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ARTICLE

Integrative taxonomy and cryptic diversity in dictyostelids: a 42% expansion of taxa known from China with conservation implications

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Abstract

An inadequate understanding of microbial eukaryotes, especially dictyostelids, threatens accurate biodiversity assessments and conservation efforts. Integrative taxonomy combining ISCC-NBS color quantification, spore morphometrics, and multi-locus phylogenetics (SSU rDNA, *atp1*) was applied to 68 dictyostelid isolates from 200 soil samples collected across China's biodiversity hotspots (Changbai Mountain, Shennongjia, and Jianfengling National Nature Reserves). We identified 28 taxa, including 17 new species, nine new varieties, and two already known species—collectively increasing global dictyostelid diversity by 15% (from 178 to 204 taxa) and expanding records from China by 42% (from 61 to 87 taxa). Crucially, five novel taxa were segregated by systematically revising the *D. purpureum* complex, with the reclassification of *D. pseudosessile* as an independent species, thus resolving both cryptic speciation and historical taxonomic ambiguities. Phylogenetic analyses validated these taxonomic revisions through distinct morphological-molecular signatures. Combined with prior findings, 18 endemic taxa are now documented from Changbai Mountain, establishing this region as a microbial diversification hotspot and advocating urgent inclusion of protists in biodiversity conservation efforts. This work provides a replicable protocol for microbial taxonomy by standardizing phenotypic descriptors and reconciling molecular-phylogenetic conflicts.

Keywords – Cryptic speciation – *Dictyostelium purpureum* complex – integrative taxonomy – microbial conservation – multi-locus phylogenetics

INTRODUCTION

While biodiversity conservation efforts predominantly focus on macro-organisms (Rodríguez et al. 2015), an inadequate understanding of certain microbial eukaryote taxonomic groups could jeopardize the accuracy of biodiversity assessments (Pawlowski et al. 2012, Geisen et al. 2018). This gap is particularly acute in dictyostelids (dictyostelid cellular slime molds, a group of fungus-like organisms) (Wijayawardene et al. 2020), where signature sequence limitations and cryptic speciation obscure true species boundaries (Mehdiabadi et al. 2009, Sheikh et al. 2018, Chittavichai

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et al. 2025, Zhang et al. 2025). Despite their ecological significance in nutrient cycling and microbial interactions (Geisen et al. 2018), protists remain underrepresented in conservation efforts, with only about 6.3% of described species assessed by the IUCN Red List (Adl et al. 2019, Bánki et al. 2025, IUCN 2025). This disparity is exacerbated by the exclusion of micro-organisms from IUCN biodiversity monitoring programs. The unresolved status of taxa such as *Coenonia denticulata* — described in 1884 but never isolated again — epitomizes how taxonomic uncertainties perpetuate conservation blind spots (Raper 1984, Sheikh et al. 2018).

Modern integrative taxonomy, combining morphometrics, molecular phylogenetics, and biogeographic analysis, has proven critical in resolving cryptic speciation in microbial eukaryotes (Boluda et al. 2019). For dictyostelids, historical reliance on subjective morphological descriptors (e.g., "grayish white to pale lemon yellow") has led to persistent classification ambiguities (Raper 1935). Although small subunit rRNA (SSU rDNA) sequences cannot identify dictyostelids to the species level alone (Chittavichai et al. 2025), recent advances in molecular techniques, such as multi-locus sequencing (SSU rDNA and *atp1*), now enable robust phylogenetic resolution of cryptic lineages (Zou et al. 2022). However, standardized quantitative frameworks for phenotypic characterization are still lacking, which hinders global biodiversity comparisons.

Herein, we address these taxonomic challenges through a systematic revision of the *Dictyostelium purpureum* complex. An integrative taxonomy framework that combines color quantification (Kelly & Judd 1976), spore morphometrics (Hagiwara 1989, Kirk et al. 2008), and multi-locus phylogenetics was developed to resolve the long-standing ambiguities within this group. This approach allowed us to critically evaluate species boundaries and uncover the cryptic diversity that has been previously neglected (Mehdiabadi et al. 2009).

Our study, conducted across three biodiversity hotspots from high, intermediate and low latitudes in China, significantly expands the known diversity of dictyostelids and reveals a substantial amount of previously unrecognized cryptic diversity (Liu et al. 2025). These discoveries underscore the prevalence of cryptic diversity in understudied microbial groups, emphasizing the urgent need for taxonomic modernization (Baldauf 2008, Pawlowski et al. 2012, Wang et al. 2019, Wang et al. 2023, Liu 2024, Wang et al. 2024). Our polyphasic approach establishes a replicable framework for protist systematics and provides a vital tool for accurate biodiversity assessment, which directly informs the development of effective conservation strategies in human-dominated ecosystems.

MATERIALS AND METHODS

Soil samples

Soil samples were collected from the Changbai Mountain National Nature Reserve in Jilin Province, the Shennongjia National Nature Reserve in Hubei Province, and the Jianfengling National Nature Reserve in Hainan Province, all of which are located in the Priority Conservation Areas of *China's Biodiversity Conservation Strategy and Action Plan (2023−2030)*. The detailed information about the collecting site was recorded in Supplementary Tables 1−2. The geographic information was downloaded from Aliyun (Aliyun), and visualized with detailed information as a collection map of China using the R packages "sf", "tidyverse", "ggplot2", and "ggspatial" with R, while the rooted tree of Fig. 1 was constructed with the Wekemo Bioincloud (Wekemo , Wickham 2016, Pebesma 2018, Wickham et al. 2019, Dunnington 2023, Pebesma & Bivand 2023, Gao et al. 2024). The map was combined with the rooted tree using Adobe Illustrator. Each collecting site had 10 quadrats, with an interval of more than 10 meters between each one. Each quadrat was a square with an area of approximately four square meters. Within each quadrat, more than 20 grams of soil was collected from each of nine randomly selected sampling points within that quadrat. The soils were transported to the laboratory and preserved at 4°C as soon as possible. All of the soils were processed within a month after collection to ensure that dictyostelids maintain their maximum abundance (Cavender & Raper 1965).

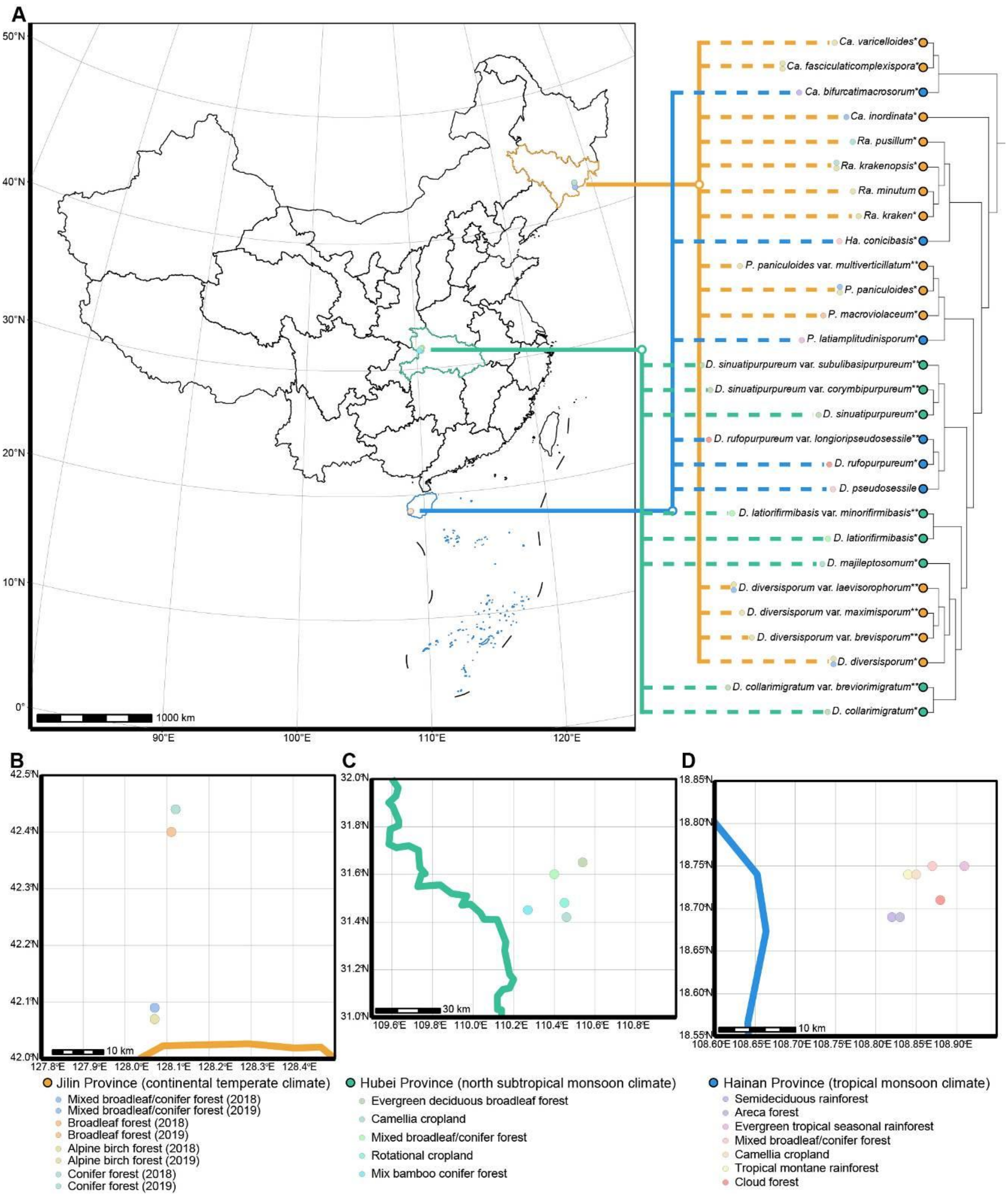

Figure 1 – Map of the collecting sites where dictyostelids were isolated. (**A**) The left side displays various collecting sites with all vegetation types from which collecting was carried out within or near three nature reserves located in different provinces (latitudes) of China, each with a distinctly different climate. Each collecting site (vegetation type) is represented by a unique color (the specific meaning of the colors are shown in the lower part of the figure). The right side is a rooted tree that shows the species relationship of dictyostelids considered in this study, * indicates a new species, and ** indicates a new variety. The connection lines between the left map and the right root tree indicate dictyostelids from different collecting sites; the color of the connection lines corresponds to the province on the left map and species points on the right root tree (yellow indicates Jilin Province, green indicates Hubei Province, and blue indicates Hainan Province), indicating from which province those species were collected. (**B**) Collecting sites in Jilin Province (Changbai Mountain National Nature Reserve and nearby areas). (**C**) Collecting sites in Hubei Province (Shennongjia National Nature Reserve). (**D**) Collecting sites in Hainan Province

(Jianfengling National Nature Reserve and nearby areas). The names of vegetation types are given below.

Isolation, cultivation, and classification

A composite soil sample (100 grams) for each collecting site was produced by combining ten grams of soil from each of ten sampling points within one collection site. An amount of 100 grams of soil from each collecting site was then mixed with 900 mL of sterile distilled water, resulting in an initial dilution of 1:10. After shaking at 280 rpm for two minutes, 5 mL of the above suspension was taken and mixed with 7.5 mL of sterile water to produce a 1:25 dilution as described in the method of Cavender and Raper (Cavender & Raper 1965). Part of the remaining initial suspension was used for pH measurements using a digital pH meter, while the others were filtered for another experiment (unpublished). Soils with pH < 6 were classified as low pH (acidic), pH 6−7 as intermediate pH (circumneutral), and pH > 7 as high pH (alkaline). Isolation and cultivation were performed using the previously established method (Zou et al. 2022), in which 0.5 mL of dilution and 0.4 mL of *Escherichia coli* were uniformly spread on a dry grass (*Setaria* spp.) agar dish for isolation. The dictyostelid isolates obtained were then transferred, along with 0.4 mL of *E. coli*, to a water agar culture dish for cultivation. Both isolation and culture dishes were incubated at 23°C. The classification of morphology, DNA extraction, and PCR amplification followed the same procedures and equipment as described by previous research (Zou et al. 2022).

Sorocarps, pseudoplasmodia, and aggregations were first observed and then subsequently photographed, measured, and analyzed using a Leica dissecting microscope equipped with 0.63× ocular lenses and 1.0× objective lenses. Photographs were taken with a Leica digital camera and accompanying software (LAS). Observations of spores and sorophores were conducted on slides using sterile water as the mounting medium. These slides were subsequently photographed, measured, and analyzed using a Zeiss light microscope equipped with 10× ocular lenses and 40× objective lenses. Photographs were taken with a Zeiss microscope camera. Morphological characteristics were compared with the original descriptions in the first published papers for each dictyostelid species. When these descriptions were incomplete, morphological characteristics were compared with authoritative monographs on the subject (Raper 1984, Hagiwara 1989). For controversial species (e.g., *Dictyostelium sphaerocephalum*), morphological features were compared with relevant revised taxonomic publications (Romeralo et al. 2007). If there are three or more significant morphological character differences compared to each known species, we regard the taxon as a new species in terms of morphology. If there are one or two significant morphological character differences, we regard it as a new variant in terms of morphology.

PCR products were sent to Sangon Biotech (Shanghai) Co., Ltd. for sequencing. Phylogenetic analysis was conducted using auto option in MAFFT for alignment, IQ-TREE 2 to construct ML (Maximum Likelihood) phylogenetic trees, ModelFinder in IQ-TREE 2 determines the best-fit model, with 10000 ultrafast bootstrap (UFBoot) replicates and 1000 SH-aLRT tests performed for branch support and testing (Anisimova et al. 2011, Kalyaanamoorthy et al. 2017, Hoang et al. 2018, Minh et al. 2020). We sequenced SSU sequences for all taxa in this paper, but *atp1* sequences were obtained for only some taxa that were difficult to identify using SSU sequences alone. Reference sequences of SSU and *atp1* (Supplementary Table 3) were downloaded from Nucleotide in NCBI or obtained from the supplementary data of Sheikh et al. (Nucleotide_[Internet] 1988, Sheikh et al. 2018). Taxonomy of dictyostelids is listed in Supplementary Table 4. Figures of dictyostelid photos were cropped, magnified proportionally, and adjusted for brightness and contrast, and combined using Adobe Photoshop. Phylogenetic trees of SSU and *atp1* were drawn in the circular formats using iTOL and in the rectangular formats using FigTree (Letunic & Bork 2024); these two formats were then combined using Adobe Illustrator. The morphological characters and sequences of dictyostelids were separately registered in MycoBank and GenBank (GenBank_[Internet] 1988, Robert et al. 2005). All of the isolates obtained in the present study were frozen in HL-5 media at −80°C and deposited in the herbarium of the Mycological Institute of Jilin Agricultural University, Changchun, China (HMJAU), and listed in Supplementary Table 4 (Cocucci & Sussman 1970).

The software versions and instrument models mentioned previously are listed in Supplementary Table 5.

RESULTS

We collected 200 soil samples from 20 collecting sites in three national nature reserves and nearby areas across three different provinces in China, all located in the eastern monsoon ecoregion and characterized by distinctly different climates. Ten soil samples were collected from each collecting site, and each site had the same type of vegetation. The collecting sites within each nature reserve and nearby areas were characterized by unique vegetation. These were 80 soil samples from the Changbai Mountain National Nature Reserve of Jilin Province (continental temperate climate zone), 50 soil samples from the Shennongjia National Nature Reserve of Hubei Province (north subtropical monsoon climate zone), and 70 soil samples from the Jianfengling National Nature Reserve of Hainan Province (tropical monsoon climate zone) (Fig. 1). The distances between these three nature reserves are all greater than 1500 kilometers. The collecting site in the Changbai Mountain National Nature Reserve had almost the same geographical coordinates in two successive collecting years (2018 and 2019).

We isolated 68 isolates of dictyostelids from 200 soil samples collected across these three nature reserves. Combining multi-locus phylogenetics (SSU rDNA, *atp1*) and standardized morphometrics (e.g., ISCC-NBS color codes, spore length/width ratios), these isolates were classified into 28 different taxa, including 17 species new to science, nine varieties new to science, and two previously known species. Notably, there were four new species (*Cavenderia bifurcatimacrosorum*, *Ca. fasciculaticomplexispora*, *Ca. inordinata*, *Ca. varicelloides*) in the genus *Cavenderia*, family Cavenderiaceae, order Acytosteliales; six new species (*Dictyostelium collarimigratum*, *D. diversisporum*, *D. latiorifirmibasis*, *D. majileptosomum*, *D. rufopurpureum*, *D. sinuatipurpureum*), one previously known species (*D. pseudosessile*), and eight new varieties (*D. collarimigratum* var. *breviorimigratum*, *D. diversisporum* var. *brevisporum*, *D. diversisporum* var. *laevisorophorum*, *D. diversisporum* var. *maximisporum*, *D. latiorifirmibasis* var. *minorifirmibasis*, *D. rufopurpureum* var. *longioripseudosessile*, *D. sinuatipurpureum* var. *corymbipurpureum*, *D. sinuatipurpureum* var. *subulibasipurpureum*) in the genus *Dictyostelium*, family Dictyosteliaceae, order Dictyosteliales; three new species (*Polysphondylium latiamplitudinisporum*, *P. macroviolaceum*, *P. paniculoides*) and one new variety (*P. paniculoides* var. *multiverticillatum*) in the genus *Polysphondylium*, family Dictyosteliaceae, order Dictyosteliales; one new species (*Hagiwaraea conicibasis*) in the genus *Hagiwaraea*, family Raperosteliaceae, order Dictyosteliales; and three new species (*Raperostelium kraken*, *Ra. krakenopsis*, *Ra. pusillum*) and one already described species (*Ra. minutum*) in the genus *Raperostelium*, family Raperosteliaceae, order Dictyosteliales. All species have been separated and included in a SSU phylogenetic analysis (Fig. 2). Closely related species, which couldn't be easily separated by SSU phylogeny, have been distinguished by *atp1* phylogenetic analysis (Fig. 3). The morphological measurements of all taxa described in this study are summarized in Supplementary Table 6.

Taxonomy

Cavenderia bifurcatimacrosorum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 4, 5

MycoBank number: 853146; GenBank accession number: SSU: PP590172.

Etymology – the name refers to the bifurcate pseudoplasmodia and the large terminal sori.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic, solitary, clustered to gregarious, erect or semierect to prone, a little sinuous, 0.2−2.6 mm in length. When clustered, 2−5 sorocarps are always clustered together and may share the same or different basal disks. Sorophores consist of several tiers of cells except tips, unbranched or with one to five short lateral branches near or below the middle, or with bifurcate dichotomous branches; rarely with 8−10 branches grown from one mound on the sorophore. Bases are clavate to round or conical with basal disks, consisting of several tiers of cells, 16.2−55.7 µm in width, with the widest points of base terminals measuring 11.9−121.8 µm. Tips are acuminate to capitate, consisting of one to several tiers of cells, 2.5−15.4 µm in width, with the widest points of tip terminals measuring 2.7−43.6 µm. Branches are reaching 150−591 µm. Branch bases are clavate, consisting of one to two tiers of cells, 8.7−17.3 µm in diam. Sori are white to pale yellow, light brownish gray (#8e8279) or grayish yellowish brown (#7e6d5a), globose, terminal sori 43−400 µm diam. Lateral sori are smaller, from 25 to 147 µm. Spores are broadly elliptical to oblong, 3.9−5.6 × 2.3−3.4 µm (length/width = 1.29−2.25), some spores large and reaching to 8.0−8.6 × 3.0−3.3 µm (length/width = 2.53−2.64), with polar granules. Aggregations are radiate at first, then shrink into a mound or secondary mounds. Pseudoplasmodia migrate with stalks, some pseudoplasmodia are bifurcate. This species belongs to the *Cavenderia* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from a forest near the Jianfengling National Nature Reserve, in mixed soil samples collected from a semideciduous rainforest at a low elevation (93−336 m) with an intermediate soil pH (pH = 6.80).

Material examined – China, Hainan Province: near the Jianfengling National Nature Reserve, 18.69º N, 108.82º E, average elevation 253.7 m. Isolated from mixed soil, February 2022, *haiban2-1* (HOLOTYPE, voucher specimen code: HMJAU MR390). Known only from Hainan Province, China.

Notes – Distinguishing features of *Cavenderia bifurcatimacrosorum* including the bifurcate pseudoplasmodia and bifurcate sorocarps, make it different from other *Cavenderia* species, except for the species with bifid, bifurcated or dichotomous structures such as *Ca. aureostabilis*, *Ca. bifurcata*, *Ca. fulva*, *Ca. parvibrachiata*, *Ca. pseudoaureostipes*, *Ca. subdiscoidea*, but the phototropic character, large sori (*Ca. aureostabilis* has sori in 60−180 µm, *Ca. bifurcata* 70−300 µm, *Ca. fulva* has terminal sori in 50−150 µm with lateral in 50−70 µm, *Ca. parvibrachiata* 43−252 µm, *Ca. pseudoaureostipes* 50−250 µm and *Ca. subdiscoidea* 50−200 µm), broadly elliptical spores (*Ca. aureostabilis* has elliptical-oblong spores in 6−10 × 3−5 µm, *Ca. bifurcata* has two types with 4.5−6.3 × 1.8−2.7 and 8−9 × 3 µm, *Ca. fulva* has elliptical-oblong 4−8 × 3−4.5 µm, *Ca. parvibrachiata* has elliptical-oblong 5.4−9.7 × 2.6−4.8 µm, *Ca. pseudoaureostipes* elliptical-oblong 6−8.5 × 3−4.5 µm and *Ca. subdiscoidea* elliptical-oblong 6−8 × 2.8−3.8 µm) and with 1−4 short lateral branches or rarely 8−10 branches grown from one mound of sorophore separate *Ca. bifurcatimacrosorum* from those species (Cavender 1976, Cavender et al. 2018, Vadell et al. 2018, Cavender et al. 2022). On the other hand, only *Ca. bifurcata* clusters near *Ca. bifurcatimacrosorum* in the SSU phylogenetic tree, and morphological distinctions have been discussed.

Cavenderia fasciculaticomplexispora Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 6, 7

MycoBank number: 853147; GenBank accession number: SSU: PP590173; PP590174.

Etymology – the name refers to the clustered sorocarps and complex spores from subglobose to oblong; the word "clustered" = Latin *fasciculatus*/*fasciculata*/*fasiculatum* with compounding form *fasciculati*--, while the word "complex" = Latin *complexus*/*complexa*/*complexum* with compounding form *complexi*--.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are clustered, prone to erect or semierect, sinuous, 0.2−4.3 mm in length. Sometimes the color of medium near the clustered bases deepens like light grayish olive (#8c8767). Sorophores consist of one to two tiers of cells except bases, unbranched or with irregular branches. Bases are round to clavate, consisting of two to several tiers of cells, 12.6−26.7 µm in width, with the widest points of base terminals measuring 16.6−28.0 µm. Tips are clavate, consisting of one tier of cells, 4.6−10.2 µm in width, with the widest points of tip terminals measuring 7.7−12.0 µm. Branches are 0.1−1.2 mm in length. Sori colors are white, occasionally a little darker, like purplish gray (#8b8589) or pinkish gray (#c1b6b3) to grayish pink (#c4aead), globose, 31−279 µm. Spores are elliptical to oblong, 3.5−7.6 × 2.4−3.4 µm (length/width = 1.32−2.38), a few small spores are subglobose to broadly elliptical, 3.2−4.9 × 2.9−3.9 µm (length/width = 1.09−1.28), all spores are with polar granules. Aggregations are mounds with short radiate streaming around, 0.5−1.5 × 0.5−1.2 mm. Aggregations have secondary centers when forming pseudoplasmodia. Pseudoplasmodia with stalks but do not migrate. This species belongs to the *Cavenderia* clade in a SSU rDNA phylogeny.

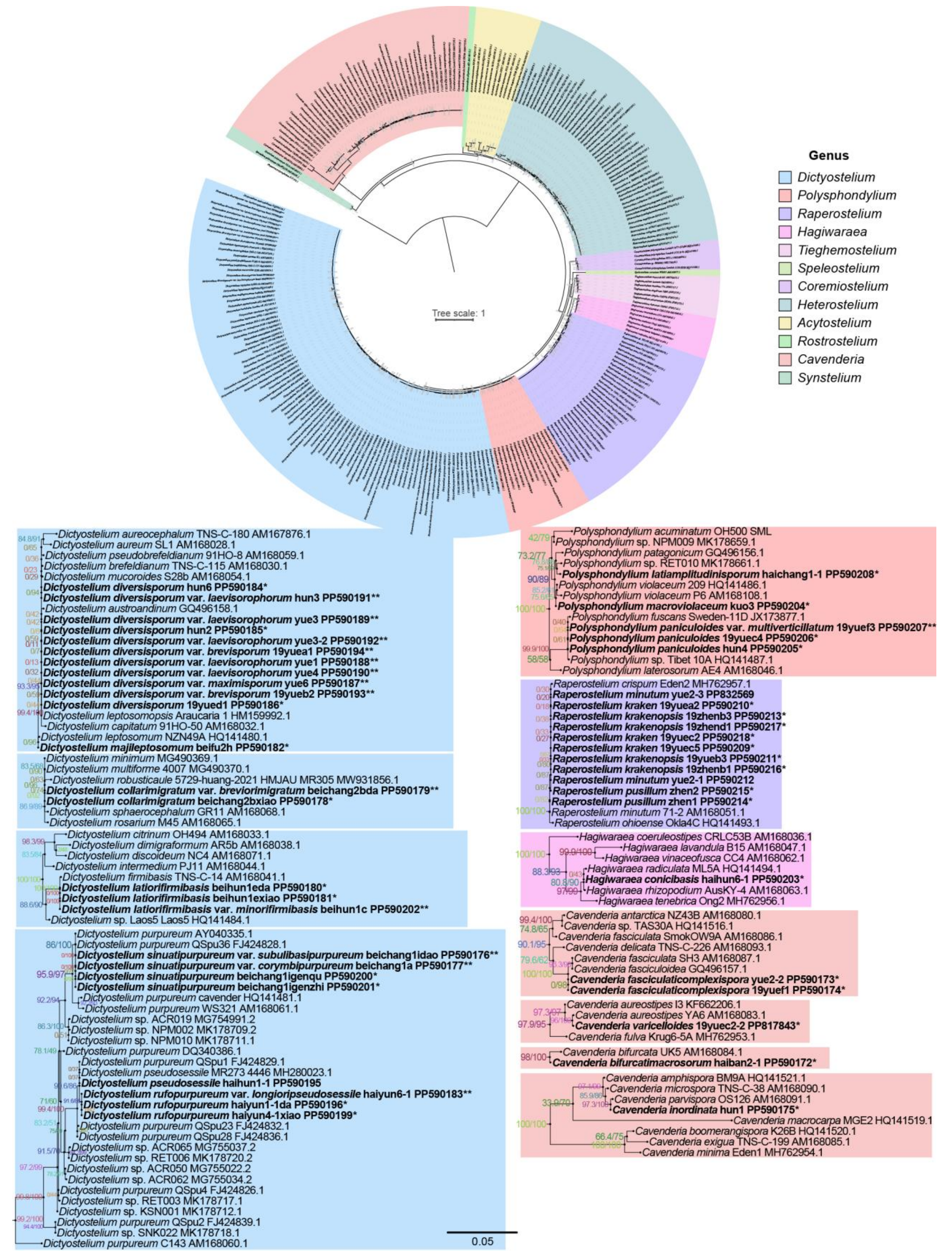

Figure 2 – SSU phylogenetic tree of dictyostelids. Isolates obtained in this study are indicated in bold, new species are marked with one asterisk (*) and new varieties are indicated with two

asterisks (**). Numbers with color represent SH-aLRT and UFBoot support values (%). The upper part of the figure displays an entire SSU phylogenetic tree with all 12 genera of dictyostelids, while the lower part of the figure shows a partial tree with specific branches of isolates in this study and adjacent species.

Figure 3 – *Atp1* phylogenetic tree of dictyostelids. Isolates considered in this study are indicated in bold, new species are marked with one asterisk (*) and new varieties are marked with two asterisks

(**). Numbers with color represent SH-aLRT and UFBoot support values (%). The upper part of the figure includes an entire *atp1* phylogenetic tree with only five genera of *atp1* dictyostelid sequences available in NCBI database, the lower part of the figure presents a partial tree with specific branches of isolates in this study and adjacent species.

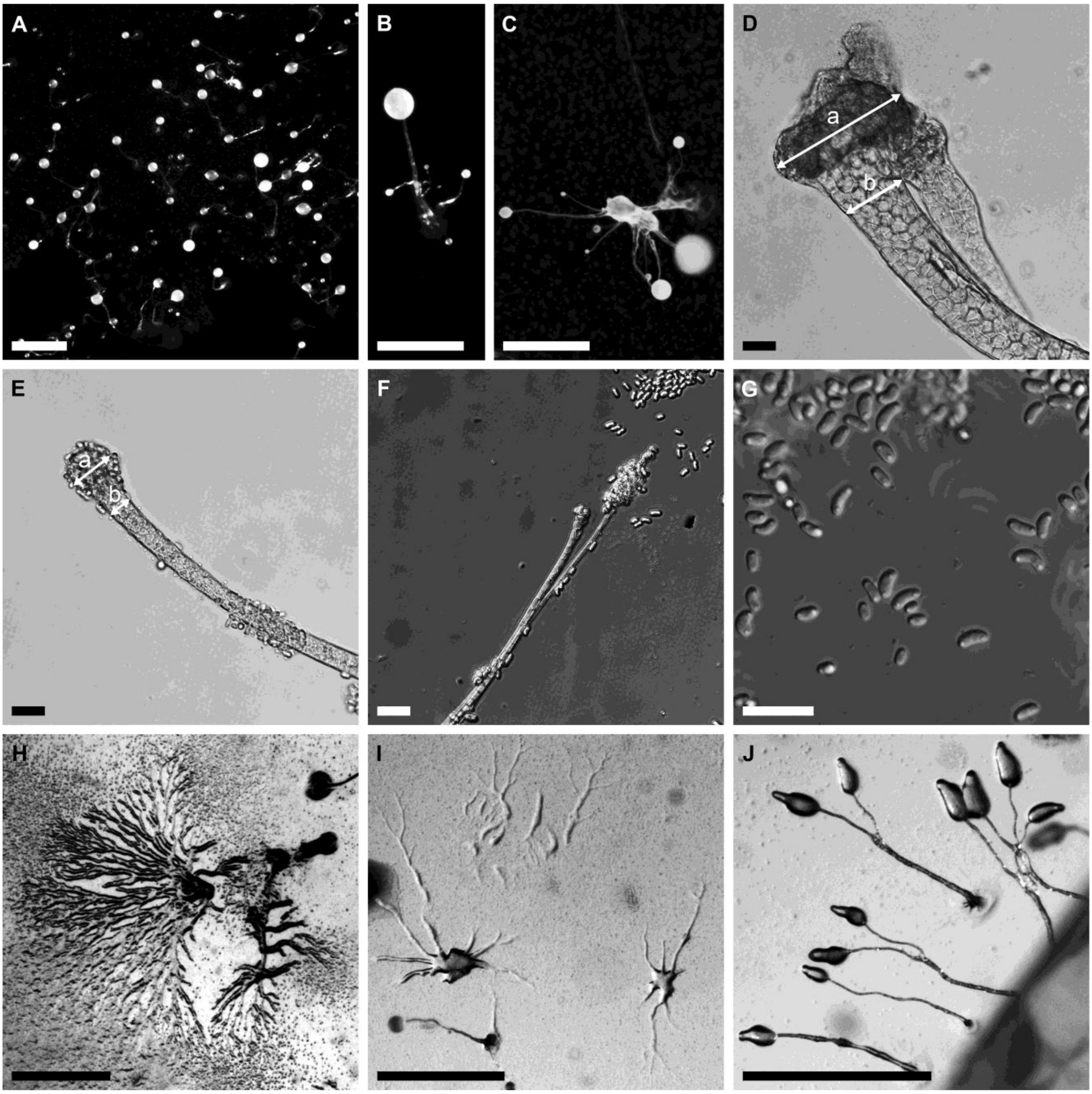

Figure 4 – Morphological features of *Cavenderia bifurcatimacrosorum*. (**A**) Gregarious sorocarps. (**B**) Sorocarp with five short branches. (**C**) Sorocarp with 8−10 branches arising from one mound on the sorophore. (**D**) Conical bases of the sorophores. Line a indicates the widest point of base terminal, line b indicates the width of the base. (**E**) Capitate tip of the sorophore. Line a indicates the widest point of tip terminal, line b indicates width of the tip. (**F**) Acuminate tips of the sorophores. (**G**) Spores with polar granules. (**H**) Early aggregation. (**I**) Late aggregations shrink into mounds. (**J**) Bifurcate and un-bifurcate pseudoplasmodia. Scale bars: A, H−J = 1 mm; B and C = 0.5 mm; D−G = 20 µm.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1821−1837 m) with an intermediate soil pH (pH = 6.03). Also isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1755−1828 m) with a low soil pH (pH = 5.32).

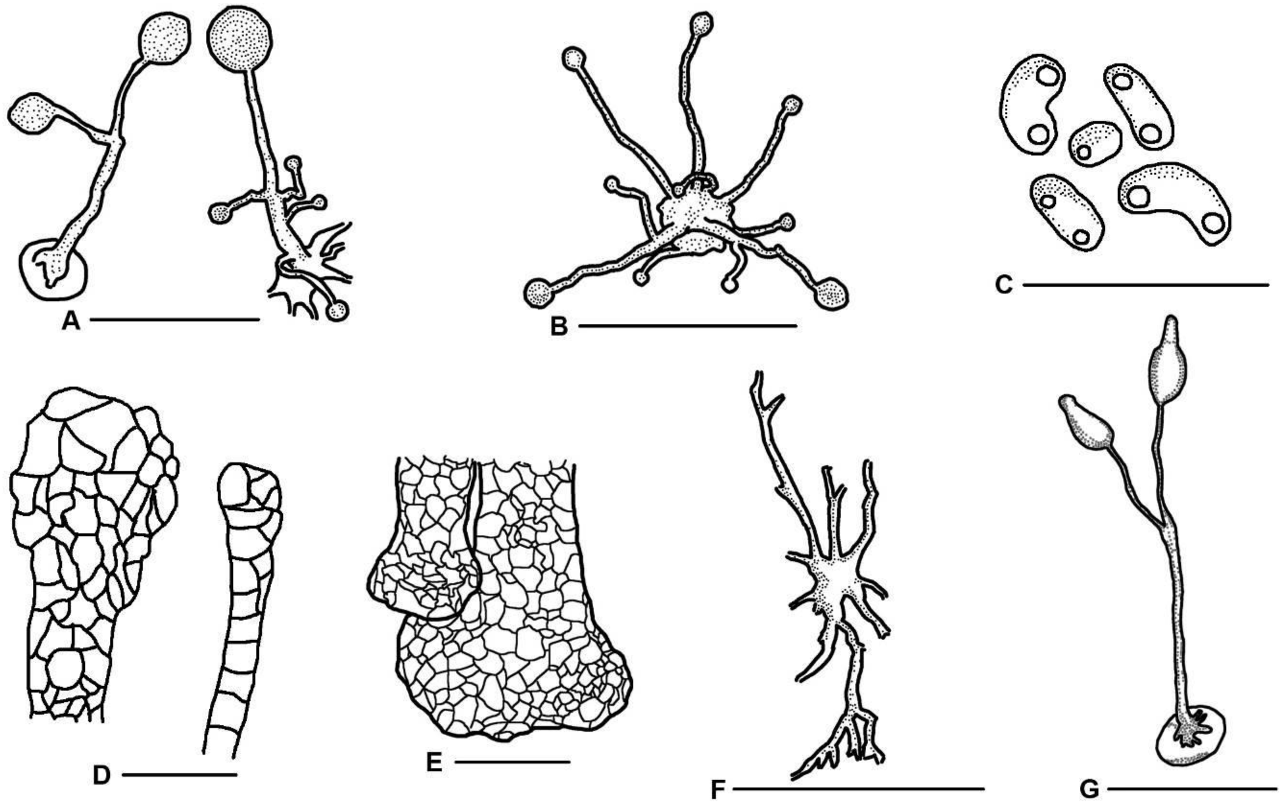

Figure 5 – *Cavenderia bifurcatimacrosorum*. (**A−B**) Sorocarps. (**C**) Spores. (**D**) Tips. (**E**) Bases. (**F**) Aggregation. (**G**) Pseudoplasmodium. Scale bars: A, G = 0.5 mm; B, F = 1 mm; C−E = 20 µm.

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1829.1 m. Isolated from mixed soils, August 2018, *yue2-2* (HOLOTYPE, voucher specimen code: HMJAU MR391). Also isolated from mixed soils of Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m, August 2019, *19yuef1*. Known only from Jilin Province, China.

Notes – Distinguishing features of *Cavenderia fasciculaticomplexispora* are including the clustered sorocarps, the smaller subglobose to broadly elliptical spores with larger elliptical to oblong ones, the aggregation pattern and the deepened medium color near the bases. In the SSU phylogenetic tree, *Ca. fasciculaticomplexispora* clusters near *Ca. fasciculata* and *Ca. fasciculoidea*, the differences between them are sorocarp size (this species has a little wider range than *Ca. fasciculoidea* (0.7−3mm), shorter than *Ca. fasciculata* (2−4 mm, occasionally to 10 mm)), complex spore size, sori size (*Ca. fasciculata* is milky-white to distinctly yellowish 60−300 µm, *Ca. fasciculoidea* is hyaline-white 40−150 (−220) µm in terminal and 25−40 µm in lateral), and the aggregations of *Ca. fasciculaticomplexispora* are obvious looser than them (Traub et al. 1981a, Vadell et al. 2011).

Cavenderia inordinata Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 8, 9

MycoBank number: 853148; GenBank accession number: SSU: PP590175.

Etymology – the name refers to the inordinate sorocarps on the medium.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are non-phototropic, gregarious, and grow in an inordinate manner on medium, prone to semierect, delicate, 0.3−2.3 mm in length. Sorophores consist of one tier of cells, colorless or white, unbranched. Bases are clavate, round to conical, sometimes curved, consisting of one to two tiers of cells, 5.1−10.5 μm in width, with the widest points of base terminals measuring 7.3−26.4 μm. Tips are acuminate, consist of one to two tiers of cells, 2.1−5.2 μm in width, and the widest points of tip terminals are 1.4−6.8 μm. Sori are white, globose, 24−212 μm in diam. Spores are elliptical to oblong, 3.2−7.1 × 1.8−3.8 μm (length/width = 1.47−2.04), rare broadly elliptical such as 3.5 × 2.7 μm (length/width = 1.28). Spores have polar granules. Aggregations are mound. Pseudoplasmodia migrate with stalks. Microcysts present 2.2−2.8 μm in diam. This species belongs to the *Cavenderia* clade in a SSU rDNA phylogeny.

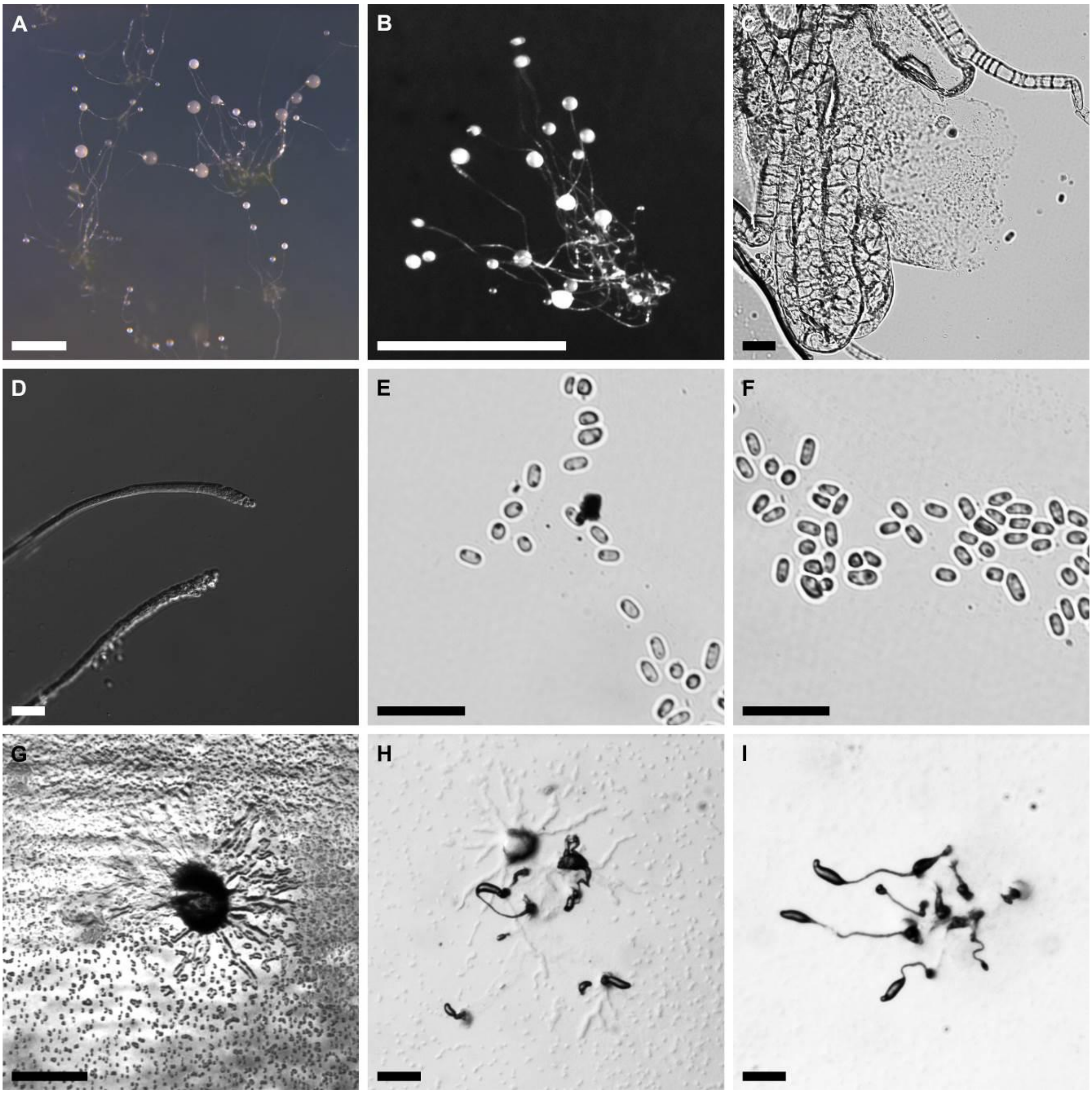

Figure 6 – Morphological features of *Cavenderia fasciculaticomplexispora*. (**A**) Sorocarps with light grayish olive medium near the bases. (**B**) Clustered sorocarps. (**C**) Clavate bases of the sorophores. (**D**) Clavate tips of the sorophores. (**E**) A few subglobose to broadly elliptical spores in the center. (**F**) Elliptical to oblong spores with polar granules. (**G**) Mounds aggregation with short

radiate streaming. (**H**) Aggregations and early pseudoplasmodia. (**I**) Clustered pseudoplasmodia with stalks but not migrating. Scale bars: A = 1 mm; B = 2 mm; C−F = 20 µm; G = 0.5 mm; H−I = 200 µm.

Distribution and ecology – Isolated from the Dell Forest of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at an intermediate elevation (1564−1620 m) with a low soil pH (pH = 5.59).

