

# A new geographical record of *Lichenostigma chlaroterae* from China

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## Abstract

This paper reports a new geographical record of a known *Lichenostigma* species from Lijiang, Yunnan Province, China. Based on morphological characteristics and phylogenetic analyses generated from multi-gene sequence data (LSU and mtSSU), the species is identified as *Lichenostigma chlaroterae*, a lichenicolous fungus growing on *Lecanora* sp. The mycelium is extremely sparse, brown, and superficial. The conidiomata are macroscopically indistinguishable, and they produce conidia that are ellipsoid, brown, smooth, but sometimes with a verrucose to echinulate ornamentation when over-mature. Each conidium comprises three to six conidial cells that are subspherical to ellipsoid. Detailed descriptions and photoplates along with molecular data of *Lichenostigma chlaroterae* are provided.

**Keywords:** Ascomycetes, Lichenicolous, Morphology, Phylogeny, Taxonomy

**Citation:** Yuan L, Thilini Chethana KW, Meng Q, Hyde KD, Zhao Q, et al. 2026. A new geographical record of *Lichenostigma chlaroterae* from China. *Studies in Fungi* 11: e027 <https://doi.org/10.48130/sif-0026-0022>

## Introduction

*Lichenostigma* was introduced by Hafellner in 1982 to accommodate the lichenicolous fungus *L. maureri* and was initially placed in Arthoniales based on ascocarp morphology<sup>[1]</sup>. The species grows on *Usnea* spp. and *Pseudevernia furfuracea* and has been reported from the Eastern Alps as well as other parts of Eurasia. Ertz et al.<sup>[2]</sup> provided the first phylogenetic study of *Lichenostigma* and synonymized two lichenicolous genera, *Diederimyces* and *Phaeosporobolus*, under *Lichenostigma*<sup>[2]</sup>. Based on the combined phylogenetic analyses of LSU and mtSSU sequence data, together with detailed morphological evidence, *Lichenostigmatales* was established within Arthoniomycetes to accommodate the family Phaeococcomycetaceae, with *Lichenostigma* designated as the type genus<sup>[2]</sup>. Phaeococcomycetaceae presently includes four genera, namely *Antarctolichenia*, *Etayoa*, *Lichenostigma*, and *Phaeococcomyces*<sup>[3]</sup>.

Presently, *Lichenostigma* comprises approximately 34 species<sup>[3,4]</sup>, with *Lichenostigma maureri* as the type species. The genus is polyphyletic, with its taxa distributed across both Lichenotheliaceae (Dothideomycetes) and Arthoniomycetes<sup>[2]</sup>. Ertz et al.<sup>[2]</sup> proposed that the genus comprises two subgenera: subgenus *Lichenostigma*, placed within Arthoniales, and corresponding to *Lichenostigma* sensu stricto, subgenus *Lichenogramma*, which is phylogenetically clustered within Dothideomycetes; these subgenera are primarily distinguished by differences in cell division. *Lichenostigma* sensu stricto divides by budding, whereas the latter produces cells through septation. The sexual morph lacks hamathecial filaments, with asci developing directly among stromatic cells; the ascus tholus may be I+ reddish and K/I+ blue, while ascospores are 1-septate, with the outer wall occasionally K/I+ blue. The asexual morph is characterized by conidiomata composed of similar globose stromatic cells, from which conidiogenous cells arise, producing multicellular, subspherical to ellipsoid conidia<sup>[2]</sup>.

The first checklist of lichenicolous fungi in China was published in 2003, reporting the occurrence of *Lichenostigma cosmopolites* on *Xanthoparmelia scabrosa* from Hong Kong<sup>[5]</sup>. In the present study, a specimen collected in China, growing on *Lecanora* sp., was examined. Based on morphological characters and phylogenetic analyses of LSU and mtSSU sequence data, the specimen was identified as *Lichenostigma chlaroterae*, representing the first geographic record of this species from China.

