Article

Insight into the Systematics of Novel Entomopathogenic Fungi Associated with Armored Scale Insect, *Kuwanaspis howardi* (Hemiptera: Diaspididae) in China

Xiu-Lan Xu 1,2,3, Qian Zeng 1,2, Yi-Cong Lv 1,2, Rajesh Jeewon 4,5, Sajeewa S. N. Maharachchikumbura 5,6, Dhanushka N. Wanasinghe 6, Kevin D. Hyde 7, Qian-Gang Xiao 3, Ying-Gao Liu 1,2 and Chun-Lin Yang 1,2,*

1 National Forestry and Grassland Administration Key Laboratory of Forest Resources Conservation and Ecological Safety on the Upper Reaches of the Yangtze River, Sichuan Agricultural University, Chengdu 611130, China; xuixialanxiao@126.com (X.-L.X.); qz1573037145@163.com (Q.Z.); Lyvyicong0616@126.com (Y.-L.C.); lyg092764@163.com (Y.-G.L.)
2 Sichuan Province Key Laboratory of Ecological Forestry Engineering on the Upper Reaches of the Yangtze River, Sichuan Agricultural University, Chengdu 611130, China
3 Research Institute of Forestry, Chengdu Academy of Agricultural and Forestry Sciences, Chengdu 611130, China; xiaogg1992@163.com
4 Department of Health Sciences, Faculty of Medicine and Health Sciences, University of Mauritius, Reduit 8083, Mauritius; rjeewon@uom.ac.mu
5 School of Life Science and Technology, University of Electronic Science and Technology of China, Chengdu 61731, China; sajeewa83@yahoo.com
6 CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 611201, China; dnaeshan@gmail.com
7 Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand; kdhyde@gmail.com
* Correspondence: yangcl0121@163.com

Abstract: This study led to the discovery of three entomopathogenic fungi associated with *Kuwanaspis howardi*, a scale insect on *Phyllostachys heteroclada* (fishtail bamboo) and *Pleioblatus amarus* (bitter bamboo) in China. Two of these species belong to *Podonectria*: *P. kuwanaspidis* X.L. Xu & C.L. Yang sp. nov. and *P. novae-zelandiae* Dingley. The new species *P. kuwanaspidis* has wider and thicker setae, longer and wider asci, longer ascospores, and more septa as compared with similar *Podonectria* species. The morphs of extant species *P. novae-zelandiae* is confirmed based on sexual and asexual morphologies. Maximum likelihood and Bayesian inference analyses of ITS, LSU, SSU, *tef1*-α, and *rpb2* sequence data provide further evidence for the validity of the two species and their placement in *Podonectriaceae* (Pleosporales). The second new species, *Microcera kuwanaspidis* X.L. Xu & C.L. Yang sp. nov., is established based on DNA sequence data from ITS, LSU, SSU, *tef1*-α, *rpb1*, *rpb2*, *act1*, *act*, *cmdA*, and *his3* gene regions, and it is characterized by morphological differences in septom numbers and single conidial mass.

Keywords: 2 new taxa; bamboo; entomopathogens; Nectriaceae; Podonectriaceae; scale insect

1. Introduction

*Podonectria* was introduced by Petch [1] to accommodate species of *Ophionectria*, which are parasitic on scale insects and have thick-walled asci, long, multisepate ascospores, and a tetracrium-like conidial stage. Ten species are listed in Index Fungorum [2]. The type species, *Podonectria coccicola* (Ellis and Everh.) Berk. & Voglino and is associated with the scale insects *Aonidiella aurantia* (Maskell), *Aspidiotus perniciosus* (Comstock), *Chrysomphalus aonidum* (Linnaeus), *Lepidosaphes beckii* (Newman), *L. Gloveri* (Packard), *Leucaspis* sp., *Parlatoria pergandii* Comstock, *P. ziziphi* Lucas, and *Unaspis citri* (Comstock) which are mainly found on Rutaceae [1,3–5]. *Puttemansia aurantii* (Henn.) Höhn, which was initially found from the...
type specimen of the asexual morph *Tetracrium auranti*ii Henn. associated with scale insect *Parlatoria ziziphi* on *Citrus aurantium* L., was also assigned to *Podonectria* as *P. auranti*ii (Henn.) Petch [1]. A new species collected from *Lepidosaphes* sp. on *Citrus nobilis* Lour. was named as *Podonectria echinata* [1]. Additionally, two new species, *P. gahnia* Dingley and *P. novae-zelandiae* Dingley, were reported by Dingley (1954) from scale insects in New Zealand [3], followed by a new fungus *P. tenuispora* Dennis collected from *Lepidosaphes ulmi* (Linnaeus) on *Calluna vulgaris* (L.) Hull [6]. Subsequently, Rossman transferred *Ophiocer*tia *coccorum* Petch, associated with *Fiorinia juniperi* Kuwana, and *Lasiosphaeria larvae*spora Cooke & Massee on an undetermined scale insect to *Podonectria*, viz. *P. coccorum* (Petch) Rossman and *P. larvae*spora (Cooke & Massee) Rossman [7]. The species *Trichonectria bamus*cola Rehm was referred as *P. bamus*cola (Rehm) Piroz. on account of scolecosporous ascospores and tetracrium-like conidia by Pirozynski [8]. However, *Podonectria bamus*cola was excluded because of its occurrence on living leaves of bamboo rather than scale insects and remained an unclassified loculoascomyete [4]. Rossman published a monograph on *Podonectria* and accepted eight species [4]. An examination of the type specimen of *T. bamus*cola further revealed that this was a synonym of *Uredinophila erinaceae* (Rehm) Rossman [9]. The genus *Podonectria* was characterized by fleshy, white to brown, uninucleate ascospore and long, multiseptated ascospores associated with scale insects [4]. Spatafora et al. [10] transferred the previously reported species *Podonectria cicadellicolida* Kobayasi & Shimizu and *P. citrina* Kobayasi & Shimizu to *Ophiocordyceps* supported by the previous phylogenetic analyses presented in Quandt et al. [11]. Yang et al. [12] found *P. sichuanensis* C.L. Yang & X.L. Xu parasitic around the ascormata of *Neostagonosporella sichuanensis* C.L. Yang, X.L. Xu & K.D. Hyde on *Phyllostachys heteroclada* Oliv.

*Microcera* (Nectriaceae, Hypocreales), typified by *Microcera coccophila* Desm. and known as the “red-headed fungus”, is mostly parasitic on scale insects with fusarium-like asexual morphs. The genus has been considered as a synonym in major taxonomic revisions of *Fusarium* Link [13–17]. A multilocus phylogenetic approach was subsequently applied to identify species in the fusarium-like clade since morphological identification was difficult [18–20]. Gräfenhan et al. [18] resurrected *Microcera* based on DNA sequence data and accepted four *Microcera* species, viz. *M. coccophila*, *M. diploa* (Berk. & M.A. Curtis) Gräfenhan & Seifert, *M. rubra* Gräfenhan & Seifert, *M. larvarum* (Fuckel) Gräfenhan, Seifert & Schroers. Lombard et al. [19] further investigated phylogenetic relationships of *Microcera* based on DNA sequence data and reported that it constitutes a lineage distantly related to *Fusarium* but closely related to *Fusella* and *Macroconia*. 

