

Jakob Emanuel Lange: The man and his mushrooms

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Abstract

Jakob Emanuel Lange (1864–1941), Danish mushroom taxonomist and illustrator, was an agricultural educator and economic philosopher. A follower and translator of the American Henry George, Lange was Headmaster of a “Small-holders High-School,” which served as a model for American folk-schools. Lange visited North America on three occasions. The first, in 1927, relied on his professional expertise; the second, in 1931, was purely mycological; and the third, 1939, was a combination of the two. All of this was lived against two World Wars and the Great Depression. This paper summarises the circumstances of Lange’s life against a background of the American mycologists of the day, the ominous events over his adult lifetime and his magnum opus, “*Flora Agaricina Danica*”, of five volumes illustrating ca. 1200 species on 200 coloured plates.

Keywords

Biography, mycologist

Chapter I. Introduction

The year was 1927. Henry Ford was wrapping up production of the “Tin Lizzy,” with 15 million on the road. With US population nudging 115 million, that was roughly one car for every 14 men, women and children, to say nothing of other companies and brands. The model T had leaf springs but no shock-absorbers and with few paved roads, automobile travel, like history, was a bumpy ride.

The United States was flexing its muscles. The era of Robber Barons had led to economic and financial strength. Names like John D. Rockefeller, Cornelius Vanderbilt, Henry Ford, Andrew Mellon and Andrew Carnegie resonate to the present day. Teddy Roosevelt had not only changed the view of the country regarding its “infinite” land holdings, but had taken on the monopolies and their lack of regulation. Railroads connected the coasts and carried the raw materials and finished products of the “Second Industrial Revolution.” The backbone of major industry, mining and manufacturing - factories, steel, logging and coal mining – was matched by budding technology, such as typewriters, cash registers and adding machines transforming how people worked. Ford had introduced the “assembly line”. The economic explosion included not only industrial growth and urban expansion, but also growth in agricultural technology, such as mechanical reapers. In a tiny corner of this juggernaut was the transfer of agricultural research in plant pathology into the hands of farmers (Petersen 2021). Mark Twain dubbed it “The Gilded Age”.

In a time of great expansion and fewer regulations surrounding wealth and business practices, circumstances were ripe for the rise of a class of extremely wealthy individuals who composed a very thin veneer of society. They wielded the power and means to

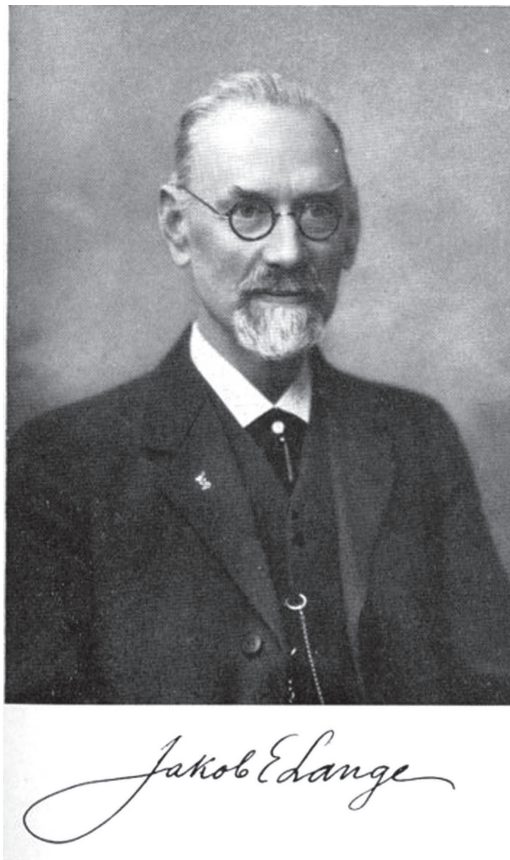


Figure 1. Jakob Emanuel Lange. Comparison of Lange’s signature reveals that it changed remarkably little over many years.

create opportunities and jobs for the working class, but often with little regard for “workers’ rights” issues, such as discrimination, exploitation, workplace conditions and low wages marked the era. Interclass battle lines were being drawn.

In spite of this disparity and inequality, at least the United States did not have to deal with royalty. This was not so in Europe. For centuries, Europe’s social structure had revolved around the royals, the clergy and favoured mercantiles. The peasants remained poor and at the service of their local authority. Only the scent of the Enlightenment sought to provide some relief to the underclasses. Such movements, of course, were not supported by the ruling class and, while the cast of characters differed from that in America, the basic parameters of the social structure were similar. For Europe, the tableau played out in the 19th century, for the United States, the 20th.

In the far-off Denmark of 1927, a modest farmer/teacher/politician named Jakob Emanuel Lange (2 April 1864–27 December 1941; Fig. 1) was already 63, in the prime of life. While Jakob Lange might not be a household name, he was to make his mark on not only the social equality movement in America, but the arcane world of mushroom taxonomy (Pearson 1946).

Born in 1864, Jakob Lange was a child of war. His father, M.T. Lange, was a vicar living in disputed territory between Germany and Denmark. His strong alter-interest was botany and, in 1858, he penned the first local flora, “The Flora of the Southern Funen Archipelago” (Lange 1858).

As a footnote to the turmoil in Europe during the mid-19th century, in 1849, a new Danish constitution tempered the absolute rule of the Danish monarchs. In 1850, after a 2-year revolution, the southern provinces of Schleswig (a Danish duchy) and Holstein (a German duchy) seceded from Denmark and allied themselves with their German-speaking neighbour to the south, Prussia. A decade of turmoil ground on, pitting neighbours against neighbours, a conflict which would harden both Danish and German nationalism, profoundly instrumental in the Rev. Lange’s attitudes about life and education. In 1862, M.T. Lange became vicar in Angel [bordering Germany], but, because he did not want to work for the German cause, he was sacked by the Germans in 1864 and had to flee to Flensburg [further north, in Denmark] and there, during the escape from Germany, Jakob Emanuel Lange was born (Buchwald 1942). In 1864, the Prussian Germans took control of Schleswig-Holstein and it was ceded to Prussia in 1866, under the Treaty of Prague (Begtrup et al. 1926; Frommers 2021). Then, in 1866, another new Danish constitution was adopted, but it was more conservative than the one of 1849 and granted more power to those who paid the highest taxes, in other words, the landowners. Society was bound for re-stratification, not egalitarianism. It was in this era that Jakob Lange grew up. Henry George would have been disappointed.

As a young man, Jakob Lange became interested in botany, working as a gardener in high-profiled gardens and going to England (Kew) and Paris (Jardins des Plantes) for two years (1885–1887). Upon his return, he accepted a job as teacher at “Dalum Landbrugsskole” as a master gardener, although without formal education. The job was for four months, but he stayed 30 years. “It soon turned out that Lange had extraordinary abilities as a teacher; he could talk, he had no problems in visualising subjects and teaching was fun for him. His route in life was now on track and it was teaching/

education in which he worked through the largest part of his life” (Buchwald 1942). At Dalum, he obtained his degree in 1887. His responsibilities included teaching young farmers botany, social economics and, interestingly, a bit of chemistry (Lange 1996). He also penned textbooks on botany (Lange 1897, 1916b) and physics (Lange 1899), each of which went through several editions.

“During his time in England, Lange heard about Henry George^[1] (Fig. 2) and became acquainted with his major work, ‘Progress and Poverty’ (George 1879). In this way, his main interest in life, social economy, was started. From his first teaching year, he started giving lectures in social economy and the next year, he wrote his first textbook, ‘Social Economy’ (Lange 1909), reprinted in a number of editions. In this way, it was Lange who introduced George’s thoughts to Denmark. Later, he made translations of some of Henry George’s books (Lange 1898, 1905, 1938c). His ideas about social economy were in focus when the so-called Land-law of 1919 was approved by the parliament, whereby ‘the peasants rights to the land, the people’s right to the land-interest’ was approved (Buchwald 1942).

“Already in his youth, through his father, [Jakob] Lange had received impressions about the popular and progressive thoughts about schools, a movement which grew in the middle of the 1800s. His father eagerly supported the small ... free schools which had been founded on Funen [a small island on Denmark’s east coast; also known as Fyn]

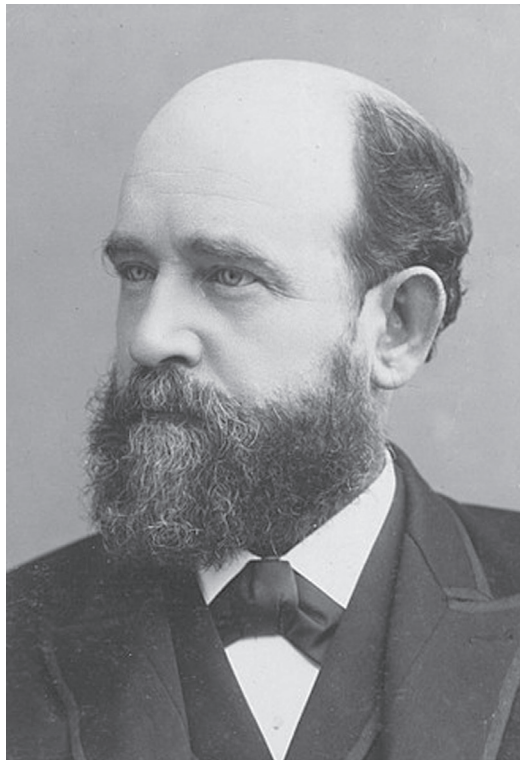


Figure 2. Henry George. Source: Wikipedia.

in the 1860s and 70s, and through this, [Jakob] Lange early became aware of “small-holders” social conditions. His attitude toward the popular context was further supported by being together with his father-in-law, free-school teacher Knud Larsen. In this way, he soon came in contact with the Danish small-holders movement and this led to his appointment as principal of “Fyns Husmandsskole”. In his leadership of this school, he enjoyed invaluable support from his wife, Mrs. Leila [Larsen] Lange (1884–1943), for whom the small-holders’ conditions were sensitive in her mind” (Buchwald 1942).

As adjunct to his participation (and subsequent teaching position) at the Dalum school, Jakob Lange also became prominent in social and political movements, over time becoming a leader of the Danish Social Liberal Party [now Det Radikale Venstre]. In 1914, he was asked to assume the superintendence of the “Husmandsskole” (“Small-holders’ school”) in Odense near Dalum on the Island of Fyn (aka Funen). He refused, professing that he was comfortable at the Agricultural Folk High-school, but the invitation was renewed in 1917. “The Great War” was at its height, Denmark was neutral and this time he accepted. Buchwald (1942): “It did not take many years before Lange threw himself into the study of the fungi, the exploration of which would become his real speciality, i.e. the difficult group, the agarics. One of the difficulties in this study is that their occurrence is restricted to a few months in the autumn. However, these conditions were in his favour, because the agricultural schools were closed in those months so the students could go home and help with the harvest – and this gave him a unique opportunity to study these fungi”.

Jakob Lange was multidimensional (Lange 1996): his pedagogical and political lives filled his days, but a growing fascination for the local mushrooms of Fyn, had, from its beginnings in the 1890s, bred a small library, growing knowledge and a cache of water-colour illustrations that were becoming known and appreciated by the Danish mycological community. Of Lange’s three trips to the United States, the first was borne of his professional occupations, the second by mushrooms and the third by both. Indeed, the impetus of his 1927 transatlantic travel had little to do with mushrooms, but everything to do with the common cause for the dignity of the working class.

Jakob’s first invitation to visit the United States had come in 1914. The fateful assassination in June of a second echelon royal lanced the abscess of ill-will in Europe and before the summer’s end, war was spreading. For America, “The Great War” (World War I), as it expanded across Europe, seemed distant. As Lange (1938b) put it, “In 1914, just after the war had started, I received an invitation from America to talk about the Danish situation, at the American teacher-organisation’s annual meeting in San Francisco, 1915. ‘It is expected you can speak an understandable English, you will be given 25 min. and a salary is not given for principle reasons.’ It was added, in a modicum of good will, that the host would arrange a paid tour of lectures in connection with the meeting. “It was flat out exciting; and I also answered yes, under one condition: that the war at that time [1915] would not be close to Denmark – and then, of course, the plan was cancelled and any thoughts of a travel to US were also cancelled”. Although Denmark remained legally and politically neutral, transatlantic ship traffic was insecure. The cancellation was followed by a 13-year hiatus for hopes for a U.S. visit.



Figure 3. Nikolaj Frederik Severin Grundtvig. Source: Wikipedia.

However, what was “the Danish situation” about which he was to speak to the American teachers organisation? Surely not Danish. In the mid-1800s sketched above, there was little movement towards equality of society by the peasantry. It was only from 1788 that farmers were freed of their attachment to the nobility, i.e. they could now live wherever they wanted. Against this grain, Nikolaj Frederik Severin Grundtvig (1783–1872; Fig. 3), a Lutheran cleric born of the upper-class, spoke of a peasantry with power within the greater population. Studies at Trinity College, London, in 1831, 1832 and 1833, helped to mature his thoughts and he began to develop the idea of a kind of folk school particularly for those who could not afford formal education, producing a peasantry ready to take its place in Danish culture and governance. His mantra was “First a Dane, then a Christian”. His followers celebrated nature through Danish language, song and history and became known as “the Happy Danes.” Using his pulpit as Lutheran pastor, his sermons reached growing congregations and, in 1844, the first “Grundtvigian high-school” was founded. Within a few years, the 1849 Constitution granted some aliquot of governance to the people, the Grundtvig movement quickly grew and, by the end of the 19th century, several hundreds of such schools had been formed, some reputable, others not so. Both the Agricultural Folk High-school at which Jakob Lange taught for 30 years and the “Husmandsskole” in Odense, to which he moved, were of the Grundtvigian tradition.

Although founded before Lange’s leadership, the Odense Folk High-school (Figs. 4, 5) had become reputable even beyond Scandinavia. As part of its popularity,

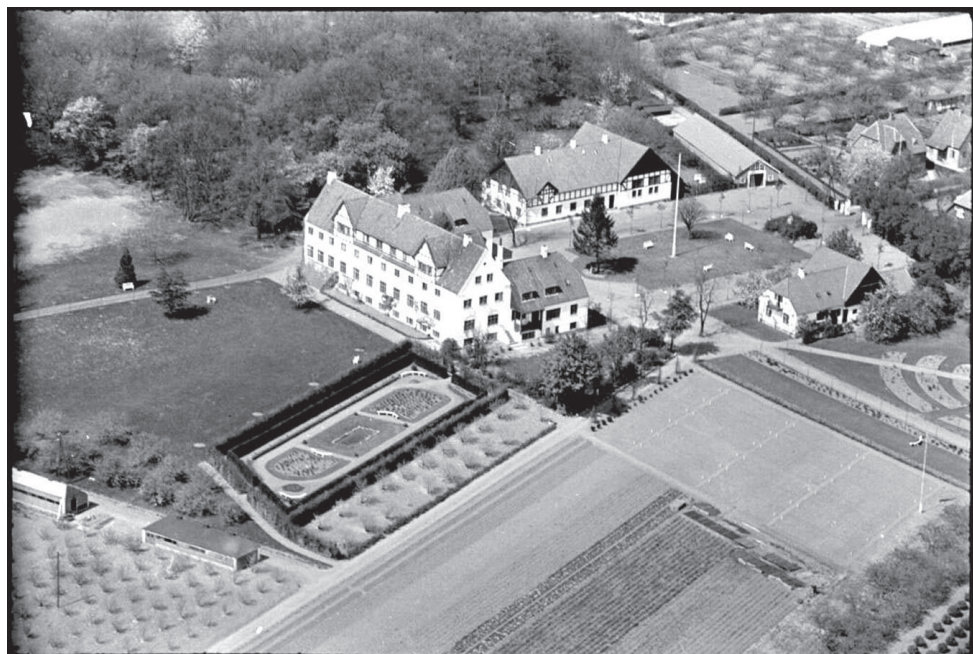


Figure 4. The Odense 'husmundsskole', probably pre-WW II. Major building and ancillary buildings. The practising farm is at lower right, the orchard is top right and lower left, the formal garden surrounded by hedge is central. Source, DKArkiv.



Figure 5. The Odense 'husmundsskole'. 1940. Source: DKArkiv.

the school played host to frequent visitors, some of whom were advocates from the United States. Lange (1938b): “One of the most important Americans who visited the school, was Dr [Philander Priestly] Claxton [1862–1957], in his time ‘commissioner of education’ [i.e. commensurate to today’s Secretary of Education], which modest title can be better translated as ‘general director for education in the United States’. Claxton was very interested in the conditions in Danish agriculture, especially because he encountered a trend which did not (without fighting) accept the minority feeling (a feeling of less- worth) which the COUNTRY-CULTURE almost all over the world has against CITY-CULTURE, not least in America. Both the [Danish folk] high-school and the ordinary village-school, with their independent teacher-families, were ideal to him. He was only too used to seeing the American country district teacher, more often female, always turning their face towards the nearest city, longing for advancement to a city-school, just as, on a dark winter night on a deserted road, you would be longing towards the cultural centre you may faintly see on the horizon over Svendborg or Bogense [two local Danish cities].” Claxton was a Tennessee native, born in a log cabin and an evangelist for state funding of rural schools. Lange: “The one among all our guests, who developed the deepest appreciation of the Danish high-school system



Figure 6. Olive Dame Campbell. Source: Wikipedia.

and thoughts about schools, was, however, Mrs. [Olive Dame] Campbell^[2] (Fig. 6). She visited first the high-schools in Scandinavia and Finland, where she found a way of organising school work, she preferred to take to the 'small farmer' society of poor mountain farmers in the Allegheny Mts. [sic], which she for her whole life had been interested in to work among and for. The book she later wrote [Campbell 1928] about Nordic high-schools is undoubtedly the most intimate understanding written about this subject and the 'small farmer' school she founded in North Carolina [John C. Campbell Folk School in Brasstown, North Carolina; Fig. 7] is in a strange way a living 'work,' which in various ways serves the 'propagation' of the 'Mountain peoples' public and socio-economic 'liberation' and prosperity. Above the entrance door to this school is a bell, given to her by Danish high-school people" (Campbell 1929). On the other side of the mountains, in Tennessee,

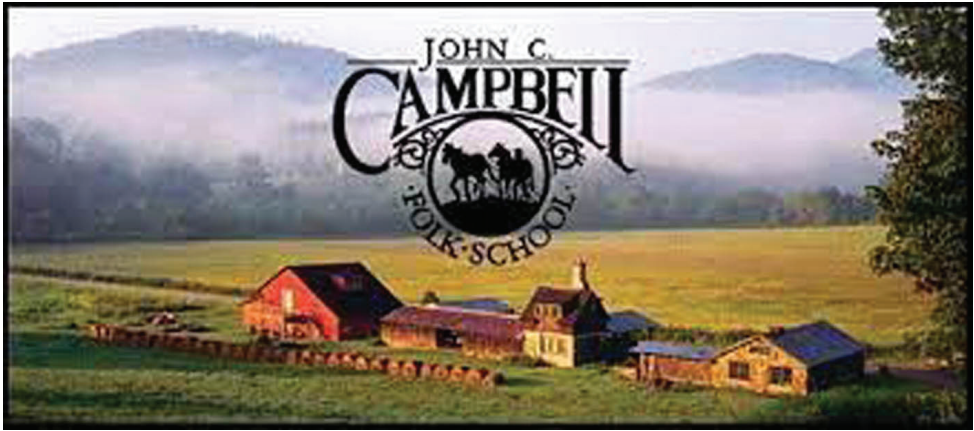


Figure 7. John C. Campbell Folkschool advertising design. Source: John C. Campbell Folkschool.

Horace Kephart was revealing the life of southern mountaineers in more whimsical prose (Kephart 1913).

Widowed in 1919, Olive Dame Campbell (1882–1954) had carried on the work of her husband, John Charles Campbell^[3] (Fig. 8), surveying and measuring the rural cultures of the southern Appalachian Mountains and conjuring what could be developed to bring education and dignity to those isolated populations (Campbell 1921, 2018). She and her friend, Margarine Butler of rural Kentucky, were each awarded fellowships from the Russell Sage and the American Scandinavian Foundations to assess the Scandinavian Folk High-School movement, curricula and ambiance.

Lange's sincerity of feelings was shared by Mrs. Campbell (1928): "The relationship of equals was certainly well maintained at Odense. Possibly the fact that the students were older and came with a serious purpose had something to do with the atmosphere of comradeship. I recall always my impression of this on my first visit, early in my stay in Denmark. When Mr. and Mrs. Lange [Fig. 9] led us down to the dining room and



Figure 8. John Charles Campbell. Source: Wikipedia.

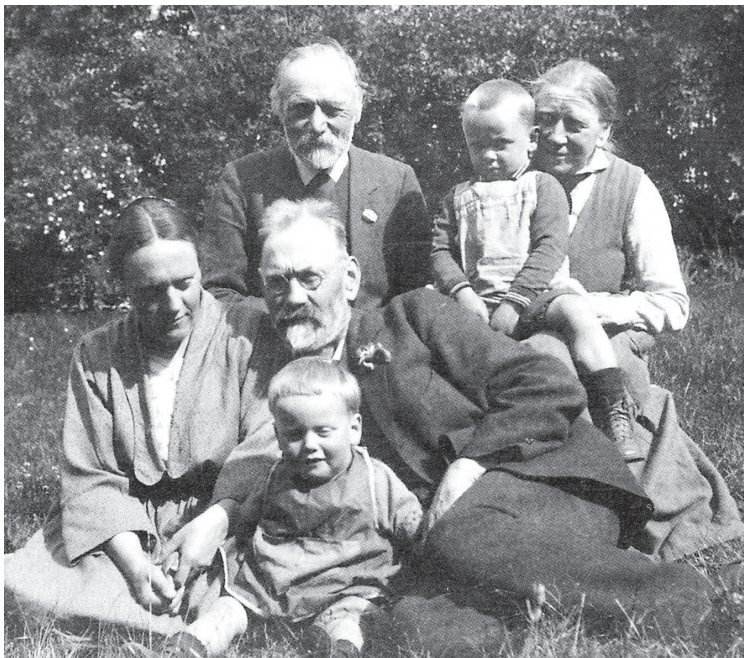


Figure 9. The Lange family. Left: Leila Lange; Centre; top, Leila's father; centre, Jakob Lange; lower, Jens Jakob Lange; Upper right, Knud Morten Lange (age perhaps 2), Johanne Lange.

found us a seat on the long benches, something ‘folkeligt’ as we say in Denmark, was to be sensed in the atmosphere – something which may have been due to equal ages, small numbers, simple food, lack of convention, or especially to Mr. Lange’s convictions and Mrs. Lange’s very warm and natural personality. Conversation was carried on freely, often across tables and even across the room. We had, I remember, barley porridge with butter and sugar, cold ham and carrots stewed in a sauce, rye bread and a pink fruit drink ... When Mr. Lange rose with ‘*Velbekomme*,’ our ‘*Tak for mad*’ (thank you for the



Figure 10. Wildflower painting by Jakob or Johanme Lange. Source: Natural History Museum of Denmark, Copenhagen.

meal) was such as we would have given in any country home”. According to school lore, the walls were decorated by paintings of local wildflowers, mostly by Jakob (Fig. 10).

Campbell (1928): “The aim of a Grundtvigian high school was to help common people qualify as active and engaged members of society, to give them a movement and the means to change the political situation from below and to be a place to meet across social strata. This atmosphere would materialize in the collegial atmosphere and mutual respect between the teaching staff and the students who would all live together in a small community transcending social classes. The egalitarian atmosphere at the schools was important. By singing, reading and exploring their surroundings, the students at a folk high school were also meant to have a joyful and uplifting time, not only to obtain educational knowledge (Warren 2012, 2021). Examinations were prohibited”.

Democratic (with small “d”) principles permeated the Odense school. “Mr. Lange told us that a committee of seven met yearly, when necessary and could dismiss the principal on six-month’s notice. Five of the committee members were from Fyn, two being selected by former students. The chairmen of the organisations of Sjælland and Jylland are *ex officio* members of the committee, but did not take an active part in the management. Mr. and Mrs. Lange got the same salary and board regardless of whether the school was prosperous or not, an arrangement which left them much freer than as if they had the burden of private ownership. They were not likely to be dismissed or interfered with unless they should become violent reactionaries in politics or radical opponents of religion, in which case ‘we would ourselves undoubtedly wish to leave’. ... A combined cultural and practical program calls for a skilled and expensive staff”.

[Experts from the Agricultural College taught at the Folk High-School in the winter, when they had spare time from regular duties during the growing seasons.] “The *Forstander* (Superintendent) can engage whom he pleases. ... The school also owns a large farm, run solely for school support although on demonstration lines. It is in the charge of one of the old students, a trained farmer. Each year, five new graduates are given the much-prized opportunity of working there for the practical training. They are permitted to remain only one year, with the exception of the cattleman who stays longer.

[The school] “stood firmly on the two essentials, family life and the relationships of equals. ... The relationship of equals was certainly well-maintained at Odense”. Campbell (1928): “The men’s course of five months takes up geography, history, literature, life of the peasantry since 1788, botany, physics, a very little chemistry, social economics, animal husbandry, anatomy, accounts and bookkeeping, gardening, plant cultivation, soils and manures, with occasional other lectures. Gymnastics is also given. The manner of teaching is much the same as in the regular folk school”. A five-month course is offered to women as well as to men although about one-third leave 1 August, after three months. Besides the usual cultural subjects, they receive cooking and sewing lessons. In addition, each woman is given a small garden plot where she raises both flowers and vegetables. Two periods of one and one-half hours a week are devoted to this work under the direction of the horticulturist. The weekly schedule shows not only subject matter, but Lange’s responsibilities in the classroom.

The durability of the Grundtvigian folk school is testified by Danebod, a small neighbourhood in Tyler, Minnesota. This tiny Danish enclave was settled in 1885 and,



Figure 11. Danebod Folkschool building. Source: Danebod.com.

almost immediately, a three-storey brick building for the school was built. For more, see bibliography under Danebod (2021a, b; Fig. 11).

In 1924, the Social Democrats became the largest party in Denmark and took the reins of government. The large Left Party (i.e. the liberals) suffered internal strife resulting in a division between the larger group, which adopted a moderate liberal attitude and a small group whose direction inclined to a more radical liberalism. In both parties, the rural population was the fulcrum, but farmers and small-holders were found in both (Hollman 1910; Begtrup et al. 1926). It was in this more radical wing that Lange was to be found.

So to the question of “the Danish situation” over which Lange was to expostulate in the United States in 1915 (the invitation of 1914): it could have been political parties in Danish politics, the Grundtvigian folk-school movement, agricultural education in Denmark or Danish professed neutrality in the growing war in Europe, in all of which Lange had more than passing expertise.

Chapter 2. 1927

In 1914, the same year as the first invitation to visit the United States, Lange began a series of published studies on the mushrooms of Denmark – with text in “understandable” English! – sometimes accompanied by montages of his own watercolours of the species involved (Fig. 12). He wrote that he had started creating the images in 1893 and, by 1914, numbered 622 (they would eventually climb to over



Figure 12. Plate of *Mycena* taxa from first instalment of Lange’s “Studies.” Source: Dansk Botanisk Arkiv.

1200). He contemplated that they would supplement his “Afbildninger af Danmarks Agaricaceer” (“Illustrations of the Agarics of Denmark;” Lange 1914), Lange’s name for his collection of aquarelles, later to become “Flora Agaricina Danica” (Lange 1969). The “Studies” series, 12 in all, extended from 1914 through 1938, three years before his death Lange (1914, 1915, 1917, 1921, 1923, 1926, 1928, 1930, 1933, 1935b, 1936a, 1938a). Already in 1888, Lange had written on potato-blight on tomatoes and his interest for this practical use of mycology continued in his pamphlet on common plant pathogenic fungi (Lange 1916), not published in some abstruse journal, but independently, so it could be distributed directly to the nearby farmers.

Two principles undergirded the “Studies” project. First, a thorough study of the agarics of Denmark had not yet been accomplished and no one was more familiar with them than Lange. Accordingly, the series furnished keys and descriptions and, where necessary, illustrations, including occasional coloured plates. Second, with the polyglot of language across Europe and Danish certainly minor amongst them and with the larger mycological community of Great Britain and the United States sharing a single language, English was preferable.

Lange was already obsessed by the notion of “agaric richness.” Starting with the first in the series, Lange’s own tally of Danish species numbers was compared to counts of Fries’ species of the same genus. Lange (1914) was always impressed that, in such a small area as the Island of Fyn (“barely 40 km in both ways”), he could produce such large numbers of species – comparable to those logged by Fries, with the exception of the Scandinavian conifer fungi. He was to expand further on his ideas after his 1931 American foray (Lange 1931, 1934).

Lange (1938b): “... in 1927, the [1914] invitation was repeated in a new form. We had at the high school eventually received many connections in socially and pedagogically interested circles abroad. And now came a request to me to talk at an international congress in Lansing (Michigan), called for by the American department of an organisation, which in English is called ‘Country Life Association’ and whose purpose was all over the world to find out and speculate in what could be done to improve life conditions in the countryside, economically, socially and by raising the information level. And furthermore, I received an invitation to talk at the old Univ[ersity] in Williamstown in Massachusetts [Williams College] at a meeting there, also of international contents, organized by a society calling themselves ‘Institute of Politics,’ really a national-economical society for information. The payment at these meetings was so ‘American’ [considerably more charitable than European] ... that the travel costs could be met. And by a row of other connected lectures (for a more European payment), it was made possible for me to bring my wife too, which became especially interesting to me since it was arranged that our travel could be extended all the way down to North Carolina, where we could be present at the inauguration of the new assembly building Mrs. Campbell had established as the centre for her new high-school”. Neither Knud Morten Lange (24 November 1919 – 10 November 2003; in 1927, eight years old and known to everyone as Morten), nor Jens Jakob Lange, their other son, were mentioned and assumedly remained at home, fully attended by the students and staff of the school.

Lange^[4] (1931): “It was an extremely interesting travel, very different from the American travels other [Danish] high-school men had taken in preceding years. For them, the main purpose was to visit the Danish small villages and religious circles, especially in ‘the Middle West,’ the States to all sides with Chicago as the centre. My travel on the contrary went through the old States, the East coast, from Maine to North Carolina and only at one point to the west, passing Niagara to Lansing in Michigan. And we did not see many Danish. On the contrary, we received a much varied and quite in-depth impression of the Americans, far more comprehensive than the Danish high-school people normally got, even after many years in the US.

“The ‘Aquitania’ was one of the largest swimming monsters of the time, with seven decks. But a sailing trip across ‘The Pond’ was anyway not very exciting: remarkably few ships are met with on the route. Days may go by without seeing any. And then when you finally reach the harbour in New York: passing the Statue of Liberty, the light of which, according to malicious tongues, is only shining outwards, not over America, the symbol of which she should be.” This observation on societal inequality, among other experiences, was a reaction to the United States’ Johnson-Reed Act of 1924, known as “The Immigration Act”. It restricted immigration to 2% of the number of nation-immigrants from each country, measured by the census of 1890. Asians were prohibited totally.

“After Medical Control [on Ellis Island, the reception centre for immigrants for decades] and other modern plagues, we finally came to the city and saw the ‘skyscrapers’ of Manhattan in front of us. The strange thing about these is that it was a BEAUTIFUL view. The reason is probably their sky-striving character (the one they share with the old Cathedrals, with which they have a certain resemblance in my memory). It is almost as if all the Cathedrals of the World have decided to meet here. And add to this their functionalistic appearance, a feeling of ‘problem solved’- mathematically correctly. In this way, it is possible, under narrow area conditions on stony ground, to build a business town for a million population. But it was strange, when you walk around in the narrow streets, which felt like the bottom of huge canyons, to see amongst them an old church, with a tower which was impressive for its time but now looked like a small, sleepy candle-snuffer, hardly reaching 1/3 towards the top of the skyscrapers from its small green churchyard in the centre of a large city’s stone desert”.

“The congress in Lansing, the capital of Michigan, took place in beautiful surroundings, at this state’s agricultural high-school [later renamed as Michigan State University]. Everywhere in America, universities – and even smaller schools – are surrounded by large parks with very old trees of beech, elm and maple and the buildings are usually large, wonderful and dominating.

“One of my best days was when I spoke to a thousand-fold audience of farmers from the area. It was almost like being home at the agricultural school to a camp – only that here there were loudspeakers and other devices at that time unknown in Denmark and a huge orchestra of about 50 musicians. ... We also had curious experiences, like at a ‘Rotary’ lunch, which was very American and took place in a large hotel in Lansing. My wife and I were, of course, placed at the head table with the other guests of

honour: to the left the beauty queen of Michigan (with her mother and fiancé), to the right 'the world champion mouth-organ player!' I had the triumph that I, although handicapped in the competition, could spell-bind the busy businessmen, who here had a short schedule, by my story about the Danish cooperative movement— for even more than 20 min, which was said to be a "record".

"At the meeting/camp in Williamstown [Williams College, Massachusetts], the old conservative university in Massachusetts (where female students were not allowed), the atmosphere was somewhat different, more upper class. It was very international. A dominant role was taken by the young H. A. Wallace^[5] – now [written in 1938] known everywhere as Roosevelt's secretary of agriculture and legislative active administrator. The British foreign-press chief talked (about England's economical policy in China); a former German Reich's finance minister shed light on Germany's economic policy after the war [World War I, reparations] etc. And here I was to talk about something so small in a world context as Danish farmers. Was it likely to be of any interest? – It was a hall the size of the Copenhagen cathedral, but luckily there was a loudspeaker – and [the talk] was OK; at least the Italian Count Sforza hurried up to my wife after the lecture and kissed her hand as a thank you: what else can you ask for? By the way, they had changed the title of my lecture. I had called it 'Progressive Peasantry' (farmers in an era of progress); but it was changed to 'Agricultural Progress'. Why, I asked? And received the answer that 'peasant population' and 'progress' were mutually exclusive - two items which could not be thought of as being related. That gave me a lot to think about.

"I shall not count the different agricultural high-schools and universities we visited during the tour. When we had the laborious tour behind us, we could with a good conscience go to Mrs. Campbell in 'the mountains'.

"While most of the villages in the southern states are 'Black,' there is a population in the Allegheny Mts. valleys which is, for America, an unusually clean and pure English-Scottish race. These mountain people constitute a 'tribe' of their own. They are descendants from an early immigration to the North Carolina lowlands, but were later forced by mass immigration from Europe into the valleys in the mountains, where they settled, whereas the other immigrants continued across the [mountains] and into Mississippi. Now they constitute a peculiar farmer-people, extremely old-fashioned, speaking practically what you would call an old-English dialect, living from pieces of old poems, homemade, traditional art-work etc., but now [find themselves] in [a general] explosion and dissolution, along with the arrival of modern central schools: highways form a net of modern culture into the valleys of the theretofore almost roadless valleys' quiet life.

"It was among these farmers and small farmers that Mrs. Campbell saw that the high-school had a mission, as already mentioned. Now she had come so far that her own agricultural farm was not alone in exemplary order, but she had founded a co-operative dairy, organized co-operative buying etc. and also in a modest way started the school. And now finally the first real house, the assembly hall made of timber-logs was finished and it was for this celebration we were invited. A lovely room, with mat brown waterboards on the walls and homemade chairs instead of benches, one from each home in the village.

“It was curious to see the population coming from near and far in their delicate [horse-drawn] chariots with picnic-baskets, babies etc, almost as you may imagine the [Danish] ‘sky-mountains parties’ (the highest point in DK is 189 m) in the old days of Blicher [a Danish poet depicting country life]. The speaker following me was President Hutchins from the Peoples’ University of Berea^[6] in neighbouring Kentucky (Berea 2021). And to the population, as for us, this celebration was a strange event, which established that now, with the new enlightenment, co-operative efforts had resulted in something real. To us, as Danish, it had the strongest effect when a small choir of the youngsters in the school sang for us in Danish a few verses of ‘I am a simple farmer’ to greet us and as an expression of the living connection to the Danish high-school and farmer-culture. ‘I sing behind the plough’ was selected as the motto for the school and is written on their emblem.

“From North Carolina, we headed for New York. Before we sailed home, we had the opportunity to participate in a Henry George gathering. It was interesting to meet men, whose names were well known to me from the information and agitation work of George’s ideas through many years. The person I had the most living impression of was Hamlin Garland, whose collections of short stories (“Main Travelled Roads” from the 1890s) was the first who gave a ‘living picture’, based on a realistic social background, of the American country population’s life and thinking. The most direct connection I had, however, was by meeting Mrs. Anne George de Mille, the youngest daughter of Henry George, who is fully occupied with the continuation of her great father’s ideas among the people of our day. At the congress we, by the way, had the impression that this was needed. The audience was mostly old people, but fortunately Mrs. de Mille and other younger people’s efforts now seem to be fruitful among the younger people.

“The most important of the veterans from Henry George’s own time, Louis F. Post^[7] and his wife Alice Thatcher Post were not present at the [Lansing] congress, but we got a very living impression of them in their home in Washington [DC]. They are now very old but fully engaged by all the important questions of our time. I made them happy by bringing my thanks for their weekly journal ‘The Public’ which through many years meant a lot to me by its progressive and bold talk”.

Almost as an after-thought, Lange mentioned a couple of mycological oddities he saw in the wilds of far-western North Carolina. The first (Lange 1934) was reported within a discussion of mycological “parallelism,” a subject expanded in a subsequent chapter of this paper. Briefly, Lange suggested that many American mushroom species resembled European agarics so closely that they were (in his terminology) “parallel”.

“One of the most peculiar cases of parallelism is the existence in America of a phosphorescent form of *Panus stipticus*. While there is no record, as far as I know, of any phosphorescence in the European form, the American one is renowned for its bright noctilucency [sic]. I myself encountered this phosphorescent form in North Carolina (Cherokee Co.) in 1927. When seen by daylight the specimens were exactly like those so commonly collected in Denmark. Whether the phosphorescence is a real specific difference or can be accounted for by atmospheric conditions (or bacteria) remains to be decided by further investigations”. The local folks were familiar with luminescence, which

was known as “foxfire.” Had Lange been present later in the year, he might have seen the “Jack O’lantern” mushroom, *Omphalotus illudens*, much more impressive than foxfire.

Lange (1931): “In North Carolina, I found a very peculiar fungus, a short-stemmed gastromycete, with an outer membrane which is very ephemeral, like grainy clay or moduling cork, which, when it disappears, reveals a smooth, egg-like pale grey-brown ‘sporehouse’, the opening of which is decorated with a star-shaped, shining cinnabar red mouth, which very aptly has been given the common name, “beauty-mouth,” most likely *Calostoma* [*lutescens*].

Surrounded by well-wishers as they were on their trip, the Langes had little opportunity to experience the exhilaration of city culture, which was in the midst of “The Roaring 20s”. The nation’s economy was growing almost too quickly, leaving the common worker behind. Not only was Prohibition, instituted in 1920, in full swing, but so were its violations. “Speakeasies” were ubiquitous. The Harlem Renaissance included the Savoy and Cotton Club; Cab Calloway, Duke Ellington and Ethel Waters performed there. The Lindy Hop and The Charleston were popular dances. The “Ziegfeld Follies” dazzled Broadway. The nation was still agog over Charles (“Lucky Lindy”) Lindbergh’s solo transatlantic aeroplane flight in May. American extravagance and exceptionalism was on display.

With their District of Columbia stop behind them, the Langes sailed for Europe in late autumn, 1927, perhaps to reach Odense in time to celebrate Morten’s birthday. Jakob seemed pleased with their tour, having delivered the message of the Danish cooperative movement and sharing experiences and philosophies with many people of similar views. The movement in the United States was represented by numerous eastern institutions, from colleges to folk schools to dreams in the minds of progressive individuals.

Chapter 3. 1931

As ethereal as the United States economy and society were during Jakob’s first visit in 1927, just so low was the country during his second, in 1931. In October, 1929, the Wall Street bubble burst, the Stock Market swooned and by 1931, there were bread lines across the country. Herbert Hoover (1874–1964) was President, but there were rumbles of disappointment. Prohibition was still the law of the land, but violations were even more prolific than during Jakob’s first US visit. “Shanty Towns” and “Hoovervilles” of displaced workers existed in the squalid shadows of all US cities. Although some of the elite families had lost everything, many others had not and societal stratification was more severe than ever. It was the juvenile stage of “The Great Depression.”

As marginal as mycology had been for Jakob’s prior visit, so his political and cultural ideas were in 1931.

The Mycological Society of America did not exist in 1931 (Fitzpatrick 1932, 1934). Mycologists met as a section of the American Academy for the Advancement of Science. Nonetheless, local to national forays took place where mycological professionals could rub shoulders over specimens and breakfasts.

Lange (1931) “This second trip had partly other purposes and therefore also a different character than the first. It was mostly about botanical items, especially, of course, research on mushrooms. During my first trip, I naturally now and then had looked at the mushroom flora in different areas and found that it was mainly composed of the same species as at home. But in the books about American mushrooms I mostly found “American” species mixed with relatively few European. It was quite clear to me that this most likely was caused by, so-to-speak, a misunderstanding of each other’s language, so what in Europe was called by one name had another name in America. [But by now] I had ... been painting portraits of Danish mushrooms for a long time - about 1000 species. And I got the idea to go there (US), bring the pictures and gather the American mycologists and discuss with them, armed with the [common] background of the pictures and in this way come closer to the ‘truth’.

“I sent my plan to the leading universities and to my private correspondents in the US and had, in this way, in 1931, planned such small mycological meetings in different areas, at Universities in the states of New York (Cornell), Michigan (Ann Arbor), Canada (Winnipeg), Oregon (Corvallis), at the Department of Agriculture in Washington [DC], in the forest- and lake-camp in the Adirondack Mountains and finally the mycological society in New York. So, it was a rather comprehensive plan, but the Americans were very interested and took good care of the arrangements. The largest approval was at Cornell where mycologists from about ten states (about 50 all told) were summoned and where a large apparatus with microscopes etc. was present and excursions arranged. The whole business had for me the important result that it was living proof of the value of such illustrated works and thus shaped the background for my thoughts of publishing my large mushroom-picture-work [*Flora Agaricina Danica*], which was realized starting in 1934 (Lange 1935a) and now is close to being finished.

“The Carlsberg-Foundation and the Rask-Ørsted-Foundation supported my plans and this along with the lecture payments made an economic balance possible, even if we were three, since both Leila and our 12-year-old son, Morten, joined the trip”.

In his English language report (Lange 1934), he gave a somewhat different itinerary. “Setting out from New York in the middle of August, my itinerary took me through Massachusetts, Vermont, the Adirondacks, Michigan, Minnesota, part of the territory south of Lake Winnipeg to the Canadian Rockies and the Pacific coast from Vancouver to Los Angeles and back to the south-eastern States, returning via Washington to New York towards the end of October”.

Lange’s purpose was not only to experience American mushrooms and to share opinions with American experts, but to exercise his concepts of ecology, distribution and taxonomy of both the mycota and flora. He was well-versed in the northern European groups. In his English report of the 1931 trip (Lange 1934), he outlined his concept of similarities between the European and North American floras (Lange 1913). “When a European botanist makes the acquaintance of the plant life of north-eastern America, he cannot avoid being impressed by the similarity of the floras on both sides of the Atlantic. To be sure, he encounters leading American genera, such as *Aster* and *Solidago*, represented by hundreds of species, which are only scantily represented in

the European flora and vice versa. But apart from these, the flora on the American side consists mainly of two types: the introduced species and the parallel ones (i.e. species which, although not identical with the European ones are so similar that it often requires a keen and practised eye to distinguish between them”).

However, did these designations also apply to the mycoflora?

Lange (1934) “That certain fungi have a universal distribution is a well-known fact. These cosmopolites are either native (e.g. many coprophilous fungi, such as Coprini) or they are introduced from one continent to another, having become established in their adopted home, sometimes even more fully than in their native land. This is true of numerous parasitic forms, such as the potato-blight (*Phytophthora infestans*), the gooseberry-mildew (*Erysiphe Mors-uvae*) and the hollyhock-rust (*Puccinia Malvacearum*)”.

“On the other hand, it is also a well-established fact that the flora of any continent, besides these cosmopolites, comprises an element of endemics: species and even genera, which are exclusively American or European. In the phanerogamic plant world, the overwhelming majority of the species are decided endemics. But what about the mycoflora? Is the main body of the American fungus-flora decidedly ‘American’ or does it consist for a large part of cosmopolitan species which are familiar to the European mycologists of old and, therefore, in common parlance are called ‘European’ species? And finally, are the specifically American species mainly parallels or are we more likely to meet with species which represent other types, widely separated from those met with in the Old World? In other words, is the American fungus-flora chiefly characterized by congruency, parallelism or incongruity?”

An anecdote was inserted: “But stronger and more lasting than any other impression is the evidence of the wonderful cosmopolitanism of the Agarics. When you have once found, in a Danish *Sphagnum*-bog, a few specimens of the ‘new’ species *Stropharia psathyroides* Lange, it gives you a shock to meet with the very same plant in a bog in Oregon, near the Pacific Coast and only an hour later to come upon *Lepiota cygnea* Lange, of which the only known specimens were theretofore those gathered in 1925, a few miles from my Danish home”.

Lange furnished examples of agarics he considered to belong to these categories and, in “*Flora Agaricina Danica*” (FAD), repeated some of his conclusions (Lange 1935b).

In America, word spread of Lange’s proposed appearance. Harry Morton Fitzpatrick (1931), a ringleader of the movement to establish a formal mycological society (Fitzpatrick 1934) and a professor at Cornell, issued an invitation: “Doctor Jacob [sic] E. Lange, well known Danish student of the mushrooms, will arrive in New York the middle of August for several weeks of collecting in the north-eastern United States and eastern Canada. He wishes to study especially the parallelism and identity of American and European species of Agaricaceae. A definite itinerary has been arranged. Inquiries regarding its details may be directed to Doctor C.W. Dodge at Pawlet, Vt.

“From August 28 to September 2 inclusive, Doctor Lange will be at Ithaca, N.Y. The region about Ithaca is especially interesting to him because Atkinson published over a period of years on locally collected materials. Fungus forays will be made daily to nearby points of interest in the effort to see a large number of species.

“In order that the conceptions of species as held by Peck, Atkinson, Kauffman and other older American workers in the group may be clearly understood, it is imperative that Doctor Lange be enabled to exchange ideas in the field with their students. To this end, American mycologists, especially those interested in mushrooms, are urged to come to Ithaca and cooperate in making these forays a success. Students with only a minor interest in the Agaricaceae will also be welcomed and the foray will be arranged in such a manner that collecting in other groups will be fruitful. Incidentally, the Atkinson herbarium has been put in good order in recent years and is now available for consultation in the new Plant Science Building at Cornell University.

“Those who plan to attend the Ithaca forays are asked to notify the undersigned at as early a date as possible. Arrangements will be made for lodging, meals and transportation at a reasonable rate. Information concerning these items or other features of the plans for the forays will be gladly given”.

On his previous trip in 1927, Lange had emoted on the New York City skyscrapers, but now in 1931, he must have marvelled over the new Art Deco-decorated Chrysler Building, opened almost simultaneously with the Stock Market crash in 1929 and then soon eclipsed by the Empire State Building some blocks south, opened in 1930. For many later years, they would dominate the city’s architecture for travellers arriving by luxury liners or later by aeroplane.

Before relating Lange’s “study-tour,” it is necessary to acknowledge the clues left in the collections made during his visit which remain in herbaria. MycoPortal (2021) can be sorted by collector and date and when searched for Lange and 1931, the result is 14 such collections, but just as important, the dates of each collection, location, in some cases, his co-collectors and the herbaria housing these specimens are disclosed.

HARVARD, CAMBRIDGE, MASSACHUSETTS (dates unknown). Lange did not detail a stop at Harvard, but his comments on some of the original mushroom illustrations by Bridgham and Krieger, commissioned by William G. Farlow, attest to his presence. Donald Pfister (1975 & pers. comm.) observed that Lange had access to more than 600 such paintings, from which only 103 plates were composed (Farlow 1929). Although the format of Lange’s “Flora Agaricina Danica” differed from that of Farlow’s “Icones”, the two publications were not totally different in concept.

VERMONT (18, 19 August). Although several destinations of Lange’s itinerary were anticipated, some were more explicit. An example of the latter was his visit to Vermont. That such a foray actually existed is confirmed by Lange’s (1941) mention of collecting *Volvaria pubescentipes* Peck. An additional sketch (Fig. 13) confirms this. MycoPortal records five such collections, all housed at the Farlow Herbarium, Harvard, perhaps indicating attendance by David Hunt Linder (1890–1946; Rusden 1947) and/or William H. (“Cap”) Weston (1890–1978; Wilson 1979).

The family home of Carroll William Dodge (1895–1988: see above) was in Pawlet, southern Vermont. He had studied at Middlebury College and, there, had come under the influence of Edward Angus Burt, who soon moved to St. Louis as Professor at Washington University and mycologist at the Missouri Botanical Garden (Petersen

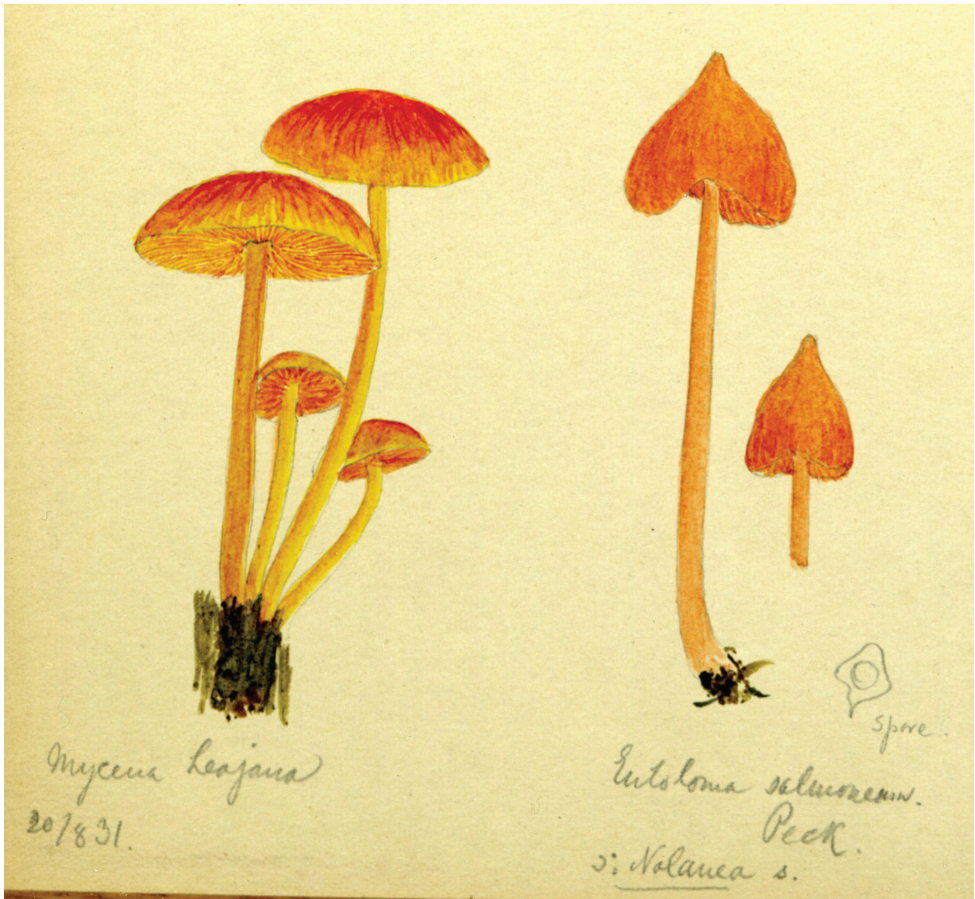


Figure 13. Lange aquarelle sketch dated 20 August 1931 (Pawlet, VT). Left: *Mycena laejaena* ("jaejana"). Right: *Entoloma salmonea*. Courtesy Natural History Museum of Denmark, Copenhagen.

2019). Dodge also moved to St. Louis and received his PhD from Washington University in 1918. After a hitch in the Army (World War I) and some time at Harvard, in 1931, he was packing his belongings for a move from Harvard to take up the position held previously by Burt. Probably, it was the family home in Vermont that the informal foray of 1931 used as headquarters.

It was the first foray for Lange in the United States and he had not yet established a routine. He took time to make eight water-colour sketches and recorded more than 40 names in his notebook.

SEVENTH LAKE, THE ADIRONDACKS, NEW YORK (20–25 AUGUST). The first widely announced stop on Lange's itinerary was a select foray in the Adirondack Mountains of New York. Fred Carleton Stewart (1868–1946), plant pathologist at Cornell, had a summer "camp" on a lake-shore in the Adirondack Mountains (Fitzpatrick, 1947; Gruff 2007) and, on more than one occasion, he opened its "spartan" facilities to mycological forays for small groups, including the Lange family in 1931 (Fig. 14).



Figure 14. The Lange family, probably in the Adirondacks in 1931. Source: Mycoologia 26(1): 2.

A typical scene was painted by Jakob, unmistakable with its “white pines” and evergreen forest and, perhaps, Seventh Lake (Fig. 15).

Lange (1941) reported that a relatively rare species, *Lactarius repraesentaneus*, was observed and he compared it to the European *L. deliciosus*. MycoPortal lists two collections, *Inocybe longicystis* and *Pholiota spumosa*. The first remains at Cornell (probably deposited by Fitzpatrick), the second at the Farlow Herbarium, again perhaps indicating attendance by Linder and/or Weston. Lange completed eight water-colour sketches and registered (questionably) some 60 names in his notebook.

Years later, in his memory of the affair, Hesler (1975) furnished a rare physical description of Jakob Lange. “... I recall that, in my good fortune, I attended the Adirondack Foray in 1932 [sic]. Lange brought with him his 200 completed plates, later published in FAD. The weather being clear and calm, one day he spread all the plates over the lawn of our cottage for us to view. I recall also that one of his paintings (a *Lepiota*) was made by Lange out on the lawn, where he used a barrel for a table and an orange crate for a stool. To complete this painting required some fifteen or twenty minutes, as I witnessed the job. It appears perhaps as one figure in either plate 12 or 13 [of FAD].

“Lange also brought with him his wife [Leila] and his son, Morten, then about 8 years old [actually 12] and, at that time, he [Morten] knew many of the agaric genera at sight. (Dr. Morten Lange has for some years now been mycologist in The University of Copenhagen [written in 1975]).



Figure 15. Jakob's painting of the scene at Seventh Lake, New York. Source: Lene Lange.

"... He (Jakob) was of rather exceptional physique, perhaps 6 ft., 4 in. height, 190 lbs., lean, good humored, a delightful personality, he spoke and wrote excellent English and, as a conversationalist, one of the best. His devotion to the people led him, while here at the foray, to visit the Penland (N.C.) Folk School". While certainly possible, Lange surely visited the John C. Campbell Folk-school, also in North Carolina.

CORNELL UNIVERSITY, ITHACA, NEW YORK (25–28 August). Although MycoPortal data show a month-long hiatus between the Adirondack foray (26.8.31) collections and those from Corvallis, Oregon (27.9.31), Lange's notebooks and paintings make the Cornell dates more precise. Fitzpatrick's announcement of the Cornell event set the dates as 28 August through to 2 Sept. In his post-tour report (Lange 1934), Lange noted that about 50 mycologists of all specialties, from some 10 states, gathered for those days. Forays visited some of Atkinson's (and his student, Calvin Kauffman) favourite collecting spots. Korf (1991; Petersen 2021) wrote that at least three of these well-known collecting grounds around Ithaca had been purchased sub rosa by Curtis Gates Lloyd (1859–1926) and were to become known as the Lloyd-Cornell Preserves. Strangely, MycoPortal lists no collections from these forays. If collections were preserved, their identifications, locations, collectors and herbaria remain undiscovered. Lange painted only two mushroom sketches (Fig. 16), the last of the entire trip, surely reflecting a more hectic routine resulting in copious notebook entries. He logged 50+ names. A list of participants has not been unearthed, but an iconic photo shows F.C. Stewart, H.M. Fitzpatrick, Vera Charles, Lange, Gertrude Burlingham, C. W. Dodge and L.R. Hesler, an august assemblage (Fig. 17).



Figure 16. Lange aquarelle sketch dated 28 August 1931 (Cornell foray). *Lactarius subpurpureus*. Courtesy Natural History Museum of Denmark Copenhagen.

Hesler's interest in the Adirondack and Cornell forays remains somewhat murky. Before and after his arrival at the University of Tennessee in 1919, he was a phytopathologist, distinctly in the mould of his Cornell PhD under H. H. Whetzel (Petersen 1978, 2021; Korf 1991). By his own recollection, Hesler's migration from plant pathology to mushroom taxonomy came much later, at about the time of the Adirondack and Cornell forays. He had begun to show interest in the fleshy fungi of the Great Smoky Mountains and was known to hitch rides on logging trains in and out of the mountains during the mushroom season. It was not until the catastrophic fire of 1934, which destroyed the entire botany department and all its faculty offices, laboratories, classrooms, library and herbarium that Hesler decided to point his career towards agronomy. What role his interaction with Lange might have had remains obscure, but he sent a signed copy of his "Mushrooms of the Great Smokies" (Hesler 1960) to Morten Lange "with personal good wishes".



Figure 17. Mycological group at Cornell. Left to right: F.C. Stewart, H.M. Fitzpatrick, Vera Charles, Jakob Lange, C. W. Dodge, Gertrude Burlingham, L.R. Hesler. Source: Cornell University.

ONTARIO (?OTTAWA; dates unknown): The discrepancy between Lange's notebook dates for Ithaca and those in Fitzpatrick's announcement may have provided enough time for a side trip mentioned only in passing in Lange's notebooks. Lange's described itinerary does not report any time in eastern Canada, but MycoPortal lists a single collection by Lange from Ontario, Canada, *Thelephora terrestris*, on 16 September 1931 – nearly two weeks after explicit Cornell and well before implicit Vancouver – with no co-collector, but improbably housed at the University of Wisconsin, perhaps a link to a co-collector.

By searching for such a link, though, it might be coincidental that, in Toronto, Herbert Spencer Jackson (1883–1951) had taken charge of the fungus herbarium at the University of Toronto in 1929. He had degrees from Cornell, Harvard and the University of Wisconsin (PhD in 1929) and was a vigorous mycological researcher (Bailey 1952). It is pure conjecture that Jackson might have come south to participate in the Cornell forays and invited Lange to return with him to Toronto.

UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN: Again, this visit was noted only marginally, but Lange noted the water-colour illustrations in the collection of Dr Howard Atwood Kelly (1858–1943), executed by Lewis Charles Christopher Krieger (1873–1940; Petersen 2019), which had been recently bequeathed to the University and housed in the herbarium. Krieger's illustrations surely rivalled those by Lange himself. No field trips or specimen numbers were recorded in Lange's notebooks.

Edwin Butterworth Mains (1890–1968; Smith 1969) was a Michigander by birth and rearing. After starting at Michigan State University, he transferred to the University of Michigan for his B.A. and earned a PhD in 1916, with Calvin H. Kauffman as major professor. After some years at Purdue University, Mains returned to become a professor at the University of Michigan in 1930 (after the debilitating illness of Kauffman). Kauffman's illness and death must have been a disappointment for Lange: Kauffman was an enthusiast of colour photography for illustrating mushrooms and had used black & white photographs for his volumes on the agarics of Michigan (Kauffman 1918), while Lange insisted on watercolours. Kauffman also had experience with western agarics and so could have prompted Lange as to what he might find there.

Bessie Bernice Kanouse (1889–1969) was also a Michigander through and through. Her B.A. was from the University of Michigan, as was her PhD in biology in 1926. She was appointed Curator of the University of Michigan Herbarium and assistant to the Director, Calvin H. Kauffman. She accompanied Kauffman on at least two collecting trips, but her own interest was in “water moulds,” on which she published (Kanouse 1927a, b).

Notably, Kauffman's student, Alexander Hanchett Smith (1904–1986) had been obliged to change professors upon Kauffman's illness and now was being supervised by Mains. Smith's M.A. was gained in 1929 and his PhD dissertation, “Investigations of two-spored forms in the genus *Mycena*” earned his PhD in 1933. Conversation with Lange could have been lively. As Atkinson and Kauffman before him had used photography (Petersen 2019), Smith was to use this medium through his entire career. Moreover, the first instalment of Lange's “Studies” series was on *Mycena* (Lange 1914), so taxonomy could have been discussed as well as methodology. Pat Rogers, currently collection manager for fungi at the University of Michigan, commented that Smith spent extended time in Nova Scotia, Canada, during the time of Lange's visit, perhaps as assistant to Lewis Edgar Wehmeyer (1897–1971; Wehmeyer 1934).

Just a few buildings away, Dow Vauter Baxter (1898–1965; Smith 1967) was a forest pathologist in the School of Natural Resources (now the School of Environment). An inveterate field botanist, he was already engaged in a long-term study in Alaska. Whether or not he met Jakob Lange is unknown to us.

A half-day's ride from Ann Arbor was East Lansing, the home of Michigan State University. In 1931, Ernst Athearn Bessey (1877–1957) was serving there as Dean of the Graduate School, building its programme in plant pathology, amongst many others. Whether he might have met Lange is unknown to us, but it would surely have been possible. In addition to his Deanship, Bessey was developing his book, “A Textbook of Mycology” (Bessey 1935).

MINNESOTA (perhaps also WISCONSIN): Although both States were merely proposed, but not further mentioned in Lange's notebooks, these States had a wealth of Scandinavian settlers and universities with strong phytopathology research faculties.

Lange's reference to a stop in Minnesota is opaque. One possibility might have been in Minneapolis, where Clyde Martin Christensen (1905–1993) was a graduate student at the University of Minnesota. Christensen (2021) obtained his B.A. there two years before (1929) and his M.S. in 1930. In 1934, he joined the faculty and was awarded his

PhD in 1937. He spent his entire career at that university until 1975 and retirement. While his research did not emphasise fleshy fungi, he wrote two popular volumes on the subject (Christensen 1943, 1946), neither of which bore reference to Lange.

The Minnesota Mycological Society was founded in 1899, as the second oldest such organisation in the country (Boston was first, four years previous). For some years, its founder, Dr Mary Whetstone,⁽⁸⁾ was corresponding secretary (Dillon 1924; Davis and Seaver 1930). Her considerable correspondence (and, apparently, associated specimens, usually fresh!) with Charles Horton Peck (1833–1917), Curtis Gates Lloyd (1859–1926), F.J. Braendle [USDA botanist in Washington, DC; dates unknown; for whom Peck (1899), found some to be new] and others often led to identifications and return letters. Clements' (1910) popular mushroom book was available, even although Clements had moved on. Given the host of Scandinavian and German settlers over this land of lakes, forests and biting flies, it would have been no wonder that mushroom hunting was popular and a European expert would have been welcome to join forays.

Although still marginally known for “pure” mycology in 1931, the University of Minnesota was a juggernaut in plant pathology, especially cereal diseases. By 1931, Elvin Charles Stakman (1885–1979) headed the Plant Pathology Department of the Division of Vegetable Pathology and Botany at the University (Peterson 2001). Amongst many other students and post-doctoral fellows, he acted as consultant to A.H.R. Buller at the Manitoba Agricultural School and was largely credited with the establishment of plant pathology in Canada. Although marginal to Jakob Lange, Stakman and his fellow faculty would have been politically cogent conversants.

WINNIPEG, MANITOBA; LONGPINE LAKE, INGOLF, ONTARIO, CANADA (14–18 Sep): Unlike the forests encountered on both coasts, south-central Canada is located at the northern rim of The Great Plains. Although less rich in large mushrooms, careful inspection of scattered large groves of aspen and/or conifers could produce results. Lange (1941) noted a collection of *Xeromphalina caudicinalis*, surely found under conifers, but MycoPortal does not record any such. Enigmatically, collection numbers from 175–190 were noted by Lange, as well as a single sketch (*Lepiota illinita*). The collection numbers overlapped those later recorded from both Lake Louise and Vancouver.

Guy Richard Bisby (1889–1958) was a professor at the Manitoba Agricultural College (later University of Manitoba) in Winnipeg. A South Dakotan by birth, Bisby earned his B.A. from South Dakota State College, his Master's degree from Columbia University (NY) and PhD from the University of Minnesota in 1918 (Purdue 2021). In 1920, Bisby moved to Winnipeg (and gained citizenship of Canada; Anonymous 1932a). In 1937, he accepted a position with CMI, Kew. His research centred in compilation of floristic lists, “The Dictionary of Fungi” (with Geoffrey Clough Ainsworth, 1905–1998) and nomenclature of fungi (Bisby 1946). Although editors changed over time, “Ainsworth & Bisby's Dictionary of the Fungi” reached its tenth edition in 2008 (Kirk et al. 2008).

Lange (1931): “One of the funniest of these gatherings - but we were only two, a Dane [mycologist] and a Canadian (+ Morten) – was when we came up to Winnipeg in southern central Canada, close to the large Lake Winnipeg. When we arrived, we were met at the station by Dr. Bisby; he immediately asked my wife if she could cook. 'Yes, at

the household level,’ she answered. ’Then the plan can be realized,’ he said. ’I have borrowed a cabin in the wilderness, 20 miles from here, there we will go for some days’”.

The cabin was actually Longpine Lake, near Ingolf, a short distance over the provincial line in Ontario. There, they lived in a cabin as noted by Bisby. His human side was revealed in a small note by Morten (Lange 1996): “The first month [of our trip] I avoided English conversation. It greatly improved when we came to Canada and lived in a hut at a lake in the forest near Winnipeg. Our host, Professor Bisby, took me on his daily tour in the canoe to the grocery store. In the quietness of the canoe, he quietly convinced me that I probably could speak English, when he was the only one to listen”.

Some details of those days can be found in MycoPortal and a search for appropriate collections in the National Herbarium of Canada at Ottawa (DAOM). Arrival in Winnipeg 14 Sep (a Monday), was spent in the town, with some time devoted to a stroll on the campus of Manitoba Agricultural College (with seven collections). It is assumed that the 15th was spent in transportation to the hamlet of Ingolf, about 145 km away; Longpine Lake was nearby. Upon arrival, only three collections were made, but on the 16th, at least 32 samples were collected and, on the 17th, 41. On the 18th, only 12 specimens were collected, but on that day, it may have been necessary to pack and head for Winnipeg.

A couple conclusions may be drawn from these data. First, Guy Bisby was a very organised host. He must have organised a drier and some way to bring at least 96 collections back to Winnipeg. Moreover, these collections were labelled appropriately and sent to Ottawa for deposit in DAOM. Second, in 96 collections, there was not a single duplicated name. Third, aside from four non-agaric fungi, all other collections bear names of mushrooms. Fourth, a rough review of collection labels shows a typical roster of autumn mushrooms, at least further east in North America, dominated by *Cortinarius*, *Lactarius* and *Russula*. Sixth, while all collections bear both Lange’s and Bisby’s names as collectors, there is no notation on the name of the identifier. It is, therefore, impossible to know if the fungi were recognised as “typically European” by Lange or by Bisby as “American” with European authors’ names.

A fellow faculty member of Bisby in Winnipeg was Arthur Henry Reginald Buller (1874–1944; Estey 1986). An immigrant from Great Britain, he arrived in Winnipeg in 1904. He was allowed to spend three or four months per year back in Birmingham, England or, later, at Kew, doing research in laboratories and libraries. By the time Lange came through southern Manitoba, Buller had published the second volume of “*Researches on Fungi*,” which would eventually (and posthumously) reach seven volumes (Buller 1922). In addition to this major achievement, Buller wrote scores of individual papers, usually in the “Transactions of the British Mycological Society”. In spite of the popularity of his pedagogical fieldtrips, whether Buller joined Lange and Bisby or whether the Langes stopped in Winnipeg is unknown to us.

Although John Dearness (1852–1954) was retired in 1922, he remained active, amongst other contributions, as co-author of “The Fungi of Manitoba” (Bisby et al. 1929, 1938). His entire mycological career, however, was spent in western Ontario and he may have met Lange if he (Lange) travelled to Ontario after the Cornell forays.



Figure 18. Jakob's painting of the scene in Banff, Alberta, Canada. Source: Lene Lange.

