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Distribution and diversity of lichenicolous fungi from western Himalayan Cold Deserts of India, including a new *Zwackhiomyces* species

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The bare rock surfaces in cold deserts provide the most extreme environmental conditions for life on Earth where specialists with particular adaptations, such as bacteria, black yeasts, fungi, mosses, lichens and microalgae can colonize. Lichens growing in these harsh conditions also use to house symptomatic and asymptomatic fungi, which are generally termed as lichenicolous and endolichenic fungi, respectively. In the present study lichenicolous fungi associated with lichens of cold deserts of India (Leh-Ladakh and Lahaul Spiti) were investigated using lichen specimens obtained from CSIR-National Botanical Research Institute including herbaria of LWG, LWU and private herbaria of Dr. D.D. Awasthi (AWAS). The new species *Zwackhiomyces lecideae*, lichenicolous on *Lecidea*, is described in detail, and a list of 36 species (including one lichenicolous lichen, *Sarcogyne sphaerospora*, and one black meristematic fungus, *Lichenothelia convexa*, that is also a facultative lichenicolous fungus) belonging to 11 families (excluding genera of uncertain taxonomic positions) infecting 39 species of lichen hosts in the study site is presented. The discovery of a new species of *Zwackhiomyces* raises the tally of its members to 36 across the world and eight from India.

Keywords: alpine, astrobiology, diversity, Mars, lichens, lichensphere, secondary fungi, taxonomy.

Cold Deserts of India by virtue of their stressed climate (i.e. higher environmental lapse rate, high wind velocity, high UV radiation, low atmospheric pressure, extreme low temperature, great diurnal fluctuations, scanty and erratic rainfall and heavy snowfall), and delimiting nutrient and exposure regime, led to the emergence of a fragile and unique ecosystem in the rain shadow regions of the Trans-Himalayan zone, which is characterised by limited trophic levels and presence of relatively few unique biodiversity elements (Rai et al. 2012), such as, bacteria, black yeasts, fungi, mosses, lichens and microalgae (Baross and Morita 1978, Herbert 1986, Russell 1990, Gounot 1991). They cover only about 2 % of the total land surface and are stretched within an area of ca. 98,660 km^2, of which ca. 82,665 km^2 can be found in Ladakh, ca. 15,000 km^2 in Himachal Pradesh and nearly 1000 km^2 in Uttarakhand and Sikkim (Negi 2002).

Rocks in such cold deserts play a prominent role as substrata (Nienow & Friedmann 1993) because (1) mechanical abrasion as compared to soil and soil crusts is slow and organisms get attached to it firmly, (2) rocks have crevices, cracks and pores that are suitable microclimatic caves for microbes and plants; and hence when conditions at the rock surface become favourable for life, the organisms, *viz*. cushion or mat forming plants (bryophytes and mosses); diminutive and bushy plants with deep penetrating tap root systems; fungi and lichens; and thick and silvery hairy indumentums] with particular adaptations (Selbmann et al. 2005, 2013, Onofri et al. 2007) start living at the absolute edge of life under the most extreme environmental conditions known on Earth. They live between the limit of adaptability and near-death, barely surviving and rarely reproducing (Friedmann & Weed 1987).

The different lineages of fungi colonizing rocks of alpine altitudes can be clustered in the following main ecological groups (modified from Sterflinger et al. 2012): (1) terricolous, epi- and endolithic lichens; (2) lichenicolous fungi; (3) fungi associated with plants (phylloplane fungi or in mycorrhizal associations) and bryophytes (Lindo and Gonzalez, 2010); (4) free living hyphomycetes and yeasts living in the soil; and (5) microcolonial fungi (MCF) living as endo- and epilithic fungi, also known as "black fungi" or "microcolonial fungi" or "meristematic

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fungi", and are among the most stress-resistant eukaryotic organisms on Earth (Ruibal et al. 2005, 2008) .

Among these five ecological groups, lichens (also called lichenised fungi) (Pereira et al. 2007, Victoria et al. 2013, Cao et al. 2017, Tripathi & Joshi 2019) express their phenotypic and phylogenetic diversity and shape the landscapes with colorful mosaics on rock surfaces. In such variably stressed situations, black fungi and lichens can occur side by side on rock, and black fungi along with lichenicolous fungi also colonize healthy lichens (Harutyunyan et al. 2008).

Lichens constitute a major component of the flora of cold desert in Trans-Himalaya (Baniya 2010) and their growth forms are known to be good indicators of habitat heterogeneities in Himalayan habitats (Baniya et al. 2012, Rai et al. 2012). They develop complex and long lived structures to shelter populations of symbiotic photobionts (Honegger 2012), and recent studies revealed that they also host a number of organisms, such as bacteria (Cardinale et al. 2008, Grube et al. 2009; Hodkinson & Lutzoni 2009, Bates et al. 2011, Grube & Berg 2009), lichenicolous fungi, which expresses symptoms (Lawrey & Diederich 2003), endolichenic fungi, which grow without symptoms in the interior of lichens (Girlanda et al. 1997, Suryanarayanan et al. 2005, U'Ren et al. 2010, Bates et al. 2012, Tripathi & Joshi 2019) and black fungi (Muggia et al. 2013, Selbmann et al. 2013, Zakharova et al. 2013). These studies have fueled the concept that lichens can also be considered miniature ecosystems (Farrar 1976, Grube et al. 2009). Recently, Santiago et al. (2015) introduced the term lichensphere in reference to Antarctic lichens, which was defined as the surface and narrow region of the lichen's thallus that may represent a protected natural microhabitat with favourable conditions (such as available nutrients and a protective barrier against the low temperature, oligotrophy, strong winds and UV radiation or a combination of these factors), which can help non-endemic non-lichenised fungi and other life forms to survive and disperse in extreme conditions.

