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Altitudinal zonation of Bryophytes on the Huon Peninsula, Papua New Guinea. A floristic approach, with phytogeographic considerations

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Abstract. The study is based on the major part of the bryophyte material collected during the Koponen-Norris expedition on the Huon Peninsula, Papua New Guinea, in 1981. Only taxa which were collected at least twice are included. Five altitudinal zones, the boundaries of which are indicated by discontinuities in the bryophyte flora, are distinguished: 0 - 300 m, 300 - 1200 m, 1200 - 2200(-2300) m, 2200(-2300) - 2800(-2900) m, and 2800(-2900) - 3400 m. These zones, each characterized by a typical species assemblage, are well in accordance with some earlier New Guinean zonation schemes based on the phanerogamic flora and vegetation. The most obvious correlations between bryophytes' altitudinal ranges on the Huon Peninsula and their general phytogeography are: New Guinean or Western Melanesian endemics, as well as Malesian endemics, are concentrated at relatively high altitudes (zones III-V); Asian - Oceanian and Asian - Oceanian - Australian taxa, notably mosses, are relatively strongly represented at low to moderate altitudes (zones I-III); species which have their main distribution in the northern hemisphere occur at high altitudes; 'cosmopolitan' species either have wide vertical ranges or are restricted to high altitudes.

Introduction

The altitudinal zonation of vegetation in the tropics is distinct and, in many regions, rather well documented (see, for example, Richards 1957: 346-368). The zones are mainly distinguished by changes in the phanerogam flora and the gross structure of the vegetation relative to altitude. Often the zone characterizations also include general observations on the abundance and species- richness of lower cryptogams, notably epiphytic ones, at different altitudes. Such general accounts of the zonation of the vegetation in New Guinea have been presented by Lane-Poole (1925), Pajmans (1976), Gressitt &

Nadkarni (1978), and Johns (1982). Robbins (1959) and Royen (1980) mainly dealt with the New Guinean mountain vegetation. The treatment of Australasian alpine bryophytes by Ramsay et al. (1986) must be mentioned in this connection, since it includes a list of the alpine mosses of New Guinea. Two studies by Seifriz (1923, 1924) on Mt. Gedeh, Java, have a bearing on the present study. In the former work he defined five vegetational 'subzones' above 4600 ft (1400 m) based on phanerogams, and in the latter reported that floristic and quantitative differences regarding mosses and lichens at different altitudes are also very profound. Despite certain lack of profoundness in Seifriz's

latter study - he was neither a bryologist nor a lichenologist - it clearly demonstrates that the altitudinal zonation of lower cryptogams closely follows that of higher plants and vegetation, and it can be considered a pioneer work in this respect.

It is currently a well-known fact that the bryophyte flora and vegetation in tropical lowland forests are poor, become richer with increasing altitude and reach their culmination in the so-called mossy forests - the terms cloud forests and mist forests have also been employed - which occur in the lower and upper montane zones (e.g. Richards 1984). The reasons for the bryological poverty of tropical lowland forests have been subject to some debate and disagreement, but it was quite convincingly pointed out by Frahm (1987), through measurements in the field and laboratory simulations, that the combination of high temperature and low light intensity is responsible for the phenomenon, since it does not allow sufficient net assimilation for bryophyte growth. With increasing altitude the mean temperature falls by about 0.4-0.7°C/100 m (Richards 1984) - lapse rates between 0.53-0.60°C have been given for the New Guinea mountains (Barry 1980) -, the tree canopy becomes lower and more open, allowing more light to penetrate to the forest interior, and the occurrence of clouds and mist become more frequent or even continuous. These factors together allow a more luxuriant bryophyte vegetation to develop.

Although numerous workers, in revisions of tropical taxa and in local or regional bryophyte floras, have given more or less detailed information regarding the altitudinal ranges of bryophytes, comprehensive and thorough studies on the altitudinal zonation of bryophytes in the paleotropical region are lacking. However, an elaborate study on the subject was carried out by Reenen & Gradstein (1983, 1984) on the Sierra Nevada de

Santa Marta, Colombia. Based on relevée analysis concerning species presence, substrate preference, and percentage cover of bryophytes, they distinguished five altitudinal bryophyte zones between 500-4100 m a.s.l. Their results are discussed in more detail in the Results and Discussion section below. Gradstein & Frahm (1987) presented a floristic study on the altitudinal zonation of mosses in NE-Peru and came up with 4 main zones two of which they further subdivided. Their results will be considered further below.

The present study surveys the altitudinal zonation of bryophytes on the Huon Peninsula, Papua New Guinea, mainly on a floristic basis. The reasons for such an approach to the problem are given below (see Materials and Methods). Some observed correlations and more or less well-defined regularities between the geographical distribution patterns of bryophytes and their altitudinal ranges on the Huon Peninsula are considered.

Materials and Methods

This study is based on the bryophytes (ca. 17500 specimens) collected by Prof. Timo Koponen (Helsinki) and Prof. Daniel H. Norris (Arcata) on the Huon Peninsula, Papua New Guinea, in 1981. The background and methods of the expedition, and introduction to the study area and its bryological exploration were presented by Koponen & Norris (1983a). At present, 31 papers under the title Bryophyte flora of the Huon Peninsula, Papua New Guinea have been published in *Acta Botanica Fennica* and *Annales Botanici Fennici*. Despite the title of these papers, the bryophyte floras of Western Melanesia (i.e. West Irian, Papua New Guinea, and the Solomon Islands) are also treated.

On the Huon Peninsula 55 moss families (Koponen pers. comm.) and 39 hepatic families (Grolle & Piippo 1984b) are

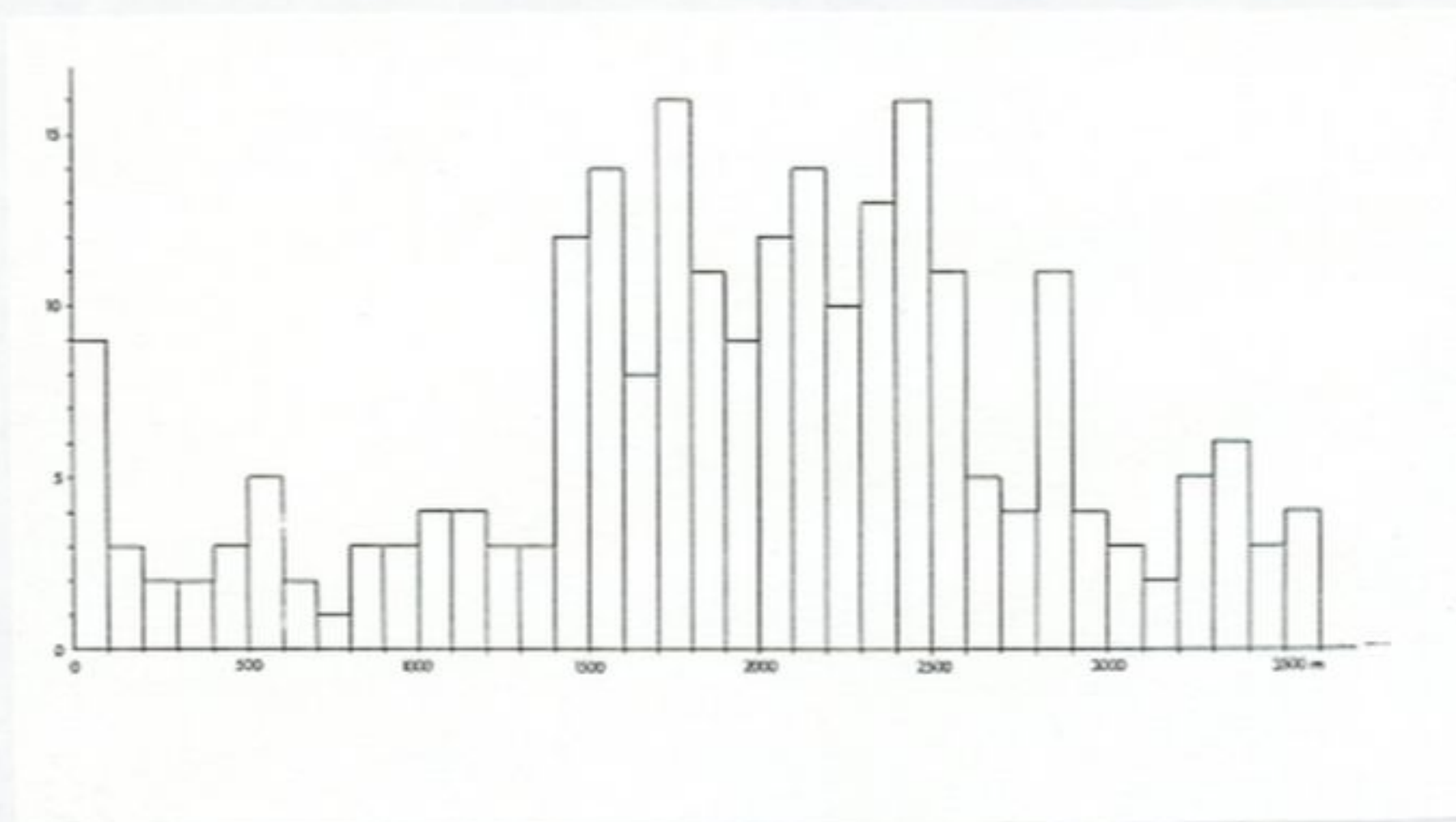


Fig. 1. The altitudinal distribution of the collecting sites of the Koponen-Norris expedition on the Huon Peninsula, Papua New Guinea, in 1981 (see Koponen & Norris 1983a). Horizontal axis: Altitude (meters above sea level). Vertical axis: Numbers of collecting sites.

quently, the present study must essentially be a floristic one, because the material and ecological information available does not allow quantitative and statistical methods to be applied, such as those utilized in Reenen & Gradstein's (1983) study.

The collecting methods of the Koponen-Norris expedition on the Huon Peninsula may result in some misinterpretation of data in the present study. First, bryophytes were not collected above 3600 meters (Koponen & Norris 1983a). This means that altitudinal amplitudes for taxa which were collected uppermost or only at ca. 3500-3600 meters can not be determined reliably. Second, the collecting intensity at different altitudes was not constant, that implies that we may have a better knowledge of the bryophyte flora at the altitudes where collecting was more intensive. However, the influence of the latter source of error is diminished by the fact that

collecting was less intensive at altitudes which a priori are known to be bryologically poorer, viz. in lowland forests on the one hand and above ca. 3000 meters on the other (cf. Fig. 1).

The primary working hypothesis used in this study is that if there is an altitudinal zonation (instead of a complete continuum) of bryophytes on the Huon Peninsula, the limits of the zones will be indicated by floristic discontinuities (cf. Gradstein & Frahm 1987). Accordingly, the altitudinal limits of the included taxa are determined. The numbers of these limits along the altitudinal gradient are graphed separately for hepatics and mosses, and for the groups together. In these graphs, the altitudinal boundaries of the taxa have been rounded off to the nearest even hundred; if the lower limit of a taxon was at, say, 650 m, it has been rounded off to 600 m, and if the upper limit of a taxon was at, say, 3250 m, it has been rounded

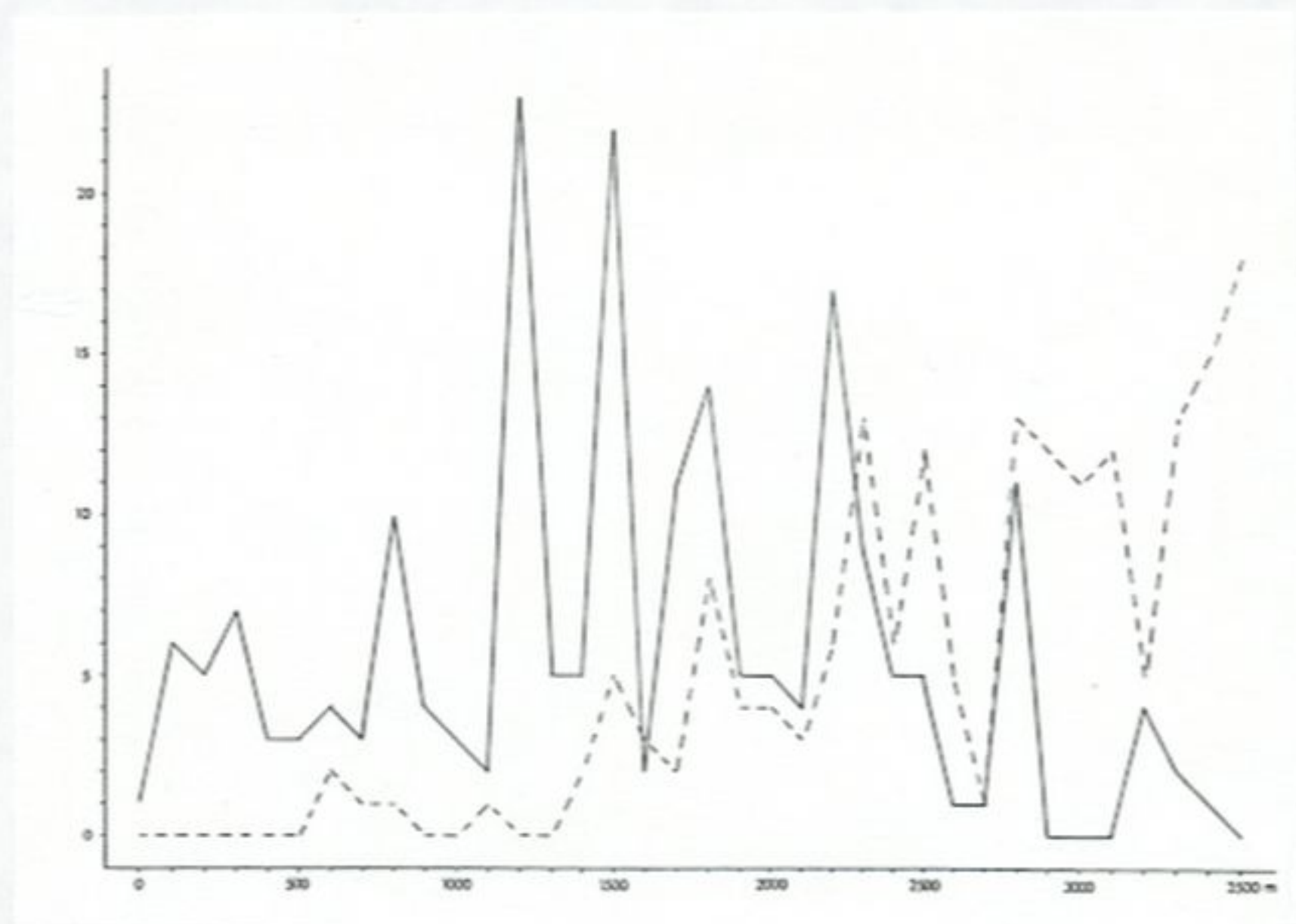


Fig. 2. The altitudinal distribution of lower (solid line) and upper (broken line) boundaries of hepatic taxa on the Huon Peninsula, Papua New Guinea. Horizontal axis: Altitude (meters above sea level). Vertical axis: Numbers of the altitudinal boundaries of the hepatic taxa.

