

Taxonomy and Phylogeny of *Peronospora* Species (Oomycota) Parasitic to *Stellaria* and *Pseudostellaria* in Korea, with the Introduction of *Peronospora casparyi* sp. nov.

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Abstract The genus *Peronospora*, an obligate biotrophic group belonging to Oomycota, causes serious damage to a variety of wild and ornamental plants, as well as cultivated crops, such as beet, rose, spinach, and tobacco. To investigate the diversity of *Peronospora* species parasitic to *Stellaria* and *Pseudostellaria* (Caryophyllaceae) plants in Korea, we performed a morphological analysis on dried herbarium specimens and molecular phylogenetic inferences based on internal transcribed spacer rDNA and *cox2* mitochondrial DNA sequences. As a result, it was confirmed that there are four species of *Peronospora* parasitic to specific species of *Stellaria* and *Pseudostellaria*, all of which were hitherto unrecorded in Korea: *P. alsinearum* (ex *Stellaria media*), *P. stellariae-aquaticae* (ex *Stellaria aquatica*), *P. stellariae-uliginosae* (ex *Stellaria alsine*), and *P. pseudostellariae* (ex *Pseudostellaria palibiniana*). In addition, *Peronospora* specimens parasitic to *Pseudostellaria davidii* differed morphologically from *P. pseudostellariae* owing to the large and ellipsoidal conidia; this morphological discrepancy was also validated by the high genetic divergence between the two species. *Peronospora casparyi* sp. nov. is described and illustrated here.

Keywords Barcoding, Caryophyllaceae, *cox2*, Diversity, Host specificity

The Oomycota is a distinct phylogenetic lineage of fungus-like microorganisms. The genus *Peronospora* (Peronosporaceae) is one of the most diverse and economically important oomycete groups, which causes the notorious downy mildew disease on a wide range of cultivated and ornamental plants. They are likely the most widespread and potentially destructive pathogens in the cultivations of sugar beet (*Beta vulgaris*), roses (*Rosa hybrida*), berries (*Rubus* spp.),

tobacco (*Nicotiana tabacum*), quinoa (*Chenopodium quinoa*), basil (*Ocimum basilicum*), and spinach (*Spinacia oleracea*) [1].

The Caryophyllaceae plants form a clade of approximately 70 genera and 2,200 species of herbs and subshrubs [2]. Although their centre of diversity is in the Mediterranean and Middle Eastern regions, they also include genera endemic to North America, South America, Africa, and Asia [3]. To date, 44 names of *Peronospora*, the third highest number following ones introduced on Fabaceae and Chenopodiaceae, have been described as the downy mildew pathogens infecting Caryophyllaceae [4]. In Korea, however, only two species, *P. campestris* (ex *Arenaria serpyllifolia*) and *P. conferta* (ex *Cerastium holosteoides*), have been reported hitherto [5].

During a survey of the diversity of Peronosporaceae in Korea, numerous samples associated with *Peronospora* have been collected on plants of two genera of Caryophyllaceae, *Stellaria* and *Pseudostellaria*. The *Stellaria* is a cosmopolitan group with about 90–120 species, but the *Pseudostellaria* is mainly distributed in Asia, with up to 20 species. So far, six species of *Peronospora* have been described on different species of *Stellaria*; *P. alsinearum* (ex *S. media*) [6], *P. media* (ex *S. media*, *S. nemorum*), *P. parva* (ex *S. holostea*) [7], *P. stellariae-aquaticae* (ex *S. aquatica* = *Myosoton aquaticum*),

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P. stellariae-uliginosae (ex *S. alsine* var. *undulata* = *S. uliginosa*) [8], and *P. stellariae-radiantis* (ex *S. radians*) [9]. Downy mildew pathogen on *Pseudostellaria* has been firstly described by Yin and Yang [10], who introduced a new species, *Peronospora pseudostellariae*, to recommend a causal agent occurring on *Ps. heterophylla*. In Korea, *Peronospora* specimens have been collected from *Pseudostellaria davidii* and *Pseudostellaria palibiniana*. The fungus on the latter plant was morphologically close to *P. pseudostellariae*. However, the specimens of *Peronospora* parasitic on *Ps. davidii* differed with *P. pseudostellariae*, especially in the size and shape of conidia. Although the feature of the oomycete in these specimens indicated the possible existence of a second species of *Peronospora* infecting *Pseudostellaria*, it was considered that more study was necessary for its introduction and classification.