These rock-inhabiting alpine lichens of Indian cold desert, to some extent face the same set of harsh environmental conditions as in Antarctica, and conceivably are home to only those organisms that can tolerate such fluctuating conditions and can persist or grow in lichens. In addition, these organisms are also coping up with the diverse and highly concentrated extracellular secondary products of their host species.

However, despite a growing body of literature on organisms associated with lichens, we still have limited knowledge of the extent of eukaryotic diversity that may be associated with lichen thalli (Lawrey & Diederich 2003, Diederich et al. 2018, Tripathi & Joshi 2019).

In India, studies concerning the fungi associated with lichens are very scarce and initiated recently (Rairkar & Patwardhan 1979; Hariharan et al. 1996; Suryanarayan et al. 2005; S. Joshi et al. 2013; Joseph & Sinha 2015; Y. Joshi et al. 2015a,b, 2016a,b,c, 2017a,b,c, 2018, 2020; Singh et al. 2017; Suryanarayan et al. 2017; Singh & Singh 2018; Tripathi et al. 2014a, b, c; Y. Joshi 2018, 2020; Tripathi & Joshi 2019), indicating that lichens shelter a variety of non-lichenised fungal species, both endolichenic and lichenicolous fungi. Though several publications dealing with lichen diversity of alpine regions of Himachal Pradesh, Jammu & Kashmir and Ladakh are available (Höeg 1953; Kumar et al. 2012, 2014; Negi & Upreti 2000; Rahim et al. 2013; Goni et al. 2015; Khare et al. 2020; Prasher & Chander 2005; Sharma & Sharma 1991, 2000; Sharma & Tayal 1992; Sharma et al. 2001; Yadav 2005), not a single manuscript has ever reported the occurrence of lichenicolous fungi from this region. It was Mikhail P. Zhurbenko, who for the first time reported lichenicolous fungi from Ladakh (Zhurbenko 2013). This paper for the first time gives an overview of the diversity of lichenicolous fungi associated with lichens of western Himalayan cold deserts of India, including a species new to science.

Materials and methods

The present study includes all species found by examination of available literature and specimens including herbaria of LWG, LWU and private herbaria of Dr. D.D. Awasthi (AWAS) provided to the author on loan basis by CSIR-National Botanical Research Institute. Samples were studied with routine mycological techniques. Macroscopic features were examined with a stereozoom dissecting microscope (Olympus SZ61). Thin hand-cut sections were made for studying the anatomy of fruiting bodies and examined under Olympus BX53 compound microscope (up to 1000×) fitted with Olympus differential interference contrast. Microscopical examination was done in water, 10 % KOH (K), lactophenol cotton blue (LCB), Melzer's reagent (MLZ), Lugol's iodine, directly (I) or after a KOH pre-treatment (K/I), Congo red (CR) solution. Measurements regarding *Zwackhiomyces lecideae* are given as follows: (minimum)(X–SD)–X–(X+SD)(maximum),

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where X is the arithmetic mean and SD the corresponding standard deviation, followed by the number of measurements (n); Q = length/width ratio.

Results

Immediately after the taxon, the hosts known from cold desert regions of India are indicated, followed by information on the distribution in India.

***Arthonia epiphyscia* Nyl.**

On thallus of *Physcia* sp. (hb LWG 20747, LWG 13355). Ladakh (Jammu & Kashmir) and Uttarakhand (Joshi et al. 2016c), and now also from Himachal Pradesh.

***Arthonia molendoi* (Frauenf.) R. Sant.**

On thallus and apothecial disc of *Caloplaca biatorina*, *Rusavskia elegans*, *Xanthoria* sp. (hb LWG 13260; LE 260 547). Himachal Pradesh, Jammu & Kashmir and Ladakh (Zhurbenko 2013, Joshi et al. 2016c).

***Carbonea vitellinaria* (Nyl.) Hertel**

On thallus of *Candelaria vitellinaria* (hb LWG 15070). Himachal Pradesh, Jammu & Kashmir and Ladakh (Poelt 1961, Hertel 1983, Awasthi 1991, Zhurbenko 2013, Joshi et al. 2016c).

***Cercidospora caudata* Kernst.**

On apothecial disc of *Calogaya biatorina*, *Rusavskia elegans*, *Xanthoria* sp. (hb LWG 008746, 23391). Himachal Pradesh, Jammu & Kashmir, Ladakh and Uttarakhand (Joshi et al. 2016c).

***Cercidospora macrospora* (Uloth) Hafellner & Nav.-Ros.**

On thallus and apothecial disc of *Protoparmeliopsis garovaglii*, *Protoparmeliopsis muralis* var. *dubyi* (hb LWG 15377; LE 261 098). Himachal Pradesh, Jammu & Kashmir and Ladakh (Zhurbenko 2013, Joshi et al. 2016c).

***Cercidospora melanophthalmae* Nav.-Ros., Calat. & Hafellner**

On thallus and apothecial disc of *Protoparmeliopsis peltata*, *Rhizoplaca chrysoleuca*, *R. melanophthalma* var. *melanophthalma*, *R. melanophthalma* var. *obscura* (hb LWG 15169, 10294, 23391). Himachal Pradesh, Jammu & Kashmir, Ladakh and Uttarakhand (Zhurbenko 2013, Joshi et al. 2016c).

***Cercidospora werneri* Nav.-Ros., Calat. & Hafellner**

On thallus and apothecial disc of *Aspicilia* sp. (hb LWG 10281). Ladakh (Joshi et al. 2016c).

***Cercidospora xanthoriae* (Wedd.) R. Sant.**

On thallus and apothecial disc of *Rusavskia elegans*. Himachal Pradesh, Jammu & Kashmir, Ladakh and Uttarakhand (Zhurbenko 2013, Joshi et al. 2016c).

