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ON THE BRYOGEOGRAPHY OF WESTERN MELANESIA

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ABSTRACT. In analysis of the distribution of 298 Western Melanesian moss species the material is divided into 11 groups according to general distribution. In addition the floristic affinities of the island of New Guinea, as well as collecting activity in Western Melanesia are presented. The material is tabulated but statistical methods or the methods of vicariance biogeography are not used in this analysis. The need is stressed for monographs on a sound cladistical basis, enabling more profound biogeographical studies.

Key words: biogeography, Musci, Papua New Guinea, Solomon Islands, West Irian.

CONTENTS

I. INTRODUCTION

In 1981 a bryological expedition was arranged by Botanical Museum, University of Helsinki and the Bryophyte Herbarium, Humboldt State University (Arcata, California) to the Huon Peninsula, Papua New Guinea. About 17 500 cryptogram specimens were collected, mainly in Madang and Morobe provinces on the Huon Peninsula but also in East and West Sepik provinces in the western part of the country. During the study all previous records of bryophytes in Western Melanesia have been documented, and many of them are verified as well. Thus the bryoflora of the whole of Western Melanesia, i.e. West Irian Papua New Guinea and the Solomon Islands is revised with a record of the general distribution of each species. The results are being published in three series. Collection of extensive material for a floristic study has also made possible many other kinds of analyses. Results can be used in studies of biogeography, vegetation and to certain extent even in ecology (Hyvönen & al. 1987).

In recent years knowledge of the biogeography of Western Melanesian biota has

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enlargened remarkably. The area, however, is still one of the most poorly known areas of the world due to the diversied fauna and flora and geographic complexity of the study area. Modern methods of vicariance biogeography give promising new tools to clear up the complex history of life in the area. In this context the bryophytes, being fairly old, including very slowly evolving groups and especially in dioicous groups with small chances of long-range dispersal are a group of plants very well suited for the study. The disadvantages are almost total lack of fossil data and still fairly poorly known phylogeny and modern distribution (cf. fig. 7).

II. Material and Methods

The study of 27 of 57 Western Melanesian moss families (Table 1 and 2) has been completed thus furnishing the bryogeographical analysis with the distribution record of 298 species and subspecific taxa. The total number of revised species in the series is 324, but some of the

Table 1. Moss families of Western Melanesia. Family names in italics are already treated in the Huon Peninsula series. Number after family name indicates number of genera in each. Number in parentheses indicates number of treated genera in the family if it was not revised as a whole.

Sphagnaceae	1	*Hedwigiaceae*	1
Andreaeaceae	1	Cryphaeaceae	3
Fissidentaceae	1	Cyrtopodaceae	1
Archidiaceae	1	Ptychomniaceae	2
Ditrichaceae	1	Prionodontaceae	1
Seligeriaceae	1	*Trachypodaceae*	2
Dicranaceae	15 (4)	Myuriaceae	2
Dicnemonaceae	3	*Pterobryaceae*	8
Leucobryaceae	7	*Meteoriacaee*	9
Calymperaceae	3	*Phyllogoniaceae*	3
Encalyptaceae	1	*Neckeraceae*	5
Pottiaceae	17	Lembophyllaceae	1
Grimmiaceae	3	Namataceae	1
Funariaceae	1	Hookeriaceae	15
Splachnaceae	3	Hypopterygiaceae	3
Bryaceae	6	Fabroniaceae	2
Leptostomataceae	1	Leskeaceae	1
Mniaceae	3	*Thuidiaceae*	4
Phyllodrepaniaceae	1	Amblystegiaceae	3
Sorapillaceae	1	Brachytheciaceae	6
Mitteniaceae	1	Entodontaceae	4
Rhizogoniaceae	4	Plagiotheciaceae	1
Hypnodendraceae	3	Sematophyllaceae	19
Meesiaceae	1	Hypnaceae	23
Bartramiaceae	4	*Rhytidiaceae*	1
Spiridentaceae	1	*Hylocomiaceae*	2
Orthotrichaceae	5	*Buxbaumiaceae*	2
Racopilaceae	2	*Polytrichaceae*	9

TABLE 2. Moss families and genera treated in the Huon Peninsula series. Number after each name indicates its number of species and subspecific taxa.

Andreaeaceae	1
Andreaea	1
Fissidentaceae	25
Fissidens	25
Archidiaceae	1
Archidium	1
Ditrichaceae	6
Garckea	1
Ditrichum	3
Distichium	1
Ceratodon	1
Seligeriaceae	1
Blindia	1
Dicranaceae	13
Atractylocarpus	1
Bryohumbertia	1
Campylopodium	1
Campylopus	10
Calymperaceae	59
Calymperes	21
Syrrhopodon	25
Mitthyridium	13
Pottiaceae	36
Weissia	2
Astomum	1
Trachycarpidium	1
Oxystegus	2
Pseudosymblepharis	1
Trichostomum	2
Timmiella	1
Anoectangium	1
Hymenostylium	1
Gymnostomum	1
Leptodontium	3
Hyophila	2
Barbula	8
Bryoerythrophyllum	2
Didymodon	3
Streptopogon	1
Tortula	1
Scopelophila	2
Tridontium	1
Grimmiaceae	3
Grimmia	1
Racomitrium	1
Schistidium	1
Bryaceae	36
Anomobryum	4
Bryum	16
Rhodobryum	2
Orthodontium	1
Mielichhoferia	2
Pohlia	2
Epipterygium	1
Brachymenium	7
Leptobryum	1
Leptostomataceae	2
Leptostomum	2
Mniaceae	8
Mnium	1
Plagiomnium	5
Orthomnion	2
Phyllodrepaniaceae	1
Mniomalia	1
Sorapillaceae	1
Sorapilla	1
Mitteniaceae	1
Mittenia	1
Rhizogoniaceae	9
Hymenodon	2
Hymenodontopsis	1
Rhizogonium	3
Pyrrhobryum	3
Racopilaceae	7
Racopilum	4
Powellia	3
Hedwigiaceae	2
Rhacocarpus	2
Trachypodaceae	4
Trachypus	2
Duthiella	1
Diaphanodon	1
Pterobryaceae	32
Calyptothecium	4

TABLE 2. (Cont'd)

Jaegerina	1	*Thamnobryum*	1
Symphysodon	5		
Symphysodontella	4	Thuidiaceae	12
Pterobryella	1	*Thuidium*	8
Trachyloma	2	*Orthothuidium*	1
Euptychium	1	*Pelekium*	2
Garovaglia	14	*Claopodium*	1
		Rhytidiaceae	1
Meteoriaceae	16	*Elmeriobryum*	1
Papillaria	2		
Meteorium	1	Hylocomiaceae	2
Floribundaria	3	*Macrothamnium*	1
Aerobryopsis	2	*Leptocladiella*	1
Aerobryidium	2		
Barbella	2	Buxbaumiaceae	3
Pseudobarbella	1	*Diphyscium*	2
Meteriopsis	2	*Buxbaumia*	1
Aerobryum	1		
		Polytrichaceae	22
Phyllogoniaceae	3	*Dawsonia*	7
Orthorrhynchium	1	*Polytrichaedelphus*	1
Cryptogonium	1	*Polytrichastrum*	1
Catagonium	1	*Polytrichum*	1
		Pogonatum	6
Neckeraceae	17	*Racelopus*	1
Neckeropsis	3	*Pseudoracelopus*	2
Himantocladium	5	*Notoligotrichum*	1
Homaliodendron	3	*Oligotrichum*	2
Pinnatella	5		

included species are not present in Western Melanesia, and others, because of nomenclatural problems, do not offer reliable distributional data. The Hepaticae will be treated in a separate study. However, some relevant hepaticological studies are cited.

