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Taxonomic identity of caricicolous *Puccinia* host-alternating on *Petasites* in Japan

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Uredinial-telial *Puccinia* fungi on *Carex shimizuensis* in Nagano Pref. and on *C. dimorpholepis* in Ibaraki Pref. were proven to host-alternate on *Petasites japonicus* by field observations and inoculation experiments. These fungi from the two localities were morphologically similar and were compared with three described *Puccinia* species that host-alternate between *Carex* species and *P. japonicus* in Japan, i.e., *P. caricis-petasitidis*, *P. caricis-flabellatae* and *P. caricis-podogynae*. The three previously described species and the newly found *Puccinia* fungi were morphologically indistinguishable at all stages of the life cycle; therefore, it was concluded that three species and the two newly found fungi are taxonomically identical, in which *P. caricis-petasitidis* has nomenclatural priority.

Key Words——*Carex*; Compositae; Cyperaceae; life cycle; Uredinales.

Uredinial-telial *Puccinia* fungi were found on *Carex shimizuensis* Franch. at Sugadaira, Nagano Pref. and on *C. dimorpholepis* Steud. at Okami, Ibaraki Pref. The *Puccinia*-infected *Carex* plants were associated with *Aecidium*-infected plants of *Petasites japonicus* (Sieb. & Zucc.) Maxim. at each location. The close association of the *Puccinia*-infected *Carex* and the *Aecidium*-infected *Petasites* plants indicated their life-cycle relationship. This paper reports experimental proof of the predicted anamorph-teleomorph relationship between the *Puccinia* on *Carex* species and the *Aecidium* on *Petasites japonicus*.

Three *Puccinia* species have been described as having a heteroecious life cycle on *Carex* species and *Pet. japonicus* in Japan, i.e., *P. caricis-petasitidis* Y. Harada (Harada, 1977), *P. caricis-flabellatae* Y. Harada and *P. caricis-podogynae* Y. Harada (Harada, 1986). All the three *Puccinia* species were described from Aomori Pref. and were stated to differ in the teliospore morphology and the number and distribution of urediniospore germ pores and to be specific on *C. sadoensis* Franch., *C. presicottiana* Boott subsp. *flabellata* (Lév. & Vant.) T. Koyama and *C. podogyna* Franch. & Savat., respectively (Harada, 1977, 1986). Determination of the taxonomic identity of the two *Puccinia* fungi found in Nagano and Ibaraki necessitated their comparison with the three previously described *Puccinia* species host-alternating on *P. japonicus* and the taxonomic reevaluation of the three described species themselves. This paper discusses the taxonomic identity of the two newly found *Puccinia* fungi and the three previously described species.

