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# A new cryptic species of the fungal genus *Acrogenospora* (Dothideomycetes, Ascomycota) from Taiwan

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ABSTRACT: *Acrogenospora taiwanica*, found on dead terrestrial wood from Taiwan, is described as a new species based on low ITS and *RPB2* identities with other species. Although the internal transcribed spacer rDNA (ITS) sequence of this species is reproducible and sufficiently comparable to that of *A. thailandica*, the 3' end cannot be aligned with that of other species. Since these ITS sequences indicate unresolved, atypical features, and ITS sequences are lacking for several other molecularly characterized species, the ITS sequences in *Acrogenospora* are shown to have limited suitability for species barcoding and phylogenetic analyses. Morphologically, the species can hardly be distinguished from *A. sphaerocephala*, *A. terricola*, and *A. thailandica*. Since *Acrogenospora* species are known to sporulate only under terrestrial conditions, their reports from submersed wood seem due to a convenient collection and incubation strategy rather than a submersed aquatic life cycle. The case of *Acrogenospora* indicates that "freshwater fungi" include a high proportion of terrestrial fungi, as this term is broadly applied to fungi that are able to grow on submersed substrates low in oxygen but sporulate only under terrestrial conditions.

KEY WORDS: *Acrogenospora taiwanica*, annellidic, aquatic fungi, barcode, monoblastic, terrestrial fungi.

## INTRODUCTION

Saprobic dematiaceous hyphomycetes show high diversity on living and dead plants, particularly plant litter and decaying wood (Ellis, 1971; Hughes, 1978; Goh *et al*., 1998, 2024; Ou *et al*., 2024). Among them, species of the genus *Acrogenospora* M.B. Ellis (Ellis, 1971) were recorded and illustrated from dead wood as early as the 19th century (Berkeley and Broome, 1859, as *Monotospora sphaerocephala* Berk. & Broome). There is no doubt that the teleomorph was *Farlowiella* Sacc. (Bao *et al*., 2020). Most species form erect, unbranched, brown conidiophores with annellidic percurrent extensions and more or less spherical, dark brown, smooth, one-celled conidia at the apex (Goh *et al*., 1998; Bao *et al*., 2020).

Up to now, 24 species have been named in *Acrogenospora* (www.indexfungorum.org). Due to the lack of discrete morphological differences, separation of species is mainly based on distinct differences in DNA sequences (Bao *et al*., 2020; Harrington *et al*., 2022). Until 1998, specimens were collected from terrestrial substrates, whereas subsequent new species were described from collections of submersed substrates (Goh *et al*., 1998; Bao *et al*., 2020; Harrington *et al*., 2022). Because of this collection strategy, the fungi were considered as "freshwater fungi" (Calabon *et al*., 2020; Li *et al*., 2024). An exception was *A. terricola* A.H. Harr. & A.E. Arnold, which was isolated from seeds in soil (Harrington *et al*., 2022). Since the present definition of "freshwater fungi" includes both "indigenous" fungi that spend their entire life cycle in water and "immigrant" organisms that primarily inhabit terrestrial environments (Park, 1972), literature on *Acrogenospora* fungi was consulted to clarify whether these definitions may fit *Acrogenospora* species.

## MATERIAL AND METHODS

Two specimens were collected in a secondary forest in Taipei City, Taiwan, at a distance of approximately 1.5 km apart and with 200 m altitudinal difference and an interval of approximately four years. Both specimens were found on rotting wood, but only the second gathering was first subjected to a moist chamber cultivation method intended for detecting slime molds (Novozhilov *et al*., 2024), i.e., after gentle air-drying, the sample was submersed in distilled water overnight. The water was then decanted, and the substrate was kept moist and regularly monitored under a dissecting microscope for the presence of fungi. Conidia of both specimens were aseptically transferred from the tip of conidiophores with an acupuncture needle to corn meal agar plates with 0.2% chloramphenicol (CMA, HiMedia Laboratories Pvt. Ltd., India). A living strain was deposited in the Bioresource Collection & Research Center (BCRC) in Hsinchu City, Taiwan. For micromorphology, the methods in Yeh *et al*. (2023) were used. Specimens on rotting wood, as well as CMA plates with fungal colonies, were dried in an electrical dryer and deposited in the fungal collection of the National Museum of Natural Science, Taichung, Taiwan (TNM).