Armored scale insects (Hemiptera: Coccoidea: Diaspididae) are major economic pests on agriculture and forestry plants, especially on fruit trees and vegetables. Diaspididae is the largest family of scale insects with 421 accepted genera and four subfamilies recognized, viz. Aneccaspideinae Borchsenius, Furcaspideinae Balachowsky, Diaspidinae Targioni Tozzetti, and Aspidiotinae Westwood. by Normark et al. [21]. The grass-feeding species, *Kuwana* sp. on bamboo, which is classified into subtribe Fioriniina Targioni Tozzetti under tribe Diaspidini Targioni Tozzetti within subfamilies Diaspidinae, are harmful to bamboo [22,23]. During our investigations of microfungi associated with bamboo in Sichuan Province, two *Podonectria* species and a *Microcera* species were isolated in association with the armored scale insect *Kuwana* sp. (Cooley) on native bamboo plants *Phyllostachys heteroclada* and *Pleiolestus amarus* (Keng) Keng. Morphological characteristics coupled with phylogenetic analyses of the combined ITS, LSU, SSU, *tef1*-a, and *rpb2* sequence dataset support the validity of the *P. kuanaspidis* X.L. Xu & C.L. Yang sp. nov. and *P. novae-zelandiae* Dingley and their placement in *Podonectriaceae*, Pleosporales. The fusarium-like species *Microcera kuanaspidis* is distinguished from similar species based on the sequences’ differences, mainly in the *tef1*-a, *acl1*, *act*, *cmdA*, *rpb1*, and *his3* regions. This is the first record of these taxa associated with scale insects in China. The taxa are compared with allied species, and comprehensive descriptions and micrographs are provided.
2. Materials and Methods

2.1. Specimen Collection and Morphological Study

During spring to autumn from 2018 to 2021, the specimens were collected from the bamboo forests located in Ya’an City and a neighboring county (Sichuan Province, China), where the environment is characterized by river valley terraces and intermountain basins and a subtropical monsoon humid climate with abundant natural resources, and it is the transition zone from Qinghai-Tibet Plateau to Chengdu Plain. Specimens documented with host, locality, time, and distribution of taxa were returned to the laboratory in suitable containers separately with the collection detail tag, and the substrate with fruiting bodies was checked following the methods described in Senanayake et al. [24]. The fungi were isolated into pure culture using single conidium obtained from sporodochia and single ascospore from ascomata parasitic on *Kuwanaspis howardi* following the isolation via spore suspension detailed in Chomnunti et al. [25]. The spore suspension was sucked into a Pasteur pipette, small drops were placed on isolation media (potato dextrose agar, PDA) in an incubator (20 °C). Then the plates were examined for single germinated spores under a dissecting microscope, and germinating spores were transferred separately for at least three new PDA plates. After incubation on PDA plates at 20 °C for 20 to 40 days depending on the growth rate, colonies were examined for their diameter, shape, and appearance. Ascomata and sporodochia were observed and photographed using a dissecting microscope NVT-GG (Shanghai Advanced Photoelectric Technology Co. Ltd., Shanghai, China) fitted with a VS-800C micro-digital camera (Shenzhen Weishen Times Technology Co. Ltd., Shenzhen, China). Dimensions of asci, ascospores, pseudoparaphyses, hairs, ascomata wall, conidia, conidiophores, and numbers of septa were based on field samples and were photographed using an Olympus BX43 compound microscope fitted with an Olympus DP22 digital camera in association with ACDSee v3.1 software. Measurements were made using Tarosoft® Image Frame Work v.0.9.7 (Tarosoft (R), Nontha Buri, Thailand). Lactophenol cotton blue reagent was used to observe the number of septa. The gelatinous appendage was observed in Black Indian ink. The type specimens were deposited at the Herbarium of Sichuan Agricultural University, Chengdu, China (SICAU). The ex-type cultures were deposited at the Culture Collection in Sichuan Agricultural University (SICAUCC), and MycoBank numbers are registered (http://www.MycoBank.org, accessed on 10 January 2021).

2.2. DNA Extraction, Amplification and Sequencing

Total genomic DNA was extracted from mycelia grown on PDA at 20 °C for 30 days, using the Plant Genomic DNA extraction kit (Tiangen, China). The internal transcribed spacer (ITS), the partial large subunit nuclear rDNA (LSU), the partial small subunit nuclear rDNA (SSU), translation elongation factor 1-alpha (*tef1*-α), the RNA polymerase II second largest subunit (*rpb2*), the large subunit of the ATP citrate lyase (*acl1*), the RNA polymerase II largest subunit (*rpb1*), β-tubulin (*tub2*), histone H3 (*his3*), translation elongation factor 1-alpha (*tef1*-α), calmodulin (*cmdA*), and actin (*act*) regions were amplified with primer pairs ITS5/ITS4 [26], LR0R/LR5 [27], NS1/NS4 [26], EF1-983F/EF1-2218R [28], fRPB2-5F/fRPB2-7cR [29], acl1-230up/acl1-1220low, RPB1-Ac/RPB1-Cr, T1/CYLTUB1R, CYLH3F/CYLH3R, EF1-728F/EF2, CAL-228F/CAL2Rd, and ACT-512F/ACT-1Rd [19], respectively.

Polymerase chain reaction (PCR) was performed in 25 μL reaction mixture containing 22 μL Master Mix (Beijing TsingKe Biotech Co., Ltd., Beijing, China), 1 μL DNA template, 1 μL each primer (10 μM). The amplification reactions were performed as described by Gräfenhan et al. [18], Lombard et al. [19], Dai et al. [30], and Wanasinghe et al. [31]. PCR products were sequenced at TsingKe Biological Technology Co., Ltd., Chengdu, China. The newly generated sequences were deposited in GenBank.

2.3. Phylogenetic Analyses

To infer relationships of our *Podonectria* taxa, a combined ITS, LSU, SSU, *tef1*-α, and *rpb2* sequences dataset was used to construct the phylogenetic tree. For *Microcera* taxa,
a combined ITS, LSU, tef1-α, rpb1, rpb2, acl1, act, tub2, cmdA, and his3 sequences dataset was used. Taxa used for phylogenetic analyses were selected based on BLAST searches and recent publications (Tables 1 and 2). DNA alignments were performed using MAFFT v.7.429 online service [32], and ambiguous regions were excluded using BioEdit version 7.0.5.3 [33]. Phylogenetic trees were inferred with maximum likelihood (ML) and Bayesian inference (BI), according to the details described in Xu et al. [34]. The finalized alignments and trees were deposited in TreeBASE (http://www.treebase.org, accessed on 10 January 2021), submission ID: 27547 and 27549, respectively.

