The araneopathogenic genus *Gibellula* (*Cordycipitaceae*: *Hypocreales*) in the British Isles, including a new zombie species on orb-weaving cave spiders (*Metainae*: *Tetragnathidae*)

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Abstract: The genus *Gibellula* (*Cordycipitaceae*: *Hypocreales*) comprises species pathogenic on and specific to spider hosts. Here, we report on the occurrence of a novel species infecting cave-dwelling, orb-weaving spiders of the subfamily *Metainae* (*Tetragnathidae*) in the British Isles. The new species, *Gibellula attenboroughii* is described and illustrated and its ecology is discussed; leading to the conclusion that infected spiders exhibit behavioural changes similar to those reported for zombie ants. The hidden diversity of the genus *Gibellula* in the British Isles is further highlighted based on fungarium records and literature searches. Two spider pathogens, previously assigned to the genus *Torrubiella*, are now transferred to the genus *Gibellula*, based on their *Granulomanus* synasexual morphs, in accordance with the one fungus-one name initiative: *Gibellula albolanata* comb. nov. and *G. aranicida* comb. nov.

INTRODUCTION

Gibellula (*Cordycipitaceae*: *Hypocreales*) is a genus specific to and pathogenic on spiders comprising over 30 accepted species (Mendes-Pereira *et al.* 2023). These authors also noted that 54 and 58 species are listed in Index Fungorum and MycoBank, respectively; highlighting the uncertainties of species delimitation within the genus. The greater majority of these taxa have a subtropical to tropical distribution (Evans 1982, Evans & Samson 1987, Samson *et al.* 1988, Samson & Evans 1992, Evans 2013, Hughes *et al.* 2016, Shrestha *et al.* 2019, Kuephadungphan *et al.* 2020, 2022, Mendes-Pereira *et al.* 2023, Nyffeler & Hywel-Jones 2024). There are few records of the genus from the British Isles with only a single species, *G. aranearum*, being recognised in the early published lists of "British entomogenous fungi" (Petch 1932a, b, Petch 1948). Subsequently, Ellis (1956) recorded *G. aranearum* on spiders in the fens and meadows of Norfolk; describing it as common from June to October which is evidenced by the large amount of material deposited in Herb K. Earlier, Mains (1950) had included *G. aranearum* as a synonym of *G. pulchra* – the type species of the genus – and this has been accepted since (Samson & Evans 1992, Roth & Van Vooren 2016, Shrestha *et al.* 2019, Mendes-Pereira *et al.* 2023); although *G. aranearum*, as described by Sydow (1922) on a spider from Papua New Guinea, remains a legitimate species in both Index Fungorum and MycoBank. There is no doubt that *G. pulchra* in the British Isles and elsewhere

is a species complex, especially since the only sequences available of *G.* "*pulchra*" are from Asia. In the phylogenetic trees of the genus published, thus far, with multiple sequences of *G.* "*pulchra*" from various localities, these do not cluster together (Mendes-Pereira *et al.* 2022; 2023). For example, Mendes-Pereira *et al.* (2023) in their in-depth study of the genus include 10 sequences; four clustering together in two widely separate groups and the other two scattered within the tree. All these originated from the tropics, whilst the type was collected in Italy (Cavara 1894). Clearly, there is a need to sequence the holotype if located, or to designate a neotype from the country of origin, in order to avoid further confusion.

During the BBC Winterwatch television series in 2021, filmed on location in Northern Ireland, a fungal-infected spider was discovered on the ceiling of an abandoned gunpowder store and provisionally identified as *G.* "*pulchra*". Images, sent by the BBC to the senior author, suggested that this was a novel species of the genus *Gibellula* and, moreover, that the reclusive cave-spider host – subsequently, identified as the orb-weaving spider *Metellina merianae* (*Tetragnathidae*: *Araneae*) – had moved to an exposed situation before death, indicating a behavioural change. These suppositions were included and discussed in the following 2022 Springwatch series after which the specimen was removed and sent for identification.

Morphological and phylogenetic analyses confirmed the taxonomic novelty of the *Gibellula* on the cave spider and its distinctiveness from the species accepted, thus far. Here, we describe the new taxon based on this specimen, as well as others discovered on two orb-spider species in cave systems on the island of Ireland. A subsequent investigation into the historical records of the genus *Gibellula* in the British Isles has revealed a hidden diversity, as well as reports of epizootics; the results of which are presented and discussed.

MATERIALS AND METHODS

Field collection

The type specimen was removed with fine forceps from the ceiling of an abandoned gunpowder storeroom at Castle Espie Wetland Centre in Northern Ireland (54°31′45.66″N, 5°41′53.16″W) and transferred to a sterile plastic tube, then air-dried for 4 d, before being sent for examination to CABI UK-Centre at Egham. Further

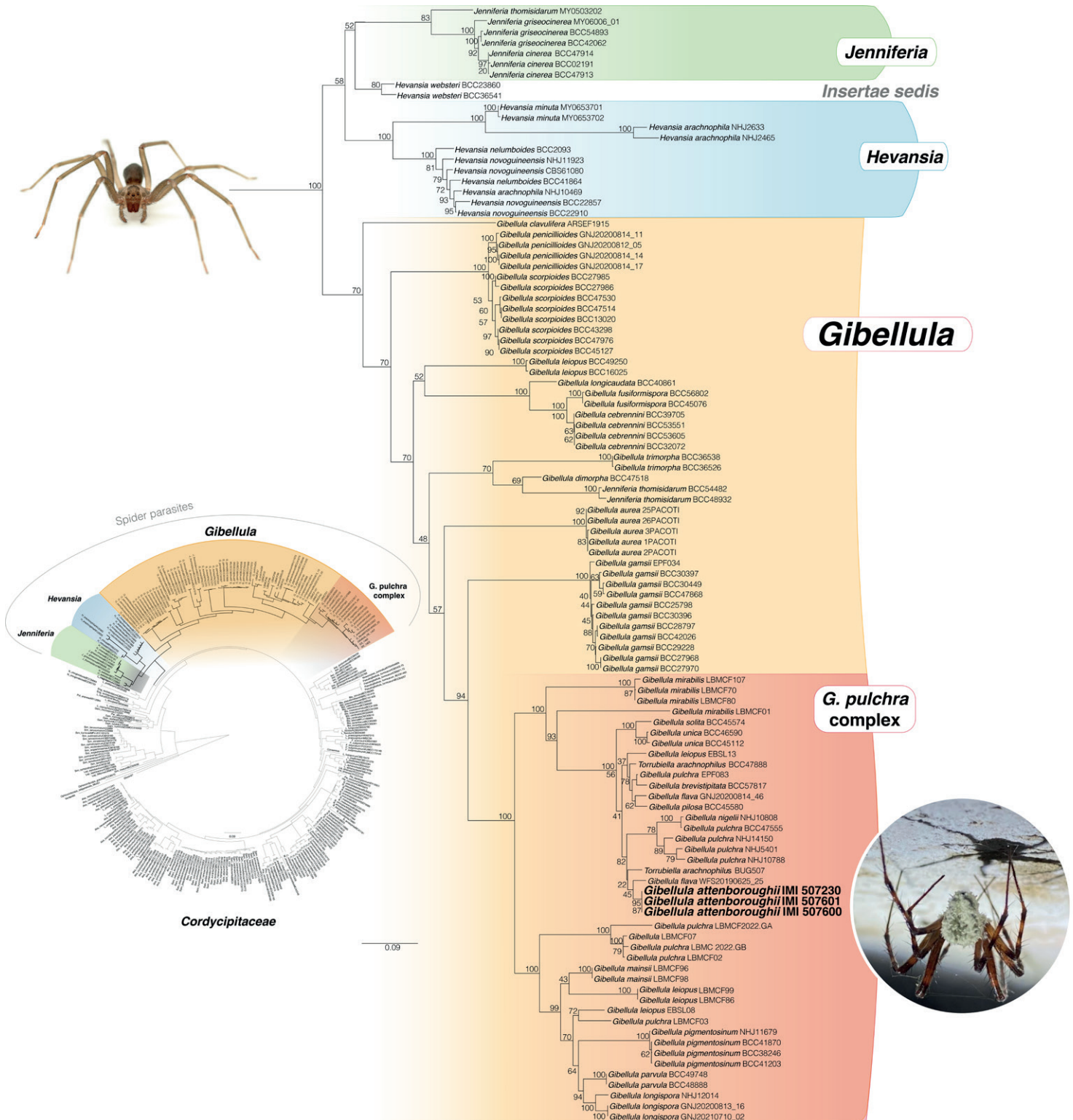**Fig. 1.** Maximum likelihood tree, obtained with a concatenated dataset of ITS, SSU, LSU, *TEF*, *RPB1* and *RPB2*, showing the clade containing the major spider pathogenic hypocrealean genera *Jenniferia*, *Hevansia* and *Gibellula*. On the left, the circular phylogeny represents the full dataset used in this study (*Cordycipitaceae*). The newly proposed species, *Gibellula attenboroughii*, is highlighted in **bold**.

specimens of *Gibellula*-infected spiders were collected from cave systems on the island of Ireland by a local speleologist (T. Fogg) and despatched in the same way. In addition, images were taken *in situ*, as well as details of the positions of the infected spiders within the cave system, particularly in relation to the light zones and the cave entrance.

Fungal isolation and DNA extraction

Dried specimens were examined with a dissecting microscope (Nikon SMZ-10, Japan) and sporulating structures were removed with a flamed needle and streaked onto tap-water agar (TWA) and potato-carrot agar (PCA; Ritchie 2002), and incubated in the dark at 20 °C until evidence of colony growth. Hyphae from the colony periphery were then transferred to fresh PCA and malt-extract agar (MEA) plates using a sterile needle.

Genomic DNA was extracted using MicroLYSIS® PLUS (Microzone Ltd., Stourbridge, UK) with a modified thermal cycling lysis profile of 1× (45 min at 65 °C, 2 min at 96 °C, 4 min at 65 °C, 1 min at 96 °C, 2 min at 65 °C and 30 s at 96 °C).

PCR and sequencing

Amplification of the whole internal transcribed spacer region (ITS), partial region of the large subunit of the nuclear ribosomal DNA (LSU), and the translation elongation factor 1-α (*TEF1*), was undertaken. The primers used were ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al*. 1990) (ITS), NL1 and NL4 (O'Donnell 1993) or LR0R and LR3 (LSU), TEF1-983F and TEF1-2218R (Rehner & Buckley 2005) (*TEF*). All PCR amplifications were performed in 20 µL volumes consisting of 1 µL of DNA template, 6 pmol of each primer, 10 µL of MegaMix-Royal (Microzone Ltd.), and made up to 20 µL with Molecular Grade water (Cytiva, Amersham, UK). Visualisation of the PCR amplicons was achieved on a 1.5 % (w/v) agarose gel in 0.5 × TBE [Tris-Borate-ethylenediaminetetraacetic acid (EDTA) buffer] stained with SafeView Nucleic Acid Stain (NBS Biologicals Ltd., UK). All PCR amplicons were then purified using MicroCLEAN (Microzone Ltd.), per manufacturer's instructions. Purified amplicons were sequenced using the Big Dye™ Terminator v. 3.1 cycle sequencing kit with 10 pmol of the same primers used for PCR, processed separately. Excess unincorporated dye terminators were removed with AutoSeq™ G-50 (Cytiva) resin columns as per the manufacturer's instructions, and suspended in 16 µL of Hi-Di™ Formamide (ThermoFisher Scientific, Hemel Hempstead, UK), followed by sequencing on an ABI 3130 Genetic Analyzer (ThermoFisher Scientific).

Molecular phylogeny

Nucleotide sequences, from both forward and reverse primers (.ab1 files), were *de novo* assembled and edited in Geneious Prime v. 2024.0.5 (Kearse *et al*. 2012). Additional sequences of SSU, ITS, LSU, *TEF*, *RPB1* and *RPB2* from related species in the *Cordycipitaceae*, selected by Araújo *et al*. (2022) and Mendes-Pereira *et al*. (2023), were downloaded from GenBank for phylogenetic analyses (Table 1). Each locus was aligned individually using MAFFT (Katoh & Standley 2013) in Geneious Prime v. 2024.0.5 (Kearse *et al*. 2012) and further concatenated into a dataset composed of 6 292 bp. The dataset consisted of 14 partitions, one for SSU and LSU and three for ITS (ITS1+5.8S+ITS2), *TEF*, *RPB1* and *RPB2*. A RAxML analysis was performed using RAxML-HPC2 v. 8.2.12 (Stamatakis 2006, 2014) on XSEDE (http://www.phylo.org/), with the GTRGAMMA+I model and 1 000 bootstrap iterations were executed to evaluate the support. Additionally, we have performed Bayesian analysis in MrBayes v. 3.2.6 (Ronquist *et al.* 2012). The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses. The substitution matrix, base frequencies, and gamma shape parameter were unlinked between data partitions, and the rate prior was set to variable (prset applyto = (all), ratepr = variable), allowing partitions to have different rates. Markov chain Monte Carlo (MCMC) runs using default parameters resulted in a low proportion of accepted swaps between adjacent Markov chains, typically less than 5 %, and independent runs did not converge after 40 M generations. Therefore, the number of attempted chain swaps was increased to 2 (nswaps = 2); two independent runs were set, each with eight simultaneous chains, temperature increment parameter set to 0.2, for 70 M generations, sampling trees every 1000th generation. The convergence diagnostic was calculated every 10 000th generation. We verified the minimal effective sample sizes (ESS > 200) and the convergence between the runs with Tracer v. 1.7 (Rambaut *et al.* 2018). The first 50 % of trees from each run were discarded as a burn-in, and the 50 % majority-rule tree with branch lengths and Bayesian posterior probabilities (BPPs) were calculated from the remaining trees. A BPP value above 0.95 was considered significant. New sequences were submitted to GenBank (Table 1). The final Newick output file from the ML analysis, was exported to Dendroscope (Huson & Scornavaca 2012) for tree layout and then edited in Adobe Illustrator.

