Multi-locus phylogeny unmasks hidden species within the specialised spider-parasitic fungus, *Gibellula* (*Hypocreales, Cordycipitaceae*) in Thailand

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Abstract: Over 80 species of hypocrealean fungi are reported as pathogens of spiders and harvestmen. Among these fungi, the genus *Gibellula* is highly regarded as a specialised spider-killer that has never been reported to infect other arthropods. While more than 20 species of *Gibellula* are known, few attempts to identify the infected spiders have been made despite the fact that the host specificity can help identify the fungal species. Here, we morphologically describe and illustrate eight new species of *Gibellula* and three new records from Thailand of known species along with the multi-gene phylogeny that clearly showed the segregation among the proposed species. Examination of the *Gibellula*-infected spider hosts identified *Oxyopidae*, *Uloboridae* and, for the first time, the ant-mimicking genus *Myrmarachne*.

Key words: araneogenous fungus, *Gibellula,* new taxa, spider predator.
Taxonomic novelties: New species: *Gibellula brevistipitata* Kuephadungphan, Tasanathai & Luangsa-ard, *G. longicaudata* Tasanathai, Kuephadungphan & Luangsa-ard, *G. longispora* Kuephadungphan & Luangsa-ard, *G. nigelii* Kuephadungphan, Tasanathai & Luangsa-ard, *G. parvula* Kuephadungphan, Tasanathai & Luangsa-ard, *G. pilosa* Kuephadungphan, Tasanathai & Luangsa-ard*, G. solita* Kuephadungphan, Tasanathai & Luangsa-ard, *G. trimorpha* Tasanathai, Khonsanit, Kuephadungphan & Luangsa-ard.

INTRODUCTION

Spiders are cosmopolitan carnivorous arthropods that play a pivotal role in maintaining the balance of ecological systems (Lee & Kim 2001) by killing 400–800 million tons of insects every year (Nyffeler & Birkhofer 2017). Nevertheless, they are predated by other animals including spiders themselves (Foelix 2011). Fungi are important, but neglected natural enemies of spiders (Evans 2013) as pathogenic fungi can be confused with saprophytic fungi on spider cadavers. Pathogenic fungi can establish dense hyphal networks that hinder species identification of the spider host. Nonetheless, *Araneomorphae* and *Mygalomorphae* spiders frequently appear to be parasitised by hypocrealean fungi (*Ascomycota*), in which over 80 species from 13 genera are reported (Shrestha *et al.* 2019).

Among the hypocrealean fungi, *Gibellula* is well-known as a pathogenic genus of spiders, but has never been found infecting any other arthropod. This genus has a very long taxonomic history. The synonymising of *G. pulchra* (the type species) with *G. leiopus*, limited access to certain holotypes, a lack of holotype sequences as well as living cultures, have created nomenclatural and taxonomic complications which unavoidably created confusion and difficulty in species identification. According to Shrestha *et al.* (2019) and our previous reports on the five new species of *Gibellula* (Kuephadungphan *et al.* 2019, 2020), there are currently 21 species accepted in this genus. *Gibellula* can be identified by producing aspergillus-like conidiophores on synnemata with the appearance

of lupines growing on the spider host. For the species that produce penicillium-like conidiophores such as *G. leiopus*, *G. clavulifera* and *G. scorpioides*, they can be distinguished from others by forming tufted synnemata fully covered with very short conidiophores. Some species possess unique distinguishing morphology, including *G. mainsii* forming mononematous conidiophores (Samson & Evans 1992), *G. brunnea* producing synnemata that widen into globose to pyriform fertile areas with pale brown, long, slender sterile tips (Samson & Evans 1992) and *G. alata* having wing-like synnemata (Petch 1932). However, other species are indistinguishable based solely on the macroscopic features. For instance, *G. cebrennini* can be discriminated from *G. fusiformispora* only by having much longer conidiophores (Kuephadungphan *et al.* 2020). As *Gibellula* is known to be linked with a *Torrubiella* sexual morph, it may occur on a spider host either with or without the presence of *Gibellula*. *Gibellula cebrennini* is an example of a species that can be found producing only *Torrubiella* perithecia on spider hosts (Kuephadungphan *et al.* 2020). *Torrubiella* was proven by phylogenetic analyses to be a polyphyletic group distributed across several genera, not only within the *Cordycipitaceae* but also the *Clavicipitaceae* (Sung *et al.* 2007, Johnson *et al.* 2009, Kepler *et al.* 2017). Considering only the hypocrealean fungi that infect spiders, *Akanthomyces* and *Hevansia* are also known to be connected with a *Torrubiella* sexual morph besides *Gibellula* (Kepler *et al.* 2017, Mongkolsamrit *et al.* 2018). To identify such fungi bearing only sexual morphs to the genus or species ranks, molecular phylogenetic analysis is highly recommended.

Thus far, 12 spider families consisting of *Agelenidae, Anyphaenidae*, *Araneidae*, *Corinnidae*, *Deinopidae*, *Linyphiidae*, *Pholcidae*, *Salticidae*, *Sparassidae*, *Theridiidae*, *Thomisidae* and *Zodariidae* have been reported as hosts of *Gibellula* (Bishop 1990, Hughes *et al*. 2016, Savić *et al*. 2016, Kuephadungphan *et al.* 2020). Our previous report suggested host-specificity in certain species of *Gibellula* (Kuephadungphan *et al*. 2020). Therein, *G. cebrennini* was found only on *Cebrenninus cf. magnus* whereas *G. pigmentosinum* and *G. scorpioides* appeared to be highly specific to *Storenomorpha* sp. (*Zodariidae*) and *Portia* sp. (*Salticidae*), respectively.

In the exploration of the diversity of the spider-parasitic fungi in Thailand, fungi tentatively identified as *Gibellula* spp. deposited in the BIOTEC Bangkok Herbarium (BBH) and the BIOTEC Culture Collection (BCC), Thailand, were selected and taxonomically studied using an integrative approach, which revealed the existence of eight new and three known taxa within the genus. The new species described herein are illustrated morphologically and phylogenetically along with the identification of their spider hosts to better understand the spider-fungus relationship.

MATERIALS AND METHODS

Fungal materials and isolation

Spiders parasitised by *Gibellula* spp. were collected from various locations throughout Thailand. The living leaves with spider cadavers attached on the underside were picked carefully, kept individually in plastic boxes and transported to the laboratory for isolation. The isolation was performed immediately after returning specimens to the laboratory. An agar plug of potato dextrose agar (PDA; fresh diced potato 200 g, dextrose 20 g, agar 15 g, in 1 L distilled water) was cut into small pieces (approximately 0.1 mm^3) using a sterile fine needle and was gently swiped over the spores located on the conidiophores along the synnemata and then placed on a PDA plate. Plates were incubated at 25 °C, roughly 12:12 light-dark cycle, and examined daily for conidial germination and also for fungal contaminants. Pure cultures were isolated onto fresh PDA plates by hyphal tip isolation. These were then allowed to grow for 6–8 wk before preparation for storage. Daily observation of conidial germination as well as fungal contamination is important. The fresh fungal specimens are stored at 4 °C until the cultures could be obtained. Notably, the longer the specimen is kept, the lesser is the chance a culture can be made. After the pure cultures of each fungus could be established onto PDA, the fungal specimens were dried at 55 °C for 24 h. All living cultures and dried specimens were then deposited in the BCC and BBH, respectively.

Morphological characterisation

Morphological characterisation of invertebrate-pathogenic fungi depends primarily on the presence of structures associated with asexual and sexual reproductive morphs on the host and the observation should be conducted at various levels from the naked eye via a dissecting microscope and compound microscope. Macroscopic features of asexual morph involve noting the number, colour, shape and length of synnemata as well as the colour of mycelia covering the host while microscopic characters involve the shape and size of vesicles, metulae, phialides, conidial heads, conidia and conidiophores including the arrangement

of conidiophores on the surface of synnemata. For the sexual morph the shapes and sizes of perithecia, asci and ascopores are noted. The fungus materials, such as phialides and conidia from the asexual morph and perithecia, asci and ascospores of the sexual morph were mounted in lactophenol cotton blue solution and measured using a compound microscope (Olympus SZ31, Olympus Corporation, Japan). Up to 10 perithecia, and 20–40 asci, part-spores, phialides and conidia were measured, and the amount of variability was calculated using standard deviation (with absolute minima and maxima in brackets) and average +/– standard deviation values. These were photographed by using an Olympus BX51 (Olympus Corporation, Japan). PDA cultures were studied for important morphological characters such as conidia and phialides.

Identification of spider hosts

To identify the spider hosts, the World Spider Catalog (2021) (https://wsc.nmbe.ch/) as well as an expert on spider taxonomy were employed. As a spider host is covered with fungi allowing only certain parts, such as the legs and cephalic region to be seen, variation in characteristics of legs and accessories such as setae, spines, and tarsal claws on legs and variation in characteristics of eyes among taxa are useful for identification. Accordingly, we used not only the necessary identification guides, *e.g.* Deeleman-Reinhold (2001), Jocqué & Dippenaar-Schoeman (2007), but also literature relating to morphological characteristics of legs, for example Deeleman-Reinhold (2009), Wolff & Gorb (2012), Wolff *et al*. (2013), Labarque *et al*. (2017), and Ramírez & Michalik (2019), and literature relating to characteristics of eyes, for example Morehouse *et al*. (2017), and Long (2021). The aforementioned literature substantially support identification of spiders.

Molecular phylogenetic analyses

Fungal mycelia were scraped out from the surface of fungal colonies actively growing on PDA and DNA subsequently extracted following the protocol previously described by Thanakitpipattana *et al.* (2020). Five nuclear DNA regions were PCR-amplified including the internal transcribed spacer regions (ITS), the nuclear large subunit (LSU) of the ribosomal DNA, translation elongation factor 1-alpha (*TEF1*), and the largest and second-largest subunits of RNA polymerase II (*RPB1* and *RPB2*). PCR reactions were done in 25 μL volumes consisting of 1× Dream *Taq* Buffer (containing 2.5 mM MgCl$_2$), 0.4 M betaine, 200 μM dNTP mix, 0.5 μM of each primer, 1 U Dream *Taq* DNA polymerase (Thermo Scientific, US) and 50 ng of DNA template.

DNA sequences were assembled using BioEdit v. 7.2.5 (Hall 1999). The alignment was conducted using MUSCLE v. 3.6 software (Edgar 2004) and manually corrected to minimise gaps. The final sequence alignment of 4 219 bps of the combined dataset was used for analyses using maximum likelihood and Bayesian inference. Maximum likelihood-based phylogeny was performed with RAxML-HPC2 on XSEDE in CIPRES Science Gateway v. 3.3 (https://www.phylo.org/) using a GTRCAT model of evolution with 1 000 bootstrap replicates (Stamatakis 2014). Bayesian analysis was performed with MrBayes on XSEDE v. 3.2.7a using the best fit models of evolution (SYM+G) selected by AIC in MrModeltest v. 2.2 (Nylander 2004). Four Markov chains were run for 5 M generations and trees were sampled every 100 generations. A burn-in value of 25 % was set that discarded the first 2 500 generations.

Estimation of divergence between closely related species

P-distances were calculated between sequences using MEGA X (Kumar *et al.* 2018). P-distances were averaged between putative species. Other closely related known taxa were included in the analysis to evaluate whether the divergence among putatively new clades would support their status as distinct species. The p-distance between *G. cebrennini* and *G. fusiformispora*, two sister species proposed in a previous taxonomic work on *Gibellula* (Kuephadungphan *et al.* 2020), was used as a threshold to discriminate between closely related species.

RESULTS

Molecular phylogeny

According to the phylogenetic tree inferred from multiple loci of 47 taxa (Fig. 1 and Table 1), seven genera including *Akanthomyces*, *Beauveria*, *Blackwellomyces*, *Cordyceps*, *Gibellula*, *Hevansia*, and *Engyodontium* (as outgroup) formed monophyletic clades that corresponded to the phylogeny-based classification of the *Cordycipitaceae* contributed by Kepler *et al.* (2017), Kuephadungphan *et al.* (2019, 2020) and Wang *et al.* (2020). All taxa pertaining to this study were distributed in the strongly supported *Gibellula* clade (100 %), which is regarded as a sister lineage to *Hevansia* – another well-known specialised spider-parasitic genus along with *Gibellula*. This multilocus-based phylogeny clearly supports the segregation of three new records of known species, eight new taxa, and seven known species within the genus. New records in Thailand are reported for *G. dimorpha*, *G. pulchra* and *G. unica*. *Gibellula dimorpha* formed a strongly supported clade with *Gibellula trimorpha*, a new species. *Gibellula brevistipitata*, *G. longicaudata*, *G. longispora*, *G. nigelii*, *G. parvula* and *G. pilosa* were recognised as new taxa with strong bootstrap supports for their phylogenetic placements.

Analyses of divergence

We calculated the p-distances between sequences constituting putative new species (*G. brevistipitata*, *G. parvula*, *G. pilosa*, *G. solita* and *G. trimorpha*), new records for Thailand (*G. dimorpha*, *G. pulchra* and *G. unica*) and between closely related known taxa in their respective clades (Fig. 1). The p-distance between *G. cebrennini* and *G. fusiformispora* (0.014 ± 0.003; ~ 1.4 % divergence) was used as a threshold of divergence between two closely related cryptic species of *Gibellula*.

Figure 2 shows the distribution of p-distances between putative new and closely related *Gibellula* species. The p-distance analysis supports *G. dimorpha*, *G. trimorpha*, *G. parvula*, *G. pigmentosinum*, *G. longispora*, *G. brevistipitata*, *G. pilosa*, *G. solita*, *G. unica*, *G. pulchra*, and *G. nigelii* as distinct species. These findings illustrate the cryptic trends in cordycipitoid morphological evolution as demonstrated in other works (Khonsanit *et al.* 2020, Kobmoo *et al.* 2019, 2021, Mongkolsamrit *et al.* 2018, 2020, Wang *et al.* 2020).

Taxonomy

Gibellula brevistipitata Kuephadungphan, Tasanathai & Luangsa-ard, ***sp. nov.*** MycoBank MB 841093. Fig. 3.

Etymology: Refers to the short stipes of synnemata.

Typus: **Thailand**, Buri Ram Province, Dong Yai Wildlife Sanctuary, Pong Kao Nature Trail, on *Thomisidae* attached to the underside of a dicot leaf, 11 Dec. 2010, *K. Tasanathai, P. Srikitikulchai, A. Khonsanit, K. Sansatchanon, W. Noisripoom, A. Saksrikrom, B. Saracam* & *S. Mongkolsamrit* (**holotype** BBH 38549, culture ex-type BCC 45580). GenBank: ITS = OK040729, LSU = OK040706, *TEF1* = OK040697, *RPB1* = OK040715.

Spider covered by a yellowish-white mycelial mat (Fig. 3A). *Synnemata* cylindrical, multiple, brownish white, becoming brown towards the tip, approximately 2 mm long, 200 µm wide, terminal part ovoid tapering towards the end, 175 µm wide (Fig. 3B). *Conidiophores* arising along the entire length of the synnemata, absent on the swollen tip, occasionally from a network of hyphae loosely attached to the host, crowded, septa conspicuous, distinctly roughened, (47.5–)58–100(–115) × 6–8(–8.5) µm, narrowing to a slender apex, and terminating in a swollen vesicle (Fig. 3C–D). *Vesicles* spherical to broadly obovoid, (7.5–)8–9(–10) µm diam (Fig. 3E). *Metulae* borne on vesicle, broadly obovoid or broadly ellipsoid, (7–)7.5–9.5(–10.5) × 5–7 µm, bearing multiple phialides (Fig. 3E). *Phialides* cylindrical to narrowly clavate, often apically thickened, (7–)7.5–9(–10) × 2–2.5(–3) µm (Fig. 3E). A vesicle together with metulae and phialides forming a spherical conidial head, (33–)34.5–37.5(–40) µm diam (Fig. 3E). *Conidia* ellipsoid or narrowly almond-shaped, (3–)3.5–4(–4.5) × 1.5–2 µm (Fig. 3F). Sexual morph and *Granulomanus* synasexual morph not observed.

Culture characteristics: Colonies on PDA attaining a diam of 2 cm in 28 d at 25 °C, white, floccose; reverse cream, becoming light brown with age at the centre (Fig. 3G). Sporulation not observed in culture.

Gibellula dimorpha Tzean, L.S. Hsieh & W.J. Wu, Mycol. Res. 102: 1350. 1998. Fig. 4.

Spider host covered by yellowish white to cream mycelial mat. *Synnema* solitary, brownish white (Fig. 4A–B). *Conidiophores* 100–175 × 5–7.5 µm. *Conidial heads* spherical, (32–)33–45(–50) µm diam (Fig. 4D). *Vesicles* globose to subglobose, 5–6(–7) µm bearing multiple metulae (Fig. 4D). *Metulae* broadly obovoid, 5–7 × 4–5 µm (Fig. 4D). *Phialides* borne on metulae, cylindrical to narrow clavate with a short neck, hyaline, 6.5–8.5 × 1.5–3 µm (Fig. 4D). *Conidia* hyaline, broadly fusiform, smooth, single or in chains, 3–5 × 1.5–2 µm (Fig. 4E). *Granulomanous* synasexual morph present, well differentiated, forming aspergillus-like conidiophores (Fig. 4C). *Conidiophores* cylindrical, septate, verrucose, (70–)94–144.5(–157.5) × 7.5–10(–11) µm (Fig. 4C, 4F). *Vesicles* well developed, often absent, globose to subglobose, smooth-walled, (4.5–)5–7 µm (Fig. 4G). Multiple metulae borne on a vesicle, occasionally hardly developed, broadly obovoid, smooth-walled, 6–7 × 4–5.5(–6) µm (Fig. 4G). *Phialides* narrowly clavate to irregularly shaped, apically thickened often with a short neck, or cylindrical bearing 1–3 denticles at the apices, smooth-walled (Fig. 4G), or irregularly shaped, polyblastic, distinctly verrucose, (6–)7.5–10(–11) × 2.5–3.5(–4) µm (Fig. 4H). *Conidia* filiform, smooth, hyaline, 10–15 × 1–1.5 µm (Fig. 4I). *Conidial head* spherical, formed by a vesicle,
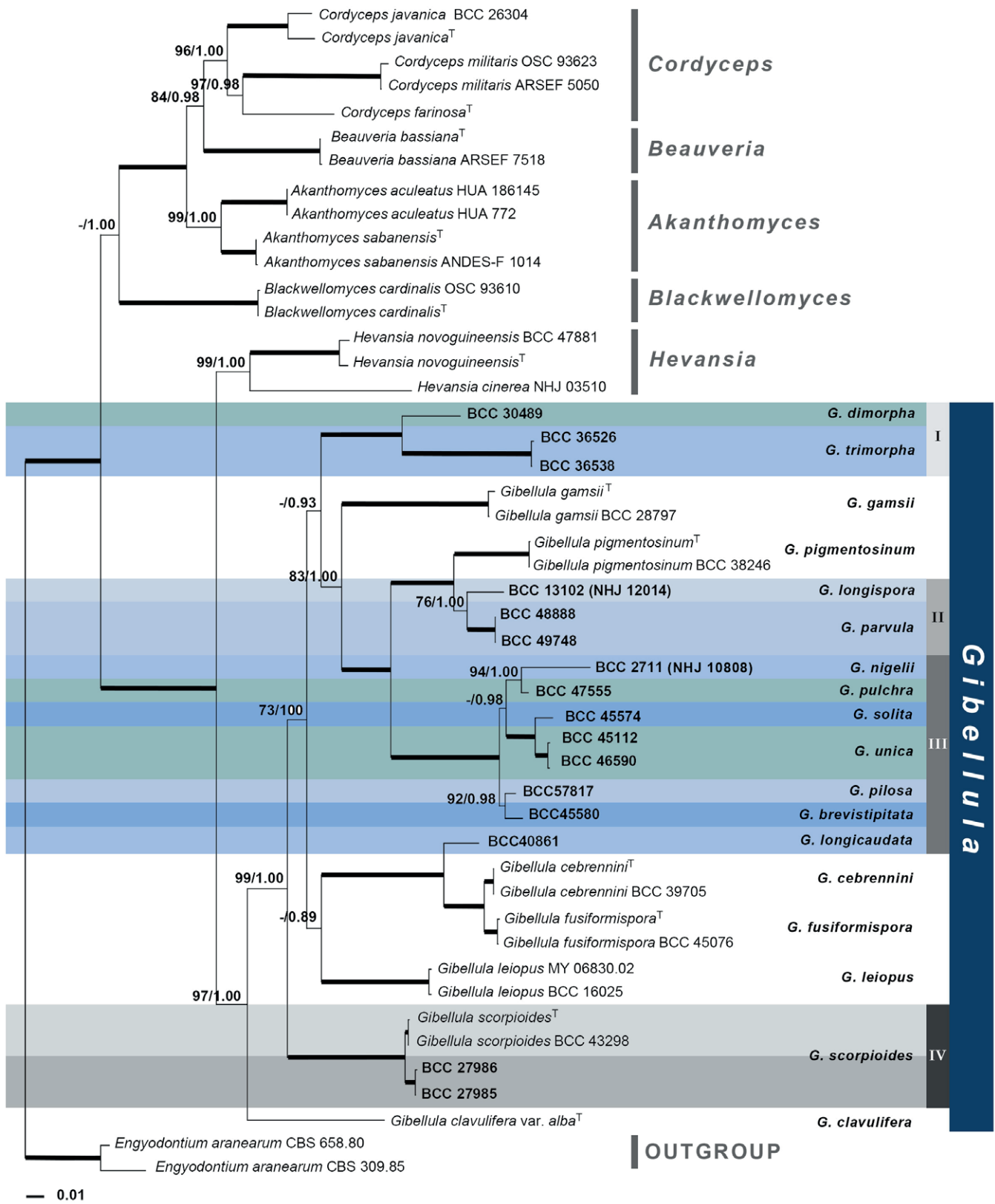
Fig. 1. RAxML tree based on the concatenated five gene datasets (ITS, LSU, *TEF1, RPB1* and *RPB2*) showing the relationship among *Gibellula* and related genera. Bootstrap proportions/ Bayesian posterior probabilities ≥ 50 % are provided above corresponding nodes; nodes with 100 % support are shown as thick lines. The ex-type strains are marked with a superscript T ([T]) and the isolates reported in this study are bold. All proposed species are highlighted in grey.

