Additions to the taxonomy of *Lagarobasidium* and *Xylodon* (Hymenochaetales, Basidiomycota)

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Abstract

*Lagarobasidium* is a small genus of wood-decaying basidiomycetes in the order Hymenochaetales. Molecular phylogenetic analyses have either supported *Lagarobasidium* as a distinct taxon or indicated that it should be subsumed under *Xylodon*, a genus that covers the majority of species formerly placed in *Hyphodontia*. We used sequences from the ITS and nuclear LSU regions to infer the phylogenetic position of the type species *L. detriticum*. Analyses confirm *Lagarobasidium* as a synonym of *Xylodon*. Molecular and morphological information show that the traditional concept of *L. detriticum* covers at least two species, *Xylodon detriticus* from Europe and *X. pruinösus* with known distribution in Europe and North America. Three species currently placed in *Lagarobasidium* are transferred to *Xylodon*, viz. *X. magnificus*, *X. pumilius* and *X. rickii*. Three new *Xylodon* species are described and illustrated, *X. ussuriensis* and *X. crystalliger* from East Asia and *X. attenuatus* from the Pacific Northwest America. The identity of *X. nongravis*, described from Sri Lanka, is discussed.

Keywords

Agaricomycetes, *Hyphodontia*, ITS, LSU, phylogeny
Introduction

The genus *Lagarobasidium* was introduced by Jülich (1974) for three corticioid species, *L. cymosum* (D.P.Rogers & H.S.Jacks.) Jülich, *L. nikolajevae* (Parmasto) Jülich and *L. pruinosum* (Bres.) Jülich (the generic type). These species possess prominent, thin- or slightly thick-walled cystidia, suburniform tetrasporic basidia and thick-walled basidiospores. Eriksson and Ryvarden (1976) concluded that *L. pruinosum* is a later synonym of *Peniophora detritica* Bourdot (Bourdot 1910), which prompted Jülich (1979) to move *P. detritica* to *Lagarobasidium*. At present, *L. detriticum* is accepted in a wide sense, with *Hyphodontia magnacystidiata* Lindsey & Gilb., *H. nikolajevae* Parmasto and *Odontia pruinosa* Bres. as synonyms (http://www.mycobank.org [accessed 07 May 2018]).

Controversies over the taxonomic position of *Peniophora detritica* emerged during the last decades. In modern morphology-based systems, it was first attributed to *Hyphodontia* J. Erikss., mainly due to hyphal characters and the shape of basidia (Eriksson 1958, Langer 1994). A second solution was introduced by Eriksson and Ryvarden (1976) who stressed the shape of cystidia and the thick-walled cyanophilous basidiospores and placed the species in *Hypochnicium*. The third option and the one chosen by Jülich (1974), was to place *P. detritica* in a genus of its own (Jülich 1974, 1979, Hjortstam and Ryvarden 2009).

Larsson et al. (2006) used the nrLSU and 5.8S genes for a phylogenetic analysis of Hymenochaetales and recovered *Peniophora detritica* nested in a fairly well-supported clade that also included several species usually classified in *Hyphodontia*. This result supported the original opinion on relationships introduced by Eriksson (1958) but also showed that *Hyphodontia* sensu Eriksson was polyphyletic. The clade with *Peniophora detritica* recovered by Larsson et al. (2006), was later identified as *Xylodon*, type species *X. quercinus*, a genus that now covers the majority of species earlier referred to *Hyphodontia* (Hjortstam and Ryvarden 2009). On the other hand, Dueñas et al. (2009) studied sequences from the ITS region and concluded that molecular information supported recognition of the separate genus *Lagarobasidium*. These same ITS sequences have been used by several subsequent researchers, who therefore maintained *Lagarobasidium* separate from *Hyphodontia* sensu lato (Yurchenko and Wu 2014, Riebesehl et al. 2015, Chen et al. 2016, Chen et al. 2017, Kan et al. 2017, Riebesehl and Langer 2017, Yurchenko et al. 2017, Chen et al. 2018).

In the present study, we revise the *Lagarobasidium detriticum* complex based on morphological and molecular methods. We propose to consider *Lagarobasidium* as a later synonym of *Xylodon* and to restore *Odontia pruinosa* as an independent species. In addition, we describe three new *Xylodon* species and make five new combinations.

Materials and methods

Morphological methods

Type material and specimens from herbaria H, S, O, GB, BPI, TAAM and BAFC were studied. Herbarium abbreviations are given according to Index Herbariorum (Thiers).
Microscopic methods are described in Miettinen et al. (2006). All measurements were made in Cotton Blue (CB, Merck 1275) with phase contrast illumination (1250×). The following abbreviations are used in microscopic descriptions: L – mean spore length; W – mean spore width; Q – mean L/W ratio; n – number of spores (hyphae, basidia) measured per number of specimens. We excluded 5% of measurements from each end of the range representing variation of basidiospores and cystidia. Excluded extreme values are given in parentheses when they differ substantially from the lower or higher 95% percentile.

**DNA extraction and sequencing**

For DNA extraction we used either the standard CTAB protocol (Griffith and Shaw 1998) or DNeasy Plant Mini kit (Qiagen, Hilden, Germany). Primers ITS1F (Gardes and Bruns 1993), ITS4 (White et al. 1990) and LR21 (Hopple and Vilgalys 1999) were used to amplify the internal transcribed spacers 1 and 2 and the 5.8S gene. LR0R, LR5 (Moncalvo et al. 2002) and LR7 (Hopple and Vilgalys 1999) were used to amplify 28S large ribosomal subunit. Polymerase chain reaction (PCR) products were purified with the Cleanup Standard kit (Evrogen Ltd, Moscow, Russia) or QIAquick PCR purification kit (Qiagen, Hilden, Germany). Sequencing reactions were performed either by the Evrogen company (Moscow, Russia) following the BigDye terminator protocol (ABI Prism) on an Applied Biosystems 3730 xl automatic sequencer (Applied Biosystems, CA, USA) with primers ITS1F and ITS4 or with an external service provided by Macrogen (South Korea) using primers ITS1, ITS4, CTB6 (http://plantbio.berkeley.edu/~bruns/), LR5 and LR3R (Hopple and Vilgalys 1999).

**Phylogenetic analyses**

DNA sequences were edited in Geneious (Biomatters Ltd, Auckland, New Zealand) or in Sequencher 5.2.4 (Gene Codes Co., Ann Arbor, MI, USA) and deposited in GenBank (Table 1). We compiled two sequence datasets. The first one contains full ITS sequences from 83 specimens. The second dataset includes ITS and nLSU sequences from 24 specimens and is a subset of the taxa in the ITS-only dataset. In both datasets, Hastodontia hastata (Litsch.) Hjortstam & Ryvarden (Hymenochaetales) was included as outgroup (Larsson et al. 2006). We generated 13 ITS and 6 nLSU sequences for this study; other sequences used in the analyses were downloaded from GenBank (Benson et al. 2018) or UNITE (Kõljalg et al. 2013) (Table 1). Alignments were calculated through MAFFT 7.407 online server (https://mafft.cbrc.jp/alignment/server/) using the L-INS-I strategy (Katoh et al. 2017) and then manually adjusted. The alignments are deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S23057).

