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STUDIES ON THE CULTURAL EXPERIMENTS OF THE FERN RUSTS OF ABIES IN JAPAN

By

Senji Kamei

(With Plates I-VII and 7 Text-figures)

I. INTRODUCTION

Among rust diseases of *Abies*, a group of species, which have their antithetic phases parasitic on ferns, is of great interest from the scientific as well as economic point of view. By the color of the spores in fresh condition these rusts are divided into two groups, namely, the white and the colored ones. To the former group belong the species of either the genus *Uredinopsis* or *Milesina*, while to the latter those of the genus *Hyalopsora*. Owing to their parasitism on ferns and firs, the genera are usually considered to be the most primitive and ancient forms of rusts (BARTHOLOMEW, 1916, ARTHUR, 1924, FAULL, 1938 b), and heteroecism is considered to have originated from these groups (DIETEL, 1904 and 1918, MOSS, 1926). Consequently they have supplied a fertile field of study for problems from the pure mycological point of view.

The firs, whose needles are usually infected, though rarely the stems also, often suffer great damage. They are sometimes ultimately killed especially when the plant is young. In Hokkaidô, *Abies Mayriana* MIYABE et KUDÔ and *A. sachalinensis* FR. SCHMIDT are widely distributed constituting the most important forest trees. In these forests, are found numerous species of ferns, some of which frequently make the dominant constituents of their undergrowth. The firs infected by fern rusts especially having the white-spored peridermia are found not only in mature trees but also in small seedlings that grow on the primeval forest floor or in nursery beds. Accordingly to investigate the taxonomy and the life history as well as the injurious effects of these rusts is one of the most interesting studies from the pathological point of view.

The investigation, however, is exceedingly perplexing in the following respects: viz., the proper taxonomic treatment of some aberrant forms and the discrimination among the species of the white *Peridermium* that live, often simultaneously, on the leaves of one and the same species of *Abies*. To overcome such difficulties it was necessary to repeat the culture experiments and to make careful comparisons or sometimes to compare them with some authentic foreign materials of nearly related species. Up to the present time, several special reports concerning the present subject have been published by the writer, but a more comprehensive one to coordinate them, together with other various new data is now needed for the complete explanation of the nature of the parasites and the diseases caused thereby.

The present report contains the results of the writer's personal observations on the life history of each of sixteen fern rust species, and also comparative studies regarding their peridermial phases as well as economic considerations on some of them.

This work has been done mainly during a long stay in the Phytopathological laboratory of the Faculty of Agriculture under the direction of Professor SEIYA ITÔ to whom the writer wishes to express his sincere thanks. To Professor Emeritus KINGO MIYABE the author is especially indebted for his constant kind help and criticisms, without which this work could not have been brought into this form. To Professors Emeritus YOSHINAO NIJIMA and OTOKUMA SHISHIDO and Professors HIROKICHI NAKASHIMA and YOSHIO SATÔ in the Forestry Institute the writer is indebted for their encouragement and help. To Professor YOSHIHIKO TOCHINAI and Assistant Professor TEIKICHI FUKUSHI the writer is indebted for their kind help and advice. To Professor Emeritus JOSEPH CHARLES ARTHUR of Purdue University, Professor JOSEPH HORACE FAULL of the Arnold Arboretum, Harvard University, Professor Emeritus SHUNSUKE KUSANO in the Tôkyô Imperial University and Professor NAOHIDE HIRATSUKA of the Tottori Agricultural College, the author is greatly indebted for their kindness in sharing their valuable specimens. The writer also acknowledges the courtesies of the following persons, Assistant Professor KYÔJIRÔ SHIMAKURA and Mr. KANEÔ HINO of this University, Mr. GEN TAZOE in the Taihoku Imperial University, Messrs. YASUSHI HARADA and SAKUO TSURUTA in the Imperial Government Forest Office, Mr. TAKESHI YAMAGUCHI in the Hokkaidô Government, Mr. TAMOTSU AIZAWA in the Government of Japanese mandate in Southern Islands and Mrs. Dr. YASU IGUCHI (née HOMMA).

II. SPECIES OF UREDINOPSIS

A. THE LIFE HISTORY STUDIES

(1) *Review of literature*

As was remarked by ARTHUR (1924), the genus *Uredinopsis* is the first of the fern rusts to have its life cycle fully worked out, which was done by FRASER. While working on the cultural studies of some heteroecious rusts in Nova Scotia, Canada, FRASER (1912) found the *Peridermium balsameum* PECK abundantly on *Abies balsamea* MILL. in all the regions visited by him. At first it was considered that the *Peridermium* mentioned above is related to a *Pucciniastrum* (CLINTON, 1908, FRASER, 1911), but later FRASER (1912) noticed that "*U. mirabilis* (PECK) Magnus was associated in a very striking way with the same *Peridermium*." Making two sets of inoculation experiments with the aecidiospores of the *Peridermium* onto *Onoclea sensibilis* he succeeded for the first time in proving that "the fern rusts of the genus *Uredinopsis* are heteroecious." In 1912, he made further cultures (FRASER, 1913) accompanied with field observations to determine positively whether the four other species of *Uredinopsis*, namely, *Uredinopsis Struthiopteridis*, *U. Osmundae*, *U. Atkinsonii* and *U. Phegopteridis* are also connected with the same *Peridermium* or not. As he considered then, that "the species of the genus *Uredinopsis* are not separated by any morphological difference, and also a number of them have their aecia on *Abies balsamea*" he was in doubt "whether they are distinct or should be included under one species." To obtain culture evidence bearing on this matter he performed his final inoculation experiments in 1913. In this case, the aecidiospores from the three sets of successful inoculations with the basidiospores of *U. americana* on *A. balsamea* and back inoculations with the obtained aecidiospores were made on five species of ferns, namely, *Onoclea sensibilis* L., *Aspidium Thelypteris* (L.) Sw., *Osmunda Claytoniana* L., *O. regalis* L. and *Phegopteris Dryopteris* (L.) FÉE. He succeeded in getting uredosori on *Onoclea sensibilis* only and accordingly concluded that "*Uredinopsis mirabilis* is a distinct species." These publications of FRASER were interpreted by one group of investigators to mean that the seven species of *Uredinopsis* published by ARTHUR (1907) are as many forms that may combine into one or smaller number of species, but others believed in their individuality though they differ from one another very slightly.

FAULL and his collaborators (FAULL, 1929) repeated FRASER's experiments mentioned above, obtaining similar results.

KLEBAHN was interested in FRASER's experiments mentioned above and also in ARTHUR and KERN's (1906) remark which was maintained by FARLOW that *Peridermium balsameum* in North America is identical with *Aecidium pseudocolumnale* KÜHN in Europe. Previously KLEBAHN (1905) had made inoculations with the aecidiospores of *A. pseudocolumnale* on six species of ferns and other plants in vain. However, afterwards, he (1916) succeeded in inoculation experiments with the basidiospores onto *Abies alba* MILL. harvesting the peridermial phase of *U. Struthiopteridis* partly thus re-proving FRASER's experiments. It is very interesting to note that HUNTER (1936 c) who intensively studied on the spermogonia of various species of Melampsoraceae, inspected the type specimens of the two species of *Peridermium* mentioned above and came to the conclusion that the specimens were identifiable as *Uredinopsis*.

In 1915-1916, WEIR and HUBERT (1917) found a *Peridermium* on the second year needles of *Abies grandis* LINDL., and the aecidiospores of the rust were successfully inoculated onto *Pteridium aquilinum* KUHN var. *pubescens* UNDERW. with positive results. From the experiment they considered that the aecidial phase is neither *Peridermium balsameum* nor *P. pseudobalsameum* ARTH. et KERN but a special stage belonging to *U. Pteridis* DIET. et HOLW. which was regarded as synonymous with *U. macrosperma* MAGN. in North America. ARTHUR (1925), JACKSON (1918), BELL (1924), FAULL (1929, 1938 b) and HUNTER (1927, 1936 c), however, took WEIR and HUBERT's *Peridermium* to be nothing but *Peridermium pseudobalsameum* as especially related to *Uredinopsis Pteridis*. Concerning WEIR and HUBERT's suggestion on the course of the development of the peridermial stage, BELL (1924) and HUNTER (1927) did not agree. In the course of his study, the writer (1930a) also obtained successful experimental proofs of the life history of a rust which has generally been known as *U. Pteridis*, parasitic on *Pteridium aquilinum* KUHN var. *japonicum* NAKAI and *Abies Mayriana*. Comparing with the American specimen of the peridermial phase mentioned above, he was able to recognize conspicuous differences regarding the morphological characters. Quite recently, FAULL (1938 b) reported that our rust form with which the writer has been concerned is to be named *U. Kameiana* FAULL sp. n. It should be separated from *U. Pteridis* which is genetically related with *Peridermium pseudobalsameum*. In the present paper, a comparative study on two species of *Peridermium* from America and Japan under

consideration is specially treated.

In 1932, the writer (1932 b) described the peridermal phases of *U. Athyrii* KAMEI, *U. Woodsiae* KAMEI, *U. hirosakiensis* KAMEI et HIRATSUKA, f., *U. intermedia* KAMEI and *U. ossaeiformis* KAMEI which were obtained from his culture experiments. In the next year the writer (1933) reported briefly on the successful cultures of *Uredinopsis Adianti*, *U. flicina* and *U. Struthiopteridis*. FAULL (1938 c) recently published the results of his cultural experiments concerning six species of *Uredinopsis* from America. Among them those of *U. longinucronata* and *U. ceratophora* were recorded for the first time.

Thus among twenty five species of *Uredinopsis* now recorded from the whole world, the life history studies of sixteen species have been heretofore reported by FRASER, KLEBAHN, WEIR & HUBERT, KAMEI and FAULL as shown in Table 84 in this paper.

DATA of the uredospore inoculations concerning some species of *Uredinopsis* were reported by FAULL (1938 c) and by the writer in this paper.

DATA of inoculations with the amphispores of some species of *Uredinopsis* were published by KLEBAHN (1916) and by the writer in this report.

(2) *Materials and methods of culture experiments*

Uredinopsis Adianti, *U. Athyrii*, *U. flicina*, *U. hirosakiensis*, *U. Kameiana*, *U. Struthiopteridis*, *U. Woodsiae*, *U. intermedia* and *U. ossaeiformis* were used for the culture experiments. These culture experiments were divided into four groups, namely, I: infection with basidiospores, II: with accidiospores obtained from basidiospore cultures, III. A: with uredospores, III. B: with amphispores and IV: with accidiospores obtained from the field. Details about the materials for the culture experiments for the respective species are treated in each section devoted to that species.

As the teleutospores of these species of *Uredinopsis* develop perfectly before winter when the host ferns are dried up, well-affected pinnae to be used for the basidiospore culture were collected in the late autumn from the field and placed inside of cotton bags which were hung up out-of-doors on the wall of the laboratory. In the following spring, taking out the material from the bags, small pieces were selected to be immersed in water for about one to two days. After taking out of the water, the material was placed inside a Petri dish and watched for the

germination of the teleutospores which usually occurred on the discolored portions of the affected fronds. As soon as germination was detected, the material with the fresh basidiospores was merely placed directly upon the fascicle of the needles of fir seedlings which were beforehand sprayed with water thoroughly and then covered with a bell-glass, the inside of which was lined with wet blotting paper. Sometimes these pots were placed inside of a large wooden case, the bottom of which was lined with moist sphagnum moss, and the case was covered with a lid after the inoculation. Two to three days after the treatment the pots were transferred to a cool place and well-watered. The fir seedlings used for the experiments were usually potted before winter. They were mostly about four to five years old (rarely two years old) which were transferred from the bed of the University nursery where fear about pre-infection was practically nil. Control plants were sometimes provided.

These inoculation experiments were conducted in the greenhouse, out-of-doors under shade, and in the corridor inside of the laboratory building. The temperatures inside of the laboratory during the day time at the periods of the various inoculation experiments were recorded to be 14°–19°C. That of inside of the greenhouse during the periods of experiments fluctuated from 5°–8°C to 30°–34°C. The temperatures of the outdoors and corridor were not recorded. In the inoculation experiments with the aecidiospores, the inocula were mostly obtained from the peridermal sori derived from artificial inoculations, but sometimes they were also obtained from the field, in which cases they were beforehand carefully inspected and accurately identified.

For the manner of the inoculations of aecidiospores and uredospores (including amphispores), two methods were adopted. In the first method, the ferns to be inoculated were usually transferred from the field into pots or foregarden before winter and the inocula were smeared by means of a clean needle on the under surface of the pinnae of the ferns. They were then covered with a bell glass, the inside of which had beforehand been wet with moistened paper. Sometimes a large wooden case was also used. After the treatment the pots were transferred to a cool place and well-watered to watch for the results expected. The second method may be called the "Petri dish method" which has already been explained in detail by CLINTON and McCORMICK (1924). In the writer's practise, the inocula were transferred onto fresh pinnae cut from the healthy potted fern plants or in the field. They were previously washed carefully with distilled water to remove dust and

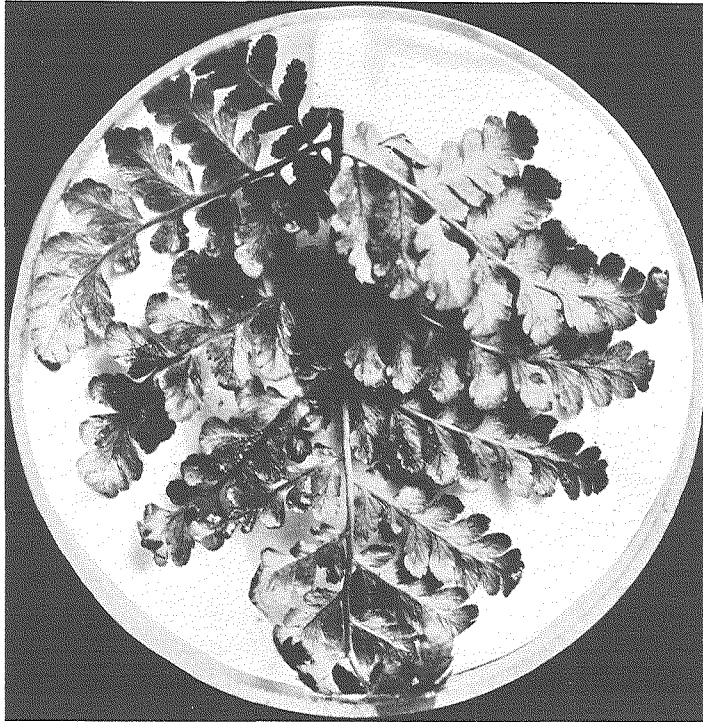


Fig. 1. Petri dish culture.

With the aecidiospores of *U. ossaeiformis* on *Abies Mayriana* collected at Morap, Prov. Iburi inoculated on fronds of *Dryopteris dilatata* var. *oblonga*. First uredospores issued after 25 days on Aug. 30, 1933. Photographed several days after. Slightly reduced.

extraneous spores and laid alive inside of clean Petri dishes (Fig. 1). The dishes were lined with wet blotting paper, and a portion of the paper was laid on the cut end of the stipe of the fern to prevent it from drying up during the investigation. The moistening of the paper was properly controlled by the subsequent occasional addition of a small quantity of distilled water by means of a pipette. After these treatments, the cover was put in place and the dish was laid in a dimly lighted place upon the laboratory desk for continued observation. The most convenient size of Petri dish was found to be 13 cm. in diameter and 3 cm. in depth. The method, by which the writer continued his experiments, corresponds apparently to that used by SALMON (1903, p. 212) with the powdery mildews or somewhat to that used by CLINTON and McCORMICK (1919) in the studies of *Cronartium ribicola* FISCH.

DE WALDHI. CLINTON and McCORMICK (1924, p. 477) advising their improved method with Petri dishes, said concerning the light condition that exposure to diffused light is less good than leaving in the direct sun light, there being advantage in overcoming the trouble with molds. The temperature in these experiments has already been mentioned above. Here it is interesting to refer to DORAN's work (1919) which treated of several rusts and in which it was reported that in the germination of the aecidiospores of *Cronartium ribicola*, the optimum temperature was 12°C and the maximum 19°C, while to the uredospores slightly higher temperatures were best suited. These grades of temperature agree respectively very well with the writer's observations. Concerning the length of the period in which the inoculated fern lives in a Petri dish under optimum condition, CLINTON and McCORMICK (1924) said "Not infrequently we have kept leaves green and alive for three or four weeks.... In one case a *Ribes* leaf, where a callus had formed and rootlets developed, remained alive for a couple of months." The writer also often found that the cut-off fern pinnae of *Dryopteris crassirhizoma* and other species could be kept alive during two months or more under favorable condition. Concerning the "disadvantage and advantage" of this method CLINTON and McCORMICK expressed themselves so fully that repetition in detail is not here needed. Briefly, in spite of the somewhat unnatural condition of the infected plants, the confirmations of the results of the aecidiospore and uredospore inoculations were in most cases sufficiently and accurately tested, because the incubation periods for the production of new sori were far shorter than the length of the alive condition of the fern leaves. Moreover, experiments by this method could be executed more easily and more concisely than by the pot method. ABE (1926) recognized similar merits of this Petri dish method when he made his inoculation experiments with *Cronartium quercuum* (COOKE) MIYABE and *Phragmidium Rosae-multiflorae* DIET. referring CLINTON and McCORMICK's publication in 1924.

1. *Uredinopsis Adianti* KOMAROV

Historical review of the fungus. KOMAROV first collected this rust in 1896 on *Adiantum pedatum* L. in Manchuria and the specimen was distributed as Fungi Rossiae Exsiccati no. 278. Afterwards, KOMAROV (1900), SACCARDO (1902), SYDOW (1915), HIRATSUKA, f. (1927 c, 1928 d, 1934 d and 1936 c), MIURA (1928), HIRATSUKA, f. and YOSHINAGA (1935), LIN (1937), FAULL (1938 b), and ITÔ (1938) published their taxonomic

studies. The life history has not been recorded except a short account made by the writer (1933).

Personal observations. Rusted fern. In the main island of Hokkaidô, the rust has been collected only from Prov. Ishikari. The first specimen that was found in our country, is that collected by Dr. NAOHARU HIRATSUKA at Jôzankei in November 1922. The writer himself gathered materials for the cultural experiments from year to year at the northern foot of Mt. Teine near Sapporo.

Uredospores. They push out from the small pustules as whitish masses. Usually the fresh spores are accompanied by a sticky substance, which was often observed under the microscope as shown in Pl. VII, fig. 1 a. Recently FAULL (1938 b) also mentioned this fact and remarked that it reveals a surprising and distinctive character hitherto unknown in the genus *Uredinopsis*. Germ pores are situated similarly as in other species.

Teleutospores. They are copiously detected just under the epidermis especially on the under surface of the discolored lesions. After the usual treatment of overwintered material, masses of basidia and basidiospores were seen covering the discolored lesions within three to four days. The basidiospores were more or less globular, measured 7.5–10.0 μ across and were colorless having smooth epispore.

Inoculations with basidiospores. Among four pots of *Abies Mayriana* and one pot of *A. sachalinensis*, successfully developed peridermia were gained in only one case as shown in Table 1.

TABLE 1. Inoculations with basidiospores of *U. Adianti*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 57	Basidiospores on <i>Ad. ped.</i> , Teine, Nov. 22, 1924	<i>A.M. I₅</i>	May 16, 1925	16	25	Corridor. Aecidia issued very abundantly (1)

(1) In those cases where no mention is made about the method of cultures it was always the pot method.

Inoculations with aecidiospores. With the aecidiospores obtained from the experiments mentioned above two sets of back inoculations were made as shown in Table 2. Positive results were obtained only on *Adiantum pedatum*, with negative results on each of five other ferns.

TABLE 2. Inoculations with accidiospores of *U. Adianti*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 51a	Accidio- spores on A.M. I ₅	<i>Adiantum pedatum</i>	Jc. 30, 1925	7	Petri dish
" b	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
" c	"	<i>Athyrium Vidalii</i>	"	—	"
" d	"	<i>Matteuccia Struthiopteris</i>	"	—	"
" e	"	<i>Woodsia polystichoides</i> var. <i>nudiusecula</i>	"	—	"
" f	"	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	"	—	"
" 59b	"	<i>Adiantum pedatum</i>	Jy. 13, 1925	10	"

The description of the peridermal phase of the present species is as follows:—

Uredinopsis Adianti KOMAROV in JACZEWSKI, KOMAROV and TRANZSCHEL, Fungi Ross. exsicc. no. 278, 1899.

Spermogonia on needles of current season, amphigenous, mostly hypophyllous, minute, inconspicuous, numerous, mostly on both sides of the midrib, honey yellow, irregularly and densely scattered on more or less discolored areas, often occupying whole surface of the leaf, isolated or confluent, situated between stomata, more or less elliptic in face view, in sections subcuticular, subconoidal to almost lens-shaped, scarcely or a little depressing the underlying epidermis, 88–165 μ broad, 55–77 μ high, averaging about 111.7 \times 61.8 μ ; apical pore mostly slit-like, parallel to long axis of the needle, 40–80 \times 16–32 μ ; spermatophores unbranched, obclavate, septate, convergent toward upper middle of the organ; spermatia narrowly ellipsoidal, 5–6 \times 1.2–1.6 μ , hyaline, smooth, colorless (Pl. IV, fig. a).

Aecidia on needles of current season, mostly hypophyllous, in two rows one on each side of the midrib, on more or less discolored parts of affected needles, closely produced or separated, white, cylindrical, up to 1 mm. high, 0.16–0.35 mm. across; peridia colorless, dehiscent at the apex; peridial cells rather firmly combined, polygonal to oblong, vertically elongated, overlapping, 20.9–41.8 \times 12.9–25.7 μ , averaging 31.97 \times 18.87 μ , with outer walls 1–2 μ thick, smooth, with inner walls 2.5–5.5 μ

thick, densely but rather stoutly verrucose; aecidiospores colorless, globose, ovoidal to ellipsoidal, $16-28 \times 13-26 \mu$, averaging $21.25 \times 18.66 \mu$, finely but closely verrucose, one side partly almost smooth; walls colorless, thin, up to 1μ thick including tubercles (Pl. VI, fig. a).

II and III have already been described by previous investigators such as the SYDOWS (1915), HIRATSUKA, f. (1936 c) and FAULL (1938 b).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures*)—in Japan (Hokkaidô).

II and III. *Adiantum pedatum* L.—in Japan (Shikoku and Hokkaidô), Manchuria and Ussuri.

2. *Uredinopsis Athyrii* KAMEI

Historical review of the fungus. This rust was established by the writer after successful inoculation experiments proving its life history. The diagnosis of the complete cycle of the fungus was for the first time published in 1932 b. Recently HIRATSUKA, f. (1932 c, 1936 c), FAULL (1938 b) and ITÔ (1938) referred to it and stated that it is found from Hokkaidô and Honshû of our country.

Personal observations. Rusted fern. In Hokkaidô, rusted specimens of *Athyrium Filix-foemina* ROTH var. *longipes* HARA have heretofore been collected from four provinces. Cultural materials for the sporidial inoculations were collected in August to November at the foot of Mt. Makkarinupuri in Prov. Iburi, where many seedlings as well as larger trees of *Abies Mayriana* grow rather densely above the undergrowth of many species of ferns.

Uredospores. The issuing of the spore masses was seen to take place even on specimens collected on Oct. 4 at Sapporo.

Teleutospores. In the germination abnormally elongated basidia attaining up to 220μ in length were found, though they were most commonly only 50μ long (cf. Pl. VII, fig. 2 e).

Inoculations with basidiospores. Among a total fifteen seedlings belonging to three species of *Abies*, seven of *A. Mayriana* were successfully inoculated producing spermogonia and aecidia as shown in Table 3. Spermogonia and aecidia were abundantly harvested on *A. Mayriana* IX₅ and I₈. The distribution of the organs on the affected needles is shown in Pl. II, fig. a. On some affected needles the parts where the spermogonia were produced were conspicuously constricted.

Inoculations with aecidiospores. With the aecidiospores produced

TABLE 3. Inoculations with basidiospores of *U. Athyrii*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of acid.	Remarks
				No. of days		
I. 21	Basidiospores on <i>Athyr. F.-f.</i> var. <i>longipes</i> , Mt. Makkari, Aug. 27, 1922	A.M. IX ₃	May 31, 1923	9	19	Greenhouse. First appearance of lesions occurred in 9 days
" 30	" Aug. 27, 1923	" V ₄	May 21, 1924	14?	21?	Greenhouse. A few acedia only were seen
" 42	"	" XV ₄	Je. 5, 1924	11	20	Greenhouse
" 65	" Nov. 12, 1924	" IX ₅	Je. 1, 1925	18	24	Corridor. 0 and I were very abundantly seen
" 74	"	" XVIII ₅	Je. 1, 1925	17	30	Outdoors
" 148	" Nov. 20, 1927	" I ₈	May 25, 1928	18	26	Laboratory. 0 and I were very abundantly seen
" 177	" Nov. 3, 1928	" XII ₉	Je. 9, 1929	14?	21?	Laboratory

on *Abies Mayriana* IX₃, XV₄, IX₅ and XII₉ inoculations were performed on six species of ferns. Resulting uredospores were seen in the cases of the proper host fern only as shown in Table 4. The inoculation on *Athyrium Vidalii*, the fern on which the related species of this rust, *U. daisenensis* HIRATSUKA, f. is parasitic, produced simply brownish discolorations within 3-7 days without forming any uredospores.

The description of the present species is as follows:—

Uredinopsis Athyrii KAMEI in Trans. Sapporo Nat. Hist. Soc. XII, p. 163, 1932.

Spermogonia on needles of current season, amphigenous, mostly hypophyllous, minute, inconspicuous, numerous, closely aggregated on discolored and more or less deformed areas, mostly on stomatal surface, especially situated between stomata, isolated or confluent, more or less elliptic in face view, margin rather entire, in sections subcuticular, slightly raised and superficial, conspicuously depressing the underlying epidermis, flattened conoidal to inverted hemispherical, 88-137.5 μ wide, 44.1-77.0 μ high, averaging 115.9 \times 61.9 μ ; apical pore mostly slit-like, parallel or oblique to long axis of the needle, 24-88 \times 12-32 μ ; spermatophores unbranched, obclavate, thickened at the basal part, convergent

TABLE 4. Inoculations with aecidiospores of *U. Athyrii*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
I. 20	Aecidio- spores on A.M. IX ₃	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	Jy. 4, 1923	12	Petri dish. Uredosori were very abundant
" 22(1)	"	"	Jy. 6, 1923	12	In greenhouse
" 22(2)a	"	"	"	6	Petri dish
" " b	"	<i>Matteuccia</i> <i>Struthiopteris</i>	Jy. 7, 1923	—	"
" " c	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
" " d	"	<i>Dryopteris Phegopteris</i>	"	—	"
" " e	"	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	"	—	"
" 36a	" XV ₄	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	Jy. 7, 1924	11	"
" " b	"	<i>Athyrium Vidalii</i>	"	?	" Discoloration appeared 3 days after, but no spores were seen
" 38	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	Jy. 10, 1924	—	Petri dish
" 43	"	<i>Athyrium Vidalii</i>	Jy. 22, 1924	?	Potted pl. in corridor. Dis- coloration appeared
" 54	" IX ₅	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	Jy. 1, 1925	—	" Observed until July 20
"	"	<i>Athyrium Vidalii</i>	Jy. 10, 1925	?	" Discolorations appeared after 7 days but no spores were seen
" 67	"	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	Aug. 10, 1925	12	Petri dish
" 91	" I ₈	"	Jy. 4, 1928	25?	"
" 27c	" XII ₆	"	Jy. 15, 1929	10	"

upward; spermatia more or less oblong to narrowly elliptic, 4.8–6.4 × 1.6–2.4 μ , averaging 5.8 × 1.9 μ , colorless, smooth (Pl. II, fig. a; IV, fig. b).

