Synopsis of Leptosphaeriaceae and Introduction of Three New Taxa and One New Record from China

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Abstract: Leptosphaeriaceae, a diverse family in the order Pleosporales, is remarkable for its scleroplectenchymatous or plectenchymatous peridium cells. Four Leptosphaeriaceae species were discovered and studied during the investigation of saprobic fungi from plant substrates in China. Novel taxa were defined using multiloci phylogenetic analyses and are supported by morphology. Based on maximum likelihood (ML) and Bayesian inference (BI) analyses, these isolates represent three novel taxa and one new record within Leptosphaeriaceae. A new genus, Angularia, is introduced to accommodate Angularia xanthoceratis, with a synopsis chart for 15 genera in Leptosphaeriaceae. This study also revealed a new species, Plenodomus changchunensis, and a new record of Alternariaster centaurae-diffusa. These species add to the increasing number of fungi known from China.

Keywords: new taxa; new record; Pleosporales; saprobic fungi; taxonomy; Xanthoceras sorbilofolium

1. Introduction

Leptosphaeriaceae is an important group of fungi in the order Pleosporales [1–6]. Leptosphaeriaceae was segregated from Pleosporaceae by Barr (1987) and was typified by Leptosphaeria Ces. & De Not. [1–3]. This family is characterized by conical or globose ascomata, scleroplectenchymatous or plectenchymatous peridium cells, cylindrical to oblong pedicellate asci, and septate reddish-brown or yellowish-brown ascospores (Figure 1) [2,4,7–14]. Although Leptosphaeriaceae is similar to Phaeosphaeriaceae, the peridium structure is morphologically distinguishable [15]. Most Leptosphaeriaceae species occur abundantly on dicotyledons, and the asexual morph can be coelomycetous (coniothyrium-like or phoma-like) or hyphomycetous [12,16,17]. Members of Leptosphaeriaceae are saprobes, hemibiotrophs, and pathogens [18–22]. Five genera Curreya, Didymolepta, Hoptamaeria, Leptosphaeria, and Ophiobolus were previously included in the family [1]. Hyde et al. [2] accepted Heterosporicola, Leptosphaeria, Neophaeosphaeria, Paraleptosphaeria, Plenodomus, and Subplenodomus in the family by integrating molecular data. Simmons [23] introduced Alternariaster to accommodate Alternariaster helianthi (=Alternaria helianthi) as the first hyphomycetous record for Leptosphaeriaceae. Trakunyingcharoen et al. [24] subsequently introduced Sphaerelopsis from Dianthus caryophyllus and Vachellia karroo. The family was revised based on morphological characteristics and phylogenetic evidence, and ten genera were accepted [4]. Several other
genera have also been added to *Leptosphaeriaceae*, such as *Heterosporicola*, *Ochraceocephala*, *Querciphoma*, *Sclerenchymomyces*, and *Praeclarispora* [8,12–14].

Figure 1. Morphology of ascomata, conidiomata, ascospores, and conidiogenous cells; and conidia of 15 genera in *Leptosphaeriaceae*. Asterisk (*) indicates the genera with synanamorphs asexual characters.
Preuss (1851) introduced *Plenodomus*, which was typified by *P. rabenhorstii* [25]. The *Plenodomus* species belong to *Leptosphaeriaceae* and are one of the members with phoma-like taxa [2,5,17]. The type material of *P. rabenhorstii* was lost, and therefore *P. lingam* (Tode) Hohn. (Sexual morph: *Leptosphaeria maculans* (Desm.) Ces. & De Not.) was replaced as the type species of *Plenodomus* [26]. Phoma-like taxa were previously classified into nine sections including *Plenodomus* based on morphological characteristics [27,28]. de Gruyter et al. [29] determined that the *Plenodomus* section was distinct from *Phoma sensu stricto* based on phylogenetic analyses and classified *Phoma* under *Didymellaceae*. The *Plenodomus* species are the causal agents of diverse diseases on different plants throughout the world [30,31]. *Plenodomus* species are also isolated as saprobes on dead branches and stems of plants [17].

*Alternariaster* was introduced by Simmons [23] to accommodate *Alternaria helianthi*, a causal agent of leaf spots of *Helianthus annuus* (sunflower) worldwide [23,32,33]. This genus was segregated from *Alternaria* based on different conidial morphology. Alves et al. [8] confirmed that *Alternariaster* is a member of *Leptosphaeriaceae* and is distinct from *Alternaria* (Pleosporaceae). Four species have been reported in *Alternariaster*, including *A. bidentis* [16], *A. centaureae-diffusae* [4], *A. helianthi* [23], and *A. trigonosporus* [2]. *Alternariaster helianthi* has been reported worldwide as a pathogen of leaf spots on sunflowers, and *Alternariaster bidentis* was reported only from Brazil, whereas *Alternariaster centaureae-diffusae* and *Alternariaster trigonosporus* were reported from Russia [2,4]. This genus has been associated with *Bidens sulphurea*, *Centaurea diffusa*, *Cirsium sp.*, and *Helianthus annuus* [2,4,16,23].

In this study, we introduce one new genus (*Angularia*), two new species (*Angularia xanthoceratis* and *Plenodomus changchunensis*), and one new record of *Alternariaster centaureae-diffusae* collected from China. The species were compared morphologically with other *Leptosphaeriaceae* species. Phylogenetic analyses were performed to confirm the taxonomic position based on maximum likelihood and Bayesian inference of combined LSU, SSU, ITS, and tub2 datasets.

2. Materials and Methods

2.1. Sample Collection and Isolation

The dried stems of *Xanthoceras sorbifolium* Bunge, *Poaceae*, and *Clematis* L. were collected from Changchun, Jilin Province and Kunming, Yunnan Province, China. The samples were preserved in plastic bags with labels describing location, date, host, and collection details. Pure fungal colonies were obtained using single spore isolation [34]. Germinating spores were transferred aseptically to potato dextrose agar (PDA), and the cultures were incubated at 25 °C. The specimens and pure cultures were deposited in the Herbarium of Mycology, Jilin Agricultural University (HMJAU), Changchun, China and International Cooperation Research Center of China for New Germplasm Breeding of Edible Mushrooms Culture Collection (CCMJ), respectively. The new taxa were registered in Mycobank [35].

