

***Inonotus chrysomarginatus*, a newly recorded species in Taiwan, and a list of Taiwan's known *Inonotus* species as well as segregated species from the genus**

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ABSTRACT

Species in Taiwan that are accepted in *Inonotus* or have been connected to the generic name are provided. Eight species are accepted in *Inonotus*, including *I. chrysomarginatus*, which is newly recorded in Taiwan. Twelve species that were previously associated with the genus *Inonotus* have now been reclassified and placed in various other genera, including *Cylindrosporus*, *Fuscoporia*, *Hymenochaete*, *Inocutis*, *Mensularia*, *Neomensularia*, *Ochrosporellus*, and *Sanghuangporus*.

Key words: *Inonotus*, molecular phylogeny, taxonomy, wood-decay fungi

Introduction

The genus *Inonotus* P. Karst., typified by *I. hispidus* (Bull.) P. Karst., belongs to Hymenochaetales Oberw. of Basidiomycota R.T. Moore (Karsten 1879). Species of *Inonotus* are white-rot fungi of angiosperm and gymnosperm wood, forming basidiocarps typically brown or brownish, annual, resupinate, effuse-reflexed or pileate. Microscopically, *Inonotus* usually has a monomitic hyphal system, simple-septate hyphae, and colorless or yellowish to brownish basidiospores.

Wagner and Fischer (2002) and Wu et al. (2022) regarded *Inonotus* as a polyphyletic group. Many studies have been conducted to revise the generic concept of *Inonotus* based on morphological and

molecular phylogenetic evidence, resulting in many species being segregated to other genera, such as *Cylindrosporus* L.W. Zhou, *Flaviporellus* Murrill, *Inonotus sensu stricto*, *Inocutis* Fiasson & Niemelä, *Inonotopsis* Parmasto, *Mensularia* Lázaro Ibiza, *Nothonotus* Y. C. Dai, F. Wu, L.W. Zhou, Vlasák & B. K. Cui, *Onnia* P. Karst, *Pachynotus* Y. C. Dai, F. Wu, L.W. Zhou & B. K. Cui, *Pseudoinonotus* T. Wagner & M. Fischer, *Rigidonotus* Y. C. Dai, F. Wu, L.W. Zhou, Vlasák & B. K. Cui, *Sanghuangporus* Sheng H. Wu, L. W. Zhou & Y. C. Dai, and *Tropicoporus* L. W. Zhou, Y. C. Dai & Sheng H. Wu (Wagner and Fischer 2002; Tian et al. 2013; Vlasák et al. 2013; Zhou et al. 2016, Wu et al. 2022).

Over the past four decades, 20 species have been associated with the genus *Inonotus* in Taiwan

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(Table 1). While many species were initially classified as *Inonotus*, they have since been transferred to other genera. Currently, seven species remain in the genus *Inonotus*: *I. chihshanyenus* (Chang and Chou 1998), *I. chilanshanus* (Chang and Chou 2000), *I. cuticularis* (Chen 1976), *I. fushanianus* (Chang 1997), *I. juniperinus* (Chen 1976), *I. rickii* (Chang and Fu 1998), and *I. rodwayi* (Dai and Wu 2002). This study provides the first report of *Inonotus chrysomarginatus* in Taiwan based on morphological and molecular phylogenetic evidence.

Materials and Methods

Morphological study

All specimens studied are deposited at the herbarium of the National Museum of Natural Science in Taiwan (TNM). Free-hand thin sections of fruiting body were prepared using three different mounting media for microscopic studies: (1) 5% (w/v) potassium hydroxide (KOH) with 1% (w/v) phloxine for observation and measurement; (2) Melzer's reagent (IKI) to test amyloidity and dextrinoidity; (3) Cotton blue (CB) to check cyanophily. The prepared slides were examined using a Leica DM2500 microscope (Leica, Wetzlar, Germany) at magnifications up to $\times 1000$.

