Multigene phylogeny and morphotaxonony of Septoria spp. from Iran along with a checklist of septoria-like taxa

Mounes Bakhshi: Research Assistant Prof., Department of Botany, Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization (AREEO), Tehran, Iran (mounesbakhshi@gmail.com)

Mahdi Arzanlou: Prof., Department of Plant Protection, Faculty of Agriculture, University of Tabriz, Tabriz, Iran

Abstract

The genus Septoria includes important plant pathogens with worldwide distribution, commonly associated with leaf spots and stem cankers of a broad range of plant hosts. In this study, eight isolates of Septoria were recovered from leaves with leaf spot on four herbaceous and woody plants from Gilan, Ardebil, East and West Azerbaijan provinces in north and northwest of Iran. The isolates were studied by applying a polyphasic approach including morphological and cultural data, and multi-gene phylogeny (LSU, ITS, ACT, TEF1-α, CAL, TUB, and RPB2). They were then identified as Septoria convolvuli on Sonchus sp., S. protearum on Solanum pseudocapsicum, S. polygonorum on Punica granatum, and S. urticae on Urtica dioica. Septoria protearum represents a new record for the mycoflora of Iran. Moreover, this research reports Sonchus sp. as new host of S. convolvuli, Punica granatum as new host of S. polygonorum, and Solanum pseudocapsicum as new host of S. protearum worldwide. Additionally, a comprehensive literature-based checklist for 102 septoria-like species known to occur on different plant species in Iran was also provided. The complete annotated list covers 78 Septoria species, eight Stagonospora, seven Sphaerulina, four Zymoseptoria, two Phloeospora, one Caryophylloseptoria, one Parastagonospora, and one Stromatoseptoria.

Keywords: Leaf spot, Mycosphaerella, phylogeny, plant pathogens, systematic

Mous Bakhshi, M.: استادیار یوزه شاخه تحقیقات بنیادی، مؤسسه تحقیقات گیاهپزشکی کشور، سازمان تحقیقات، آموزش و ترویج پژوهشی، تهران، ایران (mounesbakhshi@gmail.com)

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Introduction

The coelomycete genus *Septoria* Sacc. belongs to *Mycosphaerellaceae* (Ascomycota, Dothideomycetes, Capnodiales) and is based on *Septoria cytisi* Desm. which was first described by Desmazières (1847) as a pathogen of *Cytisus laburnum* L. (Quaedvlieg et al. 2013). This genus is characterized as having immersed, separate or aggregated (but not confluent), globose, papillate (or not), brown pycnidial conidiomata, holoblastic, determinate or indeterminate, sympodial and/or anellidic conidiogenous cells and hyaline, generally filiform, multisepate conidia, provided with broad, flat, unthickened scars (Constantinescu 1984). The multisepate filiform conidia are often considered one of the distinctive features of the genus, but other conidial shapes have also been included in the genus (Farr 1992).

The genus *Septoria* includes a number of significant plant pathogens with global distribution (Verkley et al. 2004, 2013, Quaedvlieg et al. 2013). These species are commonly associated with leaf spot diseases on many cultivated and wild plants (Verkley et al. 2004, 2013, Quaedvlieg et al. 2011, 2013). Some important plant pathogenic species include *S. apicola* Speg. on celery (Mathieu & Kushalappa 1993), and several septoria-like species now assigned to other genera, such as *Zymoseptoria tritici* (Desm.) Quaedvlieg & Crous (formerly known as *Septoria tritici* Desm.), *Zymoseptoria passerinii* (Sacc.) Quaedvlieg & Crous (syn. *S. passerinii* Sacc.) on graminicolous hosts (McDonald and Martinez 1990), and *Sphaerulina musiva* (Peck) Quaedvlieg, Verkley & Crous (syn. *S. musiva* Peck) on poplars (Feau et al. 2005), that cause severe economic losses to these crops. For most of the species, sexual morphs are unknown, but those identified, were mostly mycosphaerella-like sexual states (Crous et al. 2001, Verkley & Priest 2000, Aptroot 2006). Since January 2013, the following new rules for naming of pleomorphic fungi outlined in the International Code of Nomenclature for Algae, Fungi and Plants (ICN) a pleomorphic fungus may have only one name (Hawksworth 2011, Norvell 2011, Wingfield et al. 2012). Therefore, the name *Mycosphaerella* is restricted to the genus *Ramularia* and does not apply to species of *Septoria*, and the name *Septoria* has been accepted as the valid name (Kirk et al. 2013, Quaedvlieg et al. 2013).

