# EVIDENCE FOR CHANGES IN HOLOCENE VEGETATION AND LAKE SEDIMENTATION IN THE MARKHAM VALLEY, PAPUA NEW GUINEA

by

SAMUEL EDWARD GARRETT-JONES

Thesis submitted for the degree
of Doctor of Philosophy at the
Australian National University

Canberra October 1979

# DECLARATION

Except where otherwise acknowledged in the text, this thesis represents the original research of the author.

S. E. Garrett-Jones

*FRONTISPIECE.* Lake Wanum, Morobe Province, Papua New Guinea.

Oblique aerial view from the north-west, 8 October 1974.

# CONTENTS

# ABSTRACT

The past stability of vegetation patterns in the Markham Valley (6°30'S, 146°30'E), a lowland grassland area of Papua New Guinea, is investigated by pollen analysis of lake deposits and related palaeoecological techniques.

The predominantly organic sediments of Lake Wanum (alt. 35 m) span the last 9600 years. A $^{14}C$ chronology supports the calculation of annual pollen deposition, sediment accumulation, and carbonised particle influx rates. At Yanamugi lake (alt. 170 m), $^{14}C$ assays of the calcareous muds are influenced by variable 'hard-water error'. A tentative chronology is based on palaeomagnetic and tephra correlations.

Pollen trapping reveals very high contemporary annual deposition rates within forest, but low values over the central lake area. Surface pollen assemblages from different habitats indicate the localised nature of pollen dispersal, although a relatively 'long-distance component' from higher altitudes is also recognised.

Analysis of floristic data from the herbaceous swamp vegetation of Lake Wanum suggests the existence of two free floating root-mat associations and two or three rooted associations. Water depth appears the primary control on their distribution.

Holocene swamp communities analogous with extant associations may be identified in the palynological record of Lake Wanum. Swamp marginal conditions prevail from 9500 BP until 8200 BP when permanent shallow water becomes established. Rooted vegetation associations then predominate until about 5000 BP. Floating vegetation associations first become important at this time, and

subsequently (3000 BP to 2000 BP) come to dominate the site. A general trend towards increased water depth is indicated throughout the sequence.

Increased representation of dry-land non-forest pollen occurs from 8550 BP, and grassland taxa become more frequent from about 5350 BP. Synchronous trends in carbonised particle influx identify fire as a probable agent of vegetation change.

Little change in dry-land vegetation is recorded in the pollen sequence from Yanamugi, although recent encroachment by swamp vegetation occurs. The large proportion of 'montane' pollen and spore taxa in the earlier sediments is attributed to variable fluvial influx.

Conditions at Lake Wanum until 8200 BP may reflect the early Holocene aridity widespread in equatorial areas, although the indirect hydrologic effects of rising sea level cannot be discounted. Human impact appears the main determinant of dry-land vegetation change during much of the Holocene.

# LIST OF FIGURES

# LIST OF FIGURES

# LIST OF FIGURES

# LIST OF TABLES

# LIST OF TABLES

# LIST OF PLATES

# ACKNOWLEDGEMENTS

Papua New Guinea and Australia were equally unknown territories to me before I undertook this project. I am ever indebted to those in both countries who provided me the opportunity to share both their present and their past.

Professor Donald Walker, my supervisor, guided me towards, and through, this study. I thank him for his continued interest, patience, and championship of the cause of pellucidity over obfuscation.

I am grateful for the cooperation of numerous Papua New Guinea Government institutions and individuals. The Division of Botany, Lae, provided considerable logistic and floristic support under successive Assistant Directors, Mr J.S. Womersley, Mr Ted Henty (Acting Assistant Director, 1976) and Mr Michael Galore. Assistance was also received from the Dept of Forests, Lae, Joe Glucksman of the Fisheries Research Division, Dept of Agriculture, Stock and Fisheries, Konedobu, and the D.A.S.F. Land Utilisation Division, Boroko. Bob Johns, P.N.G. Forestry College, Bulolo, kindly allowed me access to his unpublished data. I profited from discussions with the various members of the University of Papua New Guinea, Port Moresby, and the University of Technology, Lae.

Fieldwork would have been impossible without the help and hospitality of many Papua New Guineans. Gamman and his *wantoks* from Gabensis provided labour at Lake Wanum. At Yanamugi, Nafwan and the other Yatsing villagers were kind hosts and willing helpers. Jim Croft and Neal Enright also assisted in 'mini-Mackereth' coring during 1976.

I thank the assembled members of the Dept of Biogeography and Geomorphology, almost all of whom have helped or advised. In particular, Daphne Moss and Joan Guppy for assistance with pollen identification, Alan McDonell for getting equipment from A to B faster than possible, Neal Enright for running the vegetation analysis programs, and Dr Geoff Hope for his infectious enthusiasm about all things New Guinean. Dr Ian Raine explained his computer programs to me, whilst Dr Peter Kershaw (Monash University) and Dr John Flenley could always be relied on for thought provoking ideas.

Elsewhere at A.N.U., the facilities of the Research School of Earth Sciences were used for palaeomagnetism analysis. Charles Barton assisted considerably, and provided the computer programs to plot Figs. 4.7 and 4.8. All radiocarbon samples were assayed by the A.N.U. Radiocarbon Laboratory. Much time was spent by Yvonne Pittelkow, Joint Schools' Computer Services, in bridging the chasm of the 'man/machine interface'.

Plant collections were identified by Mr R. Pullen and Dr L. Craven the Herbarium Australiense, Commonwealth Scientific and Industrial Research Organisation. Dr Russell Blong, Macquarie University, tracked down the tephras. The whole thing was painstakingly typed by Lesley Kendall, and Joan Guppy finally 'got it all together'.

The study was financed by the Australian National University while I was in receipt of a Commonwealth Scholarship and Fellowship Plan scholarship from the Australian Government.

To everyone who has eased this thesis, in any way at all, towards its ultimate destination,

*Tenkyu tumas!*

# CHAPTER 1

# INTRODUCTION

In the past quarter century or so the biogeographers' and ecologists' view of tropical vegetation has undergone considerable transformation. The geologically recent effects of continental drift and the demonstrable influence of Quaternary climatic change and man's activities in tropical regions are now fully accepted. As a consequence, the tropical rainforest can no longer be regarded as a tenuous relic of Tertiary age, subject to disturbance only within historic times, as Richards (1952) postulates:

> 'after existing thus for millions of years, the rain forest ecosystem has very recently - in most of its area only within the last 100 years or so - been rudely disturbed by the spread of western civilization to the tropics... Thus within a very short space of time the primaeval forest communities have been replaced over immense areas by cultivation, ruderal communities and seral stages. Till this change took place the Tropical Rain forest was in a stage of development not unlike the forests of Europe in the Mesolithic period, when habitation was limited to the forest fringes and restricted sites accessible by river. The subsequent destruction of the forest all over the tropics is comparable with the clearing of the European forest by agricultural peoples beginning in the Neolithic period, except that the one process has been accomplished in a few decades, while the other lasted for thousands of years.'

Raven and Axelrod (1972) review the biogeography of Australasia in the light of plate tectonics. The New Guinea highland flora consists predominantly of the more temperate Gondwanic elements, whilst the lowland vegetation is largely of Malesian origin. As a result of the juxtaposition of these diverse groups Raven and Axelrod (1972) suggest that New Guinea 'as a whole is a region of faunal and floral mixing, survival and evolution in the middle to late Tertiary.' These processes presumably continued into the Quaternary, the potential for interaction being modified by climatic fluctuation (Walker, 1972*b*).

The Quaternary era is one of dramatic and widespread climatic change. The effects of the glacial periods, particularly the most recent, have been shown from temperate and from tropical highland regions. It is now becoming clear that, at least in some areas, climatic changes associated with global glaciation had a profound effect on the tropical lowland environment and vegetation also.

The vegetation history of the African tropics is better known than any other tropical area. In particular, it is apparent that the extent of evergreen forest in East Africa was severely restricted during the last glacial (Livingstone, 1975). The region is relatively arid today, and its flora depauperate by comparison with the rest of the equatorial tropics. Richards (1973) attributes the relative lack of floral diversity to the more pronounced effects of climatic change and the longer history of human interference over the African continent.

In contrast to this view, the meagre data that are accumulating suggest climatic fluctuations of at least similar magnitude to have occurred in other tropical areas. Vegetation response to glacial age refrigeration is documented from South America (van der Hammen, 1974) and New Guinea (Bowler *et al.*, 1976, Powell and Hope, 1976).

In common with other tropical areas, the first conclusive evidence of Quaternary climatic change in New Guinea came with the identification of prior glacial landforms. Such features, reviewed by Löffler (1977), occur in both Papua New Guinea and Irian Jaya

(West Irian) on mountains exceeding the Pleistocene snow-line of approximately 3 550 m, almost 1 000 m below that of the present. The most extensive ice cover, perhaps extending as low as 3 200 m, was on Mt. Giluwe in the southern highlands. In the Saruwaged Ranges the snow-line appears slightly higher at 3 650 m to 3 700 m, possibly an artefact of tectonic uplift since the glaciation. A similarly higher snow-line existed in the still ice-capped Carstensz Mountains of Irian Jaya (Hope and Peterson, 1976) perhaps due to relatively lower Pleistocene precipitation in the west of the island.

The severe climatic conditions indicated by the lower snow-line are reflected by changes in the highland vegetation (Bowler *et al.*, 1976). The presence of upper-montane species at only 1 500 m over 30 000 years ago (Powell and Hope, 1976) and 2 550 m at 12 000 BP (Flenley, 1972) implies altitudinal depression of vegetation 'zones' by 500 m to 1 500 m. On Mt. Wilhelm (Hope, 1976*a*) vegetation depression at 2 740 m was at least 700 m until around 10 500 BP, whilst the tree-line was 1 200 m lower than today.

One can only speculate on the ecological effects of these migrations on the montane and lower altitude vegetation. It is likely that, rather than a simple shift in the altitudinal ranges of currently extant vegetation associations, there was considerable individualistic behaviour by plant species. This phenomenon is documented from other areas, both temperate and tropical, e.g. the response of *Podocarpus* on Ruwenzori to changing climatic conditions cited by Livingstone (1975). Extrapolation of the maximum vegetation zonal depression into areas below 1 500 m is untenable, as this would practically eliminate lowland forest and replace it with vegetation of montane affinity. Alternatively, considerable compression of the altitudinal range of mid-montane vegetation must be postulated were the vegetation changes in the highlands to have had no influence in the lowlands.

It is clear that both these hypotheses are too simplistic given the extreme variation in present vegetational patterns in relation to altitude, and the individualistic response of many plants. Whilst the probable effects of the demonstrated depression of higher altitude vegetation on the lowlands undoubtedly lies somewhere along this spectrum, the two extremes, i.e. no influence on lowland vegetation, or complete replacement, can probably be ruled out.

Within the more recent past, human impact on tropical vegetation is now well demonstrated. Diminishing forest cover during the past few millennia is attributed to man's activity both in East Africa (Kendall, 1969) and Central and South America (Bartlett and Barghoorn, 1973, van der Hammen, 1974). In the New Guinea highlands, archaeological evidence indicates complex agriculture perhaps 9000 years ago (Golson, 1977*b*), and forest clearance was widespread by 5000 BP (Powell *et al.*, 1975).

There is thus considerable circumstantial evidence to suggest that the vegetation of the lowland tropics has been exposed to, and may have responded to, changing environmental conditions on time-scales of millions, tens of thousands, and thousands of years. This realisation calls into question the concept of unchanging tropical lowland vegetation. In particular, the prodigious floristic diversity of the tropical rainforest can no longer be attributed to its ancient integrity.

This study attempts to identify and quantify change in the vegetation of a lowland area of Papua New Guinea over the more recent (late Quaternary) extent of this time-scale, and considers the possible determinants of any change.

## *POLLEN ANALYSIS IN THE TROPICAL LOWLANDS*

Although palynology is an established method for reconstructing Quaternary vegetation history in many temperate regions, and has been applied successfully in highland tropical areas, it is almost untested in the lowlands of the equatorial tropics. By contrast with the vegetation of temperate and, to a lesser extent, tropical highland regions, the many species of the low altitude equatorial tropics are supposedly characterised by low pollen production, and entomophilous or zoophilous pollination habit. Faegri (1966) states the pessimistic view that 'pollen analysis is simply not a method for investigating those (tropical forest) vegetational types, unless indirect conclusion can be arrived at from the presence or absence of indicators that do contribute to the pollen rain'.

The floristic diversity of the New Guinea vegetation equals that of other equatorial areas (van Balgooy, 1976), and this vast array of species poses formidable problems for pollen analysis. In addition to the task of identification of sub-fossil grains the large number of taxa involved increases the difficulty of achieving statistically reliable estimates for the values of each taxon. On the other hand, it may be more likely that 'indicator' taxa will be present.

A more fundamental problem remains the characterisation of the vegetation solely on the basis of floristic data. Pollen analytical evidence reveals, at best, only the partial floristic composition of the plant community. Ideally, a reconstruction of the past vegetation may be derived from these data by interpolation from extant communities. Yet, in the tropics, floristic classification of vegetation associations is often not feasible. In Papua New Guinea, recognition of major vegetation formations using the criteria of land-units and physiognomy (e.g. Paijmans, 1975) or physiognomy alone (Webb *et al.*, 1976) may produce more tractable results. As Walker and Guppy (1976) have shown, subjective classifications frequently do not reflect floristic changes. Analyses of lists of tree genera from 78 sites above 1 900 m revealed only one major floristic break, at 2 800 m to 3 000 m. Although altitudinal zonation below this was unsubstantiated by the floristic data, two 'nodes' of generic similarity were recognised: the genus-rich forest of environmentally stable areas, and depauperate derivatives from it.

In view of the paucity of basic ecological and palynological data it seems appropriate that initial palaeoecological research in the lowland equatorial tropics should focus on major changes in the most immediately recognisable vegetation formations. In Papua New Guinea the most striking boundaries in lowland vegetation exist between the forest, and non-forest grassland, 'woodland', or 'savanna' communities.

## *THE ORIGIN OF NEW GUINEA GRASSLANDS*

It is widely argued that, except for swamp and perhaps alpine areas, the present distribution of grasslands in New Guinea is a product of forest clearance and/or burning by man. Lane-Poole (1925), on surveying the forest of the lower Markham Valley near Yalu, hypothesised that

> 'At one time forest of this type stretched all the way along the coast between the mountains inland and the sea, and all along the vast valleys of the Markham and

> Ramu Rivers. Today, artificially formed grasslands have taken the place of the forest on the best of the land, and, in the less fertile areas, a secondary weed growth has established itself.'

Robbins (1963*a*) considers that 'tall' grassland gives way to 'short' grassland under the pressure of continued human interference. Although admitting that the most extensive grassland areas exist under conditions of low, seasonal rainfall and poor soils, he regards environmental factors as secondary to the history of human impact. Robbins sees the pattern of grassland in the Papua New Guinea highlands as reflecting the increasing antiquity of cultivation from west to east. This proposition is amplified (Robbins, 1963*b*) by interpreting the Markham Valley grasslands as lying in the wake of a route of population migration from the coast to the highland interior. 'Only thus', states Robbins, 'can the now largely abandoned Upper Markham grasslands be readily explained.' A similar contention is advanced to account for the extensive grasslands of the Sepik Plains the origin of which Reiner and Robbins (1964) correlate with population movements dated at 500 to 800 years ago by linguistic evidence.

Closer study reveals environmental factors to be of greater importance in the determination of vegetation patterns than Robbins (1963*a,b*) and Reiner and Robbins (1964) consider. Brookfield (1964) emphasises the climatic variation in the highlands in relation to grassland distribution. The Sepik grasslands have been studied by Haantgens *et al.* (1965) who demonstrate considerable edaphic influence on the vegetation. Although agreeing that the grassland is a fire-climax community, these authors regard environmental factors as at least as important in determining the character of the vegetation. Paijmans (1976) suggests that grasslands such as those of the Sepik developed from smaller grassland loci due to the use of fire, particularly in areas of poor soils and seasonal rainfall where the forest was in a precarious balance with the environment.

The survey by Holloway *et al.* (1973) reveals close relationship between the composition of the non-forest vegetation and edaphic and other environmental gradients within the Markham Valley. Eden (1974) finds a general reduction in the extent of grassland and savanna communities in southern Papua with increasing humidity. However the juxtaposition of vegetation types within similar habitats is not entirely explicable by patterns of rainfall, potential evapotranspiration, or the soil moisture availability. Eden (1974) calculates that, at rates of clearance observed today, man's cultivation activities could account for the formation of the whole grassland area within the last 2000 years. However, it is recognised that over a longer period, climatically induced vegetation changes may be of importance.

It is clear, therefore, that sole correlation between the floristic composition of non-forest vegetation and the intensity of human activity is invalid, although this concept continues to surface in the literature (e.g. Seavoy, 1975). Such a correlation can be substantiated only if the effects of all environmental variables are first accounted for. However, the character of many grassland areas is clearly maintained under present day climatic conditions by man's activity, particularly in the use of fire. The contemporary distribution of grassland provides strong circumstantial evidence that man has created, extended, or modified much of the grassland of lowland Papua New Guinea, particularly that in environmentally stressed habitats. However, extrapolation of past vegetation patterns on the basis of present distribution is at best imprecise. Palaeoecological techniques provide the most appropriate, if not the only, means to reveal the history of the vegetation and its environmental determinants.

## *AIMS OF THIS STUDY*

Three basic questions may be posed in relation to the vegetation of lowland Papua New Guinea that might be amenable to solution by palaeoecological research:

(1) Have the present patterns of lowland vegetation, particularly those of the forest and grassland associations, remained stable in the past? If not, what has been the direction and magnitude of any change?

(2) Has Quaternary environmental change, especially the climatic fluctuations demonstrable from many temperate and tropical areas, had any effect on the lowland tropical vegetation?

(3) What is man's role in influencing the vegetation and its current distribution patterns?

This study explores the extent to which palaeoecological methods can answer these problems, and, by corollary, the constraints on the use of such evidence. The central techniques employed are stratigraphic and pollen analysis of lacustrine sediments. Suitable deposits of late Quaternary age are thus required. A robust, independent chronology is essential to allow the reconstruction of the sedimentary history of the site and to provide for the use of time-area based palynological techniques. In a previously unstudied area it is particularly important to distinguish between site-specific events, and those of more widespread significance. Interpretation of stratigraphic and pollen analytical evidence of local habitats is greatly facilitated by an understanding of swamp vegetation ecology. A knowledge of the fundamental aspects of contemporary pollen dispersal is also considered essential in view of the almost total lack of knowledge about such processes in the tropical lowlands. Each of these topics is covered to some extent in this thesis. Emphasis is placed, however, on the application and interpretation of pollen analytical and stratigraphic methods in the palaeoecologically unknown environment of lowland Papua New Guinea.

## *CHOICE OF STUDY AREA*

The vegetation map of Papua New Guinea (Paijmans, 1975) shows many of the more densely inhabited lowland areas to be covered by a mosaic of forest and non-forest vegetation types. However, four major regions may be identified where non-forest vegetation predominates.

Large areas of south-west Papua New Guinea are covered by *Melaleuca* dominated savanna. Extensive areas of grassland with scattered trees of several *Eucalyptus* species occur along the coast of the Central Province, in the region of Port Moresby. These vegetation types are clearly of Australian origin, and are almost restricted in New Guinea to monsoonal areas south of the main dividing range. Their past distribution was probably substantially influenced by the considerable Pleistocene extension of land over the shallow Torres Strait shelf. For these reasons, the development of the vegetation in these savanna areas, whilst of great interest especially in relation to late Quaternary events in tropical Australia (Kershaw, 1975), is unlikely to be representative of lowland New Guinea as a whole.

The Sepik area of north-western Papua New Guinea contains large tracts of grassland. However, many of these are alluvial swamp areas and affected by changing river courses. Sites possessing deposits of suitable antiquity and continuity for palaeoecological research may well exist, but would be hard to locate.

A fourth area, the Markham Valley, has a smaller but well defined area of grassland and other non-forest vegetation. Due to the high relief and sharp environmental gradients, various forest types are also found in close juxtaposition. As with much of the northern coast of New Guinea, the land configuration was little changed during the glacial sea level minimum due to the steep off-shore shelf. The foothills along the margins of the valley contain a number of permanent lakes and swamps of potential antiquity.

Thus, whilst recognising the scientific interest of other lowland areas, this study is devoted to the palaeoecological investigation of sites within the environs of the Markham Valley, Morobe Province, Papua New Guinea.

# CHAPTER 2

# THE MARKHAM VALLEY

The Markham trough forms the eastern extension of one of the major physiographic and tectonic lineaments of Papua New Guinea. The depression follows a fault zone running approximately 300 km along the lower Ramu and Markham valleys, and extends eastward as a submarine canyon to join the 6 000 m deep New Britain trench (von der Borch, 1972).

The Markham Valley (Fig. 2.1) is bounded to the north by the Finisterre and Saruwaged Ranges that rise steeply to an altitude of over 4 000 m. To the south are the Kratke Ranges and Herzog Mountains, northern extensions of the Owen Stanley Ranges that form the backbone of the country. About 3 km wide at the Ramu divide, 360 m above sea level, the Markham Valley reaches a maximum width of 22 km at the confluence of the Leron River. The Markham River and its tributaries drain a catchment of about 12 000 km$^2$ (Löffler, 1977). Leaving the northern mountains at an altitude of *c*. 450 m, the river follows a relatively steep plain course along the southern margin of the valley. The anastomosing channel discharges into the Huon Gulf at Lae, 140 km to the south-east.

## *GEOLOGY AND GEOMORPHOLOGY*

The main features of the geology of the Markham Valley and its environs are shown in Fig. 2.2. This map and the following account are based largely on the work of Tingey and Grainger (1976), Robinson (1974), Robinson *et al*. (1974) and Jacobson (1971). Additional geomorphological data for the area may be found in Holloway *et al*. (1973) and Löffler (1977).

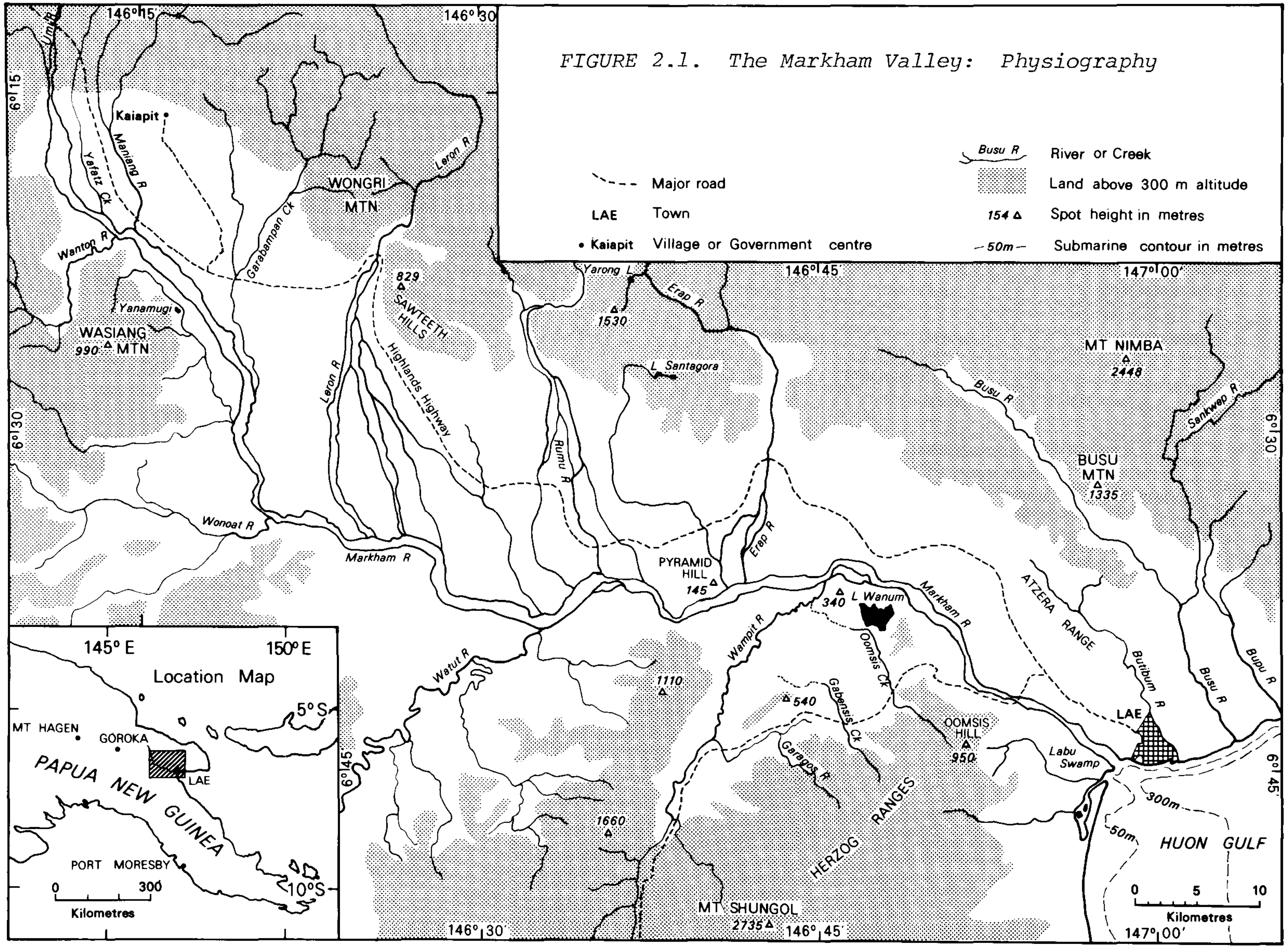


FIGURE 2.1. The Markham Valley: Physiography

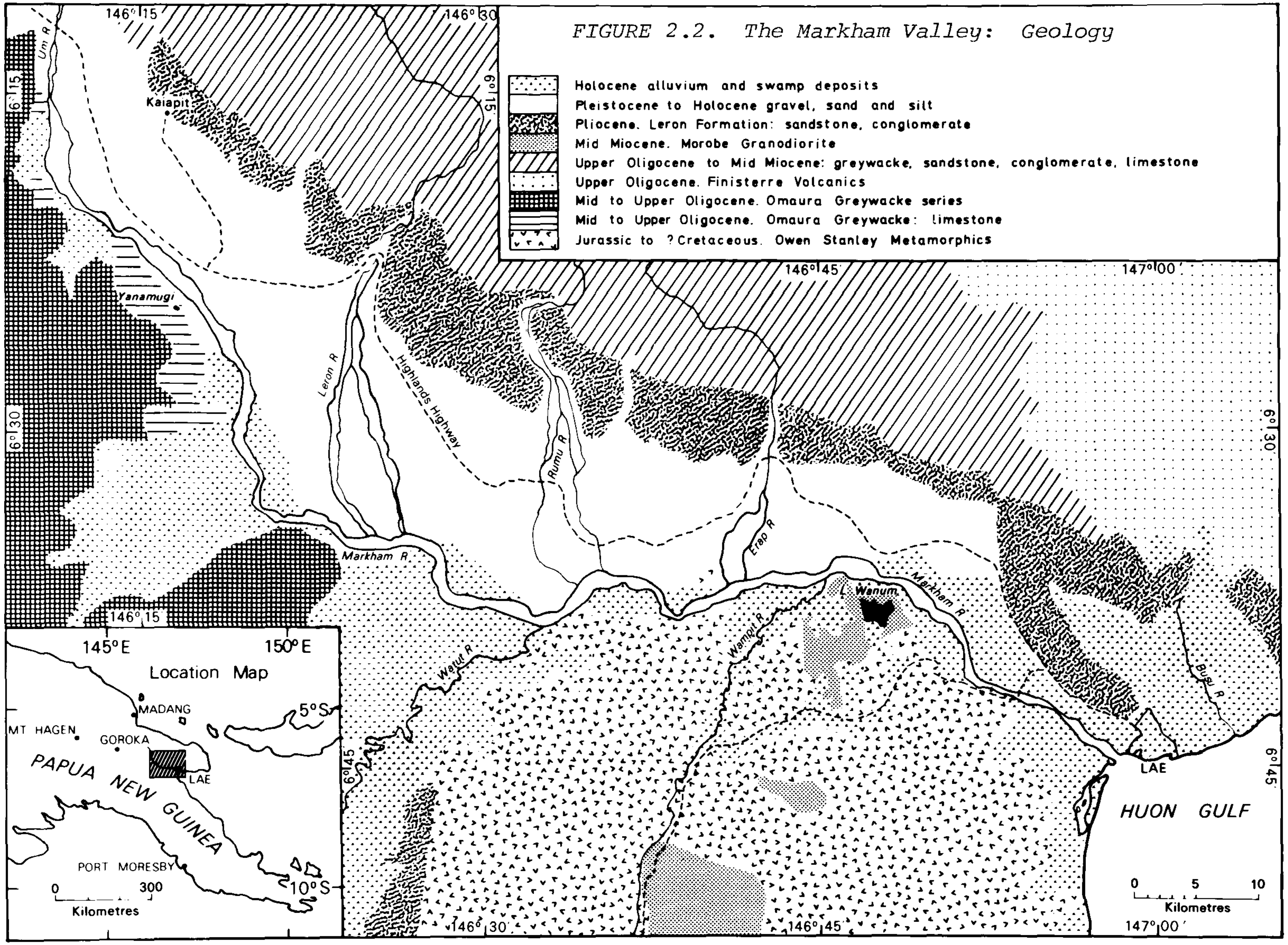


FIGURE 2.2. The Markham Valley: Geology

The Ramu-Markham fault zone is considered to have originated in middle Miocene times when the north-moving Australian Plate collided with an island arc developed on the oceanic crust of the Pacific Plate (Robinson *et al.*, 1974). The oceanic crust was thrust over the metamorphic rocks of the orogenic belt to the south; the Ramu-Markham fault zone approximating the position of the former plate boundary.

The geology of the ranges to the north and south of the Markham Valley reflects their different origin. The Oligocene to middle-Miocene sediments of the central massif of the Saruwaged Range are largely marine. Outcropping in the east of the range, the Oligocene Finisterre Volcanics were also deposited in a marine environment. The lower foothills are composed of sandstones and conglomerates of the Leron Formation, thought to be of Pliocene age. Analogous sediments are found south of the Markham in the lower Watut Valley, suggesting that a shallow sedimentary basin may have existed in the region at this time (Tingey and Grainger, 1976).

To the south-west of the Markham Valley, the bedrock consists largely of the Omaura Greywacke, an extensively folded and faulted complex of middle- to upper-Oligocene age. Limestones of this series outcrop in several places along the margin of the valley. To the east of the Watut River the Mesozoic Owen Stanley Metamorphics form the core of the Herzog Ranges. These rocks, of probable Jurassic to Cretaceous age, underwent low grade metamorphism in Eocene or Oligocene times. A later metamorphic event may have been related to the emplacement, during the middle-Miocene, of the Morobe Granodiorite batholith, isotopically dated at 12 to 14.5 million years by K-Ar and Rb-Sr techniques (Page, 1971). Granodiorite occurs along the margin of the Markham Valley in the vicinity of Lake Wanum although the greatest extent of the batholith is to the south of the study area in the Morobe Goldfields (Dow *et al.*, 1974).

The nature of the fault zone along the Markham Valley is not clearly known. The faulted southern margin of the valley may form the major boundary with the Pliocene Leron Formation underlying the valley sediments (Pettifer, 1974). Movements along the fault zone are thought to be predominantly of a left-lateral transcurrent nature, although vertical displacement of up to 1 km may also have occurred (Robinson *et al.*, 1974). Chappell (1973) sees the Markham trough as zone of, at least relative, subsidence in comparison to the rapid uplift of the surrounding mountains, particularly those to the north. The Saruwaged Ranges have undergone uplift of at least 4 000 m since the late-Miocene, making the area one of the most tectonically unstable in Papua New Guinea. Veeh and Chappell (1970) show the coast on the north-east of the Huon peninsula to have risen by up to 100 m in the past 35 000 years. Continued rapid uplift of the massif is indicated by recent faulting in the foothills of the Saruwaged Ranges. Such evidence is not found in the ranges on the southern flank of the valley. As a result of this tectonic instability, the Markham trough has become a locus of fluvial deposition. Deflection of the Markham River along the southern margin of the valley suggests that the bulk of the deposits derive from the rivers of the northern ranges. The very high sediment load of these rivers is a function of slope instability caused by the rapid uplift, although is in part due to the relative erodability of the rock types that form the Saruwaged Ranges.

Much of the alluvium in the Markham Valley is clearly fluviatile, consisting of well rounded gravel and boulders, and finer sediments. Fan deposition is active where rivers emerge from the mountain front at the northern margin of the valley. Holloway *et al.* (1973) recognise two categories. Individual fans are deposited by the larger rivers such as the Erap, Rumu, and Leron. These semi-circular fans are usually several kilometres in radius, the largest, 20 km wide, being formed by the Leron River. Many smaller fans, deposited by streams that do not reach the major rivers, coalesce laterally to form a sloping 'piedmont'. In some larger fans, particularly those of the Leron and Umi rivers, the channel is entrenched into terraced fan deposits by up to 20 m (Jacobson, 1971).

Alluvial deposition is associated with existing or prior river channels as well as with fan construction. Floodplain alluvium is predominant in the lower Markham Valley east of the Erap fan, and in the valleys of the Wampit and Watut rivers, the major southern tributaries of the Markham River. Changes in the shape and position of many active river channels since 1943 AD can be demonstrated (Holloway *et al.*, 1973).

The maximum thickness of the sediments of the Markham Valley is not known exactly. The floodplain alluvium is at least 40 m deep at the site of the Markham Bridge, whilst cores to a depth of 80 m in the piedmont alluvium have not encountered bedrock (Jacobson, 1971). A gravity survey (Pettifer, 1974) estimated the maximum depth of sediments of the southern Leron fan to be 500 to 1 000 m. A very large amount of alluvium has thus accumulated in Pleistocene and Holocene times, and the depositional and erosional processes involved continue to be active today.

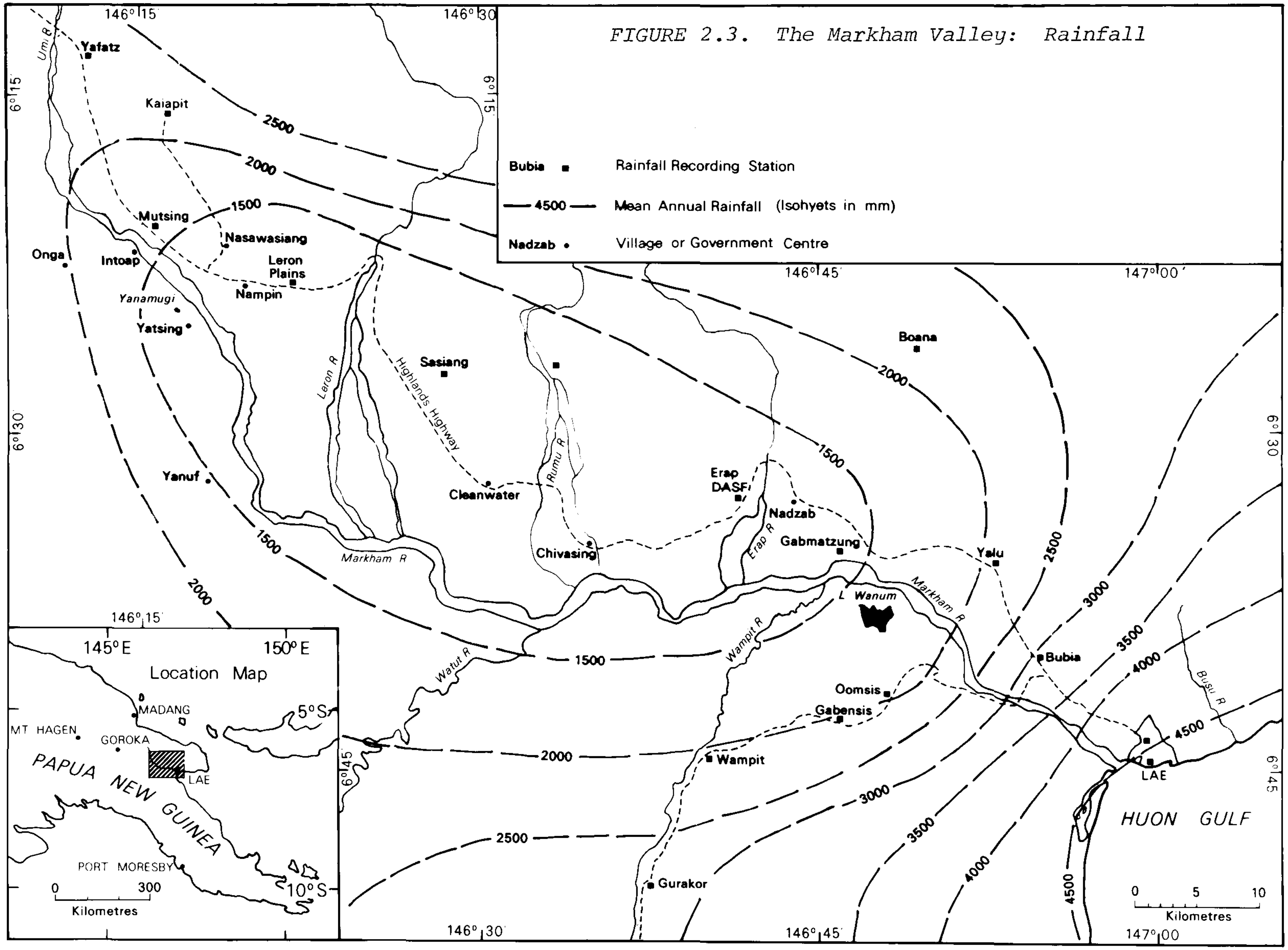
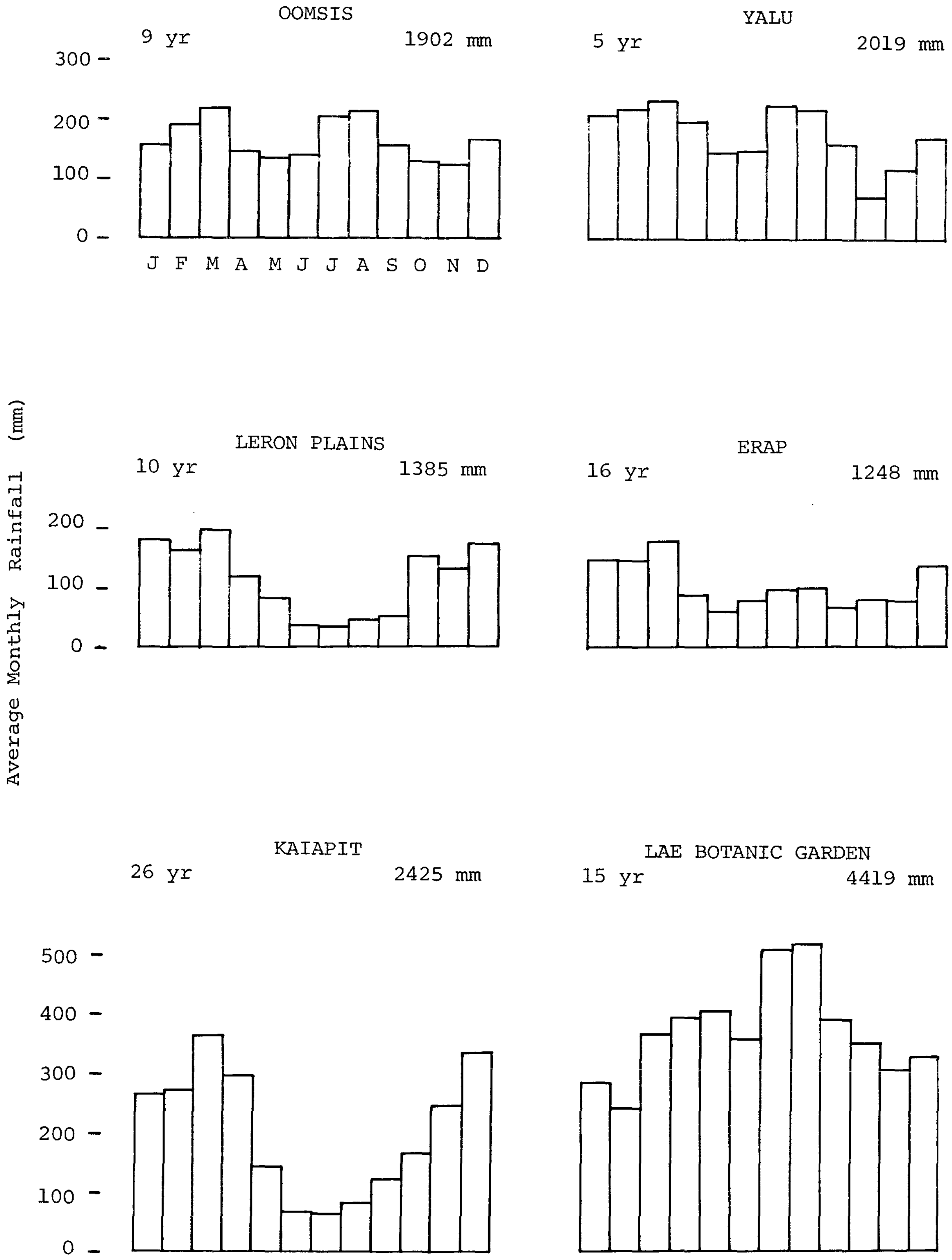


FIGURE 2.3. *The Markham Valley: Rainfall*

*FIGURE 2.4. The rainfall regime of selected Markham Valley Stations*



## *CLIMATE*

The climate of the Markham area is discussed by Holloway *et al.* (1973). Rainfall data are available for much of the region although the records of a number of stations, especially those in the central Markham Valley, are of short duration. The southern part of the valley is poorly served by weather stations, and there are no data from the area to the south of the Markham River, west of the Wampit River.