We inferred phylogenetic trees with maximum likelihood (ML), maximum parsimony (MP) and Bayesian Inference (BI) but provide only the last one since all trees show congruity of the phylogenetic signal. Substitution models were determined with the aid of TOPALi 2.5 (Milne et al. 2008) based on Bayesian information criterion
Table 1. Specimens and GenBank and UNITE accession numbers for DNA sequences used in this study.

| Species                          | Specimen voucher | GenBank or UNITE accession numbers for ITS | GenBank or UNITE accession numbers for LSU | Reference                  |
|----------------------------------|------------------|-------------------------------------------|-------------------------------------------|----------------------------|
| Hastodontia hastata (Litsch.) Hjortstam & Ryvarden | Larsson 14646 | MH638232 | MH638232 | this study |
| Lyomyces allantiporus Riebeischl, Yurchenko & E. Langer | FR-0249548, Holotype | KY800397 | KY795963 | Yurchenko et al. (2017) |
| Lyomyces crustosus (Pers.) P. Karst. | Larsson 11731 | DQ873614 | DQ873614 | Larsson et al. (2006) |
| Lyomyces erastii (Saaren. & Karis.) Hjortstam & Ryvarden | MA-Fungi 34,336 | JX857800 | | Yurchenko et al. (2017) |
| Lyomyces greseliniae (G. Cunn.) Riebeischl & E. Langer | Larsson 12971 | DQ873651 | | |
| Lyomyces mascarensis Riebeischl, Yurchenko & E. Langer | KAS-GEL4833, Holotype | KY800399 | KY795964 | Yurchenko et al. (2017) |
| Lyomyces microfasciculatus (Yurchenko & Sheng H. Wu) Riebeischl & E. Langer | TNM F24775, Holotype | JN129976 | | Yurchenko and Wu (2014) |
| Lyomyces organensis Yurchenko & Riebeischl | MSK7247, Holotype | KY800403 | KY795967 | Yurchenko et al. (2017) |
| Lyomyces orientalis Riebeischl, Yurchenko & E. Langer | KAS-GEL3400 | DQ340326 | DQ340353 | Yurchenko et al. (2017) |
| Lyomyces pruni (Lasch) Riebeischl & E. Langer | Ryberg 021018 | DQ873624 | DQ873625 | Larsson et al. (2006) |
| Lyomyces sambuci (Pers.) P. Karst. | KAS-GEL2414 | KY800398 | | Yurchenko et al. (2017) |
| Lyomyces vietnamensis (Yurchenko & Sheng H. Wu) Riebeischl & E. Langer | TNM F973, Holotype | JX179044 | | Yurchenko and Wu (2014) |
| Tylanger cerecanus (G. Cunn.) Stalpers & P.K. Buchanan | Larsson 12261 | DQ873642 | | Larsson et al. (2006) |
| Xylodon apacheriensis (Gilb. & Canf.) Hjortstam & Ryvarden | Canfield 180, Holotype | KY081800 | | Riebeischl and Langer (2017) |
| Xylodon asperti (Fr.) Hjortstam & Ryvarden | H601367 | UBD031926 | | Unpublished |
| Xylodon attenutus Spirin & Viner | Spirin 8775, Holotype | MH324476 | | this study |
| Xylodon borealis (Koris. & Saaren.) Hjortstam & Ryvarden | Spirin 9416 | MH317760 | MH638259 | this study |
| Xylodon detriticus (Bourdol) Viner & Spirin | TU115575 | UBD016473 | | Unpublished |
| Xylodon flaviporus (Berk. & M.A. Curtis ex Cooke) Riebeischl & E. Langer | ICMP13836 | AF145585 | | Paulus et al. (2000) |
| Xylodon hastifer (Hjortstam & Ryvarden) Hjortstam & Ryvarden | Ryvarden 19767, Holotype | KY081801 | | Riebeischl and Langer (2017) |
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| Species                                   | Specimen voucher | GenBank or UNITE accession numbers for ITS | GenBank or UNITE accession numbers for LSU | Reference                        |
|-------------------------------------------|------------------|---------------------------------------------|--------------------------------------------|----------------------------------|
| *Xylodon heterocystidiatus* (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl, Yurchenko & E. Langer | Wu 9209-27       | JX175045                                     |                                             | Yurchenko and Wu (2014)          |
| *Xylodon levis* Hjortstam & Ryvarden      | Wu 0808-32       | JX175043                                     | KX857820                                   | Yurchenko and Wu (2014)          |
|                                          | Wu 890714-3      |                                             | KY081802                                   | Riebesehl and Langer (2017)      |
| *Xylodon mollisimus* (L.W. Zhou) C.C. Chen & Sheng H. Wu | LWZ20160318-3, Holotype |                                             | KX007517                                   | Kan et al. (2017)                |
| *Xylodon nespori* (Bres.) Hjortstam & Ryvarden | B Nordén 030915  | DQ873622                                     |                                            |                                 |
|                                          | GEL3158          | DQ340310                                     | DQ340346                                   |                                 |
|                                          | GEL3290          | DQ340309                                     |                                            |                                 |
|                                          | GEL3302          | DQ340308                                     |                                            |                                 |
|                                          | GEL3309          | DQ340307                                     | DQ340345                                   |                                 |
| *Xylodon niemelai* (Sheng H. Wu) Hjortstam & Ryvarden | GC 1508-146      | KX857798                                     |                                            |                                 |
|                                          | GEL4998          | EU583422                                     | DQ340348                                   |                                 |
| *Xylodon nongravis* (Lloyd) Spirin & Viner | CHWC1506-2       | KX857800                                     |                                            |                                 |
|                                          | Dai 11686        | KT899668                                     |                                            |                                 |
|                                          | GC1412-22        | KX857801                                     |                                            |                                 |
|                                          | Spirin 5763      | MH324469                                     | MH656724                                   |                                 |
| *Xylodon nothofagi* (G. Cann.) Hjortstam & Ryvarden | PDD:91630        | GQ411524                                     |                                            |                                 |
| *Xylodon oviporus* (Corner) Riebesehl & E. Langer | ICMP13837        | AF145587                                     |                                            |                                 |
|                                          | KUC20130725-29   | KJ668513                                     | KJ668365                                   |                                 |
|                                          | Wu 0809-76       | KX857803                                     |                                            |                                 |
| *Xylodon paradoxus* (Schrad.) Chevall.    | FCUG 1517        | AF145572                                     |                                            |                                 |
|                                          | FCUG 2425        | AF145571                                     |                                            |                                 |
|                                          | Miettinen 7978   | FN907912                                     | FN907912                                   | Miettinen and Larsson (2011)     |
| *Xylodon prainosus* (Bres.) Spirin & Viner | Larsson 14653    | UDB024816                                    |                                            |                                 |
|                                          | Spirin 2877      | MH332700                                     |                                            |                                 |
|                                          | UC2023108        | KP814412                                     |                                            |                                 |
| *Xylodon pseudotropicus* (C.L. Zhao, B.K. Cui & Y.C. Dai) Riebesehl, Yurchenko & E. Langer | DAI 10768, Holotype |                                            |                                            |                                 |
| *Xylodon quercinus* (Pers.) Gray          | Kotiranta 27060  | MH320792                                     |                                            |                                 |
|                                          | Larsson 11076    | KT361633                                     | AY586678                                   | Ariyawansa et al. (2015)         |
|                                          | Miettinen 15050,1| KT361632                                     |                                            | Ariyawansa et al. (2015)         |
|                                          | Spirin 8565      | MH316007                                     |                                            |                                 |
|                                          | Spirin 8840      | MH320791                                     |                                            |                                 |
| *Xylodon raduloides* (Pers.) Riebesehl & E. Langer | Dai 12631        | KT203307                                     | KT203328                                   | Moncalvo et al. (2002)           |
|                                          | ICMP13833        | AF145580                                     |                                            |                                 |
| *Xylodon ramicida* Spirin & Miettinen     | Spirin 7664, Holotype | KT361634                                   |                                            | Ariyawansa et al. (2015)         |
| *Xylodon reticulatus* (C.C. Chen & Sheng H. Wu) C.C. Chen & Sheng H. Wu | GC 1512-1        | KX857808                                     |                                            |                                 |
|                                          | Wu 1109-178, Holotype | KX857805                                   |                                            |                                 |
| *Xylodon rhizomorphus* (C.L. Zhao, B.K. Cui & Y.C. Dai) Riebesehl, Yurchenko & E. Langer | Dai 12354        | KF917544                                     |                                            |                                 |