Since the morphological characters are generally conserved and specific morphological features to describe and identify *Septoria* species are rather limited (Verkley et al. 2013, Quaedvlieg et al. 2013), therefore, the taxonomy of *Septoria* is extremely complicated and reliable identification of the species of this genus based on morphological traits alone is difficult. Due to the paucity of useful morphological characters and the high level of variation therein, the identification of species of *Septoria* has mainly counted on associated host data, leading to many of the described species only being recognizable by host plant and by variation in informative supplementary characters such as conidial length, width and septation (Jørstad 1965, Sutton 1980). Of these complementary characters, conidial width appears to be the most stable (i.e. it shows the least amount of intraspecific variation) (Priest 2006). In recent years, multi-gene DNA sequence datasets are becoming an increasingly prevalent tool for taxonomy of the different groups of fungi (Bakhshi et al. 2014, 2015, Crous et al. 2009a, 2013a, Groenewald et al. 2013, Videira et al. 2015, 2016). More recently, in order to improve the delimitation of *Septoria* from allied genera and the circumscription of species within this genus, Verkley et al. (2013) applied a polyphasic approach based on multilocus DNA sequences, morphological and cultural data. The robust multi-gene (LSU, ITS, ACT, TEF1-α, CAL, TUB, and RPB2) phylogeny inferred showed that the septoria-like fungi are distributed over three main clades, establishing the genera *Septoria* str., *Sphaerulina* Sacc., and *Caryophylloseptoria* Verkley, Quaedvlieg & Crous. Their results demonstrated that, some species have wider host ranges than expected,
including hosts from more than one family (Verkley et al. 2013). The other most inclusive study was that of Quaedvlieg et al. (2013) who compared 370 isolates representing 170 species of septoria-like taxa, sampled from six continents. Their results (Quaedvlieg et al. 2013), including that of Verkley et al. (2013) defined an additional 15 genera that were formerly treated as “septoria” in the widest sense. One important outcome of this study was that although Septoria s. str. is a genus in the Mycosphaerellaceae, several of the septoria-like genera clustered outside this family, but have still retained the Septoria morphological features (Quaedvlieg et al. 2013).

Hitherto, most of the septoria-like taxa reported from Iran, have been identified based on morphological characteristics and host range (Ershad 2009, Aghajani et al. 2009, Seifbarghi et al. 2010, Azimi et al. 2011, Zahedi et al. 2012, Zafari & Razaghi 2013, Amani & Avagyan 2014, Jamali 2015) and DNA data are available for limited number of them (Quaedvlieg et al. 2011, Golmohammadi et al. 2015). Quaedvlieg et al. (2011), based on the 28s nrDNA phylogeny, showed that species that occur on graminicolous hosts e.g. S. halophila Speg. in Iran, represent an undescribed genus, for which the name Zymoseptoria Quaedvlieg & Crous was proposed. In the other study, Golmohammadi et al. (2015) studied the Septoria spp. causing leaf spot disease on poplars in Iran using species specific primers as well as morphological features. Their results revealed S. populi Desm. (currently known as Sphaerulina frondicola (Fr.) Verkley, Quaedvlieg & Crous) as the only causal agent of Septoria leaf spot disease of poplars in Iran (Golmohammadi et al. 2015). Therefore these data show that the identifications in Septoria and septoria-like fungi will have to rely on DNA sequence data to support morphological conclusions. In this regard, the aim of this study was to characterize Septoria species obtained from the infected leaves of several plant species collected from the north and northwest of Iran, based on morphology, cultural characteristics and phylogenetic analyses of the DNA sequence data (LSU, ITS, ACT, TEF1-α, CAL, TUB, and RPB2). Furthermore we have also assembled a checklist of septoria-like fungi recorded to date from Iran, in the hope that what is reported here will encourage other researchers to study the diversity of this group of fungi in Iran.

Materials and Methods

- List of the species

The list of septoria-like fungi was compiled using reports available in the literature. The list includes septoria-like taxa together with their host species and families from which they have been collected. Synonyms were identified and related to currently accepted names with the help of recent papers and the Index Fungorum (http://www.indexfungorum.org). The checklist is organized alphabetically by genus and species name.

- Sample collection, isolation and morphological characterization

Symptomatic leaves were collected in the field from different provinces, including Ardebil, Gilan, East and West Azerbaijan (Iran). Leaves were examined in the laboratory directly under a Nikon SMZ 1500 stereo microscope. Isolates were obtained in pure culture by direct transfer of cirrhi of spores from a single pycnidium onto plates containing 2% malt extract agar (MEA; Fluka, Hamburg, Germany) with a sterile fine pointed needle using a previously described procedure (Bakhshi et al. 2011). Representative cultures were deposited in the culture collection of Tabriz University (CCTU), Tabriz, Iran; the culture collection of the Iranian Research Institute of Plant Protection, Tehran, Iran; and the culture collection of the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands.

Morphological descriptions were made for isolates grown on synthetic nutrient-poor agar plates (SNA; Crous et al. 2009b) containing sterile Urtica dioica L. (stinging nettle) stems. Cultures were incubated at 25 °C under continuous near-ultraviolet light for 14–30 days to promote sporulation. Freehand sections of fungal colonies were prepared and fungal structures mounted in clear lactic acid. Observations were made
with a Nikon Eclipse 80i compound microscope with differential interference contrast (DIC) illumination at 1000 magnification and a mounted Nikon digital sight DS-fi1 high definition color camera. Thirty measurements were made of each structure, and the 95% percentiles are presented, with extremes given between brackets. Adobe Photoshop CS5 was used for the final editing of the layout of acquired images and photographic preparations. Colony macro-morphology was noted on MEA and Oatmeal Agar (OA; Crous et al. 2009b) after 2–4 wk in dark at 25 °C. Colony color was rated according to the mycological color charts of Rayner (1970).

