Cytological and Ecological Studies on the Speciation of *Lycopodium clavatum* L. in the Japanese Archipelago

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Cytological and Ecological Studies on the Speciation of *Lycopodium clavatum* L. in the Japanese Archipelago[1]

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ABSTRACT Cytological and ecological studies were made on *Lycopodium clavatum* in various habitats and localities of Japan. Among 729 individuals from 172 localities examined, 359 from 116 were of the diploid cytotype with $2n=68$, 172 from 77 were of the triploid with $2n=102$, and 198 from 77 were of the tetraploid with $2n=136$. The three cytotypes showed similar karyotypes; the median : submedian : subterminal : terminal centromeric chromosome $=30:20:25:25$ of the total complement. The meiotic chromosome configuration was 34_{II} in the diploids constantly and 68_{II} in most of the tetraploids. In the triploids, the commonest was $36_{II}+30_{I}$ and 39% SMCs had trivalents. All populations studied were divided into three population types; the sole-type where only one cytotype occurred in a population, the mixed-type A where two or three cytotypes occurred in the same population but each in a different habitat, the mixed-type B where two or three cytotypes grew sympatrically and shared the same habitat. In the sole-type and mixed-type A, the diploids preferred humid, shady, stable places; the tetraploids open, sunny, unstable places; and the triploids were intermediate between the other two cytotypes. The mixed-type B occurred in places at the early phase of succession in a plant community. Each cytotype can progress successively towards occupying its optimum habitat, from the mixed-type B to the mixed-type A and finally to the sole type. These habitat preferences of each cytotype and successional changes were found uniformly throughout the Japanese archipelago.

KEY WORDS habitat, karyotype, *Lycopodium clavatum*, meiosis, polyploid cytotype

INTRODUCTION

Lycopodium clavatum L. occurs throughout the world except Australasia and shows extreme diversification in ecological and morphological characteristics. Thus, several varieties and forms are known within this species (Spring, 1882; Baker, 1887; Nessel, 1939; Hultén, 1962; Øllgaard, 1987). However, investigations dealing with the ecological and morphological variability of this species are extremely few and inconclusive (Kallio *et al.*, 1969; Øllgaard, 1979).

Throughout the Japanese archipelago *Lycopodium clavatum* is distributed widely from Hokkaido to the Ryukyu Islands, and occurs in various vegetational zones: evergreen broad-leaved forest, deciduous broad-leaved forest, evergreen coniferous forest, and alpine meadow zones. The habitats of this species also show diversity: e.g., alpine meadows, open places in hills to high mountains, moors, roadside slopes, and shady, wooded places in hills to high mountains. Thus, its morphological characters are very diversified, and

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there is some confusion in the taxonomical treatment (Nakai, 1925; Miyabe and Kudo, 1930; Tagawa, 1959; Ching, 1982). Concerning its morphological diversity, Tagawa (1959) pointed out some correlations between individual plants and environmental factors: the plants growing in sunny places differed in color and texture from those in shady places.

The chromosome number of *Lycopodium clavatum* has been reported to be 2n = 68 from over the world: Europe, India, Formosa, Greenland, Canada, North America, Jamaica, and Ecuador (Manton, 1950; Mehra and Verma, 1957; Löve and Löve, 1958, 1966, 1976; Sorsa, 1958, 1961, 1962, 1963a, b; Walker, 1966; Tsai and Shieh, 1983; Øllgaard, 1987). In addition, 2n = 136 was reported from a Bhutanese plant (Ghatak, 1965) and 2n = 44 from a Bolivian plant (Rolleri, 1982). Meanwhile, Tanaka and Takamiya (1982) found various chromosome numbers of 2n = 68, 102, and 136 in Hiroshima Prefecture in western Japan and regarded them as diploid, triploid, and tetraploid cytotypes, respectively, assuming the basic number of the species to be x = 34. However, the cytological interrelationships among the three cytotypes are not clear, since no study has yet been done on karyotype and meiotic behavior of the chromosomes.

Takamiya and Tanaka (1982) studied many populations of *Lycopodium clavatum* in Hiroshima Prefecture and found the following differences in habitat preference among the three cytotypes: the habitat for the diploid cytotype was in humid, shady, stable places; that for the tetraploid cytotype was in open, sunny, unstable places; and that for the triploid cytotype was in between the other two. Furthermore, they suggested successional change of populations: At first, diploids, triploids, and tetraploids formed mixed-type populations in which all three cytotypes grew together and shared the same habitat. Later each cytotype separated from the others successively, and finally each occupied its op-timum habitat, thus establishing sole-type populations in which a single cytotype formed the entire population.

To date, the polyploidy related to speciation has been well studied in many pteridophytes (Mitui, 1968; Vida, 1976; Lovis, 1977; Walker, 1979, 1984; Wagner and Wagner, 1979; Haufler, 1987). But before the publication of Takamiya and Tanaka (1982) less attention had been paid to correlations between polyploidy and habitat preference (Mitui, 1968; Nakato *et al.,* 1983), and no information had been available in *Lycopodium clavatum* concerning the correlation of ecological variations and habitat preference with polyploidy.

Three cytotypes of *Lycopodium clavatum* were found in Hiroshima Prefecture, although in other places in Japan only a diploid cytotype has been reported (Takamiya and Kurita, 1983). No reports have appeared concerning polyploidy and habitat preference. This paper deals with the chromosome number, karyotype, and meiotic behavior of the chromosomes of *L. clavatum* and its ecological differentiation of habitat at various localities throughout Japan.

MATERIALS AND METHODS

I. *Sampling Sites and Methods*

Although *Lycopodium clavatum* L. has been divided into several varieties or species

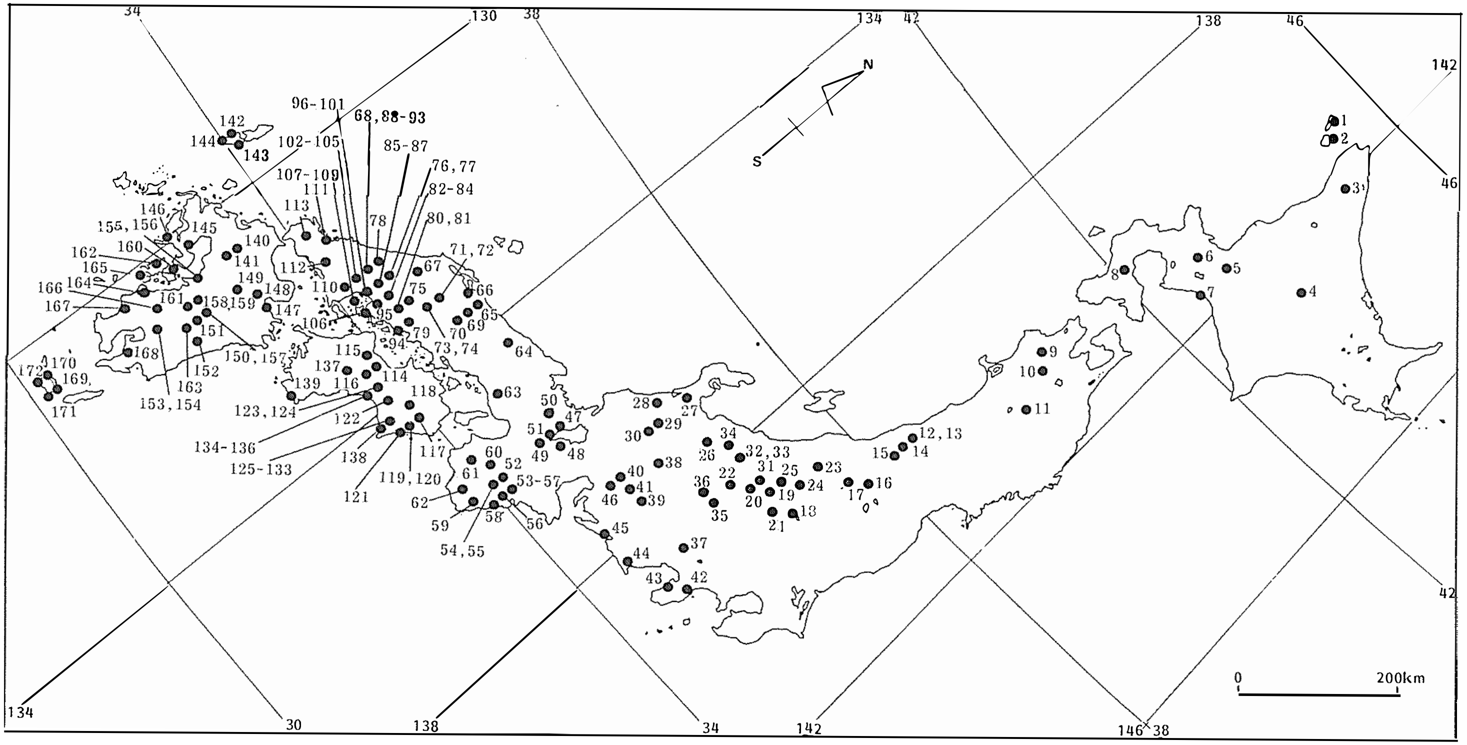

Fig. 1. A map showing the localities examined of *Lycopodium clavatum*. See Table 1 for explanations of the locality code numbers.

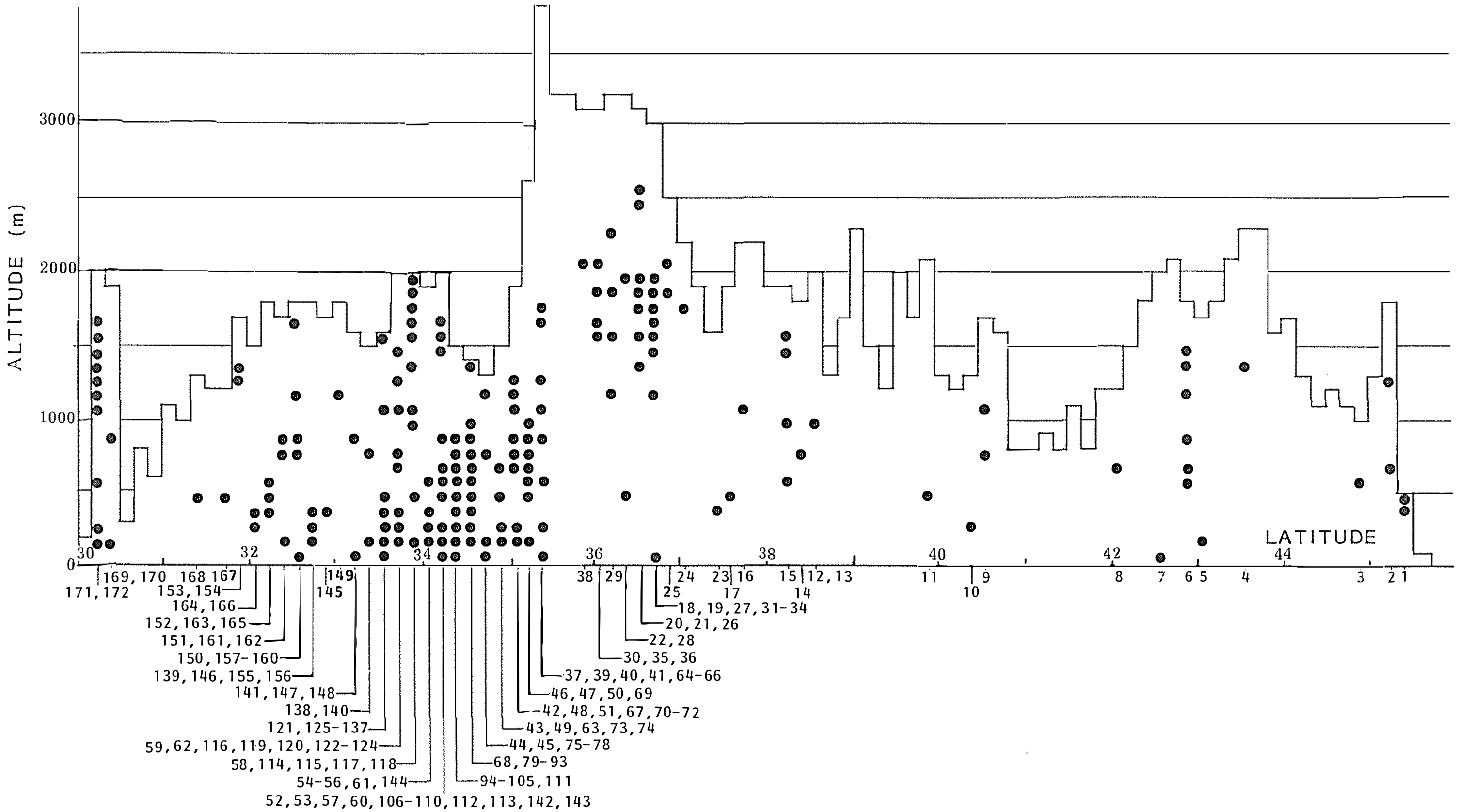

Fig. 2. A map showing the altitudinal distribution of the localities examined of *Lycopodium clavatum*. See Table 1 for explanations of the locality code numbers.

Table 1. Localities, number of individuals, and chromosome number of *Lycopodium clavatum* studied

Locality code no.	Name of studied site	Locality (Altitude)	No. of individuals showing respective chromosome number (2n)		
			68	102	136
		Hokkaido District			
Hokkaido Prefecture					
1	Rebun	Rebun Island, Rebun-cho, Rebun-gun (300–450m)	3	-	1
2	Rishiri	Rishiri Island, Rishiri-cho, Rishiri-gun (600–1200m)	1	-	1
3	Shirikoma	Mt. Shirikoma, Nakatonbetsu-cho, Esashi-gun (500m)	1	-	-
4	Kogennuma	Kogennuma, Kamikawa-cho, Kamikawa-gun (1320m)	1	-	-
5	Nopporo	Nopporo, Nopporo-cho, Ebetsu City (100m)	1	-	-
6	Muine	Mt. Muine, Sapporo City (560–1460m)	7	-	2
7	Takaoka	Takaoka-cho, Tomakomai City (60m)	1	-	-
8	Kenashi	Mt. Kenashi, Mori-cho, Kayabe-gun (600m)	1	-	-
		Tohoku District			
Aomori Prefecture					
9	Iwaki	Mt. Iwaki, Iwaki-cho, Nakatsugaru-gun (750–1000m)	2	-	1
10	Hayanose	Hayanosemori, Owani-cho, Nakatsugaru-gun (200m)	-	1	-
Akita Prefecture					
11	Hachimantai	Hachimantai, Tazawako-cho, Senboku-gun (400m)	-	-	1
Iwate Prefecture					
12	Iwaizumi	Iwaizumi-cho, Shimohei-gun (900m)	2	-	-
Yamagata Prefecture					
13	Ogoe	Ogoe, Nishikawa-cho, Nishimurayama-gun (900m)	1	-	-
14	Rokujyurigoe	Mt. Rokujyurigoe, Higashitagawa-gun (750m)	1	1	-
15	Asahi	Mt. Asahi, Asahi-cho, Higasimurayama-gun (560–1500m)	3	1	2
16	Yachidaira	Yachidaira, Iide-cho, Nishiokitama-gun (1000m)	1	-	-
Fukushima Prefecture					
17	Tokuzawa	Tokuzawa, Nishiaizu-cho, Yama-gun (500m)	-	-	1
		Kanto District			
Tochigi Prefecture					
18	Yumoto	Yumoto-cho, Nikko City (1500–1600m)	1	-	1
Gunma Prefecture					
19	Tanigawa	Mt. Tanigawa, Minakami-cho, Tone-gun (1420m)	1	-	-
20	Shirane	Mt. Shirane, Kusatsu-cho, Agatsuma-gun (1950m)	3	-	-
21	Akagi	Mt. Akagi, Hujimi-mura, Seta-gun (1350m)	1	-	-
22	Yunomaru	Mt. Yunomaru, Tsumagoi-mura, Agatsuma-gun (1950m)	1	1	-
		Chubu District			
Niigata Prefecture					
23	Komyo	Mt. Komyo, Shimoda-mura, Minamikanbara-gun (300m)	1	-	-
24	Hakkai	Mt. Hakkai, Yamato-cho, Minamiuonuma-gun (1700m)	-	-	1
25	Yomogitoge	Yomogitoge, Yuzawa-cho, Minamiuonuma-gun (1300–1500m)	4	-	-

Table 1. (continued)

Toyama Prefecture				
26 Tateyama	Mt. Tateyama, Tateyama-cho, Nakaniikawa-gun (1300–2590m)	8	-	1
Ishikawa Prefecture				
27 Yamasaki	Yamasaki, Oshimizu-cho, Hakui-gun (50m)	-	-	1
28 Kuraga	Mt. Kuraga, Kanazawa City (410m)	2	-	-
29 Iwamado	Iwamado, Oguchi-mura, Ishikawa-gun (1120–2220m)	4	-	-
30 Hakusan	Mt. Hakusan, Oguchi-mura, Ishikawa-gun (1800–2050m)	2	-	1
Nagano Prefecture				
31 Higashitate	Mt. Higashitate Yamanouchi-cho, Shimotakai-gun (1750m)	2	-	-
32 Kurohime	Mt. Kurohime, Togakushi-mura, Kamiminochi-gun (1170–1960m)	9	1	-
33 Togakushi	Mt. Togakushi, Togakushi-mura, Kamiminochi-gun (1820m)	1	-	-
34 Shirouma	Mt. Shiroumadake, Kitaazumi-gun (1800m)	-	1	-
35 Yatsu	Mt. Yatsugatake, Minamimaki-mura, Minamimaki-gun (1800m)	-	1	-
36 Kirigamine	Mt. Kirigamine, Suwa City (1550m)	1	-	-
Yamanashi Prefecture				
37 Fuji	Mt. Fuji, Narusawa-mura, Minamitosu-gun (1700m)	1	-	-
Gifu Prefecture				
38 Ontake	Mt. Ontake, Kosaka-cho, Masuda-gun (2000m)	1	-	-
39 Nenoue	Nenouekogen, Nakatukawa City (1200m)	-	-	3
40 Hisuikyo	Hisuikyo, Yaotsu-cho, Kamo-gun (200m)	-	-	1
41 Kamitoku	Kamitoku, Mizunami City (500m)	1	-	-
Shizuoka Prefecture				
42 Kurakake	Mt. Kurakake, Kannami-cho, Tagata-gun (800m)	-	-	4
43 Nekogoe	Nekogoe, Amagiyunoshima-cho, Tagata-gun (400m)	-	-	3
44 Misawa	Misawa, Kikukawa-cho, Ogasa-gun (80m)	-	1	-
45 Tateyamadera	Tateyamadera, Hamamatsu city (15m)	1	-	-
Aichi Prefecture				
46 Jokoji	Jokoji, Seto City (180m)	2	-	-
	Kinki District			
Shiga Prefecture				
47 Hira	Mt. Hira, Shiga-cho, Shiga-gun (550–960m)	8	1	2
48 Kibogaoka	Kibogaoka, Nosu-cho, Nosu-gun (180m)	-	1	1
49 Ogami	Mt. Ogami, Ozu City (450m)	2	1	2
Kyoto Prefecture				
50 Asyuu	Asyuu, Miyama-cho, Kitakuwata-gun (400m)	-	-	2
51 Hiei	Mt. Hiei, Kyoto City (620–800m)	1	3	2
Nara Prefecture				
52 Nishihara	Nishihara, Kamikitayama-mura, Yoshino-gun (540m)	2	-	-
53 Odai	Mt. Odaigahara, Kamikitayama-mura, Yoshino-gun (1580–1650m)	4	-	-
54 Zenki	Zenki, Shimokitayama-mura, Yoshino-gun (340m)	3	-	-
55 Shimokuwabara	Shimokuwabara, Shimokitayama-mura, Yoshino-gun (220m)	1	-	-

Table 1. (continued)

Mie Prefecture				
56 Nishitani	Nishitani, Kumano City (190m)	2	2	1
57 Anshinbashi	Anshinhashi, Miyagawa-mura, Taki-gun (1450m)	2	-	-
58 Okubo	Okubo, Kumano City (400m)	2	-	-
Wakayama Prefecture				
59 Honguu	Honguu, Honguu-cho, Higashimuro-gun (200m)	-	1	-
60 Koyasan	Koyasan, Koya-cho, Ito-gun (820m)	2	1	-
61 Kawai	Kawai, Shimizu-cho, Arita-gun (500m)	-	2	-
62 Kawane	Kawane, Daito-mura, Nishimuro-gun (160m)	3	-	-
Hyogo Prefecture				
63 Iimori	Mt. Iimori, Kasai City (120m)	-	2	1
	Chugoku District			
Tottori Prefecture				
64 Oginosen	Mt. Oginosen, Kokubu-cho, Iwami-gun (600–1000m)	1	3	-
65 Daisen	Mt. Daisen, Daisen-cho, Saihaku-gun (800–1600m)	1	-	1
66 Odaka	Odaka, Yonago City (80m)	-	-	2
Shimane Prefecture				
67 Sanbe	Mt. Sanbe, Ota City (600–1050m)	2	-	3
68 Michikawa	Michikawa, Hikimi-cho, Mino-gun (480m)	-	1	-
Okayama Prefecture				
69 Asanabe	Mt. Asanabewashigasen, Kawakami-mura, Maniwa-gun (850m)	-	2	-
70 Kanpa	Kanpa, Katsuyama-cho, Maniwa-gun (260m)	-	2	2
Hiroshima Prefecture				
71 Dogo	Mt. Dogo, Saijyo-cho, Hiba-gun (1130–1260m)	1	2	3
72 Hiba	Mt. Hiba, Saijyo-cho, Hiba-gun (1080–1270m)	3	1	4
73 Uenoike	Uenoike, Shyobara City (250m)	-	1	-
74 Onuka	Onuka, Tojyo-cho, Hiba-gun (650m)	-	1	1
75 Yamate	Yamate, Miyoshi City (150m)	-	3	-
76 Tenguishi	Mt. Tenguishi, Geihoku-cho, Yamagata-gun (1100m)	-	1	1
77 Taisenbaru	Taisenbaru, Geihoku-cho, Yamagata-gun (750m)	-	1	1
78 Yawata	Yawatakogen, Geihoku-cho,Yamagata-gun (750–780m)	4	4	7
79 Mikawa	Mikawa-dum, Kouzan-cho, Sera-gun (300m)	-	2	1
80 Kurokawa	Mt. Kurokawamyojin, Seranishi-cho, Sera-gun (530m)	-	1	-
81 Oguni	Oguni, Seranishi-cho, Sera-gun (350m)	1	-	-
82 Haji	Haji-dum, Yachiyo-cho, Takata-gun (250m)	28	33	46
83 Takanosu	Mt. Takanosu, Mukaibara, Takata-gun (750–860m)	5	-	2
84 Shimone	Shimone, Yachiyo-cho, Takata-gun (250m)	-	1	-
85 Sedani	Sedani, Asa-cho, Hiroshima City (100m)	-	1	-
86 Ugakyo	Ugakyo, Asa-cho, Hiroshima City (100m)	1	2	-
87 Kuchi	Kuchi, Asa-cho, Hiroshima City (200m)	1	-	1
88 Sinnyu	Mt. Shinnyu, Togouchi-cho, Yamagata-gun (830–890m)	3	3	2
89 Osorakan	Mt. Osorakan, Togouchi-cho, Yamagata-gun (920–1300m)	2	-	1
90 Tarutoko	Tarutoko-dum, Geihoku-cho, Yamagata-gun (720–760m)	2	2	3
91 Mominoki	Mominoki, Togouchi-cho, Yamagata-gun (660m)	2	-	-
92 Obara	Obara, Tsutsuga-mura, Yamagata-gun (350m)	-	1	-
93 Jippo	Mt. Jippo, Yoshiwa-mura, Saeki-gun (750m)	2	-	-

Table 1. (continued)

94 Mitsugi	Mitsugihachiman, Mitsugi-cho, Mitsugi-gun (200m)	1	-	-
95 Seno	Seno, Senogawa-cho, Hiroshima City (100m)	-	1	-
96 Kurashige	Kurashige, Itsukaichi-cho, Saeki-gun (80m)	2	6	-
97 Ege	Egedani, Yuki-cho, Saeki-gun (500m)	1	-	1
98 Gokurakuji	Gokurakuji, Hatsukaichi-cho, Saeki-gun (650m)	1	1	-
99 Aratani	Mt. Aratani, Asa-cho, Hiroshima City (450m)	2	-	-
100 Hatadao	Hatadao, Numata-cho, Hiroshima City (300m)	1	1	-
101 Otsuka	Otsuka, Numata-cho, Hiroshima City (250m)	-	-	1
102 Ushiobara	Ushiobara, Yoshiwa-mura, Saeki-gun (650m)	-	2	2
103 Iiyama	Iiyama, Saeki-cho, Saeki-gun (650m)	-	1	-
104 Uchiodani	Uchiodani, Yuki-cho, Saeki-gun (350m)	2	-	-
105 Omine	Mt. Omine, Yuki-cho, Saeki-gun (540–840m)	3	1	1
106 Haigamine	Mt. Haigamine, Kure City (600m)	-	2	1
107 Nagahama	Nagahama, Miyajima-cho, Saeki-gun (60m)	18	22	18
108 Misen	Mt. Misen, Miyajima-cho, Saeki-gun (410m)	-	2	2
109 Une	Mt. Une, Okimi-cho, Saeki-gun (200m)	1	-	1
110 Watase	Watase-dum, Ono-cho, Saeki-gun (250m)	-	1	1
Yamaguchi Prefecture				
111 Kasayama	Kasayama, Hagi City (100m)	-	1	-
112 Chomonkyo	Chomonkyo, Kawakami-mura, Abu-gun (280m)	2	-	-
113 Dogadake	Mt. Dogadake, Nagato City (450m)	-	2	1
	Shikoku District			
Ehime Prefecture				
114 Higashi	Mt. Higashiakaishi, Beshiyama-mura, Uma-gun (1000–1600m)	2	-	1
115 Ichinokawa	Ichinokawa, Ojuin-cho, Saijyo City (150m)	1	1	-
116 Kanpuu	Mt. Kanpuu, Saijyo City (1400m)	-	-	1
Tokushima Prefecture				
117 Kumohaya	Kumohaya, Kamiyama-cho, Nanishi-gun (980m)	1	-	2
118 Tsurugi	Mt. Tsurugi, Higashiiya-mura, Miyoshi-gun (1560–1900m)	12	4	3
119 Kirikosi	Kirikoshitoge, Kainan-cho, Kaifu-gun (650m)	3	-	1
120 Minanose	Minanose, Kainan-cho, Kaifu-gun (100m)	1	-	1
121 Kushikawa	Kushikawa, Kaifu-cho, Kaifu-gun (20m)	5	1	-
Kochi Prefecture				
122 Shiraga	Mt. Shiraga, Monobe-mura, Kami-gun (1200m)	-	1	-
123 Sameura	Sameura, Tosa-cho, Tosa-gun (350m)	6	-	1
124 Naragitoge	Naragitoge, Tosayama-mura, Tosa-gun (600–650m)	4	2	3
125 Segiri	Segiri, Yasuda-cho, Aki-gun (200m)	2	-	1
126 Asahide	Asahide, Umazi-mura, Aki-gun (250m)	4	-	-
127 Kitaji	Kitaji, Umazi-mura, Aki-gun (300m)	2	2	-
128 Hirano	Hirano, Umazi-mura, Aki-gun (250m)	2	-	-
129 Sakamoto	Sakamoto, Umazi-mura, Aki-gun (400m)	3	1	-
130 Kuki	Kuki, Kitagawa-mura, Aki-gun (350m)	4	-	1
131 Todoroki	Todoroki, Kitagawa-mura, Aki-gun (350m)	2	-	2
132 Ichinoue	Ichinoue, Kitagawa-mura, Aki-gun (200m)	2	-	-
133 Hiranabe	Hiranabe, Kitagawa-mura, Aki-gun (150m)	5	-	2
134 Godai	Mt. Godai, Godaisan-cho, Kochi City (90m)	-	-	1
135 Amikawago	Amikawagoe, Mitani-cho, Kochi City (420m)	-	3	3
136 Futsusegoe	Futsusegoe, Engyoji-cho, Kochi City (350m)	-	-	2

Table 1. (continued)

137 Myojin	Mt. Myojin, Agawa-mura, Agawa-gun (1500m)	-	-	1
138 Kashiwagi	Kashiwagi, Kitagawa-mura, Aki-gun (100m)	2	-	-
139 Ashizuri	Ashizurimisaki, Tosashimizu City (300m)	-	2	1
	Kyusyu District			
Fukuoka Prefecture				
140 Kosho	Mt. Kosho, Amagi City (780m)	1	-	-
141 Meotogi	Meotogi, Kusa-cho, Kurume City (80m)	-	-	1
Nagasaki Prefecture				
142 Oita	Oita, Izuhara-cho, Shimoagata-gun (150m)	10	7	1
143 Kamimisaka	Kamimisaka, Izuhara-cho, Shimoagata-gun (120m)	-	1	-
144 Uchiyama	Uchiyama, Izuhara-cho, Shimoagata-gun (150m)	12	1	-
145 Kuroki	Kuroki, Omura City (350m)	1	-	-
146 Inasa	Mt. Inasa, Nagasaki City (250m)	-	-	1
Oita Prefecture				
147 Dannoharu	Dannoharu, Oita City (80m)	-	-	1
148 Inoseto	Inoseto, Beppu City (800m)	1	-	-
149 Iidakogen	Iidakogen, Kokonoe-cho, Kusu-gun (1100m)	-	1	1
Miyazaki Prefecture				
150 Mukozaka	Mt. Mukozaka, Gokanose-cho, Nishiusuki-gun (1600m)	2	-	-
151 Obata	Obata, Shiiba-mura, Higashiusuki-gun (850m)	1	-	1
152 Osuzu	Mt. Osuzu, Tsuno-cho, Koyu-gun (440–560m)	11	3	6
153 Shiratori	Mt. Shiratori, Takaharu-cho, Nishimorokata-gun, (1200–1350m)	7	1	-
154 Ebino	Ebinokogen, Ebino-cho, Nishimorokata-gun (1100–1200m)	10	-	8
Kumamoto Prefecture				
155 Honmyoji	Honmyoji, Ikeda-cho, Kumamoto City (350m)	1	1	-
156 Tatsuta	Mt. Tatsuta, Shimizu-cho, Kumamoto City, (120m)	2	1	2
157 Hirogawara	Hirogawaradani, Yabe-cho, Kamimashiki-gun (760m)	8	1	2
158 Haki	Haki, Izumi-mura, Yatsushiro-gun (850m)	1	-	-
159 Nihonsugi	Nihonsugi, Izumimura, Yatsushiro-gun (1100m)	1	-	-
160 Maeshima	Maeshima, Matsushima-cho, Amakusa-gun (80m)	-	2	2
161 Odorigoe	Odorigoe, Itsuki-mura, Kuma-gun (750m)	1	-	-
162 Joseki	Joseki, Shinwa-cho, Amakusa-gun (150m)	1	-	-
163 Ichifusa	Ichifusa-dum, Mizukami-mura, Kuma-gun (320m)	1	1	-
164 Yude	Yude, Minamata City (250m)	2	-	-
Kagoshima Prefecture				
165 Gyojindake	Mt. Gyojindake, Nagashima-cho, Izumi-gun (300m)	-	1	-
166 Juso	Juso, Ookuti City (300m)	1	-	-
167 Imutaike	Imutaike, Kedoin-cho, Satsuma-gun (400m)	1	-	-
168 Takakuma	Mt. Takakuma, Tarumizu City (450m)	2	1	1
169 Yaku-1	Yaku Island, Kamiyaku-cho, Kumage-gun (750m)	2	-	-
170 Yaku-2	Yaku Island, Kamiyaku-cho, Kumage-gun (120m)	1	-	-
171 Yaku-3	Yaku Island, Yaku-cho, Kumage-gun (250–1650m)	11	-	-
172 Yaku-4	Yaku Island, Yaku-cho, Kumage-gun (150–1800m)	2	-	-
	Total	359	172	198

and treated as a "species complex" (Ghatak, 1965), in the present paper *L. clavatum* is interpreted in a broad sense. In total 729 individuals of *L. clavatum* were collected from 172 localities which ranged from Yaku Island (30°15′N) to Rebun Island (45°25′N), covering almost the entire range of this species in the Japanese archipelago. Their chromosome numbers were then determined.