This table lists species of *Lagarobasidium* and *Xylodon* with their specimen vouchers, GenBank or UNITE accession numbers, and references.
| Species                       | Specimen voucher | GenBank or UNITE accession numbers for ITS | GenBank or UNITE accession numbers for LSU | Reference                     |
|------------------------------|------------------|-------------------------------------------|-------------------------------------------|-------------------------------|
| Xylodon rimosissimus (Peck) Hjortstam & Ryvarden | CFMR:DLL2011-081 | KJ140600                                  |                                            | Brazee et al. (2014)          |
|                              | Ryberg 021031    | DQ873627                                  | DQ873628                                  | Larsson et al. (2006)         |
|                              | UC2022842        | KP814311                                  |                                            | Rosenthal et al. (2017)       |
|                              | UC2023109        | KP814414                                  |                                            | Rosenthal et al. (2017)       |
|                              | UC2023147        | KP814193                                  |                                            | Rosenthal et al. (2017)       |
|                              | UC2023148        | KP814194                                  |                                            | Rosenthal et al. (2017)       |
| Xylodon spatulatus (Schrad.) Kuntze | GEL2690          | KY081803                                  |                                            | Riebesehl and Langer (2017)  |
|                              | Larsson 7085     | KY081804                                  |                                            | Riebesehl and Langer (2017)  |
| Xylodon subtropicus (C.C. Chen & Sheng H. Wu) C.C. Chen & Sheng H. Wu | Wu 1508-2     | KX857806                                  |                                            | Chen et al. (2017)            |
|                              | Wu 9806-105, Holotype | KX857807                             |                                            | Chen et al. (2017)            |
| Xylodon ussuriensis Viner    | KUN1989, Holotype | MH324468                                  |                                            | this study                    |

(BIC). GTR + G (nst = 6, rates = gamma) were the best-fit models for the whole ITS region in the ITS dataset as well as in the ITS + nrLSU dataset. SYM + G (nst = 6, rates = gamma, statefreqpr = fixed(equal)) was the best-fit model for the nrLSU region in the ITS + nrLSU dataset. The suggested models were implemented in the Bayesian phylogenetic analyses. We performed Bayesian inference with MrBayes 3.2 (Ronquist et al. 2012). In the analyses, three parallel runs with four chains each, temp = 0.2, were run for 3 million generations. All chains converged to <0.01 average standard deviation of split frequencies. A burn-in of 25% was used in the final analyses.

Maximum-likelihood (ML) analysis was performed in RAxML 7.2.8 (Stamatakis 2006) implemented in Geneious. Following models suggested by TOPALi 2.5, we preferred to use the GTR model with gamma correction (GTRGAMMA) in ML analysis for both datasets. The bootstrapping was performed using the ‘Rapid bootstrapping’ algorithm with the number of bootstrap replicates set as 1000.

Maximum parsimony (MP) analysis was performed using MEGA 7 (Kumar et al. 2016). We used the Subtree-Pruning-Regrafting (SPR) algorithm using all sites. The number of bootstrap replicates was set as 1000.

Specimens examined (sequenced specimens are marked by an asterisk)

*Xylodon attenuatus.* USA. Washington: Clallam Co., La Push, *Pseudotsuga menziesii*, 8 Oct 2014, Spirin 8286a (H), Sol Duc, *Tsuga heterophylla*, 6 Oct 2014, Spirin 8133 (H); Jefferson Co., Hoh River, *Acer macrophyllum*, 20 Oct 2014, Spirin 8775* (H, holotype), *Tsuga heterophylla*, 20 Oct 2014, Spirin 8779 (H); Pend Oreille Co., Gypsy Meadows, *Picea engelmannii*, 17 Oct 2014, Spirin 8694* (H). Canada. British Columbia: Fraser-Fort George Reg. Dist., Mt. Robson Provincial Park, *Picea sp.*, 25 Jul 2015, Spirin 8900a (H).

*X. borealis.* Russia. Nizhny Novgorod Reg.: Lukoyanov Dist., Panzelka, *Quercus robur* (very rotten log), 17 Aug 2015, Spirin 9416* (H).
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* X. brevisetus. Russia. Moscow: Losiny Ostrov Nat. Park, log of *Pinus sylvestris*, 1 Oct 2016, A.Nechaev KUN2352* (H).

* X. crystalliger. Russia. Primorie: Khasan Dist., Kedrovaya Pad Nat. Res., on angiosperm wood, 25 Jul 2016, I.Viner KUN 2312* (H, holotype); ibidem 29 Jul 2017, F.Bornicov, KUN 3347 (H).

* X. detriticus. Czech Republic. Karlovarský kraj: Sokolov, Antonín mine spoil, on *Phragmites australis*, 26 May 2017, L.Zíbarová (H*); Liberecký kraj: Liberec, Uhelná, on *Calamagrostis epigejos*, 30 Oct 2017, L.Zíbarová (H*). France. Auvergne: Allier, St. Priest, on fern, 1 Sep 1909, H.Bourdot 7226 (S F204453, lectotype of *Peniophora detritica*). Italy. Lazio: Circeo Nat. Park, on *Pinus pinea* bark, 23 Oct 1984, K.H.Larsson 5496 (GB); ibidem, on fallen leaves, 24 Oct 1984, K.H.Larsson 5622 (GB); ibidem, on ferns, 24 Oct 1984, K.H.Larsson 5627 (GB).

* X. magnificus. Argentina. Tierra del Fuego: Ushuaia, Estancia Moat, on *Drimys winteri*, 21 Mar 1998, A.Greslebin 1387 (GB, paratype duplicate).

