The avocado subgroup of *Phytophthora citricola* constitutes a distinct species, *Phytophthora mengei* sp. nov.

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Key words: avocado canker pathogen, identification, Oomycete

INTRODUCTION

Among six species of *Phytophthora* affecting avocado (*Persea americana* Miller) in USA (Farr et al. 1989) *P. citricola* was identified to be the primary cause of trunk canker (Zentmyer 1973, Zentmyer et al. 1974). Feeder roots and tree trunks are the primary infection courts (Elhamalawi et al. 1995b) although the pathogen may attack main structural roots (Coffey 1987, Zentmyer et al. 1974) and fruit (Koike et al. 1987, Ouimette et al. 1988). The resultant disease is commonly known as “citricola canker” (Elhamalawi et al. 1995a). This disease first was described by Fawcett (1916) and Barrett (1917), and it has caused increasing devastation to avocado in California (Coffey et al. 1988, Coffey 1987, Elhamalawi and Menge 1994).

Our knowledge about the identity of the causal agent of avocado trunk canker has evolved over time. The pathogen was identified first as a *Pythiacystis* sp. (Fawcett 1916). A year later it was redescribed as *Phytophthora cactorum* (Lebert and Cohn) J. Schrot. (Barrett 1917). *Phytophthora citricola* was separated from *P. cactorum* by Sawada (Sawada 1927, Tucker 1931). The avocado canker pathogen subsequently was identified as *Phytophthora citricola* Sawada based on its similarity in morphology and protein banding patterns with those of other isolates of *P. citricola* (Zentmyer 1973, Zentmyer et al. 1974). While identifying the pathogen as *P. citricola*, Zentmyer and associates clearly acknowledged that the avocado canker pathogen produced smaller oogonia and oospores than did the type culture of this species. Also the avocado isolates more frequently produced irregular sporangia in greater variety than the type culture of *P. citricola* (Zentmyer 1973, Zentmyer et al. 1974). This pathogen more recently was demonstrated to belong to a subgroup within *P. citricola* based on distinct patterns of isozymes (Oudemans et al. 1994) and amplified fragment length polymorphisms (AFLP) (Bhat and Browne 2007).

The above morphological and molecular differences indicate that the avocado canker pathogen is a separate species. To test this hypothesis we performed a standard DNA fingerprinting technique based on single-stranded conformation polymorphism of PCR-
amplified ribosomal DNA (PCR-SSCP) (Gallegly and Hong 2008). This technique was developed by Kong and associates (2003) and since has been evaluated with the vast majority of the known species of Phytophthora (Hong et al unpubl data). Each different PCR-SSCP, with a few exceptions, represent a distinct species within the genus (Gallegly and Hong 2008; Kong et al 2003, 2004a). We also sequenced representative isolates and examined their morphology. This paper reports on the morphology, DNA fingerprint and sequence analysis data of this new taxon in comparison with morphologically similar species.

MATERIALS AND METHODS

Isolation and isolate maintenance.—All cultures of the new taxon examined in this study were collected from the trunk of avocado trees in southern California. Nine of the isolates, including the type culture, were isolated by Dr John Menge of the University of California at Riverside (Table 1). Single zoospore isolates of these cultures were obtained as described by Bhat and Browne (2007), and they were grown on V8 juice agar (Erwin and Ribeiro 1996). Blocks of fresh agar cultures were transferred into microtubes with sterile distilled water for long-term storage at 15 C. Five additional cultures representing several known species with similar morphology also were included in this study for comparison purposes.

Morphology.—Among the 11 isolates of the avocado trunk canker pathogen whose SSCP DNA fingerprints were identical, two (p340, p341) were selected for morphology studies. The detailed procedures are presented on pages 6 and 15 in Gallegly and Hong (2008). Sporangia were produced on disks of lima bean agar in 10% sterile soil extract under fluorescent light at 20–22 C. Hem-seed agar was used for production of the sexual organs. About 20 measurements were made of each morphological stage. Microphotographs of the organs were made with Kodak 35 mm film (Eastman Kodak Co., Rochester, New York) with 45× and 97× objectives of a Bausch & Lomb zoom microscope. Black and white negatives were converted to positive digital images with a Polaroid 35 mm scanner using Photoshop.