Locality code numbers (Loc.), names of studied sites, localities, and number of individuals whose chromosome number was determined are given in Table 1. The geographical and altitudinal distributions of studied sites are shown in Figs. 1 and 2. The maps were constructed by Horikawa's methods (1972); the geographical distribution maps are divided into squares each of which corresponds to the area of a governmental "topographic map" of 1/50000. This unit square covers an area 10 minutes in latitude by 15 minutes in longitude (Fig. 1). A unit square of the altitudinal distribution maps covers 10 minutes in latitude and 100 m in altitude (Fig. 2). Occurrence of a plant within a square is indicated by one solid circle, irrespective of the number of known studying sites. Numbers in Figs. 1 and 2 correspond to locality code numbers which appear in Table 1.

Because *Lycopodium clavatum* propagates vegetatively by longcreeping rhizomes and forms extensive colonies, the number of individuals in a population is often unclear. Thus only plants that appeared to represent distinct individuals were collected in this study.

According to the method of Takamiya and Tanaka (1982), the number of individuals sampled from a study site was determined in the following manner. When a population of *Lycopodium clavatum* was indivisible into colonies and the individuals in this population showed morphological homogeneity with respect to peduncle and pedicel length at the spike, one or more individuals were sampled. When individuals in a population showed morphological heterogeneity, individuals which covered all of the variation of the population were sampled. On the other hand, when a population was divisible into colonies, one or more individuals were sampled from each colony.

In all of the sampling materials, we analyzed only individuals whose chromosome numbers were determined. The voucher specimens of chromosome observations were deposited in the Herbarium of the Botanical Institute, Hiroshima University. The collection numbers shown throughout this paper are Takamiya's collection numbers.

II. *Ecological Studies of the Growing Places*

In the native habitats where *Lycopodium clavatum* was collected, the altitude, vegetation, light conditions, and edaphic conditions of the growing places were recorded. All of the plant species associated with *L. clavatum* were listed in Muine (Loc. 6), Tateyama (Loc. 26), Kurohime (Loc. 32), Hira (Loc. 47), Hiba (Loc. 72), Tsurugi (Loc. 118), Shiratori (Loc. 153), and Ebino (Loc. 154).

In Haji (Loc. 82) 20 quadrats of 1×1 m^2 were set in the populations of *Lycopodium clavatum* along the roadway, and the coverage and height of each plant in each quadrat were recorded according to Numata (1969). The same study was also made in Nagahama (Loc. 107) of 18 quadrats. For comparison, each quadrat's degree of succession (DS) (Numata, 1961, 1974) was calculated. The degree of succession was defined as follows:

$$DS = [(l \times d)/n] \times v$$

where l is the life span (Th: 1, H, Ch, G: 10, N: 50 and M, MM: 100 depending on Raunkiaer's life-forms), d is the summed dominance ratio (SDR3), n is the number of species, and v is the ground cover (100% cover = 1). SDR3 is (C' + H' + F')/3, where C', H', and F' are cover ratio (%), plant height ratio (%), and frequency ratio (%). Population having low DS values are at pioneer phase, but high DS values are later successional phases in a plant community.

III. *Methods for Observation of Somatic and Meiotic Chromosomes*

For the cytological studies, the materials were treated directly in the field or were transplanted and cultivated in the Botanical Institute, Faculty of Science, Hiroshima University.

The somatic chromosomes were observed in the meristematic cells of root tips. Sometimes shoot apices were also used for observations. After pretreatment with 0.05% colchicine for 6 hours at 20°C the root tips or stem apices were fixed in modified Carnoy's solution (99% ethanol : chloroform : acetic acid = 2 : 1 : 1) for over 1 hour at about 5°C. The fixed materials were macerated with 1 N HCl at 60°C for 30 seconds. They were stained with 2% aceto-orcein and then squashed.

For karyomorphological analysis, we used 32 diploid individuals from 23 localities, 12 triploids from 10, and 15 tetraploids from 12. The somatic metaphase chromosomes were arranged in the descending order of the total length of the chromosomes and the number (1, 2, 3,---) were allotted to them. The classification of mitotic chromosomes at metaphase was done according to the system proposed by Levan *et al.* (1964) and modified by Walker (1985), and other nomenclature of karyotypes follows Tanaka (1980).

For observation of meiotic chromosomes, we used a modified version of the method described by Takamiya and Kurita (1983). Young strobili of *Lycopodium clavatum* were fixed in modified Carnoy's solution (99% ethanol : chloroform : acetic acid = 3 : 1 : 1) for over 24 hours at about 5°C, and refixed with fresh fixative just before examination. Sporangia only were macerated with 1 N HCl at 60°C for 30 seconds and rinsed in distilled water. Then the sporangial walls were removed, and the spore mother cells (= SMCs) were spread on a glass slide and squashed in 2% acetocarmine. The configurations of chromosomes at diakinesis or metaphase I were examined in more than 20 SMCs in each individual. The divisions and segregations of chromosomes were observed in a hundred SMCs at each meiotic stage from anaphase I to telophase II.

The nomenclature of species follows Tagawa (1959) and Ohwi (1975).

RESULT

In this study, the somatic chromosome numbers of *Lycopodium clavatum* were determined in 729 individuals from 172 localities. Among these, 359 individuals from 116 localities were of the diploid cytotype with $2n = 68$, 172 from 77 localities were of the triploid cytotype with $2n = 102$, and 198 from 77 localities were of the tetraploid cytotype with $2n = 136$ (Table 1 and Fig. 3). No other chromosome numbers were observed. The occurrence of polyploid cytotypes in *L. clavatum* was previously reported in several

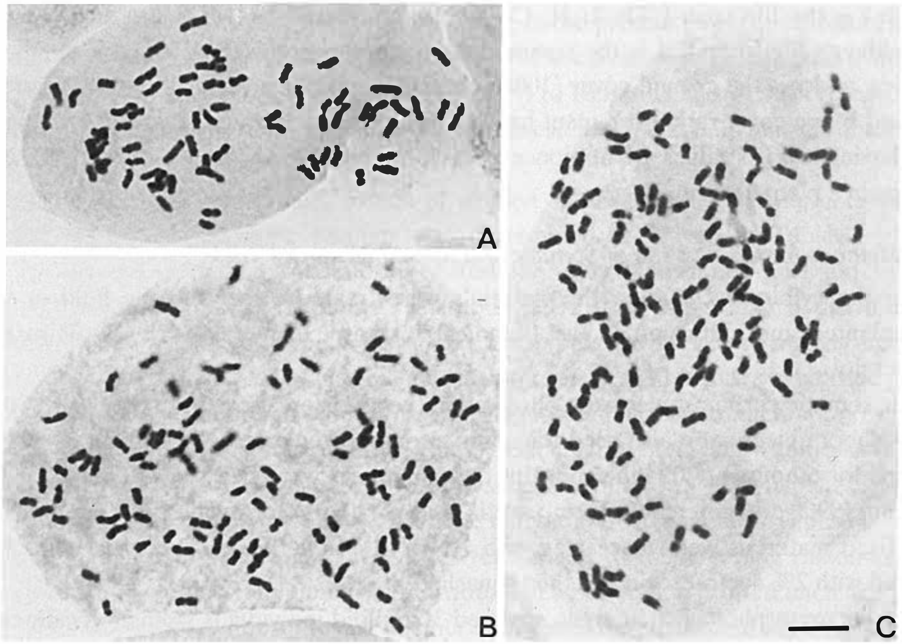

Fig. 3. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum*. A, 2n = 68, from Mt. Kirigamine, Nagano Prefecture (Loc. 36, *Takamiya 2147*). B, 2n = 102, from Yamate, Hiroshima Pref. (Loc. 75, *Takamiya 1689*). C, 2n = 136, from Mt. Hiei, Kyoto Pref. (Loc. 51, *Takamiya 1423*). Bar represents 5 μm.

localities of Hiroshima Prefecture in western Japan (Tanaka and Takamiya, 1981; Takamiya and Tanaka, 1982). Those results were confirmed in this study from many localities throughout Japan.

I. *Hokkaido District*

Lycopodium clavatum mainly occurs in the mountain regions in the Hokkaido District, and a morphologically distinct form referred to as *L. clavatum* var. *robustius* is known in high mountains (Miyabe and Kudo, 1930; Kawano, 1972; Sato, 1982). In this study, field observations and collections were made in eight localities of *L. clavatum* populations at an elevation of 60 m to 1460 m. Chromosome numbers were determined in 20 individuals, of which 16 collected from 8 localities were diploids and 4 from 3 were tetraploids. No triploid plants were found (Figs. 1, 2, 4; Table 1).

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows: On Rebun Island (Loc. 1), diploid individuals grew around the edges (alt. 300 m) and on the floor (alt. 450 m) of a *Pinus pumila* scrub, and tetraploid individuals grew in an open place (alt. 600 m). On Rishiri Island (Loc. 2), diploid individuals grew on the floor of a *Betula ermanii* forest (alt. 1200 m), and tetraploid individuals grew around the edges of a secondary open forest (alt. 600 m). In Shirikoma (Loc. 3), Kogennuma (Loc. 4) and Nopporo (Loc. 5), only diploid individuals were found on the floors of *Abies sachalinensis* forests.

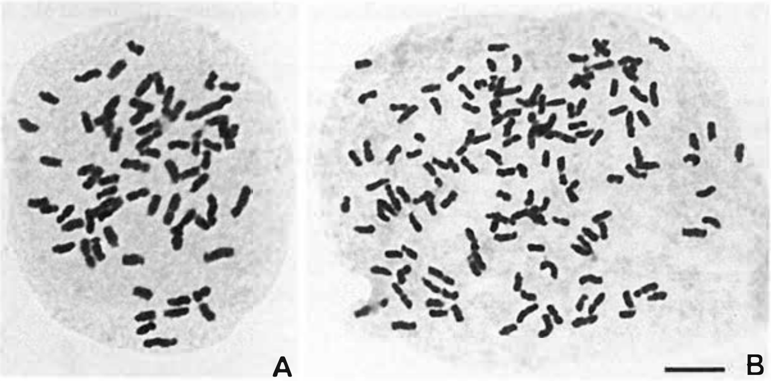

Fig. 4. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Hokkaido District. A, 2n = 68, from Mt. Muine, Sapporo City (Loc. 6, *Takamiya 1533*). B, 2n = 136, from Rishiri Island, Rishiri-gun (Loc. 2, *Takamiya 1565*). Bar represents 5 μm.

The habitats of *Lycopodium clavatum* on Mt. Muine (Loc. 6), where diploid and tetraploid cytotypes were found, are explained by a list of plants associated with *L. clavatum* (Table 2) and by a map showing collection sites (Fig. 5). The explorational route, ranging from alt. 400 m to 1460 m, crossed three vegetation zones: deciduous broad-leaved forest dominated by *Betula ermanii,* coniferous forest dominated by *Abies sachalinensis* and *Picea jezoensis*, and alpine zones dominated by *Pinus pumila.* Diploid individuals grew on the floor of a well-developed *Betula ermanii* forest (*1533*) or scrub (*1543*), around the edges of a 2–3 m tall *Sasa kurilensis* grassland (*1535*), on the floor of a *Picea jezoensis* forest (*1548*) or a *Pinus pumila* scrub (*1539*). These areas formed a shady, humid microenvironment. Diploid individuals also occurred on a sunny, humid environment on the slope along the ridge (*1544*). On the other hand, tetraploid individuals grew in a sunny, humid snowbed grassland (*1541*) and on a sunny, dry, disturbed, open place (*1546*). Diploid and tetraploid individuals were not found intermingled with one another, but occurred in different habitats.

In Takaoka (Loc. 7), only diploid individuals grew on the floor of a *Quercus mongolica* var. *grosseserrata* forest. In Kenashi (Loc. 8), only diploid individuals were found around the edges of a *Fagus crenata* forest.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in three diploid individuals (*1533, 1535, 1539* from Loc. 6) and in two tetraploids (*1565* from Loc. 2; *1541* from Loc. 6). They are described as follows:

In the diploids, the longest chromosome of the complement was 3.0 μm long and had the centromere in median position, while the shortest chromosome was 1.3 μm long and had the centromere in submedian position (Fig. 6). The chromosomes of the complement showed a gradual decrease in length from the longest to the shortest. Out of 68 chromosomes, 22 had the centromeres in the median position, 12 in the submedian position, 18 in the subterminal position, and 16 in the terminal position. Thus, the chromosome complement was categorized as the symmetric karyotype in arm ratio

Table 2. A list of plants associated with each individual of *Lycopodium clavatum* on Mt. Muine (Loc. 6)

Specimen number	*1533*	*1535*	*1539*	*1541*	*1543*	*1544*	*1545*	*1546*	*1548*
Ploidy	2x	2x	2x	4x	2x	2x	2x	4x	2x
Altitude (m)	800	1120	1350	1460	1300	1150	840	600	560
Name of species associated									
Tree Layer									
Betura ermanii	+	−	−	−	−	−	−	−	−
Picea jezoensis	−	−	−	−	−	−	−	−	+
Shrub Layer									
Pinus pumila	−	−	+	−	−	−	−	−	−
Betula ermanii	−	−	−	−	+	−	+	−	−
Alnus maximowiczii	−	−	−	−	−	−	+	−	−
Acer tschonoskii	−	+	−	−	−	−	−	−	−
Viburnum furcatum	+	+	−	−	−	−	−	−	+
Herb Layer									
Sasa kurilensis	+	+	−	−	+	+	−	−	+
Calamagrostis arundinacea	−	−	−	+	−	+	−	−	−
Carex sp.	−	−	−	−	−	−	−	+	−
Maianthemum dilatatum	−	+	−	−	−	−	−	−	−
Salix sachalinensis	−	−	−	−	−	+	−	−	−
Betula ermanii	+	−	−	−	+	−	−	−	−
Cornus canadensis	−	−	+	−	−	−	−	−	−
Schizophragma hydrangeoides	+	−	−	−	−	−	−	−	−
Coptis trifolia	−	−	−	+	−	−	−	−	−
Hypericum kamtschaticum	−	−	−	−	+	−	−	−	−
Fragaria nipponica	−	−	−	−	+	−	−	−	−
Ilex sugerokii var. *brevipedunculata*	−	−	−	−	+	+	−	−	−
Vaccinium vitis-idaea	−	−	−	+	−	−	−	−	−
Viburnum furcatum	−	+	−	−	−	−	−	−	−
Lycopodium annotinum	−	−	+	−	−	−	−	−	−
Athyrium brevifrons	−	−	−	−	+	−	+	−	+
Phegopteris polypodioides	−	−	−	−	+	−	−	−	−
Dryoteris amurensis	−	+	−	−	−	−	−	−	+

(Tanaka, 1980). No satellited chromosome was observed.

In the tetraploids, the longest chromosome of the complement was 3.0 μm long and had the centromere in the median position, while the shortest chromosome was 0.9 μm long and had the centromere in the submedian position (Fig. 7). The chromosomes of the complement showed a gradual decrease in length from the longest to the shortest. Out of 136 chromosomes, 46 had the centromere in the median position, 24 in the submedian position, 34 in the subterminal position, and 32 in the terminal position. So, the chromosome complement was categorized as the symmetric karyotype in arm ratio (Tanaka, 1980). No satellited chromosome was observed. Since the chromosome com-

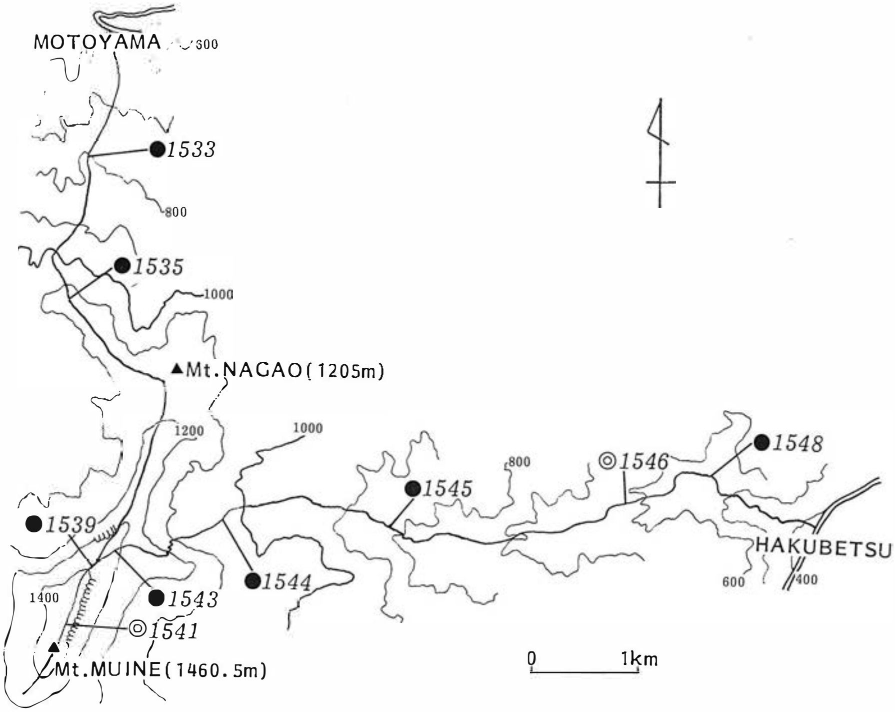

Fig. 5. A map showing the site of the collections of *Lycopodium clavatum* on Mt. Muine, Sapporo City (Loc. 6). Numbers are voucher specimen numbers. Solid circle, diploid; double circle, tetraploid.

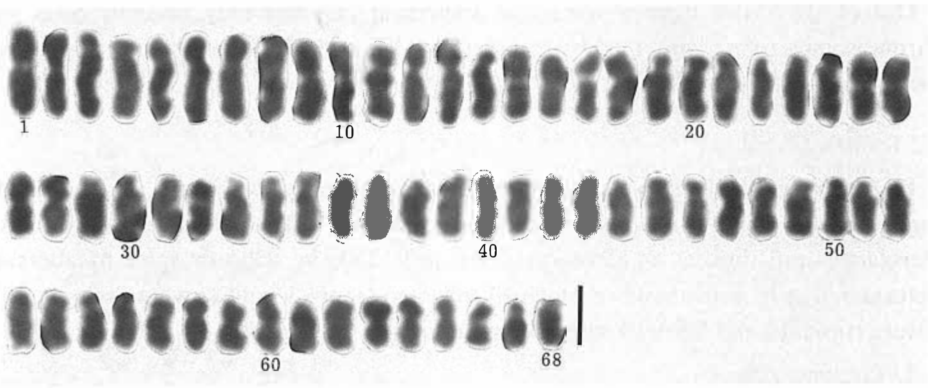

Fig. 6. Serial arrangement of the mitotic metaphase chromosomes of diploid *Lycopodium clavatum* ($2n=68$, *Takamiya 1533* from Loc. 6). Bar represents 2 μm.

plement in the tetraploid plants represent a duplication of the complement in the diploid plants, this tetraploid was thought to have an autotetraploidal nature. But there were no clear homologous chromosome sets of four in a chromosome complement.

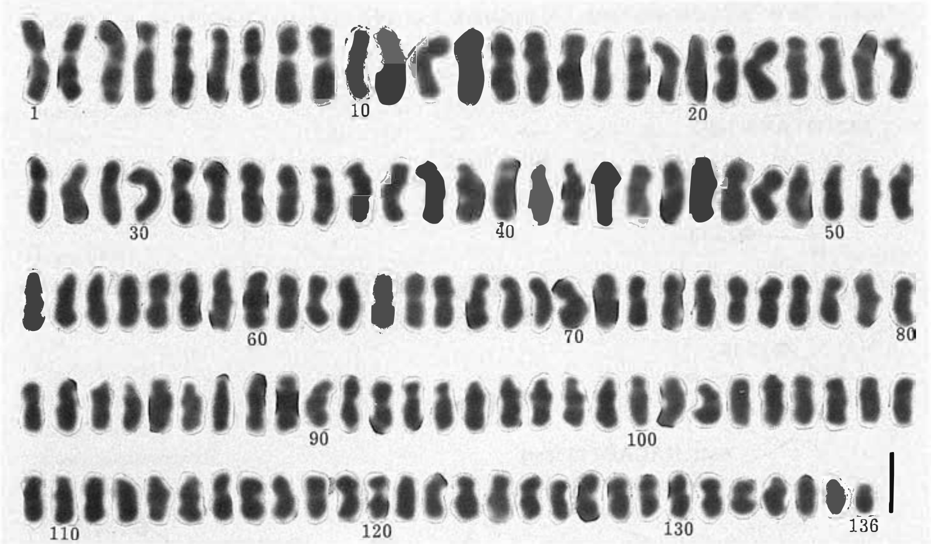

Fig. 7. Serial arrangement of the mitotic metaphase chromosomes of tetraploid *Lycopodium clavatum* (2n = 136, *Takamiya 1565* from Loc. 2). Bar represents 2 μm.

3. Meiosis

At diakinesis or metaphase I of meiosis, 42 SMCs were observed from 2 diploid individuals (*1533, 1535* from Loc. 6) and 20 SMCs from a tetraploid individual (*1565* from Loc. 2).

The diploid with 2n = 68 consistently produced only bivalent pairs of all chromosomes (34_{II}) at diakinesis or metaphase I (Fig. 8A). At each stage subsequent to metaphase I, segregations and divisions of the chromosomes were normal.

Out of 20 SMCs from a tetraploid individual, 19 had only bivalent pairs of all chromosomes (68_{II}), and 1 had $67_{II} + 2_{I}$ (Figs. 8B and C). Each stage subsequent to metaphase I was normal.

II. *Tohoku District*

In the Tohoku District, *Lycopodium clavatum* commonly occurs in the mountain regions. In this study, field observations and collections were made in nine localities of *L. clavatum* populations at an elevation of 200 m to 1500 m. Chromosome numbers were determined in 18 individuals, of which 10 collected from 6 localities were diploids, 3 from 3 were triploids, and 5 from 4 were tetraploids (Figs. 1, 2, 9; Table 1).

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows: On Mt. Iwaki (Loc. 9), diploid individuals grew around the edges (alt. 750 m) and on the floor (alt. 450 m) of *Quercus mongolica* var. *grosseserrata* forests, and tetraploid individuals grew in an open place (alt. 750 m). In Hayanose (Loc. 10), only triploid individuals were found around the edges of a *Chamaecyparis obtusa* plantation. In Hachimantai (Loc. 11), only tetraploid individuals grew on the sunny side of a roadside

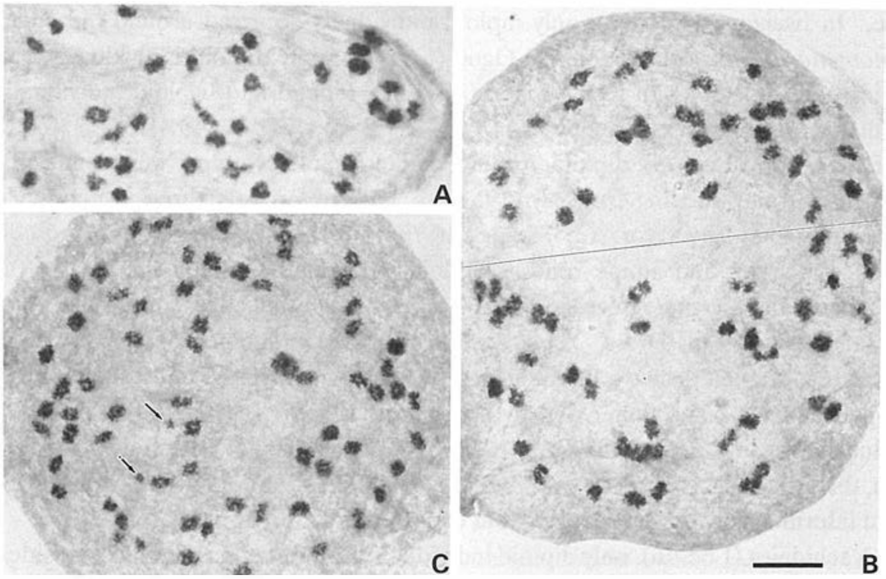

Fig. 8. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of *Lycopodium clavatum* examined in Hokkaido District. A, 2n=68=34_{II}, *Takamiya 1533* from Loc. 6. B and C, 2n=136, *Takamiya 1565* from Loc. 6 (B, 68_{II}; C, $67_{II}+2_{I}$). Arrows indicate univalents. Bar represents 10 μm.

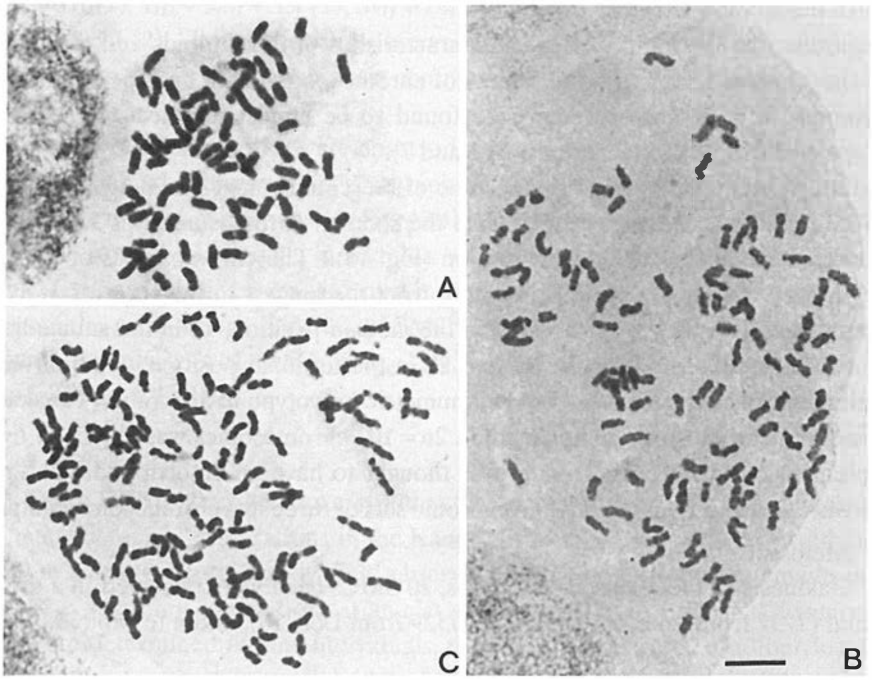

Fig. 9. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Tohoku District. A, 2n=68, from Mt. Iwaki, Aomori Prefecture (Loc. 9, *Takamiya 1526*). B, 2n=102, from Hayanose, Aomori Pref. (Loc. 10, *Takamiya 1529*). C, 2n=136, from Tokusawa, Fukushima Pref. (Loc. 17, *Takamiya 1708*). Bar represents 5 μm.

slope. In Iwaizumi (Loc. 12), only diploid individuals occurred around the edges of a *Cryptomeria japonica* plantation. In Ogoe (Loc. 13), only diploid individuals grew on a humid roadside slope. In Rokujurigoe (Loc. 14), diploid and triploid individuals grew together on a roadside slope.

On Mt. Asahi (Loc. 15), diploid, triploid, and tetraploid cytotypes were found. The explorational route, ranging from alt. 450 m to 1700 m, crossed three vegetation zones: deciduous broad-leaved forest dominated by *Fagus crenata*, coniferous forest dominated by *Abies mariesii*, and alpine zones. Diploid individuals grew on the floor of a well-developed *Fagus crenata* forest (alt. 560 m), around the edges of a *Sasa kurilensis* grassland (alt. 960 m) and a *Quercus mongolica* var. *undulatifolia* scrub (alt. 1500 m). These areas formed a shady, humid microenvironment. Triploid individuals occurred in an open cutover place dominated by *Miscanthus sinensis* (alt. 550 m). Tetraploid individuals grew in a sunny, humid, snowbed grassland (alt. 1540 m) and in a sunny, dry, open, disturbed place (alt. 1420 m). Diploid, triploid and tetraploid individuals were not found intermingled with one another, but occurred in different habitats.

In Yachidaira (Loc. 16), only diploid individuals were found on a humid roadside slope. In Tokuzawa (Loc. 17), only tetraploid individuals occurred on a roadside slope.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in two diploid individuals (*1526*, *1528* from Loc. 9), in a triploid (*1529* from Loc. 10), and in a tetraploid (*1706* from Loc. 17).

Regarding the karyomorphological characteristics of the diploids and the tetraploids from the Tohoku District, the variations of chromosome length and the positions of the centromere in each chromosome were found to be almost identical to those of each cytotype of the Hokkaido District (Fig. 6 and 7).

In the triploid, the longest chromosome of the complement was 3.2 μm and had the centromere in the median position, while the shortest chromosome was 1.3 μm and had the centromere in the submedian position (Fig. 10). The chromosomes of the complement showed a gradual decrease in length from the longest to the shortest. Out of 102 chromosomes, 34 had the centromere in the median position, 19 in the submedian position, 26 in the subterminal position, and 23 in the terminal position. The chromosome complement was categorized to be the symmetric karyotype in arm ratio (Tanaka, 1980). Because the chromosome complement in $2n=102$ chromosomes was about 1.5 times the complement of $2n=68$, this triploid was thought to have an autotriploidal nature. But there were no clear homologous chromosome sets of three in a chromosome complement.

3. Meiosis

At diakinesis or metaphase I of meiosis, 20 SMCs each were observed in a diploid individual (*1737* from Loc. 16), a triploid (*1529* from Loc. 10), and a tetraploid (*1524* from Loc. 9).

Only bivalent pairs of all chromosomes ($34_{\rm II}$) were observed in a diploid individual (Fig. 11A). Out of 20 SMCs from a tetraploid examined, 17 had only bivalent pairs of all chromosomes ($68_{\rm II}$) (Fig. 11F) and 3 had $67_{\rm II}+2_{\rm I}$. Each stage subsequent to metaphase I was normal in both cytotypes.

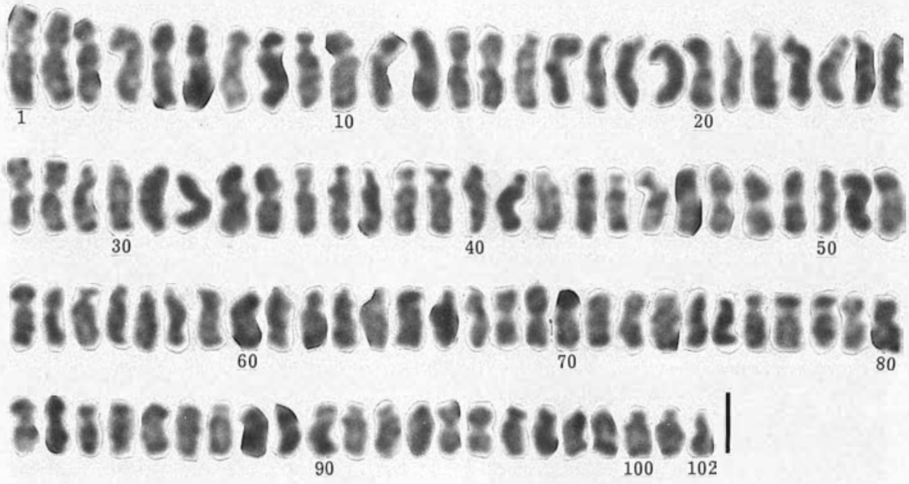

Fig. 10. Serial arrangement of the mitotic metaphase chromosomes of triploid *Lycopodium clavatum* (2n = 102, *Takamiya 1529* from Loc. 10). Bar represents 2 μm.

In a triploid individual, 11 different configurations were observed (Fig. 11B–E): $3_{III}+33_{II}+27_{I}$ (1 SMC), $2_{III}+34_{II}+28_{I}$ (2), $1_{III}+37_{II}+25_{I}$ (1), $1_{III}+35_{II}+29_{I}$ (3), $1_{III}+34_{II}+31_{I}$ (1), $1_{III}+32_{II}+35_{I}$ (1), $39_{II}+24_{I}$ (1), $38_{II}+26_{I}$ (1), $36_{II}+30_{I}$ (3), $35_{II}+32_{I}$ (4), and $34_{II}+34_{I}$ (2). Trivalents were observed in 9 of 20 SMCs, and their number per SMC varied from 1 to 3. The commonest configuration was $35_{II}+32_{I}$ and with a mean of $0.7_{III}+34.8_{II}+30.5_{I}$.

Various kinds of abnormalities were observed throughout all stages of meiosis (Fig. 12). Every SMC examined had univalents at metaphase I (Fig. 12A) and lagging chromosome or chromosome bridges at anaphase I (Fig. 12B). At telophase I or interkinesis, all SMCs examined had several micronuclei in addition to two daughter nuclei (Figs. 12C, D). At metaphase II, abnormalities were observed in 91% of SMCs (Fig. 12E, F). At anaphase II, abnormalities were observed in 92% of SMCs (Figs. 12G–J), but lagging chromosomes were found in only 2% of SMCs (Fig. 12I). At telophase II, 87% of SMCs had micronuclei (Figs. 12K, L).

