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

By

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III. SPECIES OF MILESINA

A. The life history studies

(1) *Review of literature*

The first aecidial phase of *Milesina* from artificial cultures was that of *M. Blechni* Sydow, obtained by Klebahn (1916) in 1915. From May to June, the basidiospores formed on overwintered fronds of *Blechnum Spicant* With. were inoculated on young leaves of *Abies alba, Picea Abies* (L.) Karst. and *Abies cephalonica* Loud. seedlings. They were incubated under bell-glass for six days. The results were negative in *Picea* seedlings and successful in both of two *Abies*. The mature aecidia were obtained after 31–61 days, varying according to the inoculated plants. With the aecidiospores obtained from the cultures, back inoculations were made on *Blechnum Spicant, Dryopteris spinulosa* Kunze and *Scolopendrium vulgare* Smith, resulting in positive infections on *Blechnum* fern only.

In 1924–1927, Faull and his collaborators made similar but intensive inoculation experiments with *Milesina intermedia* (Faull) Hiratsuka, f., *M. marginalis* Faull & Watson and *M. polypodophila* Faull (Faull, 1929, 1934). The collections of the teleutosporic materials and the inoculation experiments of these rusts were both made in Timagami Forest Reserve, Ontario. The experiments were always conducted out-of-doors. Hubert's celluloid cylinder method (Hubert, 1916) modified by Faull was adopted in most inoculations. In *M. intermedia* and *M. marginalis* the procedures of the experiments and the results were somewhat similar to each other. In the former species, with the basidiospores on the overwintered fronds of *Dryopteris spinulosa* var. *intermedia* Underw. and in the latter species with those on *D. marginalis* A. Gray,

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more than thirty inoculations for each species were conducted on *Abies balsamea* in June to July of two seasons. The results were that, after the appearance of lesions and spermogonia in order, the first aecidial sori were obtained after 34 days (average of 30 cases) in *Milesina intermedia,* and after 43 days (average of 38 cases) in *M. marginalis.* Reciprocal inoculations with the obtained aecidiospores were also made during August. In *M. intermedia,* resulting teleutospores were detected in the next spring in each of six cases of *Dryopteris spinulosa* and its var. *intermedia.* No infections were obtained on *Dryopteris marginalis, D. cristata* GRAY, *D. fragrans* SCHOTT and *Polystichum acrostichoides* SCHOTT. In *Milesina marginalis* resulted uredospores and teleutospores were obtained in the next spring in nine cases concerning *Dryopteris marginalis.* No infections were gained on *Dryopteris cristata, D. fragrans, D. spinulosa,* var. *intermedia, Polypodium virginianum* L. and *Polystichum acrostichoides.* In *Milesina polypodophila,* the features of the life cycle were a little different from those of the two rusts mentioned above. With the inocula derived from the overwintered fronds of *Polypodium virginianum,* fourteen basidiospore inoculations on *Abies balsamea* were carried out on June 21, 1924. The inoculated plants were closely examined from time to time thereafter. Nevertheless, during the 1924 as well as the 1925 season they showed no obvious sign of infections. "By midsummer of 1926 needles on some of the experiments were more certainly paler and samples of these were found to contain mycelium." At last in July 1927, three inoculated plants bore spermogonia and after a month longer aecidia also. "In every instance the sori were restricted to the needles of 1924." The inoculations with the aecidiospores (*Peridermium pycnogrande* BELL) were made in August 1924 on *Polypodium virginianum.* Among eighteen cases all were successful in producing uredosori or uredosori and teleutospores. The uredosori were in some experiments seen in September in the same season, but in some cases observed in June of the next year at the same time with teleutospores. *Dryopteris marginalis* and *D. intermedia* which were inoculated with the aecidiospores, revealed no infections.

On *Milesina fructuosa* (FAULL) HIRATSUKA, f., experiments were executed in the Arnold Arboretum of Harvard University by FAULL (FAULL, 1934). The teleutosporic materials were collected from a point in the State of Massachusetts. With the basidiospores on the overwintered fronds of *Dryopteris spinulosa* var. *americana* (FISCH.)

FERNALD, "two hundred and eighty-four inoculations in all were made on twenty-eight species and eight varieties of *Abies*" in May to June of 1933. The infected firs were *Abies amabilis* MURRAY, *A. balsamea*, *A. cephalonica*, *A. concolor* LINDL. & GORD., *A. Fraseri* (PURSH) POIR., *A. magnifica* MURRAY and *A. nephrolepis* MAXIM. In most of these infected firs, aecidia were produced after 34–42 days. Among these susceptible fir trees the existence of differences in their resistance to this rust was admitted. Reciprocal inoculations were not made in this species of rusts.

In 1932, EUGÈNE MAYOR (1933) obtained the uredosori of *Milesina Kriegeriana* MAGNUS by sowing the aecidiospores of a white spored *Peridermium* on *Abies alba* collected at Boudry in Switzerland on fronds of *Dryopteris spinulosa*, partially proving the life history of the rust. But his experiment was made with inocula which were "not free from the uncertainty of intermixtures" as said by HUNTER (1936 a).

In the spring of 1934, HUNTER (*l.c.*) made cultures to obtain the aecidial phases of *Milesina Scolopendrii* JAAP, *M. Dieteliana* SYDOW, *M. vogesiaca* SYDOW and *M. Kriegeriana*. The teleutospore materials were collected from Ireland and England. The experiments were made in London University. The methods of the inoculations were not particularly different from the cases above mentioned. From April 27th to 30th, the basidiospore inoculations were conducted: in *Milesina Scolopendrii* from *Scolopendrium vulgare* to *Abies alba* and *A. concolor;* in *M. Dieteliana* from *Polypodium vulgare* L. to *A. alba* and *A. concolor;* in *M. vogesiaca* from *Polystichum angulare* PRESL to *A. alba;* in *M. Kriegeriana* from *Dryopteris spinulosa* to *A. alba, A. concolor* and *A. grandis* and in the same rust from *D. Filix-mas* SCHOTT to *A. alba, A. concolor* and *A. grandis*. The resulted aecidia appeared: in *M. Scolopendrii* after 54–78 days; in *M. Dieteliana* after 80 days; in *M. vogesiaca* after 93 days; in *M. Kriegeriana* on *A. alba* after 49 days, on *A. concolor* after 49–57 days and on *A. grandis* after 37–56 days. Back inoculations were performed in June to August of the same year in all the species except *M. vogesiaca*. In *M. Scolopendrii* positive results were obtained on only *Scolopendrium vulgare* after 37–54 days while no infections occurred on *Blechnum Spicant, Dryopteris spinulosa* var. *dilatata* UNDERW. and *Polystichum angulare*. In *M. Dieteliana,* positive results were obtained on only *Polypodium vulgare* after 47–69 days, but no results on *Polystichum angulare* and *Scolopendrium vulgare*. In *M. Kriegeriana,* the aecidiospores on *Abies concolor* which originated from

Dryopteris Filix-mas were positively inoculated on *D. Filix-mas* (after 28–47 days) and on *D. spinulosa* (after 31 days). Aecidiospores of the same rust on *A. grandis* which originated from *D. spinulosa* were positively inoculated on *D. Filix-mas* and *D. spinulosa* (after 64 days). The aecidiospores on *A. alba* and *A. concolor* which originated from *D. spinulosa dilatata* were positively inoculated on *D. spinulosa dilatata*, *D. Filix-mas* (after 32 days) and *D. spinulosa intermedia* (after 47 days).

Since 1924, the writer has carried out inoculation experiments in Sapporo on *Milesina exigua* FAULL, *M. Dryopteridis* KAMEI, *M. Itôana* KAMEI, *M. jezoensis* KAMEI et HIRATSUKA, f., *M. Miyabei* KAMEI and *M. sublevis* HIRATSUKA, f. His reports (1930 b, 1931, 1932 b, 1935 a and 1935 b) have already shown some of the results of the experiments, but there are still many important data to be considered as presented in the following paragraphs.

Uredospore inoculations of some species of *Milesina* were made by KLEBAHN (1916) and also by the writer as shown in this report.

Thus among 51 species of *Milesina* now recognized, only 15 species have been proved to have the aecidial phases on *Abies* by KLEBAHN, FAULL, MAYOR, HUNTER and KAMEI as shown in Table 84 in this paper.

(2) *Materials and methods of culture experiments*

The teleutospores of *Milesina Dryopteridis*, *M. Itôana*, *M. jezoensis*, *M. Miyabei* and *M. sublevis* are formed in the early summer inside of the tissue of overwintered fronds. In *M. exigua* teleutospores often developed on current year fronds somewhat similar to cases of the species of *Uredinopsis*. So, the materials for inoculations with basidiospores were mostly collected just before the inoculation experiments in the early summer. Heavily affected fronds, bearing teleutospores on the discolored portions, were selected in the field, and brought into the laboratory. After being soaked in water, they were deposited in the moist chamber inside of Petri dishes which were placed on the desk of the laboratory. Frequently it was experienced that the basidiospores had emerged copiously just when they were collected in the field and were quite ready for prompt use. The procedures used in the inoculation experiments either in the case of basidiospores or aecidiospores were quite the same as in the case of the species of *Uredinopsis* described above in this paper.

10. **Milesina Dryopteridis** KAMEI

Historical review of the fungus. The present rust was first described by the writer (1932 b) after a partial proof of its life history. FAULL (1932) in his monograph of *Milesia* added his remarks concerning the taxonomy of this fungus. Recently HIRATSUKA, f. (1932 c, 1936 c) gave a redescription and mentioned the unrecorded localities of this rust in Hokkaidô and Honshû. Recently ITÔ & HOMMA (1938) published the description of the aecidial phase which was prepared by the present writer himself. ITÔ (1938) described this rust very recently.

Personal observations. Rusted fern. In Hokkaidô, the host, *Polystichum Standishii* C. CHR. is found as a constituent of the undergrowth of the primeval forests. The fronds are especially tenacious and adapted for the overwintering habit. Professor MIYABE gathered the rust specimen early, on May 7, 1890, at Maruyama near Sapporo. The type specimen and inoculation materials were also collected from the same place by the present writer. From the writer's own herbarium Provinces Ishikari, Iburi and Teshio may be mentioned as localities of this rust in Hokkaidô. Among 11 collections five of them are specimens on current year fronds and the earliest is dated Aug. 26. In this specimen most of the pinnae showed but slight discoloration around the uredosori. Even in the specimen obtained on Nov. 11th, the discoloration was not very prominent. But specimens of overwintered fronds collected in the earlier summer were usually heavily attacked, and the pinnae as well as petioles and stipes were seen to be covered with punctate minute pustules changing the color of the tissue to brownish or almost blackish. The discolorations of the fronds were more conspicuous on the upper surface. In such heavily affected areas teleutospores were developed inside the epidermal cells of the undersurface. In the early summer when the teleutospores had germinated, such discolored parts were covered with thin whitish films of the mass of basidiospores which were quite readily available for inoculation experiments.

Inoculations with basidiospores. Among 6 seedlings of *Abies Mayriana* inoculated in two seasons, three have shown positive results. The first appearance of yellow spots was recognized after 9 days, the spermogonia after 21–38 days and the aecidia after 71 days on Aug. 26th in only one case as shown in Pl. I, fig. c. On Sept. 1st four needles were detected to bear aecidia. Nevertheless some other affected needles were

shown even on Sept. 3rd to have spermogonia, which were vigorously producing spermatial fluid. Inside of these spermogonia there were seen such comparatively long hyphae as are shown in Pl. VII, fig. 17 f. The area in which spermogonia were produced was discolored yellowish and more or less sharply delimited and contrasted with greenish healthy portion. The lesions were seen even in November. Comparing these results with cases of the species of *Uredinopsis* and certain *Milesina,* the incubation periods up to the production of spermogonia and especially of aecidia are far longer.

TABLE 48. Inoculations with basidiospores of *M. Dryopteridis*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm. (No. of days)	App. of aecid. (No. of days)	Remarks
I. 218	Basidiospores on *Polyst. St.* Maruyama, Je. 16, 1931	*A.M.* XVI_{11}	Je. 26, 1931	38	—	Laboratory
" 279	" Moiwa, Je. 13, 1934	" III_{14}	Je. 16, 1934	73?	—	" Yellow spot appeared after 9 days
" 280	"	" IV_{14}	"	21	71	Laboratory

Inoculations with aecidiospores. Back inoculations with the aecidiospores gained from an experiment on *A. Mayriana* IV_{14} were conducted on September 10th in 1934 on cut fresh fronds of *Polystichum Standishii* laid inside of Petri dishes. Uredospores were obtained after 16 days at the two inoculated portions of the fronds (Pl. III, fig. j).

The description of the species is as follows:—

Milesina Dryopteridis KAMEI in Trans. Sapporo Nat. Hist. Soc. XII, p. 171, 1932–ITÔ & HOMMA in Trans. Sapporo Nat. Hist. Soc. XV, p. 115, 1938.

Syn. *Milesia Dryopteridis* FAULL, in Contrib. Arnold Arb. Harvard Univ. II, p. 130, 1932.

Spermogonia on needles of current season, hypophyllous, inconspicuous, distinct under the lens, scattered almost in rows on stomatiferous surface of more or less discolored and slightly deformed part, occupying a restricted portion or whole of a leaf, minute, medium in number, usually discrete, roundish in face view, colorless, in sections subcuticular, immersed, up to half of the mesophyll, flattened globose to almost

spherical, 135.6–169×110.5–166 μ; openings mostly slit-like, situated mostly on interstomatal space, elongated up to 130 μ in direction of longitudinal axis of the organ, up to 52 μ broad; spermatiophores unbranched, septate, subulate, averaging about 25 μ long, 2–4 μ broad, convergent; spermatia oblong, oblongo-cylindrical to rod-like, 5.0–7.5×1.2–2.0 μ, colorless, smooth (Pl. V, fig. a; VII, fig. 17 f).

Aecidia on needles of current season, hypophyllous, arranged in two rows, irregularly scattered on opposite sides of the midrib, on more or less discolored portions of affected needles, 2–14 per leaf, white, cylindrical, up to 2 mm. high, 0.12–0.25 mm. across; peridia colorless, rather delicate, ruptured at the apex; peridial cells mostly elongated vertically, tetragonal to hexagonal, sides unequal, margin mostly straight or rounded, slightly overlapping to make longitudinal rows, 18–24×14–20 μ, inner walls ca. 2 μ (rarely 5 μ) thick, rather finely verrucose, often striated; outer walls smooth, thin, ca. 1 μ thick; aecidiospores colorless, globoid, ovoidal or sometimes ellipsoidal, 16–25×14–23 μ, averaging 19.24×16.57 μ, closely but finely verrucose except one side where almost smooth; walls colorless, thin, up to 1 μ thick including tubercles (Pl. I, fig. c; VI, fig. j).

Uredosori hypophyllous, on more or less brownish discolored, restricted parts or sometimes on greenish areas, often on petioles or stipes, irregularly scattered, minute, pustular, covered with yellowish to brownish colored epidermis, roundish, 0.11–0.24 mm. across; peridia colorless, almost hemispherical, delicate, ruptured at the apex; peridial cells small, isodiametrically to irregularly polygonal, 6–14 μ across; walls thin, ca. 1.5 μ thick, colorless, smooth; uredospores colorless, issue as powdery white mass, short stalked, obovate, ovate oblong or broadly clavate, 22–39×14–21 μ, averaging 28.8×17.1 μ; walls thin, ca. 1 μ, colorless, sparsely and delicately echinulate (Pl. III, fig. j; VII, fig. 10 a).

Teleutosori abundant on overwintered fronds, mostly hypophyllous, on dark to almost blackish discolored areas; teleutospores within the epidermal cells, sometimes in the guard cells, more or less roundish in outline, colorless, divided into 2–20 cells with vertical septa, rarely one celled; the cells of the spores more or less roundish or polygonal, 10–22 μ long, 6–15 μ broad, with thin, colorless, smoth walls; basidiospores globoid to ellipsoidal, 7–11 μ across, colorless (Pl. VII, fig. 10 b and c).

Hosts and distribution:

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

II and III. *Polystichum Standishii* C. CHR.—in Japan (Hokkaidô and Honshû).

11. **Milesina exigua** FAULL

Historical review of the fungus. This species was named by FAULL (1931) based on a uredosporic material parasitic on *Polystichum Braunii* FÉE from Poland where it was collected by WROBLEWSKI. Since then, HIRATSUKA, f. & YOSHIDA (1932), FAULL (1932), HIRATSUKA, f. (1932 b, 1932 c, 1935 a, 1935 d, 1936 c), HIRATSUKA, f. & YOSHINAGA (1935), HIRATSUKA, f. & HASHIOKA (1937) and ITÔ (1938) presented taxonomic considerations of this rust. Thus it is now known to be distributed in Poland and in our country (Formosa, Kiushû, Honshû, Korea and Hokkaidô). The present writer (1930 b) has already published a life history study of this rust under the specific name *M. vogesiaca* and has described its spermogonial and aecidial phases.

Personal observations. Rusted ferns. HIRATSUKA, f. & YOSHIDA (*l.c.*) and HIRATSUHA, f. (1936 c) already noted the collections on *Polystichum Braunii* and *P. tripteron* from Prov. Ishikari. According to the writer's gatherings, the present rust is found also on *Polystichum aculeatum* SCHOTT var. *retroso-paleaceum* KODAMA. So, it was proved that *M. exigua* has three species of host ferns distributed through Provinces Ishikari, Iburi, Kitami and Kushiro in Hokkaidô.

From the later summer to the early winter, uredosori were seen on fronds and less frequently on stipes. Affected parts were noticed first as more or less discolored small spots, which gradually extend over the entire surface of each pinna. Discolorations were more conspicuous on the upper surface. Teleutospores develop on discolored and distorted areas by the early winter. As materials for the sporidial inoculation experiments, rusted fronds of *Polystichum aculeatum* var. *retroso-paleaceum* and *P. Braunii* were collected from Mount Moiwa and Forest Nopporo. In the case of the former fern, at least, the frond was gathered in the late autumn of the previous year to be used for cultures of the next year and positive results were usually obtained. This is rather different in comparison with other species of *Milesina* used in this study, in which teleutospores develop mostly in the early summer on the overwintered fronds. Basidia were observed to measure $50\times7\,\mu$ and basidiospores about $8\times6\,\mu$ in size as shown in Pl. VII, fig. 11 b.

Inoculations with basidiospores. Basidiospore inoculations were conducted repeatedly on the needles of three species of Japanese firs.

As shown in Table 49, eight seedlings of *Abies Mayriana*, two of *A. sachalinensis* and one of *A. firma* were infected. Successful infection was denoted by the discoloration of the affected spot, the subsequent exudation of the spermatial fluid after 13–17 days and the production of the aecidial cups in three to four weeks. The period is the shortest case among the species of *Milesina* used in this study. In one case an inoculation was made onto needles of a twig of *A. Mayriana* laid inside of a moist chamber with the result, that only spermogonia were obtained after 26 days. The late appearance of the organ must be due to the extreme abnormal condition of the inoculated plant. Upon a careful inspection of the spermogonia that were gained from inoculations, it was noted that between the spermatiophores, there were inter-

TABLE 49. Inoculations with basidiospores of *M. exigua*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm. (No. of days)	App. of aecid. (No. of days)	Remarks
I. 40	Basidiospores on *Polyst. acul.* v. *retr. pal.*, Moiwa, Aug. 1923	*A.M.* $XIII_4$	Je. 4, 1924	20	27	Greenhouse
" 72	" Oct. 25, 1924	" XVI_5	Je. 6, 1925	17	54?	Out-of-doors
" 94	" Oct. 24, 1925	" III_6	Je. 7, 1926	19	—	Laboratory
" 112	"	" XXI_6	Je. 17, 1926	20	28?	"
" 120	"	*A. s.* III_6	Je. 6, 1926	20	42?*	"
" 125	"	" $VIII_6$*	Je. 17, 1926*	20*	40?*	Out-of-doors
" 128	"	*A. f.* I_6	Je. 17, 1926	14	27	"
" 152	" Moiwa, Aug., 1927	*A.M.* V_8*	May 30, 1928	20*	27*	Laboratory
" 170	" Moiwa, Aug., 1928	" V_9	Je. 4, 1929	13	21	Out-of-doors
" 189	Basidiospores on *Polyst. Br.*, Nopporo, Apr. 20, 1930	" X_{10}	Je. 5, 1930	12	19	Laboratory
" 201	"	" XX_{10}	Je. 5, 1930	26	—	" Fir twig in Petri dish

* Data indicated by the asterisk are different from those in the writer's previous publication (1930b) which should be corrected as in this table. The inocula on *Abies* in the cases of Expt. nos. 40–170 were always obtained from the fronds of *Polystichum aculeatum* var. *retroso-paleaceum* and the previous record that they came from *P. Braunii* should here be corrected. In the inoculations on nos. 189 and 201 the inocula were obtained from the fronds of *P. Braunii*.

posed some elongated hypha-like bodies which correspond to the "flexuous hyphae," already mentioned by HUNTER (1936 c) in connection with the species of *Milesina* and other genera of Melampsoraceae. They were often somewhat inflated at the apex and surpassed the spermatiophores in length as shown in Fig. 5 a in page 139 and Pl. VII, fig. 17 g.

Inoculations with aecidiospores. After 17 days from the aecidiospore inoculations on the portions of a frond of potted *Polystichum Braunii,* several uredopustules were seen to be developed. In both of two Petri dishes, on the other hand, the pustules came out 13 days after. It happened that no inoculation was made on the fronds of *P. aculeatum* var *retroso-paleaceum,* from which plant the basidiospores in most of the inoculations were derived. But the positive result of the inoculation is beyond all doubt considering the similar cases of experiments in other related rusts.

TABLE 50. Inoculations with aecidiospores of *M. exigua*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos.	Remarks
				No. of days	
II. 44	Aecidiospores on *A.M.* XIII$_4$	*Polystichum Braunii*	Jy. 22, 1924	17	Corridor. Discoloration came after 12 days
" 88	" *A.f.* I$_6$	"	Aug. 27, 1926	13	In Petri dish

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

Milesina exigua FAULL in Journ. Arnold Arb. XII, p. 219, 1931. Syn. *Milesina vogesiaca* (non SYDOW) KAMEI in Trans. Sapporo Nat. Hist. Soc. XI, p. 146, fig. 1 B, 2 A and B, 1930.

Milesia exigua FAULL in Contrib. Arnold Arb., Harvard Univ. II, p. 100, 1932.

Milesina Polystichi-tripteri HIRATSUKA, f. in FAULL in Contrib. Arnold Arb., Harvard Univ. II, p. 102, 1932.

Spermogonia on needles of current season, amphigenous, mostly hypophyllous, colorless at first, later becoming brownish, more or less circular in face view, isolated or confluent, irregularly scattered on more or less yellowish discolored areas, mostly on stomatiferous surface, sometimes even on the midrib, minute, abundant, clearly seen with hand-lens; in sections subcuticular, immersed up to half of the leaf thickness, subspherical to flask-shaped, 122–177.5 μ broad in longitudinal sections,

148–203 μ broad in transverse sections, 110–163 μ high; openings mostly slit-like, situated on interstomatal spaces, elongated in direction of long axis of the needles, 96.8×39.6 μ in average; spermatiophores unbranched, septate, obclavate, ca. 30 μ in length, 3 μ broad, convergent; spermatia oblongo-cylindric to vermicular, 4.5–7.0×1.5–2.2 μ, with rounded or truncate ends, smooth, colorless (Pl. II, fig. i; V, fig. b; VII, fig. 17 g).

Aecidia hypophyllous, on needles of current season, arranged in two rows, one on each side of the midrib, mostly on discolored areas, irregularly scattered, 3–20 per leaf, white, cylindrical, 0.25–0.36 mm. across, 0.5 mm. in height; peridia colorless, comparatively firm, opened at the apex; peridial cells mostly vertically elongated, with unequal sides, hexagonal, margin more often rounded, overlapping, 22.5–48.3 ×11.3–25.6 μ, averaging 33.13×18.22 μ, inner walls comparatively thick, up to 4 μ including tubercles, rather coarsely verrucose, somewhat striated, outer walls thinner, about 1 μ, smooth; aecidiospores colorless, globose to ellipsoidal, 18–30×13–23 μ, averaging 22.3×18.49 μ, closely but rather coarsely verrucose except one side where almost smooth; walls thin, about 1 μ thick including tubercles, colorless (Pl. II, fig. i; VI, fig. k).

II and III are as described by previous authors such as FAULL (1932) and HIRATSUKA, f. (1936 c).

Hosts and distribution:

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

II and III. *Hypolepis punctata* METT.—in Japan (Formosa).

Microlepis strigosa PRESL—in Japan (Formosa and Shikoku).

Polystichum aculeatum SCHOTT var. *japonicum* H. CHRIST—in Japan (Honshû and Kiushû).

Polystichum aculeatum SCHOTT var. *retroso-paleaceum* KODAMA—in Japan (Honshû and Hokkaidô).

Polystichum Braunii FÉE—in Japan (Honshû and Hokkaidô) and Poland.

Polystichum tripteron PRESL—in Japan (Honshû, Hokkaidô and Korea) and Ussuri.

12. **Milesina Itôana** KAMEI

Historical review of the fungus. This rust was first described by

the writer (1935 b) and the diagnosis of all stages and the process of the life cycle have been preliminarily published. HIRATSUKA, f. (1936 c) and ITÔ (1938) recently redescribed it.

Personal observations. Rusted fern. The rust is now known only from the Provinces Ishikari, Iburi and Kushiro of Hokkaidô. As already reported by the writer, the first observations of the uredo- as well as teleutospores were made when he succeeded in obtaining positive results from tentative inoculations on the fronds of *Dryopteris crassirhizoma* with the aecidiospores of a *Peridermium* on *Abies Mayriana* collected from the Nopporo Forest on Oct. 26, 1925. Such inoculation experiments thereafter, were repeatedly made with like results. However, such uredospores as those derived from the inoculations were not obtained from the field until quite recently because of the lack of knowledge of peculiar characters in the course of development of this rust. On the 5th of April 1935, when visiting the Nopporo Forest, in a certain restricted small area, the writer was fortunate in being able to collect the first specimen of the uredosori as well as teleutospores on overwintered fronds. The collections were made from a location where a group of about 20-year old trees of *Abies Mayriana* which had been severely attacked by the white spored peridermia in the previous autumn were standing (Fig. 7a b, p. 163). The collected uredospores under the microscope were the same as the form which had issued in the previous inoculations described above. Subsequent searches made at other places inside the forest showed that the rust is rather widely distributed. In the latter part of the season, no uredosori nor teleutospores on fronds of the current season have heretofore been observed. The uredopustules were seen to appear on more or less sharply restricted and discolored intervein areas, especially in the marginal portion. Usually at first, the lesion was scarcely discolored, but gradually increased in brownish color, eventually becoming blackish.

TABLE 51. Inoculations with uredospores of *Milesina Itôana*

Exp. no.	Inocula	Date of inoc.	App. of uredos. No. of days	Remarks
III. 51	Uredospores on *Dr. crassirh.*, *Cult.* IV, 49 A. iii	Nov. 28, 1934	28	In Petri dish
" 58	" *Cult.* III, 55	Jan. 12, 1935	26	"

On the fern host in Petri dishes inoculations with the uredospores were made with the result that new pustules appeared in 26–28 days (cf. Table 51).

The teleutospores appeared near uredosori or a little apart from the sori. They were formed singly or often two to more spores attached closely together inside of one epidermal cell. Each spore 1 to 7 celled, but once a 22 to 33 celled ones were seen (cf. Pl. VII, fig. 12 b and c). Comparing with those of *M. Miyabei,* the cells of a spore were distinctly more numerous. Where teleutospores developed, the area was evenly discolored and often rather widely extended. The teleutospores were seen to be formed so abundantly that one was astonished by the fact. In the artificial cultures in Petri dishes the writer saw the formation of teleutospores after 30–97 days from the inoculations on fronds of the inoculated ferns with aecidiospores or uredospores. The germination of teleutospores was also observed on the affected fronds that were laid inside the dishes. In such cases, basidia issued from each pore of each cell of the spore and attained about 46μ in length and 4μ in breath. Materials used for inoculation experiments with sporidia were selected from overwintered fronds collected at Nopporo and Tomakomai.