several metulae and phialides, (37–)39–56(–59) µm (Fig. 4G–H). *Perithecia* produced on the mycelial mat covering the body of the spider, absent on its legs, superficial with mycelia covering the bottom two-thirds of the perithecium, ovoid narrowing towards the ostiole, reddish-brown, (640–)645–691.5(–700) × (280–)285–310 µm (Fig. 4J–K). *Asci* cylindrical, up to 688 µm long, (5–)6–7(–8) µm wide. *Asci caps*, (4–)4.5–6(–7) × (6.5–)7–8(–8.5) µm (Fig. 4L). *Ascospores* filiform, multiseptate, arranged in parallel rows, breaking into bacilliform part-spores, (5–)6–10(–12) × 1.5–2 µm (Fig. 4M).
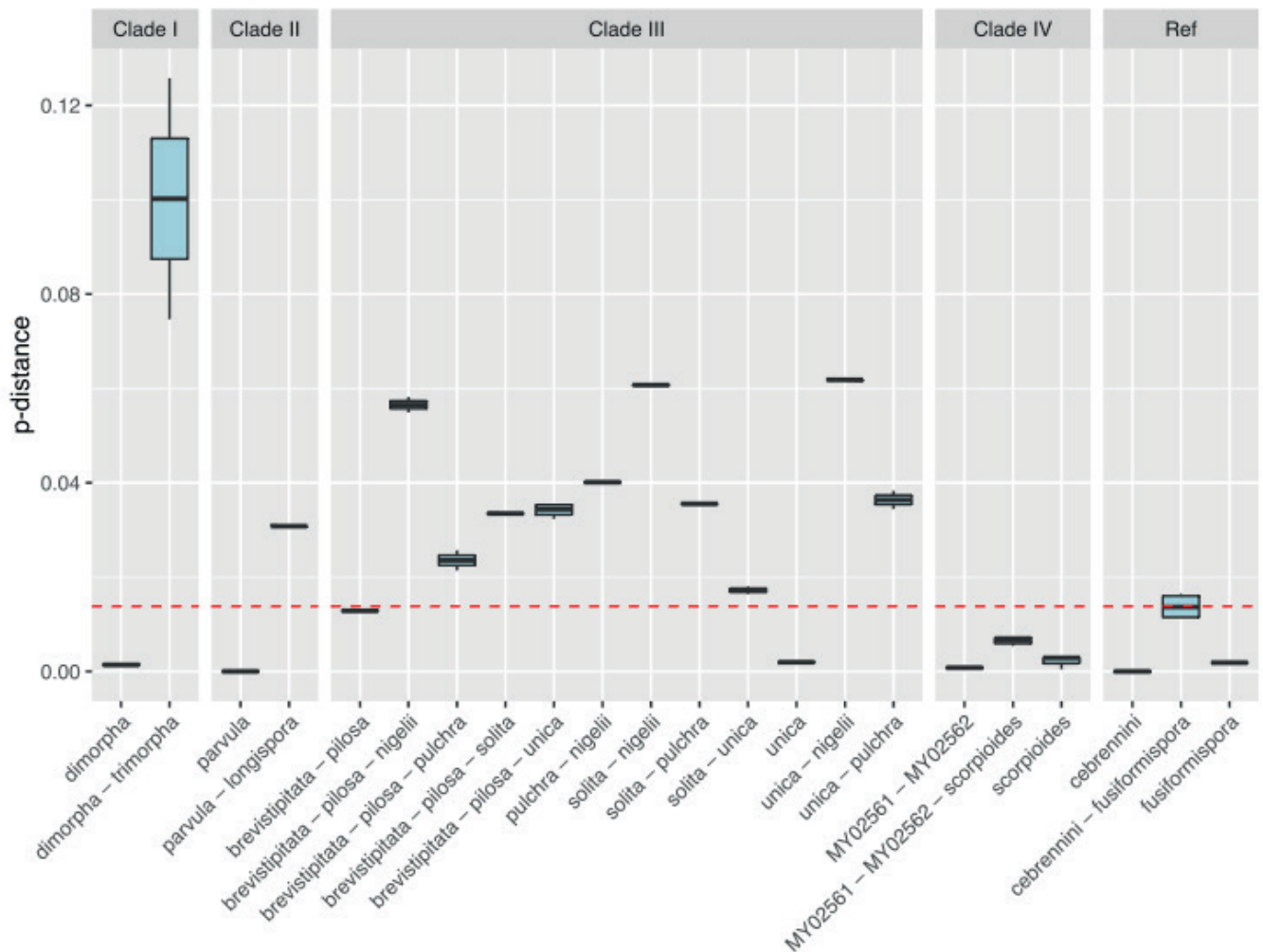
Fig. 2. Distribution of p-distances between putative new species and closely related known taxa. Within Clade III (*G. brevistipitata–G. pilosa–G. solita–G. unica–G. pulchra–G. nigelii*), all pairwise p-distances between putative species exceeded the threshold supporting their species status (*G. brevistipitata–G. pilosa–G. solita*: 0.033 ± 0.000, *G. brevistipitata–G. pilosa–G. unica*: 0.034 ± 0.001, *G. brevistipitata–G. pilosa–G. pulchra*: 0.024 ± 0.003, *G. brevistipitata–G. pilosa–G. nigelii*: 0.056 ± 0.002, *G. solita–G. unica*: 0.017 ± 0.001, *G. solita–G. pulchra*: 0.038, *G. solita–G. nigelii*: 0.069, *G. unica–G. pulchra*: 0.036 ± 0.003, *G. unica–G. nigelii*: 0.062 ± 0.000, *G. pulchra–G. nigelii*: 0.044). The p-distance between *G. brevistipitata* (BCC 45580) and *G. pilosa* (BCC 57817) is just below the threshold (0.013). However, there are sufficient distinguishing morphological characters to establish them as separate species. Pairwise p-distances also exceeded the threshold in Clade II (*G. parvula–G. longispora*: 0.031 ± 0.000), and Clade I, in which the average p-distance of *G. trimorpha–G. dimorpha* was notably greater (0.061) than for any other pair In clade IV, the average p-distances of the isolates BCC 27985 and BCC 27986 to *G. scorpioides* were well below the threshold indicating that these isolates belong to *G. scorpioides*.

Culture characteristics: Colonies on PDA attaining a diam of 2 cm in 20 d at 25 °C, white, floccose; reverse cream, becoming light brown with age at the centre (Fig. 4N). Sporulation not observed in culture.

Material examined: **Thailand**, Ranong Province, Khuan Mae Yai Mon Wildlife Sanctuary, Heo Lom Waterfall, on *Miagrammopes* sp. attached to the underside of a dicot leaf, 9 Mar. 2011, *K. Tasanathai, P. Srikitikulchai, A. Khonsanit, K. Sansatchanon* & *D. Thanakitpipattana* (BBH30489, living culture BCC 47518). GenBank: ITS = MH532884, LSU = MH394679, *TEF1* = MH521892, *RPB1* = MH521819, *RPB2* = MH521863.

Notes: *Gibellula dimorpha* was first described by Tzean *et al.* in the late 1990s and there has been no report on this species since then. In this study, we described for the first time *G. dimorpha* from Thailand; moreover, we obtained a culture of this species. Typically, *G. dimorpha* is recognised by having a *Granulomanus* conidial morph that develops aspergillus-like conidiophores and by producing broadly fusoid conidia in the *Gibellula* conidial morph. A *Granulomanus* conidiophore often bears both types of phialides:

narrowly clavate, smooth-walled phialides, which is typically found in the *Gibellula* conidial morph and irregular-shaped, rough-walled phialides with 1–3 denticles. Remarkably, the narrowly clavate phialides of the *Granulomanus* conidial morph are significantly longer, (6–)7.5–10(–11) μm, than those found in the *Gibellula* conidial morph (6.5–8.5 μm). The size of the conidial heads varies over a wide range, in which the largest is up to 59 μm diam. In comparison to the type, the Thai specimen shared similarity in shape but shows difference in size (Table 2). For instance, the Thai specimen has *Gibellula* conidiophores, *Granulomanus* phialides and conidia that are much shorter than the type whereas the part-spores of the *Torrubiella* sexual morph are slightly longer.

Gibellula longicaudata Tasanathai, Kuephadungphan & Luangsaard, *sp. nov.* MycoBank MB 841095. Fig. 5.

Etymology: Long tail, referring to the long synnema.

Typus: **Thailand**, Ranong Province, Khuan Mae Yai Mon Wildlife Sanctuary, Heo Lom Waterfall, on *Indoxysticus* sp. (*Thomisidae*) attached
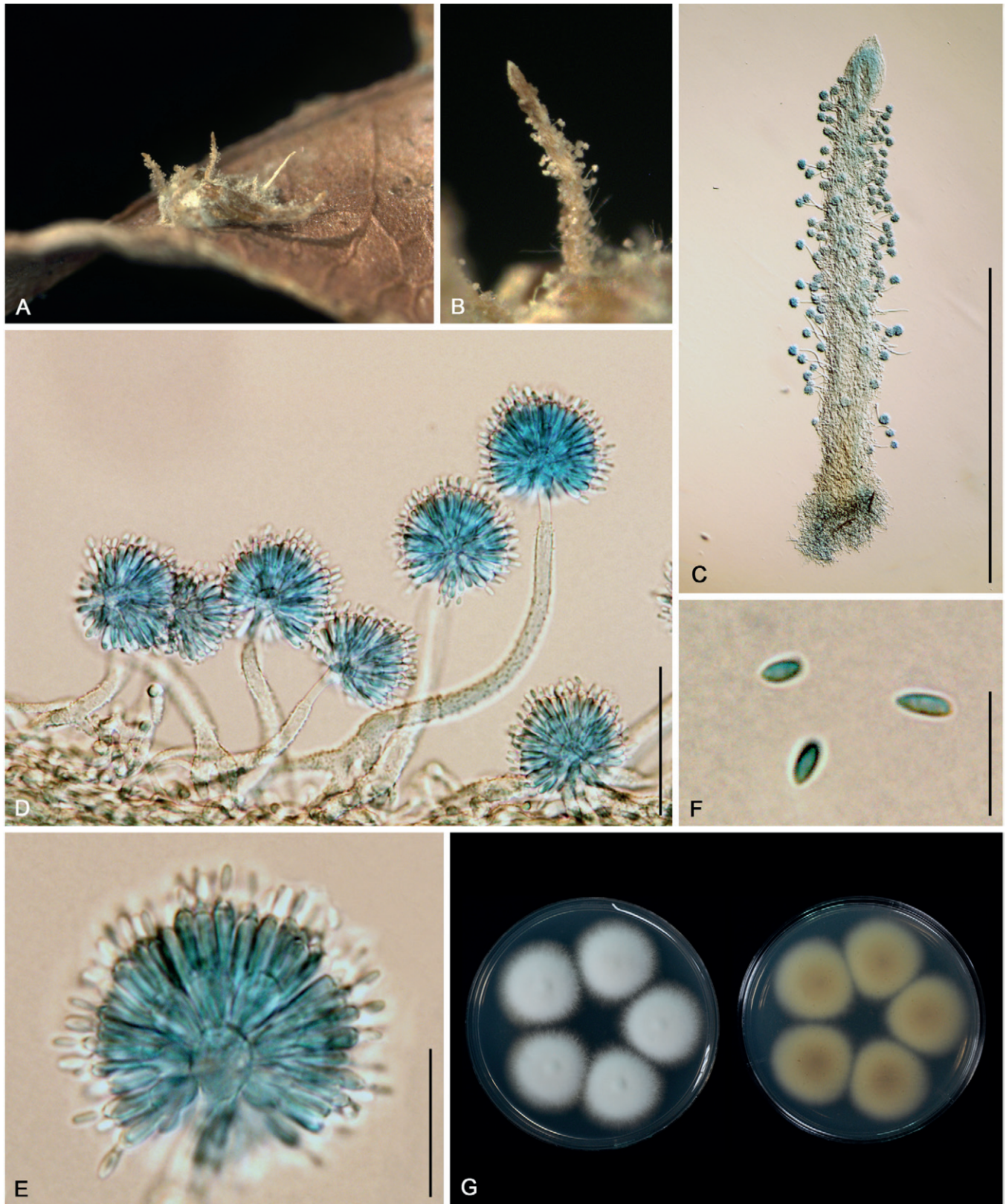
Fig. 3. *Gibellula brevistipitata*. **A.** Fungus on spider. **B–C.** Synnemata. **D.** Conidiophores showing spherical conidial heads. **E.** A conidial head bearing conidia. **F.** Conidia. **G.** Colonies obverse and reverse on PDA at 25 °C after 28 d. Scale bars: C = 1 mm; D = 50 μm; E = 20 μm; F = 10 μm.

Fig. 4. *Gibellula dimorpha*. **A.** Fungus on a spider. **B.** Part of synnema showing conidiophores. **C.** Conidiophores arising from the mycelia covering a spider's leg. **D.** Conidial head of *Gibellula* conidial stage. **E.** Conidia of *Gibellula* conidial stage. **F.** Aspergillus-like conidiophore of *Granulomanus* conidial stage. **G.** *Granulomanus* conidial stage forming typical *Gibellula* phialides. **H.** Conidial head of *Granulomanus* conidial stage showing irregular-shaped phialides. **I.** Filiform conidia of *Granulomanus* conidial stage. **J.** Perithecium occurring on the mycelial network covering the spider's body. **K.** Perithecium. **L.** Asci. **M.** Part-spores **N**. Colonies obverse and reverse on PDA at 25 °C after 20 d. Scale bars: C, K = 250 μm; F, L = 50 μm; J = 50 μm; D, G, H = 20 μm; E, I, M = 10 μm.

Table 1. List of taxa included in the multi-locus based phylogenetic analyses and their GenBank accession numbers. The isolates representing the new taxa are marked in bold.

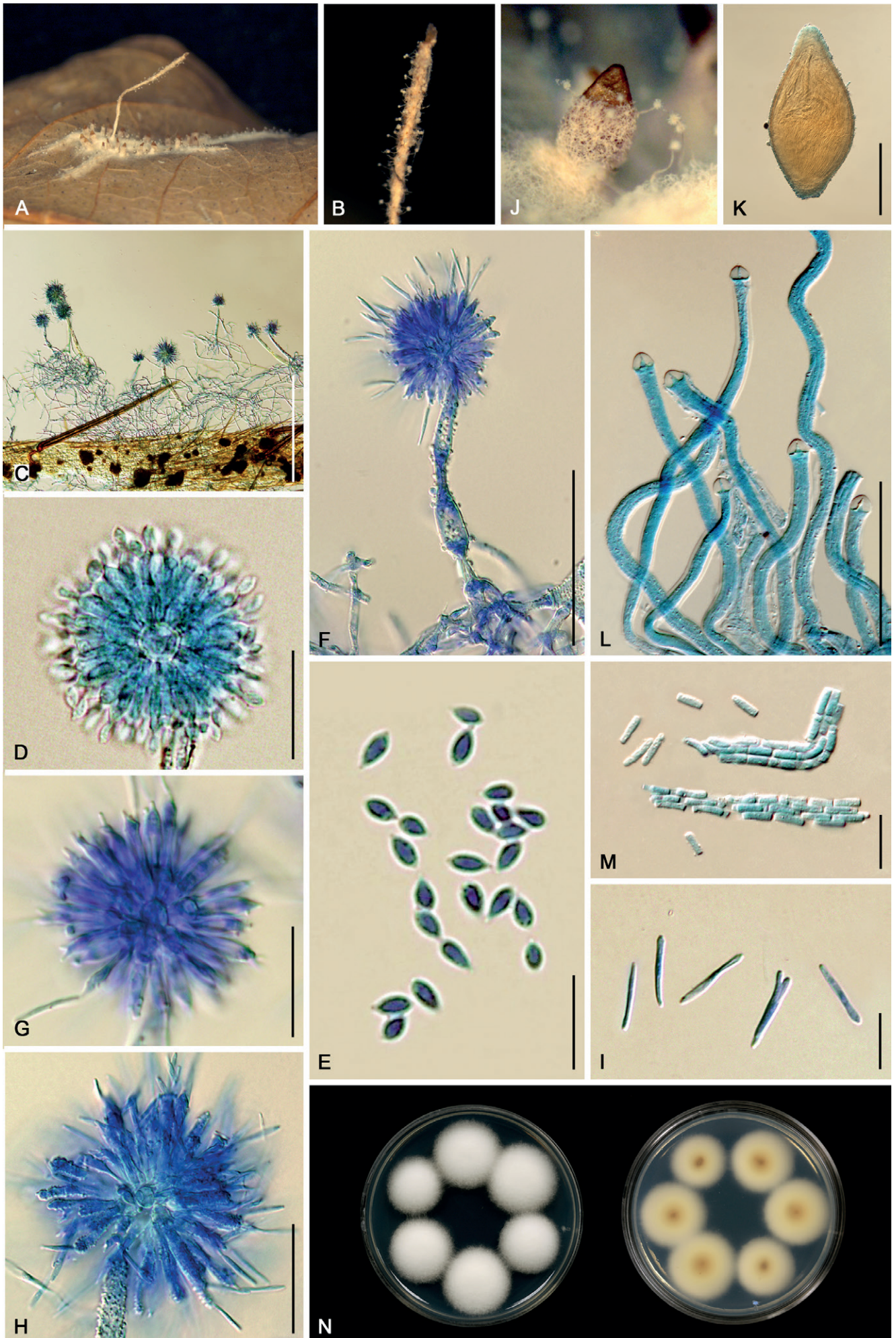| Species	Code	GenBank accession numbers					References
		ITS	LSU	*TEF1*	*RPB1*	*RPB2*	
Akanthomyces aculeatus	HUA 772	KC519371	KC519370	KC519366	–	–	Sanjuan *et al.* (2014)
	HUA 186145	–	MF416520	MF416465	–	–	Kepler *et al.* (2017)
Akanthomyces sabanensis	ANDES-F 1014	KC633245	KC633248	KC875221	–	–	Chirivi-Salomon *et al.* (2015)
	ANDES-F 1024	KC633232	KC875225	KC633266	–	KC633249	Chirivi-Salomon *et al.* (2015)
Beauveria bassiana	ARSEF 1564ᵀ	NR111594	–	HQ880974	HQ880833	HQ880905	Rehner *et al.* (2011)
	ARSEF 7518	HQ880762	–	HQ880975	HQ880834	HQ880906	Rehner *et al.* (2011)
Blackwellomyces cardinalis	OSC 93609ᵀ	–	AY184962	DQ522325	DQ522370	DQ522422	Sung & Spatafora (2004), Spatafora *et al.* (2007)
	OSC 93610	JN049843	AY184963	EF469059	EF469088	EF469106	Kepler *et al.* (2012), Sung & Spatafora (2004), Sung *et al.* (2007)
Cordyceps farinosa	CBS 111113ᵀ	AY624181	MF416554	MF416499	MF416656	MF416450	Luangsa-ard *et al.* (2005), Kepler *et al.* (2017)
Cordyceps javanica	CBS 134.22ᵀ	NR111172	NG059048	MF416504	MF416661	MF416455	Luangsa-ard *et al.* (2005), Kepler *et al.* (2017)
	BCC26304	MH532851	MH394660	MH521903	MH521825	MH521868	Helaly *et al.* (2019), Kuephadungphan *et al.* (2020)
Cordyceps militaris	ARSEF 5050	HQ880829	–	HQ881020	HQ880901	HQ880973	Rehner *et al.* (2011)
	OSC 93623	JN049825	AY184966	DQ522332	DQ522377	AY545732	Kepler *et al.* (2012), Spatafora *et al.* (2007), Sung & Spatafora (2004)
Engyodontium aranearum	CBS 309.85	JN036556	AF339526	DQ522341	DQ522387	DQ522439	Spatafora *et al.* (2007), Sung *et al.* (2001)
	CBS 658.80	LC092897	LC092916	–	–	–	Tsang *et al.* (2016)
Gibellula brevistipitata	**BCC45580**	**OK040729**	**OK040706**	**OK040697**	**OK040715**	**–**	**This study**
Gibellula cebrennini	BCC39705	MH532874	MH394673	MH521895	MH521822	MH521859	Kuephadungphan *et al.* (2020)
	BCC53605ᵀ	MT477069	MT477062	MT503328	MT503321	MT503336	Kuephadungphan *et al.* (2020)
Gibellula clavulifera var. *alba*	ARSEF 1915ᵀ	–	DQ518777	DQ522360	DQ522408	DQ522467	Spatafora *et al.* (2007)
Gibellula dimorpha	**BCC47518**	**MH532884**	**MH394679**	**MH521892**	**MH521819**	**MH521863**	**This study**
Gibellula fusiformispora	BCC 45076	MH532882	–	–	MH521823	MH521860	Kuephadungphan *et al.* (2020)
	BCC56802ᵀ	MT477070	MT477063	MT503329	MT503322	MT503337	Kuephadungphan *et al.* (2020)
Gibellula gamsii	BCC27968ᵀ	MH152529	MH152539	MH152560	MH152547	–	Kuephadungphan *et al.* (2019)
	BCC28797	MH152531	MH152541	MH152562	MH152549	MH152557	Kuephadungphan *et al.* (2019)
Gibellula leiopus	BCC16025	–	MF416548	MF416492	MF416649	–	Kepler *et al.* (2017)
	BCC49250	**OK070780**	**OK070781**	**OK070782**	**OK070783**	**OK070784**	**This study**
Gibellula longicaudata	**BCC40861**	**OK040730**	**OK040707**	**OK040698**	**OK040716**	**OK040724**	**This study**
Gibellula longispora	**NHJ 12014**	**–**	**–**	**EU369017**	**EU369055**	**EU369075**	**Johnson *et al.* (2009)**
Gibellula nigelii	**NHJ 10808**	**–**	**EU369035**	**EU369018**	**EU369056**	**EU369076**	**Johnson *et al.* (2009)**
Gibellula parvula	**BCC48888**	**OK040731**	**OK040708**	**OK040699**	**OK040717**	**OK040725**	**This study**
	BCC49748	**OK040732**	**OK040709**	**OK040700**	**OK040718**	**OK040726**	**This study**
Gibellula pigmentosinum	BCC38246	MH532872	MH394672	MH521893	MH521800	MH521855	Helaly *et al.* (2019), Kuephadungphan *et al.* (2020)
	BCC41203ᵀ	MT477071	–	MT503330	MT503323	–	Kuephadungphan *et al.* (2020)
Gibellula pilosa	**BCC57817**	**OK040733**	**OK040710**	**OK040701**	**OK040719**	**–**	**This study**
Gibellula pulchra	**BCC47555**	**MH532885**	**–**	**MH521897**	**MH521804**	**–**	**This study**
Gibellula scorpioides	**BCC27985**	**OK040734**	**MH394662**	**MH521899**	**MH521815**	**MH521857**	**This study**

Table 1. (Continued).

Species	Code	ITS	LSU	*TEF1*	*RPB1*	*RPB2*	References
				GenBank accession numbers			
BCC27986		**OK040735**	**OK040711**	**OK040702**	**OK040720**	**OK040727**	**This study**
	BCC43298	MT477074	MH394677	MH521900	MH521816	MH521858	Kuephadungphan *et al.* (2020)
	BCC47976ᵀ	MT477078	MT477066	MT503335	MT503325	MT503339	Kuephadungphan *et al.* (2020)
Gibellula solita	**BCC45574**	**OK040736**	**OK040712**	**OK040703**	**OK040721**	**–**	**This study**
Gibellula trimorpha	**BCC36526**	**OK040737**	**–**	**OK040704**	**OK040722**	**OK040728**	**This study**
	BCC36538	**MH532867**	**MH394668**	**MH521890**	**MH521817**	**MH521861**	**This study**
Gibellula unica	**BCC45112**	**OK040738**	**OK040713**	**OK040705**	**OK040723**	**–**	**This study**
	BCC46590	**MH532883**	**MH394678**	**–**	**MH521803**	**MH521866**	**This study**

Table 2. Morphological comparison between *G. trimorpha*, Thai *G. dimorpha* and the type.