Adequate temperature records are available only from Lae, Kaiapit, Bubia and Erap. However, the general temperature regime is very similar throughout the valley. The annual mean temperature is 26.2 °C at Lae, and about 1 °C higher at Erap. The hottest months are from November to February, although the mean diurnal temperature range (6.8 °C at Lae, 11.3 °C at Erap) is much greater than the annual range of mean monthly temperature. The annual range of mean monthly maxima (3.4 °C at Lae, 3.6 °C at Erap) is greater than that range of minima (2.6 °C at Lae, 2.0 °C at Erap).

Rainfall intensity and seasonality show great variation throughout the area. Figure 2.3 maps the approximate annual isohyets for the Markham Valley and environs. Monthly mean rainfall totals for selected stations are given in Fig. 2.4. Both figures are based on unpublished data collated by the Land Use Research Division of the CSIRO. The records of additional stations (Fig. 2.3) are from Holloway *et al.* (1973), and Johns (unpubl. *a*).

The incidence of rainfall in the area can be related primarily to the two patterns of atmospheric circulation that influence most of Papua New Guinea. From December to March, the 'north-west' or 'monsoon' season, low pressure vortical systems associated with the intertropical convergence zone (ITCZ) dominate the circulation. Between May and October the ITCZ is located north of the equator and has no direct influence on the area. At this time, the 'south-east trades' season, south-easterly winds moving towards the equator dominate the circulation. During April and November, when the ITCZ is moving across the region, either circulation system may predominate. Due to the great variations in topography, circulation patterns produced by anabatic and katabatic winds along the valley margins have a significant effect on local rainfall.

The south-easterlies are the only strong and persistent wind system affecting the area. They are also moist, and become increasingly unstable towards the equator. A temperature inversion, the 'trade-wind inversion', frequently occurs at low altitude. Under such conditions much of the winds' moisture is released as rain along the coastal ranges, whereas precipitation in the leeward area of the Markham Valley is unlikely. Although the coastal area is very wet throughout the year, maximum rainfall occurs during the south-easterly season. Rainfall during this season decreases very sharply inland, reflected by the reduction in annual precipitation at stations various distances from the coast (Fig. 2.3). Lae Botanic Garden receives an average of 4 419 mm $yr^{-1}$, whilst at Erap, 40 km to the west, the annual total is only 1 248 mm.

Due to the decreased influence of the south-easterly circulation, stations in the mid- and upper-Markham Valley receive nearly 40% of their rainfall during the height of the north-west season from January to March. Conversely, the central valley area is relatively dry from July to September, the degree of seasonality increasing with distance from the coast. At Erap, 21% of the total rainfall falls during these months. This proportion declines to around 10% or less at Sasiang and stations to the west. Kaiapit, and similar marginal valley areas, experience greater annual rainfall due to local circulation effects, although the seasonality of the rainfall is very similar to that of the nearby open valley stations. The lower valley area around Oomsis and Yalu is influenced equally by both circulation patterns, and rainfall distribution is less seasonal than in other areas.

A large section of the Markham Valley thus experiences a seasonally distributed annual rainfall of less than 1 500 mm. The only extensive region of the country drier than the mid-Markham is the Central Coast of Papua (Brookfield and Hart, 1966). This relative aridity is reflected by increased drought frequency and intensity, and by seasonal or annual water budget deficits. Estimates for Erap and Leron Plains stations (Holloway *et al.*, 1973) show the potential annual evapotranspiration to exceed rainfall by 460 mm and 334 mm respectively. McAlpine and Short (1974) indicate an excess of theoretical evaporation over rainfall of 555 mm $yr^{-1}$ for Erap.

## *VEGETATION AND SOILS*

Figure 2.5 shows a highly generalised map of the vegetation of the Markham region. Due to the paucity of ecological data (see Appendix II) the vegetation units mapped are largely physiognomic, similar to those proposed by Paijmans (1975). Floristic lists for specific locations within the area may be found in Lane-Poole (1925), Holloway *et al.* (1973) and Johns (unpubl. *a*).

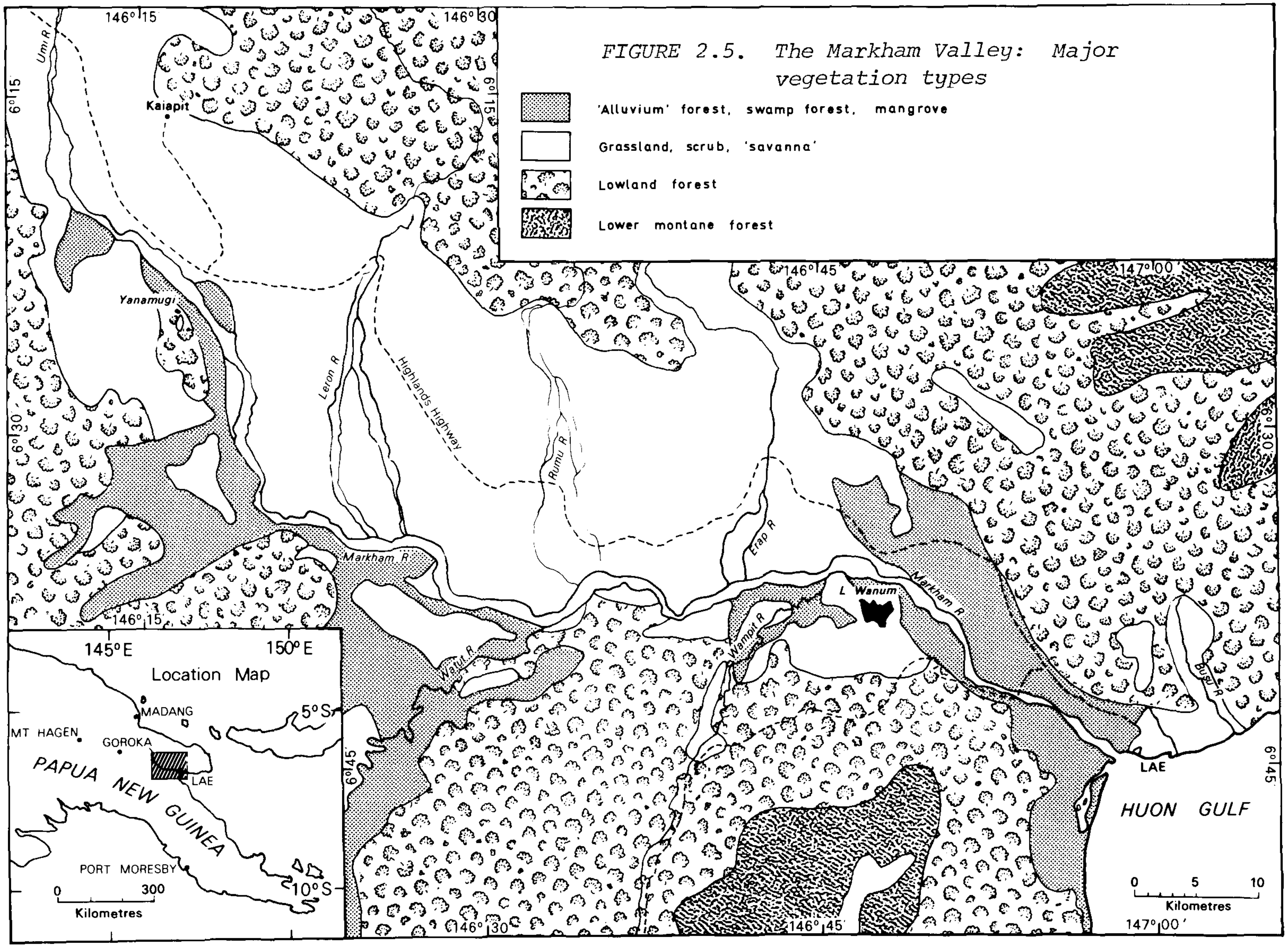


FIGURE 2.5. The Markham Valley: Major vegetation types

The vegetation units are described in a wider context by Paijmans (1975, 1976). Vegetation boundaries are mapped on Fig. 2.5 by interpolation from aerial photography, photomosaics, and LANDSAT imagery of the area. The following units are recognised:

*Grassland* comprises most of the non-forest vegetation of the area. Grass dominated vegetation occupies much of the drier central valley of the Markham, from the Erap River westwards to the margin of the Leron fan. It also covers an extensive area of the lower mountain slopes, up to about 500 m, particularly on the northern flanks of the valley. South of the Markham River, grassland is less widespread. It occurs along the floodplains of several rivers, but is most abundant over the granodiorite of the Lake Wanum area, and on the foothills in the vicinity of Wasiang Mountain. In the latter area, grasslands ascend to almost 1 000 m above sea level.

In mapping the floor of the Markham Valley, Holloway *et al.* (1973) recognise a number of non-forest vegetation alliances. A short grass association, dominated by *Themeda australis,* is found especially on active surfaces of the piedmont, and of the Leron, Umi and, to a lesser extent, Erap fans. The tall grass alliance, composed of *Imperata cylindrica* in association with *Ophiuros toncalingii* and *Saccharum spontaneum,* appears to dominate areas of deeper soil. It is particularly abundant around the margin of the Leron fan, and from this area eastward to the Erap River. Scattered trees, often *Albizia procera* or *Nauclea orientalis,* may occur either individually or in groups. In the upper valley west of the Leron Fan and along the piedmont and Garabampan fan, such trees become more abundant. Holloway *et al.* (1973) classify much of this area as 'savanna' or 'woodland'.

The grassland associations of the foothill slopes and valley floor appear essentially similar in floristic composition. In the vicinity of Lake Wanum, the grassland is almost totally dominated by *Themeda australis,* although *Arundinella setosa* also occurs. On similar slopes on the metamorphic rocks at nearby Redhill, *Imperata cylindrica* is the most abundant species. A wider diversity of grass species is seen in the wetter depressions in both areas. In such situations *Coelorhachis rottboellioides* and *Ischaemum barbatum* are particularly common.

*'Alluvium' forest* includes all substantially forested areas of the alluvial plain. Both Holloway *et al.* (1973) and Paijmans (1975) differentiate between swamp forest, and the forest of the floodplain. However, apart from small areas of floristically distinct mangrove vegetation east of Labu, and along the coast, none of the area is permanently inundated. There is perhaps an environmental gradient related to frequency and depth of flooding. Pure stands of sago (*Metroxylon sagu*) occur particularly in the lower Markham Valley where inundation is frequent, and the palm is common in the understorey at other periodically flooded sites. The floristic composition of 'alluvium' forest appears essentially similar throughout the area. Some of the more common trees encountered are *Artocarpus communis, Buchanania heterophylla, Bischofia javanica, Octomeles sumatrana, Terminalia* spp. *Neonauclea* spp. and *Ficus* spp.

'Alluvium' forest extends over most of the lower Markham floodplain. West of the Erap River it is much less widespread, although forest patches occur on some lower-fan areas, and adjacent to the Markham River. In this part of the valley, the major 'alluvium' forest tracts are south of the river, along the floodplains of the Wonoat, Watut and Wampit rivers.

*Lowland hill forest* encompasses all areas of closed canopy forest on well drained sites, below about 1 400 m. This omnibus category undoubtedly includes a wide variety of structurally and floristically different forest types. Most are dominated by evergreen broad-leaved species. However, semi-deciduous forest occurs along the southern margin of the Markham Valley in some seasonally dry areas notably the limestone foothills of Wasiang Mountain.

Some of the more abundant tree taxa recorded by Johns (unpubl. *a*) from valley side forest plots in the Oomsis-Gabensis area are *Celtis kajewskii, Intsia bijuga, Diospyros, Pimeliodendron alternifolium* and *Maniltoa*.

*Lower montane forest* (*sensu* Paijmans, 1975) is mapped at altitudes greater than 1 400 m. In the study area the unit extends over small areas of the Herzog and Saruwaged Ranges.

Where sufficient data exist, the effect of edaphic factors on the vegetation appears important. The apparent contrast between grassland on granodioritic soils and that on soils derived from metamorphic substrates has been mentioned.

The only systematic pedological study is that reported by Holloway *et al*. (1973), on the alluvial soils of the Markham Valley floor. Most soils investigated were found to be lacking in some major plant nutrients and trace elements. Drainage and topography, by their control of runoff, leaching and erosion, were found to be the most important factors influencing soil development. In the drier areas of the valley soil formation processes were considered 'more characteristic of semi-arid' than humid tropical climates. The young and unstable nature of the valley floor soils is emphasised. In many profiles, one or more ancient pedogenic phases, indicated by buried 'A-horizons', were encountered.

### *HUMAN ACTIVITY*

Although the cosmopolitan port of Lae is the country's second most populous town, the majority of the area's inhabitants live in traditional villages. Most villages are located along the foothills, or in tributary valleys, rather than in the open expanse of the Markham Valley. Population densities for the valley floor are thus low. The area between the Erap and Leron rivers has a density of only 3.4 persons $km^{-2}$. In the upper valley from the Leron to Umi rivers there are a larger number of villages and the number of persons rises to 18.5 $km^{-2}$.

The majority of the population practises subsistence agriculture in shifting gardens, although excess crops, particularly betel nut (*Areca catechu*) and coconuts, may be traded. Staple crops include the many varieties of banana (*Musa* spp.) and the coconut (*Cocos nucifera*). Sweet potato (*Ipomoea batatas*) is also important, but does not dominate the diet to the extent that it does in highland areas. Sago (*Metroxylon sagu*) is utilised in the lower Markham Valley and coastal areas, although nowhere does it appear the sole staple crop. Many other plants supplement the diet. Yams (*Dioscorea* spp.) and taro (*Colocasia esculenta*) are cultivated, and mangoes (*Mangifera indica*) may be found as shade trees in villages. A large number of plants are harvested from the wild; breadfruit (*Artocarpus altilis*) being one example. An extensive list of other food plants is given by Powell (1976). Domestic pigs are usually kept, and fishing and hunting are practised where appropriate resources are available.

Plantation agriculture is established particularly in the lower Markham Valley within 30 km of Lae. The major crops grown are coconuts and cocoa, and *Sorghum* is also widely cultivated. Many other plants have been introduced in attempts to promote village cultivation of cash crops (Holloway *et al.*, 1973) and a large cattle station is in operation at Leron Plains.

The pre-European history of the area is almost totally speculative. The two main peoples of the valley proper, the Adzera and Wampar (or Laewomba) are closely related culturally (Holzknecht, 1974). Both speak an Austronesian language, in contrast to the non-Austronesian affinities of the mountain inhabitants to the north and south (Hooley and McElhanon, 1970). No archaeological sites of any antiquity have been found within the area, although Specht and Holzknecht (1971) have recovered ceramic and stone artefacts from surficial deposits at abandoned village sites. A shallow rock shelter containing ancestoral skulls, at the southern end of Yanamugi lake, was encountered during fieldwork near Yatsing village.

Accounts of the oral and post-contact history of the lower Markham Valley (Willis, 1974, Sack, 1976) suggest widespread population movement in response to specific intertribal disputes. No sustained migration patterns are evident, however. European contact has had an increasing influence on the region since the late nineteenth century.

## *SELECTION OF SITES FOR PALAEOECOLOGICAL STUDY*

Potential sites for palaeoecological study were evaluated on the basis of the following desiderata:

(i ) probable existence of continuous sedimentary history of some antiquity,

(ii ) preservation in the sediments of macroscopic and microscopic plant remains,

(iii) sufficiently low in altitude to reflect changes in lowland vegetation,

(iv ) location in relation to vegetation associations, and

(v ) reasonable access for equipment.

Few sites fulfilled all critera. No suitable sites exist on the floor of the Markham Valley. Although some swamp areas and alluvial plains to the south of the river contain organic material, this is unlikely to have been deposited continuously, or to be of great age, given the unstable nature of the alluvial environment. Neither are such sites with a fluctuating watertable likely to preserve much pollen. Perennially inundated sites only were therefore considered, restricting the search to permanent lakes or swamps.

Several lakes are found in the foothills of the Saruwaged Range. Yarong Lake and the two Santagora Lakes (Fig. 2.1) are located between about 600 m and 800 m altitude in the headwaters of the Erap River and Wawin Creek respectively. These lakes are in an interesting position at the upper limit of major cultivation in the foothills, although may have been formed relatively recently by landslips in this unstable area. The sites might also be too elevated to reflect vegetation events in the Markham Valley. Due to their relative inaccessibility, these lakes were not investigated, although they would undoubtedly bear further study.

Possible sites also occur at low altitude in the foothills along the southern margin of the valley. Two small lakes in the forest between the Wampit and Watut rivers were observed from a light aircraft. They could not be located subsequently on aerial photographs and may be ephemeral.

Two areas were chosen for initial palaeoecological investigation. The vicinity of Mount Ngaroneno, at the southern margin of the lower Markham Valley, contains the greatest expanse of swamps and lakes in the region. Lake Wanum is by far the largest, although other lakes and swamps are also found. Several small lakes or ponds occur in the second area, the limestone region of Wasiang mountain. The largest of these, Yanamugi, appeared suitable for study.

Both areas are critically located in relation to the environmental factors outlined in this chapter. They occur on rock types uncharacteristic of most of the area, granodiorite and limestone. The prevailing rainfall regimes differ, the Lake Wanum area probably receiving 1 500 to 2 000 mm, distributed throughout the year. Yanamugi lies within the area of strongly seasonal precipitation, with an annual average of less than 1 500 mm. Grassland vegetation is abundant around both sites, although the immediate vicinity of Yanamugi is forested. These areas thus appear well sited to detect any past change in major environmental conditions or vegetation occurring in the region.

# CHAPTER 3

# SWAMP AND LACUSTRINE DEPOSITS OF THE LAKE WANUM AREA

Lake Wanum, centred on 6°38'S and 146°47'E, lies about 25 km inland from the Huon Gulf on the southern flank of the Markham Valley. It has an irregular outline and, with a maximum width of about 3 km, is the largest of a number of lakes and swamps in the vicinity. The area consists predominantly of granodiorite, extensively faulted in the upper Quaternary, which gives rise to a topography of steep slopes with rounded ridges and flat bottomed valleys. Various small swamps and lakes are found at the foot of these hills some possibly being impounded by faults (Chappell, 1973).

To the west of Lake Wanum over a narrow fault scarp lie the Erom-Erom lakes (Plate 3.1), a series of three small ponds and associated swamps. More extensive swamps and at least two other lakes are found bounding the hills to the west and south of the area. To the south-east on the edge of the granodiorite is the large expanse of Redhill Swamp (Fig. 3.1).

The Lake Wanum basin itself appears to be delimited by at least two major fault lines, along the northern and western shores. To the east the marginal hills are less steep in the immediate vicinity of the lake. The bathymetric sketch map[1] (Fig. 3.2) shows a similar trend continuing under water, the deepest part of the basin (19 m below datum) occurring near the steeply sloping northern shore.

---

[1] Compiled from echo-sounding traverses made by Joe Glucksman of the Fisheries Research Division of D.A.S.F. and the author in August 1974.

FIGURE 3.1. The distribution of lakes and swamps in the Lake Wanum area

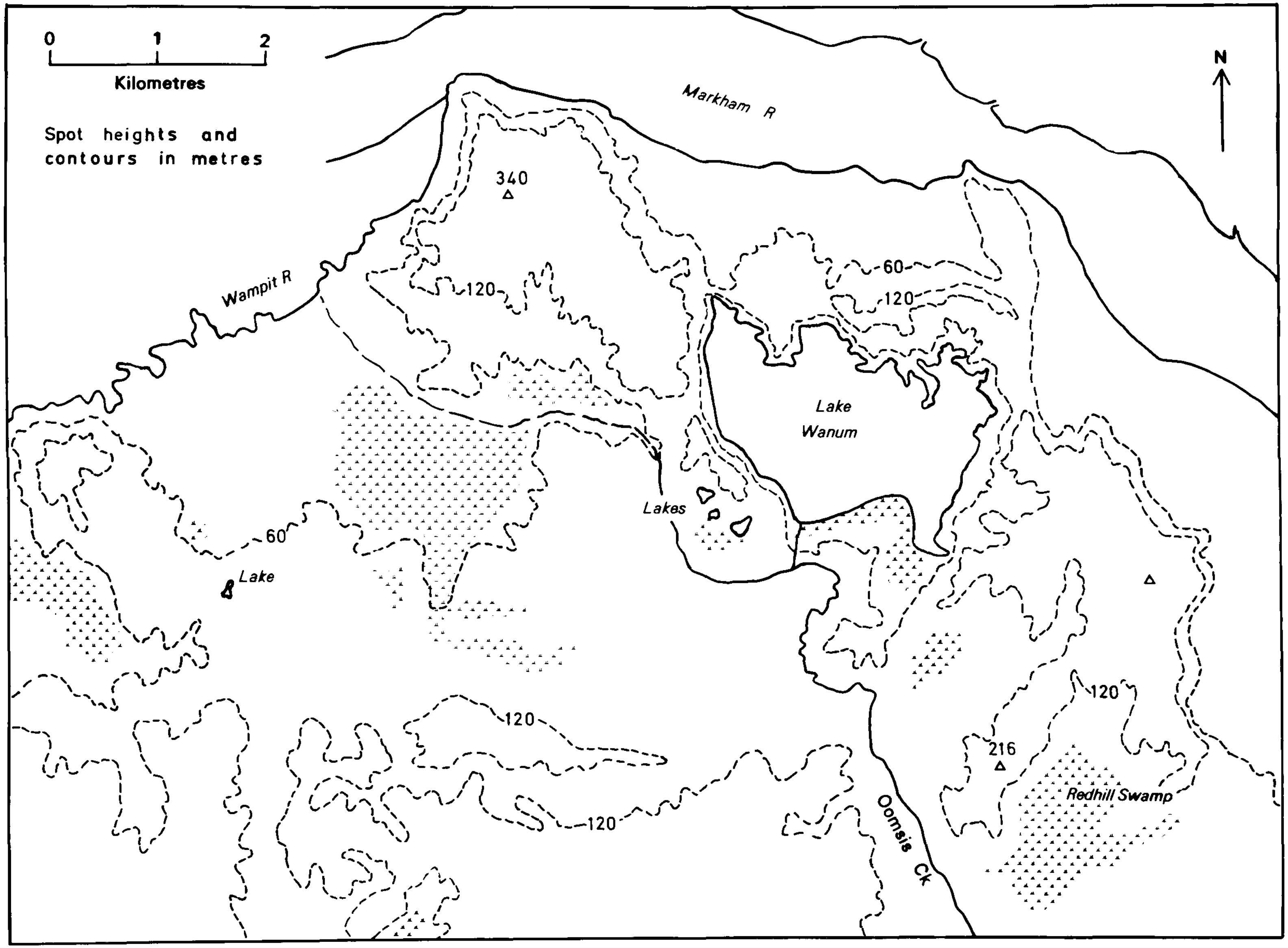


FIGURE 3.2. Lake Wanum: Bathymetric sketch map. Underwater contours are in metres

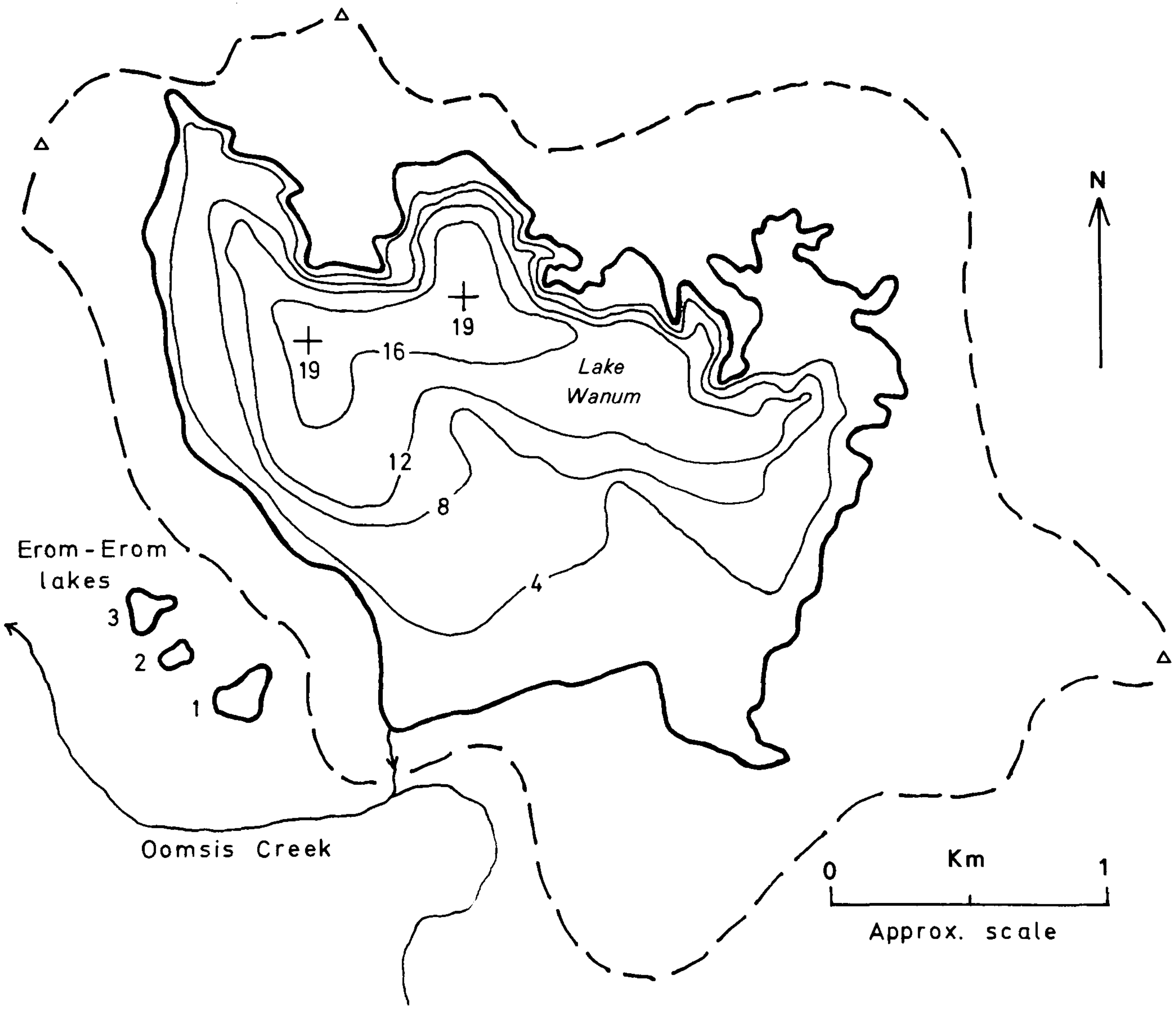


*PLATE 3.1* The Erom-Erom lakes and Lake Wanum, an oblique aerial view from the south-west. The course of Oomsis Creek is marked by riparian forest in the foreground, and the Markham River is visible in the distance.

*PLATE 3.2.* The eastern shore of Lake Wanum, an oblique aerial view from the north. Several islands of herbaceous swamp vegetation are visible in the north-east bay.

The area of open water in the basin, about 3.7 km$^2$, is fairly large in relation to the total catchment area of approximately 8 km$^2$ as measured from the map. As there is no permanent stream inflow into the lake much of its water must be derived by precipitation directly onto the lake surface, and the water is fresh and clear. The only outflow of the lake is a small channel in the extreme south-west corner of the basin that runs into Oomsis Creek. This operates only intermittently. It was observed flowing throughout the latter half of 1974, but had dried up and become overgrown by May 1976 when the lake level was apparently slightly lower. Brass (1964) reports that this channel also serves as an inflow when the creek is in flood. Oomsis Creek is the only more or less permanent watercourse in this locality although Brass also reports that it too may cease flowing under conditions of sustained dry weather.

The altitude of the water surface of Lake Wanum above sea level is not known accurately. The 1944 1:63 360 map[1] shows it as between 150 feet and 200 feet (45 to 60 m). Using the heights of nearby hills given on this map as a basis, a crude triangulation with an Abney level determined the lake surface as 34 m or 36 m above sea level. If the height for Mt. Ngaroneno given on the 1966 1:250 000 map[2] (± 340 m) is taken as correct, the lake level becomes 16 m above sea level. A similar exercise at Erom-Erom lake 2, shown on the 1 inch map as between 250 feet and 300 feet (60 to 75 m) produced figures of 41 m or 23 m for the lake surface depending on the datum height used.

---

[1] No. 0452 Nadzab 1 inch series.

[2] SB 55-10 Markham sheet.

## *STRATIGRAPHIC INVESTIGATIONS*

### *Coring techniques*

In the recovery of sediment cores for stratigraphic description the primary equipment used was a version of the Livingstone-Vallentyne stationary-piston corer incorporating the modifications of Walker (1964). The sampler was operated from a small, flat bottomed, aluminium dinghy provided with a central coring hole. This apparatus proved successful in obtaining cores of reasonable length when firmly anchored in shallow water. In open water deeper than about 5 m stable anchorage of the boat became a problem and cores longer than *c*. 4 m were difficult to obtain. Instability was overcome by positioning the boat, or subsequently a 2 m x 2 m plywood coring platform, on top of islands of floating or loosely rooted vegetation. In this way cores over 20 m in depth were recovered.

During 1976 a compact pneumatically operated corer (Mackereth, 1969) was employed to obtain cores up to 1 m long with an undisturbed sediment/water interface. The 'mini-Mackereth' was successful in recovering both a core of highly cohesive sediment from the deepest part of Lake Wanum, and cores of the uppermost sections of the highly unconsolidated marginal sediments.

All cores were extruded in the field. Those collected solely for stratigraphic description were discarded after examination. Others were sealed in polythene sheeting, and enclosed in PVC pipe for return to Canberra.