Physiology.—The two isolates (p340, p341) used in the morphology studies were incubated at 6, 10, 15, 20, 25, 28, 30, 33 and 35 C. Disks (4 mm diam) from 3 d old cultures were placed on lima bean agar in 60 mm Petri dishes, and diameters of colony growth were recorded after 2 d.

DNA extraction.—Isolates were grown in V8 juice broth as described in the Appendix to Chapter 3, Growth media and method (Erwin and Ribeiro 1996) at room temperature (ca. 23 C) for 10 d. DNA was extracted from each culture as instructed with the DNeasy® Plant Minikit (QIAGEN, Valencia, California).

DNA fingerprinting.—A standard fingerprinting (Gallegly and Hong 2008; Kong et al 2003, 2004a) was used. The only modification was that a smaller volume (2 µL) denatured PCR product was loaded for electrophoresis. In addition to the 11 isolates from avocado the type culture and another authentic culture (CBS 295.29) of P. citricola, one isolate each of P. primulae Tomlison, P. pseudosyringae T. Jung & Delatour and P. syringae (Klebahn) Klebahn (Gallegly and Hong 2008) were included for comparison (Table 1).

DNA sequencing and sequence analysis.—Two isolates from avocado were sequenced in four nuclear and mitochondrial DNA regions. The ITS regions were amplified with forward primer ITS6 (Cooke et al 2000) and reverse primer ITS4 (White et al 1990). Genes encoding β-tubulin, translation elongation factor 1α and NADH dehydrogenase subunit I were amplified as described by Kroon et al (2004). Excess primer and dNTP were removed from quantified PCR products with shrimp alkaline phosphatase and exonuclease I (USB Catalog Nos. 70092Y, 70073Z). One unit of each enzyme was added to 15 µL PCR product, incubated at 37 C for 30 min, followed by heat inactivation at 65 C for 15 min. Sequencing was performed in both directions for all regions with the same primers as for PCR by the University of Kentucky Advanced Genetic Technologies Center (Lexington, Kentucky). Sequencing was repeated at least once.

Sequences from different runs were compared with the Clustal W multiple sequence alignment at http://align.genome.jp. The consensus sequence of each isolate was aligned with those from other isolates to examine inter-isolate sequence variation. Basic local alignment search tool (BLASTn, http://ncbi.nlm.nih.gov) was used to identify the close relatives of P. mengei at the respective regions. The phylogenetic analyses with a group of selected species was carried out in TOPALI 2.5 (Milne et al 2009) with the Felsenstein-84 nucleotide substitution plus gamma rates heterogeneity model to calculate pair-wise distances, resulting in a neighbor joining tree. A total of 21 other species representing major clades (Blair et al 2008, Cooke et al 2000, Kroon et al 2004, Martin and Tooley 2005) of genus Phytophthora were selected based on the availability of type culture sequence. These sequences were published by Cooke and associates (2000) and by species authorities of P. alni subsp. alni and P. invadans (Brasier et al 2004, Brasier et al 2003), P. bisherpia (Abad et al 2008), P. melonis (Ho et al 2007), P. quercetorum (Balci et al 2008) and P. sikkimensis (Raealter et al 2007). Sequences of other sources were double-checked by sequencing the type culture in our collection to confirm its accuracy. Several species of Cooke’s clade 2 were included.

TAXONOMY

Phytophthora mengei G.T. Browne, M.E. Gallegly & C.X. Hong, sp. nov.