## Materials and methods

### Specimen collection and morphological analysis

A specimen of *Lichenostigma* was collected in 2018 from the bark of an unidentified tree hosting a *Lecanora* species in Lijiang (22°36'38.8" N, 100°10'33.5" E), Yunnan Province, China. The specimen was observed and examined using a stereo-microscope (SterEO Discovery V12, Carl Zeiss Microscopy GmbH, Germany) and a compound microscope (Nikon ECLIPSE 80i, Nikon, Japan), equipped with a Nikon DS-Ri2 digital camera (Nikon, Japan). The measurements were done with Tarosoft® Image Frame Work v0.9.7, and the morphological analysis was performed following Senanayake et al.<sup>[6]</sup>. The symbol 'x̄' indicates the mean value. Illustrations were prepared and finalized using Adobe Photoshop 2020 (Adobe Systems, San Jose, CA, USA). The specimen was deposited in the Herbarium of Lichen, Kunming Institute of Botany, Chinese Academy of Sciences (KUN-L). The Faces of Fungi number was obtained following Jayasiri et al.<sup>[7]</sup>.

### DNA extraction, polymerase chain reaction amplification, and sequencing

Genomic DNA was extracted directly from fungal fruiting bodies using the Omega Bio-Tek Kit (Anoren [Beijing] Biotechnology Co., Ltd), following the manufacturer's protocol. PCR amplification of the

LSU region was carried out with primers LR0R/LR5 following the conditions recommended by Vilgalys & Hester<sup>[8]</sup>. The mtSSU region was amplified using primers mrSSU1/mrSSU3R<sup>[9]</sup>. The PCR reaction mixture contained a total volume of 25 µL, consisting of 12.5 µL of 2 × PCR G013 Taq MasterMix with Dye (ABM, Canada), 1 µL of each primer (10 µM), 2 µL of genomic DNA, and 8.5 µL of sterile distilled water. The parameters of PCR amplifications are displayed in Table 1. The PCR products were visualized through electrophoresis on a 1% TAE gel and detected using TSJ003 GoldView nucleic acid dye (Qingke, Kunming, China). Sequencing was performed at Qingke Company, Kunming, China.

Sequence alignment and phylogenetic analyses

All newly generated sequences were checked for quality using BioEdit v7.0.9<sup>[10]</sup>. Forward and reverse sequences were assembled using DNASTAR Lasergene SeqMan Pro v7.1.0<sup>[11]</sup>. The assembled sequences were then queried against the NCBI database<sup>[12]</sup> to identify close relatives. Preliminary identification of the newly generated sequences was performed through standard BLAST searches of GenBank. For phylogenetic analyses, LSU and mtSSU gene regions from representative species of Lichenostigmatales, as well as the outgroup taxa from Arthoniales, were retrieved from GenBank (Table 2). Each gene dataset was aligned using MAFFT v7 (<https://mafft.cbrc.jp/alignment/server/index.html>), subsequently trimmed with TrimAl v1.3 software, with a gap threshold set to 0.6 for both datasets<sup>[13]</sup>. The aligned LSU and mtSSU datasets were combined into a combined matrix using SequenceMatrix v1.8, and file formats were converted using AliView v1.19<sup>[14]</sup> for further analyses. The phylogenetic tree for maximum likelihood analysis was generated using the PhyIip format, while the Nexus format was used for Bayesian inference analysis<sup>[15]</sup>. The ML analysis was performed using IQ-TREE with the ML+ rapid bootstrap setting and 1,000 replicates<sup>[16,17]</sup>. Bayesian inference was performed with MrBayes v3.1.2 to estimate Bayesian posterior probabilities (BYPP)<sup>[18]</sup>. The resulting trees were visualized using FigTree v1.4.0 (<https://tree.bio.ed.ac.uk/software/figtree>). The identification of potential species followed previously proposed species delineation approaches<sup>[19,20]</sup>.