Characters	*Gibellula trimorpha*	*Gibellula dimorpha* (New record from Thailand)	*Gibellula dimorpha* (Tzean *et al.* 1998)
***Gibellula* asexual morph**	Present	Present	Present
Mycelia	Brown	Brownish-white	White, yellowish-white to orange white
Synnemata (mm)	Brownish-white, solitary cylindrical, attenuated	Brownish-white, solitary cylindrical, attenuated	Greenish white to pale green solitary, cylindrical, attenuated curved, 5 × 200
Conidiophores (µm)	Arising from the aerial mycelium and from synnema, septate, rough-walled, 65–230 × 7–9	Arising from the aerial mycelium and from synnema, 100–175 × 5–7.5	Arising from the aerial mycelium or from synnemata, septate, thickened, conspicuous, often darkly pigmented, rough-walled, in particular at base, 140–422 × 7.1–10.3
Conidial heads (µm)	Spherical, 37–44	Spherical, 32–50	Spherical, 36–54
Vesicle (µm)	Globose to subglobose, 9–12 × 7–10	Globose to subglobose, 5–7	Globose to subglobose, 7.9 × 11.1
Metulae (µm)	Hyaline, broadly ellipsoid, 7–10 × 6–7	Broadly obovoid to cylindrical, 5–7 × 4–5	Hyaline, broadly obovoid, narrowing towards base, 7.1–11.9 × 6.4–8.7
Phialides (µm)	n/a	Hyaline, cylindrical to narrow clavate, with a short neck, 6.5–8.5 × 1.5–3	Hyaline, cylindrical to narrowly clavate, with a short neck, smooth-walled, 5.6–8.7 × 2.5–4
Conidia (µm)	Fusoid In short chains, 4–5 × 2	Hyaline, fusoid, smooth-walled, single or in chains, 3–5 × 1.5–2	Hyaline, fusoid, ellipsoidal or lemon-shaped, smooth-walled, single or catenate, 3.2–4.1 × 2–2.4
***Granulomanus* asexual morph**	Present	Present	Present
Conidiophores (µm)	Rough-walled to distinctly verrucose	Rough-walled to distinctly verrucose, 77.5–157.5 × 7.5–11	Rough-walled to distinctly verrucose, 68–140 × 5.2–7.1
Conidial heads (µm)	n/a	Spherical, 37–59	Spherical, n/a
Vesicle (µm)	n/a	Globose to subglobose, often absent, 4.5–7	Hardly developed
Metulae (µm)	n/a	Broadly obovoid, occasionally hardly developed, smooth-walled, 6–7 × 4–6	Broadly obovoid, smooth-walled, occasionally minutely warted, 5.6–8.7 × 4.4–6.4
Phialides (µm)	Holoblastic, cylindrical, clavate, flask-shaped, or irregularly shaped, rough-walled, rarely smooth, bearing 1–3 conspicuous denticles, 8–13 × 3	Holoblastic, cylindrical, clavate, or irregularly shaped, rough- or smooth-walled, bearing 1–3 conspicuous denticles, 6–11 × 2.5–4	Cylindrical, ellipsoidal, narrowly clavate, conoid, or irregularly shaped, smooth-walled, occasionally roughened, bearing 1–3 conspicuous denticles, 7.9–20.6 × 3.2–4
Conidia (µm)	Hyaline, filiform, smooth-walled, 10–19 × 1–1.5	Hyaline, filiform, smooth-walled, 10–15 × 1–1.5	Hyaline, filiform, smooth-walled, 9.1–23.8 × 0.8–2.4
Sexual morph	Present	Present	Present

Table 2. (Continued).

| Characters	*Gibellula trimorpha*	*Gibellula dimorpha* (New record from Thailand)	*Gibellula dimorpha* (Tzean *et al.* 1998)
Perithecia (µm)	Reddish-brown, superficial, scattered, ovoid, 340–690 × 200–310	Reddish-brown, superficial, scattered, ovoid, 640–700 × 280–310	Yellowish-white, superficial or partly embedded, scattered, ovoid, 490–600 × 250–320
Asci (µm)	Cylindrical, >455 × 7–10 with ascus cap	Cylindrical, >688 × 5–8 with ascus cap	Cylindrical, eight-spored, 220–310 × 6.4–8.2 with a thickened perforated apex
Apex (µm)	4–5.5 × 5–8	4–7 × 6.5–8.5	4.8–6.4 × 6.8–8.7
Ascospores (µm)	Filiform, multi-septate	Filiform, multi-septate	Filiform, multi-septate, no data × 1.6–2.4
Part-spores (µm)	Bacilliform, 3–9 × 1.5–2.5	Bacilliform, 5–12 × 1.5–2	Hyaline, cylindrical, smooth-walled, 3–8.7 × 2–2.3
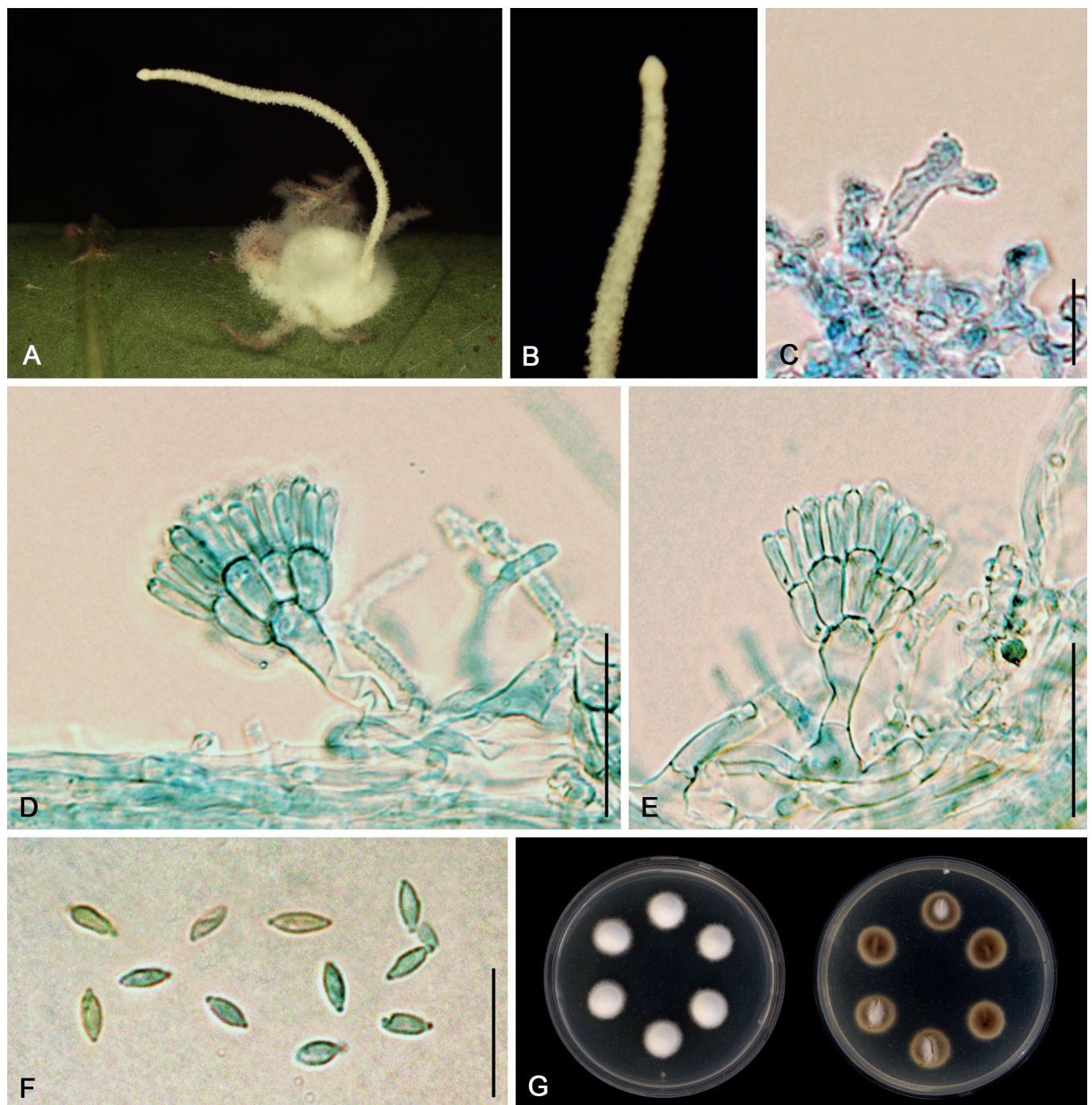
Fig. 5. *Gibellula longicaudata*. **A.** Fungus on spider. **B.** Upper part of a synnema showing a slight enlarged tip. **C.** Conidiophore showing a penicillium-like conidial head. **D–E.** *Granulomanus* phialides. **F.** Conidia. **G.** Colonies obverse and reverse on PDA at 25 °C after 20 d. Scale bars: D–E = 20 µm; C, F = 10 µm.

to the underside of dicot leaf, 9 Mar. 2011, *K. Tasanathai, P. Srikitikulchai, A. Khonsanit, K. Sansatchanon* & *D. Thanakitpipattana* (**holotype** BBH29604, culture ex-type BCC 40861). GenBank: ITS = OK040730, LSU = OK040707, *TEF1* = OK040698, *RPB1* = OK040716, *RPB2* = OK040724.

A long *synnema* arising from white mycelial mat covering the host, posterior part of a spider, greyish white, cylindrical, tufted surface, slightly tapering into sterile ovoid tip (Fig. 5A–B). *Conidiophores* crowded, smooth, enlarging upward into obovoid apices, (10–)15–28(–35) × 3–4(–5) µm, bearing multiple metulae (Fig. 5D–E). *Metulae* broadly obovoid to ellipsoid, 7–8(–10) × 3–3.5(–4) µm (Fig. 5D–E). *Phialides* borne on metulae, narrowly clavate to cylindrical, thickened at the tip, (7–)7.5–9(–10) × 2(–3) µm (Fig. 5D–E). Metulae and phialides together forming wedge-shaped conidial head. *Conidia* fusoid or occasionally ovoid with acute ends, (3–)3.5–5(–6) × 1–2 µm (Fig. 5F). *Granulomanus* synasexual morph observed, occurring on the synnema, arising from the septate hyphae loosely attached to the surface of synnema (Fig. 5C). *Conidiophores* distinctly roughened, very short, bearing polyblastic and irregularly shaped phialides with inconspicuous denticles (Fig. 5C). Sexual morph not observed.

Culture characteristics: Colonies on PDA attaining a diam of 1.1 cm in 20 d at 25 °C, floccose, white; reverse light brown, darkening with age, starting from the centre (Fig. 5G). Sporulation not observed in culture.

Gibellula longispora Kuephadungphan & Luangsa-ard, ***sp. nov.*** MycoBank MB 841091. Fig. 6.

Etymology: Refers to the long conidia.

Typus: **Thailand**, Nakhon Ratchasima Province, Khao Yai National Park, on *Myrmarachne* sp. (*Salticidae*) attached to the underside of monocot leaf, 1 Sep. 2002, *N.L. Hywel-Jones* (**holotype** BBH8638, culture ex-type BCC 13102). GenBank: *TEF1* = EU369017, *RPB1* = EU369055, *RPB2* = EU369075.

White mycelia covering the body of a spider host, occasionally its legs (Fig. 6A). Multiple synnemata produced, cylindrical, attenuated, brown when dried, 5–5.5 mm long, 175–200 µm wide, narrowing upward to a slender tip, 62.5–75 µm wide, consisting of parallel multiseptated longitudinal hyphae (Fig. 6A–C). *Conidiophores* arising from the outer layer of hyphal network loosely attached to the synnemata, crowded along the entire length of the synnemata, multiseptate, minutely roughened, (105–)159.5–290.5(–415) × (6–)8.5–11(–15) µm, abruptly narrowing to a distinct long slender stipe, bearing an aspergillus-like conidial head (Fig. 6D). *Conidial head* spherical, (37–)39–41.5(–42) µm diam (Fig. 6E). *Vesicles* terminated from apices of conidiophores, globose to subglobose, 7–8.5(–9) µm diam, bearing multiple metulae (Fig. 6E). *Metulae* broadly obovoid, (6.5–)7.5–9.5(–10) × (5.5–)6–6.5(–7) µm (Fig. 6E). *Phialides* narrowly clavate to cylindrical, (8.5–)9.5–11(–11.5) × (2.5–)3–3.5(–4) µm (Fig. 6E). *Conidia* borne on phialides, single, often in chains of up to four, bacilliform to cylindrical, (3.5–)5.5–8(–9) × 1–1.5 µm (Fig. 6F). *Granulomanus* synasexual morph and sexual morph not observed.

Culture characteristics: *Gibellula longispora* was once established in culture on PDA. DNA was extracted and sequenced but unfortunately the culture lost its viability after storage.

Notes: *Gibellula longispora* has often been used as a representative of the genus *Gibellula* in phylogenetic analyses (Johnson *et al.* 2009, Kepler *et al.* 2011, Chiriví-Salomón *et al.* 2015, Thanakitpipattana

et al. 2020). *Gibellula longispora* is in fact an invalid name which is not yet listed in the global fungal nomenclatural databases including Index Fungorum (www.indexfungorum.org) and MycoBank (www.mycobank.org). In order to validate this name, the species is therefore morphologically described and illustrated herein. The specimen BBH8638 (formerly known as NHJ12014) is reminiscent of *G. pulchra* in having numerous synnemata and producing aspergillus-like conidiophores. Nonetheless, *G. longispora* distinctly differs from the type of *G. pulchra* (Cavara 1894) not only in the length of conidia which are twice as long as those of the type (Table 3), but also from the phylogenetic evidence that *G. longispora* is more closely related to *G. parvula* than to *G. pulchra* (Fig. 1).

Gibellula nigelii Kuephadungphan, Tasanathai & Luangsa-ard ***sp. nov.*** MycoBank MB 841096. Fig. 7.

Etymology: In honour of Dr Nigel Hywel-Jones, for his outstanding contribution to our knowledge of spider-parasitic fungi.

Typus: **Thailand**, Nakhon Ratchasima Province, Khao Yai National Park, Mo Sing To Nature trail, on *Linyphiidae* attached to the underside of a dicot leaf, 16 Jun. 2000, *R. Nasit* (**holotype** BCC 2711, culture ex-type BCC 2711). GenBank: LSU = EU369035, *TEF1* = EU369018, *RPB1* = EU369056, *RPB2* = EU369076.

White mycelia growing over the spider, densely on the abdomen, occasionally on the cephalothorax and legs (Fig. 7A). *Synnema* arising from the posterior part of the host, cylindric, attenuated, approximately 3 mm long, 70 µm wide, white at the base, becoming brown to greenish brown upward, enlarging into inconspicuous swollen tip with acute apex (Fig. 7A–D). *Conidiophores* arising from outer layer of hyphal network of the synnema, absent in the lower part, scattered, occasionally septate at base, minutely roughened, (42.5–)55–85(–90) × 7.5–9.5(–10) µm, tapering abruptly in a slender apex and terminating into a swollen vesicle (Fig. 7E–F). *Vesicles* globose to subglobose, (7.5–)8.5–10.5(–11) µm diam bearing multiple metulae (Fig. 7G). *Metulae* broadly obovoid, (7–)7.5–9(–10) × (5–)5.5–6.5(–7) µm (Fig. 7G). *Phialides* borne on metulae, narrowly clavate to cylindrical, apically thickened, occasionally with very short neck, (6–)7–8(–9) × 2–2.5(–3) µm, each bearing a conidium (Fig. 7G). A vesicle, metulae and phialides forming a spherical conidial head, 38–41(–42) µm diam (Fig. 7E–G). *Conidia* ellipsoid, narrowly ovoid, sometimes with an acute end, (2.5–)3–3.5(–4) × 1–1.5 µm (Fig. 7H). *Granulomanus* synasexual morph and sexual morph not observed.

Culture characteristics: Colonies on PDA attaining a diam of 1.5 cm in 24 d at 25 °C, cottony, brownish white; reverse light brown, darkening with age, starting from the centre (Fig. 7I). Sporulation not observed in culture.

Notes: Besides *G. longispora*, *G. nigelii* (formerly known as *G. pulchra* NHJ 10808) has also frequently been included in phylogenetic analyses to represent *G. pulchra* (Johnson *et al.* 2009, Kepler *et al.* 2011, Chiriví-Salomón *et al.* 2015, Thanakitpipattana *et al.* 2020). However, morphological data indicate that NHJ10808 represents a different species. Even though *G. nigelii* and *G. pulchra* show morphological resemblance in having nearly the same microscopic characters, they can be distinguished from each other by the outer appearances. *Gibellula pulchra* typically produces numerous synnemata; however, *G. nigelii* formed only a single synnema and could thus not be assigned to the same species. In addition, the arrangement of conidiophores on

Table 3. Morphological comparison of *G. longispora*, *G. nigelii*, *G. parvula*, *G. pulchra* and *G. solita* with the type strain of *G. pulchra* and other records of the species.

Characters	G. longispora	G. nigelii	G. parvula	G. pulchra	G. solita	The type of G. pulchra (Cavara 1894)	G. pulchra (Mains 1950)	G. pulchra (Kobayasi et al. 1977)	G. pulchra (Tzean et al. 1997)	G. pulchra (Selcuk et al. 2004)
Locality	Thailand	Thailand	Thailand	Thailand	Thailand	Italy	America	Japan	Taiwan	Turkey
***Gibellula* asexual morph**	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present
Mycelia	White	White	Yellowish-white	Yellow	Yellow	—	Yellow or yellowish-white	White	White or yellowish-white	Whitish brown, pinkish when dried
Synnemata	At least 20 synnemata cylindrical attenuated	Solitary, white at the base, becoming brown to greenish-brown upward, cylindrical, with indistinct swollen tip, 3 mm × 70 µm	A pair of two yellowish-white, cylindrical, with ovoid tips	Numerous, yellowish-white, cylindrical attenuated, 5 mm × 150 µm	A group of three, brownish-white, cylindrical, attenuated, with ovoid tips, 7 mm × 175 µm	—	Numerous, yellowish-brown, cylindrical, sometimes slightly enlarged above	Numerous, cylindrical, attenuated, 4–5 mm × 400–800 µm	Solitary to numerous, cylindrical	Whitish brown, pinkish when dried cylindrical, 1.5–3 mm × 100–200 µm
Conidiophores (µm)	Crowded, minutely rough-walled, multi-septate, 105–415 × 6–15	Scattered, minutely rough-walled, septate at base, 42.5–90 × 7.5–10	Crowded, rough-walled, multi-septate	Hyaline, rough-walled, 87.5–250 × 6–10	Rough-walled, multi-septate, 62.5–180 × 7.5–10	Multi-septate, 100–120 × 7–8	Hyaline, smooth-walled, 150–600 × 7–12	Septate, 5–8 µm wide	Darkly pigmented, rough-walled, 110–640 × 7.9–10.3	Pale brown, smooth-walled, 155–170 × 6–10
Conidial heads (µm)	Spherical, 37–42	Spherical, 38–42	Spherical, 30–40	Spherical, 34–41	Spherical, 30–33	Spherical, 30–40	Spherical, 30–42	Spherical, 40–50	Spherical, 40–48	Spherical, 40–43
Vesicle (µm)	Globose to subglobose, 7–9	Globose to subglobose, 7.5–11	Globose to subglobose, 6.5–9	Ellipsoidal to globose, 9–11	Globose to subglobose, 6.5–8.5	—	Ellipsoidal, obovoid, 6.4–10	Globose, 6–8	Ellipsoidal to globose, 8.7–10.3 × 7.9–8.7	Globose, obovoid or broadly-clavate, 7.5–10
Metulae (µm)	Broadly obovoid, 6.5–10 × 5.5–7	Broadly obovoid, 7–10 × 5–7	Broadly obovoid, 6–10 × 4.5–8	Broadly obovoid, 8–10 × 6–8	Broadly obovoid, 6.5–8 × 5–7	—	Broadly obovoid, 6–12 × 4–6	Obpyriform, 8–12 × 3–4	Broadly obovoid, 7.9–9.9 × 5.2–6.4	Narrowly clavate, 7.5–8 × 1.5–2.5
Phialides (µm)	Narrowly clavate to cylindric, 8.5–11.5 × 2.5–4	Narrowly clavate to cylindric, 6–9 × 2–3	Narrowly clavate to cylindric, 6–10 × 2–4	Clavate to cylindric, 6–9 × 2–3	Narrowly clavate to cylindric, 6–7.5 × 2–2.5	—	Clavate, 6–10 × 2–3	Sub-cylindric or clavate, 7–10 × 2–2.5	Narrowly clavate with a short neck, 6.4–10.3 × 2–2.4	Cylindrical with a short neck, 6.2–7.5 × 5

Table 3. (Continued).

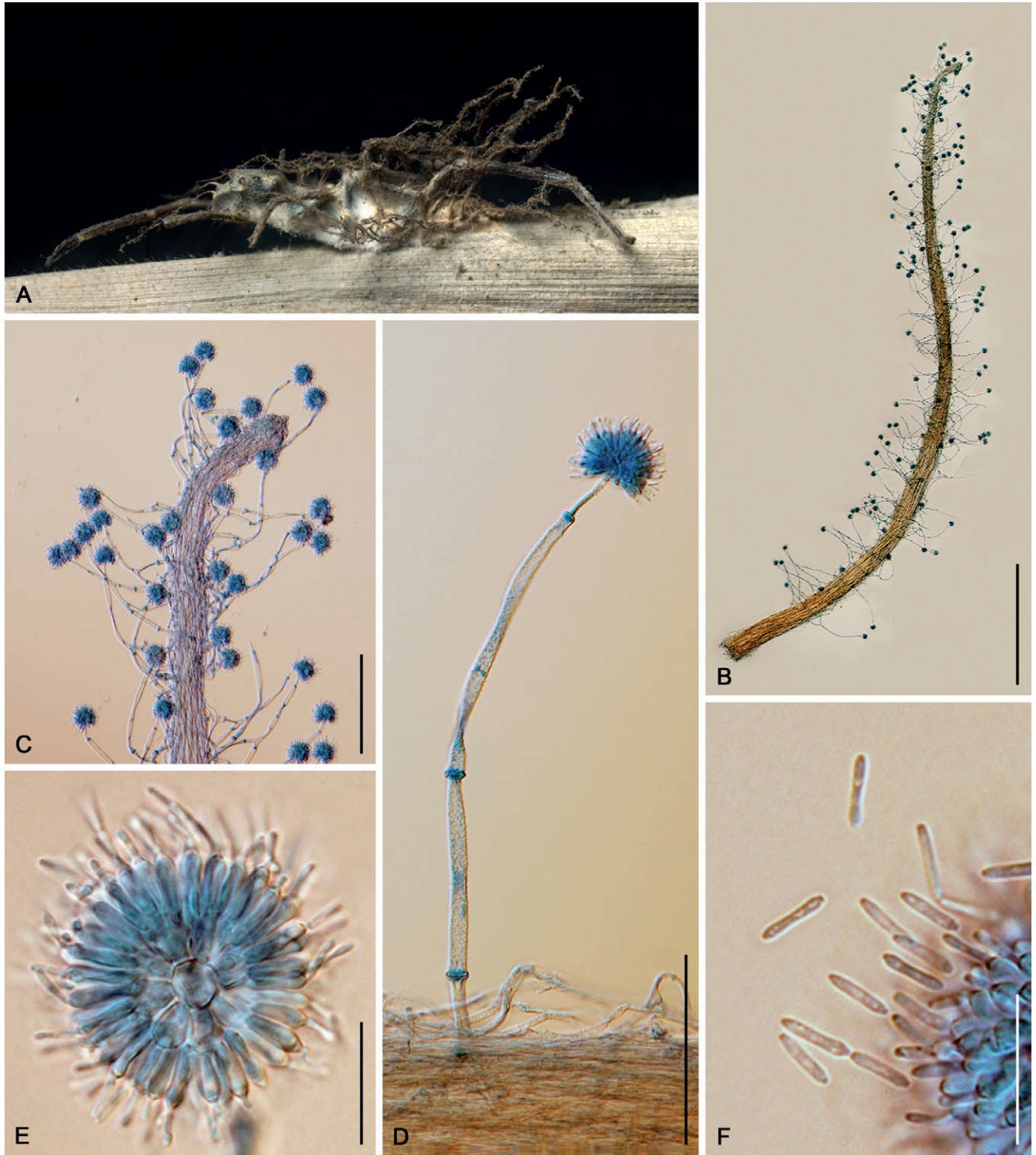| Characters	G. longispora	G. nigelii	G. parvula	G. pulchra	G. solita	The type of G. pulchra (Cavara 1894)	G. pulchra (Mains 1950)	G. pulchra (Kobayasi et al. 1977)	G. pulchra (Tzean et al. 1997)	G. pulchra (Selcuk et al. 2004)
Conidia (μm)	Bacilliform to cylindric, often in chains of up to 4 conidia, 3.5–9 × 1–1.5	Ellipsoid, narrowly ovoid, sometimes with an acute end, 2.5–4 × 1–1.5	Narrowly ovoid or narrowly ellipsoid or bacilliform, 4–6 × 2–4	Ellipsoid, 2–4 × 1–1.5	Ellipsoid to ovoid, 1.5–3 × 1–2	Cylindric to ovate-oblong, 3–4 × 1	Fusoid to fusoid-ellipsoid, 2.5–6.4 × 1.5–2.5	Single or in chains, fusiform-ellipsoidal, 4–6 × 1.5–2	Ellipsoid to fusiform, smooth-walled, 4–6 × 2–2.4	Fusiform to fusiform-ellipsoid, smooth-walled, 3–5 × 1.5–2.5
Granulomanus asexual morph	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Sexual morph	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present	Absent	Absent
Perithecia (μm)	—	—	—	—	—	—	Superficial, light yellowish brown to reddish brown above, narrowly ovoid to conoid, 550–1 200 × 230–350	Almost covered with white hypha, dark ashy grey, narrowly ovoid to conoid, 1 000–1 200 × 250–300	—	—
Asci (μm)	—	—	—	—	—	—	Narrowly cylindrical, with thickened cap, 450–660 × 4–6	Narrowly cylindrical, with thickened cap, 1.5–2.5 μm wide	—	—
Ascospores (μm)	—	—	—	—	—	—	Hyaline, filiform, multi-septate, 450–660 × 1.5	n/a	—	—
Part-spores (μm)	—	—	—	—	—	—	No data, 4–10 × 1.5	Bacilliform to cylindric, 5–7 × 1.2–1.5	—	—

Fig. 6. *Gibellula longispora.* **A.** Fungus on spider. **B.** Synnema. **C.** Upper part of synnema. **D.** Conidiophore bearing aspergillus-like conidial head. **E.** Conidial head bearing conidia. **F.** Conidia. Scale bars: B = 1 mm; C= 200 μm; D = 100 μm; E = 20 μm; F = 10 μm.

synnemata appeared to be an informative character for species discrimination – the conidiophores are scattered in *G. nigelii* but crowded in *G. pulchra*. These differences together with the phylogenetic placements suggested proposing the strain NHJ 10808 as a new species.

