# Less is better than more: reassessing the monotypic nature of Irpicodon (Amylocorticiaceae, Basidiomycota)

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Abstract. Within the family Amylocorticiaceae, conspicuous morphological affinities exist among the previously defined species Irpicodon pendulus, Plicaturopsis crispa and Plicatura nivea. With the aid of macro- and micro-morphological characters and phylogenetic evidence based on 3-gene datasets, a comprehensive reassessment of generic boundaries within these taxa was conducted. Upon reviewing the systematic position of the taxa included, the three genera emerged as a well-defined monophyletic clade. Based on the genetic divergence observed, coupled with the robust support for monophyly, similarities in ecological roles, and congruence in macro- and micromorphological characteristics, we suggest a revised genus concept that synonymizes Irpicodon (as well as Plicaturopsis) with the earliest established genus Plicatura.

Key words: Amylocorticiales, Central Europe, Hungary, indicator species, old-growth forest, phylogeny, Pinus, wood-inhabiting

# Introduction

In recent years, taxonomists have proposed numerous new fungal genera to better classify both known and newly described species into monophyletic groups. In 2019, He et al. accepted 1,928 genera within the Basidiomycota (He et al. 2019), and by 2024, their updated classification recognized 2,134 genera within the phylum (He et al. 2024). This increase of over 200 accepted basidiomycetous genera in just five years underscores the substantial progress made in fungal taxonomy and the resolution of phylogenetic relationships. These reclassifications are largely driven by advancements in molecular and genetic research, which have provided more accurate insights into the evolutionary relationships among fungi, allowing taxonomists to refine fungal taxonomy and ensure that genera reflect natural evolutionary lineages. Taxonomic studies predominantly focus on proposing new taxa, leading to less emphasis on the critical reassessment of the systematic position of formerly established genera. This is particularly evident in smaller or monophyletic genera, although revisiting these taxa – originally defined solely by morphological characteristics - using modern integrative taxonomic approaches could also facilitate

the establishment of a more natural and accurate classification system.

During a systematic survey of wood-inhabiting macrofungi in a Hungarian relict Scots pine forest in 2019, we discovered a distinctive species, currently recognized in the literature as Irpicodon pendulus. This peculiar fungus in the field reminded us of the well-known species Plicaturopsis crispa, which is primarily associated with deciduous trees in Hungary. The macromorphological similarity between the two species prompted us to investigate their potential phylogenetic relationship and to determine whether I. pendulus truly represents a genus-level distinction from its sibling taxa.

Irpicodon Pouzar is a monotypic fungal genus established in 1966, with Sistotrema pendulum Alb. & Schwein. designated as the type species (Pouzar 1966). This wood-inhabiting fungus was described by Albertini and Schweinitz (1805) based on a specimen collected in a Scots pine (Pinus sylvestris) forest in Germany. Based on morphological characteristics of the trama, Fries (1821) initially placed S. pendulum within the genus Hydnum L.; subsequently, he reclassified it into the genus Irpex Fr. based on further taxonomic considerations (Fries 1828). A variety of species exhibiting different hymenophore types were initially encompassed within this genus. However, as morphological criteria underwent refinement, species were subjected to reassignment, and Irpex evolved into a well-defined genus, supported by phylogenetic evidence (Li et al. 2022). Irpex was typified by I. lacteus (Fr.) Fr. (Clements & Shear 1931), which has a dimitic

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hyphal system, cystidia in the hymenium, and inamyloid basidiospores (Maas Geesteranus 1963). In contrast, based on examination of a specimen in the National Museum in Prague, Pouzar (1966) proved that I. pendulus (Alb. & Schwein.) Pouzar has a monomitic hyphal system, lacks cystidia in the hymenium, and basidiospores are amyloid. Based on these characteristics, he concluded that the two species cannot belong to the same genus, and I. pendulus should be classified into a new genus, which he named Irpicodon. Pouzar (1966) believed that the genus Irpicodon might be closely related to Anomoporia Pouzar and Amylocorticium Pouzar, characterized by poroid and smooth hymenophores, respectively. Subsequent phylogenetic studies confirmed the relationship between these genera, revealing that based on nuc-LSU rRNA gene sequences, the closest known species is Plicaturopsis crispa (Pers.) D.A. Reid (type species of Plicaturopsis D.A. Reid) (Parmasto 1995; Niemelä et al. 2007; Binder et al. 2010; Zhou et al. 2016). This species, however, shows a close relationship with Plicatura nivea (Fr.) P. Karst. (syn. Plicatura alni Peck), which is the type species of the earlier described genus Plicatura Peck (Ginns 1970).