Results

Phylogenetic analyses

The combined LSU and mtSSU dataset comprised 2,867 base pairs in total, with positions 1–1,826 corresponding to the LSU region and positions 1,827–2,867 representing the mtSSU region. The dataset consists of 1,231 distinct alignment patterns, with 39.97% of under-terminated characters or gaps with *Arthonia didyma*, *A. dispersa*, *Cryptothecia candida*, and *Briancoppinsia cytospora* as outgroup taxa (Fig. 1). A total of 32 strains were included in the combined analyses. The best RAXML tree with a final likelihood value of –14109.293201 is presented in Fig. 1. Estimated base frequencies were as follows: A = 0.275194, C = 0.200804, G = 0.275049, T = 0.248953, substitution rates AC = 0.791749, AG = 2.569367, AT = 1.900859, CG = 1.275594, CT = 4.854511, and GT = 1.000000. Single-gene analyses

Table 1. Genes/loci used in this study with respective PCR primers and protocols.

| Locus | Primers            | PCR: thermal cycles                                 | Ref. |
|-------|--------------------|-----------------------------------------------------|------|
| LSU   | LR5/LR0R           | (95 °C: 15 s, 55 °C: 15 s: 72 °C: 15 s) × 40 cycles | [8]  |
| mtSSU | mrSSU1/<br>mrSSU3R | (95 °C: 15 s, 55 °C: 15 s: 72 °C: 15 s) × 40 cycles | [9]  |

were also performed to evaluate topological congruence and clade stability relative to the combined-gene analyses. The single-gene analyses produced tree topologies that were consistent with those inferred from the combined gene analyses. The ML analysis generated tree topologies consistent with those from the Bayesian inference (BI) analysis, supporting the reliability of our phylogenies generated herein.

Taxonomy

*Lichenostigma chlaroterae* (F. Berger & Brackel) Ertz & Diederich, Fungal Diversity 66: 128 (2014) [MB#804672]. Fig. 2

=*Phaeosporobolus chlaroterae* F. Berger & Brackel, Herzogia 24(2): 351 (2011)

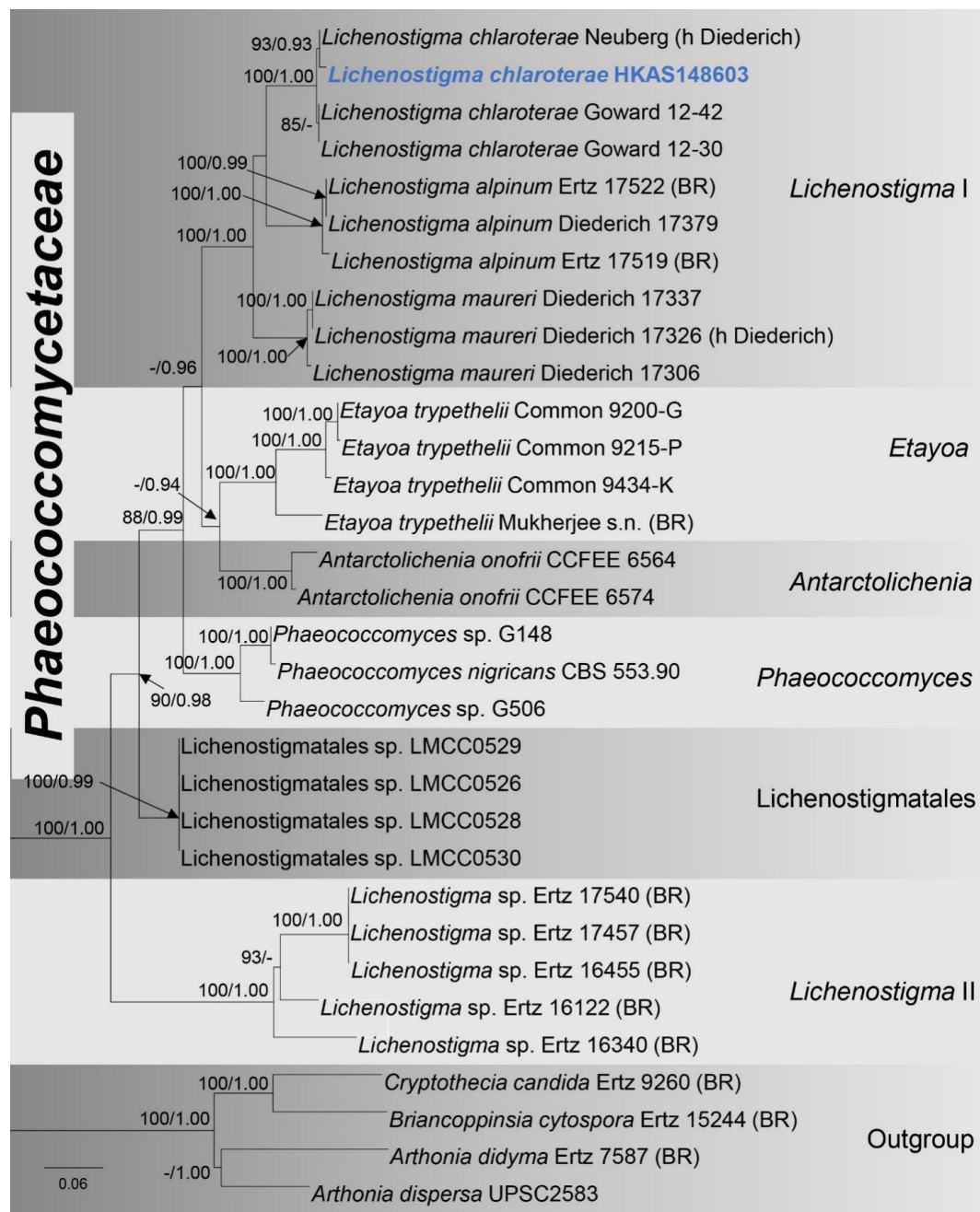
Index Fungorum: IF561182; Faces of Fungi Number: FoF 19647