The methods of genomic DNA isolation, PCR amplification, and sequencing of the internal transcribed spacers (ITS) of the rRNA genes, the partial large ribosomal RNA gene (LSU), and the gene encoding the DNA-directed RNA polymerase II second largest subunit

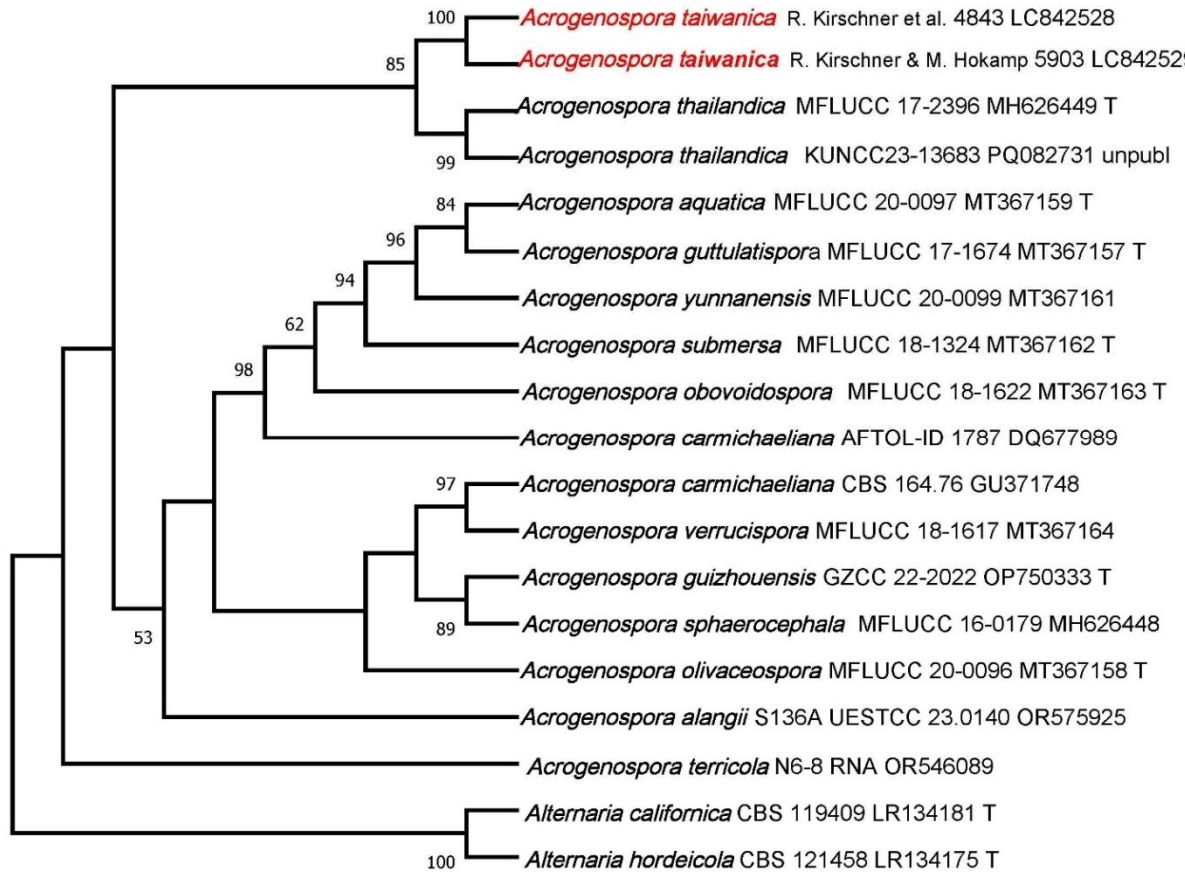


**Fig. 1.** Maximum likelihood tree of *RPB2* sequences of ***Acrogenospora*** species with ***Alternaria*** species as the outgroup with 1000 bootstrap replications (values < 50% not shown). The tree was not rooted. Voucher and GenBank accession numbers are given behind the species name. "T" indicates the ex-type strain. "Unpubl" refers to a sequence in GenBank without publication status.