Materials and Methods

Specimens examined On *Carex dimorpholepis*, Ibaraki, Kuji-gun, Satomi-mura, Okami, 31 March 1998. Y. Ono (Y. O.) & K. Ishimiya (K. I.) 4092 (T: IBA-8034); 21 Aug. 1998. Y. O. & K. I. 4220 (U, T: IBA-8163); 2 March 1999. Y. O. & K. I. 4268 (T: IBA-8219); 2 March 1999. Y. O. & K. I. 4269 (T: IBA-8220). On *C. presicottiana* subsp. *flabellata*, Aomori, Kitatsugaru-gun, Shiura-mura, Katsuragawa, 22 Oct. 1978. Y. Harada (Y. H.) 11500 (U, T; Holotype of *P. caricis-flabellatae*). On *C. podogyna*, Aomori, Nakatsugaru-gun, Nishimeya-mura, Anmon-ohashi, 13 Nov. 1979. Y. H. 11201 (U, T; Holotype of *P. caricis-podogynae*). On *C. sadoensis*, Aomori, Hirosaki, Koguriyama, 1 Dec. 1974. Y. H. 4129 (U, T: HU-741201; Holotype of *P. caricis-petasitidis*); 20 May 1975. Y. H. 11201 (U, T: HU-750501). On *C. shimizuensis*, Nagano, Chiisagata-gun, Sanada-machi, Sugadaira, 24 Aug. 1997. J. Abe (U, T: TSH-R1702); 26 April 1997, M. Kakishima (T: TSH-R1703). On *Petasites japonicus*, Aomori, Hirosaki, 14 March 1975. Y. H. (result of basidiospore inoculation of *P. caricis-petasitidis*, S. A: HU750301); 12 March 1979. Y. H. 10020 (result of basidiospore inoculation of *P. caricis-flabellatae*, S. A); 12 March 1980. Y. H. 10668 (result of basidiospore inoculation of *P. caricis-podogynae*, S, A); Ibaraki, Kuji-gun, Satomi-mura, Okami, 8 June 1990. Y. O. 2114 (S, A: IBA-4806); 7 June 1998. Y. O. & K. I. 4150 (S, A: IBA-8093); Mito, 10 May 1991. Y. O. 2336 (result of basidiospore inoculation, S, A: IBA-5692); 6 May 1998. Y. O. 4096 (result of basidiospore inoculation, S, A: IBA-8038); 6 May 1998. Y. O. 4097 (result of basidiospore inoculation, S, A: IBA-8039); Mito, 8 June 1999. Y. O. 4342 (result of basidiospore inoculation, S, A: IBA-8292); Nagano, Chiisagata-gun, Sanada-machi, Sugadaira, Aug. 1996. S. Iwamoto (S, A: TSH-R1704).

Capital letters S, A, U and T preceding the herbarium accession number denote spermogonial, aecial, uredinial

Table 1. Teliospore characteristics of *Puccinia* species host-alternating between *Carex* and *Petasites* in Japan.

Species/fungus	Specimen	Length (Mean) (μm)	Width (Mean) (μm)	Apical wall-thickening (Mean) (μm)	Pedicel length (Mean) (μm)
P. caricis-flabellatae Harada	YH-11500 (Holotype)	42.5–(52.5)–67.5	13.8–(16.9)–20.0	6.3–(8.3)–11.3	25.0–(36.2)–46.3
P. caricis-petasitidis Harada	YH-4129 (Holotype)	41.3–(49.8)–65.0	15.0–(19.1)–22.5	7.5–(11.4)–13.8	25.0–(40.0)–51.3
P. caricis-podogynae Harada	YH-11201 (Holotype)	41.3–(55.6)–67.5	15.0–(19.1)–22.5	10.0–(12.3)–15.0	18.8–(31.4)–47.5
The Okami fungus	IBA-8163	37.5–(49.7)–61.3	13.8–(18.1)–22.5	7.5–(10.7)–12.5	28.8–(37.9)–50.0
The Sugadaira fungus	TSH-R1702	40.0–(50.0)–62.5	13.8–(16.6)–20.0	6.3–(7.9)–10.0	20.0–(30.5)–47.5

and telial stage, respectively. All the above-cited specimens have been deposited in the mycological herbaria of the Faculty of Education, Ibaraki University (IBA), the Institute of Agriculture and Forestry, University of Tsukuba (TSH) and the Faculty of Agriculture and Life Science, Hirosaki University (HU).

Basidiospore inoculation Basidiospore inoculations were undertaken by the method described by Ono (1994) and Ono and Azbukina (1997). Telium-bearing leaves of *C. shimizuensis* were collected at Sugadaira, Nagano in April, 1997 and of *C. dimorpholepis* at Okami, Ibaraki in March, 1991, February, 1998 and March, 1999, respectively. The telium-bearing leaves were preserved in a refrigerator at ca. 5°C until the time when they were soaked in running tap water for 7–14 d to induce germination. Then, the leaves were cut into small pieces (ca. 2×5 mm), placed on water-saturated filter paper in a petri dish and incubated in the dark at ca. 18°C. The leaf pieces with germinated teliospores were placed on adaxial surfaces of apparently healthy leaves of the *Pet. japonicus* plants, which had been planted with loam soil in clay pots (18 cm diam). The inoculated plants were sprayed with distilled water and placed in a moist chamber at room temperature (18–22°C) for 48 h. The plants were subsequently transferred to a glasshouse for further observations. The inoculation experiments were repeated four times for the Sugadaira fungus population in 1997 and five times for the Okami fungus population, twice in 1991 and 1998 and once in 1999. In each basidiospore inoculation, two to five leaves of one or two plants were inoculated.