LAKE LOUISE, ALBERTA, CANADA (including 21 Sep): Included merely as a mention in Lange's itinerary, collection numbers 178–183 and 191–195 were recorded. These numbers overlap those from Long Pine Lake, Manitoba. There was time for a “portrait” of Banff (Fig. 18).

VANCOUVER, BRITISH COLUMBIA, CANADA (approx. 23 Sept): In an easily overlooked paper in *Mycologia* on Vancouver agarics, Jean Davidson (1930) thanked “Prof. F[rank] Dickson of this University” [Univ. of British Columbia, Vancouver] for his help in identifying her collections and the writing of the paper. English born, Frank Dickson (1891–1969; Yarwood 1970) was the first instructor of plant pathology at the University and taught forest pathology and mycology there from 1923–1956 (Estey 1994). In addition to his duties on campus, Dickson was part of the staff at the Aleza Lake Research Station (2007), over a hundred km north of Vancouver, probably during the summer months. Although only a slim chance, Aleza Lake may have been Lange's opaque reference to the Canadian Rockies. Dickson's name appears in the directory of mycologists of the British Empire (Anonymous 1932a). Morten Lange provided a photo of the family with some local Danes in front of a great tree in the vicinity of Vancouver (Fig. 19). Otherwise, little was made of the stop. Collections numbers 178–187 and 191–195 were logged, but these numbers overlap those from Manitoba and Alberta.

and the Olympics to the west. Perhaps Hotson related Calvin Kauffman's comment on west coast mushrooms: "In 1922, when Dr. C.H. Kauffman visited this state on a mycological trip, he made the remark that '... as a rule the mushrooms of Western Washington and Oregon are Friesian or new', indicating that our forms are more like those found in Sweden than those of eastern United States" (Hotson 1936). To this, Lange could add his own observations. Kauffman's (1925, 1930) papers on fungi of relatively nearby areas preceded Lange's visit and may have spurred Lange's interest in the forests of the west coast.

Perhaps Lange's visit may have spurred Hotson to put his mycological experience into words (Hotson 1934, 1936) and he encouraged students to also pursue work on the agarics (Hotson and Lewis 1934; Hotson and Stuntz 1938). In the paper with Stuntz, Lange's "*Studies*" (no. 6, 1926) and his 1934 report of his United States trip were cited. As a grace note, however, their illustrations of the agarics of the Pacific Northwest were all photographs.

They also echoed Lange's sentiments this way: "The genus [*Agaricus*] is well represented in the Pacific Northwest, but, when one wishes to identify collections made in this region, he faces an obstacle in the lack of available information concerning the local flora and also in the fact that some of the species occurring here are more closely allied to European forms than to those found in the eastern United States. To further complicate matters, the student will often find a lack of agreement among mycologists concerning the interpretation of a particular species and is apt finally to be more confused than helped by the literature he consults. This condition has been found as prevalent in Europe as in America" (Hotson and Stuntz 1938).

CORVALLIS, OREGON (approx. 27 Sept): Sanford Myron Zeller (1885–1948) was the mycologist at the Oregon Agricultural Experimental Station (associated with Oregon State University) in Corvallis. His PhD was from Washington University in St. Louis, where Edward Angus Burt was the mycologist. At the time of Lange's visit, Zeller's research emphasis was on parasitic fungi, less so on gastroid fungi (Gilkey 1949), including hypogaeous forms, the latter a group not previously investigated by Lange, but which he noted when discussing his itinerary. Together with Zeller, at least two field trips were undertaken (only 27 Sep appears in MycoPortal), although their reported destinations were hardly compatible in one day. On one foray in the vicinity of Mt. Hood, collection numbers 223–237 were recorded. On the second, to the Coast Range, Lange (1941) later reported finding his own *Lepiota cygnea*, not yet published, but theretofore known only from a couple collections from his home in Denmark (Zeller 1938), amongst collection numbers 238–248. Equally, what Lange knew as his own species, *Stropharia psathyroides* from a Danish *Sphagnum* bog, was discovered in the same habitat in Oregon. MycoPortal reports three specimens: two of *Lepiota oculata* and one of *Gomphidius nigricans*.

At the University, Helen Margaret Gilkey (1886–1972) was Professor of Botany and Curator of the Herbarium. Her Master's degree thesis entitled "Oregon Mushrooms," had led to doctoral work at the University of California and her PhD dissertation, with William Albert Setchell as major professor, was "A revision of the Tuberales (truffle fungi) of California" (Leonard 2021). With this background, she was already a

likely contact for Lange, but her talent as an artist-illustrator might well have matched Lange's insistence on accurate depictions. Lange, however, saw little value in dried herbarium specimens and coloured portraits of Tuberales were less than helpful. They might have differed over this subject. Gilkey's (1939) later magnum opus took in all of North America and was accompanied by superb illustrations.

BERKELEY, SAN FRANCISCO BAY AREA, CALIFORNIA (visit problematic): Surely, a most conjectural stop for Lange and family was the California Bay Area; San Francisco and especially the University of California, Berkeley. Lange may have seen Edwin Bingham Copeland's (1873–1963; 1904a, b) small series on new and interesting California fungi, but these papers were written years before Lange's tour, when Copeland was a student at Stanford University in Palo Alto and before his PhD from Halle, Germany. As coincidence would have it, Copeland was changing venue in 1931 from the Philippine Islands to Berkeley, where he was less familiar with mycological surroundings. Copeland was to become internationally known for his work in pteridology (Wagner 1964, 1965).

A person with a much longer career in Berkeley was William Albert Setchell (1864–1943; Drouet 1943). Setchell was already better-known in phycology than mycology, although he had acted as supervisor for Helen Gilkey's Master's degree. She may have advised the Langes to visit Setchell.

Elizabeth Eaton Morse (1864–1955; Bonar 1956), a New York City teacher, made her summer vacations into naturalistic trips, one of which was to Berkeley in 1925. There she stopped and inquired as to any summer courses in botany. There was none, so she proceeded to Yosemite National Park to collect fungi. She never returned to the east, but was put on staff at Berkeley, remaining so for many years as curator of fungi and all-round mycologist (Vellinga 2020). She could have been a candidate to take the Langes into the field in Berkeley's environs.

Elmer Drew Merrill (1876–1956; Robbins 1958) had served as Dean of Agriculture at Berkeley, but, in 1929, had moved on to become Director of The New York Botanical Garden and afterwards to the Arnold Arboretum of Harvard.

It must be written again, however, that we have no evidence that Lange stopped in the Bay Area, so his possible interaction with any of the triumvirate of botanical friends is purely conjectural.

LOS ANGELES, CALIFORNIA (dates unknown): Los Angeles appears only as a single-word mention in Lange's proposed itinerary. The nearest predictable mushroom-hunting grounds were in the mountains away from the coast, but even more improbably, mycologists were also less prolific.

One person with mycological experience and resident in the Los Angeles area was Effie Almira Southworth Spalding (1860–1947; Southworth 2021). Reportedly, she was the first woman hired in a mycological field by the USDA, including those in the Washington, DC, headquarters and her story is interesting.

Born in New England, she attended Allegheny College for a year, but transferred to the University of Michigan, where she was awarded a B.A. in 1885. She immediately became an instructor at Bryn Mawr College, near Philadelphia, on a two-year

contract. In 1887, she was hired by the USDA as the third person in the Section of Mycology, along with Erwin F. Smith and Beverly T. Galloway and moved to Washington, DC (Ristaino and Peterson 2013; American Phytopathological Society 2001). Her paper on cotton cankers was a major advancement in plant pathology. Her short paper in the “Bulletin of the Torrey Botanical Club” dealt with an assumed polypore – perhaps a large sclerotium (Southworth 1891). Five years later, she became an Assistant in Botany at the newly-established Barnard College in New York, where she must have interacted with Lucian Underwood, the mycologist at Columbia University across Broadway from Barnard. She married Volney Morgan Spalding, a botanist at the University of Michigan in 1895 and moved there. Soon, though, his health began to fail. Eventually he was diagnosed with tuberculosis and the couple moved to Tucson, Arizona. There, he worked at the Desert Botanical Laboratory of the Carnegie Institute of Washington. Retired in 1909, he spent the rest of his years in a Loma Linda, California, sanatorium, where he died in 1918. Almost immediately, Effie was hired to the faculty of the University of Southern California as Assistant Professor of Botany. There she spent her remaining years, during which she was awarded an M.A. in 1922, with a thesis entitled “Form alterations and growth in cacti,” established the herbarium and wrote occasional papers on plant pathological fungi. She died years later, in 1947. Her name was mentioned as a notable early mycologist by Maroske and May (2018).

That she was on faculty and could have met Lange in 1931, is beyond dispute, but whether they, in fact, met, is highly questionable. She would have been 71 years old and a foray or two would have been improbable. What was much more expected, however, was that Los Angeles served as the Langes’ terminus along the west coast and their departure point for return to the east.

In 1922, Bonnie C. Templeton (1906–2002) moved from Nebraska to Los Angeles. According to Wikipedia (Templeton 2021), amongst several jobs she occupied during the following decade, one was assignment as an assistant to a botanist at the California Botanical Garden in 1928. She fell in love with the work of sorting and identifying plant specimens and the following year was appointed Curator of Botany at the Natural History Museum of Los Angeles County, a position she held from 1928 until 1970. Through night courses, she earned B.A. (1941) and Master’s (1947) degrees from the University of Southern California. As was common, she was refused permission to enter a doctoral programme at USC, but obtained her PhD from Oregon State University. She was a person of wide interests and MycoPortal records two specimens of fungi she collected in 1931, both of them earlier than Lange’s time in southern California. Whether they met is lost in history.

Although preceding Southworth by several years, Alfred James McClatchie (1861–1906), a Professor at Throp Institute of Technology (now known as California Institute of Technology, “Caltech”), was an active botanist, including fungi and published two papers which included fungi of Pasadena vicinity (McClatchie 1895, 1897). McClatchie was educated at Olivet College in Michigan, with an A.B. from the University of Nebraska, with Charles Bessey, in 1890. McClatchie’s Herbarium was sold to the New York Botanical Garden and Murrill (1912b) noted that McClatchie’s

early specimens had been sent to Setchell, Ellis, Morgan, Peck, Underwood, Barnes and Hasse (the last two not familiar names to us: RHP, HK).

Also worthy of mention, Charles Fuller Baker (1872–1927; Essig 1927) collected fungi amongst many other biological groups in southern California at about the same time as McClatchie. Born in Michigan, he attended the Michigan Agricultural College (later Michigan State University). Spending much of his professional life in tropical regions, he was an inveterate collector; his entomological specimens alone numbered over 400,000. From 1899–1901, Baker was zoologist at the Alabama Polytechnic Institute and connected with the Alabama Biological Survey, where he was a colleague of Franklin Sumner Earle (1856–1929) just a few years after George Francis Atkinson (1954–1918). In 1903, Baker was on faculty at Pomona College in southern California, but his brush with the region was short-lived.

“SOUTHERN STATES” (ARIZONA, KENTUCKY, TENNESSEE; dates unknown): From MycoPortal, we know that the Langes were in the neighbourhood of Corvallis, Oregon, on 27 Sep. At that moment, however, the monitor goes black and the next time we have a firm date is 24 October, in Washington, DC. Assuming their mode of transportation as rail and Jakob’s reference to “the southern states,” we can conjecture that they took the Southern Pacific route through southern Arizona (Morten found the Grand Canyon “shocking”), New Mexico and Texas. Reference to the specific States appears only in Lange’s proposed itinerary, with no collection numbers recorded or sketches executed.

William Henry Long (1867–1947; Stevenson 1949), a Texan, obtained his B.A. from Baylor University in Waco, in 1888, after which he was appointed to faculty there until 1892, when he moved to Burleson College in Greenville. In 1899, he left Burleson to study at the University of Texas, where he received his M.A. in 1900. After nine years on faculty at North Texas State Normal School in Denton, a PhD was granted by the University of Texas in 1917. Several summers during this time, Long spent periods with G.F. Atkinson at Cornell University and, thus, rubbed shoulders with the numerous faculty and graduate students there in the Plant Pathology Department (Petersen 2021).

His professional career was at the USDA where he soon was transferred to the Office of Forest Pathology in the Bureau of Plant Industry in Washington, DC. There he found himself in a stellar group of mycologists/forest pathologists. Soon, he was appointed to head up this work in the south-western States, headquartered in Albuquerque, New Mexico. There, he stayed until retirement in 1937. Although his research emphasised tree rusts, he was interested in the gastromycetes and it was probably this that would have caught the eye of Lange. If the two met, possible field work for Lange would have been at relatively high elevation where the pine forests dominated.

From the dry southwest, the Langes would have proceeded through Louisiana, Mississippi and Georgia into North Carolina. Hesler’s comment (written in 1975) that Lange visited Penland School in western North Carolina before returning to Denmark, raises the probability that the Langes re-visited the John C. Campbell Folk-school in Brasstown, NC, only some 100 km away from Penland. Unlike the Campbell school,

founded along the same Grundtvigian principles as the Danish schools, Penland was, from its beginning in the 1920s, a school of crafts, chiefly weaving, selling the products to supplement the meagre wages of the local population (Craft Revival 2021).

WASHINGTON, D.C. (dates surrounding 24 Oct): The Langes (minus Morten) had already seen Washington during their 1927 trip (see above). Their 1931 visit was for very different reasons and now they found a goldmine of mycological activity. The discipline was represented at the US Department of Agriculture, located downtown. The Department had been established in 1862, during the Civil War and within days of the Morrill Act enabling Land-grant Colleges (Petersen 2021). Its functions were divided between two headquarters: research in one location, the herbarium in another. Mycological research centred in phytopathology, as might be expected, which occasionally spun off preserved specimens that travelled to the Smithsonian Institution on the Mall. A considerable roster of plant pathologists worked in the Department. While their research rarely dealt with agarics, they were eager field-biologists and appreciated their local mushrooms. They were (and are) notable and deserve individual sketches.

MycoPortal reports only three collections, from Glen Echo, a suburb and only collection numbers 252–255 were recorded in Lange's notebooks.

By 1931, Cornelius Lott Shear (1865–1956; Stevenson 1957) had seen numerous changes in the Department since his hiring in 1898 as Assistant Agrostologist under Frank Lamson-Scribner (1851–1938), chief of the Division of Agrostology (later succeeded by Beverly T. Galloway (Petersen 2021). In 1901, the Bureau of Plant Industry was established and absorbed much of the Department's research personnel. He was a "moving spirit" in forming the American Mycological Society, which existed from 1903–1906, also a charter member of the Mycological Society of America some thirty years afterwards. At the turn of the century, he was an active member of the short-lived Washington Mycological Club, largely composed of USDA workers. While working days, Shear earned his PhD from George Washington University in 1906. In 1923, Shear was made head of the newly-established Division of Mycology and Disease Survey in the Bureau of Plant Industry, formed by consolidation of Divisions of Mycological and Pathological Collections and the Plant Disease Survey. Shear partnered with Bernard O. Dodge (1872–1960) on a seminal paper introducing *Neurospora* as a laboratory tool. All the while, Shear was establishing himself as a scholar of fungus taxonomy and nomenclature, attending successive International Congresses to promote a uniform nomenclature code. Of note was also his partnership with Frederic Edward Clements (1874–1945) on "The Genera of Fungi," (Clements 1909) which saw both reprinting and revision (Clements and Shear 1951). An appreciation for mycological history saw collaboration with Neil Everett Stevens (1887–1949) on several papers sketching historical mycologists and their activities (Shear and Stevens 1917). Retired in 1935, Shear saw the movement of the mycological herbarium to new headquarters in Beltsville, Maryland in 1941 (Benjamin 1963; Lentz and Lentz 1968), just days before the United States entered World War II. He remained active in the mycological community, including forays, for additional years.

Vera K. Charles (1877–1954; Cash 1956, Rossman 2008) was a transplanted Pennsylvanian who moved to and lived in the District. She attended Holyoke College, but her A.B. degree was from Cornell. Straightaway, she came from Cornell to the Bureau of Plant Industry in 1903 and carried on her work in the Office of Mycological Collections and its successors from that date until her retirement from government service in 1942. While her formal occupation dealt with plant pathogens, especially of imported plants, her bulletin on “Mushrooms and other common fungi” in 1913, with Flora Patterson (Galloway 1928; Patterson and Charles 1915; Charles 1929; Rossman 2002) spawned later bulletins on the same subject (Charles 1917, 1931) and another just a few months before the Langes’ visit (Charles 1931; Rossman 2008)). Vera Charles participated in the Cornell Forays and, during Lange’s Washington visit, they were able to do some mushroom hunting in the nearby suburbs (MycoPortal). After her retirement, she spent several winters in Florida, sometimes accompanied by C.L. Shear and Gertrude Burlingham. Hesler (1975) wrote of her: “Miss Charles was a keen collector of fungi. I saw many of her collections at the Mycological Society Foray at Highlands, N.C. in 1933 where she found several which had rarely been found there before.”

Edith Katherine Cash (1890–1992) professed that her only mycological training was a night course at the USDA Graduate School. Nonetheless, her 1912 A.B. from George Washington University in history and languages got her a job at the USDA as a botanical translator in 1913. Over the following half-century, she progressed through the ranks from junior pathologist (1924) to mycologist (1956). Her “day job” in pathology was augmented by a collaboration with Vera Charles on a USDA Bulletin on common mushrooms. She was a vital part of the triumvirate of women mycologists at the USDA; Charles, Patterson and Cash.

According to Batra (1994), Miss Cash’s work on the discomycetes led to an outpouring of monographs of genera. She would have been an eager person to interact with Lange in 1931.

Another USDA mycologist was William Webster Diehl (1891–1978; Lentz 1981). With an M.A. from Iowa State University (1915), he accepted a job at Clemson College for a year, but soon moved to the USDA in 1917, as Scientific Assistant in plant pathology, but spent World War I in Ithaca, New York, learning the skills of the signal corps. In 1919, he returned to the USDA and began a career in plant pathology. He became a lecturer at George Washington University in 1927. In the 1920s, he met Curtis Gates Lloyd and, by Lloyd’s death in 1929, his (Lloyd) herbarium was left to the Smithsonian Institution, but was housed within the USDA. At the AAAS meeting in Des Moines in 1929, Diehl met W.H. Weston from Harvard and soon prepared a proposal to study *Balansia* on grasses at the Harvard Herbaria. The proposal was approved by John A. Stevenson and C.L. Shear and Diehl was on his way. There is no mention of his meeting Jakob Lange in 1931, but, in 1932, Diehl obtained his Ph.D. from Harvard. In 1941, the USDA mycological collections were moved from downtown to Beltsville, Maryland and, during World War II, Diehl was part of the fabric deterioration unit. In 1958, he retired from the USDA. Over the years, he

published with the other contemporary mycologists. Had he been in Washington over particular days, he surely would have joined Lange in the field.

Anna Eliza Jenkins (1886–1972) was a New Yorker. Born in Walton, in 1907, she enrolled at Cornell University, where she obtained a B.S. in 1911 and an M.S. in 1912. She was hired by the USDA in 1912, without a Ph.D. and she became an Assistant Scientist in the Bureau of Plant Industry. After some additional studies in Washington DC, she received her Ph.D. from Cornell in 1927. Her professional duties dealt with diseases of imported plant material, but soon she began a series of studies of particular causal organisms. She progressed through the ranks to Mycologist in 1945 (through 1952). Her distinguished career surrounded Lange's visit of 1931 and she was one of the several working mycologists in Washington at the time of his visit (O'Brien 1975). Along with many others, her collections are housed at the Agriculture Research Service installation in Beltsville, Maryland.

Another of the mycologists hired by the USDA just after the turn of the 20th century was John Albert Stevenson (1890–1979). Born in South Dakota, his early years passed in a fishing village on the shore of Lake Superior in Wisconsin (Farr 1985). His undergraduate years were spent at the University of Wisconsin, where he was taught by M. Freeman, F.C. Stakman, F.E. Clements and C. Bessey. He emerged with intentions of becoming a plant pathologist, attending George Washington University (D.C.), but leaving "ABT" (all but thesis).

Stevenson's career, like that of several other young mycologists, began with some years in the Caribbean, especially Puerto Rico (Stevenson 1975). As outlined by Farr (1985), there "he also served as librarian, plant quarantine inspector, herbarium curator, editor of Station publications, disbursing officer and assistant to the director". At the end of World War I, 1918, he left the tropics to work at the USDA as pathological inspector. Subsequently, he occupied several titled positions and, in 1927, succeeded J.R. Weir at the Mycology and Disease Survey, in charge of development of the collections. There he was under the supervision of C.L. Shear, a kindred spirit. This was his position during Lange's visit in 1931. We could not find any evidence that he joined in the 1931 forays with Lange, but he would have been enthusiastic nonetheless. Over the years, his title changed and he oversaw the move of the National Fungus Collections to Beltsville in 1941. Although he reached mandatory retirement age (70) in 1960, he continued work under a series of emeritus titles.

Stevenson was a collector. Professionally, his collections were of botanical specimens and professional books. As a second penchant, he was a philatelist. The latter two collections were more than significant. Farr (1985) offered the following anecdote: "An avid bibliophile throughout his long career, Mr. Stevenson acquired – frequently with his personal funds – all mycological or phytopathological literature available, including many old, rare and obscure publications. For example, a renowned European mycologist found some rare European books in the NFC [National Fungus Collections] that he had vainly searched for all over Europe and throughout other U.S. libraries (M.A. Donk, letter to Stevenson, March 1970)".

Stevenson's major contributions were archival (Stevenson and Cash 1936; Stevenson 1971, 1975).

BRASSTOWN, NORTH CAROLINA (21 Oct): This stop appears only on the Lange's itinerary, but must have been sentimental, as it surely was centred in the John C. Campbell Folk-school and perhaps a reunion with Olive Dame Campbell.

NEW YORK CITY (surrounding 26 Oct): Contrary to its inauspicious announcement in *Mycologia*, Lange was sent off from his American visit at an august occasion (Anonymous 1932b). "On October 26th [1931], the newly formed Society [New York Mycological Society] in collaboration with the Torrey Botanical Club and The New York Botanical Garden gave a luncheon in the American Museum of Natural History in honour of Dr. Jakob E. Lange, the Danish expert on gill fungi, who has been spending the summer in the United States. Preceding the luncheon, Dr Lange made an exhibit of several hundred water-coloured drawings of European gill fungi". As usual, there were last-minute changes in venue and arrangements. A letter from C.W. Dodge to Lange (dated 23 Oct): "We first planned to have the mycological meeting at the Museum Building at The New York Botanical Garden, but later on changed the meeting place to the American Museum of Natural History, where we expect to have luncheon at one o'clock, after which we shall meet in the Academy Room for your talk and exhibit." In short, the Langes were left to improvise. The cover charge was 60 cents.

Equally low key, Morten (Lange 1996) chronicled their arrival home in Denmark as 5 November.

With their American odyssey over, what were the repercussions?

Chapter 4. Intermission

Even as the Langes toured North America in 1931, a drought had descended over an enormous territory from Colorado to Nebraska, a condition observed by Lange (1934). For several years thereafter, drought continued, exacerbated by homesteading and ploughing in areas where rainfall was already only marginal for row crops. High winds produced dust storms month after month, year after year. By 1934, the year of Lange's (1934) report of his 1931 trip, an estimated 35 million acres of formerly cultivated land had been rendered useless for farming, while another 125 million acres—an area roughly three-quarters the size of Texas—was rapidly losing its topsoil. The worst dust storm occurred in April 1935. News reports called the event "Black Sunday". A wall of blowing sand and dust started in the Oklahoma Panhandle and spread east, depositing grit as far as New York and ships at sea. Roughly 2.5 million people left the "Dust Bowl" states (a term coined by the press) during the 1930s, one of the largest migrations in American history. As an agricultural educator, Lange must have followed this story from Funen, where such a catastrophe would have been next to impossible.

As the Langes pulled away from the American dock in fall, 1931, political jockeying was already underway for the 1932 presidential election. The Great Depression engulfed the country, and whether at fault or not, Herbert Clark Hoover (1874–1964), the President, was perceived as a non-action leader. His Republican political party shared a philosophy of a small government role, while Franklin Delano Roosevelt (1882–1945), the eventual Democratic candidate, promised a larger role of government in bringing the Depression under control and delivering aid to the people. A year later, Roosevelt won the November 1932 election (both popular and Electoral College) by a landslide, but by law, the election winner in November only took office in March of the following year, in this case, 1933. The American people had to wait for Roosevelt to act. Jakob Lange, after all, was a seasoned politician and surely was interested in the American political process. During the trip, conversations with Americans must have been animated. In Denmark, Lange's party would side with a large and liberal role for national government and he would have appreciated the Roosevelt programme more completely than that of Hoover.

Upon arrival home, there was little time to digest the kaleidoscope of the trip. By the time the Langes left for their trip, eight instalments of the "Studies" series had appeared and already plans were afoot to publish all his water-coloured mushroom "portraits" together in a more substantial form.

Morten (Lange 1996) summarised the situation: "The first wave of initiative [for *Flora Agaricina Danica*: FAD] came from an invitation to a mycological (and political) study tour to USA in 1931. The encounter with American agarics and American mycologists was very stimulating and the plan for the printing of FAD was under development. The two [Danish] professors with standing in mycology, Ø. Winge and C. Ferdinandsen...took interest in [Jakob's] plan and started hunting for the necessary economic support A hard job in those years of economic crisis".

Jakob's duties as headmaster of the Folk-school competed with mycological activity. "Specimens were collected on a morning's walk through the wood or at one or two Sunday excursions. Each year gave some new paintings" (Lange 1996). Nevertheless, Jakob penned a report, in Danish, to give other Scandinavian interested parties his impressions gathered in America (Lange 1931). For this audience, he pointed out numerous examples of identical mushrooms found on both continents, other very close fits and still others clearly different from both continents.

It took Jakob three years to gather his thoughts into written form for English-speaking colleagues (Lange 1934). He chose to publish them in *Mycologia*, then one of the journals of The New York Botanical Garden and only in the process of being adopted by the fledgling Mycological Society of America as their official print organ (Fitzpatrick 1944). Both of Lange's reports were acknowledged by "Annales Mycologici" [under "Neue Literatur", "Annales Mycologici" 33(1): 128. 1935, lists both Lange's Danish and English reports of his study tour of the US].

It is not easy to extract the core of Lange's (1934) report. Some problems seem to involve semantics – Lange's use of an English word which, to an English speaker,

creates confused concepts. Some abbreviated excerpts follow. “In other words, is the American fungus-flora chiefly characterized by *identity* [i.e. identical morphology on both continents; in short, the same morphotaxon from both continents], *parallelism* [i.e. European and American basidiomata so close morphologically that separation requires very close observation] or *incongruity* [i.e. European and American basidiomata clearly distinct]?” [sometimes, Lange used the word ‘*diversity*’] (*Italics are his*).

For Americans, it must have been a challenge to comprehend Lange’s ideas of parallelism. Whether the difference between an American mushroom and its European counterpart was 1% or 4%, distinction was distinction and at what percentage of distinction (and of what characters) did such mushrooms qualify as simply infraspecific variations: forms, varieties or subspecies? At each stop on his tour, Lange was more than willing to exhibit his illustrations, but to appreciate them, the viewer was obliged to make close observation, even to the point of using a hand-lens.

Lange (1934): “Nevertheless, I make bold to state as a preliminary result that the difference between the European and the American fungus-flora is not nearly as great as might be expected from American monographs and floras. If one turns to such publications of recent years, the general impression will be that the proportion between exclusively American species and ‘Europeans’ is about 7:3. But not only in the eastern States but also in the North and West, wherever I gathered a fairly large number of species, I found more nearly the inverse proportion: 70 per cent which were known to me from the European side of the Atlantic, against 30 per cent specifically American. Wherever a European mycologist may go in American woods, he will meet with species familiar to him. Generally, the main aspect of the American fungus-flora will be very ‘European.’ Or to put it more correctly: *The American mycoflora has more of a cosmopolitan stamp than of an exclusively American one*” [*Italics are his*].

“But what about parallelism in the world of fungi? It goes without saying that the more numerous the truly Americo-European species are, the less will be the chance of meeting with parallels. Still their number seems to be not at all insignificant.

“Altogether the number of true parallels substituting European forms in the Western Hemisphere and not found on the European side of the Atlantic, seems to be rather limited. Evidence is as yet far too incomplete to draw any final conclusions with regard to the problem of parallelism. But to my mind, the facts point in a certain direction: Everywhere in the vegetable and animal kingdom new ‘small species’ or varieties seem to arise by ‘mutation’ (sudden leaps or sidesteps from the straight path of heredity). If such new forms be equally well - or better - adapted to the natural conditions in the country where they arise, they may establish themselves there or even become the exclusive possessors of the territory hitherto occupied by the parent species. If such new forms have limited means of dispersal, they will become local species. If adapted for wide dispersal, they may gradually spread over unlimited areas.

“... in addition to the direct effect of the climatic conditions, the fungus-flora evidently is influenced by the phanerogamic vegetation, more especially by the presence or absence of certain trees [with] which the particular species is attached. This may

account for a good deal of the incongruity of the floras of Europe and America and those of the eastern and western United States”.

Lange (1934): “By far the greatest distinction in the world of fungi is not between a western and an eastern flora, but between southern and northern”.

Description of mycorrhizae had begun in the late 19th century and by 1934, the idea was well-developed, although species-to-species associations and detailed mycorrhizal anatomical studies were still 20 years ahead. Why Lange did not use the term remains obscure.

“But stronger and more lasting than any other impression is the evidence of the wonderful cosmopolitanism of the Agarics” (Lange 1934). This sentiment was not lost on the Americans. John Dearnness (1936), the Canadian mycologist, wrote: “In 1931, the veteran Danish agaricologist, Jacob [sic] E. Lange, made a trip across the middle latitudes of this continent for the express purpose of comparing the fleshy fungi of the region traversed with those of Europe. The last statement in his interesting report of the trip ... is that his strongest impression was of the evidence of the wonderful cosmopolitanism of the Agarics. He concludes with the question – Who can trace the aerial course of a spore?”

Even as the Langes made their way across North America, there was an “Announcement of formation of the Mycological Society of America at the New Orleans (1931) meeting. Its first meeting will be December 28–30 (1932) in Atlantic City” (Fitzpatrick 1931).

After a career of teaching, Jakob retired from active administration of the Odense “Husmandsskole” in 1934 (Fig. 20), but his mycological endeavours continued. As Morten (Lange 1996) later related, the first experimental plate of mushroom portraits came off the stone and was approved by the collaborators and supporters. Plans were laid for the appearance of the first volume of FAD the following year.



Figure 20. Lange family, about 1934-1935. Left to right: Morten, Jens Jakob, Jakob E., Leila. Source: Morten, 1996.

Across Europe, the 1930s had started with a conquered Germany and widespread physical and material ruin. Soon, however, disquieting words and sentiments sent signals of a new Germany (and later, Italy) echoing years of a philosophy dubbed “*Lebensraum*” (“living space”), introduced in the 19th century, but now championed by a rising personality, Adolf Hitler (1889–1945). The idea had two roots: the Aryan people were special (“*Übermenschen*”) while neighbouring people were lesser (“*Untermenschen*”); as the Aryan people needed additional soil through which to support themselves (Fig. 21), the inhabitant population must be eliminated by whatever means necessary. Intermarriage was considered a weakening of the Aryan race and therefore forbidden.

By the mid-1930s, Hitler had taken control of German government and re-armament was underway, officially “swept under the rug” by the conquering powers, themselves tired of war. Austria was gathered under the German Reich as fellow Aryans and “*Lebensraum*” was dusted off, openly threatening Poland and Czechoslovakia. Viewing the gathering clouds, Scandinavia, again, strived to stay, officially at least, neutral.

Meanwhile, Franklin D. Roosevelt took office as president on 4 March 1933 and immediately began implementing programmes to alleviate the economic crisis of “The Great Depression.” In June, he passed the National Industrial Recovery Act (NIRA),



Figure 21. Extent of “*Lebensraum*” as envisioned by Germany in 1934. Source: Wikipedia.

which gave workers the right to organise into collective representative organisations - in short, unions. Its most significant passage was:

“Employees shall have the right to organize and bargain collectively through representatives of their own choosing and shall be free from the interference, restraint or coercion of employers”. Although the NIRA was ultimately deemed unconstitutional by the Supreme Court in 1935, it was immediately

replaced by the Wagner Act legislation (the National Labor Relations Act) with the same intent and workers were encouraged to join and strengthen unions and other such organisations. Expressly excluded from the union movement were agricultural workers – but the law’s overall motive was close to the heart of Jakob Lange.

The “mid-term elections” (held in the midst of the presidential term of office) of 1934 might have reflected the “radical upheaval sweeping the country,” as the Roosevelt administration won the greatest majority either party ever held in the Senate and in the House of Representatives, 322 Democrats to 103 Republicans. Coincidentally, the strength and independence of the Executive Branch was expanded as never before.

The year 1935 brought the 10th in Lange’s (1935b) “Studies” series, this time a floristic monograph of *Cortinarius*. Taxonomy within the genus, Lange wrote, depended heavily on colours, but written descriptions were difficult to understand when colours were named, especially when non-colorimetric references were made such as “pecan” or “cream”. In other instances, the same colour was described with different terms, such as “lilac”, “lavender”, “violet”, “purple” or “bluish”. An accurately coloured “portrait”, however, by-passed such confusion. Lange was aware of Kauffman’s (1918) treatment of *Cortinarius* for Michigan or eastern United States, who cited Ridgway (1912), but did not use Ridgway’s terminology. Lange’s (1935b) sole plate was special for the instalment, not reproduced later in FAD. It is interesting that Kauffman’s (1932) post-humous offering on *Cortinarius* for “North American Flora” was not cited by Lange (1935b); perhaps this series was not part of Lange’s library.

An unexpected reader was John Dearnness (1935) in Canada. “Professor Jacob [sic] E. Lange has recently published a monograph in English of the Danish *Cortinari* in which he keys and describes 120 species, being about twenty more than half the total number of North American species described in the N[orth] A[merican] Flora. He accepts the six Friesian subgenera and keys them separately dividing each subgenus into two subsections. The quality of the keys is always proved by their use; however, a careful reader of these six examples will probably admit the author’s claim that they are so clear and plain that “a novice may be able to follow their lead without getting side-tracked on the road”.

According to Morten (Lange 1969), no. 10 in the “Studies” series appeared in July 1935 and, in November, the first part of Volume 1 of FAD was completed (Figs. 22–24). There must have been cause to celebrate – plans for the FAD series had been laid well in advance. However, a close reading of Morten’s report would indicate that several other persons were in charge of various tasks in the production and support of FAD. “Poul Larsen, Ferdinandsen and Winge have their great part in the production of the work through their pressure to secure the economic basis and in the primary development of



Figure 22. Detail from “Flora Agaricina Danica”, Vol. 1. Plate 1D. *Amanita phalloides*. Original 11 × 13.5 cm.

the printing standards to be met. N.F. Buchwald served as secretary, helped to see the pages through the press, completed the index and organized the distribution. The production was in itself a very excellent job. The technical work of transferring the pictures to the lithographic stones was done by one highly skilled man (O.R. Poulsen) and as much as ten colours were generally needed to make up the final print”. Even Lange’s inked images of cystidia, basidia and spores were faithfully reproduced in lithography. The tasks remaining for Lange were to write the text and provide the images: Morten wrote “[J.E.] Lange was no friend of long descriptions...” and Latin diagnoses only became required for nomenclature in 1935, just in time to plague the author. The plates

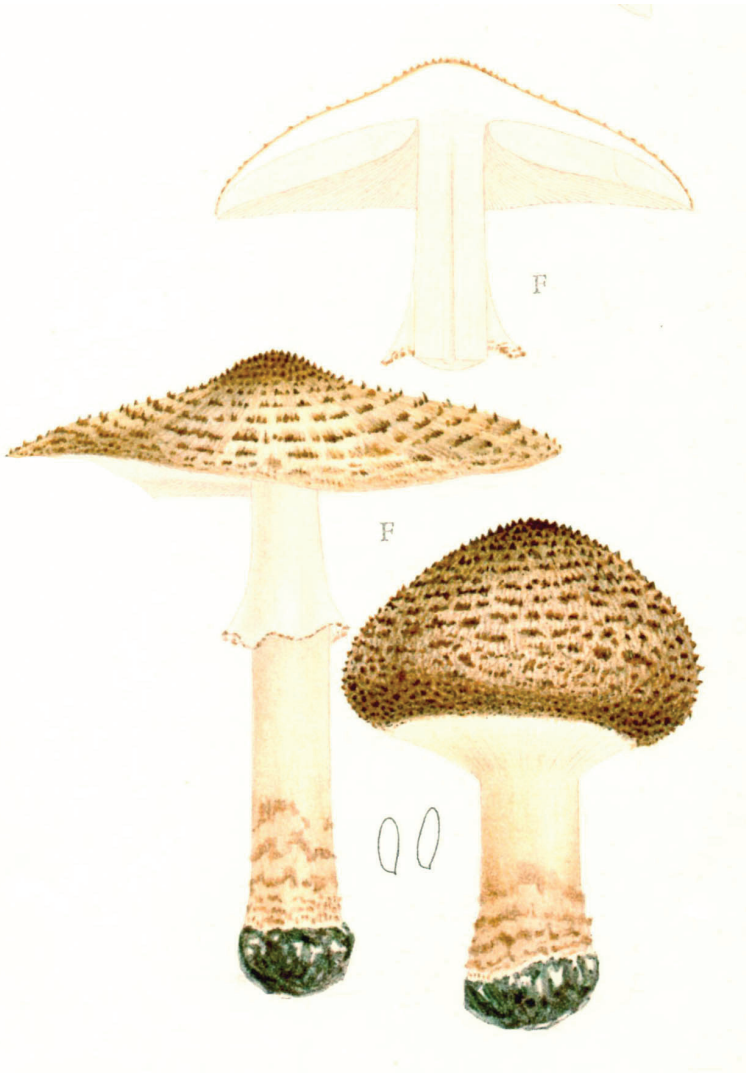


Figure 23. Detail from “Flora Agaricina Danica”, Vol. 1. Plate 10F. *Lepiota acutesquamosa*. Original 11 × 14,5 cm.

were montages of Lange’s original “portraits” on glossy paper, while the text was on quarto opaque paper of large print-face. A separately paged general introduction was culminated, but added as an introduction before Volume I, consisted of Latin diagnoses of new taxa and index of all illustrations by genus and by volume/plate. Few descriptions bore detailed geographic information; these details were included in the two notebooks mentioned by Morten (Lange 1969) and now at the Natural History Museum of Denmark, Copenhagen. Soon, in the middle of March (Lange 1936b), the second part of Volume I was produced. FAD took its position amongst contemporary and preceding illustrated works on European agarics (Petersen and Hughes 2017; Krieger 1927).



Figure 24. Detail from “Flora Agaricina Danica”, Vol. 1. Plate 40G. *Clitocybe aggregate* var. *ovispora*. Original 12.5 × 14.5 cm.

The appearance of FAD was the result of clear-eyed business collaboration, not only the realisation of a mycological dream. Years previously, Lange had already had a mycological disagreement with Ferdinandsen and Winge (1924–1925), two of the chief collaborators on FAD. It concerned proposal by the latter two of a new species of *Russula* (*R. solaris*), which Lange considered only *R. raoultii*, already described by Quélet and already known from the Danish mycoflora. Later (Studies XII: 103, 1938a), however, Lange acknowledged the new species. The three remained friends and colleagues throughout.

Such an auspicious start was bound to be recognised by the mycological community, both European and American. In the German journal, “*Annales Mycologici*” (1935 [1936], 34(2): 265) both number 10 of the “Studies” series and Volume I of FAD were simply acknowledged under “*neue literatur*”.

In Paris, Roger Heim (1936) inaugurated the new journal, “*Revue de Mycologie*”, with a review of Volume I of FAD. In part, he wrote (translation from French HK): “The world’s botanical authority, the author of ‘Studies of the Agarics of Denmark’ ...

in fact, [makes] this publication of particular importance. ... It is not only a matter of providing a very new system for the agarics, but the masterly qualities of the author – his sincerity, his clarifying spirit, his fine scientific sense – allow consideration of his personal concept for each species as a defining statement.

“He seeks – within the genera – to group the taxa in a logical way by using simple and clear distinctions. Mr. Lange is a master of this game and it is perhaps especially this charm from his publications which is retained and reappears in an agreeable way. ... Lange always insists on the precision of the descriptions by adding twigs, dung and other precise biological characters [to the illustrations], rarely recognized by other authors.

“All those who regretted that these essays were applied to a small number of genera will be fully satisfied when they learn that this Flora will be the generalization of the author’s previous observations, to which are added excellent watercolours in the sense that they are those that mycologists may desire; without too deliberately artistic effects, but scientifically complete and rigorous”.

As Volume 1 dealt with *Amanita* and *Lepiota*, Heim discussed these genera and their infrageneric taxonomy, noting differences between Lange’s arrangement and that of contemporary French authors.

“We sincerely hope that the real difficulties in these times [the Great Depression and the build-up to WW II] will not delay the publication of such a precise work, which simultaneously brings honour to the knowledgeable author and to two Danish groups which have taken on this enterprise”.

Heim (1931) was no novice in such publications. His treatise on *Inocybe*, for instance, had numerous colour plates quite similar to those used for FAD. Lange (1917) had also investigated the genus. From France, Robert Kühner (1935) also published his comprehensive treatment of *Galera*, citing unpublished coloured illustrations by several workers, including Lange.

Virtually simultaneous with Lange’s first instalment of FAD came a mushroom book from the United States, illustrations from which rivalled those by Lange. Louis C.C. Krieger had worked with W.G. Farlow (Petersen 2019) in producing water-colour figures of New England fungi, but in 1935, Krieger was mycologist of the State of New York, in the succession of Charles H. Peck. His “Popular Guide to the Higher Fungi (Mushrooms) of New York State” (Krieger 1935) and its reprinted successor, “The Mushroom Handbook” (Seaver 1936) were illustrated by a combination of photographs (not taken by Krieger) and watercolours. The quality of the latter was quite high.

The year 1935 also saw a paper on American *Mycena* taxa by Alexander H. Smith. Smith had started his graduate work under Calvin H. Kauffman at the University of Michigan, but had to switch to E.B. Mains when Kauffman was incapacitated. Under Mains’ influence, Smith obtained his PhD in 1933, with a dissertation on two-spored forms of *Mycena* in North America. He had ample reference to Lange’s 1914 study of the genus in Denmark (Lange 1914). Lange’s “Studies” series parts I and V appeared in Smith’s bibliography. Smith’s 1935 paper was the first in a series of five (Smith 1935a, b, 1936, 1937b, 1939).

Now, some twenty years after Lange's study, Smith wrote: "No comprehensive treatment of the genus *Mycena* giving proper emphasis to both microscopic and macroscopic characteristics has been published for the North American species. Atkinson had such a study in mind and, at the time of his death, he accumulated considerable information toward that end. Unfortunately, however, it was never published. Kauffman was engaged in a similar study in 1929, but withheld it from publication because he felt that it was incomplete. As a result, Kauffman's treatment of the genus in 'The *Agaricaceae* of Michigan' and that of Beardslee and Coker (1924) on the species found in North Carolina are our most reliable sources of information.

"Very little authentic European material has been available for comparison and it has been necessary to rely on published descriptions and figures". Lange (1934) acknowledged as much.

An important "*déviaton obligatoire*" is necessary. In 1922, a small paper appeared in a new journal from Germany, "Zeitschrift für Pilzkunde" and was authored by a young Rolf Singer (1906–1994; Singer 1922). It introduced the man who would become the leading agaricologist of the 20th century, not only for Europe, but worldwide. Over the next few years, he seemed to deal especially with *Russula*, but already had greater horizons in mind (Mueller and Wu 1998). In 1936, some 50 publications later, Singer (1936) introduced his overall taxonomic scheme for the agarics. His productivity and taxonomic breadth would eclipse all other individuals and his very presence would influence all writings on the subject. His new system, presciently, was written in Leningrad, the temporary home of Rolf and Martha Singer, newly-weds, reflective of the times.

In February, 1936, Hitler convinced the Chancellor of Austria to allow Germany to control the Austrian economy, citing the unity of Aryan peoples. The next month, German troops marched into the Rhineland; numerous Germans saw difficult times ahead and felt obliged to emigrate from their fatherland.

January 1937 saw the 11th instalment of the "Studies" series (Lange 1936a), this one dealing with several genera, but without a coloured plate. Two months later, the second volume of FAD appeared. In both instances the technical tasks were no longer new and especially the plates for FAD Volume II, planned well in advance, were produced almost routinely, but always under Lange's eyes. By mid-year, the publication had arrived in Michigan, where Alex Smith (1937a), now on faculty, wrote a review.

"... The first volume [of FAD] appeared in 1935 and 1936. Although the author [Lange] has confined himself to the Agaricaceae of Denmark, his work is indispensable to critical students of the family in the United States and Canada. Many of the curious and unusual species which Dr. Lange has discovered are widely distributed and are to be found both in eastern North America and along the Pacific Coast. The work is outstanding because all the species recognized in the Danish flora are described and illustrated. An unusually high degree of accuracy has been obtained in depicting and reproducing the natural colours and fine details in each species. There are keys to all the species and brief descriptions which emphasize the characters the author considers important".

Smith summarised the taxonomic outline of the two volumes. He then pointed out a few nomenclatural shortcomings. “Such errors as these are practically inevitable in a group where little authentic material exists and the literature is widely scattered. They do not detract materially from the value of the work as a whole. There is little doubt that Lange’s *Agaricina Danica* [sic] will always remain one of the outstanding contributions in Agaricology.”

A few months after the appearance of Smith’s review, he and Marcel Josserrand (Josserrand and Smith 1937) collaborated on a paper which centred on Lange’s (1934) English language report on his trip to America. Josserrand, based in Lyon, was already a leader in French mycology. Lange’s report had dealt at some length on his own observations and his conclusions about agaric distributions. The three categories he (Lange) sketched for transatlantic mushroom distributions were “identity”, “parallelism” and “incongruity” (q.v. above).

The authors wrote: “...Lange in his comments on agarics in North America discussed briefly the existence of “parallel species” in North America and in Europe. He also re-emphasised the view, which many American mycologists have long held, that, in reality, the North American fungous flora and that of Europe are characterized by the presence of a larger number of species in common than the published floras indicate. The task of accurately determining the true synonyms and the recognition of ‘parallel species’ is a very delicate one and involves a careful study of the variations of each species not only in each country, but in various regions of the same country as well as in the same locality over a period of several seasons. The co-existence of a striking character in a European and an American species does not suffice to justify the identification of the one with the other. In order to pronounce them synonyms, it is necessary to have a perfect superposition of the two series of characters. If there is the slightest doubt, it appears to be wiser not to place them in synonymy for we believe that it is incomparably less serious and less confusing to permit the existence of two names for the same plant than to designate a mixture of two species with a single name”.

It is not surprising that Josserrand & Smith should single out *Mycena* in their criticisms. In 1935, Smith was two years out of graduate school at University of Michigan, with his dissertation on two-spored forms in the genus in North America. Lange’s English report on his 1931 trip had appeared only in 1934 and the paper with Josserrand was Smith’s first chance to comment on Lange’s remarks on biogeography of *Mycena*.

Time has blurred precisely how much Lange’s 1931 trip to America – person-to-person interaction and/or probable reference to the “Studies” series (FAD had not appeared in 1931) – influenced the work of American agaricologists, but the Americans sometimes mentioned Lange explicitly or cited his publications in their bibliographies. These references are of help in telling Lange’s story, but are difficult to search out. The following are examples.

Lange may have stopped in Seattle or not, but his influence was felt nonetheless. Hotson and Stuntz (1938) mentioned Lange's (1934) report on his trip and Lange's "Studies" XII; 1938) in their paper on *Agaricus* on the west coast. Lange's mention of the sterile cells at the gill edge (cystidia) were mentioned and illustrated.

Hotson and Stuntz (1938) stated: "The genus is well represented in the Pacific Northwest, but when one wishes to identify collections made in this region, he faces an obstacle in the lack of available information concerning the local flora and also in the fact that some of the species occurring here may also be more closely allied to European forms than to those found in the eastern United States". This certainly has the ring of Lange's (1934) sentiments and also those of Kauffman (1918).

Lange's visit with S. M. Zeller in Corvallis, listed in his itinerary and vouchered by specimens included in MycoPortal, was reflected by Zeller (1938). Under *Armillaria robusta*, Zeller drew attention to the illustration by Lange (1935b). A new species, *Lepiota oculata* Lange & Zeller, collected at Hemlock, Oregon, was described and *Lepiota cygnea* Lange, pointed out by Lange (1934), was reported as collected during Lange's stay.

A year after Volume II of FAD (Lange 1937), March 1938, brought the appearance of FAD III (Lange 1938c) and, in October, the last instalment of Lange's (1938a) "Studies" series. The former was reviewed by Smith (1938), who, in a somewhat perfunctory discussion, furnished an account of the taxa and infrageneric taxonomy of *Cortinarius*, *Inocybe*, *Hebeloma* and *Pholiota*.

Chapter 5. 1939

Jakob's (1938b) recollections of his American travels were written a year before his final trip to America. Fortunately, Morten's account of the 1939 trip, although brief, is precise and accurate.

From the American side, the year opened with some equivocations on that year's foray time and location (Mains 1939). By March, dates could be posted (Linder 1939b). "The Mycological Foray will be held in the Great Smoky Mountains National Park, but with headquarters in Gatlinburg, Tennessee. In view of the fact that the meeting will be held from August 17th to 20th inclusive, during the tourist season, it is advisable that those planning to attend make reservations early at one of the following places, all within a radius of a mile: [a list of about 15 hotels & cabins]". Although we know of no evidence of an American invitation to Jakob Lange to join the foray, one must have been transmitted, perhaps from John Dearness (see below) or perhaps C.W. Dodge. Such an invitation would have coincided with other, non-mycological proposed appointments.

From Morten Lange (1996): "My father invited me on a new America trip in the summer of 1939. He had received an invitation to a mushroom congress in Tennessee

and to give a couple of lectures about [Danish] agricultural education in Washington and Pennsylvania. It looked as a new exciting trip. I should accompany as a 'qualified companion' on a five-week, somewhat frenzied, trip". (Wartime in Europe limited categories of persons embarking across the Atlantic, especially from Great Britain. Only "qualified companions" were allowed to accompany credentialed passengers) (Lange 1996).

The years leading to Lange's 1939 trip were a chronicle of turbulence. From the United States, the Roosevelt "New Deal" was not without its detractors and, on the European side, there was little but threatening news.

As early as 1922, Italy had devolved from monarchy to fascism. Benito Mussolini (1883–1945) saw his paramilitary descend on Rome and was rewarded with the prime minister's appointment. On 3 January 1925, he asserted his right to be supreme ruler and declared himself dictator of Italy.

A decade later, following Italy's 1935 invasion of Ethiopia, Germany was the second country to recognise Italy's legitimacy there. Over subsequent years, Germany's industrial might and population propelled Hitler to eclipse Mussolini. Both Hitler and Mussolini sided with Francisco Franco (1892–1975) in the Spanish Civil War (1936–1939), with Mussolini providing 50,000 troops. In 1937, Italy left the League of Nations in solidarity with Germany. Parenthetically, 1935 saw Rolf Singer and his wife forced to flee Spain for Paris.

Perhaps a useful means of communicating the events of the period is through a chronology as follows:

12 March 1938: The *Anschluss*, the annexation of Austria into Greater Germany, began as a large contingent of German troops entered Austria. The *Anschluss* ostensibly reunited ethnically similar Aryan cultures and many Austrians welcomed the German soldiers.

March 1938: Volume III of FAD appeared in the midst of threatening times (Lange 1938c).

30 September 1938: In Munich, Germany, representatives of the victorious countries of World War I ceded to Germany the Czech Sudetenland – the Czechoslovakian borders on its west, south and north. The territory included the major defences of Czechoslovakia against Germany and Poland, so the Czechs were rendered defenceless. Soon, the remaining Czech territories and the Hungarian border land were also awarded to Germany. The British Prime Minister, Arthur Neville Chamberlain (1869–1940), upon arrival home after the Munich Conference, declared its agreements as "Peace for our time".

In the context of the post-war (WW I) economic depression of the 1930s, the German National Socialist Party ("Nazi") gained popularity in part by presenting Jews as the source of a variety of political, social, economic and ethical problems permeating German society. The Nazis used racist and also medieval social, economic and religious imagery to this end. Inspired by theories of racial struggle, Hitler preached the intent of the Jews to survive and expand at the expense of Germans. The Nazis, as the governing party, ordered anti-Jewish boycotts, staged book burnings and enacted anti-Jewish

legislation. In 1935, the Nuremberg Laws defined Jews by race and mandated the total separation of “Aryans” and “non-Aryans”. These measures aimed at both legal and social segregation of Jews from Germans and Austrians. On the night of 9 November 1938, Nazis and their sympathisers destroyed synagogues and shop windows of Jewish-owned stores throughout Germany and Austria in what became known as “Kristallnacht”.

Simultaneously, people of German ancestry living abroad were encouraged to form citizens groups both to extol “Germanic virtues” around the world, but also to lobby for causes helpful to Nazi Party goals (Atlantic 2021). In the United States, the “Amerikadeutscher Volksbund” or German American Bund was formed in 1936 as “an organisation of patriotic Americans of German stock” (Atlantic 2021; Bund 2021). The Bund eventually grew to a membership in the tens of thousands. On 20 February 1939, the Bund held an “Americanisation” rally in New York’s Madison Square Garden, denouncing Jewish conspiracies, President Roosevelt and other controversial subjects. The rally, attended by 20,000 supporters and members, was protested by huge crowds of anti-Nazis (Bund 2021). As war broke out and German allegiance forced difficult choices, the German-American Bund fell apart, many of its assets were seized and its leader was arrested for embezzlement and later deported to Germany.

October 1938: The 12th and final instalment of Lange’s (1938a) “Studies” series appeared. As planned, the summary of Danish agarics had been completed.

March 1939: German army occupied Prague, Czechoslovakia, in clear violation of the Munich Agreement.

31 March 1939: In the face of the perceived German threat, Britain and Poland announced a mutual assistance pact in case of military threat, but the treaty was not signed until August. From the British Prime Minister: “... [I]n the event of any action which clearly threatened Polish independence and which the Polish Government accordingly considered it vital to resist with their national forces, His Majesty’s Government would feel themselves bound at once to lend the Polish Government all support in their power. They have given the Polish Government an assurance to this effect. I may add that the French Government have authorised me to make it plain that they stand in the same position in this matter as do His Majesty’s Government”. On 13 April, the assurance was extended to Greece and Romania. Formal signing was accomplished on 25 August.

May 1939: Germany demanded a non-aggression pact with the Scandinavian countries. Sweden and Norway rejected the idea, but Denmark accepted, which created a major physical obstacle for the Britain/Poland alliance.

Early May 1939, Volume IV of FAD appeared in Denmark (Lange 1939a, 1969). Considering the geopolitical context, in retrospect it is a wonder that the raw materials for the production - paper, ink, lithograph stone etc. - were available.

22 May 1939: Italy and Germany signed the “Pact of Steel” officially creating the Axis powers. (Japan would join in September of 1940 with the signing of the “Tripartite Pact”).

12 August 1939: The Langes, father and son, pushed off from England for New York “on a fast boat,” arriving on 18 August and immediately boarded a train headed south towards Tennessee and a “mycological congress.” Morten was impressed that



Figure 25. Mycological Society of America Foray, 1939, Gatlinburg, TN **1** Helen Smith **2** David Linder **3** L.R. Hesler **4** Robert Hagelstein **5** Arthur Stupka, Smokey Mountains National Park biologist **6** Alexander H. Smith **7** L.O. Overholts **8** Morten Lange **9** John Dearness **10** C.L. Shear **11** J.E. Lange. Source: L.R. Hesler.

they disembarked at 6:30 pm Daylight Savings time and boarded the train at 6:30 pm Standard time. Daylight Savings Time had been instituted during World War I, but afterwards had been scrapped. Roosevelt attempted to resurrect it, but it was rejected again, except for a very few States and large cities, one of which was New York. The railroads ran on Standard Time and this would persist all the way to Tennessee.

It must have been no sooner than 19 August that the Langes reached Gatlinburg, Tennessee and the 1939 foray of the Mycological Society of America. The foray was scheduled for 17 – 20 August, so the Langes had no more than a few hours with the large contingent of mycologists – just long enough to be caught in a group photo (Fig. 25). Morten later wrote (Lange 1996): “Among them [was] Alex H. Smith from Michigan, whom I agreed to visit soon for a study period. It was only realized later, in 1947”. By mutual agreement, that study period was concerned with *Coprinus*, in this case, the *C. ephemerus* group (Smith 1948; Lange 1952; Lange and Smith 1953). One can only imagine conversations between Jakob Lange and Alexander Smith, who had taken Jakob to task over their common interest in *Mycena*. Although time was severely limited, Jakob managed to make several sketches dated 20 August (Figs 26, 27).

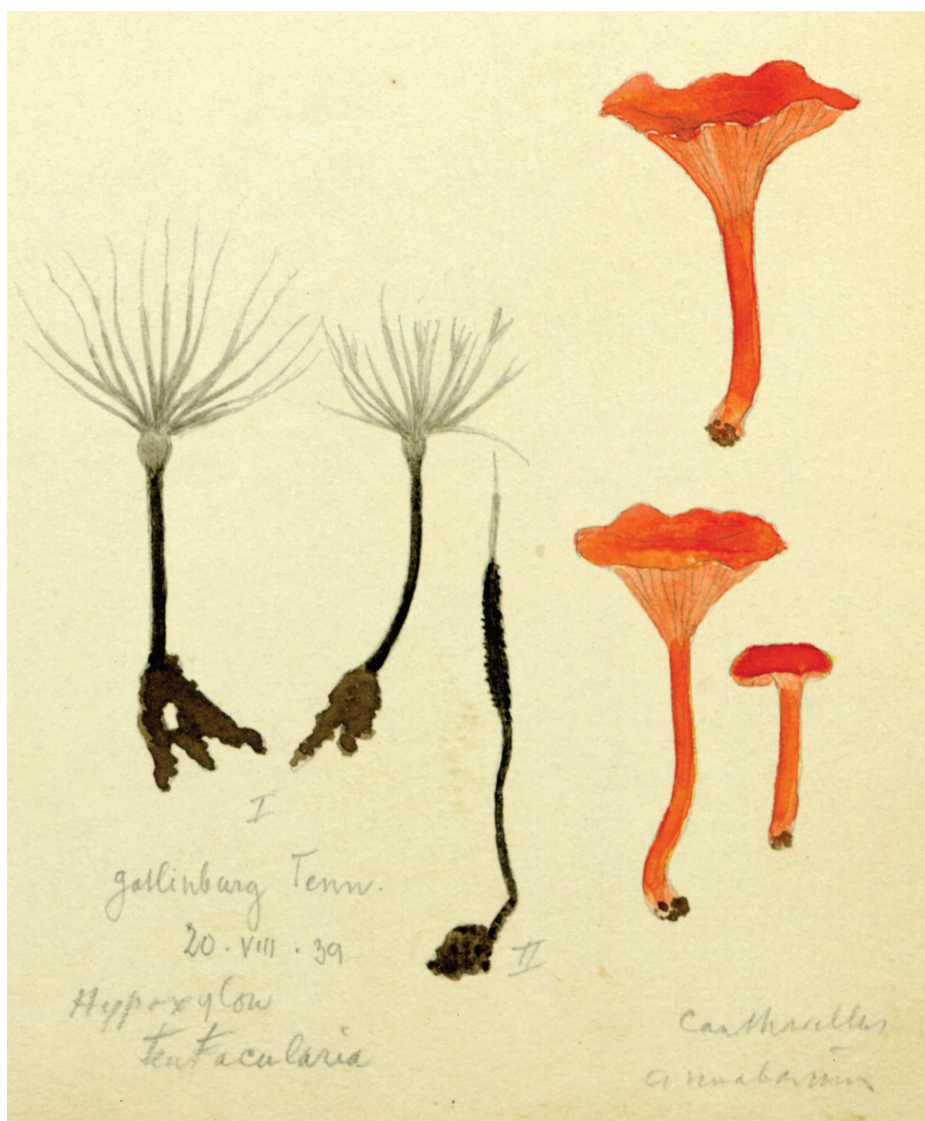


Figure 26. Lange aquarelle sketch dated 20 August 1939 (Gatlinburg, TN). Left: *Hypoxylon* “tentaculus.” Right: *Cantharellus cinnabarinus*. Courtesy Natural History Museum of Denmark, Copenhagen.

It is quite possible that a small group of mycologists remained in Gatlinburg for extra collecting and conversation. A second photo might suggest that amongst them were C.L. Shear, John Dearness and Robert Hagelstein (Fig. 28).

23 August 1939: Meanwhile, secretly, the USSR was negotiating with both Britain and Germany. The deal with Germany promised a Soviet “Sphere of Influence” including eastern Europe, the Baltic States and Finland. Joseph Stalin was attracted to this much better deal from Hitler and the USSR signed the (Vyacheslav) Molotov-(Joachim von) Ribbentrop Pact.



Figure 27. Lange aquarelle sketch dated 20 August 1939 (Gatlinburg, TN). *Lactarius indigo*. Courtesy Natural History Museum of Denmark, Copenhagen.

Morten (Lange 1996) wrote: “After four days of advanced mycology, there was room in the calendar for a fast visit to Mrs. Olive D. Campbell’s high-school in North Carolina and accordingly private mushroom trips”. This would mean about 23 August (= 4 days after arrival in Gatlinburg on 19 August). Whether Mrs. Campbell was present is doubtful, since the Langes visited her summer residence on Nantucket some days later. Nonetheless, the visit to Brasstown must have been a sentimental journey, since Jakob (with Leila) had visited there in 1927 and again (this time with Morten) in 1931. The school had built and acquired several new buildings, but perhaps more importantly, it had become the centre of a farmers’ cooperative, a dairy cooperative and



Figure 28. Mycological Society of America Foray, 1939, Gatlinburg, TN. Left to right: C.L. Shear, John Dearness, Morten Lange, Jakob Lange, Robert Hagelstein. Source: L.R. Hesler.

a growing network of crafts people. In each case, the power and leverage of individual participants had been magnified. Activities did not take the place of public education, but introduced new methods and communication, all echoes of the “Husmandsskole”. Jakob was able to execute a small number of sketches, including one of *Calostoma*, but not the one discovered by Jakob in 1927.

25 August (probably): Morten wrote (Lange 1996) “And then there was time for lectures in Washington and at Penn State College”.

In 1931, the Lange family had visited Washington, where they spent time in the field with USDA workers. Most of those folks were still in their jobs and reunions were probably pleasant. At least Cornelius Shear and Vera Charles had been at the Gatlinburg foray, lending additional familiarity.

Morten described the lectures as agricultural, not mycological and used the plural, but nothing specific is known about them. One person already known to Jakob was Henry Agard Wallace (1888–1965), then Secretary of Agriculture under Roosevelt and slated to be Roosevelt’s Vice President after the 1940 election.

Sounding much as though it could have come from Grundtvig's pen, "The Farmers' High School" was established in Pennsylvania in 1855, seven years before the land-grant act was passed. The implication, of course, was that agriculture already played a significant role in the mission of the school, reflecting the rural agrarian demographics. The first graduating class of 13 males in 1861 was the first such class at an American agriculture institution. Just as the Grundtvigian schools in Denmark, agricultural programmes at "Penn. State" included numerous short courses so students could receive education and immediately apply their new knowledge to their livelihood.

In terms of mycology, at least three faculty members were on board in 1939. Frank Dunn Kern (1883–1973), expert in rust fungi, was not only Head of the Department of Botany, but also Dean of the Graduate School. George Lorenzo Ingram Zundel (1885–1950) was plant pathology's extension representative to the farming public. Lee Oras Overholts (1890–1946) had already published several papers on polypores and had served as President of the Mycological Society of America in 1938. He had just attended the Gatlinburg foray the previous month. James Whaples Sinden (1902–1994) was becoming well-known for his development of "grain Spawn" in the mushroom industry.

In the 19th century, caves in and around Chester County, Pennsylvania, had become home for a thriving mushroom growing industry, businesses often owned and run by immigrant families. With the advent of mechanical aids, especially in ventilation, the industry went above ground and, after World War II, the area produced the lion's share of mushrooms in the United States. Pennsylvania State University evolved an advisory role to the mushroom farmers' association, later adding a research laboratory and short courses of its own to serve as extension, under the leadership of Leon R. Kneebone (1920–2020; Kneebone 2021).

1 September 1939: Lange (1996): "The 1st of September we returned to New York, [just as] the war broke out in Europe. Father's prophet, Henry George, had been dead for a long time, but his daughter – Anne George de Mille [1878–1947; married to William, brother of the film magnate C(ecil) B. de Mille] gave an elegant private dinner and we made sure to change [our reservations] to the Swedish ship 'Gripsholm'".

On that very day, Hitler, convinced that Britain would not intervene and assured that USSR would not interfere, sent troops into Poland in the face of the Munich Conference agreement and the mutual assurance pact between Poland and Britain. Within days, the USSR entered Poland from the east and the country essentially disappeared.

Great Britain immediately declared war against Germany. This was not a singular event, for British agreements with its dominions – Australia, Canada, South Africa, New Zealand and other colonies such as India and African possessions – brought them also into the War, both in Europe and across the Pacific.

September 1939: Denmark's reaction to these tumultuous events was to declare neutrality, as it had been for World War I. Danish government and society continued to function more or less normally, but always "looking over their shoulders" as their southern neighbours killed one another. The southern areas of Schleswig and Holstein were again in play. The Germans, contrary to their other incursions, considered the Danes a kind of Aryan and therefore qualified for less harsh treatment.

A stop in New York City would not have been complete without a visit to Columbia University to see John Sidney Karling (1887–1994; Anonymous 1996; Karling 2021), by then a full professor. Karling had earned his PhD there under R.A. Harper and remained on faculty. Equally, if time allowed, a side trip to the New York Botanical Garden would have been worthy, especially to meet with Fred Jay Seaver (1877–1970; Rogerson 1973; Seaver 2021), the Editor in Chief of *Mycologia* and Curator of the Herbarium.

Lange 1996: The change of transatlantic vessels “...gave us a few extra days for a fast visit on Nantucket to Mrs. Campbell’s summer residence. The Island is situated further at sea than Martha’s Vineyard and is finer. Our host had two original houses built for whaling captains”. Mrs. Campbell was now 57 years old; it had been 14 years since she had first met Jakob in Denmark.

The evident reason for the change in transatlantic schedule were widely circulating reports of German “U-boats” (submarines) plaguing shipping on Atlantic seaways. On the advice of American hosts and colleagues, bookings were changed to the “Gripsholm,” a vessel of the Swedish-American Line, which sailed under the flag of neutral Sweden. Morten (Lange 1996) described: “... and then sailing with a spotlight on the [Swedish] flag, up to the Faroe Islands [southeast of Iceland and due north of Great Britain] and inside the coast in the Norwegian archipelago from Ålesund [a town on the Norwegian coastal islands] to Göteborg [on the Swedish coast just south of Norway]. The whole development in the war [was followed] through American newspapers and as telegrams to the ship. It was tough!”

20 September 1939: The Lange men arrived home. With this, the 1939 North American visit ended, but the tension and stress of the return voyage was only enhanced by the turmoil on all sides of Denmark. Nevertheless, it must have been welcome to return to retirement at the Odense “Husmandsskole”.

Chapter 6. Epilogue

17 December 1939: As the year wound down, in Berlin, the decision was made to occupy Denmark. Within days, German troops occupied Copenhagen, violating Denmark’s neutrality. The Germans had already planned to use northernmost Denmark as a jumping off spot in an invasion of Norway.

Morning, 9 April 1940: Germany declared Denmark a protectorate as it began the invasion of Norway. Norwegian resistance was valiant, but failed and Norway capitulated on 10 June. With Denmark and Norway in its pocket, Germany controlled commerce over the Baltic Sea.

9 April 1940: The Danish envoy to the US signed an agreement under which the US would defend Greenland, a Danish protectorate. The agreement also provided the US an opportunity to erect military bases on the Island. This arrangement moved the US closer to the war without being directly involved.

12 April 1940: With Danish permission, Britain peacefully invaded the Faroe Islands, another Danish protectorate and fortified them.

