

Molecular phylogeny and morphology reveal a new wood-inhabiting fungal species in *Crustodontia* (Meruliaceae, Polyporales) from China

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Abstract

Crustodontia is characterized by resupinate, ceraceous, smooth, grandinioid to odontoid or tuberculate basidiomata, exhibiting a yellowish, brownish, or black hymenial surface that turns reddish or purplish upon application of KOH. A novel leather-like fungus, *Crustodontia electrina*, was discovered in Yunnan Province, southwestern China, and is described and illustrated here based on both morphological and molecular evidence. This species is distinguished by resupinate basidiomata, a smooth and light curry-yellow hymenial surface when fresh, a monomitic hyphal system with clamp connections on generative hyphae, subclavate cystidia, clavate to subuniform basidia, and thin-walled, ellipsoid to broadly ellipsoid basidiospores measuring $3.4\text{--}4.7 \times 2.9\text{--}3.9\ \mu\text{m}$. Phylogenetic analysis indicates that the new species forms a distinct lineage within the *Crustodontia* clade, based on internal transcribed spacer (ITS) sequences. A comprehensive description, illustrations, and results of the phylogenetic analysis of the new species are presented.

Key words: Morphology, New taxon, Phylogeny, Wood-inhabiting fungi, Yunnan Province

Introduction

Fungi play diverse and ecologically important roles in ecosystems (James *et al.* 2020). Wood-rotting fungi are a cosmopolitan group with a rich diversity in boreal, temperate, subtropical, and tropical vegetation, and they degrade lignin, cellulose, and hemi-cellulose, thereby maintaining the sustainable ecosystem cycle (Wu *et al.* 2020, Dai *et al.* 2021, Yuan *et al.* 2023). Recently, many new taxa of wood-rotting fungi have been described from southern China (Dai *et al.* 2021, Mao *et al.* 2023, Wang *et al.* 2024, Dong *et al.* 2024, 2025, Liu *et al.* 2025, Yang *et al.* 2025).

The genus *Crustodontia* Hjortstam & Ryvarden (2005: 20) belonging to Meruliaceae (Polyporales, Basidiomycota) was described by Hjortstam & Ryvarden (2005), and *C. chrysocreas* (Berk. & M.A. Curtis) Hjortstam & Ryvarden (2005: 20) was designated as the type species. Within the family Meruliaceae, *Crustodontia* is monotypic and receives strong support within the *Sarcodontia* Schulzer clade (Chen *et al.* 2021). Six species were included in the genus, the typical species *C. chrysocreas* was from the USA, and recently *C. taiwanensis* C.C. Chen & Sheng H (2021: 111), *C. nigrodontea* C.L. Zhao & R.X. Huang (2021: 111) and *C. tongxiniana* C.L. Zhao (2021: 111) were described from East Asia or New Zealand (Chen *et al.* 2021).

The genus *Crustodontia* has a wide distribution in subtropical and tropical areas. It has resupinate, ceraceous to subceraceous, smooth, grandinioid to odontoid or tuberculate basidiomata, with a yellowish, brownish, or black hymenial surface, turning to reddish or purplish with KOH, a monomitic hyphal system with clamped generative hyphae, sometimes with nodose-septate hyphae, cylindrical to ventricose cystidia, clavate basidia, ellipsoid to broadly ellipsoid thin-walled, smooth basidiospores (Hjortstam & Ryvarden 2005).

Two wood-inhabiting fungi, HMZhou 129 and HMZhou 1347, were collected from Yunnan Province, China. To clarify their taxonomic placement, morphological and phylogenetic analyses of ITS sequences were conducted, resulting in the identification of a new species. A description, illustrations and phylogenetic analysis results of this new species are provided in the present paper.

Materials and methods

Basidiocarps were photographed with a Nikon D5300 digital camera. Macro-morphological descriptions are based on field notes. Colour terms follow Petersen (1996). Macroscopic and collection details were recorded (Rathnayaka *et al.* 2025), and the fruit body was transported to a field station, where it was dried in an electronic food dryer at 45°C. Once dried, the specimens were sealed in envelopes and zip-lock plastic bags, and labelled (Zhao *et al.* 2015, 2023). All specimens studied are deposited at the herbarium of Southwest Forestry University, Yunnan Province, China (SWFC). The hymenial surface of basidiocarps was studied under a Nikon SMZ645 stereomicroscope at magnifications up to ×50. Micro-morphological data were obtained from the dried specimens and observed under a light microscope following Dai (2010).

Free-hand thin sections of basidiocarps were mounted in 5% potassium hydroxide (KOH) with 1% Phloxine B (C₂₀H₂Br₄Cl₄Na₂O₅) for observation and measurements, Melzer’s reagent for checking amyloidity and dextrinoidity, and Cotton Blue (CB) for determining cyanophily using a Nikon Eclipse E100 microscope (– 1000×). The following abbreviations were used: KOH = 5% water solution of potassium hydroxide, CB = Cotton Blue, CB– = acyanophilous, IKI = Melzer’s reagent, IKI– = both inamyloid and nondextrinoid, L = mean spore length (arithmetic average), W = meanspore width (arithmetic average), Q = variation in the L/W ratios between the specimens studied, n (a/b) = number of spores (a) measured from given number (b) of specimens (Huang *et al.* 2020). The micro-morphological data were obtained from dried specimens observed under a light microscope at 1000× oil immersion magnification (Wu *et al.* 2022, Zhao *et al.* 2023, Dong *et al.* 2024). To show the variation in spore sizes, 5% of measurements were excluded from each end of the range and shown in parentheses. At least thirty basidiospores from each specimen were measured. Stalks were excluded from basidia measurements, and the hilar appendage was excluded from basidiospores measurements (Dong *et al.* 2025). The MycoBank number will be registered in the MycoBank database (<http://www.mycobank.org>).

Genomic DNA was extracted from dried basidiomata using a cetyltrimethylammonium bromide rapid plant genome extraction kit (Aidlab Biotechnologies Co., Ltd., Beijing, China) according to the manufacturer’s instructions with some modifications (Zhao *et al.* 2012). ITS sequences were analyzed to determine the taxonomic status of *Crustodontia*. PCR was performed as described by Dong *et al.* (2024). All newly generated sequences were deposited in the GenBank database. The primer sets used for nucleotide PCR amplification, and the sequences are listed in Table 1. The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and a final extension of 72 °C for 10 min (Zhao *et al.* 2023). Sequences were aligned in MAFFT 7 ([https://mafft.cbrc.jp/alignment/ server/](https://mafft.cbrc.jp/alignment/server/)) using the “G-INS-i” strategy and adjusted manually in AliView (Hall 1999).

TABLE 1. List of species, specimens, and GenBank accession numbers of sequences used in this study.