***Cercidospora* sp.**

On thallus of *Lecanora* sp. (hb LE 261 077). Ladakh by Zhurbenko (2013).

***Endococcus perpusillus* Nyl.**

On thallus of *Acarospora badiofusca*, *Aspicilia* sp. (hb LWG 15371, LWG 13361). Himachal Pradesh and Ladakh (Joshi et al. 2016c).

***Endococcus propinquus* (Körb.) D. Hawksw.**

On thallus of *Lecidella carpathica* (hb LWG 16220). Himachal Pradesh and Uttarakhand (Joshi et al. 2016c).

***Intralichen christiansenii* (D. Hawksw.) D. Hawksw. & M.S. Cole**

On apothecial disc of *Candelariella aurella* (hb LE 260 467). Jammu & Kashmir, Ladakh and Uttarakhand (Zhurbenko 2013, Joshi et al. 2016c).

***Lichenochora verrucicola* (Wedd.) Nik. Hoffm. & Hafellner**

On thallus of *Aspicilia* sp. Ladakh (Joshi et al. 2016c).

***Lichenoconium lecanorae* (Jaap) D. Hawksw.**

On thallus of *Psora* sp. (LWG 15371). Himachal Pradesh and Uttarakhand (Joshi et al. 2016c).

***Lichenodiplis lecanorae* (Vouaux) Dyko & D. Hawksw.**

On thallus and apothecial disc of *Acarospora* sp., *Rusavskia elegans*. Himachal Pradesh, Jammu & Kashmir, Karnataka, Madhya Pradesh and Uttarakhand (Zhurbenko 2013; Joshi et al. 2015a, 2016c).

***Lichenostigma cosmopolites* Hafellner & Calat.**

On thallus of *Xanthoparmelia somloensis* (hb LWG 25939). Himachal Pradesh, Jammu & Kash-

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mir, Rajasthan, Sikkim and Uttarakhand (Zhurbenko 2013, Joshi et al. 2016c).

***Lichenostigma* cf. *elongatum* Nav.-Ros. & Hafellner**

On thallus and apothecial disc and margins of *Lecanora* sp., *Lobothallia praeradiosa* (hb LE 261 126, 261 078). Ladakh (Zhurbenko 2013).

***Lichenostigma* subgen. *Lichenogramma* sp.**

On thallus and apothecial disc *Seirophora contortuplicata* (hb LE 261 117). Ladakh (Zhurbenko 2013).

***Lichenothelia convexa* Henssen**

On thallus of *Aspicilia almorensis* (hb LWG 005192). Uttarakhand (Joshi et al. 2016c), and in the present study extending its distributional range up to Himachal Pradesh. Besides its facultative lichenicolous nature, this cosmopolitan species is a rock inhabiting black meristematic fungus (Kocourková & Knudsen 2011, Muggia et al. 2013) colonizing nearby areas of the rocks.

***Muellerella erratica* (A. Massal.) Hafellner & V. John**

On thallus and apothecial disc of *Acarospora bullata*, *Acarospora fuscata*, *Acarospora superans*, *Circinaria caesiocinerea*, *Circinaria maculata*, *Lecidea auriculata*, *Lecidella stigmatea*, *Lobothallia praeradiosa*, *Protoparmeliopsis garovaglii*, *Protoparmeliopsis muralis*, *Rhizoplaca melanophthalma*, *Rusavskia elegans* (hb LWG 10408, 13215, 13355, 15608, 15025, 16211, 16229, 005315, 15557, 15559, 15910, 15925, LWG-AWAS 2053, LWG-LWU 2460). Himachal Pradesh, Jammu & Kashmir, Ladakh, Uttarakhand (Joshi et al. 2016c), and in the present study extending its distributional range to Kerala.

***Muellerella lichenicola* (Sommerf.) D. Hawksw.**

On thallus of *Caloplaca* sp., *Caloplaca trachyphylla*, *Lecanora* sp., *Rusavskia elegans* (hb LWG 23391, 11529). Himachal Pradesh, Jammu & Kashmir, Ladakh, Uttarakhand (Joshi et al. 2016c).

***Muellerella pygmaea* (Körb.) D. Hawksw.**

On thallus and occasionally on apothecia of *Acarospora* sp., *Rusavskia elegans* (hb LE 261 177, 260 517, 260 447, 260427). Jammu & Kashmir, Ladakh (Zhurbenko 2013, Joshi et al. 2016c).

***Muellerella ventosicola* (Mudd) D. Hawksw.**

On thallus of *Rhizocarpon disporum*. Ladakh and Uttarakhand (Joshi et al. 2016c).

***Polycoccum clauzadei* Nav.-Ros. & Cl. Roux**

On thallus and apothecia of *Rusavskia elegans* (LE 261 007). Ladakh and Uttarakhand (Zhurbenko 2013, Joshi et al. 2016c).

***Polycoccum microstictum* (Leight.) Arnold**

On thallus of *Acarospora fuscata*. Himachal Pradesh (Joshi et al. 2016c).

***Polysporina subfuscescens* (Nyl.) K. Knudsen & Kocourk.**

On thallus of *Acarospora* sp., *Candelariella* sp., *Carbonea vitellinaria* (hb LWG 00594). Jammu & Kashmir, Ladakh (Joshi et al. 2016c).

***Rosellinula frustulosae* (Vouaux) R. Sant.**

On thallus of *Lecanora argopholis*, *Lecanora frustulosa* (hb LWG 14969, 15031, 15632, LE 261 017). Ladakh (Zhurbenko 2013) and extending its distibutional range up to Himachal Pradesh.