In the present study, we present the results of phenetic and molecular phylogenetic analyses for the downy mildew species parasitic to *Stellaria* and *Pseudostellaria* collected in Korea, including a presumably new taxon.

MATERIALS AND METHODS

Oomycete samples. Plants of *Stellaria* and *Pseudostellaria* with downy mildew infections were collected from different sites of Korea. Information on the dried herbarium samples selected for morphological and molecular phylogenetic analyses is provided in Table 1.

Morphological analysis. Conidiophores, conidia, and resting organs formed from the infected leaves were transferred to a drop of lactic acid on a slide glass, covered with a cover slip, and briefly heated using an alcohol

lamp. The microscope preparations were examined under brightfield- and DIC-light microscopes, and photographed using a model BX53F microscope (Olympus, Tokyo, Japan) equipped with a DigiRetina 16M digital camera (Tucsen, Fuzhou, China). Measurements were performed at $\times 400$ for conidia and $\times 100$ – $1,000$ for other organs, and reported as maxima and minima in parentheses and the mean plus and minus the standard deviation of the number of measurements given in parentheses.

DNA extraction, PCR, and sequencing. Genomic DNA was extracted from the infected host tissue using the MagListo 5M Plant Genomic DNA Extraction Kit (Bioneer, Daejeon, Korea). Two barcode markers for oomycetes, the ribosomal internal transcribed spacer (ITS) region and the mitochondrial cytochrome c oxidase subunit II (*cox2*) gene [11], were amplified with primers ITS1-O [12] and LR0 [13] and primers *cox2*-F [14] and *cox2*-RC4 [11], respectively. PCR conditions for ITS and *cox2* amplifications were identical as outlined in Choi et al. [15]. The PCR products were purified and sequenced by a DNA sequencing service (Macrogen Inc., Seoul, Korea), with the same primers used for amplification.

Phylogenetic analysis. Sequences of the ITS rDNA and the *cox2* mtDNA were edited with the DNASTAR software package ver. 5.05 (DNASTar Inc., Madison, WI, USA). Alignments of each locus were performed using the Q-INS-i algorithm [16] in MAFFT 7 [17], in addition to the reference sequences of *Peronospora* parasitic to *Stellaria* species, available in GenBank. Maximum likelihood (ML) and minimum evolution (ME) methods were used to infer the phylogenetic trees. For ML analysis, 1,000 rounds of

Table 1. Information of *Peronospora* specimens parasitic to *Stellaria* and *Pseudostellaria* in Korea

Oomycete species	Host plant	Geographic origin	Herb. No.	GenBank accession No.	
				ITS rDNA	<i>cox2</i> mtDNA
<i>P. stellariae-uliginosae</i>	<i>Stellaria alsine</i>	Korea, Chuncheon	KUS-F18827	MF784738	MF784725
<i>P. stellariae-uliginosae</i>	<i>S. alsine</i>	Korea, Chuncheon	KUS-F15790	-	MF784726
<i>P. stellariae-uliginosae</i>	<i>S. alsine</i>	Korea, Yangpyeong	KUS-F21734	MF784739	MF784727
<i>P. stellariae-aquaticae</i>	<i>S. aquatica</i>	Korea, Chuncheon	KUS-F17269	MF784740	-
<i>P. stellariae-aquaticae</i>	<i>S. aquatica</i>	Korea, Hongcheon	KUS-F17326	MF784741	MF784728
<i>P. stellariae-aquaticae</i>	<i>S. aquatica</i>	Korea, Chuncheon	KUS-F29741	MF784742	MF784729
<i>P. parva</i>	<i>S. holostea</i>	Austria, Burgenland	WU22915	AY198276	-
<i>P. parva</i>	<i>S. holostea</i>	Germany, Sachsen-Anhalt	GLM65627	-	KJ654255
<i>P. alsinearum</i>	<i>S. media</i>	Korea, Jeju	KUS-F21708	MF784743	MF784730
<i>P. alsinearum</i>	<i>S. media</i>	Korea, Jeju	KNUH88	MF784744	MF784731
<i>P. alsinearum</i>	<i>S. media</i>	Austria, Vienna	WU22876	AY198279	-
<i>P. alsinearum</i>	<i>S. media</i>	Germany, Sachsen	GLM78867	-	KJ654256
<i>P. pseudostellariae</i>	<i>Pseudostellaria palibiniana</i>	Korea, Hongcheon	KUS-F18840	MF784745	MF784732
<i>P. pseudostellariae</i>	<i>Ps. palibiniana</i>	Korea, Chuncheon	KUS-F26706	MF784746	-
<i>P. pseudostellariae</i>	<i>Ps. palibiniana</i>	Korea, Hongcheon	KUS-F24933	MF784747	MF784733
<i>P. pseudostellariae</i>	<i>Ps. palibiniana</i>	Korea, Hoengseong	KUS-F25730	MF784748	MF784734
<i>P. pseudostellariae</i>	<i>Ps. palibiniana</i>	Korea, Hongcheon	KUS-F25743	MF784749	MF784735
<i>Peronospora</i> sp.	<i>Ps. davidii</i>	Korea, Hongcheon	KUS-F18847	MF784750	MF784736
<i>Peronospora</i> sp.	<i>Ps. davidii</i>	Korea, Chuncheon	KUS-F25822	MF784751	MF784737

