Revision of Immersaria and a New Lecanorine Genus in Lecideaceae (Lichenized Ascomycota, Lecanoromycetes)

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Research

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Abstract

The species *Immersaria cupreoatra* has repeatedly been reassigned between *Bellemerea* and *Immersaria*. This caused us to reconsider the relationships between *Bellemerea* and the lecanorine species of *Immersaria*, and to question the monophyly of *Immersaria*. Among 25 genera of the family *Lecideaceae*, most have lecideine apothecia, with the exception of *Bellemerea* and *Koerberiella*, which have lecanorine apothecia. According to previous classifications, *Immersaria* included species with both lecanorine and lecideine apothecia. A five-loci phylogenetic tree (nrITS, nrlSU, RPB1, RPB2 and mtSSU) for *Lecidea* showed that *Immersaria* was split into two clades: firstly all the lecideine apothecia species, and secondly all the lecanorine apothecia species. The latter were closely related to the remaining lecanorine apothecia genera: *Bellemerea* and *Koerberiella*. Therefore, the genus concept of *Immersaria* was revised accordingly, and a new lecanorine genus *Lecaimmeria* was proposed. Furthermore, five new species for *Immersaria*, and seven new species and three new combinations for the new genus *Lecaimmeria* were proposed.

Keys to *Immersaria*, the new genus *Lecaimmeria* and allied genera were provided.

Introduction

The lichen genus *Immersaria* Rambold & Pietschmann (Rambold 1989) was originally constructed from the genus *Lecidea* Ach. in order to accommodate the species *Immersaria athroocarpa* (Ach.) Rambold & Pietschmann. The genus *Immersaria* was characterized by its brown thallus with an epinecral layer, a pruinose margin and an amyloid medulla, immersed apothecia with a somewhat reduced proper margin and *Porpidia*-type asci with eight spores, halonate and simple ascospores (Rambold 1989). Subsequently, Calatayud and Rambold (1998) enlarged the scope of the genus by including the lecanorine species, *I. mehadiana* Calat. & Rambold and *I. cupreoatra* (Nyl.) Calat. & Rambold, based on morphological characters only. Currently, eight species of *Immersaria* are known worldwide (Lücking et al. 2017), three of which have lecanorine apothecia. Three of these species were previously reported from China (Hertel 1977, Zhang et al. 2015).

The genetic position of the species *Immersaria cupreoatra* (Nyl.) Calat. & Rambold was repeatedly reassigned between *Bellemerea* Hafellner & Cl. Roux (Clauzade and Roux 1984) and *Immersaria* (Calatayud and Rambold 1998). This caused us to reconsider the relationships between *Bellemerea* and the lecanorine species of *Immersaria*, and to question the monophyly of *Immersaria*. The family *Lecideaceae* Chevall originally included all the crustose lecideoid genera, but now only 25 genera have been retained. Most of these are monospecific genera or small genera with under five species (Fryday and Hertel 2014, McCune et al. 2017). The majority of genera in *Lecideaceae* have lecideine apothecia. Three exceptions are *Bellemerea*, *Immersaria* and *Koerberiella* Stein, which have lecanorine apothecia. Only *Immersaria* has both lecanorine and lecideine apothecia, according to previous circumscription (Calatayud and Rambold 1998, Valadbeigi et al. 2011). Calatayud and Rambold (1998) indicated that the presence of “two types of ascomata” represent different stages of ontogeny. However, there was no molecular evidence that could clarify the species-level phylogenetic relationships within *Immersaria*. In the two-loci phylogenetic tree of Buschbom and Mueller (2004), the lecideine species *I. usberkica* (Hertel) N. Barbero, Nav.-Ros. & Cl. Roux were related to *Lecidea tessellata* Flörke. However, because only two loci of one lecideine species were included, their tree was insufficient to clarify the relationship of the lecanorine apothecia species in *Immersaria*.

In this study, a phylogenetic tree of *Lecideaceae*, based on five loci, was established in order to verify the monophyly of *Immersaria*. The results showed that *Immersaria* was split into two clades. One clade included all the lecideine apothecia species, was sister to *Lecidea tessellata*, *L. auriculata* Th. Fr., *Cyclohymenia epithilica* McCune & M.J. Curtis and *Porpidia albocaerulescens* group. The second clade contained all the lecanorine apothecia species and was closely related to the rest of the lecanorine apothecia genera within this family: *Bellemerea* and *Koerberiella*. Therefore, the genus concept of *Immersaria* was revised, to retain only the species which had lecideine apothecia. The lecanorine species of *Immersaria* were excluded and proposed to belong to a new genus, *Lecaimmeria* C.M. Xie, Lu L. Zhang & Li S. Wang. Furthermore, five new species for *Immersaria*, seven new species and three new combinations for the new genus *Lecaimmeria* were proposed, based on the four-loci phylogenetic trees. Keys to *Immersaria*, the new genus and allied genera are provided below.

Materials And Methods

Morphological analysis
All the materials for this study were collected in mainland China, mostly from the Qinghai-Tibetan Plateau, during the authors’ participation in The Second Tibetan Plateau Scientific Expedition and Research Program. These specimens were stored in the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences (KUN) and the Lichen Section of the Botanical Herbarium, Shandong Normal University (SDNU). Type specimens were loaned by the University of Helsinki (H) and Universität Wien (WU). High-resolution photographs of type specimens were provided by the curators of H or obtained from the website Global Plants (https://plants.jstor.org/). Morphological descriptions were made under a dissecting microscope COIX. Anatomical descriptions were based on observations made of hand-cut sections, mounted in water and using a NIKON microscope. Photographs were captured with a NIKON Eclipse 50i microscope equipped with a NIKON digital camera (DSFi2 high-definition color camera head, NIKON, Japan). The specimens were tested with a 10% aqueous solution of potassium hydroxide (K), a solution of aqueous sodium hypochlorite (C) and 3% Lugol’s iodine (I) in the medulla and the surface of thallus. Secondary metabolites of all the specimens were examined by thin-layer chromatography (TLC) methods, using Solvents A, B and C, as described by Orange et al. (2001).

**Phylogenetic analysis**

Molecular analysis was carried out on the selected specimens. Genomic DNA was extracted from dry or fresh specimens using a DNAsecure Plant Kit (Tiangen), following the manufacturer’s instructions. Five gene loci were amplified by using the following primers: ITS1F (Larena et al. 1999), ITS4 (White et al. 1990), LR0R (Rehner and Samuels 1994), LR5 (Vilgalys and Hester 1990), gRPB1a (Stiller and Hall 1997), fRPB1c (Matheny et al. 2002), RPB2-6f, RPB2-7cr (Liu et al. 1999), mrSSU1 and mrSSU3R (Zoller et al. 1999). The 25 µl PCR mixture consisted of 2 µl DNA, 1 µl of each primer, 12.5 µl 2 x Taq PCR MasterMix (Aidlab) (Taq DNA Polymerase [0.1 unit/µL], 4 mM MgCl₂, and 0.4 mM dNTPs) and 8.5 µl ddH₂O. Conditions for PCR of nrITS, nrLSU and mtSSU were set for an initial denaturation at 94 ºC for 10 min, followed by 34 cycles of denaturation at 95 ºC for 45 s, annealing at 50 ºC for 45 s, extension at 72 ºC for 45 s, and a final extension at 72 ºC for 10 min. For RPB1 and RPB2, the parameters were set to an initial denaturation at 94 ºC for 10 min, followed by 34 cycles of denaturation at 95 ºC for 45 s, annealing at 52 ºC for 50 s, extension at 72 ºC for 60 s, and a final extension at 72 ºC for 5 min. The PCR products were sequenced using Sanger technology by the company of Tsingke Biological Technology (Beijing).

The raw sequences were assembled and edited using SeqMan v.7.0 (DNAstar packages). Sequences extracted from new materials with each gene loci were aligned with additional sequences that were available from GenBank (Table 1), by using MEGA v.10.0 and an online version of MAFFT v.7.0 to generate nrITS-nrLSU-RPB1-RPB2-mtSSU or nrITS-nrLSU-RPB1-RPB2 matrices. The five or four gene matrices were combined by SequenceMatrix v.1.7.8. and the concatenated alignments were estimated by PartitionFinder 2 (Lanfear et al. 2017), based on Bayesian information criterion (BIC), to find the most appropriate nucleotide substitution model for each of the five loci.
Table 1
Sequences included in this study. The new sequences generated are in bold.

