Ganoderma ovisporum **sp. nov. (Polyporales, Polyporaceae) from Southwest China**

Hong-De Yang^{‡§,|}, Yong Ding[‡], Ting-Chi Wen^{¶§#}, Kalani Kanchana Hapuarachchi^{¤,§,|#}, De-Ping Wei^{|,¤,} §,#,«

‡ Key Laboratory of Forest Biotechnology in Yunnan, Southwest Forestry University, Kunming, China

§ The Engineering Research Center of Southwest Bio-Pharmaceutical Resources Ministry of Education, Guizhou University, Guiyang, China

| Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai, Thailand

¶ State Key Laboratory Breeding Base of Green Pesticide and Agricultural Bioengineering, Guiyang, China

The Mushroom Research Centre, Guizhou University, Guiyang, China

¤ State Key Laboratory Breeding Base of Green Pesticide and Agricultural Bioengineering, Key Laboratory of Green Pesticide and Agricultural Bioengineering, Ministry of Education, Guizhou University, Guiyang, China

« Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand

Corresponding author: Yong Ding (dingyongSWFU@163.com), Ting-Chi Wen ([tingchiwen@yahoo.com\)](mailto:tingchiwen@yahoo.com)

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Abstract

Background

Ganoderma is a white-rot fungus with a cosmopolitan distribution and includes several economically important species. This genus has been extensively researched due to its beneficial medicinal properties and chemical constituents with potential nutritional and therapeutic values. Traditionally, species of *Ganoderma* were identified solely based on morphology; however, recent molecular studies revealed that many morphology-based species are conspecific. Furthermore, some type species are in poor condition, which hinders us from re-examining their taxonomic characteristics and obtaining their molecular data. Therefore, new species and fresh collections with multigene sequences are needed to fill the loopholes and to understand the biological classification system of *Ganoderma*.

New information

In a survey of *Ganoderma* in Guizhou Province, southwest China, we found a new species growing on soil and, herein, it was identified by both morphology and phylogenetic evidence. Hence, we propose a new species, *Ganoderma ovisporum* sp. nov. This species is characterised by an annual, stipitate, laccate basidiome, with a red– brown to brownish-black pileus surface and pale white pores, duplex context, clavate pileipellis terminal cells, trimitic hyphal system, ellipsoid basidiospores with dark brown eusporium bearing coarse echinulae and an obtuse turgid appendix. Phylogenetic analyses confirmed that the novel species sisters to *G. sandunense* with high bootstrap support. Furthermore, the RPB2 sequence of *G. sandunense* is supplied for the first time. Notably, we re-examined the type specimen of *G. sandunense* and provide a more precise description of the duplex context, pileipellis terminal cells and basidia. All species collected are described and illustrated with coloured photographs. Moreover, we present an updated phylogeny for *Ganoderma*, based on nLSU, ITS, RPB2 and TEF1-α DNA sequence data and species relationships and classification are discussed.

Keywords

one new species, *Ganoderma*, morphology, phylogeny, taxonomy

Introduction

Ganodermataceae Donk is a large family of Polyporales and *Ganoderma* P. Karst is the most speciose genus in the family [\(Hapuarachchi et al. 2016a,](#page-14-0) [Hapuarachchi et al. 2017](#page-14-1), [He et al. 2019\)](#page-15-0). Before the molecular era, Polyporales with double-walled basidiospores with a pigmented endosporium ornamented with columns or ridges and a smooth hyaline exosporium were usually placed in Ganodermataceae (Moncalvo and Ryvarden 1997). This family is comprised of ten genera: *Amauroderma* Murrill, *Amaurodermellus* Costa-Rezende, Drechsler-Santos & Góes-Neto, *Foraminispora* Robledo, Costa-Rezende & Drechsler-Santos, *Furtadomyces* Leonardo-Silva, Cotrim & Xavier-Santos, *Ganoderma* P. Karst*, Haddowia* Steyaert, *Humphreya* Steyaert*, Sanguinoderma* Y.F. Sun, D.H. Costa & B.K. Cu,*Tomophagus* Murrill and *Trachyderma* Imazeki ([Richter et al. 2014](#page-18-0), [Costa-](#page-12-0)[Rezende et al. 2017](#page-12-0), [Costa-Rezende et al. 2020](#page-12-1), [Sun et al. 2020,](#page-19-0) [Leonardo-Silva et al.](#page-16-0) [2022](#page-16-0)). However, Ganodermataceae has been treated as a synonym of Polyporaceae ([Justo et al. 2017](#page-16-1)). There have been several discrepancies regarding the treatment of [Justo et al. \(2017\);](#page-16-1) in particular, the studied collection of Ganodermatoid specimens was insufficient to establish a stable taxonomic and systematic placement in a phylogenetic context because some herbarium materials have been destroyed or cannot be found, lacking molecular and morphological data and the characterised double-walled basidiospores in Ganodermataceae are quite different from those in Polyporaceae ([Cui](#page-13-0) [et al. 2019](#page-13-0), [Costa-Rezende et al. 2020](#page-12-1)). In this study, we subsequently followed [Justo et](#page-16-1) [al. \(2017\)](#page-16-1) since the phylogenetic analyses are more convincing and objective than morphological results.

