—レビュー—
Review

Cytotaxonomical Aspects of Antarctic Mosses, with Special Reference to the Proportion of Polyploidy

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南極産蘚類の細胞分類学的特徴—特に倍数性の出現頻度について

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要旨: 南極から報告された蘚苔類の染色体に関する研究をレビューし，倍数性の出現頻度とその意義について考察した．従来より維管束植物では過酷な環境の元では倍数性の出現が多いことが知られている．地球上で最も過酷な環境にあると考えられる南極で蘚類の染色体にどの様な進化的傾向があるのかを解析したところ，南極，亜南極での倍数性の出現頻度は世界中の様々な植物相の中に占める倍数性の頻度の範囲内にあることが解った．ところが，昭和基地周辺のラングホブデ雪鳥沢産の蘚類では高い倍数性頻度を示し，またここに分布するオオハリガネゴケ(*Bryum pseudotriquetrum*)では種内倍数性がみられた．雪鳥沢でみられるこれらの現象は南極という過酷な環境における倍数性の役割を理解する上で重要な示唆を与えることが予想される．

Abstract : The evolutionary tendency concerning karyological features, especially the proportion of polyploidy and infraspecific polyploidy in Antarctic mosses is reviewed. Almost all chromosome numbers reported from sub-Antarctic and maritime Antarctic are within the world-wide range of deviation of ploidy proportions. The mosses at Yukidori Valley, in the vicinity of Syowa Station, Continental Antarctica, indicate an unusually high frequency of polyploidy, containing infraspecific polyploidy, which is of particularly interest in the understanding of the role of polyploidization in the harsh Antarctic environment.

1. Introduction

The Antarctic environment is one of the harshest on the earth. The plants are exposed to bright sunlight throughout the day during the summer season, and the deep unbroken darkness of winter. The mean air temperature reaches only 0°C at Syowa Station (69°S latitude) even in the summer season. Organisms have to tolerate very low temperatures, dryness and the peculiar seasonal light conditions. The mosses distributed in Antarctica seem to have adapted and become specialized to living under such harsh conditions.

Our biological research interests in Antarctic plants are aimed towards a better understanding of the events which have occurred during the evolutionary processes and how the distribution mechanisms of the Antarctic plants have become established

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in such a harsh environment. In various explanations of the present phytogeographical aspects of Antarctic mosses (BARTRAM, 1938; VAN ZANTEN, 1971; ROBINSON, 1972; SCHUSTER, 1979), the main limitation to persistent establishment of colonies is the physiological response to the environment.

The aim of this short report is to review the chromosome studies of the Antarctic mosses and discuss whether there are any genetic phenomena that respond to such peculiar environmental conditions.

2. Polyploidization in Harsh Environments

Cytological events, such as mutation of chromosome structure and/or polyploidization (=multiplication of chromosome sets) frequently induce speciation. It is suggested that angiosperm plants at higher latitudes, higher altitudes or in harsher environments contain a higher proportion of polyploidy (*cf.* GRANT, 1981). The reason why polyploid plants occupy frequently in harsher environments is considered as follows. Gene mutation usually results in lethal or semi-lethal damage to organisms. It is difficult for diploid plants to change gene structure without any disadvantage, because they have only one pair of the genome sets, and many genes are considered to be unicates. Therefore, diploid plants rarely seem to change their genetic systems and their habits and habitats. In contrast to diploid plants, polyploid plants consist of multiple genome sets. Due to the original genome set ensuring their basic viability, additional genome sets have an ability to modify genetic systems to adapt to a new environment by gene mutation. Mosses seem to be regulated by different genetic systems. They are haplontic plants, so the normal haploid form consists of only one genome set. The haploid condition leads to conservatism for habitats or genetic systems, so this would therefore be stronger in mosses than in angiosperms. Thus, mosses are expected to be more widely distributed in harsh environments following the events of polyploidization.