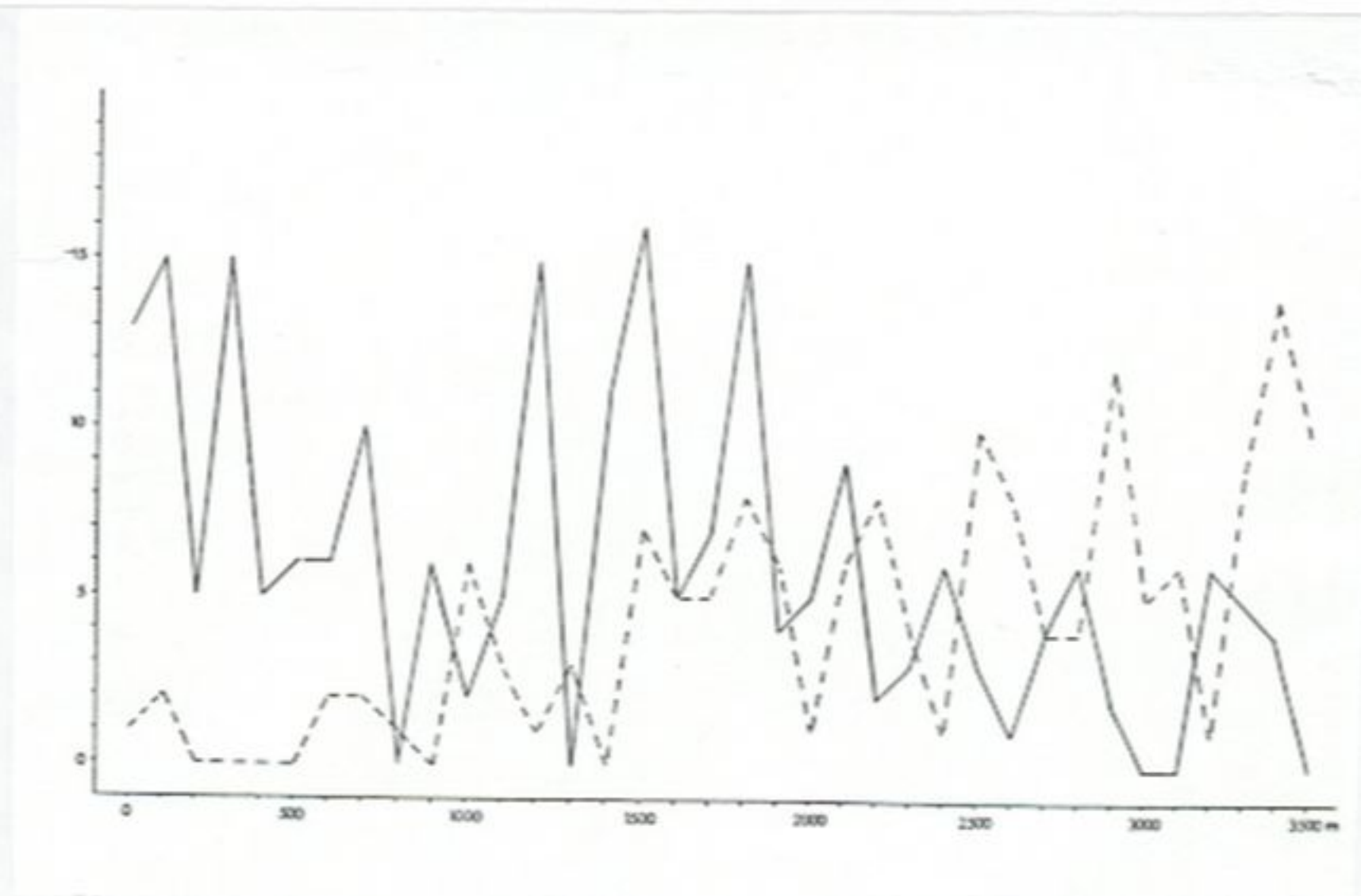


Fig. 3. The altitudinal distribution of lower (solid line) and upper (broken line) boundaries of moss taxa on the Huon Peninsula, Papua New Guinea. Horizontal axis: Altitude (meters above sea level). Vertical axis: Numbers of the altitudinal boundaries of the moss taxa.

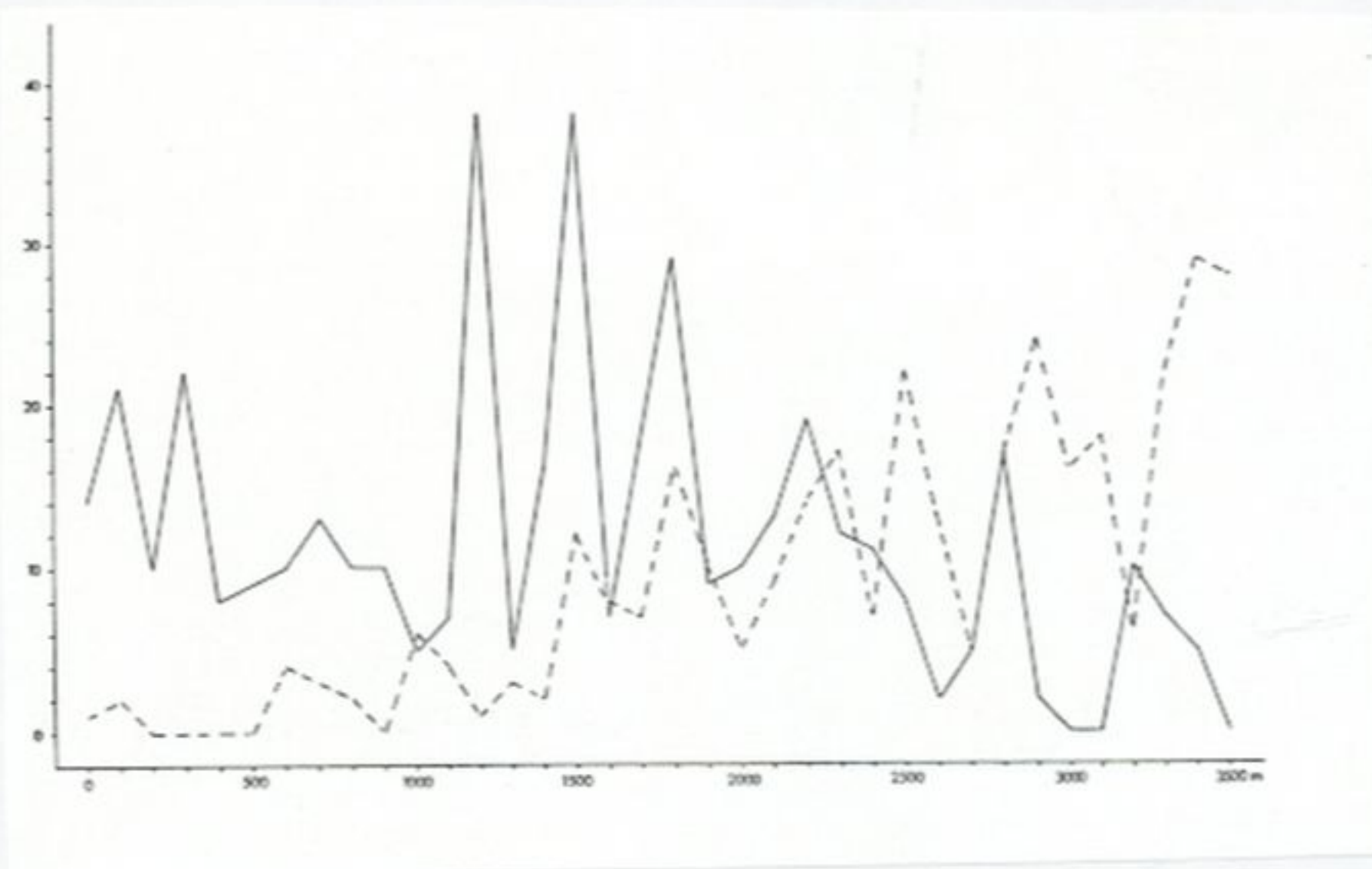


Fig. 4. The altitudinal distribution of lower (solid line) and upper (broken line) boundaries of bryophyte taxa on the Huon Peninsula, Papua New Guinea. Horizontal axis: Altitude (meters above sea level). Vertical axis: Numbers of the altitudinal boundaries of the bryophyte taxa.

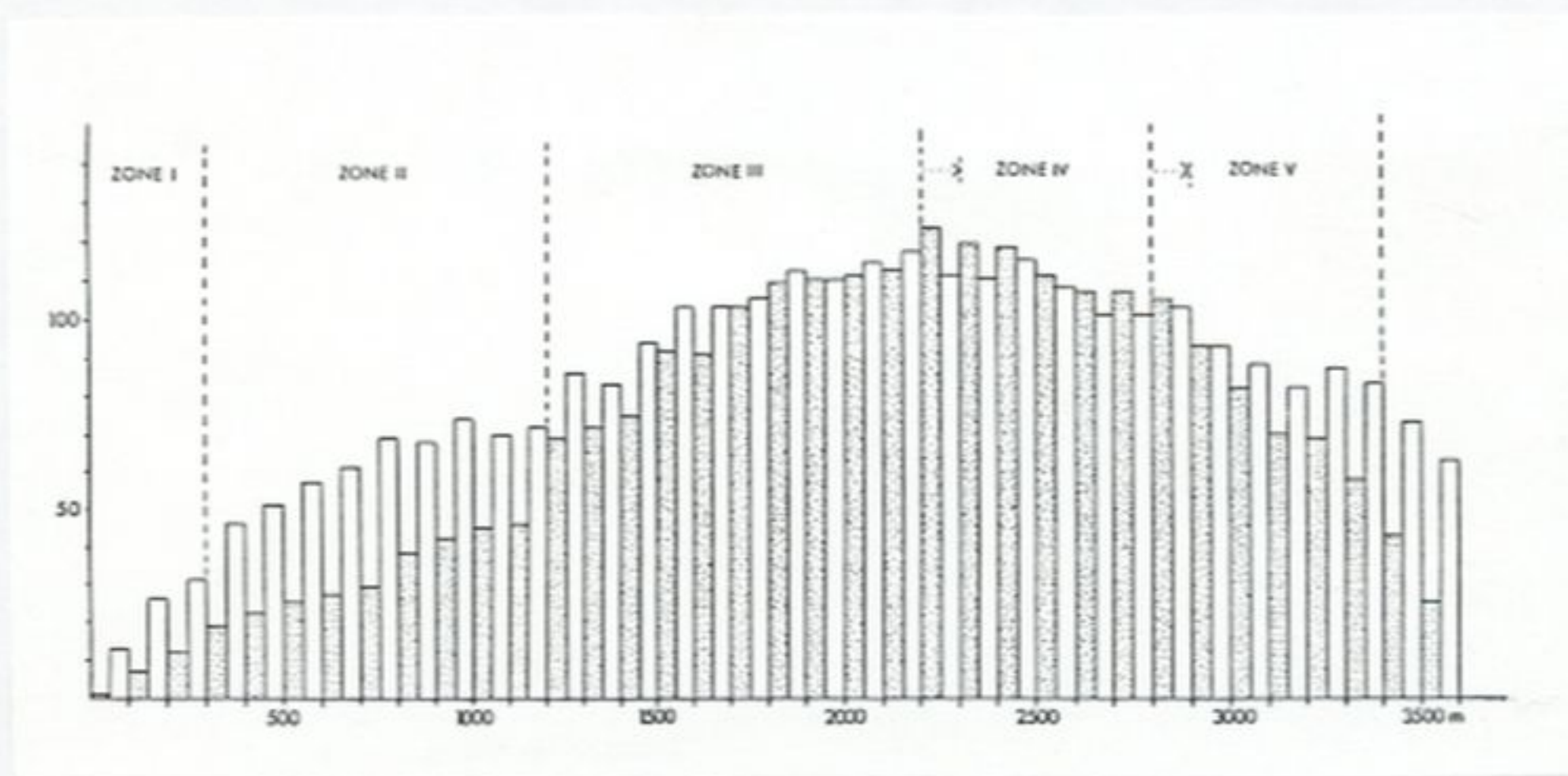


Fig. 5. The altitudinal distribution of hepatic (stippled bars) and moss (plain bars) taxa on the Huon Peninsula, Papua New Guinea. Only taxa which were collected at least twice at different altitudes are included. Horizontal axis: Altitude (meters above sea level). Vertical axis: Numbers of taxa.