- DNA extraction, PCR amplification and sequencing

Fungal isolates were grown on MEA plates for 15 days at 25 °C in the dark. Genomic DNA was extracted from mycelium according to the protocol developed by Möller et al. (1992). Seven partial nuclear genes were initially targeted for PCR amplification and sequencing, namely, 28S nrRNA gene (LSU), internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS) of the nrDNA operon, actin (ACT), translation elongation factor 1-α (TEF1-α), calmodulin (CAL), β-tubulin (TUB) and RNA polymerase II second largest subunit (RPB2). The PCR amplifications were performed in a total volume of 12.5 µL on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA). The primers, protocols and conditions for standard amplification and subsequent sequencing of the loci were according to Bakhshi et al. (2015) for LSU and ITS loci, and Quaedvlieg et al. (2013) for the remaining loci (ACT, TEF1-α, CAL, TUB, and RPB2).

The resulting fragments were sequenced in both directions using the PCR primers and the ABI Prism BigDye® Terminator Cycle Sequencing Reaction Kit ver. 3.1 (Applied Biosystems™, Foster City, CA, USA) following the protocol of the manufacturer. DNA sequencing amplicons were purified through Sephadex® G-50 Superfine columns (Sigma Aldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA) as outlined by the manufacturer. Purified sequence reactions were run on an Applied Biosystems™ 3730xl DNA Analyzer (Life Technologies Europe BV, Applied Biosystems™, Bleiswijk, The Netherlands).

- Sequence alignment and phylogenetic analysis

DNA sequence data were analyzed in MEGA (Molecular Evolutionary Genetics Analysis) ver. 6 software (Tamura et al. 2013) and consensus sequences were manually generated from the forward and reverse sequences. The consensus regions of LSU, ITS, ACT, TEF1-α, CAL, TUB, and RPB2 were blasted against the NCBI’s GenBank sequence database using Megablast to identify their closest neighbors. The obtained sequences from GenBank together with the novel generated sequences during this study, were aligned with MAFFFT ver. 7 online interface using default settings (http://mafft.cbrc.jp/alignment/server/) (Katoh & Standley 2013) for each gene and whenever necessary, manually improved in MEGA ver. 6. The alignments were concatenated with Mesquite ver. 2.75 (Maddison & Maddison 2011).

Appropriate gene models were determined using MrModeltest ver. 2.3 (Nylander 2004) and applied to each gene partition. A Bayesian phylogenetic reconstruction was performed with MrBayes ver. 3.2.2 (Ronquist et al. 2012) based on the results of MrModeltest. The heating parameter was set at 0.15 and burn-in was set to 25% and trees were saved each 1000 generations. Posterior probabilities were determined by Markov Chain Monte Carlo (MCMC) analysis in MrBayes ver. 3.2.2. Four simultaneous Markov chains were run for 10000000 generations and trees were sampled every 100th generation, until the average standard deviation of split frequencies reached a value of 0.01 (stopval = 0.01). The resulting phylogenetic tree was printed with Geneious ver. 8.1.8 (Kearse et al. 2012). All new sequences generated in this study were deposited in NCBI's GenBank nucleotide database (www.ncbi.nlm.nih.gov) (Table 1). The GenBank
accession numbers for the strains obtained from NCBI can be found in Verkley et al. (2013).

**Results and Discussion**

- Checklist of the known species of septoria-like taxa from Iran

A list containing 78 species of *Septoria*, eight species of *Stagonospora* (Sacc.) Sacc., seven species of *Sphaerulina*, four species of *Zymoseptoria*, two species of *Phloeospora*, one species of *Caryophylloseptoria*, one species of *Parastagonospora*, and one species of *Stromatoseptoria* Quaedvlieg, Verkley & Crous is shown in Table 2. The highest numbers of septoria-like taxa were recorded on the representatives of the *Poaceae* (13 species), *Apiaceae* (nine species), *Asteraceae* (nine species), *Caryophyllaceae* (seven species), and *Salicaceae* (six species) families.

The preliminary checklist of septoria-like taxa gathered here, is useful for a wide range of activities. The data will provide both an overview on the known diversity of septoria-like taxa in Iran and a basis for ongoing and future taxonomic research on this group of fungi in Iran.

- Phylogenetic analysis

Eight isolates of *Septoria* spp. recovered from four host species and four host families were subjected to multi-gene DNA sequence analyses. The seven datasets consisted of 3160 characters (including the alignment gaps), representing 66 taxa of *Septoria* spp. (including 58 taxa from NCBI, and eight taxa from this study), and *Cercospora apii* (isolate CBS 118712) as an outgroup (gene boundaries of ACT: 1–230, TEF1-α: 231–649, ITS: 650–1155, TUB: 1156–1487, LSU: 1488–2322, RPB2: 2323–2676, and CAL: 2677–3160). The respective alignments included 711 unique site patterns (90, 170, 36, 142, 23, 96 and 154 for ACT, TEF1-α, ITS, TUB, LSU, RPB2, and CAL, respectively). The 10 characters artificially introduced as spacers between partitions were excluded from the phylogenetic analysis (Fig. 1).

