Critical Revision on the Genera *Rhizosphaera* MANGIN et HARIOT and *Rhizophoma* PETRAK et SYDOW, a Little-known Fungous Group Associated with Needle Disease of Conifers

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Introduction

During the spring through the summer of 1965, an unusual outbreak of a needle blight of Japanese pines, especially of Japanese red pine, *Pinus densiflora* SIEB. et ZUCC., was recorded from the low-altitude areas throughout the central and eastern parts of Japan. Such occurrence of this needle blight has not been recorded previously in Japan, although locally restricted development of the disease has been observed several times[29)30)]. On these blighted needles a particular fungus was usually recognized and it was tentatively called a species of the genus *Rhizosphaera* or *Rhizophoma*. This epidemic occurrence of the needle blight extending over vast areas provided a good opportunity for the author to determine systematic position of the fungus. Accordingly, many fresh materials of pine and other conifers showing similar signs as those on pine were collected from various localities to examine in detail the morphology of the fungus found on them.

In the course of examination on these materials, it was found that at least three species of fungi belonging to the same genus being separable only by their spore size, were distributed in Japan. Moreover, a question whether the genera *Rhizosphaera* and *Rhizophoma* precisely differ from each other or not, came to the author's mind. To answer this question, morphology of Japanese species was comparatively studied with that of the authentic specimens of the genus *Rhizosphaera*. This paper describes the results of critical study on the genera *Rhizosphaera* and *Rhizophoma*, and gives additional information on the species belonging to these genera.

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Criticism and revision on the genera *Rhizosphaera* and *Rhizophoma*

In examining many materials collected newly or deposited in the laboratory herbarium, it was found that the fungi associated with the needle blight of pines and other conifers were divided into three groups which belonged to the same genus but were apparently distinguishable by their spore size. Concerning the determination of systematic position of these fungi, some confusion in literature has been found.

In 1907, MANGIN and HARIOT[16] who investigated a needle blight of *Abies pectinata* in Jura province of France, described a genus *Rhizosphaera* as a new member of Sphaeropsidales based on the fungus inhabiting blighted needles. The basic ground, by which they differentiated it from the hitherto known genera, was the structure of pycnidium. According to them, a stalk like bundle of brown hyphae grows up from the hyphal mass aggregated beneath the stoma, and penetrates through the stoma, then finally forms a pycnidium on the stoma. Therefore, mature pycnidia have apparent stalk and hyphal mass at their base. MANGIN and HARIOT likened the fruit-body of *Rhizosphaera abietis* MANGIN et HARIOT, the type species of the genus, to a balloon; i. e., hyphal mass was equivalent to a hanging basket, stalk to sash-chain, and pycnidium to ball.

At the same time, they recorded that there were two different ways in conidial formation. Pycnidial wall which is formed from outer hyphal layer of the stalk changes into the spore producing cells having short conidiophore. Branched brown hypha which grows upward from inner hyphal strand of the stalk, is the source of another way in its conidial formation. Conidia are produced on these hyphae at the inner part of pycnidium as if they are produced on the long slender conidiophore (Figure 5 in MANGIN & HARIOT). They, however, mentioned only the former type of conidial formation in their description, that is "sporophora brevia, simplicia, monospora".

Shortly after the time when MANGIN and HARIOT erected the genus *Rhizosphaera*, MAUBLANC[17] found that two older species would belong to this genus. One of them, *Coniothyrium pini* CORDA, was considered by him to be the same species as *Rhizosphaera abietis* MANG. et HAR. and he recombined it newly as *R. pini* (CDA.) MAUBL. having a synonym of *R. abietis*. For another species, *Sacidium abietis* OUDEMANS, he gave a new combination of *Rhizosphaera oudemansii* MAUBL. to avoid confusion with *R. abietis* MANG. et HAR. According to the description of this fungus[26], it has filiform conidiophore.

In 1914, BUBÁK[3] added one species to this genus based on his re-study of an older species, *Sphaeronema pini* DESMAZIÈRE described in 1848. He named it newly as *Rhizosphaera kalkhoffii* BUB., because the species name *pini* could not be used for it owing to the CORDA's older species, *R. pini* (CDA.) MAUBL. described in 1840. With regard to the way of conidial formation in this fungus, BUBÁK noted that the conidia were directly born on the inside cell of pycnidial wall; in other words, conidiophore was absent.

Shortly after, HÖHNEL[7] established Sclerophomaceae as a new family of Sphaeropsidales, in which he aggregated many pycnidial fungi having no conidiophore. *Rhizosphaera kalkhoffii* BUB. was transferred by him to the genus *Sclerophoma* and revived its species name *pini* as *S. pini* (DESM.) HÖHNEL. Van LUYK[14] who studied several species of the genus *Sclerophoma*

inhabiting coniferous plants, however, rejected HÖHNEL's treatment and supported BUBÁK's name for the fungus in question. He thought the genus *Sclerophoma* HÖHNEL consisted of heterogeneous fungi that needed re-examination. In 1924, PETRAK[22] discussed relative connection in the fungi belonging to the family Sclerophomaceae. It was emphasized in his conclusion that the family was composed from quite heterogeneous genera in relation to their structure and life-history, and, at least five distinguishable ways of conidial formation were observed among them.

WILSON and WALDIE[34)35)] reported two *Rhizosphaera* species, i. e. *R. pini* (CDA.) MAUBL. and *R. kalkhoffii* BUB., from Britain. They stated that British materials of *Rhizosphaera pini* always produced its conidia directly on the inside wall of pycnidium, and such long conidiophore as that noted by MANGIN and HARIOT was not observed in these materials. As to *Rhizosphaera kalkhoffii*, they noted that chief points to differentiate this species from *R. pini* were the smaller conidia and entire lack of conidiophore.

In 1927, PETRAK and SYDOW[24)], who published a result of re-examination on various pycnidial fungi having unicellular conidia, established a new genus *Rhizophoma* with a new combined species *Rhizophoma pini* (DESM.) PETR. et SYD., segregating it from the genus *Rhizosphaera*. Exactly the same reason by which WILSON and WALDIE distinguished two species of the genus *Rhizosphaera*, *R. pini* (CDA.) MAUBL. and *R. kalkhoffii* BUB. (=*Rhizophoma pini* (DESM.) PETR. et SYD.), prompted them to separate two genera, *Rhizosphaera* and *Rhizophoma*. Namely, they estimated the different ways in conidial formation between them as an important characteristic to distinguish these genera each from the other.

In 1947, WATERMAN[32)] reported *Rhizosphaera kalkhoffii* BUB. from the United States and noted its conidial formation by the budding way.

Now, if the systematic position of Japanese fungi which are summarily shown in Table 2 is judged from the description of genera *Rhizosphaera* and *Rhizophoma*, there is no doubt that they belong to the genus *Rhizophoma* PETRAK et SYDOW. However, in view of literature cited above, a question arises as to whether or not the genus *Rhizophoma* would be distinctly differentiated from the genus *Rhizosphaera*. The first reason is that the existence of conidiophore in the genus *Rhizosphaera* MANGIN et HARIOT seems to be doubtful. On the type species of the genus *Rhizosphaera*, *R. pini* (CDA.) MAUBL., the workers other than MANGIN and HARIOT, did not observe the existence of conidiophores. In addition to this fact, that the rest of dissolving contents in pycnidium are often misjudged to be a real conidiophore among the pycnidial fungi having no conidiophore has been well known[22)]. Secondly, PETRAK and SYDOW, by whom the genus *Rhizophoma* was segregated from the genus *Rhizosphaera*, did not ascertain directly the way of conidial formation in *Rhizosphaera pini* (CDA.) MAUBLANC. They accepted the existence of conidiophore in the genus *Rhizosphaera* from the description and figure made by MANGIN and HARIOT.

In order to dispose of this uncertainty, two authentic specimens of *Rhizosphaera pini* (CDA.) MAUBL. identified by MANGIN were investigated in detail. From this investigation it was revealed that the general features of this species were quite identical with those of *Rhizophoma* PETR. et SYDOW. No conidiophores were recognized and conidia were born directly on the inside wall of pycnidium or on the wall of inner hyphae. Then, it may be said that the conidiophores of *Rhizosphaera* observed by MANGIN and HARIOT are no more than the rest of dissolving hyphal wall.

Judging from the foregoing facts, it can be concluded that there is no reason to separate both genera, *Rhizosphaera* MANGIN et HARIOT and *Rhizophoma* PETRAK et SYDOW, from each other. Description for the genus *Rhizospaera* given by MANGIN and HARIOT, therefore, will be amended as follows, and the genus *Rhizophoma* PETRAK et SYDOW treated as a synonym of the genus *Rhizosphaera*.

But by conceding that the genus *Rhizophoma* was contained in the synonym of genus *Rhizosphaera*, a further problem arises. Type species of both genera have the same species name *pini*, respectively. However, it will be clear, as pointed out previously by BUBÁK[3], that *Coniothyrium pini* CORDA described in 1840, the oldest synonym *Rhizosphaera pini* (CDA.) MAUBL., possesses its nomenclature. Species name *pini* in *Rhizophoma pini* (DESM.) PETR. et SYD. which was first described by DESMAZIÈRE in 1848, therefore, could not be used under the genus *Rhizosphaera*. Then, *Rhizosphaera kalkhoffii* BUBÁK is revived again for it instead of the old species name *pini* originated from *Sphaeronema pini* DESMAZIÈRE.

In "Genera of Fungi" published in 1931, CLEMENTS and SHEAR[5] treated the genus *Ectosticta* SPEG.[26] and *Sclerochaeta* HÖHN. (=*Chaetopyrena* PASS.[9]) as synonyms of the genus *Rhizosphaera*. The author has not seen any specimens of these two genera. Judging from the description, the genus *Ectosticta* differs distinctly from the genus *Rhizosphaera* by its entirely superficial pycnidia having no hypostroma——stalk and hyphal mass——and the genus *Sclerochaeta* also differs in its superficial and setous pycnidia. Then, the author retains here the treatment by CLEMENTS and SHEAR as a problem to be cleared up in future.

Concerning the life history of the genus *Rhizosphaera* and/or *Rhizophoma*, PETRAK presumed that the perfect stage of these fungous groups was probably species of the genus *Phaeocryptopus* NAOUMOFF. On the other hand, ROHDE[25] gave a practical disproof against PETRAK's assumption, based on his isolation experiment from the conidium of *Rhizosphaera* and ascospore of *Phaeocryptopus*. According to him, cultural characters of *Rhizosphaera* species were different from those of *Phaeocryptopus*. PETRAK[23], however, once more rejected ROHDE's opinion and presented life historical schema of these fungi; i. e., *Rhizosphaera pini* (CDA.) MAUBL. was equivalent to macroconidial stage of *Phaeocryptopus nudus* (PECK) PETR., and *Rhizophoma pini* (DESM.) PETR. et SYD. to microconidial stage of it, though he did not give any practical evidence. PETRAK's supposition was accepted exactly in AINSWORTH and BISBY's "Dictionary of Fungi"[2].

It is quite doubtful, however, whether *Rhizophoma pini* (DESM.) PETR. et SYD. is the microconidial stage of *Phaeocryptopus nudus* (PBCK) PETRAK. No similarity between these two fungi has been recognized in the isolation experiments, as noted in the latter part. To clear up the genetic relation between the species of the genera *Rhizospaera* and *Phaeocryptopus* is an important problem to be solved in future.

