


ORIGINAL ARTICLE

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Redisposition of apiosporous genera *Induratia* and *Muscodor* in the Xylariales, following the discovery of an authentic strain of *Induratia apiospora*

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Abstract

Background The genus *Induratia* is based on *Induratia apiospora*, a xylarialean pyrenomycete from New Zealand with clypeate uniperitheciate stromata, hyaline apiospores and a nodulisporium-like anamorph. However, because of the lack of DNA data from the generic type, its phylogenetic affinities have remained unresolved. Recently, two fungal species with teleomorphs strikingly similar to *Induratia* were discovered in Thailand. However, they did not produce an anamorph and were found to be phylogenetically close to the species classified within the hyphomycete genus *Muscodor*, which was described after *Induratia*. Therefore, in 2020 the species of *Muscodor* were transferred to *Induratia*, and a new family Induratiaceae was proposed.

Results We have encountered an unpublished ex-holotype strain of *Induratia apiospora* among the holdings of the ATCC collection, enabling detailed morphological and molecular phylogenetic investigations. We observed the characteristic nodulisporium-like anamorph described in the original publication. Phylogenetic analyses of multigene sequence data revealed a close relationship of *Induratia apiospora* to the Barrmaeliaceae, while a close relationship to the *Induratia* species formerly classified within *Muscodor* was rejected.

Conclusions We here classify *Induratia apiospora* within the Barrmaeliaceae and consider Induratiaceae to be synonymous with the former. As the holotype specimen of *Induratia apiospora* is apparently lost, an isotype specimen from WSP is selected as lectotype. We also propose that the genus *Muscodor* is resurrected within the Xylariaceae, and formally transfer several *Induratia* species to *Muscodor*.

Keywords Fungi, Lectotypification, Sordariomycetes, Phylogeny, New combination

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Background

The taxonomy of the Sordariomycetes and other Ascomycota has changed drastically in the past decade, owing to the advent of multi-locus phylogenies, which were often combined in polyphasic studies, using morphological and chemotaxonomic data as additional evidence. The currently proposed classification of genera and higher taxa (cf. Hyde et al. 2020; Wijayawardene et al. 2022) is steadily changing as new evidence becomes available, in particular when the species that have been first described in the pre-molecular era are cultured and sequenced for the first time. A fair example are genera of the Xylariales, and especially so the Xylariaceae s. lat. where it has become evident due to the availability of molecular data that the classical discrimination of higher taxa based on ascus structure (uni-, bitunicate), fruiting bodies, anamorph-teleomorph connections and ascospore morphology alone is not feasible. This has been reflected by the recent re-organization of the families (Wendt et al. 2018), where the results of a four-locus genealogy were better in agreement with chemotaxonomy and anamorphic morphology than with the classical concept based on ascospore shape. Interestingly, the aforementioned phylogeny was even backed up at genus level by a concurrent phylogenomic study using the amino acid sequences of 4912 orthologue genes for the core genera of the Hypoxylaceae (Wibberg et al. 2021). Other families and genera of Xylariales, for which by far not that many data are available, are in bad need of further studies. It is to be expected that it will take several years more to generate sufficient amounts of data to attain a stable phylogeny. Numerous taxa are still only known from old morphological descriptions (often restricted to the teleomorphs), or have only recently been recollected and cultured to generate molecular data and study their anamorphs for the first time. These studies sometimes revealed rather unexpected phylogenetic affinities but also showed the limits of a morphocentric approach for phylogenetic assessments (Jaklitsch et al. 2014; 2016; Voglmayr et al. 2022).

Aside from attempts to re-discover fresh specimens corresponding to the old fungal taxa, it may at times also be feasible to screen the inventories of the large culture collections, since those may contain valuable reference or ex-type strains that have not been reported in the original literature. The current paper describes such a case.

The genus *Induratia* was originally described by Samuels et al. (1987) based on a single specimen from New Zealand that featured uniperitheciate stromata, asci with an amyloid ascus apparatus and apiosporous ascospores. The authors also observed a nodulisporium-like conidial stage in the mycelial culture they obtained, and this new combination had at that time given rise to the erection of a new monotypic genus. In the following decades the

genus almost remained forgotten, except that Miller and Huhndorf (2005) included a specimen they referred to as “*Induratia* sp. SMH 1255” originating from Puerto Rico in their phylogenetic study of Sordariales and other Sordariomycetes. However, Miller and Huhndorf (2005) neither included any morphological data of the specimen (which is housed in the fungarium of the University of Illinois as ILLS 82598), nor cultured it nor studied the anamorph. Samarakoon et al. (2020) later included the DNA sequences derived from this collection and provided microscopic details of the stromata and ascogenic structures. These morphological features resembled the drawings of *Induratia apiospora* by Samuels et al. (1987), even though the holotype specimen of this species has apparently been lost and could neither be located at the ZT nor the PDD herbarium. The molecular data of *Induratia* sp. SMH 1255 resembled those derived from two specimens that were freshly collected from Thailand. Moreover, they also clustered with the sequences of all hitherto described species of the genus *Muscodor*. This gave rise to the synonymisation of *Induratia* and *Muscodor*, with the former, older name taking priority over the younger *Muscodor*, and the erection of the new family Induratiaceae, which also included the similar genus *Emarcea* (Samarakoon et al. 2020).

However, we have recently encountered a culture labeled *Induratia apiospora* in the catalogue of the ATCC (Manassas, USA) via a random Google search on information on the genus on the Internet and decided to order and study it for comparison. The current paper is dedicated to the description of its characteristics and the necessary changes in the taxonomy of the Xylariales.

Methods

Morphological studies on strain ATCC 60639

A Google search for *Induratia apiospora* revealed a culture deposited as ATCC 60639 by G.J. Samuels not mentioned by Samuels et al. (1987). From discussions with two of the authors of the original paper, it was confirmed that this strain was indeed derived from the holotype specimen (O. Petrini and G.J. Samuels, personal communications). The strain *Induratia apiospora* (Samuels et al. 1987) was thus purchased from the American Type Culture Collection (ATCC, Manassas, Virginia) under the accession ATCC 60639 and cultured on Yeast-Malt agar (10 g/L malt extract, 4 g/L D-glucose, 4 g/L yeast extract, supplemented with 20 g/L agar and adjusted to pH 6.3 prior to sterilization). The mycelia were transferred to a new plate once the strain had covered the medium by excision of a 5 mm² square overgrown with mycelium on a regular basis (2–4 weeks). Plates were frequently monitored for sporulation.

For the morphological analysis of strain ATCC 60639, a small piece of sporulating mycelium was extracted and the dimensions of conidiogenous structures measured in distilled water and lactic acid. To observe the macro-morphology of the cultures, the strains were grown on Yeast-Malt agar (YM6.3; malt extract 10 g/L, yeast extract 4 g/L, D-glucose 4 g/L, agar 20 g/L, pH 6.3 before autoclaving), 2% Malt Extract Agar (MEA), Oatmeal Agar (OA, Sigma-Aldrich, Steinheim, Germany), and potato dextrose agar (PDA, Himedia, Mumbai, India) and the cultures checked at four weeks after inoculation. Photomicrographs were obtained using a DS-Fi3 camera connected to a Nikon eclipse Ni-U microscope (Nikon Europe BV, Amsterdam, Netherlands).

DNA extraction, PCR amplification and sequencing

The DNA extraction protocol and the solutions used for PCR amplification followed the description of Wendt et al. (2018). PCR programs followed Samarakoon et al. (2020), with the exemption of using the primer pair ITS1f and ITS4 (White et al. 1990) instead of ITS5 and ITS4. Briefly, the following settings were used: ITS: 94 °C for 30 s, 56 °C for 50 s, 72 °C for 60 s; LSU: LR0R/LR5: 94 °C for 30 s, 55 °C for 50 s, 72 °C for 60 s (Vilgalys and Hester 1990); SSU: NS1/NS4: 94 °C for 30 s, 54 °C for 50 s, 72 °C for 60 s (White et al. 1990); *rpb2*: fRPB2-5F/fRPB2-7cR: 95 °C for 45 s, 57 °C for 50 s, 72 °C for 90 s (Liu et al. 1999); *tub2*: T1/T22: 95 °C for 60 s, 54 °C for 110 s, 72 °C for 120 s (O'Donnell and Cigelnik 1997). PCR amplicons were purified as described in Wendt et al. (2018) and sequences generated with the Sanger sequencing method at the Microsynth sequencing company, using respective forward and reverse primers (Microsynth SeqLab GmbH, Göttingen, Germany). Sequences were assembled as a consensus sequence from both reads by using the de-novo assembly program contained in Geneious® R7.1.9 (Kearse et al. 2012). The generated and further used sequences in this study are listed with their respective GenBank Acc. No. in Table 1.

