

II. Review of literature

1. Taxonomy of *Uromyces viciae-fabae*

Uromyces viciae-fabae (Pers.) Schroet., causing the pea rust disease, is an autoecious and macrocyclic rust fungus occurring on wild and cultivated *Vicia*, *Lathyrus*, *Pisum* and *Lens* plants (Wilson and Henderson 1966; Cummins 1978; Duke 1981; Azbukina 1984; Guo and Wang 1986; Hiratsuka et al. 1992). Persoon (1794, cited from Ito 1922) first reported a rust fungus on *Vicia faba* L. as *Uredo fabae* Pers., and the fungus was later named as *Uromyces fabae* de Bary (= *U. viciae-fabae* var. *viciae-fabae*) by de Bary (1863, cited from Ito 1922). On the other hand, Persoon (1794, cited from Ito 1922) first reported a rust fungus on *Lathyrus montanus* Bernh. as *Aecidium orobi* Pers. Later, L veill  (1847) named the rust fungus on *L. montanus* as *U. orobi* L v. and stated that *U. orobi* differed from *U. fabae* because of thicker urediniospore wall. The rust fungus was commonly found on *L. montanus* (Wilson and Henderson 1966). However, J rstad (1936, cited from Wilson and Henderson 1966) merged the rust fungus into *U. viciae-fabae* because of morphological similarity in urediniospores, and he changed the status of *U. orobi* to a variety of *U. viciae-fabae*. However, the wall thickness of urediniospores was considered as a useful taxonomic character to identify the two species (or varieties) in Japan, Europe and Russia (Ito 1922, 1950; Hiratsuka 1933, 1973; G umann 1934; Wilson and Henderson 1966; Azbukina 1984; Hiratsuka et al. 1992). Furthermore, G umann (1934) stated that urediniospores of *U. fabae* on *Vicia sepium* L. showed different wall thickness, i.e.,

those on stems being thicker than those on leaves, and listed six formae speciales for *U. fabae* and three formae speciales for *U. orobi*. Likewise, Conner and Bernier (1982a, 1982b) inoculated *U. viciae-fabae* isolates from *Vicia* and *Lathyrus* on *Vicia*, *Lens*, *Pisum* and *Lathyrus* and listed eleven races for *U. viciae-fabae*.

Dietel (1900, cited from Hiratsuka and Yoshida 1930) first examined a rust fungus from *V. faba* in Japan and reported the fungus as *Uromyces fabae*. Later, Hennings (1905, cited from Hiratsuka and Yoshida 1930), Yoshinaga (1902, cited from Hiratsuka and Yoshida 1930), Yoshino (1905, cited from Hiratsuka and Yoshida 1930), Ito (1922) and Hiratsuka (1927) also examined the same fungus on *V. faba* from many places of Japan and identified as *U. fabae*. In addition, Hennings (1901, cited from Hiratsuka and Yoshida 1930) named a rust fungus collected on *Pisum sativum* L. as *U. yoshinagai* P. Henn. Subsequently, Yoshinaga (1902, cited from Hiratsuka and Yoshida 1930), Yoshino (1905, cited from Hiratsuka and Yoshida 1930) and Dietel (1905, cited from Hiratsuka and Yoshida 1930) reported the rust fungus on *P. sativum*. Contrarily, Sydow et al. (1906) reported that a rust fungus on *P. sativum* in India as *U. fabae* and they considered *U. yoshinagai* in Japan was a synonym of *U. fabae*. Moreover, Yoshino (1905, cited from Hiratsuka and Yoshida 1930) reported a rust fungi on *V. hirsuta* Koch and *V. sativa* L. as an unidentified *Uromyces*. Later, Hennings (1905, cited from Hiratsuka and Yoshida 1930) identified this *Uromyces* on the two plants as *U. fabae*. In contrast to Hennings (1905, cited from Hiratsuka and Yoshida 1930), Dietel (1905, cited from Hiratsuka and Yoshida 1930) recognized a *Uromyces* species on *V. hirsuta* as *U. ervi* West., and a *Uromyces* species on *V.*