Within the family *Amylocorticiaceae*, notable morphological affinities exist between the species *Irpicodon pendulus*, *Plicaturopsis crispa* and *Plicatura nivea*. Therefore, the aim of this study is to conduct a comprehensive review of generic boundaries within these taxa and reassess the necessity of segregating the monotypic genus *Irpicodon*, based on macro- and micro-morphological characteristics alongside phylogenetic evidence.

## Materials and methods

## Morphological examination

The specimens were collected from a relict pine forest near Fenyőfő in Hungary during 2019 and 2022, where the species exhibited considerable prevalence. Analysis of the macroscopic features of the samples relied on assessments of fresh basidiomata in conjunction with photographic documentation. Dried basidiomata are deposited in the fungarium of the Department of Botany, Hungarian University of Agriculture and Life Sciences, under the designation "BPalla". Microscopic examinations, along with photographic documentation and morphometric measurements, were conducted on slide-mounted specimens treated with Melzer's reagent. Microscopic analysis was performed at 1,000× magnification using a Zeiss Axio Imager A2 light microscope, outfitted with an AxioCam HRc camera. Quantitative measurements were executed utilizing Axio Vision Release 4.8 software. Throughout the descriptions, standard abbreviations were employed, including MR for Melzer's reagent, MR+ for amyloid reactions, L for the range of spore lengths, Lav for the mean spore length, W for the range of spore widths, Wav for the mean spore width, Q for the variation in the lengthto-width ratios, Qav for the average length-to-width ratio, and n for the number of spores measured.

#### Molecular analyses

DNA extraction from dried material was performed using the EZNA Plant DNA Kit (Omega Bio-tek, Norcross, GA, USA), following the manufacturer's protocol. Amplification of the ITS regions utilized primers ITS1F and ITS4B (White et al. 1990; Gardes & Bruns 1993), and the same primers were employed for sequencing. The primers LR0R (Rehner & Samuels 1994) and LR5 (Vilgalys & Hester 1990) were used to amplify the partial 28S nrRNA gene (LSU) of the nrDNA operon region. For amplification of the most variable region of the second largest subunit of RNA polymerase II gene (rpb2), primers fRPB2-5F/ bRPB2-7.1R (Liu et al. 1999; Matheny 2005; Matheny et al. 2007) were used. PCR reactions were carried out on a thermal cycler with the following conditions (parameters for LSU and rpb2 are shown between brackets, if different): initial denaturation at 95°C for 2 min 30 s (95°C for 5 min), followed by 35 cycles of denaturation at 95°C for 30 s (95°C for 1 min), annealing at 60°C for 30 s (55°C for 2 min), and extension at 72°C for 2 min, with a final extension at 72°C for 10 min. Purification of PCR products was conducted using an ExoSAP-IT purification kit (Amersham Biosciences), and subsequently, the purified samples were sent to the Biological Research Centre, Szeged for sequencing. Sequencing was performed using a Sanger Sequencing 3,500 Dx Series Genetic Analyzer (Applied Biosystems<sup>TM</sup>, Thermo-Fisher, Waltham, MA, United States). Raw sequences underwent editing using BioEdit (Hall 1999), with manual removal of the primers' connection region. Newly-generated sequences were submitted to GenBank. Studied voucher collections are presented in Table 1. Sequences of each locus (ITS, LSU and rpb2), together with sequences of related species downloaded from GenBank, were aligned separately with the online MAFFT v. 7.0 using the G-INS-i strategies (Katoh & Standley 2013). The alignments were checked and edited by manual adjustment in SeaView 5 (Gouy et al. 2021). Maximum Likelihood (ML) analysis was performed using RAxML in raxmlGUI2.0 (Stamatakis 2014; Edler et al. 2021) with 1,000 rapid bootstraps and GTR-GAMMA substitution model. The resulting phylogenetic tree was visualized in MEGA11 (Tamura et al. 2021).

## Results

#### Phylogenetic analyses

The three-locus molecular phylogenetic analyses of the newly generated and representative sequences of genera belonging to the *Amylocorticiaceae* were based on 39 ITS, 32 LSU and 13 *rpb2* sequences (Table 1). According to the results, the newly sequenced Hungarian samples clustered into the '*Irpicodon pendulus*' clade with strong support (ML = 100%) (Fig. 1).

