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Pleurodesmospora acaricola sp. nov. and a new record of *Pleurodesmospora coccorum* (Cordycipitaceae, Ascomycota) in Taiwan

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ABSTRACT: *Pleurodesmospora* is an anamorphic genus with two known species recorded mainly on chitinous substrates such as insects, mites, spiders, and foliicolous fungi in tropical and subtropical areas. A further fungus with similar morphology of conidiophores and conidiogenous cells was found on a dead mite on a living fern (*Angiopteris lygodiifolia*). Isolated in culture, this fungus produced white dusty colonies. Morphologically, the new strain from the mite differs from the two known *Pleurodesmospora* species by non-catenate conidia and chlamydospores and is, therefore, proposed as new species. The tea whitefly, *Aleurocanthus camelliae*, was found as new host of *Pleurodesmospora coccorum* in Taiwan. The ITS sequences of these isolates are similar to those of other *Pleurodesmospora* strains. A phylogenetic analysis of a combined ITS and TEF sequence dataset indicates the presence of cryptic species in *Pleurodesmospora*.

KEY WORDS: Acari, *Camellia sinensis*, *Engyodontium*, Hypocreomycetidae, *Pleurodesmospora acaricola*.

INTRODUCTION

Pleurodesmospora was introduced by Samson *et al.* (1980) based *P. coccorum* (Petch) Samson, W. Gams & H.C. Evans for hyaline hyphomycetes with sparsely branched macronematous conidiophores, conidiogenous pegs arranged along apical and intercalary conidiogenous cells and catenate conidia. The species has been recorded mainly on chitinous substrates such as insects, mites and foliicolous fungi in tropical and subtropical areas. This species was successfully tested for potential biological control against a coccid pest insect on macadamia trees and a whitefly on tea trees (Gutierrez-Coarite *et al.*, 2018; Han and Li, 1992). In published phylogenetic relationships based on DNA data (Seifert *et al.*, 2011: "Clavicipitaceae"; Summerbell *et al.*, 2011: Cordycipitaceae, Sung *et al.*, 2001), the genus and species was placed in close relationship with *Beauveria* and *Cordyceps* s. str. of the Cordycipitaceae, Hypocreales. In spite of these data, the genus has hitherto been considered *incertae sedis* among the hyphal Ascomycota in the biodiversity and mycological nomenclatural repositories (e.g. www.indexfungorum.org), until Chen *et al.* (2021) confirmed the placement of *Pleurodesmospora* in the Cordycipitaceae. A species with similar morphology of conidiophores and conidiogenous cells, but with non-catenate conidia, was found on a dead mite on a living fern in Taiwan. The ITS sequence of this isolate was most similar to sequences of *P. coccorum*. Because of the morphological similarity of the new species with *Engyodontium* spp., species of this genus also were included in the phylogenetic hypotheses.

MATERIALS AND METHODS

Specimens

Specimens were collected on black whitefly nymphs on living tea leaves in central Taiwan and on a dead mite on a fern leaf in northern Taiwan. Cultures were made by transferring conidia under a dissecting microscope from the dead arthropods to corn meal agar (CMA, HiMedia Laboratories Pvt. Ltd., India) complemented with 0.2% chloramphenicol. For the fungus on the mite, material from the natural substrate was preserved as permanent slide with a polyvinyl-lactophenol-cotton blue mounting (Kirschner and Chen, 2008) and as dried cultures on CMA. Original specimens on tea whiteflies were preserved by drying on an electrical dryer. The specimens were deposited in the National Museum of Natural Science, Taichung, Taiwan (TNM). A living culture of the mite-associated fungus was deposited in the Bioresource Collection & Research Center (= BCRC, Hsinchu, Taiwan).

Microscopy

For light microscopy, fresh specimens from field collections and cultures were mounted in 10% KOH. Sizes of cells were measured at 1000× magnification with an Olympus light microscope with bright field and phase contrast and given as mean value ± standard deviation of n measurements with extreme values in brackets or only as minimum and maximum values. Photographs were made with Olympus EP50 cameras, drawings were made free-hand on scaled paper. Cultivated material on CMA was processed directly for scanning electron microscopy (SEM) without chemical fixation, but in some samples

Table 1. Species, strains and sequences as used in this study. Scientific names were checked with Index Fungorum; for names as applied in GenBank see footnotes a–g. [T] in the first column (species) indicates type species of the genus, in the second column (strain), [T] indicates sequences being derived from typified material. Strain and sequence numbers were taken from GenBank. New data are indicated in bold.

