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Origin of the New Caledonian Bryophytes

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The origin of a flora is one of the most interesting and challenging topics in bryology. However, it is a very difficult problem, and considerable effort is needed to accumulate more detailed information on the distribution and taxonomy of bryophytes than is available today.

In 1982 there was a short bryological expedition to New Caledonia and Fiji (Iwatsuki & Kitagawa, 1985). Members of the party consisted of Dr. N. Kitagawa and myself. An additional member, Mr. T. Suzuki, a specialist of Fissidens, joined us for about ten days. Dr. Gordon McPherson of the Missouri Botanical Garden, who was in Nouméa at that time, helped us in many ways. During this survey, 4761 specimens of bryophytes were collected. We are still studying the specimens, but so far we have published 16 papers on the New Caledonian bryophytes.

One of the reasons we selected New Caledonia for our study area was that so many endemic taxa of bryophytes had been described from that region, as pointed out by Herzog (1926). The New Caledonian bryoflora includes many endemic or remarkable taxa, e.g., the monotypic genus *Perssoniella*, representing Perssoniellaceae, a suborder of Jungermanniales.

The small island (20,000 km2) lies about the same distance, nearly 1600 km, from New Guinea, Australia, and New Zealand. According to Good (1974) the vascular flora of New Caledonia is oceanic in isolation and continental in structure. It is of the greatest interest not only for its marked endemism but also because of its floral relationships. The vascular flora consists of 2600 species and 600 genera, which include more than 130 endemic genera in nearly 30 families. About half the genera are monotypic. Moreover, the quality of endemism is high; several of the genera form separate families (5 endemic families). These are Amboleaceae, Oceanopapaveraceae, Onchothecaceae, Paracryphiaceae, and Strasburgiaceae.

The island is comprised partly of igneous rocks, including much serpentine and partly Permian and younger sedimentary rocks. The island was probably separated from Australia 60 - 65 million years ago (end of Cretaceous).

There is only one native composite and

Table 1. Number of species of Fissidentaceae recorded in New Caledonia.

	Pursell & Reese(1982)	Iwatsuki (1982)	Iwatsuki & Suzuki (1989, in press)
Fissidens	36(29)	23(13)	27(3)
Nanobryum	0	0	1(0)
Total	36(29)	23(13)	28(3)
Endemic spp.	80.6%	56.5%	10.7%

Pacific Islands, and only a slight relationship with New Zealand.

Endemism of bryophytes in New Caledonia

Pursell and Reese (1982) compiled a list of all previously reported mosses from New Caledonia. They included 40 families, 151 genera, and 631 species, among which four genera and 318 species and infraspecific taxa (50.4%) are endemic to the island.
Kitagawa (1983) also compiled a list of New Caledonian hepatics, which consists of 32 families, 94 genera, and 449 species. Among those, 217 species (48.3%) and only one genus (Perssoniella) are endemic to the island.

Hattori (1976, 1977) reported many interesting species of *Frullania* from New Caledonia. He has shown that the Frullaniaceae have achieved remarkable speciation in New Caledonia, and more than 60% of the species of *Frullania* are endemic to the island.

Touw (1974) mentioned that modern monographic studies have reduced the number of species by 20 - 45%. He also stated that preparation of revisions and the accumulation by bryologists of collections in under-collected and phytogeographically important areas are necessary. I agree with Touw that monographic revisions of bryophytes are urgently need, and collecting of bryophytes in phytogeographically important tropical areas is also necessary to clarify the origins of the bryophyte flora.

According to Pursell and Reese (1982), 36 species of *Fissidens* are recorded from New Caledonia. The number includes 29 (80.6%) endemic species. Iwatsuki (1982) reported preliminary work on New Caledonian *Fissidens*, in which many species were reduced to synonymy, and he considered 23 species of *Fissidens*, including 13 endemic species (56.5%), to be present on the island. Adding more specimens, Iwatsuki and Suzuki (1989, in press) included 27 species of *Fissidens* and one species of *Nanobryum* in the Fissidentaceae, of which only three species (10.7%) are endemic to the island (Table 1).