* X. nongravis. Russia. Khabarovsk Reg.: Khabarovsk Dist., Ulun, on *Salix schwerinii*, 25 Aug 2012, V.Spirin 5615 (H); ibidem, on *Corylus mandshurica*, 28 Aug 2012, V.Spirin 5763* (H); Primorie Reg.: Krasnoarmeiskii Dist., Melnichnoe, on *Corylus mandshurica*, 21–23 Aug 2013, V.Spirin 6218, 6260, 6261 (H). Sri Lanka. Peradeniya, on rotten branch, T.Petch (BPI US0305211, holotype of *Polyporus nongravis*).

* X. pruinosus. Estonia. Ida-Virumaa: Kohtla-Järve, Pärnassaare, on *Betula pubescens*, 1 Oct 1958, E.Parmasto (TAAM, holotype of *Hyphodontia nikolajevae*). Finland. Helsinki: Veräjämäki, on *Salix caprea*, 4 Sep 2011, O.Miettinen 14651.4 (H). Germany, Nordrhein-Westfalen, on *Betula sp.*, W.Brinkmann (S F204462, isolecotype of *Odontia pruinosa*).

* X. rickii. Brazil. Rio Grande do Sul: S. Salvador, 5 Apr 1944, J.Rick 20847 (O, isotype of *Odontia polycystidifera*).

* X. ussuriensis. Russia. Primorie: Khasan Dist., Kedrovaya Pad Nat. Res., angiosperm wood, 24 Jul 2016, I.Viner KUN 1989* (H, holotype of *Xylodon ussuriensis*), I.Viner KUN 2103, 2186.
Results

For both datasets, the Bayesian inference returned trees with two main clades (Figures 1, 2); the largest clade is well-supported and corresponds to *Xylodon* (pp 1.0), while the other clade is unsupported and includes *Lyomyces*, the *Hyphodontia crustosa* group, *H. pruni* and *Rogersella griseliniae* (pp 0.89). Basal relationships within *Xylodon* are not resolved. *Peniophora detritica* and its allied species are nested within *Xylodon* and form a well-supported subclade together with *X. borealis* and *X. brevisetus* (Figures 1, 2). Maximum likelihood and maximum parsimony returned similar topologies and relevant support values from these analyses are indicated on nodes in Figures 1, 2.

In the ITS-only tree, three terminal branches represent new species that are described below. *Xylodon attenuatus* occurs as a sister taxon to *X. rimosissimus*; *X. crystalliger* forms a subclade with *X. astrocytiadiatus*, *X. paradoxus* and *X. heterocystidiatus*; and *X. ussuriensis* is the sister taxon to *X. detriticus* and *X. pruinosus* (Figure 1).

The results allow us to introduce new species and new combinations as follows.

*Xylodon attenuatus* Spirin & Viner, sp. nov.

Mycobank No: MB825367

Figure 3

**Type.** USA. Washington: Jefferson Co., Hoh River, on *Acer macrophyllum*, 20 Oct 2014, V. Spirin 8775 (H) – ITS sequence, GenBank MH324476.

**Etymology.** Attenuatus (lat., adj.) – exhausted, thin.

**Description.** Basidiocarp effused, up to 5 cm in widest dimension. Sterile margin white, up to 1 mm wide. Hymenial surface cream-coloured, grandinioid to odontoid; projections rather regularly arranged, from 80 µm to 200 µm high, 70–90 µm broad at base, 6–8(–9) per mm. Hyphal structure monomitic, hyphae clamped, cyanophilous. Subicular hyphae densely interwoven, thin-walled, (2–)2.4–4.6 µm in diam. (n=60/6), often short-celled, the outline of these hyphae often irregular. Tramal hyphae subparallel, thin-walled, in subhymenium densely arranged, sometimes short-celled, 2.4–3.6 µm in diam. (n=62/6). Large stellate crystals 10–13.3 µm in diam. present in subiculum and trama. Cystidia originating from subhymenium, of two types: a) subcapitate or capitate cystidia, (12–)13.5–25.1(–37)×(2.7–)3.3–5(–5.5) µm (n=80/6), b) hyphoid cystidia, (14–)16–38.3(–40.8)×2.8–4.5 (n=51/6), sometimes with crystalline cap on the top; some cystidia with granular contents in CB. Basidia suburniform, 4-spored, (12.2–)14–22(–25)×(3–)3.3–4.6(–5) µm (n=61/2), slightly thick-walled at the base. Basidiospores thin-walled, ellipsoid, (3.7–)4.1–5.5(–6)×(3–)3.4–4.5(–4.9) µm (n=180/6), L=4.85, W=3.98, Q=1.22, slightly cyanophilous.

**Distribution and ecology.** North-western USA (Washington), on angiosperm and gymnosperm wood (fallen decorticated logs).

**Remarks.** *Xylodon attenuatus* bears morphological similarity to *X. borealis*, although densely arranged hyphae, star-like crystals and a regular presence of cystidia with granular contents make it easily recognisable. The crystalline caps on hyphoid cystidia are other characteristics useful for the identification of *X. attenuatus*. 
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**Figure 1.** Phylogenetic relationships of *Xylodon* inferred from ITS sequences using Bayesian analysis. A 50% majority rule consensus phylogram. Bayesian posterior probabilities, ML bootstrap and MP bootstrap values are shown on nodes; branch lengths reflect estimated number of changes per site.
Figure 2. Phylogenetic relationships of Xylodon inferred from ITS and LSU sequences using Bayesian analysis. A 50% majority rule consensus phylogram. Bayesian posterior probabilities, ML bootstrap and MP bootstrap values are shown on nodes; branch lengths reflect estimated number of changes per site.

Figure 3. Xylodon attenuatus (holotype): a section through an aculeus b basidia c subhymenial short-celled hyphae d cystidia e basidiospores.
**Xylodon crystalliger** Viner, sp. nov.
Mycobank No: MB825368

**Figure 4**

**Type.** RUSSIA. Primorie: Khasan Dist., Kedrovaya Pad Nat. Res., on angiosperm wood, 25 Jul 2016, I.Viner KUN 2312 (H) – ITS sequence, GenBank MH324477.

**Etymology.** Crystalliger (lat., adj.) – bearing crystals.

**Description.** Basidiocarp effused, soft membranaceous, up to 6 cm in widest dimension. Sterile margin poorly defined, up to 0.3 mm wide. Hymenial surface white, minutely odontioid, i.e. covered by small peg-like hyphal projections up to 60–100 µm high, 60–75 µm broad at base, 10–15 per mm, with flattened

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**Figure 4. Xylodon crystalliger** (holotype): a section through an aculeus b apically encrusted hyphae from aculeal tips c basidiospores d basidia e cystidia f subhymenial hyphae.
fimbriate apices. Surface between projections porulose-reticulate. Hyphal structure monomitic, hyphae clamped, faintly cyanophilous. Subicular hyphae densely interwoven, often with thickened walls, 3.2–4.4 µm in diam. (n=20/2), smooth or sparsely encrusted. Tramal hyphae subparallel, thin- to clearly thick-walled, sparsely encrusted, subhymenial hyphae densely arranged, sometimes short-celled, 2.5–3.2 µm in diam. (n=20/2), sparsely encrusted. Hyphal ends at the top of projections often strongly encrusted. Cystidia of two types: a) sparsely encrusted hyphoid cystidia at the top of projections, 21.0–29.0×2.9–4.1(–4.4) µm (n=40/2), b) subcapitate or cylindrical cystidia, of subhymenial origin, rather variable in shape and size, (11.8–)14.1–25.0(–28.0)×(2.6–)2.9–4.6(–4.8) µm (n=40/2), often heavily encrusted and rarely with a stellate crystalline cap 3.5–4.5 µm in diam. Basidia suburniform, 4-spored, 13.4–18.4(–19.0)×4.2–4.7 µm (n=20/2), slightly thick-walled at the base. Basidiospores thin-walled, elliptical, occasionally with an oil-drop, (3.1–)4.2–5.1(–5.9)×(2.4–)3.3–4.2 µm (n=60/2), L=4.66, W=3.71, Q=1.26, slightly cyanophilous.

