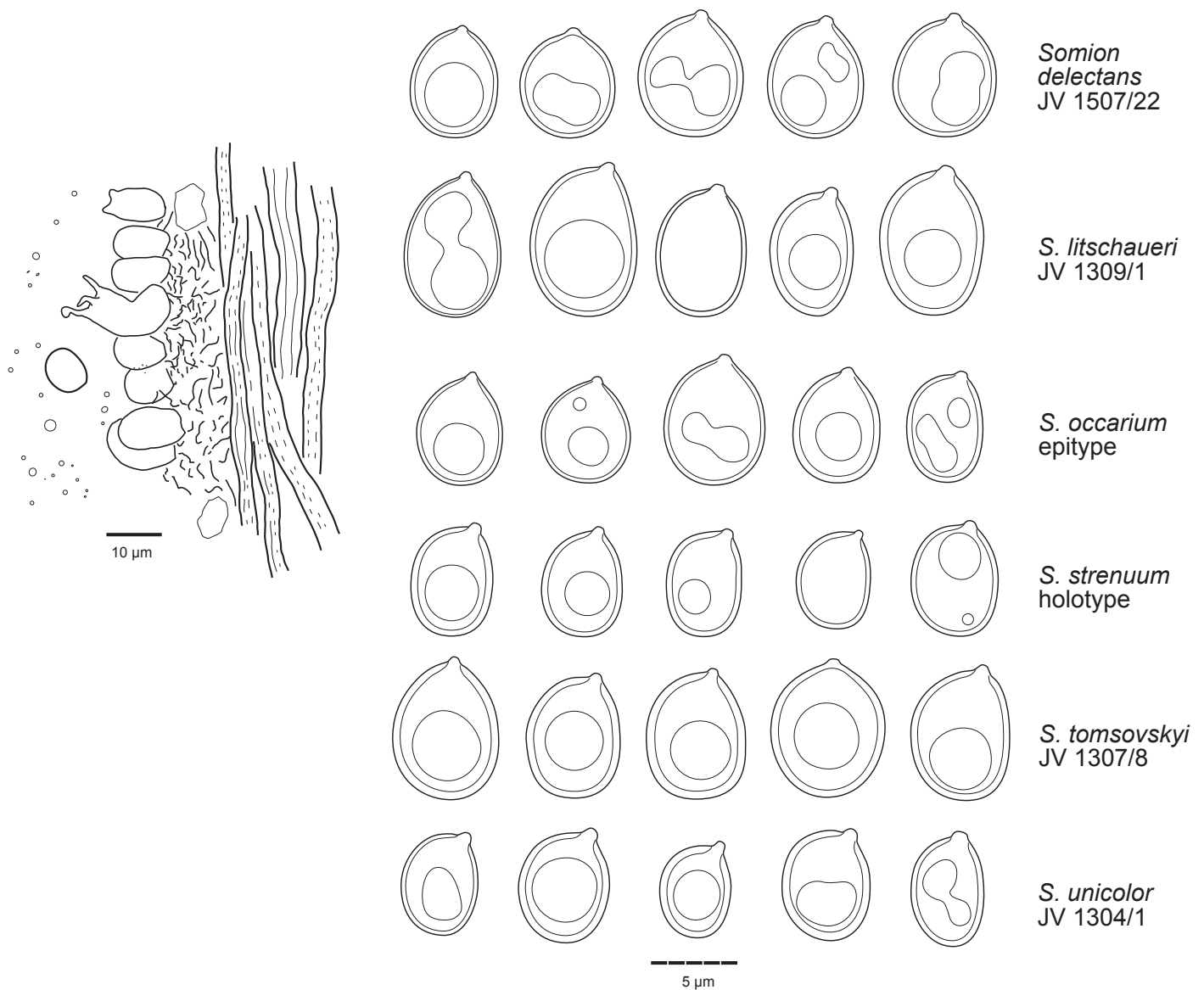
**Fig. 18.** Spores of *Somion* spp. and hyphal structure, tube trama, with subhymenium and hymenium, of *S. strenuum* (holotype).

*Notes*: This species was described as a member of *Tyromyces*, at that time a collective genus for all fleshy mono/dimitic polypores causing a white rot. ITS and *TEF1* sequences show that *T. formosanus* is a member of *Somion* and does not belong to any other species of the genus recognized here. The type is supposedly stored in the herbarium TAIF of the Taiwan Forest Research Institute, where Dr T.T. Chang worked. We wrote to TAIF requesting the type on loan in 2016 – so 17 years after the publication of the species – but were informed that no fungal material is stored in the herbarium. The herbarium staff suggested that the type specimen may still be with Dr Chang, who never replied to us. Under these circumstances, we were not able to get the type on loan. According to the original description (Chang & Chou 1999), *S. formosanum* is morphologically the most similar to *S. unicolor*. However, DNA data indicate that it is more closely related to *S. litschaueri* and *S. strenuum*. So far, *S. formosanum* is known only from two collections from the type locality.

**Somion litschaueri** (Lohwag) Vlasák & Spirin, ***comb. nov.***
MycoBank MB 849653. Fig. 18.

*Basionym*: *Spongipellis litschaueri* Lohwag, *Arch. Protistenk*. **75**: 301, 1931.

*Typus*: **Austria**, Burgenland: Sankt Margarethen im Burgenland, broken standing tree of *Quercus* sp., Oct. 1930, *K. Jusa* (**holotype** W 0132387, studied).

*Basidiocarps* annual, sessile, pilei projecting up to 10 cm. Upper surface tomentose to hirsute, azonate, yellowish to pale or bright ochraceous. Edge of pileus blunt, sterile, concolourous with pileal surface. Hymenial surface even to more-or-less convex, cream coloured to ochraceous or pale brown; pores angular to irregularly elongated, 1–3 per mm, dissepiments rather thick, first more or less even, later serrate. Section: context white to cream coloured or pale ochraceous (old herbarium specimens only), watery in fresh condition, firm, distinctly fibrillose and zonate when dry, up to 3 cm thick; tube layer tough, concolourous with pore surface, up to 3 cm thick.

 *Hyphal structure* monomitic; all hyphae with clamp connections. Context hyphae very thick-walled, interwoven or arranged in subparallel bundles, (3.9–)4.8–5.8(–7.4) μm diam.

Tramal hyphae thick-walled (lumen narrow to rather wide), subparallel, (2.8–)3.2–4.1(–5.2) µm diam. Subhymenial hyphae slightly thick-walled, 2.0–2.5 µm diam. *Basidiospores* thick-walled, broadly ellipsoid to ovoid, (6.6–)6.8–8.6(–9.1) × (4.9–)5.2–7.0(–7.7) µm, L = 7.71 µm, W = 6.00 µm, Q = 1.27–1.33.

*Distribution and ecology*: Widely distributed in Central Europe although rare. Inhabits old living and recently fallen logs of *Quercus* spp., especially *Q. cerris* (Kotlaba & Pouzar 1965).

*Notes*: This species was described from Austria (Lohwag 1931, as *Spongipellis litschaueri*) and later reported from several countries of Central Europe (summarized in Tomšovský 2012). Another *Somion* species from Europe, *S. occarium*, differs from *S. litschaueri* in having thinner and paler, often effused-reflexed basidiocarps, sinuous pores, wider tramal hyphae and smaller basidiospores. Older records of *S. litschaueri* from European part of Russia, Ukraine, and Caucasus (Bondartsev 1953) should be reconfirmed.

***Somion occarium*** (Batsch) Spirin & Miettinen, **comb. nov.** MycoBank MB 849654. Figs 1, 18.
*Basionym*: *Hydnum occarium* Batsch, *Elenchus fungorum*: 113. 1783 (conserved by Fries 1821: 412).
*Synonyms: Spongipellis suberis* Pat., *Catalogue Raisonné des Plantes Cellulaires de la Tunisie* **7**: 48. 1897.
*Leptoporus bredecelensis* Pilát ex Pilát, *Acta Musei Nat. Pragae* **9B**(2): 103. 1953.