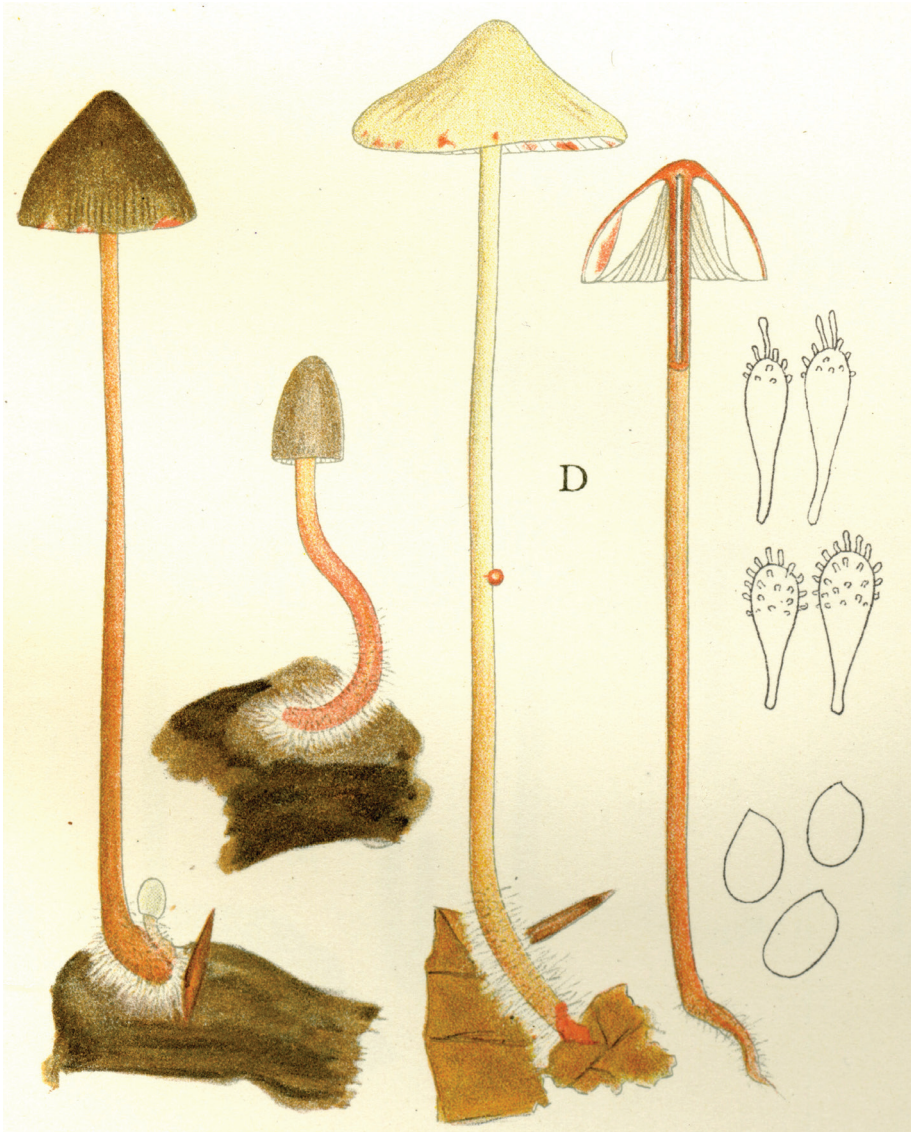


Figure 29. Detail from *Flora Agaricina Danica*. Plate 100D. *Mycena crocata*. Original 9 × 11.5 cm.

10 May 1940: The United Kingdom invaded Iceland as a pre-emptive strike, eventually turning it over to the USA in July 1941. Occupation of the Faroes, Iceland and Greenland were all attempts to preserve the northern transatlantic waterway.

Germany's occupation of Denmark and invasion of Norway convinced Mussolini that Hitler would win the war. In continental Europe, neutral Holland (15 May 1940) and Belgium (28 May 1940) also fell to the Germans.

26 May – 4 June 1940: The German army advanced over its western front, trapping large numbers of British and French troops against the British Channel, necessitating their evacuation from Dunkirk.



Figure 30. Detail from “Flora Agaricina Danica”. Plate 130E. *Galera sphagnorum*. Original 11.5 × 12 cm.

June 1940: The French military collapsed and occupation began over much of the country.

In mid-September, 1940, Volume V of FAD appeared (Figs 29–31). It had been planned as the final volume and was so. With long-term planning, it had been known that the number of plates would not reach the promised 200, so Jakob had augmented the illustrations in hand with several new ones, but without the generic organisation present in the preceding volumes. The final plates and descriptions were patched together in order to reach 200. Sometime during the production of the plates, Jakob

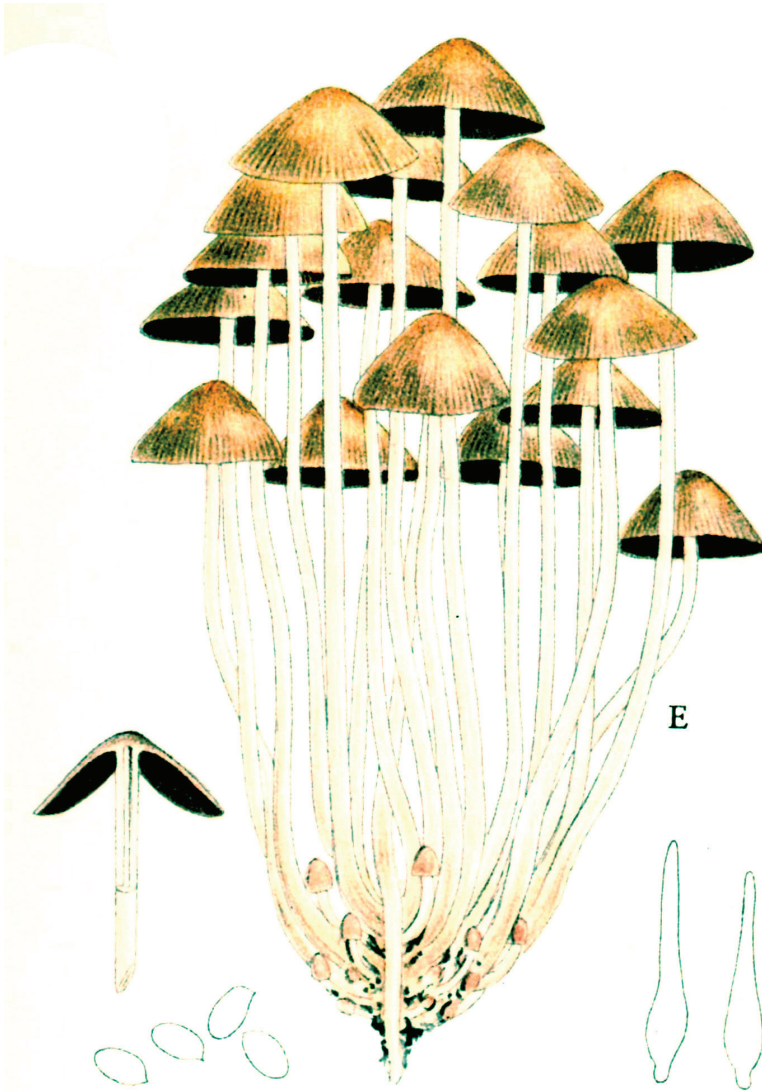


Figure 31. Detail from “Flora Agaricina Danica”. Plate 153E. *Psathyra stipitissima*. Original 9 × 12.5 cm.

designed and built a special cabinet to house a set of the original images. Even the door was customised with marquetry announcing “*Danmarks Agariceer*” (Danish mushrooms) (Fig. 32).

22 June 1941: Under “Operation Barbarossa,” Germany started its invasion of the USSR, ripping asunder the Molotov-Ribbentrop Pact.

It was surely Germany’s most grievous over-extension and the beginning of the end for Axis powers (Germany and Italy).

On the very same day, German occupation authorities in Denmark demanded that Danish communists be arrested. The Danish government complied and, in the following days, the Danish police arrested over 300 communists. Many of these, including the three communist members of the Danish Parliament, were imprisoned, in violation of the Danish constitution. On 22 August, the Danish Parliament (without its communist members) passed the “Communist Law”, outlawing the Communist Party and communist activities, in another violation of the Danish constitution. In 1943, about half of the detainees were transferred to Stutthof (Stutthof 2021) concentration camp (near the former “free city” of Danzig), where several died.

On Sunday, 7 December 1941, the air force of the Imperial Empire of Japan bombed the United States’ naval base at Pearl Harbour, Hawaii, concurrent with a declaration of war. The following day, the United States responded with its own declaration. Under the terms of the Tripartite Treaty, Germany declared war on the United States and on 11 December, the United States declared war on the Axis powers. The storm clouds of the preceding decade had broken into in a major storm.

27 December 1941, Jakob Emanuel Lange (Fig. 33) breathed his last, just a few days after Christmas, although there might not have been much to celebrate. He was 77 years of age. His occupation had been in education, especially agricultural



Figure 32. Detail of marquetry on the door of Jakob’s cabinet housing the first-run plates from “*Flora Agaricina Danica*”. Source: Lene Lange.

education and that reputation had underwritten his 1927 and 1939 trips to America. However, his preoccupation was mushrooms and especially their images (Lange 1943). This singular mindset had led to over 1000 such illustrations and their reproduction did not die with him. Morten (Fig. 34) used Jakob's portraits in a popular English language mushroom guide (Lange and Hora 1963, with several printings), later in a Danish edition (Lange and Lange 1970), with translation editions in Dutch, Finnish, French, German, Italian, Norwegian, Spanish and Swedish. Eventually, the original set of the portraits was deposited in the Botanical Museum in Copenhagen, now the Natural History Museum of Denmark, whereas the copy set is privately owned. Morten's daughter, Lene, remains a mycologist, with interest in ecology and distribution (Lange 1974; Samson 2018).

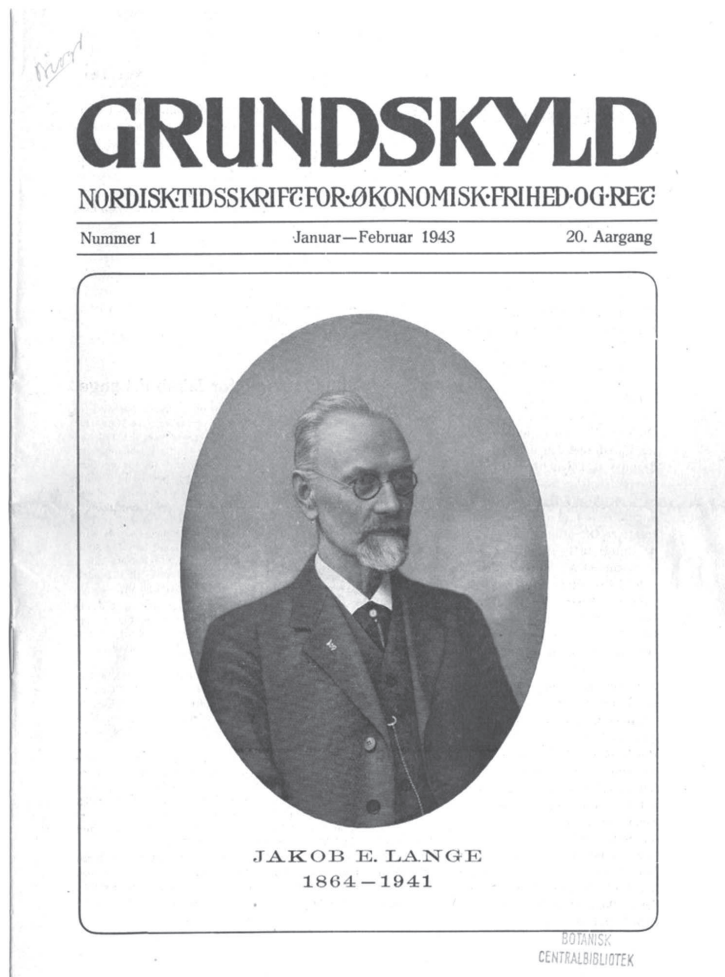


Figure 33. Jakob E. Lange on cover of “Grundskyld” (Nordic Journal of Economic Freedom and Justice). No. 1., 1943.

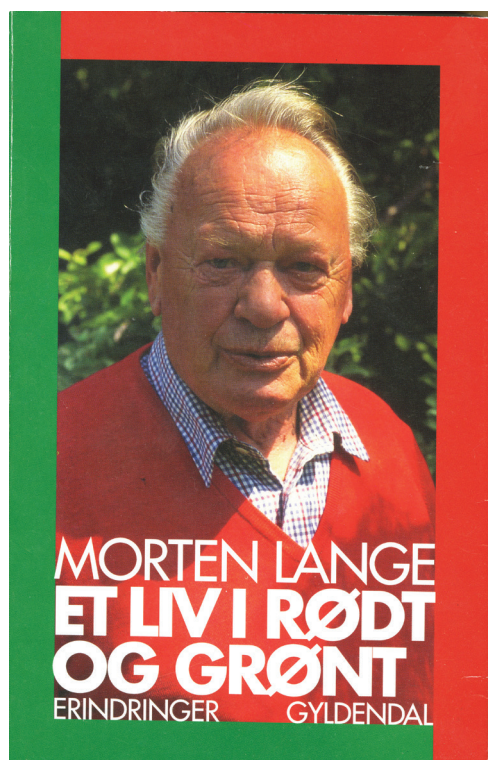


Figure 34. Knud Morten Lange in maturity. Source: on-line.

In a eulogy, A.A. Pearson (1947) reviewed FAD's five volumes as well as Jakob's life and motivation.

Far from the European theatre, Japanese forces overran the Korean Peninsula, much of China and, in 1942, extended its holdings down the Indochinese Archipelago, including Singapore and much of the "Dutch East Indies". At least two notable mycologists were swept up; E.J.H. Corner (1981) in Singapore and M.A. Donk (Maas Geesteranus 1973) in Buitenzorg (later Bogor, Indonesia). They were treated quite differently, but survived to continue productive mycological research.

29 August 1943: Germany placed Denmark under direct military occupation.

1943: German occupation authorities initiated the round-up of Danish Jews. Many Danes donned stars of David in hopes of confusing the military police. Many Jews were rescued and smuggled to neutral Sweden.

During those days, the German SS ('Schutzstaffel' or "Protective Echelon" for its origin as Hitler's personal bodyguard), expropriated the Odense "Husmandsskole" as their main headquarters for Denmark. Morten (Lange 1996): "... [father] always loved freedom and hated Nazism. In the last years of the occupation, his old home, the Small Holders' School, was taken over by the Gestapo and they made it the worst prison in

the whole country”. In the waning days of the European campaign, the Royal Airforce of Britain bombed the place into the ground^[9].

Denmark was liberated by British troops from the south in May, 1945. Within days, the war in Europe was concluded after the armies of the United States and USSR met within Germany. Germany capitulated for the second time in the 20th century. It took another year before Japan was forced to surrender after two atomic bombs were dropped on major cities.

Chapter 7. After-thoughts

This paper is a tale of a small corner of turn-of-the-20th-century mycology. Almost the entire cast was born before 1900, generally from the close of the United States’ Civil War through the “Gay ‘90s” and most lived into the decades of World War II. The cast saw economic feast and famine, repeated wars and the growth of democratic societies. It is told, for the most part, through the eyes of a non-American, a Danish man whose long working hours and imagination were occupied by cultural equality for his fellow citizens, but whose hobby was mushrooms, their forms and habitats.

In a recent Copenhagen newspaper, Politiken (8 July 2021), under the by-line, Gretelise Holm, there appeared a “chronology” about the small holders. The headline: “Small-holders are extinct, and soon we, children of the small-holders, will be gone too”. A summary follows. From 1880–90, ca. 140,000 men working in agriculture went to the cities to work there and 300,000 Danes emigrated, most to the United States. In 1899, a law established that small-holders’ farms could not exceed 3.5–5 “tønder land” (= 4.8–6.8 acres) to ensure that the small-holders would still be available as a working force for the larger farmers[!]. Later, this was changed so they could have 6–10 “tønder” (= 8–13 acres), enough to sustain an independent family. Seventy-five years ago (1946, just after World War II), the small holders’ movement had 115,636 members organised in 1317 local chapters. Between 1950 and 70, 50,000 small-holders disappeared. No matter how poor they were, the small-holders were not socialists, since they had “their own” place, although they often had to work for others as well in order to make a living. In 1993 the “Small-holders Society” changed its name to “Danish Family-farmers” and 10 years later, they fused with the larger farmers’ society and took the common name “Danish Agriculture”. The small-holders movement had withered and died.

Finally, the reporter discussed the pros and cons for the small farmers versus the large farmers. Some of the small farmers are now organised in the “Free Farmers” organisation, the homepage of which includes: “Problems with environment, biodiversity, climate, energy, distribution of the population, unemployment as well as physical and psychological health can be solved through a radical new structure, where the right to own land is spread to more hands.”

Jakob Lange had absolute confidence in his “portraits” as substitutes for long and, for him, tedious descriptions. His aquarelles, though, could not capture the variability of the taxon, but only the form and colour of the basidiomata of the single collection used as models. Colours of basidiomata were considered “true,” so his inclusion of a colour chart at the end of “Studies” part VI (on *Russula*; Lange 1926) is unexplained. Upon even rapid examination, it seems clearly done with his water-colour palette and brushes and probably added to over time, for the colours do not fit any pattern. A footnote refers to 970 completed portraits (in 1926) at the library of the Botanical Museum of the University in Copenhagen, referred to by Lange as “*Danmarks Agaricaceer*”. By 1926, American agaricologists were using Ridgway’s (1912; Petersen 2016) “Color Standards and Color Nomenclature”, while Europeans had Klincksieck and Valette (1908).

Not long before Lange’s “Studies” series commenced, came instalments of “North American Flora”, a contribution from The New York Botanical Garden, edited by and often written by William Alphonso Murrill (Murrill 1907, 1908, 1914, 1916, 1917a, b; Murrill and Burlingham 1910; Burlingham et al. 1915; Murrill et al. 1924; Overholts and Kauffman 1932), some volumes of which dealt with the Agaricales. For Lange, they would have been a disappointment, for they were models of tedious descriptions in small print, with no illustrations. Keys were provided, but employed characters which were difficult to interpret. Barnhart’s (Murrill and Barnhart 1916) bibliography was, however, exhaustive and, to this day, serves as a guide to the literature prior to 1920.

The meagre MycoPortal trail of Lange specimens are clues to his stops in 1931, reflective of his philosophy that illustrations were better than dried specimens. Noting his microscope (Fig. 35), though, gives clues to the quality of his observations of microscopic characters. Especially spore dimensions must be granted some leeway, much less cystidia. Lack of herbarium material forms an obstacle for molecular evidence of transatlantic congruence of taxa, precisely the motivation for his 1931 trip. Molecular analysis will help by facilitating proposal of epitypes. Lange’s conscious decision not to develop a herbarium of even the specimens he illustrated deprived future workers from accurately identifying and mapping the agarics of Europe (Heilmann-Clausen et al. 2019).

Lange’s admiration of Fries, who also did not keep a large herbarium, was explicit. However, Fries’ aquarelles were executed by hired professional artists, not Fries himself (Petersen and Knudsen 2016), even though he approved of each illustration. Fries’ plates may have served as models for Lange, for his uncle owned a copy of Fries’ illustrations.

Lange (1938b) related the intentions for his 1927 and 1931 trips, but we know that he did some mycological sleuthing in 1927 and some lecturing, probably on agricultural topics, in 1931. The latter trip could well have included stops purely for agricultural or educational appearances. The 1939 trip was explicitly devoted to both missions.



Figure 35. Jakob Lange at his microscope; age perhaps 60. Source: Henning Knudsen.

There is, of course, a temptation to examine Jakob Lange unidirectionally: by a mycologist as a mycologist, by a sociologist or economist as a social economist, by a politician as a politician. To do so would not do him justice. Lange was all of these, but at the bottom of it all, he was a Dane. The parting words of his memoir (Lange 1938b) were: “But the society we dare to dream about, the country of equality, must be built on the foundation of the people. It has been a happiness for me to have lived in an era and in a country, where a part of this popular character has germinated, to be able – through my information work – to guard and nurse its growth”.

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In a paper of this breadth and length, numerous people furnished information and clues to needed data. Amongst these individuals are the following.

Dr Joe Ammirati not only informed us of John Hotson, but also provided an unpublished (and undated) paper, “Fungus Collectors of the Pacific Northwest.” Dr Mary Berbee helped with information on collecting in Vancouver and especially information on Frank Dickson. Dr Dennis Desjardin suggested avenues for information on early San Francisco Bay mycology, especially the name of Bessie Southworth Spalding. Dr Don Pfister gave information about Farlow’s watercolours and Lange’s annotation of some of them. For information about the Minnesota Mycological Society, Heather Erikson has lectured and published on Dr Mary Whetstone and shared some of her data with us. John Lamprecht, Jane Onorati and David McLaughlin put us in touch with her. Megan Romberg, who works at the Agricultural Research Service in Beltsville, MD, generously searched the database there, which led us to our search of MycoPortal and also volunteered information about the early Washington Mushroom Club and forays around the District. Dr Else Vellinga at University of California, Berkeley, who wrote on E. E. Morse, furnished information about Bonnie C. Templeton, W.H. Long and C.F. Baker. She also suggested some clues to early collecting in southern California.

Lene Lange, Jakob’s granddaughter, generously supplied images of Jakob’s paintings of scenery, as well as of his marquetry. Her encouraging words were also appreciated.

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Finally and exceptionally, we extend our gratitude to the dedicated group of workers behind MycoPortal. This database of accessioned fungus collections in herbaria holds possibility not only taxon-centred, but by date, locality and collector. In this way, Lange’s collections in Ingolf, Ontario, Canada, came to light, otherwise easily missed.

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End notes

1. Henry George (1839–1897)

Henry [NMI] George was a leading American economic and political thinker, but he was also the epitome of the “rags to riches” American story. Raised under a strict Episcopalian father, he revolted against the parochial school, which was replaced by a tutor. He adopted a set of beliefs he called “deistic humanitarianism,” probably not far from present-day Secular Humanism.

His formal education ceased when he was 14 and, at 15, he shipped out as a foremast boy climbing the shrouds of a ship bound for Australia and India. That was 1855 and three years later, he disembarked in San Francisco, essentially penniless, where he settled into a job as a typesetter, unromantic but steady. He married his wife Annie, an Irish Catholic, but their four children were mainly influenced by their father’s deism and humanism.

His experience overseas and at home sowed embryonic seeds of economic thought. How could so many people exist in poverty at the same time that society seemed to become more prosperous? America seemed to magnify this incongruity. In a trip to New York City, he was amazed at the apparent paradox that the poor in that complex city of immigrants were much worse off than the poor in less developed California. He developed a philosophical concept questioning this *status quo* and began to write his thoughts: people should own the value of the product of their personal labour, but the land itself (including natural resources) should belong equally to all members of society. He argued that a single tax on land would create a more productive and just society. The more sophisticated and profitable developers of the land should pay more taxes; farmers should pay less. His words and ideas proved attractive to a wide spectrum of society and his influence grew apace. As might be expected, his popularity was chiefly in the working classes. His thoughts matured and, at age 40, he published a book, “Progress and Poverty” (George 1879), which proved to be his *magnum opus* and which eventually sold over three million copies worldwide. The philosophy became known as “Georgism” and spawned several reform movements during the Progressive Era.

One of his most enthusiastic followers was Jakob Lange in far-off Denmark. Lange would translate George’s books into Danish and expound on George’s philosophy in

his teaching, first at Dalum, then at Odense. He integrated George's principles into an overall context of social equality and education for the "small-holders."

George became widely travelled after his publications' successes, including a speaking tour of Great Britain. In his youthful zeal over Georgistic principles, Lange sought to travel to Britain to hear and meet George. Alas, there were no available passenger ships between Denmark and England to match his aspiration and time and he wound up sharing a boat with 600 pigs in order to attend George's lectures. However, as luck would have it, Lange appeared just after George had spoken and departed for his next appointment. Lange bolted after him and after a couple more missed opportunities, did, indeed, meet and talk with Henry George. Lange was only 33 when George died.

Lange's 1927 trip to the United States was due, in part, to his experiences and application of Georgist and Grundtvigian principles to Danish agricultural education. Lange came to know and befriend George's daughter, Anne George de Mille and met several influential American followers of George's philosophy.

2. Olive Dame Campbell (1882–1954)

Olive Dame Campbell was born to Lorin Low and Isabel (Arnold) Dame in Medford, Massachusetts. She married John C. Campbell in 1907 and moved to the mountains of north Georgia, where John was President of Piedmont College. From 1908 to 1912, she accompanied him through the mountains of Tennessee, Kentucky, Georgia, West Virginia and North Carolina, surveying social and economic conditions. After 1913, she established residence in Asheville, where John had been appointed Chief Executive Officer of the Southern Highlands Division of the Russell Sage Foundation. At his death in 1919, he had written only the preface and first chapter of a projected study of the Appalachian Region; she completed the manuscript, which was published under her husband's name as "The Southern Highlander and His Homeland" in 1921 (Campbell 1921).

After John's death, Mrs. Campbell became executive secretary of the Conference of Southern Mountain Workers, which he had founded; she held the position until 1928. Concurrently, in 1921, she joined the staff of the Russell Sage Foundation. In 1922, her interest in using traditional folk culture as a basis for social reconstruction led her to accept a Scandinavian-American Foundation fellowship for an eighteen-month study of adult education in Scandinavian folk schools. Based on her experiences, she wrote "The Danish Folkschool" (Campbell 1928). In 1928–29, she was instrumental in establishing the Southern Highlands Handicraft Guild, a marketing organisation for mountain craftsmen that still maintains its headquarters in Asheville.

It was during her Scandinavian study-tour that she met Jakob Lange, Headmaster of the *Fyn Husmandsskole* in Odense, Denmark. She interacted with Lange frequently and, in the preface to her book (Campbell 1928), she wrote: "I wish to acknowledge my deep indebtedness to the American Scandinavian Foundation which made this study possible ... and especially to Jakob Lange, principal of the Smallholder's School in Odense". Thus was formed a close relationship between Denmark and the United States with the cause of social equality at its core. In late 1925, Olive returned to North Carolina and established the John C. Campbell Folk School in Brasstown, Cherokee County and, in 1927, Jakob was invited to join in the celebration of the new endeavour.

In the forty years that Olive Dame Campbell lived in western North Carolina, she collected folk songs, tallied mountain schools, studied Scandinavian education, established a school, organised numerous agricultural cooperatives, wrote books, conceptualised a craft marketing guild and organised multiple conferences (Campbell and Butler 1924; Campbell 1929). While some of her accomplishments are well recognised, others have gone unnoticed because of Campbell's deference to others. During her lifetime, she wrote three books: one under her own name, one as co-author and one under her husband's name. She also wrote his biography, kept a journal of their travels and, independently, wrote numerous articles and speeches (Fariello 2015).

3. John C. Campbell (1867–1914)

In the United States, John Charles Campbell (1867–1919), a product of Williams College (B.A. 1892) and Andover University (D.D. 1895), applied his experience to education in rural settings in Alabama and the Southern Appalachian Mountains. In 1901, he was appointed as superintendent of Piedmont Collegiate Institution, in Demorest, Georgia, tucked in the foothills of Georgia's share of the Appalachian Mountain chain. The institution was new, having been founded in 1897 and served a rural population, with an enrolment of less than 400 from 1st grade to second year of college. Within a short time, Campbell was promoted to Dean and eventually to President of Piedmont. Widowed during his tenure at Piedmont, on a recuperation vacation trip to Scotland, he met and, in 1907, married Olive Arnold Dame, 15 years his junior, who shared John's deep concern about the people of "Southern Appalachia". Over more than the next decade, they attempted to determine social needs and their remedies within the Appalachian region. They set out trekking the wilderness and back roads from north Georgia to West Virginia. On occasion, they were able to travel by rail; at other times the remoteness of their destinations required they walk into deep hollows and isolated "coves" to make contact with the sequestered inhabitants. The Campbells became amongst the first to distinguish and map Southern Appalachia as a distinct region. John popularised the name Southern Highlands. In 1913, the Campbells established residence in Asheville, North Carolina, in the heart of the southern Appalachians. Across the mountains in Tennessee, Horace Kephart (1862–1931; Kephart 1913) was publishing a very different view of Southern Highland life.

The Campbells shared the same idealism and were determined to provide aid, through a combination of education and humanitarian endeavours and, as their experience grew, they heard about a far-off land where an older tradition was addressing the education and well-being of "small holders"—the Scandinavian Folk High-schools.

Upon the early death of John in 1919, Olive continued their studies. John had intended to publish a book based on their work and she finished that task (Campbell 1921).

4. Jakob Lange's impressions of America (Lange 1931; translation, HK).

Once on the road away from New York in 1931, Lange found himself in rural America. All around him were forests and farms comparable to those of Europe, but with exceptional differences. These differences, he concluded: "... are also found in the human

world. There are, of course, European elements, especially Irish, but also Scots, English, Scandinavian etc. – not to speak of the ‘coloured,’ but next to that, often distinctly felt, is something American. The American ‘farmer’ is not just straightforwardly a Danish peasant and does not have the imprint on him of a history of former suppression, of an underclass living, but also not of romantic overcapitalisation as ‘the peoples’ nucleus and strength’. But nonetheless, I was struck time after time, by how uniform Danish and American attitude could be: a certain natural feeling of equality, a certain ‘well-grounded’ feeling we met everywhere. No snobbery, but straightforward helpfulness is probably the most characterising feature which has come to be developed in the internationally mixed colonies, where ‘what can I do for you’ is the first a newcomer will hear” (Lange 1931).

“The president, the director of the Agricultural high school, Dr Butterfield, had not only a winning personality, but was an important personality of real dimensions, with radical thoughts – which, by the way, cost him his position at the high school a short time after, under pressure from reactionary capitalistic influence, felt here [Denmark] as so often in America.

“But in America you should be able to overcome a surprise, as my wife – totally unprepared – had to, when they asked her to take the podium at a meeting where I had spoken (which she proudly did, so the acclamation was practically larger and at least more heartfelt than after my lecture)”.

Some remarks on the architecture in Washington, D.C. The capital building’s “capitolium with its huge cupula makes a distinct impression – pure in the lines and powerful in the dimensions – especially when you have not seen the many copies, in smaller format, around the capitals of the individual states (e.g. in Maine and Michigan). But by the way there is a strong prominent tendency in American architecture (when something monumental is sought for) to follow classical, Greek-Roman role-models, especially when you so-to-say build in supernatural size: huge Parthenons, in snow white, polished marble, seems a little far from Greek. In opposition to this is ‘the White House,’ the President’s home, which makes an impression on you by its modest noblesse, almost as in Washington’s own house at his mansion, Mount Vernon, not far from the capital, now a common place to visit for people from all States, a kind of American Mecca.

“It is instinctively repulsive as soon as you get south of Washington, to see the distinct barrier between ‘white’ and ‘coloured’ being retained everywhere. [Lack of capitalised references to race is his.] In the waiting rooms along the railway, there is a barrier: white at one side, black at the other; the two sides even have their own ticket-hole. A ‘coloured’ – no matter how weak the negro-features may be, cannot enter a ‘white’ restaurant. Equalizing measures, e.g. common schools, have time after time been abandoned and the underclass look is everywhere connected to the negroes. But you understand anyway better having seen it yourself, why the deep ditch is so difficult to fill”.

5. Henry Agard Wallace (1888–1965)

An Iowan, Henry Agard Wallace’s father, Henry C. Wallace, served as Secretary of Agriculture under Warren G. Harding, popular Republican President, so national service was not strange to Henry A. Once graduated from Iowa State University (1910), he joined

the family weekly publication, “Wallace’s Farmer” as a writer and soon thereafter, as editor. As a professional farmer, he also founded the Hi-Bred Corn Company (Hi-bred 2021), which eventually became extremely successful. Over subsequent years, Wallace delved into numerous pursuits, from statistics and economics to religious and spiritual movements, including Georgism. After his father’s death in 1924, Henry drifted away from the Republican Party and supported Franklin Roosevelt in the 1932 election campaign. Wallace’s experience with poverty-stricken, southern, tenant farmers resonated with the Danish history of peasant culture. By American standards, Wallace supported a monumental governmental role in agriculture in harmony with Roosevelt’s New Deal policies, a view not without backlash in Congress and the U.S. Supreme Court.

During the War years, Roosevelt sent Wallace, by then Vice President, to the Soviet Union (now Russia) to report on the “collective agriculture” programmes. Unbeknownst to Wallace, he was duped by Soviet authorities and returned with a glowing report, which fed into accusations of being a Communist (with capital C), a label which became anathema as US/Soviet relationships soured. As a result, Wallace was dropped from the ticket for the 1944 election in favour of Harry S. Truman.

Jakob Lange would have found common ground with Wallace had the two met at the Williams College colloquium in 1927 or Lange’s possible lecture in Washington in 1939.

6. Berea College (1855–present)

The founding and development of Berea College mirrors both the ebbs and flows of United States history, as well as bearing a close resemblance to the aspirations of the “Small-holders High-schools” of Denmark.

Not far from Lexington, Kentucky, the Rev. John G. Fee started a one-room school in 1855 that eventually would become Berea College (Berea 2021). Fee envisioned a school that would be an advocate of equality and excellence in education for men and women of all races. Although the emancipation decree was not signed until 1865, Fee’s uncompromising faith and courage in preaching against slavery attracted the attention of Cassius M. Clay, a well-to-do Kentucky landowner and prominent leader in the movement for gradual emancipation. Clay offered Fee a 10-acre homestead on the edge of the mountains if Fee would take up permanent residence there. Fee accepted and established an anti-slavery church with 13 members on a ridge they named “Berea” after the biblical town whose populace was open-minded and receptive to the gospel (Acts 17:10).

Berea’s first teachers were recruited from Oberlin College, an anti-slavery stronghold in Ohio. Fee saw his humble church-school as the beginning of a sister institution “which would be to Kentucky what Oberlin is to Ohio, anti-slavery, anti-caste, anti-rum, anti-sin”.

The first articles of incorporation for Berea College were adopted in 1859, the year of Darwin’s “Origin of Species”. However, it also was the year Fee and the Berea teachers were driven from Madison County by southern, pro-slavery sympathisers. Fee spent the Civil War years raising funds for the school; in 1865, following Lincoln’s emancipation proclamation, he and his followers returned. A year later, the articles of incorporation were recorded and, in 1869, the college department became a reality.

Berea's commitment to interracial education was overturned in 1904 by the Kentucky Legislature's passage of the Day Law, which prohibited education of black and white students together. When the U.S. Supreme Court upheld the Day Law, Berea set aside funds to assist in the establishment of Lincoln Institute, a school located near Louisville, for black students. When the Kentucky Day Law was amended in 1950 to allow integration above the high school level, Berea was the first college in Kentucky to reopen its doors to black students.

By 1911, the number of students seeking admission to Berea was so great that the trustees amended the College's constitution to specify the southern mountain region as Berea's special field of service. The commitment to Appalachia, however, had begun as early as 1858, when the region was identified as a "neglected part of the country".

In the early 1920s, in addition to its College Department, Berea established a high school that included ungraded classes for students who had not had educational opportunities, an elementary school, a vocational school and a Normal School for teacher training. No student was charged tuition. Most students worked for the College, whether weaving on the loom or milking in the dairy.

7. Louis F. Post (1849–1928)

Louis Freeland Post was a controversial Assistant Secretary of Labor in the Woodrow Wilson administration. His collegial friendship with Jakob Lange was based on his (Post) strong and vocal approval of the political ideas of Henry George, especially his uniform tax plan, but it was his stance against anti-immigration laws, which put him at odds with powerful politicians of the day.

Deportation laws were being stringently applied when the temporary absence of the Secretary of Labor and that of the Chief Assistant coincided and left Post in charge of the Department. Post considered the operative deportation process to be a "witch hunt" and he ordered a complete review of recent deportations, dismissing 71% of them as unconstitutional. This, not unexpectedly, brought him afoul of A. Mitchell Palmer, Attorney General and J. Edgar Hoover, Head of the Justice Department's "Radical Division", an organisation committed to rooting out foreigners with "radical" intentions, and the precursor to the Federal Bureau of Investigation (FBI). As early as January 1920, Hoover's FBI began compiling a file on Post and his political leanings, but failed to find substantive evidence of radical connections on his part. A call for Post's impeachment followed, but his defence of his actions won the day and impeachment was withdrawn.

An evening with the Langes must have provided some hearty conversation on Georgist ideas and the progress of his movement on both sides of the Atlantic.

8. Mary Whetstone (1845–1929)

Dr Mary J.S. Whetstone, Corresponding Secretary of the Minnesota Mycological Society, died at the age of 84 years (Davis and Seaver 1930), just two years before the Langes passed through. As Mary J. Snoddy, she received the degree of M.D. from the University of Michigan in 1881. She attended clinics in London, Paris, Vienna, Detroit, Boston

and New York, serving on the staff of New England Hospital for Women and Children, Boston. She promoted the Northwestern Hospital for Women and Children, was an active worker for suffrage as a member of the Women's Welfare League and, in addition to her practice, was interested for many years in the study of fungi (Dillon 1924). She was a premature widow. Her husband, Allen S. Whetstone, also a physician (Univ. of Mich., M.D. 1880), died in 1909. Like so many other collectors across the country, she was a correspondent of Charles Horton Peck and Curtis Gates Lloyd.

In her first letter to Peck (3 November 1898), she introduced him to the Minnesota Mycological Club, then a group of “about 20 enthusiastic, intelligent members”. She inquired whether he would be willing to help “with difficult identifications”. Peck obliged, as he did repeatedly with scores of such collectors and a correspondence commenced, lasting for at least a decade. Descriptions accompanied dried specimens and Peck did his best to provide pertinent information.

However, just as collegial as Whetstone would have been, there was also a prodigious number of Scandinavian settlers in the neighbourhood. The Langes would have been quite at home in the field with transplanted Scandinavians.

9. The fate of the Odense Husmandsskole.

(Husmandsskole 2021a, b). The Gestapo established three main headquarters in Denmark: in Copenhagen, at Århus and on Fyn (*Fyns Stifts Landbrugsskole*). The first two were bombed by the British Royal Air Force (RAF), so the Gestapo on Fyn also expected to be bombed. For this reason, they placed huge camouflage nets over the school and surrounding buildings, so when the RAF came with six Mustangs with 225 kg bombs, they could not find the target in spite of the maps the pilots had received from the Danish resistance, who asked for the bombing! They had to fly three times over the target before they finally let the bombs fall. The Gestapo, however, had been warned by telephone from Sild-Rømø, where the Mustangs entered Danish air territory flying only 15 m above the sea, so as not to be detected by the German radar. However, they were discovered and when they arrived at the school, the Gestapo had left and the sirens only left nine minutes for people to escape before the bombs fell. Due to the cover over the buildings, the bombs were not very precise and only nine local people died, just 16 days before the end of the war! The school was rebuilt not too far away.

In memory of Jakob Lange, a monument was built, like a shrine, where he is depicted surrounded by children and people and there is a poem in his honour.

Updated taxonomy on *Gerronema* (Porotheleaceae, Agaricales) with three new taxa and one new record from China

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Abstract

Only three *Gerronema* (Porotheleaceae) species have been previously recorded in China. Here, we report collections of a fourth species in China: *G. nemorale* Har. Takah., which is widely distributed in Chinese temperate to subtropical zones. We also formally describe three new species, collected from Anhui, Fujian, and Zhejiang provinces: *G. baishanzuense* **sp. nov.**, *G. microcarpum* **sp. nov.**, and *G. zhujiang* **sp. nov.** Furthermore, we include the results of a phylogenetic analysis of Porotheleaceae based on a multi-locus (ITS + nLSU) dataset. The results, which indicate that *Gerronema* is polyphyletic, support the taxonomic recognition of the three new species. Morphological descriptions, photographs, line drawings, and comparisons with closely related taxa are presented for the new and newly recorded species. A key to the seven species of *Gerronema* in China is also provided.

Keywords

new taxon, polygenes, taxonomy, white-spored

Introduction

Gerronema Singer is a small omphalinoid genus, principally subtropical to tropical in distribution, with approximately 62 named species in Index Fungorum. Singer (1951) erected the genus *Gerronema* to accommodate three tenacious and lignicolous omphalinoid to clitocyboid species from South America and later transferred some species traditionally placed in *Omphalina* Quél. to this new genus (Singer 1964). This taxonomic definition of *Gerronema* was controversial, however, as the circumscription of *Omphalina* by Singer was notably different from that of Bigelow (Bigelow 1970; Singer 1986). Virtually all species of *Omphalina* recognized by Bigelow were included in Singer's concept of *Gerronema*, whereas species placed in *Clitocybe* (Fr.) Staude by Bigelow were retained in *Omphalina* by Singer (Bigelow 1970, 1982, 1985; Singer 1986). Furthermore, Lange (1981) treated *Gerronema* as a subgenus of *Omphalina* (subgen. *Gerronema*). Both Singer and Bigelow considered *Gerronema* to be pigment based and therefore emphasized pigmentation as a more important taxonomic character than other observed features (Bigelow 1970, 1982, 1985; Singer 1986). *Gerronema sensu* Singer, however, was considered to be heterogeneous (Cléménçon 1982; Moser 1983; Kuyper 1986; Singer 1964, 1975, 1986; Norvell et al. 1994; Antonín et al. 2008), and Redhead (1986) restricted the genus to species having sarcodimitic tissues, a concept supported by Norvell et al. (1994). Along with Redhead, Norvell et al. defined *Gerronema* as comprising lignicolous species with typical sarcodimitic tissues, and the genus was monophyletic according to this circumscription (Redhead 1986; Norvell et al. 1994). Finally, an infrageneric classification proposed by Singer divided *Gerronema* into four subgenera containing six sections on the basis of pigmentation, cystidia, hymenophoral trama, and clamp connections (Singer 1970).

In previous taxonomic studies, many authors have suggested that the genus *Gerronema* is heterogeneous (Cléménçon 1982; Moser 1983; Kuyper 1986; Antonín et al. 2008). The polyphyletic status of *Gerronema* is uncertain, however, owing to insufficient species representation and limited phylogenetic evidence, and only four *Gerronema* taxa have been analyzed in phylogenetic studies: *G. chrysophyllum* (Fr.) Singer, *G. strombodes* (Berk. & Mont.) Singer, *G. subclavatum* (Peck) Singer ex Redhead, and *G. marchantiae* Singer & Cléménçon (Lutzoni 1997; Pine et al. 1999; Hibbett and Binder 2002; Moncalvo et al. 2002; Redhead et al. 2002). Two of these species, *G. chrysophyllum* and *G. marchantiae*, have since been transferred to *Chrysomphalina* Cléménçon (Cléménçon 1982) and *Loreleia* Redhead, Moncalvo, Vilgalys & Lutzoni (Redhead et al. 2002), respectively, and the other two species, *G. subclavatum* and *G. nemorale*, are difficult to distinguish genetically (Antonín et al. 2008). According to a phylogenetic reconstruction of more than 800 euagaric taxa derived from a nuclear ribosomal large subunit RNA gene (nLSU) sequence dataset, *Gerronema* is monophyletic and belongs to the “hydropoid” clade together with *Hydropus* Kühner ex Singer s. str., *Megacollobia* Kotl. & Pouzar, *Clitocybula* (Singer) Singer ex Métrod,

and *Porotheleum fimbriatum* (Pers.) Fr. (Moncalvo et al. 2002). Matheny et al. (2006) and Antonín et al. (2019) concurred with Moncalvo et al. (2002) in the establishment of the hydropoid group and the monophyly of *Gerronema*. Matheny et al. (2006) also included *Henningomyces candidus* (Pers.) Kuntze, *Hydnopolyporus fimbriatus* (Cooke) D.A. Reid, and some *Mycena* species (*M. auricoma* Har. Takah., *M. amabilissima* (Peck) Sacc. and *M. aurantiidisca* (Murrill) Murrill) in the same subclade of the large Marasmioid clade, but they did not include any *Gerronema* species in their studies. In a taxonomic and phylogenetic study of *Clitocybula s. l.*, the hydropoid clade was found to comprise eight genera, including *Gerronema*, and was sister to other genera (Antonín et al. 2019). In 2019, Vizzini et al. assigned the hydropoid clade to Porotheleaceae, a new family; at the same time, they recognized *Gerronema* as polyphyletic on the basis of previous taxonomic studies and divided it into seven clades, designated as *Gerronema* 1 to *Gerronema* 7 (Vizzini et al. 2019). The view of *Gerronema* as polyphyletic is also supported by our studies.

Gerronema is well characterized by its lignicolous habit; omphalinoid to clitocyboid basidiomata; an umbonate or infundibuliform pileus with partly to entirely pigmented, decurrent lamellae; smooth, thin-walled, and inamyloid basidiospores; cystidia that are present or absent; and sarcodimitic tramal tissues (Singer 1951; Norvell et al. 1994). Species of *Gerronema* are widespread in subtropical to tropical regions but are also rarely distributed in temperate zones (Singer 1951, 1970; Norvell et al. 1994). Studies of *Gerronema* during the past 70 years have focused on species distributed in South America and Asia, with 11 new species and six new combinations recognized from Argentina, the USA, Brazil, Japan, India and China (Singer 1951, 1959; Liu 1995; Takahashi 2000; Desjardin et al. 2005; Latha et al. 2018; Liu et al. 2019). In contrast, few investigations of *Gerronema* taxa in Europe, Australia, and Africa have been conducted, and only one new species and two new combinations have been reported from these regions (Bañares et al. 2006; Degreef and Ndong 2007; Cooper 2014).

Only three *Gerronema* species, including two new to the genus, have previously been recognized in China (Liu 1995; Dai et al. 2010; Liu et al. 2019). In recent years, progress has been achieved in clarifying the status of mycenoid and omphalinoid fungi in China, including a new taxon reported from Zhejiang Province, China, namely, *Leucoinocybe lishuiensis* Q. Na, H. Zeng & Y.P. Ge, which is sister to *Gerronema* (Na and Bau 2018, 2019a, 2019b; Ge et al. 2021; Na et al. 2021). During our ongoing research on omphalinoid fungi, we discovered three new species belonging to *Gerronema* in subtropical China. These species are formally described here as *G. baishanzuense* Q. Na, H. Zeng & Y.P. Ge, *G. microcarpum* Q. Na, H. Zeng & Y.P. Ge, and *G. zhujiang* Q. Na, H. Zeng & Y.P. Ge. In addition, we have determined that *G. nemorale* Har. Takah., which has not previously been recorded in China, is widely distributed in the country. We accordingly present a morphological description of the new and newly recorded species, and we also provide a key for identification of the seven species of *Gerronema* currently known from China.

Materials and methods

Sample collection and morphological description

Specimens were collected in Anhui, Fujian, Jilin, and Zhejiang provinces, China, from June 2019 to August 2021. Basidiomata were photographed in their natural habitats with a Canon 90D digital camera and then dried on allochroic silica gel. Fresh fruiting bodies were recorded in the field to identify macroscopic characters. In our descriptions, color codes and notations follow Kornerup & Wanscher (Kornerup and Wanscher 1978). Microscopic features were conducted on dried specimens mounted in 5% KOH and stained with Congo red when necessary. Melzer's reagent was used to test whether spores and tissues were amyloid (Horak 2005). Twenty mature basidiospores from each basidiocarp were measured, the notation [*a/b/c*] used at the beginning of each basidiospore description indicates that *a* basidiospores from *b* basidiocarps of *c* specimens were measured. The dimensions of basidiospores and *Q* values are presented as (*d*) *e*–*f*–*g* (*h*) × (*i*) *j*–*k*–*l* (*m*), where *d* is the minimum length, *e*–*g* represents the range of at least 90% of values, *f* is the average length, and *h* is the maximum length; width (*i*–*m*) is expressed in the same manner. In addition, *Q* is the length: width ratio of a spore, and $Q \pm SD$ is the average *Q* of all basidiospores \pm the sample standard deviation (Ge et al. 2021; Liu et al. 2021; Na et al. 2021). Hyphae of the pileipellis and stipitipellis and a total of 20 basidia, cheilocystidia, and caulocystidia were measured from each collection. Author abbreviations follow those used in Index Fungorum (<https://www.indexfungorum.org>). Voucher specimens have been deposited in the Fungarium of the Fujian Academy of Agricultural Sciences (FFAAS), China.

Phylogenetic reconstruction

Genomic DNA was extracted from dried specimens using a NuClean Plant Genomic DNA kit (Kangwei Century Biotechnology Co., Beijing, China). The internal transcribed spacer (ITS) region and the nuclear large subunit (nLSU) of ribosomal DNA were respectively amplified with primer pairs ITS1/ITS4 and LR0R/LR7 (White et al. 1990; Hopple and Vilgalys 1999). The PCR thermocycling protocol (for both ITS and nLSU) was the same as reported in Ge et al. (2021). A dataset comprising sequences from 38 accessions of seven genera of Porothleaceae and *Mycena purpureofusca* as an outgroup was compiled for phylogenetic analysis. All newly generated sequences and those downloaded from GenBank are shown in Table 1. The sequences used in this study were aligned and adjusted manually using BioEdit 7.0.4.1 and Clustal X (Thompson et al. 1997; Hall 1999). In the alignment, gaps were treated as missing data. The alignment was deposited in TreeBase (submission ID: 29143; study accession URL: <http://purl.org/phylo/treebase/phyloids/study/TB2:S29143>). The best model of nucleotide evolution for the ITS and nLSU data was identified using Modeltest 2.3 (Nylander 2004). The optimized sequence dataset was analyzed using Bayesian

inference (BI) and maximum likelihood (ML) methods in MrBayes 3.2.6 and raxml-GUI 1.5b1, respectively (Ronquist and Huelsenbeck 2003; Stamatakis 2006). The BI analysis was performed for 2 million generations, with trees sampled every 100 generations. The sampled trees were subsequently summarized by using the “sump” and “sumt” commands after discarding the first 25% of iterations as burn-in. For the ML analysis, default parameters in RAxML were used with 1,000 bootstrap replicates. Phylogenetic trees were visualized with Figtree 1.4.3.

Table 1. Sequenced specimens used in phylogenetic analysis. New and newly recorded species are marked in bold.

No.	Taxa	Voucher	Locality	ITS	nLSU	Reference
				Sequences ID	Sequences ID	
1	<i>Chrysomycena perplexa</i>	MCVE:30184	Italy	MN496427	NG071251	Vizzini et al. 2019
2	<i>Clitocybula abundans</i>	STU:SMNS-B-FU-2017/00898	not indicated	MF627833	–	from GenBank
3	<i>C. familia</i>	PRM 921866	Czech	JF730327	JF730320	Antonín et al. 2011
4	<i>C. familia</i>	BRNM 736053	Slovakia	JF730328	JF730323	Antonín et al. 2011
5	<i>C. familia</i>	2319-QFB-25741	not indicated	KM406970	–	from GenBank
6	<i>C. familia</i>	STU:SMNS-B-FU-2017/00926	not indicated	MF627834	–	from GenBank
7	<i>C. familia</i>	NAMA 2017-349	not indicated	MH979253	–	from GenBank
8	<i>C. flavoaurantia</i>	D	Italy	HM191743	–	Malysheva and Morozova 2011
9	<i>C. flavoaurantia</i>	GDOR	Italy	HM191744	–	Malysheva and Morozova 2011
10	<i>C. flavoaurantia</i>	LE 262757	Russia	HM191745	–	Malysheva and Morozova 2011
11	<i>C. lacerata</i>	LE 6639	Russia	HM191746	–	Malysheva and Morozova 2011
12	<i>C. lacerata</i>	LE 262744	Russia	HM191747	–	Malysheva and Morozova 2011
13	<i>C. lacerata</i>	LE 262743	Russia	HM191748	–	Malysheva and Morozova 2011
14	<i>C. lignicola</i>	BPI M-20.989	Russia	HM191735	–	Malysheva and Morozova 2011
15	<i>C. lignicola</i>	BPI M-20.825	Russia	HM191736	–	Malysheva and Morozova 2011
16	<i>C. lignicola</i>	LE253926	Russia	HM191741	–	Malysheva and Morozova 2011
17	<i>C. lignicola</i>	LE262737	Russia	HM191742	–	Malysheva and Morozova 2011
18	<i>C. oculus</i>	AFTOL-ID 1554	USA	DQ192178	–	Matheny et al. 2006
19	<i>C. oculus</i>	3512	not indicated	KM406971	–	from GenBank
20	<i>C. oculus</i>	BIOUG24046-B03	Canada	KT695321	–	Telfer et al. 2015
21	<i>C. oculus</i>	WU 20008	Austria	LT854017	LT854017	Antonín et al. 2019
22	<i>C. oculus</i>	S.D. Russell iNaturalist # 8591258	India	MN906164	–	from GenBank
23	<i>C. oculus</i>	S.D. Russell iNaturalist # 8606755	India	MN906165	–	from GenBank
24	<i>Gerronema atrialbum</i>	AFTOL-ID 1529	USA	DQ192179	DQ192179	Matheny et al. 2006
25	<i>G. baishanzuense</i>	FFAAS0359 Holotype	China	OL985962	OL985984	This study
26	<i>G. baishanzuense</i>	FFAAS0360	China	OL985963	–	This study
27	<i>G. baishanzuense</i>	FFAAS0361	China	OL985964	OL985985	This study
28	<i>G. baishanzuense</i>	FFAAS0362	China	OL985965	OL985986	This study
29	<i>G. baishanzuense</i>	FFAAS0363	China	OL985966	OL985987	This study
30	<i>G. baishanzuense</i>	FFAAS0366	China	OL985967	OL985988	This study
31	<i>G. indigoticum</i>	HMJAU 47636	China	MK693727	MK693732	Liu et al. 2019
32	<i>G. indigoticum</i>	HMJAU 47942	China	MK693728	MK693733	Liu et al. 2019
33	<i>G. indigoticum</i>	HMJAU 47943	China	MK693729	MK693734	Liu et al. 2019
34	<i>G. keralense</i>	CAL 1666	India	MH156555	NG_064531	Latha et al. 2018
35	<i>G. kuruense</i>	CAL 1665	India	NG_159831	NG_064530	Latha et al. 2018
36	<i>G. microcarpum</i>	FFAAS0365	China	–	OL985989	from GenBank

No.	Taxa	Voucher	Locality	ITS	nLSU	Reference
				Sequences ID	Sequences ID	
37	<i>G. microcarpum</i>	FFAAS0371	China	OL985968	OL985990	from GenBank
38	<i>G. microcarpum</i>	FFAAS0372	China	OL985969	OL985991	from GenBank
39	<i>G. microcarpum</i>	FFAAS0373 Holotype	China	OL985970	OL985992	from GenBank
40	<i>G. microcarpum</i>	FFAAS0374	China	OL985971	–	from GenBank
41	<i>G. microcarpum</i>	FFAAS0375	China	OL985972	OL985993	from GenBank
42	<i>G. nemorale</i>	KACC 43599	Korea	EU883592	–	This study
43	<i>G. nemorale</i>	KACC 43600	Korea	EU883593	–	This study
44	<i>G. nemorale</i>	not indicated	Korea	EU883594	–	This study
45	<i>G. nemorale</i>	FA249	Pakistan	MN744686	–	This study
46	<i>G. nemorale</i>	FA236	Pakistan	MN744687	–	This study
47	<i>G. nemorale</i>	FA239	Pakistan	MN744688	–	This study
48	<i>G. nemorale</i>	FFAAS0377	China	OL985976	OL985997	This study
49	<i>G. nemorale</i>	FFAAS0379	China	OL985977	OL985998	This study
50	<i>G. nemorale</i>	FFAAS0382	China	OL985978	OL985999	This study
51	<i>G. nemorale</i>	FFAAS0384	China	OL985979	OL986000	This study
52	<i>G. nemorale</i>	FFAAS0388	China	OL985980	OL986001	This study
53	<i>G. nemorale</i>	FFAAS0389	China	OL985981	OL986002	This study
54	<i>G. nemorale</i>	FFAAS0392	China	OL985982	OL986003	This study
55	<i>G. nemorale</i>	FFAAS0410	China	OL985983	OL986004	This study
56	<i>G. strombodes</i>	DJL05NC72	USA	EU623639	–	Hughes et al. 2007
57	<i>G. strombodes</i>	TFB12519/ TENN60718	USA	EU623640	–	Hughes et al. 2007
58	<i>G. strombodes</i>	TFB12783/ TENN61350	USA	EU623641	–	Hughes et al. 2007
59	<i>G. strombodes</i>	TFB11947 clone C2	USA	KY242503	–	Hughes et al. 2007
60	<i>G. strombodes</i>	TFB11947 clone C3	USA	KY242504	–	Hughes et al. 2007
61	<i>G. strombodes</i>	TFB11947 clone C5	USA	KY242506	–	Hughes et al. 2007
62	<i>G. strombodes</i>	TFB14234	USA	KY242507	–	Hughes et al. 2007
63	<i>G. strombodes</i>	TFB14514	USA	KY242509	–	Hughes et al. 2007
64	<i>G. strombodes</i>	TFB11947	USA	KY271083	–	from GenBank
65	<i>G. subclavatum</i>	Redhead 5175, DAOM	not indicated	U66434	–	Lutzoni 1997
66	<i>G. subclavatum</i>	FLAS-F-60986	USA	MH016932	–	from GenBank
67	<i>G. subclavatum</i>	FLAS-F-61518	USA	MH211945	–	from GenBank
68	<i>G. subclavatum</i>	Smith-2018	USA	MK573888	–	Direct Submission
69	<i>G. subclavatum</i>	Mushroom Observer # 243440	USA	MK607510	–	Direct Submission
70	<i>G. subclavatum</i>	iNaturalist # 8545787	India	MN906021	–	from GenBank
71	<i>G. subclavatum</i>	S.D. Russell MycoMap # 6854	India	MN906138	–	from GenBank
72	<i>G. viridilucens</i>	SP307883 (SP)	Brazil	–	EF514207	Desjardin et al. 2005
73	<i>G. waikanaense</i>	PDD:87667	New Zealand	JQ694117	–	from GenBank
74	<i>G. wildpretii</i>	BRNM 788347	Madeira	LT854045	LT854043	Antonin et al. 2019
75	<i>G. xanthophyllum</i>	PRM 924657	Czech	LT854023	LT854023	Antonin et al. 2019
76	<i>G. zhujuan</i>	FFAAS0364	China	OL985973	OL985994	This study
77	<i>G. zhujuan</i>	FFAAS0370	China	OL985974	OL985995	This study
78	<i>G. zhujuan</i>	FFAAS0376 Holotype	China	OL985975	OL985996	This study
79	<i>Hydropus fuliginarius</i>	DAOM196062	USA	–	AF261368	Moncalvo et al. 2002
80	<i>H. marginellus</i>	AFTOL-ID 1720	Czech	DQ490627	DQ457674	Matheny et al. 2006
81	<i>H. marginellus</i>	OSC 112834	USA	EU669314	EU852808	from GenBank
82	<i>Leucoinocybe lishuiensis</i>	FFAAS 0111	China	MW424488	MW424492	Na et al. 2021
83	<i>L. lishuiensis</i>	FFAAS 0112	China	MW424489	MW424493	Na et al. 2021
84	<i>L. lishuiensis</i>	FFAAS 0113	China	MW424490	MW424494	Na et al. 2021
85	<i>L. lishuiensis</i>	FFAAS 0115	China	MW424491	MW424495	Na et al. 2021
86	<i>L. sp.</i>	KA12-0435	South Korea	KR673482	–	Kim et al. 2015

No.	Taxa	Voucher	Locality	ITS	nLSU	Reference
				Sequences ID	Sequences ID	
87	<i>L. sulcata</i>	CAL 1246 (HOLOTYPE)	India	KR029720	KR029721	Latha et al. 2015
88	<i>L. taniae</i>	BCN-SCM B-4064	Italy	LT854057	LT854028	Antonín et al. 2019
89	<i>Megacollybia clitocyboidea</i>	TFB11884/ TENN60766	USA	EU623658	–	Hughes et al. 2007
90	<i>M. clitocyboidea</i>	TENN62231	USA	EU623664	–	Hughes et al. 2007
91	<i>M. clitocyboidea</i>	TENN62230 clone c4	USA	EU623673	–	Hughes et al. 2007
92	<i>M. clitocyboidea</i>	TENN62230 clone c5	USA	EU623674	–	Hughes et al. 2007
93	<i>M. fallax</i>	MICH 45002	USA	EU623714	–	Hughes et al. 2007
94	<i>M. fallax</i>	TFB11561/ TENN59447	USA	EU623723	–	Hughes et al. 2007
95	<i>M. fallax</i>	DAOM208710	USA	EU623724	–	Hughes et al. 2007
96	<i>M. fallax</i>	Mushroom Observer 291302	USA	MN176984	–	Direct Submission
97	<i>M. fallax</i>	Mushroom Observer 286893	USA	MT437075	–	Direct Submission
98	<i>M. marginata</i>	TENN60752	USA	EU623685	–	Hughes et al. 2007
99	<i>M. marginata</i>	HR 91607	Czech	LT854051	–	Antonín et al. 2019
100	<i>M. platyphylla</i>	TFB11572/ TENN59523	USA	EU623712	–	Hughes et al. 2007
101	<i>M. platyphylla</i>	LE 256-2004	USA	EU623713	–	Hughes et al. 2007
102	<i>M. platyphylla</i>	10164	Italy	JF908499	–	Osmundson et al. 2013
103	<i>M. platyphylla</i>	BRNM 737654	Czech	LT854048	LT854036	Antonín et al. 2019
104	<i>M. platyphylla</i>	LE-BIN 3863	Russia	MG734826	–	from GenBank
105	<i>M. rodmani</i>	BHS2009-06	USA	GQ397989	–	from GenBank
106	<i>M. rodmani</i>	PUL F27039	USA	MW448576	–	from GenBank
107	<i>M. subfurfuracea</i>	TFB11075/ TENN59558 clone c3	USA	EU623744	–	Hughes et al. 2007
108	<i>M. subfurfuracea</i>	TFB11075/ TENN59558 clone c8	USA	EU623745	–	Hughes et al. 2007
109	<i>M. texensis</i>	DPL7405/ TENN62058 clone c1	USA	EU623725	–	Hughes et al. 2007
110	<i>M. texensis</i>	DPL7405/ TENN62058 clone c2	USA	EU623726	–	Hughes et al. 2007
111	<i>M. texensis</i>	FLAS-F-61511	USA	MH211940	–	from GenBank
112	<i>Mycena purpureofusca</i>	HMJAU 43554	China	MG654740	–	Na and Bau 2018
113	<i>Mycena purpureofusca</i>	HMJAU 43624	China	MG654741	–	Na and Bau 2018
114	<i>Mycena purpureofusca</i>	HMJAU 43640	China	MG654742	–	Na and Bau 2018
115	<i>Porothelium fimbriatum</i>	Dai 12276	China	KX081137	KX161656	from GenBank
116	<i>P. fimbriatum</i>	Dai 12289	China	KX081138	KX161654	from GenBank
117	<i>P. fimbriatum</i>	CLZhao 1120	China	MH114870	–	from GenBank
118	<i>P. fimbriatum</i>	CLZhao 2368	China	MH114871	–	from GenBank
119	<i>P. fimbriatum</i>	SWFC 006350	China	MK894078	–	from GenBank
120	<i>P. fimbriatum</i>	SWFC 006399	China	MK894079	–	from GenBank
121	<i>Trogia benghalensis</i>	CUH AM031	India	KU647630	–	Dutta et al. 2017
122	<i>T. benghalensis</i>	CUH AM122	India	MF967246	–	Dutta et al. 2017
123	<i>T. infundibuliformis</i>	KUN_HKAS63661	China	JQ031775	JQ031780	Yang et al. 2012
124	<i>T. infundibuliformis</i>	KUN_HKAS56709	China	JQ031776	JQ031781	Yang et al. 2012
125	<i>T. infundibuliformis</i>	NW1487	Thailand	MW504969	–	Direct Submission
126	<i>T. venenata</i>	KUN_HKAS54710	China	JQ031772	JQ031778	Yang et al. 2012
127	<i>T. venenata</i>	KUN_HKAS56679	China	JQ031773	JQ031779	Yang et al. 2012
128	<i>T. venenata</i>	TC2-28	China	KT968080	–	Mi et al. 2016
129	<i>T. venenata</i>	CLZhao 4141	China	MK268886	–	from GenBank

Results

Phylogenetic analysis

The concatenated dataset of 127 ITS and 50 nLSU sequences from 38 taxa of eight genera in Porotheleaceae, with the addition of one *Mycena* species as an outgroup, comprised 1,527 sites. Sequences retrieved from GenBank and those obtained in this study are listed in Table 1.

BI and ML phylogenetic analyses of the concatenated dataset were performed under the optimal evolutionary model selected for both ITS and nLSU partitions, GTR + I + G (lset nst = 6, rates = gamma, and prset statefreqpr = dirichlet [1,1,1,1]). Because the BI and ML phylogenetic reconstructions were consistent in topology, only the ML tree is shown in Fig. 1.

In the phylogenetic tree shown in Fig. 1, 17 major clades are evident. *Chrysomyцена* Vizzini, Picillo, Perrone & Dovana, *Clitocybula*, *Hydropus*, *Leucoinocybe* Singer ex Antonín, Borovička, Holec & Kolařík, *Megacollybia*, *Porotheleum* Fr., and *Trogia* form monophyletic groups, whereas *Gerronema* is polyphyletic (Vizzini et al. 2019). In the analysis of Vizzini et al. (2019), *Gerronema* was resolved into eight clades; in our tree, this number is increased to 10, including 13 species, which we have designated as *Gerronema* clades 1 to 10.

Each individual *Gerronema* clade (e.g., *Gerronema* 1, *Gerronema* 2, etc.) is sister to some subset of Porotheleaceae genera, all with high statistical support (ML bootstrap support [BS] = 100%, Bayesian posterior probability [BPP] = 1.00). Samples of the three new species and the newly recorded species are placed in *Gerronema* 1, *Gerronema* 2, *Gerronema* 6, and *Gerronema* 7 clades, where they constitute monophyletic lineages, each with high statistical support (*G. baishanzuense*, BS = 100%, BPP = 1.00; *G. microcarpum*, BS = 100%, BPP = 1.00; *G. zhujian*, BS = 100%, BPP = 1.00; *G. nemorale*, BS = 98%, BPP = 0.99; Fig. 1). The two new species *G. baishanzuense* and *G. zhujian* form a monophyletic lineage that is sister to a group comprising *Gerronema* 5 and *Gerronema* 8 clades, the latter consisting of *G. strombodes* (Berk. & Mont.) Singer and *G. kuruvense* K.P.D. Latha & Manim. *Gerronema microcarpum*, which is well supported as a species, is placed along with *G. keralense* K.P.D. Latha & Manim., a new species recently reported from India, in the *Gerronema* 1 clade (Latha et al. 2018). In contrast, *G. nemorale* is polyphyletic, with accessions of this species and *G. subclavatum* forming an unresolved lineage in the *Gerronema* 2 clade that are difficult to distinguish genetically.

The weakly supported *Gerronema* 3 clade consists of two species: *G. xanthophyllum* (Bres.) Norvell, Redhead & Ammirati and *G. waikanaense* (G. Stev.) J.A. Cooper, collected from the Czech Republic and New Zealand, respectively. Finally, *Gerronema* clades 5 to 10 comprise a single species each.

Taxonomy

Gerronema baishanzuense Q. Na, H. Zeng & Y.P. Ge, sp. nov.

Mycobank No: 842308

Figs 2–4

Diagnosis. Pileus dark brown at center, covered with dark brown fibrillose or pubescent. Stipe densely pruinose when young. Cheilocystidia present. Pileus trama with visible dark brown hyphae and coarse excrescences.

Holotype. China. Zhejiang Province, Lishui City, Qingyuan County, Baishanzu, 8 Jul 2020, Qin Na, Yupeng Ge, Yaping Hu, Hui Zeng, and Zewei Liu, *FFAAS0359* (collection no. MY0246).

Etymology. Refers to the type locality.