The *Irpicodon pendulus* samples clustered together with the group formed by *Plicatura nivea* and *Plicaturopsis crispa* samples, collectively forming a well-delineated clade with strong support (ML=100%). Based on the findings from our phylogenetic analyses, we propose

Species	Voucher Specimen	GenBank Accession Number			D.C.
		ITS	LSU	rpb2	Kelerences
Amyloceraceomyces angustisporus	He2824	MK520872	MK491337	_	Yuan et al. (2020)
Amyloceraceomyces angustisporus	He2819	MK520871	-	_	Yuan et al. (2020)
Amylocorticium subsulphureum	CFMR:HHB-13817	GU187506	GU187562	GU187773	Binder et al. (2010)
Amylocorticium canadense	MO414701	OK346339	_	_	Unpublished
Amylocorticium cebennense	CFMR:HHB-2808	GU187505	GU187561	GU187770	Binder et al. (2010)
Amylocorticium indicum	He5357	MK520874	MK491339	_	Unpublished
Amylocorticium subincarnatum	AS 95	AY463377	AY586628	_	Larsson et al. (2004)
Anomoloma albolutescens	 CFMR:L-6088	GU187507	GU187563	GU187768	Binder et al. (2010)
Anomoloma flavissimum	Dai 2968a	KT954952	KT954966	_	Song et al. (2016)
Anomoloma luteoalba	Cui 2687	KT954961	KT954975	_	Song et al. (2016)
Anomoloma myceliosum	CFMR:MJL-4413	GU187500	GU187559	GU187766	Binder et al. (2010)
Anomoloma rhizosum	Cui 9717	KT954958	KT954972	_	Song et al. (2016)
Anomoloma submyceliosum	Dai 7402	KT954964	KT954977	_	Song et al. (2016)
Anomoporia bombycina	CFMR:L-6240	GU187508	GU187564	GU187765	Binder et al. (2010)
Anomoporia kamtschatica	KHL 11072	AY463379	AY586630	_	Larsson et al. (2004)
Anomoporia vesiculosa	Cui 9523	KT954950	_	_	Song et al. (2016)
Ceraceomyces tessulatus	KHL 16429	KU518951	KU518951	_	Chikowski et al. (2016)
Ceraceomyces tessulatus	KHL 8474	AY463391	AY586642	_	Larsson et al. (2004)
Ceraceomyces atlanticus	URM85888	KX685875	KX685874	_	Chikowski et al. (2016)
Leptosporomyces galzinii	KHL 11079	EU118642	EU118642	_	Larsson (2007)
Leptosporomyces fuscostratus	RGC 121006	UDB024819	_	_	Unpublished
Leptosporomyces raunkiaeri	CFMR:HHB-7628	GU187528	GU187588	GU187791	Binder et al. (2010)
Plicatura crispa <sup>1</sup>	AFTOL-ID 1924	DQ494686	DQ470820	GU187816	Binder et al. (2010)
Plicatura crispa <sup>1</sup>	GB/KHL8615	DQ144620	DQ144620	_	Unpublished
Plicatura nivea	CBS:482.72	MH860536	MH872242	_	Vu et al. (2019)
Plicatura nivea	S.D. Russell ONT WCMB23	OR167801	_	_	Unpublished
Plicatura pendula <sup>2</sup>	GB/B.Norden	DQ144619	DQ144619	_	Chikowski et al. (2016)
Plicatura pendula	BPalla19111524	PQ722792	PQ721673	PQ678963	This study
Plicatura pendula	BPalla19111526	PQ722793	PQ721674	PQ678964	This study
Podoserpula pusio	AFTOL-ID 1522	DQ494688	DQ470821	GU187804	Binder et al. (2010)
Podoserpula aliweni	SGO 170081	MN970529	_	_	Garnica et al. (2021)
Podoserpula ailaoshanensis	BJFC ZJL2015015	KU324484	KU324487	_	Zhou et al. (2016)
Podoserpula ailaoshanensis	Liu170	KU324485	KU324488	_	Zhou et al. (2016)
<i>Podoserpula</i> sp.	FFCL1456	MT912007	MT912029	_	Garnica et al. (2021)
Jaapia argillacea	CBS:252.74	NR_119766	NG_042523	GU187788	Binder et al. (2010)
Jaapia ochroleuca	KHL 8433	EU118637	EU118637	_	Larsson (2007)

Table 1. Species, voucher specimens and GenBank accession numbers of sequences used in the phylogeny of Irpicodon pendulus and related taxa.