***Sarcogyne sphaerospora* J. Steiner**

On thallus of *Candelariella* sp. (hb LE 261 106, 260 996). This lichenicolous lichen was Ladakh (Awasthi 1991, Zhurbenko 2013).

***Sclerococcum homoclinellum* (Nyl.) Ertz & Diederich**

On thallus of *Protoparmeliopsis muralis* (hb LWG 15554). Himachal Pradesh, Madhya Pradesh (Joshi et al. 2016c), and in the present study extending its distribution to Uttarakhand.

***Sphaerellothecium contextum* Triebel**

On thallus of *Rhizoplaca chrysoleuca* (hb LWG 13186). Uttarakhand (Joshi et al. 2016c), and in the present study extending its distribution to Himachal Pradesh, Jammu & Kashmir and Ladakh.

***Stigmidium gyrophorarum* (Arnold) D. Hawksw.**

On thallus of *Umbilicaria virginis* (hb LWG 24974). Jammu & Kashmir (Zhurbenko 2013), and in the present study extending its distribution to Himachal Pradesh.

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***Stigmidium tabacinae* (Arnold) Triebel**

On thallus of *Toninia tristis* ssp. *asiae-centralis*. Jammu & Kashmir (Zhurbenko 2013, Joshi et al. 2016c), and in the present study is extending its distribution in Ladakh.

***Tetramelas pulverulentus* (Anzi) A. Nordin & Tibell**

On thallus of *Physcia* sp. (hb LWG 13304). Uttarakhand (Joshi et al. 2018), and in the present study extending its distribution to Ladakh.

***Zwackhiomyces coepulonus* (Norman) Grube & R. Sant.**

On thallus and apothecial disc of *Caloplaca* sp., *Rusavskia elegans* (hb LWG 15223, LE 260 437). Ladakh (Zhurbenko 2013), and in the present study extending its distribution to Himachal Pradesh and Uttarakhand.

***Zwackhiomyces lecanorae* (Stein) Nik. Hoffm. & Hafellner**

On thallus of *Lecanora* sp. (hb LWG 13384). Ladakh (Joshi et al. 2015a).

***Zwackhiomyces lecideae* Y. Joshi, sp. nov. – Fig. 1**
MycoBank no.: MB838128

Diagnosis. – Similar to *Z. socialis*, which differs from the new taxon in having brownish-black vegetative hyphae near the ascomata, narrower exciple [(10–15(20) µm], slightly bigger ascospores [14–17.5(20) × (4)5–7 µm (Q = 2.8)] and in host preference (*Clauzadea monticola*, *C. metzleri* and *Bacidia bagliettoana*).

Holotypus. – INDIA. Himachal Pradesh, Lahul Spiti district, Zinzibar, alt. 4200 m, on thallus of *Lecidea auriculata* colonizing exposed rocks, 4 August 2003, *leg*. D.K. Upreti & S. Chatterjee 03-001756/A (Holotype - LWG 16236).

Description. – Vegetative hyphae not observed. – Ascomata perithecioid, superficial on the thallus and lateral side of the host areoles, black, globose to subglobose, slightly flattened at the top, (100)120–130(150) × (130)135–150(160) µm, scattered to rarely crowded, sessile. Radial superficial fissures visible around the ostiole, no apparent damage and thallus deformation observed to the host. – Wall pseudoparenchymatous, of *textura angularis*, dark blackish brown both in the upper and lower part of the ascomata, K+ intense; in section 17–30 µm wide, with 6–10 layers of cells, with the inner layers of cells paler and with a thinner wall than those more external. Cells of the wall rounded to somewhat irregular in superficial view, mostly 4–8 µm diam., wall pigments deposited among the cells, granulose, turning black with K. – Hymenial gel I-, K/I orange red. – Hamathecial filaments branched, septate and anastomosing, embedded in a gelatinous mass, 1–1.5 µm wide. – Asci cylindrical to slightly clavate, shortly stipitate, 8-spored, (57)60–*72*–84(95) × (11)13–*14*–15(16) µm (n = 30), wall thickened at the apex, with a distinct ocular chamber, I+ red brown, all other parts I–, dehiscence fissitunicate. – Ascospores 1-septate, distichously to irregularly arranged, ellipsoid to somewhat soleiform, markedly constricted at the septum, lower cell narrower than the upper one and ±attenuated, hyaline, with a ±finely granulose surface, (13)14.2–*15*.6–16.0(17) × (3.5)3.8–*4.5*–5.2(6); Q = (2.6)3.0–*3.6*–4.1(4.3) (n = 30); perispore distinct, 0.5 µm. Conidiomata not seen.

Etymology. – The epithet derives its name from the host on which it is growing.

Habitat and distribution. – The new species is known only from the type locality in the alpine regions of Himalaya, growing on the thallus of *Lecidea auriculata* colonizing exposed rocks. It is assumed to be a commensalistic species, as no damage to the affected portions of the thallus of *Lecidea auriculata* has been observed.

Remarks. – The lichenicolous fungal genus *Zwackhiomyces* Grube & Hafellner belonging to the family Xanthopyreniaceae was established by Grube & Hafellner (1990). It is generally characterized by perithecioid ascomata, lack of ostiolar filaments, branched and anastomosing interascal filaments, fissitunicate asci, a distinctive pigmentation of the peridial cells produced by a granular dark brown, K+ blackish pigment, and 1-septate, hyaline and asymmetric ascospores and is represented by 35 species across the world colonizing various saxicolous and corticolous lichens (Diederich et al. 2018), of which seven were reported previously from India (viz. *Zwackhiomyces coepulonus* (Norman) Grube & R. Sant., *Z.* cf. *kiszkianus* D. Hawksw. & Miadl., *Z. lecanorae* (Stein) Nik. Hoffm. & Hafellner, *Z. physciicola* Alstrup, *Z. socialis* (Körb.) Cl. Roux, *Z. sphinctriniformis* Grube & Hafellner and *Z. sphinctrinoides* (Zwackh) Grube & Hafellner) colonizing various crustose and foliose lichens in temperate and alpine regions, except *Z. socialis* which was reported from tropical region of India (Zhurbenko 2013; Y. Joshi 2018; Joshi et al. 2016, 2018).