(*RPB2*), as well as the alignments, were the same as in Yeh *et al*. (2023). The same primers were used for the PCR and the subsequent sequencing of the PCR products. PCR and sequencing of the ITS region were repeated in one strain. DNA sequences were uploaded in GenBank (rRNA gene regions) and the DNA Data Bank of Japan (*RPB2*).

For evaluating the nucleotide variations within and between species, DNA sequences were subjected to BLAST searches in GenBank. According to the results and by following publications on *Acrogenospora* (Bao *et al*., 2020; Harrington *et al*., 2022; Li *et al*., 2024), species and *RPB2* sequences were included in an alignment (for species and sequence accessions see Fig. 1). Two species of *Alternaria* were included as the outgroup. No manual manipulations were done within the final alignment of the *RPB2* dataset comprising 640 positions (deposited in Zenodo under 10.5281/zenodo.13981080). A Maximum Likelihood analysis was done for this dataset with the Kimura 2-parameter model with Gamma distribution and 1000 bootstrap replications in the MEGA X package (Kumar *et al*., 2018). The GC content of the ITS sequence of the *Acrogenospora* specimen R. Kirschner & M. Hokamp 5903 was calculated with Genomics %G~C Content Calculator (https://www.sciencebuddies.org/science-fair-projects/references/genomics-g-c-content-calculator).

For checking the potential distribution of the *Acrogenospora* species, we used the ITS sequence of specimen R. Kirschner & M. Hokamp 5903 in the BLAST function in Global Fungi (https://globalfungi.com).

## RESULTS

### DNA sequence comparison

Two specimens of *Acrogenospora* were found at two locations at a distance of approximately 1.5 km from each other in the years 2019 and 2023. The ITS sequences of one of our two strains (R. Kirschner *et al*. 4843) after two separate amplifications were identical and differed by 2 bp between both strains. No similar sequence was found in Global Fungi. The most similar sequence after BLAST searches using the ITS of R. Kirschner *et al*. 4843 (GenBank PQ323567) was an ex-type strain of *A. thailandica* Jing Yang & Hyde (503/546 bp; 92%; GenBank MH626449). The matching regions of strains of *A. terricola* and *A. carmichaeliana* (Berk.) Rossman & Crous were less than 400 bp long. Other identified *Acrogenospora* species were not shown in the 100 highest

