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Didymella fagi sp. nov. and its anamorph *Ascochyta fagi*, causing the yellow leaf spot disease of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in Japan

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An *Ascochyta* fungus was obtained during a survey of leaf spot diseases of *Fagus crenata* in the mountains of Aomori prefecture in 1995. The pathogenicity of the fungus to *F. crenata* was confirmed by inoculation. Its teleomorph was first found on artificially infected leaves after the leaves were placed in an incubator at 5°C with a 12-h photoperiod (approximately 500 lx, daylight strip lamps) for 4 mo. The fungus was found to be the causal agent of yellow leaf spots of *F. crenata* and *Quercus mongolica* var. *grosseserrata* in the field. Comparison with similar fungi so far described from Fagaceae indicated that the anamorph is *Ascochyta fagi* and the teleomorph is an undescribed species of *Didymella*. The name *Didymella fagi* is introduced for the teleomorph. Correlation between the two morphs has been proved by cultural, morphological and pathological studies.

Key Words——anamorph-teleomorph connection; *Ascochyta fagi*; *Didymella fagi*; morphology.

In July1995, we first obtained the present fungus from leaves of *Fagus crenata* Blume during the study of leaf spot disease caused by *Discula umbrinella* (Berk. et Br.) Sutton. This fungus was found to be associated with the yellow leaf spots of *F. crenata* and *Quercus mongolica* var. *grosseserrata* (Blume) Rehd. et Wils. in the mountains of Aomori prefecture in August 1996 (Wei and Harada, 1996). It has now been identified as *Ascochyta fagi* Woronich. based on the morphology of pycnidia and conidia. Its teleomorph was produced on artificially and naturally diseased leaves after artificial overwintering treatment. Several *Mycosphaerella* species have already been described on various Fagaceae species (Ellis and Ellis, 1985; Corlett, 1991), but no *Didymella* species had been described. The teleomorph is described as *Didymella fagi*, a new species of *Didymella* Sacc.

Materials and Methods

Field surverys and collections Naturally diseased leaves of *F. crenata* and *Q. mongolica* var. *grosseserrata* with pycnidia of the fungus were collected on 2 and 18 Aug. 1995 in *F. crenata* forest near lake Towada, Aomori prefecture. To find the teleomorph of the fungus, artificially inoculated leaves of *F. crenata* with conidial isolates (Nos. 2672–2676) were placed in an incubator at 5°C with a 12-h photoperiod (approximately 500 lx, daylight strip lamps) on 18 Nov. 1995, when mature pycnidia had produced in lesions. Mature pseudothecia were produced in lesions in Apr. 1996. Artificially infected leaves of *F. crenata* with pseudothecia of the fungus were collected in Apr. 1996 in the laboratory. The teleomorph of the fungus was also developed on naturally diseased leaves of *F. crenata* and *Q. mongolica* var. *grosseserrata*, which were collected from the field in Aug. 1996 and kept in a plastic box at 1°C in the dark from 2 Aug. 1996 to Apr. 1997. Moisture of these leaves was maintained with wet filter papers. Naturally diseased leaves of *F. crenata* and *Q. mongolica* var. *grosseserrata* with the pseudothecia were collected from Feb. to Apr. 1997 after artificial overwintering in the laboratory since Aug. 1996.

Isolation and culture of the fungus Isolates of the fungus from fresh leaves were obtained by incubating the leaf tissue on potato sucrose agar (PSA). Leaves at the edge of the lesion were torn away with a sterilized knife and surface-sterilized by immersing them in 90% ethyl alcohol for 1–2 min, followed by 1% NaClO for 1–2 min, then immersed in sterilized distilled water for 1–2 min. Pieces of leaf lesions of approximately 3 mm in diam were placed into 90-mm Petri dishes containing PSA, then incubated at 20°C with a12-h photoperiod (approximately 500 lx, daylight lamps). The fungus was distinguished from other fungi by its characteristic blue colonies near the leaf discs. Hyphal tips from the colonies were then isolated onto PSA slants for storage and subsequent study.

Isolates of the fungus from the teleomorph were obtained by growing single ascospores on PSA according to Harada et al. (1974).

Growth of the fungus on agar was recorded from PSA, potato dextrose agar (PDA), malt extract agar

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(MA), yeast phosphate soluble starch agar (YpSs), Czapek agar, Richard agar and Hopkins agar (Wei et al., 1997). Plates were incubated at 20°C with a 12-h photoperiod (approximately 500 lx, daylight fluorescent strip lamps). Colony growth rates were measured on 90-mm plates with agar 5 mm deep, inoculated with a 5-mm mycelial disc.