III. *Kanto District*

In the Kanto District *Lycopodium clavatum* commonly occurs in hills or mountains. In spite of many botanical explorations in the Kanto District, no plant was collected at less than 1350 m altitude. In this study, field observations and collections were made in five localities of *L. clavatum* populations at an elevation of 1350 m to 1950 m. Chromosome numbers were determined in nine individuals, of which six collected from four localities were diploid, two from two were triploid, and one from one was tetraploid (Figs. 1, 2, 13; Table 1).

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows:

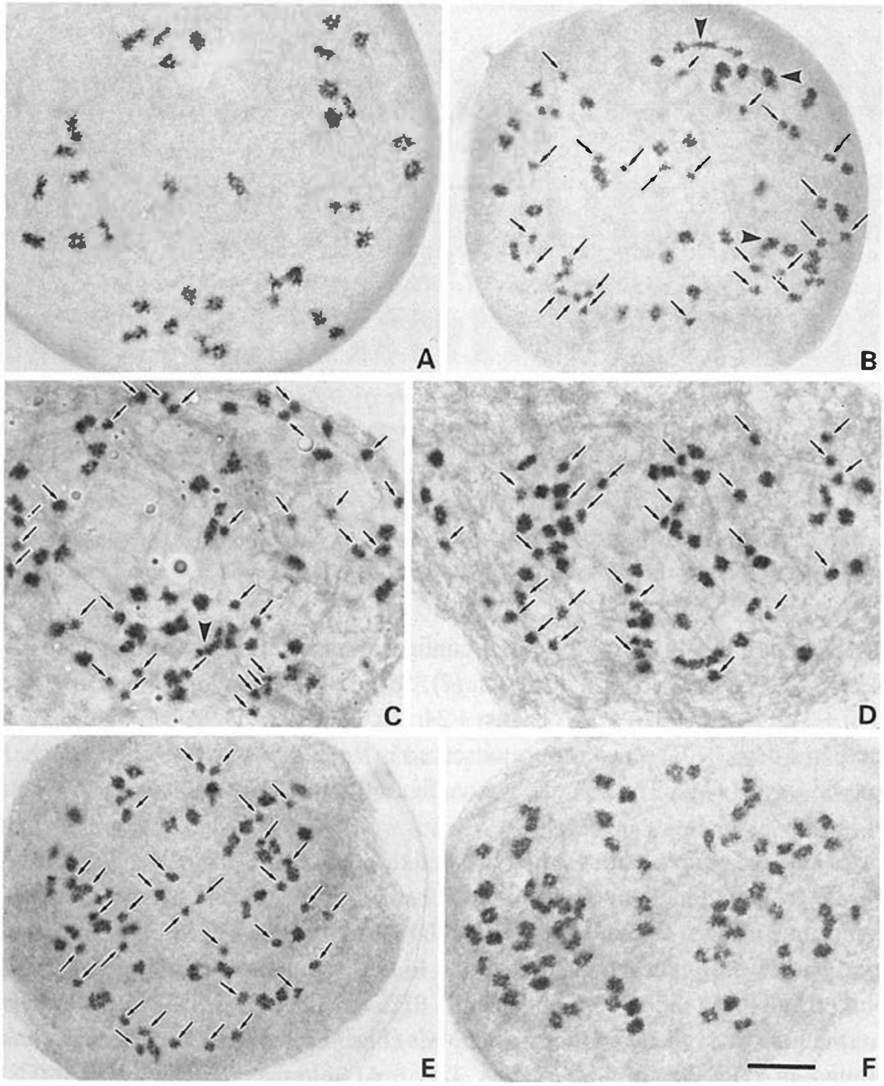

Fig. 11. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of *Lycopodium clavatum* examined in Tohoku District. A, $2n=68=34_{\text{II}}$, *Takamiya 1737* from Loc. 16. B–E, $2n=102$, *Takamiya 1529* from Loc. 10. B, $3_{\text{III}}+33_{\text{II}}+27_{\text{I}}$; C, $1_{\text{III}}+35_{\text{II}}+29_{\text{I}}$; D, $37_{\text{II}}+28_{\text{I}}$; E, $35_{\text{II}}+32_{\text{I}}$ Arrow heads and arrows indicate trivalents and univalents, respectively. F, $2n=136=68\text{II}$, *Takamiya 1524* from Loc. 9. Bar represents 10 µm.

In Yumoto (Loc. 18), diploid individuals grew around the edges of a *Quercus mongolica* var. *grosseserrata* forest (alt. 1500 m), and tetraploid individuals grew in the disturbed grassland of a skiing ground (alt. 1600 m). On Mt. Tanigawa (Loc. 19), only triploid individuals were found in a grassland near the mountaintop. On Mt. Shirane (Loc. 21), only diploid individuals grew around the edges of a *Sasa kurilensis* grassland. On Mt. Akagi (Loc. 21), only diploid individuals occurred on the floor of a *Quercus mongolica* var. *grosseserrata* forest. On Mt. Yunomaru (Loc. 22), diploid individuals grew around the edges of a *Tsuga diversifolia* forest, and triploid individuals grew in a sunny, open place.

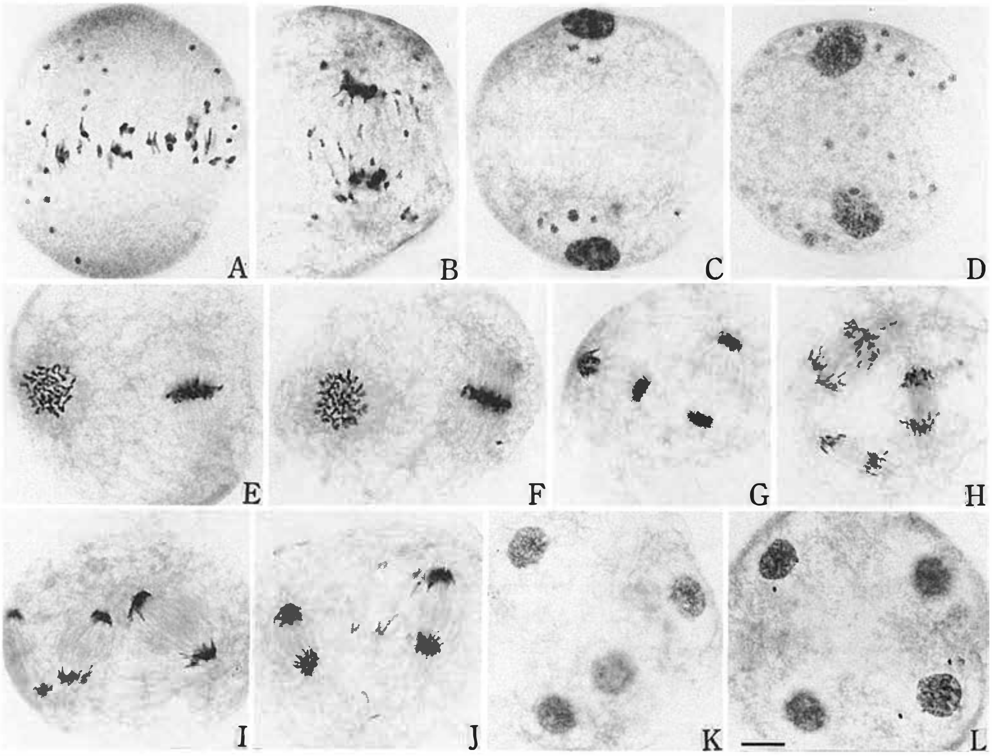

Fig. 12. Photomicrographs of SMCs at various meiotic phases of triploid *Lycopodium clavatum* with 2n = 102 (*Takamiya 1529*). A, metaphase I; B, anaphase I; C and D, telophase I or interkinesis; E and F, metaphase II; G – J, anaphase II; K and L, telophase II. In A– D, F, H– J, L, abnormal divisions are observed. Bar represents 10 μm.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in two diploid individuals (*1514*, *1520* from Loc. 20). The variations of chromosome length and the positions of the centromere in each chromosome were almost identical to those of the Hokkaido District (Fig. 6).

IV. *Chubu District*

Lycopodium clavatum commonly occurs from lowland hills up to high mountains in the Chubu District, and a morphologically distinct form referred to as *L. clavatum* var. *robustius* is known in the high mountains (Ota *et al.*, 1983; Satomi, 1983; Sugimoto, 1984). Field observations and collections were made in 24 localities of *L. clavatum* populations at an elevation of 15 m to 2590 m. Chromosome numbers were determined in 59 individuals, of which 42 collected from 17 localities were diploid, 2 from 2 were triploid, and 15 from 8 were tetraploid (Figs. 1, 2, 14; Table 1).

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows:

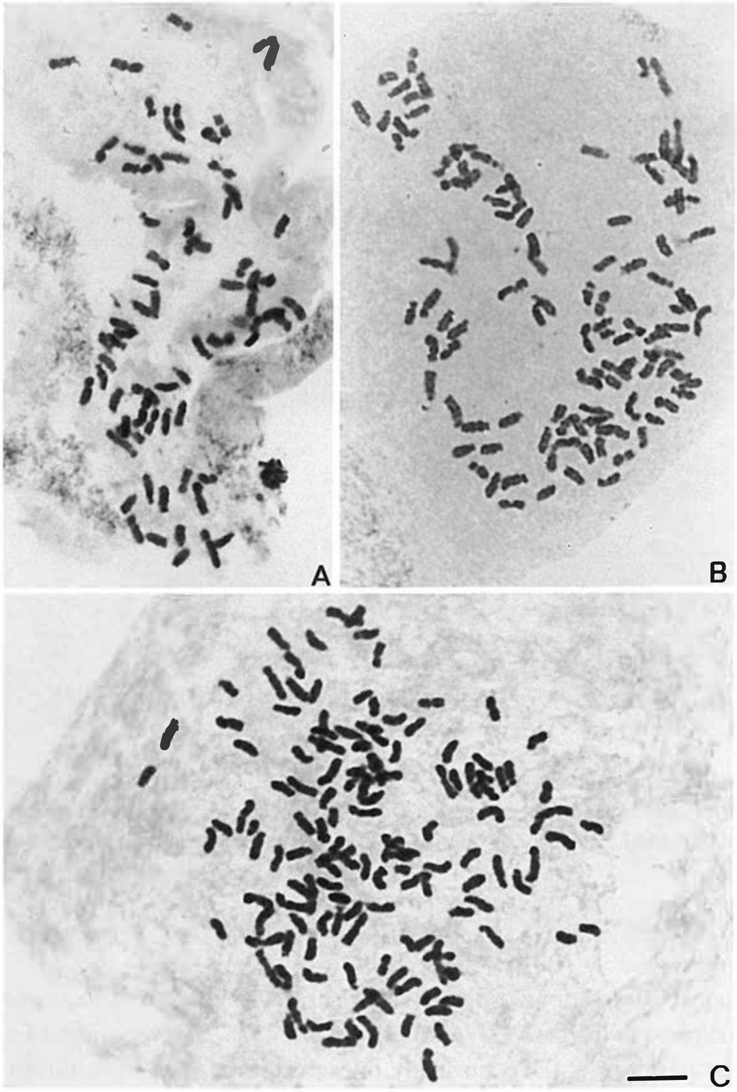

Fig. 13. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Kanto District. A, 2n = 68, from Mt. Shirane, Gunma Prefecture (Loc. 20, *Takamiya 1514*). B, 2n = 102, from Mt. Tanigawa, Gunma Pref. (Loc. 19, *Takamiya 1119*). C, 2n = 136, from Yumoto-cho, Tochigi Pref. (Loc. 18, *Takamiya 2161*). Bar represents 5 μm.

In Komyo (Loc. 23), only diploid individuals were found around the edges of a *Cryptomeria japonica* plantation. On Mt. Hakkai (Loc. 24), only tetraploid individuals grew on a grassland near the mountaintop. In Yomogitoge (Loc. 25), diploid individuals grew around the edges of a *Quercus mongolica* var. *undulatifolia* scrub and in a *Sasa kurilensis* grassland.

The habitats of *Lycopodium clavatum* on Mt. Tateyama (Loc. 26), where diploid and tetraploid cytotypes were found, are explained by a list of plants associated with *L. clavatum* (Table 3) and by a map showing collection sites (Fig. 15). The explorational

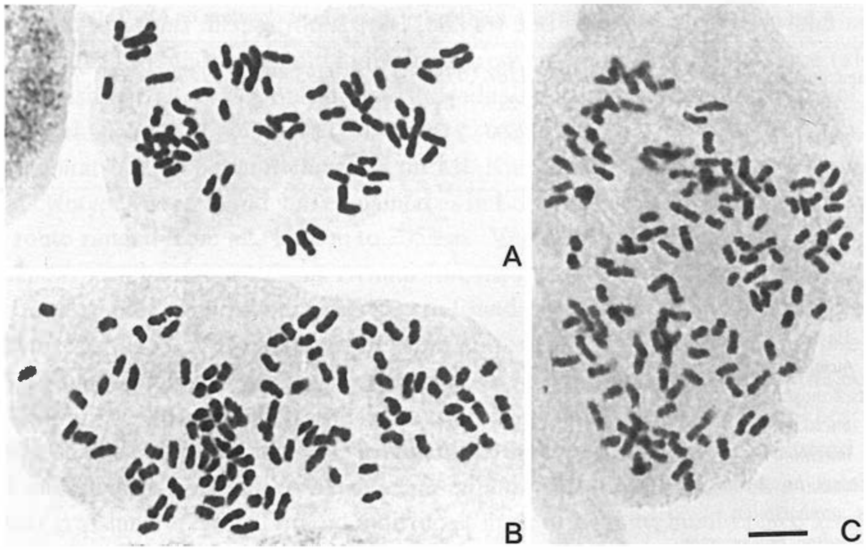

Fig. 14. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Chubu District. A, 2n = 68, from Mt. Kirigamine, Nagano Prefecture (Loc. 36, *Takamiya 1503*). B, 2n = 102, from Mt. Kurohime, Nagano Pref. (Loc. 32, *Takamiya 1119*). C, 2n = 136, from Yamasaki, Ishikawa Pref. (Loc. 27, *Takamiya 2161*). Bar represents 5 μm.

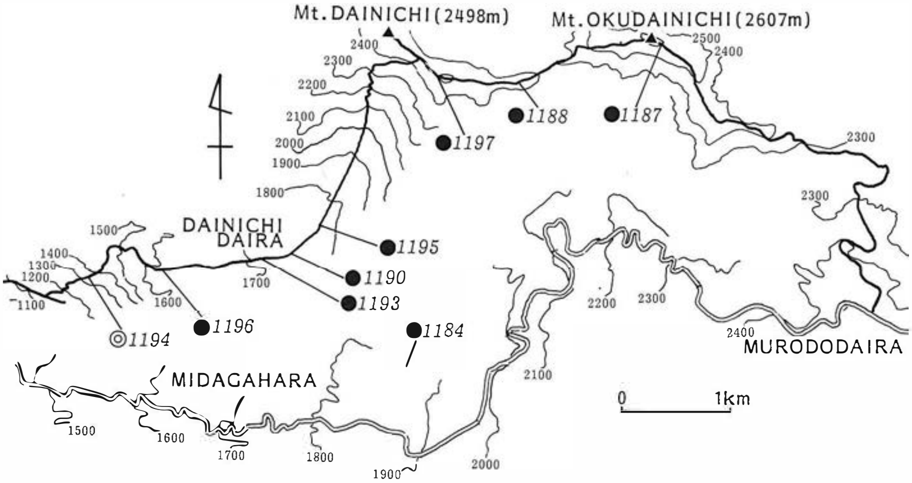

Fig. 15. A map showing the site of the collections of *Lycopodium clavatum* on Mt. Tateyama, Toyama Prefecture (Loc. 26). Numbers are voucher specimen numbers. Solid circle, diploid; double circle, tetraploid.

route ranging from alt. 1300 m to 2607 m crosses two vegetation zones: the subalpine and the alpine zones. Diploid individuals grew around the edges of a *Sasa kurilensis* grassland (*1184*), a *Tsuga diversifolia* forest (*1195*), and a *Pinus pumila* scrub (*1197*), and on the floor of *Abies mariesii* forests (*1190, 1193, 1196*) and an *Alnus* maximowiczii scrub (*1188*). These areas formed a shady, humid microenvironment. Diploid individuals also occurred

Table 3. A list of plants associated with each individual of *Lycopodium clavatum* on Mt. Tateyama (Loc. 26)

Specimen number	*1184*	*1187*	*1188*	*1197*	*1195*	*1190*	*1193*	*1196*	*1194*
Ploidy	2x	2x	2x	2x	2x	2x	2x	2x	4x
Altitude (m)	1860	2590	2430	2440	1760	1720	1705	1550	1300
Name of species associated									
Tree Layer									
Tsuga diversifolia	−	−	−	−	+	−	−	−	−
Abies mariesii	−	−	−	−	−	+	+	+	−
Shrub Layer									
Pinus pumila	−	+	−	+	−	−	−	−	−
Acer tschonoskii	−	+	+	−	−	−	−	−	−
Rosa acicularis	−	+	−	−	−	−	−	−	−
Alnus maximowiczii	−	−	+	−	−	−	−	−	−
Tripetaleia bracteata	−	−	+	−	−	−	−	−	−
Sorbus sambucifolia	−	+	−	−	−	−	−	−	−
Rhododendron brachycarpon	−	−	−	−	−	+	+	−	−
Rhododendron trinerve	−	−	−	−	+	−	−	−	−
Herb Layer									
Solidago virga-aurea var. *leiocarpa*	+	+	+	+	−	−	−	−	−
Potentilla palustris	−	+	−	−	−	−	−	−	−
Calamagrostis langsdorffii	−	+	+	+	−	−	−	−	−
Sasa palmata	+	+	+	−	+	+	+	−	−
Vaccinium uliginosum	−	−	−	+	+	−	−	−	−
Cornus canadensis	−	+	+	−	+	+	+	−	−
Rhododendron aureum	−	−	+	+	−	−	−	−	−
Rubus pedatus	+	−	−	−	+	−	−	−	−
Acer tschonoskii	+	−	−	+	−	−	−	−	−
Alnus maximowiczii	+	−	−	−	−	−	−	−	−
Vaccinium ovalifolium	−	−	−	−	−	−	−	+	−
Menziesia pentandra	−	−	−	−	−	+	+	−	−
Epigaea asiatica	−	−	−	−	−	−	+	+	−
Clintonia udensis	−	−	−	−	−	−	+	+	−
Loiseleuria procumbens	−	−	−	+	−	−	−	−	−
Gaultheria adenothrix	−	−	−	+	−	−	−	−	−

in the sunny, humid environment of an alpine meadow (*1187*). On the other hand, tetraploid individuals grew in a sunny, dry, disturbed, open place of roadside slope (*1194*). Diploid and tetraploid individuals were not found intermingled with one another, but occurred in different habitats.

In Yamasaki (Loc. 27), only tetraploid individuals occurred on a roadside slope. In Kuraga (Loc. 28), only diploid individuals grew on a humid roadside slope and on the floor of a young *Cryptomeria japonica* plantation. In Iwamado (Loc. 29), only diploid individuals were found on the floor of *Quercus mongolica* var. *grosseserrata* forests (alt. 1120 m, 1830 m) and around the edges of a *Fagus crenata* forest (alt. 1500 m) and an *Abies mariesii* forest (alt. 2200 m). On Mt. Hakusan (Loc. 30), diploid individuals grew around the edges of an *Alnus hirsuta* forest (alt. 1800 m) and on the floor of an *Abies mariesii* scrub (alt. 2050 m), and tetraploid individuals grew on a humid roadside slope (alt. 2000 m). In Higashitate (Loc. 31), only diploid individuals occurred around the edges of a *Sasa kurilensis* grassland.

The habitat of *Lycopodium clavatum* on Mt. Kurohime (Loc. 32), where diploid and triploid cytotypes were found, are explained as in Loc. 26 (Fig. 16; Table 4). The explorational route ranged from alt. 1100 m to 2053 m. Vegetation along this route consisted of *Larix leptolepia* plantations, *Fagus crenata* forests, *Betula ermanii* forests, *Abies mariesii* forests, and so on. Diploid individuals were found on the floor of well-developed *Fagus crenata* forests (*1213, 1215*) and a *Betula ermanii* forest (*1216*), a *Tsuga diversifolia* forest (*1218*), and a *Quercus mongolica* var. *grosseserrata* (*1506*) forest, and around the edges of an *Abies mariesii* forest (*1199*) and a *Larix leptolepia* plantation (*1262*). These areas formed a shady and humid microenvironment. Diploid individuals also occurred on the humid and slightly bright floor of a *Betula ermanii* scrub (*1508*) and in a sunny *Sasa kurilensis* grassland (*1210*). Triploid individuals grew in a sunny, humid place around the edges of a *Sasa kurilensis* grassland (*1214*). Diploid and triploid individuals were not found intermingled with one another, but occurred in different habitats.

On Mt. Togakushi (Loc. 33), Mt. Shiroumadake (Loc. 34), and Mt. Yatsugatake (Loc. 35), only diploid individuals grew around the edges of a 1–2 m tall *Sasa kurilensis* grassland, on a humid roadside slope, and around the edges of an *Abies mariesii* forest, respectively. On Mt. Kirigamine (Loc. 36) and Mt. Fuji (Loc. 37), only diploid individuals grew on the floor of well-developed *Quercus mongolica* var. *grosseserrata* forests. On Mt.

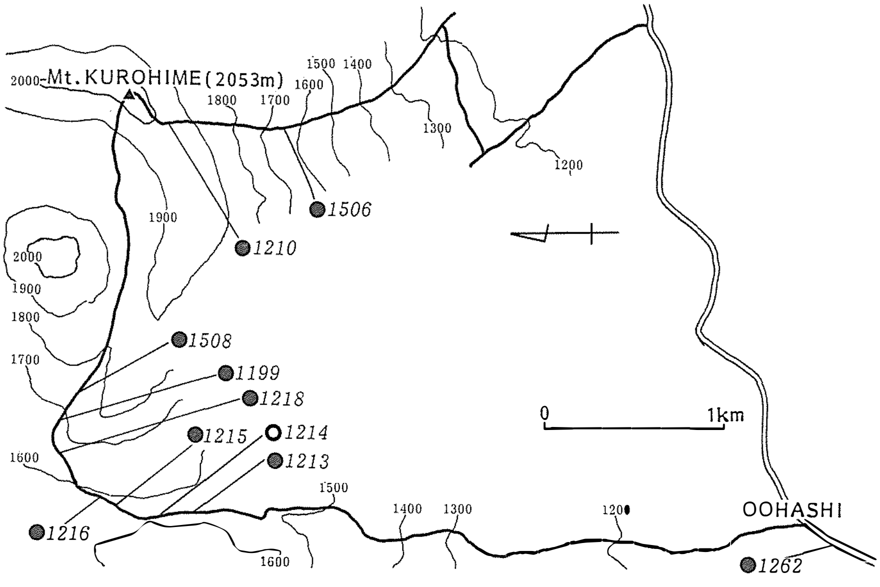

Fig. 16. A map showing the site of the collections of *Lycopodium clavatum* on Mt. Kurohime, Nagano Prefecture (Loc. 32). Numbers are voucher specimen numbers. Solid circle, diploid; open circle, tetraploid.

Table 4. A list of plants associated with each individual of *Lycopodium clavatum* at Mt. Kurohime (Loc. 32)

Specimen number	*1199*	*1210*	*1262*	*1213*	*1214*	*1215*	*1216*	*1218*	*1506*	*1508*
Ploidy	2x	2x	2x	2x	3x	2x	2x	2x	2x	2x
Altitude (m)	1670	1960	1170	1580	1590	1580	1580	1640	1655	1720
Name of species associated										
Tree Layer										
Abies mariesii	+	−	−	−	−	−	−	−	−	−
Larix leptolepis	−	−	+	−	−	−	−	−	−	−
Fagus crenata	−	−	−	+	−	+	−	−	−	−
Betula ermanii	+	−	−	−	−	−	+	−	−	−
Tsuga diverifolia	−	−	−	−	−	−	−	+	−	−
Quercus mongolica var. *grosseserrata*	−	−	−	−	−	+	−	−	+	−
Acer mono	−	−	−	+	−	+	−	−	+	−
Acer shirasawanum	−	−	−	+	−	−	−	−	+	−
Acanthopanax divaricatus	−	−	−	+	−	−	−	−	+	−
Shrub Layer										
Betula ermanii	−	−	−	−	−	−	−	−	−	+
Acer ukurunduense	+	−	−	−	−	−	+	+	−	+
Vaccinium smallii	+	−	−	−	−	−	+	−	+	+
Menziesia pentandra	+	−	−	−	−	−	+	−	−	+
Rhododendron albrechtii	+	−	−	−	−	−	−	−	−	−
Viburnum furcatum	−	−	+	−	+	−	−	−	−	−
Styrax obassia	−	−	−	−	+	−	−	−	−	−
Lindera umbellata var. *membranacea*	−	−	+	−	+	−	−	−	−	−
Euonymus melananthus	−	−	−	−	−	+	−	−	+	−
Acer tschonoskii	−	−	−	−	−	+	−	−	−	+
Rhododendron brachycarpon	−	−	−	−	−	+	+	−	−	+
Abies mariesii	−	−	−	−	−	−	−	−	−	+
Herb Layer										
Sasa kurilensis	+	+	−	+	+	+	+	+	−	+
Pteridophyllum racemosum	+	−	−	−	−	−	−	−	−	+
Oxalis acetosella	+	−	−	−	−	−	+	−	+	+
Polystichopsis mutica	+	−	−	−	−	−	+	−	−	+
Maianthemum dilatatum	−	+	−	−	−	+	−	+	−	−
Tripterospermum japonicum	−	+	−	−	−	−	−	−	−	−
Prunella vulgaris	−	−	+	−	−	−	−	−	−	−
Struthiopteris niponica	−	−	+	−	+	−	−	−	−	−
Heloniopis orientalis	−	−	−	−	+	−	−	−	−	−
Rubus pseudo-japonicus	−	−	−	−	−	−	−	+	−	+
Lycopodium annotinum	−	−	−	−	−	−	−	−	−	+
Vaccinium yatabei	−	−	−	−	−	−	−	+	−	−
Chiogenes japonica	−	−	−	−	−	−	−	+	−	−

Ontake (Loc. 38), only diploid individuals occurred on the floor of a *Tsuga diversifolia* forest. In Nenouekogen (Loc. 39) and Hisuikyo (Loc. 40), only tetraploid individuals grew on roadside slopes. In Kamitoku (Loc. 41), only diploid individuals grew on the floor of a *Pinus densiflora* forest. In Kurakake (Loc. 42) and Nekogoe (Loc. 43), only tetraploid individuals grew on roadside slopes. In Misawa (Loc. 44), only triploid individuals were found on a cutover place dominated by *Miscanthus sinensis*. In Tateyamadera (Loc. 45) and Jokoji (Loc. 46), only diploid individuals grew around the edges of a *Cryptomeria japonica* plantation and on a humid roadside slope, respectively.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in seven diploid individuals (*2654* from Loc. 25; *1195* from Loc. 26; *1739* from Loc. 29; *2147* from Loc. 30; *1218*, *1508* from Loc. 32; *1503* from Loc. 36) and in two tetraploids (*1577* from Loc. 39; *2644* from Loc. 43).

The variations of chromosome length and the positions of the centromere in each chromosome were found to be almost identical to those of each cytotype of the Hokkaido District (Figs. 6 and 7).

3. Meiosis

At diakinesis or metaphase I of meiosis, 86 SMCs were observed in 4 diploid individuals (*1508* from Loc. 32; *1503* from Loc. 36; *1572* from Loc. 42; *1573* from Loc. 46) and 20 SMCs in a tetraploid (*1577* from Loc. 39).

Only bivalent pairs of all chromosome (34_{II}) were observed in a diploid individual (Fig. 17A). Out of 20 SMCs from a tetraploid individual examined, 18 had only bivalent pairs

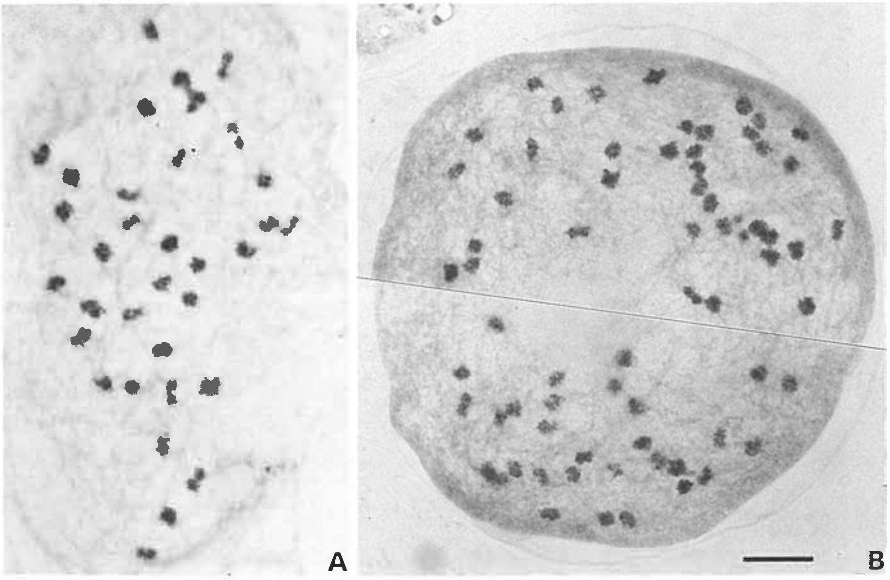

Fig. 17. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of *Lycopodium clavatum* examined in Chubu District. A, $2n = 68 = 34_{II}$, *Takamiya 2116* from Loc. 32. B, $2n = 136 = 68_{II}$, *Takamiya 1577* from Loc. 39. Bar represents 10 μm.

of all chromosomes (68_{II}) (Fig. 17B) and 2 had $67_{II}+2_{I}$. Each stage subsequent to metaphase I was normal in both cytotypes.

V. *Kinki District*

Lycopodium clavatum commonly occurs from lowland hills up to mountains in the Kinki District. Field observations and collections were made in 17 localities of *L. clavatum* populations at an elevation of 120 m to 1650 m. Chromosome numbers were determined in 57 individuals, of which 32 collected from 12 localities were diploid, 14 from 9 were triploid, and 11 from 7 were tetraploid (Figs. 1, 2, 18; Table 1).

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows: Habitats on Mt. Hira (Loc. 47), where diploid, triploid, and tetraploid cytotypes were found, are explained by a list of plants associated with *L. clavatum* (Table 5) and by a map showing collection sites (Fig. 19). The explorational route, ranging from alt. 250 m to 1057 m, crossed two vegetation zones: the evergreen broad-leaved forest and the deciduous broad-leaved forest zones. Vegetation along the route consisted of *Cryptomeria japonica* plantations, *Fagus crenata* forests, secondary forests of *Pinus densiflora,* and so on. Diploid individuals grew on the floor of a *Fagus crenata* forest (*1431, 1432*) and around the edges of a *Cryptomeria japonica* plantation (*1428, 1429*). These areas formed a shady, humid microenvironment. Diploid individuals also occurred in the humid, slightly bright

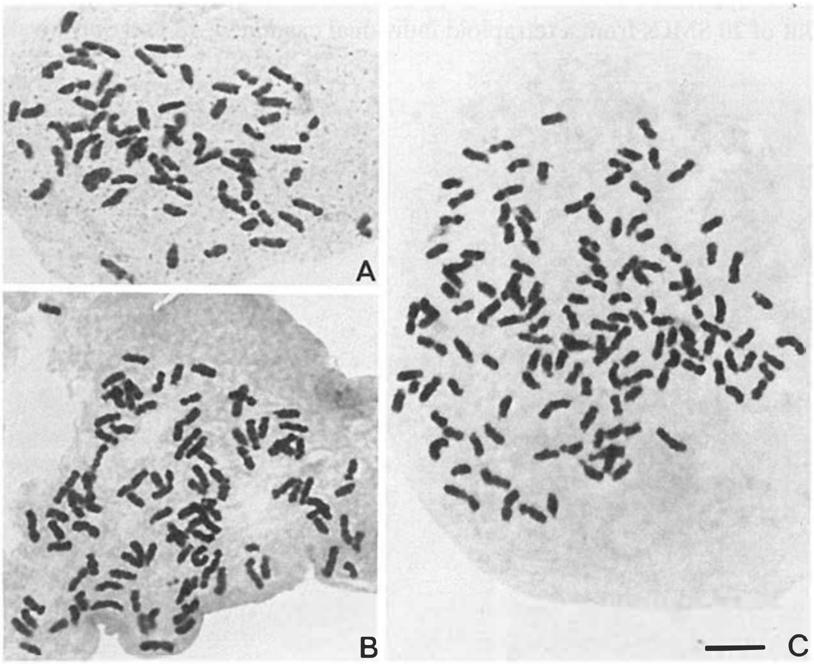

Fig. 18. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Kinki District. A, 2n = 68, (*Takamiya 1423*), B, 2n = 102, (*Takamiya 1418*), C, 2n = 136, (*Takamiya 1420*). All materials were collected from Mt. Hiei, Kyoto Pref. (Loc. 51). Bar represents 5 μm .

floor and edges of a young secondary forest dominated by *Pinus densiflora* and *Quercus serrata* (*1427, 1430*), and in the humid, sunny environment of the edges of a *Sasa tuboiana* grassland (*1426*) and on a roadside slope (*1434*). Tiploid individuals grew on a sunny cutover place (*1433*) and tetraploid indviduals grew on a sunny, dry, open roadside slope (*1424, 1425*). Diploid, triploid, and tetraploid individuals were not found intermingled with one another, but occurred in different habitats.