**Distribution and ecology.** East Asia (Russian Far East), on decayed angiosperm logs.

**Remarks.** The peg-like hymenial projections and cystidia with stellate caps are characteristic for *X. crystalliger* and make it reminiscent of *Xylodon astrocytidiatus* (Yurchenko & Sheng H. Wu) Riebesehl, Yurchenko & Langer. The latter species is known from Taiwan and differs from *X. crystalliger* by having longer basidiospores and presence of constricted and bladder-like hymenial cystidia.

*Xylodon detriticus* (Bourdot) K.H. Larss., Viner & Spirin, comb. nov.

Mycobank No: MB825366

Figures 5, 6c, 7

**Basionym.** *Peniophora detritica* Bourdot, Revue Scientifique du Bourbonnais et du Centre de la France 23: 13. 1910. ≡ *Lagarobasidium detriticum* (Bourdot) Jülich, Persoonia 10: 334. 1979. Type. France. Auvergne: Allier, St. Priest, fern, 1.IX.1909 Bourdot 7226 (lectotype S! [F204453], designated by Eriksson and Ryvarden 1976: 703).

**Description.** Basidiocarps effused, up to 5 cm in widest dimension. No differentiated margin. Hymenial surface white, smooth or warted, farinaceous. Hyphal structure monomitic, hyphae clamped, faintly cyanophilous, thin-walled. Subicular hyphae interwoven and frequently branched, (2.2–)3.0–5.9 µm in diam. (n=61/6). Tramal hyphae subparallel, subhymenial hyphae short-celled, (1.5–)1.9–3.5 µm in diam. (n=61/6). Large, rhomboid or stellate crystals abundant in trama and subiculum, 8–10.5 µm in diam. Cystidia of two types: a) large, thin-walled cystidia of subicular or tramal origin, cylindrical or clavate, rarely slightly thick-walled (wall not exceeding 1 µm thick), (30.0–)58.9–110.0(–115.0)×4.1–8.5(–9.6) µm (n=120/6), occasionally bearing 1–2 clamped septa, b) rare astrocytidiia of subhymenial origin, with a stellate crystalline cap 10–23×2–3.1 µm, in some specimens difficult to find. Basidia suburniform, 4-spored,
Additions to the taxonomy of *Lagarobasidium* and *Xylodon*...

Figure 5. Cystidial elements of *Xylodon detriticus*: a Larsson 5496 b Zíbarová 26.V.2017 c Zíbarová 30.X.2017.

(12.2–)13.1–20.0×(3.1–)3.4–5.0 μm (n=61/6), thin-walled. Basidiospores clearly thick-walled, elliptical to broadly elliptical, usually with an oil-drop, (3.3–)4.3–5.7–6.1)×3.2–4.1–4.5 μm (n=190/6), L=4.92, W=3.69, Q=1.34, cyanophilous.

**Distribution and ecology.** Europe (Czech Republic, France, Italy), on herbaceous remnants, once collected from pine bark at the same spot where it was found on fern remains.

**Remarks.** Eriksson and Ryvarden (1976) selected Bourdot 7226 (in herb. S) as lectotype. They also treated *Hyphodontia nikolajevae* and *Odontia pruinosa* as synonyms. However, the type specimens of *H. nikolajevae* and *O. pruinosa* reveal small differences from the type material and other collections of *X. detriticus* studied by us. The main
Figure 6. Basidiospores of two Xylodon species in CB: a X. pruinosus (Spirin 9994) b X. pruinosus (isotype of Hyphodontia magnacystidiata) c X. detriticus Zíbarová (26.V.2017).

Figure 7. Basidiocarp of Xylodon detriticus (Zíbarová 26.V.2017). Scale bar: 5 mm.
Additions to the taxonomy of *Lagarobasidium* and *Xylodon*...

Features of *X. detriticus* versus the two other taxa are narrower basidiospores (must be observed in cotton blue) and longer, narrower cystidia having no distinct intercalary inflation (Tables 2, 3, Figures 5, 6). Eriksson and Ryvarden (1976) attributed the differences in cystidia morphology between Bourdot’s specimen and types of *H. nikolaevae* and *O. pruinosa* to different stages of basidiocarp development. Our investigation indicates that the differences are genetic and species specific. Differences in basidiospore size and shape are detectable in CB but not in KOH, which could explain why they have gone unnoticed in earlier studies.

Hjortstam and Ryvarden (2009) added *Hyphodontia magnacystidiata* to the synonymy of *X. detriticus*. This species is, as far as we know, only known from the type, collected on dead wood of *Populus* in New York, USA (Lindsey and Gilbertson 1977). It has an odontiod basidiocarp and its cystidia are similar to those of *X. pruinlus* (Table 3, Figures 6, 8). On the other hand, the basidiospore size is very close to *X. detriticus* (Table 2). In the absence of sequenced material, it is not possible to decide whether this is an independent species or not. Considering that the single specimen was growing on wood and that *X. detriticus* is not yet found in North America, we prefer to keep *H. magnacystidiata* as a synonym of *X. pruinlus* (see below).

*Xylodon detriticus* grows on ferns and grasses, developing thin farinaceous basidiocarps. The species evidently has a more southern distribution than *X. pruinlus*. Earlier reports of *X. detriticus* from woody substrates should be treated with caution and may represent *X. pruinlus* or as yet undescribed taxa.

Figure 8. Cystidial elements and basidia of *Xylodon pruinlus* (isotype of *Hyphodontia magnacystidiata*).
Table 2. Spore measurements of five Xylodon species.