Taxon selection and molecular phylogenetic inference

To assess the affinities of the newly generated sequences within the order Xylariales, the manually curated alignment and taxon set recently presented by Voglmayr et al. 2022 was used, further restricting sequences derived from Xylariaceae from 154 to 94 taxa. The newly generated sequences of the ITS, LSU, *rpb2* and *tub2* loci were inserted into the data matrix and manually checked for consistency. The different loci were subjected to IQTree2 (Minh et al. 2020) for molecular phylogenetic inference using Maximum-Likelihood criterion with options for a partitioned analysis (Chernomor et al. 2016) of the supermatrix with prior testing for the optimal nucleotide

substitution model by using ModelFinder (Kalyaanamoorthy et al. 2017) following BIC criterion and 1000 non-parametric bootstrap (Felsenstein 1985) replicates. Concurrently, the optimal nucleotide substitution models for each locus were calculated with PartitionFinder2 (Lanfear et al. 2016) as implemented in the PhyloSuite V.1.2.2 (Zhang et al. 2020) program package and to-be-tested models restricted to the ones available in MrBayes 3.2.7a (Ronquist et al. 2012). Partitions were regarded as unlinked and testing options set to BIC optimality criterion and test strategy set to test all. A phylogenetic inference using MrBayes 3.2.7a followed, with settings used and described by Kemkuignou et al. (2022). Briefly, a random starting tree was used to calculate 200,000,000 generations with convergence controlled to arrive at an average split frequency of 0.01. Tree sampling was done every 1000 generations, of which the first 25% were discarded as “burn-in”. Four incrementally heated chains were used for the Markov Chain Monte Carlo (MCMC), with temperature set to 0.15. The BEAGLE library (Ayres et al. 2012) and a parallel Metropolis coupling for the MCMC (Altekar et al. 2004) were used to calculate in total four chains in parallel. The resulting bootstrap (bs) $\geq 70\%$ and posterior probabilities ≥ 0.95 were mapped on the respective bipartition on the found maximum-likelihood tree.

Results

Morphological studies on strain ATCC 60639

The culture we obtained from ATCC showed the following characteristics (Fig. 1):

Culture characteristics: On YM6.3 and PDA: 2.6 cm in four weeks. Mycelium white, wavy or cottony hyphal growth, margin filiform to slightly undulate, flat to slightly elevate. Reverse white to pale. On MEA: 4.2 cm in four weeks, differs by having a mycelium with a margin slightly undulate, flat. On OA: 5.8 cm in four weeks, differing to have a margin entire. The information is summarized in Table 2. **Sporulating regions:** in patches, citrine (13) olivaceous (48). Conidiogenous structure nodulisporium-like, abundant, smooth to slightly roughened. Conidiogenous cells: melanized, smooth to slightly roughened, $34.5\text{--}66.5 \times 2\text{--}3 \mu\text{m}$ ($n=23$). Conidia: hyaline with cytoplasm content melanized, smooth, ellipsoidal to obovoid, $4\text{--}6 \times 2\text{--}4 \mu\text{m}$ ($n=41$).

These characteristics (see also Fig. 2) are indeed well in accordance with what Samuels et al. (1987) had reported for *Induratia apiospora*. According to the description by Samuels et al. (1987), the anamorph is nodulisporium-like, conidiogenous cells are light brown, slightly roughened, conidia are hyaline, ellipsoidal to obovoid, $4\text{--}6 \times 2\text{--}4 \mu\text{m}$.

Table 1 Feature table listing all sequences used for molecular phylogenetic inference. GenBank sequence accession numbers, type status of taxa, country of origin and specimen/strain numbers are given in the respective columns

| Species | Specimen or strain number | Origin | Status | GenBank accession numbers | | | | References |
|-------------------------------------|---------------------------|-------------|--------|---------------------------|----------|-------------|-------------|--|
| | | | | ITS | LSU | <i>rpb2</i> | <i>tub2</i> | |
| <i>Albicollum longisporum</i> | CBS 147283 | Spain | HT | ON869286 | ON869286 | ON808465 | ON808509 | Voglmayr et al. (2022) |
| <i>Albicollum vincensii</i> | CBS 147286 | Austria | ET | ON869297 | ON869297 | ON808475 | ON808519 | Voglmayr et al. (2022) |
| <i>Amphirosellinia nigrospora</i> | HAST 91092308 | Taiwan | HT | GU322457 | N/A | GQ848340 | GQ495951 | Hsieh et al. (2010) |
| <i>Annulohypoxylon truncatum</i> | CBS 140778 | Texas | ET | KY610419 | KY610419 | KY624277 | KX376352 | Kuhnert et al. (2017), Wendt et al. (2018) |
| <i>Anthostomelloides krabiensis</i> | MFLUCC 15–0678 | Thailand | HT | KX305927 | KX305928 | KX305929 | N/A | Tibpromma et al. (2017) |
| <i>Astrocystis concavisporea</i> | MFLUCC 14–0174 | Italy | | KP297404 | KP340545 | KP340532 | KP406615 | Daranagama et al. (2015) |
| <i>Barrmaelia macropora</i> | CBS 142768 | Austria | ET | KC774566 | KC774566 | MF488995 | MF489014 | Voglmayr et al. (2018) |
| <i>Barrmaelia moravica</i> | CBS 142769 | Austria | ET | MF488987 | MF488987 | MF488996 | MF489015 | Voglmayr et al. (2018) |
| <i>Barrmaelia oxyacanthae</i> | CBS 142770 | Austria | | MF488988 | MF488988 | MF488997 | MF489016 | Voglmayr et al. (2018) |
| <i>Barrmaelia rappazii</i> | CBS 142771 | Norway | HT | MF488989 | MF488989 | MF488998 | MF489017 | Voglmayr et al. (2018) |
| <i>Barrmaelia rhamnicola</i> | CBS 142772 | France | ET | MF488990 | MF488990 | MF488999 | MF489018 | Voglmayr et al. (2018) |
| <i>Biscogniauxia marginata</i> | MFLUCC 12–0740 | France | | KJ958407 | KJ958408 | KJ958409 | KJ958406 | Daranagama et al. (2015) |
| <i>Camillea obularia</i> | ATCC 28093 | Puerto Rico | | KY610384 | KY610429 | KY624238 | KX271243 | Wendt et al. (2018) |
| <i>Clypeosphaeria mamillana</i> | CBS 140735 | France | ET | KT949897 | KT949897 | MF489001 | MH704637 | Jaklitsch et al. (2016), Voglmayr et al. (2018), Liu et al. (2019) |
| <i>Collodiscula japonica</i> | CBS 124266 | China | | JF440974 | JF440974 | KY624273 | KY624316 | Jaklitsch and Voglmayr (2011), Wendt et al. (2018) |
| <i>Creosphaeria sas-safras</i> | STMA 14087 | Argentina | | KY610411 | KY610468 | KY624265 | KX271258 | Wendt et al. (2018) |
| <i>Daldinia concentrica</i> | CBS 113277 | Germany | | AY616683 | KY610434 | KY624243 | KC977274 | Triebel et al. (2005), Kuhnert et al. (2014), Wendt et al. (2018) |
| <i>Dematophora necatrix</i> | CBS 349.36 | Argentina | | AY909001 | KF719204 | KY624275 | KY624310 | Pelaez et al. (2008), Wendt et al. (2018) |
| <i>Diatrype disciformis</i> | CBS 197.49 | Netherlands | | N/A | DQ470964 | DQ470915 | N/A | Zhang et al. (2006) |
| <i>Digitodochium amoenum</i> | CBS 147285 | Austria | ET | ON869303 | ON869303 | ON808481 | ON808525 | Voglmayr et al. (2022) |
| <i>Emarcea castanop-sidicola</i> | CBS 117105 | Thailand | HT | AY603496 | MK762717 | MK791285 | MK776962 | Duong et al. (2004), Samarakoon et al. (2020) |
| <i>Emarcea eucalyptigena</i> | CBS 139908 | Malaysia | HT | KR476733 | MK762718 | MK791286 | MK776963 | Crous et al. (2015), Samarakoon et al. (2020) |
| <i>Entalbotroma erumpens</i> | ICMP 21152 | New Zealand | HT | KX258206 | N/A | KX258204 | KX258205 | Johnston et al. (2016) |
| <i>Entoleuca mammata</i> | 100 J.D.R | France | | GU300072 | N/A | GQ844782 | GQ470230 | Hsieh et al. (2010) |
| <i>Entonaema lique-scens</i> | ATCC 46302 | USA | | KY610389 | KY610443 | KY624253 | KX271248 | Wendt et al. (2018) |
| <i>Entosordaria perfidiosa</i> | CBS 142773 | Austria | ET | MF488993 | MF488993 | MF489003 | MF489021 | Voglmayr et al. (2018) |
| <i>Entosordaria quercina</i> | CBS 142774 | Greece | HT | MF488994 | MF488994 | MF489004 | MF489022 | Voglmayr et al. (2018) |
| <i>Eutypa lata</i> | UCR-EL1 | USA | | JGI | JGI | JGI | JGI | |

