

## ***Cronartium orientale*, sp. nov., segregation of the pine gall rust in eastern Asia from *Cronartium quercuum***

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The Asian pine gall rust, which has hitherto been assigned to *Cronartium quercuum* distributed in North America, is described as *C. orientale*, sp. nov. The spermogonial and aecial states occur on hard pines, and the uredinial and telial states occur on various oaks. *Cronartium orientale* has globose, almost hyaline basidiospores in contrast to the ellipsoid, yellow-orange ones of North American *C. quercuum* s.l. Characteristics of the new rust species in morphology, DNA analysis, and host alternation are discussed.

Key Words—distribution; *Pinus*; *Quercus*; taxonomy; Uredinales.

The pine gall rust fungus *Cronartium quercuum* (Berk.) Miyabe ex Shirai has been recognized as an important pathogen of various hard pines in eastern Asia (Ito, 1974; Kondo, 1975) and North America (Peterson and Jewell, 1968; Hiratsuka and Powell, 1976; Sinclair et al., 1987). It was originally reported as *C. asclepiadium* Tul. var. *quercium* Berkeley (Berkeley, 1874) based on a *Cronartium* species on *Quercus nigra* L. and *Q. tinctoria* W. Bartr. collected in the U.S.A. Dr. Kingo Miyabe proposed the name *C. quercuum* for this fungus, and this was legitimately published by Shirai (1899).

Distinct species names had been proposed for *Cronartium* species on *Quercus* distributed in the U.S.A.: *C. fusiforme* Hedgc. et N. R. Hunt ex Cummins (Cummins, 1956), *C. cerebrum* Hedgc. et W. H. Long (Hedgcock and Long, 1914), *C. strobilinum* Hedgc. et G. G. Hahn (Hedgcock and Hahn, 1922), and *C. conigenum* Hedgc. et N. R. Hunt (Hedgcock and Hunt, 1922). Arthur (1934) included these four species in his concept of *C. quercuum*. *Cronartium cerebrum*, however, had not been validly published and was treated as a synonym of *C. quercuum* (Cummins, 1962). Aecia of *C. conigenum* and *C. strobilinum* occur on the cones of pines, and the symptoms and host range of *C. fusiforme* are different from those of *C. quercuum*. Therefore, *C. conigenum*, *C. strobilinum*, and *C. fusiforme* were recognized as distinct species from *C. quercuum* in a strict sense (Cummins, 1962; Peterson and Jewell, 1968; Peterson, 1973).

Burdsall and Snow (1977) considered *C. fusiforme* to be conspecific with *C. quercuum*, since no consistent morphological differences could be found between the two taxa. Thus they treated the former fungus as a forma specialis (f. sp.) of *C. quercuum* based on the differences of host range of pines. They also proposed other three formae speciales, f. sp. *banksianae*, f. sp. *echinatae*, and f. sp. *virginianae*.

The pine-oak rust in eastern Asia has been treated as *C. quercuum* (Shirai, 1899; Sydow and Sydow, 1915; Hiratsuka, 1960; Kim, 1963; Azbukina, 1974; Tai, 1979; Hiratsuka et al., 1992; Li and Jing, 1995). However, Ito (1939) considered the Japanese pine-oak rust to be different from Berkeley's species from North America, though he did not describe the reason. Hedgcock and Siggers (1949) used the name *C. quercuum* only for the pine-oak rust in Japan and China, and they treated the American pine-oak rust, which produces spherical galls on pine stems, as *C. cerebrum*. They recognized differences in morphological characteristics of aecial peridia between the Asian and North American *Cronartium* species.

No type specimen of *C. quercuum* was designated by either Berkeley or Miyabe. Later a telial specimen on *Quercus tinctoria* Bartr. (= *Q. velutina* Lam.) collected in Pennsylvania, U.S.A. was designated as the lectotype of *C. quercuum* (Peterson, 1973).

Because of heterogeneity in *C. quercuum* sensu lato (s.l.), in which *C. fusiforme* and Asian pine-oak rust are included, the rust group has been called *C. quercuum* complex (Kaneko et al., 1991; Kuhlman and Kaneko, 1991; Hiratsuka, 1995). In these works, differences are noted between Asian and American collections of *C. quercuum* in morphology (Kaneko et al., 1991; Kuhlman and Kaneko, 1991; Kaneko, 1992), pathogenicity to pines and oaks (Powers et al., 1991), and DNA analysis (Nakamura et al., 1998). I also have compared collections on oaks and pines from China, Korea, and the Russian Far East region with North American forms, and now conclude that *Cronartium* species on oaks from eastern Asia is a different species from North American *C. quercuum* and *C. fusiforme*. The Asian pine-oak rust is here described as a new species and taxonomic relationships among related *Cronartium* species are discussed.