This is the fourth species of this genus colonizing members of the lichen forming family *Lecideaceae* Chevall. The previous ones were *Z. berengerianus* (Arnold) Grube & Triebel (Grube & Hafellner 1990), *Z. socialis* (Körb.) Cl. Roux (Grube & Hafellner 1990; Roux 2009), and *Z. sphinctriniformis* Grube & Hafellner (Grube & Hafellner 1990). It is the first

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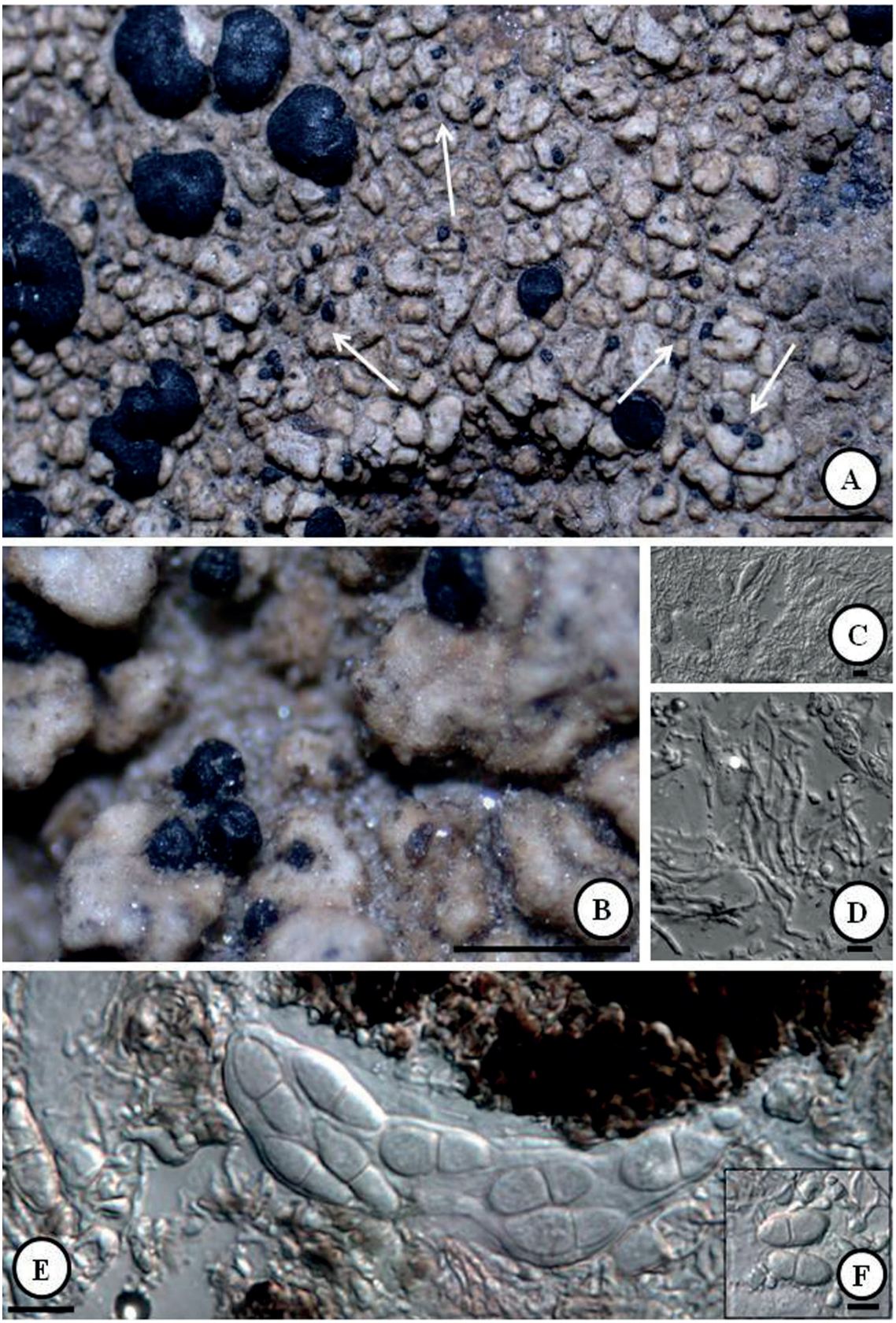

Fig. 1. *Zwackhiomyces lecideae* (holotype): A. Thallus of *Lecidea* infected by *Zwackhiomyces* (arrows indicating lichenicolous fungus). B. Magnified view of infected part. C. Immature ascus surrounded by hamathecial filaments. D. Hamathecial filaments. E. Ascus with ascospores. F. Ascospores. Scale bars: A = 1 mm, B = 0.5 mm, C–F = 10 µm.

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one colonizing members of the lichen genus *Lecidea* and is very much close to *Z. socialis*, which differs from the new taxon by brownish-black vegetative hyphae near the ascomata, narrower exciple [(10–15(20) µm)], slightly bigger ascospores [14–17.5(20) × (4)5–7 µm (Q = 2.8)] and in host prefernce (*Clauzadea monticola*, *C. metzleri* and *Bacidia baglietoana*) (Grube & Hafellner 1990). *Zwackhiomyces berengerianus*, differs from the new taxon in having obpyriform ascomata, bigger ascospores 17–24(27) × 5–8(10) µm (Q = 2.9–3.1) with a distinctly verrucose perispore, hyaline to pale brown overmature spores and host preference (*Mycobilimbia berengeriana*) (Grube & Hafellner 1990). *Zwackhiomyces sphinctriniformis*, differs from *Z. lecideae* not only in host selection (thallus of *Romjularia lucida*) but also by bigger ascomata (230–280 × 200–240 µm) and slightly bigger and wider ascopores [(15)15.5–23 × (4)4.5–6.5(8.5) µm].