random addition of sequences as well as 10,000 fast bootstrap replicates were performed with RAxML 7.0.3 [18] using the GTRCAT model. ME analysis was done using MEGA 7.0 [19] with the default settings of the program, except for replacement with the Tamura-Nei model, and the robustness of the ME tree was evaluated with 10,000 bootstrap replicates.

RESULTS AND DISCUSSION

The phylogenetic relationships of *Peronospora* species parasitic on *Stellaria* and *Pseudostellaria* species were inferred using ML and ME analyses of the ITS rDNA and *cox2* mtDNA sequences. As the tree topologies generated from ML and ME inferences were fully compatible (data not shown), except for minor differences in bootstrapping support values, only the ML tree is shown for each locus (Fig. 1A for ITS and 1B for *cox2*), with ML and ME bootstrap values higher

than 70% at first and second position above the branches.

In both ITS and *cox2* trees, the accessions of *Peronospora* originated from three species of *Stellaria* and two species of *Pseudostellaria* formed four highly supported clades; the first monophyletic clade consisting of two *Peronospora* species, *P. pseudostellariae* parasitic on *Ps. palibiniana* and *P. stellariae-uliginosae* on *Stellaria alsine*, the second of *P. stellariae-aquatica* on *Stellaria aquatica*, the third of *P. alsinearum* on *S. media*, and the fourth of an undetermined species of *Peronospora* on *Ps. davidii*. Interestingly, in the first clade, *P. pseudostellariae* and *P. stellariae-uliginosae*, were undistinguishable in both gene trees, although a specimen (KUS-F21734) of *P. stellariae-uliginosae* revealed only one substitution in the ITS sequence, providing evidence of their close genetic affinity. However, we postpone a synonymization of the epithet *P. pseudostellariae* under *P. stellariae-uliginosae* to a further study using additional