***Cronartium orientale*** S. Kaneko, sp. nov. Figs. 1–8.  
 = *Cronartium quercuum* (Berk.) Miyabe ex Shirai, Bot. Mag. Tokyo **13**: 74, 1899, pro parte; Sydow, Monogr. Ured. **3**: 573, 1915, pro parte; Ito, Mycol. Fl., Japan **2**(2): 152, 1939; Azbukina, Rust Fungi of the Soviet Far East p. 155, 1974, pro parte; Hiratsuka, f. List of Ured. Japan p. 207, 1960, pro parte; Hiratsuka et al. Rust Flora of Japan p. 253, 1992, pro parte.

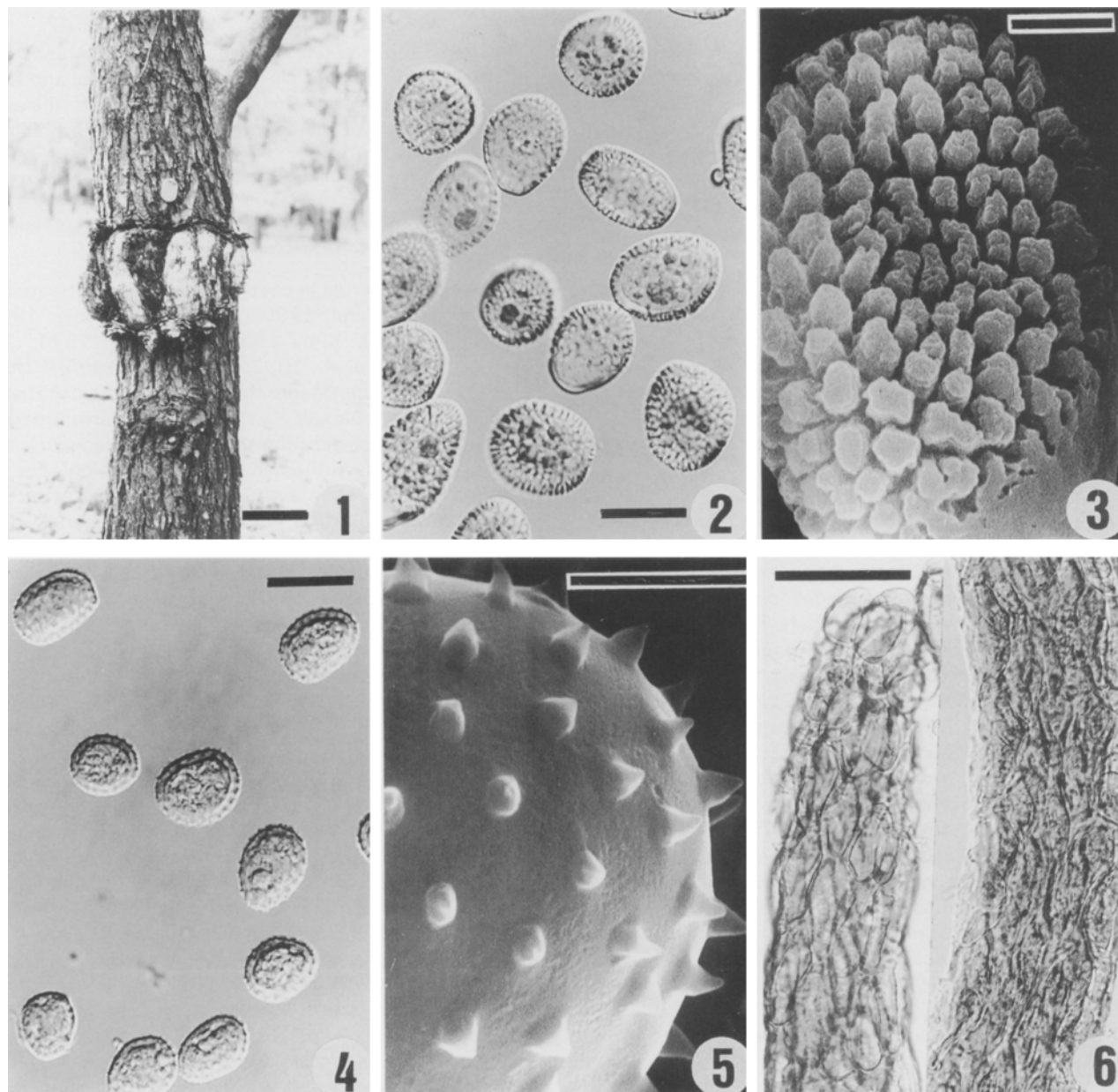
= *Cronartium quercus* (Brond.) Arthur, Kuprevicz and

Tranzshel, Crypt. Pl. USSR **4**(1): 268, 1957, pro parte.

