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Systematic placement of Lagarobasidium cymosum and description of two new species
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Abstract:	Lagarobasidium cymosum is a rare corticioid species with characteristic morphology different from other Lagarobasidium species. We used nuc rDNA 5.8S, 28S and mit 12S rDNA loci to infer the phylogenetic position of L. cymosum. Our analyses suggest that it belongs to Xylodon but is not closely related to any of the other taxa referred to Lagarobasidium. Molecular and morphological information show that the traditional concept of L. cymosum covers at least three species: Xylodon acuminatus from the Neotropics, X. cymosus from North America, and X. subtilissimus distributed in both Europe and North America. Lagarobasidium calongei is transferred to Xylodon and DNA barcodes for Lyomyces incrustatus and Xylodon hjortstamii are published for the first time.
Keywords:	Peniophora cymosa; Xylodon; Lyomyces; Hymenochaetales; phylogeny
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1 Systematic placement of *Lagarobasidium cymosum* and description of two new

2 species

3 Running Head: The systematics of *Lagarobasidium cymosum*

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11 Declarations of interest: none

12

13 **ABSTRACT**

14 *Lagarobasidium cymosum* is a rare corticioid species with characteristic

15 morphology different from other *Lagarobasidium* species. We used nuc rDNA

16 5.8S, 28S and mit 12S rDNA loci to infer the phylogenetic position of *L.*

17 *cymosum*. Our analyses suggest that it belongs to *Xylodon* but is not closely

18 related to any of the other taxa referred to *Lagarobasidium*. Molecular and

19 morphological information show that the traditional concept of *L. cymosum*

20 covers at least three species: *Xylodon acuminatus* from the Neotropics, *X.*

21 *cymosus* from North America, and *X. subtilissimus* distributed in both Europe

22 and North America. *Lagarobasidium calongei* is transferred to *Xylodon* and

23 DNA barcodes for *Lyomyces incrustatus* and *Xylodon hjortstamii* are published

24 for the first time.

25 **KEY WORDS:** *Peniophora cymosa*; *Xylodon*; *Lyomyces*; Hymenochaetales;

26 phylogeny.

27 **INTRODUCTION**

28 Jülich (1974) coined the genus *Lagarobasidium* Jülich for three corticioid

29 species with well-differentiated, thin- to slightly thick-walled cystidia,

30 suburniform tetrasporic basidia, and thick-walled basidiospores. Initially, the

31 genus included only three species, *L. cymosum* (D.P.Rogers & H.S.Jacks.)

32 Jülich, *L. nikolajevae* (Parmasto) Jülich, and *L. pruinosum* (Bres.) Jülich (the

33 generic type). Since then, six more names have been coined in

34 *Lagarobasidium*. Later, most of these taxa, including the type species, have

35 been transferred to either *Xylodon* (Pers.) Gray or *Hyphodontia* J. Erikss. sensu

36 stricto based on molecular and morphological data (Hjortstam and Ryvarden

37 2009, Riebesehl and Langer 2017, Viner et al. 2018).

38   The systematic placement of the two remaining *Lagarobasidium* species

39 has remained controversial. *Lagarobasidium cymosum* differs in having

40 acuminate cystidia more similar to other *Hyphodontia* s.l. such as *Hastodontia*

41 (Parmasto) Hjortstam & Ryvarden than to any other *Lagarobasidium* spp.

42 However, the combination of such cystidia and other characters such as thick-

43 walled cyanophilic spores precludes assigning *L. cymosum* reliably to any

44 corticioid genus. The original description of the second species, *L. calongei* M.

45 Dueñas, Tellería, Melo & M.P. Martín, clearly shows its resemblance to the

46 *Lagarobasidium* taxa transferred to *Xylodon*. However, the nuc rDNA ITS

47 sequence of the type material (FM876212) places *L. calongei* outside *Xylodon*

48 (Dueñas et al. 2009). Therefore, this species has retained its generic name.

49   Depending on taxon sampling and the chosen method for phylogeny

50 inference, our preliminary phylogenetic analysis of nuc rDNA 28S resolved *L.*

51 *cymosum* either in *Xylodon* or in its closest relative *Lyomyces* P. Karst. In order

52 to clarify the generic placement of *L. cymosum*, we compiled a 3-loci dataset

53 (nuc rDNA 5.8S, 28S (D1–D4), and mit rDNA 12S) of *Lyomyces*, *Xylodon*,

54 and allied genera—the most comprehensive such phylogenetic dataset

55 available. We describe two relatives of *L. cymosum* as new species based on

56 molecular and morphological data. Additionally, we transfer *L. calongei* to

57 *Xylodon* based on its morphology and publish DNA barcodes for *Lyomyces*

58 *incrustatus* (Kotir. & Saaren.) Hjortstam & Ryvarden and *X. hjortstamii* (Gresl.

59 & Rajchenb.) Riebesehl & Langer for the first time.

MATERIALS AND METHODS

61 *Morphological methods.*—Type specimens and collections from herbaria GB,

62 H, ISC, MA, and O were studied. Herbarium acronyms are given according to

63 Thiers (2022). Microscopic methods were described in Miettinen et al. (2006).

64 All measurements were made in Cotton Blue (CB, Merck 1275; Kenilworth,

65 New Jersey) with phase contrast illumination (1250×), which benefits over

66 bright-field microscopy are explained in Stein (1969). The following

67 abbreviations were used in microscopic descriptions: L—mean spore length;

68 W—mean spore width; Q—mean L/W ratio; n—number of elements

69 (basidiospores, basidia, cystidia, and hyphae) measured, which are followed by

70 the number of specimens studied. We excluded 5% of measurements from each

71 end of the range representing variation of basidiospores and cystidia. Excluded

72 extreme values were indicated in parentheses when they strongly differed from

73 the lower or higher 95% percentile.

74 *DNA extraction and sequencing.*—Total genomic DNA was extracted from

75 herbarium specimens using a CTAB-chloroform extraction protocol (Kutuzova

76 et al. 2017). We used standard as well as genus-specific primers to amplify

77 complete nuc rDNA ITS1-5.8S-ITS2 (ITS), nuc 28S rDNA (28S), and mit 12S

78 rDNA (12S) for the focal taxa (TABLE 1). After amplification, PCR products

79 were run on a 1.5 % agarose gel stained with GelRed staining (Biotium,

80 Fremont, California) and visualized under UV light. PCR products were

81 purified from agarose gels using a Fermentas Genomic DNA Purification Kit

82 (Thermo Fisher Scientific, Waltham, Massachusetts). Sequencing reactions

83 were performed on an ABI 3730XL DNA analyzer (Applied Biosystems) by

84 Macrogen (Amsterdam, the Netherlands). A number of additional sequences

85 used in the analyses were retrieved from partial genomes as described in Viner

86 et al. (2021). All newly produced sequences used in this study have been

87 deposited in GenBank (TABLE 2).

88 ***Phylogenetic analyses.***—In addition to our newly produced data, we retrieved

89 all relevant sequences from GenBank (Benson et al. 2018), UNITE (Kõljalg et

90 al. 2013), and the Fungal Genomics Resource (https://mycocosm.jgi.doe.gov)

91 as of 16 February 2022.

92   High variability of ITS sequences in the focal genera does not allow

93 construction of a reliable all-encompassing alignment for *Lyomyces* and

94 *Xylodon* without blunt violation of phylogenetic homology principles. In an

95 effort to meet these principles, we confined to sequences that could be reliably

96 aligned. The resulted alignment contains only the *L. cymosum* complex—this

97 corresponds to 87% threshold of pairwise similarity between sequences—and

98 *X. borealis* (Kotir. & Saaren.) Hjortstam & Ryvarden as an outgroup. The latter

99 was selected based on the highest pairwise similarity (83%) to the *L. cymosum*

100 complex.

101   We constructed two additional datasets to find the proper generic (5.8S,

102 28S and 12S) and intrageneric (28S) placement for the *L. cymosum* complex.