Ganoderma was introduced by Karsten (1881) and typified by *G. lucidum* (Curtis) P. Karst. (*syn. Polyporus lucidus; bas. Boletus lucidus* Curtis), a species with stipitate and laccate white-rot Polypore fungi [\(Karsten 1881](#page-16-2), [Pegler and Young 1973,](#page-18-1) [Moncalvo and](#page-18-2) [Ryvarden 1997,](#page-18-2) [Keypour et al. 2020\)](#page-16-3). The membership of *Ganoderma* has been subsequently extended, including species with sessile, non-laccate basidiocarps and pigmented, ellipsoid to ovoid, ornamented, double-walled basidiospores ([Murrill 1902](#page-18-3), [Pegler and Young 1973,](#page-18-1) [Steyaert 1980,](#page-19-1) [Cao and Yuan 2013](#page-12-2), [Papp 2016\)](#page-18-4). Moncalvo and

Ryvarden (1997) accepted 148 *Ganoderma* species before the molecular era, of which 65% are recognised as only one or some species, but represented different morphologybased species ([Ryvarden 2000](#page-18-5), [Smith and Sivasithamparam 2003](#page-19-2), [Torres-Torres and](#page-19-3) [Guzmán-Dávalos 2012\)](#page-19-3). Recently, 180 species of *Ganoderma* were accepted, whereas nearly 500 species are estimated worldwide, of which 60% are awaiting discovery [\(He et](#page-15-0) [al. 2019](#page-15-0), [He et al. 2022\)](#page-15-1).

Despite their economic importance, the taxonomy of *Ganoderma* remains uncertain due to a slew of confusion and misconceptions. During the past several decades, many species of *Ganoderma* have been delimited, based on the presence of stipe, laccate or non-laccate, the context of pileus and the microscopic characteristics of basidiospores ([Chang and Chen 1984](#page-12-3), [Seo and Kitamot 1998,](#page-18-6) [Wu et al. 2004](#page-20-0), [Torres-Torres and](#page-19-3) [Guzmán-Dávalos 2012](#page-19-3), [Zhou et al. 2016](#page-21-0), [Tchotet-Tchoumi et al. 2019\)](#page-19-4). In general, it is difficult and subjective to identify *Ganoderma* species solely based on morphological evidence, as their phenotypic traits are sensitive to extrinsic factors, such as illumination, ventilation and humidity [\(Szedlay et al. 1999,](#page-19-5) [Demoulin 2010](#page-14-2), [Yang and Feng 2013](#page-20-1), [Hapuarachchi et al. 2019a](#page-15-2)). Therefore, morphology-based identification brought *Ganoderma* into a state of taxonomic chaos ([Smith and Sivasithamparam 2003,](#page-19-2) [Coetzee](#page-12-4) [et al. 2015](#page-12-4), [López-Peña et al. 2019,](#page-17-0) [Náplavová et al. 2020](#page-18-7)). Compared to morphology, molecular methods have turned out to be more effective in resolving intraspecific relationships with *Ganoderma* ([Yamashita and Hirose 2016](#page-20-2), [Fryssouli et al. 2020](#page-14-3), [Gunnels et al. 2020,](#page-14-4) [Jiang et al. 2021,](#page-16-4) [Shen et al. 2021](#page-18-8)). Phylogenetic markers, such as IGS, nrSSU, ITS, nrLSU, mtSSU, β-TUB, RPB1, RPB2 and TEF1-α sequences, were independently or conjointly used to infer intraspecific relationships within *Ganoderma* ([Cao et al. 2012](#page-12-5), [Zhou et al. 2015](#page-21-1), [Xing et al. 2018,](#page-20-3) [Hapuarachchi et al. 2019a,](#page-15-2) [Liu et al.](#page-17-1) [2019](#page-17-1), [Ye et al. 2019\)](#page-20-4). In particular, the multilocus phylogeny incorporating sequences from ITS, nrLSU, TEF1-α and RPB2 was applied to give a phylogenetic framework for species delimitation in this genus ([Xing et al. 2018,](#page-20-3) [Ye et al. 2019,](#page-20-4) [Tchotet-Tchoumi et al.](#page-19-4) [2019](#page-19-4), [Wu et al. 2020,](#page-20-5) [He et al. 2021](#page-15-3), [Cao et al. 2021](#page-12-6)). Furthermore, some researchers steered using a combination of morphological, chemotaxonomic and molecular strategies to elevate a steady taxonomy for *Ganoderma* and resolve taxonomic ambiguities ([Richter et al. 2014](#page-18-0), [Welti et al. 2015\)](#page-19-6).