sativum as *U. fabae*. In 1910, Dietel reported a *Uromyces* species on *V. unijuga* Al. Br. as *U. fabae*. In addition, Sydow and Sydow (1913, cited from Hiratsuka and Yoshida 1930) identified a *Uromyces* species on *V. cracca* L. var. *japonica* Miq. in Japan as *U. fabae*. Ito (1922) treated a fungus on *Vicia*, *Lathyrus* and *Pisum* as *U. fabae*, and reported that the rust fungus was more commonly found on *Vicia*, *Lathyrus* and *Pisum* than *U. orobi* and *U. ervi*.

On the other hand, Dietel (1899, cited from Hiratsuka and Yoshida 1930) first reported a *Uromyces* fungus on *Lathyrus maritimus* Bigel collected in Tokushima Pref. as *U. orobi*. Later, Hennings (1900, cited from Hiratsuka and Yoshida 1930) re-examined the same specimens and transferred the rust fungus to *U. fabae*. However, Kusano (1902, cited from Hiratsuka and Yoshida 1930) and Dietel (1905, cited from Hiratsuka and Yoshida 1930) considered the *Uromyces* fungus on *L. maritimus* and *L. davidii* Hance as *U. orobi*. However, Ito (1922) treated the *Uromyces* species in Japan, and recognized a rust fungus on *V. unijuga* as *U. orobi* because of the thicker urediniospore wall. From 1930 to 1933, Hiratsuka examined the host specificity of *U. fabae* and *U. orobi* and listed three formae speciales for *U. fabae* and two formae speciales for *U. orobi* (Hiratsuka 1933). Later, Hiratsuka (1937) also reported that *U. fabae* was commonly found on most of *Vicia*, *Lathyrus* and *Pisum*, and *U. orobi* was commonly found on *V. unijuga*, *V. nipponica* Matsum. var. *capitata* Nakai and *L. davidii*. Similarly, Ito (1950) followed Hiratsuka's report (1937) and also reported that most of *Vicia*, *Lathyrus* and *Pisum* species were susceptible only to *U. fabae*, whereas *V. unijuga*, *V. nipponica* var. *capitata* and *L. davidii* seemed to be

susceptible only to *U. orobi*.

Recently, Hiratsuka (1973) and Hiratsuka et al. (1992) agreed with Jørstad. (1936, cited from Wilson and Henderson 1966) and changed the status of *U. orobi* to *U. viciae-fabae* var. *orobi*. Thus, they recognized that *U. viciae-fabae* var. *orobi* (= *U. orobi*) differed from *U. viciae-fabae* var. *viciae-fabae* (= *U. fabae*) in wall thickness of urediniospores (Hiratsuka 1973; Hiratsuka et al. 1992). As their morphological descriptions, urediniospore wall-thickness of *U. viciae-fabae* var. *viciae-fabae* was from 1.5 to 2.5 μm , and *U. viciae-fabae* var. *orobi* was from 2 to 3 μm . The taxonomic history of *U. viciae-fabae* var. *viciae-fabae* and *U. viciae-fabae* var. *orobi* in Japan was listed in Fig. 2.1.

2. Taxonomy of *Uromyces appendiculatus* and *Uromyces vignae*

Uromyces appendiculatus (Pers.) Unger (= *U. phaseoli* var. *typica* Arth.) and *U. vignae* Barclay (= *U. phaseoli* var. *vignae* (Barclay) Arth.) are economically important rust fungi on bean, cowpea and related legumes. The two species cause rust diseases on bean and cowpea throughout the world (Duke 1981; Thurston 1998). Persoon (1795, cited from Arthur 1934) first reported a fungus on *Phaseolus vulgaris* L. as *Uredo appendiculata* Pers. Later, Link (1816, cited from Ito 1922) named the rust fungus on *P. vulgaris* as *U. appendiculatus* (Pers.) Link. Likewise, Unger (1836, cited from Cummins 1978) named the same rust fungus on *P. vulgaris* as *U. appendiculatus* (Pers.) Unger. On the other hand, *Uromyces vignae* causes rust diseases mainly on cowpea and is widely distributed where cowpeas are grown

