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Review article

Global species diversity and distribution of the psychedelic fungal genus *Panaeolus*

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ABSTRACT

Psychedelic fungi have received considerable attention recently due to their promising treatment potential of several psychiatric disorders and medical conditions, both in clinical settings but also as a nutraceutical. Besides research, a growing number of companies are developing capacity to conduct research and clinical trials where these fungi and their products can be used, and to provide these fungi to the public market that are rapidly becoming legal across the world. Whereas *Psilocybe* species are better known as psychedelic fungi, species in *Panaeolus* are also reputed to contain the psychedelic compound psilocybin and used recreationally. For the novice, there is no contemporary scientific summary of all the species in this genus that are known to be psychedelic, compared to those that are not. The global distribution and species diversity of these brown to white, often inconspicuous mushrooms are also not summarised, nor is it known to what extent DNA sequence data that are needed for identification have been generated for all of the species in this genus. However, psychedelic *Panaeolus* species are used and moved across the world. This lack of data makes it difficult to regulate bioexploitation and apply law enforcement of these fungi and the compounds they contain, especially seen in the light of the rapid development of the related markets. The aim of this review is to summarise current scientific data and knowledge on the species biodiversity, geographical distribution, extent of sequence data for identification purposes, and the psychedelic potential of species, based on published results. The review revealed where species are mostly known from, while also indicating areas seriously lacking such biodiversity data. A significant degree of study across the world is still needed to confirm which of these species are truly psychedelic and exactly what compounds they can produce.

1. Introduction

The use of psychedelic fungi has its roots in the histories of various cultures across the world [1]. Of these, psilocybin-containing mushrooms have mostly been used in the Americas by shamans, and were consequently used recreationally by Western societies after their discovery [2–4]. Psilocybin and its related metabolite psilocin are two serotonin derivatives that are increasingly demanded in modern medicine [5–11]. When psilocybin and psilocin are consumed by an individual, these substances can cross the blood-brain barrier and act as a serotonin inhibitor, creating hallucinations and long lasting beneficial changes in the brain [12,13]. Psilocybin and psilocin are used as an alternative therapeutic tool for the treatment of major depression disorder, obsessive-compulsive disorder,

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anorexia nervosa, post-traumatic stress disorder, cluster headaches, chronic pain, and substance abuse (e.g. alcohol, cocaine, nicotine) [14–18].

Upon legalization in several countries research into medicinal aspects are exploding with small to large pharmaceutical companies starting to invest significant resources to harness the therapeutic powers of psilocybin analogues and the fungi that produce them [19–21]. Whereas these compounds can be synthesized, it is the organic nature of consuming the mushrooms that naturally produce these compounds, which appeal most to the public. Furthermore, these mushrooms are also a source of self help, or assisted help, for individuals that does not require prescriptions. Several fungal genera are known to include psychedelic species that can produce psilocybin, with *Psilocybe* being the best known [4,22].

A number of powerful psilocybin-producing species are also known in *Panaeolus* [22] with species shown to produce psilocybin, its psychoactive metabolite psilocin, and other related alkaloids [19]. Hence species of *Panaeolus,* typified by *Panaeolus papilionaceus* [23, 24], are known for their notable health benefits and hallucinogenic properties [25–35]. *P. antillarum* and *P. cyanescens* have significant antioxidant, antiviral, antibacterial and antifungal activities [33,35], while *P. cyanescens* can also be anti-inflammatory [36]. Some species that are hallucinogenic include *P. subbalteatus, P. cyanescens* and *P. cambodginiensis* [5,19,37].

Panaeolus mushrooms [Fig. 1(A–D)] are small, brown to blackish to cream to white, with conical- or bell-shaped caps, elongated slender stalks, attached gills and a purple-brown to black spore print [5,38–40]. Microscopic characteristics include spores with an apical germ pore and a cellular pileipellis [23,41]. Most *Panaeolus* species are coprophilic [42–44] but non-coprophilic species, such as *P. bisporus*, *P. subbalteatus*, and *P. cyanescens*, are also known from substrates such as wood [45,46]. They can be easily grown on a number of substrates [47]. Family and subfamily relationships of *Panaeolus* remain complex, as well as the total number of species after previous taxonomic changes [22]. The genus was classified under *incertae sedis* due to its uncertain taxonomic level and unknown broader relationships [40,48,49]. However, recently the genus was placed in the Galeropsidaceae [24], sometimes referred to as tribe Panaeoleae. This family includes *Copelandia, Panaeolina, Panaeolopsis,* and *Panaeolus* [24]. Of these genera, *Panaeolina* and *Panaeolopsis* are currently valid but not *Copelandia* [50,51], even if these names are inconsistently used in literature [52–55].

The total number of currently legitimate species in *Panaeolus* is confusing for individuals that lack taxonomic expertise and knowledge of this group. There are no up to date monographs of *Panaeolus*, but only previous studies on groups of 15 and 29 *Panaeolus* species [39,56,57]. Of these, only 16 species were linked to DNA sequence data of the ITS region at the National Library of Medicine [58]. In comparison, online taxonomic databases such as Index Fungorum [50] and Mycobank [51] show that *Panaeolus* has 179 and 202 names, respectively. Other online biodiversity databases, such as the Catalogue of Life: 2019 Annual Checklist [59], has 162 names of *Panaeolus*, while the Global Biodiversity Information Facility [60] recognises 90 names from 23,000 observations and photographs. These still include synonyms and species names moved to other genera.

A publication capturing only currently accepted species names of *Panaeolus* to know how diverse the genus is will be of substantial value to researchers, students, taxonomists, forensic investigators and amateur mycologists. Furthermore, it is not well-known and

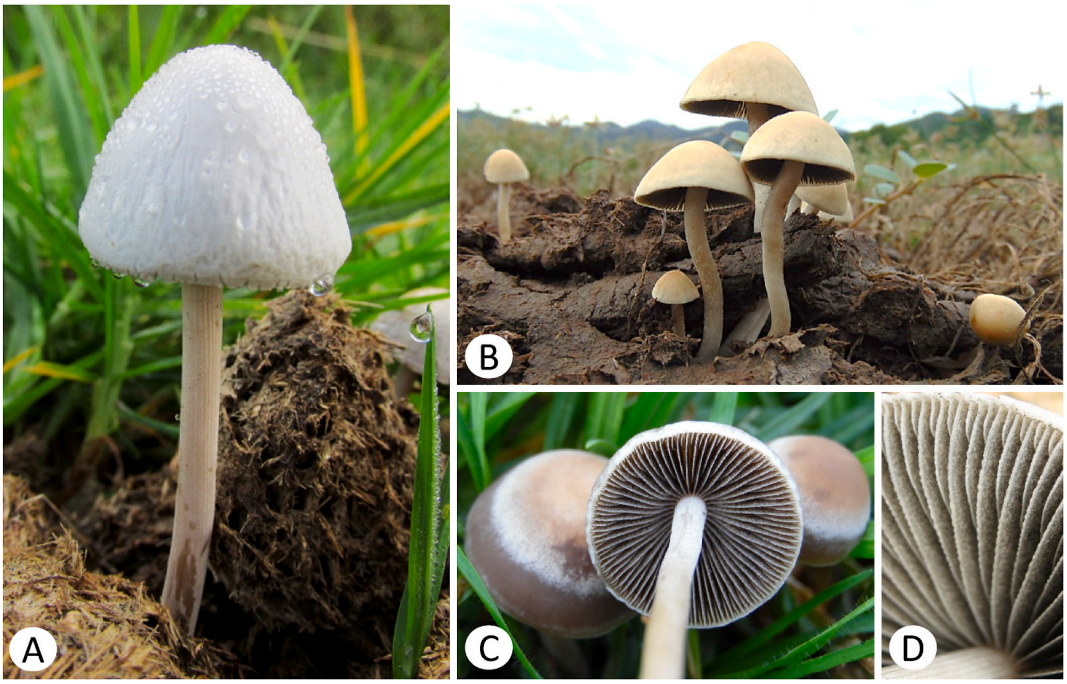

Fig. 1. (A) *Panaeolus antillarum* associated with dung (photograph by L. Popich). (B) *Panaeolus cyanescens* associated with dung, one of the most potent hallucinogenic species (photograph by J. MacGillvray). (C) *Panaeolus cinctulus* (photograph by L. Popich). (D) Mottled gills characteristic of *Panaeolus* species (photograph by L. Popich).

summarised how widely these species occur across the world. This systematic review aimed to compile only the currently accepted species, along with valuable information on each species, including type locations, global distributions as well as DNA sequence availability. The data were used to summarise the diversity and occurrences of *Panaeolus* species in each continent, region and country to show areas of the world where the genus *Panaeolus* is well studied compared to areas where there are missing data. Lastly, the extent of the state of knowledge if each species contains psychoactive compounds, or an indication thereof (i.e. bruising blue), is not recorded consistently in published literature and the scientific proof for the existence of psilocybin and psilocin in some species is thus unclear. Hallucinogenic properties captured in scientific literature were thus included in this review for each species, which differs from on the ground knowledge by those growing and using these fungi. Similarly it summarised what is known about the occurrence of psilocybin and psilocin across species only based only on published scientific proof.

2. Materials and methods

A list only of species that are currently legitimate was obtained from Dr Paul Kirk (Kew Botanical Gardens, UK) and formed the basis of the review. The approach used to obtain information is based on literature and data from Google Scholar (61) and Scopus (62) (Fig. 2) and results were summarised in Tables 1–3. Literature for *Panaeolus* each year were found using the search terms "*Panaeolus*" or "*Panaeolus* species", as well as "*Panaeolus* species", "novel species" or "sp. nov.", "first record", "first finding", "species description", "check lists", "field guides", "species distribution", "hallucinogenic", "psychedelic", "psychoactive", "bluing", "psilocybin" and "psilocin", with titles, abstracts and text searches from 1922 to 2022 (Fig. 2). Sequences found on NCBI representing ITS [63], the most variable gene region currently sequenced, was representatively sequenced across species and added to Table 1 for easy referencing. Separate datasets were compiled using Microsoft Excel to determine the diversity of species per country, region and continent. Regions were defined according to the United Nations Geoscheme (Table 4). A map was created to visualise the distribution of *Panaeolus* species using MapChart [64].