Aecidia on needles of current season, hypophyllous, isolated or closely formed, arranged in two rows one on each side of the midrib, on more or less discolored areas, occupying a part or whole of the leaf, white, cylindrical, 0.7–1.3 mm. high, 0.2–0.4 mm. across; peridia colorless,

rupturing at the apex; peridial cells rather firmly combined, overlapping, polygonal to ellipsoidal, $24.1-51.5 \times 11.3-25.7 \mu$, averaging $36.80 \times 17.64 \mu$, with inner walls coarsely verrucose, $3-7 \mu$ thick including tubercles, with outer walls smooth, $1-3 \mu$ thick; aecidiospores colorless, ellipsoidal to subglobose, $12-24 \times 10-20 \mu$, averaging $18.18 \times 16.15 \mu$, minutely verrucose except a part where almost smooth; walls thin, $0.5-3.0 \mu$ thick including tubercles (Pl. II, fig. a; IV, fig. b).

Uredosori hypophyllous, subepidermal, pustular, $0.1-0.2$ mm. across, scattered on yellowish to brownish discolored areas bounded by veins, especially near veins or marginal portions, sometimes on stipes, minute, round, covered with discolored epidermis; peridia colorless, delicate, more or less hemispherical, rupturing by a central slit; cells more or less polygonal, $12.0-18.0 \times 5.0-14.0 \mu$, averaging $12.68 \times 8.76 \mu$; walls of peridial cells about 1μ thick, hyaline, smooth, overlapping; uredospores colorless, white in mass, pushing out in filamentary tendrils, short stalked, fusiform, clavate, ellipsoidal or obovoidal, sometimes beakless and flattened or rounded at the apex, sometimes with short beak, $2-5 \mu$ long, $21-40 \times 10-15 \mu$, averaging $29.73 \times 12.39 \mu$; walls thin, about 1μ , very obscurely verrucose except two longitudinal ridges formed of minute papillae, apparently smooth in wet mounts; germ pores in pairs near both ends (Pl. III, fig. b; VII, fig. 2 a and b).

Teleutosori on fronds of current season, amphigenous, mostly hypophyllous, on discolored areas of indefinite extent; teleutospores intercellular, mostly just under the epidermis, compactly aggregated or isolated, globose to subglobose, colorless, $16-37 \times 13-25 \mu$, $1-7$ celled with vertical septa, mostly $2-4$ celled; walls thin, 1μ thick, colorless, smooth; basidiospores subglobose, $7-11 \mu$ across, colorless, smooth (Pl. VII, fig. 2 c, d and e).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures*)—in Japan (Hokkaidô).

II and III. *Athyrium Filix-foemina* ROTH var. *longipes* HARA—in Japan (Hokkaidô).

3. *Uredinopsis filicina* MAGNUS

Historical review of the fungus. This rust on *Dryopteris Phegopteris* C. CHR. was first described by C. NIESSL (MAGNUS, 1892) interogatively as a species of *Protomyces*. Afterwards, it was considered a species of *Gloeosporium* (FRANK, 1880, SACCARDO, 1884, 1892, ALLE-

SCHER, 1901) and of *Uredo* (WINTER, 1881). In 1892, MAGNUS established the new genus *Uredinopsis* basing on this rust and considered it to belong to *Phycomycetes* and not to the rust. Three years later, DIETEL incorporated this species into *Melampsoraceae*. Since that time, it has been treated as a rust fungus by many mycologists such as SACCARDO (1895), DIETEL (1895, 1897, 1928), FISCHER (1904), HARIOT (1908), BUBÁK (1908), LIRO (1908), TROTTER (1908), GROVE (1913), KLEBAHN (1914), SYDOW (1915), HIRATSUKA, f. (1936 c), FAULL (1938 b), ITÔ (1938) and others and is known to be widely distributed over the old continents throughout the northern hemisphere. In our country, the first publication of this rust was made by Dr. TOGASHI (1924) who had collected the specimens from Rebun Island, Hokkaidô. According to the subsequent reports made by HIRATSUKA, f. (1927 c, 1933 a), however, specimens were collected early in 1900 by Drs. YAMADA and HIRATSUKA respectively at Sapporo, and also by Drs. YAMADA and HANZAWA at Nikkô in Honshû. HIRATSUKA, f. (1927 b, 1929 b, 1930 a, 1934 d, 1935a, 1935 g, 1936 c) and HIRATSUKA, f. & YOSHINAGA (1935) made many collections of the present rust in the main island of Hokkaidô, southern Saghalien, Honshû, Shikoku and Korea. NAGAI and SHIMAMURA (1933) collected specimens in Kunashiri of the Kuriles. So far as the writer is aware, however, no cultural life history study of this rust has yet been reported except that in the brief notes of the writer himself (1932 b, 1933).

Personal observations. Rusted fern. While the host fern, *Dryopteris Phegopteris* is distributed widely throughout the island of Hokkaidô, the rusted materials have been found only from six provinces. Among 29 specimens examined by the writer, the August collections counted 12, September gatherings 11, while the earliest collection in a season was that of July 17. The inoculation materials onto *Abies* were obtained at Mt. Makkarinupuri and Lake Shikaribetsu where the host fern is growing associated with *Abies*.

Uredospores. Germination of the uredospores and position of the germ pores were observed to be similar to those of the related species that have already been investigated.

Amphisporae. Observations on the germination of the amphisporae of this rust were attempted by MAGNUS (1892) without success, but DIETEL (1895) made suggestions on its possible occurrence. If pieces of overwintered affected leaves bearing amphisporic sori were laid moistened in a wet chamber, usually after about 24 hours, there was

obtained a powdery whitish mass of spores protruding from the apical fissure of the pustule as already shown by WINTER (MAGNUS, 1892). For experiment, with clean needles bits of the spore mass were transferred into small drops of distilled water that were placed on the under surface of a host frond which was placed inside of a Petri dish. After about a day, by inspection of these drops under the microscope it was found that a certain number of the amphispores had germinated by tube from each corner of the spores, and in one case it was seen that the germ-tube had already branched into two small hyphae as shown in Pl. VII, fig. 3 c. The writer was able to see one to three tubes emerging from separate germ pores of a spore though the total number of pores was not determined. In many spores of this condition, both germinated and intact, the epispores were stretched by the increment of the contents induced by the absorption of water and often many vacuoles were seen surrounded with plasma. These conditions of the spores have already been illustrated by MAGNUS (1892, Pl. IX, figs. 3 and 4). It is very natural that he considered that the fungus was a Phycomycetes, because the features somewhat resemble the formation of the zoospores inside of a zoosporangium. Inoculation experiments with the amphispores thus obtained were performed in Petri dishes as well as with potted plants. The spore masses were smeared on the under surface of a fresh frond of *Dryopteris Phegopteris* by means of a clean needle. After 10-14 days, the primary uredospores appeared as shown in Table 5. So far as the successful inoculation experiments with the amphispores of this rust are concerned, there is no report up to this day except that of the writer. FAULL (1938 b, p. 7) said: "A test that settled the matter in part was

TABLE 5. Inoculations with amphispores of *U. filicina*

Exp. no.	Inocula	Date of inoc.	App. of uredos.	Remarks
			No. of days	
III. B 14'	Amphispores on <i>Dr. Pheg.</i> , Mt. Makkari, Aug. 28, 1922	Je. 2, 1923	+ (?)	Inoculated on <i>Dryopteris Phegopteris</i> in pot. In greenhouse
" 15'	" Aug. 27, 1923	May 16, 1924	10	"
" 19'	"	May 21, 1924	13	"
" 17'	"	"	14	"
" 21	Shikaribetsu, Sept. 30, 1929	Jy. 7, 1930	14	Inoculated on <i>Dryopteris Phegopteris</i> in Petri dish

eventually made by KLEBAHN (34). He sowed overwintered 'stylospores' of *U. filicina* on new leaves of their fern host in the spring." KLEBAHN (1916) had made such a test concerning *U. Struthiopteridis* but not concerning *U. filicina*.

Teleutospores. A successful attempt to observe the germination of the teleutospores of this species was first performed by DIETEL (1895). According to the present writer's observation, the germination of the teleutospores inside of overwintered materials occurred from the end of April to the latter part of May. In such a case, a stalk of the promycelium issued from each single pore on the upper wall of the cells of the teleutospores, and the length of the promycelia attained to 90μ . The basidiospores measured 4.5–7.4 by $4.8\text{--}8.1\mu$.

Inoculations with basidiospores. According to the present experiments, as shown in Table 6, after the usual procedure of inoculations on 14 seedlings of *Abies Mayriana* and 1 of *A. sachalinensis*, the spermogonia as well as the aecidia were produced on seedlings nos. II₃, X₃, X₈, IV₁₀ and XII₁₀ of *Abies Mayriana*. The aecidia were completely developed within 19–28 days. Usually after about a week to ten days the yellowish discolorations appeared. As shown in Pl. II, fig. b, the

TABLE 6. Inoculations with basidiospores of *U. filicina*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 14	Basidiospores on <i>Dr. Pheg</i> , Aug. 29, 1922, Mt. Makkari-nupuri	A.M. II ₃	May 21, 1923	?	28	Greenhouse. 0 and abundantly cropped
" 22	"	" X ₃	Je. 2, 1923	?	21	Greenhouse
" 144	" Teine, Oct. 1926	" XII ₇	Je. 19, 1927	22?	—	Laboratory
" 157	" Sept. 20, 1927	" X ₈	Je. 4, 1928	12	22?	" Aecidia scantily harvested
" 183	" Shikaribetsu, Sept. 30, 1929	" IV ₁₀	Je. 3, 1930	14	21	Laboratory
" 191	"	" XII ₁₀	Je. 7, 1930	12	19	"

discolored area, in which spermogonia were produced, was always more or less distorted. The aecidial cups on the other hand generally appeared first on still green healthy looking portions.

Inoculations with accidiospores obtained from cultures. With the accidiospores thus gained from cultures were made further inoculations resulting as shown in Table 7. The ordinary uredospores issued within 11–15 days both in the case of inoculated plants laid in Petri dishes and of potted ones. On the proper host fern, the uredospores were readily obtained, but on other ferns such as *Matteuccia Struthiopteris*, *Thelypteris palustris* var. *pubescens*, *Athyrium Filix-foemina* var. *longipes* and *Pteridium aquilinum* var. *japonicum* the results were all negative.

TABLE 7. Inoculations with accidiospores of *U. flicina*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 19	Accidiospores on A.M. II ₃	<i>Dryopteris Phegopteris</i>	Jy. 6, 1923	11	Petri dish
" 21a	"	"	"	15	Potted pl. in greenhouse
" b	"	<i>Matteuccia Struthiopteris</i>	"	—	"
" c	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
" d	"	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	"	—	"
" e	"	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	"	—	Planted pl.

The description of the peridermal phase of this species is as follows:—

Uredinopsis flicina MAGNUS in Atti d. Congr. Bot. Intern. (1892) p. 167, 1893.

Syn. *Protomyces* (?) *flicinus* NIESSL in RABENHORST'S Fungi Eur. no. 1659, 1873.

Uredo Polypodii PERS. f. *Phegopteris* WINTER in Pilze Deutsch. I, p. 253, 1881.

Gloeosporium Phegopteridis PASS. in Rev. Myc. II, 36, 1880; Sacc. Syll. Fung. III, p. 721, 1884.

G. Phegopteridis FRANK, Krankh. Pflanz., p. 611, 1880; Sacc. Syll. Fung. X, p. 463, 1892.

G. Frankii ALLESCHER, Pilze Deutsch. VII, p. 494, 1901.

Spermogonia on needles of current season, amphigenous, mostly hypophyllous, closely aggregated, isolated or often confluent, minute, numerous, inconspicuous, mostly between stomata of discolored and distorted stomatiferous areas, more or less elliptic in face view, margin rather sinuated, subcuticular, lenticular to inverted hemispherical in sectional view, $52.5-118.5\mu$ broad, $25.2-64.5\mu$ high, averaging $82.2 \times 48.1\mu$; apical pore mostly slit-like, parallel to long axis of the needle, $24-96 \times 12-32\mu$; spermatophores unbranched, rather obclavate, septate, convergent; spermatia oblong or narrowly ellipsoidal, $4.8-6.4 \times 1.9-2.4\mu$, colorless, smooth (Pl. II, fig. b; IV, fig. c).

Aecidia on needles of current season, hypophyllous, in two rows on yellowish discolored areas, occupying a part or whole of the leaf, white, cylindrical, 0.18–0.35 mm. across, 0.8–1.3 mm. high; peridia colorless, firm, rupturing at the apex; peridial cells tetragonal to hexagonal, often rounded at margin, somewhat elongated vertically, slightly overlapping, $28.8-48.3 \times 14.5-25.7\mu$, averaging $38.09 \times 19.22\mu$, with inner walls $3-6\mu$ thick including tubercles, coarsely and distinctly verrucose, sometimes a little striated, with outer walls $0.5-1.0\mu$ thick, smooth; aecidiospores colorless, globose to ellipsoidal, $12-24 \times 10-22\mu$, averaging $18.96 \times 16.44\mu$, densely but finely verrucose except a part where almost smooth; walls thin, up to 2μ thick including tubercles, colorless (Pl. II, fig. b; VI, fig. c).

II and III are as already described by previous authors such as FISCHER (1904), SYDOW (1915), HIRATSUKA, f. (1936), FAULL (1938 b) and Itô (1938).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDô (*Cultures*)—in Japan (Hokkaidô).

II and III. *Dryopteris Phegopteris* C. CHR.—in Japan (Honshû, Hokkaidô and Saghalien), Eastern Siberia, Ussuri and Europe.

4. *Uredinopsis hirosakiensis* KAMEI et HIRATSUKA, f.

Historical review of the fungus. The description of this rust on *Thelypteris palustris* var. *pubescens* was first presented by the writer (1932 b) based on the type material that was collected by Dr. NAOHARU HIRATSUKA at Hirosaki, a northern town of Honshû of our country. Recently Dr. NAOHIDE HIRATSUKA (1932 c, 1935 a, 1936 c), junior author of this rust announced that seven provinces of Honshû, six of Hokkaidô, two of Korea as well as Ussuri may be listed as its localities. Very

recently, FAULL (1938 b) and ITÔ (1938) redescribed this rust. The writer (1934) reported on injuries to fir seedlings by the peridermal phase of this rust occurring in forest nurseries.

Personal observations. Rusted fern. The materials for cultural experiments with the basidiospores were collected in the previous autumn always at the same place situated by the side of small brook at Sôen, Sapporo. The affected tissue of the fern host became yellowish at first in an area sharply restricted by the veins and veinlets, then turned into a brownish color making a distinct contrast with the fresh green portion showing a fine arrangement of variegated colors.

Uredospores. They pushed out from the fissures of the host stomata as powdery white masses and rarely as filamentary tendrils which must be attributed to the characters of the membrane of the spores. At maturity, uredospores germinated soon by means of slender germ-tubes issuing from both sides near the apex and the base of the spores (Pl. VII, fig. 7 b). The number of germ-pores varied from three to five.

Teleutospores. As the teleutospores of this species developed soon after the appearance of the uredosori, so all the specimens inspected revealed that both spore forms were found together. The germination of the teleutospores was observed after two to five day's dipping of the overwintered rusted pinnae in the water and about a day's exposure to air. An abundant mass of basidiospores and basidia was seen as a thin layer covering the lesions. Some elongated basidia were seen to attain to 70μ and the basidiospores were somewhat globose and hyaline but never provided with a colored pigment as seen in the case of some species of *Pucciniastrum*, to which there is much similarity in the morphology of the uredospores.

Inoculations with basidiospores. Among 18 plants belonging to two species of *Abies*, successful infection was obtained only on nine cases of *Abies Mayriana* as shown in Table 8. Among them, in the successful cases, yellow spots were seen usually within about ten days. Spermogonia appeared normally within 8 to 16 days and the aecidia within 19-24 days after the inoculation.

Inoculations with aecidiospores obtained from cultures. With the aecidiospores formed on *A. Mayriana* X₂, III₃ and VIII₅, inoculation experiments were performed on various ferns on which uredospores of this as well as of related species of rusts have been detected in the field. In the case of the proper host, *Thelypteris palustris* var. *pubescens*, the uredopustules issued after 8 to 13 days (rarely later). In the other

TABLE 8. Inoculations with basidiospores of *U. hirosakiensis*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of acid.	Remarks
				No. of days		
I. 10	Basidiospores on <i>Th. pal. v. pub.</i> , Sapporo, Oct. 1, 1921	<i>A.M.</i> X ₂	Je. 9, 1922	?	21	Greenhouse
" 15	" Sept. 30, 1922	" III ₃	May 24, 1923	?	20	"
" 64	" Oct. 31, 1924	" VIII ₅	Je. 1, 1925	8	24	Corridor
" 80	" "	" XXI ₅	Je. 12, 1925	28?	—	Out-of-doors
" 97	" Nov. 15, 1925	" VI ₃	Je. 8, 1926	?	23	Laboratory
" 149	" Aug. 1927	" II ₃	May 27, 1928	16	24	"
" 181	" Nov. 15, 1929	" II ₁₀	Je. 3, 1930	?	23	"
" 190	" "	" XI ₁₀	Je. 7, 1930	12	19	"
" 234	" Nov. 19, 1931	" V ₁₃	Je. 5, 1932	?	—	"

ferns inoculated, though in some cases discolorations appeared, successful formation of the uredopustules did not eventually happen in any of them. In the case of these inoculations it was possible to observe the germination of the aecidiospores. The germ-tube was seen to attain to 550–700 μ in length five days after the sowing, when the temperature varied from 10° to 12°C.

Inoculations with aecidiospores collected from the field. In the first part of July 1933, in a nursery at the Tomakomai Experimental Forest of the University the writer found many tiny seedlings of *Abies Mayriana* (Fig. 6 a & b) attacked by the peridermal phase of this rust. Careful morphological comparison with the materials gained from the artificial cultures and several check inoculation experiments with the aecidiospores were made for identification as already reported by the writer (1934). Several specimens of uredo and teleutostages were collected at the near neighborhood of the nursery bed and the facts confirmed the assumption that they were the result of infection by the peridermal phase of this rust.

The description of the species under consideration is as follows:—

Uredinopsis hirosakiensis KAMEI et HIRATSUKA, f. in KAMEI in "Trans. Sapporo Nat. Hist. Soc. XII, p. 104, 1932.

Syn. *Pucciniastrum Dietelianum* HIRATSUKA in HIRATSUKA, f. in Memoirs Tottori Agricul. Coll. IV, p. 84, 1936.

TABLE 9. Inoculations with acidiospores of *U. hirosakiensis*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 3	Acidiosp. on <i>A.M.</i> X ₂	<i>Thelypteris palustris</i> var. <i>pubescens</i>	Jy. 4, 1922	8	Potted pl. in greenhouse
7	"	"	Jy. 22, 1922	23?	"
8	" III ₃	"	Je. 16, 1923	?	Petri dish. Discoloration occurred 4 days later without spore formation
9	"	"	Je. 16, 1923	13	Petri dish
18a	"	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	Je. 28, 1923	—	Planted pl. Decayed after three days
"	"	<i>Matteuccia Struthiopteris</i>	"	—	Potted pl. in greenhouse
"	"	<i>Dryopteris Phegopteris</i>	"	—	" Small brown spot was seen
18b	"	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	Jy. 1, 1923	—	"
18c	"	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Jy. 4, 1923	—	Petri dish
52	" VIII ₅	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	Jy. 1, 1925	—	Planted pl.
61	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	Jy. 13, 1925	10	Petri dish
IV. 23a	" Tomakomai, Jy. 10, 1933	"	Jy. 12, 1933	10	Potted pl. Slight discoloration occurred after 8 days. New uredosori found after 14 days
" 23b	"	"	Jy. 16, 1933	5	Petri dish
" 23c	"	"	Jy. 22, 1933	7	"

Pucciniastrum Thelypteridis TRANZSCHEL in HIRATSUKA, f. in Memoirs Tottori Agricul. Coll. IV, p. 84, 1936.

Spermogonia on needles of current season, amphigenous, mostly hypophyllous, minute, inconspicuous, abundant, irregularly and closely scattered on yellowish discolored and deformed areas, isolated or confluent, situated between stomata, oblong, circular to polygonal in face view, margin irregularly wavy, subcuticular, raised slightly above the surface of the needle, more or less conoidal to almost hemispherical, in

sections often a little depressing the tissue beneath, 74–137 μ broad, 37–92.5 μ high, averaging 109.4 \times 64.6 μ ; apical pore a stoma or slit-like, mostly parallel to long axis of the leaf, 48–104 \times 12–64 μ ; spermatophores unbranched, obclavate, septate, convergent toward upper middle; spermatia oblong or ellipsoidal, 4.8–6.4 \times 1.6–2.7 μ , averaging 5.6 \times 1.9 μ , hyaline, smooth (Pl. II, fig. c; IV, fig. d).

Aecidia on needles of current season, rarely amphigenous, mostly hypophyllous, in two rows one on each side of the midrib, sparsely arranged on more or less discolored areas, cylindrical, rather flattened, white, 0.2–0.6 mm. across, 0.6–1.2 mm. high; peridia colorless, rupturing at the apex; peridial cells ovate to obovate, overlapping, fragile, easily separable from each other, 20.8–40.2 \times 8.1–24.1 μ , averaging 27.4 \times 14.5 μ , with inner walls 2.0–4.0 μ thick, finely striated or alveolated, with outer walls 0.6–1.0 μ thick, smooth; aecidiospores colorless, globose to ovate, 13–32 \times 12–20 μ , averaging 17.83 \times 16.24 μ , minutely verrucose except a small part where almost smooth; walls thin, up to 2 μ thick including tubercles, colorless (Pl. II, fig. c; VI, fig. d; Fig. 6 a and b).

Uredosori hypophyllous, subepidermal, scattered or in groups on yellowish discolored areas, restricted by veins or indefinitely extended, especially near veins or margin, sometimes on stipes, round, small, 0.1–0.3 mm. across, covered with pale yellowish discolored epidermis; peridia delicate, colorless, depressed hemispherical to subconoidal, ruptured at the apex; peridial cells small, hyaline, irregularly polygonal, 6.5–15.0 \times 9.0–10.7 μ , averaging 12.41 \times 9.94 μ ; walls of peridial cells thin, about 1 μ , smooth, hyaline; uredospores colorless, issuing in white powdery spore mass, short stalked, ovoidal to ellipsoidal, 16–29 \times 12–23 μ , averaging 22.8 \times 18.1 μ ; walls thin, about 1 μ , colorless, sparsely but minutely echinulated; contents hyaline; bladder cells present (Pl. III, fig. c; VII, fig. 7 a and b).

Teleutosori on fronds of current season, amphigenous, on indefinitely extended discolored areas; teleutospores intercellular, abundant, more or less compactly arranged just under the epidermis, often in a single layer, rarely scattered in the mesophyll tissue, globoid to ellipsoidal, colorless, 17.5–40.0 \times 15.5–29.0 μ , mostly 2 to 4 celled (sometimes 1 to 6 celled) with more or less vertical septa; walls thin about 1 μ , smooth, hyaline; basidiospores subglobose, 7.5–11.0 μ across, smooth, colorless (Pl. VII, fig. 7 c and d).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures and field*)

—in Japan (Hokkaidô).

II nad III. *Thelypteris palustris* SCHOTT var. *pubescens* FERNALD—in Japan (Honshû and Hokkaidô) and Ussuri.

5. *Uredinopsis Kameiana* FAULL

Historical review of the fungus. This species was quite recently established by FAULL (1938 b). He made a close comparative study on two rust forms on *Pteridium aquilinum* and *Abies* which are found in Western America and Japan. As a result he came to the conclusion that the Western American form which is lacking amphispores and related to *Peridermium pseudobalsameum* ARTH. et KERN is *Uredinopsis Pteridis* DIET. et HOLW. with which *U. macrosperma* MAGNUS is synonymous. The Japanese form, which has narrower uredospores, amphispores and a quite distinct aecidial phase, is a new species, to which FAULL gave the name of *U. Kameiana*. Heretofore, in this country except cases in Formosa whence *U. macrosperma* were recorded by HIRATSUKA, f. (1936 c) and ITÔ (1938), the rust on *Pteridium aquilinum* has been known under the designation of *U. Pteridis*. It was TOKUBUCHI (1911) who first drew attention to the presence of the species in Japan. HARA collected the same fungus in the same year in Prov. Mino and sent it to the Sydows who published it in 1912 in their *Fungi Exotici exsiccati* no. 224. Since then, references to the fungus by the name of *U. Pteridis*, have been made by IDETA (1911), FUJIKURO (1914), SHIRAI (1917, 1927), SAWADA (1928), TOGASHI & HIRATSUKA, f. (1924), ITÔ & HIRATSUKA, f. (1927), MIURA (1928), HIRATSUKA, f. (1927 c, 1928 d, 1929 b, 1930 a, 1930 d, 1932 b, 1935 a, 1935 f, 1936 c), KAMEI (1930 a), HIRATSUKA, f. & YOSHINAGA (1935) and ITÔ (1938). Thus the rust was reported from "Formosa, Hokkaidô, Honshû, Shikoku, Korea and South Saghalien" according to HIRATSUKA, f. (1936 c). Although these collections have not yet been completely inspected by the present writer, he is inclined to believe that the larger part of the specimens belong to *U. Kameiana*. On the life history of the present species, under the name of *U. Pteridis*, the writer (l. c.) has published a paper, in which he discussed his experimental data compared with the results reported in North America.

Personal observations. Rusted fern. In Hokkaidô, the rusted materials have been obtained from six provinces. Special materials used for the cultural works were mostly obtained from the same location at the northern entrance to the Nopporo Forest. Some of them were

collected at Kaributo in the Prov. of Iburi and also in the vicinity of Sapporo. A collection from Prov. Echigo gathered by Mrs. Dr. YASU IGUCHI (née HOMMA) was also used.

Uredospores. The pustules containing ordinary uredospores were comparatively large. They appeared near the veins or margins of the pinule and sometimes also on the stipe. The areas where these sori were found were discolored little at first but gradually changed into brownish patches. Whitish uredospores pushed out in a mass from an apical pore or slit or frequently from an irregular, sub-basal, lateral slit. Germ-pores were four in number, as shown in Pl. VII, fig. 4 a. The uredospores measured by the writer were $25-53 \times 11-19 \mu$, averaging $37.31 \times 15.21 \mu$.