DNA extraction, polymerase chain reaction (PCR), and sequencing

DNA from dried specimens or mycelia from pure cultures on malt extract agar (MEA) was extracted using the Plant Genomic DNA Extraction Miniprep System (Viogene-Biotek Corp., New Taipei City, Taiwan) following the manufactur-

er's protocol. Tissue disruption and homogenization were performed prior to extraction using liquid nitrogen and Tissue Lyser II (Qiagen, Hilden, Germany). The internal transcribed spacer (ITS) region of the nuclear ribosomal DNA (rDNA) was amplified using primer pairs ITS1/ITS4 or ITS1/ITS5 (White et al. 1990), while 28S rDNA was amplified using primer pairs LR0R/LR5 or LR0R/LR3 (Vilgalys and Hester 1990). PCR protocols for ITS and 28S rDNA followed Chen et al. (2021). PCR products were purified and sequenced directly by MB Mission Biotech Company (Taipei City, Taiwan). Nucleotide sequences were manually edited and assembled using BioEdit v7.2.5 (Hall 1999). All newly obtained sequences were submitted to GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) (Table 2).

Alignment and phylogenetic analyses

Sequences were aligned by MAFFT 7.409 with the G-INS-i option (Kato and Standley 2013) and manually adjusted in MEGA 10 (Kumar et al. 2018). The ITS+28S dataset was used to investigate the systematic positions of *Inonotus* species, with *Phaeotremella foliacea* (Pers.) Wedin, J.C. Zamora & Millanes selected as the outgroup. Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed using RAxML-HPC 8.0.2 (Stamatakis 2014) and MrBayes v. 3.2.6 (Ronquist et al. 2012), respectively, on the CIPRES Science Gateway (Miller et al. 2010). Sequence alignments are deposited at TreeBASE (submission number: 29839; www.treebase.org). The ML analyses were conducted using a GTRCAT model with 1,000

Table 1. Species in association with *Inonotus* in Taiwan and their redistribution.

Original name	Accepted name	Reference
<i>Inonotus chihshanyenus</i> T. T. Chang & W. N. Chou	<i>Inonotus chihshanyenus</i>	Chang and Chou (1998)
<i>Inonotus chilanshanus</i> T. T. Chang & W. N. Chou	<i>Inonotus chilanshanus</i>	Chang and Chou (2000)
<i>Inonotus chrysmarginatus</i> B. K. Cui & Y. C. Dai	<i>Inonotus chrysmarginatus</i>	Cui et al. (2011), present study