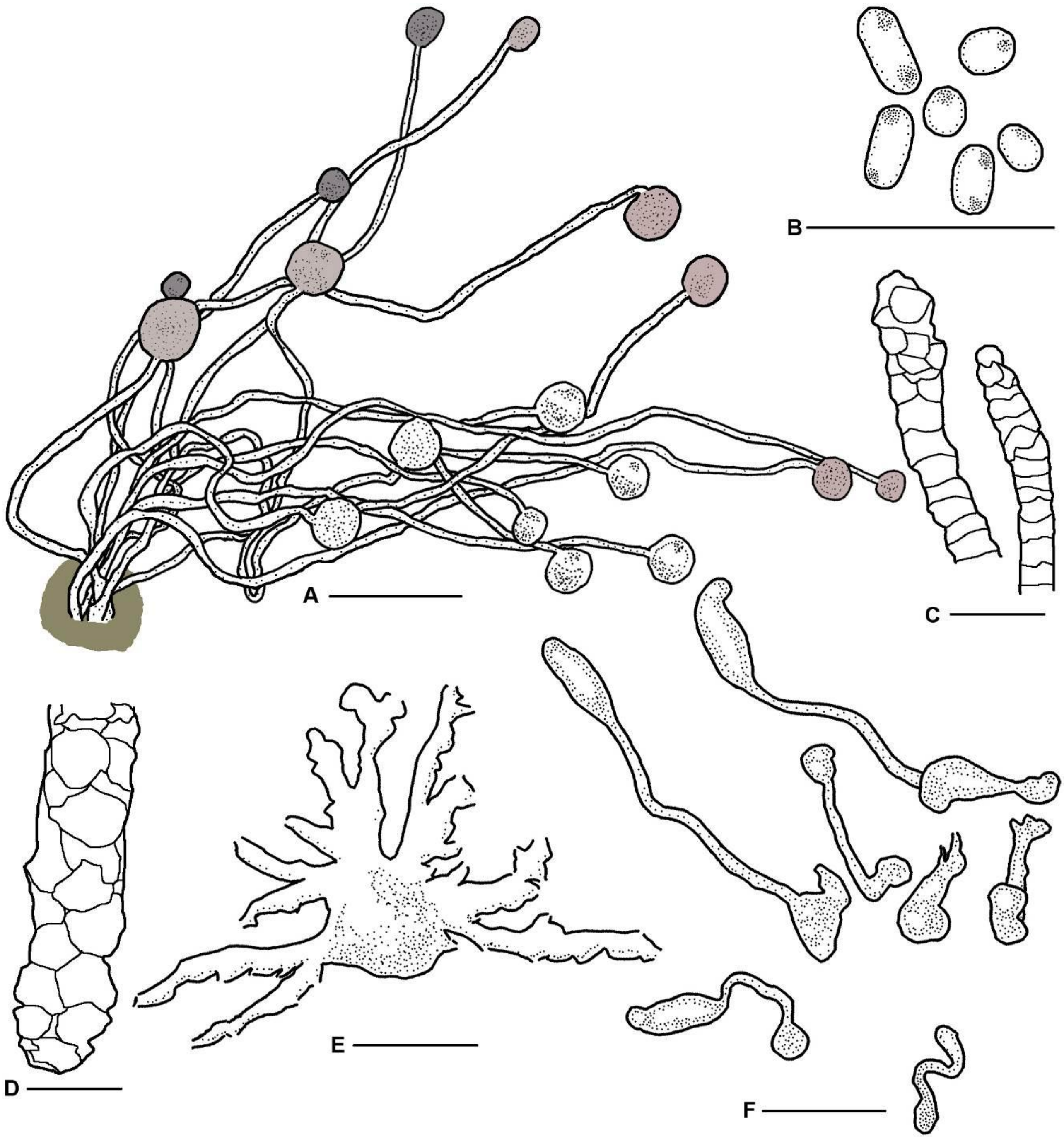

Figure 7 – *Cavenderia fasciculaticomplexispora*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tips. (**D**) Base. (**E**) Aggregation. (**F**) Pseudoplasmodia. Scale bars: A = 0.5 mm; B−D = 20 µm; E−F = 0.2 mm.

Material examined – China, Jilin Province: Dell Forest of the Changbai Mountain National Nature Reserve, 42.09º N, 128.07º E, average elevation 1594.2 m, August 2018, *hun1* (HOLOTYPE, voucher specimen code: HMJAU MR393). Known only from Jilin Province, China.

Notes – Gregarious unbranched sorocarps, colorless or white sorophores, white sori and the bases without basal disks distinguish *Cavenderia inordinata* from other *Cavenderia* species. *Cavenderia amphispora*, *Ca. microspora* and *Ca. parvispora* cluster near *Ca. inordinata* in the SSU phylogenetic tree. The distinctions among them are sorus size, spore size and base size (Hagiwara 1986, 1989, Cavender et al. 2005). *Cavenderia amphispora* has sori 30−80 µm in diam, *Ca. microspora* has 10−100 (−150) µm and *Ca. parvispora* 10−170 µm, are all smaller than *Ca. inordinata*. *Cavenderia amphispora* has larger ovoil spores 4.8−6.3 × 2.8−3.5 and smaller elliptical narrow spores 3−4.5 × 1.5−2.8 µm, *Ca. microspora* also has two types spores with 4.4−5.8 × 2.8−4.3 µm and 3.3−5.3 × 1.7−2.8 µm, *Ca. parvispora* has 4.3−6.1 × 1.8−2.8 µm, are all different with *Ca. inordinata*. *Cavenderia amphispora* has round to clavate bases with 7−22 µm in diam, *Ca. microspora* has clavate with 3−17.5 (−21.5) µm and *Ca. parvispora* has clavate with 5−25 (−36) µm, are all wider than *Ca. inordinata*.

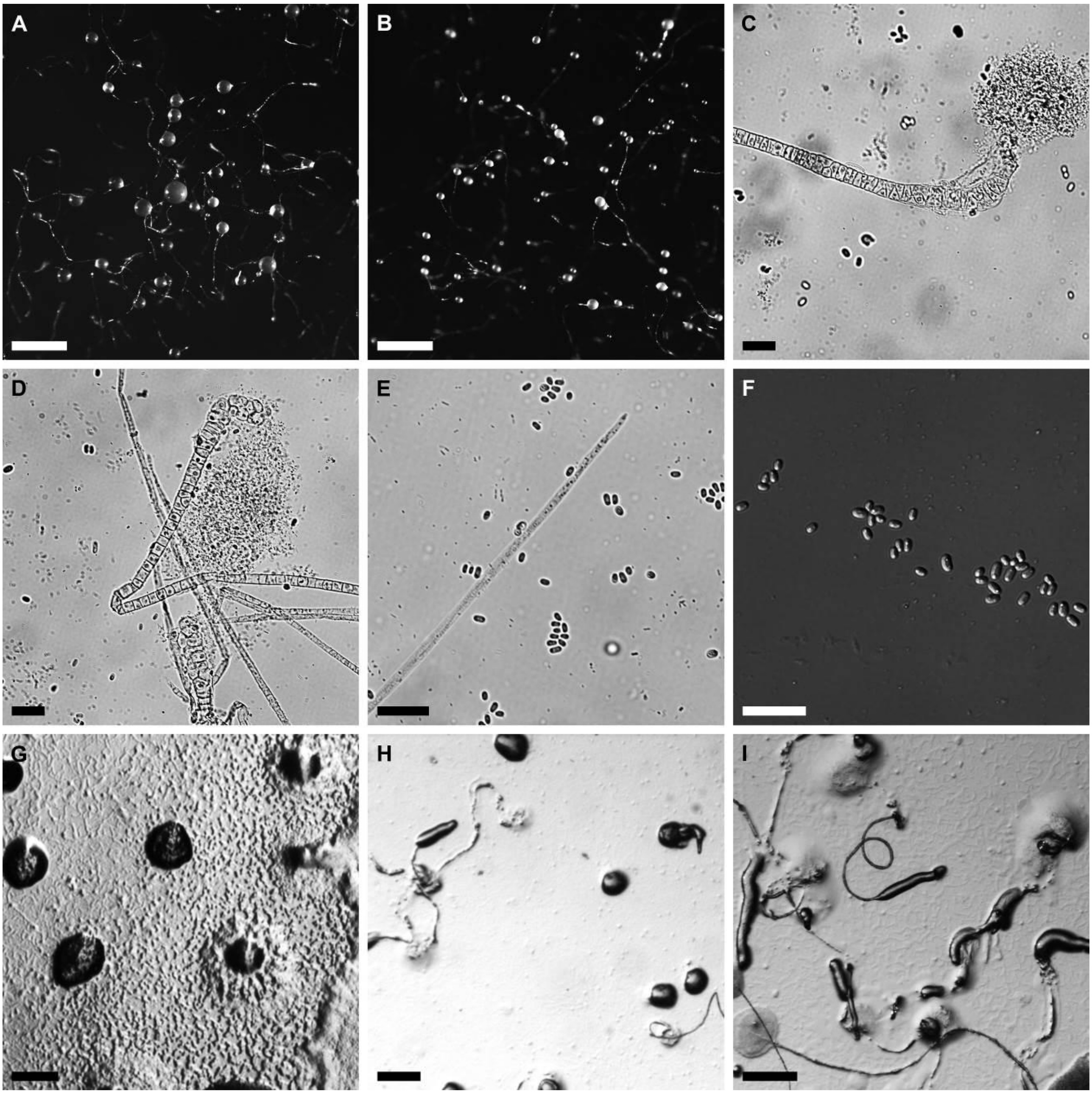

Figure 8 – Morphological features of *Cavenderia inordinata*. (**A−B**) Inordinate sorocarps. (**C)** Curved clavate base. (**D**) Curved and non-curved clavate bases. (**E**) Acuminate tip. (**F**) Spores

with polar granules. (**G**) Mound aggregations. (**H**) Aggregations and early pseudoplasmodia. (**I**) Pseudoplasmodia migrate with stalks. Scale bars: A−B = 0.5 mm; C−F = 20 µm; G−I = 200 µm.

Cavenderia varicelloides Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 10, 11

MycoBank number: 853170; GenBank accession number: SSU: PP817843. *Atp1*: PP932632.

Etymology – the name *varicelloides* refers to the resemblance of the aggregations to chickenpox (Latin: *varicella*).

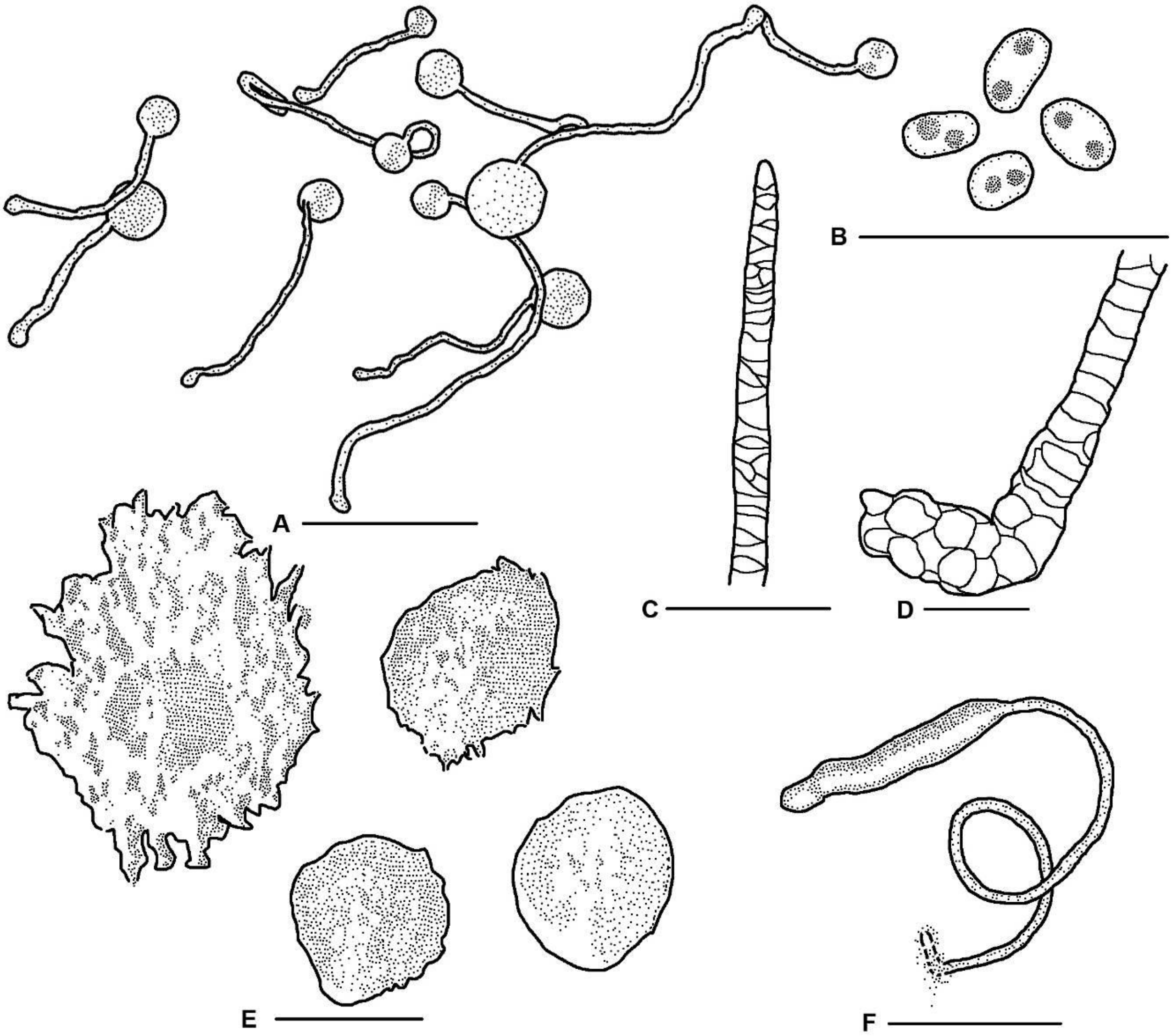

Figure 9 – *Cavenderia inordinata*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregations. (**F**) Pseudoplasmodium. Scale bars: A = 0.5 mm; B−D = 20 µm; E−F = 0.2 mm.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are without phototropic, gregarious or tightly clustered, prone to decumbent, 0.1−12.2 mm in length, unbranched or with many irregular branches. The part of sorophores near the bases is sometimes pale golden, ranging in color from deep yellow (#af8d13) to moderate olive brown (#6c541e). Branch length 0.1−3.2 mm or longer; bases of branches are clavate, consist of one tier of cells, 5.2−13.7 µm in width; branch tips are clavate, consist of one tier of cells, 2.6−4.7 µm in width. Sorophores consist of one to two tiers of cells. Bases are clavate, consisting of one to several tiers of cells, 7.3−25.9 µm in width, the widest points of base terminals measuring 7.2−32.9 µm. Tips are obtuse, capitate, clavate, or acuminate, consisting of one to two tiers of cells, 2.3−6.8 µm in width, with the widest points of tip terminals measuring 2.6−11.9 μm. Sori white, globose, 41−428 μm in diameter. Spores are elliptical to oblong, sometimes reniform, 3.8−7.3 × 2.4−4.4 μm (length/width = 1.32−2.68), occasionally large to 9.4 × 4.2 μm (length/width = 2.24), with obvious polar granules. Aggregations are small, round mounds that look like chicken pox. Pseudoplasmodia cluster with stalks, but do not migrate. Microcysts present, 3.2−3.9 × 2.9−3.8 μm. This species belongs to the *Cavenderia* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1755−1828 m) with a low soil pH (pH = 5.32).

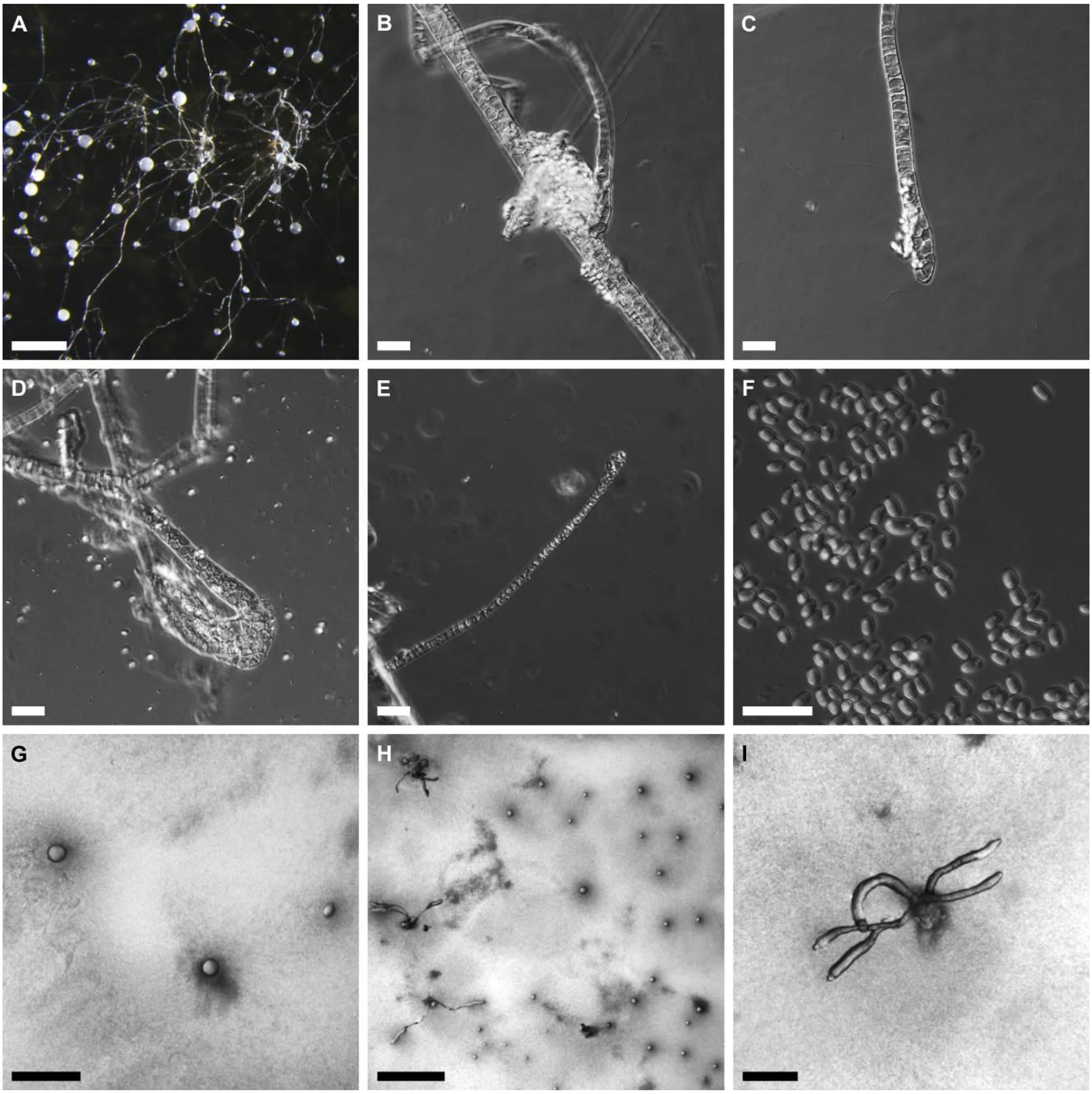

Figure 10 – Morphological features of *Cavenderia varicelloides*. (**A**) Clustered sorocarps with yellowed bases. (**B**) Branch on the sorophore. (**C**−**D**) Bases of the sorophores. (**E**) Clavate tip of the sorophore. (**F**) Spores with polar granules. (**G**) Small, round mounds form aggregations that look like chicken pox. (**H**) Aggregations and pseudoplasmodia. (**I**) Pseudoplasmodia do not migrate. Scale bars: A, G = 1 mm; B−F = 20 μm; H = 2 mm; I = 0.5 mm.

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m. Isolated from mixed soils, August 2019, *19yuec2-2* (HOLOTYPE, voucher specimen code: HMJAU MR429). Known only from Jilin Province, China.

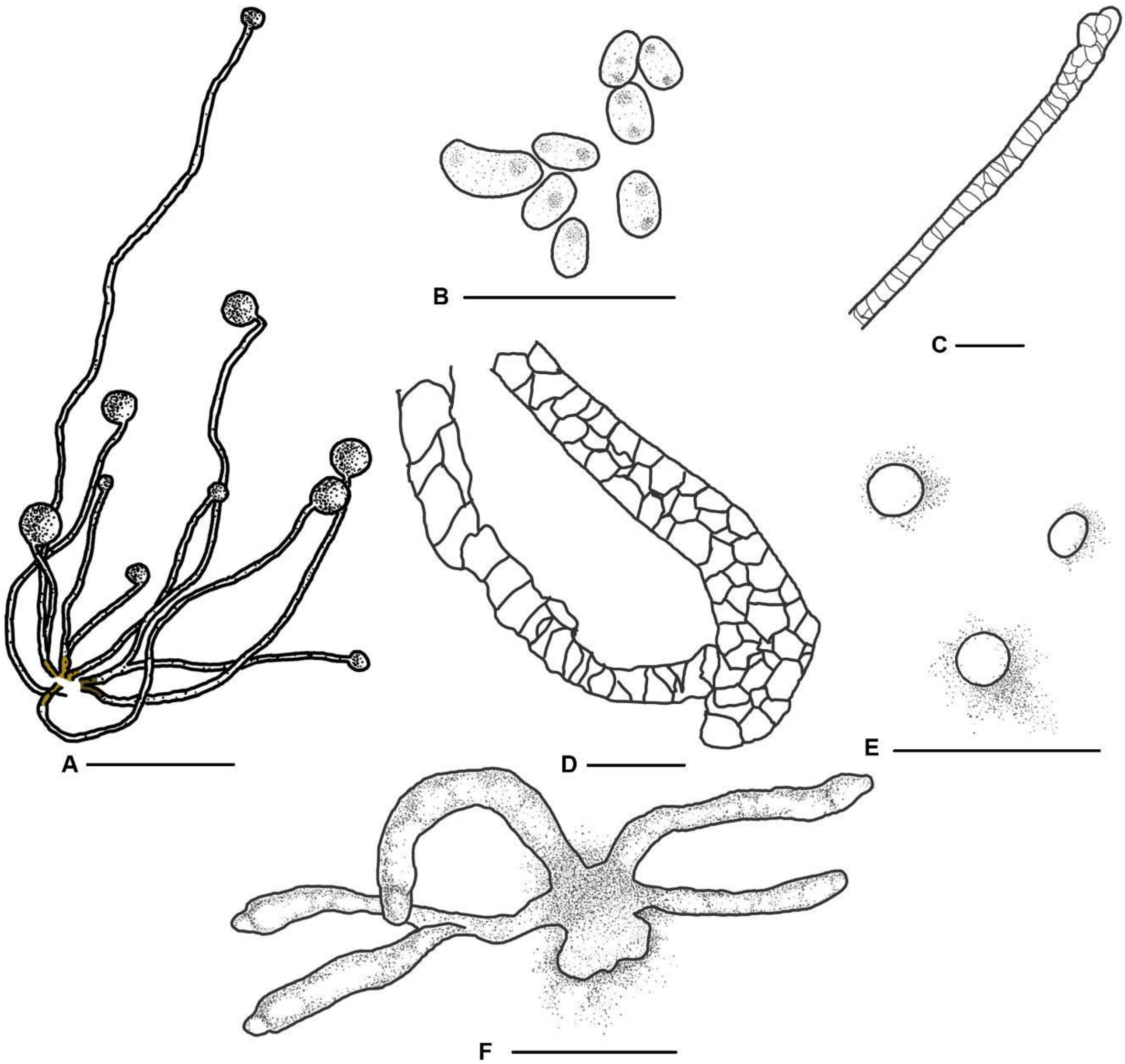

Figure 11 – *Cavenderia varicelloides*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Bases. (**E**) Aggregations. (**F**) Pseudoplasmodium. Scale bars: A, E = 1 mm; B−D = 20 µm; F = 0.5 mm.

Notes – *Cavenderia varicelloides* clusters near the species *Ca. aureostipes* and *Ca. fulva* in the SSU phylogenetic tree. On the *atp1* phylogenetic tree, *Ca. varicelloides* clusters closer with some conferred (cf.) species than *Ca. aureostipes*. On the other hand, *Ca. aureostipes*, *Ca. aureostipes* var. *helvetia*, and *Ca. delicata* are all similar to *Ca. varicelloides* in having long sorocarps that are more than 10 mm. *Cavenderia varicelloides* has the most obvious differences from the four species in small, round mound aggregations that look like chicken pox. Other morphological distinctions include sorophore color, width of tips and bases, and sorocarp habitat (Cavender et al. 1979, Hagiwara 1989, Cavender et al. 2018). Sorophores of *Ca. varicelloides* are white but yellowed near the bases, those of *Ca. aureostipes*, *Ca. aureostipes* var. *helvetia*, and *Ca. fulva* are golden-yellow, those of *Ca. delicata* are colorless. *Cavenderia varicelloides* has

2.3−6.8 µm wide tips, which are narrower than those of *Ca. aureostipes* (7−8 µm), *Ca. aureostipes* var. *helvetia* (13−19 µm), *Ca. delicata* (2.5−15.0 µm), and *Ca. fulva* (7−10 µm). Base widths of *Ca. varicelloides* (7.3−25.9 µm) are also narrower than those of *Ca. aureostipes* (25−30 µm), *Ca. aureostipes* var. *helvetia* (50−60 µm), and *Ca. fulva* (20−50 µm). *Cavenderia varicelloides* has gregarious or tightly clustered sorocarps, *Ca. aureostipes* var. *helvetia* has solitary sorocarps, and *Ca. delicata* has usually gregarious and sometimes solitary sorocarps.

Dictyostelium collarimigratum Y. Li, P. Liu et Y. Zou, sp. nov. (Figs. 2, 3, 12, 13)

MycoBank number: 853151; GenBank accession number: SSU: PP590178. *Atp1*: PP932652.

Etymology – the specific epithet refers to the collar structures and the migrating pseudoplasmodia.

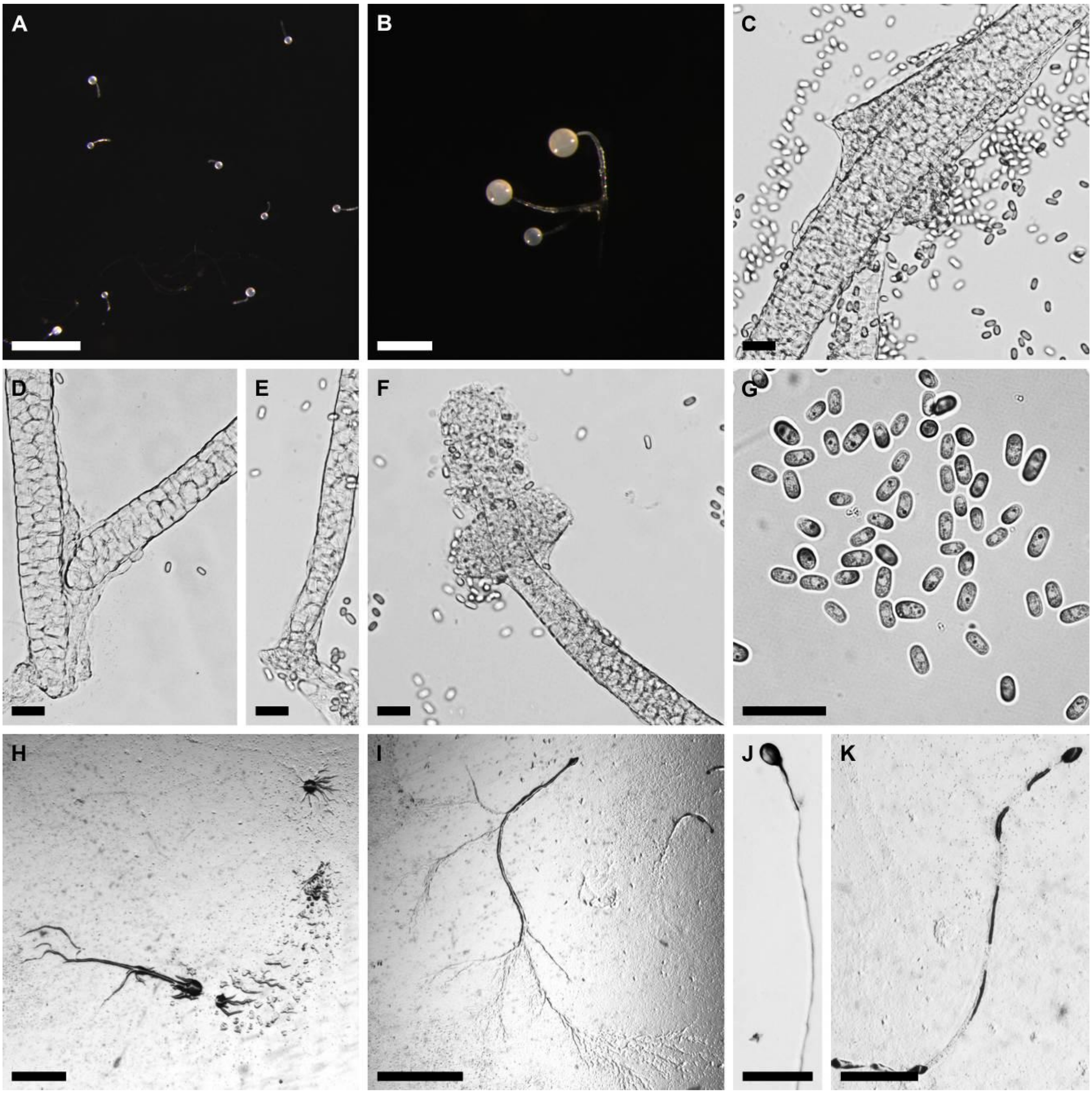

Figure 12 – Morphological features of *Dictyostelium collarimigratum*. (**A**) Solitary sorocarps. (**B**) Sorocarps with light grayish yellowish brown sori and with light orange yellow at the periphery of sori. (**C**) Expanded midpoints of the sorophores. (**D**) Clavate bases. (**E**) Base with slightly expand basal disk. (**F**) Capitate tip with a collar. (**G**) Spores with consolidated subpolar granules on one or

both sides. (**H**) Radiate aggregations. (**I**) Migrating pseudoplasmodium. (**J**) Migrating pseudoplasmodium with a continuous trail. (**K**) Migrating pseudoplasmodium with a discontinuous trail. Scale bars: A, H, K = 1 mm; B, J = 0.5 mm; C−G = 20 µm; I = 2 mm.

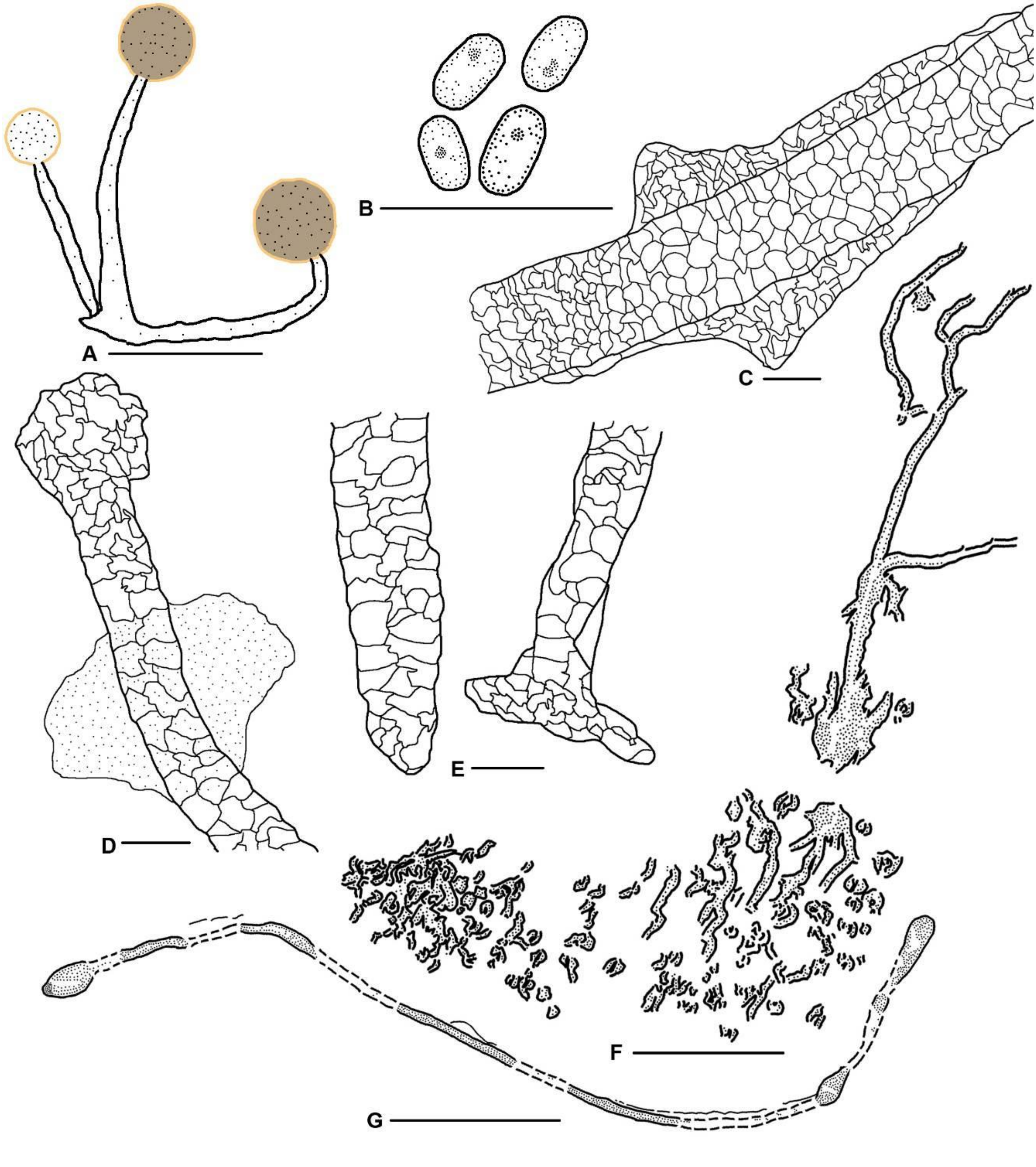

Figure 13 – *Dictyostelium collarimigratum*. (**A**) Sorocarp. (**B**) Spores. (**C**) Expanded sorophore. (**D**) Tip. (**E**) Bases. (**F**) Aggregations. (**G**) Pseudoplasmodium. Scale bars: A = 0.5 mm; B−E = 20 µm; F−G = 1 mm.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary or gregarious, sometimes two to three sorocarps clustered in one point, erect, prone to prostrate, 0.2−2.1 mm in length, unbranched or with one to two branches. Sorophores consist of several tiers of cells in width, have supporting cells, generally stout, expanded at midpoint, uneven taper in erect structures. The expanded midpoints of sorophores are 23.3−40.0 µm in width. Bases are clavate or acuminate, with one to several tiers of cells wide, 9.5−29.6 μm in width, sometimes have slightly expand basal disks (19.8−63.9 μm) at terminal cells of bases. Tips are capitate or obtuse, 9.1−25.0 μm wide, with one to several tiers of cells in width, with collars near the tips. The widest points of tip terminals are 9.1−36.5 μm. Sori are semi-hyaline, mostly white, or sometimes with cream color like light grayish yellowish brown (#ae9b82) with light orange yellow (#fbc97f) at the periphery, globose, 43−231 μm in diameter. Spores are elliptical to oblong, capsule-shaped, 5.0−11.5 × 3.2−4.6 μm (length/width = 1.45−2.83), with consolidated subpolar granules on one or both sides when observed under a microscope at 100× magnification. Aggregations are radiate, pseudoplasmodia migrate without stalks but with continuous or discontinuous trails. This species belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from Songbai Town of the Shennongjia National Nature Reserve, in mixed soil samples collected from an evergreen deciduous broadleaf forest at an intermediate elevation (1011−1424 m) with a high soil pH (pH = 7.41).

Material examined – China, Hubei Province: Songbai Town of the Shennongjia National Nature Reserve, 31.65º N, 110.54º E, average elevation 1151.2 m. Isolated from mixed soils, July 2022, *beichang2bxiao* (HOLOTYPE, voucher specimen code: HMJAU MR396). Known only from Hubei Province, China.

Notes – This species and *Dictyostelium collarimigratum var. breviorimigratum* cluster with *D. minimum* Li et al., *D. multiforme* Li et al., and *D. robusticaule* Li et al. in same clade of the SSU phylogenetic tree. On the *atp1* phylogenetic tree, *D. collarimigratum* and *D. collarimigratum var. breviorimigratum* cluster in the same clade but differ from others. They all have stout sorophores with relatively large sori, collars near tips with basal disks around bases, and the almost entirely identical SSU rDNA sequences, make these organisms really similar (Liu et al. 2019b, Zou et al. 2022). But they still have some differences in morphological characters, maybe due to the geographical isolation. *Dictyostelium minimum* has mini sorocarps (erect with 95−720 μm), white sori, globose spores without polar granules (PG−), mound-like aggregations, and not migrating pseudoplasmodia without stalks. *Dictyostelium multiforme* has several types of sorocarps (semi-erect with 0.68−1.8 mm and erect with 0.21−1.13 mm), white sori, oblong or elliptical spores with 5.8−12.6 × 3.6−5.0 μm (PG−), mound-like aggregations, and not migrating pseudoplasmodia without stalks. *Dictyostelium robusticaule* also has two types of sorocarps (larger 0.3−2.4 mm, smaller 0.1−0.2 mm) with erect, inclined, semierect or prone characters, larger sori with color white to off-white and dry out or tend to yellowish in age and smaller sori hyaline to white, larger elliptical or oblong spores with 5−7.2 × 3.2−4.7 μm with polar granules (PG+) and smaller spores with 4.7−6.5 × 3−4.3 μm (PG+), and radiate aggregations. *Dictyostelium collarimigratum* has erect, prone to prostrate 0.2−2.1 mm sorocarps, white or sometimes with cream color sori, elliptical to oblong and capsule-shaped spores with 5.0−11.5 × 3.2−4.6 μm (with consolidated subpolar granules on one or both sides), radial aggregations and migrating pseudoplasmodia with stalks. *Dictyostelium collarimigratum var. breviorimigratum* has erect to prone or prostrate sorocarps, white, or sometimes with a little cream sori, elliptical to oblong and capsule-shaped spores with 5.3−9.2 × 3.2−4.2 μm (with subpolar unconsolidated granules on one or both sides), radial aggregations and pseudoplasmodia not migrating or migrate only a short distance with stalks.

Dictyostelium collarimigratum* var. *breviorimigratum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 14, 15

MycoBank number: 853152; GenBank accession number: SSU: PP590179. *Atp1*: PP932651.

Etymology – the name refers to the pseudoplasmodia migrating a shorter distance than those of *D. collarimigratum* (from Latin *brevior*/*brevior*/*brevius*, meaning shorter).

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary, sometimes clustered with only two sorocarps, erect to prone or prostrate, 0.2−1.1 mm in length. Sorophores consist of one to several tiers of cells, taper from bases to tips. Bases are round or clavate with hook-shape, 13.1−24.5 μm in width, with two to several tiers of cells wide, sometimes have basal disks (26.3−85.1 μm). Tips are round to clavate, or capitate, 5.8−18.2 μm in width, with one to two tiers of cells in width, with collar near the tips, the widest points of tip terminals measuring 8.6−33.4 µm. Sori are mostly white, or sometimes with a little cream just like light brownish gray (#8e8279) to dark grayish yellow (#a18f60), with brownish pink (#c2ac99) at the periphery, globose, 70−287 µm in diam. Spores are elliptical to oblong, capsule-shaped, 5.3−9.2 × 3.2−4.2 µm (length/width =1.54−2.50), with subpolar unconsolidated granules on one or both sides when observed under a microscope at 100× magnification. Aggregations first are radiate, and later shrink into mounds with primary center and secondary centers. Pseudoplasmodia do not migrate or migrate a short distance with stalks. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

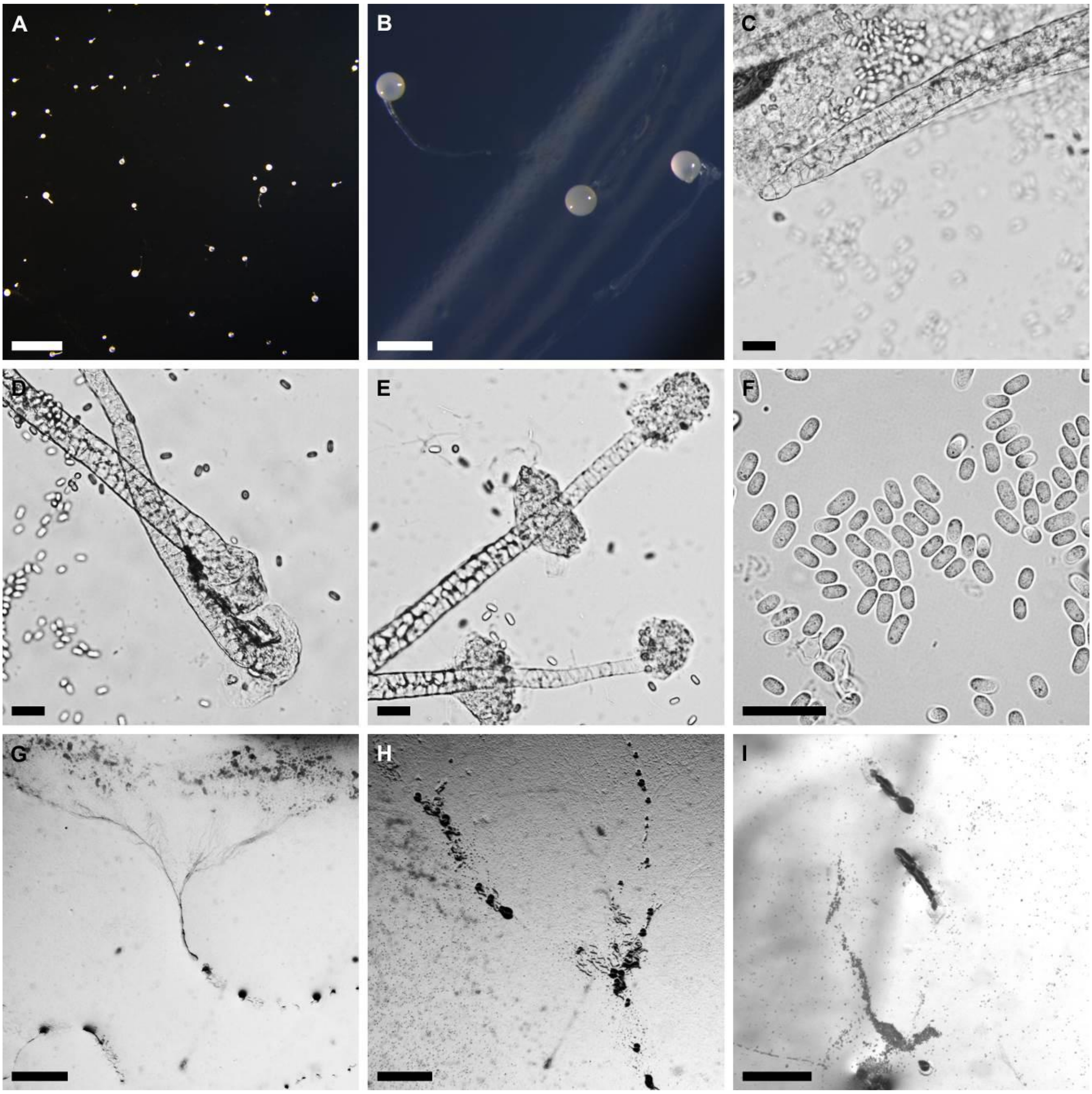

Figure 14 – Morphological features of *Dictyostelium collarimigratum* var. *breviorimigratum*. (**A**) Solitary sorocarps. (**B**) Sorocarps with light brownish gray to dark grayish yellow and with brownish pink at the periphery of sori. (**C**) Clavate base. (**D**) Bases with small basal disks. (**E**) Tips with collars. (**F**) Spores with subpolar unconsolidated granules on one or both sides. (**G**−**H**) Radiate aggregations. (**I**) Pseudoplasmodia migrate only a short distance. Scale bars: A = 2 mm; B, I = 0.5 mm; C−F = 20 µm; G−H = 1 mm.

Distribution and ecology – Isolated from Songbai Town of the Shennongjia National Nature Reserve, in mixed soil samples collected from an evergreen deciduous broadleaf forest at an intermediate elevation (1011−1424 m) with a high soil pH (pH = 7.41).