2.2. Morphological Observation

Ascomata and conidiomata characteristics of the hosts were observed using a Zeiss Stemi 2000C stereomicroscope equipped with a Leica DFC450C digital camera (Leica, Wetzlar, Germany). Hand sections of the ascomata were carried out, and the sections were mounted on a slide with a drop of distilled water. Morphological characteristics were observed and photographed using a Zeiss AX10 light microscope equipped with an Axiocam 506 digital camera. Microscopic measurements were carried out using the ZEN 3.4 (blue edition) program (ZEISS, Jena, Germany). Adobe Photoshop CC2020 (Adobe Systems, San Jose, CA, USA) was used to process the images.

2.3. DNA Extraction, PCR Amplification and Sequencing

DNA was extracted from pure culture using a NuClean PlantGen DNA Kit (CWBIO, China) following the manufacturer’s instructions. Polymerase chain reaction (PCR) was used for the amplification of the large subunit (LSU), small subunit (SSU), internal tran-
scribed spacer regions (ITS), β-tubulin (tub2), and the RNA polymerase II second largest subunit (rpb2). The LSU gene was amplified with the primers LROR and LR5 [36]; the SSU gene was amplified with the primers NS1 and NS4 [37]; the nuclear ITS was amplified with primers ITS5 and ITS4 [37]; the tub2 gene was amplified with primers T1 and Bt2b [38]; and the rpb2 gene was amplified with primers RPB2-5f2 and fRPB2-7cr [39]. The amplification reactions were performed using 20 μL PCR mixtures containing 9 μL sterilized water, 10 μL of 2× Es Taq MasterMix (Dye), 0.3 μL (10 μM) of forward and reverse primers, and 0.4 μL (200 ng/μL) of DNA template. The PCR conditions for LSU, SSU, ITS, and tub2 were as follows: 94 °C for 5 min, then 35 cycles of denaturation at 94 °C for 30 s, annealing at 53 °C for 45 s, elongation at 72 °C for 90 s, and a final extension at 72 °C for 10 min. All the PCR products were visualized on 1% agarose gels stained with standard DNA dye.

2.4. Phylogenetic Analysis

The sequence data were assembled using BioEdit v.7.2.5 [40] The closest matches for the new strains were obtained by using BLASTn searches (accessed on 13 December 2021, http://www.blast.ncbi.nlm.nih.gov/), and reference sequence data were downloaded from recent publications (Table 1) [41,42]. Didymella exigua (CBS 183.55) and D. rumicicola (CBS 683.79) were selected as the outgroup taxa. The sequences were aligned by using MAFFT version 7 (accessed on 7 March 2022, mafft.cbrc.jp/alignment/server) [43], and ambiguous nucleotides were manually adjusted by visual examination in AliView where necessary [44]. Leading or trailing gaps beyond the primer binding site were trimmed from the alignments prior to phylogenetic analyses, and the alignment gaps were treated as missing data.

Table 1. Taxa and GenBank accession numbers used in the phylogenetic analyses. The extypes are shown in bold, and newly generated sequences are shown in blue.

| Species                          | GenBank Accession Numbers                                      | ITS                  | LSU                  | SSU                  | tub2                  |
|----------------------------------|---------------------------------------------------------------|----------------------|----------------------|----------------------|----------------------|
| **Alloleptosphaeria clematidis**  | MFLUCC 17-2071 MT310604 MT214557 MT226674                      |                      |                      |                      |
| **All. italicica**               | MFLUCC 14-0934 KTA45722 KTA45714                               |                      |                      |                      |
| **All. shangrileana**            | HKAS: 112210 MT310604 MT214557 MT226674                      |                      |                      |                      |
| **Alternaria bidentis**          | CBS 134021 KC609333 KC609341                                   |                      |                      |                      |
| **Alt. bidentis**                | CBS 134185 KC609334 KC609342                                   |                      |                      |                      |
| **Alt. centaureae-diffusae**     | MFLUCC 14-0992 KT45723 KT45715 KT457430                      |                      |                      |                      |
| **Alt. centaureae-diffusae**     | MFLUCC 150009 KTA45724 KTA45716 KTA457431                      |                      |                      |                      |
| **Alt. centaureae-diffusae**     | HMJAU 60188 OL996125 OL897175 OL891810 OL898721               |                      |                      |                      |
| **Alt. helianthi**               | MFLUCC 17-2071 MT310604 MT214557 MT226674                      |                      |                      |                      |
| **Alt. helianthi**               | MFLUCC 14-0934 KTA45722 KTA45714                               |                      |                      |                      |
| **Alt. helianthi**               | MFLUCC 14-0992 KT45723 KT45715 KT457430                      |                      |                      |                      |
| **Alt. trigonosporus**           | MFLUCC 15-2237 KY674857 KY674858                               |                      |                      |                      |
| **Didymella exigua**             | CBS 183.55 GU238069 GU238213                                   |                      |                      |                      |
| **D. rumicicola**                | CBS 683.79 KT389503 KT389721                                   |                      |                      |                      |
| **Heterosporicola chenopodii**   | CBS 448.68 FJ427023 EU754187                                   |                      |                      |                      |
| **H. chenopodii**                | CBS 115.96 JF740203 EU754187                                   |                      |                      |                      |
| **H. dimorphospora**             | CBS 165.78 JF740204 EU754187                                   |                      |                      |                      |
| **H. dimorphospora**             | CBS 145.78 JF740203 EU754187                                   |                      |                      |                      |
| **Leptosphaeria cichorium**      | MFLUCC 14-1063 KTA45720 KTA45712 KTA457428                      |                      |                      |                      |
| Species                  | Host                       | Strain/Isolate          | GenBank Accession Numbers         |
|--------------------------|----------------------------|-------------------------|-----------------------------------|
|                          |                            |                         | ITS | LSU | SSU | tnb2   |
| L. conoidea              | Lunaria annua              | CBS 616.75              | JF740201 | JF740279 |      | KT389804 |
| L. doliolum              | Phlox paniculata          | CBS 155.94              | JF740207 | JF740282 |      | JT740146   |
| L. doliolum              | Rudbeckia sp.             | CBS 541.66              | JF740206 | JF740284 |      | JT740145   |
| L. doliolum              | Urtica dioica             | CBS 505.75              | JF740205 | GQ385767 | GQ385715 | JT740144 |
| L. errabunda             | Solidago sp.              | CBS 617.75              | JF740216 | JF740289 |      | JT740150   |
| L. macrocapa             | Mercurialis perennis      | CBS 640.93              | JF740237 | JF740304 |      | JT740156   |
| L. pedicularis           | Pelicularis sp.           | CBS 390.80              | JF740224 | JF740294 |      | JT740155   |
| L. sclerotoides          | Medicago sativa           | CBS 144.84              | JF740192 | JF740269 |      | JT740150   |
| L. slovacica             | Ballota nigra             | CBS 125975              | JF740248 | JF740316 |      | JT740156   |
| L. slovacica             | Ballota nigra             | CBS 438.80              | JF740247 | JF740315 |      | JT740157   |
| L. sydowii               | Senecio jacobaea          | CBS 385.80              | JF740244 | JF740313 |      | JT740157   |
| L. veronicae             | Veronica chamaedrys       | CBS 145.84              | JF740254 | JF740320 |      | JT740160   |