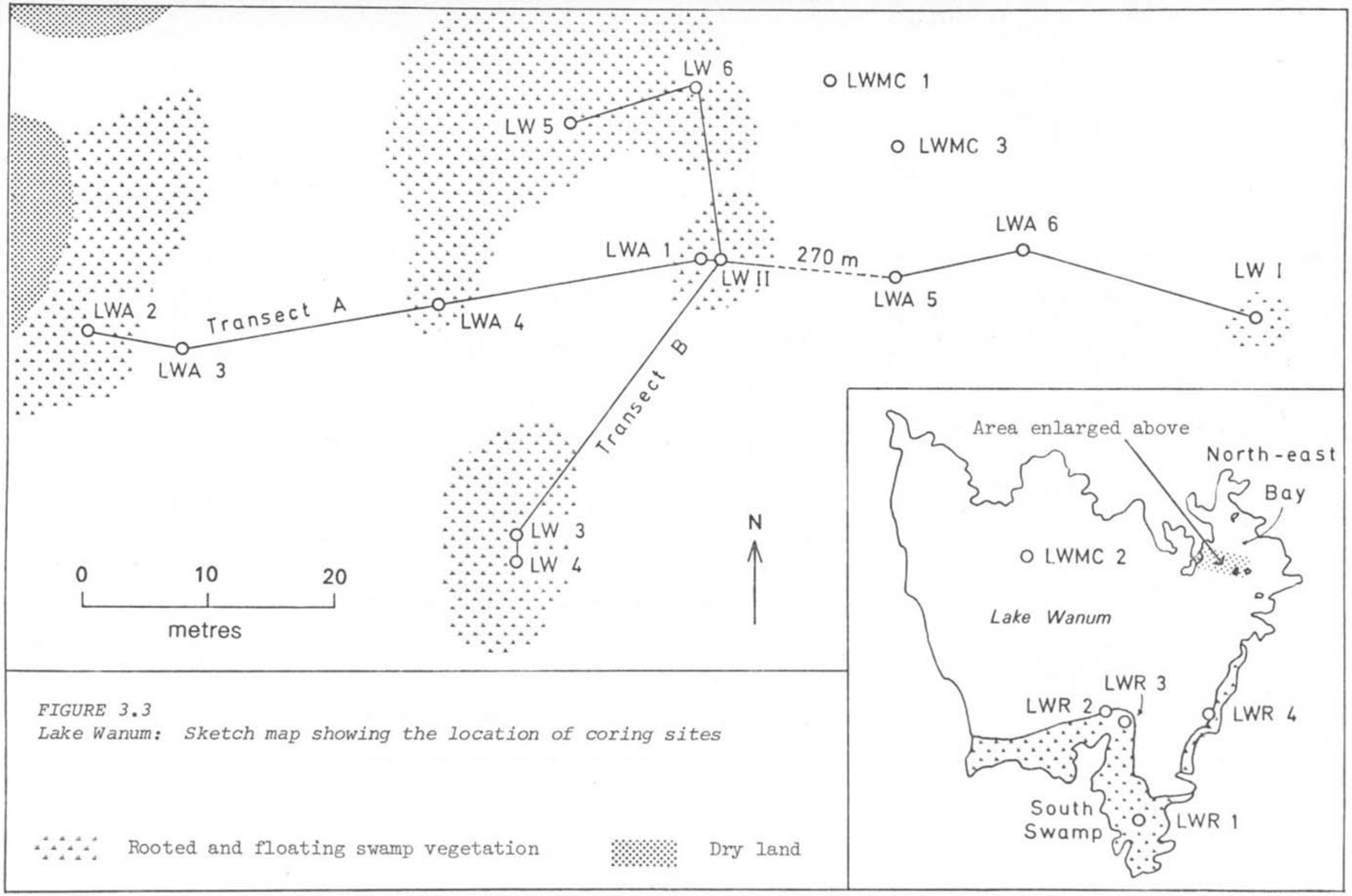
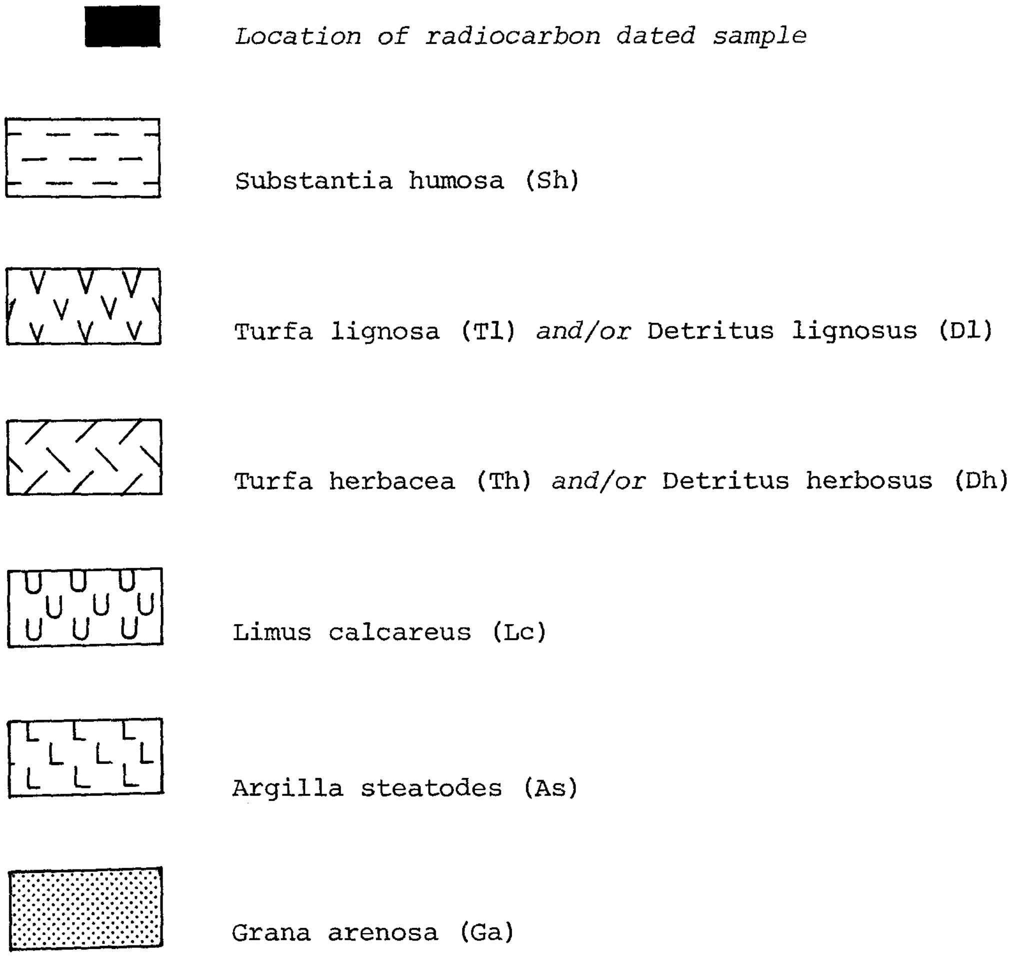


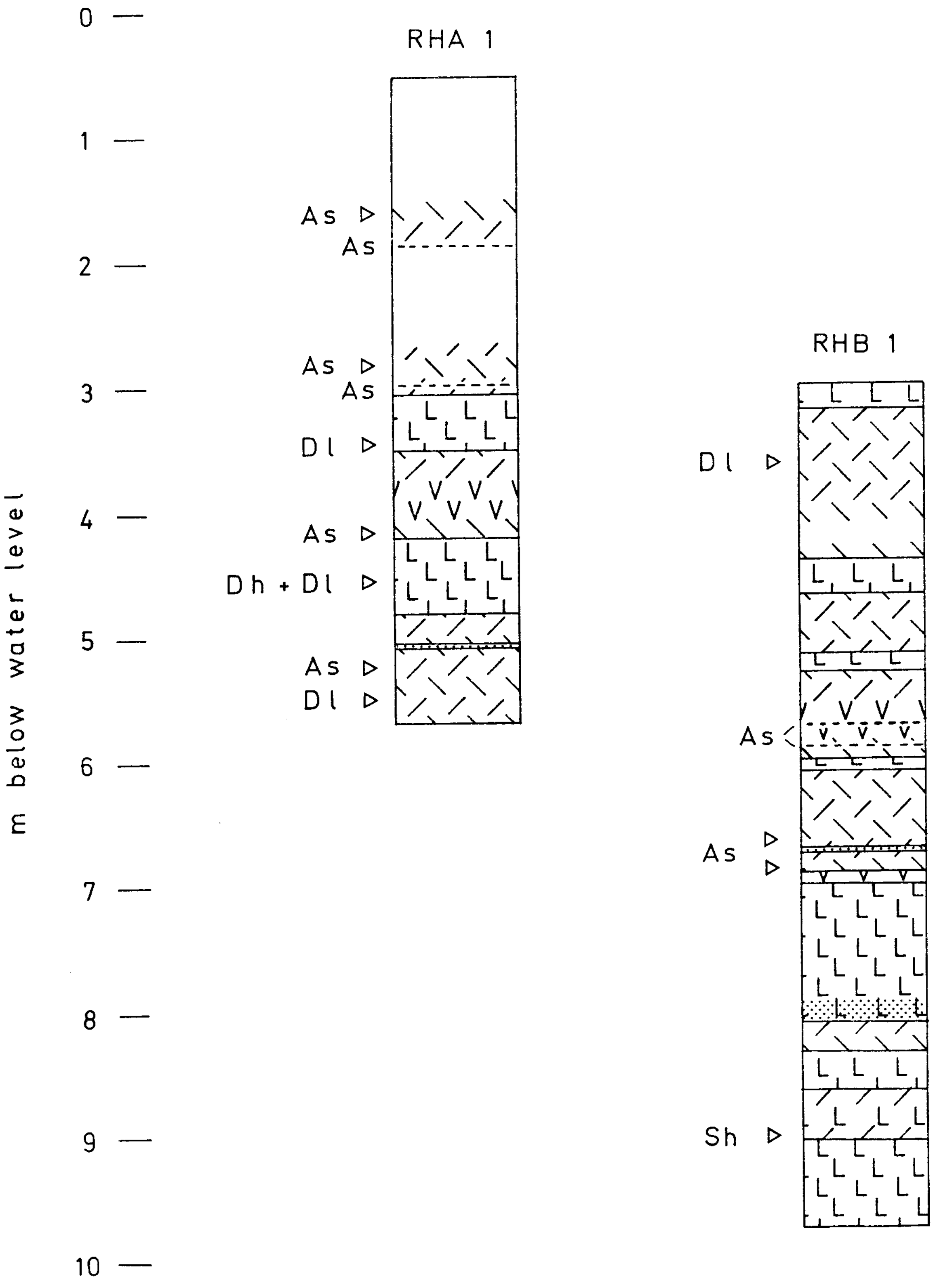
*FIGURE 3.3*
*Lake Wanum: Sketch map showing the location of coring sites*

*FIGURE 3.4. Key to stratigraphic diagrams*



*Major components only are shown in the stratigraphic column. Where two major components occur in a single horizon, both are drawn. Apart from the symbol for* Grana arenosa, *superimposed at the true stratigraphic depth, alternation of symbols within a horizon is diagrammatic only. Minor components of the deposit are identified by abbreviations at the side of the column. Narrow discrete horizons are located by a dashed line, and identified adjacent to the column. The top of each stratigraphic column represents the sediment/water interface.*

*FIGURE 3.5. Redhill Swamp: Stratigraphy of cores RHA 1 and RHB 1*



*Description of deposits*

In describing the characteristics and stratigraphy of the sediments the system of Troels-Smith (1955) is adhered to as far as practicable. Assessment of the physical properties and humicity of the deposits proved straightforward although recording of the generic terms used in the description of component elements of the deposit was less satisfactory. Many of Troels-Smith's more specialised terms are not applicable outside N.W. Europe, the region for which they were originally devised. Even the broader generic terms such as *Turfa, Detritus,* and *Limus* could not always be used with certainty as they imply a familiarity with the source of any macroscopic vegetal remains. These uncertainties are reflected in the use of alternative terms for the same horizon, or in the case of highly humified deposits use of the purely descriptive term *Substantia humosa*. As a further aid to the interpretation of the stratigraphy, a subjective description of the deposits is also given. The symbolic representation of various deposit types (Fig. 3.4) is a simplified version of Troels-Smith's system.

*The stratigraphy of Redhill Swamp*

Coring was carried out in the Lake Wanum area during two field seasons both in the basin of the lake itself (Fig. 3.3), and in the large Redhill Swamp to the south.

Two reconnaissance cores were taken near the south-eastern margin of Redhill Swamp: RHA1 located about 100 m from the edge of the swamp, and RHB1, approximately 200 m from dry land. The generalised stratigraphy of these cores is shown in Fig. 3.5. Both show a succession of grey clay (*Argilla steatodes*) bands, intercalated with predominantly organic bands of fibrous peat (*Turfa herbacea*) often including horizons of wood or woody fragments. Although both sequences contain a similar range of deposits, the stratigraphy is complex, and detailed correlation is not possible.

Passage through the swamp was extremely difficult. The water depth was too great to proceed on foot, and the dense herbaceous vegetation and frequent presence of small saplings made movement with the boat very slow. The stratigraphy suggested that the marginal areas of the swamp would be unlikely to provide any cores with a long, continuous sedimentation record. Therefore, subsequent efforts to obtain such cores for pollen analytical purposes were concentrated in the basin of Lake Wanum itself.

### *The stratigraphy of Lake Wanum*

Four reconnaissance boreholes (LWR 1 to 4) were cored in the large area of herbaceous swamp and open water vegetation, the 'south swamp', bounding the southern shore of Lake Wanum. In addition, a number of probes to determine the depth of sediments was made using the corer extension rods alone. In LWR 1 to 3 a cohesive grey plastic clay (*Argilla steatodes*) was found to underlie a shallow horizon (max. thickness 10 cm) of poorly humified fibrous organic deposit (*Turfa herbacea*). The clay was penetrated to a depth of *c*. 80 cm before its cohesive nature arrested the corer, precluding the recovery of any deeper sediments. Core LWR 4 shows a similar stratigraphy, although dark, gritty organic layers are also present. The numerous probes suggested that the thick clay layer was widespread over the whole southern area of the lake basin.

*TABLE 3.1. Stratigraphic description of core LW II*

| | | | Troels-Smith Indices | | | | | |
|---|---|---|---|---|---|---|---|---|
| Depth of horizon (cm below datum) | Colour | Structure and General Description | *Nigror* | *Elasticitas* | *Siccitas* | *Humositas* | Component Elements | Radiocarbon Samples (cm below datum) |
| 0-*c*. 200 | | Water and unconsolidated floating root-mat | - | - | - | - | | |
| *c*. 200-600 | | Water | - | - | - | - | | |
| 600-685 | Light brown | Fibrous organic sediment, slightly humified. Upper portion very wet. (No sample 600-635 cm) | 2 | 2 | 1-2 | 1-2 | *Turfa herbacea (Th)* | 645-652+<br>653-660<br>(ANU-1570) |
| 685-800 | Light brown/ grey | A heterogenous horizon of fibrous organic material admixed with grey inorganic clay. Gradual transition into the underlying horizon. | 1-2 | 2 | 2 | 2 | *Th + Argilla steatodes (As)* | 775-790<br>(ANU-1688) |
| 800-925 | Brown | Well humified, slightly fibrous organic deposit. (No sample 900-906 cm). | 2 | 2 | 2 | 3 | *Th* | |
| 925-1000 | Reddish-brown | Course fibrous organic deposit, wetter and less humified than the overlying horizon. Many well preserved rootlets present. Grades into underlying horizon. | 2 | 4 | 2 | 2 | *Th* | 923-930+<br>931-938<br>(ANU-1646) |
| 1000-1080 | Brown | Well humified organic deposit with some macroscopic plant fragments including rootlets and leaves. Fragments of yellow wood are found between 1023-1033 cm. | 2 | 2 | 2 | 3 | *?Th+Turfa lignosa (Tl)* or *Detritus lignosus (Dl)* | |
| 1080-1115 | Olive-brown | Similar to above horizon. Fine rootlets present, with woody rootlet and wood fragments between 1083-1088 cm. Gradual change into underlying horizon. | 2 | 2 | 2 | 3 | *Th + Tl* | |
| 1115-1191 | Brown | A fibrous organic horizon, although well humified, and becoming more so towards the base. In the upper part some wood and large leaves are present, penetrated by both large and fine rootlets. A solid band of light coloured wood occurs at 1188-1191 cm. | 2 | 3 | 2 | 3 | *Th+Tl* and possibly *Detritus herbosus (Dh)* | 1123-1130+<br>1131-1138<br>(ANU-1718) |
| 1191-1346 | Dark brown | A well humified horizon with fewer macroscopic organic remains. Some fine rootlets are present between 1191-1199 cm, with both fine and larger rootlets between 1219-1269 cm. Wood fragments occur from 1261-1269 cm. Between 1269-1280 cm, the deposit becomes slightly more humified and darker in colour. Large intact pieces of yellow wood are present around 1300 cm. From 1300-1346 cm scattered wood, rootlets and leaves occur. (No sample 1280-1300 cm). | 3 | 2 | 2 | 3 | *Th + Tl* | |

*TABLE 3.1. (Cont.)*

| Depth of horizon (cm below datum) | Colour | Structure and General Description | Troels-Smith Indices<br>*Nigror* | *Elasticitas* | *Siccitas* | *Humositas* | Component Elements | Radiocarbon Samples (cm below datum) |
|---|---|---|---|---|---|---|---|---|
| 1346-1348 | Light grey/ brown | A sharply defined band of grey clay, with some humified organic material and several large black fragments, possibly of carbonised wood. | 1-2 | 0-1 | 3 | - | *As* + *Substantia humosa (Sh)* + *Dl* | |
| 1348-1463 | Dark brown | Similar deposit to that between 1191-1346 cm, although slightly more humified. From about 1400-1430 cm the deposit becomes more fibrous, with some large rootlets. Towards the base, the colour becomes increasingly grey, with the inclusion of inorganic clay from the underlying horizon. | 2-3 | 3 | 2-3 | 3 | *Th* + *As* | 1443-1450+1451-1458 (ANU-1719) |
| 1463-1465 | Grey/ brown | Fairly distinct band of plastic grey clay about 1.5 cm thick. | 2 | 0-1 | 3 | - | *As* + *Sh* | |
| 1465-1487 | Olive-brown/ grey | A heterogenous admixture of slightly fibrous organic sediment and grey clay. Inorganic content decreases towards the base. | 2 | 1 | 3 | 3 | *Th* or *Sh* + *As* | |
| 1487-1488 | Grey/ brown | Band of grey clay c. 1 cm in thickness. | 2 | 0-1 | 3 | 3 | *As* + *Sh* | |
| 1488-1525 | Black | Sharp boundary between overlying clay and this slightly fibrous, well humified organic layer. Some large and fine rootlets present. Gradual transition into underlying horizon. | 3 | 3 | 3 | 3 | *Sh* or ?*Th* | |
| 1525-1711 | Olive-brown | A fine to coarse granular organic deposit, fibrous in places, with very few small rootlets. Fragments of light coloured wood occur around 1640-1643 cm. | 2 | 2 | 3 | 3-4 | *Dh* or *Detritus granosus (Dg)* + ?*As* | 1561-1570+1571-1580 (ANU-1689) |
| 1711-1712 | Orange brown | Sharp boundary between dark, almost matted organic deposit and a gritty sandy clay layer. | 2 | 0 | 3-4 | - | ?*Th* + *Grana arenosa (Ga)* + ?some *As* | 1711-1727 (ANU-1720) |
| 1712-1755 | Brown | Course organic deposit, though well humified. Noticably gritty, with some inclusions of orange-brown sand especially at 1725-1727 cm. Intact roots or twigs of light coloured wood occur at 1753 cm. | 2 | 3 | 3 | 3 | *Dh* + *Ga* + ?*Dl* | |

*TABLE 3.1. (Cont.)*

| | | | Troels-Smith Indices | | | | | |
|---|---|---|---|---|---|---|---|---|
| Depth of horizon (cm below datum) | Colour | Structure and General Description | *Nigror* | *Elasticitas* | *Siccitas* | *Humositas* | Component Elements | Radiocarbon Samples (cm below datum) |
| 1755-1770 | Dark brown | Fine organic deposit with fairly sharp upper boundary. A few large rootlets occur. Slightly gritty in places. Gradual transition into underlying horizon. | 2-3 | 2 | 3 | 4 | *Th* + *Sh* + *Ga* | |
| 1770-1862 | Reddish-brown | Very fibrous organic deposit with many large rootlets. A diffuse clay band is visible around 1799 cm, and the deposit is slightly gritty in places especially at *c.* 1800 cm. Gradual transition into underlying horizon. | 2 | 3-4 | 3 | 2-3 | *Th* + *As* + *Ga* | 1782-1790+1791-1799 (ANU-1810) |
| 1862-1881 | Brown-grey | Fibrous organic deposit admixed with clay. | 2 | 3 | 3 | 3 | *Th* + *As* | 1865-1870+1871-1880 (ANU-1645) |
| 1881-1888 | Orange/grey-brown | Fairly abrupt transition into a compact, very gritty sand/clay layer. Lower limit of this horizon more diffuse. | 2 | 0 | 3 | - | *Ga* + *As* + *Sh* | |
| 1888-1981 | Dark brown | Fibrous organic deposit. Many ?cyperaceous leaves, and some rootlet penetration. Wood fragments occur at 1890 cm and between 1909-1912 cm. | 3 | 3 | 3 | 3 | *Th* + *Dh* + *?Dl* | 1888-1890+1891-1902 (ANU-1644)<br>1960-1970+1971-1979 (ANU-1586) |

*FIGURE 3.6. Lake Wanum: Stratigraphy of cores in north-east bay Transect A*

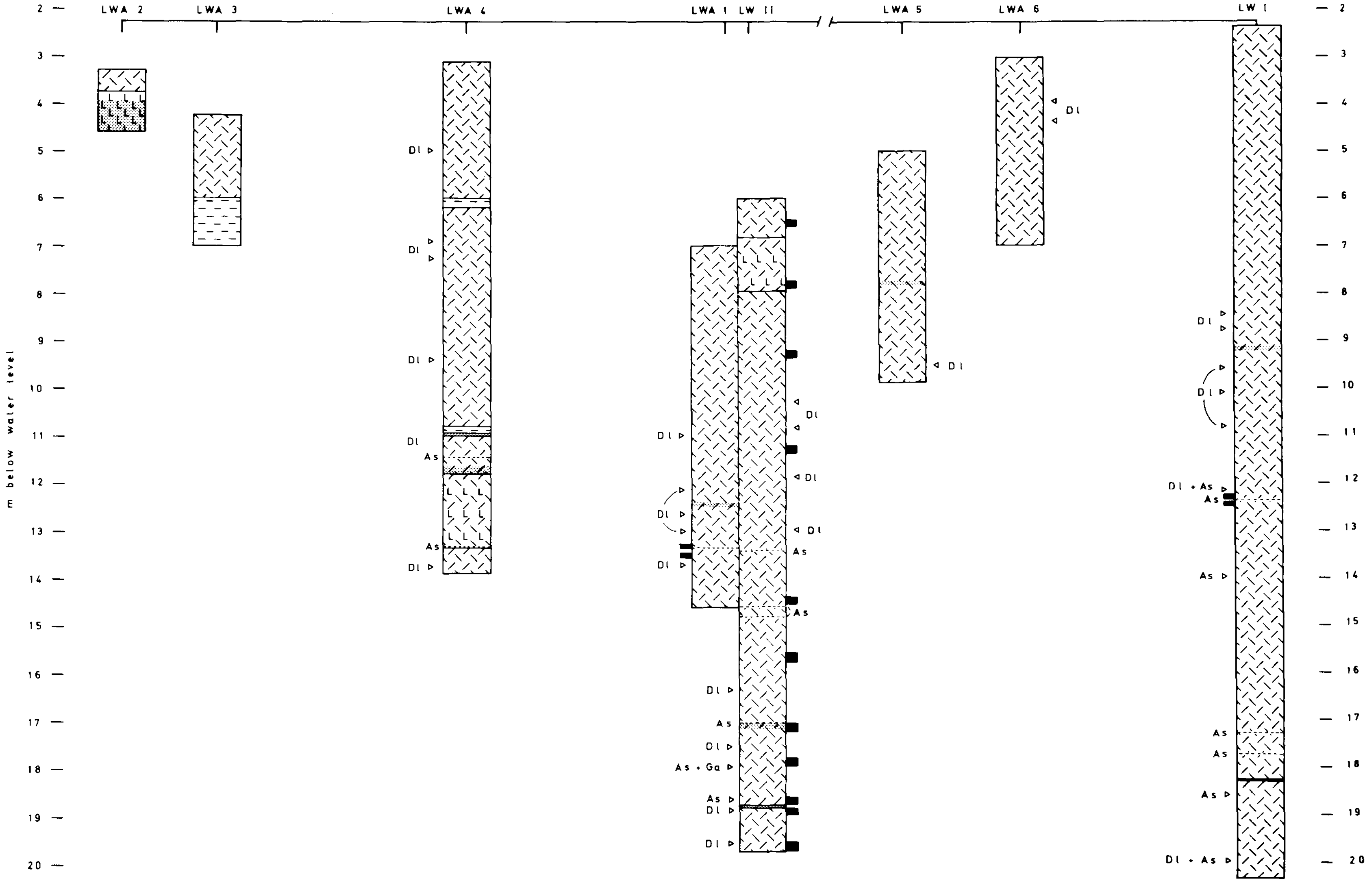
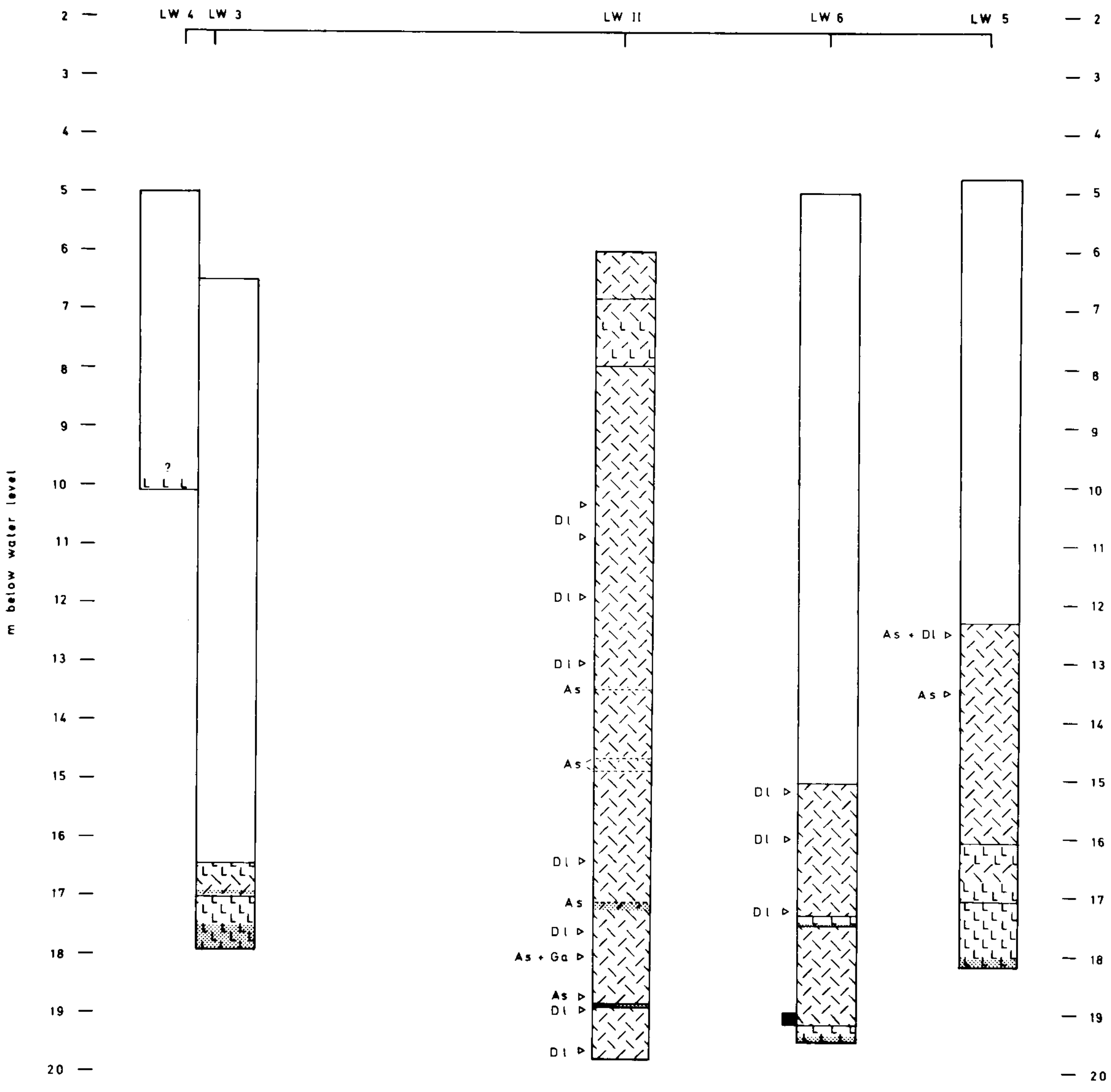


*FIGURE 3.7. Lake Wanum: Stratigraphy of cores in north-east bay Transect B*



Subsequent investigations revealed the area of shallow water and sparse intermittent swamp vegetation at the north-eastern corner of the lake, (the 'north-east bay') to contain much deeper deposits of predominantly organic sediment. Probes at several locations away from the shore reached 14 m below water level (the maximum length of rods available at the time) without encountering substantial clay bands, or harder basal sediments. The major part of the stratigraphic survey was therefore concentrated in this area (Plate 3.2).

Although some shorter cores were recovered from open-water situations the location of coring sites (shown in Fig. 3.3) was largely dictated by the presence of suitable floating vegetation to act as a relatively stable base for operations. Hence the coverage of the coring transects is not as wide as is perhaps desirable, being largely restricted to a marginal area of swamp at the western edge of the bay, and a small area in the centre of the bay.

Of the cores in transect A recovered in 1974 two, LW I and LW II, were returned to the laboratory. Further cores were taken along the line of transect B in 1976 in order to elucidate the basal stratigraphy. All except LW 4 were retained for subsequent analyses. A detailed stratigraphic description of core LW II, selected for pollen analysis, is given in Table 3.1 whilst a generalised representation of the stratigraphy of the other north-east bay cores is shown in Figs. 3.6 and 3.7.

The longer cores show a generally similar, fairly uniform stratigraphy. The major component throughout most of the sequence is a fibrous organic deposit (*Turfa herbacea*) consisting primarily of the roots and aerial stems of herbaceous swamp plants. In the upper sections of the cores this deposit is unconsolidated and poorly humified. At lower levels there is increasing occurrence of more strongly humified sediment, and in places very few macroscopic plant fragments are preserved.

The sequence of organic sedimentation is punctuated at intervals by bands, usually narrow, of plastic clay (*Argilla steatodes*), gritty clay, or sand (*Grana arenosa*). Most of these layers probably represent sediments derived by inwash from the lake shore, as they are more common in cores nearer the present water's edge. Inorganic bands also occur more frequently in the lower sections of the long cores than in the upper part. At least three cores (LW 3, 5 and 6) reach a substantial layer of plastic grey clay, sometimes admixed with a fine organic deposit, that grades into a compact gritty clay. This basal clay is presumably a decomposition product of the underlying granodiorite. Neither of the two longest cores (LW I and LW II) contacted this layer, the depth of recovery in these cases being governed by the limitations of the available coring equipment.

The basal stratigraphy suggests that the line of transect A from sites LWA 1 to LW II runs parallel to a relatively steep sided depression. Not only does the basal gritty clay occur closer to the surface towards the present shoreline, but also to the north and south of the transect line in the cores of transect B.

The two short cores LWMC 1 and LWMC 3 obtained from the north-east bay with the 'mini-Mackereth' corer show a stratigraphy similar to that found at the top of the longer cores. A shallow layer of dark brown unconsolidated organic detritus (*Detritus granosus*) is underlain by a lighter brown fibrous deposit of rootlets and other poorly humified remains of swamp vegetation (*Turfa herbacea*).

In contrast, short core LWMC 2, from under *c*. 19 m of water in the deepest part of the lake basin, consists of very different sediments. A layer of fine, predominantly organic, mud (*Limus detritosus*) grades into a more clay-rich layer containing scattered fragments of leaves of swamp plants, wood, and well humified organic material. The proportion of plastic grey clay (*Argilla steatodes*) increases until it becomes the sole constituent towards the base of the 90 cm core.

## *ANALYSIS OF ORGANIC CONTENT*

During the sampling of core LW II for pollen analysis, 71 sub-samples, each of approximately 3.9 ml, were set aside for determination of organic and inorganic content by estimate of weight loss on ignition. In order to relate this value to an appropriate gravimetric base the weighed samples were first dried in an oven at *c*. 100 °C, and the dry weight found. Each was then transferred to a crucible and ignited at 650 °C in an electric furnace for about 30 minutes. The residual ash was weighed and the loss on ignition calculated. This method, although less accurate than chemical titration methods is able to give an approximate value for the quantities of organic and inorganic sediment in most types of deposit.

The water content as a percentage of the wet weight, and loss of weight on ignition as a percentage of the dry weight, are shown in Fig. 3.8. The dry weight of the inorganic and organic fractions per ml of wet sediment is shown in Fig. 3.9. As suggested by the stratigraphic description the sediments are very wet, containing typically 90% to 95% water. A slightly lower proportion of water is found in the predominantly inorganic layers. The curve for percentage residue after ignition ('inorganic' fraction) shows generally consistent trends, with several distinct 'peaks'. All of these can be related to stratigraphic horizons previously described (Table 3.1) as containing some proportion of *Argilla steatodes* or *Grana arenosa*. This curve, and the one based on the dry weight per ml (Fig. 3.9a) which is very similar, give a better quantitative indication of the inorganic component than that obtained from the stratigraphic description alone.

The weight loss on ignition ('organic' fraction) curve (Fig. 3.9b) shows few sustained trends. The values fluctuate considerably around the mean, although there is a tendency for the fluctuations to be of smaller amplitude below about 13 m in the core. This large variation in the organic content between adjacent samples could be the result of a number of factors. However, it is unlikely that errors in weight estimation are involved to any great extent, since the consistent curve for the organic fraction frequently relies on even lower values. Inaccurate collection of the volumetric sample could account for some of the variation since the unconsolidated, often fibrous, sediment found particularly in the upper part of the core is difficult to measure precisely. Nevertheless, it is likely that a major proportion of the observed variation is actually due to short-term fluctuations in sedimentation rate of the loosely compacted heterogenous organic material. This aspect will be discussed further in relation to annual sediment accumulation and pollen deposition rates.

FIGURE 3.8. *Lake Wanum core LW II: Water content and weight loss on ignition*

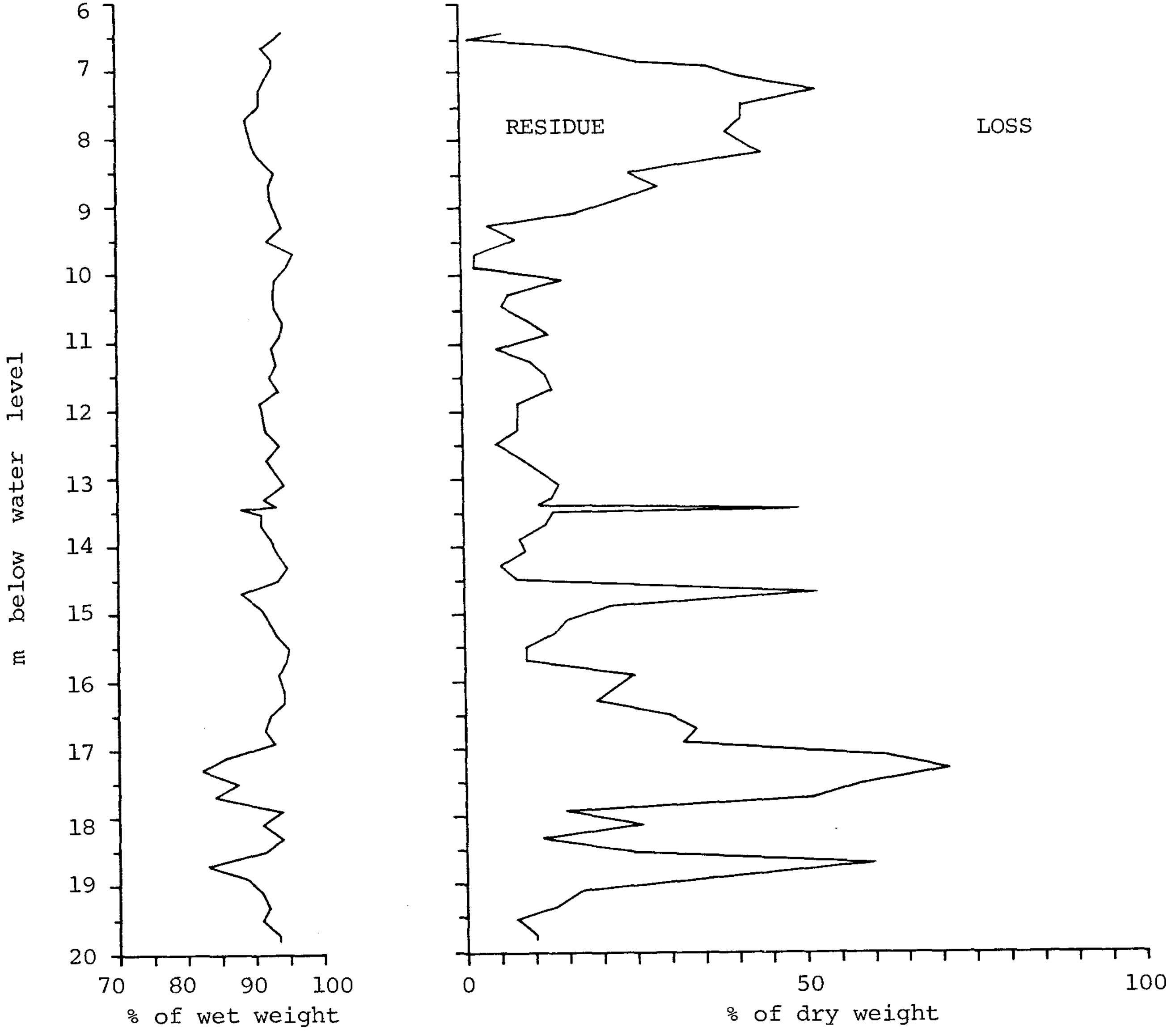


*FIGURE 3.9. Lake Wanum core LW II: Sediment density for residue- ('inorganic') and loss-on-ignition ('organic') fractions*

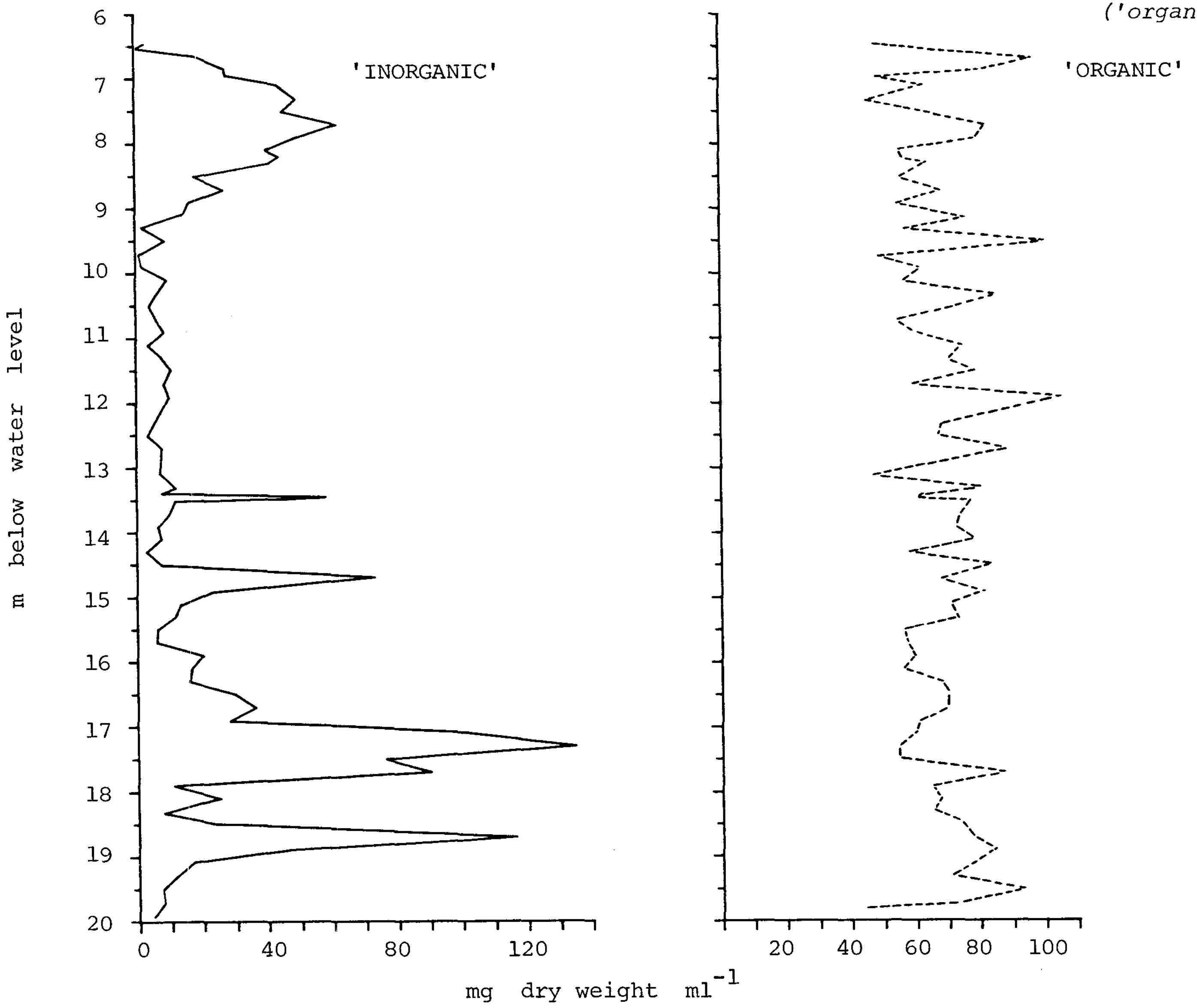


*TABLE 3.2. Radiocarbon determinations from Lake Wanum*

| Core | Depth (cm below datum) | Lab. no. | Date ± 1 S.D. |
|---|---|---|---|
| LW II | 645- 652 + 653- 660 | ANU-1570 | 260 ± 60 |
| LW II | 775- 790 | ANU-1688 | 1260 ± 100 |
| LW II | 923- 930 + 931- 938 | ANU-1646 | 2070 ± 80 |
| LW II | 1123-1130 + 1131-1138 | ANU-1718 | 3360 ± 80 |
| LW II | 1443-1450 + 1451-1458 | ANU-1719 | 4290 ± 90 |
| LW II | 1561-1570 + 1571-1580 | ANU-1689 | 4990 ± 100 |
| LW II | 1711-1727 | ANU-1720 | 5480 ± 100 |
| LW II | 1782-1790 + 1791-1799 | ANU-1810 | 6480 ± 100 |
| LW II | 1865-1870 + 1871-1880 | ANU-1645 | 7740 ± 120 |
| LW II | 1888-1890 + 1891-1902 | ANU-1644 | 8140 ± 130 |
| LW II | 1960-1970 + 1971-1979 | ANU-1586 | 9400 ± 120 |
| LWA 1 | 1330-1340 | ANU-1447 | 3820 ± 90 |
| LWA 1 | 1350-1360 | ANU-1446 | 4040 ± 100 |
| LW 6 | 1900-1908 + 1910-1918 | ANU-1826 | 9550 ± 120 |
| LW I | 1225-1235 | ANU-1449 | 2070 ± 130 |
| LW I | 1240-1250 | ANU-1448 | 2710 ± 110 |

## *CORRELATION AND DATING*

Detailed cross-correlation between cores on the basis of lithology alone is not straightforward, due to the general similarity of the organic deposits. Most of the predominantly inorganic layers, although readily discernable in individual cores can only be correlated with similar horizons in adjacent or nearby cores. The junction of the basal clay and the overlying organic deposits, whilst a distinct stratigraphic boundary, is not necessarily synchronous in all cores.

