LATE QUATERNARY VEGETATIONAL HISTORY OF THE ENGA PROVINCE OF UPLAND PAPUA NEW GUINEA

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Stratigraphies and pollen analyses are reported from three sites within 25 km east and west from Wabag in the highlands of Papua New Guinea, namely:

Sirunki, 2500 m above sea level, 32000 to 1500 yr Inferred Ages;
Inim, 2500 m above sea level, 10000 to 0 yr Inferred Ages;
Birip, 1900 m above sea level, 2300 to 0 yr Inferred Ages.

Events evidenced by these data are described against a time scale of Inferred Ages (I.A.) based on radiocarbon dates and stratigraphic considerations. The pollen analytical data from Sirunki are presented in terms of pollen recovery (deposition) rates as grains per square centimetre per year (grains $\mathrm{cm^{-2}\ a^{-1}}$) and their interpretation controlled by information about total pollen deposition rates and differential pollen production and transport at the present day.

Around Sirunki, the composition of the vegetation before 27500 I.A. is enigmatic, although almost certainly it was treeless. From then until 9000 I.A. subalpine and alpine conditions dominated except during two short periods when forest taxa grew in the catchment. Final afforestation began about 9000 I.A. but the composition of the forest did not stabilize until about 3000 years later. This relative stability was short-lived; soon after 5000 I.A. fluctuations in forest composition began. These fluctuations were associated with periodic changes in the proportion of forested to unforested land.

The Inim data lead to conclusions generally compatible with those drawn from Sirunki. However, data from the two areas differ in detail, particularly in the later onset of change in the local forests about 2000 I.A. and its intensification, coeval with a diminution in forest area, after 500 I.A.

The short record from Birip is dominated by seral changes on the crater wall itself but the main indicators of forest disturbance and unforested areas were already there at its beginning (2300 I.A.). It seems likely that general forest destruction began, or gained greater impetus, around Birip about 450 I.A.

In the most general terms, the forest taxa, recorded by pollen analysis, have behaved consistently with their present distributions and ecological relationships throughout the last 30000 years. More detailed resolution, however, exposes many deviations from this generalization. The majority of taxa are usually associated in groups which vary in their composition repeatedly during a few thousand years, yet some of the taxa occasionally behave entirely individualistically.

The establishment of forest broadly comparable with that growing around Sirunki today began about 9000 I.A., when the main components entered the catchment, but took about 2500 years to achieve balance and a repeated regeneration process. About 4500 I.A., the relationship between forest canopy trees and forest ephemerals changed from one explicable in terms of the latter's rôle in natural forest regeneration to one suggestive of the ephemerals' wide spread through the forest which could only have been achieved by degradation of the canopy.

It is suggested that a rise in the Sirunki basin's water level and the destruction of the surrounding forest about 13500 I.A. may have been due to seismic activity. The failure of the forest to re-establish there until 9000 I.A. was perhaps due to continued earth movement and partially to climatic conditions.

The vegetation record from Sirunki suggests that the mean annual temperature there was similar to that of today between 27000 I.A. and 25500 I.A. but fell irregularly thereafter until between 18500 I.A. and 16000 I.A. it was probably about 10 °C below present. The mean annual temperature rose rapidly after 16000 I.A. and was within 1 °C of its present level by 13500 I.A.

The cold episode between 18500 I.A. and 16000 I.A. corresponds with the last glacial maximum at higher altitudes in New Guinea. Pollen analytical evidence of the altitude of the forest limit and Climap Project Members (1976) estimates of sea surface temperature at that time suggest a temperature lapse rate of about 8.5 °C per 1000 m altitude (compared with 5.8 °C at present), with a firn line kept high, as the geomorphological evidence demands, by low precipitation at high altitudes.

In this coldest period the altitudinal forest limit was about 1500 m below its present level of 3800 m. There is some evidence to suggest that the highest altitude forests of that time may have been quite different from those of today, perhaps containing components of the lower mountain forest canopy as well as the plants of the present upper mountain forest. This implies that the upper mountain forest becomes a separate entity only during comparatively short excursions up the mountains during periods of relatively warm climate.

The low altitude of the forest limit during the last major cold period and its subsequent rise through 1500 m must have had substantial repercussions on the composition of the forests at lower altitudes.

Although there is no archaeological evidence, the pollen analytical data suggest human interference with the forests around Sirunki from about 4300 I.A., which for 1300 years involved clearing of the forest and the enhanced growth of ephemerals of forest and open-land. Subsequently, the forest remained generally degenerate and a new wave of clearing began about 2000 I.A. near both Sirunki and Inim which continued and intensified about 500 I.A. At the lower altitude of Birip, forests were already disturbed by the beginning of the pollen analytical record at about 2300 I.A.

1. INTRODUCTION

(a) *Geography and geology*

The island of New Guinea consists of a high mountain chain flanked by subsidiary ranges and low dissected plateaux rising diagonally from the sea between the equator and 11° south. It is about 1200 km long and 350 km wide at its widest point. Its highest mountains rise above 4000 m. Some of them, in Irian Jaya, bear snow fields and glaciers at the present day (figure 1). The tectonic movements leading to the building of the mountains are believed to have been due to the collision of crustal plates. For a long period until between 11000 and 5000 B.P. the island was joined with Australia across what is now the shallow Arafura Sea and the narrower Torres Strait (Jennings 1972). Minor earth tremors and vulcanicity are still common.

This paper reports the earliest investigations undertaken into the Quaternary vegetational history of New Guinea. They were essayed to determine the amounts and directions of vegetational change in one of the world's three main equatorial land regions. It seemed desirable to choose a montane region in order to avoid the floristic complexity of the tropical lowlands. A place on steep parts of the environmental and vegetational gradients also maximizes the probability of changes in the past having been on such a scale as to be detectable by pollen analysis.

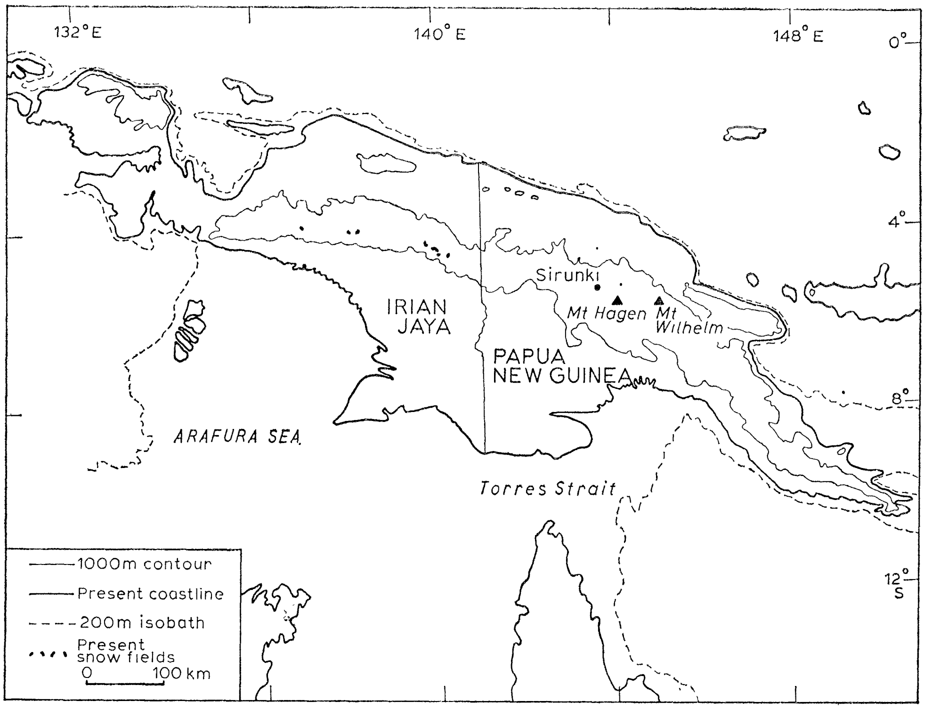


FIGURE 1. Physical features of the island of New Guinea and the location of some of the places named in the text

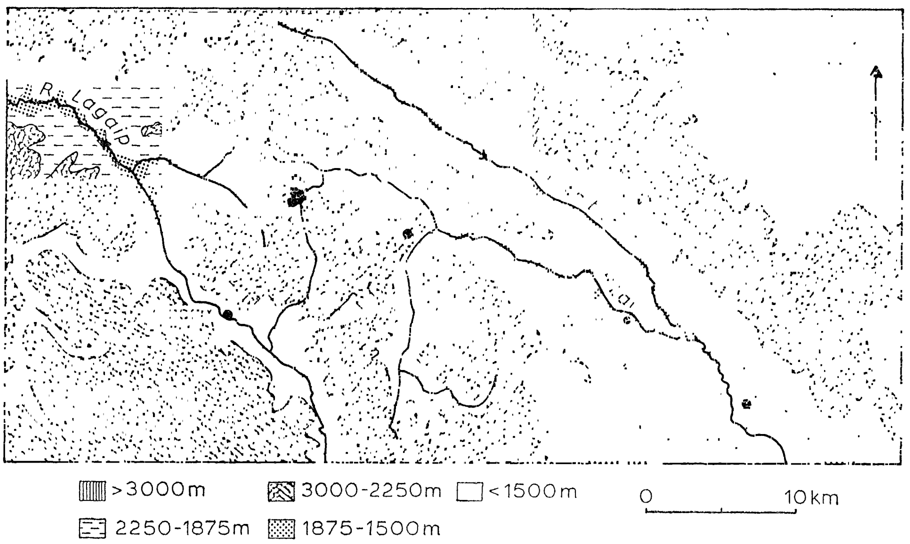


FIGURE 2. Physical features of the Enga Province showing the location of pollen analysis sites and other places mentioned in the text.

A further consideration was that the sites should be outside the range of former glaciation so as to enhance the chance of obtaining a long record, but not so far as to render correlation of major vegetational and glacial events impossible. Finally, in the conditions at that date it was important that the sites should be situated close to motorable tracks. All three sites are in the Enga Province of Papua New Guinea within 25 km east and west of Wabag (figures 2 and 3).

In the central highlands of Papua New Guinea the high mountain ranges trend northwest-southeast. They are constructed mainly from Mesozoic and Tertiary rocks and the greater part of their uplift was a Tertiary event. The ranges are separated by intramontane valleys, a few more than 50 km long and many 5 km wide, the floors of which mostly lie between about 2000 and 1500 m. The rivers draining these valleys frequently meander through thick alluvium, ultimately breaking out as gorges either northward or southward. Valley sides are steep, frequently exceeding 1:20, and ridge tops high (3000–4000 m) and narrow.

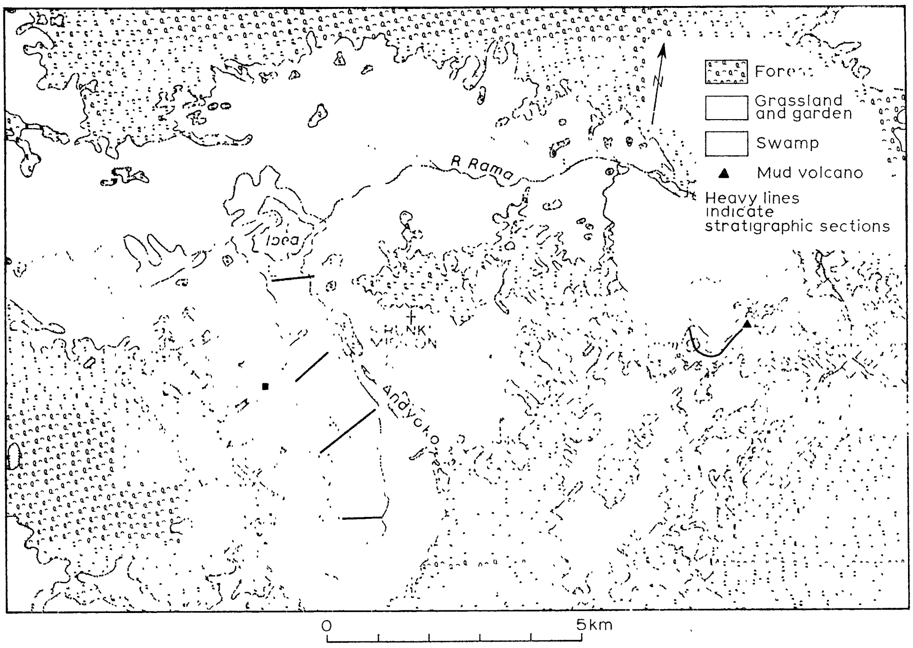


Figure 3. The Sirunki and Lake Ipea region showing main vegetation types and the positions of stratigraphic sections.

In the region around the pollen analysis sites the main intramontane valleys are those of the River Lai, its tributary the River Ambun and the River Lagaip. The River Lai and the River Ambun flow more or less eastward, but the River Lagaip flows in the opposite direction. North of the Lai–Ambun Valley the range rises to 3000 ± 200 m. Southward the ground rises somewhat less steeply to a massif dominated by Sugarloaf Mountain (3700 m) around which subsidiary peaks exceed 3000 m. The northern mountains are composed dominantly of Miocene greywacke, sandstone, conglomerate and shale. South of the Lai Valley, siltstones, shales and limestones which make up the Lagaip beds (upper Cretaceous–lower Miocene) predominate with small and isolated bands of lower Miocene Tibinini Limestone also outcropping (Dekker & Faulks 1964). There are also extensive overlays of Quaternary volcanic ash, mostly from outside the immediate area. The closest evidence of glaciation to the sites investigated is on the Doma Peaks, Mt Hagen and Mt Giluwe, which are all about 80 km distant.

(*b*) *Climate*

By comparison with the African and most of the South American montane tropics, those of Papua New Guinea have a maritime climate. In the northern summer the inter-tropical convergence zone lies some distance north of the island so that, even at the altitude of the Enga Province, the dominant air streams are southeast (trades) to east (tropical easterlies). In the southern summer the equatorial trough of low pressure runs slightly south of the island. Up to about 4500 m, therefore, dominant air flow is from the northwest at that time. Above this level, however, easterlies still predominate (Falls 1975). Hence there is no season when regional air flow does not ensure a supply of moist air to the Enga Province generally, although the actual distribution of its potential rain may be patchy due to rain-shadow and other topographical effects. The mountain valleys contain their own local circulations which in fact largely determine the frequency, timing and intensity of rainfall within the overall seasonal pattern. Most years there is no water deficit, as adequate year-round input from regional winds compensates for evaporation and run-off.

In the Enga Province, rainfall is variable throughout the year; at Wabag, with an annual average of 3015 mm, the standard deviations of monthly means varied from 16% to 49% of the means themselves during 12 years (Brookfield & Hart 1966). Nevertheless, there is usually a period from May to August during which average monthly rainfalls lie between 75 and 200 mm, followed by a somewhat erratic passage to the February–April period with averages between 200 and 330 mm per month. Mean monthly temperature varies little more than 0.5 °C from the annual mean throughout the year. At Wabag, extreme screen maxima are rarely more than 10 °C above the annual mean whilst extreme screen minima very rarely fall below 3 °C and are usually above 5 °C; extreme temperatures are most common during the less wet parts of the year (data from McAlpine *et al.* 1975).

A simple plot of mean annual temperature for Papua New Guinea stations between 200 m (avoiding the local influences on coastal stations) and 2000 m gives a lapse rate of 5.8 °C per 1000 m altitude. Extrapolated, this curve provides an estimate of 28.5 °C at sea level, almost exactly the recorded sea surface temperature in the New Guinea region (U.S. Hydrographic Office, 1969). It predicts a 2 °C annual mean at 4550 m, the average altitude of the firn line on Mt Jaya (Mt Carstensz, Irian Jaya), compared with an estimate of about 1 °C from nearby field temperature measurements there (Hope & Peterson 1975; Allison & Bennett, 1976). Mean annual maxima and minima fall at rates of 5.3 °C and 5.7 °C per 1000 m altitude. Values for annual extremes are more widely scattered but the lapse rates for the extreme summer maxima and extreme winter minima appear to be significantly smaller and greater respectively than that for the mean.

Nocturnal cold air drainage on local and regional scales is a common phenomenon in the Enga Province. On the other hand, temperature inversion was not recorded during the most likely months of 1962 near Sirunki (Walker 1966), although the basin suffered frost effects during the 1972 drought (Brown & Powell 1974).

Rain falls on most days, but periods of three to six consecutive days with less than 1 mm of rain are recorded throughout the year at Wabag. Such rainless periods are commonest between April and June when even longer ones (20 days) also occur. More prolonged droughts are rare and associated with clear skies leading to extreme daily maximum and minimum temperatures. Such a period lasted from June to November 1972 and caused extensive damage and death to crops and selected trees through water stress and frost (Brown & Powell 1974; Bureau of Meterology 1973). Events of this severity probably do not occur more frequently than once in 20 years but they precipitate significant, if temporary, demographic changes.

Of the three pollen analysis sites, Birip must experience substantially the same climate as Wapenamanda (figure 2). Sirunki and Inim are probably very similar to each other. The short run of rainfall and temperature data from Sirunki for 1962 (Walker 1966) and the rainfall records for 1967–9 (McAlpine *et al.* 1975) indicate that the rainfall distribution throughout the year corresponds with the regional pattern, that the amount of rain falling in any month is similar to that recorded for Laiagam and that mean temperatures fluctuate in phase with those at Wabag but about 2–3 °C below them.

(*c*) *Man and agriculture*

In common with most parts of the highlands of Papua New Guinea, the valleys of the Enga Province between 1500 and 2100 m are densely populated and more patchy settlement extends to about 2700 m. In some places densities close to 100 persons per km^2 are recorded. Traditionally the people live in dispersed settlements, group centres being provided by cleared dancing grounds often bordered by planted trees, some of which are exotic to the district. Sweet potato (*Ipomoea batatas*) is the staple, grown in mounded allotments moved through a group's territory which is otherwise occupied by grass fallow, regrowth woodland, swamp and forest. Forest is cleared, traditionally by polished stone axe and fire, to provide new garden areas when the fertility or amount of other available land is judged inadequate (Waddell 1972).

Pigs are the common domestic animal, their populations fluctuating with the demands of traditional exchange practices. They run, under supervision, in the grass fallows, abandoned gardens and swamps and are fed sweet potatoes when necessary.

In addition to sweet potatoes, some taro (*Colocasia esculenta*) is grown in the warmer swamps and ditches and a small proportion of the better land is used for mixed gardens. The latter provide green vegetables (e.g. *Rungia klossii*, *Amaranthus* spp.), sugar cane (*Saccharum officinarum*), winged beans (*Psophocarpus tetragonolobus*) and introduced plants such as corn (*Zea mays*). The same vegetables are sometimes planted amongst the sweet potatoes.

The forest is exploited as a source of food and other useful resources. Mammals and birds are hunted with enthusiasm but probably not with sufficient skill or regularity seriously to deplete populations. Many plant products are collected (e.g. *Castanopsis* and *Pandanus* nuts, *Ficus* leaves and bark, *Garcinia* and *Nothofagus* wood) and some trees (e.g. *Pandanus* spp.) are both conserved and planted. The collection of timber for firewood, house building and fencing is probably the activity causing greatest and most selective modification of the forest within easy reach of human settlement. However, plantations of *Casuarina oligodon* in garden fallows and the use of quick-set *Dodonaea viscosa* and *Cordyline* sp. and of cane grasses for fences reduce the potential impact considerably (Flenley 1967; Meggitt 1958; Powell 1976; Waddell 1972; Walker 1966).

The Lai Valley around Birip is closely settled and in the climatically least rigorous part of the Enga Province. Sweet potatoes mature about five months after planting and taro and banana can be grown successfully. Sirunki and Inim, by contrast, are close to the altitudinal limit of agriculture. Sweet potatoes commonly take a year to mature and only a small selection of native vegetables can be grown, although many European introductions flourish. The people of such places are the most susceptible to deprivation as a result of inclement weather, particularly drought and frost.

(*d*) *Vegetation and its environmental correlates*

The vegetation of Papua New Guinea is usually described and classified on a structural basis, limited taxonomic lists being attributed to classes to 'typify' them floristically (e.g. Paijmans 1975). In the present account such a system will be avoided wherever possible in favour of a floristically determined classification. The state of taxonomy rarely allows certain identification below the genus so that even floristic assemblages may lack ecological reality (Walker & Guppy 1976).

Lowland rainforest extends from sea level to between 900–1400 m where it passes into a floristically and structurally dissimilar mountain forest, the exact level of transition depending on local factors. Walker & Guppy (1976) recognize a significant, but less striking, floristic break between 2800 and 3000 m dividing their lower mountain forest from the upper mountain forest. At generic level the main feature is the loss of many taxa in a small altitudinal interval. The limited data available suggest that the upper mountain forest is composed of four nodal types (D, C, B and A) one of which (D) may be but a geographical variant of another (C) with which it shares its altitudinal range. Types C, B and A are progressively poorer in genera; C extends from 3000 to 3350 m, B from 3350 to 3600 m and A from 3600 m to the forest limit (*ca.* 3800 m), each boundary being modified by local conditions such as soil, aspect and cold air drainage.

The lower mountain forest is a complex of variants. Floristically it can be divided into a generically rich node (type F) and one from which an inconstant variety of genera is excluded (type E). The two are not altitudinally distinguished but type E tends to be found in places where environmental disturbances of some kind (e.g. intense gathering, Late Quaternary vulcanicity) are more evident. Other authors have recognized units such as beech forests (typified by *Nothofagus* spp.), oak forest (typified by *Castanopsis acuminatissima* and *Lithocarpus* spp.) and conifer forest (typified by *Podocarpus* spp. and *Phyllocladus hypophyllus*) which are distinct from mixed forest in which all the typifying genera occur. There is no doubt that forest stands occur for which such names can reasonably be used to describe the quantitative dominance of the gregarious plant named, but their relative status is dubious. More particularly, there is nothing to sustain the view that these types have discrete altitudinal ranges, other than those imparted by the limits of their dominants; the accompanying genera occur in several or all of the supposed 'types' and in the 'mixed' forest.

TABLE 1. TEMPERATURE CORRELATES OF MAJOR VEGETATION BOUNDARIES AND OF THE ALTITUDINAL LIMITS OF SELECTED TAXA BASED ON CALCULATED TEMPERATURE LAPSE RATES (p. 270)

(Sources of plant records: 1, specimens in Lae Herbarium (number of sheets in parentheses); 2, literature including Johns & Stevens (1971), Smith (1975*a*), Walker & Guppy (1976). Maxima and minima are rounded upwards and downwards respectively. All temperatures are subject to an error of ± 1 °C from the calculation of the lapse rates and of an unknown amount from inadequacies of plant records. l.l., Lower limit; u.l., Upper limit.)

		temperature/°C		
vegetation type or genus	source of plant data	mean annual	mean annual maximum	mean annual minimum
barren l.l.	2	1	8	< 0
tropicalpine tundra l.l.	2	4	10	< 0
forest limit u.l.	2	6	13	1
natural lower mountain grassland in cold air drainage and bog l.l.	2	10–12	17–18	6–7
upper mountain forest l.l.	2	11–12	17–18	6–7
lower mountain forest l.l.	2	20–22	25–27	14–7

TABLE 1 (*cont.*)

			temperature/°C		
vegetation type or genus		source of plant data	mean annual	mean annual maximum	mean annual minimum
Acalypha	u.l.	1 (> 90)	12	19	8
Acronychia	u.l.	2	8	14	2
Ascarina	u.l.	1 (59)	9	16	4
	l.l.	1 (59)	22	27	16
Astelia	u.l.	1 (52)	3	10	< 0
	l.l.	2	12	18	6
Castanopsis	u.l.	1 (> 140)	12	19	8
Casuarina	u.l.	1 (> 32)	12	18	7
Claoxylon	u.l.	2	11	17	6
Coprosma	u.l.	1 (> 130)	4	10	< 0
	l.l.	1 (> 130)	15	21	9
Dacrycarpus	u.l.	1 (120)	5	12	0
	l.l.	1 (120)	24	29	19
Dodonaea	u.l.	1 (42)	9	15	3
Drapetes	u.l.	1 (51), 2	1	8	< 0
	l.l.	1 (51)	11	17	6
Drimys	u.l.	2	5	12	< 0
Engelhardtia	u.l.	1 (27)	15	21	9
Evodiella	u.l.	2	8	15	3
Gentiana	u.l.	1 (133)	2	9	< 0
	l.l.	2	23	28	18
Glochidion	u.l.	2	14	20	9
Ilex	u.l.	2	10	16	5
Lithocarpus	u.l.	1 (> 100)	12	18	6
Litsea	u.l.	2	11	18	6
Macaranga	u.l.	1 (> 200)	11	17	5
Meliosma	u.l.	2	11	18	6
Myrtaceae	u.l.	2	7	14	1
Nothofagus	u.l.	1 (190), 2	11	17	5
Omalanthus	u.l.	2	9	15	4
Opocunonia	u.l.	1 (36)	12	18	7
Papuacedrus	u.l.	1 (79)	8	15	3
	l.l.	1 (79)	23	29	8
Phyllanthus	u.l.	2	12	18	6
Phyllocladus	u.l.	1 (32)	9	15	4
Piper	u.l.	2	8	15	3
Plantago major and *P. lanceolata*	u.l.	1 (7)	8	15	3
	l.l.	1 (7)	28	33	23
Plantago other *spp.*	u.l.	1 (55)	4	11	< 0
	l.l.	1 (55)	15	21	9
Podocarpus	u.l.	1 (178)	6	13	1
Polyosma	u.l.	2	7	13	1
Proteaceae	u.l.	2	11	17	5
Pygeum	u.l.	2	7	14	2
Quintinia	u.l.	1 (148), 2	6	12	0
	l.l.	1 (148)	24	29	18
Rapanea	u.l.	1 (> 300)	6	12	0
	l.l.	1 (> 300)	19	25	14
Saurauia	u.l.	1 (516)	7	14	2
Sloanea	u.l.	2	12	18	6
Sphenostemon	u.l.	2	9	15	4
Styphelia	u.l.	1 (92)	2	9	< 0
	l.l.	1 (92)	19	14	25
Trema	u.l.	1 (36)	12	18	6

Such evidence as there is indicates that the transition from lower to upper mountain forest is altitudinally consistent, although possibly somewhat higher in the west than in the east of the island; the same is true of the altitudinal limit of the forest. Although the altitudinal limit of a taxon or vegetation unit must be determined by a complex of factors, the one most consistently correlated with altitude in Papua New Guinea is mean annual temperature. The temperature correlates of the main altitudinal vegetation changes and of the altitudinal limits of a number of taxa are shown in table 1.

The lower to upper mountain forest transition also correlates roughly with the lowest level of former valley glaciation on the larger high mountains and it may be that the resultant soil differences have a strong selective effect on the vegetation above and below. It is often, but not always, about the level of longest cloud lie on average days, a factor which certainly affects both the structure and floristic composition of the forests subjected to it.

Of the commonly recognized variants within the lower mountain forest, a variant rich in *Nothofagus* Bl. subsection *Bipartitae* Steen., or 'Beech forest', seems often to grow in places either strongly disturbed in the past or subject to continuous exposure. It is suspected that this variant is transitional to a floristically more varied forest in which it plays a less dominant and gregarious rôle (Walker 1966; Hynes 1974; Johns, personal communication).

It is suspected that 'Oak forest' (*Castanopsis acuminatissima*, *Lithocarpus* spp.) is the product of intense human disturbance. *C. acuminatissima* in particular is a gregarious species, the timber of which is prized for buildings and weapon making. It regenerates freely in partially cleared forests.

'Conifer forests' are varied in their composition and occurrence but are frequently thought to be transitory after major environmental disturbance (e.g. vulcanism). They also occupy environmentally extreme sites. Cold-air drainage pockets are often ringed by the frost-tolerant *Dacrycarpus compactus* and *Papuacedrus papuanus* with *Podocarpus* spp. in the less cold places providing a transition to the surrounding, more mixed, forest. Some swamps bear a sparse cover of *Dacrydium elatum*, *Podocarpus imbricatus* and *Pandanus* sp. *Dacrycarpus compactus* also occurs in nearly pure stands at the altitudinal forest limit.

Ecotones between forest and grassland often have characteristic associations of taxa (Gillison 1970, Wade & McVean 1969) in which shrubs (e.g. *Coprosma* spp., *Olearia* spp., *Rhododendron* spp.) dominate and regenerate.

Below its altitudinal limit (2800 m) *Casuarina oligodon* grows abundantly along stream banks and gravel ridges, and is sometimes planted in fallow gardens as a timber crop. It is the commonest fence and roadside-planted tree. At higher altitudes it is replaced as a fence tree by *Dodonaea viscosa* or *Cordyline fruticosa*.

'Grasslands' are extensive in the intramontane valleys within the lower mountain forest. In swampy or riverine bottoms they may be dominated by tall cane grasses (e.g. *Miscanthus floridulus*, *Phragmites karka*, *Saccharum spontaneum*), sedges (e.g. *Elaeocharis sphacelata*, *Machaerina rubiginosa*, *Cyperus* spp.) or *Acorus calamus*. In such places fens and bogs may also develop in which *Gleichenia vulcanica*, *Lycopodium cernuum* and *Sphagnum* spp. commonly grow (Flenley 1967; Walker 1972). The effects of cold air drainage often contribute to the treelessness of already waterlogged hollows and valleys and provide habitats for otherwise subalpine plants substantially below their normal ranges (Smith 1975*a*). Such occurrences are less common, however, where sites are separated from higher altitudes by forest.

In the Papua New Guinea highlands generally, grassland occupies most valley slopes, often between patches of shrubby growth and current gardens, up to about 2600 m. There are strong reasons for supposing that much of this results from gardening of formerly forested areas and the subsequent effects of fire and pigs. Some of this type of land is part of the current short fallow cycle, some will not be gardened for decades, if ever again, some is planted unsystematically with rapidly growing timber trees (e.g. *Casuarina oligodon, Trema amboinensis*), more is studded with isolated 'regrowth' trees and shrubs (e.g. *Saurauia* spp., *Acalypha* spp.) whilst a very small proportion near the forest edge is encroached upon by pioneer forest species (e.g. *Weinmannia urdanetensis, Macaranga* spp.). It is impossible, however, certainly to separate those forest free areas created entirely by human activity from those initiated or maintained by soil instability (including landslips), waterlogging or cold air drainage. All types bear various mixtures of *Miscanthus floridulus, Imperata cylindrica, Rhododendron macgregoriae, Dodonaea viscosa, Omalanthus* spp. and many others (Flenley 1967; Powell 1970; Walker 1966).

The upper mountain forest decreases in stature, in structural complexity and floristic diversity with increasing altitude. At the generic level it is an altitudinal attenuation of the lower mountain forest but many of its species (e.g. *Pittosporum pullifolium, Coprosma papuensis*) do not occur at the lower level. Toward the forest limit (*ca.* 3800 m) a few gregarious trees (e.g. *Dacrycarpus compactus*) and shrubs (e.g. *Rapanea vaccinioides*) are especially common whilst subalpine shrubs from beyond the forest limit grow in its understorey (e.g. *Styphelia suaveolens, Trochocarpa dispersa*). The forest edge is commonly affected by the fires of hunting parties, but outlying stands of *Dacrycarpus compactus* and wood charcoal in the topsoil bears witness to its former extent (Smith 1975*b*; Wade & McVean 1969; Walker 1968).

Above the natural forest limit lies the upper mountain grassland (Smith 1975*b*), in which tussock grasses (e.g. *Poa callosa, Danthonia vestita*) grow with low shrubs (e.g. *Styphelia suaveolens, Trochocarpa dekockii*) and herbs (e.g. *Drapetes ericoides, Detzneria tubata*). Where the forest limit has been depressed, and in valleys affected by cold air ponding and impeded drainage, this upper mountain grassland merges downwards into tall tussock grassland (*Deschampsia klossii, Poa nivicola, Hierochloe redolens*) and valley bottom mires. Stands of *Cyathea*, particularly *C. atrox*, are frequently found on better drained sites in such valleys and are variously regarded as stable subalpine woodlands (Hope, personal communication) or as remnants from forest destruction (Paijmans 1975).

Alpine vegetation does not grow in the Enga Province but, from elsewhere in New Guinea, Smith (1975*b*) has distinguished tropicalpine tundra between about 4300 m (the top of the upper mountain grassland) and the permanent snowline at about 4700 m. In this zone, vegetation is discontinuous; patterned ground, shattered and bare rock are common. Amongst the herbs at this altitude are *Ranunculus saruwagedicus, Oreomyrrhis pumila,* and *Monostachya oreoboloides* together with the mosses *Rhacomitrium crispulum* and *R. lanuginosum.*

In summary, the montane vegetation of Papua New Guinea is mainly altitudinally differentiated, presumably by temperature effects, above 2800–3000 m. Except at the highest elevations (above *ca.* 4000 m), human activities are important in determining the forest-grassland balance and in modifying both forest and grassland close to habitations. Aspect, slope stability, impedence of drainage and cold-air ponding also exercise significant control on plant patterns at all elevations.

2. Pollen analysis sites (figure 2)

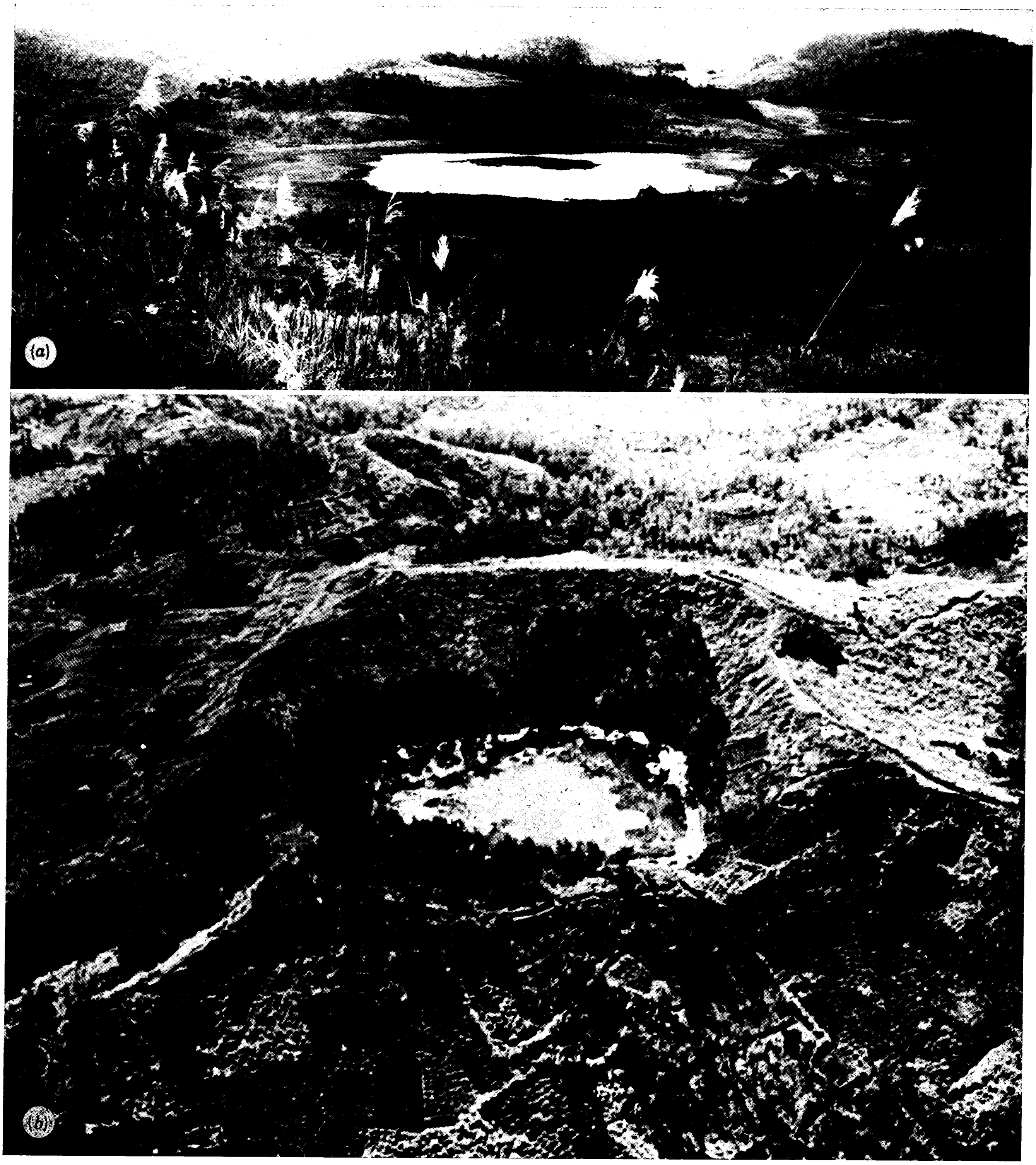
Sirunki (plate 1), 30 km west-northwest of Wabag, takes its name from a nearby settlement which has gained special identification on maps by the location there of a Christian mission since 1951. It is south of the main ridge of the Central Range which runs at 2800 to 3000 m about 12 km away. The rolling landscape immediately around Sirunki lies between 2200 and 2800 m and is formed mainly on Upper Cretaceous to Lower Miocene shales covered by as much as 2 m of yellow, close textured soil often showing evidence of disturbance associated with forest clearance and gardening. Headstreams of the River Lai and River Lagaip have cut back into this landscape and drain the northern and southern ends of the Sirunki site respectively. The site itself lies in a trough in the old rolling surface, roughly divided by fan deposits into the Kayamanda Swamp to the south and Lake Ipea (Iviva) with its associated swamps to the north. The total surface area is about 9 km^2. A fault bounds the eastern edge of the Kayamanda swamp along which Tertiary mudstones and limestones rise steeply to the Andyoko Ridge at 2800–3000 m. Elsewhere the ground rises more gently on shales cut by small watercourses. Only two substantial streams enter the swamp, each associated with an alluvial fan which together almost divide the basin across. The possibility that the fault along the edge of the Kayamanda Swamp is still active and that a variety of small tectonic movements may have affected the basin during its infilling cannot be ruled out (Guilcher 1970). There are no remnants of volcanoes in the vicinity but discontinuous ash layers are encountered in road cuttings, particularly on valley sides where they are stratified into accretions of soil. The swamp surface lies at *ca.* 2500 m.

The vegetation of the Sirunki area has been described by Walker (1966, 1972) and by Flenley (1969). It lies at the altitudinal limit of human habitation and horticulture yet 60% of the land surface within 5 km of the site is either garden or grassland; the rest is forest. Most of the forest is rather undifferentiated lower mountain type with a strong development of *Nothofagus pullei* on the slopes rising northward up the Central Range. The uppermost slopes of Andyoko and probably also of the Central Range bear upper mountain forest, at the former locality moss hung and often cloud shrouded.

Inim (plate 2) lies in a valley in the same upland block as Sirunki and 6 km west from it, poised above the deeply incised Rama headwater of the River Lai. The Inim valley is swamp filled, except for its northwestern end which harbours a lake; the total surface area of the site is about 0.3 km^2 (Flenley 1972). The origin of the impounding of a swamp and lake in the valley is obscure although usually attributed to tectonic movement (Ward 1949) and the deposition of volcanic material (Dekker & Faulks 1964). In and around the valley are several mud volcanoes which are said to be most active after heavy rain and which produce a cold slurry of limestone chips in a grey clay matrix. Emission is slow and accompanied by occasional bubbles of gas. The swamp surface lies at *ca.* 2550 m and none of the very small streams which drain into the valley penetrates it. The outflow stream from the lake runs beneath the surface in its short passage northward to leave the valley through a low rock barrier and on to join the River Rama.

The valley is well defined by slopes rising steeply southward to about 2800 m on what is an eastern extension of the Andyoko Ridge. From this high area two spurs run northward, one on each side of Inim, their tops lying about 100 m above lake level. Streams run northward, parallel with these ridges, somewhat below the level of Inim but only about a kilometre from it. Immediately north of Inim itself, the ground is broken and lies only slightly above lake level until

Lake Ipea and the swamp at Sirunki viewed from the northwest.



(*a*) Lake Inim viewed from the southwest. (*b*) The crater lake at Birip viewed from the north.

it descends steeply into the Rama Valley about 1 km from the lake. Within 5 km of the site 40% of the ground is occupied by grassland and garden, the rest being lower mountain forest (Flenley 1967, 1969).

Birip (plate 2) is a volcanic cone rising from the Lai Valley 11 km east of Wabag. At this point the main river runs at a height of 1450 m and the slopes have risen only to about 1500 m at the base of the cone about 1 km east of the river. Further northeast the ground rises gently for 2 km and then steepens reaching a 3000 m spur of Nose Mountain about 6 km from Birip. The dominant surface rocks in the area are Miocene sandstones and greywackes which are partially shrouded by Quaternary volcanic materials. Soils of the main valley slopes are orange, yellow and lateritic. The river carries a moderate load, especially after rain, and flows in a narrow flood plain. The cone itself is fairly symmetrical and steep sided. Its rim is about 450 m above the valley floor and the inner slopes fall 40 m to a crater lake about 0.03 km^2 in area. There are no streams flowing from its extremely small (*ca.* 0.15 km^2) catchment, nor is there any sign of erosion across the one low point in the rim. The water level in the lake has probably always fluctuated seasonally through the 50 cm interval currently observed, some protection against greater rise being afforded by seepage issuing as springs on the outer slopes of the cone.

The lake supports a marginal swamp about 50 m wide in which *Scirpus mucronatus* is the most prominent plant. The inner slopes are clothed by gardens, *Miscanthus floridulus* grassland and a woodland of *Casuarina oligodon* (figure 7). The Lai Valley in this reach is totally deforested and covered by grassland and garden up to about 2500 m. Above that, the slopes bear lower mountain forest.

Sirunki and Inim on the one hand and Birip on the other, separated by 30 km and by 1000 m altitude, represent the extremes of the landscapes of the Enga Province. Unfortunately, the record from Birip is too short to allow a comparative account of the vegetational history of the two areas and indications of the probable course of events at such low elevations must be drawn from sites 35 km southeast near Mt Hagen (Powell 1970; Powell *et al.* 1975).