| Taxa                  | Locality       | Voucher Specimens | GenBank accession number | nrITS | nrLSU | RPB1 | RPB2 | mtSSU |
|-----------------------|----------------|-------------------|--------------------------|-------|-------|------|------|-------|
| Amygdalaria consentiens | Greenland     | J. Buschbom 22.8.2000–56 | —            | AY532977 | —     | —    | —    | —     |
| A. elegantior         | Canada         | J. Buschbom 16.7.2000–38  | —            | AY532979 | —     | —    | —    | —     |
| A. panaeola           | USA            | J. Buschbom 3118   | —            | AY532980 | —     | —    | —    | —     |
| Bellemerea alpina     | Unknown        | Hafellner 46531   | AF332117       | —     | —     | —    | —    | —     |
| B. alpina             | Greenland      | J. Buschbom 23.8.2000–22 | —            | AY532982 | —     | —    | —    | —     |
| B. cinereorufescens   | USA            | McCune 35490      | KY800500       | —     | —     | —    | —    | —     |
| B. subsorediza        | Sweden         | J. Buschbom 25.8.2001–38a | —           | AY532983 | —     | —    | —    | —     |
| Bryoblimbia australis | Chile          | S. Pérez-Ortega 1419 | KF683092       | —     | KF683112 | —    | —    | —     |
| B. diapensiae         | Sweden         | Arup L04400       | HQ650660       | HQ660539 | —     | —    | —    | HQ660564 |
| B. hypnorum           | Unknown        | F. Jonsson & Z. Palice 10747 | KF683093 | —     | —     | —    | —    | —     |
| B. sanguineoatra      | France         | Sipman 44029      | HQ650664       | AY533005 | —     | —    | —    | —     |
| Clauzadea monticola   | USA            | A. M. Fryday 9703 | KF683090       | KF692710 | —     | —    | —    | —     |
| C. monticola          | USA            | A. M. Fryday 9728 | —            | —     | —     | KF683113 | KF683110 | —    |
| Cyclohymenia epilithica | USA          | McCune 31029      | KY800503       | KY800514 | —     | —    | —    | —     |
| C. epilithica         | USA            | McCune 31068      | KY800504       | KY800513 | —     | —    | —    | —     |
| Farnoldia jurana      | Austria        | Herbarium Tuerk 39660 | EU263920 | —     | —     | MK684889 | —    | GU074511 |
| F. jurana             | Unknown        | J. Buschbom 15.09.2001-1 | —            | AY532984 | —     | —    | —    | —     |
| Immersaria athroocarpa | China: Inner Mongolia | SDNU20190035 | MZ227390       | MZ227079 | —     | —    | MZ343462 | MZ227025 |
| I. athroocarpa         | China: Inner Mongolia | SDNU20190140 | MZ227391       | MZ227080 | MZ343432 | MZ343461 | MZ227026 |
| I. athroocarpa         | China: Inner Mongolia | SDNU20190143 | MZ227393       | MZ227081 | MZ343439 | —     | —     |
| I. athroocarpa         | China: Inner Mongolia | SDNU20190227D | MZ227394       | —     | MZ343433 | —     | —     |
| I. athroocarpa         | China: Inner Mongolia | SDNU20190227 | MZ227395       | —     | MZ343434 | —     | —     |
| Taxa       | Locality     | Voucher Specimens | GenBank accession number |
|------------|--------------|-------------------|--------------------------|
|            |              |                   | nrITS | nrLSU | RPB1 | RPB2 | mtSSU |
| I. aurantia| China: Qinghai | KUN 20-67809      | MZ227428 | MZ227101 | MZ343431 | – | MZ227031 |
| I. aurantia| China: Sichuan | KUN 20-66701      | MZ227400 | MZ227092 | – | – | – |
| I. aurantia| China: Sichuan | KUN 20-66708A     | MZ227403 | MZ227093 | MZ343427 | – | – |
| I. aurantia| China: Sichuan | KUN 20-66723      | MZ227408 | MZ227095 | – | – | – |
| I. aurantia| China: Sichuan | KUN 20-66680      | MZ227483 | MZ227087 | – | – | – |
| I. aurantia| China: Sichuan | KUN 20-66687      | MZ227485 | MZ227088 | – | – | – |
| I. aurantia| China: Sichuan | KUN 20-66692      | MZ227486 | MZ227089 | – | – | – |
| I. aurantia| China: Sichuan | KUN 20-66693      | MZ227487 | MZ227090 | – | – | – |
| I. aurantia| China: Tibet  | KUN 20-69114      | MZ227464 | MZ227116 | – | MZ343472 | – |
| I. aurantia| China: Tibet  | KUN 20-69122      | MZ227465 | MZ227117 | – | – | – |
| I. aurantia| China: Tibet  | KUN 20-69091      | MZ227461 | – | – | MZ343465 | – |
| I. aurantia| China: Tibet  | KUN 20-69094      | MZ227462 | MZ227114 | – | – | – |
| I. aurantia| China: Tibet  | KUN XY19-1290     | MZ227473 | MZ227084 | – | – | – |
| I. ferruginea| China: Sichuan | KUN 20-66697A   | MZ227399 | MZ227091 | – | – | – |
| I. ferruginea| China: Sichuan | KUN 20-67670     | MZ227426 | MZ227100 | MZ343441 | – | – |
| I. ferruginea| China: Tibet  | KUN 20-69105     | MZ227463 | MZ227115 | – | MZ343469 | – |
| I. ferruginea| China: Tibet  | KUN 20-69144     | MZ227466 | MZ227118 | MZ343417 | MZ343470 | MZ227034 |
| I. ferruginea| China: Tibet  | KUN 20-69146     | MZ227467 | MZ227119 | – | MZ343471 | – |
| I. ferruginea| China: Tibet  | KUN 20-69148     | MZ227468 | MZ227120 | – | MZ343468 | – |
| I. plumbeoolivacea | China: Qinghai | KUN 20-66889 | MZ227430 | MZ227102 | MZ343435 | MZ343467 | – |
| I. plumbeoolivacea | China: Qinghai | KUN 20-66914 | MZ227437 | MZ227103 | MZ343405 | MZ343464 | MZ227032 |
| I. plumbeoolivacea | China: Qinghai | KUN 20-66915 | MZ227438 | MZ227104 | MZ343436 | MZ343463 | MZ227033 |
| I. plumbeoolivacea | China: Qinghai | KUN 20-67896 | MZ227446 | MZ227108 | MZ343413 | – | – |
| Taxa               | Locality       | Voucher Specimens | GenBank accession number |
|--------------------|----------------|-------------------|--------------------------|
|                    |                |                   | nrITS | nrLSU | RPB1 | RPB2 | mtSSU |
| I. shangrilaensis  | China: Yunnan  | SDNU20181696      | MZ227392 |      |      |      |      |
| I. shangrilaensis  | China: Yunnan  | KUN 18-60447      | MZ227472 | MZ227083 |      |      |      |
| I. venusta         | China: Qinghai | KUN 20-66933      | MZ227439 | MZ227105 | MZ343438 |      |      |
| I. venusta         | China: Qinghai | KUN 20-66940      | MZ227441 | MZ227106 | MZ343406 |      |      |
| I. venusta         | China: Qinghai | KUN 20-68157      | MZ227452 | MZ227112 | MZ343424 | MZ343458 |      |
| I. venusta         | China: Qinghai | KUN 20-66796      | MZ227413 | MZ227097 | MZ343430 |      |      |
| I. venusta         | China: Qinghai | KUN 20-66808      | MZ227416 | MZ227098 | MZ343426 |      | MZ227028 |
| I. venusta         | China: Qinghai | KUN 20-66810      | MZ227417 | MZ227099 | MZ343428 | MZ343473 | MZ227029 |
| I. venusta         | China: Qinghai | KUN 20-66824      | MZ227421 |      | MZ343423 | MZ343460 |      |
| I. venusta         | China: Qinghai | KUN 20-66977      | MZ227444 | MZ227107 |      | MZ343466 |      |
| I. venusta         | China: Qinghai | KUN 20-2811       | MZ227480 | MZ227085 | MZ343440 |      |      |
| I. venusta         | China: Qinghai | KUN 20-2799       | MZ227481 |      | MZ343398 |      |      |
| I. venusta         | China: Qinghai | KUN 20-67959      | MZ227447 | MZ227109 | MZ343437 |      |      |
| I. venusta         | China: Qinghai | KUN 20-67965      | MZ227448 | MZ227110 | MZ343429 |      |      |
| I. venusta         | China: Qinghai | KUN 20-67969A     | MZ227449 | MZ227111 | MZ343425 |      |      |
| I. venusta         | China: Sichuan  | KUN 20-66607      | MZ227482 | MZ227086 |      |      |      |
| I. venusta         | China: Sichuan  | KUN 20-66721C     | MZ227407 | MZ227094 |      |      |      |
| I. venusta         | China: Sichuan  | KUN 20-66725      | MZ227409 | MZ227096 |      |      |      |
| I. venusta         | China: Sichuan  | KUN 20-68802      | MZ227456 | MZ227113 | MZ343399 | MZ343459 |      |
| Immersaria sp.     | Macedonia       | Malicek 7717      | MF149862 |      |      |      |      |
| Koerberiella wimmeriana | Norway         | O-L-163472     | MK812168 |      |      |      |      |
| Lecaimmeria botryoides | China: Sichuan | KUN 20-66706 | MZ227401 | MZ227046 |      |      |      |
| L. botryoides      | China: Qinghai  | KUN 20-66765      | MZ227412 | MZ227053 | MZ343400 | MZ343457 | MZ227027 |
| Taxa          | Locality       | Voucher Specimens | GenBank accession number |
|--------------|----------------|-------------------|-------------------------|
|              |                |                   | nrITS | nrLSU | RPB1 | RPB2 | mtSSU |
| L. botryoides| China: Qinghai | KUN 20-66891      | MZ227431 | – | MZ343422 | – | – |
| L. botryoides| China: Qinghai | KUN 20-66898      | – | – | MZ343408 | – | – |
| L. botryoides| China: Qinghai | KUN 20-66900      | MZ227434 | – | – | – | – |
| L. botryoides| China: Sichuan | KUN 20-66707      | MZ227402 | MZ227047 | – | – | – |
| L. botryoides| China: Sichuan | KUN 20-66711      | MZ227404 | MZ227048 | – | – | – |
| L. botryoides| China: Sichuan | KUN 20-66713      | MZ227405 | MZ227049 | MZ343403 | – | – |
| L. botryoides| China: Sichuan | KUN 20-66721A     | MZ227406 | MZ227050 | – | MZ343456 | – |
| L. botryoides| China: Sichuan | KUN 20-66730      | MZ227410 | MZ227051 | – | – | – |
| L. botryoides| China: Sichuan | KUN 20-667706     | MZ227427 | MZ227063 | – | – | – |
| L. botryoides| China: Sichuan | KUN 20-66683      | MZ227484 | MZ227045 | – | – | – |
| L. lygaea    | China: Tibet   | KUN 20-69053      | MZ227457 | – | – | – | – |
| L. iranic    | China          | SDNU20117663      | KR061347 | – | – | – | – |
| L. iranic    | China          | SDNU20117623      | KR061348 | – | – | – | – |
| L. lygaea    | China: Tibet   | KUN 20-69054      | MZ227458 | MZ227075 | – | – | – |
| L. lygaea    | China: Tibet   | KUN 20-69070      | MZ227459 | MZ227076 | – | – | – |
| L. lygaea    | China: Tibet   | KUN 20-69072      | MZ227460 | MZ227077 | – | MZ343449 | – |
| L. mongolica | China: Inner Mongolia | SDNU20190354 | MZ227389 | MZ227038 | MZ343404 | – | – |
| L. mongolica | China: Inner Mongolia | SDNU20190350 | MZ227388 | MZ227037 | – | – | – |
| L. mongolica | China: Inner Mongolia | SDNU20117851 | MZ227396 | – | – | – | – |
| L. mongolica | China: Inner Mongolia | SDNU20117613 | MZ227397 | – | – | – | – |
| L. mongolica | China: Inner Mongolia | SDNU20117399 | MZ227398 | – | – | – | – |
| L. orbicularis | China: Qinghai | KUN 20-66886B     | MZ227429 | MZ227064 | MZ343416 | – | – |
| Taxa            | Locality   | Voucher Specimens | GenBank accession number | nrITS | nrLSU | RPB1 | RPB2 | mtSSU |
|-----------------|------------|-------------------|--------------------------|-------|-------|------|------|-------|
| L. orbicularis  | China: Qinghai | KUN 20-66896    | MZ227432 MZ227065       |       |       | MZ343402 |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66899    | MZ227433 MZ227066       | MZ343401 |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66901    | MZ227435                |       |       |       |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66908    |                        | MZ227070 | MZ343415 | MZ343442 |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66909    |                        |       |       |        | MZ343394 | MZ343446 |        |
| L. orbicularis  | China: Qinghai | KUN 20-66935    | MZ227440 MZ227071       | MZ343421 |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66943    | MZ227442 MZ227072       | MZ343418 | MZ343445 |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66801    | MZ227414 MZ227054       |        |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66803    | MZ227415 MZ227055       |        |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66811    | MZ227418 MZ227056       |        |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66817    | MZ227419 MZ227057       | MZ343409 |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66821    | MZ227420 MZ227058       |        |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66826A   | MZ227422 MZ227059       | MZ343396 |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66829    | MZ227423 MZ227060       | MZ343395 |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66833    | MZ227424 MZ227061       | MZ343410 | MZ343443 | MZ227030 |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66841    | MZ227425 MZ227062       | MZ343414 |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66965    | MZ227443 MZ227073       | MZ343411 |      |        |      |        |        |
| L. orbicularis  | China: Qinghai | KUN 20-66979    | MZ227445 MZ227074       | MZ343407 | MZ343448 |        |      |        |        |
| L. orbicularis  | China: Sichuan | KUN 20-66747    | MZ227436 MZ227067       | MZ343397 | MZ343447 |        |      |        |        |
| L. orbicularis  | China: Sichuan | KUN 20-66750    |                        | MZ227068 |        |        |      |        |        |
| L. orbicularis  | China: Sichuan | KUN 20-66753    |                        | MZ227069 | MZ343412 | MZ343444 |      |        |        |
| L. orbicularis  | China: Sichuan | KUN 20-66743    | MZ227411 MZ227052       |        |      |        |      |        |        |
| L. qinghaiensis | China: Qinghai | KUN 20-3127     | MZ227471                |        |      |        | MZ343454 |      |        |
| Taxa               | Locality   | Voucher Specimens | GenBank accession number |
|-------------------|------------|-------------------|--------------------------|
|                   |            |                   | nrITS | nrLSU | RPB1 | RPB2 | mtSSU |
| L. qinghaiensis   | China:     | KUN 20-68687      | MZ227453 | –       | –     | –     | –     |
|                   | Qinghai    |                   |          |        |       |       |       |
| L. qinghaiensis   | China:     | KUN 20-68696      | MZ227454 | –       | –     | –     | –     |
|                   | Qinghai    |                   |          |        |       |       |       |
| L. qinghaiensis   | China:     | KUN 20-68698      | MZ227455 | –     | MZ343420 | MZ343450 | –     |
|                   | Qinghai    |                   |          |        |       |       |       |
| L. qinghaiensis   | China:     | KUN 20-3115       | MZ227470 | –       | –     | MZ343453 | –     |
|                   | Qinghai    |                   |          |        |       |       |       |
| L. qinghaiensis   | China:     | KUN 20–849        | MZ227469 | MZ227078 | MZ343419 | MZ343452 | MZ227035 |
|                   | Qinghai    |                   |          |        |       |       |       |
| L. tibetica       | China:     | KUN 19-64071      | –       | MZ227082 | –     | –     | –     |
|                   | Tibet      |                   |          |        |       |       |       |
| L. tibetica       | China:     | KUN XY19-1288i    | MZ227474 | MZ227039 | –     | –     | MZ227036 |
|                   | Tibet      |                   |          |        |       |       |       |
| L. tibetica       | China:     | KUN XY19-1288A    | MZ227475 | MZ227040 | –     | –     | –     |
|                   | Tibet      |                   |          |        |       |       |       |
| L. tuberculosa    | China:     | KUN 18-58856      | MZ227476 | MZ227041 | –     | –     | –     |
|                   | Gansu      |                   |          |        |       |       |       |
| L. tuberculosa    | China:     | KUN 18-58857      | MZ227477 | MZ227042 | –     | –     | –     |
|                   | Gansu      |                   |          |        |       |       |       |
| L. tuberculosa    | China:     | KUN 18-58865A     | MZ227478 | MZ227043 | –     | –     | –     |
|                   | Gansu      |                   |          |        |       |       |       |
| L. tuberculosa    | China:     | KUN 18-59835      | MZ227479 | MZ227044 | –     | –     | –     |
|                   | Gansu      |                   |          |        |       |       |       |
| L. tuberculosa    | China:     | KUN 20-68077      | MZ227450 | –       | –     | MZ343451 | –     |
|                   | Qinghai    |                   |          |        |       |       |       |
| L. tuberculosa    | China:     | KUN 20-68055      | MZ227451 | –       | –     | MZ343455 | –     |
|                   | Qinghai    |                   |          |        |       |       |       |
| Lecidea atrobrunnea | Antarctica | AAS_Convey00458       | MK620076 | –       | MK684891 | HQ660524 | MK684569 |
| L. auriculata     | Argentina  | UR00061            | MK620123 | –       | MK684941 | –     | MK684627 |
| L. berengeriana   | Unknown    | Arup L00015        | HQ650659 | HQ660537 | –     | HQ660526 | HQ660562 |
| L. confluens      | Unknown    | J. Buschbom 21.8.2001-44 | –  | AY532994 | –     | –     | –     |
| L. confluens      | Austria    | Herbarium Tuerk 39641 | –  | –       | –     | –     | –     |
| L. fuskoastra     | Sweden     | Arup L02894        | HQ650662 | HQ660541 | –     | HQ660528 | HQ660566 |
| L. grisella       | Turkey     | Trabzon 2          | HQ605931 | –       | –     | –     | –     |
| L. grisella       | Sweden     | Arup L02723        | –       | HQ660542 | –     | HQ660529 | HQ660567 |
| L. laboriosa      | USA        | F. Lutzoni et al. 03.09.05-5 | –  | KJ766586 | –     | DQ992432 | –     |
| L. laboriosa      | Unknown    | U.C. Riverside 43266UCR1 | –  | –       | MK684890 | –     | GU074503 |
| L. lapicida       | USA        | Lendemer 11081     | HQ650665 | HQ660544 | –     | HQ660530 | HQ660570 |
| Taxa                  | Locality     | Voucher Specimens          | GenBank accession number |
|----------------------|--------------|----------------------------|--------------------------|
|                      |              |                            | nrITS   | nrLSU | RPB1 | RPB2 | mtSSU  |
| *L. lithophila*      | Canada       | UR00246                    | MK620247 | –     | MK685037 | –       | MK684743 |
| *L. plana*           | Sweden       | LD L03170                  | EU259903 | –     | –     | KF683111 | – |
| *L. promiscens*      | Argentina    | UR00129                    | KX120205 | –     | MK684964 | –       | MK684661 |
| *L. silacea*         | Unknown      | AFTOL-ID 1368              | HQ650629 | –     | DQ986820 | DQ992431 | – |
| *L. silacea*         | Unknown      | Wedin 6865                 | –       |       |       |       | – |
| *L. tessellata*      | Unknown      | Herbarium Tuerk 42156      | HQ650671 | HQ660548 | –     | –     | – |
| *L. uniformis*       | USA          | Hollinger 6775             | NR_158514 | KY800515 | –     | –     | – |
| *Lecidoma demissum*  | Unknown      | AFTOL 1376                 | HQ650630 | –     | KJ766867 | DQ992445 | – |
| *Pachyphytis ozzarkana* | Unknown  | J. Buscbhomb 11.10.1997-2 | –     |       |       | AY532988 | – |
| *Poeltidea cf. perusta* | Chile   | UR00026                    | MK620106 | –     | MK684886 | –       | MK684599 |
| *P. perusta*         | Chile        | UR00039                    | MK620112 | –     | MK684888 | –       | MK684609 |
| *Porpidia alboacaerulescens* | USA | Tripp 2279                  | KJ653475 | –     | –     | DQ992443 | – |
| *P. cinereocatra*    | United Kingdom | Orange 20432              | KJ162305 | –     | –     | –     | – |
| *P. cinereocatra*    | Unknown      | J. Buscbhomb 30.8.2001-1   | –     | AY532941 | –     | –     | – |
| *P. cinereocatra*    | Unknown      | J. Guccion 1187            | –     | –     | –     | –     | KF683104 |
| *P. contraponenda*   | United Kingdom | Orange 20447              | KJ162297 | –     | –     | –     | – |
| *P. contraponenda*   | Unknown      | K. Glew 000810-2           | –     | AY532942 | –     | –     | – |
| *P. degelii*         | USA          | Tripp 2503                 | KJ653479 | –     | –     | –     | KJ653473 |
| *P. grisea*          | China        | SDNU YN0116                | KY509524 | –     | –     | –     | – |
| *P. grisea*          | Unknown      | J. Buscbhomb 25.8.1999-15  | –     | AY532951 | –     | –     | – |
| *P. hydrophila*      | United Kingdom | Orange 16218              | KJ162317 | –     | –     | –     | – |
| *P. hyposticta*      | China        | SDNU:20141385             | NR_156592 | –     | –     | –     | – |
| *P. macrocarpa*      | Austria      | Herbarium Tuerk 39740      | EU263923 | –     | –     | –     | GU074512 |
| *P. macrocarpa*      | Austria      | UR00411                    | MK620258 | –     | MK685056 | –       | MK684730 |
| *P. speirea*         | China        | SDNU20140764              | KY509523 | –     | –     | –     | – |
| *P. speirea*         | Unknown      | AFTOL 1050                 | –     | DQ986758 | DQ986829 | DQ992444 | – |
| *Rhizocarpon disporum* | Unknown   | Lutzoni 96.10.26-9 st.1 (1/2) | –     | AF356678 | –     | AY641069 | – |
Phylogenetic relationships were inferred using Bayesian inference (BI) and Maximum likelihood (ML). ML analyses were performed with RaxMLHPC using general time reversible model of nucleotide substitution with the gamma model of rate heterogeneity (GTRGAMMA or GTRCAT). The analyses were run with a rapid bootstrap analysis using 1000 replicates with data partitioned. Bayesian method was performed with MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001). Four Markov chains were run with 2 million generations for each data set and trees were sampled every 100 generations. It was ensured that the average standard deviation of split frequencies was lower than 0.01. Posterior probabilities above 0.7 and bootstrap support above 40 % were considered significant supporting values. All the trees were visualized with FigTree v 1.4.0 (Rambaut 2012).