Species Name	Sample No.	ITS	Origin	References
<i>Crustodontia chrysocreas</i>	FP-102161	AY219367	USA	Floudas and Hibbett 2015
<i>C. chrysocreas</i>	HHB-6333	KP135358	USA	Floudas and Hibbett 2015
<i>C. chrysocreas</i>	HHB-3946	KP135357	USA	Floudas and Hibbett 2015
<i>C. electrina</i>	HMZhou 129*	PV864810	China	Present study
<i>C. electrina</i>	HMZhou 1347	PV864811	China	Present study
<i>C. nigrodontea</i>	CLZhao 2758*	MT896824	China	Huang <i>et al.</i> 2020
<i>C. nigrodontea</i>	CLZhao 2729	MT896823	China	Huang <i>et al.</i> 2020
<i>C. rhododendri</i>	He 6251	PP549549	China	Li <i>et al.</i> 2025
<i>C. rhododendri</i>	CLZhao 6168*	MW732400	China	Zhao <i>et al.</i> 2023

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TABLE 1. (Continued)

Species Name	Sample No.	ITS	Origin	References
<i>C. taiwaniana</i>	Wu 9310-21	MZ636945	China	Chen <i>et al.</i> 2021
<i>C. taiwaniana</i>	GC 1703-88*	MZ636944	China	Chen <i>et al.</i> 2021
<i>C. tongxiniana</i>	CLZhao2316	MT020774	China	Huang and Zhao 2020
<i>C. tongxiniana</i>	CLZhao 2255*	MT020773	China	Huang and Zhao 2020
<i>C. vietnamensis</i>	He 5232*	PP549551	Vietnam	Li <i>et al.</i> 2025
<i>Sarcodontia crocea</i>	BRNM721609	KX831470	Czech Republic	Tomšovský 2016

Type specimens are indicated by an asterisk (*). The new strains are indicated in bold.

Results

The ITS dataset included sequences from 15 fungal specimens representing 8 species of Polyporales. The dataset had an aligned length of 897 characters, of which 443 were constant, 57 were variable and parsimony-uninformative, and 43 were parsimony-informative. Maximum Parsimony (MP) Analysis yielded 5,000 equally parsimonious trees (TL = 133, CI = 0.8496, HI = 0.1504, RI = 0.8387, RC = 0.7126). Best model for the ITS dataset estimated and applied in the Bayesian analysis: GTR+I+G.

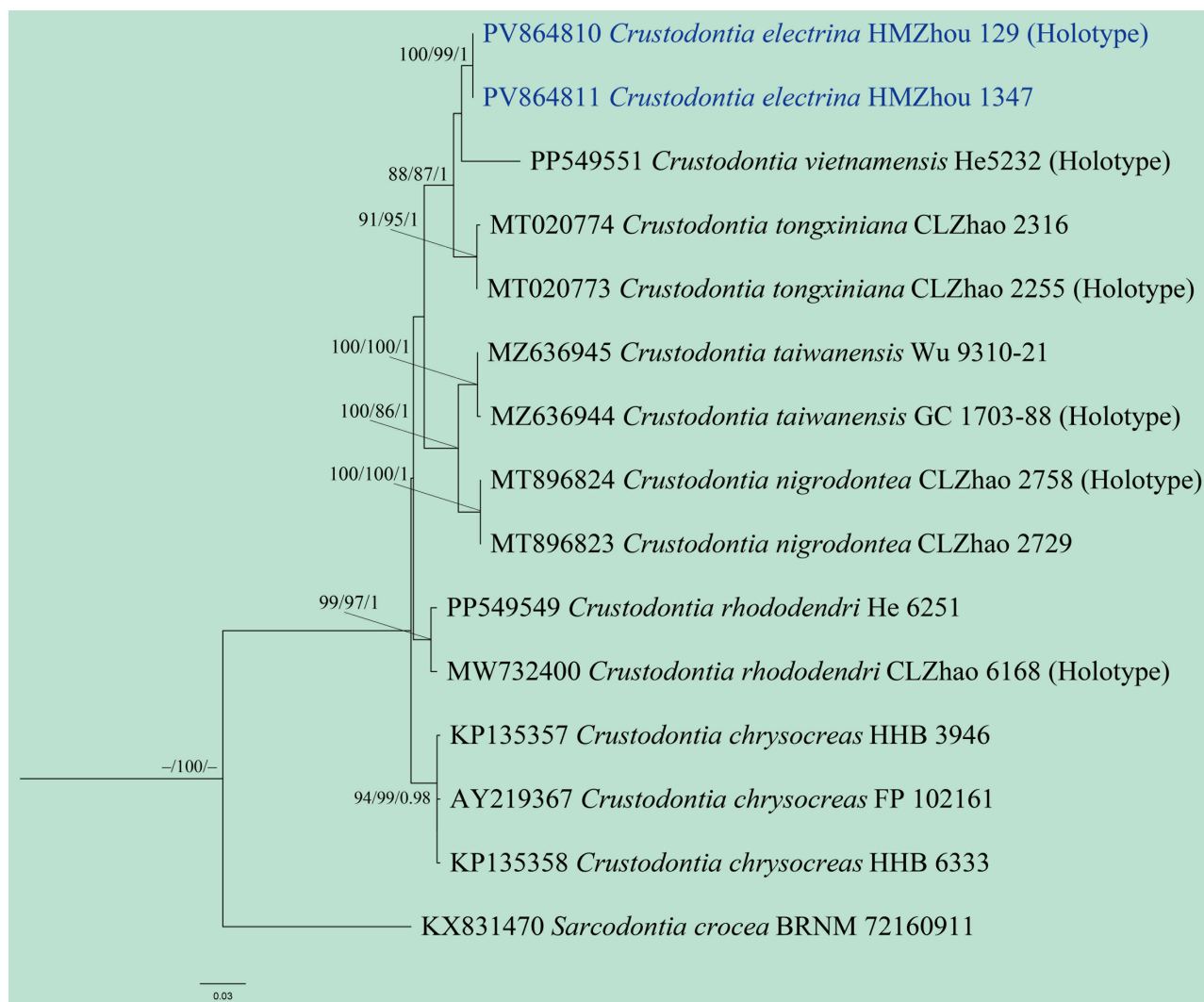


FIGURE 1. Maximum Likelihood strict consensus tree illustrating the *Crustodontia* and related species based on the combined ITS sequences. Branches are labeled with Maximum Likelihood bootstrap values (ML) $\geq 70\%$, Maximum Parsimony bootstrap values (MP) $\geq 70\%$, and Bayesian posterior probabilities (BPP) ≥ 0.95 . The newly generated sequences are in blue.

Maximum Parsimony Analysis was applied to the combined dataset, following Zhao and Wu (2017); tree construction was performed in PAUP* version 4.0b10 (Swofford 2002). All the characters were equally weighted, and the gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Max-trees were set to 5,000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1,000 replicates (Felsenstein 1985, Zhao *et al.* 2023).

Bayesian and Maximum Likelihood (ML) analyses resulted in a similar topology to the Maximum Parsimony analysis; thus, only the ML topology is presented, along with ML bootstrap support ($\geq 70\%$), MP bootstrap support ($\geq 70\%$), and Bayesian posterior probabilities (BPP ≥ 0.95) values (Fig. 1). The branches of the consensus tree that received bootstrap support for ML and MP were greater than or equal to 70%, and BPP were greater than or equal to 0.95, respectively.