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Results and Discussion

A. Altitudinal zones and their boundaries on the Huon Peninsula

The altitudinal ranges of all taxa used in this study are presented in Table 10. The numbers of lower and upper altitudinal limits of hepatic and moss taxa at different altitudes on the Huon Peninsula are graphed in Figs. 2 and 3, respectively. The numbers of these limits for the combined groups are graphed in Fig. 4.

Fig. 5 presents all of the included

bryophyte taxa along the altitudinal gradient. In general terms, the diversity increases from sea level and is highest at 2200-2300 m in the mossy forests. This implies that below approximately 2200 m the lower limits of taxa are more numerous, and apparently also more clearly concentrated at particular altitudes, than the upper ones, whereas above that altitude the gradual impoverishment of the bryoflora implies a higher amount of upper limits (Figs. 2- 4). It logically follows from this, that at lower altitudes the boundaries of the zones must mainly be based on the lower limits of individual taxa, but higher up - above 2200 m, that is - mainly upper limits should be used in the definition of the zones.

The altitudinal limits of individual hepatic taxa are most strongly concentrated at 300, 800, 1200, 1500, 1800, 2200 (- 2300), 2500, 2800, and 3400 m (Fig. 2), and those of individual moss taxa at 300, 700, 1200, 1500, 1800, 2100 (-2200), 2500, and 2900 m (Fig. 3). From Fig. 4 we observe that, when the data for both groups are combined, the highest numbers of altitudinal limits occur at 300, (800), 1200, 1500, 1800, (2200-2300), 2500, 2800-2900, and 3400 m. Although the upper limits of hepatics are still more numerous at 3500 than at 3400 m (Fig. 2), the relevance of this is doubtful (see Materials and Methods section above).

It is obvious that some of the peaks in Figs. 2-4 indicating high concentrations of altitudinal limits are artificial, caused by higher intensity of collecting at some altitudes than at others. For example, at 1700-1800 and 2400-

2500 m collecting was pursued at 16 sites, at 1500-1600 and 2100-2200 m at 14 sites. On the other hand, at 1600-1700 and 1900-2000 m collecting was less intensive, and both of these altitudes show low numbers limits. It is not easy to determine the effect on the present study of varying collecting intensities. However, it seems reasonable to hypothesize that it has a more pronounced effect in the environments which have a rich flora, such as the mossy forests, and a weaker effect in floristically poorer habitats, such as tropical lowland forests. Based on this assumption and on the previous literature, I reject as potential zone boundaries the altitudes at which the high concentrations of limits of individual taxa appear to be most artificial, namely, 1500, 1800, and 2500 m.

Because hepatics and mosses in the present data show a similar pattern of altitudinal zonation, there is no reason to treat them separately. Of course, this does not mean that some zones could not be partly characterized by a richer hepatic flora or the abundance of epiphytic mosses, but simply that it would be pointless to distinguish separate, independent zones for hepatics and mosses.

ZONE I, 0 - 300 m.

This zone is equivalent to Lane-Poole's (1925) 'Lowland forests' (see also Richards 1957: 349), and it also has exactly the same upper boundary. This lowland area embraces several different environments. These include mangroves, beach ridges and flats, swamps (saline and brackish as well as fresh water ones), alluvial

plains and fans, and typical tropical rain forests (with several canopy layers and buttressed trees, abundant lianas and vascular epiphytes). On the Huon Peninsula extensive alluvial plains and fans are restricted to a narrow belt in the western part of the southern coast (around Lae), the remaining coast being mostly formed of foothills, low mountains and a belt of grassland along the northern coast (Paijmans 1975).

During the Koponen-Norris expedition, bryophyte collecting was not very intensive below 300 m (cf. Fig. 1), but several different environments at these altitudes were visited (Koponen & Norris 1983a). As might be expected, the bryophyte flora is poor, especially in hepatics (Fig. 5). In the present material, only *Calymperes tenerum*, *Leucophanes glaucum*, and *Pinnatella mariei* are restricted to below 300 m. Another species which obviously occurs only in this zone is the swamp-dweller *Exodictyon incrassatum* (Ellis 1985, Enroth 1990). Mosses which have their lower limit at or near sea level include, some Calymperaceae (*Calymperes dozyanum*, *C. taitense*, *Mitthyridium obtusifolium*), Leucobryaceae (*Exostratum blumei*, *Octoblepharum albidum*), Neckeraceae (*Neckeropsis gracilentata*, *Pinnatella kuehliana*, *P. mucronata*, *P. nana*), Pottiaceae (*Barbula arcuata*, *B. indica*, *B. javanica*, *B. subcomosa*, *Hyophila involuta*, *Oxystegus crassicosatus*) and Thuidiaceae (*Pelekium bifarium*, *P. velatum*, *Thuidium plumulosum*). The most strongly represented hepatic family is the Radulaceae, with seven species (*Radula anceps*, *R. apiculata*, *R. javanica*, *R. koponenii*, *R. nymanii*,

Table 1. The numbers of New Guinean/Western Melanesian endemic bryophyte taxa in each altitudinal zone and their percentages of the total numbers of New Guinean/Western Melanesian endemics.

zone	I	II	III	IV	V	3400 m-
Hepatics (70 taxa)	2(3%)	7(10%)	32(46%)	39(56%)	29(41%)	15(21%)
Mosses (54 taxa)	2(4%)	6(11%)	31(57%)	23(43%)	23(43%)	16(30%)
Total 124 taxa	4(3%)	13(10%)	63(51%)	62(50%)	52(42%)	31(25%)

Table 2. The numbers of Malesian endemic bryophyte taxa in each altitudinal zone and above 3400 m, and their percentages of the total numbers of the Malesian endemics in Western Melanesia.

zone	I	II	III	IV	V	3400 m-
Hepatics (34 taxa)	0	6(18%)	27(79%)	29(85%)	21(62%)	6(18%)
Mosses (35 taxa)	2(6%)	7(20%)	17(49%)	18(52%)	22(63%)	13(39%)
Total (69 taxa)	2(3%)	13(19%)	44(64%)	47(68%)	43(62%)	19(28%)

Table 3. The numbers of SE-Asian bryophyte taxa in each altitudinal zone and above 3400 m, and their percentages of the total numbers of the SE-Asian taxa in Western Melanesia.

zone	I	II	III	IV	V	3400 m-
Hepatics (22 taxa)	1(5%)	8(36%)	14(64%)	15(68%)	11(50%)	7(32%)
Mosses (33 taxa)	4(13%)	13(41%)	28(85%)	18(56%)	8(25%)	4(13%)
Total (55 taxa)	5(9%)	21(38%)	42(76%)	33(60%)	19(35%)	11(20%)

Table 4. The numbers of Asian-Oceanian bryophyte taxa in each altitudinal zone and above 3400 m, and their percentages of the total numbers of the Asian-Oceanian taxa in Western Melanesia.

zone	I	II	III	IV	V	3400 m-
Hepatics (46 taxa)	5(11%)	17(37%)	41(89%)	28(61%)	22(48%)	11(24%)
Mosses (28 taxa)	13(46%)	23(82%)	22(79%)	13(46%)	7(25%)	3(11%)
Total (74 taxa)	18(24%)	40(54%)	63(85%)	41(55%)	29(39%)	14(19%)

Table 5. The numbers of Asian-Oceanian-Australian bryophyte taxa in each altitudinal zone and above 3400 m, and their percentages of the total numbers of Asian-Oceanian-Australian taxa in Western Melanesia.

zone	I	II	III	IV	V	3400 m-
Hepatics (10 taxa)	1(10%)	6(60%)	10(100%)	7(70%)	6(60%)	0
Mosses (21 taxa)	5(24%)	13(62%)	16(76%)	10(48%)	3(14%)	1(5%)
Total (31 taxa)	6(19%)	19(61%)	26(84%)	17(55%)	9(29%)	1(3%)

Table 6. The numbers of paleotropical bryophyte taxa in each altitudinal zone and above 3400 m, and their percentages of the total number of paleotropical taxa in Western Melanesia.

zone	I	II	III	IV	V	3400 m-
Hepatics (8 taxa)	1	1	5	6	4	3
Mosses (12 taxa)	4	9	8	4	4	3
Total (20 taxa)	5(25%)	10(50%)	13(65%)	10(50%)	8(40%)	6(30%)

Table 7. The numbers of pantropical bryophyte taxa in each altitudinal zone and above 3400 m, and their percentages of the total number of pantropical taxa in Western Melanesia.

zone	I	II	III	IV	V	3400 m-
Hepatics (6 taxa)	2	4	5	5	0	0
Mosses (10 taxa)	3	4	7	6	4	2
Total (16 taxa)	5(31%)	8(50%)	12(75%)	11(69%)	4(25%)	2(13%)

Table 8. The numbers of globally widely distributed bryophyte taxa in each altitudinal zone and above 3400 m, and their percentages of the total number of globally widely distributed taxa in Western Melanesia.

zone	I	II	III	IV	V	3400 m-
Hepatics (4 taxa)	1	2	3	3	4	1
Mosses (14 taxa)	2	6	12	11	7	4
Total (18 taxa)	3(17%)	8(44%)	15(83%)	14(78%)	11(61%)	5(28%)

R. tjibodensis, *R. vrieseana*). In addition, there occur few Frullaniaceae (*Frullania apiculata*, *F. ericoides*, *F. multilacera*) Geocalycaceae (*Heteroscyphus argutus*, *H. coalitus*), and *Dumortiera hirsuta* of the Wiesnerellaceae.

ZONE II, 300 - 1200 m.

I have accepted 1200 m as the demarcation altitude between zones II and III, because its high number of lower limits of individual bryophyte taxa is not caused by high collecting intensity. Instead, collecting at 1500 m was rather intensive, and the peaks in Figs. 2-4 at that altitude are probably artifacts. However, it should be noted that Lane-Poole (1925) placed the upper limit of his 'Foothill forests' - which I consider roughly equivalent to my zone II - at 4500-5500 ft (approximately 1350-1650 m).

Lane-Poole's (1925) account of the 'Foothill forests' gives the following general characters: The forests are not as tall as, and are less hygrophytic than, the lowland rain forests, which may be due to the lack of retention of moisture on the steeper slopes; buttressed trees are fewer; lianas and vascular epiphytes, notably ferns in the crowns of trees, are clearly less abundant; the ground-cover is mainly composed of ferns and *Elatostema* spp. (Urticaceae); the characteristic tree is *Quercus junghuhnii*; conifers (*Podocarpus*, *Araucaria*) are scarce, but become somewhat more frequent towards the upper boundary.

As can be seen from Fig. 5, the bryophyte flora in zone II is richer

than in zone I, and becomes gradually more so with increased altitude. At the lower boundary of the zone, the moss flora, suddenly becomes more diverse: 17 species have their lower limits at 300 m. As examples may be mentioned some Neckeraceae (*Himantocladium plumula*, *Homaliodendron flabellatum*, *Neckeropsis lepineana*) and Pterobryaceae (*Calypsothecium recurvulum*, *C. urvilleanum*, *Garovaglia angustifolia*, *G. elegans*, *G. powellii*). Mosses also remain more numerous than hepatics throughout the zone. A distinct feature of this zone is the strong representation of the Calymperaceae. Species such as *Calymperes afzelii*, *C. strictifolium*, *Syrrophodon muelleri*, and *Mitthyridium fasciculatum* are exclusively, or almost so, restricted zone II. Other taxa not found outside zone II are *Plagiochila longispica*, *Radula multiflora* var. *reflexilobula*, *Fissidens obscurirete*, *Aerobryidium crispifolium*, *Aerobryopsis leptostigmata*, and *Himantocladium plumula*.

ZONE III, 1200 - 2200(-2300) m.