Inoculations with basidiospores. Inoculations with basidiospores were made as shown in Table 52. The inoculation period for the production of spermogonia was 16–22 days and for aecidia, 104–119 days, employing 6 experimental seedlings (cf. Pl. I, fig. d). It is remarkable that the period needed for the issuing of the aecidia was

TABLE 52. Inoculations with basidiospores of *M. Itôana*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 283	Basidiospores on *Dr. crassirh.* Nopporo, May 12, 1935	*A.M.* I_{15}	Je. 4, 1935	16	119	Laboratory
" 284	"	" II_{15}	Je. 6, 1935	14	104	"
" 289	" Tomakomai, Je. 15, 1935	" III_{15}	Je. 20, 1935	22	104	"
" 286	" Nopporo, Je. 7, 1936	" I_{16}	Je. 10, 1936	18	116	"
" 287	"	" II_{16}	"	15	116	"
" 288	"	" III_{16}	Je. 14, 1936	20	101	"

far longer than in any other species of *Milesina* used in the present study. Compared with the North American *M. intermedia*, whose morphology is somewhat similar to that of the rust under discussion, the present fungus required a much longer period.

Inoculations with aecidiospores obtained from cultures. As indicated in Table 53, inoculations with the aecidiospores obtained from cultures were made in the autumn of 1925. Successful results were gained which showed the incubation periods to be 23 to 43 days in the case of Petri dishes and 23 days in a case of potted plants.

TABLE 53. Inoculations with aecidiospores of *M. Itôana*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos. (No. of days)	Remarks
II. 122	Aecidiosp. on *A.M.* I_{15}	*Dryopteris crassirhizoma*	Oct. 4, 1935	39	Petri dish
" 123	"	"	"	43	"
" 125a	"	" A	Oct. 16, 1935	57?*	Potted pl. in laboratory
" b	"	" B	"	—	"
" c	"	*Scolopendrium vulgare*	"	—	"
" d	"	*Polystichum Braunii*	"	—	"
" e	"	*Polystichum aculeatum* var. *restroso-paleaceum*	"	—	"
" f	"	*Polystichum Standishii*	"	—	"
" 126a	"	*Dryopteris crassirhizoma*	Nov. 4, 1935	23	Petri dish
" b	" II_{15}	"	"	39	"
" c	" III_{15}	"	"	39	"
" 131	" II_{16}	"	Nov. 19, 1936	23	Potted pl. in laboratory

* The detection of the uredosori was made somewhat later than the actual first appearance.

Inoculations with aecidiospores obtained from the field. Numerous inoculations with aecidiospores collected from the field were performed on *Dryopteris crassirhizoma* to gain uredospores of this rust in question. Among them, several results are shown in Table 54. According to these data, the incubation periods for the production of uredosori fluctuate

from 19 to 60 days. Teleutospores were also developed on some of these infected ferns.

TABLE 54. Inoculations with aecidiospores (*from the field*) of *M. Itôana* on *Dryopteris crassirhizoma*

Exp. no.	Inocula	Date of inoc.	App. of uredos. No. of days	Remarks
IV. 32a	Aecidiospores on *A. sach.*, Mt. Meakan, Sept. 15, 1933	Sept. 24, 1933	41	Inoculated on *Dryopteris crassirhizoma* in Petri dish
" 34c	" on *A. Mayr.*, Lake Panketô, Sept. 19, 1933	"	27	"
" 40ia	" Nopporo, Nov. 19, 1933	Nov. 21, 1933	50	"
" c	"	"	50	"
" d	"	"	60	"
" e	"	"	36	"
" f	"	"	50	"
" 40iia	"	Nov. 22, 1933	49	"
"*49Aib	" Nopporo, Oct. 8, 1934	Oct. 13, 1934	72?	"
" 49Aiiba′	"	"	22	"
" b′	"	"	22	"
" 49Aiiiba′	"	"	19	"
" b′	"	"	19	"
" 49Bia′	"	"	34	"
" b′	"	"	34	"
" 49Biibb′	"	"	22	"
" 49Cibb′	"	"	34	"
" 49Ciiba′	"	"	34	"
" b′	"	"	34	"
" 49Civba′	"	"	22	"
" c′	"	"	22	"

* In experiments 49 A, ten affected needless bearing several mature aecidial cups were selected for the inocula from some branchlets of the tree shown in Fig. 7 b in page 163.

The description of the species is as follows:—

Milesina Itôana KAMEI in Trans. Sapporo Nat. Hist. Soc., XIV, p. 99, pl. I, 1935.

Spermogonia on needles of current season, hypophyllous, inconspicuous, minute, rather few, 5–15 per leaf, circular to oblong in face view, colorless, clearly seen with hand-lens, mostly scattered on slightly discolored areas, especially on the stomatal areas of one side of the midrib, often on both sides, isolated or sometimes closely produced; in sections subepidermal, deeply seated up to two-thirds of the leaf thickness, almost spherical, rather large, 160–352 μ broad, 110–290 μ high, averaging about 260 μ broad, 200 μ high; openings on the epidermis as pores in the interstomatal spaces, 30.7 μ long, 23.7 μ wide; spermatiophores branched or simple, septate, 26.1 μ high, 3.1 μ broad, convergent; spermatia hyaline, unicellular, oblongo-elliptic, 4.0–6.0 × 1.0–1.6 μ, smooth, colorless (Pl. II, fig. j; V, fig. h; VII, fig. 17 h).

Aecidia mostly hypophyllous, sometimes amphigenous, on needles of current season, rather few, 1–6 per leaf, in two rows on more or less discolored portions, white, cylindrical, or often compressed laterally, 0.27–0.74 mm. across, 0.2–3 mm. high; peridia colorless, firm, rupturing at the apex; peridial cells with unequal sides, vertically elongated, tetragonal to hexagonal, margin straight, rarely rounded, overlapping in a single layer, 20.7–33.6 μ long, 12.6–23.6 μ broad, averaging about 26.2 × 18.5 μ, with outer walls smooth, ca. 1 μ thick, with inner walls closely marked by rather long tubercles, whose basal parts confluent to make ridge-like striations, 4–7 μ thick; aecidiospores colorless, globose, ovoidal or ellipsoidal, 21–31 × 16–25 μ averaging about 25.84 × 20.20 μ, closely but coarsely verrucose, one side partly almost smooth; walls up to 2.0 μ thick including tubercles, colorless (Pl. II, fig. j; VI, fig. 1).

Uredosori hypophyllous, scattered on at first sharply restricted, eventually extensive discolored areas, often on marginal portion, immersed, slightly pustular, roundish, small, 0.06–0.23 mm. in diameter, covered with dark to purplish discolored epidermis, ruptured by a centrally placed minute pore, usually situated under stomata, pushing delicate spore tendrils; peridia colorless, hemispheric, not much flattened, delicate; peridial cells colorless, isodiametric to irregularly polygonal, not overlapping, 3–22 μ across; walls colorless, less than 1 μ thick; uredospores colorless, meager in number, white in mass, short stalked, oblong or oblong-ovate, broadly clavate, pyriform to ellipsoidal, rarely more or less angular, 26–46 × 14–22 μ, averaging about 33.21 × 17.92 μ; walls thin, colorless, 0.5–0.7 μ thick, very minutely and sparsely warted, apparently smooth in wet mounts (Pl. III, fig. 1; VII, fig. 12 a).

Teleutosori abundant on overwintered fronds, amphigenous, mostly

hypophyllous, on extensive, grayish dark areas; teleutospores within the epidermal cells, colorless, rounded or irregular in outline, conforming to the shape of the host cell, sometimes isolated, sometimes compactly attached to each other and filling it, 1 to 36 celled with vertical septa, a single pore in the outer wall of each cell; the cell of the spores with thin, smooth, colorless walls, irregularly polygonal except along the free margin, 16–18×6–13 μ, averaging 12.8×8.8 μ (Pl. VII, fig. 12 b, c and d).

Hosts and distribution:

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

II and III. *Dryopteris crassirhizoma* NAKAI—in Japan (Hokkaidô).

13. **Milesina jezoensis** KAMEI et HIRATSUKA, f.

Historical review of the fungus. This rust was first described by the writer (1931) based on specimens which were collected at Mt. Kurodake, Taisetsu Mountain range, Prov. Ishikari by Dr. NAOHIDE HIRATSUKA and also on copious materials gathered at Lake Shikaribetsu, Prov. Tokachi by the writer himself. The life history was also pursued by the writer and the partial result was also published in the above mentioned paper. FAULL (1932) described this species under the genus *Milesia*, while HIRATSUKA, f. (1932 c, 1936 c) redescribed it and noted its distribution in Hokkaidô. Recently ITÔ & HOMMA (1938) and ITÔ (1938) described this rust.

Personal observations. Rusted fern. The specimens of the rust on *Polypodium virginianum* L.* have been rather meagerly obtained and heretofore four specimens from Tokachi, three from Ishikari and one from Kitami only have come to the writer's attention. At Shikaribetsu, from which place the materials for experiments have been obtained, the banks of a volcanic lake are covered with luxuriant growth of *Picea jezoensis* and *Abies Mayriana* together with some deciduous trees, such as *Tilia japonica* SIMONKAI and *Betula Maximowicziana* REGEL. Under these trees the ferns are seen grouped here and there. The diseased leaves were conspicuous for the brownish to almost blackish discolorations of the frond, on the surface of which white masses of uredospores

* In the previous paper, as the fern host of this rust, the writer (1931) published it as *Polypodium vulgare* L. which should, as here, be corrected to *Polypodium virginianum* L.

were found protruding (Pl. III, fig. m).

On the affected fronds of the current season, uredosori only were observed. Teleutospores were seen on overwintered diseased fronds. The portions, where the teleutospores are formed, were situated near the uredosori and at first sight, being scarcely discolored, seemed healthy. Germination of the teleutospores was obtained by placing well affected materials in moist chamber. The occurrence of the germination was indicated by the covering of the diseased area with a film-like layer composed of basidiospores. The period from the moistening of the materials to the beginning of the germination was found to be rather long.

Inoculations with basidiospores. Inoculation experiments were conducted during three seasons. In the two earlier seasons, spermogonia only were obtained after about 20 days. No aecidial sori were produced and infected needles mostly dropped off. In 1933, however, a seedling of *Abies Mayriana* XVI_{13} was inoculated on June 21, and yellow spots appeared on July 11 on some of the affected needles. The spot was distinctly yellowish and more or less sharply delimited from the healthy area. The pot was carefully watched taking cautions about the moisture and light conditions inside of the laboratory. On the 3rd of October, 104 days after the inoculation, a first aecidium at length appeared. Thereafter, though it was apparently healthy, the further development of the fungus seemed to be retarded by the coldness. The seedling was transferred into a greenhouse from the middle of December for continued observation. On January 26, 1934, two additional aecidia appeared,

TABLE 55. Inoculations with basidiospores of *M. jezoensis*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 197	Basidiospores on *Polyp. virg.*, Shikaribetsu, Je. 1930	*A.M.* $XVII_{10}$	Je. 19, 1930	21	—	Laboratory
" 198	"	" $XVIII_{10}$	Je. 20, 1930	22	—	"
" 199	"	" $XVIII'_{10}$	Je. 20, 1930	20	—	"
" 200	"	" XIX_{10}	Je. 19, 1930	44	—	"
" 226	" Je. 11, 1931	" $XXIV_{11}$	Je. 27, 1931	18	—	"
" 228	" Je. 1933	" XVI_{13}	Je. 21, 1933	20	104	"
" 289	" Je. 20, 1936	" IV_{16}	Je. 30, 1936	24	—	"

219 days after the inoculation. Although the same plant was left undisturbed under continued observation, no more aecidia appeared. HUNTER (1936 c) in her experiments on *Milesina Dieteliana* MAGN. which is parasitic on the nearer species of fern in Europe, found that the first spermogonium issued in 25–26 days and the aecidium 80 days after the inoculation.

Inoculations with aecidiospores. With the aecidiospores on *Abies Mayriana* XVI_{13} return inoculation experiments were made on October 25th in 1933 on fresh fronds of *Polypodium virginianum* placed inside of Petri dishes. After 28 days from the inoculation the first uredospores were to be seen. In comparison with *M. Dieteliana* of HUNTER's experiments in which the incubation periods were 47 to 69 days, the present rust has a shorter period.

Though the writer has not yet succeeded in collecting field specimens of the aecidial phase, search for it in proper season and location probably will eventually result in success.

The description of the present species as supplemented by the recent investigations now stands as follows:—

Milesina jezoensis KAMEI et HIRATSUKA, f. in KAMEI in Trans. Sapporo Nat. Hist. Soc. XII, p. 32, figs. 1–3, 1931—ITÔ & HOMMA in Trans. Sapporo Nat. Hist. Soc. XV, p. 114–115, 1938.

Syn. *Milesia jezoensis* FAULL in Contrib. Arnold Arb. Harvard Univ. II, p. 87, pl. VIII, fig. 33, a–d, 1932.

Spermogonia on needles of current season, hypophyllous, inconspicuous, scattered in rows on yellowish discolored areas, mostly on stomatiferous surface, rather few, 8–17 per leaf, isolated, minute, colorless, circular in face view; in sections subcuticular, immersed, subglobose to flask-shaped, 104–154 μ in breadth, 91–154 μ in height, averaging 127.3 $\times$115.4 μ; openings slit-like, 72.8$\times$45.5 μ in average, situated in the interstomatal spaces; spermatiophores usually simple, septate, obclavate, subulate; spermatia narrowly elliptical to oblongo-cylindrical, 6.5–9.0 μ long, 2.0–3.0 μ broad, smooth, colorless (Pl. V, fig. c; VII, 17 i).

Aecidia on needles of current season, hypophyllous, rather few, 1–5 in a leaf, arranged in two rows between spermogonia, irregularly scattered, white, cylindrical, 0.2–0.28 mm. across, about 1 mm. high; peridia colorless, rather delicate, ruptured at the apex; peridial cells vertically elongated, with unequal sides, hexagonal, oblong to elliptic, overlapping, 25.0–61.0 μ long, 12.5–33.5 μ broad, averaging 37.6$\times$21.5 μ,

inner walls rather thick, 2–3 μ, minutely verrucose or somewhat striated; outer walls thinner, about 1 μ, smooth; aecidiospores colorless, globose to ellipsoidal, 23–38 × 21–32 μ, averaging about 30.32 × 25.79 μ, closely but finely verrucose except a small part where almost smooth; walls thin, up to 1 μ, including tubercles, colorless (Pl. II, fig. k; VI, fig. m).

Uredosori hypophyllous, subepidermal, scattered or loosely grouped on yellowish to brownish, sometimes blackish colored areas, pustular, round, small, 0.16–0.5 mm. across, covered by discolored epidermis; peridia almost hemispherical, comparatively firm, colorless, opened by central pore under stomata; peridial cells small, isodiametric to irregularly polygonal, 6–22 × 4–14 μ; walls colorless, thin, about 1 μ; uredospores colorless, white in mass, broadly clavate, obovate to oblong-ovate, sometimes angular, often short stalked, 30–53 × 15–33 μ; walls thin about 1 μ, finely verrucose especially at apex, colorless (Pl. III, m; VII, fig. 13 a).

Teleutosori on overwintered fronds, mostly hypophyllous, on pale yellowish discolored areas of indefinite extent; teleutospores within the epidermal cells, one to several in a cell, often completely filling it, more or less roundish in outline, colorless, one to many celled (up to ten or more?) with vertical septa; the cells of the spores more or less polygonal, except along the free margin, 15–26 × 10–20 μ, with thin, colorless, smooth walls; basidia cylindrical to clavate, about 45 μ long, about 10 μ across; basidiospores subglobose, 11 × 7 μ, colorless, smooth (Pl. VII, fig. 13 b).

Hosts and distribution:

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

II and III. *Polypodium virginianum* L.—in Japan (Hokkaidô).

14. Milesina Miyabei KAMEI

Historical review of the fungus. This rust was first described by the writer (1932 b) naming it after Professor MIYABE who early in 1911 collected the fungus on *Dryopteris crassirhizoma* at the University Tomakomai Experimental Forest. After successfully pursuing the life history study the writer published the diagnosis of all stages. FAULL (1932) presented a synoptical description under the genus *Milesia*. HIRATSUKA, f. (1932 c, 1934 d, 1936 c), HIRATSUKA, f. & HASHIOKA (1934) redescribed it and reported on newly made collections from Honshû, Hokkaidô, Formosa and Ussuri adding a new fern host, *Dryopteris Clarkei* O. KUNTZE from Formosa. ITÔ (1938) very recently described

this rust again.

Personal observations. Rusted ferns. Dryopteris crassirhizoma is the sole host of the present rust in Hokkaidô and Honshû. Uredosori were rather large and issued in the interveined areas which appeared quite healthy at first but gradually acquired yellowish to brownish discoloration extending to a wider limit with the increment of the pustules. The uredospores issued in white filamentary spore horns that sometimes were seen to extend up to several cm. in total length. This is due to the sticky membrane and great abundance of the spores contained in a sorus. These uredospores were seen to germinate soon in the water as shown in Pl. VII, fig. 14 a. To test the incubation period and host restriction, inoculation experiments with the uredospores were carried out as shown in Table 56. Uredosori appeared within a range of 11 to 25 days, average 21 days, which is rather a shorter incubation period than that of *M. Itôana.*

The development of teleutospores was seen to be influenced by the host condition. In the field, the collections of the current year fronds have shown a few teleutospores. In the collections of overwintered fronds, on the contrary, abundant spores produced in the areas of a comparatively heavy discoloration were detected. On the other hand, on cut fronds bearing uredo-pustules placed in a moist chamber at room temperature, the development of teleutospores seemed to proceed more promptly. Thus in a specimen that was gathered at Nopporo on Dec. 8, 1925 showing apparently no marked discolorations at the time of the collection, and observed in the moist chamber as mentioned just above, teleutospores were seen after 67 days on Feb. 13, 1926. Another specimen collected on Nov. 11, 1934 at Mt. Moiwa treated in the same way also produced teleutospores after 1 month and some of them were seen to be already germinating. The writer at Nopporo on June 12, 1926 collected the fronds rusted by this fungus which were partly greenish but for the most part discolored. Inside of the collecting vasculum, abundant germination of teleutospores was seen on the lesions of the specimens mentioned above only two days later.

Inoculations with basidiospores. The inoculation experiments with basidiospores on needles of nine seedlings of *Abies Mayriana* were successful as shown in Table 57. Summarizing these data, the period of development is somewhat shorter than in the case of other species of *Milesina,* such as *M. jezoensis, M. sublevis* and *M. Itôana.*

Inoculations with aecidiospores gained from cultures. With aecidio-

TABLE 56. Inoculations with uredospores of *M. Miyabei*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos. (No. of days)	Remarks
III. A 13	Uredospores on *Dr. crassirh.*, Nopporo, Nov. 11, 1925	*Dryopteris crassirhizoma*	Nov. 16, 1923	11	Potted pl. in greenhouse
" 26a	" Makkarinupuri, Nov. 12, 1924	"	Dec. 1, 1924	24	Petri dish in laboratory
" 31	" Nopporo, Dec. 8, 1925	"	Dec. 22, 1925	23	"
" 27	" Makkarinupuri, Nov. 12, 1924	*Dryopteris monticola*	Nov. 18, 1924	—	"
" 28	"	*Dryopteris dilatata* var. *oblonga*	"	—	"
" 42	" Nopporo, Nov. 19, 1933	*Dryopteris crassirhizoma*	Dec. 1, 1933	25	" Teleutosori were detected on March 7, 1934
" 49	" *Cult.* II, no. 49, iv b	"	Nov. 4, 1934	14	"
" 53	" Moiwa, Nov. 11, 1934	"	Nov. 28, 1934	25	"
" 54	"	"	"	23	"

TABLE 57. Inoculations with basidiospores of *M. Miyabei*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm. (No. of days)	App. of aecid. (No. of days)	Remarks
I. 106	Basidiospores on *Dr. crassirh.*, Nopporo, Je. 12, 1926	*A.M.* XV_6	Je. 14, 1926	16	26	Laboratory
" 107	"	" XVI_6	"	16	26	" Yellow spot appeared after 14 days
" 108	"	" $XVII_6$	"	23	36	"
" 155	" May 27, 1928	" $VIII_8$	Je. 2, 1928	38	—	"
" 160	"	" $XIII_8$	Je. 5, 1928	29	—	"
" 203	" May 24, 1931	" I_{11}	Je. 3, 1931	28	36	"
" 204	"	" II_{11}	"	28	—	"
" 210	"	" $VIII_{11}$	Je. 9, 1931	22	31	"
" 283	" Je. 1935	" I_{15}	Je. 4, 1935	16	21	"
" 284	"	" II_{15}	Je. 6, 1935	14	19	Laboratory
" 286	" Je. 7, 1936	" I_{16}	Je. 10, 1936	18	39	" Yellow spot appeared after 11 days

spores gained from the basidiospore cultures on *Abies Mayriana* XV_6 and I_{15} back inoculations were made on *Dryopteris crassirhizoma* and *D. dilatata* var. *oblonga*. In the case of the former fern, the characteristic uredospores appeared within 12–22 days, while in the latter none appeared, as shown in Table 58.

TABLE 58. Inoculations with aecidiospores of *M. Miyabei*

Exp. no.	Inocula	Fern inoc.	Date of inoc.	App. of uredos. No. of days	Remarks
II. 78	Aecidiospores on *A. M.* XV_6	*Dryopteris crassirhizoma*	Jy. 24, 1926	22	Potted pl. in laboratory
" 121	" I_{15}	"	Oct. 4, 1935	12	"
" 128	"	"	Aug. 4, 1936	14	"
IV. 43a	" Maruyama, Je. 15, 1934	*Dryopteris dilatata* var. *oblonga*	Jy. 17, 1934	—	Fern in pot in corridor
" d	"	*Dryopteris crassirhizoma*	"	16	"
" e	"	"	"	16	"
" 44a	"	*Dryopteris dilatata* var. *oblonga*	"	—	Fern in Petri dish
" b	"	*Dryopteris crassirhizoma*	"	13	"
" 53A	" Tomakomai, Aug. 10, 1936	"	Aug. 14, 1936	17	"
" B	"	*Dryopteris dilatata* var. *oblonga*	"	—	"
" 55A	"	*Dryopteris crassirhizoma*	"	31	Fern in pot in laboratory
" B	"	*Dryopteris dilatata* var. *oblonga*	"	—	"

Inoculations with aecidiospores gained from the field. At the beginning of this study, the writer confused this rust with the aecidial phase of *M. Itôana*. After studying on the life histories of these two species, it became evident that the aecidial phase of *M. Miyabei* develops earlier and matures more rapidly than in the case of *M. Itôana*. By critical morphological study of the organs, the writer identified two specimens of the aecidial phase collected from Maruyama and Tomakomai. Check inoculations with these aecidiospores on the fern host were successful, as shown in Table 58.

The description of this rust supplemented by further studies to the original, now stands as follows:—

Milesina Miyabei KAMEI in Trans. Sapporo Nat. Hist. Soc. XII, p. 169, 1932.

Syn. *Milesia Miyabei* FAULL in Contrib. Arnold Arb., Harvard Univ. II, p. 129, 1932.

Uredinopsis dubia TRANZSCH. in HIRATSUKA, f. in Memoirs Tottori Agricul. Coll. IV, p. 94, 1936.

Spermogonia on needles of current season, hypophyllous, 7–20, averaging about 12.4 per leaf, rather few, scattered in rows on more or less discolored lesions of stomatal surface, minute, but clearly seen with hand-lens, colorless, usually isolated, rarely confluent, mostly circular but sometimes irregularly outlined; in sections subepidermal, deeply seated, almost spherical, 165–297 μ broad in longitudinal sections 132.0–231.0 μ broad in transverse sections, 174.0–243.0 μ in height; apical opening roundish, made in the interstomatal space, usually at center of the apex, sometimes at sides, 40.3×22.7 μ in average; spermatiophores simple or branched, septate, subulate, 35.9 μ long, 3.3 μ broad in average, converging toward central locules, producing spermatia in chain; spermatia oblong, cylindric to narrowly elliptic, rather small, 3.0–6.1 μ long, 1.2–2.3 μ broad, colorless, smooth (Pl. V, figs. g and i; XII, fig. 17 j).

Aecidia hypophyllous, on needles of current season, many, 4–10, averaging about 7 per leaf, scattered in two rows on both sides of the midrib, white, cylindrical, up to 2 mm. in height, 0.5 mm. across; peridium colorless, rather delicate, ruptured at the apex; peridial cells with unequal sides, vertically elongated, oblong to polygonal, very often rounded at margin, overlapping in a single layer, 20.0–41.0×11.0–26.0 μ, averaging 32.0×17.6 μ, inner walls rather thick, 2–3 μ, finely verrucose, outer walls thin, 0.3–0.6 μ, smooth; aecidiospores colorless, globose to ellipsoidal, 20–26×15–22 μ, averaging about 22.83×19.15 μ, closely but rather coarsely verrucose, except a small part where almost smooth; walls thin, up to 2 μ thick including tubercles, colorless (Pl. II, fig. 1; VI, fig. n).

Uredosori hypophyllous, scattered on at first greenish, evenly yellowish colored parts of indefinite extent, mostly near veins or marginal portion of the pinnae, pustulate, covered with yellowish discolored epidermis, 0.15–0.35 mm. in diameter, ruptured at the centrally placed

stoma in the overlying epidermis; peridia colorless, distinct, flattened hemispherical in sectional view; peridial cells colorless, roundish to polygonal, 8–22×6–14 μ; walls thin, 0.5 μ thick, colorless; uredospores white, usually issuing in filamentary spore masses, very abundant, short stalked, plectrum to bone-shaped, mostly truncated at the apex, often a little projected or rounded, never acute or pointed, slightly narrowed below, 26.0–55.5×11.0–20.0 μ; walls thin, about 1 μ thick, a little thicker at angles, smooth, with four to five indistinct germpores, often accompanied by paraphyses-like cells (Pl. III, fig. n; VII, fig. 14 a and c).

Teleutosori mostly on overwintered fronds, amphigenous, on indefinite yellowish to brownish discolored areas, often near the uredosori, sometimes apart; teleutospores within the epidermal cells, sometimes in the guard cells, often isolated, sometimes two or more spores closely produced, often compactly filling the epidermal cells, more or less roundish in outline, divided vertically into two to several cells (up to 10 or more), a single pore for each cell; the cells of the spores more or less polygonal, except along the free margin, 10–20×6–10 μ, with about 1 μ thick, colorless, smooth walls; basidia clavate or cylindrical, 50–60 μ lang, 7–9 μ broad; basidiospores ellipsoidal to ovoidal, 11–13 μ, 7–10 μ broad, smooth, colorless (Pl. VII, fig. 14 b, d and e).

Hosts and distribution:

0 and I. *Abies Mayriana* Miyabe et Kudô (*Cultures* and *field*) —in Japan (Hokkaidô).

II and III. *Dryopteris crassirhizoma* Nakai—in Japan (Honshû and Hokkaidô) and Ussuri.

Dryopteris Clarkei O. Kunze—in Japan (Formosa).

15. **Milesina sublevis** Hiratsuka, f.

Historical review of the fungus. A specimen of the fern host stage of the rust in question was first sent to Sydow by Mr. Miura who collected it at Jôzankei, Prov. Ishikari, on Oct. 17, 1909. P. and H. Sydow (1913) identified it as *Milesina Scolopendrii* Jaap. Hiratsuka, f. (1927 c) described the teleutostage of this rust under the same specific name and mentioned his collections which were made mostly in the vicinity of Sapporo. Faull (1932) basing on specimens from this locality determined them to be a variety of *Milesia Scolopendrii,* accompanying his remarks with illustrations of the uredospores. After the

present writer's transfer (1935 a) to *Milesina,* HIRATSUKA, f. (1936 c) raised this rust to specific rank and described all its stages partly making use of a manuscript on the aecidial phase that had been prepared by the present author. He mentioned as the localities, Prov. Ishikari, Iburi, Shiribeshi and Tokachi in Hokkaidô, and Prov. Kaga in Honshû. Recently ITÔ (1938) also redescribed this rust. Heretofore, however, the life history experiments on this species have not been reported except very briefly by the writer (1932 b, 1933).