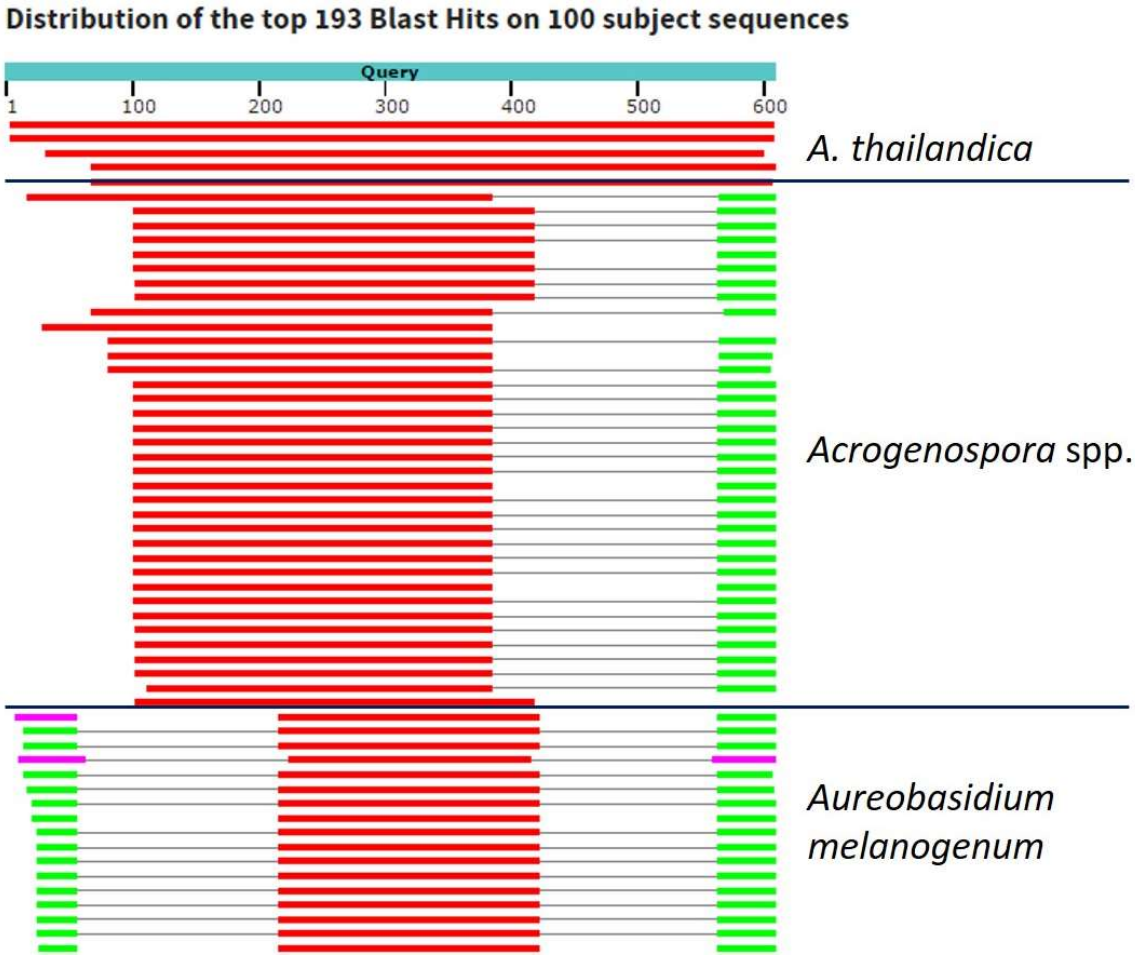


**Fig. 2.** Simplified example of a graphic summary showing a BLAST search with the ITS sequence of ***Acrogenospora taiwanica*** R. Kirschner *et al*. 4843 (GenBank PQ323567) arranged according to the maximum query cover (blast.ncbi.nlm.nih.gov; 16. Sept. 2024). The uppermost block indicates the fully alignable sequences of ***A. thailandica***, the second block includes sequences labeled as ***A. carmichaeliana***, ***A. terricola***, ***Acrogenospora*** sp., "Dothideomycetes sp.", and "Pezizomycetes sp.", which were not alignable along the approx. last 200 bp at the 3' end (presumably ITS2 region). Sequences of the lowermost block, predominantly containing ***Aureobasidium melanogenum*** and ***Aureobasidium*** sp., were alignable only in the central region (presumable 5.8S rDNA).

matches of BLAST results, but instead species of *Aureobasidium*. In the graphical summary of the BLAST results, the other sequences could not be aligned at the 3' end, which may correspond to the ITS2 region (Fig. 2). The GC content of the ITS sequence of R. Kirschner & M. Hokamp 5903 was 50.7%. For several species, such as the seven new species described by Bao *et al*. (2020), no ITS but *RPB2* sequences were available. A BLAST search with the LSU sequence PQ323569 yielded 97% (546/561 bp) identity with that of the ex-type strain of *A. thailandica*. Sequences of the LSU barcode were alignable for phylogenetic analysis, but in the majority of species, only *RPB2* sequences allowed recognition of well-supported clades. The *RPB2* sequences of the two Taiwanese strains were 100% identical to each other and had 95% identity with those of *A. thailandica*, whereas the identity was 93% or lower for the other species.

In the ML analysis of *RPB2* sequences (Fig. 1), *A. thailandica* and the new species named below as *A. taiwanica* formed a strongly supported subclade within *Acrogenospora*. The two sequences of *A. taiwanica* clustered together and sister to the two sequences of *A. thailandica*. In *A. thailandica*, two *RPB2* sequences (ca. 1000 bp) differed from each other by 6 bp, while the two species differed by ca. 100 bp in their *RPB2* sequences. Morphologically, both species showed minor differences in conidiophore lengths.

## TAXONOMIC TREATMENTS

***Acrogenospora taiwanica*** R. Kirschner, ***sp. nov.***

**Fig. 3**

Index Fungorum: IF903226

***Description*:** Based on R. Kirschner & M. Hokamp 5903 in culture on CMA, unless indicated otherwise. Colonies on CMA 6–8 mm (mean 7 mm, n = 3) in diameter after 3 weeks, cream, flat, with dense or scattered dark brown hyphae at the center, after 3–4

months becoming dark brown and strongly hairy due to numerous conidiophores.