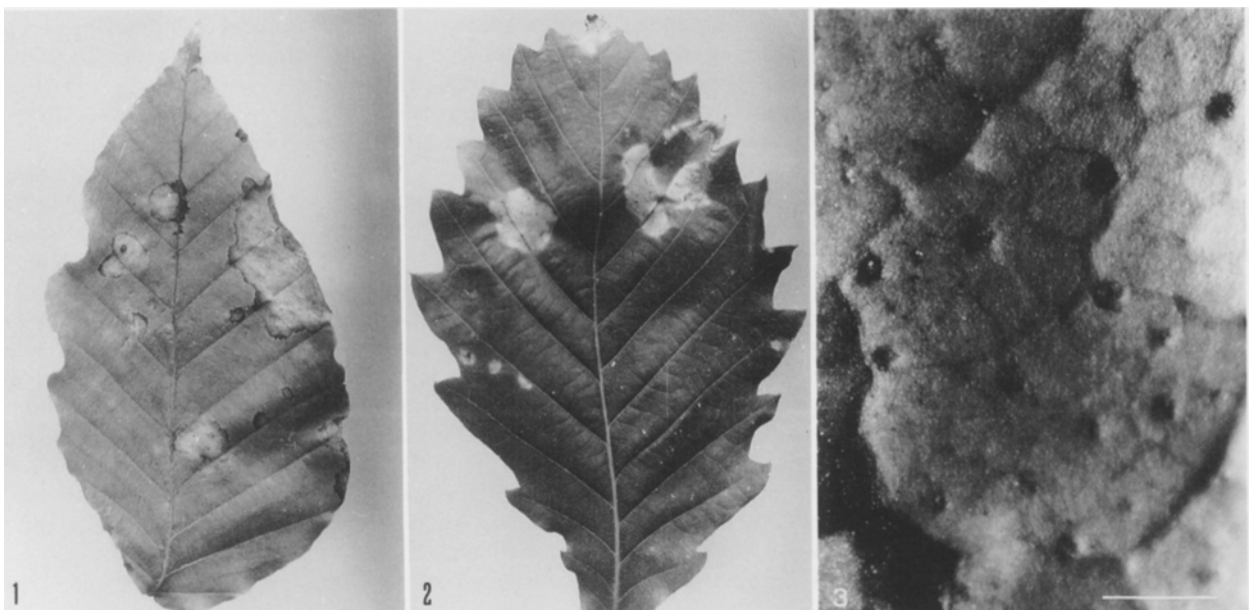
Inoculation Inoculations were made onto the leaves of 2-yr-old potted plants of *F. crenata* and *Q. mongolica* var. *grosseserrata*, which were kept in inoculation chambers near a window in the laboratory during May, or in a growth cabinet maintained at 18–22°C and about 95% relative humidity with a 12-h photoperiod (approximately 1,500 lx, daylight strip lamps). The mycelial agar discs were taken from 1- to 2-wk-old colonies grown on PSA plates at 15°C with a 12-h photoperiod (approximately 500 lx, daylight strip lamps) and placed onto either side of leaves. After lesions developed to about 10–20 mm in diam, the infected plants were moved outdoors for conidia and pycnidia to mature. Agar discs without mycelium were used to inoculate the control plants under the same conditions.

Observation Pycnidia and ascocarps on leaves were sectioned using a microtome (HM 400R, GmbH) equipped with a freezing unit (K 400, GmbH) for anatomical observation. A stereoscopic microscope and a light microscope were used for isolation and observation of the fungus. For light microscopy, materials were mounted in three mounting media: lactophenol (20 g phenol, 20 g lactic acid and 40 g glycerol in 20 ml distilled water), cotton blue (0.02 g cotton blue in 20 ml lactophenol) and distilled water. Fruit bodies produced in culture were also observed using these methods.