Personal observations. Rusted fern. The host fern, *Scolopendrium vulgare,* is distributed almost throughout the island of Hokkaidô, growing commonly under the shady parts of the forests. The rusted specimens may easily be obtained even in the immediate neighborhood of the city of Sapporo. In a specimen collected on August 23, the affected frond showed a few roundish patches of discoloration and distortions here and there to produce pustular uredosori, but no teleutospores could be found. A collection made on Nov. 13 was similar. Teleutospores were usually found fully matured on the overwintered fronds collected in the middle part of June. The writer often obtained very good materials for the morphological and biological studies of the teleutospores from Maruyama near Sapporo. The spots where teleutospores are found, were more or less evenly brownish discolored and slightly distorted. In the sections of these areas, it was revealed that the spores compactly filled the epidermal cells as well as the guard cells. They were divided into two to many cells (up to 33) by vertical septa and often also divided by a horizontal plane into two layers (cf. Pl. VII, fig. 15 c). Such features of the teleutospores of some species of *Milesina* have already been mentioned by MAGNUS (1901) in the case of *M. Kriegeriana.* He said that whether the spores of the second layer germinate or not is questionable. The basidiospores were larger than those of the related species and measured 11–15 by 5.5–9.5 μ; they were somewhat globose and smooth. HUNTER (1936 c) in the case of *M. Scolopendrii* gave a size for basidiospores which is a little smaller than that of the present species.

Inoculations with basidiospores. Inoculations with basidiospores on young needles of 13 seedlings of *A. Mayriana* were made. In these cases, yellow spots were seen before the appearance of spermogonia that occurred at 15–34 days. But aecidia were obtained in only one case, 55 days after the inoculation. In comparison with the species of *Uredinopsis* these incubation periods are far longer (cf. Table 59).

TABLE 59. Inoculations with basidiospores of *M. sublevis*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 109	Basidiospores on *Scol. vulg.*, Maruyama, Je. 1926	*A.M.* $XVIII_6$	Je. 15, 1926	15	—	Laboratory
» 110	»	» XIX_6	»	22	—	»
» 142	» Je. 1927	» X_7	Je. 19, 1927	23	—	»
» 143	»	» XI_7	Je. 22, 1927	34	—	»
» 213	» Je. 16. 1931	» XI_{11}	Je. 16, 1931	33	55	»
» 220	»	» $XVIII_{11}$	Je. 22, 1931	21	—	»

Inoculations with aecidiospores. After obtaining the aecidiospores of this species in 1931, back inoculations were at once carried out on Aug. 13 in a moist chamber on fresh fronds of *Scolopendrium vulgare* which were apparently clean from any infection of rusts. After 38 days from the inoculation on Sept. 20, the characteristic uredospores came out on the inoculated spots as shown in Pl. III, fig. o. HUNTER (1936 c) in the case of *Milesina Scolopendrii,* recorded the period of incubation as 37–54 days which is somewhat longer than that of the present species.

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

Milesina sublevis (FAULL) HIRATSUKA, f. in Memoirs Tottori Agricul. Coll. IV, p. 111, pl. III, fig. 6, 1936.

Syn. *Milesina Scolopendrii* (non JAAP) HIRATSUKA, f. in Jap. Journ. Bot. III, p. 313, 1927—KAMEI in Journ. Society of Agricul. and Forestr. Sapporo, XXIV, p. 364, 1933—SYDOW in Ann. Myc. XI, p. 110, 1913.

Milesia Scolopendrii ARTHUR var. *sublevis* FAULL in Contrib. Arnold Arb. Harvard Univ. II, p. 117, pl. VI, fig. 23, 1932.

Milesina Scolopendrii JAAP. var. *sublevis* (FAULL) KAMEI in Journ. Society of Agricul. and Forestr. Sapporo, XXVI, p. 577, 1935.

Spermogonia on needles of current season, hypophyllous, moderate in number, 10–40 to a leaf, colorless, scattered on yellowish discolored areas, especially on stomatiferous surfaces, usually discrete, rarely confluent, minute, conspicuous under hand-lens, more or less circular in face view; in sections subcuticular, immersed up to half of the leaf thickness, subspherical to flask-shaped, 100–220 μ broad, 64.0–204 μ high,

averaging 150 by 119 μ; openings more or less slit-like, located centrally or marginally in the interstomatal spaces, elongated parallel to the long axis of the needle, 19.5–97.5 × 13.0–32.5 μ, averaging 52.5 × 18.6 μ; spermatiophores usually unbranched, sometimes branched, septate, rather straight with blunt apex, 27.7 μ long, 3.4 μ thick, convergent; spermatia oblong, cylindrical to narrowly elliptical, 6.5–9.1 × 2.1–2.6 μ, hyaline, smooth (Pl. II, fig. m; V, figs. d and e; VII, fig. 17 k and l).

Aecidia on needles of current season, hypophyllous, scattered on more or less discolored areas, in two rows on both sides of the midrib, rather few, 1–9 per leaf, cylindrical, up to 0.5 mm. high, 0.13–0.3 mm. across; peridia colorless, rupturing at the apex; peridial cells mostly of equal sides, hexagonal or often isodiametric, sometimes rounded at margin, elongated vertically, slightly overlapping, 11–29 μ broad, 18–36 μ long, inner walls rather thick, 2–5 μ thick, stoutly verrucose, outer thinner, ca. 1 μ thick, smooth; aecidiospores colorless, globose to ellipsoidal, sometimes pyriform, 22–37 × 21–32 μ, averaging 31.49 × 26.67 μ, closely verrucose, except a part where almost smooth; walls thin, up to 2.5 μ including tubercles, colorless (Pl. VI, fig. o).

II and III are as described by FAULL (1932) and HIRATSUKA, f. (1936 c).

Hosts and distribution:

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

II and III. *Scolopendrium vulgare* SMITH—in Japan (Honshû and Hokkaidô).

(B) TIME OF APPEARANCE OF ORGANS

Data concerning the time of the appearance of organs in the life cycles of six species of *Milesina* observed in cultural studies are presented in the following paragraphs.

1. *Basidiospores.* As has already been stated, if the dates of inoculations with the basidiospores on the needles are granted to be those of the time of appearance of basidiospores, data concerning the species of *Milesina* used in this study are as shown below in Table 60. Comparing to the cases of other foreign species cultured by KLEBAHN (1916), FAULL (1934) and HUNTER (1936c), the dates in FAULL's cases for *M. intermedia* and *M. marginalis* were later in season than our cases, while HUNTER's dates for *M. Scolopendrii, M. Dieteliana, M. vogesiaca* and *M. Kriegeriana* were rather earlier. Comparing to the cases of

Uredinopsis from Hokkaidô that have been mentioned already the dates are distinctly later in the season.

2. *Spermogonia.* The dates of producing spermogonia from basidiospore cultures in the present six species of *Milesina* are shown in Table 60. They range in average from June 25 to July 17. Comparing to the cases in FAULL's as well as in HUNTER's experiments, these dates, though variable according to species, are not so late as in *M. intermedia* and *M. marginalis* and are not so early as in four species of *Milesina* that were cultured by HUNTER in England. Comparing to the species of *Uredinopsis* mentioned already, the dates are rather later in the season.

3. *Aecidia.* Dates of appearance of the aecidia gained from cultures of the species of *Milesina* under study are as shown in Table 60. The dates range from June 25 to Oct. 5 with the average of June 28 to Oct. 3. Compared with the foreign species which FAULL and HUNTER respectively cultured, the present dates for *M. Dryopteridis, M. Miyabei* and *M. sublevis* rather approximate to the cases of *M. polypodophila, M. intermedia* and *M. marginalis* from North America and *M. Dieteliana* and *M. vogesiaca* from Europe as shown in Table 60. In the case of *M. exigua* from the writer's cultures the dates are somewhat earlier than those species mentioned just above and close to *M. Scolopendrii* and *M. Kriegeriana* that were cultured in England. In the writer's *M. Itôana* and *M. jezoensis,* especially the former species, the aecidia are completed far later in season issuing just in the beginning of October. Comparing to the cases of *Uredinopsis* from Hokkaidô, those in the species of *Milesina* appear later in season.

4. (a) *Uredosori from inoculations with the aecidiospores gained from cultures.* The time of appearance of the uredostage gained by cultures with the aecidiospores obtained from basidiospore inoculations has already been reported by KLEBAHN (1916), KAMEI (1930b, 1935b), FAULL (1934) and HUNTER (1936a). As shown in Table 61, throughout 13 species, the dates range from Aug. 8 to Jan. 20, with the average Aug. 10 to Dec. 1. Comparing these data obtained concerning the Japanese species to the cases of foreign species, both dates of appearance more or less coincide with each other except *M. Dieteliana* from Europe, *M. Itôana* and *M. jezoensis* from Hokkaidô. In these species the uredosori appeared later in season. Comparing the dates of appearance of the uredosori originated from the aecidiospores derived from cultures in cases of rusts in *Uredinopsis* and in *Milesina,* the cases in *Milesina*

TABLE 60. Time of appearance of basidiospores, spermogonia and aecidia of the species of *Milesina* obtained from cultures

Species	Basidiospores		Spermogonia		Aecidia	
	Range	Average	Range	Average	Range	Average
*M. Blechni**	May 16–Je. 5	?	—	—	Jy. 10 ?	?
M. intermedia	Je. 27–Jy. 6	Jy. 3 (31)	Jy. 19–Jy. 25	Jy. 23 (21)	Je. 31–Aug. 11	Aug. 7 (30)
M. marginalis	Je. 27–Jy. 5	Je. 30 (38)	Jy. 17–Jy. 22	Jy. 20 (23)	Aug. 7–Aug. 19	Aug. 12 (38)
M. polypodophila	Je. 21	Je. 21 (3)	Je.	Je. (3)	Jy. 19–Jy. 25	Jy. 23 (3)
M. fructuosa	May 24–Je. 15	Je. 8 (27)	—	—	Je. 28–Jy. 25	Jy. 16 (24)
M. Scolopendrii	Apr. 27–Je. 30	May 18 (5)	May 23–Jy. 23	Je. 13 (5)	Je. 20–Aug. 5	Jy. 9 (4)
M. Dieteliana	May 2–Je. 1	May 21 (3)	May 28–Jy. 3	Je. 16 (3)	Jy. 21	Jy. 21 (1)
M. vogesiaca	Apr. 30–May 2	May 1 (2)	May 23	May 23 (2)	Aug. 3	Aug. 3 (1)
M. Kriegeriana	May 2–Je. 1	May 21 (10)	May 28–Je. 28	Je. 14 (9)	Je. 13–Jy. 24	Jy. 8 (7)
M. Dryopteridis	Je. 16–Je. 26	Je. 20 (3)	Jy. 7–Jy. 27	Jy. 17 (2)	Aug. 26	Aug. 26 (1)
M. exigua	May 30–Je. 17	Je. 6 (8)	Je. 17–Jy. 7	Je. 25 (8)	Je. 25–Jy. 2	Je. 28 (3)
M. Itôana	Je. 4–Je. 20	Je. 11 (6)	Je. 20–Jy. 19	Jy. 3 (6)	Sept. 23–Oct. 5	Oct. 1 (6)
M. jezoensis	Je. 19–Je. 30	Je. 23 (7)	Je. 10–Aug. 2	Jy. 17 (6)	Oct. 3	Oct. 3 (1)
M. Miyabei	Je. 2–Je. 14	Je. 7 (11)	Je. 20–Jy. 10	Jy. 2 (11)	Jy. 9–Jy. 20	Jy. 13 (8)
M. sublevis	Je. 15–Je. 22	Je. 19 (6)	Jy. 7–Jy. 26	Jy. 14 (6)	Aug. 10	Aug. 10 (1)
Extreme limits	May 2–Jy. 6	May 1–Je. 30	May 23–Aug. 2	May 23–Jy. 23	Je. 13–Oct. 5	Je. 28–Oct. 3

* Data for *M. Blechni* from KLEBAHN, for *M. intermedia, M. marginalis, M. polypodophila* and *M. fructuosa* from FAULL, for *M. Scolopendrii, M. Dieteliana, M. vogesiaca* and *M. Kriegeriana* from HUNTER and for the other species from the writer.

TABLE 61. Time of appearance of uredosori obtained from inoculations with aecidiospores of the species of *Milesina*

Species	Fern inoc.	Inocula	Range	Average
*M. Blechni**	*Blechnum Spicant*	c	Along in August	?
M. marginalis	*Dryopteris marginalis*	c	In spring of following year	?
M. intermedia	*Dryopteris spinulosa, D. spinulosa intermedia*	c	No uredosori formed at any time	
M. polypodophila	*Polypodium virginianum*	f	Sept. 13–Sept. 15 (–June) (F)	Sept. 14 (8) (—?)
M. Scolopendrii	*Scolopendrium vulgare*	c	Aug. 30–Sept. 18	Sept. 8 (6)
M. Dieteliana	*Polypodium vulgare*	c	Sept. 15–Oct. 19	Oct. 2 (4)
M. Kriegeriana	*Dryopteris Filix-mas, D. spinulosa*	c	Aug. 30–Sept. 15	
M. Kriegeriana	*Dryopteris Filix-mas, D. spinulosa dilatata, D. spinulosa intermedia*	c	Aug. 31–Sept. 15	
M. Kriegeriana (M)	*Dryopteris Filix-mas*	f	Aug. 10	Aug. 10 (1)
M. Dryopteridis	*Polystichum Standishii*	c	Sept. 26	Sept. 26 (1)
M. exigua	*Polystichum Braunii*	c	Aug. 8–Sept. 9	Aug. 24 (2)
M. Itôana	*Dryopteris crassirhizoma*	c	Nov. 12–Dec. 13	Dec. 1 (6)
M. Itôana	„	f	Oct. 21–Jan. 20	Nov. 27 (20)
M. jezoensis	*Polypodium virginianum*	c	Nov. 20	Nov. 20 (1)
M. Miyabei	*Dryopteris crassirhizoma*	c	Aug. 15–Oct. 16	Sept. 6 (3)
M. Miyabei	„	f	Je. 30–Sept. 14	Aug. 16 (5)
M. sublevis	*Scolopendrium vulgare*	c	Sept. 20	Sept. 20 (1)
Extreme limits			Aug. 8–Jan. 20 (–June)	Aug. 10–Dec. 1 (–?)

* The species were studied by the same authors as indicated in Table 60 except *M. Kriegeriana* (M) which was studied by MAYOR. (F) FAULL (1934) in six other experiments with aecidiospores made in August 1924 obtained uredosori in June in the next year.

are later than the cases in *Uredinopsis*.

(b) *Uredosori from inoculations with the aecidiospores gained from the field.* Inoculation experiments with the aecidiospores of some *Milesina* obtained from the field have been made already by FAULL & WATSON (FAULL, 1932), MAYOR (1933) and the writer (1935b). The present writer's results with *M. Itôana* and *M. Miyabei* agree more or less with the dates from foreign countries as well as with those dates of the appearance in inoculations with the aecidiospores derived from basidiospore cultures as shown in Table 61. Considering these results

of inoculations with the aecidiospores from cultures and from the field, the time of the appearance of uredosori in the case of *Milesina* is always later than in the case of *Uredinopsis*.

5. *Teleutospores.* Concerning the time of formation of the teleutospores of a *Milesina*, produced from inoculation experiments, there is little recorded so far. However, MAGNUS (1901) who may have made his observation on *M. Kriegeriana* inside the laboratory recorded that the spores were detected in the fall on fronds of the current season. FAULL (1934) also observing the affected fronds with uredosori of *M. marginalis* saw that the teleutospores occur in early spring on the overwintered fronds. In the writer's observations in *M. Itôana* and *M. Miyabei* on inoculated as well as collected diseased fern fronds placed inside of Petri dishes, the teleutospores were observed in February. Comparing these features of the formation of the teleutospores to those of *Uredinopsis*, the species of *Milesina* are distinctly different.

C. DEVELOPMENTAL PERIODS OF ORGANS

Periods of the development of each organ gained from artificial cultural experiments are discussed in the following paragraphs.

1. *Spermogonia.* Concerning periods of the development of spermogonia of the species of *Milesina*, the only statistical study has been reported by FAULL (1934). He mentioned periods for seven species that had previously been investigated. A slightly complemented summarization was made by the writer (1935a). In the same year four European species of *Milesina* were added to the list of those upon which life history experiments had been completed. Comparing these 15 species, among a total of 51 species now known, the shortest case in respect to the period of the development of spermogonia is that of *M. exigua* from Hokkaidô, while the longest is that of *M. polypodophila* from North America as indicated in Table 62. Among the six species of *Milesina* used for the present study, the average development period varies from 18 days in the case of *M. exigua* to 30 days in *M. Dryopteridis*. Comparing these data from this country with those of taxonomically related foreign species, for instance, in the comparison of such combinations as *M. exigua* to *M. vogesiaca*, *M. sublevis* to *M. Scolopendrii*, *M. Itôana* to *M. intermedia* and *M. jezoensis* to *M. Dieteliana*, the species of the respective combinations approximate each other. Comparing the development periods of the species of *Uredinopsis* from Hokkaidô to those of the species of *Milesina* the former ones are shorter.

2. *Aecidia.* Concerning the development period of the aecidial stage of some *Milesina,* reports have been made also by FAULL as mentioned already. Among 15 species, of which the developmental periods are known, the range is from 19 days for a case of *M. Miyabei* to three years and one month for *M. polypodophila* as shown in Table 62. Among those of the six Japanese species, the average period varies from 25 days for *M. exigua* to 110 days in the case of *M. Itôana.* In this respect, comparing the periods for taxonomically nearly related species, there is sometimes agreement among them but at other times none. In detail, in such comparisons as *M. sublevis* with *M. Scolopendrii,* or *M. jezoensis* with *M. Dieteliana,* the periods of both couples were somewhat similar. But in such cases as *M. Itôana* with *M. inter-*

TABLE 62. Developmental periods of spermogonia and aecidia of the species of *Milesina*

Species*	Hosts	Spermogonia		Aecidia	
		No. of days			
		Range	Average	Range	Average
M. Blechni	*Abies alba, A. cephalonica*	36(?)	—	35	35(1)
M. intermedia	*A. balsamea*	14–21	18(21)	32–38	34(30)
M. marginalis	"	18–23	19(23)	39–51	43(38)
M. polypodophila	"	1095		1125	
M. fructuosa	"	—	—	34–45	38(24)
M. vogesiaca	*A. alba*	21–23	22(2)	93	93(1)
M. Dieteliana	*A. alba, A. concolor*	25–26	26(3)	80	80(1)
M. Scolopendrii	*A. alba, A. concolor*	21–29	25(5)	54–78	62(4)
M. Kriegeriana	*A. alba, A. concolor, A. grandis*	21–30	22(9)	37–57	50(7)
M. Dryopteridis	*A. Mayriana*	21–38	29.5(2)	71	71(1)
M. exigua	"	13–26	18.3(8)	21–28	25.3(3)
M. Itôana	"	15–39	21.0(6)	101–119	112.3(6)
M. jezoensis	"	18–44	23.8(7)	104	104(1)
M. Miyabei	"	14–38	23.8(11)	19–39	29.3(8)
M. sublevis	"	15–34	24.6(6)	55	55(1)
Extreme limits		13–1095	18–29.5	19–1125	25.3–112.3

* The species were studied by the same authors as indicated in Table 60.

TABLE 63. Developmental period of uredosori issued from aecidiospore inoculations of the species of *Milesina*

Species*	Fern inoc.	No. of days		Remarks
		Range	Average	
M. Blechni	*Dryopteris spinulosa*	21	—	
M. marginalis	*Dryopteris marginalis*	?.	—	"Some uredinia may have formed in late fall but seen in spring of the following year"
M. intermedia	*Dryopteris spinulosa, D. spinulosa* v. *intermedia*			"No uredinia found at any time"
M. polypodophila	*Polypodium virginianum*	"37 to 42"	?	
M. Scolopendrii	*Scolopendrium vulgare*	37–54	*46*(6)	
M. Dieteliana	*Polypodium vulgare*	47–69	*58*(4)	
M. Kriegeriana	*Dryopteris Filix-mas, D. spinulosa*	28–47	*38*(4)	Aecidiospores originated from *Dryopteris Filix-mas*
"	*Dryopteris Filix-mas, D. spinulosa*	64–64	*64*(2)	Aecidiospores originated from *Dryopteris spinulosa* v. *dilatata*
"	*Dryopteris Filix-mas, D. spinulosa* v. *dilatata, D. spinulosa* v. *intermedia*	32–47	*37*(3)	
M. Dryopteridis	*Polystichum Standishii*	16	*16*(1)	Cut pinnae. Inocula obtained from culture
M. exigua	*Polystichum Braunii*	13–17	*15.0*(2)	Potted pl. Inocula obtained from culture
M. Itôana	*Dryopteris crassirhizoma*	19–60	34.0(20)	Cut pinnae. Inocula obtained from field
"	"	23	230.(1)	Potted pl. Inocula obtained from culture
"	"	23–43	36.6(5)	Cut pinnae. Inocula obtained from culture
"	Limit	19–60	*34.1*(26)	
M. jezoensis	*Polypodium virginianum*	28	*28*(1)	Cut pinnae. Inocula obtained from culture

M. Miyabei	*Dryopteris crassirhizoma*	22	22(1)	Potted pl. Inocula obtained from culture
"	"	12–14	13(2)	Cut pinnae. Inocula obtained from culture
"	"	13–31	18.4(5)	Cut pinnae. Inocula obtained from the field
"	Limit	12–31	*17.5*(8)	
M. sublevis	*Scolopendrium vulgare*	38	*38*(1)	Cut pinnae. Inocula obtained from culture
Extreme limits		12–69	13–64	
Limits of average periods			*15–64*	

* The species were studied by various authors as indicated in Table 60.

media or *M. exigua* with *M. vogesiaca,* although they are nearly related, their development periods differ considerably. Comparing the periods of *Milesina* species to those of *Uredinopsis,* those of the latter genus are far shorter than those of the former.

3. *Uredosori.* A statistical study on the developmental periods of uredosori of the species of *Milesina* was made by FAULL (1934). He collated these periods for five species that were previously known to be related to *Abies.* According to his Table 9, the periods for producing uredosori range 13–42 days in three species out of his five. KLEBAHN (1916) said that the period in *M. Blechni* was comparatively long. MAYOR (1933) reported such a period after the inoculation of the aecidiospores of *M. Kriegeriana* to be 15 days. Recently HUNTER (1936a), concerning three species including *M. Kriegeriana* published that they need 28 to 69 days. In the six species used in the present study, the uredosori from aecidiospore inoculations appear after 12 to 50 days with 15 to 38 days as the average for each species as shown in Table 63.

In the case of the uredospore inoculations as shown in Table 64, the writer obtained uredosori of *Milesina Itôana* and *M. Miyabei* in 27.0 and 24.0 days on the average respectively. From the results also it is ascertained that the developmental period in *M. Itôana* is longer than that of *M. Miyabei.*

Restricting his experiment to a certain species of our *Milesina* rusts, the writer has found, just as also in *Uredinopsis* materials, that the incubation periods for producing uredosori in the experiments in Petri

TABLE 64. Developmental period of uredosori obtained by uredospore inoculations of some *Milesina*

Species*	Fern hosts	No. of days		Remarks
		Range	Average	
M. Itôana	*Dryopteris crassirhizoma*	26–28	27.0(2)	Cut pinnae
M. Miyabei	"	23–25	24.0(3)	"

* The species were studied by the writer.

dish were usually shorter than those carried out with potted plants.

After reviewing Table 63, which contains development periods of the uredosori concerning various species of *Milesina* from this as well as foreign countries, it is learned that the period varies widely according to each species just as already remarked by FAULL (1934, p. 82). In general, however, it is very clear that the periods of the species of *Milesina* are usually longer than those of the species of *Uredinopsis*.

4. *Teleutospores.* Heretofore, there have been only meager reports on the period of the development of the teleutospores of *Milesina*. FAULL (1934) reported that the teleutospores of *M. marginalis* were detected after three weeks' incubation at the areas where previously uredosorus bearing lesions had been richly seen. He also remarked on the formation of the teleutospores of *M. intermedia* that it depends "on the earliness of the infection and the nature of the environmental conditions." In the present materials, the writer has observed alive in Petri dish in late fall a partial frond of *Dryopteris crassirhizoma* bearing an ample number of the uredosori of *M. Miyabei*, the teleutospores were seen to be developed and even germinating after 67 days from the treatment. Also in *M. Itôana*, on the host fern in Petri dish inoculated with aecidiospores, the teleutospores were seen 97 days after the inoculation. Considering these observations on the period of development of the teleutospores in each species, in general, the periods of *Milesina* species are comparatively far longer than those of the *Uredinopsis* species.

D. HOST RESTRICTION

1. *Fir hosts.* As to the restriction of species of *Milesina* to the fir hosts, FAULL (1934) summarized previously reported results relating to *M. Blechni*, *M. exigua* and *M. fructuosa*. According to his conclusion, (FAULL, 1932, p. 126 and 1934, pp. 79 and 84) in short, there is

no definite restriction or preference of the host species, that is to say, they can infect a rather wide range of species of *Abies* equally. In the life history studies of *M. Kriegeriana*, HUNTER (1936c) was equally successful to inoculate with basidiospores on needles of *Abies alba, A. concolor* and *A. grandis*. As for the writer's observations, in the case of *M. exigua*, the basidiospore inoculations were altogether successful on the needles of *Abies Mayriana, A. sachalinensis* and *A. firma*. Moreover, in *M. Itôana*, its fir hosts are proved to be *Abies Mayriana* as well as *A. sachalinensis*. These results from the investigations of HUNTER and the present writer may well support FAULL's conclusion mentioned just above.

2. *Fern hosts.* As to the production of the uredo- and teleutostages on fern hosts, the infection by the rust is strictly limited to its special proper host or hosts only. FAULL (1934) has already indicated such an inclination securing no success with aecidiospore inoculations on four species other than the proper host fern in the case of *M. intermedia*, on five species in the case of *M. marginalis* and two species in the case of *M. polypodophila*. HUNTER (1936a) also carried out test inoculations with aecidiospores of *Milesina Scolopendrii, M. Dieteliana* and *M. Kriegeriana*. In the two former rusts, negative results were obtained on ferns other than the proper special one. In *M. Kriegeriana*, successful inoculations were made on both of the two fern hosts alike. The writer also in this connection tried similar inoculations with the aecidiospores of *Milesina Itôana* derived from cultures on four other fern hosts and with the aecidiospores and uredospores of *M. Miyabei* on two other fern hosts failing to gain any uredospores in both cases as was already shown in the respective paragraphs and in Tables 53, 56 and 58.

E. DISCUSSION ON THE LIFE CYCLE

The fern rusts belonging to the genus *Milesina*, as stated by FAULL (1932, 1934), have now been found on the species of about ten genera in Polypodiaceae. Restricted to this island only, some eight *Milesina* rusts are found on each of some species or rarely more than one species of *Asplenium, Dryopteris, Polypodium, Polystichum* and *Scolopendrium*. They all, in comparison to the host ferns of *Uredinopsis* rusts, are far better fitted for the overwintering habit and some of their fronds remain "in a more or less green condition" until the next spring as mentioned by FAULL. Except for rare instances, the teleutospores develop on the

overwintered affected fronds in the next spring. An exceptional case was seen in this locality in the case of *M. exigua,* in which basidiospore materials were often collected before snow-fall and successfully inoculated on *Abies.* In the usual species, however, the teleutospore formation is associated with the production of crops of uredospores on the overwintered leaves and propagation from fern to fern as already indicated by KLEBAHN (1916) and FAULL (1932). This inclination is typically seen in this locality in the case of *M. Dryopteridis* on the fronds of *Polystichum Standishii.* On this fern, as already mentioned, one may detect a very small number of mature uredosori on less discolored lesions in the latter part of the season but in the spring on the old fronds, in about June, a profuse mass of the uredospores as well as mature teleutospores on almost blackish discoloration are seen. In the case of *M. Itôana* from this locality the conditions seem to be a little different from the cases described above. The writer has not yet obtained uredosori on current year fronds but has occasionally on the overwintered ones of *Dryopteris crassirhizoma.* The true reason for these special characters may be partly attributed to the slower development which is also generally true for other species of *Milesina* compared with the species of *Uredinopsis.* On the other hand, in *Uredinopsis,* overwintering is often accomplished by means of amphispores as well as teleutospores. But in *Milesina,* the amphispores have not yet been found, as FAULL (1932) pointed out, in any species of the genus. Considering these features the hibernation of the usual species of *Milesina* must certainly be made by the mycelia in the tissues of the affected fronds. From the mycelia new uredospores are developed after overwintering. This hibernation by mycelia was also indicated by TREBAUX (1914) in the case of *Thekopsora* and other rust fungi. Recently PADY (1935) also published similar information in *Hyalopsora.* Indeed, a species of *Milesina* must be fitted for autoecism and "may be continued indefinitely from year to year without reference to an aecial host" as said by FAULL (1932, p. 125). This is true because the same *Milesina* rust on the same fern host at the same locality is to be found in succeeding years. THURSTON (1928) already mentioned such an inclination in the case of *M. polypodophila.* The teleutospores mature at about the time when the leaves of *Abies* begin to unfold. The portions where these teleutospores are contained are usually discolored but the texture of the host tissue mostly remains quite intact unlike the case of the *Uredinopsis* species. When the germination of the spores has occurred, the promy-

celium penetrates the upper wall of the epidermal cell by a tiny pore which is clearly visible in the face view of the affected leaves. A mass of basidiospores and basidia covers the lesion presenting a whitish film-like layer.