The mycelium is extremely sparse, brown, and superficial. Asexual morph: **Conidiomata** macroscopically indistinguishable, 40–45 µm diam. × 60–70 µm high. ( $\bar{x}$  = 43 × 65 µm, *n* = 10), scattered, dark brown to black, subspherical to ellipsoid, with an indistinctly

Table 2. Taxa used in the phylogenetic analyses and their GenBank accession numbers.

| Taxa                             | Strain                        | Genbank accession number |          |
|----------------------------------|-------------------------------|--------------------------|----------|
|                                  |                               | LSU                      | mtSSU    |
| <i>Antarctolichenia onofrii</i>  | CCFEE 6564                    | MZ005697                 | –        |
| <i>Antarctolichenia onofrii</i>  | CCFEE 6574                    | MZ005692                 | –        |
| <i>Arthonia didyma</i>           | Ertz 7587 (BR)                | EU704083                 | EU704047 |
| <i>Arthonia dispersa</i>         | UPSC2583                      | AY571381                 | AY571383 |
| <i>Briancoppinsia cytospora</i>  | Ertz 15244 (BR)               | JF830770                 | JF830772 |
| <i>Cryptothecia candida</i>      | Ertz 9260 (BR)                | HQ454520                 | EU704052 |
| <i>Etayoa tryptethelii</i>       | Common 9200-G                 | KF176940                 | KF176967 |
| <i>Etayoa tryptethelii</i>       | Common 9215-P                 | KF176941                 | KF176968 |
| <i>Etayoa tryptethelii</i>       | Common 9434-K                 | KF176942                 | KF176969 |
| <i>Etayoa tryptethelii</i>       | Mukherjee s.n. (BR)           | KF176943                 | KF176970 |
| <i>Lichenostigma alpinum</i>     | Ertz 17522 (BR)               | KF176945                 | KF176972 |
| <i>Lichenostigma alpinum</i>     | Diederich 17379               | KF176944                 | KF176971 |
| <i>Lichenostigma alpinum</i>     | Ertz 17519 (BR)               | KF176946                 | KF176973 |
| <i>Lichenostigma chlaroterae</i> | Neuberg (h Diederich)         | KF176948                 | KF176975 |
| <i>Lichenostigma chlaroterae</i> | Goward 12-30                  | –                        | KF176976 |
| <i>Lichenostigma chlaroterae</i> | Goward 12-42                  | KF176949                 | KF176977 |
| <i>Lichenostigma chlaroterae</i> | HKAS 148603                   | PX885106                 | PX896563 |
| <i>Lichenostigma maureri</i>     | Diederich 17326 (h Diederich) | KF176953                 | KF176979 |
| <i>Lichenostigma maureri</i>     | Diederich 17337               | KF176952                 | KF176980 |
| <i>Lichenostigma maureri</i>     | Diederich 17306               | KF176951                 | KF176978 |
| <i>Lichenostigma</i> sp.         | Ertz 16122 (BR)               | KF176956                 | KF176982 |
| <i>Lichenostigma</i> sp.         | Ertz 16340 (BR)               | KF176957                 | KF176983 |
| <i>Lichenostigma</i> sp.         | Ertz 16455 (BR)               | KF176958                 | KF176984 |
| <i>Lichenostigma</i> sp.         | Ertz 17457 (BR)               | KF176959                 | KF176985 |
| <i>Lichenostigma</i> sp.         | Ertz 17540 (BR)               | KF176960                 | KF176986 |
| <i>Lichenostigmatales</i> sp.    | LMCC0526                      | MH259005                 | MH259138 |
| <i>Lichenostigmatales</i> sp.    | LMCC0528                      | MH259007                 | –        |
| <i>Lichenostigmatales</i> sp.    | LMCC0529                      | MH259008                 | –        |
| <i>Lichenostigmatales</i> sp.    | LMCC0530                      | MH259009                 | –        |
| <i>Phaeococcomyces nigricans</i> | CBS 553.90                    | MH873917                 | –        |
| <i>Phaeococcomyces</i> sp.       | G506                          | OP600268                 | OP600250 |
| <i>Phaeococcomyces</i> sp.       | G148                          | OP600267                 | OP600249 |

Newly generated sequences are in bold font and the unavailable sequences are indicated by ‘-’.



