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The Life Cycle of *Pogotrichum yezoense* (Dictyosiphonales, Phaeophyceae)*

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The order Dictyosiphonales, which includes the genus *Pogotrichum*, was established by SETCHELL and GARDNER (1925) primary on the basis that *Dictyosiphon foeniculaceus* possess a heteromorphic life cycle but differ from the Laminariales (SAUVAGEAU 1917) in its isogamy. Recent culture studies on the life histories of Phaeophyta were summarized by WYNNE and LOISEAUX (1976) and they showed that the order Dictyosiphonales includes various life history patterns. Although the diversities of the life history pattern and the sporangium formation have been recognized in some species of the order by means of different culture conditions, the informations of sexual process and ploidy levels of various stages are few by the reason of the frequent lack of the cytological evidence.

For the conquest of these confused points, the present work was carried out to complete the life cycle of *Pogotrichum yezoense* by culturing it from generation to generation in the laboratory. Moreover, the morphogenetical experiment under various conditions controlled by temperature and photoperiod, the cytological study on various stages of the life cycle and the crossing experiment of zoids liberated from various reproductive organs produced on various thalli were conducted.

Materials and methods

The materials used in this study were collected at first from the usual host, *Laminaria japonica* ARESCHOUG, growing on the beach of Charatsunai, Muroran, Hokkaido on March 10, 1977. At that time, the thalli had only unilocular reproductive organs. Next year, on November 29, the thalli bearing plurilocular reproductive organs were found and culture studies were conducted by using these materials. During the period of this study, many materials were collected on occasion.

For the culture study, the collected materials were wiped with clean gauze to remove diatoms and other microorganisms, and then they were rinsed several times with autoclaved seawater. These cleaned materials were stocked in a freezer regulated at 5°C more than 24 hours. For the inoculation, one fertile fragment of them was placed in a petri dish containing sterilized seawater. After a few minutes, numerous zoids were liberated. Then they were washed several times in sterilized seawater by micro-

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pipette method, and they were pipeted on a glass slide unialgally. After their settlement, this slide was transferred into a glass vessel (6.5×8.0 cm) containing 180 mℓ of PESI medium which was slightly modified PROVASORI's ES medium by TATEWAKI (1966). The culture medium was renewed monthly. Cultures were grown in freezer-incubator illuminated with cool white fluorescent lamps (ca. 2,000 lx) under the following sets of temperature-photoperiod:

	Temperature (°C)	Photoperiod (Hr light-Hr dark)
Set 1	5	14–10
Set 2	5	10–14
Set 3	10	14–10
Set 4	10	10–14
Set 5	14	14–10
Set 6	14	10–14
Set 7	18	14–10
Set 8	18	10–14
Set 9	22	14–10
Set 10	22	10–14

For the crossing experiment, the natural materials collected from October, 1977 to May, 1978, and the cultured materials were used. These experiments were set up by zoids liberated from various reproductive organs by above described method, and about 20 individuals were used for each experiment. The sexual union was examined by checking on aggregation and fusion of zoids.

For the cytological study, the thalli of various developmental stages in the life cycle were fixed in the fixative of 1:3 acetic alcohol and stained by application of aceto-iron-haematoxylin-chloral hydrate method (WITTMANN 1965). The materials used in this study were 50 natural individuals and more than 20 cultured ones in every stage. These natural plants were collected during January-May, 1978.

Results

Fertile plants collected from nature were unbranched, cylindrical multiseriate filaments, hairless, about 1–2 cm long, about 70–100 μm thick, and containing several discoid chromatophores per cell (Pl. I A). Unilocular reproductive organs were scattered on the surface of the fronds, nearly globule, about 20–30 μm in diameter (Pl. I B). Zoids from unilocular organs were pear-shaped or ovoid, 5.2–7.8×2.8–4.0 μm in size, laterally biflagellated, and containing one chromatophore and eyespot (Pl. I C).

Development of spores from unilocular sporangia in natural plants

The zoids liberated from unilocular organs did not fuse each other, but they settled on slide glass. The zoid which develops without copulation into next stage is given

the name of spore. The settled spore immediately became spherical and measured 3.6–5.7 μm in diameter (Pl. I D).

Under all the conditions examined, the developmental process of spores pursued the same cause within 14 days. Within 12–24 hours after inoculation, the settled spore began to germinate by pushing out germ tube (Pl. I E, F). The germ tube elongated and protoplast moved into the germ tube, and then it divided into two cells transversely within 2 days (Pl. I G). By successive transverse cell divisions, the germlings became uniseriate filaments, and within 7 days these filaments began to shoot out prostrate branches (Pl. I H). Their cells containing several discoid chromatophores measured 5–10 μm in breadth and 2–3 times as long as breadth in length (Pl. I I). These germlings had the dimension of 300–400 μm in diameter within 14 days.

The successive developments of the prostrate germlings were different under the various conditions, and the results obtained, which were repeated from generation to generation, were described every set of experiments, as follows:

In Set 1, within 14 days after inoculation, these prostrate germlings gave rise directly to uniseriate erect thalli (Pl. I J), and within 21 days, the maturation occurred in the uni- or bi-seriate erect thalli and these thalli produced unilocular sporangia (Pl. I K, L). In this case, the prostrate germling is not a generation but a developmental stage of the macrothallus.

In Set 3, within 14 days after inoculation, the prostrate germlings gave rise directly to uniseriate erect thalli, and within 18 days successive production and elongation of erect thalli occurred (Pl. I M, N). The cells of the erect thalli had the dimension of 10–15 μm in breadth and 1/2–3/2 times as long as breadth in length, and containing several discoid chromatophores (Pl. I O). Within 21 days, the cells of the uniseriate erect thalli divided vertically to form bi- or pauci-seriate erect thalli (Pl. I P), and a few days after, these thalli produced plurilocular reproductive organs. These were near globule and 15–20 μm in diameter, and comprised several ten compartments (Pl. I Q). On the other hand, within 30 days, the other pauci-seriate erect thalli which had no plurilocular organs developed into multiseriate erect thalli by successive cell divisions (Pl. I R), and a few days after, they began to maturate and produced unilocular sporangia (Pl. I S). These organs were near globule, 30–40 μm in diameter, and slightly larger than the unilocular sporangia produced on natural plants (Pl. I T).

In Set 5, within 14 days after inoculation, the prostrate germlings synchronously produced both plurilocular reproductive organs and uniseriate erect thalli (Pl. I U). Within 21 days, the cells of the erect thalli divided vertically to form bi-seriate erect thalli. Within 25 days the maturation occurred in the uni- or bi-seriate erect thalli and they produced plurilocular reproductive organs (Pl. I V, W). In this condition, plurilocular organs were produced on both microthallus and macrothallus.