*Typus*: Micheli, *Nova plantarum genera*: table 64, fig. 3, 1729 (**lectotype** of *Hydnum occarium* selected here, MBT 10014533). **Czech Republic**, Jihomoravský kraj, Břeclav, Valtice, 48.74931 16.79226, dead, uprooted *Quercus cerris*, 18 Nov. 2005, *Vlasák** (**epitype** of *Hydnum occarium* designated here H 7200694, MBT 10014534, studied, isoepitype JV 0511/8). **Tunisia**, El Fedja, *Quercus suber*, Jan. 1893, herb. *Patouillard* (**lectotype** of *Spongipellis suberis* FH, studied – selected by Ryvarden 1983). **Ukraine**, Zakarpatska Reg., Dilove, Mt. Menchul, *Fagus sylvatica*, Aug. 1934, *Pilát* (**holotype** of *Leptoporus bredecelensis* PRM 623854, studied).

*Basidiocarps* annual, sessile or effused-reflexed, up to 10 cm in widest dimension. Upper surface finely pubescent, sometimes indistinctly warted or striate, later almost smooth, azonate, cream coloured to pale ochraceous. Edge of pileus sharp to rather blunt, sterile, concolourous with pileal surface. Hymenial surface even to more or less concave or rarely convex, almost white to cream coloured; pores angular to sinuous, 1–3 per mm, dissepiments rather thin, serrate to dentate. Section: context white to cream coloured or pale ochraceous (old herbarium specimens only), watery in fresh condition, firm, indistinctly fibrillose and azonate when dry, up to 1 cm thick; tube layer soft, concolourous with pore surface, up to 2 cm thick.
   *Hyphal structure* monomitic; all hyphae with clamp connections. Context hyphae very thick-walled, arranged in subparallel bundles, (4.2–)5.0–6.3(–10.4) µm diam. Tramal hyphae thick-walled to more rarely slightly thick-walled (lumen distinct to capillary), subparallel, (3.0–)3.6–4.7(–5.4) µm diam. Subhymenial hyphae thin-walled, 3–4 µm diam. Basidiospores thick-walled, broadly ellipsoid to ovoid, a few subglobose, (5.3–)6.0–7.2(–7.6) × (3.9–)4.3–5.5(–6.2) µm, L = 6.60 µm, W = 5.02 µm, Q = 1.28–1.37

*Distribution and ecology*: *Somion occarium* inhabits many deciduous trees, both living and already dead but it seems to prefer *Fagus* (Ryvarden & Gilbertson 1994, as *S. delectans*). Its distribution stretches from the Mediterranean in the south to the southern part of Sweden in the north.

*Notes*: See remarks under the genus for nomenclatural details. *Somion occarium* is the European counterpart of North American *S. delectans*. Differences between these species are listed under the latter species.

***Somion strenuum*** Spirin & Vlasák, **sp. nov.** MycoBank MB 849655. Figs 1, 18.

*Typus*: **Russia**, Khabarovsk Reg., Solnechnyi Dist., Sonakh, 51.450 : 135.321, alt. 230 m, low, bushy oak forest with fire history, on living *Quercus mongolica* (basal diameter 20 cm), 15 Aug. 2014, *Spirin 7330** (**holotype** H 7200353).

*Etymology*: *Strenuus* (Lat., adj.) – strenuous, tough.

*Basidiocarps* annual or short-living perennial, sessile, pilei projecting up to 12 cm. Upper surface tomentose to hirsute, azonate, yellowish to pale ochraceous, in oldest parts fading to grey. Edge of pileus blunt, sterile, concolourous with pileal surface. Hymenial surface even to more or less concave, yellowish to pale ochraceous; pores angular, 3–4 per mm, dissepiments rather thick, uneven to serrate. Section: context cream coloured to pale ochraceous, watery in fresh condition, firm, indistinctly fibrillose and zonate when dry, up to 3 cm thick; tube layer tough, indistinctly stratified, concolourous with or slightly paler than pore surface, up to 2 cm thick.
   *Hyphal structure* monomitic; all hyphae with clamp connections. Context hyphae very thick-walled, interwoven or in subparallel bundles, (3.3–)4.2–5.1(–6.3) µm diam. Tramal hyphae very thick-walled (lumen capillary to indistinct), subparallel, (2.7–)3.2–3.8(–4.2) µm diam. Subhymenial hyphae thin- to slightly thick-walled, 3–4 µm diam. *Basidiospores* thick-walled, ellipsoid to broadly ellipsoid, (5.0–)5.2–6.4(–7.2) × (4.1–)4.2–5.3(–6.0) µm, L = 5.90 µm, W = 4.80 µm, Q = 1.19–1.26.

*Distribution and ecology*: *Somion strenuum* is distributed in temperate East Asia and restricted to *Quercus* spp. Lyubarsky & Vassilieva (1975) treated this species (as *S. litschaueri*) from oak forests and plantations in Russian Far East, where it attacks living, often rather young trees of *Q. mongolica*.

*Notes*: *Somion strenuum* has the smallest pores in the whole genus. Microscopically, it is the most similar to the North American *S. unicolor*, which has much larger pores.

***Somion tomsovskyi*** (Nakasone & Ortiz-Santana) Vlasák & Spirin, **comb. nov.** MycoBank MB 849656. Figs 1, 18.
*Basionym*: *Pseudospongipellis tomsovskyi* Nakasone & Ortiz-Santana, *Lilloa* **59** (Suppl.): 104. 2022.

*Typus*: **USA**, Arizona, Cochise County, Coronado National Forest, Chiricahua Mountains, Rucker Canyon, on *Quercus emoryi*, 27 Oct. 1967, *Gilbertson 7701* (**holotype** ARIZ AN010813; **isotype** CFMR).

*Basidiocarps* annual, sessile, pilei projecting up to 10 cm. Upper surface tomentose to hirsute, azonate, yellow to pale ochraceous, in oldest parts fading to grey. Edge of pileus blunt, sterile, concolourous with pileal surface. Hymenial surface even to more-or-less convex, yellow to pale ochraceous; pores angular, 1–1.5 per mm, dissepiments thick, uneven to serrate. Section: context cream coloured to pale ochraceous, in old herbarium specimens pale brown, watery in fresh condition, firm, distinctly fibrillose and zonate when dry, up to 4 cm thick; tube layer tough, concolourous with or slightly paler than pore surface, up to 2 cm thick.

*Hyphal structure* monomitic; all hyphae with clamp connections. Context hyphae very thick-walled, rather loosely interwoven, a few arranged in subparallel bundles, (3.1–)3.6–4.7(–5.3) µm diam. Tramal hyphae slightly or distinctly thick-walled (lumen wide to narrow), densely interwoven, (3.2–)3.8–4.8(–5.1) µm diam. Subhymenial hyphae thin- to slightly thick-walled, 3–5 µm diam. *Basidiospores* thick-walled, ellipsoid to broadly ellipsoid, (6.4–)6.8–8.3(–8.7) × (5.1–)5.5–6.8(–7.1) µm, L = 7.5 µm, W = 6.11 µm, Q = 1.22–1.23.

*Distribution and ecology*: So far known from the US Southwest and adjacent areas of Mexico inhabiting living and recently dead logs of *Quercus* spp.

*Notes*: *Somion tomsovskyi* is a close relative of *S. unicolor*. These species differ primarily in their distribution areas (US Southwest and Mexico *vs*. the North American Northeast). Microscopically, *S. tomsovskyi* differs from the rest of *Somion* species in having interwoven (not subparallel) tramal hyphae with a well-visible lumen. Two other species from North America, *S. delectans* and *S. unicolor*, have smaller basidiospores. Description and spore measurements of *S. unicolor* given by Gilbertson & Ryvarden (1987) refer to *S. tomsovskyi*.

**Somion unicolor** (Fr.) Spirin & Miettinen, **comb. nov.** MycoBank MB 849657. Fig. 18.
*Basionym*: *Polyporus unicolor* Fr., *Epicrisis Systematis Mycologici*: 458. 1838.
*Synonym*: *Boletus unicolor* Schwein., *Schriften der Naturforschenden Gesellschaft zu Leipzig* **1**: 97. 1822.

*Typus*: **USA**, North Carolina, Salem (**lectotype** of *Polyporus unicolor* selected here PH 00063495, MBT10014535, photo studied in plants.jstor.org).