Amphisporos. The writer found that amphisporos are generally seen on those specimens collected in the latter part of the season, but also once on the material that was collected on July 23rd by Prof. S. Irô in Prov. Echigo, which is the earliest one among forty specimens examined. FAULL (1938 c) pointed out the prevalent production of amphisporeic sori which so soon replaces that of ordinary uredosori. From the overwintered affected fronds, amphisporos were obtained in pure masses by moistening the materials. They were somewhat thick-walled and colorless, being whitish in mass. The contents of the spores in such a condition became turgid, vacuoles appearing abundantly. With these amphisporos the inoculation experiments on *Pteridium* host were successfully carried out producing ordinary uredospores after 11 days as shown in Table 10. These experimental results proved the

TABLE 10. Inoculations with amphisporos of *U. Kameiana*

Exp. no.	Inocula	Date of inoc.	App. of uredos.	Remarks
			No. of days	
III, B 22	Amphisporos on <i>Pteridium aquilinum</i> var. <i>japonicum</i> , Nopporo, Oct. 1932	Je. 21, 1933	11	Inoculated on <i>Pteridium aquilinum</i> var. <i>japonicum</i> in Petri dish

autoecious life cycle of this rust, explaining the fact that in the field the affected fronds of the host fern are found year after year in the same place where there is no tree of *Abies* near by. The writer observed such a case repeatedly.

Teleutospores. The portion of the diseased fern in which teleuto-

spores occur was seen to be slightly shrunken. The spores were mostly formed subepidermally in the lower surface of the frond, but sometimes also on the upper surface. Under certain conditions of the host plant, they seemed to be formed within a short period after the infection, because the writer once saw some number of newly formed teleutospores a week after the aecidiospore inoculation. Two to three days after the usual treatment of overwintered affected materials, the germination of teleutospores was indicated by a whitish film-like covering formed on the discolored portions. In this condition, the stalk of the promycelia was seen to attain to about 100μ in length, and the globular sporidia were seen to be abundantly formed measuring $7.5-11 \times 6.5-7.5\mu$ as shown in Pl. VII, fig. 4 d.

Inoculations with basidiospores. For the inoculated plants, three species of *Abies* not indigenous to Hokkaidô were used, namely, *Abies holophylla* MAXIM., *A. nephrolepis* MAXIM. and *A. balsamea* MILL. besides *A. Mayriana*. As shown in Table 11, among a total of 29 pots of seedlings of the four species of *Abies* used for repeated experiments through succeeding seasons, the writer obtained positive results in 22 pots (12 pots of *Abies Mayriana*, 2 of *A. holophylla*, 1 of *A. nephrolepis* and 7 of *A. balsamea*). In the case of *A. Mayriana*, the spermogonia appeared within 10-18 days and the peridermia within 20-25 days after the inoculations. On *A. balsamea*, which is common in North America, the period of the appearance of the spermogonia as well as of the peridermia was longer than in the other species, at most two weeks longer. Moreover, the effect on the host needles affected was more disastrous showing more marked distortion of the diseased needles. In the case of *Abies holophylla* and *A. nephrolepis* in the writer's experiments somewhat similar features were also observed but the degree was very slight.

Inoculations with aecidiospores. With the resulting aecidiospores obtained in the above described experiments on *A. Mayriana* V₃, XIV₄, VII₅, III₁₁, VIII₁₃, *A. balsamea* VI₁₃ and *A. holophylla* III₁₃, series of back inoculations were made on fronds of each of *Pteridium aquilinum* var. *japonicum* as well as of 17 other species of ferns during several succeeding seasons. As shown in Table 12, in the case of the inoculations with the aecidiospores on *Abies Mayriana* and *A. holophylla*, resulting uredospores issued respectively within 7-13 days after the inoculation both in the inoculated plants in pots and in Petri dishes. But in the case of other species of ferns no resulting spores appeared, although in some cases some discolored lesions did appear on the inoculated portions.

TABLE 11. Inoculations with basidiospores of *U. Kameiana*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of acid.	Remarks
				No. of days		
I. 17	Basidiospores on <i>Pt. aquil.</i> var. <i>jap.</i> Nopporo, Oct. 22, 1922; Maruyama, Sept. 22, 1922	<i>A.M.</i> V ₃	May 26, 1923	10	21	Greenhouse
" 41	" Nopporo, Oct. 14, 1923	" XIV ₄	Je. 5, 1924	11	21	"
" 63	" Ninoji, Prov. Echigo, Oct. 10, 1924, Y. HOMMA	" VII ₅	Je. 1, 1925	18	25	Corridor. Abundant acidia were harvested
" 136	" Nopporo, Oct. 1926	" IV ₇	Je. 9, 1927	26?	33?	Laboratory
" 151	" Oct. 22, 1927	" IV ₈	May 27, 1928	16	24	"
" 185	" Oct. 13, 1929	" VI ₁₀	Je. 3, 1930	15	23	"
" 186	"	" VII ₁₀	Je. 3, 1930	15	23	"
" 205	" May 31, 1931	" III ₁₁	Je. 4, 1931	14	22	"
" 206	"	" IV ₁₁	Je. 4, 1931	14	22	"
" 260	" Oct. 1932	" VII ₁₃	Je. 2, 1933	12	—	"
" 265	"	" VIII ₁₃	Je. 4, 1933	12	20	" Very abundant acidia were harvested
" 267	"	" IX ₁₃	Je. 5, 1933	17	29?	"
" 249	"	<i>A. helophylla</i> II ₁₃	May 30, 1933	13	25	"
" 274	"	" III ₁₃	Je. 7, 1933	(?)	40	"
" 250	"	<i>A. nephrolepis</i> I ₁₃	May 30, 1933	13	—	"
" 251	"	<i>A. balsamea</i> III ₁₃	May 30, 1933	23	48	"
" 254	"	" IV ₁₃	May 31, 1933	24	29	"
" 258	"	" V ₁₃	"	30	—	"
" 259	"	" VI ₁₃	Je. 1, 1933	22	—	"
" 262	"	" VIII ₁₃	Je. 2, 1933	(?)	46	"
" 266	"	" IX ₁₃	Je. 4, 1933	18	—	"
" 268	"	" X ₁₃	Je. 5, 1933	17	42	"

In the case of the acidiospores formed on *A. balsamea*, the inoculation experiments on the proper host fern showed eventually no uredospores. The result does not necessarily indicate that the inocula used for the experiment were impure because the morphological characters of the

peridial cells and the aecidiospores correspond exactly to those formed on the needles of *A. Mayriana* III₁₃ and V₁₃.

Inoculations with the aecidiospores from the field. On July 3, 1934, at the Teshio Experimental Forest of our University, the writer found some white peridermia attacking the needles of an about one meter high seedling of *A. sachalinensis*. After returning to Sapporo, the writer by examining the peridermia could identify it with the rust in question. Inoculations with the aecidiospores were made at once. After 4–6 days from the treatment, the discolorations appeared and the first uredopustule was observed after ten days in each of three dishes used (cf. Table 12, Exp. IV, 41). In July 1936, another specimen of the affected shoots of *A. sachalinensis* which was collected in the Teshio Forest was handed to the writer by Mr. AIZAWA of the Hokkaidô Government. After the identification of the spermogonia and the aecidia of the specimen as belonging to this species, inoculations with the aecidiospores on *Pteridium* were immediately performed. The resulting uredospores appeared after 6–8 days (cf. Table 12, Exp. IV, 51). In this case, at the inspection of the inocula, some spores were found to have germinated about one day after the treatment, as shown in Figure 2.

Comparison with the aecidial phase of U. Pteridis. Aecidiospores on the second year needles of *Abies grandis* and *A. lasiocarpa* in Western America were used by WEIR and HUBERT (1917) for successful infection experiments on bracken fern. They identified it as *U. Pteridis*. The aecidial phase, however, was recognized by JACKSON (1918), BELL (1924), ARTHUR (1925), HUNTER (1927), FAULL (1929) and HUBERT (1931) as *Peridermium pseudobalsameum*. FAULL (1938 b) recently said that he inspected the materials of WEIR and HUBERT's investigation under question and came to the conclusion that the inocula was *P. pseudobalsameum* and the resulted uredospores were those of *U. Pteridis*. Although the present writer had assumed our rust in question as similar to *U. Pteridis*, he was deeply impressed by the conspicuous differences in the morphological as well as the biological characters existing between WEIR and HUBERT's aecidial phase and that derived from his own culture experiments. Fortunately, through the generous courtesy of Professor J. C. ARTHUR the writer had a good opportunity to examine a part of the very specimen with which WEIR and HUBERT performed their inoculation experiments as well as a part of the type specimen of *P. pseudobalsameum*.

Just as FAULL (1938 b) has stated, the present writer also was able

TABLE 12. Inoculations with aecidiospores of *U. Kameiana*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 10	Aecidio- spores on <i>A. M.</i> V ₃	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	Je. 21, 1923	12	Planted pl.
" 41	XIV ₄	"	Jy. 17, 1924	10	Petri dish
" 64	VII ₅	"	Jy. 20, 1925	—	" Inoculated pl. decayed on Aug. 3
" 100	" III ₁₁	"	Jy. 14, 1931	7	Petri dish
" 105	" VIII ₁₃	"	Jy. 4, 1933	10	"
" 106	" <i>A. bals.</i> IV ₁₃	"	Jy. 17, 1933	—	" Inoculated pl. showed dis- coloration on Aug. 3, but no spores
" 107	" <i>A. hcloph.</i> III ₁₃	"	Jy. 14, 1933	13	Petri dish
" 108	" <i>A. M.</i> VIII ₁₃	"	Jy. 17, 1933	10	"
" 10	" V ₃	<i>Matteuccia Struthiopteris</i>	Je. 21, 1923	—	Potted pl. in greenhouse. Observation continued up to July 28
"	"	<i>Dryopteris Phegopteris</i>	"	—	Potted pl. in greenhouse
"	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
"	"	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	"	—	"
" 100	" III ₁₁	<i>Onoclea sensibilis</i>	Jy. 14, 1931	—	Petri dish
"	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
"	"	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	"	—	"
"	"	<i>Matteuccia Struthiopteris</i>	"	—	"
"	"	<i>Adiantum pedatum</i>	"	—	"
"	"	<i>Dryopteris Phegopteris</i>	"	—	"
" 105	" VIII ₁₃	"	Jy. 4, 1933	—	"
"	"	<i>Osmunda cinnamomea</i>	"	—	"
"	"	<i>Polystichum tripterum</i>	"	—	"
"	"	<i>Osmunda japonica</i>	"	—	"
"	"	<i>Dryopteris crassirhizoma</i>	"	—	"
"	"	<i>Athyrium acrostichoides</i>	"	—	"
IV. 41a	" <i>A. sach.</i> , Teshio, Jy. 3, 1934	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	Jy. 10, 1934	10	" Discolora- tion occurred 4 days later
" 41b	"	"	"	10	Petri dish
" 41c	"	"	"	10	"
" 51	" <i>A. sach.</i> , Teshio, Jy. 26, 1936 T. Aizawa	"	Jy. 24, 1936	8	" Uredo- spores in spore- mass were seen after 8 days

to observe spermogonia in the American specimens, though WEIR and HUBERT did not mention them. These spermogonia were sectioned after immersing the affected needle into warmed KOH solution for several hours. They were distinctly unlike those obtained from the writer's own cultures as well as from the field collection mainly in the more sparsely grown and more immersed organ. That is to say the number of the spermogonia of the foreign material was about 10 per square millimeter, while in the writer's it was 11-22, averaging 17.3 per square millimeter. They were somewhat elongated vertically and rather utricular in sectional view, and a little larger in size compared with the writer's. This sectional shape of the spermogonia was almost similar to the illustration by HUNTER (1927, fig. 2). The writer's own measurement of the spermogonia was slightly larger than that mentioned by HUNTER (l. c.) for the type specimen of *Peridermium pseudobalsameum* and by FAULL (1938 b) for that of *U. Pteridis*, although they do not differ much with each other.

In the characters of the aecidium, wide differences were observed. The most distinct difference was in the peridial cells. These cells of the American materials were much thicker in inner as well as in outer walls as shown in Fig. 3 in this paper. In a previous paper, the writer (1930 a) stated that the inner walls of the peridial cells of the aecidium of his culture measured 3-7 μ , but further investigations showed that they were much thinner making them more conspicuous in difference from those of *U. Pteridis*. The markings of the cells were so very coarse and distinct that they could not be considered as conspecific, even at a glance, compared with the writer's materials which were more delicately verrucose, as shown in Fig. 3 and Pl. VI, figs. e, p, q and r. The shape and size of the peridial cells were also not similar. Intermediate forms between peridial cells and the aecidiospores were also seen. They must correspond to that form, which ARTHUR (1925) called by the term "pseudospore." FAULL (1938 b) described it under the designation of "spore-like bodies." Compared with normal aecidiospores they were larger in size.

As to the age of the affected needles of the American material, the writer would like to say that they are of the second year, because they are much harder and thicker than those of his own cultures. FAULL (l. c.) described them as of the "second to fifth year."

In short, compared with the *Peridermium* of WEIR and HUBERT's experiment, the writer's culture can not be regarded to be the same, mainly in respect to the morphology of the spermogonia as well as of

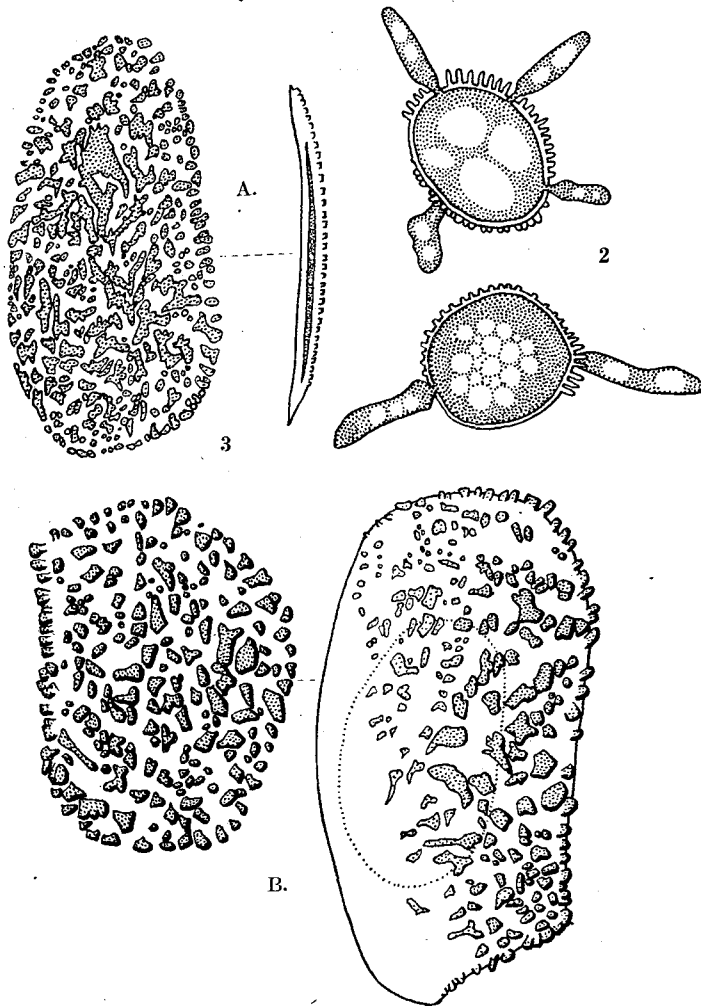


Fig. 2. Germinating aecidiospores of *U. Kameiana* on *Abies sachalinensis* from Teshio. About 1 day after sowing. $\times 1035$.

Fig. 3 A. Peridial cells of the peridermium of *U. Kameiana* on *Abies Mayriana* VIII₁₃. B. Peridial cells of the peridermium of *U. Pteridis* on *A. grandis* collected by WEIR. Left: Surface view. Right: Lateral view. $\times 1035$.

the peridial cells, and also to the age of the affected needles.

On the other hand, in the case of the type specimen of *P. pseudo-balsameum* (labelled to have been collected by BLASDALE on June 4, 1896

on *Abies grandis* at Eureka, California), unfortunately the writer was able to see spermogonia only, because the aecidial sori were very badly moulded and completely destroyed. The measurement of ten spermogonia was 104–145.5 μ in height and 97.5–162.5 μ in breadth averaging 130.0 μ in height and 124.8 μ in breadth and they were seen to be inverted hemispherical to utricular in sectional shape. Though limited to spermogonia only, the writer's observation made him instantly to think the material to be identical with WEIR's.

According to a personal communication kindly sent to the writer by Professor ARTHUR (March 27, 1931) as well as to his manual (1934), he is of opinion that the spermogonia and the aecidia of *U. Pteridis* on *Abies grandis* "do occur sparingly on the first year needles in some cases," and in his letter appended that the characters of spermogonia especially in respect to their situation is almost the same as in the writer's illustration (KAMEI, 1930 a, figs. 6 and 7), so that one is led to consider that the specimen of Western America "is not materially different from" that of Japan. However, after the careful examination of the American materials and references to literature, it is very reasonable to say that WEIR's *Peridermium* is *P. pseudobalsameum* which is synonymous with *U. Pteridis* and quite distinct from the writer's specimen, which was recently treated as a new species by FAULL (1938 b) under the name, *U. Kameiana* FAULL.

Concerning the course of development of *U. Pteridis* and *U. Kameiana* there is also a great difference. On the question in regard to the second year needles, WEIR and HUBERT (1917) presumed that the sporidia infect the needles in the latter part of the first year and the aecidia issue in the spring of the next year while BELL (1924) and HUNTER (1927) thought that this might probably not be the case. By the latter author it was remarked that the teleutospores should perhaps overwinter and the infection take place in the next spring when the needles are young. The course of the development is somewhat similar to that of *Milesina polypodophila* FAULL or *Hyalopsora Aspidiotus* MAGNUS. In the case of *U. Kameiana*, at least in this locality, the course of the life cycle does not particularly differ from that of the related species of *Uredinopsis* heretofore investigated. The teleutospores mature in the latter part of the autumn and overwinter *in situ* in the fern tissues which wither and dry up ultimately. These teleutospores germinate in the spring just before the unfolding of the fir needles and infect them. Appearance of the mature aecidia was recorded to be

between June 16 to July 11 according to the 9 successful inoculation experiments as shown in Table 24. Almost the same procedure is presumed to take place in the field also, because the writer was repeatedly able to obtain the peridermial stages on current year needles of *Abies* at Teshio in the beginning of July. The incubation period of uredosori after inoculation with aecidiospores in the part of *U. Pteridis* seems to be far longer than in our case. From WEIR and HUBERT's record one may count 36 days (from June 19 to July 25) which is about 2 to 3 times longer than in the present experiments with *U. Kameiana*, which produced uredosori within 7-13 days as shown in Tables 12 and 30. Indeed, there is a "comparatively long period of incubation" in the case of *U. Pteridis* as was said by HUNTER (1927). In the writer's experience such a longer period was seen in the case of *Milesina Itôana* and *M. sublevis* (cf. Tab. 63). The morphology, such as the shape, size and situation of spermogonia, peridial cells and aecidiospores of *U. Pteridis* reminds one of some species of *Milesina* rather than of the typical species of *Uredinopsis*. In fact, the morphological as well as the biological characters of the aecidial phase of *U. Pteridis* are somewhat like those of some species of *Milesina* and unlike the typical species of *Uredinopsis*, represented by such species as *U. Kameiana*.

The description of the peridermial phase of this rust is as follows:—

Uredinopsis Kameiana FAULL in Contrib. Arn. Arbor., Harvard Univ. XI, p. 82, pl. IV, figs. 20, a, d, 1938.

Syn. *Uredinopsis Pteridis* (non DIET. et HOLW.) Sydow, Monogr. Uredinearum III, p. 490-491, 1915, p.p.; KAMEI in Ann. Phytopath. Soc. Japan II, p. 207, 1930; HIRATSUKA, f., Monogr. Pucciniastreae, p. 61, 1936, p.p.

Uredinopsis macrosperma (non Magn.) ARTHUR in N. Amer. Fl. VII, p. 684, 1925, p.p., Manual Rusts United States & Canada, p. 5, 1934, p.p.

Spermogonia on needles of current season, amphigenous, mostly hypophyllous, inconspicuous, clearly seen by hand-lens irregularly and closely aggregate or scattered on discolored areas, numerous, minute, punctate, usually isolated, at times confluent, mostly situated at the interspaces of stomata, elliptic to oblong in face view, margin rather sinuated, honey yellow at first, later becoming reddish brown, in sections subcuticular, slightly raised, lenticular to flattened conoidal, often a little depressing and even crushing the tissues beneath, sometimes immersed,

59.2–118 μ broad, 33.3–74 μ high, 88.4 \times 49.7 μ in average; apical pore slit-like, parallel to the long axis of the leaf, 10–96 \times 10–24 μ ; spermatophores unbranched, obelavate, septate, convergent; spermatia oblong to oblong-ovate, 4.0–9.0 \times 1.2–2.0 μ , averaging 5.2 \times 1.7 μ , smooth, colorless (Pl. II, fig. d; IV, figs. e and f; VII, fig. 17 c).

Aecidia on needles of current season, amphigenous, arranged mostly on stomatiferous surface, in two rows one on each side of the midrib, on pale yellowish discolored areas occupying a part or whole of the leaf, white, cylindrical, 1.0–1.5 mm. high, 0.3–0.5 mm. across; peridia colorless, rupturing at the apex; peridial cells slightly overlapping, rather fragile, easily separating, mostly rhombic, often irregularly polygonal to oblong, 25.7–45.1 \times 12.9–28.9 μ , averaging 36.2 \times 18.8 μ , inner walls 1.5–2.0 μ thick including tubercles, obscurely verrucose, outer walls 0.5–1.0 μ thick, smooth; aecidiospores colorless, ellipsoidal to globose, 17–27 \times 12–23 μ , averaging 20.73 \times 17.41 μ , rather densely and finely verrucose except a part where almost smooth; walls colorless, thin, 1–2 μ thick including tubercles (Pl. I, fig. b; VI, fig. e; Fig. 2, 3 and 6 c).

II and III are as described by FAULL (1938 b).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures*), *Abies sachalinensis* FR. SCHMIDT (*Cultures* and *field*), *Abies nephrolepis* MAXIM. (*Cultures*), *Abies holophylla* MAXIM. (*Cultures*) and *Abies balsamea* MILL. (*Cultures*)—in Japan (Hokkaidô).

II and III. *Pteridium aquilinum* KUHN and *Pteridium aquilinum* var. *japonicum* NAKAI—in Japan (Kiushû, Shikoku, Honshû, Hokkaidô and Saghalien), China and Siberia.

6. *Uredinopsis Struthiopteridis* STÖRMER

Historical review of the fungus. The present rust was first named by C. STÖRMER in 1895 based upon a specimen on *Matteuccia Struthiopteris* TODARO found at Merradalen near Oslo. He described only the amphispores (MAGNUS, 1904, S. 119). In the same year DIETEL studied the morphology of the rust and succeeded in germinating the telentospores—the first time for *Uredinopsis*—and therefrom the genus was determined to be a rust belonging to Melampsoraceae. Ever since, it has been referred to that family by SACCARDO (1899), DIETEL (1895, 1897, 1928), ARTHUR (1907, 1934), LIRO (1908), KLEBAHN (1914), SYDOW (1915), HIRATSUKA, f. (1936 c) and FAULL (1938 b). FAULL (l. c.) recently restricted this rust to the form on *Matteuccia Struthiopteris*.

It is known to be distributed in various countries of Europe, North America and Eastern Asia. In 1912, FRASER (1913) made basidiospore inoculation onto young needles of *Abies balsamea* and obtained the characteristic white peridermia. Moreover, he secured the uredospores of this rust after inoculation with the aecidiospores of a *Peridermium* identified as *Peridermium balsameum* PECK. KLEBAHN (1916) likewise proved the heteroecism between this rust and *Abies alba*. Moreover, he made further experiments with the amphispores inoculating onto the fern host and succeeded in obtaining ordinary uredospores. FAULL (1938 c) reported having made a repetition of FRASER's cultures of this rust. Recently HUNTER (1936 c) mentioned the size of the spermogonia on *Abies balsamea*. In our country, SYDOW (1913) reported the identification of this rust that was collected in the vicinity of Sapporo by MIURA. SHIRAI (1917, 1927) twice listed this species. HIRATSUKA, f. (1927 b, 1927 c, 1929 b, 1930 a, 1930 d, 1932 b, 1936 c) made notes on collections from Hokkaidô, Southern Saghalien and Honshû. ITÔ (1938) also described this rust recently. However, little has been reported on cultural studies in Japan except those of the writer (1932 b, 1933).

Personal observations. Rusted fern. In Hokkaidô, *Matteuccia Struthiopteris*, the host fern, is commonly distributed throughout the island and usually is found in damp areas, especially inside of the forest. Well-rusted fronds used for basidiospore inoculations were collected from the Nopporo Forest, Mt. Moiwa and Morap. In these places it was noted that *Abies Mayriana* was found growing.

Uredospores. Germ-pores of the uredospores were found to be situated near the apex as well as at the basal end as in the other related species. Often two to three germ-tubes were seen issuing from these spores as is shown in Pl. VII; fig. 5 i. With the primary uredospores inoculations were made on the proper as well as on five other species of ferns on which in the field related species of rusts are found. After 14-15 days new uredospores appeared on the proper host, while none were found on the other ferns, as shown in Table 13.

Amphispores. Usually the amphispores appear late in the season in the characteristic amphispore sori. They are situated near teleutospores as indicated by DIETEL (1895). Each spore is provided with comparatively thick and distinctly pigmented walls. If the overwintered affected pinnae which bear amphispore sori are moistened, they are seen to be ruptured, pushing out dirty yellow masses of amphispores, as already observed by DIETEL (1895) and KLEBAHN (1916). DIETEL (l.c.)

TABLE 13. Inoculations with uredospores of *U. Struthiopteridis*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
III. A 1	Uredospores on <i>M. Struth.</i> , fr. <i>Cult.</i> III. B. 1	<i>Osmunda japonica</i>	May 24, 1922	—	Planted pl.
" 2	"	<i>Dryopteris Phegopteris</i>	"	—	Potted pl. in greenhouse
" 3	"	<i>Onclea sensibilis</i>	Je. 2, 1922	—	Planted pl.
"	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
" 5	"	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Je. 8, 1922	—	Potted pl. in greenhouse
" 6	"	<i>Matteuccia Struthiopteris</i>	"	14	"
" 9	" fr. <i>Cult.</i> II, 1	"	Je. 12, 1922	15	"

reported an attempt to observe the germination of these amphispores. However, he was not successful except in only one case to see "eines noch sehr kurzen Keimschlauches" that was produced from the apex of the spore. In the spring of 1924, after sowing such spore masses in small drops of distilled water laid on the under surface of a partial frond of the host fern placed in a Petri dish, the writer saw some number of germinated amphispores after 24 hours as shown in Pl. VII, fig. 5 g. The mode of the germination of the amphispores of this species has not yet been recorded in detail so far as the writer is aware. Though repeated experiments were not performed, comparison with the apparently similar case in *U. filicina* described above caused the writer to believe that such a mode of germination might always take place in this species.

With the pure mass of the amphispores obtained as described above, inoculations were performed on the fronds of the host fern, resulting in the formation of uredospores after 12–19 days as shown in Table 14. KLEBAHN (1916) performed similar experiments in May of 1914, in which on the brownish spots that appeared on the inoculated portions he succeeded at length in obtaining primary uredospores. From this fact, he said that the fungus is not restricted to heteroecism but "erhält auch nur wesentlich durch überwinterten Uredosporen." FAULL (1929) also remarked on this aspect. The present writer collected many speci-

mens of the amphisporic stage on the fern host at places where there were no trees of *Abies* near by. In such cases the perpetuation of the rust might certainly occur by natural infections by means of amphispores.