The lower limit of zone III is marked by a relatively strong increase of bryophyte taxa, notably hepatics. Several Frullaniaceae (*Frullania carrii*, *F. curvistipula*, *F. epiphylla*, *F. junghuhniana*, *F. prominula*, *F. subnigricaulis* var. *subtruncata*) and Plagiochilaceae (*Plagiochila cymata*, *P. loriana*, *P. odorata*, *P. tamiensis*, *P. trapezoidea*, *P. velata*) do not occur below this altitude. In addition to these, 12 species, belonging to the families Geocalycaceae, Jungermanniaceae, Lepidoziaceae, Lophoziaceae, Pleuroziaceae, Schistochilaceae,

and Trichocoleaceae have their lower boundaries here. Of the mosses which appear in the flora at 1200 m (13 taxa) may be mentioned *Campylopodium medium*, *Papillaria fuscescens*, *Pinnatella anacamptolepis*, *Pogonatum neesii*, *Elmeriobryum philippinensis*, and *Thuidium contortulum*. Hepatics more or less restricted to zone III include *Tylimanthus saccatus*, several Frullaniaceae, *Heteroscyphus wettsteinii*, *Jungermannia hasskarliana*, *Notoscyphus lutescens*, *Psiloclada clandestina*, *Telaranea kaindina*, *T. trisetosa*, *Porella grollei*, and *P. viridissima*. Mosses not encountered outside this zone are *Syrrhopodon japonicus*, *S. tristichus*, *Brotherobryum undulatifolium*, *Campylopodium medium*, *Microdus miquelianus*, *Fabronia curvirostris*, *Himantocladium submontanum*, *Pinnatella anacamptolepis*, *Pogonatum neesii*, and *Pyrrhobryum latifolium*.

The upper limit of zone III coincides closely with that of Lane-Poole's (1925) "Midmountain forests" (7500 ft, approximately 2300 m). At 2200 m both hepatics and mosses reach their peak, in the sense that the number of taxa is higher there than at any other altitude. According to Koponen & Norris (1983a), mossy forests occur between 1700-3300 m on the Huon Peninsula, and it is not surprising that the culmination point of the bryophyte flora and vegetation lies within these forests. It should be remembered, however, that since the development of mossy forests is dependent on the more or less continuous occurrence of mist they do not form a distinct and uniform

altitudinal zone. The topography, exposure of the slopes, prevailing wind direction, among other things determine the terms for their presence.

According to Lane-Poole (1925), the "Midmountain forests" are dominated by species of *Quercus* and several conifers, such as *Araucaria cunninghamii*, *Podocarpus spp.* and *Phyllocladus spp.* As a whole, there are fewer tree species than at the lower altitudes, and buttressed trees are entirely absent; additionally, "the ground is decidedly mossy, and the trunks and branches carry moss and lichen in crannies and nooks." (Lane-Poole 1925:221).

In general bryological terms zone III may be characterized by a gain in hepatic diversity and abundance (Frullaniaceae, Plagiochilaceae, Lepidoziaceae, Schistochilaceae), and, near the upper limit of the zone, hepatics outnumber mosses. A few large moss families, such as the Bryaceae, Dicranaceae, Fissidentaceae, and Meteoriaceae, also become more frequent and abundant. It is noteworthy that the Calymperaceae are very scarce in the upper parts of the zone. Of the species included in this study, only *Syrrhopodon prolifer* was found as high as 2400 m. The more favorable temperature/light intensity ratio, and the locally continuous dampness and occurrence of mist enhance the growth of a luxuriant and rich bryophyte vegetation.

ZONE IV, 2200(-2300) - 2800(-2900) m.

As Figs. 4 and 5 demonstrate, 2200-2300 m is the altitude where the

number of bryophyte taxa begins to decline; at 2300 m the number of the upper limits of individual taxa, notably hepatics (Fig. 2), for the first time clearly exceeds the number of the lower limits. It may be supposed that at this altitude some physical factor, or a combination of physical factors, becomes unfavorable for many bryophytes which thrive lower down on the mountains. The most obvious physical factor to restrict the growth of bryophytes at these moderately high altitudes is the lower average temperature.

As mentioned previously, Koponen & Norris (1983a) give an altitudinal range of 1700-3300 m for the mossy forests on the Huon Peninsula, and zone IV is completely within this range. However, the environments of the collecting sites of the Koponen-Norris expedition between 2200-2900 m vary from open grasslands and treefern savannahs to well developed mossy forests; in fact, only 15 of the numerous sites were described as mossy forests or elfin forests/montane rainforests approaching mossy forests.

A number of features characterize zone IV. The Dicranaceae and the Bryaceae are well represented. Members of the Polytrichaceae (*Dawsonia* spp., for example) become more abundant (*Polytrichum juniperinum* occurs lowermost at 2450 m). The Calymperaceae is virtually absent. The Neckeraceae is represented only by *Homaliodendron flabellatum*. The Leucobryaceae is represented only by two species, *Leucobryum sanctum* and *L. javense* (up to 2550 and 2900 m, respectively). The Pterobryaceae and the

Meteoriaceae are very scarce. The Thuidiaceae become scarce towards the upper boundary. Most remarkably, *Fissidens* spp. do not occur at all above the upper boundary of zone IV, and only *Fissidens plagiochiloides*, *F. strictulus* and *F. taxifolius* reach 2900 m. Mosses restricted to zone IV include *Leptobryum pyriforme*, *Braunfelsia enervis*, *Dicranodontium fleischerianum*, *Fissidens plagiochiloides*, *Dawsonia beccarii*, and *Pogonatum subtortile*. It must also be mentioned that the monotypic *Orthothuidium* (*O. curtisetum*) occurs between 2100-2900 m, and is therefore nearly restricted to this zone.

As regards hepatics, the Frullaniaceae, Geocalycaceae, Lepidoziaceae, and Plagiochilaceae are well represented. The Radulaceae become scanty, especially towards the upper boundary, and only 6 species out of the 21 included in the study occur above 2900 m. Hepatics which have their lowermost occurrences at 2200-2300 m are *Isotachis armata*, eight *Frullania* species, *Jungermannia diversiclavellata*, *J. stephaniai*, *J. herzogiana*, *Lepidozia bursifera*, *L. borneensis*, *L. holorrhiza*, *Zoopsidella caledonica*, *Chandonanthus pilifer*, *Jensenia decipiens*, *Plagiochila tecta*, *Plagiochilion braunianum*, *Pseudolepicolea grolleana*, *Radula madagascariensis*, *R. ovalilobula*, and *Schistochila schulzei*. A list of the hepatics not found outside zone IV includes *Frullania armatifolia*, *F. irregularis*, *F. papillata*, *F. pauciramea* var. *pauciramella*, *F. seriatifolia*, *F. subcaduca*, *F. subdentata*, *F. van-*

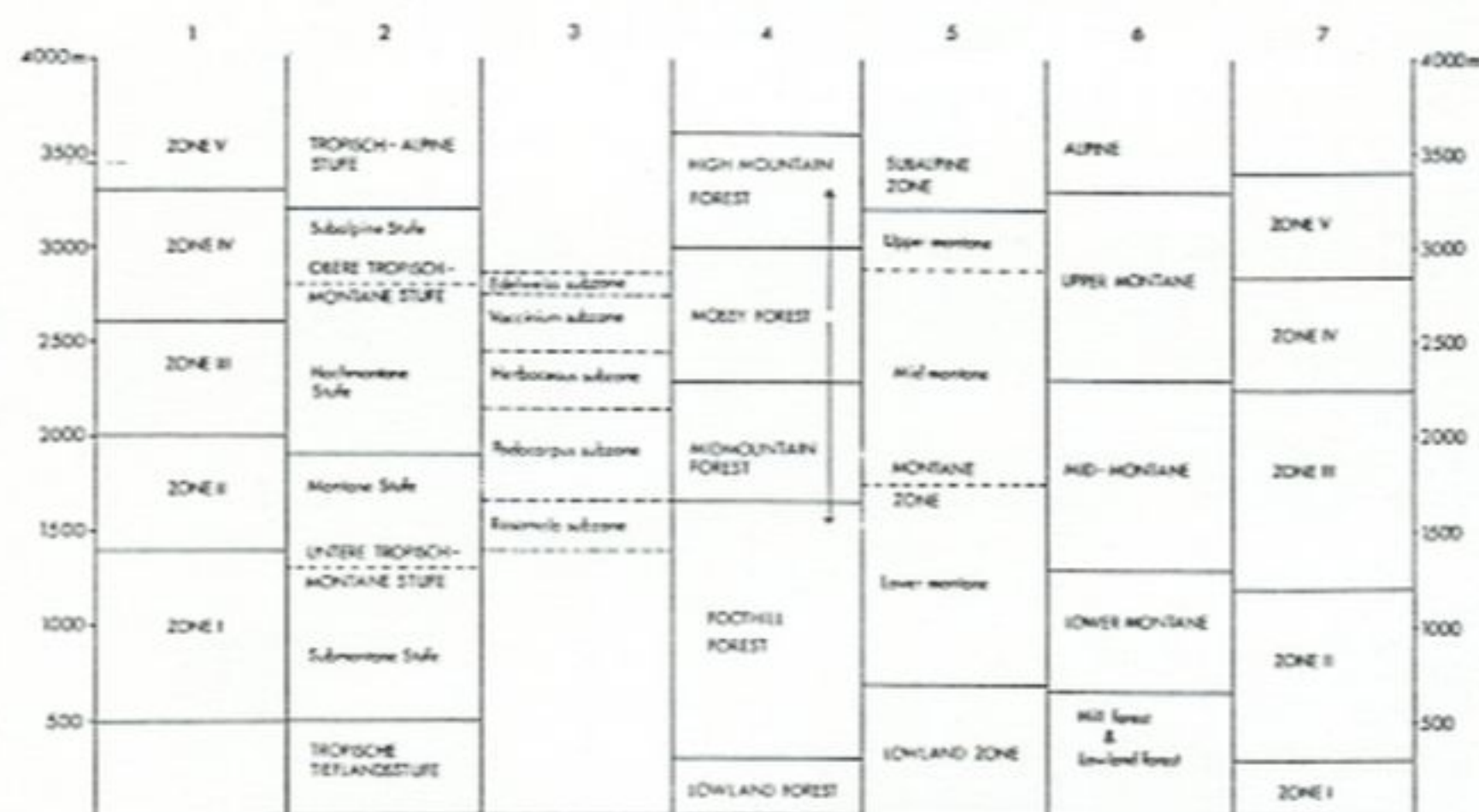


Table 9. The vertical zonation of vegetation on tropical mountains according to different authors. 1: Reenen & Gradstein 1983 (Colombia). 2: Gradstein & Frahm 1987 (Peru). 3: Seifrizz 1923, 1924 (Mt Gedeh, Java). 4: Lane-Poole 1925 (eastern New Guinea; the absolute altitudinal range of the mossy forest is indicated by arrows). 5: Johns 1982 (New Guinea). 6: Gressitt & Nadkarni 1978 (Papua New Guinea). 7: Present study (Huon Peninsula, Papua New Guinea). Capitals denote main zones, small letters subzones. 1, 2 and 7 based on bryophytes, 3-6 mainly on phanerogams.

lower limit of alpine vegetation, since some of the collecting sites at or above that altitude (along transect 6) were described as 'alpine grasslands' by Koponen & Norris (1983a). The 3400 m boundary coincides with the lower limit (3300 m) of the 'open páramo' on the Sierra Nevada de Santa Marta in Colombia (Reenen & Gradstein 1983), and the lower limit (3200 m) of the 'Tropisch alpine Stufe' in Peru (Gradstein & Frahm 1987). Consequently, my zone V apparently corresponds to the latter authors' 'Subalpine Stufe' between 2800-3200 m, and to the former authors' zone IV.

It should be noted that the studies in Colombia and Peru are based on a single transect along a mountain slope, whereas the Huon Peninsula material was collected at 16 separate transects on a number of mountain ranges (fig. 4 in Koponen & Norris 1983a). Hence, the present

study displays an average zonation in the study area, rather than a zonation on any particular mountain. Although Seifrizz's (1924) study on the altitudinal distribution of lichens and mosses on Mt Gedeh, Java, concerned only five 'subzones' between 1400-2850 m (4600-9400 ft), the bryological aspect is briefly reviewed here. The 'Rasamala subzone' (1400-1700 m, 4600-5500 ft) and the 'Herbaceous subzone' (2150-2450 m, 7000-8000 ft) are poor in bryophytes, whereas the 'Podocarpus subzone' (1700-2150 m, 5500-7000 ft) and the 'Vaccinium subzone' (2450-2750 m) are bryologically rich. According to Seifrizz (1924), there is a striking difference in the life-forms of mosses between the latter two subzones: in the *Podocarpus* subzone 'Every tree is festooned with pendent mosses', whereas in the *Vaccinium* subzone '...the mosses are compact tufted forms clinging close to the tree trunks, and forming thick reeking wet

The upper boundary of zone V, at 3400 m, should perhaps be recognized with some reservations (see Materials and Methods), and it is possible that the zone is wider than is defined here. The occurrence of a zone boundary at 3400 m is supported by the fact that a few species were collected lowermost at that altitude (*Marsupella revoluta*; *Holomitrium obliquum*, *Ditrichum sericeum*, *Rhacocarpus alpinus*, *R. purpurascens*) and the lowermost collecting sites defined as 'alpine grasslands' by Koponen & Norris (1983a) were at 3400 m. The species not common above 3400 m are rather numerous: the hepatics *Southbya grollei*, *Reboulia hemisphaerica*, *Frullania reflexistipula*, *Herbertus armitanus*, *Triandrophyllum heterophyllum*, *Jungermannia appressifolia*, *Lepidozia hasskarliana*, *L. holorrhiza*, *Plagiochila tecta*, *Schistochila nymanii*, *S. sciurea*, *Trichocolea tomentella*, and *Dumortiera hirsuta*; and the mosses *Anomobryum bulbiferum*, *A. hyalinum*, *Bryum wabagense*, *B. argenteum*, *Buxbaumia javanica*, *Dicranum armitii*, *D. blumii*, *Homaliodendron flabellatum*, *Dawsonia longifolia*, *Pogonatum cirratum*, *Leptodontium aggregatum*, *Timmiella anomala*, *Calypsothecium urvilleanum*, *Trachyloma indicum*, *Rhizogonium hattorii*, and *R. lamii*.