The abbreviations of the countries and geographical units used for records of the distribution of taxa can be found in Figs. 1 and 2. These, in many cases extremely "unnatural" units, are not the best alternative for presenting the distributional records. Collections and knowledge of the flora in the area are, however, so scattered that the use of mainly political units is obligatory. The lack of cladistic analysis in all groups except the Mniaceae (Koponen 1982) and *Hymenodon* (Rhizogoniaceae) (Karttunen & Bäck 1988) and inexact distributional information prevented the use of modern methods of vicariance biogeography (e.g. Nelson & Platnick 1981, Nelson & Rosen 1981). The study is thus restricted to a fairly general level, and only traditional methods have been used. The study is mostly descriptive, the possible reasons for particular distribution types being only briefly discussed. The inadequacy of the methods has appropriately been compared to the results obtained by phenetic methods in systematics (Wiley 1984). Thorough consideration of genetic aspect of biogeography (genetischen Pflanzengeographie, Irmscher 1929) is not possible to a sufficient extent. Similar kinds of analysis have been performed in regard to phanerogams of

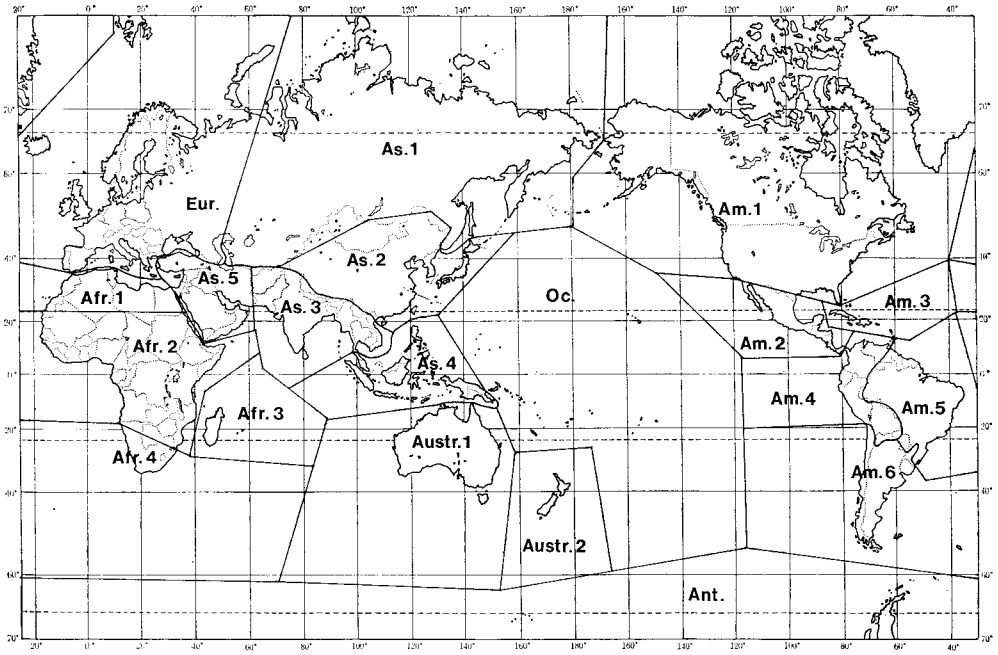

FIG. 1. Main geographical units of the world for recording general distribution of the Western Melanesian mosses, according to Wijk et al. (1964). For more detailed division used for Asia 2–4 and Oceania see Fig. 2.

larger entities (Baalogy 1971, Steenis 1986) or of adjacent regions (Morat et al. 1984). The geographical affinities of the Samoan bryophytes have been studied by Schultze-Motel (1974).

The distribution of all species was tabulated revealing that it is possible to divide the material into groups according to their overall distribution – from species with wide distribution to those endemic for the island of New Guinea. The occurrence of particular distributional types in different families can be evaluated, and recent monographs offer additional information (During 1977, Magill 1980, Miller & Manuel 1982, Zanten 1973). Analysis of local distribution might seem to be possible. However, the records still reflect more the collection activity or lack of it in Western Melanesia than the actual distributions.

III. RESULTS

A. DISTRIBUTION TYPES

Simple tabulation of the data enabled the distinction of different kinds of distribution types. The material has been divided into eleven groups. Further division is, however, in many cases warranted, and annotations are given in the following discussion. Many of the groups are also heterogeneous because the geographical entities used are of composite nature, uniting biota of different origins. The results are thus

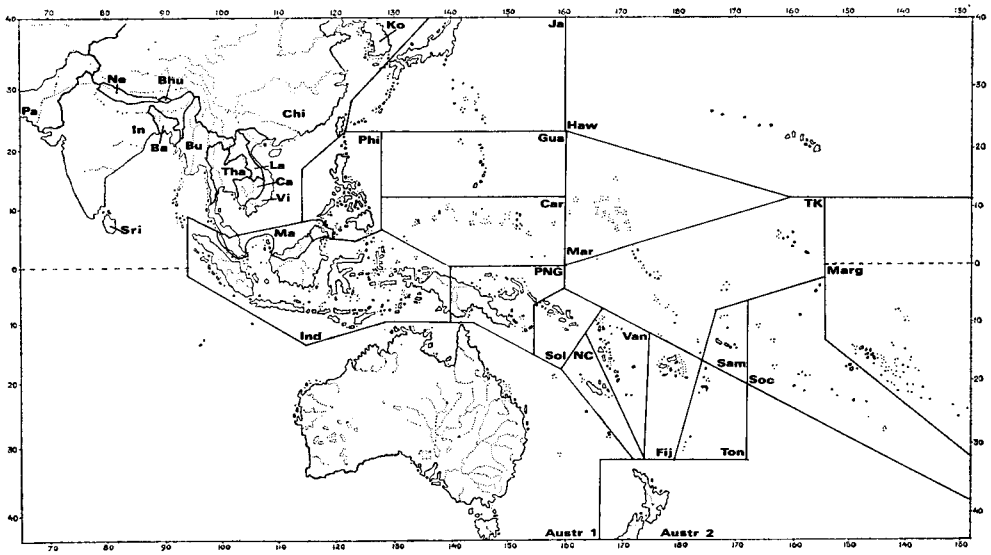

FIG. 2. Abbreviations of the countries and geographical units used for recording distribution of taxa in Western Melanesian series (Norris & Koponen 1985).