Rhizosphaera **MANGIN et HARIOT**, charact. emend., Bull. Soc. Myc. France 23 : 56, 1907; SACCARDO, Syll. Fung. 22 : 917, 1913; GROVE, Coelomycetes I, 141, 1935

Synonym : *Rhizophoma* PETRAK et SYDOW, Rept. Spec. Nov. Regn. Veg. Beih. XLII, 472, 1927

Mycelium grows within the blighted needles which are grayish brown to reddish brown in colour, aggregates beneath the stoma and forms a ball-like hyphal mass, brown to greenish brown in colour. From such hyphal mass slender hyphal strand grows up, penetrates the stoma and forms a stalk-like bundle in the stomatal cavity. Outer hypha of the bundle

continuously grows up and specializes to pycnidial wall. Inner hypha branches sparsely and fills finally within the pycnidium. At this stage many small black dots are macroscopically recognized on blighted needles in several regular rows equivalent to those of stomata. Under a hand lens, pycnidium is found to be a small black globule with white resinous mass on it, but becomes pale to yellowish brown in colour under moist condition. Pycnidium is globular to subglobular, somewhat flattened at the lower part, and has a stalk- and ball-like hypostroma at its base. Hypostroma is more clearly visible on the host plant, having thick epiderm and wide stomatal cavity. Pycnidial wall is constituted from a layer of brown-coloured hypha. Inner part of pycnidium is also constituted from prosenchymatous brown hyphae at immature stage. With its maturity, conidia are born directly from the wall of hyphae and inside wall of pycnidium, and, these inner hyphae are dissolved gradually. Consequently, mature pycnidium is filled entirely with pycnospores instead of brown hyphae. Ostiole is lacking, but pycnidium breaks out irregularly at its upper part. Conidiophore is absent, although in some cases rest of dissolving hyphal wall is incorrectly judged to be conidiophore. Pycnospore is hyaline, unicellular, ovoid, elliptic or cylindric, often somewhat irregular shaped.

Species of the genus *Rhizosphaera* MANGIN et HARIOT

Since 1907 when the genus *Rhizosphaera* was established by MANGIN and HARIOT as a monotypic member of Sphaeropsidales, three species were added to this genus, and four species are known in this genus at the present time. Morphology of these fungi reported by many workers is summarily presented in Table 1. In addition to this table, morphology and host of Japanese materials collected on various conifers are given in Table 2, and average size of conidia in each material is dotted in Figure 1 together with those of hitherto known species. Histograms of length, width and length/width ratio of conidia of Japanese materials, being separable into three groups chiefly by their spore size, are shown in Figures 2 to 4.

It is apparent from these tables and figures that morphology of the fungus included in group I of Table 2 quite agrees with that of *Rhizosphaera kalkhoffii* BUB. reported by many workers[8)6)24)26)32)34)35)]. *Pinus* is the common host between them, although the latter has been reported more often on the needle of *Picea*. From these viewpoints Japanese materials including group I are identified as *Rhizosphaera kalkhoffii* BUBÁK. Moreover, no essential differences are recognized between *Rhizosphaera kalkhoffii* BUB. and *R. radicata* NAOUM. as pointed out previously by LUYK[14)] and PETRAK and SYDOW[24)], so the latter is included in the synonyms of the former in this paper.

Group II consists of three materials, and their spore size completely overlaps those of *Rhizosphaera pini* (CDA.) MAUBLANC. It is presumed from the fact discussed above that MANGIN and HARIOT incorrectly recognized the existance of conidiophore in this species. This being so, the fungus collected on *Abies* and *Tsuga* in Japan is identified as *Phizosphaera pini* (CDA.) MAUBL., and morphological characteristics of this species will be emended in the latter part.

No identical species with the materials of group III which have largest conidia was found among the hitherto known species as shown in Table 1 and Figure 1. Their conidia are far longer than those of *Rhizosphaera pini*. In the case of *Rhizosphaera pini*, length of conidia ranges from 15 to 21.5μ (18μ in average), whereas that of group III range from 20 to 37.5μ with the average 25.1μ. On the other hand, width range of conidia in these two

Table 1. Comparison in morphology and host range of the hitherto known species of the genus *Rhizosphaera*.

Species	Host	Author	Pycnidium			Conidium	
			Size	Pore	Conidiophore	Size	Shape
Rhizosphaera pini (Cda.) Maubl.	*Abies pectinata*	Mangin & Hariot[16]	90×120		+	16～20×8	ovoid
	A. fraseri	Vuillemin[31]	64～75	+	−	17～18×7.5	oblong elliptic
	A. grandis	Saccardo[26]				16～18	oblong ovoid
	Pinus sp.	Wilson & Waldie[35]	90～120		−	16～20×8	globular to ovoid
		Grove[6]	90～120	−		16～20×8	oblong ovoid
		Kobayashi	50×122	−	−	15～20×7～9.5	elliptic to ovoid
R. oudemansii Maubl.	*Abies grandis*	Maublanc[17] Saccardo[26]	60～100		+	9～13×7～9.5	elliptic
R. radicata Naoum.	*Abies sibirica*	Naoumoff[19]	70～100	−	+	5.5～8.25×4	ovoid to oblong
	A. pectinata	Saccardo[26]					ovoid
R. kalkhoffi Bubák (=*Rhizophoma pini* (Desm.) Petr. et Syd.)	*Picea excelsa*, *P. pungens*, *P. pungens* var. *argentea*, *P. nigra*, *P. sitchensis*, *P. glauca*, *P. orientalis*, *P. schrenkiana*, *P. abies*, *Abies pectinata*, *A. nobilis*, *Pseudotsuga douglasii* *Pinus austriaca*, *P. montana*, *P. strobus*, *P. mugo*, *P. nigra*	Bubak[3]	80～150		−	7～10×3～4	ovoid to elliptic
		Wilson & Waldie[35]			−	7～10×3～4	ovoid
		Petrak & Sydow[24]	70～160	−	−	5～10×2.7～4	ovoid to elliptic
		Saccardo[26]	50			10	ovoid
		Grove[6]	80～150	−	−	7～10×3～4	ovoid
		Waterman[32]		−	−	7～10×3～5	ovoid

Table 2. Data of the genus *Rhizosphaera* collected in Japan.

	Host	Locality	Altitude	Conidia Size	Conidia Shape
I	*Pinus densiflora*	Meguro, Tokyo	<600m	5.5～ 7.5× 2.8～ 3.5μ	elliptic to ovoid
	〃	Chiba-city, Chiba Pref.	〃	6.0～ 9.0× 3.0～ 4.5	〃
	〃	Fujiyoshida, Yamanashi	〃	5.0～ 7.5× 3.0～ 3.5	〃
	〃	Minori, Ibaraki Pref.	〃	7.5～10.0× 3.8～ 5.0	〃
	Pinus thunbergii	Meguro, Tokyo	〃	6.5～ 9.0× 3.0～ 4.0	〃
	〃	Mie Pref.	〃	6.0～ 8.0× 3.0～ 4.0	〃
	〃	Chiba-city, Chiba Pref.	〃	7.0～10.0× 3.0～ 4.5	〃
	〃	Uchihara, Ibaraki Pref.	〃	6.3～ 8.8× 3.0～ 4.5	〃
	Pinus excelsa	Mito, Ibaraki Pref.	〃	7.0～10.0× 3.8～ 5.0	〃
II	*Abies veitchii*	Narusawa, Yamanashi Pref.	>1,000 m	16.3～21.3× 7.5～10.0	〃
	〃	Gotenba, Shizuoka Pref.	〃	15.0～21.3× 7.5～11.3	〃
	Tsuga diversifolia	Narusawa, Yamanashi Pref.	〃	16.3～20.0× 8.0～12.5	〃
III	*Abies mariesii*	〃	〃	20.0～26.3× 7.5～10.0	elliptic to cylindric
	Pinus pumila	Miyata, Nagano Pref.	〃	21.3～37.5× 8.8～12.5	〃
	〃 (on culture)			22.5～30.0×10.0～12.5	〃

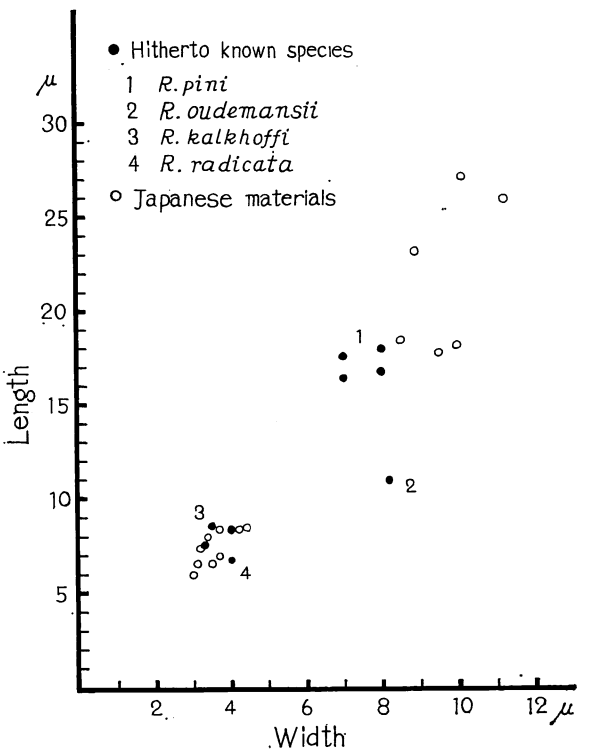

Figure 1. Average size of conidia in hitherto known species of the genus *Rhizosphaera* and in each material collected in Japan

Rhizosphaera entirely overlap each other, and no difference is recognized in their average size as shown in Table 2 and Figure 3; namely 7～12.5μ (9.3μ in average) is the case of *Rhizosphaera pini* and in the case of group III width of conidia ranges from 7.5～12.5μ (9.8μ in average). Then, group III presented in Table 2 seems to be separable fairly well from *Rhizosphaera pini* (Cda.) Maubl. by its length and length/width ratio of conidia as shown in Figures 2 and 4.