In Set 7 and 9, within 14 days after inoculation, the prostrate germlings produced

only plurilocular reproductive organs (Pl. I X), but no erect thallus was observed even if the culture was continued. These organs were intercalary (Pl. I Y) or lateral (Pl. I Z), ovoid, 20–30 × 30–70 μm in size, and comprised about several ten compartments. That is to say, only microthallus generation repeatedly occurred under these conditions.

In Set 2, 4, 6, 8 and 10, which were all short day condition, the developmental process delayed a little, but the life cycle pattern were corresponding to them under the long day condition of each temperature.

The phaeophycean hair was never observed at any stages of the life cycle.

Development of spores from plurilocular sporangia produced on cultured macrothalli

The zoids liberated from the plurilocular reproductive organs of fertile erect thalli cultured under 14°C-LD condition (Set 5) (Pl. II A, B) were pear-shaped or ovoid, 6.0–8.4 × 3.8–5.8 μm in size, slightly larger than the spores of unilocular sporangia, containing one discoid chromatophore and eyespot, and had two lateral flagella (Pl. II C). As these zoids never fused together, they must be called spores. The settled spores became spherical and measured 4.4–6.6 μm in diameter (Pl. II D). By successive transverse divisions and branching, they developed into prostrate germlings (Pl. II E, F). The subsequent development of the prostrate germlings under various conditions was closely identical with the result of the culture experiments of spores from unilocular sporangia in natural plants (Pl. II G–L).

Development of spores from plurilocular sporangia produced on cultured microthalli

The zoids liberated from plurilocular reproductive organs of fertile microthalli cultured under 18°C-LD condition (Set 7) (Pl. III A, B) were pear-shaped or ovoid, 6.6–8.6 × 3.8–6.0 μm in size, slightly larger than the spores of unilocular sporangia, containing one chromatophore and eyespot, and had two lateral flagella (Pl. III C). These zoids never fused together, so they must be called spores. The settled spores became spherical and measured 4.7–7.2 μm in diameter (Pl. III D).

Within 24 hours after inoculation, the settled spore began to germinate by pushing out germ tube and its protoplast moved into the germ tube (Pl. III E). By successive branching and transverse divisions, the germlings developed into prostrate ones (Pl. III F, G). The subsequent developments of the prostrate germlings under various conditions were identical with the result obtained from the culture studies of spores from sporangia produced on natural plants (Pl. III H–M).

Development of spores from plurilocular sporangia in natural plants

Fertile plants bearing plurilocular reproductive organs collected from nature were unbranched, cylindrical bi- or pauci-seriate filaments, hairless, 0.5–1.0 cm long, 30–70 μm thick, and had several discoid chromatophores per cell (Pl. IV A). Plurilocular repro-

ductive organs were near globule, about 20–25 μm in diameter, and comprised several ten compartments (Pl. IV B). The zoids liberated from the plurilocular reproductive organs in natural plants were pear-shaped or ovoid, 6.0–8.8 × 3.4–5.8 μm in size, slightly larger than the spores of unilocular sporangia, containing single chromatophore and eyespot and had two lateral flagella (Pl. IV C). These zoids did not fuse each other, so they must be called spores. The development of these spores under various conditions were identical with the results obtained from the culture studies of spores from plurilocular sporangia produced on cultured macrothalli (Pl. IV D–L).

Each life cycle under the fixed conditions was repeatedly completed by the route described above. By all accounts together, the effect of the controlled environmental factors on the formation of thallus form and reproductive organs of *Pogotrichum yezoense* are summerized as Table I.

Table I. Formation of erect thalli, unilocular sporangia on erect thalli, plurilocualr sporania on erect thalli and plurilocular sporangia on prostrate thalli under various culture conditions.

Temperature (°C)	Daylength	P-P	ET	E-P	E-U
5	SD	−	##	−	+
	LD	−	##	±	+
10	SD	−	###	+	###
	LD	±	###	+	###
14	SD	+	+	###	−
	LD	+	+	###	−
18	SD	###	±	−	−
	LD	###	±	−	−
22	SD	##	−	−	−
	LD	+	−	−	−

very abundant, ## abundant, + moderate, ± few, − absent, P-P=pluriocular sporangia on prostrate thalli, ET=erect thalli, E-P=plurilocular sporangia on erect thalli, E-U=unilocular sporangia on erect thalli, SD=short day condition, LD=long day condition).

Crossing experiment

The materials used in this experiments and the results obtained are shown in Table II. The experiment was carried out by all sets, but no aggregation or fusion was observed except only one case. This case was experienced in many zoids liberated from the same unilocular reproductive organ. These fused zoids had not been formed at the outside of the unilocular organ, but fused zoids which had already been formed in the organ were released from it. The fused zoids comprized 2 to about 10 cells (Pl. V A, C, E), which were clearly larger than normal zoids (Pl. V B, D). Two celled

Table II. Crossing experiments of zoids from various reproductive organs.

Material	Aggregation or Fusion
Zoids from same U	±
Zoids from U of same ET	−
Zoids from U of different ET	−
Zoids from same P of PT	−
Zoids from P of same PT	−
Zoids from P of different PT (same strain)	−
Zoids from P of different PT (different strain)	−
Zoids from same P of ET	−
Zoids from P of same ET	−
Zoids from P of different ET (same strain)	−
Zoids from P of different ET (different strain)	−

± apparent fusion, − no fusion, ET=erect thalli, PT=prostrate thalli, U=unilocular sporangia, P=plurilocular sporangia.

zoids being 7-8 μm in diameter which were larger than normal zoids had 2 eyespots and 4 flagella (Pl. V C). These fused zoids were isolated and cultured, but, in the result, they neither survived nor developed. After all, no sexual fusion was observed on any stages of the life cycle.

Cytological study

The chromosome numbers of various stages in the life cycle were observed. These stages observed (cf. the caption for Pl. VI) were as follows: 2 stages in the natural plants; 5 stages in the developmental process of spores from the unilocular sporangia produced on the natural plants; 5 stages in the developmental process of spores from plurilocular sporaniga produced on the cultured macrothalli; 5 stages in the developmental process of spores from plurilocular sporangia of the cultured microthalli.

As a result of this observation, 8-10 chromosomes were recognized in each cell of each stage, and neither meiosis nor vegetative diploidization was observed (Pl. VI A-Q).

Discussion

The species studied in this paper was described at first as *Litosiphon yezoense* YAMADA et NAKAMURA in YAMADA (1944), but the inflection of this specific epithet was incorrect. When the genus *Litosiphon* HARVEY (1849) was established on the basis of *L. pusillus* and *L. laminariae*, he described and figured the existence of hairs on the erect thalli of *L. pusillus*, but he did not refer to the hairs of *L. laminariae*. On

L. laminariae, NEWTON (1931) figured the hairs, and REINKE (1892) noted the attaching part consisting of descending rhizoidal filaments which are similar to that of the Japanese species.