Asia 2
Chi=China
Ja=Japan
Ko=Korea

Asia 3
Ba=Bangladesh
Bhu=Bhutan
Bu=Burma
Ca=Cambodia
In=India
La=Laos
Ne=Nepal
Pa=Pakistan
Si=Sikkim
Tha=Thailand
Vi=Vietnam

Asia 4
Ind=Indonesia
Ma=Malaysia, Singapore, Brunei and Sabah
PNG=Papua New Guinea
Phi=Philippines

Oceania (Oc)
Car=Carolines
Fij=Fiji
Gua=Guam
Haw=Hawaii
Mar=Marshalls
Marg=Marguesas
NC=New Caledonia
Sam=Samoa
Soc=Society Islands
Sol=Solomonas
TK=Tuvalu and Kiribati
Ton=Tonga
Van=Vanuatu

Austr 1
Australia

Austr 2
New Zealand

fairly formal, and their information content in regard to paleogeography is limited. There is no attempt at thorough phylogenetic-geographic analysis and division to distribution elements sensu Menzel & Schultze-Motel (1987).

The percentage share of each group is given in Fig. 4. The list of all species in

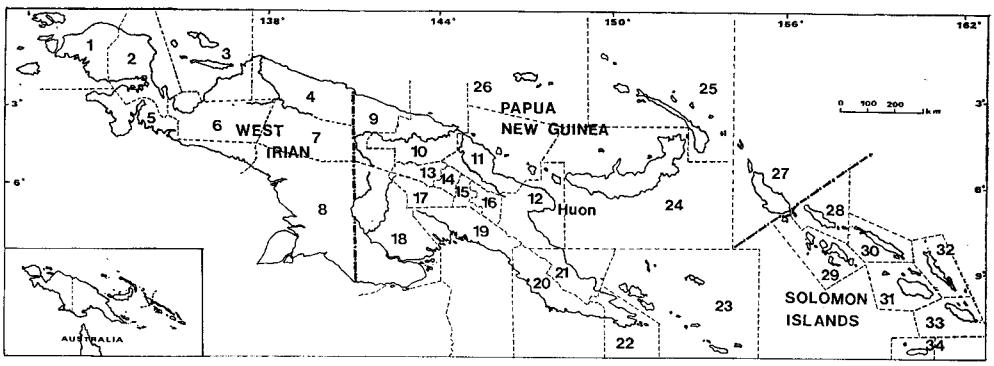

FIG. 3. Geographical units used for records of the distribution of mosses in Western Melanesia (Koponen & Norris 1983).

West Irian: 1. Sorong. 2. Manokwari. 3. Tjenderawasih. 4. Jayapura. 5. Fakfak. 6. Paniai. 7. Jayawijaya. 8. Merauke.

Papua New Guinea: 9. West Sepik. 10. East Sepik. 11. Madang. 12. Morobe. 13. Enga. 14. Western Highlands. 15. Simbu. 16. Eastern Highlands. 17. Southern Highlands. 18. Western. 19. Gulf. 20. Central. 21. Northern. 22. Milne Bay. 23. Papuan Islands. 24. New Britain. 25. New Ireland. 26. Manus. 27. Bougainville.

Solomon Islands: 28. Choiseul. 29. New Georgia Group. 30. Santa Isabel. 31. Guadalcanal. 32. Malaita. 33. San Cristobal. 34. Rennell Group.

each group can be found in Appendix 1. Varieties of some species are in this treatment given value equal to species. The total number of species are varieties included in this geographical treatment is 298.

1. New Guinea

The whole island of New Guinea is here treated as a single entity, as it is a more or less natural and much-used unit in biogeographical analysis. It has, however, been proved to be of composite nature (Hamilton 1979, Duffels 1986), and thus treating it as a single unit seems ambiguous. Provinces 1–27 (Fig. 3) are treated here as New Guinean and the Solomon Islands are treated as a separate unit.

The number of endemic species is 53, which represents ca. 18% of the entire material. Thus the amount of endemics is much lower than was presumed earlier. This is not surprising, as most of the new combinations and synonymisation presented in the studies are for species previously reported as endemics for the island. The amount might decrease still further as adjacent regions are more thoroughly studied. Many New Guinean species might well be found in other areas also. Twelve species are described as new to science, and especially in these cases it should be no suprise to find them in adjacent regions. However, endemics still form the largest of all distribution type groups.

Some of the endemics show clear affinity to the south and represent the Gondwana-element. Here can be mentioned the numerous species of *Garovaglia* of Pterobryaceae, *Dawsonia* and *Polytrichadelphus* of Polytrichaceae and *Leptostomum intermedium*

of Leptostomataceae. The large number of endemics especially in the genus *Garovaglia* was noted by During (1977), and he assumed New Guinea to be a primary speciation centre of the genus. The family as a whole is especially typical for the SE Asian area, and a large number of species of many genera are present. The other two families with many endemics, Bryaceae and Pottiaceae, are both widespread and common throughout the world. Among the endemic species the number of species with suspected affinity to the Laurasian and the Gondwana element is almost equal. In many cases the inclusion in either group is based on highly hypothetical assumptions, and opposing views on the affinity and origin of families have been presented (e.g. Smith 1972 & Schofield 1985 on Polytrichaceae).

Dawsonia papuana and *Fissidens rigidulus* var. *novaguineensis* are both endemic to Western Melanesia, i.e. they are present on New Guinea plus the Solomon Islands.

2. Malesian Region

Indonesia, Malesia, Papua New Guinea (the Solomon Islands excluded) and the Philippines are included in this entity thus corresponding to Asia 4 of Wijk et al. (1964).

The number of endemic species for this area (41) is surprisingly low, representing only ca. 14% of all taxa. The inclusion of the Solomon Islands does not remarkably increase the number because this adds only two species, *Hymenodon angustifolius* and *Pogonatum subtortile*, to the list. As expected, Pterobryaceae is represented by many species, and other families with large number of species are Dicranaceae (*Campylopus*), Calymperaceae, Rhizogoniaceae and Polytrichaeceae (*Dawsonia*), the latter two being clearly of southern Gondwanan origin.

3. SE Asia

South East Asia corresponds to Asia 2–4 of Wijk et al. (1964). The countries included in these entities are presented by Norris & Koponen (1985).

The number of Western Melanesian mosses is 44, representing ca. 15% of the material. Families such as Meteoriaceae and Pterobryaceae are well represented, with five and four species respectively. Clearly the largest group is the monotypic family Fissidentaceae with 12 species restricted to SE Asia.

4. Asian-Oceanian-Australian Species

In this heterogenus group are included all species distributed in at least two of the three mentioned areas. Most of the species have their main distribution in Asia – mostly in the Malesian region, and the genera are furnished with more species there.

Many predominantly SE Asian species share the distribution type of e.g. *Symphysodontella cylindracea* of Pterobryaceae (Fig. 5), being fairly widely distributed in the east on the Pacific Ocean islands. A similar distribution type is shared by species species clearly of the Gondwana-element (e.g. *Trachyloma* and *Garovaglia*) as well as by others, and thus the origin of the species is in many cases ambiguous.