| Species / specimen | L’ (3.8) | L (3.4) | W’ (4.2) | W (4.3) | Q’ (4.8) | Q (1.1) | n |
|-------------------|----------|---------|----------|---------|----------|---------|---|
| Xylodon attenuatus | (3.7) 4.1–5.5 (6) | 4.85 | (3.3) 3.4–4.5 (4.9) | 3.98 | (0.98) 1.06–1.38 (1.46) | 1.22 | 180 |
| Holotype | (4.3) 4.4–5.7 (5.8) | 4.86 | (3.3) 3.5–4.3 (4.7) | 3.84 | (1.1) 1.2–1.4 (1.5) | 1.27 | 30 |
| Spirin 8133 | (4.4) 4.54–5.3 (5.5) | 5.01 | (3.2) 3.8–4.6 (4.7) | 4.14 | (1.06) 1.1–1.33 (1.38) | 1.21 | 30 |
| Spirin 8286 | (4.1) 4.14–5.74 (6) | 4.98 | (3.1) 3.84–4.5 (4.5) | 4.11 | (1.02) 1.09–1.34 (1.36) | 1.21 | 30 |
| Spirin 8779 | (4) 4–5.2 (5.4) | 4.67 | (3.3) 3.2–4.3 (4.4) | 3.82 | (0.98) 1.04–1.38 (1.43) | 1.23 | 30 |
| Spirin 8900a | (3.7) 3.95–5.25 (5.6) | 4.56 | (3.4) 3.4–4.35 (4.9) | 3.94 | (1.02) 1.02–1.29 (1.37) | 1.16 | 30 |
| Spirin 8964 | (4.5) 4.6–5.6 (5.7) | 5.02 | (3.5) 3.6–4.3 (4.8) | 4.04 | (1.1) 1.1–1.4 (1.4) | 1.25 | 30 |
| Xylodon crystalliger | (3.1) 4.2–5.1 (5.9) | 4.66 | (2.4) 3.3–4.2 (4.3) | 3.71 | (1.1) 1.1–1.4 (1.6) | 1.26 | 60 |
| Holotype | (3.1) 4.2–5.1 (5.9) | 4.63 | (2.4) 3.1–3.8 (3.9) | 3.5 | (1.2) 1.2–1.5 (1.6) | 1.32 | 30 |
| Bortnickov KUN 3347 | (4.2) 4.2–5.3 (5.5) | 4.69 | (3.3) 3.6–4.2 (4.3) | 3.91 | (1.1) 1.1–1.4 (1.4) | 1.2 | 30 |
| Xylodon detriticus | (3.3) 4.3–5.7 (6.1) | 4.92 | (3.1) 3.2–4.1 (4.5) | 3.69 | (0.7) 1.1–1.6 (1.8) | 1.34 | 190 |
| Lectotype | (4.2) 4.2–6 (6.1) | 5.07 | (3.1) 3.2–4 (4.1) | 3.89 | (1.2) 1.2–1.6 (1.7) | 1.42 | 39 |
| Larsson 5496 | (3.3) 4.2–5.5 (6) | 4.87 | (3.1) 3.2–4 (4.5) | 3.61 | (0.7) 1.1–1.6 (1.8) | 1.36 | 30 |
| Larsson 5622 | (4) 4.2–5.1 (5.5) | 4.6 | (3.3) 3.4–3.9 (4) | 3.63 | (1.1) 1.1–1.4 (1.5) | 1.27 | 30 |
| Larsson 5627 | (4) 4.2–5 (5.6) | 4.69 | (3.3) 3.3–4 (4.2) | 3.73 | (1.1) 1.2–1.4 (1.4) | 1.26 | 31 |
| Zibarova 26.V.2017 | (4.4) 4.7–5.8 (5.9) | 5.26 | (3.2) 3.3–4.2 (4.3) | 3.83 | (1.1) 1.2–1.6 (1.7) | 1.38 | 30 |
| Zibarova 30.X.2017 | (4.2) 4.2–5.7 (5.9) | 4.99 | (3.2) 3.3–4 (4.2) | 3.78 | (1.1) 1.1–1.5 (1.7) | 1.32 | 30 |
| Xylodon pruinosis | (4) 4.5–5.9 (7) | 5.09 | (3.3) 3.7–4.8 (5.7) | 4.12 | (0.8) 1.1–1.4 (1.5) | 1.24 | 192 |
| Holotype of Hypodontia nikolajevae | (4.6) 4.7–6 (7) | 5.26 | (3.5) 3.8–5 (5.3) | 4.32 | (1) 1.1–1.4 (1.4) | 1.22 | 31 |
| Holotype of Odontia pruinosis | (4) 4.1–5.7 (5.9) | 4.95 | (3.5) 3.6–4.5 (4.6) | 4.03 | (1.1) 1.1–1.4 (1.4) | 1.23 | 40 |
| Spirin 2877 | (4.5) 4.7–6.1 (6.3) | 5.28 | (3.5) 3.8–5 (5.2) | 4.21 | (1.1) 1.1–1.4 (1.5) | 1.26 | 30 |
| Spirin 9350 | (4.4) 4.7–5.7 (6.2) | 5.21 | (3.5) 3.8–4.8 (5.7) | 4.17 | (0.8) 1.1–1.4 (1.5) | 1.26 | 31 |
| Spirin 9581 | (4.2) 4.2–5.8 (6.1) | 4.99 | (3.3) 3.6–4.4 (4.6) | 3.98 | (1) 1.1–1.4 (1.4) | 1.25 | 30 |
| Spirin 9994 | (4.2) 4.6–5.1 (5.3) | 4.89 | (3.3) 3.6–4.5 (4.6) | 4.04 | (1.1) 1.1–1.3 (1.4) | 1.21 | 30 |
| Holotype of Hypodontia magnacystidiatia | (4.3) 4.3–5.5 (5.6) | 4.92 | (3.1) 3.1–4 (4.2) | 3.68 | (1.1) 1.1–1.6 (1.7) | 1.35 | 30 |
| Xylodon waarensis | (4.8) 5.1–6 (6.2) | 5.48 | (3.7) 3.8–4.6 (4.8) | 4.21 | (1.2) 1.2–1.4 (1.5) | 1.3 | 92 |
| Holotype | (4.9) 5.1–5.9 (6.2) | 5.48 | (3.7) 3.8–4.6 (4.8) | 4.22 | (1.2) 1.2–1.4 (1.4) | 1.32 | 32 |
| Viner KUN 2103 | (4.8) 5–6.1 (6.2) | 5.6 | (3.8) 3.8–4.7 (4.7) | 4.24 | (1.2) 1.2–1.4 (1.5) | 1.32 | 30 |
| Viner KUN 2186 | (5) 5–5.7 (5.8) | 5.37 | (3.8) 4–4.5 (4.6) | 4.18 | (1.2) 1.2–1.4 (1.5) | 1.28 | 30 |

Xylodon magnificus (Gresl. & Rajchenb.) K.H. Larss., comb. nov.
Mycobank No: MB827074

Basionym. Hypodontia magnifica Gresl. & Rajchenb., Mycologia 92: 1160. 2000.

Type. Argentina. Tierra del Fuego: Dpto. Ushuaia, Estancia Moat, on Drimys winteri, 21 Mar 1998, M. Rajchenberg 11370 (holotype: BAFC [50038], by original designation).

For a detailed description and illustration, see Greslebin and Rajchenberg (2000). The authors compared the new species with Xylodon detriticus (as Hypodontia detriticia) and Hyphochnicium rickii. Our investigation of authentic material confirms the morphological similarity amongst these three species.
Additions to the taxonomy of *Lagarobasidium* and *Xylodon*...