Species	Strain	ITS	TEF
Acanthomyces aculeatus Lebert [T]	HUA 772	KC519371	KC519366
Akanthomyces tuberculatus (Lebert) Spatafora *et al*.	OSC 111002	JN049830[a]	DQ522338[a]
Beauveria brongniartii (Sacc.) Petch	BCC 16585	JN049867	JF416009
Beauveria caledonica Bissett & Widden	ARSEF 2567 [T]	HQ880817	EF469057
Beauveria scarabaeidicola (Kobayasi) S.A. Rehner & Kepler	ARSEF 5689	JN049827[b]	DQ522335[b]
Blackwellomyces cardinalis (G.H. Sung & Spatafora) Spatafora *et al.*	OSC 93610	JN049843[c]	EF469059[c]
Cordyceps militaris (L.) Fr. [T]	OSC 93623	JN049825	DQ522332
Engyodontium aranearum (Cavara) W. Gams *et al*.	CBS 309.85	AJ292391	DQ522341[d]
Engyodontium parvisporum (Petch) de Hoog [T]	IHEM 22910	LC092896	LC425558
Engyodontium rectidentatum (Matsush.) W. Gams *et al*.	CBS 547.82	LC092894	LC425544
Gibellula gamsii Kuephadungphan *et al*.	BCC 25798	MH152532	MH152563
Gibellula gamsii Kuephadungphan *et al*.	BCC 27968 [T]	MH152529	MH152560
Hevansia nelumboides (Kobayasi & Shimizu) Luangsa-ard *et al*.	BCC 41864	JN201871[e]	JN201867[e]
Hevansia novoguineensis (Samson & B.L. Brady) Luangsa-ard *et al*. [T]	CBS 610.80 [T]	MH532831	MH521885
Lecanicillium antillanum (R.F. Castañeda & G.R.W. Arnold) Zare & W. Gams	CBS 350.85 [T]	MH861888	DQ522350
Pleurodesmospora sp.	64-10W = F424	AF317541[f]	-
Lecanicillium psalliotae (Treschew) Zare & W. Gams	CBS 532.81	JN049846	EF469067
Pleurodesmospora sp.	ICMP 20146	MF683460[g]	-
***Pleurodesmospora acaricola* R. Kirschner**	**R. Kirschner 4968 [T]**	**MZ435417**	**LC629776**
Pleurodesmospora coccorum (Petch) Samson *et al*. [T]	CBS 458.73	MH860741	-
Pleurodesmospora coccorum (Petch) Samson *et al*. [T]	CBS 459.73	MH860742	-
Pleurodesmospora coccorum (Petch) Samson *et al*. [T]	CBS 460.73	MH860743	-
Pleurodesmospora coccorum (Petch) Samson *et al*. [T]	E1MFC	MF581039	-
***Pleurodesmospora coccorum* (Petch) Samson *et al*.** [T]	**R. Kirschner 5151**	**MZ435418**	**LC629777**
Pleurodesmospora lepidopterorum W.H. Chen *et al*.	DY 10501 [T]	MW826576	MW834317
Pleurodesmospora lepidopterorum W.H. Chen *et al*.	DY 10502	MW826577	MW834319
Purpureocillium lavendulum Perdomo *et al*.	FMR 10376	FR734106	FR775516
Purpureocillium lilacinum (Thom) Luangsa-ard *et al*. [T]	G 406	KJ443246	KJ443202
Samsoniella aurantia Mongkols. *et al*.	TBRC 7271 [T]	MF140764	MF140846
Samsoniella aurantia Mongkols. *et al*.	TBRC 7272	MF140763	MF140845

a in GenBank as *Cordyceps tuberculata;* b in GenBank as *Cordyceps scarabaeicola* sic!; c in GenBank as *Cordyceps cardinalis;* d in GenBank as *Lecanicillium tenuipes;* e in GenBank as *Cordyceps nelumboides;* f in GenBank as *Verticillium* sp. 'zealandica', as *Lecanicillium muscarium* in Marshall *et al*. (2003); g in GenBank as *Lecanicillium* sp.

with critical point drying. The samples without critical point drying were placed in low moisture and low oxygen permeable laminated bags to dry out slowly. The other samples with critical point drying were fixed on an aluminum carrier by conductive tape. All dried samples were sputtered for 120 seconds for investigating their morphology with a Hitachi TM-3000 scanning electron microscope. All illustrations were composed and edited with Adobe Photoshop CS2 9.0.

Molecular phylogenetic analyses

Nuclear DNA was isolated from freshly grown cultures, and the internal transcribed spacer (ITS) and large subunit (LSU) rDNA regions were amplified, sequenced, and edited as described by Wei and Kirschner (2017), and submitted to GenBank. For the translation elongation factor alpha 1 gene (TEF), primers TEF EF1-983F and EF1-1567R were used as described by Rehner and Buckley (2005). The sequences were submitted to the DNA Databank of Japan (DDJB) (Table 1). Similar sequences were detected with MegaBLAST at GenBank. Sequences were selected from MegaBLAST searches and the topology in Chen *et al*. (2021), with *Purpureocillium* (Ophiocordycipitaceae) chosen as outgroup (Table 1). Alignments of all sequences were created separately with the G-INS-I option of MAFFT v6.864b (Katoh *et al.*, 2005) and tested with preliminary phylogenetic estimates with neighbor joining implemented in MEGAX. For the final phylogenetic estimate with maximum likelihood (ML), a concatenated set of the evenly trimmed alignment blocks of ITS and TEF sequences with altogether 804 positions was used without any manual manipulation inside the alignment (supplementary materials). For inferring the phylogenetic positions with ML, the Tamura-Nei model with gamma distribution was chosen as best model and 1000 bootstrap replicates in MEGAX