Ganoderma has a cosmopolitan distribution and most of the species are known from tropical and sub-tropical regions (He et al. 2019). This fungus grows as saprobes or parasites on deciduous and coniferous trees and some of them are considered as plant pathogens that cause basal stem butt rot and root rot [\(Pinruan et al. 2010](#page-18-9), [Ding et al.](#page-14-5) [2020](#page-14-5), [Mafia et al. 2020,](#page-17-2) [Mohd et al. 2020\)](#page-17-3). Species of *Ganoderma* play an important role in the nutrient mobilisation process of woody plants. They possess lignocellulose– decomposing enzymes with effective mechanisms for bioenergy production and bioremediation ([Coetzee et al. 2015,](#page-12-4) [Kües et al. 2015\)](#page-16-5). In the natural environment, a basidiome has the ability to produce innumerable basidiospores that can be spread by air- or rain-driven and insect vectors ([Tuno 1999](#page-19-7), [Kadowaki et al. 2011](#page-16-6), [Almaguer et al.](#page-12-7) [2014](#page-12-7), Sadyś [et al. 2014](#page-18-10)). The infection of a plant host by pathogenic *Ganoderma* species starts with the landing of the basidiospore on the wound trunk or root, followed by

germination and colonisation [\(Rees et al. 2009,](#page-18-11) [Rees et al. 2012](#page-18-12), [Hushiarian et al. 2013](#page-15-4), [Ayin et al. 2019\)](#page-12-8). Basal stem rot caused by *G. boninense* is the main disease that leads to yield losses and death of oil palm, which account for 50% of substantial economic losses to Southeast Asia's palm oil industry ([Hushiarian et al. 2013](#page-15-4), [Lee and Chang 2016](#page-16-7), [Midot](#page-17-4) [et al. 2019\)](#page-17-4). Red roots caused by *G. philippii* are a serious disease of commercial *Acacia mangium* in Malaysia and India [\(Glen et al. 2014\)](#page-14-6). Since different *Ganoderma* species produce different characteristics and pathogenicity, species identification is difficult, which in turn, leads to significant difficulty in disease control ([Wong et al. 2012](#page-20-6)).

Ganoderma was first reported from China by Teng (1934), with four species including *G. lucidum* and one variety. More than 80 species have been introduced so far and several extensive studies have been carried out to investigate *Ganoderma* diversity in China, with new species being introduced [\(Zhao and Zhang 2000](#page-20-7), [Wu et al. 2004](#page-20-0), [Dai et al.](#page-14-7) [2009](#page-14-7), [Cao et al. 2012,](#page-12-5) [Hapuarachchi et al. 2015](#page-14-8), [Hapuarachchi et al. 2018c](#page-15-5), [Wu et al.](#page-20-8) [2019](#page-20-8), Liu et al. 2019). However, the majority of *Ganoderma* species reported from China have not been subjected to systematic studies ([Wang 2012](#page-19-8), [Hapuarachchi et al. 2016b](#page-14-9), [Hapuarachchi et al. 2018a](#page-14-10), [Wang et al. 2019](#page-19-9)). The objective of the present study is to introduce a novel *Ganoderma* species*,* from Guizhou Province, southwest China, with descriptions, colour photographs, illustrations and a multigene phylogeny.