In Kibogaoka (Loc. 48), diploid and triploid individuals grew sympatrically on a roadside slope in thin *Miscanthus sinensis* and *Pinus densiflora* seedlings. In Ogami (Loc. 49),

Table 5. A list of plants associated with each individual of *Lycopodium clavatum* on Mt. Hira (Loc. 47)

Specimen number	*1424*	*1425*	*1426*	*1427*	*1428*	*1429*	*1430*	*1431*	*1432*	*1433*	*1434*
Ploidy	4x	4x	2x	2x	2x	2x	2x	2x	2x	3x	2x
Altitude (m)	550	560	580	600	650	720	850	960	850	800	700
Name of species associated											
Tree Layer											
Fagus crenata	−	−	−	−	−	−	−	+	+	−	−
Pinus densiflora	−	−	−	+	−	−	+	−	−	−	−
Quercus serrata	−	−	−	+	−	−	−	−	−	−	−
Cryptomeria japonica	−	−	−	−	+	+	−	−	−	−	−
Sorbus commixta	−	−	−	+	−	−	−	+	−	−	−
Acer mono	−	−	−	+	−	−	+	+	+	−	−
Tritomodon companulatus	−	−	−	−	−	−	−	−	+	−	−
Acer sieboldianum	−	−	−	+	−	−	−	−	+	−	−
Acer rufinerve	−	−	−	−	−	−	+	+	−	−	−
Shrub Layer											
Hydrangea hirta	−	−	−	+	−	+	+	−	+	−	−
Clethra barbinervis	−	−	−	+	+	−	+	+	−	−	−
Hydrangea paniculata	−	−	−	+	−	−	−	−	−	−	−
Herb Layer											
Sasa tsuboiana	−	−	+	−	−	+	−	+	−	−	+
Oxalis acetosella	−	−	−	−	−	−	−	+	+	−	−
Struthiopteris niponica	−	−	−	−	+	+	−	+	−	−	+
Clethra barbinervis	−	−	−	−	−	−	−	−	−	−	+
Maianthemum dilatatum	−	−	+	−	+	+	+	+	−	−	+
Leptogramma mollissima	−	−	−	+	+	−	+	−	−	−	+
Dryopteris crassirhizoma	−	−	−	−	−	−	−	+	+	−	−
Rubus palmatus	−	+	−	−	+	−	−	−	−	+	+
Miscanthus sinensis	+	+	−	−	−	+	−	−	−	+	+
Lespedeza cyrtobotrya	+	−	−	−	−	−	−	−	−	−	+
Soridago virga-aurea var. *asiatica*	−	−	−	−	−	−	−	−	−	+	+
Haloragis micrantha	−	−	+	−	−	−	−	−	−	−	−
Athyrium vidalii	−	−	−	−	−	+	−	−	−	−	−
Rubus buergeri	−	−	−	−	+	+	−	−	−	−	−
Plantago asiatica	+	−	−	−	−	−	−	−	−	+	+

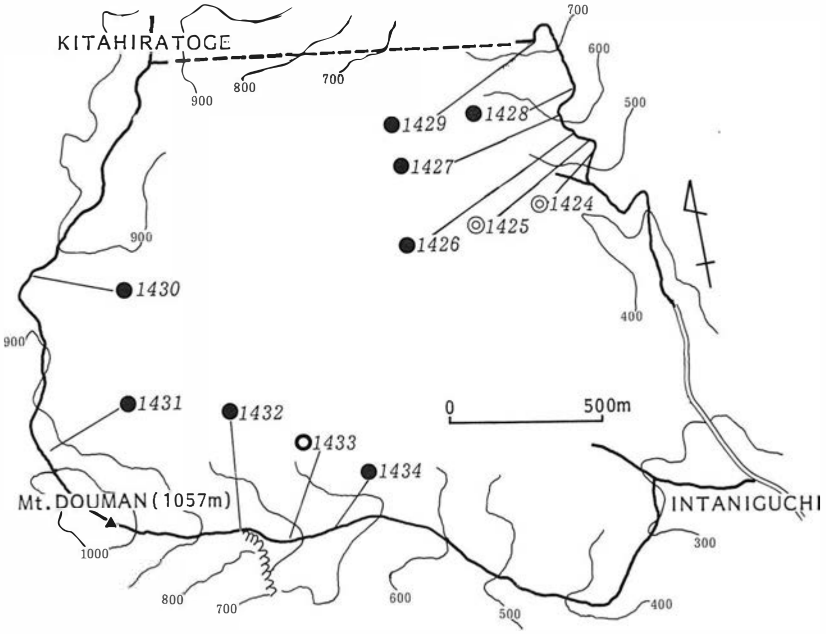

Fig. 19. A map showing the site of the collections of *Lycopodium clavatum* on Mt. Hira, Shiga Prefecture (Loc. 47). Numbers are voucher specimen numbers. Solid circle, diploid; open circle, triploid; double circle, tetraploid.

diploid, triploid, and tetraploid individuals grew intermingled around the edges of a *Pinus densiflora* forest. In Asyuu (Loc. 50), only tetraploid individuals grew on a roadside slope.

In Hiei (Loc. 51), diploid, triploid, and tetraploid were found. Diploid individuals grew around the edges of a *Chamaecyparis obtusa* plantation (alt. 620 m). Triploid individuals grew on the floor of an open secondary forest (alt. 800 m), around the edges of a *Cryptomeria japonica* plantation (alt. 750 m), and in a grassland dominated by *Miscanthus sinensis* and *Eragrostis curvule* on the roadside slope (alt. 730 m). Tetraploid individuals grew on the open roadside slope (alt. 620 m, 650 m).

In Nishihara (Loc. 52), only diploid individuals grew around the edges of a *Quercus glauca* forest. On Mt. Odaigahara (Loc. 53), only diploid individuals grew on the floor of a *Fagus crenata* forest (alt. 1580m) and around the edges of a *Sasa veitchii* grassland (alt. 1650 m). In Zenki (Loc. 54) and Shimokuwabara (Loc. 55), only diploid individuals occurred on the floor of *Cryptomeria japonica* plantations. In Nishitani (Loc. 56), diploid, triploid, and tetraploid individuals grew together on a roadside slope. In Anshinhashi (Loc. 57) and Okubo (Loc. 58), only diploid individuals grew on the floor of a *Quercus mongolica* var. *grosseserrata* forest and a *Cryptomeria japonica* plantation, respectively. In Honguu (Loc. 59), only triploid individuals were found around the edges of a *Pinus densiflora* forest. In Koyasan (Loc. 60), diploid and triploid individuals grew intermingled around the edges of a *Cryptomeria japonica* plantation. In Kawai (Loc. 61), only triploid individuals grew on a roadside slope. In Kawane (Loc. 62), only diploid individuals occurred on the floor of a *Chamaecyparis obtusa* plantation. In Iimori (Loc. 63), triploid and tetraploid individuals grew together on a roadside slope.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in three diploid individuals (*1423* from Loc. 51; *1570* from Loc. 53; *4307* from Loc. 62), in one triploid (*1421* from Loc. 51) and in three tetraploids (*1500* from Loc. 50; *1420*, *1422* from Loc. 51). Regarding the karyomorphological characteristics of diploids, triploids, and tetraploids from the Kinki District, the variations of chromosome length and the positions of the centromere in each chromosome were found to be almost identical to those of each cytotype of the Hokkaido and Tohoku Districts (Figs. 6, 7, 10).

3. Meiosis

At diakinesis or metaphase I of meiosis, 40 SMCs were observed in 2 diploid individuals (*4323* from Loc. 52; *4307* from Loc. 62), 20 SMCs each in a triploid individual (*1585* from Loc. 63), and in a tetraploid (*1002* from Loc. 48).

Only bivalent pairs of all chromosomes ($34_{\rm II}$) were observed in the diploid (Fig. 20A). Out of 20 SMCs from a tetraploid examined, 18 had only bivalent pairs of all chromosomes ($68_{\rm II}$) (Fig. 20E) and 2 had $67_{\rm II}+2_{\rm I}$. Each stage subsequent to metaphase I was normal in both cytotypes.

In a triploid individual, 13 different configurations were observed (Figs. 20B–D): $3_{\rm III}+31_{\rm II}+31_{\rm I}$ (1 SMC), $2_{\rm III}+35_{\rm II}+26_{\rm I}$ (1), $2_{\rm III}+33_{\rm II}+30_{\rm I}$ (1), $2_{\rm III}+30_{\rm II}+36_{\rm I}$ (1), $1_{\rm III}+36_{\rm II}+27_{\rm I}$ (2), $1_{\rm III}+34_{\rm II}+31_{\rm I}$ (1), $1_{\rm III}+33_{\rm II}+33_{\rm I}$ (1), $38_{\rm II}+26_{\rm I}$ (2), $37_{\rm II}+28_{\rm I}$ (3), $36_{\rm II}+30_{\rm I}$ (4), $35_{\rm II}+32_{\rm I}$ (1), $34_{\rm II}+34_{\rm I}$ (1), and $33_{\rm II}+36_{\rm I}$ (1). Trivalents were observed in 8 of 20 SMCs, and their number per SMC varied from 1 to 3. The commonest configuration was $36_{\rm II}+30_{\rm I}$, and the mean was $0.7_{\rm III}+35.1_{\rm II}+30.0_{\rm I}$.

Various kinds of abnormalities were observed throughout all stages of meiosis, resembling those of the triploids in the Tohoku District. Every SMC examined had univalents at metaphase I and lagging chromosome or chromosome bridges at anaphase I. At telophase I or interkinesis, several micronuclei in addition to two daughter nuclei were observed in 57% of SMCs. At metaphase II abnormalities were observed in 32% of SMCs. At anaphase II, abnormalities were observed in 51% of SMCs, but no lagging chromosome was found. At telophase II, 59% of SMCs had micronuclei.

VI. *Chugoku District*

Lycopodium clavatum commonly occurs from the coastal regions up to the mountains in the Chugoku District, and a morphologically distinct form referred to as *L. clavatum* var. *robustius* is known in the mountain regions (Takeda, 1984). Field observations and collections were made in 50 localities of *L. clavatum* populations at an elevation of 60 m to 1600 m. Chromosome numbers were determined in 314 individuals, of which 93 collected from 27 localities were diploids, 111 from 34 were triploids, and 110 from 27 were tetraploids (Figs. 1, 2, 21; Table 1).

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows: On Mt. Oginosen (Loc. 64), diploid individuals grew on the floor of a *Fagus crenata* forest (alt. 1000 m) and triploid individuals grew on an open roadside slope (alt. 600 m). On Mt.

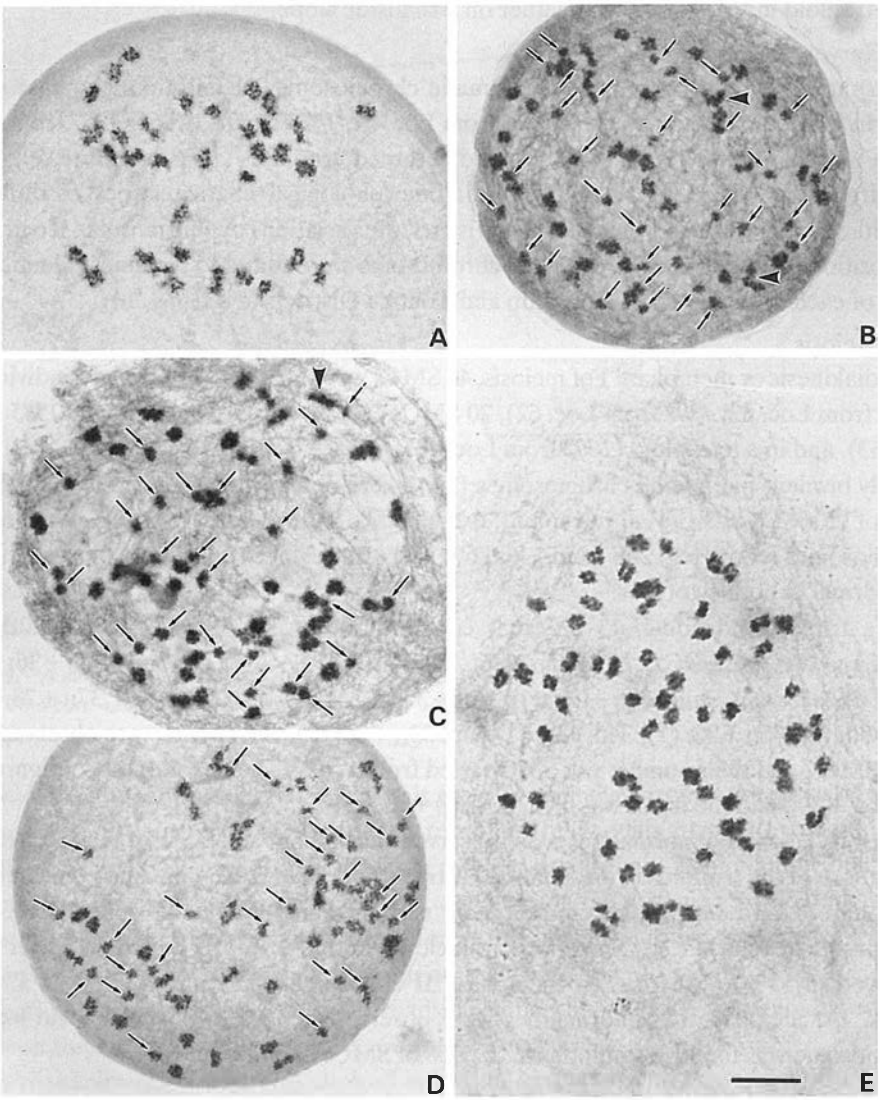

Fig. 20. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of *Lycopodium clavatum* examined in Kinki District. A, $2n=68=34_{\mathrm{II}}$, *Takamiya 4323* from Loc. 52. B–D: $2n=102$, *Takamiya 1585* from Loc. 63. B, $2_{\mathrm{III}}+33_{\mathrm{II}}+30_{\mathrm{I}}$; C, $1_{\mathrm{III}}+36_{\mathrm{II}}+27_{\mathrm{I}}$; D, $36_{\mathrm{II}}+30_{\mathrm{I}}$. Arrow heads and arrows indicate trivalents and univalents, respectively. F, $2n=136=68\mathrm{II}$, Takamiya 1002 from Loc. 48. Bar represents 10 μm.

Daisen (Loc. 65), diploid individuals grew on the floor of a *Fagus crenata* forest (alt. 800 m) and tetraploid individuals grew in an open place near the mountaintop (alt. 1600 m). In Odaka (Loc. 66), only tetraploid individuals grew on a roadside slope. On Mt. Sanbe (Loc. 67), diploid individuals grew on the floor of a *Fagus crenata* forest (alt. 1050 m) and tetraploid individuals grew on an open roadside slope (alt. 600 m). In Mitikawa (Loc. 68), only triploid individuals grew on a humid roadside slope. In Asanabe (Loc. 69), only diploid individuals occurred around the edges of a *Chamaecyparis obtusa* plantation. In Kanpa (Loc. 70), diploid and tetraploid individuals grew together on an open place of

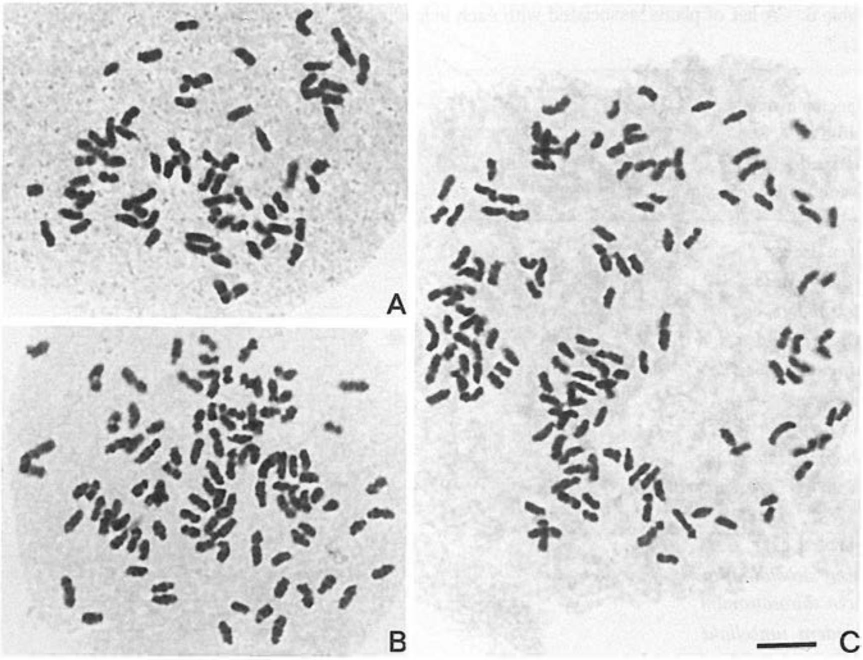

Fig. 21. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Chugoku District. A, 2n = 68, from Tarutoko, Hiroshima Prefecture (Loc. 90, *Takamiya 1441*). B, 2n = 102, from Kurashige, Hiroshima Pref. (Loc. 96, *Takamiya 1023*). C, 2n = 136, from Haji, Hiroshima Pref. (Loc. 82, *Takamiya 1467*). Bar represents 5 μm.

roadside slope. On Mt. Dogo (Loc. 71), diploid individuals were found around the edges of a *Quercus mongolica* var. *grosseserrata* forest (alt. 1130 m), and both triploid and tetraploid individuals occurred in a disturbed grassland near the mountaintop (alt. 1220–1260 m).

The habitats of *Lycopodium clavatum* on Mt. Hiba (Loc. 72), where diploid, triploid, and tetraploid cytotypes were found, are explained by a list of plants associated with *L. clavatum* (Table 6) and by a map showing collection sites (Fig. 22). The explorational route ranged from alt. 950 m to 1299 m. Vegetation along the route belonged to the broad-leaved deciduous forest zone and consisted of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* forest, *Cryptomeria japonica* and *Chamaecyparis obtusa* plantation, *Zoysia japonica* grassland near the mountaintop, and so on. Diploid individuals grew around the edges of a well-developed *Quercus mongolica* var. *grosseserrata* forest (*1174*) and a *Fagus crenata* forest (*1175*). These areas formed a shady, humid microenvironment. Diploid individuals also occurred on the humid, slightly bright floor of a young bush (*1177*). Triploid individuals grew around the sunny edges of a *Quercus mongolica* var. *grosseserrata* forest (*1181*). Tetraploid individuals grew on a sunny, dry, open place (*1180*) and in a disturbed grassland near the mountaintop (*1176, 1178, 1179*). Diploid, triploid, and tetraploid individuals were not found intermingled with one another, but occurred in different habitats.

In Uenoike (Loc. 73), only triploid individuals grew around the edges of a *Pinus den-*

Table 6. A list of plants associated with each individual of *Lycopodium clavatum* on Mt. Hiba (Loc. 72)

Specimen number	*1174*	*1175*	*1176*	*1177*	*1178*	*1179*	*1180*	*1181*
Ploidy	2x	2x	4x	2x	4x	4x	4x	3x
Altitude (m)	1190	1220	1220	1240	1260	1270	1270	1080
Name of species associated								
Tree Layer								
Fagus crenata	+	+	—	—	—	—	—	—
Ilex macropoda	—	+	—	—	—	—	—	—
Rhus javanica	—	—	—	—	—	—	—	+
Magnolia obovata	+	+	—	—	—	—	—	—
Acer mono	—	+	—	—	—	—	—	—
Acer rufinerve	—	—	—	+	—	—	—	—
Quercus mongolica var. *grosseserrata*	+	+	—	—	—	—	—	+
Shrub Layer								
Acer sieboldianum	+	+	—	—	—	—	—	—
Acer shirasawanum	—	+	—	—	—	—	—	—
Lindera umbellata	+	—	—	—	—	—	—	—
Viburnum furcatum	—	—	—	+	—	—	—	—
Ilex crenata	+	—	—	+	—	—	—	—
Clethra barbinervis	—	—	—	+	—	—	—	+
Ligustrum tschonoskii	—	+	—	—	—	—	—	+
Weigela hortensis	—	—	—	—	—	—	—	+
Herb Layer								
Rubus pectinellus	+	—	—	+	—	—	—	—
Strutiopteris niponica	+	+	—	+	—	—	—	—
Sasa palmata	—	+	—	—	—	—	—	+
Schizophragma hydrangeoides	+	—	—	—	—	—	—	—
Smilacina japonica	+	—	—	—	—	—	—	—
Oxalis griffithii	+	+	—	—	—	—	—	—
Solidago virga-aurea var. *asiatica*	—	—	—	—	+	+	—	—
Eupatorium chinense var. *simplicifolium*	—	—	+	—	—	+	—	—
Lindera obtusiloba	—	—	—	+	—	—	—	+
Corylus sieboldiana	—	—	—	+	—	—	—	+
Plantago asiatica	—	—	+	—	+	—	+	—
Poa annua	—	—	—	—	+	+	+	—
Geranium thunbergii	—	—	+	—	—	+	—	—
Ranunculus japonicus	—	—	+	—	—	—	—	—
Potentilla freyniana	—	—	—	—	+	+	—	—
Luzula capitata	—	—	—	—	+	—	+	—
Zoysia japonica	—	—	—	—	+	+	—	—
Miscanthus sinensis	—	—	+	—	—	+	—	+

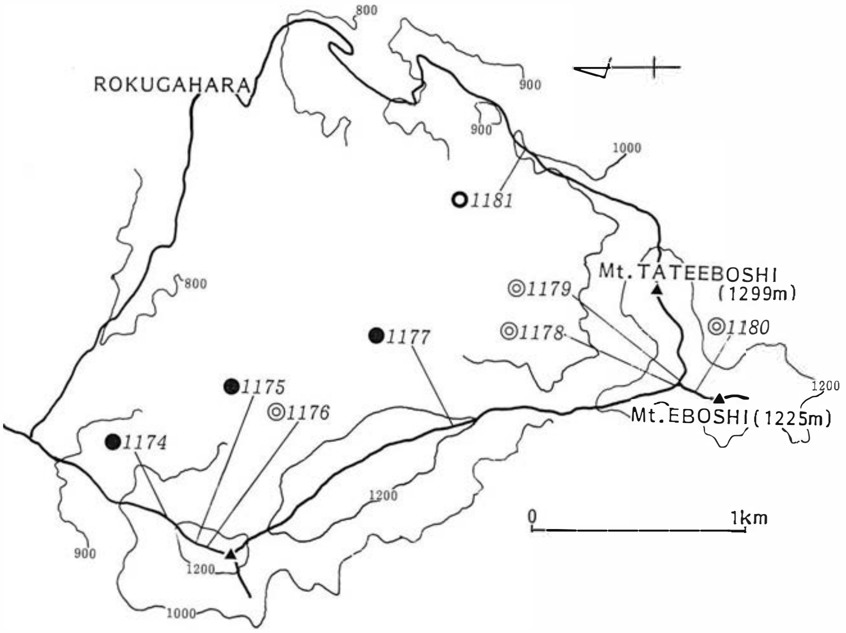

Fig. 22. A map showing the site of the collections of *Lycopodium clavatum* on Mt. Hiba, Hiroshima Pref. (Loc. 72). Numbers are voucher specimen numbers. Solid circle, diploid; open circle, triploid; double circle, tetraploid.

siflora forest. In Onuka (Loc. 74), triploid and tetraploid individuals grew together on a humid roadside slope. In Yamate (Loc. 75), only triploid individuals grew on a roadside slope. Triploid and tetraploid individuals grew intermingled in a grassland near the top of Mt. Tenguishi (Loc. 76) and in the grassland of a skiing ground at Taisenbaru (Loc. 77). In Yawatakogen (Loc. 78), diploid, triploid, and tetraploid individuals grew around the edges of a *Quercus mongolica* var. *grosseserrata* forest (alt. 780 m), on the floor of a *Quercus serrata* open forest (alt. 750 m), and on a roadside slope (alt. 750 m), respectively. In Mikawa (Loc. 79), triploid and tetraploid individuals occurred together on a roadside slope. In Kurokawa (Loc. 80), only triploid individuals grew around the edges of a *Pinus densiflora* forest. In Oguni (Loc. 81), only diploid individuals grew on the floor of a *Cryptomeria japonica* plantation.

The habitats of *Lycopodium clavatum* in Haji (Loc. 82) have already been fully described (Takamiya and Tanaka, 1982). There diploid, triploid, and tetraploid individuals were growing together within the same small areas, and there were no clear differences in habitat among the intermixed populations of the three cytotypes. Within a distance of 500 m along the road, 20 quadrats of 1 × 1 m^2 were set and Numata's (1961) degree of successions (DS) of each quadrat were calculated (Fig. 23A; Table 7). Out of 20 quadrats, 1 was occupied by only diploid individuals, 2 were only triploid, 3 were only tetraploid, 5 were diploid and triploid growing together, 6 were triploid and tetraploid together, and 3 were diploid, triploid, and tetraploid growing side by side. The values of DS ranged from 143 to 733. In diploid, triploid, and tetraploid individuals, the values of

Table 7. Floristic composition of twenty colonies of *Lycopodium clavatum* at Haji (Loc. 82)

Quadrat number	3	20	5	19	10	12	14	2	4	7
Cover of vegetation (%)	100	90	90	90	90	90	90	90	70	70
Degree of succession (DS)[a]	733	712	631	550	540	535	438	428	419	413
C[b] H[c]	C H	C H	C H	C H	C H	C H	C H	C H	C H	C H
Number of species	9	14	8	10	10	5	10	9	11	14
Lycopodium clavatum[e]	4 10	4 9	4 20	4 9	2 5	2 8	3 8	3 15	3 10	3 10
(ploidy)	(2,3)	(3,4)	(3)	(2)	(2,3)	(2,3,4)	(2,3,4)	(2,3)	(3)	(2,3)
Miscanthus sinensis	3 90	2 40	3 70	1 80	2 110	1 90	2 35	2 110	3 80	3 110
Lespedeza cyrtobotrya	—	+ 10	—	+ 5	1′ 5	+ 5	+ 10	3 150	+ 20	+ 5
Eurya japonica	2 10	—	3 30	—	—	—	—	1 15	1 10	2 15
Struthiopteris niponica	—	1′ 5	+ 5	+ 8	1′ 10	—	1′ 5	+ 10	—	+ 3
Rhododendron reticulatum	2 75	—	2 40	—	—	—	1′ 5	3 60	1 25	1′ 15
Solidago virga-aurea var. *asiatica*	1′ 45	+ 5	—	1′ 35	1′ 70	—	+ 25	—	—	—
Lyonia neziki	—	1 15	+ 10	1 20	—	1 50	+ 10	—	—	1 25
Osmunda japonica	—	1′ 8	—	—	+ 10	+ 3	+ 5	—	—	—
Pinus densiflora	1′ 25	—	—	—	3 130	—	—	—	1 55	1 65
Sasa nipponica	1 20	+ 8	—	—	—	—	+ 5	1′ 15	1′ 20	—
Hypochoeris radicata	—	—	+ 5	—	—	—	—	—	1′ 3	+ 2
Castanea crenata	—	—	—	3 300	—	—	—	—	—	—
Chamaecyparis obtusa	2 30	—	+ 15	—	—	—	—	—	1 30	1′ 10
Wisteria floribunda	—	1 20	—	1 50	—	—	—	—	—	—
Grass sp,	—	—	—	—	+ 10	—	—	1 25	—	1′ 15
Pteridium aquilinum	—	—	—	1 50	—	—	—	—	—	—
Viola sieboldii	—	+ 3	—	1′ 7	—	—	—	—	—	+ 4
Swertia japonica	—	—	—	—	—	—	—	—	+ 10	—
Aletris luteo-viridis	1′ 10	1 5	—	—	—	—	—	—	—	—
Cryptomeria japonica	—	—	—	—	—	—	—	—	—	—
Viola grypoceras	—	—	—	—	—	—	—	—	—	—
Rhododendron kaempferi	—	1 15	—	—	—	—	—	—	—	—
Ilex pedunculosa	—	—	—	—	—	—	—	1′ 20	—	—
Aster ageratoides	—	—	—	—	—	—	—	—	—	—
Sphenomeris chusana	—	—	—	—	—	—	—	—	—	—
Hypericum erectum	—	—	—	—	+ 28	—	—	—	—	—
Clethra barbinervis	—	—	—	—	—	—	—	—	—	—
Pueraria lobata	—	—	—	—	—	—	—	—	—	—
Acer crataegifolium	—	—	—	—	+ 5	—	+ 15	—	—	—
Rhus succedanea	—	+ 3	—	—	—	—	—	—	—	—
Sonchus oleraceus	—	+ 5	—	—	—	—	—	—	—	—
Pieris japonica	—	+ 3	—	—	—	—	—	—	—	—
Spiranthes sinensis	—	—	—	—	—	—	—	—	—	+ 2
Lespedeza cuneata	—	—	—	—	—	—	—	—	—	—
Equisetum arvense	—	—	—	—	—	—	—	—	—	—
Carex sp,	—	—	—	—	—	—	—	—	—	—
Haloragis micrantha	—	—	—	—	—	—	—	—	+ 15	—
Eupatorium chinense var. *sinplicifolium*	—	—	—	—	—	—	—	—	—	+ 10
Rhus javanica	—	—	—	—	—	—	—	—	—	—
Woodwardia orientalis	—	—	—	—	—	—	—	—	—	—
Erigeron canadensis	—	—	—	—	—	—	—	—	—	—
Ampelopsis brevipedunculata	—	—	—	—	—	—	—	—	—	—
Smilax china	—	—	—	—	—	—	—	—	—	—
Melamoyrum roseum var. *japonica*	—	—	—	—	—	—	—	—	—	—
Rhus trichocarpa	—	—	—	—	—	—	—	—	—	—
Lycopodium serratum	—	—	—	—	—	—	—	—	—	—
Artemisia princeps	—	—	—	—	—	—	—	—	—	—
Dryopteris fuscipes	—	—	—	—	—	—	—	—	—	—
Lysimachia japonica	—	—	—	—	—	—	—	—	—	—

a: See text.
b: Cover class: 4=coverage 75–100%, 3=50–75%, 2=25–50%, 1=5–25%, 1′=1–5%, +=0–1%.
c: Plant Height (cm).
d: SDR_3=(cover ratio + plant height ratio + frequency ratio)/3.
e: Cytotypes grown in each quadrat. 2=diploid, 3=triploid, 4=tetraploid.