The drastic decrease of endemic species from 70.6% in 1982 to 10.7% in 1989 is remarkable. However, if we compare the final figure (10.7%) with other *Fissidens* floras from relatively thoroughly investigated areas, the value (10.7%) is not unusual.

As shown in Table 2, the *Fissidens* flora of Japan (Iwatsuki & Suzuki 1982) includes 43 species, of which only two (4.7%) are endemic. The *Fissidens* flora of the Malay Peninsula (Iwatsuki & Mohamed 1987) also contains only one endemic species (4.1%) out of a total of 24 species. The *Fissidens* flora of New Guinea

Table 2. Number of species of each genus of Fissidentaceae (Musci) and Frullaniaceae (Hepaticae) in Japan, Malay Pen., Seram Is., Borneo, New Guinea, and New Caledonia. The number of endemic species to each area is indicated in parentheses.

Genera	Japan	Malay Pen.	Seram Isl.	Borneo	New Guinea	New Caledonia
Fissidentaceae (Musci)						
Fissidens	43(2)	24(1)	23(0)	--	25(2)	27(3)
Nanobryum	0	0	0	--	0	1(0)
Total	43(2)	24(1)	23(0)	--	25(2)	28(3)
Endemic	4.7%	4.1%	0%	--	8.0%	10.7%
Frullaniaceae (Hepaticae)						
Frullania	42(12)	--	45(29)	37(9)	77(48)	45(29)
Steerea	0	--	0	1(1)	0	0
Schusterella	0	--	3(3)	0	0	3(3)
Total	42(12)	--	48(32)	38(10)	77(48)	48(32)
Endemic	28.6%	--	66.7%	26.3%	62.3%	66.6%

(Norris & Koponen 1987) contains two endemic species (8.0%) out of a total of 25 species. More extensive studies on the New Guinean *Fissidens* are needed, but this percentage probably will not change drastically.

Recent revision of *Leucobryum* in New Caledonia (Yamaguchi & Iwatsuki 1987) confirmed no endemic species out of four on the island. Before the study, the New Caledonian *Leucobryum* flora contained seven endemic species (46.6%) out of a total of 15 species (Pursell & Reese 1982).

Hattori has been making a thorough study of the species of *Frullania* in tropical areas of Asia and Oceania. He particularly concerned with the New Caledonian *Frullania*, and compiled (1986) a synopsis of the genus on the island. In this synopsis, he listed 48 species of *Frullania* from New Caledonia; among them 32 species (66.6%) are endemic to the island. This figure is surprisingly large when we compare it with that of *Fissidens* (10.7%). Hattori (1982) and Hattori and Piippo (1986) reported species of Frullaniaceae from New Guinea. They reported 48 endemic species (62.3%) out of a total of 77 species recorded from New Guinea. Hattori thinks the *Frullania* flora of New Guinea may have over 100 species. Thus, this genus shows equally high endemism in New Guinea as in New Caledonia.

Differences between percentages of endemism of *Fissidens* (Musci) and *Frullania* (Hepaticae) is quite remarkable (see Table 2). However, endemic species of *Frullania* are usually abundant in many areas, such as Seram Is. (66.7%), Japan (28.6%), and Borneo (26.3%), while endemism of *Fissidens* is 10% or less in these areas. Endemisms in New Caledonia and New Guinea are high both in *Frullania* and *Fissidens*

Table 3. Distribution of Fissidens species in New Caledonia and other Circum-Pacific regions.