*Basidiocarps* annual, sessile, pilei projecting up to 10 cm. Upper surface tomentose to hirsute, azonate, yellowish to pale ochraceous, in oldest parts fading to pale grey. Edge of pileus blunt, fertile, concolourous with pileal surface. Hymenial surface even to more-or-less convex, yellowish to pale ochraceous or brownish; pores angular to sinuous, in largest basidiocarps with a tendency to radial arrangement, 1–1.5 per mm, dissepiments thick, serrate to dentate. Section: context cream coloured to pale ochraceous, in old herbarium specimens pale brown, watery in fresh condition, firm, distinctly fibrillose and zonate when dry, up to 2 cm thick; tube layer tough, concolourous with or slightly paler than pore surface, up to 3 cm thick.

*Hyphal structure* monomitic; all hyphae with clamp connections. Context hyphae very thick-walled, arranged in subparallel bundles, (3.7–)4.2–5.3(–6.2) µm diam. Tramal hyphae very thick-walled (lumen capillary), subparallel, (3.4)–

4.0–4.7(–5.3) µm diam. Subhymenial hyphae thin- to slightly thick-walled, some inflated, 3–6 µm diam. *Basidiospores* thick-walled, ellipsoid to ovoid, (5.2–)5.3–7.1(–7.3) × (4.0–)4.2–5.4(–5.9) µm, L = 6.13 µm, W = 4.78 µm, Q = 1.22–1.34.

*Distribution and ecology*: Widely distributed in the North-American Northeast inhabiting still living or recently dead trees of *Quercus* spp.

*Notes*: Schweinitz (1822) described *Boletus unicolor* from North Carolina. This name is invalid due to *Boletus unicolor* Bull. 1789. Fries (1836–1838), however, technically validated the name when he treated it as *Polyporus unicolor*, and should be cited as the valid author of the species. Schweinitz's protologue does not mention specimens. We select the single collection from the Schweinitz herbarium in PH as the lectotype. The basidiocarp is thick and with initially regular pores that split with age, 5–10 pores per cm (median 7), *i.e.*, 0.5–1 per mm. The two other *Somion* species in North America do not come into question: *S. tomsovskyi* is not found in the east coast, and *S. delectans* has smaller, less regular pores and thinner fruiting bodies. Thus, the lectotype agrees with the modern concept of the species.

*Somion unicolor* has been reported from many localities in the US Northeast and adjacent part of Canada (Lowe 1975). It seems to be restricted to *Quercus* spp. Earlier records of *S. unicolor* from the US Southwest belong to *S. tomsovskyi* (see above). *Somion delectans*, sharing the same distribution area with *S. unicolor*, differs from it in having thinner, often effused-reflexed basidiocarps, smaller pores and wider basidiospores.

## Excluded and insufficiently known species

**Cerrena maxima** (Mont.) L. Hansen, *Nat. Hist. Renell Isl. Solomon Isls*: 129. 1960.
*Synonym*: *Trametes maxima* (Mont.) A. David & Rajchenb., *Mycotaxon* **22**: 315. 1985.

*Typus*: **Cuba**, de la Sagra (**holotype** of *Trametes maxima* PC, herb. Montagne 1413, studied).

*Notes*: Ryvarden & Johansen (1980) retained this and the two following species in *Cerrena*. *Trametes maxima* is a typical member of *Trametes*.

**Cerrena meyenii** (Klotzsch) L. Hansen, *Nat. Hist. Renell Isl. Solomon Isls*: 129. 1960.
*Synonym*: *Trametes meyenii* (Klotzsch) Lloyd, *Mycological Writings* **5**(67): 14. 1918.

*Notes*: While this species has been placed in *Cerrena*, our morphological analysis and preliminary sequence data place it in the *Polyporaceae*. For now, *Trametes* is the best available genus for it.

**Cerrena sclerodepsis** (Berk.) Ryvarden, *Mem. New York Bot. Gard*. 28: 204. 1976.
*Basionym*: *Trametes sclerodepsis* Berk., Hooker's J. *Bot. Kew Gard. Misc*. **8**: 236. 1856.

*Notes*: Our morphological analysis and preliminary sequence data place this species in the *Polyporaceae*. For now, *Trametes* is the best available genus for it.

*Irpiciporus africanus* (Ipulet & Ryvarden) Nakasone, *Lilloa* **59** (Suppl.): 94. 2022.
**Basionym**: *Spongipellis africana* Ipulet & Ryvarden, *Syn. Fungorum* **20**: 97. 2005.
**Hypochnicium africanum** (Ipulet & Ryvarden) Miettinen, **comb. nov.** MycoBank MB 849658.

*Typus*: **Uganda**, Kanungu, Bwindi Impenetrable NP, Byumba, rotting log, 24 May 2003, *Ipulet F1683** (**holotype** of *Spongipellis africana* O, studied).

*Notes*: This species with hydnoid, effused-reflexed basidiocarps has septate cystidia and thick-walled, cyanophilous spores. It does not belong to the *Cerrenaceae* or *Spongipellis s. str.* Micromorphology and nrDNA sequence of the type specimen point towards *Hypochnicium* and not to *S. pachyodon* (*i.e. Irpiciporus*) as suggested by Ipulet & Ryvarden (2005) and Nakasone & Ortiz-Santana (2022). In the scheme of Maekawa *et al.* (2023), the species might belong to *Gyrophanopsis* or to a genus of its own, but we prefer a larger concept of *Hypochnicium* for now, including *Gyrophanopsis* and *H. africanum.*

*Irpiciporus cubensis* (Berk. & M.A. Curtis) Murrill, *N. Amer. Fl.* **9**: 15. 1907.
*Basionym*: *Irpex cubensis* Berk. & M.A. Curtis, *J. Linn. Soc., Bot.* **10**: 326. 1869.

*Typus*: **Cuba**, summit of Lomo del Gaso, on rotting logs, unknown collection date, *Wright 240*, Fungi Cubensis Wrightiani no. 355 (**lectotype** K – selected by Maas Geesteranus 1974: 470, **isotype** FH 00301398).

*Notes*: Description of the type were given by Maas Geesteranus (1974) and Nakasone & Ortiz-Santana (2022). According to their descriptions, the type is small and sterile, with unclear affinity. Maas Geesteranus specifically excludes conspecificity with *Cerrena zonata* and notes the specimen is irpicoid, dimitic, with clamped septa and oil-filled hyphal ends. Nakasone and Ortiz-Santana add that cylindrical cystidia (or oil hyphae) project from the hymenium. We have not seen the type, but it seems unlikely that it belongs to any genus treated here.

*Irpiciporus decolorans* (Cooke) Nakasone, *Lilloa* **59** (Suppl.): 95. 2022.
*Basionym*: *Irpex decolorans* Cooke, *Grevillea* **19**(92): 109. 1891.

*Typus*: **Cuba**, on rotting logs, unknown collection date, *C. Wright 835* (**lectotype** K(M) 62571 – selected by Maas Geesteranus 1974: 471).

*Notes*: Nakasone (2012) and Nakasone & Ortiz-Santana (2022) provide descriptions of the type, which we have not studied here. According to them, the type is richly fertile though the hymenium is degraded. Nakasone & Lindner (2012) describe a dense structure of agglutinated hyphae, small ellipsoid spores, brown colour and relatively short, and small spines. They placed it in *Cristinia* (*Agaricales*). Nakasone & Ortiz-Santana (2022) place the species in *Irpiciporus* and state that the basidiomes "change from white to brown on drying". Where this information comes from is unclear, since already Cooke in the protologue describes the caps as sooty, *i.e.* dirty brown ("*fuligineus*"). These characters make it highly unlikely that this species belongs to *Irpiciporus* with white, rather big

basidiomes and open structure. Hjortstam & Larsson (1995) suggest this species is related to *Radulodon*, though Nakasone does not describe cystidia as present in *Radulodon* spp. Ryvarden (2020b) claims it represents *Cerrena zonata*, a dimitic species. These opinions are all conflicting and the identity of this species remains ambiguous.

*Irpiciporus lacteus* (Fr.) Murrill, *North American Flora* **9**: 15. 1907.
*Synonym*: *Irpex lacteus* (Fr.) Fr., *Elenchus Fungorum* **1**: 145. 1828.

*Note*: This type species of *Irpex* belongs to *Irpicaceae*, *Polyporales* (Justo *et al.* 2017).

*Irpiciporus noharae* Murrill, *Mycologia* **1**: 166. 1909.
*Synonym*: *Lopharia mirabilis* (Berk. & Broome) Pat., *Bull. Soc. Mycol. France* **11**: 14. 1895.