Anamorphic name. *Peridermium giganteum* (Mayr) Tubeuf, Pfl. Kr. p. 429, 1895; Saccardo, Syll. Fung. **21**: 750, 1912.

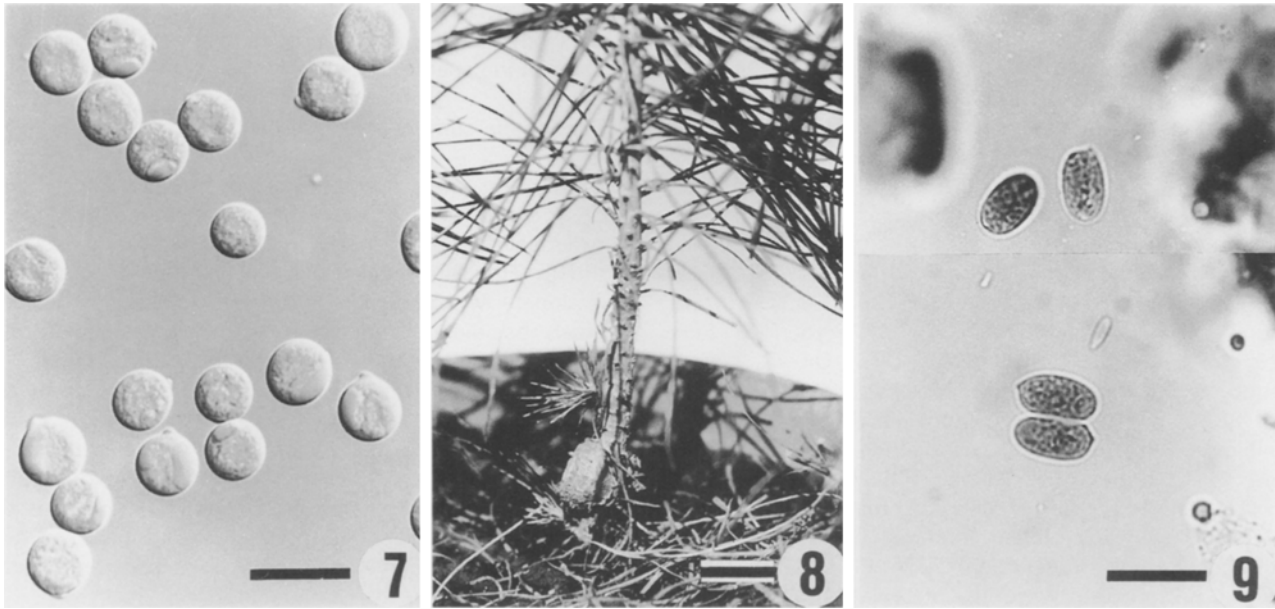
*Uredo quercus-myrsinifoliae* Hennings, Bot. Jahrb. **34**: 598, 1905; Saccardo, Syll. Fung. **21**: 803, 1912.

Spermogoniis caulogenis, planis, intracorticalibus, indeterminatis; spermatiiis obovoideis,  $5 \times 2 \mu\text{m}$ ; aeciis caulogenis, peridermioideis, intracorticalibus, posterius



Figs. 1–6. *Cronartium orientale*.

1. Gall on the stem of *Pinus densiflora* by infection with aecial state of the fungus. 2. Aeciospores on *P. densiflora* (TFM : FPH 7486). 3. SEM-micrograph of an aeciospore (TFM : FPH 7486). 4. Urediniospores on *Quercus crispula* (TFM : FPH 7397). 5. SEM-micrograph of a urediniospore (TFM : FPH 7397). 6. Apical part (left) and middle part of a telial column on *Q. crispula* (holotype). Scale bars: 1 = 20 cm; 2, 4 = 20  $\mu\text{m}$ ; 3, 5 = 5  $\mu\text{m}$ ; 6 = 100  $\mu\text{m}$ .



Figs. 7–8. *Cronartium orientale*.

7. Basidiospores on *Q. crispula* (From fresh teliospores of TFM : FPH 7397). 8. Gall produced at the base of *P. densiflora* stem 2.5 yr after inoculation with basidiospores from *Q. serrata*. Scale bars: 7 = 20  $\mu\text{m}$ ; 8 = 1 cm.