<i>Inonotus cuticularis</i> (Bull.) P. Karst.	<i>Inonotus cuticularis</i>	Chen (1976), Karsten (1879)
<i>Inonotus flavidus</i> (Berk.) Ryvarden	<i>Cylindrosporus flavidus</i> (Berk.) L.W. Zhou	Chang (1996), Zhou (2015)
<i>Inonotus formosanus</i> T. T. Chang & W. N. Chou	<i>Fuscoporia formosana</i> (T. T. Chang & W. N. Chou) T. Wagner & M. Fisch	Chang and Chou (1998), Wagner and Fisch (2002)
<i>Inonotus fushanus</i> T. T. Chang	<i>Inonotus fushanians</i>	Chang (1997)
<i>Inonotus iodinus</i> (Mont.) Murrill	<i>Hymenochaete iodina</i> (Mont.) Baltazar & Gibertoni	Chang et al. (1994), Gomes-Silva et al. (2012)
<i>Inonotus juniperinus</i> Murrill	<i>Inonotus juniperinus</i> Murrill	Chen (1976), Murrill (1908)
<i>Inonotus kanehirae</i> (Yasuda) Imazeki	<i>Neomensularia kanehirae</i> (Yasuda) F. Wu, L.W. Zhou & Y. C. Dai	Chen (1976), Wu et al. (2016)
<i>Inonotus mikadoi</i> (Lloyd) Gilb. & Ryvarden	<i>Inocutis mikadoi</i> (Lloyd) Y. C. Dai & F. Wu	Chang et al. (1994), Wu et al. (2022)
<i>Inonotus nodulosus</i> (Fr.) P. Karst.	<i>Mensularia nodulosa</i> (Fr.) T. Wagner & M. Fisch.	Chang et al. (1994), Wagner and Fisch (2001)
<i>Inonotus pachyphloeus</i> (Pat.) T. Wagner & M. Fisch.	<i>Ochrosporellus pachyphloeus</i> (Pat.) Y.C. Dai & F. Wu	Chang and Chou (2003), Wu et al. (2022)
<i>Inonotus radiatus</i> (Sowerby) P. Karst.	<i>Mensularia radiata</i> (Sowerby) Lázaro Ibiza	Tschen et al. (2000), Wu et al. (2022)
<i>Inonotus rickii</i> (Pat.) D. A. Reid	<i>Inonotus rickii</i>	Chang and Fu (1998)
<i>Inonotus rodwayi</i> D. A. Reid	<i>Inonotus rodwayi</i>	Dai and Wu (2002)
<i>Inonotus sanghuang</i> S. H. Wu, T. Hatt. & Y. C. Dai	<i>Sanghuangporus sanghuang</i> (S. H. Wu, T. Hatt. & Y. C. Dai) Sheng H. Wu, L.W. Zhou & Y.C. Dai	Wu et al. (2012), Zhou et al. (2016)
<i>Inonotus setiporus</i> (Berk.) G. Cunn.	<i>Hymenochaete setipora</i> (Berk.) S. H. He & Y. C. Dai	Chang et al. (1994), He and Dai (2012)
<i>Inonotus taiwanensis</i> Sheng H. Wu, Y. T. Lin & C. L. Chern	<i>Ochrosporellus taiwanensis</i> (S. H. Wu, Y. T. Lin & C. L. Chern) Y. C. Dai & F. Wu	Wu et al. (2018), Wu et al. (2022)
<i>Inonotus xeranticus</i> (Berk.) Imazeki & Aoshima	<i>Hymenochaete xerantica</i> (Berk.) S. H. He & Y. C. Dai	Chang et al. (1994), Gomes-Silva et al. (2012)