Materials and methods

Ganoderma samples were collected from Sandong Township, Sandu Shuizu Autonomous County, Guizhou Province, China, during the rainy season of July 2020. They were dried and preserved as outlined in [Hapuarachchi et al. \(2019b\).](#page-15-6) The materials used in this study were deposited at Guizhou University (**GACP**) and the Herbarium of Kunming Institute of Botany Academia Sinica (**HKAS**).

Morphological study

Macro-morphological characteristics were described, based on dried material and the photographs provided here. Colour codes (e.g. 8E8) are from [Kornerup and Wanscher](#page-16-8) [\(1978\)](#page-16-8). Pileus was sectioned with a razor blade and mounted in 5% potassium hydroxide (KOH) solution. Pileipellis, hyphal systems of pileus, basidia and basidiospores were observed and captured using a compound microscope (Leica DM2500) equipped with a camera. Images were measured with Leica Application Suite X (LAS X). In the description section, the number, length, width and length/width ratio of the measured basidiospores are denoted with symbols *n*, *L*, *W* and *Q*, respectively. The Faces of Fungi number was registered by following [Jayasiri et al. \(2015\)](#page-15-7).

DNA Extraction, PCR and Sequencing

Genomic DNA was extracted from dried specimens using an HP Fungal DNA Kit (OMEGA, USA) following the protocol of the manufacturer. PCR amplification was

performed in a final volume of 50 µl reaction mixture that contained 25 µl 2x BenchTopTM Taq Master Mix (Biomigas), 19 µl distilled water, 2 µl (10 µM) of each primer and 2 µl template DNA. The large subunit ribosomal RNA (LSU), the internal transcribed spacer (ITS), the translation elongation factor (TEF1-α) and the RNA polymerase II second largest subunit (RPB2) were amplified with primer pairs LROR/LR5 ([Vilgalys and Hester](#page-19-10) [1990](#page-19-10)), ITS5/ITS4 ([White et al. 1990\)](#page-20-9), EF1-983F/EF1-1567R [\(Rehner and Buckley 2017](#page-18-13)) and RPB2-5f/RPB2-7cR ([Liu et al. 1999\)](#page-17-5). PCR amplification reactions were performed with a T100 Thermal Cycler (T100™, Bio-Rad, USA). The procedures used for amplification of ITS were as follows: initial denaturation at 95°C for 3 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 58°C for 30 s, elongation at 72°C for 1 min and a final extension at 72°C for 5 min. The cycling conditions of LSU, TEF1-α and RPB2 consisted of initial denaturation at 95°C for 3 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 56°C for 30 s, elongation at 72°C for 1.3 min and a final extension at 72°C for 10 min. PCR products were verified by 1% agarose gel electrophoresis and sent to Sangon Biotech (Shanghai, China) for purification and sequencing.