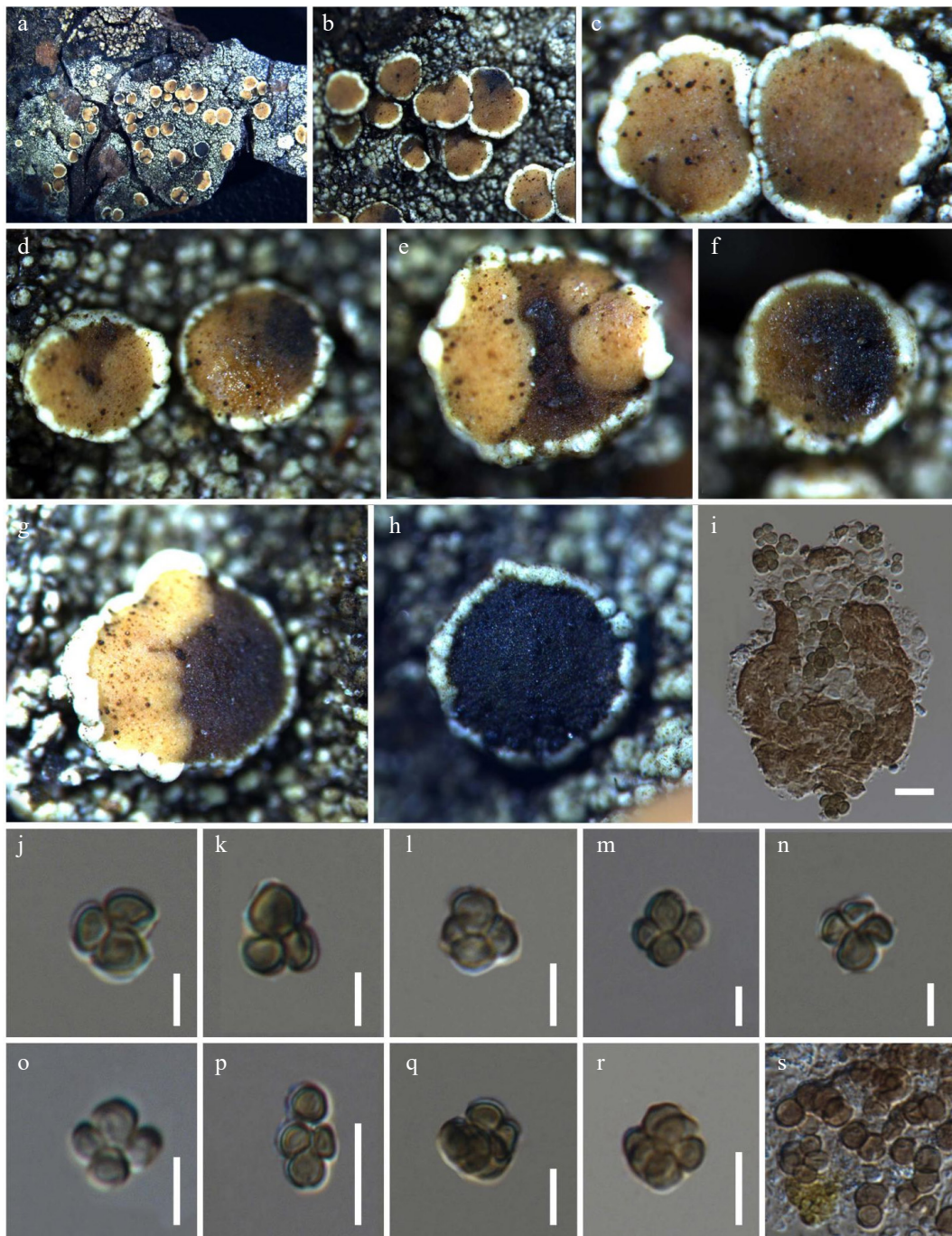
**Fig. 1** Phylogram of RA × ML analysis based on the combined LSU and mtSSU sequence datasets. Bootstrap support values for Maximum Likelihood equal to or greater than 70%, and Bayesian posterior probabilities equal to or greater than 0.90 BYPP are indicated at the nodes as ML/BYPP. The newly generated strain in this study is indicated in blue bold text. The tree is rooted with *Arthonia didyma* (Ertz 7587 BR), *A. dispersa* (UPSC2583), *Cryptothecia candida* (Ertz 9260 BR), and *Briancoppinsia cytospora* (Ertz 15244 BR).

truncated base. **Conidiophores** indistinct. **Conidiogenous cells** pale to medium brown, developing from spherical stromatic cells, shortly subcylindrical to almost ellipsoid, with an indistinctly truncate base, polyblastic. **Conidia** 4.8–6.6 × 4.4–7.1 μm ( $\bar{x}$  = 5.9 × 5.8 μm,  $n$  = 30), multicellular, composed of 3–6 cells, ellipsoid, brown, smooth, but sometimes with a verrucose to echinulate ornamentation when over-mature. **Conidial cells** 2.2–4.8 × 2.1–4.5 μm ( $\bar{x}$  = 3.3 × 3.2 μm,  $n$  = 30), subspherical to ellipsoid. Sexual morph: Unknown.

Material examined: China, Yunnan Province, Lijiang City, on a disc of *Lecanora* sp. on unidentified bark, 22°36' 38.8' N, 100°10' 33.5' E, elevation 3,351 m, 3 September 2018, V. Thiagaraja, D1L18 (HKAS148603).

Distribution: China (This study). Europe, Macaronesia, Mongolia<sup>[21]</sup>, North America<sup>[2]</sup>, Russia<sup>[21]</sup>, and South America (Bolivia).