Description. Pileus 3.0–25.5 mm in diam., hemispherical when young, becoming applanate and slightly concave at center with age, deeply infundibuliform when old, with uplifted margin, dark brown all over when young (2F8), dark brown at center and fading to light yellowish brown (2D4) towards the margin at maturity, margin light yellowish white (2A2), translucent–striate, sulcate, surface dry, with appressed dark brown (2F8) fibrillose or pubescent, margin glabrescent and brown (2F8), fibrillose or pubescent at the center with age. Context thin and fragile, yellowish white (2A2). Lamellae subdecurrent to decurrent, ascending, cream-white (3A2) to light yellowish white (2A2), faces concolorous with the sides. Stipe slender, 4.5–26.0 × 0.5–2.0 mm, hollow, cylindrical, central, straight, light whitish yellow (4A2), base yellow-brown (4D8) when old, densely pruinose on the entire surface when young, almost glabrous when old, slightly broadened at the base. Odor and taste inconspicuous.

Basidiospores [140/7/6] (6.6) 7.5–8.4–9.3 (9.8) × (4.0) 4.4–4.9–5.4 (5.6) μm [$Q = 1.65–1.74$, $Q = 1.72 \pm 0.015$] [holotype [40/2/1] (7.6) 7.9–8.6–9.5 (9.8) × (4.3) 4.5–4.9–5.5 (5.6) μm, $Q = 1.72–1.74$, $Q = 1.74 \pm 0.031$], long ellipsoid, hyaline, guttulate, thin-walled, inamyloid. Basidia 31–45 × 6–9 μm, hyaline, clavate, 4-spored. Cheilocystidia 30–48 × 8–14 μm, clavate with swollen apex, or subfusiform, hyaline, thin-walled. Pleurocystidia not seen. Lamellar trama subregular; hyphae 2–10 μm wide, thin-walled, hyaline, inamyloid. Pileus trama subregular, sarcodimitic, sometimes with dark brown (4F8) hyphae. Pileipellis a cutis, hyphae 2–6 μm wide, light yellow (2B2) to yellow (2B4), occasionally with coarse excrescences; terminal elements utriform, clavate, sometimes with sparse coarse excrescences, 25–56 × 6–10 μm, light yellowish brown (2C4) to yellowish brown (2C6) pigment in KOH; true pileocystidia absent. Hyphae of the stipitipellis 2–7 μm wide, hyaline, smooth; caulocystidia cylindrical or clavate, 39–70 × 5–14 μm, hyaline, thin-walled. All tissues nonreactive in iodine. Clamps present in all tissues.

Habit and habitat. Solitary to scattered on rotten wood, branches, and twigs in mixed forests of *Picea*, *Pinus*, *Populus*, *Quercus*, etc. Subtropical monsoon climate or subtropical humid climate.

Other specimens examined. Anhui Province, Chizhou City, Shitai County, Dayan Village, Guniujiang National Natural Reserve, 31 Aug 2019, Qin Na, Yupeng Ge, Hui Zeng, Liangliang Qi, and Junqing Yan, *FFAAS0366* (collection no. MY0260);

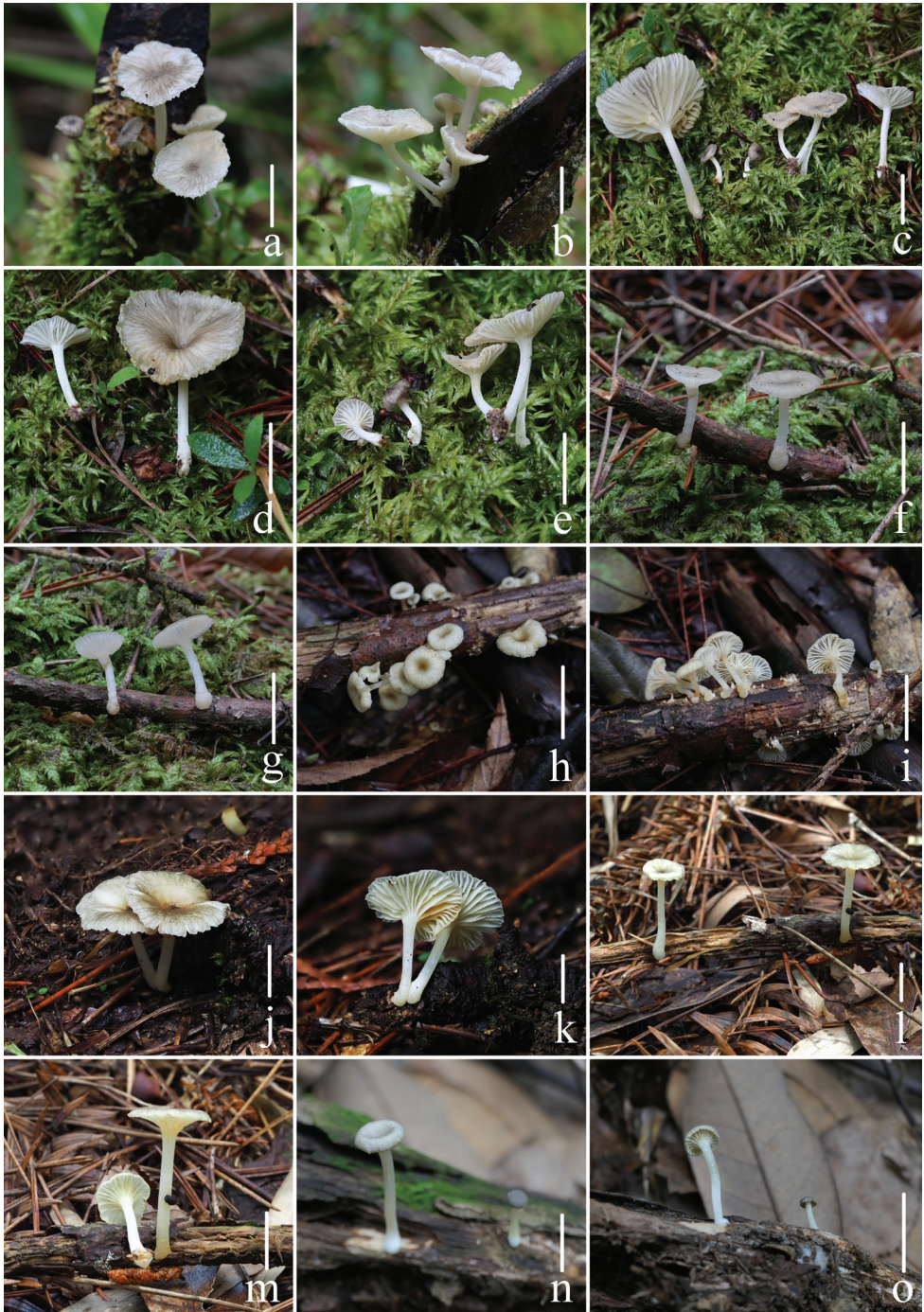


Figure 2. Fresh basidiomata of *Gerronema baishanzuense* Q. Na, H. Zeng & Y.P. Ge **a–e** FFAAS0359 (Holotype) **f–g** FFAAS0360 **h–i** FFAAS0361 **j–k** FFAAS0362 **l–m** FFAAS0363 **n–o** FFAAS0366. Scale bars: 10 mm (**a–o**). Photographs **a–e** by Qin Na; **f–g** by Junqing Yan **h–i** by Liangliang Qi **j–o** by Yupeng Ge.

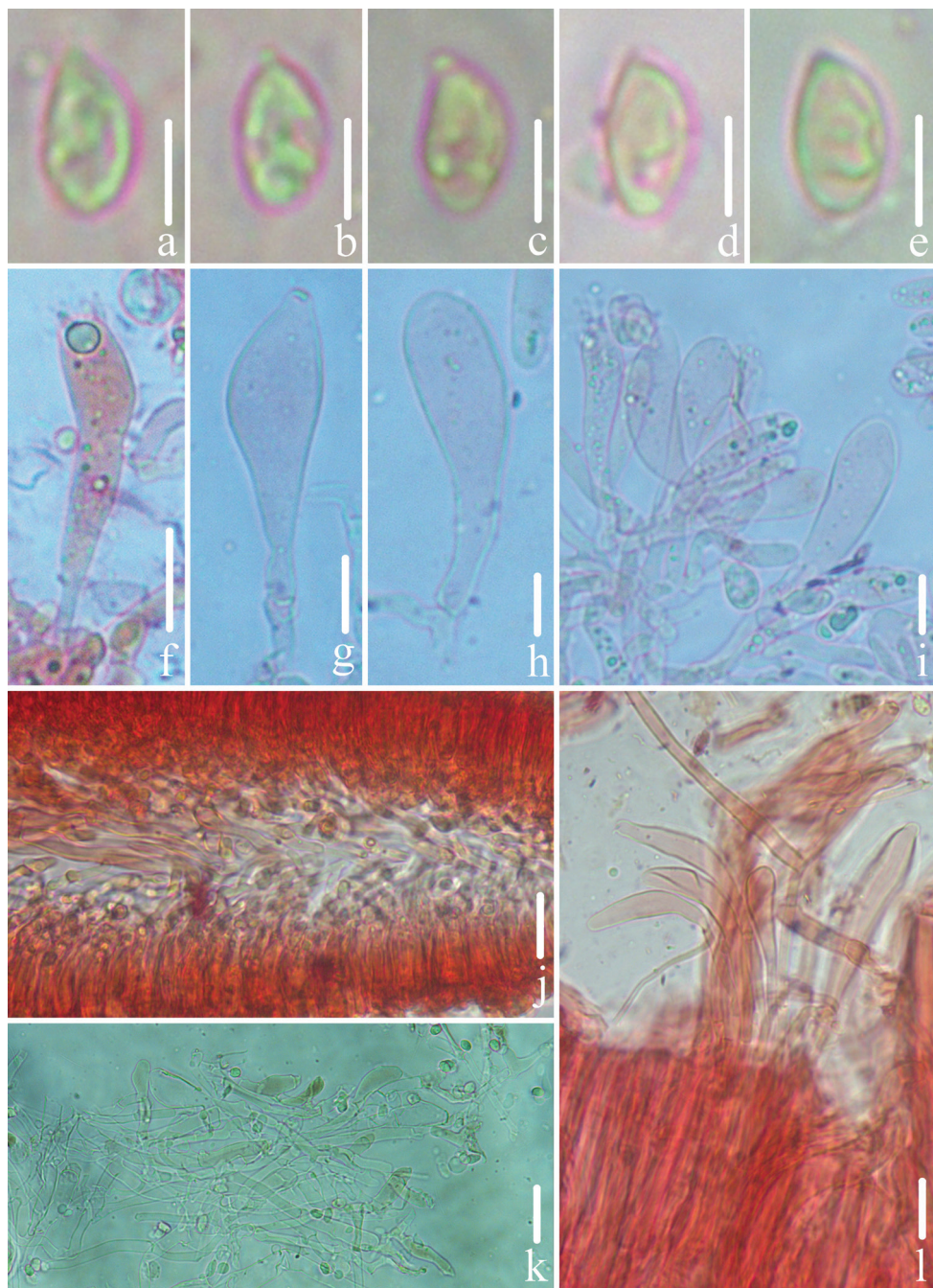


Figure 3. Microscopic features of *Gerronema baishanzuense* Q. Na, H. Zeng & Y.P. Ge. (FFAAS0359, Holotype) **a–e** basidiospores **f** basidia **g–i** cheilocystidia **j** lamellar trama **k** pileipellis **l** stipitipellis and caulocystidia. Scale bars: 5 μ m (**a–e**); 10 μ m (**f–l**).

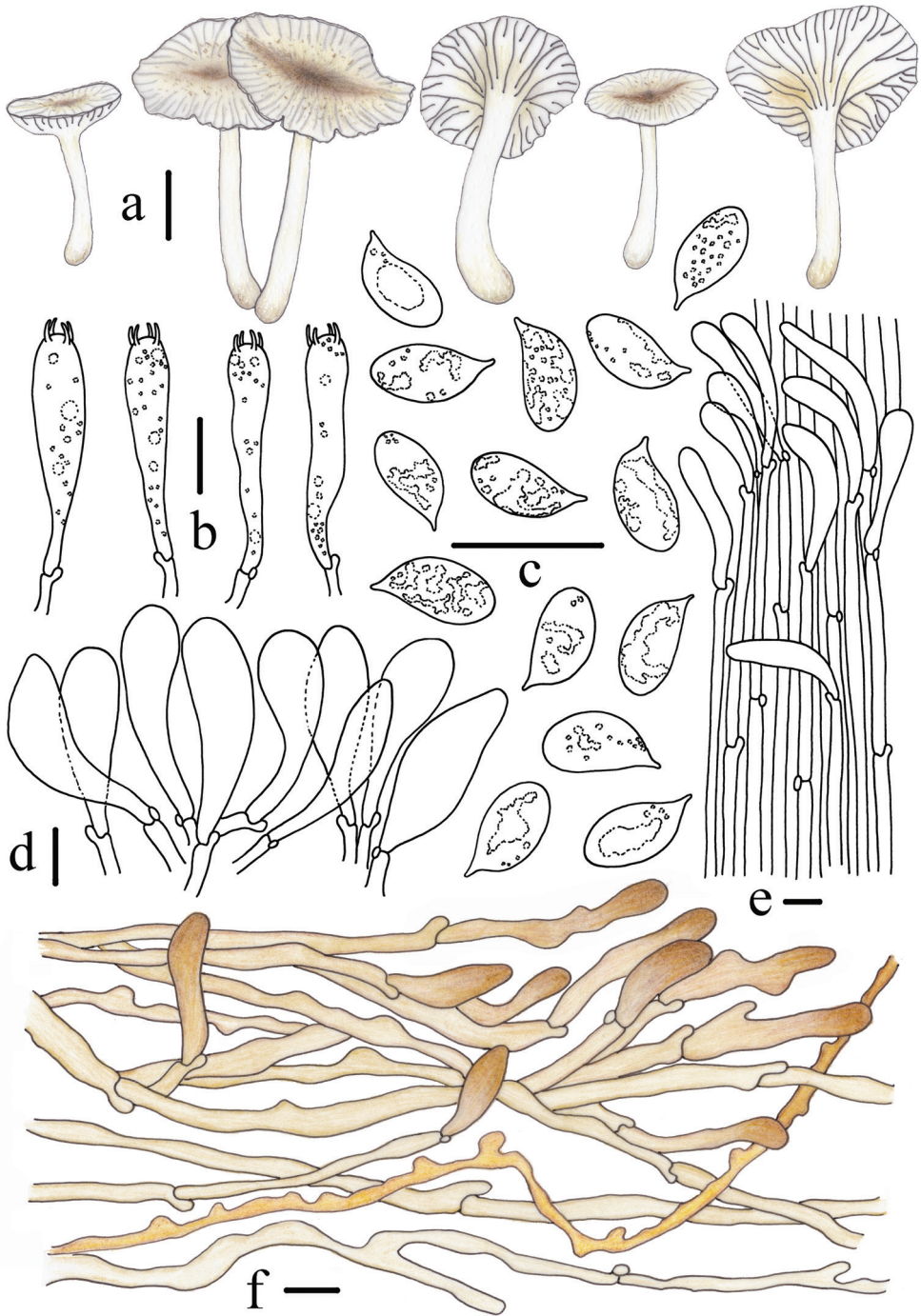


Figure 4. Morphological features of *Gerronema baishanzuense* Q. Na, H. Zeng & Y.P. Ge. (FFAAS0359, Holotype) **a** basidiomata **b** basidia **c** basidiospores **d** cheilocystidia **e** stipitipellis and caulocystidia **f** pileipellis. Scale bars: 10 mm (**a**); 10 μ m (**b–f**). Drawing by Qin Na and Yupeng Ge.

Zhejiang Province, Lishui City, Qingyuan County, Baishanzu, 24 May 2020, Qin Na, Yupeng Ge, Yaping Hu, Hui Zeng, and Zewei Liu, *FFAAS0360* (collection no. MY0247), *FFAAS0362* (collection no. MY0250); Zhejiang Province, Lishui City, Qingyuan County, Jushui Village, 27 May 2020, Qin Na, Yupeng Ge, Yaping Hu, Hui Zeng, and Zewei Liu, *FFAAS0361* (collection no. MY0249), Longquan City, Longquan Mountain, 11 Jul 2020, Qin Na, Yupeng Ge, Yaping Hu, Hui Zeng, and Zewei Liu, *FFAAS0363* (collection no. MY0251).

Remarks. *Gerronema baishanzuense* is considered to be a distinct species of *Gerronema* on account of its deeply infundibuliform pileus, decurrent lamellae, smooth and long ellipsoid basidiospores, sarcodimitic tramal tissues, cylindrical or clavate caulocystidia, and a lignicolous habitat (Singer 1986; Redhead 1986; Norvell et al. 1994). Four species with a yellow pileus have been recorded: *G. keralense*, *G. kuruvense*, *G. nemorale*, and *G. strombodes* (Singer 1970; Takashi 2009; Antonín et al. 2011; Latha et al. 2018; Takahashi 2000). *Gerronema nemorale*, originally described from Japan and later reported from the Republic of Korea, has the most morphological similarities to *G. baishanzuense*; however, the former differs in having a smaller pileus (< 20 mm in diameter) but a longer stipe (up to 40 mm), terminal elements less than 37 µm long, and much smaller caulocystidia (Takahashi 2000; Antonín et al. 2008). In contrast to *G. baishanzuense*, two new species recently reported from the Indian state of Kerala, *G. keralense* and *G. kuruvense*, are easily mistaken for the new species (Latha et al. 2018). However, the pileus of *G. keralense* lacks dark brown fibrillose or pubescent, has smaller and slightly thick-walled cheilocystidia, and the hyphae of its stipitipellis and caulocystidia are both thin- to thick-walled (Latha et al. 2018). *Gerronema kuruvense* is always distinctly yellow, has small basidiomata (pileus < 11 mm in diameter) and true pileocystidia, and lacks cheilocystidia (Latha et al. 2018). Finally, *G. strombodes*, distributed in North America and Asia, differs from *G. baishanzuense* in having larger basidiomata, a white to grayish white pileus (up to 80 mm wide), smooth pileipellis hyphae, and the absence of hymenial cystidia (Singer 1970; Antonín et al. 2008; Kim et al. 2014). *G. citrinum* (Corner) Pegler (Pegler 1983) and *G. tenue* Dennis (Dennis 1961), are allied with *G. baishanzuense*, but their lamellae edges without cheilocystidia. Moreover, *G. citrinum* has a relatively larger pileus (20–30 mm in diam.) and smaller basidiospores (6–7.5 × 3.5–4 µm), and *G. tenue* differs in having a citrine yellow pileus and an insititious stipe (Dennis 1961; Pegler 1983). *G. hungo* (Henn.) Degreef & Eyi, reported by Degreef and Ndong (2007) as a new combination, differs in yellowish orange to brownish orange pileus, ellipsoid basidiospores, and absent cheilocystidia.

***Gerronema microcarpum* Q. Na, H. Zeng & Y.P. Ge, sp. nov.**

MycoBank No: 842309

Figs 5–7

Diagnosis. Basidiomata distinctly small. A pileus a bit slimy when moist. Stipe light yellow, base turning to light brown with age. Cheilocystidia common in clavate with rounded apex, rarely fusiform. Pileipellis occasionally with coarse excrescences.



Figure 5. Fresh basidiomata of *Gerronema microcarpum* Q. Na, H. Zeng & Y.P. Ge. **a** FFAAS0365 **b** FFAAS0372 **c–d** FFAAS0375 **e** FFAAS0373 (Holotype) **f–g** FFAAS0374 **h–i** FFAAS0371. Scale bars: 10 mm (**a–i**). Photographs **a, e–i** by Yupeng Ge; **b** by Junqing Yan; **c–d** by Qin Na.

Holotype. China. Zhejiang Province, Lishui City, Qingtian County, Shigu Lake, 6 Aug 2021, Qin Na, Yupeng Ge, Junqing Yan, Zewei Liu, and Yulan Sun, *FFAAS0373* (collection no. MY0526).

Etymology. Refers to the small basidiomata.

Description. Pileus 1.5–9.0 mm in diam., at first convex, later applanate in the marginal zone, infundibuliform or deeply umbilicate in the center when old, grayish yellow (2B2) to shallow yellowish brown (2C4), shallowly sulcate, translucent–striate, smooth, a bit slimy when moist, but not hygrophanous. Context yellowish white (2A2), thin. Lamellae close to moderately close, shortly decurrent when young, whitish yellow (1A2), decurrent to deeply decurrent when old, concolorous with the sides. Stipe 5.0–18.0 × 1.0–2.0 mm, hollow or soon becoming hollow, generally central, equal or with slightly broader base, light yellow (2A2), becoming light brown (5C6) towards the base, pruinose, glabrescent when old, base covered with a few white fibrils. Odor and taste indistinctive.

Basidiospores [140/7/6] (6.1) 6.3–6.8–7.2 (7.5) × (3.3) 3.5–3.8–4.1 (4.3) μm [$Q = 1.64\text{--}1.95$, $Q = 1.80 \pm 0.059$] [holotype [40/2/1] (6.1) 6.2–6.7–7.3 (7.5) × 3.4–3.7–4.1 (4.3) μm , $Q = 1.64\text{--}1.95$, $Q = 1.81 \pm 0.066$], narrowly ellipsoid to cylindrical, hyaline in water and 5% KOH, inamyloid, smooth. Basidia 25–33 × 6–8 μm , 4-spored, clavate, hyaline. Cheilocystidia common in clavate with rounded apex, 31–35 × 5–8 μm , rarely fusiform, thin-walled and hyaline. Pleurocystidia not seen. Lamellar trama subregular; hyphae 2–5 μm wide, thin-walled, hyaline, inamyloid. Pileus trama subregular, sarcodimitic. Pileipellis a cutis, hyphae 3–6 μm wide, light yellow (2B2); terminal elements clavate, utriform, occasionally with coarse excrescences, 19–43 × 4–6 μm , light yellowish brown (2C4) to yellowish brown (2D4) pigment in KOH; true pileocystidia absent. Hyphae of the stipitipellis 2–6 μm wide, hyaline, smooth; caulocystidia long cylindrical or clavate, 26–65 × 4–9 μm , hyaline, thin-walled. All tissues nonreactive in iodine. Clamps present in all tissues.

Habit and habitat. Scattered on rotten wood and twigs in mixed evergreenbroad-leaf forests consisting of species of Fagaceae, Lauraceae, Theaceae, Ericaceae, Symplocaceae, Pinaceae, etc. Subtropical monsoon climate or subtropical humid climate.

Other specimens examined. Anhui Province, Chizhou City, Shitai County, Dayan Village, Guniujiang National Natural Reserve, 31 Aug 2019, Qin Na, Yupeng Ge, Hui Zeng, Liangliang Qi, and Junqing Yan, *FFAAS0365* (collection no. MY0259); Fujian Province, Nanping City, Wuyi Mountain, 25 Jul 2020, Qin Na, Yupeng Ge, Yaping Hu, Hui Zeng, and Zewei Liu, *FFAAS0375* (collection no. MY0544); Zhejiang Province, Hangzhou City, Tianmu Mountain, 30 Jul 2021, Qin Na, Yupeng Ge, Zewei Liu, and Yulan Sun, *FFAAS0371* (collection no. MY0424); Lishui City, Liandu District, Baiyun National Forest Park, 2 Aug 2021, Qin Na, Yupeng Ge, Zewei Liu, and Yulan Sun, *FFAAS0372* (collection no. MY0478), Qingtian County, Shigu Lake, 6 Aug 2021, Qin Na, Yupeng Ge, Junqing Yan, Zewei Liu, and Yulan Sun, *FFAAS0374* (collection no. MY0527).

Remarks. Characteristics such as tiny omphalinoid basidiomata, decurrent lamellae, inamyloid and narrowly ellipsoid to cylindrical basidiospores, sarcodimitic tramal tissues, a pileipellis with pigmented terminal elements, and long cylindrical or clavate caulocystidia

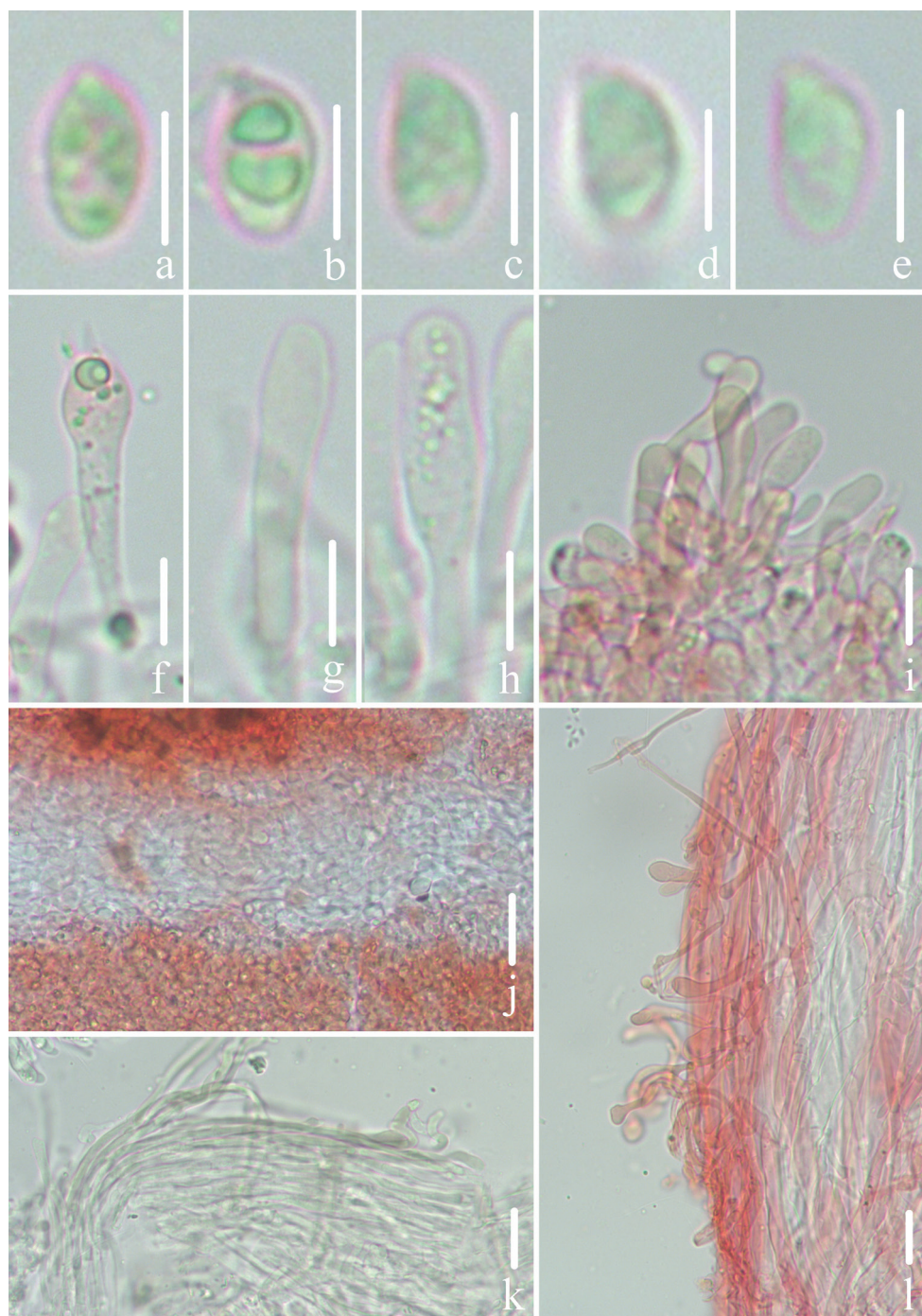


Figure 6. Microscopic features of *Gerronema microcarpum* Q. Na, H. Zeng & Y.P. Ge. (FFAAS0373, Holotype) **a–e** basidiospores **f** basidia **g–i** cheilocystidia **j** lamellar trama **k** pileipellis **l** stipitipellis and caulocystidia. Scale bars: 5 μ m (**a–e**); 10 μ m (**f–l**).

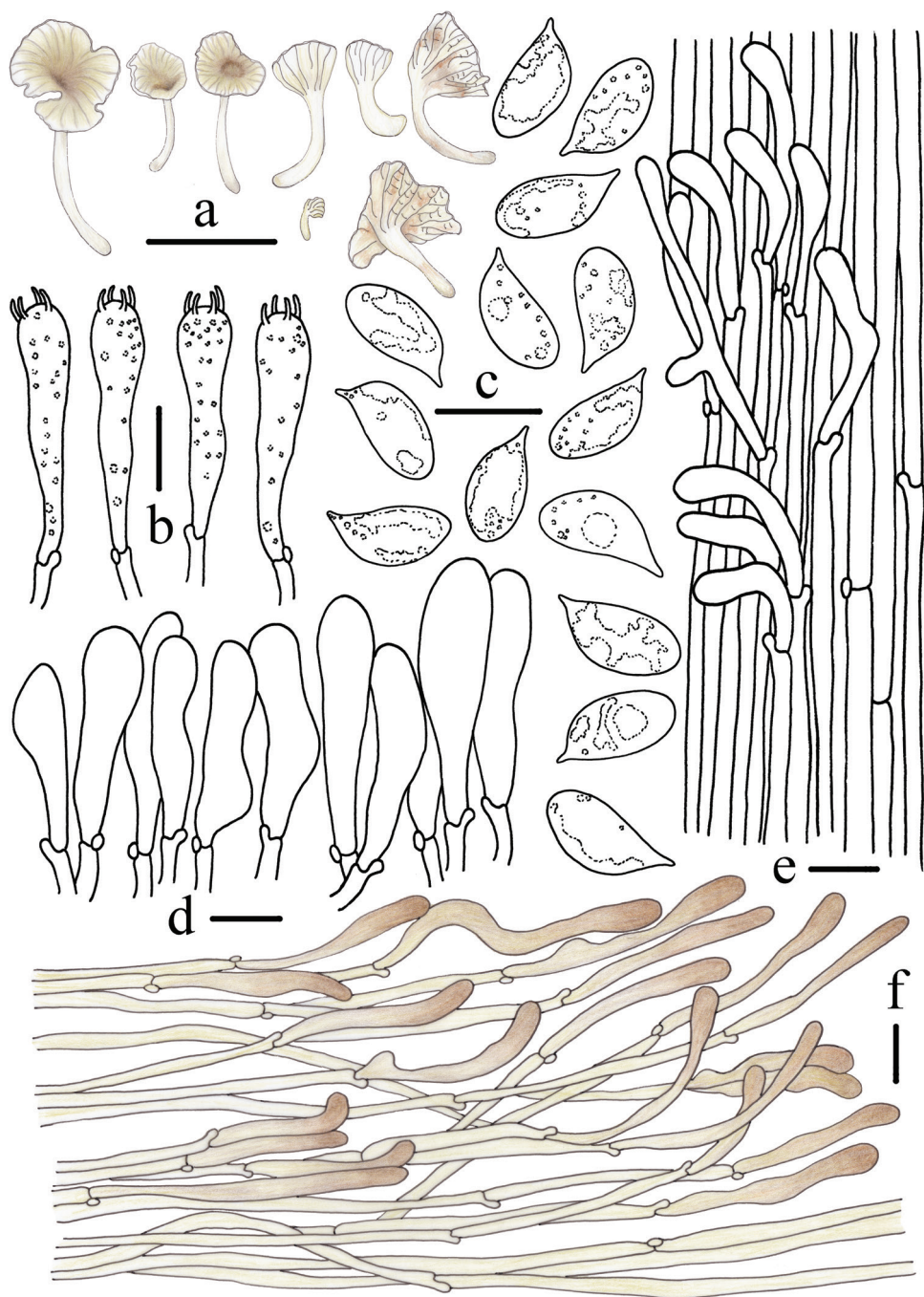


Figure 7. Morphological features of *Gerronema microcarpum* Q. Na, H. Zeng & Y.P. Ge. (FFAAS0373, Holotype) **a** basidiomata **b** basidia **c** basidiospores **d** cheilocystidia **e** stipitipellis and caulocystidia **f** pileipellis. Scale bars: 10 mm (**a**); 10 μ m (**b**, **d–f**); 5 μ m (**c**). Drawing by Qin Na and Yupeng Ge.

support the placement of this species in *Gerronema* (Singer 1970, 1986; Norvell et al. 1994). Because of its small basidiomata, decurrent lamellae, and subregular pileus trama, *G. kuruvense* is difficult to distinguish from *G. microcarpum*, but its pileus is orange yellow all over, no cheilocystidia or pleurocystidia are present, and its pileocystidia and caulocystidia are somewhat thick-walled (Latha et al. 2018). *Gerronema nemorale* has certain morphological similarities to *G. microcarpum*, namely, the presence of tiny yellowish basidiomata, decurrent lamellae, and cylindrical basidiospores (Antonín et al. 2008, 2011; Takashi 2009). However, *G. nemorale* differs in having a pileus with an olive tint, a longer stipe with conspicuous white mycelioid bristles, and larger terminal elements of the pileipellis (up to 150 μm) (Antonín et al. 2008, 2011; Takashi 2009). Compared with *G. microcarpum*, *G. subchrysophyllum* (Murrill) Singer has an olive-umber pileus fading to grayish when old, larger and ellipsoid basidiospores ($4.3\text{--}8.5 \times 2.5\text{--}6.3 \mu\text{m}$), and sometimes basidiole-like cheilocystidia (Singer 1970). *Gerronema keralense* and *G. strombodes* are easily mistaken for *G. microcarpum*, but both the two closely related species are distinguishable by their absence of cheilocystidia or their partially thick-walled pileipellis and stipitipellis (Singer 1970; Antonín et al. 2008; Latha et al. 2018; Kim et al. 2014).

***Gerronema zhujian* Q. Na, H. Zeng & Y.P. Ge, sp. nov.**

Mycobank No: 842310

Figs 8–10

Diagnosis. Pileus fuscous and densely covered with tiny, deep brown fur or scales, distinctly radially striped with darkened lines. Stipe white, upper part slight brown when old. Cheilocystidia present. Pileipellis without coarse excrescences.

Holotype. China. Fujian Province, Nanping City, Wuyi Mountain, 25 Jul. 2020, Qin Na, Yupeng Ge, Yaping Hu, Hui Zeng, and Zewei Liu, *FFAAS0376* (collection no. MY0553).

Etymology. The name refers to the centrally depressed, umbilicate basidiocarps, which resemble an eye or a loudspeaker; zhujian is a mythical one-eyed Chinese creature who is usually very noisy, like a walking loudspeaker.

Description. Pileus 8.6–18.5 mm in diam., convex to broadly convex, papillate, applanate and centrally depressed, subumbilicate to umbilicate with age, pellucid-striate to rugulo-striate, or sulcate, always \pm distinctly radially striped with darkened lines, fuliginous-fuscous (2F8) or fuscous (4F8) at center when young, grayish white (3B1) towards the margin, fading to brown (3F8) at the center, yellowish-brown (4E8) towards the margin, densely covered with tiny, deep brown (4F4) fur or scales, slightly sparse with age, with a slightly involuted margin. Context white, thin, tough. Lamellae subdecurrent to decurrent, moderately broad, pure white to yellowish-white (4A2), edges concolorous with the sides. Stipe 19.0–25.0 \times 1.0–1.5 mm, central, cylindrical, almost equal above, white, slight brown (8D3–8D4) in upper part when old, fibrous, hollow, pruinose, base slightly swollen with tiny, white fine hairs. Odorless, taste mild.



Figure 8. Fresh basidiomata of *Gerronema zhujian* Q. Na, H. Zeng & Y.P. Ge. **a–b** FFAAS0364 **c–d** FFAAS0376 (Holotype) **e–f** FFAAS0370. Scale bars: 10 mm (**a–f**). Photographs **a–b**, **e–f** by Lian-guang Qi **c–d** by Junqing Yan.

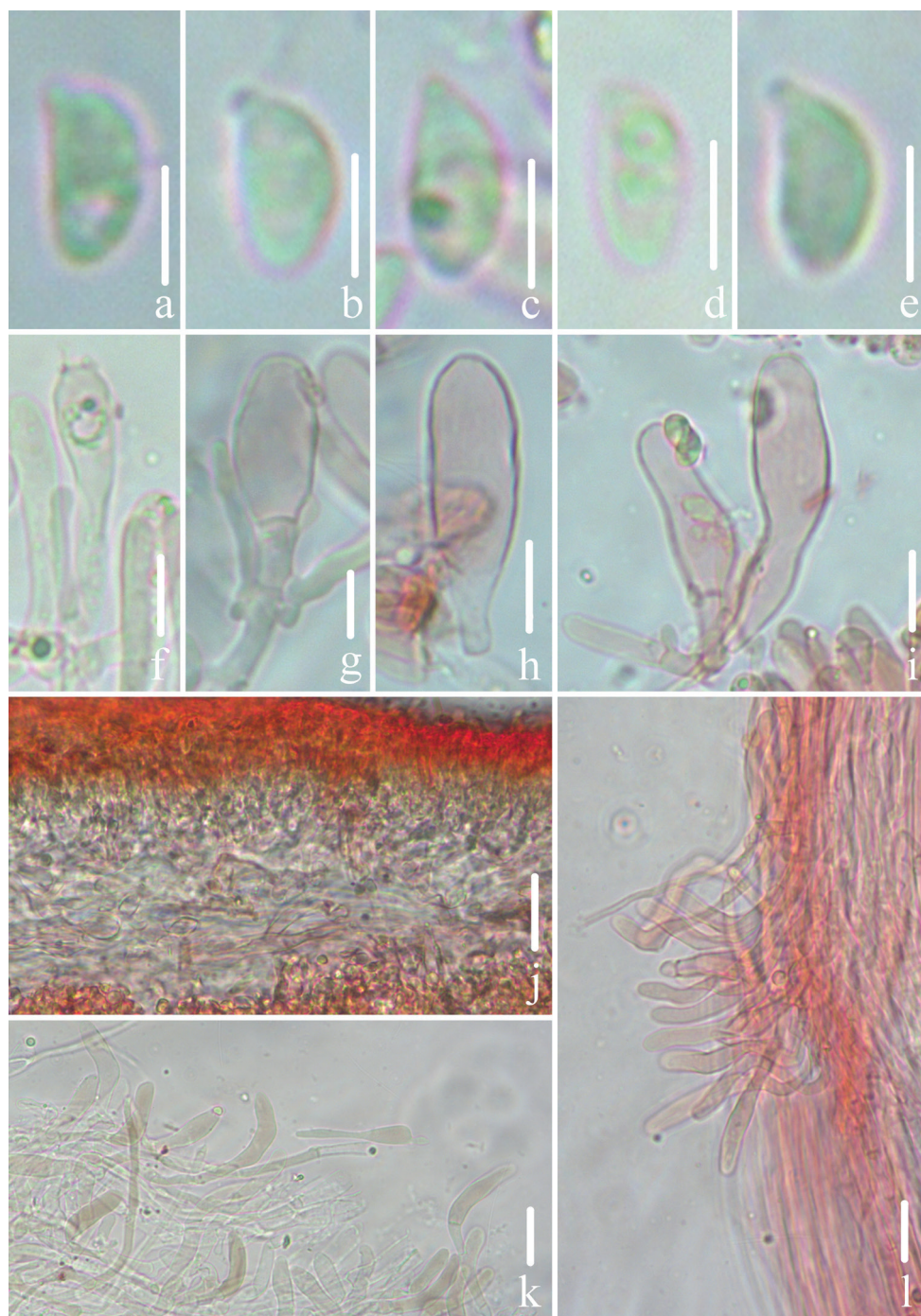


Figure 9. Microscopic features of *Gerronema zhujian* Q. Na, H. Zeng & Y.P. Ge. (FFAAS0376, Holotype) **a–e** basidiospores **f** basidia **g–i** cheilocystidia **j** lamellar trama **k** pileipellis **l** stipitipellis and caulocystidia. Scale bars: 5 µm (**a–e**); 10 µm (**f–l**).

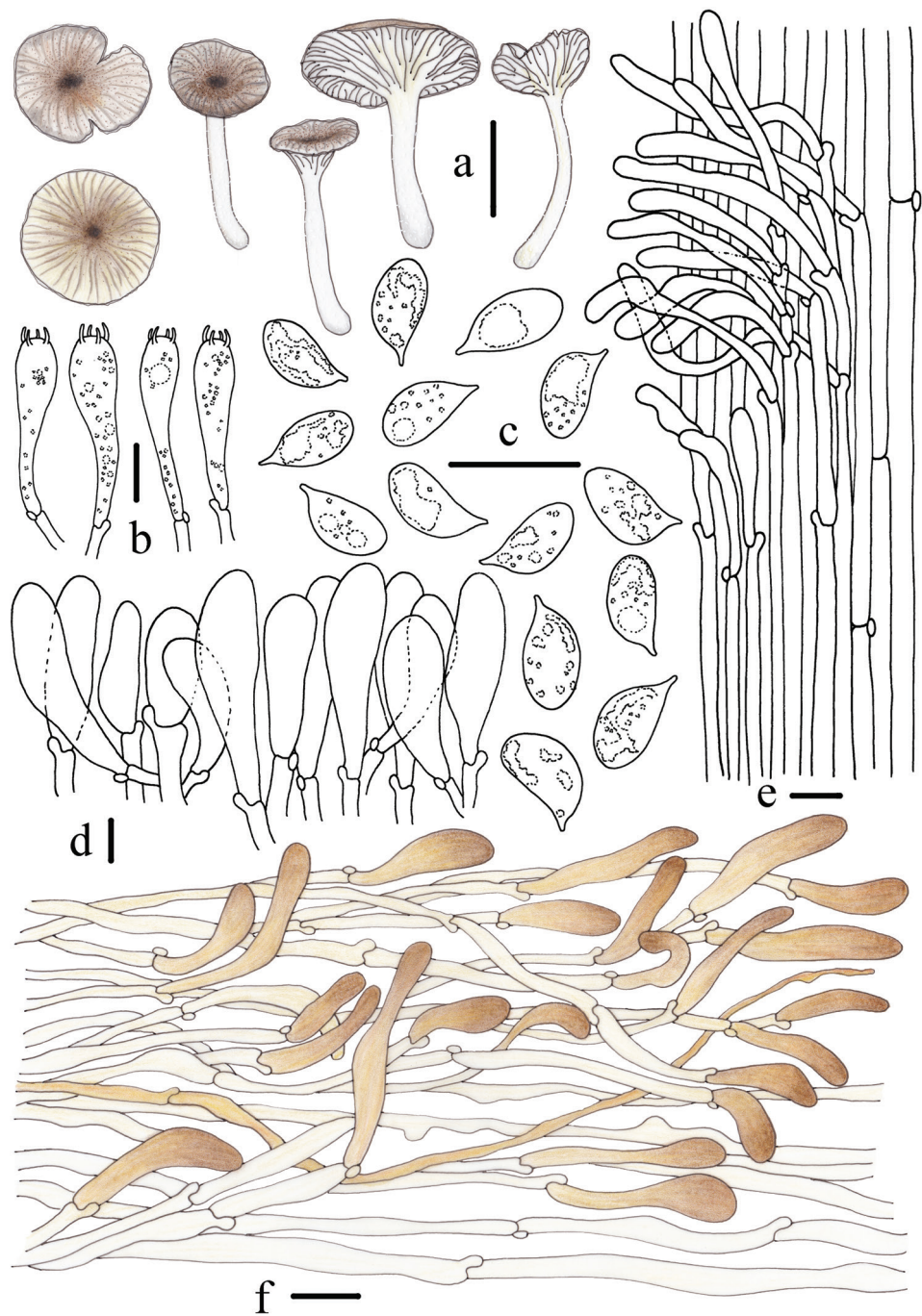


Figure 10. Morphological features of *Gerronema zhujian* Q. Na, H. Zeng & Y.P. Ge. (FFAAS0376, Holotype) **a** basidiomata **b** basidia **c** basidiospores **d** cheilocystidia **e** stipitipellis and caulocystidia **f** pileipellis. Scale bars: 10 mm (**a**); 10 µm (**b–f**). Drawing by Qin Na and Yupeng Ge.

Basidiospores [80/4/3] (6.3) 6.7–7.4–8.0 (8.5) \times (3.2) 3.7–4.1–4.6 (4.8) μm [$Q = 1.64\text{--}2.07$, $Q = 1.81 \pm 0.076$] [holotype [40/2/1] (6.3) 6.6–7.4–7.9 (8.3) \times (3.2) 3.7–4.0–4.5 (4.6) μm , $Q = 1.69\text{--}2.07$, $Q = 1.82 \pm 0.087$], narrowly ellipsoid to cylindrical, hyaline, guttulate, thin-walled, inamyloid. Basidia 28–40 \times 6–9 μm , hyaline, clavate, 4-spored. Cheilocystidia 29–46 \times 7–13 μm , subfusiform, clavate, apex usually swollen, hyaline. Pleurocystidia absent. Lamellar trama subregular; hyphae 3–8 μm wide, thin-walled, hyaline, inamyloid. Pileus trama subregular, sarcodimitic. Pileipellis hyphae 3–6 μm wide, a cutis, light yellow (2B2); terminal elements utriform or clavate, 25–49 \times 6–9 μm , light yellowish brown (2C4) to yellowish brown (2C6) pigmented, especially in the apex; true pileocystidia absent. Hyphae of the stipitipellis 2–8 μm wide, hyaline, smooth; caulocystidia long cylindrical, sometimes with rounded apex, 27–47 \times 4–8 μm , hyaline, thin-walled. All tissues nonreactive in iodine. Clamps present in all tissues.

Habit and habitat. Solitary to scattered on rotten wood, branches, and twigs in Theaceae, Fagaceae, Symplocaceae, Lauraceae, Aquifoliaceae, Ericaceae, and Pinaceae mixed forests. Subtropical monsoon climate, subtropical humid climate or subtropical maritime monsoon climate.

Other specimens examined. Anhui Province, Chizhou City, Shitai County, Dayan Village, Guniujiang National Natural Reserve, 26 Jul 2019, Qin Na, Yupeng Ge, Hui Zeng, Junqing Yan, and Liangliang Qi, FFAAS0364 (collection no. MY0256); Fujian Province, Sanming City, Mingxi County, Junzifeng National Natural Reserve, 23 Jun 2021, Qin Na, Yupeng Ge, Liangliang Qi, and Binrong Ke, FFAAS0370 (collection no. MY0296).

Remarks. *Gerronema zhujian* is unique among *Gerronema* on account of its fuscous pileus with tiny, dark brown fur or scales, its distinctly radially striping with darkened lines, cheilocystidia present and pileipellis without coarse excrescences. Two species of *Omphalina* characterized by dark pigments in the pileus—*Omphalina depauperata* (Singer) Raithelh. and *O. subpallida* (Singer) Raithelh., formerly named *G. subpallidum* Singer and *G. depauperatum* Singer, respectively, have been described from Argentina. These two species most closely resemble *G. zhujian* but differ in having a hyaline or white stipe, ellipsoid basidiospores, and no cheilocystidia (Singer 1970). *Gerronema chrysocarpum* is closely allied to *G. zhujian* on the basis of the dark brown coloration of the umbilicus of its pileus, its whitish stipe, and similarly shaped basidiospores (Liu 1995). This taxon differs from *G. zhujian* in having a viscid and glabrescent pileus, pale orange lamellar margin, and pleurocystidia (Liu 1995). Other species of *Gerronema*, such as *G. nemorale* and *G. strombodes*, have a distinctly yellow, yellowish orange, olive yellow to yellowish brown pileus, and their micromorphological features are also different (Singer 1970; Antonín et al. 2008; Latha et al. 2018).

Gerronema nemorale Har. Takah.

Figs 11–13

Description. Pileus 3.0–19.0 mm in diam., hemispherical at first, then convex with a depressed center, appanated and deeply umbilicate with age, slightly striate at the

margin in younger basidiomata, slightly translucently striate forming shallow grooves, greenish yellow (2E3), yellowish brown (2D5), olive brown (2E8), always deeper at the center, fading light yellow (5A2) towards the margin, finely tomentose when young, glabrescent with age, with a flat margin. Context white to light yellow, thin. Lamellae moderately distant to distant, decurrent, white or pale yellow (5A2), narrow, edges concolorous with the sides. Stipe 19.0–36.0 × 1.0–2.5 mm, almost equal, but swollen at the base, terete, slender, hollow, pruinose overall, glabrescent with age; base with conspicuous white mycelioid bristles. Odorless, taste mild.

Basidiospores [60/3/3] (6.8) 7.9–8.8–9.9 (10.7) × (3.7) 4.6–5.2–5.8 (6.3) μm [$Q = 1.59\text{--}1.88$, $Q = 1.70 \pm 0.065$], narrowly ellipsoid or cylindrical, hyaline, guttulate, thin-walled, inamyloid. Basidia 32–46 × 6–9 μm , hyaline, clavate, 4-spored. Cheilocystidia 27–49 × 5–9 μm , abundant, irregularly cylindric or clavate, colorless. Pleurocystidia absent. Lamellar trama subregular; hyphae 3–9 μm wide, thin-walled, hyaline, inamyloid. Pileus trama subregular, sarcodimitic. Pileipellis hyphae 2–5 μm wide, light yellow (2B2), a cutis; terminal elements cylindric or clavate, 31–50 × 4–9 μm , light yellowish brown (2C4) to yellowish brown (2C6) pigmented, especially in the apex; true pileocystidia absent. Hyphae of the stipitipellis 3–6 μm wide, hyaline, smooth; caulocystidia cylindrical or broadly clavate, 32–48 × 5–8 μm , hyaline, thin-walled. All tissues nonreactive in iodine. Clamps present in all tissues.

Habit and habitat. Solitary to caespitose on dead fallen twigs or rotten wood in mixed broadleaf–conifer forests from early spring to late autumn, common, especially in subtropical zones in China. Subtropical monsoon climate, subtropical humid climate subtropical maritime monsoon climate, or continental monsoon humid climate.

Distribution. Known from Asia (Japan, Korea, Pakistan).

Specimens examined. Anhui Province, Chizhou City, Shitai County, Dayan Village, Guniujiang National Natural Reserve, 7 Jun 2019, Qin Na, Yupeng Ge, Hui Zeng, Junqing Yan, and Liangliang Qi, *FFAAS0377* (collection no. MY0113), Qingyang County, Miaoqian Town, 2 Sep 2019, Qin Na, Yupeng Ge, Hui Zeng, Junqing Yan, and Liangliang Qi, *FFAAS0384* (collection no. MY0264); Fujian Province, Nanping City, Wuyi Mountain, 10 Aug 2021, Qin Na, Yupeng Ge, Junqing Yan, Zewei Liu, and Yulan Sun, *FFAAS0410* (collection no. MY0549), Sanming City, Junzifeng National Natural Reserve, 22 Jun 2021, Qin Na, Yupeng Ge, Binrong Ke, and Liangliang Qi, *FFAAS0390* (collection no. MY0287); Zhejiang Province, Lishui City, Qingyuan County, Wangmu, 26 May 2020, Qin Na, Yupeng Ge, Yaping Hu, Junqing Yan, and Zewei Liu, *FFAAS0379* (collection no. MY0248); Jilin Province, Tonghua City, Jian City, Wunvfeng National Forest Park, 6 Jul 2021, Qin Na, Yupeng Ge, and Zewei Liu, *FFAAS0392* (collection no. MY0364); Zhejiang Province, Lishui City, Longquan City, Zhuangbian Village, 10 Jul 2020, Qin Na, Yupeng Ge, Junqing Yan, and Zewei Liu, *FFAAS0382* (collection no. MY0254), Liandu District, Baiyun National Forest Park, 2 Aug 2021, Qin Na, Zewei Liu, *FFAAS0395* (collection no. MY0462), Qingtian County, Lanni Lake, 2 Jun 2021, Qin Na, Yupeng Ge, Junqing Yan, Yulan Sun, and Zewei Liu, *FFAAS0388* (collection no. MY0273), Jinyun County, Dayang Mountain, 3 Jun 2021, Qin Na, Yupeng Ge, and Junqing Yan, *FFAAS0389* (collection no. MY0276).

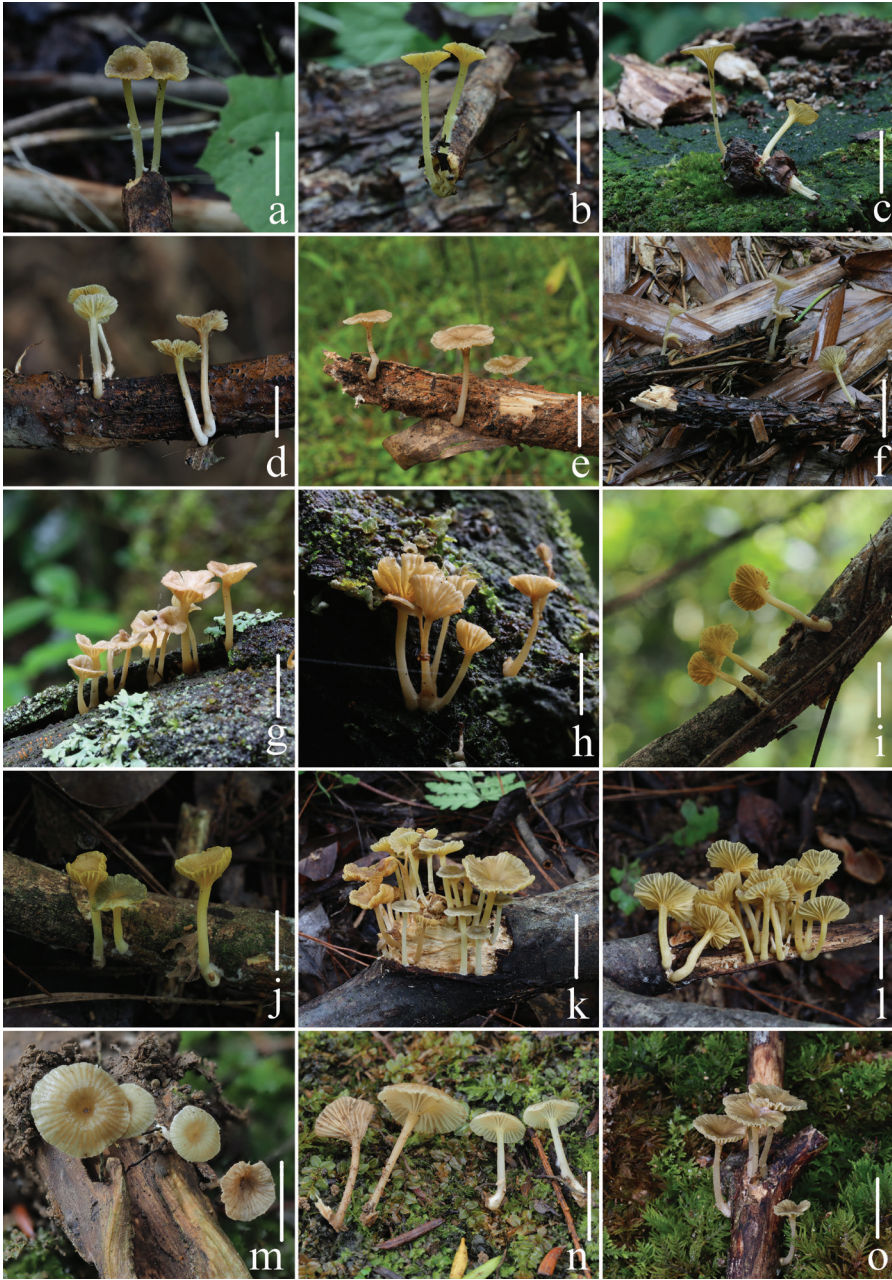


Figure 11. Fresh basidiomata of *Gerronema nemorale* Har. Takah. **a–b** MY0364 (Wunvfeng, Jian City, Liaoning Province) **c** MY0113 (Guniujiang, Shitai County, Anhui Province) **d** MY0264 (Miaoqian Town, Qingyang County, Anhui Province) **e** MY0248 (Baishanzu, Qingyuan County, Zhejiang Province) **f** MY0254 (Longquan Mountain, Longquan City, Zhejiang Province) **g–h** MY0273 (Lanni Lake, Qingtian County, Zhejiang Province) **i–j** MY0276 (Dayang Mountain, Jinyun County, Zhejiang Province) **k–l** MY0462 (Baiyun Forest Park, Lishui City, Zhejiang Province) **m–n** MY0287 (Junzifeng, Sanming City, Fujian Province) **o** MY0549 (Wuyi Mountain, Nanping City, Fujian Province). Scale bars: 10 mm (**a–o**). Photographs **a–e** by Qin Na; **f–g** by Junqing Yan; **h–i** by Liangliang Qi; **j–o** by Yupeng Ge.

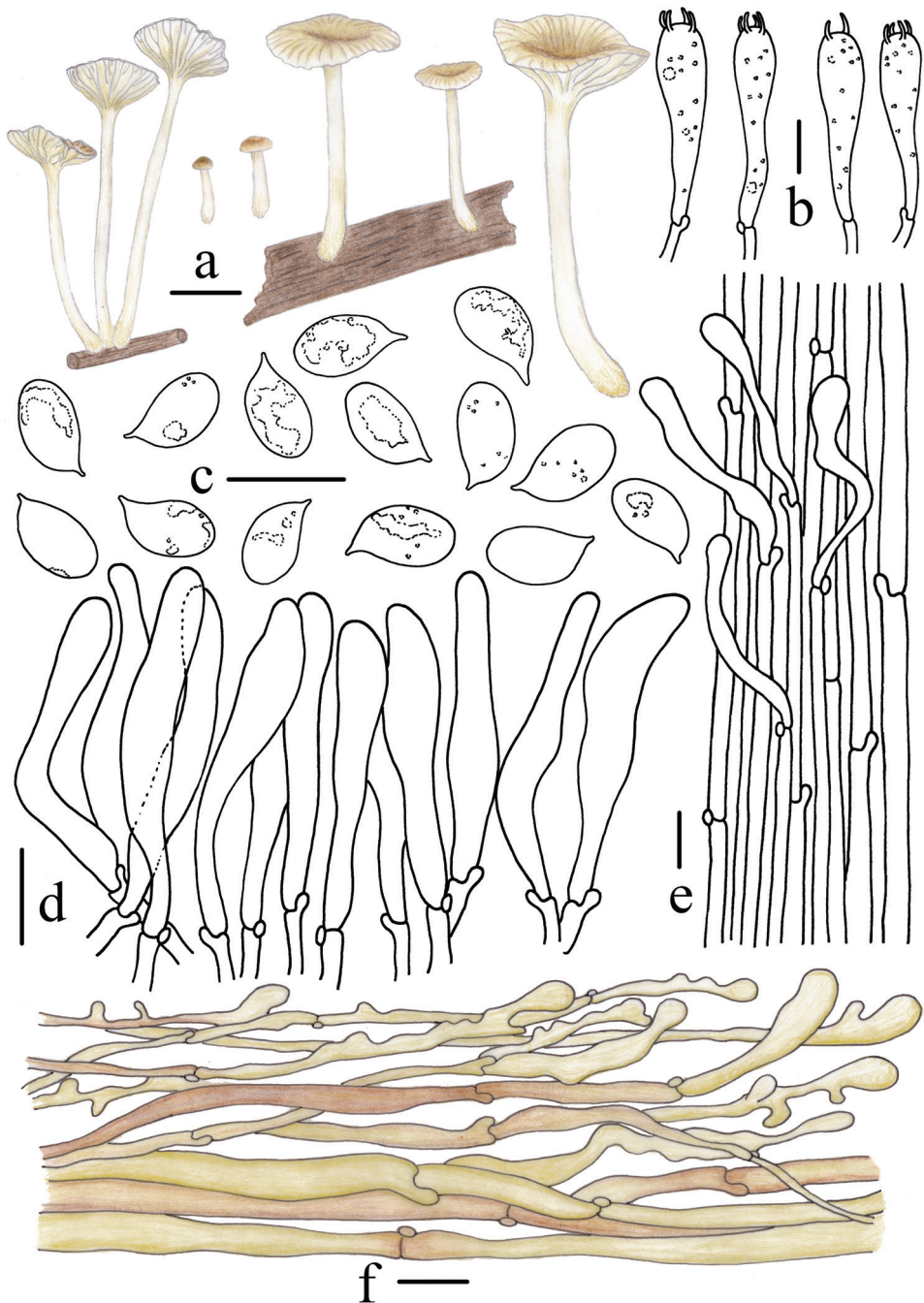


Figure 12. Morphological features of *Gerronema nemorale* Har. Takah. (FFAAS0410) **a** basidiomata **b** basidia **c** basidiospores **d** cheilocystidia **e** stipitipellis and caulocystidia **f** pileipellis. Scale bars: 10 mm (**a**); 10 μm (**b–f**). Drawing by Qin Na and Yupeng Ge.

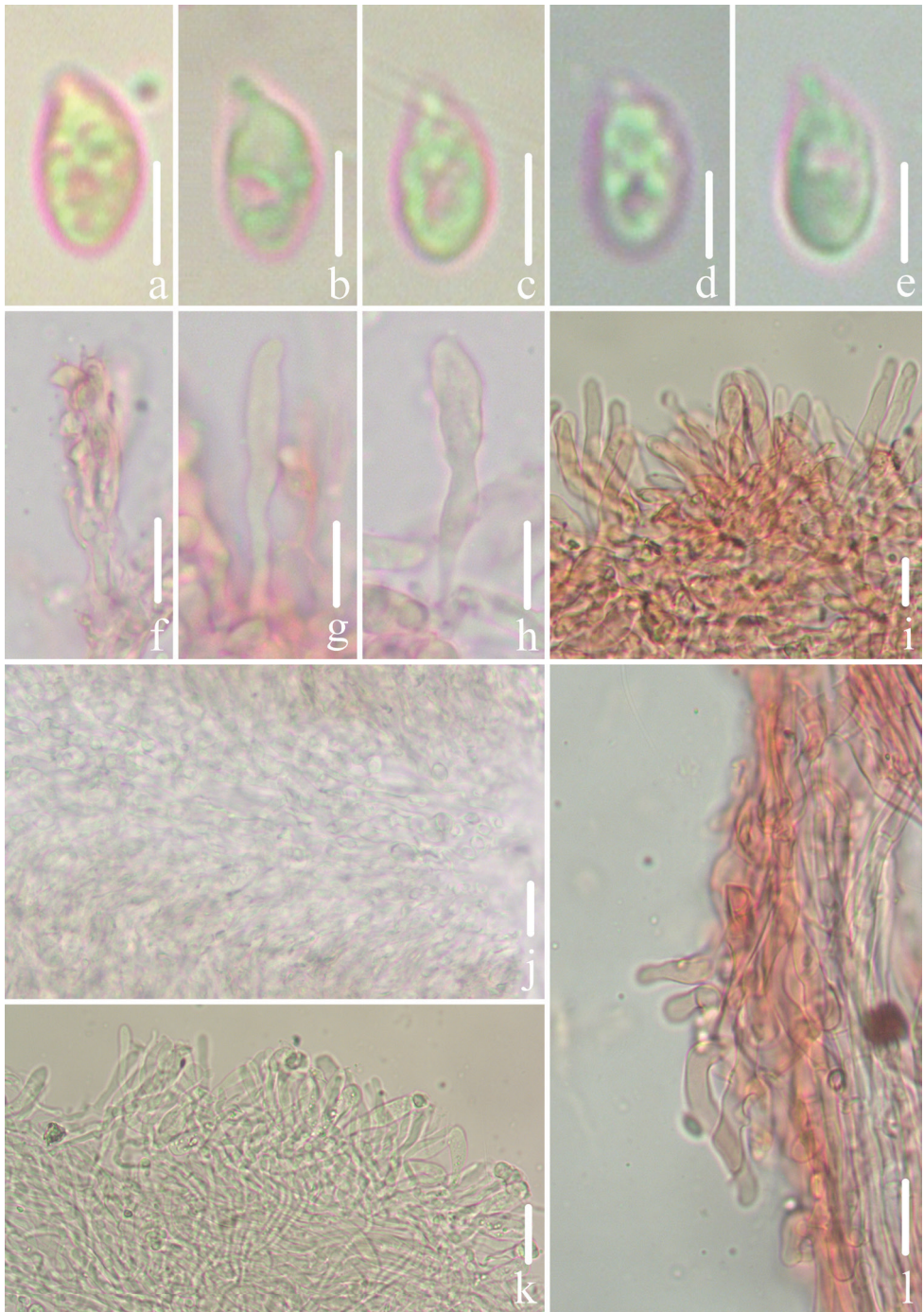


Figure 13. Microscopic features of *Gerronema nemorale* Har. Takah. (FFAAS0410) **a–e** basidiospores **f** basidia **g–i** cheilocystidia **j** lamellar trama **k** pileipellis **l** stipitipellis and caulocystidia. Scale bars: 5 μ m (**a–e**); 10 μ m (**f–l**).

Remarks. Having a sarcodimitic tissue structure, *G. nemorale* fits well within the currently restricted concept of the genus *Gerronema* (Redhead 1986; Norvell et al. 1994). *Gerronema nemorale* seems to be rather common in the East Asian region (Takahashi 2000; Antonín et al. 2008; Kim et al. 2014; Aqduş and Khalid 2021). Kim et al. (2014) has reported a basidiospore size of $6.0\text{--}8.2 \times 3.5\text{--}4.8 \mu\text{m}$ for *G. nemorale* collected from Mount Halla (Jeju Island) in southwestern Korea, which is distinctly smaller than that of other specimens from Korea, Japan, Pakistan, and our collections (Takahashi 2000; Antonín et al. 2008; Kim et al. 2014; Aqduş and Khalid 2021). *Gerronema tenue* Dennis, described from Venezuela, is allied with *G. nemorale*, but the latter differs in having a citrine yellow pileus, an insititious stipe, and lamellae edges without cheilocystidia (Dennis 1961). Another similar species, *G. corticiphilum* Lj.N. Vassiljeva, described as *G. corticiphila*, has a rarely sulfurous-colored pileus and larger and narrower basidiospores ($13\text{--}17 \times 4\text{--}5 \mu\text{m}$) (Vassiljeva 1973). In addition, *G. icterinum* (Singer) Singer from South America, now treated as *Trogia icterina* (Singer) Corner, shows some similarities with *G. nemorale* but has veined and forked lamellae and lacks cheilocystidia (Singer 1986). Another species of *Trogia*, *T. mellea* Corner, is also similar to *G. nemorale*, but can be easily distinguished from the latter in having no olivaceous tones on the pileus surface, a fuscous, pruinose pileus center and stipe, and subclavate or subventricose cheilocystidia (Corner 1966).

Discussion

Our phylogenetic analysis divided *Gerronema* into several highly supported clades containing other members of Porothleaceae, thus providing further evidence that *Gerronema* is polyphyletic (Vizzini et al. 2019). This finding is consistent with the view of Vizzini et al., who only included seven genera in Porothleaceae: *Hydropus*, *Chrysomycena*, *Clitocybula*, *Leucoinocybe*, *Megacollybia*, *Porothleum*, and *Trogia*; in addition, many taxa in this family in the sense of Redhead have a sarcodimitic structure (Redhead 1986; Vizzini et al. 2019). The phylogenetic results are in agreement with the taxonomic concept of *Gerronema* as a heterogeneous group. Although *Gerronema* was treated after its establishment as a subgenus of *Omphalina* by Lange (1981), the view of *Gerronema* as a distinct genus has been widely adopted (Redhead 1986; Norvell et al. 1994).

The phylogenetically and morphologically closest genera to *Gerronema* are *Megacollybia* and *Trogia* (Hughes et al. 2007; Antonín et al. 2019; Vizzini et al. 2019). Compared with *Gerronema*, however, *Megacollybia* is well characterized by the presence of rhizomorphs at the base of stipe and a sarcodimitic stipe structure, whereas narrow and frequently forked gills and a trichodermic pileipellis are observed in *Trogia* (Corner 1966; Hughes et al. 2007). Other groups in the same family, namely, *Hydropus*, *Chrysomycena*, *Clitocybula*, *Leucoinocybe*, and *Porothleum*, have different morphological characteristics and are genetically distant from *Gerronema* (Hausknecht et al. 1997; Antonín et al. 2008, 2019; Vizzini et al. 2019).

