DISTRIBUTION OF MOSSES IN FORMOSA

by

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Problems of plant distribution have current scientific interest, especially for taxonomists or ecologists. Because of the changes in taxonomic and nomenclatural concepts in the past few decades, modern taxonomists realize the practical importance of knowing exactly whence his specimens are derived. Actually, since the time of Hooker, it has been found that there is a close correlation between range and the best classification a botanist can make of the taxonomic unit. With wider viewpoints, the constitution and history of the flora of a given geographical area can only be explained by analysis of the range of the constituent species. The phytogeographer concerns himself not only with the distribution of plants in space but also with their distribution in time, since great changes in the distribution of plants must have taken place in the course of geological time.

Formosa, as a geographical area, offers excellent opportunities for the study of the various geobotanical problems by reason of its geographical position as well as the fundamental topographical features of the island. As a matter of fact, modern scientific research concerning the island botany was not initiated until 1854 when Robert Fortune, a Scottish botanist sent by the Royal Horticultural Society to China, visited Formosa on April 20 (Kanehira, 1936). It was with the turn of the century that the bryophytes of Formosa were first investigated (Cardot, 1905).

Works on Formosan bryophytes published since 1905 are very fragmentary and widely scattered. Bryological exploration has been limited to a number of easily accessible areas which are widely scattered over the island. No one has assembled and reported comprehensive distributional data on the mosses occurring on the island of Formosa. Therefore Formosa may be considered as a whole a very superficially explored district with respect to a bryophyte flora, although the vascular flora of the island has been

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studied by a number of Japanese botanists for decades. Even until now no critical systematic study of the entire moss flora of Formosa has ever been made based on extensively collected materials as well as specimens deposited in various herbaria. The preliminary investigation reported in this thesis was carried out mainly based upon the observations and collections of the writer even though data from reliable sources and available literature were used in taxonomic revision in the study. It is hoped that this thesis may thus serve as an up-to-date summary of our knowledge of the taxonomic composition and the correlation of the distribution patterns with the dynamic interrelationships between the mosses and the environment, which may make possible some better understanding concerning the ecological and distributional affinities of the mosses of Formosa.

Taxonomic Composition of the Moss Flora of Formosa

The moss flora of Formosa is composed of 565 species distributed among 206 genera in 46 families. Among the 565 species comprising the known moss flora of Formosa 157 species are endemic to the island. Eleven other species are represented in Formosa each by a variety. Taken as a whole, 52 varieties and nine forms of mosses belonging to 51 species, of which 28 varieties and two forms are endemic plants, occur in Formosa. It is predicted another 50 to 60 species may eventually be found in Formosa through further exploration.

Of the great number of genera present in the moss flora of Formosa 96, or 47 per cent, are represented in Formosa each by only a single species. Among these 96 genera 14 are monotypic genera, four of which, *Taiwanobryum, Horikawaea, Pseudopleuropus* and *Neodolichomitra,* are also endemic to Formosa.

In addition, the average number of species per genus is a fraction less than three. Consequently, the moss flora of Formosa is not only rich in species but also rich in genera. In other words, in the phytogeographical studies no significant difference would exist between the results from the analysis of the distributions of genera and that from the analysis of the distributions of species.

Of the 46 families represented on the island 13 families are represented in Formosa by a single genus, two of which are monotypic families. This may be an indication of the peculiarity of the moss flora of Formosa.

Distribution of Mosses in Formosa

As is known, because of the great number of lofty mountains within a narrowly limited area, the topographical conditions in Formosa are exceedingly favorable to a diversified flora. Consequently, the bryophyte flora, like the vascular flora, is very rich both in species and in communities, and the distribution of the mosses in Formosa is also broadly correlated with elevation. There is a general increase in number of species of mosses with increasing elevation below an altitude of about 2000 m, the flora is lowest in number of species of mosses in low-lying areas, even in the virgin coastal forests.