## Results

A total of 188 sequences of the nrITS, nrLSU, RPB1, RPB2 and mtSSU were generated from 75 specimens representing 65 species. Although the five-loci tree only poorly resolved the hierarchy of genera within the family Lecideaceae, nonetheless the results revealed that the genus *Immersaria* was not a monophyletic lineage. Rather, it was divided into two distant and well-supported lineages: Clade 1 which contained the lecideine apothecia species and Clade 2 which contained the lecanorine apothecia species (Fig. 1).

Clade 1 formed a highly supported clade (94% MLBS and 1.00 PP) with *Amygdalaria* Norman, *Cyclohymenia* McCune & M.J. Curtis, *Lecidea* s.str. and *Porpidia* Körb. (Fig. 1), all of which have lecideine apothecia. *Amygdalaria*, *Porpidia* and *Lecidea* s.str. were nested together, which is consistent with the results of previous research (Buschbom and Mueller 2004, Fryday et al. 2014). However, the relationships between these genera still need further research. There was a high level of support for a monophyletic lineage of lecideine apothecia species of *Immersaria*, with these being sister to the *Lecidea tessellata*, *L. auriculata*, *Cyclohymenia* and *Porpidia albocaerulescens* group. As the type species of its genus, *Immersaria athroocarpa* was included in the lineage. Thus, only those *Immersaria* species with lecideine apothecia were recognized as belonging to the genus *Immersaria*. This revised concept of the genus *Immersaria* is as follows: wax glossy thallus with an epinecral layer, immersed lecideine apothecia with a reduced margin, and *Porpidia*-type asci with halonate ascospores.

There was also a high level of support for Clade 2 as a monophyletic lineage (99% MLBS and 1.00 PP) which was clustered within the same family as the other lecanorine apothecia genera: *Bellemerea* and *Koerberiella* (Fig. 1). *Bellemerea* was the sister group of *Koerberiella* and Clade 2, but was distinguished by its white thallus and amyloid ascospores. *Koerberiella* was sister to Clade 2, but differed in the presence of spherical isidia and adnate apothecia. Although there is only a low supporting value for the node of *Koerberiella* and Clade 2, there are conspicuous differences in their morphology and sufficient differences between the bases in their nucleotide sequences. Therefore, a new genus, *Lecaimmeria*, was proposed to accommodate Clade 2, which has immersed lecanorine apothecia with a white margin, and orange epihymenium with an epinecral layer.

Two additional phylogenetic trees were constructed, based on four loci (nrITS, nrLSU, RPB1 and RPB2), in order to assess the phylogenetic position of species within *Immersaria* and *Lecaimmeria* respectively. The phylogenetic tree of *Immersaria* was comprised of one highly supported clade with six separate lineages, based on 137 sequences from 51 specimens (Fig. 2). All the species with brown, orange, rusty, irregular or aggregate thalli formed respective monophyletic lineages. *I. ferruginea* C.M. Xie & Li S. Wang formed a sister group to *I. plumbeolivacea* C.M. Xie & Xin Y. Wang, but differed in its rusty thallus and green epihymenium. *I. shangrilaensis* C.M. Xie & Lu L. Zhang formed a well-supported clade sister to *I. athroocarpa*, *I. aurantum* C.M. Xie & Li S. Wang and *I. venusta* C.M. Xie & Xin Y. Wang, but the aggregate areolae clearly distinguished *I. shangrilaensis* from these other species. The robust lineage *I. aurantum* formed a weakly supported clade sister to *I. athroocarpa* and *I. venusta*, but could be distinguished by its irregular, conspicuously orange thallus and green epihymenium. *I. athroocarpa* was sister to *I. venusta*, but differed in its convex, polygon areolae and densely crowded apothecia.

### Table

| Taxa                      | Locality | Voucher Specimens | GenBank accession number |
|---------------------------|----------|-------------------|--------------------------|
| *Romjularia lurida*       | Spain    | S. Pérez-Ortega 1372 | KF683091 KF683107 EF524328 — — |
| *R. geographicum*         | Norway   | Ihlen 941         | AF483619 AY853389 — — AF483187 |

| Specimens     | nrITS | nrLSU | RPB1 | RPB2 | mtSSU |
|---------------|-------|-------|------|------|-------|
|                |       |       |      |      |       |
The phylogenetic tree of *Lecaimmeria* was comprised of one well-supported clade with nine separate lineages, based on 195 sequences from 66 specimens (Fig. 3). *"Immersaria"* sp. and *Lecaimmeria iranica* (Valadb., Sipman & Rambold) C.M. Xie were the basal group. *"Immersaria"* sp. has only been recorded from Macedonia and *L. iranica* has been recorded from Inner Mongolia in China or from Iran. *L. tuberculosa* C.M. Xie & Xin Y. Wang was sister to *L. qinghaiensis* C.M. Xie & Li S. Wang, but conspicuously differed in its tuberculiform pycnidia. *L. mongolica* C.M. Xie & Lu L. Zhang formed a well-supported monophyletic lineage, and its population was mainly recognized by its orange, irregular areolae and gyrophoric acid content. *L. botryoides* C.M. Xie & Li S. Wang formed a highly supported sister group to *L. orbicularis* C.M. Xie & Lu L. Zhang, *L. lygaea* C.M. Xie & Lu L. Zhang and *L. tibetica* C.M. Xie & Xin Y. Wang, but differed in its crowded apothecia. *L. orbicularis* formed a highly supported sister group to *L. lygaea* and *L. tibetica*, but differed in its round apothecia and white margin of apothecia. *L. lygaea* was sister to *L. tibetica*, and differed in its black margin of areolae and well-developed prothallus between areolae.

**Discussion**

Revised boundaries of *Immersaria*

Formerly, the boundaries for *Immersaria* species were: the types of apothecia, the substances detected and the shapes of pycnidia. However, these characters were not stable characters by which to distinguish this genus. There were repeated reassignments of the lecanorine species *Immersaria cupreaatt* between *Bellemerea* and *Immersaria*. Based on many specimens from China, it was also discovered that the ostiole or stellate shapes of pycnidia appeared in different stages of ontogeny. The main substances of the genus are conuentic acid and gyrophoric acid; conuentic acid only occurs in lecideine species whereas gyrophoric acid appears in lecanorine species, with the exception of one lecideine species *I. usberkica*. Furthermore, these characters, the types of apothecia and the shapes of pycnidia, could not be applied as proper delimitations to classify species within *Immersaria*, neither were they supported by phylogeny.

The five-loci based analysis was incompatible with previous circumscriptions of the genus *Immersaria*, the members of which are currently defined by their lecideine immersed apothecia, brown areolae with an epinecral layer and brown/green epihymenium without an epinecral layer, with additional phylogenetic support. A new genus *Lecaimmeria* was established to accommodate the excluded lecanorine species. The new taxonomic system revised the classification boundaries between *Immersaria* and *Lecaimmeria*, but it may still be difficult to distinguish them in cases when apothecia are absent. In this case, they could be distinguished by their substances or by establishing the phylogenetic tree.