(Cummins 1978; Duke 1981; Guo and Wang 1986; Hiratsuka et al. 1992; Thurston 1998). Barclay (1891) first reported the rust fungus on *Vigna vexillata* (L.) A. Rich. and named it as *U. vignae* Barclay. Later, Fromme (1924) treated a rust fungus on *V. unguiculata* (L.) Walp. (= *V. sinensis* (L.) Savi ex Hassk.) as *U. vignae* and stated that the fungus differed from a fungus on *P. vulgaris* in spore morphology and host specificity. He considered *U. vignae* as a distinct species and renamed *U. vignae* as *Nigredo vignae* (Barcl.) Fromme.

However, Arthur (1934) agreed with Winter (1881, cited from Arthur 1934) and recognized the rust fungus on *Phaseolus*, *Strophostyles* and *Vigna* as *U. phaseoli* (Pers.) Wint., included three varieties, var. *typica* Arthur on *Phaseolus* spp., var. *strophostylis* Arthur on *Strophostyles* spp. and var. *vignae* (Barclay) Arthur on *Vigna* spp. According to his descriptions, these varieties showed only minor morphological differences in urediniospores and teliospores. Later, Cummins (1978) recognized *U. appendiculatus* and *U. vignae* as separate species and transferred *U. phaseoli* var. *phaseoli* and var. *strophostylis* to *U. appendiculatus* var. *appendiculatus*, and *U. phaseoli* var. *vignae* to *U. vignae*. According to Cummins (1978), *U. vignae* differed from *U. appendiculatus* in strongly superequatorial pores of the urediniospores and the smooth teliospore-walls. In contrast to Arthur (1934), Cummins (1978) considered that position of urediniospore germ-pores and teliospore wall-ornamentation were taxonomic characteristics to separate the two species.

Heath (1980; 1984) and Fernandez and Heath (1986) conducted several inoculation experiments to examine the pathogenicity of the cowpea rust fungus and

the bean rust fungus both on host and on non-host plants. The continual colonization in non-host plants inoculated either with the bean rust fungus on the cowpea rust fungus was not found. Furthermore, Kim et al. (1985) extracted proteins from *U. phaseoli* var. *typica* and *U. phaseoli* var. *vignae*, and compared number of polypeptide patterns between *U. phaseoli* var. *typica* and *U. phaseoli* var. *vignae*. The results showed that polypeptide patterns were different between the two varieties and they recognized the bean rust and the cowpea rust as separated species (Kim et al. 1985). Moreover, Elmhirst and Heath (1986; 1988) studied the coevolutionary relationships of the bean rust fungus and the cowpea rust fungus to wild and cultivated *Phaseolus* and *Vigna* from America and Africa and concluded that the bean rust had wide host range than the cowpea rust.

In Japan, Ito (1922) first recognized a rust fungus on *Phaseolus* and *Vigna* as *U. appendiculatus* (Pers.) Unger because of morphological similarity. According to Ito's (1922) descriptions, the rust fungus on *Phaseolus* and *Vigna* was autoecious and macrocyclic, possessed urediniospores with 2 pores and teliospores with wall smooth or slightly verrucose. The wall was said to be hyaline or subhyaline large hemispherical papilla. Later, Hiratsuka (1937) identified the rust fungi on *Apios fortunei* Maxim., *Lablab purpureus* (L.) Sweet (= *Dolichos lablab* L.), *P. vulgaris*, *V. angularis* (Willd.) Ohashi var. *angularis* (= *P. radiatus* var. *aurea* Prain.) and *V. umbellata* (Thunb.) Ohwi & Ohashi (= *P. pendulus* Mak.) as *U. appendiculatus*, and rust fungi on *V. unguiculata* ssp. *sesquipedalis* (L.) Verdc. (= *V. sesquipedalis* (L.) Fruwirth) and *V. unguiculata* ssp. *unguiculata* as *U. vignae*. In 1943, Ito and