REINKE (1892) established the genus *Pogotrichum* on the basis of *P. filiforme*, which is similar to the genus *Litosiphon*. At that time, he described that almost all vegetative cells of mature parts of erect thalli transformed into plurilocular sporangia and that the attachments of this species were not descending rhizoidal filaments but monostromatic basal disc. Moreover, he described and illustrated no hairs. This species had been recognized as *Litosiphon filiformis* (REINKE) BATTERS (1902) till recently.

On the other hand, KYLIN studied the life histories of *L. pusillus* (1933) and *L. filiformis* (1937), and noted the existence of minute prostrate stages in the life histories of both species. In the former species, the spores from uniseriate plurilocular sporangia developed directly into erect thalli in summer time, but in culture conducted in winter time the prostrate thalli formed unilocular and biseriate plurilocular sporangia and also erect thalli. In this case, both types of sporangia were formed on vegetative filaments, as a result, they were pedicellate or sessile. On the contrary, KYLIN's culture study on *L. filiformis* from end of April, 1935, showed that the vegetative cells of prostrate thalli transformed into plurilocular sporangia and gave rise to erect thalli. PEDERSEN (1978 a) described and photographed the transformed plurilocular sporangia and the erect thalli arising from the fertile prostrate thalli under the condition of lower temperature.

According to the absence of hair and the transformation of almost all cells of mature part of erect filaments into sporangia, as mentioned as PEDERSEN (1978 a), the Japanese species was considered to belong to the genus *Pogotrichum*. In addition to these main characters, it must be added to the generic characters given by PEDERSEN

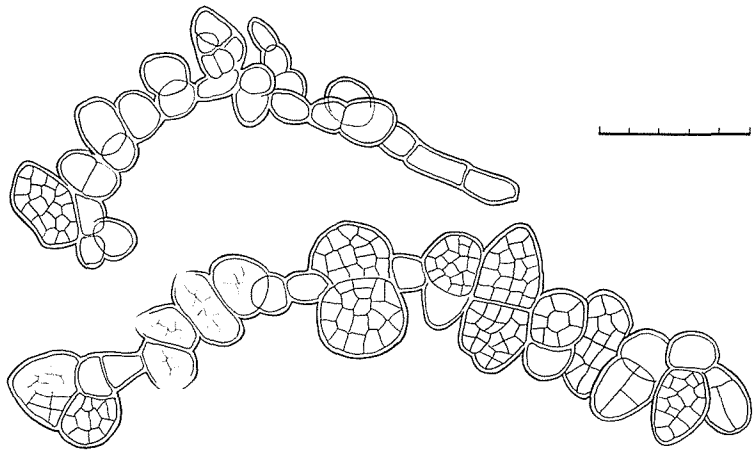


Fig. 1. Three-week old microthalli bearing plurilocular sporangia under the culture condition of Set 7. Scale shows 50 μm.

(1978 a) that the manner of sporangium formation on prostrate microthalli of *L. pusillus* (KYLIN 1933, figs. 6-7; DANGEARD 1966) is different from that of *Pogotrichum filiforme* (KYLIN 1937, fig. 3, as *Litosiphon filiformis*; PEDERSEN 1978 a) and *P. yezoense* (Fig. 1).

Pogotrichum yezoense is epiphytic mainly on the sorar part of *Laminaria* by descending filamentous rhizoids (YAMADA 1944, MIYAJI 1978). The unilocular sporangia are produced on almost all erect thalli in nature and on multiseriate erect thalli in culture condition, but the plurilocular sporangia are rarely observed on the small erect thalli throughout the growing season (MIYAJI 1978) and on the uni- or pauci-seriate erect thalli in culture condition. On the other hand, *P. filiforme* REINKE is epiphytic on the vegetative part of the host by means of small monostromatic disc, and its erect thalli produced dominantly plurilocular sporangia. By above mentioned reasons, *P. yezoense* is an independent species from *P. filiforme*. Here the authors propose following new combination:

Pogotrichum yezoense (YAMADA et NAKAMURA in YAMADA) SAKAI et SAGA, comb. nov.

Basionym: *Litosiphon yezoense* YAMADA et NAKAMURA in YAMADA, 1944, Notes on some Jap. alg. X, Sci. Pap. Inst. Algol. Res., Fac. Sci., Hokkaido Imp. Univ., vol. III, no. 1, p. 12, Fig. 1.

Since the prostrate thalli of *Pogotrichum yezoense* produced the plurilocular sporangia

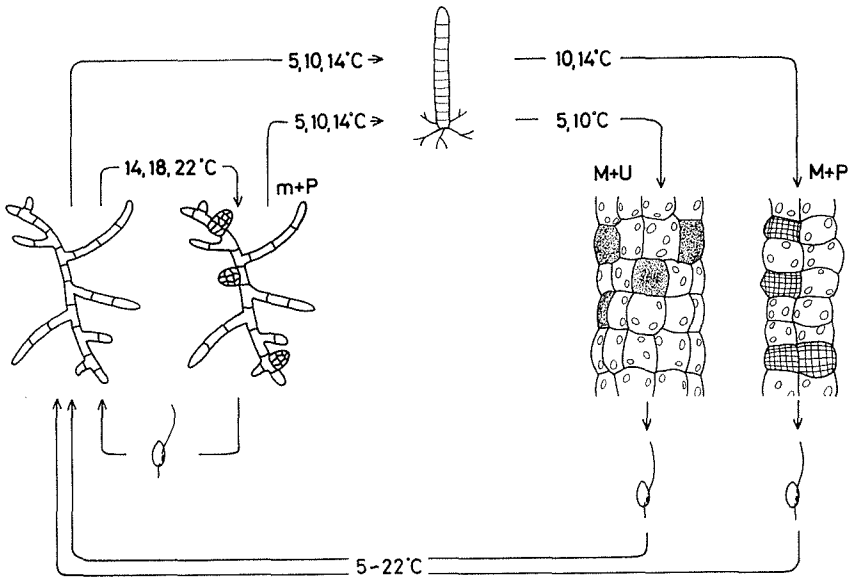


Fig. 2. Diagram summarizing life cycle of *Pogortichum yezoense* (M=macrothallus; m=microthallus; U=unilocular sporangium; P=plurilocular sporangium).

under a high temperature condition, these thalli are recognized as a generation (CHAPMAN 1961). It is termed a microthallus generation. On the other hand, the erect thalli produced unilocular or plurilocular sporangia under a low temperature condition, therefore these thalli are also recognized as a generation. It is designated a macrothallus generation. However, the prostrate germlings did not produce any reproductive organs under a low temperature condition (Sets 1-4). These prostrate ones are not a generation but one developmental stage of a macrothallus generation. Therefore, the life cycle of *Pogotrichum yezoense* is the heteromorphic alternation of generations between a macrothallus bearing unilocular or plurilocular sporangia and a microthallus bearing plurilocular sporangia (Fig. 2). But, the alternation of nuclear phase did not occur in the life cycle of this species.