The new taxon needs to be compared with *Z. heppiae* van den Boom, *Z. inconspicuus* Grube & Haf., *Z. kantvilasii* S.Y. Kondr., *Z. lecanorae* (Stein) Nik. Hoffm. & Hafellner, *Z. martinatianus* (Arnold) Triebel & Grube, *Z. peltigerae* Miadl. & Alstrup and *Z. sipmanii* Diederich & Zhurb., that have somewhat similarly sized ascospores (11–17 × 3–5.5 µm). *Zwackhiomyces heppiae* differs by semi-immersed larger perithecia (100–250 µm), smaller asci (35–55 × 15–18 µm) and different host (on thallus and apothecial disc of *Heppia arenacea*) (Boom 2010). *Zwackhiomyces inconspicuus* Grube & Hafellner differs in having bigger pseudothecia (200–250 µm), broader ascospores (4–7 µm), smaller Q value (2.5) and a different host (*Myriolecis dispersa* (Pers.) Śliwa, Zhao Xin & Lumbsch) (Grube & Hafellner 1990). *Zwackhiomyces kantvilasii* colonizing thalli of *Parmotrema* differs not only in host selection but has slightly bigger pseudothecia [140–180(200) µm], 4-spored asci and spores with four guttules (Kondratyuk 1996, Pérez-Ortega et al. 2011). *Zwackhiomyces lecanorae* differs by pyriform to obpyriform (rarely globose) bigger perithecia [(70)90–170 (200) µm], aseptate wider ascospores [(5.5)6–7.3–8.6(10) µm], smaller Q value (2.2) and different host (*Myriolecis* Clem.) (Hoffmann & Hafellner 2000). *Zwackhiomyces martinatinaus* differs by smaller pseudothecia (90–130 µm) and is a gall-inducing species colonizing the thallus of *Porpidia* Körb. (Grube & Hafellner 1990). Bigger pseudothecia (170–200 µm), thinner exciple (7–10 µm), thinner hamathecial filaments (< 1 µm) and *Peltigera* as a host, differentiate the new taxon from *Z. peltigerae* (Miadlikowska & Alstrup 1995). *Zwackhiomyces sipmanii* has 4(–6)-spored asci and the host species is *Phaeorrhiza sareptana* var. *sphaerocarpa* (Th. Fr.) H. Mayrhofer & Poelt (Diederich & Zhurbenko 2009).

Smaller pseudothecia (50–150 µm), pyriform to obovoid smaller asci (38–57 × 14–18 µm) and species of *Acarospora* A. Massal. as host differentiate *Z. argentinae* (Räsänen) D. Hawksw. & V. Atienza from the new species (Hawksworth & Atienza 1994).

Discussion

We recognized a new lichenicolous fungus and are also reporting 36 species of lichenicolous fungi [including one lichenicolous lichen (*Sarcogyne sphaerospora*) and a black meristematic fungus (*Lichenothelia convexa*) which is also a facultative lichenicolous fungus] (Kocourková & Knudsen 2011, Muggia et al. 2013) belonging to 11 families (excluding genera of uncertain taxonomic positions) inhabiting 39 lichen host species from cold desert of India (Tab. 1). Of these 36 species, 10 are confined to Lahaul & Spiti, 15 to Leh-Ladakh, while 11 species are common to both localities.

Cercidospora was the most species rich genus represented by six species, and was followed by *Muellerella* (4 species) (Tab. 1). *Muellerella erratica* was the most abundant species in the study area and recorded from 20 samples, followed by *Arthonia molendoi* (8), *Cercidospora melanophthalmae* (7), *Muellerella lichenicola* (6), *Cercidospora caudata* and *Cercidospora xanthoriae* (5 each), *Cercidospora macrospora* (4), *Rosellinula frustulosae* and *Endococcus perpusilus* (3 each); eight taxa were collected twice, while 20 were collected once, hence can be considered rare species to that locality.

It was also observed that the lichen genus *Rusavskia* was infected by the largest number of lichenicolous fungi (9), followed by *Acarospora* and *Lecanora* (6 each), *Aspicilia* and *Protoparmeliopsis* (4 each) (Tab. 2), and *Muellerella erratica* was the most infectious lichenicolous fungus infecting 8 lichen genera, followed by *Muellerella lichenicola* and *Cercidospora caudata* (3 each) (Tabs. 1, 2).

Lichenothelia convexa, a black meristematic fungus belonging to the superclass Dothideomyceta, is opportunistically growing on lichen thalli (i.e. facultative lichenicolous), where it is producing fertile structures with asci and ascospores.

Besides this, *Arthonia epiphyscia*, *Lichenothelia convexa*, *Muellerella erratica*, *Rosellinula frustulosae*, *Sclerococcum homoclinellum*, *Sphaerellothecium contextum*, *Stigmidium gyrophorarum*, *Stigmidium tabacinae*, *Tetramelas pulverulentus* and *Zwackhiomyces coepulonus* reported earlier from

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Tab. 1. Diversity of lichenicolous fungi associated with lichens of cold deserts of India.