Fig. 9. Basidiospores of *C. quercuum* on *Q. tinctoria* (Lectotype). Scale bar = 20  $\mu\text{m}$ .

erumpentibus, irregularibus, flavis, in gallis globosis vel subglobosis evolventibus, ex cellulis peridii ellipsoideis vel rhomboideis, 40–85  $\times$  19–37  $\mu\text{m}$  compositis, parietibus 4–7  $\mu\text{m}$  crassis, verrucosis; aeciosporis ellipsoideis, obovoideis vel subglobosis, 19.5–31(–35)  $\times$  15–23  $\mu\text{m}$ , parietibus hyalinis, ca. 1  $\mu\text{m}$  crassis, dense verrucosis, verrucis 1–2  $\mu\text{m}$  altis, cytoplasmate flavido; urediniis hypophyllis, sparsis, ca. 0.25 mm diam., pulverulentis, flavis, peridio tenui; urediniosporis obovoideis vel ellipsoideis, 17–29(–32)  $\times$  14–23  $\mu\text{m}$ , parietibus hyalinis, ca. 2  $\mu\text{m}$  crassis, echinulatis, cytoplasmate flavido, poris germinationis 7–12, sparsis; tellis hypophyllis, sparsis, filiformibus, rectis vel parum curvatis, 2–3 mm longis, 90–140  $\mu\text{m}$  latis, brunneis; teliosporis oblongis vel fusiformibus, 30–70  $\times$  14–27  $\mu\text{m}$ , parietibus luteo-brunneis, laevibus, 3–5  $\mu\text{m}$  crassis, poris germinationis 1 vel 2; basidiis externis; basidiosporis globosis vel subglobosis, 9.0–14.5  $\times$  8.0–13.5  $\mu\text{m}$ , parietibus tenuibus, hyalinis, cytoplasmate paene hyalino vel parum subflavido.

Holotype: On *Q. crispula* Blume (*Q. mongolica* Fisch. var. *grosseserrata* Rehd. et Wils.) (*mizunara*): Yokotemichi, Mt. Daisen, Tottori Pref., Japan, 19 Oct. 1973, collected by S. Kaneko, TFM : FPH 7391.

Isotype: Mycological Herbarium of the Institute of Agriculture and Forestry, University of Tsukuba (TSH-R 1709), Tottori Mycological Institute (TMI 21154), and National Science Museum, Tsukuba (TNS-F 101103).

Etymology: *orientale* = eastern in Latin, referring to the distribution of the species in eastern Asia.

Spermogonia on trunks or branches, flat, scattered, intracortical on globoid galls, growth indeterminate; spermatia obovoid, 5  $\times$  2  $\mu\text{m}$ . Aecia peridermioid, intracortical in origin, becoming erumpent, on globosal or sub-

globosal galls on trunks or branches, large, irregular shape, yellow; peridial cells ellipsoid or rhomboid, 40–85  $\times$  19–37  $\mu\text{m}$ , walls 4–7  $\mu\text{m}$  thick, verrucose; aeciospores ellipsoid, obovoid, or subglobose, 19.5–31(–35)  $\times$  15–23  $\mu\text{m}$ , wall hyaline, about 1  $\mu\text{m}$  thick excluding verrucae, verrucae 1–2  $\mu\text{m}$  high, densely verrucose, occasionally with a smooth spot, contents yellow. Uredinia hypophyllous, scattered, about 0.25 mm across, yellow, covered by inconspicuous hemispherical peridia; urediniospores obovoid or ellipsoid, 17–29(–32)  $\times$  14–23  $\mu\text{m}$ , wall hyaline, about 2  $\mu\text{m}$  thick, echinulate, contents pale yellow, germ pores scattered, 7–12, inconspicuous. Telia hypophyllous, scattered, forming filiform columns, straight or slightly curved, 2–3 mm long, 90–140  $\mu\text{m}$  wide, brown; teliospores oblong or fusoid, 30–70  $\times$  14–27  $\mu\text{m}$ , wall yellowish brown, smooth, 3–5  $\mu\text{m}$  thick, germ pores 1 or 2, usually in the upper half of the cells; germination occurs without dormancy, basidia external, 4-celled; basidiospores globose or subglobose, 9.0–14.5  $\times$  8.0–13.5  $\mu\text{m}$ , wall thin, hyaline, contents almost hyaline or slightly yellowish.