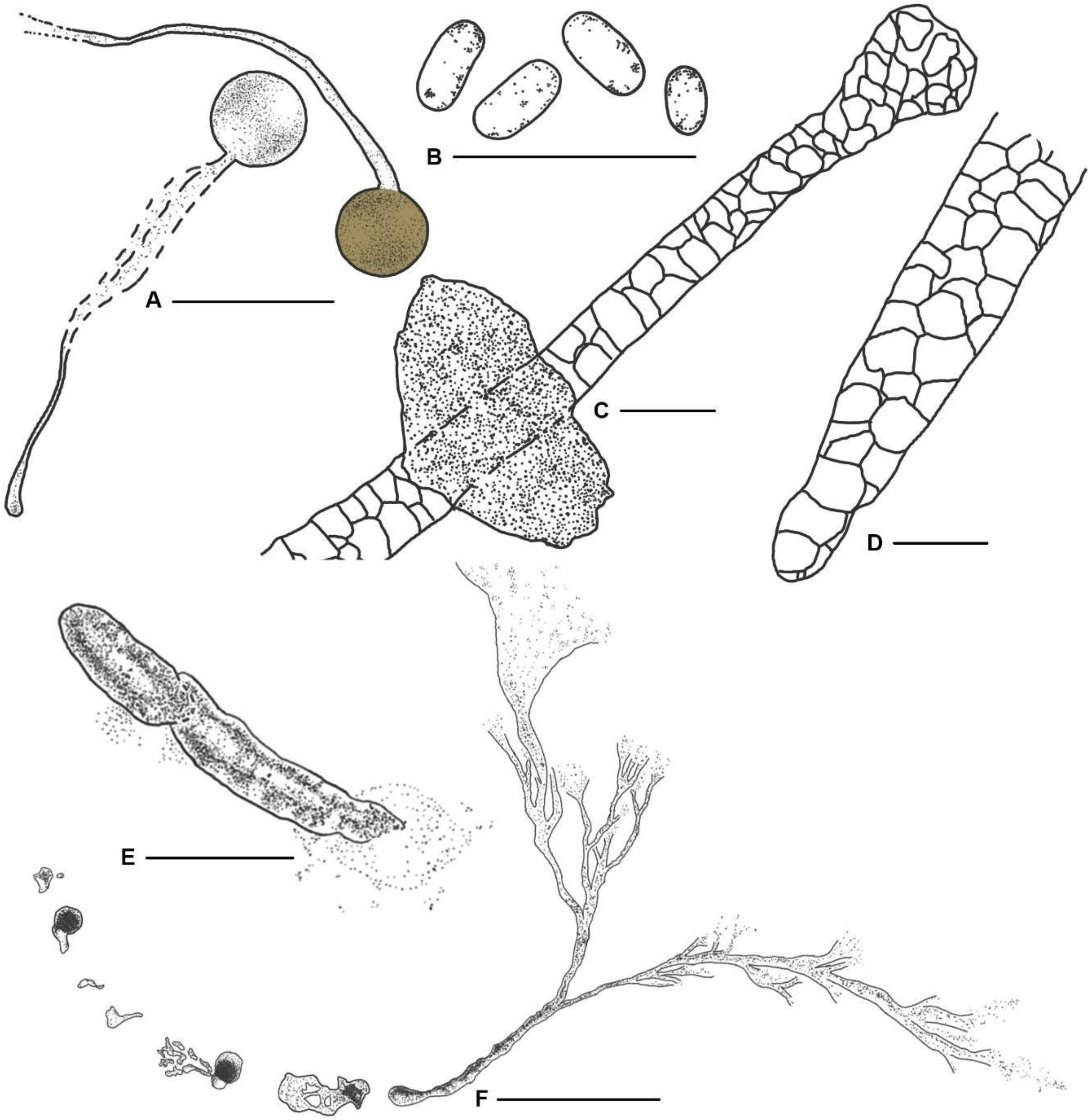

Figure 15 – *Dictyostelium collarimigratum* var. *breviorimigratum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Pseudoplasmodium. (**F**) Aggregations. Scale bars: A = 0.5 mm; B−D = 20 µm; E = 0.2 mm; F = 1 mm.

Material examined – China, Hubei Province: Songbai Town of the Shennongjia National Nature Reserve, 31.65º N, 110.54º E, average elevation 1151.2 m. Isolated from mixed soils, July 2022, *beichang2bda* (HOLOTYPE, voucher specimen code: HMJAU MR397). Known only from Hubei Province, China.

Notes – This variety has similar morphology to *Dictyostelium collarimigratum*, but this variety has spores with subpolar unconsolidated granules, and pseudoplasmodia do not migrate or migrate only a short distance. It shares the same clade as *D. collarimigratum* on the SSU and *atp1* tree.

Dictyostelium diversisporum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 16, 17

MycoBank number: 853156; GenBank accession number: SSU: PP590184; PP590185; PP590186. *Atp1*: PP932646; PP932645; PP932644.

Etymology – the name *diversisporum* refers to the various spore shapes.

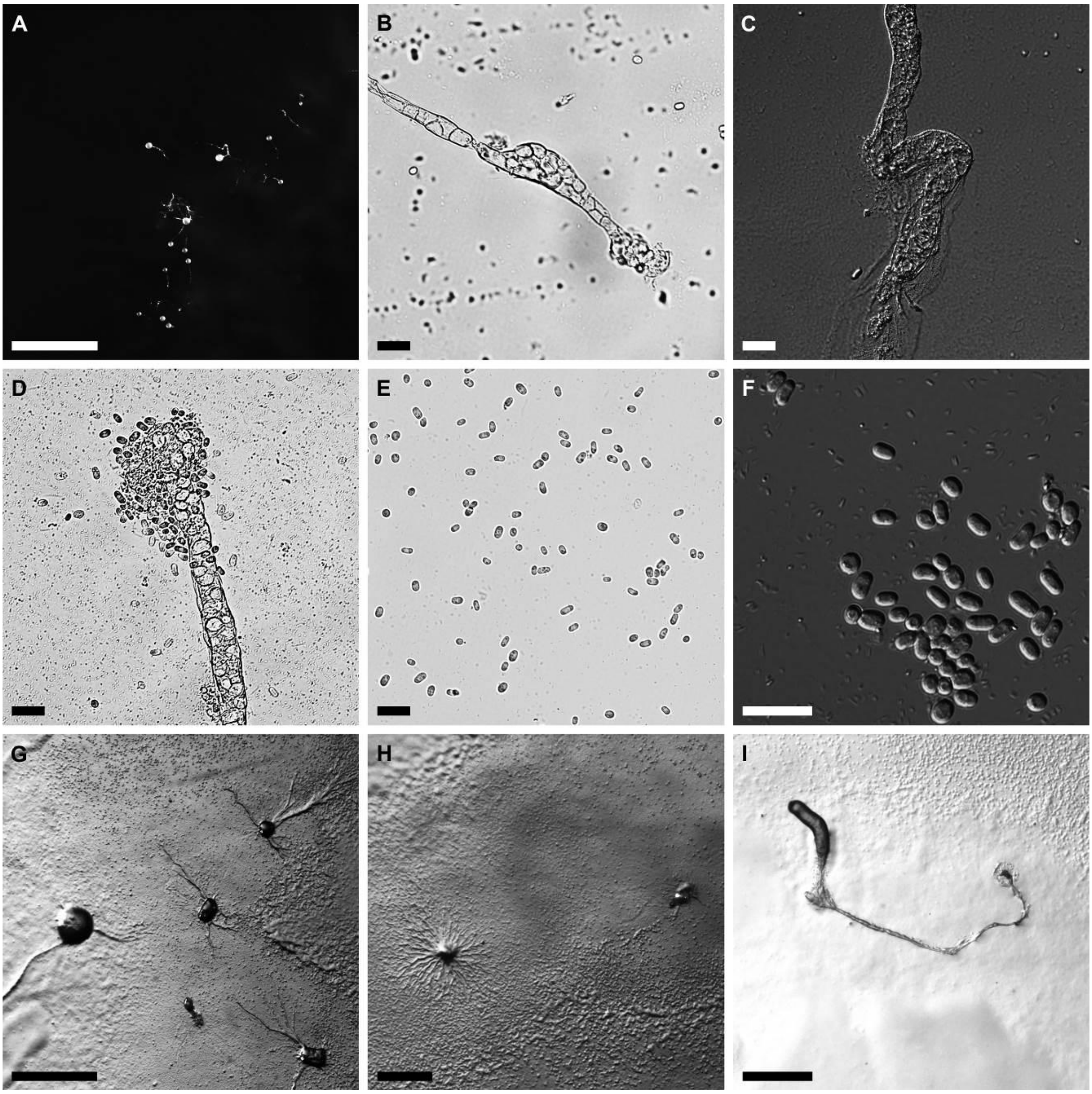

Figure 16 – Morphological features of *Dictyostelium diversisporum*. (**A**) Sorocarps. (**B**) Nodule-like cells on the sorophore. (**C**) Clavate base. (**D**) Capitate tip. (**E−F**) Various shapes of spores with consolidated or unconsolidated granules. (**G**) Radiate aggregations. (**H**) Aggregation and pseudoplasmodium. (**I**) Migrating pseudoplasmodium with a stalk. Scale bars: A = 2 mm; B−F = 20 µm; G = 1 mm; H−I = 0.5 mm.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are without phototropic or with a little phototropic, solitary to gregarious, erect or prone, prostrate, and decumbent, sori collapse and regrow new sorocarps; sorocarps are 0.5−8.4 mm in length. Sorophores consist of one to two tiers of cells in width. Sometimes sorophores are one-tier cells and two-tier cells in width for turning. Sometimes there are several nodule-like cells that occur on sorophores. Bases are clavate to round or conical, consisting of one to two tiers of cells, 5.4−18.3 µm in width, with the widest points of base terminals measuring 7.6−44.2 µm. Tips are capitate to expand clavate, sometimes hook-shape, consisting of one to two tiers cell, 4.2−16.7 µm in width, with the widest points of tip terminals measuring 6.0−38.2 µm. Sori are white, globose to citriform, 54−284 µm. Spores are amorphous shapes, including capsule-shaped, sigmoid, reniform, sunflower seed-shaped, pear-shaped, or drop-shaped, in addition to common shapes ranging from globose to bacilliform, 3.8−9.3 × 2.3−5.8 µm (length/width = 1.03−3.24), sometimes large and reaching to 10.2 × 3.8 µm (length/width = 2.68), rarely small size measuring 3.4 × 3.0 µm (length/width = 1.13), without polar granules but with consolidated or unconsolidated granules dispersed in spores. Aggregations are radiate and shrinking into mounds, 0.7−3.5 × 0.5−1.1 µm. Pseudoplasmodia migrate with stalks. Microcysts present, 3.7−5.7 µm in diameter. This species belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

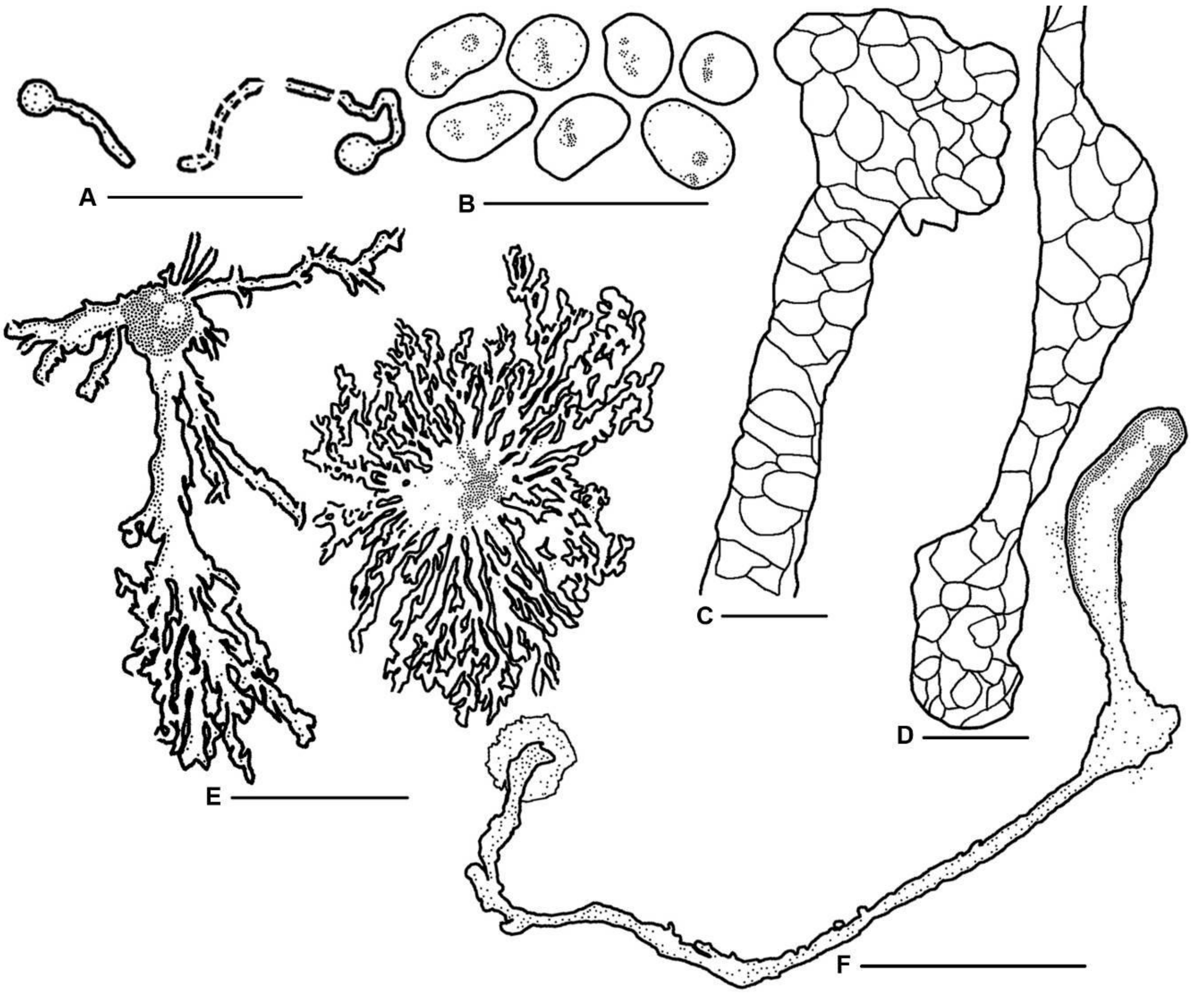

Figure 17 – *Dictyostelium diversisporum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregations. (**F**) Pseudoplasmodium. Scale bars: A = 1 mm; B−D = 20 µm; E−F = 0.5 mm.

Distribution and ecology – Isolated from the Dell Forest of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at an intermediate elevation (1564−1620 m) with a low soil pH (pH = 5.59). Also isolated from Northern

Slope of Changbai Mountain National Nature Reserve, in mixed soil samples collected from a soil sample collected in an alpine birch forest at an intermediate elevation (1755−1828 m) with a low soil pH (pH = 5.32).

Material examined – China, Jilin Province: Dell Forest of the Changbai Mountain National Nature Reserve, 42.09º N, 128.07º E, average elevation 1594.2 m. Isolated from mixed soils, August 2018, *hun6* (HOLOTYPE, voucher specimen code: HMJAU MR402); *hun2*; *hun2-2*; *hun2-3*; *hun6-2*. Also isolated from mixed soils of Northern Slope of Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m, August 2019, *19yued1*. Known only from Jilin Province, China.

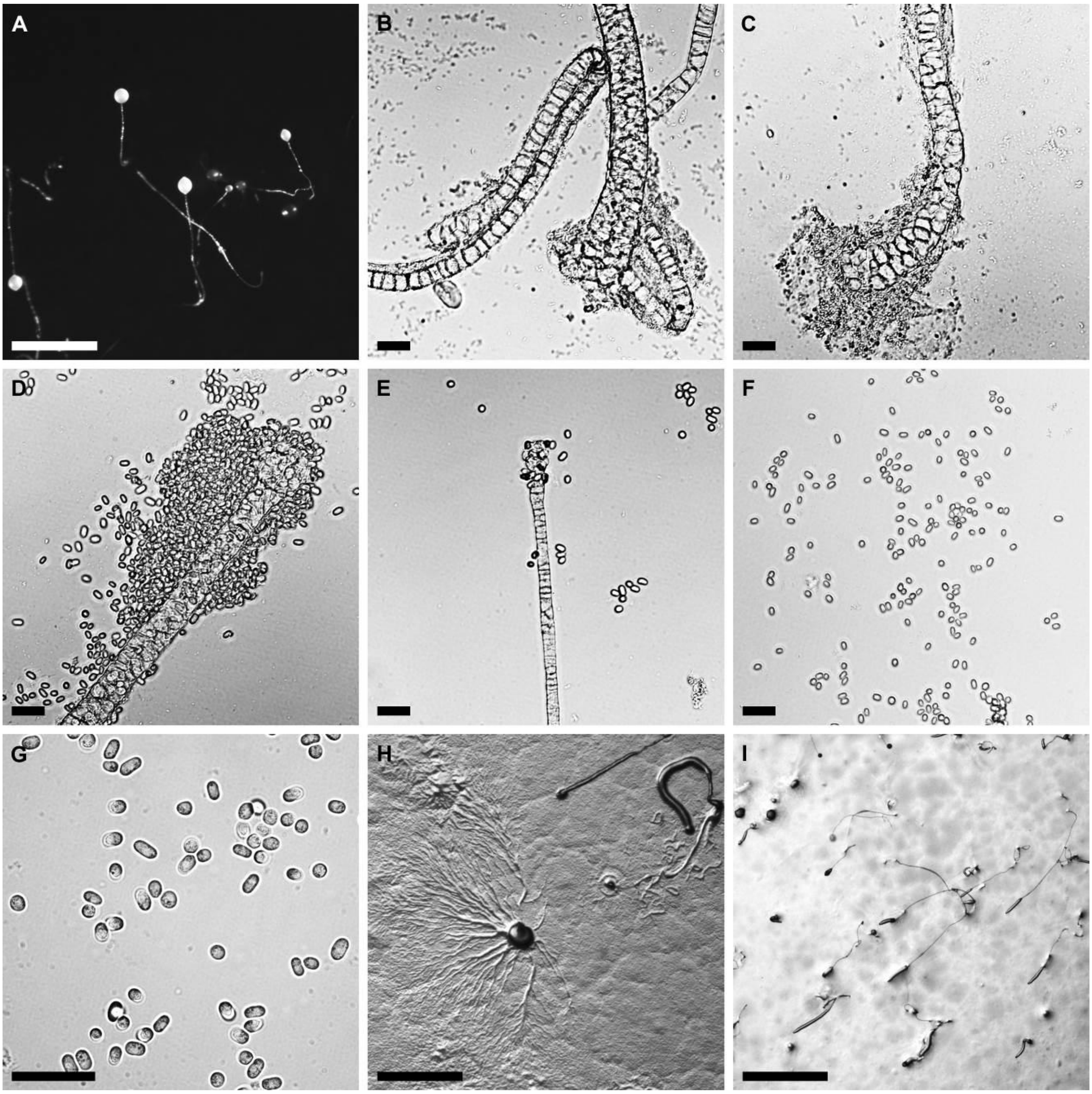

Figure 18 – Morphological features of *Dictyostelium diversisporum* var. *brevisporum*. (**A**) Sorocarps. (**B**−**C**) Round and clavate bases. (**D**−**E**) Capitate tips. (**F**−**G**) Different shapes of spores with or without granules dispersed. (**H**) Radiate aggregation and migrating pseudoplasmodium. (**I**) Phototropic pseudoplasmodia migrate with stalks, and aggregations shrink into mounds at the top-left corner. Scale bars: A, H = 1 mm; B−G = 20 μm; I = 2 mm.

Notes – *Dictyostelium diversisporum* is brought together with *D. austroandinum*, *D. capitatum*, *D. leptosomopsis*, *D. mucoroides*, and *D. pseudobrefeldianum* on close branches of the SSU phylogenetic tree. However, the *atp1* phylogenetic tree has shown it to be different from others, except for its varieties. *Dictyostelium diversisporum* has nodule-like cells on sorophores, and various spore shapes; each characteristic distinguishes this from other *Dictyostelium* species (Hagiwara 1983a, Raper 1984, Hagiwara 1996, Vadell et al. 2011). On the other hand, this species has narrower base sizes than *D. austroandinum*, *D. mucoroides*, and *D. pseudobrefeldianum*; and wider tip sizes than *D. capitatum* and *D. leptosomopsis*. The morphological differences between *D. diversisporum* and its varieties are detailed in the notes for those varieties.

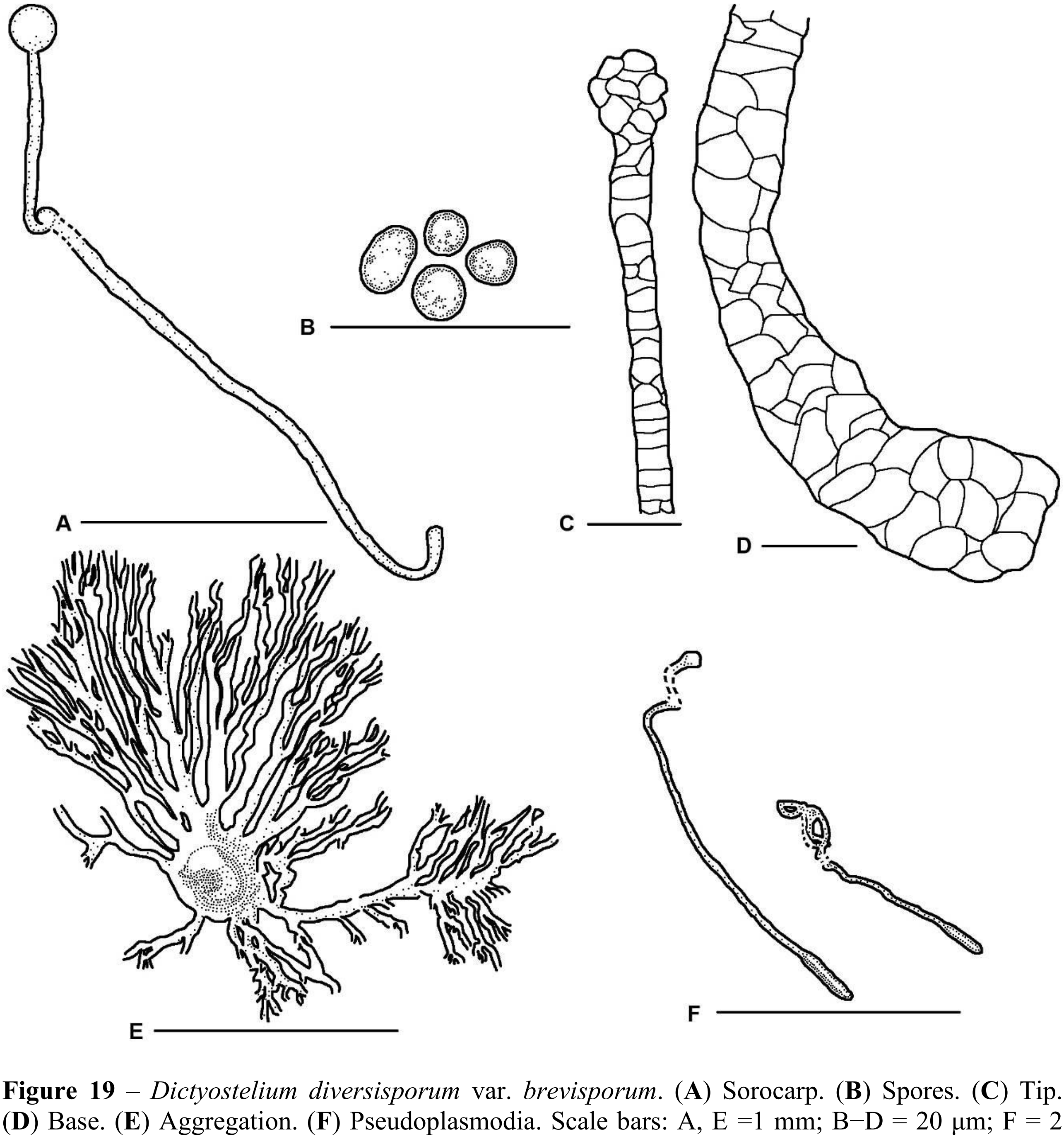

Figure 19 – *Dictyostelium diversisporum* var. *brevisporum*. (**A**) Sorocarp. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregation. (**F**) Pseudoplasmodia. Scale bars: A, E =1 mm; B−D = 20 µm; F = 2 mm.

Dictyostelium diversisporum* var. *brevisporum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 18, 19

MycoBank number: 853159; GenBank accession number: SSU: PP590193; PP590194. *Atp1*: PP932643; PP932642.

Etymology – the name refers to the shorter spores (smaller ratio of length to width) compared with *Dictyostelium diversisporum*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic, gregarious, prone to prostrate, sometimes decumbent with stoloniferous behavior, 3.2−9.5 mm in length, unbranched or with one branch. Sorocarp consists of two parts: a strong erect part and a thin prostrate part; the connecting points of two parts are the thickest and consist of two to several tiers of cells with a diameter of 20.9−55.0 μm. Sorophores consist of one to two tiers of cells. Bases are clavate, accumulate, or round, consist of one to two tiers of cells, 6.4−14.5 μm in width, the widest points of base terminals measuring 3.7−32.8 μm. Tips are capitate, consist of one to several tiers of cells, 3.8−18.1 μm in width, the widest points of tip terminals measuring 10.9−33.1 μm. Sori are white, globose or citriform, 80−250 μm in diam. Spores are globose to oblong, sometimes pear-shaped, 3.8−7.2 × 2.7−4.5 μm (length/width = 1.00−2.27), without polar granules but sometimes with granules dispersed. Aggregations are radiate at first and then shrink into mounds, 1.6−4.5 × 1.1−3.3 mm. Pseudoplasmodia migrate with stalks. Microcysts present with 3.5−5.6 × 3.2−5.6 μm. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1755−1828) with a low soil pH (pH = 5.32).

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m. Isolated from mixed soils, August 2019, *19yueb2* (HOLOTYPE, voucher specimen code: HMJAU MR408); *19yuea1*. Known only from Jilin Province, China.

Notes – *Dictyostelium diversisporum* var. *brevisporum* clusters together with *D. diversisporum*, *D. diversisporum* var. *maximisporum*, and *D. diversisporum* var. *laevisorophorum* on common branches of SSU and *atp1* tree, however, the smaller spore ratio of length to width, and the absence of nodule-like cells have distinguished it from others.

Dictyostelium diversisporum* var. *laevisorophorum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 20, 21

MycoBank number: 853158; GenBank accession number: SSU: PP590188; PP590189; PP590190; PP590191; PP590192. *Atp1*: PP932647; PP932648; PP932649.

Etymology – *laevisorophorum* refers to the smooth sorophores that are compared to *Dictyostelium diversisporum*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic, solitary to gregarious, erect, semierect, prone, to prostrate, or decumbent, 0.1−6.4 mm in length. Mostly unbranched but occasionally with only one branch on the sorocarp. Sorophores consist of one to several tiers of cells in width, usually unbranched. Bases are clavate to round or conical, curved or expanded, consisting of one to several tiers of cells in width, 5.2−19.0 μm in width, the widest points of base terminals measuring 5.5−39.5 μm. Sometimes skirt-like floccules surrounding the bases are observed under a microscope. Tips are capitate, curved, with one or two tiers of cell in width, 2.2−18.8 μm in width, the widest points of tip terminals measuring 4.2−34.5 μm. Sori are semi-hyaline, white, rarely cream at the periphery, appearing light grayish olive (#8c8767), globose, occasionally round-apiculate, 36−251 μm in diam. Spores are globose to bacilliform, sometimes reniform and sigmoid, occasionally pear-shaped, 3.5−14.6 × 2.5−5.6 μm (length/width = 1.00−3.03), without polar granules but with consolidated to unconsolidated granules. On the other hand, one spore with V-shaped has been observed, the two arms of 'V'-shape as 9.3 and 7.7 μm. Aggregations are 0.5−1.3 × 0.3−0.9 μm. Early aggregations have radial streaming, late aggregations shrink into mounds and form pseudoplasmodia. Pseudoplasmodia migrate with stalks. Microcysts present as 3.2−4.4 × 2.9−4.4 μm. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1821−1837 m) with an intermediate soil pH (pH = 6.03). Also isolated from the Dell Forest of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at an intermediate elevation (1564−1620 m) with a low soil pH (pH = 5.59).

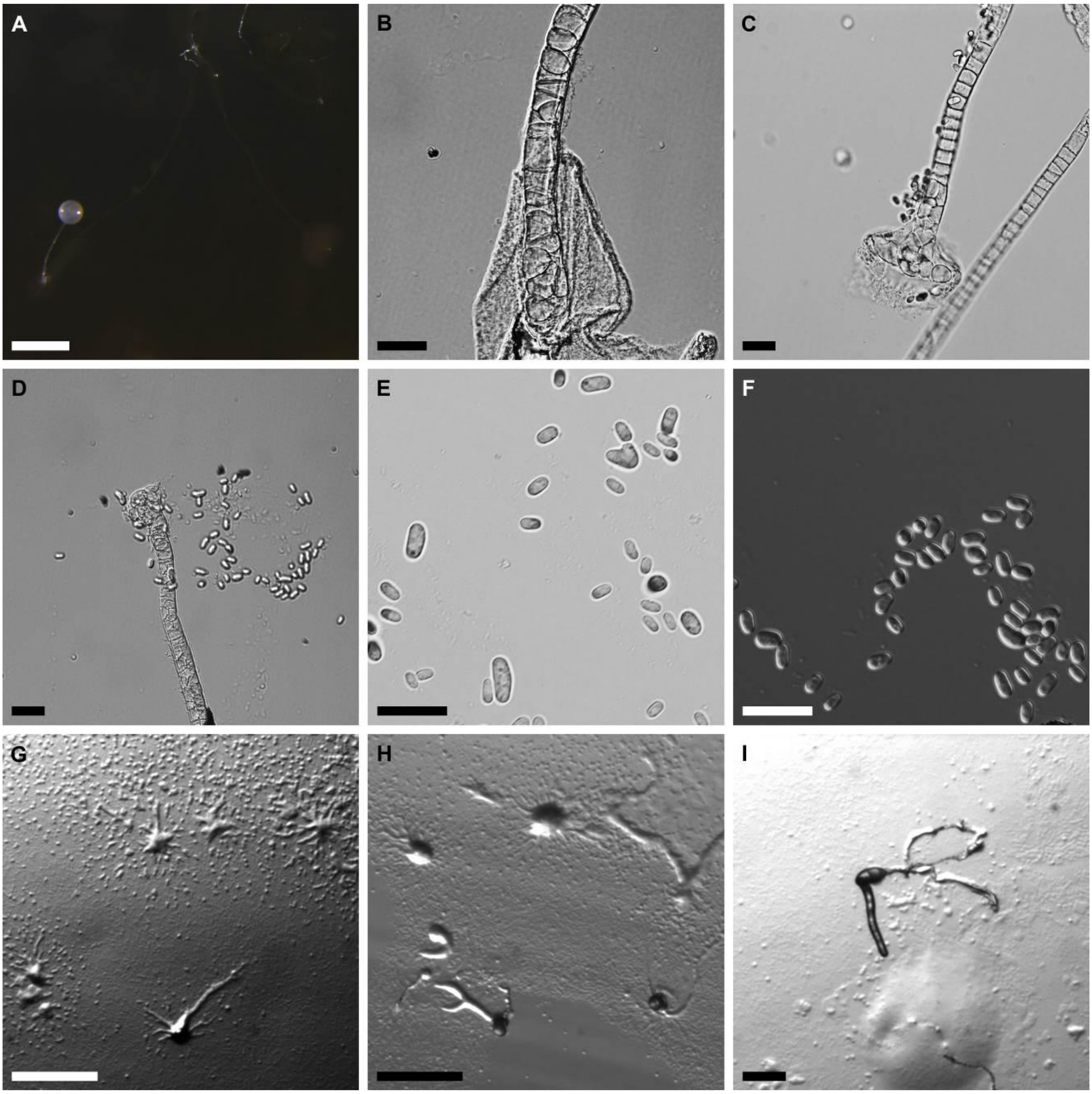

Figure 20 – Morphological features of *Dictyostelium diversisporum* var. *laevisorophorum*. (**A**) Sorocarp with light grayish olive at the periphery of white sori. (**B**−**C**) Bases. (**D**) Capitate tip. (**E**−**F**) Spores with consolidated to unconsolidated granules. (**G**) Radiate aggregations. (**H**) Aggregations and early pseudoplasmodia. (**I**) Pseudoplasmodium migrates with a stalk. Scale bars: A, G−H = 0.5 mm; B−F = 20 μm; I = 200 μm.

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1829.1 m. Isolated from mixed soils, August 2018, *yue1* (HOLOTYPE, voucher specimen code: HMJAU MR304); *yue1-2*; *yue1-3*; *yue3*; *yue3-2*; *yue3-3*; *yue4*. Also isolated from mixed soils of Dell Forest of the Changbai

Mountain National Nature Reserve, 42.09º N, 128.07º E, average elevation 1594.2 m, August 2018, *hun3*. Known only from Jilin Province, China.

Notes – *Dictyostelium diversisporum* var. *laevisorophorum* clusters together with *D. diversisporum*, *D. diversisporum* var. *maximisporum*, and *D. diversisporum* var. *brevisporum* on common branches in the SSU and *atp1* phylogenetic tree. In morphology, this variety is characterized by its smooth sorophores that lack nodule-like cells, the occasional 'V'-shape spores, and rarely a cream rim of sori.

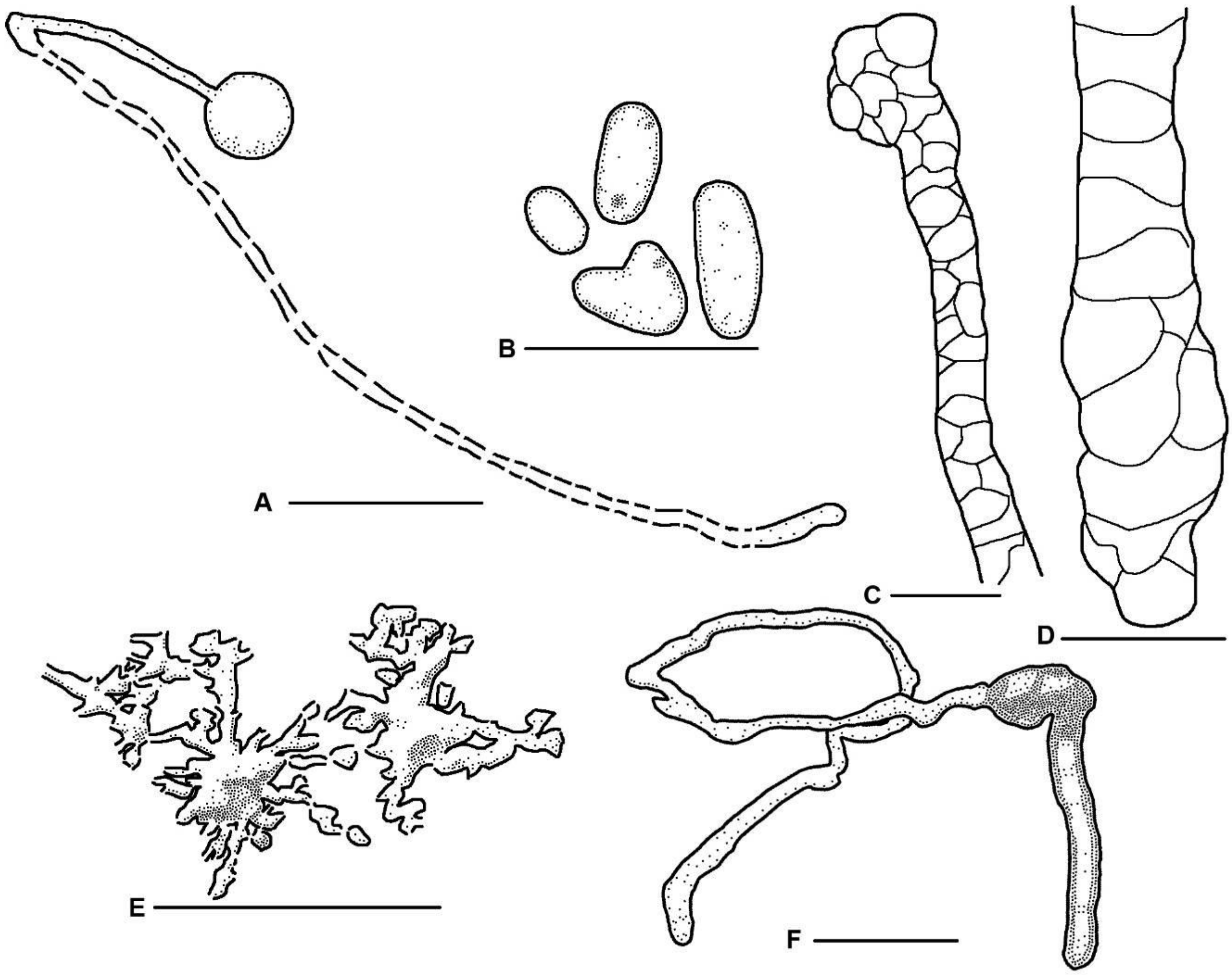

Figure 21 – *Dictyostelium diversisporum* var. *laevisorophorum*. (**A**) Sorocarp. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregations. (**F**) Pseudoplasmodium. Scale bars: A, E = 0.5 mm; B−D = 20 µm; F = 0.2 mm.

Dictyostelium diversisporum* var. *maximisporum Y. Li, P. Liu et Y. Zou, sp. nov.Figs. 2, 3, 22, 23

MycoBank number: 853157; GenBank accession number: SSU: PP590187. *Atp1*: PP932650.

Etymology – the name refers to the huge spores compared with *Dictyostelium diversisporum*.

When cultured at 23°C on non-nutrient agar, sorocarps are solitary or gregarious, 0.3−1.5 mm in length, erect or semierect to prone, unbranched or have one short branch near the base. Sorophores consist of one tier of cells, mostly buckling, some have nodule-like cells on sorophores, and buckling at the nodule-like space. Bases are clavate or round, attached a little slime, consisting of a tier cell, 8.0−17.1 µm in wide, with the widest points of base terminals measuring 11.5−23.8 µm. Tips consist of one tier of cells, a little expanded with one cell as capitate or recurve, 4.1−8.0 µm in wide, the widest points of tip terminals measuring 7.0−18.8 µm. Sori are globose, white, semi-hyaline or hyaline, diameter 73−170 µm. Spores have a lot of forms, mostly oval to bacilliform with capsule-shaped, reniform, and long "S"-shaped, as 6.1−20.7 × 2.9−7.4 µm (length/width = 1.74−4.17), rarely subglobose as 10.1 × 9.3 µm (length/width =1.09), or pear-shaped as 7.5 × 4.8 µm (length/width = 1.56), or elliptical as 10.1 × 7.1 µm (length/width = 1.42), without polar granules but sometimes with granules dispersed. Pseudoplasmodia with stalks. Microcysts 3.9−4.7 × 3.8−4.4 µm. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

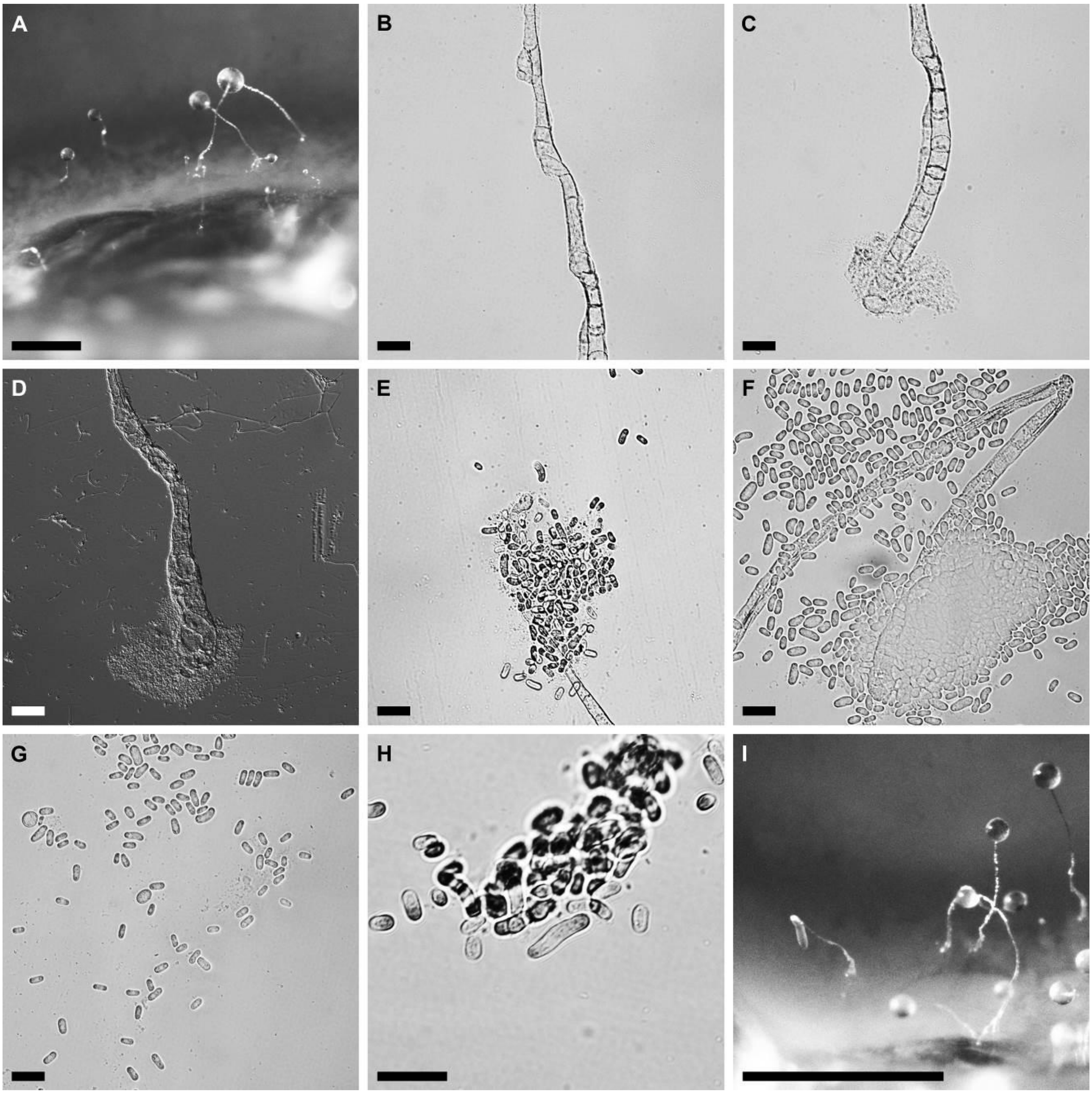

Figure 22 – Morphological features of *Dictyostelium diversisporum* var. *maximisporum*. (**A**) Sorocarps. (**B**) Nodule-like cells on the sorophore. (**C−D**) Clavate bases. (**E−F**) Capitate or recurve tips. (**G**) Spores with or without dispersed granules. (**H**) Long "S"-shape spore on the middle of picture. (**I**) Pseudoplasmodium with a stalk and sorocarps. Scale bars: A = 0.5 mm; B−H = 20 µm; I = 1 mm.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected an alpine birch forest at an intermediate elevation (1821−1837 m) with an intermediate soil pH (pH = 6.03).

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1829.1 m. Isolated from mixed soils, August 2018, *yue6* (HOLOTYPE, voucher specimen code: HMJAU MR306). Known only from Jilin Province, China.

Notes – *Dictyostelium diversisporum* var. *maximisporum* is characterized by buckling at the sorophore near the nodules, and giant spores reach a length of 20 μm. In the SSU and *atp1* phylogenetic tree, this variety clusters together with *D. diversisporum*, *D. diversisporum* var. *laevisorophorum*, and *D. diversisporum* var. *brevisporum* on common branches.

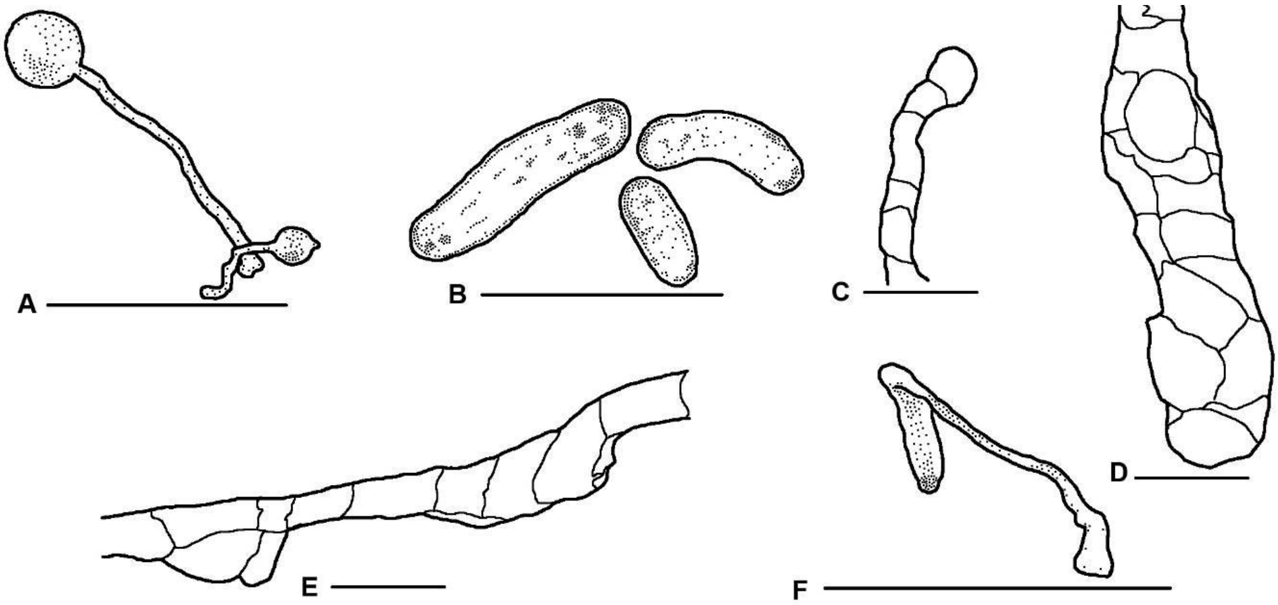

Figure 23 – *Dictyostelium diversisporum* var. *maximisporum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Nodule-like cells. (**F**) Pseudoplasmodium. Scale bars: A, F = 0.5 mm; B−E = 20 μm.