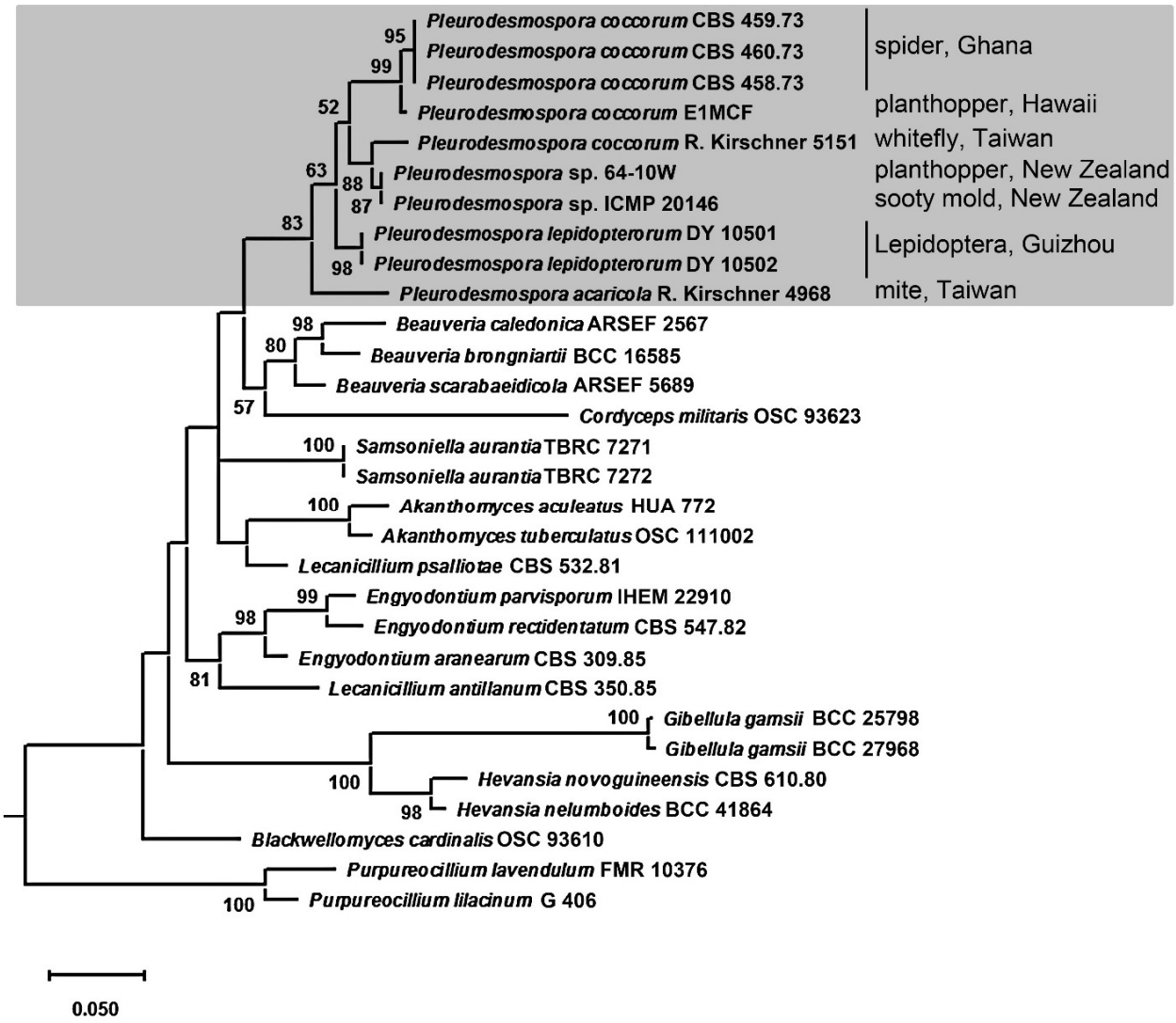

Fig. 1. Maximum likelihood tree showing estimated phylogenetic relationships of *Pleurodesmospora* strains among closely related strains of Cordycipitaceae based on a combined TEF-ITS dataset. The tree was rooted with *Purpureocillium*. Bootstrap values above 50% (1,000 replicates) are indicated at the nodes.

(Kumar *et al*., 2018). The resulting tree was rooted with *Purpureocillium* (Fig. 1).

RESULTS

DNA sequence identities in BLAST searches

The DNA sequences of the two strains from Taiwan were similar but distinct from each other, i.e. in the ITS region differed by 31 bp (5% of 583 bp), in the LSU by 8 bp (1.4% of 579 bp), and in the TEF by 26 bp (6% of 434 bp). MegaBLAST searches with the ITS sequence of the mite-associated fungus revealed highest identities (all 94%) with sequences of *P. coccorum* and *P. lepidopterorum* (length ranges 529–553/561–586 bp), and two strains from New Zealand (95%), namely a strain labeled by Marshall *et al.* (2003) as "*Lecanicillium muscarium* F424" (508/537) from a planthopper and an unpublished strain "*Lecanicillium* sp. ICMP 20146" (558/588 bp) from a sooty mold; no other gene sequences were available for these two strains. The next most similar sequences were from species of *Akanthomyces* and *Hevansia* (as "*Lecanicillium*") (all about 93% identity or lower).

ITS sequence identities of our strain from the tea whitefly with four sequences of *P. coccorum* available from GenBank (see Table 1) were 98% (length ranges between 535 and 589 bp), with two sequences of *P. lepidopterorum* 98–99% (561/570 and 566/572 bp), and 99% with those of the above mentioned strains F424 and ICMP 20146 (529/533 and 597/602 bp, respectively).