A different idea has been proposed by STEBBINS (1984, 1985): species which have already established themselves within ecosystems are usually fairly conservative. They are considered to be restricted to certain habitats. Newcomers are not usually able to settle in such stable environments. Glaciation during the Pleistocene epoch disturbed climax vegetation and provided new habitats for new colonizers. Some plants arose from the hybridization between parent species which inhabited the previously stable environment. They may have exhibited new or intermediate habits between both parents, and could survive and establish colonies in new habitats, due to lack of competition. Although hybrids usually produce sterile gametes, because of irregularities of chromosome behaviour at meiosis, polyploidization may result in the accomplishment of sexual reproduction, so that hybrid origin polyploids, namely allopolyploids, can guarantee next generations.

Newly originated polyploid plants are generally considered better adapted to harsher environments than the original ones.

3. Evolutionary Tendency of Polyploidy in Antarctic Mosses

Because of difficulties in procuring fresh specimens and maintaining active living conditions for collection of meristematic tissues, cytological investigations of

Table 1. Chromosome counts of Antarctic bryophyte reported so far. Latitude of each locality is as follows; South Georgia (54.5°S), Signy Island (60.5°S), King George Island (62°S), Syowa Station and vicinity (69°S).

Species	n	Ploidy	Source	Authors
I. Musci				
AMBLYSTEGIACEAE				
Calliergidium				
austro-stramineum	22	2	King George I.	Kuta *et al.*, 1982
Calliergon				
sarmentosum	11	1	King George I.	Kuta *et al.*, 1982
Campyliadelphus				
polygamus	11	1	Signy I.	Newton, 1980
	18	1	King George I.	Przywara *et al.*, 1984
Drepanocladus				
uncinatus	11	1	South Georgia	Newton, 1972
	20	2	King George I.	Kuta *et al.*, 1982
	30	3	King George I.	Kuta *et al.*, 1982
ANDREAEACEAE				
Andreaea				
australis	10	1	South Georgia	Newton, 1980
depressinervis	10	1	King George I.	Kuta *et al.*, 1982
gainii	10	1	King George I.	Kuta *et al.*, 1982
BARTRAMIACEAE				
Bartramia				
patens	11+m	1	Signy I.	Newton, 1980
	16	1	South Georgia	Newton, 1972
	16	1	South Georgia	Newton, 1980
	16	1	King George I.	Kuta *et al.*, 1982
Breutelia				
integrifolia	6	1	South Georgia	Newton, 1972
Conostomum				
magellanicum	8	1	King George I.	Kuta *et al.*, 1982
pentastichum	8	1	South Georgia	Newton, 1980
BRACHYTHECIACEAE				
Brachythecium				
austro-salebrosum	10	1	South Georgia	Newton, 19724
	10	1	King George I.	Kuta *et al.*, 1982
	11	1	Signy I.	Newton, 1980
	20	2	King George I.	Kuta *et al.*, 1982
BRYACEAE				
Bryum				
amblyodon	20	2	Syowa Station	Kanda and Okada, 1990
argenteum	10	1	Syowa Station	Inoue, 1976
	20	2	Syowa Station	Tatuno, 1963
pseudotriquetrum	20	2	Syowa Station	Tatuno, 1963
	20	2	Syowa Station	Inoue, 1976
	20	2	Signy I.	Newton, 1980
	20	2	Syowa Station	Kanda and Okada, 1990
	30	3	Syowa Station	Kanda and Okada, 1990
Leptobryum				
pyriforme	22+m	2	Syowa Station	Kanda and Okada, 1993

Antarctic plants have only developed very recently (Table 1). TATUNO (1963) first recorded chromosome numbers of some mosses collected from the vicinity of Syowa Station. He found a peculiar feature in Antarctic mosses, in that two out of three species were polyploid. Although *Bryum argenteum* distributed in temperate zones has a haploid* chromosome number $n=10$ (YANO, 1957; MARCHAL, 1920; JACHIMSKY, 1935; CHOPRA, 1957), the specimens collected from Antarctic, at Syowa Station and

* Contrary to higher plants having a diplontic status, the main form of mosses is haplontic.

Table 1. (Continued).