3. Chronology

Radiocarbon dates (table 2) provide the base from which the chronologies of all three sites are separately developed. In estimating an Inferred Age (I.A.) before 2000 A.D. for an event, radiocarbon ages between 350 and 6000 years B.P. have first been corrected for divergence from dendrochronological age (Damon *et al.* 1974). An event not directly dated by a radiocarbon sample has had an Inferred Age allocated to it by interpolation between corrected radiocarbon dates and the indications of stratigraphy (e.g. unconformity, varied accumulation rates). Inferred Ages are therefore subject to the error of the original radiocarbon determination, to those of its correction and to errors of interpretation involved in the interpolations. These last are highly subjective, yet it has been useful to put a value on the supposed total error as an indication of the authors' view of their probable magnitudes. Inferred Ages therefore carry an error term compounded from all these sources which has no statistical significance but indicates the range of age within which, in the authors' opinion, the event probably falls. In some instances an Inferred Age is determined from other considerations which are explained in each individual case.

Samples for radiocarbon dating could only be collected from the actual core from which detailed stratigraphic or pollen analysis data were collected in four instances. This unfortunate

TABLE 2. RADIOCARBON DATES FROM POLLEN ANALYSIS SITES

core	level in cm below sampling datum	level in cm below site datum	material	radiocarbon dating laboratory number	radiocarbon years B.P.‡	calendar years B.P.§	reference
				Sirunki			
A16	115–125	215–225	coarse detritus mud	GX3864	1275 ± 110	1253 ± 171	H. W. Kreuger (personal communication 1975)
A16	217–225	317–325	coarse detritus mud	N1522	2150 ± 75	2193 ± 170	T. Hamada (personal communication 1973)
A16	320–330	420–430	coarse detritus mud	GX3865	2850 ± 100	3050 ± 159	H. W. Kreuger (personal communication 1975)
A16†	595–610	695–710	coarse detritus mud	NSW18			
				a	3800 ± 72	4288 ± 168	J. H. Green (personal communication 1967)
				b (humic)	3950 ± 64	4498 ± 165	
A16	965–985	1065–1085	fine detritus mud	N1523	9260 ± 120	.	T. Hamada (personal communication 1973)
A16	1305–1323	1405–1423	detritus mud	N1524	14100 ± 175	.	T. Hamada (personal communication 1973)
A16†	1475–1490	1575–1590	fine detritus mud	NSW27			
				a	14200 ± 250	.	J. H. Green (personal communication 1967)
				b (humic)	14550 ± 300	.	
A16	1633–1645	1733–1745	fine detritus mud	N1525	19900 ± 320	.	T. Hamada (personal communication 1973)
A16†	2030–2045	2130–2145	fine detritus mud	NSW19			
				a	25800 ± 650	.	J. H. Green (personal communication 1967)
				b (humic)	26000 ± 650	.	
C1†	625–630	660–665	fine detritus mud	GaK1551	8400 ± 150	.	K. Kigoshi (personal communication 1968)
C1†	1695–1710	1730–1745	fine detritus mud	GaK1554	29700^{+1900}_{-1500}	.	K. Kigoshi (personal communication 1968)
C1†	1720–1725	1755–1760	fine detritus mud	NSW26			
				a	> 30000	.	J. H. Green (personal communication 1967)
				b (humic)	> 32850	.	
C8†	340–370	460–490	fine detritus mud	N1526	2580 ± 65	2709 ± 145	T. Hamada (personal communication 1973)
C8†	925–950	1045–1070	fine detritus mud	GaK1552	26200 ± 1100	.	K. Kigoshi (personal communication 1968)
C8†	950–1000	1070–1120	nekron mud	N1527	28900 ± 880	.	T. Hamada (personal communication 1973)
C8†	1010–1020	1130–1150	nekron mud	GX3645	≧ 32000	.	R. R. Pardi (personal communication 1974)
C8†	1090–1100	1210–1220	fine detritus mud	GX3644	≧ 45000	.	R. R. Pardi (personal communication 1974)
C8†	1195–1210	1315–1330	fine detritus mud	GX3643	> 37000	.	R. R. Pardi (personal communication 1974)

				Inim			
M4†	1680–1685	.	detritus mud	GaK829	3200 ± 90	3503 ± 160	Kigoshi 1967
M4†	1685–1690	.	detritus mud	GaK830	2240 ± 90	2295 ± 178	Kigoshi 1967
M4†	1690–1695	.	detritus mud	GaK831	4550 ± 100	5240 ± 181	Kigoshi 1967
M4†	1916–1921	.	compact fine detritus	GaK662	5760 ± 110	6589 ± 185	Kigoshi 1967
M4†	1921–1926	.	compact fine detritus	GaK663	7340 ± 130	.	Kigoshi 1967
M4†	1926–1931	.	compact fine detritus	GaK664	8310 ± 170	.	Kigoshi 1967
M15†	920–925	.	compact fine detritus	GaK1132	10200 ± 150	.	K. Kigoshi (personal communication 1965)
M15†	925–930	.	compact fine detritus	GaK1133	8560 ± 120	.	K. Kigoshi (personal communication 1965)
M15†	965–970	.	compact fine detritus	GaK1134	9180 ± 100	.	K. Kigoshi (personal communication 1965)
M15†	970–975	.	compact fine detritus	GaK1135	11930 ± 150	.	K. Kigoshi (personal communication 1965)
				Birip			
P14†	62–67	.	coarse detritus mud	ANU79	305 ± 90	.	Polach *et al.* 1968
P14†	67–72	.	coarse detritus mud	ANU63	2930 ± 140	3152 ± 187	Polach *et al.* 1968
P14†	72–77	.	coarse detritus mud	ANU64	275 ± 70	.	Polach *et al.* 1968
P14†	77–82	.	coarse detritus mud	ANU80	140 ± 70	.	Polach *et al.* 1968
P14†	215–220	.	coarse detritus mud	GaK825	1520 ± 100	1500 ± 158	Kigoshi 1967
P14†	220–225	.	coarse detritus mud	GaK826	1970 ± 100	1985 ± 160	Kigoshi 1967
P14†	225–230	.	coarse detritus mud	GaK827	1920 ± 90	1930 ± 154	Kigoshi 1967
P14†	230–235	.	coarse detritus mud	GaK828	2140 ± 90	2180 ± 178	Kigoshi 1967
P14†	270–275	.	fine detritus mud	GaK665	2110 ± 90	2150 ± 178	Kigoshi 1967
P14†	275–280	.	fine detritus mud	GaK666	2440 ± 90	2540 ± 183	Kigoshi 1967
P14†	280–285	.	fine detritus mud	GaK667	2120 ± 90	2160 ± 178	Kigoshi 1967

† Samples obtained from close by named core, usually by up to six multiple-shot samplings with piston sampler, and attributed to it according to depth in relation to surface and clear stratigraphic markers and pollen analysis comparisons.

‡ Based on the Libby half life of 5570 ± 30 yrs.

§ After Damon *et al.* 1974.

circumstance usually arose because of the necessity to collect several (up to six) samples from each level to be dated if the vertical spread of the sample was to be kept small. In all except a few cases separately explained below, multiple shot samples were taken with a piston sampler within a metre of the originally described cores and levels determined by reference to clear stratigraphic markers (e.g. a narrow sand layer identified by its stratigraphic associations and its depth from the surface ± 2 cm). Several millimetres of mud were cleaned from the surface of each sample used for radiocarbon dating. Table 2 lists the radiocarbon dates obtained from the core samples at all three sites.

(*a*) *Sirunki*

The occurrence of limestone in the ridge east of Kayamanda Swamp prompted the analysis of a sample of coarse detritus mud from 0–3 cm below the water covered surface of the swamp and about 500 cm from its eastern edge. The reported age of 0 ± 80 B.P. (J. H. Green, personal communication) together with the facts that pH is rarely above neutrality (Walker 1972) and exchangeable bases are low in both surface water and soil at many sampled points on the swamp, suggest that an 'old carbon error' is unlikely in age determinations of the sediments. Nevertheless, the coarsest detritus available near a significant horizon was always used for dating and in some cases separate determinations of humic acid fractions were obtained. The possibility of less subtle interference with true age determinations was minimized by avoiding sampling close to anything suspected of being detrital or reprecipitated carbonate and by the standard pretreatments of the laboratories concerned.

In the Lake Ipea Basin, three samples (N1526, N1527, GaK1552) were obtained by multiple shots with a 3 cm diameter piston corer grouped about 5 m from core C8. Three others (GX 3643, GX3644, GX3645) were taken in the laboratory from a single 5 cm diameter core taken about 20 m from C8. The detailed stratigraphy in this area is complex but comprehensible and there is no uncertainty in the attribution of the dates to appropriate levels in C8. The complexity of the stratigraphy in core C8 rendered impossible the calculation of sedimentation rates from the dates available. This was attempted for core A16, however, from which the Sirunki A pollen diagram is derived (figures 8 and 9).

The radiocarbon dates from A16 (and their standard errors) were plotted against sample depth after correction of the uppermost four dates (N1522, NSW18, GX3864, GX3865) against the dendrochronological scale (figure 4). When dates were available from bulk sample and humic acid extract, the former was used. A smooth curve relating these points was drawn by eye. A second curve of more varied gradient was then derived from the first, subjectively taking into account stratigraphic changes and probable differences in accumulation rates of the various units. This Inferred Age curve was then extrapolated to 23 m depth and 30500 I.A. Continued in the other direction it cuts the zero of the time scale about 80 cm above swamp level. No correction for this apparent anomaly is required, however, because the uppermost date lies above the top of the pollen diagram; there is also other evidence that slight erosion may recently have occurred. This curve provides Inferred Ages for individual events on core A16 and pollen diagram Sirunki A and is the basis for the calculation of rates of pollen deposition.

The stratigraphy of the deposits was interpreted in ways consistent with the main indications of the radiocarbon dates. Important periods in the history of the site were then identified throughout its deposits and Inferred Ages attributed to them by association with core A16 and, to a lesser extent, with core C8.

Among the radiocarbon dates themselves, N1524 and NSW27 are insignificantly different although 170 cm apart vertically. The smooth accumulation curve is drawn to cut a point midway between them. The material from which they derive is unlikely to have accumulated peculiarly quickly but the Inferred Age curve takes into account the possibility of rather rapid deposition between them. The five dates between 925 and 1210 cm on core C8 are from very compact mud. The two uppermost (GaK1552, N2527) are statistically separable ($p \simeq 0.05$) (Long & Rippeteau 1974) although attributed to contiguous sections of the core. The rest are beyond resolution by the radiocarbon method. For present purposes it seems reasonable to suppose that the deposits dated by these five determinations cover a period from significantly before 30000 I.A. until somewhat after (perhaps 2000 years after) 26000 I.A.

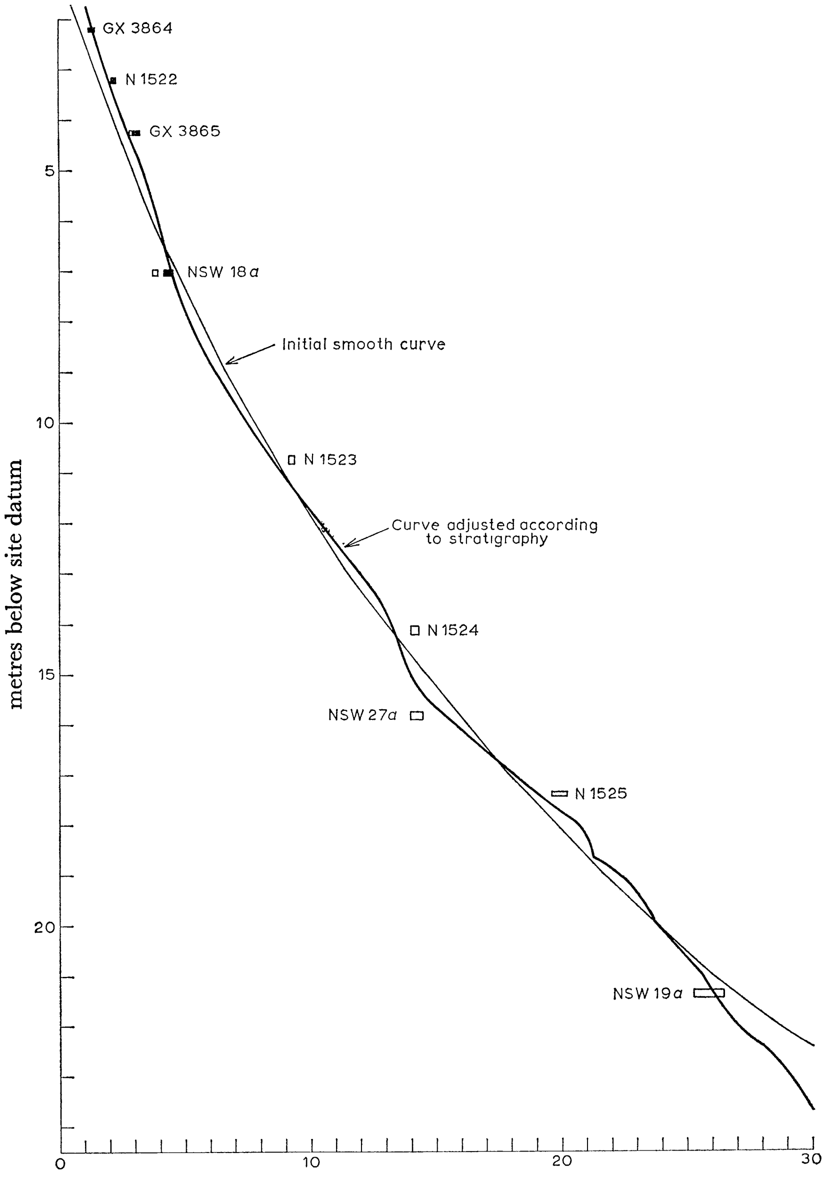


FIGURE 4. Derivation of Sirunki Inferred Age chronology.

(*b*) *Inim*

The two pairs of dates on core M15 are difficult to reconcile. Their averages, weighted according to their error terms (Long & Rippeteau 1974) are significantly different statistically (9216 ± 93, 9867 ± 135) and the accumulation of 45 cm of mud and volcanic ash between these average dates would not have been unreasonable. The big differences between contiguous samples (1640 years, 2750 years) so far exceed the difference between the averages of the pairs (651 years), however, as to discourage their separate use. Perhaps the only safe conclusion is to infer that the weighted average of the four (Long & Rippeteau 1974), namely 9696 years, lies somewhere between their extreme stratigraphic levels.

The lower three dates on core M4, although stratigraphically consistent, are unexpectedly diverse (GaK662, 663, 664). These samples came from a layer of hard compact detritus, narrow and steeply inclined at the sample site and it is possible that the site represents a long period, during which deposits were intermittently disturbed. The safe inference is that deposits above their combined level of 1916–1931 cm are probably younger than 6000 B.P. and those below probably older than 8500 B.P.

The upper three dates on core M4 (GaK829, 830, 831) also defy detailed interpretation and a conservative approach insists that all the deposits above 1680 cm could be younger than about 2000 B.P. while all those below 1695 cm could be older than about 4700 B.P. It is very unlikely, however, that the 11 m of mud above this group of samples could have accumulated in 2000 years; it is probably reasonable therefore to attribute an Inferred Age of 4000 years to the dated level.

No general explanation of the number of anomalies in the radiocarbon dates from Inim can be advanced. They render the attribution of dates to events expressed in the stratigraphy very hazardous and this has only been attempted, tentatively, in relation to three horizons.

(*c*) *Birip*

The samples were intended to date the beginning of organic accumulation and to date two thin layers of volcanic ash lying in coarse detritus mud.

GaK665, 666 and 667 are insignificantly different (at $p = 0.05$) so it is reasonable to assume that their weighted average, 2223 ± 52 or 2283 ± 105 B.P. on the dendrochronological scale, is a good indication of the onset of organic accumulation at core P14.

Of the four samples associated with volcanic ash at 225 cm in core P14, the uppermost (GaK825) is very different from the rest but in correct stratigraphical position relative to them. The close similarity between the samples immediately above and below the ash (GaK826, 827) allows the use of their weighted average, 1945 ± 67 or 1957 ± 101 B.P. on the dendrochronological scale, as an indication of its age.

Three of the four samples around the volcanic ash layer at 72 cm in core P14 are substantially 'modern' (ANU79, 64, 80), the other (ANU63) very much older. They were taken in an area traditionally used for growing *Eleocharis sphacelata* in pits and it seems likely that old mud excavated from a lower level during the process intruded into the dated material. This brings into question the true stratigraphic position of the ash layer itself.

4. STRATIGRAPHY

(a) *Sirunki*

Four transects of cores (A, B, D, E) were made across the swamp deposits and linked by more cores (C) arranged roughly along the long axis of the basin (figure 3). Together with a number of additional cores taken for special purposes, these provided 55 core records for the interpretation of the site's stratigraphic history. All the work was done with a hand operated 3 cm diameter, 1 m long piston sampler (Walker 1964) occasionally supplemented by a sleeve sampler (Thomas 1964). Cores were extruded into a metal trough and described in detail in the field. Surface levels at all the coring points were accurately surveyed with Kern level and staff and referred to a common site datum. Distances between cores on the four initial transects were measured by tape; the positions of these transects, and of other core points, were located on aerial photographs and by compass bearings on salient topographic features.

The stratigraphic sections (figure 5) are very simplified representations of the data collected and some errors have doubtless been made, particularly in relating marginal strata to their supposed counterparts more central to the basin. Many of the materials in the Lake Ipea Basin are different from those in Kayamanda Swamp so that correlations between the two are relatively uncertain.

A few more or less synchronous levels were identified throughout the deposits, controlled by the radiocarbon dates and by subjective judgements about probable facies changes from place to place. Inferred Ages were then applied to these levels as already described.

The origins of many of the deposits encountered, particularly their relationships to vegetation type and water depth, were inferred from the examination of materials currently accumulating at the surface in 91 quadrats (Walker 1972) and from the laboratory examination of samples from critical levels. Many of the cores terminated in impenetrable clay, sand and gravel, probably the colluvial border of the basin. Away from the edges, however, maximum sampling depth possible with the available equipment was reached in unconsolidated lake or swamp mud, the full depth of which remains unknown.

The Kaipare Fan is a substantial surface feature extending into the basin from the west about half way along it (figure 3). It is matched, albeit less massively, by the Putiti Fan composed of the clay deposited by the Sirunki headstream of the River Muitro, on the eastern side of the swamp. All the surface drainage from the surrounding slopes crossing these fans now runs northward into Lake Ipea. A watershed crosses the swamp just south of these features. A few metres south of it there are several pools, each only 0.5–2.0 m in diameter but more than 3 m deep. Surface water moves towards these pools through the surrounding swamp and probably leaves the area by an ill-defined course southward. It is augmented by water drainage into the swamp from the sides, the small inflow streams diffusing over the swamp surface, and meanders southward leaving the swamp basin as the River Pocketari. The stratigraphy of section D strongly suggests that whatever the origin of the two fans may have been, their periodic extensions have been such as probably to have created a barrier between the Kayamanda Swamp and the Lake Ipea basin from time to time. This is confirmed by the general dissimilarity of the deposits in the two basins and the fact that southern outflow into the River Pocketari is currently 2 m above the outflow of the River Kapupu from Lake Ipea. The morphology of the fans is also likely to have determined which basin received the waters of the headstreams of the River Muitro, the main carriers of water into the system, at any given time.

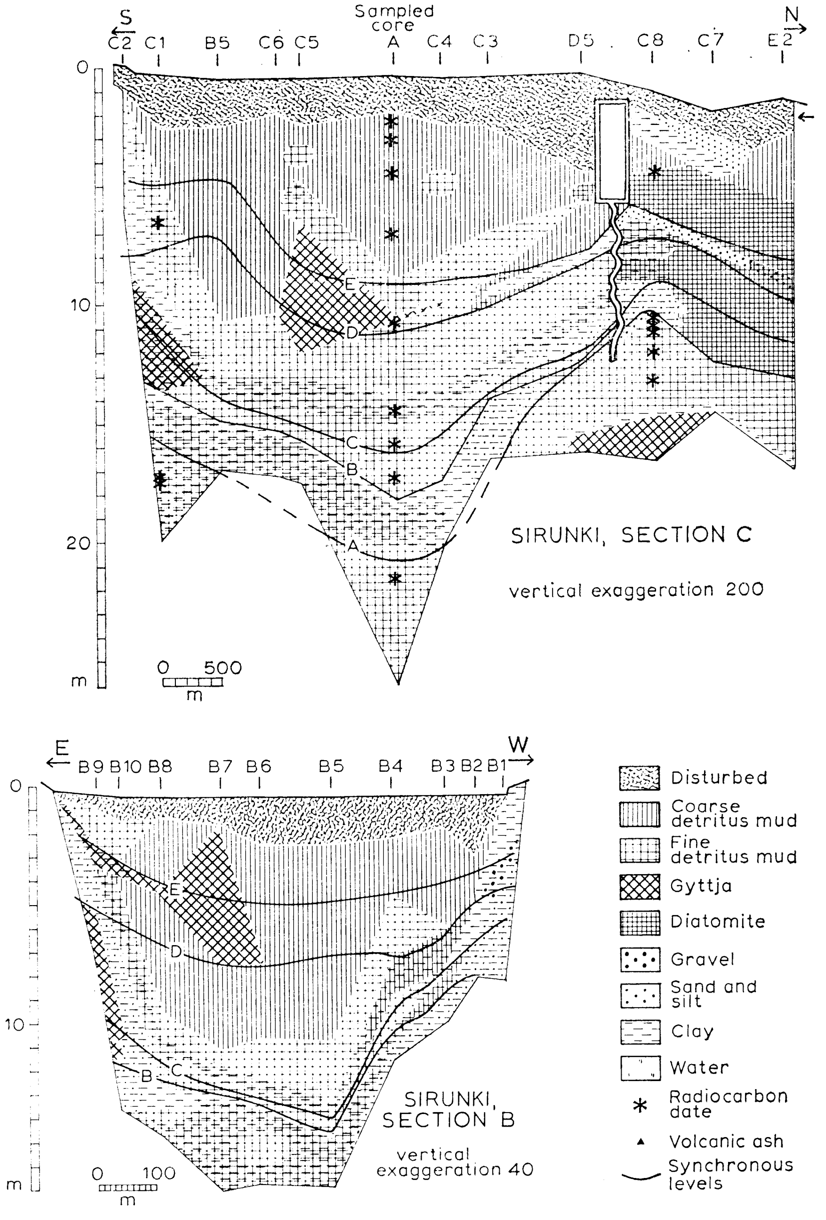


FIGURE 5. Stratigraphic sections from Sirunki. All vertical scales are from a common site datum. The heavy arrows on sections C and E mark the level of outflow from Lake Ipea. The key applies to all stratigraphic figures in this paper. The gap between D5 and C8 (section C) indicates the probability of unresolved complexity in an area not available for investigation. Synchronous levels: A, 24000 I.A.; B, 21000 I.A.; C, 15000 I.A.; D, 9000 I.A.; E, 6000 I.A.

Section D runs from the Kaipare Fan into the narrow connection between the two basins through which the River Muitro now flows northward.

The capture of the southern end of the Kayamanda Swamp may have been a relatively recent event achieved by headward erosion of a formerly minor tributary of the River Pocketari. The slopes around the present outlet suggest that, before this happened, the threshold was probably about 3 m above the present lip. However, there are several small swallow holes in the rock at this southern end of the swamp, opening about 1 m above the present outflow lip,

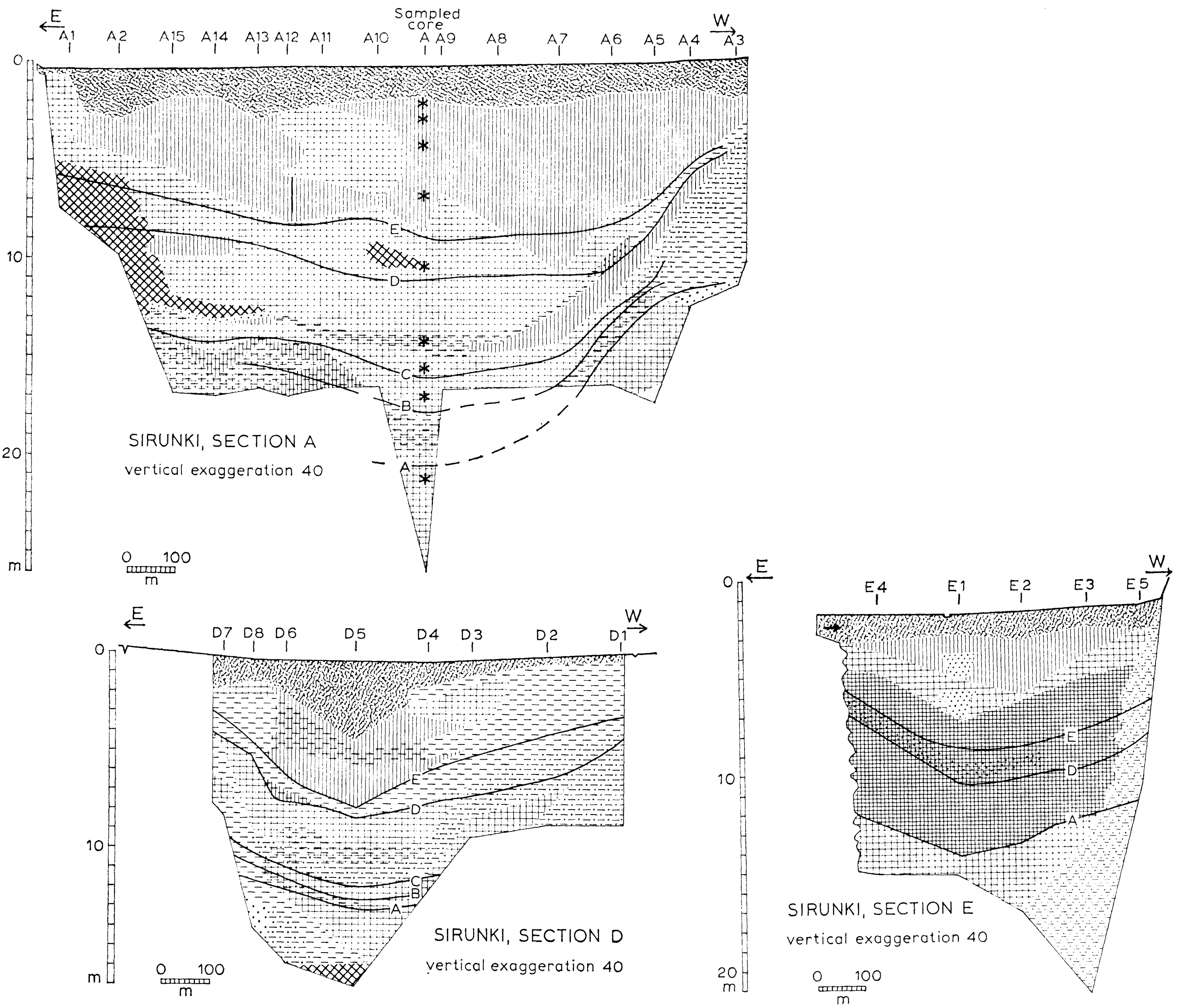


Figure 5 (continued)

which might have drained it at some time in the past. There are also traces of a narrow bench at about the same level, running for 2 km northward along both banks of the swamp.

The River Kapupu leaves Lake Ipea through a gorge deeply incised in a soil mantle over deeply weathered rock 2 m below the level of the River Pocketari outflow. The topography suggests that, prior to the incision, the overflow stood 3 to 5 m higher. Around the south-western part of the lake shore there is a clearly marked cliff about 1 m high in the organic deposits, suggesting a former lake level 0.5–1.5 m higher than at present.

32000–24000 i.a. Deposits of this period are predominantly fine detritus muds with some intercalated nekron bands and patches of calcareous mud at the margins. Clay is uncommon. In the Kayamanda Swamp Basin the highest level attributable to mud of about 24000 i.a. is consistently about 13 m below site datum (b.s.d.); in the Lake Ipea Basin it is about the same except at C8 where it lies at 10 m b.s.d. On the other hand, the 24000 I.A. level was not found *below* 14 m b.s.d. in the Lake Ipea Basin and at C8, radiocarbon dates suggest slow accumulation before that time. It seems likely that the two basins shared a common water level (above 9 m b.s.d.) throughout the period but that accumulation on the Lake Ipea side began from a higher base on the pre-existing deposits. The lake was probably moderately productive but there is no evidence of widespread marginal swamp even where the deposits of shallow water are preserved.

24000–21000 I.A. In the deeper parts of both basins, clay became a consistent component oj the deposits from the beginning of this period. In the Lake Ipea Basin fine detritus mud was substantially replaced by grey-green diatomite. In the Kayamanda Swamp Basin, fine detritus mud continued to predominate near the centre but the marginal deposits contain abundant laminated, greenish grey, sand and clay. The latter part of the period is marked by the predominance of clay to the exclusion of organic mud throughout the basin. All the deposits attributed to this period are water-laid and there is no clear evidence of a change in water level. But the relative importance of clay, with sands laminated in it at the margin, and the initiation of diatomite deposition in the Lake Ipea Basin, suggest a fall in productivity around the lake margins, exposure of the mineral soil edges or a new source of minerals and possibly slightly increased water input. The differences between the deposits in the two basins from this period through about 18000 years, whilst not necessitating their total separation, imply that the main inflow streams flowed initially into the Kayamanda Swamp Basin, contributing to its stratigraphic complexity but leaving the Lake Ipea Basin the quiet water recipient of overflow through the gap crossed by section D. It is quite probable that redistribution of surface material from the Kaipare Fan and Putiti Fan led to the southward shed of the water flowing over them. This proposition is consistent with the great thickness of sand and clay of this period at C3 and the comparative insignificance of such material at D5 and in the Lake Ipea Basin. The thickest recorded deposit of the period is somewhat uncertainly 4 m of fine detritus mud on section B, implying a mean maximum accumulation rate of 1.3 m per 1000 years.

21000–15000 I.A. Although a small admixture of clay is found, particularly near the margins, fine detritus mud and diatomite characterize the period in the Kayamanda Swamp Basin and Lake Ipea Basin respectively. At the southern end (C1), however, nekron mud accumulated suggesting remoteness from inflow and calm surface conditions with sufficient depth to inhibit overgrowth nearby. Indeed, there is no stratigraphic evidence of substantial swamps anywhere around the margin, implying some inhibition to the development of full productive potential. The maximum recorded accumulation rate is about 0.5 m per 1000 years (Section A).

15000–13500 I.A. In the central area of Kayamanda Swamp, detritus muds, now somewhat coarser, began to accumulate whilst coarse detritus mud at the margins indicates the development of productive reed swamps and mires around the edges of this basin. Clay occurs only rarely. In the deeper part of the Lake Ipea Basin diatomite continued to accumulate, although apparently discontinuous layers of fine detritus mud are probably also attributable to this period. In core C8, and in associated cores close to it, the secondary penetration of roots for 30 cm below a thin highly organic layer is assigned to this period. This could be attributable to a fall in water level from that beneath which the overgrown diatomite was deposited, to something less than 2 m above the overgrowth level, i.e. a water level below 7 m b.s.d. Alternatively, a threshold may have been reached in the infilling of the lake, the water having become shallow enough to allow the spread of swamp vegetation across the muds. In core B3 the level attributed to about 13500 I.A. lies at 7.2 m b.s.d.; it is in coarse detritus mud and from it roots penetrate downward indicating *in situ* swamp growth. In core D6, secondary penetration of roots is also found below the 13500 I.A. level although it is there as deep as 10 m b.s.d. These data suggest that, by about 13500 I.A., the water level lay between 7 and 8 m b.s.d. This is consistent with the nature of deposits found elsewhere in both basins, the deposit demanding deepest water being calcareous mud (to 10.5 m b.s.d.) (C1) and nekron (to 14 m b.s.d.) (A9). The fastest recorded accumulation rate for the period is about 1 m of fine detritus mud laid down in 1000 years (Section A).

13500–13000 I.A. During this short period, mixtures of fine and coarse detritus muds with clays and sands accumulated in the deeper parts of the Kayamanda Swamp Basin. Near the margins, clay was laid down, frequently incorporating some sand. In several places, pea-sized nodules of formerly consolidated sediment, including volcanic ash, are reworked and redeposited. This must represent a major increase in water input or a rapid rise in lake water eroding the swamp margins and causing turbulence in the lake itself. The aberrant radiocarbon date (N1524; 14000 ± 175 B.P.) from Section A is interpreted as being derived from older organic material which was exposed by erosion and transported in the turbulent water. At core C8 the level representing the earlier overgrowth is covered by clay with diatoms. The diatoms may have been derived from older sediments and the clay does not necessarily imply a rise in water level, but a pronounced change is clearly indicated with which a rise in water level is consistent. There is no obvious stratigraphic mark of this event in the deeper parts of the Lake Ipea Basin, which suggests that most of the water entered the system by streams flowing into the Kayamanda Swamp and lost much of its load there before spilling northwards. The deepest recorded deposit for this 500 year period is of 80 cm of clay mud, sand and fine detritus mud from core C5.

13000–9000 I.A. Fine detritus mud covers the 13000 I.A. level everywhere in the Kayamanda Swamp sections, except at the shallowest margins and in the southeastern deeps crossed by Section A where it is replaced by nekron. The accumulation of slightly clayey, diatomaceous, fine detritus mud up to slightly above 7 m b.s.d. at core C8 indicates conclusively that, throughout this period at least, the water had risen substantially above its former low level. Diatomite continued to accumulate in the Lake Ipea Basin. In general it seems to have been a period of more or less consistent water level during which the lake was moderately productive and mires developed around the margins of Kayamanda Swamp. The Southern end (Section B) evidently filled rapidly with detritus so that, by 9000 I.A., reed swamp was growing on a surface about 6.5 m b.s.d. as witnessed by vertical penetration of rootlets beneath it. This indicates a water level about 4.5 m b.s.d. The fastest accumulation rate recorded is 1.6 m of fine and coarse detritus muds per 1000 years on Section B, but rates rather less than 1 m per 1000 years were more common.

9000–6000 I.A. In the middle of Kayamanda Swamp, the 9000 I.A. level is marked by a change from fine detritus mud to nekron. This change is temporary in most parts but is persistant at the southern end. Toward the Kaipare Fan there is a layer of silt which, in its best development (e.g. C8), is compact, dark grey and 10 cm thick. Both the upper and lower contacts of this silt are mixed, indicating its deposition in turbulent water. In both Kayamanda Swamp Basin and Lake Ipea Basin, clay entered into the deposits of the period. In many places, particularly near the margins, there is a narrow (0.2 cm) layer of disorganized organic detritus with clear-cut upper and lower edges, and some secondary penetration of underlying deposits by roots from it, immediately above the silt. It seems that, about 9000 I.A. there was great redistribution of surface materials over and around the Kaipare Fan and that this temporarily raised the water level elsewhere in the Kayamanda Swamp Basin. Judging from the thicknesses of deposits attributable to the period on Section D, this may have been effected by the temporary blockage of the connection between the two basins. The return to pre-existing conditions probably took some time, during which local erosion and redeposition took place. Undisturbed accumulation continued in the deeper parts of the basins, however, and there is no evidence of a general lowering of water level such as occurred 6000 years earlier. By 6000 I.A. all the effects of the disturbance appear to have been overcome and purely organic accumulation was re-established.

6000–3000 I.A. This was a period of high organic productivity in the Kayamanda Swamp Basin where, under stable or slightly falling water level conditions, organic detritus built up and swamps spread inward from the margins occluding most of the open water. In the Lake Ipea Basin diatomite continued to be laid down. The maximum recorded accumulation rate is 1.3 m of coarse detritus mud per 1000 years (Section A).

< 3000 I.A. By the beginning of this period the surface of the deposits in the Kayamanda Swamp Basin lay slightly above their general level in the Lake Ipea Basin, except at the southern end of the swamp (Section B) where it was substantially higher and probably only about 2 m below the water level of the time. Renewed instability of the Kaipare Fan and Putiti Fan surfaces is evidenced by the high clay content of the muds of the period on Section D. In the Lake Ipea Basin, detritus muds supersede diatomite and substantial, but laterally discontinuous, bands of sand with turbulent contacts occur. These bands of sand cannot be matched in the Kayamanda Swamp Basin. It is proposed that the combined effects of overgrowth in the Kayamanda Swamp and rearrangement of the fan surfaces deflected the headstreams of the River Muitro to roughly their present courses, so that they issued directly into the Lake Ipea Basin, depositing sand and inhibiting diatom growth. Overgrowth of the Kayamanda Swamp then went on at an increased pace effectively eliminating back-spill from Lake Ipea and restricting open water to the vicinity of the present channel. The deep pools (p. 283) at the head of this channel are probably on the line of the former River Muitro input channel. The southern part of the Lake Ipea Basin became a watery swamp through which the river meandered to the lake at the northern end. At some, probably rather recent, time the outlet from Lake Ipea fell to its present level leaving a terrace at the lake edge and causing the river to incise the surface deposits, partially draining and lowering them. Walker (1972), from a study of the vegetation and microtopography of the present swamp surface, has suggested that slight erosion might have been taking place in the recent past. This is consistent with the Inferred Age of 500 years for the present surface at the pollen analysed core (figure 4).

(*b*) *Inim*

Twenty-one cores were taken in a line along the axis of the valley from the flanks of the main mud volcano at its northeastern end, running close by the two small cones near the centre of the swamp and crossing the lake near its northwestern end. Levels were established, a section constructed and interpretation attempted as with the Sirunki data (figures 3 and 6).

At the northwestern end (and at M20) coring bottomed on sandy clay except beneath the lake where compaction of the black fine detritus prevented further penetration. Before doing so, however, each core had passed through one or two layers of grey clay which, elsewhere along the transect, was the lowest material encountered. This grey clay rises to the surface near all three mud cones and is the same in appearance (and in its failure to react with dilute hydrochloric acid), as the clayey matrix of the mixture currently emerging from the vents of the mud volcanoes. The clay is interpreted as an effluent of these cones from which coarse flakes have settled. This sediment has been distributed by the lake water into which it oozed. Some additional force, e.g. earth tremors, may have been necessary to distribute the main clay bed so widely.

Difficulties in interpreting the few radiocarbon dates from the site demand wide limits on the periods inferred for stratigraphic events. In particular, it seems likely that the base of the grey clay may be diachronous from place to place and the best age that can be attributed to it is about 7000 ± 1000 years – although the more conservative extreme would be 6000 ± 2000 years.

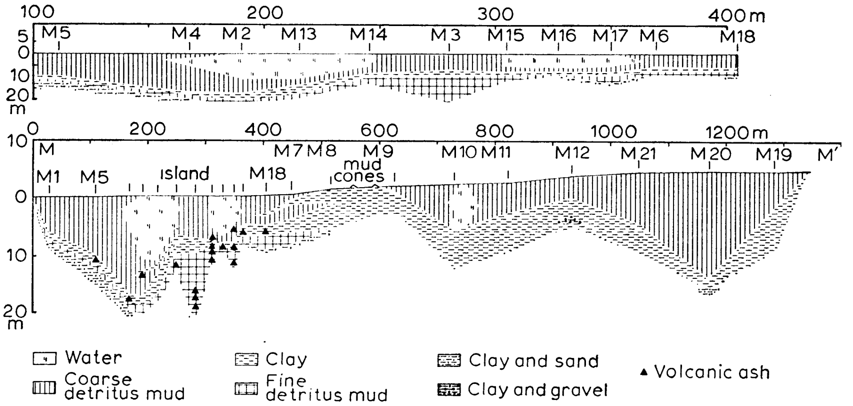


FIGURE 6. Stratigraphic sections from Inim. The upper section details the stratigraphy between borings M5 and M18 at natural scale, i.e. with 10 × less vertical exaggeration than in the lower section.

\> 7000 ± 1000 I.A. In a deep depression at the western end of the valley, lined by sands and clays, black fine detritus mud accumulated under open water conditions. It is impossible to say whether similar conditions occurred in the eastern part of the valley or whether the mud volcanoes were sufficiently active to dominate accumulation there during this period. In one core (M3) *Papuacedrus* and cf. Podocarpaceae wood was recovered from the top of the detritus mud, probably indicating the development of swamp forest.

7000 ± 1000–ca. 4000 I.A. Greater activity of the mud volcanoes, at least of the two close to the middle of the swamp, spread grey clay over all of the lake bottom. Bands of organic mud in this clay attest to the occasional establishment of swamp rafts or the redistribution of older materials from the valley sides. In general, however, the lake must have been less organically productive than before or since.

ca. 4000–0 I.A. During this period, the mud volcanoes were less active than immediately before, although on one or two occasions of rather short duration they may have been more productive than at present (cores M2, 13, 14, 18, 7 and 8). Accumulation was dominated by soft, rapidly accreted, coarse detritus mud, presumably the products of marginal swamps which quickly encroached over the basin.

The striking change in lake conditions from before 5000 I.A. to after 4000 I.A. might have resulted from the lowering of the outflow to a critical level or the physical and chemical effects of the input of volcano mud during the intervening millenium.

(*c*) *Birip*

Cores were examined from 23 points on two transects across the lake and its marginal swamps in the crater bottom (figure 3). Generally the stratigraphy found in these transects is remarkably uniform (figure 7).