However, determination of the species on group III is retained here until comparative

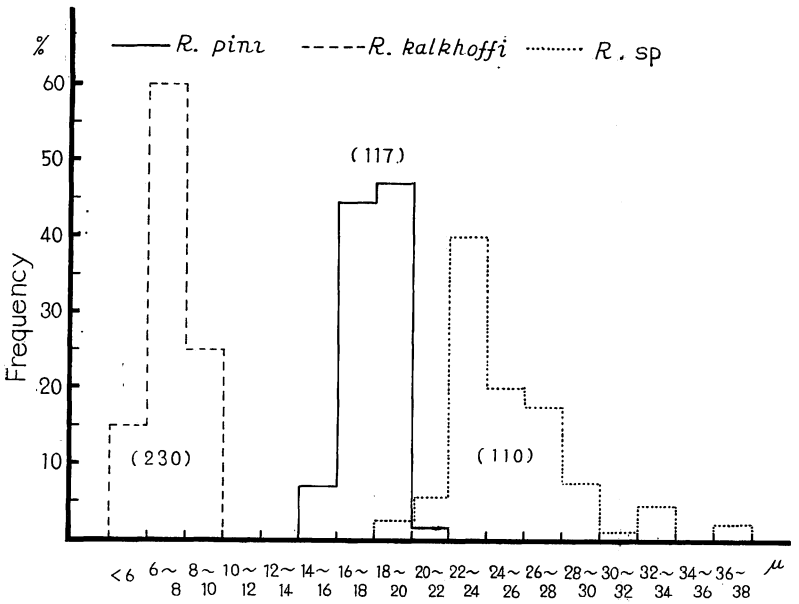

Figure 2. Histogram of length of conidia in three Japanese species of the genus *Rhizosphaera* (Total numbers of measured conidia)

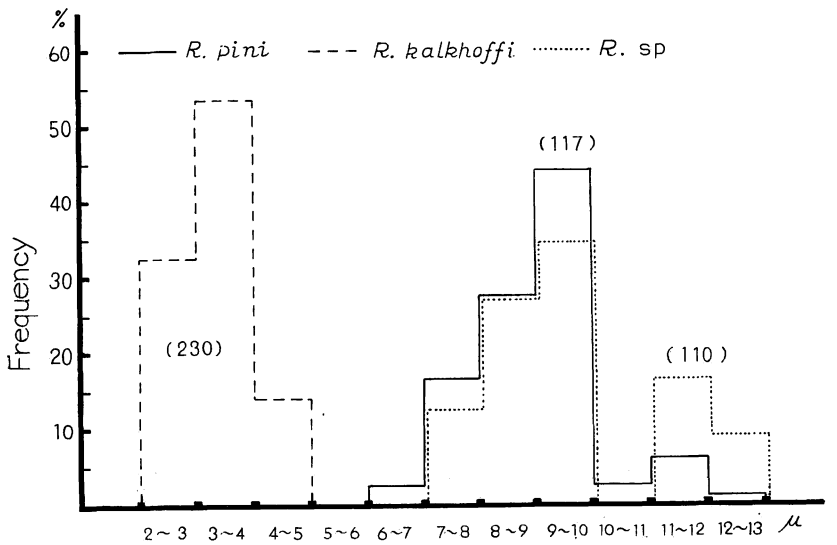

Figure 3. Histogram of width of conidia in three Japanese species of the genus *Rhizosphaera* (Total numbers of measured conidia)

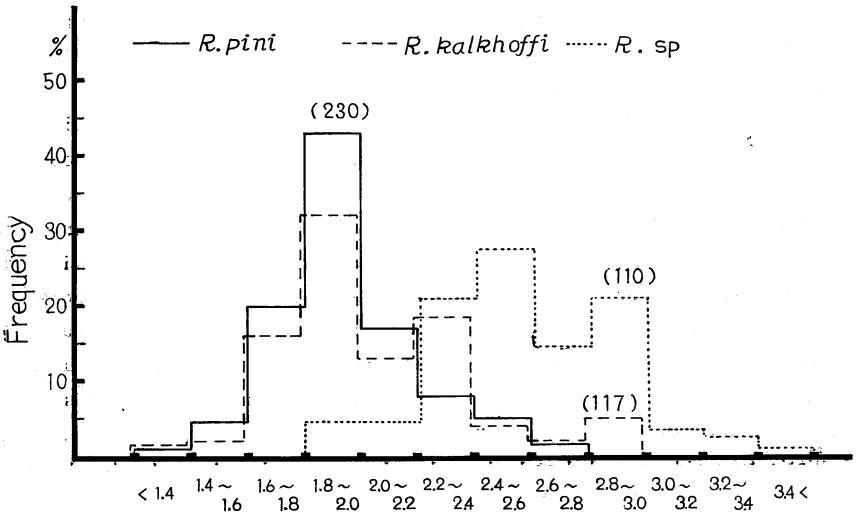

Figure 4. Histogram of length/width ratio of conidia in three Japanese species of the genus *Rhizosphaera* (Total numbers of measured conidia)

cultural and life historical studies between *Rhizosphaera pini* (Cda.) Maubl. and the fungus of group III have been conducted. Monosporous culture from the fungus collected on *Pinus pumila*, one of the materials of group III, distinctly differs from that of *Rhizosphaera kalkhoffii* Bub. (Plate 4, H), but it is still uncertain whether it also differs from that of *R. pini* or not, owing to the failure to obtain monosporous culture of the latter. As noted above, genetic connection between *Phaeocryptopus nudus* (Peck) Petr. and *Rhizosphaera kalkhoffii* Bub. was denied by the comparative cultural studies[25] (Plate 4, H). The relationship between *Phaeocryptopus nudus* and *Rhizosphaera* species other than *R. kalkhoffii* has not yet been critically investigated fully, so it seems to be necessary to supplement present knowledge by further morphological and life-historical studies based on many fresh materials and culture from them. Therefore, materials of group III presented in Table 2 are treated here as an undetermined species of genus *Rhizosphaera*.

1. ***Rhizosphaera pini*** **(Corda) Maublanc**, charact. emend. ——(Plate 1, A～E; 2, A～C; Figure 5)——Bull. Soc. Myc. France 23 : 171, 1907; Wilson & Waldie, Trans. Brit. Myc. Soc. 13 : 151～152, 1928; Grove, Coelomycetes I, p. 141～142, 1935

Synonym : *Coniothyrium pini* Corda, Icon. Fung. IV, p. 38, t. VIII, f. 105, 1840

Sacidium pini (Cda.) Fries, Summ. Veget. Scand., p. 420, 1849

Leptothyrium pini (Cda.) Saccardo, Syll. Fung. 3 : 627, 1884

Rhizosphaera abietis Mangin et Hariot, Bull. Soc. Myc. France 23 : 56～57, 1907

Mycelium grows within the blighted needles which are grayish brown to reddish brown in colour, aggregates beneath stoma and forms a ball-like hyphal mass which is brown to greenish brown in colour and 20～45×33～45μ in size. From such hyphal mass a few slender hyphal strand grow upward, penetrate the stoma and form a stalk-like bundle, 45～63×10～13μ in size, in the stomatal cavity. Outer hypha of the bundle continuously grows up and specializes to the pycnidial wall. Inner hypha branches sparsely and finally fills within the pycnidium. At this stage, many small black dots are macroscopically recognized on the

blighted needles in a few regular rows equivalent to those of stomata. Under a hand lens, pycnidium is found to be a small black globule with white resinous mass on it, but becomes pale to yellowish brown in its colour under moist condition. Pycnidium is globular to subglobular, somewhat flattened at the lower part, 50～65×55～125μ in size, and has stalk- and ball-like hypostroma at its base. Hypostroma is more distinctly visible on the host plant having thick epiderm and wide stomatal cavity. Pycnidial wall is constituted from a layer of brown hypha. Inner part of pycnidium is at first constituted from prosenchymatous brown hyphae. With its maturity, conidia are born directly on the inside wall of pycnidium and wall of inner hyphae, and, these hyphae are gradually dissolved. Consequently, the whole pycnidium is filled with many hyaline conidia instead of brown hyphae. Ostiole is lacking, but pycnidium breaks out irregularly at its upper part. Conidiophore is also lacking, although in some cases the rest of dissolving inner hyphae remains and is incorrectly taken to be conidiophore. Pycnospore is hyaline, rarely become brownish with age, unicellular, elliptic to ovoid, rounded at both ends, often somewhat irregular in shape, 15.0～21.5×7.0～12.5μ, usually 16～20×7～10μ in size.

Host : On blighted needles of *Abies pectinata* DC.[16)31)34)] *A. grandis* LIND.[6)34)35)] *A. fraseri* LIND.[1)], *A. veitchii* LIND. (Shirabe), *Pinus* sp.[26)] and *Tsuga diversifolia* MAXIM. (Kome-tsuga).

Distribution : Europe (France[6)16)31)], Britain[6)20)35)], Germany[6)], Austria[6)31)], Czechoslovakia[3)31)], Italy[6)31)]), North America (United States[1)31)]), and Asia (Japan).

Material : *Abies pectinata*——Ambert, France, II-30, 1905, by M. BREVIER (Para-type); Vorgu, France, IV-, 1908, by M. MANGIN. *Abies veitchii*——Narusawa, Yamanashi Pref., VI-22,

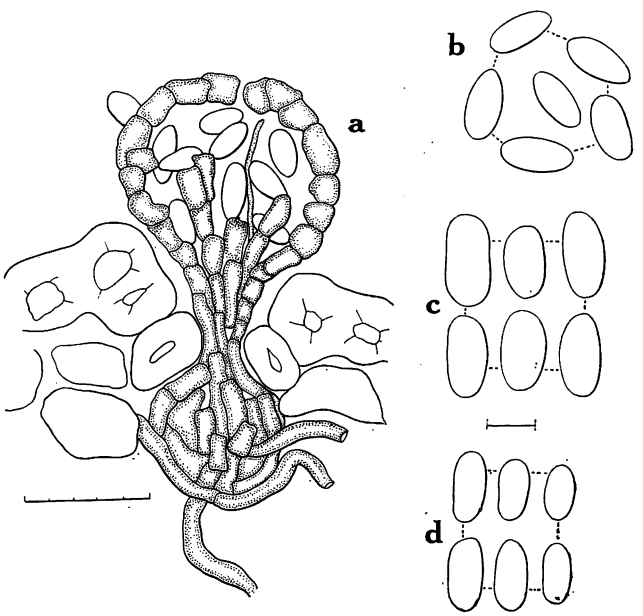

Figure 5. *Rhizosphaera pini* (CDA.) MAUBL.
a : Pycnidium having hypostroma which constitutes of stalk-like and ball-like hyphal tissue (on *Abies veitchii* LIND.) (⊔⊔⊔⊔ 50μ)
b : Conidia produced on *Abies veitehii* LIND. (⊔—⊔ 10μ)
c : Conidia produced on *Tsuga diversifolia* MAX.
d : Conidia produced on *Abies pectinata* DC.

1966, by T. KOBAYASHI & T. UOZUMI; Gotenba, Shizuoka pref., X-20, 1966, by M. SANO. *Tsuga diversifolia*——Narusawa, Yamanashi Pref., VI-22, 1966, by T. KOBAYASHI & T. UOZUMI.

Note : In Japan this species was found in the high mountain region and not on pines grown in lowland areas as shown in Table 2. No instance of serious damage caused by the present *Rhizosphaera* in Japan has been recorded, though at first this fungus attracted the attention of French mycologists in causing serious needle blight of *Abies pectinata*. Several attempts to isolate this fungus were unsuccessful, so to verify PETRAK's presumption that this species is the conidial stage of *Phaeocryptopus nudus* (PECK) PETRAK remains the object of future study.