TABLE 14. Inoculations with amphispores of *U. Struthiopteridis*

Exp. no.	Inocula	Date of inoc.	App. of uredos.	Remarks
			No. of days	
III. B 1	Amphispores on <i>M. Struth.</i> , Kotoni, Oct. 1, 1921	May 2, 1922	17	Inoculated on potted <i>Matteuccia Struthiopteris</i> in greenhouse
" 2	"	May 7, 1922	15	"
" 3	"	May 19, 1922	17	"
" 4	"	May 26, 1922	12	"
" 5	"	May 31, 1922	12	"
" 6	"	Je. 10, 1922	14	"
" 7	"	Je. 18, 1922	19	"
" 13	" Nopporo, Oct. 22, 1922	Je. 7, 1923	13	"
" 8	"	May 17, 1923	16	Petri dish
" 20	" Nopporo, Oct. 1923	May 19, 1924	17	"

Teleutospores. As the teleutospores were mostly situated subepidermally, the promycelia can easily push out of the surface of the fern frond. In such a case, the affected discolored areas were usually covered by the mass of basidia and basidiospores. In the present case, the former are elongated measuring $50-70 \times 7-9 \mu$ and the latter, globular being $7.2-11.5 \times 6.4-7.0 \mu$ in size. DIETEL (1895) stated that he had seen many branching promycelia.

Inoculations with basidiospores. As shown in Table 15, among 22 seedlings including three species of *Abies*, successful infections were obtained on each of 12 seedlings of *A. Mayriana*, 2 of *A. firma* and 1 of *A. sachalinensis* showing the resulting spermogonia after 9-15 days and aecidia after 17-24 days in the case of *A. Mayriana*. According to FRASER (1913) the spermogonia showed within 12-14 days and the aecidia within 19-21 days and the result was so successful that he could add: "practically every leaf of the young shoots being infected." KLEBAHN (1916) stated that after the appearance of yellow speckles on the surface of the affected needles the resulting peridermia issued after 23 days.

TABLE 15. Inoculations with basidiospores of *U. Struthiopteridis*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 2	Basidiospores on <i>M. Struth.</i> , Nopporo, Oct. 2, 1921	<i>A. M.</i> II ₂	May 20, 1922	12	21	Greenhouse
" 5	"	" V ₂	May 26, 1922	10	20	"
" 6	"	" VI ₂	"	9	22	"
" 16	" Oct. 2, 1922	" IV ₃	May 24, 1923	?	21	"
" 19	"	" VII ₃	May 28, 1923	10	21	"
" 23	"	" XI ₃	May 27, 1923	15	22	Corridor
" 66	" Moiwa, Oct. 25, 1924	" X ₅	Je. 1, 1925	10	24	"
" 93	" Nopporo, Oct. 26, 1925	" II ₆	Je. 7, 1926	10	?	Laboratory
" 113	"	" XXII ₆	Je. 17, 1926	?	20	"
" 116	"	" XXV ₆	Je. 24, 1926	?	21	"
" 155	" Nov. 13, 1927	" VI ₅	May 30, 1928	15	21	"
" 193	" Nov. 13, 1929	" XIV ₁₀	Je. 7, 1930	22?	—	"
" 255	" Morap, Sept. 1932	" IV ₁₃	May 31, 1933	15	22	"
" 119	" Nopporo, Oct. 26, 1925	<i>A. s.</i> II ₆	Je. 7, 1926	13	23	"
" 129	"	<i>A. f.</i> II ₆	Je. 17, 1926	14	20	"
" 132	"	" V ₆	Je. 30, 1926	?	32	"

FAULL (1938 c) reported that the yellowing of the affected needles of *Abies balsamea* appeared after 9 to 11 days from the inoculation while the spermatogonia were first observed in 10 to 15 days and the peridermia were first observed in 19 to 24 days. From the success of the writer's inoculation experiments with the basidiospores, as new hosts of the peridermal phase of this rust three species of indigenous fir trees, that is, *Abies Mayriana*, *A. sachalinensis* and *A. firma* may be added.

Inoculations with aecidiospores. As shown in Table 16, with the aecidiospores obtained from the above experiments back inoculations were made on the fronds of *Matteuccia Struthiopteris* and seven other species of ferns on which the related species of rusts are usually seen in the field. In the case of *M. Struthiopteris*, the first appearance of uredopustules was noted after 12-14 days. But in the case of other ferns, no pustules of uredospores were ever seen, although sometimes discolorations were observed. According to KLEBAHN (1916) back ino-

culations with the aecidiospores on the fern produced uredospores after 25 days. FAULL (1938 c) in similar experiments obtained the first uredosori after 10 to 11 days which were harvested 13 to 28 days later.

The description of the peridermal phase of this species is as follows:—

TABLE 16. Inoculations with aecidiospores of *U. Struthiopteridis*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 1	Aecidiospores on <i>A. M.</i> II ₂	<i>Matteuccia Struthiopteris</i>	Je. 23, 1922	14	Potted pl. in greenhouse. Discoloration appeared 10 days later
" 13	" IV ₃	"	Je. 21, 1923	13	Greenhouse.
" 14	" "	"	Jy. 4, 1923	12	Petri dish
" 73	" XXII ₈	"	Jy. 20, 1926	12	"
" 1	" II ₂	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Je. 23, 1922	—	Planted pl.
"	"	<i>Dryopteris Phegopteris</i>	"	—	"
"	"	<i>Oncoclea sensibilis</i>	"	—	"
"	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
" 15	" IV ₃	"	Je. 3, 1923	—	Petri dish.
"	"	<i>Dryopteris Phegopteris</i>	"	—	"
"	"	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	"	—	"
"	"	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	Jy. 4, 1923	—	"
" 69	" II ₀	<i>Athyrium Vidalii</i>	Jy. 10, 1926	—	"
"	"	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	Jy. 10, 1926	—	"

Uredinopsis Struthiopteridis STÖRMER in Bot. Notiser, 1895, p. 81.

Syn. *Uredinopsis Struthiopteridis* STÖRMER in ARTHUR, North Amer. Flora VII, p. 116-117, 1907, p.p.; Manual Rusts United States & Canada, p. 4, 1934, p.p.; SYDOW, Monogr. Ured. III, p. 485, 1915, p.p.; HIRATSUKA, f., Monogr. Pucciniastreae, p. 58, 1936, p.p.

Uredinopsis mirabilis (PECK) MAGNUS in RHOADS, HEDGECOCK, BETHEL and HARTLEY in Phytopathology VIII, p. 333, 1918, p.p.

Spermogonia on needles of current season, hypophyllous, minute, numerous, inconspicuous, irregularly and densely scattered on discolored

areas, mostly situated on interstomatal spaces of the stomatiferous surface, mostly isolated, sometimes confluent, elliptic, circular to polygonal in face view, often irregularly margined, honey yellow in fresh condition, in sections subcuticular, slightly raised, superficial, often depressing the epidermis or even the tissue beneath, flattened conoidal to hemispherical, $69.3-129.5 \times 29.3-74.0 \mu$, $97.2 \times 59.8 \mu$ in average; apical pore slit-like, parallel to the longitudinal axis of the needle, $32-120 \times 8-32 \mu$; spermatiphores unbranched, obclavate, septate, convergent; spermatia oblong, $4.1-6.4 \times 1.5-2.1 \mu$, colorless, smooth (Pl. IV, fig. g; VII, fig. 17a).

Aecidia on needles of current season, hypophyllous, arranged in two rows on yellowish discolored stomatiferous areas, white, cylindrical, 0.5-1.0 mm. high, 0.19-0.32 mm. across; peridia colorless, rupturing at the apex; peridial cells slightly overlapping, rhombic to hexagonal, rather fragile, $17.6-36.8 \times 9.6-20.0 \mu$, mostly $32.0 \times 17.6 \mu$, inner walls $2.0-3.0 \mu$ thick including tubercles, regularly and finely verrucose, outer ones comparatively thin, $0.3-0.5 \mu$ smooth; aecidiospores colorless, more or less globose, $18-28 \times 14-24 \mu$, averaging $22.73 \times 20.14 \mu$, closely verrucose except a part where almost smooth; walls colorless, thin, $1-2 \mu$ thick including tubercles (Pl. II, fig. e; IV, fig. g).

II and III are as described by previous authors such as DIETEL (1895), SYDOW (1915), HIRATSUKA, f. (1936 c) and FAULL (1938 b).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures*), *Abies sachalinensis* FR. SCHMIDT (*Cultures*) and *Abies firma* SIEB. et ZUCC. (*Cultures*)—in Japan (Hokkaidô).

Abies alba MILL. (*Cultures*)—in Germany.

Abies balsamea MILL. (*Cultures and field*)—in Nova Scotia.

II and III. *Matteuccia Struthiopteris* TODARO—in Japan (Honshû, Hokkaidô and Saghalien), northern, eastern and southern Europe, eastern and central North America.

7. *Uredinopsis Woodsiae* KAMEI

Historical review of the fungus. This was first described by the writer (1932 b) after finishing experiments on its genetical connection. HIRATSUKA, f. (1932 c, 1936 c) noted his collections of this rust in Hokkaidô, Southern Saghalien and Honshû. Recently he (1936 c) redescribed this fungus adding another new host fern. FAULL (1938 b) and IRÔ (1938) recently mentioned this rust.

Personal observations. Rusted fern. In the main island of Hokkaidô, *Woodsia polystichoides* EAT. var. *nadiuscula* HOOKER, one of the host ferns is distributed through all provinces (MIYABE and KUDÔ, 1930), but the rusted specimens at hand were collected only from Prov. Ishikari. Teleutospore materials to be used for inoculation experiments were collected always at the northern side of the foot of Mt. Teine, where the host fern is abundantly growing on a rocky cliff.

Uredospores. In most of the field specimens the uredospores were more or less contaminated by the amphispores in one and the same sorus even in the specimen collected as early as Sept. 18.

Amphispores. After overwintering, if seen in a moist condition, the contents of amphispores are found to be vacuolated just as in the case of *U. Struthiopteridis* and *U. filicina*. Probably the autoecious life cycle may be carried on by this spore form as in the related species.

Inoculations with basidiospores. As shown in Table 17, after the inoculation with the basidiospores in all cases of five experiments spermogonia appeared, while aecidia in only three cases. In some experiments, after a cut twig of the young shoot of *Abies Mayriana* was laid in a moist chamber it was inoculated with basidiospores by being smeared with new leaves. In these cases, however, probably because of the extremely abnormal condition of the inoculated plant, only spermogonia were obtained after a long interval and aecidia did not develop. In the case of inoculated fir IX₁₁, a considerable crop of aecidia was harvested.

TABLE 17. Inoculations with basidiospores of *U. Woodsiae*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 67	Basidiospores on <i>Woods. pol.</i> var. <i>nadiuscul.</i> , Teine Sept. 18, 1924	A. M. XI ₅	Je. 5, 1925	17	26	Corridor
" 165	" Oct. 20, 1927	" XVIII ₈	Je. 15, 1928	?	—	Cut twig in Petri dish
" 187	" Oct. 20, 1929	" VIII ₁₀	Je. 5, 1930	13	20	Laboratory
" 202	"	" XXI ₁₀	Je. 4, 1930	27?	—	" Cut twig in Petri dish
" 211	" Nov. 11, 1930	" IX ₁₁	Je. 9, 1931	?	40?	Laboratory. Aecidia were harvested abundantly

Inoculations with aecidiospores. With the aecidiospores obtained from the cultures mentioned above, three trials of back inoculation were carried out in two seasons, 1925 and 1931. Only one experiment made in 1931 using a Petri dish showed a successful result on a frond of *Woodsia* fern (Pl. III, fig. f). On July 26 after 8 days from the date of inoculation a rich production of uredosori bearing spore masses in tendrils was obtained.

The description of the present species is as follows:—

***Uredinopsis Woodsiae* KAMEI** in Trans. Sapporo Nat. Hist. Soc. XII, p. 162, 1932.

Spermogonia on needles of current season, amphigenous, mostly hypophyllous, minute, inconspicuous, numerous, irregularly and closely aggregated on discolored and deformed areas, isolated or confluent, elliptic to angular, margin often irregularly sinuated in face view, in sections subcuticular, slightly raised, lenticular to flattened conoidal, a little depressing the tissue beneath, not deeply immersed, $84.0\text{--}136.9\mu$ broad, $37.0\text{--}81.4\mu$ high averaging $107.4 \times 49.1\mu$; apical pore slit-like, parallel to longer axis of the needle, $40\text{--}120 \times 20\text{--}56\mu$; spermatophores unbranched, obclavate, septate, convergent toward upper middle part of the organ; spermatia more or less oblong, $4.5\text{--}5.6 \times 1.6\text{--}2.4\mu$, colorless, smooth (Pl. II, fig. f; IV, fig. h; VII, 17 b).

Aecidia on needles of current season, amphigenous, mostly hypophyllous, arranged in two rows on pale yellowish discolored stomatal areas, white, cylindrical, mostly 1 mm. high, 0.16–0.36 mm. wide; peridia colorless, dehiscent at the apex; peridial cells rather firmly combined, slightly overlapping, polygonal to elliptic, $22.2\text{--}37.8 \times 12.6\text{--}31.5\mu$, averaging $29.10 \times 20.12\mu$; inner walls $2\text{--}3\mu$ (rarely 5μ) thick including tubercles, minutely verrucose, outer ones $1.0\text{--}1.2\mu$ thick, smooth; aecidiospores colorless, globose to ellipsoidal, $16\text{--}26 \times 12\text{--}22\mu$, averaging $20.87 \times 17.45\mu$, finely verrucose except a part where almost smooth; walls colorless, thin, up to 2μ thick including tubercles (Pl. II, fig. f; VI, fig. g).

Uredosori hypophyllous, subepidermal, pustular, scattered on more or less discolored areas of indefinite extent, especially on leaf margin, rarely on younger part of stipes, roundish to ellipsoidal, discrete but often confluent, 0.1–0.3 mm. across, covered with yellowish to brownish discolored epidermis; peridia colorless, hemispherical to subconoidal with central rupture; peridial cells delicate, irregularly polygonal, $8.0\text{--}18.0 \times 4.0\text{--}14.0\mu$, averaging $12.03 \times 9.09\mu$; walls of peridial cells thin,

about 1μ , colorless, smooth; uredospores issue in white spore mass, each spore short stalked, ovate fusiform to ovate oblong, $20-49 \times 12-18\mu$, mostly $30.4 \times 14.8\mu$, occasionally with short stout beak, $1.5-2.5\mu$ (rarely 4μ) long, mostly rounded or flattened; walls about 1μ thick, sparsely verrucosed beside the two longitudinal serrulated ridges, formed of loosely set, blunt papillae, colorless; bladderly cells present; amphispores compacted in a peridium, often with uredospores intermingled, issue after overwintering, pulverulent, each spore colorless, obovate-polygonal to ellipsoidal or oblong, usually provided with short pedicel, $19.3-37.0 \times 11.3-22.5\mu$, averaging $27.3 \times 14.5\mu$; walls rather thick, $1-2\mu$, finely verrucose, colorless; germ-pores indistinct (Pl. VII, fig. 6 a and d).

Teleutospores on current year fronds, amphigenous, mostly hypophyllous, on discolored and distorted areas of indefinite extent; teleutospores intercellular, subepidermal, especially abundant near uredosori, sometimes scattered in the mesophyll, 1-6 celled, divided by vertical septa, globose to subglobose, often pyriform, $18-35 \times 15-27\mu$; walls thin, colorless, smooth; basidiospores subglobose, $6-9\mu$ across, colorless, smooth (Pl. VII, figs. b and c).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures*)—in Japan (Hokkaidô).

II and III. *Woodsia polystichoides* EAT. var. *nudiuscula* HOOKER and var. *Veitchii* HOOKER et BAK.—in Japan (Honshû, Hokkaidô and South Saghalien).

8. *Uredinopsis intermedia* KAMEI

Historical review of the fungus. This species was first described by the writer in 1932 (1932 b). All stages of its life cycle were also made clear. Afterwards HIRATSUKA, f., (1932 c, 1934 d and 1936 e) made notes and a redescription reporting on the collections in Hokkaidô and Honshû. FAULL (1938 b) and ITÔ (1938) also described this rust recently.

Personal observations. Rusted ferns. The hosts of this rust are restricted to two fern species. One of them, *Athyrium acrostichoides* is distributed throughout the island of Hokkaidô while the other fern, *Athyrium pterorachis* through four provinces there of (MIYABE and KUDÔ, 1930), but the rust has been collected only from the two provinces of Ishikari and Iburi. Special collections of the materials for the culture experiments were made in the autumn at Noppero and Morap, where fir

trees are growing. Some materials of *Athyrium acrostichoides* were obtained near the summit of Mt. Teine at an elevation of about 900 meters above sea level, where no trees of *Abies* were seen immediately near by.

Uredospores. The uredospores issue in a white spore mass pushing forth from the apex of the uredosori. This condition, however, was restricted to young sori such as are often seen in earlier gatherings. Most of the pustules on specimens in the writer's collections were devoid of these thin-walled uredospores. With these ordinary uredospores inoculation experiments were made to obtain the new uredosori which occurred within 8-21 days as shown in Table 18. By counter inoculations with the experimentally produced uredospores it was also proved biologically that the rusts on two different fern hosts are one and the same species.

TABLE 18. Inoculations with uredospores of *U. intermedia*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
III. A.10	Uredosp. on <i>Athyr. pteror.</i>	<i>Athyrium pterorachis</i>	Aug. 10, 1923	11	Petri dish
" 34	„ on <i>Athyr. acrost.</i>	„	Sept. 20, 1931	21	„
" 35	„	<i>Athyrium acrostichoides</i>	„	8	„

Amphisporos. The writer obtained amphisporos on the fronds of both species of the host ferns, even as early as Sept. 17. After overwintering, if moisture was provided, the amphisporos issued from the upper fissures of the pustules in whitish spore masses. With these amphisporos inoculations were made, resulting in new uredosori after 14-16 days as shown in Table 19.

TABLE 19. Inoculations with amphisporos of *U. intermedia*

Exp. no.	Inocula	Date of inoc.	App. of uredos.	Remarks
			No. of days	
III. B. 16	Amphisporos on <i>Athyr. acrost.</i>	Je. 7, 1923	15	Inoculated on <i>Athyrium acrostichoides</i> in pot in greenhouse
" 17	„	Je. 19, 1923	14	„

Teleutospores. A section of the discolored and slightly shrunken portion of the affected fern host reveals teleutospores under the epidermis especially on the under surface. They grow abundantly near the uredosori.

Inoculations with basidiospores. With the basidiospores obtained from the germinating teleutospores on two specimens of *Athyrium pterorachis*, four pots of *Abies Mayriana* were inoculated with success in two of them. With the basidiospores from four specimens of *Athyrium acrostichoides*, a total of ten pots of *Abies Mayriana* were inoculated, successfully obtaining aecidiospores in four pots. Summarizing these results as shown in Table 20, the periods for development are

TABLE 20. Inoculations with basidiospores of *U. intermedia*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 18	Basidiospores on <i>Athyr. acro.</i> , Nopporo, Oct. 20, 1922	A. M. VI ₃	May 28, 1923	10	21	In greenhouse, 0 and 1 were harvested abundantly
" 24	"	" XII ₃	Je. 6, 1923	12	21	In greenhouse.
" 68	" Oct. 26, 1924	" XII ₅	Je. 5, 1925	14	26	Laboratory
" 192	" Teine, Oct. 20, 1929	" XIII ₁₀	Je. 7, 1930	20?	—	" Spermogonia scantily seen developing slowly
" 212	" Nov. 11, 1930	" X ₁₁	Je. 9, 1931	22	31	Laboratory
" 20	" on <i>Athyr. pteror.</i> , Nopporo, Oct. 20, 1922	" VIII ₃	May 31, 1923	11	25	Greenhouse.
" 25	"	" XIII ₃	Je. 16, 1923	12	19	Greenhouse. Aecidia scantily harvested

seen to be not greatly different from those of the other species of *Uredinopsis* used in the present study.

Inoculations with aecidiospores. With the aecidiospores thus gained from experiments, back inoculations on the fronds of two corresponding as well as other ferns were performed as shown in Table 21. On the proper host ferns the new uredospores issued normally within one to two weeks (somewhat longer in Experiment II, no. 24(2), 24(3) and 27) while in the cases of other ferns the

results were negative. It was also recognized that the aecidiospores gained from the inoculations of the basidiospores on one host may alternately infect another.

TABLE 21. Inoculations with aecidiospores of *U. intermedia*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 24(1)	Aecidiospores on <i>A.M. VIII</i> ₃ (fr <i>Athyр. pterocr.</i>)	<i>Athyrium pterorachis</i>	Jy. 4, 1923	8	Petri dish
" (2)	"	"	Jy. 13, 1923	38?	In greenhouse
" (3)	"	<i>Athyrium acrostichoides</i>	"	38?	"
"	"	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	"	—	"
"	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
"	"	<i>Dryopteris Miqueliana</i>	"	—	"
" 25	"	<i>Athyrium pterorachis</i>	Jy. 24, 1923	13	Petri dish
" 28	" on <i>A.M. VI</i> ₃ (fr. <i>Athyр. acro.</i>)	<i>Athyrium acrostichoides</i>	Jy. 4, 1923	15	"
" 29	"	"	Jy. 13, 1923	15	In greenhouse
"	"	<i>Athyrium pterorachis</i>	"	15	"
"	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	"	—	"
"	"	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	"	—	"
"	"	<i>Dryopteris Miqueliana</i>	"	—	"
"	"	<i>Athyrium acrostichoides</i>	Jy. 24, 1923	19	Petri dish
" 26	" on <i>A.M. XII</i> ₃ (fr. <i>Athyр. acro.</i>)	<i>Athyrium pterorachis</i>	Jy. 27, 1923	18	"
" 27	"	"	Aug. 3, 1923	26?	"
" 103	" on <i>A.M. X</i> ₁₃ (fr. <i>Athyр. acro.</i>)	<i>Athyrium acrostichoides</i>	Aug. 5, 1931	13	"

The description of the present species is as follows:—

Uredinopsis intermedia KAMEI in Trans. Sapporo Nat. Hist. Soc. XII, p. 166, 1932.

Spermogonia on needles of current season, hypophyllous, minute, inconspicuous, few, mostly isolated, sometimes closely attached to each other, scattered in two rows on discolored stomatiferous areas, in sections

subepidermal, scarcely raising the overlying epidermis, deeply seated, globose to subglobose, $130-209\mu$ broad, $120-187\mu$ high, averaging $172.3 \times 147.3\mu$; apical pore stoma or slit-like, $32.5-84.5 \times 13.0-14.5\mu$, parallel to the long axis of the needle; spermatophores convergent toward the central cavity, unbranched or branched, clavate, subulate, producing spermatia in chain; spermatia oblongo-cylindrical, $5.6-6.7\mu$ long, $1.9-2.4\mu$ broad, colorless, smooth (Pl. II, fig. g; IV, fig. i; VII, fig. 17 e).

Aecidia hypophyllous, on needles of current season, arranged in two rows on yellowish discolored areas occupying a part or whole of the surface, 1-12 per needle, white, cylindrical, 0.6-1.2 mm. high, 0.2-0.4 mm. across; peridia colorless, opening irregularly at the apex; peridial cells rhomboidal to ovate, overlapping, $24.1-40.2 \times 14.5-29.0\mu$, averaging $34.33 \times 18.90\mu$; outer walls thin, 0.6-1.5 μ thick, smooth; inner walls 3-5 μ thick (rarely 7 μ), coarsely verrucose, often striate; aecidiospores colorless, ellipsoidal to subglobose, $13-24 \times 11-19\mu$, averaging $18.22 \times 15.42\mu$, finely verrucose except a part where almost smooth; walls colorless, thin, up to 2 μ thick including tubercles (Pl. VI, fig. i).

Uredosori hypophyllous, subepidermal, pustular, scattered on discolored areas of indefinite extent, minute, roundish, 0.1-0.23 mm. across, covered with yellowish brown epidermis, usually isolated, rarely confluent; peridia colorless, hemispherical, located under stomata; peridial cells isodiametric to polygonal, slightly elongated in the lower ones, $7.4-16.5 \times 5.9-13\mu$; walls of peridial cells thin; uredospores colorless, white in mass, irregular in form, usually wedge to fan-shaped, sometimes bone-shaped or triangular, rarely oblong or obovoidal, $15-32 \times 13-26\mu$, in average $24.3 \times 16.5\mu$; walls thin, about 1 μ thick, slightly thicker at angle, colorless, smooth, short stalked; amphispores pushing out in whitish powdery mass after overwintering, each spore colorless, ovoid, obovoid to angular, $15-25 \times 12-20\mu$, averaging $19.9 \times 15.1\mu$, with a stalk, 1.5-37 μ long; walls of amphispores ca. 1 μ thick, colorless, finely verrucose (Pl. VII, fig. 9 a, b, and d).

Teleutosori on indefinitely discolored areas of current year fronds, amphigenous, mostly hypophyllous; teleutospores intercellular, mostly compacted subepidermally in a layer, rarely in the mesophyll, colorless, pyriform, subglobose or ellipsoidal, 1 to 7 celled, mostly 3-4 celled, $19-55 \times 15-31\mu$, averaging $32.8 \times 21.8\mu$; walls colorless, thin, about 1 μ , smooth, with a pore to each cell; basidiospores more or less globular, $5.5-9.2 \times 7.4-11.1\mu$, colorless, smooth (Pl. VII, fig. 9 c, d, and e).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures*)—in Japan (Hokkaidô).

II and III. *Athyrium acrostichoides* DIELS.—in Japan (Honshû and Hokkaidô).

Athyrium pterorachis H. CHRIST—in Japan (Hokkaidô).

9. *Uredinopsis ossaeiformis* KAMEI

Historical review of the fungus. This species and its complete life cycle were first described by the writer in 1932 (1932 b). HIRATSUKA, f. (1932 c, 1935 a, 1936 c) made notes and a description mentioning its distribution in Hokkaidô, Korea and the Maritime Province of Siberia. NAGAI and SHIMAMURA (1933) reported the collection of the species from the Kuriles. FAULL (1938 b) and ITÔ (1938) respectively have made re-descriptions of this rust in recent days.

Personal observations. Rusted ferns. In the main island of Hokkaidô, both species of the host ferns, *Dryopteris dilatata* GRAY var. *oblonga* TAKEDA and *D. monticola* C. CHR. are distributed widely (MIYABE and KUDÔ, 1930). HIRATSUKA, f. noted collections from the four provinces of Ishikari, Ihuri, Tokachi and Kitami, and here may be added Prov. Kushiro as a new locality in Hokkaidô. Most of the materials used for the basidiospore inoculations were collected at Mt. Makkarinupuri and also at Nopporo where *Abies Mayriana* is found growing abundantly. Most of the inoculations were made with the basidiospores issued on the affected frond of *D. dilatata* var. *oblonga*, but sometimes also with those from *D. monticola*.

Mycelia. They are intercellular and about 4μ in thickness having colorless contents. Often they are seen to be somewhat tubercular at the portions where they are in touch with the surface of the host cells of the mesophyll. They are septated and branched. In the fixed materials of the affected fern in a week solution of Flemming's fluid, the writer found some botryose masses of hyphae inside the host cells as shown in Fig. 4 a. He was inclined to consider them as the haustoria of this rust. A somewhat similar mass of the mycelia in *Milesina polypodophila* has already been illustrated by MOSS (1926).