Morphological examination

Macro-morphological characters were based on dried material and photographed using a digital Sanyo D5100 camera. Micro-morphological characters were examined under a compound microscope (Nikon Optiphot-2, Japan), after removing synnemata with a sterilised needle and mounting them in lactophenol cotton blue or lactofuchsin.

Because of the slow establishment and growth rate, colony characteristics were observed over a 3-mo period on two kinds of media (PCA, MEA) maintained in the dark in an incubator at 20 °C.

RESULTS

Phylogenetic analysis

Our recovered topology agrees with previously published work on *Cordycipitaceae* fungi (Kepler *et al*. 2017, Araújo *et al*. 2022, Mendes-Pereira *et al*. 2023). In Fig. 1, we present the major hypocrealean groups of araneopathogenic fungi, *Jenniferia*, *Hevansia* and *Gibellula*. Our results show that the original specimen (IMI 507230), observed and reported on during the BBC Winterwatch and Springwatch series, groups within the genus *Gibellula* clustering with other collections on two orb-spider species from cave systems on the island of Ireland (IMI 507600, IMI 507601; Fig. 1), and is named herein as *Gibellula attenboroughii sp. nov*. Our newly proposed species is strongly supported and falls within the *G. pulchra* complex, but its relationship with close relative species, such as *G. flava*, is still speculative.

Table 1. Species used in this study, voucher information and GenBank accession numbers. The new species is indicated in bold text.

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
Akanthomyces aculeatus	TS772	KC519368	n/a	KC519370	KC519366	n/a	n/a
	BCC17075	GQ249958	GQ250011	GQ249983	GQ250033	n/a	n/a
A. araneicola	GY 29011	n/a	MK942431	n/a	MK955950	MK955944	MK955947
	GY 29012	n/a	MK942434	n/a	MK955951	MK955945	MK955948
A. attenuatus	CBS 170.76	n/a	MH872739	OP752153	OP762607	OP762611	OP762615
	CBS 402.78	AF339614	AJ292434	AF339565	EF468782	EF468888	EF468935
A. coccidioperitheciatus	KACC42493	KM283756	n/a	KM283780	KM283804	KM283826	KM283846
	KACC43049	KM283757	n/a	KM283781	KM283805	KM283827	KM283847
	NHJ 6709	EU369110	JN049865	EU369042	EU369025	EU369067	EU369086
A. kanyawimiae	BCC34340	n/a	MH532862	MH394666	MH521909	MH521831	MH521875
A. lecanii	TBRC 7242	n/a	MF140751	MF140718	MF140838	MF140784	MF140808
	CBS 101247	KM283770	JN049836	KM283794	DQ522359	KM283837	KM283859
	CBS 102067	KM283771	n/a	KM283795	KM283818	KM283838	KM283860
A. neocoleopterorum	GY11241	n/a	MN093295	n/a	MN097813	MN097816	MN097812
	GY11242	n/a	MN093297	n/a	MN097815	MN097817	MN097814
A. noctuidarum	BBH16595	n/a	MT356073	MT356085	MT477979	MT477995	MT478005
	BCC28571	n/a	MT356075	MT356087	MT477981	MT478009	MT478006
A. pyralidarum	BCC29197	n/a	MT356083	MT356094	MT508840	MT478003	MT477991
	BCC40869	n/a	MT356082	MT356093	MT477984	MT478002	MT477990
A. sulphureus	TBRC 7247	n/a	MF140756	MF140720	MF140841	MF140785	MF140811
	TBRC 7248	n/a	MF140758	MF140722	MF140843	MF140787	MF140812
A. thailandicus	TBRC 7245	n/a	MF140754	n/a	MF140839	n/a	MF140809
	TBRC 7246	n/a	MF140755	MF140719	MF140840	n/a	MF140810
A. tortricidarum	BCC41868	n/a	MT356077	MT356089	MT477985	MT477998	MT478008
	BCC72638	n/a	MT356076	MT356088	MT478004	MT477997	MT477992
A. tuberculatus	BCC12869	GQ249961	GQ250007	GQ249986	GQ250036	n/a	n/a
	BCC16819	GQ249962	GQ250012	GQ249987	GQ250037	n/a	n/a
A. waltergamsii	TBRC 7251	n/a	MF140747	MF140713	MF140833	MF140781	MF140833
	TBRC 7252	n/a	NR_164417	MF140714	MF140834	MF140782	MF140806

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Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
Ascopolyporus albus	BCC48976	n/a	OL331503	OL322049	OL322036	OL322057	OL322066
	BCC48975	n/a	OL331502	OL322048	OL322035	OL322056	OL322065
Asc. galloides	BCC25446	n/a	OL331510	OL322042	OL322029	OL322053	OL322060
	BCC47981	n/a	OL331511	OL322043	OL322030	OL322054	OL322061
Asc. griseoperitheciatus	BCC22358	n/a	OL331507	OL322050	OL322037	n/a	OL322067
	BCC25788	n/a	OL331508	OL322051	OL322038	OL322058	OL322068
Asc. purpuratus	BCC88388	n/a	OL331505	OL322046	OL322033	n/a	OL322064
	BCC88430	n/a	OL331506	OL322045	OL322032	OL322059	OL322063
Beauveria acridophila	MCA 1181	MF416574	n/a	MF416522	n/a	MF416628	n/a
B. amorpha	ARSEF 4149	n/a	HQ880804	n/a	HQ881006	HQ880876	HQ880948
	ARSEF 7542	n/a	HQ880805	n/a	HQ881007	HQ880877	HQ880949
B. asiatica	BUB824	MG642893	MG642836	MG642850	MG642908	MG642863	MG642878
B. australis	ARSEF 4622	n/a	HQ880790	n/a	HQ880996	HQ880862	HQ880934
	ARSEF 4580	n/a	HQ880788	n/a	HQ880994	HQ880860	HQ880932
B. bassiana	ARSEF 1564	n/a	GU734762	n/a	HQ880974	HQ880833	HQ880905
B. brongniartii	ARSEF 6215	n/a	HQ880781	n/a	HQ880990	HQ880853	HQ880925
	ARSEF 7058	n/a	HQ880773	n/a	HQ880983	HQ880845	HQ880917
	ARSEF 7268	n/a	HQ880772	n/a	HQ880982	HQ880844	HQ880916
B. caledonica	BCC16585	JF415951	JN049867	JF415967	JF416009	JN049885	JF415991
	ARSEF 2567	AF339570	HQ880817	AF339520	EF469057	EF469086	HQ880961
B. locustiphila	BUB421	MG642888	MG642831	MG642845	MG642903	MG642858	MG642873
	TS 881	JQ895525	JQ958606	JQ895535	JQ958619	JX003847	JX003845
B. malawiensis	BCC20195	n/a	MN401622	n/a	MN401448	MN401546	MN401602
B. pseudobassiana	BUB444	MG642890	MG642833	MG642847	MG642905	MG642860	MG642875
	BUB506	MG642891	MG642834	MG642848	MG642906	MG642861	MG642876
B. scarabaeidicola	YNHHCS1	MH458406	n/a	MH458408	MH458404	MH458402	MH458410
B. sinensis	ARSEF 5689	AF339574	AY245639	AF339524	DQ522335	DQ522380	DQ522431
	BUB51	MG642879	MG642824	MG642837	MG642894	MG642851	MG642864
Blackwellomyces aurantiacus	BCC85061	n/a	MT000693	MT003029	MK411599	MK411601	MT017820

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
Bla. aurantiacus	BCC85060	n/a	MT000692	MT003028	MK411598	MK411600	MT017819
Bla. calendulinus	BCC68500	n/a	MT000694	MT003030	MT017842	MT017802	MT017821
	BCC68502	n/a	MT000695	MT003031	MT017843	MT017803	MT017822
Bla. cardinalis	OSC 93610	AY184973	JN049843	AY184963	EF469059	EF469088	EF469106
	OSC 93609	AY184974	n/a	AY184962	DQ522325	DQ522370	DQ522422
Bla. lateris	MFLU 18-0663	NG_067678	NR_166258	NG_067857	MK069471	MK084615	MK079354
Bla. minutus	BCC88269	n/a	MT000696	MT003032	MT017844	MT017804	MT017823
Bla. pseudomilitaris	NBRC 101409	JN941748	JN943305	JN941393	n/a	JN992482	n/a
	NBRC 101410	JN941747	JN943307	JN941394	n/a	JN992481	n/a
Bla. roseostromatus	BCC91358	n/a	MT000697	MT003033	MT017845	MT017805	MT017824
	BCC91359	n/a	MT000698	MT003034	MT017846	MT017806	MT017825
Cordyceps araneae	BCC85065	n/a	MT000702	MT003037	MT017850	MT017810	MT017828
	BCC85066	n/a	MT000703	MT003038	MT017851	MT017811	MT017829
C. cateniobliqua	YFCC 3367	MN576765	n/a	MN576821	MN576991	MN576881	MN576935
	YFCC 5935	MN576766	n/a	MN576822	MN576992	MN576882	MN576936
C. fumosorosea	CBS 107.10	n/a	AY624184	MG665227	n/a	n/a	MG665237
	CBS 375.70	n/a	MH859721	MG665229	n/a	n/a	MG665238
C. javanica	CBS 134.22	MF416610	MH854719	MG665231	MF416504	MF416661	MF416455
	TBRC 7260	n/a	MF140744	MF140710	MF140830	MF140779	MF140803
C. lepidopterorum	TBRC 7263	n/a	MF140765	NG_067804	MF140819	MF140768	MF140792
	TBRC 7264	n/a	MF140766	MF140700	MF140820	MF140769	MF140793
C. longiphialis	YFCC 8402	NG_148882	n/a	OL468577	OL473525	OL739571	OL473536
	YFCC 8403	OL468558	n/a	OL468578	OL473526	OL739572	OL473537
C. militaris	OSC 93623	AY184977	JN049825	AY184966	DQ522332	DQ522377	n/a
C. nidus	TS903C	KY360300	n/a	KY360293	n/a	KY360296	n/a
C. pruinosa	ARSEF 5413	AY84979	JN049826	AY84968	DQ522351	Q522397	DQ522451
C. simaoensis	YFCC 8407	OL468562	n/a	OL468582	OL473530	OL739576	OL473541
	YFCC 8408	OL468563	n/a	OL468583	OL473531	OL739577	OL473542
C. subtenuipes	YFCC 6051	MN576719	n/a	MN576755	MN576945	MN576835	MN576891

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
	YFCC 6084	MN576720	n/a	MN576776	MN576946	MN576836	MN576892
C. tenuipes	ARSEF 5135	MF416612	AY624196	JF415980	KY973654	JN049896	JF416000
	BCC33299	n/a	MH532860	MH394664	n/a	MH521838	MH521877
	BCC34337	n/a	MH532861	MH394665	n/a	MH521839	MH521878
Engyodontium rectidentatum	CBS 641.74	n/a	LC092895	LC092914	LC425540	n/a	n/a
	CBS 547.82	n/a	LC092894	LC092913	LC425544	n/a	n/a
Flavocillium bifurcatum	YFCC 6101	MN576725	MN576833	MN576781	MN576951	MN576841	MN576897
Fla. acerosum	CBS 418.81	KM283762	EF641893	KM283786	KM283810	KM283832	KM283852
Fla. subprimulinum	KUMCC 17-0144	MG585320	MG585318	MG585319	MG585321	n/a	n/a
	KUMCC 17-0148	MG585316	MG585314	MG585315	MG585317	n/a	n/a
	JCM 18525	NG_073501	NR_119418	NG_067516	LC557125	n/a	n/a
Gibellula attenboroughii	**IMI 507230 [I22-1407]**	PQ036924	n/a	PQ036929	PQ046101	n/a	n/a
	IMI 507600 [I22-1423]	PQ036925	PQ036927	n/a	PQ046102	n/a	n/a
	IMI 507601 [I23-1492]	PQ036926	PQ036928	n/a	n/a	n/a	n/a
G. aurea	1PACOTI (LBMCF0003)	OK329880	n/a	OQ585967	OK392618	n/a	OL117022
	2PACOTI (LBMCF0004)	OK329881	n/a	OQ585968	OK392619	n/a	OL117023
	3PACOTI (LBMCF0005)	n/a	n/a	OQ585969	OQ658382	n/a	n/a
	25PACOTI (LBMCF0006)	n/a	n/a	OK329875	OK392624	n/a	OK315662
	26PACOTI (LBMCF0007)	n/a	OK329885	OK329876	OK392622	n/a	OK315663
G. brevistipitata	BCC57817	n/a	OK040729	OK040706	OK040697	OK040715	n/a
G. cebrennini	BCC32072+B108:B117	n/a	MT477067	n/a	MT503326	n/a	n/a
	BCC53551	n/a	MT477068	n/a	MT503327	n/a	n/a
	BCC53605	n/a	MT477069	MT477062	MT503328	MT503321	MT503336
	BCC39705	n/a	MH532874	MH394673	MH521895	MH521822	MH521859
G. clavulifera	GZUIFR-HN0801	n/a	KJ857269	n/a	n/a	n/a	n/a
	n/a	n/a	KP685596	n/a	n/a	n/a	n/a
G. clavulifera var. alba	ARSEF1915	DQ522562	JN049837	DQ518777	DQ522360	DQ522408	DQ522467
G. dimorpha	BCC47518	n/a	MH532884	MH394679	MH521892	MH521819	MH521863
G. flava	GNJ20200814-46	MW969660	n/a	MW969673	MW961413	MW980146	n/a