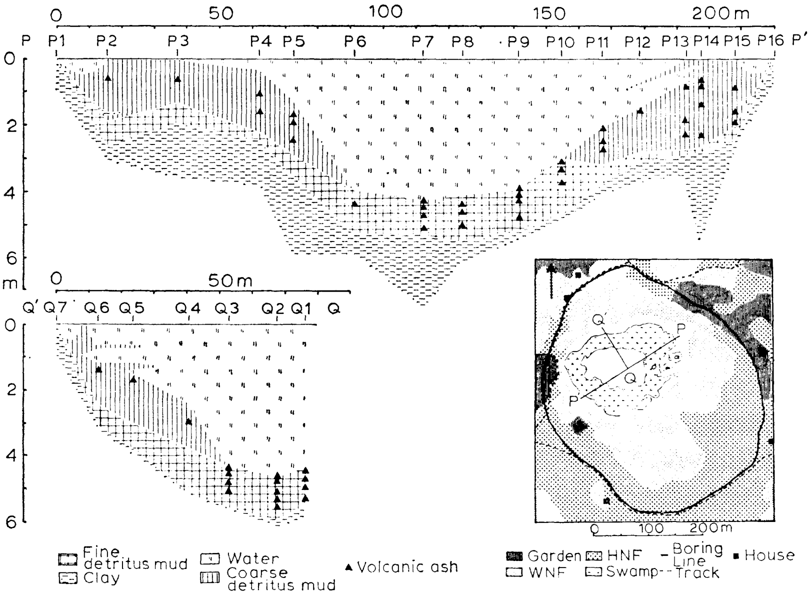


FIGURE 7. Map of the site at Birip and stratigraphic sections from the site. WNF, woody non-forest vegetation; HNF, herbaceous non-forest vegetation. Heavy line indicates crater rim.

The brown clay which seals the bottom of the basin is interpreted as a product of erosion from the inner walls of the crater before they were vegetated. The lowermost radiocarbon dates from core P14 indicate that organic accumulation had begun by 2300 I.A. (table 2). At first, fine detritus mud built up, suggesting the presence of open water over the whole of the basin, but this was soon replaced marginally by coarse detritus mud, presumably as the fringing swamp established and spread. However, fine detritus mud continued to accumulate at the centre of the basin where swamp has still not occluded the open water. Organic accumulation evidently continued now, perhaps at an enhanced rate, but there is some disturbance of the swamp surface associated with *Eleocharis sphacelata* culture.

Layers of volcanic ash, each 1 to 2 cm thick, were encountered at several points in the organic muds but defied correlation between cores and seemed not to have substantially interrupted the course of organic infilling. There is no stratigraphic evidence to suggest that the lake dried up during its history.

5. POLLEN DIAGRAMS AND GENERAL VEGETATIONAL HISTORY

(*a*) *Sirunki*

Sources of pollen. Throughout the history of Kayamanda Swamp, pollen would have reached the sampled site by the following mechanisms: (*a*) water transport from within the swamp's catchment, particularly by the headstreams of the River Muitro; (*b*) local wind dispersal, mostly from within the catchment; (*c*) valley winds, particularly those up the Rama–Lai and the Pocketari–Lagaip bringing pollen from as low as 2000 m; (*d*) regional winds carrying pollen from almost anywhere in New Guinea but principally from the southeast, east and northeast. Deposition of windborne pollen is probably almost all by rainout. Late-afternoon showers are a common concomitant of the local wind circulation and the occasional up-valley winds usually result in heavy rainstorms in the Sirunki region. It is likely that, under the formerly forested conditions, most of the pollen reached the sampled site from within its water catchment, by mechanisms (*a*) and (*b*). If pollen production in the water catchment was very much lower at times in the past but remained virtually unchanged at lower altitudes, the relative contribution of components borne by valley winds and regional winds was probably much greater; indeed it might have been greater than that more locally produced.

TABLE 3. CHARACTERISTICS OF MODERN POLLEN FALLOUT IN AND NEAR THE PINDAUNDE VALLEY, MT WILHELM (AFTER HOPE 1973, 1976)

	positions of sampled sites		
	within forest	forest edge	distant from forest
range of pollen deposition rates (grains cm^{-2} a^{-1})	2000–4600 (often $>$ 4000)	750–9000	1000–3000 (often $<$ 2000)
regional pollen (*sensu* Janssen 1966) as percentage of total pollen	10–40 (usually $<$ 30)	20–75 (usually $<$ 50)	35–85 (usually $>$ 70)

Table 3 summarizes Hope's (1973) data on present day pollen deposition in and near the Pindaunde Valley, Mt Wilhelm. These figures cannot be used directly in the interpretation of the Sirunki pollen diagram because they relate to a different topography and weather system and because the estimates of pollen deposition rate for 'fossil' material are likely to be systematically low. They indicate, however, that total pollen recovery (deposition) rates (t.p.r.) must consistently exceed 2000 grains per square centimetre per year (grains cm^{-2} a^{-1}) to imply extensive closed forest around the sampling site. Even in such circumstances, as much as 30% of the pollen may be far-travelled. More importantly, perhaps, where total pollen recovery rate consistently lies below 2000 grains cm^{-2} a^{-1}, substantially unforested conditions around the site and a 70% contribution by far-travelled grains must be suspected. This is consistent with Flenley's capture of about 1130 grains cm^{-2} a^{-1} in a Wabag rain gauge (Flenley 1973).

Based on considerations of this kind, on local weather patterns and topography and on the areal extent of land in the different altitudinal classes, the figures in table 4 provide a general guide to the interpretation of the Sirunki pollen diagram. Pollen deposition rates between 1000 and 2000 grains cm^{-2} a^{-1} require very careful interpretation.

The interpretation of the pollen diagram is also informed by what is known of the relative pollen productions and potential for travel of the taxa involved. There are few direct measurements of these values but the indications of the observations of Flenley (1967), Hope (1973) and Powell (1970) are summarized in table 5.

Flenley (1973) summarized the data on relative pollen fall out in Papua New Guinea then available to him, mostly from moss polsters beneath forest, regrowth or herbaceous vegetation. Eleven surface peat and mud samples from Kayamanda Swamp were analysed and their bulked result compared with that from a year's rain gauge collections at Wabag (table 6). The latter site was in a village surrounded by abundant secondary forest and *Casuarina* plantations; given this fact and the difference in altitude (500 m) there is satisfactory correspondence in the main taxa. Comparing these data with descriptions of the vegetation of the region (Flenley 1969; Walker 1966, 1972), it seems that *Nothofagus* and Urticaceae/Moraceae are both likely to be over-represented in the pollen rain as both produce large quantities of far-travelling pollen.

TABLE 4. THE BASIS OF INTERPRETATION OF THE SIRUNKI POLLEN DIAGRAM

	characteristics of pollen sample	
	total pollen recovery consistently < 1000 (catchment unforested)	total pollen recovery consistently > 2000 (catchment forested)
	percentage contribution from each source	
predicted pollen sources		
(*a*) beyond catchment, mostly < 2500 m	70	20
(*b*) within catchment		
(i) footslopes and marginal swamps, 2500–2550 m	10	25
(ii) middle hillslopes, 2550–2800 m	15	50
(iii) ridge tops, 2800–3000 m	5	5

TABLE 5. POLLEN PRODUCTION AND TRANSPORT

(Under-representation, equivalent-representation and over-representation refer to the amounts of pollen recovered from the ground in sample plots compared with the quantity of the living taxon in the same plots. Local, extra-local and regional are used in the sense of Janssen (1966).)

taxon	production	transport
Nothofagus	equivalent representation where dominant; elsewhere variable although usually over-represented	extra-local and regional†
Ascarina	equivalent or under-represented	extra-local and regional
Castanopsis	equivalent representation where dominant; elsewhere variable	extra-local and regional but not so strikingly so as *Nothofagus*
Phyllocladus	equivalent or under-represented	extra-local and regional, comparable with *Castanopsis*
Quintinia	variable but never over-represented	local and restricted extra-local
Podocarpus	equivalent representation	extra-local and regional
Dacrycarpus	equivalent representation	local and restricted extra-local
Elaeocarpaceae	under-represented, sometimes equivalently represented	extra-local and regional
Myrtaceae	variable but never over-represented	extra-local and regional
Claoxylon		local only
Proteaceae	variable but never over-represented	local only
Ilex	variable but never over-represented	local and restricted regional
Rapanea	equivalent to over-representation	local and restricted extra-local
Drimys	equivalent to over-representation	local and restricted extra-local
Macaranga	equivalent to over-representation	extra-local and regional†
Omalanthus	under-represented	local and restricted extra-local
Cyathea	over-represented	local and restricted extra-local
Saurauia	variable but never over-represented	local only
Trema		local and restricted extra-local†
Casuarina	over-represented	extra-local and regional†
Dodonaea	equivalent to under-represented	extra-local and regional

† Taxa often better represented away from the forest. Data generalized from Flenley (1967), Hope (1973) and Powell (1970).

Determination. The 'fossil' pollen grains have been determined by comparison with reference material accumulated from field collections and herbarium sheets. Maximum resolution of light microscopy has been used. More critical determination of some taxa, e.g. Gramineae, has been attempted using scanning electron microscopy but has not proved successful. The degree of certainty attaching to a determination is indicated by a suffix of the Benninghoff & Kapp (1962) scheme and the plants to which it probably refers are listed in table 7.

Table 6. Modern pollen fallout

(Values are percentages of pollen of total woody plants.)

	Wabag rain gauge 2000 m†	Kayamanda Swamp 2500 m
Ascarina	.	+
Nothofagus	24	29
Castanopsis	12	8
Phyllocladus	+	2
Podocarpus	.	2
Dacrycarpus	.	+
Elaeocarpus	.	+
Myrtaceae	.	+
Macaranga	2	5
Cyathea	.	8
Engelhardtia	.	3
Urticaceae/Moraceae	11	31
Casuarina	30	6
Dodonaea	4	1
Acalypha	1	.
Trema	16	4
Schefflera	.	+
Saurauia	+	.

† After Flenley (1967).

Preparation and presentation. The analysed cores were each 1 m long and were collected alternately from two holes using Walker's (1964) modification of the Vallentyne piston sampler. Each core was extruded onto polythene sheet in the field and wrapped in reinforcing mesh for transport to the laboratory. When opened for sampling, each core was measured to determine the effects, if any, of compression or shrinkage. At each sampling level a horizontal slice of mud 10 mm thick was carefully removed. A clean glass tube of 12 mm internal diameter was then thrust vertically through the centre of the mud disc so as to collect a sample of 1 ml volume. This was extruded with a glass rod, treated by standard potassium hydroxide, acetolysis and hydrofluoric acid method using standard volumes of liquids throughout. The extracted pollen grains were dehydrated by tertiary butyl alcohol and suspended in a known volume of silicone oil (AK 2000), aliquots of which were mounted for microscopic examination and counting. The chronology of Inferred Ages allows an accumulation time to be attributed to each sample, after allowing for any shrinkage, and hence the calculation of pollen recovery rates in grains $cm^{-2}\ a^{-1}$.

The remnant of each sample disc was divided into two, one half being used for the determination of bulk density, dry weight (at 100 °C) and loss on ignition.

The main pollen diagram (figure 8) shows the estimated pollen recovery rate for each taxon against depth below site datum, after allowance has been made for shrinkage or compression

TABLE 7. COMPONENTS OF THE POLLEN ANALYSIS TAXA

(The suffixes id., comp. and sim. indicate the level of identification in the Benninghoff & Kapp (1962) manner.)

taxon in pollen diagram	category in pollen diagram	family	living taxa possibly included	habit and habitat
Acaena comp.	Dg	Rosaceae id.	*Acaena*	herb of open and disturbed habitats
			Prunus	shrub or low tree of undisturbed and disturbed forest
			Potentilla	herb of open places, including mountain swamps
Acalypha id.	C	Euphorbiaceae id.	*Acalypha*	tree or tall shrub of disturbed places, particularly abandoned gardens; often planted and widely used for timber
Acanthaceae comp.	Dg	Acanthaceae comp.	*Dicliptera*	forest undergrowth shrub
			Jadunia	
			Rungia	herb, abundantly planted for food
Acronychia comp.	A	Rutaceae comp.	*Acronychia*	forest tree
			Melicope	
Amyema id.	G	Loranthaceae id.	*Amyema*	woody semi-parasite on trees
Ardisia comp.	E	Myrsinaceae comp.	*Ardisia* (and others but not *Maesa* or *Rapanea*)	forest tree
Ascarina id.	A	Chloranthaceae id.	*Ascarina*	forest tree, often reaching canopy
Astelia id. *papuana* id.	Ds	Liliaceae id.	*Astelia papuana*	low herb forming dense cushions and swards on wet soils and swamps in high mountains
Begonia comp.	G	Begoniaceae comp.	*Begonia*	herb of open places and sparse forest
Blyxa id.	E	Hydrocharitaceae id.	*Blyxa*	aquatic herb
Borreria id.	C	Rubiaceae id.	*Borreria*	herb of open moist habitats
Buddleia comp.	C	Loganiaceae comp.	*Buddleia*	
			Geniostoma	forest undergrowth shrub
Calamus comp.	C	Palmae comp.	*Calamus* and probably others	woody liane or shrub, most abundant in disturbed forest
Castanopsis/ *Lithocarpus* id.	A	Fagaceae id.	*Castanopsis*	forest tree, sometimes planted or selectively preserved, commonly reaching canopy
			Lithocarpus	forest tree, sometimes planted or selectively preserved, commonly reaching canopy
Casuarina id.	C	Casuarinaceae	probably *C. oligodon*, possibly also *C. papuana*	trees of river banks, abandoned clearings and roadsides; often planted for timber, shade and boundary marks
Caryophyllaceae id.	Dg	Caryophyllaceae id.	*Drymaria*	low or straggling herb of open or wet habitats
			Sagina	
Celtis/ *Aphananthe* id.	B	Ulmaceae id.	*Celtis*	low tree or shrub, common in regrowth
			Aphananthe	
Claoxylon id.	A	Euphorbiaceae id.	*Claoxylon*	forest tree, commonly reaching canopy
Compositae (fenestrate) id.	Dg	Compositae	*Crepis* *Elephantopus* *Sonchus* *Taraxacum*	herbs of open ground
Composite (C3P3) id.	Dg	Compositae	76 genera including *Anaphalis*, *Bidens*, *Crassocephalum*, *Erechtites*, *Gnaphalium*, *Lactuca*, *Olearia*, *Tetramolopium*	mostly herbs, but *Olearia* a shrub

TABLE 7 (*cont.*)

taxon in pollen diagram	category in pollen diagram	family	living taxa possibly included	habit and habitat
Coprosma id.	B	Rubiaceae id.	*Coprosma*	small tree or stout shrub of forests and forest edges, sometimes (e.g. *C.* cf. *papuensis*) a liane
Croton id.	C	Euphorbiaceae id.	*Croton*	shrub of open places often planted in gardens and along boundaries
Cruciferae comp.	Dg	Cruciferae comp.	Cruciferae	herbs, widespread in open habitat
Cyathea id.	B	Cyatheaceae id.	*Cyathea*	tree fern, growing within forest and amongst grasslands but also more gregariously in wet clearings and at the altitudinal forest limit
		Cyperaceae id.	sedges	
Cyp. A (pear-shaped < 40 μm)	Ds		*Cyperus* spp. *Fimbristylis* *Elaeocharis*	swamps
Cyp. B_1 (rectangular oval < 30 μm)	Ds		*Cyperus* spp. *Lipocarpha* *Kyllinga*	swamps
Cyp. B_2 = Cyp. X (computer) (rectangular oval 30–40 μm)	Ds		*Carex* spp. *Elaeocharis* *Gahnia* *Fimbristylis* *Rhynchospora* *Scirpus* spp. *Scleria*	swamps
Cyp. C (circular 25–40 μm)	Ds		*Carex* spp. *Machaerina* spp.	swamps
Cyp. D (> 40 μm)	Ds		*Carpha alpina* *Schoenus* *Uncinia*	subalpine and alpine swamps swamps swamps
Dacrycarpus id. 3 vesiculate	A	Podocarpaceae id.	*Dacrycarpus* including *Podocarpus compactus*, *P. imbricatus* and *P. papuanus*	forest tree, often gregarious and dominating canopy at altitudinal forest limit: sometimes in frost-hollows and in swamp forest
Dodonaea id.	C	Sapindaceae id.	*Dodonaea*	shrub and small tree growing in open places and commonly used for fencing, boundary marks, etc.
Drapetes id.	Ds	Thymelaeaceae id.	*Drapetes ericoides*	subalpine and alpine low shrub
Drimys id.	A	Winteraceae	*Drimys*	shrub or small tree, widely distributed
Dysophylla comp.	E	Labiatae comp.	*Dysophylla*	
Elaeocarpus comp.	A	Elaeocarpaceae id.	*Elaeocarpus*	trees and shrubs widely distributed through forests
			Sericolea	small trees and shrubs, sometimes scrambling amongst others, widely distributed in forests but perhaps most common in clearings and at high altitudes
Endiandra comp.	A	Lauraceae id.	*Endiandra*	tree used for timber
Engelhardtia id.	B	Juglandaceae	*Engelhardtia* id.	forest tree, often common in regeneration cycles
Epacridaceae/ Ericaceae id. (45–50 μm tetrads)	Ds	Epacridaceae/ Ericaceae id.	many genera	scramblers, shrubs and epiphytes
Epilobium id.	Dg	Onagraceae id.	*Epilobium*	herbs of swamps and disturbed ground, including gardens
Eriocaulon id.	E	Eriocaulaceae id.	*Eriocaulon*	erect herbs of shallow water and swamps
Evodiella	A	Rutaceae id.	*Evodiella*	forest tree

TABLE 7 (*cont.*)

taxon in pollen diagram	category in pollen diagram	family	living taxa possibly included	habit and habitat
Fagraea id.	A	Loganiaceae id.	*Fagraea*	forest tree occasionally reaching canopy
Flacourtiaceae comp.	A	Flacourtiaceae comp.	*Casearia* *Erythrospermum*	forest trees
Galium id.	D	Rubiaceae id.	*Galium*	herb of open places, including gardens, but also straggling amongst swamp plants
Gentiana id.	D	Gentianaceae id.	*Gentiana*	low herb of wet ground, particularly in subalpine places
Glochidion id.	B	Euphorbiaceae id.	*Glochidion*	low forest tree and undergrowth shrub, particularly common in regeneration cycles
Geitonoplesium id.	Dg	Liliaceae id.	*Geitonoplesium*	straggling or erect herb of sparse forest
		Gramineae id.	grasses	
Gra. A (< 20 μm psilate)	Dg			
Gra. B (20–25 μm psilate)	Dg		*Leersia*	mid-mountain grasslands and abandoned gardens
			Deschampsia	mid-mountain, subalpine and alpine grassland
Gra. C (> 25–30 μm psilate)	Dg		*Leersia*	as above
			Deschampsia	as above
Gra. D (> 30 μm psilate)	Dg			
Gra. E (< 20 μm scabrate)	Dg			
Gra. F (20–25 μm scabrate)	Dg		*Capillipedium*	mid-mountain grasslands and abandoned gardens
			Phragmites	mid-mountain swamps
Gra. G (> 25–30 μm scabrate)	Dg		*Digitaria* *Arundinella* *Capillipedium* *Miscanthus*	mid-mountain grasslands and abandoned gardens
			Agrostis *Anthoxanthum* *Poa*	mid-mountain, subalpine and alpine grasslands
			Phragmites	mid-mountain swamps
Gra. (H > 30 μm scabrate)	Dg		*Ischaemum* *Arthraxon* *Arundinella* *Miscanthus*	mid-mountain grasslands and abandoned gardens
			Agrostis *Poa* *Danthonia*	mid-mountain, subalpine and alpine grasslands
			Phragmites	mid-mountain swamps
Gunnera id.	Ds	Haloragaceae id.	*Gunnera*	large swamp herb
Haloragis/*Myriophyllum* id.	Ds	Haloragaceae id.	*Haloragis*	montane shrub and aquatic herb
			Myriophyllum	aquatic herb
Hydrocotyle comp.	Ds	Umbelliferae id.	*Hydrocotyle*	low herb of wet soils and shallow water
Hypericum sim.	Ds	Guttiferae sim.	*Hypericum*	low herb of open places and swamps
Ilex id.	A	Aquifoliaceae id.	*Ilex*	forest tree, often reaching canopy
Limnophila comp.	E	Scrophulariaceae id.	*Limnophila* and others	aquatic herb
Lindernia comp.	Ds	Scrophulariaceae id.	*Lindernia*	forest herb
			Veronica	herb of open habitats
Lobelia sim.	Ds	Lobeliaceae sim.	*Lobelia*, *Pratea* and others	aquatic and swamp herb

TABLE 7 (*cont.*)

taxon in pollen diagram	category in pollen diagram	family	living taxa possibly included	habit and habitat
Litsea id.	A	Lauraceae id.	*Litsea*	forest tree, commonly reaching canopy
Macaranga id.	B	Euphorbiaceae id.	*Macaranga*	shrub or small tree, prominent in forest regeneration cycles, at the forest edge and in abandoned clearings
Maesa comp.	A	Myrsinaceae comp.	*Maesa*, *Tapeinosperma* and others	see Myrsinaceae below
Melastoma id.	C	Melastomataceae id.	*Melastoma*	low shrub of open habitats, particularly abandoned gardens
Meliosma id.	A	Sabiaceae id.	*Meliosma*	forest tree
Mussaenda id.	B	Rubiaceae id.	*Mussaenda*	small tree of open habitats
Myrsinaceae comp.	A	Myrsinaceae comp.	*Ardisia*	forest tree often reaching canopy
			Discocalyx	small forest tree
			Maesa	forest tree or shrub
			Rapanea p.pt.	forest tree or shrub, commonest in, but not restricted to, sparse forest
Myrtaceae id.	A	Myrtaceae id.	*Decaspermum*	small forest trees and shrubs
			Octamyrtus	forest trees and shrubs
			Syzygium	forest trees and shrubs
			Xanthomyrtus	forest trees and shrubs
Nothofagus id. *brassii* comp.	A	Fagaceae id.	*Nothofagus*	forest tree, commonly reaching canopy
Nymphoides id.	E	Gentianaceae id.	*Nymphoides*	aquatic herb
Oenanthe id.	Ds	Umbelliferae id.	*Oenanthe*	swamp herb, often gregarious
Omalanthus comp.	B	Euphorbiaceae comp.	*Omalanthus* and others	shrub or small tree, commonest in forest clearings, at forest edges and regrowth
Opocunonia id.	A	Cunoniaceae id.	*Opocunonia*	forest tree, frequently reaching canopy
Osbeckia comp.	C	Melastomataceae id.	*Osbeckia*	shrub, common in regrowth
			Astronia	forest tree
			Poikilogyne	woody climber
Papuacedrus comp.	A	Cupressaceae id.	*Papuacedrus*	forest tree commonly reaching canopy
Phyllanthus id.	B	Euphorbiaceae id.	*Phyllanthus*	small trees and shrubs commonest in sparse forests and at forest edges
Phyllocladus id.	A	Podocarpaceae id.	*Phyllocladus*	forest tree, commonly reaching canopy
Piper comp.	B	Piperaceae id.	*Piper* *Macropiper*	tall, erect herbs and small shrubs of sparse forest, forest edges and clearings, sometimes planted
Planchonella comp.	A	Sapotaceae	*Planchonella*	forest trees
Plantago id.	Ds	Plantaginaceae id.	*Plantago*	low herb of open places, particularly subalpine places. *P. aundensis* above 2750 m only
Podocarpus id.	A	Podocarpaceae id.	*Podocarpus amarus* *P. brassii* *P. neriifolius* *P. pilgeri*	forest trees, commonly reaching canopy; often gregarious in cold or swampy places
Polygonum id.	Ds	Polygonaceae id.	*Polygonum*	herb of open places, often straggling amongst swamp plants
Polyosma id.	A	Saxifragaceae id.	*Polyosma*	forest trees often reaching canopy
Pontederiaceae sim.	E	Pontederiaceae sim.		swamps
Potamogeton id.	E	Potamogetonaceae id.	*Potamogeton*	aquatic and swamp herb
Potentilla id.	Dg	Rosaceae id.	*Potentilla*	low herb of open places, including gardens and subalpine areas
Proteaceae id.	A	Proteaceae id.	*Finschia*	forest trees or shrubs
			Helicia	forest tree, rarely reaching canopy

TABLE 7 (*cont.*)

taxon in pollen diagram	category in pollen diagram	family	living taxa possibly included	habit and habitat
Psychotria comp.	C	Rubiaceae id.	*Psychotria*	forest tree, sometimes reaching canopy
Pygeum id.	A	Rosaceae id.	*Pygeum*	forest shrub and small tree
Quintinia id.	A	Saxifragaceae id.	*Quintinia*	forest tree, commonly reaching canopy
Ranunculus id.	Ds	Raunuculaceae id.	*Ranunculus*	low herb of swamps and open, particularly subalpine, places
Rapanea C3P3	A	Myrsinaceae id.	*Rapanea*	forest tree and shrub commonest in, but not restricted to, sparse forest
Rapanea C_3/C_4	A	Myrsinaceae id.	*Rapanea* (montane species)	small forest tree, particularly common near altitudinal forest limit (*R. vaccinioides*)
Rubiaceae comp.	C	Rubiaceae comp.	*Amaracarpus*	forest tree
			Wendlandia	small trees and shrubs of forest remnants and regrowth
Rubus comp.	Dg	Rosaceae id.	Rosaceae genera	trees, shrubs and herbs
Rumex id.	Dg	Polygonaceae id.	*Rumex*	herb of open places including some swamps
Rutaceae/ Araliaceae/ Clusiaceae comp. (RUAR)	A	Rutaceae/ Araliaceae/ Clusiaceae comp.	*Evodia*	forest tree, commonest in regeneration cycles
			Melicope	forest tree
			Zanthoxylum	forest tree often reaching canopy
			Arthrophyllum	forest tree
			Harmsiopanax	small forest trees and shrubs
			Mackinlaya	forest tree
			Garcinia	forest tree occasionally reaching canopy
			Hypericum	herb of open moist habitats
Saurauia comp	B	Dilleniaceae id.	*Saurauia*	tree of forest regeneration cycles and open places, including abandoned gardens and grassland
			Eurya	forest shrubs and trees
Schefflera id.	A	Araliaceae id.	*Schefflera*	forest tree, frequent in regrowth from grasslands
Schizomeria id.	A	Cunoniaceae id.	*Schizomeria*	forest tree often reaching canopy
Sloanea comp.	A	Elaeocarpaceae id.	*Sloanea* and unknowns	forest tree, commonly reaching canopy
Solanum id.	C	Solanaceae id.	*Solanum*	forest herb and garden weed
Sparganium id.	E	Sparganiaceae id.	*Sparganium*	tall swamp herb
Sphenostemon id.	B	Aquifoliaceae id.	*Sphenostemon*	forest tree
Styphelia/ *Trochocarpa* id.	Ds	Epacridaceae id.	*Styphelia*	low bushy shrub of drier swamps and alpine and subalpine places, sometimes in subalpine forests
			Trochocarpa	low bush or creeping shrub of drier montane swamps and alpine and subalpine places, sometimes in subalpine forests
Symplocos id.	A	Symplocaceae id.	*Symplocos*	forest trees and shrubs
Trachymene comp.	Ds	Umbelliferae id.	*Centella*	herb of open places, particularly disturbed soil
			Oenanthe	swamp herb, often gregarious
			Oreomyrrhis	low herb of open vegetation on wet soils, alpine and subalpine places
			Trachymene	low herb of open places mostly in alpine and subalpine places

TABLE 7 (*cont.*)

taxon in pollen diagram	category in pollen diagram	family	living taxa possibly included	habit and habitat
Trema id.	B	Ulmaceae id.	*Trema*	forest tree, prominent in regeneration cycles and common in regrowth after clearing, in abandoned gardens, etc.; commonly planted for timber
Typha comp.	E	Typhaceae comp.	*Typha* and others	tall, gregarious, swamp and aquatic herb (*Typha*)
Umbelliferae id.	Ds	Umbelliferae id.	See Umbelliferae genera above	
Urticaceae/ Moraceae id.	G	Urticaceae/ Moraceae id.	*Cypholophus*	
			Elatostema	forest herb
			Pilea	forest herb
			Pipturus	forest shrub
			Ficus	forest trees and shrubs
			Streblus	forest trees and shrubs
Utricularia sim.	E	Lentibulariaceae comp.		small, lax herb of shallow water and wet mud surfaces
Veronica/ Scrophulariaceae comp.	Dg	Scrophulariaceae comp.	Scrophulariaceae genera other than *Lindernia*	
Xyris id.	E	Xyridaceae id.	*Xyris*	erect herb of shallow water and swamps
undetermined	G	including Dilleniaceae Labiatae Leguminosae *Macrozamia* Ochnaceae		
Pteridophyta				
monolete psilate id.	F			
monolete scabrate id.				
monolete verrucate id.				
trilete psilate id.	F			
trilete scabrate id.				
trilete verrucate id.				
Pteris comp.	F			

of individual cores. Samples are numbered downwards for reference. Taxa occurring rarely are not shown on the diagram but are listed in table 8. A chronology of Inferred Ages is applied as already described. Although the interpretation relies heavily on the main diagram, the data for the main taxa are also presented through the period after 15000 I.A. in a more orthodox manner, as percentages of selected totals, as an aid to comparison with diagrams from the other sites (figure 11).

The taxa contributing to the pollen diagrams have been allocated amongst eight groups according to their preferred, though not exclusive, associations, namely

A: mature forest taxa (mainly trees),
B: forest ephemeral taxa (mostly trees and shrubs including *Cyathea*),
C: open-land ephemeral taxa (mostly shrubs),
Dg: herbs of dry land (including Gramineae),
Ds: herbs of wet land (including Cyperaceae),

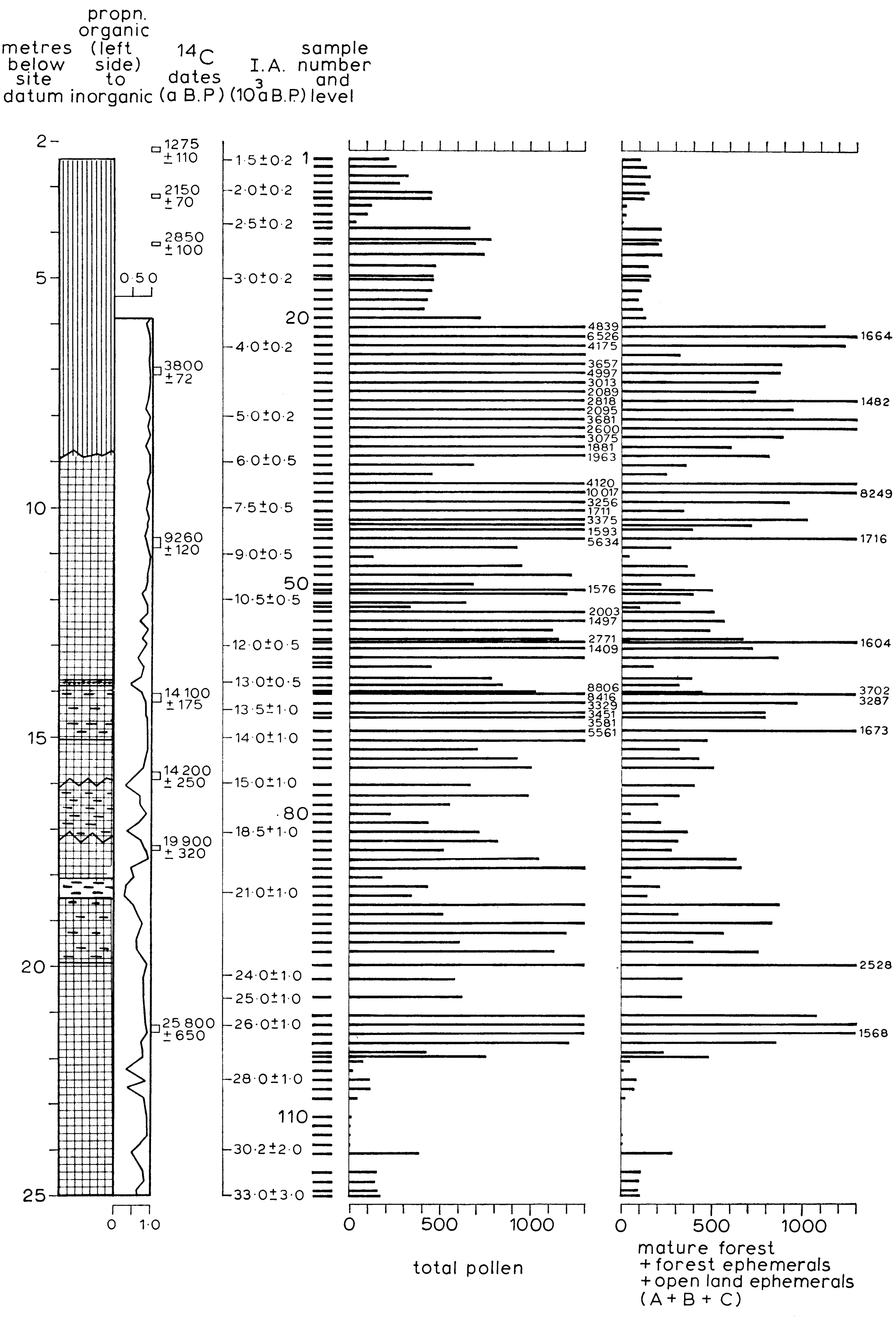
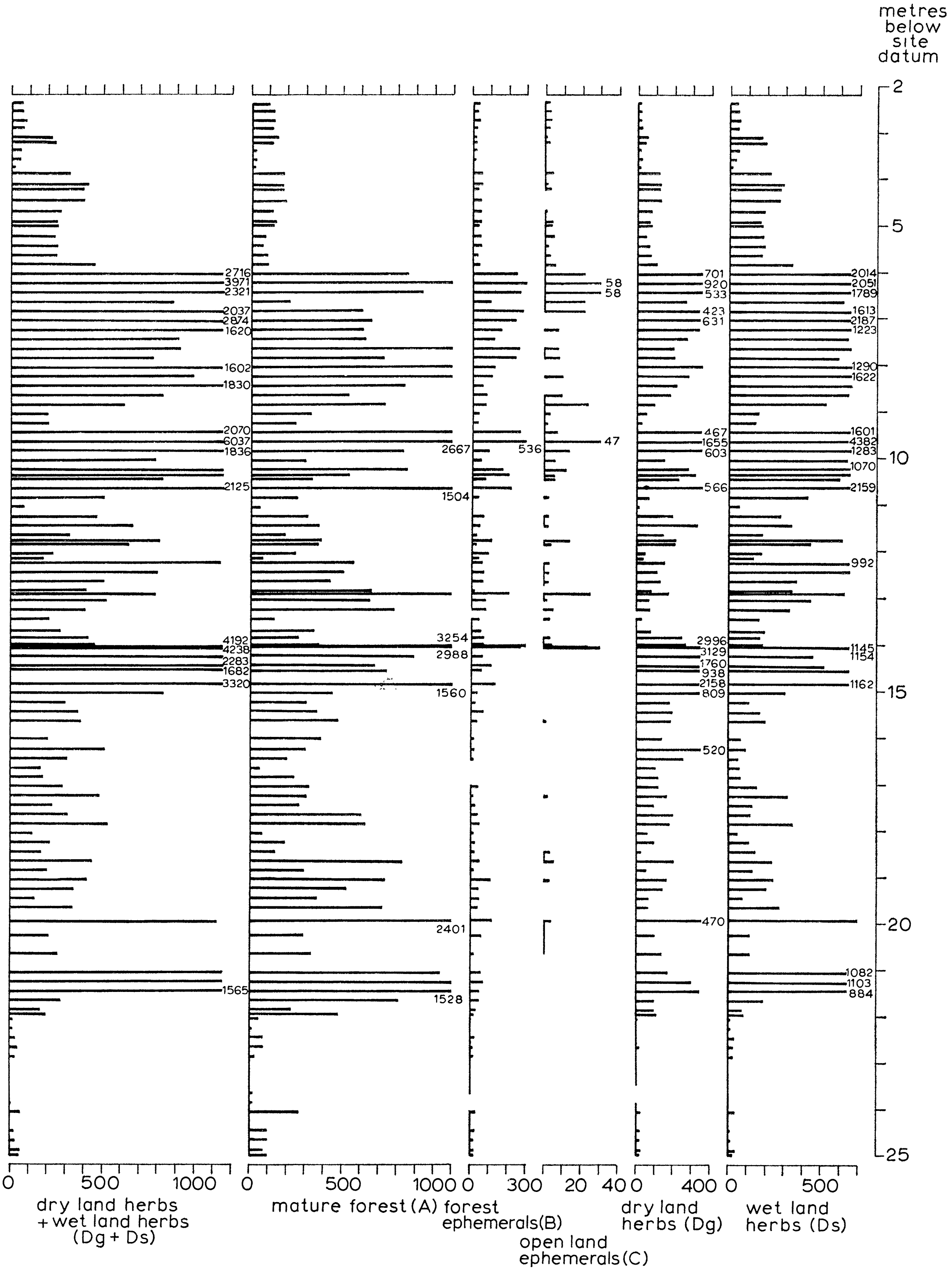


FIGURE 8. Pollen diagram A from Sirunki (2500 m). All quantities of pollen grains and spores are numbers of grains accumulated on 1 cm² of surface through 1 year. For data not included in diagram see table 8*a*.


metres below site datum
2
5
10
15
20
25
2716
3971
2321
2037
2874
1620
1602
1830
2070
6037
1836
2125
4192
4238
2283
1682
3320
1565
2667
1504
3254
2988
1560
2401
1528
536
58
58
47
701
920
533
423
631
467
1655
603
566
2996
3129
1760
938
2158
809
520
470
2014
2051
1789
1613
2187
1223
1290
1622
1601
4382
1283
1070
2159
992
1145
1154
1162
1082
1103
884
0 500 1000
dry land herbs + wet land herbs (Dg + Ds)
0 500 1000
mature forest (A)
0 300
forest ephemerals (B)
20 40
open land ephemerals (C)
0 400
dry land herbs (Dg)
0 500
wet land herbs (Ds)

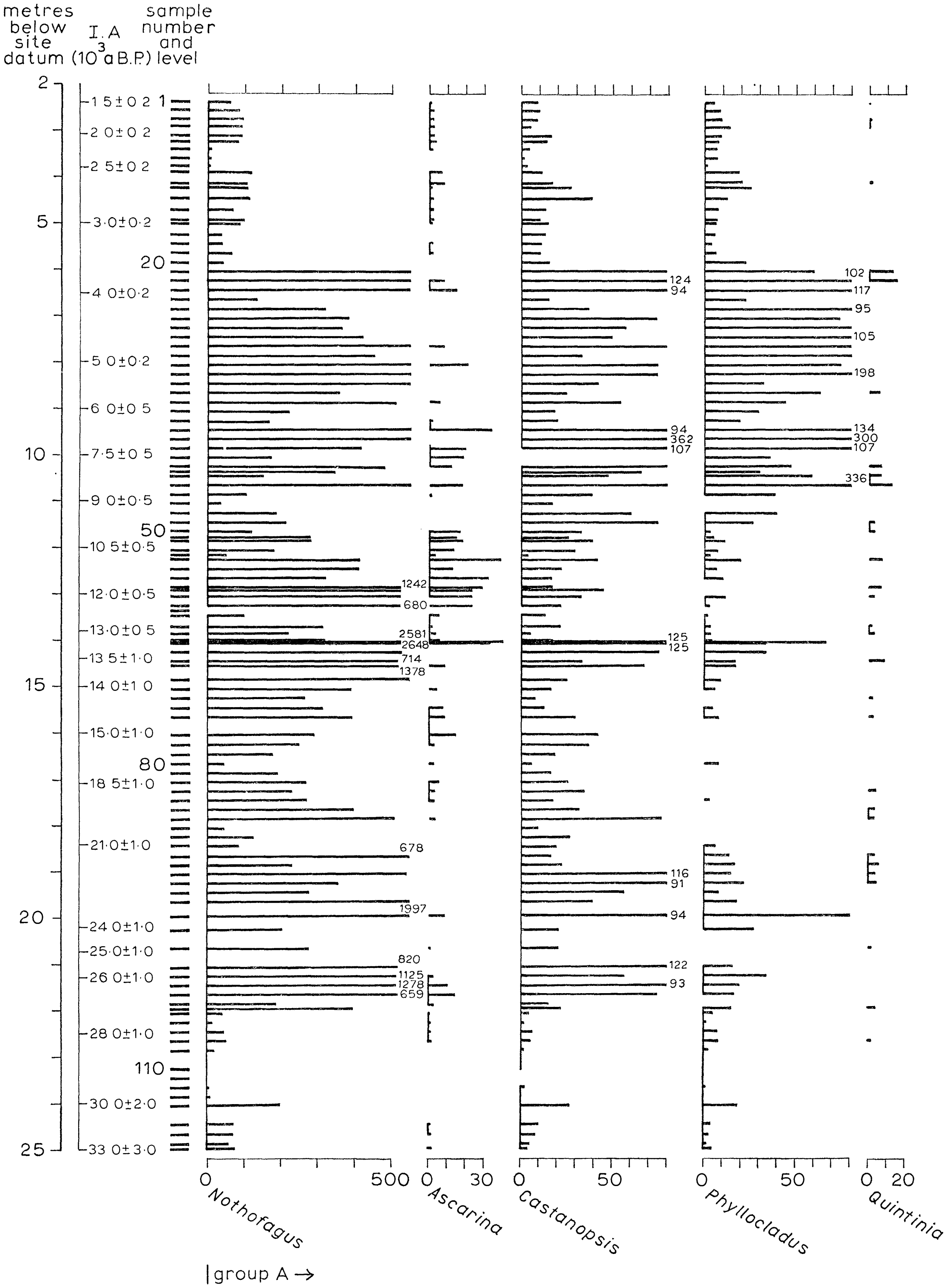
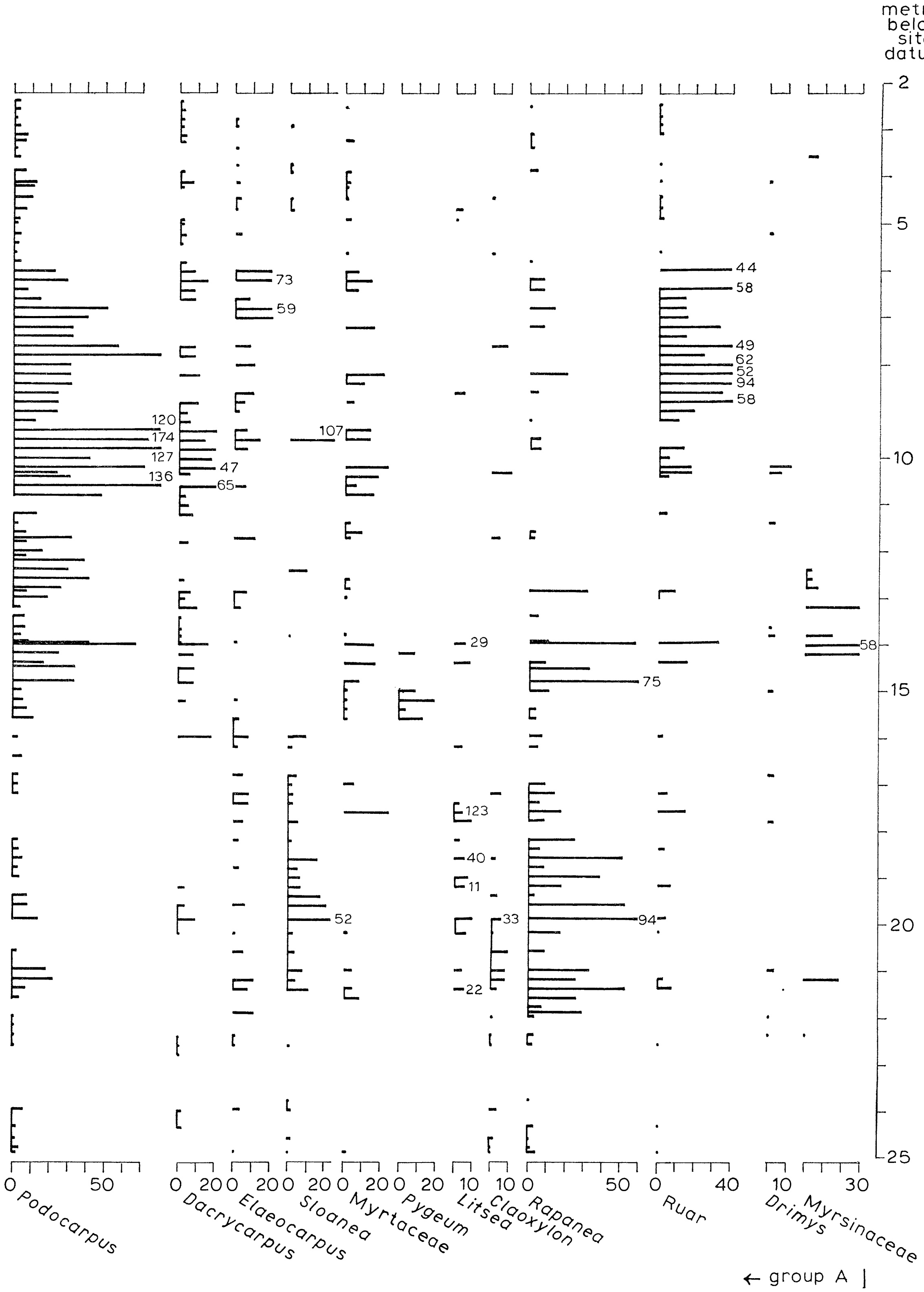