Dictyostelium latiorifirmibasis Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 24, 25

MycoBank number: 853153; GenBank accession number: SSU: PP590180; PP590181. *Atp1*: PP932654.

Etymology – the Latin adjective for "wider" is *latior*/*latior*/*latius*; *latiorifirmibasis* means the wider spores than *D. firmibasis*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic, solitary, clustered to gregarious, erect, semierect to prone, occasionally decumbent and become prostrate, sigmoid, 0.5−8.7 mm in length, rarely prostrate with stoloniferous stalks, and length reach to 10.9 mm. Sorophores are with one to several tiers of cells in width, taper from bases to tips. Mostly unbranched, a few with 1−3 short branches, branches length 323−664 μm, sometimes branches elongate to 2.3 mm. Bases are conical or expand bulbous, with basal disks, rarely round without basal disks. Bases mostly consist of two to several tiers of cells in wide, a few bases consist of one tier of cells, 10.8−51.4 μm in width, and the basal disks are 11.6−124.9 μm. Tips are clavate to capitate with one to two tiers of cells wide, 2.3−13.8 μm, with the widest points of tip terminals measuring 2.9−45.2 μm. Sori are white, semi-hyaline, spherical to round-apiculate or citriform, terminal sori 56−444 μm in diam, lateral sori 74−94 μm. Spores are oval to oblong, 5.4−9.7 × 3.0−4.5 μm (length/width = 1.67−2.51), without polar granules. Aggregations are radiate, mostly have one center but sometimes have secondary centers, 0.8−7.0 × 0.4−4.5 mm. Pseudoplasmodia with stalks. This species belongs to the *Dictyostelium* clade in 18S DNA.

Distribution and ecology – Isolated from the Shennongjia National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at an intermediate elevation (1750−1961 m) with an intermediate soil pH (pH = 6.40).

Material examined – China, Hubei Province: Shennongjia National Nature Reserve, 31.6º N, 110.4º E, average elevation 1837.9 m. Isolated from mixed soils, July 2022, *beihun1eda* (HOLOTYPE, voucher specimen code: HMJAU MR398); *beihun1a*; *beihun1d*; *beihun1exiao*. Known only from Hubei Province, China.

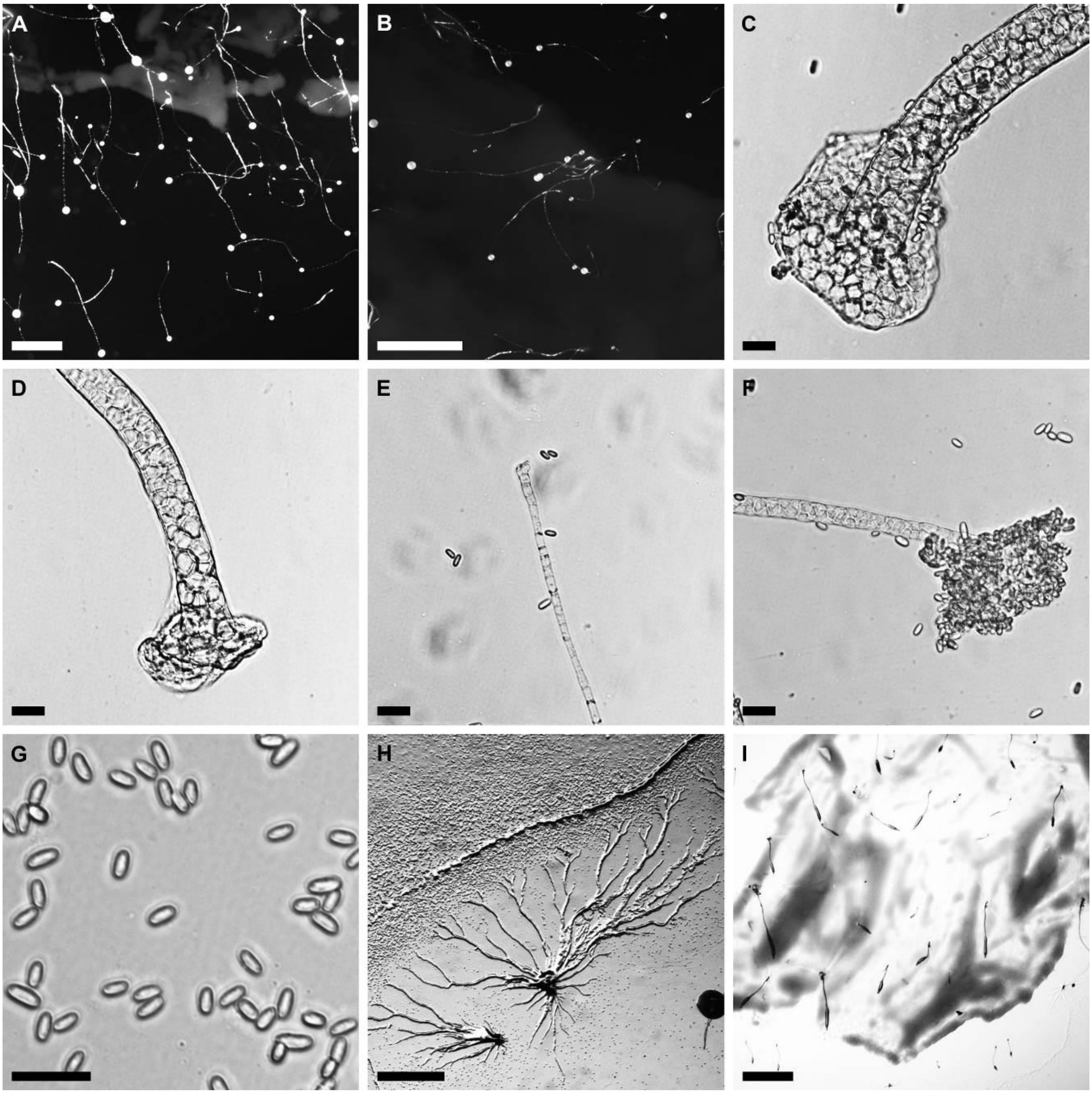

Figure 24 – Morphological features of *Dictyostelium latiorifirmibasis*. (**A**) Phototropic solitary sorocarps. (**B**) Clustered sorocarps. (**C−D**) Bases with basal disks. (**E**) Clavate tip. (**F**) Capitate tip. (**G**) Spores without polar granules. (**H**) Radiate aggregations. (**I**) Pseudoplasmodia with stalks. Scale bars: A−B, I = 2 mm; C−G = 20 µm; H = 1 mm.

Notes – Characters including basal disks, bases size, bases shape, tips shape, large white sori, tips without collar structure, large sorocarp, have been distinguished *Dictyostelium latiorifirmibasis* from other *Dictyostelium* species except *D. firmibasis*, *D. longosporum*, *D. macrocephalum* and *D. pseudobrefeldianum* (Hagiwara 1983b, Hagiwara et al. 1985, Hagiwara 1989, 1996). The morphological differences between D. *latiorifirmibasis* and the four species are discussed further below; each species has three or more differences. *Dictyostelium latiorifirmibasis* has sorophores one to several tiers of cells in width, *D. pseudobrefeldianum* with only one tier. *Dictyostelium latiorifirmibasis* has conical or expand bulbous bases with 10.8−51.4 µm in width, *D. longosporum* bases expanded and stable with 5−37.5 µm, *D. macrocephalum* has expanded bases with 9−32.5(−38.5) µm, *D. pseudobrefeldianum* bases conical with 7−27(−33) µm. *Dictyostelium latiorifirmibasis* has clavate to capitate tips with 2.3−13.8 µm in width, *D. firmibasis* has only capitate tips with 2−8(−12) µm, *D. longosporum* has only capitate tips with 2−10 µm, *D. macrocephalum* has slight widened tips with 2.5−12.5(−15) µm in width, *D. pseudobrefeldianum* has only clavate tips with 2.5−10(−17.5) µm. *Dictyostelium latiorifirmibasis* has spores 5.4−9.7 × 3.0−4.5 µm with 1.67−2.51 length/width ratio, *D. firmibasis* has spores 6.2−9.2 × 2.7−3.8 µm with 2−2.7 ratio, *D. longosporum* has spores 6.9−9 × 3.1−3.8 µm with 1.98−2.5 ratio, *D. macrocephalum* has 6.3−8.5 × 3.7−4.8 µm with 1.57−1.98 ratio. *Dictyostelium latiorifirmibasis* has solitary, clustered to gregarious, erect, semierect to prone, occasionally decumbent and become prostrate sorocarps with or without branched, *D. firmibasis* has solitary and sometimes prostrate with unbranched sorocarps, *D. longosporum* has solitary and sometimes prostrate with rarely branched sorocarps. *Dictyostelium latiorifirmibasis* has aggregations with mostly one center but sometimes secondary centers, *D. firmibasis* has centralized aggregations. Only *D. firmibasis* and *D. latiorifirmibasis* var. *minorifirmibasis* (in this paper) cluster together with *D. latiorifirmibasis* in the SSU phylogenetic tree, but *D. firmibasis* has been distinguished from the latter two in the *atp1* phylogenetic tree. Differences between *D. latiorifirmibasis* and its variety, *D. latiorifirmibasis* var. *minorifirmibasis*, are discussed in the notes for the latter.

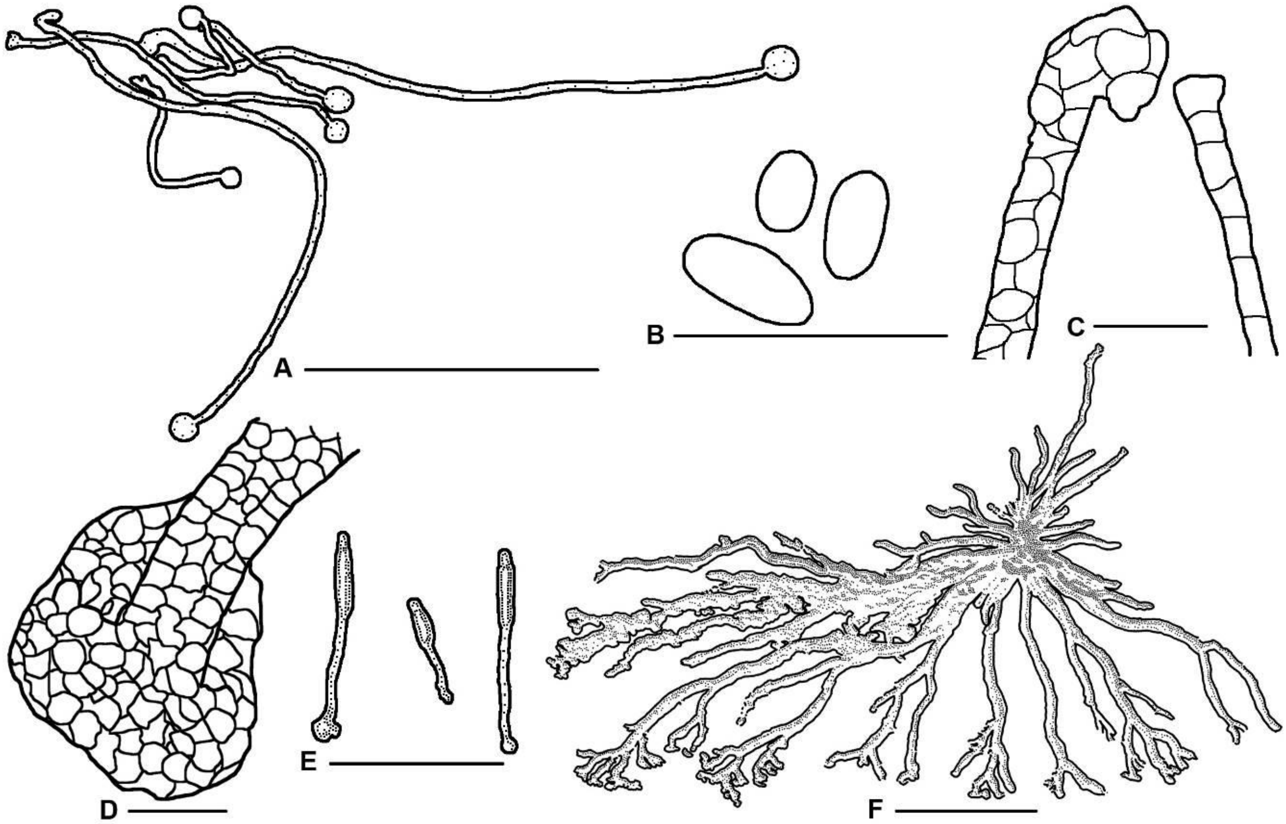

Figure 25 – *Dictyostelium latiorifirmibasis*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tips. (**D**) Base. (**E**) Pseudoplasmodia. (**F**) Aggregation. Scale bars: A, E = 2 mm; B−C = 20 µm; D = 40 µm; F = 1 mm.

Dictyostelium latiorifirmibasis* var. *minorifirmibasis Y. Li, P. Liu et Y. Zou, sp. nov.
Figs. 2, 3, 26, 27

MycoBank number: 853163; GenBank accession number: SSU: PP590202. *Atp1*: PP932653.

Etymology – the Latin adjective meaning "smaller" is *minor*/*minor*/*minus*, with compounding form *minor*--; *minorifirmibasis* means the smaller sorocarps than *D. latiorifirmibasis*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic, solitary, erect to prone, weak, 0.9−3.7 mm in length. Sorophores consist of one to two tiers of cells except bases, unbranched or rarely with one branch. Bases are round, conical, obtuse, consisting of several tiers of cells, with basal disks around, some bases connected with another bases. Bases 12.9−44.0 µm wide, and basal disks are 18.9−85.2 µm in diam. Tips are capitate or obtuse, consisting of one tier of cells, 3.1−11.7 µm in width, the widest points of tip terminals measuring 3.5−15.9 µm. Branch bases are clavate, consisting of several tiers of cells, 19.3−20.3 µm in diam. Sori are white, semi-hyaline, globose to citriform, 121−281 µm in diam. Spores are oval to bacilliform, sometimes reniform, without polar granules, 5.3−11.8 × 2.6−4.3 µm (length/width = 1.73−3.19). Aggregations have asymmetric streaming. Pseudoplasmodia with stalks. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

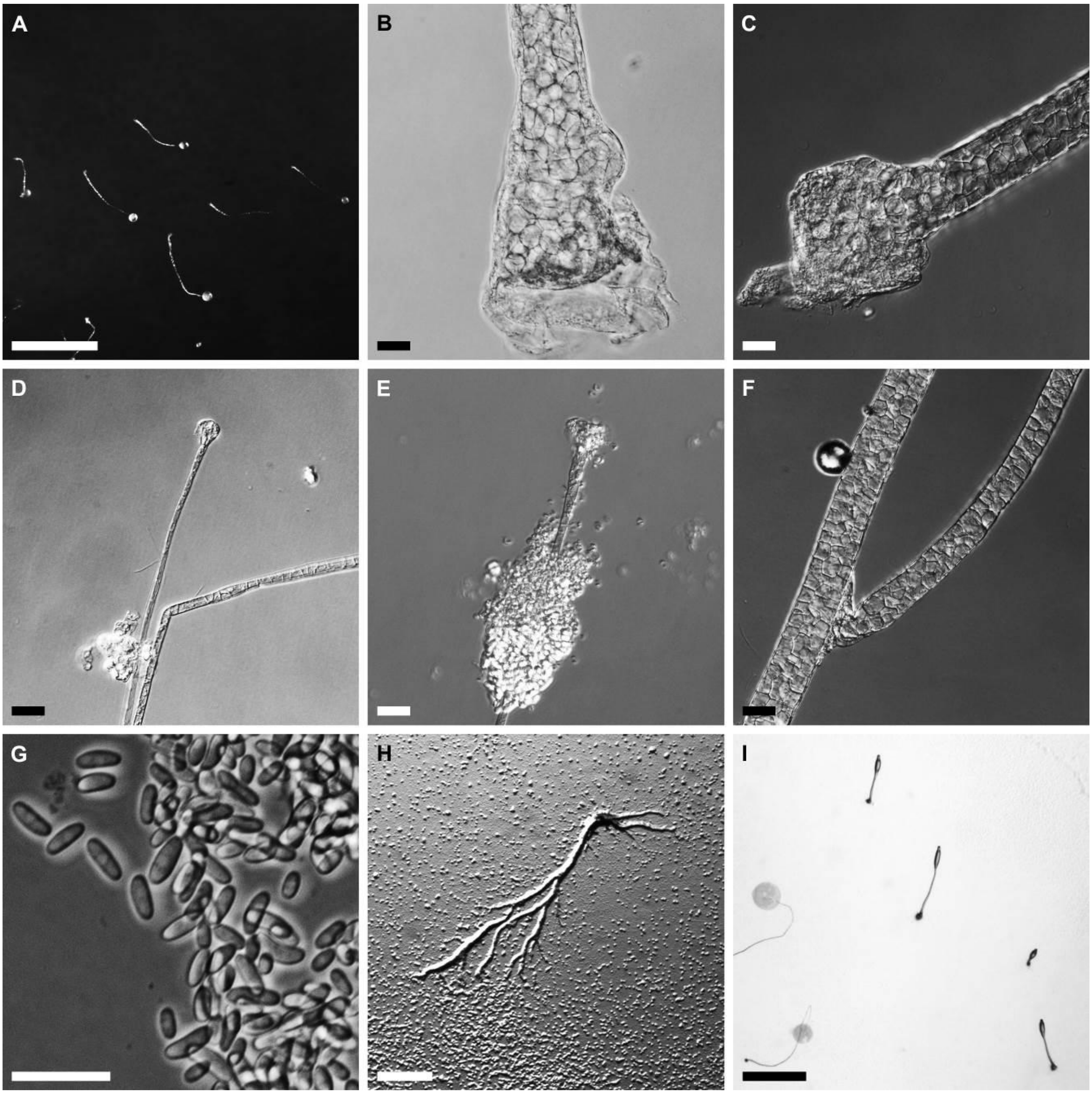

Figure 26 – Morphological features of *Dictyostelium latiorifirmibasis* var. *minorifirmibasis*. (**A**) Phototropic solitary sorocarps. (**B**) Conical base. (**C**) Base with basal disk. (**D**) Capitate tip. (**E**)

Obtuse tip. (**F**) Branch base. (**G**) Spores without polar granules. (**H**) Aggregations. (**I**) Pseudoplasmodia with stalks. Scale bars: A = 2 mm; B−G = 20 μm; H = 0.5 mm; I = 1 mm.

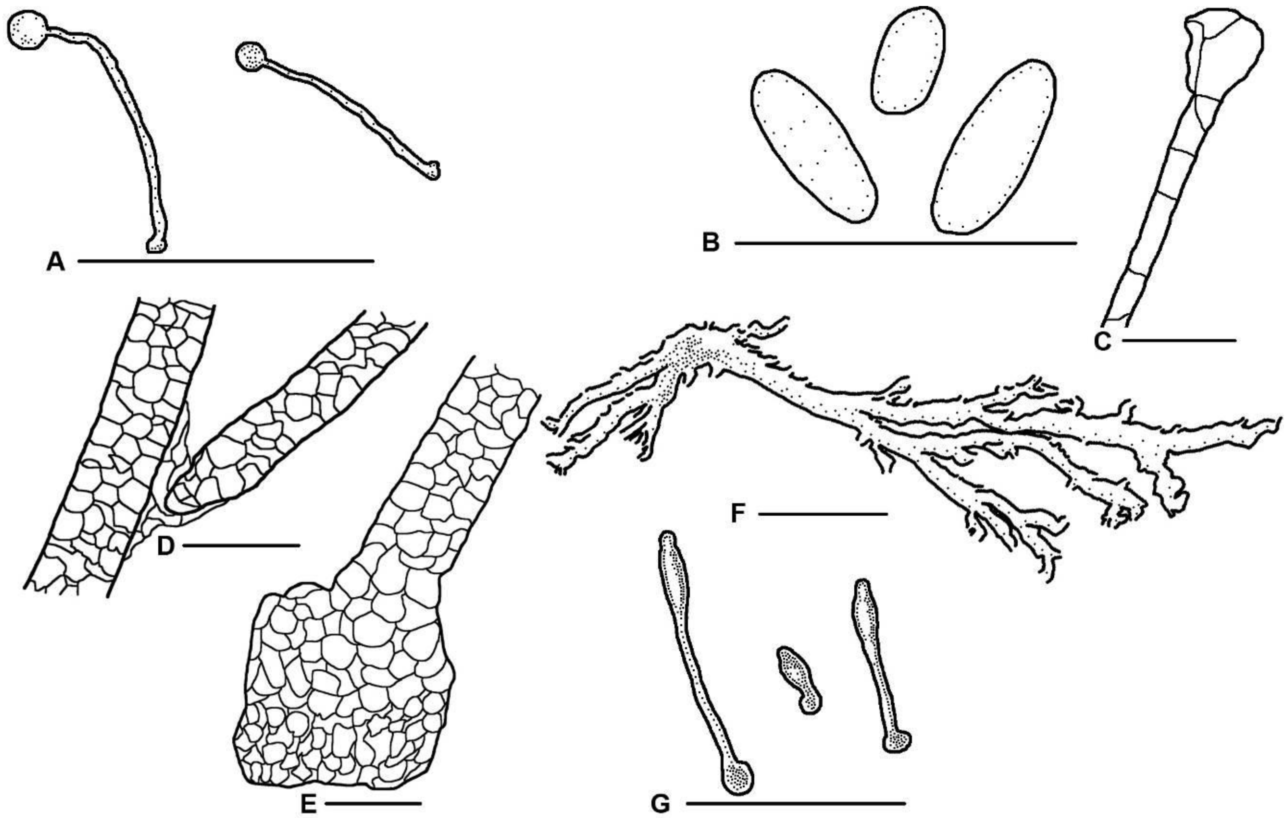

Figure 27 – *Dictyostelium latiorifirmibasis* var. *minorifirmibasis*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Branch base. (**E**) Base. (**F**) Aggregation. (**G**) Pseudoplasmodia. Scale bars: A = 2 mm; B = 20 μm; D−E = 40 μm; F = 0.5 mm; G = 1 mm.

Distribution and ecology – Isolated from the Shennongjia National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at an intermediate elevation (1750−1961) with an intermediate soil pH (pH = 6.40).

Material examined – China, Hubei Province: Shennongjia National Nature Reserve, 31.6º N, 110.4º E, average elevation 1837.9 m. Isolated from mixed soils, July 2022, *beihun1c* (HOLOTYPE, voucher specimen code: HMJAU MR417); *beihun1i*. Known only from Hubei Province, China.

Notes – The basal disks, weak sorocarps with 0−1 branch, white sori, long spores without polar granules, and base sizes make the species different with other *Dictyostelium* species. *Dictyostelium firmibasis*, *D. longosporum*, and *D. latiorifirmibasis* are similar with this species in morphology. *Dictyostelium latiorifirmibasis* var. *minorifirmibasis* has larger spores than *D. firmibasis* (6.2−9.2 × 2.7−3.8 μm) and *D. longosporum* (6.9−9 × 3.1−3.8 μm) (Hagiwara 1983b, 1984, 1989). Sorocarps of *D. latiorifirmibasis* var. *minorifirmibasis* are smaller than *D. firmibasis* in 0.5−9.69 (−11.6) mm and *D. longosporum* in 0.5−5.1 (-30) mm. *Dictyostelium latiorifirmibasis* var. *minorifirmibasis* has asymmetric streaming of aggregations, *D. firmibasis* and *D. longosporum* all have radial aggregations. *Dictyostelium latiorifirmibasis* var. *minorifirmibasis* is different from *D. latiorifirmibasis* in smaller sorocarps (0.9−3.7 mm length of *D. latiorifirmibasis* var. *minorifirmibasis* smaller than 0.5−8.7 rarely 10.9 mm of *D. latiorifirmibasis*) without clustered or gregarious formation, narrower sorophores (*D. latiorifirmibasis* var. *minorifirmibasis* is one to two tiers of cells except bases in width, *D. latiorifirmibasis* is one to several tiers of cells in width), smaller sori range (121−281 μm of *D. latiorifirmibasis* var. *minorifirmibasis*, terminal sori 56−444 μm and lateral 74−94 μm of *D. latiorifirmibasis*) and higher spore ratio of length/width (1.73−3.19

of *D. latiorifirmibasis* var. *minorifirmibasis*, 1.67−2.51 of *D. latiorifirmibasis*). *Dictyostelium latiorifirmibasis* var. *minorifirmibasis* clusters together with *D. firmibasis* and *D. latiorifirmibasis* in the SSU phylogenetic tree, but *D. firmibasis* is different in the *atp1* phylogenetic tree.

Dictyostelium majileptosomum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 28, 29

MycoBank number: 853154; GenBank accession number: SSU: PP590182.

Etymology – the Latin adjective for "larger" is *major*/*major*/*majus*; *majileptosomum* means larger spores than *D. leptosomum*.

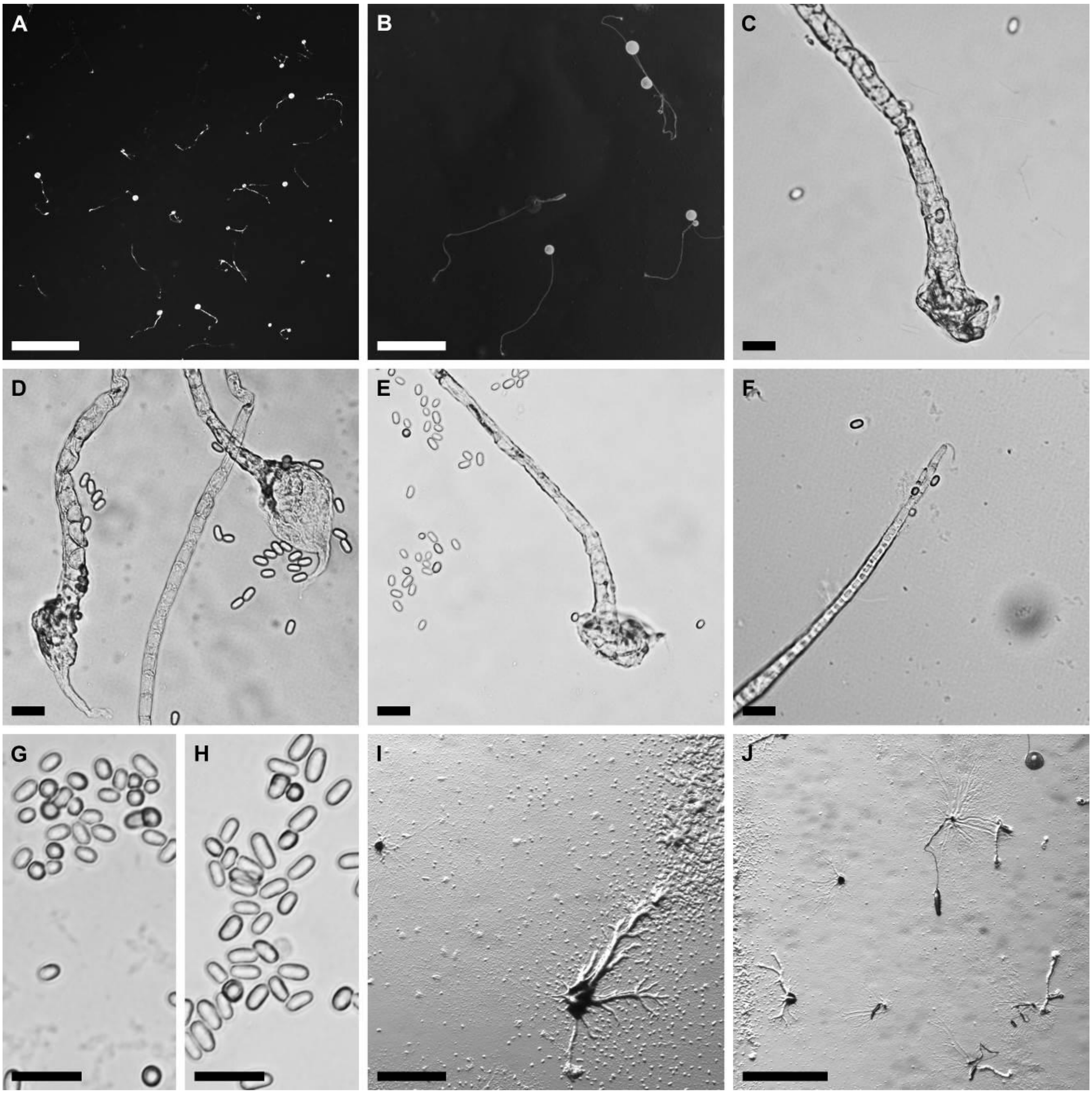

Figure 28 – Morphological features of *Dictyostelium majileptosomum*. (**A**) Sorocarps. (**B**) Pseudoplasmodium regrows from collapsed sorus. (**C**−**E**) Bases with many shapes. (**F**) Acuminate tip. (**G**−**H**) Spores with many shapes. (**I**) Radiate aggregations. (**J**) Pseudoplasmodia with stalks. Scale bars: A = 2 mm; B, J = 1 mm; C−H = 20 µm; I = 0.5 mm.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are slightly phototropic, gregarious, semierect to prone or decumbent, 0.3−3.1 mm in length. Sometimes sorocarps regrow from collapsed sori. Sorophores consist of one tier of cells in width except bases, unbranched. Bases are conical, obtuse, round, wizard-hat shape or hook, consisting of one to three tiers of cells, usually covered by a sheath. Bases widths are 7.6−26.3 µm, with the widest points of base terminals measuring 7.6−41.1 µm in diameter. Tips are obtuse, acuminate, capitate, consisting of a tier of cells wide, 4.1−6.6 µm in width, with the widest points of tip terminals measuring 3.7−7.8 µm. Sori are semi-hyaline to white, spherical to round-apiculate, 89−203 µm in diam. Spores are elliptical to oblong, 6.4−12.2 × 4.2−5.3 µm (length/width = 1.47−2.35), some are reniform with 9.4−10.9 × 4.5−5.6 µm (length/width = 1.96−2.17), some are pyriform with 8.0−9.3 × 4.6−6.3 µm (length/width = 1.48−1.72), and rarely egg-shaped with 5.5 × 3.9 µm (length/width = 1.42). Spores are without polar granules. Aggregations are with radiate steams. Pseudoplasmodia do not migrate with sorophore formation. This species belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

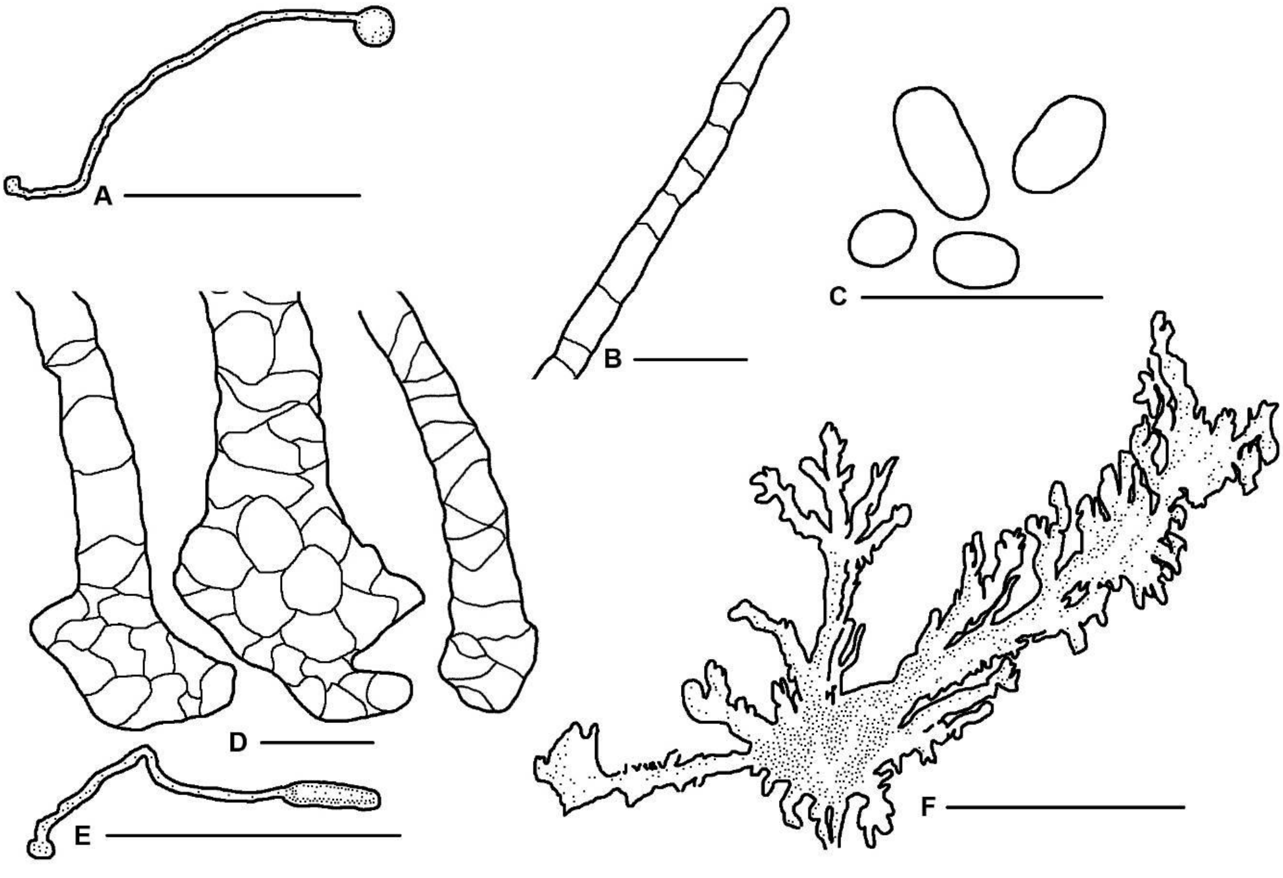

Figure 29 – *Dictyostelium majileptosomum*. (**A**) Sorocarp. (**B**) Tip. (**C**) Spores. (**D**) Bases. (**E**) Pseudoplasmodium. (**F**) Aggregation. Scale bars: A, E = 1 mm; B−D = 20 µm; F = 0.5 mm.

Distribution and ecology – Isolated from Honghua Small Town of the Shennongjia National Nature Reserve, in mixed soil samples collected from a camellia cropland at a low elevation (817−956 m) with an intermediate soil pH (pH = 6.32).

Material examined – China, Hubei Province: Honghua Small Town of the Shennongjia National Nature Reserve, 31.42º N, 110.46º E, average elevation 891.7 m. Isolated from mixed soils, July 2022, *beifu2h* (HOLOTYPE, voucher specimen code: HMJAU MR400); *beifu1b*; *beifu1f*; *beifu1g*; *beifu1j*; *beifu1k*; *beifu2a*; *beifu2c*; *beifu2e*. Known only from Hubei Province, China.

Notes – Distinguishing features of *Dictyostelium majileptosomum* including the base shape, large spore size and spore shape, white sori, and slender sorocarps without branches, make it different from other *Dictyostelium* species. SSU phylogenetic analysis showed that *D. majileptosomum* was clustered with *D. leptosomum*. The major morphological difference between them is the spore size, *D. majileptosomum* is significantly larger than *D. leptosomum* (5−6.5 × 2−3 µm) (Cavender et al. 2002). The other differences are that *D. majileptosomum* is unbranched, but *D. leptosomum* is unbranched or irregularly branched; *D. majileptosomum* has many base shapes, but *D. leptosomum* only has rounded, expanded shapes.

Dictyostelium pseudosessile (Yu Li, Pu Liu, Yue Zou, S.L. Stephenson & J.G. Hou) Y. Li, P. Liu et Y. Zou, comb. & stat. nov. Figs. 2, 3, 30, 31

Basionym. *Dictyostelium purpureum* var. *pseudosessile* Y. Li et al., BMC Evolutionary Biology 19: 78 (2019)

MycoBank number: 853160; GenBank accession number: SSU: PP590195. *Atp1*: PP932662.

Etymology – *pseudosessile* refers to the variable number sessile droplets water of sorophores.

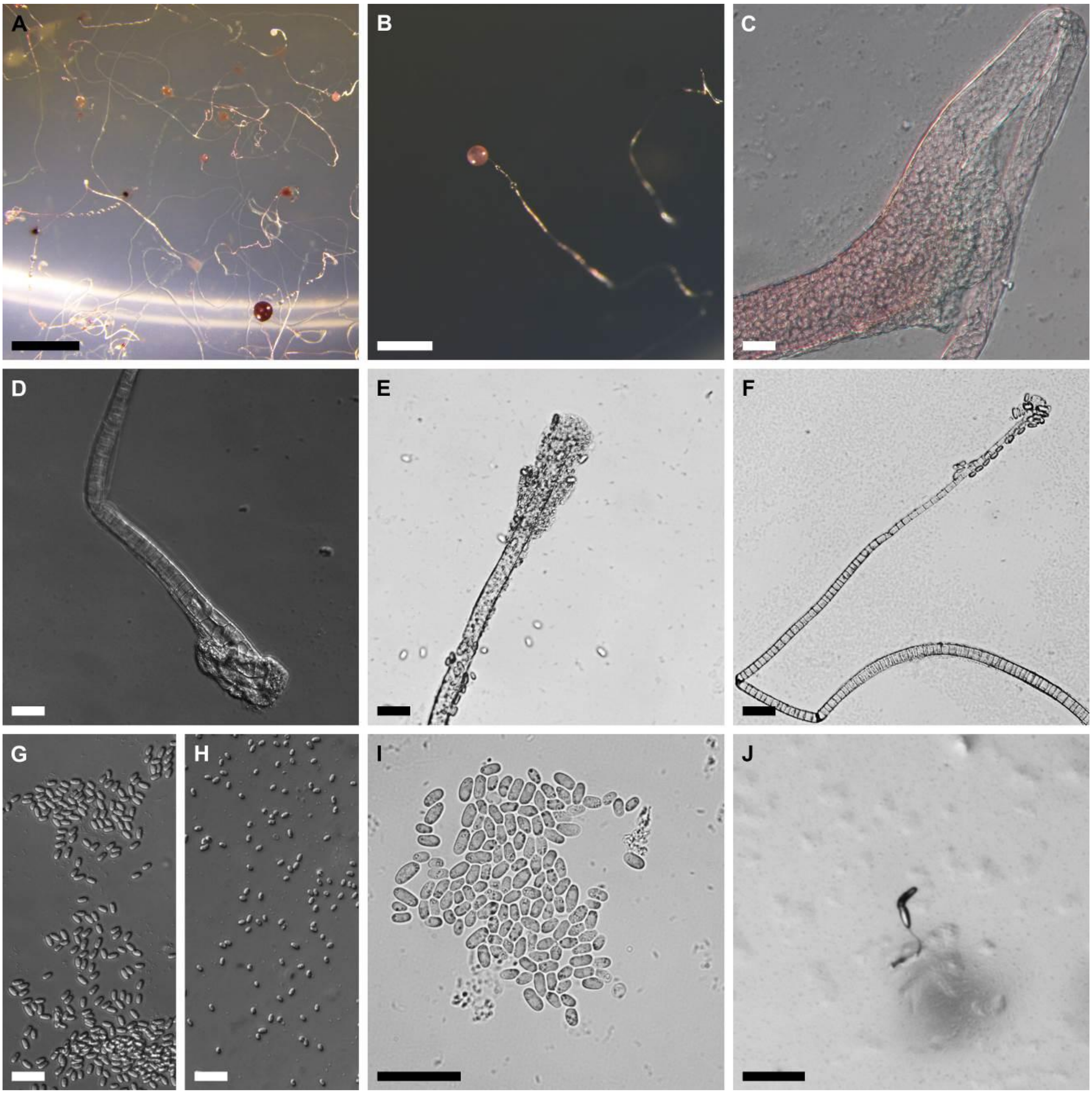

Figure 30 – Morphological features of *Dictyostelium pseudosessile*. (**A**−**B**) Sorocarps with or without pseudosessile. (**C**) Expanded midpoint of colored sorophore. (**D**) Clavate base. (**E**−**F**) Capitate tips. (**G**−**H**) Spores without obvious polar granules. (**I**) Spores with unconsolidated

granules under 100× magnification. (**J**) Pseudoplasmodium with a stalk. Scale bars: A = 2 mm; B = 0.5 mm; C−I = 20 µm; J = 200 µm.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are gregarious, prostrate at lower part and erect or semierect at upper part, with some variable number pseudosessile (sessile droplets water) adhered stalks. Sorophores consist of several tiers of cells except tips and bases, colorless to strong purplish pink (#e68fac), strong pink (#ea9399) or grayish red (#905d5d), 0.9−19.3 mm in length. Most of lower prostrate part is obviously longer than the upper erect or semierect part of the same sorophore in this study, erect part is length 0.7−5.3 mm or more. The connections of prostrate and erect part consist of several tiers of cells in width, often widen as the widest part of the whole sorophore, up to 19.1−56.3 µm or more in width. Bases are round or clavate, recurved, and consisting of one to two tiers of cells in width, 10.9−13.6 µm in width, with the widest points of base terminals measuring 11.9−17.3 µm in width. Tips are capitate, with one to two tiers of cells wide, 2.6−10.9 µm in width, with the widest points of tip terminals measuring 10.4−26.6 µm. Sori are hyaline to semi-hyaline, sori colors have a range from moderate reddish orange (#cb6d51), grayish red (#905d5d), grayish purplish red (#915f6d), dark grayish red (#543d3f), dark brown (#422518) to red reddish brown (#3e1d1e). Sori are globose, 121−621 µm. Spores are broadly elliptical to oblong, sometimes reniform, 3.5−7.8 × 2.3−3.7 µm (length/width = 1.27−2.52), without obvious polar granules but with unconsolidated granules at the polar or subpolar regions when observed under a microscope at 100× magnification. Aggregations are radiate. Pseudoplasmodia with stalks. This species belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

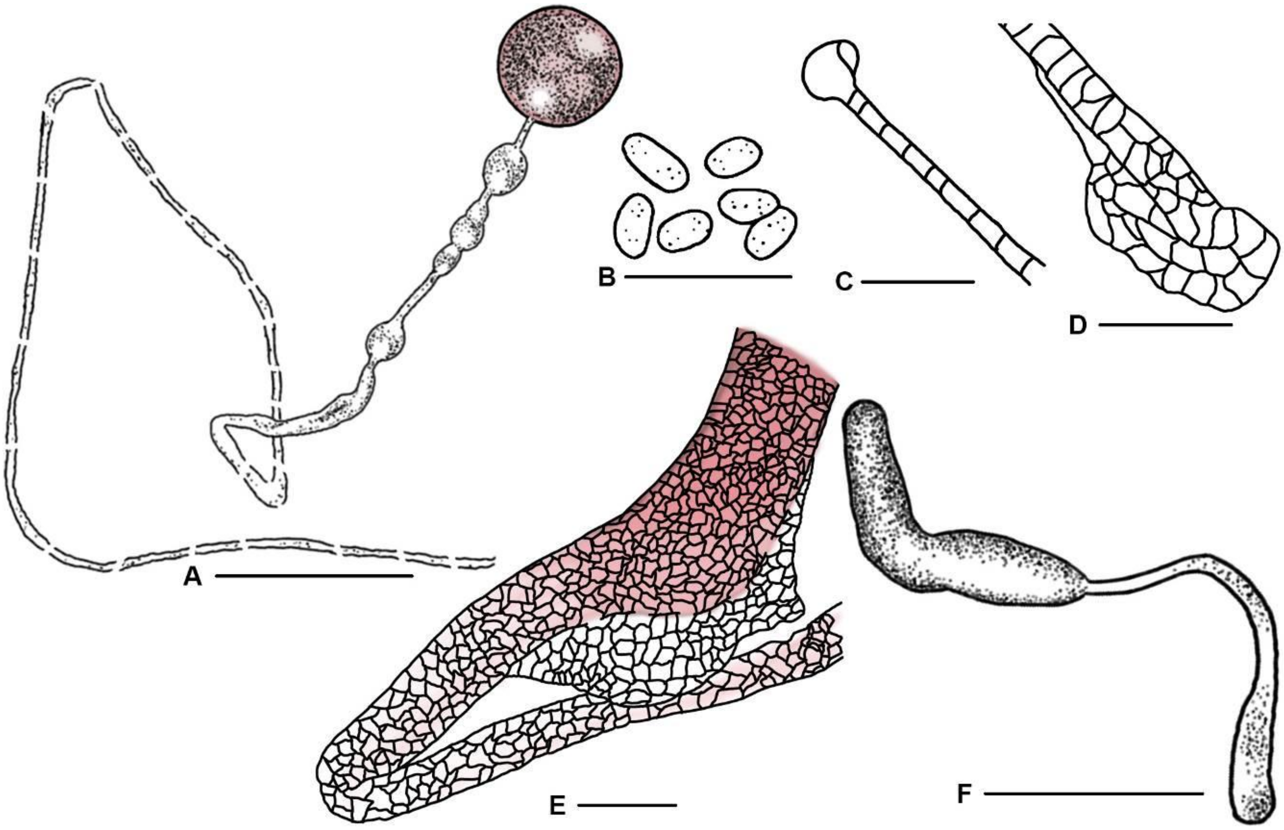

Figure 31 – *Dictyostelium pseudosessile*. (**A**) Sorocarp. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Expanded sorophore. (**F**) Pseudoplasmodium. Scale bars: A = 1 mm; B−C = 20 µm; D−E = 40 µm; F = 0.1 mm.