Table 1 (continued)

| Species | Specimen or strain number | Origin | Status | GenBank accession numbers | | | | References |
|------------------------------------|---------------------------|---------------|--------|---------------------------|----------|-------------|-------------|---|
| | | | | ITS | LSU | <i>rpb2</i> | <i>tub2</i> | |
| <i>Graphostroma platystomum</i> | CBS 270.87 | France | | JX658535 | DQ836906 | KY624296 | HG934108 | Zhang et al. (2006), Stadler et al. (2014), Koukol et al. (2015), Wendt et al. (2018) |
| <i>Hypocreodendron sanguineum</i> | J.D.R. 169 | Mexico | | GU322433 | N/A | GQ844819 | GQ487710 | Hsieh et al. (2010) |
| <i>Hypomontagnella monticulosa</i> | MUCL 54604 | French Guiana | ET | KY610404 | KY610487 | KY624305 | KX271273 | Wendt et al. (2018) |
| <i>Hypoxylon fragiforme</i> | MUCL 51264 | Germany | ET | KC477229 | KM186295 | KM186296 | KX271282 | Stadler et al. (2013), Daranagama et al. (2015), Wendt et al. (2018) |
| <i>Induratia apiospora</i> | ATCC 60639 | New Zealand | HT | OP862879 | OP862881 | OP879469 | OP879468 | This study |
| <i>Jackrogersella multiformis</i> | CBS 119016 | Germany | ET | KC477234 | KY610473 | KY624290 | KX271262 | Kuhnert et al. (2014), Kuhnert et al. (2017), Wendt et al. (2018) |
| <i>Kretzschmaria deusta</i> | CBS 163.93 | Germany | | KC477237 | KY610458 | KY624227 | KX271251 | Stadler et al. (2013), Wendt et al. (2018) |
| <i>Leptomassaria simplex</i> | CBS 147282 | Austria | ET | ON869305 | ON869305 | ON808483 | ON808527 | Voglmayr et al. (2022) |
| <i>Linosporopsis ischnothea</i> | CBS 145761 | Switzerland | ET | MN818952 | MN818952 | MN820708 | MN820715 | Voglmayr and Beenken (2020) |
| <i>Linosporopsis ochracea</i> | CBS 145999 | Germany | ET | MN818958 | MN818958 | MN820714 | MN820721 | Voglmayr et al. (2022) |
| <i>Lopadostoma turgidum</i> | CBS 133207 | Austria | ET | KC774618 | KC774618 | KC774563 | MF489024 | Jaklitsch et al. (2014), Voglmayr et al. (2018) |
| <i>Muscodor albus</i> | 9-6 | N/A | | HM034857 | HM034865 | N/A | HM034844 | Zhang et al. (2010) |
| <i>Muscodor albus</i> | MONT 620 | | HT | AF324336 | N/A | N/A | N/A | Worapong et al. (2001) |
| <i>Muscodor brasiliensis</i> | LGMF 1256 | | HT | KY924494 | N/A | MF510171 | N/A | Pena et al. (2019) |
| <i>Muscodor camphorae</i> | NFCCI 3236 | | HT | KC481681 | N/A | N/A | N/A | Meshram et al. (2017) |
| <i>Muscodor cinnanomi</i> | BCC 38842 | | HT | GQ848369 | N/A | N/A | N/A | Suwannarach et al. (2010) |
| <i>Muscodor coffeanum</i> | COAD 1842 | Brazil | HT | KM514680 | N/A | KP862881 | N/A | Hongsanan et al. (2015) |
| <i>Muscodor crispans</i> | MONT 2347 | | HT | EU195297 | N/A | N/A | N/A | Mitchell et al. (2008) |
| <i>Muscodor darjeelingensis</i> | NFCCI 3095 | | HT | JQ409997 | N/A | N/A | N/A | Saxena et al. (2014) |
| <i>Muscodor equiseti</i> | JCM 18233 | | HT | JX089322 | N/A | N/A | N/A | Suwannarach et al. (2013) |
| <i>Muscodor fengyanensis</i> | CGMCC 2862 | China | HT | HM034856 | HM034859 | HM034849 | HM034843 | Zhang et al. (2010) |
| <i>Muscodor ghooensis</i> | NFCCI 3234 | | HT | KF537625 | N/A | N/A | N/A | Meshram et al. (2015) |
| <i>Muscodor indicus</i> | NFCCI 3235 | | HT | KF537626 | N/A | N/A | N/A | Meshram et al. (2015) |
| <i>Muscodor kashayum</i> | NFCCI 2947 | | HT | KC481680 | N/A | N/A | N/A | Meshram et al. (2013) |
| <i>Muscodor musae</i> | JCM 18230 | | HT | JX089323 | N/A | N/A | N/A | Suwannarach et al. (2013) |
| <i>Muscodor oryzae</i> | JCM 18231 | | HT | JX089321 | N/A | N/A | N/A | Suwannarach et al. (2013) |
| <i>Muscodor roseus</i> | MONT 2098 | | HT | AH010859 | N/A | N/A | N/A | Worapong et al. (2002) |
| <i>Muscodor</i> sp. | SMH 1255 | | | MN250031 | AY780069 | N/A | AY780119 | Miller and Huhndorf (2005), Samarakoon et al. (2020) |
| <i>Muscodor strobilii</i> | NFCCI 2907 | | HT | JQ409999 | N/A | N/A | N/A | Meshram et al. (2014) |