Selected specimens examined:

Spermogonial and aecial states: JAPAN: On *Pinus densiflora* Sieb. et Zucc. (*akamatsu*): Hachinohe, Aomori, TFM : FPH 7485; Yanagisawa, Iwate, TFM : FPH 7392; Morioka, Iwate, TFM : FPH 7495; Ichinoseki, Iwate, TFM : FPH 7395; Tsukuba, Ibaraki, TFM : FPH 7486; Kagosaka-toge, Yamanashi, TFM : FPH 7487. On *P. thunbergii* Parl. (*kuromatsu*): Kukizaki, Ibaraki, TFM : FPH 7488; Tottori, Tottori, TFM : FPH 7489. CHINA: On *P. densiflora*: Mishan, Heilongjiang Prov., TFM : FPH 7491 (ex Mycol. Herb. Northeast For. Univ.). RUSSIA: On *P. densiflora*: Novokachalinsk, Primorsky Territory, VLA

8627.

Uredinial and telial states: JAPAN: On *Castanea crenata* Sieb. et Zucc. (*kuri*): Morioka, Iwate, TFM : FPH 7399. On *Quercus acutissima* Carr. (*kunugi*): Kokoge, Tottori, TMI 2424; Numazu, Shizuoka, TFM : FPH 376; Tottori, Tottori, TFM : FPH 7490; Kukizaki, Ibaraki (by inoculation), TFM : FPH 7491. On *Q. aliena* Blume (*naragashiwa*): Mt. Kimpu, Kumamoto, SAPA 448. On *Q. crispula*: Sapporo, Hokkaido, SAPA (no No.); Morioka, Iwate, TFM : FPH 7397; Takahagi, Ibaraki, TFM : FPH 7394; Ebinokogen, Miyazaki, TMI 5808. On *Q. dentata* Thunb. ex Murray (*kashiwa*): Muguro, Tokyo, TFM : FPH 429; Mt. Daisen, Tottori, TMI 4065; On *Q. glauca* Thunb. ex Murray (*arakashi*): Mt. Kyusho-zan, Tottori, TMI 2525. On *Q. serrata* Thunb. ex Murray (*konara*): Kushigata-mura, Ibaraki, TFM : FPH 92; Meguro, TFM : FPH 390; Hachioji, Tokyo, TFM : FPH 1552, 1966. On *Q. variabilis* Blume (*abemaki*): Komaba, Tokyo, TNS-F-195770. On introduced *Quercus*: On *Q. phellos* L.: Morioka, Iwate (by inoculation), TFM : FPH 7492. On *Q. rubra* L.: Morioka, Iwate (by inoculation), TFM : FPH 7493. CHINA: On *Q. acutissima*: Nanjing, Jiangsu Prov., TFM : FPH 7515 (ex Mycol. Herb., Chinese Acad. For.). On *Q. fabri* Hance: Pucheng, Fujian Prov., HMAS 41540. On *Q. mongolica*: Mishan, Heilongjiang Prov., TFM : FPH 7396 (ex Mycol. Herb. Northeast For. Univ.). On *Q. sponosa* David: Lijiang, Yunnan Prov., HMAS 34937. On *Q. variabilis* Blume: Mt. Daba, Sichuan Prov., HMAS 31281; Shennongjia, Hubei Prov., HMAS 57264; Nanjing, Jiangsu Prov., HMAS 31282, 43139; Quinling, Shanxi Prov., TFM : FPH 7514 (ex Mycol. Herb., Chinese Acad. For.). KOREA: On *Q. acutissima*: Tenmasan, East of Seoul, TFM : FPH 7494 (ex Mycol. Herb., For. Res. Inst. Korea). On *Q. mongolica*: Tenmasan, East of Seoul, TFM : FPH 7398 (ex Mycol. Herb., For. Res. Inst. Korea). RUSSIA: On *Q. mongolica* Fisch.: Blagovechensk, Aursk Territory, VLA 8604; Novokachalinsk, Primorsky Territory, VLA 8627; Ussuri Reserve, Primorsky Territory, VLA 1251; Shimanovsk, Aursk Territory, VLA 1252.

Other hosts from Japan – Spermogonial and aecial states: *P. luchuensis* Mayr (*ryukyu-matsu*), *P. banksiana* Lamb. (introduced from the U.S.A.), *P. nigra* Arnold (introduced from Europe), *P. pinaster* Ait. (introduced from Europe), *P. sylvestris* L. (introduced from Europe), *P. tabulaeformis* Carr. var. *mukdensis* Uyeki (introduced from China) (Hiratsuka et al., 1992), *P. ponderosa* Laws. (introduced from the U.S.A.), *P. nigra* var. *nigra* (by inoculation) (Powers et al., 1991), *P. nigra* var. *austriaca* Endlich. (introduced from Austria), *P. nigra* var. *poiretiana* Asch. (introduced from Europe), *P. montana* Miller (introduced from Europe) (Kaneko et al., 1989; Powers et al., 1991). Uredinial and telial states: *Castanopsis cuspidata* Schott. var. *sieboldii* Nakai (*sudajii*), *Q. myrsinaefolia* Blume (*shirakashi*) (Hiratsuka et al., 1992).