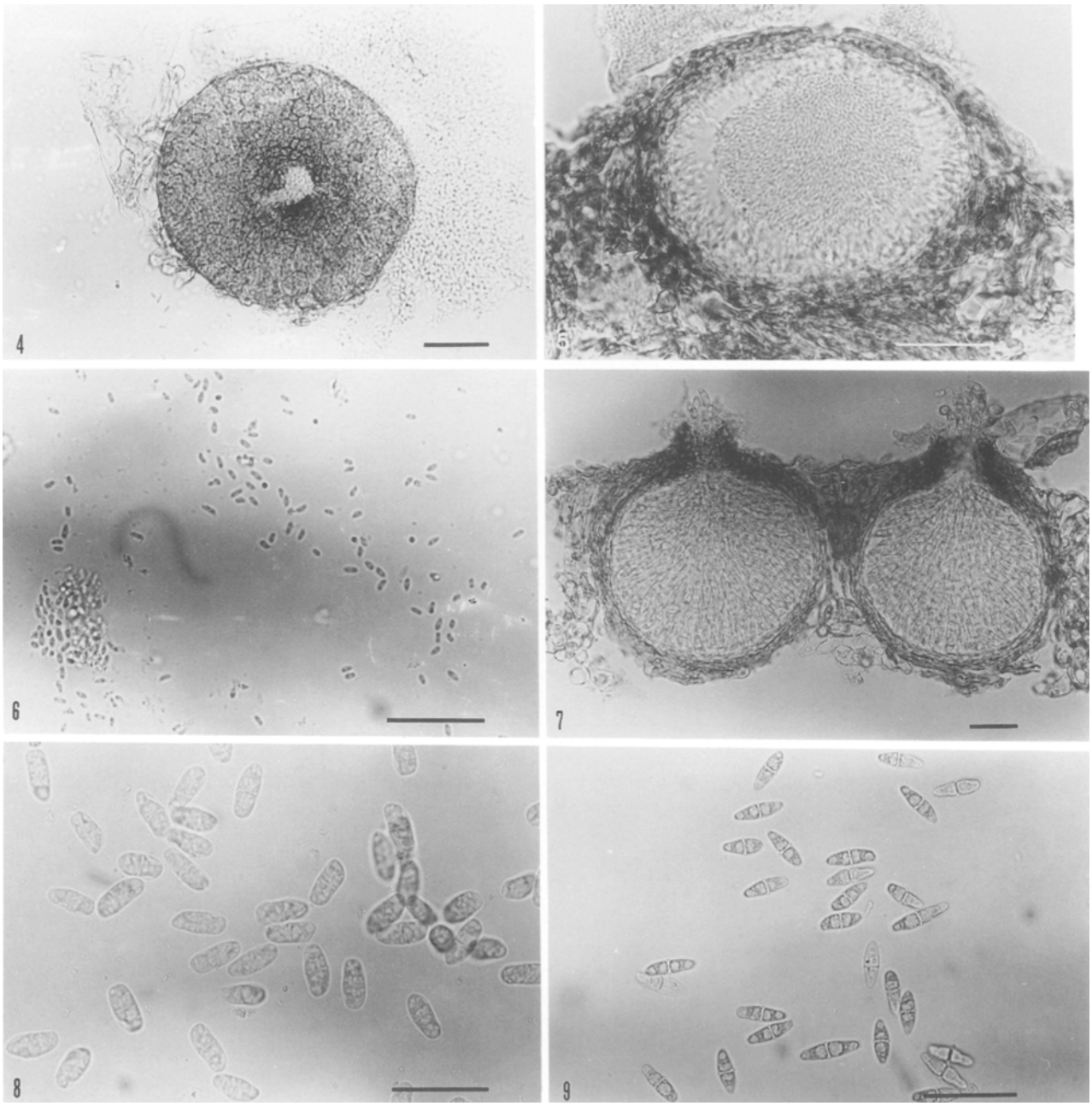
Results

Disease symptoms The first symptoms of the yellow leaf spot disease, which appeared in early Aug. on *F. crenata* and *Q. mongolica* var. *grosseserrata*, were yellow, round spots several mm across on the leaves. Subsequently, the spots enlarged, were suborbicular to oblong, up to 50 mm across on the leaves. Eventually, they extended over the whole leaf surface and resulted in premature shedding of the affected leaves (Figs. 1, 2).

We found three different types of fungal fruit bodies in the lesions at different times: In Aug., the anamorph on *F. crenata* was often observed, but the pycnidia were characteristic of *Asteromella*-like fruit bodies, the conidia were young and looked like spermatia (Figs. 3–6). In this period, we tentatively suspected that this fungus belonged to *Asteromella* Pass. et Thüm. (Sutton, 1980), but the cultures isolated from the lesions were identical to those of *Ascochyta* fungus (Nos. 2672–2781) obtained in 1995 and 1996. After placing these leaves in an incubator at 20°C with a 12-h photoperiod (approximately 500 lx, daylight strip lamps) from 2 Aug. to 30 Aug., most of *Asteromella*-like fruit bodies developed into mature pycnidia of *Ascochyta* in which two-celled conidia are produced (Figs. 7–9), while a few smaller fruit bodies developed into mature spermogonia with light brown walls, from which young pseudothecia with young pseudoparaphyses arising from a basal layer were produced. However, after placing these leaves in an incubator at 5°C with a 12-h photoperiod (approximately 500 lx, daylight strip lamps) or in a plastic box at 1°C in the dark from 2 Aug. to next Apr., all *Asteromella*-like fruit bodies developed into pseudothecia (Figs. 10–13).