Microscopic observation To examine morphology and structure of spermogonium and aecium, fresh infected materials and dried herbarium specimens were sectioned freehand under a binocular dissecting microscope. Thin sections were mounted in a drop of lactophenol solution without stain. To examine morphology and to measure size, spores were scraped from sori on herbarium specimens and mounted as described above. Fifty or 100 randomly selected spores were measured in each specimen.

For scanning-electron microscopy (SEM), rust-infected leaves from dried herbarium specimens were cut into ca. 3×3 mm pieces containing a few sori, and each piece was placed on double-adhesive tape on a specimen holder. The preparations were subsequently coated with platinum-paladium using a Hitachi E-1030 Ion Sputter and examined with a Hitachi S-4200 SEM at 15 kV

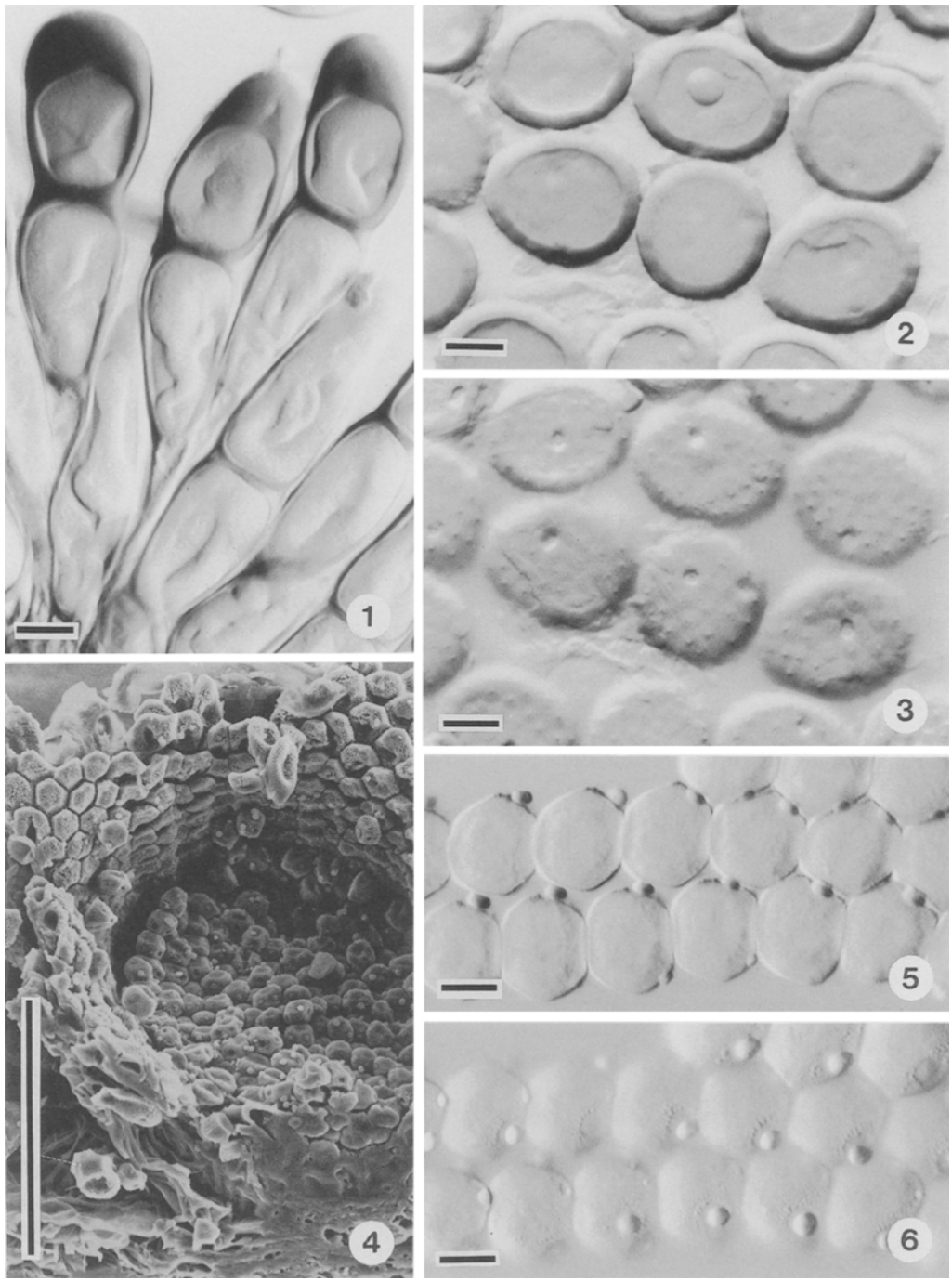
Results

Life cycle In the Sugadaira fungus, the basidiospores were successfully inoculated twice on the apparently healthy leaves of *Pet. japonicus*. Spermogonia were formed 12–15 d after the basidiospore inoculation, and aecia followed in the subsequent 10–15 d. In the Okami fungus, the basidiospores always successfully infected the *Petasites* plants, on which spermogonia appeared 5–7 d after the basidiospore inoculation and aecia were formed in the subsequent 6–7 d.