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
G. formosana	WFS20190625-25	MW036749	n/a	MW084343	MW091325	MW384883	n/a
	n/a	n/a	AB100360	n/a	n/a	n/a	n/a
G. fusiformispora	BCC56802	n/a	MT477070	MT477063	MT503329	MT503322	MT503337
	BCC45076	n/a	MH532882	n/a	n/a	MH521823	MH521860
G. gamsii	BCC25798	n/a	MH152532	MH152542	MH152563	MH152550	n/a
	BCC27968	n/a	MH152529	MH152539	MH152560	MH152547	n/a
	BCC27970	n/a	MH152530	MH152540	MH152561	MH152548	n/a
	BCC28797	n/a	MH152531	MH152541	MH152562	MH152549	MH152557
	BCC29228	n/a	MH152533	MH152543	MH152564	MH152551	MH152558
	BCC30396	n/a	MH152535	n/a	MH152566	MH152553	n/a
	BCC30397	n/a	MH152536	n/a	MH152567	MH152554	MH152559
	BCC30449	n/a	MH152534	MH152544	MH152565	MH152552	n/a
	BCC42026	n/a	MH152537	MH152545	MH152568	MH152555	n/a
	BCC47868	n/a	n/a	MH152538	n/a	MH152546	MH152556
	EPF034	n/a	JX192720	JX192753	JX192817	n/a	n/a
G. leiopus	LBMCF2022.86	OQ585788	OQ589483	n/a	OQ658391	n/a	n/a
	LBMCF2022.98	OQ585790	OQ589485	n/a	OQ658393	n/a	n/a
	LBMCF2022.99	OQ585791	OQ589486	OQ585978	OQ658394	n/a	n/a
	EBSL08 (LBMCF0011)	OK329882	OQ589488	OK329878	OK392621	n/a	OL117024
	EBSL13 (LBMCF0001)	OK329879	OK329883	OK329874	OK392625	n/a	n/a
	BCC16025	MF416602	n/a	MF416548	MF416492	MF416649	n/a
	BCC49250	n/a	OK070780	OK070781	OK070782	OK070783	OK070784
G. longicaudata	BCC40861	n/a	OK040730	OK040707	OK040698	OK040716	OK040724
G. longispora	GNJ20210710-02	OL854201	n/a	OL854212	OL981628	n/a	OL981635
	GNJ20200813-16	n/a	n/a	n/a	MW961414	MW980145	n/a
	NHJ 12014	EU369098	n/a	n/a	EU369017	EU369055	EU369075
G. mainsii	LBMCF2022.96	OQ585789	OQ589484	n/a	OQ658392	n/a	n/a
G. mirabilis	LBMCF2020.01	OQ585782	OQ589479	OQ585972	OQ658385	n/a	n/a
	LBMCF2021.70	OQ585786	OQ589481	OQ585976	OQ658389	n/a	n/a

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
	LBMCF2021.80	OQ585787	OQ589482	OQ585977	OQ658390	n/a	n/a
	LBMCF2022.107	OQ585792	n/a	OQ585979	OQ658395	n/a	n/a
G. nigelii	NHJ 10808	EU369099	n/a	EU369035	EU369018	EU369056	EU369076
G. parvula	BCC48888	n/a	NR_182399	OK040708	OK040699	OK040717	OK040725
	BCC49748	n/a	OK040732	OK040709	OK040700	OK040718	OK040726
G. penicillioides	GNJ20200812-05	n/a	MW969672	MW969664	MW961418	n/a	n/a
	GNJ20200814-11	MW969650	MW969669	MW969661	MW961415	MZ215998	n/a
	GNJ20200814-14	MW969651	MW969670	MW969662	MW961416	MZ215999	n/a
	GNJ20200814-17	MW969652	MW969671	MW969663	MW961417	n/a	n/a
G. pigmentosinum	BCC41203	n/a	MT477071	n/a	MT503330	MT503323	n/a
	BCC41870	n/a	MT477072	MT477064	MT503331	MT503324	n/a
	BCC38246	n/a	MH532872	MH394672	MH521893	MH521800	MH521855
	NHJ 11679	n/a	n/a	n/a	EU369016	EU369054	n/a
G. pilosa	BCC45580	n/a	OK040733	OK040710	OK040701	OK040719	n/a
G. pulchra	LBMCF2020.02	OQ585783	n/a	OQ585973	OQ658386	n/a	n/a
	LBMCF2020.03	OQ585784	OQ589480	OQ585974	OQ658387	n/a	n/a
	LBMCF2020.07	OQ585785	n/a	OQ585975	OQ658388	n/a	n/a
	LBMCF2022.GA	OQ585780	n/a	OQ585970	OQ658383	n/a	n/a
	LBMCF2022.GB	OQ585781	OQ589487	OQ585971	OQ658384	n/a	n/a
	NHJ 10788	EU369101	n/a	EU369036	EU369019	EU369058	EU369078
	NHJ 5401	EU369102	n/a	n/a	n/a	EU369059	EU369079
	BCC47555	n/a	MH532885	n/a	MH521897	MH521804	n/a
	NHJ14150	n/a	HM161739	n/a	HM161729	n/a	n/a
	EPF083	JX192782	JX192719	JX192752	JX192813	n/a	n/a
G. scorpioides	BCC45127	n/a	MT477075	n/a	MT503332	n/a	n/a
	BCC47514	n/a	MT477076	n/a	MT503333	n/a	n/a
	BCC47530	n/a	MT477077	MT477065	MT503334	n/a	MT503338
	BCC47976	n/a	MT477078	MT477066	MT503335	MT503325	MT503339
	BCC13020	n/a	MT477073	MH394686	MH521901	MH521814	n/a

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
	BCC27985	n/a	n/a	MH394662	MH521899	MH521815	MH521857
	BCC27986	n/a	OK040735	OK040711	OK040702	OK040720	OK040727
G. solita	BCC45574	n/a	OK040736	OK040712	OK040703	OK040721	n/a
G. trimorpha	BCC36538	n/a	MH532867	MH394668	MH521890	MH521817	MH521861
	BCC36526	n/a	OK040737	n/a	OK040704	OK040722	OK040728
G. unica	BCC46590	n/a	MH532883	MH394678	n/a	MH521803	MH521866
	BCC45112	n/a	OK040738	OK040713	OK040705	OK040723	n/a
Gamzarea humicola	LC12462	n/a	n/a	n/a	MK336028	n/a	MK335980
Gam. lunata	LC12546	n/a	n/a	n/a	MK336030	n/a	MK335982
Gam. microspora	CGMCC3.19313	NG_074898	NR_172832	NG_075269	n/a	n/a	n/a
	LC12531	n/a	n/a	n/a	MK336032	n/a	MK335984
Gam. wallacei	CBS 101237	NG_062646	NR_111267	NG_042398	EF469073	EF469102	EF469119
Hevansia arachnophila	NHJ2465	n/a	MH532899	n/a	MH521916	ON470205	ON470207
	NHJ2633	n/a	MH532900	n/a	MH521917	MH521843	MH521884
	NHJ 10469	EU369090	n/a	EU369031	EU369008	EU369047	n/a
H. koratensis	BCC01485	GQ249957	GQ250010	GQ249981	GQ250031	ON470206	ON470208
H. minuta	MY060537.01	n/a	n/a	n/a	MZ707811	MZ707826	MZ707833
	MY060537.02	n/a	n/a	n/a	MZ707812	MZ707827	MZ707834
H. nelumboides	BCC2093	MF416583	n/a	MF416530	MF416473	n/a	MF416437
	BCC41864	JN201863	JN201871	JN201873	JN201867	n/a	n/a
H. novoguineensis	BCC22910	GQ249953	GQ250003	GQ249974	GQ250024	n/a	n/a
	NHJ11923	EU369095	n/a	EU369032	EU369013	EU369052	EU369072
	CBS 610.80	n/a	MH532831	MH394646	MH521885	n/a	MH521844
	BCC22857	GQ249952	GQ250002	GQ249973	GQ250023	n/a	n/a
H. websteri	BCC36541	n/a	MH532868	MH394669	MH521889	MH521811	MH521849
	BCC23860	GQ249954	GQ250009	GQ249979	GQ250030	n/a	n/a
Jenniferia cinerea	BCC02191	GQ249956	GQ250000	GQ249971	GQ250029	n/a	n/a
	BCC47913	n/a	n/a	MH394651	n/a	MH521820	MH521850
	BCC47914	n/a	n/a	MH394652	MH521888	MH521821	MH521851

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
Jen. griseocinerea	BCC54893	n/a	MZ684093	MZ684008	n/a	n/a	n/a
	MY06006.01	n/a	n/a	n/a	MZ707815	MZ707828	MZ707837
	BCC42062	n/a	MZ684091	MZ684006	n/a	n/a	n/a
Jen. thomisidarum	BCC48932+B210:B215	n/a	MZ684095	MZ684012	n/a	n/a	n/a
	BCC54482	n/a	MZ684097	MZ684014	n/a	n/a	n/a
	MY05032.02	n/a	n/a	n/a	MZ707824	MZ707831	MZ707844
Lecanicillium antillanum	CBS 350.85	AF339585	NR_111097	AF339536	DQ522350	DQ522396	DQ522450
L. aphanocladii	CBS 797.84	KM283763	n/a	KM283787	KM283811	KM283833	KM283853
	IFM 64743	LC553289	LC553279	LC553284	LC553294	n/a	n/a
L. araneogenum	GZU1031Lea	KX845705	n/a	KX845703	KX845697	KX845699	KX845701
	GZU1032Lea	KX845706	n/a	KX845704	KX845698	KX845700	KX845702
L. coprophilum	CGMCC3.18986	NG_065751	NR_163303	NG_067818	n/a	n/a	n/a
	TBS419	MH177626	MH177615	MH177618	MH184586	MH177621	MH177623
L. dimorphum	CBS 345.37	KM283764	n/a	KM283788	KM283812	KM283834	KM283854
L. flavidum	CBS 300.70D	KM283765	MH859668	KM283789	KM283813	n/a	KM283855
	CBS 342.80	KM283766	EF641878	KM283790	KM283814	n/a	n/a
L. fungicola var. aleophilum	CBS 357.80	KM283767	n/a	KM283791	KM283815	KM283835	KM283856
L. fusisporum	CBS 164.70	KM283769	NR_111100	AF339549	KM283817	KM283836	KM283858
L. huhutii	GZUIFRhuhu	MN963916	MN944445	n/a	MT006068	MT006058	MT006063
L. longisporum	CBS 102072	KM283772	n/a	KM283796	KM283819	KM283839	KM283861
	CBS 126.27	KM283773	OP756342	KM283797	KM283820	KM283840	KM283862
L. magnisporum	CGMCC3.19304	NG_074899	NR_172833	NG_075270	n/a	n/a	n/a
L. muscarium	CBS 143.62	KM283774	n/a	NG_058106	KM283821	KM283841	KM283863
L. pissodis	BBC7	MT004819	MT004829	MT004835	MT027503	MT027506	MT027509
	CBS 118231	KM283775	n/a	KM283799	KM283822	KM283842	KM283864
L. praecognitum	MGC39	MT247062	MT247058	MT247060	MT267523	n/a	MT267525
	WA67215	NG_070677	NR_173935	NG_081473	n/a	n/a	n/a
L. psalliotae	CBS 101270	AF339607	n/a	AF339558	EF469066	EF469095	EF469113
	CBS 532.81	AF339609	JN049846	AF339560	EF469067	EF469096	EF469112

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
L. tenuipes	CBS 309.85	KM283778	JN036556	KM283802	DQ522341	KM283844	DQ522439
L. uredinophilum	CEP 054	n/a	n/a	OP752150	n/a	OP762608	OP762612
Leptobacillium filiforme	URM 7918	n/a	NR_171744	NG_075252	n/a	n/a	n/a
L. leptobactrum	CBS 774.69	n/a	MH859421	MH871192	n/a	n/a	n/a
L. leptobactrum	CBS 775.69	n/a	MH859422	MH871193	n/a	n/a	n/a
Liangia sinensis	YFCC 3103	MN576726	MN576831	MN576782	MN576952	MN576842	MN576898
	YFCC 3104	MN576727	MN576832	MN576783	MN576953	MN576843	MN576899
Microhilum oncoperae	ARSEF 4358	AF339581	n/a	AF339532	EF468785	EF468891	EF468936
Neotorrubiella chinghridicola	BCC80733	MK632121	MK632039	MK632097	n/a	MK632176	MK632149
	BCC39684	MK632122	MK632038	MK632096	MK632071	MK632181	MK632148
Niveomyces coronatus	NYO434800	ON493547	n/a	ON493606	ON513397	ON513399	ON513400
Ophiocordyceps caloceroides	MCA 2249	MF416578	n/a	MF416525	MF416470	MF416632	n/a
O. gracilis	EFCC 8572	EF468956	JN049851	EF468811	EF468751	EF468859	EF468912
O. salganeicola	Mori01	MT741705	n/a	MT741719	MT759575	MT759578	MT759580
Parengyodontium album	CBS 368.72	n/a	MH860502	MH872217	LC382183	n/a	n/a
P. formicarum	BCC84257	n/a	n/a	MT512653	MT533480	MT533473	n/a
	CBS 433.73	n/a	AY945231	n/a	n/a	n/a	n/a
	CBS 871.72	n/a	n/a	MH878295	MT863565	MT533474	n/a
Phytocordyceps ninchukispora	EGS 38.165	EF468991	n/a	EF468846	EF468795	EF468900	n/a
	EGS 38.166	EF468992	n/a	EF468847	EF468794	EF468901	n/a
Pleurodesmospora coccorum	CBS 460.73	n/a	MH860743	MH872455	n/a	n/a	n/a
	CBS 459.73	n/a	MH860742	MH872454	n/a	n/a	n/a
Ple. lepidopterorum	DY10501	n/a	MW826577	n/a	MW834317	MW834315	MW834316
Polystromomyces araneae	MY12684	n/a	n/a	n/a	MZ707825	MZ707832	MZ707845
Pseudogibellula formicarum	BCC81493	n/a	n/a	MT512652	MT863566	MT533472	n/a
Samsoniella alboaurantia	BBC5	MT004818	MT004827	MT004834	MT027502	n/a	MT027508
Sam. alpina	YFCC 5818	MN576753	n/a	MN576809	MN576979	MN576869	MN576923
	YFCC 5831	MN576754	n/a	MN576810	MN576980	MN576870	MN576924
Sam. antleroides	YFCC 6016	MN576747	n/a	MN576803	MN576973	MN576863	MN576917