The spores, which were determined by crossing experiment in this study, from all reproductive organs of this species have a potential which traces the same developmental process. The determination of the generation of this species is controlled by environmental factors mainly a temperature, that is to say, the life cycle pattern shows extensive variations by means of the setting temperature conditions. These pleomorphic life cycle patterns of this species under various temperature conditions are summerized in Fig. 3. Namely, under 5°C condition (Sets 1, 2), the only repetition of uni- or biseriate macrothallus bearing unilocular sporangia is observed (Fig. 3 A), as in *Coilodesme bulligera* (WYNNE 1972) and *Isthmoplea sphaerophora* (RUENESS 1974). Under 10°C

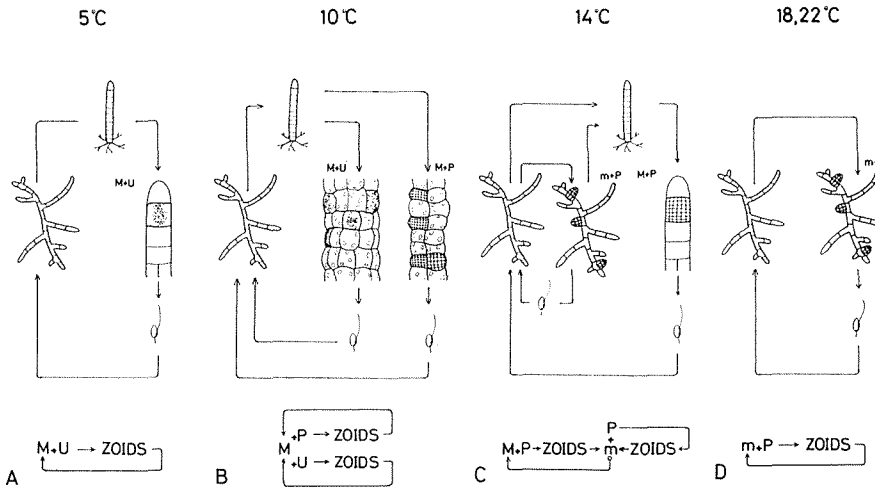


Fig. 3. Life cycle patterns of *Pogotrichum yezoense* controlled by temperature (M=macrothallus; m=microthallus; U=unilocular sporangium; P=plurilocular sporangium; +=produces reproductive organ; O⟶=produces new generation by vegetative way).

condition (Sets 3, 4), multiseriate macrothallus bearing unilocular sporangia alternates with isomorphic macrothallus bearing plurilocular one (Fig. 3 B), as in *Melanosiphon intestinalis* (WYNNE 1969). Under 14°C condition (Sets 5, 6), macrothallus bearing plurilocular sporangia alternates with microthallus bearing plurilocular sporangia (Fig. 3 C), as in *Pogotrichum filiforme* (PEDERSEN 1978 a). Under 18°C and 22°C conditions (Sets 7-10), the repetition of microthallus bearing plurilocular sporangia is suggestive of *Myrionema corunnae* of Chordariales (LOISEAUX 1970) (Fig. 3 D). As mentioned as above examples, the life cycle of this species was restricted by only temperature condition, but the whole aspect of the life cycle pattern was constructed by the results obtained under various temperature conditions. The temperature dependent expression of the generation has been known in *Desmotrichum undulatum* (RHODES 1970), *Isthmoplea sphaerophora* (EDELSTEIN *et al.* 1971) and *Hummia onusta* (*Stictyosiphon subsimplex*) (FIORE 1977) in the order Dictyosiphonales.

The life cycle of *Dictyosiphon foeniculaceus*, which is considered as the representative type of the order Dictyosiphonales, has been described to be heteromorphic, the macroscopic sporophyte bearing unilocular sporangium and the microscopic gametophyte bearing plurilocular gametangium by SAUVAGEAU (1929). Thus, it has been seemed that the basical life cycle pattern of the order Dictyosiphonales is a *Dictyosiphon* type. But, on the basis of hitherto known life cycle patterns in the Phaeophyceae, thallus sizes and, apart from the function, morphological types of reproductive organs can be combined into the following possible patterns. Cited examples are the species of the order Dictyosiphonales.

I. No alternation of generations.
   (1) Thallus (T) produces (+) plurilocular reproductive organ (pluri). *Coelocladia arctica* (PEDERSEN 1976).
   (2) T+unilocular reproductive organ (uni). *Coilodesme bulligera*, *C. fucicola* (WYNNE 1972), *Isthmoplea sphaerophora* (RUENESS 1974), *Scytothamnus fasciculatus* (ASENSI 1975 a) and *Striaria attenuata* (KORNMANN and SAHLING 1973).
   (3) T+pluri+uni. No example.

II. Isomorphic alternation of generations.
   (4) T+pluri——T+uni. *Melanosiphon intestinalis* (WYNNE 1969).
   (5) T+pluri+uni——T+pluri. No example.
   (6) T+pluri+uni——T+uni. No example.

III. Heteromorphic alternation of generations.
   (7) Microthallus (Micro) +pluri——Macrothallus (Macro) +pluri. *Desmotrichum undulatum* (RHODES 1970) and *Pogotrichum filiforme* (KYLIN 1937, as *Litosiphon*; PEDERSEN 1978 a).
   (8) Micro+pluri——Macro+uni. *Dictyosiphon foeniculaceus* (SAUVAGEAU 1917),

Isthmoplea sphaerophora (PEDERSEN 1975), *Soranthera ulvoidea* (WYNNE 1969) and *Striaria attenuata* (CARAM 1965).

(9) Micro+pluri——Macro+pluri+uni. *Corycus lanceolatus* (ASENSI 1975 b), *Hummia onusta* (FIORE 1977), *Isthmoplea sphaerophora* (EDELSTEIN *et al.* 1971), *Litosiphon pusillus* (NYGREN 1975), *Myriotrichia* sp. (LOISEAUX 1969), *Pogotrichum yezoense* and *Punctaria crouani* (DANGEARD 1966 b).

(10) Micro+uni——Macro+uni. No example.

(11) Micro+uni——Macro+pluri. No example.

(12) Micro+uni——Macro+pluri+uni. No example.

(13) Micro+pluri+uni——Macro+pluri. No example.

(14) Micro+pluri+uni——Macro+uni. *Striaria attenuata* (NYGREN 1975).

(15) Micro+pluri+uni——Macro+pluri+uni. *Coilodesme californica* (WYNNE 1972), *Litosiphon pusillus* (KYLIN 1933), *Myriotrichia clavaeformis* (PEDERSEN 1978 b) and *Phaeostrophion irregulare* (MATHIESON 1967).