Table 1 (continued)

| Species | Specimen or strain number | Origin | Status | GenBank accession numbers | | | | References |
|-----------------------------------|---------------------------|---------------|--------|---------------------------|----------|-------------|-------------|--|
| | | | | ITS | LSU | <i>rpb2</i> | <i>tub2</i> | |
| <i>Muscodora suth-epensis</i> | JCM 18232 | | HT | JN558830 | N/A | N/A | N/A | Suwannarach et al. (2013) |
| <i>Muscodora suturae</i> | MSUB 2380 | | HT | JF938595 | N/A | N/A | N/A | Kudalkar et al. (2012) |
| <i>Muscodora thailandica</i> | MFLUCC 17-2669 | Thailand | HT | MK762707 | MK762714 | MK791283 | MK776960 | Samarakoon et al. (2020) |
| <i>Muscodora tigerensis</i> | NFCCI 3172 | | HT | JQ409998 | N/A | N/A | N/A | Saxena et al. (2015) |
| <i>Muscodora vitigenus</i> | MONT P-15 | | HT | AY100022 | N/A | N/A | N/A | Daisy et al. (2002) |
| <i>Muscodora yucatanensis</i> | MEXU 25511 | | HT | FJ917287 | N/A | N/A | N/A | González et al. (2009) |
| <i>Muscodora yunnanensis</i> | CGMCC 3.18908 | China | HT | MG866046 | MG866038 | MG866059 | MG866066 | Chen et al. (2019) |
| <i>Muscodora ziziphi</i> | MFLUCC 17-2662 | Thailand | HT | MK762705 | MK762712 | MK791281 | MK776958 | Samarakoon et al. (2020) |
| <i>Magnostiolata mucida</i> | MFLU 19-2133 | Thailand | HT | MW240673 | MW240603 | MW658652 | MW775618 | Samarakoon et al. (2020) |
| <i>Nemania ethancrensonii</i> | CBS 148337 | USA | HT | ON869311 | ON869311 | ON808489 | ON808533 | Voglmayr et al. (2022) |
| <i>Nemania primolutea</i> | HAST 91102001 | Taiwan | HT | EF026121 | N/A | GQ844767 | EF025607 | Hsieh et al. (2010) |
| <i>Nemania uda</i> | CBS 148422 | Austria | | ON869312 | ON869312 | ON808488 | ON808532 | Voglmayr et al. (2022) |
| <i>Obolarina dryophila</i> | MUCL 49882 | France | | GQ428316 | GQ428316 | KY624284 | GQ428322 | Pažoutová et al. (2010), Wendt et al. (2018) |
| <i>Occultithea rosae</i> | HKAS 102393 | China | HT | MW240672 | MW240602 | MW658651 | MW775617 | Samarakoon et al. (2020) |
| <i>Oligostoma insidiosum</i> | CBS 147288 | Switzerland | ET | ON869314 | ON869314 | ON808491 | ON808535 | Voglmayr et al. (2022) |
| <i>Podosordaria mexicana</i> | WSP 176 | Mexico | | GU324762 | N/A | GQ853039 | GQ844840 | Hsieh et al. (2010) |
| <i>Poronia punctata</i> | CBS 656.78 | Australia | HT | KT281904 | KY610496 | KY624278 | KX271281 | Senanayake et al. (2015), Wendt et al. (2018) |
| <i>Pyrenopolyporus hunteri</i> | MUCL 52673 | Ivory Coast | ET | KY610421 | KY610472 | KY624309 | KU159530 | Kuhnert et al. (2017), Wendt et al. (2018) |
| <i>Rhopalostroma angolense</i> | CBS 126414 | Ivory Coast | | KY610420 | KY610459 | KY624228 | KX271277 | Wendt et al. (2018) |
| <i>Rosellinia corticium</i> | MUCL 51693 | France | | KY610393 | KY610461 | KY624229 | KX271254 | Wendt et al. (2018) |
| <i>Rostrophoxylon terebratum</i> | CBS 119137 | Thailand | HT | DQ631943 | DQ840069 | DQ631954 | DQ840097 | Tang et al. (2007), Fournier et al. (2011) |
| <i>Ruwenzoria pseudoannulata</i> | MUCL 51394 | D. R. Congo | HT | KY610406 | KY610494 | KY624286 | KX271278 | Wendt et al. (2018) |
| <i>Sarcoxyloa punctatum</i> | CBS 359.61 | South Africa | | KT281903 | KY610462 | KY624230 | KX271255 | Senanayake et al. (2015), Wendt et al. (2018) |
| <i>Spiririma gaudefroyi</i> | CBS 147284 | Spain | ET | ON869320 | ON869320 | ON808497 | ON808541 | Voglmayr et al. (2022) |
| <i>Stilbohypoxyloa elaeicola</i> | Y.M.J. 173 | French Guiana | | EF026148 | N/A | GQ844826 | EF025616 | Hsieh et al. (2010) |
| <i>Stromatoneurospora phoenix</i> | BCC 82040 | Thailand | | MT735133 | MT735133 | MT742605 | MT700438 | Becker et al. (2020) |
| <i>Thamnomycetes dendroideus</i> | CBS 123578 | French Guiana | | FN428831 | KY610467 | KY624232 | KY624313 | Stadler et al. (2010), Wendt et al. (2018) |
| <i>Xylaria apoda</i> | HAST 90080804 | Taiwan | | GU322437 | N/A | GQ844823 | GQ495930 | Hsieh et al. (2010) |
| <i>Xylaria arbuscula</i> | CBS 126415 | Germany | | KY610394 | KY610463 | KY624287 | KX271257 | Fournier et al. (2011), Wendt et al. (2018) |
| <i>Xylaria atosphaerica</i> | HAST 91111214 | Taiwan | | GU322459 | N/A | GQ848342 | GQ495953 | Hsieh et al. (2010) |
| <i>Xylaria digitata</i> | HAST 919 | Ukraine | | GU322456 | N/A | GQ848338 | GQ495949 | Hsieh et al. (2010) |

Table 1 (continued)

| Species | Specimen or strain number | Origin | Status | GenBank accession numbers | | | | References |
|---------------------------------|---------------------------|--------------------|--------|---------------------------|----------|-------------|-------------|--|
| | | | | ITS | LSU | <i>rpb2</i> | <i>tub2</i> | |
| <i>Xylaria hypoxylon</i> | CBS 122620 | Sweden | ET | KY610407 | KY610495 | KY624231 | KX271279 | Sir et al. (2016b), Wendt et al. (2018) |
| <i>Xylaria ianthinovelutina</i> | HAST 553 | French West Indies | | GU322441 | N/A | GQ844828 | GQ495934 | Hsieh et al. (2010) |
| <i>Xylaria laevis</i> | HAST 419 | French West Indies | | GU324746 | N/A | GQ848359 | GQ502695 | Hsieh et al. (2010) |
| <i>Xylaria longipes</i> | CBS 148.73 | Germany | | MH860649 | MH872351 | KU684280 | KU684204 | Vu et al. (2019), U'Ren et al. (2016) |
| <i>Xylaria oxyacanthae</i> | J.D.R. 859 | USA | | GU322434 | N/A | GQ844820 | GQ495927 | Hsieh et al. (2010) |
| <i>Xylaria polymorpha</i> | MUCL 49884 | France | | KY610408 | KY610464 | KY624288 | KX271280 | Wendt et al. (2018) |

Molecular phylogenetic inference

The alignment subjected to IQTree and MrBayes consisted of 4679 sites in total, distributed among loci corresponding to the ITS (584 sites), LSU (1329 sites), *rpb2* (1235 sites) and *tub2* (1531 sites). The generated sequence of the SSU for *Induratia apiospora* ATCC 60639 has not been used for phylogenetic reconstruction, but has been deposited under the GenBank Acc. No. OQ748100 for the scientific community to use. A detailed list of alignment features and the tested models per partition, as well as the alignments can be found in the (Additional file 1: Tables S1–S3). The final inferred tree following maximum-likelihood analysis had an lLn of -89939.9947 (Fig. 3). The topology of trees generated from the ML and Bayesian approach were identical, showing a similar arrangement of the taxa as previously presented by Voglmayr et al. (2022). Briefly, the Hypoxylaceae, Diatrypaceae, Lopadostomataceae, Graphostromataceae, Xylariaceae and Barrmaeliaceae received maximum support. The position of the latter was not resolved. Sequences derived from *Induratia* sensu Samarakoon et al. (2020; given as *Muscodor* in Fig. 3), *Spiririma gaudiefroyi* and *Emarcea* received maximum support in a clade nested inside the Xylariaceae. Surprisingly, the sequences of *Induratia apiospora* ATCC 60639 clustered in a basal position to a clade formed by *Entosordaria* and *Barrmaelia* representing the Barrmaeliaceae, each clade receiving maximum support.

Taxonomy

Our phylogenetic study showed that the ex-type strain of *Induratia* resolves within the Barrmaeliaceae. The Induratiaceae are thus regarded as a synonym of Barrmaeliaceae and *Muscodor* is resurrected. The holotype specimen of *Induratia* could still not be recovered, hence the isotype (WSP73242; MyCoPortal 2022) located at Shaw Mycology Herbarium (WSP; Washington State University) is chosen as lectotype. The genera *Emarcea*

and *Muscodor*, which were previously classified within Induratiaceae, are now formally accommodated in the Xylariaceae.