Diagnostic traits within species of *Immersaria* and *Lecaimmeria*

Species of *Immersaria* could be identified by their different thallus colors (marked in Fig. 2). *Immersaria ferruginea* and *I. plumbeoolivacea* both have a conspicuously grayish brown thallus, whereas *I. athroocarpa*, *I. aurantia*, *I. shangriilaensis* and *I. venusta* have a reddish brown thallus. *I. athroocarpa* and *I. plumbeoolivacea* (marked in Fig. 2) are species that mostly have green epihymenium whereas the other species mostly have brown epihymenium. Almost all these species contain confluentic acid, which is often accompanied by 2'-O-methylmicrophylinic acid. Planaic acid, which was firstly reported from this the genus, was only apparent in species of *I. aurantia*, *I. shangriilaensis* and *I. venusta*. All the characters discussed above were supported by phylogeny.

Species of the new genus *Lecaimmeria* could be delimited by the colors of its areolae and its margin, the existence of apothecia's margin and usually by the lack of substances. The margin of areolae (marked in Fig. 3) was usually white, but rarely black or jade green. *Lecaimmeria lygaea* could be easily distinguished by the black margin of areolae. The jade green margin occurs in *L. tuberculosa*, which grows on Qilian jade. The areolar margin of *L. qinghaiensis* is white, but is occasionally pigmented with very slightly green color. The margin of apothecia is absent in species *L. tuberculosa* and *L. iranica* whereas the apothecia of the other species have white margins. The substances in species of *Lecaimmeria* are usually absent. Gyrophoric acid was only detected in *L. botryoides*, *L. iranica* and *L. mongolica* (marked in Fig. 3). In addition, an orange thallus appeared only in *L. mongolica* and *L. tibetica*, whereas the remaining species were brownish.

**Taxonomy**

*Immersaria* Rambold & Pietschm., Bibliotheca Lichenologica 34: 239 (1989)
Type: *Immersaria athroocarpa* (Ach.) Rambold & Pietschm., in Rambold, Bibliothca Lichenol. 34: 240 (1989).

**Description**

Thallus crustose, yellow brown, red brown, orange brown or brown, sometimes with rusty colored, continuous, areolae irregular or tend to rectangular, with wax glossy, margin pruinose, areolae sometimes aggregate with black prothallus and forming bigger areolae, prothallus distinct at the margin of thallus or absent. Upper cortex with orange pigmented, epinecral layer colorless, algal layer continuous, medulla filled with gray granules, lower cortex absent. Apothecia lecideine-type, immersed, sometimes aggregate, round or irregular; disc black, flat, less concave, margin reduced, sometimes slightly raised, often poorly developed in section, pruinose or not. Exciple almost absent, sometimes developed, brown. Hymenium colorless, paraphyses simple, rare branch, anastomosing or not; epihymenium brown, green or brown green, without epinecral layer; subhymenium colorless, sometimes pale brown; hypothecium pale brown to brown. Asci *Porpidia*-type, cylindrical, eight-spored; ascospores ellipsoid, halonate, non-amyloid.

Pycnidia present or not, immersed, liner or stellate, black, margin pruinose; conidia bacilliform.

**Chemistry**

Thallus K–, C–. Medulla I+, K–, C–. Confluentic acid, often accompanied with 2’-O-methylmicophyllinic acid, planaiaic acid or no substances detected by TLC. The compound planaiaic acid is newly found in this genus.

**Ecology and distribution**

Growing on bare rock, sandstone or granite, from elevations of 3800 to 4500 m in the alpine zone of west China and elevations of 1200 to 1900 m in the steppe of north China. Worldwide distribution.

**Remarks**

Species with lecanorine apothecia were previously included in *Immersaria* (Calatayud and Rambold 1998, Valadbeigi et al. 2011), but the five-loci phylogenetic analysis excluded these species from *Immersaria*. This exclusion entails a restricted concept of the genus. *Immersaria* is defined by its orange brown, yellow brown, sometimes rusty colored thallus, the amyloid medulla, the wax glossy areolae with a pruinose margin, the black immersed lecideine apothecia with a reduced margin, the brown epihymenium and the *Porpidia*-type asci with eight halonate and non-amyloid ascospores. The members of this genus occur in alpine or steppe habitats.

Species of *Sporastatia* A. Massal. have frequently been misidentified as members of *Immersaria* because of field observations of their glossy areolae and the immersed lecideine apothecia. However, they are characterized by multispora and their radiated, yellow brown thallus. Also, *Miriquidica* Hertel & Rambold often resembles *Immersaria* by its glossy areolae and the lecideine apothecia, but differs in its black brown thallus, its *Lecanora*-type asci with non-halonate ascospores and often containing miriquidic acid. The immersed apothecia of *Immersaria* may resemble *Aspicilia* A. Massal. and *Acarospora* A. Massal., but *Aspicilia* has a white or gray thallus, the *Aspicilia*-type asci with non-halonate ascospores; *Acarospora* has multispora and a convex thallus.

Although four known species, *Immersaria carbonoidea* (J.W. Thomson) Esnault & Cl. Roux, *I. fuliginosa* Fryday, *I. olivacea* Calat. & Rambold and *I. usbekica*, currently lack molecular data, we temporarily conserved them within the *Immersaria* due to their morphology, which corresponds to that of *Immersaria*. Morphological comparisons were based on high-resolution photographs of type materials and the original descriptions.

*Immersaria athroocarpa* (Ach.) Rambold & Pietschm., in Rambold, Bibliothca Lichenol. 34: 240 (1989). — Fig. 4a–e

**Type**

Sweden [no locality, no date, no collector], H9508237 (H-Ach – lectotype!). High-resolution photographs seen.

**Description**

Thallus areolate, yellow brown, orange brown, continuous, areolae 0.25–1.0 mm in diam., often convex, regular polygon, tends to be squamalose in the margin, epruinose; margin pruinose; prothallus black, not distinct, sometimes absent. Upper cortex 32.5 µm thick,
yellow brown granules pigmented; epinecral layer 7.5 µm thick; algal layer 82.5 µm thick, cells 8.0–10.0 × 7.5 µm in diam., round; lower cortex absent. Apothecia frequent, densely crowded, immersed, 0.3–1.3 mm in diam.; disc black, rare pruinose, flat, epruinose; margin reduced. Exciple sometimes developed, 25.0 µm wide, brown. Hymenium 107.5–112.5 µm thick, colorless; paraphyses 1.0–2.0 µm wide, branched, not anastomosing; ephymenium 25.0 µm thick, brown, rare green; subhymenium 90.0 µm thick, colorless; hypothecium pale brown to brown, sometimes absent. Asci Porpidia-type, cylindrical, eight-spored; ascospores 17.5–20.0 × 10.0 µm in diam., ellipsoid, halo. Pycnidia immersed, stellate, black, margin pruinose; conidia 7.5–10.0 × 1.0 µm in diam., bacilliform.

*Chemistry:* Thallus K−, C−. Medulla I+, K−, C−. : Confluentic acid. : Unknown substance.

**Ecology and distribution**

Growing on granite in arid and semi-arid steppe habitats at elevations of 1217–1915 m. Worldwide distribution. This species is known from Inner Mongolia and Mt. Changbai (Hertel and Zhao 1982) of China.

**Remarks**

The lectotype grows on siliceous rock and contains several intact apothecia. The materials from Inner Mongolia are identical with the lectotype based on comparisons with high-resolution photographs and the description given by Hertel (1977). It is therefore treated as *I. athroocarpa* at present. Some Inner Mongolian materials contain an unknown substance but form a well-supported clade with other materials. *I. athroocarpa* is characterised by the convex, yellow brown areolae and the big sizes of ascospores. In this genus, only this species has ascospores up to 20.0 µm long.

*Immersaria usberkica* is similar to *I. athroocarpa* in its brown thallus and dense apothecia, but differs in its flat areolae, the brown ephymenium and the presence of confluentic acid and gyrophoric acid. By comparing with high-resolution photographs and the original descriptions (Hertel 1977) of *I. usberkica*, we discovered that previous reports of this species from China (Zhang et al. 2015) were due to misidentification. It is known from Algeria, Iran, Spain and the USSR (Barbero et al. 1990).

**Specimens examined** (SDNU). CHINA, Inner Mongolia, Chifeng City, Balin Youqi, Hongshilazi, 1403.2 m elev., 44°13′N, 118°44′E, on rock, 2019, Ling Hu et al. SDNU20190035; Rongshen, Wangfengou, 1217.4 m elev., 44°16′N, 118°22′E, Ling Hu et al. SDNU20190140, SDNU20190143; Erlinba, 1915.2 m elev., 44°26′N, 118°41′E, Ling Hu et al. SDNU20190227.

**Immersaria aurantia** C.M. Xie & Li S. Wang, sp. nov. – *Fungal Names* FN839738; Fig. 4f–j

**Etymology**

The epithet "aurantia" refers to the orange thallus.

**Type**

CHINA, Tibet, Sajia Co., Mula village, 4752 m elev., 28°40′N, 88°45′E, on rock, 28 Jun. 2019, Xin Yu Wang et al. XY19-1814 (KUN–holotype).

**Description**

Thallus areolate, orange, dark orange, pale orange to pale red brown, continuous, areolae 0.75–1.25 mm in diam., flat, epruinose, irregular, margin thin pruinose; prothallus not seen. Upper cortex 25.0–45.0 µm thick, orange granules pigmented; epinecral layer 12.5–37.5–62.5 µm thick, uneven; algal layer 50.0–92.5 µm thick, cells 5.0–15.0 × 5.0–10.0 µm in diam., round; lower cortex absent. Apothecia frequent, scattered, immersed or isolated from areolae, 0.3–1.3 mm in diam.; disc black, flat or concave, sometimes pruinose; margin reduced. Exciple sometimes developed, 30.0 µm wide, brown. Hymenium 55.0–82.5 µm thick, colorless; paraphyses 2.0–2.5 µm wide, only branched and anastomosing at apex; ephymenium 20.0 µm thick, green or green brown; subhymenium colorless, not distinct or absent; hypothecium brown. Asci Porpidia-type, cylindrical, eight-spored; ascospores 8.0–15.0 × 5.0–7.5 µm in diam., ellipsoid, halonate. Pycnidia rare, immersed, oblate, black, margin white; conidia 7.5 × 1.0 µm in diam., bacilliform.
Chemistry: Thallus K–, C–. Medulla I+, K–, C–. Conuentic acid, often accompanied with 2’-O-methylmicrophylinic acid. Planiaic acid. none (rare).

Ecology and distribution

Growing on rock at elevations of 3931–4229 m in the alpine zone. This species is known from Qinghai, Sichuan Province and Tibet of China.

Remarks: Immersaria aurantia is characterised by its distinct orange, irregular areolae and the mostly green epihymenium. I. athroocarpa and I. venusta are similar to I. aurantia, but I. athroocarpa differs in the convex, regular polygon areolae and the more crowded apothecia; I. venusta differs in having the yellow brown, often rusty, cracked areolae and the flat apothecia. Besides, conuentic acid and planiaic acid do not appear simultaneously in I. aurantia, whereas I. venusta always contains both of these two compounds together. The orange thallus of I. aurantia may resemble I. fuliginosa, but the latter differs in the black margin of areolae and the distinct thalliconidia.

Specimens examined (KUN). CHINA, Qinghai Province, Banma Co., 3933 m elev., 32°40′N, 100°48′E, on rock, 2020, Li-Song Wang et al. 20-66886, 3932 m elev., Li-Song Wang et al. 20-66897; Jiuzhi Co., Baiyu village, 4285 m elev., 33°14′N, 100°58′E, Li-Song Wang et al. 20-67809. Sichuan Province: Rangtang Co., Mt. Haizi, 4223 m elev., 32°20′N, 101°25′E, on rock, 2020, Li-Song Wang et al. 20-66701, 4229 m elev., Li-Song Wang et al. 20-66693, 4217 m elev., Li-Song Wang et al. 20-66680, 4221 m elev., Li-Song Wang et al. 20-66692. Tibet, Changdu City, Mangkang Co., Luoni village, 4145 m elev., 29°56′N, 98°33′E, on rock, 2020, Li-Song Wang et al. 20-69091, 4138 m elev., Li-Song Wang et al. 20-69091, 4138 m elev., Li-Song Wang et al. 20-69091, 4138 m elev., Li-Song Wang et al. 20-69094, Gatuo town, 29°39′N, 98°35′E, 3831 m elev., Li-Song Wang et al. 20-68114, 3850 m elev., Li-Song Wang et al. 20-69122; Gongga Co., Jiangtang town, 29°12′N, 90°38′E, 2019.7.23, 4560 m elev., Xin-Yu Wang et al. XY19-1287, 4556 m elev., XY19-1290; Sajia Co., Mula village, 28°40′N, 88°45′E, 2019.7.28, 4752 m elev., Xin-Yu Wang et al. XY19-1814; Angren Co., Kerangla, 29°19′N, 87°01′E, 4530 m elev., Li-Song Wang et al. 19-63635.

Immersaria ferruginea C.M. Xie & Li S. Wang, sp. nov. — Fungal Names FN839739; Fig. 5a–c

Etymology

The epithet “ferruginea” refers to the rusty brown color of the thallus.