Since 1995, only three species of *Gerronema* have been reported from China, namely, *G. albidum* (Fr.) Singer, *G. chrysocarpum* P.G. Liu, and *G. indigoticum* T. Bau & L.N. Liu (Liu 1995; Dai et al. 2010; Liu et al. 2019). The distinctly white and blue basidiomata of *G. albidum* and *G. indigoticum* can be used to distinguish those two species from our newly described and newly recorded species, and *G. chrysocarpum* has a viscid pileus and pleurocystidia (Liu 1995; Dai et al. 2010; Liu et al. 2019).

Key to seven species of *Gerronema* in China

- 1 Basidiomata not yellow or brown 2
- Basidiomata yellow to brown 3
- 2 Pileus and stipe blue *G. indigoticum*
- Pileus and stipe white *G. albidum*
- 3 Pleurocystidia present *G. chrysocarpum*
- Pleurocystidia absent 4
- 4 Pileus densely covered with deep brown fur or scales *G. zhujian*
- Pileus without fur or scales 5
- 5 Basidiomata distinctly small (Pileus < 9 mm in diam.) *G. microcarpum*
- Basidiomata moderately small (Pileus > 9 mm in diam.) 6
- 6 Cheilocystidia up to 48 μm *G. baishanzuense*
- Cheilocystidia less than 35 μm *G. nemorale*

Morphological and molecular evidence support classification of the four newly recognized/recorded species as members of *Gerronema*. The four species share an umbonate or infundibuliform pileus, decurrent lamellae, inamyloid basidiospores, clavate cystidia, and sarcodimitic tramal tissues. In addition, the four species are lignicolous in habit, growing on rotten wood or fallen twigs. *Gerronema microcarpum* is mainly distinguished from *G. baishanzuense*, *G. nemorale*, and *G. zhujian* by its distinctly small basidiomata and basidiospores. The tiny brown fur or scales on the pileus of *G. zhujian* differentiate it from the other three species. *Gerronema nemorale* is morphologically most similar to *G. baishanzuense* but can be readily discriminated on the basis of its olive-tinted pileus, larger basidiospores, and smaller caulocystidia.

Significantly, the phylogenetic relationship of *G. subclavatum* to *G. nemorale* remains unresolved given the limited genetic differentiation between these two taxa (Cooper 2014; Latha et al. 2018; Antonín et al. 2019; Vizzini et al. 2019). *Gerronema subclavatum* was formerly classified as a species in *Omphalina*; the original description is as follows: "Pileus thin, submembranaceous, subclavate or tubaeform, deeply umbilicate, glabrous, grayish brown, 6–12 mm. broad; lamellae subdistant, very decurrent, yellow; stem slender, subpruinose, often tomentose near the base, hollow, whitish, about 2.5 cm. long, 1 mm. thick; spores elliptic, 6–7.5 μm long, 4–5 μm broad" (Peck 1900). A new combination, *G. subclavatum*, was later proposed, but a detailed description was not provided (Singer 1970; Redhead 1986). Taking into account the grayish brown pileus, whitish stipe, and smaller basidiospores of *G. subclavatum*, we believe that this

species is morphologically distinct from *G. nemorale*. We therefore tentatively accept *G. subclavatum* and *G. nemorale* as two independent taxa but emphasize that sufficient sampling and a detailed appraisal of the morphological and molecular variation of *G. subclavatum* and *G. nemorale* are required to confirm this hypothesis.

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***Kodamaea hongheensis* f.a., sp. nov., *Kodamaea ovata* f.a., sp. nov. and *Kodamaea yamadae* f.a., sp. nov., three new yeast species of *Kodamaea* (Saccharomycetales, Debaryomycetaceae) from China**

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Abstract

Kodamaea includes a growing number of interesting yeasts of the family Debaryomycetaceae that are widely distributed in temperate, subtropical and tropical regions of different continents. During recent yeast collections in Henan and Yunnan Province in China, several isolates of *Kodamaea* were obtained from rotting wood, all of which represent undescribed taxa. Based on morphological and phylogenetic analyses (ITS and LSU rDNA), three new species are proposed: *K. hongheensis* f.a., **sp. nov.**, *K. ovata* f.a., **sp. nov.** and *K. yamadae* f.a., **sp. nov.** In addition, sixteen *Candida* species, which are members of the *Kodamaea* clade based on phylogenetic analysis, are transferred to *Kodamaea* as new combinations. Our results indicate high species diversity of *Kodamaea* waiting to be discovered in rotting wood from tropical and subtropical China.

Keywords

Debaryomycetaceae, 16 new combinations, Saccharomycetales, three new species, yeast taxonomy

Introduction

Kodamaea was proposed by Yamada et al. (1995a, b) to accommodate a single species, *K. ohmeri*, which was initially classified in the genus *Pichia*. Kurtzman (1998) did not accept this proposal because the entire genus *Pichia* was clearly polyphyletic and in need of careful revision. However, the discovery of four new ascosporeogenous relatives of *K. ohmeri*, namely *K. anthophila*, *K. kakaduensis*, *K. laetipori* and *K. nitidulidarum*, added further justification to the recognition of *Kodamaea* as a separate genus (Lachance et al. 1999; Rosa et al. 1999; Suh and Blackwell 2005). Subsequently, four new anamorphic species of *Kodamaea*, *K. jinghongensis*, *K. meredithiae*, *K. neixiangensis* and *K. transpacificae* have been proposed as part of the genus based on their phylogenetic placement (Freitas et al. 2013; Sylvester et al. 2015; Gao et al. 2017). In addition, more than 16 species of *Candida* are recognized as members of the *Kodamaea* clade based on phylogenetic analysis of rDNA sequences (Hsieh et al. 2010; Lachance et al. 2011; Nakase et al. 2011; Daniel et al. 2014). The *Kodamaea* clade currently consists of nine species of the genus *Kodamaea* and 16 asexual species still assigned to the genus *Candida*, making it one of the growing numbers of interesting genera tentatively assigned to the family Metschnikowiaceae (Lachance and Kurtzman 2011; Nakase et al. 2011; Freitas et al. 2013; Daniel et al. 2014; Sylvester et al. 2015; Gao et al. 2017). On the basis of multigene phylogenetic analysis of nearly entire LSU rDNA, SSU rDNA, translation elongation factor-1 α (*EF-1 α*), two RNA polymerase II subunits gene (*RPB1* and *RPB2*) and whole genome, the *Kodamaea* clade has been found to be closely related to the *Aciculoconidium* clade and should be allocated to the family Debaryomycetaceae (Kurtzman and Robnett 2013; Shen et al. 2018).

Species in *Kodamaea* are very common and inhabit a wide range of habitats, such as plant-related substrates, insects, insect frass, soil and seawater (Lachance and Kurtzman 2011; Lachance et al. 2011; Nakase et al. 2011; Freitas et al. 2013; Sylvester et al. 2015; Gao et al. 2017). Many of these species are associated with insects that occupy this ecological niche (Freitas et al. 2013; Suh and Blackwell 2005). They were isolated either directly from insects and insect frass or from common insect habitats, such as rotting wood, forest soil, mushrooms or flowers (Suh and Blackwell 2005; Hsieh et al. 2010; Lachance et al. 2011; Freitas et al. 2013; Gao et al. 2017). Significantly, *K. mesenterica* and *K. ohmeri* are also found in clinical specimens; it is thus possible that these species might act as emerging opportunistic pathogens (Lachance and Kurtzman 2011; Lachance et al. 2011).

Species of *Kodamaea* are widely distributed in temperate, subtropical and tropical regions of different continents, but most known species appear to exist in Asia, North America and South America (Suh and Blackwell 2005; Hsieh et al. 2010; Lachance et al. 2011; Nakase et al. 2011; Gao et al. 2017). The genus *Kodamaea* has been heavily studied in Asia, and 11 species of this clade were previously reported in Thailand, Japan and China. Among them, *K. loeiensis* is from Thailand (Nakase et al. 2011), while *K. fukazawae*, *K. fungicola* and *K. sagamina* are from Japan (Lachance et al. 2011). In China, *K. alishanica*, *K. hsintzibuensis*, *K. kaohsiungensis*, *K. lidongshanica* and

K. smagusa are described from Taiwan Provinces (Hsieh et al. 2010), and *K. jinghongensis* and *K. neixiangensis* are from Henan and Yunnan Provinces (Gao et al. 2017). Our studies suggest the existence of other potentially new species of the genus in China. In this study, we collected rotting wood samples from Henan and Yunnan Provinces in China. After isolation and examination, three new species of *Kodamaea* were identified based on phenotypic characteristics and phylogenetic analysis, increasing the species diversity of *Kodamaea* in China.

Materials and methods

Sample collection and isolation

Samples of rotting wood were collected in the Xishuangbanna Primeval Forest Park (Yunnan Province, China) and the Baotianman Nature Reserve (Henan Province, China). The Xishuangbanna Primeval Forest Park (21°98'N, 100°88'E) is 1355 m above sea level (MASL), with a hot and humid climate. The average annual temperature is between 16 °C and 28 °C, and the average annual rainfall is above 1,100 mm. The Baotianman Nature Reserve (33°30'44"N, 111°55'47"E) is at 1830 (MASL), with a transitional climate from a northern subtropical zone to a warm temperate zone, average annual temperature of 14–16 °C, and average annual rainfall between 800 mm and 900 mm. Forty rotting wood samples were collected, twenty from each area, during July to August in 2016 and 2017. The samples were stored in sterile plastic bags and transported under refrigeration to the laboratory over a period of no more than 24 h. Yeast strains were isolated from rotting wood samples in accordance with the methods described by Gao et al. (2017) and Zheng et al. (2017). Each sample (1 g) was added to 20 ml sterile yeast extract-malt extract (YM) broth (0.3% yeast extract, 0.3% malt extract, 0.5% peptone, 1% glucose, pH 5.0 ± 0.2) supplemented with 0.025% sodium propionate and 200 mg/L chloramphenicol in a 150 ml Erlenmeyer flask and then cultured for 3–10 days on a rotary shaker. Subsequently, 0.1 ml aliquots of the enrichment culture and appropriate decimal dilutions were spread on YM agar plates and then incubated at 25 °C for 3–4 days. Different yeast colony morphotypes were then isolated by repeated plating on YM agar. All isolates were stored in Microbiology Lab of Nanyang Normal University (NYNU; Nanyang, China), and ex-type cultures of novel yeast were deposited in the fungal collection at Westerdijk Fungal Biodiversity Institute (CBS; Utrecht, The Netherlands) and China Centre of Industrial Culture Collection (CICC; Beijing, China).

Morphological, physiological and biochemical studies

Morphological and physiological properties were determined according to Kurtzman et al. (2011). Carbon and nitrogen assimilation tests were performed using liquid media, and growth was observed for up to 4 weeks. Carbon fermentation was tested in a yeast

extract peptone (YP) base media (1% yeast extract and 2% peptone, pH 5.0 ± 0.2), and Durham tubes were used to visualize carbon dioxide production. Growth at various temperatures (30 °C, 35 °C, 37 °C and 40 °C) was assessed by streaking cells onto yeast extract peptone glucose (YPD) agar (1% yeast extract, 2% peptone, 2% glucose, 2% agar, pH 5.0 ± 0.2) plates and incubating them for ~2 weeks. Formation of true hyphae and pseudohyphae was investigated using the Dalmau plate method on both cornmeal (CM) and 5% malt extract (ME) agar plates. Induction of the sexual stage was tested by incubating single or mixed cultures of the each of the two strains on YM agar, cornmeal (CM) agar, 5% malt extract (ME) agar, V8 agar, Gorodkova agar, McClary's acetate agar or yeast carbon base plus 0.01% ammonium sulphate (YCBAS) agar at 25 °C for 2 months (Lachance and Kurtzman 2011; Sylvester et al. 2015; Gao et al. 2017).

DNA extraction, PCR amplification and nucleotide sequencing

Genomic DNA was extracted from the yeasts using the Ezup Column Yeast Genomic DNA Purification Kit according to the manufacturer's protocol (Sangon Biotech, China). The nuclear rDNA ITS1-5.8S-ITS2 (ITS) region was amplified using the primer pair ITS1/ITS4 (White et al. 1990). The D1/D2 domain of LSU rDNA was amplified using the primer pair NL1/NL4 (Kurtzman and Robnett 1998). The following thermal profile was used to amplify the ITS and LSU rDNA regions: an initial denaturation step of 2 min at 95 °C, followed by 35 cycles of 30 s at 95 °C, 30 s at 51 °C, and 40 s at 72 °C, with a final extension of 10 min at 72 °C (Lv et al. 2020). PCR products were directly purified and sequenced by Sangon Biotech Inc. (Shanghai, China). We determined the identity and accuracy of the newly obtained sequences by comparing them to sequences in GenBank and assembled them using BioEdit (Hall 1999). Newly obtained sequences were then submitted to GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; Table 1).

Phylogenetic analyses

Species in the *Kodamaea* clade with high similarity to our new species were selected for phylogenetic analyses. *Schizosaccharomyces pombe* NRRL Y-12796^T was used as an outgroup, based on Kuramae et al. (2006a). NCBI accession numbers of sequences used in the phylogenetic tree are listed in Table 1. Initial alignment of the combined ITS and partial LSU rDNA dataset was performed using the online version of MAFFT 6.0 (Katoh and Toh 2010) with manual evaluations and adjustments in BioEdit when necessary to obtain reliable and reasonable results (Hall 1999). The best-fit nucleotide substitution models for each gene were selected using jModelTest v2.1.7 (Darriba et al. 2012) according to the Akaike information criterion.

Neighbour-joining (NJ) and Maximum parsimony (MP) analyses were implemented for inferring the phylogenetic analyses by using MEGA software version 7.0 (Kumar et al. 2016). The NJ analysis was carried out using Kimura's two parameter

Table 1. DNA sequences used in the molecular phylogenetic analysis. Entries in bold are newly generated in this study.

Species	Strain	Locality	Sample	ITS	D1/D2
<i>Kodamaea arcana</i>	CBS 9883 ^T	USA	Beetle	N/A	AY242347
<i>K. alishanica</i>	CBS 11429 ^T	China	Soil	NR_159556	NG_063941
<i>K. derodonti</i>	CBS 9882 ^T	USA	Beetle	NR_111388	AY242346
<i>K. fukazawae</i>	CBS 9137 ^T	Japan	Mushroom	AB028033	AY313957
<i>K. fungicola</i>	CBS 9138 ^T	Japan	Mushroom	AB028031	AY313958
<i>K. hsintzibuensis</i>	CBS 11427 ^T	China	Soil	NR_160557	HQ999957
<i>K. kaohsiungensis</i>	CBS 11435 ^T	China	Mushroom	NR_159557	HQ999958
<i>K. leandrae</i>	CBS 9735 ^T	Brazil	Decaying fruit	NR_155222	AY449659
<i>K. lidongshanica</i>	CBS 11426 ^T	China	Fruiting body	GU126451	HQ999959
<i>K. loeensis</i>	CBS 11899 ^T	Thailand	Insect frass	NR_155223	NG_073574
<i>K. mesenterica</i>	CBS 602 ^T	Germany	Beer	NR_111297	U45720
<i>K. plutei</i>	CBS 9885 ^T	USA	Beetle	NR_111389	AY520388
<i>K. restingae</i>	CBS 8493 ^T	Brazil	Flowers Nitidulid beetles	NR_155225	AF059667
<i>K. sagramina</i>	CBS 9140 ^T	Japan	Mushroom	AB028032	AY313959
<i>K. smagusa</i>	CBS 11430 ^T	China	Mushroom	NR_111611	FJ873476
<i>K. suecica</i>	CBS 5724 ^T	Sweden	Seawater	N/A	U45732
<i>K. anthophila</i>	CBS 8494 ^T	Australia	Flowers, Nitidulid beetle	NR_155239	AF059668
<i>K. transpacific</i>	CBS 12823 ^T	Ecuador	Flowers	NR_173358	KF002564
<i>K. nitidulidarum</i>	CBS 8491 ^T	Brazil	Flower Nitidulid beetle	NR_155241	AF059665
<i>K. ovata</i>	NYNU 167144^T	China	Rotting wood	OK381035	OK381037
<i>K. ovata</i>	NYNU 1685	China	Rotting wood	OM327522	OM327519
<i>K. obmeri</i>	CBS 5367 ^T	USA	Cucumber brines	NR_121464	U45702
<i>K. jinghongensis</i>	CBS 14700 ^T	China	Rotting wood	KY213814	KY213807
<i>K. hongbeensis</i>	NYNU 17423^T	China	Rotting wood	MG255723	MG255704
<i>K. hongbeensis</i>	NYNU 17409	China	Rotting wood	OM327517	OM327518
<i>K. kakaduensis</i>	CBS 8611 ^T	Australian	Flower	NR_155240	AF092279
<i>K. laetipori</i>	CBS 9884 ^T	USA	Beetle	N/A	AY520398
<i>K. meredithiae</i>	CBS 13899 ^T	USA	soil	OK050648	KM408122
<i>K. neixiangensis</i>	CBS 14699 ^T	China	Rotting wood	KY213808	KY213820
<i>K. yamadae</i>	NYNU 168114^T	China	Rotting wood	OK381036	OK381034
<i>K. yamadae</i>	NYNU 16858	China	Rotting wood	OM327521	OM327516
<i>Metschnikowia lochheadii</i>	CBS 8807 ^T	USA	flowers	NR_164507	NG_058341
<i>M. cubensis</i>	MUCL 45753 ^T	Cuba	flowers	N/A	EU143316
<i>M. matae</i> var. <i>maris</i>	CBS 13986 ^T	Brazilian	flowers	N/A	KP241777
<i>M. cerradonensis</i>	CBS 10409 ^T	Brazil	flowers nitidulid beetles	N/A	DQ641237
<i>M. continentalis</i>	CBS 8430 ^T	Germany	flowers	N/A	DQ641238
<i>M. santaceciliae</i>	CBS 9149 ^T	Costa Rica	nitidulid beetles	N/A	DQ641242
<i>M. borealis</i>	CBS 8431 ^T	USA	beetles	N/A	DQ641243
<i>Aciculoconidium aculeatum</i>	NRRL YB-4298 ^T	USA	<i>Drosophila pinicola</i>	N/A	JQ689029
<i>Schizosaccharomyces pombe</i>	NRRL Y-12796 ^T	Jamaica, South Africa, Poland	Apple, Molass	KY105378	KY109602

Notes: Type strains are marked with T. N/A: sequences not available.

model (Kimura 1980) in the neighbour-joining method (Saitou and Nei 1987). Bootstrapping with 1,000 replicates was performed to determine branch support (Felsenstein 1985). The MP analysis was run using a heuristic search option of 1,000 search replicates with random-addition of sequences and tree bisection and reconnection (TBR) as the branch-swapping algorithm. NJ and MP bootstrap support values above 50% are shown as first and second positions above nodes, respectively.

Results

Phylogenetic analyses

The combined ITS and LSU rDNA sequences dataset was analysed to infer the interspecific relationships within the *Kodamaea* clade of the family Debaryomycetaceae. The dataset consisted of 40 sequences including the outgroup, *Schizosaccharomyces pombe* NRRL Y-12796^T. A total of 896 characters including gaps (372 for ITS and 524 for LSU rDNA) were included in the phylogenetic analysis. Both NJ and MP analyses resulted in similar tree topologies, and only the NJ tree is shown in Fig. 1.

In the NJ phylogenetic tree (Fig. 1), the genus *Kodamaea* formed a monophyletic clade distant from its related taxa of the family Debaryomycetaceae. The samples of the three new species of *Kodamaea*, *Kodamaea hongheensis*, *Kodamaea ovata* and *Kodamaea yamadae*, formed each a strongly supported sub-clade and were clearly distinct from other known species of *Kodamaea*. Two strains of *K. hongheensis* formed a unique lineage with *K. laetipori*, but with low support (NJ 57%, MP 60%). *K. ovata* clustered with *K. neixiangensis* with high support (NJ 94%, MP 90%), while *K. yamadae* clustered with *K. jinghongensis* and *K. fukazawae* with evident statistic support (NJ 87%, MP 80%).

Taxonomy

Kodamaea hongheensis C.Y. Chai & F.L. Hui, sp. nov.

MycoBank No: 842625

Fig. 2

Holotype. CHINA, Yunnan Province, Honghe Prefecture, Luxi County, in rotting wood in Jiuxi Mountain Forest Park, April 2017, K.F. Liu & Z.W. Xi (holotype NYNU 17423^T, ex-holotype CICC 33265).

Etymology. The specific epithet *hongheensis* refers to the geographic origin of the type strain, Honghe Prefecture, Yunnan.

Description. In YM broth, after 3 days at 25 °C, cells are ovoid to elongate (3–5 × 3–7 µm) and occur singly or in pairs (Fig. 2a). Sediment is formed after a month, but a pellicle is not observed. On YM agar, after 3 days at 25 °C, colonies are white to cream-colored, butyrous and smooth with entire margins. In Dalmau plate culture on CM agar, pseudohyphae are formed but not true mycelia (Fig. 2b). Asci or signs of conjugation are not seen on sporulation media. Glucose, maltose and trehalose are fermented but not galactose, sucrose, melibiose, lactose, cellobiose, melezitose, raffinose, inulin, or xylose. Glucose, glucosamine, D-xylose, sucrose, maltose, trehalose, methyl α-D-glucoside, cellobiose, salicin, melezitose, glycerol, ribitol, D-glucitol, D-mannitol, D-glucono-1, 5-lactone, 2-keto-D-gluconate, succinate, citrate and ethanol are assimilated as sole carbon sources.

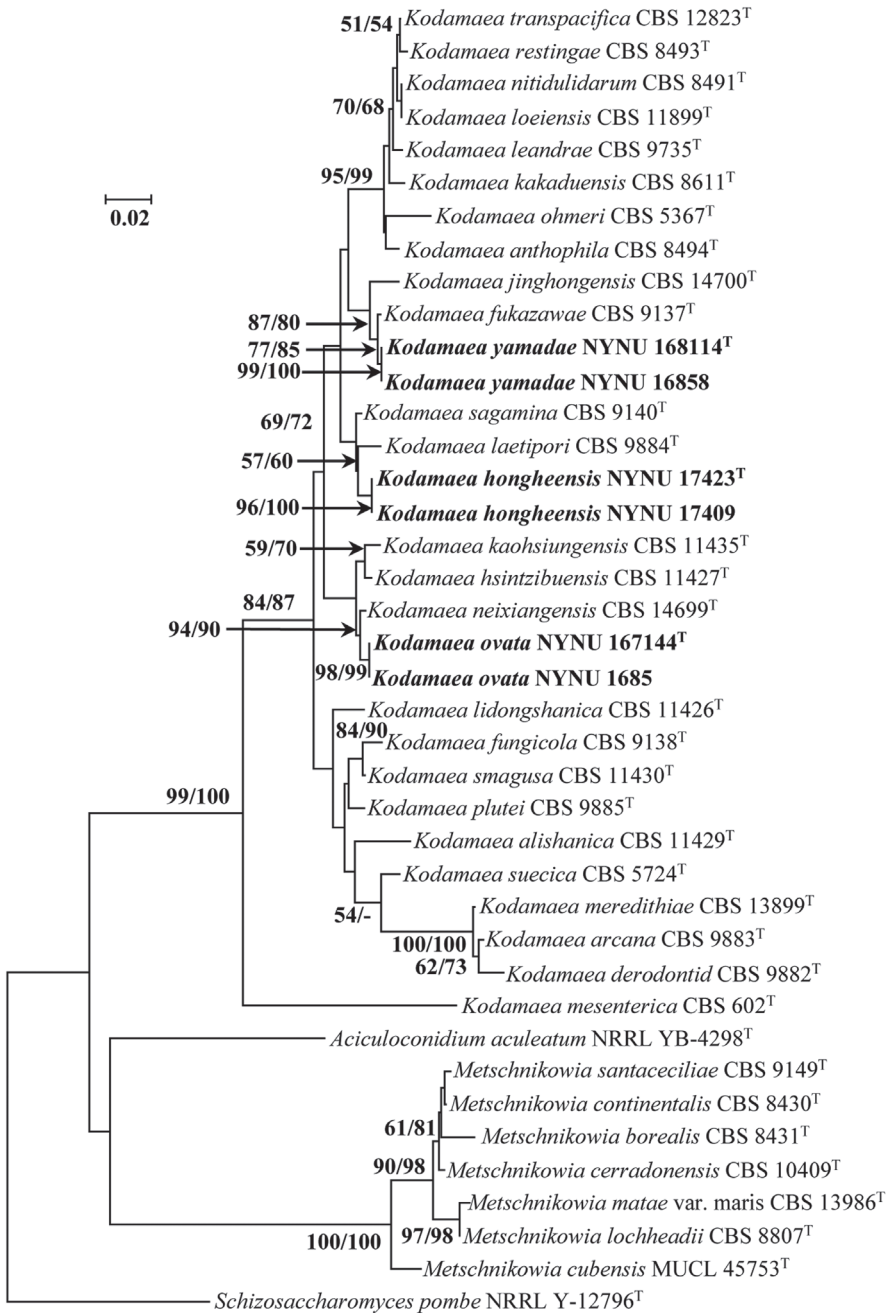


Figure 1. The NJ tree based on an analysis of a combined ITS and LSU rDNA dataset from the genus *Kodamaea* and related taxa from the family Debaryomycetaceae. *Schizosaccharomyces pombe* NRRL Y-12796^T was used as outgroup. Bootstrap support values (BS) for the neighbour-joining and maximum parsimony programs of above 50% are given at nodes based on 1000 replications, a dash (“-”) indicates a value < 50% (BS). Bar, 2% sequence difference. The strain number is indicated after the species name. The strains in this study are in bold. T, type strains.

Galactose, L-sorbose, D-ribose, D-arabinose, L-arabinose, L-rhamnose, melibiose, lactose, raffinose, inulin, erythritol, xylitol, galactitol, *myo*-inositol, D-gluconate, D-glucuronate, DL-lactate and methanol are not assimilated. L-lysine, glucosamine and D-tryptophan are assimilated as sole nitrogen sources. Nitrate, nitrite, ethylamine, cadaverine, creatine, creatinine and imidazole are not assimilated. Growth is observed at 35 °C but not at 37 °C. Growth in the presence of 0.01% cycloheximide is positive, but growth in the presence of 10% NaCl plus 5% glucose and 1% acetic acid is negative. Starch-like compounds are not produced. Urease activity and diazonium blue B reactions are negative.

Additional isolate examined. CHINA, Yunnan Province, Honghe Prefecture, Luxi County, in rotting wood in Jiuxi Mountain Forest Park, April 2017, K.F. Liu & Z.W. Xi (NYNU 17409).

Notes. Two strains NYNU 17409 and NYNU 17423, both representing *K. hongheensis*, were grouped in an independent lineage and are related to *K. laetipori*. *K. hongheensis* differed from its closest relative *K. laetipori* by 2.9% substitutions in the LSU rDNA sequence. However, the ITS sequence of *K. hongheensis* could not be successfully aligned with the type strain of *K. laetipori* because its ITS sequences are not currently available from either the NCBI GenBank database or the CBS database. Physiologically, *K. hongheensis* can be differentiated from *K. laetipori* (Lachance and Kurtzman 2011) based on growth in L-sorbose, D-arabinose, D-gluconate, and DL-lactate, which are positive for *K. laetipori* and negative for the new species. Moreover, *K. laetipori* grows in the presence of 0.1% cycloheximide and 10% NaCl plus 5% glucose, but *K. hongheensis* does not.

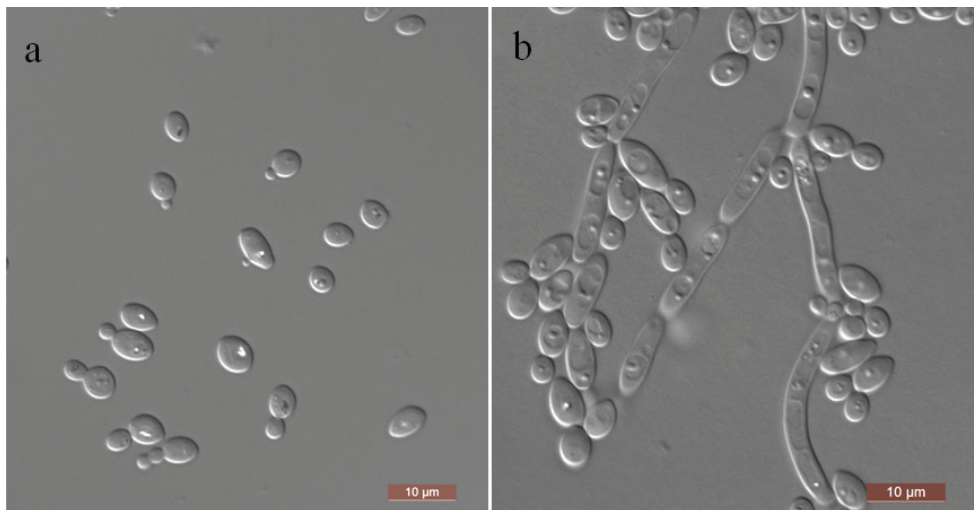


Figure 2. Morphology of *Kodamaea hongheensis* (NYNU 17423, holotype) **a** budding cells in YM broth after 3 d **b** simple pseudohyphae on CM agar after 14 d. Scale bars: 10 µm.

***Kodamaea ovata* C.Y. Chai & F.L. Hui, sp. nov.**

Mycobank No: 842623

Fig. 3

Holotype. CHINA, Henan Province, Nanyang City, the Baotianman Nature Reserve, in rotting wood under a mixed forest, July 2016, K.F. Liu & Z.W. Xi (holotype NYNU 167144^T, ex-holotype CBS 14702).

Etymology. The specific epithet *ovata* refers to the ovoid cell morphology of the type strain.

Description. In YM broth, after 3 days at 25 °C, cells are ovoid ($2\text{--}4 \times 3\text{--}5 \mu\text{m}$) and occur singly or in pairs (Fig. 3a). Sediment is formed after a month, but a pellicle is not observed. On YM agar, after 3 days at 25 °C, colonies are white to cream-colored, butyrous and smooth with entire margins. In Dalmau plate culture on CM agar, a rudimentary pseudomycelium is formed (Fig. 3b). Asci or signs of conjugation are not seen on sporulation media. Glucose, galactose, maltose and trehalose are fermented but sucrose, melibiose, lactose, cellobiose, melezitose, raffinose, inulin and xylose are not. Glucose, galactose, glucosamine, D-xylose, D-arabinose, L-arabinose, sucrose, maltose, trehalose, methyl α -D-glucoside, cellobiose, salicin, arbutin, melezitose, inulin, glycerol, ribitol, xylitol, D-glucitol, D-mannitol, galactitol, D-glucono-1, 5-lactone, 2-keto-D-gluconate, DL-lactate, succinate, citrate and ethanol are assimilated as sole carbon sources. L-sorbose, D-ribose, L-rhamnose, melibiose, lactose, raffinose, erythritol, *myo*-inositol, D-gluconate, D-glucuronate and methanol are not assimilated. Ethylamine, L-lysine and creatine are assimilated as sole nitrogen sources. Nitrate, nitrite, cadaverine, creatinine, glucosamine, imidazole and D-tryptophan are not assimilated. Growth is observed at 42 °C but not at

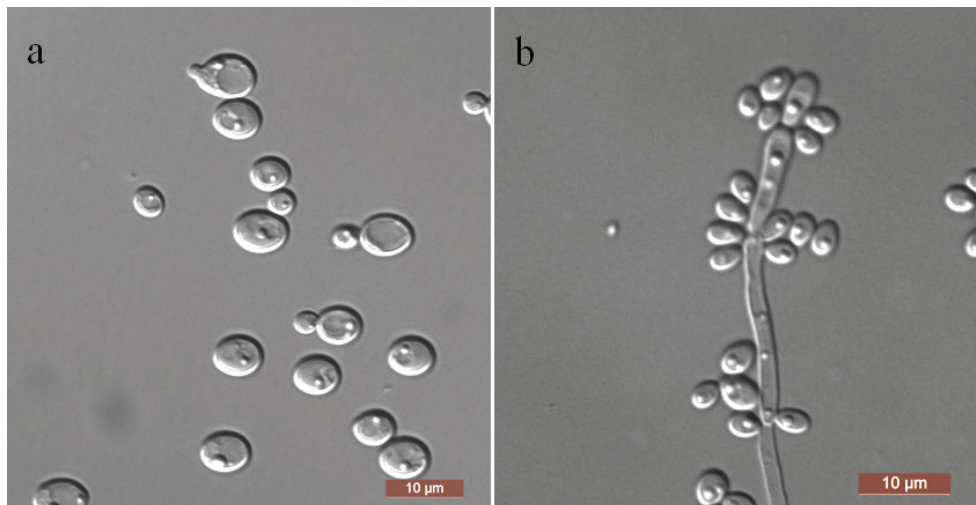


Figure 3. Morphology of *Kodamaea ovata* (NYNU 167144, holotype) **a** budding cells in YM broth after 3 d **b** pseudohyphae on CM agar after 14 d. Scale bars: 10 µm.

45 °C. Growth in the presence of 0.1% cycloheximide and 16% NaCl plus 5% glucose is positive, but growth in the presence of 1% acetic acid is negative. Starch-like compounds are not produced. Urease activity and diazonium blue B reactions are negative.

Additional isolate examined. CHINA, Henan Province, Nanyang City, the Baotianman Nature Reserve, in rotting wood under a mixed forest, July 2016, K.F. Liu & Z.W. Xi (NYNU 1685).

Notes. Two strains NYNU 1685 and NYNU 167144 representing *K. ovata* grouped in a well-supported clade and appear to be most closely related to *K. neixiangensis* (Gao et al. 2017). The nucleotide differences between the new species and the close relative *K. neixiangensis* are 1% substitutions in the LSU rDNA sequence and 4.8% substitutions in the ITS region, respectively. Physiologically, *K. ovata* can be differentiated from *K. neixiangensis* based on growth in L-arabinose, D-arabinose, DL-lactate and 16% NaCl plus 5% glucose, all of which were positive for *K. ovata* and negative for *K. neixiangensis*. Additionally, the new species ferments galactose and maltose and grows at 35 °C, but *K. neixiangensis* does not have these characteristics.

***Kodamaea yamadae* C.Y. Chai & F.L. Hui, sp. nov.**

MycoBank No: 842626

Fig. 4

Holotype. CHINA, Henan Province, Nanyang City, the Baotianman Nature Reserve, in rotting wood under a mixed forest, August 2016, K.F. Liu & Z.W. Xi (holotype NYNU 168114^T, ex-holotype CBS 14703).

Etymology. The specific epithet *yamadae* is used in honour of Y. Yamada for his proposal of the genus *Kodamaea*.

Description. In YM broth, after three days at 25 °C, cells are ellipsoidal to elongate (2–3 × 4.5–10 µm) and occur singly or in pairs (Fig. 4a). Sediment is formed after a month, but a pellicle is not observed. On YM agar, after 3 days at 25 °C, colonies are white, convex, sometimes fringed, glabrous or membranous, smooth or rugose and butyrous to tough due to filamentous growth. On Dalmau plate culture on CM agar, a rudimentary pseudomycelium is formed (Fig. 4b). Asci or signs of conjugation are not seen on sporulation media. Glucose, maltose, sucrose, trehalose and cellobiose are fermented but not galactose, melibiose, lactose, melezitose, raffinose, inulin or xylose. Glucose, galactose, glucosamine, D-ribose, D-xylose, sucrose, maltose, trehalose, methyl α-D-glucoside, cellobiose, salicin, inulin, glycerol, erythritol, ribitol, D-glucitol, D-mannitol, D-glucono-1, 5-lactone, 2-keto-D-gluconate, succinate, citrate and ethanol are assimilated as sole carbon sources. L-sorbose, D-arabinose, L-arabinose, L-rhamnose, arbutin, melibiose, lactose, raffinose, melezitose, xylitol, galactitol, *myo*-inositol, 5-keto-D-gluconate, D-gluconate, D-glucuronate, DL-lactate and methanol are not assimilated. Ethylamine, L-lysine, creatine, glucosamine and D-tryptophan are assimilated as sole nitrogen sources. Nitrate, nitrite, cadaverine, creatinine and imidazole are not assimilated. Growth is observed at 30 °C but not at 35 °C. Growth in the presence of

0.1% cycloheximide is positive, but growth in the presence of 10% NaCl plus 5% glucose and 1% acetic acid is negative. Starch-like compounds are not produced. Urease activity and diazonium blue B reactions are negative.

Additional isolates examined. CHINA, Henan Province, Nanyang City, the Baotianman Nature Reserve, in rotting wood under an oak forest, August 2016, K.F. Liu & Z.W. Xi (NYNU 16858).

Notes. Two strains NYNU 16858 and NYNU 168114, representing *K. yamadae* clustered in a well-supported clade that is closely related to *K. jinghongensis* (Gao et al. 2017) and *K. fukazawae* (Nakase et al. 1999). The nucleotide differences between *K. yamadae* and *K. jinghongensis* were 2.8% substitutions in the LSU rDNA sequences and 3.9% substitutions in the ITS region. Similarly, *K. yamadae* and *K. fukazawae* showed differences of 2.6% substitutions in the LSU rDNA sequences and 4.7% substitutions in the ITS region. Physiologically, the novel species differed from *K. jinghongensis* by its ability to ferment cellobiose and its inability to assimilate arbutin. Unlike *K. fukazawae*, the novel species was able to assimilate D-galactose, L-sorbose, inulin, D-arabinose, L-arabinose, L-rhamnose, and methanol, and was not able to grow in the presence of 0.1% cycloheximide. In all cases, identification by sequencing was the best approach.

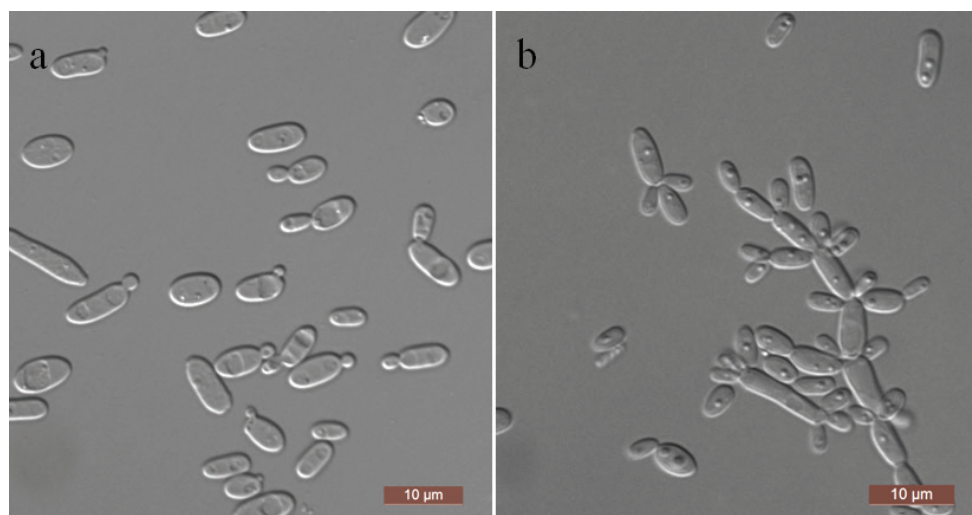


Figure 4. Morphology of *Kodamaea yamadae* (NYNU 168114, holotype) **a** budding cells in YM broth after 3 d **b** pseudohyphae on CM agar after 14 d. Scale bars: 10 µm.

Sixteen new combinations

In addition to the previously described taxa, we propose sixteen new combinations in the genus *Kodamaea* by including clade members that previously were described as species of the polyphyletic asexual genus *Candida* based on the combined ITS and LSU rDNA sequences from type strains of the genus *Kodamaea* and related taxa of the family Debaryomycetaceae.

***Kodamaea alishanica* (C.W. Hsieh) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843566

Basionym. *Candida alishanica* C.W. Hsieh, FEMS Yeast Research 10 (7): 948 (2010).***Kodamaea arcana* (S.-O. Suh & M. Blackw) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843565

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MycoBank No: 843567

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MycoBank No: 843579

Basionym. *Candida fukazawae* Nakase, M. Suzuki, Sugita, S.O. Suh & Komag, Mycoscience 40 (6): 473 (1999).***Kodamaea fungicola* (Nakase, M. Suzuki, Sugita, S.O. Suh & Komag) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843568

Basionym. *Candida fungicola* Nakase, M. Suzuki, Sugita, S.O. Suh & Komag, Mycoscience 40 (6): 470 (1999).***Kodamaea hsintzibuensis* (C.W. Hsieh) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843569

Basionym. *Candida hsintzibuensis* C.W. Hsieh, FEMS Yeast Research 10 (7): 948 (2010).***Kodamaea kaohsiungensis* (C.W. Hsieh) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843570

Basionym. *Candida kaohsiungensis* C.W. Hsieh, FEMS Yeast Research 10 (7): 948 (2010).

***Kodamaea leandrae* (Ruivo, Pagnocca, Lachance & Rosa) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 842628

Basionym. *Candida leandrae* Ruivo, Pagnocca, Lachance & Rosa, International Journal of Systematic and Evolutionary Microbiology 54(6): 62407 (2004).

***Kodamaea lidongshanica* (C.W. Hsieh) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843571

Basionym. *Candida lidongshanica* C.W. Hsieh, FEMS Yeast Research 10 (7): 948 (2010).

***Kodamaea loeiensis* (Nakase, Jindamorakot, Am-In, Ninomiya & Kawasaki) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 842627

Basionym. *Candida loeiensis* Nakase, Jindamorakot, Am-In, Ninomiya & Kawasaki, Journal of General and Applied Microbiology 57(6): 2011(388).

***Kodamaea mesenterica* ((A. Geiger) Diddens & Lodder) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843572

Basionym. *Candida mesenterica* (A. Geiger) Diddens & Lodder, Die anaskosporogenen Hefen, II Hälfte: 196 (1942).

***Kodamaea plutei* (S.-O. Suh & M. Blackw) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843573

Basionym. *Candida plutei* S.-O. Suh & M. Blackw, Mycologia 97 (1): 173 (2005)

***Kodamaea restingae* (Rosa, Lachance, Starmer, Barker, Bowles & Schlag-Edler) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 842629

Basionym. *Candida restingae* Rosa, Lachance, Starmer, Barker, Bowles & Schlag-Edler, International Journal of Systematic Bacteriology 49(1):313 (1999).

***Kodamaea sagramina* (Nakase, M. Suzuki, Sugita, S.O. Suh & Komag) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843575

Basionym. *Candida sagramina* Nakase, M. Suzuki, Sugita, S.O. Suh & Komag, Mycoscience 40 (6): 471 (1999).

***Kodamaea smagusa* (C.W. Hsieh) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843576

Basionym. *Candida smagusa* C.W. Hsieh, FEMS Yeast Research 10 (7): 948 (2010).

***Kodamaea suecica* (Rodr. Mir. & Norkrans) C.Y. Chai & F.L. Hui, comb. nov.**

MycoBank No: 843577

Basionym. *Candida suecica* Rodr. Mir. & Norkrans, Antonie van Leeuwenhoek 34: 115 (1968).

Discussion

In this study, three new species of *Kodamaea*, namely *Kodamaea hongheensis* f.a., sp. nov., *Kodamaea ovata* f.a., sp. nov. and *Kodamaea yamadae* f.a., sp. nov., from Henan and Yunnan Province in China are described and compared with similar species based on morphological and molecular data. A more comprehensive phylogenetic placement of the genus *Kodamaea* based on the combined ITS and LSU rDNA sequences is provided, including almost all representatives from GenBank database and newly generated sequences. This study provides some ideas on the species delimitation within *Kodamaea* based on morphological and phylogenetic placement evidence.

The phylogenetic relationships in *Kodamaea* have been unclear, mainly due to lacking a multigene phylogeny (Daniel et al. 2014). In this article, we used all currently known species and the new species to revise this genus, based on a phylogenetic analysis of the combined ITS and LSU rDNA sequences. As shown in Fig. 1, the genus *Kodamaea* formed a monophyletic clade with well support (NJ 99%, MP 100%). This result is similar to the results of previous phylogenetic analyses based on the D1/D2 domain of LSU rDNA sequences (Freitas et al. 2013; Gao et al. 2017). According to the nomenclature of “one fungus, one name”, sixteen asexual *Candida* species, which are members of the *Kodamaea* clade based on phylogenetic analysis, are transferred to *Kodamaea* as *K. alishanica* comb. nov., *K. arcana* comb. nov., *K. derodonti* comb. nov., *K. fukazawae* comb. nov., *K. fungicola* comb. nov., *K. hsintzibuensis* comb. nov., *K. kaohsiungensis* comb. nov., *K. leandrae* comb. nov., *K. lidongshanica* comb. nov.,

K. loeiensis comb. nov., *K. mesenterica* comb. nov., *K. plutei* comb. nov., *K. restingae* comb. nov., *K. sagramina* comb. nov., *K. smagusa* comb. nov. and *K. suecica* comb. nov.

In recent years, many new yeast species have been identified from rotting wood in China (Gao et al. 2017; Zheng et al. 2017; Lv et al. 2020). However, there is still a large number of undescribed yeast taxa in China. This study indicates that there are at least five species of *Kodamaea* isolated from rotting wood in China, including two species known previously to occur in China (*K. jinghongensis* and *K. neixiangensis*), and three novel species (*K. hongheensis*, *K. ovata* and *K. yamadae*). In China, there are still some species that need to be discovered, such as those listed under GenBank accessions KM598654 and HQ623482. Our study indicates that there is high species diversity of *Kodamaea* waiting to be discovered in rotting wood in tropical and subtropical China and nearby areas as with other genera (Lv et al. 2020).

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Two new species in *Capillidium* (Ancylistaceae, Entomophthorales) from China, with a proposal for a new combination

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Abstract

A taxonomic revision of *Conidiobolus* s.l. (Ancylistaceae, Entomophthorales) delimited all members that form capilliconidia into the genus *Capillidium*. In this study, we report two new species of *Capillidium* that were isolated in China. *Capillidium macrocapilliconidium* **sp. nov.** is characterised by large capilliconidia. *Capillidium jiangsuense* **sp. nov.** is differentiated by large capilliconidia and long, slender secondary conidiophores. Phylogenetic analyses were performed using sequences from the nuclear large subunit of rDNA (nucLSU), the mitochondrial small subunit of rDNA (mtSSU) and elongation-factor-like (*EFL*). The analyses revealed sister relationships between *Ca. macrocapilliconidium* **sp. nov.** and *Ca. globuliferus* / *Ca. pumilum* and between *Ca. jiangsuense* **sp. nov.** and *Ca. denaeosporum*. Additionally, a new combination of *Ca. rugosum* (Drechsler) B. Huang & Y. Nie **comb. nov.** is proposed herein. An identification key is provided for the ten accepted *Capillidium* species.

Keywords

Ancylistaceae, Capilliconidia, morphology, new taxa, phylogeny

Introduction

The taxonomic name *Capillidium* was first introduced as a subgenus within the genus *Conidiobolus* (Ancylistaceae, Entomophthorales) (Ben-Ze'ev and Kenneth 1982). All its members were clustered into a monophyletic group in the family Ancylistaceae, based on four molecular loci [i.e. small subunit of nuclear rDNA (nucSSU), large subunit of nuclear rDNA (nucLSU), small subunit of mitochondrial rDNA (mtSSU) and elongation-factor-like (*EFL*)] (Nie et al. 2020). Species in this genus are typically characterised by capilliconidia protruding from elongated, slender conidiophores (Nie et al. 2020). Based on this synapomorphy and a re-examination of the protologue for *Conidiobolus* s.l. species (Drechsler 1953a, b, 1954, 1955a, 1957; Srinivasan and Thirumalachar 1967, 1968; Callaghan et al. 2000), seven species so far have been recombined into the monophyletic genus *Capillidium*, including: *Ca. adiaereturum* (Drechsler) B. Huang & Y. Nie, *Ca. bangalorensis* (Sriniv. & Thirum.) B. Huang & Y. Nie, *Ca. denaeosporum* (Drechsler) B. Huang & Y. Nie, *Ca. heterosporum* (Drechsler) B. Huang & Y. Nie, *Ca. lobatum* (Sriniv. & Thirum.) B. Huang & Y. Nie, *Ca. pumilum* (Drechsler) B. Huang & Y. Nie and *Ca. rhyosporum* (Drechsler) B. Huang & Y. Nie (Nie et al. 2020).

Although *Capillidium* is a small genus with only seven accepted species, it possesses high morphological diversity. For instance, primary conidia range from 18 µm (*Ca. pumilum*) to 46 µm (*Ca. adiaereturum*) in size (Drechsler 1953a, 1955a); resting spores are present in *Ca. adiaereturum*, *Ca. bangalorensis* and *Ca. rhyosporum*, but not in *Ca. denaeosporum*, *Ca. heterosporum*, *Ca. lobatum* and *Ca. pumilum* (Drechsler 1953b, 1955a, 1957); *Ca. heterosporum* has slender conidiophores that are branched at the base and end with 2–6 terminal capilliconidia each (Drechsler 1953b), whereas other members are unbranched and end with one capilliconidia (Nie et al. 2020); although nearly all *Capillidium* species only produce capilliconidia, *Ca. adiaereturum* also produces microconidia (Callaghan et al. 2000). These important diagnostic characteristics can help mycologists form a comprehensive understanding of this fungal group.

Two species *Ca. adiaereturum* and *Ca. heterosporum* have been identified in China (Wang et al. 2010; Nie et al. 2020). Continuing investigations into Chinese *Conidiobolus* s.l. led to the discovery of two new species in the genus *Capillidium*. We describe them herein, suggest a new combination for this genus and provide an updated identification key for the species of *Capillidium*.

Materials and methods

Isolates and morphology

Plant debris was collected from Wanfo Mountain, Shucheng County, Anhui Province, China and Laoshan National Forest Park and Tianwang Town, Jiangsu Province, China. Pre-sterilised plastic bags were used to pack these plant debris samples. Isolation procedures were the same as described by Drechsler (1952) and King (1976a). Plant debris samples were incubated on inverted Petri dishes containing PDA medium

(potato 200 g, dextrose 20 g, agar 20 g, H₂O, 1 litre) at 21 °C for 4 days. The incubated dishes were examined daily under a stereomicroscope (SMZ1500, Nikon Corporation, Japan). When an entomophthoroid fungus appeared, it was transferred to a clean PDA plate for purification and then sub-cultivated for morphological studies. Microscopic structure was observed under a light microscope (BX51, Olympus Corporation, Tokyo, Japan) and imaged using a microscope-camera system (DP25, Olympus Corporation, Tokyo, Japan). The size and shape of the primary conidia, primary conidiophores, secondary conidiophores, capilliconidia etc. were measured and described using the method by King (1976a) and the type of replicative conidia were observed on 2% water agar (agar 2 g, H₂O, 1 litre). All isolates were deposited at the Research Center for Entomogenous Fungi at Anhui Agricultural University, Anhui Province, China (RCEF) and duplicated at the China General Microbiological Culture Collection Center, Beijing, China (CGMCC). A total of 13 ex-types of *Conidiobolus* s.l. were acquired from the American Type Culture Collection, Manassas, VA, USA (ATCC).

DNA extraction, PCR amplification and sequencing

Total cellular DNA was extracted using the method by Watanabe et al. (2010). For phylogenetic analyses, three loci were amplified using relevant primer pairs: LR0R (5'-ACC CGC TGA ACT TAA GC-3') / LR5 (5'-TCC TGA GGG AAA CTT CG-3') for nucLSU (Vilgalys and Hester 1990), mtSSU1 (5'-GCW GCA GTG RGG AAT NTT GGR CAA T-3') / mtSSU2R (5'-GTR GAC TAM TSR GGT ATC TAA TC-3') for mtSSU (Zoller et al. 1999) and EF983 (5'-GCY CCY GGH CAY CGT GAY TTY AT-3') / EF1aZ-1R (5'-ACA TCW CCG ACA CCC TTG ATC TTG -3') for *EFL* (Nie et al. 2012).

PCR amplification was carried out in a 50 µl mixture containing 1 µl dNTPs (200 µM), 1 µl MgCl₂ (2.5 mM), 10 µl Phusion HF buffer (5×), 1 µl primers each (0.5 µM), 100 ng genomic DNA and 0.5 µl Taq polymerase (0.04 Unit/l, Super Pfx DNA Polymerase, Cowinbioscience Co. Ltd., Shanghai, China). PCR runs were conducted under the following conditions: an initial denaturation step at 94 °C for 3 min followed by 35 cycles of denaturation at 94 °C for 1 min, annealing at 55 / 54 / 57 °C (nucLSU / mtSSU / *EFL*), extension at 72 °C for 1 min; a final extension step at 72 °C for 7 min. DNA sequences were generated on both strands by performing dideoxy-nucleotide chain termination on an ABI 3700 automated sequencer at the Shanghai Genecore Biotechnologies Company (Shanghai, China). Sequences were processed with Geneious 9.0.2 (<http://www.geneious.com>, Kearse et al. 2012) and deposited in GenBank under the accession numbers listed in Table 1.

Phylogenetic analyses

The data for the three target loci (nucLSU, mtSSU and *EFL*) were produced during this study and during our previous study (Nie et al. 2020). Sequences were retrieved from GenBank and concatenated using SequenceMatrix 1.7.8 (Vaidya et al. 2011). For this analysis, fifteen species in four closely-related genera (*Azygosporus*, *Conidiobolus*

s.s., *Neoconidiobolus* and *Microconidiobolus*) served as outgroups (Table 1). Local alignment was conducted with MUSCLE 3.8.31 (Edgar 2004) and manually refined with BioEdit v. 7.2.6 (Hall 1999). The aligned sequence matrix was deposited in TreeBase (<https://treebase.org>) under the submission ID S29102.

Phylogenetic analyses were performed using three different methods: Maximum Likelihood (ML), Maximum Parsimony (MP) and Bayesian Inference (BI). For ML and BI analyses, best-fit substitution models for each locus were estimated in Modeltest 3.7 using the Akaike Information Criterion (AIC) value (Posada and Crandall 1998). The ML phylogenetic analysis was statistically tested in RAxML 8.1.17 with 1000 bootstrap replicates (Stamatakis 2014). The BI analysis was carried out in MrBayes v.3.1.2 using Markov Chain Monte Carlo (MCMC) methods (Ronquist and Huelsenbeck 2003). Beginning with random starting trees, four MCMC chains ran simultaneously for 1 million generations. The trees were sampled once every 100 generations. These chains stopped when all convergences met and the standard deviation fell below 0.01. MP analyses were conducted using a heuristic search in PAUP* 4.0b10 (Swofford 2002). Bootstrap analyses were conducted with 1000 bootstrap replicates to determine the confidence levels of the nodes within the inferred tree topologies (Felsenstein 1985). Tree bisection-reconnection (TBR) was selected for branch swapping. Phylogenetic trees were checked with FigTree 1.4 (Rambaut 2012) and further modified with iTOL (<https://itol.embl.de/>).

Results

Phylogenetic analyses

The concatenated alignment included 30 strains, 15 of which were outgroups from *Azygosporus*, *Conidiobolus* s.s., *Microconidiobolus* and *Neoconidiobolus* (Table 1). The aligned three-locus datasets contained 1861 characters. Amongst these, 852 characters were constant, 159 were parsimony-uninformative and 850 were parsimony informative. The most parsimonious tree had a tree length (TL) consisting of 3445 steps, a consistency index (CI) of 0.5068, a homoplasy index (HI) of 0.4932, a retention index (RI) of 0.7145 and a rescaled consistency index (RC) of 0.3621. The ML and BI analyses were performed using the best models for nucLSU (TiNef+G), *EFL* (TiMef) and mtSSU (K81) partitioning. The final average standard deviation of the split frequencies was 0.0059 and the final likelihood value was -17189. The tree topology from ML analysis was identical to those obtained from MP and BI analyses. The final ML tree was generated with bootstrap support values from MP/ML analyses, as well as posterior probability values from BI analysis at each branch.

The phylogeny revealed that three strains belong to the genus *Capillidium*. The strains CGMCC 3.16169 / RCEF 6332 and CGMCC 3016168 were grouped closely with *Ca. pumilum* / *Ca. globuliferus* (100/100/1.00) and *Ca. denaesporum* (100/100/1.00), respectively.

Table 1. The species used in phylogenetic analyses.

Species	Strains*	GenBank accession numbers			References
		nucLSU	EFL	mtSSU	
<i>Azygosporus macrocapillatus</i>	CGMCC 3.16068 (T)	MZ542006	MZ555650	MZ542279	Cai et al. (2021)
<i>A. parvus</i>	ATCC 14634 (T)	KX752051	KY402207	MK301192	Cai et al. (2021)
<i>Capillidium adiaereturum</i>	ARSEF 451 (T)	KC461182	–	–	GenBank
<i>Ca. adiaereturum</i>	CGMCC 3.15888	MN061284	MN061481	MN061287	Nie et al. (2020)
<i>Ca. bangalorensis</i>	ARSEF 449 (T)	DQ364204	–	DQ364225	Chen and Huang (2018)
<i>Ca. denaesporum</i>	ATCC 12940 (T)	JF816215	JF816228	MK301181	Nie et al. (2012, 2020)
<i>Ca. globuliferum</i>	CBS 152.56 (T)	MH869095	–	–	Vu et al. (2019)
<i>Ca. heterosporum</i>	CBS 543.63	MH869973	–	–	Vu et al. (2019)
<i>Ca. heterosporum</i>	RCEF 4430	JF816225	JF816239	MK301183	Nie et al. (2012, 2020)
<i>Ca. lobatum</i>	ATCC 18153 (T)	JF816218	JF816233	MK301187	Nie et al. (2012, 2020)
<i>Ca. pumilum</i>	ARSEF 453 (T)	EF392383	–	EF392496	GenBank
<i>Ca. rhyosporum</i>	ATCC 12588 (T)	JN131540	JN131546	MK301195	Nie et al. (2018, 2020)
<i>Ca. rhyosporum</i>	CBS 141.57	MH869215	–	–	Vu et al. (2019)
<i>Ca. rugosum</i>	CBS 158.56 (T)	MH869097	–	–	Vu et al. (2019)
<i>Ca. marcocapilliconidium</i>	CGMCC 3.16169 (T)	OL830454	OL801337	OL830457	This article
<i>Ca. marcocapilliconidium</i>	RCEF 6332	OL830455	OL801338	OL830458	This article
<i>Ca. jiangsuense</i>	CGMCC 3.16168 (T)	OL830456	OL801339	OL830459	This article
<i>Conidiobolus coronatus</i>	NRRL 28638	AY546691	DQ275337	–	Lutzoni et al. (2004)
<i>C. humicolus</i>	ATCC 28849 (T)	JF816220	JF816231	MK301184	Nie et al. (2012, 2020)
<i>C. khandalensis</i>	ATCC 15162 (T)	KX686994	KY402204	MK301185	Nie et al. (2012, 2020)
<i>C. lichenicolus</i>	ATCC 16200 (T)	JF816216	JF816232	MK301186	Nie et al. (2012, 2020)
<i>C. polytocus</i>	ATCC 12244 (T)	JF816213	JF816227	MK301194	Nie et al. (2012, 2020)
<i>Microconidiobolus nodosus</i>	ATCC 16577 (T)	JF816217	JF816235	MK333388	Nie et al. (2012, 2020)
<i>M. paulus</i>	ARSEF 450 (T)	KC788409	–	–	Gryganskyi et al. (2013)
<i>M. terrestris</i>	ATCC 16198 (T)	KX752050	KY402208	MK301199	Nie et al. (2016, 2020)
<i>Neoconidiobolus couchii</i>	ATCC 18152 (T)	JN131538	JN131544	MK301179	Nie et al. (2016, 2020)
<i>N. mirabilis</i>	CGMCC 3.17763 (T)	MH282852	MH282853	MK333389	Nie et al. (2018, 2020)
<i>N. pachyzygosporus</i>	CGMCC 3.17764 (T)	KP218521	KP218524	MK333390	Nie et al. (2018, 2020)
<i>N. stromoideus</i>	ATCC 15430 (T)	JF816219	JF816229	MK301198	Nie et al. (2012, 2020)
<i>N. thromboides</i>	ATCC 12587 (T)	JF816214	JF816230	MK301200	Nie et al. (2012, 2020)

*ARSEF, ARS Entomopathogenic Fungus Collection (Ithaca, U.S.A.). ATCC, American Type Culture Collection (Manassas, U.S.A.). CBS, Westerdijk Fungal Biodiversity Institute (Utrecht, The Netherlands). CGMCC, China General Microbiological Culture Collection Center (Beijing, China). NRRL, ARS Culture Collection (Peoria, U.S.A.). RCEF, Research Center for Entomogenous Fungi (Hefei, China). T = ex-type.

Taxonomy

Capillidium macrocapilliconidium B. Huang & Y. Nie, sp. nov.

Mycobank No: 842227

Fig. 2

Etymology. *macrocapilliconidium* (Lat.), referring to the large size of its capilliconidia.

Known distribution. Jiangsu Province, China.

Typification. CHINA, Jiangsu Province, Nanjing City, Laoshan National Forest Park, 32°5'52"N, 118°35'37"E, from plant debris, 1 Dec 2018, *Y. Nie and Y. Gao*, culture ex-holotype CGMCC 3.16169 (=RCEF 6553).

Additional specimens examined. CHINA, Anhui Province, Shucheng County, Wanfo Mountain, 31°9'51"N, 116°57'86"E, from plant debris, 13 Mar 2016, X.X. Tang, culture RCEF 6332. GenBank: nrLSU = OL830455; *EFL* = OL801338; mtSSU = OL830458.

Description. Colonies on PDA at 21 °C after 3 d white, reaching ca. 28 mm in diameter, yellowish after 10 d. Mycelia hyaline, 5.5–10 µm wide, often branched. Primary conidiophores arising from hyphal segments, hyaline, 70–250 × 5–13 µm, unbranched and producing a single globose primary conidium, widening upwards near the tip. Primary conidia forcibly discharged, globose to subglobose, 25–34 × 20–28 µm, papillate or conical, 7–10 µm wide, 3–8 µm long. Secondary conidiophores short or long, arising from primary conidia, bearing a single replicative conidium similar to, but smaller than those primary ones and forcibly discharged, producing another kind of replicative conidia called capillidiconidia from slender secondary conidiophores on the 2% water agar. Capillidiconidia

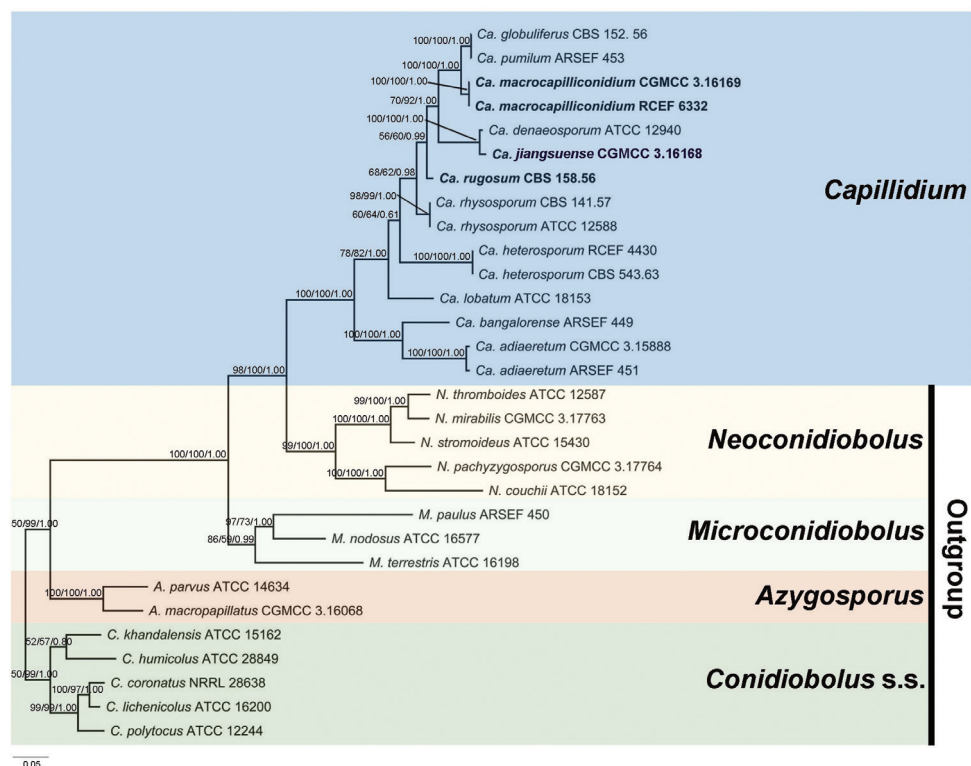


Figure 1. The phylogenetic tree of *Capillidium* constructed using Maximum Likelihood analyses on nucLSU, *EFL* and mtSSU sequences. *Conidiobolus* s.l. species were used as outgroups. New taxa are indicated by bold text. Maximum Parsimony bootstrap values ($\geq 50\%$) / Maximum Likelihood bootstrap values ($\geq 50\%$) / Bayesian posterior probabilities (≥ 0.50) of clades are provided alongside the branches. The scale bar at the lower left indicates substitutions per site.

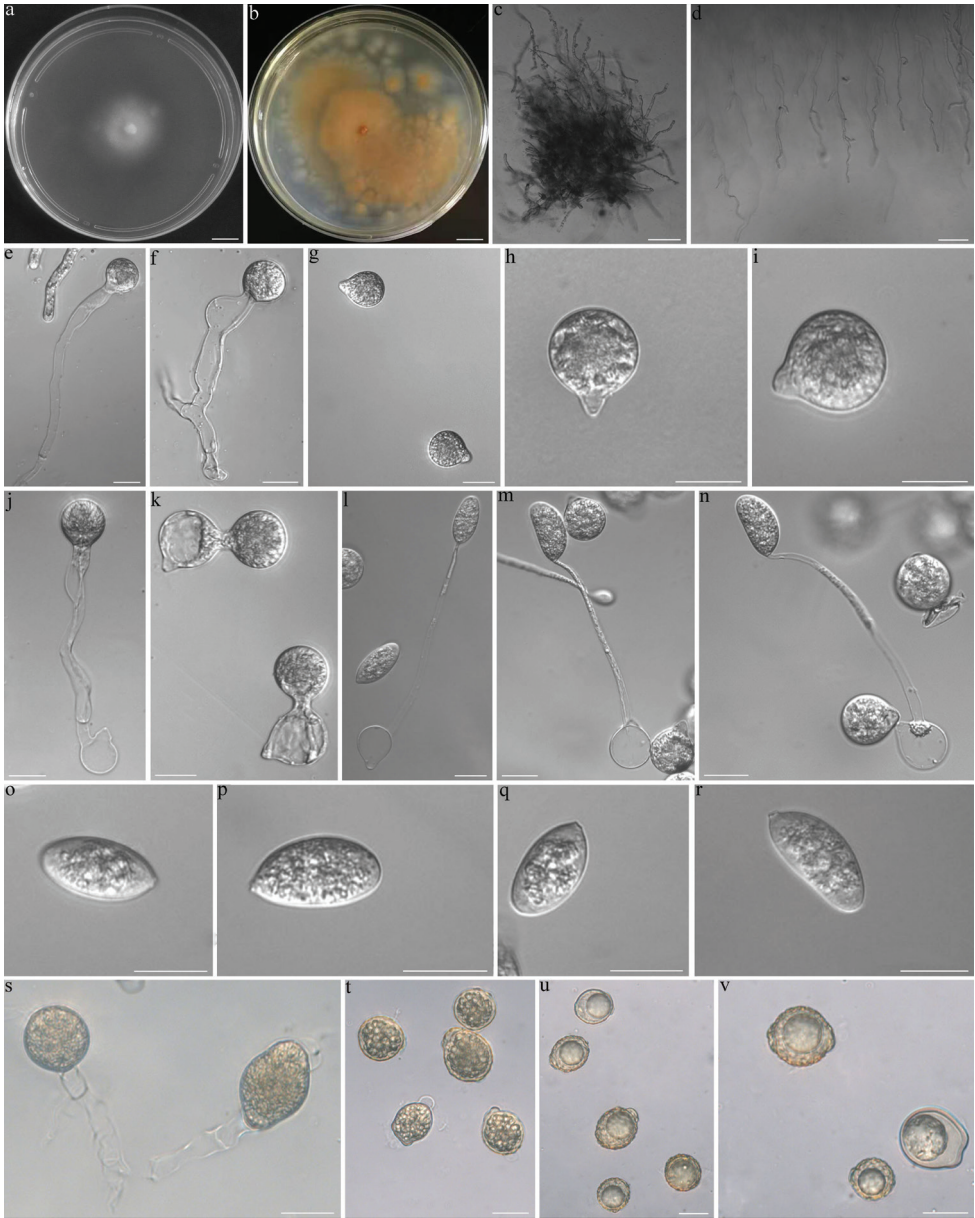


Figure 2. *Capillidium macrocapilliconidium* **a** colony on PDA after 3 d at 21 °C **b** colony on PDA after 10 d at 21 °C **c** Mycelia **d** Mycelia unbranched at the edge of the colony **e, f** primary conidiophores bearing primary conidia **g, h, i** primary conidia **j, k** primary conidia bearing a single secondary conidium **i, m, n** a primary conidium bearing a single capilliconidium **o, p, q, r** Capilliconidia **s** zygospores that were formed on adjacent segments of the same hypha **t** immature zygospores **u, v** mature zygospores. Scale bars: 10 mm (**a–b**); 100 µm (**c–d**); 20 µm (**e–v**).

colourless, elongate ellipsoidal, 25–37 μm long, 14–17 μm wide. Slender secondary conidiophores unbranched, 85–130 μm long, 4–6 μm wide at the base, tapering gradually to a width of 1–2 μm at the tip. Zygospores usually formed between adjacent segments of the same hypha after 10 d, yellowish, mostly boldly wrinkled, sometimes smooth, globose, elongate ellipsoidal or irregular, 18–35 μm long, 17–28 μm wide, with a wall 1–2 μm thick.