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
	YFCC 6113	MN576748	n/a	MN576804	MN576974	MN576864	MN576918
Sam. aurantia	TBRC 7271	n/a	MF140764	MF140728	MF140846	MF140791	MF140818
	TBRC 7272	n/a	MF140763	MF140727	MF140845	n/a	MF140817
Sam. cardinalis	YFCC 5830	MN576732	n/a	MN576788	MN576958	MN576848	MN576902
	YFCC 6144	NG_077413	n/a	MN576786	MN576956	MN576846	MN576900
Sam. coccinellidicola	YFCC 8772	ON563166	n/a	ON621670	ON676514	ON676502	ON568685
	YFCC 8773	ON563167	n/a	ON621671	ON676515	ON676503	ON568686
Sam. cristata	YFCC 6023	MN576736	n/a	MN576792	MN576962	MN576852	MN576906
	YFCC 7004	NG_077415	n/a	MN576793	MN576963	MN576853	MN576907
Sam. farinospora	YFCC 8774	ON563168	n/a	ON621672	ON676516	ON676504	ON568687
	YFCC 9051	ON563169	n/a	ON621673	ON676517	ON676505	ON568688
Sam. haniana	YFCC 8769	ON563170	n/a	ON621674	ON676518	ON676506	ON568689
	YFCC 8770	ON563171	n/a	ON621675	ON676519	ON676507	ON568690
Sam. hepiali	YFCC 7024	MN576741	n/a	MN576797	MN576967	MN576857	MN576911
	YFCC 7215	MN576742	n/a	MN576798	MN576968	MN576858	MN576912
Sam. inthanonensis	TBRC 7270	n/a	MF140759	MF140723	MF140847	MF140788	MF140813
	TBRC 7915	n/a	MF140761	MF140723	MF140849	MF140790	MF140815
Sam. kunmingensis	YHH 16002	MN576746	n/a	NG_079657	MN576972	MN576862	MN576916
Sam. lanmaoa	YFCC 6193	MN576734	n/a	MN576790	MN576960	MN576850	MN576904
	YFCC 6148	MN576733	n/a	MN576789	MN576959	MN576849	MN576903
Sam. pseudotortricidae	YFCC 9052	ON563173	n/a	ON621677	ON676521	ON676509	ON568692
	YFCC 9053	ON563174	n/a	ON621678	ON676522	ON676510	ON568693
Sam. ramosa	YFCC 6020	MN576749	n/a	MN576805	MN576975	MN576865	MN576919
Sam. tortricidae	YFCC 6013	MN576751	n/a	MN576807	MN576977	MN576867	MN576921
	YFCC 6131	NG_077418	n/a	MN576806	MN576976	MN576866	MN576920
Sam. yunnanensis	YFCC 1527	NG_077420	n/a	MN576812	MN576982	MN576872	MN576926
	YFCC 1824	MN576757	n/a	MN576813	MN576983	MN576873	MN576927
Simplicillium aogashimaense	JCM 18167	NG_068378	NR_111026	NG_068547	LC496904	n/a	n/a
	JCM 18168	LC496890	AB604004	LC496875	LC496905	n/a	n/a

Table 1. (Continued).

Species	Voucher numbers	GenBank Accession Numbers					
		SSU	ITS	LSU	TEF	RBP1	RPB2
Sim. cylindrosporum	JCM 18169	NG_068379	NR_111023	NG_069476	LC496906	n/a	n/a
Sim. formicae	MFLUCC 18-1379	NG_070121	NR_168789	NG_068624	MK926451	MK882623	n/a
Sim. lamellicola	CBS 116.25	AF339601	NR_111098	NG_042381	DQ522356	DQ522404	DQ522464
	JC-1	MT807908	MT807906	MT807907	MT826785	n/a	n/a
Sim. lanosoniveum	CG888	MT081951	MT081944	MT081957	MT140365	n/a	n/a
	CG889	MT081952	MT081943	MT081958	MT140366	n/a	n/a
	CBS 704.86	AF339602	n/a	AF339553	DQ522358	DQ522406	DQ522464
Sim. minatense	JCM 18176	NG_068380	NR_111025	NG_069477	LC496908	n/a	n/a
Sim. niveum	BCC83036	n/a	MW621499	MW620992	MW603488	MW603489	n/a
Sim. obclavatum	CBS 311.74	NG_062627	NR_111099	NG_042535	EF468798	n/a	n/a
Sim. subtropicum	JCM 18180	LC496895	NR_111024	LC496880	LC496910	n/a	n/a
Sim. sympodiophorum	JCM 18184	NG_068382	NR_111027	NG_068548	LC496912	n/a	n/a
Sim. yunnanense	YFCC 7133	NG_077412	n/a	MN576784	MN576954	MN576844	n/a
	YFCC 7134	MN576729	n/a	MN576785	MN576955	MN576845	n/a
Torrubiella arachnophilus (*G. pulchra*)	BCC47888	n/a	n/a	n/a	n/a	MH521802	MH521864
T. arachnophilus	n/a	AF327399	KP685595	AF327391	n/a	n/a	n/a
	BUG507	MH879644	n/a	MH879596	n/a	MH885445	MH879619
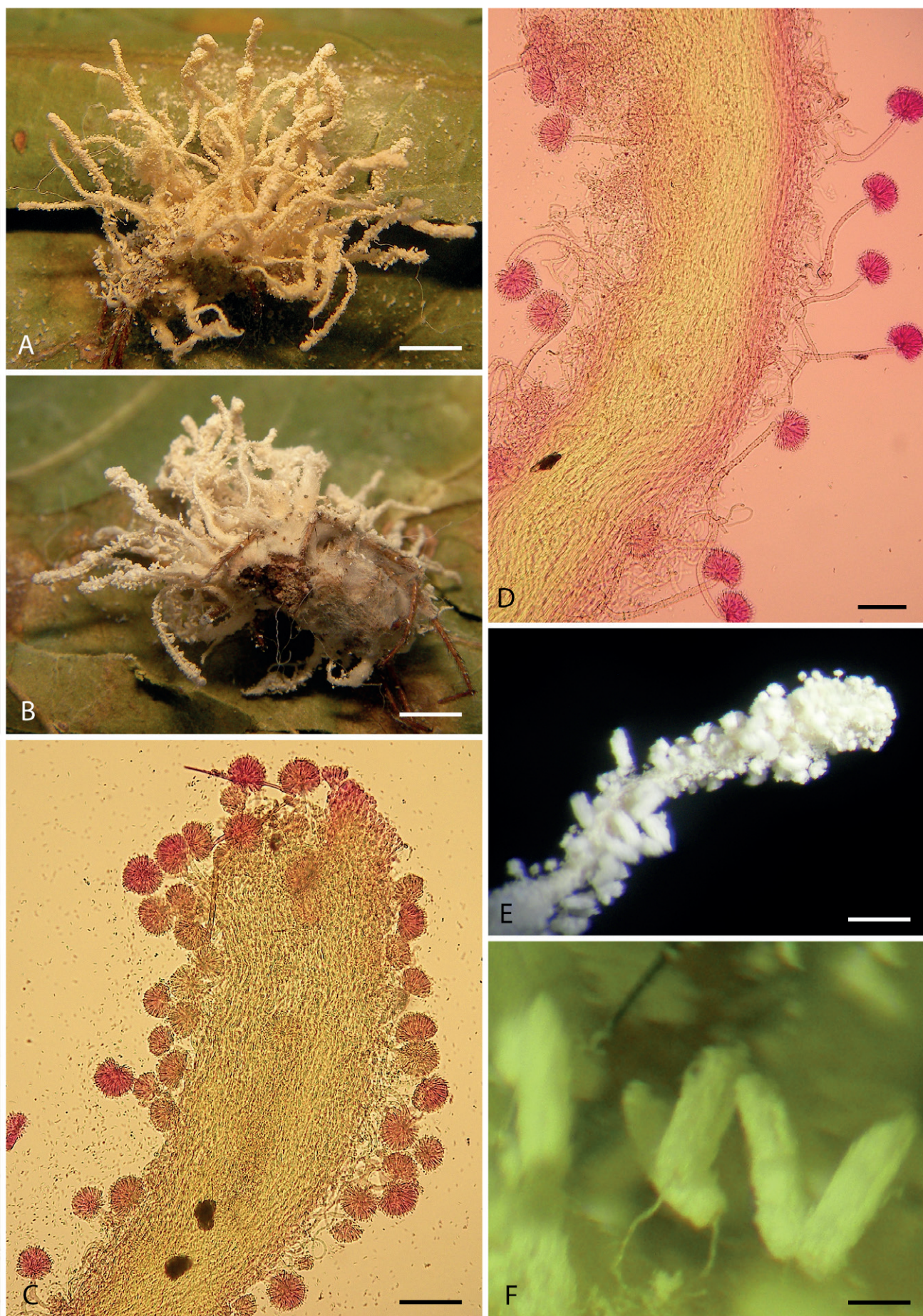
Fig. 2. *Gibellula attenboroughii*, holotype IMI 507230, on orb-weaving spider, *Metellina merianae*. **A, B.** On spider host after removal and drying, showing the multiple synnemata. **C.** Long conidiophores scattered along lower part of synnema. **D.** Short conidiophores densely clustered in terminal part of synnema. **E, F.** Dense, white spore columns on short conidiophores at apex (**E**) and long conidiophores at base (**F**). Scale bars: A, B = 1 cm; C, D = 50 μm; E = 100 μm; F = 25 μm.

Taxonomy

Based on morphology, and supported by the molecular data, a new species in the genus *Gibellula* is proposed:

Gibellula attenboroughii H.C. Evans & J.P.M. Araújo, *sp. nov.* MycoBank MB 854973. Figs 2–10.

Etymology: Named after the broadcaster and natural historian Sir David Attenborough, a pioneer of BBC natural history programmes, who – in his role as controller of BBC 2 – helped to develop the Natural History Unit; leading, indirectly, to the present nature series during which the new species was first discovered.

Typus: **UK**, Northern Ireland, County Down, Comber, Castle Espie Wetland Centre, on orb-weaving spider *Metellina merianae* (*Tetragnathidae*: *Araneae*), gunpowder store ceiling, 11 Feb. 2022, *J. Clark & M. Turley* (**holotype** dried down culture, metabolically inactive, IMI 507230; culture ex-type IMI 507230).

Paratypes: **UK**, Northern Ireland, County Fermanagh, Tullybelcoo Ground Bridge, on *Metellina merianae*, cave roof, 19 Jun. 2022, *T. Fogg*, IMI 507599. **Republic of Ireland**, County Cavan, Blacklion, Whitefathers' Caves, on *Metellina merianae*, cave roof, 19 Jun. 2022, *T. Fogg*, IMI 507600; County Cavan, Blacklion, Whitefathers' Caves, on orb-weaving spider *Meta menardi* (*Tetragnathidae*: *Araneae*), cave roof, 19 Jun. 2022, *T. Fogg*, IMI 507598; County Cavan, Blacklion, Whitefathers' Caves, on *Meta menardi*, on cave wall, 17 Oct. 2023, *T. Fogg*, IMI 507601–507603; County Cavan, Blacklion, Whitefathers' Caves, on *Metellina merianae*, *T. Fogg*, IMI 507604.
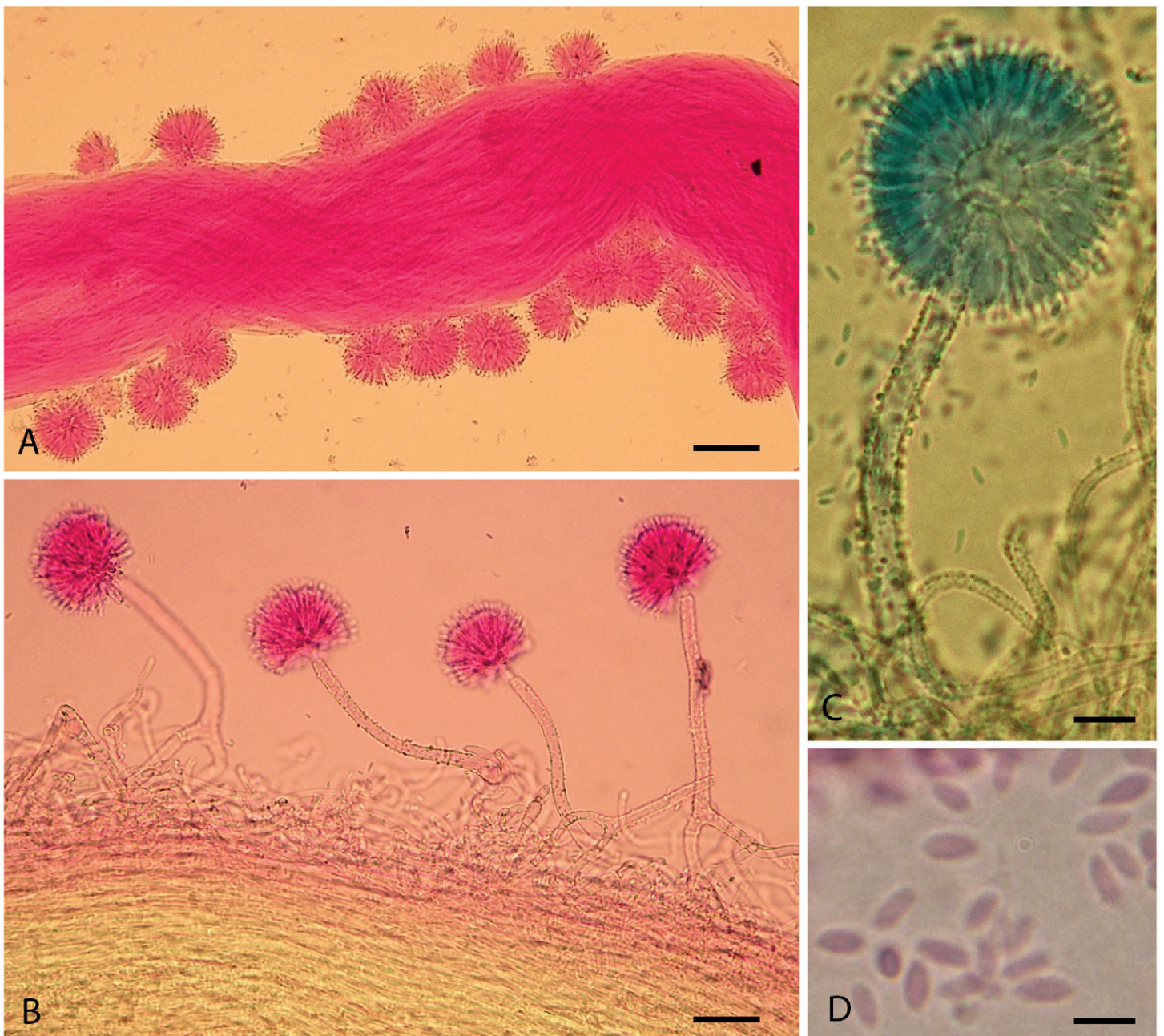
Fig. 3. *Gibellula attenboroughii*, holotype IMI 507230, conidiophore morphology. **A.** Synnema with almost astipitate conidiophores clustered towards the apex. **B, C.** Conidiophores towards the base with long, roughened stipes and short, smooth neck region. **D.** Conidia. Scale bars: A = 40 μm; B = 50 μm; C = 25 μm; D = 10 μm.