Vegetative hyphae hyaline, smooth, 1–3 µm wide, becoming pale to dark brown and monilioid around the conidiophore bases, swollen up to 6 µm, occasionally verrucose. Conidiophores densely filling the Petri dish, arising singly or occasionally in pairs from the same base, in most cases forming a foot with the shape of a reversed T, with a horizontal base that is intercalary in the supporting hypha, 12–42 µm long, 3–8 µm thick, with the stipe arising from the middle or margin of the horizontal base, with the first septum raised above the horizontal foot, sometimes with the conidiophore stipe directly arising from undifferentiated vegetative hypha; stipe cylindrical, unbranched, erect, dark brown, paler to the apex, smooth, 6–8 µm wide at the base, gradually narrowing to the apex, 4–5 µm, (180–)390–680(–850) µm long (n = 30), (on the natural substrate up to ca. 660 µm long; in R. Kirschner *et al*. 4843 up to ca. 420 µm long), with septa 13–32 µm apart, and percurrent extensions scattered along the stipe above the very base indicating the intercalary and terminal position of the conidiogenous cells. Terminal conidiogenous cell apically paler than its base or the subterminal cell, with 0–2 percurrent extensions. Conidia solitary, globose, dark brown (black and shiny under the dissecting microscope), smooth, with densely guttulate cytoplasm, with a wall 3.5–4.5 µm thick (in dried natural substrate mounted in water 3–5 µm; in dried culture of R. Kirschner *et al*. 4843: 3–6 µm in water), (19–)21.5–25 µm ($\bar{x}$ = 23 µm; n = 30) in diameter or 1 µm shorter than wide [from dried natural substrate in water mounting (20–)22–25(–26) µm ($\bar{x}$ = 23 µm; n = 30); in water mounting of dried culture of R. Kirschner *et al*. 4843: (19–)21–25(–26) µm ($\bar{x}$ = 23 µm; n = 30)]; basal hilum dark brown (contrasting against the not fully pigmented wall of young conidia), less than 1 µm thick, and 4–5 µm diam.

***Specimens examined*:** On rotting wood, Taiwan, Taipei City, ca. 25.154485 N, 121.547980 E, ca. 500 m, 17. Nov. 2019, *R. Kirschner, J.P. Abe & K. Fujii 4843* (TNM), dried culture *R. Kirschner, J.P. Abe & K. Fujii 4843-B*, living strain BCRC FU3153, DNA sequences GenBank ITS PQ323567, LSU PQ323569, *RPB2* LC842528; Taipei City, Yang Ming Shan, Qixing Mountain, 25.163472 N, 121.552222 E, ca. 744 m, 25. Aug. 2023, *R. Kirschner & M. Hokamp 5903* (TNM, **holotype**), dried culture *R. Kirschner & M. Hokamp 5903-B* (TNM), DNA sequences GenBank ITS PQ323568, *RPB2* LC842529.

## DISCUSSION

### ITS in *Acrogenospora* is not recommended for barcoding and phylogenetics

The present new species can hardly be morphologically distinguished from other *Acrogenospora* species with globose conidia, such as *A. sphaerocephala* (Berk. & Broome) M.B. Ellis, *A. thailandica*, and *A. terricola* (Harrington *et al*., 2022). The two sequences of *A. carmichaeliana* in GenBank form different lineages and belong to different species. The low ITS sequence identities (92%) and the 5% deviation in *RPB2* sequences between *A. taiwanica* and *A. thailandica* are considered to be interspecific variation. The ITS sequences of *A. taiwanica* and *A. thailandica* show strong deviation in the ITS2 region compared to other species, which precludes the usage of their ITS for phylogenetic analyses. Even for molecular species identification with BLAST and similar methods, the ITS region is limited as a species barcode because Bao *et al*. (2020) did not provide ITS sequences for their seven newly described species and did not comment on the reasons of this omission in their study. In BLAST searches, since the last ca. 200 positions of ITS sequences of *A. taiwanica* and *A. thailandica* are not alignable with those of other *Acrogenospora* species (Fig. 2) or further fungi, the ITS region should not be used for phylogenetic estimates in this genus. Although the atypical ITS sequence of *A. thailandica* was mentioned by Harrington *et al*. (2022), it was nevertheless used without comment in subsequent phylogenetic analyses (Li *et al*., 2024). The paradox that a DNA sequence works as a barcode but is not applicable for phylogenetic analyses has also been found in the basidiomycete *Quasiramularia phakopsoricola* I-Chin Wei & R. Kirschner (Kolařík *et al*., 2021; Kirschner *et al*., 2023). Since the GC content of 50.7% was balanced and not particularly low, we cannot resolve the nature of the "irregularity" of the ITS sequence as expressed in the BLAST graphic summary (Fig. 2). Since this low alignability was reproduced within the same strain and among different strains, it is not a genetic chimera. Clarification of this deviation from typical fungal ITS sequences would be helpful to further reduce the over-reliance of mycologists on this "universal" fungal barcode.