The impoverishment of the hepatic flora in zone V is clearly stronger than that of the moss flora (Fig. 5). For example, of the 46 taxa of *Frullania* included in this study, 32 occur only below this zone, and only 6 reach above 3400 m; 14 *Plagiochila* species out of 26 are represented in this zone, but only 5

above it; the Radulaceae practically vanish approximately at 3100-3250 m, just one (*Radula tjibodensis*) being encountered above 3400 m. Of the mosses, the Bryaceae, Dicranaceae, Ditrichaceae, Polytrichaceae, Pottiaceae, and perhaps also the Rhizogoniaceae are well represented. The Meteoriaceae is scarce - *Floribundaria floribunda*, *F. sparsa*, and *Meteorium buchananii* are present but not common - and vanish completely at 3250 m; the highest occurring Neckeraeae, *Homaliodendron flabellatum*, vanishes at 3350 m. Only 3 Pterobryaceae are present: *Garovaglia plumosa* is not found above 3100 m, and *Calypsothecium urvilleanum* and *Trachyloma indicum* disappear from the flora at the upper boundary of the zone.

Zone V apparently coincides in part with Lane-Poole's (1925) 'High mountain forests', but it also embraces the highermost mossy forests. Lane-Poole placed the lower limit of the 'High mountain forests' at 3050-3350 m (10000-11000 ft). The forest is taller than the mossy forest and dominated by conifers (*Dacrydium*, *Libocedrus*, *Phyllocladus*, *Podocarpus*). The climate is drier than in the lower 'cloud belt', which, along with the still lower mean temperatures, causes an impoverishment of the bryoflora. In the upper parts of zone V and above it forests are patchy and give way to alpine grasslands and heaths. This change in the vegetation is accompanied by an increase in the number of terrestrial and saxicolous bryophytes, such as numerous Bryaceae, Ditrichaceae and Polytrichaceae, and a strong

decrease in epiphytic bryophytes.

Table 9 presents a comparison of different authors' views of the altitudinal zonation of vegetation on tropical mountains. Zonation schemes under the numbers 1, 2 and 7 are based on bryophytes, 3-6 mainly on phanerogams.

As can be seen from Table 9, Reenen & Gradstein's (1983) and Gradstein & Frahm's (1987) results from Colombia and Peru, respectively, are very similar despite the different methods used. It should be noted, however, that some of the subzones of the latter authors are considered main zones by the former authors. This can not be regarded as very important, since the boundaries of the altitudinal zones (or subzones) agree very well. Gradstein & Frahm (1987: 109) conclude: 'Die Übereinstimmung dieser Ergebnisse, trotz der sehr unterschiedlichen benutzten Methoden, lässt eine Verallgemeinerung zu. Es scheint, dass sich die hier beschriebene Zonierung auf orographische und makroklimatische Bedingungen zurückführen lässt, die auch anderswo in den Anden auftreten und die nicht auf zufällige lokale Bedingungen zurückzuführen sind.'

The agreement of the above zonations from South America with those achieved in the present study is in part problematic. Obviously, my zone I (0-300 m) corresponds to Gradstein & Frahm's (1987) 'Tropische Tieflandstufe' (0-500 m), and my zone II (300-1200 m) to their 'Submontane Stufe' (500-1300 m) and to Reenen & Gradstein's (1983) zone I (500-1400 m). It is noteworthy that

Gradstein & Frahm record a considerable increase in the number of species at 1300 m, and include *Syrrhopodon prolifer* and *Jubula hutchinsiae* in the list of the species characterizing the 'Montane Stufe' between 1300-1900 m. On the Huon Peninsula a remarkable increase in the diversity of the bryoflora takes place at 1200 m, which is also the lower limit of *Syrrhopodon prolifer*; *Jubula hutchinsiae* subsp. *javanica* occurs between 1500-2800 m.

Above these zones, however, the boundaries in Colombia and Peru do not very well match those observed from the Huon Peninsula. This might be expected, because the Andes are very different in character from the mountain ranges on the Huon Peninsula. The upper boundary of my zone V, at 3400 m, probably indicates the lower limit of alpine vegetation, since some of the collecting sites at or above that altitude (along transect 6) were described as 'alpine grasslands' by Koponen & Norris (1983a). The 3400 m boundary coincides with the lower limit (3300 m) of the 'open páramo' on the Sierra Nevada de Santa Marta in Colombia (Reenen & Gradstein 1983), and the lower limit (3200 m) of the 'Tropisch alpine Stufe' in Peru (Gradstein & Frahm 1987). Consequently, my zone V apparently corresponds to the latter authors' 'Subalpine Stufe' between 2800-3200 m, and to the former authors' zone IV.

It should be noted that the studies in Colombia and Peru are based on a single transect along a mountain slope, whereas the Huon Peninsula material was collected at 16 separate transects on a number of mountain

ranges (fig. 4 in Koponen & Norris 1983a). Hence, the present study displays an average zonation in the study area, rather than a zonation on any particular mountain. Although Seifríz's (1924) study on the altitudinal distribution of lichens and mosses on Mt Gedeh, Java, concerned only five 'subzones' between 1400-2850 m (4600-9400 ft), the bryological aspect is briefly reviewed here. The 'Rasamala subzone' (1400-1700 m, 4600-5500 ft) and the 'Herbaceous subzone' (2150-2450 m, 7000-8000 ft) are poor in bryophytes, whereas the '*Podocarpus* subzone' (1700-2150 m, 5500-7000 ft) and the '*Vaccinium* subzone' (2450-2750 m) are bryologically rich. According to Seifríz (1924), there is a striking difference in the life-forms of mosses between the latter two subzones: in the '*Podocarpus* subzone' 'Every tree is festooned with pendent mosses', whereas in the '*Vaccinium* subzone' '...the mosses are compact tufted forms clinging close to the tree trunks, and forming thick reeking wet wads'. The bryofloristic differences between these two subzones are very clear. '*Papillaria fuscescens*' is 'perhaps, the most abundant of the second subzone epiphytic mosses'; common are, e.g., some other Meteoriaceae (*Floribundaria floribunda*, *F. aurea*, *Aerobryopsis longissima*), Hookeriaceae (*Hypopterygium struthiopteris*), Hylocomiaceae (*Macrothamnium macrocarpum*), Hypnodendraceae (*Hypnodendron reinwardtii*, *H. divaricatum*), and Sematophyllaceae (*Sematophyllum* spp.). The most abundant moss in the '*Vaccinium* subzone' is *Sematophyllum pinnatum* (= *Acroporium warburgii*); the Dicranaceae is

represented by *Dicranoloma assimile*, *D. braunii* and *Symblepharis reinwardtii*, and the Rhizogoniaceae by *Rhizogonium spiniforme* (= *Pyrrhobryum spiniforme*), etc. Seifríz (1924) concludes that 'no species is common to both zones'. However, Seifríz did not collect bryophytes very intensively in either zone, since he reports only 17 mosses and 3 hepatics from the '*Podocarpus* subzone', and 14 mosses and 6 hepatics from the '*Vaccinium* subzone'. In fact, many of the species which he reports as occurring only in one of his subzones have wide altitudinal distributions on the Huon Peninsula: *Aerobryopsis longissima* 400-1500 m, *Floribundaria floribunda* 100-3250 m, *Papillaria fuscescens* 1200-2400 m, *Dicranoloma assimile* 900-3500 m, and *Pyrrhobryum spiniforme* 500-2800 m. Although the floristic differences between Seifríz's (1924) 'moss zones' are obviously not quite as clear-cut as he suggested, it is evident that they really represent separate zones. In New Guinea, *Podocarpus* spp. are especially common at moderately high altitudes, in the midmountain forests of Lane-Poole (1925), or in the mid-montane forests of Johns (1982). It is likely that the bryologically poorer 'Herbaceous subzone' between 2150-2450 m on Mt Gedeh is but a local phenomenon. Indeed, on the Huon Peninsula, the richest bryoflora occurs within that range (Fig. 5). The great abundance of *Vaccinium* spp. at certain altitudes on Mt Gedeh may also be a local phenomenon, but the reported abundance of *Rhododendron* spp. in the '*Vaccinium* subzone' (Seifríz 1924, cf. also Lane-Poole 1925: 223) and Seifríz's (1924) fig. 1 (plate

17) suggest that we are dealing with a 'true' mossy forest, which, consequently, occurs between 2450-2750 m on Mt Gedeh. Thus, Seifriz's (1923, 1924) works are quite valuable locally, but their importance as general schemes of the vertical zonation of vegetation in the (paleo)tropics is more doubtful.

Lane-Poole's (1925) zonation scheme has already been discussed above. His results agree well with those reported here (cf. Table 9). The single discrepancy between our studies is that he placed the upper boundary of his "Foothill forests" at an average altitude of 1650 m (5500 ft), whereas my zone II extends only up to 1200 m. However, he allowed an altitudinal range of 1350-1650 m (4500-5500 ft) for the boundary.

The correspondence of Lane-Poole's (1925) vegetation zones with those defined here is roughly as follows:

Lowland forest, 0-300 m — Zone I, 0-300 m

Foothill forest, 300-(1350)1650 m — Zone II, 300-1200 m

Midmountain forest, 1650-2300 m — Zone III, 1200-2200(2300) m

Mossy forest (1500)2300-3050(3350) — Zone IV, (2200)2300- 2800(2900) m

High mountain forest (3050)3350-ca. 3600 m — Zone V, 2800(2900)-3400m

Gressitt & Nadkarni's (1978: fig. 2) zonation scheme is fairly similar

to the one presented in this paper (cf. Table 9). Their lowermost zone extends from sea level to 660 m. It comprises lowland rainforests in the lower part and hill forests in the upper, but the authors do not indicate any approximate altitude where the shift occurs. The lower montane zone of Gressitt & Nadkarni occurs between 660-1300 m. Therefore, my zone II embraces that zone and the hill forests below it. Gressitt & Nadkarni place the mid montane zone between 1300-2300 m, and it corresponds to the altitudinal range of my zone III. Interestingly, zones IV and V as defined here seem to subdivide Gressitt & Nadkarni's upper montane zone. Finally, they establish the lower boundary of the alpine zone at 3300 m, while on the Huon Peninsula that boundary apparently occurs at 3400 m.

A brief but important conclusion may be drawn from the close agreement of the above zonation schemes for the New Guinea vegetation. It is obvious that the altitudinal boundaries of the vegetation zones, based on phanerogamic flora and vegetation, are accompanied by distinct discontinuities in the bryophyte flora. Consequently, each zone has its characteristic bryophyte species assemblage. This makes sense since changes in the gross structure of vegetation imply changes in the physical environment within the forest interior which strongly affects the bryophyte flora and vegetation.

B. Correlations of the altitudinal zonation of bryophytes on the Huon Peninsula with their phytogeography

Hyvönen (1989a) presented lists of Western Melanesian mosses in each of the

phytogeographic units discussed below. Therefore, this list is not presented here. The abbreviations of the phytogeographical areas used are according to Wijk et. al. (1959).

1. Endemics of New Guinea or Western Melanesia (Table 1)

The endemism of the bryoflora in New Guinea was examined by Piippo et al. (1987). They concluded that most of the endemic species in Western Melanesia occur above 1500 m, with the exception of the Frieda River area, where the level of endemism is high between 200-1350 m (see Norris & Koponen 1985b, Piippo 1986). Based on the study of 22 hepatic families and 8 moss families, Piippo et al. (1987) gave endemism percentages (at the species level) of 48% for hepatics and 23% for mosses. Hyvönen (1989a) presented endemism percentage of 17% for mosses. The present study includes 25 hepatic families and 31 moss families, and their percentage of endemism, is 33% (70 out of 213 taxa) and 24% (54 out of 226 taxa), respectively. However, the last mentioned percentages include only taxa which were collected at least twice on the Huon Peninsula.

The present results agree with those of Piippo et al. (1987). The endemism level of hepatics is highest in zone IV. This might be expected, since there are numerous endemic hepatics which occur only in the mossy forests. The highest number of endemic mosses are encountered in zone III, which comprises lower montane forests and mossy forests.

The four endemics occurring in zone I are *Frullania multilacera*, *Radula koponenii*, *Fissidens vanzantennii*, and *Barbula novoguineensis*. The endemic taxa restricted to a single altitudinal zone include, *Porella grollei* (zone III), *Telaranea trisetosa* (III), *T. kaindina* (III), *Leptoscyphus huonicus* (V), *Lepicolea norrisii* (III), *Radula ovalilobula* (IV), *R. minutilobula* (V), *Metzgeria*

hispidissima (III), *Anomobryum ochii* (III), *A. hyalinum* (V), *Aerobryidium fuscescens* (III), *Garovaglia subelegans* (III), *Powellia parvula* (III), *Brotherobryum undulatifolium* (III), and *Dicnemon robbinsii* (III). It may be noted that none of the endemics occurring at low altitudes are restricted to any particular zone.

2. Malesian endemics (As 4, including species which in Oceania occur only in the Solomon Islands) (Table 2)

According to Hyvönen (1989a), ca. 15% of Western Melanesian mosses represent this distribution type.