**Neoleptosphaeria jonesii**

- Clematis vitalba
  - MFLUCC 16-1442
  - KY211869
  - KY211870
  - KY211871

**N. rubefaciens**

- Quercus
  - CBS 223.77
  - JF740243
  - JF740312

**Ochraceocephala**

- Foeniculum vulgare
  - Di3AF1 = CBS 145654
  - MN516753
  - MN516774
  - MN516743

- Pa. macrospora
  - Rumex domesticus
  - CBS 114198
  - JF740238
  - JF740305

**Pa. nitschkei**

- Cirsium spinosissimum
  - CBS 306.51
  - JF740239
  - JF740308

- Epifagus virginiana
  - CBS 101638
  - JF740230
  - JF740299

- Rubus idaeus
  - CBS 114591
  - JF740241
  - JF740310

- Rubus sp.
  - MFLUCC 14-0211
  - KT454726
  - KT454718
  - KT454733

- Eupatorium cannabinum
  - CBS 126584
  - JF740213
  - GU301828

- Eupatorium sp.
  - CBS 121.89
  - JF740194
  - JF740271

**Pa. praetermissa**

- Rubus sp.
  - CBS 145.84
  - JF740254
  - JF740320

**Pa. rubi**

- Artemisia argyi
  - KUMCC 18-0151
  - MK387920
  - MK387928

- Artemisia argyi
  - 20-0200A
  - KUMCC 20-0200A
  - MT957062
  - MT957055
  - MT957048

- Brassica rapa
  - CBS 111951
  - JF740198
  - JF740274
  - JF740102

- Brassica juncea
  - CBS 127249
  - JF740199
  - JF740275

**Pl. changhunensis**

- Poaeeae
  - HMJAU 60186
  - OL996123
  - OL984031
  - OL987916

- P. collinsoniae
  - Vitis coignetiae
  - CBS 120227
  - JF740200
  - JF740276
  - JF740156

**Pl. chrysanthemi**

- Chrysanthemum sp.
  - CBS 339.63
  - JF740253
  - GU238151
  - GU238230

**Pl. collinsoniae**

- Malus domestica
  - KNU-AP100C
  - LC550566
  - LC550568

- Malus domestica
  - KNU-20-A1
  - LC591836
  - LC591846

- Malus domestica
  - KNU-20-A2
  - LC591837
  - LC591847

- Malus domestica
  - KNU-20-A3
  - LC591838
  - LC591848

- Malus domestica
  - KNU-20-A4
  - LC591839
  - LC591849

- Malus domestica
  - KNU-20-C4
  - LC591840
  - LC591850

- Anacystis radiatus
  - CBS 375.64
  - AF39459
  - JF740277
  - JF740157

- Citrus sp.
  - ICMP:10937
  - KT309810
  - KT309635

- Satureja montana
  - CBS 120227
  - JF740200
  - JF740276
  - JF740156

**Pl. confertus**

- Anacyclus radiatus
  - CBS 375.64
  - AF439459
  - JF740277

- Erigeron canadensis
  - CBS 244.64
  - AF39460
  - JF740278
  - JF740157

- Malus domestica
  - IRAN 4159C
  = SCUA-Ahm-S41
  - MZ048609
  - MZ043102

- Brassica napus
  - SCUA-Ahm-S41-2
  - MZ04610
  - MZ043103

- Catalpa bignonioides
  - CBS 174.84
  - JF740214
  - JF740287

- Trichum aestivum
  - CBS 834.84
  - JF740215
  - JF740288

- Fraxinus angustifolia
  - F-146,176
  - MN910295
  - MN910294

- Citrus sp.
  - ICMP:10937
  - KT309810
  - KT309635

- Satureja montana
  - CBS 414.62
  - JF740222
  - JF740292

**Pl. deqinensis**

- Brassica napus
  - = SCUA-Ahm-S41
  - MZ048609
  - MZ043102

- Brassica napus
  - SCUA-Ahm-S41-2
  - MZ04610
  - MZ043103

**Pl. enteroleucus**

- Catalpa bignonioides
  - CBS 142.84
  - JF740214
  - JF740287

- Trichum aestivum
  - CBS 834.84
  - JF740215
  - JF740288

- Fraxinus angustifolia
  - F-146,176
  - MN910295
  - MN910294

- Citrus sp.
  - ICMP:10937
  - KT309810
  - KT309635

- Satureja montana
  - CBS 414.62
  - JF740222
  - JF740292

**Pl. fallaciosus**

- Eupatorium cannabinum
  - CBS 126584
  - JF740213
  - GU301828

- Eupatorium coignetiae
  - CBS 120227
  - JF740200
  - JF740276
Table 1. Cont.