2. ***Rhizosphaera kalkhoffii*** BUBÁK——(Plate 2, D～F; 3, A～D; Figure 6)——Ber. Deut. Bot. Ges. 32 : 188～190, 1914; LUYK, Ann. Myc. 21 : 133～142, 1923; WILSON & WALDIE, Trans. Roy. Scott. Arboric. Soc. 40 : 34～36, 1926; GROVE, Coelomycetes I, p. 141～142, 1935; WATERMAN, Phytop. 37 : 507～511, 1947

Synonym : *Sphaeronema pini* DESMAZIÈRE, Ann. Sci. Soc. Nat. 3, Ser. X, p. 347, 1848
Phoma pini SACCARDO, Syll. Fung. 3 : 101, 1884
Sclerophoma pini (DESM.) HÖHNEL, Sitzb. Akad. Wiss. Wien, Math. Nat. Kl. Abt. I, Bd. 118 : 1234, 1916
Rhizophoma pini (DESM.) PETRAK et SYDOW, Rept. Spec. Nov. Regni Veget. Beih. XLII, p. 472～474, 1927
Rhizosphaera radicate NAOUMOFF, Bull. Soc. Myc. France 30 : 385, 1914

General features of this species closely resemble those of *Rhizosphaera pini* (CDA.) MAUBL., the type species of this genus, so it is very difficult to distinguish them macroscopically or under a hand lens one from the other. Pycnidium is 50～95×50～115μ, and has stalk- and ball-like hypostroma which is 45～58×18～23μ and 40～58×30～50μ in size, respectively, at its base. Ostiole is lacking, but appears irregularly at the upper part of pycnidium. Conidiophore is absent. Conidia are produced directly on the inside wall of pycnidium and wall of inner hyphae. Inner hyphae dissolve with the maturity of pycnidium. Finally, pycnidium is filled with many pycnospores. Conidium is hyaline, elliptic to ovoid, unicellular, 5.0～10.0×3.0～5.0μ, usually 6～8×3～4μ in size.

Host : On blighted needles of *Picea excelsa* LINK[3)26)34)], (Oshu-tohi), *P. pungens* ENGELM.[1)-6)10)15)18)27)32)], *P. pungens* var. *argentea*[3)6)18)24)34)35)], *P. nigra* LINK[27)34)], *P. sitchensis* TRAUT. et MEYER[6)18)27)34)], *P. glauca*[6)18)27)34)], *P. orientalis* CARR.[28)34)], *P. abies*[18)28)33)], *P. schrenkiana* FISH. et MEYER[27)34)]. *Abies pectinata* DC.[6)26)34)], *A. nobilis* LIND.[6)18)34)], *A. sibirica* LEDEB.[19)26)], *Pseudotsuga douglasii* CARR.[34)], *Pinus austriaca* HOESS.[6)18)34)], *P. montana* MILL.[6)34)], *P. strobus* L.[6)], *P. mugo* POIR.[18)28)], *P. nigra* ARN.[28)], *P. densiflora* SIEB. et ZUCC.[4)12)18)29)30)] (Aka-matsu), *P. thunbergii* PARL.[4)12)18)29)30)] (Kuro-matsu), and *P. excelsa* WALL. (Himaraya-goyo).

Distribution : Europe (Russia[19)26)], Austria[3)], France[3)], Germany[6)], Czechoslovakia[8)], Norway[10)24)], Britain[6)20)21)27)34)], Ireland[6)34)], Netherland[20)27)33)]), North America(United States[1)32)], Canada[15)]), and Asia (Japan[11)]).

Material : *Pinus densiflora*——Meguro, Tokyo, VII-18, 1966, by K. TANAKA; Chiba-city, Chiba Pref., VI-25, 1965, by T. UOZUMI; Fujiyoshida, Yamanashi Pref., VII-8, 1965, by A. ENDO; Minori, Ibaraki Pref., VIII-, 1965, by H. KONDO. *P. thunbergii*——Meguro, Tokyo, VII-18, 1966, by K. TANAKA; Chiba-city, Chiba Pref., VI-25, 1965, by T. UOZUMI; Uchihara, Ibaraki Pref., VIII-, 1965, by H. KONDO, *Pinus excelsa*——Mito, Ibaraki Pref., X-3, 1966, by T. KOBAYASHI.

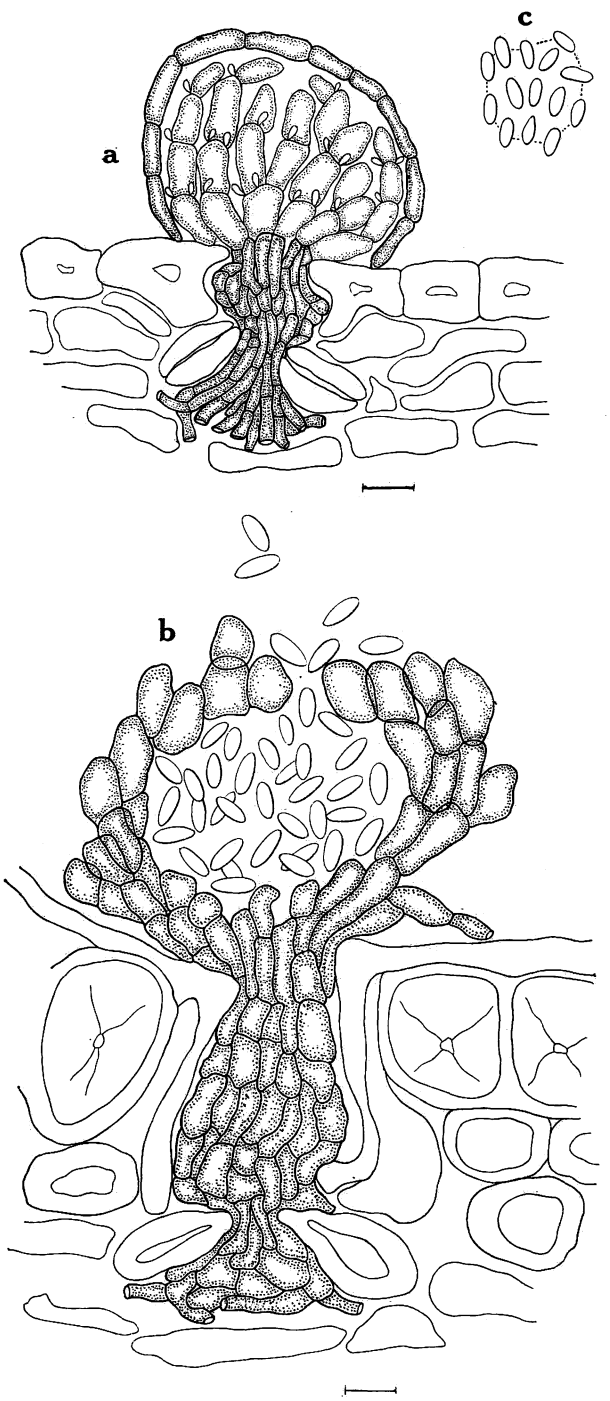

Figure 6. *Rhizosphaera kalkhoffii* Bubák
a: Immature pycnidium on *Pinus densiflora* S. et Z. showing young conidia produced directly on the wall of inner hyphae
b: Mature pycnidium on *Pinus thunbergii* Parl.
c: Conidia produced on *Pinus densiflora* S. et Z.
(⟵ 10μ)

Note: The present fungus has commonly been reported to be a causal agent of the needle blight of spruce, especially of *Picea pungens*, in Europe and North America, though it has wide host range on various conifers including pines. However, biology of this fungus has not yet been critically investigated fully. Rohde[25] and Waterman[32] obtained successfully its culture and some cultural characters on agar media were noted by them. Waterman[32] and Peace[20] pointed out the importance in determining pathogenicity of the present species as applying to coniferous plants, although they obtained only negative results. In Japan, the present fungus was first recorded by Sudo[29][30] who examined successive occurrence of the needle blight of pines caused by it in a limited area of the San-in District. In a case of epidemic outbreak of the pine needle blight during the year of 1965, Chiba[4] and Kondo[12][13] discussed the predisposing factors in pines to the present *Rhizosphaera* based on their analytical examination of the diseased stands. Kondo[12][13] also noted different susceptibility among many Japanese pine clones pertaining to the needle blight. Chiba[4] and Peace[20] suggested conclusively that infection of fungus and/or development of the disease may be stimulated by abnormal water relation onto pine or spruce brought by drought.

The present fungus was easily isolated. Two ways of germination were generally

observed. In the first, its conidium multiplicates in a budding way and the fungus gradually increases the number of secondary conidia by repeated multiplication. Hyphae grow from the mass of secondary conidia. The other case is the normal type of germination, i.e. germ-tube is born on conidium directly. In either case colony finally shows similar macroscopic appearance. Growth of colony is fairly fast and mucous conidial drops are scatteredly produced on blackish mycelial colony. Conidia are luxuriantly produced on the cultural hyphae without conidiophore as illustrated by WATERMAN[32]. Culture of the present fungus differs much from that of *Phaeocryptopus nudus* (PECK) PETR. as pointed out previously by ROHDE[25] (Plate 4, H).

3. ***Rhizosphaera* sp.**——(Plate 3, E, F; 4, A～E; Figure 7)

General features of this undetermined species of genus *Rhizosphaera* bear close resemblance to those of two *Rhizosphaera* described above. It is very difficult to distinguish these three *Rhizosphaera* macroscopically, as they differentiate only by microscopic examination one from another. Pycnidium is 65～85×70～100μ, and has stalk- and ball-like hypostroma, 55～70μ in length and 20～38×20～50μ in size, respectively. Ostiole is lacking. Conidiophore is absent. Pycnospore is produced directly on the inside wall of pycnidium and mass of inner hyphae. These inner hyphae dissolve as the pycnidium age and pycnidium is finally filled with many

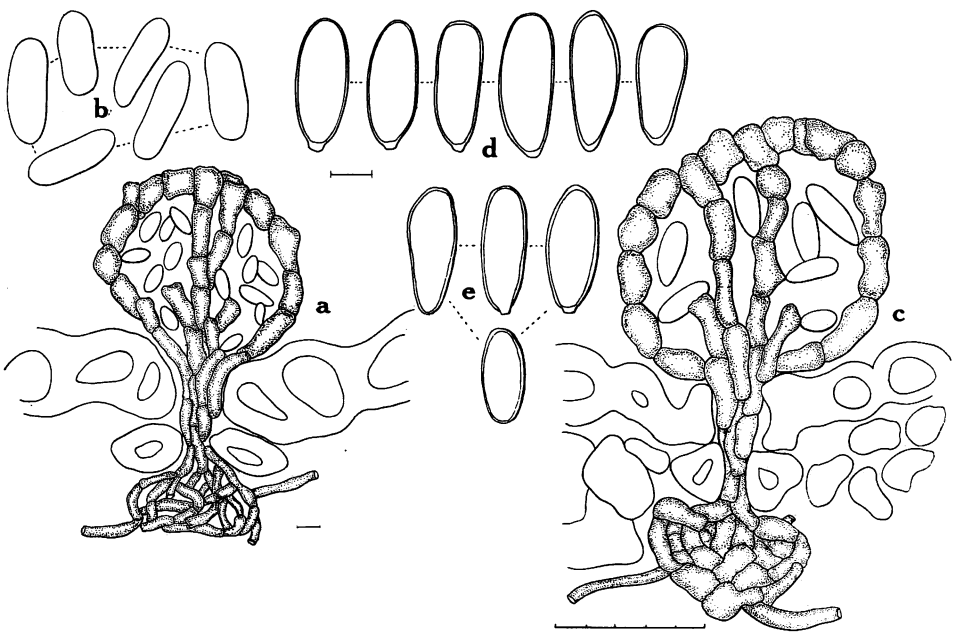

Figure 7. *Rhizosphaera* sp.

a : Pycnidium on *Abies mariesii* MAST.
b : Conidia on *Abies mariesii*
c : Pycnidium on *Pinus pumila* REGEL.
d : Conidia on *Pinus pumila*
e : Conidia on culture isolated from a material on *Pinus pumila*
(⊔⊔⊔⊔=50μ, ⊔=10μ)

conidia. Conidium is hyaline, elliptic to cylindric, unicellular, 20～37.5×7.5～12.5μ, mostly 22～28×8～12μ.