BLAST searches with the LSU sequence of the strain from a mite, however, yielded highest identities with species of *Cordyceps* (99%) and only 98% identity with *Pleurodesmospora*. BLAST searches with both TEF

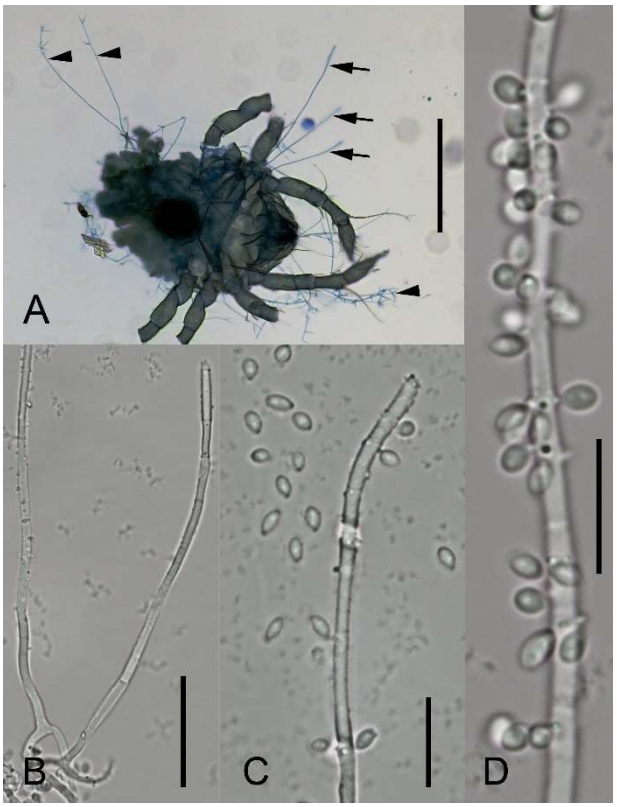

Fig. 2. ***Pleurodesmospora acaricola*** on a dead mite from ***Angiopteris lygodiifolia*** (*R. Kirschner* 4968). **A.** Photo of permanent slide, arrows indicating three conidiophores of ***P. acaricola***, arrowheads indicating conidiophores of another, *Lecanicillium*-like fungus. Stained with cotton blue. **B–D.** Material from culture on CMA. **B.** Bases of two conidiophores. **C.** Apex of conidiophore and attached as well as detached conidia. **D.** Middle part of conidiophore with conidia still attached. Scale bars = 10 µm, except A = 0.2 mm, B = 20 µm.

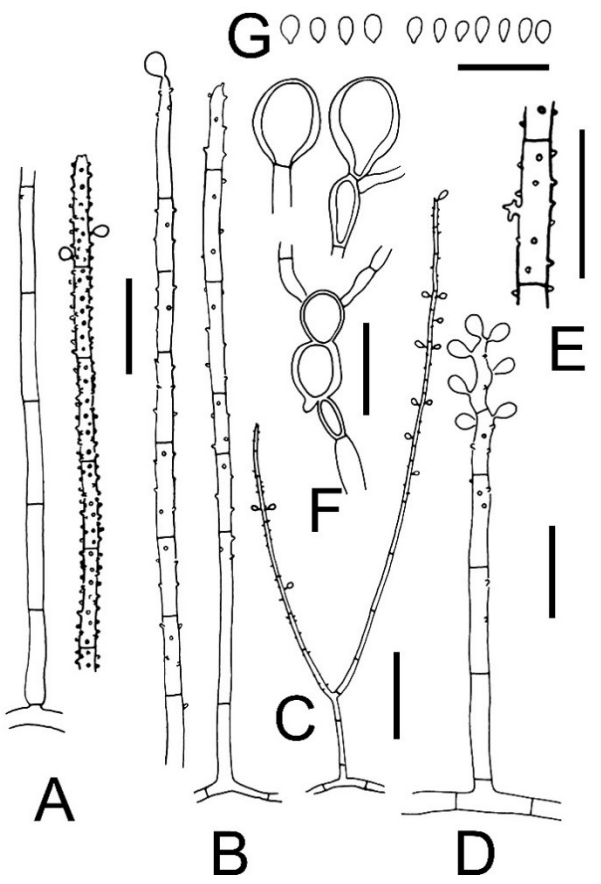

Fig. 3. Drawings of ***Pleurodesmospora acaricola***. **A.** Conidiophore base (left) and apex (right) from the mite substrate. **B–D.** Material from culture on CMA. **B.** The apex of a conidiophore (left) and a short unbranched conidiophore after conidium dehiscence (right). **C.** Branched conidiophore. **D.** Short unbranched conidiophore with numerous sympodially produced conidia still attached. **E.** Conidiogenous cell with branched peg. **F.** Chlamydospores. **G.** Conidia. Scale bars = 10 µm, except C = 20 µm.

sequences in the 100 default range of results predominantly yielded strains labeled as *Beauveria* and *Isaria* (including corresponding *Cordyceps* teleomorph names) except for an unpublished sequence of *Hevansia koratensis* (Hywel-Jones) Luangsa-ard *et al.* (all with 94–95% identity). TEF sequences have only been made available for *Pleurodesmospora* by Chen *et al.* (2021), but these were presently classified as "unverified" in GenBank and did not appear in BLAST searches.

Phylogenetic analysis

In the preliminary estimates, species of some genera appeared paraphyletic in the LSU datasets so that only ITS and TEF data were included in the final analysis. As shown in Fig. 1, the strains from GenBank labeled as *P. coccorum* and *P. lepidopterorum* formed a clade with medium support together with the two strains from Taiwan, while the strain from a mite was in a separate basal position and the strain from the tea whitefly within a poorly supported subclade comprising the other strains labeled as *P. coccorum*. The final strongly supported subclades within the *Pleurodesmospora* clade were correlated with the geographical origins and hosts from Ghana (spiders) and China, Guizhou (Lepidoptera). A clade comprising species of *Engyodontium* including *E. aranearum* (Cavara) W. Gams *et al*. [= *Lecanicillium tenuipes* (Petch) Zare & W. Gams] was well supported and distant to the *Pleurodesmospora* clade.