Table 1. GenBank accession numbers of strains in Pleosporales and Tubeufiales used for the phylogenetic analyses of Podonectria.

| Species                      | Strain/Voucher No. | GenBank Accession Numbers | References |
|------------------------------|--------------------|---------------------------|------------|
| Alternaria alternata         | CBS 916.96 T       | AF347031                  | [35]       |
| Alternaria aconidiphora      | CBS 145419 T       | LR133931                  | [36]       |
| Alternaria dactylidicola     | MFLUCC 15-0466 T   | KY703616                  | [37]       |
| Alloleptosphaeria crematidis | MFLUCC 17-2071 T   | MT310604 MT214557 MT226674 MT394736 MT394685 | [38] |
| Astragalicola amorphia       | CBS 142999 T       | MF795753 MF795973         | [39]       |
| Astragalicola vasiljevae     | MFLUCC 17-0832 T   | MG828870 MG828986 MG829098 MG829193 MG829248 | [40] |
| Bambusicola bambusae        | MFLUCC 11-0614 T   | JX442031 JX442035 JX442039 KP761722 KP761718 | [41,42] |
| Bambusicola irregularispora | MFLUCC 11-0437 T   | JX442032 JX442036 JX442040 KP761723 KP761719 | [41,42] |
| Bambusicola massarinia      | MFLUCC 11-0389 T   | JX442033 JX442037 JX442041 KP761725 KP761716 | [41,42] |
| Bambusicola splendida       | MFLUCC 11-0439 T   | JX442034 JX442038 JX442042 KP761726 KP761717 | [41,42] |
| Bambusicola dalymospora      | MFLUCC 10-0557 T   | KU940116 KU863105 KU872110 KU940188 KU940165 | [30] |
| Bambusicola pustulata        | MFLUCC 15-0190 T   | KU940118 KU863107 KU872112 KU940190 KU940165 | [30] |
| Bambusicola thailandica     | MFLUCC 11-0147 T   | KU940119 KU863108 KU872113 KU940191 KU940166 | [30] |
| Bambusicola triseptatispora  | MFLUCC 11-0166 T   | KU940120 KU863109 – – KU940167 | [30] |
| Bambusicola dimorphora       | MFLUCC 13-0282 T   | KY026582 KY000661 KY038354 – KY056663 | [37] |
| Bambusicola loculata         | MFLUCC 13-0856 T   | KP761732 KP761729 KP761735 KP761724 KP761715 | [42] |
| Bambusicola sicuanensis      | SICAUCC 16-0002 T  | MK253473 MK253532 MK253528 MK262828 MK262830 | [43] |
| Bambusicola subthailandica  | SICAU 16-0005 T    | MK253474 MK253533 MK253529 MK262829 MK262831 | [43] |
| Boeremia coffae              | CBS 109183 T       | GU237748 GU237943 – KY484678 KT389566 | [44] |
| Boeremia hirontica           | CBS 113651 T       | KY484662 – – KY484713 – KY484713 | [44] |
| Boeremia opulii              | CGMCC 3.18354 T    | KY742045 KY742199 – – KY742133 | [44] |
| Boeremia linicola            | CBS 116.76 T       | GU237754 GU237938 – KY484705 KT389574 | [44] |
| Boeremia populi              | CBS 100167 T       | GU237707 GU237939 – KY484706 – KY484706 | [44] |
| Coniothyrium telephii        | UTHSC D16-189      | LT796830 LN90732 – – – | [45] |
| Coniothyrium chiangmaiense   | MFLUCC 16-0891 T   | KY568987 KY550384 KY550385 – KY607015 | [37] |
| Coniothyrium sidae           | CBS 135108 T       | KF251149 KF251653 – KF253109 KF252158 | [46] |
| Cucurbitaria berberidis      | CBS 363.93 T       | JF740191 GQ387606 – – – | [47] |
| Decorospora gaudefrogi      | CBS 332.63 T       | AF394541 – AF394542 – – | [48] |
| Didymella poaceicola        | MFLUCC 13-0212 T   | KX965726 KX954395 – – KX898364 | [37] |
| Dothidiotrichia robiniae    | MFLUCC 16-1175 T   | MK751727 MK751817 MK751762 MK908017 MK920237 | [49] |
| Epicoccum thailandicum      | MFLUCC 16-0892 T   | KY703619 KY703620 – – – | [37] |
| Epicoccum poaceicola        | MFLUCC 15-0448 T   | KX965727 KX954396 – – KX898365 | [37] |
| Leptosphaeria cichorium      | MFLUCC 14-1063 T   | KT454720 KT454712 KT454728 – – | [50] |
| Nothophoma chromolaenae      | MFLUCC 17-1443 T   | MT214364 MT214458 MT214410 – – | [51] |
| Ophiosimulans tanaceti       | MFLUCC 14-0525 T   | KU738890 KU738891 KU738892 MG520910 – | [52,53] |
| Species                        | Strain/Voucher No. | GenBank Accession Numbers | References |
|-------------------------------|--------------------|---------------------------|------------|
| *Palmiascoma gregariascomum*  | MFLUCC 11-0175 T   | KP744452 KP744495 KP753958 – KP998466 | [54]       |
| *Parafenestella austriaca*    | CBS 145262 T       | MK356304 MK356304 – MK357576 MK357532 | [55]       |
| *Parafenestella alpina*       | CBS 145263 T       | MK356302 MK356302 – MK357574 MK357530 | [55]       |
| *Parasphiodobolus plantaginis*| MFLUCC 17-0245 T   | KY797641 KY815010 KY815012 MG520913 – | [53]       |
| *Plaesthesphaeria ampeli*     | MFLUCC 18-1641 T   | MK503797 MK503808 MK503814 MK503802 – | [56]       |
| *Podonectria coccicola*       | DAR 81026          | KU587798 KU519419 – – – | [5]        |
| *Podonectria coccicola*       | PUc515             | KU720533 KU519420 – – – | [5]        |
| *Podonectria novae-zelandiae* | PUc514             | KU720535 KU559551 – – – | [5]        |
| *Podonectria novae-zelandiae* | PUc513             | KU720538 KU559548 – – – | [5]        |
| *Podonectria novae-zelandiae* | PUc512             | KU720537 KU529802 – – – | [5]        |
| *Podonectria novae-zelandiae* | PUc511             | KU720536 KU568479 – – – | [5]        |
| *Podonectria sichuanensis*    | SICAU 16-0003 T    | MK305903 MK296471 MK296467 MK313852 MK313855 | [12]       |
| *Podonectria sichuanensis*    | SICAUCC 21-0001    | MW484988 MW462899 MW462891 MW462111 MW462118 | This study |
| *Podonectria kwawanapisdis*   | SICAUCC 21-0002 T  | MW484989 MW462900 MW462892 MW462112 MW462119 | This study |
| *Podonectria kwawanapisdis*   | SICAUCC 21-0003    | MW484990 MW462901 MW462893 MW462113 MW462120 | This study |
| *Podonectria novae-zelandiae* | SICAUCC 21-0004    | MW484991 MW462902 MW462894 MW462114 MW462121 | This study |
| *Podonectria novae-zelandiae* | SICAUCC 21-0005    | MW484992 MW462903 MW462895 MW462115 MW462122 | This study |
| *Podonectria kwawanapisdis*   | SICAUCC 21-0007    | MW484994 MW462905 MW462897 MW462116 MW462123 | This study |
| *Pseudoephidiobolus galii*    | MFLUCC 17-2257 T   | MG520947 MG520967 MG520989 MG520926 – | [53]       |
| *Pseudoprenochaeta lycopersici*| CBS 306.65 T    | AY649587 EU754205 – – – LT717680 | [57]       |
| *Pseudoprenochaeta terrestris* | CBS 282.72 T    | LT623228 LT623216 – – – LT623287 | [57]       |
| *Sclerenchymomyces clematidis*| MFLUCC 17-2180 T  | MT310605 MT214558 MT226675 MT394737 MT394686 | [38]       |
| *Seltsamia ulmi*              | CBS 143002 T       | MF795794 MF795794 MF795794 MF795882 MF795836 | [39]       |
| *Thyrostroma lycii*           | MFLUCC 16-1170 T  | MK751734 MK751824 MK751769 MK908024 MK920241 | [49]       |
| *Thyrostroma robiniae*        | MFLUCC 18-1191 T  | MK751735 MK751825 MK751770 MK908025 MK920242 | [49]       |
| *Tubeufia javonica*           | MFLUCC 12-0545 T  | KJ880034 KJ880036 KJ880035 KJ880037 – | [58]       |
| *Tubeufia chiangmaisensis*     | MFLUCC 11-0514 T  | KF301530 KF301538 KF301543 KF301557 – | [58]       |