In Formosa, the occurrence of mosses is so sparse in the lowlands that only a very limited number of species may be found; these are scarce plants of shady and relatively moist habitats By far the greatest profusion of mosses occurs on slopes between 1000 and 2500 m. where mists and clouds prevail and the humid hardwood forests grade into cloudy conifer forests. Conditions here in the damp mountain forests admit the most remarkably luxuriant growth of mosses, especially of the epiphytic forms.

It is apparent that the distributions of individual species vary enormously. Most mosses are confined to certain kinds of microhabitats; their distributions are correlated with microclimatic rather than edaphic conditions as is confirmed by their wide elevational distributions irrespective of edaphic factors. It is correct to say that the elevational range of a vast majority of the mosses is wider than that of the vascular plants in Formosa, although the latitudinal distributions of the mosses may be limited in certain parts of the island. The most striking of these is *Thuidium cymbifolium*, which extends upwards from the evergreen hill woods at low elevation into fir forests characteristic of the much elevated areas. An observation of the occurrence of the species of mosses in Formosa will make it clear enough that microclimatic factors are paramount in determining not only the range but also the relative frequency of the mosses. Therefore, it may be concluded that the appearance of the mosses in certain suitable habitats is, primarily at any rate, due to the existence there of certain particular microclimatic factors, especially the relative humidity of the atmosphere; however, it may be hazarded to say that temperature is the main component concerned.

Among the wide spread species some are generally found fairly well distributed over the island as a whole and with notably great frequency. In addition to *Thuidium cymbifolium*, these include *Pogonatum inflexum*, *Taxiphyllum taxirameum* and *Hypnum plumaeforme*. However, a number of these widely ranging species tend to show some gaps in their elevational distribution, in a way which cannot be attributed solely to direct climatic considerations. Notable examples of the somewhat discontinuous type of altitudinal distribution are *Papillaria semitorta*, *Homaliodendron microdendron*, *and Pogonatum gymnophyllum*.

It is noteworthy that the more or less common species, which form the great bulk of the moss flora, tend to show very much the same distribution, namely a concentration of species in areas at higher elevations between 1500 and 2500 m., and the general importance of the climatic factors, or more specifically the relative humidity of the atmosphere, is here particularly clear.

Also interesting are *Trematodon longicollis* and *Dicranella coarctata*, which not uncommonly grow together but which have quite different total distribution, although the former is much more frequent. In fact, the individuals of both species are widespread and plentiful. Consequently, these are the commonest species.

Another group of species is characteristic of the damp woodland covered with hill hygrophilous forests. General speaking, these are less common species which tend to show a more or less rigid restriction to one or more of a small number of major habitat

types. Therefore species in this group are mostly of local occurrence in hilly country. Moreover, the great majority of the species found at low altitudes are concentrated in the very northern part; some of them may extend from the north into the central part, but perhaps only very few, if any, ever reach as far south as the southern portion of the island. However, it is noticeable that the moss flora characteristic of the woodlands at low elevations in the south is relatively poor not only in species but also in frequency of occurrence. Species which are of wide occurrence in hilly country or in lowlands throughout the island are very few. The most striking of them is ***Hyophila rosea***, which extends from the north as far south as Heng-chun Peninsula, which is the southern tip of Formosa. Although the area of this species may be very large, the occupation appears to be very slight. In contrast, both ***Fissidens sakourae*** and ***Hyophila stenophylla***, characteristic of the low-lying areas, are widespread over the island and not only is their area large but also their occupation is relatively intense. One species deserves to be mentioned in this connection. ***Bryum argenteum*** is probably the most widely ranging species in Formosa, but its occurrence is generally well spaced, even though it may grow in great quantity and become characteristic of the alpine grassland. As a matter of fact, its distribution, at least in lowlands as well as in hilly country, takes the form of numerous but very isolated records.