Oberservations on biology and morphology of strains

Infection experiments were not conducted, but some cultures of the new mite-associated fungus were contaminated by mites with strong effect on the fungus, but not on the mites.

The morphology of the fungus on the mite seen with the light microscope (Figs. 2, 3) was confirmed by SEM (Fig. 4). This fungus produced non-catenate conidia and chlamydospores, whereas the fungus on whiteflies did not form chlamydospores, but catenate conidia (Figs. 5, 6).

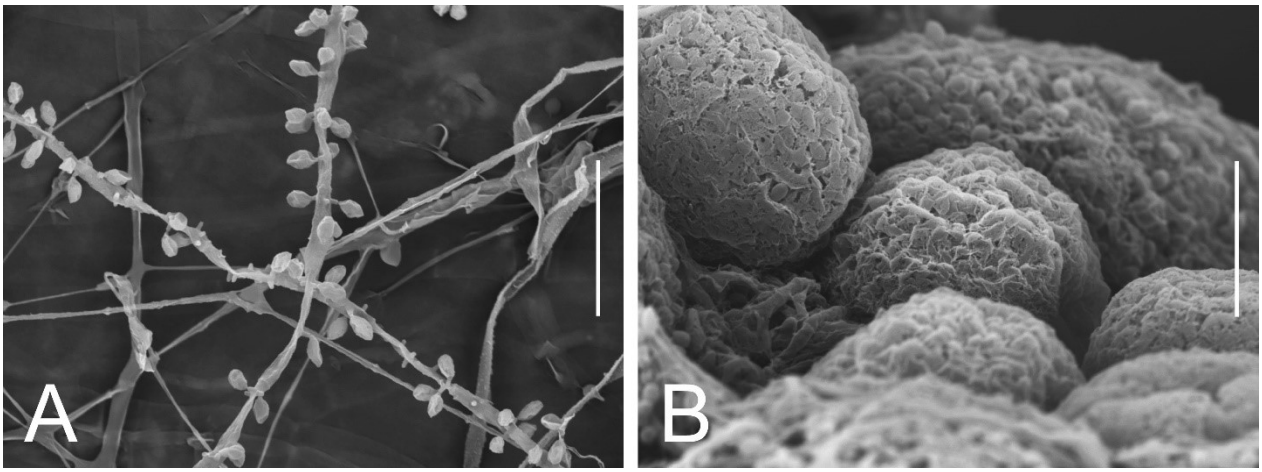

Fig. 4. Scanning electron micrographs of ***Pleurodesmospora acaricola*** (culture material). **A.** Conidiophores and conidia. **B.** Presumptive chlamydospores from the agar surface at the centre of the colony. Scale bars = 15 μm.

TAXANOMIC TREATMENT

Pleurodesmospora acaricola R. Kirschner, ***sp. nov.***
蟎生側鏈孢菌 Figs. 2–4

Index Fungorum: IF558767

***Holotype*:** TAIWAN. Taipei City, Pinglin District, Eco-Park at Tea Museum, ca. 24.9345356, 121,7137387, alt. ca. 220 m, on dead mite on living leaf of *Angiopteris lygodiifolia* Rosenst. (Marattiales), host also associated with a *Lecanicillium*-like fungus, 26. June 2020, *R. Kirschner* 4968, dried culture on CMA (TNM).

***Ex-type culture*:** BCRC FU31537.

***DNA sequences from ex-type culture (GenBank accessions)*:** ITS MZ435417, LSU MZ435415, TEF LC629776.

***Diagnosis*:** Differs from *Pleurodesmospora coccorum* and *P. lepidopterorum* by solitary conidia and by the presence of chlamydospores.

***Description*:** *Colony* on the host inconspicuous; mycelium of co-occurring *Lecanicillium*-like fungus more prominent. Colonies in culture on CMA medium at room temperature slowly growing, ca. 6 cm diam. within 3 weeks (ca. 3 mm/day), white, velvety, powdery, reverse white to cream-yellowish. Hyphae in culture on CMA hyaline, smooth, thin-walled, 1–2 μm wide. *Conidiophores* on the host erect, unbranched, hyaline, smooth, ca. 163–260 × 1.5–2 μm, in the distal third or half densely covered by minute (0.5–1 × 0.5 μm) pegs. *Conidiophores* in culture on CMA arising from hyphae, prostrate to erect, often not clearly distinct from supporting vegetative mycelium, unbranched or profusely branched, hyaline, smooth, ca. 50 to 165 μm long, 2 μm wide. *Conidiogenous cells* intercalary and terminal, cylindrical, with the same width as conidiophore, (5–)7–13(–18) μm long (n=35), forming conidiogenous pegs as on natural substrate, but more distantly dispersed. *Conidia* solitary, oblong-ellipsoidal, obovoid, smooth, on the natural substrate 2.5–3 × 2 μm, in culture 2–3(–4) × (1–)1.5–2 μm (n=35). *Chlamydospores* intercalary or lateral, ellipsoidal, oblong, clavate, short-cylindrical, hyaline, wall up to 2 μm thick, 5–10 × 4–8 μm, in SEM presumptive chlamydospores slightly larger, up to ca. 15 μm wide.