Aeciospores formed on the *Petasites* plants by the basidiospore inoculation were inoculated on either *C. shimizuensis* or *C. dimorpholepis*, from which the inoculum of the basidiospore inoculation was derived. Repeated inoculations were unsuccessful, however. Although aeciospore infection resulting in uredinio- and teliospore production on the *Carex* plants failed, the life-cycle connection between the spermogonial-aecial fungus on the *Petasites* plants and uredinial-telial fungi on the *Carex* plants both at Sugadaira and at Okami was confirmed. Because of the failure of the aeciospore inoculation, cross-inoculation to determine host range of both Sugadaira and Okami fungi was not undertaken.

Table 2. Urediniospore characteristics of *Puccinia* species host-alternating between *Carex* and *Petasites* in Japan.

Species/fungus	Specimen	Length (Mean) (μm)	Width (Mean) (μm)	Wall thickness (μm)
P. caricis-flabellatae Harada	YH-11500 (Holotype)	16.3–(19.2)–25.0	13.8–(17.0)–18.8	2.5
P. caricis-petasitidis Harada	YH-24000 (Holotype)	16.3–(20.4)–23.8	15.0–(17.8)–18.8	2.5
P. caricis-podogynae Harada	YH-11201 (Holotype)	16.3–(19.0)–23.8	13.8–(16.2)–18.8	2.5–3.8
The Okami fungus	IBA-8163	17.5–(20.8)–25.0	13.8–(17.8)–20.0	2.5–3.8
The Sugadaira fungus	TSH-R1702	18.8–(19.9)–23.8	16.3–(18.3)–20.0	2.5–3.8



Figs. 1–6. *Puccinia caricis-petasitidis sensu lato*. 1. Teliospores (IBA-8034). 2. Urediniospores fo-cused on a median plane (IBA-8163). 3. Urediniospores focused on a tangential plane (IBA-8163). 4. Aecium (TSH-R1704: SEM). 5. Aeciospores focused on a median plane (IBA-8038). 6. Aeciospores focused on a tangential plane (IBA-8038). 7. Aeciospore surface structure (TSH-R1704: SEM). Scale bar = 10 μm in Figs. 1–3, 5–7; 100 μm in Fig. 4.

