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Review Article

An overview of Keratinophilic Fungi: Ecology, Biotechnological Potential and Molecular Methods of Identification

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Abstract

This paper provides an overview of occurrence and distribution of keratinophilic fungi across their expected habitats. The study focused on their presence in soil, air, animals, and bird feather samples from diverse environments, including gardens, caves, and cold and saline habitats. These environments provide different ecological conditions that may influence the diversity, abundance, and distribution of keratinophilic fungi. The morphological and cultural characters alone are often inadequate for species-level identification; the role of molecular identification is reviewed. The need for a comprehensive survey of keratinophilic fungi from unexplored substrates, coupled with systematic investigations of their biochemical potential, is emphasized. This review also discusses the ability of keratinophilic fungi to degrade keratinous material and the mechanisms underlying this process. Various metabolites and bioactive compounds produced by these fungi, including those with antibacterial, antifungal, antitumor, and related activities, are documented. It can be concluded that fungi other than dermatophytes may also act as opportunistic pathogens. Accurate identification, integrating morphological, physiological, and molecular data, supported by reliable reference sequences from type and authenticated material, underpins all of this work. The establishment and long-term maintenance of a dedicated culture collection of these fungi also are emphasized as essential for advancing future research.

Keywords: Culture collection, Database, Extreme climate, Keratin degradation, Keratinophilic fungi, Polyphasic taxonomy, Secondary metabolites.

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1. Introduction

Keratin is a natural fibrous protein that constitutes the outermost keratinised layer of the skin, hair, horn, and its appendages in humans and animals. It contains high levels of sulfur-containing amino acids, particularly cysteine and methionine. The abundance of cysteine residues and the resulting disulfide bonds contribute substantially to the structural stability and resistance of keratin to microbial degradation. Keratin can be colonised and degraded by specialised soil microorganisms, particularly keratinophilic fungi which play an important role in the decomposition and recycling of keratinous materials in the environment (Gopinath *et al.,* 2015). These fungi share several common morphological and physiological characteristics and are members of the primitive family Gymnoascaceae. Within this family, several species are capable of degrading keratin while it is still associated with human and animal tissues. They produce keratinase and other proteolytic enzymes, which help them utilise keratin as their sole source of carbon, nitrogen, and sulphur. These fungi are primarily found in habitats visited by humans, animals, and birds where keratinous material accumulates and thus play an important role in recycling the keratinous waste in nature. Keratinophilic fungi include nonpathogenic saprophytes and pathogenic dermatophytes that cause superficial infections of the hair, skin, nails, and feathers in humans and animals.

This article provides an overview of the different habitats from which the keratinophilic fungi have been reported, followed by a discussion of their pathogenicity, identification, keratin-degrading capabilities, and the production of bioactive metabolites.

2. Distribution of Keratinophilic Fungi

2.1 Soil in General

Vanbreuseghem (1952) was the first to report dermatophyte fungi from soil. Subsequently, various researchers reported the isolation of these fungi in soils from different countries, e.g., Argentina (Mangiaterra & Alonso, 1989; Sarmiento *et al.,* 2015), Antarctica (Caretta & Piontelli, 1977; Mercantini *et al.,* 1989a/b, 1993), Australia (Rees, 1967), Bahrain (Deshmukh *et al.,* 2008), Brazil (Giudice *et al.,* 2012), Canada (Bakerspigel *et al.,* 1974), China (Zhang *et al.,* 2021), Colombia (Rogers, 1971), Egypt (Bagy, 1989; Youssef *et al.,* 1992; Zaki *et al.,* 2005), England (Baxter, 1969), France (Agut *et al.,* 1995), Germany (Böhme & Ziegler, 1969), Hungary (Zeller, 1968), Iran (Nosratabadi *et al.,* 2017; Behzadi *et al.,* 2020), Italy (Caretta *et al.,* 1992; Papini *et al.,* 1998), Jamaica (Gugnani *et al.,* 2014), Japan (Uchiyama *et al.,* 1995), Jordan (Shaqra *et al.,* 2012), Kenya (Al-Doory, 1969), Kuwait (Al-Musallam, 1990), Malaysia (Soon, 1991), and Mexico (Romero-Olivares *et al.,* 2013). New Guinea (Filipello Marchisio *et al.,* 1991), New Zealand (Marples, 1965), Nigeria (Ogbonna & Pugh, 1987), Palestine (Ali-Shtayeh *et al.,* 2002), Poland (Bohacz *et al.,* 2022; Bohacz & Możejko, 2024), Spain (Calvo *et al.,* 1984; Cano *et al.,* 1987), East Africa (Al-Doory & Kalter, 1967), Sudan (Abdalla & Osman, 2018; Ulfig *et al.,* 1997), Saudi Arabia (Rizwana *et al.,* 2012), United States (Hamm *et al.,* 2020), West Bank of Jordan (Ali-Shtayeh, 1989; Shaqra *et al.,* 2012), West Indies (Gugnani *et al.,* 2012), and Tunisia (Anane, 2012; Anane *et al.,* 2015).

The occurrence of *Microsporum gypseum* was first reported by Dey & Kakoti (1955) from soils in the Dibrugarh district of Assam, India. Subsequently, these fungi were reported from various states of India, including the Andaman Islands (Dixit & Kushwaha, 1990; Awasthi *et al.,* 1991), Assam (Deshmukh *et al.,* 2017; Gahatraj *et al.,* 2024), Bihar (Verma *et al.,* 1982; Kumari *et al.,* 1998), Chhattisgarh (Deshmukh & Shukala, 2000; Pahare *et al.,* 2018), Delhi (Randhawa & Sandhu, 1965), Goa (Deshmukh & Agrawal, 1983b), Gujarat (Deshmukh & Verekar, 2014a), Himachal Pradesh

(Deshmukh & Verekar, 2006a), Jammu and Kashmir (Garg, 1966; Deshmukh, 2002a; Sehgal *et al.,* 2011; Sharma & Sumbali, 2018), Jharkhand (Kumar *et al.,* 2012, 2013), Karnataka (Deshmukh *et al.,* 2000; Vidyasagar *et al.,* 2005), Kerala (Deshmukh, 2002b), Ladakh (Deshmukh *et al.,* 2010; Kotwal & Sumbali, 2014), Madhya Pradesh (Deshmukh & Agrawal, 1983a; Pandey *et al.,* 1990), Maharashtra (Deshmukh, 1999; Deshmukh & Verekar, 2014b; Sharma & Shouche, 2020), Orissa (Sur & Ghosh, 1980; Ghosh & Bhatt, 2000), Rajasthan (Garg. 1966; Deshmukh *et al.,* 2018; Sharma *et al.,* 2023), Tamil Nadu (Anbu *et al.,* 2004; Ramesh & Hilda, 1998; Deshmukh & Verekar, 2011b), and Uttar Pradesh (Saxena *et al.,* 2004; Nigam, 1987; Deshmukh & Verekar, 2011a). Some keratinophilic fungi and related dermatophytes can cause superficial infections in humans and animals and are therefore of potential significance to human health and welfare (Weitzman & Summerbell, 1995; De Hoog & Guarro, 1995; Gupta *et al.,* 2026).

Various distribution patterns of these fungi have been reported from different environments (Kushwaha and Guarro, 2002). They are predominantly associated with localities frequently inhabited or visited by humans and animals. Researchers have generally collected soil samples for these fungi randomly from the surface and at depths of 3–10 cm. Common habitats investigated for the occurrence of these fungi include cattle farms, gardens, roadsides, forests, watercourse banks, grasslands, animal house floors, and poultry farms (Deshmukh and Agrawal, 1983). These studies have established that keratinophilic fungi are widely distributed in soils worldwide, with a particularly high prevalence in habitats frequently inhabited by humans and animals. Since these fungi have been recorded in soils from diverse habitats and geographical regions, they are considered of epidemiological significance. Some of the major habitats in which these fungi occur and from which they have been frequently isolated are described below.

2.2 Alkaline Soil

Usar soils are alkaline, with a prominent whitish layer of excess salt on the surface and low moisture content. Such soils experience high temperatures, drought, and intense solar radiation for most of the year and are from the Usar soils of the Lucknow, Bareilly, Azamgarh, Balia, and Pratapgarh districts of Uttar Pradesh. Usar soil is an alkaline soil and covers barren lands in India. These areas are frequently visited by humans and animals. Usar soil is a white, alkaline type with a pH of 7.5–11.0 and is commonly found in areas with poor/no drainage and less percolation. These soils have scant vegetation, consisting of patches of poor grass growth. Deshmukh & Verekar (2011a) reported *Chrysosporium indicum, C. lucknowense, C. pannicola, C. tropicum, Chr*. state of *Ctenomyces serratus, Gymnascella dankailensis, Gymnoascus reessii, Microsporum gypseum, Trichophyton mentagrophytes*, and *T. terrestre* from soil samples collected from Usar soils collected from above localities. The presence of keratinophilic fungi in the Usar soils of Uttar Pradesh, India, indicates that these fungi do occur at higher alkalinity. Similarly, *Chrysosporium tropicum, Microsporum audouinii, M. canis, Trichophyton mentagrophytes,* and *T. verrucosum* were isolated from soils collected in the vicinity of Jaipur, where the pH ranges from 6.5 to 8.5 (Jain & Sharma, 2011).

2.3 Public Park Soils

Chrysosporium indicum, *C. tropicum*, *Gymnascella hyalinospora*, *Gymnoascoideus petalosporus*, *Microsporum gypseum*, and *Uncinocarpus queenslandicus* were isolated from public gardens in the Vidarbha region of Maharashtra. (Deshmukh and Verekar, 2014c). *Aphanoascus fulvescens*, *Chrysosporium indicum*, *C. tropicum*, *C. zonatum*, *Microsporum gypseum*, and *T. mentagrophytes*, together with other fungi *Aspergillus niger*, *A. flavus*, *Alternaria alternata*, *Curvularia lunata,*

Fusarium oxysporum, *Rhizopus stolonifera*, and *Scopulariopsis brevicaulis* were isolated from public parks of different locations in Riyadh (Rizwana, 2012). The high prevalence of these fungi in the soils suggests that hair and other keratinized residues from humans and animals, as well as feathers shed by birds or deposited after death, serve as substrates for microbial decomposition. Keratinophilic fungi therefore play an important role in the natural degradation of keratinized residues in soil (Sharma & Rajak, 2003).