Type

CHINA, Tibet, Changdu City, Mangkang Co., Quzika village, 4093 m elev., 29°15′N, 98°40′E, on rock, 25 Sept. 2020, Li-Song Wang et al. 20-69144 (KUN—holotype).

Description

Thallus areolate, grayish brown, rusty colored, continuous, areolae 0.5–1.25 mm in diam., flat, less convex, rectangle to polygon, epruinose; margin pruinose; prothallus black, not distinct. Upper cortex 50.0–67.5 µm thick, brown granules pigmented; epinecral layer 17.5–40.0 µm thick; algal layer 75.0–77.5 µm thick, cells 4.0–7.5–13.0 × 4.0–7.5–13.0 µm in diam., round; lower cortex absent. Apothecia frequent, densely crowded, immersed, 0.75–1.25 mm in diam.; disc black, flat, pruinose; margin pruinose, slightly raised. Exciple sometimes developed, 25.0–27.5 µm wide, brown. Hymenium 57.5–100.0 µm thick, colorless; paraphyses 1.0–2.5 µm wide, not branched, slightly anastomosing; epihymenium 15.0–32.5 µm thick, brown; subhymenium 25.0–62.5 µm thick, colorless to pale brown, rusty or dark pink; hypothecium pale brown. Asci Porpidia-type, cylindrical; ascospores not seen, or rarely seen. Pycnidia not seen.

Chemistry

Thallus K–, C–. Medulla I+, K–, C–. Confluent acid, often accompanied with 2’-O-methylmicrophylinic acid.

Ecology and distribution

Growing on quartz sandstone or granite at elevations of 3848–4227 m in the alpine zone. This species is known from Sichuan Province and Tibet of China.
Remarks: *Immersaria ferruginea* is characterized by its brown and rusty thallus, its densely crowded apothecia and its brown ephymenium. *I. ferruginea* and *I. plumbeoolivacea* were previously regarded as a single species, but it was later found that *I. ferruginea* grows on red sandstone whereas *I. plumbeoolivacea* grows on granite, and the thallus of *I. ferruginea* is rusty. The morphology of *I. ferruginea* resembles *I. carbonoidea*, but the latter differs in its dark black brown thallus, black brown hypothecium and content of nostritic acid.

**Specimens examined** (KUN). CHINA, Sichuan Province, Rangtang Co., Mt. Haizi, 4227 m elev., 32°20′N, 101°25′E, on rock, 2020, Li-Song Wang et al. 20-66967, 4221 m elev., Li-Song Wang et al. 20-67670. Tibet, Changdu City, Mangkang Co., Quzika village, 4093 m elev., 29°15′N, 98°40′E, Li-Song Wang et al. 20-69144, 4101, Li-Song Wang et al. 20-69146, 4122 m elev., Li-Song Wang et al. 20-69148; Gatuo town, 3848 m elev., 29°39′N, 98°35′E, Li-Song Wang et al. 20-69105.

*Immersaria plumbeoolivacea* C.M. Xie & Xin Y. Wang, **sp. nov.** — **Fungal Names** FN839740; Fig. 5d–f

**Etymology**

The epithet "plumbeoolivacea" refers to the lead brown thallus.

**Type**

CHINA, Qinghai Province, Banma Co., 3948 m elev., 32°40′N, 100°48′E, on rock, 9 Sept. 2020, Li-Song Wang et al. 20-66914 (KUN–holotype).

**Description**

Thallus areolate, grayish brown, continuous, areolae 0.5–1.3 mm in diam., undulate, flat, convex or concave, irregular, epruinose; margin pruinose; prothallus black, not distinct. Upper cortex 40.0 µm thick, brown granules pigmented; epinecral layer 30.0 µm thick; algal layer 62.5 µm thick, cells 10.0–15.0 × 5.0–7.5 µm in diam., round; lower cortex absent. Apothecia frequent, crowded, immersed, irregular, 0.75–1.75 mm in diam.; disc black, sometimes pruinose, flat; margin thin, pruinose, slightly raised. Exciple sometimes developed, 30.0–37.5 µm wide, brown. Hymenium 67.5–100.0 µm thick, colorless; paraphyses 2.0–2.5 µm wide, not branched, slightly anastomosing; ephymenium 37.5 µm thick, green or brown green; subhymenium 50.0–67.5 µm thick, colorless to pale brown, rusty or dark pink; hypothecium pale brown. Asci *Porpidia*-type, cylindrical; ascospores not seen. Pycnidia rare, immersed, oblate, black, margin pruinose; conidia 7.5 × 1.0 µm in diam., bacilliform.

**Chemistry**

Thallus K–, C–. Medulla I+, K–, C–. Confluentic acid, often accompanied with 2′-O-methylmicrophylinic acid.

**Ecology and distribution**

Growing on granite at elevations of 3932–3971 m in the alpine zone. This species is known from Qinghai Province of China.

Remarks: *Immersaria plumbeoolivacea* is characterized by its gray brown thallus, the areolae tend to be squamulose, with pruinose apothecia and green ephymenium. The phylogenetic results showed that *I. ferruginea* was a sister species to *I. plumbeoolivacea*, which is similar in its brown thallus and crowded apothecia, but differs in its thallus with rusty color and a brown ephymenium. The morphology of *I. plumbeoolivacea* resembles *I. carbonoidea*, but the latter has a black brown, thallus and contains traces of nostritic acid.

**Specimens examined** (KUN). CHINA, Qinghai Province, Banma Co., 3932 m elev., 32°40′N, 100°48′E, on rock, 2020, Li-Song Wang et al. 20-66889, 3948 m elev., Li-Song Wang et al. 20-66914, 3945 m elev., Li-Song Wang et al. 20-66915; Makehe, 3971 m elev., 32°42′N, 100°42′E, Li-Song Wang et al. 20-67896.

*Immersaria shangrilaensis* C.M. Xie & Lu L. Zhang, **sp. nov.** — **Fungal Names** FN839741; Fig. 6a–d

**Etymology**: The epithet "shangrilaensis" refers to the location at which the holotype was collected: "Shangri-La", a county of Yunnan Province in China.
Type

CHINA, Yunnan Province, Shangri-La County., Mt. Hong Shan, 4363 m elev., 28°7′N, 99°54′E, on rock, 18 Aug. 2018, Li-Song Wang et al. 18-60447 (KUN–holotype).

Description

Thallus areolate, yellow brown, orange brown, often appears as grayish brown. It is generally heavily pruinose, continuous, 5.75–10.0 cm across, areolae aggregated by 4–14 small areolae (often surrounded by black prothallus), small areolae up to 0.13 mm in diam., concave, or flat, irregular, pruinose; margin pruinose; prothallus black, distinct. Upper cortex 32.5–50.0 µm thick, yellow brown granules pigmented; epinecral layer 15.0–20.0 µm thick; algal layer 47.5–65.0 µm thick, cells 7.5–8.0 × 5.0 µm in diam., round; lower cortex absent. Apothecia frequent, crowded, immersed or isolated from areolae, 0.38–0.75 mm in diam.; disc black, concave to flat, aggregated, crack once mature, thin pruinose; margin reduced, slightly raised. Exciple almost absent. Hymenium 100.0–137.5 µm thick, colorless; paraphyses 2.5 µm wide, branched, anastomosing or not; epihymenium 15.0 µm thick, brown; subhymenium 55.0 µm thick, colorless; hypothecium colorless to pale brown, sometimes absent. Asci *Porpidia*-type, cylindrical, eight-spored; ascospores 7.0–9.0 × 3.0–4.0 µm, ellipsoid, halonate (sometimes not distinct). Pycnidia immersed, oblate, black, margin heavily pruinose; conidia 7.5 × 1.0 µm, bacilliform.

Chemistry

Thallus K–, C–. Medulla I+, K–, C–. Conuentic acid, planaic acid and/or 2′-O-methylmicophyllinic acid.

Ecology and distribution

Growing on granite at elevations of 4361–4503 m in the alpine zone. This species is known from Yunnan Province of China.

Remarks

The materials of *Immersaria athroocarpa* from Shangri-La county of Yunnan Province are identical with the paratype Hertel (1977) reported from the same locality, but differ from the Lectotype in its aggregate areolae, the aggregate apothecia and the smaller size of ascospores (7.0–9.0 × 3.0–4.0 µm). Based on the phenotypic and phylogenetic results, the materials from Shangri-La were treated as a new species, *I. shangrilaensis*. It is characterized by its large thallus, up to 10.0 cm in diam., the aggregate areolae and apothecia and the small size of ascospores.

Specimens examined

CHINA, Yunnan Province, Shangri-La Country, 4350–4500 m elev., on rock, 1915, Handel-Mazzetti no. 6945 = WU-Lichenes0037752 (WU); Mt. Hong Shan, 4363 m elev., 28°7′N, 99°54′E, on rock, 2018, Li-Song Wang et al. 18-60430 (KUN), Li-Song Wang et al. 18-60447 (KUN) 4503.1 m elev., Chun-Xiao Wang et al. SDNU20181696 (SDNU), 4361.9 m elev., Chun-Xiao Wang et al. SDNU20181675 (SDNU); Luquan Co., Mt. Jiaozixueshan, 3800 m elev., 2008, Hai-Ying Wang SDNU20082253 (SDNU); Lijiang City, Mt. Laojun, 26°37′N, 99°43′E, 2018, 3981m, Li-Song Wang et al. 18-60555, 18-60602 (KUN).

*Immersaria venusta* C.M. Xie & Xin Y. Wang, sp. nov. — *Fungal Names* FN839742; Fig. 6e–i

Etymology

The epithet “venusta” refers to the beautiful appearance of the thallus.

Type

CHINA, Qinghai Province, Maqing Co., Xueshan village, 4187 m elev., 34°37′N, 99°42′E, on rock, 11 Sept. 2020, Li-Song Wang et al. 20-67969 (KUN–holotype).

Description
Thallus areolate, brown, orange brown, more or less rusty, continuous, areolae 0.5–1.25 mm in diam., flat or slightly convex, irregular, tend to rectangular, often cracked, sometimes pruinose; margin pruinose; prothallus not seen. Upper cortex 37.5 µm thick, yellow brown granules pigmented; epinecral layer 12.5 µm thick; algal layer 127.5 µm thick, cells 5.0–10.0 x 5.0–7.5 µm in diam., round; lower cortex absent. Apothecia frequent, crowded, immersed or isolated from areolae, 0.6–1.0 mm in diam.; disc black, flat, epruinose; margin reduced, sometimes developed. Exciple sometimes developed, 35.0 µm wide, colorless; paraphyses 2.0 µm wide, anastomosing; epihymenium 27.5–30.0 µm thick, brown; subhymenium 62.5 µm thick, colorless; hypothecium brown. Asci Porpidia-type, cylindrical, eight-spored; ascospores 10.0–12.5 x 5.0–7.5 µm, ellipsoid, halonate. Pycnidia immersed, linear, black, margin pruinose; conidia not seen.

**Chemistry:** Thallus K–, C–. Medulla I+, K–, C–. : Conuentic acid, often accompanied with 2’-O-methylmicrophylinic acid. : Planaic acid. : none (rare).

**Ecology and distribution**

Growing on quartz sandstone or granite at elevations of 3930–4256 m in the alpine zone. This species is known from Qinghai Province of China.

**Remarks:** Immersaria venusta is characterised by its yellow brown, cracked areolae, its flat apothecia and brown epihymenium. It resembles *I. shangriiaensis* by its cracked areolae, but its areolae have the tendency to split into several patches but not aggregate like those of *I. shangriiaensis*. *I. athroocarpa* is similar to *I. venusta* in the brown appearance of its thallus and in forming a sister group in the phylogenetic tree, but it differs in its yellow brown thallus, convex areolae, densely crowded apothecia and bigger ascospores (17.5–20.0 x 10.0 µm). This species is also similar to *I. aurantia* (see notes for *I. aurantia*). The brown thallus of *I. venusta* possibly resembles *I. olivacea*, but the latter differs in its simple or one-septate ascospores, pyriform conidia and dark bluish green epihymenium. Three specimens of *I. venusta* have brown thallus, which resembles *I. plumbeoolivacea*, but they have neatly arranged, thick areolae.

**Specimens examined** (KUN). CHINA, Qinghai Province, Maqing Co., Xueshan village, 4187 m elev., 34°37′N, 99°42′E, on rock, 2020, Li-Song Wang et al. 20-67969, 20-67965; Banma Co., Yaertang village, 3930 m elev., 32°42′N, 100°42′E, Li-Song Wang et al. 20-66940. Sichuan Province, Shiqu Co., Xinrong village, 4043 m elev., 32°59′N, 98°19′E, on rock, 2020, Li-Song Wang et al. 20-68802; Rangtang Co., Mt. Haizi, 4246 m elev., 32°21′N, 101°24′E, Li-Song Wang et al. 20-66721, 20-66725.

Selected additional comparative material was examined.