Barrmaeliaceae Voglmayr & Jaklitsch, Mycol. Progr. 17(1–2): 162 (2017) [2018], emend. Cedeño-Sanchez, M. Stadler, Voglmayr & C. Lambert.

MycoBank MB 822042

Type genus: *Barrmaelia* Rappaz

≡ Induratiaceae Samarak., Thongbai, K.D. Hyde & M. Stadler, Fungal Diversity 101: 188 (2020) [MB833443], syn. nov.

Other genera in the family: *Entosordaria* Höhn. (see Voglmayr et al. 2018), *Induratia* Samuels, E. Müll. & Petrini (see below).

Saprobic on wood or bark. Stroma if present mostly in wood and blackening the surface in wide areas or in elongate bands, sometimes darker or carbonized around the ostioles; entostroma prosenchymatous, poorly developed, sometimes delimited by a black carbonized line (*Induratia*), without KOH-extractable pigments; ectostroma variable, from virtually absent, poorly developed to strongly carbonized and clypeus-like. Ascospores globose, sometimes raising the substrate, singly, in small groups or gregarious. Peridium melanized, pseudoparenchymatous to prosenchymatous. Hamathecium of numerous persistent, hyaline, septate paraphyses. Asci eight-spored, cylindrical, persistent, with inamyloid or amyloid apical ascus apparatus. Ascospores hyaline, yellow to dark brown; unicellular with or without germ slit (*Barrmaelia*), or two-celled with septum near one end, the small cell hyaline, the large cell dark brown and with an apical germ apparatus consisting of radial slits

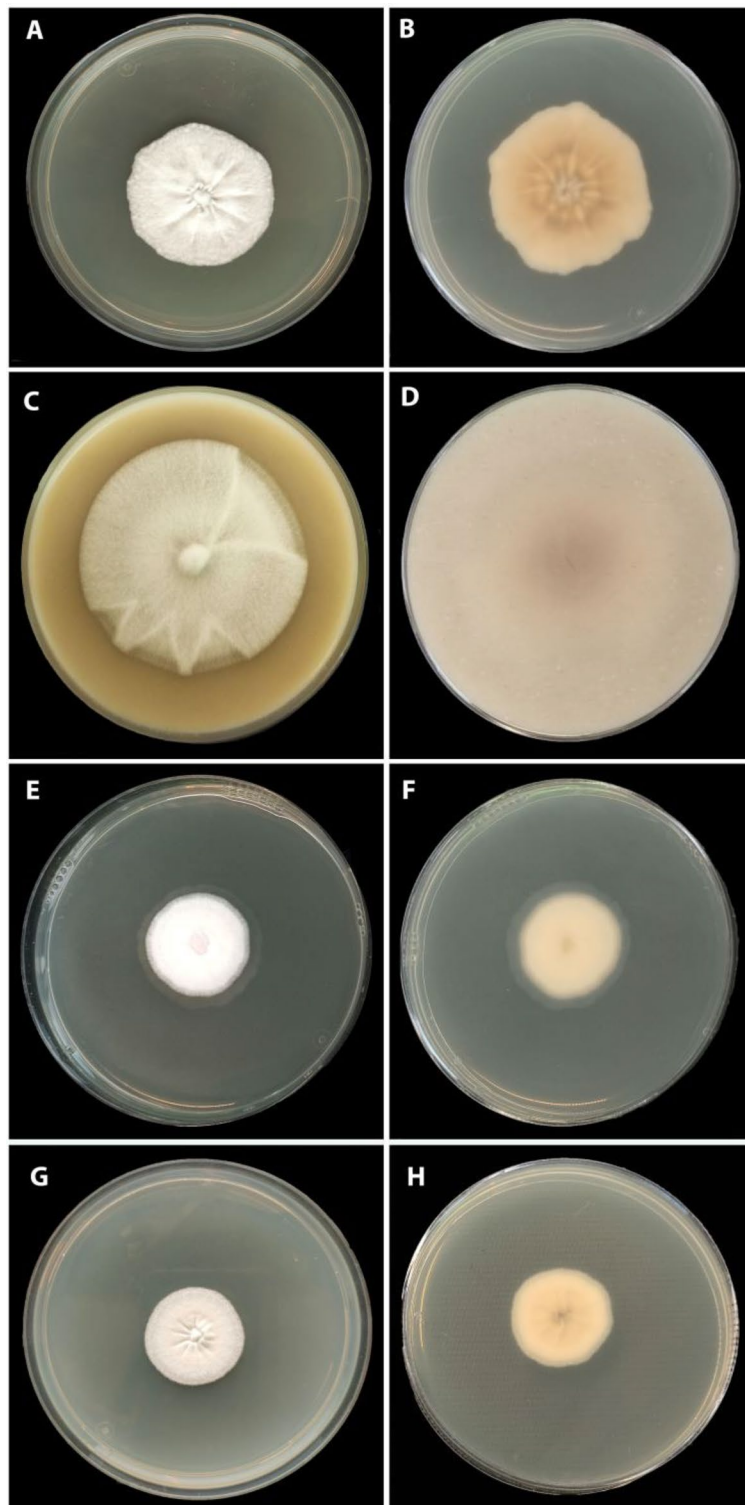
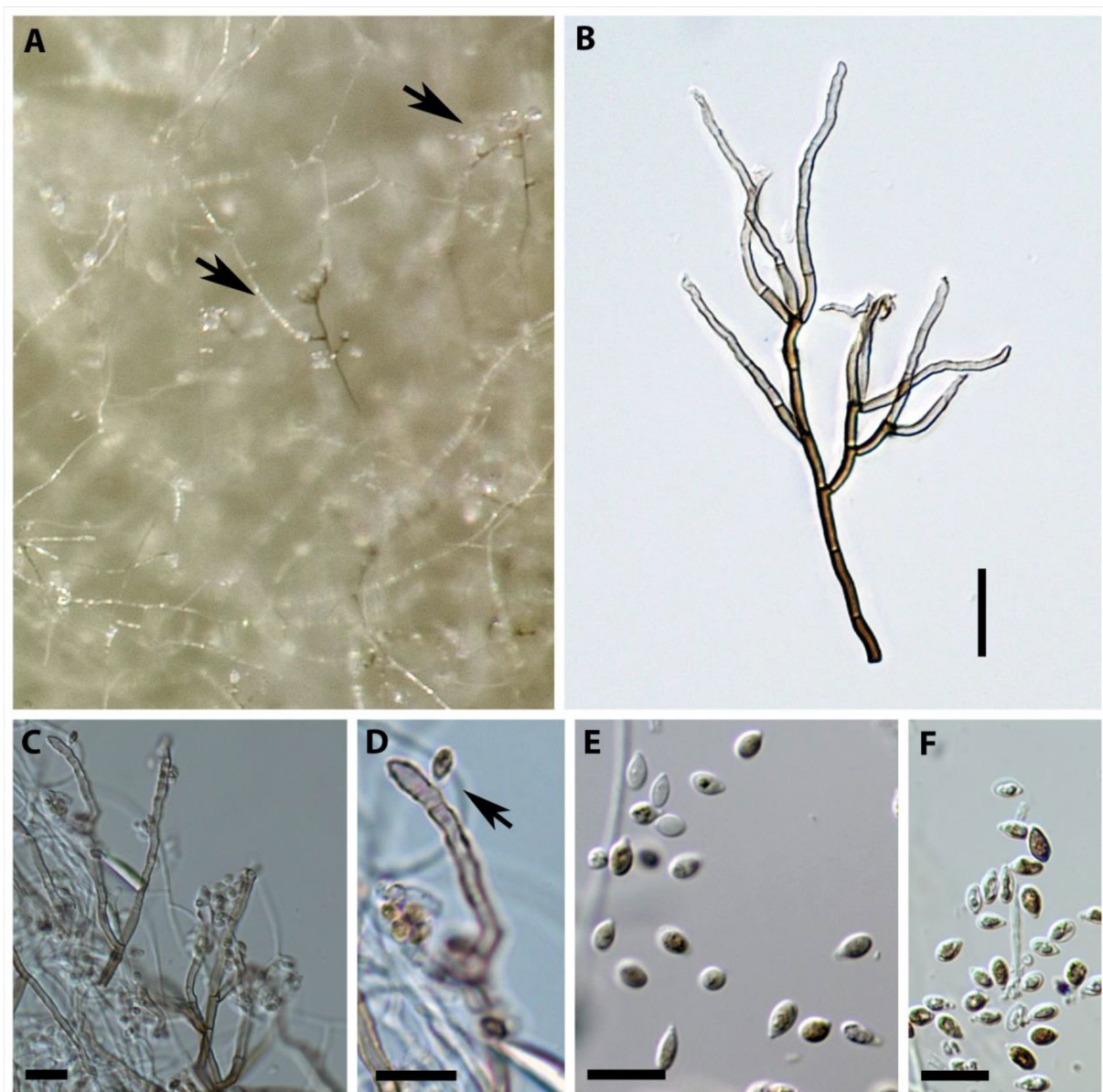