MycoBank MB 513047

Species nova homothallica, laevi-tunicata, faciliter in agaro “lima bean” dicto oogonia globosa numero medio 24.0 µm diam formans. Oosporae pterotice parietibus 2.3 µm crassis, numero medio 21.7 µm diam. Antheridia claviformia ad vel prope stipitem oogonialem affixa. Antheridia adnodiun rotundata (9.3 × 9.9 µm). Sporangia non caduca semipapillata, saepe in formis monstruosis sed
<table>
<thead>
<tr>
<th>Species</th>
<th>SSCP</th>
<th>VT</th>
<th>WVU</th>
<th>UCD</th>
<th>International</th>
<th>Host</th>
<th>Origin</th>
<th>Year</th>
<th>Alternative source</th>
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</thead>
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<td><strong>P. mengei</strong></td>
<td>Men</td>
<td>42B2</td>
<td>p340</td>
<td>M218.z1</td>
<td>MYA-4554</td>
<td><em>P. americana</em></td>
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<td>MYA-4555</td>
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<td></td>
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<td></td>
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<td>—</td>
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<td>Cil</td>
<td>33H8*</td>
<td>p396</td>
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<td><em>Citrus sinensis</em></td>
<td>Japan</td>
<td>—</td>
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<td></td>
<td></td>
<td>33J2</td>
<td>p375</td>
<td>—</td>
<td>CBS 295.29</td>
<td><em>Citrus sp.</em></td>
<td>Japan</td>
<td>1929</td>
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<td><strong>P. primulae</strong></td>
<td>Pri</td>
<td>29E9*</td>
<td>p286</td>
<td>—</td>
<td>CBS 620.97</td>
<td><em>Primula acaulis</em></td>
<td>The Netherlands</td>
<td>1997</td>
<td>WM (PD97/875)</td>
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<td><strong>P. pseudosyringae</strong></td>
<td>Pss</td>
<td>30A8*</td>
<td>p284</td>
<td>—</td>
<td>CBS111772</td>
<td><em>Quercus robur</em></td>
<td>Germany</td>
<td>1997</td>
<td>TJ(IFB-PSEU6)</td>
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<tr>
<td><strong>P. syringae</strong></td>
<td>Syr</td>
<td>21H9*</td>
<td>p187</td>
<td>—</td>
<td>ATCC34002</td>
<td><em>Citrus sp.</em></td>
<td>California</td>
<td>—</td>
<td></td>
</tr>
</tbody>
</table>

*Type culture or key isolates of respective species as designated by (Gallegally and Hong 2008).

b Data not available.

VT = Virginia Tech; WVU = West Virginia University; UCD = University of California at Davis; Internationals: those beginning with ATCC and MYA are culture reference codes of the American Type Culture Collection, CBS for the Centraal Bureau voor Schimmelcultures and IMI for the International Mycological Institute.
saepissime formis ovoideis, obpyriformibus ellipsoideisque 
apparentia. Symphodia simplicia in agaro laxa. Magnitudo 
sporangialis numero medio 62.7 × 35.2 μm (in mensura 
tota 37.4–78.2 × 27.2–44.2 μm), ratione arithmetica long-
itudinis usque latitudinis 1.8. Partes inflatae hyphales atque 
clamydosporae nullae. Temperatura maxima ad incrementum 
coloniale 30–32 C.

Holotypus: ATCC MYA 4554.

**Phytophthora mengei** G.T. Browne, M.E. Gallegly & 
C.X. Hong, sp. nov.

*Phytophthora mengei* is homothallic and forms sex 
bodies readily in lima bean and hemp-seed agars 
(Fig. 1). The oogonia average 24.0 μm diam (range 
20.4–27.2 μm) and some have tapered stalks, 
sometimes with a slight hook in the taper. Oospores are 
mostly plerotic with 2.3 μm thick walls (range 1.5– 
3.0 μm) and average 21.7 μm diam (range 18.7– 
24.5 μm). Oospores in tapered oogonia appear 
aplerotic as the taper draws away from the round 
oospores. The diclinous antheridia are paragynous 
and commonly asymmetrically capitate (Fig 1B). The 
end of the club is approximately 10 μm diam. On 
tapered oogonia the antheridia are located on the 
taper, commonly at the bottom. When placed in water 
or soil extract, mycelia on lima bean agar disks from 
3 d old cultures form abundant semipapillate sporan-
gia in fewer than 8 h under fluorescent light at room 
temperature. The apical thickened area is 2.4–3.4 μm 
deep. Bizarre shapes of sporangia occur (sickle, 
boomerang, sombrero and bluntly ellipsoid). Bluntly 
ellipsoid sporangia, sometimes with a constriction in 
the middle, average about 95 × 35 μm. Smaller ovoid 
sporangia are about 49 × 34 μm. Overall sporangia 
average 62.7 × 35.2 μm (range 37.4–95.0 × 27.2– 
44.2 μm). The length to width ratio is 1.8. Width of 
the papillae pores vary, 6.6–13.5 μm. Sporangia are 
noncaducous. Also a few sporangia are formed on 
lima bean agar where they are mostly ovoid and of 
about the same size as the ovoid ones formed in water, 
but those formed in agar sometimes appear to be 
papillate. Empty sporangia have a small plug at the 
point of pedicel attachment. Simple sympodia occur 
but sometimes a single sporangium on a long pedicel 
is seen. Hyphal swellings and clamydospores have 
not been seen, but knobby hyphae are common.