Species	In	Ja	Ch	Ta	Ma	Ph	Ja	Bo	NG	NC	Fi	So	NZ	Ha
F. zollingeri	+	+	+	+	+	+	+	+	+	+	+	+	+	.
F. zippelianus	+	+	+	+	+	+	+	+	+	+	+	.	.	.
F. ceylonensis	+	.	+	+	+	+	+	+	+	+	.	.	+	.
F. maceratus	+	+	+	+	+	+	+	+	+	+	.	.	.	.
F. laxus	+	+	+	+	+	+	+	+	+	+	.	.	.	.
F. microcladus	+	+	+	+	.	+	+	.	+	+	.	.	.	.
F. beckettii	+	+	+	.	.	.	.	.	.	+	.	.	.	.
F. bryoides var. schmidii	+	+	+	+	.	+	+	.	.	+	.	.	.	.
F. geppii	+	+	.	+	.	.	+	+	.	+	.	.	.	.
F. zippelianus var. robinsonii	+	.	+	.	+	+	.	.	.	+	.	.	.	.
F. oblongifolius	.	+	+	.	+	+	.	.	.	+	+	+	+	.
F. hollianus	.	+	+	+	+	+	+	+	+	+	+	.	.	
F. papillosus	.	+	.	+	+	+	+	+	+	+	.	.	.	.
F. bogoriensis	.	+	.	+	+	+	+	.	.	+	.	.	.	.
F. obscurirete	.	+	+	+	.	.	.	.	+	+	.	.	.	.
F. bryoides var. esquirolii	.	+	+	+	.	.	.	.	.	+	.	.	.	.
F. serratus	.	+	.	.	.	.	.	.	+	+	.	.	.	.
F. flabellulus	.	+	.	.	.	.	.	.	+	+	.	.	.	.
F. pallidus	.	.	.	.	.	.	.	+	+	+	.	.	+	.
F. dealbatus	.	.	.	.	.	.	.	.	.	+	+	.	+	.
F. pungens	.	.	.	.	.	.	.	.	.	+	+	.	+	.
F. dixonianus	.	.	.	.	.	.	.	.	.	+	+	+	.	.
F. cuspidiferus	.	.	.	.	.	.	.	.	.	+	+	.	.	.
F. pellucinervis	.	.	.	.	.	.	.	.	.	+	+	.	.	.
F. compienei	.	.	.	.	.	.	.	.	.	+	.	.	.	.
F. consociatus	.	.	.	.	.	.	.	.	.	+	.	.	.	
F. rupicola	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Nanobryum thorsboeri	.	.	.	.	.	.	.	.	.	+	.	.	.	.

Literature. E.India: Froehlich, 1953 & Gangulee, 1971; Japan: Iwatsuki & Suzuki, 1982; China: Li, 1985; Taiwan: Kuo & Chiang, 1987; Malay Pen. & Singapore: Iwatsuki & Mohamed, 1987; Philippines: Iwatsuki & Tan, 1979; Java: Fleischer,1904; Borneo: Touw, 1978; New Guinea: Norris & Koponen, 1987; New Caledonia: present paper; Fiji: Whittier, 1975; Society Islands: Whittier, 1976; New Zealand: Sainsbury, 1955; Hawaii: Pursell & Hoe, 1977.

Table 4. Spore size and endemic species of New Caledonian *Leucobryum* and Dicnemonaceae.

	Total species	Endemic(%)	Sexuality	Spores
Leucobryum*	4(0)	0%	Dioicous	Small
Dicnemonamceae**	7(7)	100%	Dioicous	Very large

*Yamaguchi & Iwatsuki, 1987.
**Allen, 1989.

as compared to other areas.

Differences in some important characters in Fissidens and Frullania

1. Habitats

Fissidens: 28 species of *Fissidens* and *Nanobryum* found in New Caledonia grow mostly on soil or rocks, and only a few species grow on tree bases or trunks of tree ferns. Some species usually grow abundantly on newly eroded soil.
Frullania: These occur mostly on trees, shrubs, decayed wood, and living leaves, and only very rarely on soil or rocks.
Differences of habitats of these two groups are remarkable: *Frullania* is essentially epiphytic, whereas *Fissidens* is essentially terricolous.

2. Sexuality and spore production

Fissidens: Among 28 taxa reported from New Caledonia, 23 taxa (82.2%) are either synoicous or autoicous, and the remaining five taxa (17.8%) are dioicous. Monoicous taxa produce spores freely.
Frullania: Most species of New Caledonia are dioicous. Hattori described perianths of many species, but he did not describe any spores.