**Bellemerea alpina** (Sommerf.) Clauzade & Cl. Roux RUSSIA, Lps. Petsamo, Pummangin vuonon N-puoli, 1938, Räsänen, V., H9503269 (H–type!); Lps. Petsamo, inter Vaitolahti et Kervanto, 1938, Räsänen, V., H9503270 (H–type!).

**Bellemerea cinereorufescens** (Ach.) Clauzade & Cl. Roux FINLAND, Ob. Simo. Anteroinen. Rantakivellä, 1920, Räsänen, V., H9503267 (H–type!); Le. Enontekiö, Kirkonkylä, 1925, Kari, L.E., H9503268 (H–type!).

**Immersaria cupreoatra** (Nyl.) Calatayud & Rambold RUSSIA, KL. Kurkijoki, Kuuppala, Himohirsi, 1934, Räsänen, V., H9503417, H9510194 (H–type!).

High-resolution photographs seen.

**Immersaria carbonoidea** (J.W. Thomson) Esnault & Cl. Roux USA, Alaska, along the Pitmegea River, 15 miles upstream from Cape Sabine, 1958, Thomson, J.W., M0082171 (M–Isotype!), G00126754 (G–isotype!).

**Immersaria olivacea** Calat. & Rambold SPAIN, Espana, Castelló: Benicàssim, Parreta Alta, 390 m elev., 1993, Calatayud, V., M0101779 (M–isotype!).

**Immersaria usbekica** (Hertel) M. Barbero, Nav.-Ros. & Cl. ALGERIA, Algerie-Atlas Tellieu, Larba, Piste de Bougara á Tablat au S-E de l’arboretum de Meindja, 1985, Esnault, J., M0101787 (M–paratype!).

Lecaimmeria C.M. Xie, Lu L. Zhang & Li S. Wang, **gen. nov.** — *Fungal Names* FN839743;
Etymology

The epithet "Lecaimmeria" refers to the immersed lecanorine apothecia of known species.

**Type:** Lecaimmeria orbicularis C.M. Xie & Lu L. Zhang, sp. nov.

Description

Thallus crustose, red brown, orange brown or dark brown, continuous or not, areolae irregular or tend to rectangular, with wax glossy, margin white or black, prothallus distinct at the margin of thallus or absent, sometimes developed between areolae. Upper cortex with orange granules pigmented, epinecral layer colorless, algal layer continuous, medulla filled with gray granules, lower cortex absent. Apothecia lecanorine-type, immersed, round or irregular; disc red brown, dark red brown or dark orange brown, flat or concave, margin present or absent, black or white, rare green, pruinose or not. Exciple reduced, tissue at the lateral sides of the hymenium corresponding to the upper cortex and the algal layer of the vegetative areolae, and to hypothecial hyphal cells when apothecia reach the margin of the areole. Hymenium colorless, paraphyses simple, rare branch, anastomosing or not, epihymenium orange, orange brown, rare brown, with epinecral layer. Asci Porpidia-type, cylindrical, eight-spored; ascospores ellipsoid, halonate, non-amyloid. Pycnidia present or absent, immersed, rare convex, liner or stellate, rare tuberculiform, conidia bacilliform.

Chemistry

Thallus K–, C–. Medulla I+, K–, C+/–. Gyrophoric acid, 4-O-demethylplanaic acid or no substances detected by TLC.

Ecology and distribution

Growing on rock, sandstone, granite or Qilian jade (rare), from elevations of 3100 to 4800 m in the alpine zone of west China and from 1200 to 1900 m in the steppe of north China. This genus is known from China, Europe, Iran, Macedonia, Mongolia, Romania and Russia.

Remarks

The five-loci phylogenetic analysis showed that these lecanorine apothecia species should be excluded from Immersaria and formed a novel lineage, thus they are here treated as a new genus Lecaimmeria. Lecaimmeria is distinguished from related genera by its glossy wax, orange or red brown areolae with margins, the amyloid medulla, the red brown immersed lecanorine apothecia with margins, the orange epihymenium with an epinecral layer and the Porpidia-type asci with eight halonate and non-amyloid ascospores. The genus is distributed in alpine areas, high altitude desert-steppe areas or high latitude steppe. Almost all the species of Lecaimmeria grow on granite or sandstone, with the exception of one species, L. tuberculosa, which grows on jade. Interestingly, the margin of pycnidia and areolae of L. tuberculosa appear with heavily jade green pruinose.

The immersed apothecia and brown thallus of Lecaimmeria often resemble those of Immersaria, but Lecaimmeria differs in its red brown lecanorine apothecia, often with a white margin, their orange epihymenium with an epinecral layer and content of gyrophoric acid. This genus is often confused with Bellemerea in its lecanorine apothecia and the Porpidia-type asci with halonate and non-amyloid ascospores, but the latter genus differs in its white thallus and amyloid ascospores.

Three species previously in Immersaria, I. cupreoatra, I. iranica and I. mehadiana, have lecanorine apothecia, but two of these, I. cupreoatra and I. mehadiana, currently lack molecular sequences. It is suggested that these three species should be transferred to Lecaimmeria, based on the following factors. Their morphology is consistent with Lecaimmeria according to molecular results and comparisons with type specimens, high-resolution photographs of the type materials and the original descriptions. One unknown "Immersaria" species from Macedonia is sister to L. iranica in the phylogenetic tree (Fig. 3), but differs in its black margin of areolae, absence of gyrophoric acid and comparison with high-resolution photograph and previous records (Malíček and Mayrhofer 2017). This unknown species with lecanorine apothecia is possibly a member of Lecaimmeria, but descriptions are lacking and the specimens were not seen. Thus, this species was temporarily retained in Immersaria.

Lecaimmeria botryoides C.M. Xie & Li S. Wang, sp. nov. — *Fungal Names* FN839744; Fig. 7a–e
Etymology
The epithet "botryoides" refers to the crowded apothecia while immature.

Type
CHINA, Sichuan Province, Aba City, Rangtang County, Haizi Mt., 4225 m elev., 32°21′N, 101°24′E, on rock, 6 Sept. 2020, Li-Song Wang et al. 20-66730 (KUN–holotype).

Description
Thallus areolate, red brown, discontinuous, areolae 0.25–1.0 mm in diam., flat, slightly concave or convex, pruinose, polygon, tend to be rectangular, margins with heavy pruinose. Prothallus black, distinct in the margin of thallus. Upper cortex 20.0–25.0 µm thick, brown; epinecral layer 22.5–47.5 µm thick; algal layer 37.5 µm thick, cells 7.5–10.0 × 7.5–10.0 µm in diam., round; lower cortex absent. Apothecia frequent, irregular, densely crowded while immature (3–6/areolae), aggregate once mature, immersed, 0.25–1.25 mm in diam.; disc red brown, flat, or concave, epruinose; margin pruinose, slightly raised. Hymenium 67.5–100.0 (–155.0) µm thick, colorless; paraphyses 2.5 µm wide, simple, only branched at the top, not anastomosing; epihymenium 25.0–30.0 µm thick, orange; epinecral layer 2.5–7.5 µm thick; subhymenium 17.5–37.5 µm thick, colorless; hypothecium colorless. Asci Porpidia-type, cylindrical, eight-spored; ascospores 7.5–8.0 × 4.0–6.0 µm in diam., ellipsoid, halonate. Pycnidia not seen; conidia not seen.

Chemistry: Thallus K–, C–. Medulla I+, K–, C+/–. ☒ Gyrophoric acid. ☐: none.

Ecology and distribution
Growing on rock at elevations of 3178–4300 m in the alpine zone. This species is known from Qinghai and Sichuan Province of China.

Remarks: Lecaimmeria botryoides is characterized by its discontinuous thallus, densely crowded apothecia while immature, and the orange epihymenium. L. orbicularis is similar to L. botryoides in its red brown thallus, but differs in its round, flat apothecia and continuous thallus. The red brown thallus of L. botryoides resembles L. cupreoatra, but the latter differs in its black margin of apothecia and its distinct black prothallus between areolae.

Specimens examined (KUN). CHINA, Qinghai Province, Banma Co., 3958 m elev., 32°40′N, 100°48′E, on rock, 2020, Li-Song Wang et al. 20-66900, 3932 m elev., Li-Song Wang et al. 20-66898, 3935 m elev., Li-Song Wang et al. 20-66891, 3178 m elev., Li-Song Wang et al. 20-66765. Sichuan Province, Rangtang Co., Mt. Haizi, 4256 m elev., 32°21′N, 101°24′E, on rock, 2020, Li-Song Wang et al. 20-66721, 4300 m elev., Li-Song Wang et al. 20-67706, 4276 m elev., Li-Song Wang et al. 20-66706, 4255 m elev., Li-Song Wang et al. 20-66707, 4274 m elev., Li-Song Wang et al. 20-66713, 4274 m elev., Li-Song Wang et al. 20-66711, 20-66705, 4225 m elev., Li-Song Wang et al. 20-66730, 4220 m elev., 32°20′N, 101°25′E, Li-Song Wang et al. 20-66683.

Lecaimmeria cupreoatra (Nyl.) C.M. Xie, comb. nov. — Fungal Names FN839745;

Type
RUSSIA, Ad Onegam, Medväschiigora, 1863, Simming, Th., H-NYL 25061 = H9508237 (H–lectotype!).

Description
Nylander (1866).

Remarks
The lectotype grows on siliceous rock and contains several intact apothecia. "Immersaria" cupreoatra has lecanorine apothecia and is related to I. lygeae in its phylogeny, therefore it was transferred to Lecaimmeria. This species has not been recorded in China (see notes for L. mongolica). The species is known from Europe, Macedonia, Mongolia and Russia (Calatayud and Rambold 1998).

Lecaimmeria iranica (Valadb., Sipman & Rambold) C.M. Xie, comb. nov. — Fungal Names FN839746;
**Type**

IRAN, Mazandaran, Haraz road, 20 km to Aamol, 36°17′N, 52°21′E, on calcareous rock, 1475 m, 7 Apr. 2006, T. Valadbeigi 9008 (TARI–holotype; B, hb. Valadbeigi–isotype). Not seen.

**Description**

Valadbeigi et al. (2011).

**Remarks**

"Immersaria" iranica has lecanorine apothecia, a distinct epinecral layer and halonate ascospores (Valadbeigi et al. 2011). The materials from China are in accordance with the materials of Iran based on comparisons with the original descriptions and the photographs given by Valadbeigi et al. (2011). The characters of this species are consistent with the new genus and the phylogenetic results showed that it was clustered with species of Lecaimmeria. Therefore, it was transferred to Lecaimmeria. This species is currently known from Iran and China.

*Specimens examined* (SDNU). CHINA, Xinjiang, Urumqi, Mt. Tianshan-glacier No.1, alt. 3800 m, on rock, 2011, Z.L. Huang SDNU0126106, SDNU20129049.

Lecaimmeria lygaea C.M. Xie & Lu L. Zhang, sp. nov. — Fungal Names FN839747; Fig. 7f–j

**Etymology**

The epithet "lygaea" refers to the dark appearance of the thallus.

**Type**

CHINA, Tibet, Changdu City, Mangkang County, Luoni Village, 4127 m elev., 29°56′N, 98°33′E, on rock, 24 Sept. 2020, Li-Song Wang et al. 20-69072 (KUN–holotype).

**Description**

Thallus areolate, dark red brown, dark brown, continuous, areolae 0.5–1.0 mm, flat, epruinose, irregular pentagonal, sometimes rectangular, fissures between areolae often filled with black prothallus; margin black, thin pruinose; prothallus black, developed between areolae, also distinct in the margin. Upper cortex 20.0 µm thick, orange brown granules pigmented; epinecral layer 15.0 µm thick; algal layer 50.0 µm thick, cells 7.5–12.5 × 7.5–12.5 µm in diam., round; lower cortex absent. Apothecia frequent, round, crowded, immersed, 0.25–0.75 mm in diam.; disc red brown, flat, or concave, epruinose; margin black, moderate thick, pruinose, raised. Hymenium 75.0–92.5 µm thick, colorless; paraphyses 2.0 µm wide, simple, unbranched, not anastomosing; epihymenium 25.0–37.5 µm thick, orange brown; epinecral layer 7.5 µm thick; subhymenium 20.0–25.0 µm thick, colorless; hypothecium absent. Asci Porpidia-type, cylindrical, eight-spored; ascospores 12.5–20.0 × 5.0–7.5 µm in diam., ellipsoid, halonate. Pycnidia immersed, stellate, black, margin pruinose; conidia 5.0 × 1.0 µm in diam., bacilliform.

**Chemistry**

Thallus K–, C–. Medulla I+, K–, C–. Unknown fatty acid.

**Ecology and distribution**

Growing on sandstone at elevations of 4095–4131 m in the alpine zone. This species is known from Tibet of China.