6		8		16		15		1		11		9		18		17		13			
80		70		90		80		80		40		90		70		90		40			
370		370		363		305		303		297		272		226		170		143			
C	H	C	H	C	H	C	H	C	H	C	H	C	H	C	H	C	H	C	H	Frequency	$SDR_3{}^d$
9		8		8		13		12		3		12		15		11		7			
3	12	3	5	2	6	1	3	3	10	4	10	4	10	3	5	3	10	4	5	20	71.2
(4)		(3,4)		(2,3)		(2,3,4)		(4)		(4)		(3,4)		(3,4)		(3,4)		(3,4)			
3	40	2	75	3	60	3	40	1	45	1	60	3	65	3	80	—		1′	50	19	87.2
—		—		—		1	10	+	10	1′	60	—		—		4	200	+	10	13	40.0
3	10	—		—		—		2	10	—		1′	30	1	15	3	45	—		10	31.5
1	10	1	8	2	10	1	5	—		—		1′	5	1	5	11	5	—		14	29.5
1′	10	—		—		1	15	1	10	—		—		—		—		—		9	27.1
—		+	8	—		—		1′	45	—		—		+	8	—		—		8	20.0
—		—		—		1	10	—		—		—		1′	25	—		—		8	19.9
—		+	7	1	10	1	10	—		—		+	3	2	13	—		—		9	19.1
—		1′	30	—		—		—		—		—		—		—		—		5	18.9
—		—		—		—		—		—		+	5	+	10	—		—		7	14.6
+	3	—		—		—		+	2	—		+	5	—		—		—		6	11.2
—		—		—		—		—		—		—		—		—		—		1	10.8
—		—		—		—		—		—		—		—		—		—		4	10.5
—		—		—		—		—		—		—		—		—		—		3	10.0
—		—		—		—		—		—		—		—		—		—		4	8.9
—		—		1′	15	—		—		—		—		—		—		+	20	3	7.8
—		—		—		—		—		—		+	3	—		—		—		4	7.3
—		+	10	—		—		+	4	—		—		—		—		—		3	6.2
—		+	2	—		—		—		—		—		—		—		—		3	6.1
+	7	—		—		+	10	—		—		+	10	—		—		—		3	5.7
—		—		+	5	+	1	—		—		—		—		+	6	—		3	5.4
—		—		—		—		—		—		—		1′	10	—		—		2	4.6
—		—		—		—		1′	12	—		—		—		—		—		2	4.3
—		—		—		—		—		—		—		+	6	—		+	30	2	4.3
—		—		—		+	2	—		—		—		—		1	12	—		2	4.3
—		—		—		—		—		—		—		—		+	5	—		2	4.1
—		—		—		—		—		—		—		1′	9	—		+	15	2	4.1
—		—		—		—		—		—		3	25	—		—		—		1	3.9
—		—		—		—		—		—		—		—		—		—		2	3.9
—		—		—		—		—		—		—		1′	12	—		—		2	3.8
—		—		—		—		—		—		—		—		+	6	—		2	3.6
—		—		—		—		—		—		—		—		+	6	—		2	3.6
+	2	—		—		—		—		—		—		—		—		—		2	3.5
—		—		—		—		—		—		1	15	—		—		—		1	2.6
—		—		+	30	—		—		—		—		—		—		—		1	2.5
—		—		—		—		1′	10	—		+	10	—		—		—		2	2.3
—		—		—		—		—		—		—		—		—		—		1	2.1
—		—		—		—		—		—		—		—		—		—		1	2.0
—		—		—		—		—		—		—		—		+	10	—		1	2.0
—		—		—		—		—		—		—		1′	10	—		—		1	2.0
—		—		—		—		—		—		—		—		+	7			1	1.9
—		—		—		—		—		—		—		+	6	—		—		1	1.9
—		—		—		—		—		—		—		—		—		—		1	1.8
+	5	—		—		—		—		—		—		—		—		—		1	1.8
—		—		—		—		—		—		—		—		—		+	5	1	1.8
—		—		—		+	5	—		—		—		—		—		—		1	1.8
—		—		—		+	5	—		—		—		—		—		—		1	1.8
—		—		—		—		—		—		—		+	2	—		—		1	1.8
—		—		—		+	1	—		—		—		—		—		—		1	1.7

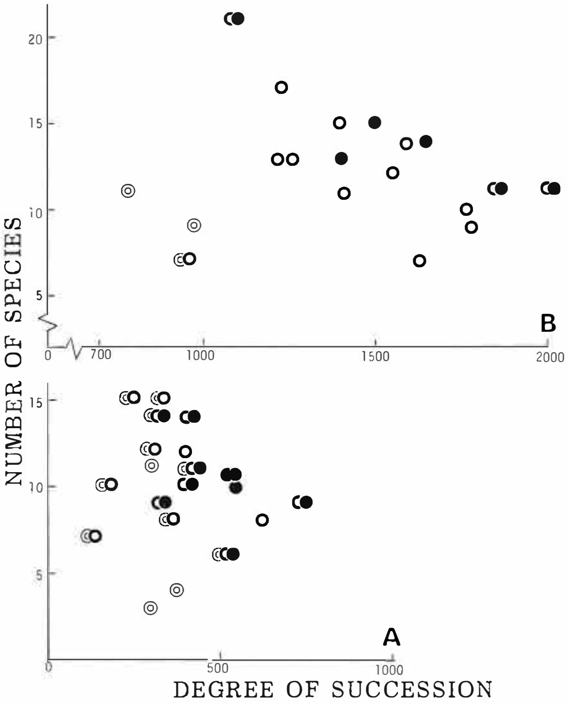

Fig. 23. The degree of succession at each of quadrats compared with number of species examined in two *Lycopodium clavatum* populations in Hiroshima Prefecture. A, Haji (Loc. 82), B, Nagahama (Loc. 107), where 20 and 18 quadrats were studied, respectively. Solid circle, diploid; open circle, triploid; double circle, tetraploid. A circle represents a quadrat and overlapping circles indicate a quadrat where two or three cytotypes were found.

DS ranged from 305–733, 143–733, and 143–535, respectively. There were some differences among the DS values of the three cytotypes; namely, the tetraploid tend to occur in earlier stages of succession, the diploid in later stages, and the triploid in a wide range.

In Takanosu (Loc. 83), diploid individuals grew around the edges of a *Chamaecyparis obtusa* plantation (alt. 750 m, 760 m), around the edges and on the floor of a *Quercus mongolica* var. *grosseserrata* forest (alt. 840 m), and tetraploid individuals grew in an open place near the mountaintop (alt. 850 m, 860 m). Only diploid individuals grew around the edge of a *Quercus serrata* forest in Shimone (Loc. 84) and a *Cryptomeria japonica* plantation in Sedani (Loc. 85). In Ugakyo (Loc. 86), diploid individuals grew around the edge of a *Cryptomeria japonica* plantation and tetraploids grew around a *Quercus serrata* forest. In Kuchi (Loc. 87), diploid and tetraploid individuals grew together on the floor of a *Cryptomeria japonica* plantation.

The detailed habitats of *Lycopodium clavatum* in Mt. Shinnyu (Loc. 88) were described previously (Takamiya and Tanaka, 1982). In this locality diploid, triploid, and tetraploid individuals occurred in different habitats.

On Mt. Osorakan (Loc. 89), diploid individuals grew on the floor of a *Cryptomeria japonica* plantation, and tetraploid individuals grew in the disturbed grassland of a skiing ground. In Tarutoko (Loc. 90), diploid, triploid, and tetraploid individuals were found around the edges of a *Quercus mongolica* var. *grosseserrata* forest (alt. 720 m), around the edges of an open forest of *Quercus serrata* (alt. 760 m), and at a roadside slope (alt. 750 m), respectively. In Mominoki (Loc. 91), only diploid individuals grew on the floor of a *Cryptomeria japonica* plantation. In Obara (Loc. 92), only triploid individuals grew on the floor of a *Chamaecyparis obtusa* plantation. On Mt. Jippo (Loc. 93) and in Mitsugi (Loc. 94), only diploid individuals grew on the floor of a *Cryptomeria japonica* plantation and around the edges of a *Quercus glauca* forest. In Seno (Loc. 95), only triploid individuals grew on the floor of a *Pinus densiflora* forest. In Kurashige (Loc. 96), diploid and triploid individuals grew together on the floor of a *Pinus densiflora* forest. In Ege (Loc. 97), diploid and tetraploid individuals grew around the edges of a *Cryptomeria japonica* plantation and on a roadside slope, respectively. In Gokurakuji (Loc. 98), diploid and triploid individuals grew together in a fen. On Mt. Aratani (Loc. 99), only diploid individuals grew on the floor of a *Chamaecyparis obtusa* plantation. In Hatadao (Loc. 100), diploid and triploid individuals grew together around the edges of a *Quercus serrata* forest. In Otsuka (Loc. 101), only tetraploid individuals occurred on a sunny roadside slope. In Ushiobara (Loc. 102), triploid and tetraploid individuals grew together around the edges of a *Chamaecyparis obtusa* plantation. In Iiyama (Loc. 103), only triploid individuals grew on a sunny roadside slope. In Uchiodani (Loc. 104), only diploid individuals occurred around the edge of a *Tsuga sieboldii* forest. On Mt. Omine (Loc. 105), diploid individuals grew on the floor of a *Cryptomeria japonica* plantation (alt. 760 m) and around the edges and on the floor of *Quercus mongolica* var. *grosseserrata* forests (alt. 820 m, 840 m). Triploid individuals grew around the edges of a *Pinus densiflora* forest (alt. 820 m), and tetraploid individuals grew on a roadside slope (alt. 540 m). On Mt. Haigamine (Loc. 106), triploid and tetraploid individuals occurred together on a roadside slope.

In Nagahama (Loc. 107), diploid, triploid, and tetraploid individuals occurred side by side within the same small areas of roadside slope where juvenile plants of *Pinus densiflora* were growing sparsely. There were no clear differences in habitats among the intermixed populations of the three cytotypes. Within a distance of 700 m along the road, 18 quadrats of 1×1 m^2 were set, and the DS value of each quadrat was calculated (Fig. 23B; Table 8). Out of 18 quadrats, 2 were occupied by only diploid individuals, 9 were only triploid, 2 were only tetraploid, 4 were diploid and triploid growing together, and 1 was triploid and tetraploid. The values of DS ranged from 783 to 1969, and higher than Haji (Loc. 82, Fig. 23A). On diploid, triploid and tetraploid individuals, the values of DS were in the ranges of 1091–1969, 927–1969, and 783–971, respectively. There were some differences among the DS values of the three cytotypes: the tetraploids tended to occur in earlier stages of succession, the diploids in later stages, and the triploids over a wide range. The tetraploids were special in that they alone occurred in habitats where the DS value and numbers of associated plants were low.

Triploid and tetraploid individuals grew together in a open place in Misen (Loc. 108), and on a roadside slope in Watase (Loc. 110). In Une (Loc. 109), juvenile diploid and tetraploid individuals occurred intermingled on a newly built roadside slope. In Kasayama (Loc. 111), only triploid individuals grew on the floor of a *Pinus densiflora* forest. In Chomonkyo (Loc. 112), only diploid individuals were found on the floor of a

Table 8. Floristic composition of eighteen colonies of Lycopodium clavatum at Nagahama (Loc. 107)

Quadrat number	9	5	18	17	10	10	8	4
Cover of vegetation (%)	80	80	70	80	60	90	70	80
Degree of succession (DS)[a]	1969	1860	1799	1774	1648	1599	1544	1502
C[b] and H[c]	C H	C H	C H	C H	C H	C H	C H	C H
Number of species	11	11	9	10	7	15	12	16
Lycopodium clavatum	2 6	3 8	2 10	2 10	2 13	3 12	2 15	1 7
(ploidy)[e]	(2,3)	(2,3)	(3)	(3)	(3)	(2,3)	(3)	(2)
Pinus densiflora	2 70	+ 23	1 20	2 70	2 45	3 100	3 120	3 65
Lyonia neziki	3 80	+ 15	1 15	2 70	1 30	2 90	2 100	1 35
Eurya japonica	1 25	2 31	—	2 100	—	1′ 25	1′ 25	2 65
Dicranopteris dichotoma	—	3 63	2 25	—	2 18	1 20	1 20	2 14
Miscanthus sinensis	2 60	—	1′ 35	—	—	—	2 80	1′ 40
Rhododendron kaempferi	1 42	—	1′ 35	—	—	1 35	2 52	1 45
Struthiopteris niponica	+ 3	—	—	1′ 10	1 8	+ 15	—	—
Pieris japonica	+ 6	1 44	1 20	—	—	1 35	1′ 24	+ 12
Sphenomeris chusana	—	—	—	10	—	1′ 20	—	1′ 15
Gleichenia japonica	—	—	—	—	1 15	2 30	—	1′ 10
Dryopteris erythrosora	—	—	—	1′ 8	1 30	+ 13	+ 5	+ 4
Melampyrum roseum var. *japonicum*	1 53	—	—	—	—	—	2 40	—
Crassocephalum crepidioides	—	+ 13	—	+ 35		—	—	—
Hydrangea luteovenosa	—	1 25	—	—	—	—	—	1 55
Rhus succedanea	+ 8	—	—	—	—	—	—	—
Eragrostis curvula	—	—	—	2 45		—	—	—
Akebia trifoliata	—	+ 3	—	—	—	+ 8	1′ 20	—
Illicium religiosum	+ 10	—	—	+ 8	—	—	+ 7	—
Abies firma	—	+ 10	—	—	—	—	—	+ 6
Osmunda japonica	—	—	—	—	—	+ 13	—	—
Lastera miqueliana	—	—	—	—	—	—	—	—
Viola maximowicziana	—	—	—	—	—	—	—	—
Paederia scandens var. *mairei*	—	—	1 15	—	—	—	—	—
Acer rufinerve	—	—	—	—	—	—	—	—
Lindera umbellata	—	—	—	—	—	1 75	—	—
Viburnum dilatatum	—	+ 12	—	—	—	—	—	—
Neolitsea sericea	—	—	—	—	—	—	—	+ 6
Mallotus japonicus	—	—	—	—	—	—	—	—
Rhamnus crenata	—	—	1′ 50	—	—	—	—	—
Rubus palmatus	—	—	—	—	—	—	—	—
Ilex pedunculosa	—	—	—	—	—	—	—	+ 15
Sonchus arvensis	—	—	—	—	—	—	—	—
Clethra barbinervis	—	—	—	—	—	—	—	—
Lastrea cystopteroides	—	—	—	—	—	—	—	—
Viola grypoceras	—	—	—	—	—	—	—	—
Quercus serrata	—	—	—	—	—	—	—	—

a: See text.

b: Cover class; 4=coverage 75–100%, 3=50–75%, 2=25–50%, 1=5–25%, 1′=1–5%, +=0–1%.

c: Plant Height (cm).

d: SDR_3=(cover ratio + plant height ratio + frequency ratio)/3.

e: Cytotypes grown in each quadrat. 2=diploid, 3=triploid, 4=tetraploid.

13	7	12	11	2	1	3	6	15	16		
70	60	80	60	80	60	90	50	40	40		
1419	1407	1402	1260	1238	1229	1091	971	927	783		
C H	C H	C H	C H	C H	C H	C H	C H	C H	C H	Frequency	SDR$_3$^{d}
14	11	16	14	18	14	22	9	7	11		
2 13	2 10	2 10	2 10	1 5	1 4	2 6	2 10	3 10	2 5	18	70.7
(2)	(3)	(3)	(3)	(3)	(3)	(2,3)	(4)	(3,4)	(4)		
3 150	3 50	3 100	1 30	3 40	1 35	2 70	2 45	1 35	2 25	18	100.0
3 100	—	1′ 15	2 65	1′ 20	1′ 15	2 20	1 35	1 35	+ 6	17	73.7
1′ 23	2 22	1′ 30	1 30	1 20	1′ 12	1 20	1′ 35	—	—	14	51.9
1′ 20	—	1′ 10	—	2 15	—	2 35	—	2 20	—	11	43.9
—	3 70	1′ 35	1 50	—	—		—	3 120	2 50	9	42.7
1′ 45	1 22	1′ 10	1 35	—	—	+ 5	—	—	1′ 20	11	39.5
+ 6	—	2 10	+ 5	2 5	1′ 5	1 10	1 4	+ 5	1 10	13	34.7
1′ 45	—	1′ 20	1′ 7	1′ 15	+ 4	—	+ 8	—	—	12	33.3
1′ 5	—	+ 6	+ 6	2 5	1 4	+ 4	+ 20	—	+ 5	11	28.9
—	—	+ 8	—	—	—	—	—	1 25	1 10	6	18.8
—	—	—	—	—	+ 2	+ 3	+ 4	—	—	8	18.0
—	—	2 45	1′ 50	—	—	—	—	—	—	4	17.8
—	+ 4	+ 30	+ 8	+ 11	—	+ 4	—	—	—	7	16.4
+ 25	—	—	—	+ 8	—	+ 8	—	—	—	5	14.8
—	+ 15	—	+ 7	—	+ 15	—	1 55	—	—	5	13.4
1 65	—	—	—	—	—	—	—	—	+ 20	3	12.3
—	+ 6	—	—	—	—	+ 8	—	—	—	5	11.0
—	—	—	+ 6	—	+ 15	—	—	—	—	5	10.9
—	—	—	—	+ 8	+ 4	+ 8	—	—	—	5	10.5
—	—	—	—	+ 3	—	+ 4	—	—	1 13	4	9.4
+ 10	—	+ 6	—	+ 3	—	1 5	—	—	—	4	9.1
—	—	+ 8	—	+ 5	+ 3	+ 3	—	—	—	4	8.1
—	+ 2	—	—	—	—	+ 5	—	—	—	3	7.2
—	—	—	—	1 40	—	+ 4	—	—	—	2	6.0
—	—	—	—	—	—	—	—	—	—	1	5.1
—	—	—	—	—	+ 8	—	—	—	—	2	4.4
—	—	—	—	—	—	+ 6	—	—	—	2	4.2
—	+ 8	—	—	—	—	+ 3	—	—	—	2	4.1
—	—	—	—	—	—	—	—	—	—	1	3.6
—	1′ 15	—	—	—	—	—	—	—	—	1	2.5
—	—	—	—	—	—	—	—	—	—	1	2.3
—	—	—	—	—	—	—	—	—	+ 15	1	2.3
—	—	—	—	1′ 6	—	—	—	—	—	1	2.2
+ 5	—	—	—	—	—	—	—	—	—	1	2.1
—	—	—	—	+ 3	—	—	—	—	—	1	2.0
—	—	—	—	—	—	+ 2	—	—	—	1	2.0

Cryptomeria japonica plantation. On Mt. Dogadake (Loc. 113), triploid and tetraploid individuals grew together on a roadside slope.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in nine diploid individuals (*1151* from Loc. 78; *1448*, *1472* from Loc. 82; *1441* from Loc. 90; *1028* from Loc. 96; *1402* from Loc. 99; *1011*, *1013*, *1017* from Loc. 107), in eight triploids (*1689* from Loc. 75; *1673* from Loc. 79; *1450*, *1452* from Loc. 82; *1442* from Loc. 90; *1406* from Loc. 102; *1005*, *1010* from Loc. 107), and in five tetraploids (*1675* from Loc. 79; *1463*, *1467* from Loc. 82; *1004*, *1009* from Loc. 107).

The variations of the chromosome length and the positions of the centromere in each chromosome were almost identical to those of each cytotype from the Hokkaido and Tohoku Districts (Figs. 6, 7 and 10).

3. Meiosis

At diakinesis or metaphase I of meiosis, 132 SMCs were observed in 6 diploid individuals (*1151* from Loc. 78; *1448*, *1472* from Loc. 82; *1402* from Loc. 99; *1011*, *1013* from Loc. 107), 124 SMCs in 6 triploid individuals (*1726–1730* from Loc. 82; *1406* from Loc. 102), and 105 SMCs in 5 tetraploid individuals (*1033* from Loc. 78; *1463*, *1467* from Loc. 82; *1004*, *1009* from Loc. 107).

Only bivalent pairs of all chromosome (34_{II}) were observed in the diploids (Fig. 24A). Out of 105 SMCs from the tetraploids examined, 97 had only bivalent pairs of all chromosomes (68_{II}) (Fig. 25A), 5 had $67_{\text{II}}+2_{\text{I}}$ (Fig. 25B), and 3 had $66_{\text{II}}+4_{\text{I}}$. Each stage subsequent to metaphase I was normal in both cytotypes.

In triploids, 23 different configurations were observed (Figs. 24C-F): $3_{\text{III}}+33_{\text{II}}+27_{\text{I}}$ (3 SMCs), $3_{\text{III}}+31_{\text{II}}+31_{\text{I}}$ (2), $3_{\text{III}}+29_{\text{II}}+35_{\text{I}}$ (2), $2_{\text{III}}+36_{\text{II}}+24_{\text{I}}$ (2), $2_{\text{III}}+35_{\text{II}}+26_{\text{I}}$ (3), $2_{\text{III}}+34_{\text{II}}+28_{\text{I}}$ (4), $2_{\text{III}}+33_{\text{II}}+30_{\text{I}}$ (3), $2_{\text{III}}+32_{\text{II}}+32_{\text{I}}$ (4), $2_{\text{III}}+31_{\text{II}}+34_{\text{I}}$ (3), $2_{\text{III}}+30_{\text{II}}+36_{\text{I}}$ (1), $1_{\text{III}}+37_{\text{II}}+25_{\text{I}}$ (1), $1_{\text{III}}+36_{\text{II}}+27_{\text{I}}$ (3), $1_{\text{III}}+35_{\text{II}}+29_{\text{I}}$ (5), $1_{\text{III}}+34_{\text{II}}+31_{\text{I}}$ (5), $1_{\text{III}}+33_{\text{II}}+33_{\text{I}}$ (7), $1_{\text{III}}+32_{\text{II}}+35_{\text{I}}$ (1), $39_{\text{II}}+24_{\text{I}}$ (5), $38_{\text{II}}+26_{\text{I}}$ (9), $37_{\text{II}}+28_{\text{I}}$ (13), $36_{\text{II}}+30_{\text{I}}$ (22), $35_{\text{II}}+32_{\text{I}}$ (13), $34_{\text{II}}+34_{\text{I}}$ (11), and $33_{\text{II}}+36_{\text{I}}$ (2). Trivalents were observed in 49 of 124 SMCs, and their number per SMC varied from 1 to 3. The commonest configuration was $36_{\text{II}}+30_{\text{I}}$, and the mean was $0.7_{\text{III}}+35.0_{\text{II}}+30.0_{\text{I}}$.

Various kinds of abnormalities were observed throughout all stages of meiosis in six triploid individuals (Fig. 26), resembling those of the triploids in the Tohoku District (Fig. 12). Every SMCs examined had univalents at metaphase I and had lagging chromosome or chromosome bridges at anaphase I (Figs. 26A, B). At telophase I or interkinesis, several micronuclei in addition to two daughter nuclei were observed in 27–72% of SMCs (Figs. 26C, D). At metaphase II, abnormalities were observed in 13–49% of SMCs (Figs. 26E, F). At anaphase II, abnormalities were observed in 10–63% of SMCs, but lagging chromosomes were found in only 0–4% of SMCs (Figs. 26G–J). At telophase II, 10–70% of SMCs had micronuclei (Figs. 26K, L).

VII. *Shikoku District*

Lycopodium clavatum in the Shikoku District commonly occurs from coastal regions to mountains, and two morphologically distinct forms referred to as *L. clavatum* var. *wal-*

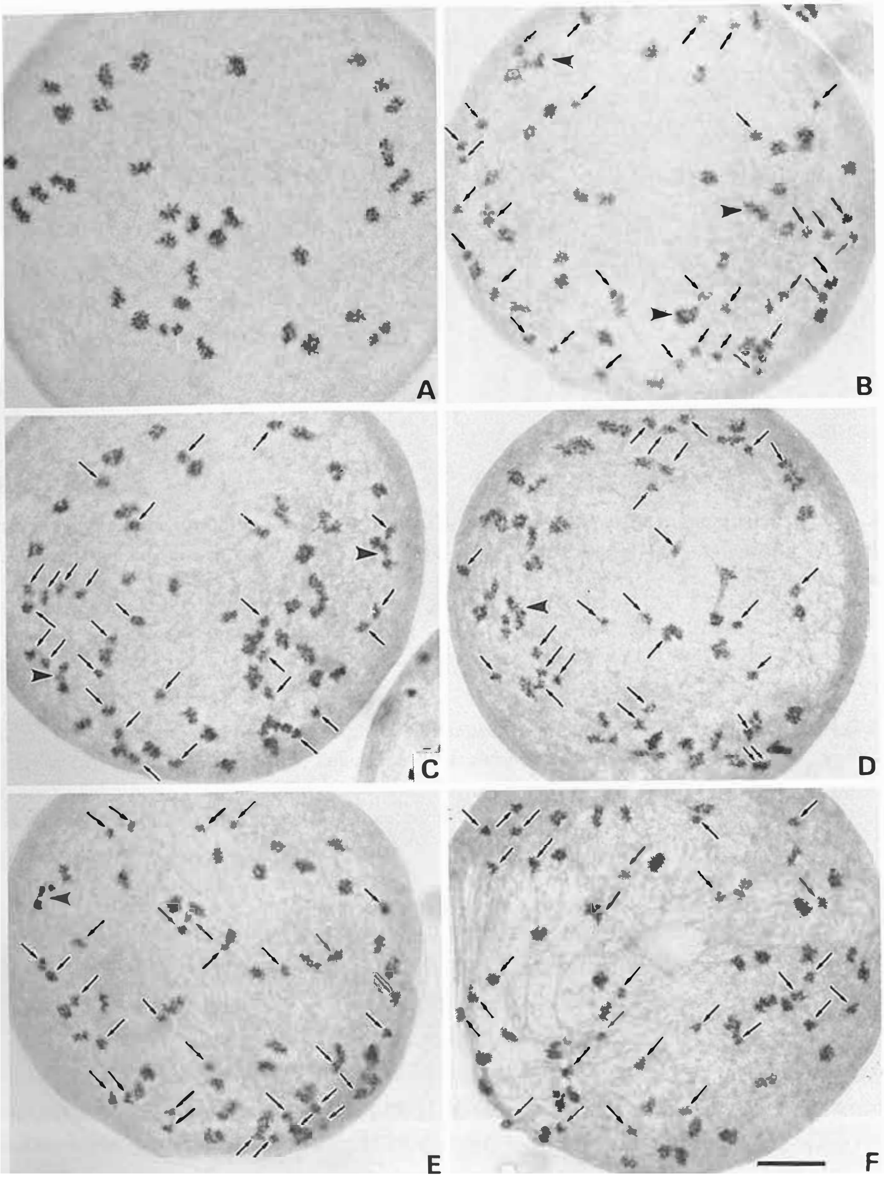

Fig. 24. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of *Lycopodium clavatum* examined in Chugoku District. A, 2n = 68 = 34II, *Takamiya 1472* from Loc. 82. B–F: 2n = 102, *Takamiya 1406* from Loc. 102. B, 3III + 29II + 35I; C, 2III + 34II + 28I; D, 1III + 37II + 25I; E, 2III + 34II + 31I; F, 37II + 28I. Arrow heads and arrows indicate trivalents and univalents, respectively. Bar represents 10 μm.

lichianum and var. *robustius* are known in the southern regions and central mountains, respectively (Tagawa, 1959). In this study, field observations and collections were made in 26 localities of *L. clavatum* populations at an elevation of 20 m to 1900 m. Chromosome numbers were determined in 108 individuals, of which 64 collected from 19 localities were diploids, 17 from 9 were triploids, and 27 from 17 were tetraploids (Figs. 1, 2, 27; Table 1).

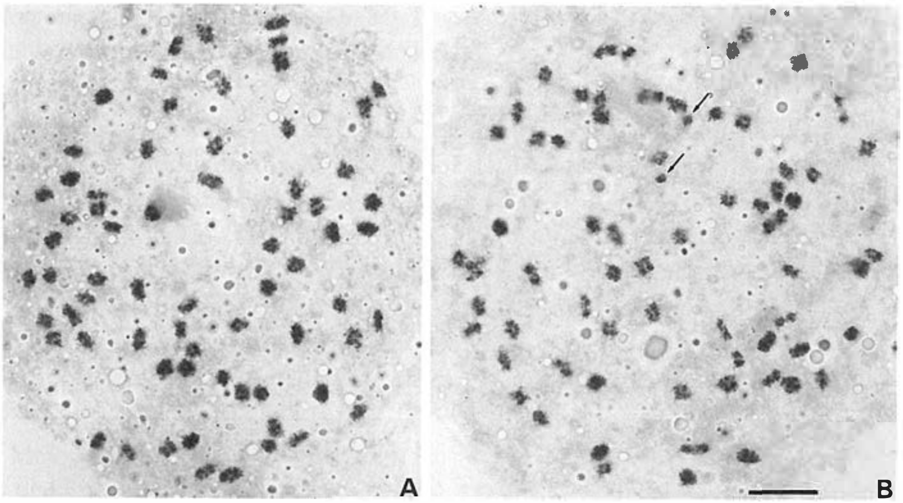

Fig. 25. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of tetraploid *Lycopodium clavatum* with 2n = 136 (*Takamiya 1467* from Loc. 82). A, 68_{II}. B, $67_{II}+2_{I}$. Arrows indicate univalent!s. Bar represents 10 μm.

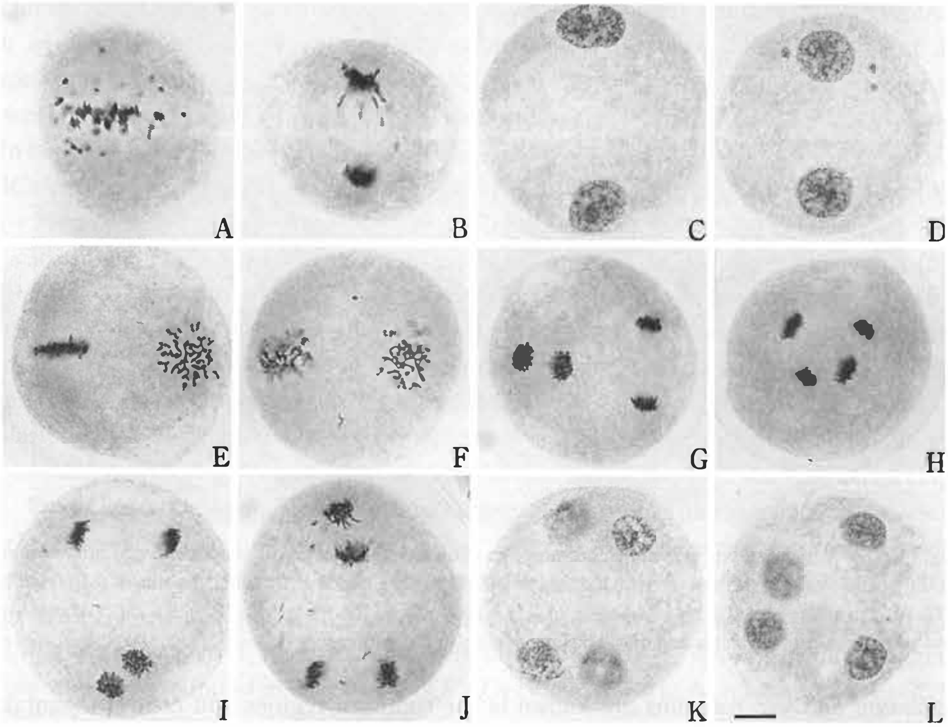

Fig. 26. Photomicrographs of SMCs at various meiotic phases of triploid *Lycopodium clavatum* with 2n = 102 (*Takamiya 1406*). A, metaphase I; B, anaphase I; C and D, telophase I or interkinesis; E and F, metaphase II; G–J, anaphase II, K and L, telophase II. In A, B, D, F, ~~H-~~J, L, abnormal divisions are observed. Bar represents 10 μm.

I,

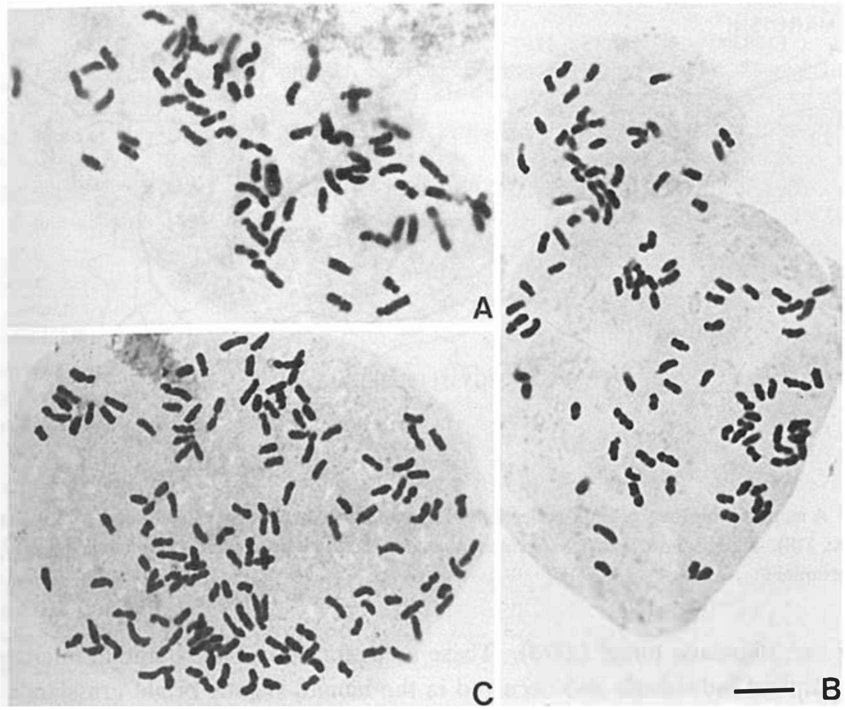

Fig. 27. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Shikoku District. A, 2n = 68, from Mt. Tsurugi, Tokushima Prefecture (Loc. 118, *Takamiya 2773*). B, 2n = 102, from Mt. Tsurugi, Tokushima Pref. (Loc. 118, *Takamiya 2784*). C, 2n = 136, from Mt. Higashiakaishi, Ehime Pref. (Loc. 114, *Takamiya 1557*). Bar represents 5 μm.