Description: Spider body *in situ* completely covered by a dense, white mycelial mat (Fig. 2A); becoming creamish yellow on drying (Fig. 2B). *Synnemata* cylindrical, numerous, from all body parts including legs, white to cream, swollen and floccose at the base, up to 250 µm diam (Fig. 2C); tapering towards the tip, 3–7(–10) mm long, 140–200 µm wide, terminal part often swollen and ovoid or club-shaped (Fig. 2D, E). *Conidiophores* produced along the entire length of the synnemata; scattered at the base with long stipes, 80–120 × 5–8 µm (Figs 2C, 3B); often becoming conspicuously crowded towards the tip and with short stipes, (10–)20–30 × 6–8 µm (Figs 2D, 3A); heads aspergilliform, occasionally with simple penicillioid heads and almost astipitate; distinctly roughened wall; septa conspicuous, 1–2; constricting to a short, smooth neck region or neck indistinct to absent; terminating in a swollen vesicle (Fig. 3B, C). *Vesicles* spherical to broadly obovoid, (8–)10–12(–13) µm diam. *Metulae* borne on vesicle, broadly obovoid or broadly ellipsoid, (8–)10–12 × (4–)6–8 µm, bearing multiple phialides. *Phialides* cylindrical to narrowly clavate, often apically thickened, 7.5–9.5 × 2.5–3.5 µm. A vesicle together with metulae and phialides forming a spherical to ovoid head measuring, (28–)32–40 × 24–40 µm diam; occasionally, much reduced in size and complexity. *Conidia* hyaline, smooth, ellipsoidal to fusoid, 4–6 × 1.5–2 µm (Fig. 3D), often adhering in long chains and forming compact, white blocks (Fig. 2E, F). *Sexual morph* and *Granulomanus synasexual morph* not observed.

In culture: On MEA, slow-growing, 0.7–0.9 cm diam after 6 wk at 20 °C, white, stromatic; turning creamish to pale brown, raised centrally, often furrowed, brown diffusate around periphery, dark brown reverse after 12 wk, 1.8–2.0 cm diam (Fig. 4A); on PCA, slower growing (1.3–1.5 cm diam after 12 wk), dark cream
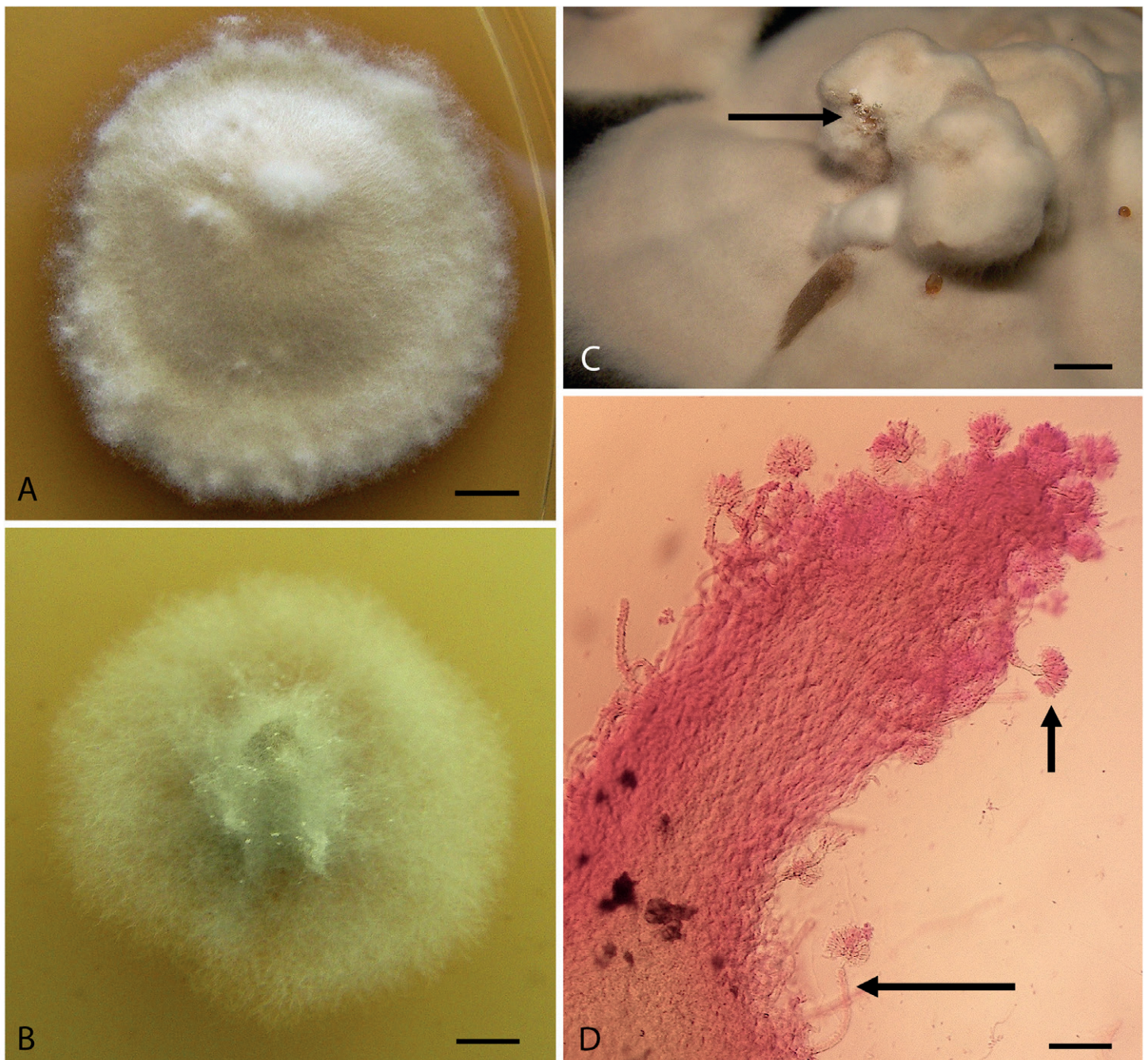

Fig. 4. *Gibellula attenboroughii*, holotype IMI 507230, in culture. **A, B.** Colony after 6 wk on MEA (**A**) and on PCA (**B**). **C.** Colony after 4 mo on MEA producing clusters of fertile synnemata (arrow) on pseudostroma. **D.** Detail of synnema with short conidiophores at apex (short arrow) and long conidiophores at base (long arrow), as on host. Scale bars: A, B = 3 mm; C = 1.5 mm; D = 60 µm.

with a greyish brown reverse (Fig. 4B); after 4 mo becoming feathery and irregular at periphery and up to 3.0 cm diam, forming chains of small, hyaline chlamydospores; occasionally developing short synnemata centrally (Fig. 4C), morphologically identical to those on the host with short conidiophores crowded at tip and longer, scattered conidiophores at base (Fig. 4D).

Paratype IMI 507601, *ex Meta menardi*, on PCA, slow-growing, 0.5-0.7 cm after 6 wk at 20 °C, white to creamish, compact, raised centrally, brown diffusate; dark brown reverse. After 3 mo, 1.8–2.0 cm, raised and cream to buff brown; producing chains of dark red chlamydospores (Fig. 8B) and scattered, typically penicillioid, conidiophores with chains of pale lilac conidia either directly from the mycelium (Fig. 8A), or from rudimentary synnemata. However, atypical aspergilliform conidiophores also occurred sporadically around the periphery (Fig. 8C, D).
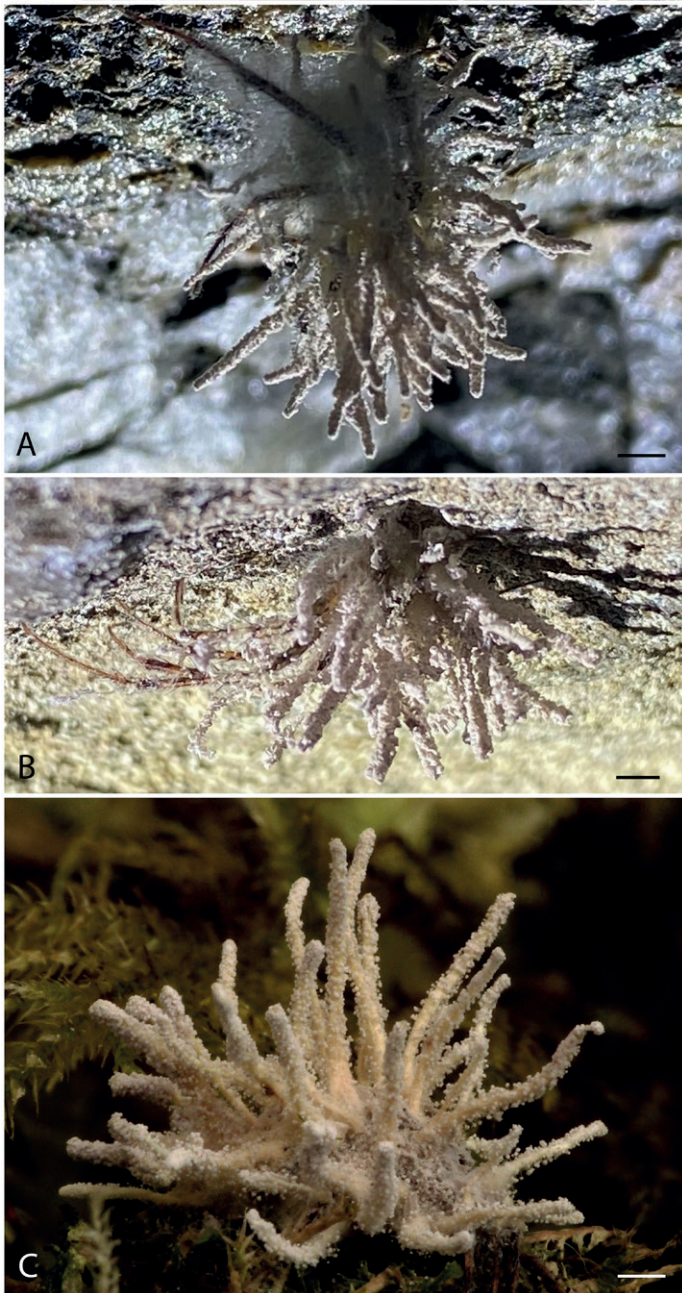
Fig. 5. *Gibellula attenboroughii* on *Metallina merianae*, paratypes *in situ*. **A.** On cave ceiling, Tullybelcoo Ground Bridge, County Fermanagh, Northern Ireland. **B.** Whitefathers' Caves, County Cavan, Republic of Ireland. **C.** On moss, Lake Vyrnwy, Powys, Wales (image: D. McNeil). Scale bars: A, B = 1.5 mm; C = 1 mm.

Notes: The holotype shows distinct features in which there is a general lack of pigmentation compared to the paratypes on the same spider host, *Metellina merianae*, which have a dense yellow mycelial covering or subiculum, with yellow synnemata and pale lilac spore heads. The compact conidial columns or blocks of spores are less evident in these paratypes. The paratypes on the much larger spider host *Meta menardi*, in which such dense spore columns are rarely observed, the conidiophores are much shorter with simple, penicillioid conidiogenous heads, formed on tapering, fir-tree-like synnemata; contrasting with the complex aspergilliform heads produced on the stouter, less tapered synnemata occurring on *Metellina merianae* (see Figs 3A, 5, 6, 7A). In fact, before the availability of the molecular data, it was considered that these morphological differences merited separation at the species level.