***Etymology*:** Referring to the discovery on a dead mite.

***Known distribution*:** Taiwan.

***Known substrates*:** Mites.

Pleurodesmospora coccorum (Petch) Samson, W. Gams & H.C. Evans, Persoonia 11(1): 68 (1980)
蚧側鏈孢菌 Figs. 5 & 6

Colonies on host white, small (only covering a small part of the host or substrate), in culture on CMA slowly to medium-slowly growing, ca. 3 cm diam. within 3 weeks or ca. 1–3 mm/day, white, velvety, powdery, reverse white to cream-yellowish. Hyphae in culture on CMA hyaline, smooth, thin-walled, 1–2 μm wide. *Conidiophores* on host ca. 75–130 μm long, 1.5–2.5 μm wide, mostly erect and unbranched, occasionally sparsely branched and prostrate, in culture on CMA arising from hyphae, prostrate to erect, often not clearly distinct from supporting vegetative mycelium, unbranched or profusely branched, hyaline, smooth, > 250 μm long, 1.5–2.5 μm wide. *Conidiogenous cells* intercalary or terminal, cylindrical, with the same width as conidiophore, 3–6 μm long, rarely up to 15 μm long, forming 1–3 μm long pegs predominantly laterally below the distal septum of intercalary conidiogenous cells or centrally on the apical conidiogenous cell. Pegs appearing more numerous and densely crowded on material from natural substrate than in freshly grown conidiophores in culture. Conidiogenous cells occasionally lanceolate, formed laterally on hyphae. Exceptionally a secondary lateral peg formed perpendicularly to the primary peg, or apically on adelophialide. *Conidia* in culture catenate (with up to 12 conidia in a chain), oblong-ellipsoidal, obovoid, smooth, 2–3.5 × 1.5–2.5 μm. *Chlamydospores* not observed.

***Specimens examined*:** Taiwan, Nantou County, Lugu Township, National Taiwan University Experimental Forest, Fenghuang Nature Education Center, tea plantation, ca. 23.730504, 120.7870132, ca. 820 m, on dead nymph of *Aleurocanthus camelliae* Kanmiya & Kasai on lower leaf side of *Camellia sinensis* (L.) Kuntze associated with other fungi such as *Tompetchia webberi* (H.S. Fawc.) Subram., 9. Apr. 2021, *R. Kirschner* 5151 (TNM); GenBank ITS MZ435418, LSU MZ435416, TEF LC629777; same place, 7. May 2021, *R. Kirschner* 5176 (TNM).

***Known distribution*:** Mainland China (e.g. Anhui, Shaanxi), Ecuador **(**Galápagos Islands), Germany(?), Ghana, Japan, Malaysia, New Zealand(?), Sri Lanka, Taiwan **(new record)**, Thailand, Uganda, USA (Florida, Hawaii) (Gutierrez-Coarite *et al.*, 2018; Li *et al.*, 1991; Matsushima and Matsushima, 1996; Samson *et al.*, 1980; www.cabri.org; www1a.biotec.or.th/tncc).

***Known substrates*:** Insects (mainly whiteflies and scale insects), mites, spiders, foliicolous fungi (Gutierrez-Coarite *et al.*, 2018; Li *et al.*, 1991; Samson *et al.*, 1980), humans (www.cabri.org; to be verified), soil (Matsushima and Matsushima, 1996).

DISCUSSION

Phylogenetic position of *Pleurodesmospora*

Our data support a systematic placement of *Pleurodesmospora* in the Cordycipitaceae (Hypocreales). Summerbell *et al.* (2011, Fig. 2, clade E) included a strain labeled as "*P. coccorum*" in their LSU rDNA sequence analysis of *Acremonium*, *Sarocladium* and closely related genera. The strain and GenBank accession for this sequence was hidden in the supplement (CBS 101284, GenBank AF339564). Sung *et al.* (2001), however, referred to SSU and LSU rDNA sequences of the same strain as "*Verticillium* sp." (CBS 101284). It showed a close relationship with species of *Beauveria*, *Cordyceps* s. str., and *Microhilum oncoperae* H.Y. Yip & A.C. Rath. Seifert *et al.* (2011) cited this publication for indicating a placement of *Pleurodesmospora* in the "Clavicipitaceae" based on "SSU" rDNA alone and missed to update the taxa treated as "Clavicipitaceae" in Sung *et al.* (2001) as the later separated family Cordycipitaceae (Sung *et al.*, 2007). Our own BLAST search using the LSU rDNA sequence of "*Verticillium* sp." (CBS 101284) showed 100% identities (734/734; 733/733 bp, respectively) with sequences of *Cordyceps ninchukispora* (C.H. Su & H.H. Wang) G.H. Sung *et al.* and *Cordyceps brevistroma* Mongkols. *et al.*, but only 98% identity with those of *Pleurodesmospora* (718/735 or 736 bp). We do not know whether the wrong labeling of this strain as *Pleurodesmospora* or simple neglect of the obscure literature records was the reason for not taking up the classification in Cordycipitaceae by databases such as GenBank, Index Fungorum and MycoBank. Chen *et al.* (2021) were apparently not aware about the previous publications placing *Pleurodesmospora* in the Cordycipitaceae. This correct placement, however, was based on wrong data in the publications prior to Chen *et al.* (2021).