Notes: the BLAST results of the LSU sequence data revealed the highest similarity to *Lichenostigma chlaroterae* (Goward 12–42) and *L. chlaroterae* (Neuberg [h Diederich]), with 99.10% and 100.00% similarity, respectively. The mtSSU sequence data showed the highest similarity to *L. chlaroterae* (Neuberg [h Diederich]) with 100.00%. In the multi-gene phylogenetic analyses, the new strain *L. chlaroterae* (HKAS148603) clustered with extant strains of *L. chlaroterae* (Neuberg [h Diederich], Goward 12–42 and Goward 12–30), with 93% ML bootstrap support and 0.93 BYPP. The strain *L. chlaroterae* (Diederich 17329) was excluded from the present



**Fig. 2** *Lichenostigma chlaroteriae* (HKAS148603). (a)–(h) Conidiomata on *Lecanora* sp. host. (i) Vertical section through conidioma. (j)–(r) Conidia. (s) Development of conidia. Scale bar: (i) = 20 µm, (j)–(r) = 10 µm.

analyses due to its unstable phylogenetic placement. The base pair comparison between our strain (HKAS 148603) and *L. chlaroteriae* (Neuberg [h Diederich]) revealed no differences in either the LSU or mtSSU regions. In comparison with *L. chlaroteriae* (Goward 12–42), sequence divergence was 0.12% (1/822 bp) in the LSU and 0.41% (3/715 bp) in the mtSSU, with no gaps detected. Similarly, comparison with *L. chlaroteriae* (Goward 12–30) showed a divergence of 0.29% (2/675 bp) in the mtSSU, while LSU comparison was not performed due to the lack of molecular data for that strain. The pairwise sequence comparison between our strain and *L. chlaroteriae* (Diederich 17329) revealed 1.26% (10/792) differences in the LSU and 1.25% (9/720) differences in the mtSSU without gaps.

*Lichenostigma chlaroteriae* was established by Ertz et al.<sup>[2]</sup> and the species was originally introduced as *Phaeosporobolus chlaroteriae* by Berger & von Bracke<sup>[22]</sup> based on material collected in Austria. It has also been reported from Germany and Portugal. In Central Europe, records range from colline to montane zones, and the species is probably more widespread<sup>[22]</sup>. The new specimen exhibits several characteristics similar to *Lichenostigma chlaroteriae*, including superficial, smooth-walled brown hyphae, warty to granular ornamentation on the outer stromatal cells, and multicellular conidia composed of nearly spherical to ellipsoidal cells. Additionally, *L. chlaroteriae* (Diederich 17329) occasionally produces a sexual stage with 1-septate brown ascospores, whereas no sexual structures have

been observed in our sample<sup>[2]</sup>. Our specimen slightly differs from the *L. chlaroterae* (Diederich 17329) in the smaller conidia ( $4.8\text{--}6.6 \times 4.4\text{--}7.1 \mu\text{m}$  vs  $[5.5\text{--}]7.1\text{--}10.2\text{--}[13] \times [5\text{--}]6.3\text{--}8.8\text{--}[11] \mu\text{m}$ ) and a smaller number of cells ( $3\text{--}6$  vs  $[3\text{--}]4\text{--}9\text{--}[16]$ )<sup>[2]</sup>.

## Discussion

Since the beginning of the 21<sup>st</sup> century, research on lichenicolous fungi in China has gradually expanded. Aptroot & Sipman<sup>[23]</sup> reported three species in Hong Kong, including two lichenicolous fungi newly recorded from China (*Lichenocodium lecanorae* and *Lichenostigma cosmopolites*)<sup>[23]</sup>. In 2003, four additional lichenicolous fungi were reported in Yunnan<sup>[24]</sup>. In the same year, a checklist of 29 known lichenicolous fungi in China was systematically compiled<sup>[5]</sup>. In 2016, *Polycoccum clauderouxii* was recorded in Qinghai<sup>[25]</sup>. Subsequently, a total of 30 lichenicolous species were reported<sup>[26]</sup>. Thiyagaraja et al.<sup>[27]</sup> reported *Sclerococcum simplex* that was reported from Yunnan, China<sup>[27]</sup>. In 2023, nine species of *Cercidospora* were documented in China. However, as these fungi were isolated from the medullary tissues of lichen thalli and reported as "black lichenicolous fungi", their true lichenicolous nature remains uncertain<sup>[28]</sup>. Subsequently, a new record of *Sclerococcum glaucomarioides* was described from Yunnan, indicating that the diversity of lichenicolous fungi in China is far from being fully revealed, especially in Yunnan<sup>[29]</sup>. However, research on lichenicolous fungi in China is limited, with nearly 60 species reported in the past 25 years, indicating that the documented diversity remains remarkably low given China's vast area and habitat heterogeneity<sup>[5,23–29]</sup>.