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows: On Mt. Higashiakaishi (Loc. 114), diploid individuals grew on the floor of a *Cryptomeria japonica* plantation (alt. 1000 m) and around the edges of a *Sasa hayatae* grassland (alt. 1600 m), and tetraploid individuals grew in a sunny, open place (alt. 1300 m). In Ichinokawa (Loc. 115), diploid and triploid individuals grew together around the edges of a *Pinus densiflora* forest. On Mt. Kanpuu (Loc. 116), only tetraploid individuals grew on a roadside slope. In Kumohaya (Loc. 117), diploid and tetraploid individuals occurred side by side on a roadside slope.

The habitats of *Lycopodium clavatum* on Mt. Tsurugi (Loc. 118), where diploid, triploid, and tetraploid cytotypes were found, are explained by a list of plants associated with *L. clavatum* (Table 9) and by a map showing collection sites (Fig. 28). The explorational route ranged from alt. 1400 m to 1957 m and crossed two vegetation zones: the broad-leaved deciduous forest and the coniferous forest zones. Vegetation along the route consisted of *Fagus crenata*, *Quercus mongolica* var. *grosseserrata* forests, *Betula ermanii* scrub, *Abies veitchii* var. *sikokiana* forest, and *Sasa hayatae* grassland near the mountaintop, and so on. Diploid individuals grew on the floor of a well-developed *Quercus mongolica* var. *grosseserrata* forest (*2772*), a *Fagus crenata* forest (*2773*), and an *Abies*

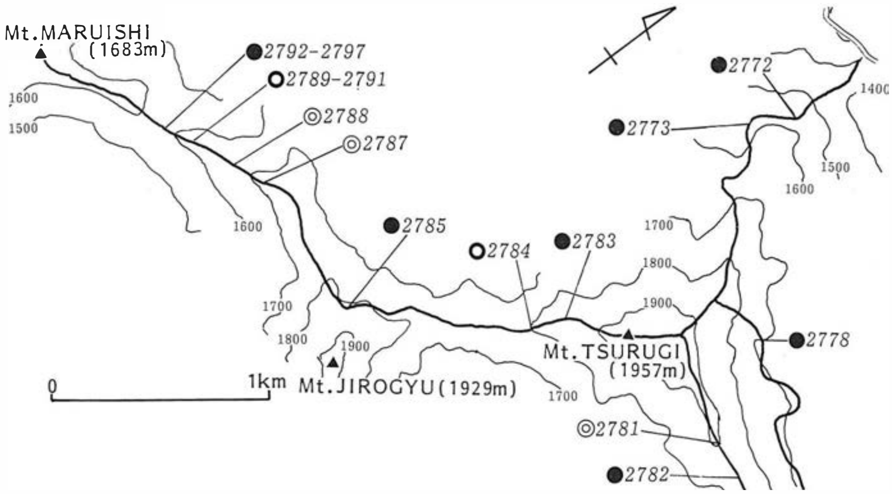

Fig. 28. A map showing the site of the collections of *Lycopodium clavatum* on Mt. Tsurugi, Tokushima Prefecture (Loc. 118). Numbers are voucher specimen numbers. Solid circle, diploid; open circle, triploid; double circle, tetraploid.

veitchii var. *sikokiana* forest (*2778*). These areas formed a shady, humid microenvironment. Diploid individuals also occurred in the humid, slightly bright grasslands (*2792–2797*) and in the sunny, dwarf grasslands (*2782, 2783, 2785*) of *Sasa hayatae*. Triploid individuals grew around the edges and in the sunny places of dwarf *Sasa hayatae* grasslands (*2784, 2789–2791*). Tetraploid individuals grew in a sunny, dry environment at the grassland edges (*2781*) and in open places (*2787, 2788*). Thus, diploid, triploid, and tetraploid individuals were not found intermingled with one another, but occurred in different habitats.

In Kirikoshi (Loc. 119) and Minanose (Loc. 120), diploid and tetraploid individuals grew intermingled on a roadside slope and around the edges of a *Pinus densiflora* forest. In Kushikawa (Loc. 121), diploid and triploid individuals grew together in an open place of roadside slope. On Mt. Shiraga (Loc. 122), only triploid individuals grew on a roadside slope. In Sameura (Loc. 123), diploid and tetraploid individuals occurred around the edges of a *Cryptomeria japonica* plantation and in an open roadside slope, respectively. In Naragitoge (Loc. 124), diploid, triploid, and tetraploid individuals grew side by side in an open place where juvenile plants of *Pinus densiflora*, *Pieris japonica*, *Eurya japonica*, etc., were growing. In Segiri (Loc. 125), diploid and tetraploid individuals grew together on a roadside slope. In Asahide (Loc. 126), only diploid individuals were found around the edge of a *Chamaecyparis pisifera* plantation. In Kitaji (Loc. 127), diploid and triploid individuals grew together in a wet rocky place where *Rhododendron macrosepalum*, etc., were growing. In Hirano (Loc. 128), only diploid individuals grew in a wet rocky place along the river. In Sakamoto (Loc. 129), diploid and triploid individuals occurred intermingled on the floor of a *Stachyurus praecox* open forest. In Kuki (Loc. 130) and Todoroki (Loc. 131), diploid and tetraploid individuals grew on a roadside slope. In Ichinoue (Loc. 132), only diploid individuals grew on a shady and humid roadside slope.

Table 9. A list of plants associated with each individual of *Lycopodium clavatum* on Mt. Tsurugi (Loc. 118)

Specimen number	*2772*	*2773*	*2778*	*2781*	*2782*	*2783*	*2784*	*2785*	*2787*	*2788*	*2789–91*	*2792–97*
Ploidy	2x	2x	2x	4x	2x	2x	3x	2x	4x	4x	3x	2x
Altitude (m)	1560	1580	1700	1900	1850	1860	1800	1870	1720	1670	1620	1580
Name of species associated												
Tree Layer												
Fagus crenata	−	+	−	−	−	−	−	−	−	−	−	−
Acer sieboldianum	+	+	−	−	−	−	−	−	−	−	−	−
Quercus mongolica var. *grosseserrata*	+	+	−	−	−	−	−	−	−	−	−	−
Abies veitchii var. *sikokiana*	−	−	+	−	−	−	−	−	−	−	−	−
Shrub Layer												
Clethla barbinervis	+	−	−	−	−	−	−	−	−	−	−	−
Sapium japonicum	−	+	−	−	−	−	−	−	−	−	−	−
Symplocos coreana	+	+	−	−	−	−	−	−	−	−	−	−
Carpinus tschonoski	+	−	−	−	−	−	−	−	−	−	−	−
Acer rufinerve	−	+	−	−	−	−	−	−	−	−	−	−
Viburnum urceolatum	−	−	+	−	−	−	−	−	−	−	−	−
Sorbus commixta	−	−	+	−	−	−	−	−	−	−	−	−
Hydrangia paniculata	−	−	−	−	−	−	−	+	+	−	−	+
Herb Layer												
Sasamorpha purpurascens	+	+	−	−	−	−	−	−	−	−	−	−
Sasa nipponica	−	+	−	−	−	−	−	−	−	−	−	−
Struthiopteris niponica	+	+	−	−	−	−	−	−	−	−	−	−
Athyrium vidalii	+	−	−	−	−	−	−	−	−	−	+	−
Dryopteris austriaca	−	−	+	−	−	−	−	−	−	−	−	−
Oxalis griffithii	−	−	+	−	−	−	−	−	−	−	−	−
Polygonum cuspidatum	−	−	+	+	+	−	−	−	+	−	−	−
Hypericum shikokumontanum	−	−	−	+	+	+	+	+	+	+	−	−
Sasa hayatae	−	−	+	+	+	+	+	−	+	−	+	+
Solidago virga-aurea var. *asiatica*	−	−	−	−	−	+	+	+	−	−	+	−
Geranium shikokianum	−	−	−	+	+	−	+	−	+	+	+	−
Gentiana scabra	−	−	−	−	−	+	+	+	−	−	+	−
Ilex dentata	−	−	−	−	−	+	−	+	−	−	+	−
Carex blepharicarpa	−	−	−	−	−	+	−	−	+	−	−	−
Calamagrostis langsdorffii	−	−	−	−	−	−	+	+	−	−	−	+
Cirsium japonicum	−	−	−	−	−	−	+	−	−	−	−	−
Aster komonoensis	−	−	−	−	−	−	−	+	−	−	−	−
Trientalis europaea	−	−	−	−	−	−	−	+	−	−	−	−
Parnassia palustris	−	−	−	−	−	−	−	+	−	−	+	−
Miscanthus sinensis	−	−	−	−	−	−	−	+	+	+	+	+
Pedicularis resupinata	−	−	−	−	−	−	−	−	−	+	−	−
Heloniopsis orientalis	−	−	−	−	−	−	−	−	−	−	+	−

In Hiranabe (Loc. 133), diploid and tetraploid individuals grew together on a roadside slope. In Godai (Loc. 134), only tetraploid individuals grew with *Miscanthus sinensis* and *Zoysia japonica* in a disturbed open place. In Amikawagoe (Loc. 135), triploid and tetraploid individuals grew together on the floor and around the edges of a juvenile *Pinus densiflora* forest. In Futsusegoe (Loc. 136) and Myojin (Loc. 137), only tetraploid individuals were found on a roadside slope and in the grassland of a skiing ground, respectively. In Kashiwagi (Loc. 138), only diploid individuals grew on the floor of a *Cryptomeria japonica* plantation. In Ashizuri (Loc. 139), triploid and tetraploid individuals grew together on a roadside slope.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in two diploid individuals (*2773* from Loc. 118; *2506* from Loc. 133), in one triploid (*2784* from Loc. 118), and in one tetraploid (*1557* from Loc. 114).

The variations of chromosome length and the positions of the centromere in each chromosome were found to be almost identical to those of each cytotype from the Hokkaido and Tohoku Districts (Figs. 6, 7, 10).

3. Meiosis

At diakinesis or metaphase I of meiosis, 41 SMCs were observed in 2 diploid individuals (*2785* from Loc. 118; *2563* from Loc. 125), 25 SMCs in a triploid individual (*2789* from Loc. 118), and 20 SMCs in a tetraploid individual (*1557* from Loc. 118).

Only bivalent pairs of all chromosomes (34_{II}) were observed in the diploids with $2n=68$ (Fig. 29A). Out of 20 SMCs from the tetraploid with $2n=136$, 18 had only bivalent pairs of all chromosomes (68_{II}) (Fig. 29F), and 2 had $67_{\mathrm{II}}+2_{\mathrm{I}}$. Each stage subsequent to metaphase I was normal in both cytotypes.

In the triploid with $2n=102$, 12 different configurations were observed (Figs. 29B–F): $3_{\mathrm{III}}+34_{\mathrm{II}}+25_{\mathrm{I}}$ (1 SMC), $2_{\mathrm{III}}+34_{\mathrm{II}}+28_{\mathrm{I}}$ (1), $1_{\mathrm{III}}+37_{\mathrm{II}}+25_{\mathrm{I}}$ (1), $1_{\mathrm{III}}+36_{\mathrm{II}}+27_{\mathrm{I}}$ (2), $1_{\mathrm{III}}+35_{\mathrm{II}}+29_{\mathrm{I}}$ (3), $1_{\mathrm{III}}+34_{\mathrm{II}}+31_{\mathrm{I}}$ (1), $1_{\mathrm{III}}+33_{\mathrm{II}}+33_{\mathrm{I}}$ (1), $38_{\mathrm{II}}+26_{\mathrm{I}}$ (1), $37_{\mathrm{II}}+28_{\mathrm{I}}$ (5), $36_{\mathrm{II}}+30_{\mathrm{I}}$ (4), $35_{\mathrm{II}}+32_{\mathrm{I}}$ (3), and $34_{\mathrm{II}}+34_{\mathrm{I}}$ (2). Trivalents were observed in 10 of 20 SMCs, and their number per SMC varied from 1 to 3. The commonest configuration was $37_{\mathrm{II}}+28_{\mathrm{I}}$, and the mean was $0.5_{\mathrm{III}}+35.6_{\mathrm{II}}+29.3_{\mathrm{I}}$.

Various kinds of abnormalities were observed throughout all stages of meiosis, similar to those of the triploids of the Tohoku District. All SMCs examined had univalents at metaphase I and had lagging chromosome or chromosome bridges at anaphase I. At telophase I or interkinesis, several micronuclei in addition to two daughter nuclei were observed in 97% of SMCs. At metaphase II, abnormalities were observed in 61% of SMCs. At anaphase II, abnormalities were observed in 58% of SMCs, but no lagging chromosome was found. At telophase II, 92% of SMCs had micronuclei.

VIII. *Kyushu District*

In the Kyushu District, *Lycopodium clavatum* commonly occurs from coastal regions up to mountains. There are two morphologically distinct forms referred to as *L. clavatum* var. *wallichianum* and var. *robustius*. The former is known in southern regions, and the later in various places (Tagawa, 1959; Tsutsui, 1988). In this study, field observations and

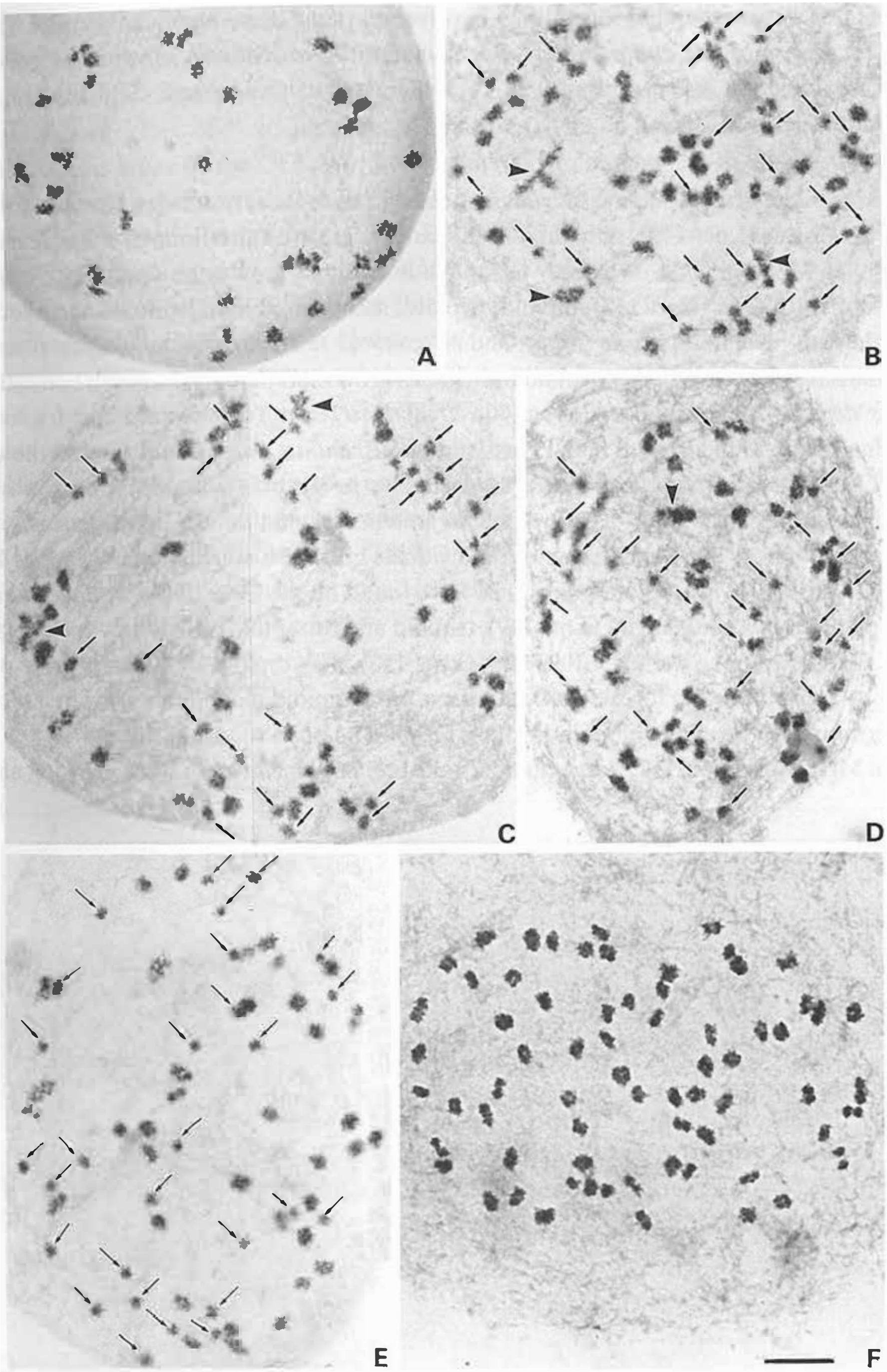

Fig. 29. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of *Lycopodium clavatum* examined in Shikoku Distirct. A, 2n = 68 = 34_{II}, *Takamiya 2785* from Loc. 118. B–E, 2n = 102, *Takamiya 2789* from Loc. 118. B, $3_{\mathrm{III}}+34_{\mathrm{II}}+25_{\mathrm{I}}$; C, $2_{\mathrm{III}}+34_{\mathrm{II}}+28_{\mathrm{I}}$; D, $1_{\mathrm{III}}+35_{\mathrm{II}}+29_{\mathrm{I}}$; E, $37_{\mathrm{II}}+28_{\mathrm{I}}$. Arrow heads and arrows indicate trivalents and univalents, respectively. F, 2n = 136 = 68II, *Takamiya 1557* from Loc. 114. Bar represents 10 μm.

collections were made in 33 localities of *L. clavatum* populations at an elevation of 80 m to 1650 m. Chromosome numbers were determined in 143 individuals, of which 94 collected from 26 localities were diploids, 22 from 13 were triploids, and 27 from 12 were tetraploids (Figs. 1, 2, 30; Table 1).

1. Growing places

The habitats of *Lycopodium clavatum* studied in each locality are described as follows: On Mt. Kosho (Loc. 140), only diploid individuals grew on the floor of a *Fagus crenata* forest. In Meotogi (Loc. 141), only tetraploid individuals grew in an open place of roadside slope. In Oita (Loc. 142), diploid, triploid, and tetraploid individuals occurred side by side with juvenile *Pinus densiflora* and *Miscanthus sinensis* in a sunny, open place. In Kamimisaka (Loc. 143), only triploid individuals grew on the floor of a scrub consisting of *Pinus densiflora* and *Quercus serrata*. In Uchiyama (Loc. 144), diploid and triploid individuals were found in a 1.5 m tall grassland of *Miscanthus sinensis* and around the edges of a *Cryptomeria japonica* plantation, respectively. In Kuroki (Loc. 145), only diploid individuals grew on the floor of a *Cryptomeria japonica* plantation. In Inasa (Loc. 146) and Dannoharu (Loc. 147), only tetraploid individuals grew in disturbed open places. In Inoseto (Loc. 148), only diploid individuals were found on the floor of a *Chamaecyparis obtusa* plantation. In Iidakogen (Loc. 149), triploid and tetraploid individuals grew together on a roadside slope. On Mt. Mukozaka (Loc. 150), only diploid individuals grew on the floor of a *Fagus crenata* forest. In Obata (Loc. 151), diploid individuals grew in a moor of *Sphagnum palustre* and triploid individuals grew on an open roadside slope.

On Mt. Osuzu (Loc. 152), large numbers of *Lycopodium clavatum* were growing along a

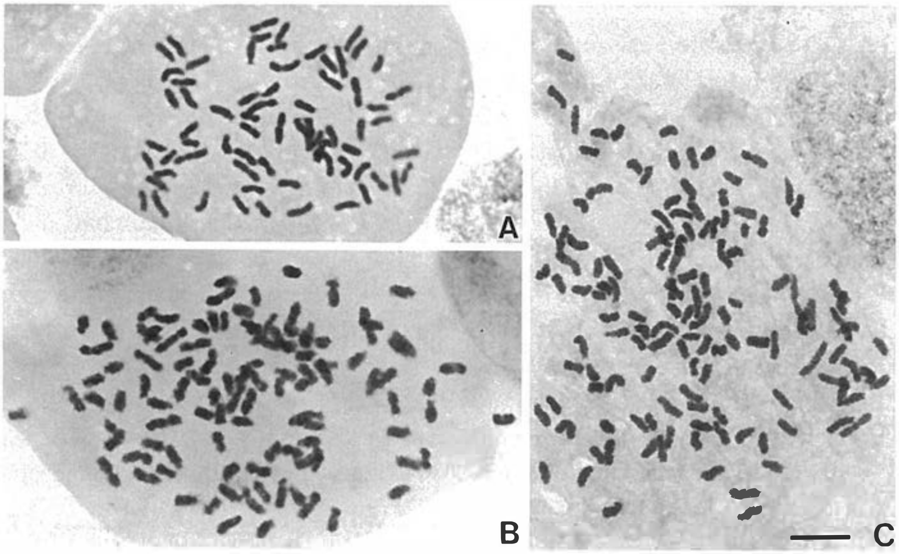

Fig. 30. Photomicrographs of mitotic metaphase chromosomes of *Lycopodium clavatum* examined in Kyushu District. A, 2n = 68, from Osuzu, Miyazaki Prefecture (Loc. 152, *Takamiya 2026*). B, 2n = 102, from Mt. Takakuma, Kagoshima Pref. (Loc. 168, *Takamiya 2124*). C, 2n = 136, from Osuzu, Miyazaki Pref. (Loc. 152, *Takamiya 2032*). Bar represents 5 μm.

woodland path ranging from alt. 400 m to 500 m, and five populations sites belonging to the evergreen broad-leaved forest zone were studied. Only diploid individuals were found around the edges of a *Cryptomeria japonica* plantation (alt. 560 m) and on the floor of a scrub consisting of *Pieris japonica*, *Lyonia neziki*, *Eurya japonica*, etc. (alt. 440 m, 460m). These areas formed a shady, humid microenvironment. At the other two sites, two or three cytotypes were found in the same place: Diploid and tetraploid individuals occurred together on a humid, bright slope (alt. 480 m) where *Dautzia crenata*, *Miscanthus sinensis*, *Boehmeria spicata*, etc., were growing. Diploid, triploid, and tetraploid individuals occurred side by side on the floor of a bush (alt. 500 m) which consisted of *Clethra barbinervis*, *Pieris japonica*, *Hydrangea luteovenosa*, *Rubus palmatus*, *Dicranopteris dichotoma*, *Sphaenomeris chusana*, *Lycopodium cernuum*, and so on. These two sites formed a bright and humid microenvironment, more disturbed than the sites where only diploids grew.

Habitats of *Lycopodium clavatum* on Mt. Shiratori (Loc. 153) and Ebinokogen (Loc. 154), where diploid, triploid, and tetraploid cytotypes were found, are explained by a list of plants associated with *L. clavatum* (Table 10, 11) and by a map showing collection sites (Fig. 31). The explorational route ranged from alt. 1100 m to 1363 m and belonged to the broad-leaved deciduous forest zone.

On Mt. Shiratori vegetation along the route consisted of *Quercus mongolica* var. *gros-*

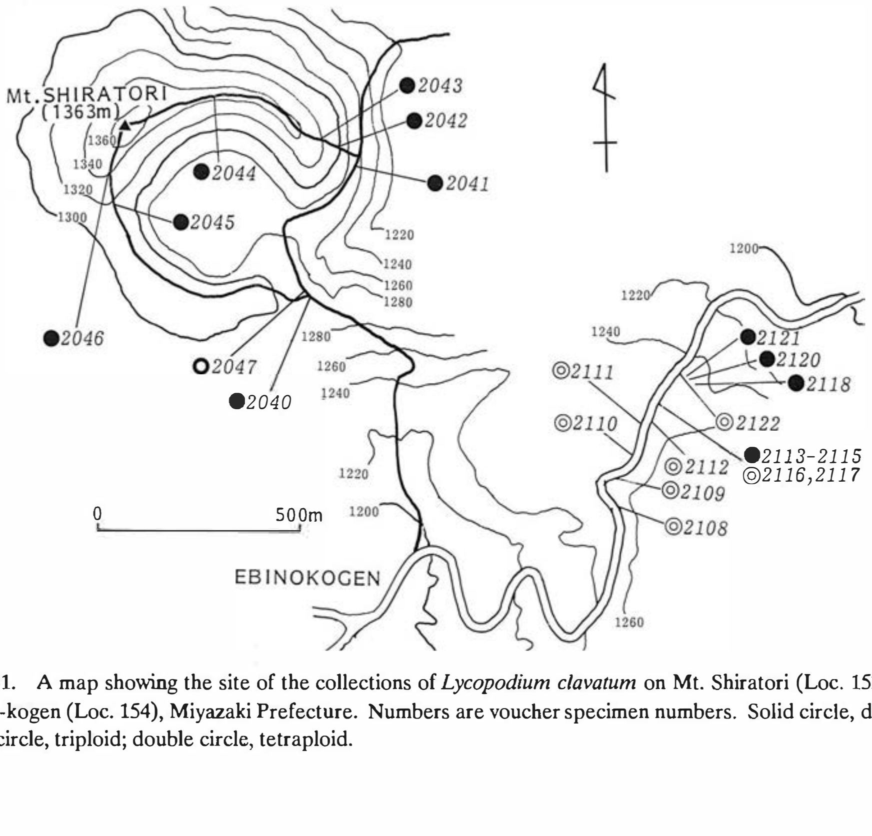

Fig. 31. A map showing the site of the collections of *Lycopodium clavatum* on Mt. Shiratori (Loc. 153) and Ebino-kogen (Loc. 154), Miyazaki Prefecture. Numbers are voucher specimen numbers. Solid circle, diploid; open circle, triploid; double circle, tetraploid.

Table 10. A list of plants associated with each individual of *Lycopodium clavatum* at Mt. Shiratori (Loc. 153)

Specimen number	*2040*	*2041*	*2042*	*2043*	*2044*	*2045*	*2046*	*2047*
Ploidy	2x	2x	2x	2x	2x	2x	2x	3x
Altitude (m)	1280	1270	1300	1320	1350	1340	1320	1280
Name of species associated								
Tree Layer								
Pinus densiflora	−	−	−	−	+	−	+	−
Clethra barbinervis	−	−	−	−	+	−	−	−
Acer sieboldianum	−	−	−	−	+	−	−	−
Shrub Layer								
Abies firma	−	−	+	−	+	−	−	−
Rhododendron obtusum	−	+	+	−	+	+	+	−
Lyonia neziki	−	+	+	−	−	−	+	+
Quercus mongolica var. *grosseserrata*	−	+	+	−	−	−	+	−
Pinus densiflora	−	+	−	+	−	+	−	−
Ilex crenata	−	−	+	−	+	−	−	−
Hydrangia paniculata	−	−	+	+	+	+	+	−
Clethra barbinervis	−	+	−	+	+	+	−	−
Rhododendron kaempferi	−	−	−	+	−	−	−	−
Wikstroemia ganpi	−	−	−	+	−	+	−	−
Hydrangea lute-ovenosa	−	−	−	+	+	−	−	−
Symplocos myrtacea	−	−	−	+	−	−	−	−
Herb Layer								
Miscanthus sinensis	+	+	−	+	+	+	−	+
Struthiopteris niponica	+	−	−	−	−	+	−	+
Ilex crenata	+	−	−	−	−	−	−	−
Pinus densiflora	+	−	−	−	−	−	−	+
Sasa sp.	−	−	+	−	−	+	−	−
Smilax china	−	−	−	+	−	+	−	−
Tripterospermum japonicum	−	−	−	+	+	−	−	−
Maianthemum dilatatum	−	−	−	+	+	−	−	−

seserrata forest, *Pinus densiflora* forest, *Rhododendron obtusum* bushes and so on. Diploids grew around the edges and on the floor of *Pinus densiflora* forests (*2044, 2046*), and on the floor of *Rhododendron obtusum* bushes (*2041, 2042*). These areas formed a shady and humid microenvironment. Diploid individuals also occurred on the humid and slightly bright floor of scrubs (*2043, 2045*) and in a sunny, humid, open place (*2040*). Triploid individuals grew in a sunny, humid open place, (*2047*). Diploid and triploid individuals were not found intermingled.

In Ebinokogen, several individuals of *Lycopodium clavatum* occurred on the disturbed slope along the roadway. Only tetraploid individuals grew at the sunny open place, intermingled with herbs and trees less than 30 cm in tall (*2108–2111*). Diploid and tetraploid grew together at a place where 50 cm tall *Miscanthus sinensis* and *Hydrangea paniculata*

Table 11. A list of plants associated with each individual of *Lycopodium clavatum* on Mt. Ebino-kogen (Loc. 154)

Specimen number Ploidy Name of species associated	*2108* 4x	*2109* 4x	*2110* 4x	*2111* 4x	*2112* 4x	*2113–15* 2x	*2116,17* 4x	*2118* 2x	*2120* 2x	*2121* 2x	*2122* 4x
Tree Layer											
Chamaecyparis obtusa	−	−	−	−	−	−[a]		+	+	−	−
Shrub Layer											
Symplocos myrtacea	−	−	−	−	−	−		+	+	−	−
Lyonia neziki	−	−	−	−	−	−		+	−	−	−
Hydrangea lute-ovenosa	−	−	−	−	−	−		+	+	−	−
Eurya japonica	−	−	−	−	−	−		+	+	−	−
Herb Layer											
Gentiana scabra	+	−	−	−	−	−		−	−	−	−
Alnus sieboldiana	+	−	−	−	−	−		−	−	−	−
Struthiopteris niponica	+	+	−	+	+	+		+	+	+	−
Smilax china	+	−	−	−	−	−		+	−	−	−
Hydrangea paniculata	−	+	+	−	+	+		+	+	+	−
Miscanthus sinensis	−	+	+	+	+	+		+	+	+	+
Aletris luteo-viridis	−	−	+	−	−	−		−	−	−	−
Quercus mongolica var. *grosesserrata*	−	−	−	+	−	−		−	−	−	−
Clethra barbinervis	−	−	−	−	+	+		−	+	+	−
Tsuga sieboldii	−	−	−	−	+	−		−	−	−	−
Abie firma	−	−	−	−	−	+		−	−	−	−
Hydrangea luteo-venosa	−	−	−	−	−	+		−	−	+	−
Drosera rotundifolia	−	−	−	−	−	+		−	−	−	−
Pteridium aquilinum	−	−	−	−	−	−		−	+	+	−
Lespedeza pilosa	−	−	−	−	−	−		−	−	+	−
Lespedeza cuneata	−	−	−	−	−	−		−	−	+	−
Lyonia neziki	−	−	−	−	−	−		−	−	+	−
Pinus densiflora	−	−	−	−	−	−		−	−	−	+

a: Specimen numbers' *2113–2117* grew in the same colony.

were growing (*2113–2117*). Along a transect line at a right angle (90°) to the roadway four individuals (*2118*, *2120*, *2121*, *2122*) were collected at 10, 8, 5, and 2 m away from the margin of the roadway, respectively. Diploid individuals *2118* and *2120* occurred on the shady, humid floor of a *Chamaecyparis obtusa* plantation. Diploid *2121*, grew in a bright, humid place with 50 cm tall *Miscanthus sinensis* plants. Tetraploid individual *2122* grew in a sunny, dry place. Thus, diploids and tetraploids occurred in different habitats in this small area.

In Honmyoji (Loc. 155), diploid and triploid individuals grew together on a open roadside slope. In Tatsuta (Loc. 156) and Hirogawara (Loc. 157), diploid, triploid, and tetraploid individuals grew side by side on a roadside slope. In Haki (Loc. 158) and Nihonsugi (Loc. 159), only diploid individuals were found on the floor of a *Cryptomeria* *japonica* plantation and around the edge of a *Quercus mongolica* var. *grosseserrata* forest, respectively. In Maeshima (Loc. 160), triploid and tetraploid individuals grew together on a roadside slope. In Odorigoe (Loc. 161) and Joseki (Loc. 162), only diploid individuals grew on the floor of a *Cryptomeria japonica* plantation and around the edges of a *Quercus glauca* forest, respectively. In Ichifusa (Loc. 163), diploid and triploid individuals occurred on the floor of a *Pinus densiflora* forest. In Yude (Loc. 164), only diploid individuals were found around the edge of a *Cryptomeria japonica* plantation. On Mt. Gyojindake (Loc. 165), only triploid individuals grew in a *Miscanthus sinensis* grassland on the roadside slope. In Juso (Loc. 166) and Imutake (Loc. 167), only diploid individuals grew around the edge of a *Cryptomeria japonica* plantation and in a *Miscanthus sinensis* grassland, respectively. On Mt. Takakuma (Loc. 168), diploid, triploids and tetraploid individuals occurred side by side on the floor of a 2–4 m tall *Pinus densiflora* forest.