Herein, the conidiophore lengths of *G. nigelii* might be inaccurate as the actual length might be longer. In general, the conidiophore is shorter the further up the synnema. To preserve the fungal specimens, only the upper part of a synnema (approximately 830 μm) was taken for the morphological study.

Gibellula parvula Kuephadungphan, Tasanathai & Luangsa-ard, *sp. nov.* MycoBank MB 841090. Fig. 8.

Etymology: Refers to the tiny spider host.

Typus: **Thailand**, Nakhon Ratchasima Province, Khao Yai National Park, Mo Sing To Nature Trail, on *Theridiidae* attached to the underside of a dicot leaf, 30 Aug. 2011, *K. Tasanathai, P. Srikitikulchai & S. Mongkolsamrit* (**holotype** BBH31330, culture ex-type BCC 49748). GenBank: ITS = OK040732, LSU = OK040709, *TEF1* = OK040700, *RPB1* = OK040718, *RPB2* = OK040726.
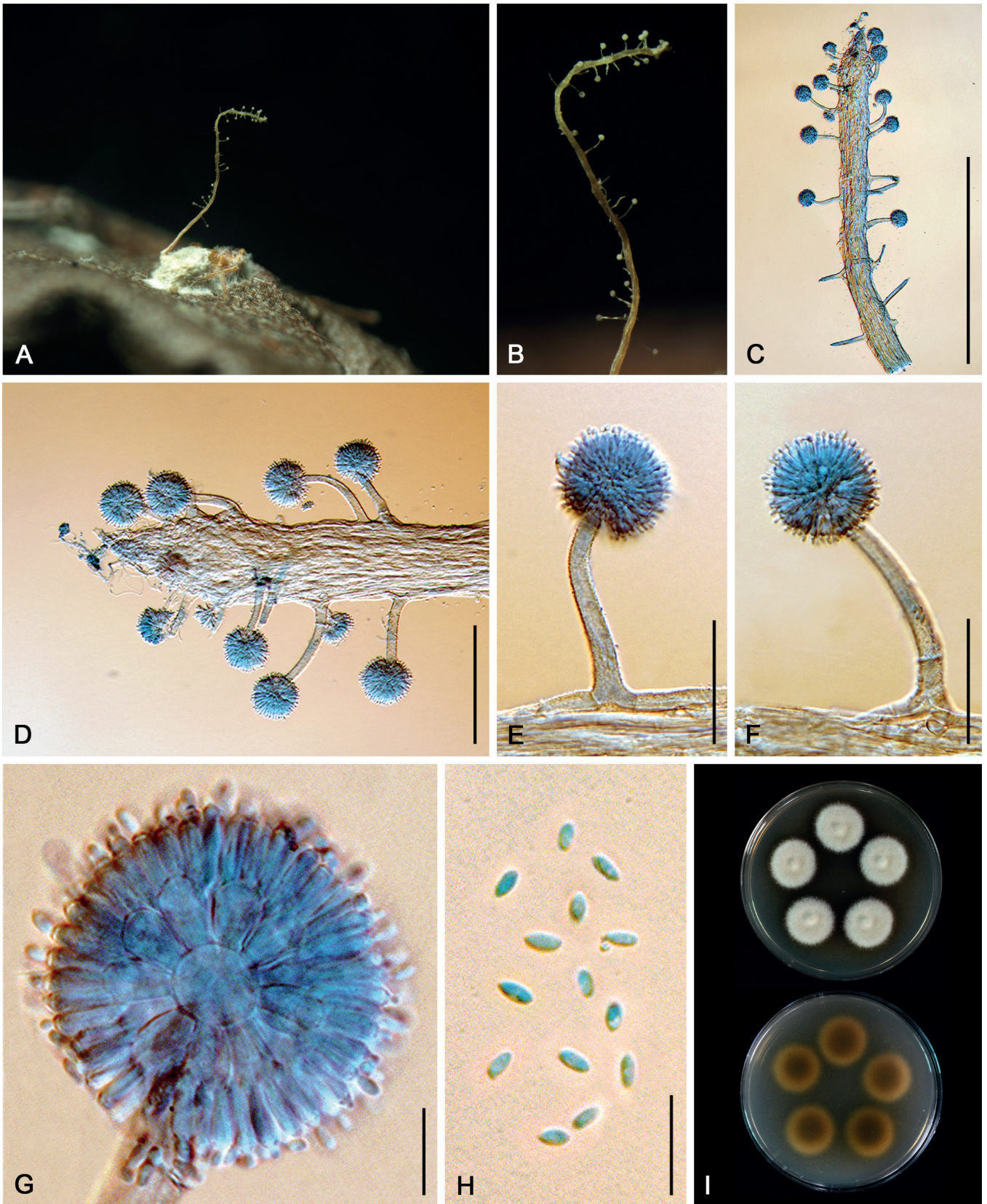
Fig. 7. *Gibellula nigelii.* **A.** Fungus on spider. **B–C.** Synnema. **D.** Upper part of a synnema showing a slight enlarged tip. **E–F.** Conidiophore showing a spherical conidial head. **G.** Conidial head bearing conidia. **H.** Conidia. **I.** Colonies obverse and reverse on PDA at 25 °C after 28 d. Scale bars: C = 500 μm; D = 100 μm; E–F = 50 μm; G–H = 10 μm.

Spider completely covered by a yellowish white mycelial mat (Fig. 8A). *Synnemata* yellowish white, a pair of two, cylindrical, swollen into an ovoid tip, 125 μm wide (Fig. 8B–C). *Conidiophores* arising from the mycelium covering the host and from a network of hyphae loosely attached to the surface of the synnemata, along its entire length, crowded, septa conspicuous, verrucose, (47.5–)85–145(–185) × (6–)8–10(–11) μm, narrowing abruptly to a slender apex, and terminating in a swollen vesicle (Fig. 8D–F). *Vesicles* globose to subglobose, (6.5–)7–8(–9) μm diam, bearing multiple broadly obovoid metulae, (6–)7–8.5(–10) × (4.5–)5–6.5(–8) μm (Fig. 8G). *Phialides* borne on metulae, narrowly clavate to cylindric with both round ends, (6–)7–9(–10) × (2–)2.5–3(–4) μm, each bearing a
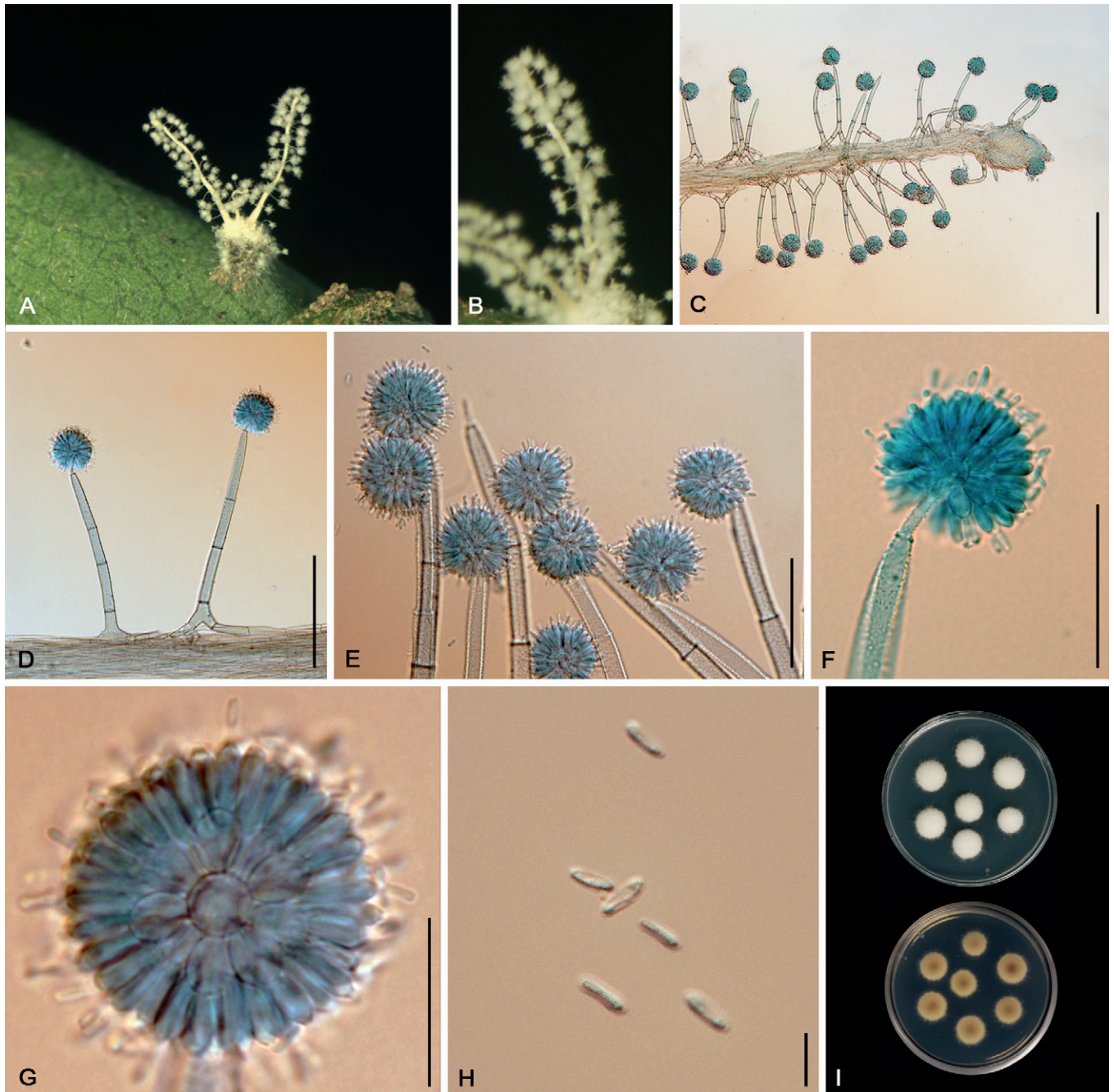
Fig. 8. *Gibellula parvula*. **A.** Fungus on spider (BBH 31330). **B.** Synnemata (BBH 31330). **C.** Upper part of a synnema showing enlarged tip (BBH 31330). **D–F.** Conidiophores showing spherical conidial heads (BBH 31330 and BBH 31446). **G.** Conidial head bearing conidia (BBH 31330). **H.** Conidia (BBH 31446). **I.** Colonies obverse and reverse on PDA at 25 °C after 20 d. Scale bars: C = 250 µm; D = 100 µm; E–F = 50 µm; G = 20 µm; H = 5 µm.

conidium or occasionally a chain of conidia. *Conidia* narrowly ovoid or narrowly ellipsoid or bacilliform, 4–5.5(–6) × (2–)2.5–3(–4) µm (Fig. 8H). Vesicle, metulae and phialides forming spherical conidial heads, (30–)33.5–37(–40) µm diam (Fig. 8D–G).

Culture characteristics: Colonies on PDA attaining a diam of 1 cm in 20 d at 25 °C, white, cottony; reverse light brown, darkening with age toward center (Fig. 8I). Sporulation not observed in culture.

Material examined: **Thailand**, Nakhon Ratchasima Province, Khao Yai National Park, Mo Sing To Nature Trail, on *Theridiidae* attached to the underside of a dicot leaf, 5 Jul. 2011, *K. Tasanathai, P. Srikitikulchai & S. Mongkolsamrit* (BBH31446, living culture BCC 48888).

Gibellula pilosa Kuephadungphan, Tasanathai & Luangsa-ard, *sp. nov.* MycoBank MB 841092. Fig. 9.

Etymology: Refers to the outer appearance of the species that is very hairy.

Typus: **Thailand**, Nakhon Ratchasima Province, KhaoYai National Park, Fern Nature Trail, on non-web builder *Araneomorphae* attached to the underside of a dicot leaf, 8 Nov. 2012, *S. Mongkolsamrit, A. Khonsanit, W. Noisripoom, P. Srikitikulchai & R. Somnuk* (**holotype** BBH35197, culture ex-type BCC 57817). GenBank: ITS = OK040733, LSU = OK040710, *TEF1* = OK040701, *RPB1* = OK040719.

Spider completely covered by yellowish-light brown mycelial mat (Fig. 9A). *Synnemata* pale brown, cylindrical, in pairs, 6 mm long,
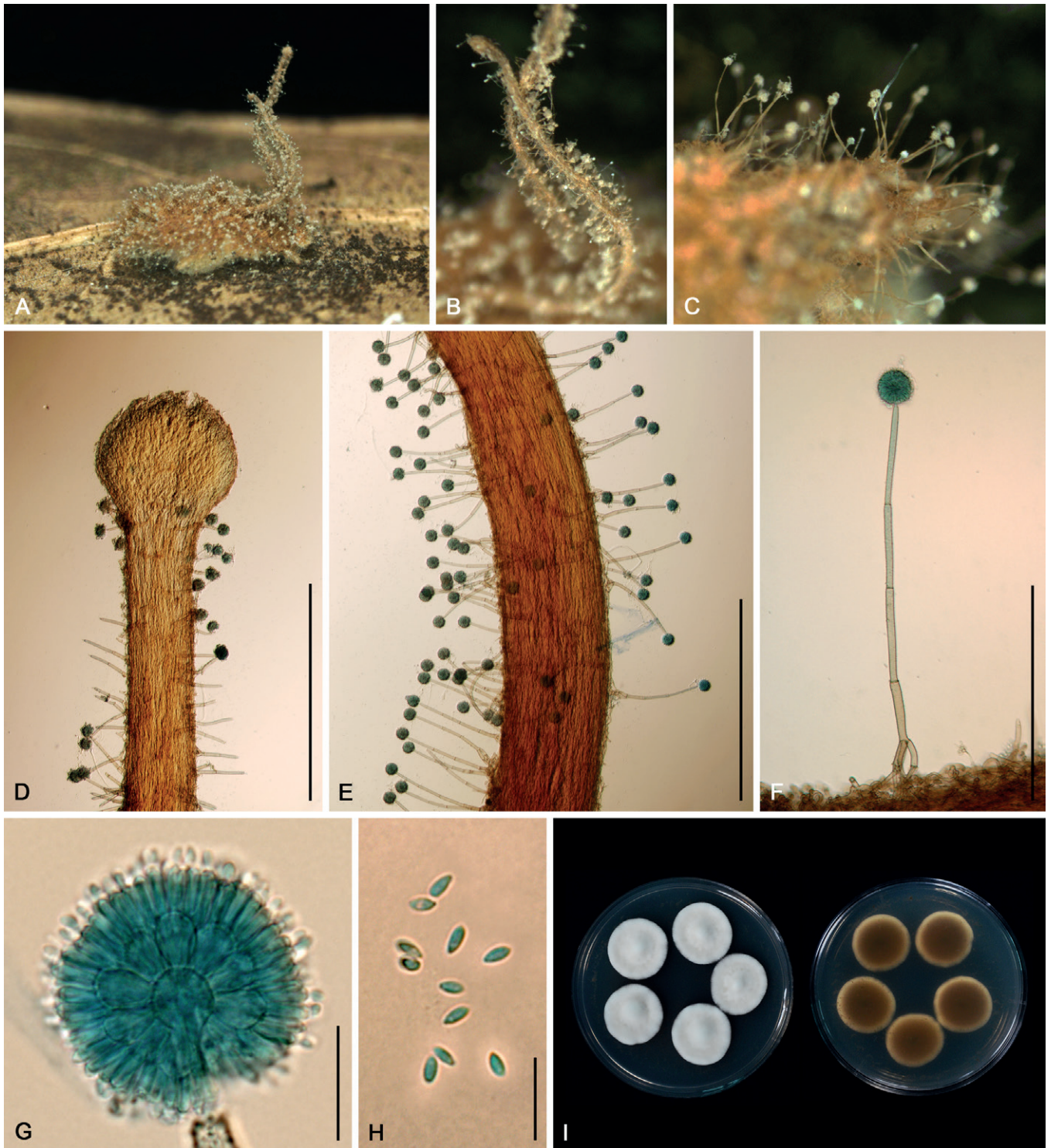
Fig. 9. *Gibellula pilosa*. **A.** Fungus on spider. **B.** Synnemata. **C.** Conidiophores arising from the mycelial mat covering the host. **D.** Upper part of a synnema showing globose tip. **E.** Part of synnema showing conidiophores. **F.** Conidiophore bearing a spherical conidial head. **G.** Conidial head bearing conidia. **H.** Conidia. **I.** Colonies obverse and reverse on PDA at 25 °C after 28 d. Scale bars: D = 1 mm; E = 500 μm; F = 250 μm; G = 20 μm; H = 10 μm.

475 μm wide, terminating in a swollen sterile globose tip, 600 μm wide (Fig. 9A–D). *Conidiophores* arising laterally from the outer layer of synnemata and from the mycelia covering all over the host, distinctly crowded, septa conspicuous, minutely roughened, (140–)151–265(–420) × (8.5–)9–11(–13.5) μm, narrowing to a slender apex, and terminating in a swollen vesicle (Fig. 9C–G). *Vesicles* spherical, (9–)10–11(–12) μm diam, bearing multiple metulae (Fig. 9G). *Metulae* broadly obovoid, (9–)9.5–11(–12) × (6–)7–8(–9) μm (Fig. 9G). *Phialides* borne on metulae, narrowly

clavate to cylindrical, 7–9(–10) × 2.5–3 μm, bearing conidia (Fig. 9G). *Conidia* narrowly almond-shaped, 3–4 × 1.5–2 μm (Fig. 9H). Vesicle, metulae, phialides forming a spherical conidial head, (41–)41.5–43(–45) μm diam (Fig. 9G). Sexual morph and *Granulomanus* synasexual morph not observed.

Culture characteristics: Colonies on PDA attaining a diam of 1.7 cm in 28 d at 25 °C, white, cottony; reverse pale brown, darkening with age toward centre (Fig. 9I). Sporulation not observed in culture.

Gibellula pulchra (Sacc.) Cavara, Atti Ist. Bot. Univ. Pavia Ser II, 3: 347. 1894. Figs 10, 11.

Spider host fully covered by yellow mycelial mat (Fig. 10A). *Synnemata* consisting of multiseptate longitudinal hyphae, numerous, arising from all over the host body, yellowish white, cylindrical, slightly narrowing towards the indistinct enlarged tip, 5 mm long, 150 μm wide (Fig. 10B–D). *Conidiophores* arising from a network of hyphae loosely attached to the surface of the synnemata along the entire length of synnemata, except for the base, roughened conspicuous, (87.5–)120–215(–250) × (6–)7.5–9(–10) μm, becoming short towards the tip of synnemata, abruptly tapering into a slender apex and terminating in a swollen vesicle, bearing a group of metulae, phialides and forming a spherical conidial head, (34–)35.5–38.5(–41) μm diam (Fig. 10C–E). *Vesicles* subglobose to globose, (9–)9.5–10.5(–11) μm diam (Fig. 10F). *Metulae* borne on vesicle, broadly obovoid, 8–9.5(–10) × 6–7(–8) μm, bearing phialides (Fig. 10F). *Phialides* narrowly clavate to cylindrical, 6–8(–9) × 2–2.5(–3) μm, each bearing a single conidium (Fig. 10F). *Conidia* ellipsoid, occasionally with an indistinct acute apex, (2–)2.5–3(–4) × 1–1.5 μm (Fig. 10G). Sexual morph and *Granulomanus* synasexual morph not observed.

Culture characteristics: Colonies on PDA attaining a diam of 1.3 cm in 20 d at 25 °C, white, cottony; reverse pale brown, becoming dark brown with age at the centre (Fig. 10H). Sporulation not observed in culture.

Material examined: **Thailand**, Nakhon Ratchasima Province, Khao Yai National Park, Mo Sing To Nature Trail, on *Salticidae* attached to the underside of a dicot leaf, 27 Apr. 2011, *K. Tasanathai, P. Srikitikulchai, S. Mongkolsamrit, A. Khonsanit, K. Sansatchanon & W. Noisripoom* (BBH30518, living culture BCC 47555).

Notes: Among *Gibellula* spp. producing aspergillus-like conidiophores, *G. longispora* bears the greatest morphological resemblance to *G. pulchra* in having almost identical macroscopic and microscopic features. They can be distinguished from each other only by the shape of conidia – *G. pulchra* typically produces cylindrical, ellipsoid to ovoid conidia (Fig. 11) whereas *G. longispora* produces only bacilliform conidia which are significantly longer than those reported for *G. pulchra*. Even though their outer appearances can easily mislead species identification, the multilocus-based phylogenetic analysis showed very clear segregation between them by placing *G. longispora* far from *G. pulchra* (Fig. 1). Considering the sister clades of *G. pulchra* and *G. nigelii*, *G. nigelii* has markedly smaller conidia (Table 3). Since the number of synnemata and the arrangement of conidiophores on synnemata are important features used effectively in species discrimination within the genus *Gibellula*, *G. pulchra* can be simply distinguished from *G. nigelii* by forming numerous synnemata with crowded conidiophores (Fig. 10A–D) whereas *G. nigelii* produces a single synnema with scattered conidiophores.

Gibellula solita Kuephadungphan, Tasanathai & Luangsa-ard, ***sp. nov.*** MycoBank MB 841094. Fig. 12.

Etymology: From the Latin '*solitus*', meaning usual, referring to the original feature of *Gibellula* of producing aspergillus-like conidiophores.

Typus: **Thailand**, Buri Ram Province, Dong Yai Wildlife Sanctuary, Pa Takong Nature Trail, on *Theridiidae* attached to the underside of a dicot leaf, 10 Dec. 2010, *K. Tasanathai, P. Srikitikulchai, A. Khonsanit,*

K. Sansatchanon, W. Noisripoom, A. Saksrikrom, B. Saracam & S. Mongkolsamrit (**holotype** BBH38545, culture ex-type BCC 45574). GenBank: ITS = OK040736, LSU = OK040712, *TEF1* = OK040703, *RPB1* = OK040721.

Yellow mycelia fully covering the spider body, occasionally on its legs (Fig. 12A). *Synnemata* brownish white in a group of three, cylindrical, attenuated, 7 mm long, 175 μm wide, narrowing to a slender apex, terminating into a swollen tip (Fig. 12B–D). *Conidiophores* scattered, arising from the outer layer of synnemata and the mycelia somewhat loosely attached to the host body and legs, multiseptate, verrucose, (62.5–)82–146(–180) × 7.5–9.5(–10) μm, becoming shorter towards the tip of synnemata, tapering abruptly to a distinct neck, enlarging into a vesicle (Fig. 12G). *Vesicle* globose to subglobose, (6.5–)7–8(–8.5) μm diam, bearing a group of metulae (Fig. 12G). *Metulae* broadly obovoid, (6.5–)7–7.5(–8) × 5–6(–7) μm. *Phialides* borne on metulae, narrowly clavate to cylindrical, 6–7(–7.5) × 2–2.5 μm, each bearing a conidium (Fig. 12G). A vesicle, metulae and phialides forming a spherical conidial head, (30–)30.5–32.5(–33) μm diam (Fig. 12G). *Conidia* ellipsoid to ovoid, occasionally globose, (1.5–)2–2.5(–3) × 1–1.5(–2) μm (Fig. 12H).

Culture characteristics: Colonies on PDA attaining a diam of 1.1 cm in 20 d at 25 °C, white, cottony; reverse pale brown, darkening with age towards the centre (Fig. 12I). Sporulation not observed in culture.