### What are morphologically reliable diagnostic characteristics?

Our measurements of *A. taiwanica* from the sparse material on the natural substrate, compared with those from abundant material in culture, as well as in living and dried conditions, showed that the range of conidium size and color appeared stable, but conidiophore length was highly variable. In all measurements, the conidia of *A. taiwanica* did not exceed 26 µm in width, which may be the single morphological difference from *A. sphaerocephala*, whose conidia are up to 30 or 33 µm in diameter (Ellis, 1971; Hughes, 1978).

Yang *et al*. (2019) proposed *A. thailandica* based on DNA sequence analysis and longer conidiophores, i.e., with lengths of 850–950 µm in *A. thailandica* compared with 155–360 µm length in *A. sphaerocephala*. Hughes (1978) identified specimens from New Zealand as *A. sphaerocephala* with conidiophore lengths reaching up to 720 µm. Conidiophore lengths of *A. taiwanica* were of a similar broad range as in *A. sphaerocephala* (Hughes, 1978); but they could become much longer in culture compared with the conidiophores on the natural substrate.

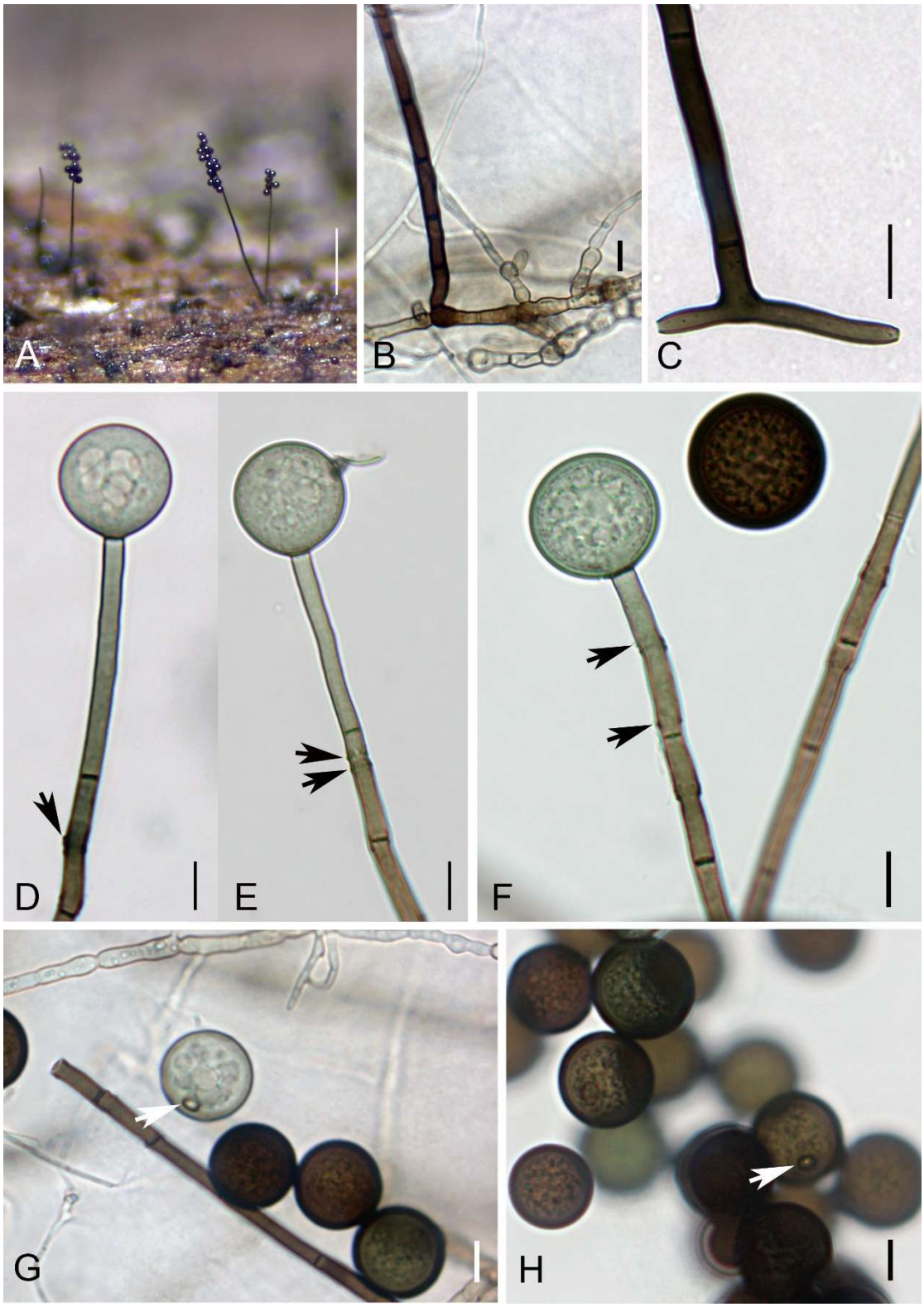


**Fig. 3.** Morphological characteristics of ***Acrogenospora taiwanica*** (*R. Kirschner & M. Hokamp 5903*, except **C**. *R. Kirschner et al. 4843*) on CMA, except A. **A.** Conidiophores on the natural substrate. **B.** Conidiophore base and hyphae. **C.** Foot-like conidiophore base. **D, E.** Apical conidiogenous cells without percurrent extensions; percurrent extensions in the subterminal cell (arrows). **F.** Conidiogenous cell with percurrent extensions (arrows). **G, H.** Detached conidia in different tinges of brown, with visible cytoplasmic content, slightly protruding darkened hilum indicated by arrow in the young, pale conidium (G) and mature conidium (H). Scale bars A = 200 µm, B–H = 10 µm.