Host and **material**: On blighted needles of *Abies mariesii* MAST. (Aomori-todomatsu)—— Narusawa, Yamanashi Pref., IX-, 1960, by Y. ZINNO, and *Pinus pumila* REGEL (Hai-matsu), Miyata, Nagano Pref., IX-, 1966, by T. KUBO.

Note: As mentioned earlier, this undetermined group is separable from the hitherto known species of the genus *Rhizosphaera* by its longer conidia. Monosporous culture from the fungus on *Pinus pumila* was obtained successfully. Dark brown-coloured colony developed on potato-sucrose agar. Its growth is comparatively slow, and small black pycnidia are scatteredly produced on the colony, then mucous conidial masses ooze out from them. Conidia produced on culture are quite identical with those on the host plant (Table 2, Figure 7 and Plate 4, F, G). It is worthy of note that the culture of *Phaeocryptopus nudus* (PECK) PETR. is quite similar to that of this isolate from *Pinus pumila* not only in its macroscopic appearance but also in the size of conidia produced on it. Verification of life-historical relationship between these two fungi remains as an important problem for future study and solution.

4. ***Rhizosphaera oudemansii*** **MAUBLANC**, Bull. Soc. Myc. France 23 : 173, 1907

Synonym : *Sacidium abietis* OUDEMANS, Contrib. Fl. Myc. Pays-Bas XVII, P. 333, 1900; SACCARDO, Syll. Fung. 16 : 992, 1902

Note: Among the hitherto known species of genus *Rhizosphaera*, *R. oudemansii* MAUBL. has been recorded only once from the Netherlands[26]. The author has not seen either its specimen or its original description and figure. According to MAUBLANC[17], however, general features and figure given by OUDEMANS as Sac*idium abietis* OUD. are quite identical with those of *Rhizosphaera pini* (CDA.) MAUBL. except for its conidia being smaller than the latter, as shown in Table 1. So, he transferred it to the genes *Rhizosphaera* from *Sacidium*, and newly named it as *R. oudemansii* MAUBL. to avoid confusion with *R. abietis* MANG. et HAR., a synonym of *R. pini* (CDA.) MAUBLANC. Judging from his treatment and from the description by SACCARDO[26], it seems highly probable that this fungus is maintained in the genus *Rhizosphaera*.

Summary

1. Justification of the genera *Rhizosphaera* MANGIN et HARIOT and *Rhizophoma* PETRAK et SYDOW was critically reexamined. The genus *Rhizophoma* lost its independency followed by the revision of misdescription of the old genus *Rhizosphaera* made by MANGIN and HARIOT.

2. Nomenclature of the species name *pini* in the type species of both genera is of *Rhizosphaera pini* (CDA.) MAUBL. described in 1840. The species name of *Rhizosphaera kalkhoffii* BUB. is, therefore, revived for *Rhizophoma pini* (DESM.) PETR. et SYD., first described in 1848, under the genus *Rhizosphaera*.

3. In the course of identification on Japanese materials, it was found that three species belonging to the genus *Rhizosphaera* were distributed in our country, two of which were the hitherto known species, namely *R. pini* (CDA.) MAUBL. and *R. kalkhoffii* BUBÁK. At the same time, *Rhizosphaera radicata* NAOUM. was treated as a synonym of *R. kalkhoffii* BUBÁK.

4. On the other species identification was retained here and its morphological and cultural characters were briefly noted. It was pointed out that the culture of *Phaeocryptopus nudus* (PECK) PETR. was quite similar to that of this undetermined *Rhizosphaera*, and further

study to verify the genetic relation between them is required.

5. Judging from the critical notes made by MAUBLANC and SACCARDO, *Rhizosphaera oudemansii* MAUBL. may remain to be the fourth species in this genus.

Literature

1) (Anonymous) : Index of plant diseases in the United States. U. S. Dept. Agr., Agr. Handb. No. **165**, (1960).

2) AINSWORTH, G. C.: AINSWORTH & BISBY's dictionary of fungi. 5th. edit., Commonw. Myc. Inst., London, (1961).

3) BUBÁK, K. F.: Eine neue *Rhizosphaera*. Ber. Deut. Bot. Ges. **32** : 188～190, (1914).

4) CHIBA, O.: On the sooty needle blight of pines (in Japanese). For. Protect. News (Tokyo) **14** : 256～260, (1965).

5) CLEMENTS, F. E. & SHEAR, C. L.: The genera of fungi. 496pp. WIILSON Co., New York, (1931).

6) GROVE, W. B.: British stem and leaf fungi (Coelomycetes) Vol. **1**. Sphaeropsidales. Cambridge Univ. Press, London, (1935).

7) HÖHNEL, F. von : Fragment zur Mykologie 965. Sitzb. Keis. Akad. Wiss. Wien, Mathem. Naturw. Kl. I, Bd. **125** : 63, (1916).

8) ——— : Fungi Imperfecti. Beiträge zur Kenntnis derserben. 3. Uber *Phoma penicillatum* FUCKEL. Hedwigia **59** : 239～240, (1918).

9) ——— : Ditto. 37. Uber *Chaetopyrena hesperidum* PASSERINI. *Ibid.* **60** : 131～132, (1919).

10) JØRSTAD, I.: Innberetning fra statsmykolog Ivar JØRSTAD om soppskydommer pa skogtraerne i arene 1926～1930. Beretning om det Norske Skogmesen 1930 : 78～96, (1931).

11) KOBAYASHI, T.: Pine sooty needle blight and its causal fungus (abs.) (in Japanese), Ann. Phytop. Soc. Japan 32 : 315, (1966).

12) KONDO, H.: Needle blight disease of pines caused by a species of the genus *Rhizophoma*: Present status of the disease in Ibaraki Prefecture and some observations on the different susceptibility among the pine clones (in Japanese). For. Protect. News (Tokyo) **14** : 208～210, (1965).

13) ——— : Different susceptibility in the Japanese pine clones selected for genetics onto the sooty needle blight (in Japanese). *Ibid.* **15** : 280～283, (1966).

14) LUYK, A. van : Uber einige Sphaeropsideae und Melanconieae auf Nädelhölzern. Ann. Myc. **21** : 133～142, (1923).

15) MACRAE, Ruth & CONNERS, I. L.: Needle blight (*Rhizosphaera kalkhoffii* BUBÁK). Ann. Rept. Canada Plant Dis. Surv. **20** (1940) : 87, (1941).

16) MANGIN, M. & HARIOT, P.: Sur le maladie du rouge du sapin pectiné dans la foret de la Savine (Jura). Bull. Soc. Myc. France **23** : 53～56, (1907).

17) MAUBLANC, M. A.: Sur la maladie des sapines produit par le *Fusicoccum abietinum*. *Ibid.* **23** : 160～173, (1907).

18) MOORE, W. C.: British parasitic fungi. Cambr. Univ. Press, London, (1959).

19) NAOUMOFF, N. : Flore mycologique de la Russie. Bull. Soc. Myc. France **30** : 385, (1914).

20) PEACE, T. R. : Pathology of trees and shrubs with special reference to Britain. Oxf. Univ. Press, London, (1962).

21) ——— & MURRAY, J. S.: Forest pathology, in Rept. For. Res. for 1956, p. 64, (1957), and

for 1956, p. 65, (1958).

22) Petrak, F.: Ubersicht und Kritik der bisher genannten Sclerophomaceen-Gattungen, in Mykologische Notizen VI. Ann. Myc. **22** : 87～104, (1924).

23) ———: Beiträge zur Systematik und Phylogenie der Gattung *Phaeocryptopus* Naoumov. *Ibid.* **36** : 9～26, (1938).

24) ——— & Sydow, H.: Die Gattungen der Pyrenomyzeten, Sphaeropsideen und Melanconieen. I Teil. Die phaeosporen Sphaeropsideen und die Gattung *Macrophoma*. Rept. Spec. Nov. Regni Veg. Beih. **42** : 472～474, (1927).

25) Rohde, T.: Uber die "schweizer" Douglasienschütte und ihren vermuten Erreger *Adelopus* spec. Mitt. Forstw. u. Forstwiss. 8 (4) : 487～514, (1937).

26) Saccardo, P. A.: Sylloge Fungorum **3** : 101, 627, (1884); **16** : 992, (1902); **22** : 874, 916, (1913); **25** : 80, 168, (1931).

27) Spaulding, P.: Diseases of North American forest trees planted abroad. U. S. Dept. Agr., Agr. Handb. No. **100**, (1956).

28) ———: Forest diseases of forest trees of the world. *Ibid.* No. **197**, (1961).

29) Sudo, Y.: Preliminary report of pine needle blight caused by a species of the genus *Rhizophoma* (in Japanese). Rept. Meet. Kansai Div. Jap. For. Soc., p. 71, (1963).

30) ———: Pine needle blight caused by a species of the genus *Rhizophoma* (in Japanese). For. Protect. News (Tokyo) **13** : 224～226, (1963).

31) Vuillemin, M. P.: Quelque champignons arboricoles nouveaux ou peu connus. Bull. Soc. Myc. France **12** : 33～44, (1896).

32) Waterman, Alma M.: *Rhizosphaera kalkhoffii* associated with a needle cast of *Picea pungens*. Phytop. **37** : 507～511, (1947).

33) Went, J. C.: Verslag van de onderzoekingen verricht in 1946 voor het Comite inzake bestudeering en bestrijding van de iepenziekte en andere boomziekten, uitgevoerd op het Phytop. Labor. "Willie Commelin Scholten" te Baarn. Meded. **42**, 12pp, (1947) (For. abs. **9**, No. 2560).

34) Wilson, M. & Waldie, J. S. L.: *Rhizosphaera kalkhoffii* Bubák, as a cause of defoliation of conifers. Trans. Brit. Roy. Scott. Arbor. Soc. **40** : 34～36, (1926).

35) ——— & ———: Notes on new or rare forest fungi. Trans. Brit. Myc. Soc. **13** : 151～156, (1928).