Sequence Alignment and Phylogenetic Analysis

The raw sequences generated in this study were assembled with ChromasPro (2.1.8). Megablast analysis was conducted using the assembled ITS and RPB2 sequences as the query to check the closely-related taxa. The taxa used in our phylogenetic analysis were selected, based on megablast results and related publications (Table [1](#page-25-0)). Alignments were performed using MAFFT v. 7 ([http://mafft.cbrc.jp/alignment/server/](http://mafft.cbrc.jp/alignment/server/index.html) [index.html](http://mafft.cbrc.jp/alignment/server/index.html), [Katoh and Standley 2013](#page-16-9)). The resulting alignments were improved manually when necessary, using BioEdit v. 7.0.5.2 ([Hall 1999](#page-14-11)). The introns in TEF and RPB2 were removed, based on the published CDS sequence in GenBank. The aligned ITS1, 5.8S, ITS2, LSU, TEF1-α and RPB2 sequences were concatenated with SequenceMatrix v. 1.7.8 ([Vaidya et al. 2011\)](#page-19-11). Maximum Likelihood (ML) analysis was performed using RAxMLHPC2 [\(Stamatakis 2014](#page-19-12)) on the CIPRES Science Gateway v. 3.3 ([Miller et al.](#page-17-6) [2010](#page-17-6)). The phylogenetic tree was inferred from four gene-partition analyses, using the GTRCAT model with 25 categories, with settings that the number of bootstrap replicates to 1,000. PartitionFinder v.2 [\(Lanfear et al. 2017](#page-16-10)) was used to estimate the best-fit model of nucleotide evolution, with the dataset subdivided into 10 data partitions (TEF 1st codon positions, TEF 2nd codon positions and TEF 3rd codon positions; RPB2 1st codon positions, RPB2 2nd codon positions and RPB2 3rd codon positions; ITS1; 5.8S; ITS2; LSU) and the following settings: branch lengths = unlinked, models = all, model selection = AICc and search = greedy. Bayesian Inference (BI) analysis was performed in the CIPRES Science Gateway using MrBayes on XSEDE v. 3.2.7a. The GTR+F+I+G4 (TEF 1st codon positions, TEF 2nd codon positions, RPB2 1st codon positions, RPB2 2nd codon positions, LSU and 5.8S), GTR+F+G4 (TEF 3rd codon positions), GTR+F+G4 (RPB2 2nd codon positions), SYM+G4 (ITS1 and ITS2) were selected as the best model. Two runs of four chains were run until the average standard deviation of split frequencies dropped below 0.01, which occurred after 2,360,000 generations**.** Tree was sampled every 1000th generation and the chain temperature was decreased to 0.05 to improve convergence. The convergence of the runs was checked using TRACER v.1.6 ([Rambaut et al. 2013\)](#page-18-14). The first 25% of the resulting samples were discarded as burn-in and posterior probabilities were calculated from the remaining sampled trees ([Larget and Simon 1999](#page-16-11)). In both ML and BY analyses, *Foraminispora concentrica* (Cui 12644) and *Foraminispora yinggelingensis* (Cui 13618) were selected as the outgroup [\(Sun et al. 2020](#page-19-0)). ML bootstrap values and BY posterior probabilities greater than or equal to 70% and 0.95, respectively, were considered significant support. The phylogenetic tree was visualised with FigTree version 1.4.0 available at [http://](http://tree.bio.ed.ac.uk/software/figtree/) tree.bio.ed.ac.uk/software/figtree/ ([Rambaut 2012\)](#page-18-15).

Taxon treatments

Ganoderma ovisporum **H.D. Yang, T.C. Wen, sp. nov.**

- IndexFungorum [IF558589](http://www.indexfungorum.org/names/NamesRecord.asp?RecordID=IF558589)
- Faces of fungi number [FoF 10099](https://bdj.pensoft.net/FoF10099)

Material

Holotype:

a. scientificName: *Ganoderma ovisporum*; kingdom: Fungi; phylum: Basidiomycota; class: Agaricomycetes; order: Polyporales; family: Polyporaceae; genus: *Ganoderma*; country: China; countryCode: CN; stateProvince: Guizhou; county: Sandu Shuizu Autonomous County; locality: Sandong Township; verbatimElevation: 612 m; verbatimLatitude: 25°70' N; verbatimLongitude: 107°96′ E; year: 2020; month: July; day: 16; habitat: Terrestrial; fieldNotes: Rotten wood, in dry dipterocarp forest and in upper mixed deciduous forest and growing up from soil; recordedBy: Hongde Yang; associatedOccurrences: HKAS123193; identifiedBy: Hongde Yang; type: HKAS123193; collectionID: SD2020071601; occurrenceID: 75774D05-5BB5-558A-B41D-FE29E21D7F32

Description

Basidiome annual, stipitate, corky, strongly laccate, becoming lighter when dry. Pileus 3 × 5 cm, up to 0.9 cm thick at the base, applanate, subreniform, upper surface redbrown (8E8) when fresh, becoming brownish-black (6C8) when dry, with slightly concentrically sulcate, radially rugose, irregularly tuberculate bumps and ridges overlying the context. Margin is slightly obtuse, yellow-brown (5D8) or concolorous with the pileus. Pore surface pale white (4A2). Pores nearly round to round, 3–4 per mm, dissepiments thin to slightly thick. Context up to 0.3 cm thick, corky, homogeneous at the periphery, becoming three-layered towards the centre, upper layer creamy-white (6E4), middle layer pale brown (6E4), lower layer brown (6D1), without concentric growth zone, black melanoid band absent. There is a line of independent or confluent, laterally arranged tubes inserted between the upper and middle layers of the context. Tubes up to 0.6 cm long, brownish (6E7). Stipe slightly darker than pileus, lateral, subcylindrical, 4-7 cm long, up to 1 cm in diam. Basidia not observed. Basidiospores (12.5–)13.0–13.5–15.0(–15.5) × (9.0–)9.5–10.0–10.5(–11.5) μ m (Q_m = 1.3, Q = 1.0–1.7, n = 30, with myxosporium), ellipsoid to broadly ellipsoid,