3. Spore size

Fissidens: Spores of most of the New Caledonian Fissidens are small, less than 20 um; only one species, *F. compienei*, endemic to the island, has spores 16-26 um.
Frullania: As noted before, no spores of New Caledonian *Frullania* were described. However, according to Miyoshi (1966), spores of Japanese species of *Frullania* are large, usually 27-80 µm. Gupta and Udar (1986) reported 21-76 µm for spores of Indian species of *Frullania.*

Origin of Fissidens and Frullania floras of New Caledonia

Evolution of bryophytes is generally thought to be very slow, compared with angiosperms. However, the rate of evolution in bryophytes varies among families and genera. Schuster (1969) considers that the Hepaticopsida is probably an old group in which evolution is generally slow except for a few families of mostly epiphytic leafy hepatics. Hattori (1982) also thinks *Frullania* evolves rather fast.

As previously explained, I selected two families of bryophytes: Fissidentaceae (Musci) and Frullaniaceae (Hepaticae) for a study of distribution. Distributions of New Caledonian species of these families are remarkably different in number of endemic species. Distribution of Fissidentaceae in New Caledonia can be explained by spore dispersal by wind.

Zanten and Pócs (1981) concluded that aerial spore transport over moderately long and long distances within the same climatological belt is

Table 5. Distribution of Frullania species in New Caledonia and other tropical regions in the world.

Species	Afr	Asi	NG	Aust	NC	Pac	NZ	Ha	Am	
Frullania										
F. serrata Gott.		+	+	+	+	+	+			
F. apiculata (Reinw. et al.) Dum.		+	+	+	+	+	+		+	
F. nodulosa (Reinw. et al.) Nees		+	+	+	+	+	+		+	+
F. riojaneirensis (Raddi) Angsr.		+	+			+	+			+
F. ericoides (Nees) Mont.		+	+	+	+	+	+			+
F. intermedia (Reinw. et al.) Dum.			+	+		+	+			+
F. monocera (Hook. et Tayl.) Tayl.			+		+	+	+	+		
var. depauperata Hatt.			+			+				
F. intermedia			+	+			+			+
fo. billardieriana (Nees et Mont.) Verd.		+	?			?				
F. junghuhniana Gott.		+	+			+				
F. intermedia var. non-appendiculata Hatt.		+				+	+			
F. reflexispipula Sande Lac.		+	+			+	+			
F. heteromorpha Schiffn.			+			+				
F. utriculata St.			+			+				
F. multilacera St.			+			+	+			
F. deflexa Mitt.						+	+			
F. novocurvirostris Hatt.						+	+			
F. hypoleucula Hatt.						+				
F. baladina Gott. ex St.						+				
var. edentata Hatt.						+				
F. baumanii Hatt.						+				
F. bella St.						+				
F. blastopetala Hatt.						+				
F. caledonica Gott. ex St.						+				
F. capillaris St.						+				
F. contracta St.						+				
F. cornuta St.						+				
F. elephantum Hatt.						+				
F. falsicornuta Hatt.						+				
F. gigantea St.						+				
F. gracilicaulis Hatt.						+				
F. huerlimannii Hatt.						+				
var. dioica Hatt.						+				
F. inflexiloba Hatt.						+				
F. kitagawana Hatt.						+				
F. ludviciae St.						+				
F. mammillosa Hatt.						+				
F. meyeniana var. dioica Hatt.						+				
F. pancheri Gott. ex St.						+				
F. pilibracteola Hatt.						+				
F. pilistipula St.						+				
F. pseudomeyeniana Hatt.						+				
F. pseudomonocrea Hatt.						+				
F. pusilla Mitt.						+				
F. scalaris Hatt.						+				
F. spinistipula St.						+				
F. subpilibracteola Hatt.						+				
F. tenuirostris St.						+				
F. tixieri Hatt.						+				
Schusterella										
S. caledonica (Schust.) Hatt.						+				
S. chevalieri (Schust.) Hatt. et al.						+				
S. microscopica (Pears.) Hatt. et al.						+				

Literature. Hattori (1986).