Uredosorus. The general structure of the pseudoperidia of uredosorus and peridial cells and the mode of development of the uredospores were seen to be not different from the cases of other species of *Uredinopsis* as is shown in Pl. VII, fig. 8 d and e.

Uredospores. The shape of the uredospores of this rust was quite different from that of the typical species of this genus. They were mostly bone-shape resembling somewhat the shape of the starch grains of *Euphorbia* (Pl. VII, fig. 8 a). Sometimes they were narrowly fan-shaped or oblong or even polygonal. Germ-pores were situated at the two ends and also near the equator, the total number being 4-6. In spite of the continued observations up to this day, amphispores have not yet been detected on either of the fern hosts. With these uredospores inoculation experiments in Petri dishes were made on healthy fern fronds transferring the uredospores on *Dryopteris dilatata* onto *D. monticola* and *vice versa*, producing new uredosori within 23-28 days.

Teleutospores. They were subepidermal and abundantly and compactly aggregated near the uredosori or around them as shown in Fig. 4 and Pl. VII, fig. 8 b, c, e. In the germination, a basidium pushed out from each cell of the spores and the mass of basidia and basidiospores made a thin layer covering the lesions. Some of the features of these germinations are shown in Pl. VII, fig. 8 b.

Inoculations with basidiospores. With the basidiospores gained from the overwintered rusted materials, inoculation experiments on the needles of 33 seedlings including three species of *Abies* were performed through five seasons. A total of 20 pots were successful as shown in Table 22. About two weeks after the inoculations, yellowish discolored lesions (*Light green to Greenish yellow*, RIDGEWAY, 1912, Pl. V, 27 b and d) were seen at each infected portion. These portions were restricted to narrow areas and more or less sharply delimited from the adjoining healthy portion (*Meadow green to Forest green*, RIDGEWAY, l. c. Pl. VI,

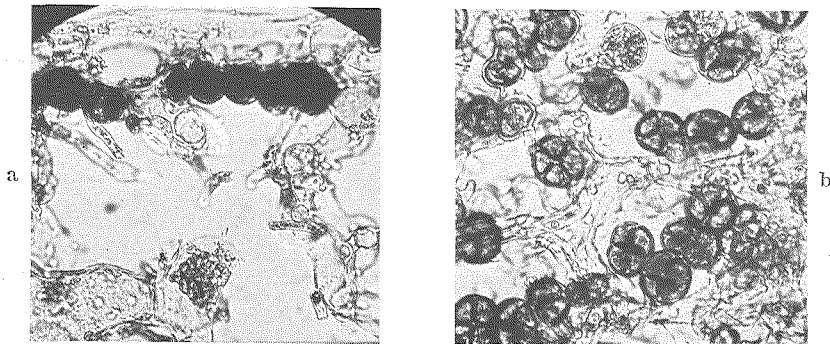


Fig. 4. Teleutospores of *Uredinopsis ossaeiformis* in the tissue of *Dryopteris dilatata* var. *oblonga*. $\times 200$. (a) Vertical section of the tissue showing the closely produced teleutospores and the haustorium-like hyphae in the host-cell. (b) Ventral face view of the same.

35 k to Pl. XVII, 29 m). The line of boundary was rather inconspicuous but occasionally clearly represented by transverse ridges against the longer axis of the needles. After the appearance of two or more of these spots on a needle they gradually united and often ultimately extended to the whole surface of the needle but sometimes were limited near apex of the leaf. The discolored parts were shrunken and eventually became reddish brown (*Cinnamon brown*, RIDGEWAY, l. c. Pl. XV). These decolorations mentioned above were noted in *Abies sachalinensis* I₆ after 13 days from the inoculation. When the decoloration became very obvious, the spermogonia began to appear about two weeks after the inoculation. They were so inconspicuous as to be visible only by the use of hand lens. They could be located by the exudation of a honey drop at each ostiole of the spermogonia. They were always hypophyllous and appeared on the stomatiferous surface. They were especially abundant at the apex of the needles and often some young leaves bore them on the entire surface. Within about three weeks the aecidial sori appeared intermingled with the spermogonia on the yellowish discolored areas or even on apparently healthy portions. The number of spermogonia per leaf was counted to be 5–19 while aecidia were 4–18. One of the abundantly infected seedlings is shown in Pl. I, fig. a. Such abundance of infection must surely be attributed to the profuse number of teleutospores that often occur in the case of the rust of the genus *Uredinopsis* which is devoid of amphispores.

Concerning the incubation period especially in regard to the production of the mature aecidial cups, considerable diversity was observed according to the plants experimented. That is, as shown in Table 22, among 16 seedlings of *Abies Mayriana*, in the Nos. I₂, III₂, IV₂, I₃, XII₄, XIX₄, VI₅, the aecidia appeared about three weeks after inoculation. But in the case of such seedlings as *Abies Mayriana* VII₂, VIII₂, I₆, XXIII₆, XXIV₆, and VI₁₁, the periods were much longer, being 4–5 weeks or more. Perhaps these delayed appearances must be attributed to the conditions of the host inoculated.

Inoculations with the aecidiospores gained from cultures. As shown in Table 23, after the inoculation on the frond of the proper host ferns the resulting uredospores appeared after 12–21 days, while in the cases of other ferns, on each of which the related species are parasitic in the field, inoculations were all unsuccessful. In germination of the aecidiospores in these cases it was observed that the germ-tubes extended up to 350 μ in length.

Inoculations with the aecidiospores gained from field. In this case, preliminary examination for the morphological characters of the spermogonia and the peridial cells of the aecidia used for the inocula was carefully made. The successful results in obtaining uredospores appeared after 9 to 27 days as indicated in Table 23, Exp. IV. One of the successful cases is illustrated in Fig. 1.

 TABLE 22. Inoculations with basidiospores of *U. ossaeiformis*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 1	Basidiospores on <i>Dry. dil.</i> var. <i>obl.</i> Nopporo, Nov. 23, 1921	A. M. I ₂	May 18, 1922	17	23	Greenhouse
" 3	"	" III ₂	May 22, 1922	20	23	"
" 4	"	" IV ₂	May 25, 1922	16	23	"
" 7	"	" VII ₂	May 27, 1922	?	30	"
" 8	"	" VIII ₂	May 31, 1922	?	35?	"
" 13	" Oct. 20, 1922	" I ₃	May 18, 1923	19	24	" Aecidia issued very abundantly
" 33	" Oct. 14, 1923	" VIII ₄	May 28, 1924	23?	?	"
" 47	"	" XX ₄	Je. 16, 1924	?	19	" Aecidia scanty and immature
" 62	" Mt. Makkari-nupuri, Nov. 12, 1924	" VI ₅	May 28, 1925	14	23	Laboratory
" 92	" Nov. 17, 1925	" I ₆	Je. 7, 1926	13	30	" Discoloration appeared 13 days later
" 114	"	" XXIII ₆	Je. 17, 1926	11	27	Laboratory
" 115	"	" XXIV ₆	Je. 24, 1926	?	36	"
" 208	" Oct. 6, 1930	" VI ₁₁	Je. 9, 1931	?	40	"
" 39	" on <i>Dry. monticola</i> , Nopporo, Oct. 14, 1923	" XII ₄	Je. 4, 1924	15	21	Greenhouse
" 45	"	" XIX ₄	Je. 14, 1924	12	23	"
" 53	"	" XXIII ₄	Je. 20, 1924	?	17	Laboratory
" 48	" on <i>Dry. dil.</i> var. <i>obl.</i> Nopporo, Oct. 14, 1923	A. f. I ₄	Je. 16, 1924	29	37	Out-of-doors
" 130	" Mt. Makkari-nupuri, Nov. 17, 1925	" III ₆	Je. 17, 1926	20	27	Laboratory
" 131	"	" IV ₆	Je. 30, 1926	15	32	"
" 118	"	A. s. I ₆	Je. 7, 1926	13	27	" Yellow spot appeared 13 days later

TABLE 23. Inoculations with aecidiospores of *U. ossaeiformis*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 2	Aecidiospores on <i>A.M.</i> III ₂	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Je. 28, 1922	17	Potted pl. in greenhouse
"	"	<i>Matteuccia Struthiopteris</i>	"	—	"
" 4	"	<i>Dryopteris Phegopteris</i>	Jy. 10, 1922	—	"
"	"	<i>Dryopteris crassirhizoma</i>	"	—	"
"	"	<i>Osmunda japonica</i>	"	—	"
"	"	<i>Polystichum Standishii</i>	"	—	"
" 6	"	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Jy. 22, 1922	20	Petri dish
" 17a	" " I ₃	"	Jy. 4, 1923	15	"
" " b	"	"	Jy. 5, 1923	12	Potted pl. in greenhouse
" " c	"	"	Jy. 28, 1923	21	Petri dish
" 17b(2)	"	<i>Thelypteris palustris</i> var. <i>pubescens</i>	Jy. 5, 1923	—	Potted pl. in greenhouse
" " (3)	"	<i>Matteuccia Struthiopteris</i>	"	—	"
" " (4)	"	<i>Athyrium pterorachis</i>	"	—	"
" " (5)	"	<i>Athyrium acrostichoides</i>	"	—	"
" " (6)	"	<i>Dryopteris Miqueliana</i>	"	—	"
" " (7)	"	<i>Dryopteris crassirhizoma</i>	"	—	"
" 37b	" XIX ₄	<i>Dryopteris monticola</i>	Jy. 10, 1924	46?	Petri dish
" 85a	" on <i>A.f.</i> III ₀	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Aug. 6, 1926	17	"
" 85b	" on <i>A.M.</i> XXIII ₀	"	"	17	"
IV. 2	" on <i>A.M.</i> Atsubetsu. Jy. 9, 1923	"	Jy. 9, 1923	10	"
"	"	<i>Dryopteris Miqueliana</i>	"	—	"
"	"	<i>Dryopteris crassirhizoma</i>	"	—	"
"	"	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Jy. 10, 1923	9	"
" 9	" Mt. Makkarinupuri, Aug. 24, 1924	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Aug. 27, 1924	16	"
" 18	" Tomakomai, Jy. 4, 1932	"	Aug. 16, 1932	14	"
" 24a	" Tomakomai, Jy. 10, 1933	"	Jy. 14, 1933	—	" Removed on Aug. 3
" " b	"	"	Jy. 15, 1933	17	"
"	"	<i>Athyrium acrostichoides</i>	"	—	" Removed on Aug. 1

IV. 24b	Aecidiospores on <i>A.M.</i> , Tomakomai, Jy. 10, 1933	<i>Athyrium pterorachis</i>	Jy. 15, 1933	—	Petri dish. Removed on Aug. 1
"	"	<i>Dryopteris crassirhizoma</i>	"	—	"
" 25a	" Jy. 22, 1933, Shigeji Ito	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Jy. 27, 1933	24	" When examined it was already matured
" 26a	" Lake Shikotsu, Jy. 10, 1933	"	"	27	Petri dish
" "b	"	"	Aug. 5, 1933	25	"
" "c	"	"	"	25	"
" "d	"	<i>Dryopteris crassirhizoma</i>	"	—	" Removed on Aug. 22
" "e	"	<i>Athyrium acrostichoides</i>	"	—	"
" 52	" Nopporo, Jy. 22, 1936	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Jy. 27, 1936	12	"

The description of the present species is as follows:—

Uredinopsis ossaeiformis KAMEI in Trans. Sapporo Nat. Hist. Soc. XII, p. 167, 1932.

Syn. *Uredinopsis obtusa* TRANZSCHEL in HIRATSUKA, f. in Memoirs Tottori Agricul. Coll. IV, p. 80, 1936.

Spermogonia on needles of current season, hypophyllous, minute, rather few, sparsely scattered in two rows on yellowish discolored stomatiferous areas, sometimes on the marginal portion, inconspicuous, honey yellow in fresh condition, usually separate, sometimes closely attached to each other, ostiole mostly central, sometimes peripheral, in sections subepidermal, deeply seated, subspherical to spherical, 192.5–270 μ broad in transverse section, 150–259 μ broad in longitudinal section, 100–241 μ high; apical pore a stoma or short slit, parallel to long axis of the needles, 18–30 μ across; spermatophores unbranched or branched, septate, convergent toward the central cavity, producing spermatia in chain; spermatia hyaline, unicellular, narrowly ellipsoidal, 3.6–6.6 \times 1.2–2.3 μ , smooth, colorless (Pl. II, fig. h; IV, fig. j; VII, fig. 17 d).

Aecidia amphigenous, mostly hypophyllous, on needles of current season, intermixed with spermogonia, scattered in two rows one on each side of the midrib, on more or less discolored areas, occupying a part or whole surface of the affected needles, 4–18 per needle, white, cylindrical, 0.2–0.5 mm. across, 0.5–1.1 mm. high, deeply seated, up to two-thirds of the thickness of the needles; peridia colorless, firm, rupturing at

the apex; peridial cells slightly overlapping, tetragonal to hexagonal, often cuneate to oblong, $25.6-43.2\mu$ long, $11.2-27.2\mu$ broad, averaging $33.64 \times 20.02\mu$; inner walls densely and finely verrucose, incompletely striated, $1-3\mu$ thick including tubercles, outer walls smooth, $0.5-1.0\mu$ thick; aecidiospores colorless, ellipsoidal to subglobose, $16-31 \times 14-23\mu$, averaging $23.40 \times 18.40\mu$, minutely and closely verrucose except a part where almost smooth; walls up to 1.5μ thick including tubercles (Pl. VI, fig. h).

Uredosori hypophyllous, occasionally on stipes, subepidermal, scattered or loosely grouped on yellowish to brownish discolored areas of indefinite extent, rather abundant near veins or margins, covered with discolored epidermis, roundish, minute, $0.15-0.3$ mm. across, ruptured by a central stomatic pore; peridia colorless, hemispherical or flattened conoidal, firm; peridial cells small, irregularly polygonal above, elongated at sides, $6.0-22.0 \times 5.5-15.0\mu$, averaging $13.20 \times 9.39\mu$; walls of peridial cells colorless, smooth, about 1μ thick; uredospores colorless, white in mass, short-stalked, bone-shaped to narrow fan-shaped, rarely oblong to subglobose, the apex truncated, projected or rounded, wider than below, $27-44 \times 13-26\mu$, averaging $35.39 \times 17.14\mu$; walls colorless, about 1.5μ thick, thicker at angles, about 3μ , smooth; colorless (Pl. III, fig. i; VII, fig. 8 a, d and e).

Teleutosori on fronds of current season, amphigenous on discolored areas of restricted or indefinite extent; teleutospores intercellular, mostly aggregated just under the epidermis and continuous, often grouped around the uredosori, rarely scattered in the mesophyll, globose to ellipsoidal or pyriform, 1-8 celled, mostly 2-4 celled, divided by vertical septa, $19-33 \times 16-30\mu$ averaging $30.4 \times 25.7\mu$; walls colorless, smooth, thin, about 1μ thick; basidiospores subglobose, $7.7-9.2 \times 5.5-7.4\mu$, colorless, smooth (Fig. 4 a and b; Pl. VII, fig. 8 b, e and e).

Hosts and distribution:

0 and I. *Abies Mayriana* MIYABE et KUDÔ (*Cultures* and *field*), *Abies firma* SIEB. et ZUCC. (*Cultures*) and *Abies sachalinensis* FR. SCHMIDT (*Cultures*)—in Japan (Hokkaidô).

II and III. *Dryopteris dilatata* A. GRAY var. *oblonga* TAKEDA—in Japan (Hokkaidô, Honshû and Korea).

Dryopteris monticola C. CHR.—in Japan (Hokkaidô).

Dryopteris amurensis C. CHR.—Maritime Province of Siberia.

B. TIME OF APPEARANCE OF ORGANS

The appearance of organs in the life cycle of any species of *Uredinopsis*, if the environmental factors are alike and the developmental process is normal, may probably differ according to species or group of species each to represent characteristic features. Data concerning the time of the appearance of each organ which were observed in cultural studies are presented below.

1. *Basidiospores*. The inocula used for the successful basidiospore inoculations on *Abies* to produce spermogonia and aecidia must contain some vigorous basidiospores when the experiments are made. So, it may be admitted that the date of the successful inoculation must correspond to the date of the appearance of the fresh basidiospores. FRASER (1913, 1914) mentioned that the dates of his inoculations with basidiospores on *Abies balsamea* were May 13 and 28 (1912) with *U. Struthiopteridis*; May 26 (1912) with *U. Osmundae*; May 27 (1912) with *U. Phegopteridis* and May 13 (1912), May 15 and May 16 (1913) with *U. americana*. KLEBAHN (1916) inoculated with the basidiospores of *U. Struthiopteridis* on *Abies alba* on May 11 (1914). From FAULL's similar experiments (FAULL, 1929, 1938 c) concerning *U. Struthiopteridis*, *U. americana*, *U. longimucronata* FAULL, *U. Phegopteridis*, *U. Osmundae* and *U. ceratophora* FAULL, we deduce the limits of the date of inoculations to be from June 10 to July 7, which is rather later in season than the dates of previous investigators.

According to the writer's experiments with nine species of *Uredinopsis* similar results were obtained as shown in Table 24. Summarizing these results, it may easily be seen that the appearances of the basidiospores are loosely concluded to be made in the period between May to June and that May 16 to June 8 in the average range. These dates of inoculations also correspond with those of the unfolding of the needles of smaller seedlings of *Abies* in Hokkaidô. However, in the case of the larger trees, especially represented by some trees planted in the arboretum of our University and observed on the unfolding of the new needles (cf. Table 25), it was rather later than in the cases of the small seedlings. This condition may explain one of the reasons why the infection on *Abies* in the field is somewhat delayed in comparison with the case of artificial inoculations using smaller seedlings.

2. *Spermogonia*. Concerning the dates of the appearance of the spermogonia of a *Uredinopsis*, FRASER (1913, 1914) published that they

TABLE 24. Time of appearances of basidiospores, spermogonia, and acidia of nine species of *Uredinopsis*

Species	Basidiospores		Spermogonia		Acidia	
	Range	Average	Range	Average	Range	Average
<i>U. Adianti</i>	May 16	May 16(1)*	Je. 1	Je. 1(1)	Je. 10	Je. 10(1)
<i>U. Athyrii</i>	May 26-Je. 5	Je. 1 (7)	Je. 9-Je. 19	Je. 15(5)	Je. 19-Jy. 1	Je. 24(5)
<i>U. flicina</i>	May 21-Je. 19	Je. 5 (6)	Je. 16-Jy. 19	Je. 18(3)	Je. 18-Je. 26	Je. 23(4)
<i>U. hirosa-kiensis</i>	May 24-Je. 12	Je. 4 (9)	Je. 9-Je. 22	Je. 14(3)	Je. 13-Jy. 1	Je. 25(7)
<i>U. Kameiana</i>	May 26-Je. 9	Je. 3 (22)	Je. 5-Jy. 5	Je. 16(11)	Je. 16-Jy. 11	Je. 24(9)
<i>U. Struthiopteridis</i>	May 20-Je. 30	Je. 5 (16)	Je. 4-Je. 29	Je. 10(9)**	Je. 10-Jy. 15	Je. 29(11)**
<i>U. Woodsiae</i>	Je. 4-Je. 9	Je. 8 (5)	Je. 18-Jy. 1	Je. 20(2)	Je. 25-Jy. 1	Je. 28(2)
<i>U. intermedia</i>	May 28-Je. 16	Je. 6 (7)	Je. 7-Jy. 1	Je. 19(6)**	Je. 18-Jy. 10	Je. 30(6)**
<i>U. ossaeiformis</i>	May 18-Je. 24	Je. 5 (20)	Je. 4-Je. 26	Je. 15(9)**	Je. 10-Jy. 30	Jy. 1(14)**
Extreme limits	May 16-Je. 30	May 16-Je. 8	Je. 1-Jy. 19	Je. 1-Je. 20	Je. 10-Jy. 30	Je. 10-Jy. 1

* Number of appearances of each organ from which average dates are obtained.

** Cases regarding *Abies Mayriana* only were considered.

TABLE 25. Dates of unfolding* of needles of *Abies* in the field

Trees/year	1931	1932	1933	1934	1935	Average
<i>Abies homolepis</i> **	Je. 4	May 30	Je. 12	Je. 9	Je. 6	Je. 6
<i>A. firma</i> **	Jy. 10	—	Je. 12	—	Je. 20	Je. 24
<i>A. Mariesii</i> **	—	Je. 10	May 29	Je. 9	May 30	Je. 4
<i>A. Mayriana</i> **	Je. 20	—	May 29	Je. 16	May 30	Je. 10
<i>A. sachalinensis</i> ***	—	Je. 10	—	—	—	Je. 10

* The unfolding here means the entire unfolding of the fascicle of needles which occurred 5-25 days after the breaking of bud scales.

** The trees were planted in the open areas of the arboretum and attained a few meters in height in 1936.

*** The trees were planted in the shady part of the arboretum and died in 1932 so that observations could not be continued.

were May 27 and June 9 (1912) with *U. Struthiopteridis*; June 10 (1912) with *U. Osmundae*; June 12 (1912) with *U. Phegopteridis* and May 23, May 25 and May 27 (1913) with *U. americana*. From FAULL's experiments (1938 c) the dates of the appearances of spermogonia of five species in American *Uredinopsis* may be computed to have occurred from June 24-July 19 in total range. According to the writer's experi-

ments, the time of the appearances of the spermogonia of nine species of *Uredinopsis* is shown in Table 24. It indicates that the limits of the average dates are from June 1 to June 20.

3. *Aecidia*. FRASER (1913, 1914) reported the dates of the appearances of the aecidia of *Uredinopsis* in Nova Scotia as follows: in *U. Struthiopteridis*, June 1 and June 10, 1912; in *U. Osmundae*, June 18, 1912; in *U. americana*, June 6, 1912, July 1 and July 3, 1913. KLEBAHN (1916) also in *U. Struthiopteridis* reported the date to be June 3, 1914. From FAULL's record (1938 c) concerning five species mentioned above we may deduce the dates to be July 3 to July 30 in outside range. According to the writer's experiments, the dates of the appearances of the aecidia after the inoculation with the basidiospores of the nine species were as shown in Table 24. The results correspond somewhat to those of the foreign scholars.

4. *Uredosori*. (a) *From inoculations with aecidiospores*. From FRASER's experiments it is learned that the uredosori issued after the inoculations of the aecidiospores in *U. Struthiopteridis* on July 6 and

TABLE 26. Time of appearances of uredosori obtained from inoculations with aecidiospores of nine species of *Uredinopsis*

Species	Fern inoc.	Inocula	Range	Average
<i>U. Adianti</i>	<i>Adiantum pedatum</i>	c*	Jy. 7-Jy. 23	Jy. 5 (2)
<i>U. Athyrii</i>	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	c	Jy. 12-Aug.24	Jy. 24 (6)
<i>U. flicina</i>	<i>Dryopteris Phegopteris</i>	c	Jy. 7-Jy. 21	Jy. 19 (2)
<i>U. hirosakiensis</i>	<i>Thelypteris palustris</i> var. <i>pubescens</i>	c	Je. 29-Jy. 23	Jy. 11 (3)
"	"	f	Jy. 21-Jy. 29	Jy. 24 (3)
<i>U. Kameiana</i>	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	c	Jy. 3-Je. 27	Jy. 20 (6)
"	"	f	Jy. 20-Aug. 1	Jy. 23 (4)
<i>U. Struthiopteridis</i>	<i>Matteuccia</i> <i>Struthiopteris</i>	c	Jy. 4-Aug. 1	Jy. 15 (4)
<i>U. Woodsiae</i>	<i>Woodsia polystichoides</i> var. <i>nudiuscula</i>	c	Jy. 26	Jy. 26 (1)
<i>U. intermedia</i>	<i>Athyrium pterorachis</i>	c	Jy. 12-Aug.14	Jy. 31 (4)
"	<i>Athyrium acrostichoides</i>	c	Jy. 19-Aug.18	Aug. 4 (4)
<i>U. ossaeiformis</i>	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	c	Jy. 15-Aug.23	Aug. 5 (7)
"	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	f	Jy. 19-Sept. 12	Aug.17 (10)
Extreme limits			Jy.29-Sept. 12	Jy. 5-Aug. 17

* The inocula designated by c were obtained from cultures and by f obtained from the field.

July 8, 1912 (two cases), in *U. Atkinsonii* on July 10, 1912, and in *U. americana* on July 5, 8 and 10, 1912 and June 21 and 24, 1913. KLEBAHN (1916) obtained the uredosori of *U. Struthiopteridis* on June 6, 1914 after similar experiments. From FAULL's records (1938 c) concerning five species of *Uredinopsis* mentioned above, we may compute that the uredosori of these species issued from July 18 to August 13 in outside range. According to the writer's experiments the dates of the appearances of the uredosori after the inoculation with the aecidiospores of the nine species of *Uredinopsis* were as shown in Table 26. The range of dates in these cases corresponds fairly well with the results reported from foreign countries. But in the cases of *U. intermedia* and *U. ossaeiformis* the average dates of the appearances of uredosori were somewhat later.

(b) *From inoculations with amphispores.* KLEBAHN (1916) in inoculation experiments with the amphispores of *U. Struthiopteridis* obtained uredosori on June 5, 1914. In the writer's cases, as shown in Table 27, the dates of the appearances of the uredosori from the similar inoculations were seen to range from May 20 to July 7. Compared with the experiments with aecidiospores, they were earlier. The cause may be the earlier date of the inoculation in the case of the amphisporic inoculations.

TABLE 27. Dates of appearances of uredosori after inoculations with amphispores of four species of *Uredinopsis*

Species	Range	Average
<i>U. flicina</i>	May 28-Je. 21	Je. 6 (4)
<i>U. Kameiana</i>	Jy. 2	Jy. 2 (1)
<i>U. intermedia</i>	Je. 22-Jy. 3	Je. 28 (2)
<i>U. Struthiopteridis</i>	May 20-Jy. 7	Je. 13 (10)
Extreme limits	May 20-Jy. 7	Je. 6-Jy. 2

5. *Teleutospores.* FRASER (1913) in his culture experiments with the aecidiospores of *U. Struthiopteridis* said, "teleutospores were present on July 30" 1912. FAULL (1938 c) said that the time seems not to be governed by the seasonal period; more likely it is determined by a nutritional influence in the lesions. FAULL (l.c.) has often found the teleutospores before midsummer has arrived. The writer also after inoculations with the aecidiospores of *U. Kameiana* on the fronds of the bracken fern detected teleutospores as early as July 3, 1923.

C. DEVELOPMENTAL PERIODS OF ORGANS

1. *Spermogonia from the inoculation experiments.* From the record of FRASER (1913, 1914) the incubation periods for producing spermogonia may be calculated to be 12-14 days with *U. Struthiopteridis*; 15 days with *U. Osmundae*; 16 days with *U. Phegopteridis* and 8-11 days with *U. americana*. From about 260 experiments by FAULL (1938 c) concerning five species of *Uredinopsis* used for cultural study, one obtains the average range for producing spermogonia as 12-14 days. In the writer's own experiments with the nine species of *Uredinopsis* at hand, the spermogonia were obtained as tabulated in Table 28.