Lichenicolous fungi	Family	Lichen host(s)	Infected part		Cold Desert	
			Th	Ap	Lahaul & Spiti	Leh-Ladakh
Arthonia epiphyscia	Arthoniaceae	*Physcia* sp.	+	–	+	+
Arthonia molendoi	Arthoniaceae	*Calogaya biatorina*, *Rusavskia elegans*	+	+	+	+
Carbonea vitellinaria	Lecanoraceae	*Candelaria* sp.	+	–	+	–
Cercidospora caudata	Incertae sedis	*Calogaya biatorina*, *Rusavskia elegans*, *Xanthoria* sp.	+	+	+	+
Cercidospora macrospora	Incertae sedis	*Protoparmeliopsis garovaglii*, *Protoparmeliopsis muralis*	+	+	+	+
Cercidospora melanophthalmae	Incertae sedis	*Protoparmeliopsis peltata*, *Rhizoplaca chrysoleuca*, *Rhizoplaca melanophthalma* var. *melanophthalma*, *Rhizoplaca melanophthalma* var. *obscura*	+	+	+	+
Cercidospora werneri	Incertae sedis	*Aspicilia* sp.	+	+	–	+
Cercidospora xanthoriae	Incertae sedis	*Rusavskia elegans*	+	+	+	+
Cercidospora sp.	Incertae sedis	*Lecanora* sp.	+	–	–	+
Endococcus perpusillus	Verrucariaceae	*Acarospora badiofusca*, *Aspicilia* sp.	+	–	+	+
Endococcus propinquus	Verrucariaceae	*Lecidella carpathica*	+	–	+	–
Intralichen christiansenii	Incertae sedis	*Candelariella aurella*	–	+	–	+
Lichenochora verrucicola	Phyllachoraceae	*Aspicilia* sp.	+	–	–	+
Lichenoconium lecanorae	Abrothallaceae	*Psora* sp.	+	–	+	–
Lichenodiplis lecanorae	Incertae sedis	*Acarospora* sp., *Rusavskia elegans*	+	–	+	–
Lichenostigma cosmopolites	Lichenotheliaceae	*Xanthoparmelia somloensis*	+	–	+	–
Lichenostigma cf. *elongatum*	Lichenotheliaceae	*Lecanora* sp., *Lobothallia praeradiosa*	+	+	–	+
Lichenostigma subgen. *Lichenogramma* sp.	Lichenotheliaceae	*Seirophora contortuplicata*	+	+	–	+
Lichenothelia convexa	Lichenotheliaceae	*Aspicilia almorensis*	+	–	+	–
Muellerella erratica	Incertae sedis	*Acarospora bullata*, *Acarospora fuscata*, *Acarospora superans*, *Circinaria caesiocinerea*, *Circinaria maculata*, *Lecidea auriculata*, *Lecidella stigmatea*, *Lobothallia praeradiosa*, *Protoparmeliopsis garovaglii*, *Protoparmeliopsis muralis*, *Rhizoplaca melanophthalma*, *Rusavskia elegans*	+	+	+	+
Muellerella lichenicola	Incertae sedis	*Caloplaca* sp., *Caloplaca trachyphylla*, *Lecanora* sp., *Rusavskia elegans*	+	+	+	+
Muellerella pygmaea	Incertae sedis	*Acarospora* sp., *Rusavskia elegans*	+	+	–	+
Muellerella ventosicola	Incertae sedis	*Rhizocarpon disporum*	+	–	–	+
Polycoccum clauzadei	Polycoccaceae	*Rusavskia elegans*	+	+	–	+
Polycoccum microstictum	Polycoccaceae	*Acarospora fuscata*	+	–	+	–
Polysporina subfuscescens	Acarosporaceae	*Acarospora* sp., *Candelariella* sp., *Carbonea vitellinaria*	+	–	–	+
Rosellinula frustulosae	Incertae sedis	*Lecanora argopholis*, *Lecanora frustulosa*	+	–	+	+
Sarcogyne sphaerospora	Acarosporaceae	*Candelariella* sp.	+	–	–	+
Sclerococcum homoclinellum	Dactylosporaceae	*Protoparmeliopsis muralis*	+	–	+	–

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Lichenicolous fungi	Family	Lichen host(s)	Infected part		Cold Desert	
			Th	Ap	Lahaul & Spiti	Leh-Ladakh
Sphaerellothecium contextum	Incertae sedis	*Rhizoplaca chrysoleuca*	+	–	–	+
Stigmidium gyrophorarum	Incertae sedis	*Umbilicaria virginis*	+	–	+	–
Stigmidium tabacinae	Incertae sedis	*Toninia tristis* ssp. *asiae-centralis*	+	–	–	+
Tetramelas pulverulentus	Caliciaceae	*Physcia* sp.	+	–	–	+
Zwackhiomyces coepulonus	Xanthopyreniaceae	*Caloplaca* sp., *Rusavskia elegans*	+	+	+	+
Zwackhiomyces lecanorae	Xanthopyreniaceae	*Lecanora* sp.	+	–	–	+
Zwackhiomyces lecideae	Xanthopyreniaceae	*Lecidea auriculata*	+	–	+	–
			35	**14**	**21**	**26**

Tab. 2. Lichen genera infected by various lichenicolous fungi.