Fig. 1 Colonies of *Induratia apiospora* (ATCC 60639) after four weeks **A, B** on MEA; **C, D** on OA; **E, F** on PDA; **G, H** on YM6.3

Table 2 Rates of growth and culture characteristics of *Induratia apiospora* ATCC60639 in four different media at four weeks of incubation

| Media | area (cm ²) | diameter (cm) | Temperature | Margin | Elevation | Mycelium color |
|-------|-------------------------|---------------|-------------|-------------------------------|------------------|----------------|
| YM6.3 | 5.5 | 2.6 | 25 °C | filiform to slightly undulate | slightly elevate | White |
| MEA | 14.0 | 4.2 | | slightly undulate | flat | White |
| OA | 26.5 | 5.8 | | Entire | slightly elevate | White |
| PDA | 5.4 | 2.6 | | filiform to slightly undulate | slightly elevate | White |

**Fig. 2** Morphology of the anamorph of the ex-type strain of *Induratia apiospora* (ATCC 60639) on YM6.3. **A** Conidiophore on surface mycelium. **B** Single nodulisporium-like conidiophore. **C, D** Conidiogenous cells. **E, F** Conidia. Scale bars: **B** 20 μ m, **E, F** 10 μ m

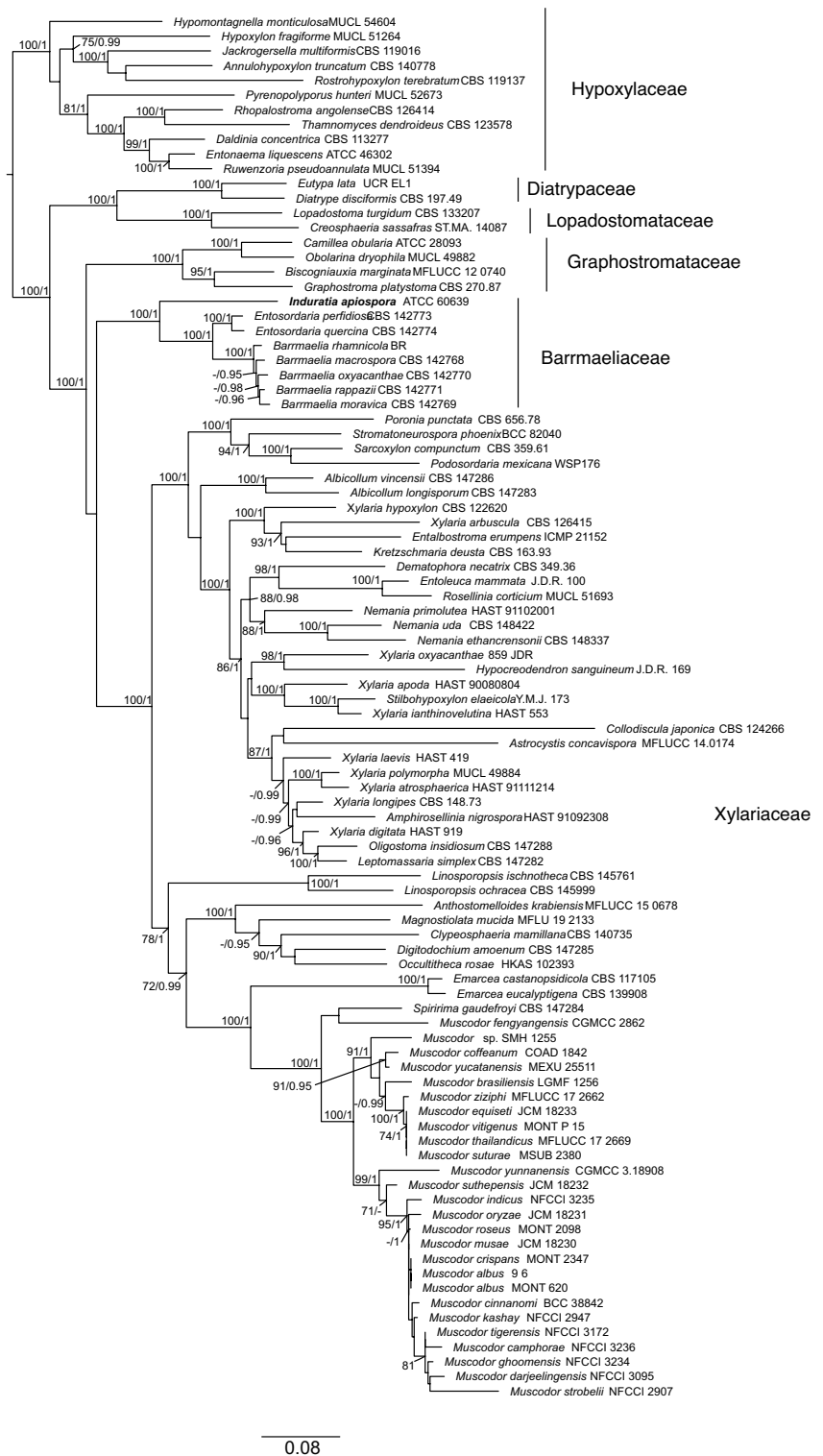


Fig. 3 Maximum Likelihood Tree (ILn = - 89939.9947) inferred from a manually edited alignment of ITS, LSU, *rbp2* and *tub2* sequences featuring sequences derived from Hypoxylaceae, Diatrypaceae, Lopadostomataceae, Graphostromataceae, Barmaeliaceae and Xylariaceae. The position of the newly generated and concatenated sequences of *Induratia apiospora* are marked in bold. Bootstrap and Bayesian posterior probabilities $\geq 70\%$ and ≥ 0.95 , respectively, are given at bipartitions

(*Entosordaria*), or hyaline, two-celled, apiosporous without germ slit (*Induratia*); allantoid, ellipsoid or fusoid, inequilateral, slightly inequilateral or nearly equilateral, with narrowly or broadly rounded ends. Anamorph, where known, libertella-like (*Barrmaelia*; Rappaz 1995), or nodulisporium-like (*Induratia*).

Key to the genera of Barrmaeliaceae

1. Ascospores one-celled, asymmetrically ellipsoid to allantoid, uniformly light to dark brown, with or without a longitudinal germ slit, without appendages; anamorph libertella-like.....*Barrmaelia*.

1. Ascospores two-celled, apiosporous, germ locus absent or consisting of apical radial slits, with or without appendages.....2

2. Ascospores with submedian septum, entirely hyaline, without germ locus, with hyaline cellular appendages at each end while still in the ascus; anamorph nodulisporium-like.....*Induratia*.

2. Ascospores with septum near one end, small ascospore cell hyaline, large ascospore cell dark brown and with an apical germ apparatus consisting of radial slits, without appendages; anamorph unknown.....
.....*Entosordaria*.

Induratia Samuels, E. Müll. & Petrini, *Mycotaxon* 28(2): 484 (1987).

Type species: *Induratia apiospora* Samuels, E. Müll. & Petrini, *Mycotaxon* 28(2): 484 and Fig. 5 (1987).