### *Palaeomagnetically based correlation*

In an attempt to establish correlations between the near-basal sediments of the north-east bay, three cores from transect B (LW 3, LW 5 and LW 6) were subjected to magnetic analysis. The intensity of the horizontal component of the natural remanent magnetisation (NRM) and the magnetic declination of the intact cores were measured on a computerised slow-speed spinner magnetometer similar to that described by Molyneux *et al.* (1972). The peaks in NRM intensity generally correspond with inorganic layers in the deposits, whereas the predominantly organic sediments show a very low level of magnetic intensity. The basal gritty clay gives a reading between that of the smooth plastic clay and the organic deposits. This may be due to the acquisition by the clay of a degree of chemical remanence on weathering. It is interesting to compare this result with that from the deep water core LWMC 2. The clay in this core shows a very high NRM intensity, which together with its smooth homogenous nature suggest that it does not represent the basal clay horizon found in the other cores analysed.

Apart from this difference, the NRM results fail to discriminate between the inorganic horizons and do not assist greatly with stratigraphic correlation.

*Dating*

In order to provide an absolute chronology for the sedimentary history of the lake basin, an independent method of dating was required. The highly organic deposits proved very suitable for $^{14}C$ assay and a suite of sixteen determinations was provided by the ANU Radiocarbon Laboratory (Table 3.2). These dated samples, the location of which is indicated in Figs. 3.5 and 3.6, form the chronological basis of the stratigraphy of the north-east bay of Lake Wanum.

Due to the complex nature of the fine stratigraphy, and the marginal setting of the coring sites, the majority of the samples for dating were chosen from the core LW II. These served as a check on the continuity of sedimentation in the core, and provided a basis for the accurate assessment of sedimentation rate during the period of deposition.

The few dates obtained from other cores serve to emphasise the problems of correlation based solely on stratigraphy. A date of 2070 ± 130 (ANU-1449) which immediately overlies a narrow but distinct clay band in core LW I can be correlated directly with a similar date of 2070 ± 80 (ANU-1646) from core LW II, some 300 m distant, where no trace of the inorganic horizon is visible. Even between cores less than 25 m apart correlation of the fine stratigraphy is ambiguous. A satisfactory description of the three dimensional extent of the various sedimentary horizons in the north-east bay area would therefore seem to require a greater number of closely spaced cores, or many more radiocarbon dates to substantiate possible correlations between the existing cores.

## *SWAMP DEVELOPMENT IN THE LAKE WANUM AREA*

At this stage it is possible to advance a preliminary hypothesis in an attempt to explain the observed features of the sedimentary sequences and the present swamp distribution in the Lake Wanum area. This model will then serve as a testable framework for the subsequent accounts of sediment and pollen deposition rates, and of the evolution of the swamp vegetation.

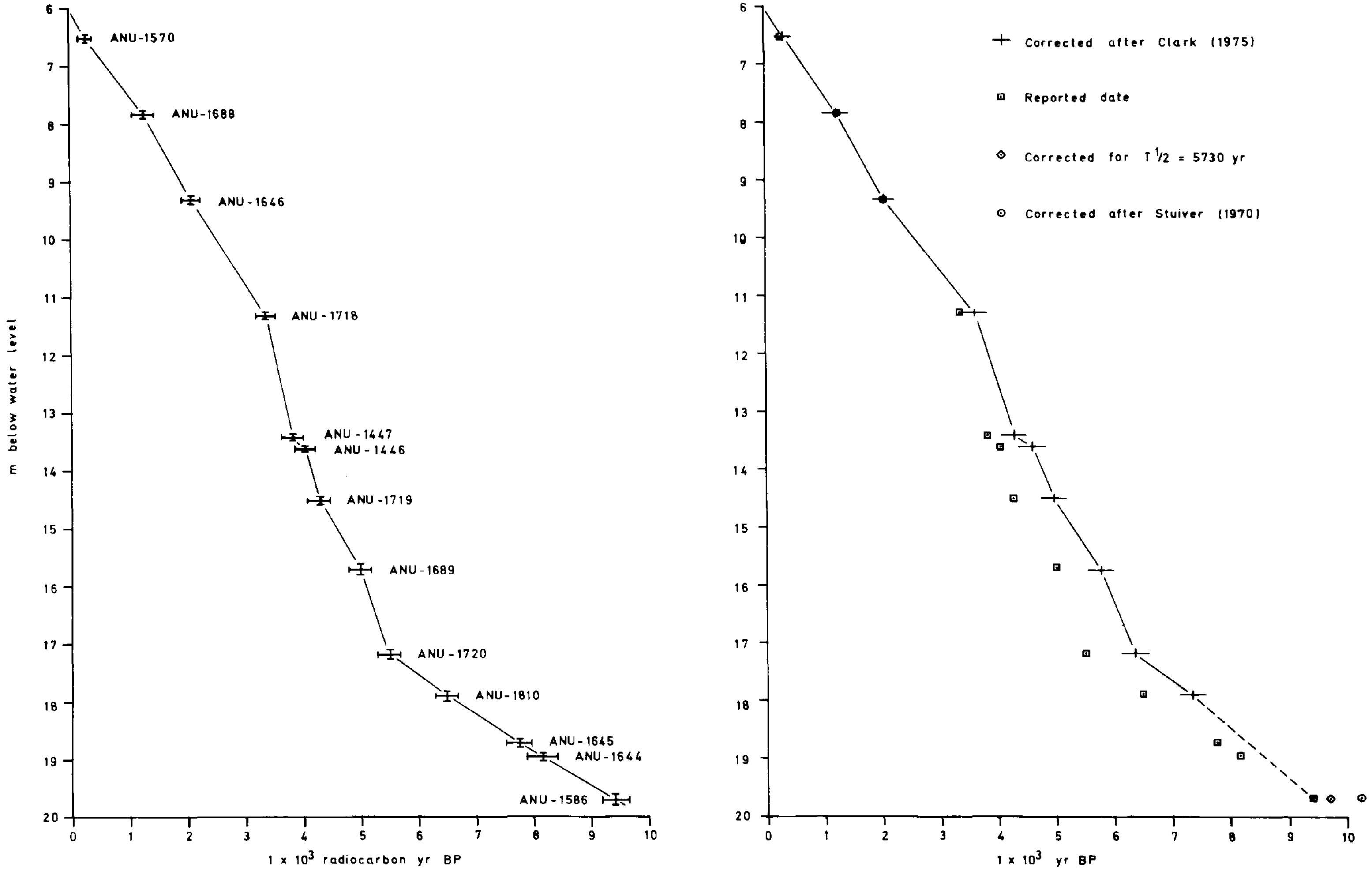
Of the sediments recovered from the north-east bay of Lake Wanum, none are similar to the fine organic mud (*Limus detritosus*) accumulating today in the deeper part of the basin. In fact, many of the cores show sedimentary sequences in their lower portions which appear more similar to those found in the shallower water situation of Redhill Swamp. It is probable that most of the sediments of the north-east bay cores were formed in less than 10 m water depth. The base of the longer cores is on average 20 m below the present water surface. If the possible effects of subsidence and sediment compaction can be discounted, this in itself suggests a progressive increase in the water level of the lake basin, above that caused by sediment infill, during the period of the sedimentary record.

There are several ways in which such an increase could possibly occur. Firstly, given a totally enclosed basin, rise in water level could be achieved by increased effective precipitation or run-off, or a combination of the two. Alternatively in a basin with at least an intermittent outflow, such as is the current situation at Lake Wanum, impedance of this outflow by organic or inorganic sedimentation could cause an increase in water level without any other change in the hydrological regime of the basin. There is perhaps some evidence for the second proposition in the topography of the lake basin, and the results of corings from the southern end of Lake Wanum. The extensive deposits of grey clay, overlain by only a thin band of organic material could be indicative of one or more episodes of inorganic deposition, presumably caused by overflow of the nearby Oomsis Creek. The presence of a similar horizon of grey clay, some of which incorporates detrital fragments of swamp vegetation, in a core from the deepest part of the lake basin could be seen as lending weight to this theory.

The hypothesis may be extended to explain the origin and distribution of other swamps and lakes in the area. The only available outflow from the Redhill Swamp basin is towards Oomsis Creek and the same situation occurs in the case of the Erom-Erom lakes, although here build-up of organic swamp sediments may also have assisted impedance of the drainage. A number of swamps are found in similar topographic locations between the hill slopes and the riparian or 'alluvium' forest of the creek area, particularly to the west of Lake Wanum.

The date of onset of organic deposition at these other swamps is largely a matter for conjecture, as the only radiocarbon dates come from the north-east bay of Lake Wanum. Here the base of the organic sediments give a date slightly older than 9500 BP. However, as this site is in a marginal area of the large lake, it is quite possible that onset of accumulation in deeper parts of the basin occurred earlier than this date.

FIGURE 3.10. Lake Wanum core LW II: Age/depth profiles for (a) uncorrected $^{14}C$ dates ($\pm$2 S.D.) and (b) recalibrated $^{14}C$ dates ($\pm$2 S.D.)



## *ESTIMATION OF ANNUAL SEDIMENT ACCUMULATION RATES*

### *The radiocarbon chronology*

The eleven radiocarbon dates from core LW II together with two correlated from an identifiable horizon in the adjacent LWA I core are shown plotted against depth in Fig. 3.10a. The physical mid-point of the sample is taken as the horizon to which the date refers. These determinations appear to provide a sound chronological basis for the estimation of annual rates of sediment and pollen deposition throughout the core. The dates follow the correct sequence, and there is no evidence of major discontinuities in sedimentation, or of any severe disturbance of the deposits. Neither is there any suggestion of a significant disequilibrium between the $^{14}C$ content of the sediments, and that of the atmosphere. Extrapolation of the rate of accumulation between the two uppermost dates to the diffuse sediment/water interface produces an apparent date close to the present. It can therefore only be assumed that a similar equilibrium has prevailed during the past.

### *Corrections to the radiocarbon timescale*

Before attempting to construct the most appropriate sediment accumulation curve consistent with both the radiocarbon dates and the observed stratigraphy, it is necessary to consider certain limitations of the dating technique itself. These have been recently summarised by Olsson (1974) and Polach (1976).

By agreement, radiocarbon laboratories report dates as calculated on the basis of Libby's proposal of 5568 ± 30 years as the half-life ($T_{\frac{1}{2}}$) of $^{14}C$ (Libby, 1949). Strictly, such determinations should be corrected in line with the accepted revised half-life of 5730 ± 30 years (Godwin, 1962). In practice this results in a small increase of about 3% in the reported age.

A more serious deviation from the absolute chronology is caused by lack of constancy, or secular variation, in the production rate of atmospheric $^{14}C$ over time. Long term increases in the production rate appear to occur in response to higher effective cosmic ray flux, perhaps due in part to decrease in the intensity of the geomagnetic field. This phenomenon was first observed by de Vries (1958), and its extent during the last 1200 years demonstrated by Willis *et al.* (1960) using a radiocarbon dated annual tree growth-ring sequence.

Subsequently a comprehensive tree-ring chronology has been constructed for the last 7500 years (Ferguson, 1970) using the wood from North American conifers *Pinus aristata* and *Sequoia gigantea*. Seuss (1967) produced the first calibration curve for the conversion of radiocarbon dates into 'absolute' ages, and his revised version (Suess, 1970) has been widely used. Several other correction curves or tables have also been produced from essentially the same tree-ring data, including those of Damon *et al.* (1972) and Ralph *et al.* (1973). The calibrations differ mainly in the degree of emphasis placed on small scale fluctuations in the atmospheric $^{14}C/^{12}C$ ratio, Suess's possessing the most 'wiggles' whilst that produced by Damon's group exhibiting only the longer term variations. Olsson (1974) synthesises these results by drawing a band covering 87% of the data points that she deems reliable.

The subjective method of obtaining the then existing calibration curves is criticised by Renfrew and Clark (1974) as being statistically unsatisfactory. As a result, Clark (1975) attempts to construct a curve using valid statistical techniques. He considers all the available data relating tree-ring ages to radiocarbon determinations, omitting over one-third not considered suitable for analysis. A calibration line is then derived using a curve fitting technique based on spline functions. The resulting curve is very similar to that drawn by Olsson (1974), but has the advantage of statistically defined confidence limits for the corrected ages.

No continuous radiocarbon dated dendrochronological sequence exists for the period before about 7500 years ago, although an extension of the existing chronology back to about 10 000 years ago is quite feasible (Ferguson, 1970). The information about atmospheric $^{14}$C production beyond this date is therefore largely based on directly or indirectly dated varve sequences. The most comprehensive of these is the revised version of the Scandinavian varve chronology originally established by De Geer (1912) and discussed in relation to the radiocarbon time-scale by Tauber (1970). The chronology is dated indirectly by correlation of pollen zones between the lake sediments and nearby radiocarbon dated autochthonous deposits.

A sequence of varves from the Lake of the Clouds, northern Minnesota, U.S.A., counted by Craig (1972), has also been employed for calibration of the radiocarbon time-scale. The varved sediments, estimated to have been deposited over the last 9500 to 10 000 years, have been directly radiocarbon dated by Stuiver (1970).

Both varve chronologies imply atmospheric $^{14}C$ deviations for the period up to 7500 years similar to those shown by the dendrochronologically based curves. Beyond this age, however, the two sequences diverge. Tauber's curve shows a trend towards the datum (19th century AD $^{14}C$ production rate) until 8500 or 9000 varve years BP when the curve levels out, and uncorrected radiocarbon ages ($T\frac{1}{2}$ = 5568) become almost synchronous with varve ages. A similar trend is shown by Stuiver's curve until about 8500 varve years ago, when the direction becomes reversed, and a continuing enrichment of atmospheric $^{14}C$ is indicated. The resulting discrepancy between the two chronologies thus becomes about 900 years at 10 000 varve years ago.

Whilst it is premature at this stage to accept either chronology as correct, the Scandinavian one does appear to be rigorously constructed, being derived from many geographically widespread varve sequences. Tauber's conclusions (Tauber, 1970) also appear to be supported by results from two other varve studies.

Vogel (1970) compares varve ages and radiocarbon dates from a Swiss site, using the varve chronology of Welten (1944). The trend in atmospheric $^{14}C$ concentration follows that postulated by Tauber until about 8500 BP. Prior to this date there appears to be a drastic reduction in $^{14}C$ production, which leads Vogel to cast doubts on the validity of the earlier section of the varve chronology.

A set of dated marine varves from Saanich Inlet, British Columbia, Canada (Yang and Fairhill, 1973), also produces results compatible with Tauber's. A decrease in atmospheric $^{14}C$ enrichment occurs until about 8500 varve years ago, values thereafter remaining close to the datum.

Such a trend may be supported by the theoretical models of Yang and Fairhill (1973), and Damon (1970). Fluctuations in the geomagnetic field intensity are assumed to follow a sinusoidal curve with a period of approximately 8000 years, peaking at about 2500 BP. The Saanich Inlet and Scandinavian results do not appear to confirm the theoretical increase in atmospheric $^{14}C$ concentration prior to about 9000 BP. This may be due to deficiencies in the model especially in relation to the time-lag in atmospheric response. This may not be constant, particularly if, as Damon (1970) suggests, the climatic influence on atmospheric $^{14}C$ levels may have been greater during the late Pleistocene period, than in more recent times.

### *The application of recalibrated radiocarbon dates*

In order to investigate the possible effects of secular radiocarbon variation on the average accumulation rate from core LW II, the following corrections were applied. Dates younger than 6500 radiocarbon years BP were adjusted for the revised half-life and for secular variation using the calibration tables of Clark (1975). For recalibration of dates older than this, it was assumed that the rate of $^{14}C$ production in the atmosphere at about 9000 BP was similar to that of the 19th century AD datum. As the uncorrected dates lie in a relatively straight line, an age/depth curve for the period 7500 to 9500 calendar years BP was approximated by connecting the oldest dendrochronologically calibrated date (ANU-1810) to the oldest date (ANU-1586) by a straight line. Possible corrections to the basal date for the revised half-life of 5730 ± 40 years and the calibration suggested by Stuiver (1970) are also indicated (Fig. 3.10b).

TABLE 3.3. *Comparison of average sedimentation rates of intervals between radiocarbon samples based on dates (A) as reported, and (B) corrected for revised half-life and secular variations*

| $^{14}$C sample interval | Mid-point of $^{14}$C sample (mm) | Depth interval (mm) | A<br>$^{14}$C date ± 1 S.D. ($T_{½}$=5568) | Time interval ($^{14}$C yr) ± 1 S.D. | Average sedimentation rate, mm $^{14}$C-yr$^{-1}$ (± 1 S.D.)<br>Min. | Mean | Max. | mean. $^{14}$C yr cm$^{-1}$ | B<br>Corrected date$^{a}$ ± 1 S.D. | Time interval (yr) ± 1 S.D. | Average sedimentation rate, mm $^{14}$C-yr$^{-1}$ (± 1 S.D.)<br>Min. | Mean | Max. | mean yr cm$^{-1}$ | % difference of mean mm yr$^{-1}$ from mean mm $^{14}$C-yr$^{-1}$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 6 000 | | - 25$^{b}$ | | | | | | - 25$^{b}$ | | | | | | | |
| A$_1$ | | 525 | | 285 + 60 | 1.52 | 1.84 | 2.33 | 5.43 | | 359 ± 78 | 1.20 | 1.46 | 1.87 | 6.84 | -20.7 | A$_1$ |
| | 6 525 | | 260 ± 60 | | | | | | 344 ± 78 | | | | | | | |
| A | | 1 300 | | 1000 ± 117 | 1.16 | 1.30 | 1.47 | 7.69 | | 903 ± 136 | 1.25 | 1.44 | 1.70 | 6.95 | +10.8 | A |
| | 7 825 | | 1260 ± 100 | | | | | | 1237 ± 112 | | | | | | | |
| B | | 1 480 | | 810 ± 128 | 1.58 | 1.83 | 2.17 | 5.47 | | 834 ± 147 | 1.51 | 1.77 | 2.15 | 5.64 | - 3.3 | B |
| | 9 305 | | 2070 ± 80 | | | | | | 2071 ± 95 | | | | | | | |
| C | | 2 000 | | 1290 ± 113 | 1.43 | 1.55 | 1.70 | 6.45 | | 1601 ± 148 | 1.14 | 1.25 | 1.38 | 8.01 | -19.4 | C |
| | 11 305 | | 3360 ± 80 | | | | | | 3672 ± 113 | | | | | | | |
| D | | 2 095 | | 460 ± 120 | 3.61 | 4.55 | 6.16 | 2.20 | | 615 ± 160 | 2.70 | 3.41 | 4.60 | 2.94 | -25.1 | D |
| | 13 400 | | 3820 ± 90 | | | | | | 4287 ± 113 | | | | | | | |
| E | | 200 | | 220 ± 135 | 0.56 | 0.91 | 2.35 | 11.00 | | 318 ± 163 | 0.26 | 0.63 | 1.29 | 15.90 | -30.8 | E |
| | 13 600 | | 4040 ± 100 | | | | | | 4605 ± 117 | | | | | | | |
| F | | 905 | | 250 ± 135 | 2.35 | 3.62 | 7.87 | 2.76 | | 363 ± 163 | 1.72 | 2.49 | 4.53 | 4.01 | -31.2 | F |
| | 14 505 | | 4290 ± 90 | | | | | | 4968 ± 113 | | | | | | | |
| G | | 1 200 | | 700 ± 135 | 1.44 | 1.71 | 2.12 | 5.83 | | 807 ± 165 | 1.23 | 1.49 | 1.87 | 6.73 | -12.9 | G |
| | 15 705 | | 4990 ± 100 | | | | | | 5775 ± 117 | | | | | | | |
| H | | 1 485 | | 490 ± 141 | 2.35 | 3.03 | 4.26 | 3.30 | | 571 ± 165 | 2.02 | 2.60 | 3.66 | 3.85 | -14.2 | H |
| | 17 190 | | 5480 ± 100 | | | | | | 6346 ± 117 | | | | | | | |
| I | | 715 | | 1000 ± 141 | 0.63 | 0.72 | 0.83 | 13.99 | | 993 ± 165 | 0.62 | 0.72 | 0.86 | 13.89 | + 0.1 | I |
| | 17 905 | | 6480 ± 100 | | | | | | 7339 ± 117 | | | | | | | |
| J | | 820 | | 1260 ± 156 | 0.58 | 0.65 | 0.74 | 15.37 | | | | | | | | |
| | 18 725 | | 7740 ± 120 | | | | | | | | | | | | | |
| K | | 225 | | 400 ± 177 | 0.39 | 0.56 | 1.01 | 17.78 | | 2061 ± 168 | 0.80 | 0.87 | 0.95 | 11.51 | +45.0 | JKL |
| | 18 950 | | 8140 ± 130 | | | | | | | | | | | | | |
| L | | 745 | | 1260 ± 177 | 0.52 | 0.59 | 0.69 | 16.91 | | | | | | | | |
| | 19 695 | | 9400 ± 120 | | | | | | 9400 ± 120$^{c}$ | | | | | | | |

[a] Corrected dates derived from the calibration curve and tables of Clark (1975)

[b] Approximate top of sediment taken as 1975 A.D.

[c] Date as reported.

The average apparent sediment accumulation results derived from the original radiocarbon dates are compared with those produced using the recalibrated dates in Table 3.3. The effect of applying the calibrations is to produce differences in sediment accumulation rates of over 30% for some dating intervals within the tree-ring calibrated section, and of 45% in the less rigorously adjusted period before 6500 radiocarbon years BP. The average accumulation rates based on the uncorrected dates display greater variation than do those based on recalibrated dates. Maximum deviation of the two occurs between approximately 2000 and 4500 radiocarbon years BP, the period that sees the most rapid sustained increase in the rate of atmospheric $^{14}C$ production. This period also encompasses the fastest average accumulation rates in the core (dating intervals D and F) and under the corrected chronology these rates become reduced substantially. Conversely, between 6500 and 9600 radiocarbon years BP, if the declining trend of atmospheric $^{14}C$ production be accepted, the corrected average accumulation rate shows an increase of 45% over that implied by the original dates.

The general trend of atmospheric $^{14}C$ concentration over the past 7500 years is now well established, and is essentially synchronous and of the same extent over the globe. However, there still remain uncertainties as to the scale and direction of fluctuations before this date. In addition, the importance of changes in the $^{14}C$ production rate showing a shorter periodicity is yet to be resolved. It may be, as Olsson (1974) has proposed, that for samples thought to represent a small duration one should employ a calibration curve, such as Suess's, that emphasises these minor fluctuations. The radiocarbon samples analysed from Lake Wanum variously represent time-spans of from about 60 to 300 years, depending on the prevailing accumulation rate. Short duration fluctuations would obviously influence the former samples to a greater extent than the latter.

Such unresolved problems in the application of radiocarbon calibration curves raise the question of the profitability of applying systematic corrections at all. The main constraint, in the current context, is the lack of an adequate calibration for the period prior to 6500 radiocarbon years ago. The trends in average sediment accumulation rate remain similar after application of the corrected dates, and there are no changes in the rate as great as an order of magnitude for any dating interval.

It was therefore decided to present the results of the sediment and pollen deposition studies on the basis of the reported radiocarbon ages alone, whilst taking into account the possible effects of gross secular variations in the interpretation. Thus all ages subsequently discussed in this thesis refer to uncorrected ($T_{\frac{1}{2}}$ = 5568) radiocarbon years BP (before present; 'present' = 1950 AD), unless indicated to the contrary.

### *The derivation of sediment accumulation rates*

The reliability of an average sediment accumulation rate based on radiocarbon determination obviously depends on the frequency and magnitude of fluctuations in the true rate, and the number of dated horizons available. Given a series of dates, there is a number of ways in which a 'best fit' curve for the accumulation rate may be derived.

In a situation where the accumulation rate is thought to be essentially static, it may be possible to fit a simple regression line to the given dates. Thus Davis and Deevey (1964) used a least-squares regression line to produce an accumulation curve for the late-glacial section of their Rogers Lake core. Ogden (1967) attempted a similar method for two other north-eastern American lakes, but found standard deviations from the regression lines to be large, and his original assumptions 'too simple'. Maher (1972) also fitted a least-squares regression to dates from Redrock Lake, Colorado, and found a good linear correlation between age and depth. However, systematic deviations from the linear trend, probably caused by increasing compaction of the older deposits, could be best explained by fitting a power (log-log) function to the data. Using a polynomial regression curve on dates from Lake Immeln, Sweden, Digerfeldt (1974) obtained a good agreement between observed and predicted ages.

Where a very large number of radiocarbon dates are available it should be acceptable to employ statistically more complex curve-fitting techniques. On the other hand, such close dating also better enables the fitting of a subjective curve expressing the 'general relationship' between the sample depth and age (e.g. Davis, 1969). Alternatively, a simple curve smoothing technique such as the calculation of a running mean for five consecutive dates, may be employed. Aaby and Tauber (1975) used this method to reconstruct rates of peat formation at Draved Mose, Denmark, as they did not wish to make the assumption of a linear accumulation rate presupposed by the use of a straight line regression. Where a substantial number of dates indicates a fairly smooth curve, there may be, as Kendall (1969) suggests, 'no apparent or statistical method more accurate than simply connecting the $^{14}C$ points... with straight lines'.

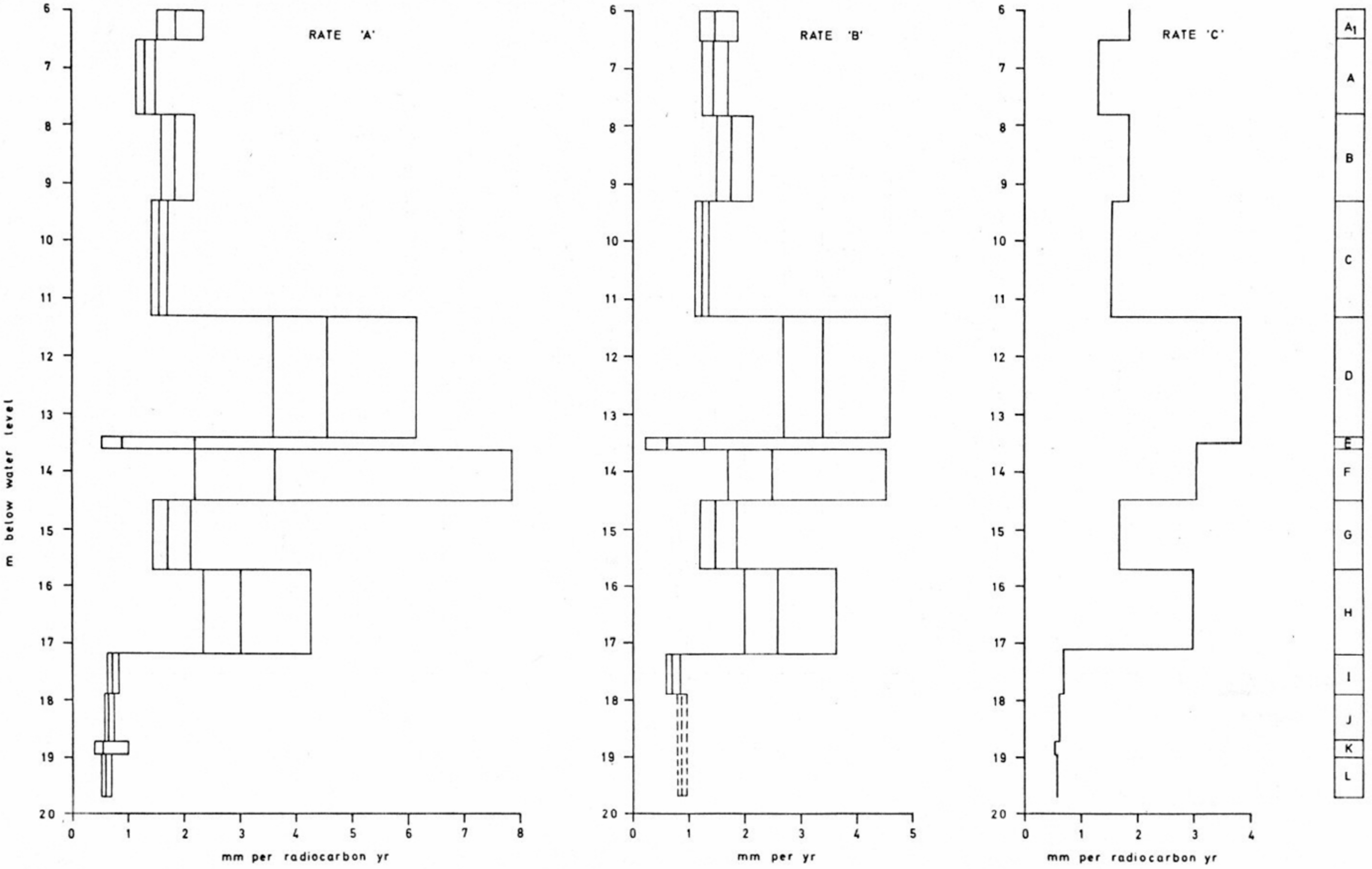
*Estimation of sediment accumulation rates for core LW II*

Examination of both the age/depth curve based on the reported radiocarbon dates, and on the recalibrated dates (Fig. 3.10) leads to the conclusion that no simple linear relationship exists between depth and age. Neither can the fluctuations in the average sediment accumulation rate (Table 3.3) be explained by autocompaction of the deposits alone. Although the accumulation is considerably lower towards the base of the core (dating intervals I-L) the sediment density profiles (Fig. 3.9) do not show a corresponding degree of increase during this time. Furthermore, the periods of most rapid apparent accumulation occur in the middle sections of the core, not towards the top as would be the case were a constant deposition rate modified only by compaction to be postulated.

It is therefore concluded that measurable change in the real accumulation rate has been operative during the time-scale represented by the core. Consequently it does not seem appropriate to derive an annual accumulation curve by fitting a simple regression model to the age/depth curve. Lack of sufficient replicated samples precludes analysis of the age/depth results using more sophisticated, non-linear statistical techniques.

A first approximation (Accumulation Rate 'A') of the annual accumulation rate (Fig. 3.11a) was therefore derived from the figures in Table 3.3. This represents the average rate of

FIGURE 3.11. Lake Wanum core LW II: Average sediment accumulation rates



apparent annual sediment accumulation, disregarding autocompaction, between pairs of radiocarbon dates. A curve produced in a similar fashion from the recalibrated dates (Accumulation Rate 'B') is shown in Fig. 3.11b. The values for minimum and maximum average rates are based on plus or minus one standard deviation of the interval between dates. This represents an overestimation as the calculation method treats each pair of dates as independent from the adjacent pairs, which is obviously not the case. It must be emphasised that the maximum and minimum limit is based only on the size of the combined radiocarbon counting errors, in relation to the length of the time interval between dates. It therefore applies only to the *average* accumulation rate and gives no direct indication of the amplitude and frequency of fluctuations around this mean. It may be reasonable to suppose that where consecutive average values are similar, fluctuations around these are generally similar also. Conversely, where averages for adjacent dating intervals are very dissimilar, this may be caused by differences in the amplitude and/or frequency of fluctuations in the accumulation rate.

A curve better representative of the actual accumulation rate needs to take into account

(a) the statistical significance of the individual radiocarbon dates and of the intervals between dates, and

(b) any evidence in the stratigraphy of discontinuities in the deposits, or abrupt changes to the rate of sediment accumulation.

Although the general sequence of dates appears valid, several of the paired ages are close in relation to their counting errors. In particular, the estimated duration of intervals E and F is less than twice the standard deviation of each interval. Using the criteria of Polach and Golson (1966) it is thus 'fairly probable' that the two age determinations defining each interval differ with statistical significance, but the exact interval between them cannot be estimated with accuracy.

The horizon encompassed by interval E is a well defined grey clay (*As*) band which possibly represents a slight unconformity, due to erosion of earlier sediment, or cessation of organic sedimentation. Lacking clear evidence, an accumulation rate for this interval is assumed that is not too dissimilar from the adjacent periods. A mean of the two dates ANU-1447 and ANU-1446 was therefore taken. Average accumulation rates were then calculated for two intervals, DE and EF, instead of three, becoming 3.85 mm $yr^{-1}$ and 3.07 mm $yr^{-1}$ respectively. This procedure serves to increase the timespan of each interval in relation to its standard deviation and also reduces the fluctuation in the average accumulation rate.

All other dating intervals are of comparatively long duration in relation to their error terms, and may therefore be taken as statistically well defined.

At two boundaries C/DE, and H/I, a change in the accumulation rate by an order of magnitude appears to be indicated. Only one of these shows a concurrent indication in the stratigraphy that might be associated with such a major change in sediment accumulation. The fourfold increase in the rate between intervals H and I appears to be marked by an horizon of gritty orange-grey clay (*Ga* + *As*) with a sharp upper boundary. This horizon produces the greatest peak on the inorganic sediment density curve (Fig. 3.9). Although an unconformity in the sequence during interval I is possible, this seems unlikely given the concordance of accumulation rates between this and the underlying periods. As the gritty clay penetrates well into the I interval, it seems more reasonable to propose a rapid increase in accumulation subsequent to this stratum, although the clay may reflect initiation of the change. The sediment analysis sample taken from 1710 to 1711 cm that includes a proportion of the clay band, was regarded as having an accumulation rate intermediate between that of intervals H and I.

A grey clay band (*As*) in interval G may also be responsible for a slight discontinuity in accumulation around 1487 to 1488 cm. This may account for the lower average accumulation rate for this period. However, no correction has been attempted.

Stratigraphic evidence for abrupt changes in the accumulation rate at the C/DE boundary is lacking. Theoretically, a 'smoother' curve would probably represent a better approximation of the actual accumulation rate at this boundary. Any such modification of the curve would however have to be extreme to affect the widely spaced samples in this section of the core. Given the acceptable radiocarbon dates, major modification was considered inappropriate, and no correction has been applied.

The average annual sediment accumulation curve, incorporating the modifications described above, is shown in Fig. 3.11c. The average accumulation rate of wet sediment for any part of the core may be read from this curve. Any sample occurring at a boundary between dating intervals is assumed to have an accumulation rate intermediate between the two.

*Gravimetric estimates of annual sediment deposition*

By applying the corrections for the average annual sediment accumulation rates to the figures for density[1] (mg dry weight $ml^{-1}$) of organic and inorganic sediment (Fig. 3.9) an estimate of annual gravimetric deposition rate for these sediment fractions may be obtained. Such estimates are shown assuming accumulation rate 'A' (Fig. 3.12) and accumulation rate 'C' (Fig. 3.13).

The main differences between the estimates based on the two accumulation rates are in the values for the inorganic sediment fraction. This curve is characterised by sharp peaks that probably represent depositional phases of short duration in relation to the dating interval in which they occur. Applying accumulation rate 'A', the highest value for inorganic deposition is found in the sample from 1710 to 1711 cm. Using the modified rate 'C', this value decreases, and the distinct clay band at 1346 to 1348 cm gives the largest peak. With the current method of dating it is impossible to resolve accurately the absolute annual deposition rate, or even the relative deposition rate for such sedimentary episodes.

As the mean value for organic sediment density (Fig. 3.9b) remains essentially similar throughout the core, variation in the annual deposition rate is very largely a product of the correction for average accumulation rate. Thus the major difference reflected in the curves derived from the two accumulation rates is in the middle section of the core. Here the higher accumulation rates suggested by rate 'A' are reflected in increased organic deposition also.