Known distribution: Japan, Korea, China, and Russia.

Bagchee (1950) reported the occurrence and host alternation of *C. quercuum* from the Shillong range in

Assam, Indian Himalaya. It probably belongs to *C. orientale*, but I was not able to examine any specimens to confirm the species name from this area.

#### Taxonomic comparisons

*Cronartium orientale* was compared morphologically with *C. quercuum* s.l. from the following herbaria in North America: Arthur Herbarium, Purdue University, U.S.A. (PUR), The New York Botanical Garden, U.S.A. (NY), National Mycological Herbarium, Canada (DAOM). Fresh basidiospore materials of *C. quercuum* f. sp. *fusiforme* collected at the Forest Pathology Laboratory, FFPRI, Japan (introduced by Dr. P. Spaine from the Forestry Sciences Laboratory, Southeastern Forest Experiment Station, Athens, U.S.A., with permission of the Plant Quarantine Office, Ministry of Agriculture, Forestry and Fishery (MAFF), Japan) and those of the four formae speciales mounted on glass slides, and sent by Dr. E. G. Kuhlman from the Forestry Sciences Laboratory, Athens, were also examined.

**Characteristics of basidiospores** For comparison of many *Cronartium* basidiospores, spores discharged from fresh telia should ideally be used. Spores from dried herbarium specimens of telia holding basidiospores are sometimes slightly smaller than fresh spores, possibly because herbarium specimens contain immature spores still attached to sterigmata. However, no remarkable differences were found in length-to-width ratios of Japanese collections between fresh spores and herbarium specimens.

Basidiospores of *C. orientale* and North American *C. quercuum* s.l. are distinctly different in morphology and color. Basidiospores of *C. orientale* are globose to subglobose (Fig. 7), and almost hyaline, while those of *C. quercuum* in North America are ellipsoid (Fig. 9) and yellow-orange, as reported previously (Kaneko et al., 1991; Kuhlman and Kaneko, 1991). The basidiospores are also clearly distinguished by length-to-width ratio, which ranges from 1.0 to 1.1 on average for *C. orientale* specimens, and from 1.3 to 1.7 for North American *C. quercuum*. Similar ratios were reported previously (Kuhlman and Kaneko, 1991).

Basidiospores of the four formae speciales in North American *C. quercuum* s.l. are readily separated into two distinct groups by morphology (Kaneko et al., 1991; Kuhlman and Kaneko, 1991). Basidiospores of *C. quercuum* f. sp. *banksianae* and *virginianae* are predominantly ellipsoidal, with length-to-width ratios of 1.6 to 1.7. *Cronartium quercuum* in a strict sense must belong to this group because the basidiospore morphology of the lectotype of *C. quercuum* on *Q. tinctoria* (Pennsylvania, U.S.A., NYBG Fungus Type Project No. 104) (Fig. 9) is identical to that of the f. sp. *banksianae* and *virginianae* group. The second group, comprising *C. quercuum* f. sp. *fusiforme* and *echinatae*, has predominantly broadly ellipsoidal basidiospores, with length-to-width ratios of 1.3 to 1.4. This evidence and the differences in isozyme analysis (Powers et al., 1989, 1991) and DNA analysis (Vogler, 1995; Vogler and Bruns, 1998) may support the

validity of *C. fusiforme* as an independent species.

**Characteristics of telia and teliospores** Telial columns of *C. orientale* (Fig. 6) are 90–140  $\mu\text{m}$  in thickness and seem to be slightly more slender than those of North American *C. quercuum*. This evidence was noted also by Hedgcock and Siggers (1949). However, no clear difference was found between the two species. No difference was found also in teliospore morphology.

**Characteristics of urediniospores** Urediniospore size is not affected by geographic or oak host source. However, slight differences are found in size and the number of spines on the spore surface between *C. orientale* and North American *C. quercuum* f. sp. *fusiforme*. Urediniospores of *C. orientale* (Fig. 5) have usually larger spines and fewer spines per unit area than those of *C. quercuum* f. sp. *fusiforme*, as reported by Kaneko et al. (1991) and Kuhlman and Kaneko (1991). However, the type specimen of *C. fusiforme* Cummins (PUR 53519 on *Q. nigra* collected by W. H. Long in Florida) had comparably large spines. In some specimens on *Quercus*, which probably do not belong to f. sp. *fusiforme*, rather conspicuous spines were observed. However, this was also not a stable feature.