| Species | Host | Strain/Isolate | GenBank Accession Numbers |
|---------|------|----------------|----------------------------|
| PL. guttulatus | – | MFLU 151876 | KT454721 KT454713 KT454729 |
| PL. hendersoniae | Pyrus malus | CBS 139.78 | JF40226 JF40296 |
| PL. hendersoniae | Salix cinerea | CBS 113702 | JF40225 JF40295 – KT266271 |
| PL. hendersoniae | Salix appendiculata | LTO | MF799790 |
| PL. influorescens | Fraxinus excelsior | CBS 143.84 | JF40228 JF40297 – KT266267 |
| PL. influorescens | Lilium sp. | PD 73/1382 | JF40229 JF40298 – KT266273 |
| PL. libanotidis | Seseli libanotis | CBS 113795 | JF40231 JF40300 – KY064059 |
| PL. lijiangensis | – | 18-0186 | MK387921 MK387959 MK387929 |
| PL. lindquistii | Helianthus annuus | CBS 381.67 | JF40233 JF40302 – |
| PL. lindquistii | Helianthus annuus | CBS 386.80 | JF40232 JF40301 – |
| PL. lingam | – | AFTOL-ID 277 | KT225526 DQ470946 DQ470993 |
| PL. lingam | Brassica oleracea | CBS 260.94 | JF40235 JF40307 – MZ073915 |
| PL. lingam | Brassica sp. | CBS 275.63 | MW810266 JF40306 – MZ073916 |
| PL. lingam | – | CBS 147.24 | MW810259 JX681097 – MZ073914 |
| PL. lupini | Lupinus mutabilis | CBS 248.92 | JF40236 JF40303 – KY064061 |
| PL. pimpinellae | Pimpenella anisum | CBS 101637 | JF40240 JF40309 – KY064062 |
| PL. salviae | Salvia glutinosa | MFLUCC: 13-0219 | KT454725 KT454717 KT454732 |
| PL. sinensis | Plukenetia sp. | MFLUCC: 17-0657 | MF072722 MF072718 MF072720 |
| PL. sinensis | Tamarindus sp. | MFLUCC: 17-0767 | MF072721 MF072717 MF072719 |
| PL. sinensis | – | KNU-GW1901 | LC550567 LC550569 LC550570 |
| PL. sinensis | Ageratina adenophora | KUCC | MT957064 MT957057 MT957050 |
| PL. sinensis | – | KUCC 18-0153 | MK387923 MK387960 MK387930 |
| PL. sinensis | – | KUCC 18-0152 | MK387923 MK387961 MK387931 |
| PL. tracheiphilus | – | 102227 | MK387924 MK387962 MK387932 |
| PL. tracheiphilus | Citrus limonia | CBS 551.93 | JF40249 JF40317 JF40104 MZ073918 |
| PL. tracheiphilus | Citrus aurantium | CBS 127250 | JF40250 JF40318 – MZ073919 |
| PL. tracheiphilus | Citrus limon | MFLUCC: 17-0767 | MUCL 38481 MW810293 MW715037 – MZ073920 |
| PL. tracheiphilus | Citrus sp. | ATCC 26007 | M2049164 MW959165 – MZ073908 |
| PL. triseptatus | Daucus carota | MFLUCC: 17-1345 | MNE48452 MN648451 – |
| PL. visci | Viscum album | CBS 122783 | JF40256 EU754195 EU754096 KY064063 |
| PL. visci | Viscum album | MFLUCC: 17-1345 | MNE48452 MN648451 – |
| PL. visci | Viscum album | CPC:33316 | MT223832 MT223924 |
| PL. visci | Viscum album | CPC:33315 | MT223831 MT223923 |
| PL. visci | Viscum album | CPC:33314 | MT223830 MT223922 |
| PL. wasabiae | Extrema wasabiae | CBS 120119 | JF40257 JF404032 – KT266272 |
| PL. wasabiae | Extrema japonicum | CBS 120120 | JF40240 JF404034 – |
| Praeclarispora | Artemisia argyi | MFLUCC: 17-0767 | MT957060 MT957053 MT957046 |
| Pr. artemisiae | Artemisia argyi | KUCC | MT957061 MT957054 MT957047 |
| Pseudolepsothapheria | Populus tremuloides | CBS 125980 | JF40221 JF40291 – |
| Pyrenochnaeta niecina | Pinus sp. | CBS 137997 | KJ696152 KJ669290 KJ669249 |
| Querciplophoma carteri | Quercus robur | CBS 105.91 | KF251209 GQ387594 GQ387533 KF252700 |
| Q. carteri | Quercus sp. | CBS 101633 | KF251210 GQ387593 GQ387532 KF252701 |
| Schleroplectenchymomyces | Clematis vitalba | MFLUCC: 17-2180 | MT310605 MT214558 MT266675 |
| Shiraia bambusicola | Phyllostachys sp. | GZAAS2 0703 | GQ845412 GQ845413 GQ460698 |
| Sh. bambusicola | Pleioblastus sp. | GZAAS2 0629 | GQ845412 GQ460698 |
| Sphaerellopsis filum | – | – | – |
| Sp. macroconidialis | Dianthus caryophyllus | CBS 170.92 | JF40256 JF404032 – KT266272 |
| Sp. macroconidialis | Allium schoenoprasum | CBS 658.78 | KF251210 JF404034 – |
| Sp. paraphysata | Cenchrus sp. | CPC:21841 | KF251210 JF404034 – |
| Subplenodomus apicola | Apium graveolens var. | CBS 285.72 | JF40196 GU238040 GU238211 – |
| Su. drobnyjacei | Eustoma exaltatum | CBS 269.92 | JF40211 JF404035 JF40100 |
| Su. drobnyjacei | Gentiana sp. | CBS 270.92 | JF40212 JF404036 – |