Heteroecism with these basidiospore inoculations onto *Abies* has been experimentally proved by several authors. It was known from these proofs that the periods for the development of spermogonia as well as aecidia are generally longer in *Milesina* than in *Uredinopsis*. A very much longer case was in *M. polypodophila*, needing three years and one month as shown by FAULL (1934). For *M. Itôana* in this locality the period is also rather longer extending for more than three months. In those species in which the development of the aecidia occurs late in season, the time in which mature aecidiospores reach the fern host, is of course delayed much toward winter. The new infection on fern by means of aecidiospores in the later autumn can not be developed into uredosori, because of the hindrance by cold weather. It happens that in this species the teleutospores are usually very abundantly produced. In contrast with that feature the uredosori, which were seen in the spring on the overwintered leaves, were very meager in number and also obscure. Whether this paucity of the uredospores is related to the abundance of the teleutospores or not is as yet undetermined. In such species as *M. Itôana*, however, basidiospores are more abundantly produced and infection of needles of *Abies* must also occur in profusion, making the species well adapted for heteroecism. In other species of *Milesina* used for the present study, new uredopustules were probably derived mainly from the reinfection of uredospores, which had been formed in the previous season. The latter course of development must be the usual one for any species of *Milesina*.

In the rusts in which the appearance of aecidia occurs late in season, the aecidial stage may overwinter *in situ* and may be collected in the next spring on second year needles. Such cases were encountered by the writer in this locality. But these collections can not be confused with such species as those in which the aecidia develop on the older needles directly as in the case of *M. polypodophila* in North America.

Among the species of *Milesina*, such a one as *M. Miyabei* in which the morphology of the fungus is somewhat nearly related to some of the species of *Uredinopsis*, the developmental period happened to be shortened and the aecidial stage was collected earlier in the season.

Conclusively, as partly indicated by the writer already (1935a),

Milesina rusts in general, must probably propagate by both modes of life cycle, autoeciously and heteroeciously, just like *Uredinopsis* rusts. The respective developmental periods of each organ, however, are generally longer resulting in a delay in the appearance. So, also in the case of the aecidial stage, the issuing of the organs in *Milesina* is later than in *Uredinopsis*. FAULL (1938b) recently announced a similar conclusion.

The species of *Milesina*, as in *Uredinopsis*, and probably also in other *Abies* rusts, while strictly restricted on fern hosts, are scarcely restrained to a single species of the fir host. Such parasitism may naturally explain how one and the same species of fir in a locality is attacked by two or more species of the same or different genera of *Abies* rusts, requiring careful taxonomic investigations of the stages on the *Abies* host. Indeed, the writer found such a case of two distinct species from genera of *Uredinopsis* and *Milesina* or *Milesina* and *Hyalopsora* infecting together even on the same single needle, each slightly differing from the other in its stage of development.

F. COMPARATIVE MORPHOLOGY

The need of comparison of the various morphological characters is similarly felt also in *Milesina* just as in the case of *Uredinopsis* which has already been remarked.

(*1*) *Spermogonium stage*

The comparative morphology of the spermogonia of some species of *Milesina* has already been studied by FAULL (1929, 1934) and HUNTER (1927, 1936c). The latter presented detailed ontogenetical descriptions of nine species accompanied with a table of morphological data and illustrations. Similar photographs of sectional views of spermogonia of *M. exigua* and *M. Itôana* were also published by the writer (1930, 1935b). Concerning materials and methods for the investigations they were similar to those described in the case of *Uredinopsis*.

1. *Color of spermogonia.* The color of the spermogonia of the species of *Milesina* is the same as those of *Uredinopsis*, and entirely hyaline.

2. *Age of the affected needles.* This is also the same as in *Uredinopsis* material and is always of the current year needles. In North America the greater age of the needles affected by *M. polypodophila* has been reported by BELL (1924) and FAULL (1929).

3. *Position of spermogonia.* So far as the writer's observations are concerned, all of the six species of material were always hypophyllous except *M. exigua* in which a minor part of the spermogonia were epiphyllous beside usual hypophyllous ones. From foreign countries, amphigenous but mostly hypophyllous ones in the cases of *M. marginalis* and *M. Blechni* are reported. FAULL (1934) noted that the spermogonia in the cases of various specimens of *M. fructuosa* are variable in respect to the position on the needles. *M. polypodophila* was stated to be the only species in America that has hypophyllous spermogonia. Recently HUNTER (1936a) announced that *M. Scolopendrii,' M. Dieteliana, M. vogesiaca* and *M. Kriegeriana* have "epiphyllous and hypophyllous" spermogonia.

4. *Distribution of spermogonia.* They were usually discrete but sometimes two to three spermogonia were seen to be closely attached to each other in the cases of *M. exigua, M. Itôana, M. Miyabei* and *M. sublevis.* The rare occurrence of such confluency of the spermogonia in the case of *M. polypodophila* was mentioned by HUNTER (1927). They were arranged almost in a line on both sides of the midrib, more or less alternating with aecidia as shown in Pl. II, figs. i, j, k and m.

5. *Number of spermogonia.* FAULL (1932) and HUNTER (1927, 1936c) respectively, have already mentioned the number of the spermogonia of some species of *Milesina,* designating them by the terms "few", "abundant", "very abundant" and "numerous". Particularly in the case of *M. polypodophila,* FAULL (1934) said the number of spermogonia on a needle varies from ten to twenty which case somewhat approaches the writer's observation on *M. Miyabei* and *M .jezoensis.*

Among six species of *Milesina* used in the present study, the total number of spermogonia as well as those per square millimeter were rather fewer in the cases of *M. Miyabei* and *M. Itôana* compared with those of other species. In a certain needle affected by *M. exigua,* the total number attained to 58. This was the greatest number seen among all the needles attacked by any species of *Milesina* used in this study. Even in this case, the number of spermogonia was far less than in any species of *Uredinopsis.* Such an occurrence is very reasonable if the number of the spermogonia per needle is presumed to be the reverse of the size of each organ. The smallest number of the organ per needle was seen in the case of *M. Itôana* and following it more numerous ones were found in the order *M. Miyabei, M. jezoensis, M. Dryopteridis, M. exigua* and *M. sublevis* as shown in Table 65. The order of the

TABLE 65. Number of spermogonia in six species of *Milesina*

Species	Hosts	Range		Average*	
		per needle	per sq. mm.	per needle	per sq. mm.
M. Dryopteridis	*A.M.* XVI_{11}, III_{14}	3–38	2–9	14.7	5.5
M. exigua	*A.f.* I_6, *A.M.* X_{10}	2–58	4–10	19.8	6.8
M. Itôana	" I_{15}	5–15	2–4	9.0	2.9
M. jezoensis	" $XVIII_{10}$, XIX_{10}	8–17	3–5	12.5	3.6
M. Miyabei	" I_{11}, II_{11}, $VIII_{11}$	7–20	2–6	12.4	4.2
M. sublevis	" XI_{11}	10–40	3–6	21.5	4.3

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

number per square millimeter was also somewhat similar.

6. *Situation of spermogonia.* (a) Face view. In the six species of *Milesina* used in this study the spermogonia were mostly situated at the stomatal areas but often were seen also in the marginal part, just alongside the stomatal areas. The occasional occurrence of the spermogonia, "upon the side of" the needles was already reported by HUNTER (1927) in the case of *M. marginalis*. In the face view of the subcuticular spermogonia, the upper central part of the organ was perceptible through thin cuticle and likewise their irregular lined pore. In subepidermal cases, on the contrary, the opening was shown as a minute pore and the upper part of the organ was quite invisible.

(b) *Sectional view.* According to their different locations the writer's six species of *Milesina* may be divided into two groups. To the subcuticular type, belong such species as *M. Dryopteridis, M. exigua, M. jezoensis* and *M. sublevis,* while to the subepidermal type such species as *M. Itôana* and *M. Miyabei.* The subcuticular ones were already known in the cases of *M. intermedia* and *M. marginalis* from North America and in the cases of *M. Dieteliana* and *M. vogesiaca, M. Kriegeriana* and *M. Scolopendrii* from Europe by the reports of HUNTER (1927, 1936c) and FAULL (1932). HUNTER (1936c) explained the form and position of the spermogonia of these foreign six rusts by the remarks "subcuticular, immersed". The subepidermal ones had previously been seen only in the case of *M. polypodophila* from North America. HUNTER (l. c.) designated them as "subepidermal, immersed". Recently HUNTER (l. c.) corrected her previous assertion about the spermogonia of *M. marginalis* by saying that they are rarely subepidermal. In her ontogenetical

studies of *M. intermedia* and *M. Kriegeriana,* she stated that in the earlier development of the organs the spermogonia originate "in the outer epidermal wall."

Concerning our species such ontogenetical studies have not been made and the observation was limited to matured stages. In the subcuticular spermogonia of our materials, some epidermal cells, at least their upper walls situated just below a spermogonium, were seen to be almost always crushed, and a thin cuticular layer was seen remaining above the apex of each spermogonium. The body of the spermogonium, so far as seen, was found to be situated in the space of a cell-cavity or much enlarged room, which probably must have been formed by the pressure exerted upon the mesophyll beneath in the course of its development. So the shape of the organ was seen in the median sectional view to be somewhat as illustrated in Pl. V. In general the peripheral tissue of the organ was seen to be composed of rather thin pseudoparenchymatic layer, and the inner surface was lined with the hymenium of converged spermatiophores intermixed with the so called "flexuous hyphae". Sometimes a few sterile spermatiophores were seen near the ostiole. The lower end of the spermogonia was seen to reach up to one-third to one-half of the leaf thickness. So comparing with the subcuticular spermogonia of *Uredinopsis,* those in the species of *Milesina* under discussion were generally immersed more deeply. In the subepidermal type, the features were somewhat similar to those of the subepidermal type of *Uredinopsis,* as for instance those in *U. ossaeiformis* and *U. intermedia.* Normally the upper part of the organ was located just under the epidermis, and the overlying host cell layer was seen often quite undisturbed. Usually near the ostiole, sterile spermatiophores were also found just under the epidermis. In such a portion, some epidermal cells were seen to be invaded by some hyphae. The peripheral portions were rather like those of *Milesina* of the subcuticular type and also those of *Uredinopsis* having subepidermal spermogonia. The lower end of the organ attained to a further depth than in the case of the subcuticular type. It reached up to two-thirds or four-fifths of the whole leaf thickness, which was almost like the limit of the depth of the aecidial organ.

7. *Size of spermogonia.* As shown in Table 66, distinctly larger diameters, vertically as well as horizontally, were seen in the cases of subepidermal spermogonia. Among two species of this type, those of *M. Itôana* were larger than in the case of *M. Miyabei.* Among the species of the subcuticular type, the spermogonia of *M. exigua* were

the largest. After these follow in order those of *M. Dryopteridis, M. sublevis* and *M. jezoensis.* HUNTER (1936c) also mentioned the size of the spermogonia of nine species of *Milesina.* Among them, *M. polypodophila* was nearly the same as *M. Miyabei* and *M. Itôana* in our materials. *M. fructuosa* (or *M. intermedia*) was indicated to have smaller organs compared with any species of the present rusts investigated. Spermogonia of other species mentioned by her were more or less near to those of the other four species of the writer's investigations.

TABLE 66. Size of spermogonia in six species of *Milesina*

Species	Range (μ)			Average (μ)*		
	Face view	Sect. view	Height	Face view	Sect. view	Height
M. Dryopteridis	110–187	134.4–184	91.6–166.5	153.5	156	136.4
M. exigua	132–176	122–185	111 –173.9	157.3	157.9	132.8
M. Itôana	160–256	172–320	172.8–288	208.3	251.5	230.4
M. jezoensis	99–165	104–154	91 –154	133.7	127.3	115.4
M. Miyabei	132–231	165–297	174 –242	190.3	223.1	213.8
M. sublevis	132–176	110–220	64 –204	147.4	150	119.4

* The number averaged was 20. The size in sectional view means that measured in a longitudinal section of the needle, and the size in face view means that measured in the upper view almost at right angles to the horizontal axis of the spermogonium. The hosts on which the materials were taken were: in *Milesina Dryopteridis, Abies Mayriana* XVI_{11}, III_{14}; in *M. exigua, A. firma* I_6; in *M. Itôana, A. Mayriana* I_{15}, II_{15}; in *M. jezoensis, A. Mayriana* $XVIII_{10}$, XIX_{10}; in *M. Miyabei, A. Mayriana* XV_6, II_{11}, and in *M. sublevis, A. Mayriana* X_7, $XVIII_{11}$.

8. *Shape of spermogonia.* (a) *Face view.* The shape of spermogonia of the six Japanese species of *Milesina* seen in face view was somewhat circular to oblong. When distinctly oblong as in the case of *M. Itôana,* the longer diameter was usually parallel to the longer axis of the needle, but rarely, at right angles or oblique. The marginal line was almost concretely circular but often a little wavy in the outline which is especially true in the case of *M. Miyabei.*

(b) *Sectional view.* Concerning the sectional view of the spermogonia of a *Milesina,* HUNTER (1936c) described it as "spherical" in the case of *M. polypodophila* and in nine other species as "hemispherical to almost spherical," "subspherical to almost spherical," "somewhat flask shaped," "hemispherical to slightly flask shaped" or "hemispherical to slightly flask shaped" or "hemispherical." In the present observations,

also they were more or less spherical to flask-shaped. Sometimes they were elongated and seen as somewhat utricular. In the subcuticular species, the apices of the organs were often a little erumpent and seen as rather subconoidal. In the subepidermal species, the organs did not rise above the level of the epidermis and were more spherical except for an occasional elongated utricular appearance. Remarks concerning the shape of the spermogonia of each species are appended as follows:—

M. Dryopteridis: flattened spherical to almost spherical.
M. exigua: subspherical to flask-shaped.
M. Itôana: almost spherical to utricular.
M. jezoensis: subglobose to flask-shaped.
M. Miyabei: almost spherical.
M. sublevis: subglobose to flask-shaped.

9. *Openings.* The openings of spermogonia of *Milesina* through which spermatia are emitted have already been described by HUNTER (1927, 1936c) and FAULL (1932, 1934). FAULL (1934, p. 70) describing spermogonia of *M. polypodophila* said, "frequently there may be a stoma more or less eccentrically located on the epidermis that covers a spermogonium. This opens wide, the opening with a jagged line of broken cuticle." According to the writer's observations, in general, the opening was made on the cuticular layer or on the epidermal cells just beside or apart from stomata. Especially in the subcuticular species, they were mostly slit-like but often roundish to irregular polygonal. Often the slit was seen extending across the entire diameter of the spermogonia. In the confluent ones, the slits of the adjacent two organs, were often running together and seen to be much elongated as in the cases of *M. exigua*. They were mostly parallel to the longer diameter of the organ, but sometimes were at right angles or oblique to it. These features were somewhat like to the subcuticular species of *Uredinopsis*. Usually the opening was made at the central portion of the cuticular layer covering the organ but, rarely, quite aside from the center. In the subepidermal species, the opening was made on the epidermis covering spermogonia locating centrally or eccentrically and seen almost always pore-like. These features are rather similar to those of *U. ossaciformis* and *U. intermedia*. The opening of the spermogonia seen in the face view for each species of the *Milesina* materials was measured as shown in Table 67.

10. *Spermatiophores.* Spermatiophores of the six species of *Milesina* used in this study were simple or branched. They arose always

TABLE 67. Size of openings of spermogonia in six species of *Milesina*

Species	Hosts	Range (μ)		Average (μ)*	
		Length	Width	Length	Width
M. Dryopteridis	*A.M.* III_{14}	39 -130	9.7-52	62.4	26.6
M. exigua	*A.f.* I_6	45 -149.5	26 -52	96.8	39.6
M. Itôana	*A.M.* (Tomakomai Imp. For.)	19.5- 58.5	13 -45	31.2	24
M. jezoensis	" $XVIII_{10}$	32.5-110.5	19.5-97.5	72.8	45.5
M. Miyabei	" II_{11}	19.5- 52	13 -32	40.9	23.7
M. sublevis	" X_7	19.5- 97.5	13 -32.5	53.3	18.8

* The number averaged was 10.

from more or less basal elongated cells and had septa especially at the basal portion. They were also straight or a little curved and tapering toward the apex on which the spermatia were constricted. In *M. Dryopteridis, M. exigua, M. jezoensis* and *M. sublevis,* the spermatiophores were shorter and less branched while in *M. Itôana* and *M. Miyabei,* they were comparatively longer and much branched. HUNTER (1936c) has already mentioned the branching of the spermatiophores from the enlarged hyphal cells of the stroma in the case of *M. vogesiaca.*

11. "Flexuous hyphae." In the conclusions and summary of her recent paper HUNTER (1936c, p. 142, No. 9) 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." She mentioned as examples such species of *Milesina: M. marginalis, M. polypodophila, M. Kriegeriana, M. Dieteliana, M. Scolopendrii* and *M. vogesiaca.* She also said in the case of *M. Scolopendrii* that "spermatia were occasionally attached to 'flexuous hyphae' but the nature of the connection was not determined. 'Flexuous hyphae' are greater in diameter for most of their length than spermatiophores and are not so much attenuated." In every one of the six species of *Milesina* used in the present studies, the same sort of hyphae were also observed by the writer. Whether or not these hyphae are truly receptive organs could not be determined. However, that the hyphae seen by the writer must surely be the same as those described and illustrated by HUNTER, is almost beyond doubt. Therefore in this paper the term is used to designate the hyphae under consideration. In the present materials, in general, the hyphae were much longer than the spermatiophores. Among them,

in some cases, a more slender hypha-like body having even diameter and rich contents was observed. But in other cases, the apex of the hyphae was markedly broadened and seen to be band-like provided with scant plasma. These organs branch or elongate from the basal cells of the stroma just as in spermatiophores. (cf. Fig. 5 a–c; Pl. VII, fig. 17, f–l). Sometimes they were clearly seen to be extended up to the upper middle of the inner space of each spermogonium, which was true in the cases of *M. exigua*, *M. jezoensis* and *M. Itôana*. They appeared at first sight to be spermatiophores but after close inspection they were seen to be far longer. HUNTER (1936c, p. 129) has already mentioned regarding *M. Dieteliana* with illustration that "the dark band lying over the spermogonium shown in Fig. 33 is made up of spermatia apparently massed around the long hyphae." The writer also observed such features in the case of the spermogonia of *M. exigua* on *Abies firma* as shown in Pl. V, fig. b.

12. *Size of spermatia.* The size of spermatia of three species of *Milesina* has already been mentioned by HUNTER (1927). Among six species of *Milesina* used in this study, comparatively large spermatia were seen in the cases of *M. Dryopteridis*, *M. exigua*, *M. jezoensis* and

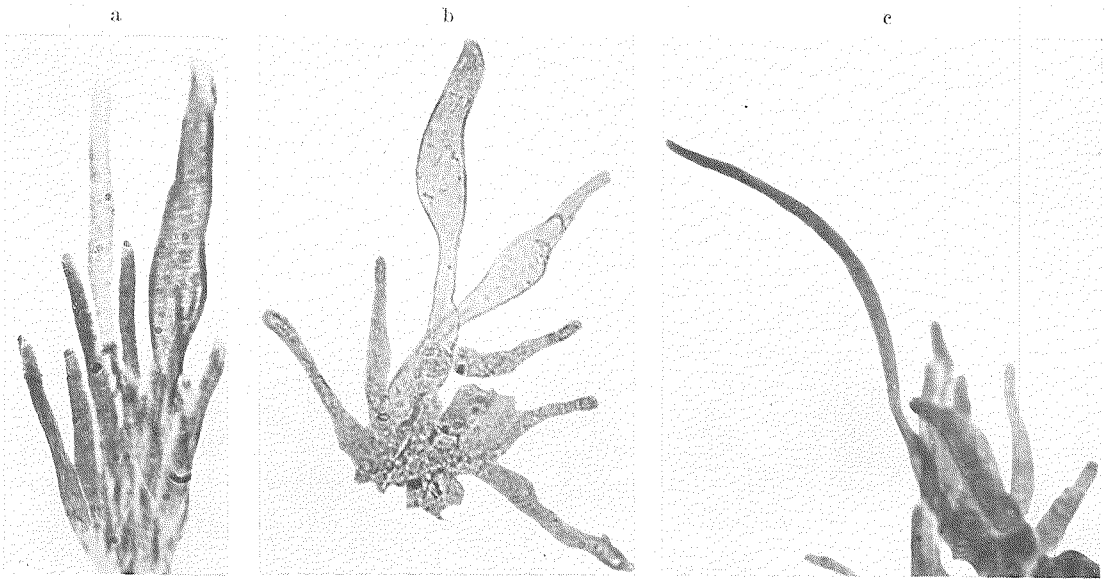

Fig. 5. "Flexuous hyphae" mingled with spermatiophores in the spermogonia of *Milesina*. ×1150. (a) *Milesina exigua* on *Abies Mayriana* XI_{10}. (b) *M. jezoensis* on *A. Mayriana* $XVIII_{10}$. (c) *M. Miyabei* on *A. Mayriana* $XIII_8$.

M. sublevis while smaller ones were seen in *M. Itôana* and *M. Miyabei*. Minute differences which existed between these species may have been derived from the calculation based on an abundant number of individuals. Some measurements taken by the writer are shown in Table 68.

TABLE 68. Size of spermatia in six species of *Milesina*

Species	Hosts		Range (μ)		Average (μ)		Ratio
			Length	Width	Length	Width	
M. Dryopteridis	*A.M.*	XVI_{11}	4–6	1.3–1.7	5.1 (10)	1.5 (")	3.40
M. exigua	"	XVI_5	4.8–7.4	1.2–2	6.1 (100)	1.5 (")	4.06
M. Itôana	"	III_{15}	3.5–6	1.0–1.9	4.7 (100)	1.3 (")	3.61
M. jezoensis	"	IV_{16}	5–7.5	1.2–2	6.1 (70)	1.8 (")	3.38
M. Miyabei	"	XV_6	3–6.1	1.2–2.3	4.2 (100)	1.5 (")	2.80
M. sublevis	"	X_7	6.5–9.1	2.1–2.6	7.5 (10)	2.5 (")	3.00

13. *Shape of spermatia.* HUNTER (1927) said in *M. polypodophila*, that the spermatia are "elongate". FAULL (1932) said in *M. marginalis*, *M. intermedia* and *M. polypodophila* that they are "narrowly ellipsoid" or "narrowly elliptical." In the six species used in the present studies they were narrowly elliptic, or oblongo-cylindric. The ratio of the longer and shorter diameters shows that the former are 2.8 to 4 times the latter. This is not so different from the cases of *Uredinopsis* (cf. Table 38). Both ends were mostly rounded, but often truncated or sometimes pointed. In the shape of spermatia only, however, clear specific distinctions could not be observed by the writer.

(2) *Aecidium stage*

Of comparative studies on the morphology of the aecidium stages of some *Milesina*, there has as yet been no publication except short accounts by the writer (1935b). The materials used were obtained from fresh as well as dried specimens that came from cultures and field collections. The methods of study were the same as in the case of *Uredinopsis*.

1. *Age of needles on which aecidia appear.* Among twelve species of *Milesina* of which the aecidial phases have heretofore been observed, only *M. polypodophila* in North America produces aecidia on "third year" old needles. In the six species of *Milesina* used in this study, the aecidia of every species appeared on the current year needles as seen in other species.

2. *Position of needles on which aecidia appear.* The position on needles of *Abies* where aecidia of the species of *Milesina* appear, so far recorded, was always on the undersurface except in one species, namely *M. Itôana,* in which case some aecidia were produced also on the upper surface of the affected needles.

3. *Number of aecidial sori per affected needle.* WILSON (1924) in the case of *Aecidium pseudocolumnale* KÜHN, a probable form of a certain species of *Milesina,* stated the number of aecidial cups to be 3–9 per needle. Those of the six species used in this study are tabulated in Table 69. As shown there, although clear limits between the species cannot be discerned in respect to the number of the aecidia, yet it is impossible to overlook that the average number was less compared with those in the species of *Uredinopsis.*

TABLE 69. Number of aecidial sori in six species of *Milesina* per affected needle

Species	Hosts	Range	Average
M. Dryopteridis	*A.M.* IV_{14}	2–14	8.3 (6)
M. exigua	*A.f.* I_6, *A.M.* V_9	3–20	10.1 (20)
M. Itôana	*A.M.* I_{15}, II_{15}, III_{15}	1– 6	2.0 (22)
M. jezoensis	" $XVIII_{10}$, XVI_{13}	1– 5	3.0 (5)
M. Miyabei	" $VIII_{11}$	4–10	7.0 (15)
M. sublevis	" XI_{11}	1– 9	3.1 (11)

4. *Dimension of aecidial sorus.* (a) *Height of the aecidial cups.* According to the present observations, the height of the aecidial cups ranged from 0.5 to 3.6 mm. Comparatively high cases were seen in *M. Itôana* and *M. Miyabei,* while the lower cases were in *M. exigua* and *M. sublevis* as shown in Table 70.

TABLE 70. Height of aecidial cups in six species of *Milesina*

Species	Hosts	Height (mm.)
M. Dryopteridis	*A.M.* XVI_{11}	Up to 2
M. exigua	*A.f.* I_6, *A.M.* III_6	0.5
M. Itôana	*A.M.* II_{15}	Up to 3
M. jezoensis	" XVI_{13}	1
M. Miyabei	" II_{11}	Up to 3.6
M. sublevis	" XI_{11}	0.5

(b) *Diameter of aecidial cups.* The diameter of the aecidial cups was measured as shown in Table 71. The largest one was seen in *M. Itôana* and more delicate ones were shown in *M. Dryopteridis.*

TABLE 71. Diameters of aecidial cups in six species of *Milesina*

Species	Hosts	Range (μ)		Average (μ)*		Ratio
		Long diam.	Short diam.	Long diam.	Short diam.	
M. Dryopteridis	*A.M.* XVI_{11}	126–210	—	182.7**	—	—
M. exigua	*A.f.* I_6, *A.M.* III_6	240–360	200–360	291.6	283	1.03
M. Itôana	*A.M.* II_{15}	378–737	273–550	473.6	363.6	1.30
M. jezoensis	" XVI_{13}	220–275	165–242	256.6	209	1.22
M. Miyabei	" II_{11}	187–275	176–275	246.4	228	1.08
M. sublevis	" XI_{11}	176–297	165–275	239.8	208.4	1.15

* The number averaged was always 10 except *M. jezoensis* in which it was only 3.

** The diameter in the case of *M. Dryopteridis* was measured only in the direction of the longitudinal axis of the needle while in the other five species it was measured both in longer and shorter axes of each organ.

(c) *Shape of aecidial cups.* The outer shape of aecidial cups was generally cylindrical. Of the six species a rather flat one having oblong horizontal shape was seen in the case of *M. Itôana,* while those of *M. exigua* and *M. Miyabei* were almost cylindric as indicated by the ratio of the longer and shorter diameters shown in Table 71. In general, the longer diameters were directed along the longer axis of the needles.