TABLE 28. Developmental periods of spermogonia and acedia of nine species of *Uredinopsis* on *Abies Mayriana*

Species	Spermogonia		Aecidia	
	No. of days			
	Range	Average	Range	Average
<i>U. Adianti</i>	16	16.0 (1)	25	25.0 (1)
<i>U. Athyrii</i>	9-18	14.6 (5)	19-30	23.8 (5)
<i>U. filicina</i>	9-15	12.6 (3)	19-28	22.2 (4)
<i>U. hirosakiensis</i>	8-16	12.0 (3)	19-24	22.0 (7)
<i>U. Kameiana</i> *	10-18	14.0 (11)	20-25	22.3 (9)
<i>U. Struthiopteridis</i> *	9-15	11.7 (9)	17-24	21.4 (11)
<i>U. Woodsiae</i>	13-17	15.0 (2)	20-26	23.0 (2)
<i>U. intermedia</i>	10-22	13.5 (6)	19-31	23.8 (6)
<i>U. ossaciformis</i> *	11-20	15.2 (10)	17-40	25.5 (14)
Extreme limits	8-22	11.7-16.0	17-40	21.4-25.5

* Cases regarding *Abies Mayriana* only were considered.

Comparing these data on the developmental periods of the spermogonia with those of FRASER as well as of FAULL, one sees that the American authors' are within the limits of the present writer's.

2. *Aecidia from the inoculation experiments.* From FRASER's results (1913, 1914) the appearances of the acedia of three species of *Uredinopsis* are known to be after 18-21 days for *U. Struthiopteridis*; 23 days for *U. Osmundae*; and 16-24 days for *U. americana*. KLEBAHN (1916) stated that the first acedia of *U. Struthiopteridis* came out 25

days after the inoculation. FAULL (1938 c) made note on the period that in about 260 experiments with five species of *Uredinopsis* the range of average periods was 20-25 days. In the nine species used in the present study, the results obtained are shown in Table 28. These data, though not quite accurately, somewhat agree with those of foreign investigators. Of course, these periods may vary according to the various conditions of the inoculated plants themselves and their environments. For instance, among 16 seedlings of MAYR's fir inoculated with *U. ossaeiformis* the aecidia on some seedlings appeared after much longer periods than those on other seedlings as already shown in the paragraph describing the rust in question. However, the aecidia of *U. intermedia* and *U. ossaeiformis* were apparently longer in making their appearance than those of other species of the materials either in range or in average. In this respect, they are somewhat nearly related to usual species of *Milesina* to which some morphological characters of these two species are similar. On the other hand, slight differences were indicated in the developmental period of the aecidial stage in connection with the different host species of *Abies* observed under apparently identical environmental conditions. FAULL (1934) has published such instances in the case of *Milesina fructuosa* (FAULL) HIRATSUKA, f. that was inoculated on *Abies* hosts explaining in this connection that "it cannot be assumed that some species of *Abies* may not be immune to *M. fructuosa*, nor that susceptible species differ from one another in their resistance to this rust." In the present experiments, in the cases of *U. ossaeiformis* and *U. Struthiopteridis*, the appearance of the mature peridermia on *Abies firma* was a little later than on *A. Mayriana*. Likewise in the case of *U. Kameiana* the mature peridermia on *Abies Mayriana* were observed to be rather earlier than on *A. holophylla* and *A. balsamea* as shown in Table 29.

3. *Uredosori*. (a) *Periods for appearances of uredosori in the artificial inoculation with aecidiospores*. FRASER (1913, 1914) in his inoculation experiments with experimentally produced aecidiospores of *U. americana* obtained uredosori after 7 and 8 days from the inoculations. KLEBAHN (1916) in similar experiments with *U. Struthiopteridis* gained uredospores after 16 days. FAULL (1938 c) recorded the results from similar experiments concerning five American species of *Uredinopsis*. From his Table 24, it is learned that the period varied from seven to thirty days. According to the writer's inoculation experiments by means of aecidiospores obtained from the cultures with nine

TABLE 29. Developmental periods of aecidium stages of three species of *Uredinopsis* on different species of *Abies* host

Species	Hosts	Range	Average
		No. of days	
<i>U. ossaeiformis</i>	<i>A. Mayriana</i>	17-36	25.1 (15)
"	<i>A. sachalinensis</i>	27	27.0 (1)
"	<i>A. firma</i>	27-37	31.3 (3)
<i>U. Kameiana</i>	<i>A. Mayriana</i>	21-25	22.3 (9)
"	<i>A. holophylla</i>	25-40	32.5 (2)
"	<i>A. balsamea</i>	29-46	41.2 (4)
<i>U. Struthiopteridis</i>	<i>A. Mayriana</i>	20-24	21.3 (11)
"	<i>A. sachalinensis</i>	23	23.0 (1)
"	<i>A. firma</i>	20-32	26.0 (2)

species of *Uredinopsis*, the developmental periods up to the perfection of the uredosorus were found to vary from five to twenty-seven days as shown in Table 30. Average period according to each experiment of the species ranged from 5.0 to 17.9 days. Among nine species, the average periods of *U. ossaeiformis* and *U. intermedia* were somewhat longer than in the cases of the remaining seven species. An unusually longer period for the incubation of uredosori was also reported by FAULL in *U. longimacronata* which needed 16-30 days. The longer periods seen in our two species mentioned above may reasonably be attributed to their peculiar nature, approaching to *Milesina*. Comparing the periods in the two kinds of experimental plants, that is, the potted plants and the cut fronds, it was shown that the periods in the latter cases were generally shorter than in the cases of the former as shown in Table 30. Here it is very interesting to refer to CLINTON and McCORMICK's paper (1924), in which a similar conclusion is derived from their culture experiments on some rusts.

(b) *Periods for appearances of uredosori obtained from inoculation with uredospores.* FAULL (1938 c) reported that the incubation periods of uredosori produced in many inoculation experiments with the uredospores of *U. Osmundae* ranged from 8 to 18 days. As shown in Table 31, the development periods in 7 cases with three species of *Uredinopsis* were determined to range from 8 to 28 days with 8 to 25 days in average. For *U. Struthiopteridis* alone the period ranges from 14 to 15 days and is somewhat approximate to that of *U. Osmundae*

TABLE 30. Developmental periods of uredosori issued from aecidiospore inoculations of nine species of *Uredinopsis*

Species	Fern inoculated	Range	Average	Condition of hosts
		No. of days		
<i>U. Adianti</i>	<i>Adiantum pedatum</i>	7-10	8.5 (2)	Cut pinnae
<i>U. Athyrii</i>	<i>Athyrium Filix-foemina</i> var. <i>longipes</i>	12	12.0 (1)	Potted pl.
"	"	6-12	10.2 (5)	Cut pinnae
Limit	"	6-12	10.6 (6)	
<i>U. filicina</i>	<i>Dryopteris Phegopteris</i>	15	15.0 (1)	Potted pl.
"	"	11	11.0 (1)	Cut pinnae
Limit	"	11-15	13.0 (2)	
<i>U. hirosakiensis</i>	<i>Thelypteris palustris</i> var. <i>pubescens</i>	8	8.0 (1)	Potted pl.
"	"	10-13	11.5 (2)	Cut pinnae
"	"	7-10*	8.5 (2)	Potted pl.
"	"	5*	5.0 (1)	Cut pinnae
Limit	"	5-13	8.8 (6)	
<i>U. Kameiana</i>	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	12	12.0 (1)	Potted pl.
"	"	7-13	10.0 (5)	Cut pinnae
"	"	8-10*	9.5 (4)	"
Limit	"	7-13	10.0 (10)	
<i>U. Struthiopteridis</i>	<i>Matteuccia Struthiopteris</i>	13-14	13.5 (2)	Potted pl.
"	"	12-12	12.0 (2)	Cut pinnae
Limit	"	12-14	12.7 (4)	
<i>U. Woodsiae</i>	<i>Woodsia polystichoides</i> var. <i>nudiuscula</i>	8	8.0 (1)	Potted pl.
<i>U. intermedia</i>	<i>Athyrium acrostichoides</i>	15	15.0 (1)	Potted pl.
"	"	13-19	15.6 (3)	Cut pinnae
"	<i>Athyrium pterorachis</i>	15	15.0 (1)	Potted pl.
"	"	8-18	13.0 (3)	Cut pinnae
Limit	"	8-19	14.7 (8)	
<i>U. ossaeiformis</i>	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	15-21	18.0 (5)	Cut pinnae
"	"	12-17	14.5 (2)	Potted pl.
"	"	9-27*	17.9 (10)	Cut pinnae
Limit	"	9-27	17.2 (18)	
Extreme limits		5-27	5.0-17.9	
Limits of average period for species			8.0-17.2	

* Aecidiospores used for inocula were collected from the field, while others obtained from cultures.

of FAULL mentioned above. In *U. Struthiopteridis* and *U. intermedia* the periods somewhat agree with those in the inoculations with the aecidiospores.

TABLE 31. Developmental periods of uredosori produced by uredospore inoculations of some *Uredinopsis*

Species	Range	Average	Host inoc.	Condition of hosts
	No. of days			
<i>U. Struthiopteridis</i>	14-15	14.5 (2)	<i>Matteuccia Struthiopteris</i>	Pottel pl.
<i>U. intermedia</i>	11-21	16.0 (2)	<i>Athyrium pterorachis</i>	Cut pinnae
"	8	8.0 (1)	<i>Athyrium acrostichoides</i>	Cut pinnae
<i>U. ossaeiformis</i>	22-28	25.0 (2)	<i>Dryopteris dilatata</i> var. <i>oblonga</i>	Cut pinnae

(c) *Periods for appearances of uredosori obtained from inoculations with amphispores.* According to KLEBAHN (1916) in his experiments with the amphispores of *U. Struthiopteridis* on ferns the brownish discolorations occurred after about 20 days and the white spore horns appeared after about 25 days. In the present experiments in 17 cases with the amphispores of 4 species of *Uredinopsis*, results were obtained as shown in Table 32. These periods are apparently similar to those of the inoculations with aecidiospores described above.

TABLE 32. Developmental periods of uredosori produced as the result of amphispore inoculations of some *Uredinopsis*

Species	Range	Average	Host inoc.	Condition of hosts
	No. of days			
<i>U. filicina</i>	10-14	12.8 (4)	<i>Dryopteris Phegopteris</i>	Potted pl.
<i>U. Kameiana</i>	11	11.0 (1)	<i>Pteridium aquilinum</i> var. <i>japonicum</i>	Cut pinnae
<i>U. Struthiopteridis</i>	12-19	14.7 (8)	<i>Matteuccia Struthiopteris</i>	Potted pl.
"	16-17	16.5 (2)	"	Cut pinnae
<i>U. intermedia</i>	14-16	15.0 (2)	<i>Athyrium acrostichoides</i>	Cut pinnae

4. *Teleutospores.* FRASER (1913) in his inoculation experiments with the aecidiospores of *U. Struthiopteridis* detected the teleutospores on the infected fronds after 28 days from the inoculations. FAULL (1938 c) in five of the inoculation experiments of *U. longimucronata*

found the teleutospores on the infected fronds after 23–31 days. The writer in similar inoculation experiments with *U. Kameiana* found the corresponding teleutospores in the frond of the inoculated *Pteridium* host after about 10 days. Compared with the foreign cases, the writer's case was far shorter in formative period. To know why such a difference exists is left for future investigations.

D. HOST RESTRICTION

1. *Fir hosts.* Concerning the restriction of the occurrence of the peridermial phase of *Uredinopsis* species on *Abies*, FAULL (1938 c) already has said that there is apparently a generic host restriction, but few tests or observations have been made with respect to specific host resistance or specific rust aggressiveness. He mentioned also the results of heretofore published data on the cases in which the number of species of *Abies* proved to be inoculated by each special species of *Uredinopsis* and also the cases in which the number of the species of *Uredinopsis* each proved to attack special species of *Abies*. Including further experiments of the writer, the following revised presentation may be offered concerning the rusts in our country.

TABLE 33. The host relationship of the species of *Abies* to those of *Uredinopsis*

(A)	
Rust species	Species of <i>Abies</i> which are proved to be susceptible to special species of <i>Uredinopsis</i>
<i>Uredinopsis Struthiopteridis</i>	<i>Abies alba</i> , <i>A. balsamea</i> , <i>A. firma</i> , <i>A. Mayriana</i> and <i>A. sachalinensis</i>
<i>U. Kameiana</i>	<i>Abies balsamea</i> , <i>A. holophylla</i> , <i>A. Mayriana</i> , <i>A. nephrolepis</i> and <i>A. sachalinensis</i>
<i>U. ossaeiformis</i>	<i>Abies firma</i> , <i>A. Mayriana</i> and <i>A. sachalinensis</i>
(B)	
Species of <i>Abies</i>	Species of <i>Uredinopsis</i> which are proved to be parasitic on special species of <i>Abies</i>
<i>Abies balsamea</i>	<i>Uredinopsis americana</i> , <i>U. Atkinsonii</i> , <i>U. ceratophora</i> , <i>U. Kameiana</i> , <i>U. longimucronata</i> , <i>U. Osmundae</i> , <i>U. Phegopteridis</i> and <i>U. Struthiopteridis</i>
<i>A. Mayriana</i>	<i>Uredinopsis Adianti</i> , <i>U. Athyrii</i> , <i>U. filicina</i> , <i>U. hirosakiensis</i> , <i>U. intermedia</i> , <i>U. Kameiana</i> , <i>U. ossaeiformis</i> , <i>U. Struthiopteridis</i> and <i>U. Woodsiae</i>
<i>A. sachalinensis</i>	<i>Uredinopsis Kameiana</i> , <i>U. ossaeiformis</i> and <i>U. Struthiopteridis</i>
<i>A. firma</i>	<i>Uredinopsis ossaeiformis</i> and <i>U. Struthiopteridis</i>

2. *Fern hosts.* Heretofore, fern host restrictions of the species of *Uredinopsis* have been recorded by FRASER (1914), KAMEI (1930 a) and FAULL (1938 c). FAULL described the results of his experiments concerning *U. Struthiopteridis*, *U. americana*, *U. longimucronata*, *U. Phegopteridis* and *U. Osmundae*. The writer made similar experiments concerning eight species used as the materials in this study, as have already been treated in the respective section of each species and as summarized in Table 34.

TABLE 34. Summarizing results of inoculations testing fern host restrictions in *Uredinopsis*

Rust species	Fern hosts that indicated positive results	Fern hosts that indicated negative results
<i>U. Adianti</i>	<i>Adiantum pedatum</i>	<i>Athyrium Vidalii</i> , <i>Matteuccia Struthiopteris</i> , <i>Pteridium aquilinum</i> var. japonicum, <i>Thelypteris palustris</i> var. pubescens and <i>Woodsia polystichoides</i> var. nudiuscula
<i>U. Athyrii</i>	<i>Athyrium Filix-foemina</i> var. longipes	<i>Athyrium Vidalii</i> , <i>Dryopteris Phegopteris</i> , <i>Matteuccia Struthiopteris</i> , <i>Pteridium aquilinum</i> var. japonicum and <i>Thelypteris palustris</i> var. pubescens
<i>U. filicina</i>	<i>Dryopteris Phegopteris</i>	<i>Athyrium Filix-foemina</i> var. longipes, <i>Matteuccia Struthiopteris</i> , <i>Pteridium aquilinum</i> var. japonicum and <i>Thelypteris palustris</i> var. pubescens
<i>U. hirosakiensis</i>	<i>Thelypteris palustris</i> var. pubescens	<i>Athyrium Filix-foemina</i> var. longipes, <i>Dryopteris dilatata</i> var. oblonga, <i>D. Phegopteris</i> and <i>Matteuccia Struthiopteris</i>
<i>U. Kameiana</i>	<i>Pteridium aquilinum</i> var. japonicum	<i>Adiantum pedatum</i> , <i>Athyrium acrostichoides</i> , <i>A. Filix-foemina</i> var. longipes, <i>Dryopteris crassirhizoma</i> , <i>D. Phegopteris</i> , <i>Matteuccia Struthiopteris</i> , <i>Onoclea sensibilis</i> , <i>Osmunda cinnamomea</i> , <i>O. japonica</i> , <i>Polystichum tripterum</i> and <i>Thelypteris palustris</i> var. pubescens
<i>U. Struthiopteridis</i>	<i>Matteuccia Struthiopteris</i>	<i>Athyrium Filix-foemina</i> var. longipes, <i>A. Vidalii</i> , <i>Dryopteris dilatata</i> var. oblonga, <i>D. Phegopteris</i> , <i>Onoclea sensibilis</i> , <i>Pteridium aquilinum</i> var. japonicum and <i>Thelypteris palustris</i> var. pubescens
<i>U. intermedia</i>	<i>Athyrium acrostichoides</i> and <i>A. pterorachis</i>	<i>Dryopteris dilatata</i> var. oblonga, <i>D. Miqueliana</i> and <i>Thelypteris palustris</i> var. pubescens
<i>U. ossaeiformis</i>	<i>Dryopteris dilatata</i> var. oblonga and <i>D. monticola</i>	<i>Athyrium acrostichoides</i> , <i>A. pterorachis</i> , <i>Dryopteris crassirhizoma</i> , <i>D. Phegopteris</i> , <i>D. Miqueliana</i> , <i>Matteuccia Struthiopteris</i> , <i>Osmunda japonica</i> , <i>Polystichum Standishii</i> and <i>Thelypteris palustris</i> var. pubescens

E. DISCUSSION OF THE LIFE CYCLE

In the species of *Uredinopsis* that have been described up to this day, their host ferns, as recently mentioned by FAULL (1938 b), were known to be one to several species of various genera belonging to Polypodiaceae and Osmundaceae. FAULL (l.c.) listed thirteen genera of fern hosts. In Hokkaidô, as to the nine species of rusts under discussion, ten species of fern belonging to the genera, *Matteuccia*, *Woodsia*, *Dryopteris*, *Athyrium* and *Pteridium*, serve for the hosts. In these ferns, the fronds are mostly dead before snow-fall and the mycelium as well as the uredosori in the infected tissues are also dried up ceasing further growth. But the teleutospores and also the amphispores, being provided with hibernating ability, enter into the resting period when the host fern begins to die at the beginning of winter. So, these teleutospores in *Uredinopsis* should distinctly be considered as resting spores, although GÄUMAN (1926) said that they cannot be called teleutospores in the true sense. In some species of *Uredinopsis*, amphispores and teleutospores are formed together on one and the same frond of a host fern. So the abundance of the latter spore form is naturally restrained by the formation of the former spore form, just as suggested recently by CUMMINS (1936). FAULL (1938 c) recently said that "teliospores are abundant for all species growing in regions in which *Abies* is native." According to the personal observations of the writer specimens which possess an abundant number of amphispores were frequently seen to have a very meager quantity of teleutospores. Such an inclination was especially revealed on such specimens of *U. filicina*, *U. Kameiana* and *U. Struthiopteridis* as were used for basidiospore inoculation experiments. After overwintering, the teleutospores begin to germinate in the season from May to June at the time when the needles of *Abies* begin to unfold. FAULL (1929) has described in these cases, how the promycelium penetrates the cell wall of the epidermis of the fern host. In most cases, such areas, where the teleutospores are formed, were seen to be discolored and slightly shrunken. In the germination of the teleutospores such areas are covered by the accumulation of basidiospores and basidia presenting a whitish film-like layer. If the basidiospores thus germinated from these teleutospores were inoculated on the young needles of *Abies* just unfolded, they infect the leaves easily; and the spermogonia were seen on the discolored areas after about two weeks and the aecidia after about 3-4 weeks on the usual hosts. The results

of the infection experiments done by FRASER (1913, 1914), KLEBAHN (1916) and FAULL (1929, 1938 c) and the writer respectively in their independent experiments more or less agree with each other in these respects. The mature peridermial cups soon rupture at the apex to disperse the mature aecidiospores. According to FAULL (1938 c) concerning five species of *Uredinopsis* such a rupture occurs one to two days following the first appearance of the peridermia. If these spores were laid on the surface of the frond of a fern and opportunities were given for their germination, the germ-tube enters into the stomata to be developed into mycelia, that migrate through the intercellular spaces of the mesophyll of the fern hosts, and the uredosori are formed after about two weeks, though often somewhat longer in some species. In the neighborhood of the uredosori, the teleutospores are also formed on the apex of the hyphal branches, probably soon after the perfection of the uredosori. From the writer's observation on *U. Kameiana* and that of FAULL on five species of *Uredinopsis*, the incubation period from the inoculation of the aecidiospores to the formation of the new teleutospores was ascertained to be about one month at most. These teleutospores mature in the fall of every season and enter into the resting stage in the Hokkaidô. Consequently, in a mature teleutospore after germination beginning its developmental course of the heteroecious life cycle, under uninterrupted conditions, it will go through its course in the usual succession and again return by and by to the teleutospores after about two months so far as some species of *Uredinopsis* are concerned. Actually, the mature peridermia of the species of *Uredinopsis* develop perfectly, either in the culture or in the field, commonly from the end of June to the beginning of July. This is different from the typical species of *Milesina* which usually perfect their peridermia later in the season. However, one exceptional case was reported in *U. Pteridis* from Western America as already explained. In that species the peridermia appear after a longer developmental period on the second to fifth year needles of *Abies* somewhat similar to some species of *Milesina* and *Hyalopsora*. In this connection, WEIR and HUBERT (1917) explained on the life cycle that the teleutospores germinate in the late summer to infect *Abies* in the same season, and the rust overwinters as mycelium in the *Abies* leaf to produce aecidia in the following spring. But these assumptions must probably not be the case considering from the remark by HUNTER (1927) as well as the writer's conclusions obtained from the experimental results done on many species of fern rusts in Hokkaidô. WEIR and

HUBERT's opinion was merely deduced from assumption based upon the fact that the rust appears on the second year needles of *Abies* and not from the result of experiments upon which reasonable explanations must be based. As the life history experiments on *U. Pteridis* are yet incomplete, repeated trials are very desirable to learn for certain the course of development of this interesting species.

Further, the appearances of the uredo and teleutostages on fern hosts are also earlier in season than in the case of *Milesina* species. In *U. ossaeiformis*, however, the periods needed for the perfection of peridermial cups and uredosori were found to be slightly longer than in the case of the other usual species. Such elongation of the periods may indicate a character approaching the species of *Milesina*. If so, it corresponds quite well to some morphological characters that are nearly related to *Milesina*. In short, in the cases of the usual species of *Uredinopsis*, the course of the life cycle on firs and ferns is not particularly dissimilar from the cases of *Milesina*, but the developmental periods of each organ are somewhat shorter and appear earlier in season. Such knowledge of the differential developmental periods existing between two related genera of the white spored rusts is very important for the sake of the distinctive criteria of the species on *Abies* supplementing those of the morphological characters. According to FAULL (1938 c) the sequence of the appearance of these white rusts on *Abies* under natural conditions, is (1) *Uredinopsis*, (2) *Uredinopsis* and *Milesina*, (3) *Milesina*.

On the other hand, that the overwintered amphispores of some species of *Uredinopsis* infect the same fern host in the spring to produce ordinary uredospores was proved by KLEBAHN (1916) and the writer. The autoecious life cycle by means of the amphispores is proved beyond all doubt, as has already been mentioned by many authors such as DIETEL (1895), FAULL (1929, 1938 c), GÄUMAN (1926), ARTHUR (1934), CUMMINS (1936) and HIRATSUKA, f. (1936 c). Accordingly, one can find the same amphisporic rusts in the same locations every year, where there are no species of *Abies* growing immediately near by.

Moreover, near Sapporo, considering from the examination of specimens, it is concluded that if the conditions of the host are favorable, the amphisporic sori are developed already in the latter part of June to the first part of July, increasing especially toward the fall of the year. It is, however, interesting to note that in the rusts that have amphispores in their life cycle, the peridermial phases are also found to exist. For

instance, in *U. Kameiana* in the Hokkaidô, the peridermial sori were detected on fir leaves. Also, in *U. Struthiopteridis* a similar phase was reported to have been observed by FRASER in Nova Scotia. Considering these facts, it may be asserted that these amphisporic rusts may lead either kind of life cycle according to the conditions even in the same locality.

In the case of non-amphisporic rusts, the perpetuation of the same rust is sometimes observable in the locality where there are no trees of *Abies* growing near by. The present writer has observed such a case in *U. hirosakiensis* in some locations. By what means of overwintering the species of this rust group do propagate may probably be as suggested by FAULL (1938 b), who pointed out the ordinary uredospores as the actual agency. But on this point experimental proof is yet needed.

Concerning the host restriction of the species of *Uredinopsis*, as already said, the restriction to the fir hosts is rather loose while to the fern hosts, generally it is strictly limited only to a particular host or hosts. This fact is very significant in the study of fir rusts that have relation to some rusted ferns, because the several species of different fern rusts may affect at the same time even a single tree of a certain species of *Abies* in the same locality.

F. COMPARATIVE MORPHOLOGY

It has already been stated that the genus *Uredinopsis*, like other fern rusts, is a rather difficult group of rust fungi considered from the taxonomical as well as biological point of view. Accordingly, careful comparative studies on the morphology of these rusts are very desirable for the clear understanding of each species itself and for the affinity relationship with other kindred rusts. The need is especially keen in the stages of the peridermial phase. The following discussion may serve in some degree to throw light on the subject.

(1) *Spermogonium* stage

That the morphological characters of the spermogonia may be used in the taxonomy of the rust fungi was already stated in the works of FISCHER (1904), ARTHUR (1904), ARTHUR and KERN (1906), FAULL (1929) and HUNTER (1927, 1936 c). Restricted to *Uredinopsis*, the SYDOWS (1915) who referred *Peridermium balsameum* to *U. Struthiopteridis* inserted the spermogonial diagnosis as a part of the generic characters. ADAMS (1919 a) described the morphology of spermogonia of "*Perider-*

mium balsameum" which he referred to *U. americana*. BELL (1924), who also admitted that "*Peridermium balsameum*" was synonymous to several species of *Uredinopsis*, described the morphology of spermogonia in order to distinguish it from three other rusts on *Abies* in the district of Ontario. ARTHUR (1925, 1934) in the generic characters also mentioned this point and recently defined them thus, "Pyenia without paraphyses, often sunken into the tissues beneath the cuticle." He described the spermogonia of three species of *Uredinopsis* in his monograph. FAULL (1929) also gave critical notes on the morphological characters of the spermogonia common to the species of *Uredinopsis*. His opinion was that "in general there is a characteristic type of each genus" and "in some cases the forms within a type are distinctive for individual species." Recently the same author (1938 b) gave a precise description of the characters of the spermogonia in the species of *Uredinopsis*. HUNTER treated the spermogonia of six species of this genus. In her previous paper (1927) she summarized the morphology of the spermogonia in a tabular form, touching on the age of the host leaf, the shape, size and position of the spermogonia and the size of the spermatia. In another paper (1936 c) all the species of *Uredinopsis* studied by HUNTER were considered to belong to the "immersed" subdivision and to have spermogonia which are "hemispherical to conoidal" in sectional view.

As to the Japanese species, they have been already described by the writer (1932 b, 1934), but in this paper they may well be once more described comparatively.