A total of 31 species, including *Aphanoasus fulvescens, Arthroderma tuberculatum, Chrysosporium carmichaelii, Chrysosporium georgii, C. indicum, C. keratinophilum, C. queensladicum*, *C. tropicum 1*, *C. xerophilum, C. zonatum, Ctenomyces serratus, Geomyces pannorum, Gymnoascus hyalinospora, M. gypseum, M. vanbreuseghmii, M. mannum, Malbranchea pulchella, Microsporum fulvum, Myceliophthora vellera, Nannizzia gypsea, T. varrucosum*, *T. mentagrophytes,* along with other fungi including *Aspergillus clavatus, A. flavus, A. niger, A. parasiticus, Absidia repens, Acremonium implicatum, Aspergillus candidus, Chaetomium globosum, Curvularia lunata, Gliocladium* sp., *Mucor pusillus,* and *Verticillium tenuipes*, were isolated from 25 parks of Agra, Kanpur, and Lucknow, Uttar Pradesh (Singh & Kushwaha, 2010). In another survey, Deshmukh & Verekar (2012) recorded *Arthrographis kalrae*, *Auxarthron conjugatum*, *C. indicum*, *C. queensl&icum*, *C. zonatum, Gymnascella dankaliensis*, *G. hyalinospora, M. gypseum, Myriodontium keratinophilum*, *Trichophyton mentagrophytes*, and *Uncinocarpus reesii* from five public parks of Mumbai (Deshmukh & Verekar, 2012). Keratinophilic fungi from soils of several parks in Shiraz included *Chrysosporium* sp., *Microsporum gypseum, M. fulvum,* and *Malbranchea* sp., *Phialophora reptans, Bipolaris spicifera, Bionectria ochroleuca, Ochroconis constricta, Scedosporium dehoogii, Cephalosporium curtipes, Nectria mauritiicola, Scedosporium apiospermum*, along with species of *Fusarium*, *Acremonium, Penicillium, Chaetomium, Scopulariopsis,* and *Tritirachium* sp. The majority of these fungi were recovered from the soils where pH ranged from 7 to 8. (Pakshir *et al.,* 2013).

The occurrence of these fungi can be attributed to the presence of common birds and rat burrows, which are also seen in the garden. Inadequate fencing and protection may also allow domestic animals, including buffaloes, cows, bullocks, horses, and pigs, to occasionally enter these parks. Public Parks are frequently visited by residents for morning and evening walks, and some visitors bring their pets along with them. Certain areas of the park are designated for children and include swings, slides, and small playgrounds, resulting in considerable human activity and frequent disturbance of the soil. The activity of humans and animals contributes keratinous materials, such as hair, feathers, and other animal-derived residues, to the soil. In addition, animal faeces, and other organic matter provide nutrient-rich substrates that may support the persistence and growth of keratinophilic fungi. Consequently, the presence of these fungi in public parks may have potential implications for human and animal health, particularly among individuals who frequently use these recreational spaces (Verekar & Deshmukh, 2017).

2.4 Grazed Pastures

The keratinophilic fungi recovered from these habitats included *Arthroderma multifidum*, *A. uncinatum*, *Clonostachys rosea*, *Engyodontium album*, *Chrysosporium* sp., *C. keratinophilum*, *Malbranchea* sp., *Microsporum* sp., *M. vellerum*, *Paecilomyces carneus*, *P. lilacinus*, *Pochonia chlamydosporia*, *Trichophyton ajelloi*, *T. terrestre*, and *Verticillium* sp. Among these, *Trichophyton ajelloi* and *P. lilacinus* were isolated from soils of long-term fold-grazed pastures in national parks of Slovakia and a non-fold-grazed pasture in Sierra Stolicke vrchy. Fold-grazed pastures showed a higher abundance of keratinophilic fungi than non-fold-grazed pastures. The comparatively lower

occurrence of keratinophilic fungi in the non-fold-grazed pasture may be associated with the soil's low pH, which may have restricted their growth and persistence (Javoreková *et al.,* 2012).

2.5 Potted Plant Soils

Potted plants are commonly maintained indoors in houses, including bathrooms, bedrooms, family kitchens, and living rooms, as well as in hotels and offices. Singh et al. (2009a, b) investigated the occurrence of keratinophilic fungi in soil associated with potted plants collected from 15 localities in Kanpur, India. The fungi isolated included *Aphanoascus terreus*, *A. keratinophilius*, *Arthroderma cuniculi*, Chrysosporium indicum, *C. keratinophilum*, *C. queenslandicum, C. pannicola, C. sulfureum, C. merdarium, C. zonatum, C. tropicum, Ctenomyces serratus, Malbranchea pulchella, Microsporum gypseum,* and *Trichophyton vanbreseghmii*. Other fungi recovered included *Acremonium* sp., *Acremonium implicatum, A. hennbertii, Botryotrichum piluliferum*, and *Verticillium tenuipes.* In another study, *Microsporum gypseum*, *M. cookie*, and *Chrysosporium* sp. were isolated from the soil associated with potted plants in hospitals in Sari, Iran (Hedayati *et al.,* 2004). The occurrence of these fungi in potted plants soil, particularly within hospital environments, is noteworthy because such plants may serve as potential environmental reservoirs and sources of fungal exposure, especially for susceptible individuals.

2.6 Arable Soils

Chrysosporium sp., *Chrysosporium tropicum*, *Ctenomyces serratus, Ctenomyces vellereus*, *Myceliophthora vellerea*, *Chrysosporium pannorum*, *Microsporum gypseum,* and *Trichophyton ajelloi* and other fungi, *Acremonium rutilum*, *Akanthomyces lecanii, Cladosporium cladosporioides, Clonostachys rosea*, *Cunninghamella elegans*, *Fusarium oxysporum, Fusarium solani, Fusarium* sp., *Gliocladium* sp., *Lecanicillium psalliotae, Metacordyceps chlamydosporia, Metarhizium marquandii, Oidiodendron griseum, Paecilomyces* sp., *Penicillium glabrum, Penicillium simplicissimum, Penicillium* sp., *Purpureocillium lilacinum, Rhizopus stolonifera, Sarocladium kiliense, Sarocladium strictum, Talaromyces purpureogenus, Trichoderma* sp., *Trichoderma virens,* and *Verticillium* sp. were isolated from the sampled collected from the Lublin province (south-eastern Poland) on two private farms in Sobieszyn and Żulice belonging to the University of Life Sciences in Lublin and were collected in early autumn. This study concludes that fungal communities colonizing and decomposing native keratin in different soils exhibit greater similarity when differences in soil properties are smaller, and vice versa: the larger the differences in soil properties, the lower the species similarity (Bohacz *et al.,* 2022).

2.7 Rice Fields

Microsporum gypseum, *M. canis*, *Trichophyton terreste*, *Trichophyton* sp., *T. ajelloi, Chrysosporium keratiophilum, Aspergillus fumigatus, Penicillium* sp., and Mycelia sterilia were isolated from soil samples collected from two rice fields in Madras, India. This study indicates that the incidence of keratinophilic fungi in the rice field soils is stable with a fairly high incidence in spite of the variation in the climatic conditions and disturbance by constant human interference during cultivation practices (Sundaram, 1987).

In another survey, *Chrysosporium carmichaeli, C. georgii, C. gourii, C. indicum, C. Keratinophilium, C. lobatum, C. merdarium, C. pannicola, C. queenslandicum, C. tropicum,* and *Chrysosporium* anamorph of *Arthroderma cuniculi, C.* anamorph of *Arthroderma curreyi C.* anamorph of *Pechtinotricum illiase, C.* anamorph of *Rollandina vriesii* were isolated from soil samples collected at

the different growth stages of paddy cropping viz. transplanting, tillering, milking and maturation, from different paddy fields of the Dayalbagh region of Agra (India), the region lies in the tropical environment, in an alluvial plain near the bank of the major Yamuna river system (Shrivastava *et al.,* 2008). It should be noted that the paddy fields in the studied areas are situated adjacent to the Yamuna River, with sandy, porous soil. During waterlogged conditions, all pores remain filled with water, which reduces the rate of oxygen diffusion, resulting in poor aeration and, in turn, affecting the distribution of keratinophilic fungi (Nigam & Kushwaha, 1993). Based on this study, it can be concluded that the occurrence of keratinophilic fungi is mainly influenced by biotic interference and the presence of keratinous substrates in the soil. The survival and occurrence of keratinophilic fungi are also influenced by other ecological factors.

3. Antarctic Environment

Antarctica is the most isolated and southernmost continent on Earth. Its persistently freezing temperatures and extensive ice cover create extreme environmental conditions (Convey *et al.,* 2024). The average annual temperature ranges from approximately −10 °C along the coast to −60 °C in the highest parts of the interior. In coastal regions, temperatures may exceed 10 °C during summer and fall below −40 °C in winter. In the elevated inland regions, summer temperatures may rise to approximately −30 °C, whereas winter temperatures can fall below −80 °C. The lowest temperature ever recorded at Earth's surface was −89.2 °C, recorded at Vostok Station in Antarctica. Low temperatures, extreme aridity, and the limited and sporadic availability of nutrients constitute major environmental constraints in such extreme habitats. Despite these conditions, fungi and bacteria can persist and grow through diverse physiological adaptations, including oligotrophic strategies that enable efficient utilization of scarce nutrient resources. (Parkinson *et al.,* 1989). Various workers have reported keratinophilic fungi, viz. *Geomyces pannorum*, *Malbranchea gypsea*, *Malbranchea* sp, *Microsporum gypseum*, *M. megellanicum*, *Trichophyton mentagrophytes* and *T. terrestre* along with other fungi from Antarctica (Caretta & Piontelli, 1977; Mario Comerio & Mac Cormack, 2004). Mercantini et al. (1993) reported *Aphanoascus fulvescens*, *C. carmichaelii*, *Geomyces pannorum* var *pannorum, G. pannorum* var *vinaceus, Malbranchea gypsea*, and T. *mentagrophytes* from the dust samples collected in various rooms on the Italian scientific base and from soil in proximity to the base of Antarctica. The presence and persistence of keratinophilic fungi in polar regions may reflect their adaptation to the extreme environmental conditions prevailing in these habitats.