Figs. 1–3. Symptom of the disease caused by the fungus.
1. Infected leaf of *Fagus crenata*. 2. Infected leaf of *Quercus mongolica* var. *grosseserrata*. 3. Surface view of young pycnidia on a leaf of *F. crenata*. Scale: 3=400 μm.



Figs. 4–9. *Ascochyta fagi*.
4. Surface view of ostiole of a pycnidium. 5. Vertical section of *Asteromella*-like conidioma. 6. Young conidia. 7. Vertical section of mature pycnidial conidioma. 8. Conidia from naturally diseased leaves. 9. Conidia from artificially infected leaves. (All from *Fagus crenata* leaves). Scales: 30 μm.

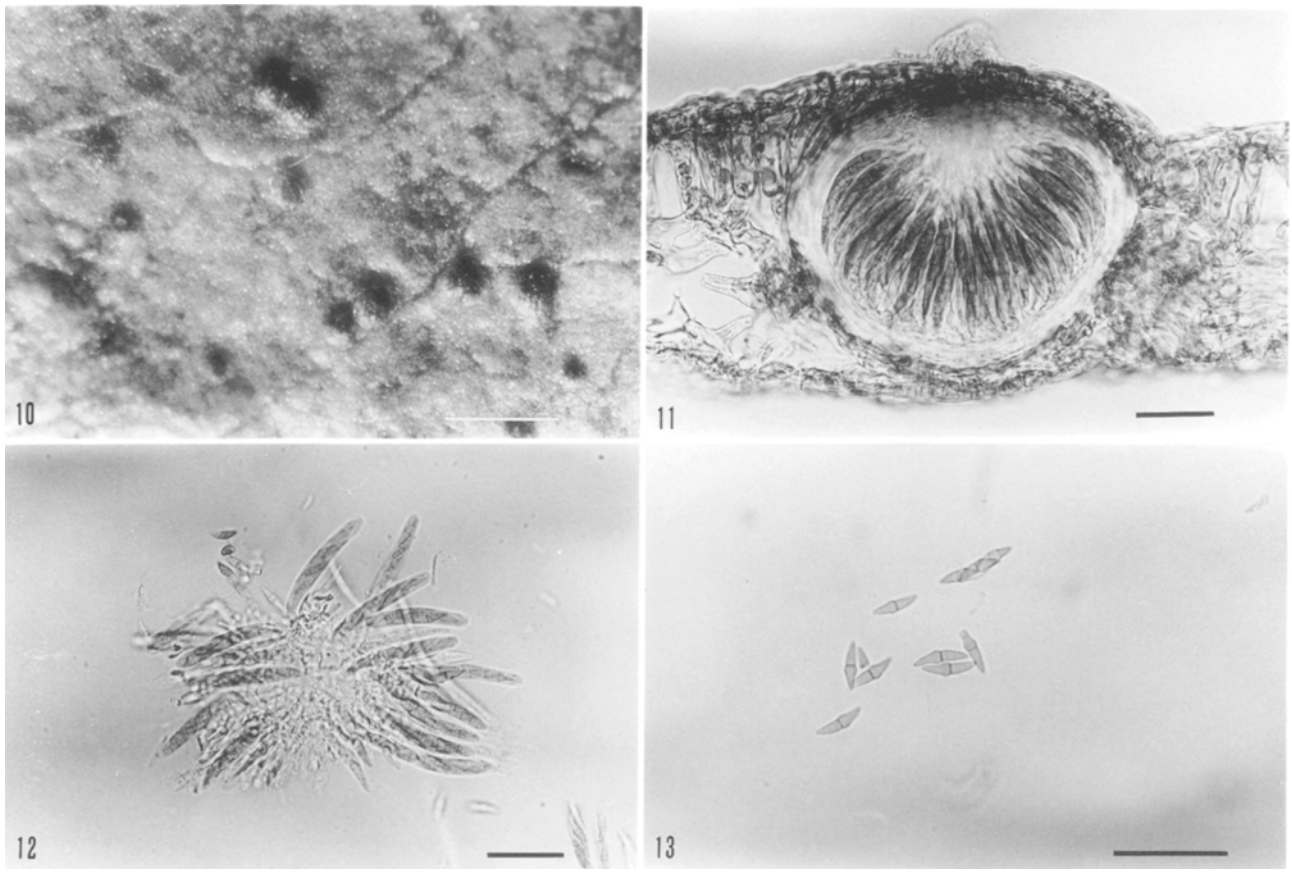
The spots of *Q. mongolica* var. *grosseserrata* are usually larger than those of *F. crenata* in nature, but few *Asteromella*-like fruit bodies or *Ascochyta* pycnidia could be observed, even though the fungus was frequently obtained by culture isolation. After artificial overwintering treatment under the same conditions, very few pseudothecia of this fungus were seen in lesions of *Q. mongolica* var. *grosseserrata* leaves.