In the phylogenetic tree, the two specimens (HMZhou 129 and 1347, collected from Yunnan Province) clustered with *C. vietnamensis* from Vietnam, with relatively low support values, well below the thresholds of 70% for ML, 70% for MP, and 0.95 for BPP; thus, this clade lacks reliable statistical support. In contrast, the new species *Crustodontia electrina* formed a monophyletic entity with high support (100% BS, 99% BT, and 1.00 BPP).

Taxonomy

Crustodontia electrina Quan Li. & H.M. Zhou, *sp. nov.* Figs. 2–4.

Mycobank: 864131

Holotype—CHINA. Yunnan Province, Zhaotong, Yiliang County, Wumengshan National Nature Reserve, Wangfu Waterfall, 27°83' N, 104°29' E, 1700 m, on dead angiosperm root, 17 Aug 2024, HMZhou 129 (SWFC 00100129).

Etymology—*Electrina* (Lat.) refers to the curry-yellow basidiomata.

Description—Basidiomata annual, widely effused, smooth, ceraceous. Hymenial surface smooth, light curry-yellow when fresh, becoming lighter or yellowish toward margin, becoming purplish black in KOH, slightly cracked when dry, 150–200 μm thick in section; margin white or concolorous with hymenial surface, thinning out.

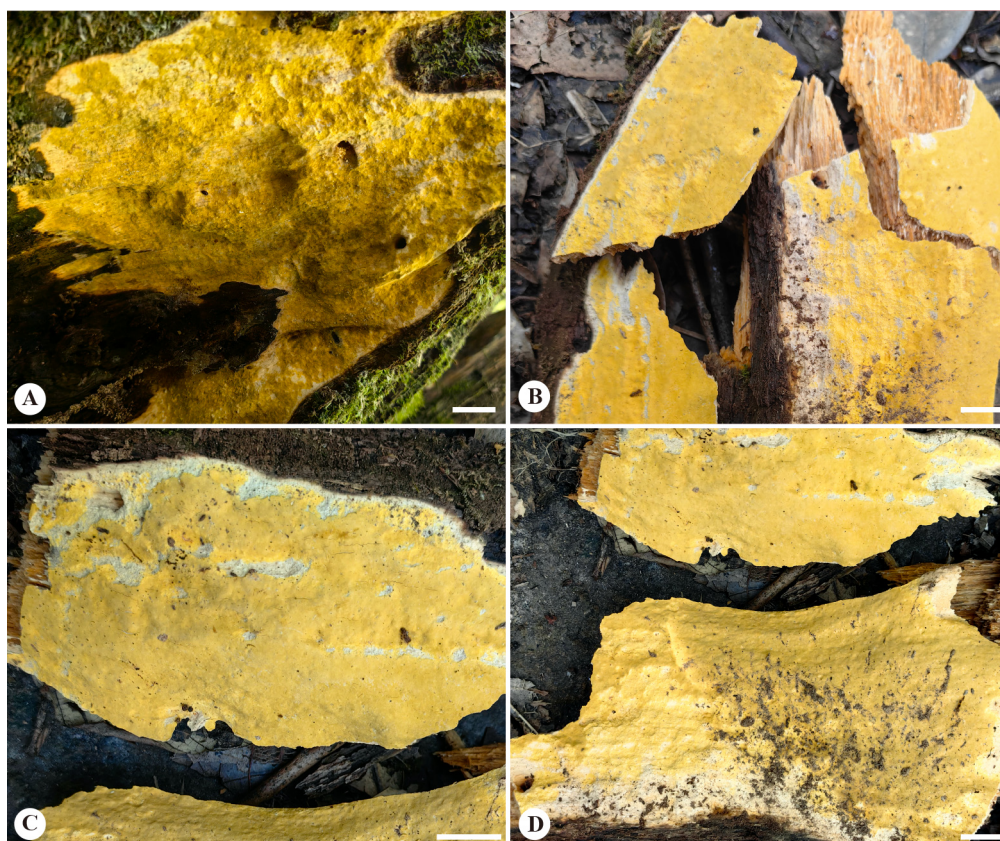


FIGURE 2. Basidiomata of *Crustodontia electrina* (A HMZhou 129 holotype, B–D HMZhou 1347). Scale bars: A–D = 1 cm.