FIGURE 8 (continued). For description see page 300.


metres below site datum
2
5
10
15
20
25
120
174
127
136
47
65
73
59
107
52
29
123
40
11
22
33
75
94
44
58
49
62
52
94
58
58
0
50
0 20
0 20
0 20
0 20
0 20
10
10
0
50
0
40
10
30
Podocarpus
Dacrycarpus
Elaeocarpus
Sloanea
Myrtaceae
Pygeum
Litsea
Claoxylon
Rapanea
Ruar
Drimys
Myrsinaceae
← group A |

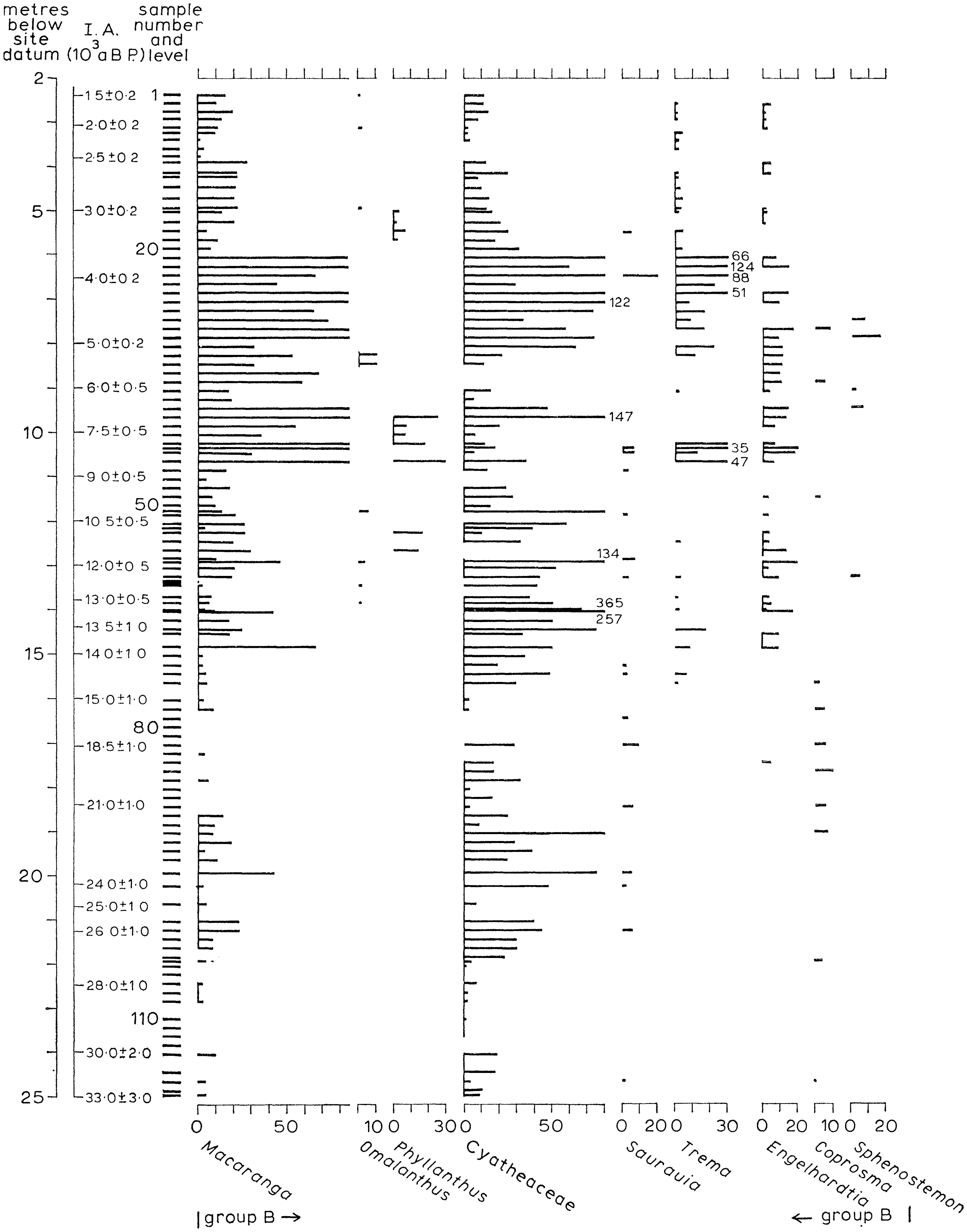
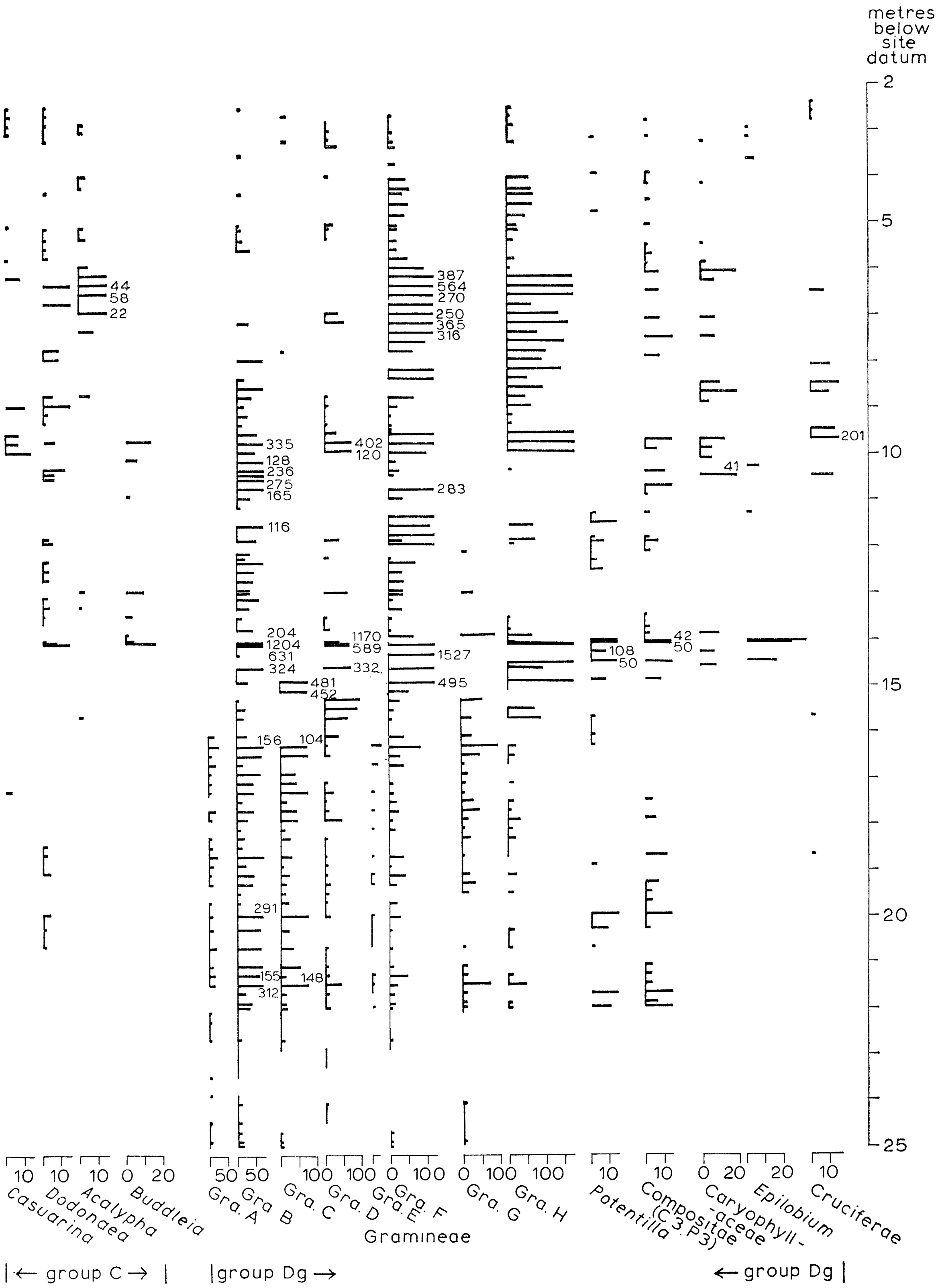


FIGURE 8 (continued). For description see page 300.


metres below site datum
2
5
10
15
20
25
44
58
22
387
564
270
250
365
316
335
128
236
275
165
402
120
201
41
283
116
204
1204
631
324
1170
589
332
42
50
108
50
1527
481
452
495
156
104
291
155
148
312
10 10 10 0 20
Casuarina
Dodonaea
Acalypha
Buddleia
50 50 100 100 0 100 0 100 100
Gra. A
Gra. B
Gra. C
Gra. D
Gra. E
Gra. F
Gra. G
Gra. H
Gramineae
10 10 0 20 20 10
Potentilla
Compositae (C3.P3)
Caryophyll-aceae
Epilobium
Cruciferae
|← group C → |
|group Dg →
← group Dg |

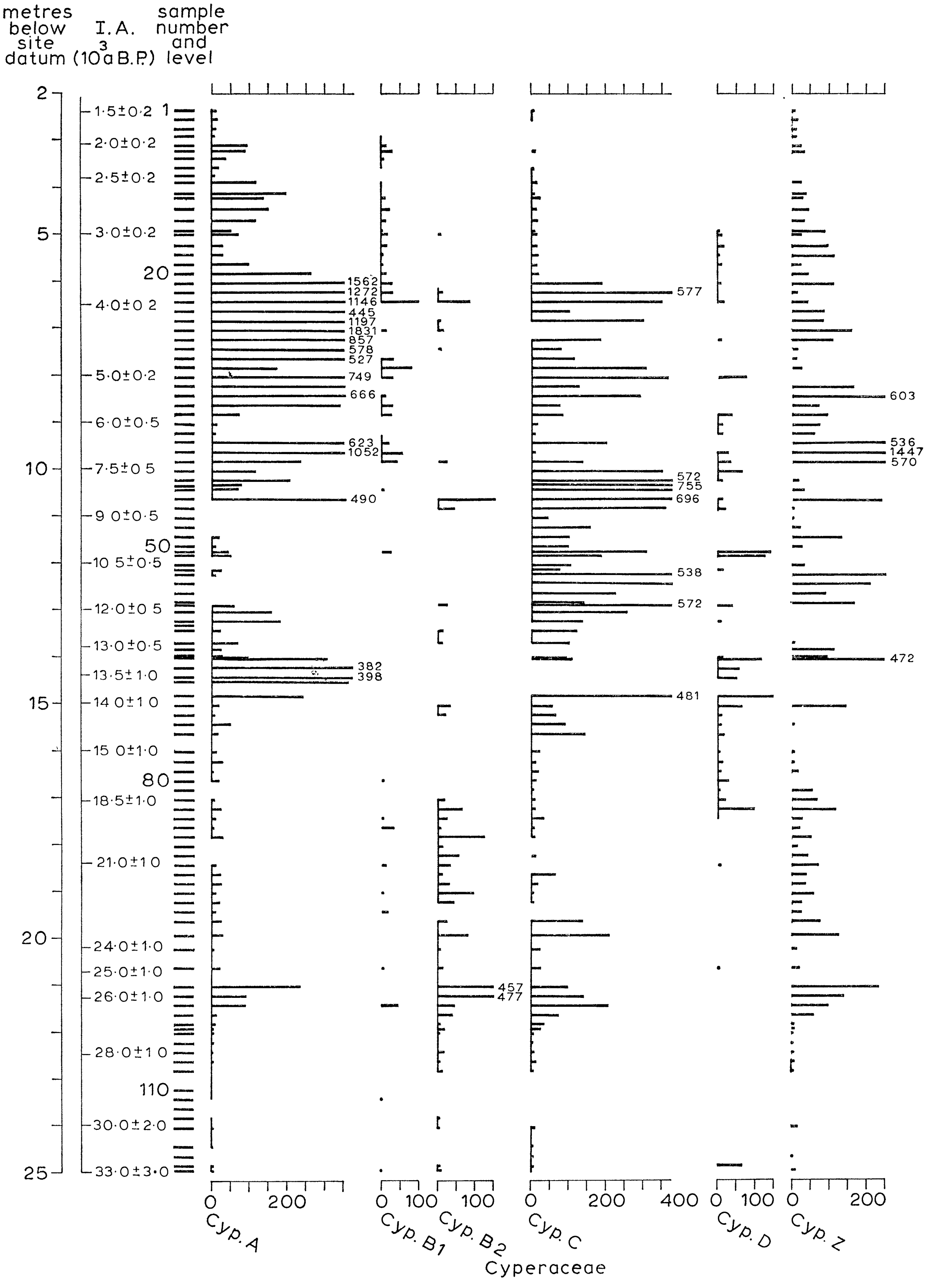
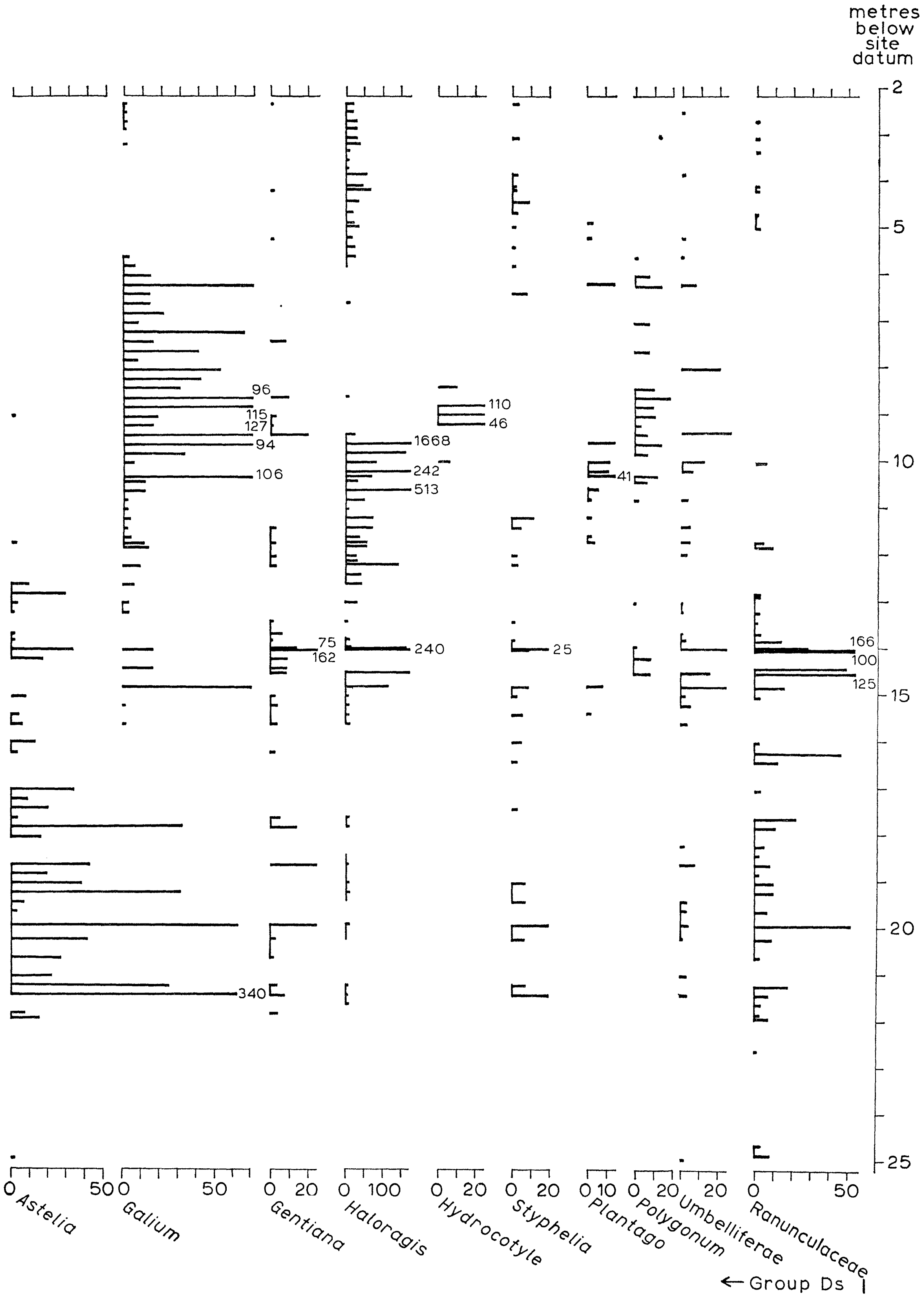


FIGURE 8 (continued). For description see page 300.


metres below site datum
2
5
10
15
20
25
96
115
127
94
106
340
75
162
1668
242
513
240
110
46
25
41
166
100
125
0 50
0 50
0 20
0 100
0 20
0 20
0 10
0 20
20
0 50
Astelia
Galium
Gentiana
Haloragis
Hydrocotyle
Styphelia
Plantago
Polygonum
Umbelliferae
Ranunculaceae
← Group Ds |

E: aquatics,
F: Pteridophyta (excluding *Cyathea*),
G: taxa of unknown or grossly ambiguous associations.

Table 7 shows these allocations.

In discussing the pollen diagram this classification of vegetation is used in addition to several general terms already used to describe the present vegetation (pp. 272 *et seq.*). In this context, however, the use of the latter terms is not intended to imply exact correspondence with a living analogue, discussion of which is reserved to a later section (pp. 335 *et seq.*).

The pollen diagram has not been divided into biostratigraphic zones because it is dominated by indications of change, rather than stability, which can be described against the timescale of Inferred Ages. This leads to a more discursive initial description but one which does least violence to the data.

Description and interpretation. Between 33000 and 30000 I.A. total pollen recovery (t.p.r.) is very low, certainly indicating unforested, indeed hardly vegetated, conditions. The only pollen and spores which may have been locally derived belong to Gramineae and *Cyathea*, although the latter's capacity for distant dispersal renders even this problematical. The deposits of the following millennium contained practically no pollen but from then until about 27500 I.A. (105)† the record is comparable with the first period with less *Cyathea* and more Cyperaceae. It is noteworthy that between 33000 and 27500 I.A. there is no significant occurrence of alpine or subalpine herbs.

Between 27500 and 27000 I.A. the record changes dramatically. By about the latter date (101) total pollen recovery values indicate that forest must have established in the catchment where it persisted until about 25500 I.A. (99). The values for *Rapanea* and *Cyathea*, amongst others, suggest that elements of upper mountain forest were nearby whilst *Astelia* and the Cyperaceae argue for subalpine swamps. On the other hand, there can be little doubt that *Nothofagus* and *Castanopsis* indicate something akin to lower mountain forest within the catchment or very close by, an environment also shared by *Phyllocladus*, *Podocarpus*, *Sloanea*, *Ascarina* and Elaeocarpaceae. There was, as yet, no substantial overgrowth of the lake.

The following 1500 years saw the catchment virtually treeless again. Possibly a few shrubs of the upper mountain forest survived but total pollen recovery values are much lower than for the immediately preceding period and grasses and *Astelia* dominate the locally produced pollen.

From about 24000 I.A. (96) to about 14000 I.A. (73) total pollen recovery values fluctuate but only occasionally exceed 1000 and sometimes fall below 500 grains $\mathrm{cm}^{-2}\ \mathrm{a}^{-1}$. This must imply that, for the greater part of the time, the catchment was unforested but that for some of it forest plants probably grew only a little way below swamp altitude and occasionally entered the catchment. It is virtually certain that *Phyllocladus*, *Podocarpus*, *Dacrycarpus* and *Castanopsis* never did so after about 21000 I.A. (90) and unlikely that *Nothofagus* did. *Rapanea* and *Cyathea* – intermittently with other mountain taxa – probably persisted in favourable enclaves in the catchment until about 18500 I.A. (82). From about 16000 I.A. (78) a systematic series of changes takes place in the mature forest pollen suggesting reassortment or movement outside the catchment. First, *Nothofagus* and *Ascarina* rise whilst *Castanopsis* falls. Then, as the first two pass their peaks, *Podocarpus*, Myrtaceae and *Pygeum* increase. At the same time, *Cyathea* becomes common again after near extinction. This is a part of the diagram in which the total pollen

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† Numbers in parentheses are sample numbers in pollen diagrams.

recovery sometimes rises close to 1000 grains cm^{-2} a^{-1} and it is probable that some of the expanding taxa began to enter the catchment and that patches of upper mountain forest become consistently established there before 14000 I.A.

Although the relative contributions of wetland and dryland herb pollen were not radically different between 24000 I.A. and 14000 I.A., the former normally just exceeded the latter until about 18500 I.A. (82) and was lower than it thereafter. The same date also marked a distinct change amongst the wetland components themselves. Some of the sporadically occurring herbs (e.g. *Gentiana*, Umbelliferae) and the shrub *Styphelia* had already been unrepresented since 20000 I.A. (85) or earlier but, from 18500 I.A., a formerly consistent group of *Astelia*, Cyperaceae B2 and Cyperaceae Z also occurred only intermittently. Cyperaceae B2 pollen contains sedges tolerant of deep water (e.g. *Scirpus mucronatus*, *Rhynchospora* sp.) and might have represented the patchy marginal reedswamps of the time; equally it might have been the product of hillside sedge – *Astelia* mires. Quantitatively this group was not replaced but Cyperaceae A and C continued at low levels whilst Cyperaceae D began to be consistently recorded; it was these three Cyperaceae which later took part in a phased recrudescence of the wetland taxa beginning shortly after 15000 I.A.

The composition of the grasslands also changed but at about 15000 I.A. (77). From that time the formerly fairly consistent Gramineae A, B and E virtually disappeared from the record whilst Gramineae G suffered a similar fate a thousand years later. Their places were taken by increases in taxa already present (e.g. Gramineae D, F, H) some of which became the common grasses of subsequent periods.

The general stratigraphy of the basin indicates that marginal reedswamps began to develop, perhaps in lowered water conditions, from about 15000 I.A. In the pollen analysed core, this date corresponds with a change from a slightly clayey to a clayless fine detritus mud in a series of variously clayey organic deposits, and the end of low loss on ignition values. The rise of Cyperaceae C at about this time was probably related to these stratigraphic phenomena, i.e. to strictly hydroseral events, but it is unlikely that the grasses were similarly directly involved. 18500 I.A., although marked by a minor stratigraphic change at the pollen analysis site, had no special significance in the general stratigraphy.

The 500 years following 14000 I.A. (to sample 69) undoubtedly witnessed the occupation of the catchment by lower mountain forest, with upper mountain forest above, perhaps above a height of 2800 m and in the cold hollows at lower elevations. Total pollen recovery rate is generally greater than 2000 grains cm^{-2} a^{-1}. The sequence of changes which began about 16000 I.A. beyond the rim of the catchment now continued in it. *Nothofagus* was certainly common but first *Podocarpus* then *Castanopsis* and *Phyllocladus* increased their rôles. So did *Macaranga*, whilst *Trema* and *Engelhardtia* occurred fitfully but in amounts suggesting their presence within the catchment. Some of the *Cyathea* represented by the increased catch of its spores may have been in the forest itself, but more likely it shared with *Rapanea* and the Myrtaceae the more rugged and exposed slopes above 2800 m. *Dacrycarpus* is first consistently represented in the pollen diagram during this period and probably, together with the persisting *Astelia*, mostly occupied cold, damp, hollows. The sequence of changes in the wetland flora, which began about 15000 I.A., culminated during this period in the abundance of Cyperaceae A together with *Galium*, Umbelliferae, *Ranunculus*, *Polygonum*, Haloragaceae and Cyperaceae D. This is consistent with the general stratigraphic evidence for overgrowth and small water depths in the basin itself, particularly as the category Cyperaceae A contains those sedges (e.g. *Cyperus globosus*, *C. unioloides*, *Fimbristylis* sp.) which do not normally tolerate water deeper than 5 cm. The contributions of different taxa to the dryland herbs had begun to change at about 15000 I.A. and the process culminated during this period in the dominance of Gramineae F and H. These categories could contain *Phragmites* and *Miscanthus*, the first of which might have grown in the watery swamps and the second on raw or peaty soils. The presence of *Potentilla* and Compositae, however, reinforce the indication of Gramineae H, that substantial well drained areas around the basin remained unforested.

The exceptionally high total pollen recovery values of samples 67 and 68 (> 8000 grains $\mathrm{cm}^{-2}\ \mathrm{a}^{-1}$; *ca.* 13250 I.A.) may be artefacts of unusually slow deposition of a narrow and otherwise not specially identified layer of sediment. This is particularly likely since all ecological categories in the pollen flora participate in them. Within each category, however, there are some striking indications. Amongst the trees of lower mountain forest, *Nothofagus* and *Ascarina* increased their representation fourfold over the immediately previous period, *Podocarpus* and *Phyllocladus* doubled their values but *Castanopsis* increased very little above the level to which it had built during the previous 500 years. The components of the upper mountain forest, however, fared comparatively badly and probably were virtually lost from the catchment. Amongst the forest ephemerals only *Cyathea* increased comparably with *Nothofagus* whilst some (e.g. *Trema*) were strikingly low. On the other hand, the open land ephemerals *Dodonaea* and *Buddleia* were recorded in substantial quantities, the first having been absent since about 21000 I.A., the second never having been recorded before.

The abundance of dryland herb pollen increased only about half as much as did that of mature forest trees. Moreover, the grasses which asserted themselves were not those which had grown to importance during the preceding 500 years but Gramineae B and D. All Compositae, *Potentilla* and *Epilobium* increased in some degree.

Amongst the sedges, Cyperaceae A and D actually diminished from their earlier values whilst Cyperaceae C and Z resumed something of their former importance. Other swamp herbs reacted variously but it is clear that swamp development in the basin was arrested or reverted to a course begun 500 years earlier.

The overriding impression is that this was a short period witnessing some major vegetation changes. Some of them, such as the virtual extinction of upper mountain forest from the catchment and the diminution of open land relative to forest, continued trends already in train. Others, such as the preponderance of *Nothofagus* in the forest and the reassortment amongst grasses and sedges were, in a sense, reversions to earlier conditions. Yet others, particularly the arrival of *Dodonaea* and *Buddleia* were new beginnings.

Immediately in the wake of these changes, total pollen recovery values fall to levels which strongly imply that by 12500 I.A. the forest had disappeared from the catchment and *Cyathea* 'woodland', sedgy swamps and depauperate grassland probably remained. It is probably significant that there is strong stratigraphic evidence for a rise in water level, accompanied by erosion and redeposition, culminating about 13000 I.A.

From about 13000 I.A., total pollen recovery values suggest that afforestation of the catchment was erratic, although commoner between 12500 I.A. and 10500 I.A. than at other times. Throughout the period, *Nothofagus* is the dominant pollen type but between 12000 I.A. (58) and 10000 I.A. (50) *Ascarina* and *Podocarpus* are its main companions with some *Phyllocladus*. *Castanopsis* is very low until 10500 I.A. (54) when it begins to rise, reaching a maximum between 10000 I.A. (50) and 9000 I.A. when it was almost certainly not in the catchment. At about this latter level, *Dacrycarpus* pollen begins to occur more abundantly in relation to other forest trees, suggesting its occupation of frost hollows in the catchment itself.

Cyathea spores remain in abundance, which probably indicates the presence of tree-fern woodlands in the catchment but this was less certainly the case after 10000 I.A. (50) when *Dodonaea* pollen also disappears from the record for the time being. The significance of these vegetation changes is discussed below (p. 328).

Changes in representatives of dry land flora, involving *Potentilla* and Compositae, began at about 11000 I.A. (56) and culminated in high pollen values of Gramineae F between 10500 I.A. (52) and 9500 I.A. (48). Amongst the wetland plants, Cyperaceae accelerated its expansion begun at 13000 I.A. and was joined at about 12000 I.A. (59) by quantities of Cyperaceae Z. Although pollen of Cyperaceae C persists in considerable quantity, both sedges in fact fall considerably at about 10500(54), as *Galium*, Haloragaceae and *Styphelia* become more abundant than they formerly had been, all indicating the progression of hydroseres on organic soils, almost certainly around the basin's edge. Apart from four isolated records much later, *Astelia* pollen disappears from the diagram at 10000 I.A. (50).

From 9000 I.A. to about 6000 I.A. (35) a sequence of pollen analytical events is recorded which strongly suggests continued *verlandung* around the sampled site. These events, in order, are (i) high values of Cyperaceae C plus Haloragaceae, (ii) relatively substantial values of Cyperaceae D+B1 with maintained Haloragaceae, (iii) high Cyperaceae A, Cyperaceae Z and *Galium*, (iv) relatively low Cyperaceae, absence of *Haloragaceae*, relatively high *Galium* and abundant *Hydrocotyle*. During the same period, however, *Sparganium* and *Xyris*, suggestive of water 25–100 cm deep, were consistently present. *Polygonum* was also frequent and consistent and it is tempting to wonder whether some of the pollen from Gramineae F and H might in fact have come from *Phragmites*. The implications of these seemingly contradictory indications are that, from an earlier more or less open-water lake edged with reedswamp, the surroundings of the sampled site passed to a mosaic of areas of fairly advanced accumulation, perhaps floating mats, on which much of the surface was vegetated and the remaining water predominantly less than 30 cm deep, and others in which the water was as much as 1 m deep. Such a situation exists on parts of the Kayamanda Swamp at the present day. It is quite consistent with the temporary rise of water level indicated in the general stratigraphy.

Following these events, Cyperaceae A and C clearly dominated the area around the sampled site. Judging from the falls in *Xyris*, *Sparganium*, *Dysophila* and *Galium* values by about 3000 I.A. and the return of Haloragaceae about then, mud accumulation had reduced the commonest depth of free water to about 5 cm and a more or less uniform sedge swamp probably covered a large area around the sampled site.

Total pollen recovery values indicate that from 9000 I.A. until about 1500 I.A. (1) most of the pollen originated in the catchment, with the possible exception of short periods at about 6000 I.A. (36 and 37) and 2000 I.A. (7, 8 and 9). Initially a forest in which *Nothofagus*, *Ascarina*, *Castanopsis*, *Phyllocladus* and *Podocarpus* were all significant trees and in which *Quintinia*, Myrtaceae and RUAR (probably *Euodia*, but possibly others from Rutaceae, Araliaceae and Clusiaceae) were represented, quickly occupied the catchment. *Dacrycarpus* temporarily sank to insignificance (perhaps associated with the instabilities attested by the stratigraphy at this time) but soon returned to persist, presumably in the colder hollows, until about 6000 I.A. (35). The dominant grass group of the period was Gramineae B, a type unlikely to have been associated with swamps and which was well represented from much earlier times; it almost certainly came from the coldest hollows around the swamp edge. Accompanying the grasses were *Potentilla*, also an ancient component, and the relatively new ones Caryophyllaceae and Cruciferae.

Although many forest taxa initially entered the catchment, their quantitative relationships (or the pollen analytical expression of these relationships) did not stabilize until about 8000 I.A. (42) (p. 328). By that time, and for the next 1500 years (to sample 37), *Castanopsis* and *Phyllocladus* had lost some of their initial importance and a forest comparatively richer in *Nothofagus*, *Ascarina*, *Podocarpus*, Myrtaceae and RUAR had asserted itself with *Macaranga*, *Phyllanthus* and *Engelhardtia* its most important ephemerals. Sample 38 was also the last grass rich sample for some time. This period was also notable for the first and most significant occurrence of *Casuarina* (samples 40, 39 and 38; about 7500–7000 I.A.), probably at lower altitudes beyond the confines of the catchment.

Although samples 36 and 37 have relatively low total pollen recovery values and are transitional to a new balance in the dryland vegetation, it seems unlikely that forest vacated the catchment. This was a time of local overgrowth or floating mat formation at the sampled site which probably temporarily accelerated accumulation giving spuriously low total pollen recovery values for which no correction has been made.

6500–5000 I.A. (37–30) witnessed a decidedly simplified forest dominated by *Nothofagus* in the catchment. Forest ephemerals lay at levels explicable in terms of regeneration gaps and by 5500 I.A. (33) *Dodonaea*, *Acalypha* and *Casuarina* (probably from outside the catchment) had disappeared for the time being, as had the grasses (notably Gramineae D) indicative of open ground for so long past. *Dacrycarpus* was lost slightly earlier suggesting that the coldest hollows were not now cold enough to harbour grass and frost-hollow forests. It was perhaps the most stable period in the history of the Sirunki forests and it lasted only 1500 years.

The abundance of *Nothofagus* pollen began to fall at about 5000 I.A. and continued to do so until about 4000 I.A. (24). For the first two thirds of this period, *Castanopsis* increased then fell to a minimum by the end of it. *Phyllocladus* was less clearly affected, although its pollen, too, shows a marked minimum in the single sample 24. *Podocarpus* and RUAR curves are not particularly sensitive but Elaeocarpaceae are represented in unprecedented amounts as *Castanopsis* values fall. The very great numerical reduction in *Nothofagus* pollen is not wholly compensated by the rises in other values with the result that the forest ephemerals, which themselves either fall slightly or stay more or less the same, *increase* relative to the mature forest tree pollen. Nevertheless, *Trema* and *Macaranga* were more consistently present than ever before, *Cyathea* increased and *Sphenostemon* and *Dodonaea* occurred. It seems very likely that the period in fact saw a real reduction in *Nothofagus* and an increase in *Castanopsis* until about 4300 I.A. (26). The mechanism of this change might have been sufficient to account for the greater importance of *Trema*, *Cyathea* and *Macaranga* but it is difficult to avoid the conclusion that some slight forest destruction was also under way (p. 339). The drift of the Gramineae (mainly Gramineae F) curve may corroborate this but its movements parallel those of the Cyperaceae values, at a time of very active swamp overgrowth, so closely that it is perhaps better not to attribute any *general* significance to the grass values.

At the level of sample 25 there is a pronounced increase in *Trema* values, accompanied by a surge of *Acalypha* (open land ephemeral). These increases correspond to the beginning of the fall in *Castanopsis* and continue until 3700 I.A. (21) at which level RUAR, Elaeocarpaceae and Myrtaceae sink to insignificance. The high levels of *Trema* and *Acalypha* are maintained in spite of a numerically much superior resurgence of *Nothofagus*, *Castanopsis*, *Phyllocladus* and

Elaeocarpaceae in samples 23, 22 and 21, from about 4000 until about 3700 I.A. There can be no doubt, therefore, that, whatever changes in forest composition were afoot from 5000 I.A., they were interrupted by partial destruction of the forests in the catchment between 4300 and 4000 I.A. In the forest that regenerated, *Castanopsis* and Elaeocarpaceae regained the levels of abundance they had achieved immediately before their fall but *Podocarpus* increased only feebly and *Phyllocladus* continued to falter. *Dacrycarpus* re-entered the record in small but significant quantity at a time when *Trema* and *Acalypha* expanded, and it remained until about 3000 I.A. (15).

The overgrowth of the sampled site by tall reedswamp at about 3700 I.A. and the lack of 'absolute' pollen catch data from analogous situations at the present day renders impossible comparisons based on pollen recovery rates before and after that date. The possibility of small vegetation changes (e.g. density of reed stems) affecting pollen accumulation rate even renders comparisons between samples above the 3700 I.A. level (21) hazardous. Interpretation of this uppermost part of the pollen diagram rests more heavily on changes in relative pollen abundances and must therefore be correspondingly tentative.

The regeneration of the forest between 4000 and 3700 I.A. was short-lived and the abundance of forest ephemerals and open-land ephemerals continued until about 3000 I.A. (17). Among the former, however, *Trema* and *Macaranga* lost their dominance to *Cyathea* and *Phyllanthus. Casuarina* is recorded erratically for the first time in about 3000 years. Towards the end of this period it seems that *Castanopsis* might have fared better than other forest trees but, in the recovery which began about 3000 I.A., it was *Nothofagus* which expanded most strongly, at least for a single generation (14). At the same time the former balance amongst the forest ephemerals was restored although their total contribution to the pollen rain, and that of the open land ephemerals, diminished. There followed a short period during which *Castanopsis* once again rose and fell, the forest ephemerals and open land ephemerals were substantially reduced and the swamp and dry land herbs increased slightly.

At about 2500 I.A. the total pollen recovery value was exceedingly low and its rise was slow during the following 300 or 400 years. This may be a stratigraphic artefact. In the relative pollen abundances the onset of this phase is not particularly marked but, as it progresses, *Castanopsis* and *Phyllocladus* rise preferentially, as do *Trema* and *Cyathea* at the expense of *Macaranga*. By about 2000 I.A. (6), however, *Nothofagus* had overtaken the expansion of the other trees and *Macaranga* had regained supremacy amongst the forest ephemerals. From that time until about 1500 I.A. (the top of the diagram) *Nothofagus* continued to increase in relation to other forest trees but there was some diminution in mature forest compared with forest ephemerals and open land ephemerals. The overall balance amongst these three main components returned roughly to the condition seen between 2500 and 2800 I.A. Among the open land ephemerals, however, *Casuarina* and *Dodonaea*, rather than *Acalypha*, were the most consistent and numerically important plants; they must have been within the Sirunki catchment.

From about 2000 I.A., the wet land herbs, and to a lesser extent the grasses, were substantially reduced. Among them, however, there were changes in the relative contributions of the different sedges and Haloragaceae became relatively very abundant. This argues a return to somewhat deeper water conditions and sparser sedge cover.

In summary, the nature of the vegetation in the catchment before 27500 I.A. is enigmatic, although the weight of evidence favours alpine barrens. From then until 9000 I.A. subalpine conditions dominated and trees and shrubs were sparse, except for the periods 27500–25500

I.A. and 14000–13250 I.A. which witnessed excursions of lower mountain forest taxa into the catchment. The final afforestation began about 9000 I.A. By 6500 I.A. a *Nothofagus*-rich forest had achieved a dominance which was maintained for 1500 years. However, shortly after 5000 I.A., fluctuations in forest composition began which were associated with periodic changes in the proportion of forested to unforested land and which certainly directly affected the catchment from 4300 I.A. onwards.

(*b*) *Inim*

Sources of pollen. Although Inim must share the same regional pollen sources as Sirunki, its size and position differentiate it from that site in relation to other sources.

Under more or less totally forested conditions, 90% of the pollen received by Inim was probably derived from its own swamps, the slopes immediately around it (covering an altitudinal interval of 2500 to 2600 m) and a very small component from as high as 2800 m. When these slopes were not forested, however, there would be greater opportunity for the intrusion of pollen borne up the Rama-Lai valleys from as low as 2000 m although the sheltered position of the Inim site behind the flanks of these valleys would still afford it considerable protection.

Determination. Pollen grains were determined in the manner described for Sirunki. The smaller reference collection available at the time, however, resulted in more tentative determination of some forms than proved necessary subsequently; in a few cases names have been attributed to pollen grains counted from Inim on the basis of later experience.