HOLOTYPUS: ATCC MYA-4554 here designated; a 
cryopreserved specimen of M218.z1 originally isolated 
from *Persea americana* by J. Menge (USA, California). 
GenBank EU748545.

Additional strains examined.—TABLE II.

**Etymology.**—‘*mengei*’ refers to the originator (Dr 
John Menge) of the type culture and eight additional 
avocado isolates used in this study.

**RESULTS**

*Temperature-growth relation.*—Daily growth rates on 
lima bean agar for p340 and p341 were respectively 
0 mm at 6, 33 and 35 C, 5 mm at 10 C, 5 and 8 mm at 
15 C, 13 and 11 mm at 20 C, 15 and 13 mm at 25 C, 
6 mm at 28 C and 5 mm at 30 C. Thus the minimum 
temperature for colony growth was 6–10 C, the 
optimum about 25 C, and the maximum 30–33 C.

**SSCP analysis.**—The 11 isolates of *P. mengei* pro-
duced an identical PCR-SSCP pattern that was distinct 
from four reference species (Fig. 2). Comparatively 
both top and bottom bands of *P. mengei* were faster

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**Fig. 1.** Diagnostic morphological characters of *Phy-
tophthora mengei*. A, B. Young oogonia and antheridia 
showing asymmetric capitate antheridia. C, D. Mature 
sexual bodies with plerotic oospores. E. Hyphae with knobs 
and short projections. F. Ovoid and bluntly ellipsoid 
semipapillate sporangia, one with two papillae. G. A bizarre 
sombrero-shaped sporangium. H. Ellipsoid sporangia, one 
with a constriction. I. A single bluntly ellipsoid sporangium. 
Bars = 10 μm.

**Habitat.**—This pathogen is found in the trunks, main 
structural roots and fruit of infected avocado trees in 
southern California, USA.
moving than bands of the other Phytophthora spp. used as references.

Sequence analysis and phylogenetic position of P. mengei.—Both isolates of P. mengei had identical complete sequences in ITS1-5.8S-ITS2 region of rDNA (EU748545, EU748546, 753 bp), and partial sequences of β-tubulin gene (899 bp), translation elongation factor 1α (869 bp) and NAHD dehydrogenase subunit I (792 bp). Sequence alignments of the ITS regions indicated that this new species is clustered with P. botryosa Chee, P. colocasiae Racib. and P. meadii McRae (Fig. 3). Phylogenetically this species is closer to P. siskiyouensis Reeser and E.M. Hansen, P. capsici Leonian, P. tropicalis Aragaki and J.Y. Uchida than P. citricola. Compared to P. siskiyouensis P. mengei has two insertions at sites 108 and 406, one deletion at 15 and five substitutions at 136, 143, 401, 531 and 689 respectively. Similarly this new species has one insertion at site 400 and seven substitutions at 94, 96, 124, 142, 419, 725 and 737 when compared to P. tropicalis. In contrast P. mengei differs from P. citricola by having a long gap at sites 59–69, three insertions at 414, 415 and 730 and nine substitutions at 58, 70, 133, 134, 153, 411, 443 and 748 respectively. Sequence alignments of the other three regions (data not shown) support the phylogenetic analysis of the ITS region.

Table II. Morphological characters of Phytophthora mengei and other homothallic-paragynous-semipapillate species of Phytophthora