The hepatics in this group show similar altitudinal distributions with the New Guinean or Western Melanesian endemics discussed above. The percentages are very high in the zones III and IV. Interestingly, mosses have a somewhat different altitudinal distribution. The number of Malesian endemic mosses rises continuously from zone I to zone V, and decreases only above 3400 m. These results do not seem to be in accordance with the reported strong affinities to Malesia of the New Guinean lowland phanerogam flora (e.g. Smith 1980).

None of the hepatics and only two mosses (*Barbula pseudo-ehrenbergii*, *Thamnobryum ellipticum*) of this distribution type occur in zone I. Species restricted to a specific zone include *Triandrophyllum heterophyllum* (zone V), *Lepidozia borneensis* (IV), *Heteroscyphus wettsteinii* (III), *Frullania armatifolia* (IV), *Aerobryidium crispifolium* (II), *Rhizogonium lamii* (V), *Dawsonia beccarii* (IV), *Oligotrichum javanicum* (V), *Pogonatum subtortile* (IV), *Buxbaumia javanica* (V), *Leptodontium aggregatum* (V), *Himantocladium submontanum* (III), *Microdus miquelianus* (III), *Braunfelsia enervis* (IV), and *Fabronia curvirostris* (III).

3. SE-Asian distribution (As 2 - 4, including taxa which in Oceania occur only in the Solomon Islands) (Table 3)

About 14% of Western Melanesian mosses have a SE-Asian distribution (Hyvönen 1989a).

SE-Asian hepatics and mosses are best represented in zones III and IV. However, when compared with the Malesian endemics, the SE-Asian species are clearly more numerous at lower altitudes, notably in zone II. The single hepatic and the four mosses with this distribution pattern in zone I are *Radula vrieseana*, *Fissidens hollianus*, *F. zippelianus*, *Barbula javanica*, and *B. subcomosa*. Species occurring only in one altitudinal zone include *Southbya grollei* (V), *Plagiomnium succulentum* (III), *Orthodontium infractum* (V), *Aerobryopsis leptostigmata* (II), *Pogonatum neesii* (III), *Dicranodontium fleischerianum* (IV), and *Leucobryum neilgherrense* (III).

4. Asian-Oceanian distribution (Table 4)

About 14% of Western Melanesian mosses belong to this distribution type (Hyvönen 1989a).

This group is more strongly represented at low altitudes (zones I and II) than any of the preceding distribution groups. In the three groups dealt with above, hepatics had the highest number of taxa in zone IV instead of zone III, where most of the Asian-Oceanian distribution hepatics are concentrated. Significantly, mosses are even more strongly represented at lower altitudes, the highest number of species being encountered in zones II and III, but also the lowermost zone is relatively rich in moss taxa. The moss flora also shows a more abrupt impoverishment at high altitudes, especially in zone V and above that, than the hepatic flora. The strong representation of Asian-Oceanian bryophytes at low altitudes is readily explained by the fact that high mountains in Oceania are very few. Many of the Oceanian islands are geologically young, and they must have received their bryophytes mainly

from SE-Asia and Australasia, and rather extensive bryophyte migration from these regions to Oceania has taken place at low altitudes.

Asian-Oceanian species encountered in only one altitudinal zone on the Huon Peninsula comprise *Pleurozia conchifolia* (III), *Jackiella javanica* (III), *Frullania gracilis* (III), *F. trichodes* (III), *F. immersa* (III), *Treubia insignis* (III), *Radula amentulosa* (V), *R. acuminata* (III), *Plagiochila longispica* (II), *Notoscyphus lutescens* (III), *Calymperes strictifolium* (II), *Syrrhopodon japonicus* (III), and *Fissidens obscurirete* (II).

5. Asian-Oceanian-Australian distribution (Table 5)

Asian-Oceanian-Australian species are relatively few in Western Melanesia, comprising only 11% of the moss flora (Hyvönen 1989a). As might be expected, they show a similar overall altitudinal distribution pattern as the Asian-Oceanian species discussed above, but mosses of this distribution type are not as commonly encountered in the two lowermost zones. Species present in only one altitudinal zone include *Jungermannia hasskarliana* (III), *Syrrhopodon muelleri* (II), *S. tristichus* (III), *Himantocladium plumula* (II), and *Leucophanes glaucum* (I).

6. Asian-Australian distribution

This distribution group is a small one in Western Melanesia; only 4% of the mosses belong here (Hyvönen 1989a). Of the species included in the present study, only 3 hepatics and 7 mosses are regarded as Asian-Australian, *Jungermannia appressifolia* (V), *Tylimanthus saccatus* (III-V), *Zoopsisidella caledonica* (IV), *Dawsonia longifolia* (III-V), *Dicranum dicarpum* (III-IV), *Fissidens*

nymanii (II-III), *Orthomnion elimbatum* (II-V), *Orthorrhynchium elegans* (III-V), *Powellia subelimbata* (II-III), and *Tridontium tasmanicum* (III).

Koponen & Norris (1986) regarded *Powellia subelimbata* as endemic to New Guinea, but according to Zanten & Pócs (1981: 533), it has been collected also in Queensland.

Most of the species named above have their main distributions in Asia, whence they probably have dispersed to Australia. An obvious exception is *Powellia subelimbata*, which Zanten & Pócs (1981), following the terminology of Smith (1980), considered to represent an Australian element, encountered in New Guinea in eucalyptus woodlands and savannahs. Koponen & Norris (1986) report that on the Huon Peninsula this species also occurs in gardens and disturbed forests.

The low number of taxa in this phyto-geographic group prevents reliable conclusions as to their altitudinal zonation on the Huon Peninsula. It can be noted that none of the taxa occur in zone I, and only three are encountered in zone II. They seem to be mainly distributed within zones III-V.

7. Transpacific distribution

This type of distribution is represented only by 1 hepatic and 3 mosses: *Frullania gaudichaudii* (zones II-III), *Barbella cubensis* (II-III), *Campylopus aureus* (IV-V, and up to 3600 m), and *Trichostomum crispulum* (III-IV). The total range of *Frullania gaudichaudii* is inadequately known, since its presence in Australia is not certain (Hattori 1982). The small number of transpacific taxa prevents any reliable conclusions, but it seems that these taxa are mainly distributed at moderate altitudes between 1000-3000 m.

8. Paleotropical distribution (Table 6)

Only about 4% of the Western Melanesian mosses are paleotropical in distribution (Hyvönen 1989a).

The hepatics in this group are *Pleurozia gigantea* (III-V and above), *Psiloclada clandestina* (III), *Heteroscyphus splendens* (III), *Frullania apiculata* (I-V), *Wiesnerella denudata* (II-IV), *Radula madagascariensis* (IV), *Metzgeria consanguinea* (III-V and above), *Gottscheia schizopleura* (IV-V and above), and the mosses *Calymperes dozyanum* (I-II), *Calymperes taitense* (I-II), *Mitthyridium fasciculatum* (II), *Floribundaria floribunda* (I-V and above), *Neckeropsis lepinea* (II-III), *Pinnatella mariei* (I), *Rhodobryum aubertii* (II-III), *R. giganteum* (III-V), *Brachymenium nepalense* (II-V and above), *Trachypus bicolor* (III-V and above), *Leucophanes octoblepharioides* (II-III), and *L. angustifolium* (II-III). *Pinnatella mariei* has recently been reported from Africa (Mattila & Enroth, 1990).

As the relatively scanty material suggests, there seem to be slight differences between the altitudinal distributions of paleotropical hepatics and mosses on the Huon Peninsula. The hepatics tend to occur at somewhat higher altitudes than the mosses, the only hepatic present in zones I and II being *Frullania apiculata*. Most paleotropical mosses occur in zones II and III on the Huon Peninsula.

9. Pantropical distribution (Table 7)

Pantropical mosses represent 5% of the Western Melanesian flora

(Hyvönen 1989a).

The species included here are *Heteroscyphus argutus* (I-III), *Frullania ericoides* (I-IV), *F. arecae* (III-IV), *Metzgeria epiphylla* (IV), *M. albinea* (II-IV), *M. australis* (II-IV), *Bryum apiculatum* (I-III), *B. billarderi* (III-V and above), *B. coronatum* (III-V), *Ceratodon stenocarpus* (IV-V and above), *Calymperes afzelii* (II), *C. tenerum* (I), *Fissidens asplenioides* (III-IV), *Syrrhopodon prolifer* (III-IV), *Octoblepharum albidum* (I-III), and *Pyrrhobryum spiniforme* (II-IV). The last mentioned species was 'with some reservations' considered a 'cosmopolitan' by Hyvönen (1989a). However, judged from the distribution map in Iwatsuki (1972: 131), it seems reasonable to regard it as pantropical (see also Menzel & Schultze-Motel 1987).

In addition Hyvönen (1989a) and Menzel & Schultze-Motel (1987) regard *Bryum billarderi* as a pantropical species. Ochi (1985) writes: 'Pan-tropical, but extending up or down to temperate regions in the Northern and Southern hemispheres'. Based on information in Norris & Koponen (1987), Hyvönen (1989a) considered *Fissidens asplenioides* a transpacific species, but the map in Schuster (1983) shows a pantropical range (see also Menzel & Schultze-Motel 1987). In this study the species is included in the pantropical element.

It is noteworthy that pantropical hepatics do not occur in zone V or above. The two mosses encountered above 3400 m are *Bryum billarderi* and *Ceratodon stenocarpus*. It should be mentioned in this connection that Norris & Koponen (1988) doubt whether *C. stenocarpus* can be kept separate from the 'cosmopolitan' *C. purpureus*. The meager material

available suggests that, in general, pantropical mosses are most numerous at moderate to relatively high altitudes (zones II-IV). This altitudinal distribution is rather similar to that of the whole bryophyte flora included in this study (cf. Fig. 5).

10. Southern hemisphere distribution

In the present study, hepatics are not represented in this type of distribution, and there are only 4 mosses: *Bryum clavatum* (zones II-V), *Catagonium nitens* (IV-V), *Ditrichum difficile* (III-V), and *Rhacocarpus purpurascens* (lowest at 3400 m). According to Ochi (1985), in the tropics *Bryum clavatum* occurs only at high altitudes, but on the Huon Peninsula it has rather a wide altitudinal amplitude between 700-3300 m. Menzel & Schultze-Motel (1987) considered *Rhacocarpus purpurascens* a pantropical species, but since it is apparently restricted to the southern hemisphere, I prefer to follow Hyvönen (1989a). Menzel & Schultze-Motel (1987) give an altitudinal distribution of 2100- 4400 m for *R. purpurascens* in Peru.

Although the number of taxa representing this distribution type is very small, it may, with some reservations, be concluded that they mostly occur at relatively high altitudes, mainly in zones IV and V. This seems to have some relevance, since *Bryum clavatum*, *Catagonium nitens* and *Rhacocarpus purpurascens* apparently belong to the Gondwanaland element (Hyvönen 1989a), which in New Guinea mainly occurs on mountains and is scarce in the lowlands (Smith 1980).

11. Mainly northern hemisphere

distribution

According to Hyvönen (1989a), only ca. 5% of Western Melanesian mosses belong to this distribution type. Of the bryophytes included in this study, the hepatics *Jungermannia sphaerocarpa* (zone V) and *Marsupella revoluta* (only above 3400 m) have a mainly northern hemisphere distribution. Eight mosses are included here: *Pogonatum urnigerum* (zone V and above), *Bryum microerythrocarpum* (III-V and above), *Anomobryum julaceum* (IV-V and above), *Epipterygium tozeri* (II-IV), *Pohlia elongata* (V and above), *Bryoerythrophyllum ferruginascens* (III-V and above), *Didymodon rigidicaulis* (III-V and above), and *Fissidens taxifolius* (III-IV). It is well-known that in the tropics, temperate species mostly occur at high altitudes. This is supported by the present data. It should be noted, however, that on the Huon Peninsula *Epipterygium tozeri* occurs as low as 750 m (zone II), and *Fissidens taxifolius* at 1400 m (zone III).

12. Miscellaneous distribution

Two hepatics may be placed here. *Chandonanthus hirtellus* has a mainly paleotropical distribution, but it is also known from British Columbia (Canada) and New Zealand (Miller et al. 1983: 79). *Plagiochila sciophila* also occurs in Arkansas, North America (Piippo 1989). Inoue (1984: 127) writes: '*Plagiochila sciophila* is the most common and most polymorphic taxon...; it is distributed very widely in tropical - temperate regions of the Paleotropics and Neotropics, but lacking from the African continent.' It is possible that the total range of this variable taxon is still inadequately known. Both *Chandonanthus hirtellus* and *Plagiochila sciophila* have wide altitudinal ranges on the Huon Peninsula. The former occurs between 1200-3500 m (zones III-V and above) and the latter between 350-2800 m (zones II-IV).

The three mosses included in this distribution are *Campylopodium medium*, *Homali dendron flabellatum* and *Timmiella anomala*. The main distribution of *Campylopodium medium* is Asian-Oceanian- Australian, but it is also known from Puerto Rico and Chile. On the Huon Peninsula it was collected between 1200-2000 m (zone III). *Timmiella anomala* has a wide distribution in North America, Central America, Europe and Asia (Japan, India). From the Paleotropics it is only known from Papua New Guinea and the Philippines. The collections from the Huon Peninsula come from relatively high altitudes (2100-3400 m, zones III-V), which would suggest that this is a northern hemisphere species (group 11 above). My decision to regard *Timmiella anomala* as a plant of a 'miscellaneous distribution' is based on Hyvönen (1989a) and the opinion of Norris & Koponen (1989): 'Several species are included in the world list of this genus but careful review of the described species may well show them all conspecific with *Timmiella anomala*.'