Notes: The superscript T represents ex-type or ex-epitype isolates. “–” means that the sequence is missing or unavailable. New sequences are listed in bold. Abbreviations. CBS: Centraalbureau voor Schimmelcultures, Utrecht, Netherlands; CGMCC: China General Microbiological Culture Collection Center; DAR: New South Wales Plant Pathology Herbarium, Orange Agricultural Institute, Orange, NSW, Australia; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; PUcS: unspecified; UTHSC: Fungus Testing Laboratory of the University of Texas Health Science Center at San Antonio, San Antonio, TX, USA; SICAUCC: Sichuan Agricultural University Culture Collection, Sichuan, China; SICAU: Herbarium of Sichuan Agricultural University, Sichuan, China.
Table 2. GenBank accession numbers of strains in Nectriaceae used for the phylogenetic analyses of *Microcera*.

| Species                        | Strain/Voucher No. | GenBank Accession No. | References                      |
|-------------------------------|--------------------|-----------------------|--------------------------------|
| Cosmospora coccinea          | CBS 3417.60 T      | HQ697613 KM232121 KM231698 KM231590 HQ897127 KM232162 KM232142 HQ977777 KM231947 KM232096 | [18,19] |
| Cosmospora cymosa             | CBS 762.40 T       | HQ697614 KM232122 KM231599 KM231531 HQ897128 KM232163 KM232143 HQ977778 KM231948 KM232097 | [18,19] |
| Dioscorea epiphora           | CBS 125494 + TG 208-11 | HQ697692 KM232127 KM231404 KM231358 HQ897311 KM231697 KM232248 HQ977756 KM231935 KM232092 | [18,19] |
| Dioscorea elodes             | CBS 125495 + TG 208-56 | HQ697693 KM232126 KM231403 KM231355 KM231821 KM232247 KM231947 KM232092 KM232091 | [18,19] |
| Fusiscola coccinea           | BBA 6679 T + IMI 104868 + NRRL 21827 | KM231065 – – – HQ897790 US8108 – – – HQ977701 – – – | [18] |
| Fusiscola cymosa              | CBS 857.85 + BBA 64599 + NRRL 20645 | KM231067 – KM231406 – KM231823 KM231699 KM232250 HQ977744 KM231955 KM232094 | [18] |
| Fusiscola cymosa              | BBA 62201 T + IMI 85601 + NRRL 20429 | KM231069 – – – – AF285792 – – – HQ977705 – – – | [18] |
| Fusiscola cymosa              | CBS 581.78 + ATCC 18084 + MAFF 238445 + NRRL 2047 | KM231070 KM231228 KM231405 KM231597 KM231522 KM231698 KM232249 HQ977720 KM231954 KM232093 | [18,19] |
| Microcera papilionacearum     | CBS 125495         | HQ697691 KM231235 KM231411 KM231561 HQ697268 KM231794 KM232254 HQ977756 KM232096 KM232096 | [18,19] |
| Microcera leptosphaeriae      | CBS 717.74         | KM231062 KM231236 KM231410 KM231564 KM231827 KM231757 KM232257 KM231930 JT735693 KM232099 | [18,19] |
| Microcera leptosphaeriae      | CBS 10085 + CBS F16100 | KM231063 KM231234 KM231412 KM231562 HQ897310 KM231755 KM232253 HQ977755 KM231930 KM232097 | [18,19] |
| Microcera copephila           | CBS 310.34 + NRRL 13960 | HQ697841 KM231232 KM231410 KM231560 HQ897794 KM231753 – – – HQ977705 JT735692 – – – | [18,19] |
| Microcera dispora             | CBS 785.79 + BBA 62773 + NRRL 13966 | KM231069 – – – – HQ897817 – – – HQ977763 – – – | [18,19] |
| Microcera larvarum            | SICAUC11 21-0006 T | MW462325 MW462326 MW462327 MW462325 MW462325 MW462325 MW462325 MW462325 MW462325 MW462325 This study | [18,19] |
| Microcera larvarum            | SICAUC11 21-0009 | MZ044537 MZ044538 MZ044539 MZ044540 MZ044541 MZ044544 MZ044545 MZ044546 MZ044547 MZ044548 This study | [18,19] |
| Microcera larvarum            | CBS 169.30         | HQ897655 – – EU460049 EU460049 EU460049 – HQ977717 – – EL360025 | [18,19] |
| Microcera larvarum            | CBS 75.79 + BBA 62299 + MAUC 19043 + NRRL 2047 | KM231060 KM231230 KM231408 KM231599 KM231825 KM231701 KM232252 KM231287 KM231957 KM231957 | [18,19] |
| Microcera larvarum            | CBS 78.45 + CBS 137944 | – – – – – – – – – – – – | [18,19] |
| Microcera rubra               | CBS 63.76 T + BBA 62480 + NRRL 20475 | HQ697693 KM231233 KM231609 EU460050 HQ977920 KM232153 HQ977676 JP400948 EL360018 | [18,19] |
| Pseudocosmospora regregiata   | CBS 125891 T + G.J.S. 90-56 | – – – – – – – – – – – – | [18,19] |
| Pseudocosmospora nipetillicia | CBS 137944 T + A.R. 4952 | – – – – – – – – – – – – | [18,19] |
| Pseudocosmospora emarginata   | CBS 137944 T + A.R. 4952 | – – – – – – – – – – – – | [18,19] |
| Zellulathidium fusiforme      | CBS 504.67         | KM231076 KM231249 KM231436 – KM231639 KM231720 KM232272 KM232415 KM231976 KM232010 | [18,19] |
| Zellulathidium fusiforme      | CBS 231.97         | KM231077 KM231246 KM231435 KM231593 KM231536 KM232271 KM232414 KM231975 KM232010 | [18,19] |

Notes: superscript T represents ex-type or ex-epitype isolates. “–” means that the sequence is missing or unavailable. New sequences are listed in bold. Abbreviations: A.R.: Amy Y. Rossman, USDA-ARS, MD, USA; ATCC: American Type Culture Collection, U.S.A.; BBA: Julius Kühn-Institute, Institute for Epidemiology and Pathogen Diagnostics, Berlin and Braunschweig, Germany; CBS: Centraalbureau voor Schimmelcultures, Utrecht, Netherlands; C.H.: Cesar S. Herrera, University of Maryland, MD, USA; G.J.S.: Gary J. Samuels, USDA-ARS, MD, USA; IMI: International Mycological Institute, CABI-Bioscience, Egham, UK; MAFF: MAFF Genebank, National Institute of Agrobiological Sciences, Ibaraki, Japan; MUCL: Mycothèque de l’Université Catholique de Louvain, Belgium; NRRL: Agricultural Research Service Culture Collection, USA; TG: T. Grafenhan collection.
3. Results

3.1. Phylogenetic Analyses

Phylogenetic analyses of a combined five-gene dataset (ITS, LSU, SSU, tef1-α, rpb2) comprised 62 taxa, and the tree is rooted with *Tubeufia javanica* Penz. & Sacc. (MFLUCC 12-0545) and *T. chiangmaiensis* Boonmee & K.D. Hyde (MFLUCC 11-0514) (Tubeufiaceae, Tubeufiales). The alignment contained 5721 characters (LSU = 1046, ITS = 821, SSU = 1176, tef1-α = 1507, rpb2 = 1171), including gaps. The best scoring RAxML tree with a final likelihood value of −40,064.587233 is presented. The matrix had 2539 distinct alignment patterns, with 46.29% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.244598, C = 0.248213, G = 0.265992, T = 0.241197, with substitution rates AC = 1.565487, AG = 3.743698, AT = 1.774643, CG = 1.114196, CT = 7.131582, GT = 1.000000. The gamma distribution shape parameter α = 0.240760, and the Tree-Length = 3.685780.