---

[1] i.e. bulk density

*FIGURE 3.12. Lake Wanum core LW II: Gravimetric sediment deposition rates based on accumulation rate 'A'*

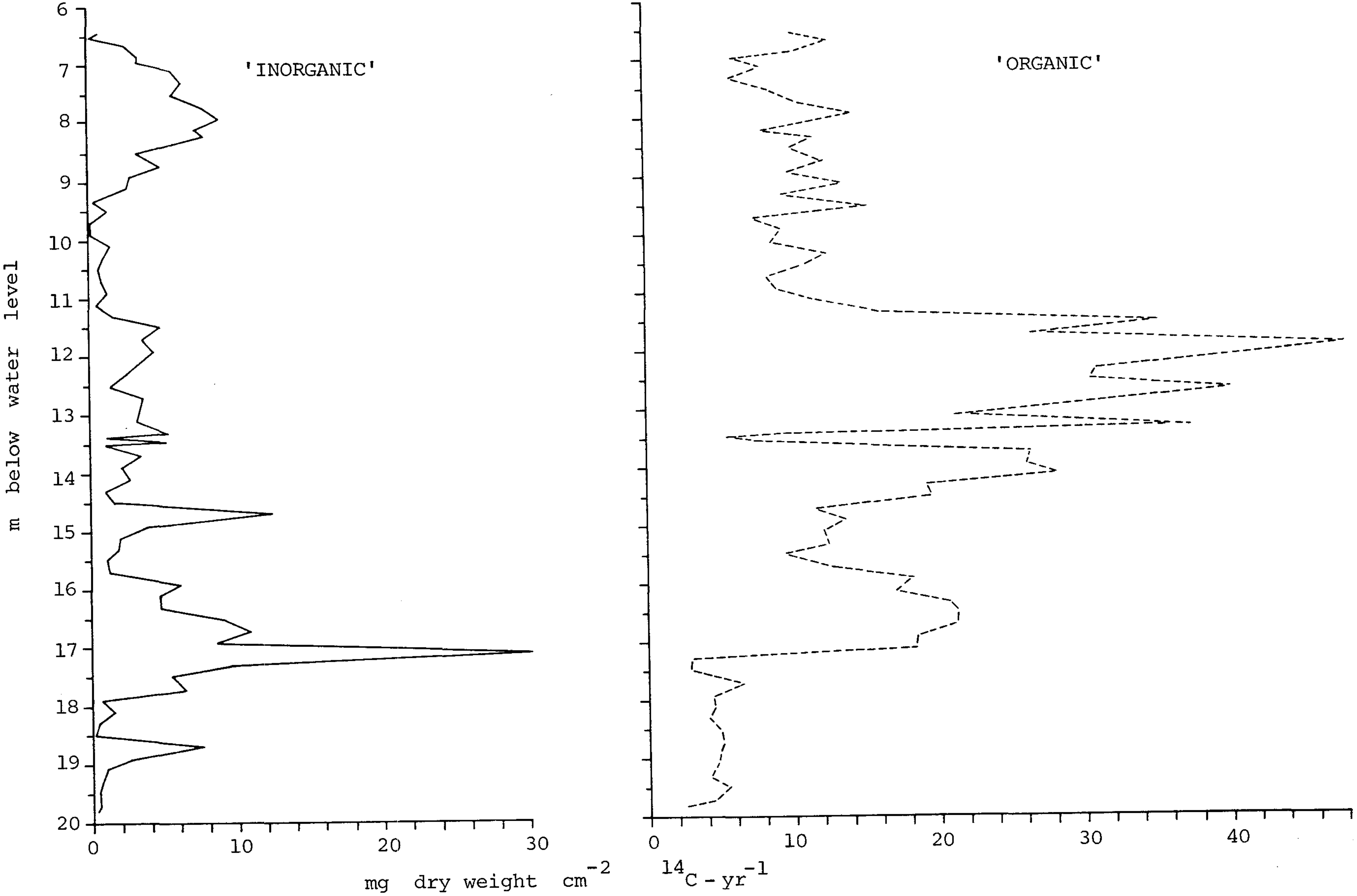
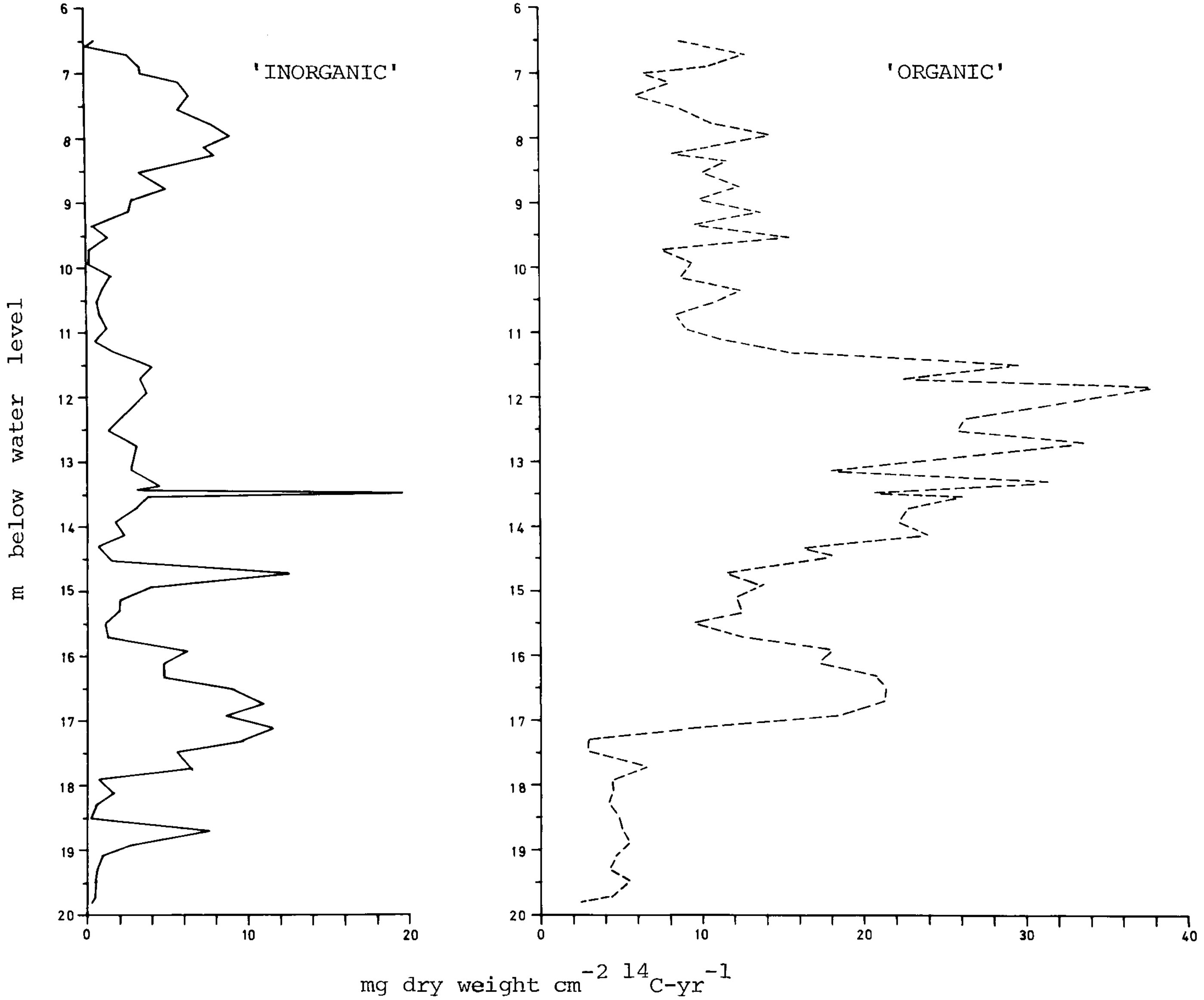


FIGURE 3.13. *Lake Wanum core LW II: Gravimetric sediment deposition rates based on accumulation rate 'C'*



## *SUMMARY OF MAJOR TRENDS IN THE SEDIMENTATION OF CORE LW II*

The main trends in the average sediment accumulation rates and annual gravimetric deposition rates in core LW II may be summarised by dividing the sequence into three zones as follows.

(1) From the base of the core at about 9500 BP until *c.* 5500 BP (6300 years corrected age).

(2) A period following this of about 2000 years until approximately 3400 BP.

(3) The uppermost part of the core representing deposits from about 3400 BP to the present.

The lowest zone exhibits a low but fairly constant average sediment accumulation rate of between 0.5 mm $yr^{-1}$ and 1.0 mm $yr^{-1}$. Although the deposits are predominantly organic two peaks occur in the inorganic deposition rate. These are produced by horizons containing gritty orange-grey clay (*Ga* + *As*) rather than the plastic grey clay (*As*) more common above.

The middle zone possesses the most rapid accumulation rate and the highest values for both organic and inorganic fractions. A number of phases of grey clay sedimentation occur within the predominantly organic matrix. The most intense of these appear to be of short duration. This zone also displays the largest apparent fluctuations in accumulation rate.

In the uppermost zone, the average accumulation rate appears to stabilise at between 1 mm $yr^{-1}$ to 2 mm $yr^{-1}$. Although the sediment is mainly organic without discrete clay bands, there is a gradual increase in inorganic sedimentation rising to a peak at about 1300 BP, and thence declining towards the top of the core.

This three-zone generalisation may be the most appropriate level of resolution at which to review the accumulation and deposition rates from the core. Stratigraphic corroboration for gross changes in the accumulation rate is generally lacking. Certainly, the changes apparently represented in the central section of the core must be interpreted with circumspection, this being the period both of greatest fluctuation in sediment accumulation, and of the most rapid sustained change in atmospheric radiocarbon concentration yet demonstrated.

## *COMPARISONS WITH OTHER CORES*

Although there are few horizons in the other cores from Lake Wanum that can be correlated either by radiocarbon dates or stratigraphic markers, it is possible to derive gross accumulation rates for several other cores.

Within the western part of the north-east bay, cores LW II and LW 6 possess closely similar average accumulation rates (1.46 mm yr$^{-1}$ and 1.48 mm yr$^{-1}$ respectively) for their total periods of sedimentation. During about 4000 BP to the present, core LWA 1 appears to record a slightly higher accumulation rate tha~~t~~n LW II, although this could be explained by lack of recovery of the uppermost highly unconsolidated material. LWA 4 also shows a similar, or perhaps slightly higher accumulation rate than LW II for this period.

The most rapid accumulation rate for any period is shown by the upper section of core LW I. Here the interval between a date of 2070 BP and the present is represented by 955 cm of loosely compacted fibrous organic deposit (*Th*) giving an average accumulation rate of 4.6 mm yr$^{-1}$. This figure is more analogous to the highest estimate for the accumulation rate of dating interval D in core LW II than with the synchronous deposits from the latter core.

Extrapolation of possible accumulation rates to the south swamp suggests an accumulation time of perhaps only two to six years for the thin cover of organic deposit in that area.

Such comparisons indicate that the sedimentation results from core LW II may be representative of more general conditions in the western part of the north-east bay. Although the range of deposits found in the cores from the central area of the bay is similar there are differences in the stratigraphy and accumulation rates by comparison with the cores from the western margin of the bay. This divergence could be explained by the presence of dry land between the two coring areas. Given a lower water level, this is quite feasible, as solid ground occurs under less than 1 m of water about 50 m south-west of LW I coring site. The possibility of a less continuous water surface must therefore be taken into account when attempting to interpret the results from core LW II in terms of events in the Lake Wanum basin as a whole.

# CHAPTER 4

## SWAMP AND LACUSTRINE DEPOSITS OF YANAMUGI

Yanamugi ($6^{\circ}24'$S, $146^{\circ}17'$E) is a small lake located on the southern margin of the Markham Valley, about 85 km W.N.W. of the Huon Gulf and 1 km N.W. of the village of Yatsing. The site was first visited briefly during 1974, stratigraphic coring being carried out in 1976. Work in both years took place during the dry season (May to September) as access to the area from the Highlands Highway is by fording the Markham River.

The valley at this point is flanked on the south by a localised outcrop of limestone, part of the extensive Omaura Greywacke unit of Middle to Upper Oligocene age (Tingey and Grainger, 1976) that forms nearby Wasiang Mountain (alt. 990 m). As shown by Fig. 4.1 Yanamugi lies to the west of the first ridge, enclosed on three sides by limestone scarps (Plates 4.1 and 4.2). The area to the north, a shallow lip leading to the Markham Valley, is a small swamp dominated by sago (*Metroxylon sagu*). It is likely that this provides an intermittent outflow for the lake. Sina Creek, a permanent watercourse originating in Wasiang Mountain some kilometres to the north, flows close to the lake basin at the edge of the valley. There does not appear to be a permanent connection between the lake and the creek.

Yanamugi lake is approximately 300 m by 190 m in extent, with a surface area of about 3.5 ha. Its exact altitude is not known. Pocket aneroid barometer readings showed the water surface as about 170 m above sea level, 5 m above the plain of the nearby Markham River, similarly measured. The recent detailed survey by Holloway *et al.* (1973), however, gives the latter value as 200 m above mean sea level.

*FIGURE 4.1. Sketch map of the Yatsing area*

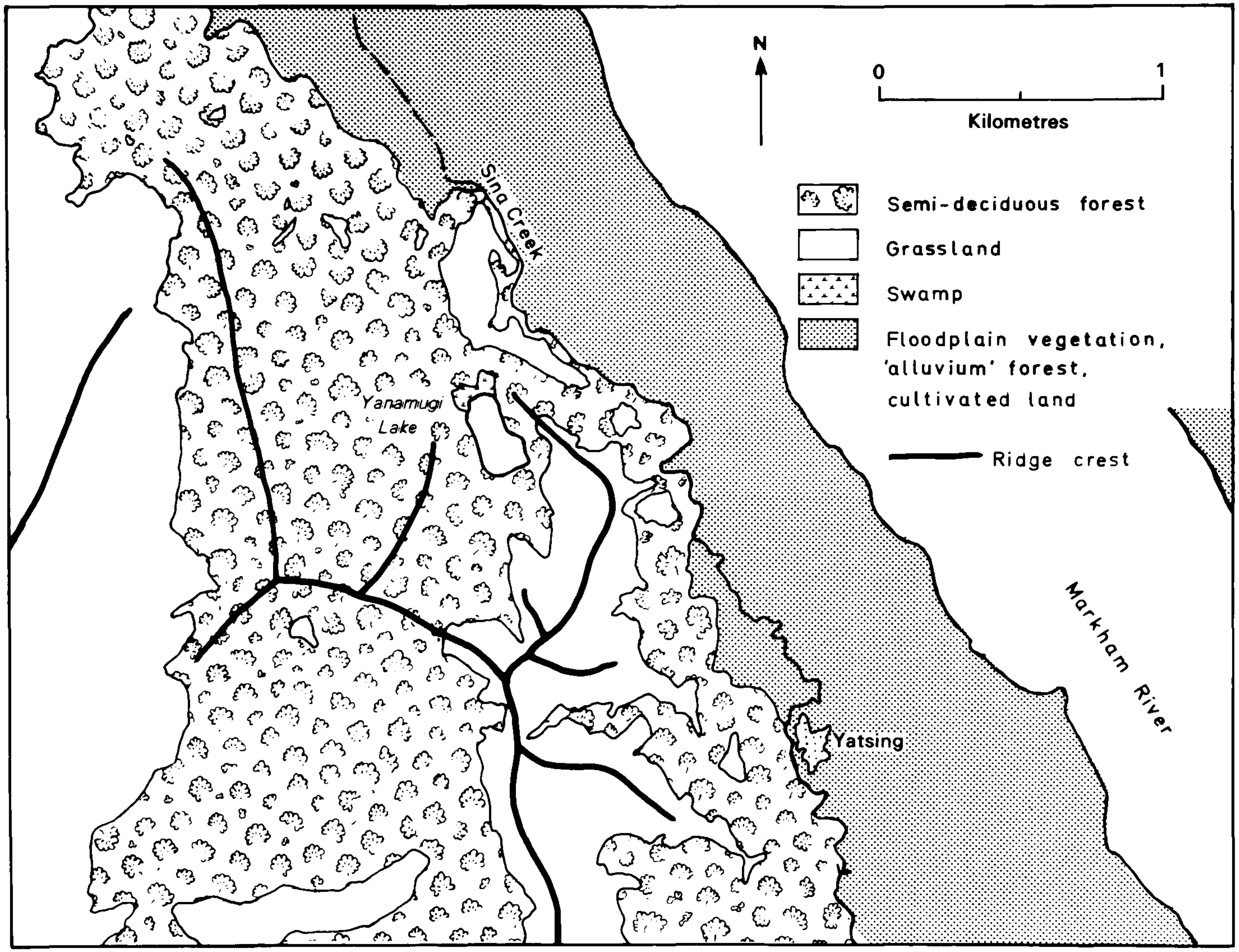
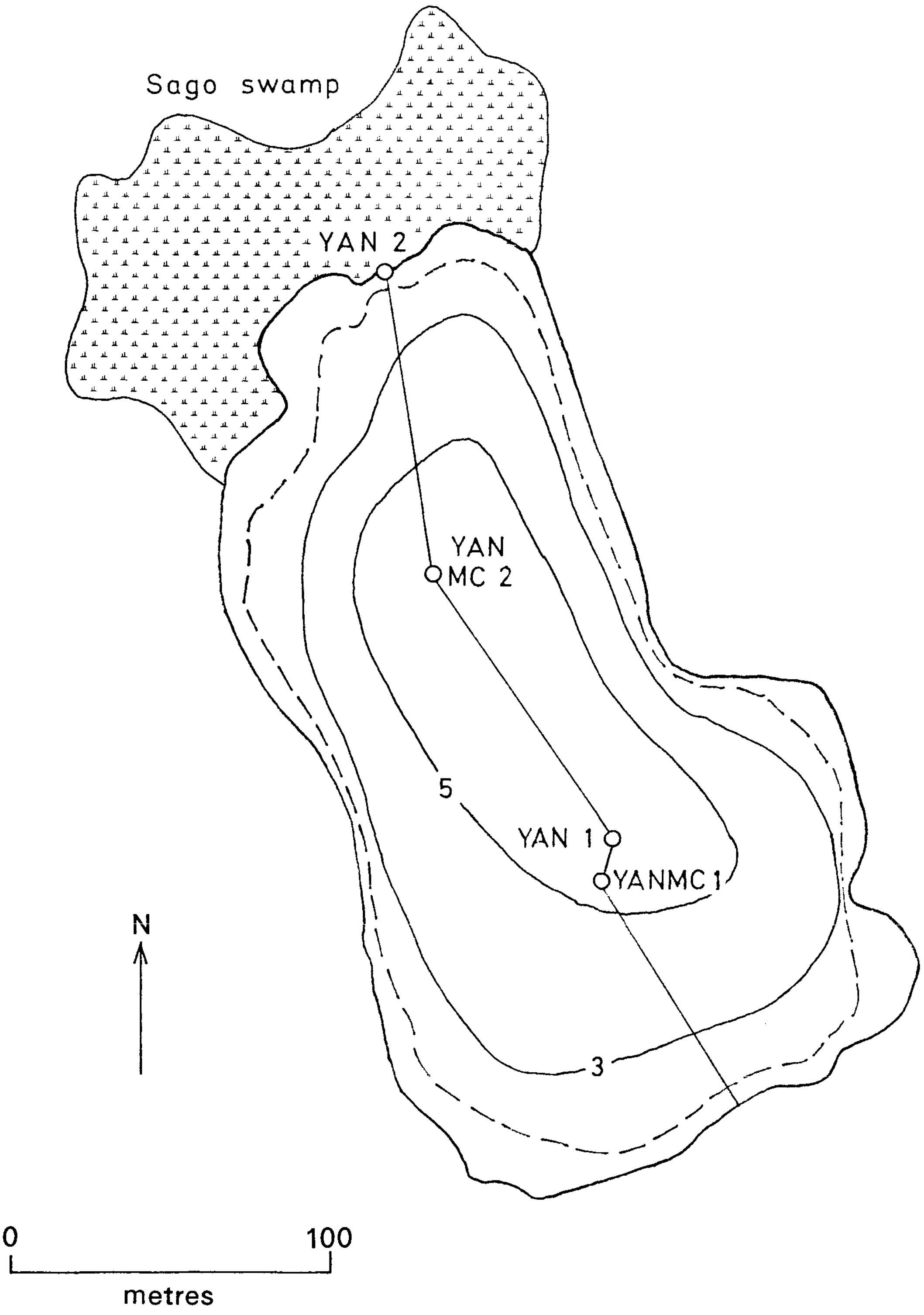


*PLATE 4.1.* Yanamugi lake, an oblique aerial view from the east. Much of the grassland to the south has been recently burnt.

*PLATE 4.2.* Yanamugi lake from the south. The semi-deciduous nature of the surrounding forest is clearly apparent. The plain of the Markham Valley is seen in the distance.

FIGURE 4.2. *Yanamugi: Bathymetry and core locations. The dotted line shows the approximate extent of emergent aquatic vegetation. Underwater contours are in metres.*



Three sounding transects established the gross bathymetry of the lake basin (Fig. 4.2). The maximum water depth recorded was 5.25 m and much of the central area is a level bottomed basin just over 5 m deep. The sides of the basin tend to be steeper along the western and eastern shores. Water marks on the surrounding limestone suggest that the lake level may have been higher in the past, although whether this is a consistent wet season occurrence, or a less frequent phenomenon, is not known.

The origin of the lake basin remains a matter for speculation. It may have formed as a solution feature in the limestone, as conspicuous dolines do exist within the area. One, about 5.5 km south of Yanamugi, forms a small circular pond with a fluctuating water level. A legend of the local Adzera people (Holzknecht, 1973) invokes spirit-induced earth movements. This may indeed have some basis in fact, either in relation to karstic collapse or as a reflection of the tectonically active nature of the whole region.

## *STRATIGRAPHIC INVESTIGATIONS*

### *Coring techniques*

Apparatus similar to that used at Lake Wanum was employed for stratigraphic investigations at Yanamugi. However, coring was performed from the anchored boat, and no casing was used. The locations of all cores obtained are shown in Fig. 4.2. A 4.5 m core (YAN 1) was recovered from under 5.25 m of water using the hand operated piston sampler. It proved impossible to penetrate sediments deeper than this under open water due to instability of anchorage and the lack of core casing. A second long core (YAN 2) 10.35 m in length was therefore obtained by securing the boat to swamp vegetation over shallow water at the margin of the sago swamp in the north of the basin. The corer was thus able to sample the compact sediments to a depth of 11.52 m below water level, whilst an auger bit penetrated a further 1.65 m without striking bedrock.

In addition, two sediment/water interface cores (YANMC 1 and YANMC 2) were collected using the Mackereth one-metre corer. All cores were returned to Canberra for analysis.

### *The stratigraphy of Yanamugi*

A diagrammatic representation of the generalised stratigraphy of all Yanamugi cores is shown in Fig. 4.3. A more detailed account of YAN 2, the longest core and that selected for pollen analysis, is given in Table 4.1.

The three cores from the central area of the lake basin consist predominantly of inorganic deposits, two basic sediment types being recognised under Troels-Smith's classification (Troels-Smith, 1955):

(i ) *Limus calcareus* (*Lc*) is a usually light yellowish-brown coloured, sometimes granular, calcareous mud or marl that reacts vigorously with cold dilute hydrochloric acid. When dry, the mud can be crushed readily with only slight pressure. A predominantly autochthonous origin is suggested for this sediment.

(ii) The second major inorganic component of the deposits is a sticky, plastic grey clay, *Argilla steatodes* (*As*), consisting of very fine mineral particles. In the Yanamugi cores a proportion of diatomaceous clay *Limus siliceus organogenes* (*Lso*) may also be present in these horizons. The clay produces no reaction with hydrochloric acid and becomes extremely hard on drying. With the exception of any diatom fraction this clay is probably allochthonous in origin, perhaps derived from the insoluble residue of the surrounding limestone.

FIGURE 4.3. *Generalised stratigraphy of Yanamugi*

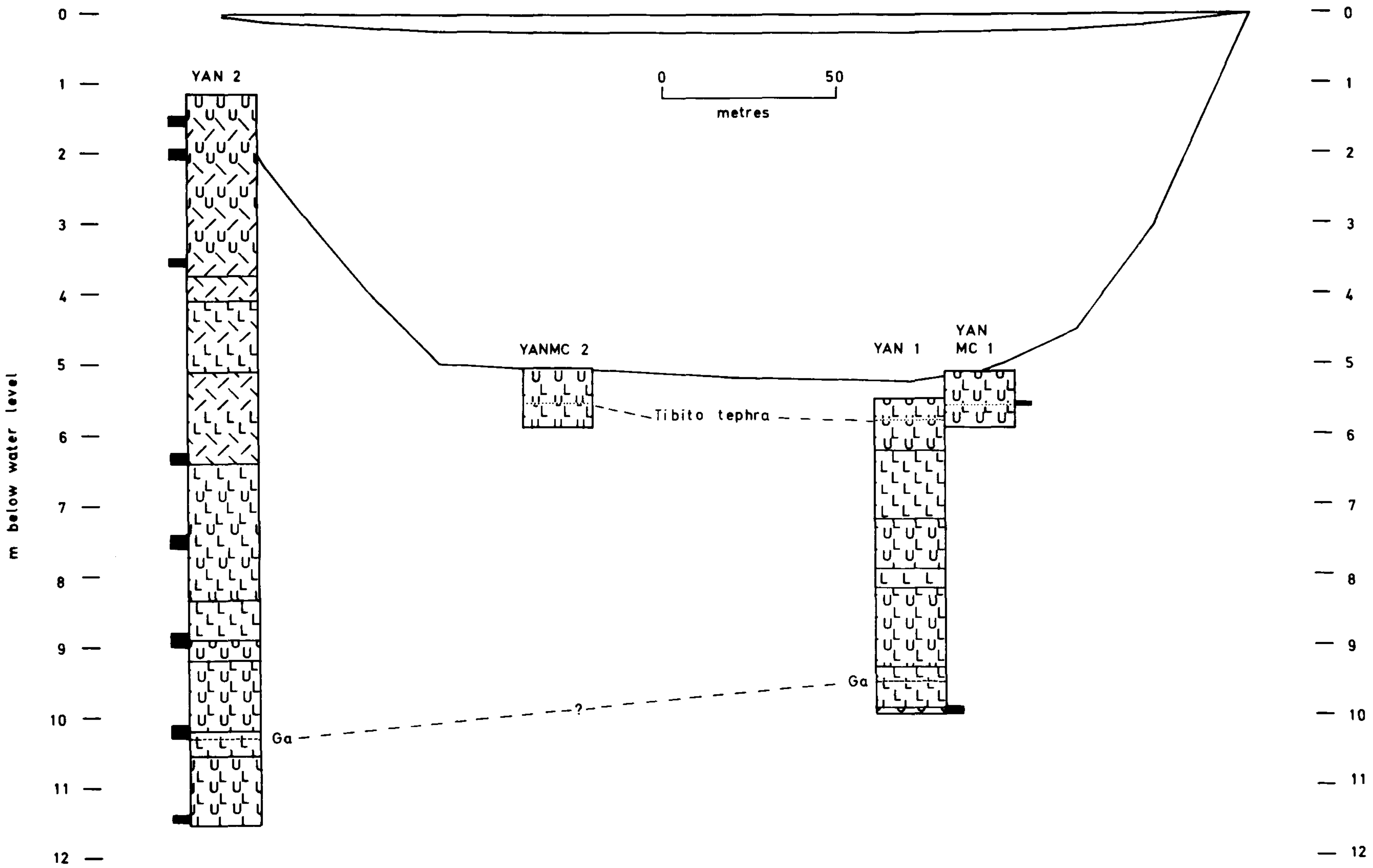


*TABLE 4.1. Stratigraphic description of core YAN 2*

| Depth of horizon (cm below datum) | Colour | Structure and General description | Troels-Smith Indices | | | | Component Elements | Radiocarbon Samples (cm below datum) |
|---|---|---|---|---|---|---|---|---|
| | | | *Nigror* | *Elasticitas* | *Siccitas* | *Humositas* | | |
| 115-240 | Light yellowish-brown | Granular calcareous mud containing fine rootlets and wood fragments in places. Darker bands of higher organic content are found at several levels within this horizon. Some shell fragments occur at 219 cm. | 2 | 2 | 2 | 2 | *Limus calcareus (Lc), Turfa herbacea (Th) + Argilla steatodes (As)* | 147-160 (ANU-1875)<br>193-200+ 201-208 (ANU-1876) |
| 240-375 | Light brown | Less granular than above horizon. Darker organic bands occur in places, and macrophytic remains are scattered throughout. | 1 | 2 | 2 | 3 | *Lc + Detritus herbosus (Dh)* | 348-360 (ANU-1876) |
| 375-382 | Dark brown | Fibrous, crumbly organic horizon containing woody fragments. | 3 | 3 | 2 | 2 | *Dh, Lc + Detritus lignosus (Dl)* | |
| 382-394 | Light brown | Granular calcareous mud. | 1 | 2 | 2 | - | *Lc + Limus detritosus (Ld)* | |
| 394-411 | Dark brown | An organic layer with a distinct upper boundary. Towards the base of this horizon occur large fragments of hard, reddish wood. | 3 | 3 | 2 | 3 | *Ld + Dl* | |
| 411-469 | Light grey | Gradual transition into wet grey clay containing some small woody fragments and other minor organic inclusions. Small shells occur around 468 cm. | 2 | 1 | 2 | 1 | *As, Dh + Dl* | |
| 469-512 | Light grey | Clay matrix containing various plant remains, including rootlets and spines. (No sample 480-503 cm). | 2 | 1 | 2 | 1 | *As, Dh + Th* | |
| 512-578 | Light grey-brown/ dark brown | A sharp angular transition into a clay horizon containing large quantities of macrophytic remains including rootlets and ?spines. Bands of dense plant detritus occur at 516-547 cm and 552-559 cm. | 1-2 | 3 | 2 | 1 | *Dh + As* | |
| 578-608 | Light grey-brown | Angular transition into clay matrix containing many small reddish-brown rootlets. | 2 | 2 | 2 | 1 | *As, Dh + Lc* | |
| 608-640 | Light grey | Clay matrix containing plant detritus of stems, rootlets and wood throughout. Large fragments of pale wood occur between 635-640 cm. | 2 | 1 | 2 | 1 | *As, Th + Dl* | 625-630+ 631-640 (ANU-1841) |

*TABLE 4.1. (Cont.)*

| | | | Troels-Smith Indices | | | | | |
|---|---|---|---|---|---|---|---|---|
| Depth of horizon (cm below datum) | Colour | Structure and General description | *Nigror* | *Elasticitas* | *Siccitas* | *Humositas* | Component Elements | Radiocarbon Samples (cm below datum) |
| 640 - 832 | Light grey/ yellow-brown | Complex alternation between sticky clay, and granular calcareous mud. Minor organic fragments occur, and some shells are found between 736-790 cm. | 2 | 0 | 3 | 3 | *As + Lc* | 740-750+<br>751-760<br>(ANU-1866) |
| 832 - 871 | Light grey/ grey | A homogenous horizon of smooth plastic clay. Colour varies slightly through the horizon. | 2 | 0 | 3 | - | *As* | |
| 871 - 917 | Yellow-brown | Granular calcareous mud. | 2 | 0 | 3 | - | *Lc* | 880-890+<br>891-900<br>(ANU-1867) |
| 917 -1017 | Yellow-brown/ light grey | A heterogenous mixture of calcareous mud and plastic clay, although fairly discrete bands of both clay and mud are present in places. A few macrophytic remains are found. | 2 | 0 | 3 | 3 | *Lc + As* | 1011-1030<br>(ANU-1869) |
| 1017-1052 | Light grey | Predominantly plastic clay layer, with some admixture of calcareous mud. A distinct gritty horizon, darker in colour, and containing macrophytic remains occurs between 1032-1037 cm. | 2 | 0 | 3 | 3 | *As, Lc + Dl* | |
| 1052-1152 | Yellow-brown/ light grey | Sediments predominantly of calcareous mud, more granular and stratified than in upper horizons. Bands of increased clay content, some quite discrete, also occur. A few macroscopic organic fragments occur within the calcareous mud. | 2 | 0 | 3 | - | *Lc + As* | 1138-1150<br>(ANU-1842) |
| 1152-1153 | Dark brown | A very compact, well humified organic horizon. | 3 | 1 | 3 | 3 | *Dh* or *Substantia humosa (Sh)* | |

The marginal core, YAN 2, also consists mainly of these two sediment types from its base up to approximately 640 cm. The upper levels of the core contain an increasing quantity of macroscopic plant and other organic remains. As noted earlier, Troels-Smith's classification is difficult to use accurately in the case of organogenic deposits containing unfamiliar macroscopic plant remains. In the YAN 2 core most such horizons suspected of being detrital in origin probably fall within the categories of *Detritus herbosus* (*Dh*) or *Detritus lignosus* (*Dl*) when plant fragments greater than 2 mm in size are present, or *Limus detritosus* (*Ld*) where such fragments are absent. Where a deposit contains macroscopic plant remains apparently *in situ*, it may be classified as *Turfa herbacea* (*Th*).

In several sections of the cores the various horizons appear to follow a rhythmic pattern on too small a scale to indicate in either Fig. 4.3 or Table 4.1. A typical sequence, from the base, may be described as:

(i ) a distinct band of light grey clay (*As*) 0.3 cm - 0.5 cm thick;

(ii ) a grey-brown admixture of clay, calcareous mud and often fine organic detritus (*As*, *Lc* and *Ld*) 3 - 8 cm thick grading into

(iii) light brown calcareous mud (*Lc*) 3 - 10 cm thick having a distinct upper boundary with the grey clay band of the next sequence.

However, in other parts of the cores where alternate horizons of grey clay and calcareous mud exist, no such regular small scale sequence is apparent.

A further notable horizon occurs as a narrow distinct band in the three open-water cores at about 50 cm below the sediment/water interface. The compact gritty mineral layer, 1 cm to 1.5 cm thick, appears almost black when wet, but dries to a dark greenish colour. The suspicion that this might represent the Tibito tephra, a widespread volcanic ash thought to have emanated from Long Island about 150 km to the north-east (Blong, in prep.), was confirmed by particle size and trace element analyses[1] of a sample from core YANMC 1 (R.J. Blong, pers. comm.). At least one other dark-coloured gritty horizon occurs in the stratigraphy of the two longer cores from Yanamugi. Although this may also be of volcanic origin, no similar attempt has been made to match this horizon with any of the many known ash-falls of Holocene age.

*ANALYSIS OF ORGANIC CONTENT*

A total of 54 samples was taken from core YAN 2 for measurement of water content and estimation of the organic fraction by loss of weight on ignition. Methods were similar to those described for the Lake Wanum samples, except that a larger volume (7.8 ml) of sediment was used. Although the samples were ignited at a slightly lower temperature (550 °C) in order to minimise decomposition of $CaCO_3$, this method may still overestimate the organic content of highly calcareous samples.

Both the percentile water content and residue on ignition curves (Figs. 4.4a and 4.4b) show good correlation with the stratigraphy of the core. The water content is generally correlated with the 'organic' fraction (percentage weight loss) of the

---

[1] Particle size analysis: (only fraction coarser than 4ø measured):
Mo (mean particle size) 3.5ø
$D_{10}$ (coarsest 10%) 2.5ø
o (sorting coefficient) 3.3ø
Trace element analysis:
Sr 661 ppm, Zr 51 ppm, Rb 34 ppm, Y 25 ppm.

*FIGURE 4.4. Yanamugi core YAN 2: Water content and weight loss on ignition*

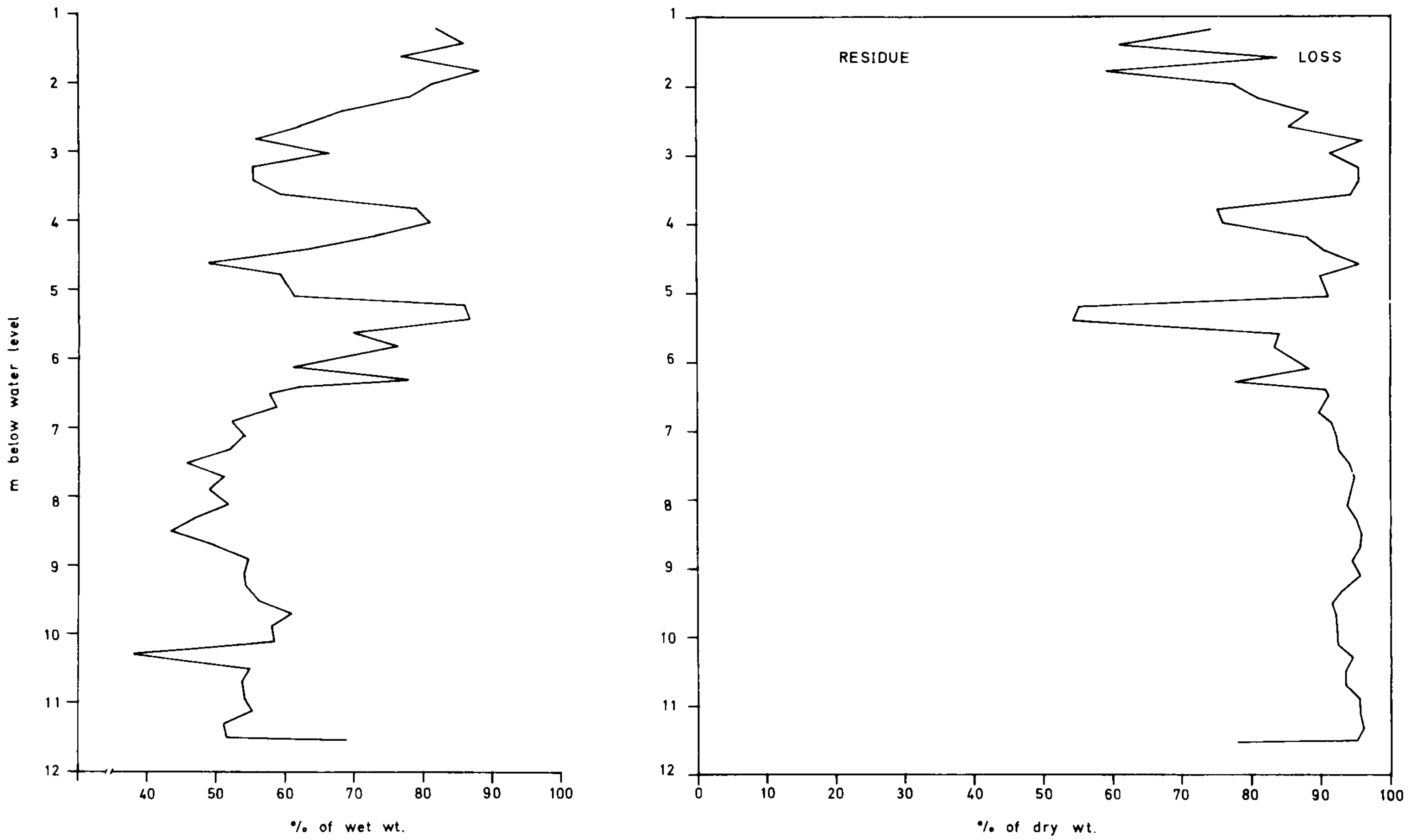
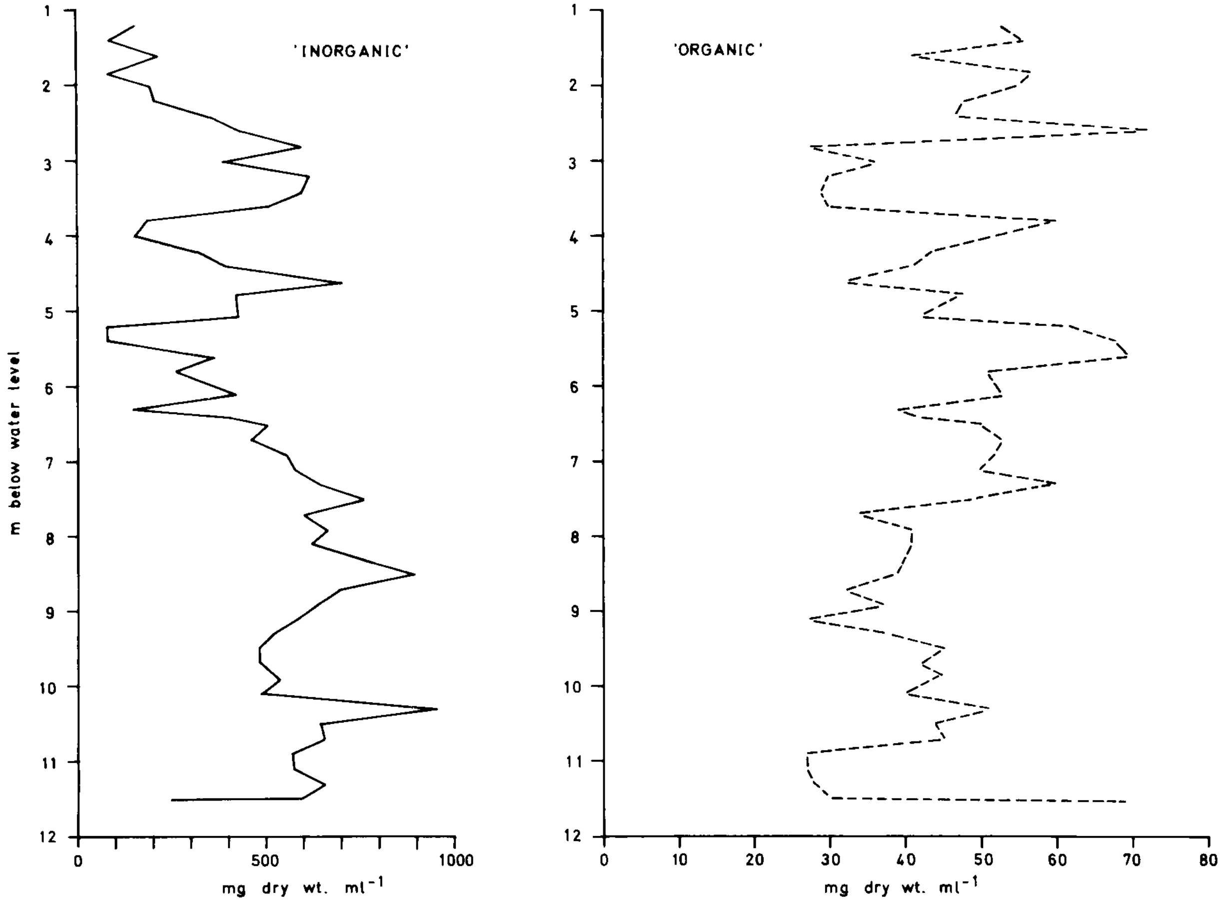


*FIGURE 4.5. Yanamugi core YAN 2: Sediment density for residue- ('inorganic') and loss-on-ignition ('organic') fractions*



sediment. Both of these curves show increases above *c.* 640 cm in the core, reflecting the greater preponderance above this level of horizons containing substantial plant remains. Conversely the percentage residue after ignition ('inorganic' fraction) shown in Fig. 4.4b is higher below 640 cm where the deposits consist predominantly of grey clay (*As*) and calcareous mud (*Lc*) and, apart from the basal sample, the 'organic' fraction comprises less than 10% of the total dry weight.