In the low-lying coastal areas environmental conditions are extreme and, therefore, provide a very specialized kind of habitat which supports only a few particular species. ***Hyophila rosea*** is the only moss species that was found and collected in the virgin coastal forest which is distributed along the coast of Heng-chun Peninsula. The extreme poverty of occurrence of mosses in the very low-lying areas is apparently due to the presence of salt in the atmosphere.

The northern species form another group of mosses in distribution on the island. Latitudinally, these species may be of wide occurrence over the island wherever subalpine conditions prevail. In other words, their occurrence is predominantly restricted to the subalpine areas, particularly the cold woods. In fact, the altitudinal range of these species may not be so wide as that of those so-called common species widely distributed over the slopes between 1000 and 2000 m. or higher, but the individuals of these species of mosses are frequently exceedingly plentiful, and usually characterize the forest floor in the fir forest or mixed conifer woods. Species such as ***Ptilium crista-castrensis***, ***Hylocomium proliferum*** and ***Pleurozium schreberi*** are the extreme examples of this type of distribution. As is known, ***Rhacomitrium heterostichum*** is probably another instance of the same thing.

A few species of mosses in Formosa are characteristic of the alpine grassland, but they grow only in places where it is well exposed and free from the competition of grasses. These are largely members of Pottiaceae and Polytrichaceae, in addition to ***Bryum argenteum***. In most cases they usually grow in great abundance but their occurrences are almost entirely well spaced.

Correlation of the Distribution of Mosses and Vascular Plants in Formosa

The vegetational zonation of mountains is particularly distinctive in Formosa. The vegetation of the island is composed mainly of two climax formations, one of which is forest and the other alpine tundra. The former occupies nearly the whole area of the mountain slopes while the latter is limited to areas above 3500 m. The altitudinal zonation of the forest formation is conspicuously evident in the distinctive altitudinal distribution of the hardwood forest and conifer forest. Within either the hardwood or the conifer zone lower and upper slopes are distinguishable. The altitudinal limits of the zones are equivalent to the latitudinal limits of the zones of the earth, each of which is characterized by vegetation dominated by a particular floristic element. Thus, the forest vegetation types characteristic of the altitudinally zonal slopes range from those of the boreal and subalpine conifer forests to those of the subtropical and tropical evergreen hardwoods.

In Formosa the altitudinal distribution of mosses is generally matched by that of the arboreal species which dominate the forest vegetation. As was previously pointed out, the occurrence of mosses is very scanty in the lowlands and over much of the hilly country even though the island flora is very rich. By far, the greatest profusion of mosses occurs in the evergreen damp woods covering the subtropical upper slopes of the hardwood forest zone. Conditions here admit the most remarkably luxuriant growth of mosses, especially of the epiphytic species and pendulous forms, which are known to be quite similar to those characteristic of the tropical rain-forest. Here in the broad-leaved evergreen mountain forests distributed over the slopes below 2000 m., the forest-floor is frequently covered with a dense carpet of liverworts, mosses and filmy ferns; the trees are often covered with mosses, lichens and ferns and herbaceous seed plants, and every log is covered with translucent, moist greenery.

In the shady dense forest stands, the trunks of trees are mostly or even completely covered with massive mats of various species of mosses. Furthermore, even the small branches of trees or shrubs may be covered with largely pendulous masses of gold-hued mosses, such as *Pilotrichopsis dentata, Aerobryidium taiwanense, Meteoriopsis formosana, Neckeropsis lepineana, Barbella rufifolioides, Pseudobarbella levieri, P. laxifolia, Calyptothecium japonicum,* and *C. cuspidatum.* Those most characteristic members of mosses inhabiting the upright trunks of trees are represented by species of *Homaliodendron, Pinnatella, Pterobryum, Meteorium,* and by *Pireela formosana,* and *Leucoloma molle.* Besides, terrestrial mosses are also found in abundance. One finds *Rhizogonium spiniforme* of common occurrence on humus in deep shade while *Bryum ramosum* frequently thrives as mesophytes on cliff or ledges. Species such as *Philonotis socia, P. plumulosa* and *Bryum coronatum* frequently appear on ground in wet places along the roadside where they are moderately sheltered by the forest canopy. Similarly, species which appear to be pioneers colonizing mineral soil, such as *Trematodon longicollis, Dicranella coarctata*

and *Pogonatum inflexum*, are commonly found densely covering the ground in extensive patches in relatively open areas.