The materials used for the study included specimens obtained from cultural studies as well as from field collections. The affected needles were fixed in CARNOY'S fluid or FLEMING'S week solution. They were mostly embedded in paraffin and sectioned with a microtome into about 10μ in thickness. The preparations were stained with safranin alone, or safranin in combination with DELAFIELD'S haematoxylin or light green. Sometimes hand sections were also used. In measuring the surface dimensions of the organs, fixed materials soaked in a mixture of chloroform and alcohol to remove the chlorophyll were especially suitable. Measurements of the height of the spermogonia were mainly obtained from the longitudinal sections along the longer axis of the needle.

1. *Color of the spermogonia.* In regard to the color of the spermogonia of some *Uredinopsis*, statements have already been made

by the SYDOWS (1915), FAULL (1929, 1938 b), KAMEI (1930 a, 1932 b 1934), HUNTER (1927) and HIRATSUKA, f. (1936 c). In nine species of *Uredinopsis* materials, they were all colorless.

2. *Age of the affected needles.* The age of the affected needles, on which the spermogonia of some *Uredinopsis* rusts appear, has already been stated by FAULL (1929, 1938 b), HUNTER (1927) and KAMEI (1930 a, 1932 b, 1934) to be in the first year. Regarding *U. Pteridis*, however, it was said by HUNTER (1927) that the spermogonia were on leaves of the second year of *Abies grandis*, while by ARTHUR (1934) that they issue "sparingly on first year leaves, abundantly on second year leaves with the aecidia." FAULL (1938 b) stated that the affected needles are second to fifth year. Concerning our materials on nine species, they were all on first year leaves. So, in the case of *U. Kameiana*, the age of the affected needles is quite dissimilar from that in the case of *U. Pteridis* of North America though the rust has been considered heretofore to be conspecific.

3. *Position of spermogonia.* The SYDOWS (1915) on one species; ARTHUR (1925, 1934) on five species; HUNTER (1927, 1936 c) on six species and FAULL (1938 b) on ten species of *Uredinopsis* said that the spermogonia are hypophyllous. ADAMS (1919 b) on *Peridermium balsameum* said that the spermogonia "are commonly found developing on both surfaces of the leaf." The present writer's study on nine species, leads him to divide them into two groups in this aspect. To the amphigenous group, belong the species *U. Adianti*, *U. Athyrii*, *U. hirosakiensis*, *U. filicina*, *U. Kameiana* and *U. Woodsiae*. To the hypophyllous group, belong *U. Struthiopteridis*, *U. intermedia* and *U. ossaeiformis*. In the amphigenous type, the most of the spermogonia appear to be hypophyllous while a small number of them are epiphyllous.

4. *Distribution of spermogonia.* The SYDOWS (1915) said about the spermogonia in *U. Struthiopteridis* that they are "sparsis," while BELL (1924) about those of *Peridermium balsameum* (referred to as "*Uredinopsis* on fern") "irregularly scattered," ARTHUR (1925) in *U. americana* and *U. Pteridis* "scattered," HUNTER (1927, 1936 c) and FAULL (1938 b) in *U. Atkinsonii* "usually isolated, very seldom confluent" and in *U. americana* "rarely confluent." According to the present writer's study, among nine species, the spermogonia were mostly scattered and discrete, but often confluent with each other. Sometimes they were developed very near the aecidia. HIRATSUKA, f. (1936 c) recently treated this point almost as stated in this paper.

5. *Number of spermogonia.* ARTHUR (1925, 1934) on *U. americana* said about the number of spermogonia that they are "few" and on *U. Pteridis* "rather numerous" or "moderately abundant." HUNTER (1927) said on *U. Osmundae* that they are "fewer" than on other related species, while on *U. Pteridis* "numerous." KAMEI (1930 a, 1932 b) has already made some statement on this aspect regarding some species in the Hokkaidô. In the present study on each nine species of rusts in question, the number of spermogonia per affected leaf and per square millimeter were carefully counted by means of a magnifying lens as shown in Table 35. In every species, except *U. intermedia* and *U. ossaeiformis*, the number of spermogonia per affected leaf varied from 10 to 211. The average number per leaf varied from 61.1 to 128.9 according to the species. The number per square millimeter varied from 4 to 30 averaging 17.3 to 22.3 according to the species. In *U. intermedia* and *U. ossaeiformis*, the number per leaf and per square millimeter was always less than in the other 7 species under discussion. Those of the above two rusts are somewhat near in number to those of *Milesina Miyabei* and *M. Itôana*, of which the type of the spermogonia is also similar in morphology.

TABLE 35. Number of spermogonia in 9 species of *Uredinopsis*

Species	Hosts	Range		Average*	
		per needle	per sq. mm.	per needle	per sq. mm.
<i>U. Adianti</i>	A.M. I ₅	10-186	14-30	128.9	22.3
<i>U. Athyrii</i>	" I ₈	10-100	11-32	61.1	18.5
<i>U. filicina</i>	" X ₈	25-113	4-22	72.5	18.1
<i>U. hirosakiensis</i>	" VI ₀	33-175	6-22	77.0	18.2
<i>U. Kameiana</i>	" VIII ₁₃	42-210	11-22	119.2	17.3
<i>U. Struthiopteridis</i>	A.s. II ₀	38-211	10-30	111.2	19.9
<i>U. Woodsiae</i>	A.M. IX ₁₁	45-124	13-29	88.7	21.4
<i>U. intermedia</i>	" X ₁₁	1- 17	2- 5	10.9	3.7
<i>U. ossaeiformis</i>	" XII ₈ ; A.f. IV ₀	5- 19	1- 6	11.4	3.4

* Average number of needles and areas examined for the number of spermogonia was in each case 10.

6. *Situation of spermogonia.* (a) *Face view.* For the inspection of the spermogonia in this respect, fixed materials were observed under a low-powered lens. In the usual seven species of *Uredinopsis*,

the organs were in every case situated on stomatal areas especially, in the spaces between stomata. In *U. intermedia* the ostioles were situated in the interstomatal spaces. In *U. ossaeiformis* they were always covered by the stomata so far as the writer has observed.

(b) *Sectional view.* ADAMS (1919 b) in *Peridermium balsameum* (referred to as *U. americana*) spoke of the spermogonia as depressing the tissues beneath and "giving the appearance of being subepidermal," while by HUNTER (1927) they are said to be subcuticular. Also in *Peridermium pseudobalsameum* (*U. Pteridis*), ARTHUR and KERN (1906) said them to be subepidermal, while later they were considered to be subcuticular by ARTHUR (1925). HUNTER (1927, 1936 c) and FAULL (1938 b) also in this species as well as some other American species stated them to be subcuticular. For the designation of the situation, HUNTER (1936 c) and FAULL (1938 b) used the term "immersed." In the usual seven species of *Uredinopsis* treated in this study, the spermogonia were always seen to be subcuticular (cf. Pl. IV, figs. a-h). Generally the organs develop inside the space between the cuticle and the outer walls of the epidermal cells. The organs frequently do not sink under the level of the epidermal cells appearing as if superficial. Often, however, the basal part was seen depressing or crushing the upper walls of epidermal cells to occupy the cell cavities or even depressing the underlying subepidermal cells. In such a case, the situation is represented by the term "immersed" as seen in the cases of *U. filicina* and *U. Athyrii*. In *U. ossaeiformis* and *U. intermedia*, the whole organ, even the maturer one, was situated under the epidermis. At maturity, the uppermost part of the organ was attached to or even raising the surface of the lower walls of the epidermis. Rarely some hyphae were seen in the inside of the cavities of a few epidermal cells just above the apex of the spermogonia. The organs have developed inside the mesophyll tissue and were seen to immerse more freely, so that they ultimately attained up to the depth of the two-thirds of the whole thickness of the needles; almost as deep as that of the aecidial sori. The peripheral part of each of these subepidermal spermogonia was surrounded by a thin pseudoparenchymatic mat of hyphae.

7. *Size of spermogonia.* ARTHUR (1925) and HUNTER (1927, 1936 c) mentioned the size of the spermogonia of *U. americana* and *U. Pteridis*. For those of *U. Phegopteridis*, *U. Osmundae*, *U. Atkinsonii*, *U. Struthiopteridis* similar data were also presented by HUNTER (1936 c). FAULL (1938 b) added those of *U. longimucronata* FAULL and *U. ceratophora*

FAULL. The size of the spermogonia of some Japanese species of *Uredinopsis* was mentioned by KAMEI (1930 a, 1932 b and 1934). The dimensions of the spermogonia of the materials at hand were measured as shown in Table 36. In these measurements the horizontal diameters were obtained both from the sectional and face views. In the sectional view, the measurements were made on the median sectional plane of the organs, but in the face view they were made along the shorter diameter of the organs which was almost at a right angle to the longer diameter. Owing to the variously directed situations of the spermogonia, the two directions along which the measurement were performed did not necessarily quite agree with both axes of the host needles. Moreover, it rarely happened that the sizes obtained from the face view exceeded those of the sectional view. At any rate, from the data obtained, in respect to the size of the organ, the species may be divided into two groups, the smaller and the larger. To the former group, belong those having subcuticular spermogonia as in the case of seven species of *Uredinopsis*. To the latter group belong two species of *Uredinopsis* having subepidermal spermogonia, viz., *U. intermedia* and *U. ossaeiformis*. Among the former group, those of *U. filicina* and *U. Kameiana*

TABLE 36. Size of spermogonia in nine species of *Uredinopsis*

Species	Range (μ)			Average (μ)*		
	Face view	Sect. view	Height	Face view	Sect. view	Height
<i>U. Adianti</i>	80-112	88 -165	46 - 77	100.0	111.7	61.8
<i>U. Athyrii</i>	80-112	88 -137.5	44.1- 77	91.6	115.9	61.9
<i>U. filicina</i>	56- 96	52.5-118	25.2- 64.5	74.4	82.2	48.1
<i>U. hirosakiensis</i>	80-128	74 -137	37 - 92.5	103.2	109.4	64.6
<i>U. Kameiana</i>	72-104	59.2-118	33 - 74	88.4	81.7	49.7
<i>U. Struthiopteridis</i>	72-120	69.3-129.5	29.3- 74	99.3	97.2	59.8
<i>U. Woodsiae</i>	80-120	84 -136.9	37 - 81.4	97.6	107.4	49.1
<i>U. intermedia</i>	121-198	143 -209	121 -187	161.2	172.3	147.3
<i>U. ossaeiformis</i>	154-220	137 -242	110 -207	187.0	180.5	161.6

The hosts from which the measurements were obtained are as follows:—
U. Adianti: A.M. I₅, *U. Athyrii*: A.M. I₅, *U. filicina*: A.M. II₅, X₅ and IV₁₀.
U. hirosak.: A.M. X₂ and VIII₅, *U. Kameiana*: A.M. V₃ and VIII₁₀, *U. Struthiopt.*:
A.f. II₆, A.M. IV₃ and X₅, *U. Woods.*: A.M. XI₅ and IX₁₁, *U. interm.*: A.M. XII₅
and VIII₅, *U. ossaeif.*: A.M. I₅ and A.f. IV₆.

* The average number was always of 20, except *U. intermedia* in which it was only of 12.

were smaller than those of the other species, especially of *U. Adianti* and *U. hirosakiensis*. In the case of *U. Struthiopteridis*, HUNTER (1936 c) recently gave measurements almost approximating the writer's on *Abies Mayriana*.

Among spermogonia of the species having larger spermogonia, the measurements for *U. intermedia* were smaller than those for *U. ossaeiformis*. They were in size somewhat near to those of *Milesina Itôana* and *M. Miyabei* in Hokkaidô.

8. *Shape of spermogonia.* The shape of the spermogonia was observed in two aspects, namely from above and as sectional view.

(a) *Face view.* The shape of the spermogonia in face view has not yet been reported in detail. In the usual seven species of *Uredinopsis* they were more or less elliptic to oblong in face view. The longer diameter of each organ was usually parallel but often oblique to the long axis of the affected needles. In the subepidermal ones of the two species, the shape from above appeared almost circular. General remarks regarding the shape of the organ of each species as viewed from above are as follows:

U. Adianti: elliptical, sometimes angular, often having irregular outline.

U. Athyrii: elliptical to circular having rather entire marginal line.

U. filicina: elliptical to circular having rather sinuate border line.

U. hirosakiensis: oblong, circular to polygonal, margin often irregular.

U. Kameiana: elliptical to oblong having irregular margin.

U. Struthiopteridis: elliptical, circular to polygonal, margin often entire.

U. Woodsiae: elliptical, circular to angular, margin not entire.

U. intermedia: almost circular.

U. ossaeiformis: more or less circular with irregular margin.

(b) *Sectional view.* On the shape of the sectional view of the spermogonia of some species of *Uredinopsis* descriptions have already been made by the SYDOWS (1915), BELL (1924), ARTHUR (1925, 1934), HUNTER (1927, 1936 c), KAMEI (1930 a, 1932 b, 1934), HIRATSUKA, f. (1935 e) and FAÛLL (1938 b). Among these authors, HUNTER (1936 c) who studied most extensively on the spermogonia of six American species of *Uredinopsis* applied the terms "hemispherical" or "hemispherical, shallow" or "hemispherical, vertically elongated" according to the

species. FAULL (1938 b) described them as "inverted hemispherical." In the present study, the sectional shape of the organ of the usual seven species was found to be somewhat variable in different materials of the same species. Among them, however, superficial and subconoidal shape were seen in the cases of *U. Adianti*, *U. hirosakiensis*, *U. Kameiana* and *U. Woodsiae* (cf. Pl. IV, figs. a, d, e, f and h). Rather immersed and lens to hemispherical shape was seen in the case of *U. Athyrii* and *U. filicina* as shown in Pl. IV, figs. b and c. Confluent spermogonia were more frequently seen in the cases of *U. Adianti*, *U. Kameiana* and *U. Woodsiae*. In such a case, the sectional shape was somewhat different from that of isolated organs. In the case of subcuticular spermogonia, they approximated to or assumed somewhat similar shape to those of a usual species of *Milesina*. In detail, the spermogonia of *Uredinopsis* were more superficial and more frequently bordered with irregular outlines. FAULL (1929) also said that the spermogonia of *Milesina intermedia* and *Uredinopsis americana* may be distinguished from each other by the shape of the organ and the length of the basal cells as well as by the compactness of the spermatophores. In *U. ossaeiformis* and *U. intermedia* the organs were more or less spherical as shown in Pl. IV, figs. i and j. Sometimes they were vertically a little elongated and somewhat piriform. These sectional shapes are also like those of the spermogonia of *Milesina Itôana* and *M. Miyabei*. For distinction between them one must rely upon other criteria such as the characters of the peridial cells and the developmental period.

9. *Openings*. HUNTER (1927, 1936 c) mentioned the dimensions of the openings of the spermogonia of *U. Atkinsonii*, *U. Phegopteridis*, *U. Osmundae* and *U. americana*. In the usual species of *Uredinopsis*, openings were mostly elongated to become lens-shape or slit-like in face view. Sometimes they were so broadened as to appear angular to roundish. They were mostly situated at the central place of each organ and were usually elongated parallel with the longer axis of the needles. Sometimes in the confluent organs, the openings also become united and much elongated. The length of the opening was sometimes so small as to be about one-fourth of the organ, but often it attained to the whole diameter of the spermogonia. The writer's measurements on those of nine Japanese species are collated in Table 37. HUNTER's data on the dimensions in *U. Osmundae* somewhat approximate those of the present seven ordinary species of *Uredinopsis*, but in the case of the other three American species, her measurements are much smaller than the writer's.

In *U. ossaeiformis*, the openings were always stomatal slit-like and almost elliptic in shape. Brownish substance was usually seen to be oozing out from or deposited under the stomata. In *U. intermedia*, openings were in interstomatal spaces and appeared to be pore or short slit-like. In this respect also the two species of *Uredinopsis* approach near to *Milesina Itôana*, *M. Miyabei* and *M. polypodophila*.

TABLE 37. Size of openings of spermogonia in nine species of *Uredinopsis*

Species	Hosts	Range (μ)		Average (μ)*	
		Length	Width	Length	Width
<i>U. Adianti</i>	A.M. I ₅	40-80	16-32	61.6	24.0
<i>U. Athyrii</i>	" I ₅	24-88	12-32	59.2	17.0
<i>U. filicina</i>	" IV ₁₀	24-86	12-32	56.2	18.4
<i>U. hirosakiensis</i>	" VIII ₅	48-104	12-64	79.2	27.6
<i>U. Kameiana</i>	" VIII ₁₃	10-96	10-24	56.7	14.6
<i>U. Struthiopteridis</i>	A.f. II ₆	32-120	8-32	72.0	19.2
<i>U. Woodsiae</i>	A.M. IX ₁₁	40-120	20-56	82.4	34.8
<i>U. intermedia</i>	" X ₁₁	32.5-84.5	13-45.5	50.7	29.9
<i>U. ossaeiformis</i>	A.f. IV ₆	32.5-39.0	19.5-19.5	35.8	19.5

* The average number was of 10 in all species except *U. ossaeiformis* in which it was only of 2.

10. *Spermatiphores*. ADAMS (1919 b) on the spermatiphores of the spermogonia of *Peridermium balsameum* said that "they are broad at the bases, short and tapering towards their free ends which converge towards the upper central region of the hemispherical fruit body." HUNTER (1927) once said on the spermatiphores of *Uredinopsis*, "the basal cells are long and tubular, narrowing toward their upper ends" and "this was thought to be an aid in distinguishing *Uredinopsis* species from *Milesina* species" but in the second report (1936 c) she amended her statement by saying that the feature is likewise found in the species of *Milesina*. FAULL (1938 b) stated, in most of the American *Uredinopsis*, "spermatiphores unbranched, septate, with large basal cell." In the usual species of the present *Uredinopsis* materials, the spermatiphores were always somewhat tapering toward the apex, septated and simple as shown in Pl. VII, fig. 17 a-f. They originated from the basal cell of the hyphal mat of each spermogonium and converged toward the upper middle of the organ, where almost no space was observable unlike the case of some *Milesina* species. The minute morphological differences

according to the species in respect to this point, have not yet been fully observed. In the two species of *Uredinopsis* in which the subepidermal spermogonia are seen, the spermatophores were distinctly branched at the basal portions as well as from the basal cells of the stroma (cf. Pl. VII, fig. 17 d). So, in this point the two types of spermogonia could be distinguished.

11. "*Flexuous hyphae.*" HUNTER (1936 c) in the species of *Milesina* recently described the presence of "flexuous hyphae," which term was first used by CRAIGIE (1933) in the case of *Puccinia Helianthi* SCHW. In her conclusion and summary (No. 6) HUNTER said "the spermogonia of the Melampsoraceae lack paraphyses. But 'flexuous hyphae' possibly receptive organs, extending beyond the aperture of the spermogonium have been found in numerous species of the Melampsoraceae." In *U. intermedia* and *U. ossaeiformis* there were also frequently seen characteristic paraphyses-like organs situated between spermatophores. They were unseptated, thicker in diameters and longer than spermatophores (Pl. VII, fig. 17 d and e). They were often somewhat inflated at the apex. The writer has often observed similar organs also in the species of *Milesina*, which will be mentioned later. From this character also these two species mentioned above are reasonably presumed to be closely related to *Milesina*. Whether the hyphae in question are truly such as CRAIGIE reported in *Puccinia* or not can not here be stated definitely, but the identity of the hyphae with HUNTER's description in *Milesina* is beyond all doubt.

12. *Size of spermatia.* The size of the spermatia of some species of *Uredinopsis* has been previously described by HUNTER (1927, 1936 c) in several species of *Uredinopsis*. FAULL (1938 b) mentioned size of the spermatia of *U. longimucronata*, *U. Phegopteridis* and *U. Struthiopteridis*. About Japanese species, previous mention on this respect has been made by KAMEI (1930 a, 1932 b). Comparing the spermatia of the nine species of *Uredinopsis* now under consideration some definite differences according to the species were noted. However, a fully accurate statement of the size differences must await the calculation of a greater number. In this study, as shown in Table 38, only twenty spores for each species were carefully selected from fixed and preserved materials gained from the inoculation experiments. So far as the measurements are concerned, the longest case was seen in *U. Adianti* and the shortest in *U. Athyrii*, the thickest case in *U. hirosakiensis* and the thinnest in *U. Struthiopteridis*. Comparing with the measurement

of *U. Struthiopteridis* by FAULL (1938 b) the writer's quite agrees with his. Concerning *U. ossaeiformis* and *U. intermedia* in which the spermatogonia are subepidermal and somewhat related to *Milesina*, the size of the spermatia was rather more similar to usual species of *Uredinopsis* than to some species of *Milesina*. Comparing with HUNTER's data on *U. Atkinsonii*, *U. Phegopteridis*, *U. Osmundae* (1927) and *U. americana* (1936 c) the present species were universally somewhat larger in respect to the length of the spermatia but their thickness was almost the same.

13. *Shape of spermatia.* ADAMS (1919 b, p. 56) in *Peridermium balsameum*, said that the shape of spermatia is "elliptical and pointed at both ends." HUNTER (1936 c) in *U. Atkinsonii* and *U. americana*, stated that the shape of the spermatia is "oval." In the present materials the mature spermatia were more or less narrowly elliptic to almost elliptic. The ratio of the longer and shorter diameters shows that the former is 2.7 to 4 times the latter. The end of each spore was either truncated, subapiculated or rounded. Larger rod-like shape was especially predominant in the case of *U. Adianti* and the shorter, almost elliptical spores were seen in *U. hirosakiensis*, *U. Kameiana*, *U. Athyrii* and *U. Woodsiae*. The shape of the spermatia of *U. intermedia* and *U. ossaeiformis* was not essentially different from that of the usual species of *Uredinopsis*. Previous statements on this point of the Japanese species were made by KAMEI (1930 a, 1932 b).

TABLE 38. Size of spermatia in nine species of *Uredinopsis*

Species	Hosts	Range (μ)		Average (μ)*		Ratio
		Length	Width	Length	Width	
<i>U. Adianti</i>	A.M. I ₅	5.0-6.0	1.2-1.6	5.27	1.30	4.05
<i>U. Athyrii</i>	" I ₈	4.0-4.5	1.2-1.5	4.03	1.26	3.19
<i>U. filicina</i>	" X ₃	4.0-5.0	1.2-1.9	4.61	1.39	3.31
<i>U. hirosakiensis</i>	" VIII ₅	4.0-5.0	1.2-2.0	4.23	1.54	2.74
<i>U. Kameiana</i>	" III ₁₁	3.5-5.5	1.0-2.0	4.23	1.39	3.04
<i>U. Struthiopteridis</i>	A.f. II ₀	4.0-5.0	1.0-1.9	4.47	1.25	3.57
<i>U. Woodsiae</i>	" XI ₇	4.0-5.5	1.2-2.0	4.75	1.43	3.32
<i>U. intermedia</i>	" X ₁₁	4.0-6.0	1.2-2.0	4.95	1.53	3.23
<i>U. ossaeiformis</i>	A.f. IV ₀	4.0-5.0	1.2-2.0	4.26	1.45	2.93

* The number of specimens averaged was always 20.

(2) *Aecidium stage*

Concerning the aecidium stage of the species of *Uredinopsis*, FRASER

(1913), who connected several species of *Uredinopsis* to *Peridermium*, revealed the difficulty in distinguishing each species by the morphological characters. KLEBAHN (1914) referring to FRASER's experiments just mentioned above, said that these groups must be of biologic species similar to the cases of *Caeomas* on *Larix* and *Peridermiums* on *Pinus* needles which were produced from his experiments. BLASDALE (1919) stated the aecidial stage of *Uredinopsis* to be similar to *Coleosporium*, which is quite different in the shape and color of the aecidium. ARTHUR (1925, 1934) also recognized the very close morphological characters of the aecidia of some American *Uredinopsis*. HUNTER (1927, 1936 c) who laid great stress on the taxonomic value of the morphology of spermogonia treated the characters of aecidium sori as of minor importance. However, from his own experience, the present writer cannot disregard those minute, but constant morphologic differences existing between each aecidium stage, particularly in peridial cells of the different species of *Uredinopsis*. Our example, in which this feature was most conspicuously represented, has been published by the writer (1934). It is very interesting to refer here to such publications by KLEBAHN (1914), ARTHUR and KERN (1914), MIYABE (1915), COLLEY and others (1927) and FAULL (1938 a, 1938 b) all of whom recognized more or less striking morphological differences of each aecidium of various species of *Caeoma* and *Peridermium*. In this study, the following comparisons are made in the hope that they may explain more clearly the distinctions existing among the materials under consideration.

For the materials used in the study of peridial cells, fresh as well as herbarium specimens were used. As the markings of the peridial cells are so minute and delicate that they are insufficiently differentiated by the ordinary magnifications, they were always inspected by means of combinations of the lenses such as Zeiss compensation oculars and Zeiss apochromatic objective having a focal distance of 2 mm. and numerical aperture of 1.3. The materials used for aecidiospore measurements were also obtained from fresh as well as herbarium specimens. In the latter case, the spores were mounted in a dilute solution of KOH (0.01 percent diluted with distilled water) and in the former case mounted directly in distilled water. Measurements were made with a well-calibrated microscope so adjusted as to make one section of the micrometer equivalent to 1 micron.

1. *Age of needles on which aecidia appear.* As for *U. americana* and *U. Osmundae*, ARTHUR (1925, 1934) said that the aecidia grow on

needles of the current season. KAMEI (1930 a, 1932 b, 1934) also stated that such is common to the Japanese species. About *U. Pteridis* of North America, however, American authors such as WEIR and HUBERT (1917), HUBERT (1931),¹ ARTHUR (1925, 1934), FAULL (1929, 1938 b), HUNTER (1927, 1936 c) and BOYCE (1938) stated that aecidia occur on second year or second to fifth year needles. But in *U. Kameiana* peculiar to Japan, the needles affected are always of the current season.

2. *Position of needles on which aecidia appear.* WEIR and HUBERT (1917) in *U. Pteridis* said that the aecidia issue hypophyllously. ADAMS (1919 b) stated that the aecidia of *U. americana* are "formed irregularly in two rows on the underside of the leaves." In *U. americana* and *U. Osmundae* it was reported by ARTHUR (1925, 1934) that the aecidia appear hypophyllously. FAULL (1938 b) also said respecting several species of *Uredinopsis* that the aecidia are "hypophyllous." In the present writer's nine species, the aecidia of *U. Athyrii*, *U. filicina*, *U. Struthiopteridis* and *U. intermedia* were all hypophyllous. In *U. Adianti*, *U. hirosakiensis*, *U. Kameiana*, *U. Woodsiae*, and *U. ossaeiformis* the aecidia were mostly hypophyllous but some of them epiphyllous. Concerning those nine species almost similar statements have previously been made by KAMEI (1930 a, 1932 b).