4. Cold Deserts

Ladakh is a high-altitude cold desert union territory in northern India, spanning roughly 59,000 square kilometers between the Karakoram and Great Himalayan ranges. Known as the "Land of High Passes", its terrain is defined by towering mountains, deep river valleys, and high-elevation salt lakes, and constitutes the highest plateau, with an elevation of approximately 3,000 ft, and lies between latitudes 30°N–36°N and longitudes 76°E–79°E. The area experiences temperatures ranging from 3–35 °C in summer to −20 to −45 °C in winter.

During a survey of keratinophilic fungi in the cold desert region of Ladakh, soil samples were collected from various localities including Pangong Tso, Chang La, Durbuk, Khardung La, Tangste, Lukung, Magnetic Hill, Phey village, Leh, and Nimmu. Samples were obtained from a range of habitats, including pastures, glaciers, roadside, lake banks, uncultivated soil, cultivated soil, river banks, and roadside soil. The survey resulted in isolation of *Amauroascus kuehnii*, *Aphanoascus keratinophilus*, *A. terreus*, *Auxarthron alboluteum*, *A. conjugatum*, *Chrysosporium articulatum*, *C. minutisporosum*, *C. mephiticum*, *C. siglerae*, *Chrysosporium* sp., *C. tropicum*, *C. submersum*, *C.* state

of *Ctenomyces serratus*, and *Geomyces pannorum* (Deshmukh *et al.,* 2010). The recovery of these taxa from diverse habitats demonstrates the occurrence and ecological adaptability of keratinophilic fungi under the extreme environmental conditions prevailing in the Ladakh cold desert. In another survey, soil samples collected from Khardung (14,738 ft) yielded *Chrysosporium inops*, *C. merdarium*, *C. queenslandicum*, *Chrysosporium* anamorph of *Gymnoascus demonbreunii*, along with several other fungal taxa (Kotwal & Sumbali, 2014, 2022).

5. Glacier banks

Keratinophilic fungi were isolated from soil samples collected from glacier banks of Gulmarg, Khilanmarg, Sonamarg, and Tangmarg of the Kashmir Valley of Jammu and Kashmir. Gulmarg and Sonamarg in Sind or Aru in Lidder are all above 8000 feet, where the temperature hovers around 15°C and the mean temperature in July never exceeds 10°C at 10,000 to 12,000 feet. Even colder sites are encountered at higher altitudes. The fungal isolates were *Chrysosporium keratinophilum*, *C. tropicum*, *Chrysosporium* state of *Ctenomyces serratus*, *Geomyces pannorum*, *Malbranchea sp.*, *Microsporum gypseum* complex, *Microsporum nanum*, *Microsporum vanbreuseghemii*, *Trichophyton ajelloi*, *Trichophyton terrestre,* and *Uncinocarpus reesii* (Deshmukh, 2002a).

6. Wildlife Sanctuaries

In the wildlife sanctuary, the keratinous material, viz. hair and feathers, is added to the environment, and keratinophiles survive on these substrates. Ten species of seven genera were isolated, viz. *Aphanoascus durus, A. fulvuscence, Arthrographis kalrae, Auxarthron conjugatum, Chrysosporium indicum, C. tropicum, C. zonatum, Chrysosporium* state of *Ctenomyces serratus, Microsporum gypseum*, and *Trichophyton mentagrophytes*, were isolated from different sites in the vicinity of Gir Forest National Park and Wildlife Sanctuary, Gujarat, India (Deshmukh & Verekar, 2014a). Sharma et al. (2013) reported a new fungus, *Auxarthronopsis bandhavgarhensis*, reported from Bandhavgarh National Park, Madhya Pradesh, India.

The soil samples collected from Periyar Wildlife Sanctuary, Kerala, India, yielded *Arthroderma simii, Chrysosporium indicum, C. keratinophilum, C. pannicola, Gymnoascella hylinospora, Malbranchea aurantiaca, Microsporum gypseum* complex, and *Trichophyton terrestre*. Periyar Wildlife Sanctuary is known for rich fauna, including elephants, tigers, bison, and spotted deer. The occurrence of these fungi in The Periyar Wildlife Sanctuary can be due to the presence of animals and birds with less human interference (Deshmukh, 2002b).

In another survey, keratinophilic fungi, viz. *Chrysosporium queenslandicum, C. xerophilum* and *Malbranchea gypsea*, were isolated from the soils of Pin Valley National Park (Himachal Pradesh, India), famous for herds of Asiatic ibex (*Capra ibex*), Snow Leopard (*Uncia uncia*) and Himalayan blue sheep (*Pseudois nayaur*). These results reflect their adaptation to the cold climatic conditions prevailing in the Pin Valley National Park (Deshmukh & Verekar, 2006a). The occurrence of these fungi in the Wildlife Sanctuary is indicative that they may be a source of superficial infections to humans and animals, on the one hand. On the other hand, these fungi may be playing an important role in decomposing the keratinic matter added to the soil by human and animal activity (Deshmukh & Verekar, 2014a).

7. Cattle houses

Chrysosporium indicum, C. tropicum, Malbracehea aurantiaca, Microsporum gypseum, Trichophyton rubrum, and *T. mentagrophytes*, together with other saprophytic fungi, viz., *Aspergillus fumigatus, A.*

flavus, A. niger, A. Terreus, *Acremonium* sp., *Alternaria sp., Curvularia lunata, Fusarium oxysporium, Humicola insolens, Penicillium sp., Paecilomyces variotii,* and *Scytalidium* sp. were isolated from the soils collected from cattle houses located in and around the Bilaspur town of Chhattisgarh state in Central India. The presence of these fungi on cattle farms is attributed to the addition of keratinous material to the soil by animals. The presence of infective propagules of pathogenic geophilic dermatophytes originating from saprobic sources is transmitted, directly or indirectly, by the combined effects of the warm, humid environment of Chhattisgarh. The infection can spread from the pet animals to humans (Pahare *et al.,* 2018). In previous survey *Acremonium spp., Chrysosporium Anamorph of Arthroderma curreyi, C. keratinophilum, C. merdarium, C. pannicola, C. pseudomerdarium, C. queenslandicum, Chrysosporium* Anamorph of *Rollandina vriesii, C. sulfureum, C. xerophilum, Emmonsia parva, Geomyces pannorum, Keratinophyton terreum, Microsporum boullardii, M. fulvum Penicillium* spp., *Sporotrichum* spp., *Trichophyton mentagrophytes, T. mentagrophytes* var. *erinaceid*, *T. simii and T. terrestre* were isolated from soils collected from the cattle farm of semi-arid soils of Agra. The study also indicates that the maximum number of fungi is recorded in the winter season compared to the rainy and summer seasons (Saxena *et al.,* 2004).

8. Piggery Soils

During a survey of keratinophilic fungi in piggery soils from Ranchi, Jharkhand (India), several species were isolated, including *Aspergillus niger*, *Alternaria alternata*, *A. terreus*, *A. flavus*, *Chrysosporium* sp., *Curvularia lunata*, *Fusarium oxysporum*, *F. solani*, *Mucor pusillus, Penicillium chrysogenum*, *Penicillium* sp., *Rhizopus stolonifera, Trichoderma harzianum*, *T. reesei*, and *T. viride* (Kumar *et al.,* 2012). The majority of the isolated fungi were secondary colonisers on keratin baits. Pig farm soil is relatively less explored as a habitat for keratinophilic fungi. Therefore, further investigation of this environment is warranted to determine the occurrence and diversity of true keratinophilic species in pig farm soils.

9. Birds and their environment

Healthy bird feathers harbour a diverse range of fungi, including keratinophilic fungi, which may serve as potential reservoirs for disseminating potential pathogens of clinical importance, as they can travel great distances. These fungi can be transmitted from parents to offspring since they occur in the bird nests (Pugh 1972). Some fungal associations with birds are thought to be species-specific. Various workers reported these fungi from birds and their environment (Sarangi & Ghosh, 1991; Deshmukh, 2004b; Nardoni & Mancianti, 2021). The species most frequently isolated include *Aphanoascus reticulisporus*, *Auxarthron conjugatum*, *Chrysosporium indicum*, *C. pannicola*, *C. tropicum*, *Gymnoascoideus petalosporus*, *Malbranchea pulchella*, *Mal. fulva. Microsporum gypseum*, *M. fulvum*, *Microsporum* sp., *Myriodontium keratinophilum*, *Pseudoarachniotus* f*lavoluteus*, *P. roseus*, *Rollandina capitata*, *R. hyalinospora*, *Trichophyton mentagrophytes*. Mandeel et al. (2011) isolated different keratinophilic fungi, viz. *Arthroderma tuberculatum, Chrysosporium keratinophilum*, *C. tropicum, C. merdarium, C. luteum, C. parvum, C. pruinosum, C. asperatum, Scopulariopsis sp., Sepedonium* spp., and *Trichophyton terrestris* from 10 migratory birds, viz. Budgerigar, Ringneck, Lovebird, Pigeon, Alexandrian parrot, Amazon parrot, African grey, Quail, Duck, and Chicken, from different countries arriving in Bahrain. Deshmukh & Verekar (2011b) reported the occurrence of *Auxarthron conjugatum*, *Chrysosporium fluviale*, *C. indicum*, *C. tropicum*, *Chrysosporium* state of *Ctenomyces serratus*, *Gymnoascus petalosporus,* and *Microsporum gypseum* complex from various sites in the vicinity of Vedanthangal Water Bird Sanctuary. While surveying

keratinophilic fungi from feathers, remains of animal food, pellets, and excrement of 9 nests of wetland Marsh harrier (*Circus aeruginosus*), Grey heron (*Ardea cinerea*), Mute swan (*Cygnus olor*), Coot (*Fulica atra*), Great crested grebe (*Podiceps cristatus*), Black-headed gull (*Larus ridibundus*), Common gull (*Larus canus*), Common tern (*Sterna Hirundo*) and Black tern (*Chlidonias niger*) from southeast Poland (the Lublin region) *Aphanoascus fulvescens*, *Arthroderma cifferii*, *A. cuniculi*, *A. curreyi*, *A. insingulare*, *A. quadrifidum*, *A. uncinatum*, *Chrysosporium keratinophilum*, *Ch. pannicola*, *Ch. quenslandicum*, *Ch. tropicum*, *Myceliophthora* an. *Arthroderma tuberculatum*, *Chrysosporium* an. *A. curreyi*, *Chrysosporium* an. *Renispora flavissima*, *Ctenomyces serratus*, *Microsporum cookie*, *M. fulvum*, *M. gypseum*, *Myceliophthora* an. *Ct. serratus*, *Nannizzia gypsea*, *Trichophyton ajelloi*, and *T. terrestris* were isolated (Kornillowicz-Kowalska *et al.,* 2011).