Species	n	Ploidy	Source	Authors
Pohlia				
cruda	11	1	South Georgia	Newton, 1972
var. *imbricata*	11	1	Signy I.	Newton, 1980
	22	2	King George I.	Kuta *et al.*, 1982
nutans	22	2	South Georgia	Newton, 1972
	33	3	King George I.	Kuta *et al.*, 1982
wahlenbergii	11	1	King George I.	Przywara *et al.*, 1984
DICRANACEAE				
Chorisodontium				
aciphyllum	12	1	King George I.	Kuta *et al.*, 1982
Dicranella				
hookeri	26	2	South Georgia	Newton, 1972
Dicranoweisia				
antarctica	13	1	Signy I.	Newton, 1980
	13	1	King George I.	Przywara *et al.*, 1984
grimmiacea	13	1	King George I.	Przywara *et al.*, 1984
Distichium				
austro-georgicum	14+m	1	South Georgia	Newton, 1972
DITRICHACEAE				
Ceratodon				
purpureus	13	1	Syowa Station	Tatuno, 1963
	13	1	Syowa Station	Inoue, 1976
	13	1	King George I.	Przywara *et al.*, 1984
ENCALYPTACEAE				
Encalypta				
rhaptocarpa	13	1	King George I.	Kuta *et al.*, 1982
GRIMMIACEAE				
Grimmia				
asperitricha	13	1	South Georgia	Newton, 1980
syntrichiacea	13	1	South Georgia	Newton, 1980
Racomitrium				
crispulum	13	1	South Georgia	Newton, 1972
Schistidium				
antarctici	13	1	King George I.	Przywara *et al.*, 1984
POLYTRICHACEAE				
Dendroligotrichum				
squamosum	7	1	South Georgia	Newton, 1972
Polytrichum				
alpinum	7	1	South Georgia	Newton, 1980
	7	1	King George I.	Kuta *et al.*, 1982
alpestre	7	1	South Georgia	Newton, 1972
juniperinum	7	1	King George I.	Kuta *et al.*, 1982
piliferum	7	1	South Georgia	Newton, 1972
	7	1	King George I.	Kuta *et al.*, 1982
Psilopilum				
antarcticum	7	1	South Georgia	Newton, 1972
trichodon	7	1	South Georgia	Newton, 1980

Langhovde, showed $n=20$, corresponding to the diploid form (Tatuno, 1963). However, at the present time, the Antarctic species of *Bryum argenteum* with $n=20$ can be considered a cytotype of *B. pseudotriquetrum* (as *B. inconnexum*. Horikawa and Ando, 1967).

Bryum pseudotriquetrum (primarily identified as *B. inconnexum*, an endemic species to the Antarctica) had $n=20$. This species is also a cosmopolitan moss, and its chromosome number has been studied by many investigators (*cf.* Fritsch, 1982).

Table 1. (Continued).

Species	n	Ploidy	Source	Authors
POTTIACEAE				
Pottia				
austro-georgica	26	2	Syowa Station	Inoue, 1976
heimii	26+2m	2	Syowa Station	Inoue, 1976
	26	2	King George I.	Przywara *et al.*, 1984
Tortula				
conferta	24	2	King George I.	Przywara *et al.*, 1984
excelsa	12	1	King George I.	Przywara *et al.*, 1984
fuscoviridis	12	1	King George I.	Przywara *et al.*, 1984
grossiretis	24	2	King George I.	Przywara *et al.*, 1984
	36	3	King George I.	Przywara *et al.*, 1984
	ca.40	3?	King George I.	Przywara *et al.*, 1984
robusta	7	1	South Georgia	Newton, 1972
	12	1	South Georgia	Newton, 1980
serrata	13	2?	South Georgia	Newton, 1972
II. Hepaticae				
ANEURACEAE				
Riccardia				
georgiensis	10	1	South Georgia	Newton, 1980
	20	2	South Georgia	Newton, 1980
CEPHALOZIELLACEAE				
Cephaloziella				
exiliflora	16+2m	2	South Georgia	Newton, 1980
	16+2m	2	King George I.	Ochyra *et al.*, 1982
GYMNOMITRIACEAE				
Herzogobryum				
teres	8+m	1	King George I.	Ochyra *et al.*, 1982
JUNGERMANNIACEAE				
Barbilophozia				
hatcheri	8+m	1	King George I.	Ochyra *et al.*, 1982
	18	2	King George I.	Ochyra *et al.*, 1982
Lophozia				
excisa	27	3	King George I.	Ochyra *et al.*, 1982
LOPHOCOLEACEAE				
Leptoscyphus				
expansus	8+m	1	South Georgia	Newton, 1980
Lophocolea				
willii	8+m	1	South Georgia	Newton, 1980
Pachyglossa				
dissitifolia	9	1	King George I.	Ochyra *et al.*, 1982
LOPHOZIACEAE				
Roivainenia				
jacquinotii	9	1	South Georgia	Newton, 1980
SCAPANIACEAE				
Blepharidophyllum				
densifolium	8+m	1	South Georgia	Newton, 1980
SCHISTOCHILACEAE				
Schistochila				
aberrans	8+m	1	South Georgia	Newton, 1972