103 The 28S dataset contains all major *Xylodon* clades and sequences of *Lyomyces*

104   and *Fasciodontia* Yurchenko & Riebesehl—the three genera are closely related

105   according to the multigene analyses in Wang et al. 2021. *Hastodontia* was

106   selected as an outgroup. The more conservative 28S locus allows for

107   assembling a reliable alignment across all these genera without discarding of

108   extensive poorly aligned fragments from further analyses. To compensate for

109   the weaker phylogenetic signal compared to ITS, we utilized a relatively large

110   fragment of 28S: domains D1–D4.

111   We chose a mitochondrial locus (12S) to supplement two nuclear ones

112   (5.8S+28S) for our concatenated dataset. 12S has already proven useful for

113   phylogenetic analyses of corticioid Hymenochaetales in Wang et al. (2021) and

114   Kolařík and Vohník (2017). Besides that, as a multicopy DNA locus, 12S

115   significantly increases the chances of successful PCR reaction. This was

116   especially relevant with extremely thin basidiocarps of the *L. cymosum*

117   complex. We have conducted independent analyses of the mitochondrial and

118   nuclear loci to corroborate the complimentary of the datasets. The resulted

119   topologies (not shown here) were similar and had no mutually exclusive

120   supported clades. The apparent difference was in lower clade support due to

121   the weaker phylogenetic signal of loci analyzed separately.

122   Alignments were calculated through the MAFFT 7.429 online server

123   (https://mafft.cbrc.jp/alignment/server/) using the L-INS-I strategy (Katoh et al.

124   2017). After removing unalignable fragments, the length of the alignment and

125   the number of parsimony informative characters were correspondingly 1292

126 and 276 bp for the 28S alignment; 2144 and 359 bp for the 5.8S+28S+12S

127 concatenated alignment; 361 and 43 bp for the ITS alignment.

128   We inferred rooted phylogenetic trees with maximum likelihood (ML)

129 and Bayesian Inference (BI). Nucleotide substitution models for BI were

130 chosen with TOPALI 2.5 (Milne et al. 2008) based on the Bayesian

131 information criterion (BIC). We performed BI using MrBayes 3.2 (Ronquist et

132 al. 2012). In these analyses three parallel runs with four chains each and other

133 default parameters were run for one million generations. A burn-in of 25% was

134 used in the final analyses, ensuring the average standard deviation of split

135 frequencies had reached <0.01 for all data sets. When depicting phylograms,

136 the support for nodes is indicated when posterior probabilities are ≥0.90. For

137 ML analyses, IQ-TREE 1.2.2 (Nguyen et al. 2015) with the best-fitted model

138 option was used. Bootstrapping was performed using the standard

139 nonparametric bootstrap algorithm with the number of replicates set to 1000.

140 Support for nodes is indicated with bootstrap values ≥80.

141 **RESULTS**

142 BI and ML resulted in similar topologies for each analysis and relevant support

143 values were indicated at nodes in Figs. 1–3. Both 5.8S+28S+12S and 28S

144 analyses returned trees with a highly supported *Xylodon*/*Lyomyces* clade, to

145 which the *Lagarobasidium cymosum* complex belonged (Fig. 1, 2). The

146 analyses did not resolve basal relationships within the *Xylodon*/*Lyomyces*

147 cluster with high support. The *L. cymosum* species complex, represented by the

148 newly described *X. acuminatus* and *X. subtilissimus*, clustered at the deepest

149 split of *Xylodon*. Former *Lagarobasidium* taxa were not resolved as a

150 monophyletic clade: *X. detriticus* (Bourdot) K.H. Larss., Viner & Spirin and *X.*

151 *pruinosus* (Bres.) Spirin & Viner (the type of *Lagarobasidium*) ended up in a

152 clade distant from the *L. cymosum* complex in both 5.8S+28S+12S and 28S

153 phylogenies (Fig. 1, 2). Our ITS analyses suggested at least three species in the

154 *L. cymosum* complex with *X. acuminatus* likely representing a species complex

155 itself (Fig. 3). *Lyomyces incrustatus* and *X. hjortstamii* clustered together with

156 other *Lyomyces* and *Xylodon* species correspondingly (Fig. 1, 2).

157   There were a number of 28S sequences with questionable species

158 assignment. The 28S sequence of Zhao 17855 (MW713737), the paratype of

159 the recently described *L. fumosus* C.L. Zhao, clustered together with *L.*

160 *incrustatus* in a clade, which was distant from the holotype of *L. fumosus*, Zhao

161 8188. The two sequences of *L. fumosus* had only a 93.5 % similarity, or 90 bp

162 difference. ITS of the corresponding specimens (MW713744 and MW713745)

163 were also clearly different, with a 94.2 % of pairwise similarity, or 37 bp

164 difference. Sequences of *L. fumosus* in the original alignment in TreeBASE (ID

165 27305) do not match any of the *L. fumosus* sequences deposited to GeneBank.

166 Similarly with *X. laceratus* C.L. Zhao, 28S (OL619266) of its holotype, Zhao

167 9892, clustered together with *X. tropicus* C.L. Zhao and was different from

168 another *X. laceratus* Zhao 9841 (OL619265), which was cited in the

169 protologue. The two sequences had only a 94.9 % similarity, or 70 bp

170 difference. That was, however, not the case with ITS of the same *X. laceratus*

171 specimens (OL619257 and OL619258): they both seem to belong to one

172 species. We, however, could not check the original alignment as it is not

173 searchable in TreeBase. Finally, the 28S sequence of the holotype of *X.*

174 *gossypinus* C.L. Zhao & K.Y. Luo, Zhao 8375 (MZ663813), is similar to its

175 paratype, Zhao 4465 (MZ663812), with the proviso that MZ663813 is missing

176 a 72 bp stretch of nucleotides in the middle of the sequence, so we discarded it

177 from the analyses.

178   Morphological differences between species in *Xylodon* and *Lyomyces*

179 complex are often small, but we have found reliable characters to distinguish at

180 least three species, which were previously covered by the traditional concept of

181 *Lagarobasidium cymosum*. We introduce two new species in the complex

182 supported by the results of our molecular and morphological analyses.

183 **TAXONOMY**

184 ***Xylodon acuminatus*** Viner & K.H. Larsson, sp. nov. FIG. 4

185 MycoBank MB 843702

186 *Typification*: BRAZIL. PERNAMBUCO: Jaqueira, Frei Caneca Reserve, Mata

187 do Cerrado Quenqo, an isolated fragment of Atlantic rain forest (Mata

188 Atlântica), on angiosperm bark, N -8.71590 E -35.84018 ±400 m, 21 Apr 2013,

189 *K.H. Larsson 16029* (holotype GB, isotype URM). GenBank: ITS+28S =

190 ON197552.

191 *Etymology*: *acuminatus* (Latin), acuminate, in reference to the acute cystidia.

192 *Description*: Basidiocarps effused, pruinose, arid, 0.1–0.2 mm thick,

193 prominent, up to 10 cm in widest dimension, no distinct margin. The color of

194 different basidiocarps varies from grayish to ochraceous. Hyphal structure

195 monomitic, hyphae clamped, thin- to slightly thick-walled, subparallel;

196 subicular (1.5) 1.8–3.6 (4) μm diam (n = 60/6), subhymenial 1.7–3.2 (3.5) μm

197 diam (n = 60/6). Cystidia frequent, projecting, hyaline, acuminate, thick-walled

198 along the proximal half, thinning to thin-walled closer to the apex (29) 34.2–

199 62.9 (87) × (2.3) 3.3–6.0 (6.5) μm (n = 124/6). Rarely, cystidia have one or two

200 adventitious internal septa without a clamp. The tips of cystidia are sometimes

201 pin-shaped and often bend in mounted slides. Basidia four-sterigmate, ovoid to

202 broadly suburniform, sometimes slightly thick-walled at the base 6.5–12 × 3.3–

203 5.9 μm (n = 60/6). Basidiospores smooth, thick-walled, ellipsoid to subglobose,

204 3.8–5.2 × 3–4.3 (5) μm (n = 181/6), L = 4.59, W = 3.79, Q = 1.22, apiculus

205 prominent.