Remarks: Lecaimmeria lygaea is characterized by its dark brown thallus, black margin of its areolae, black prothallus which filled the fissures between areolae, dark orange apothecia and its orange brown epihymenium. *L. cupreoatra* and *L. mehadiana* are similar to *L. lygaea*, but *L. cupreoatra* has a discontinuous thallus, with each areola surrounded by black prothallus, dark red brown to black brown apothecia without margin. *L. mehadiana* has a white margin of areolae, black brown apothecia, brown
epihymenium and contains 4-O-demethylplanaic acid. The phylogenetic results show that *L. tibetica* was a sister species to *L. lygaea*. They are similar in chemistry, but differ in its orange brown thallus and dark orange brown apothecia.

*Specimens examined* (KUN). CHINA, Tibet, Changdu City, Mangkang Co., Luoni village, 4099 m elev., 29°56′N, 98°33′E, on rock, 2020, Li-Song Wang et al. 20-69054, 4131 m elev., Li-Song Wang et al. 20-69070, 4127 m elev., Li-Song Wang et al. 20-69072, 4095 m elev., Li-Song Wang et al. 20-69053.

Lecaimmeria mehadiana (Calatayud & Rambold) C.M. Xie, *comb. nov.* – *Fungal Names* FN839748;

**Type**

ROMANIA, Caras-Severin Comitat, Mehadia, Strajot Mtn., on rock, 1994, Rambold, G.W., M0101781 (M–holotype!), M0101780, M0101782, M0101783 (M–isotype!). High-resolution photographs seen.

**Description**

Calatayud and Rambold (1998).

**Remarks**

"*Immersaria* mehadiana" has lecanorine apothecia and is related to *L. lygaea* and *L. cupreoatra* in the appearance of dark brown thallus, therefore it has been transferred to *Lecaimmeria*. This species is characterized by its greyish prothallus, dark brown apothecia and the brown epihymenium. It is only known from Romania (Calatayud and Rambold 1998).

Lecaimmeria mongolica C.M. Xie & Lu L. Zhang, *sp. nov.* – *Fungal Names* FN839749; Fig. 8a–e

**Etymology**

The epithet "mongolica" refers to the collection of the holotype within Inner Mongolia, an autonomous region of China.

**Type**: CHINA, Inner Mongolia: Chifeng City, Balinyouqi, Han Mountain, 1445m elev., 44°11′N, 118°44′E, on rock, 22 Jul. 2019, Z.T. Zhao et al. SDNU20190354 (SDNU–holotype).

**Description**

Thallus areolate, orange, continuous, areolae 0.4–0.8 mm in diam., epruinose, neatly arranged, irregular, tend to be rectangular, margin pruinose; prothallus black, not distinct. Upper cortex 20.0 μm thick, brown granules pigmented; epinecral layer 5.0–7.5 μm thick; algal layer 87.5 μm thick, cells 7.5–12.5 × 7.5–12.5 μm in diam., round; lower cortex absent. Apothecia frequent, crowded, immersed or isolated from areolae, 0.25–0.75 mm in diam.; disc red brown, flat, slightly convex, epruinose; margin pruinose. Hymenium 62.5–82.5 μm thick, colorless; paraphyses 2.5 μm wide, unbranched, not anastomosing; epihymenium 42.5 μm thick, orange; epinecral layer 5.0–10.0 μm thick; subhymenium 30.0–37.5 μm thick, colorless; hypothecium absent. Asci *Porpidia*-type, cylindrical, eight-spored; ascospores 10.0–17.5 × 6.0–7.5 μm in diam., ellipsoid, halonate. Pycnidia immersed, oblate, rare ellipsoid, black, margin pruinose; conidia 5.0 × 1.0 μm in diam., bacilliform.

**Chemistry**

Thallus K–, C–. Medulla I+, K–, C–. Gyrophoric acid.

**Ecology and distribution**

Growing on granite at elevations of 1400–2000 m in steppe or mountains. This species is known from Inner Mongolia of China.

**Remarks**

This species was once reported as "*Immersaria* cupreoatra" from China (Zhang et al. 2015) but after comparing with the type materials this was found to be a misclassification. Also, the phylogenetic results showed that these materials formed a well-
supported lineage belonging to *Lecaimmeria*. Therefore, here it has been treated as a new species, *Lecaimmeria mongolica*. It is characterized by its orange brown thallus, red brown apothecia with a distinct white margin and content of gyrophoric acid. *L. cupreoatra* resembles *L. mongolica* by containing gyrophoric acid, but it differs in its dark black brown thallus and the black margin of its apothecia. *L. tibetica* is similar to *L. mongolica* in its orange thallus, but differs in its smaller, dark orange apothecia and that no substance can be detected by TLC.

*Specimens examined* (SDNU). CHINA, Inner Mongolia: Chifeng City, Balin Youqi, Mt. Qingyangcheng, 1445 m elev., 43°35′N, 117°30′E, on rock, 2019, Zun-Tian Zhao et al. SDNU20190350; Han Shan, 1563 m elev., 44°11′N, 118°44′E, on rock, Zun-Tian Zhao et al. SDNU20190354; A’ershan City, Mt. Jiguan, 1500 m elev., on rock, 2011, Yu-Liang Cheng SDNU20124912, 1400 m elev., Dai-Feng Jiang SDNU20124859; Ke Qi, Huanggangliang, 2000 m elev., on rock, Pan-Meng Wang SDNU20117613, Xing-Ran Kou SDNU20117399.

*Lecaimmeria orbicularis* C.M. Xie & Lu L. Zhang, sp. nov. — *Fungal Names* FN839750; Fig. 9a–e

**Etymology**
The epithet "orbicularis" refers to the round shape of the apothecia.

**Type**
CHINA, Sichuan Province, Rangtang Co., Gangmuda village, 3800 m elev., 32°18′N, 101°3′E, on rock, 7 Sept. 2020, Li-Song Wang et al. 20-66753 (KUN–holotype).

**Description**
Thallus areolate, red brown, rare orange brown, continuous, areolae 0.25–1.0 mm, flat, occasionally wrinkled, tend to rectangular, fissures between areolae often filled with black prothallus, margin pruinose; prothallus black, developed between areolae, also distinct in the margin. Upper cortex 42.5–57.5 µm thick, brown granules pigmented; epinecral layer 5.0–20.0 µm thick; algal layer 70.0–112.5 µm thick, cells 10.0–15.0 × 7.5–10.0 µm in diam., round; lower cortex absent. Apothecia frequent, less crowded, immersed or isolated from areolae, 0.5–1.25 mm in diam.; disc red brown, flat, round, epruinose; margin white, slightly raised. Hymenium 75.0–112.5 µm thick, colorless; paraphyses 2.5 µm wide, simple, unbranched, not anastomosing; epihymenium 17.5–30.0 µm thick, orange; epinecral layer 5.0–15.0 µm thick; subhymenium 30.0–62.5 µm thick, colorless; hypothecium absent. Asci *Porpidia*-type, cylindrical, eight-spored; ascospores 12.5–15.0 × 5.0–6.0 µm in diam., ellipsoid, halonate. Pycnidia not seen.

**Chemistry**
Thallus K–, C–. Medulla I+, K–, C–. None.

**Ecology and distribution**
Growing on granite or sandstone at elevations of 3730–4200 m in the alpine zone. This species is known from Qinghai and Sichuan Provinces of China.

**Remarks:** *Lecaimmeria orbicularis* is characterized by its orange brown thallus, neatly arranged areolae, and round, flat apothecia. *L. botryoides* is similar to *L. orbicularis* (see notes for *L. botryoides*). *L. mongolica* might be confused with *L. orbicularis* due to its big apothecia with a white margin, but differs in its red brown thallus and distribution in steppes. The red brown thallus of *L. cupreoatra* resembles that of *L. orbicularis*, but differs in the black margin of its apothecia and its distinct black prothallus between areolae.

*Specimens examined* (KUN). CHINA, Qinghai Province, Jiuzhi Co., Nianbaoyuze, 4200 m elev., 33°14′N, 100°58′E, on rock, 2020, Li-Song Wang et al. 20-66811, 20-66829, 20-66801, 20-66826A, 20-66821, 20-66805, 20-66833, 20-66817, 20-66841; Banma Co., Nianbaoyuze, 3930 m elev., 32°40′N, 100°48′E, Li-Song Wang et al. 20-66909, 20-66908, 20-66896, 20-66886B, 20-66899, 20-66935, 20-66943; Zhiqingsongduo town, 3712 m elev., 33°24′N, 101°25′E, Li-Song Wang et al. 20-66965; Suohurima village, 4029 m elev., 33°23′N, 100°57′E, Li-Song Wang et al. 20-66979. Sichuan Province, Rangtang Co., Gangmuda village, 3800 m elev., 32°18′N,
Lecaimmeria qinghaiensis C.M. Xie & Li S. Wang, sp. nov. — Fungal Names FN839751; Fig. 9f–i

Etymology

The epithet "qinghaiensis" refers to the location in which the holotype was collected, in "Qinghai", a province of China.

Type

CHINA, Qinghai Province, Yushu City, Zaduo County, Sahuteng town, 4634 m elev., 32°55′N, 95°46′E, on rock, 20 Sept. 2020, Li-Song Wang et al. 20-68698 (KUN—holotype).

Description

Thallus areolate, yellow brown, rusty, continuous, areolae 0.5–1.5 mm in diam., flat, epruinose; margin pruinose, occasionally green pigmented; prothallus black, distinct at the margin. Upper cortex 27.5–37.5 µm thick, brown granules pigmented; epinecral layer 12.5–20.0 µm thick; algal layer 57.5–92.5 µm thick, cells 7.5–12.5 × 5.0–12.5 µm in diam., round; lower cortex absent. Apothecia frequent, immersed or isolated from areolae, round or somewhat irregular while immature, ellipsoid and tend to be rectangular for occupying the whole areolae once mature, 0.25–1.25 mm in diam.; disc brown, dark red brown, flat, occasionally with fissure when mature, epruinose; margin white, slightly raised. Hymenium 52.5–62.5 µm thick, colorless; paraphyses 2.0–2.5 µm wide, unbranched, not anastomosing; epihymenium 25.0–30.0 µm thick, dark orange brown; epinecral layer 7.5–17.5 µm thick; subhymenium 50.0–62.5 µm thick, colorless; hypothecium absent. Asci Porpidia-type, cylindrical, eight-spored; ascospores 8.0–15.0 × 5.0–7.5 µm in diam., ellipsoid, halonate not distinct. Pycnidia rare, immersed, flat, slightly convex, liner, stellate, graphidoid once mature, black, margin pruinose; conidia not seen.

Chemistry

Thallus K–, C–. Medulla I+, K–, C–. None.

Ecology and distribution

Growing on rock at elevations of 4622–4815 m in the alpine zone. This species is known from Qinghai Province of China.

Remarks: Lecaimmeria qinghaiensis is characterized by the yellow brown, rusty thallus, the red brown apothecia often occupying the whole areolae at maturity, and the dark orange brown epihymenium. The phylogenetic results showed that L. tuberculosa was sister species to L. qinghaiensis which is similar in the appearance of thallus, but differs in the brown, never rusty thallus, the red brown apothecia, and the green, tuberculiform pycnidia. The red brown thallus of L. qinghaiensis resembles L. iranica, but differs in the rusty thallus and the white margin of apothecia.

Specimens examined (KUN). CHINA, Qinghai Province, Zaduo Co., Sahuteng town, 4634 m elev., 32°55′N, 95°46′E, on rock, 2020, Li-Song Wang et al. 20-68698, 4637 m elev., Li-Song Wang et al. 20-68687, 4622 m elev., Li-Song Wang et al. 20-68696; 4790 m elev., 33°31′N, 95°8′E, Xin-Yu Wang et al. 20–849; Zaqing village, 4815 m elev., Xin-Yu Wang et al. 20–849.

Lecaimmeria tibetica C.M. Xie & Xin Y. Wang, sp. nov. — Fungal Names FN839752; Fig. 10a–e

Etymology: The epithet "tibetica" refers to the location from which the holotype was collected: “Tibet”, an autonomous region of China.

Type

CHINA, Tibet, Gongga Co., Jiangtang town, 4557 m elev., 29°12′N, 90°38′E, on rock, 9 Sept. 2019, Xin-Yu Wang et al. XY19-1291 (KUN—holotype).
**Description**

Thallus areolate, orange brown, epruinose, areolae 0.3–0.5 mm in diam., irregular, upper surface uneven, margin lacking, pruinose; prothallus black, distinct at the margin. Upper cortex 17.5–32.5 µm thick, brown granules pigmented; epinecral layer 10.0–20.0 µm thick; algal layer 75.0 µm thick, cells 7.5–10.0 × 7.5–10.0 µm in diam., round; lower cortex absent. Apothecia rare, immersed or isolated from areolae, 0.25–0.5 mm in diam.; disc dark orange brown, epruinose, flat, slightly convex; margin pruinose. Hymenium 105.0–137.5 µm thick, colorless; paraphyses 2.5 µm wide, unbranched, not anastomosing; epihymenium 25.0 µm thick, orange; epinecral layer 12.5 µm thick; subhymenium almost absent, colorless; hypothecium absent. Asci *Porpidia*-type, cylindrical, eight-spored; ascospores 12.5–15.0 × 5.0–6.0 µm in diam., ellipsoid, halonate. Pycnidia immersed, oblate, black, margin pruinose; conidia 5.0 × 1.5–2.0 µm in diam., bacilliform.