Preparation and presentation. The collection of material in the field and its laboratory preparation followed the methods described for Sirunki except that no attempt was made to measure pollen recovery rates. The pollen diagram therefore presents only relative changes from level to level, calculated on the bases indicated. At each level, at least 200 pollen grains and spores were counted, incorporating at least 150 grains of forest trees. Pollen taxa were attributed to eight groups as for Sirunki.

Lacking the indications of pollen recovery rates and an adequate radiocarbon chronology, the interpretation of the Inim diagrams must be tentative and crude.

Correlation of the two Inim diagrams (figures 9 and 10). The grey clay is probably substantially younger than 8000 I.A. in core M15; in M4 it lies between 8000 and 4000 I.A., perhaps between 5500 and 4000 I.A. This, and the general distribution of this clay in the relevant part of the basin, allows its use as a stratigraphical marker for the correlation of the two pollen diagrams. Due allowance was made for discontinuities of different and unknown lengths at the top and bottom of the clay in both diagrams. This general correlation is confirmed by the absence of certain pollen taxa (e.g. *Astelia*) which are characteristic of the lower levels of M15 from the mud immediately below the clay in M4 and by the presence of characteristic percentages of others (e.g. *Macaranga*, *Casuarina*) in and above the clay in both diagrams.

The water gap in core M4 emphasises the possibility of contemporaneous accumulation at two levels, the one on a floating mat, the other by inwash beneath it. For present purposes, however, it will be assumed that the detritus accumulating at the bottom of the water gap was derived mostly from the base of the mat above so that the pollen diagram represents a continuous record of vegetation change.

Description and interpretation. For a long period (M15, 19–6),† probably ending about 9500 I.A., the Inim Valley slopes were covered by grassland and damp soil herbfield, perhaps with patches

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† Letters and numbers in parentheses refer to the pollen diagrams; succeeding numbers refer to the sample numbers of that diagram.

of *Cyathea* here and there. Initially (to M15, 19), damp habitats, rich with subalpine and alpine shrubs and herbs (e.g. *Astelia*, *Drapetes*, *Plantago* cf. *aundensis*) and other less cold demanding taxa (e.g. *Gentiana*) and *Styphelia suaveolens*, were commoner than in the later part of the period. Forests were probably distant from the catchment.

Before about 7000 I.A. (M15, 6–4; M4, 25–22), a slight increase in forest ephemerals and lower grassland and wetland plant representation (particularly the fall of *Astelia* and the loss of *Drapetes*, *Plantago* cf. *aundensis* and *Styphelia*), suggest a period of steady vegetation change during which trees began to enter the catchment, amongst them *Dacrycarpus*, *Ascarina* and Elaeocarpaceae. In the muds under the island there is a stratigraphic indication of possible localized overgrowth by swamp forest.

From about 7000 to about 3000 I.A. (M15, 4–1; M4, 22–16) lower mountain forest was established in the catchment. Its composition is difficult to assess but it is likely that it was predominantly *Nothofagus* with other taxa such as *Castanopsis*, *Phyllocladus* and *Podocarpus* erratically attaining limited importance. Open land ephemerals strengthened their representation slightly but both grasses and sedges diminished markedly. Among the sedges, the taxa evidently changed; there are also erratic and high values of some swamp plants (e.g. *Oenanthe*) which is consistent with the change from organic to inorganic sedimentation in the basin. None the less, more taxa representing organic substrata, notably Haloragacae and *Gentiana*, remained in quantity, presumably on marginal swamps over which the clay from the mud volcanoes did not flow. *Casuarina* and *Dodonaea* were present consistently but in such small quantities as probably to have come from beyond the catchment.

The next thousand years or so (M4, 16–11) witnessed a strong diminution in dry land herbs and open-land ephemerals and somewhat lower levels of forest ephemerals than formerly, but an increase in wet land plants, particularly sedges. This implies that there was a period of undisturbed forest growth in the catchment and an overgrowth of the basin edge by reed swamp. Within the forest, some taxa (e.g. *Castanopsis*, *Phyllocladus*, *Podocarpus*) consolidated at the expense of others (e.g. *Dacrycarpus*, Elaeocarpaceae, Myrtaceae). Amongst the forest ephemerals, *Trema* assumed the importance formerly held by *Macaranga*.

From 2000 until about 500 I.A. (M4, 11–4) the most notable change was an expansion of grasses and a return of *Casuarina* in consistent, although very small, amounts. Within the forest, some taxa which were commoner before 3000 I.A. (e.g. *Dacrycarpus*, Myrtaceae) returned, if somewhat erratically, whilst others (e.g. *Podocarpus*) behaved less consistently than immediately before. There is instability, too, amongst the forest ephemerals. It seems likely that the forests of the region were subjected to more disturbance during this period than immediately before and that this had local expression in the catchment by the inhibition of forest regeneration and the maintenance of gaps filled by grasses.

During the last 500 years it seems that the components of the forest have behaved increasingly erratically, and that their total contribution to the pollen rain has declined substantially. This was primarily the result of very active spread of swamp vegetation across the basin but was also accompanied by increasing *Casuarina* while, among the forest ephemerals, *Trema* rose spectacularly. All these changes suggest that the forests of the region became even less stable than before and that the area of open ground increased. Not very long ago this regional tendency resulted in the replacement of some forest by open ground within the Inim catchment.

FIGURE 9.

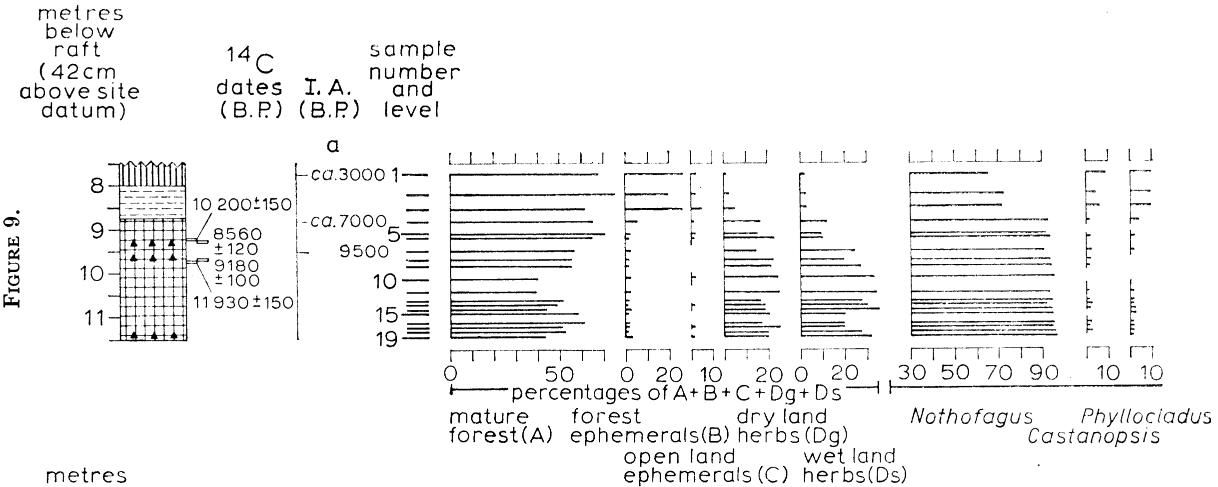


FIGURE 10.

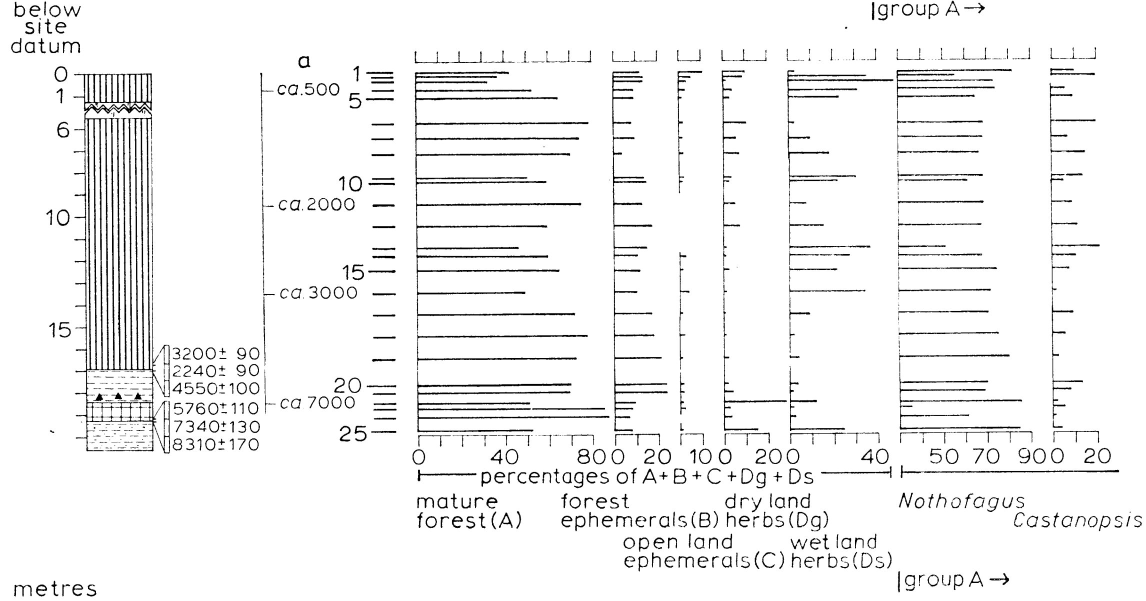


FIGURE 11.

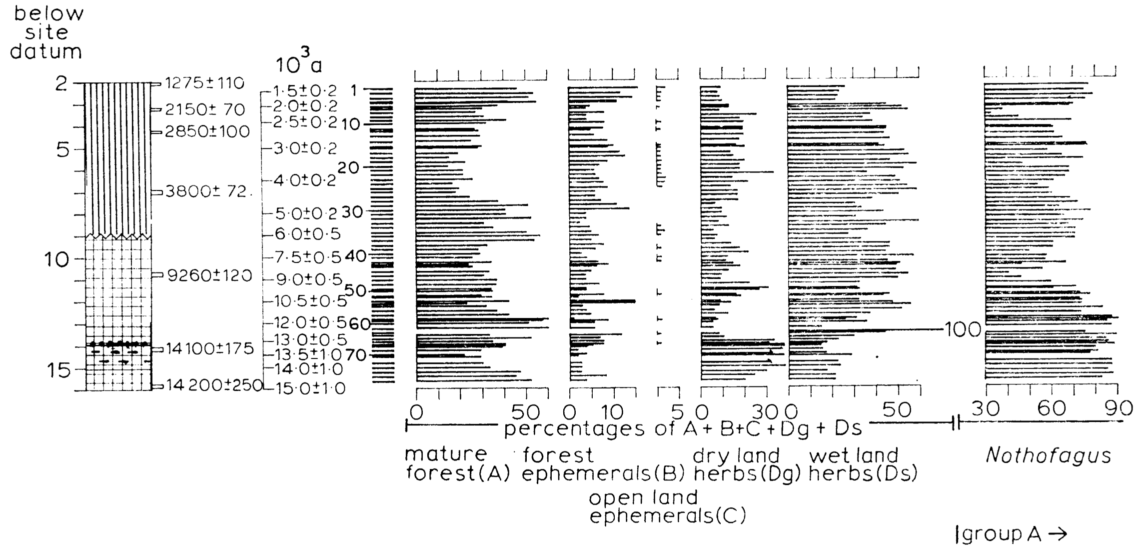


FIGURE 9. Pollen diagram M15 from Lake Inim (2550 m). Quantities are percentages of a number of bases described in the text and used also in figures 10 and 11.

FIGURE 10. Pollen diagram M4 from Lake Inim (2550 m). Quantities are percentages of same bases used in figures 9 and 11.

FIGURE 11. Pollen diagram from Sirunki (2500 m). Quantities are percentages of same bases used in figures 9 and 10 recalculated from data displayed in figure 8.

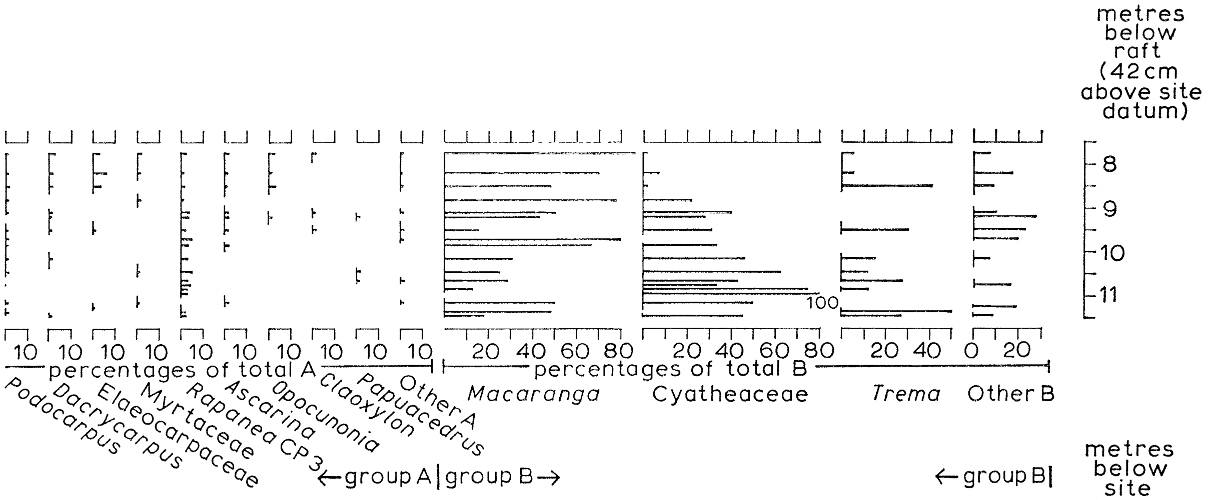


FIGURE 9 (continued).

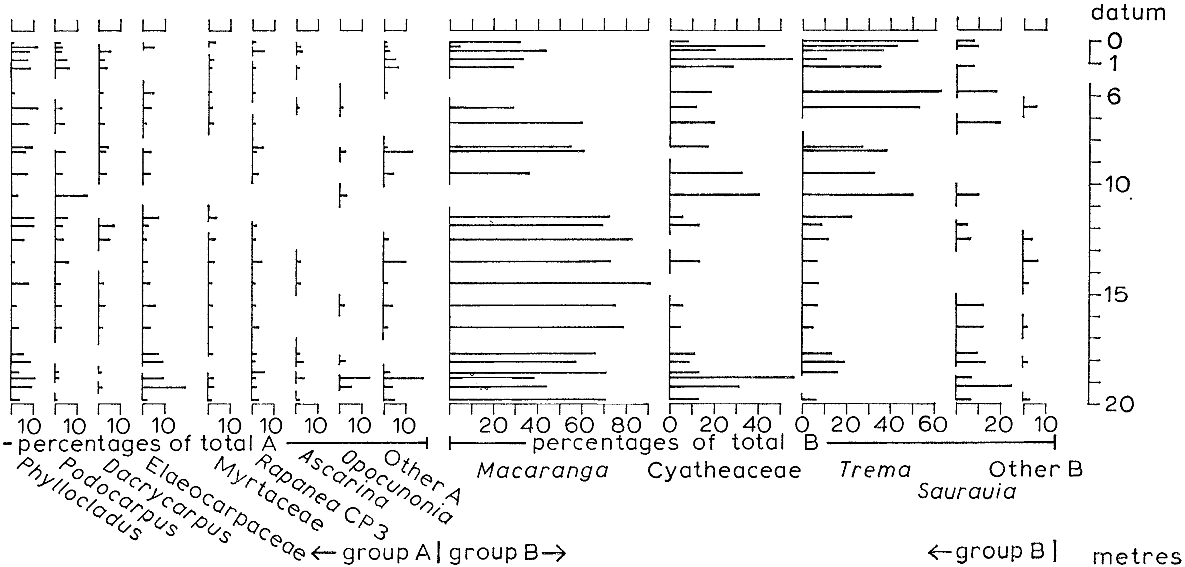


FIGURE 10 (continued).

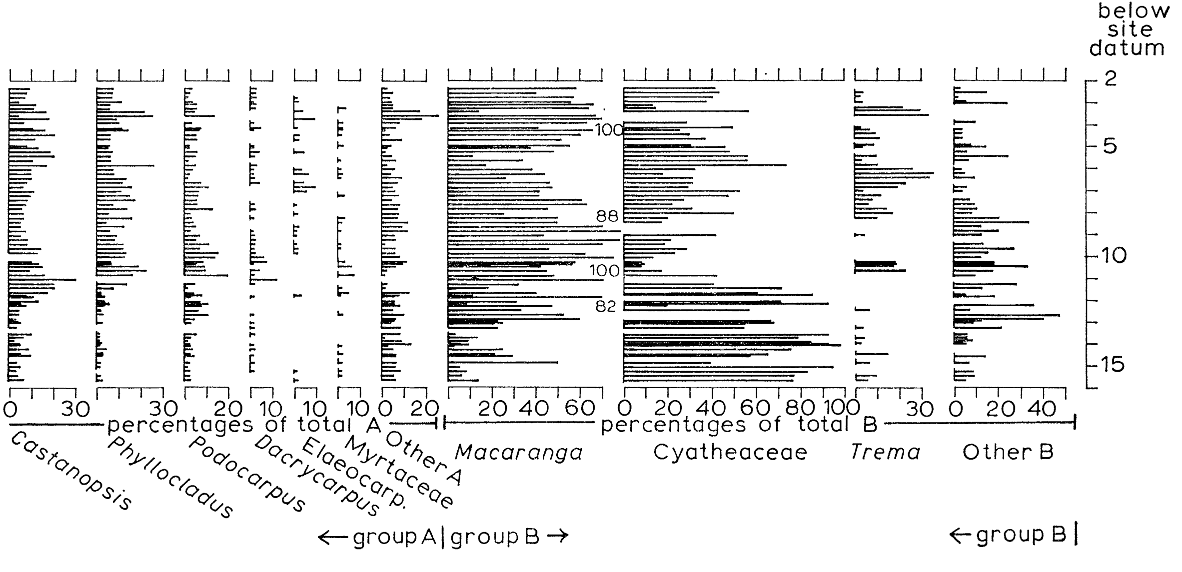


FIGURE 11 (continued).

FIGURE 9 (continued).

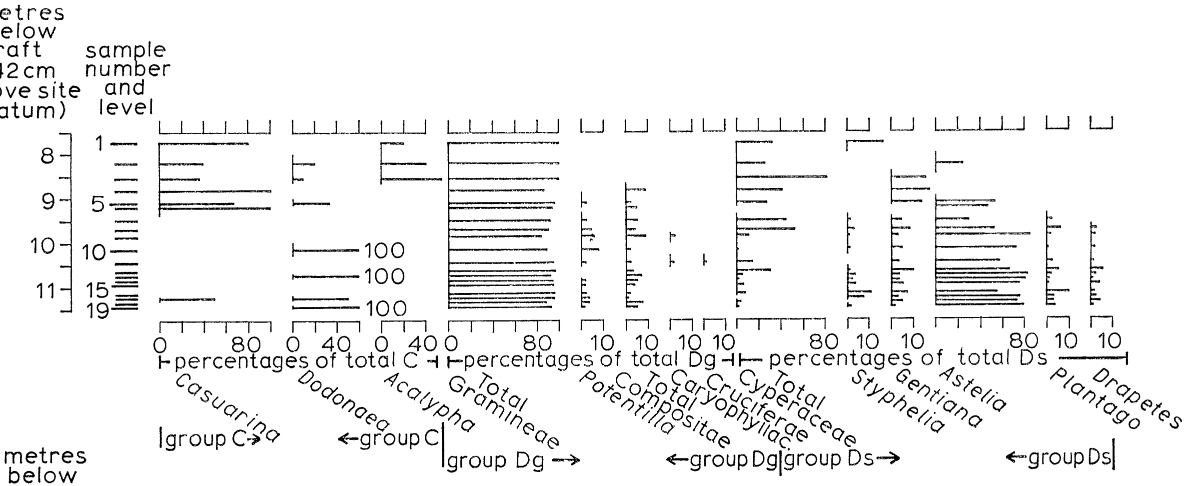


FIGURE 10 (continued).

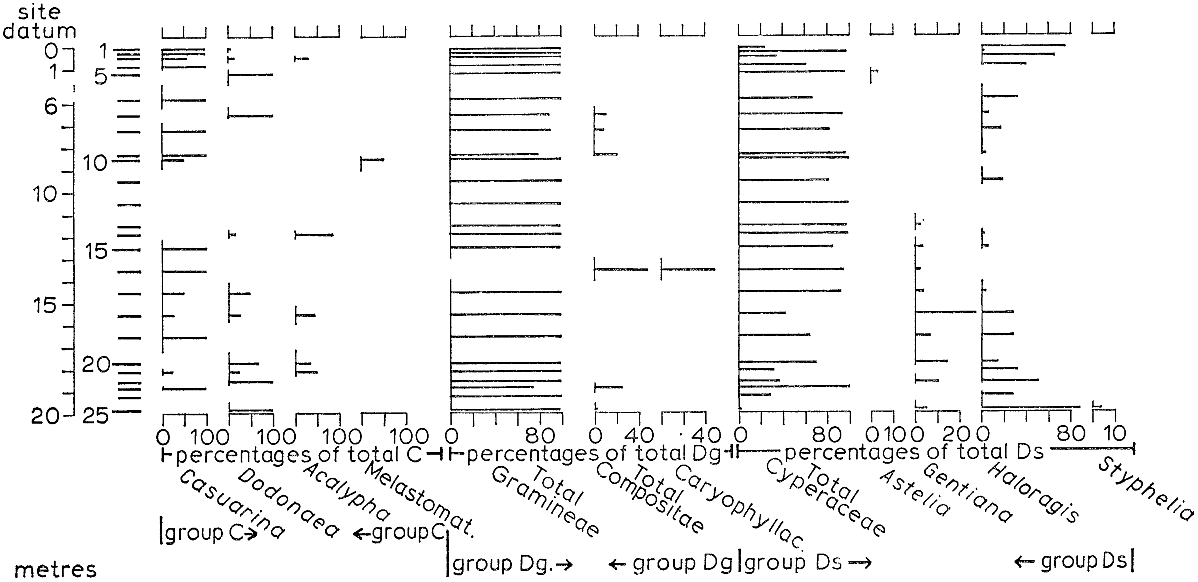
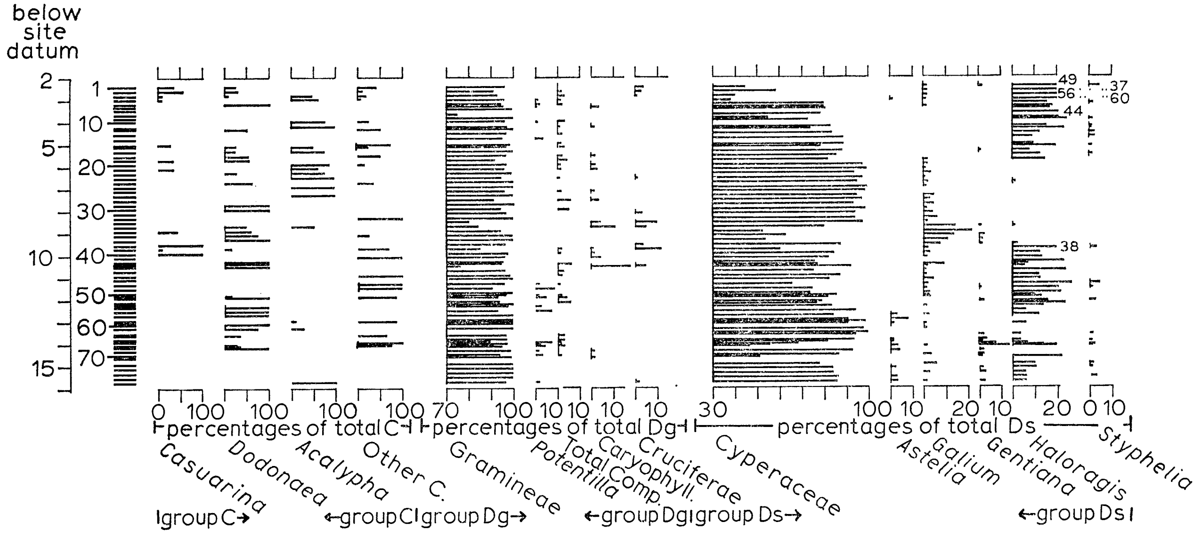


FIGURE 11 (continued).



FIGURES 9–11 (continued). For description see page 316.

(*c*) *Birip*

Sources of pollen. A substantial proportion of the pollen accumulated in the lake mud must have come from plants growing inside the crater, a land area of about 12 hectares with a vertical relief of only 40 m. When the production of such local pollen was low, however, the regional component might have made an equal or greater contribution, particularly in some of the far travelling types, e.g. *Nothofagus*, *Casuarina*. This regional component might most realistically be thought to have come from the slopes of the immediately adjacent Lai Valley between about 1500 and 2000 m but some almost certainly came from up and down the valley and even from the ridge which rises to 3000 m only 5 km northeast of the site. Because of the isolation of the lake, the regional pollen could reach it only by direct fallout, mostly in rain, but some from within the crater may have been transported by trickles of water down the soil surface and across the marginal swamp.

Collection of samples, preparation, determination and presentation. The same procedures as at Inim were used throughout. Some samples were taken from the Thomas (1964) sampler in the field, others from 3 cm diameter piston sampler cores in the laboratory.

Description and interpretation. From 2300 (13) until 1700 I.A. (10) grass pollen was abundant, probably being derived from the newly vegetated slopes within the crater. Similarly, the Cyperaceae pollen is indicative of narrow sedge swamps which became established around the lake's edge. This process continued interruptedly but appears to have accelerated from about 500 I.A. (6). It is likely that, in these early stages at least, the forest pollen came from beyond the crater itself. Its slow diminution, compared with that of forest ephemerals and open land ephemerals, was probably due to increasing contributions from the latter as, for example, *Macaranga*, *Cyathea*, *Casuarina* and Urticaceae/Moraceae colonised the crater walls. From 1500 to 750 I.A. (9–7) rising *Castanopsis* values may indicate that this tree entered the catchment leading to an apparent temporary stability in the ratio of mature forest to other components of the pollen rain.

Shortly afterwards, however, the mature forest began to decline at an accelerated rate and the former dominance of *Macaranga* amongst the forest ephemerals was replaced by one of *Trema*. This was closely followed at about 300 I.A. (5) by substantial increases in *Dodonaea* and rather later (200 I.A., 3) by a rise in the already common *Casuarina*. This must be interpreted either as a local change in the vegetation within the crater in a direction contrary to its conversion to a mixed forest cover, or a more widespread destruction of forest which had repercussions on the vegetation within the crater. The latter is the more likely explanation and would be consistent with the increasing importance of *Nothofagus* amongst the forest pollen from about 300 I.A. (5) due to its relatively large *regional* contribution.

It is clear that although mature forest grew in the vicinity of Birip, the main indicators of disturbance and unforested areas were already present by 2300 I.A., that mature forest was probably never established inside the crater and that a period of forest destruction began in the locality about 450 I.A. continuing to the present day.

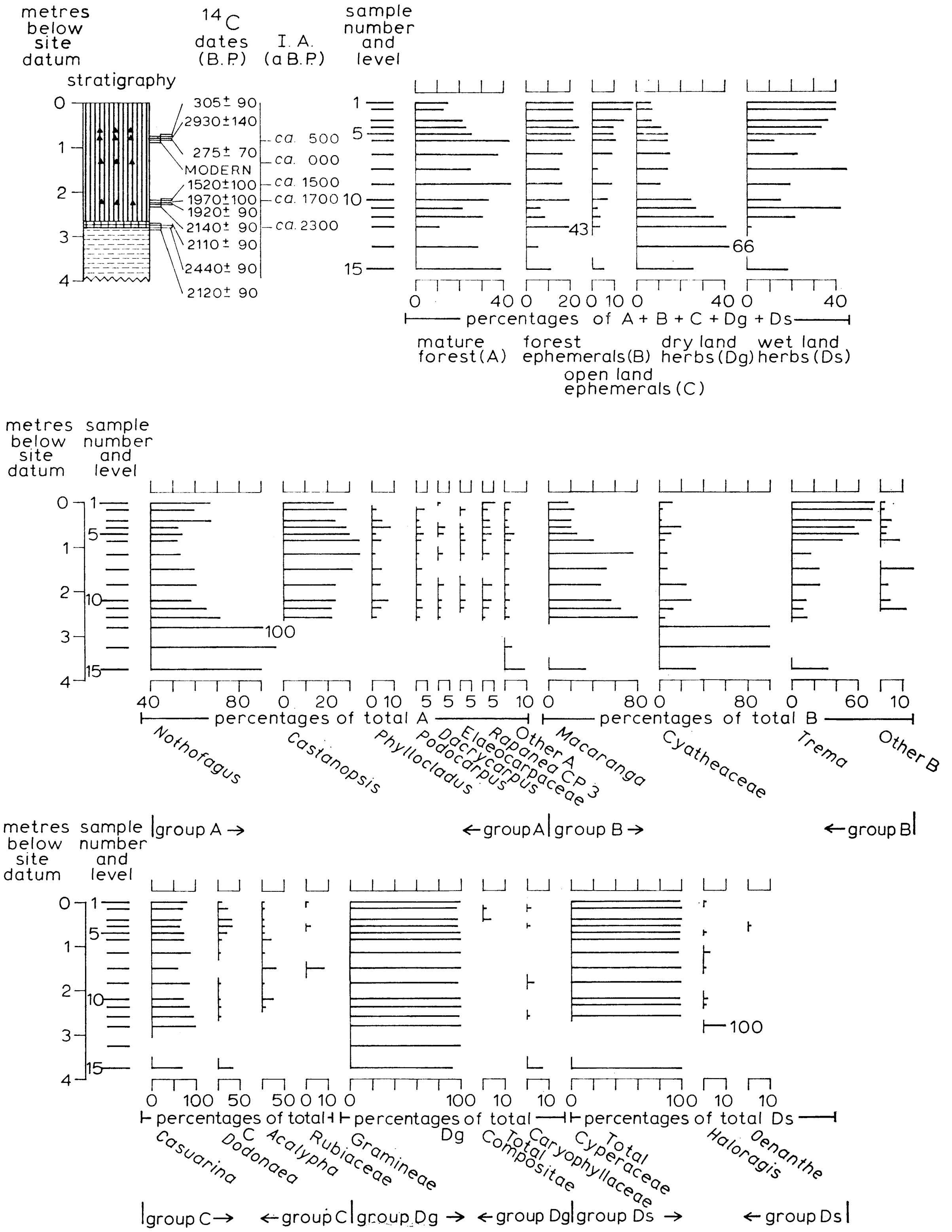


FIGURE 12. Pollen diagram from Birip (1900 m). Quantities are percentages of a number of bases described in the text and used also in figures 9, 10 and 11.

TABLE 8*a*. OCCURRENCE OF TAXA

	group A																group B			
taxon sample level (cm)	*Opocunonia*	*Schefflera*	*Evodiella*	*Meliosma*	*Acronychia*	Flacourtiaceae	Proteaceae	*Papuacedrus*	*Endiandra*	*Ilex*	*Planchonella*	*Maesa*	*Sapindus*	*Fagraea*	*Polyosma*	*Symplocos*	*Glochidion*	*Celtis/Aphananthe*	*Mussaenda*	*Capparis*
237	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
255	3	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
275	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
292	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
312	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
324	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
340	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
360	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
376	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
390	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
414	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
424	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
448	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
471	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
493	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
502	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
525	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
545	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
565	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
585	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
605	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
625	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
645	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
665	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
685	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
705	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
725	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
745	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
765	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
785	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
805	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
825	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
845	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
865	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
885	0	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
905	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
925	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
945	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0
965	0	1	0	0	0	0	0	0	0	0	1	0	3	0	0	0	4	0	0	0
985	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1025	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
1035	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
1045	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1065	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1085	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0
1145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1165	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1178	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1185	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1205	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1215	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1245	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

of taxa rarely encountered in pollen analyses at Sirunki, or not shown graphically

oup B			group C							group Dg						group Ds						
Mussaenda	*Capparis*	*Piper*	*Solanum*	*Psychotria*	*Calamus*	*Osbeckia*	*Melastoma*	Rubiaceae	*Borreria*	*Acaena*	*Rubus*	Compositae: fenestrate	*Veronica*	*Rumex*	*Geitonoplesium*	*Oenanthe*	*Trachymene*	Ericaceae	*Gunnera*	*Drapetes*	Lythraceae	*Lindernia*
0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Pteridophytes									
Lythraceae	*Lindernia*	*Pteris*	trilete psilate	trilete scabrate	trilete verrucate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	total pollen and spore count
0	0	0	0	0	0	120	0	13	0	5	745
0	0	0	0	3	67	4	0	25	0	11	846
0	0	0	0	7	194	3	0	11	4	25	103
0	0	0	14	6	135	6	0	11	2	7	940
0	0	0	0	1	22	1	0	2	2	19	454
0	0	0	0	0	2	3	0	3	3	14	451
0	0	0	0	0	1	1	0	8	0	9	127
0	0	0	0	1	0	1	0	0	6	0	103
0	0	0	0	0	4	0	0	1	0	1	34
0	0	0	1	0	15	3	0	17	1	25	669
0	0	0	0	3	46	1	0	18	9	18	783
0	0	0	0	0	40	6	0	6	0	12	698
0	0	0	0	1	38	6	0	11	4	8	743
0	0	0	0	0	1	3	0	5	10	6	476
0	0	0	0	0	3	1	0	10	4	10	464
0	0	0	0	0	1	6	0	4	5	4	470
0	0	0	0	0	2	3	0	10	3	5	439
0	0	0	0	1	0	5	0	14	2	12	434
0	0	0	0	0	0	5	0	6	0	7	414
0	0	0	0	0	0	3	0	32	3	13	730
0	0	0	0	8	0	3	0	30	16	5	663
0	0	0	0	0	0	10	0	21	3	5	894
0	0	0	1	0	0	1	0	8	0	1	572
0	0	0	0	0	0	1	0	3	0	1	183
0	0	0	0	6	0	0	0	35	9	1	501
0	0	0	2	0	0	6	0	94	4	5	617
0	0	0	0	0	0	5	0	14	6	0	372
0	0	0	0	0	0	9	0	3	1	0	258
0	0	0	0	0	0	4	0	11	1	1	348
0	0	0	0	0	0	2	0	16	0	2	259
0	0	0	0	0	0	1	0	28	1	4	354
0	0	0	0	0	0	0	0	5	0	1	250
0	0	0	0	0	0	0	0	1	0	0	296
0	0	0	0	0	0	2	0	9	0	1	392
0	0	0	0	0	2	0	0	1	1	0	409
0	0	0	0	0	2	1	0	6	6	10	861
0	0	0	0	0	2	1	0	0	0	4	581
0	0	0	0	0	1	1	0	3	1	5	615
0	0	0	0	0	0	7	0	10	0	14	1495
0	0	0	0	0	1	2	0	10	0	4	486
0	0	0	0	1	0	1	0	5	0	6	290
0	0	0	0	0	0	0	0	7	2	3	572
0	0	0	0	0	0	2	0	3	1	4	469
0	0	0	0	0	3	3	0	6	0	0	270
0	0	0	0	1	17	8	0	5	0	0	955
0	0	0	0	0	3	33	0	0	2	14	1097
0	0	0	0	0	0	3	0	0	0	0	53
0	0	0	0	0	0	9	0	3	0	22	416
0	0	0	0	6	0	9	0	12	1	5	538
0	0	0	0	0	0	16	0	0	1	9	299
0	0	0	0	0	3	7	0	3	2	2	694
0	0	0	0	0	3	0	0	0	0	0	524
0	0	0	0	0	2	0	0	3	0	1	201
0	0	0	0	0	0	1	0	1	1	2	106
0	0	0	0	0	0	1	0	0	0	4	626
0	0	0	0	5	0	0	0	5	0	1	468

1205	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1215	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1245	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1265	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
1285	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1292	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
1305	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1325	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1345	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1355	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1371	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1385	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1399	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1403	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1405	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
1425	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1445	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1455	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1485	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1505	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1525	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1545	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
1565	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1604	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1625	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1645	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1665	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1685	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1705	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1725	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1745	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1765	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1785	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1805	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1825	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1845	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1865	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1885	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1905	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1925	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1945	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1965	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1995	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2025	0	0	1	0	8	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2065	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2145	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2165	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2185	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2195	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2205	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2245	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2265	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
2285	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2325	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2345	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2365	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2385	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2405	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2445	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2467	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2487	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2497	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	2	0	0	0	0	3	0	0	2	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	4	5	0	0	0	0	8	0	0	0	1	0
0	0	0	0	0	0	0	0	0	0	0	9	1	0	1	0	0	0	0	0	6	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

0	0	0	0	0	2	0	0	3	0	1	201
0	0	0	0	0	0	1	0	1	1	2	106
0	0	0	0	0	0	1	0	0	0	4	626
0	0	0	0	5	0	0	0	5	0	1	468
0	0	0	0	0	1	0	0	1	0	0	351
0	0	0	0	0	3	1	0	0	0	0	362
0	0	0	0	0	0	8	0	0	9	5	866
0	0	0	0	1	0	11	0	8	0	9	1174
0	0	0	0	0	3	9	0	4	0	1	1146
0	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	1	0	2	0	2	378
0	0	0	0	0	1	2	0	2	0	4	658
0	0	0	0	0	0	6	0	2	0	9	704
0	0	0	0	0	0	8	0	1	0	3	740
1	0	0	0	0	1	14	0	4	2	3	1061
0	0	0	0	2	2	8	0	2	0	1	1014
0	0	0	0	0	0	3	0	1	0	2	389
0	0	0	0	0	0	19	0	0	1	4	416
0	0	0	0	0	0	0	0	0	1	0	312
0	0	0	0	0	0	2	0	1	0	3	670
0	0	0	0	0	0	3	0	2	1	4	766
0	0	0	0	0	0	1	0	0	0	0	387
0	0	0	0	0	3	2	0	4	0	4	518
0	0	0	0	2	0	7	0	1	0	0	566
0	0	0	0	0	0	12	0	1	0	1	258
0	0	0	2	0	0	0	0	0	0	2	381
0	0	0	2	0	0	0	0	0	0	0	212
0	0	0	0	0	0	0	0	0	0	0	86
0	0	0	0	0	0	0	0	0	0	0	168
0	0	1	3	0	7	0	0	2	0	1	257
0	0	0	0	0	0	0	0	0	0	0	293
0	0	0	0	0	0	1	0	0	0	0	187
0	0	0	0	0	0	2	0	0	0	3	373
0	0	2	0	0	0	0	0	0	0	1	467
0	0	0	0	0	1	1	0	0	0	0	65
0	0	0	0	0	0	0	0	0	0	0	160
0	0	0	0	0	0	0	0	1	0	0	125
0	2	0	0	0	4	1	2	0	0	0	519
0	0	0	0	0	1	1	0	0	0	3	193
0	0	3	27	1	3	49	1	4	0	4	466
0	0	0	11	0	2	47	0	1	0	8	343
0	0	2	2	0	0	1	0	3	0	2	174
0	0	0	0	0	1	0	0	0	0	0	323
0	0	0	8	0	3	6	1	2	0	4	839
0	0	0	4	0	4	3	0	0	3	0	644
0	1	0	1	0	1	1	2	1	0	3	694
0	0	0	5	0	0	2	0	0	0	4	654
0	0	0	3	9	1	5	0	0	0	0	803
0	0	1	3	0	0	0	0	0	0	5	897
0	0	0	0	0	0	6	0	0	0	0	330
0	0	0	0	0	0	2	0	0	0	0	114
0	0	0	1	0	2	0	1	1	0	1	205
0	0	0	2	2	0	0	0	0	0	5	259
0	0	0	1	0	2	1	0	0	0	0	82
0	0	0	2	3	3	0	0	1	0	0	388
0	0	0	3	0	0	1	0	0	2	3	410
0	0	0	1	0	0	0	0	0	0	1	86
0	0	0	0	0	0	0	0	0	0	0	18
0	0	0	0	0	0	0	0	0	0	0	16
0	0	0	0	0	0	0	0	0	0	0	17
0	0	0	0	1	1	0	0	0	0	0	79
0	0	0	3	0	1	1	1	2	0	3	196
0	0	0	5	0	1	0	0	5	0	4	155
0	0	0	2	0	0	0	0	2	0	1	140
0	0	0	3	0	1	0	0	0	0	2	153
0	0	0	0	0	0	2	0	1	0	3	170

TABLE 8*b*. OCCURRENCE OF TAXA RARELY ENCOUNTERED IN THE BO

	group A											group B				group Dg			
taxon sample level (cm)	*Quintinia*	*Pygeum*	*Litsea*	*Schefflera*	*Claoxylon*	*Meliosma*	*Papuacedrus*	*Ilex*	*Rapanea* C3/C4	Rutaceae/Araliaceae/ Clusiaceae	*Drimys*	*Glochidion*	*Omalanthus*	*Engelhardtia*	*Coprosma*	Compositae C3P3	Compositae fenestrate	Cyperaceae A	Cyperaceae C
0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
20	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	56
40	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	36
80	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	18
115	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	2	34
580	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2
650	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	16
720	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	24
830	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	11	28
850	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38
950	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	5	8
1050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8
1150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	34
1185	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	56
1250	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	23	5
1350	0	0	0	5	2	0	0	0	0	0	0	0	0	0	1	1	0	0	48
1450	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	6	20
1550	0	0	0	3	0	0	9	0	0	0	0	0	0	0	0	0	0	0	3
1650	0	0	0	2	1	0	0	1	0	0	0	0	0	1	0	0	0	3	3
1771	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	3
1809	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
1853	0	2	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	11	6
1880	0	0	0	0	0	19	0	0	0	0	11	0	0	0	0	0	1	2	1
1920	0	0	0	1	4	0	0	0	1	0	0	0	0	0	0	0	0	0	2
1980	0	0	0	0	1	0	1	0	0	8	0	0	0	1	0	0	1	0	2