206 *Ecology and distribution*: *Xylodon acuminatus* as treated here is a Neotropical

207 species. It can grow on decayed wood as well as on bark of living trees and on

208 dead polypores.

209 *Other specimens examined*: BRAZIL. RIO GRANDE DO SUL: São Salvador,

210 on angiosperm wood, 1939, *J. Rick 16874* (PACA FR 16874, O F-506069);

211 SÃO PAULO: Santos, Cananéia, the Ilha do Cardoso State Park, on

212 angiosperm wood, 2 Feb 1987, *L. Ryvarden 24882* (GB). COSTA RICA.

213 GUANACASTE PROVINCE: Tenorio Volcano National Park, Rancho Capu,

214 on a dead polypore from an angiosperm tree, 16 Jul 2001, *K.H. Larsson 11524*

215 (GB); PUNTARENAS PROVINCE: Monte Verde, Santa Elena Cloud Forest

216 Reserve, Youth Challenge trail, on bark of a living angiosperm tree, 13 Jul

217 2001, *K.H. Larsson 11294* (GB). ECUADOR. ORELLANA PROVINCE:

218 Yasuni National Park, on angiosperm bark, 1 Oct 2008, *L. Tedersoo 2008-10-*

219 *01* (TU110044). VENEZUELA. AMAZONAS STATE: Sanmaria, close to

220 Puerto Ayacucho, on angiosperm wood, 21 Apr 1999, *H. R. Urbina 216* (GB).

221 *Notes*: We have only two sequenced specimens of *X. acuminatus* at our

222 disposal while the third sequence included in the analysis (GU054154) came

223 from an environmental study. Considering genetic differences, the *X.*

224 *acuminatus* clade, as shown in Fig. 3, might be a species complex although we

225 found no morphological differences to support this. More comprehensive

226 sampling (both in terms of number of DNA loci and sequenced specimens) and

227 ideally mating tests will be required to resolve this problem.

228   Morphologically, *X. acuminatus* is distinguished from both *X. cymosum*

229 and *X. subtilissimus* by smaller basidia and spores. The basidiocarps are

230 prominent in dried condition, which is not the case for *X. subtilissimus* with

231 thin and inconspicuous basidiocarps. Cystidia in *X. acuminatus* differ from *X.*

232 *cymosus* by having a more delicate, thin-walled distal part, which often appears

233 bent in microscope preparations.

234   Before this study, the Brazilian taxon *Peniophora grisea* Rick ex Rick

235 (in Rambo (Ed.) Iheringia Sér. Bot. 4: 110. 1959) had been considered a

236 younger synonym of *Lagarobasidium cymosum* (Baltazar et al. 2016). We,

237 however, do not find this name referable to the *L. cymosum* complex and *X.*

238 *acuminatus* in particular. For a detailed discussion, see the taxonomy section of

239 *P. grisea*.

240 ***Xylodon calongei*** (M. Dueñas, Telleria, Melo & M.P. Martín) Viner, comb.

241 nov.

242 MycoBank MB 843704

243 Basionym: *Lagarobasidium calongei* M. Dueñas, Telleria, Melo & M.P.

244 Martín, Anales del Jardín Botánico de Madrid 66(S1): 42, 2009

245 Typus: PORTUGAL. AZORES: Pico, S. Roque, Meia Encosta de Sta. Luzia,

246 Travessa de Cima, on decayed wood, 26 Feb 2005, *M.T. Telleria 16187Tell*

247 (MA-Fungi 73256—holotype).

248 *Notes*: Dueñas et al. (2009) published ITS sequences of *Lagarobasidium*

249 *detriticum* (Bourdot) Jülich and a new similarly looking species from the

250 Azores, *L. calongei* (FM876211 and FM876212, respectively). They came to

251 the conclusion that *Lagarobasidium* was a good genus, which resolved as a

252 clade separate from any *Hyphodontia* sensu lato. Later Viner et al. (2018) and

253 Riebesehl et al. (2019) indicated an issue with data quality in Dueñas et al.

254 (2009). Their sequence of *L. detriticum* (FM876211) is based on a

255 misidentification or contamination during the laboratory process: it is fully

256 identical to several sequences of *Hyphoderma roseocremeum* (Bres.) Donk, a

257 species pertaining to Polyporales (e.g. UNITE database UDB031922). Blasting

258 FM876212 (allegedly *L. calongei*) against public databases does not return any

259 close hits. That sequence can hardly be attributed to any *Hyphodontia* neither

260 to Hymenochaetales.

261 Introducing *L. calongei* as a new species, Dueñas et al. (2009) indicated

262 characteristic thick-walled cystidia as a sole qualitative feature distinguishing it

263 from all other *Lagarabasidium*. Later Viner et al. (2018) have described a

264 similar species from Asia, *X. ussuriensis* Viner. We have studied the holotypes

265 of both species and find the same types of cystidia in both with the only

266 reliable micromorphological feature distinguishing the two species being larger

267 spores in *L. calongei.* The phylogenetic analyses in Viner et al. (2018) have

268 resolved *X. ussuriensis* as a member of *Xylodon* in the same highly supported

269 clade with two other former *Lagarobasdium* species: *X. pruinosus* (the generic

270 type of *Lagarabasidum*) and *X. detriticus*.

271   Considering all the above, we find it highly unlikely that FM876212

272 refers to the type of *L. calongei*. In an effort to corroborate our conclusion, we

273 endeavored to produce ITS for the type of *L. calongei* but failed to generate

274 even a fragment of ITS. Apparently, a freshly collected specimen from the

275 Azores would allow producing a DNA barcode for this species but it might not

276 be collected in the near future. Although we failed to support our conclusion

277 with molecular data, we feel that leaving *L. calongei* in a confusing status as

278 the last remaining *Lagarobasidium* species would be disadvantageous.

279 Therefore, we propose here the new combination *X. calongei*.

280 ***Xylodon cymosus*** (D.P. Rogers & H.S. Jacks.) Viner & Miettinen, comb. nov.

281 FIG. 5

282 MycoBank MB 843705

283 Basionym: *Peniophora cymosa* D.P. Rogers & H.S. Jacks., Canadian Journal

284 of Research 26(2): 133, 1948.

285 = *Lagarobasidium cymosum* (D.P. Rogers & H.S. Jacks.) Jülich, Persoonia

286 8(1): 84. 1974.

287 = *Hypochnicium cymosum* (D.P. Rogers & H.S. Jacks.) K.H. Larss. &

288 Hjortstam, Mycotaxon 5(2): 477. 1977.

289 Typus: USA. NORTH CAROLINA: Highlands, on coniferous wood, 17 Aug

290 1933, *G. V. Martin* 1321 (ISC-v-0046857—holotype).

291 *Description*: Basidiocarps effused, pruinose, arid, 0.1–0.2 mm thick,

292 prominent, up to 3 cm in widest dimension, no distinct margin. The color of

293 different basidiocarps varies from cream to ochraceous. Hyphal structure

294 monomitic, hyphae clamped; subicular hyphae slightly thick-walled,

295 subparallel, (2) 2.5–4.1 μm diam (n = 40/4), subhymenial hyphae slightly

296 thick-walled, subparallel, 1.8–3.5 μm diam (n = 40/4). Cystidia frequent,

297 projecting, hyaline, acuminate, thick-walled along the whole length including

298 tip (29)33–62 (72) × (3) 3.4–5 (5.5) μm (n = 80/4); often with one (rarely two)

299 adventitious internal septa without a clamp. The tips of cystidia are sometimes

300 pin-shaped. Basidia four-sterigmate, broadly suburniform, distinctly thick-

301 walled at the base (7) 9–17 × (3.5) 4–6 μm (n = 40/4). Basidiospores smooth,

302 thick-walled, ellipsoid to subglobose, 4.1–5.3 (6) × 3.2–4.7 (5.7) μm (n =

303 120/4), L = 4.87, W = 4.07, Q = 1.20, apiculus prominent.