5. *Peridial cells of the aecidia.* (a) *Combination of peridial cells.* In the species of *Milesina* used in this study, the mode of the combination of peridial cells of the aecidia was not essentially different from that of *Uredinopsis* mentioned already. They were joined firmly with each other and more or less overlapped at each end. The way in which the cells are joined with each other was also apparently similar to the species of *Uredinopsis* studied already.

(b) *Shape of peridial cells.* In their descriptions of the peridial cells of the aecidia in the species of *Milesina,* FAULL (1932), HUNTER (1936c) and HIRATSUKA, f. (1936c) used the term "polygonal" or "irregularly polygonal." According to the present observations on the six species of *Milesina,* generally speaking, the cells were polygonal but also

their ends were somewhat roundish. In the species of *Milesina*, just as in the case of *Uredinopsis*, though clear distinctions of the species can not be made by the shape of the peridial cells only, yet there may be admitted two types in the shape of cells. The one is those that have rather oblong shape in face view. The other is that group in which the cells are somewhat polygonal. To the former type, the peridial cells of *M. Miyabei*, *M. exigua* and *M. jezoensis* belong, while those of *M. sublevis*, *M. Itôana* and *M. Dryopteridis* belong to the latter type.

(c) *Size of peridial cells in face view.* Size of the peridial cells of the aecidia in some species of *Milesina* in face view has been stated in the specific descriptions by ARTHUR (1925), FAULL (1932), KAMEI (1930, 1932b, 1935b), HUNTER (1936c) and HIRATSUKA, f. (1936c) respectively. In this study, fifty peridial cells for each species were measured as shown in Table 72. As far as these results are concerned, it must be admitted that the smallest size is indicated in *M. Dryopteridis* and the largest one in the case of *M. jezoensis*.

TABLE 72. Size of peridial cells of the aecidia in six species of *Milesina*

Species	Hosts	Range (μ)		Average (μ)	
		Length	Width	Length	Width
M. Dryopteridis	*A.M.* IV_{14}	18 -24	14 -20	21.32	15.72
M. exigua	" $XIII_4$	22.5-48.3	11.3-25.7	33.13	18.22
M. Itôana	" I_{15}	20.7-33.6	12.6-23.6	26.25	18.52
M. jezoensis	" XVI_3	25.2-61	12.5-33.5	37.63	21.58
M. Miyabei	" XV_6	20 -41	11 -26	32.00	17.66
M. sublevis	" XI_{11}	13 -36	11 -29	27.58	18.18

(d) *Thickness of inner cell walls of peridial cells.* The thickness of peridial cells of the aecidia in some *Milesina* has been given in the specific descriptions by FAULL (1932), KAMEI (1932b, 1935b), and HIRATSUKA, f. (1936c). Slight differences in the thickness of the inner cell-walls of peridial cells of the aecidia in the species of *Milesina* materials were observed as shown in Table 73. Especially thicker inner walls in the case of *M. Itôana* were observed, while especially thinner ones in the cases of *M. jezoensis* and *M. Miyabei*.

(e) *Markings of inner walls of peridial cells.* The markings of the inner surface of peridial cells of the aecidia in six species of *Milesina*

TABLE 73. Thickness of inner walls of the peridial cells of the aecidia in six species of *Milesina*

Species	Hosts	Range (μ)*
M. Dryopteridis	*A.M.* IV_{14}	2–5
M. exigua	*A.f.* I_6	2–4
M. Itôana	*A.M.* I_{15}	4–7
M. jezoensis	" XVI_{13}	2–3
M. Miyabei	" XV_6	2–3
M. sublevis	" XI_{11}	2–5

* The number of peridial cells measured was variable.

presented some characteristic features just like in the species of *Uredinopsis*. FAULL (1932), KAMEI (1930b, 1932b, 1935b), HUNTER (1936c) and HIRATSUKA, f. (1936c) have given characteristics in their descriptions. In the present cases, *M. Itôana* and *M. jezoensis* had tubercles confluent to make longitudinal ridges enabling them to be designated by the term "rugose". Sculptures were more distinct in *M. Itôana*. In *M. Dryopteridis, M. exigua, M. Miyabei* and *M. sublevis* the tubercles were rather so arranged as to be characterizable by the term "verrucose". Among them, more stout markings were seen in *M. sublevis* as shown in Pl. VI, fig. o. Rather finely but regularly arranged and more or less roundish tubercles were seen in the case of *M. Miyabei* (Pl. VI, fig. n). Comparing the markings in the cases of *M. Dryopteridis* and *M. exigua*, those of the former are finer than those of the latter. (Pl. VI, fig. j). In comparison with the markings in the cases of *Uredinopsis* species, though slightly different specifically, generic distinctions can not be observed. Summary statements of the markings of peridial cells of the aecidia for each species are as follows:—

M. Dryopteridis: rather finely verrucose and somewhat striated.
M. exigua: rather coarsely verrucose and somewhat striated.
M. Itôana: adorned with longer and coarser tubercles which in their basal portions are confluent in longitudinal ridges.
M. jezoensis: minutely and obscurely verrucose and somewhat striated.
M. Miyabei: finely verrucose.
M. sublevis: stoutly and coarsely verrucose.

6. *Aecidiospores.* (a) *Variation in size of aecidiospores.* The

variation in the spore size gained from cultures is only mentioned here. For each of the six species of *Milesina,* 100 spores were measured. The spore size variation and differenees in means of the aecidiospores are shown respectively in Tables 74 and 75. In comparison with the cases of *Uredinopsis* species, at least so far as the present materials are concerned, the size of the aecidiospores of *Milesina* attained a higher limit both in length and in width. Among the six species of *Milesina,* it was indicated that those species having larger length also had greater width. Among them all, *M. sublevis* had the largest diameters in both directions. Following this species, the order of longer spores was *M. jezoensis, M. Itôana, M. Miyabei, M. exigua* and *M. Dryopteridis.* HUNTER (1936a) mentioned the size of aecidiospores of *M. Scolopendrii, M. Dieteliana, M. vogesiaca* and *M. Kriegeriana.* Those species attained in every case to larger limits in both diameters than in any of the present species investigated.

According to Table 75, the differences in means of the aecidiospores of the six species in *Milesina* were all of sufficient significance to be admitted as specific differences. Among them the amount (difference in means divided by probable error of the difference) attained to the largest extreme in the case of the length difference existing between *M. exigua* and *M. jezoensis.* Contrariwise, the smallest extreme was seen in the case of the length difference between *M. exigua* and *M. Miyabei.*

(b) *Shape of aecidiospores.* The shape of an aecidiospore of *Milesina Blechni* was illustrated by KLEBAHN (1916). In some species of *Milesina* this aspect has also heretofore been described in taxonomic treatises but no comparative study has been reported. As shown in Table 76, the shape of the aecidiospores of the six species of *Milesina* derived from culture experiments was always more or less ellipsoidal, that is, the length exceeded by 16–27 percent of the width of each spore. In comparison with the species of *Uredinopsis* there were no marked differences in the shape of the spores because the ratio of length and width of the species of *Uredinopsis* was approximately similar to those of *Milesina.*

(c) *Thickness of walls of aecidiospores.* The thickness of the walls of aecidiospores of some species of *Milesina* has also been mentioned in taxonomic descriptions. In the six species of the present materials, the thinner walls in the cases of *M. Dryopteridis, M. exigua* and *M. jezoensis* were seen to be as shown in Table 77.

TABLE 74. Variation and constants of size of aecidiospores in six species of *Milesina* obtained from cultures on *Abies Mayriana*

Species	Hosts	Spore classes (μ)	Constants		
		Length			
		13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38	Mean (μ)	St. dev.	C. o. var.
M. Dryopteridis	*A.M.* IV_{14}	3 8 25 24 22 10 3 3 1 1	19.24±0.11	1.66±0.07	8.66±0.41
M. exigua	" III_6	1 4 8 20 25 20 14 5 1 1 1	22.31±0.12	1.87±0.07	8.42±0.40
M. Itôana	" I_{15}	3 2 4 9 28 25 9 10 6 2 2	25.84±0.13	1.97±0.09	7.62±0.36
M. jezoensis	" XVI_{13}	1 5 2 13 9 9 19 10 10 4 7 3 5 1 2	30.32±0.21	3.14±0.14	10.35±0.49
M. Miyabei	" XV_6	7 16 20 23 17 12 5	22.83±0.11	1.59±0.07	6.98±0.33
M. sublevis	" XI_{11}	1 1 3 4 6 5 12 17 20 9 5 8 4 5	31.49±0.19	2.87±0.13	9.11±0.43
		Width			
M. Dryopteridis	*A.M.* IV_{14}	4 14 32 34 9 4 2 1	16.57±0.09	1.35±0.06	8.13±0.38
M. exigua	" III_6	1 5 5 8 9 19 21 14 8 9 1	18.49±0.14	2.20±0.10	12.48±0.59
M. Itôana	" I_{15}	1 7 16 41 23 8 2 1 1	20.20±0.08	1.30±0.06	6.45±0.30
M. jezoensis	" XVI_{13}	5 8 11 14 12 15 7 6 8 7 4 3	25.79±0.18	2.81±0.13	10.89±0.22
M. Miyabei	" XV_6	1 11 16 26 38 7 1	19.15±0.08	1.23±0.06	6.45±0.31
M. sublevis	" XI_{11}	2 5 5 12 14 8 13 15 7 12 4 3	26.67±0.18	2.69±0.12	10.08±0.48

TABLE 75. Summary of differences in means of measurements of aecidiospores of six species of *Milesina*

Species	Difference in means (μ)		Difference in means div. by probable error of the difference	
	Length	Width	Length	Width
M. Dryopteridis & *M. exigua*	3.07±0.16	1.92±0.16	19.18	12.00
„ & *M. Itôana*	6.60±0.17	3.53±0.12	38.82	29.41
„ & *M. jezoensis*	11.08±0.23	9.22±0.20	48.17	46.10
„ & *M. Miyabei*	3.59±0.15	2.58±0.12	23.93	21.50
„ & *M. sublevis*	12.25±0.22	10.10±0.20	55.68	50.50
M. exigua & *M. Itôana*	3.53±0.17	1.79±0.16	20.76	11.12
„ & *M. jezoensis*	8.01±0.24	7.30±0.23	33.37	31.73
„ & *M. Miyabei*	0.52±0.16	0.66±0.16	3.25	4.12
„ & *M. sublevis*	9.18±0.22	8.18±0.23	41.72	35.56
M. Itôana & *M. jezoensis*	4.48±0.24	5.59±0.20	18.66	27.95
„ & *M. Miyabei*	3.01±0.17	1.05±0.11	17.70	9.54
„ & *M. sublevis*	5.65±0.23	6.47±0.19	24.56	34.05
M. jezoensis & *M. Miyabei*	7.49±0.23	6.64±0.20	32.55	33.20
„ & *M. sublevis*	1.17±0.28	0.88±0.25	4.17	3.52
M. Miyabei & *M. sublevis*	8.66±0.22	7.52±0.20	39.36	37.60

TABLE 76. Ratio of length and width of aecidiospores of *Milesina* materials

Species	*M. Dryopteridis*	*M. exigua*	*M. Itôana*	*M. jezoensis*	*M. Miyabei*	*M. sublevis*
Ratio	1.16	1.20	1.27	1.17	1.19	1.18

TABLE 77. Thickness of walls of aecidiospores of *Milesina* materials

Species	*M. Dryopteridis*	*M. exigua*	*M. Itôana*	*M. jezoensis*	*M. Miyabei*	*M. sublevis*
Wall thickness (μ)*	up to 1	up to 1	2	1	2	2.5

* The number of aecidiospores measured was variable.

(d) *Wall markings of aecidiospores of Milesina materials.* Minute differences in markings of aecidiospores, though present, could not be considered as a mark of specific differentiation in the species of *Milesina* materials.

G.

Key to six species of Milesina from Hokkaidô for the phases on fir hosts

1 { Spermogonia subepidermal, comparatively large, deeply immersed.....2
  { Spermogonia subcuticular, rather small, not so deeply immersed.....3

2 { Peridium of aecidia stout, tubercles on inner walls of the peridial cells rather coarse and somewaht striated.....*M. Itôana*
  { Peridium of aecidia delicate, tubercles on inner walls of peridial cells rather fine and verrucose.....*M. Miyabei*

3 { Aecidiospores comparatively large sized.....4
  { Aecidiospores comparatively small sized.....5

4 { Peridial cells of aecidia rather large and finely verrucose on inner surface..... .....*M. jezoensis*
  { Peridial cells of aecidia rather small and coarsely verrucose on inner surface.... .....*M. sublevis*

5 { Peridial cells of aecidia comparatively small sized.....*M. Dryopteridis*
  { Peridial cells of aecidia comparatively large sized.....*M. exigua*

IV. SPECIES OF HYALOPSORA

THE LIFE HISTORY STUDIES

Review of literature

So far as published reports show, among fourteen species of *Hyalopsora* now recognized, only two species have had their life cycle fully established. They are *Hyalopsora Aspidiotus* MAGNUS and *H. aculeata* KAMEI. Regarding *H. Aspidiotus*, culture experiments have been done by KLEBAHN, BUBÁK, MAYOR, WEIR and HUBERT, BELL and FAULL & DARKER up to this day. In May 1903, KLEBAHN (1905) using basidiospores of this rust produced on *Dryopteris Linnaeana* C. CHR. executed inoculations on young shoots of *Abies alba* MILL., *Picea Abies* KARST., *Larix decidua* MILL. and *Pinus sylvestris* L., all without success. BUBÁK (1906) having failed in almost similar experiments in 1904, thought that the aecidia might probably be produced on the cones of some conifers. In May 1914, KLEBAHN (1916) tried repeated cultures similar to those made in 1903. In spite of the abundant supply of basidiospores on needles of *Abies* he was able to obtain nothing in the same season except yellow flecks that appeared on inoculated leaves. In the next spring, he was able to detect spermatia and spermogonia produced on affected needles of the previous season. However, failing

to see the expected aecidia for which he should have waited another year, he concluded that this rust would not carry out its heteroecious cycle and the overwintering might be accomplished by means of amphispores. BARTHOLOMEW (1916) suggested that the occurrence of heteroecism in the species of *Hyalopsora* would just be as in *Uredinopsi*, of which genus the heteroecism had already been proved at that time in North America. WEIR and HUBERT (1918) reported also that they had made unsuccessful inoculations with basidiospores on the species of *Abies*, *Tsuga* and *Pteridium*. MAYOR (1923, 1925) meanwhile continued his observations perseveringly and succeeded in the proof of the complete life cycle at Boudry in Switzerland. In June 1919, he saw seedlings of *Abies alba* in the field bearing spermogonia on two-year old needles and aecidia on three-year old ones. They were growing among *Dryopteris Linnaeana* rusted by the species under consideration. In 1920, collecting the teleutospores on the rusted host fern from the same place, the basidiospore inoculation on *Abies alba* were performed. However, he was not successful in obtaining the aecidium just as in the case of KLEBAHN's trial. In 1922, on the other hand, with the aecidiospores collected from the field, inoculations were successfully made on *Dryopteris Linnaeana*, on which also the teleutospores were detected in the next spring. In 1923, he again made basidiospore inoculations on *Abies alba* and succeeded in obtaining spermogonia on April 30th 1924 on two-year old needles and aecidia on April 11th 1925 on three-year old ones. Thus the assumption that the fungus requires a period of four years for the completion of the life cycle was confirmed. Not being aware of these experiments of Mayor in Europe, BELL (1924) collected the aecidial phase on *Abies balsamea* at Lake Timagami, Ontario and considered it as a new species, naming it *Peridermium pycnoconspicuum* BELL. On June 24th 1922, inoculations with the aecidiospores were carried out on *Dryopteris Linnaeana* and typical uredo-pustules were obtained after 18 days. He thought that his experiment was "the first evidence obtained by means of inoculation that *Hyalopsora* is a heteroecious rust, and that its aecial stage actually exists on a conifer." In 1923, FAULL & DARKER (1924) reported that they had made similar experiments to BELL's and recorded the incubation period as 22 days, from June 20th to July 12th.

Contrasting with the complex and long-lived course of the life cycle of *Hyalopsora Aspidiotus*, the writer has had the privilege to report (KAMEI, 1932a) another type of the life cycle found in the case of *H.*

aculeata. From observations in cultures and in the field, it was made clear that although the morphology of the spermogonia and aecidia of our fungus is not very different from those of *H. Aspidiotus*, the appearance of both organs in our case occurs in the current year needles of *Abies Mayriana*. It is just the same as in some species of *Milesina*. Detailed explanation of the data obtained concerning the life cycle of *H. aculeata* is given in the following paragraphs.

MAGNUS (1895) in *H. Aspidiotus* suggested the occurrence of new infection by means of amphispores after overwintering resulting in an autoecious life cycle. DIETEL (1911) in *H. Polypodii* found by experiments that the fungus winters over on the ferns by means of uredospores. WEIR and HUBERT concluded that *H. Aspidiotus* and *H. Polypodii* in North America winter over by means of teleutospores. PADY (1935), however, said that hibernation is made by mycelia in the case of *H. Aspidiotus*.

16. **Hyalopsora aculeata** KAMEI

Historical review of the fungus. This species was described by the writer (1932a), and a partial report on the results of his taxonomical and biological observations has already been published. HIRATSUKA, f. (1932b, 1932c, 1935c, 1935f, 1936c), and HIRATSUKA, f. & UEMURA (1932a) also described this rust. The species has been collected from South Saghalien, Hokkaidô, Honshû, Shikoku, and Kiushû according to HIRATSUKA, f. (1936c). The same author formerly (1932a) included a rust on *Spicantopsis amabilis* NAKAI also in this species, but recently (1936c) separated it giving the name *Milesina Kameiana* HIRATSUKA, f. ITÔ & HOMMA (1938) and ITÔ (1938) also described this rust more recently.

Personal observations. Rusted fern. Spicantopsis nipponica NAKAI var. *japonica* NAKAI, the host fern is widely distributed throughout the island of Hokkaidô. In the vicinity of Sapporo, the fern commonly grows in the forests and the rusted materials are easily obtained from such a forest as Nopporo, where the primeval vegetation is still preserved. In the early summer when the needles of *Abies* are about to unfold, the uredosori were seen to be issued particularly on the upper surface of the overwintered fronds. These pustules were easily noticed because of the golden colored powdery masses of the uredospores pushing out from them. The sori were comparatively larger. Very stout

pseudoperidia were formed (cf. Pl. VII, fig. 16 c and d). Germpores are indistinct but can be seen when heated in lactic acid. The writer has seen 2–3 pores in the same equatorial plane. Around the uredospores there are seen bladdery, thin-walled paraphyses-like cells. The number of uredosori increases on overwintered fronds in the spring, when teleutospores are going to mature. Affected fronds and pinnae were often seen to be hypertophied or distorted. This is different from the case of *H. Polypodii,* the host fern of which rust was said by DIETEL (1911) to be not deformed. The portions, where teleutospores are formed, were more or less discolored, when the spores are matured. The spores were mostly observable in epidermal cells of undersurface. From the beginning to the middle part of June when teleutospores had begun to germinate, undersurface of fronds was entirely covered by masses of basidiospores except for two longitudinal sterile areas. Germination of teleutospores and mode of production of basidia were apparently the same as in the case of the species of *Milesina.*

Peridermium from cultures. Inoculation experiments with basidiospores. As shown in Table 78, inoculation experiments with basidiospores were made on needles of *Abies Mayriana* seedlings throughout three seasons. Out of seven seedlings six have showed spermogonia on leaves of the current year after 22–37 days, while the time of appearance of yellow spots was observed in two cases to be 15–17 days from the inoculation. The spermogonia thus obtained from cultures were distinctly larger in size and fewer in number in comparison with the cases of the usual species of *Uredinopsis* and *Milesina.* According to the observations made on 21 affected needles of *A. Mayriana* $XIII_6$, the number of spermogonia was 6–15 per needle and in average 8.8. This number quite agrees with the case of *M. Itôana,* as already shown in Table 65. They were hypophyllous, mostly on stomatiferous surfaces, slightly raised above the surface of needles, and almost elliptic in face view (Pl. II, fig. n). In section, they were subepidermal and flattened conoidal to lens-form as shown in Pl. V, fig. f. The aecidial sorus did not develop well in any of the pots experimented. In one affected leaf of *A. Mayriana* $XXII_6$, however, an imperfectly grown sorns was observed just beside a mature spermogonium. It had already differentiated into aecidia which contained a considerable number of immature aecidiospores that had characteristic orange yellow contents. Other than this the writer was not able to find any trace of aecidial sorus in spite of careful inspection of all inoculated seedlings.

Peridermium from the field. While failing to obtain mature aecidial cups originated from inoculations with basidiospores, search for the aecidial phase in the field was continued in the meantime. In the first part of November 1936, the writer found at Nopporo Forest some number of current year needles of a small seedlings of MAYR's fir bearing orange colored aecidia. Comparatively large and conspicuous spermogonia were characteristic. The diseased seedlings were quite close to fronds of *Spicantopsis nipponica* var. *japonica* affected by this rust in question. A week after, by eager search for similar materials at the place where the affected fern used for inoculations with basidiospores had previously been collected, the writer obtained 20 small diseased seedlings (Fig. 7 d, p. 163). On these, one to sixteen affected leaves per seedling, and one to twelve aecidial sori and two to fifteen spermogonia per needle were counted. One seedling was observed to have different leaves on one and the same branch bearing aecidial phases of this rust as well as those of *Milesina Itôana*. Owing to the coldness of the later part of the season, affected needles were rather injured, yet they bore a few fresh sori which could be used for inoculation experiments with aecidiospores. By placing these rusted needles in moist chamber the pure mass of aecidiospores was obtained. Inoculations were made with them from 11th to 20th of November on the undersurface of *Spicantopsis* fronds. Among three sets of treated fronds, two of the cut ones showed slight discolorations at the inoculated portions after seven weeks, and on Jan. 11th 1937 after 52–63 days the expected typical uredosori appeared on the marginal portion of the upper face of the fronds (cf. Pl. III, fig. p). In the potted fern although inoculations were performed, the frond was seen to be shrunken after a short period producing no uredospores. This must be due to the dessication of the treated plant. From these successful inoculation experiments by means of aecidiospores, it may be admitted that the *Peridermium* from Nopporo is the aecidial phase of this rust in question. If so, it is now possible to assert definitely that in this rust the aecidial sori develop perfectly in the year of inoculation with basidiospores just as in the case of the typical species of *Milesina*. The mycelia would probably hibernate in the fern to form teleutospores on overwintered fronds. Teleutospores produce basidiospores which will infect needles of *Abies* in the early summer. This life cycle is also like that of the usual species of *Milesina* and not as stated by DIETEL (1911) and MAGNUS (1895) respectively in *Hyalopsora Aspidiotus* and *H. Polypodii*. It is very in-

teresting to note that the life cycle of this rust in question, in which the morphology of the uredospores and teleutospores is somewhat similar to some species of *Milesina,* also is like that of some typical species of *Milesina* such as *M. Kriegeriana,* and not like the typical species of *Hyalopsora* represented by such as *H. Aspidiotus.*

TABLE 78. Inoculations with basidiospores of *H. aculeata*

Exp. no.	Inocula	Fir inoc.	Date of inoc.	App. of sperm.	App. of aecid.	Remarks
				No. of days		
I. 104	Basidiospores on *Spic. nipp.* v. *jap.*, Nopporo, Je. 12, 1926	*A.M.* XIII$_6$	Je. 13, 1926	24	—	Laboratory
" 105	"	" XIV$_6$	"	24	—	"
" 139	" Je. 23, 1927	" VII$_7$	Je. 19, 1927	22	—	"
" 140	"	" VIII$_7$	"	37	—	"
" 141	"	" IX$_7$	"	23	—	"
" 229	" Je. 24, 1931	" XXVI$_{11}$	Je. 29, 1931	28	—	"

The description of the present species is as follows:—

Hyalopsora aculeata KAMEI in Trans. Sapporo Nat. Hist. Soc. XII, p. 128, figs. 1–3, 1932; HIRATSUKA, f. & UEMURA in Trans. Tottori Soc. Agricul. Sci. IV, p. 22–25, 1932, p.p.; ITÔ & HOMMA in Trans. Sapporo Nat. Hist. Soc. XV, p. 115–116, 1938.

Spermogonia on needles of current season, hypophyllous, scattered on slightly yellowish discolored and somewhat hypertrophied areas, usually in two rows, one on each side of the midrib, 2–15 per leaf, alternating irregularly with aecidia, covered by yellowish brown discolored epidermis, oblong or elongated elliptical in face view, in section subepidermal, subconoidal to lenticular, rather deeply seated, large, 300–600 μ long, 100–300 μ high, 160–440 μ broad; openings more or less slit-like, located centrally, more or less elongated, parallel to the longer axis of the spermogonia, 248.3 × 54.6 μ in average; spermatiophores obclavate, 30–50 μ long, 3–5 μ broad, hyaline; spermatia oblongo-elliptic, 7.0–9.5 × 2.5–3.2 μ, smooth, hyaline, ends rounded but sometimes truncated (Pl. II, fig. n; V, fig. f; VII, fig. 17 m).

Aecidia on needles of current season, hypophyllous, scattered on

more or less yellowish discolored and somewhat hypertrophied areas, in two rows one on each side of the midrib, more or less cylindrical, 1–12 per leaf, 0.3–0.48 mm. in diameter, deeply seated; peridia delicate, colorless, rupturing at the apex; peridial cells isodiametric to irregularly polygonal, slightly overlapping, easily separable, 30–54×22–38 μ, outer walls ca. 2 μ thick, smooth, inner walls 6–9 μ thick, closely marked with medium long tubercles; aecidiospores orange yellow, globoid to broadly ellipsoidal, 33–58×30–47 μ, closely but finely verrucose except a part where almost smooth; walls colorless, 2–3 μ thick including tubercles.

Uredosori mostly epiphyllous, more abundant near margin of the frond, scattered or aggregated, on slightly discolored parts, roundish, small, 0.3–0.7 mm. across, bullate, sometimes confluent, rather brownish, dehiscent by apical rupture, pulverulent; peridia colorless, firmly combinated, subepidermal, hemispherical; each cell isodiametric to irregularly polygonal, upper cell rather higher, thick-walled, the lower flattened, thin-walled, 18.5–26.0×7.4–14.8 μ; walls 2–6 μ thick, colorless; uredospores golden yellow, mostly ovoidal or broadly ellipsoidal, subglobose to angular, 40.7–62.9×31.5–34.0 μ; walls thin, 1–2 μ, colorless, scattered regularly with stout spines; germ-pores inconspicuous, scattered; a few paraphyses-like cells intermixed with spores (Pl. III, fig. p; VII, fig. 16, b, c and d).

Teleutosori on overwintered fronds, mostly hypophyllous, on more or less discolored areas, restricted to the parts other than stomatal surface; teleutospores within the epidermal cells, more or less roundish in outline, almost colorless, mostly 1 to 5 celled, with vertical septa, 29.6–51.8 μ long, 12.9–18.5 μ broad, 16.5–29.6 μ high; walls thin, ca. 1 μ, smooth, colorless; basidia more or less clavate, about 30 μ long, about 10 μ thick; basidiospores globose, 8–11 μ across, colorless, smooth (Pl. VII, fig. 16 a and e).

Hosts and distribution:

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

II and III. *Spicantopsis nipponica* NAKAI var. *japonica* NAKAI —in Japan (Hokkaidô, Honshû, Shikoku and Kiushû).

V. ECONOMIC CONSIDERATIONS

There are only a few reports bearing upon the economic considerations of the diseases caused by rusts on ferns and firs. In such a place

as Hokkaidô, where fir trees constitute one of the main natural resources, the problem of the injury done to them is of economic importance. FRASER (1912) in his report on the "Cultures of Heteroecious Rusts" mentioned *Peridermium balsameum,* which is now considered to be a group of aecidial phases of some *Uredinopsis* and *Milesina,* and said that "this Peridermium was found abundantly on *Abies balsamea* (L.) MILL. in all regions of Nova Scotia." BELL (1924) laid stress on "a determination of the amount and the effect of the injury caused to their hosts by the various species of *Uredinopsis*" (probably including some species of *Milesina* also) as a problem worthy of special attention. BOYCE (1938, p. 186) who included many species of fern rusts in "Needle Rusts of Balsam Firs" said that "they cause some damage to seedlings and small saplings occasionally killing plants but usually retarding their growth." KAMEI (1934) in his report on *U. hirosakiensis* remarked on the possibility of distinguishing white-spored *Peridermium,* the method of identification and the measurement of amount of the damage done to fir seedlings by it. FAULL (1924, 1930, 1934, 1938c) also touched on the problem under consideration. In his publication in 1934 he dwelt on the topic of the injurious effect of some *Milesina* on fir trees, saying that "economically certain Milesian rusts are of some importance with respect to the unfavorable effect they exercize on the natural reproduction of *Abies. Milesia polypodophila* and *M. fructuosa* are noteworthy examples. The former causes unsightly and worthless plants of *A. balsamea* and the latter may kill or hold in check seedlings and saplings where the balsam fir is associated with rusted ferns. It is apparent from culture experiments that *M. fructuosa* is potentially a menace to young *A. magnifica.* Whenever intensive studies are being conducted in regions in which *Abies* constitutes a part of the forest stand, for the purpose of quantitatively forecasting forest successions, fern rusts as influencing factors should not be disregarded."