Distribution and ecology – Isolated from the Jianfengling National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at a low elevation (785−797 m) with a low soil pH (pH = 5.51).

Material examined – China, Hainan Province: Jianfengling National Nature Reserve, 18.75º N, 108.87º E, average elevation 790.7 m. Isolated from mixed soils, February 2022, *haihun1-1* (EPITYPE, voucher specimen code: HMJAU MR410). This species is known from Hainan Province and Yunnan Province, China.

Notes – The sori are delicate, after opening the culture dish cover, sori would fall and break on agar medium shortly, and the pseudosessile would also dry up and disappear soon after opening the culture dish cover. The reasons for this are likely due to the climate changed: the culture lab is located in northeast of China with dry air from northerly continental monsoons, and *Dictyostelium pseudosessile* has only been found in tropical areas of China (Wang et al. 2017, Liu et al. 2019a). In the previous study, the length and the width of spores can be up to 10 and 5 μm, but the maximum length is 7.8 μm with maximum width 3.7 μm in this study (Liu et al. 2019a). The differences between *D. pseudosessile* with *D. purpureum* Olive are the pseudosessile, widening connections of sorophores, and lighter color of sori. The sori color of almost black when mature in *D. purpureum* has never been observed in *D. pseudosessile* in this or previous studies (Raper 1984, Liu et al. 2019a).

Liu et al. (2019a) designated this organism as a variety named *Dictyostelium purpureum* var. *pseudosessile*, and we have isolated it from the Hainan Province of China again. Maximum-likelihood analysis showed this organism as a cryptic species of the complex species *D. purpureum* in the SSU phylogenetic tree. However, the distinguishing morphological characteristics make the organism really different from other cryptic species of *D. purpureum*. And *atp1* phylogenetic analysis also made it stand out. Thus, we redefined it as a species instead of a variety and described it herein.

Dictyostelium rufopurpureum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 32, 33

MycoBank number: 853161; GenBank accession number: SSU: PP590196; PP590199. *Atp1*: PP932660; PP932661.

Etymology – the name refers to the reddish purple sori (from Latin *rufus*/*rufa*/*rufum*, meaning reddish).

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic to a little phototropic, solitary to gregarious, prone to prostrate, sometimes decumbent, sinuous, 0.3−10.2 mm in length, sometimes up to 15.1 mm or even longer. Sorophores are colorless, or white to strong reddish purple (#9e4f88), grayish reddish purple (#836479), or dark purple (#563c5c); rarely moderate reddish orange (#cb6d51) near the tips; rarely observed pseudosessile adherents to the upper sorophores; sorophores consist of one to several tiers of cells in width, taper from middle to two terminals, sometimes with supporting cells near the middle part. The middle of sorophores have a width of 12.9−58.4 μm. Bases are round to clavate, sometimes expanded conical, consisting of one to two tiers of cells, 4.5−23.9 μm in width, the widest points of base terminals measuring 4.8−25.6 μm. Bases sometimes expand or with slime sheath, shape of slime sheath resembles basal disk, with 18.7−46.4 μm of sheath. Tips are capitate or clavate to obtuse, consisting of one to several tiers of cells, 2.6−17.0 μm in width, the widest points of tip terminals measuring 6.6−31.0 μm. Sori are hyaline or semi-hyaline, reddish purple as pale violet (#9690ab), pale reddish purple (#aa8a9e), light reddish purple (#b784a7), strong purplish pink (#e68fac), brilliant violet (#7e73b8), light purple (#b695c0), moderate reddish purple (#915c83), moderate purplish red (#a8516e), strong red (#bc3f4a), moderate red (#ab4e52), grayish purplish red (#915f6d), grayish reddish purple (#836479), dark reddish purple (#5d3954), dark purplish red (#673147), dark red (#722f37), deep reddish brown (#56070c), very dark red (#3f1728), dark reddish brown (#3e1d1e), dark brown (#422518), globose to citriform, 47−293 μm in diam. Spores are elliptical to oblong, sometimes reniform, 4.3−8.7 × 2.4−4.5 μm (length/width = 1.63−2.29), rarely large to 9.1 × 5.1 μm (length/width = 1.78), with unconsolidated granules at the polar or subpolar. Aggregations are radial. Pseudoplasmodia migrate with stalks. This species belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from main peak of the Jianfengling National Nature Reserve, in mixed soil samples collected from a cloud forest at an intermediate elevation (936−1375 m) with a low soil pH (pH = 5.12).

Material examined – China, Hainan Province: main peak of the Jianfengling National Nature Reserve, 18.71º N, 108.87º E, average elevation 1148.7 m. Isolated from mixed soils, February 2022, *haiyun1-1da* (HOLOTYPE, voucher specimen code: HMJAU MR411); *haiyun4-1xiao*. Known only from Hainan Province, China.

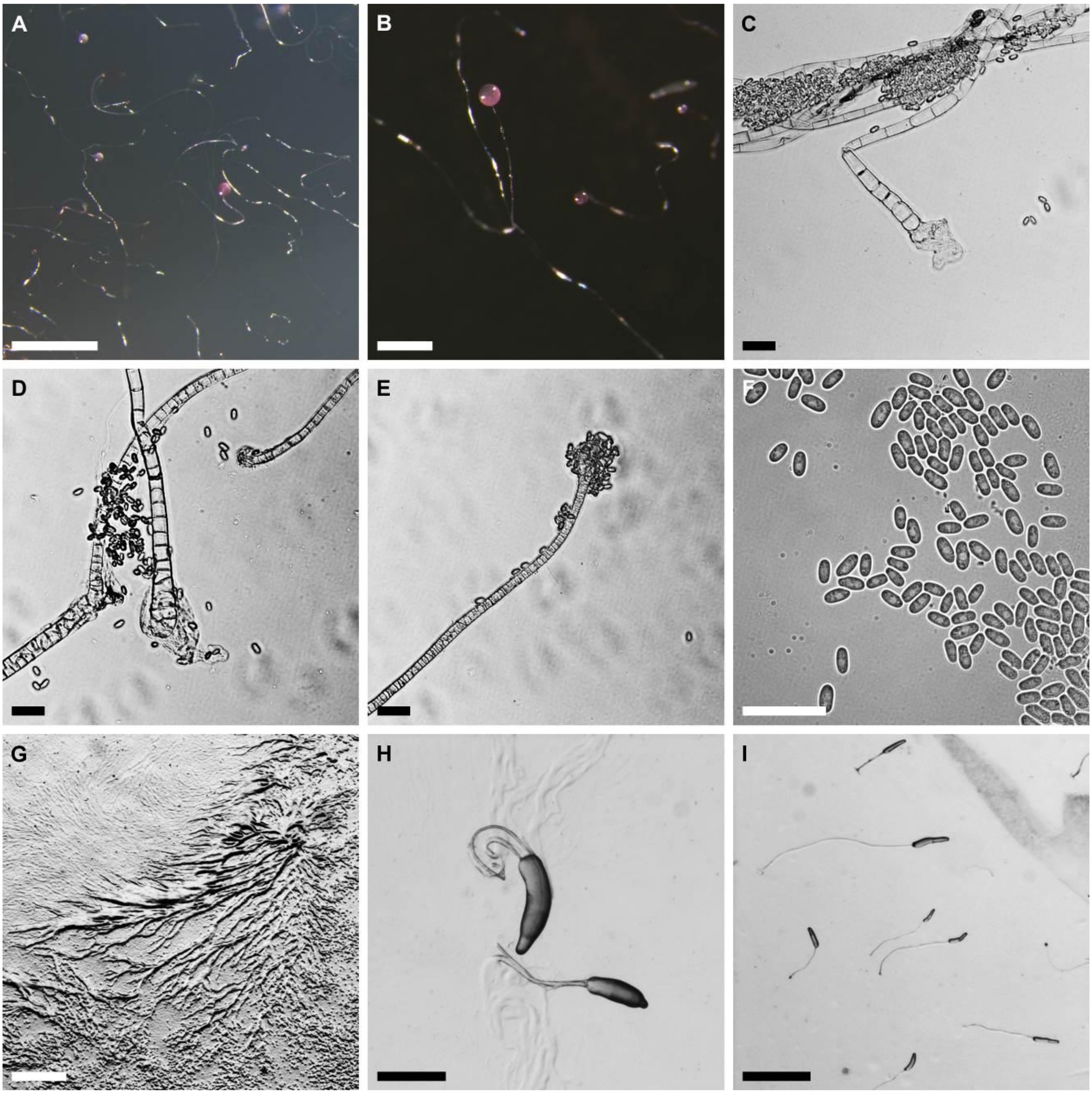

Figure 32 – Morphological features of *Dictyostelium rufopurpureum*. (**A**) Sorocarps. (**B**) A few pseudosessile adherent to the upper sorophore of sorocarp. (**C−D**) Round and clavate bases. (**E**) Capitate tips. (**F**) Spores with unconsolidated granules at the polar or subpolar regions under 100× magnification. (**G**) Radiate aggregations. (**H**) Migrating pseudoplasmodia with stalks. (**I**) Phototropic pseudoplasmodia. Scale bars: A, I = 1 mm; B, G−H = 0.5 mm; C−F = 20 μm.

Notes – *Dictyostelium rufopurpureum* has clustered with the species of this paper as *D. rufopurpureum* var. *longioripseudosessile* and *D. pseudosessile* in the SSU phylogenetic tree, and they all cluster into the former *D. purpureum* clade. But the *atp1* phylogenetic tree has shown that *D. rufopurpureum* and *D. rufopurpureum* var. *longioripseudosessile* are distinct from *D. pseudosessile*. The differences among the three taxa are discussed in the notes on *D. rufopurpureum* var. *longioripseudosessile*. Sorocarps of *D. rufopurpureum* are solitary to gregarious, prone to prostrate, sometimes decumbent; *D. purpureum* has solitary, erect or semierect, then inclined sorocarps (Raper 1984). Sori of *D. rufopurpureum* are reddish purple with 47−293 µm in diam; *D. purpureum* has larger and darker color of sori, with color ranging from dark vinaceous purple to almost black when mature, and a diameter of 125−450 µm. As part of clarifying and defining the internal distinctions within the complex species *D. purpureum*, we have separated *D. rufopurpureum* from *D. purpureum* as a new species.

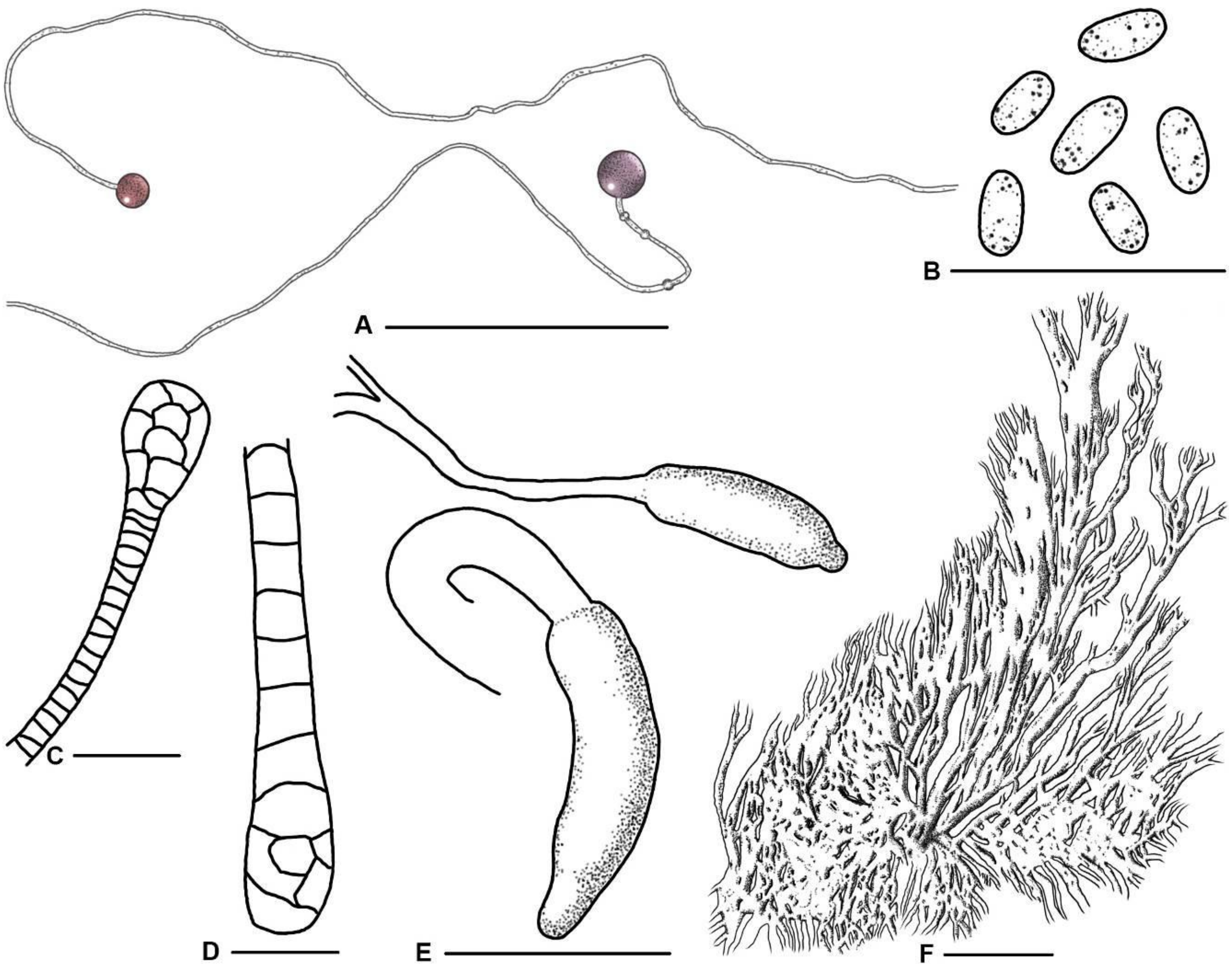

Figure 33 – *Dictyostelium rufopurpureum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Pseudoplasmodia. (**F**) Aggregation. Scale bars: A = 1 mm; B−D = 20 µm; E−F = 0.5 mm.

Dictyostelium rufopurpureum* var. *longioripseudosessile Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 34, 35

MycoBank number: 853155; GenBank accession number: SSU: PP590183. *Atp1*: PP932659.

Etymology – the Latin adjective "longer" is *longior*/*longior*/*longius* with the compounding form *longior*--; *longioripseudosessile* means the sorocarp has many pseudosessile and also has a higher spore ratio of length/width and a longer spore size than *D. rufopurpureum*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are gregarious, without phototropic or with lightly phototropic, semierect to prone, rarely decumbent with a stoloniferous habit, with several pseudosessile adhered to stalks, 0.6−7.7 mm in length. Sorophore are one to three tiers of cells wide, colorless to pale purple (#aa98a9). Bases are clavate to round, consist of one to two tiers of cells in width, often covered with strong slime sheath, 5.6−22.6 µm in width, with the widest points of base terminals measuring 6.7−25.2 µm. Tips are capitate, with one to two tiers of cells wide, 2.1−11.8 µm wide, the widest points of tip terminals measuring 5.3−32.2 µm. Sori are semi-hyaline, with colors of reddish gray (#8f817f), grayish purple (#796878), grayish reddish purple (#836479), pale reddish purple (#aa8a9e), grayish purplish pink (#c3a6b1), moderate purplish pink (#d597ae), grayish purplish red (#915f6d), and dark grayish reddish brown (#43302e), globose, 74−272 µm in diam. Spores are oval to bacilliform, sometimes reniform, 4.8−12.2 × 2.6−4.8 µm (length/width = 1.66−3.36), with unobvious unconsolidated polar granules. Aggregations are radial. Pseudoplasmodia migrate with stalks. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

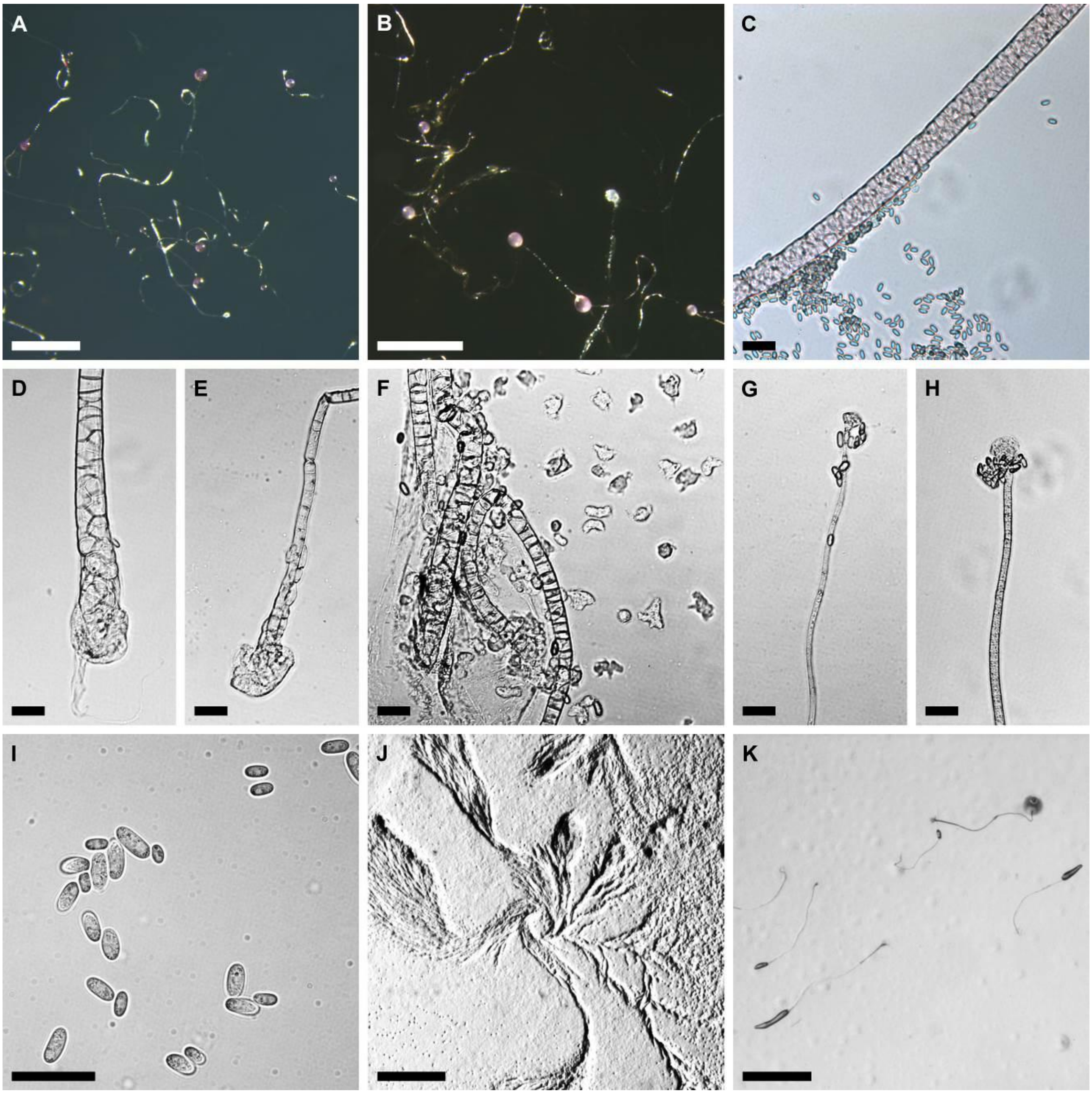

Figure 34 – Morphological features of *Dictyostelium rufopurpureum* var. *longioripseudosessile*. (**A**−**B**) Gregarious sorocarps with or without several pseudosessile adhered to stalks. (**C**) Unexpanded midpoint of colored sorophore. (**D**−**E**) Round and clavate bases. (**F**) Many

myxamoebae near bases. (**G−H**) Capitate tips. (**I**) Spores with unobvious unconsolidated polar granules under 100× magnification. (**J**) Radiate aggregations. (**K**) Pseudoplasmodia migrate with stalks, which are not phototropic. Scale bars: A−B, J−K = 1 mm; C−I = 20 µm.

Distribution and ecology – Isolated from main peak of Jianfengling National Nature Reserve, in mixed soil samples collected from a cloud forest at an intermediate elevation (936−1375 m) with a low soil pH (pH = 5.12).

Material examined – China, Hainan Province: main peak of Jianfengling National Nature Reserve, 18.71º N, 108.87º E, average elevation 1148.7 m. Isolated from mixed soils, February 2022, *haiyun6-1* (HOLOTYPE, voucher specimen code: HMJAU MR401). Known only from Hainan Province, China.

Figure 35 – *Dictyostelium rufopurpureum* var. *longioripseudosessile*. (**A**) Sorocarp. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Pseudoplasmodia. (**F**) Aggregation. Scale bars: A = 0.5 mm; B−D = 20 µm; E−F = 1 mm.

Notes – The pseudosessile structure of *Dictyostelium rufopurpureum* var. *longioripseudosessile* looks similar to the species *D. pseudosessile* and *D. rufopurpureum* introduced in this paper. The differences between them include spores, sorophores, habitat of sorocarps, tip sizes, and sori diameter. *Dictyostelium rufopurpureum* var. *longioripseudosessile* has longer spores and a higher spore ratio than *D. pseudosessile* with 3.5−7.8 × 2.3−3.7 µm (length/width = 1.27−2.52), and *D. rufopurpureum* with 4.3−8.7 × 2.4−4.5 µm (length/width =

1.63−2.29). The sorophores of *D. rufopurpureum* var. *longioripseudosessile* are slenderer without widening connections, both *D. pseudosessile* and *D. rufopurpureum* are all with middle widen sorophores. Sorocarps of *D. rufopurpureum* var. *longioripseudosessile* are rarely decumbent, on the other hand, most sorocarps of *D. pseudosessile* are prostrate. *Dictyostelium rufopurpureum* var. *longioripseudosessile* has narrower capitate tips with one to two tiers of cells wide, measuring 2.1−11.8 µm, compared to the capitate or clavate to obtuse tips of *D. rufopurpureum*, which have one to several tiers of cells wide, measuring 2.6−17.0 µm. *Dictyostelium pseudosessile* has sori 121−621 µm in diameter, which are larger than those of *D. rufopurpureum* (47−293 µm in diameter) and *D. rufopurpureum* var. *longioripseudosessile* (74−272 µm in diameter).

Apart from the structures of pseudosessile and the lighter color of sori of *D. rufopurpureum* var. *longioripseudosessile*, the spores of *D. rufopurpureum* var. *longioripseudosessile* with 4.8−12.2 × 2.6−4.8 µm are also larger than those of *D. purpureum* with 5−8 (+) × 2.5−3.2 µm (Raper 1984). As part of clarifying and defining the internal distinctions within the complex species *D. purpureum*, we have separated *D. rufopurpureum* var. *longioripseudosessile* away from *D. purpureum* as a new variety.

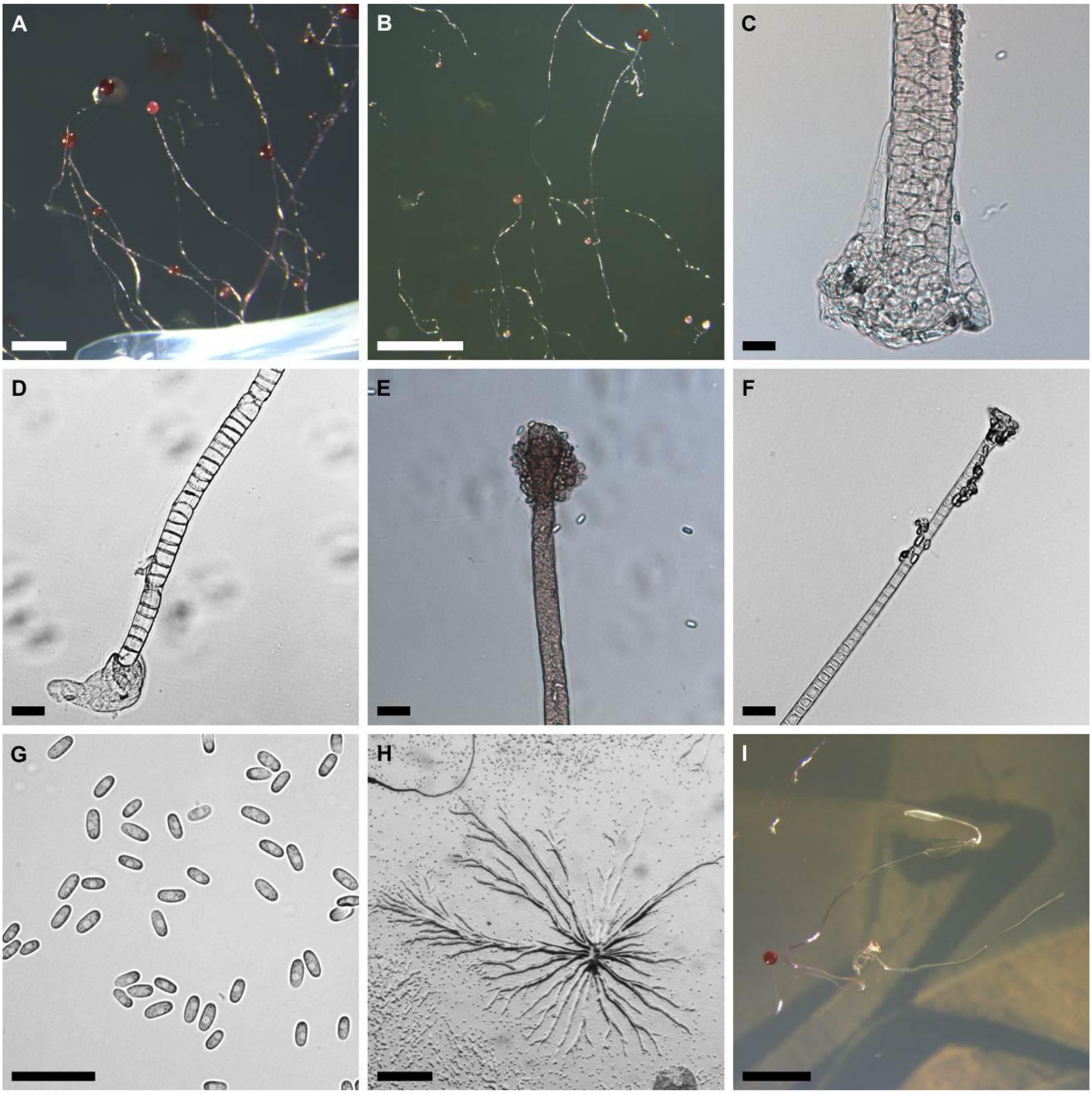

Figure 36 – Morphological features of *Dictyostelium sinuatipurpureum*. (**A−B**) Sorocarps with or without small hyaline drops. (**C−D**) Conical and clavate bases. (**E−F**) Capitate tips. (**G**) Spores with some unconsolidated granules dispersed under 100× magnification. (**H**) Radiate aggregations. (**I**) Pseudoplasmodium with a colored stalk, and a sorocarp with some looped structures at the lower part of the sorophore. Scale bars: A, I = 1 mm; B = 2 mm; C−G = 20 μm; H = 0.5 mm.

Dictyostelium sinuatipurpureum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 36, 37

MycoBank number: 853162; GenBank accession number: SSU: PP590200; PP590201. *Atp1*: PP932657; PP932658.

Etymology – the Latin adjective meaning "sinuate" is *sinuatus*/*sinuata*/*sinuatum*, with *sinuatipurpureum* standing for the purple sori and lower sinuous sorophores.

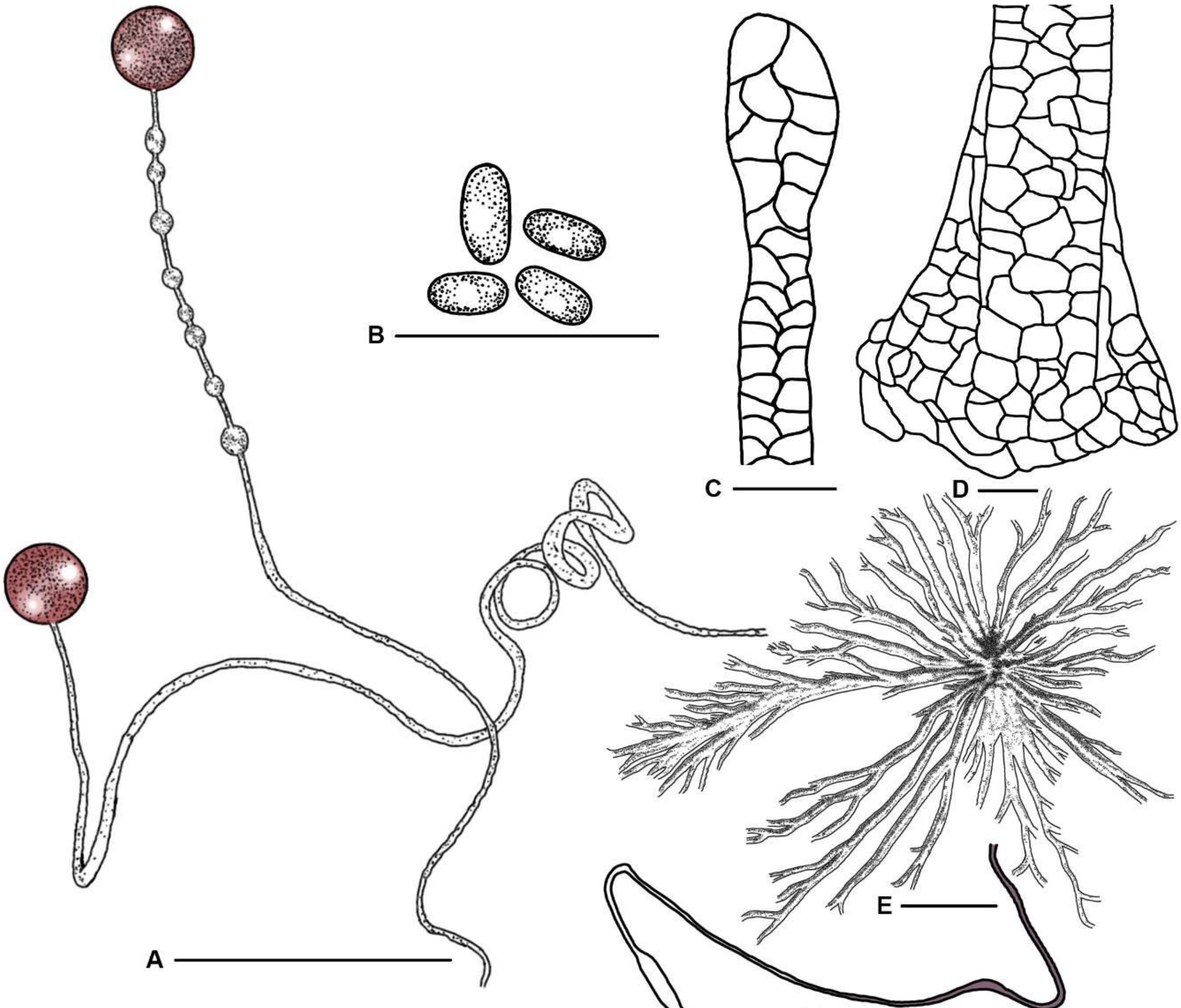

Figure 37 – *Dictyostelium sinuatipurpureum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregation. (**F**) Pseudoplasmodium. Scale bars: A, F = 1 mm; B−D = 20 μm; E = 0.5 mm.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary, sinuous, semierect or prone to semi-prostrate, 0.3−13.6 mm in length, phototropic, without branches, occasionally with a really small sorocarp (about 180 μm) adhering at the base. Sorocarp sometimes with a loop or flexuous structure at the lower part of sorophore. The sorocarp have many prominences at upper part of sorophore, small hyaline drops would appear on the prominences, the drops with prominences would disappear with time. When sori dropped, new small sorocarps would regrow from fallen sori. Sorophores are colorless to pale reddish purple (#aa8a9e) and moderate purple (#86608e), semi-hyaline, taper from bases to tips. Bases are clavate, round, obtuse, conical, consisting of one to several tiers of cells wide, 8.5−44.6 µm in width, the widest points of base terminals measuring 8.3−74.1 µm. Tips are capitate, consisting of one to two tiers of cells wide, 3.0−11.7 µm in width, the widest points of tip terminals measuring 4.4−31.5 µm. Sori are purple with a serious color as dark yellowish pink (#c48379), grayish reddish orange (#b4745e), grayish red (#905d5d), moderate red (#ab4e52), strong reddish brown (#882d17), dark red (#722f37), moderate reddish brown (#79443b), deep brown (#593319), deep reddish brown (#56070c), dark reddish brown (#3e1d1e), dark brown (#422518), globose to citriform, 61−345 µm in diam. Spores are oval to oblong, 5.1−8.3 × 2.8−3.7 µm (length/width = 1.74−2.37), without polar granules but with some unconsolidated granules dispersed in spores. Aggregations are radiate, 1.8−6.5 × 0.7−3.2 mm. Pseudoplasmodia migrate with stalks. Stalks of pseudoplasmodia are colorless to light grayish brown (#958070), light grayish reddish brown (#977f73), grayish purple (#796878), grayish reddish purple (#836479), moderate purple (#86608e), grayish reddish brown (#674c47), and dark grayish purple (#50404d). This species belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from Songbai Town of the Shennongjia National Nature Reserve, in mixed soil samples collected from an evergreen deciduous broadleaf forest at an intermediate elevation (1011−1424 m) with a high soil pH (pH = 7.41).

Material examined – China, Hubei Province: Songbai Town of the Shennongjia National Nature Reserve, 31.65º N, 110.54º E, average elevation 1151.2 m. Isolated from mixed soils, July 2022, *beichang1igenqu* (HOLOTYPE, voucher specimen code: HMJAU MR415); *beichang1igenzhi*. Known only from Hubei Province, China.

Notes – The drops of this species are different from pseudosessile of *Dictyostelium pseudosessile* in prominences of sorophores; the prominence structure has not been observed in *D. pseudosessile*. *Dictyostelium sinuatipurpureum* clusters with *D. sinuatipurpureum* var. *subulibasipurpureum*, *D. sinuatipurpureum* var. *corymbipurpureum*, and *D. purpureum* in the SSU phylogenetic tree, and *D. sinuatipurpureum* also clusters with the two varieties in the *atp1* phylogenetic tree. The differences between this species and the other two new varieties are detailed in the notes on those varieties. *Dictyostelium sinuatipurpureum* is different from *D. purpureum* in sorocarp length, sorus color, base size, and tip size (Raper 1984). *Dictyostelium sinuatipurpureum* has sorocarps in 0.3−13.6 mm length; *D. purpureum* is variable in length, often reaching several centimeters in unidirectional light. *Dictyostelium sinuatipurpureum* has purple sori, *D. purpureum* has sori in dark vinaceous purple to almost black when mature. *Dictyostelium sinuatipurpureum* has tips 3.0−11.7 µm in width and bases 8.5−44.6 µm in width, while *D. purpureum* is commonly 20−40 µm in width below and tapers to half that diameter within the sorus. As part of clarifying and defining the internal distinctions within the complex species *D. purpureum*, we have separated *D. sinuatipurpureum* away from *D. purpureum* as a new species.

Dictyostelium sinuatipurpureum* var. *corymbipurpureum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 38, 39

MycoBank number: 853150; GenBank accession number: SSU: PP590177. *Atp1*: PP932655.

Etymology – the Latin noun for “cluster” is *corymbus*; *corymbipurpureum* means the clustered sorocarps with purple sori.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are clustered to gregarious, curved, erect to prone, sometimes decumbent, 0.3−8.0 mm in length, unbranched, or with 1−4 branches. Sorophores are brilliant purple (#d399e6), semi-hyaline, consist of one to several tiers of cells in width. Sorophores curl near the bases and sometimes form a ring-like structure (similar to *Dictyostelium annularibasimum*) or a spiral conformation. Bases are conical, round or clavate, one to several tiers of cells wide, sometimes with basal disks. Bases are 9.1−79.4 µm in width, basal disks 81.2−248.8 µm. Tips are capitate, obtuse to conical, consisting of one or two tiers of cells in width, 3.3−15.1 µm wide, the widest points of tip terminals measuring

12.5−48.6 μm. Sori are dark purple to almost black as deep brown (#593319), blackish purple (#291e29), reddish black (#282022), brownish black (#28201c), globose to citriform, 39−828 μm in diam. Spores are oval to bacilliform, sometimes are reniform and sigmoid with large sizes, 5.1−14.8 × 2.3−4.5 μm (length/width = 1.80−4.03), without polar granules. Aggregations are radiate. Pseudoplasmodia migrate with stalks. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from Songbai Town of the Shennongjia National Nature Reserve, in mixed soil samples collected from an evergreen deciduous broadleaf forest at an intermediate elevation (1011−1424 m) with a high soil pH (pH = 7.41).

Material examined – China, Hubei Province: Songbai Town of the Shennongjia National Nature Reserve, 31.65º N, 110.54º E, average elevation 1151.2 m. Isolated from mixed soils, July 2022, *beichang1a* (HOLOTYPE, voucher specimen code: HMJAU MR395). Known only from Hubei Province, China.

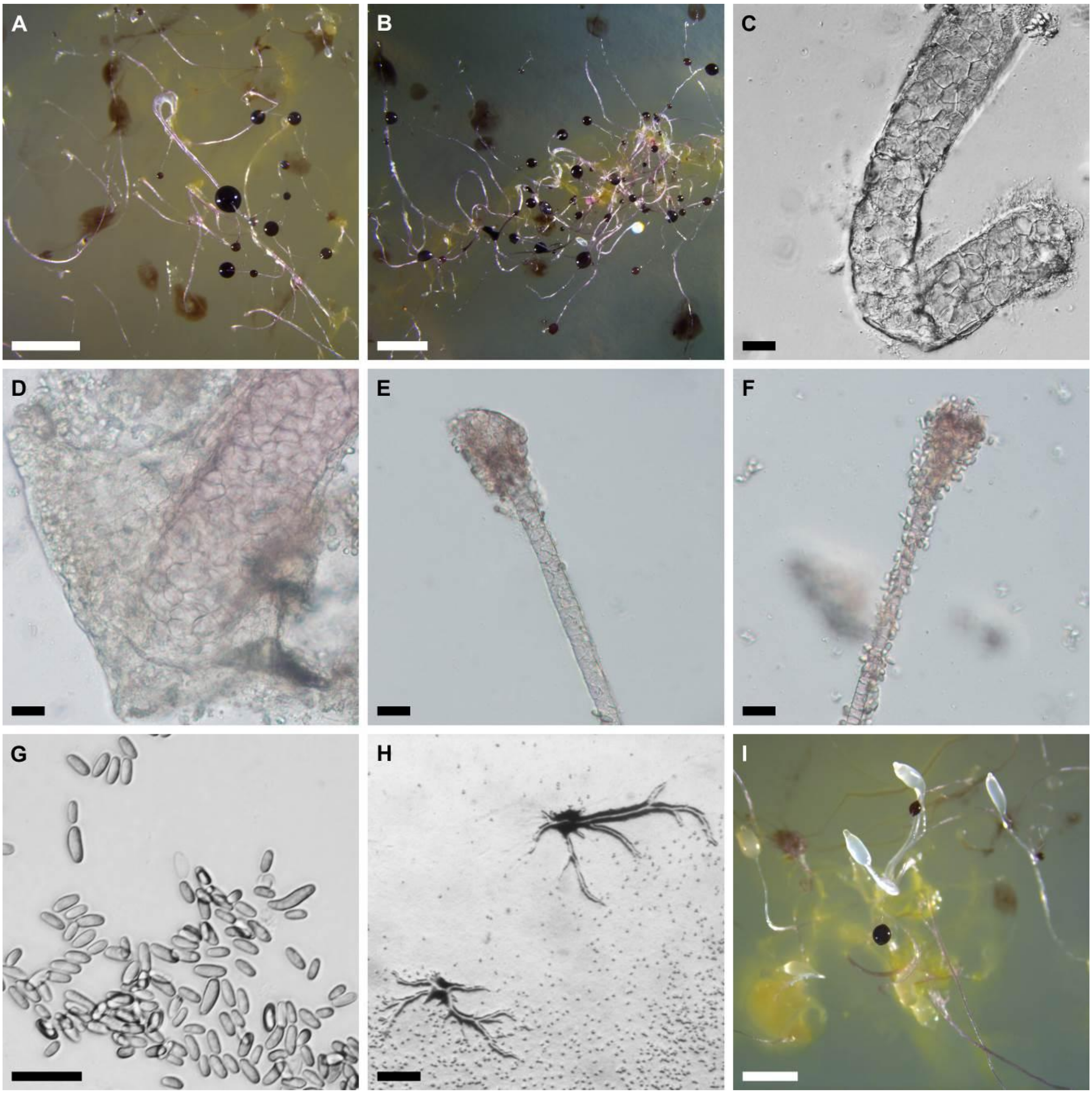

Figure 38 – Morphological features of *Dictyostelium sinuatipurpureum* var. *corymbipurpureum*. (**A−B**) Sorocarps with dark sori. (**C−D**) Bases with or without basal disks. (**E−F**) Capitate tips.

(**G**) Spores without polar granules. (**H**) Radiate aggregations. (**I**) Pseudoplasmodia migrate with stalks. Scale bars: A−B = 2 mm; C−G = 20 µm; H = 200 µm; I = 1 mm.

Notes – *Dictyostelium sinuatipurpureum* var. *corymbipurpureum* can be distinguished by clustered and sometimes decumbent sorocarps from solitary and semierect or prone to semi-prostrate sorocarps of *D. sinuatipurpureum*; and solitary, erect or semi-erect, then inclined sorocarps of *D. purpureum* (Raper 1984). The large spores of 5.1−14.8 × 2.3−4.5 µm (length/width = 1.80−4.03) are also different from 5.1−8.3 × 2.8−3.7 µm (length/width = 1.74−2.37) spores of *D. sinuatipurpureum* and 5.0−7.2(−8) × 2.5−3.2 µm spores of *D. purpureum*. Sori of *D. sinuatipurpureum* var. *corymbipurpureum* are 39−828 µm larger than sori of *D. sinuatipurpureum*, which have a size of 61−345 µm, and larger than *D. purpureum*, which have a size of 125−450 µm. In addition, the sori colors of *D. sinuatipurpureum* var. *corymbipurpureum* are dark purple to almost black and darker than the purple of *D. sinuatipurpureum*. The features discussed above distinguish *D. sinuatipurpureum* var. *corymbipurpureum* from *D. purpureum*. As part of clarifying and defining the internal distinctions within the complex species *D. purpureum*, we have separated *D. sinuatipurpureum* var. *corymbipurpureum* away from *D. purpureum* as a new variety.