304 *Ecology and distribution*: *Xylodon cymosus* is a rare conifer dwelling species,

305 so far known from the temperate and boreal zones of eastern North America.

306 *Specimens examined*: CANADA. ONTARIO: Bear Island, Lake Timagami, on

307 partly decayed coniferous wood, 19 Aug 1936, *R. Biggs 10785* (GB-0103557);

308 *10837* (GB-0103556). USA. NORTH CAROLINA: Highlands, on coniferous

309 wood, 17 Aug 1933, *G. V. Martin* 1321 (holotype of *Peniophora cymosa*, ISC-

310 v-0046857); Swain Co. Great Smoky Mountains National Park, Clingmans

311 Dome, on a natural stump of *Abies fraseri*, 1 Oct 2015, *O. Miettinen 19606*

312 (H7200259).

313 *Notes*: *Xylodon cymosus* can be distinguished from other similar-looking taxa

314 treated here by more pronounced thickening of the cell walls in cystidia: even

315 the acute tips are clearly thick-walled. Besides they develop adventitious septa

316 more often than cystidia in *X. acuminatus* and *X. subtilissimus*. These two

317 features are important in identifying North American *cymosus*-looking

318 specimens since *X. cymosus* might share the same habitat with its relative *X.*

319 *subtilissimus* (see below). According to our phylogenetic analyses (Fig. 3), the

320 closest relative of *X. cymosus* is neotropical *X. acuminatus*. In addition to

321 stable morphological differences across all studied specimens, non-overlapping

322 geographical distribution prevents confusing between these two species.

323 ***Xylodon subtilissimus*** Viner & Spirin, sp. nov. FIG. 6

324 MycoBank MB 843703

325 *Typification*: RUSSIA. LENINGRAD REGION: Tikhvin District, Korbenichi,

326 old-growth (ca. 140 years old) spruce forest with ferns, on a very rotten log of

327 *Picea abies*, N 60.143216 E 34.486059, 22 Aug 2018, *V. Spirin 12228*

328 (holotype H7074041). GenBank: ITS+28S = ON188818.

329 *Etymology*: *subtilissimus* (Latin), the most subtle, in reference to the most

330 inconspicuous basidiocarp among all *Xylodon* species we are aware of.

331 *Description*: Basidiocarps effused, pruinose, arid, 0.1 mm thick, prominent, up

332 to 10 cm in widest dimension, no distinct margin. The color of different

333 basidiocarps varies from cream to grayish. Hyphal structure monomitic,

334 hyphae clamped; subicular hyphae slightly thick-walled, subparallel, 1.9–4.2

335 μm diam (n = 90/9), subhymenial hyphae thin- to slightly thick-walled,

336 subparallel, 1.8–4 μm diam (n = 90/9). Cystidia frequent, projecting, hyaline,

337 acuminate, thick-walled along the proximal half, thinning to thin-walled closer

338 to the apex (22) 34–62 (87) × (2.3) 3–5.5 (7) μm (n = 180/9); rarely with one

339 adventitious septum. The tips of cystidia are sometimes pin-shaped. Basidia

340 broadly suburniform, slightly thick-walled at the base 10–18.5 (23) × 3.8–6.2

341 μm (n = 92/9). Most basidia have four sterigmata, however, rare one-sterigmate

342 basidia also present in some specimens; in this case, the single sterigma is quite

343 long, up to 11 μm. Basidiospores smooth, thick-walled, ellipsoid to subglobose,

344 (4.1) 4.6–6 (6.9) × (3) 3.8–5.1 (5.4) μm (n = 272/9), L = 5.19, W = 4.35, Q =

345 1.20, apiculus prominent.

346 *Ecology and distribution*: *Xylodon subtilissimus* is a rare species occurring on

347 well-decayed conifer wood. All studied specimens came from boreal and

348 temperate Europe but one environmental sequence (EU689272) derives from

349 soil sampled in Quebec, Canada.

350 *Other specimens examined*: GERMANY. BAVARIA: Bayerisch Eisenstein,

351 Großer Arbersee und Arberseewand Nature Reserve, inside a rotten trunk of

352 *Picea*, 4 Sep 1990, *H. Grosse-Brauckmann 4731* (GB-0103552). NORWAY.

353 NORD-TRØNDELAG: Stjørdal, 12 km south of Stjørdal near Nyvollskjølen

354 on the south side of the river Nævra, 15 Sep 1983, *T. Hallingbäck 1983.09.15*

355 (GB-0103550); SØR-TRØNDELAG: Orkdal municipality, Songli, Bjørndalen,

356 on *Pinus* wood, 27 Aug 1982, *K. Hjortstam 12847* (GB-0103551). POLAND.

357 LESSER POLAND PROVINCE: Zakopane, Tatry National Park, on a stem

358 and stump of *Picea*, 17 Sep 1973, *K.-H. Larsson & N. Hallenberg 2924* (GB-

359 0103553); *2928* (GB-0103554); *2932* (GB-0103555). SWEDEN.

360 VÄSTERGÖTLAND: Jonstorpsmossen Nature Reserve, Hunneberg, inside a

361 strongly decayed stump of *Picea abies*, 7 Oct 1997, *B. Lindahl 1997-10-07*

362 (GB-0103546).

363 *Notes*: *Xylodon subtilissimus* has the most insignificant basidiocarps among all

364 known *Xylodon* species so that it nearly disappears after drying. We selected

365 Spirin 12228 as the holotype since it is the only specimen we managed to

366 sequence, while Hjortstam 12847 has the most prominent basidiocarp among

367 all *X. subtilissimus* cited here.

368 **Peniophora grisea** Rick ex Rick (in Rambo (Ed.) Iheringia Sér. Bot. 4: 110.

369 1959) MycoBank MB 335786

370 *Typification*: BRAZIL. RIO GRANDE DO SUL: São Leopoldo, 1931, J. Rick

371 16780 (lectotype PACA, FR 16780) (selected here, MBT 10006687).

372 *Notes*: Rick described *Kneiffia grisea* Rick from Brazil without citing any

373 specimens (Rick 1934). *K. grisea* Rick turned out to be illegitimate as a later

374 homonym of *Kneiffia grisea* Berk. & M.A. Curtis. A new name, *Peniophora*

375 *grisea* Rick ex Rick (in Rambo (Ed.) Iheringia Sér. Bot. 4: 110. 1959), was

376 published posthumously with a reference to *K. grisea* Rick. Thus, Rick's

377 species has been mechanically validated.

378   Three specimens from Rick's herbarium were cited in the description of

379 *P. grisea*: FR 16780, FR16847, and FR16874. Baltazar et al. (2016) have

380 reported that FR 16780 is sterile and unidentifiable and FR16847 belongs to

381 *Subulicystidium perlongisporum* Boidin & Gilles. FR16874 was identified as a

382 member of the *L. cymosum* complex in both Baltazar et al. (2016) and

383 Hjortstam and Ryvarden (1982). We agree with this identification and, more

384 precisely, we find FR16874 pertaining to the newly proposed *X. acuminatus*.

385   In an attempt to typify *K. grisea*, Baltazar et al. (2016) accepted FR

386 16780—the only extant specimen with a date concordant with the publication

387 of this taxon—as its holotype. At the same time, they selected FR 16874

388 (identified as *L. cymosum*) as its epitype; this selection made *P. grisea* a

389 younger synonym of *L. cymosum.* In our opinion, this typification is not

390 correct. If no specimens were mentioned in the protologue, which is the case

391 for *K. grisea*, it is not definite that there were no elements additional to the

392 original material than extant FR 16780. We refer to the code (Ex. 2 Note 1 Art.