The gravimetric sediment concentration estimates (mg dry weight $ml^{-1}$) for the 'organic' and 'inorganic' fractions (Figs. 4.5a and 4.5b) show a general concordance with the percentage curves. Despite some differences they tend to emphasise the previously described correlations with the stratigraphy. The highest value for 'inorganic' sediment concentration is now shown to be produced by the dark gritty horizon around 1030 cm. Although these data eliminate ambiguities caused by variation in the water content of the sediments, their fuller interpretation obviously requires knowledge of annual deposition rates.

### *PALAEOMAGNETISM OF YANAMUGI CORES*

Despite the fairly complex stratigraphy of Yanamugi the range of limnic deposits is very similar in all cores, making cross-correlation difficult. As initial studies showed the sediments to possess an adequate level of natural remanent magnetisation (NRM), measurements of the horizontal component of NRM intensity and of magnetic declination were made on all cores, using the apparatus described in Chapter 3. The aims in applying this technique to the Yanamugi sediments were to facilitate fine correlation between cores, and to elucidate the gross sedimentology of the deposits.

The utility of rapid, non-destructive methods of measuring various magnetic parameters on intact sediment cores has been demonstrated by Molyneux *et al.* (1972). Thompson *et al.* (1975) were able to correlate stratigraphy within a large lake (Lough Neagh, Northern Ireland) on this basis alone, whilst Oldfield and his co-workers (Oldfield, 1977, Oldfield *et al.*, 1978) have used the technique to detect tephra sequences in lakes up to 80 km apart in the Papua New Guinea highlands.

The importance of palaeomagnetic indices in palaeolimnology lies in their relationship to events within the catchment area of the lake. As Thompson (1973) and Oldfield *et al.* (1978) have shown, in many lakes the parameters of NRM intensity and susceptibility are largely a function of events within the drainage basin. Specifically, they may be associated with the influx of allochthonous detrital material consequent on soil erosion. However, the relationship between intensity and susceptibility, or the susceptibility-related parameter $IRM_{sat}$ (saturation isothermal remanent magnetism), appears to vary in different situations. In Lake Windermere, north-west England, and Lough Neagh the horizontal NRM intensity is directly correlated with the carbon content of the sediments (Thompson, 1973). Measurements of susceptibility and IRM on Lough Neagh sediments, however, point to a positive relationship between high values of these indices and an accelerated supply of mineral detritus from the catchment area (Thompson *et al.*, 1975). In nearby Lough Fea, a much smaller lake, horizontal intensity, susceptibility and IRM all correlate well with chemical and pollen-analytical evidence for erosion of the drainage basin (Oldfield *et al.*, 1978).

It seems premature therefore to formulate a general hypothesis on the relationship between erosion and the various magnetic parameters. Many different factors are involved, their importance varying between individual lake basins. Oldfield *et al.* (1978) conclude that most available evidence points to the transportation of primary magnetite into the sediments as the main agent, although secondary enhancement of magnetic minerals during soil formation is also involved. A third potential source, formation of ferri-magnetic minerals at the sediment/water interface is also suspected, but remains unproven.

Results of the palaeomagnetic analysis of the Yanamugi short cores are given in Fig. 4.7, and results from the two longer cores appear in Fig. 4.8. Horizontal intensity of NRM in mA $m^{-1}$ (1 mA $m^{-1} = 1 \times 10^{-6}$ Gauss) is shown on a logarithmic scale, whilst declination (secular variation) is plotted relative to the mean for each core section. As these sections were neither oriented in relation to a known compass bearing nor to each other, and were also extruded under field conditions, the declination results have limited significance. The results are presented for possible evidence of sediment disturbance not an artefact of the coring techniques.

Comparison of the NRM intensity results with stratigraphy in the two long cores suggests some correlations. In YAN 2 high NRM intensity readings appear to be associated with horizons of

*FIGURE 4.6. Yanamugi core YAN 2: (a)NRM intensity measurements normalised on the basis of dry weight. (b) Normalised NRM intensity* versus *inorganic sediment density*

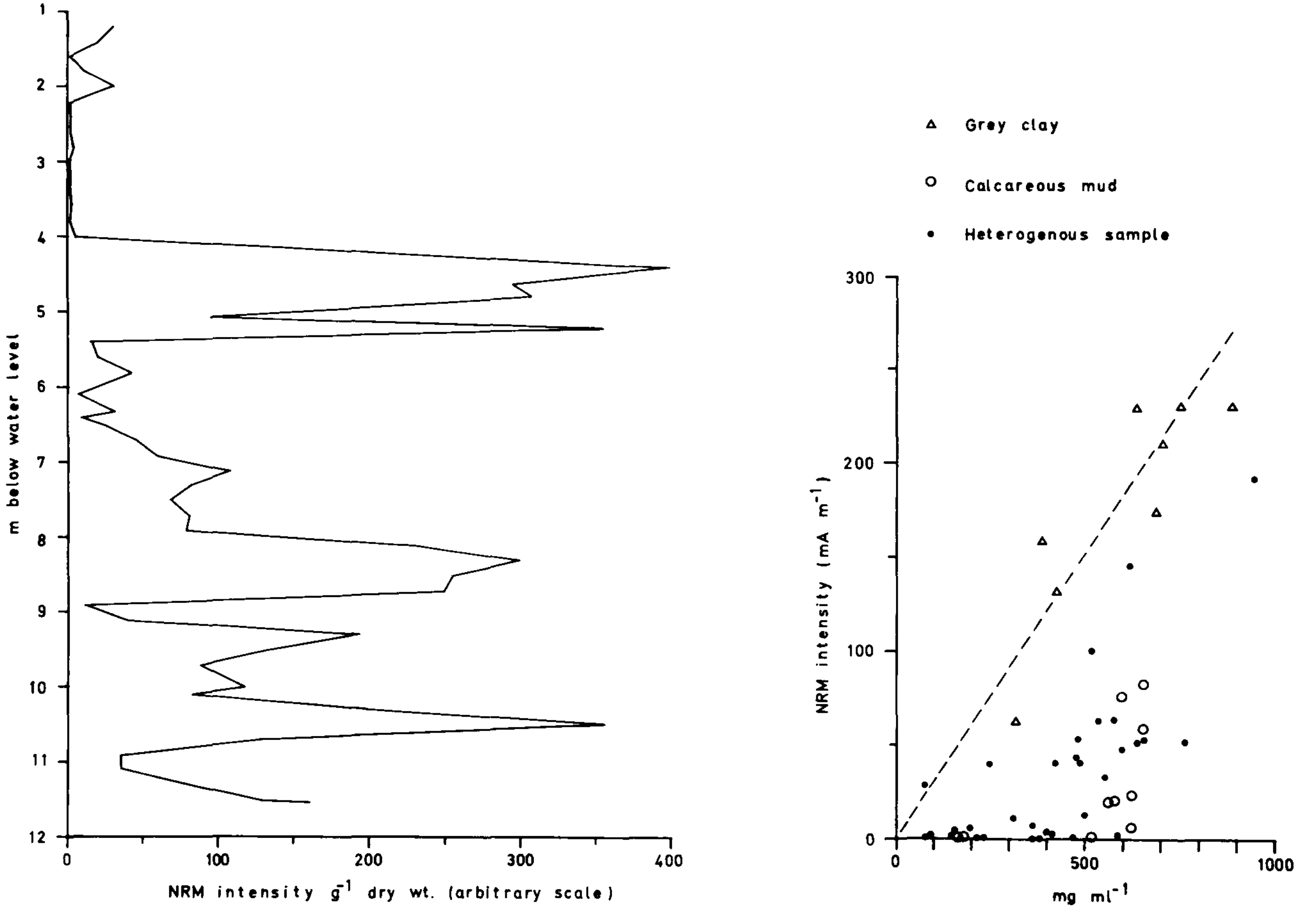


*FIGURE 4.7. Yanamugi: Palaeomagnetism of short cores*

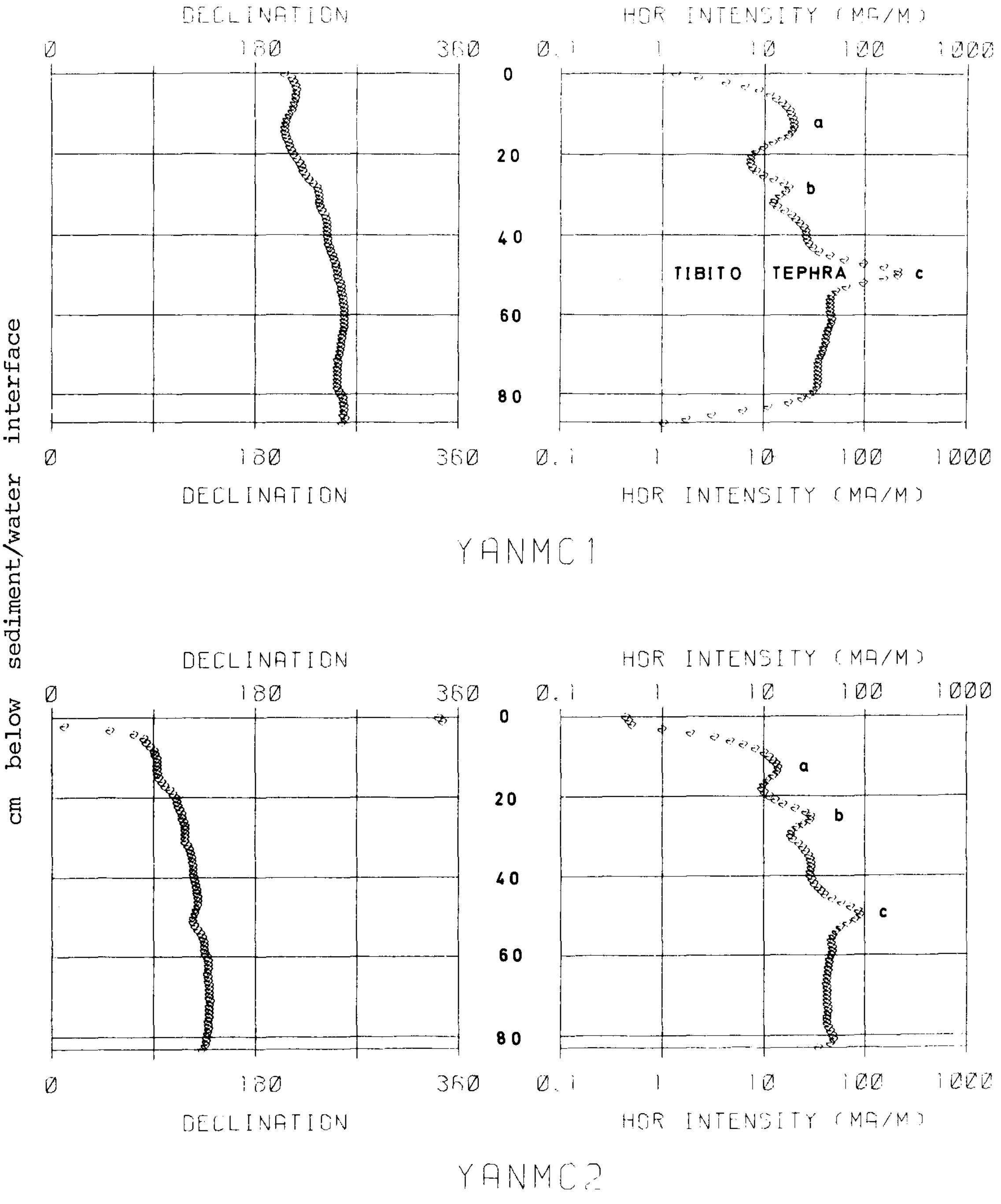
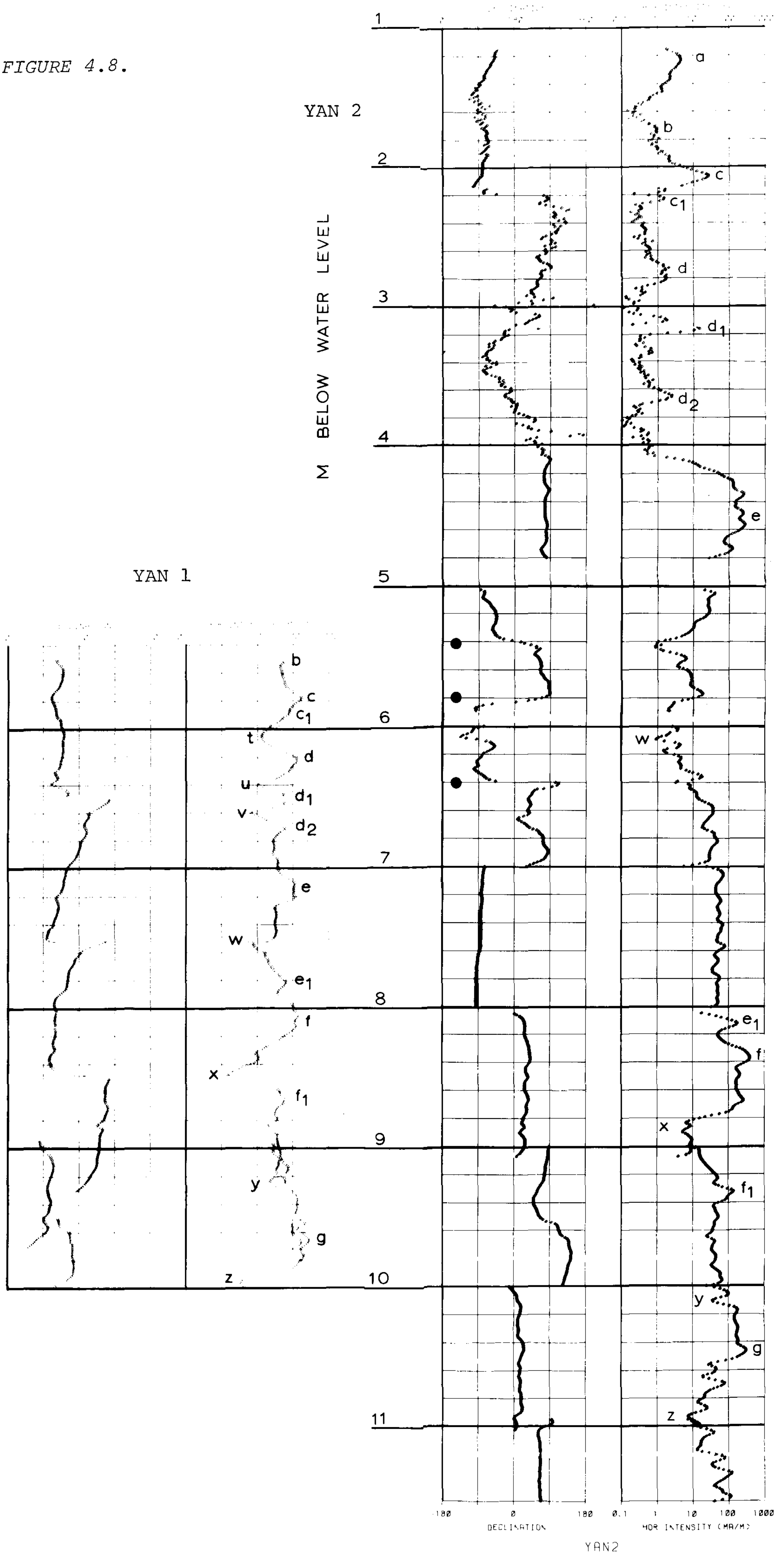


*FIGURE 4.8. Yanamugi: Palaeomagnetism of long cores. Palaeomagnetic declination (left column) and horizontal NRM intensity (right column) of (a) core YAN 1 and (b) core YAN 2. Legends for the columns are as in Fig. 4.7. Solid circles indicate major declination shifts not artefacts of the coring procedure. Letters indicate suggested NRM intensity correlations between cores (see text).*

FIGURE 4.8.


YAN 2
M BELOW WATER LEVEL
YAN 1
1
2
3
4
5
6
7
8
9
10
11
a
b
c
c1
d
d1
d2
e
e1
f
f1
g
t
u
v
w
x
y
z
-180
0
180
0.1
1
10
100
1000
DECLINATION
HOR INTENSITY (MA/M)
YAN2

substantial grey clay (*As*) content. Conversely, low intensity values occur in levels consisting predominantly of calcareous mud (*Lc*), e.g. 880-910 cm, or with a higher organic content (220-400 cm and 540-640 cm). This trend may be seen more clearly by normalising the intensity measurements of the 54 weighed samples to a dry weight basis (Fig. 4.6a) rather than the volumetric one of Fig. 4.8. The relationship between gross sediment composition and NRM intensity is shown in Fig. 4.6b by plotting the magnetic values against the dry weight of the 'inorganic' fraction. Samples apparently consisting predominantly of either grey clay or calcareous mud are indicated, whilst other samples are heterogenous in composition. Although few data points thus remain, a more or less linear relationship between mass and NRM intensity of the clay samples emerges. The calcareous mud samples exhibit no such trend, the data points being highly scattered.

The correlation between grey clay horizons and peak NRM intensity measurements is also apparent in core YAN 1. The only high NRM intensity values not associated with sediment of high clay content are those just above 580 cm, corresponding with the narrow Tibito tephra band. This concurs with the results of Oldfield *et al.* (1978) who obtained high measurements of intensity and susceptibility on the Tibito tephra (their 'Ash 4') and other recent ash falls.

It thus tentatively appears that the presumably allochthonous grey clay carries at least the greater proportion of the NRM intensity measured. However, further magnetic analyses, in particular susceptibility measurements on separate samples, and other sedimentological studies are obviously desirable to validate this hypothesis and to establish the nature of the magnetic minerals involved.

## *CORRELATION AND DATING*

### *Palaeomagnetically based core correlation*

Comparison of declination measurements between cores does not appear to be very useful for correlation purposes. Values for YAN 1 and the lower part of YAN 2 are internally consistent, although some sections of YAN 1 show considerable drift in declination. This may be attributable to non-vertical coring or disturbance during core extrusion. Values in the upper part of YAN 2 are often associated with low intensity measurements and are therefore likely to be unreliable. Between 500 cm and 700 cm in core YAN 2, a number of apparent excursions in the declination measurements cannot be explained as damage to the core during collection or handling. Three of these, indicated in Fig. 4.8b, are particularly intense showing 180° shifts within a few centimetres. Occurring in one core only, they cannot be related to secular variations in the geomagnetic field. These horizons therefore reflect some feature of the sedimentary regime either during or post-deposition, such as slumping, or other disturbance.

As demonstrated above, the NRM intensity of the sediment appears to be largely dependent on the proportion of grey clay, or in specific horizons volcanic tephra, in the sample. If the sedimentary regime throughout the basin has been substantially similar at any given time, correlation between cores on the basis of their NRM intensity should therefore be possible.

The concordance between NRM intensity measurements on the short cores YANMC 1 and YANMC 2 (Fig. 4.7) is remarkable considering the distance of over 100 m between the two sampling sites. The highest NRM intensity peak in each core is given by the Tibito tephra horizon, labelled (c), at about 50 cm below the sediment/ water interface, although the absolute value is slightly greater in YANMC 1. The general trend of declination (Fig. 4.7) is also similar between these cores. The long core YAN 1, adjacent to YANMC 1, shows good correlation of NRM intensity measurements with the short cores. The value for the tephra horizon is very similar to that of YANMC 1, although absolute values tend to decline below this horizon to a greater extent than in the short core. Although the top-most sediment was not collected at YAN 1, there is perhaps still a slight indication of the second NRM intensity peak (b).

The greatest differences in the NRM intensity results for the most recent sediments are shown by the marginal core YAN 2. However, tentative correlation with the other cores is still possible. Absolute NRM intensity values for the top portion of this core are far smaller than those from the cores of the deeper basin, presumably due to the higher proportion of water and organic detritus in the marginal sediments. The greatest peak (c) may again be attributed to the Tibito tephra, although this does not appear as a discrete stratigraphic horizon. The distinct NRM intensity peak at the top of YAN 2 is probably correlated with (a) in the other cores although alternatively it may represent horizon (b).

Cross correlation between the two longer cores below the Tibito tephra horizon on the basis of NRM intensity results (Fig. 4.8) is less straightforward. Differences in water content and sediment compaction lead to great variation in absolute NRM intensity values. Only the general sequence of changes can be used for correlation and the method is therefore sensitive to missing or poorly represented horizons in either core.

An empirical approach was taken in an attempt to match NRM intensity changes in the two cores. YAN 1 was designated the 'reference' sequence as this core shows a more consistent stratigraphic and palaeomagnetic record. Being from the deepest part of the lake, it is also more likely to be representative of the sediments of the basin as a whole. NRM intensity peaks greater than 100 mA $m^{-1}$, were labelled from (c), the Tibito ash-fall, to (g), with 'minor' peaks less than this value being given subscripted letters (e.g. $e_1$). Horizons of relatively low NRM intensity, generally less than 10 mA $m^{-1}$, were identified by the letters (t) to (z).

Transfer of these designated horizons to core YAN 2 is made difficult by the generally low and erratic values for NRM intensity present in the upper part of the core. The Tibito tephra horizon (c) has already been identified, and three subsequent minor peaks (greater than 1 mA $m^{-1}$) below this may correlate with horizons (d), ($d_1$) and ($d_2$) from core YAN 1. The first major peak in YAN 2, around 450 cm, probably represents horizon (e) although the absolute values in YAN 2 are again smaller. The next intensity peak (812 cm) in YAN 2 is probably ($e_1$) and the succeeding high values representative of horizon (f), underlain as they are by some of the lowest readings (x) in this part of the core. From (x) to (z) the NRM intensity traces of the two cores are very similar, both in relative trend and in absolute values. A transient peak at ($f_1$) is followed by slowly increasing values until the sustained peak of (g) and subsequent decline in intensity at the (z) horizon.

Other interpretations of the intensity data are possible: e.g. the sequence (w) to (f) in YAN 2 is somewhat similar to that labelled (x) to (g) in YAN 1. However the proposed correlation is the simplest supported by the NRM intensity data. It allows for least variation in sedimentation rates between the two cores, although considerable fluctuation does still exist, particularly in the middle section of the cores. The suggested correlation of these middle sections is less firmly based than that for the uppermost horizons, or for the levels below about 800 cm in both cores.

It is apparent that, whilst such a closely correlated sequence would be of great value in estimating relative sedimentation rates within different parts of the lake basin, the proposed correlation is not sufficiently robust to stand alone. Independent evidence on stratigraphic correlation and chronology from other sources is required to substantiate any such inferences based on the palaeomagnetic data.

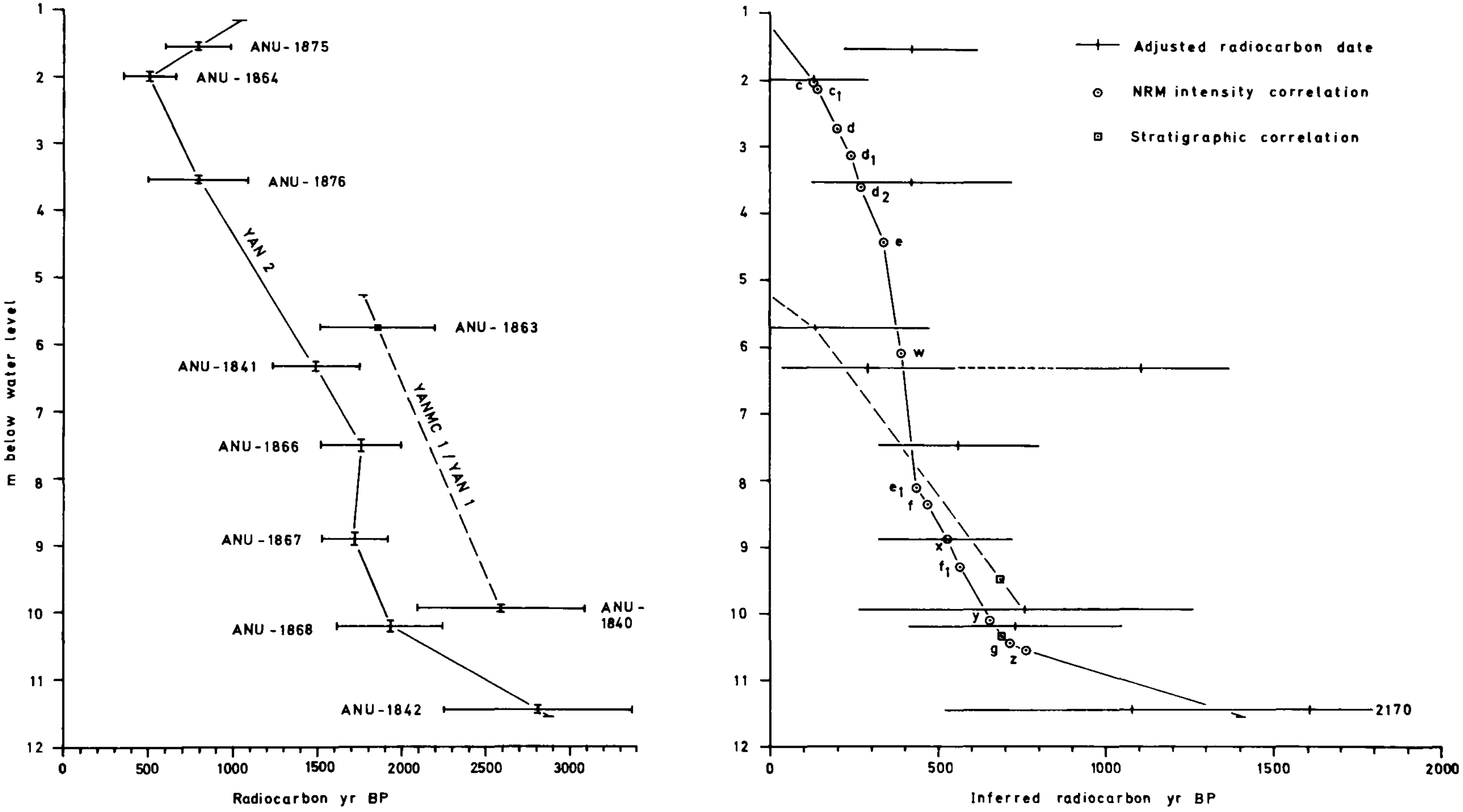
### *Radiocarbon dating*

Results of radiocarbon assays on samples from Yanamugi are shown in Table 4.2. Eight determinations were made on sediments from core YAN 2, and one from each of cores YAN 1 and YANMC 1. When the reported ages are plotted against depth (Fig. 4.9a), a number of inconsistencies become apparent, suggesting that the $^{14}C$ dates do not reflect accurately the true age/depth relationship of the sediments.

*TABLE 4.2. Radiocarbon determinations from Yanamugi*

| Core and depth (cm) | Laboratory No. | Reported Age | Material dated |
|---|---|---|---|
| YAN 2<br>147 - 160 | ANU-1875 | 800 ± 100 | Calcareous mud with some rootlet penetation. |
| YAN 2<br>193 - 208 | ANU-1864 | 510 ± 80 | Calcareous mud with ?organic detritus including some wood fragments. |
| YAN 2<br>348 - 360 | ANU-1876 | 800 ± 150 | Mainly calcareous mud, with a few organic inclusions. |
| YAN 2<br>625 - 640 | ANU-1841 | 1490 ± 130 | Grey plastic clay, with some organic detritus and wood fragments. |
| YAN 2<br>740 - 760 | ANU-1866 | 1760 ± 120 | Grey clay and calcareous mud. |
| YAN 2<br>880 - 900 | ANU-1867 | 1720 ± 100 | Calcareous mud with some grey clay. |
| YAN 2<br>1011 - 1030 | ANU-1868 | 1930 ± 160 | Grey plastic clay. |
| YAN 2<br>1138 - 1150 | ANU-1842 | 2810 ± 280 | Calcareous mud and grey clay. |
| YANMC 1<br>44 - 49 | ANU-1863 | 1860 ± 170 | Calcareous mud. |
| YAN 1<br>988 - 1000 | ANU-1840 | 2490 ± 250 | Calcareous mud. |

*FIGURE 4.9. Yanamugi: (a) Radiocarbon determinations (± 2 S.D.) and (b) inferred age/depth profile (± 2 S.D.)*



Several 'inversions' occur in the series of dates from core YAN 2. However, due to the close temporal spacing of the determinations in relation to their stated counting errors, only one such pair of dates, ANU-1875 and ANU-1864, possesses an age difference significantly larger (more than 2 S.D.) than the combined counting error associated with their interval. Indeed, three dates (ANU-1866, ANU-1867, and ANU-1868) are so close as to be indistinguishable with any statistical confidence.

More serious is the 'apparent age' anomaly of the surface sediment of the deeper lake basin as shown by the date of 1860 ± 170 (ANU-1863) from core YANMC 1. Accepting this date would imply either a dramatic decrease in sedimentation rate in the upper 50 cm of this core, or a substantial hiatus in the stratigraphic record, or both. Neither appears likely in view of the relatively uniform stratigraphy and excellent palaeomagnetic correlation of the upper part of the three deep-basin cores.

By simple extrapolation of dates ANU-1840 and ANU-1863, the apparent age of the surface sediments is 1780 BP. The error is verified by the identification of the Tibito tephra at about 50 cm below the sediment-water interface in all three deep-basin cores, and underlying ANU-1863 in YANMC 1. This ash-fall has been tentatively dated at 1700 AD (Blong, in prep.) although Ball and Johnson (1976) report two slightly younger radiocarbon dates, 1720 ± 75 AD, and 1750 ± 65 AD. The rounded estimate of 1700 AD, or about 130 $^{14}C$ years BP allowing for the probable effect of variations in the atmospheric radiocarbon ratio (Clark, 1975), is accepted here. The radiocarbon date of 1860 ± 170 (ANU-1863) is thus at least 1730 years too old.

It may be possible to use this apparent age as a correction factor for other radiocarbon determinations from similar sediments as Davis (1969) has done. However it is obvious that a uniform correction figure cannot be applied to all of the radiocarbon results from Yanamugi. Age determinations substantially younger than 1730 BP have been obtained from the upper sections of core YAN 2, although these dates also appear too old. If the palaeomagnetic correlation of the Tibito tephra horizon (c) is valid, then ANU-1864 from core YAN 2 should give an age comparable with that of ANU-1863 from YANMC 1. Whilst ANU-1864 is 1350 $^{14}C$ years younger than the latter date, it is still 380 $^{14}C$ years older than the proposed age of the tephra.

There may be several possible explanations for this non-uniform error in the radiocarbon values. Contamination with particulate carbonate from the Oligocene limestone country rock can be excluded as a result of the acid pretreatment of all samples. The influence of allochthonous organic detritus or dissolved humic products cannot be ruled out, although there does not seem to be a sufficient source of ancient organic material within the Yanamugi catchment. Fractionation of $^{13}C$ by submerged freshwater plants may produce apparent radiocarbon ages perhaps 145 ± 130 years older than contemporary terrestrial carbon sources. As the latter are used as standards when calculating radiocarbon 'ages', such an effect should ideally be taken into account. However, although in practise the extent of the error is 'almost indeterminable' (Polach, 1976) it is not thought to produce $^{14}C$ dating discrepancies as large as those exhibited in Yanamugi.

The most likely factor causing these anomalous results is the effect of the surrounding limestone on the water chemistry of the lake, and thus on the isotopic content of the lacustrine organisms. Radiocarbon-free ancient carbonate enters the water causing it to become depleted in $^{14}C$ with relation to the atmospheric reservoir. Submerged aquatic plants and animals can metabolise this source of carbon (Deevey and Stuiver, 1964) and, in so doing, become markedly depleted in $^{14}C$ compared to organisms utilising atmospheric $CO_2$ as their source. Deevey *et al.* (1954) calculated apparent ages of up to 2000 years from radiocarbon assays of contemporary aquatic organisms from a hard-water lake. Extrapolating from raised-bog radiocarbon chronologies correlated by pollen analysis, Willkomm and Erlenkeuser (1973) found age anomalies of up to 1600 years for the sediments of 22 lakes. Similarly, estimates of apparent ages of up to 3000 years have been demonstrated from surface sediments and aquatic plants of a Finnish lake (Donner *et al.*, 1971). These figures from temperate lakes are also matched by results from tropical hard-water lakes in lowland Guatemala that show similar age anomalies of up to 2000 years (Deevey, 1978).

Only submerged organisms obtain a proportion of their carbon from dissolved carbonates. Deevey *et al.* (1954) further demonstrated that emergent aquatic plants and *Nuphar*, and presumably other genera of water lilies, incorporate solely atmospheric carbon, as do terrestrial plants. Shotton (1972) reports the effect of this 'hard-water error' in a Danish late-glacial sequence. Radiocarbon determinations from algal muds produced dates over 1500 years older than assays of terrestrial material from synchronous horizons. Thus where the sediment is derived from more than one of these sources, the apparent radiocarbon age of the deposit may, as Olsson (1974) stresses, 'vary throughout one core, and from place to place, even within a lake, for deposits of the same real age'.

Such is clearly the case at Yanamugi. The age anomaly of each radiocarbon sample is dependent on the proportion of the organic carbon from different sources that it contains. The largest anomalies can be expected from the cores of the deeper basin where much of the organic sediment probably derives from submerged macrophytes and plankton. Conversely, the youngest apparent ages should occur in material containing visible evidence for the presence of emergent- or floating-leaved aquatic, or terrestrial plant remains.

## *AN ECLECTIC CHRONOLOGY FOR THE YANAMUGI SEDIMENTS*

Below the dated Tibito tephra horizon radiocarbon determinations provide the sole chronological control on which to base estimates of annual sedimentation rate within the lake basin. It is imperative, therefore, to obtain the best estimate of the apparent age anomaly for each radiocarbon sample.

The maximum correction, for the near surface sediments of the deep basin, is shown by ANU-1863 to be about 1730 years. As the sediments appear generally similar throughout YAN 1, this correction has been applied to ANU-1840, adjusting the basal date of this core to 760 ± 250 BP.

The minimum demonstrable error of 380 years (ANU-1864) comes from the swamp-margin deposits of the upper part of YAN 2. This correction figure has been applied to the other two determinations (ANU-1875 and ANU-1876) from this stratigraphic zone. Recalculated at 420 ± 100 BP, ANU-1875 still appears too old by at least 200 years as it lies above the Tibito tephra. The minimal error of ANU-1864 may be due to the presence in the sample of wood fragments, absent from the other determinations.

In the lower levels of YAN 2, where macroscopic organic remains are generally absent, a different correction factor must be applied. Assuming the revised basal date of YAN 1 to be valid then the dark gritty horizon around 951 cm in this core, 40 cm above ANU-1840, must be younger than 760 BP. This horizon is found in YAN 2 at a depth of 1035 cm, 15 cm below the midpoint of sample ANU-1868, reported as 1930 ± 160 BP. The apparent age error of the sample is thus greater than 1170 years, and therefore a correction of 1200 years has been deducted from the reported age of ANU-1868, and from the other dates (ANU-1867 and ANU-1866) in this stratigraphic zone.

Sample ANU-1841 lies in a region of heterogenous stratigraphy containing both considerable grey clay and plant detritus. Thus the age error cannot be extrapolated reliably from samples either above or below it. Recalculation applying both the 380 year and 1200 year correction suggests that, using the criterion of best fit with the other revised dates, the age anomaly of this sample lies between these two figures, though closer to the larger.

Applying the 1200 year correction, the basal date of YAN 2, ANU-1842, becomes 1610 ± 280. However, the sediments of this zone more closely resemble the calcareous mud of the deeper basin and a correction closer to 1730 years may be more appropriate for this sample.

Although all dates lie within the period of known secular variation in the atmospheric radiocarbon ratio, no further correction has been made in view of the large arbitrary adjustments already applied. The amended radiocarbon determinations produce the apparently reasonable age/depth relationship shown in Fig. 4.9b. Where alternative corrections are proposed (ANU-1841 and ANU-1842), both are indicated. However, counting errors, already large on most samples due to the low carbon content of the sediments, become proportionally much larger for the now younger dates. Calculation of precise sedimentation rates for radiocarbon dated intervals thus becomes impossible.

An alternative approach to the chronology of the sediments was therefore attempted. This model, based on the stratigraphic and NRM intensity correlation between the long cores, rests on three assumptions:

(1) that the inferred age of ANU-1840 (760 ± 250) is correct,

(2) that all stratigraphic and NRM intensity correlations proposed above are valid and

(3) that the sedimentation rate of core YAN 1 between its base and the Tibito tephra is linear.

All of these propositions may be disputed. The first does not affect relative sedimentation rate estimates between cores but an increase in the inferred age would produce uniformly lower annual values. The possibility of different interpretations of the NRM intensity data is discussed above. The third proposal is unlikely to be true, although a core from a central location should exhibit less variation than one from a marginal situation. To some extent this assumption is borne out by the stratigraphy of the two cores.