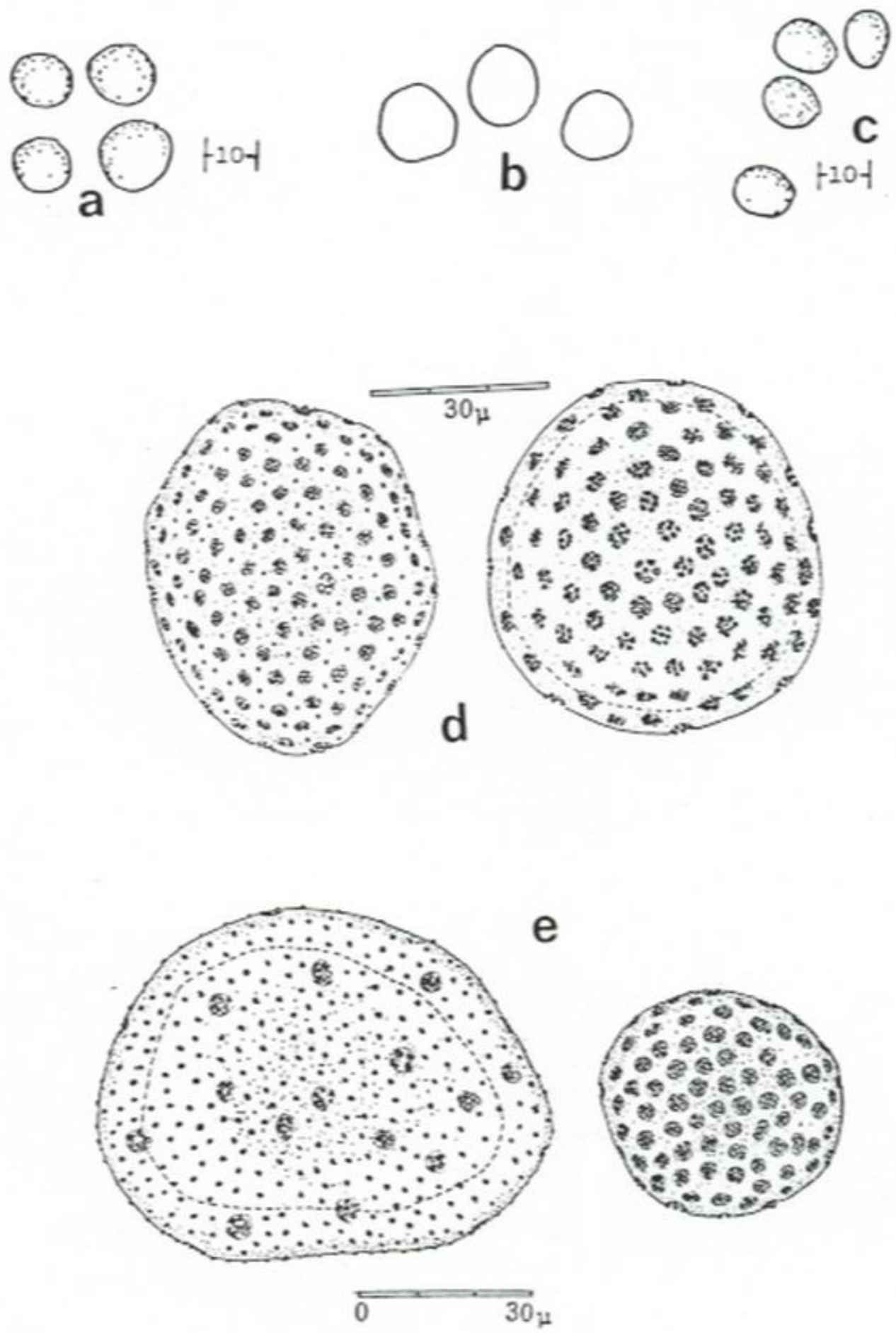

Fig. 1. Spores of *Fissidens* (Musci) and *Frullania* (Hepaticae). a, *Fissidens pellucinervis* Bartr. b, *F. flabellulus* Thwait. et Mitt. c, *F. cuspidiferus* Dix. d, *Frullania muscicola* Steph., e, *F. kagoshimensis* Steph. d, e, after Miyoshi (1966).

Gupta and Udar (1986) reported 21-76 um for spores of Indian species of *Frullania.*

Origin of Fissidens and Frullania floras of New Caledonia

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As previously explained, I selected two families of bryophytes: Fissidentaceae (Musci) and Frullaniaceae (Hepaticae) for a study of distribution. Distributions of New Caledonian species of these families are remarkably different in number of endemic species. Distribution of Fissidentaceae in New Caledonia can be explained by spore dispersal by wind.