*Notes*: Nakasone & Ortiz-Santana (2022), who studied the type, conclude it represents *Lopharia mirabilis*, a distinctive species in the *Polyporaceae*. This is also the conclusion of Ryvarden (2020b).

*Irpiciporus rajchenbergii* Nakasone, *Lilloa* **59** (Suppl.): 95. 2022.

*Typus*: **Brazil**, São Leopoldo, 1931, *Rick* (**holotype** BPI 0259635).

*Notes*: Nakasone described this species without sequence data and based on an old specimen of Rick from southern Brazil (Nakasone & Ortiz-Santana 2022). The description points towards *Irpiciporus*, but since her concept of the genus is heterogeneous, another opinion on its identity would be desirable.

*Irpiciporus tanakai* Murrill, *Mycologia* **1**: 167. 1909.
*Synonym*: *Antrodia tanakae* (Murrill) Spirin & Miettinen, [as 'tanakai'], *Mycologia* **105**: 1572. 2013 [2014].

*Note*: This species belongs to *Antrodia sensu stricto* (*Fomitopsidaceae*, *Polyporales*; Spirin *et al.* 2013).

*Irpiciporus tulipiferae* (Schwein.) Murrill, *Bull. Torrey Bot. Club* **32**: 472. 1905.
*Synonym*: *Irpex lacteus* (Fr.) Fr., *Elenchus Fungorum* **1**: 145. 1828.

*Note*: Maas Geesteranus (1974) showed the type belongs to *Irpex lacteus*.

*Irpiciporus xuchilensis* (Murrill) Y.C. Dai & Chao G. Wang, *Mycol. Progr.* **21**(73): 8. 2022.
*Basionym*: *Coriolus xuchilensis* Murrill, *Bull. New York Bot. Gard.* **8**: 143, 1912.
**Bjerkandera xuchilensis** (Murrill) Miettinen, **comb. nov.** MycoBank MB 849659.

*Typus*: **Mexico**, Veracruz, Xuchiles, near Cordoba along Rio Blanco, 17 Jan. 1910, *WA & EL Murrill 1171* (**holotype** of *Coriolus xuchilensis* NY 00705008, studied).

*Notes*: Zhao *et al.* (2017) and Wang & Dai (2022) published *Irpiciporus* sequences of one Ecuadorian specimen under this name (GenBank KX161650, KX161659). Those sequences are unique among the available sequences, so this specimen

represents another species in the genus *Irpiciporus*. However, the correct name is not *I. xuchilensis*. We have studied the type of *C. xuchilensis*. It clearly belongs to *Bjerkandera*, though it is beyond the scope of this paper to determine to which of the currently recognized species in that genus. New species of *Bjerkandera* have been recently described from tropical Americas, and they should be reviewed against this older species name. Coming back to the *Irpiciporus* specimen, we leave it formally without a name, since we consider it possible that older names may exist for it for instance among the species Murril described.

***Polyporus albostygius*** Berk. & M.A. Curtis, *J. Linn. Soc., Bot*. **10**: 309. 1869.
*Synonym*: *Rigidoporus albostygius* (Berk. & M.A. Curtis) Rajchenb., *Revista de Investigaciones Agropecuarias Serie 5, Patología vegetal*: 72. 1984.

*Typus*: **Cuba**, unknown collection date, *Wright 583* (K – **lectotype** of *Rigidoporus albostygius* designated by Ryvarden (1984), **isotype** FH 290626, studied).

*Note*: Though sometimes listed as a synonym of *Lividopora vincta*, this species belongs to *Meripilaceae*.

***Polyporus bistratosus*** Berk. & Cooke, *J. Linn. Soc. Bot*. **15**: 384. 1877.

*Typus*: **Brazil**, Amazon, Paricatuba, River Purua, 8 Sep. 1974, *Trail 74* (**holotype** K(M) 192256, studied).

*Notes*: Another species sometimes listed as a synonym of *L. vincta*. It belongs to *Meripilaceae*.

***Polyporus hyposclerus*** Berk. ex Cooke, *Grevillea* **10**(55): 103. 1882.

*Typus*: **Australia**, Queensland, Brisbane, unknown collection date, *Broome* (**holotype** K(M) 192252, studied).

*Notes*: A supposed synonym of *L. vincta*. The type is sterile and in bad condition, but it is a species of *Fomitopsis*.

***Pseudolagarobasidium calcareum*** (Cooke & Massee) Sheng H. Wu, *Acta Bot. Fenn*. **142**: 112. 1990.

*Notes*: Nakasone & Lindner (2012) suggested that this species is a synonym of *P. pronum* described from Sri Lanka. Its status as a separate species should be revised; see further notes under *P. pronum*.

***Pseudolagarobasidium concentricum*** (Cooke & Ellis) Hjortstam, *Mycotaxon* **54**: 190. 1995.
*Synonym*: *Pirex concentricus* (Cooke & Ellis) Hjortstam & Ryvarden, *Mycotaxon* **24**: 289. 1985.

*Note*: This North American species is the type of *Pirex* and belongs to *Phanerochaetaceae* (*Polyporales;* Justo et al. 2017).

*Pseudolagarobasidium conspicuum* (Pouzar) Nakasone, *Mycotaxon* **130**: 378. 2015.
*Basionym*: *Hyphoradulum conspicuum* Pouzar, *Česká Mykol*. **41**: 26. 1987.

***Crustomyces conspicuus*** (Pouzar) K.H. Larss., **comb. nov.** MycoBank MB 849660.

*Typus*: **Czech Republic**, Central Bohemia, Karlštejn, Velka Hora, *Cornus mas*, 2 Oct. 1981, *Pouzar* (**holotype** of *Hyphoradulum conspicuum* PRM 834886; **isotype** GB*, studied).

*Notes*: This is the type species of the monotypic genus *Hyphoradulum* Pouzar. Nakasone (2015) placed it in *Pseudolagarobasidium*. We managed to generate an ITS sequence from an isotype deposited in herb. GB. BLAST searches against GenBank showed close affinity with *Crustomyces*, which belongs to *Cystostereaceae*, *Agaricales*. Li *et al.* (2022) recently published a phylogenetic analysis of *Cystostereaceae*. We conducted a phylogenetic analysis of the ITS region from a selection of the dataset used in Li *et al.* along with the *H. conspicuum* sequence and a few new *Crustomyces* sequences (Fig. 19). *Hyphoradulum conspicuum* was recovered as a sister taxon to *Crustomyces tephroleucus* within a strongly supported clade corresponding to the expanded genus concept of *Crustomyces* introduced by Li *et al.* (2022). This wider *Crustomyces* includes *Cystidiodontia* (type *Cystidiodontia artocreas* = *C. laminifera*) and *Rigidotubus* (type *Rigidotubus tephroleucus*). We follow this circumscription of *Crustomyces* and suggest that also *Hyphoradulum* should be placed there.

***Radulodon acaciae*** G. Kaur, Avneet P. Singh & Dhingra, *Mycotaxon* **127**: 111. 2014.

*Notes*: This species likely belongs to *Pseudolagarobasidium*, and Nakasone & Ortiz-Santana (2022) considered it a synonym of *P. acaciicola* based on the original description. In our view the protologue (Kaur et al. 2014) is not sufficient to make any firm conclusions about its identity.

***Radulodon americanus*** Ryvarden, *Canad. J. Bot*. **50**: 2074. 1972.

*Typus*: **Canada**, British Columbia, Prince George, *Populus tremuloides*, 25 Aug. 1945, *Foster* (**holotype** DAOM 16599, studied).

*Note*: Type species of *Radulodon*, but possibly a synonym of *R. erikssonii*, see remarks under that species.

***Radulodon copelandii*** (Pat.) N. Maek., *Rep. Tottori Mycol. Inst*. **31**: 93. 1993.
*Synonym*: *Radulomyces copelandii* (Pat.) Hjortstam & Spooner, *Kew Bulletin* **45**: 314. 1990.

*Notes*: This species described from the Philippines belongs to *Radulomyces* (Nakasone 2001). Nakasone *et al.* (2021) provide sequences under this name from southern China.

***Radulodon indicus*** Jyoti & Dhingra, *Syn. Fungorum* **32**: 38. 2014.

*Notes*: Described from Jammu, India. Its authors compare the species to *Radulodon pseudomucidus*, which is a synonym of *Radulomyces copelandii* (Nakasone *et al.* 2021). We have not seen material, but the description points towards *Radulomyces*.