**Note:** ITS = Internal Transcribed Spacer; LSU = Large Subunit; SSU = Small Subunit; **ITS LSU SSU** = GenBank Accession Numbers; **tab2** = GenBank Accession Numbers.
Phylogenetic analyses of individual and multiloci phylogenetic analyses (ITS, LSU, SSU, and tub2) were performed to determine the phylogenetic placement of the isolated taxa. Maximum likelihood analysis was performed using RAxML-HPC2 on XSEDE on the CIPRES web portal (accessed on 7 March 2022, http://www.phylo.org/portal2/) [45–47]. The GTR + GAMMA model of nucleotide evolution was used for the datasets, and RAxML rapid bootstrapping of 1000 replicates was performed. The best-fit evolutionary models for individual and combined datasets were estimated under the Akaike Information Criterion (AIC) using jModeltest 2.1.10 on the CIPRES web portal for posterior probability [48]. The GTR model was the best model for all the datasets. Bayesian inference analyses were performed using MrBayes v. 3.2.6 on the CIPRES web portal [49]. Simultaneous Markov chains were run for seven million generations, and trees were sampled every 100th generations.

FigTree v. 1.4 [50] was used to visualize phylogenetic trees. The phylogram was edited by using Adobe Illustrator CS v. 6. All newly generated sequences were deposited in GenBank. All the alignments and trees were deposited in TreeBASE (Submission ID: 29394 and 29395).

3. Results
3.1. Phylogenetic Analyses

The combined LSU, SSU, ITS, and tub2 datasets comprised 138 strains, including our newly sequenced strains. Multiloci data were concatenated, which comprised 2958 characteristics, including gaps (ITS: 1–643, LSU: 644–1509, SSU: 1510–2573, and tub2: 2574–2970). The RAxML analysis yielded a best scoring tree (Figure 2) with a final ML optimization likelihood value of $-19828.46$. The matrix had 928 distinct alignment patterns, with 39.78% undetermined characteristics or gaps. Estimated base frequencies were as follows: $A = 0.240304$, $C = 0.229231$, $G = 0.271334$, and $T = 0.259131$; substitution rates $AC = 1.321448$, $AG = 2.815733$, $AT = 1.680962$, $CG = 0.694608$, $CT = 5.562821$, and $GT = 1.000000$; proportion of invariable sites $I = 0.704486$; and gamma distribution shape parameter $\alpha = 0.555544$.

Phylogenetic trees generated from the Bayesian and maximum likelihood analyses had similar topologies (Figure 2 and Figure S1). However, in the Bayesian analysis, Alloleptosphaeria shangriiana did not cluster within the Alloleptosphaeria clade, but was sister to the Schleroplectenchymyces species with low support (0.72 BPP). The MLBP values (left) and BPP values (right) are provided near each node (Figure 2). For the Bayesian analysis, a total of 10,338 trees were sampled after the 20% burn-in with a stop value of 0.009971.

| Species            | Host                      | Strain/Isolate | ITS Accession Numbers | LSU Accession Numbers | SSU Accession Numbers | tub2 Accession Numbers |
|-------------------|---------------------------|----------------|-----------------------|-----------------------|-----------------------|------------------------|
| Su. galicola      | Galium sp.                | MFLU 15-1368   | KY554204              | KY554199              | –                     | –                      |
| Su. valerianae    | Valeriana officinalis     | CBS 499.91     | JF740252              | JF740319              | –                     | –                      |
| Su. valerianae    | Valeriana officinalis     | CBS 630.68     | JF740251              | GU238150              | GU238229              | –                      |
| Su. violicola     | Viola tricolor            | CBS 306.68     | FJ427083              | GU238156              | GU238231              | KT389849               |
| Tzeanania taiwanensis | Ophiocordyceps macroacicularis | NTUCC 17-005 | MH461123              | MH461120              | MH461126              | MH461132               |
| T. taiwanensis    | Ophiocordyceps macroacicularis | NTUCC 17-006 | MH461124              | MH461121              | MH461127              | MH461133               |
Figure 2. The best scoring RAxML tree of Leptosphaeriaceae based on a concatenated ITS, LSU, SSU, and tub2 datasets. The tree is rooted with *Didymella exigua* (CBS 183.55) and *D. rumicicola* (CBS 683.79). RAxML bootstrap support values $\geq 70\%$ (ML, left) and Bayesian posterior probabilities $\geq 0.90$ (BPP, right) are shown near the nodes. The new isolates are in blue. The type strains are in bold and marked with T.
**Leptosphaeriaceae** was strongly supported in the maximum likelihood and Bayesian analyses (100% ML/1.00 BPP). Within **Leptosphaeriaceae**, **Heterosporicola**, **Leptosphaeria**, **Neoleptosphaeria**, **Ochraceocephala**, **Praeclarispora**, **Querciphoma**, and **Schleroplectenchymyces** strongly supported clades (100% ML/1.00 BPP) were formed. **Alternariaster** (98% ML/1.00 BPP) and **Sphaerellopsis** (97% ML/1.00 BPP) formed strongly supported clades, while **Alloleptosphaeria** and **Plenodomus** were only moderately supported in the maximum likelihood analyses (73% ML and 79% ML, respectively). The newly introduced genus formed an independent lineage basal to **Sphaerellopsis** with 35% ML/0.81 BPP support. A new genus **Angularia** is therefore introduced within **Leptosphaeriaceae**. The newly generated taxa **Plenodomus changchunensis** (HMJAU 60186 and HMJAU 60187) clustered with **Plenodomus lindquistii** with 100% ML/1.00 BPP support, while the strain HMJAU 60188 formed a strongly supported clade with **Alternariaster centaureae-diffusae** taxa (Figure 2).