Zanten and Pócs (1981) concluded that aerial spore transport over moderately long and long distances within the same climatological belt is possible. This is probably a common phenomenon for spores smaller than ca. 25 um. Spores of mosses are usually smaller than 25 um. I studied the moss flora of the Bonin and Volcano Islands (Iwatsuki 1985), and found that the moss flora of these islands is very similar to that of the Ryukyu Archipelago, which is about 1600 km west of the Bonin Islands. The moss flora of the Bonin and Volcano Islands is not related to that of Guam, which is about 1450 km southward. This suggests that spores of mosses were carried by westerly winds from the Ryukyu Archipelago to the Bonin and Volcano Islands.

As mentioned before, many species of *Fissidens* recorded from New Caledonia are monoicous (autoicous or synoicous) and many specimens are fertile. Their spores are small, less than 20 um in diameter. Many of them occur on newly eroded soil, trail side banks, etc. Their distribution can be explained by spore dispersal.

In 1972, Iwatsuki discussed spore dispersal of mosses, and wrote 'According to the present distribution of bryophytes we cannot assume that wind is a very effective agent for long-range dispersal, except for a few weedy species.' From distributional data on New Caledonian *Fissidens*, many of them are 'weedy' species.

As shown in Table 3, many species of Fissidentaceae, especially those of *Fissidens*, are common to Asia. Some species have pantropical distribution, including Asia, Oceania, the Americas, and Africa. *Fissidens* species with pantropical distribution will increase when we study more specimens from tropical Americas and Africa. For example, recently Iwatsuki and Suzuki (1982) pointed out that *Fissidens mangarevensis (=F. oblongifolius)* might be found in tropical America.

At the moment, we have only seven species of New Caledonian Fissidentaceae common to Australia, but I am sure this number will increase when Australian *Fissidens*, especially in northern tropical areas, have been thoroughly investigated. *Nanobryum thorsbornei* Stone, a very interesting tiny species, is recorded only in northern Queensland and New Caledonia. This species may be a reduced form of *Fissidens*, and might be better classified in the genus *Fissidens*. The genus *Nanobryum* has been recorded in Africa, Australia, and New Caledonia.

As a whole, the New Caledonian *Fissidens* flora is very closely related to that of tropical Asia. Long range dispersal by

Table 6. Species number of *Frullania* and its 11 subgenera, *Steerea* and *Schusterella* occurring in Borneo, New Guinea, and New Caledonia. The number of endemic species to each area is indicated in parentheses.

Genera & subgenera	Borneo	New Guinea	New Caledonia
Frullania	38(9)	77(48)	39(26)
1.Frullania	13(3)	28(20)	5(1)
2.Rostratae	1(0)	3(2)	2(1)
3.Diastoloba	5(2)	3(0)	9(9)
4.Meteoriopsis	1(0)	1(0)	1(1)
5.Homotropantha	6(2)	11(6)	4(0)
6.Fusiorielligerae	2(1)	3(1)	1(1)
7.Australes	1(1)	2(2)	1(1)
8.Saccophora	1(0)	1(0)	0
9.Trachycolea	7(0)	23(17)	15(11)
10.Huerlimannia	0	0	1(1)
11.Chonanthelia	1(0)	2(0)	0
Steerea	1(1)	0	0
Schusterella	0	0	2(2)
Total	39(10)	77(48)	41(28)
Endemic spp.	25.7%	62.3%	68.3%

probably Gondwanalandic in derivation. However, they seem to have become highly differentiated on this small island. They include *Schusterella*, a small genus of the Frullaniaceae whose center of differentiation is New Caledonia; all three species of *Schusterella* are endemic to New Caledonia.

The subgenus *Diastaloba* of *Frullania* is strongly differentiated, and nine species are endemic to the island. Furthermore, the monotypic subgenus *Huerlimannia* is known only from this island (Table 6).

The *Frullania* flora of New Caledonia includes only four species that are common to Australia and New Zealand. However, there are eleven species common to New Guinea, nine species to the Malay Archipelago, and nine species to the Pacific Islands. The lesser number of species common to Australia and New Zealand is difficult to explain, but after a detailed study of more specimens from northern Australia, this number might be much greater.

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