***Radulodon licentii*** (Pilát) Ryvarden, *Česká Mykol*. **30**(1): 40. 1976.
*Synonym*: *Radulomyces licentii* (Pilát) Parmasto, *Conspectus Systematis Corticiacearum*: 111. 1968.
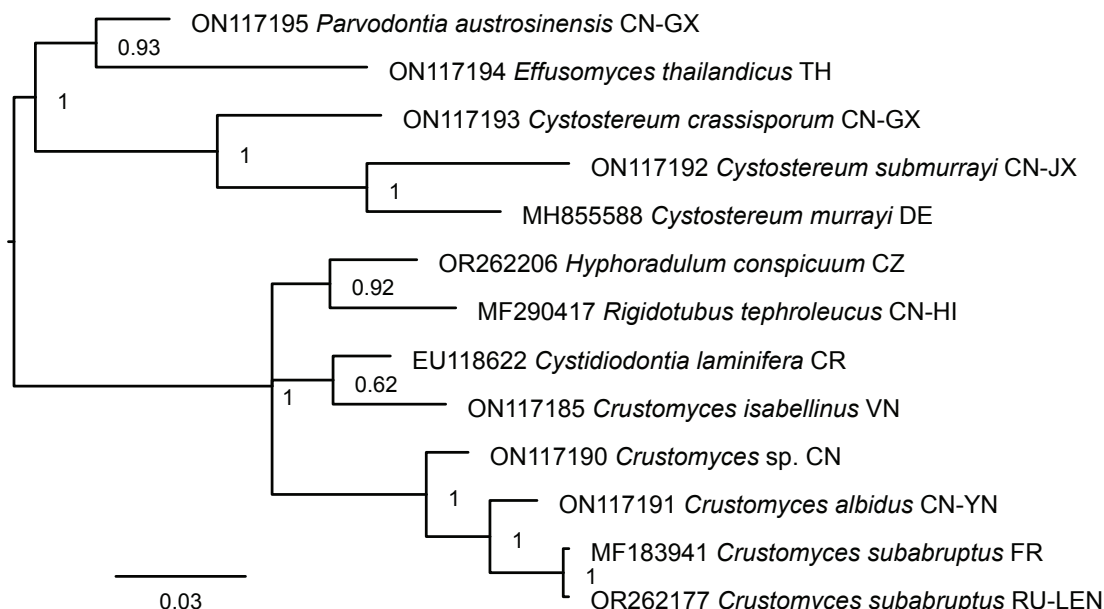
**Fig. 19.** Bayesian consensus phylogram of *Cystostereaceae* based on ITS sequences. Countries (and states) of origin are denoted with ISO 3166 codes.

*Note*: Nakasone *et al*. (2021) accept this species described from North China in *Radulomyces* (*Agaricales*) and provide DNA data from Southwest China and Taiwan.

**Radulodon pseudomucidus** (Petch) Stalpers, *Folia Cryptog. Estonica* **33**: 137. 1998.

*Note*: Nakasone *et al*. (2021) consider this a synonym of *Radulomyces copelandii* (*Agaricales*).

**Radulodon subquercinus** (Henn.) Hjortstam & Ryvarden, *Mycotaxon* **10**: 285. 1980.

*Notes*: Type of the genus *Phaneroites*, this acystidiate species reminds *Phanerochaete sensu lato* and does not belong to the *Cerrenaceae*. Hjortstam (1987) considered *Phanerochaete radulans* Hallenb. a synonym.

**Rigidoporus hypobrunneides** Corner, *Beih. Nova Hedwigia* **86**: 165. 1987.

*Typus*: **Malaysia**, Pahang, Cameron Highland, 31 Jul. 1934, *Corner* (**holotype** E 00159712, photograph studied).

*Notes*: As the name indicates, Corner (1987) considers this species similar to *R. hypobrunneus* (= *Lividopora benetosta*). He mentions that it has bigger pores, which brings *Lividopora facilis* to mind. We have not studied the type under microscope, but the photograph is of a light-colored resupinate polypore, whose mid-sized tubes have turned partly brown. Corner mentions that *R. hypobrunnea* has thick-walled, heavily encrusted cystidia ("extrahymenial setae"), while he only mentions thin-walled, narrow cystidia in *R. hypobrunneides*. This tells us that *R. hypobrunneides* is not a species of *Lividopora* and certainly not an older name for *L. facilis.* It could rather be a member of the *Meripilaceae*. Hattori (2001), who studied the type, mentions that it is moldy, indicating that Corner's spore measurements may refer to mold spores. Hattori left the specimen as *Rigidoporus* sp.

**Spongipellis caseosa** (Pat.) Ryvarden, *Occas. Pap. Farlow Herb. Cryptog. Bot*. **18**: 11. 1983.
**Basionym**: *Leptoporus caseosus* Pat., *Ann. Mycol*. **5**(4): 365. 1907.

*Typus*: **Brazil**, São Paulo, Caminas, Mar. 1897, *Noack* (**lectotype** FH 00258975, studied – typified by Ryvarden 1983).

*Notes*: Light-coloured, monomitic with thick-walled generative hyphae, spores slightly cyanophilous and slightly thick-walled, ellipsoid. Hymenium has collapsed in the type. These characters may imply *Somion*, but we cannot exclude *Ryvardenia*. Spores are smaller than in the described species of *Ryvardenia* (Rajchenberg 1994) or *Somion*. Modern collections and/or revision of the type material are needed to confirm its identity.

**Spongipellis eberhardtii** Pat., *Bull. Soc. Mycol. France* **36**: 176. 1920.

*Typus*: **Vietnam**, Annam, Lang Biang, sur Pin, Eberhardt 196 (**lectotype** FH 00258973, studied – typified by Ryvarden 1983).

*Notes*: Fleshy mid-sized polypore with regular, pinkish pores, large, ellipsoid, thick-walled spores, monomitic with very wide and thick-walled, clamped hyphae, partly agglutinated, changing colour upon drying. We do not know the true affinity of this species, and we are not aware of any modern collections. In our opinion it does not belong to any genus in the *Cerrenaceae* or *Spongipellis sensu stricto*.

**Tyromyces irpiceus** Corner, *Beih. Nova Hedwigia* **96**: 143. 1989.

*Notes*: Corner (1989) described this species from Brazil. According to his description, the species has small pilei and lamellate to irpicoid hymenophore, and Corner compares it with *Irpiciporus* and *Spongipellis sensu lato*. According to the protologue, the species is acystidiate and monomitic with thick-walled clamped hyphae. Corner describes the ellipsoid, mid-sized spores as thin-walled. We have not seen the type, but this species should be kept in mind when dealing with Neotropical

*Irpiciporus* and *Somion*. Hattori (2002) did not mention this species in his type studies.

***Tyromyces sublamellatus*** Corner, *Beih. Nova Hedwigia* **96**: 199. 1989.

*Notes*: Corner (1989) likens this Malaysian species to *T. irpiceus*, which in turn he considers similar to *Irpiciporus*. Judging from Corner's description, this might be a species of *Irpiciporus*. However, Hattori (2003) reports the species as dimitic and having gloeocystidia, relating it to *Abortiporus roseus*. Clearly this species does not belong to *Irpiciporus*.

## Specimens studied

*Acanthodontia cirrhatina.* **Malaysia**, Sabah (see **holotype**). **Indonesia**, Sumatera Barat, Sijunjung, Bukit Tujuh, alt. 550 m, dicot, 23 Jul. 2009, *Miettinen 13717*\* (ANDA, H).

*Cerrena albocinnamomea.* **China**, Jilin, Antu, Changbai Mts, on *Tilia*, 3 Sep. 1993, *Dai 997* (H, **paratype**); *Acer*, 5 Sep. 1993, *Dai 1085* (H, **paratype**); *Acer mono*, 15 Sep. 1998, *Niemelä 6372* (H); dicot, 26 Aug. 2005, *Miettinen 10511*\* (H).

*Cerrena 'gilbertsonii'.* **Guadeloupe**, Basse-Terre, Grande Anse, dicot, unknown collection date, *D. Vlasák*\* (JV 1609/29, H). **Mexico** (see type).