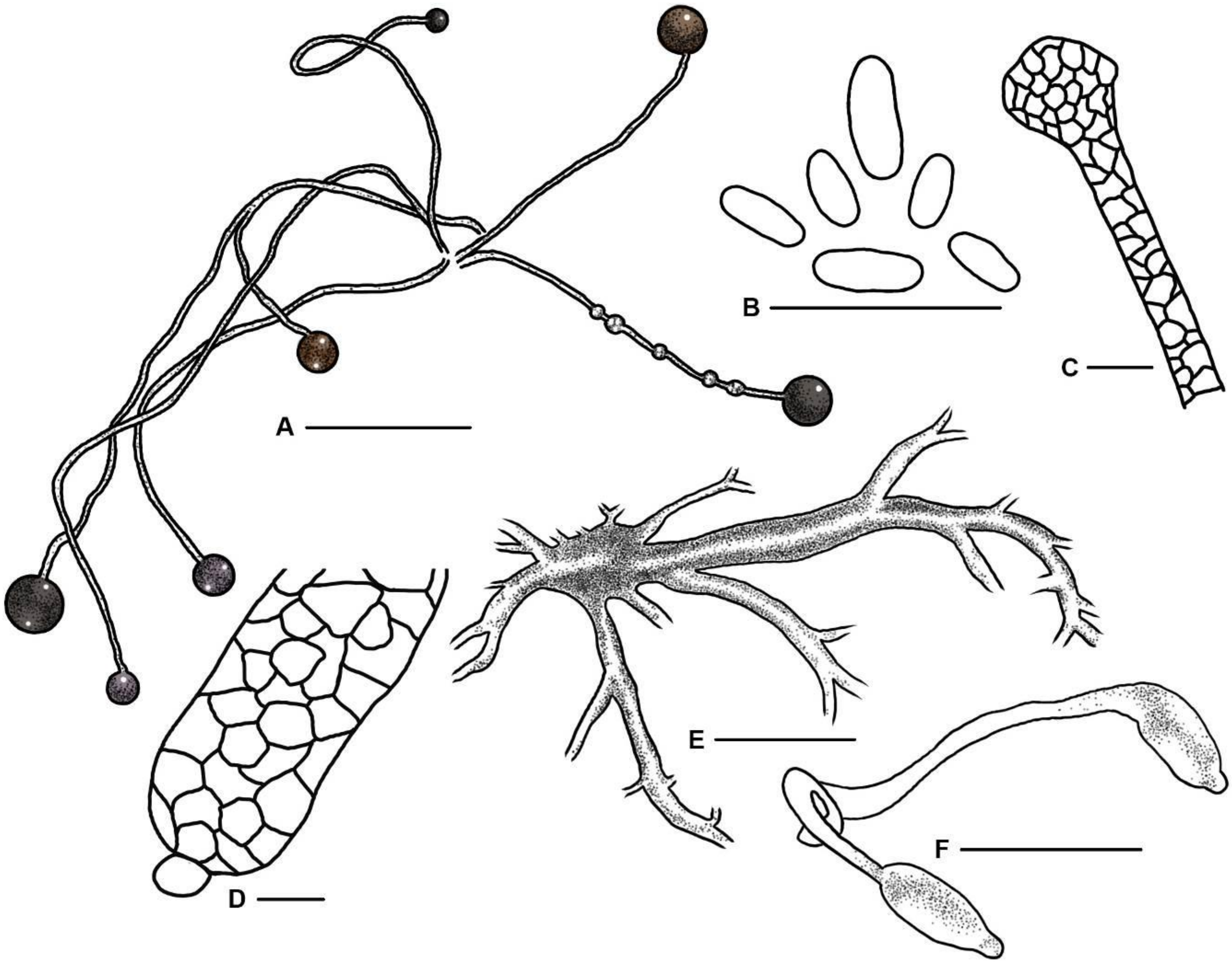

Figure 39 – *Dictyostelium sinuatipurpureum* var. *corymbipurpureum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregation. (**F**) Pseudoplasmodia. Scale bars: A = 2 mm; B−D = 20 µm; E = 0.2 mm; F = 1 mm.

Dictyostelium sinuatipurpureum* var. *subulibasipurpureum Y. Li, P. Liu et Y. Zou, sp. nov.
Figs. 2, 3, 40, 41

MycoBank number: 853149; GenBank accession number: SSU: PP590176. *Atp1*: PP932656.

Etymology – the Latin noun for "awl" is *subula*; and for "base" is *basis*; *subulibasipurpureum* means the purple sori and clavate or round base sometimes with an awl-shape terminal.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary, slight phototropic or without phototropic, prone to prostrate, with stoloniferous behavior, 0.6−4.4 mm in length. Sorophores consist of one to two tiers of cells wide, expanding slightly with several tiers of cells wide at the connection point, measuring 17.6−25.8 µm, and taper from the expanded connection point to the stoloniferous part and erect part. Bases are clavate or round, sometimes bases expanded then with terminal acuminate like an awl, with one to two tiers of cells wide, 6.3−22.1 µm in width, the widest points of base terminals measuring 8.4−22.1 µm, and the awl-shape base terminals measuring 4.4−8.7 µm in width. Tips are capitate to clavate, consisting of one tier of cells, 2.8−9.9 µm in width, with the widest points of tip terminals measuring 5.0−21.9 µm. Sori are purpure as grayish red (#905d5d), moderate reddish brown (#79443b), dark brown (#422518), globose, 70−193 µm in diam. Spores are oval to oblong, 5.0−8.2 × 2.6−3.4 µm (length/width = 1.78−2.44), occasionally spores are large and up to 10.0 × 3.5 µm (length/width = 2.86), spores without polar granules but with unconsolidated granules dispersed. Aggregations are radiate, with obvious strong but interrupted streams, 0.8−3.1 × 0.3−1.3 mm in size. At the end of aggregation, stream shrank into a mound and grew a pseudoplasmodium. Pseudoplasmodia migrate with stalks. This variety belongs to the *Dictyostelium* clade in a SSU rDNA phylogeny.

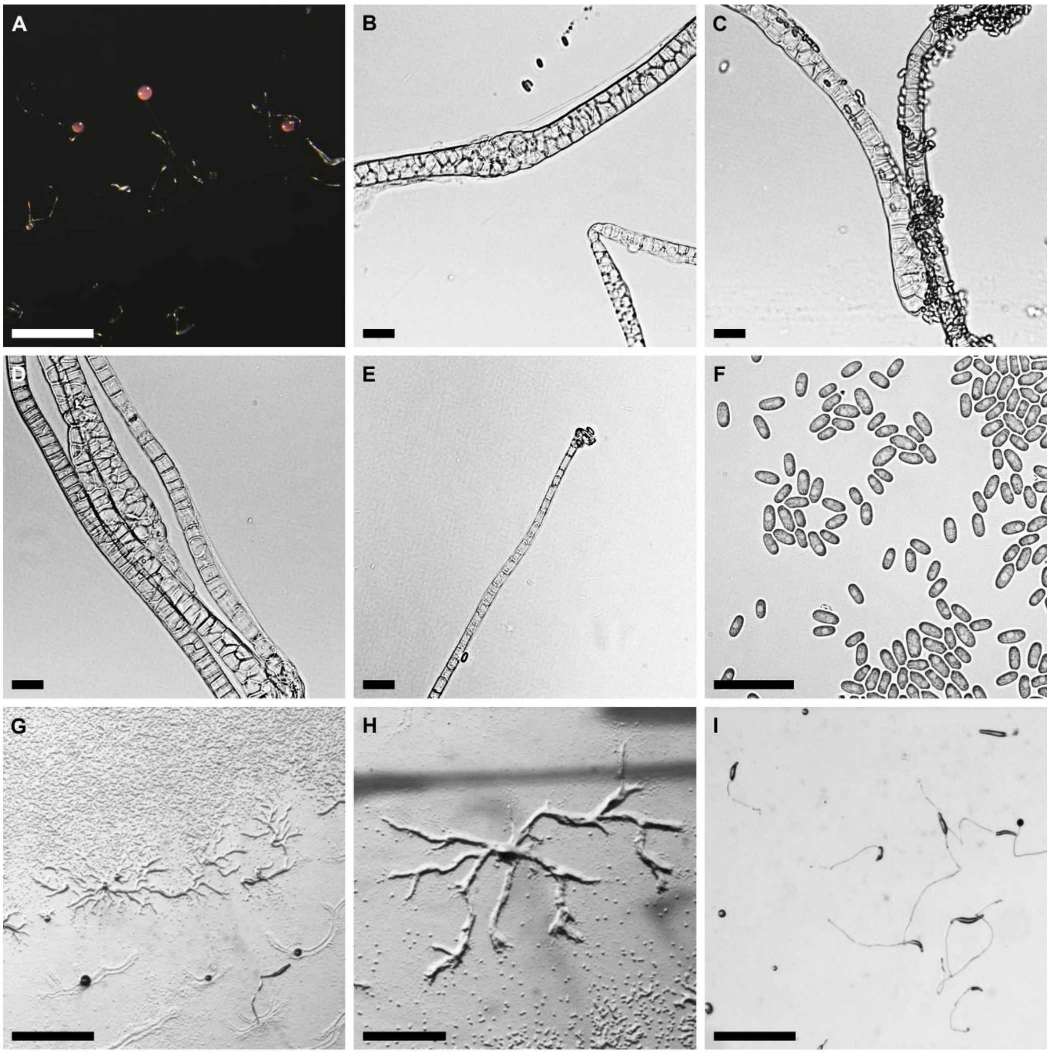

Figure 40 – Morphological features of *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum*. (**A**) Solitary sorocarps. (**B**) The expanded connection point on sorophore. (**C−D**) Bases and

sorophores. (**E**) Capitate tip. (**F**) Spores without polar granules but with unconsolidated granules under 100× magnification. (**G**) Aggregations and pseudoplasmodium. (**H**) Radiate aggregation. (**I**) Migrating pseudoplasmodia with stalks. Scale bars: A, G, I = 1 mm; B−F = 20 µm; H = 0.5 mm.

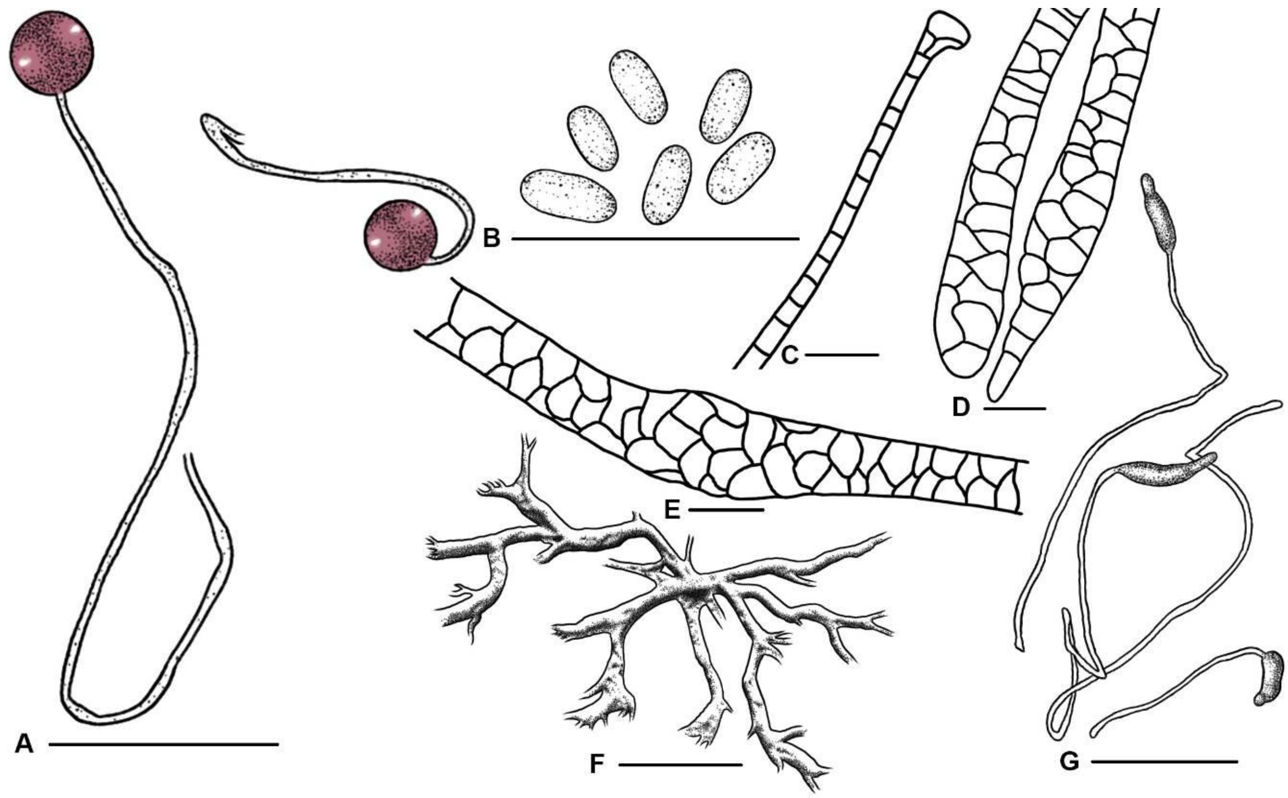

Figure 41 – *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Bases. (**E**) Expanded sorophore. (**F**) Aggregation. (**G**) Pseudoplasmodia. Scale bars: A, F−G = 0.5 mm; B−E = 20 µm.

Distribution and ecology – Isolated from Songbai Town of the Shennongjia National Nature Reserve, in mixed soil samples collected from an evergreen deciduous broadleaf forest at an intermediate elevation (1011−1424 m) with a high soil pH (pH = 7.41).

Material examined – China, Hubei Province: Songbai Town of the Shennongjia National Nature Reserve, 31.65º N, 110.54º E, average elevation 1151.2 m. Isolated from mixed soils, July 2022, *beichang1idao* (HOLOTYPE, voucher specimen code: HMJAU MR394). Known only from Hubei Province, China.

Notes – *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum* has clustered with *D. sinuatipurpureum* var. *corymbipurpureum* and *D. sinuatipurpureum* in the SSU and *atp1* phylogenetic tree, and they all cluster into the former *D. purpureum* clade. *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum* has clavate or round bases, sometimes with awl-shape terminals; the latter three species lack the structure (Raper 1984). *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum* has 70−193 µm sori smaller than 39−828 µm of *D. sinuatipurpureum* var. *corymbipurpureum*, 61−345 µm of *D. sinuatipurpureum*, and 125−450 µm of *D. purpureum*. *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum* has narrower bases, measuring 6.3−22.1 µm, compared to 9.1−79.4 µm of *D. sinuatipurpureum* var. *corymbipurpureum* and 8.5−44.6 µm of *D. sinuatipurpureum*. *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum* has prone to prostrate sorocarps with stoloniferous behavior; *D. purpureum* owns erect or semi-erect, then inclined sorocarps. Comparing with *D. sinuatipurpureum*, the aggregation streaming of *D. sinuatipurpureum* var. *subulibasipurpureum* is obviously sparse. *Dictyostelium sinuatipurpureum* var. *subulibasipurpureum* has lighter sori color with purple than *D. sinuatipurpureum* var. *corymbipurpureum* with dark purple to almost black sori, and

D. purpureum with sori dark vinaceous purple to almost black when mature. The spores of *D. sinuatipurpureum* var. *subulibasipurpureum* measure 5.0−8.2(−10.0) × 2.6−3.4(−3.5) μm with a length/width ratio of 1.78−2.44(−2.86), which are smaller than those of *D. sinuatipurpureum* var. *corymbipurpureum* with 5.1−14.8 × 2.3−4.5 μm and a ratio of 1.80−4.03, and larger than those of *D. purpureum* with 5.0−7.2(−8) × 2.5−3.2 μm. The features discussed above distinguish *D. sinuatipurpureum* var. *subulibasipurpureum* from *D. purpureum*. As part of clarifying and defining the internal distinctions within the complex species *D. purpureum*, we have separated *D. sinuatipurpureum* var. *subulibasipurpureum* away from *D. purpureum* as a new variety.

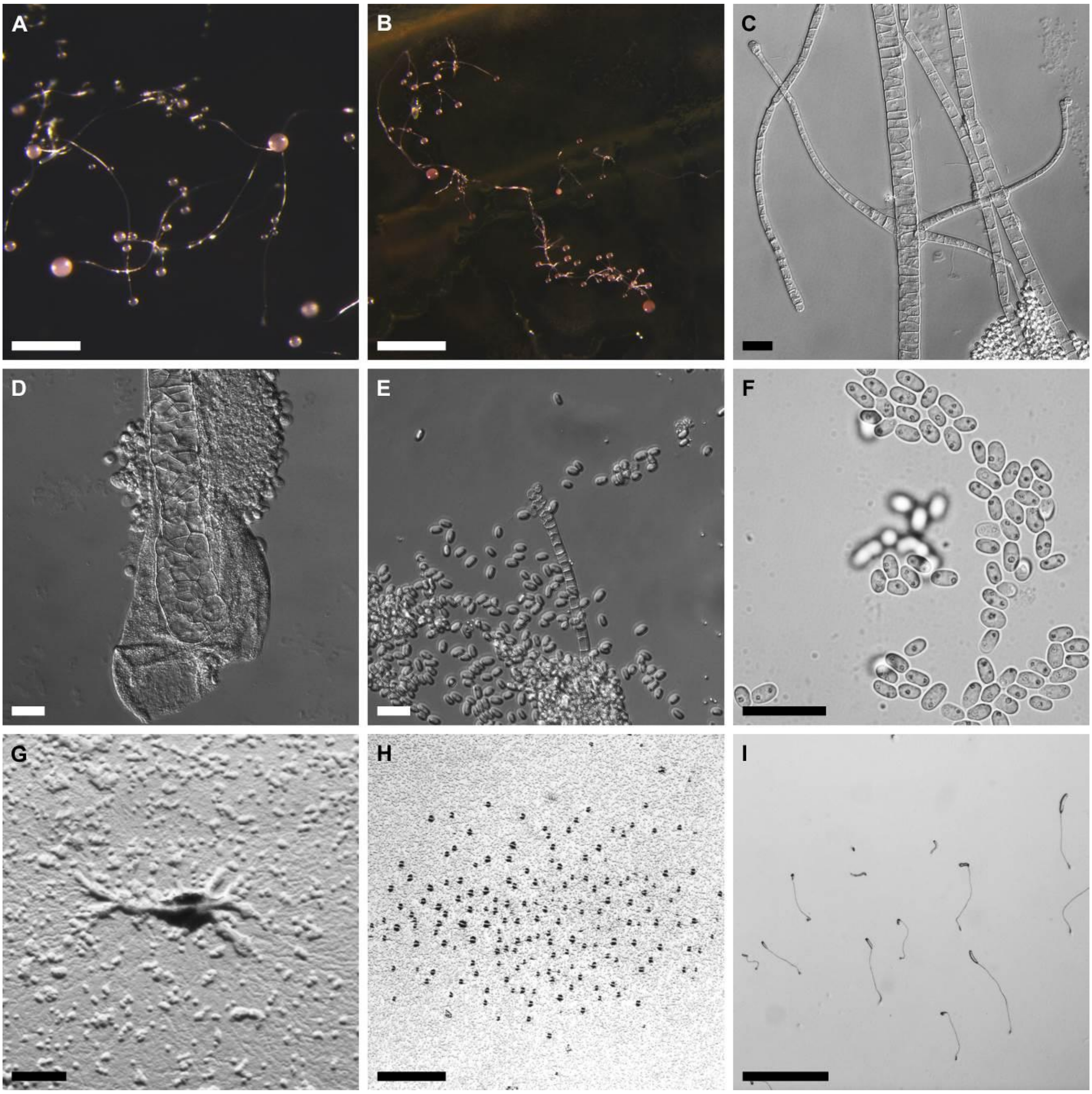

Figure 42 – Morphological features of *Polysphondylium latiamplitudinisporum*. (**A**−**B**) Gregarious sorocarps. (**C**) Whorl branches on the sorophore. (**D**) Base is covered by slime. (**E**) Obtuse tip. (**F**) Spores with polar granules under 100× magnification. (**G**) Early aggregation with short streaming. (**H**) Mound aggregations with secondary centers. (**I**) Migrating phototropic pseudoplasmodia with stalks. Scale bars: A = 0.5 mm; B, H−I = 1 mm; C−F = 20 μm; G = 200 μm.

Polysphondylium latiamplitudinisporum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 42, 43

MycoBank number: 853168; GenBank accession number: SSU: PP590208.

Etymology – the name refers to the wide range of spore sizes.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic, gregarious, erect or prone to prostrate, sometimes decumbent, sometimes sigmoid, 0.2−12.4 mm in length, unbranched or with whorl branches. Sorocarps have 1−8 whorls, with 1−5 branches on each whorl nude. Terminal segments are 173−978 μm in length, and node lengths are 77−997 μm. Branches are 68−863 μm in length. Bases of branches are round, consisting of one tier of cells, 3.3−9.7 μm in width. Tips of branches are capitate to clavate, consisting of one tier of cells, 2.0−6.8 μm in width. Sorophores consist of one to two tiers of cells except bases. Bases are round to clavate, consisting of one to two tiers of cells, 9.4−35.2 μm in width, the widest points of base terminals measuring 9.9−40.8 μm. Tips are obtuse, capitate, sometimes lack sori at terminal, consisting of one to two tiers of cells, 3.3−11.7 μm in width, the widest points of tip terminals measuring 3.0−15.1 μm. Terminal sori are pink or light purple, from dark yellowish pink (#c48379), dark pink (#c08081) to grayish purple (#796878), globose, 54−219 μm in diam. Lateral sori are colorless to grayish purple (#796878) or grayish reddish purple (#836479), globose, 27−96 μm in diam. Spores are elliptical to bacilliform, sometimes reniform, 4.2−10.8 × 2.6−5.0 μm (length/width = 1.34−3.52), with consolidated polar or subpolar granules. Aggregations are mounds with many secondary centers. Pseudoplasmodia migrate with stalks. This species belongs to the *Polysphondylium* clade in a SSU rDNA phylogeny.

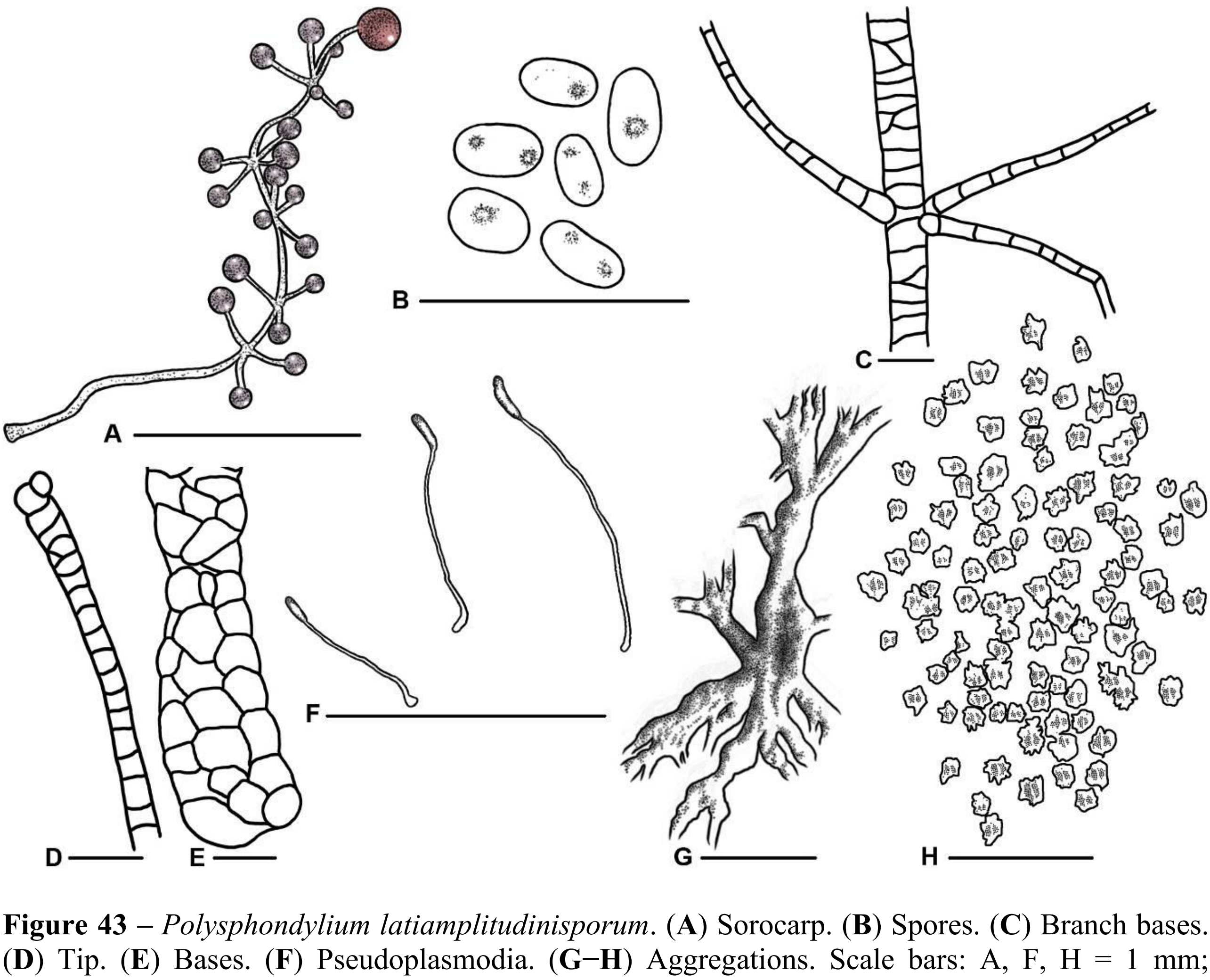

Figure 43 – *Polysphondylium latiamplitudinisporum*. (**A**) Sorocarp. (**B**) Spores. (**C**) Branch bases. (**D**) Tip. (**E**) Bases. (**F**) Pseudoplasmodia. (**G−H**) Aggregations. Scale bars: A, F, H = 1 mm; B−E = 20 μm; G = 0.2 mm.

Distribution and ecology – Isolated from the Jianfengling National Nature Reserve, in mixed soil samples collected from an evergreen tropical seasonal rainforest at a low elevation (672−707 m) with a low soil pH (pH = 5.34).

Material examined – China, Hainan Province: Jianfengling National Nature Reserve, 18.75º N, 108.91º E, average elevation 696.3 m. Isolated from mixed soils, February 2022, *haichang1-1* (HOLOTYPE, voucher specimen code: HMJAU MR421). Known only from Hainan Province, China.

Notes – This species is distinguished from other species of *Polysphondylium* by a wider range of terminal segment lengths, base widths, sorocarp sizes, and spore sizes, except for *P. violaceum* and *P. laterosorum* (Cavender 1970, Raper 1984, Vadell et al. 2011, Perrigo et al. 2013, Vadell & Cavender 2018). Other than the range of sori sizes and spore sizes, there is one more difference in the aggregation pattern between *P. latiamplitudinisporum* with *P. violaceum*. *Polysphondylium latiamplitudinisporum* has aggregations in mounds with secondary centers, while *P. violaceum* has radial aggregations with secondary centers. *Polysphondylium latiamplitudinisporum* is significantly different from *P. laterosorum* due to the presence of sessile sori in *P. laterosorum*.

Polysphondylium macroviolaceum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 44, 45

MycoBank number: 853165; GenBank accession number: SSU: PP590204.

Etymology – the name refers to the larger sori and spores of this species compared to *Polysphondylium violaceum*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary or gregarious, erect or prone, sometimes prostrate, 2.5−7.0 mm in length, sometimes up to 9.9 mm when prostrate. Sorophores are colorless to brilliant violet (#7e73b8) or grayish violet (#554c69), have whorls or irregular branches, and sometimes have irregular branches near the bases. Each sorocarp has 1−11 whorls. Each whorl has 1−5 branches, mostly 3−4 branches. Sometimes with sinuous sorophores which have a strong “S” shape in the lower portion near the bases. Sorophores are strong and tapering from bases to tips. Terminal segments are 289−980 µm in length. Bases are obtuse or clavate, occasionally digitate, covered by slime, usually with many tiers of cells in wide, 13.4−33.7 µm in width, with the widest points of base terminals measuring 11.2−96.3 µm. Tips are acuminate, capitate, or obtuse, with one or two tiers of cells wide, 6.8−13.5 µm in width, the widest points of tip terminals measuring 4.3−23.4 µm. Branches consist of one, two, or more tiers of cells in width, 87−996 µm in length. Sometimes branches can reach up to 1153 µm on prostrate stalks. The bases of branches are round or obtuse, consisting of one to several tiers of cells, 8.8−26.7 µm wide. The tips of branches obtuse to clavate or capitate, consisting of one to two tiers of cells, 4.2−12.3 µm wide. Sori are purple, ranging from moderate purple (#86608e), dark reddish purple (#5d3954), dark purple (#563c5c), dark grayish purple (#50404d), to dark brown (#422518), globose, terminal sori are a little larger than lateral sori, sometimes sorophores may lack terminal sori. Terminal sori are 131−256 µm in diameter, while lateral sori are 42−218 µm in diameter. Spores are subglobose to oblong, sometimes reniform, usually 3.2−7.8 × 2.8−4.2 µm (length/width = 1.10−2.24), but sometimes longer and up to 9.3−11.3 × 3.7−4.5 µm (length/width = 2.46−2.90), with polar granules, but sometimes polar granules are unobvious. This species belongs to the *Polysphondylium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from Northeast Asia Botanical Garden near the Changbai Mountain National Nature Reserve, in mixed soil samples collected from a broadleaf forest at a low elevation (728−763 m) with a high soil pH (pH = 7.15).

Material examined – China, Jilin Province: Northeast Asia Botanical Garden near the Changbai Mountain National Nature Reserve, 42.4º N, 128.11º E, average elevation 748.3 m. Isolated from mixed soils, August 2018, *kuo3* (HOLOTYPE, voucher specimen code: HMJAU MR308); *kuo5*. Known only from Jilin Province, China.

Notes – Comparing with other known species of *Polysphondylium*: *P. laterosorum* has sessile sori, whereas this species does not (Cavender 1970). *Polysphondylium fuscans* and *P. patagonicum* have branch whorl numbers of less than five, while this species has up to eleven whorls (Vadell et al. 2011, Perrigo et al. 2013). *Polysphondylium violaceum* has terminal sori 100−200 µm in diam, *P. acuminatum* has sori 170−220 µm, while this species has terminal sori measuring 131−256 µm (Raper 1984, Vadell & Cavender 2018). *Polysphondylium violaceum* has lateral sori 35−75 µm in diameter, while this species has 42−218 µm. *Polysphondylium violaceum* has spores measuring 5−8 × 2.5−3 µm, *P. acuminatum* has spores measuring 6.5−9 × 3−4.5 µm, while this species has spores measuring 3.2−11.3 × 2.8−4.5 µm. *Polysphondylium acuminatum* has terminal segments with length of 600−800 µm, whereas this species has terminal segments ranging from 289−980 µm in length. This species is different from *P. paniculoides* var. *multiverticillatum* and *P. paniculoides* due to the panicle-like branches of the latter two; and different from *P. latiamplitudinisporum* due to the narrower sorocarp sizes and spore ratio compared to *P. latiamplitudinisporum*. This species clusters nearby *P. violaceum* in the SSU phylogenetic tree.

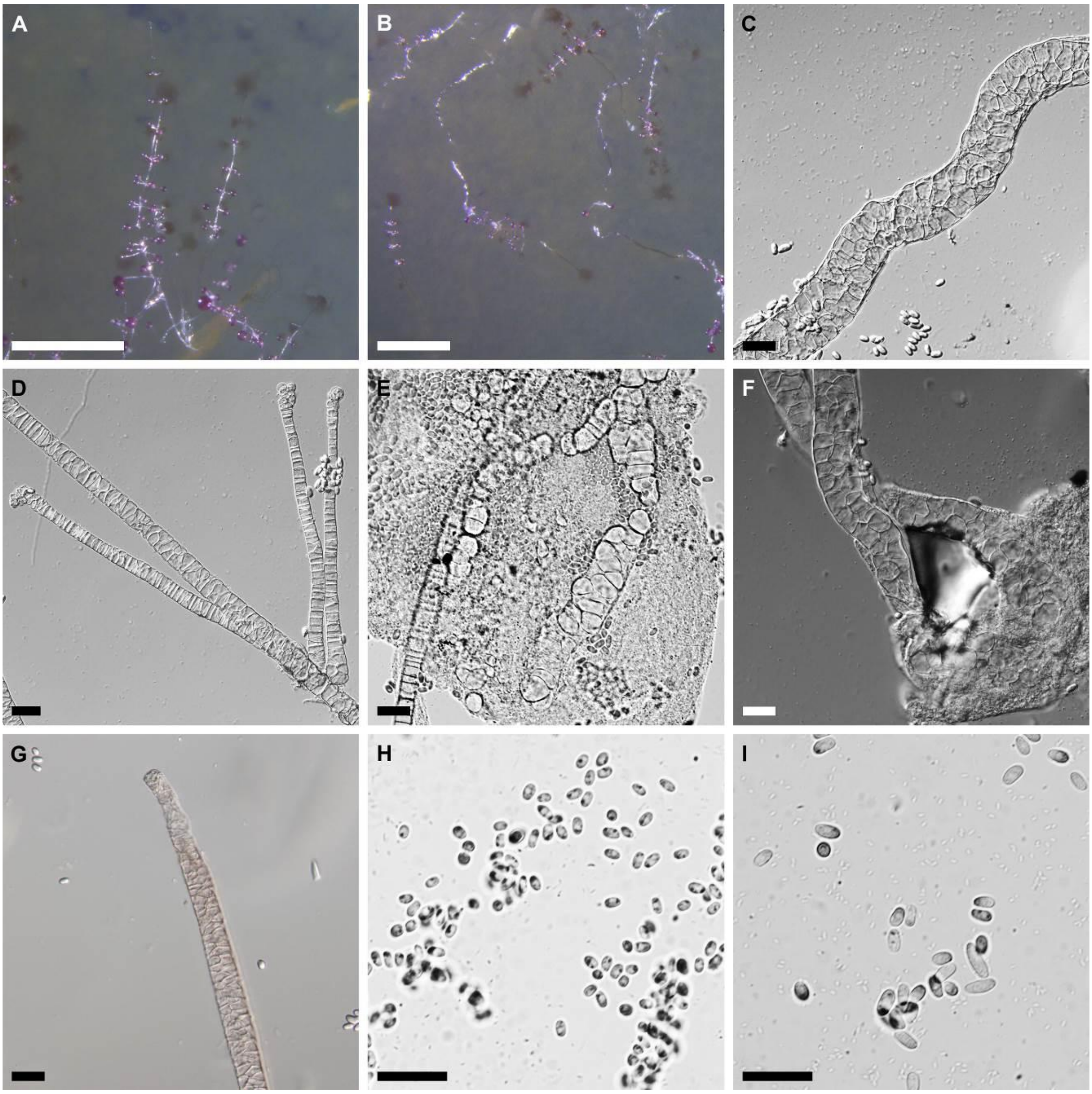

Figure 44 – Morphological features of *Polysphondylium macroviolaceum*. (**A**−**B**) Sorocarps have or lack terminal sori. (**C**) Sorophores sinuous with strong "S" shape in the lower portion near the bases. (**D**) Whorl branches on the sorophore. (**E**−**F**) Bases are covered by slime. (**G**) Obtuse tip.

(**H−I**) Small and large spores with polar granules or with unobvious polar granules. Scale bars: A−B = 2 mm; C−I = 20 µm.

Polysphondylium paniculoides Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 46, 47

MycoBank number: 853166; GenBank accession number: SSU: PP590206; PP590205. *Atp1*: PP932663; PP932665.

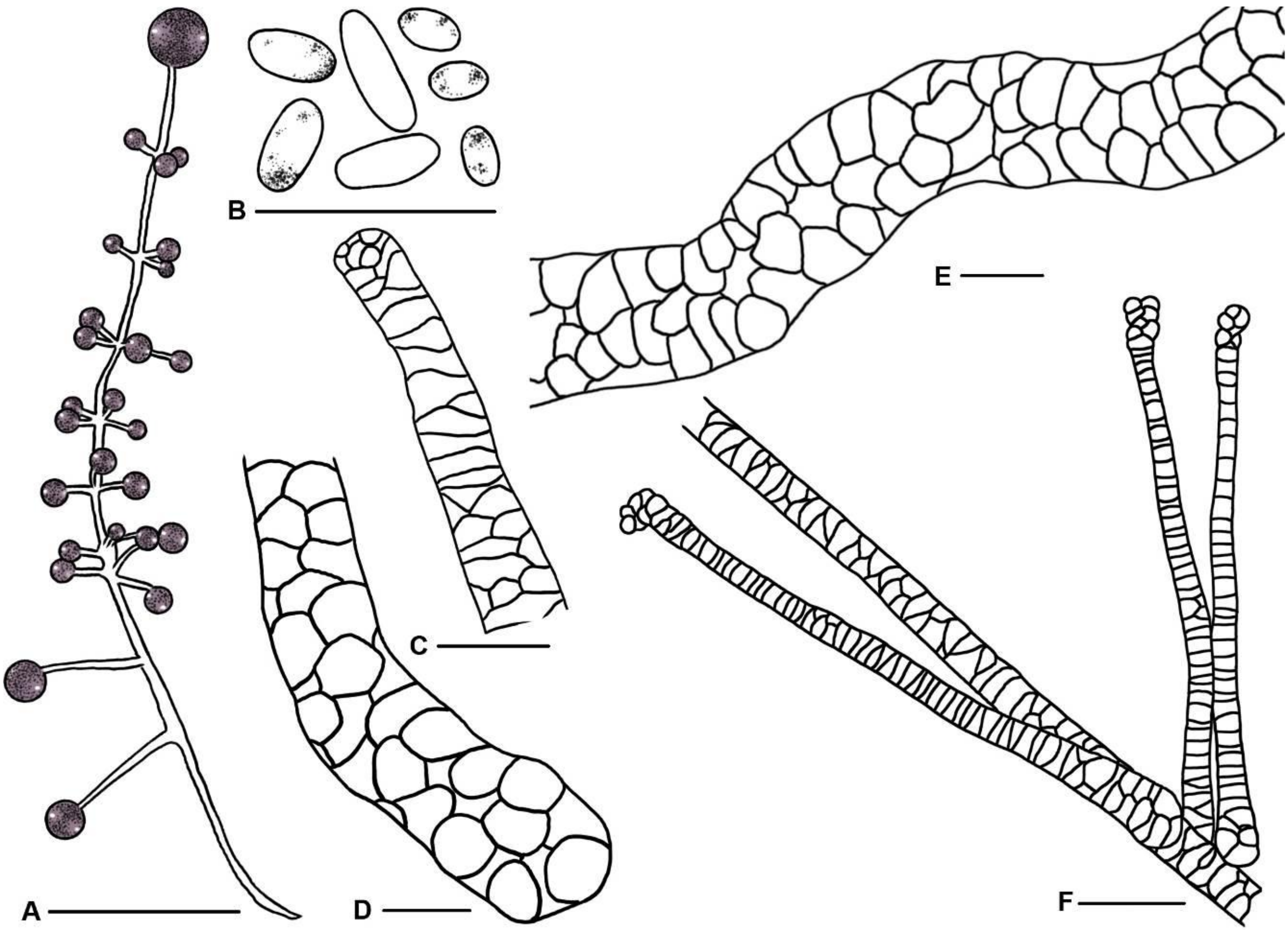

Figure 45 – *Polysphondylium macroviolaceum*. (**A**) Sorocarp. (**B**) Spores. (**C**) Tip. (**D**) Bases. (**E**) Sinuous sorophore. (**F**) Branches. Scale bars: A = 1 mm; C−E = 20 µm; F = 40 µm.

Etymology – the name refers to the panicle-like pattern of branching.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary, without phototropic, erect, prone, or prostrate to decumbent, a few are unbranched. Sorocarps always bifurcate and divide into two almost equal lengths at the lower part of the sorocarps, each dichotomous branch could bifurcate into more new branches, the bifurcate branches sometimes have crowded branches with whorls, or irregular branches. When branches are whorls, 1−4 whorls on each bifurcate branch, usually 1−6 branches on each whorl, but branch numbers of each whorl could reach 10 or more. The whole sorocarp appears to be in a panicle-like form. Sorocarps 0.2−5.9 mm in length. When sorocarps bifurcate, the lower parts (un-bifurcate part) are 0.4−2.8 mm, and the upper parts (bifurcate parts) are 1.1−5.1 mm in length. Whorl branches consist of one to two tiers cell in width, and 75−581 µm in length, a few single branches could reach 1.5 mm in length. Bases of branches are conical to round with one to several tiers of cells wide, 5.7−21.1 µm in width. Tips of branches are obtuse to capitate with one to two tiers of cells in width, 2.9−13.8 µm in width. Terminal segments are 348−900 µm in length. Sorophores consist of two to several tiers of cells, strong and tortuous or irregular, taper from bases to tips, colorless, white or light reddish purple (#b784a7) to very light purple (#d5badb). Bases are mostly enlarged, clavate, round, bulbous, conical, or digitate, consisting of two to several tiers of cells in width, 18.7−46.4 μm in width, with the widest points of base terminals measuring 27.9−64.0 μm. Some bases are obtuse, consisting of several tiers of cells, 43.8−61.9 μm in width, with the widest points of base terminals measuring 37.3−68.0 μm. A few bases are acuminate, consisting of several tiers of cells wide with 43.2 μm in width, the widest points of acuminate terminals measuring 11.0 μm. Sometimes many filaments stayed near the base. Tips are clavate, capitate, or obtuse, consisting of one to several tiers of cells, 2.0−19.3 μm in width, the widest points of tip terminals measuring 12.1−37.4 μm. Sori are globose, with a series of purple to brown colors, ranging from brilliant purple (#d399e6), deep pink (#e4717a), pale reddish purple (#aa8a9e), dark purplish pink (#c17e91), light reddish purple (#b784a7), light violet (#8c82b6), grayish reddish purple (#836479), moderate purplish red (#a8516e), grayish red (#905d5d), strong reddish brown (#882d17), to dark reddish purple (#5d3954), sometimes lateral sori could shrink and the color deepen to moderate red (#ab4e52). Terminal sori are 42−422 μm in diam, usually larger than lateral sori, lateral sori are 48−185 μm in diam. Spores are oval to bacilliform, sometimes reniform, 5.2−11.5 × 2.7−4.8 μm (length/width = 1.71−3.24), with conspicuous polar granule. Aggregations have two types, one with long and finely radial streams around center mounds, 1.1−3.1 × 0.4−2.7 mm; another are mounds with 4−8 ample short radiate streams, 0.3−0.8 × 0.2−0.7 mm. Pseudoplasmodia are mostly bullet-shaped with stalks, sometimes bifurcated. This species belongs to the *Polysphondylium* clade in a SSU rDNA phylogeny.