Notes: In comparison with *G. unica* which was phylogenetically placed close to *G. solita* as a sister clade (Fig. 1), *G. solita* can be easily distinguished from *G. unica* in mostly having ovoid conidia with the length almost twice shorter as well as distinctly producing shorter conidiophores. However, it might be difficult to tell them apart based solely on the outer appearances as they both produce a single to a few long synnemata.

Gibellula trimorpha Tasanathai, Khonsanit, Kuephadungphan & Luangsa-ard, ***sp. nov.*** MycoBank MB 841089. Fig. 13.

Etymology: Refers to the three different reproductive morphs occurring simultaneously on a single specimen.

Typus: **Thailand**, Phetchabun Province, Nam Nao National Park, Headquarter Nature Trail, on *Salticidae* attached to the underside of a dicot leaf, 6 May 2009, *K. Tasanathai, P. Srikitikulchai, S. Mongkolsamrit & T. Chohme* (**holotype** BBH27981, culture ex-type BCC 36526). GenBank: ITS = OK040737, *TEF1* = OK040704, *RPB1* = OK040722, *RPB2* = OK040728.

Spider host covered by brown mycelial mat. *Synnema* arising directly from the host abdomen, erect, cylindrical, short stipe, white, 3 mm long, composed of parallel, densely compacted hyphae (Fig. 13A). *Conidiophores* hyaline, septate, 65–230 × 7–9 μm (Fig. 13B–C). *Conidial heads*, 37–44 μm diam (Fig. 13C). *Vesicle* ellipsoidal, subglobose to globose, smooth, hyaline, 9–12 × 7–10 μm. *Metulae* broadly ellipsoidal, hyaline, smooth occasionally, 7–10 × 6–7 μm. *Conidia* fusiform, in short chains, 4–5 × 2 μm. *Conidiophores* of *Granulomanus* synasexual morph present, well-differentiated, roughened to distinctly verrucose, particularly around the base. *Phialides* holoblastic, cylindrical, clavate, flask-shaped, to irregularly shaped, mostly verrucose, rarely smooth, with one to three conspicuous denticles, 8–13 × 3 μm, bearing solitary, long, filiform conidia. *Conidia* smooth, hyaline, 10–19 × 1–1.5 μm (Fig.
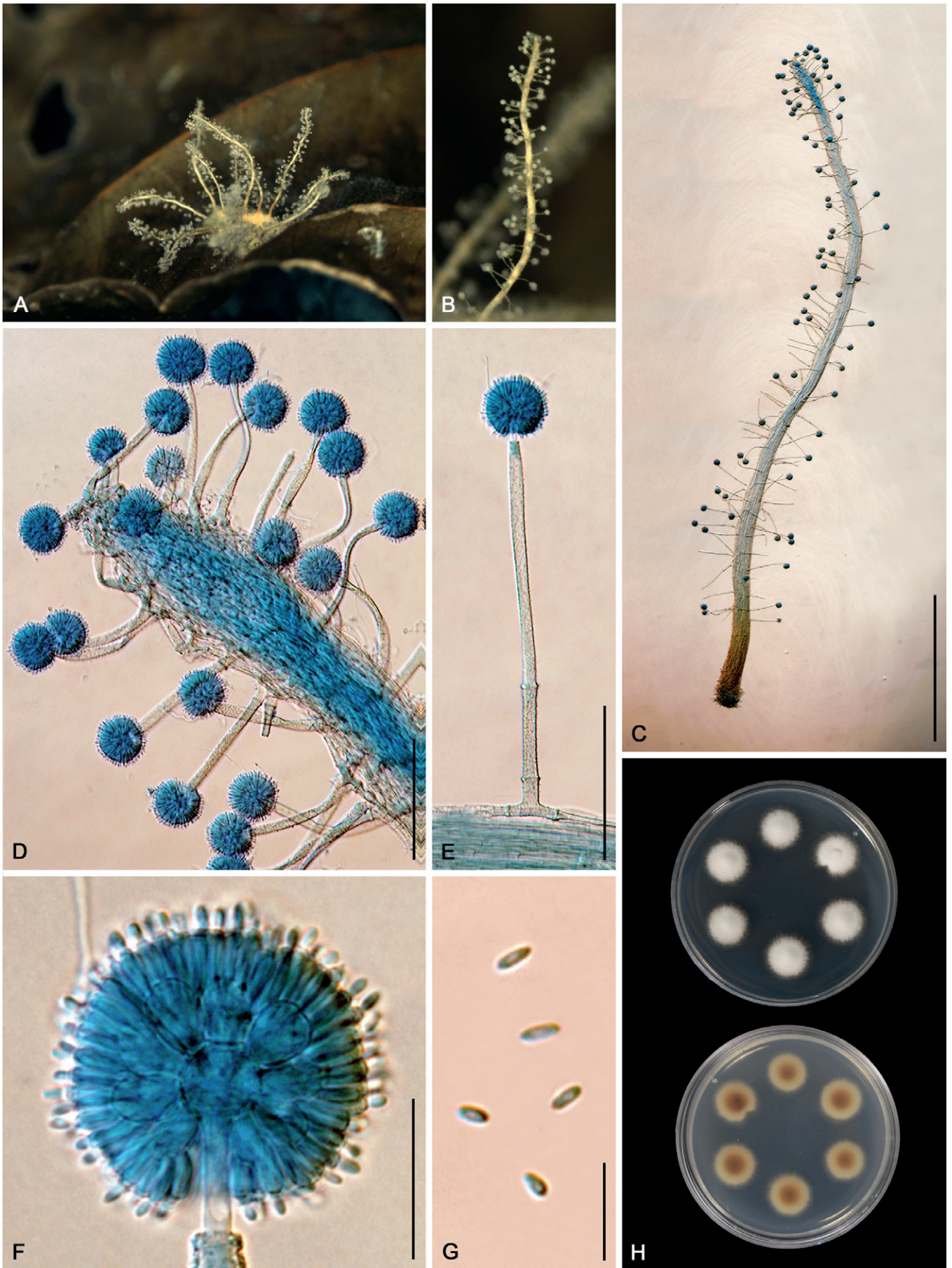
Fig. 10. *Gibellula pulchra*. **A.** Fungus on spider. **B–C.** Synnemata. **D.** Upper part of synnema showing a slight enlarged tip. **E.** Conidiophore showing a spherical conidial head. **F.** Conidial head bearing conidia. **G.** Conidia. **H.** Colonies obverse and reverse on PDA at 25 °C after 20 d. Scale bars: C = 1 mm; D–E = 100 µm; F = 20 µm; G = 10 µm.
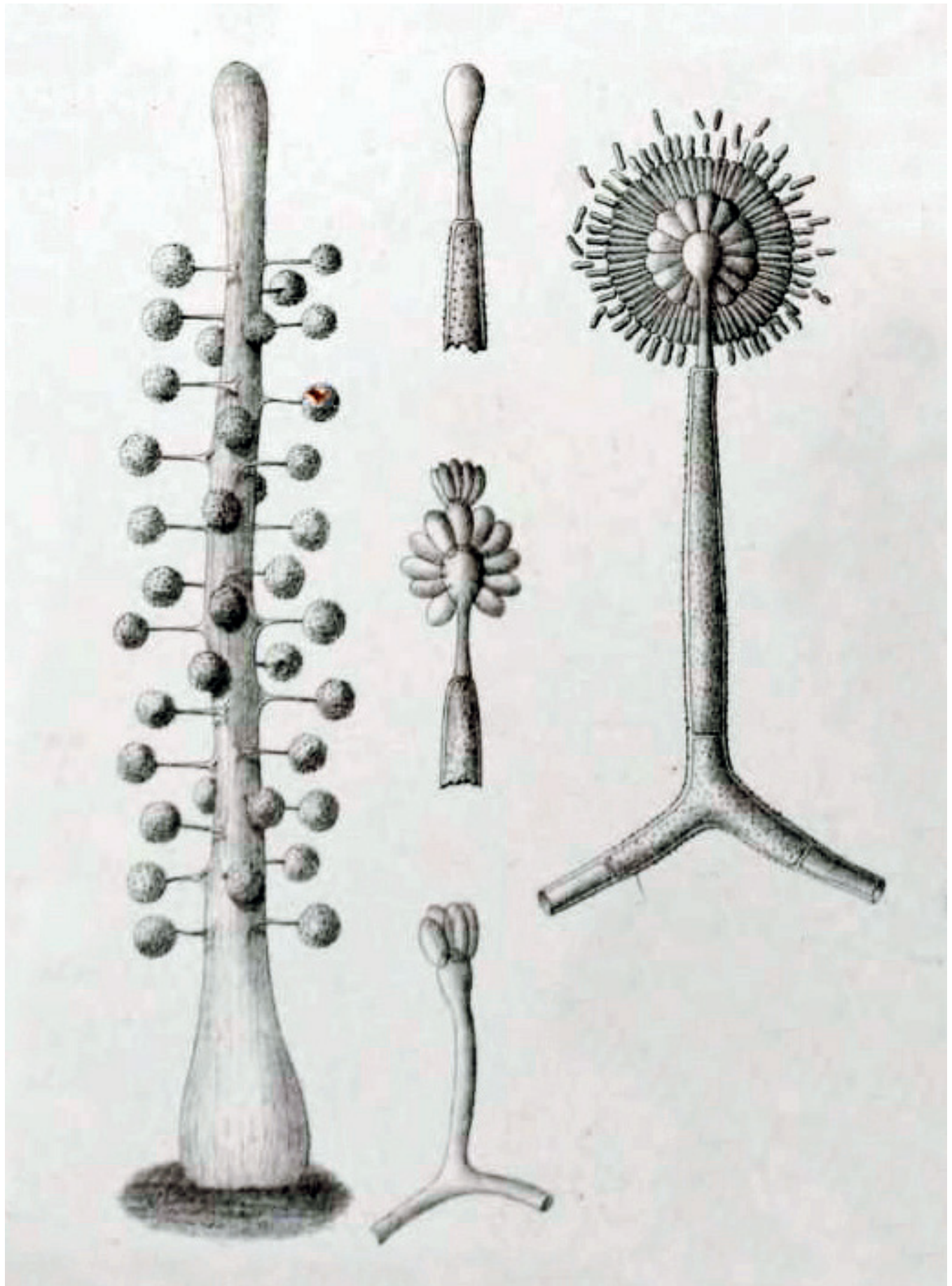
Fig. 11. *Gibellula pulchra* (Sacc.) Cavara, Atti Ist. Bot. Univ. Pavia Ser II, 3: 347. 1894.
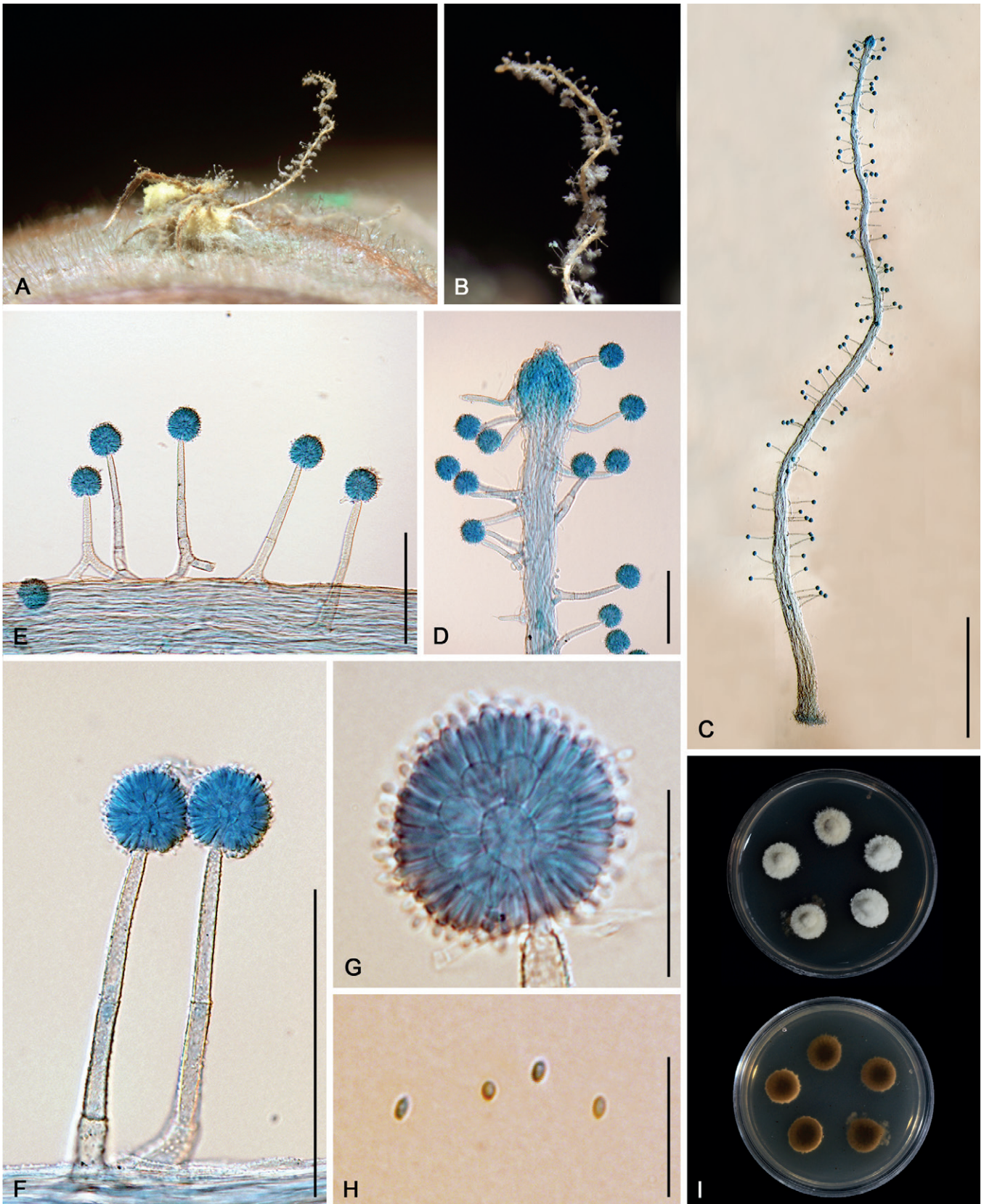
Fig. 12. *Gibellula solita*. **A.** Fungus on spider. **B–C.** Synnema. **D.** Upper part of synnema showing a swollen tip. **E–F.** Conidiophores showing spherical conidial heads. **G.** Conidial head bearing conidia. **H.** Conidia. **I.** Colonies obverse and reverse on PDA at 25 °C after 20 d. Scale bars: C = 1 mm; D–F = 100 µm; G = 25 µm; H = 10 µm.

13D). Sexual morph present. *Perithecia* occurring on the mycelial mat covering the host body, superficial, ovoid, reddish-brown, two-third covered with the loose network of mycelia, (340–)470–690 × (200–)214–282(–310) µm (Fig. 13E). *Asci* cylindrical, 340–530 × (7–)7.5–9(–10) µm. *Asci caps*, 4–5(–5.5) × (5–)6–7.5(–8) µm (Fig. 13F–G). *Ascospores* filiform, multiseptate, breaking into bacilliform part-spores, (3–)4–6(–9) × 1.5–2(–2.5) µm (Fig. 13H).
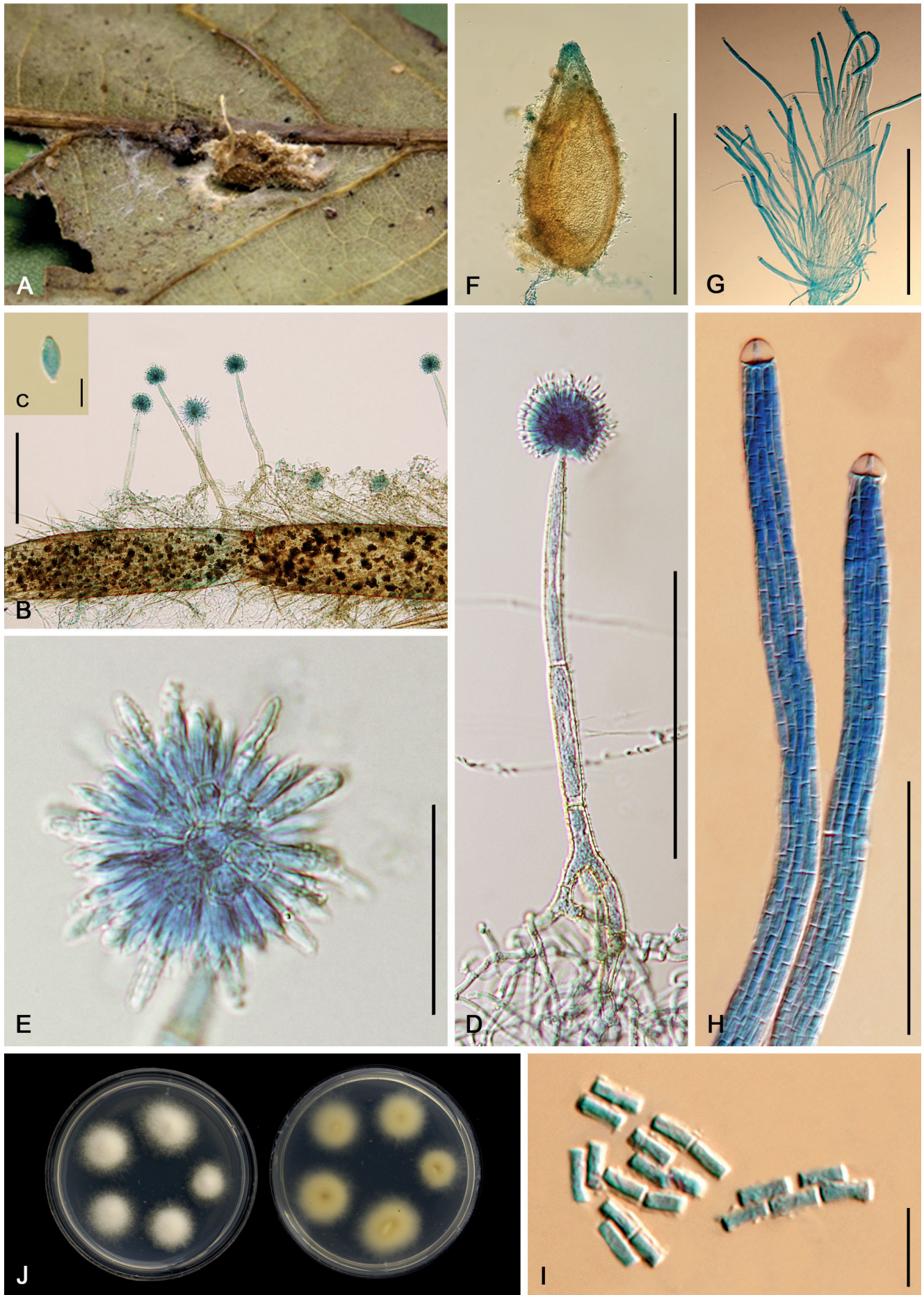
Fig. 13. *Gibellula trimorpha*. **A.** Fungus on a spider. **B.** Conidiophores arising from the mycelia covering the spider's leg. **C.** Conidium. **D.** Conidiophore of *Gibellula* conidial stage. **E.** *Granulomanus* conidial stage forming aspergillus-like conidial head. **F.** Perithecium. **G.** Asci. **H.** Asci with ascus caps. **I.** Part-spores. **J.** Colonies obverse and reverse on PDA at 25 °C after 20 d. Scale bars: F = 500 μm; B, G = 250 μm; D = 100 μm; H = 50 μm; E = 20 μm; I = 10 μm; C = 2 μm.

Culture characteristics: Colonies on PDA attaining a diam of 1.5 cm in 20 d at 25°C, white, velvety; reverse cream, becoming pale brown with age towards the centre (Fig. 13l).

Material examined: **Thailand**, Phetchabun Province, Nam Nao National Park, Headquarter Nature Trail, on *Oxyopidae* attached to the underside of a dicot leaf, 6 May 2009, *K. Tasanathai, P. Srikitikulchai, S. Mongkolsamrit & T. Chohme* (BBH29456, living culture BCC 36538).

Notes: *Gibellula trimorpha* shows morphological resemblance to *G. dimorpha* (Tzean *et al.* 1998*)* in bearing three different reproductive morphs consisting of a *Gibellula* conidial morph, *Granulomanus* conidial morph and *Torrubiella* sexual morph. It displays a distinct feature of aspergillus-like conidiophores bearing both *Gibellula* and *Granulomanus* phialides. Morphological comparison between *G. trimorpha* and *G. dimorpha* did not show any significant difference as all characters share similarity in shape and size falling within nearly the same ranges (Table 2)*,* making it difficult to discriminate these two species based solely on morphology. Even so, the phylogenetic evidence highly supported *G. trimorpha* as a new species.

Gibellula unica L.S. Hsieh, Tzean & W.J. Wu, Mycologia 89: 312. 1997. Fig. 14.

Spider host covered by white mycelial mat. *Synnemata* cylindrical, attenuated, in groups of 2–3, white to brownish white (Fig. 14A–B). *Conidiophores* arising laterally from the outer layer of synnemata and directly from the mycelial mat covering the host, scattered, septate, roughed, (225–)235–273(–280) × (7.5–)8–11(–12) μm, terminating in a swollen vesicle (Fig. 14C–D). *Conidial heads* spherical, (28–)32–39(–40) μm diam (Fig. 14D). *Vesicles* subglobose to globose, 4–6 μm diam. *Metulae* broadly obovoid, 5–7(–9) × (3–)3.5–5(–6) μm. *Phialides* borne on metulae, broadly cylindrical to clavate, (5–)7–9(–10) × 2–3 μm, bearing a conidium. *Conidia* narrowly ellipsoid, (3–)4–5 × 2 μm (Fig. 14E). *Granulomanus* synasexual morph present, occurring on the synnemata or the mycelial mat covering the host, forming conidiophores or branched hyphae bearing polyblastic, irregularly shaped phialides (Fig. 14F–G). *Conidiophores* septate, roughened, 39.5–44.5 × 5–6 μm, abruptly narrowing toward the apex, forming a vesicle. *Vesicles* obovoid, 7.5 μm diam. *Metulae* broadly obovoid or irregularly shaped, 7.5 × 6 μm. *Phialides* broad cylindrical to clavate, 6–10(–11.5) × 3.5–4 μm (Fig. 14F), developing multiple denticles, each bearing a filiform conidium, (6–)17–22(–23) × 1 μm (Fig. 14H). Sexual morph not observed.

Table 4. Morphological comparison of Thai *G. unica* and the ex-type specimen.