In another survey, *Aphanoascus fulvescens, Chrysosporium keratinophilum, C. luteum*, *C. pannorum, C. pruinosum, C. tropicum, Microsporum gypseum, Myriodontium* sp., *Scopulariopsis brevicaulis*, *Sepedonium sp., Trichophyton terrestre* were recovered from terrestrial birds (*Alectoris rufa, Columba palumbus, Corvus coronae, Erithacus rubecula, Gallus gallus domesticus, Phasianus colchicus, Pica pica, Turdus merula*) and from four waterfowl (*Anas clypeata, Anas crecca, Anas platyrhynchos, Anas querquedula, Gallinago gallinago*), from the province of Pisa, Tuscany, Italy (Nardoni & Mancianti, 2021). These studies indicate that migratory birds can serve as vectors for the dispersal of a variety of keratinophilic fungi from one geographical location to another.

10. Poultry Farms

A poultry farm is an important source of keratinophilic and toxigenic fungi and provides a favourable environment for their growth. A poultry environment encompasses birds, cages, transporting vehicles, litter, feed residues, and waste-disposal or dumping areas, all of which may contribute to the accumulation and dissemination of fungal propagules. Several researchers have reported the occurrence of keratinophilic fungi in soils from poultry farms (Kaul & Sumbali, 1997; Deshmukh & Shukla, 2000; Anbu *et al.,* 2004; Lokeshwari *et al.,* 2026). Such soils are typically rich in organic matter and are generally neutral to weakly alkaline in nature, providing favourable conditions for the growth and proliferation of these fungi. Kaul & Sumbali (1998–99) reported high concentrations of organic carbon, nitrogen, phosphorus, potassium, magnesium, calcium, and iron in the soil of this habitat. During survey of keratinophilic fungi in poultry farm soil, in the Bilaspur district of Chhattisgarh (India) several species were isolated, including *C. indicum*, *C. lucknowense*, *C. pannicola*, *C. queenslandicum*, *Chrysosporium* I, *Chrysosporium* II, *C. tropicum*, *C. zonatum*, *Chrysosporium* state of *Arthroderma tuberculatum*, *Geomyces pannorum*, *Malbranchea pulchella*, *Microsporum gallinae*, *Trichophyton mentagrophytes* and *T. simii* (Deshmukh & Shukala, 2000). In another survey, Kaul & Sumbali (2000a, b) isolated *C. indicum, C. keratinophilum*, *C. queenslandicum*, *C. tropicum*, and *Malbranchea chrysosporoidea* from the feathers of chickens (*Gallus domesticus*). They also reported C. *keratinophilum, C. queenslandicum*, *C. tropicum*, *C. pannorum,* and *Malbranchea flava* from poultry-farm soil in Jammu. The high frequency of these fungi on bird feathers may be attributed to the fact that birds spend considerable time on the ground, thereby facilitating the deposition and accumulation of feathers and other keratinous materials in the soil. The very high frequency of these fungi in poultry-farm soil may be associated with the substantial accumulation of poultry droppings and other keratinous remains, such as feathers and claws, as reported by Kaul & Sumbali (2000a). These fungi have also been recovered from poultry farms in Namakkal and from poultry-feather dumping grounds in Chennai. The isolated fungi included *Chrysosporium keratinophilum*, the *Chrysosporium* state of *Arthroderma tuberculatum*, *Geomyces pannorum*, *Microsporum gypseum*, and *Trichophyton mentagrophytes* (Anbu *et al.,* 2004).

11. Emu Farms

Deshmukh et al. (2021) reported *Aphanoascus terreus*, *A. verrucosus*, *Arthroderma tuberculatum, Ctenomyces serratus*, *Gymnascella dankaliensis*, *Gymnoascoideus petalosporus, Microsporum gypseum,* and *Uncinocarpus orissi* from feathers collected from emus (*Dromaius novaehollandiae*) from 7 emu farms in the Raigad and Thane districts of Maharashtra (India). The results indicate that the emu is an important source of keratinophilic fungi and may play a significant role in the decomposition and recycling of keratinous materials deposited in the soil. Some of these fungi may also act as causative agents of disease in humans and animals.

12. Coastal Habitats

The coastal areas are an environment for human activity, migratory birds, and burrowing animals. These activities contribute keratinous material to coastal soils, thereby supporting the growth of these fungi. Hence, this habitat is a rich source of keratinophilic fungi. Guerra-Mateo et al. (2025) reported *Onygenales* from marine sediments and recovered *Aphanoascus crassitunicatus, A. fulvescens, Byssoonygena ceratinophila, Deilomyces minimus, Gymnascella (Gl.) dankaliensis, Gl. nodulose, Gl. udagawae, Gymnoascoideus alboluteus, Gymnoascus exasperates, G. reessii, G. uncinatus, Malbranchea irregularis, M. longispora, M. multiseptata, M. ostraviensis, M. sinuata, M. sedimenticola, M. seminuda, M. parafilamentosa, M. sexualis, M. zuffiana, Myriodontium keratinophilum, Narasimhella hyalinospora, N. poonensis, Sporendonema casei* were isolated from marine sediments collected from the coast of Catalonia (Spain) and these fungi are keratinophilic in nature. It was concluded that marine sediments of the western Mediterranean Sea serve as reservoirs of rare and novel Onygenalean fungi. (Guerra-Mateo *et al.,* 2025). In another survey, *Chrysosporium* species, *Microsporum gypseum*, and *Trichophyton ajelloi* were reported from 11 beaches of the East Sea in Korea (Lee *et al.,* 2011). Katiyar & Kushwaha (1997) reported *C. keratinophilum*, *C. tropicum*, and *Chrysosporium* sp. from sand of the Mediterranean Sea, which is characterized by low organic matter. Deshmukh & Agrawal (1983b) reported *Chrysosporium indicum*, *C. tropicum*, and *Chrysosporium* sp. I (UAMH 4438) *Chrysosporium* sp. II (UAMH 4441), *Chrysosporium* state of. *Ctenomyces serratus*, *Microsporum gypseum* complex, and *Trichophyton mentragrophytes* were reported from Anjuna, Calangute, Colva, Miramar, and Vagator beaches of Goa. The occurrence of keratinophilic fungi in a saline environment may be due to the availability of fungi to tolerate elevated salinity. A preference for keratin material in such habitats. Several studies have examined the influence of salinity on fungal growth and survival and have demonstrated the widespread occurrence of keratinophilic fungi in saline environments (Kishimoto & Baker, 1969; Larrondo & Calvo, 1989; Ulfig *et al.,* 1987; Deshmukh, 1999). Pugh & Mathison (1962) reported the highest abundance of *Chrysosporium* in coastal soils, which they attributed to enrichment by bird droppings and fish debris that favoured the growth of aleurosporic fungi. The relatively high abundance of these fungi in coastal soils may also be associated with human activities and the presence of marine birds and burrowing animals.

13. Salt Pan Soils

Salt pans are very common in coastal habitats and are used for large-scale salt production by the salt industry. Sea water flows into the salt pans during the high tides and brings keratinic material, which includes hairs of both humans and animals, feathers of migratory birds, and wool fragments from blankets. The keratinophilic fungi & related dermatophytes degrade the keratin in the salt pans during the 3–4 months of salt formation. Deshmukh (2004a) recovered *Chrysosporium indicum*, *Microsporum gypseum* complex, *C. tropicum*, *Chrysosporium* state of *Ctenomyces serratus*, *C.*

fluviale, *Malbranchea aurantiaca*, *Malbranchea* sp., *Trichophyton mentagrophytes*, *T. terrestre*, and *Uncinocarpus reesii* while studying keratinophilic fungi from soils around salt pans in Mumbai. The findings of this study suggest that the soil of salt pans and surrounding environments constitutes a unique ecological niche that favours the occurrence and distribution of keratinophilic fungi and related dermatophytes.

14. Meteoritic Crater

The soil samples collected from the Lonar meteorite crater (Maharashtra state, India) yielded *Aphanoascus durus*, *A. punsolae*, *Auxarthron kuehnii*, *C. indicum*, *C. tropicum*, *Chrysosporium* sp., and *Chrysosporium* state of *Ctenomyces serratus*. The water of the crater is highly alkaline and contains various salts and minerals of sodium, chloride, carbonates, fluorides, and bicarbonates. Lonar Lake is surrounded by a dense green forest, home to numerous bird and animal species. The presence of keratinophilic fungi in such an unusual environment indicates that birds and animals introduce keratin-containing material, such as feathers & hairs into the crater, thereby supporting their growth. (Deshmukh & Verekar, 2006b).

15. Sambhar Lake

Deshmukh et al. (2018) reported that *Auxarthron conjugatum, Chrysosporium indicum, C. tropicum*, *Ctenomyces serratus*, *Gymnascella dankaliensis*, *Gymnoascoideus petalosporus, Keratinophyton durus*, and *Uncinocarpus reesii* were recovered from the soil samples collected from various sites in the vicinity of Sambhar Lake, Rajasthan, India. The other fungi recovered from these soil samples, were *Acremonium* sp., *Alternaria daucifolii, Aspergillus aculeatus, Aspergillus versicolor, Aureobasidium pullulans, Bipolaris rostrate, Bipolaris stenospila, Chaetomium globosum, Cladosporium cladosporioides, Cochliobolus verruculosus, Curvularia spicifera, Exophiala spinifera, Fusarium nematophilum, Fusarium oxysporum, Fusarium solani, Humicola fuscoatra, Myrothecium verrucaria, Nigrospora oryzae, Penicillium verruculosum, Sarocladium implicatum, Sarocladium strictum, Syncephalastrum racemosum, Trichoderma virens, Thielavia subthermophila, Torulaherbarum,* and *Yunnania penicillata.* From this study, it can be concluded that the keratinophilic flora of Sambhar Lake differs from that of other regions of India, possibly owing to the distinctive climatic and environmental conditions prevailing in the area, together with the influence of human activities.