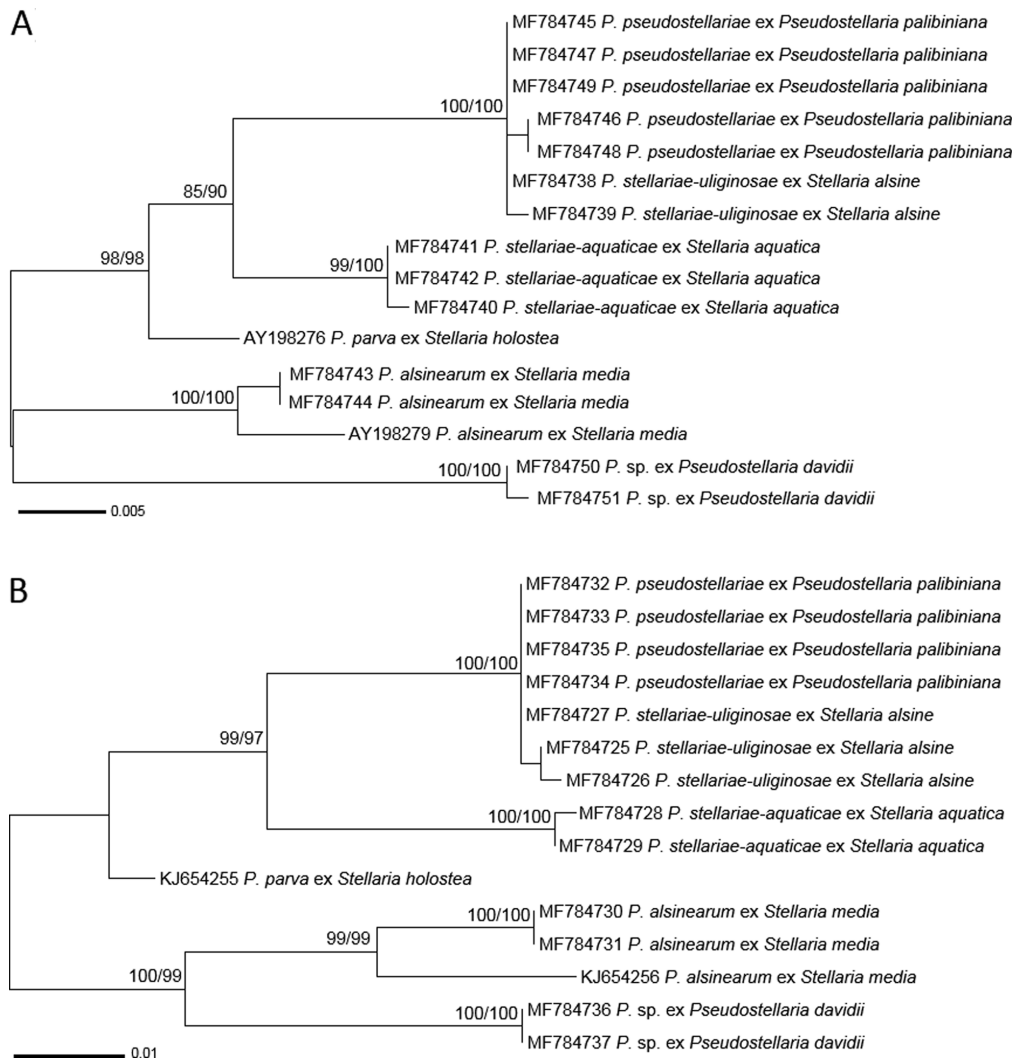


Fig. 1. Maximum likelihood trees based on the complete internal transcribed spacer (ITS) (ITS1, 5.8S rDNA, and ITS2) sequences (A) and the *cox2* mitochondrial DNA sequences (B), with support values in minimum evolution inference. Bootstrapping support values (maximum likelihood/minimum evolution) higher than 70% are given above the branches. The scale bar equals the number of nucleotide substitutions per site.

samples and more variable gene markers. In the third clade of *P. alsinearum*, despite all specimens originating from the same host plant species, *S. media*, a significant level of genetic divergences were found, which was most likely due to the distance in the geographic origin: two samples were obtained from Korea, but the remaining from Austria (ITS: AY198279) and Germany (*cox2*: KJ654256).

The specimens from *Ps. davidii* were placed as an independent group from *Peronospora* species on *Stellaria*, as well as *P. pseudostellariae*, and the phylogenetic distances were considerably greater. Their genetic distance from *P. pseudostellariae* was approximately 5.36% (43 out of 802 characters were different) in the ITS sequences and 7.97% (43 out of 539 characters) in the *cox2* sequences. Morphological characteristics of *Peronospora* on *Ps. davidii* markedly differed from those of *P. pseudostellariae*. In the specimens assumed to belong to the new species, the conidia were ellipsoidal, which noticeably distinguished them from the conidia of *P. pseudostellariae* (Fig. 3); a ratio of length to width of *Peronospora* sp. was (1.21–)1.31–1.54(–1.64) (av. 1.43), while the latter was (1.12–)1.20–1.42(–1.50) (av. 1.29). The conidial size of the former species measured av. $26.64 \times 18.72 \mu\text{m}$, which are much larger than the latter (av. $18.24 \times 14.12 \mu\text{m}$). Concerning the length of conidiophores, the former (180–)210–300(–330) μm were shorter than the latter (110–)170–380(–440) μm .

The range of natural hosts of two *Peronospora* species on *Pseudostellaria* hints at an intimate oomycete/plant association. The genus *Pseudostellaria* was subdivided into two series, Glochidiatae and Mamillatae, among which the latter further split into two subseries, Verticillate and Distantes. *Pseudostellaria heterophylla* and *Ps. palibiniana*, the host plants of *P. pseudostellariae*, both belong to the subseries Verticillate, while *Ps. davidii*, the host of *Peronospora* sp., belongs to Distantes [20, 21]. Nonetheless, this correspondence may have resulted from host-shift driven speciation (pseudo-cospeciation), rather than long-term coevolution, as well observed in other downy mildews [22].

Taxonomy. Based on the molecular phylogenetic and morphological data, we reported four previously unknown species in Korea, namely *P. alsinearum*, *P. stellariae-aquaticae*, *P. stellariae-uliginosae*, *P. pseudostellariae*, and *P. casparyi* sp. nov.