In the phylogenetic analyses, the genera within Lichenostigmales formed a monophyletic clade, with the exception of *Lichenostigma*, which appeared polyphyletic. This polyphyletic nature of *Lichenostigma* was also reported by Ertz et al.<sup>[2]</sup> highlighting the need for further studies, particularly due to the lack of molecular data for many species within the genus. Recently, Muggia et al.<sup>[30]</sup> introduced a new endolichenic genus, *Antarctolichenia*, within the order and the genus was collected from the Antarctic continent, which showed a close phylogenetic relationship with the genus *Etayoa*. A similar phylogenetic placement was observed in the present study. Further, our newly obtained strain of *L. chlaroterae*, together with previously reported strains of the same species, formed a well-supported clade with *L. alpinum*. This clade formed a sister clade to the type species, *L. maureri*, with strong statistical support (100/1.00).

*Lichenostigma* is a cosmopolitan genus that has been reported from a wide range of regions worldwide<sup>[2,21,31]</sup>. This study represents the second record of the genus *Lichenostigma* from China. Previously, *L. cosmopolites* was reported on *Xanthoparmelia scabrosa* from Hong Kong, China<sup>[23]</sup>. *Lichenostigma cosmopolites* is widely distributed in extratropical regions of both hemispheres (Africa, Asia, Australia, Europe, North America, and South America), occurring mainly in lowlands of temperate regions and at mid elevations or higher in tropical regions<sup>[32]</sup>. *Lichenostigma chlaroterae*, a relatively common species in Europe, has been reported from North America<sup>[2]</sup>. This species primarily colonizes *Lecanora* and other lichens, such as *Buellia griseovirens*, *Fuscidea lightfootii*, and *Graphis pulverulenta*<sup>[2,33,34]</sup>. Here, we report the first occurrence of *L. chlaroterae* in China. This record further expands the known distribution of the species in East Asia.

## Author contributions

The authors confirm their contributions to the paper as follows: conceptualization, data curation, and formal analysis: Yuan L, Thilini Chethana KW, Meng Q, Thiyagaraja V; funding acquisition: Meng Q, Thiyagaraja V, Hyde KD; investigation, methodology, and writing – original draft: Yuan L, Thilini Chethana KW, Meng Q, Thiyagaraja V; project administration: Yuan L, Thiyagaraja V; supervision: Thilini Chethana KW, Meng Q, Thiyagaraja V; writing – review and editing: Thilini Chethana KW, Meng Q, Hyde KD, Zhao Q, Thiyagaraja V. All authors reviewed the results and approved the final version of the manuscript.

## Data availability

All the data used are included in the article. The sequences are cited by their accession numbers and are available from GenBank.

## Acknowledgments

This study is supported by the Major Science and Technology Projects and Key R&D Plans/Programs, Yunnan Province (202202AE090001); Vinodhini Thiyagaraja thanks the Chinese Research Fund (Project No. E1644111K1) entitled 'Flexible Introduction of the High-Level Expert Program', the Kunming Institute of Botany, Chinese Academy of Sciences; Qingfeng Meng thanks the National Natural Science Foundation of China (No. 32560002).

## Conflict of interest

The authors declare that they have no conflict of interest.

## Dates

Received 5 November 2025; Revised 29 March 2026; Accepted 8 May 2026; Published online 18 September 2026

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