4.1. Asian-Oceanian Species

This group can clearly be divided still further into two subgroups.

Nineteen species are present only in the Malesian region (As 4), and 23 species of the group are more widespread in Asia. These are more western in their distribution, as most of them are found on only one or a few island groups of the Pacific, and none of the species are more widespread in the latter area than in Asia. This applies fairly well also to the first sub-group, as only *Brachymenium indicum*, *Calymperes couguiense Himantocladium flagelliferum* are more widespread in the Pacific area than in SE Asia. Inclusion as a sub-group under the Malesian or SE Asian region might thus be as warranted. However, as noted above, the paleogeographic origin of many taxa is disputed.

Families Neckeraceae and Pterobryaceae are well represented in both sub-groups.

4.2. Asian-Oceanian-Australian Species

This group of species is more homogenous than the one mentioned above. Generally the species still have their main distribution in Asia, but the number of more clearly Oceanian-Australian species is higher. Widespread in these areas are, for example: *Aerobryopsis wallichii*, *Racopilum cuspidigerum*, *Syrrhopodon tristichus*, *S. croceus*, *Mitthyridium constrictum* and *Himantocladium cyclophyllum*.

As can be seen even from this list, the family Calymperaceae is well represented. *Garovaglia powellii*, *Mniomalia semilimbata*, *Papillaria flexicaulis* and *Syrrhopodon perarmatus* are species more widespread in Australian and the Pacific regions than in Asia. The affinity of the Western Melanesian species of genus *Mitthyridium* to Australia was noted by Reese et al. (1986). Their modern distribution in northern Queensland is probably of recent origin, and like many ferns of similar habitats they are part of the tropical Malesian flora-element (Page & Clifford 1981). This assumption is further corroborated by the fact that no endemic species of the genus are present in Australia.

4.3. Asian-Australian Species

The share of species of the Gondwana-element is more pronounced than is that of two groups above. The distribution of *Mittenia plumula* and *Tridontium tasmanicum* is peculiar, because they are absent from northern Queensland and restricted to southern Australia and New Zealand (Norris & Koponen 1989). They clearly represent the southern Gondwana-element as does *Orthorrhynchium elegans* of Phyllogoniaceae. *Astomum platystegium* and *Powellia subelimbata* are plants with restricted distribution, which have been found only from New Guinea and northern Queensland, Australia (Norris & Koponen 1989, Zanten & Pócs 1981). *Orthomnion elimbatum*, *Bryum australe* and *Sorapilla papuana* are also species shared by the island of New Guinea and Australia.

5. Transpacific Distributions

The bryological affinities between America and Eastern Asia is a subject that has been much studied, e.g. by Crum (1972), Iwatsuki (1972), Iwatsuki and Sharp (1967, 1968), Schofield (1965), Sharp (1972) and Sharp and Iwatsuki (1965). Normally more northern latitudes of Asia have been dealt with in these studies, and the amount of shared or vicariant species relative to the Americas is remarkable. The distribution of

some of these plants may extend as far south as to New Guinea. The three species showing this kind of distribution in the present material are *Barbella cubensis*, *Campylopus* and *Trichostomum crispulum*. *Fissidens asplenioides* is a plant with still wider distribution, as it is found in all parts of the Americas and from Japan to New Zealand. The fifth species with trans-Pacific distribution is *Tortula caroliniana*. It is mainly American in its distribution, the only known occurrence on other side of the Pacific Ocean being in New Guinea as reported by Norris and Koponen (1989).

6. Paleotropical Species

Species can be called paleotropical when they are widespread in all other tropical areas except America. Of the New Guinean mosses, here belong many species of the family Calymperaceae; *Calymperes taitense*, *C. dozyanum* and *Mitthyridium fasciculatum*. *Syrrhopodon involutus*, a representative of a genus belonging to the southern Gondwana-element, has a similar distribution but is present apparently also in Tierra del Fuego in southernmost South America (Reese et al. 1986). *Floribundaria floribunda* (Meteoriaceae) and *Neckeropsis lepineana* (Neckeraceae) are also widely distributed plants occurring in tropical areas of all continents of the paleotropics. *Rhodobryum aubertii* (Bryaceae) and *Calymperes serratum*, *C. spiculosus* and *Syrrhopodon trachyphyllus* (Calymperaceae) belong here also, although their distribution is more restricted that those of the species mentioned above. *Brachymenium nepalense* and *Rhodobryum giganteum* (Bryaceae) and *Trachypus bicolor* (Trachypodaceae) are widely spread in the paleotropics, but they are absent from Australia.

7. Pantropical Species

Pantropical species are present on all continents in tropical areas. Ochi (1985) gives *Bryum apiculatum*, *B. billarderii*, *B. cellulare*, *B. coronatum* and *Brachymenium exile* of Bryaceae as pantropical species. Distribution of all *Bryum*-species is extended also outside tropical areas in both Northern and Southern Hemispheres. *Ceratodon stenocarpus* has a similar distribution but is confined to subtropical latitudes, not reaching further north nor south. Species of the family Calymperaceae are also numerous in this group: *Calymperes lonchophyllum*, *C. afzelii*, *C. erosum*, *C. palisoti*, *C. tenerum*, *Syrrhopodon gardneri* and *S. prolifer*, the latter two being confined to larger land masses only (Rees et al. 1986). Reese and Mohammed (1985) suspect *C. tenerum* to be an introduced species in Africa and America. *Fissidens zollingeri* (Fissidentaceae) and *Garckea flexuosa* can also be mentioned here, although their distribution is not as wide as that of other species of the group.

8. Southern Hemisphere Species

Species restricted to the Southern Hemisphere are all with wide and scattered modern distribution. *Ditrichum difficile*, *Catagonium nitens*, *Notoligotrichum australe* and *Rhacocarpus purpurascens* belong here. The last three belong to genera confined totally or mostly to Southern Hemisphere representing the Gondwana-element. Ochi (1985) gives *Bryum clavatum* as a subantarctic species occurring in tropical areas only at high altitudes. This group corresponds more or less to the Andean-circumsubantarctic

group of Menzel and Schultze-Motel (1987).

9. Species with Mainly Northern Hemisphere Distribution

Many species of this group resemble the *Bryum clavatum* mentioned above, as, being plants of severe climatic conditions, they are found in tropical latitudes only at high elevations. They are widely spread in Northern and Southern Hemispheres. Here belong *Grimmia affinis*, *Racomitrium languinosum* and *Schistidium apocarpum* of Grimmiaceae and *Polytrichastrum longisetum* and *Pogonatum urnigerum* of Polytrichaceae. Distribution of *Plagiomnium rostratum* (Mniaceae), *Bryum microerythrocarpum* (Bryaceae) and *Bryoerythrophyllum recurvirostre*, *B. ferruginascens* and *Didymodon rigidicaulis* of Pottiaceae is also wide at temperate latitudes, and in the tropics they are mostly found only at higher altitudes. *Anomobryum julaceum*, *Epipterygium tozeri* and *Pohlia elongata* (Bryaceae), as well as *Fissidens taxifolius* may also be mentioned here. Their ecology and distribution differ, however, from those of the Polytrichaceae and Grimmiaceae mentioned above.