Mycobank MB 130900

Holotype: New Zealand, North Island, Hokianga Co., Waipoua State Forest, near Yakas Track, on decorticated wood, 30 May 1982, G.J. Samuels and P. Johnston (PDD 44399, lost). **Lectotype:** (designated here, MBT 10010382) New Zealand North Island, Hokianga Co., Waipoua State Forest, near Yakas Track, on decorticated wood, 30 May 1982, G.J. Samuels and P. Johnston (WSP73242).

Ex-type culture: ATCC 60639, deposited by G.J. Samuels; duplicates sent to CBS under accession CBS 149733 and ICMP 24754.

Resurrection of *Muscodor*

The genus *Muscodor* is now placed in the Xylariaceae, where it had originally been accommodated based on phylogenetic relationship, however anamorph morphology, a traditionally important character for the characterization of Xylariales, is still lacking. Below we list all species that were formerly accepted in *Muscodor*,

including those that have been invalidly described in the original publications. The typifications have already been corrected and changed by Samarakoon et al. (2020) according to the rules of the International Code of Nomenclature for Algae, Fungi, and Plants (ICN), when those designations were validated in *Induratia*. We here introduce new combinations for these *Induratia* names in *Muscodor*.

Muscodor Worapong, Strobel & W.M. Hess, *Mycotaxon* 79: 71 (2001).

Type species: *Muscodor albus* Worapong, Strobel & W.M. Hess, *Mycotaxon* 79: 71 (2001).

≡ *Induratia alba* (Worapong, Strobel & W.M. Hess) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Other accepted species

Muscodor brasiliensis (L.C. Pena, Serviński & V. Kava ex Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sánchez, M. Stadler, Voglmayr & C. Lambert, **comb. nov.**

Mycobank MB 846432

Basionym: *Induratia brasiliensis* L.C. Pena, Serviński & V. Kava ex Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 196 (2020).

[originally described as: *Muscodor brasiliensis* L.C. Pena, Serviński & V. Kava, *Microbiol. Res.* 221: 32 (2019), nom. inval., Art. 40.7 (Shenzhen)]

Muscodor camphorae Meshram, N. Kapoor, G. Chopra & S. Saxena [as '*camphora*'], *Mycosphere* 8(4): 571 (2017).

≡ *Induratia camphorae* (Meshram, N. Kapoor, G. Chopra & S. Saxena) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor cinnamomi Suwannar., Bussaban, K.D. Hyde & Lumyong, *Mycotaxon* 114: 19 (2011) [2010].

≡ *Induratia cinnamomi* (Suwannar., Bussaban, K.D. Hyde & Lumyong) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor coffeanus A.A.M. Gomes, Pinho & O.L. Pereira [as '*coffeanum*'], in Hongnan et al., *Cryptog. Mycol.* 36(3): 368 (2015).

≡ *Induratia coffeana* (A.A.M. Gomes, Pinho & O.L. Pereira) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor crispans A.M. Mitch., Strobel, W.M. Hess, Pérez-Vargas & Ezra, *Fungal Divers.* 31: 41 (2008).

≡ *Induratia crispans* (A.M. Mitch., Strobel, W.M. Hess, Pérez-Vargas & Ezra) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor darjeelingensis (Meshram, N. Kapoor & S. Saxena ex Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sanchez, M. Stadler, Voglmayr & C. Lambert, ***comb. nov.***

Mycobank MB 846443

Basionym: *Induratia darjeelingensis* Meshram, N. Kapoor & S. Saxena ex Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 198 (2020).

[originally described as: *Muscodor darjeelingensis* Meshram, N. Kapoor & S. Saxena, *Sydowia* 66(1): 61 (2014), nom. inval., Art. 40.7 (Shenzhen)]

Muscodor equiseti Suwannar. & Lumyong, in Suwannarach, Kumla, Bussaban, Hyde, Matsui & Lumyong, *Ann. Microbiol.* 63(4): 1350 (2013).

≡ *Induratia equiseti* (Suwannar. & Lumyong) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor fengyangensis (Chu L. Zhang ex Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sanchez, M. Stadler, Voglmayr & C. Lambert, ***comb. nov.***

Mycobank MB 846442

Basionym: *Induratia fengyangensis* Chu L. Zhang ex Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 198 (2020).

[originally described as: *Muscodor fengyangensis* Chu L. Zhang, *Fungal Biol.* 114(10): 801 (2010), nom. inval., Art. 40.1 (Shenzhen)]

Muscodor ghoomensis S. Saxena, M. Gupta & Meshram, *Sydowia* 67: 136 (2015).

≡ *Induratia ghoomensis* (S. Saxena, M. Gupta & Meshram) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor heveae (Siri-Udom & Lumyong ex Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sanchez, M. Stadler, Voglmayr & C. Lambert, ***comb. nov.***

Mycobank MB 846436

Basionym: *Induratia heveae* Siri-Udom & Lumyong ex Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 199 (2020).

[originally described as: *Muscodor heveae* Siri-Udom & Lumyong, *Ann. Microbiol.* 66(1): 442 (2015), nom. inval., Art. 40.7 (Shenzhen)]

Muscodor indicus S. Saxena, M. Gupta & Meshram [as '*indica*'], *Sydowia* 67: 136 (2015).

≡ *Induratia indica* (S. Saxena, M. Gupta & Meshram) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor kashay (Meshram, N. Kapoor & S. Saxena ex Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sanchez, M. Stadler, Voglmayr & C. Lambert, ***comb. nov.***

Mycobank MB 846437

Basionym: *Induratia kashay* Meshram, N. Kapoor & S. Saxena ex Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 199 (2020).

[originally described as: *Muscodor kashayum* Meshram, N. Kapoor & S. Saxena, *Mycology* 4(4): 198 (2013), nom. inval., Art. 40.7 (Shenzhen)]

Muscodor musae Suwannar. & Lumyong, in Suwannarach, Kumla, Bussaban, Hyde, Matsui & Lumyong, *Ann. Microbiol.* 63(4): 1347 (2013).

≡ *Induratia musae* (Suwannar. & Lumyong) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 193 (2020).

Muscodor oryzae Suwannar. & Lumyong, in Suwannarach, Kumla, Bussaban, Hyde, Matsui & Lumyong, *Ann. Microbiol.* 63(4): 1349 (2013).

≡ *Induratia oryzae* (Suwannar. & Lumyong) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 194 (2020).

Muscodor roseus Worapong, Strobel & W.M. Hess, *Mycotaxon* 81: 467 (2002).

≡ *Induratia rosea* (Worapong, Strobel & W.M. Hess) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 194 (2020).

Muscodor strobilii Meshram, S. Saxena & N. Kapoor, *Mycotaxon* 128: 96 (2014).

≡ *Induratia strobilii* (Meshram, S. Saxena & N. Kapoor) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 194 (2020).

Muscodor suthepensis Suwannar. & Lumyong, in Suwannarach, Kumla, Bussaban, Hyde, Matsui & Lumyong, *Ann. Microbiol.* 63(4): 1349 (2013).

≡ *Induratia suthepensis* (Suwannar. & Lumyong) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 194 (2020).

Muscodor suturae Kudalkar, Strobel & Riy.-Ul-Hass. [as ‘*sutura*’], *Mycoscience* 53(4): 322 (2012).

≡ *Induratia suturae* (Kudalkar, Strobel & Riy.-Ul-Hass.) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 194 (2020).

Muscodor thailandicus (Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sánchez, M. Stadler, Voglmayr & C. Lambert, *comb. nov.*

Mycobank MB 846434

Basionym: *Induratia thailandica* Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 194 (2020).

Muscodor tigerensis (S. Saxena, Meshram & N. Kapoor ex Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sánchez, M. Stadler, Voglmayr & C. Lambert, *comb. nov.*

Mycobank MB 846438

Basionym: *Induratia tigerensis* S. Saxena, Meshram & N. Kapoor ex Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 199 (2020).

[originally described as: *Muscodor tigerensis* S. Saxena, Meshram & N. Kapoor, *Ann. Microbiol.* 65(1): 53 (2014) [2015], [as ‘*tigerii*’], nom. inval., Art. 40.7 (Shenzhen)].