*Cerrena multipileata.* **Brazil**, Parana, Mandirituba, alt. 850 m, 20 Apr. 1993, *de Meijer 2623* (O, H); Santa Catarina (see type). **Costa Rica**, San José, Cerro Vueltas, alt. 2 000 m, 18 Jul. 2001, *Ryvarden 43881* (O, H\*); Puntarenas, Santa Elena, dicot, 28 & 29 Jul. 2014, *Vlasák*\* (JV 1407/63, H). **Guatemala**, Huehuetenango, San Mateo Ixtatán, alt. nearly 3 000 m, 21 Nov. 2006, *Kout A36*\* (JV 0611/A36).

*Cerrena unicolor.* **China**, *Hu* (**lectotype** of *Polystictus prosector* BPI 0315073, LC23787, selected by Stevenson & Cash 1936: 137). **Finland**, Etelä-Häme, Lammi, Pappilankylä, *Betula*, 10 Sep. 1997, *Niemelä 6098* (H); Pohjois-Karjala, Tohmajärvi, Rouanaho, *Betula*, 30 Jun. 1970, *Niemelä* (H); Kainuu, Hyrynsalmi, Latvakorvensuo, *Betula pubescens*, 26 Sep. 2010, *Miettinen 14197* (H); Suomussalmi, Soidinkangas, *B. pubescens*, 30 Sep. 2004, *Miettinen 9443*\* (H); Kittilän Lappi, Kittilä, Pallas-Ounas National Park, *B. pubescens*, 21 Aug. 1990, *Niemelä 5352* (H). **Kyrgystan**, Jalal-Abad, Aksy, Arkyt village, *Craetagus*, 31 Jul. 2007; *Uotila 47588*\* (H 7200336). **USA**, Minnesota, Waseca, Janesville, Willis Lake, dicot, 21 Aug. 2013, *Miettinen 16729* (H 7005991); New York, Essex Co., Huntington wildlife forest, Arbutus lake, dicot, 17 Sep. 2013, *Miettinen 16901* (H).

*Cerrena zonata.* **Australia**, Trowutta Arch, 17 Apr. 2008, *Gates*\* (H). **China**, Yunnan, Kunming Bot. Garden, 30 Jul. 2005, *Miettinen 9773*\* (H); Chuxiong, Zixishan, dicot, 2 Aug. 2005, *Miettinen 9889.1*\* (H). **Indonesia**, Sumatera Barat, Lima Puluh Kota, Gunung Sago, dicot, 25 Jul. 2009, *Miettinen 13798*\* (ANDA, H). **Japan**, Tokyo, *Quercus*, Oct. 1908, *Kusano & Nohara* (**type** of *Irpiciporus japonicus* Murrill NY 00985353). **Nepal** (see type).

*Crustomyces conspicuus.* **Czech Republic** (see type).

*Crustomyces subabruptus.* **Russia**, Leningrad reg, Tikhvin, Gorodokskoe, *Populus tremula*, 28 Jul. 2012, *Spirin 4826*\* (H).

*Irpiciporus branchiformis.* **Tanzania**, Tanga, Lushoto, Mazumbai Forest Res., dense forest, on dead wood, 15 Dec. 1995, *Niemelä 5937* (H)\*; see also type.

*Irpiciporus mollis.* **USA**, Florida, Escambia Co., Pensacola, *Quercus* sp., 25 Nov. 1914, *Bartholomew* (Fungi Columbiani #4545, H); Manatee Co., Braden river trail, dicot, 8 May 2016, *Dollinger 770*\* (JV, H), Bradenton, dicot, 10 Oct. 2016, *Dollinger 962* (JV); Massachusetts, Worcester Co., Worcester, *Acer saccharum*, 20 Oct. 2013, *Miettinen 17338* (H); New Hampshire, Carroll Co., Chocorua, *Acer* sp., Aug. 1908, *Farlow 334* (H ex FH); New Jersey (?), *Quercus* sp., Sep. 1879, *Ellis* (North American Fungi #320, H); Pennsylvania, Philadelphia, Wissahickon Creek, *Fagus virginiana*, Aug. 2008, *Vlasák* (JV 0808/45, H); Bucks Co., Ralph Stover State Park, *Quercus* sp., Aug. 2001, *Vlasák* (JV 0108/115, H); South Carolina, Santee River, *Ravenel* (herb. *Curtis 1729* in K – **lectotype**); Virginia, Prince William Co., Woodbridge, *Liriodendron tulipifera*, Sep. 2007, *Vlasák*\* (JV 0709/174, H).

*Irpiciporus pachyodon.* **Bulgaria**, Burgas, Strandzha Nat. Park, *Quercus* sp., 25 Oct. 2007, *Heilmann-Clausen 07–286*\* (H). **Czech Republic**, Jihočeský kraj, Hluboká nad Vltavou, *Quercus petraea*, Nov. 1993, *Vlasák*\* (JV 9311/1, H); Středočeský kraj, Průhonický park, *Quercus rubra*, 1 Nov. 2016, *Kotlaba*\* (JV 1611/1); Vysočina, Velký Špičák, *Fagus sylvatica*, 2 Oct. 2004, *Vampola 199* (H ex MJ). **France**, Var, Forêt de Janas, *Q. suber*, 20 Dec. 1987, *David* (H, O ex LY). **Italy**, Piedmont, Alessandria, Bosio, Capanne di Marcarolo Nat. Regional Park, *Quercus* sp., 16 Oct. 2019, *Spirin 13785* (H). **Portugal**, Estremadura, Setúbal, Alto da Guerra, *Q. suber*, 8 Apr. 1978, *Melo 327* (H ex LISU).

*Lividopora armeniaca.* **Malaysia** (see type).

*Lividopora benetosta.* **China**, Hunan, Sangzhi, Badagongshan NR, 23 Sep. 2000, *Härkönen K778*\* (H); Wulingyuan World Heritage Site, 15 Sep. 1999, *Härkönen K8*\* (H); Yunnan, Xishuangbanna, Botanical Garden, dicot, 5 Aug. 2005, *Miettinen 9978.2* (H); 6 Aug. 2005, Miettinen 10020 (H); Biosphere Reserve, Menglun, *Moraceae*?, 9 Aug. 2005, *Miettinen 10142.1* (H); Jinghong, Mandian village, 15 Aug. 2005, *Miettinen 10333* (H); Mandian Water Fall surroundings near Jinghong, 17 Aug. 2005, *Miettinen 10394.1*, *10396.2* (H); Primeval Forest Park near Jinghong, 13 Aug. 2005, *Miettinen 10225*\* (H). **French Polynesia** (see type). **Indonesia**, Nusa Tenggara Barat, Lombok Utara, Bentek, dicot, 29 Dec. 2011, *Miettinen 15238* (BO, H), *15243* (BO, H); *Theobroma cacao*, 29 Dec. 2011, *Miettinen 15252* (BO, H); Papua, Jayapura Reg, Cyclop Mountains, *Fabaceae* (?), 22 Aug. 2004, *Miettinen 9127.1* (H); dicot, 29 Aug. 2004, *Miettinen 9176.2*\* (H); *Sapindaceae/Meliaceae* (?), 29 Aug. 2004, *Miettinen 9166.5*\* (H); dicot, 29 Aug. 2004, *Miettinen 9188.1* (H); 14 Dec. 2007, *Miettinen 12080.1* (MAN, H); Papua Barat, Manokwari Reg, Amberbaken, River Anjii/Wepai near Saukorem, dicot, 1 Nov. 2010, *Miettinen 14287* (H); Riau, Indragiri Hulu, Bukit Aluran Babi, dicot, 2 Jul. 2004, *Miettinen 8823.2*\* (H); Pelalwan, Teluk Meranti, dicot, 25 Jul. 2004, *Miettinen 9026.2* (BO, H); Sumatera Barat, Pesisir Selatan, Muara Sako, dicot, 22 Apr. 2002, *Miettinen 6026* (BO, H); Padang, Limau Manis, 13 Jul. 2008, *Miettinen 13011.3* (ANDA, H); Ulu Gadut, dicot, 28 Jul. 2009, *Miettinen 13884.1*, *13891* (ANDA, H); Sijunjung, Bukit Sebelah, 22 Jul.