16. Hospitals Dust

Chrysosporum keratinophilum, C. tropicum, C. anum, C. lobatum, Ctenomyces serratus, Malbranchea flava, M. gypsea, Microsporum gypseum, M. Nanum, Trichophyton mentagrophytes, T. Terrestre, T. ajelloi, and other species, including *A. flavus, A. flumigatus, A. terreus, A. versicolor, A. candidus, Alternaria alternata, Absidia spinosa, Candida albicans, Candida parapsilosis, Cephalosporium curtipes, Chaetomium subterraneum, Cladosporium cladosporioides, C. herbarum, Fusarium moniliforme sensu lato, F. oxysporum, F. solani, Geotrichum candidum, Gliocladium catenulatum, Mucor racemosus, Paecilomyces fusisporus, Penicillium funiculosum, P. chrysogenum, Rhizopus stolonifera, Trichoderma viride, T. aggregate, Verticillium luteoalbum, Acremonium kiliense, Curvularia lunata, Trichothecium roseum,* were isolated from corridor dust samples were collected from hospitals of Gulbarga city, Karnataka, India. This study reveals that hospital corridor dust is a good source of keratinophilic fungi (Vidyasagar *et al.,* 2005).

17. Veterinary Clinic

Chrysosporium keratinophilum, C. panorrum, C. tropicum, Chrysosporium sp., Chrysosporium state of *Arthroderma tuberculatum, Microsporum canis, M. gypseum, Trichophyton ajelloi, T. mentagrophytes,* and *T. terrestre* were isolated from 400 samples collected from the floors of 50 private veterinary clinics of in the province of Tuscany, Italy (Mancianti & Papini, 1996). Keratinophilic fungi in veterinary clinics may be due to keratinous material shed by infected pets, such as skin, hair & nails. Mites on animals can be another source of transmission of these fungi in veterinary clinics. Such veterinary clinics may serve as potential reservoirs of keratinophilic fungi, thereby posing a possible risk of exposure and infection to humans and animals visiting these facilities.

18. Animals

Aphanoascus fulvuscens, Arthroderma tuberculatum, Chrysosporium keratinophilum, C. tropicum, Microsporum gypseum, M. nanum, Trichophyton mentagrophytes, T. verrucosum, were isolated from the hair of cows, *Chrysosporium evolceanui, C. keratinophilum, C. pannorum, C. tropicum, Trichophyton verrucosum*, were recovered from the hair of donkeys, *Chrysosporium keratinophilum, C. tropicum, Microsporum audouinii, M. nanum, Trichophyton equinum, T. mentagrophytes, T. verrucosum, from Rabbits***,** *Cbrysosporium keratinophilum, C. pannorum, Microsporum canis, M. gypseum, M. nanum, Trichophyton ajelloi, T. mentagrophytes*, from Cats, and *Chrysosporium asperatum, C. keratinophilum, C. tropicum, Trichophyton mentagrophytes*, from Dogs of the West Bank of Jordan (Ali-Shtayeh *et al.,* 1988a). Cats, cows, and rabbits seem to be the most important of these animals in the transmission and persistence of *Trichophyton mentagrophytes*, whereas cows, donkeys, and rabbits are important in the transmission and persistence of *T. verrucosum*; these two species were the most common dermatophytes in all animals examined (Ali-Shtayeh *et al.,* 1988b). *Aphanoascus fulvuscens*, *Arthroderma cunieuli*, *A. curreyi*, *A. tubereulatum*, *Chrysosporium asperatum*, *C. evolceanui, C. indicum*, *C. pannorum*, *C. tropicum, Ctenomyces serratus*, *Microsporum canis, M. gypseum, M. nanum, Trichophyton concentrieurn, T. equinum, T. georgiae, T. longifusus, T. mentagrophytes,* and *T. verrucosum* were isolated from sheep of of the West Bank of Jordan (Ali-Shtayeh, 1989). In another survey, keratinophilic fungi with special reference to dermatophytes were recovered from the coat of dogs and cats living in the cities of Mexico and Nezahualcoyotl in the Metropolitan area of Mexico. *Chrysosporium* spp., *Microsporum gypseum, M. canis, T. mentagrophytes,* and *T. terrestre* were isolated from the coat of cats, and *Chrysosporium* spp., *Microsporum gypseum, M. canis, T. ajelloi, T. mentagrophytes, and T. terrestre* were isolated from the coat of dogs (Guzman-Chavez *et al.,* 2000). It was found that an animal in contact with other animals had a higher probability of getting the same fungus, including dermatophytes. Due to the particular behaviors of cats, such as taking soil baths and grooming, they are more prone than dogs to harbor keratinophilic fungi in their haircoats. The mite *Tyrophagus putrescentiae* was found associated with *M. canis* and may be responsible for transmitting fungi amongst animals (Caretta *et al.,* 1989). The occurrence of these fungi on these animals can pose a risk of dermatophytic infections to humans and animals. The majority of the keratinophilic fungi found on the hair of domestic animals are either obviously pathogenic or have been recorded from various animal and human lesions; thus, these animals represent an important reservoir for many medically important fungi.

19. Pathogenic Fungi

Species of *Chrysosporium* have been reported from immunocompromised patients, causing various types of mycoses (Anstead *et al.,* 2012). Sigler et al. (1998) reported *Chrysosporium zonatum* as the

causative agent of bronchial lavage in a female in Chiba and from a male in Kyushu. From a 15-year-old male, *C. zonatum* was also isolated from chronic granulomatous disease (CGD) (Roilides *et al.,* 1999). *Chrysosporium zonatum* has been reported to cause pneumothorax in a 56-year-old male resident of southeast New Mexico (Siddiqui & Zimmerman, 2016). *Chrysosporium* spp. viz., *C. kreiselii* and *C. zonatum* were isolated from lesions on the skin of horses in Kazakhstan. The *C. kreiselii* strain was isolated in association with the opportunistic pathogen strain *A. alternata* No. 15.23.7.1H, while the *C. zonatum* strain was isolated in monoculture (Kukhar *et al.,* 2025).

Myriodontium keratinophilum, the teleomorph of *Neoarachnotheca keratinophila,* was found to cause sinusitis (Maran *et al.,* 1985). There was a report on the isolation of Gymnascella dankaliensis from superficial human infections (De Hoog & Guarro, 1995). Other species of *Gymnascella*, i.e., *G. hyalinospora, were* reported from invasive pulmonary infection in a patient with acute myelogenous leukaemia (Iwen *et al.,* 2000). Lysková (2007) reported *Chrysosporium queenslandicum*, *C. sulfureum*, *C. tropicum*, *Malbranchea pulchella*, and *Myriodontium keratinophilum* from infections of the skin and nails of patients in the Moravian-Silesian Region of the Czech Republic. *Geomyces pannorum* var. *pannorum* was isolated from superficial infection of the skin of a healthy man (Gianni *et al.,* 2003). Zelenková (2006) reported *Chrysosporium pannorum* (Link) Hughes from the fingernails of male and female patients from the Slovak Republic.

Chrysosporium anamorph of *Nannizziopsis vriesii* (CANV) was found to cause Nannizziomycosis in 1991 in day geckos (Phelsuma sp.) and in 1997 in three different species of chameleons (*Calumma parsonii*, *Chamaeleo lateralis*, and *C. jacksoni*) (Paré *et al.,* 1997). Later on, it was found to cause Nannizziomycosis in bearded dragons (*Pogona vitticeps*), and the disease was named YFD (Bowman *et al.,* 2007; Abarca *et al.,* 2009), salt-water crocodiles (Thomas *et al.,* 2002), bearded dragons (Bowman *et al.,* 2007; Hedley *et al.,* 2010), green iguanas (Iguana iguana) (Han *et al.,* 2010), and girdled lizards (Hellebuyck *et al.,* 2010). Nannizziomycosis has also been reported in several lizard and crocodilian species (Mitchell & Walden, 2013). *Nannizziopsis* spp. Infections have been reported in Africa, Asia, Europe, North America, Australia, and New Zealand (Stchigel *et al.,* 2013; Paré & Sigler, 2016; Sigler *et al.,* 2013; Peterson *et al.,* 2020). *Nannizziopsis guarroi* is the most frequently reported in bearded dragons, but infection with *N. chlamydospora*, *N. draconii*, and *N. barbatae* has also been reported as a cause of nannizziomycosis in bearded dragons (Johnson *et al.,* 2011; Sigler *et al.,* 2013; Gentry *et al.,* 2021). Several cases of cutaneous and systemic infection attributed to *N. dermatidis* have been reported in chameleons and geckos (Sigler *et al.,* 2013). *Nannizziopsis crocodili* was isolated in saltwater crocodile (*Crocodylus porosus*) farms; forty-eight hatchlings died (Wellehan & Divers, 2019). *N. crocodili* was identified from juvenile Johnston's crocodile (*C. johnstoni*) during an outbreak of severe multifocal dermatitis (Hill *et al.,* 2019). *N. barbatae* was identified from four wild lizard species in Australia (Peterson *et al.,* 2020). *Chrysosporium* anamorph of *Nannizziopsis vriesii* was found to cause fatal mycotic dermatitis in brown tree snakes (*Boiga irregularis*) (Nichols *et al.,* 1999) and free-ranging pygmy rattlesnakes (*Sistrurus catenatus*) in Florida, United States (Cheatwood *et al.,* 2003).