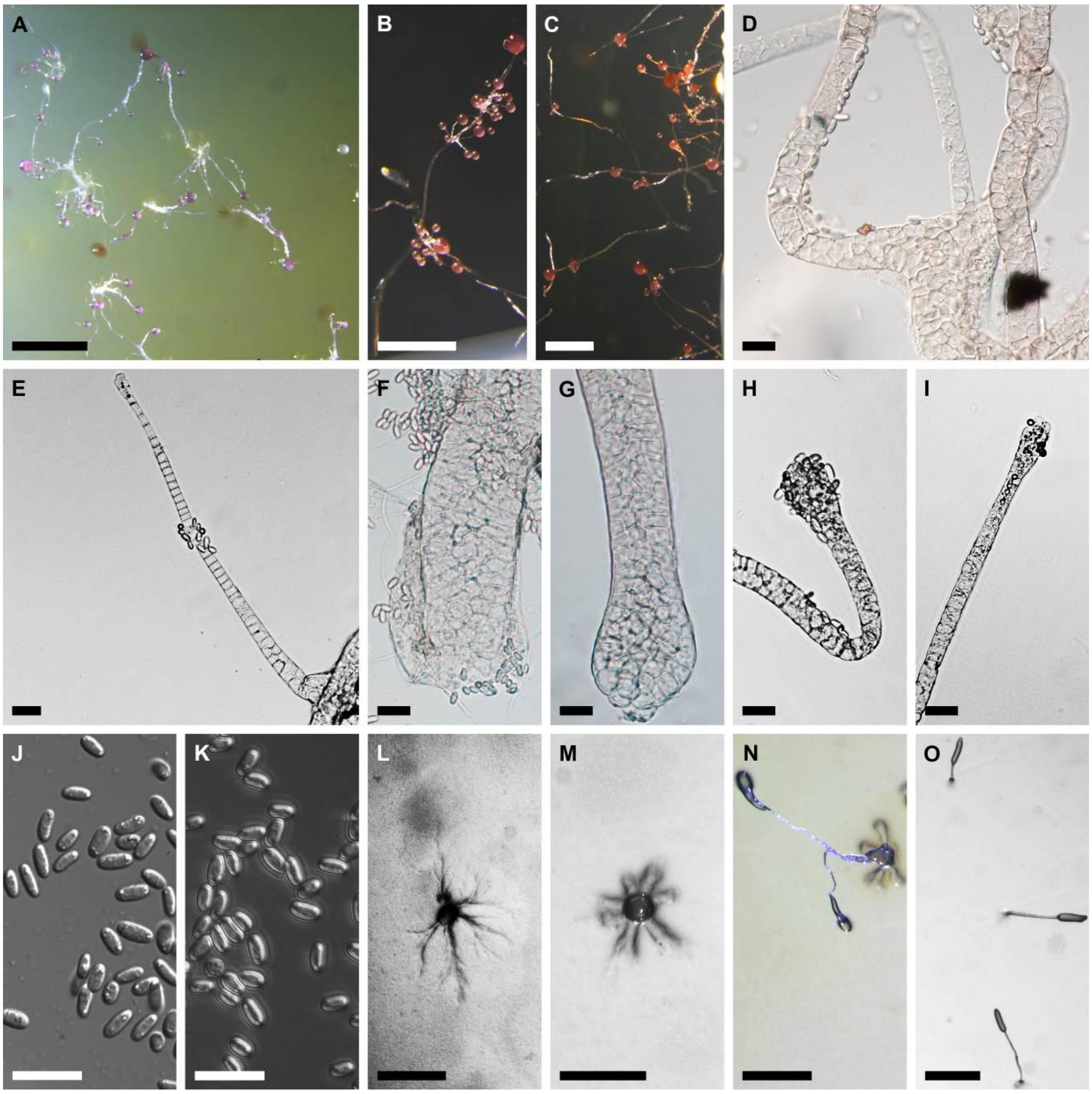

Figure 46 – Morphological features of *Polysphondylium paniculoides*. (**A**−**C**) Panicle-like and un-bifurcate sorocarps with whorl branches. (**D**) Bifurcate portion of the sorophore. (**E**) Branch of the

whorl. (**F−G**) Obtuse and bulbous bases. (**H−I**) Capitate and clavate Tips. (**J−K**) Spores with conspicuous polar granule. (**L−M**) Aggregations with two types. (**N−O**) Bifurcate and not bifurcate pseudoplasmodia. Scale bars: A = 2 mm; B−C, L, O =1 mm; D−K = 20 µm; M−N = 0.5 mm.

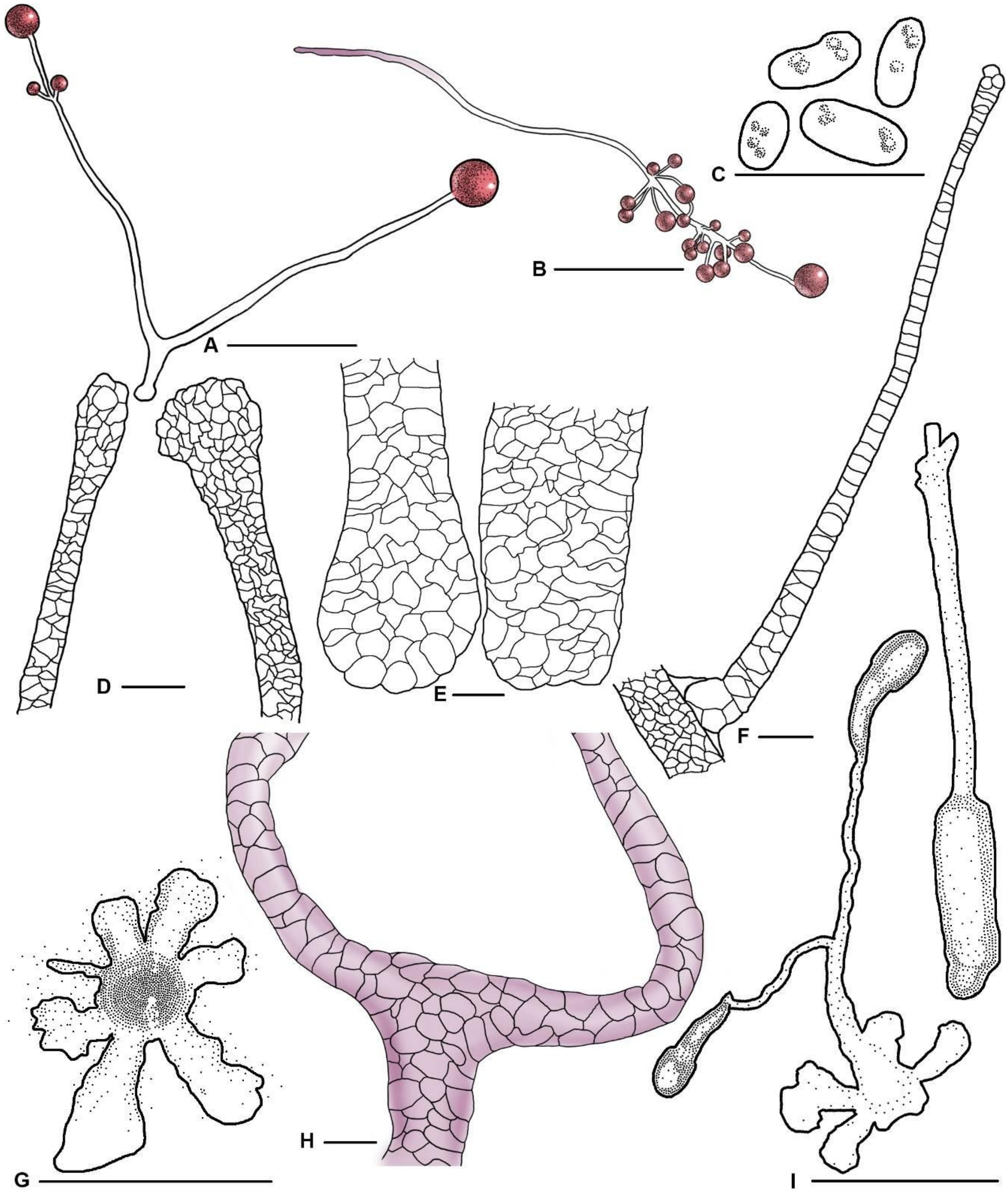

Figure 47 – *Polysphondylium paniculoides*. (**A−B**) Sorocarps. (**C**) Spores. (**D**) Tips. (**E**) Bases. (**F**) Branch. (**G**) Aggregation. (**H**) Bifurcate sorophore. (**I**) Pseudoplasmodia. Scale bars: A−B = 1 mm; C−F, H = 20 µm; G, I = 0.5 mm.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1755−1828 m) with a low soil pH (pH = 5.32). Also isolated from the Dell Forest of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at an intermediate elevation (1564−1620 m) with a low soil pH (pH = 5.59).

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m. Isolated from mixed soils, August 2019, *19yuec4* (HOLOTYPE, voucher specimen code: HMJAU MR419); *19yuec3*. Also isolated from mixed soils of Dell Forest of the Changbai Mountain National Nature Reserve, 42.09º N, 128.07º E, average elevation 1594.2 m, August 2018, *hun4*; *hun4-2*; *hun4-3*. Known only from Jilin Province, China.

Notes – This species clusters with *Polysphondylium paniculoides* var. *multiverticillatum* in the SSU and *atp1* phylogenetic tree. The differences between them are described in the notes on *P. paniculoides* var. *multiverticillatum*. *Polysphondylium paniculoides* is distinct from other species of *Polysphondylium* due to its special panicle-like branches and bifurcated sorogens, which are significantly different from those of other species (Raper 1984, Vadell et al. 2011, Perrigo et al. 2013, Vadell & Cavender 2018). This species is similar to *Dictyostelium dichotomum* in terms of the bifurcate structure, but other morphological characteristics are different, such as sori color, spore sizes, and sorocarp sizes (Vadell & Cavender 2007).

Polysphondylium paniculoides* var. *multiverticillatum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 48, 49

MycoBank number: 853167; GenBank accession number: SSU: PP590207. *Atp1*: PP932664.

Etymology – the Latin adjective meaning "whorled" is *verticillatus*/*verticillate*/*verticillatum*; *multiverticillatum* means the sorocarps with more whorls but fewer bifurcate structure than *Polysphondylium paniculoides*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are phototropic, solitary to gregarious, sigmoid, strong, erect, prone to prostrate, 1.0−6.8 mm in length. Sorocarps sometimes unbranched or with whorl branches but without bifurcate structure, and sometimes with bifurcate dichotomous branches. Dichotomous branches could also bifurcate into secondary dichotomous branches, dichotomous branches may have few or no whorl branches on the stalks. When sorocarps bifurcate, the lower parts (un-bifurcate part) are 0.3−0.6 mm, and the upper parts (bifurcate parts) are 1.2−3.7 mm in length. Sorocarps could have 1−5 whorls, and each whorl have 1−7 short branches. The branches on whorls are 0.1−0.5 mm in length. Branch bases on whorls are round, consist of one to several tiers of cells, 8.7−20.8 µm in width. Branch tips on whorls are obtuse to clavate, consist of one tier of cells, 4.9−8.7 µm in width. Terminal segments are 378−945 µm in length. Sorophores are colorless or light reddish purple (#b784a7) to light purple (#b695c0), consisting of several tiers of cells. Bases are round to clavate, consisting of two to several tiers of cells, 16.3−77.9 µm in width, with the widest points of base terminals measuring 19.0−76.9 µm. Tips are obtuse, clavate, consisting of one to several tiers of cells, 9.2−18.0 µm in width, the widest points of tip terminals measuring 8.9−25.6 µm. Sori are purple to brown colors ranging from light purple (#b695c0), dark purplish pink (#c17e91), grayish red (#905d5d), to moderate reddish brown (#79443b), globose. Terminal sori are 92−263 µm in diam, lateral sori are 44−206 µm in diam. Spores are elliptical to oblong, sometimes reniform, 5.1−10.6 × 2.6−4.1 µm (length/width = 1.44−2.60), with unobvious polar granules or subpolar granules. Aggregations are typical radiate, with thin or thick streams, 1.0−5.3 × 0.9−3.1 mm. Pseudoplasmodia migrate with stalks. This variety belongs to the *Polysphondylium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1755−1828 m) with a low soil pH (pH = 5.32).

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain, National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m. Isolated from mixed soils, August 2019, *19yuef3* (HOLOTYPE, voucher specimen code: HMJAU MR420). Known only from Jilin Province, China.

Notes – This variety has the same SSU rDNA and *atp1* sequence as *Polysphondylium paniculoides*, but sorocarps of *P. paniculoides* var. *multiverticillatum* have fewer bifurcate structures. When sorocarps bifurcate, the lower part (un-bifurcate part) and upper parts (bifurcate parts) of *P. paniculoides* var. *multiverticillatum* are all shorter than *P. paniculoides*. Spore ratio of *P. paniculoides* var. *multiverticillatum* is also smaller, but aggregations are a little larger. In another time, *P. paniculoides* var. *multiverticillatum* has a phototropic character, while *P. paniculoides* is not phototropic.

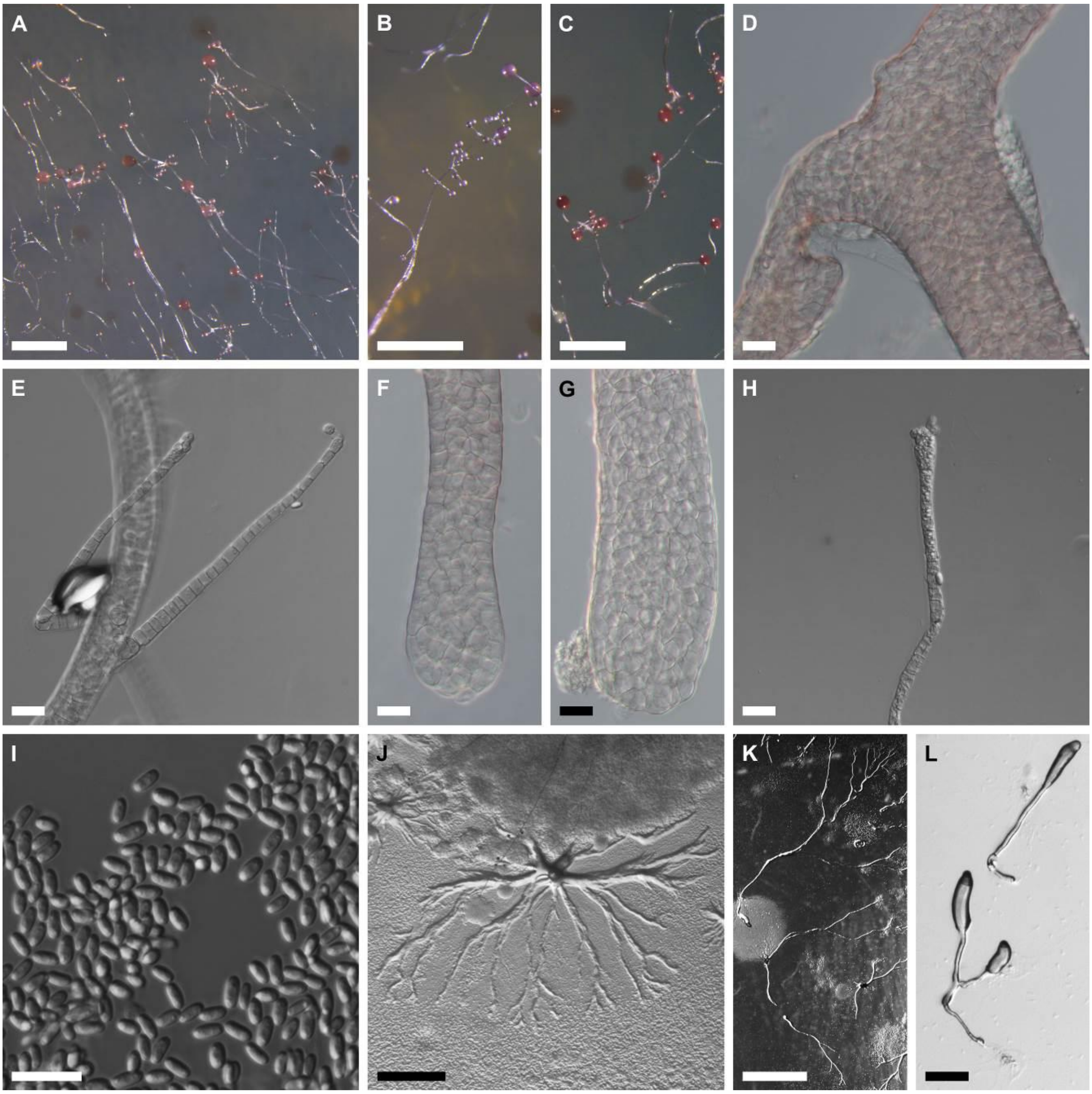

Figure 48 – Morphological features of *Polysphondylium paniculoides* var. *multiverticillatum*. (**A**) Panicle-like and un-bifurcate sorocarps are phototropic. (**B**) Sorocarp with whorl branches but without bifurcate structure (**C**) Sorocarp forms a panicle-like form with bifurcate structure. (**D**) Bifurcate part of the sorophore. (**E**) Branches of the whorl. (**F−G**) Round and clavate bases. (**H**) Clavate Tip. (**I**) Spores with unobvious polar granules or subpolar granules. (**J**) Radiate aggregation. (**K−L**) Migrating pseudoplasmodia with stalks. Scale bars: A−C, J = 1 mm; D−I = 20 µm; K = 2 mm; L = 200 µm.

Hagiwaraea conicibasis Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 50, 51

MycoBank number: 853164; GenBank accession number: SSU: PP590203.

Etymology – the Latin adjective meaning "conical" is *conicus*/*conica*/*conicum*; *conicibasis* means the bases encapsulated in a conical mass.

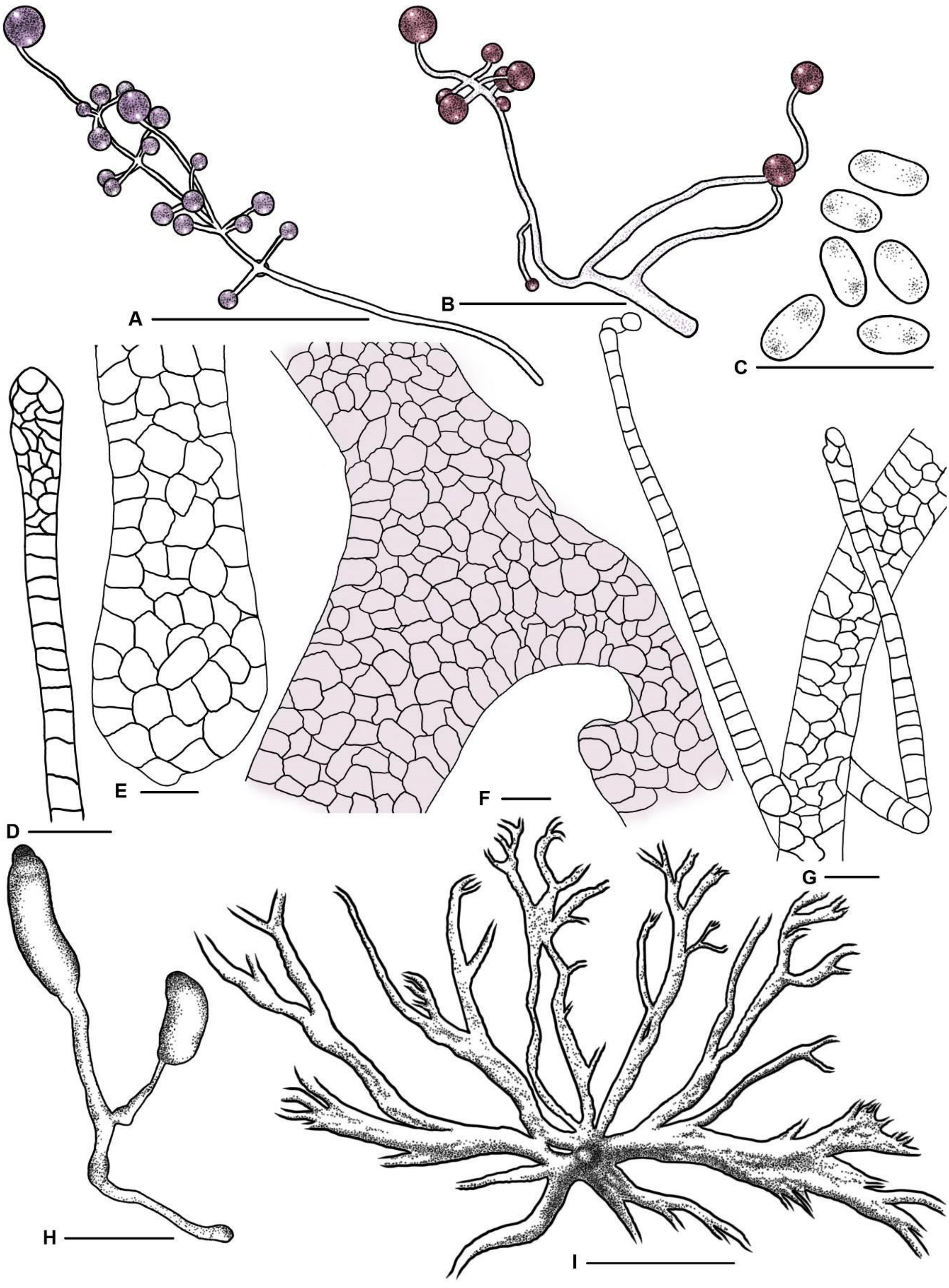

Figure 49 – *Polysphondylium paniculoides* var. *multiverticillatum*. (**A−B**) Sorocarps. (**C**) Spores. (**D**) Tip. (**E**) Base. (**F**) Bifurcate sorophore. (**G**) Branchs. (**H**) Pseudoplasmodium. (**I**) Aggregation. Scale bars: A−B, I = 1 mm; C−G = 20 μm; H = 0.2 mm.

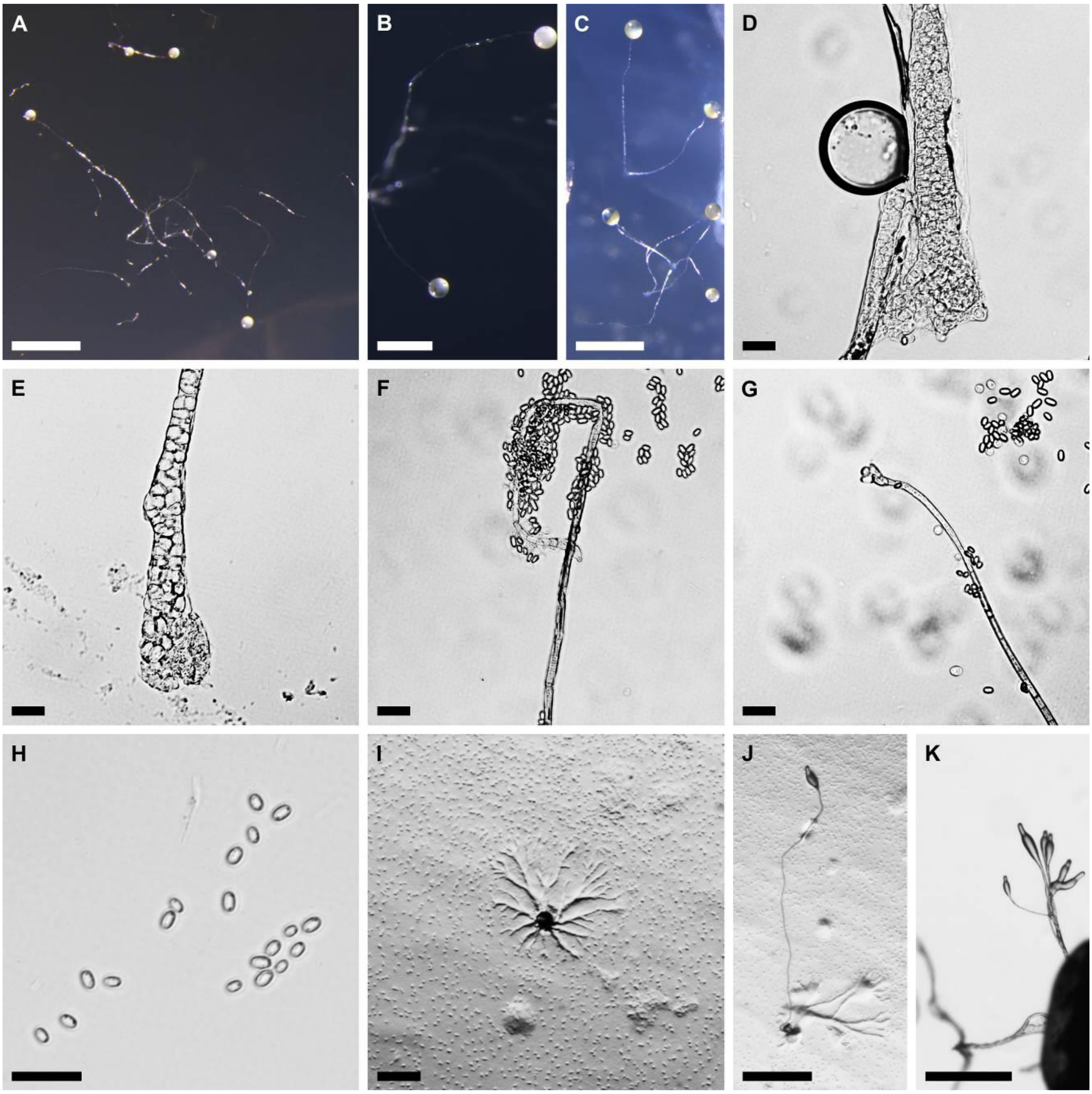

Figure 50 – Morphological features of *Hagiwaraea conicibasis*. (**A−C)** Sorocarps with yellow to grayish olive sori. **(D−E**) Conical and round bases. (**F−G**) Clavate elongated and capitate tips. (**H**) Spores with polar granules. (**I**) Radiate aggregation. (**J−K**) Migrating pseudoplasmodia with stalks. Scale bars: A, C = 1 mm; B, J−K = 0.5 mm; D−H = 20 µm; I = 200 µm.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary, clustered, or coremium-like with 2 to 5 sorocarps, erect to prone, 0.4−5.6 mm in length, usually unbranched, sometimes with one branch near the base. Branches are 0.4−1.1 mm in length. Sorocarps usually grow from a mass of cells; the cell mass appears similar to a conical flask or round-bottom flask when the light is incident only from the bottom side. Sorophores consist of one to several tiers of cells. Bases are round, conical, or expand with hook-shape, consisting of one to several tiers of cells. Bases are 8.4−30.2 µm in width, with the widest points of base terminals measuring 11.5−57.1 µm. Bases are often encapsulated in the cell of conical mass. Tips are clavate, capitate, obtuse, or elongated cell, consisting of one to several tiers cell, 3.3−16.7 µm in width, with widest points of tip terminals measuring 5.2−25.7 µm. Sori are semi-hyaline, yellow to grayish olive, ranging in color from pale yellow (#f3e5ab), light yellow (#f8de7e), grayish yellow (#c2b280), yellowish gray (#bfb8a5), light grayish olive (#8c8767), grayish olive (#5b5842), to olive gray (#57554c), globose, 32−304 µm in diameter. Spores are capsule-shaped, elliptical to oblong, 4.3−8.7 × 2.5−4.7 µm (length/width = 1.44−2.19), with polar granules. Microcysts are present with 4.5−6.9 × 4.4−6.7 µm. Pseudoplasmodia with stalks. This species belongs to the *Hagiwaraea* clade in a SSU rDNA phylogeny.

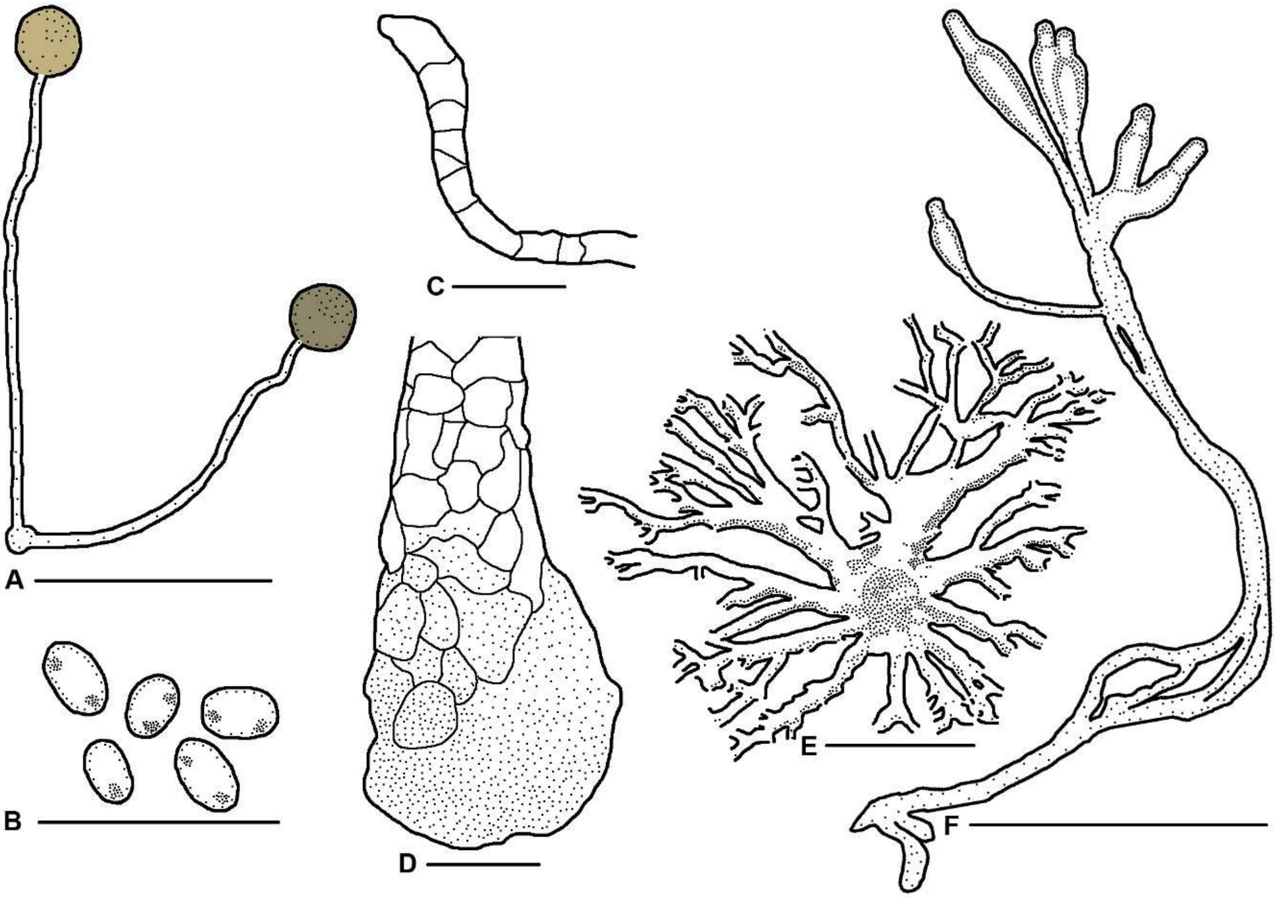

Figure 51 – *Hagiwaraea conicibasis*. (**A**) Sorocarp. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregation. (**F**) Pseudoplasmodium. Scale bars: A = 1 mm; B−D = 20 µm; F = 0.5 mm; E = 0.2 mm.

Distribution and ecology – Isolated from the Jianfengling National Nature Reserve, in mixed soil samples collected from a mixed broadleaf/conifer forest at a low elevation (785−797 m) with a low soil pH (pH = 5.51).

Material examined – China, Hainan Province: Jianfengling National Nature Reserve, 18.75º N, 108.87º E, average elevation 790.7 m. Isolated from mixed soils, February 2022, *haihun6-1* (HOLOTYPE, voucher specimen code: HMJAU MR418). Known only from Hainan Province, China.

Notes – The species clusters with *Hagiwaraea radiculata* and *Ha. rhizopodium* in the SSU phylogenetic tree. The bases of *Ha. conicibasis* encapsulated in a conical flask or round-bottom flask cell mass can be distinguished from later two species (Raper & Fennell 1967, Landolt et al. 2008). In morphological features, *Ha. conicibasis* has sorocarps (0.4−5.6 mm) and branches (0.4−1.1 mm), which are longer than 0.3−1.5 mm length sorocarps and 0.07−0.2 mm length branches of *Ha. radiculata*; and bases (8.4−30.2 µm) of *Ha. conicibasis* are narrower than 50−90 µm width bases of *Ha. radiculata*. On the other hand, *Ha. conicibasis* is different with *Ha. rhizopodium* in spores, base shapes and sizes. *Hagiwaraea rhizopodium* with the two sizes spores of 10−13 × 3−4 µm and 6.0−8.0 × 3.0−3.5 µm are narrower than those of *Ha. conicibasis*. The bases of *Ha. conicibasis* are round, conical, or expand with hook-shape, with 8.4−30.2 µm in width; *Ha. rhizopodium* has strongly dissected crampon-like bases with 25−50 µm in width. At the same time, *Ha. coeruleostipes* also has a color that is white to faintly cream-colored and pale yellow; however, the basal disks, thinner tips (4−7 µm), and blue-purple sorophores make it different from *Ha. conicibasis* (Raper & Fennell 1967).

Raperostelium kraken Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 52, 53

MycoBank number: 853169; GenBank accession number: SSU: PP590209; PP590210; PP590218. *Atp1*: PP932633; PP932634.

Etymology – the name refers to the multiple sorophores sharing a common base, resembling the sea monster *Kraken* from book "*The Natural History of Norway*" as 'full of arms, or branches.'

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary, gregarious to clustered, erect or semierect to prone, sometimes sinuous, 0.2−1.1 mm in length; usually unbranched, but sometimes with 1−3 branches. Sometimes 2−13 sorophores (rarely more and reaching up to 21 sorophores) share a common base; the overall shape looks like the sea monster *Kraken* and was called a Kraken structure by us. Sorophores consist of one to three tiers of cells. Basal disks are sometimes present, but not obvious under the Kraken structure. Bases are round or irregular in shape, sometime adhered by slime, consisting of one to several tiers of cells, 8.0−25.4 µm in width, with the widest points of base terminals measuring 17.1−266.7 µm, but sometimes can be more than 300 µm wider. Tips are acuminate, obtuse, consisting of one tier of cells, 1.9−9.1 µm in width, with the widest points of tip terminals measuring 1.9−6.1 µm. Sori are white, semi-hyaline, globose or citriform, 28−134 µm in diameter. Spores are abnormal, globose to oblong: globose spores are 3.1−3.9 × 3.0−3.8 µm (length/width = 1.00−1.05); subglobose spores are 3.1−4.3 × 2.7−3.8 µm (length/width = 1.07−1.15); broadly elliptical spores are 3.4−5.0 × 2.8−4.2 µm (length/width = 1.16−1.30); elliptical spores are 3.8−6.5 × 2.6−4.5 µm (length/width = 1.31−1.65); oval spores are 4.1−6.6 × 2.5−3.7 µm (length/width = 1.66−1.86); oblong spores are 5.3−8.4 × 2.6−4.3 µm (length/width = 1.93−2.33). Some spores have circular polar granules, some have consolidated polar granules, and others have unconsolidated polar granules. Aggregations are small mounds with flat, blocky streaming. Pseudoplasmodia with stalks. Microcysts present with 2.9−4.4 × 2.9−4.1 µm. Globose or subglobose structures with an irregular or prickly surface have present near the spores, 5.4−9.1 µm in diameter. This species belongs to the *Raperostelium* clade in a SSU rDNA phylogeny.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1755−1828 m) with a low soil pH (pH = 5.32).

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m. Isolated from mixed soils, August 2019, *19yuec5* (HOLOTYPE, voucher specimen code: HMJAU MR422); *19yuea2*; *19yuec2*. Known only from Jilin Province, China.

Notes – *Raperostelium kraken* has clustered with *Ra. krakenopsis*, *Ra. pusillum*, and *Ra. minutum* in same clade of the SSU phylogenetic tree. However, the four species all have different characteristics in morphology. Firstly, *Ra. kraken*, *Ra. krakenopsis*, and *Ra. pusillum* all have clustered sorocarps, except *Ra. minutum*. Secondly, the sorocarps with several sorophores sharing a common base (Kraken structure) have been observed in *Ra. kraken*, *Ra. krakenopsis*, and *Ra. pusillum*, but *Ra. minutum* and other *Raperostelium* species do not have this characteristic (Raper 1941, Cavender et al. 1979, Hagiwara 1983b, 1989, Cavender et al. 2002, Cavender et al. 2005, Cavender & Vadell 2006, Romeralo et al. 2009, Cavender et al. 2013, Cavender et al. 2018, Perrigo et al. 2020). Thirdly, *Ra. kraken*, *Ra. krakenopsis*, and *Ra. pusillum* have distinct polar granules in spores, but *Ra. minutum* only has unobvious polar granules or lacks polar granules. These characters differentiate *Ra. kraken*, *Ra. krakenopsis*, and *Ra. pusillum* from *Ra. minutum*.

On the other hand, *Raperostelium kraken* is also different with *Ra. krakenopsis*, and *Ra. pusillum*. The structure of Kraken (several sorophores sharing a common base) in *Ra. kraken* has more sorophores, specifically more than half of the sorocarps have 2−13, rarely up to 21 sorophores sharing a base in *Ra. kraken*; a few sorocarps have two, rarely three to four sorophores sharing a base in *Ra. krakenopsis*; and infrequent sorocarps have 4−9 sorophores sharing a base in *Ra. pusillum*. Both *Ra. krakenopsis* and *Ra. pusillum* have clavate, conical, round bases, but bases of *Ra. kraken* are round and irregular. The widest points of *Ra. kraken* base terminals (17.1−266.7 μm, sometimes more than 300 μm in width) are obviously wider than *Ra. krakenopsis* (9.4−76.8 μm) and *Ra. pusillum* (4.5−29.1 μm). Finally, *Ra. kraken* has widely varying shapes of spores (from globose to oblong); the ratio of *Ra. kraken* spores (length/width = 1.00−2.33) has a broader range than *Ra. krakenopsis* (length/width = 1.16−2.01) and *Ra. pusillum* (length/width = 1.52−1.97).

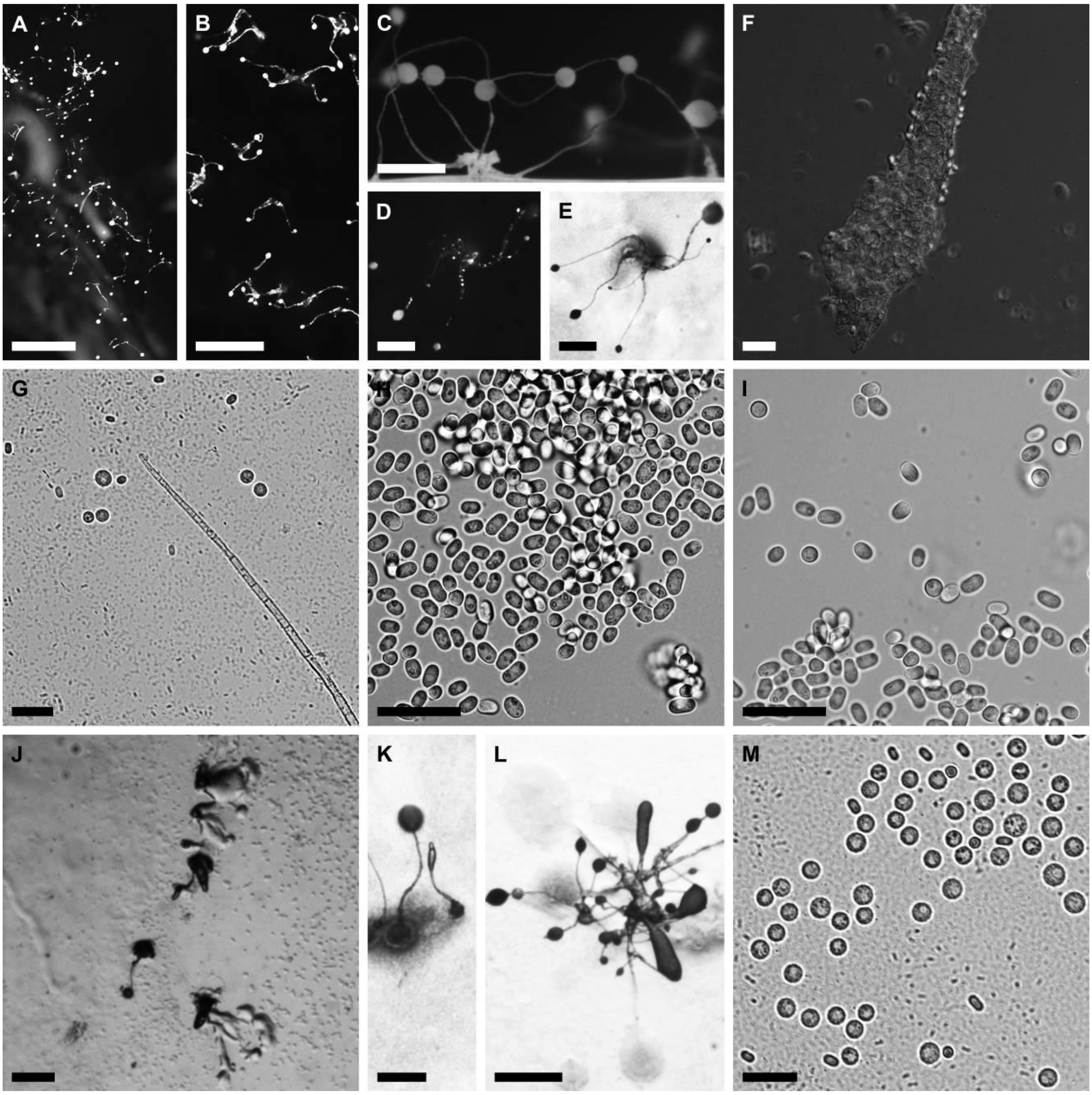

Figure 52 – Morphological features of *Raperostelium kraken*. (**A**−**B**) Non-Kraken and Kraken sorocarps. (**C**−**E**) Side-view and top-view of sorocarps with Kraken-like structures. Picture D was taken under lateral light, while picture E was the same sorocarp taken with bottom light. (**F**) Round and a little irregular base of the sorophore. (**G**) Acuminate tip of the sorophore. (**H**−**I**) Different ratio of spores with consolidated and unconsolidated polar granules. (**J**) Small aggregations with flat, blocky streaming. (**K**−**L**) Pseudoplasmodia of non-Kraken and Kraken-like structures. (**M**) Globose or subglobose structures with an irregular surface. Scale bars: A = 2 mm; B = 1 mm; C−E, J−L = 200 μm; F−I, M = 20 μm.

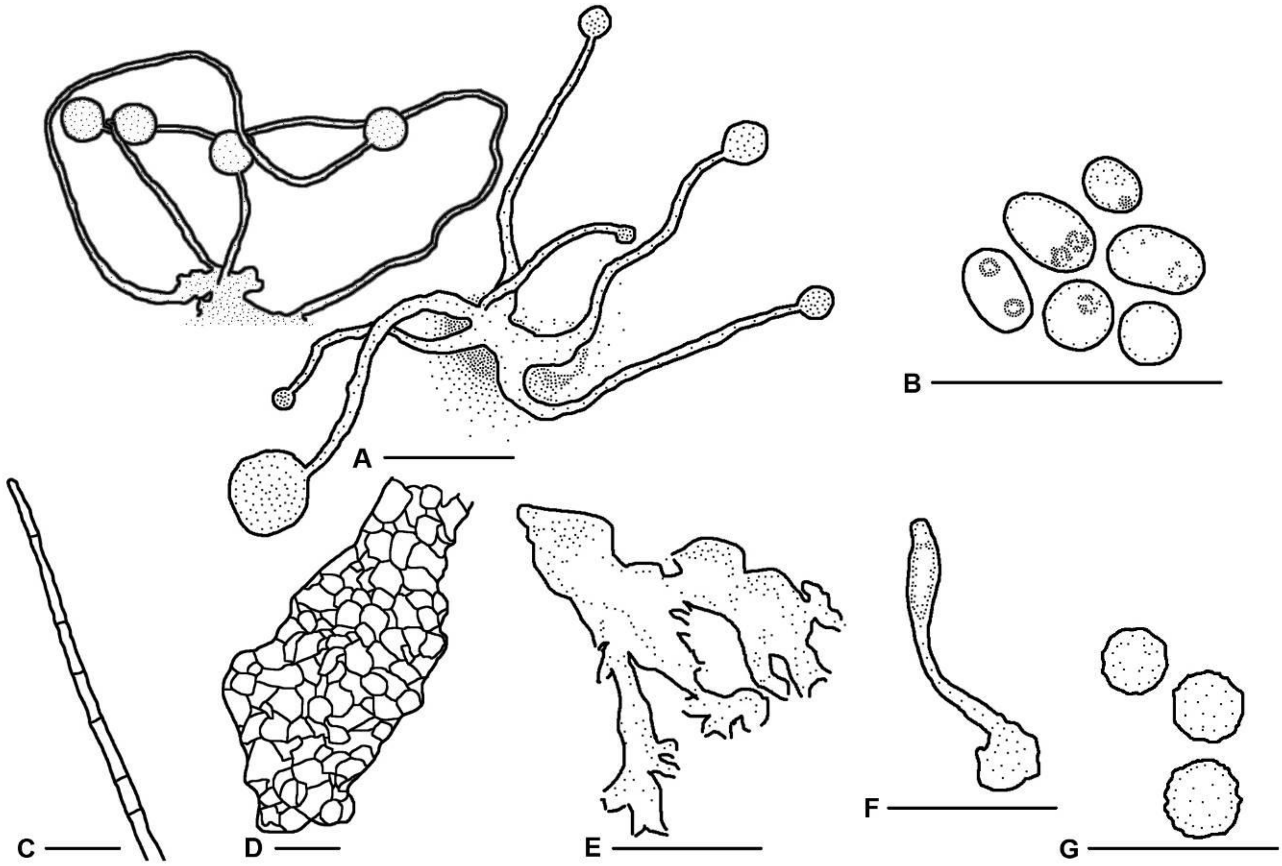

Figure 53 – *Raperostelium kraken*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregation. (**F**) Pseudoplasmodium. (**G**) Globose or subglobose structures. Scale bars: A, E−F = 0.2 mm; B−D, G = 20 μm.

Moreover, in the *atp1* phylogenetic tree, the four species (*Raperostelium kraken*, *Ra. krakenopsis*, *Ra. pusillum*, and *Ra. minutum*) have clustered in four different clades.