Characters	*G. unica* from Thailand	*G. unica* (Tzean *et al.* 1997)
Locality	Thailand	Taiwan
Host	*Pholcidae*	*Arachnida*
***Gibellula* anamorph**	Present	Present
Mycelia	White	White
Synnemata	White to brownish-white, cylindrical, attenuated, in groups of 2–3	Yellowish grey, cylindrical, attenuated, in groups of 5–6, 4–5 mm × 96–184
Conidiophores (μm)	Arising from the synnemata and the mycelial mat covering the host, scattered, septate, rough-walled, 225–280 × 7.5–12	Arising from the synnemata and the mycelial mat covering the host, scattered or densely compacted, septate, rough-walled, 122–244 × 6.4–13.5
Conidial heads (diameter, μm)	Spherical, 28–40	Spherical, 40–52
Vesicle (diameter, μm)	Globose to subglobose, 4–6	Ellipsoidal, subglobose to globose, 7.1–9.9 × 5.6–7.9
Metulae (μm)	Broadly obovoid, 5–9 × 3–6	Broadly ellipsoidal, obovoid, 5.6–9.1 × 4.8–7
Phialides (μm)	Broadly cylindrical to clavate, 5–10 × 2–3	Broadly cylindrical to ellipsoidal with a short neck, apically thickened, 6.4–9.5 × 2.8–4.2
Conidia (μm)	Narrowly ellipsoid, 3–5 × 2	Fusiform, occasionally apiculate, in short chains, 4.0–6.8 × 1.6–2.2
***Granulomanus* anamorph**	Present, formed both aspergillus- and granulomanus-like conidiophores	Present, formed both aspergillus- and granulomanus-like conidiophores
Conidiophores (μm)	Occurring on the synnemata and the mycelial mat covering the host, septate, rough-walled, 39.5–44.5 × 5–6	Occurring particularly around the base of the synnemata, septate[1], rough-walled[1], (No data)
Vesicle (diameter, μm)	Obovoid, 7.5	Subglobose[1], (No data)
Metulae (μm)	Broadly obovoid, 7.5 × 6	Broadly ellipsoidal[1], (No data)
Phialides (μm)	Broadly cylindrical to clavate, 6–11.5 × 3.5–4	Holoblastic, cylindrical, clavate, flask-shaped to irregularly shaped, with 1–3 denticles, 6.8–11.9 × 3.2–4
Conidia (μm)	Filiform, 6–23 × 1	Filiform, 11.1–17.5 × 1.0–1.6
Teleomorph	Absent	Absent

[1]Based on the species description contributed by Tzean *et al.* (1997).
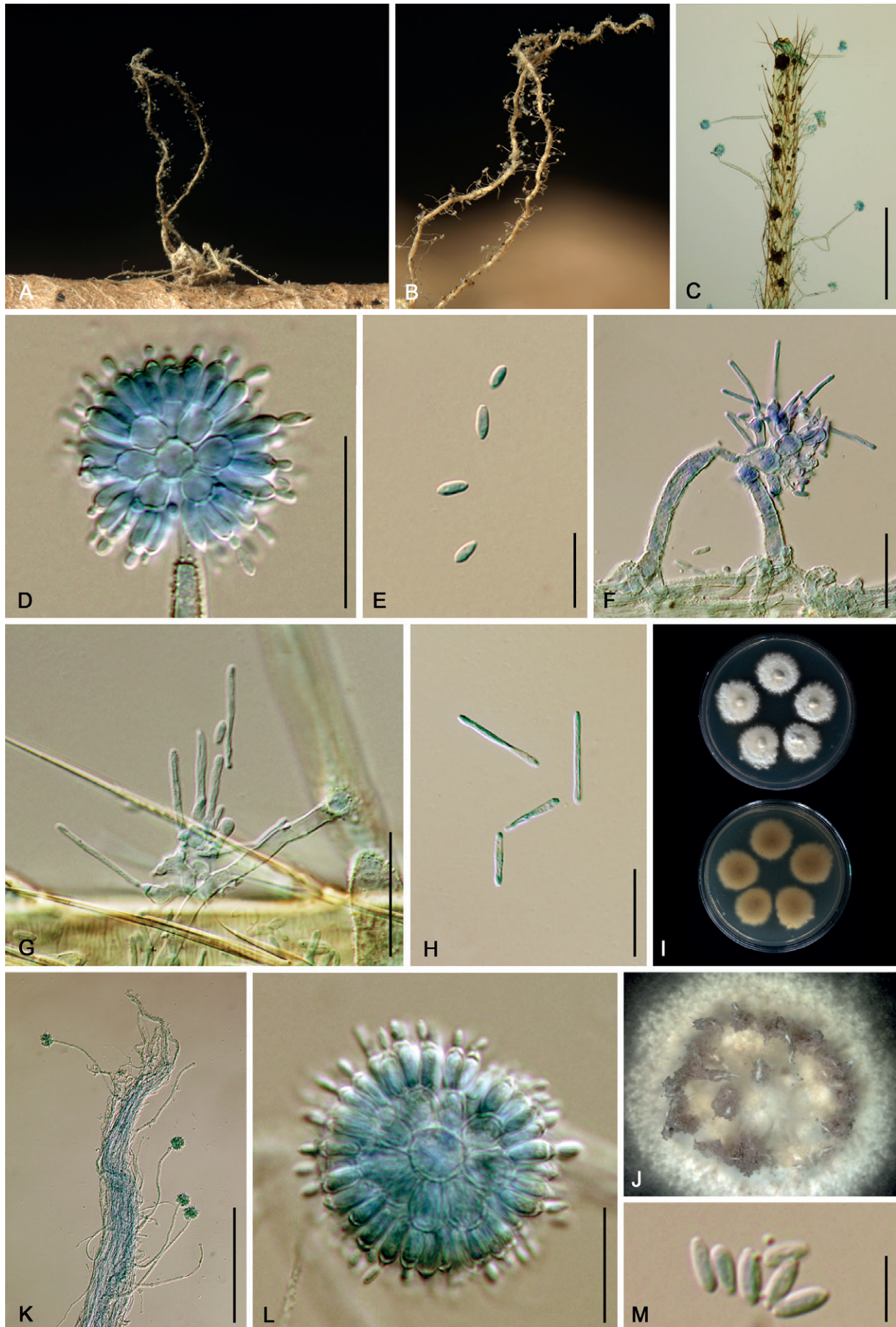
Fig. 14. *Gibellula unica*. **A.** Fungus on spider (BBH30027). **B.** Part of synnema showing conidiophores (BBH30034). **C.** Conidiophores arising from the mycelia covering a spider's leg (BBH30034). **D.** Conidial head of *Gibellula* conidial stage (BBH30034). **E.** Conidia of *Gibellula* conidial stage (BBH30034). **F.** *Granulomanus* conidial stage forming aspergillus-like conidiophores (BBH30034). **G.** Typical *Granulomanus* conidial stage occurring on the mycelial network covering a spider's leg. **H.** Filiform conidia of *Granulomanus* conidial stage. **I.** Colonies obverse and reverse on PDA at 25 °C at 28 d. **J.** Grayish-brown synnema formed on PDA after a month. **K.** Part of a synnema formed on PDA showing aspergillus-like conidiophores. **L.** Conidial head produced on PDA. **M.** Conidia produced on PDA. Scale bars: C = 500 µm; J = 200 µm; D, F, G, K, L = 20 µm; E, H = 10 µm; M = 5 µm.

Culture characteristics: Colonies on PDA attaining a diam of 1.7 cm in 28 d at 25 ºC, floccose, forming irregular margin, white to yellowish-white, reverse light brown, darkening towards the centre with age (Fig. 14I). Sporulation occurring after a month, forming synnemata in a circle, powdery, brownish grey. *Synnemata* composed of loose hyphae, white, becoming yellowish white toward base, cylindrical, tapered toward the apex, curved (Fig. 14J). *Conidiophores* crowded, septate, roughened, 192–227(–239) × (5–)6–8.5(–9) µm. *Conidial heads* spherical, (27–)29–33(–35) µm diam (Fig. 14K). *Vesicles* spherical, 7–9(–10) µm diam. *Metulae* borne on vesicle, obovoid, (5–)5.5–7.5(–10) × 4–6 µm, bearing multiple phialides. *Phialides* broad cylindrical to clavate, 5–6.5(–8) × 2–3 µm. *Conidia* narrow ellipsoid, (3–)4–5 × 1–2 µm (Fig. 14M).

Materials examined: **Thailand**, Kalasin Province, Phu Si Than Wildlife Sanctuary, Khok Pa Si Community Forest, on *Pholcidae* attached to the underside of dicot leaf, 24 Oct. 2010, *A. Khonsanit* (BBH30027, living culture BCC 45112 and BBH30034, living culture BCC 46590).

Notes: Besides *G. trimorpha* and *G. dimorpha*, *G. unica* is also known to have a *Granulomanus* conidial morph producing aspergillus-like conidiophores along with a *Gibellula* conidial morph. Nonetheless, *G. unica* can be distinguished from *G. trimorpha* and *G. dimorpha* by producing narrowly ellipsoidal *Gibellula* conidia instead of fusoid conidia. Moreover, its asexual-sexual link has not yet been found. Herein, we report *G. unica* from Thailand for the first time since the species was described *(*Tzean *et al.* 1997*)*. We also provide the description of colony morphology and the evidence of sporulation on an artificial medium. The Thai specimens were found to be very similar to the type of *G. unica* by having all morphological features in common. The Thai specimens only show slight differences in the size of *Gibellula (*shorter than type*)* and *Granulomanus (*longer than type*)* conidia *(*Table 4*)*. As the *Granulomanus* conidial morph could not be observed in specimen BBH30027, *G. unica* does not always produce a *Granulomanus* conidial morph along with a *Gibellula* morph.

DISCUSSION

Among *Gibellula* spp., *G. pulchra* has the longest and the most complicated nomenclatural history (Figs 10, 11). Several species were synonymised with *G. pulchra* (see Shrestha *et al.* 2019) causing confusion in the taxonomy of the genus. As *G. pulchra* is a cosmopolitan species, it has been recorded from many countries including Hawaii (USA), Puerto Rico, Venezuela, Guyana, Trinidad, Chile, Papua New Guinea (Mains 1950), Ghana (Samson & Evans 1973), Japan (Kobayasi 1977), Solomon Islands (Humber & Rombach 1987), Canada (Strongman 1991), Ecuador (Samson & Evans 1992), South Africa (Rong & Botha 1993), Taiwan (Tzean *et al.* 1997), Turkey (Selçuk *et al.* 2004), Thailand (Luangsa-ard *et al.* 2007) and Brazil (Costa 2014). According to the species description contributed by Mains (1950), Humber & Rombach (1987) and Tzean *et al.* (1997), *G. pulchra* can occur either in the absence or presence of a *Torrubiella* sexual morph or *Granulomanus* synasexual morph. Synnemata are numerous or solitary, clavate to cylindrical, yellow or yellowish white to brown or white or greyish or violet, violaceous brown to brown with age or when dried, sometimes slightly enlarged upwards of the tip, and consist of multiseptated longitudinal hyphae. Conidiophores arise from a network of hyphae loosely attached to the surface of the synnemata or occasionally from the mycelia

covering the host body or legs. They are usually rough-walled and arranged in a hymenium along the length of synnemata, each abruptly tapering into a slender apex which subsequently enlarges into a globose, subglobose or obovoid vesicle which bears multiple broadly obovoid metulae. Phialides borne on metulae are narrowly clavate, thickened apically and sometimes extended into a short neck. A vesicle, together with multiple metulae and phialides, form a spherical head that bear either ovoid, fusoid, fusoid-ellipsoid or ellipsoid conidia. Conidia can be found singly or in chains. Based on these descriptions, the species proposed herein as *G. longispora*, *G. nigelii*, *G. parvula* as well as *G. solita* seemed to fit well with previous identifications as *G. pulchra*.

Based on our continuous survey and study of *Gibellula*, over 2 000 specimens exhibiting *Gibellula* traits have been collected, of which around 5 % were preliminarily identified as *G. pulchra*. However, multilocus phylogenetic analyses showed many of them to represent new species, including *G. pigmentosinum*. From our observations, *G. pulchra* can be recognised only by producing numerous whitish, greyish, yellowish to violaceous, cylindrical, attenuated, long synnemata with a tapered tip or slightly enlarged tip, long aspergillus-like conidiophores densely crowded on the surface and along the entire length of synnemata and forming fusoid to ellipsoid conidia either singly or in chains. These descriptions exclude *G. nigelii*, *G. parvula* and *G. solita* from *G. pulchra sensu lato* as they produce a single, a pair of two and a group of three synnemata, respectively, as well as *G. longispora* which produces long bacilliform conidia. Considering the specimen BBH30518, its morphology is strongly reminiscent of *G. pulchra* by having all characters similar to *G. pulchra* in both shape and size (Table 3). Owing to a lack of DNA sources of the type as well as the loss of original material, comparison between our specimen and the holotype is infeasible. To solve the problem of the lost holotype and a lack of its DNA sequences, epitypification and neotypification have been suggested (Ariyawansa *et al.* 2014). Nevertheless, our specimen with affinity to *G. pulchra* could not be designated as either epitype or neotype according to the epitypification and neotypification principle that the epitype or neotype should be obtained from the same location as the type, in this case Italy.

Considering the phylogenetic placements of *G. longispora*, *G. nigelii*, *G. parvula*, *G. pulchra* and *G. solita*, they were distinctly placed in different relatively well-supported clades representing separate species, consistent with morphology-based classification. Since these species have most of the morphological characters in common, only a few can be used to tell them apart. In our study the number of synnemata appears to be an informative feature that can discriminate *G. parvula*, *G. nigelii* and *G. solita* from *G. longispora*, and *G. pulchra* and *G. nigelii* from *G. parvula* and *G. solita*, whereas the shape of conidia can be used to distinguish *G. longispora* from *G. pulchra* and *G. parvula* from *G. solita*. However, due to the limited number of specimens studied for each taxon these observations may change.

Microscopic features including vesicles, metulae and phialides are considered to be inappropriate features for discriminating species that produce aspergillus-like conidiophores, because the sizes of these characters often fall into the same ranges with nearly identical shapes. Vesicles are commonly globose to subglobose, metulae are broadly obovoid to obovoid whereas phialides are often narrowly clavate to cylindrical. In addition to these characters, conidiophore length can sometimes appear to be a misleading feature. As conidiophores become shorter upwards the synnema, the length of conidiophores thus varies depending on where they are observed. Owing to the fact that fungal herbaria are

supposed to preserve specimens under the best condition which forbids studying a whole synnema, particularly when only a single synnema is produced, the actual range of conidiophore lengths is rarely recorded.

The conidiophores of *G. brevistipitata* and *G. pilosa* can be measured along the entire length of synnemata, which is particularly useful for distinguishing these species. These two species produced aspergillus-like conidiophores that are at least twice as short in *G. brevistipitata* (47.5–)58–100(–115) µm than *G. pilosa* (140–)151–265(–420) µm (Table 5). Besides the length of conidiophores, the shape of synnemal tips and the length of synnemata are considered to be reliable characters for differentiating closely related species within *Gibellula*, including *G. brevistipitata* and *G. pilosa,* that are phylogenetically regarded as sister taxa (Fig. 1). *Gibellula brevistipitata* forms distinctly short synnemata with slightly enlarged ovoid tips, whereas *G. pilosa* produces longer synnemata with globose to subglobose apices (Fig. 6). *Gibellula pilosa* can be easily recognised at first glance by the numerous long conidiophores on the mycelia covering the host body and legs.

Among the proposed new species, *G. longicaudata* is the only one that produces penicillium-like conidiophores (Fig. 5). Thus far, only *G. clavulifera*, *G. leiopus* and *G. scorpioides* are known to produce such conidiophores. Based on morphology, *G. longicaudata* was found to be rather close to *G. scorpioides* by having a long cylindrical synnema arising from the posterior part of the spider host, and producing very short penicillium-like conidiophores bearing fusoid conidia. Table 6 shows the comparison of important morphological characters between these species. Interestingly, *G. longicaudata* was phylogenetically placed far from the ex-type strain of *G. scorpioides*, but rather close to *G. cebrennini* and *G. fusiformispora* that have penicillium-like conidiophores (Fig. 15B) instead of aspergillus-like conidiophores (Fig. 15A).

In this study, we also newly reported *G. dimorpha* and *G. unica* from Thailand. These two species are well-known to form a *Granulomanus* conidial morph that can develop aspergillus-like conidiophores. The Thai specimen BBH30034 was found to be morphologically similar to *G. unica* from Taiwan in having white mycelia, a few synnemata on the spider hosts, aspergillus-like conidiophores bearing narrowly ellipsoid conidia and a *Granulomanus* synasexual morph forming gibellula-like conidiophores. The morphological characters of the specimens from different countries showed the same shapes and sizes falling into the same ranges with some minor differences (Table 4, see notes for the species). In contrast, specimen BBH30489 was morphologically reminiscent of *G. dimorpha* (Tzean *et al.* 1998). Based on the comparison of morphological characters between BBH30489 and the type, they share similarities in shape but not size of characters (Table 2, also see notes for the species). The morphological differences between these specimens and a lack of DNA sequence data corresponding to the type have thus left us to question whether our specimen truly represents a new species or falls within the species boundary of *G. dimorpha*. To avoid introducing taxonomic confusion by proposing a new species from the fungus that might later turn out to be the described species, we decided to assign *Gibellula* strain BBH30489 to *G. dimorpha*. With regard to its sister clade, *G. trimorpha* appeared to be very much closer to *G. dimorpha* in having all morphological characters in common which could easily mislead species identification. Nevertheless, the molecular traits segregated them into two taxa (Fig. 1). Although morphological data of some certain characters of *G. trimorpha* remains incomplete, the molecular evidence was

sufficient to propose it as a new species.

Recently, Lücking *et al.* (2020) raised awareness of how not only phenotypes can mislead the identification of cryptic species, but also how a single morphologically well-defined species can possess a complex genetic structure. The approach of integrative (polyphasic) taxonomy is highly suggested for accurate species delimitation to overcome these obstacles. For closely related species with typically few distinguishing characters, phylogeny-based classification and identification is important. Nevertheless, it is sometimes questionable whether the observed genetic divergence between putative species could be considered as sufficient for proposing a new species. One approach is to use the genetic distance between known sister species in a given taxonomic group as a threshold for assignment of species status (Baker & Bradley 2006). Although this approach is not widespread in fungal taxonomy, it has been used successfully in some studies (*Ophiocordyceps unilateralis*: Kobmoo *et al.* 2012, *O. myrmecophila*: Khonsanit *et al.* 2019) and is useful for proposing new species. Using the divergence between *G. cebrennini* and *G. fusiformispora* as the threshold, *G. longicaudata*, *G. longispora*, *G. nigelii*, *G. parvula*, *G. pilosa*, *G. solita* and *G. trimorpha* could be proposed as new species. Particular attention should be paid to the taxa BCC45580 and BCC57817 in which the divergence between them was just below the threshold. However, the morphological evidence strongly supported the segregation between them. From the integrative phylogeny considering the morphological and genetic data together, *G. brevistipitata* and *G. pilosa* were thus proposed to accommodate these taxa, respectively.

To identify species of invertebrate-parasitic fungi those that have a narrow host range or are restricted to a single host, host specificity was suggested to be a very informative character (Johnson 1968, Evans *et al.* 2011, Vialle *et al.* 2013, Araújo *et al.* 2018).

The identification of the spider hosts of *Gibellula* spp. at the family ranks was first made by Van der Bijl (1922), who reported *Lycosidae* as a host of *G. haygarthii*, which is now synonymised with *G. pulchra* (Shrestha *et al.* 2019). Later, many attempts were made to identify the hosts of several species of *Gibellula* at the genus and species ranks (Petch 1948, Samson & Evans 1973, 1977, Strongman 1991, Costa 2014, Savić *et al.* 2016). Nevertheless, host specificity has not yet been clearly determined for most *Gibellula* species. For instance, the host morphologies of *G. leiopus* and *G. pulchra* reported by Savić *et al.* (2016) and Strongman (1991), respectively, seemed not to fit well the concepts of the individual species. In our previous study, we also attempted to identify the spider hosts parasitised by four new species of *Gibellula* (Kuephadungphan *et al.* 2020). Therein, *Cebrenninus cf. magnus*, *Storenomorpha* sp. and *Portia* sp. appeared to be exclusively associated to *G. cebrennini*, *G. pigmentosinum* and *G. scorpioides*, respectively, whereas the family *Deinopidae* was described for the first time as a host for *G. fusiformispora*. In total, *Gibellula* hosts have been reported among 16 spider families thus far (Table 7).

Salticidae is the largest family of spiders, and several *Gibellula* species have been reported to parasitise salticid spiders, including *G. pulchra* in this study, confirming a previous study by Samson & Evans (1973). Besides *G. pulchra*, other species of *Gibellula* parasitising salticid spiders include *G. clavulifera* (Samson & Evans 1977), *G. clavulifera* var. *alba* (Humber & Rombach 1987) and three new species reported in this study (*G. longispora*, *G. pilosa* and *G. trimorpha*). *Gibellula trimorpha* also appeared on *Oxyopidae* indicating that is not restricted to a single spider species and can infect a broad host range across multiple spider families.

Table 5. Morphological comparison of accepted species within *Gibellula* and all species proposed herein.

Species	Distribution	Synnemata	*Gibellula* anamorph					Granulomanus-like asexual morph		
			Conidiophores	Vesicles	Metulae	Phialides	Conidia	Conidiophores	Phialides	Conidia
G. alata	Sri Lanka (Petch 1932) Ghana (Samson & Evans 1973)	Up to 12, white, up to 0.8 mm long, 0.1 mm wide	Aspergillus-like	—	—	—	Oblong-oval or clavate, 4–9 × 2–4 µm	—	—	—
G. brevistipitata	Thailand	In a group of 5, cylindrical, brownish-white, becoming brown towards the tip, 2 mm long, 200 µm, swollen ovoid tip	Aspergillus-like, 47.5–115 × 6–8.5 µm, distinctly roughened	Spherical to broadly obovoid, 7.5–10 µm diam	Broadly obovoid or ellipsoidal, 7–10.5 × 5–7 µm	Cylindrical to narrowly clavate, 7–10 × 2–3 µm	Ellipsoidal, 3–4.5 × 1.5–2 µm	n/d	n/d	n/d
G. brunnea	Brazil (Samson & Evans 1992)	Multiple, with a stout yellow-tan stipe, 0.2–0.8 × 0.2–0.4 cm, broadening into globose to pyriform fertile area, 0.5–0.8 × 0.8–1.4 cm, and narrowed into a pale brown compact acuminate sterile tip	Aspergillus-like, 350 µm long, distinctly verrucose at the base	Ellipsoidal to globose, verrucose, pigmented, 10–15 µm diam	Ellipsoidal to obovoidal, smooth to roughened walled, hyaline, 10–12 × 6–9 µm	Mostly cylindrical also ellipsoidal, smooth to verrucose, pigmented, 10–15 × 3–4 µm	Fusiform, 8–10 × 2–2.5 µm	Mostly arising from the base of synnemata, verrucose, darkly pigmented, bearing 2–5 conidiogenous cells	Cylindrical, ellipsoidal, with 1–3 distinct denticles, smooth-walled	Filiform, 10–21 × 1–1.5 µm
G. cebrennini	Thailand (Kuephadungphan et al. 2020)	Single, white to cream, slightly enlarged toward the sterile tip	Aspergillus-like, 45–150 µm long, scattered verrucose	Broadly ellipsoidal to globose, 23–33.5 µm diam	Obovoidal, 5–9 × 3–6.5 µm	Narrowly obovoid, 4–9 × 1.5–3.5 µm	Fusiform, 4–9 × 1.5–3.5 µm	Mostly arising from the mycelial mat covering the host body	Polyblastic and irregularly shaped with multiple denticles	Filiform, 6–12 × 1–1.5 µm
G. clavata	Ecuador (Samson & Evans 1992)	Single, rarely paired, broadly clavate, 4–6 mm long, with a compact stipe, 1.5–2 x 0.1–0.2 mm, broadening into an ellipsoidal, pink to lilac fertile area	Aspergillus-like, 30–50 µm long, slightly verrucose at the base	Ellipsoidal to globose, verrucose, 5–8 µm diam	Ellipsoidal to obovoidal, smooth, hyaline, 6–7.5 × 4–5 µm	Cylindrical, smooth, hyaline, 5.5–7.5 × 2-3 µm	Fusiform, 6–7 × 2–2.7 µm	Arising from irregularly branched hyphae, bearing solitary conidiogenous cells	Flask-or irregularly shaped with 1–2 distinct denticles, 5–15 × 3–5.5 µm, smooth-walled	Filiform, 12–15 × 1–1.5 µm
G. clavispora	China (Chen et al. 2014)	Solitary, cylindrical, slender, scattered, attenuated, acuminate sterile tip	Aspergillus-like, 96–113 µm long, scattered	Obovate, hyaline, smooth-walled	Obovate,smooth-walled, 7.6–8.6 × 3.2 µm	Clavate, smooth-walled, with a short neck, 8.6–10.8 × 2.2 µm	Clavate to ellipsoidal, 5.4–6.5 × 1.1–2.2 µm	Absent	—	—
G. dabieshanensis	China (Huang et al. 1998)	—	Aspergillus-like, smooth-walled	—	—	Cylindrical, 7.9–10.8 × 1.8–2.9 µm	Fusiform, 3.2–4 × 1.1–1.8	Present	—	—

Table 5. (Continued).

| Species | Distribution | Synnemata | Gibellula anamorph | | | | | Granulomanus-like asexual morph | | |
			Conidiophores	Vesicles	Metulae	Phialides	Conidia	Conidiophores	Phialides	Conidia
G. dimorpha	Taiwan (Tzean et al.1998) Thailand (Luangsa-ard et al. 2010) Japan (Okuzawa 2012) Brazil (Costa 2014)	Solitary, attenuated, brownish-white, cylindrical, 5 mm x 200 µm	Aspergillus-like, 140–422 × 7.1–10.3 µm, roughened	Globose to subglobose, 7.9 × 11.1 µm	Broadly obovoid, 7.1–11.9 × 6.4–8.7 µm	Cylindrical to narrowly clavate, 5.6–8.7 × 2.5-4 µm	Fusoid, ellipsoidal to lemon shaped, 3.2–4.1 × 2–2.4 µm	Rough-walled to distinctly verrucose, 68–140 × 5.2–7.1 µm	Cylindrical, ellipsoidal, narrowly clavate, with 1–3 conspicuous denticles, 7.9–20.6 × 3.2–4 µm, smooth walled	Filiform, 9.1–23.8 × 0.8–2.4 µm
G. fusiformispora	Thailand (Kuephadungphan et al. 2020)	Single or in pairs, cream to light brown swollen sterile tip with acute apex	Aspergillus-like, 23–83 µm long, crowded verrucose	Subglobose to globose, 6–8 µm diam	Obovoid to broadly obovoid, 7–10 × 4.5-6 µm	Narrowly obovoid, 7-10 × 2-3 µm	Fusiform, 3.5-6 × 1.5-2.5 µm	Absent	Absent	Absent
G.gamsii	Thailand (Kuephadungphan et al. 2019)	Single or in groups of three, yellowish white to pale yellow, 5–15 mm long, short stipe and clavate brush-like fertile area terminating in a wing-like, yellow to gloden brown sterile tip	10–91 µm long, scattered verrucose	Ellipsoidal to globose, 6–10 × 5–10 µm diam	Ellipsoidal to obovoidal, 6–8.5 × 4–6 µm	Mostly oblong-elliptical, 6.5–8.5 × 1.5–3 µm	Fusiform, 3.5-5 × 1.5–2.5 µm	n/d	n/d	n/d
G.leiopus	Austria (Tkaczuk et al. 2011) Brazil (Costa 2014) Canada (Mains 1950) Czech Republic (Kubátová 2004) Ghana (Samson & Evans 1973) Japan (Kobayasi & Shimizu 1977) Mexico (Sánchez-Peña 1990) Sweden (Lundquist 1998, referred in Kubátová 2004) Taiwan (Tzean et al. 1997) Trinidad (Evans & Samson 1987) US (Mains 1950)	Yellow to whitish, cylindrical , 1.5–8 mm long, 80–300 µm wide	Penicillium-like, very short, crowded, smooth	Broadly obovoid or obpyriform, 10–18 × 4.5–8 µm	Broadly obovoid to ellipsoid, 7.5–12 × 3–5 µm	Narrowly clavate to subcylindric, 7.5–12 × 2.5–3.5 µm	Fusoid to fusoid-ellipsoid, 3–8 × 1–2 µm, singly or in short chains	n/d	n/d	n/d

Table 5. (Continued).