**Table 1. Collection details and GenBank accession numbers of *Septoria* isolates included in phylogenetic analysis**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Isolate</th>
<th>Host</th>
<th>LSU</th>
<th>ITS</th>
<th>ACT</th>
<th>TEF1-α</th>
<th>CAL</th>
<th>TUB</th>
<th>RPB2</th>
</tr>
</thead>
<tbody>
<tr>
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<td><em>Sonchus</em> sp.</td>
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<td>MF540</td>
<td>MF540</td>
<td>MF540</td>
<td>MF540</td>
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<td>MF540</td>
<td>MF540</td>
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<td>MF540</td>
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Table 2. Septoria-like species known from Iran

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<th>Taxon</th>
<th>Host</th>
<th>Family</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caryophylloseptoria lychnidis (Desm.) Verkley, Quaedvlieg &amp; Crous (= S. lychnidis Desm.)</td>
<td>Melandrium pratense Roehl.</td>
<td>Caryophyllaceae</td>
<td>Ershad 2009</td>
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<tr>
<td>Phloeospora maculans (Berenger) Allesch.</td>
<td>Morus sp.</td>
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<td>Ashkan et al. 2011</td>
</tr>
<tr>
<td>Ph. ulmi (Fr.) Wallr.</td>
<td>Ulmus minor Miller</td>
<td>Ulmaceae</td>
<td>Ershad 2009</td>
</tr>
<tr>
<td>Septoria acerina Peck</td>
<td>Acer velutinum Boiss.</td>
<td>Aceraceae</td>
<td>Ershad 2009</td>
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<tr>
<td>S. aesculicola (Fr.) Sacc.</td>
<td>Aesculus hippocastanum L.</td>
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</tr>
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<td>S. alhagiae S. Ahmad</td>
<td>Alhagi sp.</td>
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<td>Azimi et al. 2011</td>
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<td>S. alnicola Cooke</td>
<td>Alnus glutinosa (L.) Gaertn.</td>
<td>Betulaceae</td>
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<td>Antirrhinum majus L.</td>
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<td>S. apiicola Speg.</td>
<td>Apium graveolens L.</td>
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<td>Ershad 2009</td>
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<td>S. astragali Desm. (= Phaeoseptoria astragali (Desm.) Vasyag.)</td>
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</tr>
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<td>Poaceae</td>
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<td>S. capraeae Westend.</td>
<td>Salix triandra L.</td>
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<td>S. caricina Brunaud</td>
<td>Carex depauperata Curtis ex With.</td>
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<td>C. pendula Huds.</td>
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<td>S. cirsii Niessel</td>
<td>Cirsium arvense Scop.</td>
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<td>Ershad 2009</td>
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<td>Silene sp.</td>
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<td>Ershad 2009</td>
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<td>Epilobium hirsutum L.</td>
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<td>Ershad 2009</td>
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<tr>
<td>S. eremuricola Byzova</td>
<td>Eremurus sp.</td>
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<td>Azimi et al. 2011</td>
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<tr>
<td>S. erigerontis Peck</td>
<td>Cnyza bonariensis (L.) Cronq., Erigeron sp.</td>
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<tr>
<td>S. erulisina Petr.</td>
<td>Ferula foetida Regel, F. ovina</td>
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<tr>
<td>S. festucae Died.</td>
<td>Festuca sp.</td>
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<tr>
<td>S. gallica Sacc.</td>
<td>Colchicum robustum (Bunge) Stefanov</td>
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<tr>
<td>S. gladioli Pass.</td>
<td>Gladiolus</td>
<td>Iridaceae</td>
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Table 2 (contd)