According to these examples which have been known up to the present, microthallus always produces plurilocular reproductive organ and sometimes accessory unilocular one is produced on it. On the other hand, macrothallus produces unilocular reproductive organ, except the case of III (7), and sometimes plurilocular one is accessorily produced on it. Occasionally there are some cases that the life cycle pattern is different in the same genus, for example *Coilodesme* (WYNNE 1972). Moreover, it is different even in the same species, for example *Striaria attenuata* (CARAM 1965, KORNMANN and SAHLING 1973, NYGREN 1975) and *Isthmoplea sphaerophora* (EDELSTEIN *et al.* 1971, RUENESS 1974, PEDERSEN 1975). On the other hand, as shown in this study, there is a species which shows different life cycle patterns under settled temperature conditions. According to the examples described above, the members of this order have a peculiarity that the life cycle pattern is apt to transform. Thus the present authors consider that there is no representative life cycle pattern but manifold patterns in the order Dictyosiphonales.

Results obtained by the crossing experiment on *Pogotrichum yezoense* show that the sexual process is not observed at any stages of the life cycle. That is to say, the zoids liberated from unilocular and plurilocular reproductive organs of both microthallus and macrothallus developed in the same manner with zoospores or parthenogametes (some textbooks described the plurilocular sporanigum the gametangium). Thus the authors recognized all reproductive organs of this species the sporangia. However, apparently fused spores liberated from the same unilocular sporangium are observed, but these fused spores never germinate. The sexual process has been known in only 5 species of this order, so far as they know, for example *Dictyosiphon foeniculaceus* (SAUVAGEAU 1917, ARASAKI 1940), *Striaria attenuata* (CARAM 1965), *Litosiphon pusillus* (DANGEARD 1966 a), *Soranthera ulvoidea* (WYNNE 1969) and *Hummia onusta* (FIORE 1977). And in the cases of *S. attenuata* and *L. pusillus*, it has been reported that

sexual fusion occurred between zoids from unilocular reproductive organs. On the other hand, it has been known that the fusion of zoids from unilocular sporangia produced on *Ectocarpus* is not a sexual fusion but a result of incomplete cell separation during sporogenesis (MÜLLER 1975). And the present authors conclude that the fusion of spores from unilocular reproductive organs is a result of accidental or abnormal process as shown in the present study.

According to the present cytological study on natural and cultured thalli, the chromosome number was 8-10 at all stages in the life cycle. Namely, in the case of *Pogotrichum yezoense*, neither meiosis nor vegetative diploidization occurred, and sexual process was lacking at any stages of the life cycle. And a basical haploid chromosome number of Dictyosiphonales has been considered to be 8-13 (COLE 1967). According to these facts, it is clear that alternation of nuclear phases does not occur throughout the life cycle of this species and the nuclear phases at all stages are haploid (n=8-10). Although there have been few cytological studies corresponded to various stages of the life cycle in other species of the order, the present species from Muroran seems to be a parthenogenetic species or population. On the other stand point of view, the present authors presume that it is no necessity that the nuclear phases always alter synchronously with the alternation of generations.

In the case of *Ectocarpus*, the germlings could develop into the gametophytes or sporophytes independently of the nuclear phase (MÜLLER 1967). In *Alaria*, the gametophytes or sporophytes had been induced by apospory and apogamy (NAKAHARA and NAKAMURA 1973). Moreover, in the case of *Pogotrichum yezoense* examined in the present study, successive generation was determined not by nuclear phase but by temperature. According to these facts, it can be considered that the nuclear phase, which seems to have full genetic informations in spite of the change of gene dosage that is shown by the term of haploid or diploid, could not determine the generation or morphological phase. Consequently, the generation is not always determined by nuclear phase, but the phenotypic expression is easily influenced by certain environmental factors which may regulate the gene activation or the enzyme reaction.

Summary

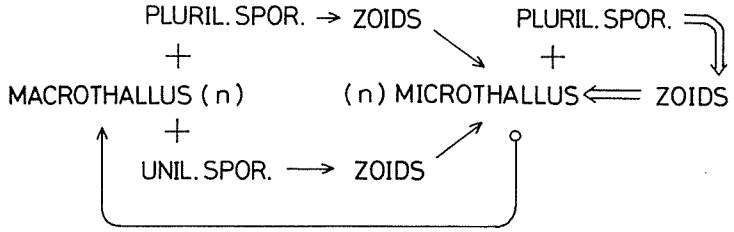
Pogotrichum yezoense from Muroran, Hokkaido, was investigated to clarify the entire life cycle, sexual evidence and nuclear phase in laboratory cultures.

The life cycle of this species was controlled by environmental factors mainly a temperature. Under 5°C condition, the life cycle pattern showed the repetition of the uni- or bi-seriate macrothallus bearing unilocular sporangia. Under 10°C condition, it also showed the repetition of the multiseriate macrothallus bearing unilocular or plurilocular sporangia. Under 14°C condition, it showed an alternation between the macrothallus bearing plurilocular sporangia and the microthallus bearing plurilocular sporangia. Under

18°C and 22°C conditions, it showed the repetition of the microthallus bearing plurilocular sporangia.

The sexual process was not observed at any stages of the life cycle. There was no alternation of nuclear phases throughout the life cycle, and the nuclear phases at all the stages were haploid (n=8–10). The present species from Muroran is considered to be a parthenogenetic species or population.

The entire life cycle of *Pogotrichum yezoense* shows heteromorphic alternation of generations between a macrothallus bearing unilocular or plurilocular sporangia and a microthallus bearing plurilocular sporangia, and is summarized by the following diagram.



(n=8–10)

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PLATE I

Development of spores from unilocular sporangia in natural plants

A. Mature plant from nature.
B. Unilocular sporangia of mature plant.
C. Spore liberated from unilocular sporangium.
D. Settled spore.
E. 12-hour old germling.
F. 1-day old germling.
G. 2-day old two-celled germling.
H, I. 7-day old prostrate thallus.
J. 14-day old uniseriate erect thallus (Set 1).
K. Unilocular sporangia produced on 21-day old uniseriate erect thallus (Set 1).
L. Unilocular sporangia produced on 21-day old biseriate erect thallus (Set 1).
M–O. 14-day old uniseriate erect thalli (Set 3).
P. 21-day old biseriate erect thallus (Set 3).
Q. Plurilocular reproductive organs produced on 25-day old biseriate erect thallus (Set 3).
R. 30-day old multiseriate erect thallus (Set 3).
S, T. Unilocular sporangia produced on 35-day old multiseriate erect thallus (Set 3).
U. Plurilocular reproductive organs and uniseriate erect thalli produced on 14-day old prostrate thallus (Set 5).
V. Plurilocular reproductive organs produced on 25-day old uniseriate erect thallus (Set 5).
W. Plurilocular reproductive organs produced on 25-day old biseriate erect thallus (Set 5).
X. Plurilocular reproductive organs produced on 14-day old prostrate thallus (Set 7).
Y. Intercalary plurilocular reproductive organ produced on 14-day old prostrate thallus (Set 7).
Z. Lateral plurilocular reproductive organs produced on 14-day old prostrate thallus (Set 7).