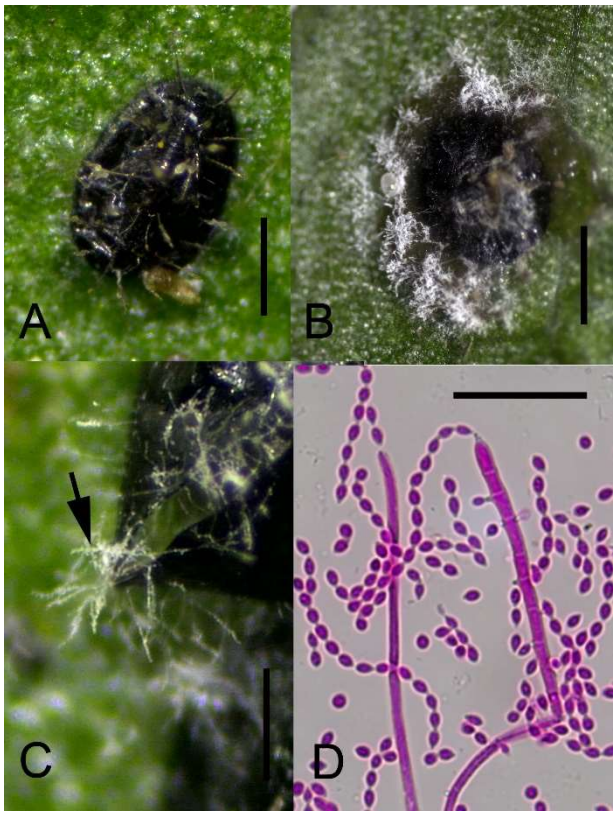

Fig. 5. *Pleurodesmospora coccorum* on *Aleurocanthus camelliae* on *Camellia sinensis* (*R. Kirschner 5151* and *5176* from April and May 2021 and the same locality). **A.** Relatively undamaged host. **B, C.** White mycelium and conidiophores on infected hosts at different magnifications. **D.** Conidiophores and conidia from material in culture on CMA, stained with phloxine. Scale bars A, B, C = ca. 0.4 mm, D = 20 µm.

In our analysis, *P. acaricola* was basal to the other species of *Pleurodesmospora*. Morphologically it differs by the non-catenate conidia and by its chlamydospores from the other two accepted species. Since molecular data, morphological characteristics and the chitinous substrate are more similar to those of species of *Pleurodesmospora* than to species of any other genus, we tentatively extend the morphological genus concept to include non-catenate conidia and placed the species from the mite into *Pleurodesmospora*.

Difficulties of morphological identification

Our list of localities for *P. coccorum* includes those of strain databases (Germany: www.cabri.org; Thailand: www1a.biotec.or.th/tncc), since in some cases we could not trace the corresponding publications. The strain CBS 100825 from a patient with psoriasis from Germany (www.cabri.org) to our knowledge is the single one from a human source and should be verified; perhaps it was confused with *Engyodontium album* (Limber) de Hoog which is morphologically similar to *Pleurodesmospora* (see below) and has been recorded in the context of human diseases (Hoog *et al.*, 2000). The morphological plasticity

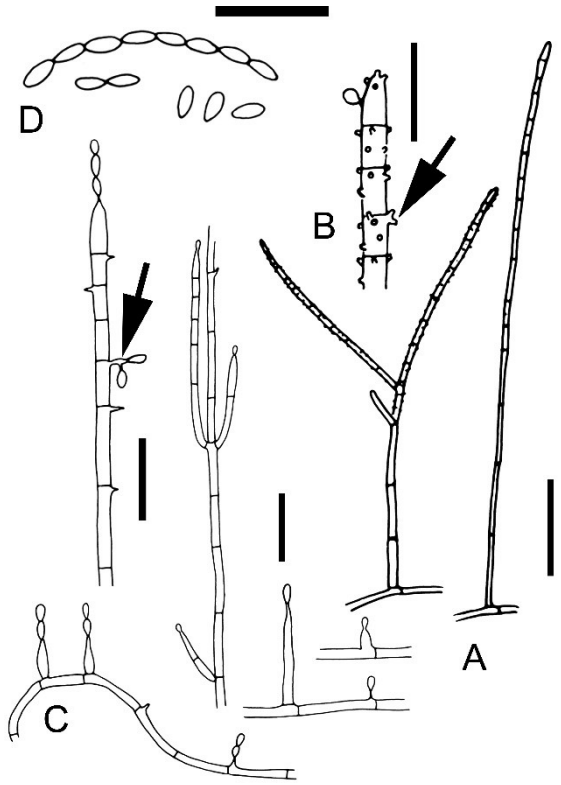

Fig. 6. Drawings of ***Pleurodesmospora coccorum***. **A, B.** A sparsely branched as well as a simple erect conidiophore and apex of conidiophore (**B**) from host insect; the arrow indicates a furcate conidiogenous peg. **C.** Conidiophores with intercalary and discrete conidiogenous cells on prostrate and erect conidiophores from culture on CMA; the arrow indicates a furcate conidiogenous peg. **D.** Conidia. Scale bars = 10 µm, except A = 20 µm.

of the species in situ and in vitro was illustrated by Petch (1925) and Li *et al.* (1991), particularly showing a higher density of conidiogenous loci along the conidiogenous cell in nature compared to more scattered arrangement in culture. The difficulty of morphological separation of these species is illustrated by Petch (1931) who synonymized the two species described previously by himself in different genera, *G. coccorum* (Petch, 1925) and *Rhinotrichum album* Petch (Petch, 1926), which was confirmed by subsequent authors (Samson *et al.*, 1980). A species separated based on minutely differences of sizes for ca. 1 µm, *Rh. depauperatum* Charles, was also synonymized with *P. coccorum* (Samson *et al.*, 1980). When *P. lepidopterorum* was described, a similar range of minute morphological variation between the two species of *Pleurodesmospora* was claimed (Chen *et al.*, 2021).