In Hokkaidô, as was said by KUDÔ (1925, p. 217) "two firs (*Abies sachalinensis* and *Abies Mayriana*) are both plentiful, the first-named being common in northern and north-eastern parts, either forming pure forests or associated with *Picea jezoensis* and *Picea Glehni,* while the second is common in the south either alone or associated with *Picea jezoensis* and broad-leaf trees." Under these forest trees, many species of ferns are growing in the undergrowth either solely or intermingling with other shrubs and herbs. As parasites on fronds or stipes of these ferns, there are now recorded 23 rust species distributed in three genera,

which affect some 30 species of ferns among a total of some 70 in Hokkaidô. Among these rusts, some are cosmopolitic, some are indigenous, some are very prevalent and some are found to a rather limited degree. In as much as a species of *Abies* is capable of being affected by many species of those fern rusts as well as other rusts, a collection of aceidial phase must be carefully identified for the determination of the proper species. For this purpose, cultures as well as comparative studies have been made as already stated. Thus the morphological, biological, as well as symptomatical characters of each of the rust materials have been accurately described so that they may be safely available for the identification of field materials. After such a careful determination of the species, the damage effected on the part of the fir host was examined. These features for six representative rusts are treated in the following sections.

1. *Uredinopsis hirosakiensis* KAMEI et HIRATSUKA, f. From the end of June to the beginning of July, characteristic aecidial phase of this rust of the species were frequently collected from the field in the Provinces Ishikari and Iburi. An adequate example of the injury in this connection was observed in a case found in the forest nursery of the Tomakomai University Experimental Forest. The injury was restricted to new leaves made conspicuous by maculae of pale discoloration or of a reddish tint and deformed to a certain extent. Careful observations of each affected needle showed that this discoloration occupied a half or more of the entire length, but was sometimes restricted to a small portion in the middle of each leaf. The discolored area was light-yellow and more or less sharply delimited from the healthy deep-green portions. The boundary between affected and healthy areas was at times very abrupt or at times rather transitional. Often on such a discolored portion a more or less rosy to dark-reddish coloration appeared, which was extended to entire faded areas or often was limited to a narrow region at the leaf margin. Such a coloration was more conspicuous on the upper surface. The deformation of leaves was sometimes slightly hypertrophic or sometimes showed a conspicuous shrinkage, which was especially distinct where aecidia were found close together. Sometimes the shrinkage was seen to occur very suddenly from the middle portion or sometimes on the basal portion of the affected leaf. Affected leaves were mostly curved flexuously and seemed to be slightly more elongated than healthy ones. Diseased needles were seen not only amongst those of well grown seedlings but also appeared in poorly

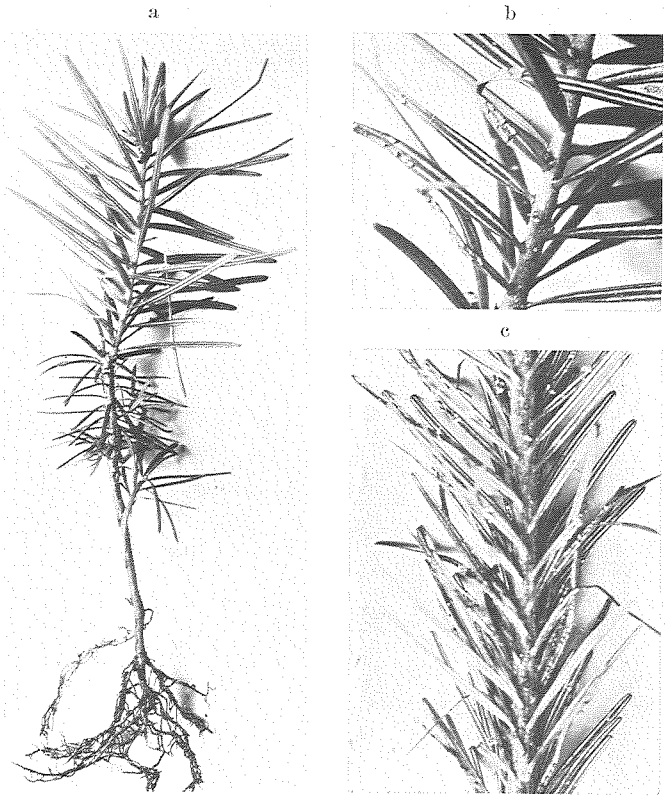

Fig. 6. Affected fir seedlings.

(a) and (b) Three-year old seedling of *Abies Mayriana* affected with *Uredinopsis hirosakiensis*, collected on July 6, 1937 at Tomakomai University Experimental Forest. (a) ×2/3. (b) ×1.7.

(c) A branchlet of an about ten-year old seedling of *A. sachalinensis* affected with *U. Kamciana*, collected on July 20, 1936 at Teshio National Forest. Slightly enlarged.

developed ones. Such an affected seedling is shown in Fig. 6 a and b. When the present writer first saw the *Peridermium* on needles of *Abies Mayriana* seedlings at the nursery bed (Plot No. 4) at Tomakomai, he attempted to count the number of affected seedlings taking three different standard areas (1 square meter) and obtained from each area 58.7, 56.4 and 41.1 percent respectively as the number of diseased seedlings. Mr. Shigeji Itô, from whom the writer requested a further survey of the injury over the entire area including nine plots of nursery beds, reported in detail the features and extent of the damage on

seedlings of *A. Mayriana* accompanied with several packages of diseased specimens. A considerable number of affected needles selected from each specimen were inspected and found to be the same as those from Plot No. 4 above mentioned. The number of diseased young seedlings 2 to 10-years old attained a total of 20368, varying 6 to 51 percent according to the plot. Moreover, the writer found the same *Peridermium* also on needles of numbers of larger seedlings grown in plantation plots in the 21st division in Horonai Working Section of this University Forest. To estimate the amount of diseased leaves per seedling, a careful inspection was made of each of 50 seedlings taken from Plot. No. 4. It was ascertained that 1 to 11 needles were attacked per seedling. As the total needles of a new branch numbered 2 to 239, the percentage of attacked leaves remains only 19 percent at most, as shown in Table 79. Upon the inspection of *Peridermium* specimens in the writer's herbarium, a diseased specimen of seedlings was discovered that had been collected from the nursery bed in the University ground at Sapporo dated June 30, 1920. The leaves were also unusually elongated and distorted. The number of diseased needles was counted as 300 and the seedling recorded to be five years old.

2. *Uredinopsis ossaeiformis* KAMEI. In the later part of July 1936, in a restricted area in the Nopporo Forest the writer's attention was attracted to a peculiar white *Peridermium* affecting some number of 15-year old seedlings to a considerable degree. From the morphological characters of the spermogonia and aecidia, the rust was assumed to be *U. ossaeiformis*, and successful check inoculations made immediately with the aecidiospores (cf. Table 23, IV, 52) affirmed the presumption. Slight distortion and conspicuous discoloration were observed at the affected part of those needles at the portion where aecidia and spermogonia were formed and sometimes a very slight rosy coloration was also seen. By these symptoms of the affected needles as well as by the time of issuing of aecidia, this rust can be discriminated from cases of *Milesina Miyabei* and *M. Itôana* with which the spermogonia of the present species were apparently similar in morphology. In the inspection of Nopporo materials, the writer has seen, as shown in Table 80, that some small number of diseased leaves affected by this rust in question, were simultaneously affected by *Milesina Itôana*. In alcoholic materials of such diseased needles, aecidia as well as spermogonia of the two rusts were seen to be situated in two adjoining areas. The spermogonia of *M. Itôana* were almost always in especially hypertrophied parts and seen

TABLE 79. Number of diseased needles in seedlings of *Abies Mayriana* in Tomakomai forest nursery (Plot No. 4) rusted by *U. hirosakiensis*

No. of seedlings	No. of diseased needles in ratio to healthy ones per each branchlet					Total no. of diseased needles	Percent of diseased needles
	I brl.	II brl.	III brl.	IV brl.	V brl.		
1	1/14	1/32				2	4
2	1/33					1	3
3	1/21	0/25				1	2
4	1/44					1	2
5	2/66					2	3
6	1/20	1/43				2	3
7	2/21					2	10
8	6/32					6	19
9	2/27	2/23	5/76			9	7
10	2/25	2/28	2/21	5/87		11	7
11	3/44	1/51	1/26	1/17		6	4
12	2/50	0/30				2	3
13	4/43	3/169				7	3
14	2/85	0/110	5/136			7	2
15	1/88	0/77	0/30			1	1
16	3/89					3	3
17	3/41					3	7
18	3/60	1/61				4	3
19	2/51					2	4
20	2/33					2	6
21	4/49					4	8
22	1/36					1	3
23	2/28					2	7
24	3/75	2/56				5	4
25	1/67					1	1
26	1/38					1	3
27	2/44					2	5
28	3/59					3	5
29	1/33					1	3
30	1/74					1	1
31	1/51					1	2
32	2/47					2	4
33	1/63					1	2
34	7/70	0/30	0/35			7	5
35	1/37					1	3
36	7/75	2/36				9	8
37	1/40					1	3
38	2/28	1/32	0/30			3	3
39	2/46	1/39				3	4
40	3/80					3	4
41	2/65	3/39				5	5
42	1/68					1	1
43	3/43	0/73	4/102			7	3
44	5/63					5	8
45	3/70					3	4
46	1/61	0/37	0/62	3/58	1/66	5	2
47	1/41					1	2
48	2/24	1/38				3	5
49	3/65					3	5
50	3/38					3	8
Range						1–11	1–19
Average						3.24	4.34

to have attained to the stage of the beginning of the exudation of spermatia, while aecidial sori were not yet protruded remaining in immature condition. In the case of *U. ossaeiformis*, on the contrary, spermogonia were then entirely effected and already turned brownish in color, while aecidia had already reached to matured condition and bladder cups were wholly erumpent. So the two rust species can never be confused by the experienced eye. Of course, just as shown in Table 80, among needles of one branch, those which were affected by *M. Itôana* exclusively were also mingled with needles that were restrictedly infected by *U. ossaeiformis*. In one location in Nopporo Forest, where the specimens were collected, fronds of *Dryopteris dilatata* var. *oblonga* rusted by *U. ossaeiformis* as well as of *D. crassirhizoma* infested by *M. Itôana* were seen. So the condition just shown above must be considered to occur naturally. Number of needles affected by *U. ossaeiformis* and *M. Itôana* are shown in Table 80.

TABLE 80. Number of affected needles of branchlets of *Abies Mayriana* affected by *U. ossaeiformis* and *M. Itôana*

No. of branchlets	*U. ossaeiformis*		*M. Itôana*		Total		
	No. of affected needles	Percent	No. of affected needles	Percent	Healthy needles	Affected needles	Percent of diseased needles
1	20	9.0	11	4.4	192	31	14
2	28	26.0	7	6.4	71	35	33
3	19	8.6	8	3.6	195	27	12
4	5	1.4	12	3.3	320	17	5
5	10	17.6	4	4.7	71	14	16
6	24	9.9	4	1.6	214	28	12
7	6	1.6	36	9.9	319	42	12
8	21	9.1	13	5.6	195	34	15
9	12	9.1	10	3.4	268	22	8
10	11	5.1	7	4.0	154	18	10
11	49	15.9	15	4.9	241	64	21
12	4	5.0	6	7.5	69	10	13
Limits	4–49	1.4–26.0	4–36	1.6–9.9	69–320	10–64	5–33
Average	17.41	9.85	11.08	4.94	192.41	28.50	14.33

3. *Uredinopsis Kameiana* FAULL. In July 1936, Mr. AIZAWA in the Hokkaidô Government kindly brought to the writer three small

branchlets of *Abies sachalinensis* chosen from rusted seedlings that were found at Working Section No. 40 of the Teshio National Forest. The white *Peridermium,* with which needles were heavily affected was proved to be the rust in question, by the writer's careful inspection and inoculation experiments as shown above (cf. Table 12 IV, 51). In the specimens received from AIZAWA, each affected leaf was discolored at the apical part and slight deformation as well as elongation was also observed (Fig. 6, c p. 157). Special coloration as seen in the case of *U. hirosakiensis* was not distinctly indicated. Demarcation between diseased and healthy portions was distinctly shown. Small sized and aggregated spermogonia and fragile thin walled peridial cells of aecidia were the same as those obtained from artificial inoculations. The number of affected needles of three branchlets received were counted to be 157, 120 and 41 out of 333, 292 and 141 leaves respectively corresponding to 47.1, 41.09 and 29.0 percent for each branchlet and 39.1 percent in entire average. According to AIZAWA's personal observations at the actual location at Teshio, the plantation area is situated at the summit of an elongated hill not far from the sea shore. The area had recently been burned over and thereafter gradually restored to the present vegetation. At present, it is covered principally with *Sasa* bushes intermingled with abundant bracken fern which is heavily infected with *Uredinopsis Kameiana.* Fir seedlings which had attained to the age of about 10 years and 1 meter in height were transplanted in strips. Almost 150 out of 3000 seedlings per hectare were attacked and about two-thirds of the total number of the current year needles were affected. The moist weather which is very common at the locality in the early summer may easily induce the germination of teleutospores and basidiospores thus produced would easily infect needles just above. The disease was said to have occurred from two to three years before. As shown in the section on this rust under question, similar materials of the diseased Sachalin fir were also collected from Teshio University Experimental Forest, but the extent of the damage done was not fully studied.

4. *Milesina Itôana* KAMEI. As already explained, the economic concern in regard to the aecidial phase of this rust is very great because of its eminent prevalence in our locality. The outer feature of diseased needles were characteristic by the stouter and rather flattened aecidial cups erumpent usually on the undersurface and rarely also on the upper surface. Following the development of aecidial cups, the adjoining tissue was often seen to be splitted longitudinally, accompanied

with brownish healing tissue at the margin of the fissures. Affected leaves were frequently hypertrophied and very brittle. The decoloration of diseased needles was observed to occupy the whole of the leaf surface or limited to only a part of them. The aecidia usually stand up firmly late in the season. Microscopic characters differing from the related species have already been discussed. Thus the aecidial stage of this rust was very characteristic and identification is an easy matter. The rust was limited to leaves of young small seedlings on the floor of the forest as well as on much taller trees attaining to 20 meters or more. In the larger tree, the damage suffered from the parasite may not be great resulting in only a certain decrease in the vigor owing to the diseased condition and in the earlier failing of needles. But in the case of seedlings which have a smaller number of needles the affection of a few leaves even leads to a disastrous damage or frequently to death when the greater part of needles are affected and shed. FAULL (1934) already in *M. fructuosa* said that it may kill or hold in check seedlings and saplings where the balsam fir is associated with rusted ferns. In order to gain additional information, how seriously needles of branches of the host plant are affected, was studied by a special survey of a diseased tree as described in the following lines. In the autumn of 1934, especially abundant infection was observed on needles of 20-year old trees of *Abies Mayriana* planted in a small restricted area (0.24 hectare) situated about half a mile from the northern entrance of Nopporo Forest. A particular young tree about two meters in height among them was chosen for the examination of the damage. It is shown in Fig. 7 a and b. Twenty eight branchlets were selected to be used for counting the number of affected needles. The obtained data are shown in Table 81. According to the result, the number of affected needles per each branchlet varies 8 to 70 and the percentage of diseased ones amounts to 10 to 83 suggesting some considerable damage upon the growth of the tree. Check inoculation experiments by means of aecidiospores were performed as shown already in the section on the rust in question. Almost similar damage to fir needles by the same rust was frequently experienced at various other parts within the boundaries of this forest at the same season of each year. Moreover, from such other localities as Lake Shikotsu, Tomakomai Imperial Forest, Tomakomai University Forest in Prov. Iburi, and Oboro National Forest in Prov. Kushiro, specimens of the rust were also collected in large numbers suggesting a wide distribution. Further, the writer gathered this

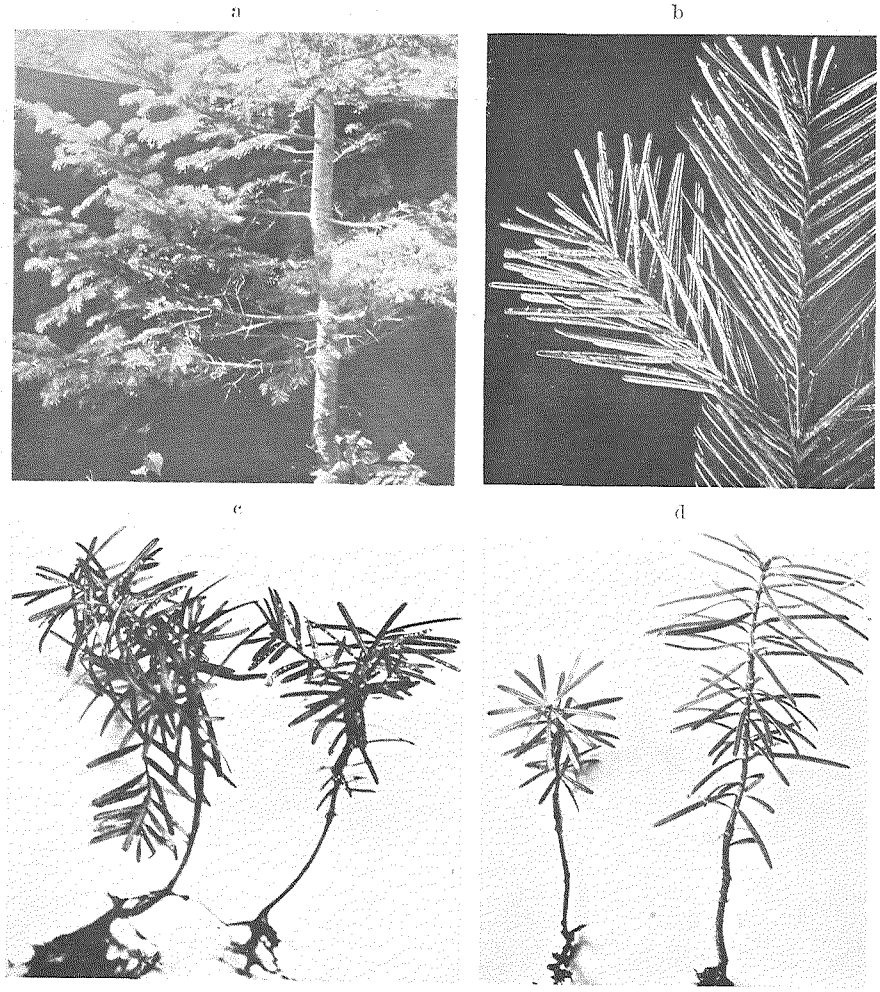

Fig. 7. Affected firs.
(a) An about twenty-year old tree of *Abies Mayriana* affected with *Milesina Itôana* at Nopporo Forest. Photographed on Oct. 8, 1934. ×1/22. (b) A part of an affected branchlet of the same tree. slighly reduced. (c) Small seedlings of *A. sachalinensis* affected with *M. Itôana* collected on Sept. 14, 1933 at Mt. Meakan. ×2/3. (d) Three-year old seedlings of *A. Mayriana* affected with *Hyalopsora aculeata*, collected on Nov. 13, 1936 at Nopporo Forest. ×3/5.

Peridermium on small seedlings of *Abies sachalinensis* at a location half way up Mt. Meakan (cf. Fig. 7, c). The above remarks must lead one to admit that the injury by this rust is very considerable from the

economic point of view.

5. *Milesina Miyabei* KAMEI. Materials used for the examination regarding the damage done to needles of *Abies* by *Milesina Miyabei* were collected from Tomakomai University Experimental Forest on Aug. 10,

TABLE 81. Number of needles of a tree of *Abies Mayriana* affected by *M. Itôana* at Nopporo Forest

No. of branchlets	Length of branchlets (cm.)	No. of diseased needles	Total no. of needles	Percent of diseased needles
1	5.5	17	92	18
2	4.2	20	72	28
3	17.3	70	205	34
4	9.0	54	163	33
5	7.5	41	136	30
6	3.5	20	62	32
7	5.5	24	94	26
8	5.2	28	58	48
9	6.0	31	63	49
10	7.0	51	102	50
11	7.0	40	101	40
12	7.8	49	131	37
13	3.5	14	50	28
14	3.2	8	43	19
15	4.5	19	47	40
16	5.5	22	79	28
17	5.0	21	66	32
18	5.5	26	51	51
19	3.0	11	29	38
20	4.0	25	56	45
21	4.2	32	58	55
22	1.4	15	18	83
23	2.5	14	28	50
24	5.7	34	90	38
25	5.2	29	73	40
26	5.3	51	77	66
27	5.1	31	83	37
28	6.0	52	99	53
Limits	1.4–17.3	8–70	18–205	18–83
Average	5.54	30.32	79.50	40.21

1936 by Mr. T. YAMAGUCHI. Check inoculations to aid identification were successfully made as shown already (cf. Table 58, Exp. IV, Nos. 53 and 55). Affected seedlings were grown at a certain place in the forest and attained to the age of twelve years measuring about 1 meter in height. Especially the upper needles of each branchlet were attacked. Each affected needle at the maturation of aecidial cups was slightly discolored but showed almost no hypertrophy and distortion of the tissue. These features were different from such cases as those of *Milesina Itôana* and *Uredinopsis ossaeiformis,* whose spermogonia are, however, morphologically of the same type as the species in question. A total of 45 branchlets were counted for affected leaves as shown in Table 82, and the percentage of the total number of needles was found to vary from 11–46 with an average of 26%. In this case also some affected needles were seen to be simultaneously affected with another white rust that has comparatively large spermogonia (probably *M. Itôana*) and those that were infected with another one that has smaller spermogonia (probably *Uredinopsis hirosakiensis*) as shown in Table 82. On Sept. 28, 1936, from the same location in the Tomakomai Forest, the same *Peridermium* was still collected though a little changed in its outer appearance. Two other specimens of diseased MAYR's fir were collected from Mt. Maruyama near Sapporo and also from Ochiai Forest. The former consisted of branchlets removed from a large tree. Check inoculations by aecidiospores were successful (cf. Tab. 58, IV, Nos. 43 and 44). The latter specimen included two small seedlings attaining about seven centimeters in height and two years in age. With the specimen check inoculation was not successfully made, but in morphology of spermogonia and peridial cells it was so similar, that the writer instantly determined it as the rust in question. In these seedlings one-third to one-half of the number of new needles were diseased, which probably may have affected the healthy development of the fir seedlings.

6. *Hyalopsora aculeata* KAMEI. Data concerning this rust were derived from special observations on affected seedlings collected in the autumn of 1936 at Nopporo Forest. The affected needles showed slight hypertrophy and elongation but no marked distortion nor demarcation between healthy and diseased areas. The affected tissue was pale yellowish green just as shown in cases of some *Milesina.* Frequently the midrib was seen in face view to be conspicuously discolored. Other characteristics were orange colored aecidial sori and markedly large spermogonia. Needles affected by the rust in question were "rather

TABLE 82. Number of needles of branchlets of *Abies Mayriana* seedlings affected by *Milesina Miyabei*

No. of branchlets	Length of branchlets (cm.)	No. of diseased needles	Total no. of needles	Percent of diseased needles
1	8.7	19	128	15
2	6.0	17	73	23
3	7.2	16	72	22
4	4.3	5	34	15
5	3.1	4	26	15
6	6 5	15	71	21
7	4.4	13	49	27
8	6 5	9	83	11
9	4.7	5	16	11
10	1.5	2	13	15
11	15.3	50	229	22
12	11.5	47	138	34
13	11.7	38	155	25
14	8.0	22	69	32
15	8.0	20	70	29
16	7.0	26	89	29
17	6 5	12	74	16
18	13.5	45	205	22
19	9.0	47	130	36
20	10.0	30 (+2*)	140	21
21	7.2	23 (+2*)	83	28
22	10.2	60	168	36
23	7.0	39	85	46
24	12.1	39 (+1*)	240	16
25	16.7	23	137	17
26	15.5	20 (+1*)	130	15
27	17.0	10	59	17
28	10.4	9	67	13
29	12 0	26	142	18
30	10.0	14	83	17
31	8.0	25	104	24
32	7.0	7	64	11
33	6.0	6	49	12
34	15.0	35	206	17
35	10.0	38 (+3*)	119	32
36	10.0	30(+2*+1§)	125	24
37	6.3	5	64	8
38	6.5	20	70	29
39	4.0	6 (+1*)	32	19
40	16.0	29	258	11
41	10.5	27 (+4*)	151	18
42	10.0	31 (+1§)	143	22
43	5.0	4	56	7
44	5.3	11 (+2*)	47	23
45	4 5	7	33	21
Limits	1.5–17.0	2–60	13–258	7-46
Average	8.79	21.93	102.42	20.93

* Some rust that had not yet developed aecidia, but was seen only in spermogonia, which probably may be identified as *Milesina Itôana*.

§ Some rust that had not yet perfectly developed aecidia and may probably be identified as *Uredinopsis hirosakiensis*.

sparsely scattered" among fascicles of leaves of the entire branchlet as already reported by BELL (1924, p. 23) in the case of *H. Aspidiotus*. The seedlings which bore affected leaves, so far as observed, varied from tiny ones about three years old and 6.5 cm. in height to medium sized ones that have attained an age of about six years and 22 cm. in height (cf. Fig. 7, d). But the number of affected needles was only 1–16 per seedling. Rarely, leaves on the same branch were found to be affected by this rust and *Milesina Itôana* simultaneously. Among twenty branchlets that were taken from small trees having various heights the amount of the damage was as shown in Table 83. The degree of damage done by this rust appears to be not so great as that of some species of *Milesina* and *Uredinopsis*. It is also rather like the case of *H. Aspidiotus*

TABLE 83. Number of affected needles of *A. Mayriana* by *Hyalopsora aculeata*

No. of branchlets	Length of branchlets (cm.)	Total no. of needles	No. of diseased needles	Percent
1	1.8	19	2	11
2	2.3	23	2	9
3	1.6	21	3	14
4	1.1	19	1	5
5	1.5	18	9	50
6	1.2	21	4	19
7	4.0	27	1	4
8	2.0	17	2	12
9	1.9	20	6	30
10	1.2	18	3	17
11	1.0	15	1	7
12	1.2	17	1	6
13	1.1	9	1	11
14	0.7	9	1	11
15	1.4	16	1	6
16	2.0	23	1	4
17	1.2	17	2	12
18	1.7	20	2	10
19	3.2	39	2	5
20	7.5	102	1	1
Limits	0.7–7.5	9–102	1–9	1–50
Average	1.43	23.50	2.30	12.25

of which it was remarked (MAYOR, 1923) "infection never takes place on a large scale which accounts for these stages having been so long overlooked."