Use scale in A for A, M, N, P, R, S, U & X; scale in B for B, I–L, O, Q, T, V, W, Y & Z; scale in F for C–G; scale in H for H. Scale A & H show 100 μm; scale B & F show 10 μm.

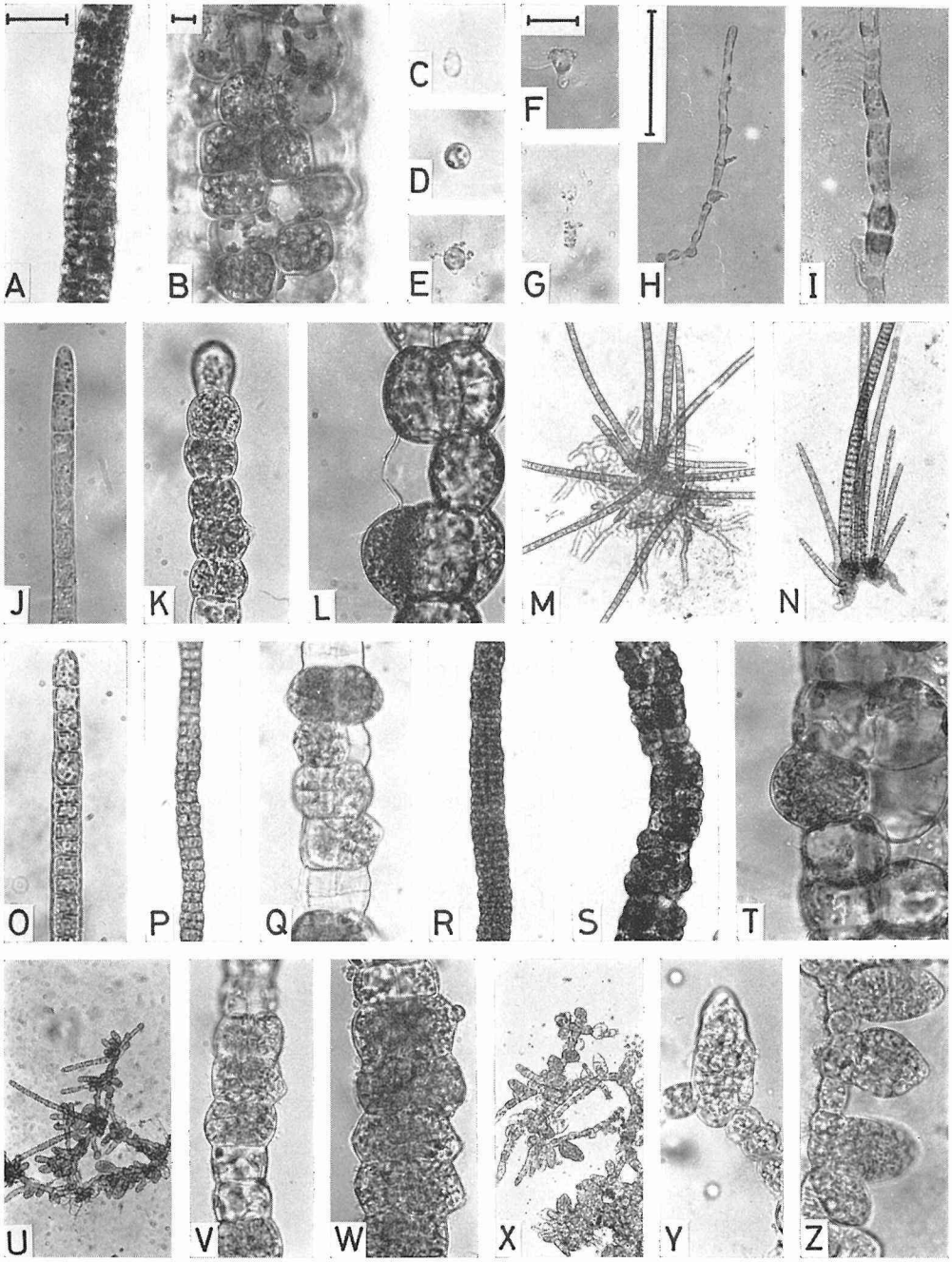
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PLATE II

Development of spores from plurilocular sporangia produced on cultured macrothalli

A. Biseriate erect thallus with plurilocular sporangia cultured under Set 5.
B. Plurilocular sporangia just liberating spores.
C. Spore liberated from plurilocular sporangium.
D. Settled spore.
E. 2-day old two-celled germling.
F. 7-day old prostrate thallus.
G. Unilocular sporangium produced on 21-day old uniseriate erect thallus (Set 1).
H. Plurilocular sporangia produced on 25-day old biseriate erect thallus (Set 3).
I. Unilocular sporangia produced on 35-day old multiseriate erect thallus (Set 3).
J. Plurilocular reproductive organs produced on 14-day old prostrate thallus (Set 5).
K. Plurilocular sporangia produced on 25-day old uniseriate erect thallus (Set 5).
L. Plurilocular reproductive organs produced on 14-day old prostrate thallus (Set 7).

Use scale in A for A, F, J & L; scale in B for B, G, H & K; scale in C for C-E; scale in I for I. Scale A & I show 100 μm; scale B & C show 10 μm.

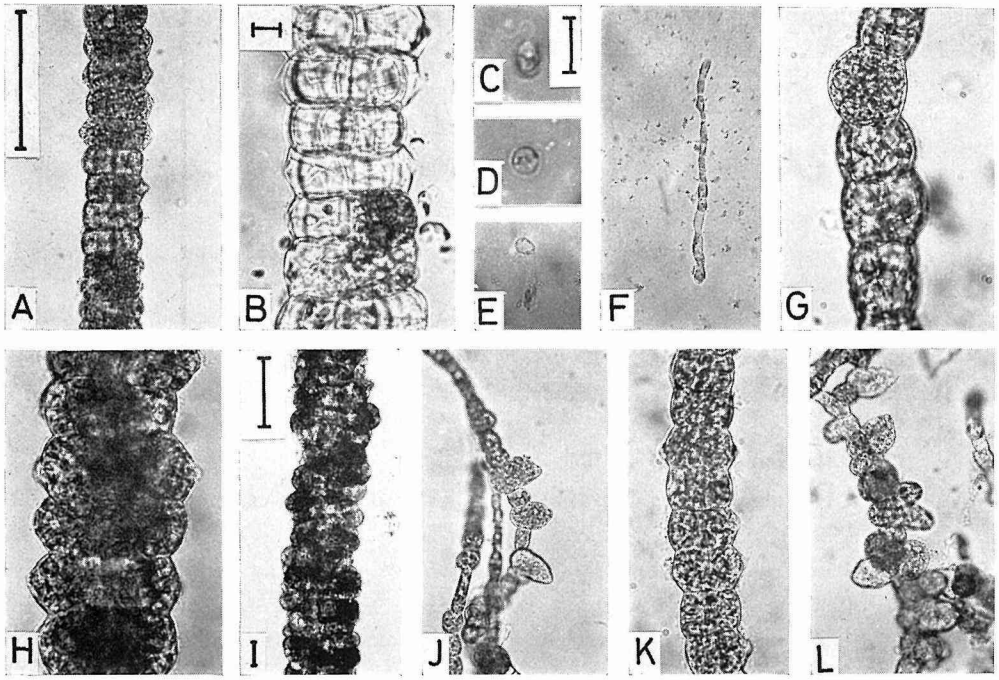
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PLATE III

Development of spores from plurilocular sporangia produced on cultured microthalli.