Peronospora alsinearum Casp. (Fig. 2)

Basionym: *Peronospora alsinearum* Casp., Monatsbericht. König. Akad. Wiss. Berlin 1855: 330 (1855) [MB#223417].

Description: Down hypophyllous, yellowish to brownish, consisting of scattered patches of conidiophores, rarely of a more or less dense structure. Conidiophores hyaline, slender, (200–)240–350(–390) μm long; trunk straight to slightly curved, (60–)100–220(–260) μm long ($n = 50$), of more or less uniform width, (6.3–)7.3–10(–11) μm wide at the middle, basal end not differentiated, rarely slightly bulbous, callose plugs absent; branching elaborate, sub- to dichotomous, in

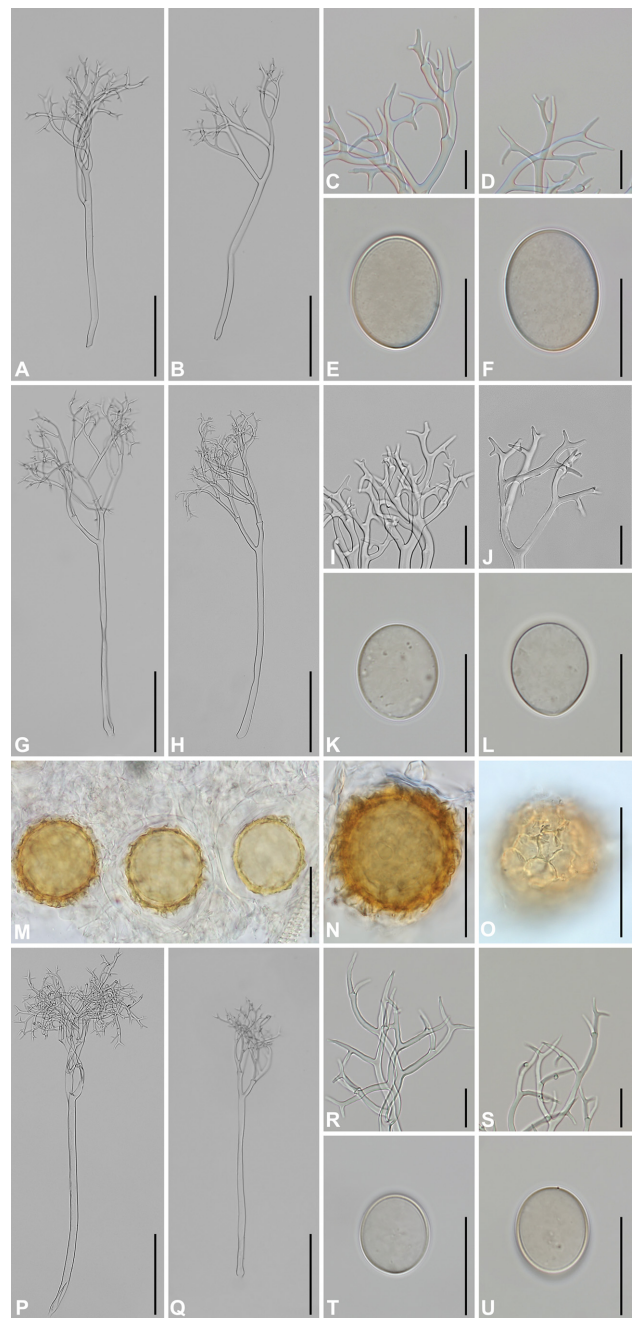


Fig. 2. Morphological characteristics of three *Peronospora* species parasitic on *Stellaria* species, *P. alsinearum* ex *Stellaria media* (A–F), *P. stellariae-aquaticae* ex *Stellaria aquatica* (G–O), *P. stellaria-uliginosae* ex *Stellaria alsine* (P–U). A, B, G, H, P–Q, Conidiophores; C, D, I, J, R, S, Ultimate branchlets; E, F, K, L, T, U, Conidia; M–O, Resting organs (scale bars: 100 μm for conidiophores, 20 μm for ultimate branchlets and conidia, and 40 μm for resting organs).