TABLE 8*c*. OCCURRENCE OF TAXA RARELY ENCOUNTERED IN THE POLLEN A

	group A						group B					group Dg			group Ds				
taxon sample level (cm)	*Quintinia*	*Sloanea*	Proteaceae	*Rapanea* C3/C4	Rutaceae/Araliaceae/ Clusiaceae	*Drimys*	*Symplocos*	*Phyllanthus*	*Saurauia*	*Engelhardtia*	*Coprosma*	Compositae C3P3	Compositae fenestrate	*Epilobium*	Cyperaceae A	Cyperaceae C	*Galium*	*Haloragis*/*Myriophyllum*	*Oenanthe*
774	1	0	0	0	0	0	0	0	4	0	1	0	0	0	0	2	0	3	0
821	0	0	0	1	0	0	0	0	10	0	0	0	0	0	0	1	0	0	1
854	0	1	1	0	0	0	0	0	5	0	0	0	0	0	5	0	0	0	0
882	0	0	0	0	0	0	0	0	0	0	0	2	0	1	6	1	0	3	4
911	0	0	0	0	0	1	0	1	0	0	0	1	0	0	8	0	0	1	0
920	0	0	0	0	0	0	0	1	0	1	0	2	1	0	12	0	0	1	0
950	1	0	1	0	0	0	0	0	2	0	1	2	1	0	54	0	0	6	0
970	0	0	0	0	1	0	0	0	0	1	0	3	0	1	6	0	0	0	0
985	0	0	0	0	0	0	0	0	0	0	0	9	0	0	1	0	0	0	0

THE BOLLEN ANALYSES OF THE INIM M4 CORE, OR NOT SHOWN GRAPHICALLY

group Ds							group E					group F								group G	
Cyperaceae A	Cyperaceae C	Cyperaceae D	*Oenanthe*	Ericaceae	*Polygonum*	Umbelliferae	*Eriocaulon*	*Sparganium*	*Xyris*	*Nymphoides*	*Typha*	*Pteris*	trilete scabrate	trilete verrucate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	Urticaceae/Moraceae	total pollen and spore count
0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	40	0	0	0	1	8	303
0	56	0	0	0	0	0	2	0	0	0	0	3	0	0	6	3	7	3	0	2	233
2	36	0	0	0	0	0	0	0	0	0	0	0	0	0	4	5	2	0	1	3	250
1	18	0	0	0	0	0	0	0	0	0	0	1	0	0	22	3	0	0	1	2	139
2	34	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	1	2	179
0	2	0	0	0	0	0	0	0	1	0	8	1	0	0	0	0	7	5	2	3	249
0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	6	230
0	24	0	0	0	0	0	0	0	11	0	0	0	0	0	1	2	3	2	3	3	237
1	28	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	0	0	1	154
0	38	0	0	0	0	0	0	0	6	0	1	2	0	0	3	0	3	5	1	2	220
5	8	0	0	0	0	0	0	0	1	0	1	0	0	0	11	5	2	11	9	6	298
1	8	0	0	0	0	0	0	0	0	0	1	0	0	0	3	1	1	1	0	4	83
0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	1	3	2	168
2	56	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	8	244
3	5	0	2	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	5	185
0	48	0	0	0	1	0	0	0	0	0	0	0	0	0	6	1	1	1	1	0	167
6	20	0	0	0	0	0	0	0	0	1	0	0	2	0	1	4	1	4	4	4	365
0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	5	4	3	15	458
3	3	3	0	0	0	0	0	0	0	0	0	0	0	0	2	2	3	2	0	12	380
2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	2	33	233
0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	3	6	0	1	25	251
1	6	0	0	1	0	0	0	0	0	0	0	0	0	1	3	1	6	0	5	3	462
2	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	1	0	2	4	250
0	2	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	2	0	13	3	312
0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	5	450

OLLEN ANALYSES OF THE INIM M15 CORE, OR NOT SHOWN GRAPHICALLY

group Ds					group E				group F							group G	
Oenanthe	Ericaceae	*Gunnera*	Umbelliferae	Cruciferae	*Ranunculus*	*Eriocaulon*	*Nymphoides*	*Blyxa*	trilete scabrate	trilete verrucate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	Urticaceae/Moraceae	total pollen and spore count
0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	42	343
1	0	1	0	0	0	0	0	1	0	0	0	1	2	0	3	54	380
0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	45	300
4	0	0	0	0	0	0	0	0	0	0	1	0	28	1	2	5	229
0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	1	3	365
0	0	0	0	0	1	0	0	0	0	0	5	0	7	3	0	8	341
0	0	0	0	0	4	0	0	0	1	0	1	0	0	0	0	8	449
0	2	0	3	0	4	0	0	0	1	0	0	0	0	0	0	4	346
0	0	0	2	0	6	0	0	0	0	0	1	0	0	0	1	8	525

911	0	0	0	0	0	1	0	1	0	0	0	1	0	0	8	0	0	1	0
920	0	0	0	0	0	0	0	1	0	1	0	2	1	0	12	0	0	1	0
950	1	0	1	0	0	0	0	0	2	0	1	2	1	0	54	0	0	6	0
970	0	0	0	0	1	0	0	0	0	1	0	3	0	1	6	0	0	0	0
985	0	0	0	0	0	0	0	0	0	0	0	9	0	0	1	0	0	0	0
1015	0	0	0	0	0	0	0	0	1	0	0	3	0	0	28	0	1	2	0
1045	0	0	0	0	0	1	0	0	0	0	0	2	1	0	50	0	0	0	0
1065	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	4	0	0	1
1075	0	0	0	0	0	0	0	0	1	0	0	6	0	0	0	1	0	1	0
1085	0	0	0	0	0	0	0	0	0	0	0	4	0	0	9	0	0	1	0
1095	0	0	0	0	0	0	0	0	0	0	0	3	0	0	5	1	0	0	0
1115	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
1125	0	0	0	0	0	0	0	0	1	0	0	1	0	0	3	0	0	0	0
1135	0	0	0	0	0	0	0	0	0	0	0	7	0	0	1	0	0	0	5
1145	0	0	0	0	0	0	0	0	1	0	0	3	1	0	13	0	0	0	0

TABLE 8*d*. OCCURRENCE OF TAXA RARELY ENCOUNTERED IN THE POLLEN ANAI

	group A									group B				group Dg	group Ds			
taxon sample level (cm)	*Ascarina*	*Quintinia*	*Opocunonia*	Myrtaceae	*Schefflera*	*Claoxylon*	Proteaceae	*Rapanea* C3/C4	*Drimys*	*Glochidion*	*Omalanthus*	*Saurauia*	*Engelhardtia*	Compositae C3P3	Cyperaceae A	Cyperaceae C	*Eriocaulon*	*Xyris*
0	1	0	0	0	0	1	0	0	0	0	2	0	0	0	192	0	0	0
15	0	0	0	0	0	2	0	0	0	0	0	3	0	1	311	0	1	1
40	0	0	0	1	0	0	0	0	0	0	0	5	0	1	168	0	0	0
55	3	0	0	0	0	0	0	0	0	1	1	3	0	0	233	0	0	0
70	3	0	1	1	0	0	0	1	0	0	0	3	0	0	185	0	0	0
85	3	0	0	3	0	0	1	0	0	0	0	10	0	0	58	1	0	0
117	0	2	1	0	0	0	0	0	0	0	0	0	0	0	85	0	0	4
150	0	1	0	1	0	0	0	0	0	0	0	9	1	0	215	0	0	2
183	0	1	0	1	0	0	0	0	0	0	0	2	0	0	66	0	0	0
218	0	0	1	0	2	0	0	0	0	0	1	3	0	0	67	0	0	0
236	0	0	1	0	0	0	0	0	0	0	0	4	1	0	264	0	0	0
258	1	0	0	2	0	0	0	0	0	0	0	0	0	0	105	0	0	0
280	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
325	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
375	0	0	0	1	0	1	0	0	0	0	0	0	0	0	10	0	0	0

0	0	0	0	0	1	0	0	0	0	0	5	0	7	3	0	8	341
0	0	0	0	0	4	0	0	0	1	0	1	0	0	0	0	8	449
0	2	0	3	0	4	0	0	0	1	0	0	0	0	0	0	4	346
0	0	0	2	0	6	0	0	0	0	0	1	0	0	0	1	8	525
0	0	0	4	0	7	0	0	0	0	0	0	0	1	0	2	1	627
0	3	0	0	1	5	0	0	0	0	0	0	0	2	0	0	6	547
1	0	0	0	0	4	1	0	0	0	0	2	0	0	0	0	3	339
0	0	0	1	0	3	0	0	0	0	0	0	1	0	1	0	8	448
0	1	0	3	0	1	0	2	0	0	0	0	0	1	0	0	1	439
0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	413
0	4	0	0	0	4	0	0	0	0	0	0	0	0	0	1	0	342
0	1	0	2	0	2	0	0	0	0	0	1	0	0	0	2	4	478
5	6	0	0	0	5	0	0	0	0	0	0	0	0	0	1	5	477
0	0	0	0	0	3	0	0	0	1	0	1	0	0	0	1	3	439

LEN ANALYSES AT BIRIP, OR NOT SHOWN GRAPHICALLY

group E						group F						group G		
Eriocaulon	*Xyris*	*Limnophila*	*Nymphoides*	*Typha*	*Blyxa*	trilete scabrate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	*Amyema*	Urticaceae/Moraceae	total pollen and spore count
0	0	12	13	0	0	0	0	5	0	0	1	0	41	584
1	1	0	11	0	0	0	0	5	1	2	2	0	42	883
0	0	0	13	0	0	0	2	3	1	2	0	0	47	544
0	0	0	67	0	1	0	3	2	2	0	3	0	47	837
0	0	0	15	1	0	1	2	0	0	0	3	0	79	727
0	0	0	1	0	1	0	1	1	0	0	1	0	126	658
0	4	0	0	0	0	0	9	0	1	0	2	0	53	483
0	2	0	0	0	0	2	9	2	0	0	0	0	90	609
0	0	0	0	0	0	0	3	1	1	0	2	1	27	378
0	0	0	0	0	0	0	6	8	2	0	5	0	48	538
0	0	0	0	0	0	0	0	1	1	0	1	0	38	852
0	0	0	0	0	0	0	2	0	8	0	1	0	13	520
0	0	0	0	0	0	0	2	0	2	3	0	0	1	95
0	0	0	0	0	0	0	0	0	2	3	1	0	1	194
0	0	0	0	0	0	0	1	0	3	0	0	0	2	80

	± closely associated within group																
Living Vegetation Genus	*Ascarina*	*Macaranga*	*Nothofagus*	*Podocarpus*	*Castanopsis*	*Phyllocladus*	*Claoxylon*	*Litsea*	*Rapanea* (C3C4)	*Sloanea*	Gra. C	Gra. E	Gra. G	Gra. F	Gra. H	*Dacrycarpus*	Myrtaceae
1111																	
Harmsiopanax	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Omalanthus†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Xanthomyrtus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
1112																	
Eurya†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Zanthoxylum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1121																	
Rapanea	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
11221																	
Acronychia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Castanopsis†	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Engelhardtia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helicia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lithocarpus	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Litsea	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Trema†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
11222																	
Arthrophyllum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Garcinia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Opocunonia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Podocarpus† *imbric.*	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyllocladus	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
12111																	
Ascarina	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nothofagus	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sloanea†	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
12112																	
Macaranga†	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Syzygium†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
1212																	
Claoxylon	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Saurauia†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spiraeopsis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2111																	
Decaspermum†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Elaeocarpus†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Evodiella	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sericolea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
212																	
Cyathea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Podocarpus†	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Schefflera†	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE 9. OCCURRENCE OF POLLEN ANALYSIS TAXA IN LIVING VEGETATION TYPES

taxa in pollen diagrams

generally associated in period of occurrence within group

forest: partial floristic groups according to Walker & Guppy (1976)

	Myrtaceae	*Dodonaea*	*Engelhardtia*	*Trema*	*Acalypha*	*Casuarina*	*Coprosma*	*Saurauia*	*Glochidion*	*Omalanthus*	Compositae (fenestrate)	*Polygonum*	Cyp. A	Cyp. C	*Galium*	*Astelia*	*Gentiana*	*Potentilla*	*Styphelia*	*Ranunculus*	*Buddleia*	*Cyathea*
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·
·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
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	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
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	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
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	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

individualistic															insignificant quantities							
	Cyathea	Elaeocarpaceae	*Quintinia*	RUAR	Compositae (C3P3)	Cyp. B2	Cyp. D	Cyp. Z	*Epilobium*	Gra. B	Gra. D	*Haloragis*	*Hydrocotyle*	*Plantago*	Umbelliferae	*Evodiella*	*Opocunonia*	Proteaceae	*Pygeum*	*Rapanea*	*Schefflera*	*Drapetes*
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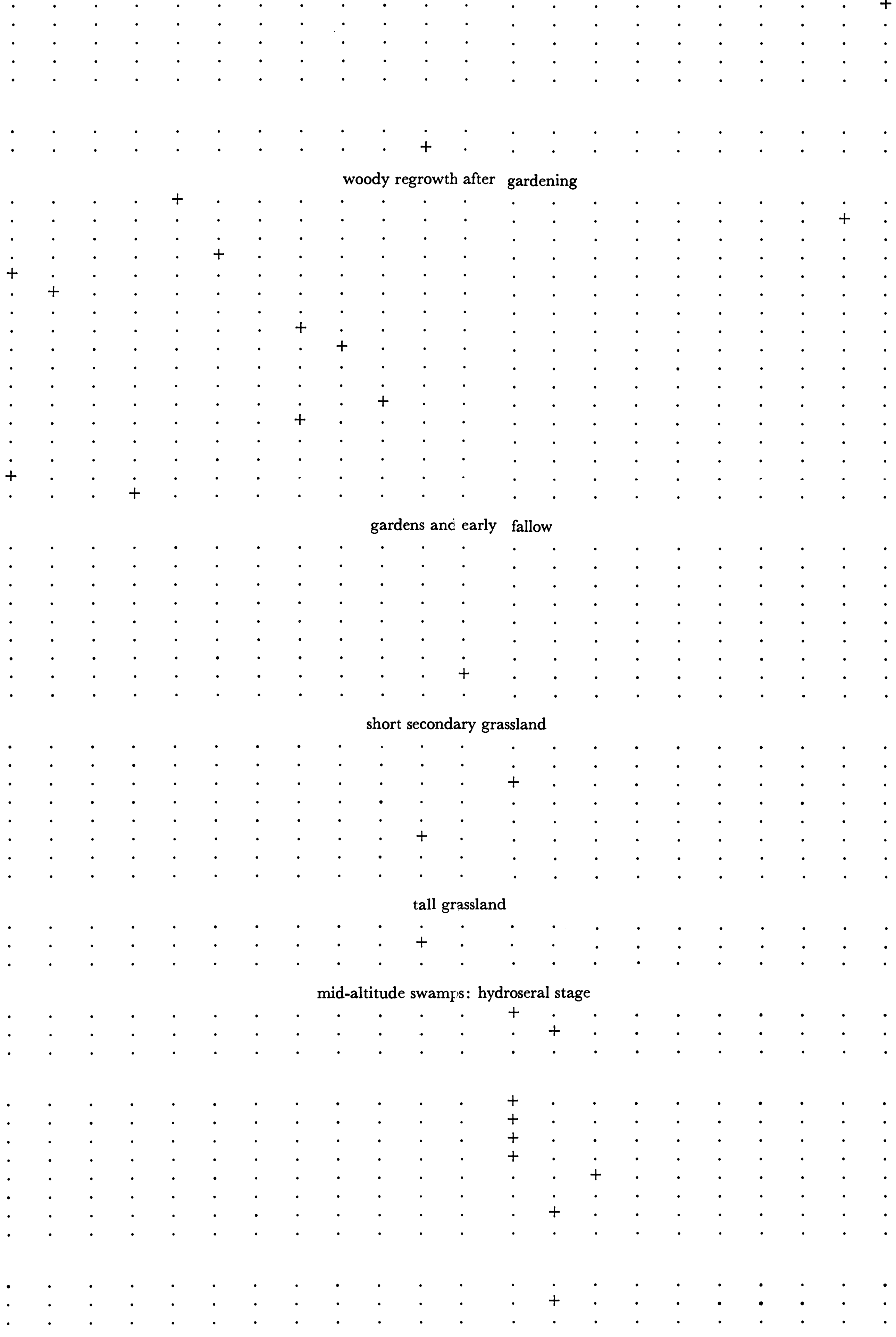
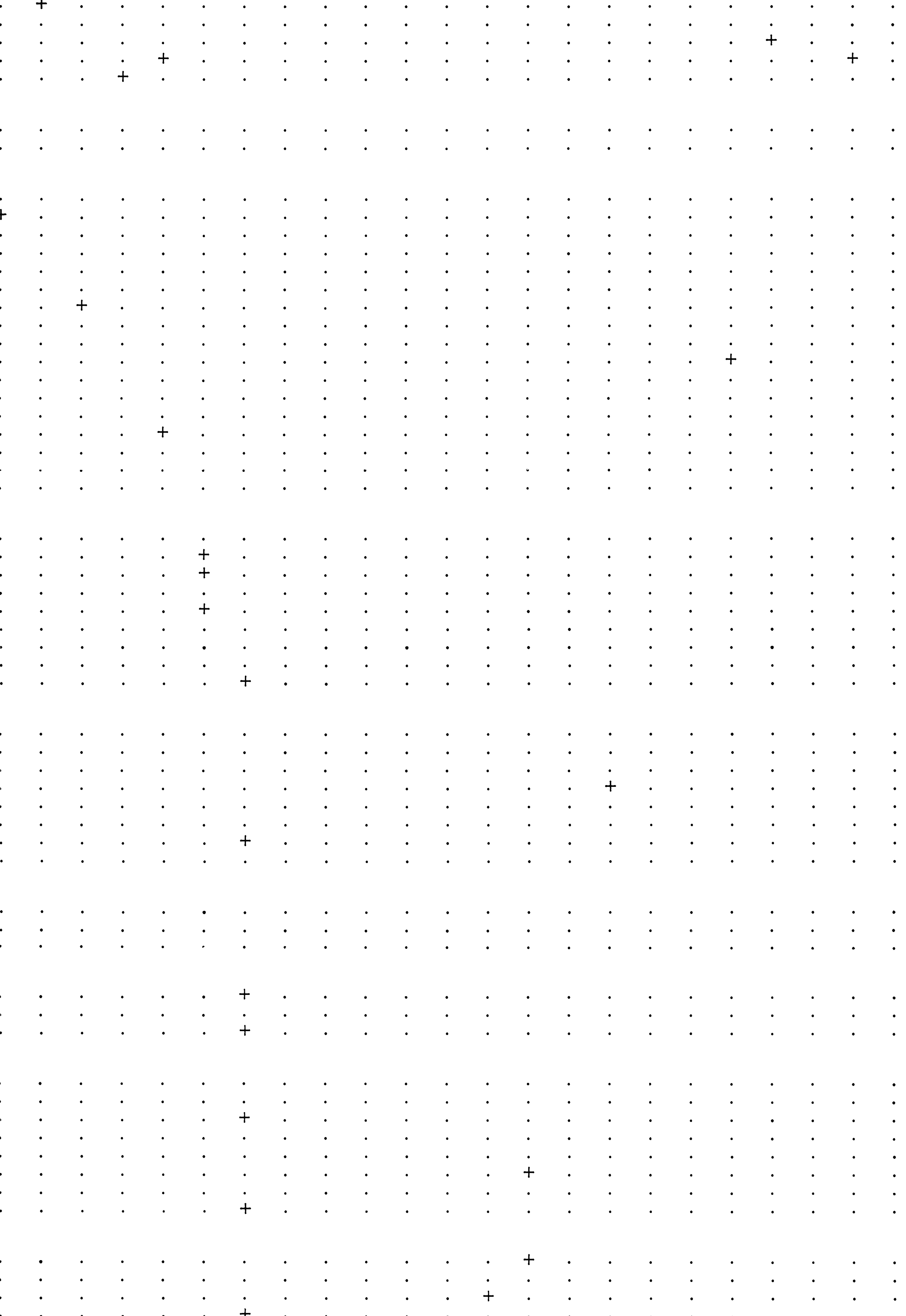

woody regrowth after gardening
gardens and early fallow
short secondary grassland
tall grassland
mid-altitude swamps: hydroseral stage



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† Genera occurring more than once among vegetation types.

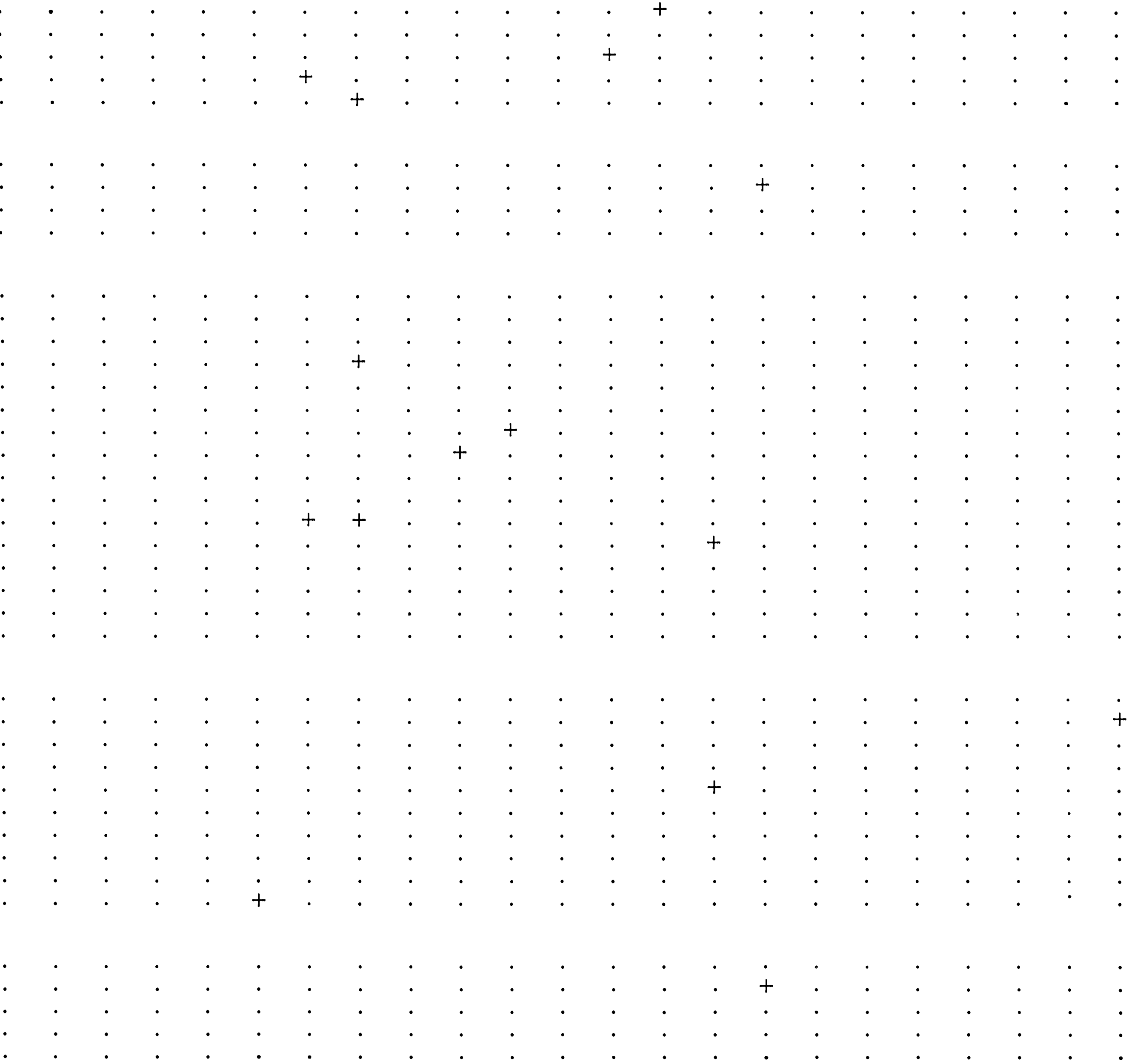


Table 11. Derivatio

period years I.A.	vegetation of catchment	stratigraphy	lowest estimate of mean ann criteria
1500–5000	lower mountain forest with periodic clearings after 4300 I.A.	detritus mud	*Dacrycarpus* commoner; changing significanc of forest ephemerals
5000–6500	lower mountain forest	detritus mud, nekron and diatomite	*Trema* and *Phyllanthus* absent; *Casuarina* polle catchment
6500–8000	lower mountain forest comparatively rich in *Nothofagus*	detritus mud, nekron and diatomite with clay layers	*Nothofagus* commoner than before; *Dacrycarp* common
8000–9000	lower mountain forest components	detritus muds, nekron and diatomite with clay layers	*Trema* and *Phyllanthus* excluded; *Dacrycarpus* *Quintinia* sometimes high
9000–13000	forest tree growth erratic amongst grasslands, *Cyathea* 'woodlands' and frost-hollow vegetation	fine detritus mud and diatomite	temperature excluding lower mountain fores time to time; *Astelia* fitfully present
13000–13500	lower mountain forest, *Nothofagus* predominating	re-deposited organic and inorganic matter including volcanic ash; rise in water level	*Castanopsis*, *Trema* etc. still not in catchment lower mountain forest probably also absent
13500–14000	lower mountain forest with upper mountain forest above and some frost-hollow vegetation	culmination of overgrowth around margins, secondary penetration of older deposits by reedswamp roots: fine detritus mud and diatomite at centre of basin	*Castanopsis*, *Trema*, *Macaranga* still not in catc of which still occupied by lower mountain f including *Dacrycarpus*
14000–15000	patchy subalpine grasslands and upper mountain forest	coarse detritus mud at margins, fine detritus mud and diatomite in centre of basin	*Pygeum and Evodiella* only precariously establi catchment amongst subalpine grassland
15000–16000	predominantly unforested but some subalpine shrubs enter catchment	fine detritus and nekron muds and diatomite	*Rapanea* erratic, possibly far travelled; *Astelia*
16000–18500	unforested, alpine grassland and herbfield	fine detritus mud and diatomite with rare clay	absence of *Rapanea*, *Cyathea* and very low tot recovery; absence of *Astelia*
18500–21000	predominantly unforested but some subalpine shrubs and rarely trees	fine detritus mud and diatomite with rare clay	*Rapanea* and *Cyathea* in quantities implying so from swamp; *Astelia* in moderate quantity
21000–24000	predominantly unforested but some trees occasionally	fine detritus mud and diatomite becoming progressively inorganic particularly at margins	*Rapanea* and *Quintinia* at lowest temperature when present and sometimes absent
24000–25500	alpine and subalpine herbfield, grassland and a few shrubs	fine detritus and nekron muds	*Astelia* at lowest temperature tolerance; alpin dominant; *Rapanea* distant
25500–27000	upper and lower mountain forest elements and subalpine swamps	fine detritus and nekron muds	*Rapanea* in forest-limit abundance; *Astelia* co
27500–33000	barren to poor sedge swamps and possibly some *Cyathea*	fine detritus and nekron muds	apparent lack of vegetation

Corrections for Table 9. tall grassland once among

ERIVATION OF POSSIBLE MEAN ANNUAL TEMPERATURES FROM SIRUNKI POLLEN ANALYSIS DATA

f mean annual temp.		highest estimate of mean annual temp.		ra estir mear tem
	temp °C	criteria	temp. °C	min.
significance	10	*Acalypha* in clearing beginning 4300 I.A.	15	10
uarina pollen not reaching	11	*Dacrycarpus* uncommon	15	11
; *Dacrycarpus*	11	*Trema* and *Phyllanthus* present; *Casuarina* and *Glochidion* pollen reaching catchment	14	11
Dacrycarpus and	11	*Astelia* absent, *Castanopsis* present	13	11
ntain forest trees from nt	oscillating 10–12	vegetation not climatically significant	13	10
catchment although also absent	12	changes not climatically significant	13	12
not in catchment, much mountain forest	11	all lower mountain forest components in catchment; upper mountain forest plants on surrounding hills or frost-hollows	13	11
usly established in assland	7	Myrtaceae, *Pygeum* and *Evodiella* imply closed upper mountain forest amongst which are patches of open ground producing the low *Astelia* values; trace of *Trema* pollen suggests lower mountain forest close to catchment; overgrowth of lakes active with grassland components changing	10	7
led; *Astelia* low	4	beginning of changes in lower mountain forest components outside catchment	7	4
ry low total pollen	2	lack of positive tundra indicators; grasses predominant	6	2
mplying some distance quantity	4	*Ascarina* probably and *Nothofagus* possibly, but both rarely, in catchment	11	4
nperature tolerance ent	4–6	*Sloanea*, *Nothofagus*, *Castanopsis* occasionally in catchment	13	4
ance; alpine grasslands	3	*Rapanea* and *Acronychia* in catchment, *Astelia* in middle of range	9	3
Astelia common	6–12	*Castanopsis*, *Sloanea*, *Nothofagus* in catchment	> 13	6
	1	*Cyathea* spores and organic mud	4	1

range of estimates of mean annual temp. °C		most probable range of estimates of mean annual temp. °C		range of estimates in relation to present mean annual temp. at 2500 m (14 °C), °C		most probable range of estimates in relation to present mean annual temp. at 2500 m (14 °C), °C	
min.	max.	min.	max.	min.	max.	min.	max.
10	15	12	14	−4	+1	−2	0
11	15	13	15	−3	+1	−1	+1
11	14	12	14	−3	0	−2	0
11	13	12	13	−3	−1	−2	−1
10	13	10	13	−4	−1	−4	−1
12	13	12	13	−2	−1	−2	−1
11	13	12	13	−3	−1	−2	−1
7	10	8	10	−7	−4	−6	−4
4	7	4	6	−10	−7	−10	−8
2	6	3	5	−12	−8	−11	−9
4	11	5	10	−10	−3	−9	−4
4	13	7	13	−10	−1	−7	−1
3	9	5	9	−11	−5	−9	−5
6	> 13	10	14	−8	< −1	−4	0
1	4	vegetation possibly under non-climatic control		−13	−10	?	?

6. The associations of taxa

The canopy genera of the living forest can be divided into floristic groups (Walker & Guppy 1976). Non-forest vegetation types can also be more loosely typified by genera which are frequently, and more or less exclusively, reported from them. Some components of all these groups are recorded in the pollen diagrams. Where a pollen analysis group is preferentially represented in one or two of the floristic groups of the living vegetation, the latter provide the closest living analogues to the vegetation represented by it (table 9). Comparison with the full lists then provides hints as to additional genera which may have been present but are unrepresented in the pollen analyses.

The same data from the living forest can be used in another way without reference to floristic or vegetation units. A number of genera represented in the pollen diagram are selected and the plots in the living vegetation (from Walker & Guppy 1976) in which each occurs, are identified. The frequency of occurrence of all other genera (down to 0.7) in each set of plots so typified is then calculated. The values give some measure of the probability that the significant occurrence of a taxon in the pollen diagram indicates also the presence of other genera in the vegetation of the time (table 10).

In the pollen diagrams the taxa are arranged in groups according to their most general ecological significance. Within and between groups, however, the courses of some curves are consistently related and, to some, more precise ecological implications can be attributed.

The pollen curves can be considered on a variety of time scales. At their most coarse, say at a scale of about 5000 years, the associations of taxa do little more than restate the features of the general vegetation history, emphasizing the importance and generality of changes occurring between 30000 and 25000 I.A. and between 15000 and 10000 I.A. Major consistencies between associations in the pollen record and in the living vegetation are apparent. Thus, *Nothofagus*, *Castanopsis*, *Phyllocladus*, *Podocarpus*, *Ascarina* and *Macaranga* march together in the pollen diagrams and all fall in Walker & Guppy's (1976) forest floristic groups 1122 and 1211 which are best represented in their lower mountain forest. *Dacrycarpus* and Myrtaceae form a pair on this scale, insignificant before 15000 I.A. and running only indecisively with the first group thereafter. *Rapanea* and RUAR (Rutaceae, Araliaceae, Clusiaceae) form a contrasting pair, the first most important before 10000 I.A., the second after that date.

Although *Engelhardtia*, *Sloanea*, *Litsea*, *Trema*, some Myrtaceae and some RUAR, belong to the same living floristic groups as *Nothofagus* and its pollen analysis associates, they do not behave similarly in the pollen diagrams. *Sloanea* and *Litsea*, together with *Claoxylon*, are important before 15000 I.A. but insignificant afterwards. By contrast, *Engelhardtia* and *Trema* occur significantly only after 15000 I.A. and, after 10000 I.A., are somewhat paralleled by *Phyllanthus* and *Acalypha*. These four genera certainly now flourish best in actively regenerating forests which were only fleetingly present in the Sirunki catchment before 15000 I.A., while *Engelhardtia* has apparently fairly high temperature demands. *Sloanea*, *Litsea* and *Claoxylon* today grow up to 2900, 2950 and 3050 m respectively and their contrasting occurrence with *Trema*, *Acalypha* and *Phyllanthus*, all with altitudinal limits at 2900 m, cannot therefore be explained by temperature differences before and after 15000 I.A. However, *Sloanea*, *Litsea* and *Claoxylon* seem to be most abundant in forest which is mist-shrouded. At lower altitudes, *Sloanea* at least benefits temporarily from slight forest disturbance. All three seed abundantly. The small seeds of *Sloanea* are windborne from large dehiscent fruits while the smaller fruits of *Litsea* and *Claoxylon*

TABLE 10. ASSOCIATIONS IN EXISTING FOREST BETWEEN GENERA REPRESENTED IN THE POLLEN DIAGRAMS AND THOSE NOT SO REPRESENTED

(Each number indicates the proportion of vegetation plots in which a genus unrepresented in the pollen diagrams (rows) occurs with one recorded by pollen analysis (columns). Genera present in both total data sets are bold in the left hand column although not all of them reach sufficiently high correlations with other taxa to be included in the columns. Data from Walker & Guppy (1976).)

associated genera predicted from vegetation plots	genus in pollen diagram											
	Ascarina	*Casta-nopsis*	*Dacry-carpus*	*Elaeo-carpus*	*Macar-anga*	*Notho-fagus*	*Phyllo-cladus*	*Podo-carpus*	*Quin-tinia*	*Rapanea*	*Sloanea*	*Trema*
	Number of vegetation plots in which recorded											
	25	8	32	55	34	27	9	46	35	68	22	5
Amaracarpus	.	.	.	.	.	.	.	.	.	.	.	0.6
Ardisia	.	.	.	.	.	0.7	.	.	.	.	.	.
Arthrophyllum	.	.	.	.	.	.	0.8	.	.	.	.	.
Ascarina	*	.	.	.	.	.	.	.	.	.	0.7	.
Bubbia	0.7	.	.	.	.	.	0.9	.	.	.	.	.
Carpodetus	.	0.9	.	.	.	.	.	.	.	.	.	0.8
Casearia	.	.	.	.	.	.	0.7	.	.	.	.	.
Castanopsis	.	*	.	.	.	.	.	.	.	.	.	1.0
Cinnamomum	.	.	.	.	.	.	0.8	.	.	.	.	.
Claoxylon	.	.	.	.	.	.	0.7	.	.	.	.	.
Cyrtandra	.	.	.	.	.	.	0.7	.	.	.	.	.
Cryptocarya	0.7	0.8	.	.	0.9	0.9	1.0	.	.	.	0.9	0.8
Cyathea	0.9	0.8	0.8	0.9	0.9	0.9	0.9	1.0	0.9	0.8	0.8	0.8
Daphniphyllum	.	.	.	.	.	.	1.0	.	.	.	.	.
Dimorphanthera	0.8	.	0.8	0.8	0.7	0.8	0.9	0.9	0.8	0.8	0.7	0.8
Drimys	0.9	.	0.9	0.9	0.8	.	0.9	0.9	0.9	0.9	0.9	.
Dysoxylum	.	.	.	.	.	.	0.7	.	.	.	.	.
Elaeocarpus	1.0	0.8	.	*	0.9	0.9	1.0	0.8	0.8	0.7	0.9	.
Eurya	0.9	1.0	.	0.8	0.9	1.0	1.0	0.7	.	.	1.0	1.0
Euodia	.	0.8	.	.	.	0.7	0.7	.	.	0.7	.	0.6
Ficus	.	1.0	.	.	0.7	0.7	1.0	.	.	.	0.8	1.0
Garcinia	.	.	.	.	.	.	0.7	.	.	.	.	.
Glochidion	.	1.0	.	.	0.8	0.8	1.0	.	.	.	0.9	1.0
Guioa	.	0.8	.	.	.	.	0.8	.	.	.	.	0.6
Harmsiopanax	.	.	.	.	.	.	.	.	.	.	.	0.8

Helicia	.	.	.	.	.	.	0.7	.	.	.	.	.
Ilex	.	.	.	.	.	.	0.8	.	.	.	.	.
Levieria	.	.	.	.	.	.	0.7	.	.	.	.	.
Macaranga	0.8	1.0	.	.	*	0.9	1.0	.	.	.	0.9	1.0
Nastus	.	.	.	.	.	.	.	.	.	.	.	0.6
Nothofagus	0.7	.	.	.	0.7	*	0.9	.	.	.	0.9	.
Neolitsea	.	.	.	.	.	.	0.7	.	.	.	.	.
Olearia	.	.	0.7	.	.	.	.	.	.	.	.	.
Omalanthus	0.7	0.8	.	.	0.7	0.7	.	.	.	.	0.7	.
Opocunonia	.	.	.	.	.	.	0.7	.	.	.	.	.
Pandanus	0.8	.	.	.	0.8	0.9	1.0	.	.	.	0.8	.
Perottetia	.	.	.	.	.	.	0.8	.	.	.	.	.
Phaleria	.	.	.	.	.	.	0.7	.	.	.	.	.
Phyllanthus	.	0.8	.	.	.	.	.	.	.	.	.	0.8
Pittosporum	.	.	.	.	.	.	0.9	0.8	.	.	.	.
Podocarpus	0.7	.	.	0.7	0.7	0.7	0.9	*	0.7	.	0.7	.
Polyosma	0.9	.	.	0.8	0.9	0.9	1.0	0.8	0.7	.	0.9	.
Polyscias	.	0.8	.	.	.	.	.	.	.	.	.	1.0
Prunus	0.9	0.9	.	0.9	0.9	1.0	1.0	0.9	0.8	0.8	1.0	0.6
Psychotria	.	.	.	.	.	0.7	0.9	.	.	.	0.7	.
Rapanea	0.8	.	1.0	0.9	0.8	0.8	1.0	0.8	0.9	*	0.9	.
Rhododendron	.	.	.	.	.	.	0.8	.	.	.	.	.
Rubus	0.7	0.8	0.7	0.7	0.7	0.7	.	0.8	0.8	0.7	.	1.0
Saurauia	0.8	1.0	.	0.8	0.9	1.0	1.0	0.7	.	.	1.0	1.0
Schefflera	0.8	0.9	.	0.8	0.9	0.9	1.0	0.9	.	0.7	0.9	1.0
Schizomeria	0.7	.	.	.	0.8	0.9	1.0	.	.	.	0.9	.
Schuurmansia	.	0.9	.	.	.	.	.	.	.	.	.	0.6
Sericolea	0.8	.	.	0.7	.	0.7	.	.	.	.	0.7	.
Sloanea	.	.	.	.	.	0.7	0.7	.	.	.	*	.
Sphenostemon	.	0.8	.	.	.	0.7	.	.	.	.	.	0.8
Streblus	0.8	.	.	.	0.8	0.9	0.8	.	.	.	0.9	.
Symplocos	1.0	0.9	0.8	0.9	0.9	0.9	1.0	0.9	0.9	0.8	1.0	0.6
Syzygium	0.9	.	.	0.8	0.9	0.9	0.9	0.8	0.8	.	0.9	0.8
Timonius	0.8	0.8	.	0.7	0.9	1.0	1.0	.	.	.	0.9	0.6
Trema	.	.	.	.	.	.	.	.	.	.	.	*
Weinmannia	.	.	.	.	.	0.7	0.9	.	.	.	0.7	.
Wilkiea	.	.	.	.	.	.	0.7	.	.	.	0.7	.
Xanthomyrtus	0.7	0.8	.	.	0.8	0.9	1.0	.	.	.	0.9	0.6

are distributed by birds and mammals. It is possible, therefore, that these genera had a significance in pioneer forests or in relics left by a retreating forest limit that is not obvious in the less labile conditions of today. *Coprosma* and *Saurauia*, with higher altitudinal limits, occupy this kind of position now and evidently also did so then. It may be that 15000 I.A. roughly marked the time of transition from dominantly pioneer vegetation to forests with well ordered regeneration (involving *Trema*, etc.) in the Sirunki region generally, or that the falling temperature of the time created open areas below the altitudinal tree line (p. 331).

As a group, the open land ephemerals effectively began about 13000 I.A. *Dodonaea* is the only one consistently present after that, *Buddleia* giving way to *Casuarina* and *Acalypha* at 7000 I.A.

Among the herbs, Gramineae B and F with tricolporate Compositae occur throughout the pollen diagram consistently with their having components at the present day in high mountains and in cleared land. Cyperaceae A, C and Z, which have similar distributions in time, are likely to derive from marginal swamps of kinds now common around Sirunki and Inim. *Astelia*, *Gentiana*, *Styphelia*, *Potentilla* and *Ranunculus* form a group commonest between 30000 and 10000 I.A. and best represented today in tundra, alpine and subalpine grassland, mire and heath.

With some exceptions, therefore, fluctuations of the main pollen curves on the 5000 year scale are comprehensible by comparison with the composition of the major vegetation types of upland Papua New Guinea at the present day.