393 9.1), which exemplifies such a case. Therefore, FR 16780 is not the holotype.

394 If made before 1 January 2001, such typification would have been considered a

395 correctable error: FR 16780 would have become the lectotype automatically.

396 However, after that date, the code plainly requires the use of the word

397 "lectotypus" or its equivalent term for lectotypification (Art. 9.21). It means

398 that Baltazar et al. (2016) were not able to cite any types referable to *K. grisea*,

399 which is a requirement for an effective epitypification (Art. 9.7). Therefore, *K.*

400 *grisea* has remained formally untypified to date.

401   In accordance with the simplest way to avoid the use of a problematic

402 name, we select FR 16780 as the lectotype of *P. grisea* but refrain from

403 formalizing the epitypification of Baltazar et al. (2016). Considering that the

404 identity of *P. grisea* is unclear even after the lectotypfication and that the

405 protologue does not agree with the *L. cymosum* complex, we do not find that

406 name applicable to Neotropical relatives of *L. cymosum*.

407 **DISCUSSION**

408 The relative scarcity of easily recognizable morphological traits in fungi led to

409 highly permissive generic descriptions based on arbitrarily selected sets of

410 characters in the pivotal 18th and 19th century taxonomical works. With the

411 advent of modern microscopy and molecular techniques, many old large genera

412 subsequently turned out to be a plethora of unrelated phylogenetic clades.

413 Inconveniently, molecular data still create alternative scenarios of how to

414 delimit genera, as morphology doesn't clearly favor one solution.

415 Morphological traits may evolve rapidly: closely related species can develop

416 different basidiocarp types, etc. Vellinga et. al. (2015) addressed most of the

417 phylogenetic pitfalls of establishing new fungal genera by stressing the

418 monophyly requirement for introduced genera as well as for the group from

419 which it is separated and the group to which it is added. They also encourage

420 taxonomists to consider different possible options of delimiting genera to better

421 integrate all available supporting information and to avoid creating a

422 taxonomic turmoil just for the sake of establishing more genera.

423   In this study, we showed that the *X. cymosus* complex is resolved at the

424 deepest split of the *Xylodon* clade. This phylogenetic position, reinforced by a

425 unique set of micromorphological characters, could have been used as the basis

426 for erecting a new genus without taxonomic consequences for *Xylodon*.

427 However, we deem this option to be unfavorable for the following reasons. The

428 backbone of the *Xylodon* phylogeny, including the placement of the *X. cymosus*

429 complex, is not well supported (Fig. 1). Adding more DNA loci and taxa to the

430 analyses might resolve it in some other place inside of the *Xylodon* clade. If it

431 happens with the *X. cymosus* clade defined as a genus of its own, *Xylodon*

432 would become paraphyletic. In order to restore its monophyly, one of the two

433 consequences will occur: the added "*cymosus*" genus will be synonymized with

434 the older *Xylodon* or vice versa all newly emerged monophyletic *Xylodon*

435 clades (aside from the clade with the generic type *X. quercinus* (Pers.) Gray)

436 will be raised to the genus level. To avoid such taxonomic turbulence, we

437 choose to add this group to *Xylodon* and thus further expand its generic

438 concept.

439   The discussion on the generic placement of the *X. cymosus* complex

440 touches on a bigger issue regarding the generic concept of *Xylodon*. In our

441 opinion, its two closest relatives, genera *Lyomyces* and *Fasciodontia* as

442 currently circumscribed, can hardly be morphologically delineated from

443 species-rich and morphologically versatile *Xylodon* (which has nomenclatural

444 priority). As a result, the recognition of *Lyomyces* and *Fasciodontia* as separate

445 genera is based solely on their monophyly in phylogenetic analyses. The

446 *Lyomyces* situation is even more precarious as the recent attempt to show its

447 monophyly (Wang et al. 2021) has apparent methodological flaws discussed by

448 Viner et al. (2021).

ACKNOWLEDGEMENTS

LITERATURE CITED

462 Baltazar JM, Da Silveira RM, Rajchenberg M. 2016. Type studies of J. Rick's

463 corticioid homobasidiomycetes (Agaricomycetes, Basidiomycota) housed in

464 the Herbarium Anchieta (PACA). Phytotaxa 255(2):101–132.

465 Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Ostell J, Pruitt KD,

466 Sayers EW. 2018. GenBank. Nucleic Acids Research 46(D1):D41–D47.

467 Dueñas M, Telleria MT, Melo I, Martín MP. 2009. *Lagarobasidium calongei*

468 (Aphyllophorales, Basidiomycota), a new species of corticioid fungi from

469 Azores Islands. Anales del Jardín Botánico de Madrid 66(S1):41–46.

470 Hjortstam K, Ryvarden L. 1982. Studies in tropical Corticiaceae

471 (Basidiomycetes) IV. Type studies of taxa described by J. Rick. Mycotaxon

472 15:261–276.

473 Hjortstam K, Ryvarden L. 2009. A checklist of names in *Hyphodontia* sensu

474 stricto—sensu lato and *Schizopora* with new combinations in *Lagarobasidium*,

475 *Lyomyces*, *Kneiffiella*, *Schizopora*, and *Xylodon*. Synopsis Fungorum 26:33–

476 55.

477 Hopple JS, Vilgalys R. 1994. Phylogenetic relationships among coprinoid taxa

478 and allies based on data from restriction site mapping of nuclear rDNA.

479 Mycologia 86:96–107.

480 Katoh K, Rozewicki J, Yamada KD. 2017. MAFFT online service: multiple

481 sequence alignment, interactive sequence choice and visualization. Briefings in

482 Bioinformatics 20:1160–1166.

483 Kolařík M, Vohník M. 2018. When the ribosomal DNA does not tell the truth:

484 the case of the taxonomic position of *Kurtia argillacea*, an ericoid mycorrhizal

485 fungus residing among Hymenochaetales. Fungal biology 122(1):1–18.

486 Kutuzova IA, Kokaeva LY, Pobendinskaya MA, Krutyakov YuA, Skolotneva

487 ES, Chudinova EM, Elansky SN. 2017. Resistance of *Helminthosporium solani*

488 strains to selected fungicides applied for tuber treatment. Journal of Plant

489 Pathology 99:635–642.

490 Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AF, Bahram M,

491 Bates ST, Bruns TD, Bengtsson-Palme J, Callaghan TM, Douglas B, Drenkhan

492 T, Eberhardt U, Dueñas M, Grebenc T, Griffith GW, Hartmann M, Kirk PM,

493 Kohout P, Larsson E, Lindahl BD, Lücking R, Martín MP, Matheny PB,

494 Nguyen NH, Niskanen T, Oja J, Peay KG, Peintner U, Peterson M, Põldmaa K,

495 Saag L, Saar I, Schüßler A, Scott JA, Senés C, Smith ME, Suija A, Taylor DL,

496 Telleria MT, Weiss M, Larsson K-H. 2013. Towards a unified paradigm for

497 sequence-based identification of fungi. Molecular Ecology 22:5271–5277.

498 Landvik S. 1996. *Neolecta*, a fruit-body producing genus of the basal

499 ascomycetes, as shown by SSU and LSU rDNA sequences. Mycological

500 Research 100:199–202.

501 Martin KJ, Rygiewicz PT. 2005. Fungal-specific PCR primers developed for

502 analysis of the ITS region of environmental DNA extracts. BMC Microbiology

503 5:1–11.

504 Miettinen O, Niemelä T, Spirin W. 2006. Northern *Antrodiella* species: the

505 identity of *A. semisupina*, and type studies of related taxa. Mycotaxon 96:211–

506 240.

507 Milne I, Lindner D, Bayer M, Husmeier D, McGuire G, Marshall DF, Wright

508 F. 2008. TOPALi v2: a rich graphical interface for evolutionary analyses of

509 multiple alignments on HPC clusters and multi-core desktops. Bioinformatics

510 25:126–127.