Just as in the hardwoods, environmental conditions in the conifer forests are also favorable for the growth and development of mosses, and the luxuriant growth of mosses also characterizes the vegetation aspect there. In many cases trunks, even branches, of trees characteristic of the lower slopes of the conifer forest zone are so densely covered with bryophytes as to resemble the rich moss communities which are commonly found to be of maximum development in the hardwoods distributed below the conifer forests in question. Moreover, the components of the abundant growth of the rich bryophyte vegetation even include a number of tropical and subtropical species. Characteristic epiphytes include *Meteoriella soluta, Chrysocladium retrorsum, Isothecium subdiversiforme* and species of *Homaliodendron*. Those commonly found on ground, either rocks or humus, are represented by species as *Fleischerobryum longicolle, Syrrhopodon japonicus* and *Pogonatum grandifolium* in addition to species of *Gollania, Hypnum, Dicranum, Leucobryum*, and *Plagiothecium*. Splendid massive mats of species of *Bartramia* are not uncommonly found covering damp cliffs or ledges in densely stocked stands. In relatively open or exposed areas one finds *Pogonatum urnigerum, Oncophorus wahlenbergii, Ptychomitrium formosicum* and species of *Rhacomitrium* of frequent occurrence on rocks at higher altitudes.

Terrestrial mosses usually attain their most luxuriant growth in the cold woods characteristic of the upper slopes of the conifer forest zone where mosses of pendulous forms gradually diminish. In the fully stocked fir stands, the gravelly or rocky forest-floor is usually covered with extensive dense carpets of mosses. These mossy carpets are frequently composed entirely of *Ptilium crista-castrensis*, or more often woven by a mixture of *Hylocomium proliferum* and *Pleurozium schreberi*. Under certain circumstances, *Mnium punctatum*, which is a hygrophilous upright form, alone forms pure patches of considerable extent, and thus characterizes the ground vegetation in the cold woods. However, this species is more often scattered or intermixed with the mosses just mentioned above in the fir forests or occasionally in hemlock stands distributed on the tops or ridges of some of the high mountains. Among those of common occurrence in moderately stocked woods or somewhat open areas in the subalpine regions are species of *Polytrichum, Grimmia, Rhacomitrium, Oncophorus* and *Ptychomitrium* growing chiefly on rocks. Besides, only a very limited number of species of mosses are usually found in sunny places. *Bryum argenteum* and a few species in Pottiaceae are the familiar and prominent examples.

Often almost nothing represents cryptogamic vegetation above the timber line except for a few species of mosses and lichens occurring sparsely on rocks of various dimensions. Among the mosses noteworthy are species of *Ulota, Grimmia*, and *Andreaea*.

According to what has just been stated, it is demonstrated that the distribution of floristic elements in the Formosan moss flora parallels that of the corresponding elements among the seed plants. This is especially noticeable with reference to the subalpine

and boreal mosses which occupy the same altitudinal zones as the subalpine and boreal conifers. Therefore it may be stated that the distribution of mosses is generally correlated with that of the vascular plants.

However, it must be noted that bryophytes frequently exhibit patterns different from their floristic counterparts of higher plants in distribution. Some species are found restricted to certain stations but others are commonly wide ranging mosses. A number of species of mosses may be found in the woods which are ecologically different from those with which they are usually associated. Consequently, some diversification of the distributional ranges of mosses from those of their related higher plants is found; this is particularly noticeable in regard to the altitudinal ranges of some tropical or subtropical forms of mosses occurring in Formosa. It is, of course, a matter of observation that mosses generally are more widespread than their commonly associated higher plants. Apparently, the divergence between the distributional ranges of the mosses and their floristic counterparts lies in the fact that mosses are more sensitive to micro-environmental factors, especially the relative humidity of the atmosphere prevailing over the microhabitat; in fact, this seems to be the limiting micro-environmental factor to the occurrence or distribution of mosses, a fact which undoubtedly accounts for the wider ranges of a majority of species of mosses.