bootstrap replicates to yield a best-scoring tree with proportional bootstrap values (BS). For the BI analyses, jModelTest 2 (Darriba et al. 2012) was used to estimate the best-fit substitution model based on the Akaike information criterion, with the GTR+I+G model selected for the ITS+

28S dataset. The MCMC algorithm was run for four runs with four chains each for 1,000,000 generations, sampling one tree every 100 generations to produce a total of 10,000 trees. The first 25% of trees were discarded as burn-in, and the remaining trees were used to construct a 50%

Table 2. Species and sequences used in the phylogenetic analyses. Sequences newly generated in this study were shown in boldface.

Scientific name	Voucher specimen	GenBank no.		Country	Reference
		28S	ITS		
<i>Cylindrosporus flavidus</i>	Dai 13213	KP875561	KP875564	China	Zhou (2015)
<i>Donkioporiella mellea</i>	LWZ 20140622-12	KX258955	KX258957	China	Qin et al. (2016)
<i>Fomitiporella subinermis</i>	Dai 15114	KX181344	KX181308	China	Ji et al. (2017)
<i>Fomitiporella umbrine</i>	CBS 303.66	AY059036	–	Unknown	Wagner and Fischer (2002)
<i>Fomitiporella robiniae</i>	CBS 211.36	AY059038	–	Unknown	Wagner and Fischer (2002)
<i>Fuscoporia formosana</i>	TFRI 799	AY059034	–	Unknown	Wagner and Fischer (2002)
<i>Fuscoporia torulosa</i>	Dai 15518	MN810023	MN816732	Unknown	Chen et al. (2020)
<i>Hymenochaete cyclolamellata</i>	CBS 100106	AF385163	–	Unknown	Wagner and Fischer (2002)
<i>Hymenochaete setiporus</i>	Cui8349	JQ279638	JQ279516	Unknown	Unpublished
<i>Hymenochaete xeranticus</i>	Cui9209	JQ279635	JQ279519	Unknown	Unpublished
<i>Inocutis mikadoi</i>	SFC 980601-12	–	AY640936	Unknown	Wu et al. (2022)
<i>Inocutis rheades</i>	86-922	–	AY624994	Germany	Wagner and Fischer (2001)
<i>Inocutis tamaricis</i>	CBS 384.72	MH872221	AY558604	Italy	Wagner and Fischer (2001)
<i>Inonotus chrysomarginatus</i>	Wu 0407-6	OP962472	KP030785	Taiwan	This study
<i>Inonotus chrysomarginatus</i>	Wu 1906-1	OP962473	OP965381	Taiwan	This study
<i>Inonotus chrysomarginatus</i>	Yuan 3506-21	OP962471	–	China	This study
<i>Inonotus cuticularis</i>	QFB-888	–	AF237730	Unknown	Germain et al. (2002)
<i>Inonotus hispidus</i>	Wang 552	KP030768	KP030781	Germany	Wagner and Fischer (2001)
<i>Inonotus micantissimus</i>	URM90186	MG576125	MG576057	Brazil	Unpublished
<i>Inonotus rickii</i>	Dai 12996	MH101019	KC479128	China	Zhu et al. (2019)
<i>Inonotus rodwayi</i>	Wu 2007-1	OP962474	OP965380	Taiwan	This study
<i>Inonotus rodwayi</i>	Wu 9908-1	OP962475	–	Taiwan	This study
<i>Inonotus chihshanyenus</i>	TFRI 708	AY059039	–	Taiwan	Wagner and Fischer (2002)
<i>Laetiporus sulphureus</i>	TW 241	AF311049	–	Unknown	Wagner and Fischer (2001)
<i>Mensularia nodulosa</i>	87-115	AF311016	–	Unknown	Wagner and Fischer (2001)
<i>Mensularia radiata</i>	TW 704	AF311018	–	Germany	Wagner and Fischer (2001)
<i>Ochrosporellus hymenonitens</i>	SMDB 14733	–	NR173360	Unknown	Unpublished
<i>Ochrosporellus taiwanensis</i>	Wu 1408-1	LC214362	LC214359	Taiwan	Wu et al. (2018)
<i>Ochrosporellus tricolor</i>	Dai 16181	KX832919	–	Unknown	Ren (2018)
<i>Phaeotremella foliacea</i>	97-1117	AF311051	–	Unknown	Wagner and Fischer (2001)
<i>Phaeolus schweinitzii</i>	818-96	AF311050	–	Unknown	Wagner and Fischer (2001)
<i>Phylloporia pectinata</i>	R. Coveny 113	AF411823	–	Unknown	Wagner and Ryvarden

<i>Phylloporia ribis</i>	82-828	AF311040	–	Unknown	(2002) Wagner and Fischer (2001)
<i>Phellinus fastuosus</i>	Dai 18292	MH390381	MH390411	Viet Nam	Unpublished
<i>Porodaedalea pini</i>	Dai & Niemela 28	MH152369	MH152347	Finland	Unpublished
<i>Porodaedalea yunnanensis</i>	Dai 3072	MH152380	MG585282	China	Unpublished
<i>Sanghuangporus sanghuang</i>	Cui 14419	MF772810	MF772789	China	Zhu et al. (2019)
<i>Sanghuangporus vaninii</i>	Cui 14082	MF772814	MF772793	China	Zhu et al. (2019)
<i>Tropicoporus linteus</i>	JV 0904-64	JX467701	JQ860322	USA	Tian (2013)
<i>Tropicoporus tropicalis</i>	CBS 617.89	AY059037	AF534077	Unknown	Wagner and Fischer (2002)

majority-rule consensus phylogram with Bayesian posterior probabilities (BPPs), until the average standard deviation of split frequencies fell below 0.001. The phylogram was visualized and edited using TreeGraph 2 (Stöver and Müller 2010).