<p>| S. glycines Hemmi | Glycine max (L.) Merr. | Fabaceae | Ershad 2009 |
| S. guepini Oudem. | Euphorbia amygdaloides L. | Euphorbiaceae | Ershad 2009 |
| S. hederae Desm. | Hedera helix L. | Araliaceae | Ershad 2009 |
| S. heraclei Desm. ex Fr. | Heracleum sp. | Apiaceae | Ershad 2009 |
| S. jaculella R. Sprague | Bromus danthoniae Trin. | Poaceae | Ershad 2009 |
| S. jasmini Roum. | Jasminum officinale L. | Oleaceae | Ershad 2009 |
| S. koeleriae Cocc. &amp; Morini | Lophochloa phleoides (Vill.) Reichenb. | Poaceae | Ershad 2009 |
| S. lactucae Pass. | Lactuca sativa L. | Asteraceae | Ershad 2009 |
| S. lepyrodiclidis Petr. | Lepidodictis holostoides L. | Caryophyllaceae | Ershad 2009 |
| S. meliae Syd. &amp; P. Syd., | Melia azedarach L. | Meliaceae | Azimi et al. 2011 |
| S. mercurialis Westend. | Mercurialis perennis L. | Euphorbiaceae | Ershad 2009 |
| S. ornithogalea Sacc. | Beta vulgaris L. | Liliaceae | Ershad 2009 |
| S. phalaridis Cocc. &amp; Morini | Phalaris paradoxa L. | Poaceae | Seifbarghi et al. 2010 |
| S. phytolaccaceae Cavara | Phytolacca decandra L. | Phytolaccaceae | Ershad 2009 |
| S. plantaginis (Ces.) Sacc. | Plantago lanceolata L. | Plantaginaceae | Ershad 2009 |
| S. polygonina Thuem. | Polygonum lapathifolium L. | Polygonaceae | Ershad 2009 |
| S. rechingeri Petr. | Rheum ribes L. | Polygonaceae | Ershad 2009 |
| S. ribis (Lib.) Desm. | Ribes uva-crispa L. | Saxifragaceae | Ershad 2009 |
| S. rivini Brunaud | Falcaria vulgaris Bernh. | Apiaceae | Ershad 2009 |
| S. rubiae (Pat.) Bubák &amp; Ranoj. | Rubia tinctorum L. | Rubiaceae | Ershad 2009 |
| S. rubiae-tinctorum Unamumo | R. tinctorum | Rubiaceae | Ershad 2009 |</p>
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<th>Family</th>
<th>Reference</th>
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<tr>
<td><em>S. saponariae</em> (DC.) Savi &amp; Becc.</td>
<td>Silene sp.</td>
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<td><em>S. sigesbeckiae</em> Siemaszko</td>
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<td><em>S. sonchi</em> Sacc.</td>
<td>Sonchus oleraceus L.</td>
<td>Asteraceae</td>
<td>Zafari &amp; Razaghi 2013</td>
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<td><em>S. thelygoni</em> Sacc.</td>
<td>Theligonum cynocrambe L.</td>
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<td><em>S. urticae</em> Desm. &amp; Rob.</td>
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<td>Ershad 2009</td>
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<td><em>S. viciosoi</em> Gonz. Frag.</td>
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<td>Apiaceae</td>
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<td>Papaveraceae</td>
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<td>Citrus sp.</td>
<td>Rutaceae</td>
<td>Ershad 2009</td>
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<td>Convolvulus tricolor L.</td>
<td>Convolvulaceae</td>
<td>Ershad 2009</td>
</tr>
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<td>Erysimum sp.</td>
<td>Brassicaceae</td>
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<td>Linaria elaine Mill.</td>
<td>Scrophulariaceae</td>
<td>Ershad 2009</td>
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<td>Nerium oleander L.</td>
<td>Apocynaceae</td>
<td>Ershad 2009</td>
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<td>Sonchus oleraceus</td>
<td>Asteraceae</td>
<td>Ershad 2009</td>
</tr>
<tr>
<td><em>Sphaerulina aceris</em> (Libert) Verkley, Quaedvlieg &amp; Crous (=<em>Phloeospora aceris</em> (Lib.) Sacc.)</td>
<td><em>Acer</em> velutinum Boiss. var. velutinum, <em>Acer</em> sp.</td>
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<td>Ershad 2009</td>
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<tr>
<td><em>Sph. berberidis</em> (Niessl) Quaedvlieg, Verkley &amp; Crous (=<em>S. berberidis</em> Niessl)</td>
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<td><em>Sph. cercidis</em> (Fr.) Quaedvlieg, Verkley &amp; Crous (=<em>S. cercidis</em> Fr. ex Lév.)</td>
<td>Cercis siliquastrum L.</td>
<td>Fabaceae</td>
<td>Ershad 2009</td>
</tr>
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<td><em>Sph. cornicola</em> (DC.: Fr.) Verkley, Quaedvlieg &amp; Crous</td>
<td>Cornus australis C.A. Mey., C. sanguinea</td>
<td>Cornaceae</td>
<td>Ershad 2009</td>
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<td><em>Sph. frondicola</em> (Fr.) Verkley, Quaedvlieg &amp; Crous</td>
<td>Populus alba, P. euphratica Olivier, P. nigra L., <em>Populus</em> sp.</td>
<td>Salicaceae</td>
<td>Ershad 2009</td>
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Table 2 (contd)