Phylogenetic trees generated from ML and BI analyses were similar in overall topologies. Phylogeny from the combined sequence data analysis indicates that all the Pleosporalean families are monophyletic with strong bootstrap support values (Figure 1). Three species grouped with taxa in *Podonectria* with 100% ML and 1.00 BYPP support. A species (SICAUCC 21-0004, SICAUCC 21-0005) clustered with *P. novae-zelandiae* in a clade with 99% ML and 1.00 BYPP statistical support. Our novel species *P. kuwanaspidis* constitutes a moderately supported independent lineage (82% ML/– BYPP statistical support) between *P. novae-zelandiae* and *P. coccicola*.

DNA sequences of four known species of *Microcera* and our new taxon, *M. kuwanaspidis*, were used in the analyses. The combined dataset comprised 24 taxa within Nectriaceae and two outgroup taxa in Tilachlidiaceae (Table 2). The alignment contained 7447 characters (ITS = 638, LSU = 831, acl1 = 1041, act = 673, cmdA = 778, his3 = 530, rpb1 = 741, rpb2 = 874, tef1-α = 631, tub2 = 710), including gaps. The tree is rooted with *Tilachlidium brachiatum* (Batsch) Petch (CBS 363.97, CBS 505.67). The best scoring RAxML tree with a final likelihood value of −50,074.064664 is presented. The matrix had 3327 distinct alignment patterns, with 28.65% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.233349, C = 0.272026, G = 0.255053, T = 0.239571, with substitution rates AC = 1.285610, AG = 3.696293, AT = 1.292257, CG = 0.967004, CT = 6.115076, GT = 1.000000. The gamma distribution shape parameter α = 0.261457, and the Tree-Length = 2.372705. In the concatenated phylogenetic analyses of ML and BI, all species of *Microcera* analyzed clustered in a well-supported clade (ML = 100%, BYPP = 1.00) with a close affinity to *Fusicolla* and *Macroconia* (Figure 2). *Microcera kuwanaspidis* is related to *M. coccophila* in a subclade with 100% ML and 1.00 BYPP statistical support.

3.2. Taxonomy

**Podonectriaceae** H.T. Dao & Rossman, Mycological Progress 15(5): 47 (2016) amended. MycoBank number: MB 815827

Type genus: *Podonectria* Petch, Trans. Br. mycol. Soc. 7(3): 146 (1921).

*Parasitic* fungus on scale insects, other fungi, or substrates previously colonized by other fungi. **Sexual morph:** Stromata byssoid, well-developed or scant, white to brown or dark-brown. Ascomata solitary or aggregated, superficial on or immersed in the stroma, globose to subglobose, obpyriform or ovoid, cream white to light yellow, or brown to dark brown, covered with hairs or absent. The hamathecium comprises numerous reticulate, filiform, septate, branched, pseudoparaphyses. Asci 8-spored, bitunicate, long clavate to cylindric. Ascospores long clavate to long cylindric, or vermiform, multiseptate. **Asexual morph:** Tetracrium-like. Sporodochia formed directly on cushion-shaped, white, orange, or brown, and hard stroma. Conidiophores moniliform. Conidia usually 1–4 “arms”, narrowed toward the apex, joined at the basal cell, multiseptate.

Notes: The family Podonectriaceae was introduced to accommodate *Podonectria* by Dao et al. [5], in which descriptions of conidia, ascomata, asci, and ascospores were lacking. Here we emend those descriptions and the habitats of Podonectriaceae with the inclusion of fungi or substrates previously colonized by other fungi and not only scale
insects [4,5,8,12]. This broadens the taxonomic concept of Podonectria, which is further supported by molecular analyses in this study.

*Podonectria nova-zelandiae* Dingley, Trans. & Proc. Roy. Soc. N.Z. 81: 496 (1954) (Figures 3 and 4).

Figure 1. Phylogram generated from RAxML analysis based on ITS, LSU, SSU, tef1-α, and rpb2 Scheme 70. and Bayesian posterior probabilities (BYPP, right) equal to or greater than 0.95 are indicated at the nodes respectively. The sequences from ex-type strains are in bold. The newly generated sequence is in red.
clustered in a well-supported clade (ML = 100\% \text{,} BYPP = 1.00) with a close affinity to \textit{Fusicolla} and \textit{Macroconia} (Figure 2).

\textit{Microcera kuwanaspidis} is related to \textit{M. coccophila} in a subclade with 100\% ML and 1.00 BYPP statistical support.

Figure 2. Phylogram generated from RAxML analysis based on combined ITS, LSU, \textit{tef1-\alpha}, \textit{rpb1}, \textit{rpb2}, \textit{acl1}, \textit{act}, \textit{tub2}, \textit{cmdA}, and \textit{his3} sequence data of \textit{Microcera} isolates. Bootstrap support values for maximum likelihood (ML, left) higher than 70\% and Bayesian posterior probabilities (BYPP, right) equal to or greater than 0.95 are indicated at the nodes respectively. The sequences from ex-type strains are in bold. The newly generated sequence is in red.

3.2. Taxonomy

\textbf{Podonectriaceae} H.T. Dao & Rossman, Mycological Progress 15(5): 47 (2016)

amended.

\textbf{MycoBank number}: MB 815827

\textbf{Type genus}: \textit{Podonectria} Petch, Trans. Br. mycol. Soc. 7(3): 146 (1921).

\textbf{Parasitic fungus on scale insects, other fungi, or substrates previously colonized by other fungi.}

\textbf{Sexual morph}: Stromata byssoid, well-developed or scant, white to brown or dark-brown.

\textbf{Ascomata}: solitary or aggregated, superficial on or immersed in the stroma, globose to subglobose, obpyriform or ovoid, cream white to light yellow, or brown to dark
Figure 3. *Podonectria novae-zelandiae* (SICAU 21-0005). (a,b) Ascomata and sporodochia on host substrate. (c) Section through ascoma. (d) Peridium. (e,f) Hairs covering on ascoma. (g) Pseudoparaphyses. (h) Ocular chamber. (i–k) Asci. (l–p) Ascospores. (q) Germinated ascospores. (r,s) Colonies on PDA after 18 days. Scale bars: (a,b) 200 μm, (c) 100 μm, (d) 50 μm, (e–g) 20 μm, (h) 10 μm, (i–q) 20 μm.
Podonectria novae-zelandiae (SICAU 21-0004). (a–c) Sporodochia and ascomata on host substrate. (d–f) Immature conidia. (g–j) Mature conidia. (k,l) Conidiophores. (m,n) Colonies on PDA after 20 days and 60 days. (o) Germinated conidium. Scale bars: (a–c) 500 µm, (d–k) 20 µm, (l,o) 10 µm.