Notes. *Capillidium macrocapilliconidium* is characterised by having larger capilliconidia compared to other *Capillidium* species. It produces yellowish and wrinkled zygospores like *Ca. rhysosporum* (Drechsler 1954). However, *Ca. macrocapilliconidium* has larger capilliconidia than *Ca. rhysosporum* (25–37 \times 14–17 μm in *Ca. macrocapilliconidium* vs. 12–32 \times 6.5–16 μm in *Ca. rhysosporum*). *Ca. macrocapilliconidium* is phylogenetically distant from *Ca. rhysosporum* (Fig. 1) and most closely related to *Ca. pumilum*. It is distinguished from *Ca. pumilum* by larger primary conidia (25–34 \times 20–28 μm in *Ca. macrocapilliconidium* vs. 9–18 \times 7.3–14 μm in *Ca. pumilum*) and capilliconidia (25–37 \times 14–17 μm in *Ca. macrocapilliconidium* vs. 8.8–12 \times 5–7.5 μm in *Ca. pumilum*) (Drechsler 1955b).

***Capillidium jiangsuense* B. Huang & Y. Nie, sp. nov.**

MycoBank No: 842228

Fig. 3

Etymology. *jiangsuense* (Lat.), referring to the region where the fungus was isolated.

Known distribution. Jiangsu Province, China.

Typification. CHINA, Jiangsu Province, Jurong City, Tianwang Town, 31°6'94"N, 119°26'91"E, from plant debris, 25 Mar 2018, *Y. Nie*, culture ex-holotype CGMCC 3.16168 (=RCEF 6545).

Description. Colonies on PDA at 21 °C after 3 d white, reaching ca. 21 mm in diameter. Mycelia haline, often unbranched, vegetative hyphae filamentous, 5–10 μm wide. Primary conidiophores unbranched, producing a single primary conidium, widening upwards near the tip, 50–240 \times 6–10 μm . Primary conidia forcibly discharged, subglobose to turbinate, 21–31 \times 12–29 μm . Papilla 4–10 μm wide, 2–4 μm long. Replicative conidia two kinds on 2% water agar, arising from primary conidia, one similar and smaller to the primary conidia, the other elongate and passively detached, 17–32 \times 10–15 μm . Slender secondary conidiophores unbranched, 65–120 μm long, 2.5–3 μm wide at the base, tapering gradually to a width of 1 μm at the tip. Resting spore not observed.

Notes. Morphologically, the present isolate resembles *Ca. denaeosporum* because of the size of its primary conidia (13–32 \times 6–21 μm in *Ca. denaeosporum* vs. 21–31 \times 12–29 μm in *Ca. jiangsuense*) (Drechsler 1957). However, *Ca. denaeosporum* has larger capilliconidia (10–18 \times 6–10 μm in *Ca. denaeosporum* vs. 17–32 \times 10–15 μm in *Ca. jiangsuense*) and longer, more slender secondary conidiophores (35–65 μm in

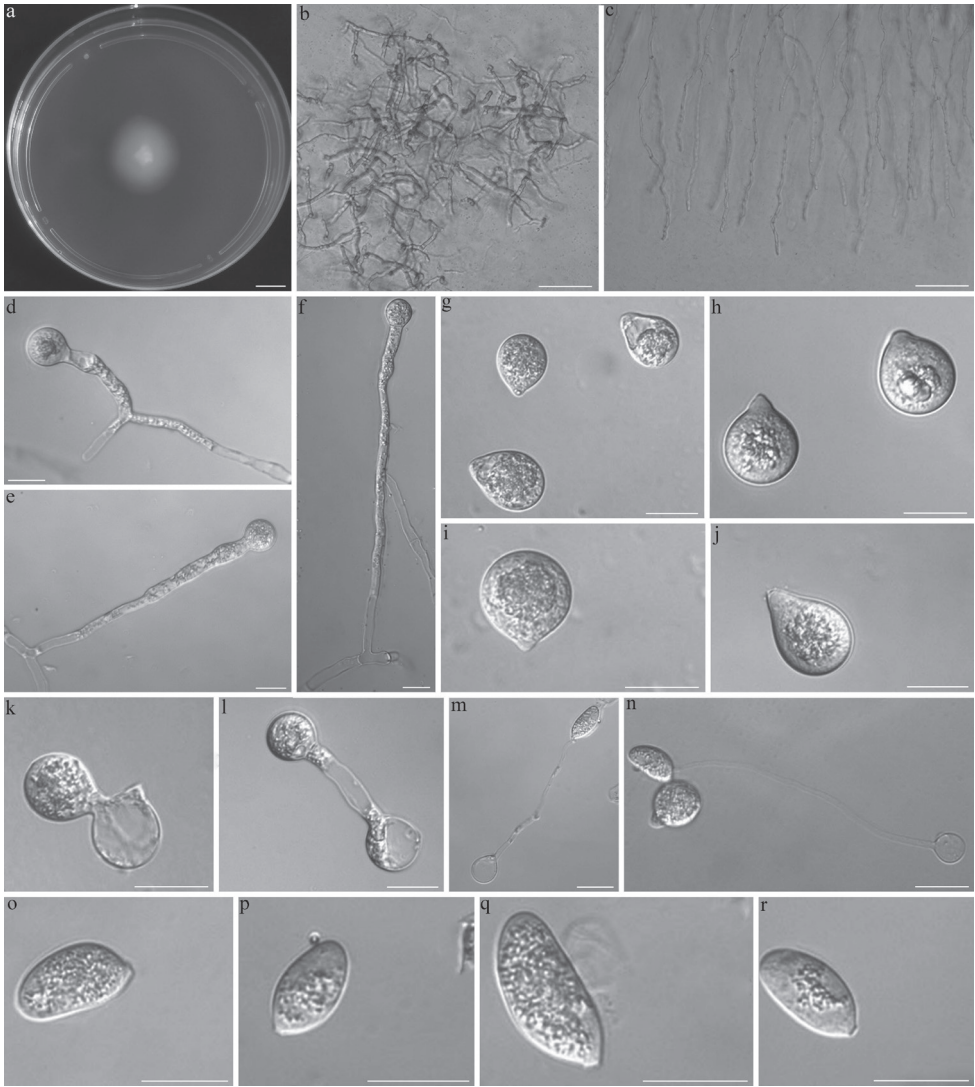


Figure 3. *Capillidium jiangsuense* **a** colony on PDA after 3 d at 21 °C **b** Mycelia **c** Mycelia unbranched at the edge of the colony **d, e, f** primary conidiophores arising from mycelia segments **g, h, i, j** primary conidia **k, l** secondary conidia arising from primary conidia **m, n** primary conidia bearing a single capilliconidium **o, p, q, r** Capilliconidia. Scale bars: 10 mm (**a**); 100 µm (**b, c**); 20 µm (**d–r**).

Ca. denaeosporum vs. 65–120 µm in *Ca. jiangsuense*) (Drechsler 1957). Although they grouped together with relatively little divergence on the phylogram, DNA similarity levels between the two species are only around 97.9% (nucLSU) (Nie et al. 2012). This evidence supports the present isolate being a new species, which we have named *Capillidium jiangsuense* sp. nov.

***Capillidium rugosum* (Drechsler) B. Huang & Y. Nie, comb. nov.**

MycoBank No: 842229

Basionym. *Conidiobolus rugosus* Drechsler, Am. J. Bot. 42: 437 (1955).**Description.** Refer to Drechsler (1955a).**Notes.** The ex-type living culture is ATCC 12586 (United States, New Jersey, Moorestown, 25 February 1954, Drechsler). Historically, *Conidiobolus rugosus* was synonymised with *Co. heterosporus* (King 1976b). However, we have re-established its taxonomic status at the species level, based on the phylogeny herein and the morphological traits of the capilliconidia.**Discussion**

From the 1950s–1970s, a total of eight *Conidiobolus* species have been reported to produce capilliconidia, including *Conidiobolus denaeosporus*, *Co. globuliferus*, *Co. heterosporus*, *Co. inordinatus*, *Co. lobatus*, *Co. pumilus*, *Co. rhyosporus* and *Co. rugosus* (Drechsler 1953a, b, 1954, 1955a, b, 1956, 1957; Srinivasan and Thirumalachar 1968). Based on the numerical taxonomy of *Conidiobolus* (King 1976a, b, 1977), four species were rejected. *Co. rugosus* was considered synonymous with *C. heterosporus*. On the other hand, *Conidiobolus denaeosporus*, *Co. globuliferus* and *Co. inordinatus* were considered synonymous with *Co. pumilus*. Consequently, only four species forming capilliconidia were accepted into this genus. Based on this synapomorphy, the subgenus *Capillidium* was erected in the latter taxonomic study of *Conidiobolus* (Ben-Ze'ev and Kenneth 1982; Humber 1989). Interestingly, it appears that *Co. adiaeretus* and *Co. bangalorensis* develop both microconidia and capilliconidia (Callaghan et al. 2000). Unfortunately, there was no molecular evidence at the time to support these morphological results. Recently, we summarised molecular data from available *Conidiobolus* s.l. ex-types and identified a monophyletic lineage of *Capillidium* producing capilliconidia. Since then, some taxonomic revisions have been conducted. For example, *Co. denaeosporus* was separated from *Co. pumilus* and recombined into *Capillidium*. *Co. adiaeretus* and *Co. bangalorensis* were also recombined into *Capillidium*. In total, *Capillidium* now has seven accepted species.

Conidiobolus heterosporus (= *Capillidium heterosporum*) and *Co. rugosus* share distinct morphological characteristics. For instance, *Co. heterosporus* bears no resting spores and has conidiophores that are often branched at the base and bear 2–6 terminal capilliconidia (Drechsler 1953a). The conidiophores of *Co. rugosus*, though, have yellowish zygo-spores with wrinkled or smooth surfaces, are unbranched and bear a single capillicondium (Drechsler 1955b).

Based on a phylogenetic analysis of three gene regions (nucLSU, mtSSU and *EFL*), the ex-type of *Co. rugosus* (Strain No: CBS 158.56) and *Co. heterosporus* diverged into two distinct lineages. Consequently, we identified *Co. rugosus* as an independent species and recombined it into *Capillidium* as a new combination: *Capillidium rugosum*

(Drechsler) B. Huang & Y. Nie comb. nov. On a side note, while researchers previously considered *Co. denaeosporus* (= *Ca. denaeosporum*), *Co. globuliferus* and *Co. inordinatus* to be synonymous with *Co. pumilus* (= *Ca. pumilum*) (King 1976b), the present phylogeny confirmed that *Co. denaeosporus* (= *Ca. denaeosporum*) is an independent species and *Co. globuliferus* is synonymous with *Co. pumilus* (= *Ca. pumilum*). More molecular evidence is needed to clarify the taxonomic status of *Co. inordinatus*.

Capillidium bangaloreense may be another *Capillidium* species that forms microspores, based on its close phylogenetic relationship with *Ca. adiaeretum*. Besides microspores, these two species possess another morphological characteristic that is distinctive compared with the other members of *Capillidium*, that being the width between the primary conidiophores and the hyphae (Drechsler 1955a; Srinivasan and Thirumalachar 1967). This could explain why *Ca. adiaeretum* and *Ca. bangaloreense* are grouped into a single clade in the phylogenetic tree (Fig. 1). However, *Ca. bangaloreense* should be re-examined and more evidence should be supplied to confirm that this clade is in a separate taxon.

With the current description of *Azygosporus*, most members of *Conidiobolus* s.l. have now received suitable taxonomic placements. Yet, there are still many other taxonomic challenges to be resolved in the future, such as replacing the missing ex-type *Co. utriculosus* and assigning *Co. coronatus* as the epitype of *Conidiobolus* s.s., isolating lost ex-types to confirm their taxonomic placements etc. (Nie et al. 2018, 2020, 2021; Cai et al. 2021). For the first time, this study used partial sequence data from nucLSU, mtSSU and *EFL* genes to identify two new species of *Capillidium* from China, increasing the total number of species in the genus to ten. A key to the species of *Capillidium* is provided below.

Key to the Species of *Capillidium*

- 1 Capilliconidia and microconidia produced, the width of primary conidiophores offers a pronounced dimensional contrast with the mycelial filaments **2**
- Only capilliconidia produced, the width of primary conidiophores offers a similar dimensional contrast with the mycelial **3**
- 2 Primary conidia larger, up to 46 µm, chlamydospores produced ***Ca. adiaeretum***
- Primary conidia smaller, less than 25 µm, zygosporangia produced ***Ca. bangaloreense***
- 3 Slender conidiophores branched at the base, bearing 2–6 terminal capilliconidia ***Ca. heterosporum***
- Slender conidiophores unbranched at the base, bearing a single capilliconidia **4**
- 4 Resting spores of zygosporangia produced, yellowish, mostly wrinkled, sometimes smooth **5**
- Resting spores not observed **6**

5	Primary conidia and zygospores larger, more than 30 µm	7
–	Primary conidia and zygospores smaller, less than 25 µm	
 <i>Ca. rugosum</i> comb. nov.	
6	Primary conidia larger, more than 30 µm	8
–	Primary conidia smaller, less than 26 µm	9
7	Capilliconidia larger, up to 37 µm	<i>Ca. macrocapilliconidium</i> sp. nov.
–	Capilliconidia smaller, less than 32 µm	<i>Ca. rhyosporum</i>
8	Capilliconidia larger, 17–32 × 10–15 µm, primary conidiophores longer, 50–240 µm	<i>Ca. jiangsuense</i> sp. nov.
–	Capilliconidia smaller, 10–18 × 6–10 µm, primary conidiophores shorter, 15–50 µm	<i>Ca. denaeosporum</i>
9	Primary conidia larger, 21–26 × 20–24 µm, capilliconidia larger, 18–25 × 8–10 µm	<i>Ca. lobatum</i>
–	Primary conidia smaller, 9–18 × 7.3–14 µm, capilliconidia smaller, 8.8–12 × 5–7.5 µm	<i>Ca. pumilum</i>

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Two new species of *Boletopsis* (Bankeraceae, Thelephorales) from Southwest China

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Abstract

Two new species of *Boletopsis*, *B. macrocarpa* and *B. tibetana*, are described and illustrated from Southwest (SW) China based on morphology, ecology and phylogenetic analyses by the internal transcribed spacer regions (ITS) and the large subunit of nuclear ribosomal RNA gene (nLSU). *Boletopsis macrocarpa* is characterized by big basidiocarps (up to 18 cm in diam), guttulate basidiospores, and the presence of gloeoplerous hyphae in context and growing in pure forest of *Pinus yunnanensis*. *Boletopsis tibetana* is characterized by smaller pores (3–4 per mm), the presence of gloeoplerous hyphae in pileipellis, and the growth in forests of *Picea*. Phylogenetically, the two new species are grouped in two independent lineages nested in *Boletopsis*. In addition, one sample from Northeast China is temporarily treated as *Boletopsis* sp. 1 because of the single sample; another Chinese sample from SW China is sister to *B. grisea* in phylogeny, and it is treated as *B. cf. grisea* because the morphological difference between *B. cf. grisea* and *B. grisea* is indistinct. Furthermore, the main characteristics of *Boletopsis* species are listed, and a key to accepted species of *Boletopsis* is provided.

Keywords

Ectomycorrhizal fungi, phylogeny, taxonomy

Introduction

Boletopsis Fayod was established by Fayod based on *B. leucomelaena* (Pers.) Fayod originally described from Europe (Niemela and Saarenoksa 1989) and is characterized by annual basidiocarps with poroid hymenophore and central to lateral stipes,

generative hyphae with clamp connections, and angular to tubercular, hyaline to pale brownish basidiospores which are negative in Melzer's reagent (Ryvarden and Melo 2017). Previously, seven species, *B. grisea* (Peck) Bondartsev & Singer, *B. leucomelaena*, *B. mediterraneensis* G. Moreno et al., *B. watlingii* Blanco-Dios (= *B. perplexa* Watling & Jer. Milne, Nom. inval., Blanco-Dios 2018), *B. smithii* K.A. Harrison, *B. nothofagi* J.A. Cooper & P. Leonard and *B. atrata* Ryvarden, were accepted in the genus, and the first four species have a distribution in Europe (Ryvarden and Melo 2017), *B. grisea*, *B. watlingii* and *B. smithii* occur in North America (Watling and Milne 2008), and *B. nothofagi* and *B. atrata* were described from New Zealand and Thailand, respectively (Hjortstam and Ryvarden 1982; Cooper and Leonard 2012). Five of these seven species were analyzed by molecular techniques (Watling and Milne 2008; Cooper and Leonard 2012; Crous et al. 2019). In addition, *Boletopsis subsquamosa* (L.) Kotl. & Pouzar and *B. subcitrina* Corner were recorded in *Boletopsis* (Kotlába and Pouzar 1957; Corner 1989), but the former was considered as a synonym of *Albatrellus ovinus* (Schaeff.) Kotl. & Pouzar (Donk 1974; Ryvarden and Gilbertson 1993), and the latter was treated as *Cornerporus subcitrinus* (Corner) T. Hatt. (Hattori 2001).

Boletopsis is the ectomycorrhizal fungal genus in the family Bankeraceae, phylogenetically, *Boletopsis* is sister to *Hydnellum* P. Karst. and *Sarcodon* Qué. ex P. Karst (Cooper and Leonard 2012; Mu et al. 2021; Crous et al. 2019). Morphologically, *Boletopsis* is distinguished from other genera in the family by poroid hymenophore.

Species of *Boletopsis* are edible mushrooms in SW China, and they are sold in the local markets as "black bear's-paw fungi", but their scientific names are unknown. During an investigation on forest macrofungi in China, sampling efforts of *Boletopsis* were especially focused on, and the ecology of these samples was recorded. The aim of this study is to clarify the species of *Boletopsis* in China and to expound phylogenetic relationships among members in the genus.

Materials and methods

Molecular phylogenetic studies

Eleven samples of *Boletopsis* were collected from Liaoning Province, Xizang Autonomous Region (Tibet) and Yunnan Province in China and deposited in the Herbarium of the Institute of Microbiology, Beijing Forestry University (BJFC). Potential host trees of *Boletopsis* spp. were observed from field trips. The macro-morphology was based on fresh and dried specimens. The color terms in descriptions followed Anonymous (1969) and Petersen (1996). Micro-morphology was studied at magnifications 1000×, using a Nikon Eclipse 80i microscope with phase contrast illumination. The Melzer's reagent, Cotton Blue and 5% KOH were used in the study. Drawings were made with the aid of a drawing tube. In the text the following abbreviations were used: IKI = Melzer's reagent, IKI– = non-dextrinoid and non-amyloid, KOH = 5% potassium hydroxide, CB = Cotton Blue, CB– = acyanophilous, L = mean basidiospores length (arithmetic average of all basidiospores), W = mean

basidiospores width (arithmetic average of all basidiospores), Q = variation in the L/W ratios between the specimens studied, n = number of basidiospores measured from number of specimens.

DNA extraction and amplification

A cetyltrimethyl ammonium bromide (CTAB) rapid plant genome extraction kit (Aidlab Biotechnologies Co. Ltd., Beijing, China) was used to extract DNA from dried specimens following the manufacturer's instructions with some modifications (Chen et al. 2015, 2016). PCR reactions were performed in the 0.2 mL tubes, along with 1 μ L DNA, 29 μ L specified primers. The ITS primers pairs were ITS5 and ITS4 (White et al. 1990); the nLSU primers pairs was LR0R and LR7 (Vilgalys and Hester 1990). The optimal annealing temperature and cycles were generated as: an initial denaturation at 95 °C for 3 min, followed by 34 cycles at 94 °C for 40 s, annealing at 54 °C (sometimes at 56 °C) and extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR procedure for nLSU was: initial denaturation at 94 °C for 1 min, followed by 34 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 1 min and extension at 72 °C for 1.5 min, and a final extension at 72 °C for 10 min.

Phylogenetic analyses

Fifty-three sequences used in phylogenetic analyses are listed in Table 1, including 24 sequences generated by this study and another 29 downloaded from the National Center for Biotechnology Information (NCBI) which mainly adapted from Cooper and Leonard (2012) and Crous et al. (2019). *Sarcodon imbricatus* (L.) P. Karst. was used as outgroup (Crous et al. 2019).

Raw chromatograms were aligned and edited using BioEdit Sequence Alignment Editor (Hall 1999), especially those chromatograms with double peaks at the start and the end of sequences. The ITS and nLSU sequences were aligned using MAFFT 7 online (<https://mafft.cbrc.jp/alignment/server/>), and applying the interactive refinement method of G-INS-I (Katoh and Standley 2013). For aligned sequences, the ambiguous regions at the start and the end were deleted. Sequence alignment was deposited at TreeBASE (<http://purl.org/phylo/treebase/>; submission ID 29052).

The Maximum likelihood (ML) and Bayesian inference (BI) methods were used to conduct phylogenetic trees with ITS + nLSU matrix. The best-fit model was selected by ModelFinder (Kalyaanamoorthy et al. 2017), adopting Akaike information criterion (AIC). The model GTR + F + I + G4 was selected as the best-fit model for the ITS + nLSU matrix, $\text{lset nst} = 6$, $\text{rates} = \text{invgamma}$ in Bayesian analysis. ML analysis was constructed by RaxmlGUI 1.2 (Stamatakis 2006). We performed default parameters in the ML analysis. A Bayesian tree was produced by MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) using the same model as ML analysis. Four Markov chains were run for 2 million generations for the analysis. Trees were sampled every 1000th generation. The first 25% of sampled trees were discarded as burn-in, whereas others were used to construct a 50% majority consensus tree and for calculating Bayesian posterior probabilities (BPPs).

Table 1. Information on the sequences used in this study.

Species	Sample	Location	Hosts	GenBank Accession No.	
				ITS	nLSU
<i>Boletopsis grisea</i>	UPS F-120382	Sweden	<i>Pinus sylvestris</i>	MN536751	MN535646
<i>Boletopsis grisea</i>	UPS F-153996	Sweden	<i>Pinus sylvestris</i>	MN536742	MN535641
<i>Boletopsis grisea</i>	AB 16-09-113	France	<i>Abies alba</i>	MN536743	–
<i>Boletopsis grisea</i>	AB 17-09-52	France	<i>Abies alba</i>	MN536744	–
<i>Boletopsis grisea</i>	AH 42971	Spain	<i>Pinus pinea</i>	MN536747	MN535642
<i>Boletopsis grisea</i>	AH 44091	Spain	<i>Pinus pinaster</i>	MN536748	MN535643
<i>Boletopsis grisea</i>	Rec 227658	USA	<i>Tsuga canadensis</i>	EF457899	–
<i>Boletopsis grisea</i>	Rec 227659	USA	<i>Pinus sylvestris</i>	EF457902	–
<i>Boletopsis</i> cf. <i>grisea</i>	Dai 23070	China	<i>Pinus</i> , <i>Quercus</i>	OL673003	OL672990
<i>Boletopsis leucomelaena</i>	UPS F-173290	Sweden	<i>Picea abies</i>	MN536739	MN535638
<i>Boletopsis leucomelaena</i>	UPS F-575617	Sweden	<i>Picea</i> , <i>Populus</i>	MN536740	MN535639
<i>Boletopsis macrocarpa</i>	Dai 21780	China	<i>Pinus yunnanensis</i>	OL673004	OL672991
<i>Boletopsis macrocarpa</i>	Dai 22727	China	<i>Pinus yunnanensis</i>	OL673007	OL672994
<i>Boletopsis macrocarpa</i>	Dai 22728	China	<i>Pinus yunnanensis</i>	OL673005	OL672992
<i>Boletopsis macrocarpa</i>	Dai 22729	China	<i>Pinus yunnanensis</i>	OL673006	OL672993
<i>Boletopsis macrocarpa</i>	Dai 22748	China	<i>Pinus yunnanensis</i>	OL673008	OL672995
<i>Boletopsis macrocarpa</i>	Dai 23064	China	<i>Pinus yunnanensis</i>	OL673009	OL672996
<i>Boletopsis macrocarpa</i>	Dai 23065	China	<i>Pinus yunnanensis</i>	OL673010	OL672997
<i>Boletopsis mediterraneensis</i>	AB 06-10-343	France	<i>Cedrus atlantica</i>	MN536717	–
<i>Boletopsis mediterraneensis</i>	AB 15-11-97	France	<i>Cedrus atlantica</i>	MN536736	–
<i>Boletopsis mediterraneensis</i>	AH 44070	Spain	<i>Pinus nigra</i>	MN536724	MN535630
<i>Boletopsis mediterraneensis</i>	AH 44080	Spain	<i>Pinus</i>	MN536723	MN535629
<i>Boletopsis mediterraneensis</i>	FR 2016250	France	<i>Pinus halepensis</i>	MN536726	–
<i>Boletopsis mediterraneensis</i>	ML 410112B	Cyprus	<i>Pinus nigra</i>	MN536719	–
<i>Boletopsis nothofagi</i>	PDD 96007	New Zealand	<i>Nothofagus fusca</i>	JQ417193	–
<i>Boletopsis</i> sp. 1	Dai 22172	China	<i>Pinus</i>	OL673011	OL672998
<i>Boletopsis tibetana</i>	Dai 20896	China	<i>Picea balfouriana</i>	OL673012	OL672999
<i>Boletopsis tibetana</i>	Dai 20897	China	<i>Picea balfouriana</i>	OL673013	OL673000
<i>Boletopsis watlingii</i>	Holden E150627 (E)	UK	<i>Pinus sylvestris</i>	DQ408766	–
<i>Boletopsis watlingii</i>	Wat. 28788 (E)	UK	<i>Pinus sylvestris</i>	DQ408767	–
<i>Boletopsis watlingii</i>	SMI 350	Canada	Unknown	FJ845401	–
<i>Sarcodon imbricatus</i>	Dai 20314	China	Unknown	OL676807	OL678542
<i>Sarcodon imbricatus</i>	NIFoS 1676	–	Unknown	MF421106	–

New sequences are shown in bold.

Results

Molecular phylogeny

A total of 33 ITS and 20 nLSU sequences were used in the phylogenetic analyses. The Bayes analysis and Maximum likelihood analysis resulted in a similar topology with an average standard deviation of split frequencies = 0.006494. All samples of *Boletopsis* form a monophyletic clade. Among the Chinese materials, the specimen Dai 23070 is sister to *B. grisea* samples from Europe and North America with a stable support (100/1). The specimen Dai 22172 has singleton position as a lineage, specimens Dai 20896 & 20897 and Dai 21780, 22727, 22728, 22729, 22748, 23064 & 23065 are

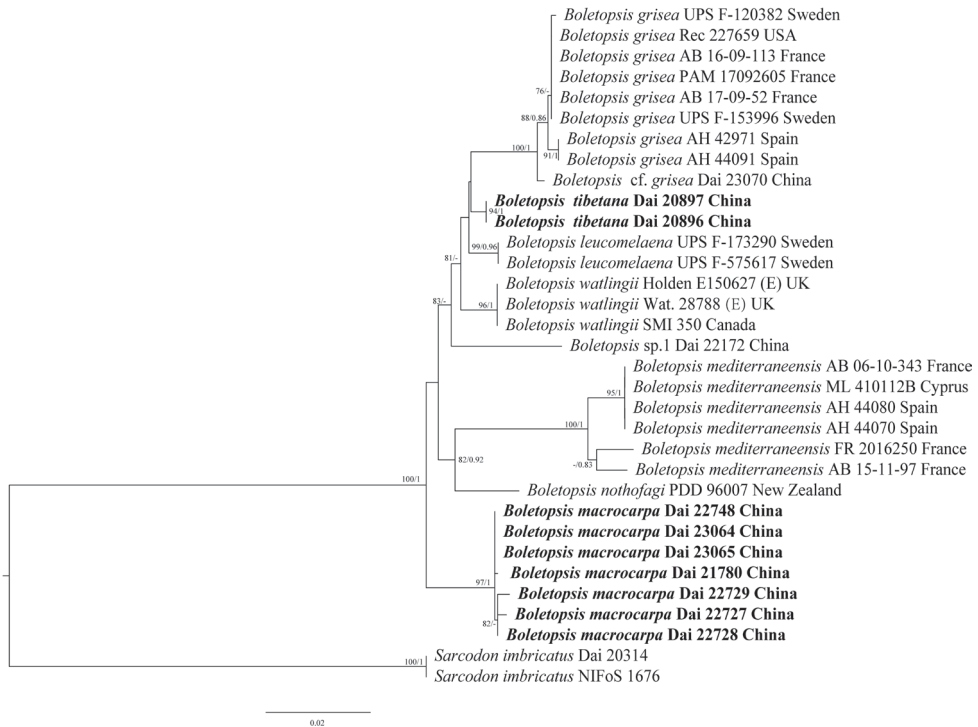


Figure 1. Phylogeny of species in *Boletopsis* generated by maximum likelihood based on ITS + nLSU sequence data. Branches are labeled with maximum likelihood bootstrap $\geq 75\%$ and Bayesian posterior probabilities ≥ 0.80 , respectively. New species are in bold.

grouped respectively in two lineages with high support (97/1, 94/1). So, two species are described from nine specimens grouped in two independent lineages nested in *Boletopsis* clade, and specimens Dai 23070 and Dai 22172 are treated as *Boletopsis* cf. *grisea* and *Boletopsis* sp. 1, respectively (Fig. 1).

Taxonomy

Boletopsis macrocarpa Y.C. Dai, F. Wu & H.M. Zhou, sp. nov.

Mycobank No: 843792

Figs 2A, 3

Diagnosis. Differs from other *Boletopsis* species by largest basidiocarps (up to 18 cm in diam) with grayish brown to dark gray upper surface, gloeoplerous hyphae present in context, guttulate basidiospores, and the fact that it grows in forests of *Pinus yunnanensis* at high altitude with open and slightly dry environments in SW China.

Holotype. CHINA, Yunnan Province, Nujiang, Lanping County, Xinchengqiao National Forest Park, on ground in forest of *Pinus yunnanensis*, alt. 3000 m, 2 September 2021, Dai 22728 (BJFC037301).

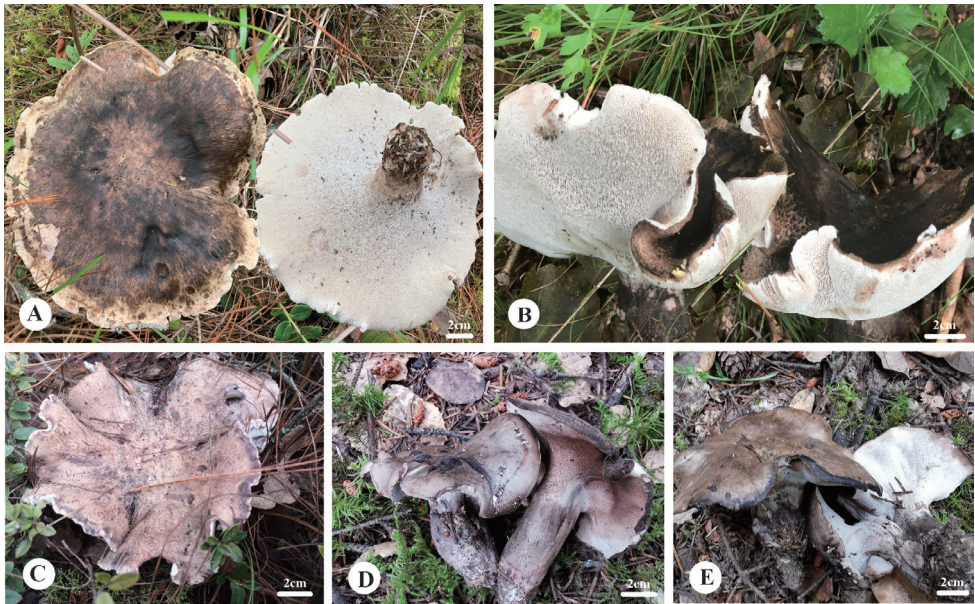


Figure 2. Basidiocarps of *Boletopsis* in China **A** *B. macrocarpa* (Dai 22728) **B** *B. sp. 1* (Dai 22172) **C** *B. cf. grisea* (Dai 23070) **D–E** *B. tibetana* (Dai 20896 and Dai 20897).

Etymology. *Macrocarpa* (Lat.): referring to the species having largest basidiocarps.

Fruiting bodies. Basidiocarps annual, terrestrial, centrally stipitate, solitary. Pilei circular or irregular, slightly depressed at center, with undulate and sharp margin, up to 18 cm in diam and 3 cm thick at center when fresh. Pileal surface grayish brown (5/6E4) with cream margin (4A2/3) when fresh, becoming blackish blue (20F8) to black upon drying, smooth, azonate. Pore surface white when fresh, becoming clay-buff (6D4) to fawn (7D/E4) upon drying; pores round to angular, some irregular, 1–3 per mm, mature pores bigger than juvenile ones; dissepiment thin, even to slightly lacerate. Context white when fresh, become pale mouse-gray (7C2) when dry, brittle, up to 2.5 cm thick when fresh. Tubes concolorous with pore surface, brittle, up to 5 mm long when fresh. Stipe pale ash-gray (19C2) when fresh, become mouse-gray (9F3) when dry, up to 6 cm long and 4 cm in diam when fresh.

Hyphal structure. Hyphal system monomitic; generative hyphae with clamp connections; gloeoplerous hyphae present, usually 3–11 μm in diam.

Pileipellis. Pileipellis hyphae hyaline, thin- to thick-walled, 4–9 μm in diam; gloeoplerous hyphae rarely present; tissue darkening in KOH.

Context. Contextual hyphae hyaline, thick-walled, rarely branched, interwoven, distinctly inflated, 5–25 μm in diam; gloeoplerous frequently hyphae present, thin-walled, reflective in Melzer's reagent.

Stipitipellis. Stipitipellis hyphae hyaline, usually thick-walled with a wide lumen, rarely branched, parallel along stipe, straight, uniform, 4–12 μm in diam; gloeoplerous hyphae rarely present.

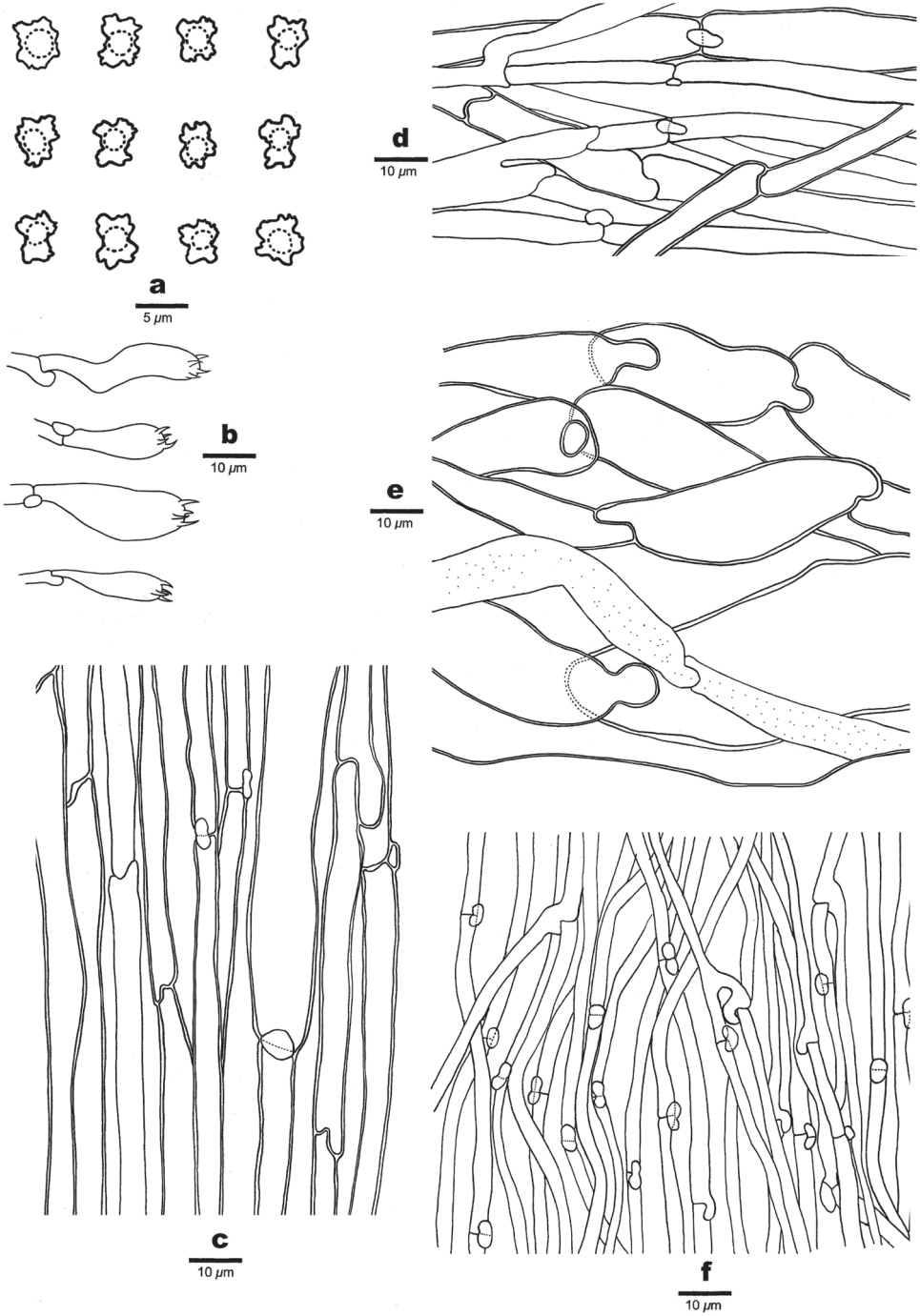


Figure 3. Microscopic structures of *Boletopsis macrocarpa* (Holotype) **a** basidiospores **b** basidia **c** stipitipellis hyphae **d** pileipellis hyphae **e** hyphae from context **f** hyphae from trama.

Tubes. Tramal hyphae hyaline, thin-walled, occasionally branched, interwoven, uniform, 2–4 μm in diam; gloeoplerous hyphae rarely present; cystidia and cystidioles absent; basidia clavate, tetrasterigmatic with a basal clamp connection, $14\text{--}19 \times 6\text{--}7 \mu\text{m}$.

Spores. Basidiospores angular to tubercular with irregular ornaments, hyaline, thin-walled, with a guttule, IKI–, CB–, $(4.5\text{--})4.8\text{--}6(-6.2) \times (3.7\text{--})4\text{--}5 \mu\text{m}$, $L = 5.22 \mu\text{m}$, $W = 4.31 \mu\text{m}$, $Q = 1.20\text{--}1.22$ ($n = 90/3$).

Additional specimens examined (paratypes). CHINA, Yunnan Province, Chuxiong, Wuding County, on ground in forest of *Pinus yunnanensis*, alt. 2400 m, 23 September 2021, Dai 23064 (BJFC037635), Dai 23065 (BJFC037636); Dali, Jianchuan County, Laojunshan Nature Reserve, on ground in forest of *Pinus yunnanensis*, alt. 3100 m, 29 August 2020, Dai 21780 (BJFC035681); Nujiang, Lanping County, Luoguqing Nature Reserve, on ground in forest of *Pinus yunnanensis*, alt. 3000 m, 3 September 2021, Dai 22748 (BJFC037321); Xinchengqiao National Forest Park, on ground in forest of *Pinus yunnanensis*, alt. 3000 m, 2 September 2021, Dai 22727 (BJFC037300), Dai 22729 (BJFC037302).

***Boletopsis tibetana* Y.C. Dai, F. Wu & H.M. Zhou, sp. nov.**

MycoBank No: 843793

Figs 2D–E, 4

Diagnosis. Differs from other *Boletopsis* species by smaller pores (3–4 per mm), the presence of gloeoplerous hyphae in pileipellis and context, and the fact that it grows in the forest of *Picea* in Tibet, SW China.

Holotype. CHINA, Tibet, Linzhi, on ground in the forest of *Picea balfouriana*, alt. 2900 m, 23 August 2019, Dai 20896 (BJFC032554).

Etymology. *Tibetana* (Lat.): referring to the species having a distribution in Tibet.

Fruiting bodies. Basidiocarps annual, terrestrial, centrally stipitate, solitary to confluent. Pilei convex, or irregular, with undulate and incurved margin, up to 7 cm in diam and 1 cm thick at center when fresh. Pileal surface vinaceous buff (4C4) to clay buff (6D4) when fresh, becoming mouse-gray (9F3) to black upon drying, smooth, azonate; margin concolorous with pileal surface. Pore surface white when fresh, become fawn (7D/E4) when bruised, ash-gray (19C2) when dry; pores round to angular, 3–4 per mm; dissepiment thin, entire to slightly lacerate. Context white when fresh, become ash gray (19C2) when dry, rigid, up to 9 mm thick when dry. Tubes concolorous with pore surface, brittle, up to 1 mm long when dry. Stipe concolorous with pileal surface, cylindrical or tapering to the base, up to 6 cm long and 2 cm in diam when fresh.

Hyphal structure. Hyphal system monomitic; generative hyphae with clamp connections; gloeoplerous hyphae present, usually 3–11 μm in diam.

Pileipellis. Pileipellis hyphae hyaline, thin-walled, with finger-shaped tips, 5–7 μm in diam; gloeoplerous hyphae frequently present, thin-walled, strongly reflective in Melzer's reagent; tissue darkening in KOH.

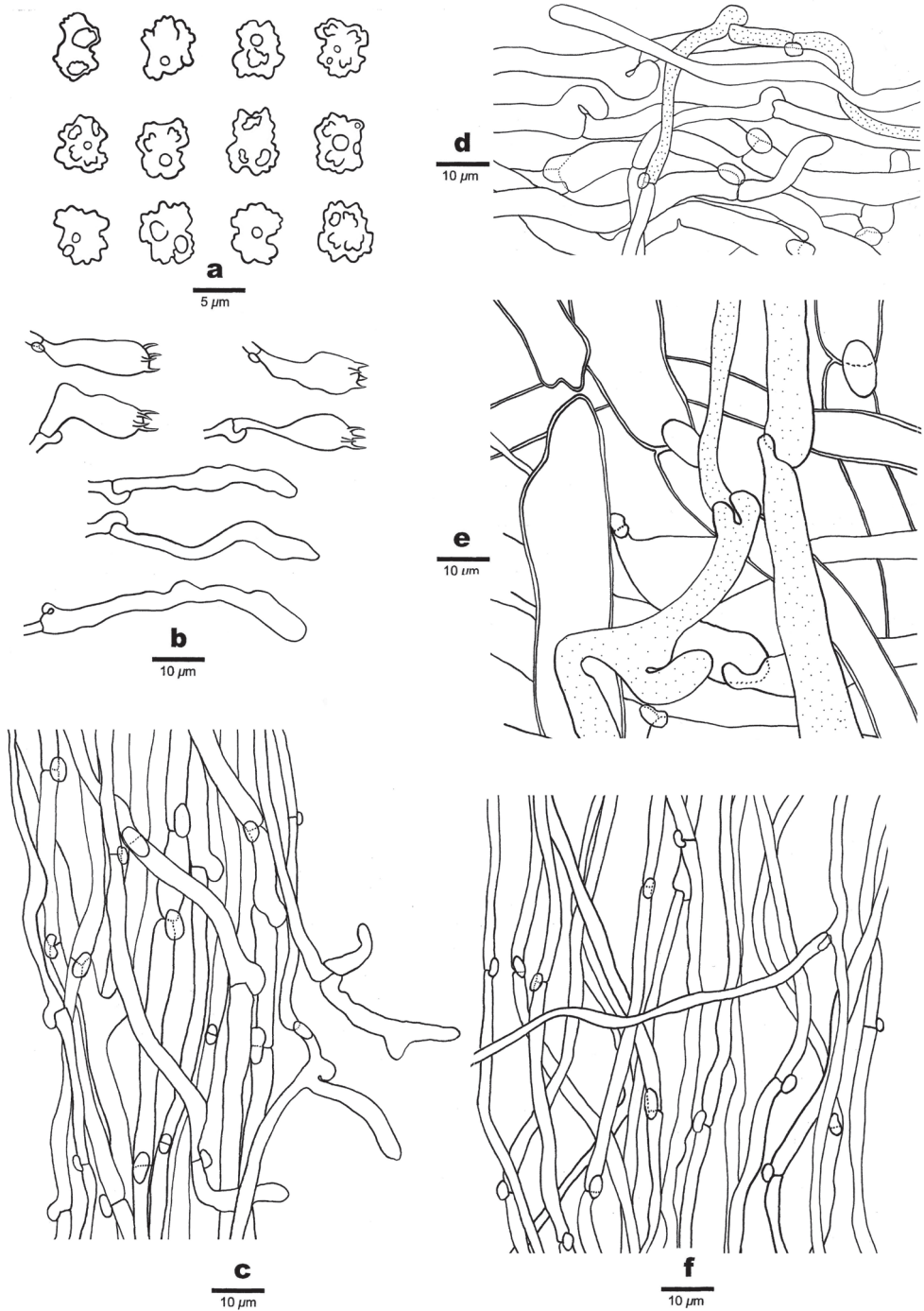


Figure 4. Microscopic structures of *Boletopsis tibetana* (Holotype) **a** basidiospores **b** basidia and basidioles **c** stipitipellis hyphae **d** pileipellis hyphae **e** hyphae from context **f** hyphae from trama.

Context. Contextual hyphae hyaline, thick-walled, rarely branched, interwoven, distinctly inflated, 6–22 μm in diam; gloeoplerous hyphae present, thin-walled, strongly reflective in Melzer's reagent.

Stipitipellis. Stipitipellis hyphae hyaline, thin- to thick-walled, frequently branched, subparallel along stipe, straight, uniform, 2–6 μm in diam; gloeoplerous hyphae rarely present.

Tubes. Tramal hyphae hyaline, thin-walled, occasionally branched, loosely interwoven, uniform, 2–4 μm in diam; gloeoplerous hyphae rarely present; cystidia and cystidioles absent; basidia clavate, tetrasterigmatic with a basal clamp connection, 13–25 \times 6–8 μm ; basidioles clavate, 22–40 \times 3–4 μm .

Spores. Basidiospores angular to tubercular with irregular ornaments, hyaline, thin-walled, IKI–, CB–, 5–6.5(–7) \times 4–5(–5.2) μm , L = 5.55 μm , W = 4.41 μm , Q = 1.22–1.29 (n = 60/2).

Additional specimen examined (paratype). CHINA, Tibet, Linzhi, on ground in forest of *Picea balfouriana*, alt. 2900 m, 23 August 2019, Dai 20897 (BJFC032555).

Discussion

Previously seven species of *Boletopsis* were accepted mostly based on morphological examination, and five were confirmed by phylogenetic analyses (Cooper and Leonard 2012). In the present study, four distinct taxa of *Boletopsis* were found in China: *B. macrocarpa*, *B. tibetana*, *B. cf. grisea* and *B. sp. 1* based on morphological and molecular evidence, and the phylogenetic relationship of seven *Boletopsis* taxa is analyzed (Fig. 1). The former two new species are proposed, but the latter two taxa require further collections and analyses.

Morphologically, *Boletopsis macrocarpa* and *B. mediterraneensis* share similar pileal surface, almost the same shape and size of basidiospores, and both species take *Pinus* as a potential host (Table 2), but the former has white fresh context which was unchanged when cut and hyaline basidiospores, while the latter has pale gray fresh context, becoming pale red when cut and hyaline to pale yellow-brown (Crous et al. 2019). In addition, *B. macrocarpa* has a distribution in SW China, while *B. mediterraneensis* is known in the Mediterranean area. *Boletopsis grisea* resembles *B. macrocarpa* by almost the same size of pores and basidiospores, but the former has uniform grayish tinges for all upper surface, its gloeoplerous hyphae are present at pileipellis (Ryvarden and Melo 2017), while the upper surface is grayish brown to dark gray with cream margin and the gloeoplerous hyphae present in context in *B. macrocarpa* (Table 2).

Boletopsis tibetana resembles *B. grisea* by almost the same shape and size of basidiospores. However, the latter species has bigger pores (1–3 per mm vs. 3–4 per mm, Table 2), and both species are phylogenetically distantly related. In fact, *Boletopsis tibetana* has pores as 3–4 per mm, and other *Boletopsis* species have pores 1–3 per mm, so it is easily distinguished *B. tibetana* from other *Boletopsis* species.

Table 2. A comparison of morphology, ecology and distribution of *Boletopsis* species.

Species	Type Locality	Basidiocarps in diam (cm)	Pileal surface when fresh	gloeoplerous hyphae	Pores/ mm	Basidiospores (µm)	Guttules in basidiospores	Hosts	Distribution	References
<i>B. atrata</i>	Thailand	2–5	black	–	2–3	4.5–6 in diam	–	<i>Quercus, Castanea</i>	Asia and North America	Hjortstam and Ryvarden 1982
<i>B. grisea</i>	Norway	5–18	gray–white to silvery gray, gray–brown, or brownish vinaceous	frequent in pileipellis	1–3	5–6.2 × 4–5	present	Pinaceae	Europe and North America	Watling and Milne 2008; Ryvarden and Melo 2017
<i>B. leucomelaena</i>	Norway	Up to 10	deep grayish to black	rarely present	1–3	5–6.5 × 4–5	present	mostly <i>Picea</i>	Europe	Ryvarden and Melo 2017
<i>B. macrocarpa</i>	China	12–18	grayish brown to dark gray	present in context	1–3	4.8–6 × 4–5	present	<i>Pinus</i>	Asia	This study
<i>B. mediterraneensis</i>	Spain	4–12	pale gray, brownish gray to ochraceous brown or dark brown	–	1–3	4.5–6.7 × 3.3–5.2	–	mostly <i>Pinus, Cedrus</i>	Europe	Crous et al. 2019
<i>B. nothofagi</i>	New Zealand	1–8	gray	present in context	2–3	5.3 × 4.1	–	<i>Nothofagus</i>	Oceania	Cooper and Leonard 2012
<i>B. smithii</i>	USA	4–5	dull orange	–	2–3	5.5–7 × 4.5–5.6	absent	–	North America	Harrison 1975
<i>B. tibetana</i>	China	5–7	vinaceous buff to clay buff	present in pileipellis	3–4	5–6.5 × 4–5	absent	<i>Picea</i>	Asia	This study
<i>B. watlingii</i>	UK	4–7	dark fuliginous brown to gray–brown	present in pileipellis	1–3	4.5–4.8 × 3.5–4.5	present	<i>Pinus</i>	Europe and North America	Watling and Milne 2006, 2008; Ryvarden and Melo 2017

Two species in *Boletopsis*, *B. atrata* and *B. smithii*, have so far no DNA data available, and their relationships with our new species are still unknown. Morphologically, *B. atrata* can be distinguished from our two new species by its small basidiocarps (2–5 cm in diam), verruculose basidiospores with regular ornaments (Hjortstam and Ryvarden 1982), while our new species have big basidiocarps (5–18 cm in diam), angular to tubercular basidiospores with irregular ornaments. *Boletopsis smithii* is different from our new species by its dull orange and smaller basidiocarps (4–5 cm in diam), and inflated hyphae (up to 17 µm in diam) in pileipellis and stipitipellis (Harrison 1975).

Although the specimen Dai 22172 forms an independent lineage nested in *Boletopsis* clade in our phylogeny (Fig. 1), it is temporarily treated as *Boletopsis* sp. 1 because of the single sample. The taxon is characterized by the presence of scales at pileal margin, a bulbous stipe base, dentate pores, the presence of cystidioles, and the fact that it grows in a forest dominated by *Pinus sylvestris* var. *mongolica* in NE China.

All European and North American samples of *Boletopsis grisea* clustered together with a support (88/0.86), and a single Chinese sample Dai 23070 is sister to them (100/1). We treat the sample Dai 23070 as *B. cf. grisea* because no distinct morphological difference has been found between them to date. More samples and a multi-locus phylogeny are needed to clarify the status of the Chinese *Boletopsis cf. grisea*.

Species of *Boletopsis* form ectomycorrhizae with certain host plants, and the potential host trees may help to identify species, for instance, *Boletopsis leucomelaena* is usually associated with *Picea abies* (L.) Karst. In Europe (Niemela and Saarenoksa 1989), and *B. nothofagi* are usually accompanied by *Nothofagus* in Oceania (Cooper and Leonard 2012). Almost all *Boletopsis* species are found in the Northern Hemisphere except *B. nothofagi*; most *Boletopsis* species grow coniferous trees in temperate areas and two species are known from more than one continent (Watling and Milne 2008; Ryvarden and Melo 2017). According to our field inventory, the two Chinese new species were found in temperate zone, and *Boletopsis macrocarpa* seems to prefer to pine forest at high altitude with open and slightly dry environments; *Boletopsis tibetana* was found in coniferous forest dominant by spruce at high altitude with cold and humid environments. Previously numerous new species have been found in SW China (Dai et al. 2021; Wang et al. 2021), and the present paper confirms the fungal diversity is very rich in the montane forests of East Himalayas.

The main morphological characteristics, ecology and distribution of the accepted species of *Boletopsis* are summarized in Table 2.

A key to accepted species of *Boletopsis* in the world

- 1 Basidiospores verruculose with regular ornaments..... *B. atrata*
- Basidiospores oblong, angular to tubercular with irregular ornaments..... 2
- 2 Basidiospores < 5 µm long *B. watlingii*
- Basidiospores > 5 µm long 3
- 3 Pileal surface dull orange when fresh..... *B. smithii*
- Pileal surface vinaceous, grayish brown, dark gray or brownish to black when fresh..... 4

- 4 Pores 3–4 per mm.....***B. tibetana***
 – Pores 1–3 per mm.....**5**
 5 Basidiospores oblong to tuberculate; associated to *Nothofagus* forest, distribution in Oceania.....***B. nothofagi***
 – Basidiospores angular to tuberculate; associated to *Picea* or *Pinus* forest, distribution in Northern Hemisphere.....**6**
 6 Upper surface grayish brown with cream margin when fresh; distribution in Asia.....***B. macrocarpa***
 – Upper surface brownish gray to blackish without cream margin when fresh; distribution in Europe and North America**7**
 7 Context pale gray, becoming pale red when cut***B. mediterraneensis***
 – Context white, becoming darker when cut.....**8**
 8 Pileus dark gray to blackish, flesh brittle, usually associated to *Picea* forest
***B. leucomelaena***
 – Pileus grayish to grayish brown, flesh tough, usually associated to *Pinus* forest***B. grisea***

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A compendium of macrofungi of Pakistan by ecoregions

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Abstract

Macrofungi form fruiting bodies that can be detected with the naked eye in the field and handled by hand. They mostly consist of basidiomycetes, but also include some ascomycetes. Mycology in Pakistan is still in its infancy, but there have been many historical reports and checklists of macrofungi occurrence from its 15 ecoregions, which range from Himalayan alpine grasslands and subtropical pine forests to deserts and xeric shrublands. In this work, we searched and reviewed the historical literature and the GenBank database for compiling a comprehensive list of macrofungi reported from Pakistan to date. We recorded 1,293 species belonging to 411 genera, 115 families and 24 orders. These occurrences were updated taxonomically following the classification system currently proposed in the Index Fungorum website. The highest represented order by taxon number is Agaricales (47%) with 31 families, 146 genera and 602 species, followed by Polyporales (11%), Russulales (9%) and Pezizales (8%). Genera occurrence reported therein are presented for each ecoregion to the best of our ability given the data. We also discussed the currently known macrofungi diversity between different ecoregions in Pakistan. Overall, this work should serve as a solid foundation for the inclusion of Pakistan macrofungi in global biodiversity and conservation studies.

Keywords

Biodiversity, conservation, ecoregions, fungi, taxonomic list

Introduction

Fungi are amongst the most diverse groups of organisms on earth. There have been numerous estimates regarding the total number of fungi worldwide. Bisby and Ainsworth (1943) recorded the total number to be about 100,000 and later, Hawksworth (1991) hypothesised the total number of fungal species to be 1.5 million. Later, Blackwell (2011) estimated the total number of fungi to be around 3.5 – 5.1 million. More recently, Hawksworth and Lücking (2017) predicted the total number to be in the range of 2.8 to 3.8 million. To date, 149,974 species have been recognised (Index Fungorum 2021). The current rate of fungal species discovery per year averages at 2,000 as compared to 1,000 to 2,000 a decade ago (Cheek et al. 2020).

Macrofungi form fruiting bodies that can be detected with the naked eye in the field and handled by hand. They mostly consist of basidiomycetes, but also include some ascomycetes. They play many essential roles in ecosystems as mutualists, pathogens, decomposers or saprotrophs (Volk 2013). Some are edible, medicinal or toxic to humans. About 20,000 macrofungal species have been recognised worldwide (Hawksworth 2001), but many belong to cryptic species complexes and many more await discovery, particularly from poorly explored regions of the world.

A major hindrance of traditional systematics in fungal discovery and identification is the presence of limited taxonomic features (Wu et al. 2019). The traditional identification techniques utilised morphological features, ecological characters, physiology and biochemistry of tissues (Wang et al. 2016). The boom in molecular methods in the 1980s and a remarkable paper by White et al. (1990) describing rRNA primers in fungi spurred the beginning of molecular data utilisation in fungal classification and species identification. Phylogenetic studies have shown that morphologically similar taxa might belong to different lineages (e.g. Hibbett et al. 1997; Moncalvo et al. 2002). DNA sequences can also be helpful for detecting and distinguishing amongst cryptic taxa sharing similar morphological traits (e.g. Moncalvo and Buchanan 2008; Schoch et al. 2012; Wu et al. 2019).

Before the partition of British India, mycoflora of the region (presently India and Pakistan) was listed by Butler and Bisby (1931) and Mundkur (1938). These checklists recorded only 198 species of this region expanding on 30,000 square miles (77700 km²). Later, Ahmad et al. (1997) recorded about 4,500 fungal taxa in a list that included all groups of fungi, i.e. macrofungi as well as microfungi and lichens. In the last two decades, many new records and description of new species have been added, based on morphological characters alone or in combination with molecular data (e.g. Sarwar et al. 2011; Saba et al. 2019a; Bashir et al. 2020a; Khalid in press), but none of these was comprehensively addressing macrofungal diversity in Pakistan and the ecoregions of their occurrence.

From a biodiversity conservation perspective, ecologists have been concerned about the factors that affect the delimitation of ecological units and how it affects our knowledge of ecological processes (Weins et al. 1985; Gosz 1991). Numerous efforts have been made to categorise geographical zones with analogous features. In a remarkable paper, Olson et al. (2001) defined ecoregions as broad areas of land or

water that consist of geographically distinct assemblages of taxa, natural communities and environmental conditions. They presented an ecoregion map for its utilisation at global as well as regional scales. They based their map on biogeographic information and this was built with the collaboration of more than 1,000 experts in biogeography, taxonomy, conservation biology and ecology from all over the world. Ecoregions were classified by taking into account biogeographic features like endemism, species richness and special evolutionary perspectives. The unique feature of this global biodiversity map is that it focuses on species allocation and communities more precisely than the earlier models, based on biophysical characters, for instance, rainfall and temperature (Holdridge 1967; Walter and Box 1976; Schultz 1995; Bailey 1998) or vegetation structure (UNESCO 1969; de Laubenfels 1975; Schmidhüsen 1976). In Olson et al. (2001), the terrestrial world is divided into 14 biomes, eight biogeographic realms and 867 ecoregions; out of which, nine biomes, two realms and 15 ecoregions are found in Pakistan. This country covers a wide altitudinal range from sea level (Arabian Sea) to the second highest peak of the world, K2. The variety of ecoregions from Himalayan alpine grasslands and subtropical pine forests to deserts and xeric shrublands promotes a great deal of fungal diversity that still remains largely unaccounted for.

In this study we compiled a compendium of macrofungi reported from Pakistan to date from searches in the historical literature as well as in the GenBank database. We have included fungi with prominent fruiting bodies visible to the naked eye in this taxonomic list. We have excluded taxa in Ascomycota which are immersed or half immersed structures, galls or non-prominent fruiting structures on animal dung. We also categorised the reported macromycetes into ecoregions, based on available data.

Materials and methods

Compendium of Macromycetes of Pakistan

For compiling a comprehensive compendium of macromycetes of Pakistan, data were gathered from extensive literature searches of checklists and published papers, as well as in the GenBank sequence database. Sequence data in GenBank (2020, 2021) was retrieved using a Python script written by Santiago Sanchez-Ramirez (available upon request) on 09-10-2020 for Basidiomycota and on 22-06-2021 for Ascomycota. The list was arranged following the current classification system in Index Fungorum (2021) with great care about eliminating synonymy.

Division of Macromycetes of Pakistan into Ecoregions

In order to attribute ecoregion occurrence of the taxa we retrieved, we used their locality-based information to consult various repositories, such as Ecoregion 2017 (Dinerstein et al. 2017), DOPA explorer (Dubois et al. 2018) and the ArcGis

search tool (2021). Ecoregion allocation of genera was graphically represented on an MS excel spreadsheet for analyses. Genera were listed in rows and ecoregions in columns. The presence or absence of a genus in an ecoregion was scored “1” or “0”, respectively. The sum and percentage of each genus in each ecoregion were then calculated.

Results

Table 1 provides a comprehensive record of the macrofungal biota of Pakistan known to date, to the best of our knowledge. It lists 1,293 species belonging to 411 genera, 115 families and 24 orders. Out of which, 1,117 species, 338 genera, 83 families and 16 orders belong to Basidiomycota and 176 species, 73 genera, 32 families and eight orders are from Ascomycota. The source reference in Table 1 indicates that most entries are from the extensive checklist by Ahmad et al. (1997; 874 entries). The highest order recorded is Agaricales (27%) with 31 families, 146 genera and 602 species, followed by Polyporales (11%), Russulales (9%) and Pezizales (8%). The orders of least occurrences are Atheliales, Leotiales and Trechisporales representing one taxon in a single genus and family. The proportion of respective families, genera as well as species are shown in Fig. 1.

Table 2 indicates the ecoregions from which each genus was recorded. Fig. 2 shows that the highest macrofungal diversity is found in the western Himalayan

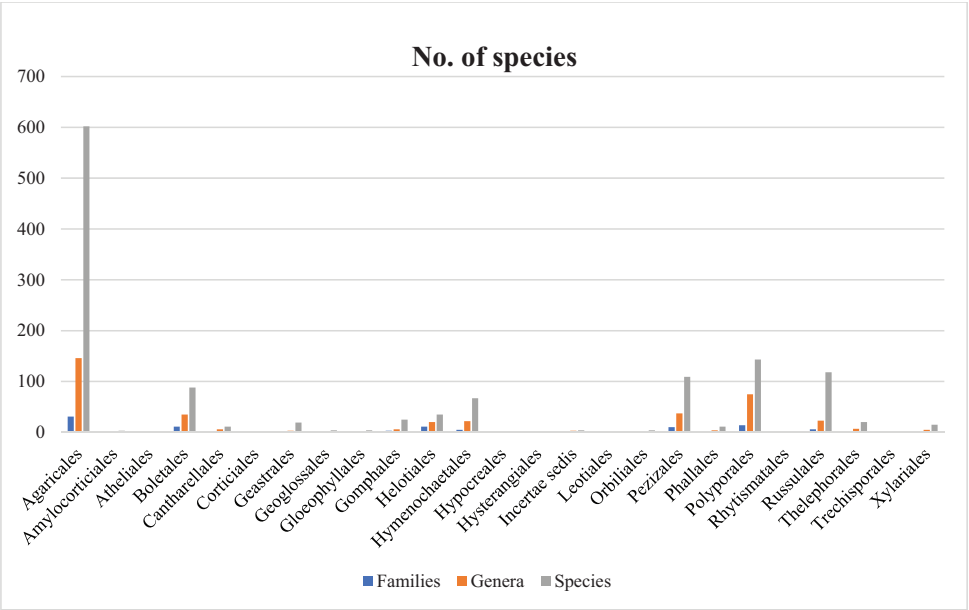


Figure 1. The Bar graph showing number of families, genera and species per order.

broadleaf forests (36%) followed by north-western thorn scrub forests (25%). In addition, Himalayan subtropical pine forests have rich macrofungal diversity with 17% taxa representation, followed by western Himalayan subalpine conifer forests with 13% distribution. The Karakorem West Tibetan Plateau alpine steppe and Baluchistan xeric woodlands show 5% or lesser distribution. On the other hand, the Indus River Delta, Arabian Sea mangroves, Thar Desert, Sulaiman range alpine meadows, East Afghan montane conifer forests, Registan north Pakistan sandy desert, south Iran Nubo-Sindian desert and semi-desert, Rann of Kutch seasonal marsh, as well as the north-western Himalayan alpine scrub and meadows have 0–2% macromycetes record.

Biomes and macrofungi occurrence details therein are presented in the supplementary document labelled “Macrofungi_list_by_biomes_and_ecoregions_of_Pakistan”, whereas supplementary table entitled “Detailed_compendium_of_macrofungi_of_Pakistan” contains thorough information about synonymy, locality and taxa level ecoregion allocation.

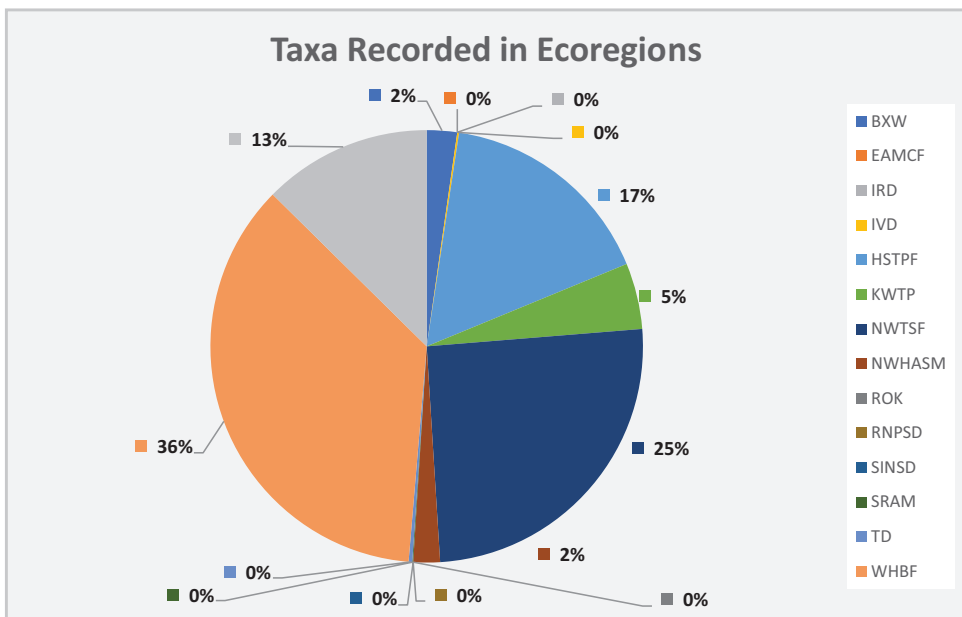


Figure 2. Percentage of macrofungi taxa in different ecoregions of Pakistan. Where, *BXW* = Baluchistan Xeric woodlands, *EAMCF* = East Afghan montane conifer forests, *IRM* = Indus River Delta Arabian Sea mangroves, *IVD* = Indus Valley Desert, *HSTPF* = Himalayan subtropical pine forests, *KWTP* = Karakorem West Tibetan Plateau alpine steppe, *NWTSF* = North-western thorn scrub forest, *NWHASM* = North-western Himalayan alpine scrub & meadows, *RNPSD* = Registan north Pakistan sandy desert, *ROK* = Rann of Kutch seasonal marsh, *SINS* = South Iran Nubo-Sindian desert & semi-desert, *SRAM* = Sulaiman Range Alpine meadows, *WHBF* = Western Himalayan broadleaf forests, *WHSACF* = Western Himalayan subalpine conifer forests, *TD* = Thar Desert.