### 3.2. Taxonomy

**Angularia** R. Xu, Phukhams. & Y. Li, gen. nov.

**MycoBank Number:** 843307.

**Etymology:** referring to the angular peridium of the type species.

**Description:** Saprobic on decaying wood or herbaceous plant material in terrestrial habitats. **Sexual morph:** Undetermined. **Asexual morph:** **Conidiomata** pycnidial, solitary, sometimes aggregated, uniloculate, immersed in host substrate, dark brown to brown, globose, coriaceous. **Ostioles** absent. **Conidiomatal wall** thick-walled, multilayered, scleroplectenchymatous cells thick at base, composed of **textura angularis**, lined with a thick hyaline layer bearing conidiogenous cells. **Conidiophores** reduced to conidiogenous cells. **Conidiogenous cells** enteroblastic, phialidic, determinate, discrete, subcylindrical to truncate, smooth-walled, hyaline, arising from the inner layers of conidiomata. **Conidia** fusiform, truncate at both ends, aseptate, hyaline, smooth.

**Type species:** **Angularia xanthoceratis** R. Xu, Phukhams. & Y. Li.

**Notes:** **Angularia** is introduced for a strongly supported lineage comprising **Angularia xanthoceratis** (1.00 BPP, Figure 2). **Angularia** formed a distinct lineage to **Alternariaster**, **Ochraceocephala**, **Plenodomus**, **Praeclarispora** and **Sphaerellopsis** based on multiloci phylogenetic analyses. For individual loci, **Angularia** formed a sister clade distinct from **Heterosporicola** (ITS) and formed a sister clade distinct from **Pseudoleptosphaeria_etheridgei** (LSU). **Leptosphaeriaceae** species are remarkable for having superficial to semi-immersed, shiny ascomata or conidiomata, with thick, multilayers of scleroplectenchymatous or pseudoparenchymatous tissue types [4]. The fungus has semi-immersed to immersed conidiomata, black, with a multilayer scleroplectenchymatous-type tissue (Figure 3). **Angularia** is similar to **Plenodomus** and **Alternariaster** in having peridium with scleroplectenchymatous cells [4]. **Angularia** is also similar to **Plenodomus** and **Sphaerellopsis** in having **textura angularis** cells in the conidiomatal wall [4,24]. However, **Angularia** and **Ochraceocephala** differ substantially in morphology. **Ochraceocephala** has long and branched conidiophores, and the branching is commonly irregularly verticillate, while the conidiophores of **Angularia** are reduced to conidiogenous cells. **Ochraceocephala** has hyaline to yellowish, mostly sand to olive yellow, and mostly globose to subglobose conidia, while **Angularia** has hyaline and fusiform conidia; the conidia are smaller than in our new genus (4.8 vs. 18.7 × 3.6 vs. 5.4 µm).
Angularia xanthoceratis R. Xu, Phukhams. & Y. Li, sp. nov. (Figure 3).

MycoBank Number: 843308.

Etymology: referring to the host genus, Xanthoceras.

Holotype: HMJAU 60197.

Description: Saprobic on dead stems of Xanthoceras sorbifolium. Sexual morph: Undetermined. Asexual morph: Conidiomata 180–220 × 195–224 µm (\(\bar{x} = 200 \times 210 \mu m, n = 5\)), pycnidial, solitary, aggregated, uniloculate, immersed in host substrate, globose, thick-walled, subcoriaceous to coriaceous at the outer layers, dark brown to brown, without distinct ostioles. Ostioles absent. Conidiomatal wall 20–46 µm wide, thick, multilayered, scleroplectenchymatous cells, outer layer composed of 6–8 layers of dark brown to brown cells of textura angularis, lined with a thick hyaline layer bearing conidiogenous cells. Conidiophores reduced to conidiogenous cells. Conidiogenous cells 7.8–20.8 × 1.7–3.5 µm (\(\bar{x} = 14.3 \times 2.6 \mu m, n = 20\)), enteroblastic, phialidic, determinate, discrete, subcylindrical to truncate, smooth-walled, hyaline, arising from the inner layers of conidiomata. Conidia 13–24.5 × 4–7 µm (\(\bar{x} = 18.7 \times 5.4 \mu m, n = 30\)), fusiform, truncate at both ends, aseptate, hyaline, smooth-walled.

Culture characteristics: Colonies on PDA reaching 20 mm in diameter after 2 weeks at 25 °C. Cultures from above, dome-shaped in the center, milky white radiating outward, dense, round, creeping hyphae; reverse dark at the center, light orange radiating outward.

Material examined: CHINA, Jilin Province, Changchun, on dead stem of Xanthoceras sorbifolium (Sapindaceae), 15 September 2021, Rong Xu, HMJAU 60197 (holotype); extype living culture, CCMJ5013.
GenBank accession numbers: LSU = OM295682, SSU = OM295681, ITS = OM295683, and tub2 = OM304358

Notes: Angularia xanthoceratis is distinct from the closely related Sphaerellopsis species in conidial characteristics (Figure 3). Angularia xanthoceratis has fusiform, smooth-walled, hyaline, aseptate conidia, which are truncate at both ends, while Sphaerellopsis has fusoid-ellipsoidal, occasionally Y-shaped or digitate, subcylindrical to ellipsoid or globose, pale brown, 0–1(−3)-euseptate conidia [24]. In a BLASTn search, the LSU sequence of Angularia xanthoceratis was 99.55% similar to Leptosphaeria etheridgei (CBS 125980) with 96% query cover which translates to 95.6% similarity. The ITS region was 97.44% similar to Leptosphaeria sp. (C1-BC63) with 82% query cover which translates to 79.9% similarity. A pairwise comparison of the ITS region revealed 119 bases pair differences (18.39%) between A. xanthoceratis and Sphaerellopsis macroconidialis, while the tub2 region was 98 bases pair different (24.62%).

Plenodomus changchunensis R. Xu, Phukhams. & Y. Li, sp. nov. (Figure 4)

![Figure 4. Plenodomus changchunensis (HMJAU 60186, holotype). (a) Appearance of conidiomata on host substrate; black arrow indicates the conidiomata of P. changchunensis on the host. (b) Vertical section of conidioma. (c) Ostiolar canal. (d) Section of conidioma wall. (e–g) Conidiogenous cells and conidia. (h–l) Conidia. (m) Culture characteristics on PDA after three weeks at 25 °C. Scale bars: (b) = 100 μm; (c,e,l) = 20 μm; (d) = 50 μm; and (f–k) = 5 μm.