MycoBank number: MB 304079

Habitat associated with scale insects *Kuwanaspis howardi* on *Phyllostachys heteroclada*. Sexual morph: Stromata byssoid, brown, well-developed, and covered the scale insects. Ascomata solitary, rarely aggregated, superficial on the byssoid stroma, concomitant with sporodochia, light yellow, covered with long hairs, 150–415 µm high (x̄ = 240 µm, n = 20), 100–350 µm wide (without hairs) (x̄ = 192 µm, n = 30). Hairs 60–280 µm long, multiseptate, 3–6.5 µm wide, straight, or curved, abundant, hyaline, slightly narrowed toward the apex, 1–2.5 µm thick-walled (n = 30). Peridium 60–100 µm thick, usually wider at the base, composed of hyaline suborbicular cells forming textura angularis, the cells measuring...
5.5–12 × 4.5–10 µm (⌀ = 8.9 × 7.0 µm, n = 20). *Hamathecium* 1.5–3 µm diameter (⌀ = 2.3 µm, n = 30), 1 µm diameter at the apex, longer than the asci, numerous, filiform, curved, septate, branched pseudoparaphyses. *Asci* 220–340 × 18–26 µm (⌀ = 267 × 21 µm, n = 20), 8-spored, bitunicate, cylindrical, straight, or curved, rounded at apex. *Ascospores* 100–160 × 7–10 µm (⌀ = 138 × 9 µm, n = 30), fasciculate, parallel, long-clavate, rounded at ends, multisepate, 10–22 septa with slight constriction, curved, hyaline, smooth. *Asexual morph: Stromata* hard, white to grey-brown, cushion-shaped, formed directly on host scales with 1–4 sporodochia. *Sporodochia* erupted, white, yellowish to grey-brown, scattered or aggregated. *Conidiophores* inconspicuous, short, 1–2 celled, the cells 3–7 × 4–10 µm (⌀ = 5.0 × 7.5 µm, n = 30), usually globose, subglobose, or shortly cylindrical, attached with 1–2 conidiogenous cells. *Conidiogenous cells* 3–7 × 4–11 µm (⌀ = 7.3 × 6.5 µm, n = 30), globose or ellipsoidal. *Conidia* usually with two and three “arms”, occasionally one and four “arms”, each “arm” varies in length and slightly divergent, 85–163 µm long (⌀ = 117 µm, n = 70), 7–11 µm wide (⌀ = 9 µm, n = 70) with 11–25 septa, mature conidium tapering toward the acute apex. All “arms” of single conidium joined at a basal oval or irregular cell, measuring 4–7 × 5–10 µm (⌀ = 5.3 × 7.1 µm, n = 40).

Material examined: CHINA, Sichuan Province, Ya’an City, Lushan County (102°55’58.13″ E, 30°15’24.07″ N, Alt. 1116 m), on scale insect *Kuwanaspis howardi*, 10 June 2020, Xiu-lan Xu, XXL202006006 (SICAU 21-0005), living culture SICAUCC 21-0005; ibid. XXL202006005 (SICAU 21-0004), living culture SICAUCC 21-0004.

Culture characters: Conidia germinate on PDA within 12 h, and the cultures grow slowly on PDA. Colonies reach 2 cm in diameter after 25 days. Colonies from single conidia are flocculent and hard, with irregular margins. The mycelium is creamy white to light lemon yellow starting at the center but gradually becoming brown to dark brown after 20 days. Aerial hyphae cluster and raise straightly, measuring 2–3 µm diam. Conidia develop on small, sparsely distributed mycelial clumps after two months. Conidiophores moniliform, branched, multi-celled, and longer than those in nature. Conidia commonly have three “arms”, occasionally two and four “arms”, rarely one and five “arms”, each “arm” with 17–22 septa, measuring 115–145 µm long, 6.5–10 µm wide (⌀ = 128 × 7.9 µm, n = 30). Ascospores germinate on PDA within 12 h, and the cultures grow slowly on PDA. Colonies reach 1 cm in diameter after 20 days. Colonies from single ascospores are cottony, with regular margin; the mycelium is creamy white to yellow; and the back of colonies is brown, with concentric rings.

Notes: Here, we follow the recommendation of Rossman et al. [62] by adopting *Podonectria* over *Tetracrium*. The asexual morph of *P. novae-zelandiae* was reported by Dao et al. [5], and was supported with morphology and molecular data. Our observations agree with the descriptions provided by Rossman [4] and Dao et al. [5]. Nucleotide comparison of ITS and LSU (SICAUCC 21-0005) reveals high similarity to *P. novae-zelandiae* (isolate PUcS13, similarities = 473/476 (99%), 0 gaps (0%); similarities = 517/518 (99%), 0 gaps (0%), respectively) in Dao et al. [5]; however, the latter lack SSU, *tef1*-α, and *rpb2* sequences for further comparisons. The conidia produced here in culture were similar to those on scale insects in the field.

*Podonectria kuwanaspidis* X.L. Xu & C.L. Yang sp. nov. (Figure 5)
Figure 5. *Podonectria kuwanaspidis* (SICAU 21-0002, holotype). (a) Ascomata on or around the scale host (red arrow). (b) Aggregated ascomata. (c) Solitary ascomata. (d) Section through ascoma. (e) Peridium. (f) Hairs covering ascoma. (g) Pseudoparaphyses. (h–k) Asci. (l–n, q–u) Ascospores. (o, p) Colonies on PDA after 25 days and 50 days. (v, w) Germinated ascospores. Scale bars: (a) 500 μm, (b, c) 200 μm, (d) 100 μm, (e) 50 μm, (f–n) 20 μm, (q–w) 20 μm.

MycoBank number: MB 838465

*Etymology:* In reference to the generic name for the associated scale insect. Holotype: SICAU 21-0002.

*Habitat* associated with scale insects *Kuwanaspis howardi* on *Phyllostachys heteroclada.*

*Sexual morph:* Stromata byssoid, white or brown, well-developed and covering the scale insects, or forming a thin, white, and byssoid layer, which spreads out from the scale over...
the stem. *Ascomata* solitary to aggregated, superficial on byssoid stroma around the scale hosts, or extending far beyond the scale byssoid stroma, globose to subglobose, creamy white to dirty white, covered with hairs, 200–590 μm high (σ = 424 μm, n = 20), 140–600 μm wide (σ = 346 μm, n = 70). *Hairs* 30–120 μm long, 0–4 septa, 8–16 μm wide at the base, 2–7 μm wide at the apex, abundant, hyaline, distinctly narrowed toward the apex, 2–4.5 μm thick-walled (n = 40). *Ostiole* 40–100 μm wide. *Peridium* 40–170 μm thick (σ = 72 μm, n = 30), usually wider at the base, composed of hyaline elongated cells forming *textura prismatica* to *textura angularis*, becoming globose toward outside, the cells measuring 6.5–15 × 8–20 μm (σ = 10 × 14 μm, n = 30). *Hamathecium* 1.5–3.5 μm in diameter (σ = 2.2 μm, n = 40) at the base, 1 μm diameter at the apex, longer than the asci, numerous, filiform, curved, septate, branched pseudoparaphyses.