According to previous reports, this species has various chromosome numbers, such as n=10, 10+m, 20, 20+m, and 33 (maybe 30+3m). INOUE (1976), KANDA and OKADA (1990, 1993) undertook cytological studies of mosses collected from the Syowa Station area. Many aspects of their results were similar to those in TATUNO's (1963) report. From these results, it has become clear that there is a very high (80%) proportion of polyploidy (Table 2).

In contrast to this high proportion of polyploidy in mosses at Syowa Station, continental Antarctica, the polyploid proportion at lower latitudes in the sub-

Table 2. Ploidy proportion and latitude at Antarctic and sub-Antarctic regions.

Area (lat.)	Haploid	Polyploid	Total	Ploidy %
South Georgia (54.5 ° S)	26	3	29	10
Signy Island (60.5 ° S)	5	1	6	17
King George Island (62 ° S)	19	8	27	30
Syowa Station (69 ° S)	1	3*	5	80

*: contains one species showing intraspecific polyploidy.

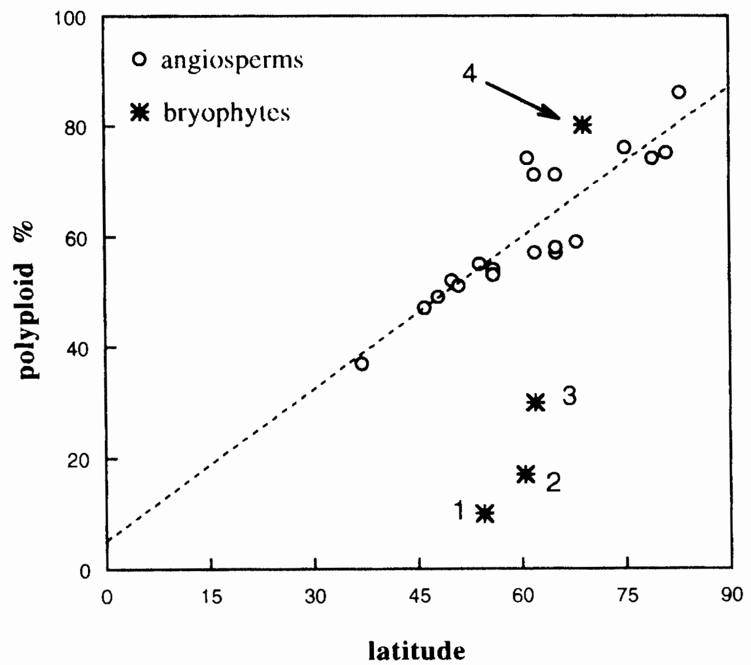

Fig. 1. Relation between latitude and proportion of polyploidy. Average of polyploid % of bryophytes in the world is ca. 25%. Numerals in figure represent as 1; South Georgia, 2; Signy Island, 3; King George Island 4; vicinity of Syowa Station. Refer angiosperm data to GRANT *(1981, Table 24.1).*