The extremely variable *Homali dendron flabellatum* (zones II-V) has rather a wide range in the tropical regions, where it remains unrecorded only from continental Africa and (possibly) large areas of the Neotropics. In the latter region (at least on the islands of the Caribbean) the species has been known as *H. decompositum* (see Enroth 1989b).

13. Global distribution ('cosmopolitan' (Table 8))

As might be expected this group comprises mostly 'weedy' plants, which often occur in exposed, man-made habitats, and usually grow on soil or cliffs and rocks (cf. Hyvönen 1989a). However, of the four hepatics included here *Lophocolea bidentata* is exclusively, and *Metzgeria leptoneura* mainly, epiphytic. The two other hepatics, *Dumortiera hirsuta* and *Reboulia hemisphaerica* are epigeaic or epilithic.

The Pottiaceae is represented by eight species, all occurring on soil and/or boulders and rocks: *Anoetangium aestivum*, *Barbula indica*, *Hymenostylium recurvirostre*, *Hyophila involuta*, *Lepto-*

HEPATICAE**Acrobolbaceae (Piippo 1985a)**

Tylimanthus saccatus (Hook.)
Mitt. (1700-2400 m)

Adelanthaceae (Piippo 1984b)

Wettsteinia inversa (Sande Lac.)
Schiffn. (2500-3100 m)

Arnelliaceae (Piippo 1985a)

Southbya grollei N. Kitag.
(3250-3400 m)

Aytoniaceae (Piippo 1988b)

Asterella khasyana (Griff.)
Pandé et al. (1300-2900 m)
Reboulia hemisphaerica (L.)
Raddi (1500-3400 m)

Balantiopsiaceae (Piippo 1984a)

Balantiopsis ciliaris Hatt.
subsp. *novoguineensis* Hatt.
(1500-2500 m)
Isotachis armata (Nees) Gott.
(2200-3100 m)

Cephaloziaceae (Grolle & Piippo 1984a; Piippo 1984b)

Nowellia borneensis (De Not.)
Schiffn. (2100-2250 m)

Odontoschisma naviculare
(Steph.) Grolle (1800-2450 m)

Frullaniaceae (Hattori & Piippo 1986)

Frullania apiculata (Reinw. et
al.) Dum. (100-3200 m)

F. appendistipula Hatt. (2300-
3500 m)

F. arecae (Spreng.) Gott.

(1500-2400 m)

F. armatifolia Verd. (2300-
2800 m)

F. armitiana Steph. (1500-
3500 m)

F. attenuata Steph. (900-2800
m)

F. bergmanii Hatt. (1500-2600
m)

F. carrii Kamim. & Hatt.
(1200-1500 m)

F. curvistipula Steph. (1200-
2200 m)

F. cuspidifolia Steph. (1700-
3300 m)

F. echinantha Hatt. (2800-3200
m)

F. epiphylla Hatt. (1250-1500
m)

F. ericoides (Nees) Mont. (0-
2900 m)

F. eymae Hatt. (600-2200 m)

F. errans Verd. var.
angulistipula Hatt. (2200-2300
m)

F. falsisinuata Hatt. fo.
parvistylata (Hatt.) Hatt. &
Piippo

(3300-3400 m)

F. gaudichaudii (Nees &
Mont.) Nees & Mont. (550-2000
m)

F. gracilis (Reinw. et al.) Dum.
(1700-2300 m)

F. immersa Steph. (1300-1400
m)

F. irregularis Hatt. & Piippo
(2200-2600 m)

F. junghuhniana Gott. var.
tenella (Sande Lac.) Grolle &
Hatt.

(1200-3350 m)

F. leeuwenii Verd. (800-1800 m)
F. macgregorii Steph. (2800-3600 m)
F. multilacera Steph. (200-1800 m)
F. nepalensis (Spreng.) Lehm. & Lindenb. (2000-2600 m)
F. nobilis Steph. var. *cochleata* (Steph.) Hatt. & Piippo (2200-2300 m)
F. orientalis Sande Lac. (600-2500 m)
F. papillata Steph. (2200-2900 m)
F. papuana Verd. (3300-3600 m)
F. pauciramea Steph. (1300-3000 m)
— var. *pauciramella* Hatt. & Piippo (2200-2800 m)
F. prominula Hatt. & Streim. (1200-1500 m)
F. pullei (2200-3500 m)
F. reflexistipula Sande Lac. (1400-3400 m)
F. reimersii Verd. (2800-3500 m)
F. saepis-dentata Hatt. & Streim. (1730-1800 m)
F. schusteriana Hatt. (1700-2300 m)
F. seriatifolia Steph. (2000-2900 m)
F. serrata Gott. fo. *crispulodentata* Verd. (1500-2300 m)
F. serrata var. *hamatispina* (Hatt.) Hatt. (800-3300 m)
F. serrata subsp. *spinistipula* (Hatt.) Hatt. (1000-2500 m)
F. subcaduca Hatt. (2400-2800 m)
F. subdentata Steph. (2200-2900 m)
F. subnigricaulis Hatt. var. *subtruncata* Hatt. (1200-1700 m)
F. trichodes Mitt. (1450-2230 m)

F. van-zantennii Kamim. & Hatt. (2300-2500 m)

Geocalycaceae (Piippo 1985b)

Heteroscyphus acutangulus (Schiffn.) Schiffn. (1200-3300 m)
H. argutus (Reinw. et al.) Schiffn. (200-1600 m)
H. aselliformis (Reinw. et al.) Schiffn. (1200-3000 m)
H. coalitus (Hook.) Schiffn. (200-3100 m)
H. sarawaketanus Piippo (3250-3550 m)
H. splendens (Lehm. & Lindenb.) Grolle (1800-2300 m)
H. tridentatus (Sande Lac.) Grolle (1850-3600 m)
H. wettsteinii (Schiffn.) Schiffn. (1700-2000 m)
H. zollingeri (Gott.) Schiffn. (350-1600 m)
Leptoscyphus huonicus Piippo (2800-3100 m)
Lophocolea bidentata (L.) Dum. (2850-3300 m)
L. ciliolata (Nees) Gott. (1800-3100 m)
L. costata (Nees) Gott. (1500-3100 m)
L. levieri Schiffn. (1400-3500 m)
Saccogynidium muricellum (De Not.) Grolle (1500-2500 m)

Gymnomitriaceae (V na & Piippo 1989)

Marsupella revoluta (Nees) Dum. (3400-3570 m)

Haplomitriaceae (Piippo 1984a)

Haplomitrium blumii (Nees) Schust. (1100-3550 m)

Herbertaceae (Piippo 1984a)

Herbertus armitanus (Steph.) H. A. Miller (1700-3400 m)
H. circinatus (Steph.) H. A.

Miller (1950-3500 m)

H. longifissus Steph. (1900-3500 m)

Triandrophyllum heterophyllum (Steph.) Grolle (3250-3400 m)

Jackiellaceae (Piippo 1985a)

Jackiella javanica Schiffn. (1500-2000 m)

Jubulaceae (Piippo 1984b)

Jubula hutchinsiae (Hook.) Dum. subsp. *javanica* (Steph.) Verd. (1500-2800 m)

Jungermanniaceae (Vana & Piippo 1989)

Jungermannia appressifolia Mitt. (2800-3350 m)

J. comata Nees var. *novaeguineae* Vana (1300-2300 m)

J. diversiclavellata Amak. & Grolle (2300-3300 m)

J. hasskarliana (Nees) Mitt. (1250-2000 m)

J. herzogiana Vana (2300-3550 m)

J. hirticalyx Steph. (750-2300 m)

J. sphaerocarpa Hook. (3200-3250 m)

J. stephanii (Schiffn.) Amak. (2280-3550 m)

J. stricta (Schiffn.) Steph. (1200-3550 m)

J. tetragona Lindenb. (800-1400 m)

J. truncata Nees (800-2450 m)

J. virgata (Mitt.) Steph. (800-1800 m)

Notoscyphus lutescens (Lehm.) Mitt. (1450-1700 m)

Lepicoleaceae (Piippo 1984a, 1988a)

Lepicolea norrisii Piippo (1900-2300 m)

L. rara (Steph.) Grolle (1800-

3500 m)

Mastigophora diclados (Brid.) Nees (900-3500 m)

Lepidoziaceae (Grolle & Piippo 1984a; Piippo 1984b, 1985c, pers. comm.)

Hygrolembidium boschianum (Sande Lac.) Schust. (2450-3300 m)

Kurzia pallida Piippo (2400-3550 m)

Lepidozia bursifera Hatt. & Grolle (2200-3000 m)

L. borneensis Steph. (2300-2700 m)

L. cladorrhiza (Reinw. et al.) Gott. et al. (1900-3100 m)

L. ferdinandi-muelleri Steph. (1200-2400 m)

L. gwamii Piippo (2800-3550 m)

L. hasskarliana (Lindenb.) Steph. (1500-3350 m)

L. holorrhiza (Reinw. et al.) Gott. et al. (2200-3350 m)

L. stahlia Steph. (2500-3500 m)

L. trichodes (Reinw. et al.) Nees (1000-2500 m)

L. wallichiana Gott. (1200-3500 m)

Psiloclada clandestina Mitt. (1800-2300 m)

Telaranea kaindina Grolle (1800-2250 m)

T. lawesii (Steph.) Grolle (1200-3100 m)

T. trisetosa (Steph. emend. Grolle) Grolle (1350-2300 m)

Zoopsidella caledonica Schust. (2200-2600 m)

Zoopsis liukiensis Horik. (1000-3000 m)

Lophoziaceae (Vana & Piippo 1989b)

Anastrophyllum revolutum Steph. (1800-3600 m)

Andrewsianthus cavifolius Grolle & Vana (2500-3600 m)

A. bidens (Mitt. ex Steph.)
Schust. (2450-3600 m)
Anomacaulis flaccidus (Steph.)
Grolle (2100-2900 m)
Chandonanthus hirtellus
(Web.) Mitt. (1200-3500 m)
C. pilifer Steph. (2200-3600 m)
Denotarisia linguifolia (De
Not.) Grolle (1500-3500 m)
Gottschelia schizopleura
(Spruce) Grolle (2600-3600 m)
Jamesoniella flexicaulis (Nees)
Schiffn.
Syzygiella securifolia (Nees)
Inoue (1500-2500 m)

Makinoaceae (Piippo 1988c)
Makinoa crispata (Steph.)
Miyake (1500-3000 m)

Metzgeriaceae (Piippo pers.
comm.)
Metzgeria consanguinea
Schiffn. (1750-3550 m)
M. epiphylla Evans (2750-
2900 m)
M. hispidissima Steph. (2000-
2200 m)
M. albinea Spruce (300-2800
m)
M. australis Steph. (1100-2350
m)
M. macveanii Kuwah. (2850-
3500 m)
M. hattorii Kuwah. (1500-
3100 m)
M. leptoneura Spruce (400-
3550 m)

Pallaviciniaceae (Grolle &
Piippo 1986)
Jensenia decipiens (Mitt.)
Grolle (2300-3600 m)
Pallavicinia ambigua (Mitt.)
Steph. (800-1750 m)
Podomitrium malaccense
(Steph.) D. H. Campb. (400-
2450 m)
Symphogyna rectidens Grolle
(1700-2400 m)

S. similis Grolle (1600-2900 m)

Plagiochilaceae (Piippo 1989)
Plagiochila abietina (Nees)
Lindenb. (1500-3300 m)
P. arbuscula (Brid. ex Lehm. &
Lindenb.) Lindenb. (1600-3000
m)
P. cymata Inoue & Grolle
(1200-2100 m)
P. decidua Inoue & Grolle
(2500-3000 m)
P. dendroides (Nees) Lindenb.
(1500-3300 m)
P. gymnoclada Sande Lac.
(1500-3600 m)
P. hampeana Gott. (1900-3500
m)
P. javanica (Swartz) Dum.
(500-3300 m)
P. kurokawae Inoue (2800-
3500 m)
P. longispica Mitt. (300-600 m)
P. loriana Steph. (1200-2800
m)
P. odorata Inoue & Grolle
(1200-2800 m)
P. propinqua Sande Lac. (800-
2000 m)
P. pulvinata Steph. (2000-3550
m)
P. renitens (Nees) Lindenb.
(1800-3300 m)
P. schusteri Inoue & Grolle
(2500-3600 m)
P. sciophila Nees (350-2800 m)
P. seemannii Mitt. (300-1800
m)
P. singularis Schiffn. (1800-
2800 m)
P. sumatrana Schiffn. (800-
1500 m)
P. tamiensis Steph. (1200-
3000 m)
P. tecta Inoue & Grolle (2200-
3400 m)
P. teysmannii Sande Lac. (400-
1800 m)
P. trapezoidea Lindenb. (1200-
3300 m)

P. ulata Inoue & Grolle (1500-1600 m)

P. velata Inoue & Piippo (1250-2500 m)

Plagiochilium braunianum (Nees) Hatt. (2300-3500 m)

P. oppositum (Reinw. et al.) Hatt. (1500-3600 m)

Pleuroziaceae (Piippo 1984a)

Pleurozia conchifolia (Hook. & Arnott) Aust. (1700-2200 m)