Explamation of plates

Plate 1

Rhizosphaera pini (Corda) Maublanc

A: Blighted needles showing minute black pycnidia on the under leaf surface (A piece of PARATYPE specimen on *Abies pectinata* DC. deposited in France). ×1.2

B: Do. On *Abies veitchii* Lind. ×1.3

C: Enlarged needles showing a number of pycnidia arranged into two streaks. On *Tsuga diversifolia* Max. ×2.5

D: Do. On *A. veitchii*. ×2.5

E: Closed masses of pycnidia having white resinous substance on them. On *A. pecticata*. ×15

F: Pycnidium having apparent stalk- and ball-like hypostroma on *A. pectinata*. Stained by KOH. ×370

Plate 2

Rhizosphaera pini (CORDA) MAUBLANC

A: Pycnidium on *Abies veitchii* LIND. ×370

B: Conidia on *A. pectinata* DC. ×500

C: Conidia on *A. veitchii*. ×500

Rhizosphaera kalkhoffii BUBÁK

D: Diseased seedlings of pines in Asakawa nursery. (Photograph by Mr. T. UOZUMI)
Front row: Heavily blighted seedlings of *Pinus densiflora* SIEB. et ZUCC.
Back row: Seedlings of *P. thunbergii* PARL. infected very slightly

E: Mature pycnidia broken out irregularly on their upper wall. On *P. thunbergii*. ×210

F: Do. On *P. densiflora*. ×210

Plate 3

Rhizosphaera kalkhoffii BUBÁK

A: Heavily blighted needles of *Pinus densiflora* SIEB. et ZUCC. (Photograph by Mr. UOZUMI). ×1/2

B: Closed mass of pycnidia forming regular row. On *P. densiflora* (Photograph by Mr. T. UOZUMI). ×25

C: Conidia on *P. densiflora*. ×500

D: Conidia on *P. thunbergii*. ×500

Rhizosphaera sp.

E: Blighted needles of *Abies mariesii* MAST. showing minute black pycnidia on the under leaf surface. ×2

F: Blighted needles of *Pinus pumila* REGEL. ×1.5

Plate 4

Rhizosphaera sp.

A: Closed mass of pycnidia forming regular row of black globules. On *Abies mariesii* MAST. ×20

B: Do. On *Pinus pumila* REGEL. ×15

C: Pycnidium on *Abies mariesii*. ×370

D: Pycnidium on *Pinus pumila*. ×370

E: Conidia on *Abies mariesii*. ×500

F: Conidia on *Pinus pumila*. ×500

G: Conidia produced on culture isolated from the conidium on *Pinus pumila*. ×500

Test-tube cultures of *Rhizosphaera* and *Phaeocryptopus* (After a month on potato-sucrose agar). ×2/3

H: Left: *Rhizosphaera kalkhoffii* BUBÁK isolated from *Pinus densiflora* S. et Z.
Middle: *Rhizosphaera* sp. isolated from *Pinus pumila* REGEL.
Right: *Phaeocryptopus nudus* (PECK) PETRAK isolated from *Abies homolepis* S. et Z. (two colonies).

針葉樹すす葉枯病菌の属および種の再検討

小　林　享　夫[1]

（要　　旨）

1965 年の春から夏にかけて，東北南部から甲信，東海地方の広範囲にわたって，天然生あるいは人工植栽マツ林に一種の葉枯性病害が大発生した。従来この葉枯性病害は関東あるいは山陰地方において局部的な発生が知られていたのみで，今回のような広域大発生の記録はまったくなかった。したがって本病および病原菌に関する知見はほとんどなく，病原と考えられる菌の同定もなされず，たんに *Rhizophoma* 属あるいは *Rhizosphaera* 属の一種であろうとされていたにすぎない。そこでこの広域大発生を機に，本病および病原菌の調査研究がとりあげられ，筆者は病原菌の所属の同定を担当して，内外の標本および文献によって調査を開始した。

調査にあたってはまず日本各地産のマツ類標本を収集するとともに，マツと相似た病標徴をしめす他の針葉樹の標本をも採集につとめた。これらの新鮮な標本および保存標本によってその形態調査をおこなった結果，わが国には，同一属に属し，たがいに相似た病標徴を呈する菌が少なくとも 3 種類あることがわかった（Table 2, Figure 1～4）。これらの菌は外観的にはまったく区別することが難しく，おもに分生胞子の大きさによって類別される。

この 3 種の菌は，文献によって記載のみから判断すると，Petrak と Sydow[24] が 1927 年に *Rhizosphaera* 属から分離独立させた，*Rhizophoma* 属とその特徴がまったく一致する。元来，*Rhizosphaera* 属は 1907 年 Mangin と Hariot[16]によって *Abies pectinata* DC. 上の菌をもとにして創設された不完全菌類球殻菌科の一属である。*Rhizosphaera* 属は柄子殻下部に気孔を貫通する柄と気孔直下の菌糸塊（近代分類用語では両者をあわせて hypostroma 殻下子座という）を有するという特徴によって新設された。Mangin らはこの形態を気球になぞらえ，菌糸塊を吊籠，柄を吊鎖，柄子殻を浮球にたとえたが，同時に分生胞子形成方法についてもふれ，ひとつは柄子殻内層の短い分生子梗上に生じ，いまひとつは柄子殻下部からのびる長細い菌糸状の分生子梗上に頂生するとした。かれらは，その挿図(第 5 図)にはこの両型の分生子梗を描いたが，正式の属の記載文中には前者の短い分生子梗しかのべていない。そのご本属には 3 種が加えられ，現在 4 種が知られている。Wilson と Waldie[35]とはイギリス産の本属菌 2 種についてのべ，本属のタイプ種 *Rhizosphaera pini* (Cda.) Maubl. の英国産標本には Mangin らのいう細長い分生子梗はみられず，分生胞子は柄子殻壁から直接芽生すること，いまひとつの *R. kalkhoffii* Bub. はまったく分生子梗を欠き，この点と分生胞子の大きさのちがいが両者の類別点であることを指摘した。Petrak らは，Wilson らが種の類別点とした分生胞子形成方法のちがいを重視し，属を分ける価値を認めて *Rhizosphaera kalkhoffii* Bub. をもとにして *Phizophoma* 属を分離独立させたのである。

ところが Wilson らがのべたように，*Rhizosphaera* 属のタイプ種において，分生子梗の存在をみてい

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るのは創設者 MANGIN らのみであること，また PETRAK[22] が指摘したように，分生子梗なしに分生胞子を芽生もしくは内生する柄子殻菌類群では，しばしば成熟過程において溶失直前の菌糸または細胞の膜壁が残って，あたかも分生子梗と見誤まられやすいこと，さらに PETRAK らは *Rhizosphaera pini* (CDA.) MAUBL. について標本からではなく MANGIN らの記載から分生子梗の存在を認めて，分生子梗を欠く *R. kalkhoffii* BUB. と属を異にしうるとしていること，などから，本来この両属の菌が果たしてその分生胞子形成方法に本質的差異があるかどうかに疑問がもたれた。

この疑問を解消するためにおこなったフランス，パリの国立自然科学博物館保存の *Rhizosphaera pini* (CDA.) MAUBL. の paratype をふくむ標本2点の調査は，分生胞子が殻内菌糸細胞膜および柄子殻内壁から直接芽生し，分生子梗をもたないことをしめし，また溶失途中の殻内菌糸の膜のみが MANGIN らの描いた図のように残っているのも確認され，MANGIN らの属の記載のうち分生子梗に関する部分は誤まりであることがあきらかになった。したがって，*Rhizosphaera* 属の特徴は一部修正され，同時に，これによって PETRAK らが *Rhizophoma* 属を独立させた主たる理由は消失するので，*Rhizophoma* 属はふたたび *Rhizosphaera* 属に統合され，その異名となる。

この両属はタイプ種がそれぞれ同じ種名 *pini* を有するので，同一属に統合する場合いずれかの種名はそのまま用いられない。*Rhizosphaera pini* (CDA.) MAUBL. は 1840 年に記載された *Coniothyrium pini* CORDA にもとづいており，一方 *Rhizophoma pini* (DESM.) PETR. et SYD. は 1848 年に記載された *Sphaeronema pini* DESMAZIÈRE をもとにしている。したがって先命権は *Rhizosphaera pini* にあり，*Rhizophoma pini* は *Rhizosphaera* 属の下では *pini* の種名を用いることができない。そこで，この種の異名のなかで2番目に古い種名である *Rhizosphaera kalkhoffii* BUBÁK がふたたび復活する。

一方 CLEMENTS と SHEAR[5] は *Ectosticta* SPEG. 属と *Sclerochaeta* HÖHN. (=*Chaetopyrena* PASS.[9]) 属を *Rhizosphaera* 属の異名として処理している。筆者はこの両属菌の標本をみていないが，いずれも広葉樹にのみ生ずること，記載からすると両者ともまったく表生の柄子殻を生じ，後者はさらに柄子殻に剛毛があること，などから本報においてはこの両属を *Rhizosphaera* 属の異名とすることは保留した。

さきにのべた日本産の本属菌3種のうち2種は既知の種に該当し (Table 1, 2, Figure 1)，それぞれ *Rhizosphaera pini* (CDA.) MAUBL. および *R. kalkhoffii* BUB. と同定された。あとの1種は分生胞子が大きく既知種に該当するものがない。しかしまだ資料が少ないこと，ハイマツ上の標本からの単胞子培養が *Phaeocryptopus nudus* (PECK) PETRAK の培養に似ており，後者が培養上に生ずる分生子の大きさが前者のそれに一致し，この両者の同根関係についての検討が必要であることから，ここではこの *Rhizosphaera* 属菌の種名の決定は留保し，たんに *Rhizosphaera* 属の一種としておく。

NAOUMOFF がロシアから報告した *Rhizosphaera radicata* NAOUM. は，LUYK[14] や PETRAK ら[24]が指摘し，また Table 1, Figure 1 にみられるように，その形態が *Rhizosphaera kalkhoffii* BUB. によく一致するので，その異名として処理した。

オランダから OUDEMANS が報告した *Rhizosphaera oudemansii* MAUBL. は，はじめ *Sacidium abietis* OUD. として記載されたが，MAUBLANC[17]の再検査により *Rhizosphaera* 属に移され，同時に *R. pini* (CDA.) MAUBL. の異名である *R. abietis* MANG. et HAR. との種名の重複混乱をさけるため新たに命名されたものである。わが国には本種に該当するものがなく，またその原標本もみることができなかったが，MAUBLANC や SACCARDO[26] の報告から判断して *Rhizosphaera* 属の種と考えてよいものと思われる。

なお，本属菌の生活史に関し PETRAK ははじめその完全時代は多分 *Phaeocryptopus* 属であろうと想定した。これに対して ROHDE[25] は両属菌の分離培養をおこない，*Phaeocryptopus nudus* (PECK) PETR. および *P. gaeumanni* (ROHDE) PETR. と *Rhizosphaera kalkhoffii* BUB. および *R. pini* (CDA.) MAUBL. とのあいだには同根関係はないとした。ところが PETRAK[28] はふたたび RHODE の見解に反ばくし，ROHDE の培養比較実験は不完全であり疑わしいとして，*Rhizosphaera pini* は *Phaeocryptopus nudus* の大形分生胞子世代であり，*R. kalkhoffii* は小形分生胞子世代にほかならないと主張した。AINSWORTH と BISBY[2] の „菌類辞典" は PETRAK の説をそのままうけ入れている。PETRAK のこの ROHDE の培養実験に対する反ばくは一理あるところである*が，後半の仮説設定に対しては何らの具体的証拠をあげていない。筆者らの分離実験においては，少なくとも *Rhizosphaera kalkhoffii* BUB. と *Phaeocryptopus nudus* (PECK) PETRAK との間には，ROHDE の指摘と同様，まったく同根関係のないことがあきらかであった。しかし *Rhizosphaera kalkhoffii* 以外の種と *Phaeocryptopus* 属菌，*Phaeocryptopus nudus* 以外の種と *Rhizosphaera* 属菌とのあいだの同根関係の有無については，今後検討を必要とされる問題である。

以上のべてきた諸点を整理し，日本産の針葉樹類すす葉枯病菌の属，種名を次にしめし，終わりに本属菌の検索表を付す。

Rhizosphaera **MANGIN et HARIOT**, charac. emend., Bull. Soc. Myc. France **23** : 56, 1907; SACCARDO, Syll. Fung. **22** : 917, 1913; GROVE, Coelomycetes **I**, p. 141, 1935.