<sup>1</sup>as Plicaturopsis crispa; <sup>2</sup>as Irpicodon pendulus

reclassifying the genera *Irpicodon* and *Plicaturopsis* under the genus *Plicatura*. Within the genus *Plicatura*, the species *Irpicodon pendulus*, as well as *Plicatura nivea* and *Plicaturopsis crispa*, form two distinct clades, justifying a subgeneric classification (Fig. 1). Considering that the combination *Plicatura crispa* (Pers.) Rea was already published by Rea (1922), the proposal of a new combination is only necessary for *Irpicodon pendulus*.

## Taxonomy

*Plicatura* subgen. *Irpicodon* (Pouzar) Palla, V. Papp & Dima, comb. & stat. nov.

MycoBank MB 856843

Basionym: Irpicodon Pouzar, Folia Geobot. Phytotax. Bohemoslov. 1: 371. 1966.

Plicatura pendula (Alb. & Schwein.) Palla, V. Papp& Dima, comb. nov.(Fig. 2)

MycoBank MB 856842

Basionym: *Sistotrema pendulum* Alb. & Schwein., Consp. fung. (Leipzig): 261. 1805; Typus: Germany, on *Pinus sylvestris*, (Tab. VI, fig. 7. [image!]).

Synonyms: *Hydnum pendulum* (Alb. & Schwein.) Fr., Syst. Mycol. (Lundae) 1: 413. 1821.

 $\equiv$  *Irpex pendulus* (Alb. & Schwein.) Fr., Elench. Fung. (Greifswald) 1: 143. 1828.

 $\equiv$  *Xylodon pendulus* (Alb. & Schwein.) Kuntze, Revis. Gen. Pl. (Leipzig) 3(3): 541. 1898.

 $\equiv$  *Irpicodon pendulus* (Alb. & Schwein.) Pouzar, Folia Geobot. Phytotax. Bohemoslov. 1: 371. 1966.

= Sistotrema conchatum Ehrenb., Sylv. Mycol. Berol. (Berlin): 30. 1818.

**Description**. Basidiomata annual, growing in small clusters, and loosely attached to the substrate; mostly pileate, dimidiate, or basally substipitate, flabelliform or lobed; thin (approximately 1 mm thick) and small, up to 2.5 cm wide, with a softly ceraceous texture; initially whitish to pale cream on the upper surface when young, later becoming yellowish to yellowish-brown, except for the margin; surface from nearly smooth to radially wrinkled.



0.1

Figure 1. Phylogenetic placement of *Plicatura pendula* (in bold) and delimitation of redefined *Plicatura* within the family *Amylocorticiaceae* based on ML inference of the ITS+28S+*rpb2* data set. Numbers on nodes represent bootstrap values greater than 50%. The scale bar indicates the number of expected substitutions per site.

Hymenophore whitish to pale cream, characterized by variable shapes and irregularly aculeate or almost radially arranged flat to lamelloid teeth. Hyphal system monomitic, generative hyphae with clamp-connections and measuring 3–4 µm in width, sparsely interwoven, and with thin inamyloid, indextrinoid, and acyanophilous walls; the upper surface of the basidioma composed of closely appressed hyphae, without forming a pellicle. Cystidia none. Basidia thin-walled and narrowly clavate, with a basal clamp connection and 4 sterigmata, measuring  $14-19 \times 4-5 \mu m$ . Basidiospores suballantoid to reniform, thin-walled, smooth, with amyloid, indextrinoid, and acyanophilous walls, measuring  $L = (3.73)4.12 - 4.44 - 4.72(5.27) \mu m$ , Lav = 4.45  $\mu$ m; W = (1.99)2.11–2.29–2.40(3.01)  $\mu$ m, Wav = 2.34  $\mu$ m; Q = (1.53)1.71–1.89–2.11(2.39), Qav = 1.93 (n=50).

**Notes.** The basidiomata of *Plicatura nivea* are also annual, similarly soft and lax, resupinate to dimidiate with an upperside that is whitish when young, later turning pale beige-brown; however, the hymenophore is initially smooth, then distinctly and irregularly plicate