P. gigantea (Web.) Lindb. (1200-3500 m)

Porellaceae (Piippo 1984a)

Porella acutifolia (Lehm. & Lindenb.) Trev. (300-1800 m)

P. geheebii (Steph.) Hatt. (600-2800 m)

P. grollei Hatt. (1800-2100 m)

P. viridissima (Mitt.) Grolle var. *novoguineensis* (Hatt.) Hatt. (2000-2300 m)

Pseudolepicoleaceae (Piippo 1984a)

Pseudolepicolea grolleana (Schust.) Grolle in Piippo (2200-3550 m)

Temnoma setigerum (Lindenb.) Schust. (1850-2850 m)

Radulaceae (Yamada & Piippo 1989)

Radula acuminata Steph. (1700-1900 m)

R. amentulosa Mitt. (2800-ca.3100 m)

R. anceps Sande Lac. (100-2200 m)

R. apiculata Sande Lac. ex Steph. (100-1900 m)

R. densifolia Castle (750-3000 m)

R. javanica Gott. (40-800 m)

R. koponenii Yamada & Piippo (100-650 m)

R. lacerata Steph. (900-2500 m)

R. madagascariensis Gott. (2200-2600 m)

R. minutilobula Yamada & Piippo (2850-3100 m)

R. multiflora Gott. ex Schiffn. var. *reflexilobula* Grolle & Yamada (900-1100 m)

R. norrisii Yamada & Piippo (2100-3000 m)

R. nymanii Steph. (200-1900 m)

R. ovalilobula Yamada (2200-2800 m)

R. parvitexta Steph. (2100-2900 m)

R. retroflexa Tayl. (350-3250 m)

- - var. *fauciloba* (Steph.) Yamada (350-1900 m)

R. sharpii Yamada (750-2850 m)

R. subpallens Steph. (1450-2400 m)

R. tjibodensis Goebel ex Schiffn. (100-3600 m)

R. vrieseana Sande Lac. (100-600 m)

Scapaniaceae (Piippo 1985a)

Scapania javanica (1500-3600 m)

Schistochilaceae (Piippo 1984a)

Schistochila aligera (Nees & Blume) Jack & Steph. (1250-3200 m)

S. antara Grolle (1500-2900 m)

S. blumii (Nees) Trev. (1200-2800 m)

S. nymanii Steph. (800-3400 m)

S. philippinensis (Mon.) Jack & Steph. (500-3000 m)

S. schultzei (Steph.) (2200-3200 m)

S. sciurea (Nees) Schiffn. (1800-3350 m)

Targioniaceae (Piippo 1988b)

Cyathodium foetidissimum
Schiffn. (600-1500 m)

Treubiaceae (Piippo 1988c)
Treubia insignis Goebel (1800-2100 m)

Trichocoleaceae (Piippo 1984a)
Trichocolea breviseta Steph. (1250-3100 m)
T. tomentella (Ehrh.) Dum. s. lat. (800-3350 m)

Wiesnerellaceae (Piippo 1988b)
Dumortiera hirsuta (Sw.) Nees (200-3400 m)

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Bryaceae (Koponen & Norris 1984, 1985b)
Anomobryum bulbiferum Bartr. (2000-3400 m)
A. hyalinum T. Kop. & Norris (2900-3400 m)
A. julaceum (Gaertn. et al.) Schimp. (2400-3600 m)
A. ochii T. Kop. & Norris (1500-1800 m)
Brachymenium huonii T. Kop. & Norris (3250-3600 m)
B. nepalense Hook. in Schwaegr. (700-3600 m)
- - var. *globosum* Bartr. (1200-1800 m)
B. wabagense (Bartr.) T. Kop. & Norris (1800-3400 m)
Bryum apiculatum Schwaegr. (0-1500 m)
B. argenteum Hedw. (1750-3350 m)
B. billarderi Schwaegr. (2000-3500 m)
B. capillare Hedw. (700-2500 m)
B. clavatum (Schimp.) C. Müll. (700-3300 m)
B. coronatum Schwaegr. (1500-3000 m)

B. microerythrocarpum C. Müll. & Kindb. in Macoun (1700-3500 m)

B. perdecurrens Bartr. (1500-3500 m)

B. pseudoblandum T. Kop. & Norris (2000-3500 m)

B. russulum Broth. & Geh. (1400-2200 m)

Epipterygium tozeri (Grev.) Lindb. (750-2400 m)

Leptobryum pyriforme (Hedw.) Wils. (2200-2900 m)

Orthodontium infractum Dozy & Molk. (2800-3100 m)

Pohlia elongata Hedw. (2800-3600 m)

P. flexuosa Hook. (1600-3600 m)

Rhodobryum aubertii (Schwaegr.) Thér. (400-2300 m)

R. giganteum (Schwaegr.) Par. (1500-3000 m)

Buxbaumiaceae (Hyvönen 1986)
Buxbaumia javanica C. Müll. (3300-3400 m)

Calymperaceae (Reese et al. 1986)
Calymperes afzelii Sw. (500-600 m)

C. dozyanum Mitt. (0-1200 m)

C. strictifolium (Mitt.) G. Roth (500-650 m)

C. taitense (Sull.) Mitt. (50-1000 m)

C. tenerum C. Müll. (0-100 m)

Syrrhopodon japonicus (Besch.)

Broth. (1800-1900 m)

S. muelleri (Dozy & Molk.) Sande Lac. (400-1000 m)

S. prolifer Schwaegr. (1200-2400 m)

S. tristichus Nees ex Schwaegr. (1800-2100 m)

Mitthyridium fasciculatum (Hook. & Grev.) Robins. (500-1000 m)

M. obtusifolium (Lindb.) Robins. (200-1000 m)

Dicnemonaceae (Norris & Koponen 1990a)

Dicnemon novaeguineae (Dix.) B.

Allen (2100-3500 m)

D. robbinsii (Bartr.) B. Allen (1500-2000 m)

Dicranaceae (Frahm et al. 1985; Norris & Koponen 1990a)

Atractylocarpus comosus Dix. (2700-3600 m)

A. novoguineensis (Broth. & Geh.) Norris & T. Kop. (2450-3600 m)

Braunfelsia dicranoides (Dozy & Molk.) Broth. (1800-3550 m)

B. enervis (Dozy & Molk.) Par. (2450-2700 m)

Brotherobryum undulatifolium Zanten (1800-2200 m)

Bryohumbertia walkeri (Mitt.) J.-P. Frahm (1800-2900 m)

Campylopodium medium (Duby) Giese (1200-2200 m)

Campylopus aureus Bosch & Sande Lac. (2600-3600 m)

C. austrosubulatus Broth. & Geh. (3300-3550 m)

C. clemensiae Bartr. (1200-3300 m)

C. comosus (Schwaegr.) Bosch & Sande Lac. (1800-3300 m)

C. crispifolius Bartr. (1500-3300 m)

C. exasperatus (Nees & Blume) Brid. (1700-3600 m)

-- var. *lorentzii* (Fleisch.) J.-P. Frahm (2500-3400 m)

C. involutus (C. Müll.) Jaeg. (750-2850 m)

C. macgregorii Broth. & Geh. (3300-3550 m)

C. umbellatus (Arnott) Par. (1300-3600 m)

Dicranella papua-palustris Norris & T. Kop. (1900-3570 m)

Dicranodontium fleischerianum Schultze-Motel (2330-2500 m)

Dicranum arfakianum C. Müll. ex Geh. (1800-2500 m)

D. armittii C Müll. (1000-3400 m)

D. assimile Hampe (900-3500 m)

D. blumii Nees (1100-3400 m)

D. braunii C. Müll. ex Dozy & Molk. (1480-2500 m)

D. cutlackii Norris & T. Kop. (2800-3500 m)

D. dicarpum Nees in Spreng. (1800-2900 m)

D. geluense (Herz.) Norris & T. Kop. (1800-3100 m)

D. rugifolium (Bartr.) Norris & T. Kop. (2800-3600 m)

Holomitrium austroalpinum Bartr. (2550-3100 m)

H. obliquum Salm. (3400-3600 m)

H. stenobasis Dix. (2400-3550 m)

Microdus miquelianus (Mont.) Besch. in Par. (1800-2200 m)

Symblepharis reinwardtii (Dozy & Molk.) Mitt. (3250-3570 m)

Trematodon longicollis Michaux (1750-2450 m)

Ditrichaceae (Norris & Koponen 1988)

Ceratodon stenocarpus Bruch & Schimp. ex C.Müll. (2430-3600 m)

Distichium capillaceum (Hedw.) B.S.G. (2850-3600 m)

Ditrichum colijnii Dix. (3250-3600 m)

D. difficile (Duby) Fleisch. (1900-3300 m)

D. sericeum Bartr. (3400-3570 m)

Fabroniaceae (Norris & Koponen 1990b)

Fabronia curvirostris Dozy & Molk. (2070-2200 m)

Fissidentaceae (Norris & Koponen 1987)

Fissidens asplenioides Hedw. (1480-2500 m)

F. braunii (C.Müll.) Dozy & Molk. (300-2600 m)

F. flabellulus Thwait. & Mitt. (880-2550 m)

F. flexifolius Bartr. (1100-2400 m)

F. geminiflorus Dozy & Molk. (750-2200 m)

F. hollianus Dozy & Molk. (0-1600 m)

F. nobilis Griff. (750-2100 m)

F. nymanii Fleisch. (900-1700 m)

F. obscurirete Broth. & Par. in Broth.

(600-1100 m)
F. plagiochiloides Besch. (2100-2900 m)
F. rigidulus C. Müll. subsp. *novaguineensis* Brugg. (1500-2400 m)
F. strictulus C. Müll. (1400-2900 m)
F. taxifolius Hedw. (1400-2900 m)
F. vanzanteni Brugg. (200-2600 m)
F. wichurae Broth. & Fleisch. (1700-2600 m)
F. zippelianus Dozy & Molk. in Zoll. (100-1300 m)

Grimmiaceae (Koponen & Norris 1986)
Racomitrium javanicum Dozy & Molk. in Zoll. (3250-3550 m)

Hedwigiaceae (Koponen & Norris 1986)
Rhacocarpus alpinus (Wright) Par. (3400-3600 m)
R. purpurascens (Brid.) Par. (3400-3600 m)

Hylocomiaceae (Koponen & Norris 1985a)
Leptocliadiella flagellaris T. Kop. & Norris (1700-3000 m)
Macrothamnium hylocomioides Fleisch. (1600-3600 m)

Leptostomataceae (Koponen & Norris 1985b)
Leptostomum intermedium Broth. (2000-3500 m)
L. perfectum Bartr. (3350-3550 m)

Leucobryaceae (Enroth 1990a)
Exostratum blumei (Nees ex Hampe) L.T. Ellis (100-1750 m)
E. sullivantii (Dozy & Molk.) L.T. Ellis (900-1300 m)
Leucobryum javense (Brid.) Mitt. (1500-2900 m)
L. neilgherrense C. Müll. (1450-1600 m)
L. sanctum (Brid.) Hampe (1450-2550 m)

Leucophanes angustifolium Ren. & Card. (300-1800 m)
L. glaucum (Schwaegr.) Mitt. (0-20 m)
L. octoblepharioides Brid. (500-1450 m)
Octoblepharum albidum Hedw. (0-1450 m)

Meteoriaceae (Norris & Koponen 1985a)
Aerobryidium crispifolium (Broth. & Geh.) Fleisch. (750-1000 m)
A. fuscescens Bartr. (1400-2200 m)
Aerobryopsis longissima (Dozy & Molk.) C. Müll. (400-1500 m)
A. leptostigmata (Geh.) Fleisch. (700-1100 m)
Aerobryum speciosum Dozy & Molk. (1800-2400 m)
Barbella cubensis (Mitt.) Broth. (1000-1800 m)
Floribundaria floribunda (Dozy & Molk.) Fleisch. (100-3250 m)
F. pseudofloribunda Fleisch. (100-1700 m)
F. sparsa (Mitt.) Broth. (1800-3200 m)
Meteoriopsis reclinata (C. Müll.) Fleisch. (400-2400 m)
M. squarrosa (Hook.) Fleisch. in Broth. (1500-2400 m)
Meteorium buchananii (Brid.) Broth. (400-3200 m)
Papillaria flexicaulis (Wils.) Jaeg. (1500-2400 m)
P. fuscescens (Hook.) Jaeg. (1200-2400 m)
Pseudobarbella ancistrodes (Ren. & Card.) Manuel (500-1900 m)

Mniaceae (Koponen & Norris 1983b)
Orthomnion elimbatum (Nog.) T. Kop. (350-3300 m)
Plagiomnium cordatum T. Kop. & Norris (2500-3600 m)
P. integrum (Bosch & Sande Lac.) T. Kop. (350-3500 m)
 - - var. *subelimbatum* (Dix.) T. Kop. & Norris (1250-1900 m)
P. succulentum (Mitt.) T. Kop. (1550-1900 m)

Neckeraceae (Enroth 1989a)
Himantocladium plumula (Nees) Fleisch. (350-650 m)
H. submontanum Enroth (1500-2100 m)
Homaliodendron flabellatum (Sm.) Fleisch. (300-3350 m)
Neckeropsis gracilentata (Bosch & Sande Lac.) Fleisch. (0-800 m)
N. lepineaana (Mont.) Fleisch. (350-1900 m)
Pinnatella anacamptolepis (C. Müll.)