異名：*Rhizophoma* PETRAK et SYDOW, Rept. Spec. Nov. Regni Veget. Beih. **42** : 472, 1927.

1. ***Rhizosphaera pini*** **(CORDA) MAUBLANC**, charac. emend.,——(Plate 1, A～E, Plate2, A～C, Figure 5)——Bull. Soc. Myc. France **23** : 171, 1907; WILSON & WALDIE, Trans. Brit. Myc. Soc. **13** : 151～152, 1928; GROVE, Coelomycetes **I**, p. 141～142, 1935.

異名：*Coniothyrium pini* CORDA, Icon. Fung. Ⅳ, t. Ⅷ, f. 105, 1840

Sacidium pini (CDA.) FRIES, Sum. Veget. Scand., p. 420, 1849

Leptothyrium pini (CDA.) SACCARDO, Syll. Fung. **3** : 627, 1884

Rhizosphaera abietis MANGIN et HARIOT, Bull. Soc. Myc. France **23** : 53～68, 1907

寄主：*Abies pectinata* DC.[16)31)34)], *A. grandis* LIND.[6)34)35)], *A. fraseri* LIND.[1)], *Pinus* sp.[26)], シラベおよびコメツカの針葉に生ずる。

分布：欧州（フランス[6)16)31)]，イギリス[6)20)35)]，ドイツ[6)]，オーストリア[6)31)]，チェコスロバキア[3)31)]，イタリア[6)31)]），北米（アメリカ[1)31)]）およびアジア(日本)。

資料：*Abies pectinata* DC. 2 点（MANGIN の同定による，Paratype 1 点を含む），シラベ2点およびコメツガ1点。

記事：Table 2 にみられるように，わが国では亜高山地帯に分布し，低地のマツ類にはみとめられなかった。欧州ではおもに旱害と関連してモミ類の葉枯（落葉）病菌として記録されている。数回試みた本菌の分離実験はいずれも不成功（不発芽）に終わり，培養の比較によって PETRAK の仮説を吟味することはできなかった。

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* この点については，*Phaeocryptopus* 属菌の培養的性質を詳述しなければならないので，ここでは深く論議しない。

2. ***Rhizosphaera kalkhoffii*** BUBÁK——(Plate 2 : D～E, Plate 3 : A～D, Figure 6)——Ber. Deut. Bot. Ges. **32** : 188～190, 1914; LUYK, Ann. Myc. **21** : 133～142, 1923; WILSON & WALDIE, Trans. Roy. Scott. Arb. Soc. **40** : 34～36, 1926; GROVE, Celomycetes **I**, p. 141～142, 1935; WATERMAN, Phytop. **37** : 507～511, 1947

異名：*Sphaeronema pini* DESMAZIÈRE, Ann. Sci. Soc. Nat. **3**, Ser. X, p. 347, 1848.

Phoma pini SACCARDO, Syll. Fung. **3** : 101, 1884

Sclerophoma pini HÖHN., Sitzb. Akad. Wiss. Wien, Math. Nat. Kl. Abt. I, Bd. **118** : 1234, 1916

Rhizophoma pini (DESM.) PETRAK et SYDOW, Rept. Spec. Nor. Regni. Veget. Beih. **42** : 472～474, 1927

Rhizosphaera radicata NAOUMOFF, Bull. Soc. Myc. France. **30** : 385, 1914

寄主：オウシュウトウヒ[3)26)34)], シトカトウヒ[6)18)27)34)], *Picea pungens*[1)6)10)15)18)27)32)], *P. pungens* var. *argentea*[3)6)18)24)34)35)], *P. nigra* LINK[27)34)], *P. glauca*[6)18)27)34)], *P. orientalis* CARR.[28)34)], *P. abies*[18)28)33)], *P. schrenkiana* FISH. et MEYER[27)34)], *Abies pectinata* DC.[6)26)34)], *A. nobilis* LIND.[6)18)34)], *A. sibirica* LEDEB.[19)26)], ダグラスファー[34)], *Pinus austriaca* HOUSS[6)18)34)], *P. mugo* POIR[18)28)], *P. nigra* ARN[28], モンタナマツ[6)34)], ストローブマツ[6)], アカマツ[4)11)12)13)29)30)], クロマツ[4)11)12)13)29)30)] およびヒマラヤゴヨウの針葉に生ずる。

分布：欧州(ロシア[19)26)], オーストリア[3)], フランス[3)], ドイツ[6)], チェコスロバキア[3)], ノルウエー[10)24)], イギリス[6)20)21)27)34)], アイルランド[6)34)], オランダ[20)27)33)]), 北米 (アメリカ[1)32)], カナダ[15]) およびアジア (日本[4)11)12)13)29)30)])。

資料：アカマツ4点, クロマツ4点およびヒマラヤゴヨウ1点。

記事：本菌は Table 2 にみられるように, 他の2種と異なり, 標高1,000m 以下の低地帯でマツ類にのみ産する。欧米では一般にトウヒ類の葉枯 (落葉) 病菌として知られている。本属既知種のなかでは最も分布, 寄主範囲が広く, 報文も比較的多いが, 生態等の詳しい調査研究はほとんどなされておらず, ROHDE[25)] と WATERMAN[32)] が分離培養をおこなって若干の培養的特徴をのべているほかは, PEACE[20)], WATERMAN[32)] がトウヒ類に接種実験をしたが陰性に終わったことを記述しているにすぎない。

わが国では周藤[29)30)]が山陰地方における本菌によるマツの葉枯性病害の発生状況をのべたのが最初の報告である。1965 年の大発生に際して千葉[4)], 近藤[12)]らは発生環境, 発病誘因等について調査観察結果を解析して報告し, 千葉によって本菌によるマツの病害がすす葉枯病と正式に命名された。近藤[12)18)]はさらにアカマツ, クロマツの多くのクローンを調べ, すす葉枯病罹病程度がクローン間で顕著な差のあることを報じた。さらに千葉[4)], PEACE ら[21)]によれば, マツ, トウヒなどの本菌による感染あるいは発病は, 乾燥等による樹体内水分の消費, 供給のアンバランスによって誘発促進されるらしいという。

本菌分生胞子は容易に発芽管を生じ, あるいは芽生増殖をおこなう。両発芽型のいずれからも, のちには同一の菌そうを発達する。発育は良好で, WATERMAN[32)] が図示したように, 菌糸より直接分生胞子を芽生し, 黒色菌そう表面に液滴状の分生胞子粘塊を散生あるいは一面に生ずる。*Phaeocryptopus nudus* (PECK) PETRAK の菌そうはこれとまったく異なり, ROHDE[25)] が指摘したように, 両者の間の同根関係は否定される。

3. ***Rhizosphaera* sp.**——(Plate 3 : E, F, Plate 4:A～G, Figure 7)

寄主および資料：アオモリトドマツおよびハイマツ各1点の針葉に生ずる。

記事：ここにあげた資料の菌は *Rhizosphaera pini* (Cda.) Maubl. とは分生胞子長あるいは分生胞子の長さと幅の比によって類別される(Table 2, Figure 1～4)。2つの資料のうち，ハイマツ上の分生胞子から分離した培養は，*Rhizosphaera kalkhoffii* Bub. のそれとはまったく異なるが，*R. pini* (Cda.) Maubl. の分離に失敗したため，この両者の培養比較ができなかった。一方 *Phaeocryptopus nudus* (Peck) Petr. の培養の一般的特徴および培地上に形成された分生胞子の大きさが，ハイマツから分離された *Rhizosphaera* 菌株のそれとよく似ている。このことから，この群の菌と *Phaeocryptopus* 属菌との関係をさらに多くの資料とその分離培養によって検討する必要があり，ここでは種名の決定を留保した。

***Rhizosphaera* 属菌の検索表**（括弧内の種は本邦未記録種）

A_1：分生胞子は小さく（10μ 以下），卵形ないし楕円形，低地に産しマツ類に生ずる
……*R. kalkhoffii* Bub.

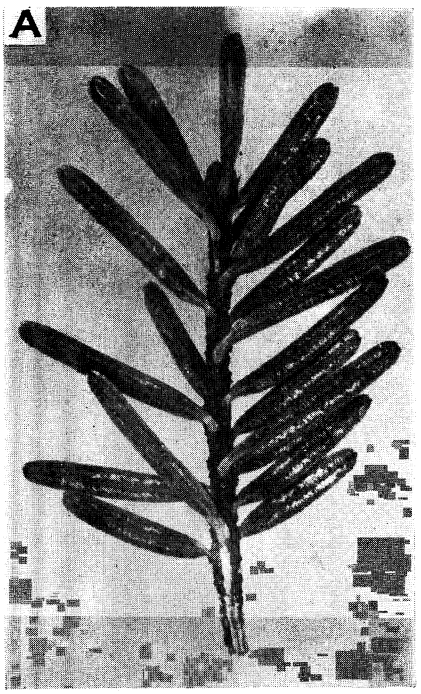
A_2：分生胞子は大きく（10μ 以上），楕円形ないし長楕円形

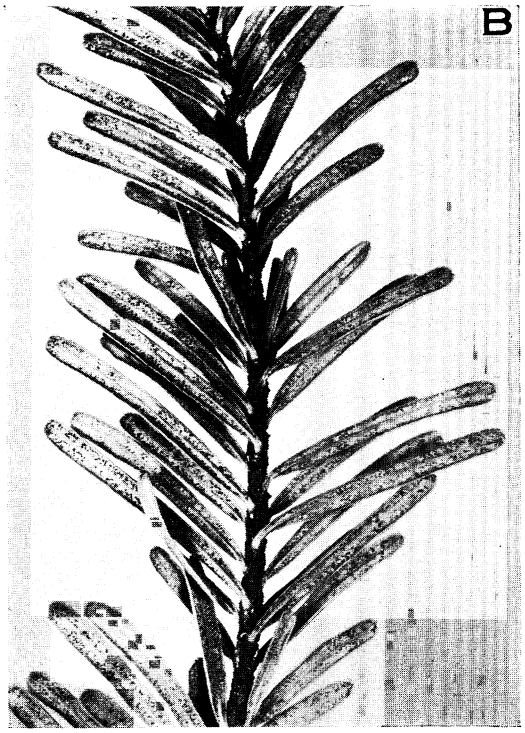
B_1：分生胞子は 9～13×7～9.5μ，楕円形……(*R. oudemansii* Maubl.)