(Ginns 1970, Eriksson et al. 1981). This species is similar to P. pendula in terms of major micromorphological features. Its hyphal system is also monomitic, consisting of hyphae with clamp connections; cystidia are absent, and basidia are 4-sterigmate with a basal clamp connection; the basidiospores are narrower, allantoid, but also smooth, thin-walled, and amyloid (Eriksson & Ryvarden 1976; Eriksson et al. 1981). Regarding the micromorphological characteristics, P. crispa shows significant similarity to P. pendula; its hyphal system is also monomitic and composed of generative hyphae with clamp connections, lacking cystidia, and its basidia are 4-sterigmate, and subclavate to subcylindrical. The basidiospores are somewhat smaller and narrower  $[L = (3.43)3.64 - 3.85 - 4.00(4.19) \mu m, Lav = 3.81 \mu m;$  $W = (0.99)1.17 - 1.24 - 1.33(1.53) \mu m$ ,  $Wav = 1.25 \mu m$ ; Q = (2.41)2.82 - 3.06 - 3.37(3.97), Qav = 3.10; n = 50],allantoid, but also thin-walled, smooth, and amyloid. The size, shape, and appearance of the basidiomata of the two species also show a resemblance, but P. crispa can be easily distinguished by its radially folded hymenophore (Pouzar 1966; Eriksson et al. 1981).



**Figure 2**. Basidiomata of *Plicatura pendula* in the old Scots pine forest of Fenyőfő, Hungary (A–F). A – BPalla20102912; B – BPalla20102914; C – BPalla19111525; D – BPalla19111527; E – BPalla19111524; F – BPalla19111526. Photos: V. Papp.

Specimens examined. HUNGARY. Győr-Moson-Sopron County, Bakony Mts, forestry region of Bakonyszentlászló, Fenyőfő, in old Pinus sylvestris forest characterized by the sandy Festuco vaginatae-Pinetum sylvestris association, on Pinus sylvestris log, 47°21.2960'N, 17°46.077'E, 8 Jun. 2019, leg. B. Palla & V. Papp (BPalla1906084); on Pinus sylvestris log, 47°21.3890'N, 17°46.3850'E, 15 Nov. 2019, leg. B. Palla & V. Papp (BPalla19111524); on Pinus sylvestris log, 47°21.321'N, 17°46.536'E, 15 Nov. 2019, leg. B. Palla & V. Papp (BPalla19111525); on Pinus sylvestris log, 47°21.3460'N, 17°46.4770'E, 15 Nov. 2019, leg. B. Palla & V. Papp (BPalla19111526); on Pinus sylvestris log, 47°21.3790'N, 17°46.473'E, 15 Nov. 2019, leg. B. Palla & V. Papp (BPalla19111527); on Pinus sylvestris log, 47°21.3490'N, 17°46.4750'E, 29 Oct. 2020, leg. B. Palla & V. Papp (BPalla20102912); on Pinus sylvestris log, 47°21.3880'N, 17°46.47'E, 29 Oct. 2020, leg. B. Palla & V. Papp (BPalla20102914).

## Discussion

Within the order *Amylocorticiales* resupinate basidiomata are dominant, although effused, effused-reflexed, nearly pileate and multistoried pileate-stipitate structures also occur, exhibiting a variety of hymenial configurations (Hibbett et al. 2014). Recently, 14 genera have been accepted within *Amylocorticiales* (He et al. 2024), including *Plicatura*, *Plicaturopsis* and *Irpicodon*. The classification of aphyllophoroid basidiomycetes at the genus level has consistently sparked debate and is susceptible to subjectivity, particularly in cases where concepts are proposed solely based on morphological characteristics, leading to subjective criteria for classification. Integrative taxonomic studies have revealed the need to reclassify certain clades of previously morphologically delimited, but phylogenetically distinct, lineages into newly described genera in numerous cases (e.g., Papp & Dima 2018; Wang & Dai 2022; Wu et al. 2022; Liu et al. 2023; Miettinen et al. 2023). However, there were also examples of taxa previously considered as distinct genera, which have been merged based on insights derived from phylogenetic studies (e.g., Justo & Hibbett 2011; Gorjón et al. 2021; Spirin et al. 2024; Kõljalg et al. 2024). The science of ranking is inherently subjective (Liu et al. 2016), so when a taxon represents a basal group within a phylogenetic clade, delineating genus boundaries requires individualized assessment and careful evaluation.