(5–)6–7 orders, branches slightly curved; ultimate branchlets mostly in pairs or rarely single, sub-straight to slightly curved to sigmoid, (3–)5–12(–14) μm long, (1.2–)1.5–2.3(–2.6) μm wide at the base ($n = 30$), apex subtruncate or obtuse. Conidia bright yellowish, broadly ellipsoidal to

ellipsoidal, (23–)24–29(–30) μm long (av. 26.97), (18–)19–22(–23) μm wide (av. 20.76), with a ratio of length to width of (1.13–) 1.20–1.36(–1.43) (av. 1.30, $n = 50$), greatest width median, rarely supra-median, tip rounded, base narrowing to rounded; germination at the side of conidia, producing germ tubes, up to 100 μm long. Resting organs not seen.

Habitat: Infested leaves of *Stellaria media*.

Specimen examined: Korea, Jeju-do, Jeju-si, Hallasan National Park, 33°28'11" N, 126°29'37" E, 3 Dec 2004, H. D. Shin and Y. J. Choi, KZITFG000000013 (KUS-F21011); also see Table 1.

Note: Two species of *Peronospora*, *P. alsinearum* [6] and *P. media* [7], have been described on *Stellaria media*, but Gustavsson [23] thought that the latter species is conspecific with *P. alsinearum*. All morphological characteristics of the Korean samples are consistent with the descriptions for *P. alsinearum* [7, 23]. This is the first record of *P. alsinearum* in Korea.

Peronospora stellariae-aquaticae Sawada (Fig. 2)

Basionym: *Peronospora stellariae-aquaticae* Sawada, sec. Sawada 1927, Descript. Cat. Formosa Fungi: 58 (1925) [MB#278783].

Description: Down hypophyllous, whitish to greyish, consisting of dense patches of conidiophores, Conidiophores hyaline, slender, (210–)280–470(–550) μm long; trunk straight to slightly curved, (90–)150–360(–420) μm long ($n = 50$), of more or less uniform width, (6–)8–11(–13) μm , basal end not differentiated, rarely slightly bulbous, callose plugs absent; branching elaborate, sub- to dichotomous, 5–6(–7) orders, branches slightly curved; ultimate branchlets mostly in pairs or rarely single, straight to slightly curved, (3–)5–10(–12) μm long, (1–)1.5–3(–3.5) μm wide at the middle ($n = 30$), apex subtruncate or obtuse. Conidia pale olivaceous, broadly ellipsoidal, (16–)17–21(–22) μm long (av. 19.55), (14–)15–18(–19) μm wide (av. 16.51), with a ratio of length to width of (1.05–)1.13–1.37(–1.45) (av. 1.18, $n = 50$), greatest width median, rarely supra-median, tip rounded, base rounded or narrowing, pedicel absent or hardly visible as a scar to slightly protruding; germination at the side of conidia, producing germ tubes, up to 300 μm long, often various globose swellings and whirling. Resting organs rarely present and visible as yellow to brown spot on leaves. Oospores plerotic to aplerotic, globose, (32–)37–45(–52) μm diameter, yellowish, 2–3.5 μm thick wall.

Habitat: Infested leaves of *Stellaria aquatica*.

Specimen examined: Korea, Gangwon-do, Hoengseong-gun, Chudong-ri, 37°28'42" N, 128°01'34" E, 8 Sep 2011, H. D. Shin & Y. J. Choi, KZITFG000000015 (KUS-F26123); also see Table 1.

Note: This is the first record of *P. stellariae-aquaticae* in Korea. The morphological features of the present specimen are consistent with the original description by Sawada [24], except that conidia in the Korean sample (av. 19.55 \times 16.51 μm) are somewhat smaller than those of the original description (av. 21.1 \times 17.6 μm).

Peronospora stellariae-uliginosae Sawada (Fig. 2)

Basionym: *Peronospora stellariae-uliginosae* Sawada, see Sawada 1927, Descript. Cat. Formosa Fungi: 59 (1925) [MB#278785].

Description: Down on to lower surface of leaves but rarely on stems, greyish to yellowish, consisting of dense patches of conidiophores. Haustoria hyphal, branched, filling the host cell almost completely. Conidiophores hyaline, slender, (170–)280–520(–600) μm long; trunk straight to slightly curved, (50–)140–310(–400) μm long ($n = 50$), of more or less uniform width, (6–)7–10(–11) μm wide at the middle, callose plugs absent; branching elaborate, sub- to dichotomous, in (5–)6–7 orders, branches slightly curved; ultimate branchlets mostly in pairs, rarely single, sub-straight to slightly curved, (4–)6–8(–10) μm long, (1–)1.3–1.5(–1.8) μm wide at the base ($n = 30$), apex subtruncate or obtuse. Conidia brightly yellowish, ellipsoidal, (14–)15–19(–20) μm long (av. 17.40), (12–)13–15(–16) μm wide (av. 14.24), with a ratio of length to width of (1.06–)1.11–1.31(–1.36) (av. 1.22, $n = 50$), greatest width median, rarely supra-median, tip rounded, base rounded or narrowing, pedicel absent or hardly visible as a scar to slightly protruding; germination at the side of conidia, producing germ tubes, often various swellings and whirling. Resting organs not seen.