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<th>Species</th>
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<th>Family</th>
<th>Source</th>
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<td><em>Sph. westendorpii</em> Verkley, Quaedvlieg &amp; Crous (≡<em>S. rubi</em> Westend.)</td>
<td><em>Rubus sp.</em></td>
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<td>Ershad 2009</td>
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<td><em>Stagonospora alliina</em> (Woron.) Petr.</td>
<td><em>Allium porrum</em> L.</td>
<td><em>Liliaceae</em></td>
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<td><em>St. calystegiae</em> (Westend.) Bubák (≡<em>S. calystegiae</em> Westend.)</td>
<td><em>A. schoenoprasum</em> L., <em>Allium sp.</em></td>
<td><em>Convolvulaceae</em></td>
<td>Ershad 2009</td>
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<td><em>St. citrorum</em> Petr.</td>
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<td><em>Rutaceae</em></td>
<td>Ershad 2009</td>
</tr>
<tr>
<td><em>St. iranica</em> Petr. &amp; Esfand.</td>
<td><em>Lathyrus incurvus</em> Willd.</td>
<td><em>Fabaceae</em></td>
<td>Ershad 2009</td>
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<td><em>St. tussilaginis</em> Died.</td>
<td><em>Tussilago farfara</em> L.</td>
<td><em>Asteraceae</em></td>
<td>Ershad 2009</td>
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<td><em>Stagonospora</em> sp.</td>
<td><em>Actinidia chinensis</em> Planch.</td>
<td><em>Dilleniaceae</em></td>
<td>Ershad 2009</td>
</tr>
<tr>
<td><em>Stromatoseptoria castaneicola</em> (Desm.) Quaedvlieg, Verkley &amp; Crous (≡<em>S. castaneicola</em> Desm.)</td>
<td><em>Heracleum persicum</em> Desf. ex Fischer</td>
<td><em>Apiaceae</em></td>
<td>Ershad 2009</td>
</tr>
<tr>
<td><em>Zymoseptoria brevis</em> M. Razavi, Quaedvlieg &amp; Crous</td>
<td><em>Castanea sativa</em> Mill.</td>
<td><em>Fagaceae</em></td>
<td>Ershad 2009, Quaedvlieg et al. 2011</td>
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<tr>
<td><em>Z. halophila</em> (Speg.) M. Razavi, Quaedvlieg &amp; Crous (≡<em>S. halophila</em> Speg.)</td>
<td><em>Phalaris minor</em></td>
<td><em>Poaceae</em></td>
<td>Ershad 2009, Quaedvlieg et al. 2011</td>
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<tr>
<td></td>
<td><em>L., Triticum aestivum,</em></td>
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</table>
Fig. 1. Consensus phylogram (50% majority rule) of 272 trees resulting from a Bayesian analysis of the combined seven-gene (LSU, ITS, ACT, TEF1-α, CAL, TUB, and RPB2) sequence alignment using MrBayes ver. 3.2.2. The scale bar indicates 0.02 expected changes per site. The tree was rooted to Cercospora apii (CBS 118712).

The results of MrModeltest, recommended a K80+G for ACT, ITS and TUB, SYM+G for RPB2, GTR+G for TEF1-α and RPB2, HKY+I+G for LSU, and GTR+I+G for CAL. The TEF1-α, LSU and CAL partitions had dirichlet base frequencies, whereas the remaining partitions (ACT, ITS, TUB and RPB2) had fixed (equal) base frequencies. The Bayesian analysis lasted 135000 generations and saved a total of 272 trees. After discarding the first 25% of sampled trees for burn-in, the consensus trees and posterior probabilities (PP) were calculated from the remaining 204 trees (Fig. 1).

- Taxonomy

The Consolidated Species Concept (Quaedvlieg et al. 2014) was employed in this study to distinguish *Septoria* species from Iran. Based on the phylogenetic analyses, the eight isolates from various plants were grouped in four species clades. The following species of the genus *Septoria* have been identified in the present investigation:

1. *Septoria convolvuli* Desm., Annls Sci. Nat., sér. 2, Bot. 17: 108 (1842) (Fig. 2)
Morphology on SNA: Conidiomata pycnidial, dark brown to black, single, 70–160 µm in diameter, or merged to small clusters of up to 350 µm in diameter, olivaceous to brown, formed mostly on the agar surface; Conidiogenous cells hyaline, often discrete, narrowly to broadly ampulliform with a relatively elongated neck, holoblastic, proliferating percurrently with indistinct annellations, sometimes also proliferating sympodially, 8–25 × 2.5–3.5(-5) µm. Conidia filiform to filiform-cylindrical, straight or slightly to distinctly curved, attenuated in the upper cell to a narrowly rounded or more or less pointed apex, narrowly truncate at the base, 1–3(-5)-septate, hyaline, contents moderately rich in minute oil-droplets and small granular material, (19–)32–43(-50) × 1.5–2.5 µm.

Culture characteristics: Colonies on MEA surface folded, radially striated, immersed mycelium very dark chestnut to black, aerial mycelium almost absent, superficial pycnidial conidiomata releasing pale flesh or milky white droplets of conidial slime, the margin irregular to ruffled, colorless to pale buff, reaches 15 mm in 4 wk.

Specimens examined: Iran: Ardebil province, Moghan, on Sonchus sp., Oct. 2011, M. Bakhshi (CCTU 1062 = CBS 136120).

Notes: Septoria convolvuli has been reported on different plants of Convolvulaceae (Verkley et al. 2013, Farr & Rossman 2017) and it was assumed to be host-specific to this family (Verkley et al. 2013). So far, this species has been reported from Iran on C. sepium and C. arvensis (Ershad 2009). In this investigation, S. convolvuli was found for the first time on Sonchus sp. (Asteraceae), therefore, the supposed single-family host range of S. convolvuli, included one additional family Asteraceae.