Species	Distribution	Synnemata	Gibellula anamorph					Granulomanus-like asexual morph		
			Conidiophores	Vesicles	Metulae	Phialides	Conidia	Conidiophores	Phialides	Conidia
G. longicaudata	Thailand	Single, greyish-white, cylindrical, tufted surface, sterile broadly ovoid tip	Penicillium-like, 10–35 × 3–5 µm, crowded, smooth	n/d	Broadly obovoid to ellipsoidal, 7–10 × 3-4 µm	Narrowly clavate to cylindrical, 7–10 × 2–3 µm	Fusoid, 3–6 × 1-2 µm	Arising from the septate hyphae	Distinctly roughened, very short, bearing polyblastic and irregularly shaped	n/d
G. longispora	Thailand	At least 20, cylindrical, attenuated, 5–5.5 mm × 175–200 µm	Aspergillus-like, 105–415 × 6–15 µm, crowded, minutely roughened	Globose to subglobose, 7–9 µm diam	Broadly obovoid, 6.5–11 × 5.5–7 µm	Narrowly clavate to cylindrical, 8.5–11.5 × 2.5–4 µm	Bacilliform to cylindrical, 3.5–9 × 1–1.5 µm	n/d	n/d	n/d
G. mainsii	Brazil (Samson & Evans 1992)	Vegetative mycelium hyaline, smooth-walled or irregularly verrucose, mostly 2–2.5 µm wide but occasionally thinner, 1.5–2 µm	Aspergillus-like, up to 350 µm in length, hyaline, smooth-walled	Ellipsoidal to globose, 10–15 µm diam	Ellipsoidal to obovoid, 10–12 × 6–9 µm	Cylindrical with a short neck, 10–13 × 3–4 µm	Fusiform, smooth-walled, 8–10 × 2–2.5 µm	n/d	n/d	n/d
G. mirabilis	Ecuador (Samson & Evans 1992)	Paired, pale to golden yellow, 1.5–2 × 0.6–1 mm, consisting of a short stipe and clavate brush-like fertile area, terminating in a short, golden brown sterile tip	Aspergillus-like, 80 µm long, slightly verrucose at the base	Ellipsoidal to globose, smooth to verrucose, 8–10 µm diam	Ellipsoidal to obovoidal, smooth, hyaline, 6–9 × 5–8 µm	Broadly cylindrical to ellipsoidal, smooth, hyaline, 5.5–7.5 × 3–4 µm	Fusiform, 5–7 × 2–3.5 µm	Arising from irregularly branched hyphae, bearing solitary or densely whorled conidiogenous cells	Flask or irregularly shaped with 1–2 distinct denticles, 5–12 × 3–4 µm, smooth-walled	Filiform, 14–25 × 1–1.5 µm
G. nigelii	Thailand	Single, white at the base becoming brown to greenish-brown upward, cylindrical, attenuated, 3 mm long, 70 µm wide, swollen tip with acute apex	Aspergillus-like, 42.5–90 × 7.5–10 µm, scattered, minutely roughened	Globose to subglobose, 7.5–11 µm diam	Broadly obovoid, 7–10 × 5–7 µm	Narrowly clavate to cylindrical, 6–9 × 2–3 µm	Ellipsoidal, 2.5–4 × 1–1.5 µm	n/d	n/d	n/d

Table 5. (Continued).

Species	Distribution	Synnemata	Gibellula anamorph					Granulomanus-like asexual morph		
			Conidiophores	Vesicles	Metulae	Phialides	Conidia	Conidiophores	Phialides	Conidia
G. pulchra	Austria (Tkaczuk *et al.* 2011) Belgium (Bosselaers 1984) Brazil (Costa 2014) British Guiana (Mains 1950) Canada (Strongman 1991) Chile (Mains 1950) Ecuador and Brazil (Samson & Evans 1992) Ghana (Samson & Evans 1973) Mexico (Sánchez-Peña 1990) Papua New Guinea (Mains 1950) Poland (Bałazy 2004) Solomon Islands (Humber & Rombach 1987) Spain (Santamaria & Girbal 1996) Taiwan (Tzean *et al.* 1997) Trinidad (Mains 1950) Turkey (Selçuk *et al.* 2004) USA (Mains 1950) Venezuela (Mains 1950)	Numerous, yellowish-brown, cylindrical	Aspergillus-like, 150–600 × 7–12 μm, smooth-walled	Ellipsoidal to obovoidal, 6.4–10 μm diam	Broadly obovoid, 6–12 × 4–6 μm	Clavate, 6–10 × 2–3 μm	Fusoid to ellipsoid, 2.5–6.4 × 1.5–2.3 μm	Absent	Absent	Absent
G. parvula	Thailand	A pair of two, yellowish-white, cylindrical with ovoid tips	Aspergillus-like, 47.5–185 × 6–11 μm, crowded, rough-walled	Globose to subglobose, 6.5–9 μm diam	Broadly obovoid, 6–10 × 4.5–8 μm	Narrowly clavate to cylindrical, 6–10 × 2–4 μm	Narrowly ovoid or ellipsoid or baciliform, 4–6 × 2–4 μm	n/d	n/d	n/d
G. pigmentosinum	Thailand (Kuephadungphan *et al.* 2020)	Single or in pairs, white becoming yellowish white at the base	Aspergillus-like, 55–226 μm long, crowded verrucose	Mostly globose, 5–10 μm diam	Broadly obovoid, 5.5–10 × 3–7.5 μm	Obovoid to clavate, 5–9 × 2–4.5 μm	Obovoid, 2.5–5.5 × 1–3 μm	Arising from irregularly branched hyphae	Irregularly shaped with one or more conspicuous denticles, mostly smooth	Filiform, 16–22.5 × 1–1.5 μm
G. pilosa	Thailand	A pair of two, light brown, cylindrical with globose tips, 6 mm × 475 μm	Aspergillus-like, 140–420 × 8.5–13.5 μm, crowded, minutely roughened	Spherical, 9–12 μm diam	Broadly obovoid, 9–12 × 6–9 μm	Narrowly clavate to cylindrical, 7–10 × 2.5–3 μm	Almond shaped, 3–4 × 1.5–2 μm	n/d	n/d	n/d

Table 5. (Continued).

Species	Distribution	Synnemata	*Gibellula* anamorph					Granulomanus-like asexual morph		
			Conidiophores	Vesicles	Metulae	Phialides	Conidia	Conidiophores	Phialides	Conidia
G. scorpioides	Thailand (Kuephadungphan et al. 2020)	Single, arising all over the host, 15–20 mm long with blunt tip	Penicillium-like, 20–30 µm long, stout, smooth, mostly biverticillate	Absent or hardly developed, bearing multiple metulae	Obovoid, 7–15 × 2–7 µm	Broadly cylindrical, 9–14 × 2–4 µm	Fusiform, 5–9 × 1.5–3 µm	Absent	Absent	Absent
G. shennongjiaensis	China (Zou et al. 2016)	Solitary, arising from mycelial mat, cylindrical, attenuated	Aspergillus-like, 77–107 µm long, distinctly roughened	—	Ellipsoidal, 5.4–7.6 × 2.1–4.3 µm	Clavate with a short neck, smooth, hyaline, 5.4–10.8 × 1.1–2.2 µm	Cylindrical or fusiform, 3.2–6.5 × 1.1–1.6	Present on culture	—	—
G. solita	Thailand	In a group of three, cylindrical, attenuated, 7 mm long, 175 µm wide, brownish white, swollen tip	Aspergillus-like, 62.5–180 × 7.5–10 µm, verrucose	Globose to subglobose, 6.5–8.5 µm diam	Broadly obovoid, 6.5–8 × 5–7 µm	Narrowly clavate to cylindrical, 6–7.5 × 2–2.5 µm	Ellipsoidal to ovoid, 1.5–3 × 1–2 µm	n/d	n/d	n/d
G. trimorpha	Thailand	Single, cylindrical, short stipe, white, 3 mm long	Aspergillus-like, 65–230 × 7–9 µm	Subglobose to globose, 9–12 × 7–10 µm	Broadly ellipsoidal, 7–10 × 6–7 µm	Not observed	Fusiform, in short chains, 4–5 × 2 µm	Well-differentiated, roughened to distinctly verrucose,	Cylindrical, clavate, flask- or irregularly shaped, mostly verrucose with 1–3 conspicuous denticles, 8–13 × 3 µm	Filiform, 10–19 × 1–1.5 µm
G. unica	Taiwan (Tzean et al. 1997) Thailand (Luangsa-ard et al. 2010, this study) Japan (Okuzawa 2012)	In a group of 5–6, arising all over the host, cylindrical, slender acuminate towards the apex, yellowish grey, 4–5 mm × 96–184 µm, fertile along the length	Aspergillus-like, 112–244 × 6.4–13.5 µm, distinctly verrucose along the length	Ellipsoidal, subglobose to globose, smooth, hyaline, 7.1–9.9 × 5.6–7.9 µm	Broadly ellipsoidal to obovoidal, smooth, hyaline, 5.6–9.1 × 4.8–7.0 µm	Broadly cylindrical to ellipsoidal, smooth, hyaline, 6.4–9.5 × 2.8–4.2 µm	Fusiform, occasionally apiculate, 4.0–6.8 × 1.6–2.2 µm	Mostly arising from the base of synnemata, verrucose	Cylindrical, clavate, flask- or irregularly shaped, verrucose, with 1–3 conspicuous denticles, 6.8–11.9 × 3.2–4.0 µm	Filiform, 11.1–17.5 × 1.0–1.6 µm

Table 6. Morphological comparison of Thai *G. longicaudata* and three varieties of *G. clavulifera* (Data partly after Tzean *et al.* 1997).

Characters	*G. leiopus* (Mains 1950)	*G. longicaudata*	*G. scorpioides* (Kuephadungphan *et al.* 2020)	*G. clavulifera* var. *clavulifera*	*G. clavulifera* var. *alba* (Humber & Rombach 1987)	*G. clavulifera* var. *major* (Tzean *et al.* 1997)
Locality	USA	Thailand	Thailand	n/a	Solomon Islands	Taiwan
Host	Spider	*Arachnida*	*Portia* sp.	n/a	*Euophrys cf. trivittata*	*Arachnida*
***Gibellula* anamorph**	Present	Present	Present	Present	Present	Present
Mycelia	Yellow to whitish	White	Greyish- or brownish-white	Lilac	White	White to yellowish-white
Synnemata (length × width)	Yellow to whitish, cylindrical, 1.5–8 mm long, 80–300 μm wide	Solitary, greyish-white, whip-like, slightly tapering into sterile broadly ovoid tip, arising from the posterior of the host abdomen	Solitary, greyish- or brownish-white, whip-like with blunt end, arising from the posterior of the host abdomen	Solitary, greyish to purple, stout, short, cylindrical	Mononematous	Solitary, white to yellowish-white, whip-like
Conidiophores (μm)	Hyaline, smooth-walled, enlarged upward, broadly obovoid or obpyriform, 10–18 × 4.5–8	Hyaline, smooth-walled, enlarged upward into obovoid apices, 10–35 × 3–5	Hyaline, smooth-walled, 20–30 × 4	Brown, smooth-walled, 97.3 × 5.4	Hyaline, long and stout, smooth to asperulate, 100 × no data	Hyaline, smooth- to slightly roughed-walled, up to 140 × 4.8–7.1
Metulae (μm)	—	Broadly obovoid to ellipsoid, 7–10 × 3–4	Narrowly obovoid to cylindrical, 7–15 × 2–7	Cylindrical, 11.6–15.4 × 3.8–5	Cylindrical or clavate, 9–15 × 3–4	Clavate to cylindrical, in groups of 3–10, 12.7–19.8 × 4–5.6
Phialides (μm)	Narrowly clavate to sub-cylindrical, 7.5–12 × 2.5–3.5	Narrowly clavate to cylindrical, apically thickened, 7–10 × 2–3	Broadly cylindrical, apically thickened, often with distinct short neck, 9–14 × 2–4	Cylindrical, in groups of 2–4, 13–17 × 3–3.5	Cylindrical, in groups of 2–6, 10–12.4 × 1.5–2.5	Ampulliform to cylindrical, in groups of 2–8, 12.7–19.8 × 3.6–6
Conidia (μm)	Fusoid to fusoid-ellipsoid, 3–8 × 1–2	Fusoid or occasionally ovoid with an acute end, 3–6 × 1–2	Fusiform, 5–9 × 1.5–3	Purplish in mass, fusiform to cylindrical, 6–9 × 1.7–2	Pure white in mass, fusiform, 5–7.5 × 1.5–2	Pure white in mass, fusiform to broadly fusiform, often distinctly apiculate at both ends, 7.1–13.9 × 2.4–5.6
***Granulomanus* anamorph**	Absent	Present	Absent	Present	Present	Present
Phialides (μm)	—	Polyblastic, irregular, rough-walled, arising from a synnema	—	Holoblastic, cylindrical or irregular, pigmented, arising from hyphae, 10–18 × 3–4	Holoblastic, irregular, smooth-walled, arising from hyphae, 9–15 × 3–5	Verticillate, holoblastic, cylindrical to flask-shaped, arising from stipe, 9.5–14.6 × 2.7–4.4
Conidia (μm)	—	n/d	—	Hyaline, filiform, smooth-walled, 11–17 × 1.2–1.5	Hyaline, baciliform, often swollen at one end, smooth-walled, 20–30 × 0.5–1.5	Hyaline, smooth- to slightly roughed-walled, up to 140 × 4.8–7.1, baciliform to filiform, apiculate or round end, smooth-walled, 15.9–34.1 × 1.3–2.4

Table 6. (Continued).

Characters	G. leiopus (Mains 1950)	G. longicaudata	G. scorpioides (Kuephadungphan et al. 2020)	G. clavulifera var. clavulifera	G. clavulifera var. alba (Humber & Rombach 1987)	G. clavulifera var. major (Tzean et al. 1997)
Teleomorph	Present	Absent	Present	Absent	Present	Absent
Perithecia (µm)	Ovoid, 550–900 × 230–350	—	Superficial, one-third immersed in the loose network of mycelia, mostly arranged in groups, reddish-yellow to light honey-brown, ovoid, 750–870 × 310–380	—	Superficial, one-third immersed in the loose network of mycelia, bright to reddish-yellow or light honey-brown, ovoid, up to 600 × 150–250	—
Asci (µm)	Cylindrical, 400–600 × 5–6	—	Cylindrical, over 550 × 3–7, with ascus tips, 4–5 × 3–4	—	Cylindrical, up to 125 × 5–7, with ascus tips, 5–6 × 5–6	—
Ascospores (µm)	Filiform, multi-septate	—	Cylindrical, multi-septate, often break into part-spores	—	Vermiform, septate, 8 per ascus, each breaks into 8 part-spores	—
Part-spores (µm)	Cylindrical	—	Baciliform, 9–22× 1.5–2	—	Baciliform, 7–10 × 1.5–2	—
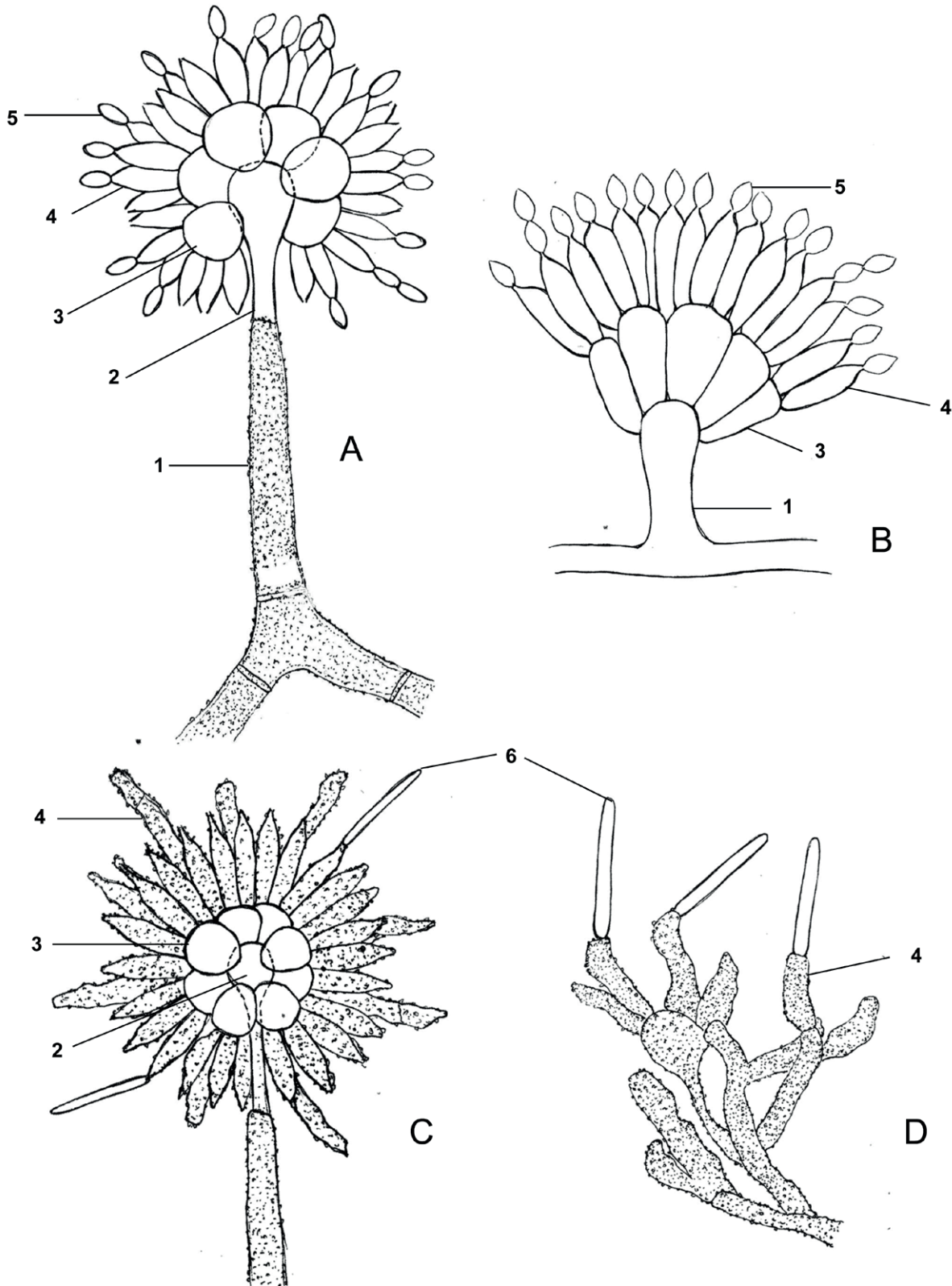
Fig. 15. Illustration of *Gibellula* and *Granulomanus* anamorphs. **A.** Aspergillus-like conidiophore of *Gibellula*. **B.** Penicillium-like conidiophore of *Gibellula*. **C.** Aspergillus-like conidiophore of *Granulomanus*. **D.** *Granulomanus* anamorph. **1.** Conidiophore. **2.** Vesicle. **3.** Metulae. **4.** Phialide. **5.** Conidium of *Gibellula*. **6.** Conidium of *Granulomanus*.

According to Shrestha *et al.* (2019), *Linyphiidae*, the second largest family of spiders after the *Salticidae* (World Spider Catalog 2021) has so far been reported as the hosts of only a few species of hypocrealean fungi including *Cordyceps* sp. from Panama (Nentwig 1985), *G. pulchra* and *Torrubiella albolanata* from the British Isles (Petch 1944, 1948) and *Gibellula* sp. from Brazil (Costa 2014). In this study, this spider family was found to be infected by *G. nigelii*.

Interestingly, although at least 46 species of *Linyphiidae* spiders have been reported in Thailand, none of them have previously been reported to be mummified by any hypocrealean fungi. Therefore, to our knowledge, this study includes the first report of *Linyphiidae* as the host of hypocrealean fungi from Asia.

Theridiidae, also known as tangle-web spiders, cobweb spiders, and comb-footed spiders is one of the largest spider families in

Table 7. Classification of spiders parasitised by *Gibellula*. Those encountered in the current study are in bold. The data compiled in part from Shrestha *et al.* (2019).