*Microconidia* distinguish apical cell and basal cell. Slightly curved, slender toward each end, 3–8 septate, mostly 5–6–7 septate, difficult to determine.

**Asexual morph**: Undetermined.

**Material examined**: CHINA, Sichuan Province, Ya'an City, Lushan County (102° 55' 58.13" E, 30° 15' 24.07" N, Alt. 1116 m), on scale insect *Kuwanaspis howardi*, 10 June 2020, Xiulian Xu, XXL202006002 (SICAU 21-0002, holotype), ex-type culture, SICAUCC 21-0002; ibid. XXL202006003 (SICAU 21-0003, paratype), living culture SICAUCC 21-0003. ibid. Yucheng District, Kongping Township (103° 2' 59.87" E, 29° 50' 8.56" N, Alt. 1133 m), on scale insect *Kuwanaspis howardi*, 19 September 2018, Xiulian Xu, YCL201810014 (SICAU 21-0007, paratype), living culture SICAUCC 21-0007.

Culture characters: Ascosores germinating on PDA within 12 h, and the cultures grow slowly on PDA. Colonies reach 2 cm in diameter after 25 days. Colonies from single ascospores are cottony, cling to the medium, with regular margin; the mycelium is creamy white to pale yellow but gradually becomes pale brown after 30 days.

Notes: This new taxon resembles species of *Podonectria*, in having superficial, bright, or lightly colored fruiting bodies and hairs obscuring the outer wall of ascoma. Morphologically *Podonectria kuanaspidis* is comparable with *P. novae-zelandiae*. It has shorter (30–120 vs. 60–280 μm) and thicker-walled hairs (2–4.5 vs.1–2.5 μm), longer and narrower ascospores (150–240 × 5–7 μm vs. 100–160 × 7–10 μm). The ITS base-pair comparison between *Podonectria kuanaspidis* (SICAUCC 21-0002) and phylogenetically affiliated *P. sicianensis* (SICAU 16-0003) reveals 15% (including 20 gaps, 4%) nucleotide differences; the nucleotide differences in the SSU, LSU, *tef1*-α, and *rpb2* region between them are 1% (0 gaps, 0%), 3% (5 gaps, 0%), 4% (0 gaps, 0%), and 10% (0 gaps, 0%), respectively. Hence, we describe our collection as a new species in Podonectria, as recommended by Jeewon and Hyde [63].

*Nectriaceae* Tul. & C. Tul., Select. fung. carpol. (Paris) 3:3 (1865)

*Microcera* Desm., Annls Sci. Nat., Bot., sér. 3 10:359 (1848)

*Microcera kuanaspidis* X.L. Xu & C.L. Yang sp. nov. (Figure 6)

**Basionym**: *Podonectria kuanaspidis* Xu, XXL202006002 (SICAU 21-0002, holotype), ex-type culture, SICAUCC 21-0002; ibid. XXL202006003 (SICAU 21-0003, paratype), living culture SICAUCC 21-0003; ibid. Yucheng District, Kongping Township (103°2'59.87" E, 29°50'8.56" N, Alt. 1133 m), YCL201810014 (SICAU 21-0007, paratype), living culture SICAUCC 21-0007.

**Etymology**: In reference to the generic name for the associated scale insect.

**Holotype**: SICAU 21-0006.

**Habitat associated with scale insects** *Kuwanaspis howardi* on bamboo. **Sexual morph**: Undetermined. **Asexual morph**: Stromata 500–690 μm long, 410–600 μm wide (σ = 614 × 524 μm, n = 20), ellipsoid, orange-red, completely covering a single scale insect, or absent. Sporodochia 190–280 μm long, 150–300 μm wide (σ = 240 × 227 μm, n = 20), formed singly on the margin of the stroma, or rarely in groups of one to three on the margin of the scale covers. Conidiophores with developing macroconidia form a pink upright mass. *Macroconidia* 80–95–120 μm long × 6.5–8.5 (σ = 107 × 7.3 μm, n = 20) μm wide, hyaline, cylindrical, slightly curved, slender toward each end, 3–8 septate, mostly 5–6–7 septate, difficult to distinguish apical cell and basal cell. *Microconidia* and *chlamydospores* were not observed.

**Material examined**: CHINA, Sichuan Province, Ya'an City, Lushan County (102°55'58.13" E, 30°15'24.07" N, Alt. 1116 m), on scale insect *Kuwanaspis howardi* on *Phyllostachys hetero-
clada, 10 June 2020, Xiu-lan Xu, XXL202006007 (SICAU 21-0006, holotype), ex-type culture SICAUCC 21-0006, additional GenBank Number: SSU = MW462896; CHINA, Sichuan Province, Meishan City, Hongya County (103°14′2.64″ E, 29°41′53.07″ N, Alt. 538 m), on scale insect Kuwanaspis howardi on Pleioblastus amarus, 9 March 2021, Chun-lin Yang, YCL202103001 (SICAU 21-0009, paratype), living culture SICAUCC 21-0009, additional GenBank Number: SSU = MZ029435.

**Figure 6.** Microcera kuwanaspidis (SICAU 21-0006, holotype). (a,b) Stromata and sporodochia on host substrate. (c–e) Conidiophore with developing macroconidia. (f) Germinated conidium. (g–l) Macroconidia. (m) Colonies on PDA after 12 days. Scale bars: (a,b) 200 µm, (c–e) 50 µm, (f–l) 20 µm.

Culture characters: Colonies from a single macroconidium on PDA grow slowly and reach approximately 2.2 cm in diameter after 12 days at 25 °C, circular, flat, whitish to bright orange with white mycelium on the surface forming concentric circles, and the back of colonies is bright orange.

Notes: Distinguished from the red-headed fungus Microcera coccophila [18,64], in which the sporodochium is usually formed in groups on margin of dead scale or their covers accompanied with perithecia surround the edge of scale covers. However, this new species
has distinct stroma covering the host, with a single sporodochium at the edge and without perithecia being discovered. Furthermore, although they are similar in size, *Microcera kuwanaspidis* is different from *M. coccophila* (CBS 310.34) with 100% ML and 1.00 BYPP support; however, striking base-pair differences are noted, viz. 1% (0 gaps, 0%), 1% (0 gaps, 0%), 1% (0 gaps, 0%), 13% (23 gaps, 4%), 4% (0 gaps, 0%), 3% (0 gaps, 0%), 5% (3 gaps, 0%), and 9% (6 gaps, 1%) in the ITS, LSU, *rpb2*, *tef1-α*, *acl1*, *act*, *cmdA*, and *his3* DNA sequence data, respectively. According to the guidelines of Jeewon and Hyde [63], our collection is proposed as a new species.