On old leaves of *F. crenata*, there were numerous fruit bodies of *Discosia artocreas* (Tode) Fr., but they were infrequent in leaf lesions colonized by the present fungus.

Description

Didymella fagi C. Z. Wei et Y. Harada, sp. nov.
Figs. 10–13

Pseudothecia epiphylla vel hypophylla, subcuticular-



Figs. 10–13. *Didymella fagi*, the teleomorph of *Ascochyta fagi*.
10. Surface view of pseudothecia on a leaf. 11. Vertical section of a pseudothecium. 12. Asci with ascospores. 13. Ascospores. (All from *Fagus crenata* leaves). Scales: 10=400 μm; 11–13=30 μm.

ia, globosa vel ovata, hyalina vel brunneola, singula, ostiolata, 70–170 μm lata, 70–140 μm alta. Paries 10–20 μm crassus, ex cellulis 2–4-stratis flavidis isodiametricis compositus. Pseudoparaphyses filiformes, simplices, 4–5-septatae, 42.5–55 μm longae, 1–1.3 μm crassae, hyalinae, persistentes. Asci bitunicati, clavati vel cylindracei, apice rotundati, octospori, 35–58×6-9 μm. Ascosporae distichae in ascis, fusoideae, medio 1-septatae, ad septum constrictae, ad apices duos attenuatae, brunneae, 11–15×3–5 μm.

Pseudothecia epiphyllous, sometimes hypophyllous, subcuticular, globose or ovate, 70–170 μm wide by 70–140 μm high, hyaline to yellowish brown, ostiole 15 μm across. Ascomatal wall of textura angularis, composed of 2–4 layers of cells, 10–20 μm thick. Pseudoparaphyses thread-like, simple, hyaline, 1–1.3 μm wide, 4–5-septate, 42.5–55 μm long, persistent. Asci bitunicate, clavate or cylindrical, with round apex, long-stalked, 8-spored, 35–58×6–9 μm. Ascospores biseriate in the ascus, fusoid, medianly 1-septate, constricted at the septum, widest near the septum, tapering towards both apices, distichous, brunneolous, 11–15×3–5 μm.

Status anamorphicus. *Ascochyta fagi* Woronich.

Holotypus: Japan. Honshu, Aomori prefecture, Hirosaki. On inoculated *Fagus crenata* leaves by conidia isolate cultures (Nos. 2672–2676), 30 March 1996, C. Z. Wei and Y. Harada (No. 23475), kept in the Herbarium of the Faculty of Agriculture, Hirosaki University.

Etymology: *fagi*=from the generic name of the host plant.

Host: *Fagus crenata* and *Quercus mongolica* var. *grosseserrata*.

Known distribution: Japan. Aomori prefecture.

Anamorph

Ascochyta fagi Woronich., Vestn. Tiflisskogo Bot. Sada **28**: 22. 1913. Figs. 4–9

Pycnidia usually epiphyllous, sometimes hypophyllous, immersed, becoming erumpent, yellowish or brown, globose or ovate, (60–)100–125(–175)μm in diam, ostiolate. Ostiole almost round, up to 15 μm wide, surrounded by brown cells. Pycnidial wall of textura angularis, composed of 2–4 layers of cells thick, the outermost layer light brown, the inner layers hyaline. Conidiogenous cells phialidic, simple, globose, arising from the cells of the innermost layer of pycnidial wall, 5–7.5 μm in diam, hyaline. Conidia shortly cylindrical with slightly flattened or rounded base, hyaline, medianly uniseptate, slightly or not constricted at the septum, gut-

tulate, smooth, 15–18 × 5–7.5 μm.

Specimens examined: Japan, Aomori prefecture. Sukayu spa, Aomori City. Teleomorph-on *Fagus crenata* leaves, 20 Dec. 1996, C. Z. Wei and Y. Harada (No. 23987); 17 Jan. 1997, C. Z. Wei (No. 24015); 27 Jan. 1997, C. Z. Wei (Nos. 24019, 24020); 27 Jan. 1997, 25 Feb. 1997, C. Z. Wei (No. 24024); 27 Feb. 1997, C. Z. Wei (No. 24025); C. Z. Wei (No. 24031). On *Quercus mongolica* var. *grosseserrata* leaves, C. Z. Wei (No. 24032). Anamorph-on *Fagus crenata* leaves, 2 Aug. 1996, C. Z. Wei and Y. Harada (No. 23652) containing *Discosia artocreas*; C. Z. Wei and Y. Harada (Nos. 23593–23598), 19 Aug. 1996; C. Z. Wei and Iwama (Nos. 23653, 23657); On inoculated *Fagus crenata* leaves by single ascospore isolate culture (No. 2781), 31 May 1996, C. Z. Wei (Nos. 23535–23538). On *Quercus mongolica* var. *grosseserrata* leaves, C. Z. Wei and Y. Harada (Nos. 23599–23604, 23651).