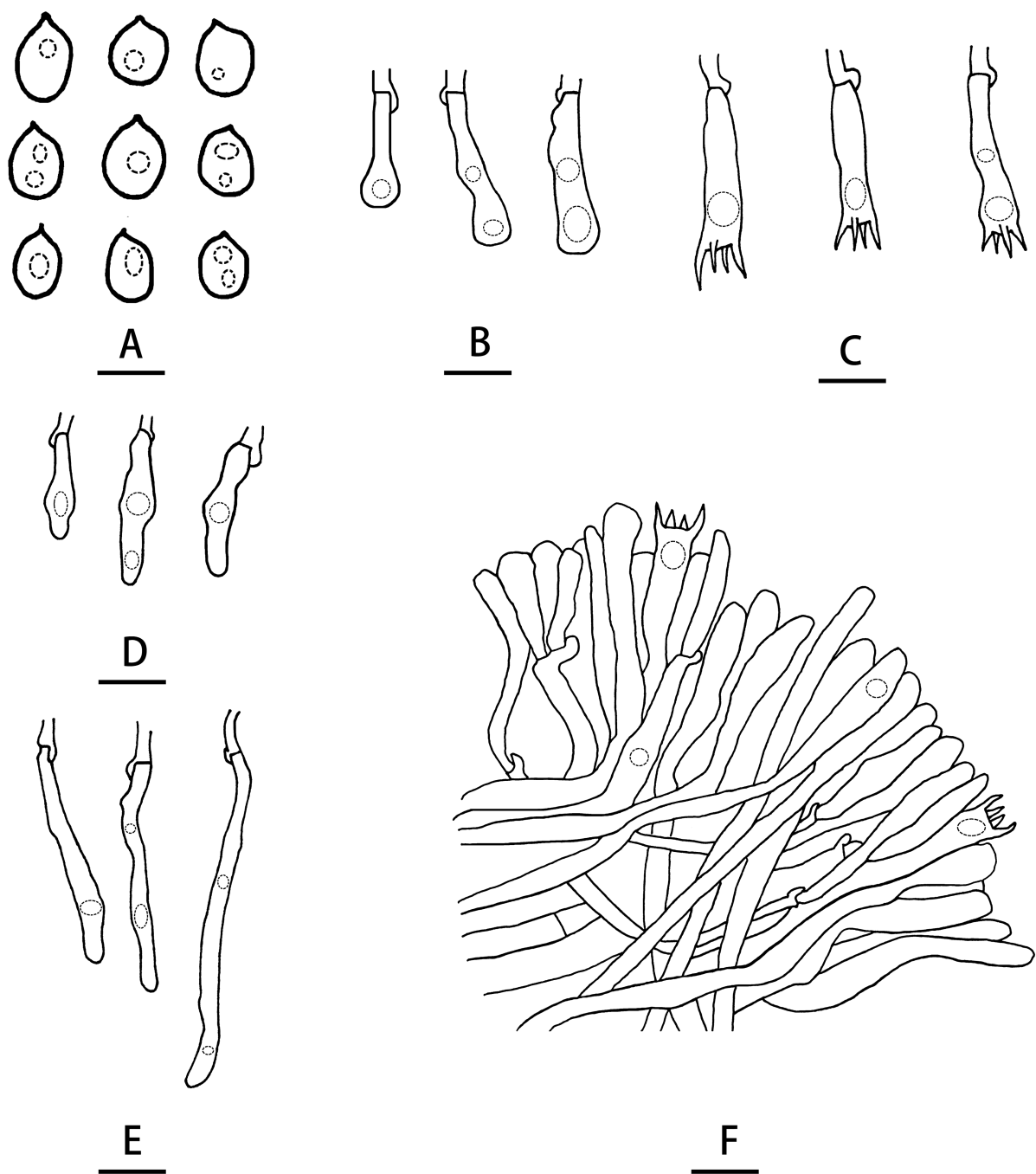


FIGURE 3. Microscopic features of *Crustodontia electrina* (HMZhou 129, holotype). **A.** Basidiospores. **B.** Basidioles. **C.** Basidia. **D.** Cystidioles. **E.** Cystidia. **F.** Hymenium. Scale bars: A = 5 μ m, B–F = 10 μ m.

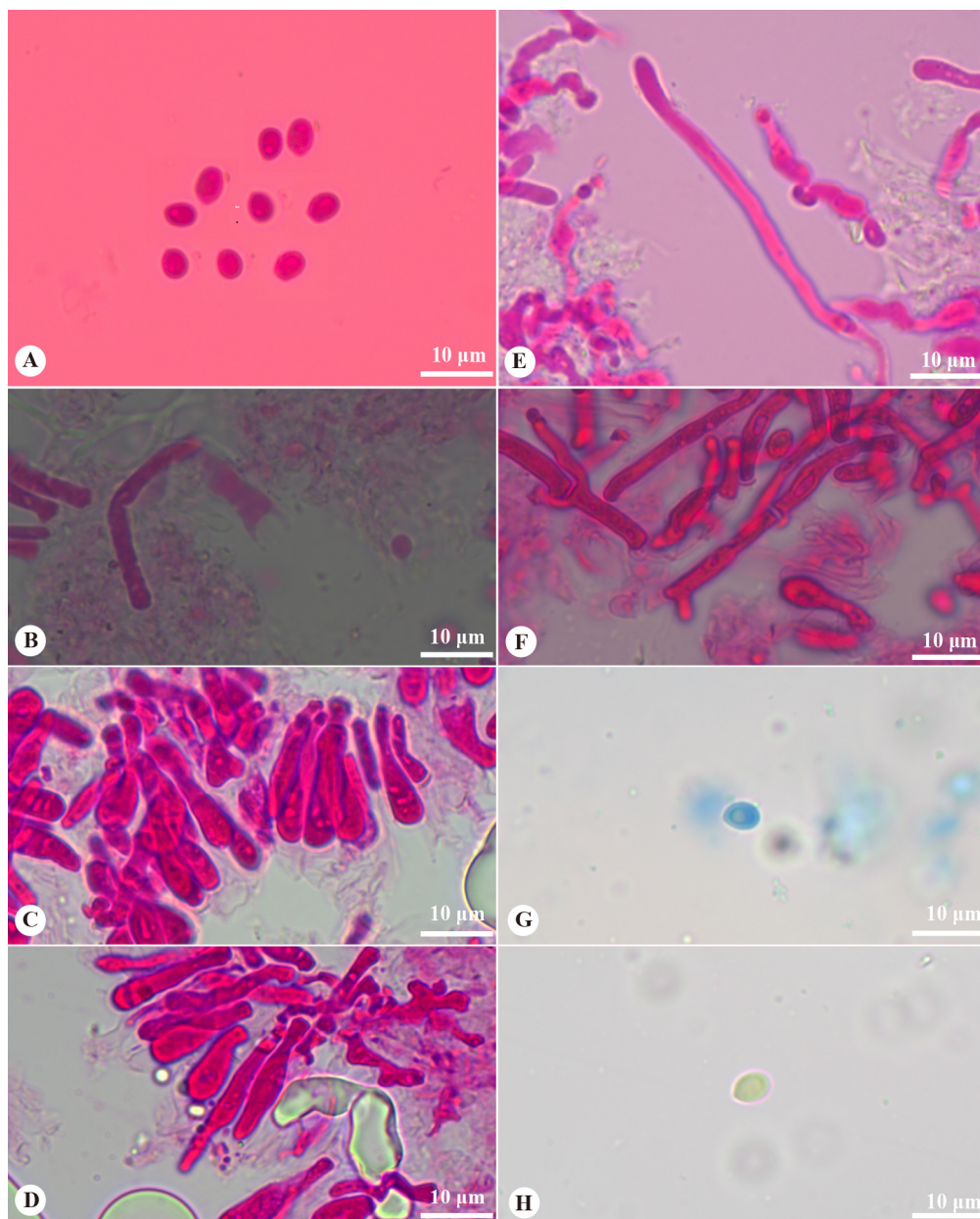


FIGURE 4. Microscopic features of *Crustodontia electrina* (HMZhou 129, holotype) in Cotton Blue, Melzer and Phloxine B reagent. **A.** Basidiospores. **B.** Basidia. **C.** Basidioles. **D.** Cystidiolate. **E.** A Cystidium. **F.** Clamp connections of hyphae. **G.** Basidiospores stained with Cotton Blue. **H.** Basidiospores stained with Melzer's reagent.

Hyphal system—Monomitic; generative hyphae with clamp connections. Subhymenium not clearly differentiated from subiculum; hyphae colorless, interwoven, 2–4 µm diam, walls up to 0.6 µm thick, moderately branched. Yellow resinous materials abundantly embedded among hyphae. Cystidia subclavate, thin-walled, 29–42 × 2–3 µm. Cystidioles subfusiform, with obtuse apex, thin-walled, 16–20 × 2–5 µm. Basidia clavate to subuniform, thin-walled, 4-sterigmate, often guttulate, 15–23 × 4–5.5 µm. Basidiospores ellipsoid to broadly ellipsoid, colorless, thin-walled, smooth, often with 1–2 guttules, IKI–, CB–, (3.1–)3.4–4.7(–5.0) × (2.6–)2.9–3.9(–4.3) µm, L = 4.1 µm, W = 3.3 µm, Q = 1.2 µm (n = 64/2).

Other specimens examined (Paratype): CHINA. Yunnan Province, Zhaotong, Yiliang County, Wumengshan National Nature Reserve, 27°83' N, 104°29' E, 1700 m, on fallen angiosperm trunk, 16 Apr 2025, HMZhou 1347 (SWFC 00101347).