2008, *Miettinen 13674.1* (ANDA, H). **Malaysia**, Sabah, Ranau, Poring, dicot, 19 Jun. 2013, *Miettinen 16397.2* (SNP 33655, H), *Miettinen 16416* (SNP 33667, H). **New Zealand**, Rotorua, between lakes Rotoiti-Rotoehu, Hongi's track, 14 Apr. 2004, *Hallenberg 15301** (O). **Philippines**, Zamboanga, San Ramon, 12 May 1904, *Copeland 743* (**type** of *Poria porphyrophaea* NY 00742723). **Puerto Rico**, Luquillo, El Yunque National Forest, Bisley, *Dacryodes excelca* (?), 7 Jan. 2014, *Miettinen 18019* (H); Sabana, *Cecropia*, 8 Jan. 2014, *Miettinen 18035** (H); 12 Jan. 2014, *Miettinen 18133* (H); 14 Jan. 2014, *Miettinen 18140* (H); Yokahú tower, 14 Jan. 2014, *Miettinen 18135** (H). **Samoa**, unknown collection date, *Lloyd 5042* (**lectotype** of *Poria fumosa* BPI US0318515, **isotype** FH 290621). **Sri Lanka**, Gangaruwa, Dec. 1913, *Petch 3930* (**lectotype** of *Poria hypobrunnea* K(M) 56199). **US Virgin Islands**, St John, Virgin Islands NP, 8 Feb. 2012, *Justo 513** (H). **Vietnam**, Thanh Hóa, 20 Apr. 1892, *Bon 5294* (**lectotype** of *Poria fulvobadia* FH 290623).

*Lividopora facilis*. **Indonesia**, Riau (see type).

*Lividopora subvincta*. **Kenya**, Taita-Taveta, Taita Hills, Ngangao, dicot, 24 Nov. 2017, *Savchenko 171124/1505* (H 7008794); dicot, 29 Nov. 2017, *Savchenko 171129/1309A** (H 7008878). **Zimbabwe** (see type).

*Pseudolagarobasidium belizense*. **Brazil**, Pará, Vicinal Das Paranarense, Municipio de Aveiro, *Hevea brasiliensis*, unknown collection date, *Gazis VPB197** (H). **Costa Rica**, Guanacaste, Reserva Biologica Lomas Barbudal, angiosperm, 14 Jul. 2001, *KH Larsson 11363** (O, H).

*Lividopora vincta*. **Brazil**, Amazon, Rio Uaupés, Ipanoré ("Panuré"), on dead trees, Feb. 1853, *Spruce 178* (**lectotype** of *Polyporus carneopallens* K(M) 192248, **isotype** FH 00290615). **Costa Rica**, San José, Ciudad Colon, alt. 800 m, 23 Jul. 1963, *Lowe L-13218-Sp* (CFMR). Puntarenas, Tarcoles, Villa LaPaz, dicot, 22 Apr. 2017, *Vlasák** (JV 1704/102). **Dominican Republic** (K, type). **USA**, Florida, Alachua Co., Gainesville, dicot, 24 Nov. 2013, *Miettinen 17916.1** (H).

*Pseudolagarobasidium calcareum*. **Taiwan**, Nantou, Sun-Moon Lake, *Castanopsis kusanoi*, 26 Oct. 1988, *Wu 881026–18* (H 7003571).

*Pseudolagarobasidium subvinosum*. **Taiwan**, Hualien, Hsiulin Hsiang, *Leucaena leucocephala*, Sep. 1986, *Wu 8609* (H 7003570).

*Pseudolagarobasidium venustum*. **Brazil**, São Paulo, Cananeia, Ilha do Cardoso, dicot, 2–5 Feb. 1987, *Ryvarden 24717* (GB, **paratype**), see also **holotype**. **Colombia**, Magdalena, Parque Nacional Tayrona, Estacion Canaveral, 17–19 Jun. 1978, *Ryvarden 15910B* (GB, paratype). **Costa Rica**, unknown collection date, *Carranza 120929** (O); Guanacaste, Tempisque, Reserva Biologica Lomas Barbudal, on decaying dicot wood, 14 Jul. 2001, *K.H. Larsson 11363** (GB). **Puerto Rico**, Luquillo, Sabana, Bisley, dicot, 6 Jun. 1997, *K.H. Larsson 10040** (GB).

*Radulodon americanus*. **Canada** (see type).

*Radulodon casearius*. **USA**, Fungi Caroliniani Exsiccati by H.W. Ravenel, fasc. III, 20. "*Hydnum trichodontium*", *Quercus* sp. (H).

*Radulodon erikssonii*. **Finland**, Pohjois-Häme, Vesijaon luonnonpuisto, 21 Sep. 2018, *Pennanen 3886** (H); Pohjois-Savo, Savonlinna, Haukiniemi, *Populus tremula*, 9 Nov. 2018, *Pennanen 3794** (H); Pieksänmaa, Kivimäki, *P. tremula*, 29 Sep. 2006, *Miettinen 10977* (H). **Norway** (see type). **Switzerland**, Ticino, Losone, Maia, *P. tremula*, 30 Apr. 1988, *Martini** (GB 0181279).

*Somion delectans*. **USA**, Maine. York Co., Kittery Point, *Carya ovata*, Oct. 1922, *Thaxter 799* (H ex FH); New Jersey, Carroll Co., North Conway, *Betula* sp., Sep. 2008, *Vlasák 0809/62** (JV); Ohio, Cincinnati, fallen log, unknown collection date, *Morgan 106* (BPI – **isotype**); Pennsylvania, Montgomery Co., Green Lane State Park, *Carya* sp., Jul. 2015, *J. Vlasák Jr.** (JV 1507/22, H); Chester Co., Phoenixville, *Acer rubrum*, Nov. 2018, *J. Vlasák Jr.** (JV 1811/9).

*Somion litschaueri*. **Czech Republic**, Jihomoravský kraj, Valtice, *Quercus cerris*, 10 Sep. 1998, *Vampola 198* (H ex MJ); 3 Sep. 2013, *Vlasák** (JV 1309/1, H). **Slovakia**, Zvolen, Čertova Skala Nat. Res., *Quercus* sp., 4 Sep. 2013, *Vlasák** (JV 1309/7, H).

*Somion occarium*. **Czech Republic**, Jihočeský kraj, Jindřichův Hradec, Suchdol nad Lužnicí, *Fagus sylvatica*, Oct. 2013, *Hlásek** (JV 1310/23, H); Jihomoravský kraj (see epitype); Vysočina, Doupě, *F. sylvatica*, 17 Nov. 1994, *Vampola* (H ex MJ, *Polyporales* Exsiccati Čechoslaviacae 149). **Sweden**, Skåne, Kullaberg, Brunnby, *F. sylvatica*, 20 Nov. 2009, *KH Larsson 14261** (GB). **Tunisia**, El Fedja, *Quercus suber*, Jan. 1893, herb. *Patouillard* (**lectotype** of *Spongipellis suberis* FH). **Ukraine**, Zakarpatska Reg., Dilove, Mt. Menchul, *F. sylvatica*, Aug. 1934, *Pilát* (**holotype** of *Leptoporus bredecelensis* PRM 623854).

*Somion strenuum*. **China**, Liaoning, Anshan, Qian Mts. Park, *Quercus* sp., 22 Aug. 2005, *Miettinen 10456** (H). **Russia**, Khabarovsk Reg., Komsomolsk Dist., Boktor, *Quercus mongolica*, 18 Aug. 2013, *Spirin 6112** (H); Solnechnyi Dist., Igdomi, *Q. mongolica*, 6 Sep. 2016, *Spirin 10989* (H); Sonakh (see type); Ulchskii Dist., Susanino, *Q. mongolica*, 27–29 Aug. 1976, *Alanko 31049, 31153* (H).

*Somion tomsovskyi*. **Mexico**, San Luis Potosí, Ciudad de Maiz, 23 May 1963, *Lemke* (H ex O). **USA**, Arizona, Cochise Co., Chiricahua, *Quercus hypoleucoides*, 6 Oct. 1967, *Gilbertson 7638* (H ex O); 5 Sep. 2012, *J. Vlasák Jr.** (JV 1209/55, H); *Quercus* sp., 19 Jul. 2013, *J. Vlasák Jr.** (JV 1307/8, H); Pima Co., Madera Canyon, *Quercus* 20 Nov. 2016, *J. Vlasák Jr.** (JV 1611/1).