Murayama described a rust fungus on *A. fortunei* as a new species, *U. dispersus* Hiratsuka ex S. Ito & Murayama, but they did not describe the morphological differences between *U. dispersus* and *U. appendiculatus* on *Phaseolus*, *Vigna* and *Lablab*. Ito (1950) reported that *Uromyces* species on *Phaseolus*, *Vigna*, *Apios* and *Lablab* were separated into three species, the *U. appendiculatus* on *P. vulgaris*, *V. angularis* var. *nipponensis* (Ohwi) Ohwi (= *P. minimus* f. *typicus* Hosokawa), *P. coccineus* L. (= *P. multiflorus* Willd.), *V. angularis* var. *angularis*, *V. umbellata* and *L. purpureus*, the *U. vignae* on *V. unguiculata* ssp. *sesquipedalis* and *V. unguiculata* ssp. *unguiculata*, and the *U. dispersus* on *A. fortunei*. However, Ito (1950) did not describe morphological differences among the three *Uromyces* species. Hirata (1952) described a rust fungus on *V. angularis* var. *angularis*, *V. angularis* var. *nipponensis* and *V. umbellata* as a new species, *Uromyces azukicola* S. Hirata. According to Hirata (1952), the rust species on the three host plants showed sufficient morphological differences from *U. appendiculatus* and *U. vignae* and could not infect and sporulate on *P. vulgaris*, *P. coccineus* L., *V. unguiculata* ssp. *unguiculata* and *L. purpureus*.

In 1973, Hiratsuka agreed with Arthur (1934) and changed the status of *U. appendiculatus*, *U. azukicola*, *U. dispersus* and *U. vignae* to four varieties of *U. phaseoli*, var. *phaseoli*, var. *vignae*, var. *azukicola* (Hirata) Hiratsuka, f. and var. *dispersus* (Hiratsuka, f.) Hiratsuka, f. Hiratsuka (1973) did not recognize *U. appendiculatus*, *U. azukicola*, *U. dispersus* and *U. vignae* as separate species because of morphological similarity between these species. He also considered that

the position of urediniospore germ-pores and size variations of urediniospores and teliospores were not sufficient morphological characteristics to recognize separate species. Currently, Hiratsuka et al. (1992) recognize the position of urediniospore germ-pores and putative host specificity as important taxonomic characteristics to separate *U. appendiculatus* and *U. vignae*. Thus, they transferred *U. phaseoli* var. *phaseoli* on *P. vulgaris* to *U. appendiculatus* var. *appendiculatus*, *U. phaseoli* var. *azukicola* on *V. angularis* var. *angularis*, *V. angularis* var. *nipponensis* and *V. umbellata* to *U. appendiculatus* var. *azukicola*, *U. phaseoli* var. *dispersus* on *A. fortunei* to *U. appendiculatus* var. *dispersus*, and *U. phaseoli* var. *vignae* on *V. unguiculata* and *L. purpureus* into *U. vignae*. According to Hiratsuka et al. (1992), *U. appendiculatus* had 2 (rarely 3) germ-pores on equatorial or subequatorial position, and *U. vignae* had 2 (rarely 3) germ-pores near the apex (Hiratsuka et al. 1992). Moreover, varieties of *U. appendiculatus* were distinguished from each other based on size of urediniospores and teliospores (Hiratsuka et al. 1992). *Uromyces appendiculatus* var. *dispersus* had larger urediniospores than *U. appendiculatus* var. *appendiculatus* and *U. appendiculatus* var. *azukicola*. *Uromyces appendiculatus* var. *appendiculatus* had larger teliospores than *U. appendiculatus* var. *azukicola*. The taxonomic history of *U. appendiculatus* and *U. vignae* in Japan was listed in Fig. 2.2.