Grand and Moore (1972) examined *Cronartium* urediniospores by scanning electron microscopy (SEM), and reported no differences among North American *C. quercuum* (American pine host unspecified). It appears difficult to differentiate *C. quercuum* s.l. and *C. orientale* based on surface characteristics of urediniospores.

Two other pine cone rusts produce urediniospores on *Quercus* trees in North America. Urediniospores of *C. conigenum* (PUR 5143 on *Q. rubra*, inoculated by G. G. Hedgcock,  $21.0 \times 25.0 \mu\text{m}$  on average; unnumbered PUR specimen on *Q. oblongifolia* collected by E. Bethel in Arizona,  $19.0 \times 24.5 \mu\text{m}$  on average) were observed to be significantly larger than those of *C. orientale* and *C. quercuum* s.l. Urediniospores of the other cone rust, *C. strobilinum* (PUR 5163 on *Q. virginiana*; PUR 5083 on *Q. gouglassii*; PUR 52812 on *Q. alba*), were of similar size to those of *C. orientale* and *C. quercuum*.

**Characteristics of aeciospores and aecial peridia** No differences were found in aeciospore and peridium morphology between *C. orientale* and North American *C. quercuum* s.l.

**Morphology in the specimens from other regions in eastern Asia** Basidiospores on *Quercus* spp. from China, Korea, and the Russian Far East are globose and almost hyaline. No morphological differences have been found in any other spore stages between collections from Japan and the other eastern Asian countries. Consequently, the *Cronartium* species on *Quercus* from China, Korea, and the Russian Far East should also be called *C. orientale*.

**DNA analysis** In isozyme analysis (Powers et al., 1989, 1991) and nucleotide sequences from the ITS region (Vogler, 1995; Vogler and Bruns, 1998), clear differences were found within the North American *C. quercuum* s.l. No Asian forms have been employed in these analyses.

Our research group (Nakamura et al., 1998) compared ITS regions of ribosomal DNA between Japanese

sources and *C. quercuum* f. sp. *fusiforme* by restriction fragment length polymorphism (RFLP) analysis and nucleotide sequences using aeciospores. Six collections from *P. densiflora* and four collections from *P. thunbergii* from Japan, and five collections from the native American pines were examined. The RFLP patterns with the three enzymes *Dra* I, *Hinf* I, and *Taq* I showed clear differences between the Japanese sources and the American *C. quercuum* f. sp. *fusiforme*. Nucleotide sequences of the ITS2 region confirmed the clear distinction between the Japanese collections and f. sp. *fusiforme*, i.e., the size of the ITS2 region in the Japanese collection was 220 base pairs and that in f. sp. *fusiforme* was 225 base pairs. Comparisons with sequence data (Vogler and Bruns, 1998) obtained from GenBank database on the other formae speciales in *C. quercuum* s.l. showed that the Japanese collections are distinct from *C. quercuum* in North America. In sequence analyses on the ITS region by the UPGMA (Sneath and Sokal, 1973) similarity dendrogram and the neighbor-joining method (Saitou and Nei, 1987), the Japanese collections were placed in a different lineage from the four American formae speciales in *C. quercuum*, and were closer to the cone rust *C. conigenum* than to *C. quercuum* (Nakamura et al., 1998). Based on isozyme analysis and sequence data on the ITS region, Vogler and Bruns (1998) indicated that the cone rusts *C. conigenum* and *C. strobilinum* are separate species from *C. quercuum*. These molecular data support the morphological differences between Asian and American collections in pine-oak *Cronartium* rusts and indicate the validity of *C. orientale* as an independent species.

#### Host alternation

The host alternation of *C. orientale* has been proved by Shirai (1899), Hiratsuka and Yoshida (1931), Hiratsuka (1932), Hiratsuka and Sato (1984), and Kondo (1969, 1970, 1975). Kondo (1975) suggested the existence of two physiological strains of the rust, a *P. densiflora* – *Q. serrata* strain and a *P. thunbergii* – *Q. acutissima* strain, based on inoculation experiments. The two strains were designated as *C. quercuum* f. sp. *densiflorae* and f. sp. *thunbergii* by Kuhlman and Kaneko (1991).

I conducted several inoculation experiments with aeciospores obtained from *P. densiflora* and *P. thunbergii* (Table 1). The host ranges of f. sp. *densiflorae* and f. sp. *thunbergii* were not completely different from each other. However, lighter infection or only flecks without urediniospore production were observed when aeciospores of f. sp. *thunbergii* were inoculated on *Q. serrata* and when those of f. sp. *densiflorae* were inoculated on *Q. acutissima*.