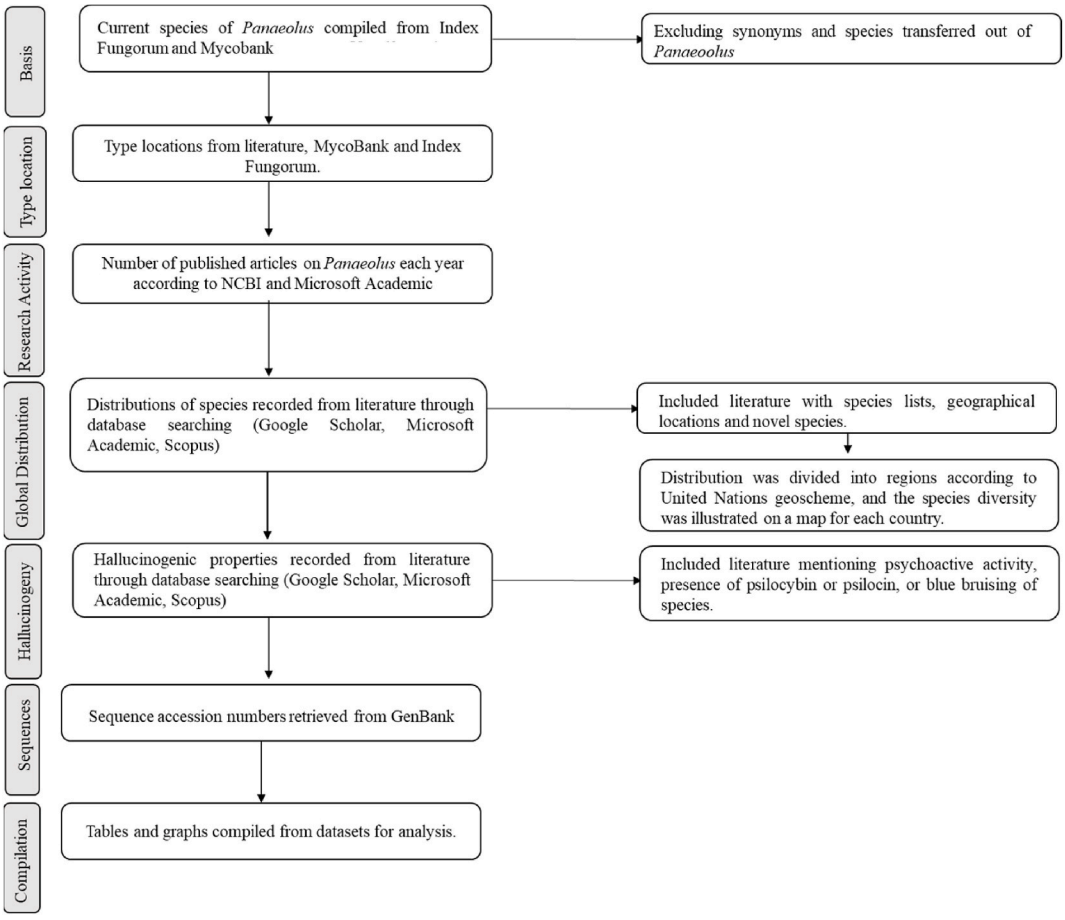

Fig. 2. A pipeline for creating the referral datasets of *Panaeolus*, including characteristics of species in the genus such as the diversity, distribution, hallucinogenic properties and available DNA data.

Table 1
Published records of *Panaeolus* species distribution across the world.

No.	Species	Type location	Distribution	References	ITS Accession Number (NCBI)
1	*Panaeolus acidus* Sumst.1905	USA	USA.	[115]	–
2	*Panaeolus acuminatus* (P. Kumm.) Quél. 1872	France	Italy; British Isles; Brazil; India; Argentina; Iran; China; Morocco; Spain; Turkey; Macedonia; Poland; Australia; Austria; Slovakia; Scotland; Serbia; USA; Czech Republic; Croatia; France.	[23,116–125]	MH856251.1; MH856250.1; JF908518.1; MW376698.1; MW352021.1.
3	*Panaeolus affinis* (E. Horak) Ew. Gerhardt 1996	Papua New Guinea	Papua New Guinea.	[39]	–
4	*Panaeolus africanus* Ola'h 1969	Central African Republic	India; Chad; Republic of Central Africa; Sudan.	[25,49,57,126]	–
5	*Panaeolus albellus* Massee 1902	Thailand	Thailand.	[74,127,128]	–
6	*Panaeolus albovelutinus* (Rick) Raithelh. 1995	Brazil	Brazil	[129]	–
7	*Panaeolus alcis* M.M. Moser 1984	Sweden	Italy; Poland; India; Sweden.	[75,126,130,131]	KM982723.1; MW597122.1.
8	*Panaeolus alveolatus* Peck 1902	USA	USA.	[132,133]	–
9	*Panaeolus annulatus* Natarajan & Raman 1983	India	India.	[126,134]	–
10	*Panaeolus anomalus* (Murrill) Sacc. & Trotter 1925	Jamaica	Jamaica	[135]	–
11	*Panaeolus antillarum* (Fr.) Dennis 1961	Venezuela	India; Kenya; Uganda; Tanzania; British Isles; China; South Africa, Australia, Italy, East Falkland; Ukraine; Brazil; Poland; Thailand; Philippines; United States of America; Mexico; Iceland; Taiwan; Thailand; Indonesia; Sierra Leone; Netherlands; Austria; Argentina; Spain; Panama; Venezuela.	[49,73,74,78,83,95,96,119,123,126,130,136–147]	MF497586.1; MF497585.1; JF908515.1; KR998382.1.
12	*Panaeolus ater* (J.E. Lange) Kühner & Romagn. ex Bon 1985	Denmark	India; British Isles; USA; Denmark; Australia; Russia; Israel; Japan; Sri Lanka; Germany; Central Russia; Morocco; Macedonia; Turkey; Italy; Indonesia; Jordan; Greece; Scotland.	[25,45,49,78,100,117,119,123,126,148–154]	–
13	*Panaeolus atrobalteatus* Pegler & A. Henrici 1998	British Isles	British Isles.	[155]	–
14	*Panaeolus axfordii* Y. Hu, S.C. Karunarathna, P.E. Mortimer & J.C. Xu 2020	China	China.	[7]	NR169700.1; MN482689.1.
15	*Panaeolus bernicis* A.M. Young 1989	Australia	Australia.	[119]	–
16	*Panaeolus bisporus* (Malençon & Bertault) Ew. Gerhardt 1996	Morocco	USA; Morocco; Spain, South Africa.	[39,46,156]	MT110229.1; MG966283.1.
17	*Panaeolus bolombensis* Beeli 1928	Congo	Congo.	[157]	–
18	*Panaeolus cambodginiensis* Ola'h & R. Heim 1969	Colombia	Brazil; Mexico; Colombia; Hawaii.	[57,139,158,159]	AB158633.1.
19	*Panaeolus campanuloides* Guzmán & K. Yokoy. 1979	Papua New Guinea	Papua New Guinea.	[160]	–
20	*Panaeolus chlorocystis* (Singer & R.A. Weeks) Ew. Gerhardt 1987	USA	USA.	[39,46,161]	–
21	*Panaeolus cinctulus* (Bolton) Sacc. 1887	Brazil	Italy; Brazil; Poland; Mexico; Morocco.	[130,131,139,162,163]	MH590045.1; MW241166.1; MW352022.1.
22	*Panaeolus conicodiffractus* (Rick) Raithelh. 1995	Brazil	Brazil	[129]	–
23	*Panaeolus convexulus* Singer 1965	Chile	Argentina; Chile.	[164,165]	
24	*Panaeolus cyanescens* Sacc. 1887		Brazil; India; Hawaii; Indonesia; Italy; Phillipean; Australia; Germany; Japan; Mexico; USA; Hungary (single occurrence); Thailand; Sri Lanka; Venezuela, South Africa.	[45,93,119,126,139,140,158,159,163,166–170]	MW452990.1; MW018891.1; MK855518.1; MK855517.1; MK855516.1; MK855515.1; MH547103.1; KU640172.1; KU640168.1; KT002152.1; HM035084.1; EU834287.1.

(*continued on next page*)

Table 1 (*continued*)

No.	Species	Type location	Distribution	References	ITS Accession Number (NCBI)
25	*Panaeolus cyanoannulatus* Atri, M. Kaur & Amand. Kaur 2014	India	India.	[49,171]	–
26	*Panaeolus cylindrosporus* E. Ludwig 2001	Germany	Germany	[172]	–
27	*Panaeolus desertorum* (Velen. & Dvořák) E.F. Malysheva, G. Moreno, Svetash. & M. Villarreal 2019	Spain	Spain.	[86]	–
28	*Panaeolus diffractus* (Rick) Raithelh. 1995	Brazil	Brazil	[129]	–
29	*Panaeolus digressus* Peck 1895	USA	USA.	[173]	–
30	*Panaeolus fimicola* (Pers.) Gillet 1878	France	Italy; Australia; USA; Jamaica; Puerto Rico; Brazil; Austria; Denmark; British Isles; Ireland; Spain; Switzerland; Morocco; Japan; Korea; Mongolia; Germany; Brazil; India; Macedonia; Argentina; Norway; Slovak; Turkey; Mexico; Iran; Thailand; Panama; Nigeria; Finland; Egypt; France; Poland.	[25,74,96,119,123, 126,130,139,149, 165,174–185]	MT451924.1; MN894012.1; JF908519.1; JF908514.1; MK394183.1; MT347601.1.
31	*Panaeolus fimicoloides* A. Pearson 1950	South Africa	South Africa.	[186,187]	–
32	*Panaeolus fontinalis* A.H. Sm. 1948	USA	USA; Mexico.	[188]	–
33	*Panaeolus fraxinophilus* A.H. Sm. 1948	USA	USA.	[116,189]	–
34	*Panaeolus georgii* Szem. 1944	Hungary	Hungary.		–
35	*Panaeolus goossensiae* Beeli 1928	Congo	Hawaii; Congo.	[105,157,190]	–
36	*Panaeolus griseofibrillosus* (Rick) Raithelh. 1995	Brazil	Brazil	[129]	–
37	*Panaeolus guttulatus* Bres. 1893	Italy	Italy, Iran, Greece, Turkey	[191–194]	MH592651.1, LC458688.1, KU725994.1, KU725993.1
38	*Panaeolus hippophilus* E.H.L. Krause 1928	Germany	Germany.		–
39	*Panaeolus hygrophanus* Velen. 1921	Czech Republic	Czech Republic.	[195]	–
40	*Panaeolus indicus* Sathe & J.T. Daniel 1979	India	India.	[196]	–
41	*Panaeolus lentisporus* Ew. Gerhardt 1996	Papua New Guinea	Papua New Guinea.	[39]	–
42	*Panaeolus lepistercoris* Atri, M. Kaur & Amand. Kaur 2014	India	India.	[171]	–
43	*Panaeolus lepus-stercus* Atri, M. Kaur &A. Kaurin 2014	India	India.	[49,126,171]	–
44	*Panaeolus lignicola* Rick 1930	Brazil	Brazil.	[139]	–
45	*Panaeolus linnaeanus* S. Imai 1938	Japan	Japan.	[197]	–
46	*Panaeolus microsporus* Ola'h & Cailleux 1969	Central African Republic	Republic of Central Africa.	[25,57]	–
47	*Panaeolus moellerianus* Singer 1960	Macquarie Is.	Faeroes Islands; Antarctic; Argentina; Macquire Island.	[25,165,174,198]	–
48	*Panaeolus niveus* Velen. 1921	Czech Republic	Czech Republic.	[195]	–
49	*Panaeolus olivaceofuscus* Raithelh. 1977	Argentina	Argentina.	[165,174,199]	–
50	*Panaeolus olivaceus* F.H. Møller 1945	Føroyar (Faeroe Islands)	Czeckoslovakia; Denmark; Finland; British Isles; Sweden; Switzerland; Australia; Morocco; Macedonia; Iran; Poland; Faeroe Islands; Turkey; Italy; Austria; France; India.	[25,95,123,149,179, 200–206]	MH593015.1; MH285992.1; MF955153.1.
51	*Panaeolus paludosus* Cleland 1933	Australia	China; Australia.	[207,208]	MK278434.1
52	*Panaeolus panaiensis* Copel. 1905	Philippines	Philippines.	[209]	–
53	*Panaeolus papilionaceus* (Bull.) Quél. 1872	France	Italy; USA; Bahamas; Cuba; Puerto Rico; San Vincent Island; Brazil; Chile;	[23,25,44,68,74, 122,123,125,126,	MH632116.1; MW915589.1; MW633031.1; MK397571.1;