3. *Number of aecidial sori per affected needle.* Up to the present, the number of aecidial sori of any species of *Uredinopsis* has not been reported. As shown in Table 39, among the usual seven species of *Uredinopsis*, 38 sori per leaf in one case of *U. Kameiana* was the most abundant example, while on the other hand, there were observed such

TABLE 39. Number of aecidial sori in nine species of *Uredinopsis* per affected needle

Species	Hosts	Range	Average
<i>U. Adianti</i>	A.M. I ₃	1-30	11.2 (50)*
<i>U. Athyrii</i>	" IX ₃ , IX ₅ , I ₃	10-32	14.6 (16)
<i>U. filicina</i>	" II ₃	2-16	8.3 (12)
<i>U. hirosakiensis</i>	" X ₂ , VIII ₅ and Tomakomai material	1-19	7.2 (121)
<i>U. Kameiana</i>	" IV ₈ , III ₁₁ , VIII ₁₃	2-38	13.4 (35)
<i>U. Struthiopteridis</i>	" V ₂ , A.f. II ₆ ; A.M. IV ₃ , XII ₆	5-22	12.0 (12)
<i>U. Woodsiae</i>	" IX ₁₁	4-36	15.4 (10)
<i>U. intermedia</i>	" VIII ₃ , XII ₃ , XII ₅	1-12	6.3 (59)
<i>U. ossaeiformis</i>	" XX ₄	4-18	10.1 (23)

* The number inside of parentheses shows number of needles observed.

cases as only one sorus on a diseased leaf in several species. Generally, there was indicated an inclination for groups of species which have an abundant number of spermogonia, also to have an abundance of aecidial sori. In those species such as *U. ossaeiformis* and *U. intermedia*, in which a smaller number of spermogonia were seen, the number of aecidial sori also attained to rather a small average.

4. *Dimensions of aecidial sori.* (a) *Height of aecidium cups.* Concerning the height of the aecidium cups of the species of *Uredinopsis*, in *U. Pteridis* WEIR and HUBERT (1917) stated it to be 1.5–2.6 mm.; ARTHUR (1925) 0.7–1.0 mm. and FAULL (1938 b) up to 2 mm. FAULL (l.c.) also on 15 other species mentioned that they vary from 0.3–2 mm. Regarding some species of Japan, the present writer (1930 a, 1932 b) has made mention of this point in the descriptions. The result of the present study is presented in Table 40. Throughout all the materials, the height ranges from 0.5 to 1.5 mm., and only in this respect they can not be distinguished from each other.

TABLE 40. Height of aecidial cups in nine species of *Uredinopsis*

Species	Hosts	Height (mm.)*	Species	Hosts	Height (mm.)
<i>U. Adianti</i>	A.M. I ₅	Up to 1.0	<i>U. Struthiopteridis</i>	A.f. II ₀	0.5–1.0
<i>U. Athyrii</i>	" I ₈	0.7–1.3	<i>U. Woodsiae</i>	A.M. IX ₁₁	1.0
<i>U. flicina</i>	" II ₃	0.8–1.3	<i>U. intermedia</i>	" VIII ₃ , XII ₅ , XII ₅	0.6–1.2
<i>U. hiroasakiensis</i>	" VIII ₅	0.6–1.2	<i>U. ossaeiformis</i>	A.f. IV ₀	0.5–1.1
<i>U. Kameiana</i>	" VIII ₁₃	1.0–1.5			

* The number of specimens from which the ranges were determined varied considerably.

(b) *Diameters of aecidial cups.* Regarding the diameters of the aecidium cups of *Uredinopsis*, WEIR and HUBERT (1917) on *U. Pteridis* stated it to be 0.2–0.4 mm., ARTHUR (1925) on the same species, 0.4–0.6 mm. and *U. americana*, 0.2–0.5 mm., FAULL (1938 b) in 16 species of *Uredinopsis* stated that they vary from 0.1 to 0.5 mm. The writer (1930 a, 1932 b) gave figures for some species of *Uredinopsis*. As shown in Table 41, in which are collated the measurements of ten mature aecidial cups for each species of *Uredinopsis*, the range of the longer diameters is indicated to be 160 to 600 μ and that of the shorter diameters 160–440 μ . The largest diameters were observed in the case of *U. hiroasakiensis* while the smallest in *U. Adianti*. But so far as the dia-

meters only are concerned, a person can hardly discriminate one species from another.

TABLE 41. Diameters of acedial cups in nine species of *Uredinopsis*

Species	Range (μ)		Average (μ)*		Ratio
	Long. diam.	Short. diam.	Long. diam.	Short. diam.	
<i>U. Adianti</i>	160-320	160-264	254.4	225.6	1.12
<i>U. Athyrii</i>	240-400	184-360	308.8	260.4	1.18
<i>U. filicina</i>	200-320	176-280	273.6	252.8	1.08
<i>U. hirosakiensis</i>	360-600	240-440	450.8	364.0	1.23
<i>U. Kameiana</i>	280-400	260-360	340.0	300.0	1.13
<i>U. Struthiopteridis</i>	200-320	192-320	258.4	240.0	1.07
<i>U. Woodsiae</i>	240-400	160-360	319.2	278.4	1.14
<i>U. intermedia</i>	210-357	189-336	256.1	241.9	1.06
<i>U. ossaeiformis</i>	275-363	241-363	302.5	288.1	1.04

* The number of specimens averaged was 10. The host plants from which the materials were gained were the same as those indicated in Table 40.

5. *Peridial cells.* (a) *Combination of peridial cells.* Concerning the combination of the peridial cells of some species of *Uredinopsis*, WEIR and HUBERT (1917) described it in *U. Pteridis* to be "overlapping," while ARTHUR (1925) in *U. Pteridis* and *U. americana*, "somewhat overlapping." The writer (1930 a, 1932 b) and HIRATSUKA, f. (1936 c) respectively on some species, described them as "overlapping" or "slightly overlapping." FAULL (1938 b) in American species described them as "overlapping" or "much overlapping." In the materials of this study, the acedium cups are made of many longitudinal rows of cells that abutted side by side and at maturity broke at the apex of the cups and did not split longitudinally as in the cases of *Roestelia*. Also in most of the materials, peridial cells of each longitudinal row were more or less overlapping at each end and usually rather firmly jointed with each other. In *U. hirosakiensis* and less markedly in *U. Kameiana*, however, the cell combinations were rather loose so that if a bit of mature peridium were mounted in water and pressed gently the cells were usually seen to be separated from one another.

(b) *Shape of peridial cells.* WEIR and HUBERT (1917) on *U. Pteridis* spoke of the cells as "majority rhomboid." ARTHUR (1925) in *U. americana* and *U. Pteridis* described them to be "polygonal or angularly ellipsoid in face view." FAULL (1938 b) called them

"polygonal, elongated vertically." Each peridial cell of our materials, as already shown by KAMEI (1930 a, 1932 b), was much flattened, the thickness being commonly far less than the length and breadth and the side view being mostly long and thin. So, in the loose mounts of a bit of the peridium in most cases the face view was seen while the side view was quite rarely seen. As for the materials concerned, generally speaking, the cells were rather elongated vertically and seen to be irregularly tetragonal or pentagonal to hexagonal, while very often also they were rounded at the margin to present an elliptical or oval appearance. But they were not so long and narrow as seen in those of some species of *Pucciniastrum*, of which have already been described by KLEBAHN (1899), DARKER (1929) and HIRATSUKA, f. (1936 c) respectively. To conclude, there hardly exist any clear discriminative criteria among the species of *Uredinopsis* as far as the shape of the peridial cells only is concerned.

(c) *Size of peridial cells in face view.* Also concerning the size of the peridial cells of some species of *Uredinopsis*, statements have already been made by WEIR and HUBERT (1917), ARTHUR (1925), KAMEI (1930 a, 1932 b), and FAULL (1938 b). In the present study the size of 50 mature peridial cells of each species was measured as shown in Table 42. The longer cells were found in *U. filicina*, *U. Athyrii* and *U. Kameiana* and the shorter ones in *U. Struthiopteridis*, *U. hirosakiensis* and *U. Woodsiae*. The wider cells were seen in *U. Woodsiae* and *U. filicina* and narrower ones in *U. hirosakiensis*. Comparing with those of *U. Struthiopteridis* described by FAULL (1938 b) the writer's measurements in the same species are somewhat smaller.

TABLE 42. Size of peridial cells in nine species of *Uredinopsis*

Species	Hosts	Range (μ)		Average (μ)	
		Length	Width	Length	Width
<i>U. Adianti</i>	A.M. I ₅	20.9-41.8	12.9-25.7	31.97	18.87
<i>U. Athyrii</i>	" IX ₃	24.1-51.5	11.3-25.7	36.80	17.64
<i>U. filicina</i>	" X ₃	28.8-48.3	14.5-25.7	38.09	19.22
<i>U. hirosakiensis</i>	" VIII ₅	20.9-40.2	8.1-24.1	28.52	16.45
<i>U. Kameiana</i>	" IV ₈	25.7-45.1	12.9-28.9	36.22	18.76
<i>U. Struthiopteridis</i>	" XXII ₆	17.6-36.8	9.6-20.8	27.49	15.19
<i>U. Woodsiae</i>	" XI ₅	22.2-37.8	12.6-31.5	29.10	20.12
<i>U. intermedia</i>	" VI ₃	24.1-40.2	14.5-29.0	34.33	18.90
<i>U. ossaeiformis</i>	A.f. IV ₆	25.6-43.2	11.2-27.2	33.64	20.02

(d) *Thickness of peridial cells.* In nine species of *Uredinopsis*, the thickness of the peridial cells of the aecidia were measured as shown in Table 43. The thicker inner walls were seen in *U. Athyrii*, *U. filicina* and *U. intermedia*, while the thinner ones in the cases of *U. Kameiana* and *U. Struthiopteridis*. In the outer walls the thicker ones were seen in *U. Athyrii* and *U. Adianti*, while the thinner in *U. Struthiopteridis*. The writer (1930 a) previously gave the thickness of the inner walls of *U. Kameiana* as 3-7 μ and the outer almost 1 μ . Further investigations, however, revealed that the inner walls are still thinner indicating a more great difference comparing to the measurements of *U. Pteridis* in Western America which heretofore has been treated as conspecific with *U. Kameiana*. ARTHUR (1925) in *U. americana* said the inner walls were 4-7 μ and the outer ones 1-3 μ , while FAULL (1938 b) gave for the inner walls 2.5-3.0 μ and for the outer 1.0-1.2 μ . The writer (1932 b, 1934) already described concerning some species of our country in this respect. In *U. Struthiopteridis*, comparing to the measurement of FAULL (1938 b), the thickness of the outer wall is thinner in the case of our material.

TABLE 43. Thickness of peridial cell-walls in nine species of *Uredinopsis*

Species	Hosts	Range	
		Inner walls(μ) *	Outer walls(μ)
<i>U. Adianti</i>	A.M. I ₅	2.5-5.5	1.0-2.0
<i>U. Athyrii</i>	" IX ₃	3.0-7.0	1.0-3.0
<i>U. filicina</i>	" X ₃	3.0-6.0 (Rarely 10)	0.5-1.0
<i>U. hirosakiensis</i>	" VIII ₅	2.0-4.0	0.6-1.0
<i>U. Kameiana</i>	" VI ₃	1.5-2.0	0.5-1.0
<i>U. Struthiopteridis</i>	" XII ₆	2.0-3.0	0.3-0.5
<i>U. Woodside</i>	" IV ₈	2.0-3.0 (Rarely 5)	1.0-1.2
<i>U. intermedia</i>	" XXII ₀	3.0-5.0 (Rarely 7)	0.6-1.5
<i>U. ossaeiformis</i>	" XI ₅	1.0-3.0	0.5-1.0

* Inner wall thickness here means the thickness of walls including tubercles. The number of peridial cells examined varied considerably.

(e) *Markings of inner walls of peridial cells.* Heretofore, on *U. americana* and *U. Pteridis* in North America and on some species of our *Uredinopsis*, the markings of the peridial cells have been reported

in the descriptions made by WEIR and HUBERT (1917), ARTHUR (1934), KAMEI (1930 a, 1932 b, 1934), HIRATSUKA, f. (1936 c) and FAULL (1938 b). There is no published comparative study, and it has generally been believed that there are "no morphological differences in the aecidial stage" as concluded by ARTHUR (WEIR and HUBERT, 1917, p. 327). Following the suggestion by Professor MIYABE, and referring to publications by KERN (1910, 1911) on *Gymnosporangium*, the writer inspected very carefully the markings of the inner surface in the cells of aecidia of our materials in *Uredinopsis* and recognized considerable distinctions especially under high-power lens. The markings, that is, the arrangement of elevated projections in the intervening lower spaces as well as the shape of each projection or tubercle showed some constant differences according to the species as already shown by the writer (1934). The markings seen in face view can be grouped into three types, namely, the finely verrucose type, the coarsely verrucose one and the striately or alveolately marked one. Under the types, the characters of the markings for each species are explained by the following remarks, and also by Pl. VI, figs. a-i.

1. *Finely verrucose type.*

- a) The tubercles are slender, tubular and closely studded, regular in projectional shape *U. Adianti*
- b) The tubercles are slender, tubular and less closely studded, regular in projectional shape *U. Woodsiae*
- c) The tubercles are more slender, tubular, and closely studded, regular in projectional shape *U. Struthiopteridis*

2. *Coarsely verrucose type.*

- a) The tubercles are coarser, low, sparsely distributed, irregular in projectional shape *U. Kameiana*
- b) The tubercles are coarser, more elevated, sparsely distributed, regular in projectional shape *U. flicina*
- c) The tubercles are coarser, low, closely distributed, regular in projectional shape *U. intermedia*
- d) The tubercles are coarser, more elevated, closely distributed, regular in projectional shape *U. Athyrii*

3. *Finely striate type.*

- a) The tubercles are ridge-like, very often connected with each other in an alveolar manner *U. hiroasakiensis*

b) The tubercles are finer, low, connected to make longitudinal striations *U. ossaeiformis*

The existence of these distinctions in the markings of the peridial cells of some other species of *Uredinopsis* can also be recognized from the descriptions made recently by FAULL (1938 b). It is very reasonable that COLLEY et al. (1927) in the study of the *Peridermium* of a *Cronartium* remarked "further work will probably show peridial characters to be as important for the *Peridermium* group as KERN (6) has found them to be for *Gymnosporangium*."

6. *Aecidiospores*. (a) *Variation in size of aecidiospores*. Concerning the size of the aecidiospores of some species of *Uredinopsis*, WEIR and HUBERT (1917), ARTEUR (1925, 1934), KAMEI (1930 a, 1932 b, 1934) and FAULL (1938 b) respectively reported data derived from their original observations. In the present paper, the variation in the size of the aecidiospores obtained from the writer's own culture works is presented in the following pages. The writer measured 200 mature aecidiospores of each of the nine species of *Uredinopsis* under question, all of which came from artificial culture experiments. Conditions of the experimental host plants were assumed to be approximately similar. Here, by the length and the width are meant the distance from the end of the tubercles on one side of the spores to the end of the tubercles on the other side of the spore axis. The biometric constants of each species are as shown in Table 44. From the table, it may be seen that the longer spores appear in *U. ossaeiformis*, *U. Struthiopteridis* and *U. Adianti* while the shorter ones in *U. hirosakiensis* and *U. Athyrii*. The wider spores are seen in *U. Struthiopteridis*, *U. Adianti* and *U. ossaeiformis*, while the narrower ones in *U. intermedia*, *U. Athyrii*, *U. hirosakiensis* and *U. filicina*.

As shown in Table 45, the difference of the size of aecidiospores of each species was always significant in both diameters or in either of the two diameters except in only one case, namely in the comparison of *U. Kameiana* with *U. Woodsiae*, where the differences of two diameters are both so small that they must be considered alike and can not be admitted as different species so far as the data are concerned. From this fact one can imagine that some species of *Uredinopsis* are very similar in the size of aecidiospores. In such a case, for their distinction, one must rely upon other criteria. Concerning *U. Struthiopteridis*, the measurements of aecidiospores given by FAULL (1938 b) are rather

TABLE 44. Variation and constants of size of aecidiospores in nine species of *Uredinopsis* obtained from cultures on *Abies Mayriana*

Species	Hosts	Spore classes (μ)																													Constants		
		Length																													Mean (μ)	St. deviat.	C. of var.
		10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31										
<i>U. Adianti</i>	A.M. I ₅	1 3 14 15 42 42 35 26 9 6 2 3 2																													21.25±0.09	2.07±0.07	9.76±0.33
<i>U. Athyrii</i>	" IX ₃	2 2 7 20 43 42 38 27 8 5 2 4																													18.18±0.09	1.91±0.06	10.50±0.50
<i>U. filicina</i>	" II ₃	1 2 7 15 26 34 30 35 28 15 3 4																													18.96±0.10	2.11±0.07	11.15±0.37
<i>U. hirosakiensis</i>	" VIII ₆	1 2 9 22 47 53 43 17 5 1																													17.83±0.07	1.48±0.05	8.31±0.28
<i>U. Kameiana</i>	" III ₁₁	1 2 15 37 49 49 23 5 9 4 4 2																													20.73±0.08	1.93±0.07	9.21±0.31
<i>U. Struthiopteridis</i>	" IV ₃	2 3 16 21 50 48 31 15 10 3 1																													22.73±0.08	1.75±0.05	7.69±0.26
<i>U. Woodsiae</i>	" IX ₁₁	3 15 11 30 27 39 28 18 14 12 3																													20.87±0.11	2.29±0.08	10.98±0.37
<i>U. intermedia</i>	" VI ₃	1 1 5 16 48 49 36 29 8 5 1 1																													18.22±0.08	1.66±0.05	9.12±0.31
<i>U. ossaeiformis</i>	" I ₃	1 2 4 10 6 24 30 21 32 32 16 11 4 3 3 1																													23.40±0.12	2.69±0.09	11.49±0.43
		Width																															
<i>U. Adianti</i>	A.M. I ₅	1 2 12 18 28 34 33 33 24 7 4 2 1 1																													18.66±0.10	2.18±0.07	11.70±0.39
<i>U. Athyrii</i>	" IX ₃	1 2 4 7 13 29 65 39 28 6 6																													16.15±0.07	1.72±0.06	10.59±0.59
<i>U. filicina</i>	" II ₃	1 3 4 8 10 30 39 44 29 23 7 1 1																													16.44±0.09	2.01±0.07	12.15±0.41
<i>U. hirosakiensis</i>	" VIII ₅	4 2 17 38 49 49 32 7 2																													16.24±0.06	1.49±0.05	9.21±0.31
<i>U. Kameiana</i>	" III ₁₁	1 1 4 18 31 51 47 27 14 4 1 1																													17.41±0.07	1.63±0.05	9.37±0.32
<i>U. Struthiopteridis</i>	" IV ₅	1 1 6 12 19 34 38 42 31 11 5																													20.14±0.09	1.96±0.07	9.73±0.33
<i>U. Woodsiae</i>	" IX ₁₁	2 7 19 37 37 43 32 12 8 2 1																													17.45±0.09	1.82±0.06	10.45±0.35
<i>U. intermedia</i>	" IV ₃	1 4 7 30 69 50 26 9 4																													15.42±0.06	1.36±0.04	8.85±0.29
<i>U. ossaeiformis</i>	" I ₃	1 3 20 33 47 45 28 19 2 2																													18.40±0.02	1.63±0.05	8.87±0.29

TABLE 45. Summary of differences in means of measurements of aecidiospores
 in nine species of *Uredinopsis*

Species		Difference in means (μ)		Difference in means div. by probable error of the difference	
		Length	Width	Length	Width
<i>U. Adianti</i>	& <i>U. Athyrii</i>	3.07±0.13	2.51±0.12	23.61	20.91
"	& <i>U. flicina</i>	2.29±0.13	2.22±0.13	17.61	17.07
"	& <i>U. hirosakiensis</i>	3.42±0.11	2.42±0.12	31.09	20.16
"	& <i>U. Kameiana</i>	0.52±0.12	1.25±0.12	4.33	10.41
"	& <i>U. Struthiopteridis</i>	1.48±0.12	1.48±0.13	12.33	11.38
"	& <i>U. Woodsiae</i>	0.38±0.14	1.21±0.13	2.71	9.31
"	& <i>U. intermedia</i>	3.03±0.12	3.24±0.12	25.25	27.00
"	& <i>U. ossaeiformis</i>	2.15±0.15	0.26±0.10	14.33	2.60
<i>U. Athyrii</i>	& <i>U. flicina</i>	0.78±0.13	0.29±0.11	6.00	2.63
"	& <i>U. hirosakiensis</i>	0.35±0.11	0.09±0.09	3.18	1.00
"	& <i>U. Kameiana</i>	2.55±0.12	1.26±0.10	21.25	12.60
"	& <i>U. Struthiopteridis</i>	4.55±0.12	3.99±0.11	37.91	36.27
"	& <i>U. Woodsiae</i>	2.69±0.14	1.30±0.11	19.21	11.81
"	& <i>U. intermedia</i>	0.04±0.12	0.73±0.09	0.33	8.11
"	& <i>U. ossaeiformis</i>	5.22±0.15	2.25±0.07	34.80	32.14
<i>U. flicina</i>	& <i>U. hirosakiensis</i>	1.13±0.12	0.20±0.11	9.41	1.81
"	& <i>U. Kameiana</i>	1.77±0.13	0.77±0.11	9.83	7.00
"	& <i>U. Struthiopteridis</i>	3.77±0.13	3.70±0.13	29.00	28.47
"	& <i>U. Woodsiae</i>	1.91±0.13	1.01±0.13	14.69	7.77
"	& <i>U. intermedia</i>	0.74±0.13	1.02±0.11	5.69	9.27
"	& <i>U. ossaeiformis</i>	4.44±0.16	1.96±0.09	27.75	21.77
<i>U. hirosakiensis</i>	& <i>U. Kameiana</i>	2.90±0.11	1.17±0.09	26.36	13.00
"	& <i>U. Struthiopteridis</i>	4.90±0.11	3.90±0.11	44.54	35.45
"	& <i>U. Woodsiae</i>	3.04±0.13	1.21±0.11	23.38	11.00
"	& <i>U. intermedia</i>	0.39±0.11	0.82±0.08	3.54	10.25
"	& <i>U. ossaeiformis</i>	5.57±0.14	2.16±0.07	39.78	30.85
<i>U. Kameiana</i>	& <i>U. Struthiopteridis</i>	2.00±0.11	2.73±0.11	18.18	24.81
"	& <i>U. Woodsiae</i>	0.14±0.13	0.04±0.11	1.07	0.36
"	& <i>U. intermedia</i>	2.51±0.11	1.99±0.09	22.81	22.11
"	& <i>U. ossaeiformis</i>	2.67±0.14	0.99±0.07	19.07	14.14
<i>U. Struthiopteridis</i>	& <i>U. Woodsiae</i>	1.86±0.14	2.69±0.13	13.28	20.69
"	& <i>U. intermedia</i>	4.51±0.11	4.72±0.11	41.00	42.90
"	& <i>U. ossaeiformis</i>	0.67±0.14	1.74±0.09	4.78	19.33
<i>U. Woodsiae</i>	& <i>U. intermedia</i>	2.65±0.14	2.03±0.11	18.92	18.45
"	& <i>U. ossaeiformis</i>	2.53±0.16	0.95±0.09	15.80	10.55
<i>U. intermedia</i>	& <i>U. ossaeiformis</i>	5.18±0.14	2.98±0.06	37.00	49.66

smaller than those of the writer.

(b) *Shape of aecidiospores.* Concerning the shape of the aecidiospores of *Uredinopsis*, WEIR and HUBERT (1917), ARTHUR (1925, 1934), KAMEI (1930 a, 1932 b, 1934) and FAULL (1938 b) said that they are "broadly ellipsoid or globoid" or "globoid to ellipsoidal." KLEBAHN (1916) illustrated an aecidiospore of *U. Struthiopteridis* which he had obtained from his basidiospore culture experiment. As shown in Table 46, in which is indicated the ratio of the breadth and length, almost globose spores are seen in the case of *U. hirosakiensis*, while more elongated and somewhat elliptic ones are seen in the cases of *U. Kameiana*, *U. Woodsiae* and *U. intermedia*.

TABLE 46. Ratio of length and width of aecidiospores in nine species of *Uredinopsis*

Species	Ratio
<i>U. Adianti</i>	1.14
<i>U. Athyrii</i>	1.12
<i>U. filicina</i>	1.15
<i>U. hirosakiensis</i>	1.09
<i>U. Kameiana</i>	1.19
<i>U. Struthiopteridis</i>	1.13
<i>U. Woodsiae</i>	1.19
<i>U. intermedia</i>	1.27
<i>U. ossaeiformis</i>	1.12

TABLE 47. Thickness of walls of aecidiospores in nine species of *Uredinopsis*

Species	Wall thicken. incl. tub. (μ)
<i>U. Adianti</i>	0.6-2.0*
<i>U. Athyrii</i>	0.5-3.0
<i>U. filicina</i>	0.7-2.0
<i>U. hirosakiensis</i>	1.0-2.0
<i>U. Kameiana</i>	1.2-2.0
<i>U. Struthiopteridis</i>	1.0-2.0
<i>U. Woodsiae</i>	1.0-2.0
<i>U. intermedia</i>	1.0-2.0
<i>U. ossaeiformis</i>	1.0-1.5

* The number of aecidiospores measured varied considerably.

(c) *Thickness of walls of aecidiospores.* Concerning the thickness of the walls of the aecidiospores of *Uredinopsis*, data have been presented on *U. Struthiopteridis*, *U. Pteridis*, *U. mirabilis*, *U. Osmundae*, *U. longimucronata*, *U. ceratophora*, *U. Atkinsonii* and *U. Phegopteridis* by SYDOW (1915), WEIR and HUBERT (1917), ARTHUR (1925, 1934) and FAULL (1938 b) in foreign countries. In the case of the Japanese species information has already been given by KAMEI (1930 a, 1932 b). In the present nine species, the wall thickness including tubercles ranged from 0.5 to 3.0 μ slightly differing according to the species (cf. Table 47).

(d) *Wall markings of aecidiospores of nine species of Uredinopsis.* Heretofore the markings of aecidiospores of some species of *Uredinopsis*

have been described by WEIR and HUBERT (1917), ARTHUR (1925, 1934), KAMEI (1930 a, 1932), HIRATSUKA, f. (1936 c) and FAULL (1938 b) by the terms "coarsely and closely verrucose," "coarsely verrucose," "minutely verrucose," "verrucose" or "densely verrucose." In the present materials, the minute differences in the markings of the aecidiospores, represented by such items as size, shape and arrangements of the tubercles may exist, but they could not be used as criteria in identifying species.

G.

*Key to nine species of Uredinopsis from Hokkaidô
for the phases on fir hosts*

1	{	Spermatogonia subcuticular, comparatively small, typically superficial, lenticular to subconoidal	2
		Spermatogonia subepidermal, comparatively large, deeply immersed, spherical ..	8
2	{	Inner surface of the peridial cells of aecidia verrucose	3
		Inner surface of the peridial cells of aecidia alveolar <i>U. hirosakiensis</i>	
3	{	Inner surface of the peridial cells of aecidia finely verrucose	4
		Inner surface of the peridial cells of aecidia coarsely verrucose	5
4	{	Tubercles of the peridial cells rather dense	6
		Tubercles of the peridial cells rather sparse	7
5	{	Walls of the peridial cells rather thick	<i>U. Athyrii</i>
		Walls of the peridial cells rather thin	<i>U. filicina</i>
6	{	Tubercles of the peridial cells short and thin	<i>U. Struthiopteridis</i>
		Tubercles of the peridial cells long and thick	<i>U. Adianti</i>
7	{	Tubercles of the peridial cells rather long	<i>U. Woodsiae</i>
		Tubercles of the peridial cells rather short	<i>U. Kameiana</i>
8	{	Tubercles of the peridial cells rather coarse, aecidiospores smaller.	<i>U. intermedia</i>
		Tubercles of the peridial cells rather fine and often slightly striated, aecidiospores larger	<i>U. ossaciformis</i>