511 Nguyen L-T, Schmidt HA, Von Haeseler A, Minh BQ. 2015. IQ-TREE: a fast

512 and effective stochastic algorithm for estimating maximum-likelihood

513 phylogenies. Molecular Biology and Evolution 32:268–274.

514 Rick JE. 1934. Monographia Thelephoracearum resupinatarum

515 Riograndensium. Brotéria Série Trimestral: Ciências Naturais 3(2):66–80.

516 Rick JE. 1959. Basidiomycetes Eubasidii in Rio Grande do Sul-Brasilia 2.

517 Thelephoraceae. Iheringia, Botânica 4:61–124.

518 Riebesehl J, Langer E. 2017. *Hyphodontia* s.l. (Hymenochaetales,

519 Basidiomycota): 35 new combinations and new keys to all 120 current species.

520 Mycological Progress 16:637–666.

521 Riebesehl J, Yurchenko E, Nakasone KK, Langer E. 2019. Phylogenetic and

522 morphological studies in *Xylodon* (Hymenochaetales, Basidiomycota) with the

523 addition of four new species. MycoKeys 47:97–137.

524 Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S,

525 Larget B, Liu L, Suchard M, Huelsenbeck JP. 2012. MrBayes 3.2: efficient

526 Bayesian phylogenetic inference and model choice across a large model space.

527 Systematic Biology 61:539–542.

528 Stein F. 1969. Particle size measurements with phase contrast microscopy.

529 Powder Technology 2:327–334.

530 Thiers B [continuously updated]. Index Herbariorum: a global directory of

531 public herbaria and associated staff New York Botanical Garden's Virtual

532 Herbarium. [cited 2022 Feb 04]. Available from: http://sweetgumnybgorg/

533 science/ih/

534 Vellinga EC, Kuyper TW, Ammirati J, Desjardin DE, Halling RE, Justo A,

535 Læssøe T, Lebel T, Lodge DJ, Matheny PB, Methven AS, Moreau P-A,

536 Mueller GM, Noordeloos ME, Nuytinck J, Ovrebo CL, Verbeken, A. 2015. Six

537 simple guidelines for introducing new genera of fungi. IMA Fungus, 6(2):65–

538 68.

539 Viner I, Bortnikov F, Ryvarden L, Miettinen O. 2021. On six African species

540 of *Lyomyces* and *Xylodon*. Fungal Systematics and Evolution 8:163–178.

541 Viner I, Spirin V, Zíbarová L, Larsson K-H. 2018. Additions to the taxonomy

542 of *Lagarobasidium* and *Xylodon* (Hymenochaetales, Basidiomycota).

543 MycoKeys 41:65–90.

544 Wang XW, May TW, Liu SL, Zhou LW. 2021. Towards a natural

545 classification of *Hyphodontia* sensu lato and the trait evolution of basidiocarps

546 within Hymenochaetales (Basidiomycota). Journal of Fungi 7:478.

547 White TJ, Bruns T, Lee S, Taylor JW. 1990. Amplification and direct

548 sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA,

549 Gelfand DH, Sninsky JJ, White TJ, eds. PCR protocols: A guide to the

550 methods and applications. New York: Academic Press. p. 315–322.

551 **LEGENDS and FOOTNOTES**

552 **Figure 1.** Phylogenetic relationships of *Xylodon* and *Lyomyces* inferred from

553 the 5.8S+28S+12S concatenated dataset using BI analysis. Bayesian posterior

554 probabilities followed by ML bootstrap values are shown at nodes; branch

555 lengths reflect estimated number of changes per site.

556 **Figure 2.** Phylogenetic relationships of *Xylodon* and *Lyomyces* inferred from

557 28S sequences using BI analysis. Bayesian posterior probabilities followed by

558 ML bootstrap values are shown at nodes; branch lengths reflect estimated

559 number of changes per site.

560 **Figure 3.** Phylogenetic relationships of the *Xylodon cymosus* species complex

561 inferred from ITS sequences using BI analysis. Bayesian posterior probabilities

562 followed by ML bootstrap values are shown at nodes; branch lengths reflect

563 estimated number of changes per site.

564 **Figure 4.** *Xylodon acuminatus* (holotype): Bar = 20 μm.

565 **Figure 5.** *Xylodon cymosus* (holotype): Bar = 20 μm.

566 **Figure 6.** *Xylodon subtilissimus* (holotype): Bar = 20 μm.

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Alloclavaria purpurea Miettinen 18831

Tubulicrinis chaetophorus Spirin 12616

Kneiffiella barba-jovis Spirin 10622 — 0.99/-

Kneiffiella subalutacea Miettinen 12026.2 — 1/100

Kneiffiella pilaecystidiata Helo 1517 — 1/87

Kneiffiella microspora Miettinen 11418 — 1/100

Kneiffiella alutacea Miettinen 21701

Kneiffiella abdita Miettinen 22165 — 0.98/85

Kneiffiella curvispora Pennanen 4040

0.96/-

Hastodontia hastata Larsson 14646

Hastodontia halonata Larsson 9252 — 0.96/-

Hyphodontia subdetritica Savchenko TU114869 — 0.99/100

Hyphodontia pallidula Kotiranta 18839

Hyphodontia alutaria Miettinen 13500.2 — -/93

Fasciodontia bugellensis Larsson 8195

1/99

Lyomyces pruni Spirin 12682 — 0.99/-

Lyomyces crustosus Spirin 12603

Lyomyces sambuci sl Miettinen 11705 — 0.99/93 — 1/100

Lyomyces griseliniae Larsson 5289

Lyomyces sp. Savchenko AS171126/0918

1/100

Xylodon subtilissimus Spirin 12228

Xylodon nespori Viner 2019_59 — 0.92/-

Xylodon angustisporus Ryvarden 50691b — 0.90/-

Xylodon pruinosus Viner 2019_21

Xylodon hyphodontinus Savchenko AS171124/1235

Xylodon crystalliger KUN3347 — 1/93

Xylodon paradoxus Oivanen PO109

Xylodon mollissimus Miettinen 12791.1

Xylodon pseudotropicus Miettinen 16558.2

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0.99/-

Xylodon asperus Spirin 11923

Xylodon ovisporus KUC8140

Xylodon spathulatus Spirin 12007

0.03

1/97 *Hastodontia halonata* Finn Oldervik
Hastodontia hastata Larsson 14646
1/100 *Fasciodontia bugellensis* Larsson 13832
Fasciodontia yunnanensis Zhao 6280
Lyomyces pruni Spirin 12682
Lyomyces vietnamensis He 3260
0,99/91 *Lyomyces crustosus* Spirin 12630
Lyomyces ochraceoalbus Zhao 10474
1/100 *Lyomyces ochraceoalbus* Zhao 4385
Lyomyces ochraceoalbus Zhao 4725
Lyomyces ochraceoalbus Zhao 6224
0,95/- 1/98 *Lyomyces niveus* Zhao 6431
Lyomyces niveus Zhao 6442
Lyomyces niveus Zhao 6474
Lyomyces niveus Zhao 6483
0,99/83 *Lyomyces niveus* Zhao 6565
1/100 *Lyomyces macrosporus* He 6179
Lyomyces macrosporus Zhao 4516
1/100 *Lyomyces elaeidicola* He 6360
Lyomyces elaeidicola He 6378
0,97/87 1/100 *Lyomyces microfasciculatus* He 2651
Lyomyces microfasciculatus Zhao 5109
-/100 *Lyomyces wuliangshanensis* He 3498
Lyomyces wuliangshanensis He 4765
Lyomyces sp. Savchenko AS171126/0918
0,99/82 0,99/84 *Lyomyces fissuratus* Zhao 4352
1/100 *Lyomyces fissuratus* Zhao 4394
Lyomyces fissuratus Zhao 9784
Lyomyces fissuratus Zhao 4299
0,99/86 *Lyomyces fissuratus* Zhao 4577
Lyomyces griseliniae Larsson 12971
1/100 *Lyomyces fumosus* Zhao 8188
Lyomyces densiusculus Ryvarden 44818
0,99/- *Lyomyces bambusinus* Zhao 4831
1/100 *Lyomyces sambuci* sl He 6108
Lyomyces sambuci sl He 6576
0,99/- 1/100 *Lyomyces fumosus* Zhao 17855
Lyomyces incrustatus Viner 2019 203
0,99/- *Lyomyces sambuci* sl Miettinen 11705
1/100 *Lyomyces orientalis* He 3616
0,99/81 *Lyomyces orientalis* He 3686