VI. CONSOLIDATED TABLES

TABLE 84. RECORD OF THE CULTURES PROVING RELATIONSHIPS BETWEEN THE SPECIES OF FERN RUSTS AND THEIR ALTERNATE PHASES

1. *Uredinopsis*

No.	Rust	O. I. hosts	II. III. hosts	Kinds* of cult.	Authors and place of publication
1.	*U. Struthiopteridis*	*Abies balsamea*	*Matteuccia Struthiopteris*	A.B.	FRASER, Mycologia, **5**: 235, 1913
2.	*U. Osmundae*	"	*Osmunda Claytoniana*	A.	"
	"	"	"	B.	FAULL, Journ. Arnold Arb., **19**: 419, 1938
3.	*U. Atkinsonii*	"	*Thelypteris palustris* var. *pubescens*	B.	FRASER, Mycologia, **5**: 236, 1913
4.	*U. Phegopteridis*	"	*Dryopteris Linnaeana*	A.	"
	"	"	"	B.	FAULL, Journ. Arnold Arb., **19**: 413, 1938
5.	*U. americana*	"	*Onoclea sensibilis*	A.B.	FRASER, Mycologia, **5**: 236, 1913
6.	*U. Pteridis*	*Abies grandis*	*Pteridium aquilinum* var. *lanuginosum*	B.	WEIR & HUBERT, Am. Journ. Bot. **4**: 330, 1917
7.	*U. Kameiana*	*Abies Mayriana*	*Pteridium aquilinum* var. *japonicum*	A.B.	KAMEI, Ann. Rep. Jap. Phytopath. **2**: 212–214, 1930
8.	*U. Athyrii*	"	*Athyrium Filix-foemina* var. *longipes*	A.B.	KAMEI, Journ. Facult. Agric. Hokk. Imp. Univ. **47**: 11–42, 1940
9.	*U. Woodsiae*	"	*Woodsia polystichoides* var. *nudiuscula*	A.B.	" **47**: 41–42, 1940
10.	*U. hirosakiensis*	"	*Thelypteris palustris* var. *pubescens*	B.	KAMEI, Trans. Sapporo Nat. Hist. Soc. **13**: 157, 1934
	"	"	"	A.	KAMEI, Journ. Facult. Agric. Hokk. Imp. Univ. **47**: 20–21, 1940

11.	*U. intermedia*	*Abies Mayriana*	*Athyrium acrostichoides, A. pterorachis*	A.B.	KAMEI, Journ. Facult. Agric. Hokk. Imp. Univ. **47**: 45–46, 1940
12.	*U. ossaeiformis*	"	*Dryopteris dilatata* var. *oblonga, D. monticola*	A.B.	" **47**: 49–50, 1940
13.	*U. Adianti*	"	*Adiantum pedatum*	A.B.	" **47**: 9, 1940
14.	*U. filicina*	"	*Dryopteris Phegopteris*	A.B.	" **47**: 17–18, 1940
15.	*U. ceratophora*	*Abies balsamea*	*Cystopteris bulbifera*	A.	FAULL, Journ. Arnold Arb., **19**: 425, 1938
16.	*U. longimucronata*	"	*Athyrium angustum*	A.B.	" **19**: 411, 1938

2. *Milesina*

17.	*M. Blechni*	*Abies alba, A. cephalonica*	*Blechnum spicant*	A.B.	KLEBAHN, Zeitschr. f. Pfl. Kr., **26**: 262–264 1916
18.	*M. marginalis*	*Abies balsamea*	*Aspidium marginale*	A.B.	FAULL, Journ. Arnold Arb. **15**: 58–59, 1934
19.	*M. intermedia*	"	*Dryopteris spinulosa intermedia*	A.B.	" **15**: 56–57, 1934
20.	*M. polypodophila*	"	*Polypodium virginianum*	A.B.	" **15**: 60–61, 1934
21.	*M. fructuosa*	*Abies balsamea* and other six species of *Abies*	*Dryopteris spinulosa* var. *fructuosa*	A.	" **15**: 63, 1934
22.	*M. exigua*	*Abies Mayriana, A. firma, A. sachalinensis*	*Polystichum Braunii, P. aculeatum* var. *retrosopaleaceum*	A.B.	KAMEI, Trans. Sapporo Nat. Hist. Soc. **11**: 143–146, 1930
23.	*M. jezoensis*	*Abies Mayriana*	*Polypodium virginianum*	A.	" **12**: 31, 1931
	"	"	"	B.	KAMEI, Journ. Facult. Agric. Hokk. Imp. Univ. **47**: 111, 1940
24.	*M. Dryopteridis*	"	*Polystichum Standishii*	A.B.	" **47**: 97–98, 1940

25.	*M. Miyabei*	*Abies Mayriana*	*Dryopteris crassirhizoma*	A.B.	KAMEI, Journ. Facult. Agric. Hokk. Imp. Univ. **47**: 113–114, 1940
26.	*M. sublevis*	"	*Scolopendrium vulgare*	A.B.	" **47**: 118–119, 1940
27.	*M. Kriegeriana*	*Abies alba*	*Dryopteris Filix-mas*	B.	MAYOR, Bull. Soc. Neuchât. Sco. Nat. **58**: 1933
	"	" *A. concolor, A. grandis*	*D. spinulosa*	A.	HUNTER, Journ. Arnold Arb. **17**: 32, 1936
28.	*M. Scolopendrii*	*Abies alba, A. concolor*	*Scolopendrium vulgare*	A.B.	" **17**: 28–32, 1936
29.	*M. Dicteliana*	*Abies alba A. concolor*	*Polypodium vulgare*	A.B.	"
30.	*M. vogesiaca*	*Abies alba*	*Polystichum angulare*	A.	" **17**: 28, 1936
31.	*M. Itôana*	*Abies Mayriana, A. sachalinensis*	*Dryopteris crassirhizoma*	A.B.	KAMEI, Trans. Sapporo Nat. Hist. Soc. **14**: 98, 1935

3. *Hyalopsora*

32.	*H. Aspidiotus*	*Abies alba*	*Dryopteris Linnaeana, D. Robertiana*	A.B.	MAYOR, Bull. Soc. Neuchât. Sci. Nat. **47**: 1923
33.	*H. aculeata*	*Abies Mayriana*	*Spicantopsis nipponica* var. *japonicum*	A.	KAMEI, Trans. Sapporo Nat. Hist. Soc. **12**: 125–126, 1932
	"	"	"	B.	KAMEI, Journ. Facult. Agric. Hokk. Imp. Univ. **47**, 152, 1940

* The kinds of culture are A and B, where A means basidiospore culture and B aecidiospore.

TABLE 85. SUMMARY OF ORIGINAL CULTURE EXPERIMENTS PERFORMED BY THE WRITER

A. *Inoculations with basidiospores and aecidiospores*

§ Inocula obtained from	Inoculated on	Result	Times of expt.	The year in which experiments performed
Uredinopsis Adianti (Tab. 1 and 2)				
Adiantum pedatum	*Abies Mayriana*	+	1	1925
Abies Mayriana	*Adiantum pedatum*	+	2	"

Abies Mayriana	*Thelypteris palustris* var. *pubescens*	−	1	1925
,,	*Athyrium Vidalii*	−	1	,,
,,	*Matteuccia Struthiopteris*	−	1	,,
,,	*Woodsia polystichoides* var. *nudiuscula*	−	1	,,
,,	*Pteridium aquilinum* var. *japonicum*	−	1	,,

Uredinopsis Athyrii (Tab. 3 and 4)

Athyrium Filix-foemina var. *longipes*	*Abies Mayriana*	+	7	1923, 1924(2)*, 1925(2), 1926, 1929
Abies Mayriana	*Athyrium Filix-foemina* var. *longipes*	+	7	1923(3), 1924, 1925, 1928, 1929
,,	*Matteuccia Struthiopteris*	−	1	1923
,,	*Thelypteris palustris* var. *pubescens*	−	2	1923, 1924
,,	*Dryopteris Phegopteris*	−	1	1923
,,	*Pteridium aquilinum* var. *japonicum*	−	2	1923, 1925
,,	*Athyrium Vidalii*	−	3	1924(2), 1925

Uredinopsis filicina (Tab. 6 and 7)

Dryopteris Phegopteris	*Abies Mayriana*	+	6	1923(2), 1927***, 1928, 1930(2)
Abies Mayriana	*Dryopteris Phegopteris*	+	2	1923(2)
,,	*Matteuccia Struthiopteris*	−	1	1923
,,	*Thelypteris palustris* var. *pubescens*	−	1	1923
,,	*Athyrium Filix-foemina* var. *longipes*	−	1	1923
,,	*Pteridium aquilinum* var. *japonicum*	−	1	1923

Uredinopsis hirosakiensis (Tab. 8 and 9)

Dryopteris Thelypteris	*Abies Mayriana*	+	9	1922, 1923, 1925, 1925***, 1926, 1928, 1930(2), 1932***
Abies Mayriana	*Thelypteris palustris* var. *pubescens*	+	4	1922(2), 1923, 1925
,,	,,	?	1	1923**
,,	*Pteridium aquilinum* var. *japonicum*	+	2	1923, 1925

Abies Mayriana	*Matteuccia Struthiopteris*	−	1	1923
"	*Dryopteris Phegopteris*	−	1	1923
"	*Athyrium Filix-foemina* var. *longipes*	−	1	1923
"	*Dryopteris dilatata* var. *oblonga*	−	1	1923
" ***	*Thelypteris palustris* var. *pubescens*	−	3	1933(3)

Uredinopsis Kameiana (Tab. 11 and 12)

Pteridium aquilinum var. *japonicum*	*Abies Mayriana*	+	12	1923, 1924, 1925, 1927, 1928, 1930(2), 1931(2), 1933(2), 1933***
"	*A. holophylla*	+	2	1933(2)
"	*A. nephrolepis*	+	1	1933***
"	*A. balsamea*	+	7	1933(4), 1933(3)***
Abies holophylla	*Pteridium aquilinum* var. *japonicum*	+	1	1933
A. Mayriana	"	+	5	1923, 1924, 1931, 1933(2)
"	*Matteuccia Struthiopteris*	−	2	1923, 1931
"	*Dryopteris Phegopteris*	−	3	1923, 1931, 1933
"	*Thelypteris palustris* var. *pubescens*	−	2	1923, 1931
"	*Athyrium Filix-foemina* var. *longipes*	−	2	1923, 1931
	Onoclea sensibilis	−	1	1931
"	*Adiantum pedatum*	−	1	1933
"	*Osmunda cinnamomea*	−	1	1933
"	*Polystichum tripteron*	−	1	1933
"	*Osmunda japonica*	−	1	1933
"	*Dryopteris crassirhizoma*	−	1	1933
"	*Athyrium acrostichoides*	−	1	1933
A. sachalinensis	*Pteridium aquilinum* var. *japonicum*	+	4	1934(3), 1936

Uredinopsis Struthiopteridis (Tab. 15 and 16)

Matteuccia Struthiopteris	*Abies Mayriana*	+	13	1922(3), 1923(3), 1925, 1926(3), 1928, 1930***, 1933
"	*A. sachalinensis*	+	1	1926
"	*A. firma*	+	2	1926(2)

Abies Mayriana	*Matteuccia Struthiopteris*	+	4	1922, 1923(2), 1926
"	*Dryopteris dilatata* var. *oblonga*	−	1	1922
"	*Dryopteris Phegopteris*	−	2	1922, 1923
"	*Onoclea sensibilis*	−	1	1922
"	*Thelypteris palustris* var. *pubescens*	−	2	1922, 1923
"	*Pteridium aquilinum* var. *japonicum*	−	2	1923, 1926
"	*Athyrium Filix-foemina* var. *longipes*	−	1	1923
"	*Athyrium Vidalii*	−	1	1926

Uredinopsis Woodsiae (Tab. 17)

Woodsia polystichoides var. *nudiuscula*	*Abies Mayriana*	+	5	1925, 1928***, 1930***, 1930, 1931
Abies Mayriana	*Woodsia polystichoides* var. *nudiuscula*	+	1	1931

Uredinopsis intermedia (Tab. 20 and 21)

Athyrium acrostichoides	*Abies Mayriana*	+	5	1923(2), 1925, 1930***, 1931
A. pterorachis	"	+	2	1923(2)
Abies Mayriana	*Athyrium pterorachis*	+	6	1923(6)
"	*Athyrium acrostichoides*	+	5	1923(4), 1931
"	*Dryopteris dilatata* var. *oblonga*	−	2	1923(2)
"	*Thelypteris palustris* var. *pubescens*	−	2	1923(2)
"	*Dryopteris Miqueliana*	−	2	1923(2)

Uredinopsis ossaeiformis (Tab. 22 and 23)

Dryopteris dilatata var. *oblonga*	*Abies Mayriana*	+	13	1922(5), 1923, 1924(2) 1925, 1926(3), 1931
D. monticola	"	+	3	1924(3)
D. dilatata var. *oblonga*	*Abies firma*	+	3	1924, 1926(2)
"	*Abies sachalinensis*	+	1	1926
Abies Mayriana	*Dryopteris dilatata* var. *oblonga*	+	6	1922(2), 1923(3), 1926
"	*D. monticola*	+	1	1924
"	*D. Phegopteris*	−	1	1922
"	*Osmunda cinnamomea*	−	1	1922

Abies Mayriana	*Polystichum Standishii*	—	1	1922
"	*Thelypteris palustris* var. *pubescens*	—	1	1923
"	*Matteuccia Struthiopteris*	—	2	1922, 1923
"	*Athyrium pterorachis*	—	1	1923
"	*A. acrostichoides*	—	1	1923
"	*Dryopteris Miqueliana*	—	1	1923
"	*D. crassirhizoma*	—	1	1923
"	*D. dilatata* var. *oblonga*	+	9	1923(2), 1924, 1932, 1933(4), 1936
" ****	*D. Miqueliana*	—	1	1923
"	*D. crassirhizoma*	—	3	1923, 1933(2)
"	*Athyrium acrostichoides*	—	2	1933(2)
"	*A. pterorachis*	—	1	1933
Abies firma	*Dryopteris dilatata* var. *oblonga*	—	1	1926

Milesina Dryopteridis (Tab. 48 and p. 98)

Polystichum Standishii	*Abies Mayriana*	+	3	1931***, 1934***, 1934
Abies Mayriana	*Polystichum Standishii*	+	1	1934

Milesina exigua (Tab. 49 and 50)

Polystichum aculeata var. *retroso-paleaceum*	*Abies Mayriana*	+	6	1924, 1925, 1926, 1926***, 1928, 1929
"	*A. sachalinensis*	+	2	1926(2)
"	*A. firma*	+	1	1926
Polystichum Braunii	*A. Mayriana*	+	2	1930, 1930***
Abies Mayriana	*Polystichum Braunii*	+	1	1924
A. firma	"	+	1	1926

Milesina Itôana (Tab. 52, 53 and 54)

Dryopteris crassirhizoma	*Abies Mayriana*	+	6	1935(3), 1936(3)
Abies Mayriana	*Dryopteris crassirhizoma*	+	7	1935(6), 1936(1)
"	*Scolopendrium vulgare*	—	1	1935
"	*Polystichum Braunii*	—	1	1935
"	*P. aculeatum* var. *retroso-paleaceum*	—	1	1935
"	*P. Standishii*	—	1	1935
" ****	*Dryopteris crassirhizoma*	+	20	1933(7), 1934(13)
*Abies sachalinensis***	"	+	1	1933

Milesina jezoensis (Tab. 55 and p. 111)

Polypodium virginianum	*Abies Mayriana*	+	7	1930(4), 1931, 1933, 1936***
Abies Mayriana	*Polypodium virginianum*	+	1	1933

Milesina Miyabei (Tab. 57 and 58)

Dryopteris crassirhizoma	*Abies Mayriana*	+	11	1926 (3), 1928 (2)***, 1931***, 1931(2), 1935 (2), 1936
Abies Mayriana	*Dryopteris crassirhizoma*	+	3	1926, 1935, 1936
„ ****	„	+	5	1934(3), 1936(2)
„	*Dryopteris dilatata* var. *oblonga*	−	4	1934(2), 1936(2)

Milesina sublevis (Tab. 59 and p. 119)

Scolopendrium vulgare	*Abies Mayriana*	+	6	1926(2)***, 1927(2)***, 1931, 1931***
Abies Mayriana	*Scolopendrium vulgare*	+	1	1931

Hyalopsora aculeata (Tab. 78 and p. 152)

Spicantopsis nipponica var. *japonica*	*Abies Mayriana*	+	6	1926(2)***, 1927(3)***, 1931***
*Abies Mayriana***	*Spicantopsis nipponica* var. *japonica*	+	2	1936(2)

§ The inocula obtained from ferns were basidiospores and from firs aecidiospores.

* The number inside the parentheses is the number of times of culture experiments.

** Cases that were not clearly shown by the resulting uredosori.

*** Cases that did not produce aecidia.

**** Cases in which aecidiospores for inoculations were obtained from the field.

B. *Inoculations with uredospores and amphispores*

Inocula obtained from	Inoculated onto	Result	Times of expt.	The year in which experiments performed
Uredinopsis filicina (Tab. 5)				
§ *Dryopteris Phegopteris*	*Dryopteris Phegopteris*	+	5	1923, 1924(3), 1930

Uredinopsis Kameiana (Tab. 10)

§ *Pteridium aquilinum* var. *japonicum*	*Pteridium aquilinum* var. *japonicum*	+	1	1933

Uredinopsis Struthiopteridis (Tab. 13 and 14)

§§ *Matteuccia Struthiopteris*	*Matteuccia Struthiopteris*	+	2	1922(2)
"	*Thelypteris palustris* var. *pubescens*	−	1	1922
"	*Dryopteris Phegopteris*	−	1	1922
"	*D. dilatata* var. *oblonga*	−	1	1922
"	*Onoclea sensibilis*	−	1	1922
"	*Osmunda japonica*	−	1	1922
§ *Matteuccia Struthiopteris*	*Matteuccia Struthiopteris*	+	10	1922(7), 1923(2), 1924

Uredinopsis intermedia (Tab. 18 and 19)

§§ *Athyrium pterorachis*	*Athyrium pterorachis*	+	1	1923
§§ *Athyrium acrostichoides*	*A. acrostichoides*	+	1	1931
"	*A. pterorachis*	+	1	1931
§ *Athyrium acrostichoides*	*A. acrostichoides*	+	2	1923(2)

Uredinopsis ossaeiformis (p. 47)

§ *Dryopteris dilatata* var. *oblonga*	*D. monticola*	+	1	1924
§ *D. monticola*	*D. dilastata* var. *oblonga*	+	1	1934

Milesina Itôana (Tab. 51)

§§ *Dryopteris crassirhizoma*	*Dryopteris crassirhizoma*	+	2	1934, 1935

Milesina Miyabei (Tab. 56)

§§ *Dryopteris crassirhizoma*	*Dryopteris crassirhizoma*	+	7	1923, 1924, 1925, 1933, 1934(3)
"	*D. monticola*	−	1	1924
"	*D. dilatata* var. *oblonga*	−	1	1924

§ Amphispores were used as inocula.

§§ Uredospores were used as inocula.

VII. SUMMARY

1. Studies on the taxonomy and biology of fern rusts of *Abies* are very important from the pathological point of view in Hokkaidô, where fir trees are economically of great value and commonly associated with ferns in the field. In the present paper, there is described the writer's work with special regard to the cultural life history concerning sixteen species included in genera of *Uredinopsis, Milesina* and *Hyalopsora* made during past 15 years. For each species of materials, a historical review of researches on the fungus and personal observations accompanied with its description are presented.

2. To obtain distinguishing criteria, intensive comparative studies of the spermogonial and aecidial phases were made. Comparing spermogonia of each species, it may either be classed into subcuticular or subepidermal type. The shape, size and number were different for each type. Subepidermal spermogonia of the species of *Uredinopsis* and *Milesina* differed little, while subcuticular spermogonia of the species of *Uredinopsis* were generally smaller and more superficial than those of the species of *Milesina*.

3. Comparing markings of peridial cells of aecidia of all the species, they may be divided into finely verrucose type, coarsely verrucose type and striate (including alveolar markings) type. Aecidiospores of the species of *Uredinopsis* were generally smaller than those of the species of *Milesina* though they are indistinguishable in color and shape.

4. Keys to the species of *Uredinopsis* and *Milesina* based upon morphological characters of spermogonial and aecidial phases are given.

5. Spermogonial and aecidial phases of *Uredinopsis Kameiana* FAULL on *Abies Mayriana* in Hokkaidô are conspicuously different from those of *U. Pteridis* DIET. et HOLW. on *Abies grandis* in Western America though they have been heretofore considered conspecific.

6. For each species of all white spored materials, the relative time of the appearance and the development period of the organ of each stage developed from cultures were compared. Organs of the species of *Uredinopsis* appeared generally earlier with shorter periods of development than those of the species of *Milesina*.

7. It is concluded that the species of *Uredinopsis* and *Milesina* are not closely restricted to any particular species of *Abies*, but they are closely restricted to particular species of fern.

8. In the normal development of heteroecious life cycle in the

typical species of *Uredinopssi*, so far as artificial cultures are concerned, the period from the germination of overwintered teleutospores to the formation of new teleutospores again after the infection of aecidiospores is found to cover only a little more than two months.

9. That overwintered amphispores may infect the same fern host was proved in *Uredinopsis filician, U. Kameiana, U. intermedia* and *U. Struthiopteridis*. The germination of amphispores was also observed in cases of *U. filicina* and *U. Struthiopteridis*.

10. Considering the overwintering habit of the host fern, the development of teleutospores and uredosori as well as the lack of amphispores, species of *Milesina* in this locality are reasonably assumed to hibernate by the mycelium.

11. In *Hyalopsora aculeata*, according to the writer's investigations, the course of a life cycle was completed within one season. It is different from that of *Hyalopsora Aspidiotus*, which is known to require four years for the completion of a life cycle. Such a character well corresponds to the typical species of *Milesina*, with which *H. aculeata* somewhat agrees in morphological characters.

12. The amount of damage to *Abies* was estimated by counting affected needles of branchlets for the cases of *Uredinopsis hirosakiensis, U. Kameiana, U. ossaeiformis, Milesina Itôana, M. Miyabei* and *Hyalopsora aculeata*.

13. In Hokkaidô, the current year needles of *Abies* were seen to be affected by species of *Uredinopsis* early in the season and later by some of *Milesina* and *Hyalopsora aculeata*. Sometimes two species of the same genus or of different genera of the rust fungi were found infecting together on one and the same needle or branchlet. Among these, *Uredinopsis hirosakiensis* was observed to occur on needles of especially small seedlings in nursery beds, while *Milesina Itôana* to affect current year needles of young and mature fir trees as well as those of tiny seedlings on the floor of the forest. From these facts, it may easily be accepted that fern rusts of this locality, at least some of them represented by such as *M. Itôana*, may exert considerable damage upon the natural reproduction of fir seedlings retarding the growth or reducing the number of seedlings themselves. In such a case, all the rusted ferns should promtly be destroyed for the sake of the health of the fir trees.

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EXPLANATION OF PLATES

PLATE I.

Successfully inoculated fir seedlings with basidiospores of various species of fern rusts.

Fig. a. *Abies Mayriana* I_3, inoculated with *Uredinopsis ossaeiformis* on May 18, 1923. Aecidia began to issue about three weeks after inoculation and continued to become profuse ultimately. ×1/3.

Fig. b. *A. Mayriana* IV_8, inoculated with *U. Kameiana* on May 27, 1928. Aecidia began to issue 24 days after inoculation on current year needles only. Photographed on June 28, 1928. About natural size.

Fig. c. *A. Mayriana* IV_{11}, inoculated with *Milesina Dryopteridis* on June 16, 1934. Aecidia began to appear from August 26th. Slightly enlarged.

Fig. d. *A. Mayriana* I_{15}, inoculated with *M. Itôana* on June 4, 1935. Aecidia began to appear from Oct. 1, 1935. About 1/2.

PLATE II.

Face views of affected fir needles producing aecidial phases of various species of fern rusts. Photographed in June 1933. Taken with reflected light unless otherwise stated and magnified in every case about 17 times.

Fig. a. *Abies Mayriana* I_8, successfully inoculated with *U. Athyrii.*

Fig. b. *A. Mayriana* IV_{10}, successfully inoculated with *U. filicina.*

Fig. c. *A. Mayriana* VI_6, successfully inoculated with *U. hirosakiensis.*

Fig. d. *A. Mayriana* $VIII_{13}$, successfully inoculated with *U. Kameiana.*

Fig. e. *A. Mayriana* II_6, successfully inoculated with *U. Struthiopteridis.*

Fig. f. *A. Mayriana* IX_{11}, successfully inoculated with *U. Woodsiae.*

Fig. g. *A. Mayriana* X_{11}, successfully inoculated with *U. intermedia.* Photographed with transmitted light.

Fig. h. *A. Mayriana* VI_5, successfully inoculated with *U. ossaeiformis.*

Fig. i. *A. firma* I_6, successfully inoculated with *Milesina exigua.*

Fig. j. *A. Mayriana* affected with *M. Itôana* collected at Tomakomai Imperial Forest, Division 301, on Sept. 28, 1932.

Fig. k. *A. Mayriana* XIX_{10}, successfully inoculated with *M. jezoensis.*

Fig. l. *A. Mayriana* I_{11}, successfully inoculated with *M. Miyabei.*

Fig. m. *A. Mayriana* $XVIII_{11}$, successfully inoculated with *M. sublevis.* Photographed with transmitted light.

Fig. n. *A. Mayriana* IX_7, successfully inoculated with *Hyalopsora aculeata.*

PLATE III.

Pinnae of various species of fern affected with the uredostages of various species of rusts.

Fig. a. *Adiantum pedatum* affected with *Uredinopsis Adianti.* Collected at Jôzankei, Prov. Ishikari on Sept. 23, 1934. Slightly enlarged.

Fig. b. *Athyrium Filix-foemina* var. *longipes* affected with *U. Athyrii.* Collected at Botanic Garden Sapporo on Oct. 4, 1932. About natural size.

Fig. c. *Thelypteris palustris* var. *pubescens* affected with *U. hirosakiensis.* It shows many uredosori that issued after the inoculation experiments with accidiospores on Mayrian fir seedlings collected at Tomakomai in July 1933. Inoculated in Petri dish on July 21th. ×1.3.

Fig. d. *Dryopteris Phegopteris* affected with *U. filicina.* Collected at Mt. Makkarinupuri on Aug. 27, 1923. About natural size.

Fig. e. *Matteuccia Struthiopteris* affected with *U. Struthiopteridis.* Collected at Maruyama near Sapporo in September 1929. Slightly enlarged.

Fig. f. *Woodsia polystichoides* var. *nudiuscula* affected with *U. Woodsiae.* Collected at Mt. Teine on Oct. 20, 1929. About natural size.

Fig. g. *Pteridium aquilinum* var. *japonicum* affected with *U. Kameiana.* Collected at Nopporo on Oct. 19, 1929. Enlarged.

Fig. h. *Athyrium pterorachis* affected with *U. intermedia*. Collected at Mt. Teine on Sept. 28, 1924. Slightly enlarged.

Fig. i. *Dryopteris dilatata* var. *oblonga* affected with *U. ossaeiformis*. Collected at Mt. Makkarinupuri on Aug. 24, 1924. About natural size.

Fig. j. *Polystichum Standishii* affected with *M. Dryopteridis*. It shows uredosori (×) that issued after the inoculation of aecidiospores produced after the inoculation with basidiospores on *Abies Mayriana* IV_{14}. Inoculated on June 16, 1931 and produced 70 days after inoculation in Petri dish. About natural size.

Fig. k. *Polystichum Braunii* affected with *M. exigua*. Collected at Nopporo Forest in October 1929. Enlarged.

Fig. l. *Dryopteris crassirhizoma* affected with *M. Itôana*. It shows uredosori issued on Dec. 4, 1933, 27 days after the inoculation with aecidiospores on *A. Mayriana* collected at Lake Shikotsu. About natural size.

Fig. m. *Polypodium virginianum* affected with *M. jezoensis*. Collected at Shikaribetsu on June 6, 1930. Photographed on June 24. Slightly enlarged.

Fig. n. *Dryopteris crassirhizoma* affected with *Milesina Miyabei*. Collected at Mt. Makkarinupuri on Oct. 6, 1930. Uredospores are issuing in filamentary masses. ×2.

Fig. o. *Scolopendrium vulgare* affected with *M. subelvis*. It shows uredosori that issued after the inoculation of aecidiospores which were produced on *A. Mayriana* XI_{11}. About natural size.

Fig. p. *Spicantopsis nipponica* var. *japonica* affected with *Hyalopsora aculeata*. It shows uredosori that issued from the aecidiospore inoculation. About natural size.

PLATE IV.

Median vertical sections of spermogonia of various *Uredinopsis* rusts.

Fig. a. Closely attached mature spermogonia of *U. Adianti* from longitudinal section of leaf of *Abies Mayriana* I_5. ×310.

Fig. b. A mature spermogonium of *U. Athyrii* from longitudinal section of leaf of *A. Mayriana* I_8. ×310.