On the basis of the morphological characteristics of the young fruit bodies of the anamorph, the fungus could be placed in *Asteromella* (Sutton, 1980). Although it has conspicuously light-colored fruit bodies, the typical structure of the conidiogenous apparatus and the small, rod-shaped conidia, which developed into mature conidia after detaching from the conidiogenous cells within the conidioma after keeping in an incubator at 20°C, demonstrate that the fruit bodies are young pycnidia of *A. fagi* (Figs. 4–8). However, several smaller fruit bodies developed into mature spermogonia with light brown walls, from which young pseudothecia were produced in an incubator at 20°C; and all of light-colored fruit bodies developed into pseudothecia after artificial overwintering at low temperatures. The results indicated that young fruit bodies of the fungus could also serve as spermogonia at low temperatures, from which pseudothecia are produced in a way typical of *Pleospora* development (Wei, 1997). The *Asteromella*-like typical structure of the conidiogenous apparatus seems to be a kind of undeveloped conidiomata, from which mature pycnidia developed at normal temperatures or pseudothecia developed at low temperatures.

Cultural characteristics Single ascospores usually germinated from both ends on water agar at 15°C and produced about 45 μm long germ tubes after 24 h (Fig. 14), but single conidia usually germinated from one end in water at 15°C after 12 h and produced about 110–140 μm long germ tubes (Fig. 15). Colonies from ascospores (No. 2781) and conidia (No. 2672) were morphologically identical on PSA. Colonies raised, aerial mycelium gray, reverse of colonies yellowish, usually blue to green (Fig. 16). The fungus grew in the range of 1 to 30°C with the optimum temperature of 20°C. Colonies on PSA, PDA, MA and YpSs attained a diameter of 60.5 to 85 mm in 20 d at 20°C. Growth on Czapek and Richard's agars was limited, with colony diam averaging 24 mm on Richard's, and 79 mm on Czapek's but with very thin mycelia. Colonies grown on Hopkins agar and CMA covered about 57 and 70 mm respectively under the same conditions.

The fungus did not sporulate on agar media within 20 d at 20°C. Conidial formation began on PSA after 30 d at 15°C. Pycnidia gray to black, scattered, single, rarely confluent, globose, ostiolate, 95–175 × 95–170 μm (Fig. 17). Ostiole almost round, sometimes with neck, up to 15 μm wide. Conidiogenous cells hyaline, round, phialidic, 5–7.5 μm in diam. Conidia hyaline, uniseptate, gutullate, 10–15 × 3–5 μm (Fig. 18). After the culture plates were moved to 20°C and kept for about 20 d, the pycnidia and conidia became bigger with diam averaging 150–375 μm and 14–22 μm respectively, with ostioles 25 μm across. Conidia produced in culture were usually longer than those produced on the host.