Spider	*Gibellula*	Reference
Agelenidae		
Urocoras longispinus	*Gibellula* sp.	Savić *et al.* (2016)
Anyphaenidae		
Iguarima censorial	*Gibellula* sp.	Costa *et al.* (2014)
Anyphaenid spider	*G. leiopus*	Costa *et al.* (2014)
Araneidae		
Eustala sp.	*Gibellula* sp.	Costa *et al.* (2014)
Corinnidae		
Trachelas aff. *robustus*	*G. leiopus*	Costa *et al.* (2014)
Deinopidae		
Deinopid spider	*G. fusiformispora*	Kuephadungphan *et al.* (2020)
Linyphiidae		
Gongylidium rufipes	*G. pulchra*	Petch (1948)
Linyphiid spiders	**G. nigelii**	**This study**
	Gibellula sp.	Costa *et al.* (2014)
Lycosidae		
Lycosid spider	*G. pulchra*	Van der Bijl (1922)
Oxyopidae		
Oxyopid spider	**G. trimorpha**	**This study**
Pholcidae		
Metagonia aff. *beni*	*Gibellula* sp.	Costa *et al.* (2014)
Pholcid spiders	**G. unica**	**This study**
Salticidae		
Corythalia sp.	*Gibellula* sp.	Costa *et al.* (2014)
Euophrys nr. *trivittata*	*G. clavulifera* var. *alba*	Humber & Rombach (1987)
***Myrmarachne* sp.**	**G. longispora**	**This study**
Portia sp.	*G. scorpioides*	Kuephadungphan *et al.* (2020)
Salticid spiders	*G. clavulifera*	Samson & Evans (1977)
	G. pilosa	**This study**
	G. pulchra	Samson & Evans (1973), **this study**
	G. trimorpha	**This study**
	Gibellula sp.	Strongman (1991)
Sparassidae		
Caayguara cupepema	*Gibellula* sp.	Costa *et al.* (2014)
Tetragnathidae		
Metellina (= *Meta*) *merianae*	*Gibellula cf. leiopus*	McNeil (2012)
Theridiidae		
Episinus cognatus	*Gibellula* sp.	Costa *et al.* (2014)
Helvibis longicauda	*Gibellula cf. pulchra*	Gonzaga *et al.* (2006)
Hetschia gracilis	*Gibellula* sp.	Costa *et al.* (2014)
Janula biocorniger	*Gibellula* sp.	Costa *et al.* (2014)
Theridion evexum	*Gibellula* sp.	Costa *et al.* (2014)
Theridiid spiders	**G. parvula**	**This study**
	G. solita	**This study**

Table 7. (Continued).

Spider	*Gibellula*	Reference
Thomisidae		
Cebrenninus cf. *magnus*	*G. cebrennini*	Kuephadungphan *et al*. (2020)
Tmarus spp.	*Gibellula* spp.	Costa *et al*. (2014)
Indoxysticus sp.	**G. longicaudata**	**This study**
Thomisid spider	**G. brevistipitata**	**This study**
Uloboridae		
Miagrammopes sp.	**G. dimorpha**	**This study**
Zodariidae		
Epicratinus aff. *takutu*	*Gibellula* sp.	Costa *et al*. (2014)
Storenomorpha sp.	*G. pigmentosinum*	Kuephadungphan *et al*. (2020)

the world, ranking among the top five most diverse families with over 120 described genera (World Spider Catalog 2021). Certain genera including *Achaearanea*, *Argyrodes*, *Carniella*, *Chrysso*, *Coleosoma*, *Coscinida*, *Dipoena*, *Episinus*, *Janula*, *Latrodectus*, *Meotipa*, *Parasteatoda*, and *Theridion* (Knoflach 1996, Chotwong & Tanikawa 2013, Wongprom & Košulič 2016, Chaiphongpachara *et al*. 2019, World Spider Catalog 2021, Petcharad & Tanikawa, unpublished data) have been recorded from Thailand but none has previously been reported to be hosts of hypocrealean fungi. Nonetheless, other members of this family are known to be exclusively associated with *Gibellula*, including *Helvibis longicauda* that was found to be parasitised by *Gibellula* cf. *pulchra* (Gonzaga *et al*. 2006), and *Neopisinus* cf. *cognatus*, and *Janula bicornigera* that were the hosts of two unidentified *Gibellula* (Marques *et al*. 2011, Costa 2014, World Spider Catalog 2021). In the current study, *G. parvula* and *G. solita* were also found growing on members of *Theridiidae*. However, the host could not be identified at the species nor genus rank. Host identification is important for further study of the fungus/host interaction as the fungus may require specific nutrients from certain hosts, or the physiology or behaviour of the spider could facilitate the fungal infection. Gonzaga *et al*. (2006) noted different susceptibility of two *Theridiidae* species (*Chrysso intervales* and *H. longicauda*) to *Gibellula* fungal attack. These spiders are known to share similarities in body size, web placement as well as habitat selection; however, the latter appeared to encounter *Gibellula* more frequently in nature.

Myrmarachne is a family of ant-mimetic spiders that was found to include a host of *G. longispora* in this study. It is worth pursuing whether *G. longispora* can be found on other spiders beyond *Myrmarachne* or not. As the exoskeleton structure is different between insects and spiders (Evans 2013, Machałowski 2020), a focus on pathogenic fungi parasitising *Myrmarachne* spiders and the ant species mimicked by the spider would provide insight on whether the exoskeleton is the main factor driving the evolution of *Gibellula*. Interestingly, as *Myrmarachne* spiders tend to be herbivores or nectarivores rather than carnivores in comparison with other spiders (Jackson *et al*. 2001, Jackson *et al*. 2008, Nyffeler *et al*. 2017, Hashimoto *et al*. 2020), nutrients could be a key factor driving the speciation of *G. longispora*.

In the spider family *Pholcidae*, *Metagonia* aff. *beni* was reported as a host of an unidentified *Gibellula* (Costa 2014). In this study, two isolates were assigned to *G. unica* that parasitised unidentified species of *Pholcidae*. The morphology of the aforementioned specimen illustrated by Costa (2014) is reminiscent of *G. unica*

by the outer appearance and the presence of both *Gibellula* and *Granulomanus* anamorphic states on the same specimen. *Metagonia* is distributed only in the Americas (World Spider Catalog 2021); hence, the *Pholcidae* host of *G. unica* identified in this study is unlikely to belong to *Metagonia*.

Miagramopes sp. is a member of the spider family *Uloboridae*, which is mainly distributed in tropical and subtropical regions (World Spider Catalog 2021) and was found herein to be parasitised by *G. dimorpha*. This fungus is a cosmopolitan species reported in Taiwan (Tzean *et al*. 1998), Thailand (Luangsa-ard *et al*. 2010), probably Brazil (Costa 2014), and Japan (Shrestha *et al*. 2019).

Thomisidae are widely known as crab spiders with more than 2 100 species currently described. Only a few among them have ever been reported as prey for the invertebrate-parasitic fungi. This includes *Cebrenninus* cf. *magnus* as the host for *G. cebrennini* (Kuephadungphan *et al*. 2020), *Tmarus* for *Gibellula* spp. (Costa 2014) and unidentified thomisid spiders for *Torrubiella albolanata* (Petch 1944) and *Torrubiella fusiformis* (Kobayasi & Shimizu 1982). Based on Ramírez (2014), Wongprom & Košulič (2016), World Spider Catalog (2021), in addition to *Cebrenninus*, there are 16 *Thomisidae* genera reported in Thailand including *Amyciaea*, *Angaeus*, *Boliscus*, *Borboropactus*, *Camaricus*, *Epidius*, *Misumenops*, *Oxytate*, *Pagida*, *Pharta*, *Platythomisus*, *Runcinia*, *Smodicinodes*, *Thomisus*, *Tmarus*, *Zygometis*. However, in the present study, *G. longicaudata* was found on an *Indoxysticus* host that we report as *Thomisidae* cf. *Indoxysticus*. To our knowledge, this is the first report of *Indoxysticus* in Thailand. Furthermore, *G. brevistipitata* was also found in this study to parasitise a *Thomisidae* host; however, the host could not be identified unequivocally to even the genus rank.

Identifying a spider to the species rank is challenging, which is made more difficult when dealing with a spider fully covered with fungal mycelia that obscure the spider's morphological features. The tarsal claws and scopulate are the most informative characters when the legs appear to be the only part slightly covered by fungal mycelia (Kuephadungphan *et al*. 2020). However, the identification of such a spider to the species rank without severely damaging the fungus highly requires experienced araneologists, and preferably, fresh specimens from fieldwork (Savić *et al*. 2016, Kuephadungphan *et al*. 2020). To promote the investigation of araneophagous fungi, we herein provide a simple protocol of how to handle the specimens in the Methods section. To enable the isolation of spider-parasitic fungi, the parasitised spiders are preferably delivered to mycologists within the same day they are

collected. The molecular data generated from pure cultures often gives much more accurate identification to the species level when it is not feasible to obtain DNA from the fungal stroma. In the case that the specimens cannot be transferred to mycologists or within a day, they can be stored at 4 °C or air-dried. However, the longer they are stored, the lower chance they can be established in cultures.

During our field work for this study, several observations were made that raise the possibility of manipulation of spider behaviour by *Gibellula* during infection. *Gibellula* were noticeably found only on *Araneomorphae* spiders, whereas these fungi have never been reported on *Mygalomorphae* (Shrestha *et al.* 2019, Kuephadungphan *et al.* 2020), suggesting that *Gibellula* is only able to infect the very thin body surface of the former. The exoskeletal parts of the abdomen and leg joints are much thinner than that of other body parts (Jocqué & Dippenaar-Schoeman 2007, Pérez-Miles 2020, Göttler *et al.* 2021a, b) and are much softer after molting (Baerg 1926, Stefoff 2009, Foelix 2011), making them the most vulnerable entry parts for infection, as well as the joints which are composed by thin membranes. *Gibellula* infection thus probably initiates from spores that contact the abdomen or leg joints during molting, which then invade the haemocoel and proliferate via a budding yeast-like phase (Evans 2013), eventually reaching the cephalothorax in which a brain is located and spreading to the appendages via hemolymph. Once the fungus has invaded the brain, the spider's behaviour could be manipulated to enhance fungal growth and dispersal creating "zombie" spiders. The indirect evidence supporting zombie spiders includes 1) the frequency of *Gibellula*-infected cadavers that were found to be firmly attached to the underside of leaves (97.67 %, n = 43) (Kuephadungphan & Petcharad unpubl. data), seems to be not a coincidence as in nature, spiders could randomly stay on the upper surface and underside of leaves (Petcharad pers. obs., Jackson 1986, Li *et al.* 1999, Pekár 2005, Huber & Schütte 2009, Suter *et al.* 2011, Roff & Haddad 2015, Uetz & Dillery 2017, Guarisco 2018), and 2) the cadavers of web-building spiders, such as *Theridiidae* that were found dead off their webs where they spend much of their life time on (Gonzaga *et al.* 2006, Kuephadungphan & Petcharad, unpubl. data) seems to be abnormal. In addition, signs of behaviour manipulation by *G. scorpioides* on the spider assassin *Portia* were reported previously (Kuephadungphan *et al.* 2020). With their thin exoskeleton, desiccation is a significant stress to *Araneomorphae* spiders (Oxbrough *et al.* 2005, Ziesche & Roth 2008, Canal *et al.* 2015, Kwok & Eldridge 2016) and moisture is a limiting factor for araneophagous fungi to grow (Hajek & Leger 1994). The propensity of *Gibellula*-infected spiders to be found on the underside of leaves could be a consequence of behavior for maintaining moisture via avoidance of sunlight exposure.

CONCLUSIONS

A survey of the spider-parasitic genus *Gibellula* led to the discovery of eight new taxa along with three new records from Thailand of previously described species. Among the new species, *G. nigelii* was herein proven to represent a new taxon that had previously been used to represent the type species *G. pulchra* in the phylogeny of *Cordycipitaceae*. New data validate *G. longispora* as a species. Divergence within the genus was estimated from DNA sequence data and shown to be useful in species delimitation of closely related taxa. In addition to the morphological descriptions and DNA sequence data of the fungi, the spider hosts were carefully examined to determine whether the host specificity can aid in species identification of *Gibellula* and to extend our understanding of the spider-fungus association. Most of the spiders being examined could be identified to the family rank. Although this did not give much information on the species delimitation of *Gibellula*, several observations of the hosts indicated aspects of the interaction between spiders and *Gibellula* that are worth further pursuing such as behavioural modification.

Accepted names for *Gibellula*

The following taxa are accepted species of *Gibellula* based on their species descriptions and/or phylogenetic placements. These has been compiled in part from Shrestha *et al.* (2019).

Gibellula alata Petch, Annls. mycol. 30: 391. 1932. MycoBank MB 256143.

Gibellula brunnea Samson & H.C. Evans, Mycologia 84: 301. 1992. MycoBank MB 358123.

Gibellula cebrennini Tasan. *et al.*, MycoKeys 72: 21. 2020. MycoBank MB 835113.

Gibellula clavata Samson & H.C. Evans, Mycologia 84: 306. 1992. MycoBank MB 358125.
Synonym: *Torrubiella clavata* Samson & H.C. Evans, Mycologia 84: 306. 1992.

Gibellula clavispora Z.Q. Liang *et al.*, Mycotaxon 131: 111. 2016. MycoBank MB 810567.

Gibellula clavulifera (Petch) Samson & H.C. Evans, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 80: 131. 1977. MycoBank MB 314478.
Basionym: *Spicaria clavulifera* Petch, Trans. Br. mycol. Soc. 16: 238. 1932.
Synonym: *Gibellula clavulifera* var. *clavulifera* (Petch) Samson & H.C. Evans, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 80: 131. 1977.

***Gibellula clavulifera* var.** *alba* Humber & Rombach, Mycologia 79: 376. 1987. MycoBank MB 132411.
Synonym: *Torrubiella ratticaudata* Humber & Rombach, Mycologia 79: 376. 1987.

***Gibellula clavulifera* var**. *major* Tzean *et al.*, Mycologia 89: 311. 1997. MycoBank MB 437910.

Gibellula dabieshanensis B. Huang *et al.*, Mycosystema 17: 110. 1998. MycoBank MB 446535.

Gibellula dimorpha Tzean *et al.*, Mycol. Res. 102: 1350. 1998. MycoBank MB 446667.
Synonym: *Torrubiella dimorpha* Tzean *et al.,* Mycol. Res. 102: 1350. MycoBank MB 446666.

Gibellula fusiformispora Tasan. *et al.*, MycoKeys 72: 26. 2020. MycoBank MB 835114.

Gibellula gamsii Kuephadungphan, *et al.*, Mycol. Prog. 18: 138. 2018. MycoBank MB 825141.

Gibellula leiopus (Vuill. ex Maubl.) Mains, Mycologia 42: 313. 1950. MycoBank MB 485289.
Basionym: *Gibellula arachnophila* f. *leiopus* Vuill. ex Maubl., Bull. Soc. mycol. France 36: 42. 1920. MycoBank MB 137604.
Synonym: *Gibellula araneae* Sawada, Rep. Dept Agric., Govern. Res. Inst. Formosa, Spec. Bull. Agric. Exp. Station Formosa 35: 114. 1928. MycoBank MB 257173.

Gibellula perexigua (Kobayasi) Koval, Klavitsipital'nye Griby SSSR (Kiev): 57. 1984. MycoBank MB 132451.

Gibellula mainsii Samson & H.C. Evans, Mycologia 84: 300. 1992. MycoBank MB 358122.

Gibellula mirabilis Samson & H.C. Evans, Mycologia 84: 310. 1992. MycoBank MB 358126.

Gibellula pigmentosinum Tasan. *et al.*, MycoKeys 72: 27. 2020. MycoBank MB 835112.

Gibellula pulchra (Sacc.) Cavara, Atti Ist. bot. R. Univ. Pavia 3: 347. 1894. MycoBank MB 215909.

Basionym: *Corethropsis pulchra* Sacc., Michelia 1: 84. 1877. MycoBank MB 206516.

Synonyms: *Gibellula araneaurum* P. Syd., Bot. Jb. 57: 321. 1922. MycoBank MB 257177.

Gibellula arachnophila f. *macropus* Vuill., Bull. Soc. mycol. Fr. 36: 41. 1920. MycoBank MB 137624.

Gibellula haygarthii Van der Byl, Trans. Roy. Soc. South Africa 10: 149. 1922. MycoBank MB 266863.

Gibellula globosa Kobayasi & Shimizu, Bull. natn. Sci. Mus., Tokyo, B 8: 45. 1982. MycoBank MB 114288.

Gibellula globosostipitata Kobayasi & Shimizu, Bull. natn. Sci. Mus., Tokyo, B 8: 49. 1982. MycoBank MB 114291.

Gibellula suffulta Speare, Phytopathology 2: 137. 1912. MycoBank MB 216044.

Gibellula tropicalis Sawada, Special Publ. Coll. Agric. Natl. Taiwan Univ. 8: 231. 1959. MycoBank MB 331320.

Gibellula scorpioides Tasan., *et al.*, MycoKeys 72: 30. 2020. MycoBank MB 835115.

Gibellula shennongjiaensis X. Zou *et al.*, Mycosystema 35: 1163. 2016. MycoBank MB 814470.

Gibellula unica L.S. Hsieh *et al.*, Mycologia 89: 312. 1997. MycoBank MB 437911.

Residual species of *Gibellula*

The following species of *Gibellula* could not be confidently assigned to the genus as their morphologies did not fit the concept of the genus or the molecular phylogeny presented is inconclusive or unavailable.

Gibellula arachnophila (Ditmar) Vuill., Bull. Séanc. Soc. Sci. Nancy, Sér. 3 11: 156. 1910. MycoBank MB 227937.

Basionym: Isaria arachnophila Ditmar, Deutschlands Flora, Abt. III. Die Pilze Deutschlands 1–4: 111, t. 55. 1817. MycoBank MB 203061.

Note: Mains (1950) and Evans & Samson (1987) stated that this Ditmar's fungus actually was *Akanthomyces araneaurum* (Petch) Mains.

Gibellula araneicola Sawada, Special Publ. Coll. Agric. Natl. Taiwan Univ. 8: 231. 1959. MycoBank MB 331319.

Note: Tzean *et al.* (1997) doubted the identity of *G. araneicola* Sawada that produces an isarioid morph instead of *Gibellula*.

Gibellula aspergilliformis (Rostr.) Vuill., Bull. Séanc. Soc. Sci. Nancy, Sér. 3 11: 158. 1910. MycoBank MB 521547.

Basionym: *Isaria aspergilliformis* Rostr., Botan. Zbl. 57: 185. 1894.

Note: Petch (1932) expressed doubt towards the identity of *G. aspergilliformis* because of the narrow metulae and spherical conidia in chains present in this species were uncommon features of *Gibellula*.

Gibellula capillaris Morgan, J. Mycol. 11: 50. 1905. MycoBank MB 215873.

Note: According to Mains (1950), the description of *G. capillaris* did not fit the concept of *Gibellula* and re-examination of the type specimen is infeasible as it is no longer in a good condition.

Gibellula curvispora Y.F. Han *et al.*, Mycosystema 32: 778. 2013. MycoBank MB 516621.

Note: Judging by the species illustration, *Gibellula curvispora* does not fit the concept of *Gibellula*. Importantly, its ITS sequence appeared close to *Bionectriaceae*.

Gibellula formosana Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa. 19: 1. 1919. MycoBank MB 646527.

Note: Mains (1950) expressed doubt on the assignment of *Gibellula formosana* Sawada to the genus since it was found infecting a moth while Kobayasi suggested that it resembled *Isaria japonica*.

Gibellula eximia Höhn., Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 83: 37. 1907. MycoBank MB 216040.

Note: The species description of *Gibellula eximia* does not fit *Gibellula* (Petch 1932).

Gibellula elegans Henn., Hedwigia 41: 148. 1902. MycoBank MB 216113.

Note: Since *Gibellula* is well-known as an obligate parasite of spiders, Mains (1950) reported that the assignment of *G. elegans* to this genus might be erroneous, as this species is found parasitising locusts.

Gibellula petchii Humber & Rombach, Mycologia 79: 380. 1987. MycoBank MB 132409.

Basionym: *Cylindrophora araneaurum* Petch, Trans. Br. mycol. Soc. 27: 85. 1944. MycoBank MB 285924.

Synonym: *Granulomanus araneaurum* (Petch) de Hoog & Samson, Persoonia 10: 70. 1978. MycoBank MB 314729.

Notes: It is still unclear whether the species name should be retained or abandoned. *Gibellula petchii* was proposed to accommodate *Cylindrophora araneaurum*, which was originally described as the conidial morph of *Torrubiella albolanata* and later elevated to generic rank as a new genus, *Granulomanus* (Petch 1944, de Hoog 1978, Humber & Rombach 1987). From the point of view of Humber & Rombach (1987), *Granulomanus* should be synonymised with *Gibellula* as it almost never occurs in the absence of *Gibellula* and/or its torrubiella-ike teleomorph. *Cylindrophora araneaurum* (≡*Granulomanus araneaurum*) was henceforth synonymised with *G. petchii*. On the other hand, Samson & Evans (1992) argued that *Granulomanus* naturally occurs independently on spider hosts either with or without *Gibellula*. Thus, the genus should be retained as an independent asexually typified genus resulting in rejection of *G. petchii*. According to a recent taxonomic revision of the *Cordycipitaceae*, which was largely based on molecular data, several generic names including *Granulomanus* were suppressed (Kepler *et al*. 2017). Nevertheless, the taxonomic dilemma of *G. petchii* cannot yet be resolved owing to the lack of sequence data.

Gibellula phialobasia Penz. & Sacc., Malpighia 15: 252. 1902. MycoBank MB 216177.

Note: Petch (1932) expressed doubt towards the identity of *G. phialobosia* because of its flask-shaped phialides regarded as an uncommon feature of *Gibellula*.

KEY TO *GIBELLULA* SPECIES

Aspergillus-like conidiophores 1
Penicillium-like conidiophores 12

1a.   Mononematous .... ***G. mainsii***
1b   Synnematous 2

2a.   Synnematal shape wing-like structure .... ***G. alata***
2b.   Synnematal shape globose to pyriform fertile area with a short sterile stipe .... ***G. brunnea***
2c.   Synnematal shape clavate 3
2d.   Synnematal shape cylindrical 5

3a.   Conidiophores 30–50 µm in length .... ***G. clavata***
3b.   Conidiophores longer than 50 µm 4

4a.   Conidial heads (31–)37–42.5(−48) µm diam bearing fusoid to fusoid-ellipsoid conidia, smooth-walled, hyaline, (3–)3.5–5(−5.5) × (1–)1.5–2.5(−3) µm .... ***G. gamsii***
4b.   Conidial heads 25–40 µm diam bearing fusoid conidia, 5–7 x 2–3.5 µm .... ***G. mirabilis***

5a.   1 synnema 6
5b.   2–5 synnemata. 9
5c.   More than 5 synnemata 11

6a.   *Granulomanus* synasexual morph present 7
6b.   *Granulomanus* synasexual morph absent 8

7a.   Conidiophores aspergillus-like .... ***G. dimorpha/G. trimorpha***[1]
7b.   Conidiophores irregular-shaped .... ***G. cebrennini***

8a.   Conidia ellipsoid, narrowly ovoid, sometimes with an acute end, (2.5–)3–3.5(−4) × 1–1.5 µm .... ***G. nigelii***
8b.   Conidia ellipsoid to ovoid, occasionally globose, (1.5–)2–2.5(−3) × 1–1.5(−2) µm .... ***G. solita***
8c.   Conidia cylindrical or fusoid, 3.2–6.5 × 1.1–1.6 µm ....***G. shennongjiaensis***

9a.   Synnematal tips regular, not swollen .... ***G. unica***
9b.   Synnematal tips globose .... ***G. pilosa***
9c.   Synnematal tips ovoid 10

10a. Conidia ellipsoid or narrowly almond-shaped, (3–)3.5–4(−4.5) × 1.5–2 µm .... ***G. brevistipitata***
10b. Conidia fusiform to broadly fusoid conidia, (3.5–)4–5(−6) × 1.5–2(−2.5) µm .... ***G. fusiformispora***
10c. Conidia narrowly ovoid or narrowly ellipsoid or bacilliform, 4–5.5(−6) × (2–)2.5–3(−4) µm .... ***G. parvula***
10d. Conidia broadly almond-shaped, (2.5–)3.5–5(−5.5) × 1–2(−3) µm .... ***G. pigmentosinum***

11a. Conidia fusoid to ellipsoid .... ***G. pulchra***
11b. Conidia bacilliform .... ***G. longispora***
11c. Conidia clavate .... ***G. clavispora***

12a. Mononematous .... ***G. clavulifera* var. *alba***
12b. Synnematous 13

13a. Numerous synnemata 14
13b. A single synnema 15

14a. Conidia fusoid or fusoid-ellipsoid, 3–8 × 1–2 µm .... ***G. leiopus***
14b. Conidia fusoid, 3.2–4 × 1.1–1.8 µm .... ***G. dabieshanensis***

15a. Synnematal tip swollen .... ***G. longicaudata***
15b. Synnematal tip regular, not swollen 16

16a. Conidia filiform .... ***G. clavulifera***
16b. Conidia fusoid .... ***G. scorpioides***
16c. Conidia bacilliform .... ***G. clavulifera* var. *major***

[1] *Gibellula dimorpha* and *G. trimorpha* showed identical morphology. Only molecular data could distinguish one from the other.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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