Results

Molecular Phylogeny

This study produced 7 new sequences from three species, with 2 for ITS and 5 for 28S (Table 2). The ITS+28S dataset included 37 species, with 25 ITS sequences and 36 28S sequences. The final alignment had a total of 2364 characters including gaps, of which 31% were parsimony-informative. Phylograms inferred from the BI and ML methods showed a highly similar tree topology; thus, only the ML phylogram with BS and BPPs values is shown. (Fig. 1). Within the in-group, specimens of the newly recorded *I. chrysomarginatus* formed a monophyletic lineage with strong supports (BS = 100; BPPs = 1).

Key to species in association with *Inonotus* in Taiwan

1. Hyphal system monomitic 2
1. Hyphal system dimitic 19
 2. A black line present in the context; basidiospores thin-walled 3
 2. A black line absent in the context in most species; if present, basidiospores thick-walled 6
3. Hymenial setae < 20 µm high, ventricose *Cylindrosporium flavidus*
3. Hymenial setae > 20 µm high, acute 4
 4. Pore 1–3 per mm; basidiospores < 3 µm high *Hymenochaete setipora*
 4. Pore > 3 per mm; basidiospores > 3 µm high 5
5. Basidiospores < 2 µm broad *Hymenochaete xerantica*
5. Basidiospores > 2 µm broad *Hymenochaete iodine*
6. Basidiospores CB+; setae hooked 7
 6. Basidiospores usually CB–; setae, if present, usually straight 8
7. Basidiocarps resupinate to nodulose-pileate; basidiospores < 4 µm broad *Mensularia nodulosa*
7. Basidiocarps often imbricate-pileate; basidiospores > 4 µm broad *Mensularia radiata*

- 8. Basidiocarps resupinate *Inonotus chilanshanus*
- *Inonotus chihshanyenus*
- 8. Basidiocarps effused-reflexed, pileate or stipitate 9
- 9. Hyphoid setae absent 10
- 9. Hyphoid setae present 14
- 10. Basidiospores < 4.5 μm high; hymenial setae present 11
- 10. Basidiospores > 4.5 μm high; hymenial setae absent 12
- 11. Basidiospores > 2.5 μm broad, colorless..... *Inonotus juniperinus*
- 11. Basidiospores < 2.5 μm broad, colorless to pale yellow *Fuscoporia formosana*
- 12. Pores < 3 per mm; basidiospores > 6 μm high *Inonotus fushanianus*
- 12. Pores > 3 per mm; basidiospores < 6 μm high 13
- 13. Basidiospores < 4 μm broad *Inocutis mikadoi*
- 13. Basidiospores > 4 μm broad *Inonotus juniperinus*