Xylodon angustisporus Ryvarden 50691
1/100 **Xylodon acuminatus* Larsson 16029*
**Xylodon subtilissimus* Spirin 12228*
Xylodon hyphodontinus Savchenko AS171124/1235
1/100 *Xylodon laceratus* Zhao 9892
1/100 *Xylodon tropicus* Zhao 3351
Xylodon tropicus Zhao 3395
Xylodon tropicus Zhao 3397
1/100 *Xylodon nespori* Nordon 030915
Xylodon nespori Viner 2019 59
Xylodon borealis Spirin 10911
1/85 *Xylodon gossypinus* Zhao 4465
1/100 *Xylodon pruinosus* Nilsson 990902
1/85 *Xylodon pruinosus* Viner 2019 21
Xylodon detriticus Miettinen 22106
1/100 *Xylodon flocculosus* Zhao 18342
Xylodon flocculosus Zhao 18379
Xylodon flocculosus Zhao 18394

0,98/- *Xylodon dissiliens* Ryvarden 44817
Xylodon laceratus Zhao 9841
Xylodon crystalliger KUN3347
Xylodon paradoxus Oivanen PO109
0,97/- *Xylodon xinpingensis* Zhao 9125
0,99/95 *Xylodon xinpingensis* Zhao 9174
Xylodon cystidiatus Savchenko AS171128/1625B
Xylodon mollissimus Miettinen 12791.1
Xylodon nongravis Viacheslav Spirin 5615
1/97 1/100 *Xylodon macrosporus* Zhao 10226
Xylodon macrosporus Zhao 2379
Xylodon macrosporus Zhao 2488
Xylodon macrosporus Zhao 3238
Xylodon sp. Larsson 12386
Xylodon sp. Berglund 1117
1/100 *Xylodon montanus* Zhao 8118
Xylodon montanus Zhao 8179
1/100 *Xylodon* sp. Zhao 210
Xylodon sp. Zhao 214
1/100 *Xylodon* sp. Zhao 215
1/100 *Xylodon bambusinus* Zhao 11211
Xylodon bambusinus Zhao 11215
Xylodon bambusinus Zhao 11219
Xylodon bambusinus Zhao 11224
Xylodon bambusinus Zhao 11310

Xylodon pseudotropicus Miettinen 16558.2
Xylodon verecundus Larsson 12261
1/99 *Xylodon ramicida* Spirin 7670
Xylodon quercinus Spirin 12030
Xylodon attenuatus Spirin 8714
Xylodon rimossisimus Miettinen 12026.1
Xylodon hjortstamii Gorjón 3187
0,99/95 *Xylodon sinensis* Zhao 11120
Xylodon sinensis Zhao 9197
Xylodon pseudolanatus HHB-10703-Sp
Xylodon asperus Nilsson 2004b
-/98 *Xylodon asperus* Spirin 11923
Xylodon nothofagi ICMP 13839
Xylodon flaviporus MA Fungi 79440
0,99/83 *Xylodon ovisporus* ICMP 13835
0,93/- *Xylodon ovisporus* KUC8140
Xylodon raduloides Dai 12631
1/100 *Xylodon niemelaei* GC 1508-146
0,97/82 *Xylodon niemelaei* Savchenko TU114922
Xylodon apacheriensis Miettinen 16686
0,99/86 *Xylodon spathulatus* Spirin 12007
0,98/100 *Xylodon spathulatus* Wu 1307-42

0.02

Figure. Phylogenetic tree.

Xylodon borealis Spirin 10911

Xylodon cymosus Miettinen 19606

Xylodon acuminatus LX042233-122-012-D07

0,99/100

Xylodon acuminatus Tedersoo 2008-10-01

0,99/99

Xylodon acuminatus Larsson 16029

Xylodon subtilissimus BPACtl2T0 2H

Xylodon subtilissimus Spirin 12228

0,99/88

Xylodon subtilissimus G4459

Xylodon subtilissimus S460

Xylodon subtilissimus IH.M09

0.02

Table 1. Primers used in this study.

Primer name	Sequence	Target DNA locus	Binding site	Direction	Reference
ITS5	GGAAGTAAAAGTCGTAACAAGG	ITS, ITS1	18S	fwd	White et al. 1990
ITS2	GCTGCGTTCTTCATCGATGC	ITS1	5.8S	rev	White et al. 1990
58A1F	GCATCGATGAAGAACGC	ITS2	5.8S	fwd	Martin and Rygiewicz 2005
ITS2.2r Xyl	TTATCACACCGCATATATGC	ITS2	ITS2	rev	Viner et al. 2021
ITS2.2f Xyl	CTTCYCTTGAATGYATTA	ITS2	ITS2	fwd	Viner et al. 2021
ALR0.2	GATATGCTTAAGTTCAGCGGG	ITS, ITS2	28S	rev	Riebesehl and Langer 2017
LR22	CCTCACGGTACTTGTTCGCT	ITS	28S	rev	Vilgalys lab, Duke University (https://sites.duke.edu/vilgalyslab/files/2017/08/rDNA-primers-for-fungi.pdf)
JS1	CGCTGAACTTAAGCATAT	28S	28S	fwd	Landvik 1996
LR7	TACTACCACCAAGATCT	28S	28S	rev	Hopple and Vilgalys 1994
MS1	CAGCAGTCAAGAATATTAGTCAATG	12S	12S	fwd	White et al. 1990
MS2	GCGGATTATCGAATTAAATAAC	12S	12S	rev	White et al. 1990

1   **Table 2.** GenBank and UNITE accession numbers for DNA sequences used in

2   this study. Sequences downloaded from the Fungal Genomics Resource

3   indicated as JGI. New sequences are in bold.

Species	Specimen	ITS	28S	12S
Alloclavaria purpurea	Miettinen 18831	**ON188807**	**ON188807**	**ON228494**
Fasciodontia bugellensis	Larsson 13832	OK273855	OK273855	**ON228480**
Fasciodontia yunnanensis	Zhao 6280		MZ146327	
Hastodontia halonata	Finn Oldervik	**ON188810**	**ON188810**	**ON228482**
Hastodontia hastata	Larsson 14646	MH638232	MH638232	**ON228492**
Hyphodontia alutaria	Miettinen 13500.2	**ON188811**	**ON188811**	**ON228488**
Hyphodontia pallidula	Kotiranta 18839	**OP620785**	**OP620785**	**OP620779**
Hyphodontia subdetritica	Savchenko TU114869	**OP620786**	**OP620786**	**OP620780**
Kneiffiella abdita	Miettinen 22165	**ON188809**	**ON188809**	**ON228493**
Kneiffiella alutacea	Miettinen 21701	**ON188808**	**ON188808**	**ON228491**
Kneiffiella barba-jovis	Spirin 10622	**ON188812**	**ON188812**	**ON228489**
Kneiffiella curvispora	Pennanen 4040	**OP620787**	**OP620787**	**OP620781**
Kneiffiella microspora	Miettinen 11418	**OP620788**	**OP620788**	**OP620782**
Kneiffiella pilaecystidiata	Helo 1517	**OP620789**	**OP620789**	**OP620783**
Kneiffiella subalutacea	Miettinen 12026.2	**OP620790**	**OP620790**	**OP620784**
Lyomyces bambusinus	Zhao 4831		MW264919	
Lyomyces crustosus	Spirin 12630	OK273832	OK273832	**ON228478**
Lyomyces densiusculus	Ryvarden 44818	OK273853	OK273853	
Lyomyces elaeidicola	He 6360		MW507035	
Lyomyces elaeidicola	He 6378		MW507036	
Lyomyces fissuratus	Zhao 4299		MW713731	
Lyomyces fissuratus	Zhao 4352		MW713732	
Lyomyces fissuratus	Zhao 4394		MW713733	
Lyomyces fissuratus	Zhao 4577		MW713734	
Lyomyces fissuratus	Zhao 9784		MW713735	
Lyomyces fumosus	Zhao 8188		MW713736	
Lyomyces fumosus	Zhao 17855		MW713737	
Lyomyces griseliniae	Larsson 12971	OK273851	OK273851	**ON228485**
Lyomyces incrustatus	Viner2019_203	**ON197553**	**ON197553**	
Lyomyces macrosporus	He 6179		MW507034	
Lyomyces macrosporus	Zhao 4516		MW264920	
Lyomyces microfasciculatus	He 2651		MW507027	
Lyomyces microfasciculatus	Zhao 5109		MW264921	
Lyomyces niveus	Zhao 6431		MZ262526	
Lyomyces niveus	Zhao 6442		MZ262527	
Lyomyces niveus	Zhao 6474		MZ262528	
Lyomyces niveus	Zhao 6483		MZ262529	
Lyomyces niveus	Zhao 6565		MZ262531	
Lyomyces ochraceoalbus	Zhao 10474		MZ262525	