10. Miscellaneous Species

Species that cannot be included in any of the geographical groups mentioned above are listed here. *Campylopodium medium* (Dicranaceae) is a species with wide distribution in Asia, the western Pacific and Australia; thus it could be included in group 4 of the Asian-Oceanian-Australian species. However, it is found also in America in Puerto Rico and Chile.

The rest of the group is formed of four species of the family Pottiaceae. *Scopelophila cataractae* and *S. ligulata* are found in Europe, America, Africa and Asia. *Timmiella anomala* is a more northern plant, being collected in Europe but not in Africa. *Streptopogon eryhtrodontus* is a species of tropical America and Africa with disjunct occurrence in New Guinea.

11. Widely Distributed Species

Probably there are no truly cosmopolitan plants except certain algae, but traditionally the term has been used for extremely widely distributed plants showing no affinity to any particular continent or vegetation zone. In many cases the range of these plants has been enlarged by human activities — intentional or accidental, the latter being true in regard to mosses. Thus more or less weedy plants form the bulk of the group. *Bryum argenteum* and *Leptobryum pyriforme* are weeds common on man-made habitats. *Bryum capillare* thrives also on disturbed habitats, although it is not as clearly a weed as are the two species mentioned above. *Polytrichum juniperinum* and *Distichium capillaceum* can as well be classified in this group. One of the most common weedy mosses at temperate latitudes – *Ceratodon purpureus* – is in Western Melanesia replaced by pantropical and the very similar *C. stenocarpus*. The relationship of two is problematic, and further study is needed (Norris & Koponen 1989).

Not quite as widely spread as the species mentioned above are many species of Pottiaceae, i.e. *Anoectangium aestivum*, *Barbula indica*, *Gymnostomum aeruginosum*, *Hymenostylium recurvirostre*, *Hyophila involuta*, *Leptodontium viticulosoides*, *L.*

flexifolium, *Oxystegus tenuirostris*, *Trichostomum brachydontium* and *Weissia controversa*. Most of these are confined to, or are more common on open habitats, thus being more or less weedy plants. *Andreaea rupestris* and *Pyrrhobryum spiniforme* can be included with some reservations in this group.

B. Floristic Affinities

In Fig. 6 can be seen the number and percentage share of Western Melanesian mosses found in other areas. Clearly, New Guinea shares most of its moss flora with other Malesian areas, i.e. Malaysia, Indonesia and the Philippines. These results are by no means surprising, as most of the biota has a similar geography (terrestrial vertebrates are an exception, being more or less Australian), Climatic barriers relative to Australia have also been important in reducing the influence of the latter area (Gressitt 1982), Recent cladistic studies on the biogeography of the area (Duffels 1986, Schuh & Stonedahl 1986) have revealed the biota of New Guinea to be of a composite nature. The data of Schuh and Stonedahl (1986) also indicate a closer relationship of New Guinea to Africa than to Australia. Such a conclusion is neither demonstrated nor

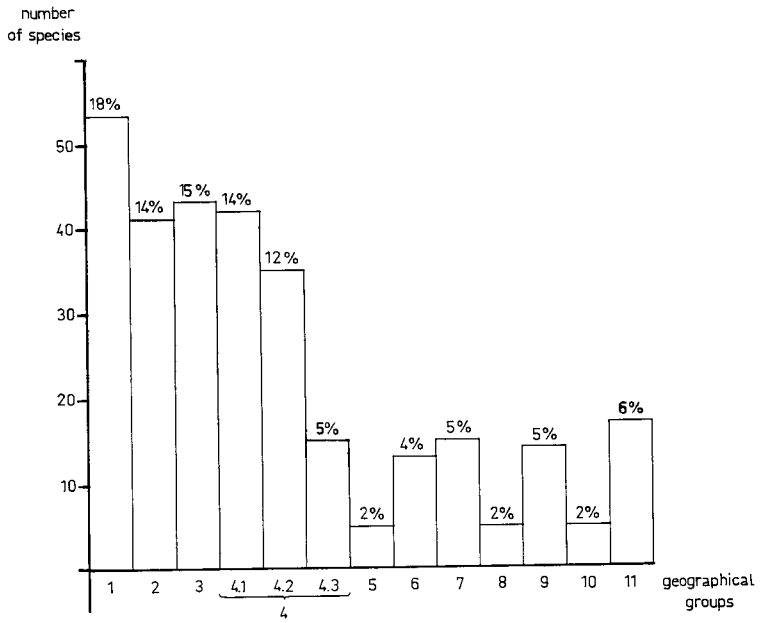

Fig. 4. Percentage share of moss species in each geographical group (see text). Total number of species included in this treatment 298. 1. Endemics of New Guinea. 2. Endemics of Malesian region. 3. SE Asian species. 4. Asian-Oceanian-Australian species: 4.1. Asian-Oceanian species. 4.2. Asian-Oceanian-Australian species. 4.3. Asian-Australian species. 5. Transpacific species. 6. Paleotropical species. 7. Pantropical species. 8. Southern Hemisphere species. 9. Species with mainly Northern Hemisphere distribution. 10. Miscellaneous species. 11. Widely distributed species.

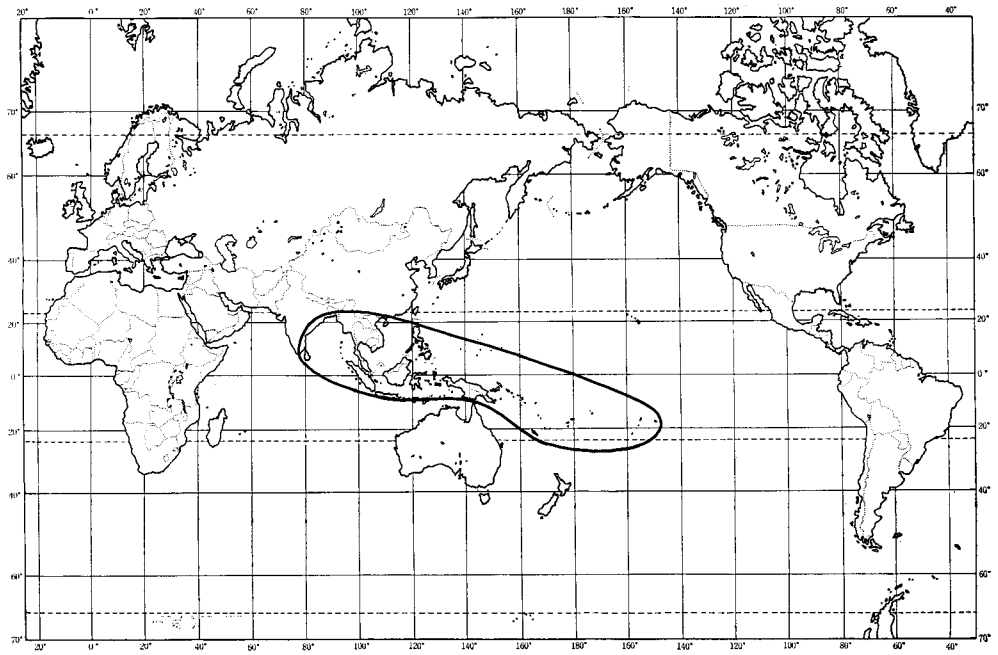

FIG. 5. The world distribution of *Symphysodontella cylindracea* (Mont.) Fleisch. (after Magill 1980).

contradicted by the present limited bryological information. The number of shared taxa with Africa and Australia are 65 and 94. However, the fact that only a few species represent a truly Australian element must be kept in mind. Many families or genera (e.g. Leptostomataceae) are, however, clearly the ancient Gondwana-element like many phanerogams of the area (e.g. genus *Nothofagus* and family Araucariaceae).