In Yaku-1 (Loc. 169), only diploid individuals grew around the edge of a *Cryptomeria japonica* forest. In Yaku-2 (Loc. 170), only diploid individuals grew on a roadside slope. In Yaku-3 (Loc. 171), only diploid individuals were found around the edge and on the floor of *Cryptomeria japonica* forests (alt. 1000–1200 m), on the floor of *Rhododendron metternichii* var. *yakushimanum* scrubs (alt. 1350–1500 m), in the humid open places (alt. 1450–1650 m), and on the roadside slope (alt. 250 m, 550 m). In Yaku-4 (Loc. 172), only diploid individuals grew on the humid roadside slope. On Yakushima Island triploids and tetraploids were not found.

2. Karyotype

Morphological observations of the somatic chromosomes at mitotic metaphase were made in four diploid individuals (*2700* from Loc. 142; *2026* from Loc. 152; *1304, 1307* from Loc. 171), in one triploid (*2124* from Loc. 168) and in one tetraploid (*2032* from Loc. 152).

The variations of chromosome length and the positions of the centromere in each chromosome were found to be almost identical to those of each cytotype from the Hokkaido and Tohoku Districts (Figs. 6,7, and 10).

3. Meiosis

At diakinesis or metaphase I of meiosis, 65 SMCs were observed in 3 diploid individuals (*2033* from Loc. 152; *3297* from Loc. 156; *1304* from Loc. 171), 21 SMCs in a triploid individual (*2124* from Loc. 168), and 40 SMCs in 2 tetraploid individuals (*2112, 2122* from Loc. 154).

Only bivalent pairs of all chromosomes (34_{II}) were observed in the diploids (Fig. 32A). Out of 43 SMCs from 2 tetraploids examined, 40 had only bivalent pairs of all chromosomes (68_{II}) (Fig. 32F) and 3 had $67_{\mathrm{II}}+2_{\mathrm{I}}$. Each stage subsequent to metaphase I was normal in both cytotypes.

In a triploid individual, 12 different configurations were observed (Figs. 32B–E): $3_{\mathrm{III}}+33_{\mathrm{II}}+27_{\mathrm{I}}$ (1 SMC), $2_{\mathrm{III}}+34_{\mathrm{II}}+28_{\mathrm{I}}$ (2), $2_{\mathrm{III}}+32_{\mathrm{II}}+32_{\mathrm{I}}$ (1), $1_{\mathrm{III}}+37_{\mathrm{II}}+25_{\mathrm{I}}$ (1), $1_{\mathrm{III}}+36_{\mathrm{II}}+27_{\mathrm{I}}$ (1), $1_{\mathrm{III}}+35_{\mathrm{II}}+29_{\mathrm{I}}$ (2), $1_{\mathrm{III}}+32_{\mathrm{II}}+35_{\mathrm{I}}$ (1), $39_{\mathrm{II}}+24_{\mathrm{I}}$ (1), $37_{\mathrm{II}}+28_{\mathrm{I}}$ (4), $36_{\mathrm{II}}+30_{\mathrm{I}}$ (2), $35_{\mathrm{II}}+32_{\mathrm{I}}$ (3), and $33_{\mathrm{II}}+36_{\mathrm{I}}$ (2). Trivalents were observed in 9 of 21 SMCs, and their number per SMC varied from 1 to 3. The commonest configuration was $37_{\mathrm{II}}+28_{\mathrm{I}}$, and the mean was $0.7_{\mathrm{III}}+35.2_{\mathrm{II}}+29.5_{\mathrm{I}}$.

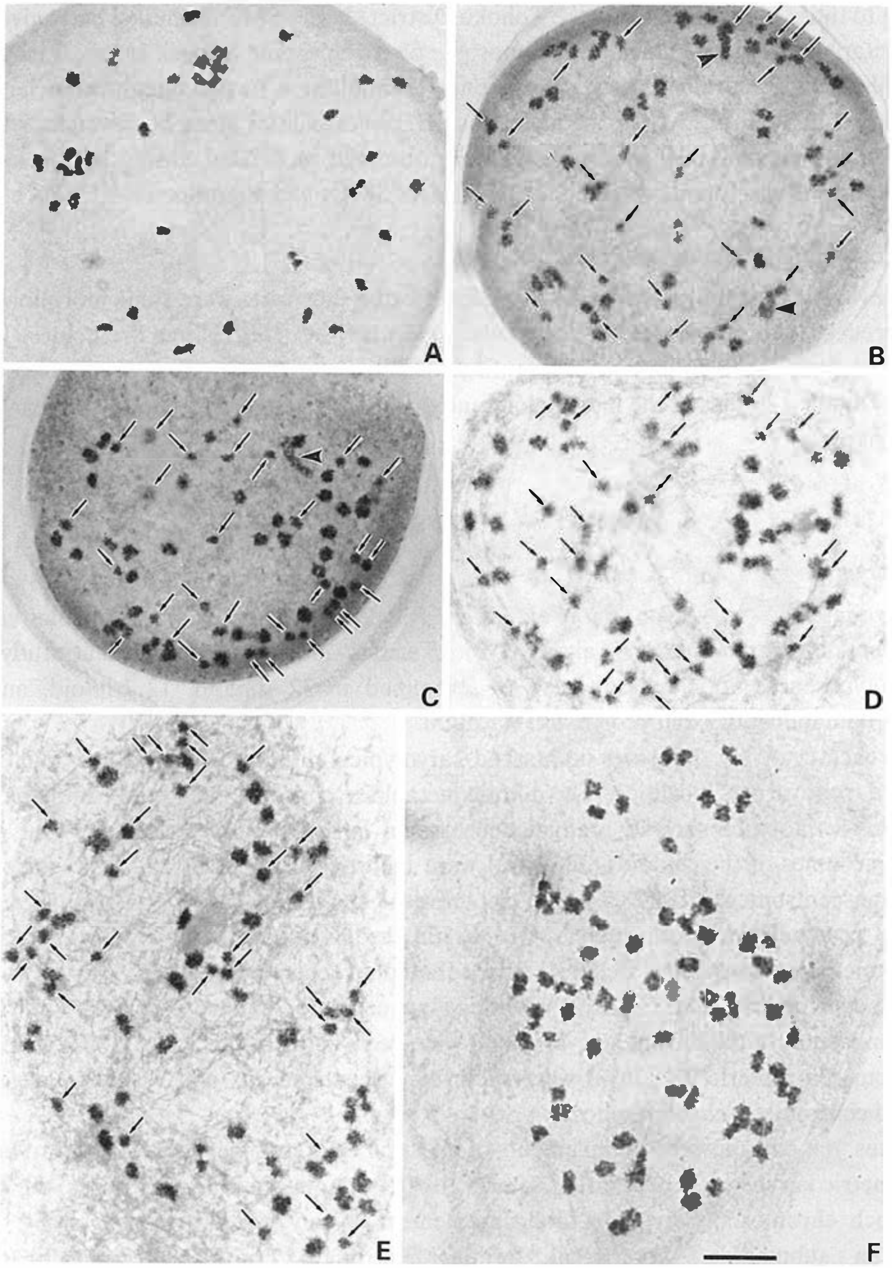

Fig. 32. Photomicrographs of meiotic chromosomes at diakinesis in SMCs of *Lycopodium clavatum* examined in Kushu District. A, $2n=68=34_{\mathrm{II}}$, *Takamiya 2033* from Loc. 152. B–E, $2n=102$, *Takamiya 2124* from Loc. 168. B, $2_{\mathrm{III}}+34_{\mathrm{II}}+28_{\mathrm{I}}$; C, $1_{\mathrm{III}}+35_{\mathrm{II}}+29_{\mathrm{I}}$; D, $37_{\mathrm{II}}+28_{\mathrm{I}}$; E, $35_{\mathrm{II}}+32_{\mathrm{I}}$. Arrow heads and arrows indicate trivalents and univalents, respectively. F, $2n=136=68_{\mathrm{II}}$, *Takamiya 2112* from Loc. 154. Bar represents 10 μm.

Various kinds of abnormalities were observed throughout all stages of meiosis, resembling to those of the triploids in the Tohoku District. Every SMC examined had univalents at metaphase I and had lagging chromosome or chromosome bridges at anaphase I. At telophase I or interkinesis, several micronuclei in addition to two daughter nuclei were observed in 42% of SMCs. At metaphase II, abnormalities were observed in 40% of SMCs. At anaphase II, abnormalities were observed in 38% of SMCs, but no lagging chromosome was found. At telophase II, 52% of SMCs had micronuclei.

IX. *External Morphology* of *Three Cytotypes*

Previously, Takamiya and Tanaka (1982) reported that there were some morphological differences in three cytotypes of *Lycopodium clavatum* from Hiroshima Prefecture. In the present study these differences are confirmed throughout the Japanese archipelago (Fig. 33). Detailed studies of the morphology and taxonomy of each cytotype will appear in future papers.

DISCUSSION

I. *Karyotype*

To date no karyotype data for plants of Lycopodiaceae are available except *Lycopodium casuarinoides* (Takamiya and Tanaka, 1983). In the present study, the karyotypes at mitotic metaphase were examined in 32 diploid, 12 triploid, and 15 tetraploid individuals of *Lycopodium clavatum*.

In each cytotype, there was no marked karyotypical difference among individuals collected from various localities. The mitotic metaphase chromosome of the complement in all three cytotypes showed gradual decrease in length in each cytotype. Out of 68 chromosomes of the diploids, 22 (32%) were median centromeric, 12 (18%) were submedian centromeric, 18 (28%) were subterminal centromeric, and 16 (24%) were terminal centromeric chromosomes. Out of 102 chromosomes of the triploids, 34 (33%) were median centromeric, 19 (19%) were submedian centromeric, 26 (25%) were subterminal centromeric, and 23 (23%) were terminal centromeric chromosomes. Out of 136 chromosomes of the tetraploids, 46 (34%) were median centromeric, 24 (18%) were submedian centromeric, 34 (25%) were subterminal centromeric, and 32 (24%) were terminal centromeric chromosomes.

Thus, the chromosome complements of all three cytotypes were categorized to be the symmetric karyotype in arm ratio (Tanaka, 1980). Among the three cytotypes, the ratios of each chromosomal type to total complement closely resembled each other: The median : submedian : subterminal : terminal centromeric chromosomes = ca. 30% : ca. 20% : ca. 25% : ca. 25% of the total complement. With respect to this, the triploids and the tetraploids were found to have autopolyploidal natures. But there were no clear homologous chromosome sets of three or four in the chromosome complement of the triploids and the tetraploids, respectively.

Fig. 33. Fertile aerial shoots of three cytotypes of Lycopodium clavatum. A–H, diploids. I–L, triploids. M–T, tetraploids. A, *Takamiya 2661* (Loc. 25); B, *2782* (Loc. 118); C, *1543* (Loc. 6); D, *1013* (Loc. 107); E, *1017* (Loc. 107); F, *2005* (Loc. 12); G, *2730* (Loc. 144); H, *2440* (Loc. 124); I, *1529* (Loc.10); J, *2719* (Loc. 142); K, *1025* (Loc. 96); L, *2784* (Loc. 118); M, *1557* (Loc. 39); N, *1565* (Loc. 2); O, *2109* (Loc. 154); P, *1524* (Loc. 9); Q, *2003* (Loc. 24); R, *3846* (Loc. 117); S, *1003* (Loc. 78); T, *2116* (Loc. 154). Bar represents 10 cm.

II. *Meiosis*

The meiotic behavior of chromosomes was observed in 20 diploid, 10 triploid, and 12 tetraploid individuals of *Lycopodium clavatum*.

Meiotic chromosome-pairings in diploids with 2n = 68 were complete and normal, and formed 34_{II} at diakinesis or metaphase I in 426 SMCs observed. Out of 248 SMCs examined in tetraploids with 2n = 136, almost all 227 (92%) had only bivalent pairs of all chromosomes (68_{II}) at diakinesis or metaphase I, 18 (7%) had $67_{\text{II}}+2_{\text{I}}$, and 3 (1%) had $66_{\text{II}}+4_{\text{I}}$. No multivalent was observed. Each stage subsequent to metaphase I was complete and normal in both cytotypes. Thus, diploids and tetraploids seemed to be fertile and stable cytotypes, and to propagate sexually.

In the triploids, 210 SMCs at diakinesis or metaphase I were examined. Results are summarized in Table 12. The following meiotic configurations were frequently observed: $2_{\text{III}}+34_{\text{II}}+28_{\text{I}}$, $1_{\text{III}}+36_{\text{II}}+27_{\text{I}}$, $1_{\text{III}}+35_{\text{II}}+29_{\text{I}}$, $1_{\text{III}}+34_{\text{II}}+31_{\text{I}}$, $1_{\text{III}}+33_{\text{II}}+33_{\text{I}}$, $38_{\text{II}}+26_{\text{I}}$, $37_{\text{II}}+28_{\text{I}}$, $36_{\text{II}}+30_{\text{I}}$, $35_{\text{II}}+32_{\text{I}}$, and $34_{\text{II}}+34_{\text{I}}$. The commonest configuration was $36_{\text{II}}+30_{\text{I}}$, and the mean was $0.7_{\text{III}}+3.5_{\text{II}}+29.9_{\text{I}}$. Trivalents were observed in 39% of SMCs, and their number per SMC varied from one to three. These results indicate that among three genomes (= chromosome complements, x = 34) of the tripioid, two are homologous and the remaining one is partly homologous with the other two.

In 162 SMCs (77%), the proportion of bivalents was slightly higher than numerically estimated from the number of trivalents. For example, if there is a trivalent in a SMC, one expects, 33 bivalents and 33 univalents as a balance. Any increase in the number of bivalents from such an estimation should indicate the extent of intragenomic pairing within the remaining univalents of the extra set of chromosomes. There were two to ten univalents which formed one to five extra bivalents, respectively. In pteridophytes, intragenomic pairing has been documented only from colchicine-induced autotriploid *Adiantum capillus-veneris* (Verma, 1977, 1978). Therefore, our finding in *Lycopodium clavatum* is the first such report in nature.

The frequency of abnormality at each stage of meiosis in the triploid examined is summarized in Table 13. Various kinds of abnormalities such as lagging chromosomes or chromosome bridges were observed throughout all stages of meiosis. In spite of the fact that all SMCs had lagging chromosomes at anaphase I, only a few (0–4%, mean 1.4%) had lagging chromosomes at metaphase II. This finding indicates that two sister chromatids of each univalent chromosome separate only at metaphase II. While the same behavior of univalents observed in triploid *Lycopodium clavatum* has been seen and named as Drosera-type meiosis (Rosenberg, 1909), there have been no reports on this meiotic type in pteridophytes.

If triploids are fertile and propagate sexually, then the chromosome number of their progeny will show several variations, because chromosome segregation is irregular and each spore has a varied chromosome number. But no chromosome number other than 2n = 102 was observed. Therefore, triploids were found to be sterile and are assumed to propagate only vegetatively.

Table 12. Meiotic chromosome configurations in the triploid cytotypes (2n=102)

Configurations	Individual numbers, and number of SMCs observed										Total
	1529	*1585*	*1406*	*1726*	*1727*	*1728*	*1729*	*1730*	*2789*	*2124*	
$3_{III} + 34_{II} + 25_{I}$	—	—	—	—	—	—	—	—	1	—	1
$3_{III} + 33_{II} + 27_{I}$	1	—	1	1	—	—	1	—	—	1	5
$3_{III} + 31_{II} + 31_{I}$	—	1	—	—	1	—	—	1	—	—	3
$3_{III} + 29_{II} + 35_{I}$	—	—	1	—	—	1	—	—	—	—	2
$2_{III} + 36_{II} + 24_{I}$	—	—	1	—	—	—	—	1	—	—	2
$2_{III} + 35_{II} + 26_{I}$	—	1	1	—	2	—	—	—	—	—	4
$2_{III} + 34_{II} + 28_{I}$	2	—	2	1	—	1	—	—	1	2	9
$2_{III} + 33_{II} + 30_{I}$	—	1	1	1	—	1	—	—	—	—	4
$2_{III} + 32_{II} + 32_{I}$	—	—	—	—	1	—	1	2	—	1	5
$2_{III} + 31_{II} + 34_{I}$	—	—	2	—	—	—	—	1	—	—	3
$2_{III} + 30_{II} + 36_{I}$	—	1	—	—	—	—	1	—	—	—	2
$1_{III} + 37_{II} + 25_{I}$	1	—	1	—	—	—	—	—	1	1	4
$1_{III} + 36_{II} + 27_{I}$	—	2	1	1	—	1	—	—	2	1	8
$1_{III} + 35_{II} + 29_{I}$	3	—	—	—	2	1	—	2	3	2	13
$1_{III} + 34_{II} + 31_{I}$	1	1	1	1	1	—	1	1	1	—	8
$1_{III} + 33_{II} + 33_{I}$	—	1	—	2	1	2	2	—	1	—	9
$1_{III} + 32_{II} + 35_{I}$	1	—	—	1	—	—	—	—	—	1	3
$39_{II} + 24_{I}$	1	—	2	—	2	—	—	1	—	1	7
$38_{II} + 26_{I}$	1	2	1	1	1	2	4	—	1	—	13
$37_{II} + 28_{I}$	—	3	3	2	3	1	2	2	5	4	25
$36_{II} + 30_{I}$	3	4	2	5	4	3	5	3	4	2	35
$35_{II} + 32_{I}$	4	1	1	2	3	3	2	2	3	3	24
$34_{II} + 34_{I}$	2	1	—	2	1	4	1	3	2	2	18
$33_{II} + 36_{I}$	—	1	—	—	—	—	1	1	—	—	3
Total SMCs observed	20	20	21	20	22	20	21	20	25	21	210
Mean III	0.7	0.7	1.1	0.6	0.6	0.6	0.5	0.7	0.5	0.7	0.7
II	34.8	35.1	35.2	34.9	35.5	34.8	35.1	34.7	35.6	35.2	35.1
I	30.5	30.0	28.5	30.4	29.3	30.9	30.3	30.7	29.3	29.5	29.9

III. *Geographical Distribution of the Three Cytotypes*

Diploids were widespread at nearly all localities examined, which ranged from Yaku Island, Kagoshima Prefecture (Loc. 172; 30°15'N) to Rebun Island, Hokkaido (Loc. 1; 45°25'N) and from alt. 15 m to 2590 m (Fig. 34). Triploids occurred at various localities ranging from Mt. Takakuma, Kagoshima Prefecture (Loc. 168; 31°30'N) to Hayanose, Aomori Prefecture (Loc. 10; 40°30'N), and from alt. 20 m to 1950 m (Fig. 35). Triploids were abundant in western Japan, while they were not found in Hokkaido. Tetraploids were also detected at various localities ranging from Mt. Takakuma, the same as the southern limit of the triploids, to Rebun Island, the same as the northern limit of the diploids (Fig. 36). Altitudinal distribution of tetraploids ranged from 60 m to 2050 m. Thus, the ranges of geographical and altitudinal distribution were found to decrease in the

Table 13. Frequency of abnormal divisions at each meiotic phase in the triploid cytotypes

Phase of meiosis		Individual numbers, and frequency of abnormal SMCs										Mean
		1529	*1585*	*1406*	*1726*	*1727*	*1728*	*1729*	*1730*	*2789*	*2124*	
1st	Metaphase	100	100	100	100	100	100	100	100	100	100	100.0
	Anaphase	100	100	100	100	100	100	100	100	100	100	100.0
	Telophase	100	57	72	63	59	44	67	27	97	42	62.8
2nd	Metaphase	91	32	13	36	46	35	49	41	61	40	44.4
	Anaphase[a]	2	0	2	4	2	3	1	0	0	0	1.4
	Anaphase[b]	90	51	8	52	53	59	62	57	58	38	52.8
	Telophase	87	59	10	53	60	68	70	61	92	52	61.2

a: With lagging chromosomes.
b: Without lagging chromosomes.

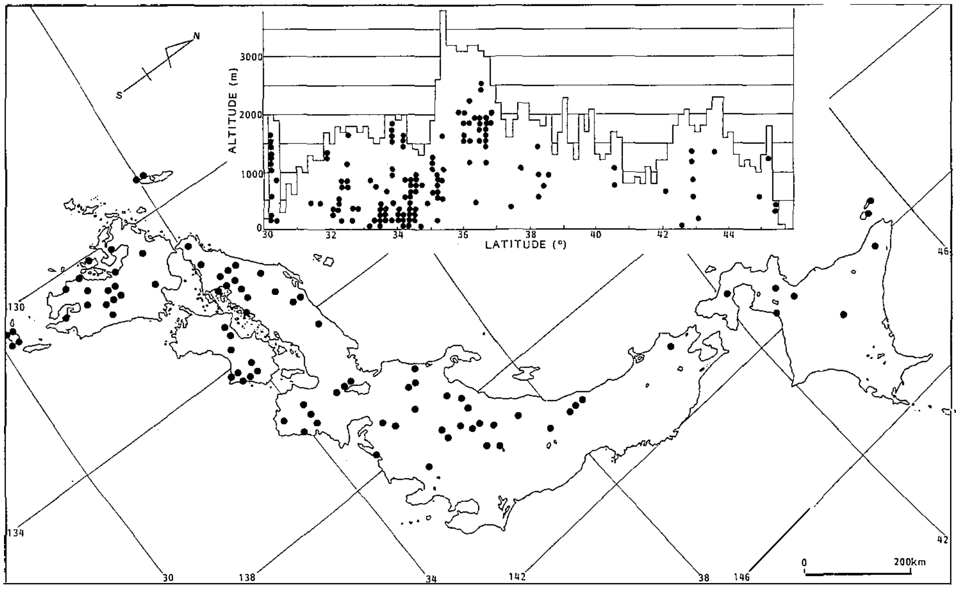

Fig. 34. A map showing distribution of diploid *Lycopodium clavatum* examined in this study.

order of diploids, tetraploids, and triploids.

In some pteridophytes, geographical differentiations between ancestral diploid and derived polyploid cytotypes in the Japanese archipelago have been reported for the following species: *Woodwardia orientalis* (Mitui, 1968), *Dryopteris erytrosora* (Hirabayashi, 1974), *Pteris dispar* (Nakato, 1981), and *Lepisorus thunbergianus* (Mitui, 1968; Takei, 1974, 1978; Mitui *et al.*, 1987; Nakato *et al.*, 1983). In these species, the ancestral diploid cytotype occurs in southern regions and the derived polyploidal cytotypes in northern regions. On the other hand, the diploid cytotype of *Lycopodium serratum* occurs in cool-temperate regions, while the tetraploid occurs in warm-temperate regions of the Japanese

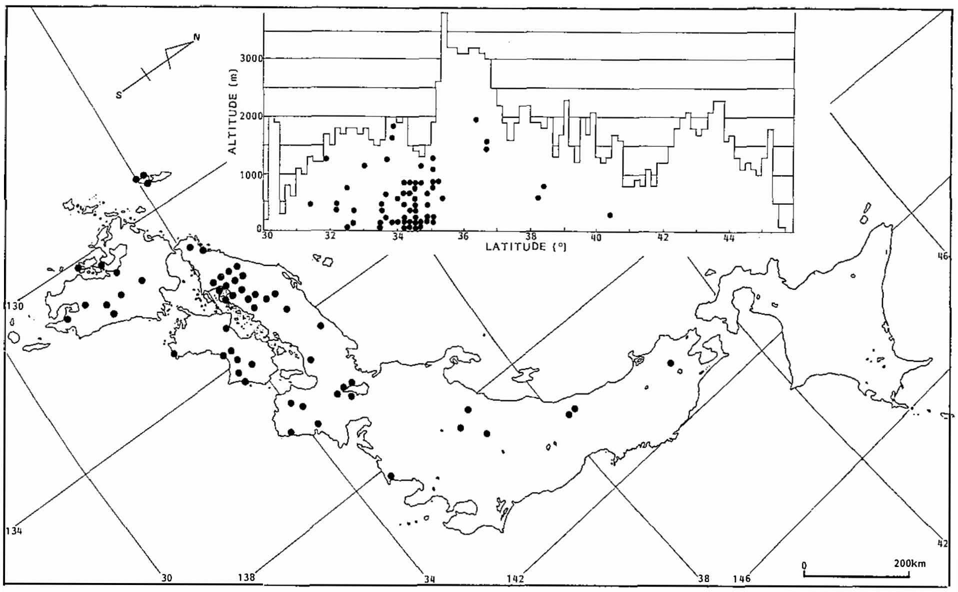

Fig. 35. A map showing distribution of triploid *Lycopodium clavatum* examined in this study.

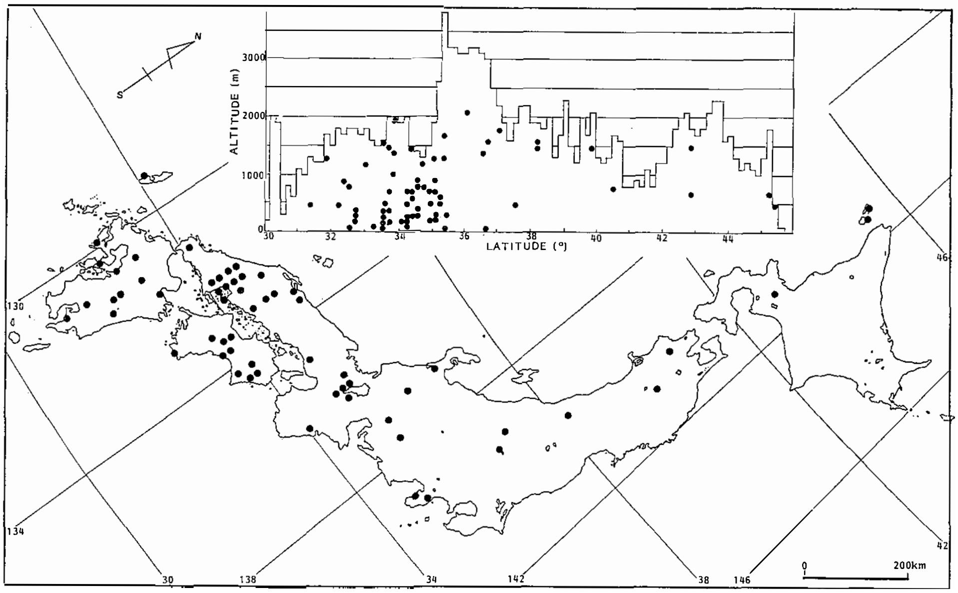

Fig. 36. A map showing distribution of tetraploid *Lycopodium clavatum* examined in this study.

archipelago (Takamiya and Kurita, 1983). There was no distinct difference, however in geographical distribution of diploid, triploid and tetraploid cytotypes of *Lycopodium clavatum* regarding altitude and latitude.

IV. *Habitat of the Three Cytotypes and Their Population Types*

Previously, Takamiya & Tanaka (1982) divided the populations of *Lycopodium* *clavatum* from Hiroshima Prefecture into three categories: (1) "sole-type", characterized by a single cytotype occupying an entire population, (2) "mixed-type A", characterized by two or three cytotypes occupying together the same population but each occurring in a different habitat, (3) "mixed-type B", characterized by two or three cytotypes occupying together the same population and sharing the same habitat. The population of *L. clavatum* examined in this study can also be divided into these three categories.

In addition, habitats of *Lycopodium clavatum* can be classified into five habitat-types: (1) "habitat-type A" – sunny, dry, disturbed, open places where the cover of vegetation is scanty (less than 50%) and tree species are less than 20 cm tall; (2) "habitat-type B" – sunny, slightly wet, open places where the cover of vegetation is 50–80% and tree species are juvenile and 20–100 cm tall; (3) "habitat-type C" – bright, slightly wet places where the cover of vegetation is over 80%, *L. clavatum* is covered with other plants, and tree species are over 1 m height and form an open forest; (4) "habitat-type D" – bright (but darker than above three types), humid places such as the floor of scrubs and open forests, and the edges of forests; (5) "habitat-type E" – close, dark, humid, stable places such as the edge and floor of well-developed forests. The habitats are darker, wetter, and ecologically more stable in the order of A, B, C, D, and E.

1. Sole-type

Sole-type populations of the diploid cytotype were found in 59 localities where 110 individuals in 69 colonies were examined cytologically (Table 14). In this type of population, diploid individuals occurred in the following growing places: dry or humid roadside slopes, grasslands of *Sasa* spp., an alpine meadow, a grassland of *Miscanthus sinensis*, the floor of a *Pinus densiflora* forest, the floor of a *Rhododendron serpyllifolium* scrub, the floor of a *Rhododendron metternichii* var. *yakushimanum* scrub, the floor and edges of *Cryptomeria japonica* plantations, the floor and edges of a natural forest of *C. japonica*, the floor and edges of *Chamaecyparis obtusa* plantations, the floor and edges of *Fagus crenata* forests, the floor and edges of *Quercus mongolica* var. *grosseserrata* forests, the floor of a *Q. mongolica* var. *undulatifolia* scrub, the edges of *Quercus glauca* forests, the floor of *Betula ermanii* forests, the edges of a *Tsuga sieboldii* forest, the floor of a *Tsuga diversifolia* forest, the floor of *Abies sachalinensis* forests, and the floor and edges of *Abies mariesii* forests. The habitats of these diploid individuals were various: roadside slopes, grassland, alpine meadow, and natural forests and plantations of coniferous, deciduous, and evergreen broad-leaved trees. While diploid individuals have high adaptability, they were found to choose mainly humid, shady, stable places.

Sole-type populations of the triploid cytotype were found in 18 localities where 21 individuals in 18 colonies were examined cytologically (Table 15). In this type of population, triploid individuals occurred in the following growing places: roadside slopes, a grassland, a cutover place, the floor and edges of *Pinus densiflora* forests, the floor and edges of *Quercus serrata* forests, the floor of a *Cryptomeria japonica* plantation, and the floor and edges of *Chamaecyparis obtusa* plantations. Because these habitats were always manmade places or secondary forests, the triploid individuals might have a tendency to grow in relatively new and ecologically transitional places. The sole-type populations of triploid individuals occurred mainly in western Japan, especially in the Chugoku District

Table 14. Growing places of the diploid cytotypes in the sole-type population

Growing place	Locality code number[a]	Habitat type[b]	Number of individuals examined[c]
humid open place	170	B	2
roadside slope	170	B	1
	171	B	2
	172	B	2
	13	C	1
	16	C	1
	28	C	1
	46	C	2
	132	C	2
in *Sasa kurilensis* grassland	20	C	1
	25	C	2
	31	D	2
	33	D	1
edge of *Sasa veitchii* grassland	53	C	2
alpine meadow	34	C	1
in *Miscanthus sinensis* grassland	167	C	1
floor of young *Cryptomeria japonica* plantation	28	C	1
in *Rhododendron serpyllifolium* scrub	128	C	2
floor of *Pinus densiflora* forest	41	D	1
floor of scrub of *Pieris japonica* etc.	152	D	3
edge of *Quercus glauca* forest	52	D	2
	94	D	1
	162	D	1
edge of *Cryptomeria japonica* plantation	45	D	1
	152	D	1
	166	D	1
	12	E	2
	23	E	1
	164	E	2
floor of *Cryptomeria japonica* plantation	138	D	2
	161	D	1
	54	E	3
	55	E	3
	58	E	2
	81	E	1
	91	E	2
	93	E	2
	112	E	2
	145	E	1
	158	E	1
edge of *Chamaecyparis obtusa* plantation	69	D	2
floor of *Chamaecyparis obtusa* plantation	99	D	2
	62	E	3
	148	E	1
edge of *Chamaecyparis pisifera* plantation	126	D	4

Table 14. (continued)

edge of *Quercus mongolica* var. *grosseserrata* forest	159	D	1
floor of *Quercus mongolica* var. *grosseserrata* forest	57	D	2
	7	E	1
	21	E	1
	29	E	2
edge of *Tsuga sieboldii* forest	104	E	2
edge of *Fagus crenata* forest	8	D	1
	29	D	1
floor of *Fagus crenata* forest	53	E	2
	140	E	1
	150	E	2
edge of *Cryptomeria japonica* forest	169	D	2
	170	E	4
floor of *Rhododendron metternichii* var. *yakushimamum* scrub	170	E	3
floor of *Tsuga diversifolia* forest	38	E	1
edge of *Quercus mongolica* var. *undulatifolia* scrub	25	E	2
floor of *Betula ermanii* forest	36	E	1
	37	E	1
floor of *Abies sachalinensis* forest	3	E	1
	4	E	1
	5	E	1
edge of *Abies mariesii* forest	29	E	1
floor of *Abies mariesii* forest	35	E	1

a: Locality code numbers correspond to those which appeared in Table 1, Fig. 1 and Fig. 2.
b: The symbol of habitat type.
c: Number of individuals examined cytologically.

where 61% of this type of population was found (Tables 1, 15).