Table 1. A compendium of macrofungi of Pakistan. Note:FOP refers to checklist ‘Fungi of Pakistan’ (Ahmad et al. 1997).

Phylum/Order	Family	Genus	Species	Authority	Source
Basidiomycota/ Agaricales	Agaricaceae	<i>Agaricus</i>	<i>arvensis</i>	Schaeff.	FOP
			<i>bisporiticus</i>	Nawaz, Callac, Thongklang & Khalid	GenBank (KJ575608); Thongklang et al. (2014)
			<i>bisporus</i>	(J.E. Lange) Imbach	GenBank (KU170542); Sultana et al. (2011)
			<i>bitorquis</i>	(Quel.) Sacc.	GenBank (KU170541); FOP
			<i>bolorhizus</i>	Berk. & Broome	FOP
			<i>callipelus</i>	Berk. & Broome	FOP
			<i>campestris</i>	L.	Razaq et al. (2014)
			<i>dulcidulus</i>	Schulzer	Razaq et al. (2014)
			<i>endoxanthus</i>	Berk. & Broome	GenBank (MK101039); FOP
			<i>glabriusculus</i>	S. Hussain	GenBank (MK751855); Hussain and Sher (2019)
			<i>goossensiae</i>	Heinem.	GenBank (KU170540)
			<i>gregariomyces</i>	J.L. Zhou & R.L. Zhao	GenBank (MK101032)
			<i>hemilasius</i>	Berk. & Broome	FOP
			<i>heterocystis</i>	Heinem. & Gooss.-Font.	GenBank (KU170543)
			<i>inoxydabilis</i>	Heinem.	GenBank (KU170539)
			<i>latiumbonatus</i>	S. Hussain	GenBank (MK751859) ; Hussain and Sher (2019)
			<i>lateriticolor</i>	Heinem.	FOP
			<i>latipes</i>	Berk.	FOP
			<i>pakistanicus</i>	H. Bashir, A.N. Khalid, L.A. Parra & Callac	GenBank (MG669256); Bashir et al. (2018)
			<i>placomycetes</i>	Peck.	FOP
			<i>pseudopratesensis</i>	(Bohus) Bohus	GenBank (MK123324)
			<i>punjabensis</i>	Qasim, A. Ashraf & Khalid	GenBank (KT985908); Chen et al. (2016)
			<i>rufolbus</i>	Berk.	FOP
			<i>semotus</i>	Fr.	FOP
			<i>sinoplacomycetes</i>	P. Callac & R.L. Zhao	GenBank (KY741891)
			<i>squalidus</i>	Massee	FOP
			<i>sparsisquamosus</i>	H. Bashir, S. Hussain, A.N. Khalid & H. Ahmed	GenBank (MG669253); Sultana et al. (2011); Bashir et al. (2018)
			<i>sylvaticus</i>	Schaeff.	Sultana et al. (2011)
			<i>trisulphuratus</i>	Berk.	GenBank (KU170545); FOP; Sultana et al. (2011)
			<i>woodrowii</i>	Massee	FOP
			<i>xanthodermus</i>	Genev.	GenBank (KU170544)
		<i>Baeospora</i>	<i>myosura</i>	(Fr.) Singer	FOP
		<i>Battarrea</i>	<i>phalloides</i>	(Dicks.) Pers.	FOP; Yousaf et al. (2013a)
		<i>Chamaemyces</i>	<i>fracidus</i>	(Fr.) Donk.	FOP
		<i>Chlorophyllum</i>	<i>hortense</i>	(Murrill) Vellinga	GenBank (KM350689)
			<i>molybdites</i>	(G. Mey.) Massee	GenBank (MN577080); Razaq and Shahzad (2012)
		<i>Coprinus</i>	<i>palaeotropicum</i>	Z.W. Ge & A. Jacobs	GenBank (MN577079)
			<i>rachodes</i>	(Vittad.) Vellinga	FOP; Sultana et al. (2011)
			<i>comatus</i>	(Muell. Ex Fr.) S.F. Gray	GenBank (HE819398); FOP; Razaq et al. (2014c)
			<i>hookeri</i>	Berk.	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Agaricaceae	<i>Cystoderma</i>	<i>amianthinum</i>	(Scop.) Fayod	FOP
		<i>Cystodermella</i>	<i>cinnabarina</i>	(Alb & Schwein.) Harmaja	Razaq et al. (2013c)
			<i>granulosa</i>	(Batsch) Harmaja	FOP
		<i>Cystolepiota</i>	<i>pseudogranulosa</i>	(Berk. & Broome) Pegler	FOP
		<i>Disciseda</i>	<i>cervina</i>	(Berk.) Hollos	FOP
		<i>Echinoderma</i>	<i>asperum</i>	(Pers.) Bon	FOP; Razaq et al. (2013a)
		<i>Hymenagaricus</i>	<i>alphitochrous</i>	(Berk. & Broome) Heinem.	FOP
		<i>Lepiota</i>	<i>albogranulosa</i>	Qasim & Khalid	Qasim et al. (2015b)
			<i>anthomyces</i>	(Berk. & Broome) Sacc.	FOP
			<i>brunneoincarnata</i>	Chodat & C. Martin	Razaq et al. (2013b)
			<i>ceramogenes</i>	(Berk. & Broome) Sacc.	FOP
			<i>cholistanensis</i>	H. Bashir, Usman & Khalid	Bashir et al. (2020a)
			<i>cingulum</i>	Kelderman	GenBank (MN240457)
			<i>clypeolaria</i>	(Bull.) P. Kumm.	GenBank (KJ906506)
			<i>cristata</i>	(Bolton) P. Kumm.	FOP; Razaq et al. (2013a)
			<i>eriphaea</i>	(Berk. & Br.) Sacc.	FOP
			<i>erythrogramma</i>	(Berk. & Br.) Sacc.	FOP
			<i>himalayensis</i>	Khalid & Razaq	Razaq et al. (2012a)
			<i>ignivolvata</i>	Bousset & Joss. ex Joss.	Sultana et al. (2011)
			<i>laborensis</i>	Qasim & Khalid	GenBank (KT186609); Qasim et al. (2016)
			<i>lepidophora</i>	(Berk. & Broome) Sacc.	FOP
			<i>leprica</i>	(Berk. & Broome) Sacc.	FOP
			<i>magnispora</i>	Murrill	Sultana et al. (2011)
			<i>metulispora</i>	(Berk. & Broome) Sacc.	FOP
			<i>micropholis</i>	(Berk. & Broome) Sacc.	FOP
			<i>ochraceofulva</i>	P.D. Orton	Sultana et al. (2011)
			<i>pardalota</i>	Sacc.	FOP
			<i>revelata</i>	(Berk. & Broome) Sacc.	FOP
			<i>subincarnata</i>	J.E. Lange	FOP; Razaq et al. (2013b)
			<i>vellingana</i>	Nawaz & Khalid	Nawaz et al. (2013)
		<i>Leucoagaricus</i>	<i>asiaticus</i>	Qasim, Nawaz, & Khalid	Ge et al. (2015)
			<i>badhamii</i>	(Berk. & Broome) Singer	Sultana et al. (2011)
			<i>badius</i>	S. Hussain, Pfister, Afshan & Khalid	Hussain et al. (2018b)
			<i>brunneus</i>	Z. Ullah, Jabeen & Khalid	Ullah et al. (2019)
			<i>laborensiformis</i>	S. Hussain, H. Ahmad, Afshan & Khalid	Hussain et al. (2018b)
			<i>laborensis</i>	Qasim, T. Amir & Nawaz	Qasim et al. (2015a)
			<i>leucothites</i>	(Vittad.) Wasser	FOP
			<i>nivalis</i>	(W.F. Chiu) Z.W. Ge & Zhu L. Yang	GenBank (MK106148); Jabeen et al. (2020a)
			<i>meleagris</i>	(Gray) Singer	FOP
			<i>pabbiensis</i>	S. Jabeen & A.N. Khalid	GenBank (MG973423); Usman and Khalid (2018)
			<i>pakistaniensis</i>	S. Jabeen & A.N. Khalid	GenBank (KU647726); Hussain et al. (2018b)
			<i>serenus</i>	(Fr.) Bon & Boiffard	FOP; Sultana et al. (2011)
			<i>sultanii</i>	S. Hussain, H. Ahmad & Khalid	Hussain et al. (2018b)
			<i>umbonatus</i>	S. Hussain, H. Ahmad & Afshan	GenBank (KU647737); Hussain et al. (2018b)
			<i>viriditinctus</i>	(Berk. & Broome) J.F. Liang, Zhu L. Yang & J. Xu	FOP
		<i>Leucocoprinus</i>	<i>birnbaumii</i>	(Corda.) Singer	GenBank (KJ717764); FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Agaricaceae	<i>Leucocoprinus</i>	<i>cepaestipes</i>	(Sw. ex Fr.) Pat.	FOP
			<i>zeylanicus</i>	(Berk.) Boedijn	FOP
		<i>Macrolepiota</i>	<i>dolichaula</i>	(Berk & Broome) Pegler & R.W. Rayner	GenBank (KJ643334); Fiaz et al. (2014)
			<i>excoriata</i>	(Schaeff.) Wasser	GenBank (KJ643333); Fiaz et al. (2014)
			<i>procera</i>	(Scop.) Singer	FOP
		<i>Micropsalliota</i>	<i>venenata</i>	Bon	Sultana et al. (2011)
			<i>arginea</i>	(Berk. & Broome) Pegler & R.W. Rayner	FOP
			<i>brunneosperma</i>	(Berk. & Broome) Höhn.	FOP
		<i>Montagnea</i>	<i>plumaria</i>	(Berk. & Broome) Höhn.	FOP
			<i>arenaria</i>	(DC) Zeller	FOP
		<i>Mycenastrum</i>	<i>corium</i>	(Guers.) Desv.	FOP
		<i>Podaxis</i>	<i>pistillaris</i>	(L.) Fr.	FOP
		<i>Phellorinia</i>	<i>herculeana</i>	(Pers.) Kreisel	Sultana et al. (2011); Yousaf et al. (2012b)
		<i>Schizostoma</i>	<i>laceratum</i>	Ehrenb. ex Fr.) Lév.	FOP
			<i>mundkuri</i>	(S. Ahmad) Long & Stouffer	FOP
		<i>Tulostoma</i>	<i>ahmadii</i>	H. Hussain & Khalid	GenBank (KP738711); Hussain et al. (2015b)
			<i>amnicola</i>	Long & S. Ahmad	FOP
			<i>australianum</i>	Lloyd	FOP
			<i>balanoides</i>	Long & S. Ahmad	FOP
			<i>brumale</i>	Pers.	FOP
			<i>cineraceum</i>	Long	FOP
			<i>crassipes</i>	Long & S. Ahmad	FOP
			<i>egranulosum</i>	Lloyd	FOP
			<i>evanescens</i>	Long & S. Ahmad	FOP
			<i>exitum</i>	Long & S. Ahmad	FOP
			<i>hygrophilum</i>	Long & S. Ahmad	FOP
			<i>inonotum</i>	Long & S. Ahmad	FOP
			<i>ladbaerens</i>	Lloyd	FOP
			<i>macalpineanum</i>	Lloyd	FOP
			<i>mussooriense</i>	Henn.	FOP
			<i>occidentale</i>	Lloyd	FOP
			<i>operculatum</i>	Long & S. Ahmad	FOP
			<i>parvissimum</i>	Long & S. Ahmad	FOP
			<i>perplexum</i>	Long & S. Ahmad	FOP
			<i>pluriosteum</i>	Long & S. Ahmad	FOP
			<i>puncticulosum</i>	Long & S. Ahmad	FOP
			<i>squamosum</i>	(J.F. Gmel.) Pers.	GenBank (KT285883); Hussain et al. (2015b)
			<i>volvulatum</i>	I.G. Borshch.	FOP
			<i>vulgare</i>	Long & S. Ahmad	FOP
			<i>xerophilum</i>	Long	FOP
		<i>Xanthagaricus</i>	<i>flavidorufus</i>	(Berk. & Broome)	FOP
				Little Flower, Hosag. & T.K. Abraham	
			<i>pakistanicus</i>	S. Hussain, Afshan & H. Ahmad	GenBank (KY621555); Hussain et al. (2018c)
			<i>subaeruginosus</i>	(Berk. & Broome)	FOP; Hussain et al. (2018c)
				S. Hussain	
	Amanitaceae	<i>Amanita</i>	<i>ahmadii</i>	Jabeen, I. Ahmad, M. Kiran, J. Khan & Khalid	GenBank (MF070490); Jabeen et al. (2019)
			<i>battarrae</i>	(Boud.) Bon	Tulloss et al. (2001); Sultana et al. (2011)

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Amanitaceae	<i>Amanita</i>	<i>caesarea</i>	(Scop.) Pers.	FOP
			<i>ceciliae</i>	(Berk. & Broome) Bas	FOP
			<i>cinnamomescens</i>	Tulloss, S.H. Iqbal, A.N. Khalid & Bhandary	Tulloss et al. (2005)
			<i>cinis</i>	S. Ullah, A.W. Wilson, Tulloss & Khalid	Ullah et al. (2019b)
			<i>emodotrygon</i>	Mehmood, Tulloss, K. Das, Hosen & R.P. Bhatt	Ullah et al. (2019b)
			<i>flavipes</i>	S. Imai.	FOP; Tulloss et al. (2001)
			<i>glarea</i>	Jabeen, M. Kiran & Sadiquallah	GenBank (KY817310); Jabeen et al. (2017c)
			<i>griseofusca</i>	J. Khan & M. Kiran	GenBank (MH241055); Kiran et al. (2018)
			<i>hemibapha</i>	(Berk. & Broome) Sacc.	FOP
			<i>longistriata</i>	S. Imai	FOP
			<i>mansehraensis</i>	M. Saba, Haelew. & A.N. Khalid	Saba et al. (2019b)
			<i>muscaria</i>	(L.) Lam.	GenBank (MK719200), FOP
			<i>olivovaginata</i>	S. Ullah, Tulloss & Khalid	Ullah et al. (2019a)
			<i>orsonii</i>	Ash. Kumar & T.N. Lakh.	GenBank (KU248132); Tulloss et al. (2001)
			<i>pantherina</i>	(DC.) Krombh	FOP; Sultana et al. (2011)
			<i>pakistanica</i>	Tulloss, S.H. Iqbal & Khalid	GenBank (KX061523); Tulloss et al. (2001)
			<i>pallidorosea</i>	P. Zhang & Zhu L. Yang	GenBank (KY621476); Kiran et al. (2017)
			<i>phalloides</i>	(Vaill. ex Fr.) Link	FOP
			<i>porphyria</i>	Alb. & Schwein.	FOP
			<i>pseudovaginata</i>	Hongo	GenBank (MT277138); Naseer and Khalid (2020a)
			<i>rubescens</i>	Pers.	FOP; Niazi et al. (2009)
			<i>subjunquillea</i>	S. Imai	GenBank (MH998627); Ishaq et al. (2019a)
			<i>vaginata</i>	(Bull.) Lam.	FOP
			<i>verna</i>	(Bull. Ex Fr.) Roques	FOP
			<i>virosa</i>	Bertill.	FOP
			<i>watlingii</i>	Kumar, BhattAsh. Kumar & T.N. Lakh.& Lakhapal.	FOP
		<i>Saproamanita</i>	<i>nana</i>	(Singer) Redhead, Vizzini, Drehmel & Contu	FOP
		<i>Limacella</i>	<i>delicata</i>	(Fr.) Earle ex Konrad & Maubl.	FOP
		<i>Limacellopsis</i>	<i>guttata</i>	(Pers.) Zhu L. Yang, Q. Cai & Y.Y. Cui	FOP
		<i>Zhuliangomyces</i>	<i>pakistanicus</i>	Usman & Khalid	GenBank (MN240881); Usman and Khalid (2020a)
	Bolbitaceae	<i>Bolbitius</i> <i>Conocybe</i>	<i>illinitus</i>	(Fr.) Redhead	FOP
			<i>titubans</i>	(Bull.) Fr.	FOP
			<i>khasiensis</i>	(Berk.) Watling	FOP
			<i>macrocephala</i>	Kühner & Watling	FOP
			<i>mesospora</i>	Kühner ex Watling	FOP
			<i>pubescens</i>	(Gillet) Kühner	FOP
			<i>punjabensis</i>	A. Izhar, H. Bashir & Khalid	GenBank (MK637515); Izhar et al. (2019)
			<i>rickenii</i>	(Jul. Schäff.) Kühner	FOP
			<i>semiglobata</i>	Kühner & Watling	FOP
			<i>semiglobata</i> var. <i>campanulata</i>	Hauskn.	GenBank (MT994769)
			<i>tenera</i>	(Schaeff.) Kühner	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Bolbitaceae	<i>Descolea</i>	<i>flavannulata</i>	(Lj.N. Vassiljeva) E. Horak	Niazi et al. (2007)
			<i>quercina</i>	J. Khan & Naseer	GenBank (MF966634); Khan et al. (2017a)
	Callistosporiaceae	<i>Callistosporium</i>	<i>luteo-olivaceum</i>	(Berk. & M.A. Curtis) Singer	GenBank (KJ101607); Saba and Khalid (2014a)
			<i>Macrocybe</i>	<i>gigantea</i> (Masse) Pegler & Lodge	GenBank (LK932287); Razaq et al. 2016b
	Clavariaceae	<i>Pseudolaccaria</i>	<i>pachyphylla</i>	(Fr.) Vizzini & Contu	GenBank (KJ906503)
		<i>Clavaria</i>	<i>rosea</i>	Fr.	FOP
			<i>vermicularis</i>	Batsch	FOP
			<i>Clavulinopsis</i>	<i>corniculata</i> (Schaeff.) Corner	FOP
	Cortinariaceae	<i>Cortinarius</i>	<i>acetosus</i>	(Velen.) Melot	Razaq et al. (2014)
			<i>brunneocarpus</i>	Razaq & Khalid	GenBank (MN738695); Song et al. (2019)
			<i>bulliardii</i>	(Pers.) Fr.	FOP
			<i>cinnamomeus</i>	(L.) Gray	FOP
			<i>claricolor</i>	(Fr.) Fr.	Sultana et al. (2011)
			<i>delibutus</i>	Fr.	Sultana et al. (2011)
			<i>elegantissimus</i>	Rob. Henry	Sultana et al. (2011)
			<i>gentilis</i>	(Fr.) Fr.	Sultana et al. (2011)
			<i>hinnuleus</i>	Fr.	FOP
			<i>longistipitatus</i>	M. Saba, S. Jabeen, Khalid & Dima	GenBank (MF872641); Saba et al. (2017)
			<i>leucopus</i>	(Bull.) Fr.	GenBank (JN133921)
			<i>melanotus</i>	Kalchbr.	Sultana et al. (2011)
			<i>olivaceofuscus</i>	Kühner	Sultana et al. (2011)
			<i>pakistanicus</i>	A. Naseer & A. N. Khalid	Naseer et al. (2020b)
			<i>percomis</i>	Fr.	Sultana et al. (2011)
			<i>pseudotorvus</i>	A. Naseer, J. Khan & A.N. Khalid	GenBank (MN864286); Naseer et al. (2020b)
			<i>purpureus</i>	(Bull.) Bidaud, Moënné- Locc. & Reumaux	FOP
			<i>rufo-olivaceus</i>	(Pers.) Fr.	Sultana et al. (2011)
			<i>sanguineus</i>	(Wulfen) Gray	Sultana et al. (2011)
			<i>subturbinateus</i>	Rob. Henry	Sultana et al. (2011)
			<i>violaceus</i>	(L.) Gray	Sultana et al. (2011)
	Crepidotaceae	<i>Crepidotus</i>	<i>applanatus</i>	(Pers.) P. Kumm.	FOP
			<i>caspari</i>	Velen.	FOP
			<i>epibryus</i>	(Fr.) Quel.	FOP
			<i>mollis</i>	(Schaeff.) Staude	FOP
	Cyphellaceae	<i>Simocybe</i>	<i>centunculus</i>	(Fr.) P. Karst.	Razaq and Shahzad (2017)
		<i>Chondrostereum</i>	<i>purpureum</i>	(Pers.) Pouzar	FOP
	Entolomataceae	<i>Clitocella</i>	<i>mundula</i>	(Lasch) Kluting, T.J. Baroni & Bergemann	FOP
			<i>popinalis</i>	(Fr.) Kluting, T.J. Baroni & Bergemann	Sultana et al. (2011)
		<i>Clitopilus</i>	<i>apalus</i>	(Berk. & Broome) Petch	FOP
			<i>hobsonii</i>	(Berk.) P.D. Orton	FOP
			<i>peri</i>	(Berk. & Broome) Petch	FOP
			<i>pinsitus</i>	(Fr.) Joss.	FOP
		<i>Entoloma</i>	<i>scyphoides</i>	(Fr.) Singer	Sultana et al. (2011)
			<i>cetratum</i>	(Fr.) M.M. Moser	Sultana et al. (2011)
			<i>gnophodes</i>	Berk. & Broome) E. Horak	FOP
			<i>gnaphalodes</i>	(Berk. & Broome) E. Horak	FOP
			<i>incanum</i>	(Fr.) Hesler	FOP
			<i>iodnephes</i>	(Berk. & Broome) Pegler	FOP
			<i>mougeotii</i>	(Fr.) Hesler	Sultana et al. (2011)

Phylum/Order	Family	Genus	Species	Authority	Source	
Agaricales	Entolomataceae	<i>Entoloma</i>	<i>papillatum</i>	(Bres.) Dennis	Sultana et al. (2011)	
			<i>polycolor</i>	Blanco-Dios	FOP	
			<i>shandongense</i>	T. Bau & J.R. Wang	GenBank (MT255022); Haelewaters et al. (2020)	
		<i>Leptonia</i>	<i>gnaphodes</i>	(Berk. & Broome) Sacc.	FOP	
		<i>Rhodocybe</i>	<i>truncata</i>	(Schaeff.) Singer	Sultana et al. (2011)	
			<i>subgilva</i>	(Berk. & Broome) Pegler	FOP	
	Hygrophoraceae	<i>Arrhenia</i>	<i>epichysium</i>	(Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys	FOP	
			<i>Hygrocybe</i>	<i>acutoconica</i>	(Clem.) Singer	Sultana et al. (2011)
		<i>bresadolae</i>	Quel.	FOP		
		<i>chlorophana</i>	(Fr.) Wunsch	FOP		
		<i>conica</i>	(Schaeff.) P. Kumm.	FOP; Sultana et al. (2011)		
		<i>nigrescens</i>	(Quél.) Kühner	Sultana et al. (2011)		
		<i>ovina</i>	(Bull.) Kühner	Sultana et al. (2011)		
		<i>spadicea</i>	(Scop.) P. Karst. [as 'Hydrocybe']	Sultana et al. (2011)		
		<i>Hygrophorus</i>	<i>alboflavescens</i>	A. Naseer & A.N Khalid	GenBank (MK066232); Naseer et al. (2019b)	
			<i>agathomus</i>	Fr. (Fr.)	FOP	
			<i>chrysodon</i>	(Batsch) Fr.	Razaq et al. (2014b)	
			<i>marzuolus</i>	(Fr.) Bres.	Razaq and Shahzad (2005a)	
			<i>pudorinus</i>	(Fr.) Fr.	GenBank (MK066233); Naseer et al. (2019b)	
			<i>scabrellus</i>	A. Naseer & A.N Khalid	Genbak (MK066234); Naseer et al. (2019b)	
		Hydnangiaceae	<i>Laccaria</i>	<i>amethystina</i>	Cooke	FOP
				<i>bicolor</i>	(Maire) P.D. Orton	Sultana et al. (2011)
				<i>glioderma</i>	(Fr.) Maire	FOP
	<i>laccata</i>			(Scop.) Cooke	Sultana et al. (2011)	
	<i>obiensis</i>			(Mont.) Singer	Sultana et al. (2011)	
	<i>tortilis</i>			(Bolton) Cooke	Sultana et al. (2011)	
	Hymenogas- traceae	<i>Galerina</i>	<i>marginata</i>	(Batsch) Kühner	FOP	
		<i>Gymnopilus</i>	<i>aeruginosus</i>	(Peck.) Singer	FOP	
			<i>chrysimyces</i>	(Berk.) Manjula	FOP	
			<i>chrysomyces</i>	(Berk.) Pegler.	FOP	
			<i>chrysites</i>	(Berk.) Singer	FOP	
			<i>dunensis</i>	H. Bashir, Jabeen & Khalid	GenBank (MK088247); Bashir et al. (2020b)	
			<i>holocrocinus</i>	(Berk.) Singer	FOP	
			<i>hybridus</i>	(Gillet) Maire	FOP	
			<i>junonius</i>	(Fr.) P.D. Orton	FOP	
			<i>lepidotus</i>	Hesler	GenBank (MK584298); Bashir et al. (2018)	
			<i>penetrans</i>	(Fr.) Murrill.	GenBank (MF136815); Khan et al. (2017b)	
			<i>sapineus</i>	(Fr.) Murrill	FOP	
			<i>swaticus</i>	J. Khan, Sher & Khalid	GenBank (MF149864); Khan et al. (2017b)	
		<i>Hebeloma</i>	<i>anthracophilum</i>	Maire	Sultana et al. (2011)	
			<i>atrocoerulea</i>	(Fr.) Singer.	FOP	
			<i>aff. Lutense</i>		GenBank	
			<i>mesophaeum</i>	(Pers.) Quél.	FOP; Razaq et al. (2017)	
			<i>pusillum</i>	J.E. Lange	FOP	
	<i>sinapizans</i>		(Paulet) Gillet	Sultana et al. (2011)		
	<i>theobrominum</i>		Quadr.	Razaq et al. (2017)		
	<i>bohémica</i>		Velen.	Sultana et al. (2011)		
	<i>Naucoria</i>		<i>conicopapillata</i>	(Henn.) Sacc. & P. Syd.	FOP	

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Hymenogasteraceae	<i>Naucoria</i>	<i>salicis</i>	P.D. Orton	FOP
		<i>Phaeocollybia</i>	<i>pakistanica</i>	J. Khan, Sher & Khalid	GenBank (KY007615); Khan et al. (2016a)
	Inocybaceae	<i>Psilocybe</i>	<i>coronilla</i>	(Bull.) Noordel.	FOP
			<i>semilanceata</i>	(Fr.) P. Kumm.	Sultana et al. (2011)
		<i>Inocybe</i>	<i>aff. amblyspora</i>	Kühner	GenBank (HG796912)
			<i>aff. cryptocystis</i>	D.E. Stuntz	GenBank (HG796963)
			<i>aff. glabripes</i>	Ricken	GenBank (HG796964)
			<i>aff. hirtella</i>	Bres.	GenBank (HG796965)
			<i>aff. nitidiuscula</i>	(Britzelm.) Lapl.	GenBank (HG796966)
			<i>ahmadii</i>	Farooqi, Niazi & Khalid	GenBank (KX254462); Farooqi et al. (2017)
			<i>amblyspora</i>	Kühner	GenBank (KX254462)
			<i>amicta</i>	Kokkonen & Vauras	GenBank (KJ686344); Saba et al. (2015)
			<i>argillacea</i>	(Pers.) Singer	FOP
			<i>asterospora</i>	Quel.	FOP; Sultana et al. (2011)
			<i>caroticolor</i>	T. Bau & Y. G. Fan	GenBank (MH473144); Naseer et al. (2019c)
			<i>cryptocystis</i>	D.E. Stuntz	GenBank (KF679812)
			<i>dulcamara</i>	(Pers.) P. Kumm.	FOP
			<i>fibrosa</i>	(Sowerby) Gillet	Sultana et al. (2011)
			<i>flocculosa</i>	Sacc.	FOP
			<i>fuscidula</i>	Velen.	Sultana et al. (2011)
			<i>glabripes</i>	Ricken	FOP; Sultana et al. (2011)
			<i>geophylla</i>	P. Kumm.	FOP; Sultana et al. (2011); Razaq and Shahzad (2017)
			<i>hirtella</i>	Bres.	Sultana et al. (2011)
			<i>inocybium</i>	NA	FOP
			<i>kobistanensis</i>	Jabeen, I. Ahmad & Khalid	GenBank (KP316243); Jabeen et al. (2016a)
			<i>leptocystis</i>	G.F. Atk	GenBank (KX254461); Farooqi et al. (2017)
			<i>napipes</i>	J.E. Lange	Sultana et al. (2011); Razaq and Shahzad (2017)
			<i>nitidiuscula</i>	(Britzelm.) Lapl.	GenBank (HE862959); Ilyas et al. (2013a)
			<i>oblectabilis</i>	(Britz.) Sacc.	FOP
			<i>posterula</i>	(Britzelm.) Sacc.	FOP
			<i>praetervisa</i>	Quél.	Sultana et al. (2011)
			<i>pyriodora</i>	(Pers.) P. Kumm.	FOP
			<i>shawarensis</i>	A. Naseer & A.N. Khalid	GenBank (KY616964); Naseer et al. (2017b)
			<i>vaccina</i>	Kühner	Sultana et al. (2011)
		<i>Inosperma</i>	<i>adaequatum</i>	(Britzelm.) Matheny & Esteve-Raventos	Sultana et al. (2011)
			<i>bongardii</i>	(Weinm.) Matheny & Esteve-Rav.	FOP
			<i>erubescens</i>	(A. Blytt) Matheny & Esteve-Rav.	FOP; Sultana et al. (2011)
		<i>Mallocybe</i>	<i>agardhii</i>	(N. Lund) Matheny & Esteve-Rav.	Razaq and Shahzad (2017)
		<i>Pseudosperma</i>	<i>velutina</i>	Saba & Khalid	Saba and Khalid (2020)
			<i>brunneoumbonatum</i>	Saba & Khalid	GenBank (MG742419); Saba et al. (2020b)
			<i>flavorimosum</i>	Jabeen & Khalid	GenBank (MG495391); Jabeen and Khalid (2020)
			<i>himalayense</i>	(Razaq, Khalid & Kobayashi) Matheny & Esteve-Rav.	GenBank (MH745140); Liu et al. (2018)

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Inocybaceae	<i>Pseudosperma</i>	<i>mimicum</i>	(Masse) Matheny & Esteve-Rav	GenBank (KJ546158); Saba et al. (2015)
			<i>pakistanense</i>	(Z. Ullah, S. Jabeen, H. Ahmad & A.N. Khalid)	GenBank (MF588965); FOP; Ullah et al. (2018)
			<i>rimosum</i>	(Bull.) Matheny & Esteve-Rav.	FOP; Sultana et al. (2011)
			<i>squamatum</i>	(J.E. Lange) Matheny & Esteve-Rav.	FOP
		<i>Langermannia</i>	<i>wahlbergii</i>	(Fr.) Dring	FOP
		<i>Apioperdon</i>	<i>pyriforme</i>	(Schaeff.) Vizzini	FOP
		<i>Bovista</i>	<i>bovistoides</i>	(Cooke & Masse) S. Ahmad	FOP
			<i>concinna</i>	S. Ahmad	FOP
			<i>himalaica</i>	Yousaf, Krieisel & Khalid	GenBank (JN411938); Yousaf et al. (2012a)
			<i>longispora</i>	Krieisel	FOP
			<i>lycoperdoides</i>	(Cooke) S. Ahmad	FOP
			<i>plumbea</i>	Pers.	GenBank (JX183694); Yousaf et al. (2014)
			<i>polymorpha</i>	Krieisel	FOP
			<i>pusilla</i>	(Batsch) Pers.	FOP
			<i>trachyspora</i>	(Lloyd) Krieisel	FOP
		<i>Bovistella</i>	<i>japonica</i>	Lloyd	Yousaf et al. (2012b)
		<i>Bryoperdon</i>	<i>acuminatum</i>	(Bosc) Vizzini	FOP
		<i>Calvatia</i>	<i>ahmadii</i>	Khalid & S.H. Iqbal	Khalid and Iqbal (2004)
			<i>craniiformis</i>	(Schwein.) Fr.	FOP
			<i>cyathiformis</i>	(Bose) Morgan	FOP
			<i>fragilis</i>	(Quél.) Morgan	GenBank (AJ486958)
			<i>lilacina</i>	(Mont. & Berk.) Henn.	Genbank (MN544913); Haelewaters et al. (2020)
		<i>Lycoperdon</i>	<i>atropurpureum</i>	Vittad.	FOP
			<i>curtisii</i>	Berk.	GenBank (MK414502)
			<i>echinella</i>	(Pat.) S. Ahmad	FOP
			<i>excipuliforme</i>	(Scop.) Pers.	FOP; Yousaf et al. (2012b)
			<i>glabrescens</i>	Berk.	FOP
			<i>laborenses</i>	N. Yousaf & A.N. Khalid	GenBank (MK414506); Yuan et al. (2020)
			<i>molle</i>	Pers.	Razaq and Shahzad (2005b)
			<i>perlutum</i>	Pers.	FOP
			<i>pratense</i>	Pers.	GenBank (MK414499); FOP
			<i>pseudocurtisii</i>	N. Yousaf & A.N. Khalid	GenBank (MK414505); Yuan et al. 2020
			<i>rimulatum</i>	Peck	FOP
			<i>setiferum</i>	Demoulin	FOP
			<i>subterranea</i>	Ahmad	FOP
			<i>umbrinum</i>	Pers.	FOP
	Lyophollaceae	<i>Hypsizygus</i>	<i>marmoreus</i>	(Peck) H.E. Bigelow	FOP
		<i>Lyophyllum</i>	<i>decastes</i>	(Fr.) Singer	FOP
			<i>nigrescens</i>	Hongo	FOP
		<i>Sagaranelia</i>	<i>tesquorum</i>	(Fr.) V. Hofst., Cléménçon,	FOP
		<i>Tephroclybe</i>	<i>anthracophila</i>	Moncalvo & Redhead	FOP
			<i>aff. platypus</i>	(Lasch) P.D. Orton	GenBank (KY947353)
		<i>Termitomyces</i>	<i>acriumbonatus</i>	(Kühner) M.M. Moser	GenBank (MT179690); Usman and Khalid (2020b)
			<i>clypeatus</i>	Usman & Khalid	FOP
				R. Heim,	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Lyophollaceae	<i>Termitomyces</i>	<i>eurrhizus</i>	(Berk.) R. Heim	FOP
			<i>furfuracea</i>	(Fr.) Gillet	FOP
			<i>le-testui</i>	(Pat.) R. Heim	FOP
			<i>microcarpus</i>	(Berk. & Broome) R. Heim	FOP; Sultana et al. (2011); Sultana et al. (2014)
			<i>rabuorii</i>	Otieno	Sultana et al. (2011)
			<i>sheikhpurensis</i>	Izhar, Khalid & H. Bashir	Izhar et al. (2020)
			<i>striatus</i>	(Beeli) Heim	FOP
			<i>umkouwaaan</i>	(Cooke & Massee) D.A. Reid	GenBank (KJ703245); Hussain et al. (2015c)
	Macrocytidiaceae	<i>Macrocytidia</i>	<i>cucumis</i>	(Pers.) Joss.	FOP
	Marasmiaceae	<i>Chaetocalathus</i>	<i>niduliformis</i>	(Murrill) Singer	FOP
		<i>Collybiopsis</i>	<i>biformis</i>	(Peck) R.H. Petersen	GenBank (MT162681)
			<i>diminuta</i>	(Berk. & Broome) R.H. Petersen	FOP
			<i>peronata</i>	(Bolton) R.H. Petersen	Sultana et al. (2011)
		<i>Crinipellis</i>	<i>rubiginosa</i>	Pat.	FOP; Sultana et al. (2011)
			<i>scabella</i>	(Alb. & Schwein.) Murrill	FOP; Sultana et al. (2011)
		<i>Marasmius</i>	<i>atrorubens</i>	(Berk.) Mont.	FOP
			<i>corrugatiformis</i>	Singer	FOP
			<i>ferrugineus</i>	Berk. & Broome	FOP
			<i>graminum</i>	(Lib.) Berk.	FOP
			<i>griseoviolaceus</i>	Petch	FOP
			<i>haematocephalus</i>	(Mont.) Fr.	FOP
			<i>ochropus</i>	Singer	FOP
			<i>oreades</i>	(Bolton) Fr.	GenBank (HF546217); Razaq et al. (2013d)
			<i>palmivorus</i>	Sharples	GenBank (MN559682)
			<i>pulcherripes</i>	Peck	FOP
			<i>rotula</i>	(Scop.) Fr.	FOP
			<i>ruforotula</i>	Singer	FOP
			<i>tubulatus</i>	Petch	FOP
	Mycenaceae	<i>Mycena</i>	<i>epipterygia</i>	(Scop.) Gray	FOP
			<i>galericulata</i>	(Scop.) Gray	FOP
			<i>haematopus</i>	(Pers.) P. Kumm.	FOP
			<i>inclinata</i>	(Fr.) Quél.	Sultana et al. (2011)
			<i>leptocephala</i>	(Pers.) Gillet	Sultana et al. (2011)
			<i>metata</i>	(Fr.) P. Kumm.	FOP
			<i>pura</i>	(Pers.) P. Kumm.	FOP; Razaq et al. (2014)
			<i>stipticus</i>	(Bull.) P. Karst	FOP
		<i>Panellus</i>	<i>tenuipes</i>	(Schwein.) A.H. Sm.	FOP
		<i>Xeromphalina</i>	<i>corneipes</i>	(Fr.) Redhead & A.H. Sm.	GenBank (KY648897)
	Mythicomycetaceae	<i>Mythicomycetes</i>			
	Niaceae	<i>Merismodes</i>	<i>anomala</i>	(Pers.) Singer	FOP
	Omphalotaceae	<i>Anthracoephyllum</i>	<i>nigritum</i>	(Lév.) Kalchbr.	FOP
		<i>Gymnopus</i>	<i>androsaceus</i>	(L.) Della Magg. & Trassin.	Sultana et al. (2011)
			<i>barbipes</i>	R.H. Petersen & K.W. Hughes	GenBank (MK450334); Saba et al. (2020a)
			<i>dryophilus</i>	(Bull.) Murrill	FOP; Sultana et al. (2011)
			<i>dysodes</i>	(Halling) Halling	GenBank (MT114698); Saba and Khalid (2020c)
			<i>erythropus</i>	(Pers.) Antonín, Halling & Noordel.	Sultana et al. (2011)
			<i>fusipes</i>	(Bull.) Gray	FOP; Sultana et al. (2011)
			<i>hirtellus</i>	(Berk. & Broome) Desjardin & B.A. Perry	FOP
			<i>ocior</i>	(Pers.) Antonín & Noordel.	GenBank (MK122769)
			<i>subnudus</i>	Ellis ex Peck) Halling	GenBank (MK307636)

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Omphalotaceae	<i>Omphalotus</i>	<i>olearius</i>	(DC.) Singer	FOP; Razaq and Shahzad (2017)
		<i>Marasmiellus</i>	<i>biformis</i>	(Peck) J.S. Oliveira	Oliveira et al. (2019)
			<i>candidus</i>	(Fr.) Singer	GenBank (KJ906507); FOP
			<i>confluens</i>	(Pers.) J.S. Oliveira	FOP; Sultana et al. (2011)
			<i>inoderma</i>	(Berk.) Singer ex Furneaux	FOP
			<i>longistipes</i>	Muh. Ali, Niazi & Khalid	Haelewaters et al. (2020)
			<i>luxurians</i>	(Peck) J.S. Oliveira	GenBank (KF803761); Saba and Khalid (2014c)
			<i>menehune</i>	(Desjardin, Halling & Hemmes) J.S. Oliveira.	GenBank (KF803762); Saba and Khalid (2014c)
			<i>ramealis</i>	(Bull.) Singer	FOP; Sultana et al. (2011)
			<i>subnudus</i>	(Ellis ex Peck) J.S. Oliveira.	Oliveira et al. (2019)
		<i>Mycetinis</i>	<i>alliaceus</i>	(Jacq.) Earle ex A.W. Wilson & Desjardin	Sultana et al. (2011)
			<i>scorodoni</i>	(Fr.) A.W. Wilson & Desjardin	Sultana et al. (2011)
		<i>Rhodocollybia</i>	<i>butyracea</i>	(Bull.) Lennox	FOP
			<i>maculata</i>	(Alb. & Schwein.) Singer	FOP; Sultana et al. (2011)
			<i>prolixa</i>	(Fr.) Antonín & Noordel	Sultana et al. (2011)
			<i>utrorensis</i>	A. Sattar, M. Kiran & Khalid	GenBank (MH220536); Sattar et al. (2018)
	Physalacriaceae	<i>Armillaria</i>	<i>mellea</i>	(Vahl) P. Kumm	Sultana and Rizwana (2007)
			<i>omnituens</i>	(Berk.) Sacc.	FOP
		<i>Armillariella</i>	<i>mellea</i>	(Vahl) P. Karst	FOP; Sultana et al. (2011)
			<i>vara</i>	(Berk.) Sacc.	FOP
		<i>Desarmillaria</i>	<i>tabescens</i>	(Scop.) R.A. Koch & Aime	Sultana et al. (2011)
		<i>Flammulina</i>	<i>phlegmatica</i>	(Berk.) Sacc.	FOP
			<i>velutipes</i>	(Curtis) Singer	FOP
			<i>yunnanensis</i>	Z.W. Ge & Zhu L. Yang	GenBank (MN388767)
		<i>Hymenopellis</i>	<i>radicata</i>	(Relhan) R.H. Petersen	FOP; Sultana et al. (2011)
		<i>Strobilurus</i>	<i>esculentus</i>	(Wulfen) Singer	Sultana et al. (2011)
			<i>tenacellus</i>	(Pers.) Singer	GenBank (KY070339)
		<i>Xerula</i>	<i>pudens</i>	(Pers.) Singer	FOP; Sultana et al. (2011)
			<i>strigosa</i>	Zhu L. Yang, L. Wang & G.M. Muell.	GenBank (LK932286)
	Pluteaceae	<i>Pluteus</i>	<i>ephebeus</i>	(Fr.) Gillet	FOP
			<i>escharites</i>	(Berk. & Broome) Sacc.	FOP
			<i>fusconigricans</i>	(Berk. & Broome) Sacc.	FOP
			<i>laeticeps</i>		FOP
			<i>leoninus</i>	(Schaeff.) P. Kumm.	FOP
			<i>palumbinus</i>	(Berk.) Sacc.	FOP
			<i>pellitus</i>	(Pers.) P. Kumm.	FOP
			<i>petasatus</i>	(Fr.) Gillet	FOP
			<i>pulverulentus</i>	Murrill	FOP
			<i>squamosa</i>	(Pers. ex Fr.) Kummer	FOP
			<i>variabilicolor</i>	Babos	GenBank
		<i>Volvariella</i>	<i>bingensis</i>	(Beeli) Shaffer	Sultana et al. (2014)
			<i>castanea</i>	(Masse) G.C. Rath	FOP
			<i>media</i>	(Schumach.) Singer	FOP
			<i>pusilla</i>	(Pers.) Singer	FOP
			<i>taylorii</i>	(Berk. & Broome) Singer	FOP
			<i>woodrowiana</i>	(Masse) Manjula	FOP
		<i>Volvopluteus</i>	<i>earlei</i>	(Murrill) Vizzini, Contu & Justo	GenBank (MT353644)
			<i>gloiocephalus</i>	(DC.) Vizzini, Contu & Justo	FOP; Sultana et al. (2011)
	Pleurotaceae	<i>Acanthocystis</i>	<i>gemmellari</i>	Inzenga) Konrad & Maubl	FOP

Phylum/Order	Family	Genus	Species	Authority	Source	
Agaricales	Pleurotaceae	<i>Hohenbuebelia</i>	<i>atrocaerulea</i>	(Fr.) Singer	FOP	
			<i>petaloides</i>	(Bull.) Schulzer	FOP	
			<i>reniformis</i>	(G. Mey.) Singer	FOP	
		<i>testudo</i>	(Berk.) Pegler	FOP		
		<i>Nothopanus</i>	<i>candidissimus</i>	(Sacc.) Kühner	FOP	
		<i>Pleurotus</i>	<i>atricapillus</i>	(Batsch.) Singer	FOP	
		<i>cystidiosus</i>	O.K. Mill.	GenBank (KR149589); Hussain et al. (2015a)		
		<i>djamor</i>	(Rumph. ex Fr.) Boedijn	GenBank (KX056435)		
		<i>dryinus</i>	(Pers.) P. Kumm.	Sultana et al. (2011)		
		<i>flabellatus</i>	Sacc.	FOP		
		<i>membranaceus</i>	Massee	FOP		
		<i>nebrodensis</i>	(Inzenga) Quél.	FOP		
		<i>ostreatus</i>	(Jacq.) P. Kumm.	FOP		
		<i>Resupinatus</i>	<i>applicatus</i>	(Batsch) Gray	FOP	
		<i>poriaeformis</i>	(Pers.) Thorn, Moncalvo & Redhead	FOP		
		Porothelaceae	<i>Phloeomana</i>	<i>speirea</i>	(Fr.) Redhead	Sultana et al. (2011)
		Psathyrellaceae	<i>Britzelmayria</i>	<i>multipedata</i>	(Peck) D. Wächt. & A. Melzer	FOP
			<i>Coprinellus</i>	<i>campanulatus</i>	S. Hussain & H. Ahmad	Hussain et al. (2018a)
				<i>disseminatisimilis</i>	S. Hussain	Hussain et al. (2018a)
				<i>disseminatus</i>	(Pers.) J.E. Lange	FOP; Razaq et al. (2014)
	<i>marculentus</i>		(Britzelm.) Redhead, Vilgalys & Moncalvo	FOP		
	<i>micaceus</i>		(Bull.) Vilgalys, Hopple & Jacq. Johnson	FOP		
	<i>ovatus</i>		M. Kamran & S. Jabeen	Kamran and Jabeen (2020)		
	<i>radians</i>		(Desm.) Vilgalys, Hopple & Jacq. Johnson	FOP; Sultana et al (2014)		
	<i>tenuis</i>		S. Hussain	Hussain et al. (2018a)		
	<i>Coprinopsis</i>		<i>atramentaria</i>	(Bull.) Redhead, Vilgalys & Moncalvo	GenBank (KM977767); FOP; Sultana et al. (2011)	
	<i>cinerea</i>		(Schaeff.) Redhead, Vilgalys & Moncalvo	Razaq et al. (2014)		
	<i>lagopus</i>		(Fr.) Redhead, Vilgalys & Moncalvo	FOP; Sultana et al. (2011)		
	<i>lagopides</i>		(P. Karst.) Redhead, Vilgalys & Moncalvo	FOP		
	<i>macropus</i>		(Berk. & Broome) Redhead, Vilgalys & Moncalvo	FOP		
	<i>patouillardii</i>		(Quél.) Gminder	FOP; Sultana et al. (2011)		
	<i>Homophron</i>		<i>spadiceum</i>	(P. Kumm.) Örstadius & E. Larss.	FOP	
	<i>Parasola</i>		<i>auricoma</i>	(Pat.) Redhead Vilgalys & Hopple.	GenBank (KY461721); FOP; Hussain et al. (2018d)	
	<i>conopilea</i>		(Fr.) A. Pearson & Dennis	Sultana et al. (2011)		
	<i>glabra</i>		S. Hussain, Afshan, H. Ahmad & Khalid	GenBank (KY621805); Hussain et al. (2018d)		
	<i>lilatincta</i>		(Bender & Ulje), Redhead, & Hopple	GenBank (KP886462); Hussain et al. (2016)		
	<i>malakandensis</i>	S. Hussain, Afshan & H. Ahmad	GenBank (KP738713); Hussain et al. (2017)			
	<i>plicatilis</i>	(Curtis) Redhead, Vilgalys & Hopple	FOP			
	<i>pseudolactea</i>	Sadiquallah, S. Hussain & Khalid	GenBank (KY621799); Hussain et al. (2018d)			
	<i>schroeteri</i>	(P. Karst.) Redhead, Vilgalys & Hopple	GenBank (KY461722)			

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Psathyrellaceae	<i>Parasola</i>	<i>setulosa</i>	(Berk. & Broome) Redhead, Vilgalys & Hopple	FOP; Sultana et al. (2011)
		<i>Psathyrella</i>	<i>atomata</i>	(Fr.) Quél.	Sultana et al. (2011)
			<i>ammophila</i>	(Durieu & Lév.) P.D. Orton	Sultana et al. (2011)
			<i>artemisiae</i>	(Pass.) Konrad & Maubl.	Sultana et al. (2011)
			<i>bipellis</i>	Quél.) A.H. Sm.	Sultana et al. (2011)
			<i>candolleana</i>	(Fr.) Maire	GenBank (KJ917666); FOP; Sultana et al. (2011)
			<i>corrugis</i>	(Pers.) Konrad & Maubl.	FOP; Sultana et al. (2011)
			<i>efflorescens</i>	(Sacc.) Pegler	FOP
			<i>flavogrisea</i>	(Berk.) Pegler	FOP
			<i>hirta</i>	Peck	Sultana et al. (2011)
			<i>nana</i>	(Massee) Manjula	FOP
			<i>piluliformis</i>	(Bull.) P.D. Orton	FOP
			<i>spadiceogrisea</i>	(Schaeff.) Maire	FOP
			<i>spintrigera</i>	(Fr.) Konr & Maubl.	FOP
		<i>Punjabia</i>	<i>pakistanica</i>	(Usman & Khalid) D. Wächt. & A. Melzer	GenBank (MH366737); Hussain et al. (2018a)
				Fr.	GenBank (MN178555); FOP
	Schizophyllaceae	<i>Schizophyllum</i>	<i>commune</i>		FOP
			<i>radiatum</i>	Fr.	FOP
	Strophoriaceae	<i>Sramatoscypha</i>	<i>fimbriata</i>	(Fr.) Donk.	FOP
		<i>Agrocybe</i>	<i>arvalis</i>	(Fr.) Singer	Sultana et al. (2011)
			<i>broadwayi</i>	(Murrill) Dennis	FOP
			<i>manibotis</i>	Pegler	FOP
			<i>pediades</i>	(Fr.) Fayod	GenBank (MK791714), FOP
			<i>stercoraria</i>	Pegler	FOP
		<i>Deconica</i>	<i>vervacti</i>	(Fr.) Singer	Sultana et al. (2011)
			<i>coprophila</i>	(Bull.) P. Karst.	FOP
			<i>merdaria</i>	(Fr.) Noordel.	FOP
			<i>montana</i>	(Pers.) P.D. Orton	FOP
			<i>pseudobullacea</i>	(Petch) Ram.-Cruz & Guzmán	FOP
		<i>Hypholoma</i>	<i>elongatum</i>	(Pers.) Ricken	Sultana et al. (2011)
			<i>fasciculare</i>	(Huds.) P. Kumm.	FOP; Sultana et al. (2011)
			<i>marginatum</i>	J.Schröt.	Sultana et al. (2011)
			<i>radicosum</i>	J.E. Lange	Sultana et al. (2011)
		<i>Kuehneromyces</i>	<i>mutabilis</i>	(Schaeff.) Singer & A.H. Sm.	FOP
		<i>Melanotus</i>	<i>proteus</i>	(Sacc.) Singer	FOP
		<i>Pholiota</i>	<i>aurivella</i>	(Batsch) P. Kumm.	FOP
			<i>gummosa</i>	(Lasch) Singer	GenBank (MT995199)
			<i>lubrica</i>	(Pers.) Singer	FOP
			<i>lucifera</i>	(Lasch.) Quél.	FOP
			<i>populnea</i>	(Pers.) Kuyper & Tjall.-Beuk.	FOP
			<i>spumosa</i>	(Fr.) Singer	FOP
			<i>squarrosa</i>	(Vahl) P. Kumm.	FOP
			<i>tuberculosa</i>	(Schaeff.) P. Kumm.	Sultana et al. (2011)
			<i>semiglobata</i>	(Batsch) Redhead, Moncalvo & Vilgalys	FOP
				(Curtis) Quél.	FOP
		<i>Stropharia</i>	<i>aeruginosa</i>	(Peck) Zeller	GenBank (MN957717)
			<i>ambigua</i>	M.B. Khan, Fiaz & A. N. Khalid	GenBank (MK141060); Khan et al. (2019)
			<i>atroferruginea</i>		
	Tricholomataceae	<i>Leucopaxillus</i>	<i>paradoxus</i>	Costantin & L.M. Dufour Boursier [as 'paradoxa']	Sultana et al. (2011)

Phylum/Order	Family	Genus	Species	Authority	Source
Agaricales	Tricholomataceae	<i>Leucopaxillus</i> <i>Tricholoma</i>	<i>gentianeus</i>	(Quel.) Kotl.	FOP; Sultana et al. (2011)
			<i>aurantium</i>	(Schaeff.) Ricken	FOP
			<i>elegans</i>	G. Stev.	FOP
			<i>lascivum</i>	(Fr.) Gillet	FOP
			<i>matsutake</i>	(S. Ito & S. Imai) Singer	GenBank (MT448907)
			<i>myomyces</i>	(Pers.) J.E. Lange	GenBank (HF546219)
			<i>terreum</i>	(Schaeff.) P. Kumm.	FOP
			<i>ustale</i>	(Fr.) P. Kumm.	Razaq et al. (2014)
			<i>vaccinum</i>	(Schaeff.) P. Kumm.	FOP; Sultana et al. (2011)
			<i>decora</i>	(Fr.) Singer	FOP
			<i>flammula</i>	Métrod ex Holec	GenBank (FR822742); Razaq et al. (2012c)
			<i>inamoenum</i>	(FR.) Gill	Sultana et al. (2011)
			<i>rutilans</i>	(Schaeff.) Singer	FOP
			<i>sulphurescens</i>	Bres.	Sultana et al. (2011)
	Tubariaceae	<i>Cyclocybe</i>	<i>erebia</i>	(Fr.) Vizzini & Matheny	GenBank (MT994783), FOP
			<i>Flammulaster</i>	(Fr.) Earle ex Vellinga	FOP
		<i>Tubaria</i>	<i>carpophilus</i>	(Berk. & Broome) Pegler	FOP
			<i>fulvoalbus</i>	(Pers.) Fayod	FOP
			<i>conspersa</i>	(Pers.) Gillet	FOP
	Typhulaceae	<i>Pistillaria</i>	<i>furfuracea</i>	(Pers.) Corner	FOP
			<i>filiformis</i>	Corner	FOP
		<i>Clitocybe</i>	<i>dealbata</i>	(Sowerby) P. Kumm.	FOP
			<i>fragrans</i>	(With.) P. Kumm.	Sultana et al. (2014)
			<i>infundibuliformis</i>	(Schaeff.) Quél.	FOP; Sultana et al. (2011)
			<i>metachroa</i>	(Fr.) P. Kumm	Sultana et al. (2011)
			<i>nebularis</i>	(Batsch) P. Kumm.	Sultana et al. (2011)
			<i>squamulosa</i>	(Pers.) P. Kumm.	Sultana et al. (2011)
			<i>vibecina</i>	(Fr.) Quél.	FOP
		<i>Clitocybula</i>	<i>lacerata</i>	(Scop.) Métrod	FOP
		<i>Crucibulum</i>	<i>laeve</i>	(Huds.) Kambly	FOP
		<i>Collybia</i>	<i>macra</i>	Sacc.	FOP
			<i>reineckeana</i>	Henn.	FOP
		<i>Cyathus</i>	<i>triplicata</i>	(Berk.) Sacc.	FOP
			<i>limbatus</i>	Tul. & C. Tul.	FOP
			<i>olla</i>	(Batsch) Pers.	GenBank (MH593250)
		<i>Fistulina</i>	<i>stercoreus</i>	(Schwein.) De Toni	FOP
			<i>hepatica</i>	(Schaeff.) With.	FOP
		<i>Infundibulicybe</i>	<i>gibba</i>	(Pers.) Harmaja	GenBank (MT994778); FOP
			<i>kotanensis</i>	M Ishaq, Fiaz & A.N. Khalid	GenBank (MN017278); Ishaq et al. (2019b)
			<i>macrospora</i>	M. Ali, J. Khan, Niazi & Khalid	GenBank (MT548910); Ali et al. (2020)
		<i>Lactocollybia</i>	<i>epia</i>	(Berk. & Broome) Pegler	FOP
			<i>variicystis</i>	D.A. Reid & Eicker	GenBank (MN250288)
		<i>Lepista</i>	<i>caffrorum</i>	(Kalchbr. & McOwen) Singer	FOP
			<i>irina</i>	(Fr.) H.E. Bigelow	GenBank (KJ194172); FOP
			<i>nuda</i>	(Bull.) Cooke	Sultana et al. (2011)
			<i>sordida</i>	(Schumach.) Singer	FOP
			<i>platyphylla</i>	(Pers.) Kotl. & Pouzar	FOP; Sultana et al. (2011)
		<i>Melanoleuca</i>	<i>cinereifolia</i>	(Bon) Bon	GenBank (KJ182965); Saba and Khalid (2014b)
			<i>dirensis</i>	F. Nawaz, Jabeen & Khalid	GenBank (KU556797); Nawaz et al. (2017)
			<i>excissa</i>	(Fr.) Singer	FOP
			<i>graminicola</i>	Kühner & Maire	Genbank (KX908113); Nawaz et al. (2017)

Phylum/Order	Family	Genus	Species	Authority	Source		
Agaricales	Typhulaceae	<i>Melanoleuca</i>	<i>kashmirensis</i>	R. Khurshed, Z. Ullah, Jabeen, H. Ahmad & Khalid	GenBank (MK541789); Ullah et al. (2020a)		
		<i>Paralepista</i>	<i>flaccida</i>	(Sowerby) Vizzini	FOP; Razaq et al. (2014)		
		<i>Secotium</i>	<i>acuminatum</i>	Mont.	FOP		
		<i>Phaeolepiota</i>	<i>aurea</i>	(Matt.) Maire	FOP; Razaq et al. (2014)		
		<i>Trogia</i>	<i>infundibuliformis</i>	Berk. & Broome	FOP		
	Incertae sedis	<i>Leucocybe</i>	<i>connata</i>	(Schumach.) Vizzini, P. Alvarado, G. Moreno & Consiglio	GenBank (HE819396); FOP; Razaq et al. (2012b)		
		<i>Henningsomyces</i>	<i>candidus</i>	(Pers.) Kuntze	FOP		
		<i>Panaeolus</i>	<i>acuminatus</i>	(P. Kumm.) Quél.	Sultana et al. (2011)		
			<i>cyanescens</i>	Sacc.	FOP		
			<i>fimicola</i>	(Pers.) Gillet	FOP; Sultana et al. (2011)		
			<i>papilionaceus</i>	(Bull.) Quél.	GenBank (HE819397); Razaq et al. (2012b)		
			<i>rickenii</i>	Hora.	FOP; Sultana et al. (2011)		
			<i>semiovatus</i>	(Sowerby) S. Lundell & Nannf.	FOP		
		Amylocorticiales	Amylocorticiaceae	<i>Anomoloma</i>	<i>myceliosum</i>	(Peck) Niemelä & K.H. Larss.	FOP
			Incertae sedis	<i>Athelia</i>	<i>rolfsii</i>	(Curzi) C.C. Tu & Kimbr.	GenBank
<i>Plicatura</i>	<i>crispa</i>			(Pers.) D.A. Reid	FOP		
Atheliales	Atheliaceae		<i>Amphinema</i>	<i>byssoides</i>	(Pers.) J. Erikss	FOP	
Boletales	Boletaceae		<i>Aureoboletus</i>	<i>gentilis</i>	(Quél.) Pouzar	Razaq and Shahzad (2013)	
		<i>Boletus</i>	<i>barrowsii</i>	Thiers & A.H. Sm.	Niazi (2008)		
			<i>edulis</i>	Bull.	FOP; Razaq and Shahzad (2013)		
			<i>erythropus</i>	Krombh.	FOP		
			<i>himalayensis</i>	Jabeen, Sarwar & Khalid	Sarwar et al. (2018a)		
			<i>pakistanicus</i>	S. Sarwar & Khalid	GenBank (JQ178324); Sarwar and Khalid (2014)		
			<i>reticulatus</i>	Schaeff.	Niazi (2008); Razaq and Shahzad (2013)		
			<i>reticuloceps</i>	(M. Zang, M.S. Yuan & M.Q. Gong) Q.B. Wang & Y.J. Yao	GenBank (KJ131224)		
			<i>subvelutipes</i>	Peck	FOP		
		<i>Butyriboletus</i>	<i>appendiculatus</i>	(Schaeff.) D. Arora & J.L. Frank	FOP		
		<i>Caloboletus</i>	<i>calopus</i>	(Pers.) Vizzini	FOP		
		<i>Chalciporus</i>	<i>piperatus</i>	(Bull.) Bataille	Sultana et al. (2011); Razaq and Shahzad (2013)		
		<i>Cyanoboletus</i>	<i>pulverulentus</i>	(Opat.) Gelardi, Vizzini & Simonini	FOP		
		<i>Hortiboletus</i>	<i>kobistanensis</i>	A. Naseer, S. Sarwar & A.N. Khalid	GenBank (MK002767); Naseer et al. (2019a)		
			<i>rubellus</i>	(Krombh.) Simonini, Vizzini & Gelardi	GenBank (KJ802928); Sarwar et al. (2016)		
<i>Leccinum</i>	<i>aurantiacum</i>	(Bull.) Gray	Razaq and Shahzad (2017); Sultana et al. (2011)				
	<i>scabrum</i>	(Bull.) Gray	Sultana et al. (2011); Razaq and Shahzad (2017)				
	<i>ustale</i>	(Berk.) E. Horak	FOP				
	<i>versipelle</i>	(Fr. & Hök) Snell	Razaq and Shahzad (2017)				
<i>Leccinellum</i>	<i>crociopodium</i>	(Letell.) Della Magg. & Trassin.	Razaq and Shahzad (2017)				
	<i>pseudoscabrum</i>	(Kallenb.) Mikšik	Razaq and Shahzad (2017)				
<i>Neoboletus</i>	<i>luridiformis</i>	(Rostk.) Gelardi, Simonini & Vizzini	GenBank (KJ802930); Sarwar et al. (2016)				

Phylum/Order	Family	Genus	Species	Authority	Source
Boletales	Boletaceae	<i>Phylloporus</i>	<i>bibulosa</i>	(Lloyd) Ryv.	FOP
			<i>brunneiceps</i>	N.K. Zeng, Zhu L. Yang & L.P. Tang	GenBank (KY679591); Naseer et al. (2017a)
			<i>rhodoxanthus</i>	(Schwein.) Bres.	Sultana et al. (2011)
		<i>Porphyrellus</i>	<i>porphyrosporus</i>	(Fr. & Hök) E.-J. Gilbert	FOP; Razaq and Shahzad (2017)
			<i>parasiticus</i>	(Bull.) Šutara	FOP
		<i>Pseudoboletus</i>	<i>lupinus</i>	(Fr.) Costanzo, Gelardi, Simonini & Vizzini	Sultana et al. (2011)
		<i>Rubroboletus</i>	<i>longistipitatus</i>	D. Chakr. K. Das & S. Adhikari	GenBank (MK518064); Ullah et al. (2019a)
			<i>strobilaceus</i>	(Scop.) Berk.	FOP
		<i>Tylopilus</i>	<i>felleus</i>	(Bull.) P. Karst	Razaq and Shahzad (2017)
			<i>pseudoscaber</i>	Secr. ex A.H. Sm. & Thiers	GenBank (KJ775785); Sarwar et al. (2014a)
			<i>sultanii</i>	S. Sarwar, Khalid & Niazi,	GenBank (KJ775786); Sarwar et al. (2014a)
		<i>Xanthoconium</i>	<i>separans</i>	(Peck) Halling & Both	Gardezi (2003); Razaq et al. (2014)
			<i>dryophilus</i>	(Thiers) N. Siegel, C.F. Schwarz & J.L. Frank	Gardezi (2003)
			<i>fulvus</i>	Sarwar, I. Ahmad & Khalid	Hernández-Restrepo et al. (2016)
		<i>Xerocomus</i>	<i>ferrugineus</i>	(Schaeff.) Alessio	FOP
			<i>indicus</i>	Singer	FOP
			<i>rubellus</i>	Quél.	Niazi (2008)
			<i>subtomentosus</i>	(L.) Quél	Sultana et al. (2011); Razaq and Shahzad (2013)
	Coniophoraceae	<i>Coniophora</i>	<i>arida</i>	(Fr.) P. Karst.	FOP
			<i>fusispora</i>	(Cooke & Ellis) Cooke	FOP
		<i>Gyrodontium</i>	<i>sacchari</i>	(Spreng.) Hjortstam	FOP
	Diplocystidiaceae	<i>Gomphidius</i>	<i>glutinosus</i>	(Schaeff.) Fr.	FOP
		<i>Gyrodon</i>	<i>lividus</i>	(Bull.) Sacc.	Razaq and Shahzad (2017)
	Gastrosporiaceae	<i>Astraeus</i>	<i>hygrometricus</i>	(Pers.) Morgan	FOP; Yousaf et al. (2014)
		<i>Gastrosporium</i>	<i>simplex</i>	Mattir.	FOP
	Gomphidiaceae	<i>Chroogomphus</i>	<i>helveticus</i>	(Singer) M.M. Moser	FOP
			<i>pakistanicus</i>	M. Kiran & A.N. Khalid	GenBank (MK509771); Kiran et al. (2020)
			<i>pruinosis</i>	M. Kiran & A.N. Khalid	GenBank (MK509769); Kiran et al. (2020)
			<i>roseolus</i>	Y.C. Li & Zhu L. Yang	GenBank (LT576117); Razaq et al. (2016a)
			<i>rutilus</i>	(Schaeff.) O.K. Mill.	FOP
			<i>mollusca</i>	(Fr.) Pouzar	FOP
			<i>pinastri</i>	(Fr.) Ginns & Weresub	FOP
	Hygrophoropsidaceae	<i>Melanogaster</i>	<i>durissimus</i>	Cooke	FOP
			<i>flavus</i>	Petch	FOP
	Rhizopogonaceae	<i>Rhizopogon</i>	<i>albus</i>	(Cooke & Massee) Priest	GenBank (MN295477)
	Sclerodermataceae	<i>Pisolithus</i>	<i>tinctorius</i>	(Mont.) E. Fisch.	GenBank (KF802173); Razaq and Shahzad (2004)
			<i>aff. cepa</i>	Pers.	GenBank (HG796946)
			<i>areolatum</i>	Ehrenb.	Yousaf et al. (2012c)
		<i>Scleroderma</i>	<i>aurantium</i>	(L.) Pers.	GenBank (KF802172)
			<i>bovista</i>	Fr.	GenBank (KF802171); FOP
			<i>cepa</i>	Pers.	FOP
			<i>chevalieri</i>	Guzmán	Yousaf et al. (2012c)
			<i>dictyosporum</i>	Pat.	Yousaf et al. (2012c)
			<i>flavidum</i>	Ellis & Everh.	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Boletales	Sclerodermataceae	<i>Scleroderma</i>	<i>sinnamariense</i>	Mont.	FOP
			<i>verrucosum</i>	(Bull.) Pers.	FOP
	Serpulaceae	<i>Serpula</i>	<i>lacrymans</i>	(Wulfen) J. Schröt.	GenBank (AJ557312), FOP
	Suillaceae	<i>Suillus</i>	<i>americanus</i>	(Peck) Snell	GenBank (KX213755); FOP; Sarwar et al. (2011)
			<i>bovinus</i>	(L.) Roussel	Sultana et al. (2011); Razaq and Shahzad (2016)
			<i>brevipes</i>	(Peck) Kuntze	Sarwar et al. (2011); Sarwar and Khalid (2014b)
			<i>collinitus</i>	(Fr.) Kuntze	Sultana et al. (2011); Sarwar and Khalid (2014b)
			<i>flavidus</i>	(Fr.) J. Presl	Sarwar et al. (2012); Sarwar and Khalid (2014b)
			<i>granulatus</i>	(L.) Roussel	FOP; Sarwar et al. (2014b)
			<i>grevillei</i>	(Klotzsch) Singer	FOP
			<i>himalayensis</i>	B. Verma & M.S. Ready	GenBank (KR056819); Sarwar et al. (2018b)
			<i>luteus</i>	(L.) Roussel	Razaq and Shahzad (2016); Sultana et al. (2011)
			<i>marginielevatus</i>	S. Sarwar, Khalid & Dentinger	GenBank (KJ361512); Sarwar et al. (2015)
			<i>placidus</i>	(Bonord.) Singer	FOP; Sultana et al. 2011
			<i>tomentosus</i>	Singer	FOP; Niazi (2008); Sarwar and Khalid (2014b)
			<i>triacicularis</i>	B. Verma & M.S. Reddy	GenBank (KM677929); Sarwar et al. (2015)
			<i>viscidus</i>	(L.) Roussel	Razaq et al. (2019)
		<i>Suillellus</i>	<i>luridus</i>	(Schaeff.) Murrill	FOP
			<i>queletii</i>	(Schulzer) Vizzini, Simonini & Gelardi	FOP
	Tapinellaceae	<i>Pseudomerulius</i>	<i>aureus</i>	(Fr.) Jülich	FOP
		<i>Tapinella</i>	<i>atrotoментosa</i>	(Batsch) Šutara	FOP
Cantharellales	Aphelariaceae	<i>Aphelaria</i>	<i>panuoides</i>	(Fr.) E.-J. Gilbert	FOP
			<i>ceracea</i>	Corner	FOP
	Hydnaceae	<i>Cantharellus</i>	<i>cibarius</i>	Fr.	FOP
			<i>coralloides</i>	(L.) J. Schröt.	FOP
			<i>cinerea</i>	(Bull.) J. Schröt.	FOP
		<i>Clavulina</i>	<i>cinerea var. gracilis</i>	Rea, Trans	FOP
			<i>rugosa</i>	(Bull.) J. Schröt	FOP
			<i>cinereus</i>	(Pers.) Pers.	GenBank (MF374488); Naseer and Khalid (2018)
		<i>Hydnum</i>	<i>repandum</i>	L.	FOP
			<i>rufescens</i>	Fr.	FOP
		<i>Multiclavula</i>	<i>mucida</i>	(Pers.) R.H. Petersen	FOP
Corticiales	Punctulariaceae	<i>Dendrocorticium</i>	<i>polygonioides</i>	(P. Karst.) Donk	FOP
Geastrales	Vuilleminiaceae	<i>Cytidia</i>	<i>salicina</i>	(Fr.) Burt.	FOP
	Geastraceae	<i>Geastrum</i>	<i>argenteum</i>	Cooke	FOP
			<i>clelandii</i>	Lloyd	FOP
			<i>corollinum</i>	(Batsch) Hollós	FOP
			<i>coronatum</i>	Schaeff. ex J. Schröt.	FOP
			<i>drummondii</i>	Berk.	FOP
			<i>fimbriatum</i>	Fr.	Razaq and Shahzad (2007)
			<i>lageniforme</i>	Vittad.	FOP
			<i>lageniforme var. ahmadii</i>	Stanck.	FOP
			<i>minimum</i>	Schwein.	FOP
			<i>nanum var. nanum</i>	Pers.	FOP
			<i>panjabense</i>	S. Ahmad	FOP

Phylum/Order	Family	Genus	Species	Authority	Source		
Geastrales	Geastraceae	<i>Geastrum</i>	<i>rufescens</i>	Pers.	FOP		
			<i>saccatum</i>	Fr.	FOP		
			<i>striatum</i>	DC.	FOP		
			<i>velutinum</i>	Morgan	FOP		
			<i>triplex</i>	Jungh.	FOP		
		<i>Myriostoma</i>	<i>coliforme</i>	(Dicks.) Corda	Yousaf et al. (2013b)		
		<i>Sphaerobolus</i>	<i>ingoldii</i>	Geml, D.D. Davis & Geiser	GenBank (MN957515)		
Gloeophyllales	<i>Gloeophyllaceae</i>	<i>Gloeophyllum</i>	<i>stellatus</i>	Tode	FOP		
			<i>sepiarium</i>	(Wulfen) P. Karst.	FOP		
			<i>striatum</i>	(Fr.) Murrill	FOP		
			<i>subferrugineum</i>	(Berk.) Bondartsev & Singer	FOP		
Gomphales	Clavariadelphaceae	<i>Neolentinus</i>	<i>lepideus</i>	(Fr.) Redhead & Ginns	FOP; Razaq et al. (2018)		
		<i>Clavariadelphus</i>	<i>elongatus</i>	J. Khan, Sher & Khalid	GenBank (MG768846); Sher et al. (2018)		
			<i>pakistanicus</i>	Hanif & Khalid	GenBank (HQ379937); Hanif et al. (2014)		
			<i>pistillaris</i>	(L.) Donk	FOP		
			<i>subfastigiatus</i>	V.L. Wells & Kempton	GenBank (JX275756); Hanif and Khalid (2013)		
			<i>truncatus</i>	Donk	FOP		
			<i>Gomphus</i>	<i>clavatus</i>	(Pers.) Gray	FOP	
				<i>megasporus</i>	Corner	FOP	
				<i>Phaeoclavulina</i>	<i>abietina</i>	(Pers.) Giachini	Nasim et al. (2008)
					<i>flaccida</i>	(Fr.) Giachini	FOP
			<i>Ramaria</i>	<i>auraea</i>	(Schaeff.) Quél.	Razaq and Shahzad (2005c)	
				<i>botrytis</i>	(Pers.) Bourdot	FOP	
	<i>flava</i>	(Schaeff.) Quél.		FOP			
	<i>flava var. flava</i>	(Schaeff.) Quél.		FOP			
				<i>flavescentoides</i>	Hanif & Khalid	GenBank (KC357769); Hanif et al. (2019)	
				<i>formosa</i>	(Pers.) Quél.	Nasim et al. (2008)	
				<i>fragillima</i>	(Sacc. & P. Syd.) Corner	FOP	
				<i>moelleriana</i>	(Bres. & Roum.) Corner	FOP	
				<i>pallida</i>	(Schaeff.) Ricken	FOP	
				<i>soluta</i>	(P. Karst.) Corner	FOP	
				<i>stricta</i>	(Pers.) Quél.	FOP	
				<i>subaurantiaca</i>	Corner	FOP	
				<i>Turbinellus</i>	<i>floccosus</i>	(Schwein.) Earle ex Giachini & Castellano	FOP
				Lentariaceae	<i>Lentaria</i>	<i>acuminata</i>	Berk.
<i>micheneri</i>						(Berk. & M.A. Curtis)	FOP
Hymenochaetales				Hymenochaetaeaceae	<i>Aurificaria</i>	<i>surculus</i>	Corner
	<i>indica</i>	(Masse) D.A. Reid	FOP				
	<i>Coltricia</i>	<i>bambusicola</i>	(Henn.) D.A. Reid			FOP	
		<i>cinnamomea</i>	(Jacq.) Murrill			FOP	
		<i>perennis</i>	(L.) Murrill			GenBank (MN892531); FOP	
	<i>Fomitiporia</i>	<i>punctata</i>	(P. Karst.) Murrill		FOP		
		<i>robusta</i>	(P. Karst.) Fiasson & Niemelä		FOP		
		<i>Fuscoporia</i>	<i>callimorpha</i>		(Lév.) Groposo, Log.-Leite & Góes-Neto	FOP	
					<i>ferruginosa</i>	(Schrad.) Murrill	FOP
					<i>senex</i>	(Nees & Mont.) Ghob.- Nejh.	FOP
					<i>torulosa</i>	(Pers.) T. Wagner & M. Fisch.	FOP
					<i>Hymenochaete</i>	<i>cinnamomea</i>	(Pers.) Bres.