This species sometimes has a Kraken structure that grows several twisted stalks from a common base on medium, reminiscent of the legendary *Kraken*, in which a monster reaches out with many tentacles and attacks boats from the sea surface (Pontoppidan 1755, Denys de Montfort 1801). This is also the reason why the species is named.

Raperostelium krakenopsis Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 54, 55

MycoBank number: 854075; GenBank accession number: SSU: PP590211; PP590213; PP590216; PP590217. *Atp1*: PP932636; PP932637; PP932635.

Etymology – the name refers to the overall resemblance of this species to *Raperostelium kraken*.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary to gregarious, occasionally cluster with two sorocarps, erect to prone, 0.1−1.0 mm. Kraken structures present as a few sorocarps grow two sorophores on one common base and rarely grow three to four sorophores on one common base. Usually unbranched, sometimes with 1−3 branches near the base. Branches are 50−296 μm in length. Bases are clavate, conical, round, consisting of one to several tiers of cells, 6.6−19.8 μm in width, with the widest points of base terminals measuring 9.4−76.8 μm. Tips are acuminate, obtuse, capitate, consisting of one tier of cells, 1.2−5.8 μm in width, with the widest points of tip terminals measuring 1.5−7.1 μm. Sori are semi-hyaline, white, globose, 16−150 μm in diameter. Spores are broadly elliptical to oblong, sometimes reniform: broadly elliptical spores are 5.1−6.8 × 4.4−5.2 μm (length/width = 1.16−1.30); elliptical spores are 4.4−5.3 × 2.7−3.3 μm (length/width = 1.60−1.63); oval spores are 4.8−7.1 × 2.8−3.8 μm (length/width = 1.70−1.85); oblong spores are 6.7−7.7 × 3.5−3.8 μm (length/width = 1.91−2.01). All spores have polar granules. Aggregations are mounds. Pseudoplasmodia with stalks but do not migrate. Microcysts present, 3.9−4.7 µm in diameter. Round myxamoebae cells appearing near bases have been observed, 3.4−5.9 µm in diameter. This species belongs to the *Raperostelium* clade in 18S DNA.

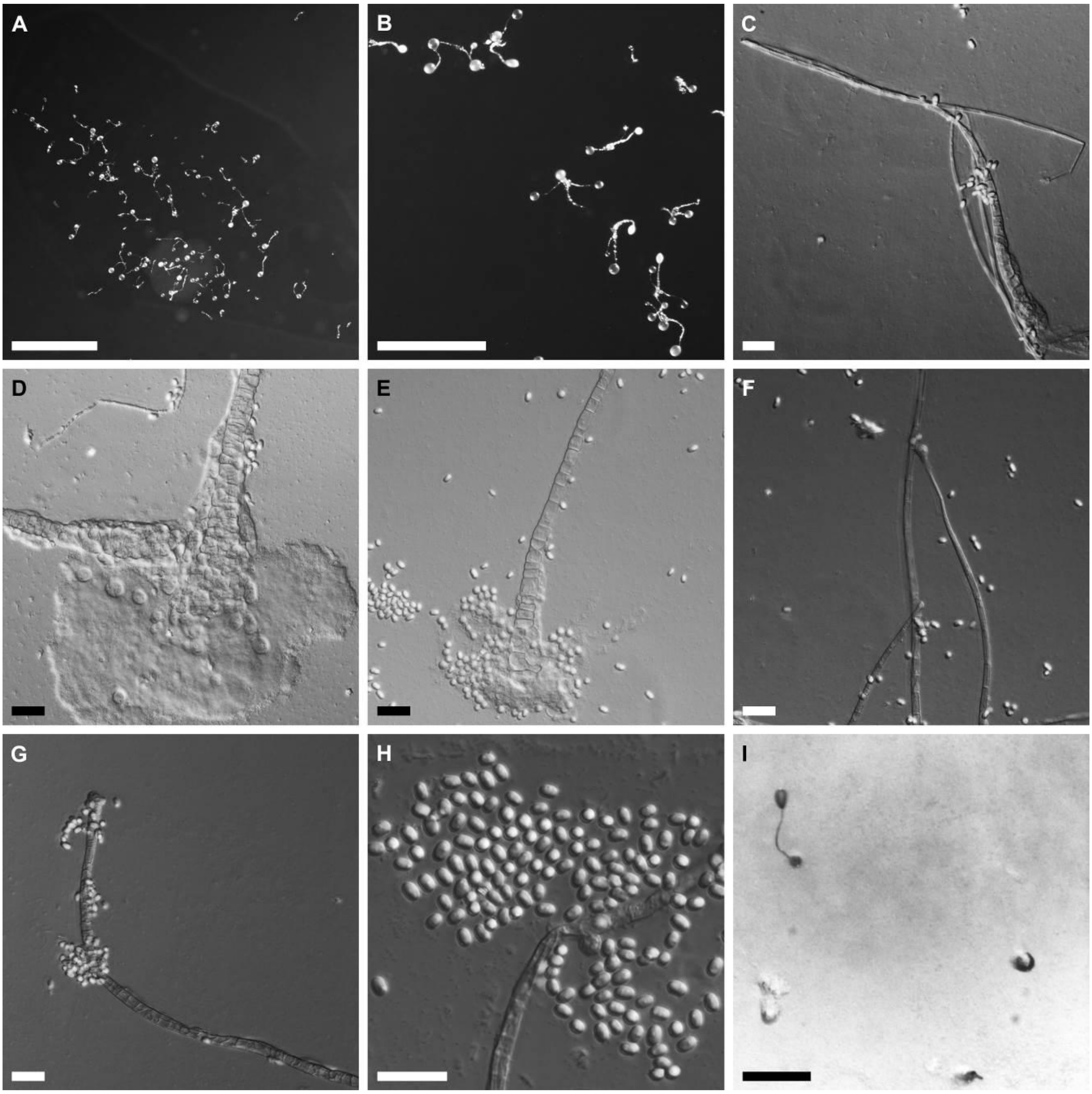

Figure 54 – Morphological features of *Raperostelium krakenopsis*. (**A**−**B**) Solitary to gregarious sorocarps with Kraken structures. (**C**) Whole sorophore. (**D**−**E**) Conical and round bases of the sorophores. Myxamoebae cells was appearing near bases in picture E. (**F**−**G**) Acuminate, obtuse and capitate tips of the sorophores. (**H**) Different shapes of spores with polar granules. (**I**) Mound aggregation and pseudoplasmodium with stalk. Scale bars: A = 2 mm; B = 1 mm; C−H = 20 µm; I = 200 µm.

Distribution and ecology – Isolated from the Beauty Pine Park near the Changbai Mountain National Nature Reserve, in mixed soil samples collected from a conifer forest at a low elevation (714−721 m) with an intermediate soil pH (pH = 6.03). Also isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1755−1828 m) with a low soil pH (pH = 5.32).

Material examined – China, Jilin Province: Beauty Pine Park near the Changbai Mountain National Nature Reserve, 42.44º N, 128.12º E, average elevation 717.3 m. Isolated from mixed soils, August 2019, *19zhenb3* (HOLOTYPE, voucher specimen code: HMJAU MR425); *19zhenb1*; *19zhend1*. Also isolated from mixed soils of Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1799.2 m, August 2019, *19yueb3*. Known only from Jilin Province, China.

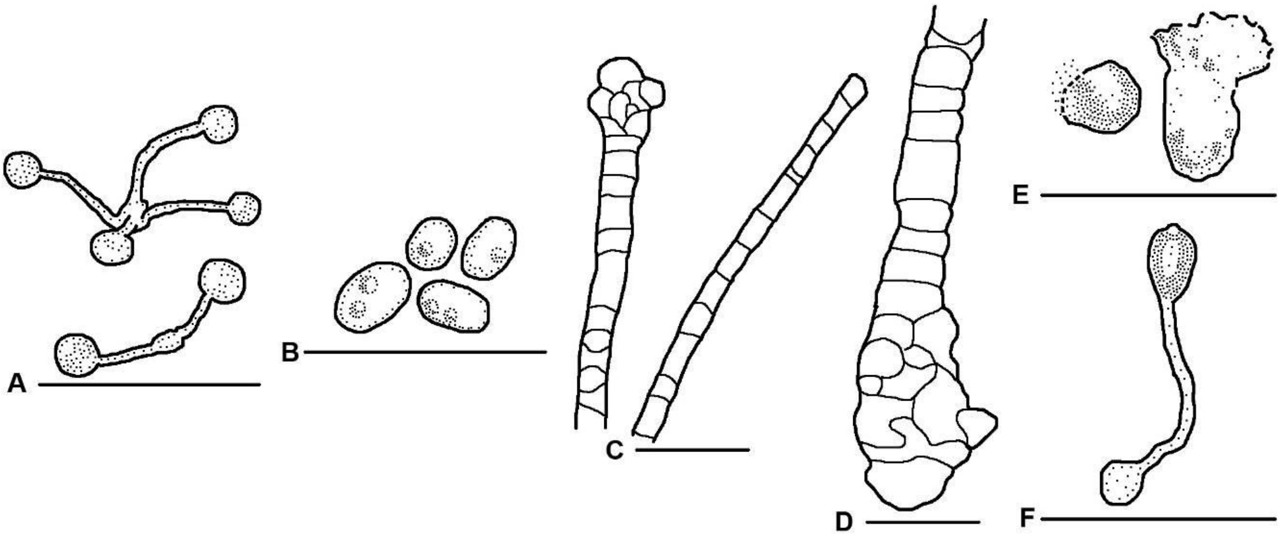

Figure 55 – *Raperostelium krakenopsis*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tips. (**D**) Base. (**E**) Aggregations. (**F**) Pseudoplasmodium. Scale bars: A = 0.5 mm; B−D = 20 μm; E−F = 0.2 mm.

Notes – This species has clustered with *Raperostelium kraken*, *Ra. minutum*, and *Ra. pusillum* in the same clade of the SSU phylogenetic tree, but in different clades of the *atp1* phylogenetic tree. In morphology, clustered sorocarps, the Kraken structure (two, or rarely three to four sorophores grown on one base), and polar granules make *Ra. krakenopsis* different from *Ra. minutum* (Raper 1941). Morphological distinctions between *Ra. krakenopsis* and *Ra. kraken* are also discussed in the commentary on *Ra. kraken*. Finally, the differences between *Ra. krakenopsis* and *Ra. pusillum* are in branches, sorophore number of Kraken structure, bases, and spore ratio. *Raperostelium krakenopsis* usually has no branches, sometimes has 1−3 branches near the base; *Ra. pusillum* has no or one branch. A few sorocarps of *Ra. krakenopsis* have two sorophores on one base, while rare sorocarps have three to four sorophores on one base, fewer than the infrequent sorocarps of *Ra. pusillum* with 4−9 sorophores on one base. *Raperostelium krakenopsis* has one to several tiers of base cells wide, while *Ra. pusillum* has one to two tiers of base cells wide; and the widest points of base terminals in *Ra. krakenopsis* (9.4−76.8 μm in width) are also wider than *Ra. pusillum* (4.5−29.1 μm in width). Lastly, spore ratio of *Ra. krakenopsis* (length/width = 1.16−2.01) is broader than of *Ra. pusillum* (length/width = 1.52−1.97).

In the *atp1* phylogenetic tree, *Raperostelium krakenopsis* clusters with *Ra. kraken* and *Ra. minutum* closer than *Ra. pusillum*. The Kraken structure and wider base terminals make this species very similar to *Ra. kraken*.

Raperostelium minutum (Raper) S. Baldauf, S. Sheikh & Thulin, Protist 169: 23 (2018)
Figs. 2, 3, 56, 57

Basionym. *Dictyostelium minutum* Raper, Mycologia 33: 634 (1941)

GenBank accession number: SSU: PP590212; PP832569. *Atp1*: PP932638; PP932639.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary or gregarious, erect to prone, 0.2−1.3 mm, sometimes with a few branches. Sorophores consist of one tier of cells in width, curved. Bases are clavate to conical, sometimes adhere slime, consisting of one tier of cells in width, 7.2−13.5 μm in width, with the widest points of base terminals measuring 8.1−21.7

µm. Tips are acuminate or a little capitate, consisting of one tier of cells in width, 2.6−5.5 µm in width, with the widest points of tip terminals measuring 2.0−7.0 µm. Sori are white, globose, 72−143 µm in diameter. Spores are oblong to elliptical, 4.5−7.2 × 2.3−4.3 µm (length/width = 1.32−2.40), with unobvious polar granules or without polar granules. Aggregation are mounds. Pseudoplasmodia migrate with stalks. Microcysts present, 3.2−4.5 µm in diameter. Irregular globose or subglobose macrocysts present near the bases, 10.3−12.9 × 9.3−12.8 µm. This species belongs to the *Raperostelium* clade in 18S DNA.

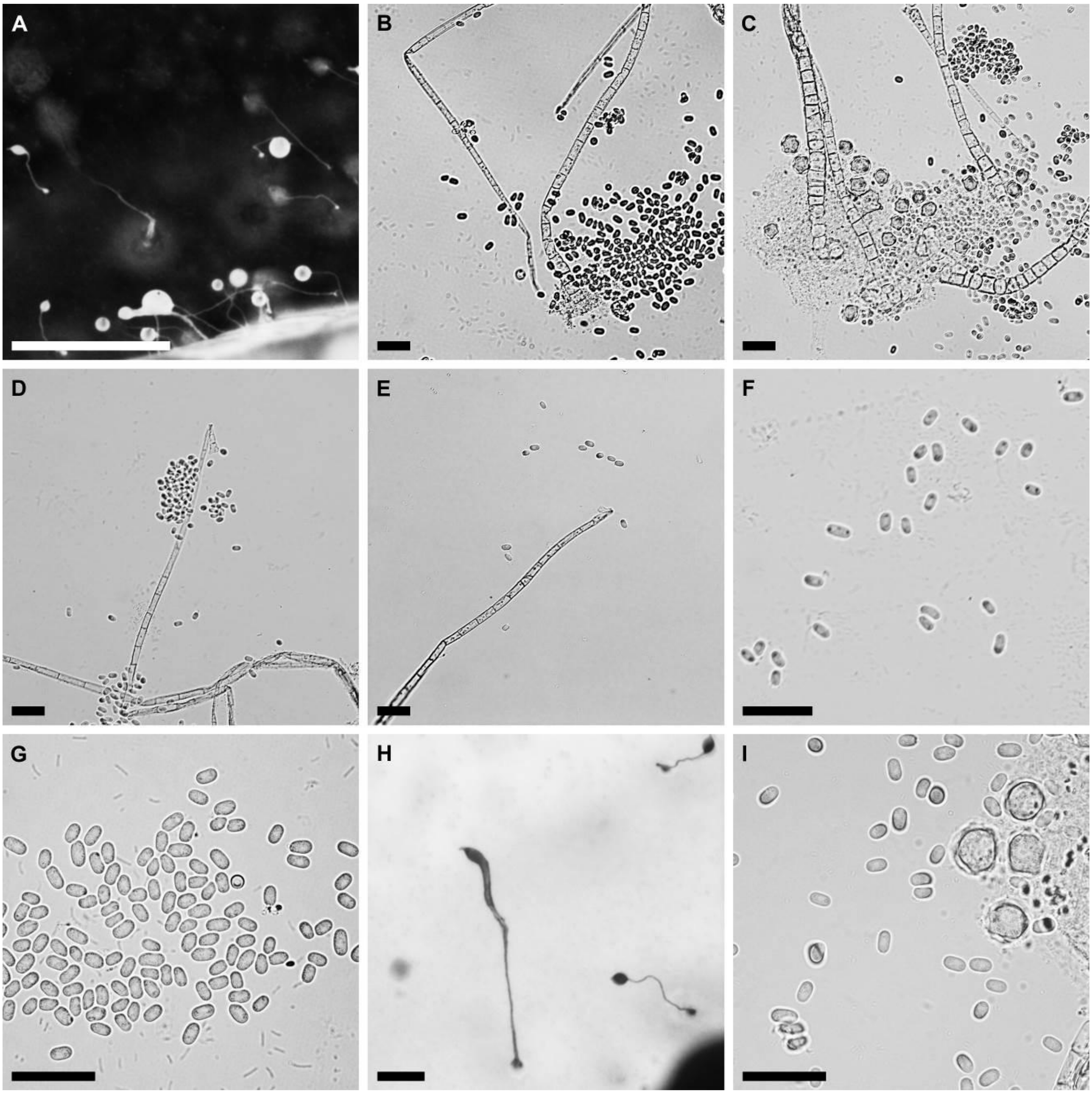

Figure 56 – Morphological features of *Raperostelium minutum*. (**A**) Erect to prone sorocarps. (**B**) Clavate base. (**C**) Base and macrocysts. (**D**−**E**) Acuminate or a little capitate tips. (**F**) Spores with unobvious polar granules. (**G**) Spores without polar granules under 100× magnification. (**H**) Pseudoplasmodium migrates with a stalk. (**I**) Macrocysts and spores under 100× magnification. Scale bars: A = 1 mm; B−G, I = 20 µm; H = 200 µm.

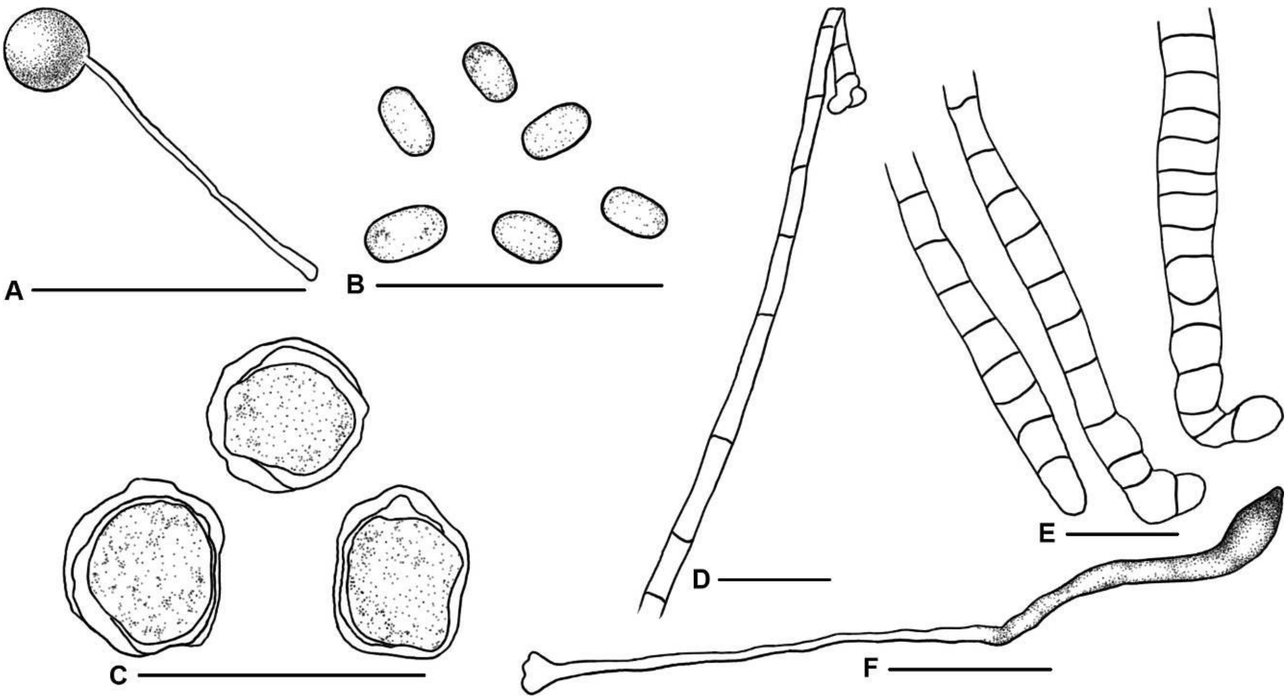

Figure 57 – *Raperostelium minutum*. (**A**) Sorocarp. (**B**) Spores. (**C**) Macrocysts. (**D**) Tip. (**E**) Bases. (**F**) Pseudoplasmodium. Scale bars: A = 0.5 mm; B−E = 20 μm; F = 0.2 mm.

Distribution and ecology – Isolated from the Northern Slope of the Changbai Mountain National Nature Reserve, in mixed soil samples collected from an alpine birch forest at an intermediate elevation (1821−1837 m) with an intermediate soil pH (pH = 6.03).

Material examined – China, Jilin Province: Northern Slope of the Changbai Mountain National Nature Reserve, 42.07º N, 128.07º E, average elevation 1829.1 m. Isolated from mixed soils, August 2018, *yue2-1*; *yue2-3*. This species is known from America, Canada, China, Germany, India, Italy, Japan, Kenya, Mexico, New Zealand, Nepal, Norway, Pakistan, Portugal, Puerto Rico, Russia, Spain, Sweden, Switzerland, Tanzania, Thailand, Uganda, Yugoslavia.

Notes – *Raperostelium minutum* is a species found worldwide (Cavender 1978, Traub et al. 1981b, Hagiwara 1989, Cavender et al. 1995, Stephenson et al. 1997, Stephenson et al. 1999, Swanson et al. 1999, Cavender et al. 2002, Romeralo & Lado 2006, 2008, Sathe et al. 2010, Cavender et al. 2012, Perrigo et al. 2013, Seephueak & Petcharat 2014, Liu et al. 2020). The isolates *yue2-1* and *yue2-3* had almost the same 18S rDNA sequences as *Ra. minutum*. The morphology of this species in this paper had narrower bases (7.2−13.5 μm in diameter) than those described for *Ra. minutum* (12−18 μm in diameter) in 1941 (Raper 1941), and branches of isolates *yue2-1* and *yue2-3* were also infrequent instead of frequently branched as described in 1941. However, the bases of *Ra. minutum* described in 1989 were 6.5−22.5 μm in diameter, and the branches were also described as unbranched or sparsely and irregularly branched in that paper, indicating that the morphology here is normal. More importantly, the frequent macrocysts and spores with unobvious polar granules or without polar granules identified the species as *Ra. minutum*.

Raperostelium pusillum Y. Li, P. Liu et Y. Zou, sp. nov. Figs. 2, 3, 58, 59

MycoBank number: 830539; GenBank accession number: SSU: PP590214; PP590215. *Atp1*: PP932640; PP932641.

Etymology – The name *pusillum* refers to the tiny sorocarps.

When cultured at 23°C on non-nutrient agar with *E. coli*, sorocarps are solitary, gregarious to clustered, erect to prone, 0.3−1.1 mm, unbranched or with one branch. Infrequent 4−9 sorophores share a common base. Sorophores consist of a single tier cell in width, slightly taper from bases to tips. Bases are clavate, round to conical, slightly expand, consisting of one to two tiers of cells, 5.1−17.6 μm in width, with the widest points of base terminals measuring 4.5−29.1 μm. Tips are acuminate or capitate, consisting of one tier cell, 2.4−6.3 μm in width, with the widest points of tip terminals measuring 1.2−8.6 μm. Sori are semi-hyaline, white, globose, 59−135 μm in diameter. Spores are elliptical to oblong, capsule-shaped, 4.8−8.2 × 2.8−4.7 μm (length/width = 1.52−1.97), with conspicuous polar granules. Aggregation are mounds. Pseudoplasmodia with stalks. This species belongs to the *Raperostelium* clade in 18S DNA.

Distribution and ecology – Isolated from the Beauty Pine Park near the Changbai Mountain National Nature Reserve, in mixed soil samples collected from a conifer forest at a low elevation (703−746 m) with an intermediate soil pH (pH = 6.51).

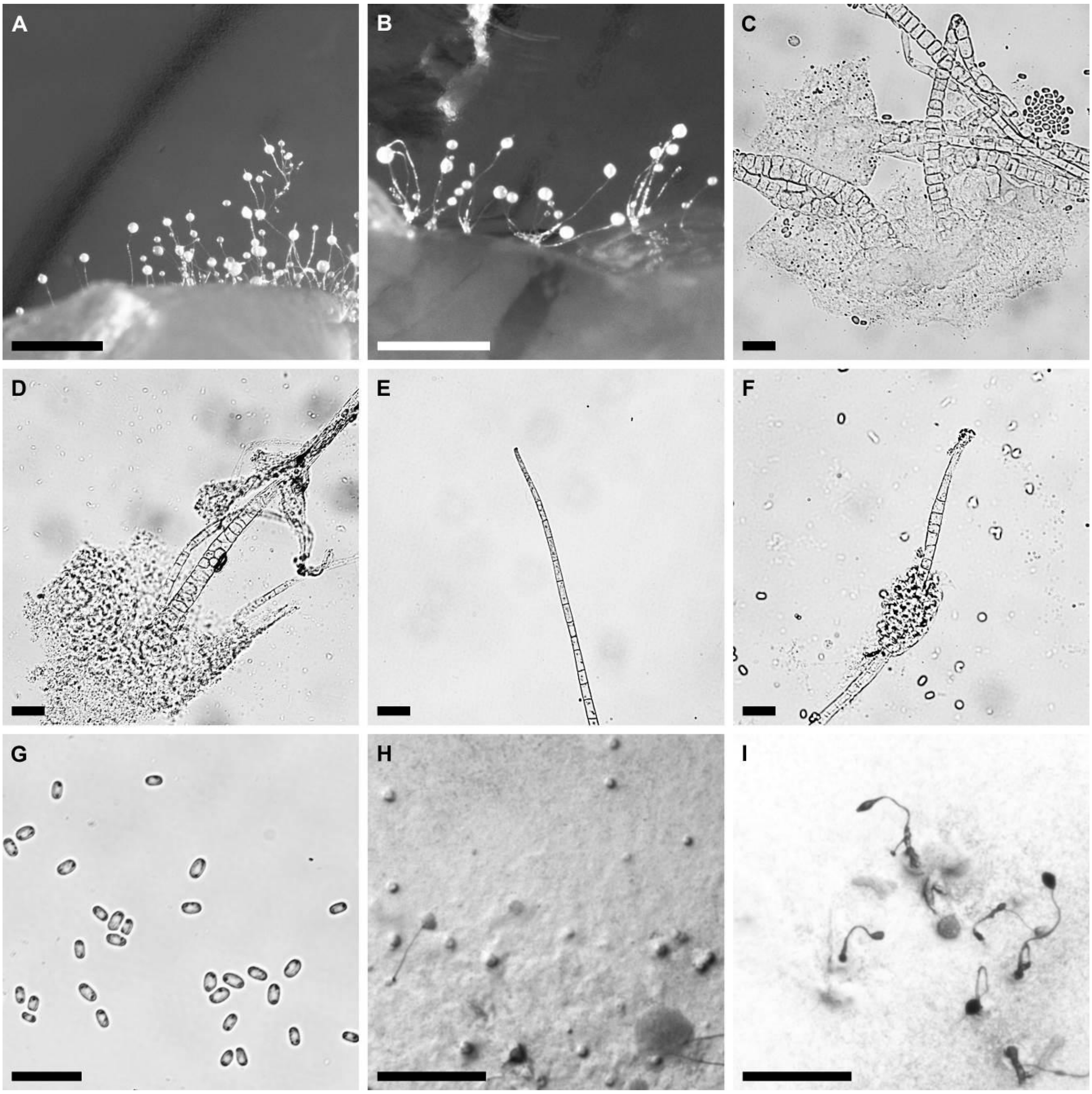

Figure 58 – Morphological features of *Raperostelium pusillum*. (**A**) Erect to prone sorocarps. (**B**) Sorocarps with several sorophores sharing a common base. (**C−D**) Clavate, round to conical bases. (**E−F**) Acuminate or capitate tips. (**G**) Spores with conspicuous polar granules. (**H**) Mound aggregations. (**I**) Migrating pseudoplasmodia with stalks. Scale bars: A−B = 1 mm; C−G = 20 μm; H−I = 0.5 mm.

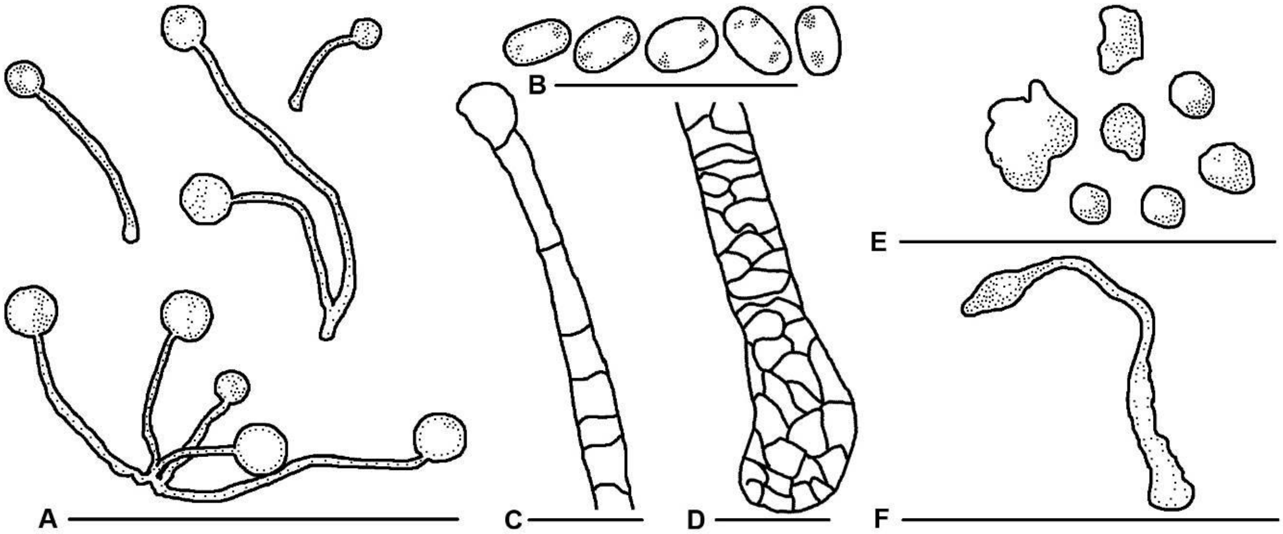

Figure 59 – *Raperostelium pusillum*. (**A**) Sorocarps. (**B**) Spores. (**C**) Tip. (**D**) Base. (**E**) Aggregations. (**F**) Pseudoplasmodium. Scale bars: A = 1 mm; B−D = 20 µm; E−F = 0.5 mm.

Material examined – China, Jilin Province: Beauty Pine Park near the Changbai Mountain National Nature Reserve, 42.44º N, 128.12º E, average elevation 724.3 m. Isolated from mixed soils, August 2018, *zhen1* (HOLOTYPE, voucher specimen code: HMJAU MR311); *zhen2*. Known only from Jilin Province, China.

Notes – *Raperostelium pusillum* has clustered with *Ra. kraken*, *Ra. krakenopsis*, and *Ra. minutum* in the same clade of the SSU phylogenetic tree, but in different clades of the *atp1* phylogenetic tree. Kraken structure (infrequent sorocarps with 4−9 sorophores share a common base), clustered sorocarps, and narrower spore ratio make *Ra. pusillum* different from *Ra. minutum*. The distinctions between *Ra. pusillum*, *Ra. kraken*, and *Ra. krakenopsis* are also discussed in the commentary on the latter two species.

In the *atp1* phylogenetic tree, *Raperostelium pusillum* is distinct far away from *Ra. kraken*, *Ra. krakenopsis*, and *Ra. minutum*. In morphology, the largest difference between *Ra. pusillum* and the latter three species is a narrower spore ratio. Spore ratio of *Ra. pusillum* is 1.52−1.97, of *Ra. kraken* is 1.00−2.33, of *Ra. krakenopsis* is 1.16−2.01, and of *Ra. minutum* in this study is 1.32−2.40. Difference of spore ratio in *Ra. pusillum* is only 0.45, smaller than 1.33 in *Ra. kraken*, 0.85 in *Ra. krakenopsis*, and 1.08 in *Ra. minutum*.

Key to dictyostelid species and varieties in this study

1. Sorocarps with whorled branches 2
1. Sorocarps lacking whorled branches 5
2. Sorocarps with panicle-like branching (repeated dichotomies and whorls) 3
2. Sorocarps without panicle-like branching 4
3. Repeated dichotomies and whorls ....*Polysphondylium paniculoides*
3. Branches predominantly whorled with fewer dichotomies than *P. paniculoides* ....
....*P. paniculoides* var. *multiverticillatum*
4. Sori purple; spores subglobose to oblong..*P. macroviolaceum*
4. Sori pink or light purple; spores elliptical to bacilliform ....*P. latiamplitudinisporum*
5. Sorocarps with "Kraken structure" 6
5. Sorocarps without "Kraken structure" 8
6. 2−13, rarely up to 21 sorophores per shared base; spores polymorphic (globose to oblong) ....
....*Raperostelium kraken*
6. ≤ 9 sorophores per shared base.. 7
7. Bases one to several tiers of cells wide ....*Ra. krakenopsis*

7. Bases one to two tiers of cells wide..*Ra. pusillum*
8. Sori light purple to dark brown 9
8. Sori white, or yellow to grayish olive, or cream color 14
9. Sorophores with pseudosessile sori 10
9. Sorophores without pseudosessile sori 12
10. Larger sori (121−621 µm); bases not covered slime sheath ....*Dictyostelium pseudosessile*
10. Smaller sori (47−293 µm); bases covered slime sheath 11
11. Sorophores with widen middle connections ....*D. rufopurpureum*
11. Sorophores without widening connections.............*D. rufopurpureum* var. *longioripseudosessile*
12. Spore ratio smaller (length/width = 1.47−2.37) ....*D. sinuatipurpureum*
12. Spore ratio larger (length/width = 1.78−2.86 or 1.80−4.03) 13
13. Sori dark purple to almost black............................*D. sinuatipurpureum* var. *corymbipurpureum*
13. Sori purpure .... *D. sinuatipurpureum* var. *subulibasipurpureum*
14. Macrocysts present ....*Ra. minutum*
14. Macrocysts absent.. 15
15. Spores with polar granules or subpolar granules 16
15. Spores without polar granules or subpolar granules.. 22
16. Sorophores with subpolar granules.. 17
16. Spores with polar granules... 18
17. Pseudoplasmodia migrate with continuous or discontinuous trails.................*D. collarimigratum*
17. Pseudoplasmodia not migrating or migrate only a short distance with stalks................................
....*D. collarimigratum* var. *breviorimigratum*
18. Sorocarps could up to 12.2 mm in length..*Cavenderia varicelloides*
18. Sorocarps < 6 mm in length.. 19
19. Bases wider, could up to 55.7 µm in width ....*Ca. bifurcatimacrosorum*
19. Bases < 35 µm in width 20
20. Spores ratio wider (length/width = 1.09−2.38)................................ *Ca. fasciculaticomplexispora*
20. Spores ratio narrower (1.28 ≤ length/width ≤ 2.19) 21
21. Tips acuminate with 2.1−5.2 µm in width...*Ca. inordinata*
21. Tips clavate, capitate, obtuse, or elongated cell, with 3.3−16.7 µm in width ....
....*Hagiwaraea conicibasis*
22. Bases with basal disks 23
22. Bases without basal disks 24
23. Sorocarps 0.5−8.7 mm length, rarely up to 10.9 mm .... *D. latiorifirmibasis*
23. Sorocarps < 4 mm length..*D. latiorifirmibasis* var. *minorifirmibasis*
24. Tips 4.1−6.6 µm in width, with the widest points of tip terminals measuring 3.7−7.8 µm............
....*D. majileptosomum*
24. Tip widths could up to 8.0 µm or more, with the widest tip terminals up to 18.8 µm or more.......
.... 25
25. Sorophores with nodule-like cells 26
25. Sorophores smooth that lack nodule-like cells 27
26. Spores highly polymorphic with longest spore 10.2 × 3.8 µm .... *D. diversisporum*
26. Spores could be exceptionally long (> 20 µm).....................*D. diversisporum* var. *maximisporum*
27. Spores ratio narrower (length/width = 1.00−2.27) ....*D. diversisporum* var. *brevisporum*
27. Spores ratio wider (length/width = 1.00−3.03)................*D. diversisporum* var. *laevisorophorum*

DISCUSSION

Coordinated field sampling for species in geographical areas and habitats along with more taxonomic revisions of species groups should enhance our understanding of any taxonomic group (Costello et al. 2013). This will improve our knowledge of related species and better protect biodiversity. Collecting dictyostelids from nature and revising details of their classification could improve our understanding of the taxonomy and provide more germplasm resources of this group.

The new species and new varieties have greatly enriched our knowledge of the dictyostelids. Prior to this study, 178 taxa of dictyostelids had been described worldwide, including 172 species and six varieties (www.indexfungorum.org, accessed on 01 January 2025). The new taxa isolated and identified in this study increased the total to 189 species and 15 varieties, representing an increase of nearly 15% compared to the total reported previously. Only 61 species and one variety of dictyostelids were previously known from China. In this study alone, the number of species and varieties has increased by nearly 42% of the total number recorded in China (Liu et al. 2020, Zhu et al. 2021, Zou et al. 2022, Zhang et al. 2023a, Zhang et al. 2023b, Zhang et al. 2024a, Zhang et al. 2024b). Study of these new species is important for a better understanding of protists, particularly dictyostelids, as it helps identify community composition patterns in China and provides a more complete understanding of the complexity of ecosystems, and thus is beneficial for protecting biodiversity from a microcosmic perspective (Enkhtur et al. 2021, Prosekov et al. 2022).

We also have clarified and defined the internal distinctions of the complex species *Dictyostelium purpureum*, which was found to encompass several hidden species that were not well defined, and separated two species and three varieties new to science from it (Mehdiabadi et al. 2009). Actually, morphological features of *D. purpureum* have been interpreted slightly differently as described by Raper (1984) and Hagiwara (1989) based on the original description of Olive (1901) (Olive 1901, Raper 1984, Hagiwara 1989). With the development of molecular biology, Mehdiabadi et al. (2009) showed that genetic variation and cryptic species occur within *D. purpureum* (Mehdiabadi et al. 2009). Since then, the problems have not been addressed properly, and many organisms that displayed differential genetic and morphological variation throughout the world were still classified into species or varieties of *D. purpureum* (Rollins et al. 2010, Stephenson & Landolt 2011, Yulo & dela Cruz 2012, Cavender & Cavender 2013, Vadell et al. 2018, Liu et al. 2019a, Liu et al. 2019c). After deliberate consideration, we defined to separate the organisms away from *D. purpureum* as new species and new varieties: *D. rufopurpureum*, *D. rufopurpureum* var. *longioripseudosessile*, *D. sinuatipurpureum*, *D. sinuatipurpureum* var. *corymbipurpureum*, and *D. sinuatipurpureum* var. *subulibasipurpureum* by morphological and phylogenetic distinctions, with *D. purpureum* sensu Raper (1984) corresponding to Olive's *D. purpureum* (Olive 1901, Raper 1984). We also corrected the concept of a species, *D. pseudosessile*, which was identified as the variety *Dictyostelium purpureum* var. *pseudosessile* before due to the cryptic species problem of *D. purpureum* (Liu et al. 2019a).

Actually, we considered separating *Dictyostelium purpureum* and those hidden species into a new genus distinct from the genus *Dictyostelium*. The reddish to purple sori, along with the colorful, long but sturdy sorophores, gave these organisms a high level of identifiability. Meanwhile, these organisms occupied a distinct clade that is parallel to and separated from other *Dictyostelium* species on the SSU phylogenetic tree (Fig. 2). However, the phylogenetic analysis of *atp1* could not distinguish *D. purpureum*, along with its hidden species, from other *Dictyostelium* species, unlike the SSU phylogeny (Fig. 3). The *atp1* sequence has been shown to complement the SSU sequence in identifying dictyostelids (Zou et al. 2022). This means that *D. purpureum* and the hidden species cannot be distinguished from *Dictyostelium* as a new genus.

Consistently, the descriptions of the color of dictyostelids were ambiguous. Phrases such as "grayish white to pale lemon yellow" or "present white to off-white with abundant slime at first…tend to become yellowish in age" made it difficult to distinguish between the similar colors (Raper 1935, Zou et al. 2022). For this, we suggested defining color determination in dictyostelids using ISCC-NBS color charts (Kelly 1964). ISCC-NBS color charts were widely used in the study of microbiology (Hoang et al. 2007, Tan et al. 2015, Liang et al. 2020). And the ISCC-NBS color charts could easily be found on the internet (Foster 2007). With a high color accuracy screen, photos of dictyostelids can be accurately compared to the ISCC-NBS color charts on a personal computer. It could reduce the subjective opinions of researchers on colors and be more effective in avoiding ambiguous descriptions about the color of dictyostelids; this approach has also been applied in the characteristic description of species on this paper.

Finally, we added some new characters of dictyostelids for identification purposes (the widest points of base and tip terminals, and ratio of spores), parenthetically, to differentiate species in more detail. In the meanwhile, we linked some spore shape descriptions with the spore ratio, referring to spores of Fungi and dictyostelids (Hagiwara 1989, Kirk et al. 2008). To be specific, these spore descriptions were specified as globose or spherical (length/width = 1.00−1.05), subglobose (length/width = 1.06−1.15), broadly elliptical (length/width = 1.16−1.30), elliptical (length/width = 1.31−1.65), oval (length/width = 1.66−1.90), oblong (length/width = 1.91−2.99), and bacilliform (ratio is more than 3.0). While other descriptions were merely of shapes, they include but are not limited to capsule-shaped (a common shape that resembles a capsule), reniform (also called fabiform, another common shape that is curved and resembles a human kidney), sigmoid (also called "S"-shaped, which curved like the letter "S"), long "S"-shaped (seems like a stretched sigmoid shape), V-shaped (seems like two capsule-shaped spores stick the ends together like the letter "V"), drop-shaped (which appears like a drop, that ratio as globose or subglobose but with one side pointed), pear-shaped (also called pyriform, with a ratio that is broadly elliptical or elliptical spore but one side is obviously narrower than another side), sunflower seed-shaped (seems like a sunflower seed or a stretched pear-shaped spore, but ratio larger as oval or longer spore), egg-shaped (with a ratio similar to an elliptical spore, but resembling a chicken egg), and fusiform (also called spindle-like, where the two sub-sides are obviously narrower than midpoint of spores).

With the developments in molecular biology technology, identification using DNA can be in much greater detail, and more species or genera have been published on since this approach became available (Sheikh et al. 2018, Perrigo et al. 2020, Cavender et al. 2022). SSU sequences were not able to provide all the necessary information for identification (Fontaneto 2011); *atp1* sequences complemented it and were further confirmed in our study. On the other hand, traditional morphology could also improve with digital techniques and more refined definitions. Meanwhile, the dictyostelids exhibited morphological distinctions despite having almost identical sequences, highlighting the importance of traditional morphology, such as the new varieties identified in this study. In addition, after nearly 40 years of studying history in China, many new species and new varieties discussed in this paper have been discovered, revealing that an abundant species diversity of dictyostelids was hidden within the vastness of this land.

Looking forward

Five species (*Dictyostelium culliculosum*, *D. longigracilis*, *D. macrosoriobrevipes*, *D. recurvibasicum*, and *Heterostelium recretum*) were found only in the Changbai Mountain National Nature Reserve or in the piedmont of Changbai Mountain in previous studies (He & Li 2008, Liu & Li 2017, Zou et al. 2022, Zhang et al. 2024a, Zhang et al. 2024b). Our integrative study reveals that Changbai Mountain harbors 18 endemic taxa of dictyostelids, including nine new species and four new varieties described herein. The 18 endemic dictyostelid taxa collectively account for nearly 9% of all dictyostelid taxa worldwide. This concentration of endemism—spanning two orders (Dictyosteliales and Acytosteliales), four families, and five genera—challenges the traditional paradigm that higher latitudes harbor lower dictyostelid diversity (Perrigo et al. 2013). Previous studies have shown that protist species that are rare or unique to a continent may be ecologically important and could be of conservation interest (Fontaneto 2011). To safeguard this unique biodiversity, we propose the following evidence-based strategies:

Microhabitat Protection Zone: Prioritize mid-elevation place (1550−1850 m), where 11 endemic taxa were identified, comprising 61% of the unique species of Changbai Mountain zone, according to our soil sampling data from mixed broadleaf/conifer forests and alpine birch forests.

IUCN Red List Assessments: Collaborate with the IUCN to develop standardized protocols for microbial eukaryote assessments, addressing current biases toward micro-organisms (IUCN 2025).

Community-Driven Monitoring: Train local rangers in standardized sampling protocols to track population trends of key dictyostelids. Integrate data into citizen science platforms, such as the Catalogue of Life (Bánki et al. 2025), to enhance public engagement and ensure long-term data sustainability.

Our polyphasic taxonomic workflow—combining morphometrics (three or more distinct morphological characteristics as criteria for a new species and one or two distinct morphological characteristics as criteria for a new variety), ISCC-NBS color quantification, and multi-locus phylogenetics (a unique phylogenetic clade for a new species)—provides a replicable model to accelerate microbial conservation efforts globally.

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DECLARATION ON CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

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