Without many further radiocarbon determinations, such a proposition forms the only available basis for comparison.

The age-depth curve for YAN 2 derived from this model is shown on Fig. 4.9b, alongside the revised radiocarbon chronology. The model shows good agreement with the radiometric dates although the broad counting-error terms of the latter could obviously encompass alternative interpretations also.

*ESTIMATION OF SEDIMENTATION RATES*

The tentative chronology now constructed allows for estimation of relative sedimentation rates between cores and, for some intervals, of annual sediment influx.

The dated Tibito tephra horizon, and good NRM intensity correlation form a sound basis for calculation of the sedimentation rate of all cores for the last 275 years or so (Table 4.3). Average annual deposition rates of the three cores from the deep basin (YAN 1, YANMC 1, and YANMC 2) are very similar for this period at between 1.64 to 1.93 mm. The marginal core YAN 2 exhibits a much more rapid mean deposition rate than the other cores at 3.85 mm $yr^{-1}$. An apparent decrease during the most recent interval in this core may be due to failure to collect the uppermost unconsolidated portions of the sediment.

Estimates of the sedimentation rates for the two long cores below the Tibito tephra (Table 4.4) are calculated on the basis of stratigraphic and NRM intensity correlations proposed above. In both cores the mean annual deposition rates appear over three times higher for the period below the ash horizon than for that above. Only below 10 m in core YAN 2 do annual rates approach the values estimated for the most recent period. The ratio of the

*TABLE 4.3. Relative and absolute sedimentation rates for the last 275 years*

| Horizon | Estimated age A.D. | YAN 2 Depth (cm) | YAN 2 Interval (cm) | YANMC 2 Depth (cm) | YANMC 2 Interval (cm) | YAN 1 Depth (cm) | YAN 1 Interval (cm) | YANMC 1 Depth (cm) | YANMC 1 Interval (cm |
|---|---|---|---|---|---|---|---|---|---|
| Surface | 1975 | *c.* 100 | | 0 | | *c.* 525 | | 0 | |
| | | | 23 | | 13 | | 27 | | 14 |
| a | | 123 | | 13 | | - | | 14 | |
| | | | 40 | | 13 | | | | 9 |
| b | | 163 | | 26 | | 552 | | 23 | |
| | | | 43 | | 24 | | 26 | | 22 |
| Tibito Tephra c | 1700 | 206 | | 50 | | 578 | | 45 | |
| Total sediment depth | | | 106 | | 50 | | 53 | | 45 |
| Mean sedimentation rate (mm $yr^{-1}$) | | | 3.85 | | 1.82 | | 1.93 | | 1.64 |

TABLE 4.4. *Comparison of sedimentation rates in cores YAN 1 and YAN 2 prior to 1700 A.D.*

| | | | YAN 1 | | | YAN 2 | | | |
|---|---|---|---|---|---|---|---|---|---|
| Horizon | Inferred age ($^{14}$C yr BP) | Interval ($^{14}$C yr) | Depth (cm) | Interval (cm) | Sedn. rate (mm yr$^{-1}$) | Depth (cm) | Interval (cm) | Sedn. rate (mm yr$^{-1}$) | Ratio of sedimentation rates YAN 2:YAN 1 |
| Tibito Tephra c | 130 | | 578 | | | 206 | | | |
| | | 15 | | 9 | 6.64 | | 10 | 6.67 | 1.00 |
| $c_1$ | 145 | | 587 | | | 216 | | | |
| | | 55 | | 36 | " | | 59 | 10.73 | 1.62 |
| d | 200 | | 623 | | | 275 | | | |
| | | 40 | | 27 | " | | 41 | 10.25 | 1.55 |
| $d_1$ | 240 | | 650 | | | 316 | | | |
| | | 30 | | 21 | " | | 47 | 15.67 | 2.36 |
| $d_2$ | 270 | | 671 | | | 363 | | | |
| | | 70 | | 44 | " | | 82 | 11.71 | 1.77 |
| e | 340 | | 715 | | | 445 | | | |
| | | 50 | | 35 | " | | 165 | 33.00 | 4.97 |
| w | 390 | | 750 | | | 610 | | | |
| | | 45 | | 31 | " | | 202 | 44.89 | 6.77 |
| $e_1$ | 435 | | 781 | | | 812 | | | |
| | | 35 | | 24 | " | | 25 | 7.14 | 1.08 |
| f | 470 | | 805 | | | 837 | | | |
| | | 60 | | 40 | " | | 53 | 8.83 | 1.33 |
| x | 530 | | 845 | | | 890 | | | |
| | | 35 | | 21 | " | | 42 | 12.00 | 1.81 |
| $f_1$ | 565 | | 866 | | | 932 | | | |
| | | 90 | | 59 | " | | 80 | 8.89 | 1.34 |
| y | 655 | | 925 | | | 1012 | | | |
| | | 35 | | 26 | " | | 23 | 6.57 | 0.99 |
| ?Tephra | 690 | | 951 | | | 1035 | | | |
| | | 25 | | 14 | " | | 11 | 4.40 | 0.66 |
| g | 715 | | 965 | | | 1046 | | | |
| | | 45 | | 31 | " | | 11 | 2.44 | 0.37 |
| z | 760 | | 996 | | | 1057 | | | |

mean sedimentation rate of YAN 2:YAN 1 is very similar (2.03) to that for the period above the tephra (1.99). However, considerable differences in sedimentation rate between the two cores do appear to exist. In the interval between NRM intensity peaks (e) and ($e_1$), values for YAN 2 are nearly five to seven times higher than those for YAN 1, with estimated mean deposition rates of up to 45 mm per year. Given such a rapid accumulation rate, an annual origin could be postulated for some of the rhythmic sedimentary sequences characteristic of parts of this section. Towards the base of the palaeomagnetically correlated section the sedimentation rate of YAN 2 appears to decline considerably in relation to that of YAN 1.

Below 1057 cm in YAN 2 sedimentation rate can be estimated only by extrapolation to the revised ages for ANU-1842. The two alternative inferred ages for the basal date produce mean sedimentation rates for this period of 1.02 mm or 2.72 mm per year respectively.

Although these estimates may provide an indication of the major trends in sediment influx to YAN 2, some deviations from the basic assumptions of the correlation model are apparent. The sedimentation rate of YAN 1 is demonstrably not linear, the most recent deposits showing a much slower accumulation rate. In addition the basal age of YAN 2 is not known with sufficient precision to allow calculation of accumulation rates for the lowest section of the core. Therefore, systematic translation of the proposed age/depth results into annual deposition rates is not considered appropriate, except perhaps for the period above the Tibito tephra.

## *THE SEDIMENTARY HISTORY OF YANAMUGI*

Data presented in this chapter provide reasonable if circumstantial evidence on the depositional history of the Yanamugi basin. The chronology is tenuous, and therefore absolute ages and sedimentation rates cannot be ascribed with much certainty.

The lake basin appears to be fairly young. The oldest deposits augered are probably over 2500 years old, although the maximum age of those recovered in the cores may be nearer to 1600 BP.

The stratigraphic record of the deep-basin core YAN 1 suggests that the sedimentary regime has remained essentially similar for the past 800 years or so. In contrast, at the site of core YAN 2 now a swamp margin, stratigraphic evidence indicates a transition from a previously open water depositional regime. Apart from a compact organic band at the base of this core, the earliest horizons reflect slow sedimentation of predominantly calcareous mud. From around 700 BP, influx into the sediments of the presumably allochthonous grey clay increases. There is some evidence for a phase of rapid clay deposition around 400 BP when calculated accumulation rates reach nearly 45 mm per year. Although based solely on the proposed palaeomagnetic correlation model, such an interpretation also accords with both the radiocarbon data and the anomalous shifts in magnetic declination recorded in this region of the core. Influx during this period of predominantly grey clay is also indicated in YAN 1, although the deposition rate appears much lower than that from the marginal core. In the absence of evidence for major water level changes it may be hypothesised that the influx of allochthonous clay hastened the infilling of the northern end of the basin. Thus from about 300 BP there is increasing evidence in YAN 2 for the close proximity of swamp vegetation, revealed by the greater proportion of organic detritus in the sediments.

The deposits of the last few centuries suggest a decrease in the input of grey clay to all areas of the lake, together with a general reduction in annual sedimentation rates.

# CHAPTER 5

# HERBACEOUS SWAMP VEGETATION OF THE MARKHAM VALLEY

A knowledge of the ecology of contemporary aquatic vegetation is an essential prerequisite to the palaeoecological study of any swamp or lacustrine system. Macroscopic and microscopic plant remains comprise the greater part of most organic deposits and changes in their assemblages can reveal information on the hydrology and nutrient status of the lake or swamp. However, such potential can be realised only with a sound understanding of the ecology of the component species, both individually and collectively.

There is a paucity of such ecological data from tropical freshwater habitats in general, and from those of the Australasian region in particular. Although the state of knowledge has improved since the review by Walker and Gregory (1965), most accounts present a geographical-scale synthesis without comprehensive floristic data or quantitative estimates of species importance (e.g. Taylor, 1959, Holloway *et al.*, 1973, and Paijmans, 1976).

More detailed, and of necessity localised, ecological studies exist (Wade and McVean,1969, Flenley, 1972, and Hope, 1976*b*) but these are of sub-alpine and highland bogs under climatic and other environmental conditions very different from those prevailing in the lowlands. The most comparable data may therefore come from north-east Queensland, Australia, where Kershaw (1978) has studied a wide range of aquatic vegetation types from three sites on the Atherton Tableland.

The swamp vegetation of four sites in the Markham Valley was investigated as a basis for the interpretation of modern and past swamp communities. Systematic ecological sampling was restricted to Lake Wanum, the largest site and that with the greatest diversity of herbaceous swamp vegetation. At the other three sites, the Erom-Erom lakes, Redhill swamp and Yanamugi lake, partial species lists were compiled and the vegetation associations described subjectively.

### *SURVEY OF HERBACEOUS SWAMP VEGETATION AT LAKE WANUM*

A survey was made of the two main herbaceous swamp areas at Lake Wanum, the south swamp (Plate 5.1) and the western margin of the north-east bay. Six transect lines were laid subjectively to include what appeared to be the major vegetation associations. Of the transects across the south swamp, A and F were aligned approximately north-south, transect B south-west to north-east, and transect C south-south-west to north-north-east. In the north-east bay, transect D followed the alignment of the western end of stratigraphic transect 'A' (see Fig. 3.3), transect E being parallel and about 40 m to the north. Fifty-eight quadrats 1.5 m square were set at regular intervals of 20 m, or in the north-east bay 10 m, along these transects. All vascular plant species encountered were collected for identification. A total enumeration of each quadrat was made, the percentage cover of each taxon being estimated on a five-point scale:

| | |
|---|---|
| + | presence only, cover less than 5% |
| 1 | cover 5 - 24% |
| 2 | cover 25 - 49% |
| 3 | cover 50 - 74% |
| 4 | cover 75 - 100% |

The score for each quadrat was not constrained to total four or less, since many minor species might occur, and distinct layering was often present in the vegetation. The growth habit of each individual taxon was noted, as was the average shoot height of emergent plants, and evidence of flowering or spore production. In addition to the vegetation observations, the percentage of bare ground and open water in each quadrat was estimated and the approximate water depth determined using coring rods as probes.

The complete floristic data for all swamp quadrats are shown in Table 5.1. Taxa encountered, but not sampled in any quadrat include *Ficus drupacea, Hyptis capitata, ?Sarcocephalus* sp. (21053)[1], *?Anthocephalus cadamba* (21074) and *Metroxylon sagu*. Two additional quadrats located in the damp grassland-swamp boundary recorded the grasses *Themeda australis, Phragmites karka,* and *Coelorhachis rottboellioides,* the sedge *Fimbristylis dichotoma,* ferns *Cyclosorus* sp. (21050) and *Stenochlaena palustris,* and herbs *Uraria lagopodioides, Premna herbacea, Ipomoea gracilis, Pouzolzia hirta,* and *Euphorbia hypericifolia.*

### *ANALYSIS OF SWAMP QUADRAT DATA*

In order to erect a numerically based classification of the herbaceous swamp vegetation, a multivariate analysis was performed on the floristic data of Table 5.1. All values recorded as '+' were first set to 0.5. The technique of sums-of-squares analysis (program SSA) presented by Orloci (1975) was then employed. This hierarchical polythetic clustering method uses the coefficient of Euclidian distance as a similarity measure for the formation of groups. The coefficient, calculated by program EUCD, may be derived from either

---

[1] ANU collection number. Voucher specimens are in the Herbarium, Botany Division, Lae, with selected duplicates at the Herbarium Australiense, CSIRO, Canberra.

TABLE 5.1. *Floristic and cover-abundance data from herbaceous swamp quadrats at Lake Wanum*

| Common species | | Area | SOUTH SWAMP | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | NORTH-EAST BAY | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Transect | A | | | | | | | B | | | | | | | | | | | | | C | | | | | | | | | | | | | | | | | F | | | | | | | | D | | | | | | E | | | | | | |
| | | Quadrat No. | 01 | 02 | 03 | 04 | 05 | 06 | 07 | 08 | 09 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 |
| • | 1 | NELUMBO NUCIFERA | 0 | + | 0 | 0 | 2 | + | + | + | 1 | + | 3 | 3 | 1 | 1 | 0 | 2 | 2 | 4 | 4 | 2 | 2 | 0 | + | + | 1 | 0 | 0 | 0 | 1 | + | 4 | 4 | 4 | 4 | 2 | 3 | 4 | + | 3 | 2 | 3 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| • | 2 | NYMPHOIDES INDICA | 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 | 1 | 0 | + | + | 1 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 |
| | 3 | NYMPHAEA PUBESCENS | 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 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 4 | NYMPHAEA SP. (21060) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 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 | NYMPHOIDES SP. (21059) | 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 |
| • | 6 | CERATOPHYLLUM DEMERSUM | 0 | 0 | 0 | 0 | + | 0 | + | + | 0 | 0 | 2 | + | + | 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 |
| | 7 | VALLISNERIA SP. (21020) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 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 | NEPHROLEPIS HIRSUTULA | 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 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 1 | + | 0 | 1 | + | 2 | + | 2 | 2 | 0 | 3 |
| • | 9 | STENOCHLAENA PALUSTRIS | + | 0 | 1 | 1 | 0 | + | 2 | 0 | 0 | 4 | 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 | 1 | 2 | 1 | + | 0 | 0 | 1 |
| • | 10 | CYCLOSORUS SP. (21050) | 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 | 0 | 0 | 0 | 0 | 1 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 11 | CERATOPTERIS THALICTROIDES | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 12 | ACROSTICHUM AUREUM | 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 |
| | 13 | MICROSORIUM SP. (21067) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + | 0 | 0 | + |
| • | 14 | HYPOLYTRUM NEMORUM | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 2 | 3 | 3 | 4 | 4 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 1 | + | 1 | 0 | 1 | + | 2 | + | 2 | + | 1 | 1 | 1 | + | + | 1 |
| | 15 | CYPERUS PLATYSTYLIS | 0 | 2 | 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 |
| | 16 | CYPERUS POLYSTACHOS | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 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 | ELEOCHARIS DULCIS | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 18 | SCIRPUS GROSSUS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 19 | FUIRENA CILIARIS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 |
| • | 20 | LEERSIA HEXANDRA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | + | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | + | 3 | 0 | + | 2 | + | 0 | + | + | 1 | 3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 21 | SACCIOLEPIS MYOSUROIDES | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 22 | SACCIOLEPIS INDICA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 23 | PHRAGMITES KARKA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 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 |
| | 24 | LUDWIGIA OCTOVALVIS | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 |
| | 25 | LUDWIGIA HYSSOPIFOLIA | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 26 | PANDANUS SP. (21062) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 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 |
| | 27 | ALSTONIA SPATULATA | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 28 | UNCARIA GAMBIR | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 |
| | 29 | COLOCASIA SP. (21055) | 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 |
| | 30 | MERREMIA GEMELLA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 31 | IPOMOEA GRACILIS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 32 | CAYRATIA TRIFOLIA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 33 | ARACEAE SP. (21064) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 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 |
| | 34 | MARSDENIA SP. (21066) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 |
| | 35 | NEPENTHES MIRABILIS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 |
| | 36 | SPATHOGLOTTIS PLICATA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 |
| | 37 | THRIXSPERMUM AMPLEXICAULE | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 |

*FIGURE 5.1. Dendrogram of sums-of-squares analysis on floristic data from Lake Wanum, normalised by quadrat*

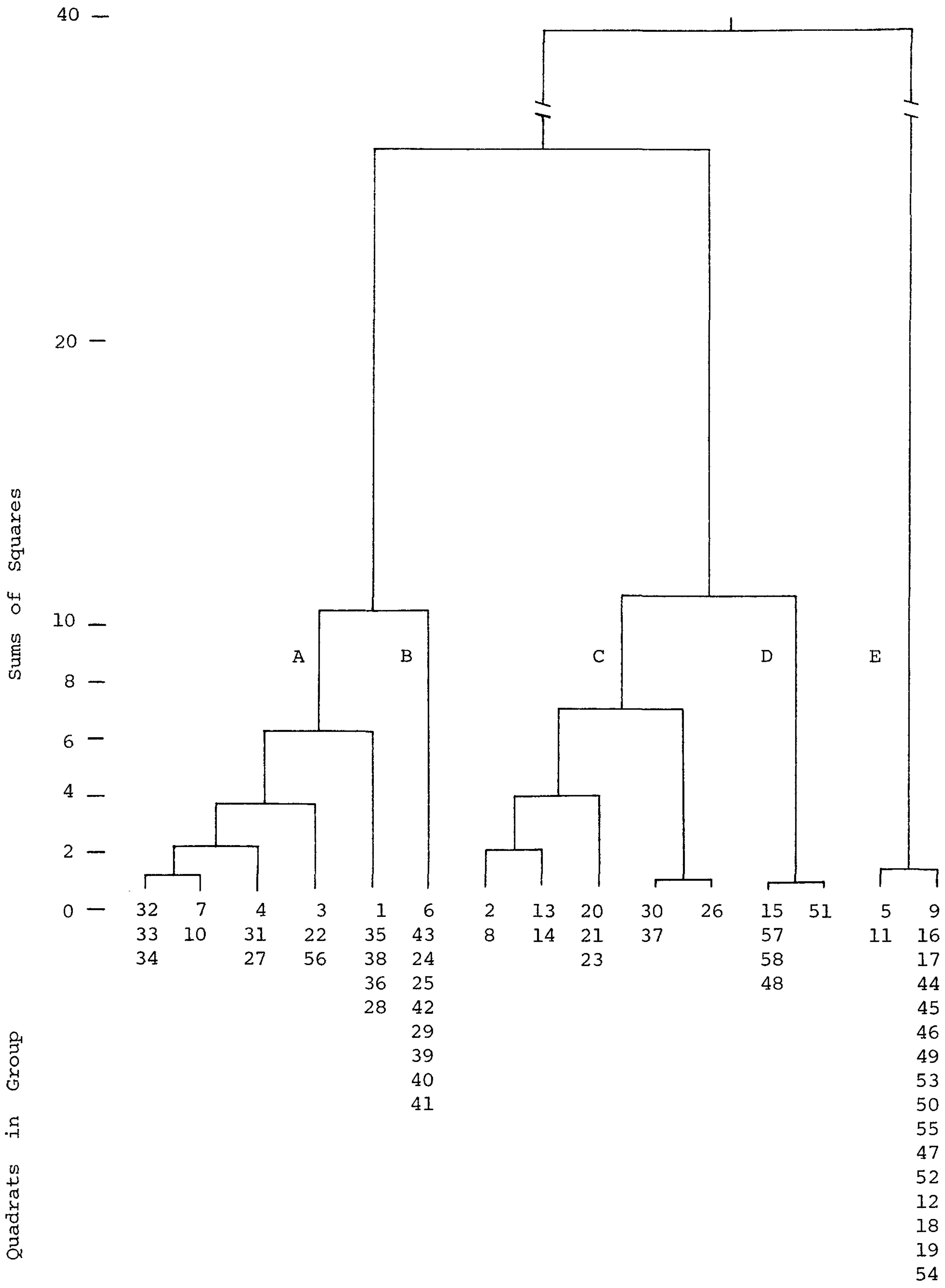


*TABLE 5.2. Herbaceous swamp data matrix grouped by sums-of-squares analysis, normalised by quadrat*

| | | GROUP A | | | | | | | | | | | | | | | | GROUP B | | | | | | | | | GROUP C | | | | | | | | | | GROUP D | | | | | GROUP E | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 01 | 03 | 08 | 07 | 10 | 22 | 27 | 28 | 31 | 32 | 33 | 34 | 35 | 36 | 38 | 56 | 06 | 24 | 25 | 29 | 39 | 40 | 41 | 42 | 43 | 02 | 04 | 13 | 14 | 20 | 21 | 23 | 26 | 30 | 37 | 15 | 49 | 51 | 57 | 58 | 05 | 09 | 11 | 12 | 16 | 17 | 18 | 19 | 44 | 45 | 46 | 47 | 48 | 50 | 52 | 53 | 54 | 55 |
| 1 | NELUMBO NUCIFERA | . | . | . | + | + | . | . | . | . | . | . | . | . | . | . | 1 | + | + | 1 | . | . | . | . | 1 | + | + | + | 1 | 1 | 2 | 2 | + | . | . | . | . | 2 | + | . | . | 2 | 1 | 3 | 3 | 2 | 2 | 4 | 4 | 4 | 4 | 4 | 4 | 3 | 4 | 3 | 2 | 3 | 3 |
| 2 | NYMPHOIDES INDICA | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | + | + | . | + | . | . | . | + | 1 | 1 | + | . | . | . | . | . | 2 | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 3 | NYMPHAEA PUBESCENS | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | + | . | . | . | . | . | . |
| 4 | NYMPHAEA SP. (21060) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | + | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 5 | NYMPHOIDES SP. (21059) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | + | . | . | . | . | . | . | . | . | . | . | . | . | . | + | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 6 | CERATOPHYLLUM DEMERSUM | . | . | . | + | . | . | . | . | . | . | . | . | . | + | . | . | . | . | + | + | . | + | + | . | . | . | + | + | . | . | + | . | . | . | . | + | . | . | . | . | + | . | 2 | + | . | . | 1 | + | . | . | . | . | . | . | . | . | + | . |
| 7 | VALLISNERIA SP. (21020) | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 8 | NEPHROLEPIS HIRSUTULA | 3 | + | 1 | + | . | + | + | 1 | 1 | + | 2 | + | 2 | 2 | 3 | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 9 | STENOCHLAENA PALUSTRIS | + | 1 | 1 | 2 | 4 | + | + | . | 1 | 1 | 2 | 1 | + | . | 1 | + | + | . | . | . | . | . | + | . | + | . | . | . | . | + | . | . | . | . | . | 1 | + | + | + | + | . | . | . | . | . | . | . | . | . | . | . | + | . | . | + | . | . | . |
| 10 | CYCLOSORUS SP. (21050) | . | 1 | + | . | + | 1 | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | + | + | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 11 | CERATOPTERIS THALICTROIDES | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 12 | ACROSTICHUM AUREUM | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 13 | MICROSORIUM SP. (21067) | . | . | . | . | . | . | . | . | . | . | + | + | + | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 14 | HYPOLYTRUM NEMORUM | 1 | 1 | 2 | 1 | . | + | 1 | + | 2 | + | 1 | 1 | 1 | + | 1 | 1 | 2 | 2 | 3 | 2 | 3 | 4 | 4 | 2 | 3 | . | . | + | . | . | . | + | . | + | + | . | . | + | + | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 15 | CYPERUS PLATYSTYLIS | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | 1 | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 16 | CYPERUS POLYSTACHOS | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 17 | ELEOCHARIS DULCIS | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 18 | SCIRPUS GROSSUS | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 19 | FUIRENA CILIARIS | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 20 | LEERSIA HEXANDRA | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | + | . | . | . | . | + | 1 | . | . | . | . | 3 | 3 | 2 | 3 | 4 | . | . | . | . | . | . | . | . | . | . | . | + | . | + | + | . | + | + |
| 21 | SACCIOLEPIS MYOSUROIDES | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 22 | SACCIOLEPIS INDICA | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 23 | PHRAGMITES KARKA | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . |
| 24 | LUDWIGIA OCTOVALVIS | . | . | . | . | . | . | + | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 25 | LUDWIGIA HYSSOPIFOLIA | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 26 | PANDANUS SP. (21062) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | 2 | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . |
| 27 | ALSTONIA SPATULATA | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 28 | UNCARIA GAMBIR | . | + | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 29 | COLOCASIA SP. (21055) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 30 | MERREMIA GEMELLA | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 31 | IPOMOEA GRACILIS | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | + | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 32 | CAYRATIA TRIFOLIA | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . |
| 33 | ARACEAE SP. (21064) | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 34 | MARSDENIA SP. (21066) | . | . | . | . | . | . | . | + | . | + | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 35 | NEPENTHES MIRABILIS | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 36 | SPATHOGLOTTIS PLICATA | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 37 | THRIXSPERMUM AMPLEXICAULE | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |

the raw data, or from normalised quadrat vectors (the 'chord' distance). Normalisation sets the sum of all vectors to unity, thus effectively comparing relative rather than absolute abundance of taxa between quadrats. Unfortunately, no facility is available for normalisation of data on the basis of within-taxon rather than within-quadrat vectors. An 'inverse' (taxon-grouping) analysis of the raw data produced an unsatisfactory dendrogram showing excessive 'chaining' of the more abundant commonly occurring taxa only. The quadrat groups, or vegetation associations, formed are therefore interpreted subjectively on the basis of apparent similarities in the floristic and environmental attributes.

Sums-of-squares analysis was performed on three versions of the floristic data set: the raw data, the normalised data, and a subset of the normalised data. This last group of eight taxa represents the 'common' species, defined as those with ten or more occurrences. The subset also happens to include the most generally abundant, or physiognomically dominant, taxa. Analysis of the full, normalised data appears to give the most tractable classification of the vegetation. The dendrogram of quadrat groupings thus produced is shown in Fig. 5.1 and their floristic composition is displayed in Table 5.2. Five groups of quadrats are defined at the sums-of-squares value 10:

### *Group A: Deep-water, floating root-mat, association*

This group of 16 quadrats is characterised by the co-occurrence of three species: the large sedge *Hypolytrum nemorum*, the erect fern, *Nephrolepis hirsutula*, and the straggling fern *Stenochlaena palustris*. Associated with these species in the denser stands are *Microsorium* sp. (21067), also an erect fern, and several dicotyledons, amongst them *Nepenthes mirabilis,* and *Uncaria gambir.* The orchids *Spathoglottis plicata* and *Thrixspermum amplexicaule* are often found along the margins of the floating root-mat islands. This association predominates in many areas where the water is deeper than 2 m, although vegetation of somewhat similar floristic composition may occur in shallower water. It is, however, the only association consistently found in water deeper than 4 m, and may occur in areas up to 8 m deep.

*Group B: Shallow water,* Hypolytrum nemorum, *association*

Quadrats in this group are dominated by dense tussocky stands of *Hypolytrum nemorum* with shoots up to 2 m above water level. The only widespread associates are *Nelumbo nucifera* and the submerged *Ceratophyllum demersum,* found in open water between the *Hypolytrum* tussocks, although *Stenochlaena palustris* is locally common. This vegetation is characteristic of many areas with a water depth of about 1.5 m. Two quadrats (29 and 39) from areas of floating root-mat in deeper water consist of similar, almost monospecific *Hypolytrum* stands, and are classified with this association.

*Group C: Mixed aquatic association*

The 10 quadrats of this group are floristically diverse, and heterogenous in their species composition. *Nelumbo nucifera, Nymphoides indica* and *Hypolytrum nemorum* are frequent occurrences, although none dominates. *Cyperus platystylis, Pandanus* sp. (21062) and *Araceae* sp. (21064) are locally abundant. A number of quadrats from the submerged margin of floating root-mats are also included in this group. With the exception of these sites, the association is generally found in water 1 m to 2 m deep.

*Group D:* Leersia hexandra *root-mat association*

A small but distinctive group of five quadrats dominated by *Leersia hexandra* comprise this association. This grass often forms a low floating root-mat in areas shallower than 2.5 m. *Stenochlaena palustris*, though never abundant, is a consistent associate.

*Group E:* Nelumbo nucifera *open water association*

The 18 quadrats of this large association are characterised by almost pure stands of *Nelumbo nucifera* in otherwise open water, typically 1.5 m deep. Other species, in particular floating-leaved and submerged aquatics, occur, but none is common. *Leersia hexandra* is found in some quadrats.

Analysis of the non-normalised raw data produces a slightly different allocation of quadrats to groups (Fig. 5.2). At the sums-of-squares value 100, four groupings are recognised. Floristic groups B, the *Hypolytrum nemorum* association, and D, the *Leersia hexandra* association remain unchanged. However, quadrats of the heterogenous group C, the mixed aquatic association, become equally redistributed between groups A, the deep-water root-mat, and E, the *Nelumbo nucifera* associations.

A third analysis, using the normalised records of the 'common' species only, results in the classification shown in Fig. 5.3. At the sums-of-squares value 12, group D is the only one to remain totally intact. The quadrats of group C again become redistributed, this time between groups B and E. Quadrats 4, 27 and

*FIGURE 5.2. Dendrogram of sums-of-squares analysis on floristic data from Lake Wanum, non-normalised*

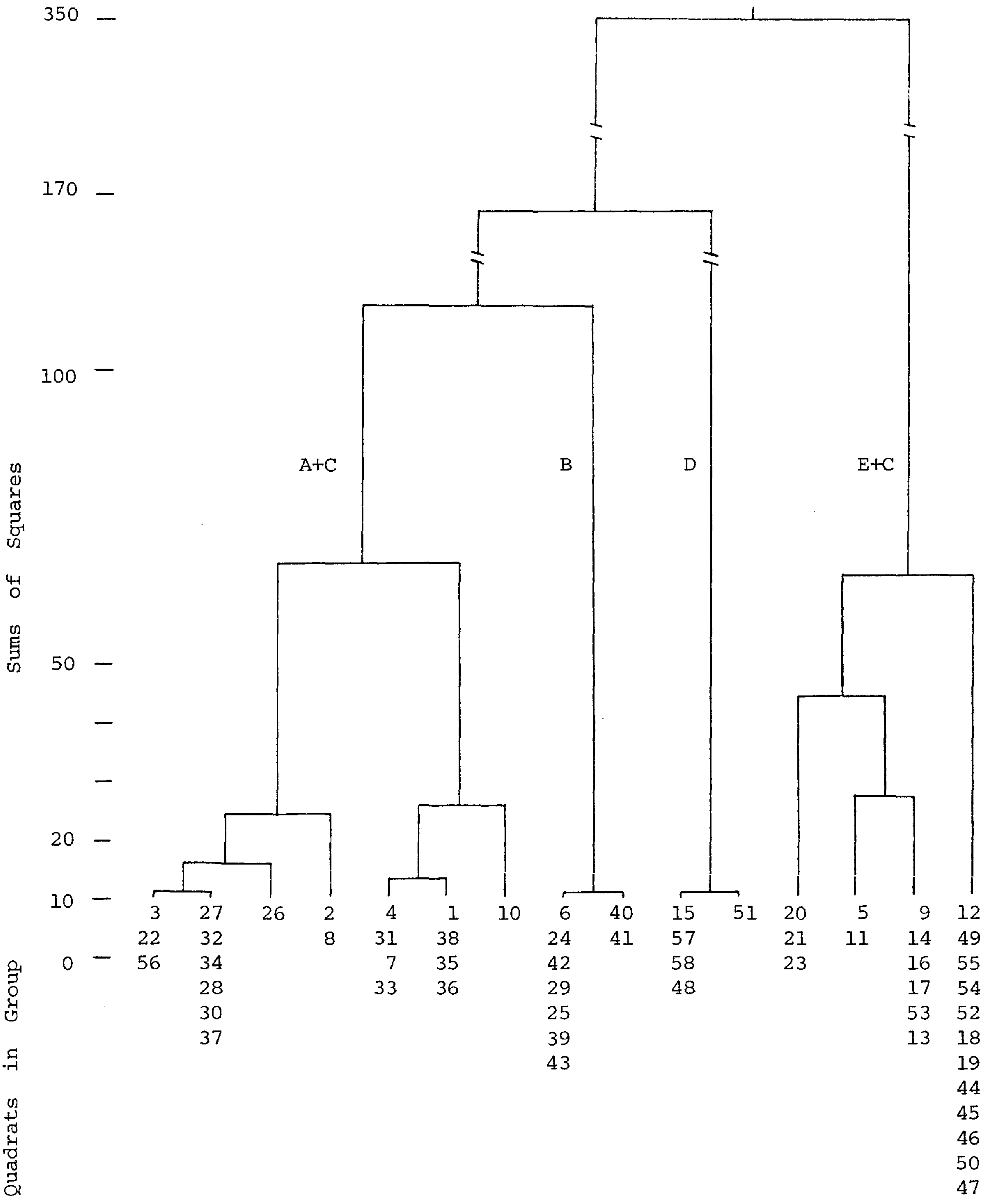
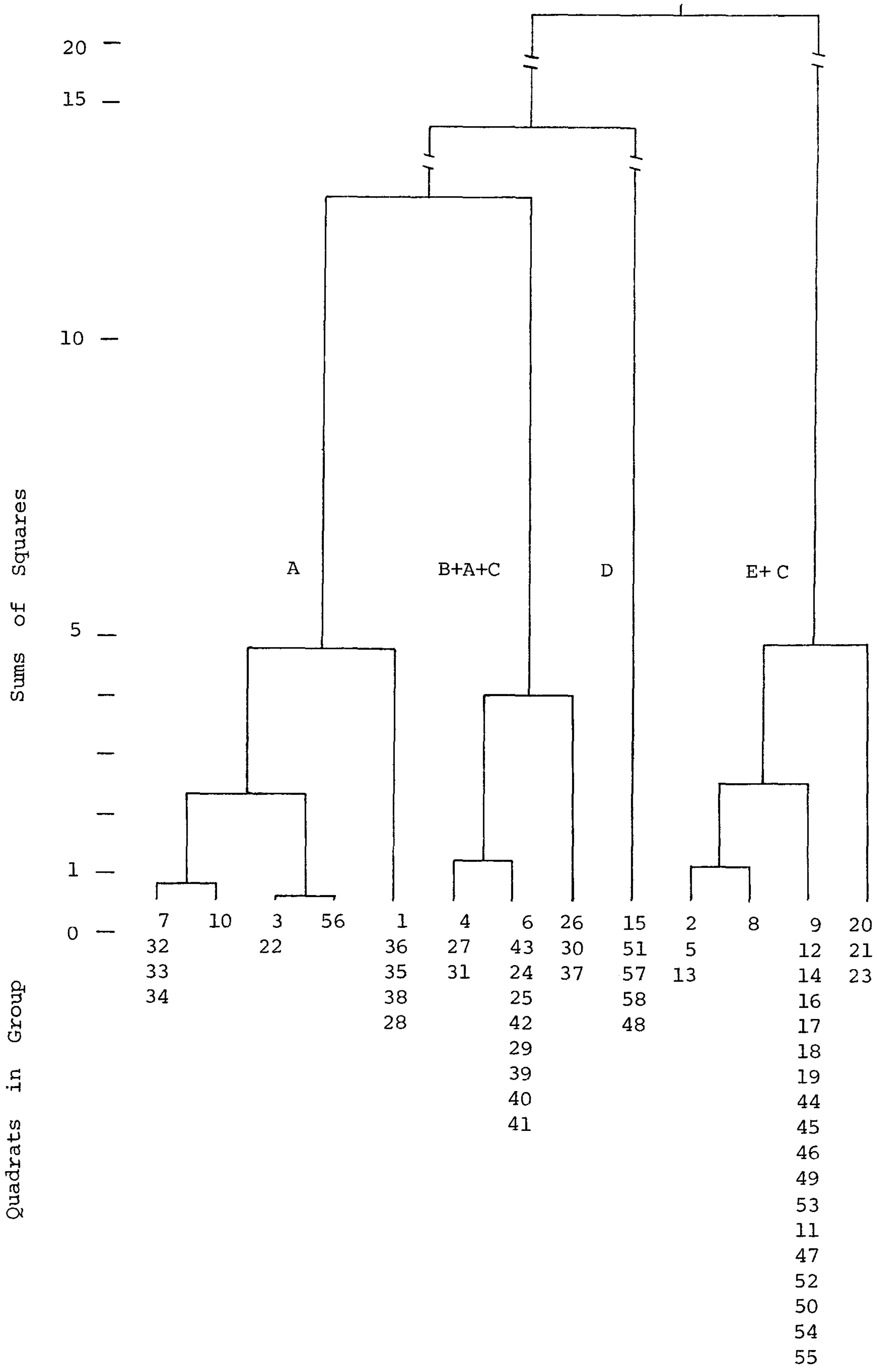


*FIGURE 5.3. Dendrogram of sums-of-squares analysis on floristic data from Lake Wanum, common taxa only, normalised by quadrat*



31 with their relatively high values for *Hypolytrum* are allocated to group B, the *H. nemorum* association, rather than to the floristically more diverse association of group A.

Despite these differences, the major features of the floristic classification remain intact. This suggests that the classification is relatively robust and insensitive to minor differences in the analytical technique. Four or five main vegetation associations occur, of which four can be defined by the small number of species that dominate them floristically and physiognomically.

## *THE DISTRIBUTION OF HERBACEOUS SWAMP ASSOCIATIONS IN THE LAKE WANUM AREA*

The herbaceous swamp associations described above frequently occur in small scale mosaics, and are therefore difficult to map. This is especially true in the south swamp area of Lake Wanum where all associations are represented to some extent. The *Nelumbo nucifera* association, group E, occurs here over a wide area (Plate 5.2), and also along the southern and eastern shores of the lake. Group C, the mixed aquatic association is also predominant in the south swamp. The *Leersia hexandra* floating root-mat association, group D, is also more common in the south swamp, although small areas do occur in the vegetation of the north-east bay. The shallow water *Hypolytrum nemorum* association of group B dominates large areas of the south swamp but is also found along the eastern shore of the lake, and forms the small islands of vegetation in the middle of the north-east bay. The generally deeper water of the western margin of the north-east bay is dominated by the floating root-mat vegetation of group A (Plate 5.3). All but two quadrats sampled from the area fall into this association.