It is posited here that these differences are due to ecotypic variation with the complete absence of light and air movement within the underground gunpowder store leading to loss of pigmentation and the spores adhering in columns. Within the cave system, especially in the threshold zone favoured by *Metellina merianae*, there would be both diffuse light and air currents to dislodge and disperse the conidia resulting in a decreased incidence of long chains or blocks of spores. The simpler, more open and penicillioid conidiogenous heads usually forming on *Meta menardi* would lead to less adhesion of the spores and the general absence of spore columns or blocks. In old cultures derived from the paratypes on *Meta menardi*, rudimentary synnemata bearing short penicillioid conidiophores were observed, as well as long conidiophores with complex aspergilliform heads producing spore blocks arising directly from the mycelium (Fig. 8D).

Ecology

Although *Metellina merianae* was moved to this genus many years ago (Bristowe 1939), some authors still maintain it in the genus *Meta* together with *M. menardi* (Roberts 1995). The latter author even stated that "this move is incorrect; it may well be reversed in the future and is not followed here". However, the latest molecular phylogenetic study of metaine spiders (*Metainae*; *Tetragnathidae*) shows that *Meta menardi* and *Metellina merianae* are not congeneric within the sub-family *Metainae* (Kallal & Hormiga 2018). These two orb-spider species occupy overlapping niches within cave systems and, typically, *Metellina merianae* inhabits the shallow threshold or twilight zone in and around cave entrances (Novak *et al*. 2010, Hesselberg *et al*. 2019), which is where the infected paratypes were found. *Meta menardi*, however, is more prevalent in the so-called dark zone but has an optimal adaptation to the epigean/hypogean ecotone, according to Novak *et al*. (2010), so that the two species can and do occur together (Mammola & Isaia 2018). In fact, in one instance, infected *Meta menardi* and *Metellina merianae* specimens were found *ca*. 3 cm apart on a cave wall, some 20 m from the entrance (see Fig. 10A).

Metellina merianae also favours man-made habitats, such as culverts and cellars, and, in the case of the holotype, in a gunpowder store. In all instances, the infected spiders had moved from their concealed lairs or webs and died exposed on the cave roof or wall and the store ceiling. Similarly, this host when infected by *Gibellula* was also found in an exposed position around the rocky shores of upland lakes in Wales (McNeil 2012). At the time, the fungus was tentatively identified – based on

the received images (see Fig. 5C) – as being close to *G. leiopus* (H.C. Evans, pers. comm., 2012). No specimens were received for examination and none have been deposited officially but it is considered highly probable that this record on *Metellina merianae* from Wales is the new species *G. attenboroughii*; having similar densely-packed, white to pale yellow synnemata, although the stipes are distinctly pigmented and tan-coloured towards the base.

Infected specimens of *Meta menardi*, or the European cave spider, were collected freely exposed on the cave ceiling, typically, within the dark zone (T. Fogg, pers. comm., June 2022; see Figs 6, 9C). *Meta menardi*, like *Metellina merianae*, is a sit-and-wait predator – building a similar planar orb-web – but can also adapt to off-web foraging (Novak *et al.* 2010, Hesselberg *et al.* 2019). However, the life-style of both spider species in cave systems is cryptic, often concealing themselves in close proximity to their webs. The fact that *Gibellula*-infected spiders are found in prominent positions on the roof or ceiling of their subterranean habitats indicates a behavioural change, possibly manipulated by the fungus, in which the sporulating cadavers would be exposed to the air currents circulating through the caves promoting the release and subsequent dispersal of the dry spores through the system. In the case of the suspected infection of *Metellina merianae* by *G. attenboroughii* in Wales (McNeil 2012, Evans 2013, Hughes *et al.* 2016), the spiders appear to have moved from the entrances of rock fissures or similar natural or man-made niches, to die on the surrounding or overhanging sphagnum moss, as there are no cave systems in this lakeside locality (H.C. Evans, pers. obs., September 2022).

The ecological significance of the vastly-different sporulating heads – complex and aspergilliform on *Metellina merianae*; simple and penicillioid on *Meta menardi* – is difficult to interpret.
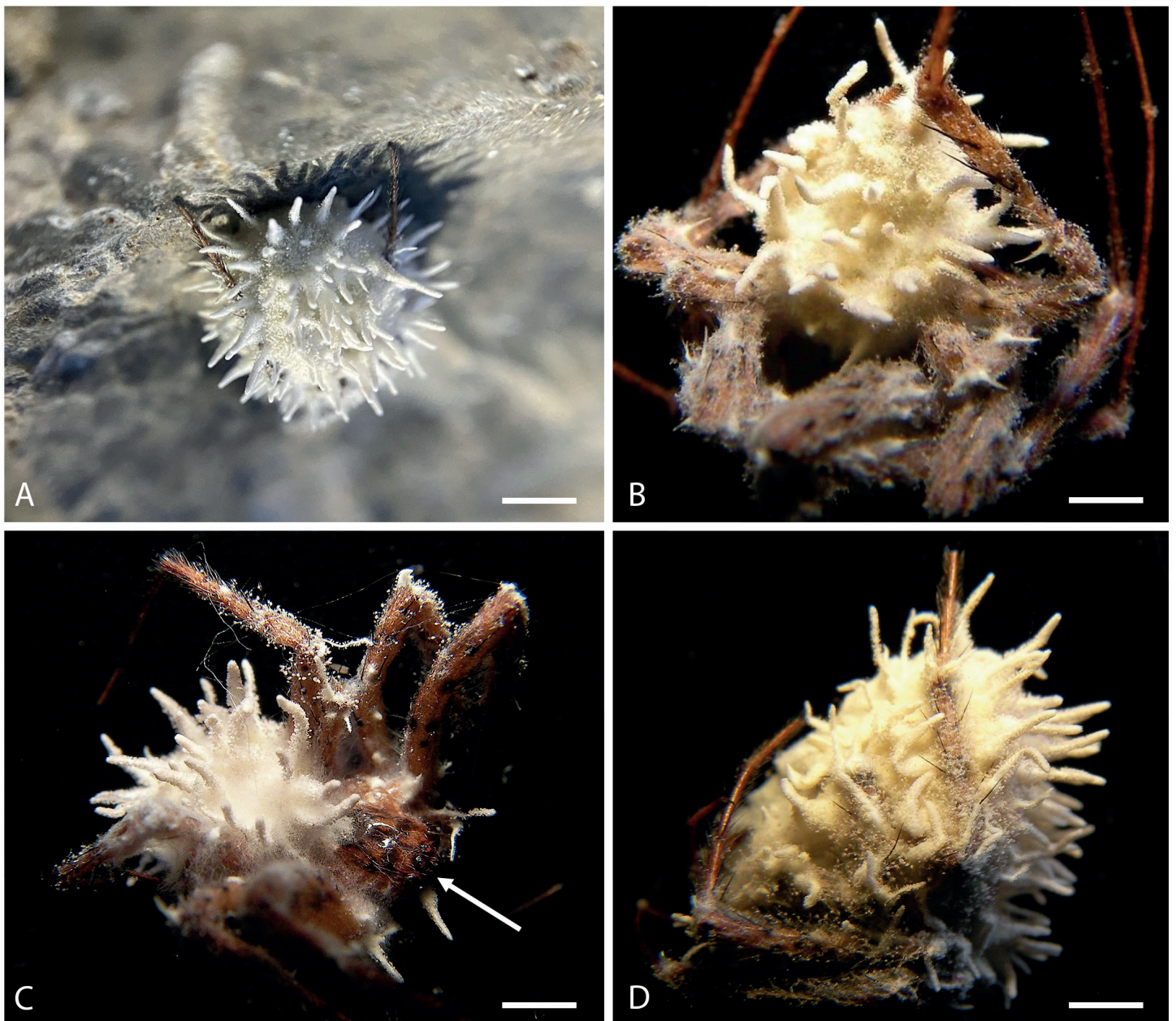

Fig. 6. *Gibellula attenboroughii* paratypes, on orb-weaving spider *Meta menardi*. **A.** Paratype IMI 507601, *in situ*, attached to cave wall above River Barran, with multiple white synnemata covering dorsal surface, Whitefathers' Caves, County Cavan, Republic of Ireland. **B.** After drying to show multiple creamish synnemata on ventral abdomen. **C.** Paratype IMI 507603, after drying; note the free conidiophores on the legs and the naked head region with prominent eyes arrow. **D.** Paratype IMI 507602, after drying, hanging from a thread above river, showing abundant synnematal production on both dorsal and ventral surfaces. Scale bars: A = 4 mm; B–D = 3 mm.

Undoubtedly, the aspergilliform head produces significantly more spores than the more open penicillioid form and this may relate to the host niche within the cave with *Metellina merianae* being exposed to a different microclimate – such as drier conditions and increased air movement, especially when the infected host dies around or outside the cave entrance – compared to *Meta menardi* occupying the deeper recesses of the cave.

Mycoparasites

Mycoparasites were also observed *in situ* on *Gibellula*-infected spiders within the cave systems; being described originally as "blobs" (T. Fogg, pers. comm., Fig. 10B). Culture isolates taken from them were identified as close to *Nodulisporium* (Fig. 10C, D); whilst others were found and subsequently isolated from dried specimens following examination under a stereoscopic microscope. These included engyodontium- and lecanicillium-like isolates, with the latter also producing a torrubiella-like morph in culture.
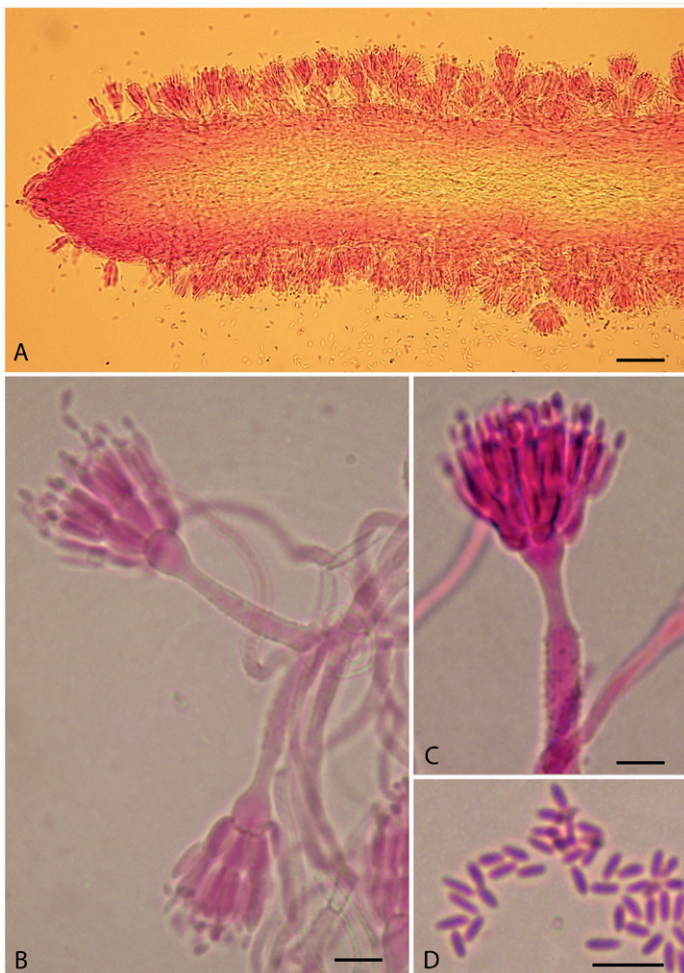
Fig. 7. *Gibellula attenboroughii*, micro-morphology on *Meta menardi*, paratype IMI 507601. **A.** Detail of upper part of synemma showing tapering apex and densely-crowded, penicillioid conidiophores (compare Fig. 2D). **B.** Conidiophores showing short, lightly-roughened stipes and simple penicillioid heads. **C.** Detail of conidiophore head with prominent, smooth neck region. **D.** Conidial chain. Scale bars: A = 50 µm; B–D = 10 µm.

Historical overview

The entomopathogenic mycobiota of the British Isles has never been studied systematically and most of the knowledge is based on the work of Tom Petch in the 1930s and 1940s, which was covered in his presidential address to the Yorkshire Naturalists' Union (1932a) and culminated in a list of "British entomogenous fungi" (Petch 1932b), with a subsequent revision (Petch 1948). Later, these lists were updated in a series of entomological publications based on new records which appeared in the literature, as well as in foray reports, but these were catalogued and indexed under the arthropod host rather than the fungal pathogen (Leatherdale 1958, 1962, 1966, 1970). This resulted in a final list of 106 fungal taxa of which 16 species were assigned to spider (*Araneae*) hosts, with only a single species of *Gibellula*, *G*. "*aranearum*", being recognised.

Many of the "post-Petch" fungal records on spiders listed by Leatherdale (1970) were based on reports by amateur collectors in the publications of local natural history societies in England; most notably, in East Anglia (Ellis 1956) and the Midlands (Evans 1967). There have been few publications since, with the exception of that by an amateur collector in the parochial newsletter *Shropshire Entomology* (McNeil 2012), which merited attention because of the "astronomical" number of specimens collected of: "A small but quite spectacular spider pathogen [*Gibellula cf. leiopus*] which produced 102 specimens from Lake Vyrnwy (mid-Wales) on a visit in December 2011" (McNeil 2012; see Fig. 5C). A similar number of specimens were also collected from the nearby Lake Bala (D. McNeil, pers. comm., 2012). These records are especially intriguing; not least, as it was in the depths of winter in a temperate mountainous area and *Gibellula* is a genus typically associated with spider hosts in the tropics and sub-tropics (Evans 1982, Evans & Samson 1987, Samson *et al*. 1988, Samson & Evans 1992, Evans 2013, Hughes *et al*. 2016, Shrestha *et al*. 2019, Kuephadungphan *et al*. 2020, 2022, Mendes-Pereira *et al*. 2023). The latter authors accepted 31 species in the genus – although, as stated earlier, significantly more are listed in Index Fungorum and MycoBank – many of which have been described in recent years from Asia and a far cry from the eight species listed in the original monograph on *Gibellula* (Samson & Evans 1992).