In 2009, Mycotic Granuloma of a Black Rat Snake (*Pantherophis obsoletus*) was caused by *Ophidiomyces ophidiicola*. *Ophidiomyces ophidiicola* was first described in 2009 as *Chrysosporium ophidiicola* in a black rat snake (*Pantherophis obsoletus*) presenting severe subcutaneous facial swelling, causing displacement of cranial anatomical features (Rajeev *et al.,* 2009), and in pygmy rattlesnakes (*Sistrurus catenatus*) in Florida, United States (Cheatwood *et al.,* 2003). Ophidiomycosis is thought to affect only snakes, with cases reported worldwide in colubrid snakes (e.g., *Pantherophis*

sp., *Nerodia* sp., *Natrix* sp., *Lampropeltis* sp., *Thamnophis* sp.), viperids (e.g., *Agkistrodon* sp., *Crotalus* sp., *Sistrurus* sp.), Acrochordidae, and boids, elapids, and pythonids (Meier *et al.,* 2018; Wellehan & Divers, 2019).

There are reports of infection of other *Chrysosporium* species in multiple reptile species. *Chrysosporium guarroi* was isolated from pet green iguanas (*Iguana iguana*) from different areas of Spain (Abarca *et al.,* 2008, 2010) and Turkey (Kahraman *et al.,* 2015). *Chrysosporium queenslandicum* was isolated from a garter snake (Vissiennon *et al.,* 1999). In the review by Paré & Jacobson (2007), it is reported that *Chrysosporium keratinophilum, C. tropicum, and Chrysosporium* spp. can be causal agents of cutaneous and systemic mycoses in reptile species. Saidi et al. (1994) reported *Chrysosporium tropicum* from the comb lesion in two breeds of chicken in India. These reports indicate that the species of *Chrysosporium* may be regarded as opportunistic pathogens.

20. Identification of Keratinophilic Fungi

Precise identification of keratinophilic fungi is important not only for understanding their taxonomic diversity and ecological distribution but also for evaluating their potential pathogenicity and keratin-degrading abilities (Deshmukh & Verekar, 2014c; Kushwaha & Guarro, 2002; Zhang *et al.,* 2021). Conventionally, these fungi have been identified using conventional cultural and morphological characteristics, including colony colour, texture, pigmentation, growth patterns, conidial morphology, microscopic structures, and physiological characteristics (Deshmukh & Verekar, 2014c; Dehghan *et al.,* 2019; Ogórek *et al.,* 2019; Kukhar *et al.,* 2025). Although these characters provide valuable initial information, morphological identification alone may not always be adequate for correct species-level identification (Dehghan *et al.,* 2019; Brandt *et al.,* 2005).

Molecular identification has become a crucial component of fungal taxonomy due to several limitations associated with conventional morphological identification (Zhang *et al.,* 2019; Dukik *et al.,* 2019). Many keratinophilic fungi exhibit similar cultural and microscopic characteristics; closely related species may share similar morphological characters, making their identification difficult, particularly when diagnostic structures are poorly developed or absent (Labuda *et al.,* 2024; Zhang *et al.,* 2019; Kukhar *et al.,* 2025). Some fungi fail to produce characteristic reproductive structures under laboratory conditions, and others exhibit atypical morphology depending on incubation temperature, culture medium, environmental conditions, and culture age (Kukhar *et al.,* 2025; Ogórek *et al.,* 2019; Brasch *et al.,* 2026). Molecular methods help in the identification even when typical morphological features are unavailable (Brasch *et al.,* 2026; Kaur *et al.,* 2026; Brandt *et al.,* 2005). As confirmed in a study, morphological identification of *Microsporum gypseum* was later revised through ITS sequencing to *Nannizzia fulva*, and *Chrysosporium* sp. isolates were resolved into *Chrysosporium shanxiense* and *Chrysosporium keratinophilum* (Dehghan *et al.,* 2019). Likewise, isolates from equine skin lesions, which were initially diagnosed morphologically as *Trichophyton mentagrophytes*, were later found to be *Chrysosporium zonatum* and *Chrysosporium kreiselii*, which were confirmed through ribosomal gene sequencing (Kukhar *et al.,* 2025). Similarly, another study reported that a *Chrysosporium* species can cross-react with a commercial *Histoplasma capsulatum* probe, which could only be correctly identified using sequence analysis (Brandt *et al.,* 2005).

Morphological characteristics may be inadequate to discriminate members of species complexes or species that are closely related; the DNA sequence analysis provides additional discriminatory features that enable more accurate species-level identification (Shams-Ghahfarokhi & Razzaghi-Abyaneh, 2021; Hamied, 2022; Garces *et al.,* 2016). Molecular approaches can reveal genetically

distinct species that are morphologically identical, indistinguishable, or very similar (Labuda *et al.,* 2024; Zhang *et al.,* 2019; Dukik *et al.,* 2019); this is very important in keratinophilic fungi, where many taxa have been previously clustered under obvious morphological species concepts (Kidd *et al.,* 2023; Kandemir *et al.,* 2021). The phylogenetic revisions of *Arthrodermataceae* and *Onygenales* using multilocus phylogenetic analyses have resolved earlier conflated genera such as *Microsporum*, *Trichophyton*, *Nannizzia*, *Guarromyces*, *Arthroderma*, *Paraphyton*, *Ctenomyces*, *Lophophyton*, and *Epidermophyton* (Ogórek *et al.,* 2019; Kandemir *et al.,* 2021; Dukik *et al.,* 2019; Zhang *et al.,* 2019). Precise molecular identification improves the characterization of keratinophilic fungal communities in different ecological habitats and keratin-containing substrates (Srivastava, 2022; Deshmukh & Verekar, 2014c; Zhang *et al.,* 2020, 2021), and offers a reliable foundation for studying their diversity, distribution, and ecological significance (Kandemir *et al.,* 2021; Kushwaha & Guarro, 2002; Deshmukh & Verekar, 2014c).

An important aspect of molecular identification is the choice of an appropriate genetic marker. Even though the Internal Transcribed Spacer (ITS) region is considered the universal DNA barcode for fungi, it does not offer enough discriminatory power for all fungal genera or species (Shams-Ghahfarokhi & Razzaghi-Abyaneh, 2021; Ferreira *et al.,* 2019). Different fungal genera have different rates of genetic divergence, evolutionary histories, and levels of sequence variation (Kidd *et al.,* 2023; Kandemir *et al.,* 2021). Subsequently, a specific gene region that efficiently differentiates species in one genus may fail to differentiate closely related species in another genus. The choice of molecular markers thus depends on the taxonomic group under study and the discriminatory ability of the selected gene region (Zhang *et al.,* 2019, 2020; Kandemir *et al.,* 2021).

Different genes evolve at different rates: some regions gather mutations quickly and are useful for distinguishing closely related species, while others are more conserved and are suitable for recognising organisms at higher taxonomic levels (M.-Y. Zhang *et al.,* 2026; Shams-Ghahfarokhi & Razzaghi-Abyaneh, 2021). The ITS region is extremely useful for initial fungal identification because it contains variable sequences flanked by relatively conserved regions, which ease PCR amplification (Ferreira *et al.,* 2019). Though closely related species may share highly similar or identical ITS sequences, in which case additional protein-coding genes are required to resolve species-level relationships (Z. Zhang *et al.,* 2019, 2021; Kandemir *et al.,* 2021; Shams-Ghahfarokhi & Razzaghi-Abyaneh, 2021).

Different genera possess different patterns of variation at the genetic level (Table 1). Multilocus phylogenetic studies incorporating LSU, ITS, *β-tubulin*, *translation elongation factor 3 (TEF3), ribosomal protein 60S L10 (RP60S), RPB1*, and *RPB2* have been used to re-examine the ecology and phylogeny of the order Onygenales (Kandemir *et al.,* 2021), while studies on *Ctenomyces* used *RPB2*, ITS, and *EF1A* to delimit species (Z. Zhang *et al.,* 2019). Combined LSU and ITS phylogenies have also been used to resolve novel *Keratinophyton* species (Labuda *et al.,* 2024), and multilocus datasets including *EF1A*, *RPB2*, *MCM7*, LSU, and ITS have been applied to characterize the family *Thelebolaceae* and establish the new generas *Solomyces, Scedosporium* and *Pseudogymnoascus* (Z. Zhang *et al.,* 2020). Using additional gene regions helps in providing independent phylogenetic information, and combining multiple loci helps in improving the resolution of phylogenetic trees, mostly when closely related species cannot be distinguished using a single marker (Kandemir *et al.,* 2021; Z. Zhang *et al.,* 2020, 2021; M.-Y. Zhang *et al.,* 2026).

The choice of a gene region is also influenced by the availability of reliable reference sequences from type and authenticated specimens in the databases (Brandt *et al.,* 2005; Kidd *et al.,* 2023). A marker can have good theoretical discriminatory power but merely limited practical utility if suitable reference sequences are not available (Brandt *et al.,* 2005). These differences signify why fungal identification should not depend on a single molecular marker for all genera (Shams-Ghahfarokhi & Razzaghi-Abyaneh, 2021; Kidd *et al.,* 2023). Instead, a group-specific or a genus-specific molecular identification strategy should be adopted (Kaur *et al.,* 2026; Brasch *et al.,* 2026). A consolidative approach combining cultural, morphological, molecular, and phylogenetic evidence delivers a more robust framework for the identification and characterization of keratinophilic fungi (Kushwaha & Guarro, 2002; Dukik *et al.,* 2019; Ogórek *et al.,* 2019).

Table 1. Recommended genera and specific molecular markers for the identification of keratinophilic fungi.