Among the lower mountain forest trees which are consistently present in the Sirunki catchment (or closely below it) from about 14000 I.A., pollen analytical parallelism is maintained down to periodicities of 2000 years or less. This is not so clearly the case amongst the trees and shrubs which are most abundant before 10000 I.A., however. Thus *Sloanea* exhibits its highest values between about 24000 and 21000 I.A. when *Rapanea* is also high, but does not reflect other maxima of *Rapanea*. *Sloanea* and *Litsea* begin among high *Nothofagus* and *Castanopsis* values at about 26000 I.A. but achieve their highest levels as the latter fall; *Claoxylon* behaves similarly but disappears more quickly. *Sloanea*, *Litsea* and *Claoxylon* must have remained as relics as the lower mountain forest retreated (p. 335). High *Rapanea* values are associated in modern pollen fallout studies with the presence of *R. vaccinioides* at and above the altitudinal forest limit. Overall, the pollen analysis record of these genera suggests that before 14000 I.A. they were opportunists, sometimes pioneers and sometimes relics persisting several generations; some still demonstrate this behaviour today while others do not clearly do so.

As a group, the forest ephemerals for the most part rise and fall with the mature forest trees until about 5000 I.A. After that date they persist, being relatively important in periods of low total forest pollen suggesting that these lows reflect widespread degradation of the forest and greater areal importance of early regeneration stages.

Among the grasses common throughout the Sirunki diagram there is general parallelism down to the 2000 year periodicity between groups D, F and H, all of which contain alpine or subalpine genera as well as some genera which grow in lower clearings. Gramineae B has a course contrasting in detail with D, F and H. Groups A, C, E and G, all commonest before 14000 I.A., behave independently of one another on shorter time scales. Perhaps B and C together below 14000 I.A. represent alpine and subalpine *Deschampsia klossii*.

Before about 15000 I.A. there is some parallelism between the Cyperaceae A, B, C and Z curves which is not maintained amongst them, or other sedges, thereafter. It seems that before this date the wetland herbs were reacting more or less in unison to generally limiting environmental conditions; after it they entered seral situations and behaved independently, each attaining ascendancy for a millenium or two in turn.

Departures from behaviour consistent with impressions gained from living vegetation become more marked when the pollen diagrams are resolved into units shorter than 2000 years in length. This is best achieved by selecting a period of general vegetational constancy, as indicated by total and individual pollen fallout values, and displaying the performance of each taxon separately throughout that period. For each taxon, the mean number of pollen grains per square centimetre of deposit per year for the period is calculated and the deviation from this mean at each sample level expressed as a percentage of that mean. A plot of these deviations then illustrates the changing success of the taxon throughout the period concerned. In the present instance three contiguous sections of the diagram, namely 15000–8000, 8000–3500 and 3500–1500 I.A., have been separately treated covering the time from the beginnings of replacement of alpine and subalpine vegetation by forests in the Sirunki catchment. Curves for selected taxa are shown in figure 13 with the sample levels arranged on a linear time scale.

In the brief forest period beginning about 14000 I.A. and culminating at about 13250 I.A. the main components, *Nothofagus*, *Castanopsis*, *Phyllocladus* and *Macaranga*, became established together and, apart from *Castanopsis* which fell earlier than the rest, deteriorated together. *Ascarina*, as in the later forest period, has its maxima narrowly related to those of *Nothofagus* with which it is very closely associated in analyses of living vegetation. *Trema* and *Engelhardtia* are similarly related to optimal forest development in the early period and in the earliest stages of the later period.

From about 13000 to 9000 I.A. the indications from forest pollen fallout are that lower mountain forest was only intermittently represented in the Sirunki catchment. The histories of individual taxa confirm this and suggest that, on the whole, they reached there individually at different times in response to differing environmental pressures and with dissimilar rates of migration and distances to travel. Thus, *Nothofagus*, *Ascarina*, *Engelhardtia* and *Dacrycarpus* were probably briefly in the catchment between 12500 and 10750 I.A. but most vigorously so at different times within that period and each for a very few generations. The implication is that, during a time when the area was environmentally marginal for growth of lower mountain forest or occupied by upper mountain forests unrepresented by pollen analysis, taxa otherwise closely associated behaved with individual opportunism.

The main forest period in the Sirunki catchment began about 9000 I.A., all the main taxa first expanding together but oscillating greatly for about 2500 years.

In the lower mountain forest after 6500 I.A., a few taxa were relatively consistent in their relationship according to the indications of their pollen abundances resolved at scales less than 2000 years. Thus *Castanopsis*, *Phyllocladus* and *Podocarpus* or *Macaranga* and *Engelhardtia* are rarely more than a sample apart in either upward or downward trends, or in peaks or minima of their pollen curves. Those taxa most closely associated in this way, e.g. *Nothofagus* and *Ascarina*, *Phyllocladus* and *Podocarpus*, are equally close when analysed in living forests. Yet they do not respond exactly together, so that at any time the composition of the forest, even in terms of these trees, is but one of a spectrum of possible quantitative compositions. The rates and directions of responses are generally consistent with known ecologies (e.g. canopy trees against ephemerals) but relationships are never unique in the sense of the decreasing success of one taxon being always accompanied by an improvement in another.

There is sometimes a hint of system within the variety, presumably attributable to life span

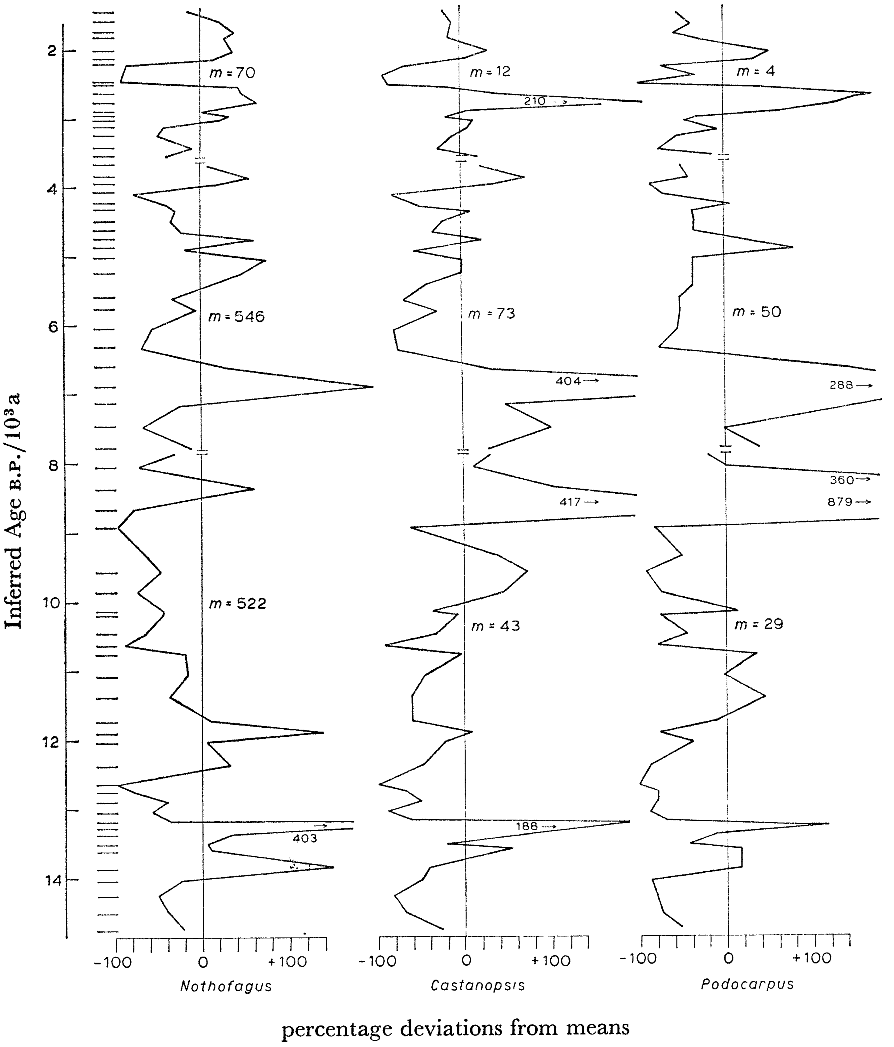


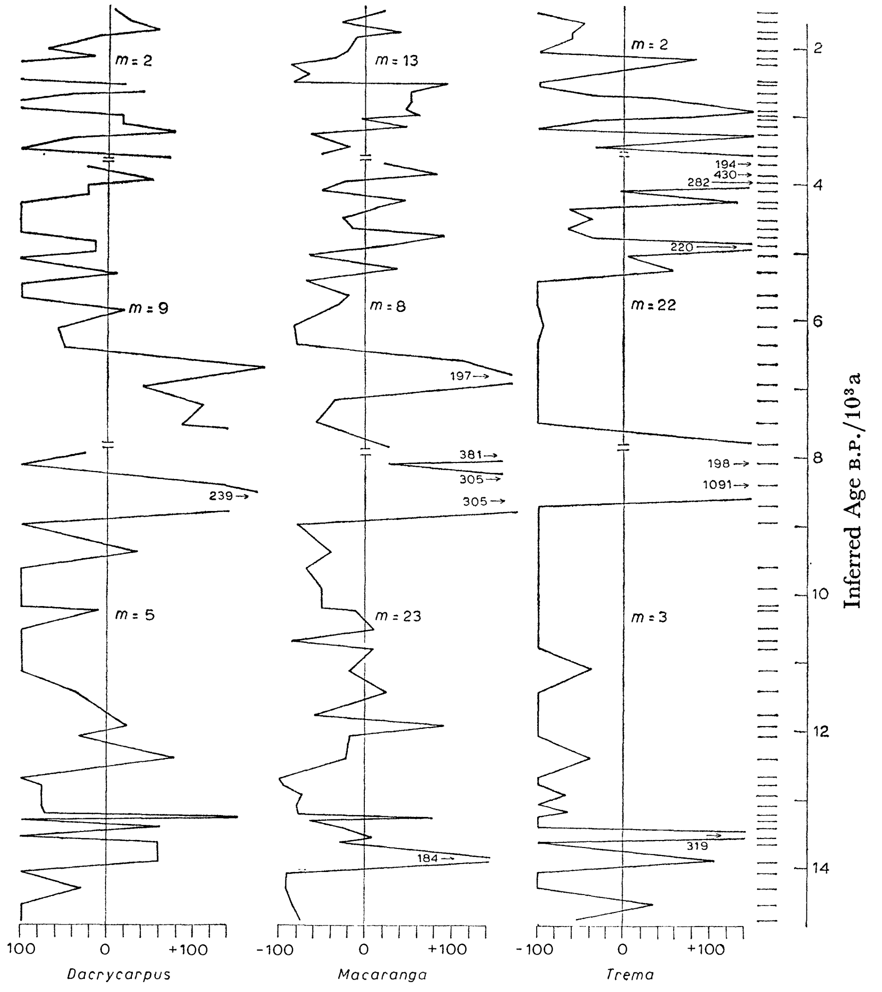
FIGURE 13. Variations in 'performance' of selected taxa, as measured by changes in the deviation of quantity of pollen of each from its mean quantity through the same time period. For further explanation see text. *m*, Mean for period between breaks in vertical line.

or aspects of regeneration strategy. Thus, *Nothofagus* and *Castanopsis* pollen curves, on this time scale, usually rise more or less synchronously but are less certainly correlated in their falls. Some movements, although in unison on a 2000 year scale, act contrarily for short periods within it. For instance, *Macaranga* and *Nothofagus* generally march together despite detailed antagonism such as that seen about 4500 I.A. when the pause in the fall of *Nothofagus* is the occasion for a temporary peak of *Macaranga*. Such behaviour is explicable in terms of known differences of regeneration time and responses to temporary environmental variations.

A few pollen types seem to behave entirely independently of all others on this scale; some (e.g. *Dacrycarpus*) correspond in this to their occurrence at present, others (e.g. Elaeocarpaceae), do not.

Finally, the association of taxa may be consistent but different within each of two periods as is the case of *Macaranga* and *Trema* before and after about 3500 I.A.

The associations between taxa at Inim are difficult to discern because of inadequate



percentage deviations from means

FIGURE 13 (continued).

chronological control and the relative basis of the pollen counts. All that can be said is that, within these limitations, such conclusions as can be drawn agree with those from Sirunki. For instance, on the largest scale of resolution, *Astelia*, *Styphelia*, *Plantago*, *Drapetes*, *Potentilla* and *Ranunculus* together occur before about 10000 I.A. but not thereafter. *Casuarina* begins at about 10000 I.A. *Macaranga* and *Trema* are present, the latter intermittently, throughout the diagram but do not assume real significance before some time between 10000 and 8000 I.A.

A few similarities are apparent in the detailed relationships of some taxa. Thus *Ascarina* occurs only with the higher *Nothofagus* values, *Podocarpus* and *Phyllocladus* run parallel courses closely similar to that of *Castanopsis*, *Nothofagus* behaves contrarily to *Castanopsis* before about 2000 I.A. (but sympathetically thereafter) and *Trema*, whilst in general paralleling *Casuarina*, in detail is antagonistic to it.

The record from Birip is too short to test the consistency of relationships between its taxa which were probably dominated by seral events around the crater wall.

In the most general terms, e.g. as components of a loosely defined lower mountain forest in the past 30000 years, the higher taxa of the Papua New Guinea mountains have behaved as their present distributions and ecological relationships might have led us to expect. Resolved in detail, however, this is not universally true. A few taxa are closely and mutually related at all times whilst the success of others seems to bear no relationship to the quantities of other taxa present. The majority of taxa, however, lie between these extremes; they are usually quite closely associated in groups which, during a few thousand years (i.e. a few generations), vary somewhat in their composition repeatedly but on occasion behave entirely individualistically. There are degrees of affiliation and of their constancy through time.

7. Vegetation synthesis and dynamics

Before about 10000 I.A. the forests in the Sirunki catchment were co-eval with grassland and fragments of alpine vegetation there. They developed where these communities were formerly more extensive and in decaying gave place to the forests. Because very few components of modern upper mountain forest are represented in the pollen analyses, it is difficult to know whether anything strictly analogous to it was present during that period. Some components (e.g. *Rapanea* cf. *vaccinioides*, *Coprosma*) were certainly present as were others (e.g. *Podocarpus*, *Cyathea*) only some of whose species belong to the upper mountain forest today. But *Dacrycarpus*, now a gregarious timber line plant (*D. compactus*) did not grow in the catchment more than fleetingly until about 14000 I.A., 13000 years after the earliest indications of persistent forest of some kind. Lower mountain forest certainly occupied the catchment at about 14000 I.A. Before it, upper mountain forest components were there but not in sufficient variety, nor producing enough pollen, to be confidently interpreted as the closed formation they make today. For reasons which are at present obscure but which may have had stratigraphic as well as vegetational repercussions (p. 310), lower mountain forest more or less vacated the catchment between about 13000 and 9000 I.A. leaving it to herbs and *Cyathea* woodlands. Little that might be thought of as upper mountain forest was present at this time, suggesting that climatically the area was already unsuitable (too warm) for it. The presence of *Dodonaea* indicates that some of its niches were being filled with more warmth demanding, shade intolerant, woody plants.

The establishment of lower mountain forest after this period involved all its main taxa. *Phyllocladus*, *Podocarpus* and *Castanopsis* pollen curves rose first, closely followed by *Nothofagus*. For about 1000 years after 8250 I.A., all the high forest trees were less successful, *Nothofagus* and *Ascarina* particularly so, whilst *Macaranga* and *Trema* were more than usually abundant. By 7500 I.A. another surge of canopy trees had begun; this passed into steadier conditions by 6500 I.A. It seems possible that expansion into newly available niches from nearby forests at about 9000 I.A. created a large mosaic forest in which each taxon was represented by more or less even aged stands. As these died together, after about 500 years, ephemerals became comparatively very important in the forest cover until a second surge of canopy trees at 7500 I.A. Competition, and probably the arrival of more species, led to a mosaic of smaller units of differing ages and therefore smaller amplitude and periodicity in pollen production.

The establishment of lower mountain forest with repeated fluctuations in its composition and with wavelengths of about 2000 to 1000 years (or two to four generations of the longer lived trees) therefore took about 2500 years after the main components had entered the area. It was a period of differentiation and increase in sociological complexity in a newly expanding plant community.

Superimposed on the periodicities of 1000 to 2000 years, are shorter lived variations with time spans as short as 400 years (about twice the sampling interval) or a single generation of canopy tree. Indeed, these shortest period fluctuations might mainly be the expressions of regeneration seres in small gaps originating from the death of a single canopy tree. The longer fluctuations, however, must reflect changes in the populations of taxa generally and synchronously experienced over a wide area. They may be determined environmentally or be the products of interactions of differing life-spans of the plants involved. Perhaps the pattern of death of *Nothofagus* commonly remarked in today's forests (Cartledge *et al.* 1975) is part of the mechanism of changes on this time scale.

From about 4500 I.A. the behaviour of the forest ephemerals in relation to the canopy trees changes. Before that date, the fluctuations of the two categories, down to a scale of about 500 years, were closely parallel. Above it, peaks of canopy genera are usually shared by forest ephemerals but, with the exception of the trough around 2250 I.A., the ephemerals do not sink comparably during low periods of the former. The parallelism before 4500 I.A. is consistent with the idea of a constant proportion of ephemerals in the forest as a whole, albeit clustered at any one time in small regeneration gaps. Their behaviour after 4500 I.A. suggests that the ephemerals were widespread throughout the forest and able to respond quickly and independently to fluctuations in the canopy trees of the order of 1000 years. This could only have been achieved by a 'degradation' of the forest, that is the loss of a proportion of its canopy trees; present day analogues are to be found between Sirunki and Inim and in the Marapamanda hills.

8. The physical environment

Both the stratigraphic records and the pollen diagrams exhibit events which it is tempting to attribute to major changes in the physical environment independent of plants, animals or man. The four determinants of this kind which it is necessary to consider in the Papua New Guinea uplands are tectonic movement, vulcanism, temperature change and the incidence of drought.

Tectonic movements take place today and must have done so during the period of accumulation at Sirunki and Inim (Guilcher 1970; Dekker & Faulks 1964). There is no indication of rapid or large movements nor any direct disturbance, such as faulting of the deposits in the basins. However, earth tremors are commonly felt in the district, whilst elsewhere in Papua New Guinea, earthquakes devastating vegetation and drainage have been observed recently (Pain 1972; Pain & Bowler 1973; Simonett 1967) and are strongly indicated in the past (Pain 1975). Landslip scars of unknown ages may be seen in the Sirunki–Inim area.

Accumulations of volcanic ash are common in the western highlands of Papua New Guinea as well as elsewhere in the country (Pain & Blong 1976). Close to their origins (e.g. Kaugel Valley near the volcanic Mt Giluwe) they may blanket valleys to a depth of 7 m (Pain 1973). They are more often encountered as layers a few centimetres to a metre in thickness intercalated in soil profiles, exposed by roadside cuttings and as thin layers and lenses in swamp deposits. Not all such ashes originated in the western highlands of Papua New Guinea. Indeed, the only likely large sources there during the late Quaternary are Mt Giluwe, Sugarloaf and the Doma Peaks, whilst Birip itself was evidently a minor source sometime shortly before 2300 I.A. There are also at least two layers of volcanic ash intercalated in the muds at Birip and several such at Inim but at Sirunki they were recorded only rarely. This is partly a reflection of the authors' inexperience at the time most of the field work was carried out and subsequent examination of some cores in the laboratory has established that some silt layers are indeed volcanic ash. It is also possible that the abundance of diatoms in the past in the Lake Ipea Basin was a product of volcanic ash enrichment, as might also be the turquoise colouration of some of the diatom rich muds there. The turquoise colour is particularly marked in the Lake Ipea Basin deposits from 24000 to 21000 I.A. and again after 13500 I.A. Indeed, the reworked and redeposited material in the Kayamanda Swamp Basin and the diatomaceous clay at the fringe of the Lake Ipea Basin assigned to the period 13500 to 13000 I.A. certainly contain volcanic ash, perhaps redistributed from older deposits around the edges of the basin. In the Sirunki district an olive ash layer, often 50–100 cm thick, commonly lies in the soil profile one to two metres below the surface. If this ash had fallen during the investigated period at Sirunki it should be evident in the swamp stratigraphy and might have significantly affected the vegetation. Pain & Blong (1976) include this ash with the Tomba Tephra which originated from the caldera complex of Mt Hagen about 70 km southeast of Sirunki certainly more than 30000 and probably before 50000 years ago (Pain & Blong 1976).

If this age is correct, the ash fall might have contributed to the barren conditions evidenced by the Sirunki pollen diagram between 33000 and 27500 I.A. and provided a source for later redistribution, particularly between 24000 and 21000 I.A. and about 13500 I.A.

Blong, Hughes & Golson (personal communication) have assembled a large number of radiocarbon dates associated with volcanic ash layers in the swamps of the Wahgi Valley, 110 km southeast of Sirunki. Although they record at least nine distinct ashes since 6500 B.P., none has been recovered from between that date and 13000 B.P. at the earliest. However, three are dated, rather loosely, from 13000 back to 16000 B.P. and possibly earlier. It is possible, therefore, that these events might have directly provided some of the material which accumulated in the Sirunki swamp from 13500 to 13000 I.A.

If the raising of the water level at Sirunki about 13500 I.A., the reworking of its marginal deposits during the following 500 years, the destruction of the forests and their failure to re-establish complete and permanent cover until 9000 I.A. have a single prime cause other than climate, it is likely to have been volcanic ash showers or seismic activity. The only known ash shower sufficient to affect forests so drastically is that represented in the Sirunki soil profiles and known to be of much greater age. Moreover, it is difficult to believe that it would have taken 4000 years for the forest completely to cover a soil so blanketed. Besides, such a quantity of ash should have left an easily recognisable stratum in the undisturbed deposits near the centres of the basins if it were large enough to have blocked the outflow from Lake Ipea and so raised the water level in the basin. On the other hand, if the ash were to have been deposited much earlier, before most of the lake and swamp deposits investigated, its redistribution could have been due to a minor earthquake which would also have been sufficient to cause landslips blocking the narrow gorge through which the River Kapupu leaves Lake Ipea. A period of repeated tremors during the following 4000 years could certainly have kept the soil mantle around Sirunki unstable and account for the erratic and partial success of tree growth there, particularly if the climate were also marginal. It might also account for the wide spread of grey clay across the swamp from the mud volcano at Inim (p. 288). An implication of such an explanation is that seismic activity has been less common since 9000 I.A.

An alternative explanation for the stratigraphic sequence between 15000 and 13000 I.A. might be that there was a decrease in rainfall, or increase in evaporation, which lowered the lake level substantially and allowed swamp to grow over lake mud. From considerations of world palaeoclimatology it is inconceivable that evaporation could have been higher then than now. Given the same evaporation, a rainfall less than half that of today would have been needed to turn the Sirunki basin into a closed lake and permit the further lowering of its water level. It is highly unlikely that such a change can have taken place (p. 270). It is possible, however, that periods of unusually high or concentrated rainfall contributed to the instability of the Kaipare Fan and led to the deposition of inorganic sediments around its edge at about 9000 I.A. and after 3000 I.A. Minor seismic activity might also have been involved.

During the period since 6500 I.A. there have been fluctuations in the amount and composition of the forest pollen fallout. Although the movements of the different pollen curves (figure 13) are not exactly synchronous, by and large they fall from peaks at about 5000, 4000 and 2750 I.A. Lacking a chronology of ash showers for the Sirunki district, it is impossible to establish correlation between any such events and the vegetation changes. There is no correlation with the Wahgi Valley ashes (Blong, Hughes & Golson, personal communication) except between the 2750 I.A. vegetation change at Sirunki and two ashes in the Wahgi Valley, one dated about 2500 I.A., the other to 3000 I.A., and the presumed last eruption of Birip (> 2300 I.A.).

Some of the shorter fluctuations of the forest taxa after 6500 I.A. may have resulted from periods of unusually frequent transitory droughts, and the frosts which commonly accompany them, which are known to have significant effects on natural vegetation at about the altitude of Sirunki (Bureau of Meteorology 1973; Brown & Powell 1974).

It is reasonable to suppose that temperature change might have influenced the vegetation of this region during a part of the period under consideration. The high mountains of Papua New Guinea were glaciated down to between 2750 and 3300 m (Löffler 1972; Galloway *et al.* 1973) by ice which began to retreat from Mt Wilhelm at 14000–15000 B.P., from Mt Albert Edward and Mt Giluwe at 13000 B.P. and from Mt Jaya (Mt Carstensz) before about 14000 B.P. (Hope & Peterson 1975; Hope personal communication). In the vegetation histories of Sirunki and Inim the contrast between the period before 15000 I.A., during which forests were uncommon and alpine or subalpine plants were common amongst the herbs, and the forest-dominated time which followed, invites explanation related to temperature.

Qualitatively, temperature conditions roughly comparable with today's must have become established by 6500 I.A. when relatively stable lower mountain forest occupied the Sirunki–Inim area. From 14000 until 6500 I.A. the climate was evidently colder for part of the time, as witness the persistence of subalpine plants, but vulcanism and earthquakes probably also contributed to the determination of some of the vegetation changes. The time between 33000 and 14000 I.A. was evidently the coldest, interspersed with some less extreme periods. The lake and swamp stratigraphy is consistent with this interpretation, organic productivity being restricted before 15000 I.A. and at its greatest after 6000 I.A. Pollen analysis and stratigraphic data are not always in detailed accord, however. Thus, the clay content of the muds between 24000 and 21000 I.A. suggests more rigorous environmental conditions than immediately before or after, yet the vegetation indicates a slightly higher temperature; perhaps volcanic ash falls contributed directly to the mud at that time.

A more detailed and quantitative reconstruction can be made by selecting periods in the vegetation history and attributing a temperature range to each of them by analogy with the temperature correlates of appropriate taxa at the present day. Table 11 sets out the argument for each period and the resulting plot of probable temperature change at Sirunki is shown in figure 14. For each period the range indicated by extreme interpretations of the data, including different assessments of relative pollen transport and production, is given. Within this range a narrower one is selected, based on the authors' judgement of the relative weight to be attached to the contributions to the wider range. Finally, allowance is made for chronological uncertainties, by indicating the possible time range of each boundary.

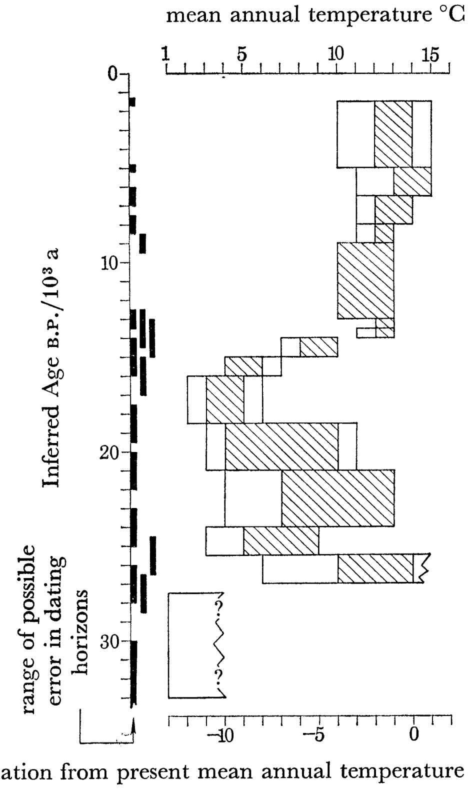


FIGURE 14. Estimates of the march of temperature at Sirunki based on the calculations in table 12. For each time span the total horizontal spread represents the extreme limits between which the mean annual temperature must have lain; the shaded sections show the more probable limits based on informed judgement as well as facts.

The evidence from before 27500 I.A. is difficult to interpret. The pollen diagram indicates negligible, totally herbaceous, species-poor vegetation throughout the period and virtually barren land from 30000 to 29000 I.A. Yet organic muds accumulated in the Kayamanda Swamp Basin and Lake Ipea. True, some of this accumulation is almost certainly *dy*, soil humates brought into solution and reprecipitated in the lake, a material consistent with erosion of pre-existing organic soils in the catchment. By analogy with the present day, such barren conditions, if wholly climatically determined, imply mean annual temperatures at least 10 °C and more probably greater than 12 °C below those of the present day. This is at least 1 °C lower than the lowest temperatures indicated by pollen analysis between 18500 and 16000 I.A. and 2 °C lower than the lowest possible estimate from the maximum extent of glaciation (p. 333). The possibility that a major volcanic ash shower blanketed the region shortly before this time has already been mentioned. It would be injudicious to attribute environmental conditions to the period dogmatically without further evidence.

It seems that temperatures may have approached those of the present day between 27000 and 25500 I.A. but thereafter fell, albeit fluctuatingly, until between 18500 and 16000 I.A., the greatest temporary fall occurring between 25000 and 24000 I.A. The maximum difference throughout the total period is estimated at 12 °C, a rate of fall of rather less than 2 °C per millennium. However, the lower limit for the warmest period is the same as the upper limit for the coldest (8 °C below present), so that no temperature change is *essential* to the explanation of the data. Between these extremes lies the authors' preferred hypothesis that the temperature fell irregularly from about 1 °C below present to about 10 °C below present between 26500 and 18500 I.A., a mean rate of 1.3 °C per millennium.

The temperature rise after the 18500–16000 I.A. cold period was evidently faster than the fall before it until about 14000 I.A. when lower mountain forest again became established, albeit fleetingly, in the catchment, and temperatures there were within 2 °C of present. Depending on the boundaries selected, rates of 1.5 °C to 5.5 °C per 1000 years can be justified; the authors' considered preference is for a mean of 3 °C per millennium between 10 °C below present at 16500 I.A. and 1 °C below present at 13500 I.A.

It has already been suggested that non-climatic factors might mainly have inhibited the persistence of total forest cover between 13000 and 9000 I.A. It is also possible that temperatures fluctuated, reaching means as low as 4 °C below present day temperatures. But by 9000 I.A. mean annual temperature was within a degree of its present value and by 6500 I.A. probably little different from its present-day value. Since that time no vegetation changes have occurred for which it is necessary to invoke climatic reasons. It is true that the vegetation established by then was relatively insensitive to changes of a degree or two which might therefore have occurred without registration in the pollen diagram.

Although there is a possibility of an earlier glaciation of the New Guinea mountains which may prove to be about 30000 years old (Hope & Peterson 1975), the main evidence of glaciation is provided by suites of valley moraines ascending the major high mountains from about 3000 m. The radiocarbon dating of deposits behind such moraines, associated with pollen analysis, indicate that retreat began between 14500 and 15500 years ago (Hope & Peterson 1975). This is consistent with the indications of mean annual temperature increase beginning at Sirunki at about 16000 I.A. and leads to the suggestion that the last glacial maximum in New Guinea was in the 18500 to 16000 I.A. period. Hope (1976) shows that the altitudinal tree line on Mt Wilhelm did not respond until about 10000 B.P. by which date, however, forest similar to that of the present day occupied a site at 2740 m. It is likely that the difference in immediacy of response between Sirunki and Mt Wilhelm was associated with the distance of relict forests from the sites and local geographical conditions. Yet the fact that the rise of the forest edge did not begin confidently on Mt Wilhelm until about 10000 B.P. is consistent with the impersistence of forest near Sirunki until about 9000 I.A. and suggests a climatic component in the inhibition of its development there. Indeed there was still ice on Mt Wilhelm until about 9000 I.A. (Hope & Peterson 1975) and the present hypothetical snowline of Papua New Guinea was probably not reached until more than a thousand years later, which is entirely consistent with the Sirunki vegetation record. There is no indication from Sirunki or Inim of renewed cooling evidenced by high altitude moraines and minor depression of tree lines on Mt Jaya and Mt Wilhelm (Hope & Peterson 1975; Hope 1976), but this may reflect insensitivity of the forest vegetation to its effects.

Assuming, as a result of the above discussion, that at 18000 B.P. the firn line stood about 3500 m above present sea level, say 3600 m above the sea level of the time, the temperature lapse rate between there and Sirunki altitude must have been between 1 and 5 °C per 1000 m altitude, depending on the estimate chosen for Sirunki (figure 14). The mean of these, namely

3 °C per 1000 m, is significantly smaller than the modern lapse rate. However, the Climap Project Members' (1976) model estimates sea surface temperatures in the equatorial west Pacific about 2 °C below present at 18000 B.P. Applying this to a sea level about 100 m below present leads to lapse rate estimates per 1000 m between 9.2 °C and 7.7 °C on the basis of Sirunki data and 7 °C from the firn line position.

The present forest limit lies at about 3800 m and at 6 °C mean annual temperature. At 18000 I.A. the Sirunki firn line based lapse rate estimate places it between below sea level and 2500 m above sea level. The first extreme is absurd whilst the Sirunki evidence itself suggests that the second is somewhat too high. The Climap Project Members' firn line based lapse rate puts the 18000 I.A. forest limit about 2750 m above present sea level which is above that indicated by the evidence of pollen analysis from Sirunki. However, the Climap Project Members' Sirunki (mid-range estimate) based calculation of 2250 m for the forest limit corresponds more closely with that derived from the pollen analyses. If the Climap Project Members' estimate is correct a lapse rate considerably greater than that of the present day is implied, namely something between 8 and 9 °C per thousand metres altitude. This would be consistent with a forest limit between 2400 and 2100 m above present sea level but implies a firn line between 3000 and 2700 m above present sea level, i.e. 500–800 m below that indicated by geomorphological evidence.

Only a very low lapse rate could explain the altitudinal distance between the forest limit and the firn line at 18000 I.A. if it were totally temperature controlled or if the present forest limit is not more substantially below its minimum temperature tolerance at present than is suspected. The extrapolation of such a lapse rate downwards leads to absurd conclusions. All other indications favour a lapse rate greater than that of the present, namely between 6 and 9 °C per 1000 m, and must lead to the possibility that the firn line was kept high by lack of precipitation at high altitudes. This is not at variance with the assertion that the vegetation never suffered from lack of water because a much greater diminution below present would be necessary to cross the vegetation tolerance threshold than would significantly affect the amount of snow accumulation to be expected. Moreover, a mechanism for affecting the highest altitudes in this way, without significantly reducing precipitation below, is available if high altitude dry air were more or less perennially, instead of occasionally, to subside into the highest New Guinea altitudinal range, perhaps an expected concomitant of a greater lapse rate (cf. McVean 1968; Hnatiuk *et al.* 1976).

If this were the mechanism, it could be that the general warming beginning at about 16000 I.A. reduced the frequency and depth of cold dry air subsidence and allowed progressively more effective penetration of wet surface winds to high altitudes, so maintaining the actual firn line more or less stable as the theoretical firn line rose toward it. Until the two coincided, deglaciation would be erratic, punctuated by still-stands and readvances marked by staircases of terminal moraines as in the Mt Wilhelm valleys. It may be that it took until 9000 I.A. for balance to be achieved, shortly before permanent snow vacated the summit of Mt Wilhelm. In the meantime the response of the vegetation might have been episodic, affected by the generally rising temperature, local effects of increased snow precipitation and the persistence of cold katabatic winds from the snow fields. This might well have contributed to the failure of forest to persist around Sirunki until 9000 I.A.

If the theoretical and actual snowlines had risen to about 4500 m by 8500 I.A. (cf. Hope & Peterson 1975) and the sea surface temperature had reached about 27 °C (i.e. 1 °C above its mean 18000 I.A. level), the lapse rate would have been about 5.7 °C per 1000 m altitude, i.e. insignificantly different from its present day value.

In summary, the contributions of different environmental factors to vegetational development before 27500 I.A. are uncertain. It seems, however, that from temperatures approaching those of the present day about 27000 to 25500 I.A., cooling proceeded until the time of the last glacial maximum between 18500 and 16000 I.A. At the beginning of deglaciation the temperature rose rapidly to within 3 to 1 °C below present day levels by 14000 to 13000 I.A. Thereafter, somewhat lower temperatures and repeated earth movements probably combined first to destroy the forest and then to inhibit its widespread development. These influences were overcome by about 9000 I.A. so that by 6500 I.A. temperatures comparable with those of the present day were established. There are indications that the temperature lapse rate at the last glacial maximum was much greater than now, but it is likely that modern values were reached by about 8500 I.A.

9. PLANT GEOGRAPHIC IMPLICATIONS

The height of the altitudinal forest limit has evidently shifted substantially during the past 33000 years (table 12, figure 15). Events before 27000 I.A. clearly need elucidation beyond the capacity of the present data. There is little doubt, however, that in the Wabag region the tree line fell from about 26000 I.A. to about 18000 I.A. at a mean rate between 17 and 8 m per century and rose between about 17000 I.A. until 15500 I.A. at a mean rate between 33 and 25 m per century; rates of 15 and 30 m per century are the most probable for the two processes respectively.

Falling mean annual temperature and its frequently associated conditions (e.g. increasingly frequent frosts at lower altitudes) affects established trees by reducing metabolic rates, growth and seed production, by directly damaging tissues (e.g. by frost) and by reducing regeneration. The effects of a given temperature reduction on metabolism, growth and seed production might be roughly the same for all montane trees and frost damage is more likely to affect the upper mountain forest trees because of their lower stature. Regeneration might also be inhibited to an equivalent degree in all forest types and so the composition of a stressed forest will depend mainly on the longevity of the canopy trees. The mean life spans of trees of the upper mountain forest probably range between about 50 and 200 years whilst those of the canopy trees of lower mountain forest are probably closer to 500 years. Because of this difference, the upper mountain forest would disappear from a given altitudinal interval faster than would the remnant canopy of lower mountain forest in a similar, but absolutely lower, interval. The thinned upper edge of the lower mountain forest would doubtless accommodate most, if not all, of the taxa which now, and formerly, grow in the upper mountain forest so that the tree line forest would be of a composition unknown at the present day and one in which the longest lived, least cold susceptible, components of the present lower mountain forest may have had a part. This is consistent with the pollen record of *Sloanea* and *Litsea* during this period.

Whether or not temperatures were constant for long enough during the cold period of 18500–16000 I.A. for the forests to differentiate into units comparable with those of the present day, the subsequent rapid rise in mean annual temperature would have strongly favoured those trees which reproduce prolifically and early and the seeds of which travel far. This is consistent with the Sirunki data for components of both upper and lower mountain forests. It implies, too, that the upper mountain forest as it is known today might have taken several thousands of

Table 12. Derivation of forest limit altitude estimates from Sirunki data (table 11) displayed in figure 14

	period in years I.A.	8000–9000		13000–14000		16000–18500		25500–27000		27500–33000	
		min.	max.	min.	max.	min.	max.	min.	max.	min.	max.
		maximum range									
	temperature at Sirunki °C	11	13	11	13	2	6	6	> 13	1	4
	difference from forest limit temperature (6 °C) °C	5	7	5	7	−4	0	0	> 7	−5	−2
lapse rate 8.5 °C per 1000 m	altitudinal equivalent of temperature difference m	588	823	588	823	−470	0	0	> 823	−769	−235
	altitude above present sea level m	3088	3323	3088	3323	2030	0	2500	> 3323	1731	2265
lapse rate 5.8 °C per 1000 m	altitudinal equivalent of temperature difference m	862	1207	862	1207	−689	0	0	> 1206	−862	−344
	altitude above present sea level m	3362	3707	3362	3707	1811	0	2500	> 3706	1638	2156
		most probable range									
	temperature at Sirunki °C	12	13	12	13	3	5	10	14	?	?
	difference from forest limit temperatures (6 °C) °C	6	7	6	7	−3	−1	4	8	?	?
lapse rate 8.5 °C per 1000 m	altitudinal equivalent of temperature difference m	706	823	706	823	−353	−117	470	941	?	?
	altitude above present sea level m	3206	3323	3206	3323	2147	2383	2970	3441	?	?
lapse rate 5.8 °C per 1000 m	altitudinal equivalent of temperature difference m	1034	1207	1034	1207	−517	−172	689	1379	?	?
	altitude above present sea level m	3534	3707	3534	3707	1983	2328	3189	3879	?	?

years to form or reform in more or less its present position. If, as has been suggested (p. 333), the persistence of snow down to about 3500 m until about 10000 I.A. inhibited the upward spread of forest above about 3400 m for about 3500 years, this would further have delayed differentiation within the upper mountain forest.

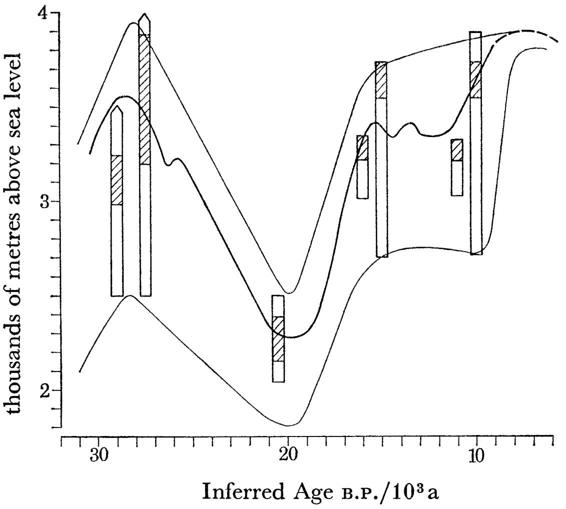


FIGURE 15. Estimates of altitudinal forest limit fluctuations derived from Sirunki pollen analyses. Each vertical column relates to a selected time; within it the shaded part indicates the range of the most probable altitude and the unshaded parts the extreme limits of possibility. The heavy curve traces the most probable continuous movement of the forest limit, the lighter curves the extreme upper and lower possibilities.

All these considerations suggest that the upper mountain forest flora is one which can be accommodated within the lower mountain forest and which becomes a separate entity only during its periodic excursions to altitudes beyond the tolerance of the rest of the trees of the lower mountain forest, excursions which have probably occupied but a small proportion of the Quaternary Period as a whole.

The last glacial maximum probably saw the forest limit depressed to about 2300 m in the Wabag region. It is impossible to tell how generally applicable to New Guinea as a whole this was, but throughout the island it is likely that the forest limit did not lie outside the extreme estimates from the Sirunki data, namely 2500 and 1800 m. A depression of 1500 to 2300 m would require that the tree species now occupying the full altitudinal range of New Guinean forests must have lived in only 60 % of that range, since there was no commensurate lowering of sea level at the time. The possibility has been suggested above that the occupants of the uppermost 800 m today were accommodated in a now unfamiliar forest type occupying a smaller altitudinal interval below the tree line. It may be, indeed, that sociological changes of this kind occurred throughout the altitudinal range of the forests, in which case some at quite low altitudes with long lived trees may still only be recovering from it. Alternatively, the altitudinal range of each taxon might have been narrowed in response to the greater lapse rate of the time. Whatever the mechanism employed, the lowering of the tree line and the environmental pressures which caused it must have significantly affected the forest composition at lower altitudes.