The maximum length in culture was identical to the minimum length of *A. thailandica* on the natural substrate (Yang *et al*., 2018). Although most of the recently newly described species were cultivated, no information about sporulation in culture was provided (Yang *et al*., 2018; Bao *et al*., 2020; Li *et al*., 2024). An exception was the description of *A. terricola* from culture on malt extract agar with sterilized pine needles (Harrington *et al*., 2022). We do not know whether abundant sporulation in our specimens on CMA is specific to *A. taiwanica*. Whether conidiophore length is a good marker in a genus characterized by repeated percurrent conidiophore extensions, particularly when only a single specimen is available, seems questionable.

Although different shades of brown can be seen in conidia from the same microscopic slide (Fig. 3), comparison of living material from culture with that from dried material from culture and natural substrate mounted in water all showed the same tinge of brown at maturity with similar thickness in the semitransparent cell wall, and still discernible granular cytoplasmic content. This is the single morphological difference from *A. terricola*, with strongly opaque conidium walls (Harrington *et al*., 2022). Diverse tinges of brown described by different authors (Bao *et al*., 2020), however, may also depend on the age of the specimen, light intensity and color of the microscope, or subjective perception of the observer and should not be overstressed as major characteristics for taxonomic purposes (Li *et al*., 2024).

Our finding of a further cryptic species in *Acrogenospora* supports the suggestion of a much higher diversity in this genus than previously anticipated and that *A. sphaerocephala*, as identified in the past, may comprise different cryptic species (Bao *et al*., 2020).