As already noted, the geographic entities used above are highly artificial and even delusive from a paleogeographical point of view. Part of the moss flora clearly represent Laurasian or Gondwanaland element. However, in many cases inclusion in either group is highly hypothetical. Some groups, especially those showing the typical Malesian-Western Pacific distribution pattern (Fig. 5.) may just as well be placed in either of the large groups. An interesting theory has been proposed in regard to *Pogonatum* by Smith (1972) and may well be applied also to other groups. It is hypothetized that the ancestor of the genus *Pogonatum* may have been rafted to the north on the Indian subcontinent, and from there the species have gradually attained their present distribution.

C. Collecting Activity

As already mentioned in the introduction, the record of species in different provinces of Western Melanesia reveals mainly the collecting activity and not the real distribution of a particular plant.

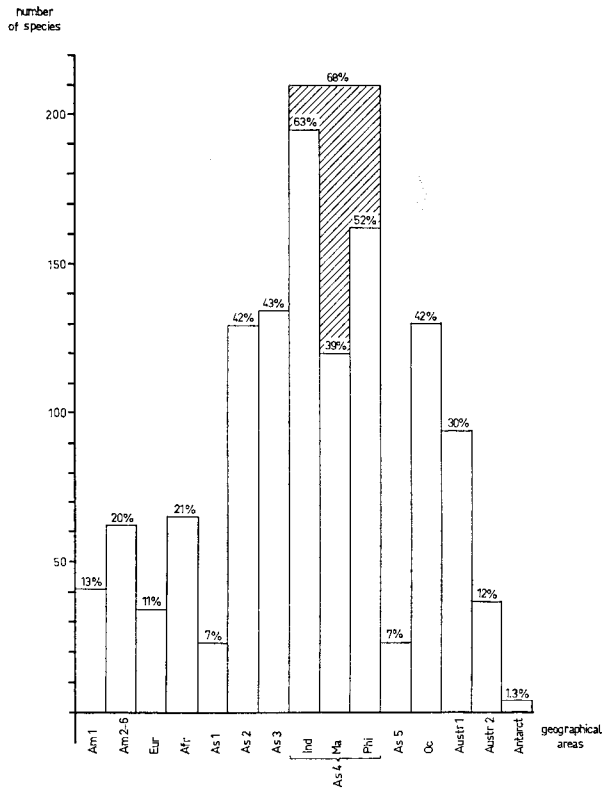

FIG. 6. Floristic affinities of Western Melanesian moss flora. Percentage of shared species with each area indicated over each column. Total number of included species 309.

As can be seen in Fig. 7, West Irian and the Solomon Islands are generally less well known than are the provinces of Papua New Guinea. The reliability of the results in regard to the Solomon Islands is distorted by the fact that many New Guinean mosses are not distributed as far east as the Solomon Islands. However, it is clear that the islands are poorly known bryologically. There are no records of mosses from the island of Santa Isabel. The situation is not much better for Choiseul and Malaita as there is only one record from each.

The difficulty of access to West Irian has been the main reason for the poor collecting activity in the western part of the island of New Guinea. Morobe province of Papua New Guinea clearly is the best known area in the whole region — the material at hand shows that 80% of the mosses known from Western Melanesia have also been found in this province. Of the Papua New Guinean provinces the island of New Britain is the least known area with only 13 records of moss species. On the main island the Gulf Province is the least known part with only 14 records. However, this latter province may possess a very small flora because it is mainly tropical, swampy flatlands

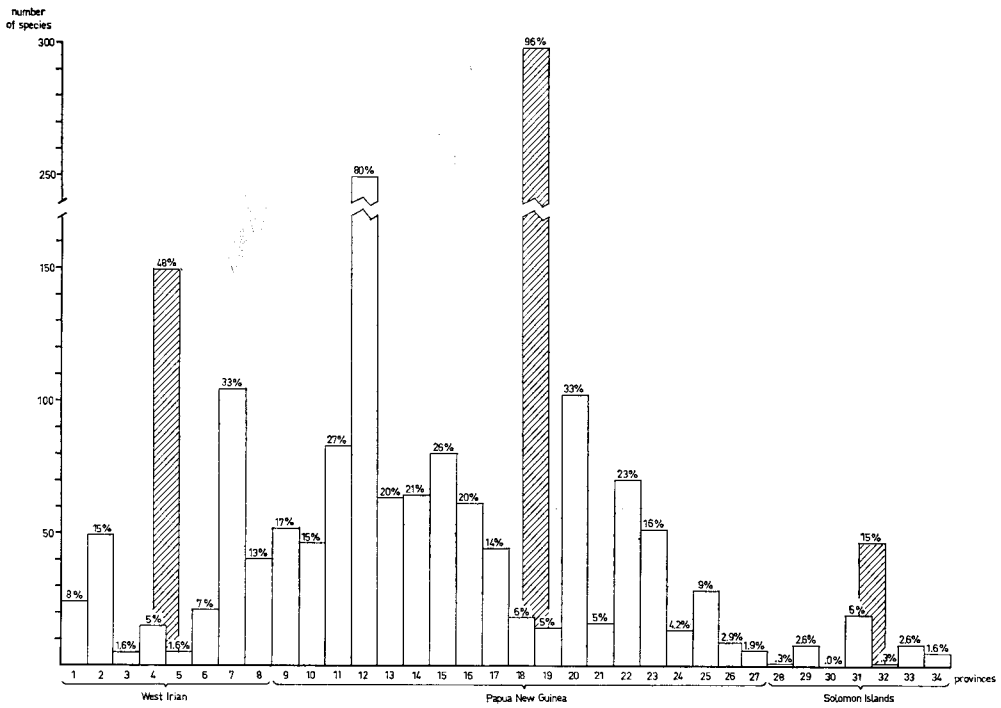

FIG. 7. Moss-collecting activity in the provinces of Western Melanesia. Percentage share of moss species records in the particular province indicated over each column. Shaded columns show percentage representation in West Irian, Papua New Guinea and Solomon Islands. Total number of included species 311.

which do not offer ideal conditions for the growth of mosses. The moss flora of tropical lowland forests can be extremely poor (Richards 1984). The number of suitable habitats is naturally much greater in the provinces with high mountains, such areas containing the greatest number of bryophyte species on earth.