The earliest record of *Gibellula* in the British Isles would appear to be by Cooke (1892), who listed *Isaria arachnophila* under the common name, "European Spider Isaria", but without locality details. Petch (1931, 1932c) considered this to be a synonym of *Gibellula* "*aranearum*" and he confirmed British records of this species on spiders in the counties of Cambridgeshire, Hampshire, Somerset, Surrey and Worcestershire. In his revised list (Petch 1948), he also included multiple records from Norfolk and Suffolk where one of the hosts was identified as the red-legged spider, *Gongylidium rufipes* (*Linyphiidae*). Petch (1948) also listed *G. rufipes* as a host of *Torrubiella albolanata* in the Norfolk Broads with the purported asexual state described as *Cylindrophora aranearum* both of which had been described earlier as new species (Petch 1944). Later, Ellis (1956) expanded on his collections from Norfolk where this species was said to be common in marshes throughout the county making "upwards of ninety collections of this fungus regularly from May to October each year from 1942 to 1956"; adding that he had made recent collections in Bedfordshire and Berkshire. These collections from various broads in Norfolk have been examined in Herb K

and the host is always a small spider (2–3 mm) with distinctive reddish legs, matching the description of *Gongylidium rufipes*, with the ascomata buried in a white subiculum and an absence of *Gibellula* synnemata (Fig. 11A). The same host-pathogen association also appears to be common in mainland Europe, with Nyffeler & Hywel-Jones (2024) reporting the occurrence of *T. albolanata* in Denmark and illustrating fresh specimens showing yellow perithecia buried in a snow-white subiculum. Later collections made by Ellis from Cumbria and Devon were also examined but one of the Devon specimens is atypical, with the ascomata buried amongst lilac-coloured *Gibellula* synnemata rather than a *Granulomanus* subiculum. *Cylindrophora aranearum* has since been recognised as belonging to the genus *Granulomanus*, a synasexual morph of *Gibellula* (Samson & Evans 1977, de Hoog 1978, Samson *et al*. 1988). According to Index Fungorum and MycoBank, *Torrubiella albolanata* is a legitimate or current name; whilst *Cylindrophora aranearum* and *Granulomanus aranearum* are considered to be synonyms of *Gibellula arachnophila* by Index Fungorum. In contrast, MycoBank recognises *Granulomanus aranearum* as a legitimate species with *Cylindrophora aranearum* as a synonym.

Another *Torrubiella* species, *T. aranicida* also occurs on spiders in the Norfolk fens and, like *T. albolanata*, it lacks the *Gibellula* asexual morph (Petch 1948, Ellis 1956). In the Petch collection at RBG Kew, the prominent orange-coloured ascomata are scattered superficially on the body and legs of a large spider
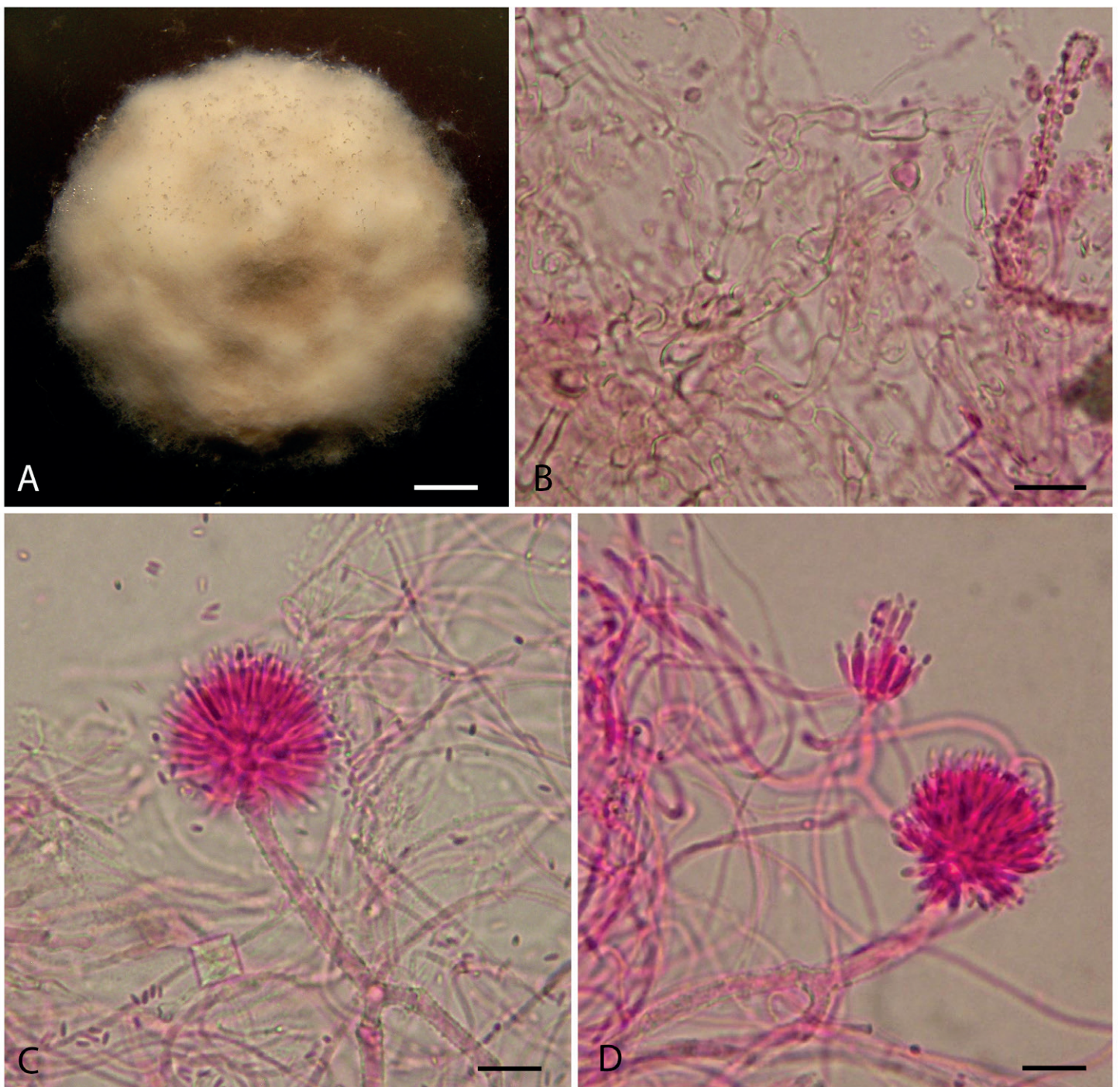

Fig. 8. *Gibellula attenboroughii*, paratype IMI 507601, *ex Meta menardi, in vitro*. **A.** Colony after 3 mo on PCA with aspergilliform conidiophores produced directly from the mycelium. **B.** Chlamydospore-like structures and verrucose hyphae from the subiculum. **C.** Aspergilliform conidiophore arising from the mycelium. **D.** Aspergilliform and penicillioid conidiogenous heads on the mycelium. Scale bars: A = 3 mm; B–D = 15 μm.

(10–12 mm) collected "under hanging moss on a cliff face" in Yorkshire (Petch 1948; see Fig. 11C): a significantly bigger spider than *Gongylidium rufipes* (2–3 mm), the host of *T. albolanata* (Fig. 11A). The latter species has also been recorded on another *Linyphiidae* spider, *Leptorhoptrum robustum* from sewage filter beds in Warwickshire (Duffy 1997). And, more recently, a species close to *T. aranicida* has been collected on the funnel-web spider, *Coelotes atropos* (*Amaurobiidae*), under a log in Devon (G. Lyons, pers. comm. 2023; IMI 507605). This large spider (9–10 mm) has only traces of the *Granulomanus* synasexual morph on the body, which is characterised by the translucent to pale cream ascomata (Fig. 11F), which turn a yellow orange colour when dried (Fig. 11E). Petch (1944) noted this colour change, describing the fresh ascomata as "pellucid, but dull orange when dry". In the type diagnosis of *T. aranicida* – on the spider *Aranea lucifuga* (= *Gnaphosa lucifuga*, *Gnaphosidae*) from France – the ascomata are described as "ochracea vel ochracea-aurantiaca" or yellowish-brown to orange (Boudier 1885; see Fig. 11D). Later, Boudier (1887) returned to the same site but earlier in the season and reported an asexual morph on the same spider host which he described and illustrated as *Isaria cuneispora*

sp. nov. (Fig. 11B). Petch (1944) considered this to be a species of *Cylindrophora* and, possibly, *C. aranearum* as associated with *Torrubiella albolanata*: now accepted as a synonym of *Granulomanus* (de Hoog 1978). Although it would appear that the *Gibellula* morph is rarely or never produced in either *Torrubiella albolanata* or *T. aranicida*, the genus *Gibellula* is now considered to be the legitimate generic name in the one fungus-one name classification (Kepler *et al*. 2017), with *Granulomanus* and, therefore, *Torrubiella* as synonyms.

In accordance with the *Code* protocol, the following new combinations are proposed:

Gibellula albolanata (Petch) H.C. Evans, **comb. nov.** MycoBank MB 856522.
Synonyms: *Torrubiella albolanata* Petch, *Trans. Brit. Mycol. Soc.* **27**: 85. 1944.
Cylindrophora aranearum Petch, *Trans. Brit. Mycol. Soc.* **27**: 85. 1944.
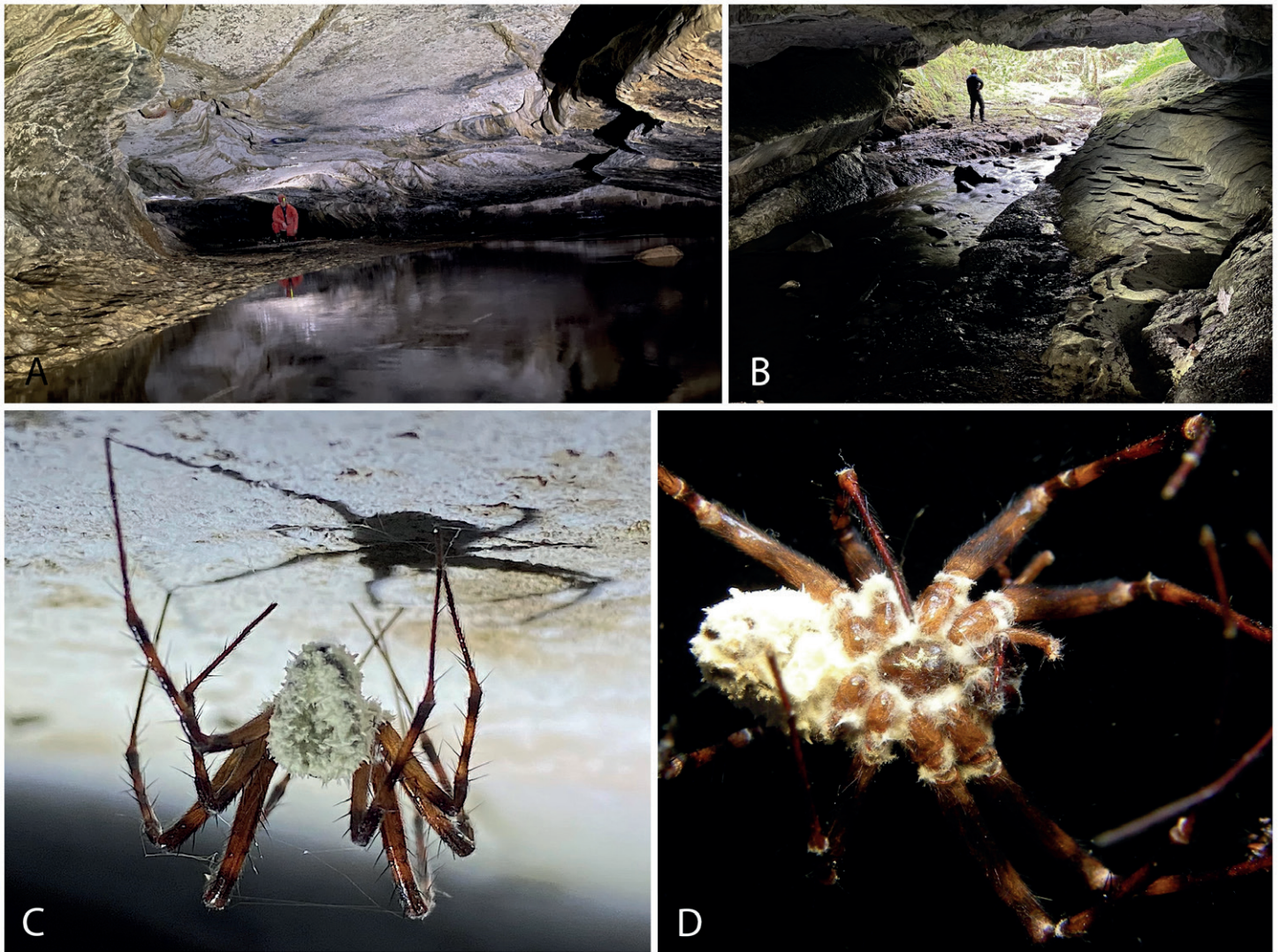*Granulomanus aranearum* (Petch) de Hoog & Samson, *Persoonia* **10**: 70. 1978.

Fig. 9. *Gibellula attenboroughii*, habitat and paratype IMI 507598, on *Meta menardi*. **A.** Whitefathers' Caves, showing the dark zone above the River Barran, County Cavan, Republic of Ireland. **B.** Entrance and twilight zone. **C.** Infected spider *in situ*, on cave ceiling, showing early infection with immature synnemata on compact, white subiculum, the specimen was found immediately above the figure in the centre. **D.** Dried specimen, showing creamish-yellow subiculum covering ventral abdomen. Scale bars: C = 0.5 mm; D = 0.25 mm.