In the inoculation experiment with basidiospores obtained from *Q. serrata*, galls developed on the seedlings of *P. densiflora* (Table 2, Fig. 8). In contrast, *P. thunbergii* and several American pines remained uninfected. These results of inoculation experiments with aeciospores and basidiospores indicate the existence of the two formae speciales of *C. orientale*. The two forms could not be distinguished by RFLP analysis with the

Table 1. Results of oak inoculations with aeciospores of *Cronartium orientale*.

Host species	Aeciospore source		Date of inoculation	Days for the first appearance of uredinia	Days for the first appearance of telia
	Locality and date of collection	<i>Quercus</i> species inoculated			
<i>Pinus densiflora</i>	Hachinohe, Aomori, 17 May 1985	<i>Q. acutissima</i>	20 May 1985	F <sup>1)</sup>	
		<i>Q. serrata</i>		27**	
<i>Pinus densiflora</i>	Tsukuba, Ibaraki, 17 Apr. 1991	<i>Q. acutissima</i>	23 Apr. 1991	6*	39
		<i>Q. acutissima</i>		—	
		<i>Q. acutissima</i>		9*	28
		<i>Q. crispula</i>		8*	
		<i>Q. rubra</i>		—	
		<i>Q. rubra</i>		—	
		<i>Q. serrata</i>		8**	30
		<i>Q. serrata</i>		8**	
<i>Q. serrata</i>	8*				
<i>Pinus densiflora</i>	Kagosaka-toge, Yamanashi, 23 May 1990	<i>Q. crispula</i>	25 May 1990	29*	
		<i>Q. serrata</i>		22**	
		<i>Q. serrata</i>		23**	
<i>Pinus densiflora</i>	Morioka, Iwate, 5 June 1991	<i>Q. acutissima</i>	12 June 1991	F	
		<i>Q. serrata</i>		9**	
		<i>Q. serrata</i>		9**	
<i>Pinus thunbergii</i>	Tsukuba, Ibaraki, 10 May 1991	<i>Q. acutissima</i>	11 May 1991	11***	35
		<i>Q. crispula</i>		F	
		<i>Q. crispula</i>		12*	30
		<i>Q. rubra</i>		13*	
		<i>Q. rubra</i>		12*	30
		<i>Q. rubra</i>		12*	
		<i>Q. serrata</i>		11*	35
		<i>Q. serrata</i>		11*	
<i>Pinus thunbergii</i>	Kukizaki, Ibaraki, 19 Apr. 1991	<i>Q. acutissima</i>	24 Apr. 1991	7**	
		<i>Q. acutissima</i>		6**	
		<i>Q. serrata</i>		6*	
		<i>Q. serrata</i>		6*	
<i>Pinus thunbergii</i>	Tottori, Tottori, 21 Apr. 1991	<i>Q. acutissima</i>	30 Apr. 1991	10	
		<i>Q. acutissima</i>		10	
		<i>Q. serrata</i>		F	27
		<i>Q. serrata</i>		F	30

\*\*\*, \*\*, and \* indicate heavy, medium, and light infection, respectively; <sup>1)</sup>F indicates only fleck without urediniospore production.

three enzymes *Dra*I, *Hinf*I, and *Taq*I (Nakamura et al., 1998).

The degree of infection differed slightly between *Q. serrata* and *Q. crispula* in experiments with aeciospores of the same origin. To ascertain whether other biological forms exist, more experiments are needed including evergreen oaks as host plants for inoculation.

Field surveys have shown that many American pine species were resistant, but *P. montana* and *P. sylvestris* from Europe were very susceptible to *C. orientale* (Kaneko et al., 1989; Powers et al., 1991), suggesting that the fungus could be a threat to European pine forests if it is introduced there.

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Table 2. Results of pine inoculations with basidiospores of *Cronartium orientale*.

Pinus species inoculated	Number of seedlings inoculated	% seedlings that developed galls	
		1 yr after inoculation	2 yr after inoculation
<i>P. densiflora</i>	69	4.3	5.8
<i>P. thunbergii</i>	86	0	0
<i>P. banksiana</i>	50	0	0
<i>P. echinata</i>	69	0	0
<i>P. elliotii</i>	84	0	0
<i>P. taeda</i>	63	0	0
<i>P. virginiana</i>	94	0	0

Inoculum: Basidiospores produced from telia on *Quercus serrata* collected at Kouma, Iwate Pref. on 9 Sept. 1986.

Age of seedlings: 80 d.

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