IV. CONCLUDING REMARKS

The material at hand represents only part of the moss flora, and results might be altered when all taxa have been treated. The lack of thorough knowledge of some groups may hide many biogeographic mistakes. Insufficient cladistic analysis of the moss flora prevents the use of modern methods of vicariance biogeography and thus monographs with a sound cladistic basis are needed to furnish the biogeographic analysis with reliable data. However, the strong affinity to Asia can clearly be seen. The number of endemic moss species for New Guinea is surprisingly low when compared for example with the results obtained from the study of hepatics (Piippo 1988). The percentage share of endemic species in some hepatic genera is as high as c. 80%

and for the whole group ca. 40% (Piippo 1988). However, many of the hepatic groups are insufficiently known, and some of them treated with an extremely narrow species concept and without use of modern research methods. Critical revisions, like those made by Piippo (1984) and Grolle and Piippo (1986) have decreased the number of species. Some of the hepatic groups are supposed to be in a very active stage of evolution and include a large amount of endemics (Schuster 1983). When these groups (Plagiochilaceae, Radulaceae, Frullaniaceae and Lejeuneaceae) are set aside, we get still an extremely high figure (ca. 30%, Piippo pers. comm.) when compared with 18% for mosses.

According to Paijmans (1976) ca. 13% of the phanerogam genera are endemic to the island, a percentage comparable to that of the endemic moss species and supporting the view that evolution in bryophytes is in general much slower than in phanerogams (Iwatsuki 1972). At the species level the approximated values of endemism for the latter group are extremely high, reaching 90% (Royen 1980).

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Appendix 1

The number after family name indicates the number of taxa in each family. Sp. nov. indicates that the particular species has been described in the Huon Peninsula series.

1. Endemic Species of New Guinea (53 taxa, c. 18%)

Bryaceae 13
Anomobryum bulbiferum sp. nov.
A. hyalinum sp. nov.
A. ochii sp. nov.
Brachymenium wabagense sp. nov.
B. gracile
B. huonii sp. nov.
B. nepalense var. *globosum*
Bryum papuanum
B. perdecurrens
B. pseudoblandum sp. nov.
B. sclerodictyon
Leptostomum intermedium
Mielichhoferia novoguineensis

Buxbaumiaceae 1
Diphyscium loriae

Calymperaceae 1
Mitthyridium megamorphum

Dicranaceae 1
Campylopus clemensiae

Ditrichaceae 2
Ditrichum colijnii
D. sericeum

Fissidentaceae 3
Fissidens flexifolius
F. rigidulus var. *novaguineensis*
F. vanzantenii

Hylocomiaceae 1
Leptocladiella flagellaris sp. nov.

Meteoriaceae 1
Aerobryidium fuscescens

Mniaceae 2
Plagiomnium cordatum sp. nov.
P. integrum var. *subelimbatum*

Polytrichaceae 4
Dawsonia papuana (endemic to Western Melanesia)
D. pullei
Oligotrichum novae-guineae
Polytrichadelphus archboldii

Pottiaceae 7
Barbula novo-guinensis
B. pachyloma
B. robbinsii
Didymodon coffeatus sp. nov.
D. wisselii
Hyophila streimannii sp. nov.
Trachycarpidium echinatum

Pterobryaceae 12
Calyptothecium integrifolium
Garovaglia binsteadii
G. brassii
G. crispa
G. plumosa
G. robbinsii
G. subelegans
G. zantenii
Pterobryella papuensis
Symphysodon longicuspis
S. piliferus
Trachyloma concavifolium

Racopilaceae 2
Powellia parvula
Racopilum squarrifolium

Seligeriaceae 1
Blindia myer-dreesii

Thuidiaceae 2
Orthothuidium curtisetum sp. nov.
Thuidium longissimum

2. Endemics of Malesian Region (41 taxa, c. 14%)

Bryaceae 2
Bryum russulum
Mielichhoferia hymenodonta

Buxbaumiaceae 1
Buxbaumia javanica

Calymperaceae 1
Syrrhopodon hispidissimus

Dicranaceae 5
Atractylocarpus comosus
Campylopus austrosubulatus
C. crispifolius
C. exasperatus
C. macgregorii

Grimmiaceae 1
Racomitrium javanicum

Hedwigiaceae 1
Rhacocarpus alpinus

Hylocomiaceae 1
Macrothamnium hylocomioides

Leptostomataceae 1
Leptostomum intermedium

Meteoriaceae 2
Aerobryidium crispifolium
Barbella flagellifera

Neckeraceae 2
Himantocladium submontanum
Thamnobryum ellipticum

Polytrichaceae 8
Dawsonia beccarii
D. gigantea
D. grandis
D. lativaginata
Oligotrichum javanicum
Pogonatum microphyllum
P. subtortile
P. tubulosum

Pottiaceae 2
Barbula pseudo-ehrenbergii
Leptodontium aggregatum

Pterobryaceae 8
Calyptothecium extensum
Garovaglia bauerlenii
G. compressa

G. mujuensis
Symphysodon neckeroides var. *tjibodensis*
S. splendens
Symphysodontella convoluta
S. parvifolia

Racopilaceae 1
Racopilum verrucosum

Rhizogoniaceae 5
Hymenodon angustifolius
H. pilifer var. *sericeus*
Hymenodontopsis stresemannii
Rhizogonium hattorii
R. lamii

3. SE Asian Species (44 taxa, c. 15%)

Archidiaceae 1
Archidium birmannicum

Bryaceae 1
Orthodontium infractum

Buxbaumiaceae 1
Diphyscium involutum

Calymperaceae 1
Mitthyridium cardotii

Dicranaceae 3
Bryohumbertia walkeri
Campylopus comosus
C. involutus

Fissidentaceae 12
Fissidens autoicus
F. flabellatum
F. gemmiflorus
F. hallianus
F. laxus
F. microcladus
F. papillosus
F. plagiochiloides
F. serratus
F. strictulus
F. wichurae
F. zippelianus

Meteoriaceae 5
Aerobryopsis leptosigmata
Aerobryum speciosum
Floribundaria sparsa
Meteriopsis squarrosa
Pseudobarbella ancistrodes

Mniaceae 4
Minium lycopodioides
Orthomnion loheri
Plagiomnium integrum
P. succulentum

Neckeraceae 2
Homaliodendron microdendron
Pinnatella anacamptolepis

Polytrichaceae 2
Pogonatum neesii
Racelopus pilifer

Pottiaceae 2
Barbula javanica
B. subcomosa

Pterobryaceae 4
Calyptothecium urvilleanum
Garovaglia plicata
Jaegerina luzonensis
Symphysodontella attenuatula

Rhizogoniaceae 1
Pyrrhobryum latifolium

Rhytidiaceae 1
Elmeriobryum philippinense

Thuidiaceae 2
Thuidium contortulum
T. sparsifolium

Trachypodaceae 2
Diaphanodon blandus
Duthiella flaccida

4. Asian-Oceanian-Australian Species

4.1 Asian-Oceanian Species (42 species, c. 14%)

Species occurring in Asia only in Malesian region (As 4) are marked with (*).