Genera	Molecular Markers	References
Achaetomium	ITS, LSU, *rpb2*, *tub2*, *tef-1α*, *CaM*	Sastoque *et al.,* 2025
Acremonium	ITS, LSU	Liu *et al.,* 2025
Ajellomyces	ITS, LSU	Rodríguez-Andrade *et al.,* 2021
Akanthomyces	ITS, SSU, *tef-1α*, *rpb1*, *rpb2*	Shahbaz *et al.,* 2026
Alternaria	ITS, *GAPDH*, *rpb2*, *tef-1α*, *Alt a 1*, *EndoPG*, OPA10-2	He *et al.,* 2026
Aphanoascus	ITS, LSU	Zhang *et al.,* 2024
Arachnomyces	ITS, LSU	Rodríguez-Andrade *et al.,* 2021
Arthroderma	ITS, *β-tub*, *rpb2*	Baert *et al.,* 2026
Aspergillus	*cmdA*, *rpb2*, *tub2*	Tan *et al.,* 2026
Aureobasidium	ITS, LSU, *rpb2*, *tef-1α*, *tub*	Senwanna *et al.,* 2026
Auxarthron	LSU	Zhang 2017
Auxarthronopsis	ITS	Zhang *et al.,* 2021
Beauveria	*tef-1α*, *rpb1*, *rpb2*, Bloc	Xu *et al.,* 2026
Bionectria	ITS, *β-tub*	Luo *et al.,* 2010
Bipolaris	ITS, *GAPDH*, *tef-1α*	Ahmadpour *et al.,* 2025
Bisifusarium	ITS, *rpb2*, *tef-1α*, *tub2*	Crous *et al.,* 2026
Blastomyces	ITS, LSU, *PRP8*, *β-tub*, *act*	Maphanga *et al.,* 2020

Candida	ITS, D1/D2 LSU	Liu *et al.,* 2026
Canomyces	ITS, LSU, SSU	Sharma & Shouche, 2020
Cephalosporium	ITS, *β-tub*, *his3*	Saleh *et al.,* 2004
Chaetomium	ITS, LSU, *rpb2*, *tub2*	Sastoque *et al.,* 2026
Chrysosporium	ITS	Han *et al.,* 2022
Cladosporium	ITS, *tef-1α*, *act*	Dai *et al.,* 2025
Clonostachys	ITS, LSU, *tef-1α*, *tub2*, *rpb2*	Cuevas-Jacquez *et al.,* 2026
Ctenomyces	ITS, LSU, SSU	Sharma & Shouche, 2020
Cunninghamella	ITS, D1/D2 LSU, *tef-1α*	Letícia Ferreira de Lima *et al.,* 2026
Currahmyces	ITS, LSU, SSU	Sharma & Shouche, 2020
Curvularia	ITS, *GAPDH*, *tef-1α*	Jaffey *et al.,* 2025
Deilomyces	ITS, LSU	Guerra-Mateo *et al.,* 2025
Emmonsia	ITS, LSU, *rpb2*, *tub2*, *TEF3*	Jiang *et al.,* 2018
Exophiala	ITS, LSU, *tub2*, *tef-1α*	Wu *et al.,* 2026
Fusarium	*tef-1α, rpb2*, *rpb1*, *CaM*, *tub2*	Crous *et al.,* 2026
Geomyces	ITS, LSU, *MCM7*, *rpb2*, *tef-1α*	Zhang *et al.,* 2020
Geotrichum	ITS, D1/D2 LSU	Zhu *et al.,* 2024
Gymnascella	ITS, LSU, *TUB*, *tef-1α*, *TEF3*, *rpb1*, *rpb2*, *rpl10*	Kandemir *et al.,* 2022
Gymnoascoideus	ITS, LSU, *tub2*	Guerra-Mateo *et al.,* 2025
Gymnoascus	LSU	Zhang *et al.,* 2017
Hortaea	ITS, D1–D2 LSU, *rpb2*	Czachura *et al.,* 2021
Humicola	ITS, LSU, *rpb2*, *tub2*	Nogueira *et al.,* 2025
Keratinophyton	ITS, LSU	Shi *et al.,* 2026
Lecanicillium	ITS, LSU, *tef-1α*, *rpb2*, *tub2*	Lee *et al.,* 2025
Malbranchea	ITS, LSU	Rodríguez-Andrade *et al.,* 2021

Malbranchea	ITS, LSU, *tub2*	Guerra-Mateo *et al.,* 2025
Metacordyceps	ITS, SSU, *tef-1α*, *rpb1*	Wen *et al.,* 2017
Metarhizium	ITS, LSU, SSU, *tef-1α*, *rpb1*, *rpb2*	Peng *et al.,* 2026
Microascus	ITS	Tan *et al.,* 2026
Microsporum	ITS	Kandemir *et al.,* 2022
Mucor	ITS	Zhao *et al.,* 2023
Myceliophthora	ITS, *rpb2*, *tef-1α*	Phurbu *et al.,* 2024
Apinisia	ITS, LSU	Li *et al.,* 2023
Myrothecium	ITS, LSU, *rpb2*, *tef-1α*, *tub2*, *cmdA*	Lu *et al.,* 2025
Nannizzia	ITS, LSU, *tub2*, *tef-1α*, *TEF3*, *rpb1*, *rpb2*, *rpl10*	Kandemir *et al.,* 2022
Nannizziopsis	ITS, LSU	Wu *et al.,* 2026
Narasimhella	ITS, LSU	Kandemir *et al.,* 2022
Nectria	ITS, LSU, *act*, *tub2*, *rpb1*, *tef-1α*	Hirooka *et al.,* 2012
Nigrospora	ITS, LSU, *tef-1α*, *tub2*	Liu *et al.,* 2026
Ochroconis	ITS, LSU, SSU, *act*, *tub2*, *tef-1α, rpb2*	Wei *et al.,* 2022
Oidiodendron	ITS, LSU, *MCM7*, *rpb1*	Okubo *et al.,* 2025
Onychocola	ITS, LSU	Sun *et al.,* 2019
Ophidiomyces	ITS	Sigler 2013
Paecilomyces	ITS, *tub2*, *CaM*	Spetik *et al.,* 2022
Penicillium	ITS, *tub2*, *rpb2*, *CaM*	Sastoque *et al.,* 2026
Phialophora	ITS, LSU	Torres-Garcia *et al.,* 2023
Phoma	ITS, LSU, *act*, *cal*, *tub2*,	Ramos Romero *et al.,* 2021
Pseudoarachniotus	ITS, LSU, *tub2*, *tef-1α*, *TEF3*, *rpb1*, *rpb2*, *rpl10*	Kandemir *et al.,* 2022
Pseudoarthropsis	ITS, LSU	Rodríguez-Andrade *et al.,* 2021
Pseudomalbranchea	ITS, LSU	Rodríguez-Andrade *et al.,* 2021

Purpureocillium	ITS, LSU, *tef-1α*, *rpb1*, *rpb2*	Chang *et al.,* 2026
Renispora	ITS, LSU, *tub2*, *tef-1α*, *TEF3*, *rpb1*, *rpb2, rpl10*	Kandemir *et al.,* 2022
Rhizopus	ITS, *act*, *tef-1α*	Abe *et al.,* 2010
Sarocladium	ITS, LSU, *rpb2*, *tef-1α*	Zhao *et al.,* 2026
Scedosporium	ITS	Tan *et al.,* 2026
Scopulariopsis	LSU, *tef-1α*, *tub2*	Wang *et al.,* 2025
Scytalidium	ITS, LSU	Manawasinghe *et al.,* 2025
Sepedonium	ITS, *rpb2, tef-1α*	Cornax *et al.,* 2021
Spiromastigoides	ITS, LSU	Rodríguez-Andrade *et al.,* 2021
Sporendonema	ITS, LSU	Kandemir *et al.,* 2024
Syncephalastrum	ITS, LSU	Yadav *et al.,* 2025
Talaromyces	ITS, *cmdA*, *rpb2, tub2*	Tan *et al.,* 2024
Torula	ITS, LSU, SSU, *tef-1α*, *rpb2,*	Hyde *et al.,* 2023
Trichoderma	ITS, *tef-1α*, *rpb2*	Nascimento *et al.,* 2023
Trichophyton	ITS, *GAPDH*, *tub2, tef-1α*	Čmoková *et al.,* 2020
Trichothecium	ITS, LSU, *rpb2*, *tef-1α*	Chen *et al.,* 2025
Tritirachium	ITS	Alves *et al.,* 2022
Uncinocarpus	ITS, LSU	Rodríguez-Andrade *et al.,* 2021
Verticillium	ITS, *act*, *tef-1α*, *GAPDH*, *TS*	Inderbitzin *et al.,* 2011
Yunnania	ITS, LSU, *tef-1α*	Woudenberg *et al.,* 2017

Abbreviations *act*: Actin; *Alt a 1*: *Alternaria alternata* allergen 1; *CaM/Cal*/*cmdA*: Calmodulin; D1/D2 LSU: D1/D2 domains of the Large Subunit ribosomal RNA gene; *EndoPG*: Endopolygalacturonase; *GAPDH*: Glyceraldehyde-3-phosphate dehydrogenase; *his3*: Histone H3; *MCM7*: Minichromosome Maintenance Complex Component 7; OPA10-2: Random Amplified Polymorphic DNA (RAPD) primer OPA10-2; *PRP8*: Pre-mRNA Processing Factor 8; ITS: Internal Transcribed Spacer; LSU: Large Subunit Ribosomal RNA gene; *rpb1*: RNA Polymerase II largest subunit 1; *rpb2*: RNA Polymerase II second largest subunit; SSU: Small Subunit Ribosomal RNA gene; *tef-1α*: Translation Elongation Factor 1-alpha; *tef3*/*TEF3*: Translation Elongation Factor 3; *TS*: Tryptophan synthase; *tub2*/*tub*/*TUB*/*β-tub/Bloc*: *β-tubulin* gene; *rpl10*: Ribosomal Protein L10

21. Keratin Degradation

Keratins are water-insoluble and highly resistant to degradation by animal or plant proteolytic enzymes due to their high cysteine content, intermolecular disulfide-bond cross-linking, hydrogen bonding, and hydrophobicity (Feroz *et al.,* 2020). Based on their sulphur content, keratins can be divided into two groups, including hard keratin (containing 5% sulphur), which is found in feathers, horns, hair, and nails, and soft keratin (containing 1% sulphur), which is found in skin and calluses (Wang *et al.,* 2016; Anbesaw, 2022). The invasion of hair by dermatophytes has been investigated with light and electron microscopy under natural and experimental conditions. The stages by which detached hairs are attacked by keratinophilic fungi are as follows: (1) cuticle lifting, (2) cortical erosion, (3) penetrating organs, and (4) colonisation of the medulla (Barlow & Chattaway, 1955; English, 1963). It was also recognized that these stages overlap one another during the process of infection with *M. gypseum* (Kanbe & Tanaka, 1982). studied the in vitro degradation of human hair by various soils inhabited by keratinophilic fungi was studied by Deshmukh & Agrawal (1982, 1985), and it was observed that the in vitro breakdown of hair is characterized by the release of protein, peptides, and amino acids and results in the marked alkalinization of the medium. Microscopic examination showed extensive hair damage and extensive rupturing of the hair cuticle. The predominant keratinolytic fungi include the genera *Chrysosporium, Aspergillus, Trichophyton, Trichoderma, Fusarium, Penicillium*, and *Acremonium* (Adelere & Lateef, 2016; Anbesaw, 2022).