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Table 1 (*continued*)

No.	Species	Type location	Distribution	References	ITS Accession Number (NCBI)
			Colombia; Uruguay; Venezuela; Czeckoslovakia; Finland; British Isles; Ireland; Macedonia; Norway; Russia; Spain; Sweden; Switzerland; Morocco; Ukraine; South Africa; Uganda; China; Hong Kong; India; Israel; Japan; Korea; Kuwait; Philippines; Australia; Sri Lanka; Germany; Netherlands; Argentina; Turkey; Taiwan; Iran; Egypt; Poland; Austria; Thailand; Croatia; Paraguay; Iceland; France.	[130,148,174,179, 181,183,200,203, 210]	MK500858.1; MN258670.1; LC481956.1; MK028487.1; MK439503.1; LC458685.1; MH979305.1; MF156263.1; MH169580.1; MH100727.1; MH100681.1; MF628989.1; LT716041.1; KF830093.1; KC414234.1.
54	*Panaeolus plantaginiformis* (Lebedeva) E.F. Malysheva 2019	Russia	Argentina; Peru; Russia; Asia	[86]	–
55	*Panaeolus pseudoguttulatus* Hauskn. & Krisai 2009	Austria	Austria.	[146]	–
56	*Panaeolus pseudopapilionaceus* Copel. 1905	Philippines	Philippines.	[209,211]	–
57	*Panaeolus regis* De Seynes 1901	France	France.	[212]	–
58	*Panaeolus reticulatus* Overh. 1916	USA	Macedonia; USA; Slovakia.	[149,213]	–
59	*Panaeolus rickenii* Hora 1960	British Isles	Australia; Brazil; India; Spain; Iran; Poland; Siberia; Korea; Argentina; Turkey; Greece; Austria; British Isles.	[100,165,174,179, 181,214–219]	JF908516.1; KY559329.1; MK966650.1; MK966649.1; MK966648.1; JF908523.1; MK351680.1.
60	*Panaeolus rubricaulis* Petch 1925	Sri Lanka	Papua New Guinea; Sri Lanka; Vietnam.	[25,44,220]	–
61	*Panaeolus rufus* Overh. 1916	USA	USA.	[213]	–
62	*Panaeolus semiglobatus* (Murrill) Sacc. & Trotter 1925	USA	USA; Mongolia	[135,221]	–
63	*Panaeolus semilanceatus* Peck 1909	Canada	Ireland; Australia.	[25,119,222]	–
64	*Panaeolus semiovatus* (Sowerby) S. Lundell & Nannf. 1938	Germany	Italy; British Isles; Brazil; India; Indonesia; Morocco; Argentina; Macedonia; Spain; Macedonia; Colombia; Mongolia; Falkland Island; Hawaii; Canada; USA; Turkey; Poland; Thailand; Croatia; Mexico; Bulgaria; Kazakhstan; Iceland.	[66,68,73,74,105, 117,123,125,126, 130,131,139,143, 149,165,174,200, 223–232]	MH856012.1; MT712776.1; MK386836.1; JF908517.1; MH856675.1; MK386822.1; MF955154.1.
65	*Panaeolus squamulosus* Velen. 1921	Czech Republic	Czech Republic.	[195]	–
66	*Panaeolus subbalteatus* (Berk. & Broome) Sacc. 1887	British Isles	USA; Guadalupe; Martinique; Argentina; Brazil; British Isles; Iceland; Italy; Russia (including Siberia); South Africa; India; Japan; Papua New Guinea; Philippines; Australia; New Zealand; Hawaii; Germany; Brussels; Belgium; India; Iran; Bulgaria; Canada.	[25,126,158,163, 174,179,230,233]	MW192454.1; MH855554.1; MH855553.1; MH855551.1; MH855550.1; MN960188.1; MN622762.1; MF955157.1; MF955156.1; MF955155.1; JF961370.1; AB092794.1; MH855552.1; MZ197976.1.
67	*Panaeolus subfirmus* P. Karst. 1889	Finland	Italy; Poland; Argentina; Iran; Greece; Falkland Islands; Turkey; Finland.	[73,123,130,131, 174,179,234,235]	–
68	*Panaeolus sylvaticus* Silva-Filho & Cortez 2019	Brazil	Brazil.	[88,139]	–
69	*Panaeolus texensis* V.E. Tyler & A.H. Sm. 1963	USA	USA.		–
70	*Panaeolus tirunelveliensis* (Natarajan & Raman) Ew. Gerhardt 1996	India	India; Hawaii; Cambodia.	[39,45,49]	–
71	*Panaeolus tropicalis* Ola'h 1969	Cambodia	Brazil; Cambodia; Republic of Central Africa; Mexico; Hawaii; India.	[126,139,158,159, 236]	JF961377.1.
72	*Panaeolus uliginicola* (Speg.) Sacc. 1891	Argentina	Argentina.	[174,237]	–
73	*Panaeolus uliginosus* Jul. Schäff. 1947	Germany	Slovakia; France; Germany; Canada.	[212,238–240]	AY129363.1.
74	*Panaeolus variabilis* Overh. 1916	USA	USA.	[213]	–

(*continued on next page*)

Table 1 (*continued*)

No.	Species	Type location	Distribution	References	ITS Accession Number (NCBI)
75	*Panaeolus venenosus* Murrill 1916	USA	British Isles; USA.	[201,241]	–
76	*Panaeolus venezolanus* Guzmán 1978	Venezuela	Mexico; Venezuela; India.	[25,126,242]	–
77	*Panaeolus westii* (Murrill) Murrill 1942	USA	USA	[243]	–

3. Results

3.1. Literature

In this review, 258 articles were studied for information on the 77 *Panaeolus* species that are currently legitimate (Table 1). Publications on *Panaeolus* mushrooms have up to now slightly increased, but especially in popular literature, as indicated by Google Scholar searches (Fig. 3). The number of citations of published literature on *Panaeolus* has also increased. This trend that is most evident over the last decade, probably is a result of the increase in the interest in psilocybin and psilocin containing species of the genus.

3.2. Type locations

In North America, the United States of America (USA) has 13 type locations for species from out of the 77 currently legit species, and one type species from Canada (Table 1). In South America (9 species), three species have been described from type locations in Brazil, two more from Venezuela, two from Argentina, one from Chile, and one from Colombia. In Asia (12 species), India has six species described from type locations, one species in Japan, one species from China, two species from the Philippines, one species from Thailand and another from Cambodia. In Europe (19 species), species were described from type locations all over the continent, including three species from the United Kingdom, one from Austria, three from Czech Republic, one from Denmark, one from Finland, four from France, three from Germany, one from Hungary, one from Spain and one from Sweden. The Oceania region (five species) has two species described from type locations in Australia, and three from Papua New Guinea. Six species have been described from type locations in Africa and include two species from Central African Republic, two more from Congo, one species from Morocco, and one from South Africa.

3.3. Distribution and diversity

The highest known species diversity of *Panaeolus* occurs in Asia (32 species) (Fig. 4). This is followed by South America (27 species) and Europe (26 species). North America had 21 species, while Oceania, with Australia, New Zealand and Melanesia, had 19 species of *Panaeolus*, and Africa 16 species.

Some species have a wide geographic distribution from multiple continents whereas others appear to have a restricted distribution and are currently known from one or a few countries (Table 1). Twenty eight species of *Panaeolus* are intercontinental and occur on more than two continents. Some examples include *P. cinctulus, P. rickenii, P. subbalteatus, P. tropicalis, P. africanus, P. ater, P. subfirmis, P. olivaceus, P. fimicola, P. papilionaceus, P. semiovatus, P. ulignosus, P. antillarum* and *P. cyanescens*. Species that are only known intra-continental but occur in more than one location include *P. cambodginiensis, P. convexulus, P. moellerianus, P. bisporus, P. alcis* and *P. fontinalis*. However, the majority of species have only been recorded at their type locations (*P. olivaceofuscus, P. ulignosa, P. benicis, P. pseudoguttulatus, P. atrobalteatus, P. axfordii, P. bolombensis, P. hygrophanus, P. niveus, P. squamulosus, P. georgii, P. desertorum. P. lignicola, Pa. sylvaticus, P. annulatus, P. cyanoannulatus, P. indicus, P. lepistercoris, P. lepus-stercus, P. affinis, P. campanuloides, P. lentisporus, P. panaiensis, P. pseudopapilionaceus, P. fimicoloides, P. albellus, P. acidus, P. alveolatus, P. chlorocystis, P. digressus, P. fraxinophilus, P. rufus, P. texensis,* and *P. variabilis*).

In Asia with the highest diversity, division of data from published records into regions according to the United Nations Geoscheme shows showed that most *Panaeolus* species are recorded in southern Asia, south-eastern Asia, and eastern Asia with 23, 15 and 13 species, respectively (Table 2, Figs. 5 and 6). Western Asia has ten known species and central Asia only has a single species from Kazakhstan, namely *P. semiovatus*, which is also a widely distributed species.