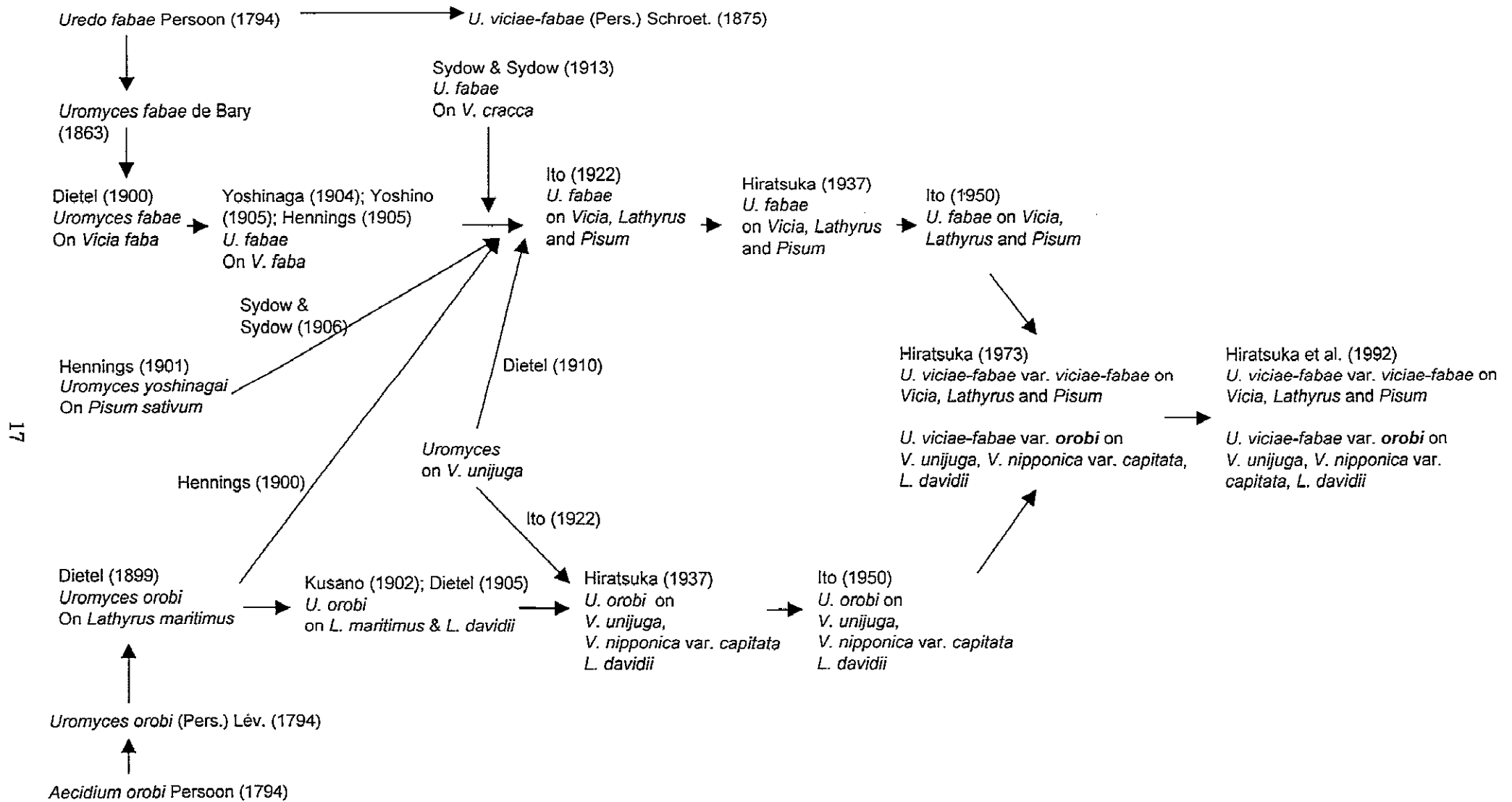


Fig. 2.1. The taxonomic history of *Uromyces viciae-fabae* on *Vicia*, *Lathyrus* and *Pisum* in Japan.