Antarctica and maritime Antarctica is lower (Table 2) (NEWTON, 1972, 1980, 1984; KUTA *et al.*, 1982; OCHYRA *et al.*, 1982; PRZYWARA *et al.*, 1984). NEWTON (1972, 1980) thoroughly counted chromosome numbers of bryophytes from South Georgia and Signy Island, South Orkney Islands, and found a low value of polyploid % within these floras (Fig. 1). She concluded that the incidence of polyploidy did not increase with latitude in the southern hemisphere. Further, NEWTON (1984) summarized karyological reports of bryophytes from the world so far, and drew a graph (NEWTON, 1984) expressing the frequency of each chromosome number. According to the graph, about 25% of bryophytes are polyploid. The proportions of polyploidy at three localities in the sub-Antarctica and maritime Antarctica seemed to be included within the range of this deviation. This also seems to be the case in the Arctic region. STEERE (1954) reported no significant difference between the polyploid proportion of Arctic mosses and that of Californian mosses.

The regression line in Fig. 1 expresses significant correlations between latitude and polyploid proportion in the angiosperm floras. However, the evolutionary tendency of Antarctic and sub-Antarctic bryophytes is extremely different from that of angiosperms. The evolutionary tendency of Antarctic mosses relating to polyploidy is not clear on the whole, as mentioned above. The only exception is found in mosses surrounding Syowa Station. It is interesting to find reasons for the frequency of polyploid mosses distributed around Syowa Station. Whether the environmental conditions in the vicinity of Syowa Station are exceptional, or whether this represents a real phenomenon in the continental Antarctic region may be clarified by further investigations.

4. Infraspecific Polyploidy at the Yukidori Valley

KANDA and OKADA (1990) found infraspecific polyploidy, $n=20$ and 30, diploid and triploid of $x=10$, respectively, in *Bryum pseudotriquetrum* collected from Langhovde. Both specimens were collected from the same locality at Yukidori Valley. Similar findings have been made by NEWTON (1980). The specimens of *Bartramia patens* collected from Signy Island showed $n=11+1m$, while those from South Georgia $n=16$. She noted that cytological heterogeneity was not surprising for the great morphological variation associated with *B. patens*. In the case of *Bryum pseudotriquetrum* collected from Yukidori Valley, diploid and triploid specimens inhabited the site sympatrically (or parapatrically) and did not show distinctive morphologies from each other (KANDA and OKADA, 1990).

Yukidori Valley has a rich vegetation for continental Antarctica. This is the main reason why the region is recognized as a nature reserve site, "Site of Special Scientific Interest" (SSSI). It would be interesting to know whether diploid and triploid specimens inhabit sites segregatively, or what factors effect polyploidization of the species. Unfortunately, for these specimens, the exact locations have not been recorded, nor the relative position between them, so that we can not draw further biological conclusions for these mosses. *Bryum pseudotriquetrum* is distributed over a wide-range of localities through the equator to the polar zone, and shows a remarkable polyploid series from a haploid level to a triploid level. As pointed out by KANDA and OKADA (1990), this species exhibits increasing polyploidization with higher latitude. The relationships between ploidy levels and latitude may express, in general, the physiological response of plants to low temperature. It is also interesting to know whether further high ploidy levels are distributed at other extreme environments such as Yukidori Valley.

In cases of bryophytes, polyploidy confers genetic isolation (NEWTON, 1984). Moss hybrids between different ploidy levels have not been reported so far. Further, diploid and triploid specimens have not shown different morphological characters (KANDA and OKADA, 1990). What do these facts mean? In general, a biological species is considered to have a capacity to breed with an individual belonging to the same species, to establish its status within the ecosystem, and to display an indistinguishable morphology. From the former view, both diploid and triploid belong to different species, while both are the same species from the last view. The detailed analysis of habitat segregation of different ploidy levels at the same locality, in this case the Yukidori Valley, may provide answers to this puzzle.

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