**Chemistry**

Thallus K–, C–. Medulla I+, K–, C–. None.

**Ecology and distribution**

Growing on quartz sandstone at elevations of 4310–4583 m in the alpine zone. This species is known from Tibet of China.

**Remarks:** *Lecaimmeria tibetica* is characterized by the orange brown thallus, the black pigmented of areolae margin, and the dark orange brown and small size of apothecia. *L. tibetica* is similar to *L. mongolica* (see notes for *L. mongolica*). The red brown apothecia of *L. cupreoatra* resembles *L. tibetica*, but differs in its dark red brown thallus and the presence of gyrophoric acid.

**Specimens examined** (KUN). CHINA, Tibet, Gongga Co., Jiangtang town, 4583 m elev., 29°12′N, 90°38′E, on rock, 2019, Xin-Yu Wang et al. XY19-1288, 4557 m elev., XY19-1291, 4560 m elev., XY19-1280; Dingri Co., Zhaguozhong, 4310 m elev., 28°35′N, 86°53′E, Li-Song Wang et al. 19-64071.

*Lecaimmeria tuberculosa* C.M. Xie & Xin Y. Wang, sp. nov. — *Fungal Names* FN839754; Fig. 10f–i

**Etymology**

The epithet “tuberculosa” refers to the tuberculiform of the pycnidia.

**Type**

CHINA, Gansu Province, Zhangye City, Sunan Co., Along the way from Sunan to Qilian, 3928 m elev., 38°37′N, 99°28′E, on rock, 30 May 2018, Li-Song Wang et al. 18-58865 (KUN–holotype).

**Description**

Thallus areolate, red brown, continuous, areolae 0.5–1.25 mm in diam., slightly convex, epruinose; margin pruinose, often with jade green pigmented; prothallus not distinct. Upper cortex 27.5 µm thick, orange granules pigmented; epinecral layer up to 27.5 µm thick, uneven, sometimes absent; algal layer 50.0 µm thick, cells 6.0–10.0 × 6.0–10.0 µm in diam., round; lower cortex absent. Apothecia frequent, scattered, immersed, 0.3–0.6 mm in diam.; disc red brown, concave, epruinose; margin absent. Hymenium 55.0–82.5 µm thick, colorless; paraphyses 2.5 µm wide, unbranched, not anastomosing; epihymenium 15.0–30.0 µm thick, orange; epinecral layer 5.0 µm thick, discontinuous; subhymenium 37.5 µm thick, colorless; hypothecium colorless. Asci *Porpidia*-type, cylindrical, eight-spored; ascospores 6.0–12.5 × 3.0–5.0 µm in diam., ellipsoid, halonate. Pycnidia stellate, strongly convex, rarely immersed, forming tuberculiform, black, margin pruinose; conidia 3.0–4.5 × 1.0 µm in diam., oblong to bacilliform.

**Chemistry**

Thallus K–, C–. Medulla I+, K–, C–. None.

**Ecology and distribution**
Growing on the Qilian jade or sandstone at elevations of 3928–4124 m in the alpine zone. This species is known from Qinghai Province and Gansu Province of China.

Remarks: Lecaimmeria tuberculosa is characterized by its red brown thallus, the jade green pruinose at the margin of its areolae, its red brown, concave apothecia without a proper margin and tuberculiform pycnidia. L. qinghaiensis is similar to L. tuberculosa (see notes for L. qinghaiensis). L. tuberculosa usually grows on jade, and interestingly the margin of pycnidia and areolae of the species are heavily jade green pigmented. L. iranica resembles L. tuberculosa by the absence of apothecia margin, but differs in its immersed pycnidia and white margin of its areolae.

Specimens examined (KUN). CHINA, Qinghai Province, Gande Co., Qingzhen village, 4124 m elev., 34°11′N, 100°12′E, on rock, 2020, Li-Song Wang et al. 20-68077, 4145 m elev., Li-Song Wang et al. 20-68055. Gansu Province, Zhangye City, Sunan Co., along the way from Sunan to Qilian, 3928 m elev., 38°37′N, 99°28′E, on rock, 2018, Li-Song Wang et al. 18-58856, 18-58857, 18-58865, 18-59835.

Key to Lecaimmeria and allied genera

1 Apothecia lecanorine-type. ................................................................. 2
Apothecia lecideine-type. .................................................................. 5
2 Apothecia adnate; Isidia spherical. .............................................. Koerberiella
Apothecia immersed; Isidia absent. ................................................ 3
3 Thallus surface wax glossy, orange or red brown. ......................... Lecaimmeria
Thallus surface not glossy, white. .................................................... 4
4 Asci Aspicilia-type, ascospores non-halonate. .......................... Aspicilia
Asci Porpidia-type, ascospores halonate, amyloid. ......................... Bellemerea
5 Epinecral layer absent. ................................................................. 6
Epinecral layer present. ................................................................. 8
6 Asci Lecanora-type; often containing miriquidic acid. ............... Miriquidica
Asci not Lecanora-type; not containing miriquidic acid. .............. 7
7 Asci Lecidea-type, ascospores non-halonate. ............................. Lecidea
Asci Porpidia-type, ascospores halonate. ....................................... Porpidia
8 Thallus surface dark brown; Asci Lecanora-type, ascospore non-halonate. ........................................ Miriquidica
Thallus surface orange or red brown; Asci Porpidia-type, ascospores halonate. ........................................... Immersaria

Key to species of Immersaria in this study

1 Thallus grayish brown; Apothecia crowded. ............................... 2
Thallus reddish brown; Apothecia rarely crowded. ....................... 3
2 Thallus rusty; Apothecia over 1.3 mm in diam.; Epihymenium brown; growing on red sandstone. ......................... I. ferruginea
Thallus never rusty; Apothecia never over 1.3 mm in diam.; Epihymenium green; growing on granite. ......................... I. plumbeoolivacea
3 Thallus orange, areolae irregular. ........................................... I. aurantia

Thallus not orange, areolae irregular, polygon or rectangle. ........................................... 4

4 Thallus up to 10 cm across, areolae aggregated by several smaller areolae and black prothallus. .............................................................. I. shangrilaensis

Thallus not up to 10 cm across, areolae not aggregated. ........................................... 5

5 Thallus areolae convex, not rusty, not cracked; Ascospores over 15 µm long. .................. I. athroocarpa

Thallus areolae flat, often rusty, cracked; Ascospores never over 15 µm long. .... I. venusta

**Key to species of Lecaimmeria in this study**

1 Prothallus distinct and filled the fissures between areolae. ........................................... 2

Prothallus only distinct at the margin. ................................................................. 4

2 Areolae margin white; Apothecia black brown; containing 4-O-demethylplanaic acid. .............................................................. L. mehadiana

Areolae margin black; Apothecia dark red brown; containing gyroboric acid or no substance detected by TLC. ........................................... 3

3 Thallus discontinuous, prothallus continuous, distinct and encircle every areolae; Apothecia dark red brown, margin absent. ........................................... L. cupreoatra

Thallus continuous, prothallus discontinuous, not encircle every areolae; Apothecia dark orange, margins present. ........................................... L. lygaea

4 Thallus orange. ................................................................. 5

Thallus reddish brown. ................................................................. 6

5 Apothecia red brown; containing gyroboric acid. ........................................... L. mongolica

Apothecia dark orange; no substance detected by TLC. ........................................... L. tibetica

6 Apothecia margin absent. ................................................................. 7

Apothecia margin present. ................................................................. 8

7 Areolae margin white; Epiphyemenium brown; Pycindia immersed, liner or stellate. ........ L. iranica

Areolae margin green; Epiphyemenium orange; Pycindia convex, tuberculiform. ............ L. tuberculosa

8 Thallus rusty; Apothecia occupy the whole areolae. ........................................... L. qinghaiensis

Thallus not rusty; Apothecia do not occupy the areolae. ........................................... 9

9 Apothecia irregular, crowded while immature, aggregate when mature. ........ L. botryoides

Apothecia round, rarely crowded, not aggregate. ........................................... L. orbicularis

**Declarations**

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Authors’ contributions

The manuscript was initially drafted by C.M. Xie, X.Y. Wang and L.L. Zhang. The authors commented on the draft in several rounds and provided substantial modifications. All authors read and approved the final manuscript.

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Availability of data and materials

All sequence data generated for this study (Table 1) can be accessed via GenBank: https://www.ncbi.nlm.nih.gov/genbank/.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

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Figures
Figure 1

Phylogenetic tree constructed from Maximum likelihood analyses in Lecideaceae based on the concatenated nrITS-nrLSU-RPB1-RPB2-mtSSU dataset. Maximum likelihood bootstrap probabilities above 40% (left) and Bayesian inference posterior probabilities above 0.7 (right) are given at the nodes.
Figure 2

Phylogenetic tree constructed from Maximum likelihood analyses in Immersaria based on the concatenated nrITS-nrLSU-RPB1-RPB2 dataset. Maximum likelihood bootstrap probabilities above 40% (left) and Bayesian inference posterior probabilities above 0.7 (right) are given at the nodes. Solid brown rectangle: thallus brown; solid orange rectangle: thallus yellow brown to orange brown; solid red rectangle: thallus rusty; hollow brown rectangle: thallus pale yellow brown. Solid green circle: green epihymenium; solid gray circle: without apothecia; hollow green circular: brown epihymenium.
Figure 3

Phylogenetic tree constructed from Maximum likelihood analyses in Lecaimmeria based on the concatenated nrITS-nrLSU-RPB1-RPB2 dataset. Maximum likelihood bootstrap probabilities above 40% (left) and Bayesian inference posterior probabilities above 0.7 (right) are given at the nodes. Solid purple rectangle: areolae margin white; solid gray rectangle: areolae margin black; hollow purple rectangle: areolae margin jade green pigmented. Solid blue circle gyrophoric acid; hollow blue circle: none.
Figure 4

Immersaria athroocarpa (a–e SDNU20190227). a–b. Thallus; c. Apothecial anatomy; d. Ascus; e. Ascospores. I. aurantia (f–j KUN XY19-1290). f–g. Thallus; h. Apothecial anatomy; i. Asci; j. Ascospores. — Scale bars: a, b, f, g = 1 mm; c, h = 20 μm; d, e, i, j = 10 μm.
Figure 5

Immersaria ferruginea (a-c KUN 20-69144). a–b. Thallus; c. Apothecial anatomy. l. plumbeoolivacea (d–f KUN 20-66914). d–e. Thallus; f. Apothecial anatomy. – Scale bars: a–b, d–w = 1 mm; c, f = 20 μm.
Figure 6

Immersaria shangrilaensis (a–d KUN 18-60430). a–c. Thallus; d. Apothecial anatomy. I. venusta (e–i KUN 20-66725). e–f. Thallus; g. Apothecial anatomy; h. Asci; i. Asci and paraphyses. — Scale bars: a–c, e–f = 1 mm; d, g, h, i = 20 μm.
Figure 7

Lecaimmeria botryoides (a–e KUN 20-66730). a–b. Thallus; c. Apothecial anatomy; d. Asci; e. Ascospores. L. lyagea (f–i KUN 20-69070). f–g. Thallus; h. Apothecial anatomy; i. Asci; j. Ascospores. — Scale bars: a–b, f–g = 1 mm; c, h = 20 μm; d, e, i, j = 10 μm.
Figure 8

Lecaimmeria mongolica (a–e SDNU20190354). a–b. Thallus; c. Apothecial anatomy; d. Asci; e. Ascospores. — Scale bars: a–b = 1 mm; c = 20 μm; d–e = 10 μm.
Figure 9

Lecaimmeria orbicularis (a–e KUN 20-66753). a–b. Thallus; c. Apothecial anatomy; d. Asci; e. Ascospores. L. qinghaiensis (f–i KUN 20-68696). f–g. Thallus; h. Apothecial anatomy; i. Asci. — Scale bars: a–b, f–g = 1 mm; c, h, i = 20 μm; d, e = 10 μm.
Figure 10

Lecaimmeria tibetica (a–e KUN XY19-1288). a–b. Thallus; c. Apothecial anatomy. d. Ascii; e. Ascospores. L. tuberculosa (f–i KUN 18-58864). f. Thallus; g. Pycnidia; h. Apothecial anatomy; i. Ascii; j. Ascospores. — Scale bars: a–b, f–g = 1 mm; c = 20 μm; d, e, i, j = 10 μm; h = 50 μm.