MycoBank Number: 843304

Holotype: HMJAU 60186

Etymology: referring to Changchun city where this fungus was collected.

Description: Saprobic on dead stems of Poaceae. Asexual morph: Undetermined. Sexual morph: Undetermined.

Conidiomata 163–192 × 193–245 μm (x = 175 × 207 μm, n = 5), pycnidial, solitary or in groups of 2–5, erumpent, aggregated, globose to subglobose, depression in the middle, thick-walled, subcoriaceous to coriaceous at the outer layers, dark brown to black, ostiolate. Ostiolytes 20–45 μm, central, papillate, ovoid, filled with short periphyses. Conidiomatal wall 24–48 μm wide, thick, multilayered, outer layer composed of 8–10 layers of dark brown to brown cells of textura angularis, lined with a thick hyaline layer bearing conidiogenous cells. Conidiophores reduced to conidiogenous cells. Conidiogenous cells 2.8–5.8 × 1.5–2.8 μm (x = 4.1 × 2 μm, n = 30), enteroblastic, phialidic, determinate, smooth-
walled, hyaline. **Conidia** 5–7.6 × 2–3.4 µm (x = 6.2 × 2.7 µm, n = 50), oblong or oval, slightly curved toward the ends, rounded ends, aseptate, hyaline, smooth-walled.

**Culture characteristics:** Colonies on PDA reaching 30 mm diam. after 3 weeks at 25 °C. Cultures from above, gray in the center, milky white radiating outward, dense, circular, creeping hyphae, grayish-green at the margins; reverse dark at the center, milky white radiating outward. Yellow pigmentation diffused into the media.

**Material examined:** CHINA, Jilin Province: Changchun, on dead twigs of **Poaceae** sp., 20 May 2021, C. Phukhamsakda, HMJAU 60186 (holotype); ex-type living culture, CCMJ5011; HMJAU 60187 (isotype), ex-isotype living culture, CCMJ5012.

**GenBank accession numbers:** LSU = OL897174, SSU = OL984031, ITS = OL996123, and **tub2** = OM009247

**Notes:** **Plenodomus changchunensis** (CCMJ5011 and CCMJ5012) formed a sister clade distinct from **Plenodomus lindquistii** with 99% ML/1.00 BPP support based on phylogenetic analysis of the concatenated ITS, LSU, SSU, and **tub2** datasets (Figure 2). **Plenodomus changchunensis** is similar to **P. lindquistii** in the size of conidia [51]. This species can be distinguished from **P. lindquistii** (CBS 381.67) by 34 nucleotides in the ITS region (34/643 in the ITS region and 0/866 in the LSU region). In the BLASTn search, the closest match to the LSU and ITS sequences of **P. changchunensis** were 100% and 89.57% similar to **Leptosphaeria** sp. (PHY-30) and **P. lindquistii** (MCN535002) with 95% query cover which translates to a 95% and 85.1% similarity, respectively. **Plenodomus changchunensis** was found associated with a grass near the water resources in temperate regions. Therefore, this fungus is introduced as a novel species.

**Alternariaster centaureae-diffusae** R.H. Perera, Bulgakov, Ariyawansa & K.D. Hyde, in Fungal Diversity, 74: 32 (2015), new host record and new geological record (Figure 5)

**Description:** Saprobic on dried stems of **Clematis** sp. **Sexual morph:** Ascomata 170–360 × 146–290 µm diam., solitary or in groups of 2–10, erumpent, semi-immersed or nearly superficial, uniloculate, globose to subglobose, coriaceous, black, ostiolate. Ostiole papillate, black, filled with periphyses. Periphyses aseptate, with a blunt apex, hyaline. **Peridium** 40–75 µm wide (x = 57.5 µm, n = 10), comprising thick-walled cells of textura globularis, inner layer composed of flattened cells of textura angularis, 5–10 rows of scleroplastenchymatous cells, outer layer thick, black. Hamathecium 2.5–3.8 µm wide, dense, distinctly septate, branched, cellular pseudoparaphyses, hyaline, embedded in a gelatinous matrix. **Asci** 110–140 × 10–14 µm (x = 125 × 12 µm, n = 20), 8-spored, bitunicate, fissitunicate, cylindrical to cylindric-subclavate, with a short bulbous pedicel, rounded at the apex. **Ascospores** 80–138 × 2.3–4.3 µm (x = 109 × 3.3 µm, n = 40), fasciculate, filiform, 14–16-septate, constricted at the apical septum, apical cell swollen, conical, yellowish-brown, smooth-walled, with a mucilaginous cap. **Asexual morph:** Undetermined.

**Material examined:** CHINA, Yunnan Province, dead aerial branch of **Clematis** spp., 24 April 2021, (HMJAU 60188).

**Host associations:** **Centaurea diffusa**, **Clematis** spp. ([4] and this study).

**GenBank accession numbers:** LSU = OL897175, SSU = OL981810, ITS = OL996125, and **tub2** = OL898721

**Notes:** **Alternariaster centaureae-diffusae** was originally described from the dead stems of **Centaurea diffusa** Lam. in Russia [4]. The new isolate (HMJAU 60188) has similar morphology to the type strain of **A. centaureae-diffusae** (MFLU 15–1521) in having fasciculate, filiform, constricted at the apical septum, conical, yellowish-brown ascospores with swollen apical cell [4]. A pairwise comparison of the sequences of the new isolate (HMJAU 60188) with the type species of **A. centaureae-diffusae** revealed minor differences. The new isolate clustered in the same clade as the type strain of **A. centaureae-diffusae** (Figure 2). Therefore, we report **A. centaureae-diffusae** on **Clematis** spp. as a new host and new geological record.
isolate clustered in the same clade as the type strain of *Alternariaster centaureae-diffusae* (Figure 2).

Therefore, we report *Alternariaster centaureae-diffusae* on *Clematis* spp. as a new host and new geological record.