Are there cryptic species in *Pleurodesmospora*?

The phylogenetic analysis indicated correlation of molecular data with hosts or with geographical distribution when the same host was collected in the same locality. The three strains of *P. coccorum* labelled with CBS accession numbers in Fig. 1 and Table 1 were from spiders in Ghana (Samson *et al.*, 1980). To these strains, a further strain from a planthopper (Auchenorrhyncha) in Haiwaii (Gutierrez-Coarite *et al.*, 2018) was more closely related than another strain also from a planthopper from New Zealand which was more closely related to a strain from New Zealand, but isolated from a sooty mold (GenBank, unpublished). This unpublished strain supports including fungicolous strains in *Pleurodesmospora* as suggested by Samson *et al.* (1980). Our own strain from a black whitefly (Aleyrodidae) in Taiwan appeared more isolated from the other strains of *P. coccorum* s. lat. from other areas. The two strains of *P. lepidopterorum* were from lepidopteran pupae from Guizhou in China (Chen *et al.*, 2021), and the strain of *P. acaricola* from a mite from Taiwan. Because of this geographic pattern and the recent molecular-based segregation of *P. lepidopterorum*, there might be several cryptic species in the species complex hitherto considered as *P. coccorum*. It cannot be excluded that all these strains, except *P. acaricola*, are geographic variants of the same species, *P. coccorum*. The recent explosion of new names, however, in Cordycipitaceae (Kepler *et al.*, 2017), for example in *Beauveria* (Rehner and Buckley, 2005; Bustamante *et al.*, 2019), rather suggests the presence of a not yet fully unraveled high diversity of cryptic species in *Pleurodesmospora*.

Suggestions for disentangling cryptic species in *Pleurodesmospora*

The type of *P. coccorum* is based on a specimen on "black *Aleyrodes*" from mango in Sri Lanka (Samson *et al.*, 1980), which clearly indicates a whitefly (Aleyrodidae), although Samson *et al.* (1980) interpreted this host as "blak (sic!) scale". Most likely because Petch (1925) found a similar fungus first on a scale insect, he chose *Gonatorrhodiella coccorum* Petch for the scientific name, indicating scale insects as hosts because he believed that the fungi on the scale insects and on black Aleyrodidae were the same species. Among the hitherto known hosts of *Pleurodesmospora* fungi, the host of the type specimen from Sri Lanka seems to be most closely related to the black tea whitefly from Taiwan. Investigation of *Pleurodesmospora* species on whiteflies and scale insects in Sri Lanka with molecular approaches could contribute to clarification. We assume that the specimens on whiteflies in Asia will reveal to be more closely related to *P. coccorum* in the strict sense, whereas the strains derived from other hosts and regions may receive new species names.

A further species on scale insects, *Rhinotrichum album* Petch in Sri Lanka, another one on mites, *Rh. depauperatum* Charles in Florida, and a fungicolous species, *Aphanocladium meliolae* (Hansf.) W. Gams in Uganda, were all considered synonyms of the type species by Samson *et al.* (1980), who provided information on further hosts. These names should also be

re-examined with molecular methods based on specimens on similar hosts in the same countries as the type specimens for disentangling the taxonomy of *Pleurodesmospora*. With such data, it should also be possible to identify strains isolated from dead plant material or soil, which are presently considered as *P. coccorum* (Matsushima and Matsushima, 1996).

Phylogenetic position of *Engyodontium*

Engyodontium is similar to *Pleurodesmospora* by the occurrence of polyphialidic conidiogenous cells whose pegs bear a single conidium each (Gams *et al.*, 1984), whereas in *P. coccorum* we found phialide-like lanceolate conidiogenous cells which are also typical for *Engyodontium*. Particularly in *E. aranearum*, conidiogenous pegs occur not only on terminal, but also on intercalary conidiogenous cells (Gams *et al.*, 1984). In our analysis, however, the clade comprising *Engyodontium* species, including the type species, *E. parvisporum* (Petch) de Hoog, is distantly related to *Pleurodesmospora*. *Engyodontium* is rarely considered in phylogenetic analyses of the Cordycipitaceae; *E. aranearum* is often presented under its synonym *Lecanicillium tenuipes* (Petch) Zare & W. Gams so that the polyphyletic *Lecanicillium* unnecessarily appears in a further clade (e.g. Chen *et al.*, 2021; Tsang *et al.*, 2016). The type species of *Lecanicillium*, *L. lecanii* is conspecific with *Akanthomyces lecanii* (Zimm.) Spatafora *et al*., thus the genus name has become a synonym of *Akanthomyces* and should no longer be available (Kepler *et al.*, 2017). Kepler *et al.* (2017) consequently used *E. aranearum* in their analyses without emphasizing that this name should replace the later *L. tenuipes*. When suggesting changing *E. aranearum* to *L. tenuipes*, Zare and Gams (2001) mentioned that they had no data of other *Engyodontium* species. *Engyodontium* is now well supported in molecular analyses and differs morphologically by its polyphialidic conidiogenous cells from "*Lecanicillium*" species (Gams *et al.*, 1984; Zare and Gams, 2001).

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