Discussion

DNA sequence-based classification and identification have become the standard methods in fungal taxonomy (Hibbett *et al.* 2007, Xu 2020, Lücking *et al.* 2021, Zhou *et al.* 2023, Qin *et al.* 2025, Wang *et al.* 2025). This study describes *Crustodontia electrina*, discovered in Yunnan Province, southwestern China, as a new species based on phylogenetic analyses and morphological characteristics. The species is distinguished by curry-yellow basidiomata, subclavate cystidia, subfusiform cystidioles, and ellipsoid to broadly ellipsoid basidiospores.

In phylogeny, *Crustodontia electrina* clusters with *C. vietnamensis* and *C. tongxiniana* as a clade with high support values (88% ML, 87% MP, and 1.00 BPP). However, *C. vietnamensis* has bigger basidiospores ($4.5\text{--}5 \times 3\text{--}3.5 \mu\text{m}$ vs. $3.4\text{--}4.7 \times 2.9\text{--}3.9 \mu\text{m}$, He *et al.* 2025). Additionally, the cystidia of *C. vietnamensis* are longer and thinner ($20\text{--}28 \times 3.5\text{--}4.5 \mu\text{m}$ vs. $17\text{--}22 \times 5\text{--}7 \mu\text{m}$, He *et al.* 2025).

The four additional species of *Crustodontia*: *C. taiwanensis*, *C. nigrodontea*, *C. rhododendri*, and *C. chrysocreas*, each represent distinct evolutionary lineages. *Crustodontia electrina* and *C. taiwanensis* both exhibit a purplish-black reaction in KOH; however, *C. taiwanensis* possesses smaller cystidia ($18\text{--}21 \times 2\text{--}5 \mu\text{m}$) compared to *C. electrina* ($29\text{--}42 \times 2\text{--}3 \mu\text{m}$, Chen *et al.* 2021). *C. chrysocreas* is characterized by subclavate cystidia and shorter basidiospores ($3.4\text{--}4.7 \mu\text{m}$) relative to those of *C. electrina* ($5\text{--}6 \mu\text{m}$, Hjortstam & Ryvarden 2005). Furthermore, *C. nigrodontea* and *C. rhododendri* differ from *C. electrina* by their black and ochraceous basidiomata (Huang *et al.* 2022).

Polypoid fungi represent a significant group of wood-inhabiting basidiomycetes. As key decomposers in forest ecosystems, they are responsible for extensive white rot and brown rot of wood. In recent years, considerable attention has been directed toward brown-rot fungi within the order Polyporales (Dai *et al.* 2021), leading to the description of numerous new species from China based on morphological and phylogenetic analyses (He *et al.* 2025). Advanced approaches, including molecular phylogeny and omics technologies, are expected to further facilitate the discovery of novel polypoid fungi (Zhao *et al.* 2015). Yunnan Province, recognized as one of the world's biodiversity hotspots, harbors a rich diversity of fungal species (Zhao *et al.* 2023, Guo *et al.* 2026). Our study contributes to the conservation of fungal biodiversity in this region.

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References

- Binder, M., Justo, A., Riley, R., Salamov, A., Lopez-Giraldez, F., Sjökvist, E., Copeland, A., Foster, B., Sun, H., Larsson, E., Larsson, K.H., Townsend, J., Grigoriev, I.V. & Hibbett, D.S. (2013) Phylogenetic and phylogenomic overview of the Polyporales. *Mycologia* 105: 1350–1373.
<https://doi.org/10.3852/13-003>
- Chen, C.C., Chen, C.Y. & Wu, S.H. (2021) Species diversity, taxonomy and multi-gene phylogeny of phlebioid clade (Phanerochaetaceae, Irpicaceae, Meruliaceae) of Polyporales. *Fungal Diversity* 111: 337–442.
<https://doi.org/10.1007/s13225-021-00490-w>
- Chowdhary, A., Kathuria, S., Agarwal, K. & Meis, J.F. (2014) Recognizing filamentous basidiomycetes as agents of human disease: a review. *Medical Mycology* 52: 782–797.
<https://doi.org/10.1093/mmy/myu047>
- Crozier, J., Thomas, S.E., Aime, M.C., Evans, H.C. & Holmes, K.A. (2006) Molecular characterization of fungal endophytic morphospecies isolated from stems and pods of *Theobroma cacao*. *Plant Pathology* 55: 783–791.
<https://doi.org/10.1111/j.1365-3059.2006.01446.x>
- Dai, Y.C. (2010) Hymenochaetaceae (Basidiomycota) in China. *Fungal Diversity* 45: 131–343.
<https://doi.org/10.1007/s13225-010-0066-9>
- Dai, Y.C., Cui, B.K., Yuan, H.S. & Li, B.D. (2007) Pathogenic wood-decaying fungi in China. *Forest Pathology* 37: 105–120.