Morphology In the Okami fungus, teliospores were variable in shape, mostly clavate to oblong-ellipsoid, rounded, truncate or conical at the apex; slightly to moderately constricted at the septum, attenuate toward the base, and 37.5–61.3 × 13.8–22.5 μm in size (Fig. 1; Table 1). The wall was light chestnut-brown and prominently thickened at the apex (7.5–12.5 μm). The pedicel was persistent and 28.8–50.0 μm long. Teliospores of the Sugadaira population were similar to and did not seem to be morphologically distinct from those of the Okami population (Table 1).

Urediniospores of the two geographically separated populations were also similar; mostly obovoid-ellipsoid or broadly ellipsoid and 17.5–25.0 × 13.8–20.0 μm in size

Table 3. Urediniospore germ pores of *Puccinia* species host-alternating between *Carex* and *Petasites* in Japan.

Species/fungus	Specimen	2, infraequatorial	2, equatorial	3, equatorial	4, equatorial
P. caricis-flabellatae Harada	YH-11500 (Holotype)	2*	22	65	11
P. caricis-petasitidis Harada	YH-24000 (Holotype)	2	15	76	7
P. caricis-podogynae Harada	YH-11201 (Holotype)	2	11	68	19
The Okami fungus	IBA-8163	0	17	79	4
The Sugadaira fungus	TSH-R1702	1	20	73	6

* Frequency in 100 observed urediniospores.

(Fig. 2; Table 2). The wall was evenly 2.5–3.8 μm thick, cinnamon-brown and completely echinulate (Fig. 3). Number and distribution of urediniospore germ pores were variable. When the urediniospore was divided longitudinally into three zones, i.e., apical, equatorial and basal zones, most urediniospores in the two geographically separated populations possessed three germ pores at the equatorial zone (Fig. 3; Table 3).

As with the uredinio- and teliospores, no significant difference was observed in aecium and aeciospore morphology of the two fungus populations. Spermogonia were subepidermal and globose, flask-shaped or depressed ovoid, 110–185 μm high and 115–135 μm wide. Aecia were cupulate surrounded by a well-developed peridium that ruptures and becomes reflected upon maturity (Fig. 4). Aeciospores were subglobose or depressed ellipsoid, often angular and 12.5–22.5 × 10.5–17.5 μm in size (Fig. 5; Table 4). The wall was ca. 1 μm thick, colorless and verrucose with refractive granules on the upper side (type 5 of Savile, 1973; Fig. 6, Table 4).

Discussion

Identity of the two geographically separate fungi The *Puccinia* fungi on *C. shimizuensis* at Sugadaira, Nagano and on *C. dimorpholepis* at Okami, Ibaraki have the same heteroecious life cycle with *Pet. japonicus* as the common spermogonial-aecial host, as proven by field observations and artificial inoculations. Beside having the same life cycle, as shown in Tables 1–4, the two fungi are morphologically indistinguishable at all stages of the life cycle. The same heteroecious life cycle and morphological similarity indicate that the two geographically separated fungi constitute a single species under the species concept of interbreeding populations reproductively isolated from others, which is adopted from Mayr and Ashlock (1991).

As stated previously for caricicolous rust fungi (Ono, 1983), two morphologically similar fungal populations may be recognized as distinct and placed in different taxa if they exhibit distinct host specificity, taxa being species, subspecies, varieties or formae speciales depending on how well their biology is understood. Thus, morphologically indistinguishable rust populations may be recognized as distinct species if they have different life cycles with different spermogonial-aecial host(s) and distinct ranges of uredinial-telial host(s).