Habitat: Infested leaves and stems of *Stellaria alsine*.

Specimen examined: Korea, Gangwon-do, Chuncheon-si, Bongmyeong-ri, 37°50'20" N, 127°47'00" E, 4 Nov 2004, H. D. Shin & Y. J. Choi, KZITFG000000016 (KUS-F20953); also see Table 1.

Note: *Peronospora stellariae-uliginosae* has been described on *Stellaria uliginosa* (now, a synonym of *S. alsine*). The conidial size of the Korean samples is somewhat smaller than ones of the original description [24]. This is the first record of *P. stellariae-uliginosae* in Korea.

Peronospora pseudostellariae G. Y. Yin & Z. S. Yang (Fig. 3)

Basionym: *Peronospora pseudostellariae* G. Y. Yin & Z. S. Yang, Acta Mycol. Sin.: 161 (1994) [MB#413721].

Description: The attacked tissues show spots of 6–10 mm diameter on leaves, often covering much larger areas by coalescing, pale green to yellowish, margin diffuse; the tissues are necrotic and brittle. Down hypophyllous, whitish, consisting of scattered to conglomerated patches of conidiophores. Conidiophores hyaline, slender, (250–)300–470(–600) μm long; trunk straight, (110–)170–380(–440) μm long ($n = 50$), of more or less uniform width, (5.8–)7.3–11.2(–12.7) μm wide below the first branch, 6–10 μm at the base, basal end not differentiated, rarely slightly bulbous and then up to 13 μm wide, callose plugs absent; branching elaborate, monopodial to subdichotomous, in 6–7(–8) orders, branches slightly curved; ultimate branchlets in pairs or single, from substraight to slightly curved, (3.5–)5–8.5(–10) μm long, (1.1–)1.35–2.25(–2.5) μm wide at the base ($n = 30$), apex subtruncate or obtuse. Conidia pale olivaceous, broadly ellipsoidal, (15–)16–20(–21) μm long (av. 18.24), (12–)13–15(–16) μm wide (av. 14.12), with a ratio of length

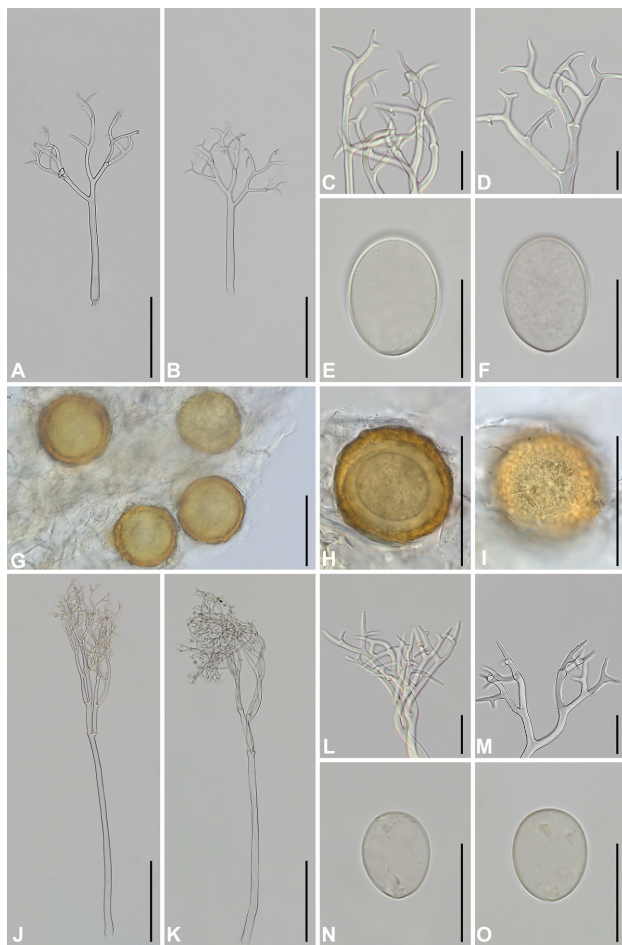


Fig. 3. Morphological characteristics of *Peronospora casparyi* sp. nov. parasitic on *Pseudostellaria davidii* (A–I) and *Peronospora pseudostellariae* on *Pseudostellaria palibiniana* (J–O). A, B, J, K, Conidiophores; C, D, L, M, Ultimate branchlets; E, F, N, O, Conidia; G–I, Resting organs (scale bars: 100 μ m for conidiophores, 20 μ m for ultimate branchlets and conidia, and 40 μ m for resting organs).