Table 3. Measurements of cystidial elements of *Xylodon detriticum* and *X. pruinosus*.

| Species / specimen | L' (n) | L (n) | W (n) | W (n) | n |
|--------------------|--------|-------|-------|-------|---|
| *Xylodon detriticum* (30) | 58.9–110 (115) | 85 (4) | 4.1–8.5 (9.6) | 6.3 | 120 |
| Lectotype (67) | 69.9–96.7 (110) | 83.8 (4) | 4–9.1 (9.2) | 6.5 | 20 |
| Larsson 5496 (30) | 45.2–108.2 (112) | 81.2 (4.1) | 4.3–7 (7.2) | 5.7 | 20 |
| Larsson 5622 (30) | 45–103 (110) | 82.7 (4.1) | 4.3–7.5 (8.5) | 5.7 | 20 |
| Larsson 5627 (50) | 58.7–104.6 (110) | 79.1 (4.4) | 4.8–8.9 (9.6) | 6.4 | 20 |
| Zibarova 26.V.2017 (80) | 83.8–103.3 (110) | 95.1 (4) | 5.4–8.1 (8.5) | 7.1 | 20 |
| Zibarova 30.X.2017 (67) | 73.7–112.2 (115) | 87.7 (4) | 5–7.4 (7.5) | 6.3 | 20 |
| *Xylodon pruinosus* (35) | 44–84 (107) | 61.9 (4) | 4.9–10.9 (12.4) | 7.2 | 146 |
| Holotype of *Hyphodontia nikolajevae* (41) | 43–95 (99) | 64 (4) | 5–12 (12) | 7.7 | 21 |
| Isolectotype of *Odontia pruinosa* (43) | 45.9–80.4 (107) | 64 (4.6) | 5.3–10.6 (12.4) | 7.3 | 20 |
| Spirin 2877 (35) | 42.6–80 (80) | 58.4 (4) | 4.8–7.9 (8) | 6.2 | 20 |
| Spirin 9350 (41) | 44.8–83.2 (86) | 61.8 (4.6) | 4.7–10 (10.7) | 7.2 | 20 |
| Spirin 9581 (49) | 51.8–84.1 (86) | 64.6 (4.9) | 5–9 (11) | 7.1 | 20 |
| Spirin 9994 (45) | 45.8–75.3 (81) | 58.9 (5.3) | 5.6–10.2 (10.8) | 7.8 | 20 |
| Isotype of *Hyphodontia magnacystidiata* (48) | 51–95 (104) | 75.8 (4.1) | 6–12 (14) | 8.4 | 25 |

*Xylodon nongravis* (Lloyd) C.C. Chen & Sheng H. Wu, in Chen et al. 2018: 349

Figure 9

Basionym. *Polyporus nongravis* Lloyd, Mycol. Writings 6 (61): 891. 1919.

Type. Sri Lanka. Peradeniya, on rotten branch, T.Petch (holotype BPI [305211]).

Wu (2000) re-described and illustrated this poroid species as *Hyphodontia nongravis* (Lloyd) S.H. Wu. Our specimens collected in the Russian Far East fit well with his description. One of these collections (Spirin 5763) was sequenced and proved to

Figure 9. Basidiocarp of *Xylodon nongravis* (Spirin 5763). Scale bar: 5 mm.
be close to other sequences of *H. nongravis* available in GenBank. The species undoubtedly belongs to the core *Xylodon* clade (Figure 1) where it has been combined by Chen et al. (2018). However, the type specimen of *Polyporus nongravis* possesses small but clear morphological differences from our collections: in particular, wider pores (2–3 per mm in the type, 3–4 per mm in East Asian specimens) and broader trimal hyphae (4–6 µm vs. 3–4.5 µm in diam.), as well as broader, predominantly subglobose basidiospores, 3.9–4.7×3.6–4.2 µm (n=30/1), L=4.27, W=3.97, Q=1.08 (vs ovoid-ellipsoid, 4.0–5.2×3.0–4.1 µm (n=60/2), L=4.74, W=3.46, Q=1.38 in East Asian specimens). An epitype for *P. nongravis* from the *locus classicus* is needed to reintroduce this species based on modern methods and to clarify the taxonomic status of *X. nongravis* sensu East Asia.

*Xylodon pruinosus* (Bres.) Spirin & Viner, comb. nov.
Mycobank No: MB825369
Figures 6 a,b, 8, 10, 11

**Basionym.** *Odontia pruinosa* Bres., Annales Mycologici 18 (1–3): 43. 1920. ≡ *Lagarobasidium pruinatum* (Bres.) Jülich, Persoonia 8: 84. 1974.

**Type.** Germany. Nordrhein-Westfalen, Lengerich, W.Brinkmann (lectotype L [L 0053271], designated by Jülich 1974: 84).

≡ *Hyphodontia nikolajevae* Parmasto, Conspectus Systematis Corticiacearum: 213. 1968. Type: Estonia. Ida-Virumaa, Kohtla-Järve, Pärnassaare, on *Betula pubescens*, 1 Oct 1958, E.Parmasto (holotype: TAAM [9683], by original designation).

≡ *Hyphodontia magnacystidiata* Lindsey & Gilb., Mycotaxon 5: 315. 1977. Type: USA. New York, Franklin County, Paul Smith’s, on *Populus tremuloides*, 12 Sep 1965, R.L.Gilbertson 5481 (holotype: BPI [266395], by original designation).

**Description.** Basidiocarps annual, resupinate, up to 5 cm in widest dimension. Margin poorly differentiated, pruinose. Hymenial surface greyish-white or pale cream-coloured, grandinoid to odontoid; projections rather regularly arranged, from 100 µm to 250 µm high, 80–100 µm broad at base, 6–8 per mm. Hyphal structure monomitic, hyphae clamped, faintly cyanophilous, thin-walled. Subicular hyphae interwoven and frequently branched, 2.2–4.7(–6.1) µm in diam. (n=60/6). Trimal hyphae subparallel, subhymenial hyphae short-celled, 2.0–3.5(–3.9) µm in diam. (n=60/6). Stellate crystals abundant in trama, subiculum and subhymenium, 4.4–8.3 µm in diam. Cystidia large, thin-walled, of subicular, trimal or subhymenial origin, clavate to spatuliform, often with an intercalary inflation, sometimes slightly thick-walled (wall not exceeding 1 µm thick), rarely forked, (35.0–)44.0–84.0(–107.0)×(4.0–)4.9–10.9(–12.4) µm (n=121/6), occasionally bearing 1–2 clamped septa. Basidia suburniform, 4-spored, (12.0–)14.0–20.8(–24.0)×3.4–4.2(–5.5) µm (n=60/6), thin-walled. Basidiospores clearly thick-walled, ellipsoid to broadly ellipsoid, usually with an oil-drop, (4.0–)4.5–5.9(–7.0)×(3.3–)3.7–4.8(–5.7) µm (n=192/6), L=5.09, W=4.12, Q=1.24, cyanophilous.
Additions to the taxonomy of Lagarobasidium and Xylodon...

Figure 10. Cystidial elements of Xylodon pruinosus: a Spirin 9581 b Spirin 2877 c holotype of Hyphodontia nikolajevae.

Figure 11. Basidiocarp of Xylodon pruinosus (Spirin 2877). Scale bar: 5 mm.

Distribution and ecology. Europe (Estonia, Finland, Germany, Norway, Russia – up to Ural Mts.), North America, on medium-decayed wood of angiosperms.