ovoid, brown, double-walled, with a dark brown eusporium bearing coarse echinulae and an obtuse turgid appendix, overlaid by a hyaline, smooth myxosporium. Pileipellis hymeniodermiformic, yellowish-brown, terminal cells clavate, entire, brown (5D6), thick-walled, hollow, $18-29 \times 6-11$ µm. Hyphal system trimitic, generative hyphae 3.5–6 μ m in diam., hyaline, colourless, thin-walled with clamp connections; skeletal hyphae 3–6 μm in diam., thick-walled to nearly solid, sometimes branched; binding hyphae 1.5–3 μm in diam., thick-walled, nearly solid, colourless (Fig. [1](#page-22-0)).

Etymology

Referring to the ovoid basidiospores.

Notes

Ganoderma ovisporum clusters with *G. sandunense* in the multigene phylogenetic tree (Fig. 3), the former is similar to the latter by having 98% and 97% homology in ITS and RPB2 sequence data, respectively. These two species are similar in having wide ovoid basidiospores and inhabiting deciduous coniferous mixed forests. However, *G. ovisporum* differs from *G. sandunense* in having inconspicuously concentric rings near the pileus margin, lateral stipe and shorter pileipellis terminal cells (18–29 × 6–11 μm), while conspicuously concentric zones and verticallyarranged ridges or grooves, central stipe and longer pileipellis terminal cells (50–95 × 8–13.5 μm) have been observed in the latter. By considering both phylogenetic evidence and morphological observations, we conclude our collection is a new species in *Ganoderma.*

Ganoderma sandunense **Hapuar., T.C. Wen & K.D. Hyde**

- IndexFungorum [IF555784](http://www.indexfungorum.org/names/NamesRecord.asp?RecordID=IF555784)
- Faces of fungi number [FoF05659](https://bdj.pensoft.net/FoF05659)

Material

Holotype:

a. scientificName: *Ganoderma sandunense*; kingdom: Fungi; phylum: Basidiomycota; class: Agaricomycetes; order: Polyporales; family: Polyporaceae; genus: *Ganoderma*; country: China; countryCode: CN; stateProvince: Guizhou; county: Sandu Shuizu Autonomous County; verbatimElevation: 590 m; verbatimLatitude: 24°54′N; verbatimLongitude: 107°53′E; year: 2018; month: January; day: 25; habitat: Terrestrial; fieldNotes: Rotten wood, growing up from the soil; recordedBy: Ting-Chi Wen; associatedOccurrences: GACP18012501; identifiedBy: Kalani Hapuarachchi; type: GACP18012501; collectionID: GACP18012501; occurrenceID: 120BD4C3-248E-50D0-84F4-ECA73DDE47E7

Description

Basidiome annual, stipitate, corky, strongly laccate. Pileus hemispherical, projecting 8 cm, up to 4 cm wide and 1.5 cm thick. Pileal surface reddish-black (8E8) to brownishblack (6C8), with distinctly concentrically sulcate, vertically-arranged ridges or grooves. Margin obtuse, concolorous with the pileus. Pore surface whitish-yellow (4A2) to light brown (6D4). Pores nearly circular, 3–5 per mm, dissepiments thin. Context up to 0.5 cm thick, inconspicuous triplex, fawn (5C5) to creamy-white (5A1) to dark brown (5E6), without concentric growth zone, black melanoid band absent. There is a line of independent or confluent, laterally-arranged tubes inserted between the upper and middle layer of the context. Tubes up to 1.2 cm long, dark brown (7F8). Stipe slightly darker than pileus, central, subcylindrical, up to 8 cm, 0.5 cm in diam. Basidia broadly ellipsoid, 21–25.5 × 13.5–17.5 μm, with four sterigmata. Basidiospores (12.3–)13.2–13.7–14.2(–15.7) × (9.0–)10–10.3–10.6(–12.5) μm (Qm = 1.3, $Q = 1.0 - 1.7$, $n = 30$, with myxosporium), ellipsoid to broadly ellipsoid, brown (7E5). Pileipellis cells clavate like, entire, brownish-orange (5C5), 50–95 × 8–13.5 μm. Hyphal system trimitic, generative hyphae 4-6 μm in diam., hyaline, colourless, thin-walled with clamp connections; skeletal hyphae 3.5–6 μm in diam., thick-walled to nearly solid, sometimes branched; binding hyphae 1-2 μm in diam., thick-walled, nearly solid, colourless (Fig. [2\)](#page-23-0).