to width of (1.12–)1.20–1.42(–1.50) (av. 1.29, $n = 50$), greatest width median, wall ca. 0.4 μ m thick; pedicel absent or hardly visible as a scar to slightly protruding; germination at the randomly located sites of the wall, producing germ tubes, up to 240 μ m long, often various globose swellings and whirling. Resting organs not seen.

Habitat: Infested leaves of *Pseudostellaria palibiniana*.

Specimens examined: Korea, Gangwon-do, Chuncheon-si, Bongmyeong-ri, 37°46'23" N, 127°48'44" E, 5 Jun 2012, H. D. Shin and Y. J. Choi, KZITFG000000014 (KUS-F26706); also see Table 1.

Note: *Peronospora* materials from *Ps. palibiniana* are in agreement with the description of *P. pseudostellariae* [10]. Yin and Yang [10] reported *Pseudostellaria heterophylla* as the original host plant of *P. pseudostellariae*, but the present study added *Ps. palibiniana*, a common wild plant in Korea [25, 26], as a new host of the species. This is the first

record of this species in Korea. So far, the distribution of *P. pseudostellariae* has been restricted to China [10, 27], but the present study suggests that this species may be commonly present in East Asia.

Peronospora casparyi Jae S. Lee & Y. J. Choi, sp. nov. (Fig. 3) [MB#823746]

Etymology: Named in honour of Robert Caspary, who has first recorded the downy mildew species parasitic on the genus *Stellaria* s. lat. (including *Pseudostellaria*).

Description: The attacked tissues show 3–8 mm spots on leaves, covering much larger areas by coalescing, pale green to yellowish, margin diffuse to vein limited; the tissues are finally necrotic and brittle. Down hypophyllous, whitish, consisting of scattered to rarely dense patches of conidiophore. Haustoria hyphal, branched, filling the host cell almost completely. Conidiophores hyaline, slender, (180–)210–300(–330) μ m long; trunk straight to slightly curved, (100–)120–180(–200) μ m long ($n = 50$), of more or less uniform width, (5–)6–8(–9) μ m wide below the first branch, 7–10 μ m at the base, basal end not differentiated, rarely slightly bulbous and then up to 14 μ m wide, callose plugs absent; branching elaborate, monopodial, in 5–6(–7) orders, branches slightly curved; ultimate branchlets in pairs or single, from slightly curved to sigmoid, (5–)8–12(–15) μ m long, (1–)1.5–2.8(–3.3) μ m wide at the base ($n = 30$), apex subtruncate or obtuse. Conidia pale olivaceous, ellipsoidal, (23–)24–29(–30) μ m long (av. 26.64), (16–)17–21(–22) μ m wide (av. 18.72), with a ratio of length to width of (1.21–)1.31–1.54(–1.64) (av. 1.43, $n = 50$), greatest width median, rarely supra-median, tip rounded, base rounded or narrowing, wall ca. 0.5 μ m thick; pedicel absent or hardly visible as a scar to slightly protruding; germination at the randomly located sites of the wall, producing germ tubes, often various swellings and whirling. Resting organs commonly present and clearly visible as brown to dark brown dots on both upper and lower surfaces of infected leaves; oogonia irregular to broadly ellipsoidal to globose, 44–62 μ m diam., wall wrinkled, yellowish, irregularly 1–2 μ m thick; oospores plerotic, globose, 30–45 μ m diam., brownish, wall 2–3 μ m thick, verrucose, periplasm yellowish to brown.

Habitat: Infested leaves of *Pseudostellaria davidii*.

Typus: Korea, Gangwon-do, Chuncheon-si, Bongmyeong-ri, 37°50'20" N, 127°47'00" E, on the leaves of *Pseudostellaria davidii* affected by downy mildew disease, 4 Nov 2004, H. D. Shin & Y. J. Choi (KZITFG000000025—holotypus; KUS-F26707— isotypus).

Distribution: South Korea.

Additional specimens examined: see Table 1.

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