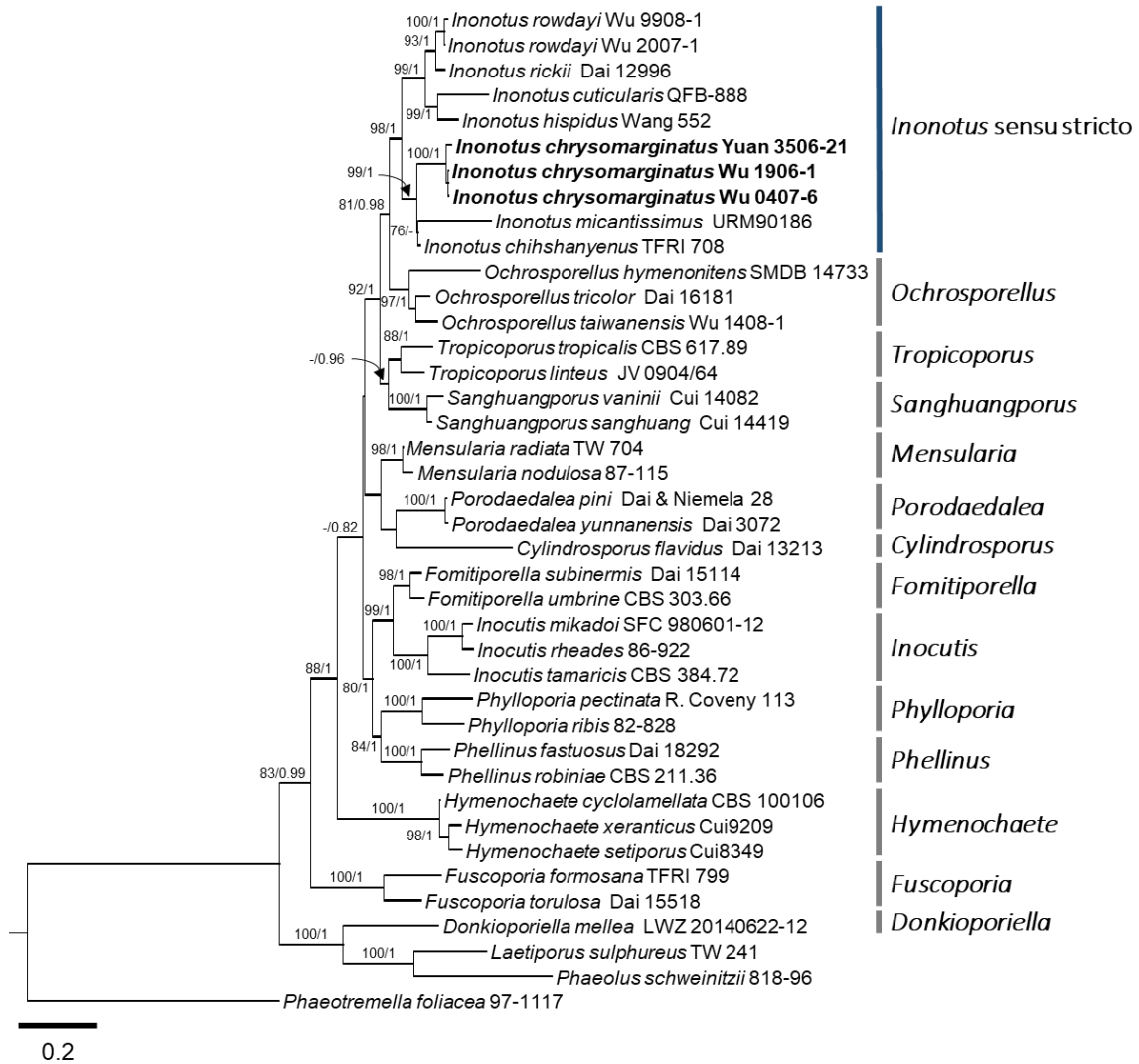


Fig. 1. The phylogram inferred from maximum likelihood (ML) and Bayesian inference (BI) analyses using the ITS+28S rDNA sequences. Nodes are respectively labeled with ML bootstrap $\geq 70\%$ (left) and BPPs ≥ 0.9 from Bayesian analyses (right). *Inonotus chrysomarginatus* was shown in boldface. Bar: number of substitutions per site.

- 14. Hymenial setae absent; chlamydospores present *Inonotus rickii*
- 14. Hymenial setae present; chlamydospores absent 15
- 15. Basidiocarps annual; basidiospore > 6 μm high 16
- 15. Basidiocarps perennial; basidiospore < 6 μm high 17
- 16. Pores 4–5 per mm; hymenial setae hooked *Inonotus cuticularis*
- 16. Pores 1–2 per mm; hymenial setae ventricose *Inonotus rodwayi*
- 17. Basidiospores > 4 μm broad
..... *Inonotus chrysomarginatus*
- 17. Basidiospores < 4 μm broad 18
- 18. Dissepiments entire; hymenial setae < 9 μm broad
..... *Ochrosporellus pachyphloeus*
- 18. Dissepiments lacerate; hymenial setae > 9 μm broad
..... *Ochrosporellus taiwanensis*
- 19. Context duplex; setae hooked
..... *Neomensularia kanehirae*
- 19. Context homogeneous; setae ventricose
..... *Sanguangporus sanguang*

Taxonomy

Inonotus chrysomarginatus B. K. Cui & Y. C. Dai, Mycological Progress 10:108. 2011.