Ecological Factors Influencing the Distribution of Mosses in Formosa

A thorough knowledge of brycecology is fundamental to a full understanding of bryology. The relations between the distributions of bryophytes and environmental factors have been occasionally noted or discussed in various bryological works by a number of bryologists. As far as is known, the various distribution patterns of mosses in Formosa are determined primarily by ecological relationships.

With regard to plant distribution,climate is generally classified into four components, and most fundamental among them is the temperature of the atmosphere. Next in importance to temperature comes moisture. Besides, light and wind are usually to be regarde as secondary. In Formosa the temperature conditions are always more or less at an optimum, and plant growth generally continues all the year round. However, the temperature values actually tend to be widely modified under the influence of the great number of lofty mountains since elevation of the land has the general effect of reducing the normal latitudinal values of temperature. Temperatures still play an important role in the latitudinal distributions of mosses and also are responsible, in part, for the presence of particular floristic elements in various elevational zones in Formosa.

Apparently, the moisture content of the air is of prime importance as far as the distribution of the mosses in Formosa is concerned. In general, rainfall is abundant but varies greatly with elevation as well as with topography. The high and continuous humidity favors the development of particularly luxuriant growth of epiphytic mosses in the mountain forests at intermediate elevations where mists and clouds prevail. Actually

over much of the slopes rainfall is extremely heavy and rainy days are very frequent. Apparently, the concentration of a vast number of species in the damp mountain forests between 1000 and 2500 m. is closely correlated with the prevalence of cloud and mists which is often a matter of topography together with wind. In connection with the moisture factor, the occurrence of mosses in great abundance in the woods is due to the fact that evaporation is significantly reduced because of the reduction of air movement, limited radiation, and low vapour pressure deficit. However, the writer is convinced that the moisture content or relative humidity of the atmosphere appears to be a fundamental, if not limiting, distributional factor, at least with regard to the local distribution of mosses in Formosa.

Among the epiphytic mosses many are found on the trunks of broad-leaved trees while others are characteristic of conifers. Furthermore, the distributional ranges of these mosses as well as the level at which the species of mosses occur on the trees are also correlated with a number of environmental factors. Accordingly, various patterns of distribution of mosses on the trees are usually recognized in the same forest community. In fact, the distribution of bryophytes on trees has attracted the interest of a great many bryologists, and works dealing with one or another of its phases have been published at various times. A number of factors have been investigated for correlation studies of the distribution of mosses on various trees. However, the occurrence of mosses on the trees as well as the restriction of some species to particular groups of arboreal species are believed to be correlated with bark factors, such as pH, texture, field moisture, water-holding capacity and rate of water absorption of the bark, each of which may impress a quite different pattern of distribution on the mosses. According to Billings and Drew (1938) the values of these factors decrease with height above the ground. Moreover, the zonation of bryophytic communities could be correlated with the changing water relationships of the bark. However, the matter in relation to the occurrence of mosses on a tree at different levels may not be quite so simple. Rather, these variations are biological reflections of the holocoenotic influence of the environmental conditions which appear to be combinations of relative humidity, light intensity, topography and bark factors prevailing over the microhabitats.

As regards the terrestrial mosses it may be said that some amount of soil is of primary necessity for their growth. In this connection, the importance of the edaphic factors in the distribution of mosses must be recognized. In fact, mosses occurring noticeably on limestone often exhibit anomalous distribution because of their specific edaphic requirement.

In reference to the discontinuous type of altitudinal distribution of certain species in Formosa, it is believed that the present distribution is a reflection of the climatic changes that have occurred on the island and, therefore, cannot be explained by the existing factors.