*Somion unicolor*. **Canada**, Ontario, Renfrew Co., Petawawa Forest Station, *Quercus borealis*, Aug. 1937, *Lewis* (H ex DAOM 9080). **USA**, Missouri, Perry Co., Perryville, dead logs, 1884, *Demetrio* (Rabenhorst-Winter's Fungi Europaei #3330, H); New Jersey, Atlantic Co., Hammonton, Wharton State Forest, *Quercus* sp., 15 Apr. 2013, *J. Vlasák Jr. 1304/1** (JV, H); Burlington Co., Batsto Village, *Quercus* sp., Aug. 2017, *J. Vlasák Jr. 1708/10** (JV, H); *Acer rubrum*, Jan. 2021, *J. Vlasák Jr. 2102/2** (JV).

*Trametes meyenii*. **Indonesia**, Nusa Tenggara Barat, Lombok Utara, Bentek, dicot, 29 Dec. 2011, *Miettinen 15249* (BO, H); Papua Barat, Teluk Wondama, Werianggi-Werabur, 7 Sep. 2004, *Miettinen 9274* (BO, H).

*Trametes sclerodepsis*. **Ecuador**, Orellana, Yasuni NP, 12 Mar. 2002, *Ryvarden 44671A* (O, H).

## DISCUSSION

We have inferred a phylogeny of the family *Cerrenaceae* with a 6-marker dataset to revise its classification at the genus level. Balancing morphological data and phylogenetic information, we have adopted a scheme of seven genera. Other schemes would also be feasible for the family: three large genera (*Cerrena*, *Irpiciporus*, and *Somion*), six genera (as in the seven-genus solution but *Lividopora* included in *Cerrena*) or nine small genera (as in the seven-genus solution, but *Cerrena* and *Somion* divided into two each). The latter are fairly similar phylogenetically to the seven-genus solution, but genera in them would be more difficult to define morphologically. The phylogenetically simplest three-genus solution is worthy of further comments.

Nomenclaturally, the three-genus option would cause many more changes to the *status quo* than the other options. On the positive side, the three genera would be phylogenetically more distinct (distant) than in the other solutions, and therefore likely more robust over time, when more species are discovered and added to the phylogenetic estimate. In the other schemes, compulsory modifications are more likely, when species that do not fit to genera, for instance within the *Cerrena-Pseudolagarobasidium* clade, turn up. However, we cannot work with the unknown, and the above-mentioned point of view should not be overemphasized. Our sampling covers all forested continents and is tolerably representative of genus diversity in the family.

If we were to define genera for the hydnoid members of the family in isolation, then division into *Irpiciporus* (incl. *Radulodon*) and *Pseudolagarobasidium* would be well justified both morphologically and phylogenetically. However, once polypores are added, either *Pseudolagarobasidium* would need to be included in a morphologically heterogeneous *Cerrena* (the three-genus solution), or the *Irpiciporus* clade would need to be divided into three genera (the seven-genus solution we have adopted, Fig. 3). Either way, the solution no longer appears optimal from the isolationist perspective.

Defining genera from the polypore perspective, division into four (*Irpiciporus*, *Somion*, *Cerrena*, and *Lividopora*) is the most natural solution morphologically, and the one we have adopted here, even if it causes splitting of hydnoid taxa. The three-genus solution (*Cerrena* incl. *Lividopora*, *Irpiciporus*, and *Somion*) could be morphologically somehow justified. Again, when hydnoid taxa are added, the *Irpiciporus* concept becomes more diluted and *Cerrena sensu lato* would include nearly monomitic, hydnoid species of *Pseudolagarobasidium*, making it a yet more difficult concept morphologically.

We have chosen here the seven-genus solution as the one optimizing morphological recognition with phylogenetic signal, while minimizing nomenclatural changes. In doing so we have had to abandon easy-to-define genera for hydnoid fungi. This underlies the importance of integrating different morphogroups and their research traditions when making conclusions on higher-level taxonomy. Polypores and corticioid fungi in particular are very often intermixed above the genus level, as is the case of the *Cerrenaceae*, *Irpicaceae*, *Polyporaceae*, and *Steccherinaceae* to give a few examples from the *Polyporales*. Our seven-genus solution avoids placing strictly hydnoid and poroid species in the same genus, which would have been the case for the three-genus solution.

Can the family *Cerrenaceae* be defined morphologically? Definition in the strict sense is not feasible, as is the case for most families in the *Polyporales*. A few general characters are shared by all the known species: mid-sized spores that are slightly cyanophilous if they are thick-walled, mid-sized to large basidia, hyphal structure that is never agglutinated, aggressive white rot; many, if not all species, are tree parasites or pathogens. These characters are found in many other families in *Agaricomycetes* and even as a combination are not unique to the *Cerrenaceae*.

We have focused on morphological and phylogenetic characters of the *Cerrenaceae*. Ecologically this family contains only species that inhabit trees, though quite many species are able to colonize living trees already and some are considered tree diseases. Some wood decay fungi are able to grow in soil as well, but this does not seem to be the case with the *Cerrenaceae*. When compiling ITS sequences for this study, we searched the UNITE database for species that belong to this family. UNITE contains many unique sequences, mostly soil-derived, not available through GenBank, but only few additional sequences were found through UNITE in this case, indicating that they are not an important component of soil funga.

Representatives of all the genera in the *Cerrenaceae* have been studied for their cultural morphology in varying degree with the exception of *Acanthodontia,* which has not been cultivated to our knowledge. In particular, *Cerrena unicolor* has been studied for its enzymes associated with white rot (see Introduction). When grown on agar plates, members of the family produce fast-growing, white, well-spaced mycelium cottony on the surface, with clamps in part of the septa, conidia, and they show signs of laccase and peroxidase activity (David 1969, Setliff 1972a, Stalpers 1978, Woods & Ginns 2006). In this sense the *Cerrenaceae* are rather uniform, but with the current sampling of a single specimen and species per genus, little can be said on how the genera differ in their cultural characters, if at all. The above-mentioned set of characters is also not unique to the *Cerrenaceae*, and for instance in the key of Stalpers (1978), the family appears in different parts of the key intermixed with unrelated species. It would appear that cultural characters are not very useful for the systematics of the *Cerrenaceae*.

Surprisingly, only one high-quality genome sequence, *Cerrena unicolor*, has been produced for the whole family, by the US Joint Genome Institute. Even this genome is not yet public, though it is visible in the Mycocosm database (Grigoryev *et al*. 2013). It is a typical white-rot polypore genome in size and in its gene count of carbohydrate active enzymes such as class II peroxidases and other genes associated with wood decomposition. Considering how easy the *Cerrenaceae* are to culture and due to their economic importance as tree pathogens, we would expect more high-quality genome sequences to be published soon, enabling comparative genomics.

We will end this paper with a note on the intriguing ecology of the *Cerrenaceae*. *Cerrena unicolor* is spread by several species of the woodwasp (*Siricidae*) genera *Tremex* and *Eriotremex* (Stillwell 1964, Tabata & Abe 1995, Pažoutová & Šrůtka 2007, Schiff *et al*. 2012). The symbiosis between woodwasp and *Amylostereum* (*Russulales*) is well-documented, but so far, no other fungi than *Amylostereum* and *Cerrena* are known to be associated with woodwasps. Could other species of *Cerrena* be associated with insects in a similar manner? And to expand, many species in this family attack living trees as mentioned in the introduction. In addition to *Cerrena*, also *Pseudolagarobasidium* and *Somion* are pathogenic; *Lividopora* spp. are known to be

tree pathogens but also endophytes, *i.e.* present as mycelium in healthy plant tissues. Could insect association provide a route for these species to enter living trees?

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**Supplementary Material: http://fuse-journal.org/**

**Fig. S1.** Bayesian consensus tree of *Cerrenaceae* based on nrDNA ITS and LSU sequences. Countries (and states) are denoted with ISO 3166 codes.

**Fig. S2.** Bayesian consensus tree of the *Cerrenaceae* based on mitochondrial SSU sequences.

**Fig. S3.** Bayesian consensus tree of the *Cerrenaceae* based on mitochondrial *ATP6* sequences.

**Fig. S4.** Bayesian consensus tree of the *Cerrenaceae* based on nuclear *RPB1* sequences.

**Fig. S5.** Bayesian consensus tree of the *Cerrenaceae* based on nuclear *TEF1* sequences.