The results of our phylogenetic analysis based on a 3-gene dataset (ITS, LSU, rpb2) supported the monophyly of the Plicatura clade (incl. P. nivea, P. crispa, P. pendula) with a statistically high bootstrap value (ML = 100%). Phylogenetic analyses revealed two distinct subgeneric clades within the genus Plicatura. Plicatura nivea and P. crispa, which typically colonize deciduous trees, are identified as closely related sister species. In contrast, P. pendula, which is specialized to Scots pine, occupies an early-divergent lineage within the clade. The continuous decomposition of dead wood by wood-decay macrofungi increases their interactions with host plants, driving the fungi to undergo evolutionary adaptations. However, Zhang et al. (2024) found that wood-decay macrofungi do not exhibit significant evolutionary adaptations to gymnosperms, but show substantial adaptations to angiosperms. Therefore, the evolutionary divergence within the two subgenera of the Plicatura genus may have been driven by host plant specialization. Nevertheless, the angiosperm-associated P. crispa has also been observed on conifers in North America (Ginns & Lefebvre 1993). In contrast, P. pendula is exclusively associated with gymnosperms, particularly Pinus sylvestris (Eriksson & Ryvarden 1976; Kotiranta & Saarenoksa 1993; Dai et al. 2004; Bernicchia & Gorjón 2020).

Species of the accepted genera within the Amylocorticiales mainly form corticioid and resupinate basidiomata and produce various types of hymenophore (e.g., smooth, merulioid, or poroid) (Binder et al. 2010; Hibbett et al. 2014; He et al. 2024). Compared to other genera in the order, members of the Plicatura clade are readily distinguishable by their pendant fan-shaped effused-reflexed basidiomata (Larsson 2007). The historical genus-level segregation of species within this clade (Reid 1964; Pouzar 1966) was primarily driven by overemphasizing the hymenophore structure as a taxonomic criterion. This perspective is deeply rooted in the history of macrofungal taxonomy, dating back to the works of Christiaan Hendrik Persoon and Elias Magnus Fries (Persoon 1794; Fries 1821, 1823, 1829), who based their classification primarily on the type of hymenophore. Although over time increasingly complex fungal classification systems have been proposed, and their methodologies and taxonomic systems have influenced mycological practices, especially in the pre-molecular era. However, phylogenetic analyses have revealed that certain macromorphological features, including hymenophore types, can exhibit considerable variation even among closely related species, and alone do not necessarily warrant genus-level differentiation (Runnel et al. 2019; Meiras-Ottoni et al. 2021; Zhang et al. 2022). Therefore, we consider that the inclusion of *Irpicodon* within *Plicatura* (the former characterized by dimidiate basidiomata and an irregularly aculeate hymenophore) would not significantly impact the taxonomic integrity of the latter genus. Such an inclusion would be further reinforced if *Plicaturopsis*, which also has a distinct, merulioid hymenophore, is treated under the genus *Plicatura*.

Considering that the genus name (unlike names of other higher taxa) is part of the binomial, and is also used by individuals outside of taxonomy, unnecessary changes to these names should be avoided. At the same time, splitting well-defined monophyletic groups into smaller, distinct genera can hinder the understanding of species relationships and complicate scientific communication. While the segregation of certain genera is often necessary to preserve monophyly, we believe that where possible, it is preferable to broaden the genus boundaries, as this approach can promote greater taxonomic stability. In the case of the fungal group discussed in this study, instead of recognizing three genera (Plicatura, Plicaturopsis, and Irpicodon), a two-genus classification (Plicatura and Irpicodon) could be applied. However, the most stable solution is to consolidate all species into a single, broader monophyletic genus Plicatura.

## Conclusions

Upon reassessing the systematic position of the monotypic genus Irpicodon, we unveiled that it constitutes a well-defined clade together with the genus Plicatura (including Plicaturopsis) based on both phylogenetic and morphological evidence. Based on the genetic divergence observed in this study, coupled with the robust support for monophyly, similarities in ecological role as wood-decaying white-rot fungi, and congruence in macro- and micromorphological characteristics, we suggest a revised and enlarged genus concept by synonymizing Irpicodon (as well as *Plicaturopsis*) with the earlier established genus Plicatura. The habitat and morphological characteristics of P. pendula (subgen. Irpicodon), especially the structure of its hymenophore, make it distinctly identifiable in the field, distinguishing it from the other two species, P. nivea and P. crispa (subgen. Plicatura). Nevertheless, we believe that these differences are insufficient to warrant the recognition of the Plicatura clade as comprising two or even three separate genera. Furthermore, both the toothlike and the wrinkled hymenophore should be considered autapomorphies of the species. Unlike synapomorphies, autapomorphies that occur individually in only one species are not suitable for taxonomic conclusions. Thus, in this case, an expanded genus Plicatura represents the clearest phylogenetic solution. Although the determination of genus boundaries can be influenced by individual

perspectives in addition to the objective evaluation of results, we hope that this work can serve as an example for the examination and taxonomic assessment of monophyletic groups where dividing into multiple genera is not necessarily required, or where the merging of previously morphologically separated genera could be justified.

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