A. Prostrate thallus with plurilocular sporangia cultured under Set 7.
B. Plurilocular sporangia just liberating spores.
C. Spore liberated from plurilocular sporangium.
D. Settled spore.
E. 2-day old two-celled germling.
F. 3-day old germling.
G. 7-day old prostrate thallus.
H. Unilocular sporangia produced on 21-day old uniseriate erect thallus (Set 1).
I. Plurilocular sporangia produced on 25-day old biseriate erect thallus (Set 3).
J. Unilocular sporangia produced on 35-day old multiseriate erect thallus (Set 3).
K. Plurilocular sporangia produced on 14-day old prostrate thallus (Set 5).
L. Plurilocular sporangia produced on 25-day old uniseriate erect thallus (Set 5).
M. Plurilocular sporangia produced on 14-day old prostrate thallus (Set 7). Use scale in A for A & J; scale in B for B, H, I & L; scale in C for C–F; scale in G for G, K & M. Scale A & G show 100 μm; scale B & C show 10 μm.

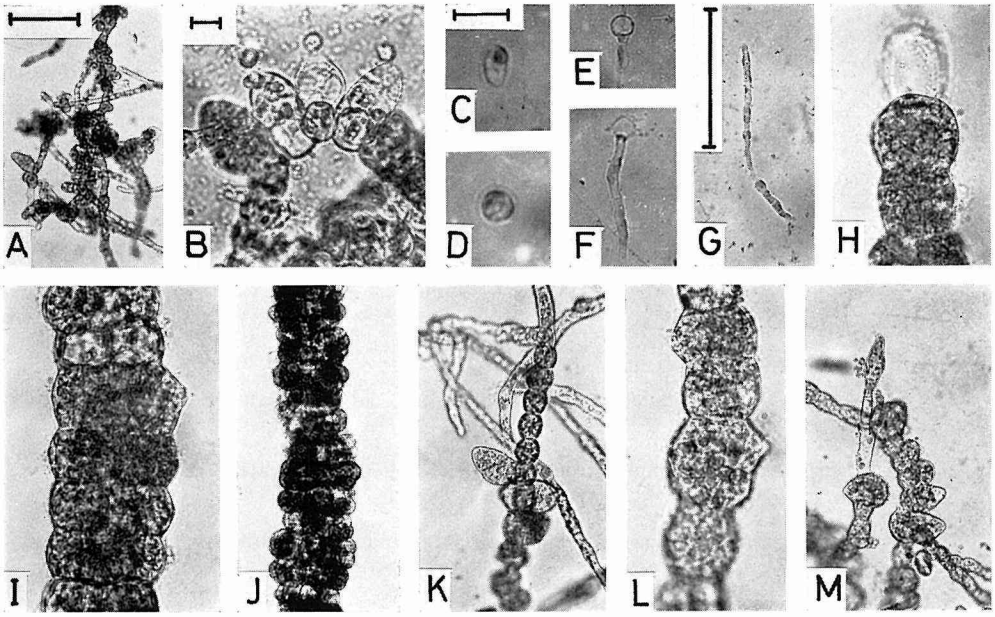
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Plate IV

Development of spores from plurilocular sporangia in natural plants

A. Mature plant from nature.
B. Plurilocular sporangia of mature plant.
C. Spore liberated from plurilocular sporangium.
D. Settled spore.
E. 1-day old germling.
F. 7-day old prostrate tahllus.
G. Unilocular sporangia produced on 21-day old uniseriate erect thallus (Set 1).
H. Plurilocular sporangia produced on 25-day old biseriate erect thallus (Set 3).
I. Unilocular sporangia produced on 35-day old multiseriate erect thallus (Set 3).
J. Plurilocular sporangia produced on 14-day old prostrate thallus (Set 5).
K. Plurilocular sporangia produced on 25-day old uniseriate erect thallus (Set 5).
L. Plurilocular sporangia produced on 14-day old prostrate thallus (Set 7).

Use scale in A for A & I; scale in B for B, G, H & K; scale in C for C-D; scale in F for F, J & L. Scale A & F show 100 μm; scale B & C show 10 μm.

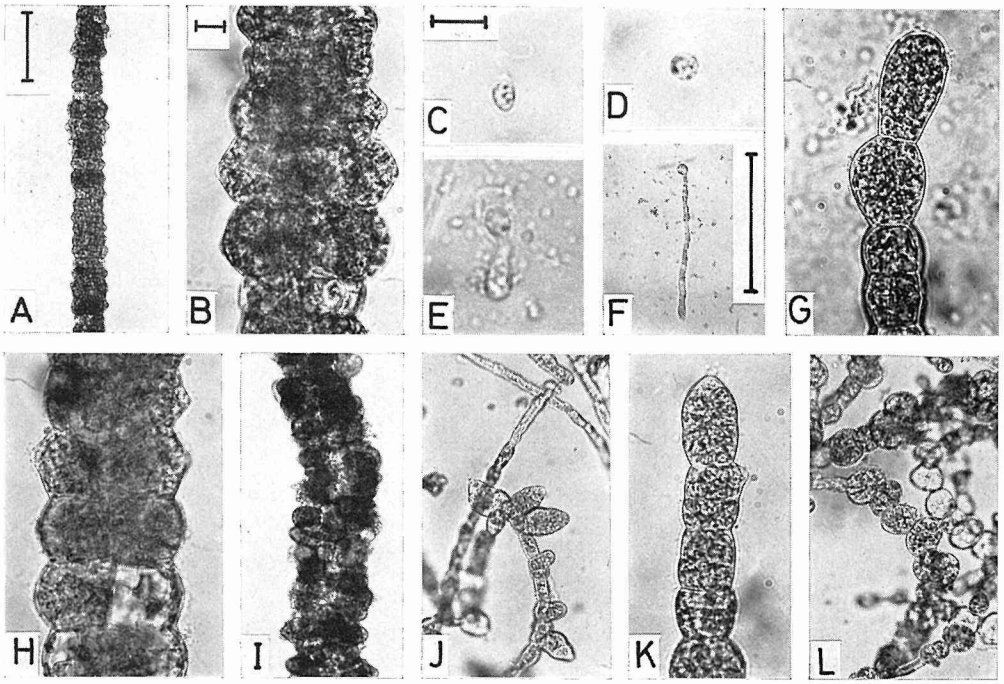
Plate V

Fused zoids liberated from the same unilocular sporangium

A. Fused zoids comprised of several zoids.
B. Non fused zoid.
C. Fused zoid comprised of two zoids.
D. Non fused zoid.
E. Fused zoid comprised of about ten zoids.