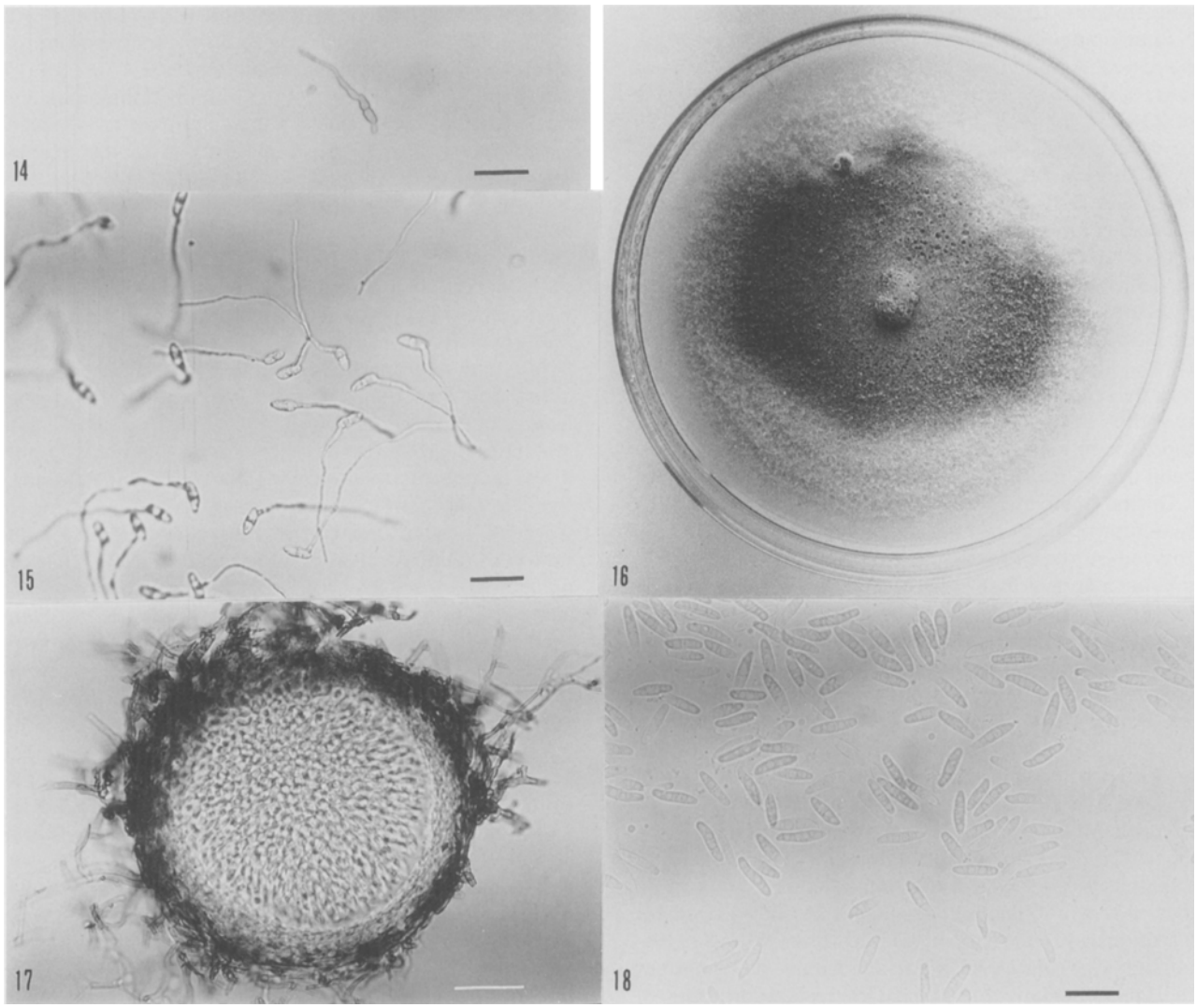
Pathogenicity Inoculation on either side of the leaves of *F. crenata* and *Q. mongolica* var. *grosseserrata* could cause the infection. Lesions were noted on mature leaves of *F. crenata* as early as 5 d after inoculation, reaching 10–15 mm in diam 2 wk after inoculation on the lower leaf surface; and lesions caused by inoculation on the upper leaf surface were smaller, reaching 1–5 mm after 2 wk. Symptoms of the disease caused by inoculation with cultures of ascospore isolates (No. 2781) and conidia isolates (Nos. 2672–2676) were identical. Lesions on young leaves in the laboratory were first black, then turned yellow within several days after the potted plants were placed outdoors. Usually the lesions on mature leaves were also first yellow. Light seems affect the color of lesions, because lesions on plants outside were yellower than those in the laboratory. Cross-inoculation experiments demonstrated the fungus isolated from *F. crenata* is the same as that isolated from *Q. mongolica* var. *grosseserrata*. No apparent symptoms were observed on the leaves of control plants.

Pycnidia and conidia produced on inoculated leaves were morphologically similar to those on naturally diseased leaves, but the pycnidia were bigger than those on naturally diseased leaves, 140–230 × 120–200 μm. Conidia were (9–)11–17.5 μm long, usually 5 μm wide (Fig. 9). Production of pycnidia and conidia on inoculated *F. crenata* leaves using ascospore cultures confirmed the connection between the teleomorph and anamorph of the fungus.

Discussion

The genus *Ascochyta* Lib. comprises over 600 formally described species, of which the majority are plant pathogens with a worldwide distribution (Punithalingam, 1979). Recently a reappraisal of all the *Ascochyta* species on Monocotyledones has been made by Punithalingam (1979, 1988) based on the morphology of known species and the host plants. Usually identification of *Ascochyta* is conducted according to the host genus or family (Sun et al., 1995). It seems conceivable that a taxonomy based on host families rather than host genera or species may provide an appropriate circumscription of the genus based on our results.