Lyomyces ochraceoalbus	Zhao 4385		MZ262521	
Lyomyces ochraceoalbus	Zhao 4725		MZ262522	
Lyomyces ochraceoalbus	Zhao 6224		MZ262523	
Lyomyces orientalis	He 3616		MW507030	
Lyomyces orientalis	He 3686		MW507031	
Lyomyces pruni	Spirin 12682	OK273833	OK273833	**ON228483**
Lyomyces sambuci	He 6108		MW507033	
Lyomyces sambuci	He 6576		MW507037	
Lyomyces sambuci	Miettinen 11705	OK273852	OK273852	**ON228487**
Lyomyces vietnamensis	He 3260		MW507028	
Lyomyces wuliangshanensis	He 3498		MW507029	
Lyomyces wuliangshanensis	He 4765		MW507032	
Lyomyces sp.	Savchenko AS171126/0918	**ON188813**	**ON188813**	**ON228486**
Tubulicrinis chaetophorus	Spirin 12616	**ON188814**	**ON188814**	**ON228495**
Xylodon acuminatus	Larsson 16029	**ON197552**	**ON197552**	
Xylodon acuminatus	LX042233-122-012-D07	GU054154		
Xylodon acuminatus	Tedersoo 2008-10-01	UDB014084		
Xylodon angustisporus	Ryvarden 50691b	OK273831	OK273831	**ON228490**
Xylodon apacheriensis	Miettinen 16686	OK273835	OK273835	
Xylodon asperus	Nilsson 2004b	DQ873606	DQ873607	
Xylodon asperus	Spirin 11923	OK273838	OK273838	**ON228467**
Xylodon attenuatus	Spirin 8714	OK273839	OK273839	**ON228472**
Xylodon bambusinus	Zhao 11211	MW394658	MW394651	
Xylodon bambusinus	Zhao 11215	MW394661	MW394652	
Xylodon bambusinus	Zhao 11219	MW394659	MW394653	
Xylodon bambusinus	Zhao 11224	MW394662	MW394654	
Xylodon bambusinus	Zhao 11310	MW394660	MW394655	
Xylodon borealis	Spirin 10911	OK273846	OK273846	
Xylodon crystalliger	KUN3347	OK273842	OK273842	**ON228479**
Xylodon cymosus	Miettinen 19606	**ON197554**		
Xylodon cystidiatus	Savchenko AS171128/1625B	OK273850	OK273850	
Xylodon detriticus	Miettinen 22106	OK273844	OK273844	
Xylodon dissiliens	Ryvarden 44817	OK273856	OK273856	
Xylodon flaviporus	MA Fungi 79440	MH260071	MH260066	
Xylodon flocculosus	Zhao 18342		MW980779	
Xylodon flocculosus	Zhao 18379		MW980780	
Xylodon flocculosus	Zhao 18394		MW980781	
Xylodon gossypinus	Zhao 4465		MZ663812	
Xylodon gossypinus	Zhao 8375		MZ663813	
Xylodon hjortstamii	Gorjón 3187	**ON188816**	**ON188816**	**ON228473**
Xylodon hyphodontinus	Savchenko AS171124/1235	OK273848	OK273848	**ON228476**
Xylodon laceratus	Zhao 9841		OL619265	
Xylodon laceratus	Zhao 9892		OL619266	
Xylodon macrosporus	Zhao 10226		MZ663817	

Xylodon macrosporus	Zhao 2379		MZ663814	
Xylodon macrosporus	Zhao 2488		MZ663815	
Xylodon macrosporus	Zhao 3238		MZ663816	
Xylodon mollissimus	Miettinen 12791.1	**ON188815**	**ON188815**	**ON228481**
Xylodon montanus	Zhao 8118		OL619267	
Xylodon montanus	Zhao 8179		OL619268	
Xylodon nespori	Nordon 030915	DQ873622	DQ873622	
Xylodon nespori	Viner 2019_59	OK273834	OK273834	**ON228477**
Xylodon niemelaei	Savchenko TU114922	OK273836	OK273836	
Xylodon niemelaei	GC 1508-146		KX857816	
Xylodon nongravis	Spirin 5615	OK273849	OK273849	
Xylodon nothofagi	ICMP 13839	AF145582	MH260064	
Xylodon ovisporus	ICMP 13835	AF145586	MH260063	
Xylodon ovisporus	KUC8140	JGI	JGI	JGI
Xylodon paradoxus	Oivanen PO109	OK273843	OK273843	**ON228474**
Xylodon pruinosus	Viner 2019_21	OK273845	OK273845	**ON228475**
Xylodon pruinosus	Nilsson 990902	DQ677507	DQ677507	
Xylodon pseudolanatus	HHB-10703-Sp	OK273847	OK273847	
Xylodon pseudotropicus	Miettinen 16558.2	OK273854	OK273854	**ON228466**
Xylodon quercinus	Spirin 12030	OK273841	OK273841	**ON228469**
Xylodon raduloides	Dai 12631		KT203328	
Xylodon ramicida	Spirin 7670	**ON188817**	**ON188817**	**ON228468**
Xylodon rimosissimus	Miettinen 12026.1	OK273840	OK273840	**ON228470**
Xylodon sinensis	Zhao 11120		MZ663819	
Xylodon sinensis	Zhao 9197		MZ663818	
Xylodon sp.	Berglund 1117	DQ873633	DQ873634	
Xylodon sp.	Larsson 12386	DQ873612	DQ873612	
Xylodon sp.	Zhao 210		MN654918	
Xylodon sp.	Zhao 214		MN654919	
Xylodon sp.	Zhao 215		MN654920	
Xylodon spathulatus	Spirin 12007	OK273837	OK273837	**ON228471**
Xylodon spathulatus	Wu 1307-42		KX857810	
Xylodon subtilissimus	BPACtl2T0_2H	EU689272		
Xylodon subtilissimus	G4459		UDB0239643	
Xylodon subtilissimus	IH.M09		UDB062035	
Xylodon subtilissimus	S460		UDB0111079	
Xylodon subtilissimus	Spirin 12228	**ON188818**	**ON188818**	**ON228484**
Xylodon tropicus	Zhao 3351		OL619269	
Xylodon tropicus	Zhao 3395		OL619270	
Xylodon tropicus	Zhao 3397		OL619271	
Xylodon verecundus	Larsson 12261		DQ873643	
Xylodon xinpingensis	Zhao 9125		MW394649	
Xylodon xinpingensis	Zhao 9174		MW394650	

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