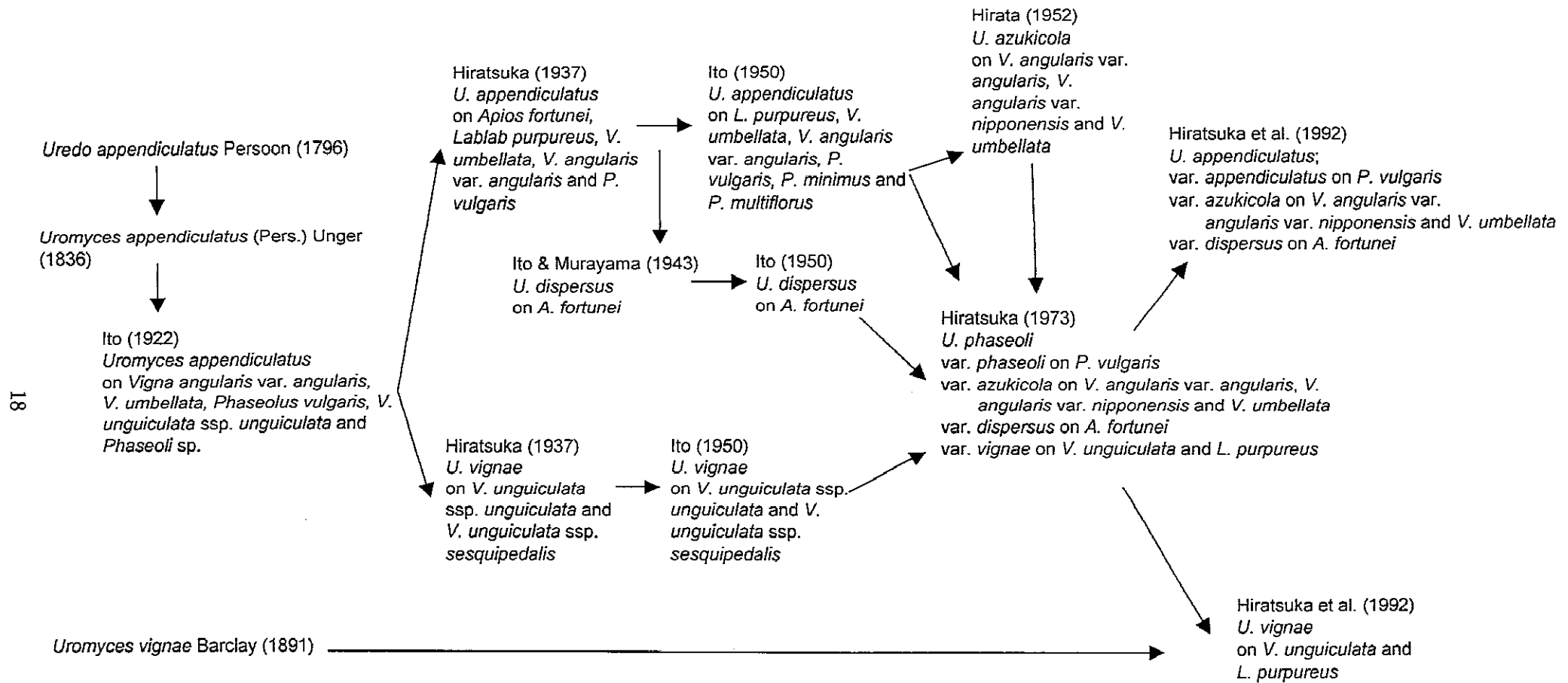


Fig. 2.2. The taxonomic history of *Uromyces appendiculatus* and *U. vignae* on *Phaseolus*, *Vigna*, *Apios* and *Lablab* in Japan.