It has already been noted that the poverty of the occurrence of mosses in the lowlands is very pronounced because of the adversity of the environmental conditions. Moreover,

through the agency of man, especially in the destruction of the original vegetation over vast low-lying areas, it is very probable that some local indigenous low-altitude forms of mosses may have been exterminated, even though it is, of course, always difficult to be sure that any species has actually disappeared.

In view of what has been said, it would be evident that the occurrence of mosses at any station is related to climatic variations. Consequently, the local distribution of the mosses generally indicates the mosaic of the environmental conditions prevailing over the microhabitats, which are the products of the interaction of climatic, edaphic and biotic factors at each station.

Summary and Conclusions

Formosa offers excellent opportunities for the study of the various geobotanical problems because of the geographical position and the fundamental topographical features of the island. Tree growth is the prominent feature of the island; the mountain slopes remain primarlycovered by primeval or virgin forests of different types.

The island moss flora is particularly rich not only in species but also in genera. It possesses a high degree of endemism which would testify the antiquity of the island. The modern Formosan moss flora is demonstrated to be a complex mixture of species of great diversity in affinities.

In Formosa, the occurrence of mosses is so sparse in the lowlands that only a very limited number of species may be found. The greatest profusion of mosses occurs in evergreen damp woods on slopes between 1000 and 2500 m. A few species of mosses are characteristic of the alpine grassland, growing only in places where it is well exposed and free from the competition of grasses. Almost nothing represents cryptogamic vegetation above the timber line except for a few species of mosses and lichens occurring sparsely on rocks of various dimensions.

The distribution of mosses is generally correlated with that of the vascular plants, even though bryophytes frequently exhibit patterns different from their floristic counterparts of higher plants in distribution and are more widespread than their commonly associated higher plants. The distributional ranges of these mosses as well as the level at which the species of mosses occur on the trees are correlated with a number of environmental factors, and the moisture content or relative humidity of the atmosphere appears to be a fundamental distributional factor, at least with regard to the local distribution of mosses in Formosa.

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臺灣苔類植物之分佈

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臺灣近代苔藓植物的採集與研究始于 1864 年以後。最初由歐美植物園特派採集人員及英國駐臺外交官員等在濱海各地及交通較爲便利之淺山地區採集高等植物標本及搜集臺灣特產經濟觀賞植物的種子和苗木，並附帶採得一些苔藓植物標本。繼後于 1903 年始有法籍傳教士 Faurie 來臺大量採集苔藓植物標本，然採集地區則限於臺灣本島北部，即現今臺北縣屬區域。其後臺灣苔藓植物漸受日本植物學家之重視；時有日本植物學者來臺採集標本，初係以採集種子植物爲主而獲得較多的苔藓植物標本。再後于 1930 年代以後日本苔藓植物學者如野口及堀川氏等均曾專程先後數度來臺調查並採集苔藓植物標本。臺灣光復以後，植物調查工作雖然亦有開展，本省林業試驗所且曾先後兩度派遣森林調查隊入山調查，而且調查範圍遍及臺灣本島各地山區，然而苔藓植物並未受人重視。近年臺灣大學楊寶瑜教授雖曾發表有關臺灣蘚類植物 (liverworts) 之研究報告，惟苔藓植物之搜集工作始終沒有正常開展，研究工作幾乎完全停頓。

再者今日以前中外學者所發表的有關臺灣苔藓植物的報告，概限於分類方面，且多係零星片段的報告，分佈生態記錄亦不具備。至於臺灣本島全地區苔藓植物生態綜合研究與地理分佈方面之資料則完全沒有。

本篇係就著者四年來在臺灣本島各地區採集觀察並參攷多種文獻資料和鑑訂實際標本的初步報告。限於個人學識淺薄，遺漏缺欠與謬誤之處實所難免，尙希各方先進與同好諒之教之。