4. Discussion

Mycologists have questioned the exact familial placement of *Podonectria* since the beginning of its establishment. Dingley [3] placed the genus in Clavicipitaceae (Hypocreales). Rossman transferred it into the Pleosporaceae (Pleosporales) due to its bitunicate asci rather than the unitunicate asci found in Hypocreales [4,7]. Barr transferred *Podonectria* to Tubeufiaceae [65], which was erected [66] to accommodate pleosporaceous taxa that are typically hyper saprobic on other fungi or substrates previously colonized by other fungi, hyperparasitic on foliicolous fungi, parasitic on scale insects, or occasionally parasitic on living leaves. This treatment was followed by subsequent authors [9,67–69]. However, Tubeufiaceae, which was comprehensively reviewed by Boonmee et al. [70], was accommodated in a new order, Tubeufiales [58]. This placement was followed by Wijayawardene et al. [71,72] and Hongsanan et al. [73]. However, Dao et al. [5] proposed Podonectriaceae, a new family in Pleosporales, to accommodate this genus, which was confirmed by ITS and LSU data. This placement was supported by Yang et al. [12], in which *Podonectria sichuanensis* was identified based on morphological characteristics and phylogenetic analyses. Based on the phylogenetic results of combined ITS, LSU, SSU, *tef1-α*, and *rpb2* data in this current study, we confirm Podonectriaceae as an accepted family in the suborder Pleosporineae [49]. Podonectriaceae is phylogenetically closely related to Pseudopyrenochaetaceae that has been established to accommodate two species, viz. *Pseudopyrenochaeta lycopersici* and *P. terrestris* [37]. However, the two families are morphologically distinct. Pseudopyrenochaetaceae has pycnidial conidiomata, filiform conidiophores, and aseptate, cylindrical to allantoid conidia, whereas Podonectriaceae comprises sporodochial conidiomata, moniliform or inconspicuous conidiophores, and 1–4 armed, multiseptated conidia. In addition, the coelomycete genera *Tetracarium* that has septate tetraradiate conidia [74,75] was documented as the anamorph associated with *Podonectria gahnia* according to substrate observation [4]. However, the association is somewhat confused, as it lacks further phylogenetic investigations and taxonomic studies. Identical molecular sequences of *Podonectria novae-zelandiae* in our study confirmed the link between the sexual morphs and asexual morphs in *Tetracarium*. *Podonectria* was reported to be associated with scale insects on various hosts in previous studies [1,4,5,38]. In this paper, we isolated *Podonectria sichuanensis* (SICAUCC 21-0001) on the ascomata of *Neostagonosporella sichuanensis* in our sampling site and confirm that the *Podonectria* species are not only parasitic on scale insects but also on other fungi or substrates previously colonized by other fungi [12]. According to published studies, most species of *Podonectria* are associated with armored scale insects, in addition to being associated with the mostly reported hosts *Citrus aurantium* L. and *C. nobilis* Lour. (Rutaceae) [1,4] and the known host plants associated with *Podonectria* are *Calluna vulgaris* Salisb. (Ericaceae), *Gaulinia setifolia* (A. Rich) Hook.f., *G. xanthocarpa* (Hook.f.) Hook. f. (Cyperaceae), *Juniperus bermudiana* L. (Cupressaceae), *Olearia rani* Druce ( Asteraceae), *Phyllostachys heterochlada* (Poaceae) and *Podocarpus ferrugineus* G. Benn. ex D. Don (Podocarpaceae) [3–5,12].

Gräfenhan et al. [18] reported an association of *Microcera* to *Fusarium*, *Cladostereum*, *Mycogloea* Pat., *Mycoeleo* L.S. Olive, *Tetracarium* Henn., and accepted four species in *Microcera*. Nowadays, taxonomic concepts based on multi-gene phylogenetic inference have provided a deeper understanding of phylogenetic relationships than those based on individual
gene regions [76–79]. Recently, combined ITS-LSU-ef1-a-act1-act-mdm1-act-mdm2 datasets were used to clarify intraspecific and intergeneric relationships within Nectriaceae [19], and combined ITS-LSU-ef1-a-act-mdm1-act-mdm2 datasets were similarly used for Hypocreales [80]. In this paper, Microcera kuwanaspidis can be distinguished from M. coccophila and is established as new species on account of base-pair differences, especially in the ef1-a (13%), act1 (4%), act2 (5%), and his3 (9%). The Microcera species have been mostly reported associated with armored scale insects on citrus (Rutaceae), viz. Aonidiella aurantii, Lepidosaphes beckii, Unaspis citri, and Quadraspidiotus perniciosus on Pyrus communis, Prunus domestica and P. cerasus (Rosaceae), as well associated with nut scale Eulecanium tiliae (Hemiptera: Coccidae) on Salix sp. (Salicaceae) and Fraxinus excelsior (Oleaceae), and an unknown scale insect on Broussonetia kazinoki × B. papyrifera (Moraceae), Laurus nobilis (Lauraceae), and Citrus maxima (Rutaceae), and apple trees [18,60,64].

In China, the entomopathogenic fungi associated with scale insects was mainly focused on commercial Citrus plants in the 1990s. Verticillium lecanii (Zimm) Viegas is the most common fungus that is parasitic on scale insects on Citrus since its discovery from Guizhou Province in 1982 [81]. Subsequently, Aschersonia duplex Berk., Beauveria bassiana (Bals.-Criv.) Vuill., Fusarium jwuanum Henn., F. moniliforme Sheld., Microcera coccophila, Nigrospora sphaerica (Sacc) Mason, and Podonectria coccicola have also been reported to be associated with the scale insects on citrus [82–84]. Microcera and Podonectria were commonly encountered on scale insects within tree canopies and occurred throughout the year but were more noticeable under wet and humid conditions [5,64,85,86], consistent with the observations in this study. Presently, Microcera coccophila and Podonectria coccicola have been the most commonly and worldwide recorded species on scale insects, especially on orange trees [1,4,7,85–89]. This paper provides new records for three entomopathogenic fungi, Podonectria kuwanaspidis, P. novae-zelandiae, and Microcera kuwanaspidis on armored insect scale from bamboo in China. According to the field observation from 2015 to 2020, the three species are commonly associated with Kuwanaspidis howardi on native bamboo, especially on Phyllostachys heteroclada, and they effectively cause the scale insect hosts to be infected, which ultimately results in death. As documented by Rossman [4] and Dao et al. [64], the role of entomopathogens in the biological control of destructive scale insects on citrus trees was usually controlled by chemical sprays. These entomopathogenic fungi should be further screened to assess their potential for commercial development as biological control agents.

Author Contributions: X.-L.X. and C.-L.Y.: conceptualization. X.-L.X.: data curation. X.-L.X. and C.-L.Y.: formal analysis, methodology, and writing—original draft. X.-L.X. and Q.-G.X.: funding acquisition. X.-L.X., C.-L.Y., Q.Z. and Y.-C.L.: investigation. Q.-G.X. and Y.-G.L.: project administration. C.-L.Y.: supervision. C.-L.Y., R.J., S.S.N.M., D.N.W. and K.D.H.: writing—review and editing. All authors contributed to the article and approved the submitted version. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Chengdu Science and Technology Bureau (2019040509).

Informed Consent Statement: Not applicable.

Data Availability Statement: The datasets presented in this study can be found in the NCBI GenBank (https://www.ncbi.nlm.nih.gov/), MycoBank (http://www.MycoBank.org) and TreeBASE (http://www.treebase.org) (all accessed on 18 July 2021).

Acknowledgments: Xiulan Xu acknowledges the Sichuan Agricultural University for providing laboratory facilities, and Konstanze Bensch is thanked for the nomenclatural correction of the name. D.W. would like to thank the CAS President’s International Fellowship Initiative (No. 2021FYB0005) and Postdoctoral Fund from the Human Resources and Social Security Bureau of Yunnan Province.

Conflicts of Interest: The authors declare no conflict of interest.

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