In Europe, most *Panaeolus* species are recorded in eastern Europe (20 species) and southern Europe (17 species), while western Europe has 15 species and northern Europe records 13 species. In South America, *Panaeolus* has a diversity of 21 species, while in North America, 21 species have also been recorded. Central America and the Caribbean have nine and three species recorded, respectively. In Australia and New Zealand, 12 and two species have been recorded, while Papua New Guinea in the Melanesia region, have five species recorded. Africa has the lowest diversity of *Panaeolus* compared to its size (Fig. 4). Northern Africa has the highest diversity on the continent with eight species of *Panaeolus*, while Central Africa only has five species, southern Africa four species and eastern and western Africa each having two recorded species.

Table 2
Global distribution of *Panaeolus* according to continent, region and country.

Continent	Species per continent	Regions	Species per region	Country	Species per country
Asia	*Panaeolus acuminatus*	Central Asia	*Panaeolus semiovatus*	Kazakhstan	*Panaeolus semiovatus*
	P. africanus	Eastern Asia	*P. acuminatus*	China	*P. acuminatus*
	P. albellus		*P. antillarum*		*P. antillarum*
	P. alcis		*P. ater*		*P. axfordii*
	P. annulatus		*P. axfordii*		*P. paludosus*
	P. antillarum		*P. cyanescens*		*P. papilionaceus*
	P. ater		*P. fimicola*	Japan	*P. ater*
	P. axfordii		*P. linnaeanus*		*P. cyanescens*
	P. cyanescens		*P. paludosus*		*P. fimicola*
	P. cyanoannulatus		*P. papilionaceus*		*P. linnaeanus*
	P. fimicola		*P. rickenii*		*P. papilionaceus*
	P. guttulatus		*P. semiglobatus*		*P. subbalteatus*
	P. indicus		*P. semiovatus*	Mongolia	*P. fimicola*
	P. lepistercoris		*P. subbalteatus*		*P. papillionaceus*
	P. lepus-stercus				*P. semiglobatus*
	P. linnaeanus				*P. semiovatus*
	P. olivaceus			Korea	*P. fimicola*
	P. paludosus				*P. papilionaceus*
	P. panaiensis				*P. rickenii*
	P. papilionaceus			Taiwan	*P. antillarum*
	P. pseudopapilionaceus				*P. papilionaceus*
	P. rickenii	South-Eastern Asia	*P. albellus*	Cambodia	*P. tirunelveliensis*
	P. rubricaulis		*P. antillarum*		*P. tropicalis*
	P. semiglobatus		*P. ater*	Thailand	*P. albellus*
	P. semiovatus		*P. cyanescens*		*P. antillarum*
	P. sepulchralis		*P. fimicola*		*P. fimicola*
	P. solidipes		*P. panaiensis*		*P. papilionaceus*
	P. subbalteatus		*P. papilionaceus*		*P. semiovatus*
	P. subfirmus		*P. pseudopapilionaceus*	Vietnam	*P. rubricaulis*
	P. tirunelveliensis		*P. rubricaulis*	Indonesia	*P. antillarum*
	P. tropicalis		*P. semiovatus*		*P. ater*
	P. venezolanus		*P. subbalteatus*		*P. cyanescens*
			P. tirunelveliensis		*P. semiovatus*
			P. tropicalis	Philippines	*P. panaiensis*
					P. papilionaceus
					P. pseudopapilionaceus
					P. subbalteatus
		Southern Asia	*P. acuminatus*	India	*P. acuminatus*
			P. africanus		*P. africanus*
			P. alcis		*P. alcis*
			P. annulatus		*P. annulatus*
			P. antillarum		*P. antillarum*
			P. ater		*P. ater*
			P. cyanescens		*P. cyanescens*
			P. cyanoannulatus		*P. cyanoannulatus*
			P. fimicola		*P. fimicola*
			P. guttulatus		*P. indicus*
			P. indicus		*P. lepistercoris*
			P. lepistercoris		*P. lepus-stercus*
			P. lepus-stercus		*P. olivaceus*
			P. olivaceus		*P. papilionaceus*
			P. papilionaceus		*P. rickenii*
			P. rickenii		*P. semiovatus*
			P. rubricaulis		*P. sepulchralis*
			P. semiovatus		*P. solidipes*
			P. sepulchralis		*P. subbalteatus*
			P. solidipes		*P. tirunelveliensis*
			P. subbalteatus		*P. tropicalis*
			P. subfirmus		*P. venezolanus*
			P. tirunelveliensis	Sri Lanka	*P. ater*
			P. tropicalis		*P. cyanescens*
			P. venezolanus		*P. papilionaceus*
					P. rubricaulis
				Iran	*P. acuminatus*
					P. fimicola
					P. guttulatus
					P. olivaceus
					P. papilionaceus

(*continued on next page*)

Table 2 (*continued*)

Continent	Species per continent	Regions	Species per region	Country	Species per country
					P. rickenii
					P. subbalteatus
					P. subfirmus
		Western Asia		Israel	*P. ater*
					P. papilionaceus
				Jordan	*P. ater*
				Kuwait	*P. papilionaceus*
				Turkey	*P. acuminatus*
					P. acuminatus
					P. fimicola
					P. guttulatus
					P. olivaceus
					P. papilionaceus
					P. rickenii
					P. semiovatus
					P. subfirmus
Americas	*P. acidus*	Northern America	*P. acuminatus*	Canada	*P. semiovatus*
	P. acuminatus		*P. antillarum*		*P. subbalteatus*
	P. antillarum		*P. chlorocystis*		*P. uliginosus*
	P. ater		*P. digressus*	USA	*P. acidus*
	P. bisporus		*P. cyanescens*		*P. acuminatus*
	P. cambodginiensis		*P. fimicola*		*P. antillarum*
	P. chlorocystis		*P. papilionaceus*		*P. ater*
	P. cinctulus		*P. reticulatus*		*P. bisporus*
	P. convexulus		*P. semiovatus*		*P. chlorocystis*
	P. cyanescens		*P. acidus*		*P. cyanescens*
	P. digressus		*P. ater*		*P. digressus*
	P. fimicola		*P. bisporus*		*P. fimicola*
	P. fontinalis		*P. subbalteatus*		*P. fontinalis*
	P. lignicola		*P. texensis*		*P. papilionaceus*
	P. moellerianus		*P. variabilis*		*P. reticulatus*
	P. olivaceofuscus		*P. venenosus*		*P. rufus*
	P. papilionaceus		*P. rufus*		*P. semiovatus*
	P. reticulatus		*P. uliginosus*		*P. semiglobatus*
	P. rickenii				*P. subbalteatus*
	P. rufus				*P. texensis*
	P. semiovatus				*P. variabilis*
	P. subbalteatus				*P. venenosus*
	P. subfirmus				*P. westii*
	P. sylvaticus	Caribbean	*P. papilionaceus*	Bahamas	*P. papilionaceus*
	P. texensis		*P. subbalteatus*	Cuba	*P. papilionaceus*
	P. tropicalis		*P. fimicola*	Guadalupe	*P. subbalteatus*
	P. uliginosus			Jamaica	*P. fimicola*
	P. variabilis				*P. anomalus*
	P. venenosus			Martinique	*P. subbalteatus*
	P. venezolanus			Puerto Rico	*P. fimicola*
					P. papilionaceus
				San Vincent Island	*P. papilionaceus*
		Central America	*P. antillarum*	Mexico	*P. antillarum*
			P. cambodginiensis		*P. cambodginiensis*
			P. cinctulus		*P. cinctulus*
			P. cyanescens		*P. cyanescens*
			P. fimicola		*P. fimicola*
			P. fontinalis		*P. fontinalis*
			P. semiovatus		*P. semiovatus*
			P. venezolanus		*P. venezolanus*
			P. tropicalis		*P. tropicalis*
				Panama	*P. antillarum*
					P. fimicola
		South America	*P. acuminatus*	Argentina	*P. acuminatus*
			P. antillarum		*P. antillarum*
			P. convexulus		*P. convexulus*
			P. fimicola		*P. fimicola*
			P. moellerianus		*P. moellerianus*
			P. olivaceofuscus		*P. olivaceofuscus*
			P. papilionaceus		*P. papilionaceus*
			P. rickenii		*P. rickenii*
			P. semiovatus		*P. semiovatus*
			P. subbalteatus		*P. subbalteatus*

(*continued on next page*)

Table 2 (*continued*)

Continent	Species per continent	Regions	Species per region	Country	Species per country
			P. subfirmus		*P. subfirmus*
			P. uliginicola		*P. uliginicola*
			P. cambodginiensis	Brazil	*P. acuminatus*
			P. cinctulus		*P. antillarum*
			P. cyanescens		*P. cambodginiensis*
			P. sylvaticus		*P. cinctulus*
			P. tropicalis		*P. cyanescens*
			P. lignicola		*P. fimicola*
			P. convexulus		*P. papilionaceus*
			P. subfirmus		*P. rickenii*
			P. venezolanus		*P. semiovatus*
					P. subbalteatus
					P. sylvaticus
					P. tropicalis
					P. lignicola
				Chile	*P. convexulus*
					P. papilionaceus
				Colombia	*P. cambodginiensis*
					P. papilionaceus
					P. semiovatus
				Falkland Island	*P. antillarum*
					P. semiovatus
					P. subfirmus
				Paraguay	*P. papilionaceus*
				Uruguay	*P. papilionaceus*
				Venezuela	*P. antillarum*
					P. cyanescens
					P. papilionaceus
					P. venezolanus
Europe	*P. acuminatus*	Northern Europe	*P. acuminatus*	Denmark	*P. ater*
	P. alcis		*P. alcis*		*P. fimicola*
	P. antillarum		*P. antillarum*		*P. olivaceus*
	P. ater		*P. ater*	Faeroe Islands	*P. moellerianus*
	P. atrobalteatus		*P. atrobalteatus*		*P. olivaceus*
	P. bisporus		*P. fimicola*	Finland	*P. subfirmus*
	P. cinctulus		*P. olivaceus*		*P. fimicola*
	P. cyanescens		*P. papilionaceus*		*P. olivaceus*
	P. cylindrosporus		*P. rickenii*		*P. papilionaceus*
	P. fimicola		*P. semilanceatus*	Iceland	*P. antillarum*
	P. georgii		*P. semiovatus*		*P. subbalteatus*
	P. hippophilus		*P. subbalteatus*	Norway	*P. fimicola*
	P. niveus		*P. venenosus*		*P. papilionaceus*
	P. olivaceus			Sweden	*P. alcis*
	P. panaiensis				*P. olivaceus*
	P. plantaginiformis				*P. papilionaceus*
	P. papilionaceus			British Isles	*P. acuminatus*
	P. pseudoguttulatus				*P. antillarum*
	P. regis				*P. ater*
	P. reticulatus				*P. atrobalteatus*
	P. rickenii				*P. fimicola*
	P. semilanceatus				*P. olivaceus*
	P. semiovatus				*P. papilionaceus*
	P. squamulosus				*P. rickenii*
	P. subbalteatus				*P. semilanceatus*
	P. subfirmus				*P. semiovatus*
	P. uliginosus				*P. subbalteatus*
	P. venenosus				*P. venenosus*
		Western Europe	*P. acuminatus*	Austria	*P. acuminatus*
			P. antillarum		*P. antillarum*
			P. ater		*P. fimicola*
			P. cyanescens		*P. olivaceus*
			P. cylindrosporus		*P. papilionaceus*
			P. fimicola		*P. pseudoguttulatus*
			P. hippophilus		*P. rickenii*
			P. olivaceus		*P. semiovatus*
			P. papilionaceus	Belgium	*P. subbalteatus*
			P. pseudoguttulatus	France	*P. acuminatus*
			P. regis		*P. fimicola*
			P. rickenii		*P. olivaceus*