Fig. 2. Septoria convolvuli (CBS 136120): a. Culture on MEA, b–c. Conidiogenous cells, d–g. Conidia (Bars = 10 µm).
2. *Septoria polygonorum* Desm., Annls Sci. Nat., sér. 2, Bot. 17: 108 (1842) (Fig. 3)

Morphology on SNA: Conidiomata pycnidial, brown to black, subglobose to lenticular, formed mostly on the nettle stems, 70–110 µm in diameter, with a single ostiolum up to 45 µm wide, conidiomatal wall composed of angular cells up to 8 µm in diameter. Conidiogenous cells proliferating sympodially and rarely percurrently, hyaline, discrete, cylindrical or narrowly to broadly ampulliform, holoblastic, 8–20 × 4–6 µm. Conidia filiform, filiform-cylindrical, slightly curved to flexuous or sigmoid, hyaline, attenuated gradually to a narrowly rounded to pointed apex, attenuated more abruptly towards the truncate base, 1–4-septate, not or only inconspicuously constricted around the septa, with several minute oil-droplets and granular contents in each cell 25–58 (~70) × 1.5–2(~2.5) µm.

Culture characteristics: Colonies on MEA surface folded, immersed, very dark chestnut to olivaceous-black, aerial mycelium on elevated surface scanty, but near margin forming felty rosy buff or grey-olivaceous hyphae, superficial pycnidial conidiomata releasing dirty white to flesh droplets of conidial slime, with an irregular or somewhat undulating, ruffled, glabrous, colorless to rosy buff margin, reaches 10 mm in 4 wk. Colonies on OA plane, spreading, dark olivaceous, immersed mycelium olivaceous-black, aerial mycelium scanty, grey-olivaceous; conidiomata developing mostly immersed in the agar, in concentric zones, releasing droplets of rosy-buff or dirty white conidial slime, with an even, regular dark green margin, reaches 25 mm in 4 wk.

Specimens examined: Iran: Gilan province, Talesh, on *Punica granatum* L., Oct. 2012, M. Bakhshi (CCTU 1103; CCTU 1103.1).

Notes: So far, *Septoria polygonorum* has been reported from Iran on *Polygonum lapathifolium* and *Po. persicaria* (Ershad 2009). *Septoria polygonorum* has been previously known only on the members of the family *Polygonaceae* (Verkley et al. 2013, Farr & Rossman 2017), but here surprisingly, it was found to be also associated with Pomegranate (*Punica granatum, Lythraceae*).
3. **Septoria protearum** Viljoen & Crous, S. Afr. J. Bot. 64: 144 (1988) (Fig. 4)
Morphology on SNA: Conidiomata pycnidial, globose to lenticular, single or merging into complexes up to 220 µm in diameter, formed mostly on the nettle stems, brown to black, the wall composed of brown textura angularis with cells up to 10 µm in diameter. Conidiogenous cells hyaline, discrete or integrated in simple, 1–(2)-septate conidiophores, cylindrical or narrowly to broadly ampulliform, proliferating sympodially or percurrently with a distinct neck of variable length, holoblastic, with indistinct annellations, 6–10(–14) × 2.5–3(–4) µm. Conidia filiform to cylindrical, straight to slightly curved or flexuous, rounded to somewhat pointed at the tip, attenuated gradually or more abruptly towards the narrowly truncate base, 1–3-septate, not constricted at the septa, hyaline, contents with several minute oil-droplets, (12–)17–25(–30) × 1–1.5(–2) µm.
Culture characteristics: Colonies on MEA surface folded, immersed, faintly salmon in the center, dark bluish-olivaceous in outer region, sporulating in the center with spores in large pale salmon droplets oozing from pycnidial complexes; with an even, (vinaceous) buff to somewhat colorless undulating margin, reaches 30 mm in 4 wk. Colonies on OA plane, spreading, dark olivaceous, immersed, aerial mycelium scarce, grey-olivaceous, with few grey tufts; conidiomata developing mostly immersed in the agar, in concentric zones, olivaceous-black, releasing droplets of dirty white conidial slime, with an even dark green margin, reaches 28 mm in 4 wk.
Specimens examined: Iran: Gilan province, Talesh, on *Solanum pseudocapsicum* L., Apr. 2012, M. Bakhshi (CCTU 1132 = CBS 135979; CCTU 1132.1).

Notes: In the past, *Septoria protearum* was only known from the members of *Proteaceae* family (Crous et al. 2004), however, recently based on the combination of morphological and multi-gene phylogenetic analysis, it has been demonstrated that, it is a plurivorous species with multiple family-associations including *Anacardiaceae*, *Araceae*, *Araliaceae*, *Aspleniaceae*, *Asteraceae*, *Oleaceae*, *Orchidaceae*, *Rutaceae*, *Boraginaceae*, *Oleandraceae*, *Rosaceae*, and *Rutaceae* (Crous et al. 2013b, Verkley et al. 2013). *Septoria protearum* is a new record for the mycobiota of Iran. Moreover, this investigation is the first report of the species on *Solanum pseudocapsicum* in the world, thus a further family, *Solanaceae* was added to the host range of this species.