Gibellula aranicida (Boud.) H.C. Evans, **comb. nov.** MycoBank MB 856523.
Synonyms: *Torrubiella aranicida* Boud., *Revue mycol.*, *Toulouse* **7**: 227. 1885.
Isaria cuneispora Boud., *Revue mycol.*, *Toulouse* **9**: 158. 1887.

DISCUSSION

Spiders play a key role in ecosystem functioning (Nyffeler & Birkhofer 2017) and, therefore, their parasites and pathogens should warrant especial attention. However, until recently, their associated mycobiota – the entomogenous, entomopathogenic or, more accurately, araneopathogenic fungi – has largely been ignored. Evans (2013) discussed this "no-man's land" between mycologists and arachnologists where, historically, there has been little or no attempt by either group of taxonomists to interpret host-pathogen interactions and to identify both the organisms involved. In the last decade, this situation has changed and more emphasis is now being given to host identification and the ecological significance of these fungi, most notably, in relation to the genus *Gibellula* (Hughes *et al*. 2016, Shrestha *et al*. 2019, Kuephadungphan *et al*. 2020, 2022, Durkin *et al*. 2021, Mendes-Pereira *et al*. 2023, Nyffeler & Hywel-Jones 2024).

Within the species in the genus *Gibellula* described, thus far, the greater majority produce only the asexual morph. In a few species, however, only the sexual morph and the *Granulomanus* synasexual morph are found. Within the small sample size recorded here from the British Isles, all three morphs are represented: as, for example, in *Gibellula albolanata* which produces perithecia embedded in a subiculum of *Granulomanus* and, *G. aranicida* in which ascospores appear to be the dominant spore-dispersal form; contrasting with *G. attenboroughii* where spore density is maximised in the aspergilliform *Gibellula* heads. The evolutionary pressures to either limit or optimise spore production – or, indeed, to opt for asexual *vs* sexual reproduction – can only be speculated upon, as is the form and function of the *Granulomanus* synasexual morph. The diversity of the *Gibellula* morph was highlighted and illustrated, as "Variations on a theme", by Evans & Samson (1987). Since then, the number of described species has burgeoned, as has the range of *Gibellula* forms (Samson & Evans 1992, Evans 2013, Shrestha *et al*. 2019,
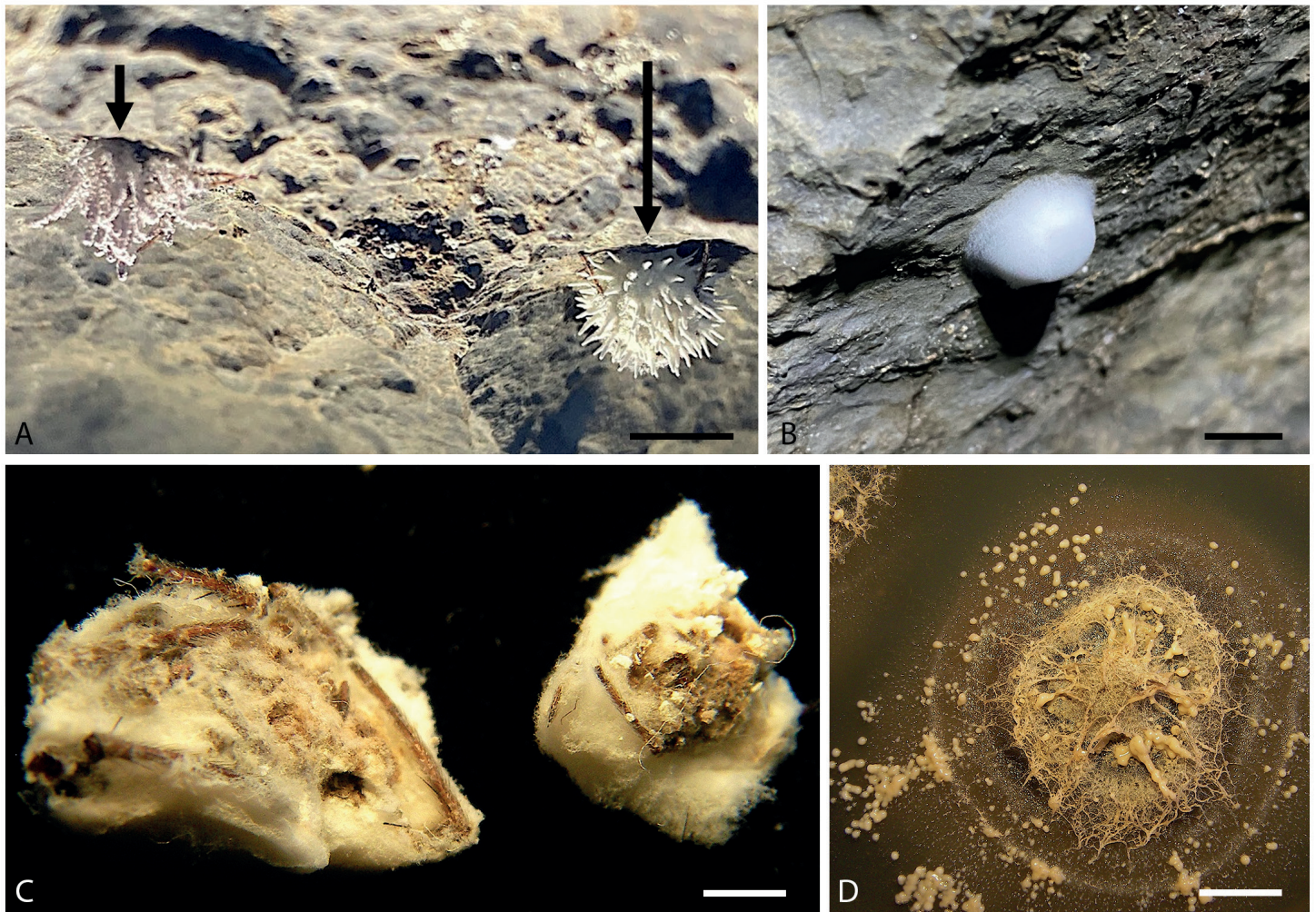

Fig. 10. *Gibellula attenboroughii in situ* on orb spiders and mycoparasite macro-morphology. **A.** On orb spiders, *Metellina merianae* (left, short arrow), and *Meta menardi* (right, long arrow), on cave ceiling, Whitefathers' Caves; showing differences in synnematal morphology. **B.** Same site, with *Meta menardi* completely overgrown by nodulosporium-like mycoparasite, forming a 'slimy blob'. **C.** Dried specimens showing the larger *Meta menardi* on left and smaller *Metellina merianae* on right. **D.** Mycoparasite after 1 mo on PCA, forming slimy colonies. Scale bars: A, B = 5 mm; C = 2 mm; D = 10 mm.

Kuephadungphan *et al.* 2020, 2022, Mendes-Pereira *et al.* 2023). Doubtless, there are many more species to be found with equally complex and bizarre morphologies.

With the benefit of host identification, it has become possible to better understand the spider-pathogen interactions and, crucially, to assess the impact of infection on host behaviour. Earlier studies on ant-fungal interactions led to the concept of zombie-ant fungi (Evans 2002, Evans *et al.* 2011, Bekker *et al.* 2014, Hughes *et al.* 2016, Araújo *et al.* 2018, Araújo & Hughes 2019). Hughes *et al.* (2016) provided the first circumstantial evidence that infected spiders also change behaviour and move from their characteristic concealed niches to die in elevated or freely-exposed situations, typically, on the undersides of

leaves in the understorey of tropical forests. This behavioural manipulation has since been reported by Arruda *et al.* (2021), Durkin *et al.* (2021) and Mendes-Pereira *et al.* (2022) for *Gibellula*-infected spiders in the humid tropics and sub-tropics. Here, we posit that temperate cave spiders also alter their behaviour when infected by *Gibellula* species facilitating the release and dispersal of fungal spores and, in effect, replicating the manipulation of ants by *Ophiocordyceps* species.

Finally, the data unearthed during the herbarium and literature searches indicate that there is a hidden diversity in the British Isles and that many more species of *Gibellula* remain to be discovered. Moreover, the ecological impact on their spider hosts could be significant with epizootics being reported in
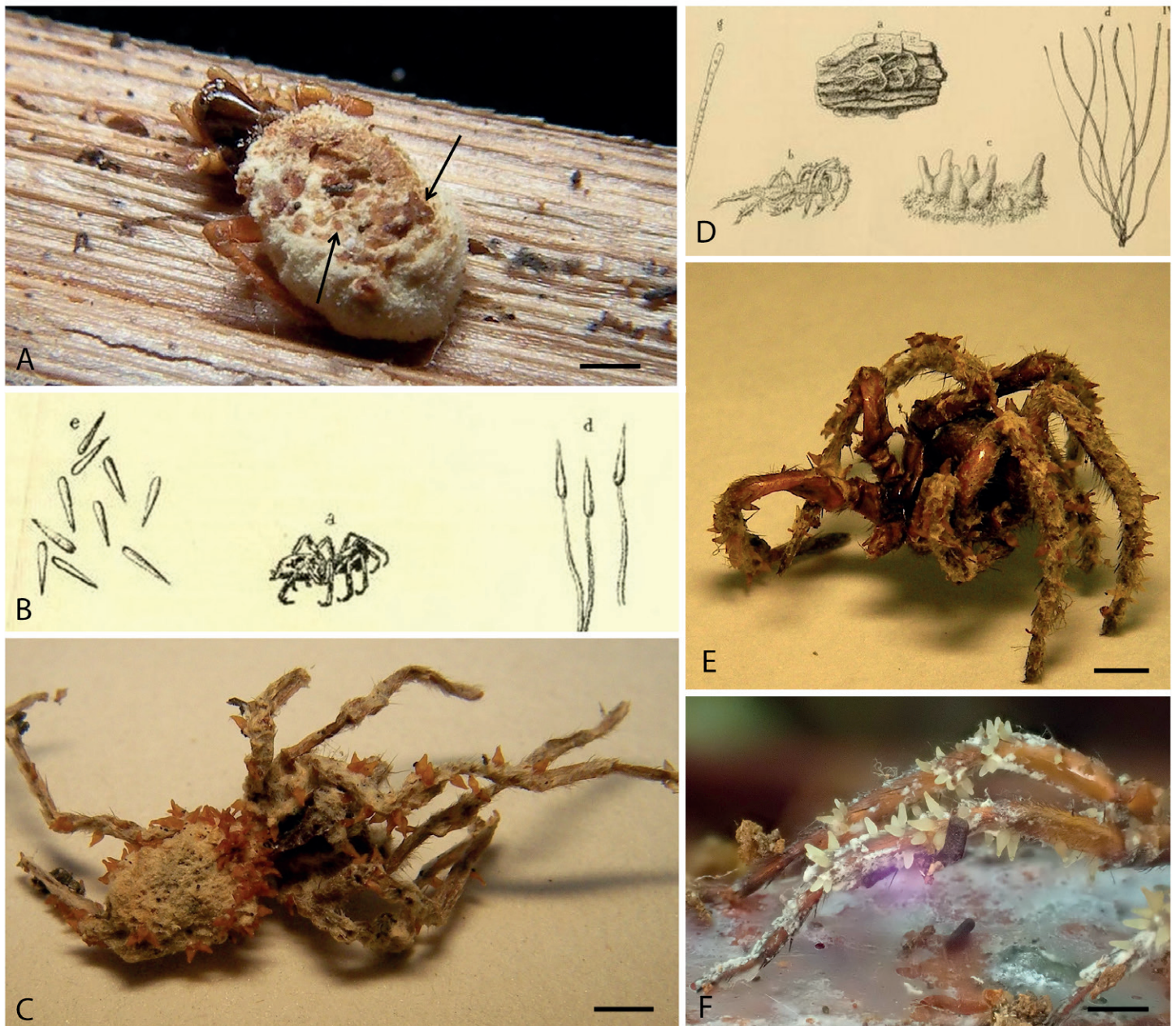

Fig. 11. New *Gibellula* combinations. **A.** *Gibellula albolanata comb. nov.*, type of *Torrubiella albolanata* on the red-legged spider, *Gongylidium rufipes* (*Linyphiidae*), fen sedge, Norfolk, 1942 (*ex* Herb K), showing the yellow ascomata (arrow) embedded in a white subiculum. **B.** Type illustration of *Isaria cuneispora* on *Gnaphosa lucifuga* (*Gnaphosidae*), from France (Boudier 1887), showing the *Granulomanus* synasexual morph of *G. albolanata*. **C.** *Gibellula aranicida comb. nov.*, labelled as *Torrubiella aranicida*, from Yorkshire, 1936 (*ex* Petch collection, Herb K), showing the yellow-orange ascomata scattered on the spider legs and body. **D.** Type illustration of *Torrubiella aranicida*, on *Gnaphosa lucifuga*, France (Boudier 1885). **E, F.** *Gibellula aranicida* on the funnel-web spider, *Coelotes atropos* (*Amaurobiidae*) collected by G. Lyon, under a log, Devon, 2023, dried fungarium specimen, IMI 507605; note the scattered yellow ascomata. **F.** Close-up of the spider legs taken *in situ*, showing the white or pellucid ascomata in the fresh specimen (image, G. Lyon), as described by Petch (1944). Scale bars: A = 1 mm; C, E = 2 mm; F = 0.6 mm.

Norfolk and Wales (Ellis 1956, McNeil 2012) – similar to those recorded on spiders in the humid tropics (Evans 1974, 1982, Samson & Evans 1973, 1977, Mendes-Pereira *et al.* 2022, 2023) – and these have now been analysed in detail by Nyffeler & Hywel-Jones (2024). Thus, their role in spider-population dynamics warrants further study, as does the metabolites they produce which enable them to exploit such a highly-specific ecological niche.

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