(*continued on next page*)

Table 2 (*continued*)

Continent	Species per continent	Regions	Species per region	Country	Species per country
			P. semiovatus		*P. papilionaceus*
			P. subbalteatus		*P. regis*
			P. uliginosus		*P. uliginosus*
				Germany	*P. ater*
					P. cyanescens
					P. cylindrosporus
					P. fimicola
					P. hippophilus
					P. papilionaceus
					P. subbalteatus
					P. uliginosus
				Netherlands	*P. antillarum*
					P. papilionaceus
				Switzerland	*P. fimicola*
					P. olivaceus
					P. papilionaceus
		Eastern Europe	*P. acuminatus*	Bulgaria	*P. semiovatus*
			P. alcis		*P. subbalteatus*
			P. antillarum	Czech Republic	*P. hygrophanus*
			P. ater		*P. acuminatus*
			P. cinctulus		*P. niveus*
			P. fimicola		*P. squamulosus*
			P. olivaceus	Hungary	*P. cyanescens*
			P. papilionaceus		*P. georgii*
			P . panaiensi	Poland	*P. acuminatus*
			P. plantaginiformis		*P. alcis*
			P. rickenii		*P. antillarum*
			P. semiovatus		*P. cinctulus*
			P. subfirmus		*P. fimicola*
			P. subbalteatus		*P. olivaceus*
			P. niveus		*P. papilionaceus*
			P. squamulosus		*P. rickenii*
			P. cyanescens		*P. semiovatus*
			P. georgii		*P. subfirmus*
			P. reticulatus	Russia (based on all name variations)	*P. ater*
			P. uliginosus		*P. panaiensis*
					P. plantaginiformis
					P. subbalteatus
				Slovakia	*P. acuminatus*
					P. reticulatus
					P. uliginosus
				Ukraine	*P. antillarum*
					P. papilionaceus
		Southern Europe	*P. acuminatus*	Croatia	*P. acuminatus*
			P. alcis		*P. papilionaceus*
			P. antillarum		*P. semiovatus*
			P. ater	Greece	*P. ater*
			P. bisporus		*P. guttulatus*
			P. cinctulus		*P. rickenii*
			P. cyanescens		*P. subfirmus*
			P. fimicola	Italy	*P. acuminatus*
			P. olivaceus		*P. alcis*
			P. papilionaceus		*P. antillarum*
			P. reticulatus		*P. ater*
			P. rickenii		*P. cinctulus*
			P. semiovatus		*P. cyanescens*
			P. subbalteatus		*P. fimicola*
			P. subfirmus		*P. guttulatus*
					P. olivaceus
					P. papilionaceus
					P. semiovatus
					P. subbalteatus
					P. subfirmus
				Serbia	*P. acuminatus*
				Spain	*P. acuminatus*
					P. antillarum
					P. bisporus
					P. desertorum
					P. fimicola

(*continued on next page*)

Table 2 (*continued*)

Continent	Species per continent	Regions	Species per region	Country	Species per country
					P. papilionaceus
					P. rickenii
					P. semiovatus
				Republic of Macedonia	*P. acuminatus*
					P. ater
					P. fimicola
					P. olivaceus
					P. papilionaceus
					P. reticulatus
					P. semiovatus
Oceania	*P. acuminatus*	Australia and New Zealand	*P. acuminatus*	Australia	*P. acuminatus*
	P. affinis		*P. albovelutinus*		*P. antillarum*
	P. albovelutinus		*P. antillarum*		*P. ater*
	P. antillarum		*P. ater*		*P. bernicis*
	P. ater		*P. bernicis*		*P. cyanescens*
	P. bernicis		*P. cyanescens*		*P. fimicola*
	P. campanuloides		*P. fimicola*		*P. olivaceus*
	P. cyanescens		*P. olivaceus*		*P. paludosus*
	P. fimicola		*P. paludosus*		*P. papilionaceus*
	P. lentisporus		*P. papilionaceus*		*P. rickenii*
	P. olivaceus		*P. rickenii*		*P. semilanceatus*
	P. paludosus		*P. semilanceatus*		*P. subbalteatus*
	P. papilionaceus		*P. subbalteatus*	New Zealand	*P. albovelutinus*
	P. rickenii				*P. subbalteatus*
	P. rubricaulis	Melanesia	*P. affinis*	Papua New Guinea	*P. affinis*
	P. semilanceatus		*P. campanuloides*		*P. campanuloides*
	P. subbalteatus		*P. lentisporus*		*P. lentisporus*
			P. rubricaulis		*P. rubricaulis*
			P. subbalteatus		*P. subbalteatus*
Africa	*P. acuminatus*	Northern Africa	*P. acuminatus*	Egypt	*P. fimicola*
	P. africanus		*P. ater*		*P. papilionaceus*
	P. antillarum		*P. bisporus*	Morocco	*P. acuminatus*
	P. ater		*P. cinctulus*		*P. ater*
	P. bisporus		*P. fimicola*		*P. bisporus*
	P. bolombensis		*P. olivaceus*		*P. cinctulus*
	P. cinctulus		*P. papilionaceus*		*P. fimicola*
	P. fimicola		*P. semiovatus*		*P. olivaceus*
	P. fimicoloides				*P. papilionaceus*
	P. goossensiae				*P. semiovatus*
	P. microsporus	Western Africa	*P. fimicola*	Nigeria	*P. fimicola*
	P. olivaceus		*P. antillarum*	Sierre Leone	*P. antillarum*
	P. papilionaceus	Middle/Central Africa	*P. africanus*	Central African Republic	*P. africanus*
	P. semiovatus		*P. microsporus*		*P. microsporus*
	P. subbalteatus		*P. tropicalis*		*P. tropicalis*
	P. tropicalis		*P. bolombensis*	Chad	*P. africanus*
			P. goossensiae	Congo	*P. bolombensis*
					P. goossensiae
		Eastern Africa	*P. antillarum*	Kenya	*P. antillarum*
			P. papilionaceus	Uganda	*P. antillarum*
					P. papilionaceus
				Tanzania	*P. antillarum*
		Southern Africa	*P. antillarum*	South Africa	*P. antillarum*
			P. fimicoloides		*P. fimicoloides*
			P. papilionaceus		*P. papilionaceus*
			P. subbalteatus		*P. subbalteatus*

3.4. Distribution of *Panaeolus* species per country

Using published literature [63,64] (Tables 1 and 2), a constructed map shows that 78 countries have records of *Panaeolus* (Fig. 6). However, many others lacked records (light grey). On average, countries with records had between one to six species (blue). Below follows a more detailed summary of trends per country for each continental region (Figs. 5 and 6, Table 2).

3.4.1. Asia

South eastern Asia has species reported from Cambodia, Thailand, Vietnam, Indonesia and the Philippines, while Malaysia, Myanmar and Singapore lack records. In the southern Asia region, India has the highest diversity of species, with 22 species. Countries surrounding India and Iran such as Afghanistan, Bangladesh, Bhutan, Maldives, Nepal and Pakistan lack records of *Panaeolus* species. Central Asia only has a report from Kazakhstan, namely of the commonly occurring *P. semiovatus*, and lacks reports from Kyrgyzstan,

Table 3
Reported hallucinogenic characteristics of *Panaeolus* species.

	Species	Hallucinogenic	Bluing	Psilocybin	Psilocin	References
1	*Panaeolus acuminatus*	N	–	N	N	[104,158,244]
2	*P. affinis*	Y	–	–	–	[190]
3	*P. africanus*	Y	Y	Y	Y	[25,158,190,236,245,246]
4	*P. antillarum*	Y?	N	Y?	Y?	[25,190,246]
5	*P. ater*	N	–	N	N	[25,190,246]
6	*P. bisporus*	Y	Y	–	–	[46,247]
7	*P. cambodginiensis*	Y	Y	Y	N	[9,98,158,236,245,248]
8	*P. campanuloides*	Y	–	Y	N	[9,158,246]
9	*P. chlorocystis*	Y	Y	–	–	[25]
10	*P. cinctulus*	Y	Y	–	–	[249]
11	*P. cyanescens*	Y	Y	Y	Y	[9,97,98,104,158]
12	*P. cyanoannulatus*	Y	Y	–	–	[87]
13	*P. fimicola*	Y	Y	Y	Y	[9,25,98,158]
14	*P. fontinalis*	N	–	N	N	[9,158,250]
15	*P. fraxinophilus*		–	N	–	[9,158]
16	*P. goossensiae*	N	–	N	N	[9,190]
17	*P. microsporus*	Y	Y	N	Y	[9,25,158,236]
18	*P. moellerianus*	Y	–	–	–	[25,198]
19	*P. olivaceofuscus*	Y	Y	–	–	[251]
20	*P. olivaceus*	Y	Y	Y	N	[25,98,252]
21	*P. papilionaceus*	N	N	N	N	[9,25]
22	*P. reticulatus*	Y	–	–	–	[25]
23	*P. rickenii*	N	–	N	N	[9,25,253]
24	*P. rubricaulis*	Y	–	–	–	[220]
25	*P. semilanceatus*	Y	–	–	–	[254]
26	*P. semiovatus*	N	–	N	N	[158,190]
27	*P. subbalteatus*	Y	Y	Y	N	[9,25,98,158,244,245,255,256]
28	*P. tropicalis*	Y	Y	Y	Y	[9,105,158]
29	*P. uliginosus*	N	–	N	N	[9]
30	*P. venenosus*	Y	–	–	–	[244,245,252,257]
31	*P. venezolanus*	Y	–	–	–	[25,258]
	TOTAL Yes	20	13	8	5	
	TOTAL No	8	2	10	12	
	TOTAL uncertain from publications	1	0	1	1	
	TOTAL unknown from publications	1	16	12	13	

Tajikistan, Turkmenistan, Uzbekistan. Western Asia has reports of *Panaeolus* species from Israel, Jordan, Kuwait and Turkey, but no reports from Armenia, Azerbaijan, Bahrain, Cyprus, Georgia, Iraq, Lebanon, Oman, Qatar, Saudi Arabia, State of Palestine, Syrian Arab Republic, United Arab Emirates, and Yemen. Of the reported species some species only have records from their type locations, such as *P. albellus* from Thailand, *P. annulatus, P. cyanoannulatus, P. indicus, P. lepistercoris, P. lepus-stercus* from India, *P. axfordii* and *P. paludosus* from China, and *P. linnaeanus* from Japan.