Phylum/Order	Family	Genus	Species	Authority	Source
Hymenochaetales	Hymenochaetaceae	<i>Hymenochaete</i>	<i>cruenta</i>	(Pers.) Donk	FOP
			<i>leonina</i>	Berk. & M.A. Curtis	FOP
			<i>patelliformis</i>	G. Cunn.	FOP
			<i>rheicolor</i>	(Mont.) Lév.	FOP
			<i>rubiginosa</i>	(Dicks.) Lév.	FOP
			<i>semistupposa</i>	Petch	FOP
		<i>Hydnoporia</i>	<i>villosa</i>	(Lev) Bres.	FOP
			<i>xerantica</i>	(Berk.) S.H. He & Y.C. Dai	FOP
		<i>Inocutis</i>	<i>tabacina</i>	(Sowerby) Spirin, Miettinen & K.H. Larss.	FOP
			<i>dryophila</i>	(Berk.) Murrill	FOP
		<i>Inonotus</i>	<i>tamaricis</i>	(Pat.) Fiasson & Niemelä	FOP
			<i>cuticularis</i>	(Bull.) P. Karst.	FOP
		<i>Phellinopsis</i>	<i>hispidus</i>	(Bull.) P. Karst.	FOP
			<i>pachyphloeus</i>	(Pat.) T. Wagner & M. Fisch.	FOP
		<i>Phellinus</i>	<i>peristrophidis</i>	S. Ahmad	FOP
			<i>tabacinus</i>	(Mont.) G. Cunn.	FOP
		<i>Phellinus</i>	<i>tinctorius</i>	(Quél.) S. Ahmad	FOP
			<i>triqueter</i>	P. Karst.	FOP
		<i>Phellinus</i>	<i>conchata</i>	(Pers.) Y.C. Dai	FOP
			<i>allardii</i>	(Bres.) S. Ahmad	FOP
		<i>Phellinus</i>	<i>badius</i>	(Cooke) G. Cunn.	FOP
			<i>caryophylli</i>	(Racib.) G. Cunn.	FOP
		<i>Phellinus</i>	<i>contiguus</i>	(Pers. ex Fr.) Bours. & Galz.	FOP
			<i>fastuosus</i>	Lév.) S. Ahmad	FOP
		<i>Phellinus</i>	<i>gilvus</i>	(Schwein.) Pat.	FOP
			<i>gilvus var. scruposus</i>	(Fr.) Ahmad	FOP
		<i>Phellinus</i>	<i>igniarius</i>	(L.) Quél.	FOP
			<i>laevigatus</i>	(P. Karst.) Bourdot & Galzin	FOP
		<i>Phellinus</i>	<i>nilgheriensis</i>	(Mont.) G. Cunn.	FOP
			<i>pectinatus</i>	(Klotzsch) Quél.	FOP
		<i>Phellinus</i>	<i>pini</i>	(Brot.) Pilát	FOP
			<i>pini var. abietis f. microspora</i>	Pilat.	FOP
		<i>Phellinus</i>	<i>purpureagilvus</i>	(Petch.) Ryvarden	FOP
			<i>ribis</i>	(Schumach.) Quél.	FOP
		<i>Phellinus</i>	<i>ribis f. gymnosporiae</i>		FOP
			<i>ribis f. lycil</i>		FOP
		<i>Phellinus</i>	<i>rimosus</i>	(Berk.) Pilat.	FOP
			<i>ribis</i>	(Schumach.) Ryvarden	FOP
		<i>Phellinus</i>	<i>tiliae</i>	L.W. Zhou	GenBank (MN080232)
			<i>chrysites</i>	(Berk.) Ryvarden	FOP
		<i>Porodaedalea</i>	<i>himalayensis</i>	(Y.C. Dai) Y.C. Dai	GenBank (MK995632)
			<i>indica</i>	Spirin, Y.C. Dai & Vlasák	GenBank (MN829552)
		<i>Pseudoinonotus</i>	<i>dryadeus</i>	(Pers.) T. Wagner & M. Fisch.	FOP
			<i>tibetica</i>	Y.C. Dai & S.H. He	GenBank (MT050549)
		<i>Onnia</i>	<i>tomentosa</i>	(Fr.) P. Karst.	FOP
			<i>linteus</i>	(Berk. & M.A. Curtis) L.W. Zhou & Y.C. Dai	FOP
		<i>Xanthoporia</i>	<i>radiata</i>	(Sowerby) Tjura, Zmitr., Wasser, Raats & Nevo	Razaq and Shahzad (2017)
			<i>arguta</i>	(Fr.) J. Erikss.	FOP
		<i>Hyphodontiaceae</i>	<i>pallidula</i>	(Bres.) J. Erikss.	FOP
			<i>latemarginatus</i>	(Durr. & Mont.)	FOP
		<i>Oxyporaceae</i>	<i>populinus</i>	(Schumach.) Donk	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Hymeno- chaetales	Rickenellaceae	<i>Peniophorella</i>	<i>pubera</i>	(Fr.) P. Karst.	FOP
	Schizoporaceae	<i>Schizopora</i>	<i>paradoxa</i>	(Schrad.) Donk	FOP
		<i>Xylodon</i>	<i>raduloides</i>	Riebesehl & Langer	FOP
	Incertae sedis	<i>Trichaptum</i>	<i>abietinum</i>	(Pers. ex J.F. Gmel.) Ryvarden	FOP
Hysterangiales	Phallogastraceae	<i>Protuberia</i>	<i>biforme</i>	(Fr.) Ryvarden	FOP
			<i>clathroidea</i>	Dring	FOP
			<i>maracuja</i>	Möller	FOP
Phallales	Phallaceae	<i>Colus</i>	<i>hirudinosus</i>	Cavalier & Séchier	FOP
		<i>Itajahya</i>	<i>rosea</i>	(Delile) E. Fisch.	GenBank (KF481955); FOP; Moreno et al. (2013)
		<i>Lysurus</i>	<i>borealis</i>	(Burt) Henn.	FOP
			<i>pakistanicus</i>	S.H. Iqbal, Kasuya, Khalid & Niazi	Iqbal et al. (2006)
		<i>Phallus</i>	<i>periphragmoides</i>	(Klotzsch) Dring	FOP
			<i>calongei</i>	G. Moreno & Khalid	GenBank (KF481955); Moreno et al. (2009)
			<i>celebicus</i>	Henn.	FOP
			<i>hadriani</i>	Vent.	GenBank (KF481956); Moreno et al. (2013)
			<i>impudicus</i>	L.	FOP
			<i>indusiatus</i>	Vent.	FOP
			<i>rubicundus</i>	(Bose.) Fr.	FOP
			<i>subtrametes</i>	(Pilat.)	FOP
Polyporales	Fomitopsidaceae	<i>Antrodia</i>		(Murrill) Zmitr.	GenBank (KR610980)
		<i>Brunneoporus</i>	<i>juniperinus</i>	(Durieu & Mont.) Zmitr. & Malysheva	GenBank (MT491098)
		<i>Cellulariella</i>	<i>warnieri</i>	(Curr.) Tura, Zmitr., Wasser & Spirin	FOP
		<i>Phaeodaedalea</i>	<i>incerta</i>	(Berk.) Zmitr.	FOP
		<i>Pilatoporus</i>	<i>ostreiformis</i>	(Fr.) Zmitr.	FOP
		<i>Ranadivia</i>	<i>stereoides</i>	(P. Karst.) Audet	FOP
		<i>Resinoporia</i>	<i>crassa</i>	(Alb. & Schwein.) Kotl. & Pouzar	FOP
		<i>Rhodofomes</i>	<i>roseus</i>		
	Dacrybolaceae	<i>Jahnporus</i>	<i>oreinus</i>	Spirin, Vlasák & Miettinen	GenBank (MN178648)
		<i>Fomitopsis</i>	<i>annosa var indicus</i>	(Wakef.) S. Ahmad	FOP
			<i>pinicola</i>	(Sw.) P. Karst.	FOP
			<i>rufolaccata</i>	(Bose) Dhanda	FOP
	Panaceae	<i>Postia</i>	<i>tephroleuca</i>	(Fr.) Jülich	FOP
		<i>Panus</i>	<i>rudis</i>	Fr.	FOP
	Irpicaceae	<i>Bysomerulius</i>	<i>corium</i>	(Pers.) Parmasto	FOP
		<i>Ceriporia</i>	<i>ferrugineocincta</i>	(Murrill) Ryvarden	FOP
			<i>leptoderma</i>	(Berk. & Broome) Ryvarden	FOP
			<i>xylostromatoides</i>	(Berk.) Ryvarden	FOP
		<i>Gloeoporus</i>	<i>thelephoroides</i>	(Hook.) G. Cunn.	FOP
		<i>Flavodon</i>	<i>flavus</i>	(Klotzsch) Ryvarden	GenBank (MN888947)
		<i>Irpex</i>	<i>flavus</i>	Klotzsch	FOP
			<i>lacteus</i>	(Fr.) Fr.	GenBank (KM977778)
		<i>Leptoporus</i>	<i>mollis</i>	(Pers.) Quél.	FOP
		<i>Trametopsis</i>	<i>cervina</i>	(Schwein.) Tomšovský	FOP
	Laetiporaceae	<i>Laetiporus</i>	<i>sulphureus</i>	(Bull.) Murrill	FOP; Razaq and Shahzad (2016)
		<i>Phaeolus</i>	<i>schweinitzii</i>	(Fr.) Pat.	GenBank (MN109971); FOP; Razaq and Shahzad (2016)
			<i>weberiana</i>	(Bres. & Henn. ex Sacc.) Ryv.	FOP
Meruliaceae		<i>Climacodon</i>	<i>pulcherrimus</i>	(Berk. & M.A. Curtis) Nikol.	FOP
		<i>Hydnophlebia</i>	<i>chrysorhiza</i>	(Eaton) Parmasto	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Polyporales	Meruliaceae	<i>Irpiciporus</i>	<i>pachyodon</i>	(Pers.) Kotl. & Pouzar	FOP
			<i>Phlebia</i>	(Pers.) M.P. Christ.	FOP
			<i>sedimenticola</i>	(S. Ahmad) S. Ahmad	FOP
			<i>tremellosa</i>	(Schräd.) Nakasone & Burds.	FOP
		<i>Sarcodontia</i>	<i>spumea</i>	(Sowerby) Spirin	FOP
		<i>Scopuloides</i>	<i>hydroides</i>	(Cooke & Massee)	FOP
				Hjortstam & Ryvarden	
			<i>leprosa</i>	(Bourdöt & Galzin) Boidin, Lanq. & Gilles	FOP
	Meripilaceae	<i>Rigidoporus</i>	<i>lineatus</i>	(Pers.) Ryvarden	FOP
			<i>microporus</i>	(Sw.) Overeem	FOP
			<i>ulmarius</i>	(Sowerby) Imazeki	FOP; Razaq and Shahzad (2016)
			<i>vinctus</i>	(Berk.) Ryvarden	FOP
			<i>zonalis</i>	(Berk.) Imazeki	FOP
	Phanerochaeta-ceae	<i>Bjerkandera</i>	<i>adusta</i>	(Willd.) P. Karst.	FOP; Razaq and Shahzad (2016)
		<i>Aporium</i>	<i>carayae</i>	(Schw.) Teixeira and Rogers	FOP
		<i>Hyphodermella</i>	<i>corrugata</i>	(Fr.) J. Erikss. & Ryvarden	FOP
		<i>Phaeophlebiopsis</i>	<i>ravenelii</i>	(Cooke) Zmitr.	FOP
		<i>Phlebiopsis</i>	<i>gigantea</i>	(Fr.) Jülich	FOP
			<i>papyrina</i>	(Mont.) Boid.	FOP
		<i>Porostereum</i>	<i>spadiceum</i>	(Pers.) Hjortstam & Ryvarden	FOP
		<i>Rhizochaete</i>	<i>filamentosa</i>	(Berk. & M.A. Curtis) J. Erikss	FOP
	Podoscyphaceae	<i>Abortiporus</i>	<i>biennis</i>	(Bull.) Singer	Razaq and Shahzad (2016); Khan et al. (2016b)
		<i>Podoscypha</i>	<i>elegans</i>	(G. Mey.) Pat.	GenBank (MH858811)
			<i>parvula</i>	(Lloyd) D.A. Reid	FOP
			<i>petalodes</i>	(Berk.) Boidin	FOP; GenBank (DQ917655)
	Polyporaceae		<i>pusilla</i>	(Berk.) Ryvarden	FOP
			<i>warneckeana</i>	(Henn.) Ryvarden	FOP
		<i>Cerioporus</i>	<i>leptocephalus</i>	(Jacq.) Zmitr.	FOP
			<i>squamosus</i>	(Huds.) Quél.	GenBank (MN888950); FOP; Razaq and Shahzad (2016)
			<i>varius</i>	(Pers.) Zmitr. & Kovalenko	FOP
		<i>Coriolus</i>	<i>hirtellus</i>	(Fr.) Murrill	FOP
		<i>Coriolopsis</i>	<i>occidentalis</i>	(Klotzsch) Murrill	FOP
		<i>Cystostiptoporus</i>	<i>indicus</i>	Dhanda & Ryvarden	FOP
		<i>Daedalea</i>	<i>dickinsii</i>	Yasuda	GenBank (KR019739); FOP
			<i>pusillus</i>	(Lev.) Singer	FOP
			<i>quercina</i>	(L.) Pers.	FOP
		<i>Daedaleopsis</i>	<i>confragosa</i>	(Bolton) J. Schröt.	FOP
		<i>Earliella</i>	<i>scabrosa</i>	(Pers.) Gilb. & Ryvarden	GenBank (MN888942)
		<i>Epithele</i>	<i>typhae</i>	(Pers.) Pat.	FOP
		<i>Favolus</i>	<i>grammocephalus</i>	(Berk.) Imazeki	FOP
			<i>tenuiculus</i>	P. Beauv.	FOP
		<i>Fomes</i>	<i>ajazii</i>	S.M. Hussain	FOP
			<i>borneoensis</i>	(Lloyd) S. Ahmad	FOP
			<i>fomentarius</i>	(L.) Fr.	FOP; Razaq and Shahzad (2016)
			<i>semitostus</i>	(Berk.) Cooke	FOP
		<i>Funalia</i>	<i>floccosa</i>	(Jungh.) Zmitr. & Malysheva	FOP
			<i>hispida</i>	(Bagl.) M.M. Chen	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Polyporales	Polyporaceae	<i>Funalia</i>	<i>leonina</i>	(Klotzsch) Pat.	FOP
			<i>Ganoderma</i>	Staeysart.	FOP
		<i>Ganoderma</i>	<i>ahmadii</i>	(Fr.) Pat.	FOP; Razaq and Shahzad (2017)
			<i>applanatum</i>	(Fr.) Pat.	FOP
			<i>australe</i>	(Fr.) Pat.	FOP
			<i>flexipes</i>	Pat.	FOP
			<i>leucocontextum</i>	T.H. Li, W.Q. Deng, Sheng H. Wu, Dong M. Wang & H.P. Hu	GenBank (MK713839)
			<i>lucidum</i>	(Curtis) P. Karst.	GenBank (KX610998)
			<i>resinaceum</i>	Boud.	FOP
			<i>tornatum</i>	(Pers.) Bres.	FOP
		<i>Grammothele</i>	<i>fuligo</i>	(Berk. & Broome) Ryvarden	FOP
		<i>Hexagonia</i>	<i>discopoda</i>	Pat. & Har.	FOP
		<i>Lopharia</i>	<i>cinerascens</i>	(Schwein.) G. Cunn.	FOP
			<i>papyracea</i>	(Bres.) D.A. Reid	FOP
		<i>Lentinus</i>	<i>arcularius</i>	(Batsch) Zmitr.	FOP
			<i>brumalis</i>	(Pers.) Zmitr.	FOP
			<i>crinitus</i>	(L.) Fr.	FOP
			<i>multicolor</i>	Berk.	FOP
			<i>prolifer</i>	(Pat. & Har.) D.A. Reid	FOP
			<i>squarrosulus</i>	Mont.	FOP
		<i>Lenzites</i>	<i>tigrinus</i>	(Bull.) Fr.	GenBank (EU543989)
			<i>betulinus</i>	(L.) Fr.	GenBank (MN888944); FOP
			<i>platyphyllus</i>	Lev.	FOP
			<i>Perenniporia</i>	(Jacq.) Donk	FOP
		<i>Picipes</i>	<i>medulla-panis</i>	(Pers.) Zmitr. & Kovalenko	Razaq and Shahzad (2016)
			<i>badius</i>	(H.J. Xue & L.W. Zhou)	GenBank (MN888945)
			<i>submelanopus</i>	J.L. Zhou & B.K. Cui	
			<i>Polyporellus</i>	(Fr.) P. Karst.	FOP
		<i>Polyporus</i>	<i>picipes</i>	(Bull.) Fr.	FOP
			<i>biennis</i>	Bose	FOP
			<i>calcuttensis</i>	(Pers.) Fr.	FOP
			<i>umbellatus</i>	(Durieu & Mont.) Cooke	FOP; Razaq et al. (2014)
		<i>Poria</i>	<i>latemarginata</i>	Schard. ex Fr.	FOP
			<i>paradoxa</i>	(Lév.) Kotl. & Pouzar	FOP
		<i>Pyrofomes</i>	<i>demidoffi</i>	(H. Schrenk) Vlasák & Spirin	FOP
			<i>juniperinus</i>	(Fr.) Murrill	FOP
		<i>Tomophagus</i>	<i>colossus</i>	Berk.	FOP
		<i>Trametes</i>	<i>cingulata</i>	(Pers.) Bres.	FOP
			<i>corrugata</i>	(Spreng.) Fr.	GenBank (MN888943); FOP
			<i>elegans</i>	(Lév.) Zmitr., Wasser & Ezhov	FOP
			<i>flavida</i>	Pilat.	FOP
			<i>ijubarskii</i>	Berk.	FOP
			<i>incana</i>	(Berk.) Sacc.	FOP
			<i>lactinea</i>	(Pers.) Gilb. & Ryvarden	FOP
			<i>ochracea</i>	(Pers.) Justo	FOP
			<i>polyzona</i>	(Schumach.) Pilát	FOP
			<i>pubescens</i>	Pat. & Har.	FOP
			<i>roseola</i>	(L.) Fr.	FOP
			<i>suaveolens</i>	Berk.	FOP
			<i>tephroleuca</i>	Berk.	FOP
			<i>trogii</i>	(L.) Lloyd	GenBank (KU697312); Razaq et al. (2014)
			<i>versicolor</i>		

Phylum/Order	Family	Genus	Species	Authority	Source		
Polyporales	Polyporaceae	<i>Truncospora</i>	<i>livida</i>	(Kalchbr. ex Cooke) Zmitr.	FOP		
			<i>tephropora</i>	(Mont.) Zmitr.	FOP		
	Incrustoporiaceae	<i>Tyromyces</i>	<i>chioneus</i>	(Fr.) P. Karst.	FOP		
			<i>gollanii</i>	(Masse) S. Ahmad	FOP		
	Pycnoporellaceae	<i>Pycnoporellus</i>	<i>fulgens</i>	(Fr.) Donk.	FOP		
			<i>Pycnoporus</i>	<i>cinnabarinus</i>	(Jacq.) P. Karst.	FOP	
			<i>Pycnoporus</i>	<i>sanguineus</i>	(L.) Murrill	FOP	
	Sparassidaceae	<i>Sparassis</i>	<i>crispa</i>	Wulf. ex Fr.	FOP		
			<i>laminosa</i>	Fr.	FOP		
			<i>latifolia</i>	Y.C. Dai & Zheng Wang	GenBank (KF866226)		
	Steccherinaceae	<i>Cabalodontia</i>	<i>queletii</i>	(Bourdort & Galzin) Piątek	FOP		
			<i>Odontia</i>	<i>bicolor</i>	(Alb. & Schwein. ex Fr.) Quel.	FOP	
			<i>calcicola</i>	(Bourdort & Galzin) Kóljalg	FOP		
	Incertae sedis	<i>Antrodiella</i>	<i>oleaginea</i>	Overh. ex Ryvarden	FOP		
			<i>Mycorrhaphium</i>	<i>stereoides</i>	(Cooke) Maas Geest.	FOP	
			<i>Steccherinum</i>	<i>ochraceum</i>	(Pers. ex J.F. Gmel.) Gray	FOP	
			<i>Amaropostia</i>	<i>stiptica</i>	(Pers.) B.K. Cui, L.L. Shen & Y.C. Dai	FOP	
			<i>Hypochnicium</i>	<i>punctulatum</i>	(Cooke) J. Erikss.	FOP	
			<i>Phanerodontia</i>	<i>chrysosporium</i>	(Buds.) Hjortstam & Ryvarden	GenBank (EU543990)	
			Auriscalpiaceae	<i>Auriscalpium</i>	<i>vulgare</i>	Gray	FOP
<i>Lentinellus</i>					<i>micheneri</i>	(Berk. & M.A. Curtis) Pegler	FOP
<i>ursinus</i>					(Fr.) Kuhner	FOP	
Bondarzewiaceae					<i>Albatrellus</i>	<i>roseus</i>	J. Khan, Sher & Khalid
	<i>Amyloporus</i>	<i>campbellii</i>	(Berk.) Ryvarden	FOP			
	<i>succulentus</i>	Jia J. Chen & L.L. Shen	GenBank (MK929297)				
	<i>Bondarzewia</i>	<i>dickinsii</i>	(Berk.) Jia J. Chen, B.K. Cui & Y.C. Dai	FOP			
Hericiaceae	<i>Heterobasidion</i>	<i>amyloideopsis</i>	Saba, C.L. Zhao, Khalid & Pfister	Genbank (KT598384); Zhao et al. (2017)			
		<i>insulare</i>	(Murrill) Ryvarden	FOP			
		<i>linzhiense</i>	Y.C. Dai & Korhonen	GenBank (MH233930); Saba et al. (2018)			
		<i>orientale</i>	Tokuda, T. Hatt. & Y.C. Dai.	GenBank (MH233931); Saba et al. (2018)			
		<i>cirrhatum</i>	(Pers.) Nikol.	GenBank (MN513042); Khan et al. (2020)			
		<i>clathroides</i>	(Pall.) Pers.	FOP			
		<i>coralloides</i>	(Scop.) Pers.	FOP			
		<i>erinaceus</i>	(Bull.) Pers.	FOP			
		<i>Laxitextum</i>	<i>bicolor</i>	(Pers.) Lentz	FOP		
		Peniophoraceae	<i>Asterostroma</i>	<i>laxum</i>	Bres.	FOP	
<i>Dichostereum</i>	<i>pallescens</i>			(Schwein.) Boidin & Lanq.	FOP		
<i>rhodosporum</i>	(Wakef.) Boidin & Lanq.			FOP			
<i>Duportella</i>	<i>velutina</i>			Pat.	FOP		
<i>tristricula</i>	(Berk. & Broome) Reinking			GenBank (MH858266)			
<i>Lachnocladium</i>	<i>fulvum</i>			Corner	FOP		
<i>Peniophora</i>	<i>cinerea</i>			(Pers.) Cooke	FOP		
<i>versiformis</i>	(Berk. & M.A. Curtis) Bourdort & Galzin			FOP			
<i>Scytinostroma</i>	<i>cystidiatum</i>			Boidin	FOP		
<i>portentosum</i>	(Berk.& Curt.) Donk			FOP			
Russulaceae	<i>Russula</i>	<i>abbottabadensis</i>	Saba & Adamčík	GenBank (MZ364137); Adamčík et al. (2019)			
		<i>adusta</i>	(Pers.) Fr.	Sultana et al. (2011)			

Phylum/Order	Family	Genus	Species	Authority	Source
Russulales	Russulaceae	<i>Russula</i>	<i>ahmadii</i>	Jabeen, Razaq, Niazi, I. Ahmad & Khalid	Genbank (KU535608); Jabeen et al. (2017b)
			<i>amethystina</i>	Quél.	GenBank (KT953612)
			<i>amoenicolor</i>	Romagn.	Sultana et al. (2011)
			<i>anthracina</i>	Romagn.	GenBank (KR011879), Jabeen et al. (2016b)
			<i>aurea</i>	Pers.	FOP
			<i>aurantioflava</i>	Kiran & Khalid	GenBank (MN130074); Adamčík et al. (2019)
			<i>azurea</i>	Bres.	FOP
			<i>badia</i>	Quel.	FOP
			<i>brevipes</i>	Peck	Niazi et al. (2006)
			<i>brunneopurpurea</i>	Jabeen & Khalid	GenBank (KT953613); Jabeen et al. (2017a); Ahmad et al. (2019)
			<i>caerulea</i>	Fr.	Sultana et al. (2011)
			<i>cessans</i>	A. Pearson	GenBank (KF679816)
			<i>chloroides</i>	(Krombh.) Bres.	FOP
			<i>cinnabarina</i>	Berk.	FOP
			<i>consobrina</i>	(Fr.) Fr.	Sultana et al. (2011)
			<i>cyanoxantha</i>	(Schaeff.) Fr.	FOP; Razaq et al. (2019)
			<i>decipiens</i>	(Singer) Bon	Sultana et al. (2011)
			<i>delica</i>	Fr.	FOP
			<i>densifolia</i>	Secr. ex Gillet	FOP
			<i>emetica</i>	(Schaeff.) Pers.	FOP
			<i>fellea</i>	(Fr.) Fr.	FOP
			<i>foetentoides</i>	Razaq, Khalid & Niazi	GenBank (HE647707); Razaq et al. (2014a)
			<i>foetida</i>	C. Martin	FOP
			<i>grata</i>	Britzelm.	FOP; Razaq et al. (2019)
			<i>integra</i>	(L.) Fr.	FOP
			<i>livescens</i>	(Batsch). Bataille	GenBank (KM596858); Jabeen et al. (2015b)
			<i>maculata</i>	Quél.	Sultana et al. (2011)
			<i>mansehraensis</i>	Saba, Caboň & Adamčík	GenBank (KU886598)
			<i>nitida</i>	(Pers.) Fr.	Razaq et al. (2019)
			<i>olivacea</i>	(Schaeff.) Fr.	Razaq et al. (2019)
			<i>paludosa</i>	Britzelm.	Razaq et al. (2019); Sultana et al. (2011)
			<i>pelargonia</i>	Niolle	Razaq et al. (2019); Sultana et al. (2011)
			<i>pectinatoides</i>	Peck	FOP
			<i>queletii</i>	Fr.	FOP
			<i>quercus-flori-bundae</i>	M. Kiran & Adamčík	GenBank (MN053391); Crous et al. (2019)
			<i>rosea</i>	Pers.	FOP; Sultana et al. (2011); Razaq et al. (2019)
			<i>rhodopodus</i>	Zvára	FOP
			<i>risigallina</i>	(Batsch) Sacc.	GenBank (KF679818)
			<i>romellii</i>	Maire	Razaq et al. (2019); Sultana et al. (2011)
			<i>rubricolor</i>	Jabeen, Naseer & Khalid	Jabeen et al. (2020b)
			<i>sanguinea</i>	Fr.	FOP
			<i>shanglaensis</i>	S. Ullah, Khalid & Fiaz	GenBank (MK579183); Ullah et al. (2020b)
			<i>sichuanensis</i>	G.J. Li & H.A. Wen	GenBank (KM596859); Saba and Khalid (2015)
			<i>swatica</i>	Sarwar and Hanif	Genbank (MK389374); Sarwar et al. (2019)
			<i>torulosa</i>	Bres.	Sultana et al. (2011)

Phylum/Order	Family	Genus	Species	Authority	Source
Russulales	Russulaceae	<i>Russula</i>	<i>tuberculosa</i>	R. Heim	FOP
			<i>velenovskiyi</i>	Melzer & Zvára	FOP
			<i>vinosa</i>	Lindblad	Sultana et al. (2011)
			<i>violacea</i>	Quél.	Sultana et al. (2011)
			<i>xerampelina</i>	(Schaeff.) Fr.	FOP
		<i>Thelephora</i>	<i>atlanticus</i>	Bon.	Sultana et al. (2011)
			<i>badiosanguineus</i>	Kühner & Romagn.	FOP
			<i>controversus</i>	Pers.	Sultana et al. (2011)
			<i>deliciosus</i>	(L.) Gray	FOP; Sultana et al. 2011
			<i>determinus</i>	Gröger	Sultana et al. (2011)
			<i>hatsudake</i>	Nobuj. Tanaka	FOP
			<i>helvus</i>	(Fr.) Fr.	Razaq and Shahzad (2012)
			<i>lacunarum</i>	Romagn. ex Hora	Sultana et al. (2011)
			<i>mediterraneensis</i>	Llistos. & Bellù	GenBank (MK607609)
			<i>obscuratus</i>	(Lasch) Fr.	Sultana et al. (2011); Razaq and Shahzad (2012)
			<i>pubescens</i>	Fr.	Razaq and Shahzad (2012)
			<i>quietus</i>	(Fr.) Fr.	Sultana et al. (2011)
			<i>romagnesii</i>	Bon	Sultana et al. (2011)
			<i>sanguifluus</i>	(Paulet) Fr.	GenBank (HE615155); FOP; Sultana et al. 2011; Ilyas et al. (2013b)
		<i>Lactifluus</i>	<i>scrobiculatus</i>	(Scop.) Fr.	FOP; Sultana et al. (2011)
			<i>semisanguifluus</i>	R. Heim & Leclair	GenBank (HF559377); Sultana et al. (2011)
			<i>torminosus</i>	(Schaeff.) Pers.	FOP; Sultana et al. (2011)
			<i>vietus</i>	(Fr.) Fr.	Sultana et al. (2011)
			<i>violascens</i>	(J. Otto) Fr.	Sultana et al. (2011)
			<i>scrobiculatus</i>	(Scop.) Fr.	FOP
			<i>brunneoviolascens</i>	(Bon) Verbeken	Sultana et al. (2011)
			<i>glaucescens</i>	(Crossl.) Verbeken	Razaq et al. (2014)
			<i>pergamenus</i>	(Sw.) Kuntze	Sultana et al. (2011)
			<i>piperatus</i>	(L.) Roussel	FOP; Sultana et al. (2011); Razaq and Shahzad (2012)
			<i>rugatus</i>	(Kühner & Romagn.) Verbeken	Sultana et al. (2011)
			<i>vellereus</i>	(Fr.) Kuntze	Sultana et al. (2011)
			<i>volemus</i>	(Fr.) Kuntze	Khan and Sher (2016c)
	Stereaceae	<i>Acanthofungus</i>	<i>ahmadii</i>	(Boidin) Sheng H. Wu, Boidin & C.Y. Chien	FOP
			<i>Aleurodiscus jacksonii</i>	S. Ahmad	FOP
		<i>Amylostereum chaillatii</i>	(Pers.) Boidin		FOP
		<i>Gloeocystidiellum porosum</i>	(Berk. & M.A. Curtis) Donk		FOP
		<i>Stereum</i>	<i>elegans</i>	(G. Mey.) Fr.	FOP
			<i>frustulosum</i>	(Pers.) Fr.	FOP
			<i>gausapatum</i>	(Fr.) Fr.	FOP
			<i>hirsutum</i>	(Willd.) Pers.	FOP
			<i>ostrea</i>	(Blume & T. Nees) Fr.	FOP
			<i>princeps</i>	(Jungh.) Lév.	FOP
			<i>rugosum</i>	Pers.	FOP
			<i>sanguinolentum</i>	(Alb. & Schwein.) Fr.	FOP
		<i>Xylobolus</i>	<i>subpileatus</i>	(Berk. & M.A. Curtis) Boidin	FOP
			<i>caeruleoporus</i>	(Peck) Audet	Sultana et al. (2011)
Incertae sedis	Incertae sedis	<i>Neoblatrellus</i>	<i>caeruleoporus</i>	(Bres.) K.H. Larss. & Hjortstam	FOP
Trechisporales	Hydnodontaceae	<i>Brevicellicium</i>	<i>olivascens</i>	(Pers.) Boidin	FOP
	Bankeraceae	<i>Boletopsis</i>	<i>leucomelaena</i>	(Pers.) Fayod	FOP
		<i>Hydnellum</i>	<i>caeruleum</i>	(Hornem.) P. Karst.	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Thelephorales	Bankeraceae	<i>Hydnellum</i>	<i>concrescens</i>	(Pers.) Banker	FOP
			<i>earlianum</i>	Banker	FOP
	Thelephoraceae	<i>Sarcodon</i>	<i>imbricatus</i>	(L.) P. Karst.	FOP
		<i>Phellodon</i>	<i>niger</i>	(Fr.) P. Karst.	FOP
			<i>anthocephala</i>	(Bull.) Fr.	FOP
		<i>Thelephora</i>	<i>arbuscula</i>	Corner	FOP
			<i>atra</i>	Weinm.	FOP
			<i>caryophyllea</i>	(Schaeff.) Pers.	FOP
			<i>fucoides</i>	Corner	FOP
			<i>iqbalii</i>	Nasir & Hanif	GenBank (JX241471); Khalid and Hanif (2017)
		<i>Tomentella</i>	<i>palmata</i>	(Scop.) Fr.	FOP
			<i>penicillata</i>	(Pers.) Fr.	FOP
			<i>terrestris</i>	Ehrh. ex Fr.	FOP
			<i>bryophila</i>	(Pers.) M.J. Larsen	FOP
			<i>coriaria</i>	(Peck) Bourdot & Galzin	FOP
			<i>griseo-cinnamomea</i>	Wakef.	FOP
			<i>punica</i>	(Alb. & Schwein.) J. Schröt.	FOP
	Incertae sedis	<i>Dendrothele</i>	<i>acerina</i>	(Pers.) P.A. Lemke	FOP
		<i>Geoglossum</i>	<i>umbratile</i>	Sacc.	FOP
Ascomycota/ Geoglossales	Geoglossaceae	<i>Trichoglossum</i>	<i>hirsutum</i>	(Pers.) Boud.	FOP
			<i>octopartitum</i>	Mains	FOP
Helotiales	Calloriaceae	<i>Calloria</i>	<i>urticae</i>	(Pers.) J. Schröt. ex Rehm	GenBank (MN957392)
			<i>mollisioidea</i>	(Sacc. & Briard) B. Hein	FOP
	Cenangiaceae	<i>Chlorencoelia</i>	<i>torta</i>	(Schwein.) J.R. Dixon	GenBank (MN957580)
			<i>rufo-olivacea</i>	(Alb. & Schwein.) Korf	FOP
	Helotiaceae	<i>Cyathicula</i>	<i>coronata</i>	(Bull.) Rehm	FOP
			<i>cyathoidea</i>	(Bull.) Thüm.	FOP
		<i>dolosella</i>	<i>dolosella</i>	(P. Karst.) Dennis	FOP
			<i>egenula</i>	(Rehm) E. Müll.	FOP
			<i>calyculus</i>	(Fr.) W. Phillips	FOP
		<i>Hymenoscyphus</i>	<i>scutula</i>	(Pers.) W. Phillips	FOP
			<i>scutula</i> var. <i>scutula</i>	(Pers.) W. Phillips	FOP
			<i>subferrugineus</i>	(Nyl.) Dennis	FOP
		<i>vitigenus</i>	<i>vitigenus</i>	(De Not.) Dennis	FOP
			<i>macrospora</i>	(Peck) Baral	FOP
	Lachnaceae	<i>Incrucipulum</i>	<i>ciliare</i>	(Schräd.) Baral	FOP
			<i>arida</i>	(W. Phillips) Dennis	FOP
		<i>Lachnellula</i>	<i>calyciformis</i>	(Batsch) Dharne	FOP
			<i>bicolor</i>	(Bull.) P. Karst.	FOP
		<i>Lachnum</i>	<i>corticale</i>	(Pers.) Nannf.	FOP
			<i>indicus</i>	(E.K. Cash) J.H. Haines & Dumont	FOP
			<i>mollissimum</i>	(Fuckel) P. Karst.	FOP
			<i>pudibundum</i>	(Quél.) J. Schröt.	FOP
			<i>himalayensis</i>	E. Müll. & Dennis	FOP
	Mollisiaceae	<i>Tapesia</i>	<i>fusca</i>	(Pers.) Fuckel	FOP
			<i>rosae</i>	(Pers.) Fuckel	FOP
	Pezizellaceae	<i>Allophylaria</i>	<i>subhyalina</i>	(Rehm) Baral	FOP
			<i>citrina</i>	(Hedw.) Gray	FOP
		<i>chionea</i>		(Fr.) Kuntze	FOP
	Ploettnerulaceae	<i>Pyrenopeziza</i>	<i>lavaterae</i>	E. Müll. & S. Ahmad	FOP
	Rutstroemiaceae	<i>Rutstroemia</i>	<i>bolaris</i>	(Batsch) Rehm	FOP
			<i>firma</i>	(Pers.) P. Karst.	FOP
	Sclerotiniaceae	<i>Moellerodiscus</i>	<i>berberidis</i>	Dumont	FOP
			<i>fuscum</i>	(E. Müll. & Dennis) Raitv.	FOP
	Thelebolaceae	<i>Thelebolus</i>	<i>crustaceus</i>	(Fuckel) Kimbr.	FOP
	Incertae sedis	<i>Cistella</i>	<i>geelmuydenii</i>	Nannf.	FOP

Phylum/Order	Family	Genus	Species	Authority	Source
Rhytismatales	Cudoniaceae	<i>Cudonia</i>	<i>circinans</i>	(Pers.) Fr.	FOP
	Hyaloscyphaceae	<i>Hyaloscypha</i>	<i>luteola</i>	S. Ahmad	FOP
Leotiales	Leotiaceae	<i>Leotia</i>	<i>lubrica</i>	(Scop.) Pers.	FOP
Orbiliales	Orbiliaceae	<i>Hyalorbilia</i>	<i>erythrostroma</i>	(W. Phillips) Baral & G. Marson	GenBank (MN957494)
		<i>Orbilia</i>	<i>auricolor</i>	(A. Bloxam) Sacc.	FOP
			<i>curvatisspora</i>	Boud.	FOP
			<i>leucostigma</i>	(Fr.) Fr	FOP
Hypocreales	Bionectriaceae	<i>Hydropisphaera</i>	<i>erubescens</i>	(Roberge ex Desm.) Rossman & Samuels	GenBank (MN957491)
	Hypocreaceae	<i>Trichoderma</i>	<i>alutaceum</i>	Jaklitsch	FOP
Xylariales	Hypoxylaceae	<i>Daldinia</i>	<i>bakeri</i>	Lloyd	FOP
			<i>concentrica</i>	(Bolton) Ces. & De Not.	FOP
			<i>vernica</i>	Ces. & De Not.	FOP
	Xylariaceae	<i>Podosordaria</i>	<i>kurziana</i>	(Curr.) P.M.D. Martin	FOP
			<i>leporina</i>	(Ellis & Everh.) Dennis	FOP
			<i>nigripes</i>	(Klotzsch) P.M.D. Martin	FOP
			<i>pyramidata</i>	(Berk. & Broome) P.M.D. Martin	FOP
		<i>Poronia</i>	<i>indica</i>	S. Ahmad	FOP
			<i>polyporoides</i>	Henn.	FOP
		<i>Xylosphaera</i>	<i>ehrenbergii</i>	(Henn.) Dennis	FOP
		<i>Xylaria</i>	<i>hirtella</i>	Wakef.	FOP
			<i>hypoxylon</i>	(L.) Grev.	FOP
			<i>mali</i>	Fromme	FOP
			<i>melliisii</i>	(Berk.) Cooke	FOP
			<i>polymorpha</i>	(Pers.) Grev.	FOP
Pezizales	Ascobolaceae	<i>Ascobolus</i>	<i>americanus</i>	(Cooke & Ellis) Seaver	FOP
			<i>denudatus</i>	Fr.	FOP
			<i>elegans</i>	J. Klein	FOP
			<i>furfuraceus</i>	Pers.	FOP
			<i>immersus</i>	Pers.	FOP
			<i>leveillei</i>	Boud.	FOP
			<i>michaudii</i>	Boud.	FOP
			<i>minutus</i>	Boud.	FOP
			<i>perplexans</i>	Massee & E.S. Salmon	FOP
			<i>quezelii</i>	Faurel & Schotter	FOP
			<i>scatigenus</i>	(Berk. & M.A. Curtis)	FOP
				Brumm.	
			<i>subglobosus</i>	Seaver	FOP
		<i>Saccobolus</i>	<i>citrinus</i>	Boud. & Torrend	FOP
			<i>depauperatus</i>	(Berk. & Broome) E.C. Hansen	FOP
			<i>glaber</i>	(Pers.) Lambotte	FOP
			<i>succineus</i>	Brumm.	FOP
			<i>truncatus</i>	Velen.	FOP
			<i>versicolor</i>	(P. Karst.) P. Karst.	FOP
	Ascodesmidaceae	<i>Ascodesmis</i>	<i>macrospora</i>	W. Obris	FOP
			<i>microscopica</i>	(P. Crouan & H. Crouan)	FOP
				Le Gal	
			<i>sphaerospora</i>	W. Obris	FOP
			<i>nigricans</i>	Tiegh.	FOP
		<i>Lasiobolus</i>	<i>papillatus</i>	(Pers.) Sacc.	FOP
			<i>trichoboloides</i>	S.R. Khan & J.L. Bezerra	FOP
	Discinaceae	<i>Gyromitra</i>	<i>esculenta</i>	Pers. ex Fr.	FOP
			<i>infula</i>	(Schaeff.) Quel.	FOP
			<i>khanspurensis</i>	Jabeen & Khalid	GenBank (MF116159); Krisai-Greilhuber et al. (2017)

Phylum/Order	Family	Genus	Species	Authority	Source	
Pezizales	Discinaceae	<i>Discina</i>	<i>ancilis</i>	(Pers.) Sacc.	FOP	
	Helvellaceae	<i>Helvella</i>	<i>acetabulum</i>	(L.) Quél.	FOP	
			<i>albella</i>	Quél.	GenBank (MN814023)	
			<i>atra</i>	J. König	GenBank (KF679807); FOP	
			<i>bachu</i>	Q. Zhao, Zhu L. Yang & K.D. Hyde	GenBank (MN959917)	
			<i>crispa</i>	(Scop.) Fr.	FOP	
			<i>cupiliformis</i>	Razaq et al., (2014)	Sultana et al. (2011)	
			<i>elastica</i>	Bull.	FOP	
			<i>involuta</i>	Q. Zhao, Zhu L. Yang & K.D. Hyde	GenBank (MW447509)	
			<i>lacunosa</i>	Afzel.	FOP	
			<i>leucopus</i>	Pers.	Razaq et al. (2014)	
			<i>monachella</i>	(Scop.) Fr.	Razaq et al. (2014)	
			<i>pezizoides</i>	Afzel.	FOP	
			<i>villosa</i>	Schaeff.	FOP	
		Morchellaceae	<i>Paxina</i>	<i>queletii</i>	(Bres.) Stangl	FOP
			<i>Morchella</i>	<i>crassipes</i>	(Vent.) Pers.	GenBank (KP670934)
				<i>deliciosa</i>	Fr.	GenBank (MW558089)
				<i>esculenta</i>	(L.) Pers.	FOP; GenBank (MT957957)
				<i>elata</i>	Fr.	GenBank (MT977069)
				<i>pakistanica</i>	Jabeen & Khalid	GenBank (KX306760); Hernández-Restrepo et al. (2016)
				<i>pulchella</i>	Clowez & Franç. Petit	GenBank (MF400857); Badshah et al. (2018)
	<i>tridentina</i>			Bres.	GenBank (MT584841)	
	<i>Verpa</i>			<i>bohémica</i>	(Krombh.) J. Schröt.	FOP
	<i>Ahmadea</i>			<i>dalanensis</i>	Aman & Khalid	GenBank (MT645090); Aman et al. (2020)
	<i>Iodophanus</i>			<i>carneus</i>	(Pers.) Korf	FOP
	<i>Ionopezia</i>		<i>gerardii</i>	(Cooke) Van Vooren	FOP	
	Pezizaceae		<i>Mattirolomyces</i>	<i>spinosus</i>	(Harkn.) Kovács, Trappe & Alsheikh	GenBank (MT649183); FOP; Aman et al. (2020)
			<i>Pachyphlodes</i>	<i>conglomerata</i>	(Berk. & Broome) Doweld	GenBank (HG797006)
			<i>Paragalactinia</i>	<i>michellii</i>	(Boud.) Dennis	GenBank (JN836749); Ashraf et al. (2012)
			<i>succosa</i>	(Berk.) Van Vooren	GenBank (JN588568); Ashraf and Khalid (2012)	
			<i>succosella</i>	(Le Gal & Romagn.) Van Vooren	GenBank (KM199729); Jabeen et al. (2015a)	
		<i>Plicaria</i>	<i>trachycarpa</i>	(Curr.) Boud.	FOP	
		<i>Peziza</i>	<i>badiofusca</i>	(Boud.) Dennis	FOP	
			<i>cerea</i>	Bull.	FOP	
			<i>micropus</i>	Pers.	FOP	
			<i>pakistanica</i>	(S. Ahmad) S. Ahmad	FOP	
			<i>repanda</i>	Pers.	FOP	
			<i>vesiculosa</i>	Pers.	FOP	
			<i>violacea</i>	Pers.	FOP	
			Pyronemataceae	<i>Terfezia</i>	<i>arenaria</i>	(Moris) Trappe
		<i>Aleuria</i>		<i>aurantia</i>	(Pers.) Fuckel	FOP
				<i>boudieri</i>	(Höhn.) J. Moravec	FOP
	<i>Aleuria</i>	<i>murreana</i>		S. Ahmad	FOP	

Phylum/Order	Family	Genus	Species	Authority	Source		
Pezizales	Pyronemataceae	<i>Byssonectria</i>	<i>fusispora</i>	(Berk.) Rogerson & Korf	FOP		
		<i>Cheilymenia</i>	<i>granulata</i>	(Bull.) J. Moravec	FOP		
			<i>pulcherrima</i>	(P. Crouan & H. Crouan) Boud.	FOP		
			<i>theleboloides</i>	(Alb. & Schwein.) Boud.	FOP		
		<i>Geopora</i>	<i>ahmadii</i>	Saba, T. Ashraf, Khalid & Pfister	GenBank (KY805996); Saba et al. (2019a)		
			<i>arenicola</i>	(Lév.) Kers	FOP		
			<i>arenosa</i>	(Fuckel) S. Ahmad	FOP		
			<i>cooperi</i>	Harkn.	Ashraf and Khalid (2012)		
			<i>cooperi</i> f. <i>cooperi</i>		GenBank (JN558642)		
			<i>foliacea</i>	(Schaeff.) S. Ahmad	FOP		
			<i>pinyonensis</i>	Flores-Rent. & Gehring	GenBank (MK583663)		
			<i>summeriana</i>	(Cooke ex W. Phillips) M. Torre,	GenBank (MN860070)		
			<i>Geopyxis</i>	<i>alpina</i>	Höhn.	Khalid et al. (2000)	
				<i>majalis</i>	(Fr.) Sacc.	FOP	
			<i>Humaria</i>	<i>hemisphaerica</i>	(E.H. Wigg.) Fuckel	FOP	
			<i>Neottiella</i>	<i>hetieri</i>	Boud.	FOP	
			<i>Octospora</i>	<i>humosa</i>	(Fr.) Dennis	FOP	
				<i>plumbeoatra</i>	(E.K. Cash) D.C. Pant & V.P. Tewari	FOP	
				<i>umbrina</i>	(E.K. Cash) S. Ahmad	FOP	
			<i>Otidea</i>	<i>alutacea</i>	(Pers.) Massee	GenBank (MN495937)	
				<i>leporina</i>	(Batsch) Fuckel	FOP	
			<i>Pyronema</i>	<i>omphalodes</i>	(Bull.) Fuckel	FOP	
				<i>domesticum</i>	(Sowerby) Sacc.	GenBank (MN957610)	
			<i>Sepultariella</i>	<i>semiimmersa</i>	(P. Karst.) Van Vooren, U. Lindem. & Healy	FOP	
			<i>Scutellinia</i>	<i>scutellata</i>	(L.) Lambotte	FOP	
			<i>Trichophaea</i>	<i>gregaria</i>	(Rehm) Boud.	FOP	
				<i>woolhopeia</i>	(Cooke & W. Phillips) Boud.	FOP	
			Sarcoscyphaceae	<i>Komposcypha</i>	<i>waterstonii</i>	(Seaver) Pfister	FOP
			Sarcosomataceae	<i>Plectania</i>	<i>melastoma</i>	(Sowerby) Fuckel	FOP
				<i>Sarcoscypha</i>	<i>coccinea</i>	(Gray) Boud.	FOP
					<i>occidentalis</i>	(Schwein.) Sacc.	FOP
			Tuberaceae	<i>Tuber</i>	<i>puberulum</i>	Berk. & Broome	FOP
			Incertae sedis	<i>Coprotus</i>	<i>albidus</i>	(Boud.) Kimbr.	FOP
					<i>dextrinoideus</i>	Kimbr., Luck-Allen & Cain	FOP
					<i>granuliformis</i>	(P. Crouan & H. Crouan) Kimbr.	FOP
					<i>leucopocillum</i>	Kimbr., Luck-Allen & Cain	FOP
					<i>ochraceus</i>	(P. Crouan & H. Crouan) J. Moravec	FOP
				<i>niveus</i>	(Fuckel) Kimbr., Luck-Allen & Cain	FOP	
				<i>sexdecimsporus</i>	(P. Crouan & H. Crouan) Kimbr. & Korf	FOP	
		Pulvinulaceae		<i>Pulvinula</i>	<i>orichalcea</i>	(Cooke) Rifai	FOP
		Tarzettaceae		<i>Tarzetta</i>	<i>bronca</i>	(Peck) Korf & J.K. Rogers	FOP
				<i>catinus</i>	(Holmsk.) Korf & J.K. Rogers	FOP	
				<i>cupularis</i>	(L.) Lambotte	FOP	

Genus	Total species	BXW	EAMCF	IRM	IVD	HSTPF	KWTP	NWTSF	NWHASM	ROK	RNPSD	SINSD	SRAM	TD	WHBF	WHSACF
Hyphodontia	2	○	○	○	○	●	○	○	○	○	○	○	○	○	●	○
Hypholoma	4	○	○	○	○	●	○	○	○	○	○	○	○	○	●	●
Hypochnicium	1	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○
Hypsizygus	1	○	○	○	○	○	○	○	○	○	○	○	○	○	●	○
Incrucipulum	1	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○
Infundibulicybe	3	○	○	○	○	●	○	○	○	○	○	○	○	○	●	○
Inocutis	2	●	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Inocybe	30	○	○	○	○	●	●	○	○	○	○	○	○	○	●	●
Inonotus	7	●	○	○	○	●	○	●	○	○	○	○	○	○	●	○
Inosperma	3	○	○	○	○	○	○	○	○	○	○	○	○	○	●	○
Iodophanus	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Ionopezia	1	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○
Ipex	2	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Irpiciporus	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Itajahya	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Jahnoporus	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Komposcypha	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Kuehneromyces	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	●
Laccaria	6	○	○	○	○	●	○	○	●	○	○	○	○	○	●	○
Lachnellula	2	○	○	○	○	○	○	○	○	○	○	○	○	○	●	○
Lachnocladium	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Lachnum	5	○	○	○	○	●	○	○	○	○	○	○	○	○	●	○
Lactarius	20	○	○	○	○	●	●	○	●	○	○	○	○	○	●	○
Lactifluus	7	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Lactocollybia	2	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Laetiporus	1	○	○	○	○	●	●	○	○	○	○	○	○	○	○	○
Langermannia	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Lasiobelonium	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Lasiobolus	2	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Laxitextum	1	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○
Leccinellum	2	○	○	○	○	○	●	○	○	○	○	○	○	○	○	○
Leccinum	4	○	○	○	○	○	●	○	○	○	○	○	○	○	○	○
Lentaria	3	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Lentinellus	2	○	○	○	○	○	○	●	○	○	○	○	○	○	○	●
Lentinus	7	○	○	○	○	○	○	●	○	○	○	○	○	○	○	●

[illegible]

[illegible]

[illegible]

Genus	Total species	BXW	EAMCF	IRM	IVD	HSTPF	KWTP	NWTSF	NWHASM	ROK	RNPDS	SINSD	SRAM	TD	WHBF	WHSACF
Trichoglossum	3	○	○	○	○	●	○	●	○	○	○	○	○	○	●	○
Tricholoma	8	○	○	○	○	○	●	○	○	○	○	○	○	○	●	○
Tricholomopsis	5	○	○	○	○	○	●	○	●	○	○	○	○	○	●	○
Trichophaca	2	○	○	○	○	○	○	○	○	○	○	○	○	○	●	○
Trogia	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Tropicoporus	1	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Truncospora	2	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Tubaria	2	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Tuber	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Tulostoma	25	●	○	○	○	○	●	○	○	○	○	○	○	○	○	○
Turbinellus	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Tylophilus	3	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Tyromyces	2	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Velutaria	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Verpa	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Volvariella	6	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Volvopluteus	2	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xanthagaricus	3	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xanthoconium	3	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xanthoporia	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xerocomus	4	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xeromphalina	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xerula	2	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xylaria	5	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xylobolus	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xylodon	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Xylospheera	1	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Zhuliangomyces	2	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○

Where, **BXW** = Baluchistan xeric woodlands, **EAMCF** = East Afghan montane conifer forests, **IRM** = Indus River Delta Arabian sea mangroves, **IVD** = Indus valley desert, **HSTPF** = Himalayan subtropical pine forests, **KWTP** = Karakoram west Tibetan plateau alpine steppe, **NWTSF** = North-western thorn scrub forest, **NWHASM** = North-western Himalayan alpine scrub & meadows, **RNPDS** = Registan north Pakistan sandy desert, **ROK** = Rann of Kutch seasonal marsh, **SINSD** = South Iran Nubo-Sindian desert & semi-desert, **SRAM** = Sulaiman range Alpine meadows, **WHBF** = Western Himalayan broadleaf forests, **WHSACF** = Western Himalayan subalpine conifer forests, **TD** = Thar Desert.

Discussion

The compendium presented in Table 1 gives an overview of the macrofungal diversity of Pakistan known to date. It largely reposes on the checklist by Ahmad et al. (1997; 866 entries) published over two decades ago and its recent update (Khalid, *in press*), as well as taxa recently described with the use of molecular data, for example, *Russula foetenoides* (Razaq et al. 2014), *Leucoagaricus lahorensis* (Qasim et al. 2015a), *Tulotoma ahmadii* (Hussain et al. 2015b), *Phaeocollybia pakistanica* (Khan et al. 2016a), *Descolea quercina* (Khan et al. 2017a), *Amanita griseofusca* (Kiran et al. 2018), *Leucoagaricus brunneus* (Ullah et al. 2019), *Ahmadea dalanensis* (Aman et al. 2020) etc. Numerous edible mushrooms naturally occur in Pakistan including *Agaricus bisporus*, *Boletus edulis*, *Termitomyces umkowaan*, *Macrocybe gigantea*, *Morchella esculenta* (morels), *Ahmadea dalanensis* (truffles), *Pleurotus cystidiosus*, *Marasmius oreades*, *Phellorinia herculeana*, *Cantharellus cinereus* (chanterelle), *Coprinus comatus* and more. Siddiqui et al. (2020) worked on the cultivation potential of two wild indigenous species of *Agaricus*, i.e. *A. bisporus* and *A. subrufescens* and obtained promising results for spawn production locally. In the future, more edible mushrooms can be worked on for their possible cultivation and commercialisation prospects.

We recorded 1,293 species belonging to 411 genera, 115 families and 24 orders. For comparison, Vaco-Palacios and Franco-Molano (2013) listed 1,239 macrofungal species from Colombia. Flores et al. (2012) reported 315 taxa, 163 genera and 20 orders from Guatemala. Kinge et al. (2020) recently presented an elaborate checklist of macrofungi in South Africa listing 1,008 species, 251 genera and 72 families. For comparison with a well-studied area, 3,173 species have been reported from Quebec (mycoquébec.org). Approximately 20,000 species of macrofungi are known worldwide (Hawksworth 2001). Unsurprisingly, since Agaricales is the largest order of macrofungi (Money 2016), it is by far the most commonly represented order with 47% species in the present taxonomic list followed by Polyporales (11%), Russulales (9%) and Pezizales (8%).

The highest number of taxa was recorded in the western Himalayan broadleaf forests ecoregion, which belongs to the temperate broadleaf and mixed forest biome and has been reported to be the richest in central China and eastern North America (Zhao et al. 1990; Martin et al. 1993). The second highest diversity was found in the north-western thorn scrub forests, which are categorised under deserts and xeric shrublands. This thorn scrub is considered as a degraded form of tropical dry forests (e.g. Champion and Seth 1968; Puri et al. 1989). This ecoregion includes semi-arid to arid climatic zones and a mean annual rainfall of less than 750 mm and a temperature range of 45 degrees or more in summers to temperatures dropping below freezing point in winters. Furthermore, ecoregions in tropical and subtropical coniferous forests and temperate coniferous forest biomes also show good macrofungal taxa representation. The ecoregion of western Himalayan subalpine conifer forests plays an important ecological role to vanguard the alpine meadows to the north. For instance, many Himalayan birds and mammals migrate seasonally between the steep mountain

slopes, relying on adjacent habitats when the original ones are disturbed. Likewise, large-scale collection of morel mushrooms (*Morchella spp.*) from this ecoregion by local people for export overlaps with the breeding season of many pheasants and some mammals. Therefore, maintaining the biodiversity composition and ecological processes within this geologically young, highest mountain range on Earth requires particular conservation policies for this unique ecoregion (Wikramanayake et al. 2002). Finally, the ecoregions of flooded grasslands and savannahs, mangroves and montane grasslands and shrublands have either less than five percent or no representation. So, clearly there are missing data due to very limited exploration in several regions.

Although the data presented here will be useful to taxonomists, ecologists and conservation biologists, conclusive trends cannot be drawn as there are gaps in data due to extensive sampling in a few ecoregions, whereas other areas have been either neglected or unexplored. Therefore, the unexplored ecoregions of Pakistan need to be sampled extensively to give a full picture of the fungal diversity and endemism therein. Many countries and regions around the world have identified and listed endemic species, including the United States (Stein 2002), Russia (Griffin 1999), the Tuscan Region in Italy (Foggi et al. 2014) and New Caledonia (Wulff et al. 2013). The International Union for Conservation of Nature (IUCN) recently published a report on endemic threatened species on the Red List for each country (IUCN 2019). Redhead (1997) listed rare macrofungi of British Columbia, Canada, for each ecoregion. More recently, Enns et al. (2020) generated a list of endemic species, including a few fungal species as well, highlighting the status of target species for conservation.

In conclusion, this study provides a comprehensive list of macrofungi recorded in Pakistan as of the year 2020 and their known distribution by ecoregions. The otherwise scattered data have now been arranged and are available to be utilised by mycologists and other scientists as well as by amateur citizens. Most importantly, it can serve as a baseline information for further conservation studies and policy-making. Furthermore, these data also highlight the need for more sampling from less sampled areas like Sindh and Baluchistan Provinces. Our next step is to develop an online portal for fungi of Pakistan, where revisions of the current compendium can be done and new reports can be continuously added.

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Supplementary material I

Macrofungi list by biome and ecoregion of Pakistan

Authors: Nourin Aman

Data type: Base data for biomes and ecoregions of Pakistan

Explanation note: WWF description data for biomes and ecoregion of Pakistan is compiled in one document for readers ease of understanding of ecoregions present in Pakistan. The source of data is WWF official site, wikipedia and Dopa explorer. However, author added macrofungal genera recorded from each ecoregion.

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Link: <https://doi.org/10.3897/mycokeys.89.81148.suppl1>

Supplementary material 2

Detailed taxonomic checklist of macrofungi of Pakistan

Authors: Nourin Aman, Abdul Nasir Khalid & Jean-Marc Moncalvo

Data type: Checklist with detailed references, localities, biome and ecoregion

Explanation note: The detailed references and localities of each taxon is given and allocated biome and ecoregion according to localities mentioned in references consulted.

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