Bryaceae 2
*Brachymenium indicum**
Pohlia flexuosa

Calymperaceae 11
*Calymperes aeruginosum**
*C. couguiense**
C. fasciculatum
C. porrectum
*C. strictifolium**
*C. subulatum**
Mitthyridium undulatum
Syrrhopodon albovaginatus
*Syrrhopodon aristifolius**
S. japonicus
S. loreus

Fissidentaceae 3
Fissidens braunii
F. nobilis
F. obscurirete

Meteoriaceae 2
*Floribundaria pseudofloribunda**
Papillaria fuscescens

Neckeraceae 7
*Himantocladium flagelliferum**
*H. giulianettii**
*Neckeropsis gracilenta**
*Pinnatella kuehliana**
P. mariei (also in Afr 3)
P. mucronata
*P. nana**

Polytrichaceae 3
Pogonatum cirratum
*Pseudoracelopus misimensis**
*P. philippinensis**

Pottiaceae 3
Barbula arcuata
*Oxystegus crassicostatus**
Pseudosymblepharis angustata

Pterobryaceae 4
Calyptothecium recurvulum
Garovaglia angustifolia
*Symphysodon neckeroides**
*Symphysodontella cylindracea**

Racopilaceae 1
Racopilum spectabile

Thuidiaceae 6
Claopodium prionophyllum
*Pelekium bifarium**
P. velatum
*Thuidium brotheri**
T. cymbifolium
T. glaucinum

4.2 Asian-Oceanian-Australian Species (35 taxa, c. 12%)

Bryaceae 1
Bryum pachytheca

Trachypodaceae 1
Trachypus humilis

Calymperaceae 14
Calymperes schmidtii
Mitthyridium constictum
M. luteum
M. obtusifolium (disjunct in Chile)
M. repens
M. subluteum
Syrrhopodon ciliatus
S. confertus
S. croceus
S. fimbriatulus
S. muelleri
S. parasiticus
S. perarmatus
S. tristichus

Dicranaceae 1
Campylopus umbellatus

Meteoriaceae 4
Aerobryopsis wallichii
Meteorium buchananii
Meteoriopsis reclinata
Papillaria flexicaulis

Neckeraceae 3
Himantocladium cyclophyllum
H. plumula
Homaliodendron exiguum

Phyllodrepaniaceae 1
Mniomalia semilimbata

Phyllogoniaceae 1
Cryptogonium phylloconioides

Pottiaceae 1
Weissia edentula

Pterobryaceae 4
Eupthychium setigerum
Garovaglia elegans
G. powellii
Trachyloma indicum

Racopilaceae 2
Powellia involutifolia
Racopilum cuspidigerum

Rhizogoniaceae 2
Rhizogonium graeffeanum
Pyrrhobryum medium

4.3 Asian-Australian Species (16 taxa, c. 5%)

Bryaceae 1
Bryum australe

Calymperaceae 3
Mitthyridium crassum
M. flavum
M. jungguilianum

Fissidentaceae 3
Fissidens ceylonensis
F. crassinervis
F. nymanii

Mitteniaceae 1
Mittenia plumula

Mniaceae 1
Orthomnion elimbatum

Neckeraceae 1
Neckeropsis nanodisticha

Phyllogoniaceae 1
Orthorrhynchium elegans

Polytrichaceae 1
Dawsonia longifolia

Pottiaceae 2
Astomum platystegium
Tridontium tasmanicum

Racopilaceae 1
Powellia subelimbata

Sorapillaceae 1
Sorapilla papuana

5. Transpacific Distributions (5 species, c. 2%)

Dicranaceae 1
Campylopus aureus

Fissidentaceae 1
Fissidens asplenioides

Pottiaceae 3
Barbella cubensis
Tortula caroliniana
Trichostomum crispulum

6. Paleotropical Species (13 species, c. 4%)

Species marked with * are absent from Australia.

Bryaceae 3
*Brachymenium nepalense**
Rhodobryum aubertii
*R. giganteum**

Calymperaceae 7
Calymperes dozyanum
C. serratum
C. spiculosus
C. taitense
Mitthyridium fasciculatum
Syrrhopodon involutus
S. trachyphyllus

Meteoriaceae 1
Floribundaria floribunda

Neckeraceae 1
Neckeropsis lepineana

Trachypodeceae 1
*Trachypus bicolor**

7. PANTROPICAL SPECIES (15 species, c. 5%)

Bryaceae 5
Brachymenium exile
Bryum apiculatum
B. billarderii
B. cellulare
B. coronatum

Calymperaceae 7
Calymperes afzelii
C. erosum
C. lonchophyllum
C. palisotii
C. tenerum
Syrrhopodon gardneri
S. prolifer

Ditrichaceae 2
Ceratodon stenocarpus
Garckea flexuosa

Fissidentaceae 1
Fissidens zollingerii

8. SOUTHERN HEMISPHERE SPECIES (5 species, c. 2%)

Bryaceae 1
Bryum clavatum

Ditrichaceae 1
Ditrichum difficile

Phyllogoniaceae 1
Catagonium nitens

Polytrichaceae 1
Notoligotrichum australe

Racopilaceae 1
Rhacocarpus purpurascens

9. SPECIES WITH MAINLY NORTHERN HEMISPHERE DISTRIBUTION (14 species, c. 5%)

Bryaceae 4
Anomobryum julaceum
Bryum microeryhtrocarpum
Epipterygium tozeri
Pohlia elongata

Fissidentaceae 1
Fissidens taxifolius

Grimmiaceae 3
Grimmia affinis
Racomitrium lanuginosum
Schistidium apocarpum

Mniaceae 1
Plagiomnium rostratum

Polytrichaceae 2
Polytrichastrum longisetum
Pogonatum urnigerum

Pottiaceae 3
Bryoerythrophyllum ferruginascens
B. recurvirostre
Didymodon rigidicaulis

10. MISCELLANEOUS SPECIES (5 species, c. 2%)

Dicranaceae 1
Campylopodium medium

Pottiaceae 4
Scopelophila cataractae
S. ligulata
Streptopogon erythrodontus
Timmiella anomala

11. WIDELY DISTRIBUTED SPECIES (17 species, c. 6%)

Andreaeaceae 1
Andreaea rupestris

Bryaceae 3
Bryum argenteum
Bryum capillare
Leptobryum pyriforme

Ditrichaceae 1
Ditrichum capillaceum

Polytrichaceae 1
Polytrichum juniperinum

Pottiaceae 10
Anoectangium aestivum
Barbula indicum
Gymnostomum aeruginosum
Hymenostylium recurvirostre
Hyophila involuta
Leptodontium flexifolium
L. viticulosoides
Oxystegus tenuirostris
Trichistomum brachydontium
Weissia controversa

Rhizogoniaceae 1
Pyrrhobryum spiniforme