Fig. 2

≡ *Ochrosporellus chrysomarginatus* (B. K. Cui & Y. C. Dai) Y. C. Dai & F. Wu



Fig. 2. Basidiocarps of *Inonotus chrysomarginatus*. a, b. Wu 0407-6 (TNM F0016564). c, d. CWN 05456 (TNM F0016206).

Description. See Cui et al. (2011).

Specimens examined. TAIWAN. Nantou County, Puli Town, on trunk of living *Machilus zuihoensis*, 28 Jul 2004, leg. S.H. Wu et al., *Wu 0407-6* (TNM F0016564). Taichung City, North District, National Museum of Natural Science, 120°39'E 24°10'N, 100 m, on rotten wood, 07 Jun 2002, leg. W.N. Chou, *CWN 05456* (TNM F0016206); 26, Jul 2002, leg. W.N. Chou, *CWN 05601* (TNM F0016210).

Habitat. On living angiosperm tree such as *Machilus* and rotten wood.

Distribution. Known from tropical to subtropical areas of China (Hainan) (Cui et al. 2011) and Taiwan (present study).

Discussion

In Taiwan, *Inonotus chrysomarginatus* specimens were identified as *Ochrosporellus pachyphloeus* due to their similar appearance (Wu et al. 2018). Nevertheless, *O. pachyphloeus* has smaller pores, 7–9 per mm in *O. pachyphloeus*; 5–8 per mm in *I. chrysomarginatus*, and narrower basidiospores, (3.3–)3.7–4.3(–4.9) × (2.6–)2.7–3.9(–4.1) μm in *O. pachyphloeus*; (4.3–)4.7–6(–6.4) × (3.8–)4–5(–5.3) μm in *I. chrysomarginatus* (Dai 2010, Cui et al. 2011). *Inonotus chrysomarginatus* resembles *I. indurescens* Y. C. Dai and *O. taiwanensis* in having setal hyphae and hymenial setae. However, *I. indurescens* differs from *I. chrysomarginatus* by having curved and penetrating hyphoid setae, subulate or ventricose hymenial setae and narrower basidiospores measured (3.8–)4–5.7(–6) × (2.8–) 3.2–4.1(–4.4) μm in Dai and Zhou (2000), while *O. taiwanensis* differs by having setal hyphae with

1–3 branches near the base and smaller basidiospores measured 3.8–4.9 × 2.9–3.7 μm in Wu et al. (2018). *Inonotus chrysomarginatus* can also be confused with *O. tricolor* because both species have hyphoid setae, hymenial setae, and broadly ellipsoid to subglobose, yellowish basidiospores, but the latter species has smaller pore sizes and basidiospores measured (3.8–) 3.9–4.8(–4.9) × (3–)3.1–4(–4.1) μm (Dai 2010).

Wu et al. (2022) transferred *I. chrysomarginatus* to the genus *Ochrosporellus* based on morphological characteristics, but the present study placed it in *Inonotus* with strong supports (Fig. 1) (BS = 98; BPPs = 1).

Some *Inonotus* species in Taiwan, e.g., *I. chilanshanus*, *I. fushanianus*, and *I. juniperinus*, still lack molecular data and their phylogenetic placement is uncertain.

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臺灣新記錄種 *Inonotus chrysomarginatus*，以及臺灣已知的 *Inonotus* 種類和從該屬移出的物種清單

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摘 要

本文除了提供臺灣已確認的織孔菌屬真菌，也列出曾與織孔菌屬名相連結的種類。屬於織孔菌屬共有八種，包含臺灣新記錄金邊織孔菌 (*I. chrysomarginatus*)。其它曾與 *Inonotus* 屬名相連結的 12 種，目前被歸類在不同的屬中，包括 *Cylindrosporus*、*Fuscoporia*、*Hymenochaete*、*Inocutis*、*Mensularia*、*Neomensularia*、*Ochrosporellus* 和 *Sanghuangporus*。

關鍵詞：織孔菌屬、分子親緣關係、分類學、木腐真菌