S. No.	Lichen genera	Lichenicolous fungi
1	*Acarospora* A. Massal.	*Endococcus perpusillus*, *Lichenodiplis lecanorae*, *Muellerella erratica*, *Muellerella pygmaea*, *Polycoccum microstictum*, *Polysporina subfuscescens*
2	*Aspicilia* A. Massal.	*Cercidospora werneri*, *Endococcus perpusillus*, *Lichenochora verrucicola*, *Lichenothelia convexa*
3	*Calogaya* Arup, Frödén & Søchting	*Arthonia molendoi*, *Cercidospora caudata*
4	*Caloplaca* Th. Fr.	*Muellerella lichenicola*, *Zwackhiomyces coepulonus*
5	*Candelaria* A. Massal.	*Carbonea vitellinaria*
6	*Candelariella* Müll. Arg.	*Intralichen christiansenii*, *Polysporina subfuscescens*, *Sarcogyne sphaerospora*
7	*Carbonea* (Hertel) Hertel	*Polysporina subfuscescens*
8	*Circinaria* Link	*Muellerella erratica*
9	*Lecanora* Ach.	*Cercidospora macrospora*, *Cercidospora* sp., *Lichenostigma* cf. *elongatum*, *Muellerella lichenicola*, *Rosellinula frustulosae*, *Zwackhiomyces lecanorae*
10	*Lecidea* Ach.	*Muellerella erratica*, *Zwackhiomyces lecideae*
11	*Lecidella* Körb.	*Endococcus propinquus*, *Muellerella erratica*
12	*Lobothallia* (Clauzade & Cl. Roux) Hafellner	*Muellerella erratica*, *Lichenostigma* cf. *elongatum*
13	*Physcia* (Schreb.) Michx.	*Arthonia epiphyscia*,*Tetramelas pulverulentus*
14	*Protoparmeliopsis* M. Choisy	*Cercidospora macrospora*, *Cercidospora melanophthalmae*, *Muellerella erratica*, *Sclerococcum homoclinellum*
15	*Psora* Hoffm.	*Lichenoconium lecanorae*
16	*Rhizocarpon* Ramond ex DC.	*Muellerella ventosicola*
17	*Rhizoplaca* Zopf	*Cercidospora melanophthalmae*, *Muellerella erratica*, *Sphaerellothecium contextum*
18	*Rusavskia* S.Y. Kondr. & Kärnefelt	*Arthonia molendoi*, *Cercidospora caudata*, *Cercidospora xanthoriae*, *Lichenodiplis lecanorae*, *Muellerella erratica*, *Muellerella lichenicola*, *Muellerella pygmaea*, *Polycoccum clauzadei*, *Zwackhiomyces coepulonus*
19	*Seirophora* Poelt	*Lichenostigma* subgen. *Lichenogramma* sp.
20	*Toninia* A. Massal.	*Stigmidium tabacinae*
21	*Umbilicaria* Hoffm.	*Stigmidium gyrophorarum*
22	*Xanthoparmelia* (Vain.) Hale	*Lichenostigma cosmopolites*
23	*Xanthoria* (Fr.) Th. Fr.	*Cercidospora caudata*

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diverse phytogeographical regions of India are extending their known distributional range in India.

Conclusions

As lichens can host a wide range of associated fungi with varied ecologies, specificities, and biological behaviours (Lawrey & Diederich 2003), yet, these lichenicolous fungi cannot express their phenotypes without their hosts and have received little attention so far both in basic and applied research. By supporting the growth of 36 species of lichenicolous fungi, the lichens of Indian cold desert are not only helping other life forms besides themselves to survive, colonise and disperse in extreme environments, but also making themselves a potential cradle of fungal diversity in India.

Though rhizospheres and bryospheres which have always been explored for their diverse fungal metacommunities and novel compounds throughout the world, the lichensphere (a term applied for Antarctic lichens, here also applied for lichens of alpine regions) has not been widely explored and can offer a chance to comprehensively explore the host selectivity patterns of their fungal associates and novel compounds. The fungal communities present in the lichensphere might offer an interesting model for studying the co-evolution of symbiosis under extreme conditions, and also the influence of the lichensphere on the biodiversity of other organisms will help in understanding the complexities of the biological web in extreme conditions (Bridge & Spooner 2012).

In comparison to the most extremophilic and extremotolerant organisms on Earth, i.e. bacteria and archaea, lichens, lichenicolous fungi, microcolonial fungi and hyphomycetes do not require a relatively constant level of water potential beyond 14.5 MPa [which is a prerequisite of bacteria and archaea with the exception of some cyanobacteria (Danin 1983, Buedel et al. 2009a, b)], and can survive easily under matric water stress conditions in a re-cultivable state by forming thick-walled spores (Conley et al. 2006), and hence are considered superior survival organisms with respect to bacteria and archaea. Because of this, black fungi, rock inhabiting fungi, and some lichens are today assumed to be the most stress resistant [against solar radiation, radioactivity, desiccation, oligotrophic conditions even allowing them to survive space and Martian conditions (Onofri et al. 2008)] eukaryotic organisms known on Earth (de Hoog & Grube 2008) and are treated as model organisms for Astrobiology (Onofri et al. 2004, de Vera 2012, https://en.wikipedia.org/wiki/List_of_microorganisms_tested_in_outer_space) and for gamma radiation experiments (Dadachova & Casadevall 2008).

Of the known and widely used model lichens for exobiological studies (*Aspicilia fruiticulosa*, *Buellia frigida*, *Circinaria gyrosa*, *Rhizocarpon geographicum*, *Rusavskia elegans* and *Xanthoria parietina*), *Rh. geographicum*, *Ru. elegans* and *X. parietina* also occur in India, and are infected by various lichenicolous fungi. As described earlier, *Ru. elegans* is infected by nine species of lichenicolous fungi, while genera *Aspicilia*, *Circinaria* and *Rhizocarpon* are infected by 4, 1 and 1 species, respectively, hence this study recommends that besides using the above mentioned model lichens, species of the lichen genera *Acarospora*, *Calogaya*, *Caloplaca*, *Carbonea*, *Lecanora*, *Lecidea*, *Lecidella*, *Lobothallia*, *Protoparmeliopsis*, *Rhizoplaca*, *Umbilicaria* and *Xanthoparmelia* along with their lichenicolous fungi may also be tested for astrobiological studies in the near future. Besides this these cold desert lichens should also be searched out for their endophytes and surface fungi along with some novel compounds.

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