Use scale in A for A & B; scale in C for C-E. Scale A shows 100 μm; scale C shows 10 μm.

[SAKAI-SAGA] PLATE IV



[SAKAI-SAGA] PLATE V

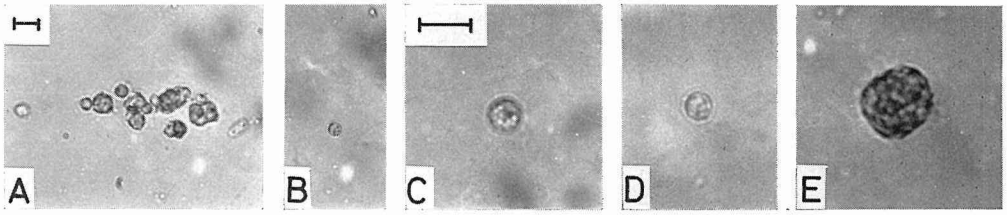
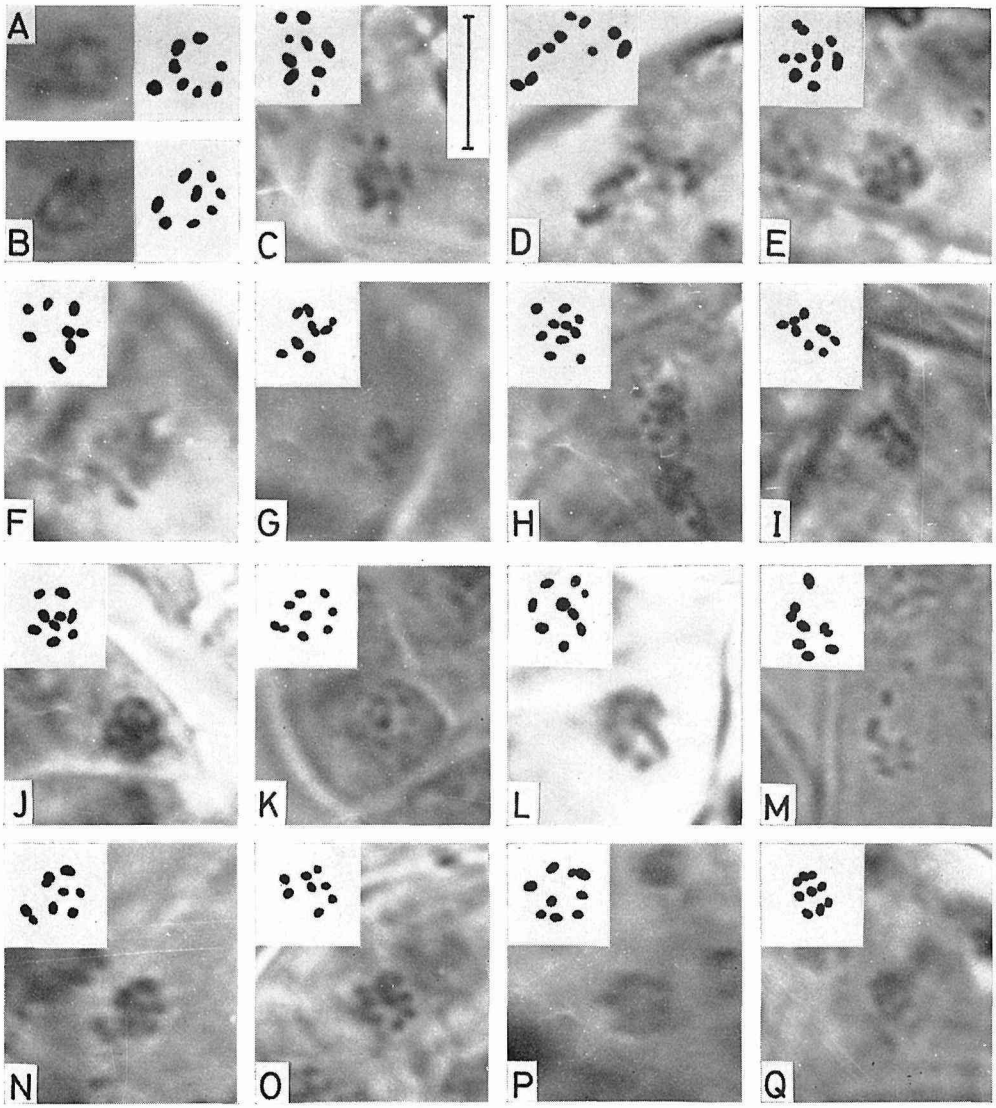


PLATE VI

Chromosomes of *Pogotrichum yezoense*

A. Vegetative cell in erect thallus collected from nature.
B. Unilocular sporangium in erect thallus collected from nature.
C. Vegetative cell in prostrate thallus derived from zoid of unilocular sporngium.
D. Vegetative cell in prostrate thallus derived from zoid of plurilocular sporangium in erect thallus.
E. Vegetative cell in erect thallus derived from zoid of unilocular sporangium.
F. Vegetative cell in erect thallus derived from zoid of plurilocular sporangium in erect thallus.
G. Unilocullar sporangium in erect thallus derived from zoid of unilocular sporangium.
H. Plurilocular sporangium in erect thallus derived from zoid of unilocular sporangium.
I. Unilocular sporangium in erect thallus derived from zoid of plurilocular sporangium in erect thallus.
J. Plurilocular sporangium in erect thallus derived from zoid of plurilocular sporangium in erect thallus.
K. Plurilocular sporangium in prostrate thallus derived from zoid of unilocular sporangium.
L. Plurilocular sporangium in prostrate thallus derived from zoid of plurilocular sporangium in erect thallus.
M. Vegetative cell in prostrate thallus derived from zoid of plurilocular sporangium in prostrate thallus.
N. Vegetative cell in erect thallus derived from zoid of plurilocular sporangium in prostrate thallus.
O. Plurilocular sporangium in prostrate thallus derived from zoid of plurilocular sporangium in prostrate thallus.
P. Plurilocular sporangium in erect thallus derived from zoid of plurilocular sporangium in prostrate thallus.
Q. Unilocular sporangium in erect thallus derived from zoid of plurilocular sporangium in prostrate thallus.

Use scale in C for A-Q. Scale shows 5 μm.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