Notes

Ganoderma sandunense was introduced by [Hapuarachchi et al. \(2019b\)](#page-15-6) with ITS sequence. In addition, the description of its basidia is absent in their publication. In this study, the holotype of *G. sandunense* was loaned from Herbarium (**GACP**) and re-examined. We have refined this species with a more detailed illustration. Furthermore, we provided RPB2 sequence data of this species, which is an important phylogenetic marker used for intraspecific delimitation within *Ganoderma*.

Identification keys

Analysis

Phylogenetic analyses

Eight sequences of ITS, LSU and RPB2 were successfully amplified, but we failed to obtain the TEF1-α sequence from the two specimens HKAS123193 and GACP20071602. The newly-generated sequences and sequences from GenBank represented 132 specimens from 66 species, of which 21 were the type. The combined alignment of sequences comprised 3028 characters of 606, 1020, 809, 593 belonging to TEF1-α, RPB2, ITS and LSU, respectively. The final ML optimisation log-likelihood was -17354.28. The Bayesian Inference stopped at 2915000 generations when the average standard deviation of split frequencies reached 0.009904. The tree topologies derived from ML and BY were identical. Therefore, only the ML tree is shown (Fig. [3\)](#page-24-0). The new species *G. ovisporum* and *G. sandunense* formed an individual clade in the phylogenetic tree (Fig. 3).

Discussion

In this study, both phylogeny and morphology support *G. ovisporum* as a new species*.* Morphologically, it resembles other dark-coloured, laccate, stipitate *Ganoderma* species. However, it can be distinguished by having larger (12.5–15.5 × 9.0–11.5 μm), wide ovoid, dark brown-pigmented basidiospores. It is mostly similar to *G. sandunense* in having brownish-black pileus and similarly-sized basidiospores, as well distribution in Guizhou Province [\(Hapuarachchi et al. 2019b](#page-15-6)). The former species is distinct from the latter by having a lateral stipe and shorter pileipellis terminal cells $(18-29 \times 6-11 \text{ }\mu\text{m})$. Phylogenetically, *G. ovisporum* and *G. sandunense* are closely related, forming a distinct clade with basal position with strong support.

Ganoderma was extensively researched by the Chinese because it applied to medicine and food, together with the symbolic happiness and immortality culture, those being recognised as long as 2,000 years ago ([Hapuarachchi et al. 2016b](#page-14-9), [Hapuarachchi et al.](#page-15-8) [2018b,](#page-15-8) [Li et al. 2018](#page-17-7), [Cui et al. 2019](#page-13-0), [Du et al. 2021\)](#page-14-12). Chinese taxonomists emphasised the morphological characteristics, such as stipe, pileus, pores, context, pileipellis terminal cells and basidiospores as keys to identity ([Zhao 1989](#page-20-10), [He and Yu 1989](#page-15-9), [Zhang 1997](#page-20-11)). Keeping this method, [Zhao and Zhang \(2000\)](#page-20-7) recorded 76 *Ganoderma* species from China, providing detailed illustrations. [Wu and Dai \(2005\)](#page-20-12) identified 77 *Ganoderma* species with full description and colour photographs*.* Studies have been implemented to revise the taxonomy of *Ganoderma* in China by using molecular and morphology methods in the recent decade. The results indicated at least 23 species names are synonyms and confirmed that 24 species are distributed in China, 16 of which possess laccate basidiomes [\(Wang 2012](#page-19-8), [Chao 2013,](#page-12-9) [Xing 2019](#page-20-13)). Since then, six species with laccate basidiomes have been described from China: *G. bambusicola, G. dianzhongense, G. esculentum, G. sandunense, G. shanxiense* and *G. weixinense* (

[Hapuarachchi et al. 2019b](#page-15-6), [Liu et al. 2019](#page-17-1), [Ye et al. 2019](#page-20-4), [Wu et al. 2020,](#page-20-5) [He et al. 2021](#page-15-3)). *Ganoderma* taxonomy has undergone tremendous changes since both phenotypic features and phylogeny were used to delineate species ([Gottlieb et al. 2000](#page-14-13), [Hapuarachchi et al. 2018c](#page-15-5), [Hapuarachchi et al. 2018a,](#page-14-10) [Lin and Yang 2019](#page-17-8), [Tchotet-](#page-19-4)[Tchoumi et al. 2019,](#page-19-4) [He et al. 2022](#page-15-1)). Based on the aforementioned characteristics, we have provided a dichotomous key to 22 laccate species, including our new species from China.