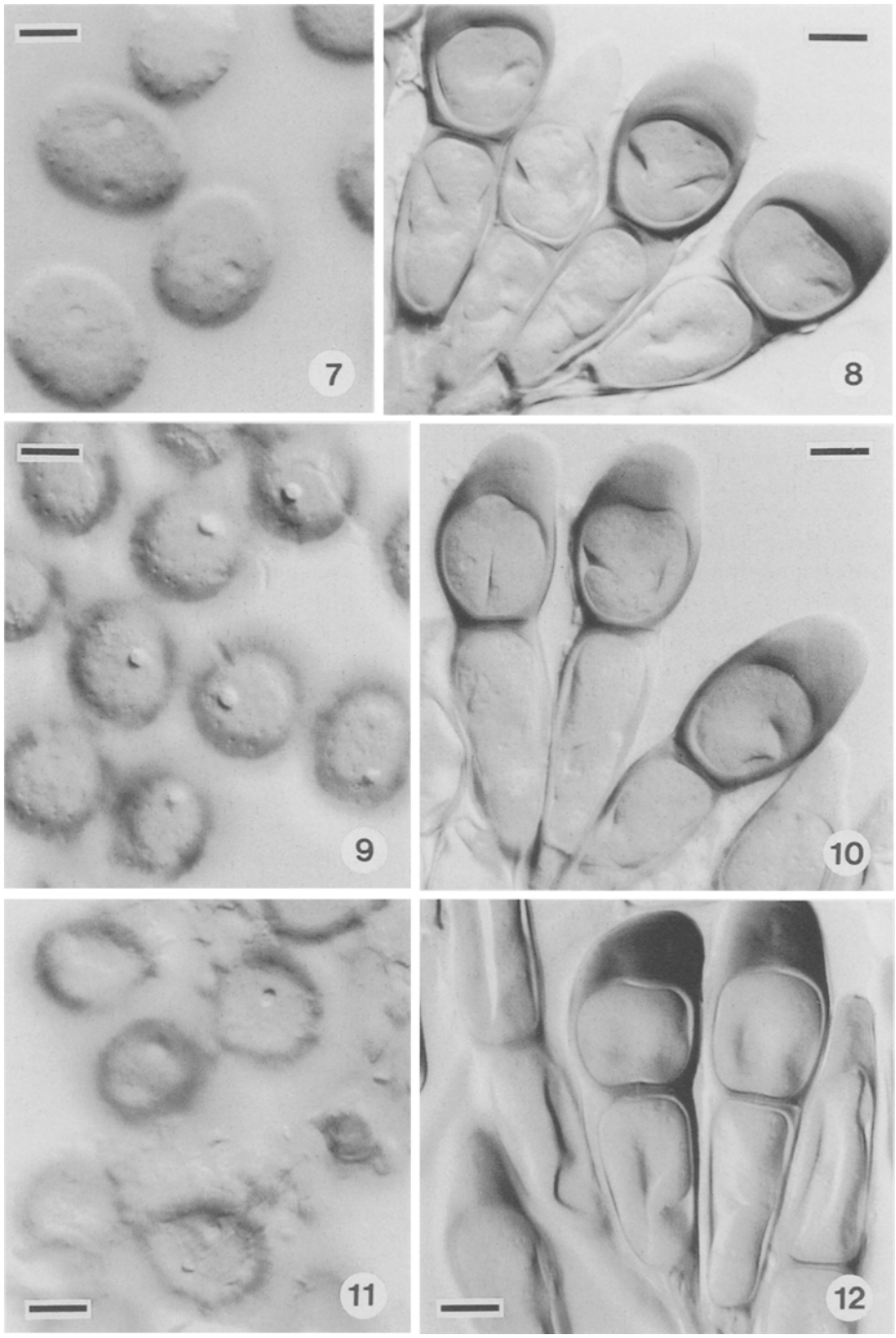
For rust populations that are morphologically indistinguishable, have similar uredinial-telial hosts and share common spermogonial-aecial host(s), it would be practical to treat them as a single species. Thus circumscribed species might be found to be composed of two or more reproductively isolated populations, i.e., two or more species, by additional properties to be found in future study. Accordingly, it is concluded that the geographically separated *Puccinia* fungi under discussion constitute a single species.