If, at the height of the last glacial episode, the altitudinal forest limit stood at about 2300 m, most of the now treeless subalpine and alpine parts of New Guinea would have been connected above this altitude, albeit somewhat tortuously in places. However, the Sarawaged Range would have remained quite separate as would the Kratke Mountains and the Mt Victoria–Mt Albert Edward Massif and at least two other sections of the Owen Stanley Range. Smith (1975*a*) has pointed out that the high New Guinea mountains in general hold a large number of their herbaceous angiosperm species in common, a circumstance to which their former near continuity over perhaps 2000 years doubtless contributed.

The bottoms of the great intramontane valleys of Papua New Guinea commonly lie within a few hundreds of metres of 1500 m. When the altitudinal tree line was most depressed (between about 18500 and 16000 I.A.) these valleys must have lain within the upper mountain forest or a forest different from anything known today (p. 335) no matter which of the possible temperature lapse rates is employed. They would also be within the range of common night frosts and cold air ponding to which their topographies would be particularly conducive. It is likely that treeless patches became established there as a result of these locally cold conditions as well as of impeded drainage. It is conjectural whether these persisted until the supposed stabilization of the temperature lapse rate at about 9000 I.A. If they did they might well have provided the nuclei from which grasslands spread to occupy most of these valleys, largely as a result of human activity now attested near Mt Hagen 9000 years ago (Golson, personal communication).

10. HUMAN INTERACTIONS

The earliest remains attributable to human activity in the Papua New Guinea highlands date from about 26000 B.P. (Bulmer 1975; White *et al.* 1970). It has been argued that the occurrence of pigs there, well authenticated from 6500 B.P., and probably dating back to 10000 B.P. (Bulmer 1975), was accompanied by some sort of agriculture (Bulmer 1966; White 1972) although Bulmer (1975) and Golson & Hughes (1976) have suggested that the animal might have reached New Guinea independently of man. In the Wahgi Swamps near Mt Hagen, Golson (1976 and personal communications) has discovered extensive but intermittently operated drainage systems which he associates with horticulture back to at least 6000 B.P. and undoubtedly human modification of the land surface as early as 9000 B.P. Powell *et al.* (1975) have reported pollen evidence from the same region, indicating vegetation disturbance which is assumed to have been produced by human activity before 5000 B.P. There have been no archaeological investigations in the Enga Province itself.

Even if a sufficiently cold-tolerant staple crop were available, it is unlikely that people would be able to live permanently above 2800 m in the Sirunki–Inim region today without substantial improvement in clothing and housing. The limiting temperature and wetness this implies was probably not realized at Sirunki–Inim altitude between 27000–25500 I.A., 24000–21000 I.A. and after 9000 I.A. and only uncertainly and intermittently so between 14000–9000 I.A. During these periods climatic conditions did not directly prevent human settlement, but at other times they could have done so. Nevertheless, even when permanent settlement was precluded, seasonal hunting and gathering parties might have made substantial use of the region, particularly when the altitudinal forest limit lay above or not far below it, namely at times between 25500 and 19500 I.A. and between 15000 and 9000 I.A.

The pollen diagrams contain taxa which are currently strongly associated with human activities, such as *Acalypha* and *Casuarina* which are planted today, *Trema* and *Dodonaea* which are conserved and abundantly used, and *Castanopsis* and *Nothofagus* which are selected from the forests for building purposes (Powell 1976). The most simplistic interpretation might equate the occurrence of open land ephemerals, known to be used now (e.g. *Acalypha*, *Casuarina*, *Dodonaea*), with human occupation, particularly if associated with high values for forest ephemerals (e.g. *Trema*, *Macaranga*) which would presumably have been encouraged by the selective or general felling of canopy trees. By this argument, human disturbance of the forest could be carried back, intermittently, to 13000 I.A. (*fide Dodonaea*). There is positive evidence to suggest that the period from 13000 to 9000 I.A. was relatively treeless, a condition to which low temperatures, seismic instability and volcanic ash showers may have contributed (pp. 330, 334). Although humans might have taken advantage of this situation for hunting, as Hope & Hope (1976) have suggested for earlier forest-grassland interfaces, there is no archaeological evidence that they did so, nor do the vegetational data require it.

Casuarina grows only sparingly in the Sirunki–Inim region, which is only 300 m below its absolute altitudinal limit in Papua New Guinea, many of the artificial habitats in which it might grow (were they at lower altitudes) being occupied by *Dodonaea*. However, it produces large amounts of pollen which travels far and such long distance transport doubtless accounts for its occurrence from about 10000 I.A. in the Inim record. Nevertheless, the occurrence of substantial amounts of *Casuarina*, together with *Glochidion* whose altitudinal limit today is only 2500 m, from about 7500 to 7000 I.A. deserves attention. The evidence is insufficient to prove that *Casuarina* and *Glochidion* were growing within the catchment; certainly it was not a period notable for high proportional representation of forest ephemerals or grasses, nor is it especially evident in the Inim diagram. However, there is no escaping the facts that *Casuarina* and *Glochidion* were growing in the Wabag region by 10000 I.A. and that they were either more abundant or closer to Sirunki between 7500 and 7000 I.A. than either before or immediately afterward.

Compelling evidence for forest reduction at Sirunki beginning at about 4300 I.A. comes from falls in the abundance of pollen of some canopy trees together with marked increases in *Trema*, *Macaranga* and *Engelhardtia*, the first major surge of *Acalypha* and isolated high values of *Dodonaea*. Some of the open land created at this time persisted until about 3000 I.A. despite the partial regeneration of forest from about 4000 I.A. There was no major volcanic ash shower at the time which could have accounted for these changes, whilst the plants involved are not indicative of a new temperature régime. Moreover, it was not recorded at Inim, suggesting that, although substantial, the forest destruction was restricted to the Sirunki catchment. The activities of humans, whilst not proven, are strongly implied. Moreover, the scale and persistence of the clearing suggests residence and gardening rather than occasional hunting visits.

It was at about this time that the forest composition changed, apparently irreversibly during the span of the Sirunki pollen diagram, to one which throughout phases of canopy tree regeneration nevertheless remained degraded compared with its condition between 6500 and 4500 I.A. Data from Inim do not permit analysis of an appropriate kind so there is no test of the regional generality of this condition. Nevertheless, it is tempting to suppose that were there human habitation around Sirunki before 4500 I.A., it was of a kind which did not alter the natural regeneration pattern of the forest sufficiently to influence the pollen fall-out, whereas after that date, however intermittent the actual clearings, impact on the forest resulting from them and from continual exploitation of canopy trees and ephemerals was of a new order of magnitude.

Superimposed on this general degradation of the forest was a second, less dramatic, clearing event beginning about 2000 I.A. and continuing for at least 500 years to the top of the Sirunki diagram. *Acalypha* was not prominent in it, but *Dodonaea* and *Casuarina* were, the amounts of pollen suggesting that both were now growing within the Sirunki catchment. There is evidence of disturbance around Inim at about the same time, including the inhibition of forest regeneration and the development of grassy gaps. This continued until about 500 I.A. when it was intensified, *Casuarina* and *Trema* and open ground indicators becoming very abundant in relation to canopy trees.

In the record from Birip, the contributions of the seral vegetation within the crater and that from the forests beyond are difficult to separate. Clearly, however, open land ephemerals including *Casuarina* and *Acalypha* were present in the area from the beginning of organic accumulation at about 2300 I.A. The great expansion of *Trema*, *Casuarina* and *Dodonaea*, accompanied by smaller rises in *Saurauia* and *Acalypha*, from about 300 I.A. must have been the results of more intensive forest disturbance, probably beyond as well as within the crater.

Although, lacking dated archaeological material from the region, the evidence must be only circumstantial, it seems likely that human interference with the natural forest dynamics in the Sirunki–Inim region began about 4500 I.A. and was accompanied by positive and substantial clearance around Sirunki itself. Although these clearings were not maintained after about 3000 I.A. the forest continued to be used and from about 2000 I.A. clearing was renewed on a smaller scale around both sites. It is likely that the forest around Birip was already degraded by this time and that at both Inim and Birip the most intense clearance began, presumably leading directly to the present balance between forest, regrowth, grassland and garden.

The making of clearings almost certainly implies that human communities were resident in the area concerned, i.e. between 4300 and 3000 I.A. near Sirunki and more or less continuously after 2000 I.A. throughout the region. More generalized degradation of the forest from 4500 I.A. onward did not necessitate settled residence so much as avid exploitation by hunting and gathering parties. Such activities and gardening are often two aspects of one subsistence system so that only changes in location of settlement are necessary to explain their apparent alternation in the pollen record. Sirunki and Inim are now close to the altitudinal limit of continuous human residence which is largely imposed by the intolerance of the staple crop, *Ipomoea batatas*, of colder conditions. The earliest clearance and presumably settlement date for that area is about 4300 I.A., a date within the period of slightly greater ice extent in Irian Jaya and active periglaciation on Mt Wilhelm (Hope & Peterson 1975) and therefore no warmer than, if as warm as, today. *I. batatas* has greater tolerance of cold than any other potential staple, so whatever the staple of the New Guinea Highlands' people before the introduction of *I. batatas* it was something with less cold tolerance (e.g. *Colocasia esculenta*) (Powell 1976). It could be argued therefore, that clearings at 2500 m about 4300 years ago could only have been justified if *I. batatas* had already reached Papua New Guinea almost 4000 years before the commonly accepted date and 3000 before that preferred by Golson (1976). A preferable explanation is probably that native trees, such as *Pandanus*, were at that time sufficiently prolific to sustain settlement together with hunting and the encouragement of other useful plants, such as *Acalypha*, by forest clearing in a subsistence system now lost from Papua New Guinea.

11. Conclusions

The present data, together with those of Hope (1976) and Powell *et al.* (1975), conclusively demonstrate that profound changes in the distribution of major vegetation types have taken place during the past 30000 years. The most striking of these were dominantly upward and downward movements of major vegetation types, but the mechanism of such movements also resulted in reassortment of the taxa within them. An indication of the magnitude of these shifts is given by the probability that the altitudinal forest limit now stands 1500 m higher than it did between 18500 and 16000 I.A. Of the environmental variables which might have prompted such changes, air temperature, of which the mean annual value is the most useful available measure, is the most likely candidate. The indications are that temperatures changed by amounts and at rates which effected major vegetation movements in the Papua New Guinea mountains continuously from 27000 I.A. or earlier until about 9000 I.A. or later.

In their hypothetical reconstruction of climate and vegetation of New Guinea and northern Australia, Nix & Kalma (1972) used a mean air temperature 3.5 °C below present, a precipitation half of the present and an evaporation 0.8 of the present for the time of 'the later stages of sea level lowering and global cooling due to glaciation at high latitudes (approximately 20000 B.P.)'. By 17000 to 14000 B.P. they suggest that temperatures might have risen close to present values at sea level but remained lower at high altitudes; precipitation remained as before but evaporation rose to 1.25 its present values. The maximum glaciation of Papua New Guinea and the greatest depression of its forest limit fall between the first and second of these periods. However valid Nix & Kalma's (1972) estimates of temperature and precipitation might be for what is now northern Australia, the southern fringe of New Guinea and the former land between, they did not apply in the highlands of Papua New Guinea. It has already been argued (p. 334) that rainfall may have been lower than it is at present above 2500 m but not sufficiently so as to affect the distribution of major vegetation types. This suggests that Nix & Kalma's proposed low level is too extreme; their temperature estimates are clearly greatly at variance with those from the evidence of pollen analysis. Yet, given the high temperature lapse rates of the time and the quite different controls on rainfall and evaporation in the lowlands, Nix & Kalma's (1972) position for the southern border of closed rainforest in New Guinea is probably correct. It runs along the foot of the mountains and emphasizes further the extreme spatial restriction of the total rainforest at the time of the last glacial maximum.

Soon after the climate became sufficiently stable to allow the main vegetation types to assume and maintain roughly their present distributions, there began changes in the balance of the component taxa, indicative of structural changes. They started about 4500 years ago in the Sirunki region and continued to the present day. There is little doubt that they were induced by human activity within and peripheral to areas used horticulturally. It is clear that in order to study the dynamics of vegetation unscathed by man, sites will have to be very carefully selected.

Yet, even in such places, the probability of continuous change other than the cyclical replacement of components in an enduring mixture, is now clearly established. The stability of vegetation depends on a great variety of things but mostly on the relationship between the longevity of plants in a 'community' and the rates of change in significant environmental variables such as temperature. In the Sirunki region the greatest stability was reached for no more than three generations of the dominant canopy trees. Moreover, the lowering of the altitudinal forest limit and the constraining of the lowland forest southward (Nix & Kalma 1972) at the height of the last glaciation, must have produced forests of composition or distribution (or both) different from anything witnessed today. Since the stresses which produced this were not finally alleviated until about 6000 years ago, i.e. six to 12 generations of canopy trees before the present, it is very likely that sociological adjustments are still going on throughout the forests of New Guinea.

The indications of world palaeoclimatology now favour the notion of more or less continuous climatic change throughout the Quaternary Period. The longest periods of relative stability were roughly contemporary with 'glacials' whilst 'interglacials' have been but a small part of the total time span of the Quaternary. This being the case, the forests of the glacial maximum in Papua New Guinea were presumably similar to those which lived there for the greater part of Quaternary time. Rather than think of them as temporary and stressed accommodations to a passing climatic perturbation, it is perhaps nearer the truth to see today's vegetation as containing many units with short histories and probably insecure futures. Thus the upper mountain forest occupies ground most of which has probably been unforested for the greater part of the Quaternary Era. Moreover, it is composed of plants which must be able to survive either in small isolated stands or mixed with the components of other forest types for very long periods. The characteristics which endow these plants with the capacity for survival under such circumstances and for periodic excursions into treeless terrain are worthy of investigation. Most Quaternary vegetation history is about such excursions.

Data of the kind presented here further call into question the rigid application of 'climax' theory. It seems likely that, during the Quaternary at least, the climate might never have been sufficiently stable anywhere in the world to allow the establishment and persistence of plant communities in which the only changes are directly associated with their own maintenance. The tendency toward increasing stability with time clearly exists but its achievement falls short of the ideal to varying degrees.

The record of the association of taxa and of the synthesis and breakdown of vegetation types also throws light on the nature of plant communities and the mechanism of migration. Whilst some taxa occur together through a variety of environmental vicissitudes with great fidelity, others with which they are often associated behave with striking independence on longer time scales. This leads to the supposition that a stand of vegetation contains taxa of both types, some less specifically essential to its functioning than others.

Finally, returning to the simple fact of vegetation change itself, it is now abundantly clear that its magnitude in the New Guinean tropics has been as great as at higher latitudes in both hemispheres.

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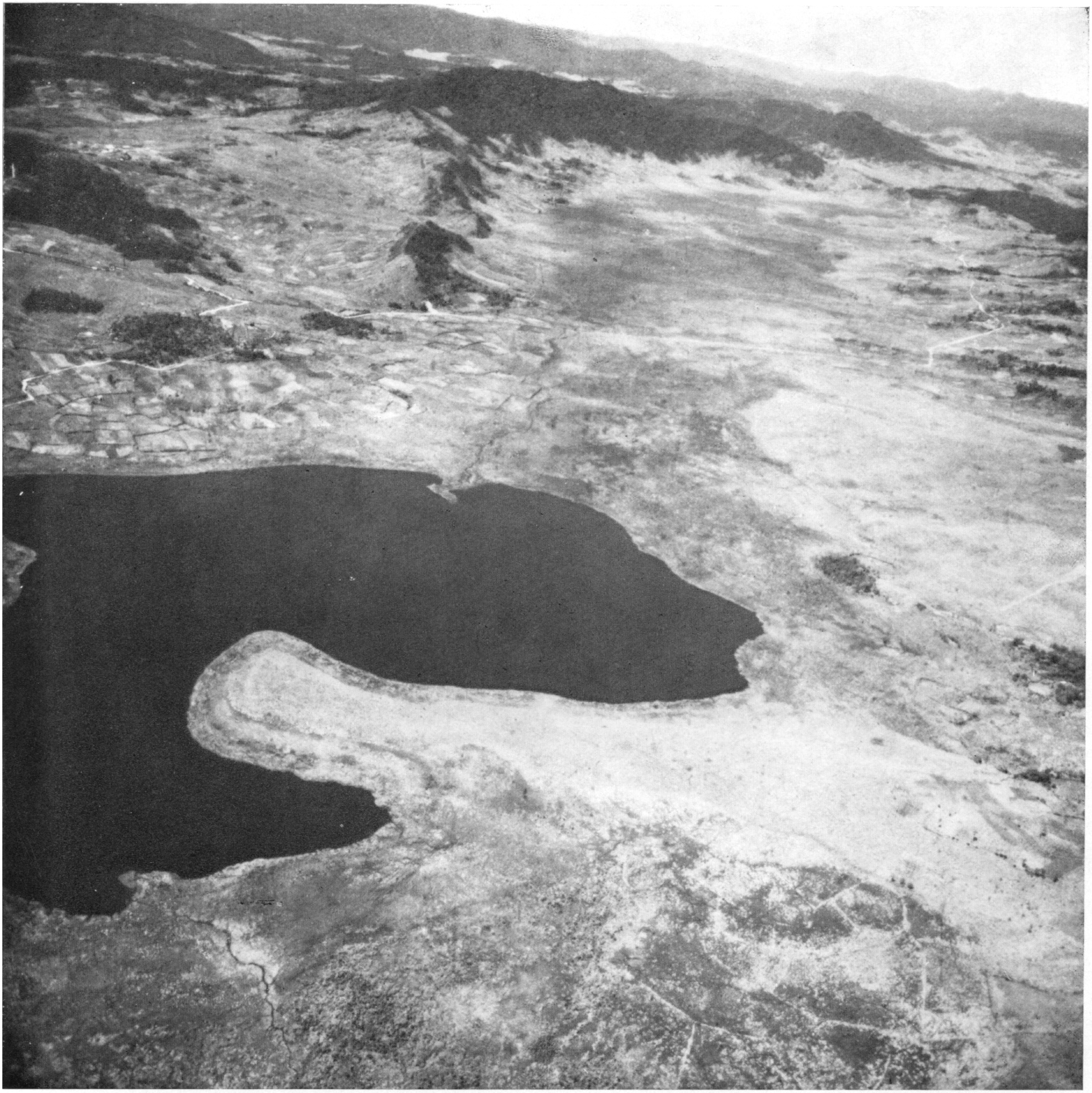
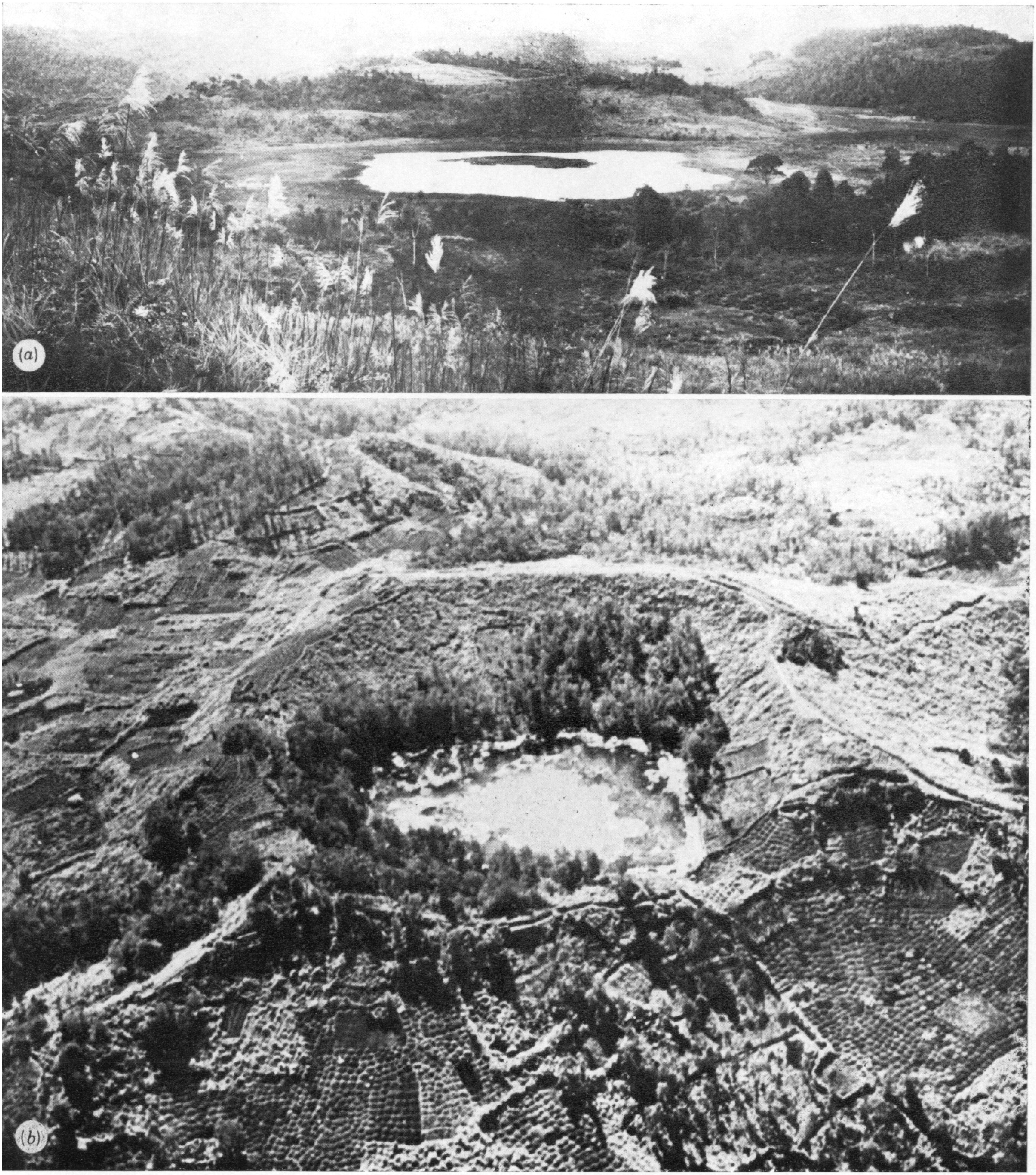


Lake Ipea and the swamp at Sirunki viewed from the northwest.



(*a*) Lake Inim viewed from the southwest. (*b*) The crater lake at Birip viewed from the north.

TABLE 8a. OCCURRENCE OF TAXA RARELY ENCOUNTERED IN POLLEN ANALYSES AT SIRUNKI, OR NOT SHOWN GRAPHICALLY

taxon	group A																group B					group C							group Dg						group Ds							Pteridophytes									
sample level (cm)	*Opocunonia*	*Schefflera*	*Rapanea*	*Meliosma*	*Acronychia*	Flacourtiaceae	Proteaceae	*Pittosporum*	*Elaeocarpus*	*Ilex*	*Planchonella*	*Maesa*	*Sapindus*	*Fagraea*	*Polyosma*	*Symplocos*	*Glochidion*	*Celtis/Aphananthe*	*Mussaenda*	*Coprosma*	*Piper*	*Solanum*	*Psychotria*	*Coleus*	*Osbeckia*	*Melastoma*	Rubiaceae	*Borreria*	*Acaena*	*Rubus*	Compositae: fenestrate	*Vernonia*	*Rumex*	Caryophyllaceae	*Oenanthe*	*Trachymene*	Ericaceae	*Gunnera*	*Drapetes*	Lythraceae	*Lindernia*	*Pteris*	trilete psilate	trilete scabrate	trilete verrucate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	total pollen and spore count
237	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	120	0	13	0	5	743
255	3	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	67	4	0	25	0	11	848
275	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	7	104	3	0	11	4	25	103
292	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	14	6	136	0	0	11	2	7	940
312	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	1	0	2	2	19	454
324	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	3	3	14	451
340	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	3	0	9	127
360	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	8	0	103
376	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	1	34
390	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	15	8	0	17	1	25	689
414	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	29	1	0	18	0	18	743
424	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	6	0	6	0	12	698
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1265	0	0	0	0	0	0	0	0	0	0	[illegible]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	351
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1785	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	1	467
1805	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	66
1825	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	190
1845	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	125
1865	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	4	1	2	0	0	0	519
1885	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	3	193
1905	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	27	1	3	41	1	4	0	4	196
1925	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	2	17	0	1	0	8	342
1945	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	1	0	3	0	2	174
1965	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	323
1985	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	3	8	1	2	0	4	430
2025	0	0	0	0	8	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	3	0	0	3	0	611
2065	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	2	1	0	3	694
2105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	2	0	0	0	4	651
2125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	5	0	0	0	0	303
2145	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	537
2165	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	330
2185	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	114
2195	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	1	0	1	205
2205	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	3	250
2225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	82
2245	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	3	0	0	1	0	0	353
2255	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	2	3	419
2265	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	86
2285	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78
2305	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
2365	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
2385	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	55
2405	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	1	1	2	0	3	130
2425	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	5	0	0	3	0	4	153
2467	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	1	140
2487	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	2	153
2495	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	3	150

Table 8a. Occurrence of taxa rarely encountered in the pollen analyses of the Inim M4 core, or not shown graphically

	group A											group B				group Dg		group Ds							group E					group F								group G	
taxon / sample level (cm)	*Quintinia*	*Pygeum*	*Trema*	*Schefflera*	*Clethra*	*Meliosma*	*Papuacedrus*	*Ilex*	*Rapanea* C3/C4	Rutaceae/Araliaceae/ Clusiaceae	*Drimys*	*Glochidion*	*Omalanthus*	*Engelhardia*	*Gymnostoma*	Compositae C3P3	Compositae fenestrate	Cyperaceae A	Cyperaceae C	Cyperaceae D	*Oenanthe*	Ericaceae	*Polygonum*	Umbelliferae	*Eriocaulon*	*Sparganium*	*Xyris*	*Nymphoides*	*Typha*	*Pteris*	trilete scabrate	trilete verrucate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	Urticaceae/Moraceae	total pollen and spore count
0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	40	0	0	0	1	8	303
20	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	56	0	0	0	0	0	2	0	0	0	0	3	0	0	6	3	7	3	0	2	233
40	0	0	0	1	0	1	0	0	0	0	0	0	5	0	0	0	0	2	30	0	0	0	0	0	0	0	0	0	0	0	0	0	4	5	2	0	1	3	260
80	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	1	18	0	0	0	0	0	0	0	0	0	0	1	0	0	22	3	0	0	1	3	139
135	1	0	0	1	6	1	1	1	0	0	0	0	0	0	0	0	0	2	34	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	1	2	179
580	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	3	1	0	0	0	0	7	5	2	3	240
650	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	6	230
720	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	24	0	0	0	0	0	0	0	11	0	0	0	0	0	1	2	3	2	3	3	237
830	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	11	28	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	0	0	1	164
900	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	0	0	0	0	0	0	0	6	0	1	2	0	0	3	0	3	5	1	2	220
950	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	5	8	0	0	0	0	0	0	0	1	0	1	0	0	0	11	5	2	11	3	6	299
1060	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	0	0	0	0	0	0	0	0	0	1	0	0	0	3	1	1	1	0	4	83
1150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	34	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	1	3	2	109
1185	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	56	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	3	244
1250	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	23	5	0	2	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	6	5	185
1350	0	0	0	6	2	0	0	0	0	0	0	0	0	0	1	1	0	0	28	0	0	0	1	0	0	0	0	0	0	0	0	0	8	1	1	1	1	0	107
1450	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	1	0	0	2	0	1	4	1	4	4	4	306
1550	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	5	4	3	15	408
1660	0	0	0	2	1	0	0	1	0	0	0	0	0	1	0	0	0	3	3	3	0	0	0	0	0	0	0	0	0	0	0	0	2	2	3	2	0	12	380
1771	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	3	33	233
1808	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	3	6	0	1	25	251
1865	0	3	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	11	0	0	0	1	0	0	0	0	0	0	0	0	0	1	3	1	6	0	5	3	462
1880	0	0	0	0	4	29	0	0	0	0	11	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	1	0	2	4	250
1920	0	0	0	1	4	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	2	0	13	9	312
1990	0	0	0	0	1	0	1	0	0	6	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	5	250

Table 8b. Occurrence of taxa rarely encountered in the pollen analyses of the Inim M15 core, or not shown graphically

	group A						group B					group Dg			group Ds									group E				group F							group G	
taxon / sample level (cm)	*Quintinia*	*Sloanea*	Proteaceae	*Rapanea* C3/C4	Rutaceae/Araliaceae/ Clusiaceae	*Drimys*	*Symplocos*	*Phyllocladus*	*Macaranga*	*Engelhardia*	*Gymnostoma*	Compositae C3P3	Compositae fenestrate	*Plantago*	Cyperaceae A	Cyperaceae C	*Galium*	*Haloragis*/*Myriophyllum*	*Gonocarpus*	Ericaceae	*Gunnera*	Umbelliferae	Cruciferae	*Ranunculus*	*Eriocaulon*	*Nymphoides*	*Elyna*	trilete scabrate	trilete verrucate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	Urticaceae/Moraceae	total pollen and spore count
771	1	0	0	0	0	0	0	0	4	0	1	0	0	0	0	2	0	3	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	42	343
821	0	0	0	1	0	0	0	0	10	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	2	0	0	54	353
834	0	1	1	0	0	0	0	0	5	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	1	0	1	45	300
852	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1	0	3	4	0	0	0	0	0	0	0	0	0	0	1	0	28	1	2	5	229
911	0	0	0	0	0	1	0	1	0	0	0	1	0	0	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	1	3	365
920	0	0	0	0	0	1	0	1	0	1	0	2	1	5	13	0	0	1	0	0	0	0	0	1	0	0	0	0	0	5	0	7	3	0	8	341
950	1	0	1	0	0	0	3	0	2	0	1	2	1	0	24	0	0	6	0	0	0	0	0	4	0	0	0	1	0	1	0	0	0	0	6	449
970	0	0	0	0		0	5	0	0	1	0	3	0	1	5	0	0	0	0	2	0	3	0	4	0	0	0	1	0	0	0	0	0	0	4	316
985	0	0	0	0	0	0	0	0	0	0	0	8	0	0	1	0	0	0	0	0	0	2	0	6	0	0	0	0	0	1	0	0	0	1	8	528
1015	0	0	0	0	0	0	0	0	1	0	0	3	0	0	25	0	1	2	0	0	0	4	0	5	0	0	0	0	0	0	0	1	0	2	1	627
1045	0	0	0	0	0	1	0	0	0	0	0	2	1	0	50	0	0	0	0	3	0	0	1	5	0	0	0	0	0	0	0	2	0	0	6	547
1065	0	0	0	0	0	0	0	0	0	0	0	2	0	0	7	4	0	0	1	0	0	0	0	4	1	0	0	0	0	2	0	6	0	0	3	230
1075	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	3	0	0	0	0	0	0	1	0	1	0	8	168
1085	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	7	0	3	0	1	0	2	0	0	0	0	0	1	0	0	1	480
1095	0	0	0	0	0	0	0	0	0	0	0	3	0	3	5	1	0	0	0	0	6	0	0	1	0	0	0	0	0	1	0	0	0	0	2	113
1115	0	0	0	0	0	0	1	0	0	0	0	4	1	0	0	0	0	0	0	4	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	342
1125	0	0	0	0	0	0	0	0	1	0	0	1	0	0	3	0	0	0	0	7	0	3	0	2	0	0	0	0	0	2	0	0	0	2	4	478
1135	0	0	0	0	0	0	0	0	4	0	0	7	0	0	1	0	0	0	3	6	0	5	0	3	0	0	0	0	0	0	0	0	0	1	5	477
1145	0	0	0	0	0	0	0	0	1	0	0	3	1	0	33	0	0	0	0	0	0	6	0	4	0	0	0	1	0	2	0	0	0	1	3	339

Table 8c. Occurrence of taxa rarely encountered in the pollen analysis at Birip, or not shown graphically

	group A									group B				group Dg	group Ds		group E						group F						group G		
taxon / sample level (cm)	*Ascarina*	*Quintinia*	*Olearia*	Myrtaceae	*Sloanea*	*Clethra*	Proteaceae	*Rapanea* C3/C4	*Drimys*	*Glochidion*	*Omalanthus*	*Macaranga*	*Engelhardia*	Compositae C3P3	Cyperaceae A	Cyperaceae C	*Eriocaulon*	*Xyris*	*Limnophila*	*Sparganium*	*Typha*	*Elyna*	trilete scabrate	trilete other	monolete other	monolete psilate	monolete scabrate	monolete verrucate	*Acalypha*	Urticaceae/Moraceae	total pollen and spore count
0	1	0	0	0	0	1	0	0	0	0	2	0	0	0	102	0	0	0	12	13	0	0	0	0	6	0	0	1	0	40	534
15	0	0	0	0	0	2	0	0	0	0	0	3	0	1	311	0	1	1	0	11	0	0	0	0	5	1	2	2	3	42	583
40	0	0	0	1	0	0	0	0	0	0	0	5	0	1	168	0	0	0	0	13	0	0	0	2	3	1	2	0	0	47	644
55	3	0	0	0	0	0	0	0	0	1	1	3	0	0	233	0	0	0	0	67	0	1	0	3	2	2	0	3	0	47	837
70	3	0	1	1	0	0	0	1	0	0	0	3	0	0	186	0	0	0	0	15	1	0	1	2	0	0	0	3	0	79	727
85	3	0	0	3	6	0	1	0	0	0	6	19	0	0	56	1	0	0	0	1	0	1	0	1	1	0	0	1	0	126	654
117	0	2	1	0	0	0	0	0	0	0	0	0	0	0	86	6	0	4	0	0	0	0	0	0	0	1	0	2	0	53	283
150	0	1	0	1	0	0	0	0	0	0	0	0	1	0	210	0	0	2	0	0	0	0	2	8	2	0	0	0	6	90	609
153	0	1	0	1	0	0	0	0	0	0	0	2	0	0	60	0	0	0	0	0	0	0	0	3	1	1	6	2	1	87	376
218	0	0	1	0	2	0	0	0	0	0	1	3	0	0	67	0	0	0	0	0	5	0	0	6	8	2	0	3	0	43	538
238	0	0	1	0	0	0	0	0	0	0	0	4	1	0	254	0	0	0	0	0	0	0	0	0	1	1	0	3	0	39	462
258	1	0	0	2	0	0	0	0	0	0	0	0	0	0	106	0	0	0	0	0	0	0	0	2	0	8	0	1	0	13	526
280	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	3	0	0	1	96
325	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	1	0	1	104
375	0	0	0	1	0	1	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	1	0	3	0	0	0	2	80

TABLE 9. OCCURRENCE OF POLLEN ANALYSIS TAXA IN LIVING VEGETATION TYPES

	taxa in pollen diagrams																																																									
	closely associated within group															generally associated in period of occurrence within group																					individualistic															insignificant quantities							
Living Vegetation Genera	Ascarina	Macaranga	Nothofagus	Podocarpus	Castanopsis	Phyllocladus	Claoxylon	Ilex	Rubiaceae (CIC4)	Sloanea	Gra. C	Gra. E	Gra. G	Gra. I	Gra. H	Dacrycarpus	Myrtaceae	Dodonaea	Engelhardia	Trema	Acalypha	Casuarina	Coprosma	Saurauia	Glochidion	Omalanthus	Compositae (Lactucae)	Polygonum	Cyp. A	Cyp. C	Galium	Astelia	Gentiana	Potentilla	Styphelia	Ranunculus	Buddleia	Cyathea	Elaeocarpaceae	Quintinia	R.U.A.R.	Compositae (CBPs)	Cyp. B2	Cyp. D	Cyp. Z	Epilobium	Gra. B	Gra. D	Haloragis	Hydrocotyle	Plantago	Umbelliferae	Evodiella	Opocunonia	Proteaceae	Pygeum	Rapanea	Schefflera	Drapetes
forest: partial floristic groups according to Walker & Guppy (1976)																																																											
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Harmsiopanax	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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† Genera occurring more than once among vegetation types.

TABLE 11. DERIVATION OF POSSIBLE MEAN ANNUAL TEMPERATURES FROM SIRUNKI POLLEN ANALYSIS DATA

period years B.P.	vegetation of catchment	stratigraphy	lowest estimate of mean annual temp.		highest estimate of mean annual temp.		range of estimates of mean annual temp. °C		most probable range of estimates of mean annual temp. °C		range of estimates in relation to present mean annual temp. at 2500 m (14 °C), °C		most probable range of estimates in relation to present mean annual temp. at 2500 m (14 °C), °C	
			criteria	temp. °C	criteria	temp. °C	min.	max.	min.	max.	min.	max.	min.	max.
1500–5000	lower mountain forest with periodic clearings after 4300 B.P.	detritus mud	*Dacrycarpus* commoner; changing significance of forest ephemerals	10	*Acalypha* in clearing beginning 4300 B.P.	15	10	15	12	14	−4	+1	−2	0
5000–6500	lower mountain forest	detritus mud, nekron and diatomite	*Trema* and *Phyllocladus* absent; *Casuarina* pollen not reaching catchment	11	*Dacrycarpus* uncommon	15	11	15	13	15	−3	+1	−1	+1
6500–8000	lower mountain forest comparatively rich in *Nothofagus*	detritus mud, nekron and diatomite with clay layers	*Nothofagus* commoner than before; *Dacrycarpus* common	11	*Trema* and *Phyllocladus* present; *Casuarina* and *Glochidion* pollen reaching catchment	14	11	14	12	14	−3	0	−2	0
8000–9000	lower mountain forest components	detritus muds, nekron and diatomite with clay layers	*Trema* and *Phyllocladus* excluded; *Dacrycarpus* and *Quintinia* sometimes high	11	*Astelia* absent, *Castanopsis* present	13	11	13	12	13	−3	−1	−2	−1
9000–13000	forest tree growth erratic amongst grasslands, *Cyathea* 'woodlands' and frost-hollow vegetation	fine detritus mud and diatomite	temperature excluding lower mountain forest trees from time to time; *Astelia* fitfully present	oscillating 10–12	vegetation not climatically significant	13	10	13	10	13	−4	−1	−4	−1
13000–13500	lower mountain forest, *Nothofagus* predominating	re-deposited organic and inorganic matter including volcanic ash; rise in water level	*Castanopsis*, *Trema* etc. still not in catchment although lower mountain forest probably also absent	12	changes not climatically significant	13	12	13	12	13	−2	−1	−2	−1
13500–14000	lower mountain forest with upper mountain forest above and some frost-hollow vegetation	culmination of overgrowth around margins, secondary penetration of older deposits by reedswamp roots; fine detritus mud and diatomite at centre of basin	*Castanopsis*, *Trema*, *Macaranga* still not in catchment, much of which still occupied by lower mountain forest including *Dacrycarpus*	11	all lower mountain forest components in catchment; upper mountain forest plants on surrounding hills or frost-hollows	13	11	13	12	13	−3	−1	−2	−1
14000–15000	patchy subalpine grasslands and upper mountain forest	coarse detritus mud at margins, fine detritus mud and diatomite in centre of basin	*Pygeum* and [illegible] only precariously established in catchment amongst subalpine grassland	7	Myrtaceae, *Pygeum* and [illegible] imply closed upper mountain forest amongst which are patches of open ground producing the low *Astelia* values; trace of *Trema* pollen suggests lower mountain forest close to catchment; overgrowth of lakes active with grassland components changing	10	7	10	8	10	−7	−4	−6	−4
15000–16000	predominantly unforested but some subalpine shrubs enter catchment	fine detritus and nekron muds and diatomite	*Rapanea* erratic, possibly far travelled; *Astelia* low	4	beginning of changes in lower mountain forest components outside catchment	7	4	7	4	6	−10	−7	−10	−8
16000–18500	unforested, alpine grassland and herbfield	fine detritus mud and diatomite with rare clay	absence of *Rapanea*, *Cyathea* and very low total pollen recovery; absence of *Astelia*	2	lack of positive tundra indicators; grasses predominant	6	2	6	3	5	−12	−8	−11	−9
18500–21000	predominantly unforested but some subalpine shrubs and rarely trees	fine detritus mud and diatomite with rare clay	*Rapanea* and *Cyathea* in quantities implying some distance from swamp; *Astelia* in moderate quantity	4	*Ascarina* probably and *Nothofagus* possibly, but both rarely, in catchment	11	4	11	5	10	−10	−3	−9	−4
21000–24000	predominantly unforested but some trees occasionally	fine detritus mud and diatomite becoming progressively inorganic particularly at margins	*Rapanea* and *Quintinia* at lowest temperature tolerance when present and sometimes absent	4–6	*Sloanea*, *Nothofagus*, *Castanopsis* occasionally in catchment	13	4	13	7	13	−10	−1	−7	−1
24000–26500	alpine and subalpine herbfield, grassland and a few shrubs	fine detritus and nekron muds	*Astelia* at lowest temperature tolerance; alpine grasslands dominant; *Rapanea* distant	3	*Rapanea* and *Acronychia* in catchment, *Astelia* in middle of range	9	3	9	5	9	−11	−5	−9	−5
26500–27500	upper and lower mountain forest elements and subalpine swamps	fine detritus and nekron muds	*Rapanea* in forest-limit abundance; *Astelia* common	6–12	*Castanopsis*, *Sloanea*, *Nothofagus* in catchment	> 13	6	> 13	10	14	−8	> −1	−4	0
27500–33000	barren to poor sedge swamps and possibly some *Cyathea*	fine detritus and nekron muds	apparent lack of vegetation	1	*Cyathea* spores and organic mud	4	1	4	vegetation possibly under non-climatic control		−13	−10	?	?

Corrections for Table 9. tall grassland once among