Ganoderma could originate from Southeast Asia and later dispersal to the Northern Hemispheres, the Southern Hemispheres and the neotropics before 30 Mya years, during which species radiation and diversification events happened ([Moncalvo and](#page-17-9) [Buchanan 2008\)](#page-17-9). Overviewing *Ganoderma* species worldwide, [Imazeki \(1939\)](#page-15-10) concluded using subgenera *Euganoderma* and *Elfvingia* to accommodate species with laccate and non-laccate characters, respectively. In this study, a phylogenetic analysis was carried out using combined LSU, ITS, TEF1-α and RPB2 sequences from 66 species that included species previously placed in the above two subgenera. The topology of our phylogenetic tree is consistent with the morphology that the laccate species and nonlaccate species tend to form groups. It is worth mentioning that the new species *G. ovisporum* group with the laccate species of *G. carnosum*, *G. dianzhongense*, *G. leucocontextum*, *G. lucidum*, *G. oregonense*, *G. sandunense*, *G. shandongense*, *G. shanxiense*, *G. tsugae* and *G. weixiensis* had strong support in both ML and Bayesian analyses. Those species were found in only or few ecological niches, except the widely cultivated *G. leucocontextum*, *G. lucidum and G. tsugae* ([Gottlieb et al. 2000,](#page-14-13) [Moncalvo](#page-17-9) [and Buchanan 2008](#page-17-9), [Hapuarachchi et al. 2018b,](#page-15-8) [Lin and Yang 2019](#page-17-8)). Therefore, many *Ganoderma* species are geographically restricted ([He et al. 2022](#page-15-1)). However, the phylogenetic tree in the case of the laccate species *G. pfeifferi* and *G. mutabile* grouped with the non-laccate species *G. adspersum*, *G. australe*, *G. eickeri*, *G. ellipsoideum*, *G. gibbosum*, *G. knysnamense*, *G. lobatum*, *G. podocarpense* and *G. williamsianum*, indicating *Euganoderma* and *Elfvingia* are polyphyletic ([Gottlieb et al. 2000\)](#page-14-13)*.* However, in fact, they are similar in having a substipitate to sessile basidiome and living as saprobes or parasites [\(Hapuarachchi et al. 2018c,](#page-15-5) [Tchotet-Tchoumi et al. 2019\)](#page-19-4). Consequently, biogeographic patterns and convergent evolution could explain the population structure and evolution of *Ganoderma*. Thus, a phylogeography study would help better understand the evolution of *Ganoderma*.

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Figure 1.

Ganoderma ovisporum (HKAS123193, holotype). **a**–**b** Basidiome; **c** Pileus; **d** Pore surface; **e** Pores; **f** Sections of pileus**; g**–**i** Pileipellis terminal cell; **j–m** Basidiospores; **n** Skeletal hyphae; **o** Generative hyphae; **p** Binding hyphae. Scale bars: g = 50 µm; h–i = 30 µm; j**–**m = 10 µm; n

 $= 100 \text{ µm}$; o = 10 µm ; p = 100 µm .

Figure 2.

Ganoderma sandunense (GACP18012501, holotype). **a** Basidiome; **b** Pore surface; **c** Sections of pileus; **d**–**e** Pileipellis terminal cell; **f** Basidia**; g**–**j** Basidiospores; **k** Skeletal hyphae and binding hyphae; **l** Generative hyphae; **m** Binding hyphae. Scale bars: d–e= 50 μm; f–h = 20 μm; i–j = 10 μm; k = 100 μm; l–m = 50 μm.

Figure 3.

Phylogram for *Ganoderma* generated from Maximum Likelihood analysis of ITS, LSU, TEF1-α and RPB2 sequence data. Bootstrap support values for Maximum Likelihood and maximum parsimony greater than 70% and posterior probabilities of Bayesian Inference ≥ 0.95 are given above branches. Type specimens are marked with letter (T) and new species in this study are indicated in red.

Table 1.

The species, specimens and GenBank accession numbers of sequences used in this study