Taxonomic identity of *Puccinia caricis-flabellatae* and *P. caricis-podogynae* with *P. caricis-petasitidis* Three *Puccinia* species host-alternating between *Carex* species and *Pet. japonicus* have been described as distinct in Japan. *Puccinia caricis-petasitidis* was the first to be described and was characterized by globose or subglobose urediniospores (Fig. 7) of 18–21 × 16–20 μm in size with 2–4 subequatorial or scattered germ pores and broadly clavate teliospores of 40–55 × 15–20 μm in size with moderate constriction at the septum (Fig. 8; Harada, 1977). This fungus was assumed to be specific on *C. sadoensis*, giving negative results upon inoculation onto *C. thunbergii* Steud., *C. heterolepis* Bunge and *C. forficula* Franch. & Savat. (Harada, 1977).

Table 4. Aeciospore characteristics of *Puccinia* species host-alternating between *Carex* and *Petasites* in Japan.

Species/fungus	Specimen	Length (Mean) (μm)	Width (Mean) (μm)	Wall thickness (μm)	Surface structure type**
P. caricis-flabellatae Harada	YH-10021*	15.0–(16.7)–20.0	12.5–(14.7)–16.3	ca.1.0	type 5
P. caricis-petasitidis Harada	YH-4143*	13.8–(17.5)–20.0	12.5–(15.3)–17.5	ca.1.0	type 5
P. caricis-podogynae Harada	YH-10668*	15.0–(16.8)–20.0	12.5–(14.5)–17.5	ca.1.0	type 5
The Okami fungus	IBA-8095	15.0–(16.7)–20.0	12.5–(14.6)–17.5	ca.1.0	type 5
The Okami fungus	IBA-8038*	12.5–(17.7)–22.5	12.5–(15.2)–17.5	ca.1.0	type 5
The Sugadaira fungus	TSH-R1704	14.5–(16.8)–19.5	10.5–(14.0)–17.5	ca.1.0	type 5

* Aeciospores formed by basidiospore inoculation.
** The type is according to Savile's (1973) classification.



Figs. 7–12. *Puccinia caricis-petasitidis sensu lato*. 7. Urediniospores focused on a tangential plane (YH-4129: Holotype of *P. caricis-petasitidis*). 8. Teliospores (YH-4129: Holotype of *P. caricis-petasitidis*). 9. Urediniospores focused on a tangential plane (YH-11500: Holotype of *P. caricis-flabellatae*). 10. Teliospores (YH-11500: Holotype of *P. caricis-flabellatae*). 11. Urediniospores focused on a tangential plane (YH-11201: Holotype of *P. caricis-podogynae*). 12. Teliospores (YH-4129: Holotype of *P. caricis-podogynae*). Scale bar = 10 μm.

The second species, *P. caricis-flabellatae*, was characterized by obovate or broadly ellipsoid urediniospores (Fig. 9) of 18–21 × 15–19 μm in size with 2–3 primarily equatorial germ pores and broadly clavate or ellipsoid teliospores of 45–75 × 15–20 μm in size with strong constriction at the septum (Fig. 10; Harada, 1986). This species seems to be restricted to *C. presicottiana* subsp. *flabellata*, giving negative results upon inoculation onto *C. heterolepis*, *C. podogyna*, *C. sadoensis*, and *C. stipata* Muhl. (Harada, 1986).

The third species, *P. caricis-podogynae*, was stated to possess globose or subglobose urediniospores (Fig.

11) of 18–21 × 15–19 μm in size with 3–4 (rarely 2 or 5) equatorial gem pores and broadly clavate or ellipsoid teliospores of 50–70 × 13–19 μm in size with weak constriction at the septum (Fig. 12; Harada, 1986). This species was assumed to be specific on *C. podogyna*, giving negative results upon inoculations onto *C. sadoensis*, *C. heterolepis*, *C. forficula*, *C. olivacea* Boott var. *angustior* and *C. shimizuensis* (Harada, 1986).

Our measurements of the type specimens of the three species are slightly different from the original description (Tables 1–4). The longest teliospore of *P. caricis-flabellatae* was ca. 8 μm shorter and that of *P. caricis-petasitidis* was 10 μm longer than the original description (Table 1). The shortest teliospore of *P. caricis-flabellatae* was 2.5 μm shorter and that of *P. caricis-podogynae* was ca. 9 μm shorter than the original description (Table 1). Except for the difference in the size range, no significant difference in the measurements was detected among the three type specimens. As stated in the original description, the teliospores of *P. caricis-flabellatae* appear to be more strongly constricted at the septum than are those of two other species. However, the degree of constriction at the septum of the teliospores is variable and the difference among the specimens is not prominent (Figs. 8, 10, 12).