<https://doi.org/10.1111/j.1439-0329.2007.00485.x>

- Dai, Y.C., Yang, Z.L., Cui, B.K., Wu, G., Yuan, H.S., Zhou, L.W., He, S.H., Ge, Z.W., Wu, F., Wei, Y.L., Yuan, Y. & Si, J. (2021) Diversity and systematics of the important macrofungi in Chinese forests. *Mycosystema* 40: 770–805.
<https://doi.org/10.13346/j.mycosystema.210036>
- Dai, Y.C., Yang, Z.L., Cui, B.K., Yu, C.J. & Zhou, L.W. (2009) Species diversity and utilization of medicinal mushrooms and fungi in China. *International Journal of Medicinal Mushrooms* 11: 287–302.
<https://doi.org/10.1615/IntJMedMushr.v11.i3.80>
- Dong, J.H., Chen, M.L., Chen, M., Li, Q., Zhu, Y.J., Zhang, X.C., Zhou, C.Q., Li, W., Muhammad, A., Zhou, H.M., Jabeen, S. & Zhao, C.L. (2025) Notes, outline, taxonomy and phylogeny of wood-inhabiting Agaricales. *Mycosphere* 16 (1): 2599–2711.
<https://doi.org/10.5943/mycosphere/16/1/16>
- Dong, J.H., Li, Q., Yuan, Q., Luo, Y.X., Zhang, X.C., Dai, Y.F., Zhou, Q., Liu, X.F., Deng, Y.L., Zhou, H.M., Muhammad, A. & Zhao, C.L. (2024) Species diversity, taxonomy, molecular systematics and divergence time of wood-inhabiting fungi in Yunnan-Guizhou Plateau, Asia. *Mycosphere* 15: 1110–1293.
<https://doi.org/10.5943/mycosphere/15/1/10>
- El-Gharabawy, H.M., Leal-Dutra, C.A. & Griffith, G.W. (2021) *Crystallicutis* gen. nov. (Irpicaceae, Basidiomycota), including *C. damiettensis* sp. nov., found on *Phoenix dactylifera* (date palm) trunks in the Nile Delta of Egypt. *Fungal Biology* 125 (6): 447–458.
<https://doi.org/10.1016/j.funbio.2021.01.004>
- Felsenstein, J. (1985) Confidence intervals on phylogenetics: An approach using bootstrap. *Evolution* 39: 783–791.
<https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Floudas, D. & Hibbett, D.S. (2015) Revisiting the taxonomy of *Phanerochaete* (Polyporales, Basidiomycota) using a four gene dataset and extensive ITS sampling. *Fungal Biology* 119: 679–719.
<https://doi.org/10.1016/j.funbio.2015.04.003>
- Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R.A., Henrissat, B., Martínez, A.T., Otilar, R., Spatafora, J.W., Yadav, J.S., Aerts, A., Benoit, I., Boyd, A., Carlson, A., Copeland, A., Coutinho, P.M., de Vries, R.P., Ferreira, P., Findley, K., Foster, B., Gaskell, J., Glotzer, D., Görecki, P., Heitman, J., Hesse, C., Hori, C., Igarashi, K., Jurgens, J.A., Kallen, N., Kersten, P., Kohler, A., Kues, U., Kumar, T.K.A., Kuo, A., LaButti, K., Larrondo, L.F., Lindquist, E., Ling, A., Lombard, V., Lucas, S., Lundell, T., Martin, R., McLaughlin, D.J., Morgenstern, I., Morin, E., Murat, C., Nagy, L.G., Nolan, M., Ohm, R.A., Patyshakuliyeva, A., Rokas, A., Ruiz Dueñas, F.J., Sabat, G., Salamov, A., Samejima, M., Schmutz, J., Slot, J.C., John, F.St., Stenlid, J., Sun, H., Sun, S., Syed, K., Tsang, A., Wiebenga, A., Young, D., Pisabarro, A., Eastwood, D.C., Martin, F., Cullen, D., Grigoriev, I.V. & Hibbett, D.S. (2012) The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* 336: 1715–1719.
<https://doi.org/10.1126/science.1221748>
- Guo, W., Jiang, Q. & Zhou, H. (2026) Morphological characteristics and phylogenetic analyses revealed *Lopharia guangdongensis* sp. nov. (Polyporaceae, Basidiomycota) from Southern China. *Phytotaxa* 739 (3): 245–259.
<https://doi.org/10.11646/phytotaxa.739.3.1>
- Hall, T.A. (1999) Bioedit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
<https://doi.org/10.1021/bk-1999-0734.ch008>
- He, M.Q., Zhao, R.L., Hyde, K.D., Begerow, D., Kemler, M., Yurkov, A., McKenzie, E.H.C., Raspé, O., Kakishima, M., Sánchez-Ramírez, S., Vellinga, E.C., Halling, R., Papp, V., Zmitrovich, I.V., Buyck, B., Ertz, D., Wijayawardene, N.N., Cui, B.K., Schoutteten, N., Liu, X.Z., Li, T.H., Yao, Y.J., Zhu, X.Y., Liu, A.Q., Li, G.J., Zhang, M.Z., Cao, B., Antonín, V., Boekhout, T., Silva, B.D.B.D., Crop, E.D., Decock, C., Dima, B., Dutta, A.K., Fell, J.W., Geml, J., Ghobad-Nejhad, M., Giachini, A.J., Gibertoni, T.B., Gorjón, S.P., Haelewaters, D., He, S.H., Hodkinson, B.P., Horak, E., Hoshino, T., Justo, A., Lim, Y.W., Menolli Jr, N., Mešić, A., Moncalvo, J.M., Mueller, G.M., Nagy, L.G., Nilsson, R.H., Noordeloos, M., Nuytink, J., Orihara, T., Ratchadawan, C., Rajchenberg, M., Silva-Filho, A.G.S., Sulzbacher, M.A., Tkalčec, Z., Valenzuela, R., Verbeken, A., Vizzini, A., Wartchow, F., Wei, T.Z., Weiß, M., Zhao, C.L. & Kirk, P.M. (2019) Notes, outline and divergence times of Basidiomycota. *Fungal Diversity* 99: 105–367.
<https://doi.org/10.1007/s13225-019-00435-4>
- Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lücking, R., Lumbsch, H.T., Lutzoni, F., Matheny, P.B., McLaughlin, D.J., Powell, M.J., Redhead, S., Schoch, C.L., Spatafora, J.W., Stalpers, J.A., Vilgalys, R., Aime, M.C., Aptroot, A., Bauer, R., Begerow, D., Benny, G.L., Castlebury, L.A., Crous, P.W., Dai, Y.C., Gams, W., Geiser, D.M., Griffith, G.W., Gueidan, C., Hawksworth, D.L., Hestmark, G., Hosaka, K., Humber, R.A., Hyde, K.D., Ironside, J.E., Kõljalg, U., Kurtzman, C.P., Larsson, K.H., Lichtwardt, R., Longcore, J., Miadlikowska, J., Miller, A., Moncalvo, J.M., Mozley-Standridge, S., Oberwinkler, F., Parmasto, E., Reeb, V., Rogers, J.D., Roux, C., Ryvarden, L., Sampaio, J.P., Schüssler, A., Sugiyama, J., Thorn, R.G., Tibell, L., Untereiner, W.A., Walker, C., Wang, Z., Weir, A., Weiss, M., White, M.M., Winka, K., Yao, Y.J. & Zhang,