3.4.2. North America, Central America, the Caribbean and South America

In North America, the United States of America (USA) had 20 species of which two also occurred in Canada, namely *P. semiovatus* and *P. subbalteatus*. Canada had reports of a third species, namely *P. ulignosus*, which does not occur in the USA. Given that two species found in Canada are also found in the United States, there are possibly more species. Checklists of North American fungi list detailed descriptions of many of these species including *P. campanulatus, P. cintulus, P. cyanescens, P. semiovatus, P. solidipes* and *P. subbalteatus* [65–67].

Central America and the Caribbean have nine recorded species, all of which were also found in Mexico. Three species appear to be widely distributed in Central America and the Caribbean, namely *P. papilionaceus*, *P. subbalteatus* and *P. fimicola*. In the Caribbean islands, *P. papilionaceus* occurs in the Bahamas, Cuba, Puerto Rico and San Vincent Island, *P. subbalteatus* occurs in Guadalupe and Martinique, and *P. fimicola* in Jamaica and Puerto Rico.

South America has 21 recorded species of *Panaeolus*, mostly observed from Argentina, Brazil and Colombia [68]. *P. papilionaceous* and *P. subbalteatus* occurs all over South America [69]. *P. cyanescens* and *P. antillarum* are reported from Brazil [68,70,71], *P. venezolanus* from Venezuela [72], and *P. cubensis* from Colombia. *P. antillarum, P. papilionaceus, P. subfirmis* and *P. semiovatus* were reported on the Falkland Islands from horse and cattle dung [73]. Across both American continents *P. antillarum* is thus widely reported [74]. Furthermore, in South America species such as *P. papilionaceous* and *P. subbalteatus* are widespread across the continent.

Species that are restricted to the USA include *P. aciduc, P. alveolatus*, *P. chlorocystis, P. digressus, P. faxinophilus, P. rufus, P. texensis,* and *P. variabilis*. Species form the USA but with restricted global distributions include *P. fontinalis* (USA and Mexico), *P. goossensiae* (USA and Congo), *P. bisporus* (USA, Morocco and Spain) and *P. venenosus* (USA and British Isles). In South America, *P. convexulus* is only recorded in Argentina and Chile. *P. cambodginiensis* is only reported from Brazil, Mexico, and Colombia, but then also recorded from the USA. *P. venezolanus* is found in Mexico and Venezuela, also with a report from India. *P. moellerianus* appears to occur far south in the Faeroes Islands, Antarctic, Argentina and Macquire Island. *P. lignicola* and *P. sylvaticus* are only located from their type locations in

Table 4
United Nations Geoscheme (data from https://unstats.un.org/unsd/methodology/m49/). The United Nations Geoscheme divides the world into regions and sub-regions. This assignment is for statistical convenience and does not imply any assumption regarding political or other affiliation of countries or territories.

Region	Sub-region	Countries and territories
Africa	Northern Africa	Algeria, Egypt, Libya, Morocco, Sudan, Tunisia, Western Sahara.
	Eastern Africa	British Indian Ocean Territory, Burundi, Comoros, Djibouti, Eritrea, Ethiopia, French Southern Territories, Kenya, Madagascar, Malawi, Mauritius, Mayotte, Mozambique, Réunion, Rwanda, Seychelles, Somalia, South Sudan, Uganda, United Republic of Tanzania, Zambia, Zimbabwe.
	Middle/Central Africa	Angola, Cameroon, Central African Republic, Chad, Congo, Democratic Republic of the Congo, Equatorial Guinea, Gabon, Sao Tome and Principe.
	Southern Africa	Botswana, Eswatini, Lesotho, Namibia, South Africa.
	Western Africa	Benin, Burkina Faso, Cabo Verde, Côte d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Saint Helena, Senegal, Sierra Leone, Togo.
Americas	Latin America and the Caribbean	Caribbean: Anguilla, Antigua and Barbuda, Aruba, Bahamas, Barbados, Bonaire, Sint Eustatius and Saba, British Virgin Islands, Cayman Islands, Cuba, Curaçao, Dominica, Dominican Republic, Grenada, Guadeloupe, Haiti, Jamaica, Martinique, Montserrat, Puerto Rico, Saint Barthélemy, Saint Kitts and Nevis, Saint Lucia, Saint Martin (French Part), Saint Vincent and the Grenadines, Sint Maarten (Dutch part), Trinidad and Tobago, Turks and Caicos Islands, United States Virgin Islands Central America: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama South America: Argentina, Bolivia (Plurinational State of), Bouvet Island, Brazil, Chile, Colombia, Ecuador, Falkland Islands (Malvinas), French Guiana, Guyana, Paraguay, Peru, South Georgia and the South Sandwich Islands, Suriname, Uruguay, Venezuela (Bolivarian Republic of).
	Northern America	Bermuda, Canada, Greenland, Saint Pierre and Miquelon, United States of America.
Asia	Central Asia	Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan.
	Eastern Asia	China, Democratic People's Republic of Korea, Japan, Mongolia, Republic of Korea.
	South - Eastern Asia	Brunei Darussalam, Cambodia, Indonesia, Lao People's Democratic Republic, Malaysia, Myanmar, Philippines, Singapore, Thailand, Timor-Leste, Vietnam.
	Southern Asia	Afghanistan, Bangladesh, Bhutan, India, Iran, (Islamic Republic of), Maldives, Nepal, Pakistan, Sri Lanka.
	Western Asia	Armenia, Azerbaijan, Bahrain, Cyprus, Georgia, Iraq, Israel, Jordan, Kuwait, Lebanon, Oman, Qatar, Saudi Arabia, State of Palestine, Syrian Arab Republic, Turkey, United Arab Emirates, Yemen.
Europe	Eastern Europe	Belarus, Bulgaria, Czech Republic, Hungary, Poland, Republic of Moldova, Romania, Russian Federation, Slovakia, Ukraine.
	Northern Europe	Åland Islands, Channel Islands (Guernsey, Jersey, Sark), Denmark, Estonia, Faroe Islands, Finland, Iceland, Ireland, Isle of Man, Latvia, Lithuania, Norway, Svalbard and Jan Mayen Islands, Sweden, United Kingdom of Great Britain and Northern Ireland.
	Southern Europe	Albania, Andorra, Bosnia and Herzegovina, Croatia, Gibraltar, Greece, Holy See, Italy, Malta, Montenegro, Portugal, San Marino, Serbia, Slovenia, Spain, Republic of Macedonia.
	Western Europe	Austria, Belgium, France, Germany, Liechtenstein, Luxembourg, Monaco, Netherlands, Switzerland.
Oceania	Australia and New Zealand	Australia, Christmas Island, Cocos (Keeling) Islands, Heard Island and McDonald Islands, New Zealand, Norfolk Island.
	Melanesia	Fiji, New Caledonia, Papua New Guinea, Solomon Islands, Vanuatu.
	Micronesia	Guam, Kiribati, Marshall Islands, Micronesia (Federated States of), Nauru, Northern Mariana Islands, Palau, United States Minor Outlying Islands.

Brazil, and *P. olivaceofuscus* and *P. uliginicola* in Argentina.

Areas that lack published records of *Panaeolus* species in North America include Greenland, Saint Pierre and Miquelon, according to the names of the United Nations Bioschemes. Countries in the Caribbean and Central America still lacking records of *Panaeous* species include British Virgin Islands, Cayman Islands, Curaçao, Dominica, Grenada, Montserrat, Saint Barthélemy, Saint Lucia, Saint Martin (French Part), Sint Maarten (Dutch part), Trinidad and Tobago, Turks and Caicos Islands, United States Virgin Islands, and Bouvet Island. South American countries that do not have any reported *Panaeolus* species are Anguilla, Antigua and Barbuda, Aruba, Barbados, Bonaire, Bolivia, Ecuador, French Guiana, Guyana, Peru, Sint Eustatius and Saba, South Georgia, Suriname, and the South Sandwich Islands.

3.4.3. Europe

A significant amount of literature is available on the coprophilous agarics of Europe [68], including records of *Panaeolus* from 26 different countries. The continent is well studied and *Panaeolus* species are widespread. Across Europe *P. subbalteatus* and *P. acuminatus* are the most widely distributed species [5,69].

In Northern Europe *P. alcidis* was recorded in Sweden [68,75] and *P. antillarum, P. papilionaceus* and *P. semiovatus* in Iceland [68,76,77]. These and eight other species were recorded in the British Isles [68,78], which were also the country in the region with the most records. In southern Europe, regions around Italy were quite diverse after 13 species were recorded [79]. Other countries having numerous species included Austria and Germany in Western Europe (eight each) and Poland (10 species) in Eastern Europe.

The Czech Republic had the rare species *P. hygrophanus, P. niveus* and *P. squamulosus* reported from only their type locations. In Austria *P. pseudoguttulatus*m and in France *P. regis*, were recorded only from their type locations. *P. semilanceata* has only been described from Ireland and Australia, and *P. atrobalteatus* from the British Isles. *P. desertorum* is only recorded at its type location in Spain.