<table>
<thead>
<tr>
<th>Morphological character</th>
<th>P. mengei</th>
<th>P. citricola</th>
<th>P. primulae</th>
<th>P. pseudosyringae</th>
<th>P. siskiyouensis</th>
<th>P. syringae</th>
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<tbody>
<tr>
<td>Number of isolates or reference</td>
<td>11</td>
<td>2</td>
<td>30</td>
<td>30</td>
<td>27.8</td>
<td>28</td>
</tr>
<tr>
<td>Oogonium (μm)</td>
<td>26</td>
<td>31</td>
<td>38</td>
<td>30</td>
<td>27.8</td>
<td>28</td>
</tr>
<tr>
<td>Antheridia</td>
<td>10</td>
<td>10.5</td>
<td>14</td>
<td>10</td>
<td>8.6–11.6 × 9.5–13.3</td>
<td>10</td>
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<tr>
<td>Oospore</td>
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<td></td>
<td></td>
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<td>Fitness</td>
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<td>Plerotic</td>
<td>Aplerotic</td>
<td>Plerotic</td>
<td>Aplerotic</td>
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<tr>
<td>Mean diameter (μm)</td>
<td>22</td>
<td>28</td>
<td>30</td>
<td>27</td>
<td>24.6</td>
<td>26</td>
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<tr>
<td>Diameter range (μm)</td>
<td>—</td>
<td>—</td>
<td>25.5–34.0</td>
<td>—</td>
<td>22.5–25.8</td>
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<tr>
<td>Wall thickness (μm)</td>
<td>2.3</td>
<td>1.5</td>
<td>2.5</td>
<td>1.0</td>
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<td>4.0</td>
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<td>Sporangia</td>
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<td>1 x w mean (μm)</td>
<td>62.7 × 35.2</td>
<td>56.3 × 37.8</td>
<td>57.1 × 44.8</td>
<td>40.8 × 30.6</td>
<td>55 × 36</td>
<td>42.0 × 31.0</td>
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<tr>
<td>1/w ratio</td>
<td>1.78</td>
<td>1.48</td>
<td>1.26a</td>
<td>1.44</td>
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<td>1.35</td>
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<td>Caducityb</td>
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<td>—</td>
<td>—</td>
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<td>Hyphal swellingc</td>
<td>—</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>—</td>
<td>+</td>
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<tr>
<td>Temperature-growth relation</td>
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<tr>
<td>Maximum (C)</td>
<td>30–33</td>
<td>31</td>
<td>&lt; 27</td>
<td>&lt; 27</td>
<td>30</td>
<td>23</td>
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<td>Growth rate at optimum (mm d⁻¹)</td>
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<td>—</td>
<td>4.6</td>
<td>6.2–8.5</td>
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<td>8</td>
<td>3</td>
<td>2</td>
<td>8</td>
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</table>

a Only ovoid sporangia measured, bizarre sporangia up to 300 μm occasionally occur.
b − = non-caducous, + = caducous.
c − = not present, + = not common, ++ = common.

DISCUSSION

Comparative DNA fingerprinting and sequence analyses, as well as morphological examinations, indicated that the avocado subgroup of P. citricola constitutes a new, separate species, and we named it Phytophthora mengei sp. nov. This new species is phylogenetically closer to P. siskiyouensis, P. capsici and P. tropicalis than P. citricola. Separation of P. mengei from P. citricola is supported by studies of morphology (Zentmyer et al 1974), isozymes (Oudemans et al 1994) and AFLP (Bhat and Browne 2007). Phytophthora mengei can be easily differentiated from its close relatives by sequence analysis. Also it can be easily distinguished from these relatives and other

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<td>Number of isolates or reference</td>
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<td>(Gallegly and Hong 2008)</td>
<td>(Gallegly and Hong 2008)</td>
<td>(Reeser et al 2007)</td>
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<td>Oogonium (μm)</td>
<td>26</td>
<td>31</td>
<td>38</td>
<td>30</td>
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<td>28</td>
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<td>Antheridia</td>
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<td>8.6–11.6 × 9.5–13.3</td>
<td>10</td>
</tr>
<tr>
<td>Oospore</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fitness</td>
<td>Plerotic</td>
<td>Plerotic</td>
<td>Aplerotic</td>
<td>Plerotic</td>
<td>Aplerotic</td>
<td>Plerotic</td>
</tr>
<tr>
<td>Mean diameter (μm)</td>
<td>22</td>
<td>28</td>
<td>30</td>
<td>27</td>
<td>24.6</td>
<td>26</td>
</tr>
<tr>
<td>Diameter range (μm)</td>
<td>—</td>
<td>—</td>
<td>25.5–34.0</td>
<td>—</td>
<td>22.5–25.8</td>
<td>—</td>
</tr>
<tr>
<td>Wall thickness (μm)</td>
<td>2.3</td>
<td>1.5</td>
<td>2.5</td>
<td>1.0</td>
<td>—</td>
<td>4.0</td>
</tr>
<tr>
<td>Sporangia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 x w mean (μm)</td>
<td>62.7 × 35.2</td>
<td>56.3 × 37.8</td>
<td>57.1 × 44.8</td>
<td>40.8 × 30.6</td>
<td>55 × 36</td>
<td>42.0 × 31.0</td>
</tr>
<tr>
<td>1/w ratio</td>
<td>1.78</td>
<td>1.48</td>
<td>1.26a</td>
<td>1.44</td>
<td>1.5</td>
<td>1.35</td>
</tr>
<tr>
<td>Caducityb</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.5</td>
<td>0.3</td>
</tr>
<tr>
<td>Hyphal swellingc</td>
<td>—</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>—</td>
<td>+</td>
</tr>
<tr>
<td>Temperature-growth relation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum (C)</td>
<td>30–33</td>
<td>31</td>
<td>&lt; 27</td>
<td>&lt; 27</td>
<td>30</td>
<td>23</td>
</tr>
<tr>
<td>Growth rate at optimum (mm d⁻¹)</td>
<td>14.5</td>
<td>—</td>
<td>—</td>
<td>4.6</td>
<td>6.2–8.5</td>
<td>—</td>
</tr>
<tr>
<td>Phylogenetic clade</td>
<td>2</td>
<td>2</td>
<td>8</td>
<td>3</td>
<td>2</td>
<td>8</td>
</tr>
</tbody>
</table>