- N. (2007) A higher-level phylogenetic classification of the Fungi. *Mycological Research* 111 (5): 509–547.
<https://doi.org/10.1016/j.mycres.2007.03.004>
- Hjortstam, K. & Ryvarden, L. (2005) New taxa and new combinations in tropical corticioid fungi (Basidiomycotina, Aphyllophorales). *Synopsis Fungorum* 20: 33–41.
- Huang, R.X. & Zhao, C.L. (2020) Three new species of *Phlebia* (Polyporales, Basidiomycota) based on the evidence from morphology and DNA sequence data. *Mycological Progress* 19: 753–767.
<https://doi.org/10.1007/s11557-020-01591-7>
- Huang, R.X., Luo, K.Y. & Zhao, C.L. (2020) *Phlebia nigrodontea* sp. nov. in Meruliaceae (Polyporales) with a black hymenial surface. *Phytotaxa* 458: 195–206.
<https://doi.org/10.11646/phytotaxa.458.3.2>
- James, T.Y., Stajich, J.E., Hittinger, C.T. & Rokas, A. (2020) Toward a fully resolved fungal tree of life. *Annual Review of Microbiology* 74: 291–313.
<https://doi.org/10.1146/annurev-micro-022020-051835>
- Justo, A., Miettinen, O., Floudas, D., Ortiz-Santana, B., Sjökvist, E., Lindner, D., Nakasone, K.K., Niemelä, T., Larsson, K.H. & Ryvarden, L. (2017) A revised family-level classification of the Polyporales (Basidiomycota). *Fungal Biology* 121 (9): 798–824.
<https://doi.org/10.1016/j.funbio.2017.05.010>
- Kumar, A.K. & Sharma, S. (2017) Recent updates on different methods of pretreatment of lignocellulosic feedstocks: a review. *Bioresources and Bioprocessing* 4: 7.
<https://doi.org/10.1186/s40643-017-0137-9>
- Kumar, P., Barrett, D.M., Delwiche, M.J. & Stroeve, P. (2009) Methods for pretreatment of lignocellulosic biomass for efficient hydrolysis and biofuel production. *Industrial and Engineering Chemistry Research* 48: 3713–3729.
<https://doi.org/10.1021/ie801542g>
- Larsson, K.H., Larsson, E. & Kõljalg, U. (2004) High phylogenetic diversity among corticioid homobasidiomycetes. *Mycological Research* 108: 983–1002.
<https://doi.org/10.1017/s0953756204000851>
- Lee, S.O., Kim, H.Y., Choi, G.J., Lee, H.B., Jang, K.S., Choi, Y.H. & Kim, J.C. (2009) Mycofumigation with *Oxyporus latemarginatus* EF069 for control of postharvest apple decay and *Rhizoctonia* root rot on moth orchid. *Journal of Applied Microbiology* 106: 1213–1219.
<https://doi.org/10.1111/j.1365-2672.2008.04087.x>
- Li, T., Le-Gao, J., Huang, J.H., Gu, L., Zou, J. & Wu, X.J. (2021) *Phlebiopsis xuefengensis* sp. nov. from *Gastrodia elata* (Orchidaceae) in Hunan Province, Southern China. *South African Journal of Botany* 142: 299–304.
<https://doi.org/10.1016/j.sajb.2021.06.034>
- Li, Y., Bateman, C.C., Skelton, J., Jusino, M.A., Nolen, Z.J., Simmons, D.R. & Hulcr, J. (2017) Wood decay fungus *Flavodon ambrosius* (Basidiomycota: Polyporales) is widely farmed by two genera of ambrosia beetles. *Fungal Biology* 121: 984–989.
<https://doi.org/10.1016/j.funbio.2017.08.004>
- Li, Y., Cao, Y.F., Nakasone, K.K., Liu, S.L., Huang, M.R. & He, S.H. (2025) Species diversity, taxonomy, multi-gene phylogeny, and divergence times of Meruliaceae (Polyporales, Basidiomycota). *Mycology* 16 (3): 1–42.
<https://doi.org/10.1080/21501203.2024.2443216>
- Li, Y., Simmons, D.R., Bateman, C.C., Short, D.P., Kasson, M.T., Rabaglia, R.J. & Hulcr, J. (2015) New fungus-insect symbiosis: culturing, molecular, and histological methods determine saprophytic *Polyporales mutualists* of *Ambrosiodmus ambrosia* beetles. *PLOS One* 10: e0137689.
<https://doi.org/10.1371/journal.pone.0137689>
- Liu, Z.B., Yuan, Y., Dai, Y.C., Liu, H.G., Vlasák, J., Zeng, G.Y., He, S.H. & Wu, F. (2025) Global diversity and systematics of Hymenochaetaceae with non-poroid hymenophore. *Fungal Diversity* 131: 1–97.
<https://doi.org/10.1007/s13225-025-00552-3>
- Lücking, R., Aime, M.C., Robbertse, B., Miller, A.N., Aoki, T., Ariyawansa, H.A., Cardinali, G., Crous, P.W., Druzhinina, I.S., Geiser, D.M., Hawksworth, D.L., Hyde, K.D., Irinyi, L., Jeewon, R., Johnston, P.R., Kirk, P.M., Malosso, E., May, T.W., Meyer, W., Nilsson, H.R., Öpik, M., Robert, V., Stadler, M., Thines, M., Vu, D., Yurkov, A.M., Zhang, N. & Schoch, C.L. (2021) Fungal taxonomy and sequence-based nomenclature. *Nature Microbiology* 6 (5): 540–548.
<https://doi.org/10.1038/s41564-021-00888-x>
- Mäkinen, M., Larrondo, L.F., Putnam, N., Gelpke, M.D.S., Huang, K., Chapman, J., Helfenbein, K.G., Ramaiya, P., Detter, J.C., Larimer, F., Coutinho, P.M., Henrissat, B., Berka, R., Cullen, D. & Rokhsar, D. (2019) Genome description of *Phlebia radiata* 79 with comparative genomics analysis on lignocellulose decomposition machinery of phlebioid fungi. *BMC Genomics* 20: 430.
<https://doi.org/10.1186/s12864-019-5817-8>