Although most of Europe has been well investigated, there are countries with no *Panaeolus* species recorded. In northern Europe

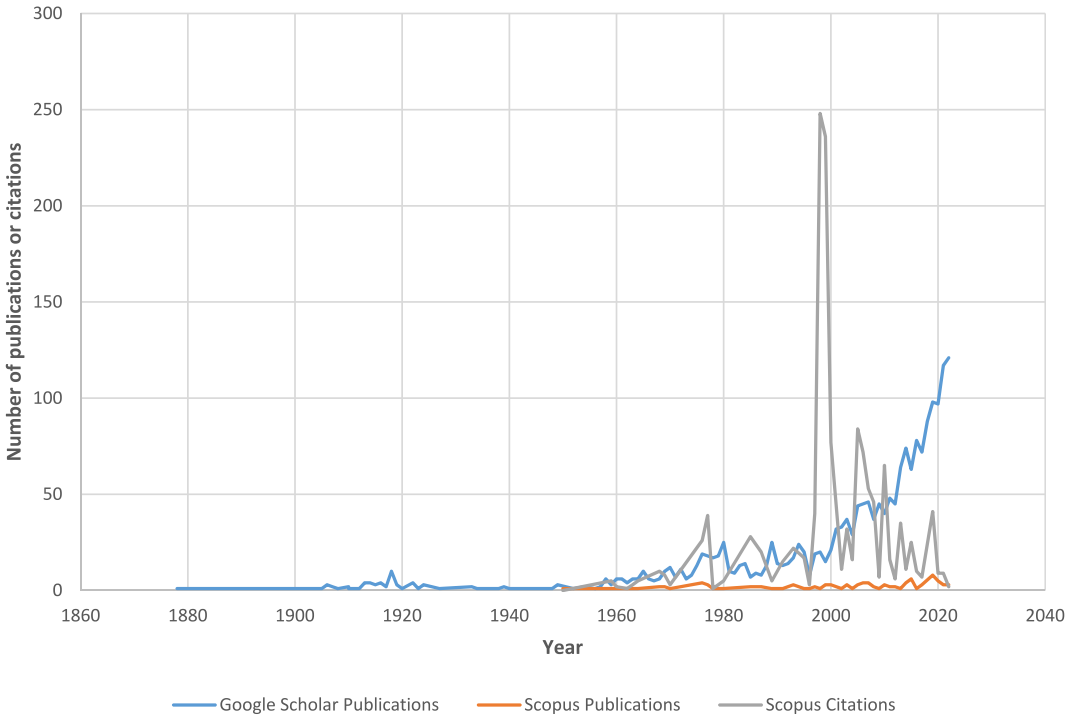

Fig. 3. Number of publications and citations per year for *Panaeolus* based on Microsoft Academic [114] and Scopus (2022) [58] (accessed on 15 January 2023).

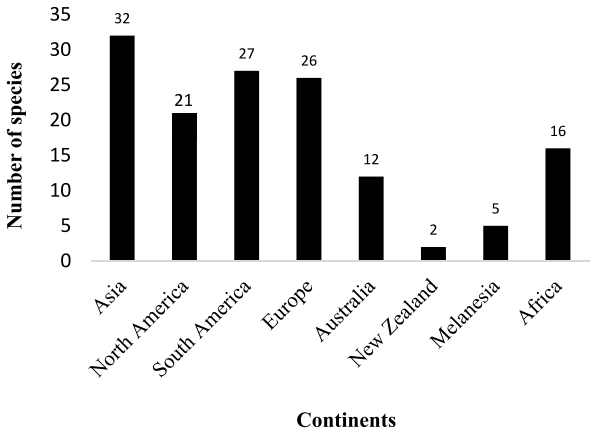

Fig. 4. An overview of the distribution of *Panaeolus* in different continents of the world according to published literature.

many islands had no records, including Åland Islands, Channel Islands (Guernsey, Jersey, Sark), Svalbard and Jan Mayen Islands, as well as the countries Estonia, Isle of Man, Latvia, and Lithuania. In eastern Europe countries such as Belarus, Republic of Moldova, and Romania do not have records of *Panaeolus* species. In Southern Europe, Albania, Andorra, Bosnia and Herzegovina, Gibraltar, Holy See, Malta, Montenegro, Portugal, San Marino and Slovenia lack records of *Panaeolus* species. In Western Europe, only a small region remains void of records, including Liechtenstein, Luxembourg and Monaco.

3.4.4. Oceania

The Oceania region consists out of Australia and New Zealand, Melanesia (containing Fiji, New Caledonia, Papua New Guinea, Solomon Islands, Vanuatu) and Micronesia (Guam, Kiribati, Marshall Islands, Federated States of Micronesia, Nauru, Northern Mariana Islands, Palau, United States Minor Outlying Islands). Only Australia, New Zealand and Papua New Guinea have recorded records. No records were found of *Panaeolus* species in Micronesia, inclusive of Guam, Kiribati, Marshall Islands, Nauru, Northern Mariana Islands, Palau and United States Minor Outlying Islands. In the Melanesia region countries including Fiji, New Caledonia,

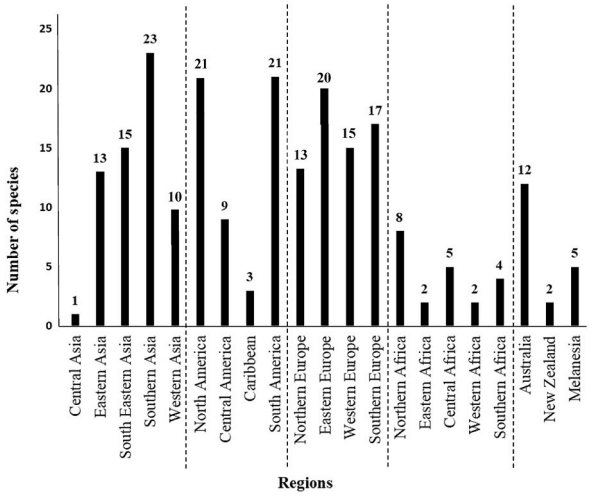

Fig. 5. An overview of *Panaeolus* distribution in different regions across the world according to publications.

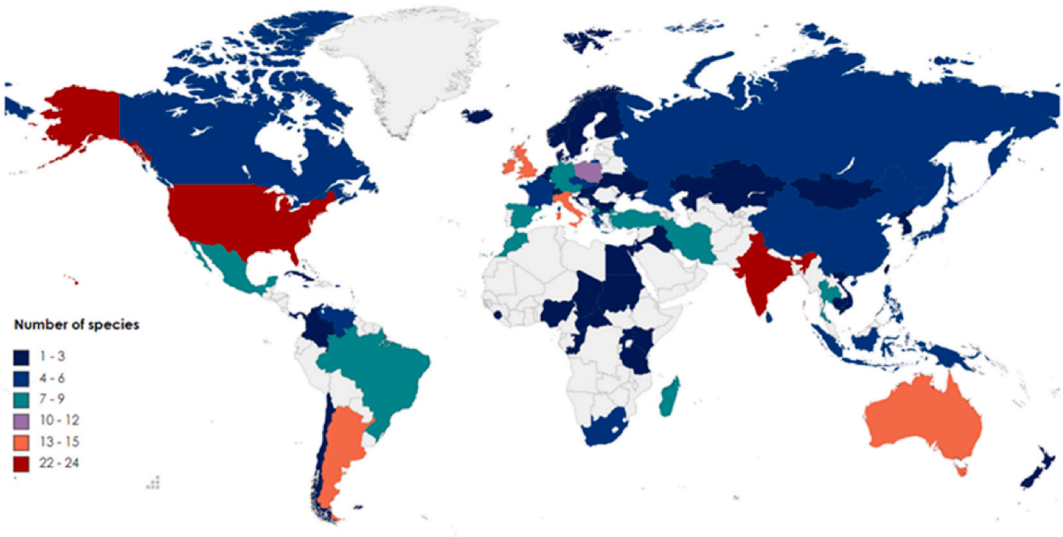

Fig. 6. A distribution map of *Panaeolus* across the world. Zero records are presented as grey, countries with one to six species are presented as blue, which fades to a red in countries that have 13–24 records. Created from published literature (Table 1) and illustrated using Mapchart [62]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Solomon Islands, and Vanuatu lacked species.

Australia has 12 species including some of the most widely spread global species such as *P. fimicola, P. papilionaceus, P. semilanceata* and *P. subbalteatus*. New Zealand only has two species, namely *P. albovelutinus* and *P. subbalteatus*. The Melanesia region has five species, all from Papua New Guinea, namely *P. affinis*, *P. campanuloides*, *P. lentisporus*, *P. rubricaulis* and *P. subbalteatus*, with *P. affinis, P. campanuloides* and *P. lentisporus* restricted from this country. Australia has an indigenous species *P. bernicis*, only known from the type location, as well as a rare species, *P. paludosus*, only found in Australia and China.

3.4.5. Africa

Northern Africa has the highest known diversity of *Panaeolus* but only from two countries, with eight species from Morrocco, while *P. fimicola* and *P. papilionaceus* also occur in Egypt. Southern Africa has four species recorded from South Africa only, including *P. antillarum*, *P. fimicoloides*, *P. papilionaceus* and *P. subbalteatus* [80–82]. Eastern Africa has two species, namely *P. antillarum* and *P. papilionaceus*, recorded in Kenya, Uganda and Tanzania [68,74,83]. Western Africa recorded *P. fimicola* and *P. antillarum* from Nigeria and Sierre Leone, respectively, and Middle Africa recorded five species, namely *P. africanus*, *P. microsporus*, *P. tropicalis*, *P. bolombensis*, and *P. goossensiae,* from Central African Republic, Chad and the Congo [5]. Africa has three species that have only been recorded from their type locations including *P. bolombensis* from the Congo, *P. fimicoloides* from South Africa, and *P. microsporus*

described in the Republic of Central Africa.

A large number of countries lack published records of *Panaeolus*, and Africa appears to be the most poorly studied with regards to the biodiversity of *Panaeolus*. These include Algeria, Libya, Sudan, Tunisia, and Western Sahara in northern Africa. In eastern Africa, no *Panaeolus* records exist from British Indian Ocean Territory, Burundi, Comoros, Djibouti, Eritrea, Ethiopia, French Southern Territories, Madagascar, Malawi, Mauritius, Mayotte, Mozambique, Réunion, Rwanda, Somalia, South Sudan, Zambia, and Zimbabwe. Angola, Democratic Republic of the Congo, Equatorial Guinea, Gabon, Sao Tome and Principe in central Africa, and Lesotho, and Namibia in Southern Africa, and Benin, Burkina Faso, Cabo Verde, Côte d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Saint Helena, Senegal, Togo in Western Africa lack records.