**Terminology for conidiogenesis**

Annellidic conidium ontogeny in *Acrogenospora* was considered enteroblastic by some authors (Cole and Samson, 1979; Seifert *et al*., 2011), but holoblastic by others (Ellis, 1971) or both (Minter *et al*., 1982). The percurrent extensions do not only occur in a single conidiogenous cell, which gives rise to conidia whose outer cell wall layer extends from the inner cell wall layer of the conidiogenous cell, i.e. enteroblastically formed conidia (Hawksworth *et al*., 1995), but also at such long distances along the conidiophore that a new septum is formed distally to the percurrent extension, and the newly delimited distal cell is formed holoblastically. Since all cell wall layers of this conidiogenous cell are involved in conidium production, this conidium is holoblastically formed. This pattern was described and illustrated in detail for *A. sphaerocephala* by Minter *et al*. (1982). They used this example to illustrate that applying the terms "holoblastic" and "enteroblastic" for conidiogenesis merely refers to two extremes which are connected by intergrading processes. As Minter *et al*. (1982) concluded, generalizing the separate steps of conidiogenesis under either of these terms was imprecise and led to confusion. Since "percurrent proliferation/extension" and "annellidic" are sufficiently descriptive terms without the need to define the cell layer that is involved in conidium development, Goh *et al*. (1998) and Harrington *et al*. (2022) correctly used only these terms in *Acrogenospora* and avoided the term "holoblastic" in this genus.

**Are most "freshwater fungi" hypoxia-tolerant terrestrial fungi?**

Several species of *Acrogenospora* were first characterized from terrestrial habitats until Goh *et al*. (1998). Subsequently, they were predominantly found on submersed wood (Goh *et al*., 1998; Bao *et al*., 2020; Li *et al*., 2024), with the exception of *A. terricola* (Harrington *et al*., 2022). Sridhar *et al*. (2010), however, clearly distinguished between damp chamber incubation of samples collected from freshwater habitats for up to 6 months with sporulation under terrestrial conditions, and aquatic bubble chamber incubation with trapping of conidia from aquatic sporulation. A species identified as *A. sphaerocephala* exclusively belonged to the group of damp chamber incubation, where the fungus was the second most common species among their collections. The same fungus was also identified as one of the most common species on submersed wood in damp chamber incubation in the Philippines (Cai *et al*., 2003). In these two ecological studies, the species were morphologically identified as *A. sphaerocephala*, but this may also include other, morphologically similar species such as *A. thailandica* (Bao *et al*., 2020). The habitat of these *Acrogenospora* specimens, according to both studies, is terrestrial with respect to sporulation, and aquatic merely by the ability of the mycelium to survive under submersed conditions. This ability may help litter fungi to survive periods of inundation after rainfall. Fungi present in terrestrial litter as spores or hyphae may also survive when the litter becomes submersed in permanent water bodies (Park, 1972). Such litter is collected while sampling for "freshwater fungi" and incubated in moist-chambers, i.e., under terrestrial conditions in order to allow the fungi to grow out and sporulate. In detecting fungi from submersed litter, therefore, this substrate does not indicate the major natural habitat of the sporulating stage but rather an ingenious and convenient sampling strategy of the researchers, which saves them the time of washing and soaking terrestrial litter in water before incubation (Barbosa *et al*., 2024). The absence of common mold genera (e.g. *Aspergillus*, *Penicillium*) in the records of "freshwater fungi" may be based on natural washing off of nutrients and conidia as well as limited nutrient availability in the lignocellulosic substrate. This, together with oxygen depletion, may further limit the survival of fungi on submersed substrates. Whether the fungi merely tolerate submersion in water or also

sporulate under aquatic conditions, however, is often not discriminated in the literature. The present terms "freshwater fungi" or "aquatic fungi" include all submersion-tolerant fungi in a very broad definition. Tolerance to submersion in water is correlated with low oxygen content, i.e., hypoxia-tolerance (Metzler *et al*., 1993). It is easier to find examples of fungi that could weakly tolerate submersion, e.g., typical wood decay Basidiomycota (Malan, 2004) and powdery mildews (Erysiphaceae; Blumer, 1967), than to enumerate all fungi which can be found in freshwater habitats without discrimination between "native" and "immigrant" species (Calabon *et al*., 2020). In the case of *Acrogenospora*, it could be assumed that at least in dematiaceous hyphomycetes collected from freshwater samples, the proportion of truly aquatic fungi e.g. "native" (Park, 1972) may be small compared to "immigrant" terrestrial species.

## ACKNOWLEDGMENTS

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