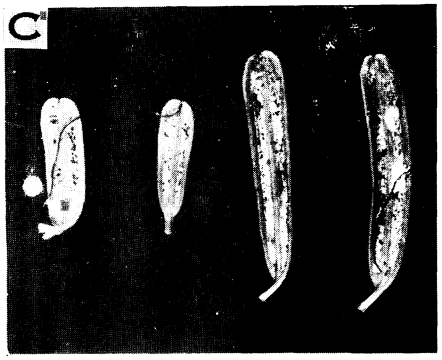
B_2：分生胞子は 15μ 以上，高地に産し，亜高山性樹種に生ずる。

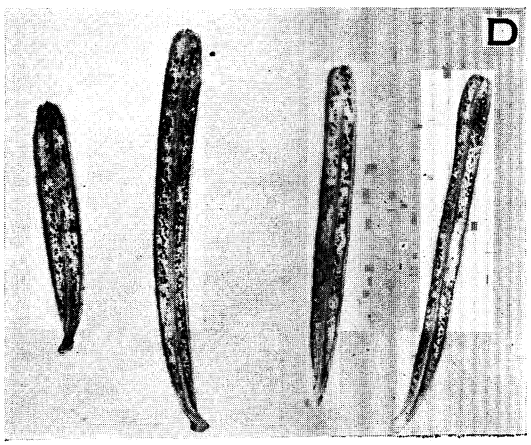
C_1：分生胞子は 16～20×8～10μ……*R. pini* (Cda.) Maubl.

C_2：分生胞子は 22～28×8～12μ……*R.* sp.


A

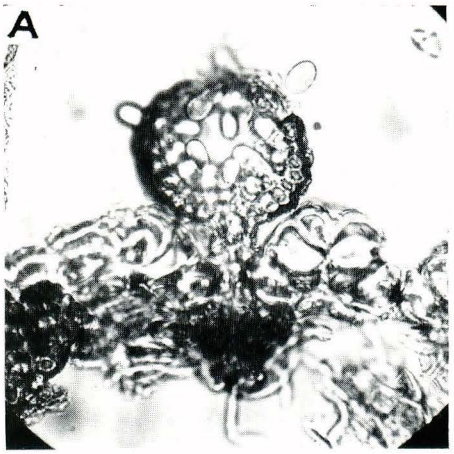

B

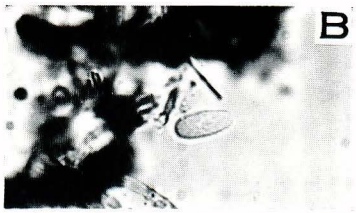

C


D


F


E


A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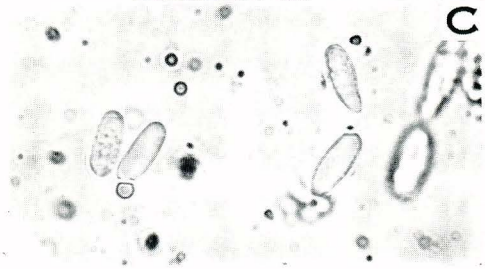
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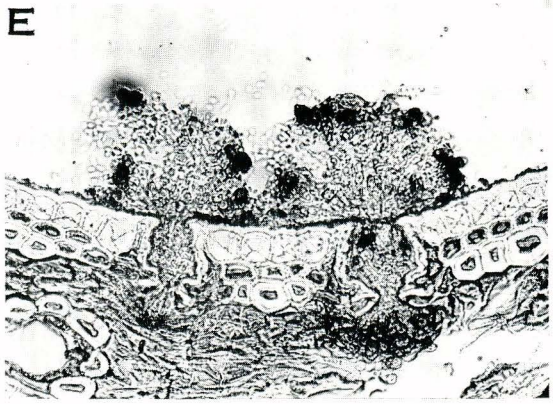
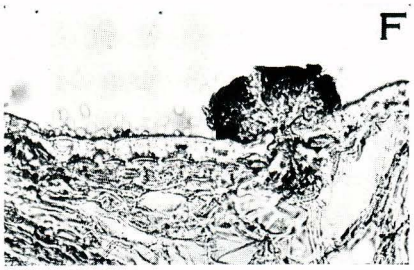

E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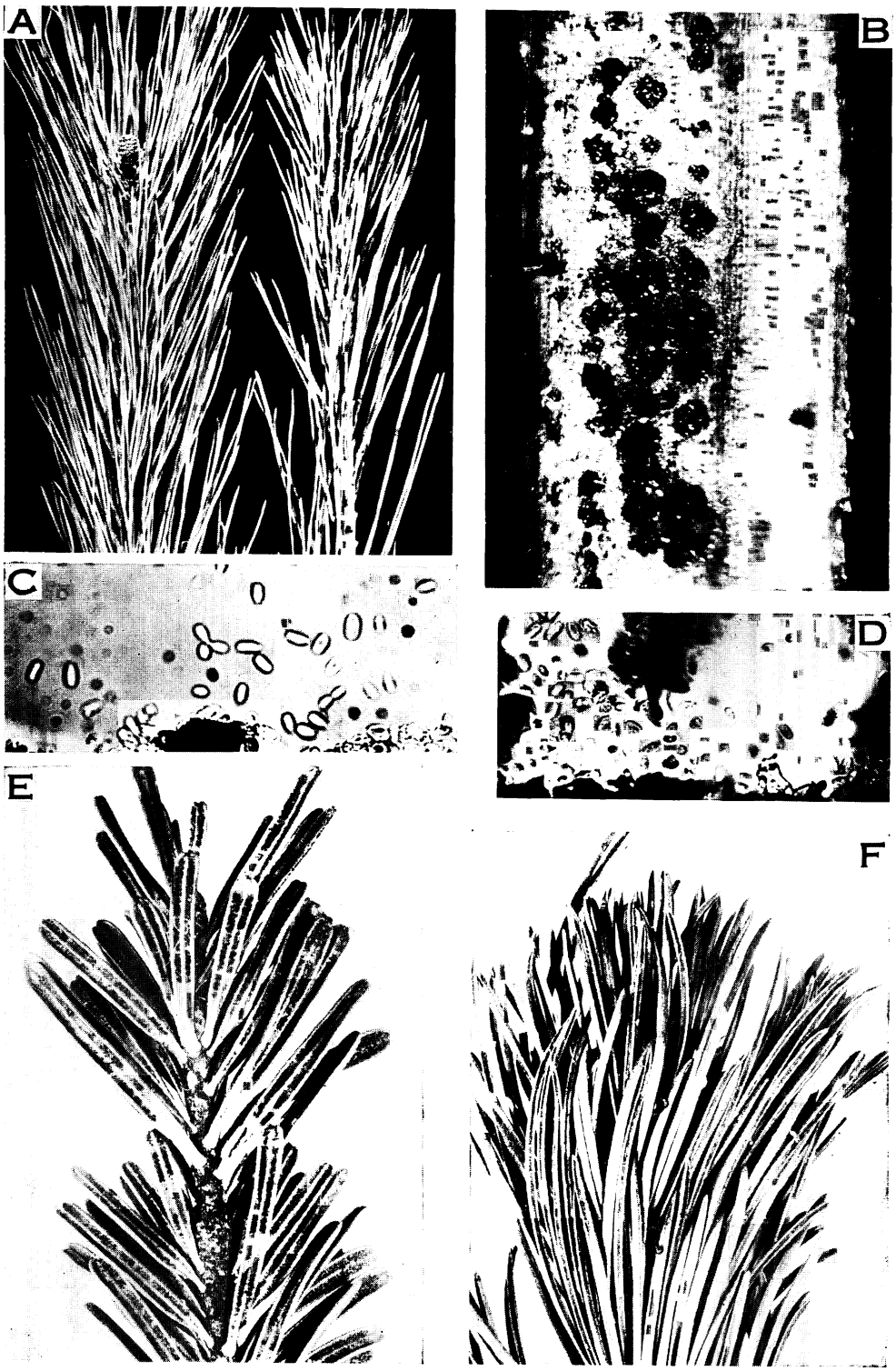
D


A
B
C
D
E
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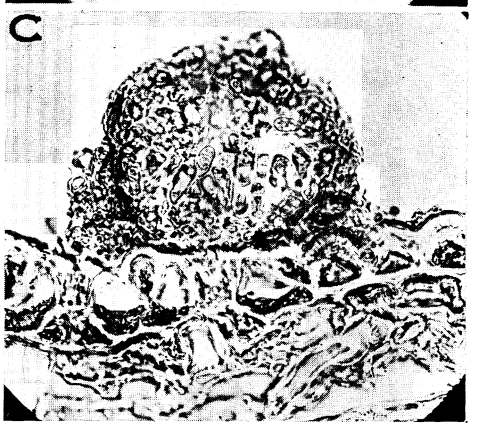
A


B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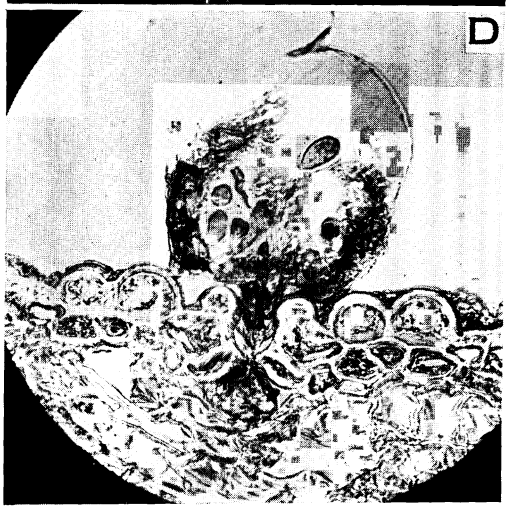
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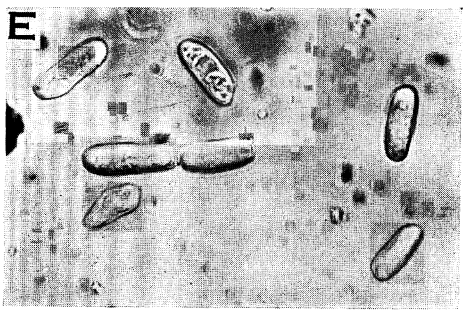
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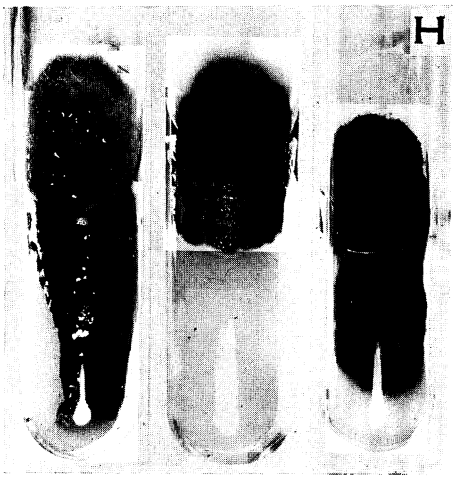
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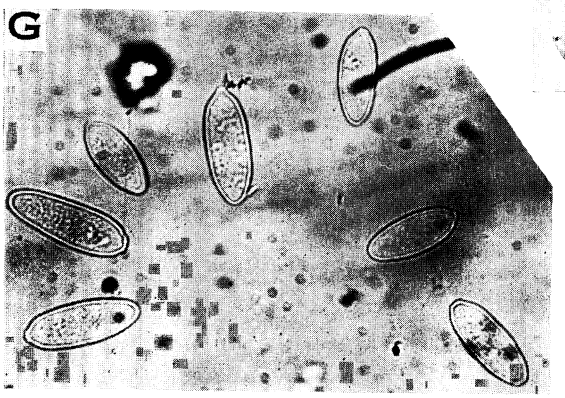
G


F