There are four *Ascochyta* species on Fagaceae: *A. quercus* Sacc. et Speg. and *A. irpina* Sacc. et Trott. on leaves of *Quercus*; *A. fagi* on leaves of *Fagus*; and *A. praecox* Velenovsky' on stumps of *Fagus* and *Betula*



Figs. 14–18. Culture characteristics of the fungus.
14. Germinating ascospore. 15. Germinating conidia. 16. Colony of a single ascospore culture (No. 2781) on PSA after 20 d at 15°C with a 12-h photoperiod (approximately 500 lx, daylight fluorescent strip lamps). 17. Vertical section of a pycnidium in culture. 18. Conidia produced in culture. Scales: 30 μm.

Table 1. Comparative morphological data of closely related species of *Ascochyta* on Fagaceae.

Fungus	Present fungus	*A. quercus* (Saccardo, 1931)	*A. irpina* (Saccardo, 1931)	*A. praecox* (Velenovsky', 1922)	*A. fagi* (Melnik, 1977)
Host	*F. crenata*, *Q. mongolica* var. *grosseserrata*	*Quercus*	*Q. ilicis*	*Fagus* and *Betuta*	*F. orientalis*
Pycnidia	(60–)100–125(–175)μm	120–150 μm	80–100 μm		up to 100 μm
Conidia	15–18 × 5–7.5 μm	7–14 × 3–4.5 μm	7–11 × 3–3.5 μm	7–9 μm	(13–)15–18 × 5–6 μm

(Velenovsky', 1922; Saccardo, 1931; Melnik, 1977). Although the descriptions of these fungi are far from adequate (Table 1), the present fungus could be identified as *A. fagi* based on the morphology.

The fungus was the causal agent of the yellow leaf spot disease of *F. crenata* and *Q. mongolica* var. *grosseserrata*. It could sometimes be obtained during isolation of *D. umbrinella* from *F. crenata* leaves, but its pycnidia are difficult to find. When the yellow spot disease of *F. crenata* and *Q. mongolica* var. *grosseserrata* was first found in field on 2 Aug. 1996, the causal agent was not at once thought to be *Ascochyta* species, be-

cause the pycnidia were still young, and no mature conidia were observed (Figs. 3–6). Such conidiomata serve as young pycnidia at normal temperature or as a premature form of the teleomorph at low temperature (Wei, 1997). A similar anamorph was thought to be a premature form of *Didymosphaeria petrakiana* Sacc. (Butin and Kehr, 1995).

Many *Ascochyta* species have been described, but few teleomorphs have been found among them, especially for woody plant pathogens (Sivanesan, 1984). Numerous species of *Didymella* have been described, but many are only imperfectly known. *Didymella* is often confused with *Mycosphaerella* John. Corbaz (1957) discussed the problems of species identification and the separation of *Didymella* and *Mycosphaerella*. However, the delimitation of the genus *Didymella* has often been questioned. Von Arx (1987) thought *Mycosphaerella* species never include *Ascochyta* or *Phoma* anamorphs. The presence of pseudoparaphyses in *Didymella* is usually used to separate the fungi from *Mycosphaerella*, but they are not always apparent in mature ascomata. We observed that the pseudothecia were developed from their young pycnidia, and this can explain why the pseudothecia and pycnidia are identical in shape and wall anatomy.

There are four species of *Mycosphaerella* on leaves of *Fagus* and about six species on *Quercus* (Ellis and Ellis, 1985; Corlett, 1991), but the typical *Didymella* morphology of the present fungus readily distinguished it from these fungi. *Pseudodidymella fagi* C. Z. Wei, Y. Harada et Katumoto is morphologically close to *Didymella*, but the stromatic wall of ascocarps is different from the pseudothecia wall of the present fungus (Wei et al., 1997).

The brown ascospores and light-colored ascomatal wall of the present fungus resemble those of *Didymosphaeria petrakiana* Sacc. (Butin and Kehr, 1995), for which a new combination *Phaeodothis winteri* (Niessl) Aptroot was made (Aptroot, 1995), but *D. fagi* has relatively smaller ascospores and asci and its ascomatal wall has 3–4 layers. The present teleomorph is better accommodated in *Didymella* rather than *Didymosphaeria*, because the latter has clypeate ascomata and trabeculate pseudoparaphyses (Kohlmeyer and Volkmann-Kohlmeyer, 1990).

The life cycle of the pathogen seems similar to the typical life history of the genus *Mycosphaerella* and *P. fagi* (Sivanesan, 1984; Wei et al., 1997). Infection occurs on young leaves in early summer, and the host tissues are killed within a limited area causing necrotic, yellow spots on the leaf. During August, the conidial states occur on these spots. The pseudothecia and ascospores mature over winter in a saprophytic environment of growth.

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