No significant differences were observed among the urediniospores from the three type specimens (Table 2). The most significant difference in the urediniospores of the three species was stated to be in the number and distribution of germ pores, i.e., 2–4 subequatorial or scattered in *P. caricis-petasitidis*, 2–3 equatorial in *P. caricis-flabellatae* and 3–4 (rarely 2 or 5) equatorial or scattered in *P. caricis-podogynae* (Harada, 1977, 1986). Distribution of the germ pores is highly variable, primarily because spores are distorted rather than ellipse oriented to the longitudinal axis. When the spores are longitudinally divided into three zones, the number and distribution pattern are found to be similar among the three species: most of the spores examined possess 3 equatorial germ pores (Figs. 7, 9, 11; Table 3).

In the morphology of aeciospores formed on the *Petasites* plants by the basidiospore inoculation, no significant difference was observed among the three species (Table 4).

These observed similarities noted upon the reexamination of the type specimens lead to the conclusion that the three described species are actually a single species, and that *P. caricis-petasitidis* has nomenclatural priority. Putative host specificity of the species is not conclusive and needs further investigation to see if the host specificity actually causes reproductive isolation of the rust populations or if the degree of host specificity is at a stage at which the different rust populations are recognized as formae speciales.

Following the conclusion that *P. caricis-petasitidis* embraces the rust populations formerly named *P. caricis-flabellatae* and *P. caricis-podogynae*, it is also concluded that the *Puccinia* populations on *C. shimizuensis* at Sugadaira, Nagano and on *C. dimorpholepis* at Okami, Ibaraki belong to *P. caricis-petasitidis*. The description of *Puccinia caricis-petasitidis* is revised as follows:

Puccinia caricis-petasitidis **Y. Harada**, Trans. mycol. Soc. Japan 18: 173. 1977.

Synomyms: *Puccinia caricis-flabellatae* Y. Harada, Trans. mycol. Soc. Japan 27: 359. 1986.

Puccinia caricis-podogynae Y. Harada, Trans. mycol. Soc. Japan 27: 362. 1986.

Spermogonia mostly epiphyllous or petiolicolous, subepidermal, subglobose or depressed obovoid, 100–185 μm high and 100–170 μm wide, Aecia mostly hypophyllous or petiolicolous, peridiate, cupulate: aeciospores subglobose, often angular, 12–23 × 10–20 μm, the wall ca. 1 μm thick, colorless, verrucose with refractive granules at upper side. Uredinia mostly hypophyllous, brown, powdery; urediniospores subglobose, obovoid or ellipsoid, 16–25 × 13–20 μm, the wall evenly 2.5–3.8 μm thick, cinnamon-brown, completely echinulate, germ pores (2–)3(–5) mostly equatorial. Telia hypophyllous, black, pulvinate; teliospores clavate, obovoid ellipsoid, oblong ellipsoid, rounded, truncate or conical at the apex, weakly to moderately constricted at the septum, attenuate toward the base, 37–70(–75) × 12–23 μm, the wall chestnut-brown, 5–15 μm thick at the apex, the pedicel colorless, persistent, 18–55(–70) μm long.

Holotype: On *Carex sadoensis* Franch., Japan, Aomori Pref., Hirosaki, Oguriyama, 1 Dec. 1974, Y. Harada 4129 (HU741201).

Host and geographic distribution: *C. dimorpholepis*-Ibaraki and Fukushima; *C. presicottiana* subsp. *flabellata*-Aomori; *C. podogyna*-Aomori; *C. sadoensis*-Aomori; *C. shimizuensis*-Nagano; *Pet. japonicus*-Hokkaido, Aomori, Fukushima, Ibaraki and Nagano.

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