- Mao, W.L., Wu, Y.D., Liu, H.G., Yuan, Y. & Dai, Y.C. (2023) A contribution to *Porogramme* (Polyporaceae, Agaricomycetes) and related genera. *IMA Fungus* 14: 5.
<https://doi.org/10.1186/s43008-023-00110-z>
- Martin, R., Gazis, R., Skaltsas, D., Chaverri, P. & Hibbett, D.S. (2015) Unexpected diversity of basidiomycetous endophytes in sapwood and leaves of *Hevea*. *Mycologia* 107: 284–297.
<https://doi.org/10.3852/14-206>
- Martinez, D., Larrondo, L.F., Putnam, N., Gelpke, M.D.S., Huang, K., Chapman, J., Helfenbein, K.G., Ramaiya, P., Detter, J.C., Larimer, F., Coutinho, P.M., Henrissat, B., Berka, R., Cullen, D. & Rokhsar, D. (2004) Genome sequence of the lignocellulose degrading fungus *Phanerochaete chrysosporium* strain RP78. *Nature Biotechnology* 22: 695–700.
<https://doi.org/10.1038/nbt967>
- Ogura-Tsujita, Y., Gebauer, G., Xu, H., Fukasawa, Y., Umata, H., Tetsuka, K., Kubota, M., Schweiger, J.M.I., Yamashita, S., Maekawa, N., Maki, M., Isshiki, S. & Yukawa, T. (2018) The giant mycoheterotrophic orchid *Erythrorchis altissima* is associated mainly with a divergent set of wood-decaying fungi. *Molecular Ecology* 27: 1324–1337.
<https://doi.org/10.1111/mec.14524>
- Pratt, J.E., Niemi, M. & Sierota, Z.H. (2000) Comparison of three products based on *Phlebiopsis gigantea* for the control of *Heterobasidion annosum* in Europe. *Biocontrol Science and Technology* 10: 467–477.
<https://doi.org/10.1080/09583150050115052>
- Qin, G.F., Qin, W.M., Wang, H.C., Zhao, J., Korhonen, K., Chen, J., Dai, Y.C. & Yuan, Y. (2025) Phylogeny and species diversity of *Armillaria* in China based on morphological, mating test, and GCPSR criteria. *Mycology* 16 (2): 777–811.
<https://doi.org/10.1080/21501203.2024.2404121>
- Rathnayaka, A.R., Tennakoon, D.S., Jones, G.E., Wanasinghe, D.N., Bhat, D.J., Priyashantha, A.H., Stephenson, S.L., Tibpromma, S. & Karunarathna, S.C. (2025) Significance of precise documentation of hosts and geospatial data of fungal collections, with an emphasis on plant-associated fungi. *New Zealand Journal of Botany* 63 (2–3): 462–489.
<https://doi.org/10.1080/0028825x.2024.2381734>
- Rungjindamai, N., Pinruan, U., Choeyklin, R., Hattori, T. & Jones, E.B.G. (2008) Molecular characterization of basidiomycetous endophytes isolated from leaves, rachis and petioles of the oil palm, *Elaeis guineensis*, in Thailand. *Fungal Diversity* 33: 139–161.
- Ryvarden, L. & Melo, I. (2017) *Poroid Fungi of Europe*. Fungiflora, Oslo, 431 pp.
- Sánchez, C. (2009) Lignocellulosic residues: biodegradation and bioconversion by fungi. *Biotechnology Advances* 27: 185–194.
<https://doi.org/10.1016/j.biotechadv.2008.11.001>
- Sayari, M., Babaeizad, V., Ghanbari, M.A.T., Rahimian, H., Borhani, B., Mohammadi, M.M. & Nasiri, J.S. (2012) First report of *Hyphodermella rosae* causing dry fruit rot disease on plum in Iran. *Plant Disease* 96: 1228–1228.
<https://doi.org/10.1094/PDIS-10-11-0825>
- Suetsugu, K., Matsubayashi, J. & Tayasu, I. (2020) Some mycoheterotrophic orchids depend on carbon from dead wood: novel evidence from a radiocarbon approach. *New Phytologist* 227: 1519–1529.
<https://doi.org/10.1111/nph.16409>
- Swofford, D. (2002) *PAUP*. Phylogenetic analysis using parsimony (*and Other Methods); Version 4.0b10*. Sinauer Associates, Massachusetts, USA.
<https://doi.org/10.1111/j.0014-3820.2002.tb00191.x>
- Thomas, S.E., Crozier, J., Aime, M.C., Evans, H.C. & Holmes, K.A. (2008) Molecular characterisation of fungal endophytic morphospecies associated with the indigenous forest tree, *Theobroma gileri*, in Ecuador. *Mycological Research* 112: 852–860.
<https://doi.org/10.1016/j.mycres.2008.01.008>
- Tomšovský, M. (2016) *Sarcodontia crocea* (Basidiomycota, Polyporales) is unrelated to *Spongipellis*. *Phytotaxa* 288 (2): 197–200.
<https://doi.org/10.11646/phytotaxa.288.2.12>
- Wang, C.G., Dai, Y.C., Kout, J., Gates, G.M., Liu, H.G., Yuan, Y. & Vlasák, J. (2024) Multi-gene phylogeny and taxonomy of *Physisporinus* (Polyporales, Basidiomycota). *Mycosphere* 15: 1455–1521.
<https://doi.org/10.1080/21501203.2024.2379476>
- Wang, C.G., Wu, Y.D., Zhang, X., Dai, Y.C., Li, Z.H. & Yuan, Y. (2025) Studies in phylogeny and divergence times of Irpicaceae and Meripilaceae (Polyporales, Basidiomycota), with an emphasis on *Ceriporia* and *Meripilus* including ten new species. *IMA Fungus* 16: e161336.
<https://doi.org/10.3897/imafungus.16.161336>
- Wijayawardene, N.N., Hyde, K.D., Al-Ani, L.K., Tedersoo, L., Haelewaters, D., Rajeshkumar, K.C. & Zhao, R. (2020) Outline of Fungi and fungus-like taxa. *Mycosphere* 11: 1060–1456.
<https://doi.org/10.5943/mycosphere/11/1/8>
- Wu, F., Yuan, H.S. & Zhou, L.W. (2020) Polypore diversity in South China. *Mycosystema* 39: 653–682.

<https://doi.org/10.13346/j.mycosystema.200087>

- Wu, F., Zhou, L.W., Vlasák, J. & Dai, Y.C. (2022) Global diversity and systematics of Hymenochaetaceae with poroid hymenophore. *Fungal Diversity* 113: 1–192.
<https://doi.org/10.1007/s13225-021-00496-4>
- Wu, F., Zhou, L.W., Yang, Z.L., Bau, T., Li, T.H. & Dai, Y.C. (2019) Resource diversity of Chinese macrofungi: edible, medicinal and poisonous species. *Fungal Diversity* 98: 1–76.
<https://doi.org/10.1007/s13225-019-00432-7>
- Xiao, P. & Kondo, R. (2019) Biodegradation and bioconversion of endrin by white rot fungi, *Phlebia acanthocystis* and *Phlebia brevispora*. *Mycoscience* 60: 255–261.
<https://doi.org/10.1016/j.myc.2019.04.004>
- Xu, J. (2020) Fungal species concepts in the genomics era. *Genome Biology* 63 (9): 459–468.
<https://doi.org/10.1139/gen-2020-0022>
- Yang, Y., Xu, Y., Wang, L., Jiang, Q.Q., Su, J.Q., Li, R., Zhou, H.M. & Zhao, C.L. (2025) Multigene phylogeny of seven wood-inhabiting fungal orders in Basidiomycota, and proposal of a new genus and thirteen new species. *Mycosphere* 16 (1): 245–295.
<https://doi.org/10.5943/mycosphere/16/1/4>
- Yuan, Y., Bian, L.S., Wu, Y.D., Chen, J.J., Wu, F., Liu, H.G., Zeng, G.Y. & Dai, Y.C. (2023) Species diversity of pathogenic wood-rotting fungi (Agaricomycetes, Basidiomycota) in China. *Mycology* 14 (3): 204–226.
<https://doi.org/10.1080/21501203.2023.2238779>
- Zhao, C.L. & Wu, Z.Q. (2017) *Ceriporiopsis kunmingensis* sp. nov. (Polyporales, Basidiomycota) evidenced by morphological characters and phylogenetic analysis. *Mycological Progress* 16: 93–100.
<https://doi.org/10.1007/s11557-016-1259-8>
- Zhao, C.L., Cui, B.K. & Dai, Y.C. (2012) New species and phylogeny of *Perenniporia* based on morphological and molecular characters. *Fungal Diversity* 58: 47–60.
<https://doi.org/10.1007/s13225-012-0177-6>
- Zhao, C.L., Cui, B.K., Song, J. & Dai, Y.C. (2015) Fragiliporiaceae, a new family of Polyporales (Basidiomycota). *Fungal Diversity* 70: 115–126.
<https://doi.org/10.1007/s13225-014-0299-0>
- Zhao, C.L., Qu, M.H., Huang, R.X. & Karunarathna, S.C. (2023) Multi-gene phylogeny and taxonomy of the wood-rotting fungal genus *Phlebia* s.l. (Polyporales, Basidiomycota). *Journal of Fungi* 9 (3): 320.
<https://doi.org/10.3390/jof9030320>
- Zhou, H.M., Dai, Y.C., Vlasák, J., Liu, H.G. & Yuan, Y. (2023) Updated systematics of *Trichaptum* s.l. (Hymenochaetales, Basidiomycota). *Mycosphere* 14 (1): 815–917.
<https://doi.org/10.5943/mycosphere/14/1/11>