4. **Septoria urticae** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 8: 24 (1847) (Fig. 5)
Morphology on SNA: Conidiomata pycnidial, formed mostly on the nettle stems, pale brown to dark brown, subglobose to lenticular, 80–210 µm in diameter, with a single ostiolum, or ostioli barely differentiated; conidiogenous cells hyaline, mostly discrete, narrowly or broadly ampulliform with a relatively narrow neck, holoblastic, proliferating sympodially and percurrently with somewhat distinct annellations on an elongated neck, 6–13 × 3–6.5 µm; conidia cylindrical, straight or slightly curved, with a narrowly rounded apex, attenuated towards the narrowly truncate base, 1–7(–9)-septate, not constricted around the septa, hyaline, with several minute indistinct oil-droplets and numerous granules in each cell, (30–)40–60(–70) ×1.5–2(–3) µm.
Culture characteristics: Colonies on MEA surface folded, immersed, very dark chestnut to olivaceous-black, aerial mycelium on elevated surface scanty, but near margin forming felty white or grey-olivaceous hyphae, superficial pycnidial conidiomata releasing dirty white to flesh droplets of conidial slime, with an even or somewhat undulating, ruffled, colorless to rosy buff margin, reaches 18 mm in 4 wk. Colonies on OA spreading, remaining almost plane, grey-olivaceous, aerial mycelium woolly-floccose, white, well-developed in the center, with an even to slightly ruffled, margin reaches 19 mm in 4 wk.


Fig. 4. *Septoria protearum* (CBS 135979): a. Culture on MEA, b. Culture on OA, c. Conidiomata on stinging nettle stem, d–f. Conidiogenous cells, g–i. Conidia (Bars = 10 µm).
Fig. 5. *Septoria urtica* (IRAN 2767C): a. Culture on MEA, b. Culture on OA, c. Conidiomata on stinging nettle stem, d. Conidiogenous cells, e–g. Conidia (Bars = 10 μm).

**Host family index for septoria-like taxa from Iran**

The taxa reported from Iran are listed below according to the host family:

**Aceraceae**
- *Septoria acerina*
- *S. convolvuli*
- *Sphaerulina aceris*

**Apiaceae**
- *Septoria apiicola*
- *S. cumulata*
- *S. ferulina*
- *S. heraclei*
- *S. petroselini*
- *S. rivini*
- *S. sii*
- *S. viciosoi*
- *Stagonospora sp.*

**Apopynaceae**
- *Septoria sp.*

**Araliaceae**
- *Septoria hederae*

**Asteraceae**
- *Septoria chrysanthemella*
- *S. cirsii*
- *S. erigerontis*
- *S. lactucae*
- *S. sigebeckiae*
- *S. silybi*
- *S. sonchi*
- *Septoria sp.*
- *Stagonospora tussilaginis*

**Berberidaceae**
- *Sphaerulina berberidis*

**Betulaceae**
- *Septoria alnicola*

**Brassicaceae**
- *Septoria lepidii*
- *S. sisymbrii*
- *Septoria sp.*

**Caprifoliaceae**
- *Septoria ebuli*

**Caryophyllaceae**
- *Caryophylloseptoria lychnitis*
- *Septoria carthusianorum*
- *S. cerasii*
S. dianthi
S. dimera
S. lepyrodiclidis
S. saponariae

Chenopodiaceae
Septoria atriplicis

Convolvulaceae
Septoria convolvuli
Septoria sp.
Stagonospora calystegiae

Cornaceae
Septoria corni-maris
S. cornina
Sphaerulina cornicola

Cyperaceae
Septoria baudysiana
S. caricina
S. caricicola
S. riparia
Stagonospora caricinella

Dilleniaceae
Stagonospora sp.

Euphorbiaceae
Septoria guepini
S. mercurialis

Fabaceae
Septoria alhagiae
S. astragali
S. glycines
Sphaerulina cercidis
Stagonospora iranica
S. meliloti

Fagaceae
Stromatoseptoria castaneicola

Hippocastanaceae
Septoria aesculicola

Iridaceae
Septoria gladioli

Lamiaceae
Septoria bornmülleri

Liliaceae
Septoria eremuri
S. eremuricola
S. gallica
S. ornithogalea
Septoria sp.

Lythraceae
Septoria polygonorum

Meliaceae
Septoria meliae

Moraceae
Phloeospora maculans

Musaceae
Septoria eumusae

Oleaceae
Septoria fraxini
S. jasmini

Onagraceae
Septoria epilobii

Papaveraceae
Septoria sp.

Phytolaccaceae
Septoria phytolaccae

Plantaginaceae
Septoria plantaginis

Poaceae
Parastagonospora nodorum
Septoria bromi var. bromi
S. cynodontis
S. festucae
S. jaculella
S. koeleriae
S. phalaridis
S. triseti
Stagonospora dolosa
Zymoseptoria brevis
Z. halophila
Z. passerinii
Z. tritici

Polygonaceae
Septoria polygonina
S. polygonorum
S. rechingeri

Ranunculaceae
Septoria clematidis

Rosaceae
Sphaerulina westendorpii
Sph. oxyacanthae

Rubiacceae
Septoria cruciatae
S. rubiae
S. rubiae-tinctorum

Rutaceae
Septoria sp.
Stagonospora citrorum

Salicaceae
Septoria botuliformis
S. candida
S. capraeae
S. davatchii
S. didyma
Sphaerulina frondicola

Saxifragaceae
Septoria ribis

Scrophulariaceae
Septoria antirrhini
S. digitalis
Septoria sp.

Solanaceae
Septoria protearum

Thelygonaceae
Septoria thelygoni

Ulmaceae
Phloeospora ulmi

Urticaceae
Septoria urticae
Acknowledgements

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