Sole-type populations of the tetraploid cytotype were found in 18 localities where 25 individuals in 18 colonies were examined cytologically (Table 16). In this type of population, tetraploid individuals occurred in the following growing places: roadside slopes, grassland of a skiing ground, open places, and grasslands near the mountaintop. Thus, the habitat of tetraploid individuals are sunny, open, unstable places that are highly disturbed.

Concerning type of habitat, the sole-type population of diploid individuals was not found in habitat-type A (Table 14, 17). For diploids, the frequency increased gradually from habitat-type B to E. It was highest in habitat-type E in which almost half of the sole-type diploid population was found, 33 colonies (48%) and 54 individuals (49%). For triploids, sole-type populations were found from habitat-type A to E but mostly in B and C, 14 colonies (78%) and 15 individuals (71%). For tetraploids, the occurrence of sole-type populations was highest in habitat-type A, 13 colonies (72%) and 13 individuals (52%), and this type of population was not observed in habitat-types C to E.

From the above observations, some clear differences in the habitats of each cytotype

Table 15. Growing place of the triploid cytotypes in the sole-type population

Growing place	Locality code number[a]	Habitat type[b]	Number of individuals examined[c]
roadside slope	75	A	3
	61	B	2
	68	B	1
	103	B	1
	122	B	1
	165	B	1
grassland	19	B	1
cutover place dominated by *Miscanthus sinensis*	44	C	1
edge of *Pinus densiflora* forest	59	C	1
	73	C	1
	80	C	1
floor of *Pinus densiflora* forest	95	C	1
	111	C	1
edge of *Quercus serrata* forest	84	C	1
floor of *Quercus serrata* scrub	143	C	1
floor of *Cryptomeria japonica* plantation	85	D	1
floor of *Chamaecyparis obtusa* plantation	92	D	1
edge of *Chamaecyparis obtusa* plantation	10	E	1

a: Locality code numbers correspond to those which appeared in Table 1, Fig. 1 and Fig. 2.
b: The symbol of habitat type.
c: Number of individuals examined cytologically.

appear. The habitats of the diploid individuals are ecologically stable places, those of the tetraploid individuals are unstable places, and those of the triploid individuals are intermediate.

2. Mixed-type A

Mixed-type A populations were found in 32 localities (Table 18). Among them, 7 localities consisted of triploid and tetraploid individuals, 15 of diploid and tetraploid individuals, and 10 of diploid, triploid, and tetraploid individuals. No mixed-type A population of triploids and tetraploids was found. The altitudinal distribution patterns of each cytotype in each mixed-type A population are shown in Fig. 37. The patterns are various, and there is no clear relationship between altitude and ploidy level.

The diploid cytotypes occurring in the mixed-type A populations were found in 32 localities where 118 individuals at 78 colonies were examined. In this type of population, diploid individuals occurred in the following growing places: humid open places, grasslands of *Sasa* sp., an alpine meadow, grasslands of *Miscanthus sinensis*, a moor of *Sphagnum*, the floor and edges of *Pinus densiflora* forest, floor and edges of *Chamaecyparis obtusa* plantations, the floor and edges of *Cryptomeria japonica* plantations, the edges of a *Larix leptolepia* plantation, the floor and edges of *Fagus crenata* forests, the floor and the edges of *Quercus mongolica* var. *grosseserrata* forests, the edges

Table 16. Growing place of the tetraploid cytotypes in the sole-type population

Growing place	Locality code number[a]	Habitat type[b]	Number of individuals examined[c]
open place	146	A	1
	147	A	1
roadside slope	11	A	1
	17	A	1
	27	A	1
	39	A	3
	40	A	1
	50	A	2
	101	A	1
	116	A	1
	134	A	1
	141	A	1
	42	B	4
	43	B	3
	66	B	2
	136	B	2
slope of skiing ground	137	A	1
grassland	24	B	1

a: Locality code numbers correspond to those which appeared in Table 1, Fig. 1 and Fig. 2.
b: The symbol of habitat type.
c: Number of individuals examined cytologically.

Table 17. Number of colonies and individuals of *Lycopodium clavatum* at respective habitat type in the sole-type population

		Habitat type					
		A[a]	B	C	D	E	Total
2x	colony	0 (0)[b]	4 (6)	12(17)	20(29)	33(48)	69
	individual	0 (0)	7 (6)	17(15)	32(29)	54(49)	110
3x	colony	1 (6)	7(39)	7(39)	2(11)	1 (6)	18
	individual	3(14)	8(38)	7(33)	2(10)	1 (5)	21
4x	colony	13(72)	5(28)	0 (0)	0 (0)	0 (0)	18
	individual	13(52)	12(48)	0 (0)	0 (0)	0 (0)	25
Total	colony	14(13)	17(16)	18(17)	22(21)	34(32)	105
	individual	16(10)	28(18)	23(15)	34(22)	55(35)	156

a: The symbol of habitat type.
b: Percent.

Table 18. Growing places of each cytotype in the mixed-type A populations examined

Locality code number[a]	Growing places, habitat types and number of individuals examined cytologically		
	2x	3x	4x
22	edge of *Tsuga diversifolia* forest, (1[b], E[c])	open place, (1, B)	–
32	floors of *Fagus crenata, Betula ermanii, Tsuga diversifolia,* and *Quercus mongolica* var. *grosseserrata* forest, (2, E; 1, E; 2, E; 1, D); floor of *Betula ermanii* scrub (1, E); in *Sasa kurilensis* grassland, (1, C); edges of *Abies mariesii* forest, (1, D) and *Larix leptolepis* plantation, (1, D)	edge of *Sasa kurilensis* grassland, (1, D)	–
64	floor of *Fagus crenata* forest, (1, D)	open roadside slope, (3, A)	–
86	edge of *Cryptomeria japonica* plantation, (1, E)	edge of *Quercus serrata* forest, (2, C)	–
144	under *Miscanthus sinensis* grassland, (12, C)	edge of *Cryptomeria japonica* plantation, (1, C)	–
151	moor of *Sphagnum palustre,* (1, C)	open roadside slope, (1, A)	–
153	edge and floor of *Pinus densiflora* forest, (2, C); floor of *Rhododendron obutusum* bush, (2, D); floor of scrub (2, E); wet open place, (1, B)	sunny open place, (1, B)	–
1	floor and edge of *Pinus pumila* scrubs, (2, E; 1, D)	–	open place, (1, A)
2	floor of *Betula ermanii* forest, (1, E)	–	edge of secondary open forest, (1, B)
6	floor of *Betula ermanii* forest, (1, E); floor of *Betula ermanii* scrub; edge of *Sasa kurilensis* grassland, (1, C; 1, D); floor of *Picea jezoensis* forest, (1, E); floor of *Pinus pumila* scrub, (1, E); wet, open place, (1, B)	–	snow-bed grassland, (1, B); open place, (1, A)
9	edge of *Fagus crenata* forest, (1, E); floor of *Quercus mongolica* var. *grosseserrata* forest, (1, E)	–	open bare area, (1, A)
18	edge of *Quercus mongolica* var. *grosseserrata* forest, (1, E)	–	slope of skiing ground, (1, A)
26	in *Sasa kurilensis* grassland, (1, D); edge of *Pinus pumila* scrub, (1, E); floor of *Abies mariesii* forest, (1, E); edge of *Tsuga diversifolia,* (1, E); floor of *Betula maximowiczii* scrub, (1, D); alpine meadow, (1, C)	–	dry open place, (1, A)

Table 18. (continued)

30	edges of *Alnus hirsuta* and *Abies mariesii* forest, (1,D; 1,D)	–	humid roadside slope, (1,B)
65	floor of *Fagus crenata* forest, (1,E)	–	open place, (1,A)
67	floor of *Fagus crenata* forest, (2,E)	–	roadside slope, (3,B)
83	edges of *Chamaecyparis obtusa* plantation, (2,E); edge and floor of *Quercus mongolica* var. *grosseserrata* forest, (2,E; 1,D)	–	open place, (2,A)
89	floor of *Cryptomeria japonica* plantation, (2,D)	–	slope of skiing ground, (1,A)
97	edge of *Cryptomeria japonica* plantation, (1,E)	–	roadside slope, (1,A)
114	floor of *Cryptomeria japonica* plantation, (1,E); edge of *Sasa hayatae* grassland, (1,D)	–	sunny open slope, (1,A)
123	edge of *Cryptomeria japonica* plantation, (6,C)	–	open roadisde place, (1,A)
154	floor of *Chamaecyparis obtusa* plantation, (2,E); under *Miscanthus sinensis* grassland, (1,C)	–	open roadside slope, (3,A); open roadside slope, (3,B)
15	floor of *Fagus crenata* forest, (1,E); edge of *Sasa kurilensis* grassland, (1,C); edge of *Quercus mongolica* var. *undulatifolia* scrub, (1,D)	cutover place dominated by *Miscanthus sinensis*, (1,B)	open place, (1,B); open bare area, (1,A)
47	floor of *Fagus crenata*, (2,E) and young secondary forest, (1,C); edgesof *Cryptomeria japonica* plantation, (2,D), young secondary forest, (1,C) and *Sasa tuboiana* grassland, (1,C); wet roadsid slope, (1,B)	cutover place, (1,A)	open roadside slope, (2,A)
51	edge of *Chamaecyparis obtusa* plantation, (1,D)	floor of young *Pinus densiflora* forest, (1,C); edge of *Cryptomeria japonica* plantation, (1,D); roadside slope coveredby *Eragrostis curvula*, (1,B)	open roadside slope, (1,A)
71	edge of *Quercus mongolica* var. *grosseserrata* forest, (1,E)	grassland, (2,B)	grassland, (3,B)
72	edge of *Quercus mongolica* var. *grosseserrata* and *Fagus crenata* forest, (1,E; 1,E); floor of young bush, (1,C)	edge of *Quercus mongolica* var. *grosseserrata* forest, (1,C)	open place (1,A); grassland, (2,B)
78	edge of *Quercus mongolica* var. *grosseserrata* forest, (4,D)	floor and edge of *Quercus serrata* forests, (2,D; 2,C)	open roadside slope, (7,A)

Table 18. (continued)

88	edge of *Quercus mongolica* var. *grosseserrata* forest, (1,E); floorand edge of *Fagus crenata* forests, (1,E; 1,D)	floor of *Pinus densiflora* open forest, (3,C)	open roadside slope, (2,A)
90	edge of *Quercus mongolica* var. *grosseserrata* forest, (2,E)	edge of *Quercus serrata* open forest, (2,C)	roadside slope, (3,A)
105	floor of *Cryptomeria japonica* plantation, (1,E); edge and floor of *Quercus mongolica* var. *grosseserrata* forests, (1,D; 1,E)	edge of *Pinus densiflora* forest, (1,C)	roadside slope, (1,B)

a: Locality code numbers correspond to those which appeared in Table 1, Fig. 1, and Fig. 2.
b: Number of individuals examined cytologically.
c: Symbols of habitat types.

of a *Q. mongolica* var. *undulatifolia* scrub, the floor of *Betula ermanii* forests, the floor of a *Alnus maximowiczii* scrub, the edges of an *Alnus hirsuta* forest, the floor of a *Rhododendron obtusum,* the floor and edges of a *Tsuga diversifolia* forest, the floor of *Picea jezoensis* forests, the floor and the edges of *Abies mariesii* forests, the floor of a *Abies veitchii* var. *sikokiana* forest, and the floor and the edges of *Pinus pumila* scrub.

The habitats of these diploid individuals were various: humid open places, grassland, alpine meadow, moor, and natural forests and plantations of coniferous and deciduous broad-leaved trees. It seems that diploid individuals in the mixed-type A populations have high plasticity but they tend to grow mainly in humid, shade, stable places similar to those preferred by the diploid individuals in the sole type populations.

The triploid cytotypes occurring in the mixed-type A populations were found in 17 localities where 36 individuals at 25 colonies were examined. In this type of population, triploid individuals occurred in the following growing places: open places or cutover places, roadside slopes, grasslands, the floor and edges of open forests of *Pinus densiflora* or *Quercus serrata*, the edge of a *Cryptomeria japonica* plantation, and the edges of *Quercus mongolica* var. *grosseserrata* forest. Thus, triploid individuals can easily tolerate various environmental conditions from unstable and transitional places to stable and shady places.

The tetraploid cytotypes occurring in the mixed-type A populations were found in 25 localities where 51 individuals at 30 colonies were examined. In this type of population, tetraploid individuals occurred in the following growing places: sunny, dry, open places, roadside slopes, disturbed grassland in skiing grounds, and manmade grassland. These places are open, sunny, and unstable places, the same as habitats of the tetraploids in the sole-type populations.

Concerning the type of habitat, diploid individuals belonging to the mixed-type A population were not found the habitat-type A (Table 19). The frequency increased gradually from habitat-type B to E, and was highest in habitat-type E in which almost a half was found, 38 colonies (49%) and 49 individuals (42%). Triploid individuals belonging to the mixed-type A populations were found widely in habitat-type A to E, occurring

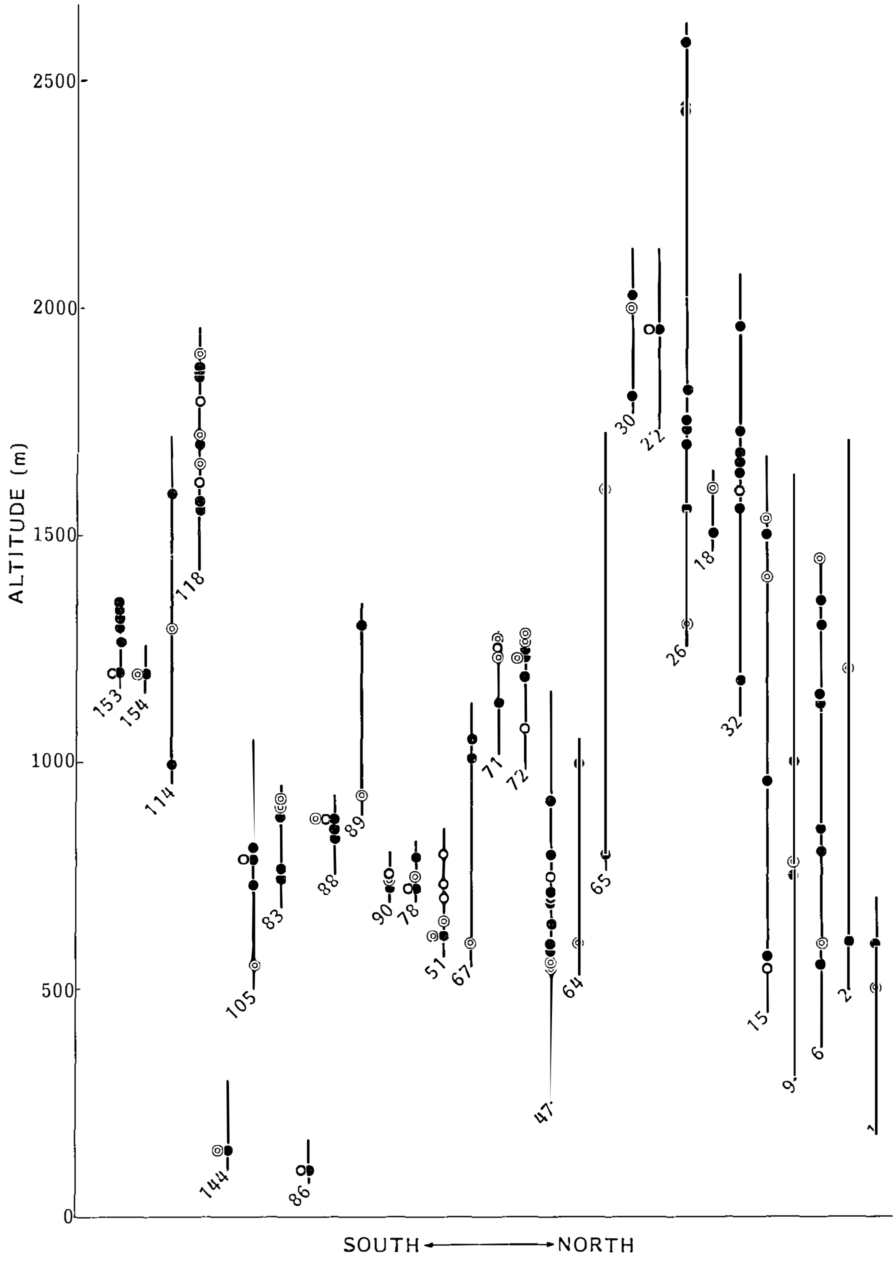

Fig. 37. Schematic representation of the altitudinal distribution of three cytotypes of *Lycopodium clavatum* examined at each the mixed type B population. Numbers are locality code numbers. Length of vertical lines correspond to the surveyed area in each locality. Solid circle, diploid; open circle, triploid; double circle, tetraploid.

mostly in type B and C: 17 colonies (68%) and 25 individuals (70%). The occurrence of tetraploid individuals of mixed-type A populations was highest in habitat-type A, 20 colonies (66%) and 34 individuals (67%). They were not found in habitat-types C to E.

Table 19. Number of colonies and individuals of *Lycopodium clavatum* at respective habitat type in the mixed-type A population

		Habitat type					
		A[a]	B	C	D	E	Total
2x	colony	0 (0)[b]	3 (4)	15 (19)	22 (28)	38 (49)	78
	individual	0 (0)	3 (3)	33 (28)	33 (28)	49 (42)	118
3x	colony	5 (20)	8 (32)	9 (36)	3 (12)	0 (0)	25
	individual	7 (19)	10 (28)	15 (42)	4 (11)	0 (0)	36
4x	colony	20 (66)	10 (4)	0 (0)	0 (0)	0 (0)	30
	individual	34 (67)	17 (33)	0 (0)	0 (0)	0 (0)	51
Total	colony	22 (17)	20 (16)	24 (19)	25 (19)	38 (29)	129
	individual	38 (19)	30 (15)	48 (24)	37 (18)	49 (24)	202

a: The symbol of habitat type.
b: Percent.

There is a strong resemblance between the mixed-type A and the sole-type populations in values of frequency of each cytotype in its particular habitat-type.

It is clear from the above observations that the habitat differences among the three cytotypes in the sole-type populations can also be found in the mixed-type A populations.

3. Mixed-type B

Mixed type B populations were found in 48 localities (Table 20). Among them, 13 localities consisted of diploid and triploid individuals without differences of habitat preference, 15 consisted of triploid and tetraploid individuals, 10 of diploid and tetraploid individuals, and 19 of diploid, triploid, and tetraploid individuals. This type of population occurred only in western Japan, except for one locality (Loc. 14) in the Tohoku District (Fig. 38).

The habitats of mixed-type B population consisting of diploid and tetraploid individuals were roadside slopes, a humid rocky place, a fen, the floor and edges of a *Pinus densiflora* forest, the edges of a *Quercus serrata* forest, and the edges of a *Chamaecyparis obtusa* plantation. The habitats of the mixed-type B with diploid and tetraploid individuals were roadside slopes, the floor of a juvenile forest of *Pinus densiflora*, and the edges of a *Chamaecyparis obtusa* plantation. The habitats of triploid and tetraploid individuals were roadside slopes, a grassland near the mountaintop, a skiing ground, the edges of an open plantation of *Chamaecyparis obtusa*, the floor and edges of a juvenile *Pinus densiflora* forest. The habitats of diploid, triploid, and tetraploid individuals were the sunny open places, the roadside slopes, the open forest floor of *Pinus densiflora*. In all the cases mentioned above, there were no clear differences in the habitat preference of each cytotype. The mixed-type B populations were found in either newly or continuously disturbed places. Therefore, populations of this type could occur in places in the early phase of secondary succession.

Table 20. Growing places of the each cytotypes in the mixed type-B population examined

Growing place	Locality code number[a]	Habitat type[b]	Number of individuals examined		
			2x	3x	4x
open roadside slope	14	A	1	1	-
	70	A	2	2	-
	121	A	5	1	-
roadside slope	125	B	2	1	-
	155	B	1	1	-
humid rocky place	127	B	2	2	-
fen	98	C	1	1	-
edge of *Cryptomeria japonica* plantation	60	C	2	1	-
edge of *Quercus serrata* forest	99	C	1	1	-
edge of *Pinus densiflora* forest	115	C	1	1	-
floor of *Pinus densiflora* forest	96	C	2	6	-
	163	C	1	1	-
floor of *Stachyurus praecox* open forest	129	C	3	1	-
open roadsid slope	109	A	1	-	1
	154	A	3	-	1
roadside slope	117	B	1	-	2
	119	B	3	-	1
	130	B	4	-	1
	131	B	2	-	2
	133	B	5	-	2
	151	B	2	-	5
floor of juvenile *Cryptomeria japonica* plantation	87	B	1	-	1
edge of *Pinus densiflora* forest	120	C	2	-	1
open roadsid slope	63	A	-	2	1
	106	A	-	2	1
	108	A	-	2	2
roadside slope	48	B	-	1	1
	73	B	-	1	1
	79	B	-	2	1
	110	B	-	1	1
	113	B	-	2	1
	139	B	-	2	1
	149	B	-	1	1
	160	B	-	2	2
grassland near the mountaintop	76	B	-	1	1
slope of skiing ground	77	B	-	1	1
edge of *Chamaecyparis obtusa* plantation	102	B	-	2	2
edge and floor of juvenile *Pinus densiflora* forest	135	B	-	3	3
open roadsid slope	56	A	2	1	2
	157	A	8	1	2
roadside slope	82	B	28	33	46
	107	B	18	22	18
	156	B	2	1	2
	152	C	5	3	1

Table 20. (continued)

sunny open place	124	B	4	2	3
	142	B	10	7	1
edge of juvenile *Pinus densiflora* bush	49	B	2	1	2
floor of *Pinus densiflora* open forest	168	B	2	1	1

a: Locality code numbers correspond to those which appeared in Table 1, Fig. 1 and Fig. 2.
b: The symbol of the habitat type.

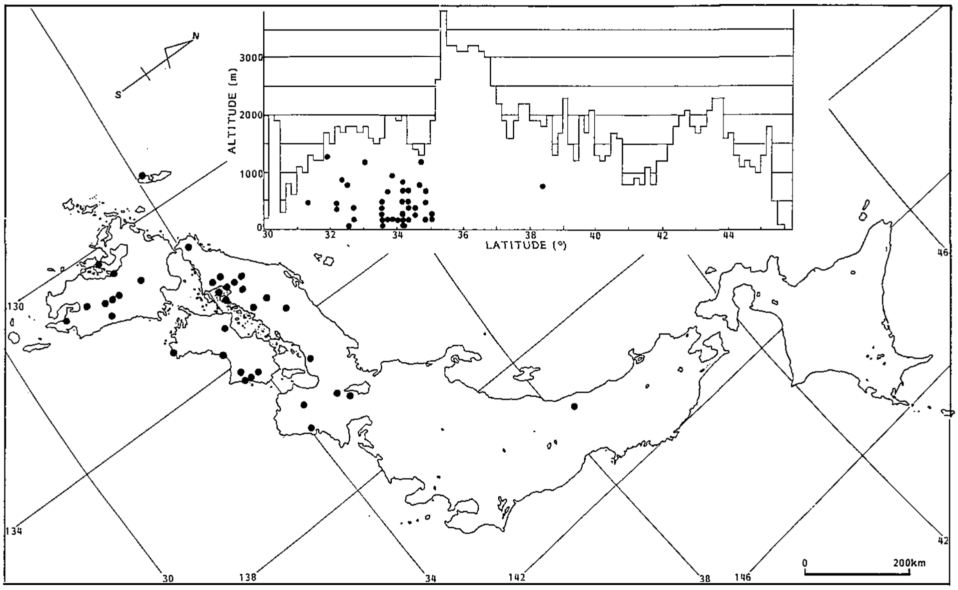

Fig. 38. A map showing distribution of the mixed type B population of *Lycopodium clavatum* examined in this study.

Concerning the type of habitat, mixed-type B populations did not occur in habitat-type D to E (Table 20, 21). Some differences among these type of populations were found. The mixed-type B with diploid and triploid individuals occurred in the habitat-type A to C, and was most frequent in habitat-type C (54%). The populations with diploid and tetraploid individuals occurred in the habitat-type A to C, and was most frequent in the habitat-type B (70%). The population with triploid and tetraploid individuals occurred in the habitat-type A and B, not in C, and was most frequent in B (82%). The populations with diploid, triploid and tetraploid occurred in habitat-type A to C, and was most frequent at in B (70%). Therefore, mixed-type B populations consisting of triploids and tetraploids ought to be formed from the mixed type B consisting of diploid, triploid and tetraploid; this occurs through the disappearance of populations in the habitat-type C and of all diploid individuals. On the other hand, the mixed-type B populations consisting of diploid and triploid individuals ought to have originated from mixed-type B consisting of diploid, triploid, and tetraploid individuals; this occurs through the increase of popula-

Table 21. Number of colonies and individuals of *Lycopodium clavatum* at respective habitat type in the mixed-type B population

		Habitat type					
		A[a]	B	C	D	E	Total
2x+3x	colony	3(23)[b]	3(23)	7(54)	0 (0)	0 (0)	13
	2x individual	8(33)	5(21)	11(46)	0 (0)	0 (0)	24
	3x individual	4(20)	4(20)	12(60)	0 (0)	0 (0)	20
2x+4x	colony	2(20)	7(70)	1(10)	0 (0)	0 (0)	10
	2x individual	4(17)	18(75)	2 (8)	0 (0)	0 (0)	24
	4x individual	2(12)	14(82)	1 (6)	0 (0)	0 (0)	17
3x+4x	colony	3(18)	14(82)	0 (0)	0 (0)	0 (0)	17
	3x individual	6(24)	19(76)	0 (0)	0 (0)	0 (0)	25
	4x individual	4(20)	16(80)	0 (0)	0 (0)	0 (0)	20
2x+3x+4x	colony	2(20)	7(70)	1(10)	0 (0)	0 (0)	10
	2x individual	10(12)	66(81)	5 (6)	0 (0)	0 (0)	81
	3x individual	3 (4)	67(92)	3 (4)	0 (0)	0 (0)	73
	4x individual	3 (4)	72(95)	1 (1)	0 (0)	0 (0)	76
Total	colony	10(20)	32(64)	8(16)	0 (0)	0 (0)	50
	2x individual	22(17)	90(70)	17(13)	0 (0)	0 (0)	129
	3x individual	13(11)	91(77)	14(12)	0 (0)	0 (0)	118
	4x individual	9 (8)	102(90)	2 (2)	0 (0)	0 (0)	113

a: The symbol of habitat type.
b: Percent.

tions in habitat-type C and the disappearance of the tetraploids. These successional dynamics were demonstrated quantitatively in Haji (Loc. 82) and Nagahama (Loc. 107) by comparison of DS values (Fig. 23).

V. *Habitat Preferences of Each Cytotype and the Vegetational Succession of Growing Places*

From the above observations it seems that *Lycopodium clavatum* adapts to the vegetational succession of the growing place by changes in the growth of diploid, triploid, and tetraploid cytotypes in each population (Fig. 39).

With the progress of secondary succession, the frequency of tetraploid cytotypes decreases gradually from the mixed-type B populations consisting of diploid, triploid, and tetraploid cytotypes. Subsequently, triploid cytotypes decrease from the mixed-type B populations consisting of diploids and triploids. In other words, the composition of each population changes, step by step, from the mixed-type B population to the mixed-type A population and finally reaches the sole-type population. In the formation of the sole-type population of each cytotype, diploid cytotypes come to occupy the mature stage of vegetational succession, triploid cytotypes are most frequent in the seral stage, and tetraploid

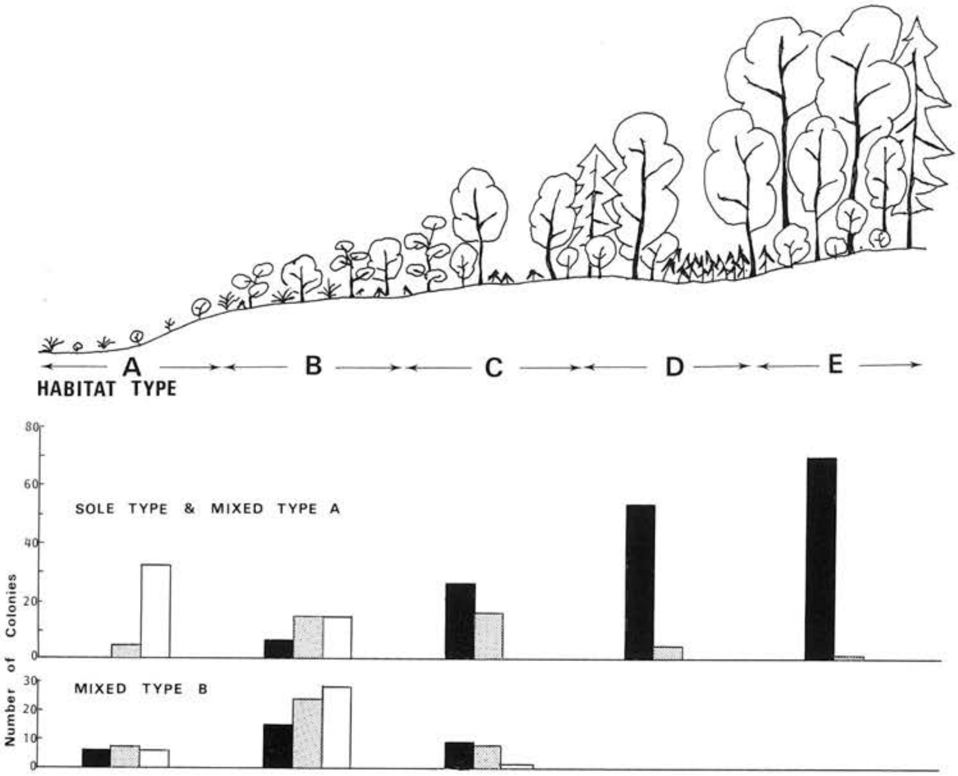

Fig. 39. Schematic representation of the habitat-type and number of colonies of *Lycopodium clavatum* occurring at respective habitat-types. Solid bars, diploid colonies; dotted bars, triploid; open bars, tetraploid.

cytotypes come to occupy the places where the progress of vegetational succession was prevented by disruptive influences and which remain fixed at the pioneer stage.

The correlations between polyploidy and habitat preferences in *Lycopodium clavatum* that were previously suggested in Hiroshima Prefecture (Takamiya and Tanaka, 1982), are confirmed in this study encompassing various places and vegetational zones throughout Japan. The differences in the ecological requirement of habitat between ancestral diploid cytotypes and derived polyploid cytotypes have been discussed in many phanerogams (Stebbins, 1971, 1979, 1984, 1985; Lewis, 1979; Ehrendorfer, 1979; Grant, 1981; Watanabe, 1987). In many pteridophytes much effort has gone into the study of polyploidy and speciation (Mitui, 1968; Vida, 1976; Lovis, 1977; Walker, 1979, 1984; Wagner and Wagner, 1979; Haufler, 1987), while only a few studies have dealt with correlations between polyploidy and habitat preference. In *Phegopteris decursive-pinnata*, the diploid individuals were found in the shady and wet places, but the tetraploid individuals were found in sunny places (Mitui, 1968). On the other hand, in epiphytic *Lepisorus thunbergianus*, the diploid individuals occurred in the dry places, but tetraploid and hypertetraploid individuals occurred in the wet places in Oita Prefecture, western Japan (Takei, 1978). Such differentiation of habitat was not observed in the *L. thunbergianus* from the Kanto District, central Japan (Nakato *et al.* 1983). In any case, correlations between habitat preference and vegetational succession of the growing places have not been discussed in these species.

Lastly, except for Japanese materials, there is only one report about tetraploid *Lycopodium clavatum* collected from Bhutan (Ghatak, 1965) and none about the triploid among reports of the chromosome numbers of *L. clavatum* (cf. Löve *et al*., 1977; Goldblatt, 1981, 1984, 1985, 1988). However, polyploidy in *L. clavatum* in many localities and the sympatric populations of these three cytotypes suggest that polyploidization might be a significant factor in the distinct ecological variation of *L. clavatum* indigenous to Japan.

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