**Figure 5.** *Alternariaster centaureae-diffusae* (HMJAU 60188). (a) Appearance of ascomata on host substrate. (b) Vertical section of ascoma. (c) Ostiole with periphyses. (d) Close-up of peridium. (e,g,h) Immature and mature asci. (f) Pseudoparaphyses. (i,j) Fissitunicate asci. (k) Top part of ascospore. (l–o) Ascospores. (j,n,o) Ascospores were stained in cotton blue. Scale bars: (b) = 200 μm; (c,d,f–j,l–o) = 50 μm; (e) = 100 μm; and (k) = 20 μm.

4. Discussion

Molecular biology has helped to elucidate the phylogenetic relationships among members of *Dothideomycetes*, particularly among several phoma-like taxa [13,52]. Multi-loci analyses based on LSU, SSU, ITS, *tub2*, *rpb2*, and *tef-1* sequences have been widely used to define species boundaries in *Leptosphaeriaceae* and other families of *Dothideomycetes* [13,52,53]. We carried out phylogenetic analyses with a concatenated dataset of five loci (ITS, LSU, SSU, *tub2*, and *rpb2*) for *Leptosphaeriaceae* members. The final alignment included 138 strains representing 132 ingroup taxa and six outgroup strains. However, the *Plenodomus* species were polyphyletic and mixed with *Alternariaster*, *Ochraceoccephala*, and *Praeclarispora* taxa. It is often encouraged to use additional taxon-specific secondary barcode loci to delineate taxa.
We therefore compared the phylogenetic informativeness of \(\text{tub}2\) (52 sequences translated to 37.7%) and \(\text{rpb}2\) (46 sequences translated to 33.3%) sequences of \text{Leptosphaeriaceae}. Our study shows that the polyphyletic topology of the \text{Plenodomus} group is due to the \(\text{rpb}2\) gene (Figures S2–S4). This could be due to a lack of \(\text{rpb}2\) barcodes in several related taxa, but the \(\text{rpb}2\) gene can be useful for delineation at the genus level [12,41]. In contrast, using the \(\text{tub}2\) gene provides a better resolution at the species level within the genera (Figure 2). Therefore, we performed phylogenetic analyses of \text{Leptosphaeriaceae} species with a concatenated dataset of ITS, LSU, SSU, and \(\text{tub}2\) loci. Three new species of \text{Leptosphaeriaceae} were revealed from China based on multilocus phylogeny combined with morphology.

The phylogeny from our analyses is similar to several previous studies [4,12,13]. The \text{Leptosphaeriaceae} taxa clustered in fifteen clades based on the ITS, LSU, SSU, and \(\text{tub}2\) datasets. A novel genus \text{Angularia} is also introduced in \text{Leptosphaeriaceae} to accommodate a new species, \text{A. xanthoceratis}. Conidial characteristics are the primary morphological characteristics that distinguish \text{Angularia} from the allied genus \text{Sphaerellopsis} (Figure 1). \text{Plenodomus} formed a separate clade, sister to \text{Ochraceocephala}, and revealed a novel species \text{P. changchunensis} with strong support. Many new genera have been introduced in \text{Leptosphaeriaceae} [2,4,8,12–14,23], which indicates that this family has a high degree of fungal diversity and distribution.

\text{Plenodomus lingam} was chosen to be the representative type species of \text{Plenodomus} over \text{P. rabenhorstii} Preuss [14,54]. There are 36 epithets listed under \text{Plenodomus} in Species Fungorum (2022) and 107 epithets in MycoBank. The host specificity of \text{Plenodomus} has not yet been clarified as species have been recorded from various plant families (\text{Asteraceae, Fabaceae, Lamiaceae, and Liliaceae}) [9]. In our study, \text{P. changchunensis} was found on \text{Poaceae}, which suggests that the \text{Leptosphaeriaceae} species are widely associated with many types of substrates. Members of \text{Plenodomus} appear to be cosmopolitan, as they have been recorded in both temperate and tropical countries (China, Greece, France, Japan, Netherlands, Peru, and Spain) [55].

\text{Alternariaster centaureae-diffusae} has been isolated from \text{Centaurea diffusa} Lam. (\text{Asteraceae}) in Shakhty city, Rostov region, Russia [4]. In this study, it was isolated from \text{Clematis spp. (Ranunculaceae)} in Kunming, Yunnan province, China. Therefore, our study extended the host range of \text{A. centaureae-diffusae} even though the environment of the two cities is different (temperate and subtropical). Therefore, we speculate that this species could be found in different environments and hosts [56].

Fungal diversity and taxonomy are constantly changing, necessitating a continuous assessment [57–59]. It is especially significant when taxa are described from genera that usually accommodate pathogens [60,61]. For example, \text{Plenodomus} and \text{Alternariaster} are the causal agents of blackleg disease and leaf spots of \text{Helianthus annuus} (sunflower) worldwide [31,32,62,63]. The discovery of novel species in a pathogenic genus could also indicate the discovery of emerging pathogens that can cause damage to economically important crops [64,65]. The formation of new fungi species has been reported to be intricately linked to their evolutionary relationships and ecological roles [20]. These phenomena can also occur when species are associated with different hosts and environments, as in the case of \text{A. centaureae-diffusae} in this study. The presence of the \text{Alternariaster} and \text{Plenodomus} species in different substrates reflects their ecological importance. Further studies focusing on fungal diversity from different niches are needed to understand the relationships between these organisms in ecosystems.

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/10.3390/jof8050416/s1, Figure S1: Phylogram generated from Bayesian inference analysis based on combined ITS, LSU, SSU, and \(\text{tub}2\) sequence data. Figure S2: Phylogram generated from maximum likelihood analysis based on combined ITS, LSU, SSU, \(\text{tub}2\), and \(\text{rpb}2\) sequence data. Figure S3: Phylogram generated from maximum likelihood analysis based on combined ITS, LSU, SSU, and \(\text{rpb}2\) sequence data. Figure S4: Phylogram generated from maximum likelihood analysis using \(\text{rpb}2\) sequence data. Figure S5: Phylogram generated from maximum likelihood analysis using \(\text{tub}2\) sequence data.
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