a Only ovoid sporangia measured, bizarre sporangia up to 300 μm occasionally occur.
b − = non-caducous, + = caducous.
c − = not present, + = not common, ++ = common.
Phytophthora mengei will be placed in the homothallic-paragynous-semipapillate group of the morphological key by Gallegly and Hong (2008). The other species in this group are *P. citricola*, *P. syringae*, *P. pseudosyringae*, *P. primulae* and *P. porri*. Based on its original description *P. siskiyousensis* will be placed in this group. The differences of these species are that *P. mengei* has smaller oogonia, no hyphal swellings, and has asymmetric capitate antheridia on many of the oogonia. The sporangia of *P. mengei* are similar to those of *P. primulae* and differ from those of the other species in the group by forming many large, bizarre shapes. However the oogonia of *P. mengei* are much smaller than those of *P. primulae* (24 vs. 38 μm) and the maximum temperature for colony growth is higher (31 vs. < 27 °C). This new species also can be easily separated from *P. capsici* and *P. tropicalis*. *Phytophthora mengei* is homothallic and produces noncaducous semipapillate sporangia, whereas *P. capsici* and *P. tropicalis* are heterothallic and produce conspicuously papillate sporangia. In addition sporangia of *P. tropicalis* are caducous with long pedicels.

*P. mengei* and *P. siskiyousensis* are mostly similar morphologically. The oospores of *P. mengei* are plerotic, whereas those of *P. siskiyousensis* are aplerotic. Also the oogonial sizes of these two species differ.

![Polyacrylamide gel electrophoresis](image)

**Fig. 2.** Polyacrylamide gel electrophoresis of amplified ribosomal DNA internal transcribed spacer 1 region with primers ITS6 and ITS7 of 11 isolates of *Phytophthora mengei* (Lanes 2–12) and two authentic isolates of *Phytophthora citricola* (Lanes 13 and 14) and one isolate of *P. syringae*, *P. primulae* and *P. pseudosyringae* (Lanes 15–17 respectively). Lanes 1 and 18 are single-stranded DNA (ssDNA) ladders.

![Neighbor joining phylogenetic tree](image)

**Fig. 3.** Neighbor joining phylogenetic tree based on the sequences of the ITS regions of *Phytophthora mengei* with its close relatives and other species representing different clades of genus *Phytophthora*.
slightly (26.0 vs. 27.8 μm). The antheridia of *P. mengei* and those of *P. siskiyouensis* are described respectively as being asymmetrically capitate and capitate. Also sporangia of these two species are similar but those of *P. mengei* appear to be more irregularly shaped. The maximum growth temperature for *P. mengei* is slightly higher than that for *P. siskiyouensis*, whereas the minimum temperature for growth is lower for *P. siskiyouensis*. Variability among isolates of these two species could render the above discussion moot.

**ACKNOWLEDGMENTS**

We thank Dr Patricia M. Eckel at the Missouri Botanical Garden, St Louis, Missouri, for her assistance in preparing the Latin diagnosis.

**LITERATURE CITED**