Remarks. The type specimen of Hyphodontia nikolajevae Parmasto reveals no essential differences from the type and other collections of X. pruinosus studied by us. On average, Xylodon pruinosus has wider basidiospores than X. detriticus (Table 2).
**Xylodon pumilius** (Gresl. & Rajchenb.) K.H. Larss., comb. nov.  
Mycobank No: MB827075

**Basionym.** *Hyphodontia pumilia* Gresl. & Rajchenb., Mycologia 92: 1162. 2000.

**Type.** Argentina. Chubut. Dpto Luquínéo, Lago Engaño, on *Nothofagus pumilio*, 19 Apr 1996, A.Greslebin 650 (holotype BAFC [50031], by original designation).

The presence of both hymenial, capitate cystidia and enclosed, tubular to moniliform cystidia with homogenous contents strongly stained by cotton blue, make this species morphologically reminiscent of *Xylodon brevisetus* and *X. tuberculatus*. *X. pumilius* differs from both by a smooth hymenium and thick-walled basidiospores.

**Xylodon rickii** (Hjortstam & Ryvarden) K.H. Larss., comb. nov.  
Mycobank No: MB827076

**Figure 1**

**Basionym.** *Hypochnicium rickii* Hjortstam & Ryvarden, Mycotaxon 15: 271. 1982.  
≡ *Odontia polycystidifera* Rick, Iheringia, Sér. Bot. 5: 163. 1959. Nom. inval. (Code Art. 40.1).

**Type.** Brazil. S. Salvador, 5 Apr 1944, Rick 20847 (holotype PACA, by original designation).

For a description, see Hjortstam and Ryvarden (1982). Gorjón (2012) could not verify the presence of large capitate cystidia, similar to those present in *X. magnifica* and included in the original description by Hjortstam and Ryvarden (1982). We restudied the isotype in herbarium O and can confirm that these large cystidia do exist, which supports a possible position of this species close to *X. detriticus* and *X. pruinosus*.

**Xylodon ussuriensis** Viner, sp. nov.  
Mycobank No: MB825356

**Figure 12**

**Type.** RUSSIA. Primorie: Khasan Dist., Kedrovaya Pad Nat. Res., on angiosperm wood, 24 Jul 2016, I.Viner KUN 1989* (H) – ITS sequence, GenBank MH324468.

**Etymology.** Ussuriensis (lat., adj.) – from the river Ussuri in Russian Far East and adjacent China.

**Description.** Basidiocarps effused, up to 10 cm in longest dimension. Sterile margin white to pale ochraceous, floccose, up to 1 mm wide. Hymenial surface pale ochraceous, grandinioid to odontoid; projections rather regularly arranged, from 100 µm to 250 µm high, 90–110 µm broad at base, 6–8(–9) per mm. Hyphal structure monomitic, hyphae clamped, faintly cyanophilous, thin-walled. Subicular hyphae interwoven, (3.0–)3.4–6.2 µm in diam. (n=30/3). Tramal hyphae subparallel, sub-
Additions to the taxonomy of *Lagarobasidium* and *Xylodon*...

Hymenial hyphae short-celled, 1.9–3.9 μm in diam. (n=30/3). Large rhomboid or stellate crystals rarely present in trama and subiculum, 10–19 μm in diam. Cystidia of three types: a) large, thin- or fairly thick-walled (wall up to 2.8 μm thick) cystidia of subicular, tramal or subhymenial origin, cylindrical, spathuliform, almost capitate or with one intercalary inflation at the upper part, (64.0–)71.0–188.9(–220.0)×(5.0–)5.7–9.4(–11.9) μm (n=30/3), often apically encrusted by large rhomboid crystals, b) astrocytidia of subhymenial origin, bearing a stellate crystalline cap 15–17×4.5–4.8 μm, sometimes rare, c) cystidia of subhymenial origin, thin-walled, varying from fusoid to cylindrical or submoniliform, rarely forked, 40.0–84.0(–92.0)×5.0–9.0(–11.4) μm (n=30/3). Basidia suburniform, 4-spored, 14.7–22.8(–24.0)×3.4–4.9 μm (n=30/3),

*Figure 12. Xylodon ussuriensis* (holotype): a section through an aculeus b basidia, basidioles and hymenial cystidia c thick- and thin-wall tramal cystidia d thick- and thin-wall subhymenial cystidia e astrocytidia f basidiospores h short-celled hyphae from aculei.
thin-walled. Basidiospores clearly thick-walled, ellipsoid to broadly ellipsoid, usually with an oil-drop, (4.8–)5.1–6.0×3.8–4.6 µm (n=92/3), L=5.48, W=4.21, Q=1.30, cyanophilous.

**Distribution and ecology.** East Asia (Russian Far East – Primorie), on decayed angiosperm wood; seemingly not rare in secondary oak-dominated forest.

**Remarks.** The distinctly thick-walled tubular cystidia of *X. ussuriensis* make it different from other *Lagarobasidium*-like species treated here. Subhymenial astrocytidia found in *X. ussuriensis* are also present in some specimens of *X. detriticus* although they are apparently rare in the latter species.

**Discussion**

Our study confirms the results from Larsson et al. (2006) and Larsson (2007) that *Peniophora detritica* clusters with *Xylodon quercinus*, the type species of *Xylodon*. Here we also show that *Peniophora pruinosa*, the type of *Lagarobasidium*, belongs in *Xylodon* and is a sister species to *X. detriticus*. This contradicts the results published by Dueñas et al. (2009) who came to the conclusion that *Lagarobasidium* was a genus separate from *Hyphodontia* sensu lato. As support for that result, they published ITS sequences of *L. detriticum* and the new species *L. calongei* (GenBank FM876211 and FM876212, respectively). However, at least the sequence of *L. detriticum* (FM876211) seems to be based on a misidentification or contamination during the laboratory process. This sequence is 100% identical to several sequences of *Hyphoderma roseocremeum*, a species belonging in Polyporales (e.g. UNITE database UDB031922).

Blasting FM876212 against public sequence databases does not return any reliable results, which, if the sequence is correct, suggests that the species does not belong in *Xylodon*. Remaining species referred to *Lagarobasidium* and not already discussed include *L. cymosum* (D.P. Rogers & H.S. Jacks.) Jülich and *L. subdetriticum* (S.S. Rattan) J. Kaur & Dhintra. The former has been placed in *Hypochnicium* because of the thick-walled basidiospores but numerous subulate cystidia makes it a deviating element in that genus. Only access to sequence information can disclose its relationships. *Lagarobasidium subdetriticum* was originally described in *Hyphodontia* and should be retained in that genus also when the genus is taken in a restricted sense (Hjortstam and Ryvarden 2009).

For the phylogenetic analyses of *Hyphodontia* sensu lato, only nuclear ribosomal genes have so far been applied. All published results confirm that *Hyphodontia* sensu lato is polyphyletic and that most species can be referred to one of three clusters, viz *Hyphodontia* sensu stricto, the *Kneiffiella* cluster and the *Xylodon* cluster (including *Lyomyces*). Within these clusters the relationships are not well resolved when the ribosomal genes are the sole source for genetic information. On such detailed level, analyses become highly sensitive to sampling and outgroup choice. It is clear that both a wider sampling and more markers must be included in analyses in order to establish a stable genus level classification for all species that have been referred to *Hyphodontia* in a wide sense.
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