Keratinases are unique enzymes that hydrolyse both soft and hard keratin proteins (Lange *et al.,* 2016). These enzymes are categorized into three main types: serine proteases, metalloproteases, and cysteine proteases, each distinguished by their catalytic mechanisms, structural configurations, and substrate affinities (Lokeshwari *et al.,* 2026). These enzymes act synergistically to cleave disulfide bonds and peptide linkages, enabling efficient keratin breakdown. Different levels of keratinase activity reported in *Aspergillus* spp., *Chrysosporium* spp., *Fusarium* spp., *Trichophyton* spp., *Penicillium* spp. *Microsporum* sp. (Fakhfakh *et al.,* 2011; Rajput *et al.,* 2010 ;Mukesh *et al.,* 2024; Sharma *et al.,* 2017; Lokeshwari *et al.,* 2026). The biotechnological application of the enzyme keratinase can be in agriculture, biogas production, animal feed, cosmetics and pharmaceuticals, detergent additives, and in the textile and leather industry (Fig. 1)

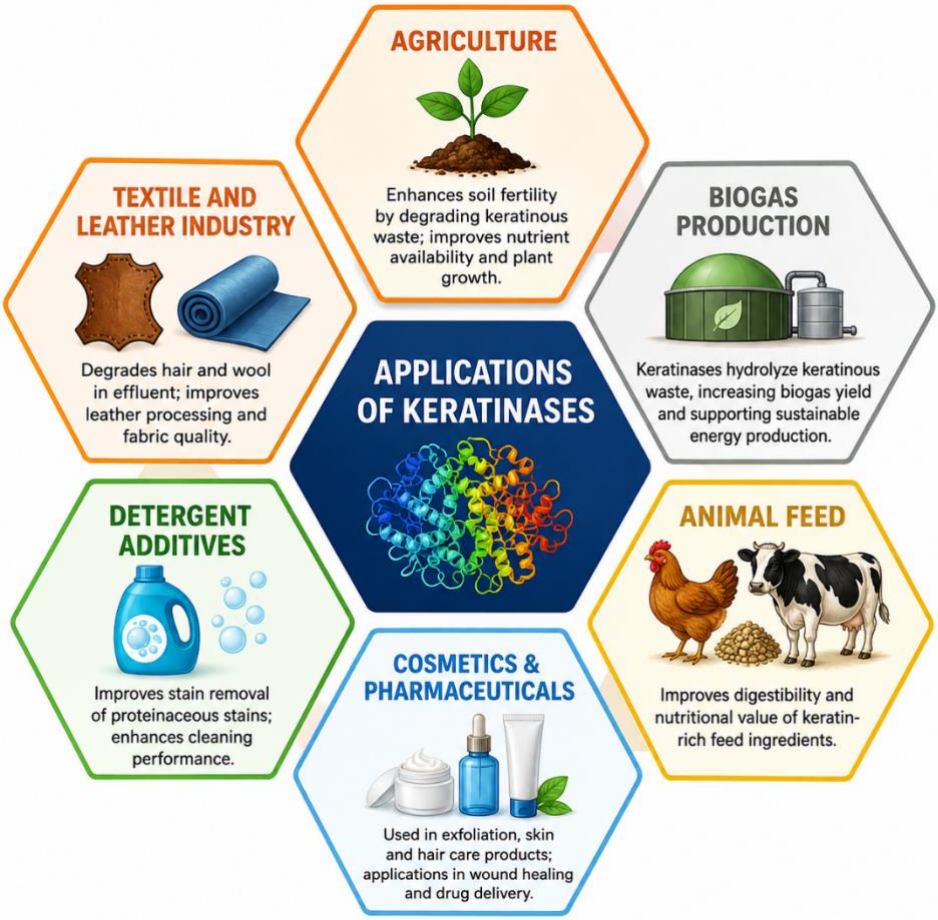

Fig.1. Biotechnological applications of keratinase

22. Bioactive Metabolites from Keratinophilic Fungi

The keratinophilic fungi are known to produce diverse chemical compounds, viz., alkaloids, polyketides, lactones, terpenoids, peptides, and steroids. Among keratinophilic fungi, the genera *Chrysosporium* and *Malabranchea/Auxarthons* are prolific producers of bioactive compounds. The secondary metabolites isolated from *Chrysosporium* have various bioactive activities: Adenopeptin and TMC-69 cytotoxic compounds (Hayakawa *et al.,* 1998; Kohno *et al.,* 2001), Chryscandin antibacterial activity (Yamashita *et al.,* 1984a, b), L-Arginyl-D-allothreonil-L-phenylalanine antifungal (Koenig *et al.,* 1973). Semicochliodinol A and B, enzyme inhibition (Fredenhagen *et al.,* 1997). *Auxarthron* produces various bioactive activities: rumbrin lipid peroxidase inhibitor (Yamagishi *et al.,* 1993), Austrocortilutein and auxarthrol H cytotoxic (Tian *et al.,* 2021), Auxarthrones A-E antifungal (Li *et al.,* 2017), Dimethyl fumarate nematicidal (Burness *et al.,* 2014), 4-benzyl-3-phenyl-5H-furan-2-one vasodilator activity (Hosoe*et al.,* 2005).

The production of antiviral substances, i.e., acetyl aranotin, aporaratrotin and aranotin A, by Arachniotus aureus (Neuss *et al.,* 1968), and antifungal compounds such as aranorosin, aranorosinol A, and aranorosinol B by Pseudoarachniotus roseus (Roy *et al.,* 1988, 1992)

Known compounds floccosin, an antifungal, and floccosic acid, an antibacterial compound, were produced by an anthropophilic dermatophyte, *Epidermophyton floccosum* (Blank *et al.,* 1969).

Microsporum gypseum and *Trichophyton violaceum* are known to produce antimicrobial substances. Major antimicrobial compounds include Fusidic acid, penicillins, quinone antibiotics, gypsetin, and 6-APA by *M. gypseum* (Uri *et al.,* 1963; Elander *et al.,* 1969; Shinohara *et al.,* 1994). Vioxanthin and xanthomagnin, possessing antimicrobial properties, were produced by *T. violaceum* (Blank *et al.,* 1966), while T. mentagrophytes was found to produce antibiotics of the penicillin group (Subrahmanyam, 1980).

Tropical and subtropical countries such as India support particularly high diversity because warm temperatures, seasonal moisture, and abundant keratin substrates create favorable conditions for their growth and persistence.

23. Outlook

Researchers have investigated these fungi across a wide range of environments, including various soil types, birds, bird nests, and animal farms. However, the diversity of keratinophilic fungi in unexplored habitats remains largely unknown, particularly the presence of novel strains and their potential pathogenicity to humans and animals. Greater attention is therefore required to elucidate the ecological factors governing the distribution and survival of these fungi, as well as the environmental conditions that influence the formation of anamorphic and teleomorphic states. Systematic investigations of dermatophytes and related keratinophilic fungi from unexplored and extreme habitats are warranted, particularly in heated and self-heated materials, environments with low or extreme pH, and habitats with high concentrations of salts and other solutes. Such studies may provide valuable insights into the ecological adaptability, distribution, diversity, and pathogenic potential of these fungi.

Reliable identification is the foundation for all of this work. Morphology alone often cannot separate closely related species or species complexes, and misidentifications, including cross-reactivity of a *Chrysosporium* species with a commercial *Histoplasma capsulatum* probe, have been corrected only through sequencing. Future surveys of unexplored habitats should therefore combine cultural and morphological characters with DNA sequence data from the outset. No single marker suits every genus. ITS is an effective first-line barcode but may be identical in closely related species. Genus- or group-specific multilocus strategies (for example, LSU, β-tubulin, TEF3, RPB1, RPB2, EF1A, MCM7, and RP60S) should be adopted, as summarized in Table 1. Marker choice is also limited by the availability of sequences from type and authenticated specimens in public databases. Depositing such sequences should be a priority, especially for taxa from India and other under-studied regions, where novel taxa and cryptic species are likely to turn up.

For more than 70 years, researchers have investigated keratinophilic fungi and isolated them from soil, birds and their associated environment, healthy animal skin, and disease specimens. However, well-documented culture collections and reference specimens of these fungi remain limited in India. The establishment and maintenance of such collections would be of immense value to younger scientists by providing access to authentic and well-characterized strains for taxonomic, ecological, physiological, and biotechnological studies. It is therefore highly important to establish culture collections containing both standard reference strains and diverse isolates representing the ecological and geographical diversity of keratinophilic fungi. Taxonomic identification in such collections should integrate classical morphological and physiological criteria with molecular biological criteria (genus-specific multilocus sequencing, with sequences linked to the preserved strains and deposited in public databases) to ensure accurate and reliable identifications. Keratinophilic fungi have also proved

to be prolific producers of biologically active compounds and structurally novel metabolites, highlighting their potential for pharmaceutical and biotechnological applications. A systematic classification and evaluation of the bioactive molecules produced by different species, together with their ecological distribution, would therefore be valuable for identifying promising strains and metabolites for further investigation.

In addition, these fungi can degrade keratinous materials into peptides and amino acids via keratinase. Keratinase has important industrial applications, including the removal of hair from animal hides during leather processing. Selected or genetically modified strains with enhanced keratinolytic activity could potentially be developed for the large-scale degradation of keratin-rich waste into peptides and amino acids. The resulting hydrolysates may serve as protein-rich supplements in poultry and other animal feeds, while keratinase itself can be used in the leather industry.

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