Muscodor vitigenus Daisy, Strobel, Ezra & W.M. Hess, in Daisy, Strobel, Ezra, Castillo, Baird & Hess, *Mycotaxon* 84: 45 (2002).

≡ *Induratia vitigena* (Daisy, Strobel, Ezra & W.M. Hess,) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 196 (2020).

Muscodor yucatanensis M.C. González, A.L. Anaya, Glenn & Hanlin, *Mycotaxon* 110: 365 (2009).

≡ *Induratia yucatanensis* (M.C. González, A.L. Anaya, Glenn & Hanlin) Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 196 (2020).

Muscodor yunnanensis (C.L. Zhang ex Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sánchez, M. Stadler, Voglmayr & C. Lambert, *comb. nov.*

Mycobank MB 846435

Basionym: *Induratia yunnanensis* C.L. Zhang ex Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 199 (2020).

[originally described as: *Muscodor yunnanensis* C.L. Zhang, in Chen et al., *Mycosphere* 10(1): 193 (2019), nom. inval., Art. 40.8 (Shenzhen)]

Muscodor ziziphi (Samarak., Thongbai, K.D. Hyde & M. Stadler) Cedeño-Sánchez, M. Stadler, Voglmayr & C. Lambert, *comb. nov.*

Mycobank MB 846433

Basionym: *Induratia ziziphi* Samarak., Thongbai, K.D. Hyde & M. Stadler, *Fungal Divers.* 101(1): 196 (2020).

Notes

The specimen SMH 1255 from Puerto Rico, originally studied by Miller and Huhndorf (2005) and later by Samarakoon et al. (2020), has so far been treated as a member of the genus *Induratia*. It should henceforth be treated as a species of *Muscodor*, as its phylogenetic affinities are with the latter genus. Even though the species has not been formally described, the taxonomic name associated with the GenBank Acc. Nos for its DNA sequences ought to be changed.

Emarcea Duong, Jeewon & K.D. Hyde, *Stud. Mycol.* 50(1): 255 (2004).

Mycobank MB 500070.

Type species: *Emarcea castanopsidicola* Duong, Jeewon & K.D. Hyde, *Stud. Mycol.* 50(1): 255 (2004).

Notes

Since the genus *Emarcea* is phylogenetically closely related to the species in the *Muscodor* clade, it is again classified within the Xylariaceae, together with the *Muscodor* species discussed above.

Discussion

Multi-locus molecular phylogenetic analysis proved to serve as a powerful tool to emend placements of taxonomic groups in the Xylariales over the last years, exemplified by the erection of the Barrmaeliaceae to accommodate a phylogenetically distinct and well-supported clade of *Barrmaelia* and *Entosordaria* (Voglmayr et al. 2018). Other examples include the emendation of the Hypoxylaceae in concordance with chemotaxonomic information (Wendt et al. 2018) or the resurrection of *Dematophora*, distinguished from *Rosellinia* species by its synnematal geniculosporium-like anamorph and often a phytopathogenic lifestyle (Wittstein et al. 2020). Regarding the recent synonymisation of *Muscodor* with *Induratia* (Samarakoon et al. 2020), some doubts remained on the validity of that approach, e.g., because the anamorph described by Samuels et al. (1987) was hitherto not observed in the *Muscodor* cultures, which seem to be unable to sporulate. The proposed taxonomy of Samarakoon et al. (2020) was based on the rather similar teleomorphs of *M. thailandicus* (\equiv *I. thailandica*) and *M. ziziphi* (\equiv *I. ziziphi*) and the *Muscodor* sp. (\equiv *Induratia* sp.) specimen reported by Miller and Huhndorf (2005) and characterized by Samarakoon et al. (2020), featuring typical xylariaceous asci and apiospores. The results of the corresponding phylogenies unfortunately did not include any sequences of *Induratia* before erection of its eponymous family, due to a lack of access to molecular data to compare (Samarakoon et al. 2020). Only two years later, Voglmayr et al. (2022) found that DNA sequences of *Spiririma* (\equiv *Helicogermis*) *gaudefroyi*, clustered within the Induratiaceae clade. Since *S. gaudefroyi* features dark ascospores, this gave reason to challenge the concept of restricting apiosporous Xylariales to the Induratiaceae. In our study, the ex-holotype culture of *Induratia apiospora* isolated by Samuels et al. (1987) clustered in a basal position with *Barrmaelia* and *Entosordaria*, while the position of the Barrmaeliaceae

remained unchanged. As the *Induratia* spp. transferred from *Muscodor* showed no relationship with the ex-holotype culture of *I. apiospora*, the genus *Muscodor* is resurrected. Furthermore, this implied that the Induratiaceae cannot be retained as an own family, from a phylogenetic perspective, but should be merged with Barrmaeliaceae (Voglmayr et al. 2022). Morphological characters formerly used to segregate the Induratiaceae from other members of the Xylariaceae, i.e. the presence of apiosporous ascospores, can apparently not serve beyond species discrimination. The resurrected *Muscodor* still showed a paraphyletic structure, indicated by a clade formed by *Spiririma* and *Muscodor fengyangensis*, which may result in further re-arrangements in the future, e.g., when a larger number of anamorph/teleomorph relationships has been established.

Serious degrees of synapomorphies are well documented within the Xylariaceae, illustrated by the paraphyly of the genus *Xylaria*, and so far it has not been possible to resolve this problem even by extensive taxon sampling (Hsieh et al. 2010; Voglmayr et al. 2018, 2022; Voglmayr and Beenken 2020). A similar situation was previously encountered for another family in the Xylariales, the Hypoxylaceae. An important feature of the Hypoxylaceae is the prolific secondary metabolism of its members, which has long been exploited for chemotaxonomic purposes. Recently, it was possible to match chemotaxonomic data by performing genome mining for secondary metabolite-encoding biosynthesis gene clusters (Wibberg et al. 2021; Kuhnert et al. 2021) after sequencing of the full genomes of some representative strains using 3rd generation techniques with phylogenomic approaches. This example indicates the feasibility to sample for additional phenotypic data, i.e. data about the secondary metabolism, and attempting to link it with phylogenetic data on a larger scale to explore taxonomic affinities. Almost all Xylariales are well-known to be very prolific secondary metabolite producers, and in particular *Muscodor* species are known to produce volatile antibiotics. Therefore, following the previously presented example of the Hypoxylaceae, we suggest the inclusion of chemotaxonomic data and in particular studies on the non-volatile metabolites, combined with robust synthetic chemistry enabling the identification of the produced metabolites for the future.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40529-023-00372-1>.

Additional file 1. Images of the isotype located in the Shaw Mycological Herbarium (WSP), provided by Monique H. Slipher, are shown in Fig. S1. Auxiliary information and characteristics covering the molecular

phylogenetic analysis as well as the alignment are given in the Tables S1–S3.

Acknowledgements

We thank Anke Skiba for expert technical assistance and, Adrienne Stanton, Peter Johnston, Gary J. Samuels, Orlando Petrini, for valuable correspondence in the course of our search for the type of *Induratia apiospora*. Monique H. Slipher is thanked for providing information and images about the state of the isotype of *I. apiospora* located in WSP. This article is dedicated to the memory of Prof. Jack D. Rogers

Author contributions

CL: conceptualization, supervision, analysis, writing—original draft preparation; HV: analysis; MCS: methods and analysis; RS: methods and analysis; MS: analysis, writing—original draft preparation, resources; KB: analysis, writing—review and editing. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding

Open Access funding enabled and organized by Projekt DEAL. MCS gratefully acknowledges a PhD stipend from The National Secretariat of Science, Technology and Innovation of the Republic of Panama (SENACYT) and the Institute for the Development of Human Resources (IFARHU). We are also grateful to the LifeScience Foundation (Munich) for a PhD stipend for CL. MS would like to thank the Deutsche Forschungsgemeinschaft for a Research Unit grant in the SPP 1991 (TaxonOmics).

Data availability

All data except for the DNA sequences, which are deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) are available in the manuscript or the Additional file 1.

Declarations

Competing interests

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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Received: 21 November 2022 Accepted: 25 March 2023

Published online: 13 April 2023

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