3.5. DNA sequences of Panaeolus

Of the 77 legitimate *Panaeolus* species, sequences of the ITS region are available for 18 species on Genbank [58]. These include recent novel species and species that are widely occurring such as *P. antillarum, P. sphinctrinus P. acuminatus*, *P. antillarum*, *P. campanulatus*, *P. retirugis*, *P. rickenii*, *P. semiovatus P. alcis*, *P. bisporus*, *P. foenisecii* and *P. papilionaceus*. *P. cambodginiensis*, *P. subbalteatus*, *P. campanulatus* and *P. retirugis* (Table 1). Only one ex-type sequence, namely that of the ITS sequence for *P. axfordii*, exist. Whereas Large and Small Subunit sequences for the ribosomal operon are available these have low resolution power at the species level, but will be helpful for the resolution of deeper relationships of the genus. Only one Translation Elongation Factor sequence for a *P. papilionaceus* strain is available, and no other genes that are normally used for multi-gene phylogenies at the species level have been sequenced. Genome sequences are available but thus far only for *P. papilionaceus* and *P. cyanescens* [84].

3.6. Panaeolus hallucinogenic species

Indications of hallucinogenic properties have been recorded for only 22 *Panaeolus* species (Table 3) out of the 77 total number of species (29%). As many as 20 species were recorded to be hallucinogenic in published literature, and eight species were reported as non-hallucinogenic, including *P. acuminatus, P. ater, P. fontinalis, P. fraxinophilus, P. goossensiae, P. rickenii, P. papilionaceus, P. semiovatus* and *P. uliginosus*. Bruising was recorded for 13 species (17%), leaving 64 species lacking descriptions of presence of absence of bruising. Psilocybin was recorded in eight species (10% of total number) and psilocin in five species (6%). Psilocybin was not found in any trace amounts in 10 species and similarly, psilocin was not found in 12 species. Species that are shown to contain both psilocybin and psilocin include only four species, namely *P. africanus, P. cyanescens, P. fimicola,* and *P. tropicalis*. Psilocybin can be found in four species, which lack psilocin, namely *P. campanuloides, P. cambodiginensis, P. olivaceus*, and *P. subbalteatus*. One species, namely *P. microsporus,* has concentrations of psilocin but lacks psilocybin. Hallucinogenic species that remain unexplored for psilocybin and psilocin are 12 and 13 species, respectively, including *P. affinis, P. bisporus, P. chlorocystis*, *P. cinctulus, P. cyanoannulatus* and *P. olivaceofuscus,* to name a few (Table 4).

A third of the known hallucinogenic species are widely distributed and occur on three or more continents, including *P. acuminatus*, *P. cinctulus*, *P. cyanescens*, *P. fimicola*, *P. olivaceus*, *P. reticulatus, P. semilanceatus* and *P. rickenii*. However, two thirds of the known hallucinogenic species have limited distributions, including *P. rubricaulis* (from Papua New Guinea, Sri Lanka and Vietnam), *P. moellerianus* (Faeroes Islands, Antarctic, Argentina and Macquire Island), *P. microsporus* (Republic of Central Africa), *P. chlorocystis* (USA), *P. campanuloides* (Papua New Guinea), *P. africanus* (India, Chad, Republic of Central Africa and Sudan) and *P. affinis* (Papua New Guinea) (Tables 1 and 2). The extent to which this distribution has been aided by human movement and use of these mushrooms is unrecorded.

4. Discussion

The systematic review of 258 articles, and the records of Index Fungorum, showed that 77 species are currently in *Panaeolus* [50, 51]. More species have thus been added since those listed in previous monographs [23,39,85]. The increase is a result of the discovery of novel species from across the world and subspecies being brought to species rank, while other species were also transferred to other genera such as to *Galeropsis* [86]. Six novel species have been described in the last decade, including *P. axfordii* [7], *P. cyanoannulatus* [87], *P. desertorum* [86], *P. lepus-stercus* [87], *P. lignicola* [87] and *P. sylvaticus* [88].

The distribution of *Panaeolus* species was found to span across 78 countries. The highest diversity was in Asia with reports from numerous countries such as India, Sri Lanka, Iran, Japan, China, and Thailand. South America and North America had the highest diversity observed from Brazil, Argentina, the USA, and Mexico. Europe had species reported from each region but the most species were from the United Kingdom, Italy, Poland, Austria and Germany. Australia has a high diversity of *Panaeolus* with 12 species. Africa is known to have *Panaeolus* biodiversity but has the least number of records of species across countries. Numerous other countries across the world also still lack reports of any *Panaeolus* species. Evidence of rare species existed, since numerous species are only known from their type locations. In contrast, some species occurred commonly across the world.

The geographic trends reported in this study most likely reflect the availability of mycological skills and access to funding, rather than true biodiversity [89,90]. The global distributions could also be attributed to the recreational use of hallucinogenic species and their often illegal spread through trade, cultivation and human consumption. This is because species that are notably hallucinogenic usually also occur widely, such as *P. cyanescens, P. fimicola, P. olivaceus, P. papilionaceus, P. subbalteatus*, and *P. tropicalis*. These better known species may also be confused with morphologically slightly different species, which could actually represent novel species.

As many as 20 *Panaeolus* species are hallucinogenic. Previously nine [91] and 13 [25] hallucinogenic *Panaeolus* species were

known. An additional seven species have now been recognised, with *P. axfordii* the most recently described [7]. Psilocybin-containing species are often, but not always, identified by a strong blue staining reaction described when bruised on the cap or stem due to the oxidative reaction between the air and psilocybin [92,93]. *P. fimicola, P. cyanescens* and *P. rickenii* are a few bluing species that are widely distributed [94–97]. However, presence or absence of bruising are often not reported in publications.

Blueing and hallucinogenic properties of species have been reported by end-users, and the presence of psilocin and psilocybin could perhaps be assumed from these reactions. However, relatively few scientific studies focused on establishing whether both psilocin and psilocybin are actually present, including across all of the known species. The presence of psilocybin and psilocin was confirmed in fruiting bodies for *P. africanus*, *P. ater, P. cambodginiensis, P. campanulatus, P. castaneifolius, P. cyanescens, P. fimicola, P. microspores, P. sphinctrinus, P. subbalteatus* and *P. tropicalis*. The highest levels of psilocybin was regularly found to be in *P. cyanescens* fruiting bodies [8,93,106]. Furthermore, alkaloid detection studies for all of the other known related alkaloids [19] have not yet been published. Chemical methods to detect psilocybin and psilocin include gravity flow liquid chromatography, liquid chromatography-mass spectrometry, thin layer chromatography, gas chromatography, high-performance liquid chromatography, and capillary zone electrophoresis [37,57,93,98–105].

The concentration of psilocybin and psilocin can vary appreciably within a collection of mushrooms and between species that are widely distributed [97]. For example, collections of *P. cyanescens* from Hawaii contained significantly higher levels of psilocybin compared to collections from Australia and Thailand, which barely contained traces [8,97]. Variation in concentrations of psilocybin and psilocin between specimens of the same species was also found in *P. campanulatus, P. castaneifolis, P. foenisecii, P. microspores, P. sphinctrinus* and *P. subbalteatus* [8,93,106]. There have also been instances where a species is reported both with and without psilocybin and psilocin [25,95], for example samples of *P. antillarum* from Poland contained no psilocybin or psilocin [95], but sampled did contain psilocybin and psilocin in Taiwan [107]. Misidentification of species could be the largest problem contributing to the confusion concerning published chemical studies of psychoactive fungi [25]. Psilocybin and psilocin amounts varied even in the same mushroom specimen (e.g. camp, stem, gills) [9]. This could be due to several factors including age, growing and drying conditions, and specific parts of mushrooms used for psilocybin testing [98].

For any new species, it is common practice that novel species of *Panaeolus* are also characterized using at least the internal transcribed spacer (ITS) region as part of their taxonomical description, as has been done for the recently discovered species *P. axfordii*, *P. plantaginiformis* and *P. desertorum* [7,108]. Numerous DNA extraction protocols exist, while in some studies DNA extraction methods were modified for more efficient DNA extractions to aid identifying mushrooms of hallucinogenic genera based on DNA sequence data [61,109]. Of the 77 known *Panaeolus* species, sequences of the ITS region are available for only 18 species on Genbank [58]. Because the remaining species still need to be sequenced, this results in poor species coverage for the genus that may skew and bias DNA sequence comparison results. Moreover, only one type specimens has representative sequence, namely that of *P. axfordii*. Obtaining more ex-type sequences will be vital to fully ascertain species affiliations of samples since the often indistinct, highly variable morphologies of these fungi can lead to misidentifications. Additional regions, such as the translation elongation factor, beta-tubulin, large subunit and small subunit of rRNA [110–112], should also be tested for species resolution and consistently be sequenced with the ITS region to confirm results through multi-gene analyses, which would solidify understanding of species relationships.

5. Conclusion

Panaeolus species occur across the globe. Since the first record of *P. papilionaceus* in 1872, a total of 77 species have been recorded and many more will be discovered. This is especially evident from the fact that numerous countries still have no records of *Panaeolus*, and that the true biodiversity of the genus is poorly represented in sequence data. There are at least 20 psychoactive species that belong to the genus and at least 10 species that can be considered medically valuable because they are proven to contain psilocybin. However, analysis showed that this aspect across all of the species in *Panaeolus* is still poorly studied based on sound experimental data, and not just invaluable, but unpublished, experiences by the community that uses these mushrooms recreationally or as self-medication.

Current and future regulation of these fungi and their products for psycho-assisted therapy, in clinical settings, and trade and product development by pharmaceutical and nutraceutical companies (nutraceutical companies being companies obtaining additional value from natural products other than nutrition) [19], will not be possible without up-to-date databases from various parts of the world. Such species databases should include geographical distributions, flagged geographical areas still lacking any data, whether species are rare or commonly occurring, threatened and in need of conservation, what their hallucinogenic properties are, and the extent of study as well as of use. Such information should aid studies and regulation of species of interest for bioexploitation. However, more complete surveys on the biogeography of *Panaeolus* spp. will be needed to service the various levels of regulation (biodiversity, ethics and knowledge sharing with traditional communities, conservation, commercialization, trade, use and movement of biological material, strain development, and clinical aspects) required by individual countries, and to protect their natural resources and cultural heritage against illegal trade and movement [4,19,22,113].

This review only assimilated facts that have been published in scientific literature and not word-of-mouth knowledge from the recreational community, or the more confidential data on species and strains used by industry. Whereas all effort was placed to have the review as complete and correct as possible, there are most likely areas to be improved or corrected, records that have been missed, and new records that will continuously have to be added. Furthermore, considerable more knowledge exist about the psychoactive properties of *Panaeolus* species by the recreational community and industry, and strains and species with different properties are being collected from across the world to be developed and refined with differing psilocybin content and properties. This knowledge also needs to be incorporated more actively in scientific literature and regulation schemes to better protect the important resource that presents *Panaeolus* biodiversity.

Author contribution statement

All authors listed have significantly contributed to the development and the writing of this article.

Data availability statement

Data included in article/supp. material/referenced in article.

Additional information

No additional information is available for this paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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