Fig. c. Two mature spermogonia of *U. filicina* from longitudinal section of leaf of *A. Mayriana* X_3. ×310.

Fig. d. Two closely attached spermogonia of *U. hirosakiensis* from transverse section of leaf of *A. Mayriana* III_3. ×330.

Fig. e. Confluented spermogonia of *U. Kameiana* from longitudinal section of leaf of *A. Mayriana* VII_5. ×310.

Fig. f. A mature spermogonium of *U. Kameiana* from longitudinal section of leaf of *A. Mayriana* VII_5. ×330.

Fig. g. A mature spermogonium of *U. Woodsiae* from longitudinal section of leaf of *A. Mayriana* X_5. ×310.

Fig. h. Two spermogonia of *U. Woodsiae* from longitudinal section of leaf of *A. Mayriana* IX_{11}. ×310.

Fig. i. A mature spermogonium of *U. intermedia* from longitudinal section of leaf of *A. Mayriana* X_{11}. ×310.

Fig. j. A mature spermogonium of *U. ossaeiformis* from transverse section of leaf of *A. Mayriana* collected in July 1932 at Mórap, Prov. Iburi. ×310.

PLATE V.

Median vertical sections of spermogonia of various *Milesina* rusts.

Fig. a. Two mature spermogonia of *M. Dryopteridis* from transverse section of leaf of *Abies Mayriana* IV_{14}. ×310.

Fig. b. A mature spermogonium of *M. exigua* from transverse section of a leaf of *A. firma* L. Note spermatia are being produced accompanied with so called "flexuous hyphae" from the ostiole to constitute band-like mass. ×310.

Fig. c. A mature spermogonium of *M. jezoensis* from transverse section of leaf of *A. Mayriana* $XVIII_{10}$. ×310.

Fig. d. A mature spermogonium of *M. sublevis* from transverse section of leaf of *A. Mayriana* $XVIII_{11}$. Somewhat flattened one. ×310.

Fig. e. A mature spermogonium of *M. sublevis* from longitudinal section of leaf of *A. Mayriana* $XVIII_{11}$. Somewhat globose one. ×310.

Fig. f. A mature spermogonium of *Hyalopsora aculeata* from longitudinal section of leaf of *A. Mayriana* $XIII_6$. ×52.

Fig. g. Two mature spermogonia of *Milesina Miyabei* from transverse section of leaf of *A. Mayriana* II_{11}. ×108.

Fig. h. A mature spermogonium of *M. Itôana* from transverse section of leaf of *A. Mayriana* collected at Tomakomai Imperial Forest (Division 301) on Sept. 28, 1932. ×310.

Fig. i. A spermogonium of *M. Miyabei* same as in Fig. g. ×310.

PLATE VI.

Face view of the peridial cells of aecidia of various species of fern rusts magnified 900 times except figures q and r in which magnified 310 times.

Fig. a. *Uredinopsis Adianti* on *Abies Mayriana* I_5.

Fig. b. *U. Athyrii* on *A. Mayriana* IX_8.

Fig. c. *U. filicina* on *A. Mayriana* II_3.

Fig. d. *U. hirosakiensis* on *A. Mayriana* $VIII_5$. Note conspicuous alveolar markings.

Fig. e. *U. Kameiana* on *A. Mayriana* $VIII_{13}$.

Fig. f. *U. Struthiopteridis* on *A. Mayriana* VI_2.

Fig. g. *U. Woodsiae* on *A. Mayriana* IX_{11}.

Fig. h. *U. ossaeiformis* on *A. Mayriana* I_3, accompanied with an aecidiospore. Note somewhat striate markings.

Fig. i. *U. intermedia* on *A. Mayriana* XII_3.

Fig. j. *Milesina Dryopteridis* on *A. Mayriana* IV_{11}.

Fig. k. *M. exigua* on *A. firma* I_6.

Fig. l. *M. Itôana* on *A. Mayriana* collected at Nopporo Forest on Oct. 8, 1934.

Fig. m. *M. jezoensis* on *A. Mayriana* XVI_{13}.

Fig. n. *M. Miyabei* on *A. Mayriana* XV_6.

Fig. o. *M. sublevis* on *A. Mayriana* XI_6.

Fig. p. *Uredinopsis Pteridis* on *Abies grandis* collected by Dr. J. R. Weir at Priest River, Idaho, in U.S.A. on June 11, 1916. A part of the specimen that was used in the inoculation experiments made by Drs. Weir and Hubert. Note more conspicuous and far coarser markings comparing with those

of *U. Kameiana* in Fig. c which was previously considered as *U. Pteridis.*

Fig. q. The same in lower magnification. Note very thick walled peridial cells.

Fig. r. *U. Kameiana* on *Abies Mayriana* VIII$_{13}$. Accompanied with three aecidiospores that were obtained from the writer's inoculation experiments. Note distinct difference of markings compared with Fig. q.

PLATE VII.

Uredo and teleutostages of various species of fern rusts. Drawn by means of camera lucida and magnified 240 times unless otherwise stated.

Fig. 1. *U. Adianti.* a. The uredospores in sticky substance. b. Uredospores in water. c. Teleutospores in face view of the affected fern frond.

Fig. 2. *U. Athyrii.* a. Uredospores in water. b. A uredospore in dry state. c. Teleutospores in sectional view of the host tissue. d. Teleutospores in face view of the affected fern frond. e Two promycelia.

Fig. 3. *U. filicina.* a. Amphispores in wet and dry states. b. Uredospores in water. c. Amphispores in germination. d. Teleutospores in sectional view of an affected frond.

Fig. 4. *U. Kameiana.* a. Uredospores in water, in germination and in dry state. b. An amphispore in dry state. c. Amphispores just before germination. d. Teleutospores intact and in germination.

Fig. 5. *U. Struthiopteridis.* a. Uredospores in water. b. Uredospores in dry state. c. Teleutospores in sectional view of the affected frond. d. A promycelium and basidiospores. e. A teleutospore in the beginning of germination. f. Amphispores. g. Germinating amphispores. h. Cells of a pseudoperidium of a uredosorus. i. Germinating uredospores.

Fig. 6. *U. Woodsiae* on *Woodsia polystichoides* var. *nudiuscula.* a. Uredospores in wet and dry states. b. Teleutospores in face view of the affected frond. c. Promycelia and basidiospores. d. Amphispores in wet and dry states.

Fig. 7. *U. hirosakiensis.* a. Uredospores in dry and wet states. b. Uredospores in germination. c. Teleutospores in subepidermal position in the host tissue. d. Teleutospores in face view of the affected frond.

Fig. 8. *U. ossaeiformis.* a. Uredospores issued on *Dryopteris monticola.* b. A teleutospore in germination. c. Teleutospores in sectional and face views of the affected fern of *Dryopteris dilatata* var. *oblonga.* d. A uredosorus under the stomatal slit of the same host. e. A uredosorus in median vertical section showing surrounding teleutospores on *Dryopteris monticola.*

Fig. 9. *U. intermedia.* a. Uredospores from *Athyrium pterorachis* in water. b. Amphispores in water mostly derived from *Athyrium pterorachis.* c. Promycelia accompanied by basidiospores. d. Amphisporic sori and teleutospores in the sectional view of the affected frond of *Athyrium acrostichoides.* ×136. e. Teleutospores on the face view of the affected frond of *Athyrium pterorachis.*

Fig. 10. *Milesina Dryopteridis* on *Polystichum Standishii.* a. Uredospores in wet and dry states. b. Teleutospores in epidermal cells in face view of the host fern. c. The same in section of the affected frond.

Fig. 11. *M. exigua* on *Polystichum aculeatum* var. *retroso-paleaceum*. a. Uredospores in wet and dry states. b. Promycelia and basidiospores. c. Teleutospores in epidermal cells of the host fern in face view.

Fig. 12. *M. Itôana*. a. Uredospores. b. Teleutospores. c. A young teleutospore in a host epidermal cell. d. Teleutospores in a host epidermal cell in the time of germination.

Fig. 13. *M. jezoensis*. a. Uredospores. b. Germinating teleutospores.

Fig. 14. *M. Miyabei* on *Dryopteris crassirhizoma*. a. Uredospores in water. The right end one is germinating. b. Mature teleutospores in face view when they are germinating. c. Part of a uredosorus in face view showing structures of the pseudoperidium. d. Basidiospores. e. Young teleutospores.

Fig. 15. *M. sublevis*. a. Uredospores. b. Teleutospores in sectional view of the host tissue. c. Teleutospores in sectional view of the host tissue showing double layers of spores. d. A promycelium and basidiospores.

Fig. 16. *Hyalopsora aculeata*. a and e. Teleutospores in host epidermal cells. a. Face view. e. Sectional view. b. Uredospores in wet and dry states. c. A part of the pseudoperidium of a uredosorus in face view. d. Sectional view of the pseudoperidium.

Fig. 17. Spermatiophores and "flexuous hyphae" of various species of the fern rusts. a. Spermatiophores of *Uredinopsis Struthiopteridis* in a spermogonium on *Abies Mayriana* $XXII_6$. ×560. b. Spermatiophores of *U. Woodsiae* in a spermogonium on *A. Mayriana* $XVIII_8$. ×560. c. Spermatiophores of *U. Kameiana* in a spermogonium on *A. Mayriana* VII_{10}. ×560. d. Spermatiophores and a "flexuous hypha" in a spermogonium of *U. ossaeiformis* on *A. Mayriana* collected at Morap in July 1932. ×560. e. Spermatiophores and "flexuous hyphae" in a spermogonium of *U. intermedia* on *A. Mayriana* X_{11}. ×575. f. Spermatiophores and a "flexuous hypha" in a spermogonium of *Milesina Dryopteridis* on *A. Mayriana* III_{14}. ×575. g. Spermatiophores and "flexuous hyphae" in a spermogonium of *M. exigua* on *A. Mayriana* XI_{10}. ×575. h. Spermatiophores and "flexuous hyphae" in a spermogonium of *M. Itôana* on *A. Mayriana* II_{15}. ×575. i. Spermatiophores and "flexuous hyphae" in a spermogonium of *M. jezoensis* on *A. Mayriana* $XVIII_{10}$. ×575. j. Spermatiophores and "flexuous hyphae" in a spermogonium of *M. Miyabei* on *A. Mayriana* $XIII_8$. ×575. k. Spermatiophores in a spermogonium of *M. sublevis* on *A. Mayriana* X_7. ×560. l. Spermatiophores and "flexuous hyphae" in a spermogonium of *M. sublevis* on *A. Mayriana* X_7. ×240. m. Spermatiophores in a spermogonium of *Hyalopsora aculeata* on *A. mayriana* $XXII_6$. ×560.

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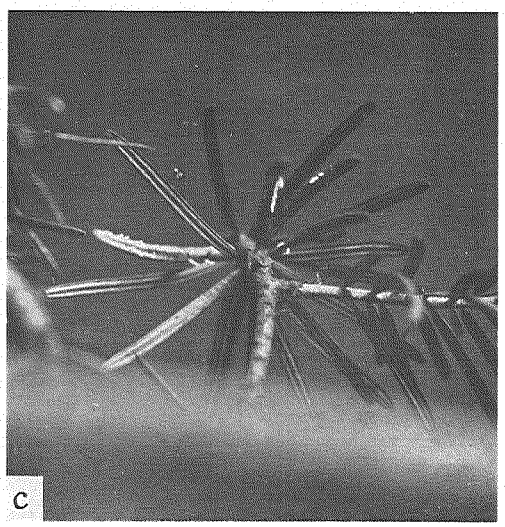
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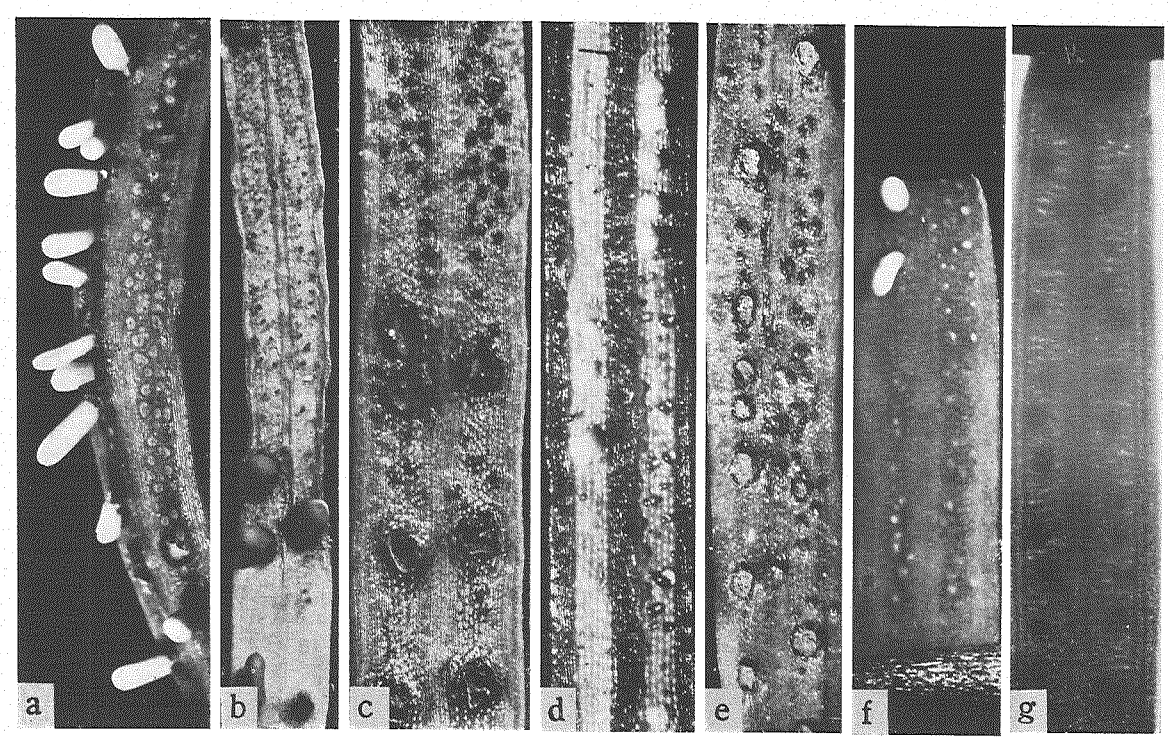
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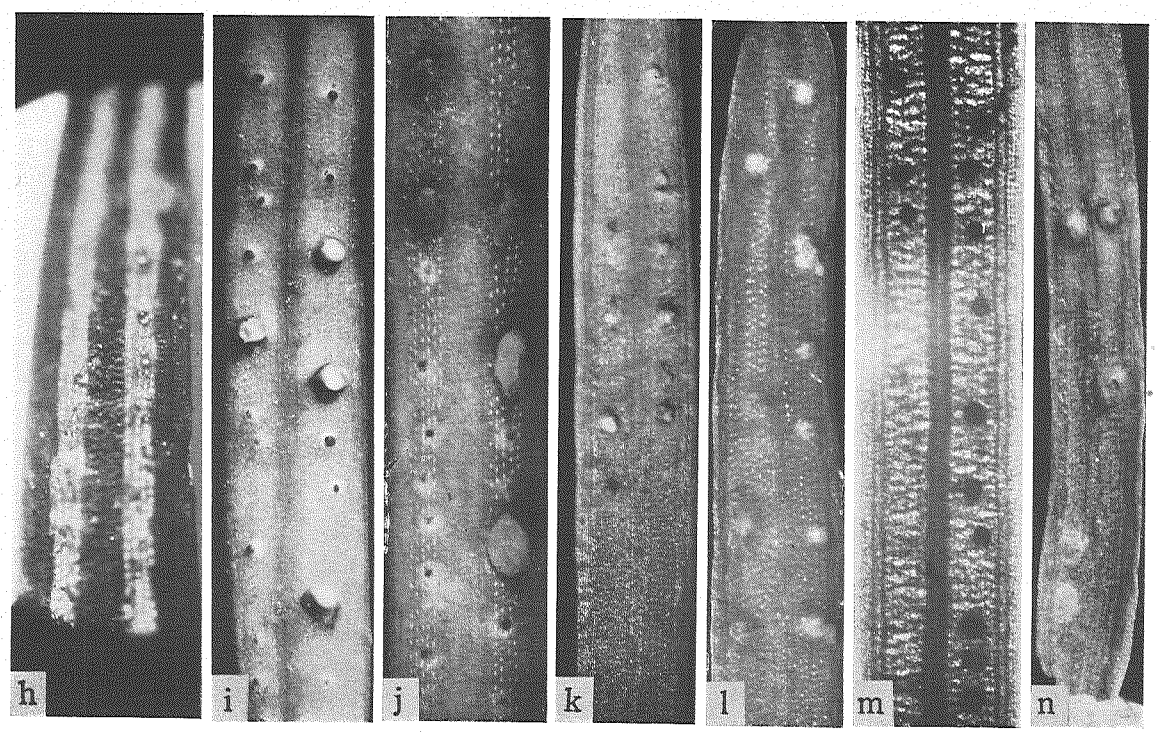
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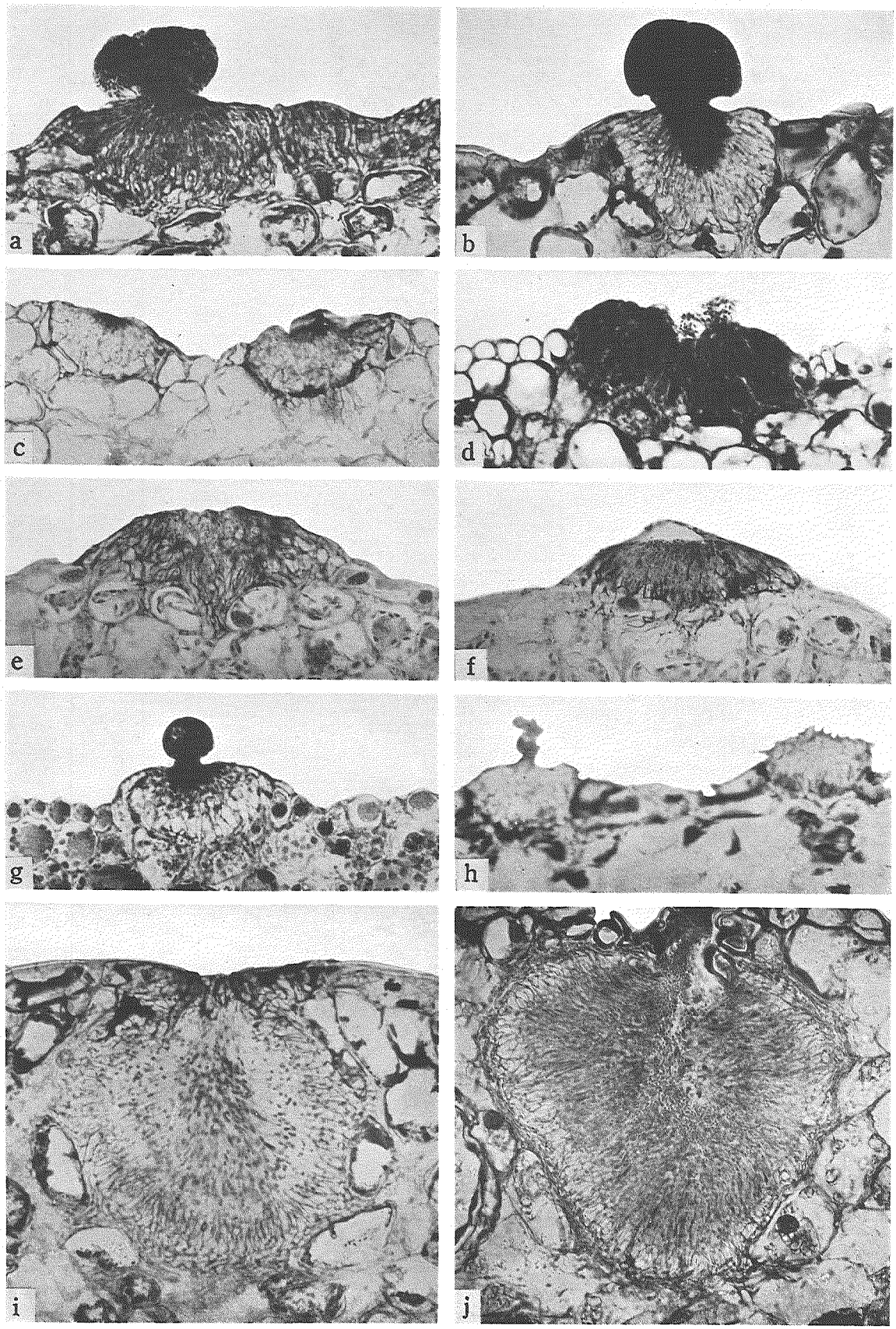
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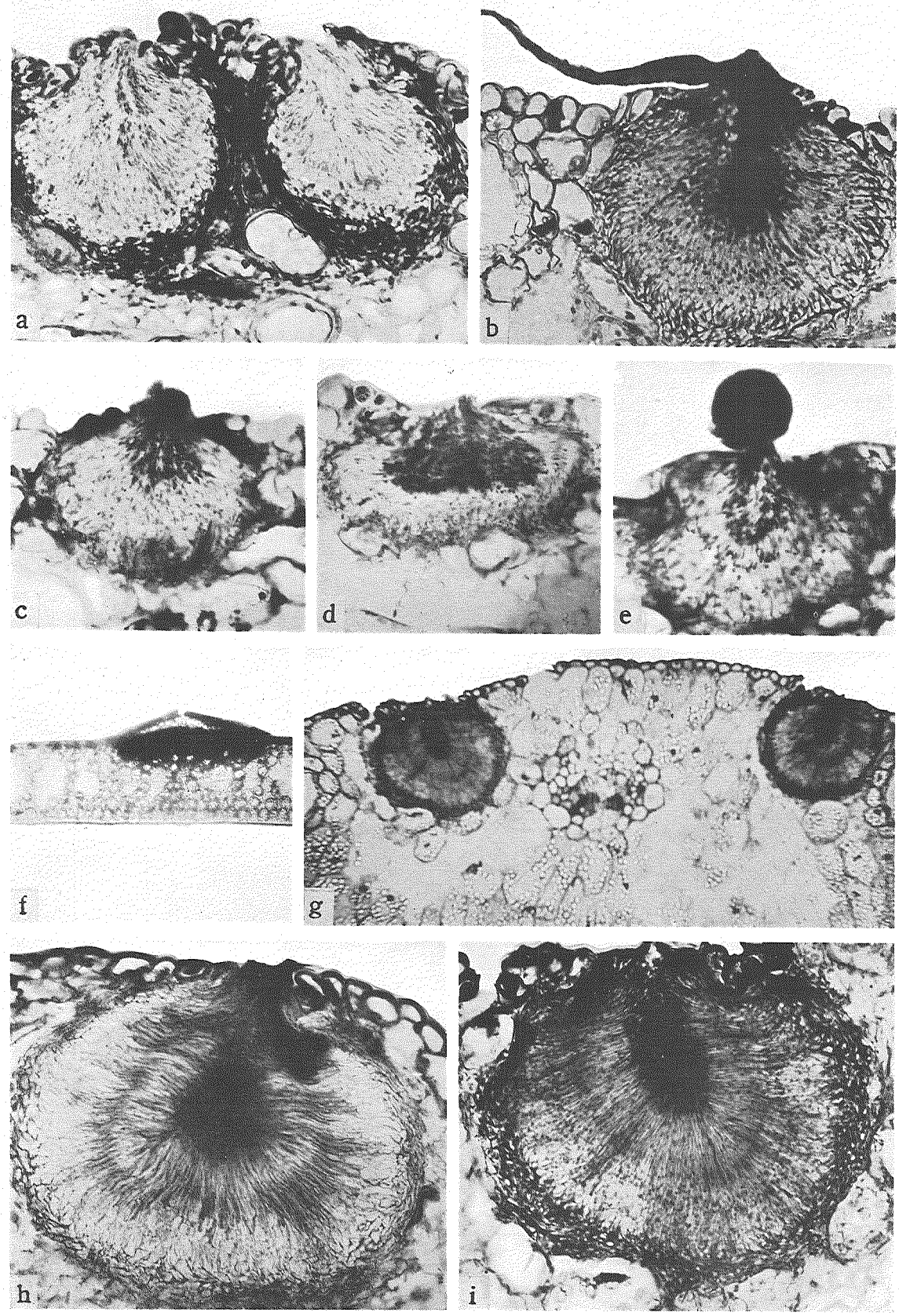
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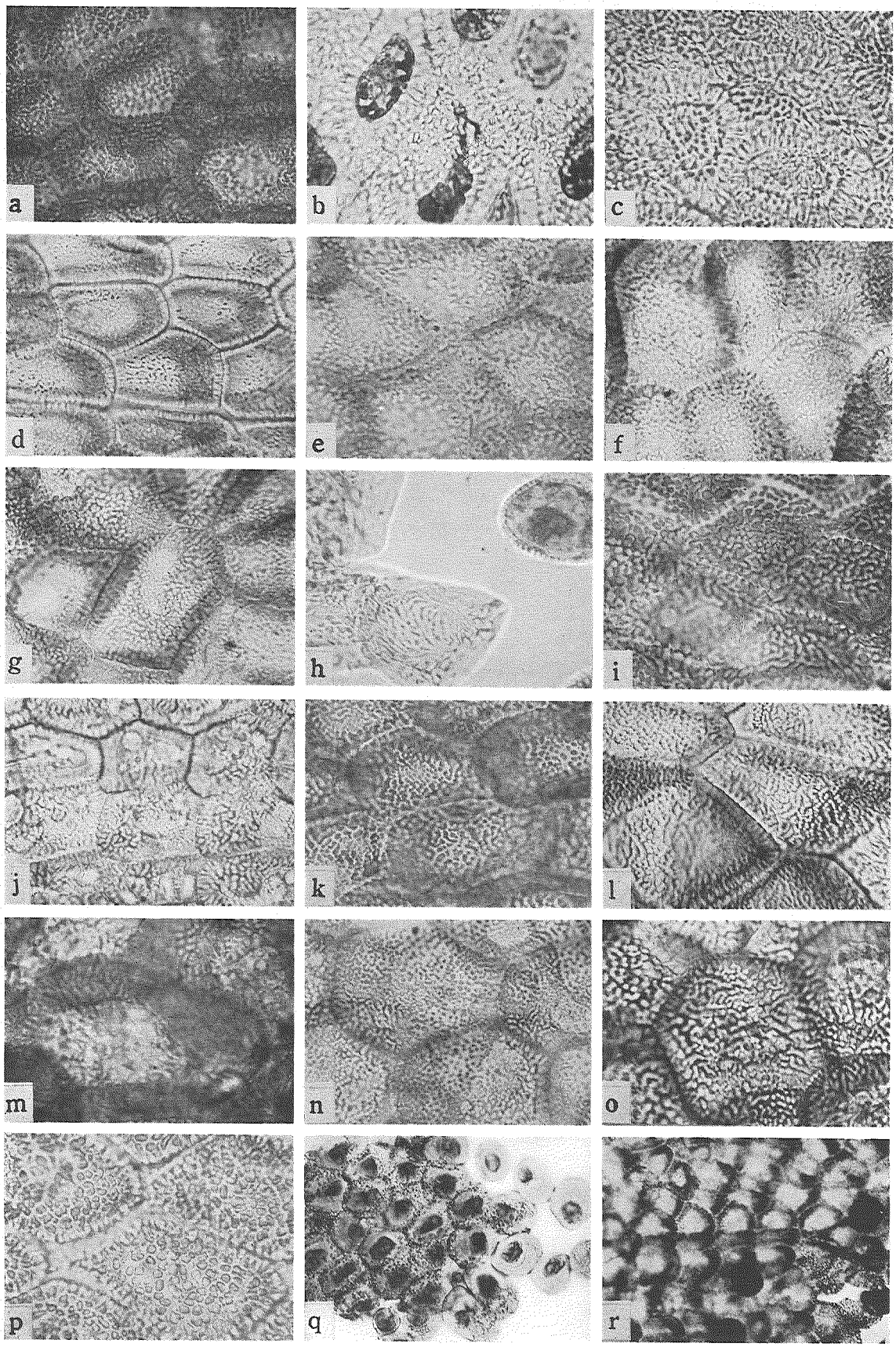
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