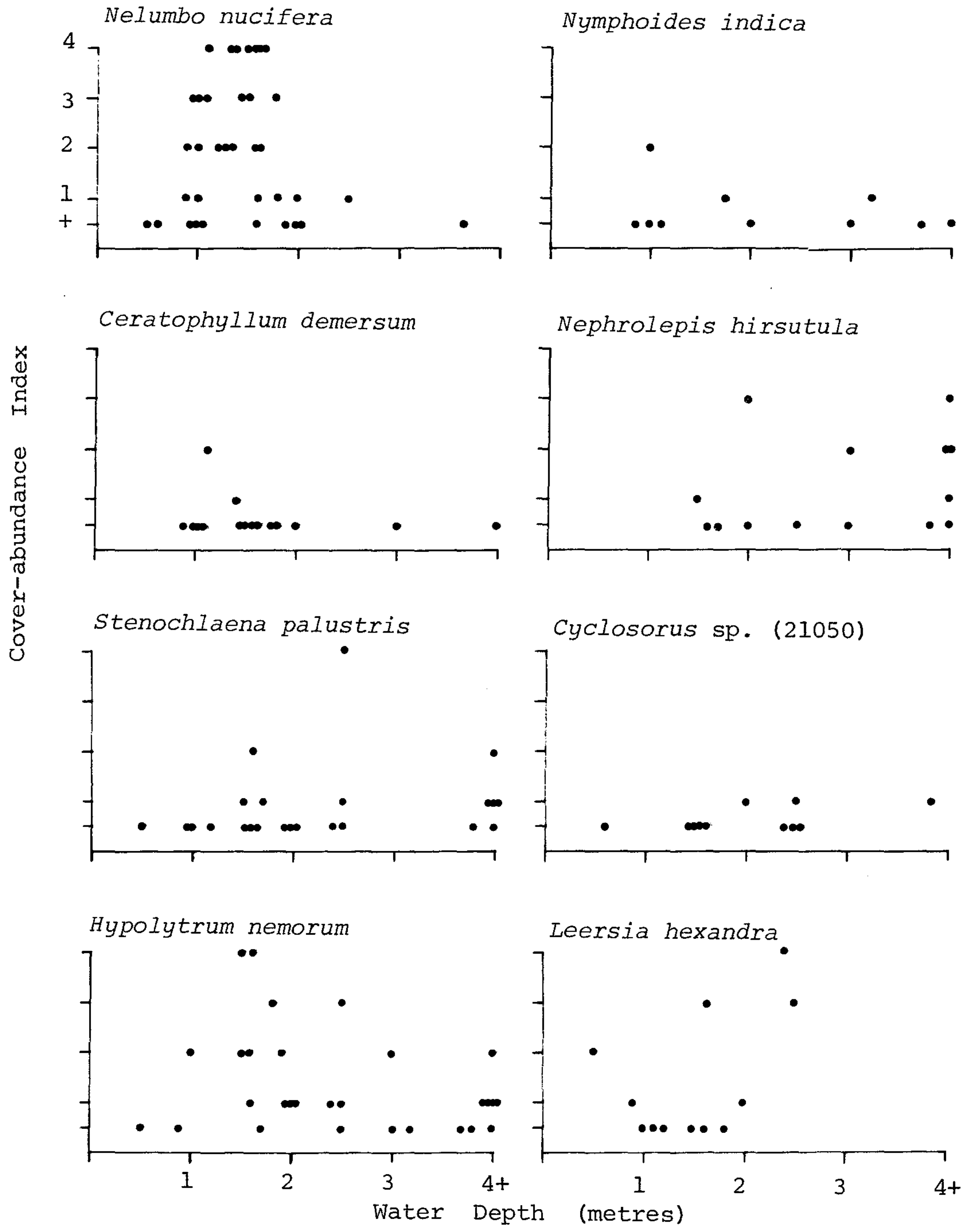
*PLATE 5.1.* The extensive south swamp of Lake Wanum. Grass-covered Mount Ngaroneno (alt. 340 m) is visible to the north-west.

*PLATE 5.2. Hypolytrum nemorum* and *Stenochlaena palustris* encroaching on open water stands of *Nelumbo nucifera*, south swamp, Lake Wanum.

*PLATE 5.3.* Floating root-mat vegetation in deep water at the western margin of the north-east bay, Lake Wanum. The sedge *Hypolytrum nemorum* and erect fern *Nephrolepis hirsutula* dominate the mat. *Stenochlaena palustris,* a straggling fern, is also seen.

*PLATE 5.4.* Aquatic vegetation at the northern end of Yanamugi. *Nymphoides indica* covers much of the open water less than 3 m in depth. Sago palm, *Metroxylon sagu,* is visible in the right background.

*FIGURE 5.4. Cover-abundance of common herbaceous swamp taxa from Lake Wanum in relation to water depth*



Associations similar to those recognised at Lake Wanum appear to make up the herbaceous swamp vegetation around the Erom-Erom lakes. Here, the slope of the shoreline is gradual, and a distinct zonation of vegetation is apparent. Waterlogged grassland with such species as *Coelorhachis rottboellioides* gives way to a floating *Leersia hexandra* root-mat, similar to group D. Other taxa may be present, including species of *Sacciolepis*, and the twining *Merremia* sp. (21165). Isolated shoots of *Nelumbo nucifera* may also occur, and in deeper water the species forms an almost monospecific association, similar to that of group E at Lake Wanum. The area between each of the small lakes and the riparian forest of Oomsis Creek is occupied by dense herbaceous swamp vegetation. Although these areas were not surveyed, they appear to be dominated by *Hypolytrum nemorum*, either rooted or in floating vegetation similar to groups B and A at Lake Wanum.

## *ENVIRONMENTAL DETERMINANTS OF VEGETATION DISTRIBUTION*

As indicated above, the major environmental factor controlling the distribution of the various herbaceous swamp associations is water depth. In some areas zonation of vegetation is related to increasing water depth. More usually, a mosaic of vegetation associations occurs and it becomes more difficult to assess the influence of the water depth on their floristic composition. The edges of floating root-mats can form a shallow 'micro-environment' in otherwise deeper water.

The abundance of each of the 'common' species in relation to water depth is shown in Fig. 5.4. Some of the taxa can be seen to occupy fairly restricted depth ranges, whilst others are more ubiquitous.

Most occurrences of *Nelumbo nucifera* are recorded from 0.75 m to 2 m of water, the two data points from deeper areas being associated with the edge of floating root-mat communities. The species is least common in the deep water root-mat association of group A. *Nymphoides indica* although never abundant is found growing in up to 5 m of water. It is surprisingly infrequent in shallow places dominated by *Nelumbo nucifera*. The widespread *Hypolytrum nemorum* exhibits a bi-modal distribution. The first abundance peak is associated with the quadrats of group B where the sedge dominates, and the second coincides with the deep water floating root-mat association of group A. The co-dominants of *H. nemorum* in this association, *Nephrolepis hirsutula* and *Stenochlaena palustris* show similar abundance patterns, although neither is as common as *H. nemorum* in shallow water. *Nephrolepis hirsutula* is almost entirely restricted to the quadrats of group A, and was not recorded growing in areas of water shallower than 1.5 m. *Stenochlaena palustris* is present throughout all groups although is more common in floating root-mat vegetation. In the quadrats sampled, *Leersia hexandra* is restricted to water shallower than 2.5 m. *Cyclosorus* sp. (21050) occurs in quadrats of group A in the south swamp with water depths generally of less than 2.5 m. However it is totally absent from this association in the north-east bay, where the water is deeper than 4 m. Its place appears to be taken by *Microsorium* sp. (21067), restricted to the group A quadrats in this area. Although often free-floating, *Ceratophyllum demersum* is commonly associated with shallow water areas less than 2 m deep.

The availability of shelter from wind and wave action may also affect the distribution of some species. *Nymphoides indica* and *Eleocharis dulcis* are seldom found in exposed situations, but tend to congregate in between tall stands of other vegetation.

The composition of the substrate provides a further factor that may influence the distribution of a species. The south swamp is largely underlain by minerogenic grey clay, as are the shallow margins of the south and east shores of the lake. In the north-east bay the substrate is predominantly organic. Differences in the vegetation and floristics of the two areas have been described above, and some may reflect the contrasting substrates. Kershaw (1978) recorded *Nymphaea gigantea* only from sites lacking a large accumulation of organic material, and suggested that the species might require a mineral substrate. At Lake Wanum, *Nymphaea pubescens* and *Nymphaea* sp. (21060) are present in the vegetation of the south swamp, but not in that of the north-east bay. However, the great difference in general water depth rather than their contrasting substrates probably accounts for the major variations in herbaceous swamp vegetation between these two areas.

## *HISTORICAL CHANGES IN HERBACEOUS SWAMP VEGETATION AROUND LAKE WANUM*

The existence of a chronological series of aerial photographs of the lower Markham Valley makes it possible to trace recent changes in the herbaceous swamp vegetation around Lake Wanum.

The earliest photographs available are those reproduced in the wartime Allied Geographical Section terrain studies handbooks and reports (A.G.S. 1942, 1943*a*, 1943*b*, 1943*c*). Oblique aerial photographs dated February and March 1943 indicate the extent of herbaceous swamp along the southern margin of the lake to be very similar to that of 1974. However, no open water is visible in Lake Erom-Erom 1, apparently a swamp at that date. A series of vertical aerial photographs dated September 1956[1] show similar features although there appears to have been slight encroachment of swamp vegetation into the open water of the south-east corner of Lake Wanum. Substantial islands of vegetation are present in the centre of the north-east bay, and a swamp remains on the site of Erom-Erom 1.

The most dramatic changes are documented by a run of photographs from November 1969[2]. A vast encroachment of vegetation into open water along the southern and eastern margins is shown extending towards the 4 m bathymetric contour (Fig. 3.2). Many of the small embayments along the north shore of the lake are also vegetated, and there is an extension of the swamp islands in the north-east bay. The open water of Lake Erom-Erom 3 is also reduced by swamp growth. However, at Lake Erom-Erom 1, a considerable body of open water is visible for the first time.

Large scale vertical photographs of sections of Lake Wanum taken during 1971 indicate a reversal of previous conditions. The south-east corner of the lake[3] is still considerably infilled with what appear to be stands of *Nelumbo nucifera*. However, some

---

[1] CAJ 53-5053 NADZAB 25 000 ft. 27 September 1956
[2] QASCOPHOTO NG 99 2163 25 000 ft. 30 November 1969
[3] QASCOPHOTO NG 155 8729 6 500 ft. 27 July 1971

tracts of open water are once again present, especially along the eastern shore. A photograph[1] of the north-west area suggests a slight diminution of aquatic vegetation cover in some of the embayments.

Ground and aerial observations made during 1974 and 1976 indicated the area of open water in Lake Wanum to be very similar to that in 1943. The south-east corner was again free of swamp vegetation, and the islands in the north-east bay were noticeably less extensive than in 1956 or 1969. Lake Erom-Erom 1 contained much open water, as in 1969, although between 1974 and 1976 there appeared to be a slight increase in the area of *Nelumbo nucifera* in the eastern branch.

Most of the observed vegetation changes could be explained by fluctuation in the water level of Lake Wanum and the Erom-Erom lakes. The extension of *Nelumbo nucifera* and other vegetation into the areas indicated in 1969 would require a drop in the lake level to at least 2 m below that of 1974. Evidence does exist for a recent slight rise in water level. Dead *Phragmites karka* stems may be found in areas of open water where the grass does not now grow. Numerous dead trees occur along the margin of the swamp forest and around the shores of the lake, presumably killed by inundation. A small decrease in the level of Lake Wanum was recorded between 1974 and 1976. During 1974, the outlet to Oomsis Creek flowed constantly, whereas 18 months later the channel was found dry and overgrown.

---

[1] QASCOPHOTO NG 144 4747 10 000 ft. 21 March 1971.

The opposite directions of apparent water level change in Lake Wanum and Lake Erom-Erom 1 suggest that local hydrological conditions are more important than any general climatic effects. Factors possibly influencing local hydrology are multifarious and almost impossible to quantify. Considerable extension of the Gabensis cocoa plantation immediately adjacent to the Lake Wanum south swamp took place between 1956 and 1969. Resulting erosion may have had a direct effect on the swamp forest or on the hydrology of Oomsis Creek. The suggested increase in water level of Lake Erom-Erom 1 could have been caused by further impoundment by the extensive swamp vegetation between the lake and Oomsis Creek.

One other biotic factor may be of importance in recent vegetation change. Lake Wanum is now well stocked with *Tilapia mossambica* despite heavy exploitation by the local inhabitants. These exotic fish were introduced into the lake by the D.A.S.F., reportedly during 1966, and their increasing population may have made some impact on the swamp and aquatic vegetation.

Whatever the causes, the evidence documents considerable and rapid change in swamp vegetation over the last few decades. The vegetation associations appear dynamic rather than successional, responding to minor changes in environmental conditions. This conclusion becomes of great importance when attempting to reconstruct the development of the swamp vegetation over a much longer time-scale.

## *THE VEGETATION OF REDHILL SWAMP*

The vegetation of Redhill swamp differs from that of the lake marginal areas of Lake Wanum and Erom-Erom. At Redhill there is practically no open water and the basin appears fairly shallow.

The stratigraphy (Chapter 3) suggests that much of the swamp is floating on at least 3 m of water. Examination of the vegetation showed it to be a well developed root-mat association with a floristic composition similar to that of group A at Lake Wanum. The co-dominants of this group, *Hypolytrum nemorum, Stenochlaena palustris* and *Nephrolepis hirsutula* are all present. However, the floating vegetation of Redhill is more complex both floristically and physiognomically than that of Lake Wanum. The herbaceous vegetation may be up to 3 m high and many additional species are found including *Alstonia spatulata,* a small tree with a balsa-like trunk and root-system, and the sago palm, *Metroxylon sagu.*

The gentle slope of the south-eastern edge of the swamp basin provides a habitat for shallow water and periodically inundated vegetation. Within the perennial swamp are found, along with the species named above, *Alstonia scholaris, Nepenthes mirabilis* and *Dysophylla verticillata.* Also included in the swamp margin and periodically waterlogged grassland areas are *Lycopodium cernuum, Coelorhachis rottboellioides, Alyxia floribunda* and *Coleus scutellarioides.* In the damp shrubby grassland fringing the swamp *Timonius timon* and *Ilex arnhemensis* are very common, and *Terminalia, Trichospermum, Schuurmansia henningsii* and *Desmodium gyroides* are also encountered.

There is no evidence for any major change in the swamp vegetation from the aerial photographs available for 1956 and 1971. This is not surprising since, if as suggested most of the swamp is floating, only extreme changes in the hydrology would be reflected by visible changes in the vegetational associations.

## *SWAMP AND AQUATIC VEGETATION AT YANAMUGI*

The largest area of swamp vegetation at Yanamugi is the *Metroxylon sagu* dominated association to the north of the lake. *Phragmites karka* is also common in this area. In water deeper than *c.* 1.2 m the sago swamp gives way to a zone of *Eleocharis dulcis* whilst in open water up to 3 m deep *Nymphoides indica* dominates (Plate 5.4).

There is little swamp vegetation along the western and eastern shores of the lake where the slope of the basin is steeper (Fig. 4.2). However, other small areas of herbaceous swamp vegetation occur along the shallower margins of the lake. A bay in the south-east corner is dominated by the emergent aquatic herbs *Polygonum attenuatum* and *Phyla nodiflora,* as well as *Phragmites karka* and *Eleocharis dulcis.*

In areas of open water *Nymphoides indica* is the most common floating-leaved hydrophyte, although *Nymphaea pubescens* is also found. The submerged aquatics *Najas graminea* and *Ceratophyllum demersum* occur in water up to 4.2 m deep.

Small areas of floating root-mat vegetation exist in sheltered embayments along the south-west shore of the lake. Species forming these associations include *Acrostichum aureum, Ceratopteris thalictroides, ?Scirpus grossus* and several grasses, probably *Leersia hexandra* and species of *Sacciolepis.* Scattered individuals of *Metroxylon sagu, Stenochlaena palustris* and *Nephrolepis* occur in shallow water or periodically inundated situations around the lake.

Available aerial photography[1] reveals no appreciable change in swamp and aquatic vegetation between 1962 and 1971.

## *SWAMP VEGETATION OF THE MARKHAM VALLEY AND OTHER TROPICAL AREAS*

It would be improper to generalise about lowland freshwater swamp communities in Papua New Guinea on the basis of four localised sites, only one of which has been studied in any detail. However, tentative comparisons can be made both between the different sites in the Markham Valley, and with similar environments in other tropical areas.

The vegetation associations of Lake Wanum and the Erom-Erom lakes appear very similar, reflecting their proximity and identical geology. The differences between these two sites and Redhill swamp may result from several factors. The latter's location on the boundary of the granodiorite and metamorphic rocks may give rise to the suggested shallower basin morphometry and perhaps even to differing nutrient supply to the swamp.

Yanamugi is very different from the other sites in its geology, morphometry, sedimentology and climatic regime. Two of the major dominant species in the Lake Wanum area, *Hypolytrum nemorum* and *Nelumbo nucifera,* are missing from the swamp vegetation at Yanamugi and two others, *Stenochlaena palustris* and *Nephrolepis hirsutula*, are much less common. Nevertheless, the vegetation is otherwise floristically and physiognomically fairly similar, with the *Metroxylon sagu* palm and various swamp grasses being more abundant.

---

[1] C.A.J. 195 LERON 5031 25 000 ft. 1 February 1962
QASCOPHOTO C.A.J. 1284 ONGA 1284 23 000 ft. 25 May 1969
QASCOPHOTO MARKHAM VALLEY NG 138 1578 10 000 ft. 22 January 1971

There are very few similarities between the lowland swamps studied and the alpine and sub-alpine bogs of Papua New Guinea and West Irian described by Wade and McVean (1969) and Hope (1976*b*). These communities are structurally very different, and do not possess any species in common with the lowland sites. The few congeneric plants are mainly grasses and sedges.

At Kayamanda, an extensive valley swamp at a lower altitude (2 500 m), Walker (1972*a*) identifies 15 floristic groups falling into 8 major vegetation units. Only four species recorded, *Lycopodium cernuum, Sacciolepis indica, Phragmites karka* and *Dysophylla verticillata,* and six genera including four sedges, *Nymphoides* and *Polygonum* are common to the Markham Valley. No floating vegetation was encountered, although the northern sector of the swamp around Lake Ipea was not sampled. Flenley (1972) describes floating vegetation from nearby Lake Inim (2 550 m) although the floristic composition differs totally from that found in the lowland sites studied.

In contrast, striking similarities exist between the swamp and aquatic vegetation of the Atherton Tableland (alt. 750 m) north-east Queensland (Kershaw, 1978) and that of the Markham Valley. Six species (*Ceratophyllum demersum, Cyperus platystylis, Eleocharis dulcis, Leersia hexandra, Nymphoides indica* and *Ludwidgia octovalvis*) and six additional genera found at these sites are also recorded from the Markham Valley. Kershaw (1978) recognises three ecologically definable communities: free water dominated by *Nymphoides indica, Cyclosorus gongylodes* dominated floating root-mat, and fixed root-mat comprised of tussocks of *Blechnum indicum*. These communities appear structurally similar to three of the vegetation associations defined at Lake Wanum. In both areas, ferns play an important role in the swamp vegetation. *Cyclosorus* species are frequently found in herbaceous swamp areas of Papua New Guinea (Paijmans, 1976) and occur at Lake Wanum. *Stenochlaena palustris* is a widespread inhabitant of swamp forest and mangrove communities of south-east Asia (Holttum, 1932) and Papua New Guinea (Paijmans, 1976) although it is not found in northern Queensland.

The herbaceous swamp vegetation of the four sites investigated exhibits basic similarities both in floristic composition and physiognomy. Differences tend to be expressed floristically rather than structurally, even though the missing species may be important dominants in other sites. Floristic and structural similarities between these swamps and related environments in northern Queensland and south-east Asia appear much greater than those between lowland and high-altitude sites within New Guinea.

# CHAPTER 6

# THE DETERMINATION OF POLLEN AND CHARCOAL DEPOSITION RATES

Ever since the inception of Quaternary pollen analysis it has been realised that, for both statistical and ecological reasons, the interpretation of fluctuations in the interdependent curves of the standard 'percentage' pollen diagram, has serious limitations. L. von Post in his famous address of 1916 (von Post, 1918, 1967) stated that 'obviously it would have been desirable from various points of view to use figures giving the absolute frequencies instead of the relative measures that are indicated by percentage figures'. Although he also discussed the total pollen content of peat layers von Post realised that such figures would be difficult to interpret due to differences in the rate of peat accumulation within and between bog sites. He therefore considered it 'especially desirable to investigate the feasibility of producing comparable absolute frequency figures' (von Post, 1967).

Some authors have since published diagrams calculated on the basis of pollen content per unit of sediment, assuming changes in sedimentation rate to be of only minor importance at the particular site (Livingstone and Estes, 1967, Sims, 1973). However, it is only with the widespread application of independently derived chronologies, in particular from radiocarbon dating and other isotopic techniques, that the production of comparable absolute frequency figures for pollen deposition, as envisaged by von Post, has become feasible.

Due to the increased effort necessary in absolute pollen analysis, and the scarcity of sites suitable for precise dating, it is perhaps natural that the initial work in this area focussed on problems that could not be adequately resolved using the existing relative pollen frequency technique alone. Thus the transition from late-glacial to early post-glacial conditions was investigated both in North America (Davis and Deevey, 1964) and the British Isles (Pennington and Bonny, 1970). Absolute pollen frequencies have also been used to reinterpret Mesolithic clearance phases of previously analysed British sites (Pennington, 1973, Sims, 1973). A number of longer diagrams from late-Pleistocene and Holocene sequences in the U.S.A. have now been published (Davis, 1969, Waddington, 1969, Maher, 1972, and Craig, 1972).

The question therefore arises as to whether it is worthwhile to attempt a systematic estimation of pollen deposition rates from a tropical lowland situation, given the current state of palynological knowledge about such areas. The only published pollen deposition rate diagram from the equatorial tropics is that of Kendall (1969) from Lake Victoria, East Africa. Livingstone (1975) comments that Kendall's results show 'an accuracy of vegetation reconstruction that has not yet been matched from any other site in Africa'. Of particular interest to the present study, the results show that an apparent increase in grass pollen in the upper levels of the core is an artefact of the relative calculation method, and in fact, whereas forest pollen decreases in absolute frequency, the deposition rate of grassland types remain comparatively stable.

Given the availability of radiocarbon chronologies from the two Markham Valley sites, it was therefore considered appropriate to attempt the estimation of pollen deposition rates in the analysed cores. A preparation technique facilitating quantitative handling of the sediment samples was therefore adopted.

The terms 'absolute' diagram or pollen frequency and 'pollen influx' should not be used without qualification. As Maher (1972) has emphasised, 'absolute' is really a misnomer: such pollen results are estimates that are always stated relative to some other quantity. In addition, the term may also be ambiguous (Davis, 1969) as it does not specify whether pollen concentrations or pollen deposition rates are involved. Nor is 'pollen influx' considered appropriate as, according to Pennington (1973), not all pollen entering a lake basin becomes permanently incorporated into the sediments.

Pollen analytical results from this study are therefore expressed:

(a) in relative frequency terms, as percentages of a given base sum,

(b) as concentration of grains and spores per unit volume of sediment, in this case 1 ml ('pollen concentration'), and

(c) as a figure for pollen deposition rate (PDR) defined as number of palynomorphs deposited per $cm^2$ of sediment surface per year. This value is obtained by adjusting the pollen concentration for the appropriate sediment accumulation rate.

### *DETERMINATION OF POLLEN CONCENTRATION*

The determination of the concentration of pollen and spores in a sediment sample involves a three-stage process:

(1) the sampling of an accurately measured amount of the sediment,

(2) the counting of a known proportion of the pollen and spores in the processed sediment, and

(3) extrapolation from this count, within statistically stated limits, to give an estimate of the total number of pollen grains in the original sample of sediment.

### *Sediment sampling*

Since the final aim is to relate pollen deposition to a volumetric measure, i.e. number of grains per unit area per unit depth (representing time), most workers have based their estimates on an initial volume of sediment (e.g. Davis, 1969, Waddington, 1969, Maher, 1972) although others (Durkee, 1964, Jørgensen, 1967) have preferred a sample of known dry weight. A volumetric sample is more difficult to collect and measure accurately than is one taken on the basis of dry weight, and a variety of techniques have been devised to produce samples of a standard size. Davis (1969) packed the sediment into a spatula of known volume. A method involving less risk of error caused by compaction is the use of a small-scale coring device to remove cylindrical samples of sediment from measured slices of the core. Such a technique has been used by Waddington (1969), and in a more mechanised form by Engstrom and Maher (1972). Alternatively the volume of the sample can be measured by displacement in an accurately calibrated measuring cylinder (Bonny, 1972, Pennington, 1973).

Once a measured sediment sample has been obtained, it may be prepared in either of two ways to produce slides in which the pollen content can be related to that of the original sample.

### *Quantitative preparation techniques*

*Marker grain method*: Benninghoff (1962) outlined the now common technique of adding, before processing, a known quantity of exotic pollen grains as markers. The ratio of marker grains to fossil grains counted is then used to calculate the number of fossils in the original sediment sample. This method has been further elaborated by Matthews (1969), Waddington (1969), and Maher (1972).

Craig (1972), and Swain (1973) use polystyrene microspheres as markers rather than an exotic pollen type. Both versions of this method provide an easy means to compensate for any loss of material during preparation of the sample, if it can be assumed that the markers become evenly distributed throughout the sediment, and act in the same way as fossil sporomorphs. Not wishing to make such assumptions, Kirkland (1967) and Bonny (1972) added the exotic grains only in the later stages of slide preparation.

The 'marker grain' method requires an accurate assessment of the number of exotic grains added to the preparation. Often a homogenous suspension of the marker is made and an estimate of the pollen concentration derived by counting aliquots of this suspension on haemocytometer or ordinary microscope slides. Known fractions determined by mass (Matthews, 1969, Bonny, 1972) or volume (Waddington, 1969, Maher, 1972) are then added to the sediment preparation. A simpler method is to add an appropriate number of commercially available tablets, described by Stockmarr (1971), containing known quantities of a particular spore or pollen type as a marker. For best results the ratio of fossil grains to added marker grains should be about 2:1 (Maher, 1976).

*Aliquot technique*: A second established method does not involve the use of any exotic marker, but requires strict quantitative handling of the sample throughout all stages of the preparation procedure. A homogenous suspension of the processed sediment is produced and known aliquots transferred onto microscope slides. This may be done either by pipetting a measured volume (Davis, 1965, 1966), by weight (Jørgensen, 1967), or by settling the whole of the suspension onto cover-slips of known area in an evaporation tray using the method described by Battarbee (1973) and Battarbee and McCallan (1974). To maintain accuracy, loss of sample during processing must be minimised, or some estimate of this loss independently obtained.

The method adopted for routine counting of slides depends on the initial choice of preparation technique. The evaporation tray method produces a random distribution of grains over the whole area of the cover-slip thus permitting analysis of only a proportion of the slide. Any other method leads to slides in which the pollen grains or other microfossils are not randomly distributed (Brookes and Thomas, 1967, Battarbee, 1973). Thus it is desirable to count as much of the whole slide as possible, although if marker grains have been used regularly spaced traverses over a portion of the slide may be adequate.

### *Choice of method*

Both the 'marker grain' and aliquot methods are capable of producing accurate and reproducible results if all sources of error are identified and quantified in the manner of Davis (1965) and Maher (1972, 1976). An attempt at such precision in the determination of the pollen concentration of lake sediments and pollen traps from the Markham Valley could not be theoretically justified. It was considered that only large and consistent fluctuations of pollen deposition rate would be interpretable, given the current state of knowledge about processes of pollen dispersal and sedimentation in the tropical lowland environment.

The 'marker grain' method was considered the more time-consuming, and suitable exotic grains or microspheres were not readily available. Use of the aliquot method therefore seemed appropriate, if proven sufficiently accurate to reveal moderate variations in pollen concentration. Of the aliquot methods, the evaporation-tray technique of Battarbee and McCallan appears straightforward and accurate. However, the random distribution of grains on the slide is upset if any are moved to facilitate identification. As this is essential when dealing with the largely unknown pollen flora of the lowland tropics, this method was rejected in favour of a version of the volumetric aliquot technique of Davis.

*The volumetric preparation technique*

Before sampling the sediment cores their dimensions were checked for any shrinkage due to water loss since collection. In most cases shrinkage was minimal. Selected cores were sampled for pollen at 10 cm or 20 cm intervals and around marked stratigraphic boundaries. For each sample a horizontal slice 10 mm thick was cut from the core with a sharp knife and transferred to a small petrie dish. A cylindrical portion was then excised using an accurately made glass tube with an internal diameter of 11.28 mm. This produced a sample of about 1 ml that was transferred to a weighed glass vial, sealed and weighed. The remainder of the slice was used for the determination of water and organic carbon content.

The measured sediment was then processed using, in the main, standard palynological preparation techniques (Faegri and Iversen, 1964) summarised in Table 6.1. No estimation was made for loss of sample during preparation, although major spillage was noted and the sample not used for estimation of pollen concentration. All samples required sieving to produce countable slides. Large volumes of water were used to ensure maximum recovery of pollen

*TABLE 6.1. Summary of preparation techniques*

| Treatment | Time | Purpose | Samples treated |
|---|---|---|---|
| Cold 10% HCl | 10 mins | Removal of $CaCO_3$ | Calcareous samples only (all samples from YAN 2, YANMC 1) |
| Hot 5% KOH or NaOH | 20 mins | Removal of humic acids and deflocculation | All samples |
| Sieving through *c.* 150 µm terylene mesh | - | Removal of coarse organic and inorganic particles | All samples |
| Cold 40% hydrofluoric acid | 12 to 18 hours | Removal of moderate quantities of silica | Most fossil samples |
| $ZnBr_2$ heavy-liquid separation | - | Separation of organic matter from large amounts of mineral sediments | Highly inorganic sediments only (most samples from YAN 2, YANMC 1) |
| Acetylation ('Acetolysis') technique (Erdtman, 1952) | 3 mins | Removal of excessive cellulose | All samples |
| Ultra-sonic bath | 10 secs or less | Break-up of large particles | Excessively clumped samples only |
| Dehydration in ethanol series | - | Removal of water prior to mounting in silicone oil | All samples |

and spores from the sieve. The heavy liquid separation procedure was also a potential source of error due to retention of pollen, and this was used on all sediment samples from Yanamugi cores.

After dehydration in ethanol, the sample was suspended in a measured volume (10 ml or 15 ml depending on the quantity of sediment remaining) of tertiary-butyl-alcohol (TBA). A small magnetically operated stirring rod or 'flea' was introduced and the suspension stirred automatically until homogenous. Working within a laminar flow cabinet,aliquots of 0.02 ml taken using an 'Eppendorf' automatic micropipette with disposable plastic tips were transferred onto a drop of silicone oil (Wacker AK 2000) on a warmed microscope slide, and the TBA evaporated. Sufficient aliquots were added to produce a slide of suitable density for pollen analysis. In practise this ranged from one to seventeen aliquots (0.02 to 0.34 ml) with most slides containing the material from between 0.1 to 0.2 ml of TBA. When all TBA had evaporated, a 38 x 22 mm cover-slip was positioned and sealed with clear lacquer.

Samples were analysed using a Carl Zeiss (Oberkochen) photo-microscope, employing a magnification of X 160 or X 400 for routine scanning of the slide. Identification of well known types was made at X 400 whilst a X 100 planapochromatic oil-immersion objective was used for final identification of problem grains and investigation of unknowns at a magnification of X 1600.

Only a proportion of each slide was counted. Traverses across the narrow axis of the slide were made, usually at 1 mm intervals, along the whole width of the cover-slip. For a few slides, mainly the very dense pollen trap content preparations, the interval was increased to 2 mm or even more, but traverses were always regularly spaced over the whole slide area. With an interpupillary distance of 70 mm, the proportion of the slide scanned with the various combinations of magnification and traverse interval was measured as:

| | Traverse Interval | | |
|---|---|---|---|
| Proportion counted | 1 mm | 2 mm | 4 mm |
| At X 160 | 0.87 | 0.435 | 0.2175 |
| At X 400 | 0.35 | 0.175 | 0.0875 |

The pollen content of each preparation was thus estimated by calculating:

$$\text{concentration} = T \times \frac{V_p}{V_s \times C}$$

Where T = total number of pollen and spores counted per sample

$V_p$ = Volume of preparation suspension

$V_s$ = Volume of TBA transferred to slides

C = Proportion of each slide counted.

As the volume of sediment taken was in all cases 1 ml this formula represents the concentration of sporomorphs per ml.

*Assessment of accuracy*: The percentage of the total suspension analysed ranged from 0.01% to 0.35% for pollen traps, and 0.19% to 3.65% for sediment cores. 'Typical' values were 0.03% for traps and 0.5% to 1.75% for cores. These figures are of the same order as those used by Davis (1965), although the method used varied from Davis' in several ways. The most significant were use of smaller volumes of suspension and aliquot, and counting of only a proportion of each slide. As all of these factors could lead to greater inaccuracy, the precision of the adopted technique was tested.

Three tablets of *Lycopodium clavatum*, batch 212761 (Stockmarr, 1971) were dissolved in 10% HCl and the spores suspended in 10 ml of TBA. Maher (1976) has calibrated the spore concentration of this batch at 12 489 per tablet, with a standard deviation (S.D.) of 491. The concentration of the suspension was thus 37 467 with the standard deviation calculated as

$$S.D._n = \sqrt{n} \times S.D._1$$

Where $S.D._n$ = standard deviation of n tablets
$S.D._1$ = standard deviation of one tablet
n = number of tablets

although Maher states that this may tend to underestimate the true value for standard deviation.

The total number of spores used represents a typical value for pollen concentration per ml in the sediment cores studied.

Four series of volumetric aliquot slides were then produced from this suspension, representing the mid range of actual volumes counted from the sediment preparations. The slides were analysed at a magnification of X 160, and a traverse interval of 1 mm. For each series of counts, the arithmetic mean ($\bar{x}$), standard deviation (S.D.), variance ($S.D.^2$) and coefficient of variation (V) were calculated (Table 6.2).

As expected, the mean number of spores counted per slide was directly proportional to the number of aliquots per slide. The correlation coefficient (r) between these two variables is greater than +0.99. The coefficient of variation generally decreases with increased number of spores, indicating greater precision for larger counts. The exception is the most concentrated series (0.2 ml per slide) where the higher value for V may be due to excessive clumping of the large number of spores on the slide.

The variance of a Poisson distributed population approximates the mean (Gregory, 1968). Calculations of variance for the *Lycopodium* counts give values around and below the mean, suggesting a distribution varying between 'homogeneous' and Poisson (Kendall, 1969). In order to test the fit of the counts to a Poisson distribution, the method used by Davis (1965) was employed. For Poisson distributed data the product of the formula

$$\frac{\Sigma(x - \bar{x})^2}{\bar{x}}$$

is approximately chi$^2$ distributed (Cochran, 1954). Chi$^2$ was therefore calculated using this formula (Table 6.2). Deviation from a Poisson fit was not significant for any series of slides.

Table 6.3 compares the results obtained by counting the aliquot series with those expected from the spore content of the tablets determined with an electronic particle counter (Maher, 1976). The counts are consistently larger than the expected values, the percentage difference increasing with size of aliquot. This pattern of divergence is not easy to explain, but as all values were well within 10% of those predicted, they were considered acceptable within the context of the study.

*Estimation of confidence limits*: Accepting the Poisson fit of the data, it may be assumed that the number of pollen and spores counted (T) is equivalent to the mean number for a given aliquot size, and therefore to the variance. The 95% confidence interval

*TABLE 6.2. Results of replicate counts on slides containing different volumes of* Lycopodium clavatum *suspension*

| Vol. of slide (ml) | No. of slides counted | Range of counts | $\bar{x}$ | S.D.$^2$ | S.D. | V (%) | chi$^2$ | d.f. |
|---|---|---|---|---|---|---|---|---|
| 0.02 | 6 | 57- 73 | 65.33 | 26.23 | 5.12 | 7.84 | 2.41 | 5 |
| 0.08 | 6 | 256-293 | 275.00 | 146.33 | 12.10 | 4.40 | 3.19 | 5 |
| 0.14 | 6 | 460-515 | 481.50 | 345.25 | 18.58 | 3.86 | 4.30 | 5 |
| 0.20 | 5 | 661-732 | 704.80 | 808.76 | 28.44 | 4.04 | 4.80 | 4 |

*TABLE 6.3. Comparison of results obtained by counting slides containing different volumes of* Lycopodium clavatum *suspension with those expected from the given content of the spore tablets*

| % of suspension counted | $\bar{x}$ no. counted | $\bar{x}$ no. expected | % difference of count from expected |
|---|---|---|---|
| 0.174 | 65.33 | 65.19 | + 0.21 |
| 0.696 | 275.00 | 260.77 | + 5.46 |
| 1.218 | 481.50 | 456.36 | + 5.51 |
| 1.740 | 704.80 | 651.94 | + 8.11 |

for a count can therefore be given as approximately twice the square root of the count. Thus the formula for the estimation of pollen concentration, with 95% confidence limits, becomes

$$T \times \frac{V_p}{V_s \times C} \pm 2\sqrt{T} \times \frac{V_p}{V_s \times C}$$

This formula provides an overestimate of the confidence limit if the grains are more homogenously distributed, and an underestimate if the occurrence of grains is more variable than in a Poisson distribution. Precision may be increased by counting a larger number of grains by increasing the proportion of the total suspension analysed.

*Sources of error:* Counts of sub-fossil grains from core samples were examined for excessive variance, indicating possible divergence from Poisson distribution. Of eleven samples with counts from two or three slides of equal volume, one-third showed excessive variance above the mean. This may indicate a non-Poisson distribution, although the number of replicate slides and counts is low.

The experimental results suggest that homogenisation of the suspension and aliquot pipetting can be achieved with accuracy. Similarly the counting technique, at least where a large proportion of the slide has been scanned, seems reliable. Excessive small-scale clumping on the slide, either through high pollen concentration or large amounts of debris, causes greater variability in the count. The effect of this can be reduced by counting the whole slide, or reducing the concentration of material.

Any deficiency in the estimate of pollen concentration per unit volume of sediment is therefore more likely to be the result of other factors. Although none was quantitatively assessed, and is not therefore encompassed by the stated confidence limits, the main sources of error are thought to be:

(a) Inaccuracy in sediment sampling. Replicates were not taken, but inspection of the samples suggests that, in reasonably fine homogenous organic or mineral sediments, the error was within ± 5%. For coarser material, especially poorly humified and fibrous organic deposits, the method was less accurate.

(b) Loss of material during preparation. The extent of this depends on the processing techniques used. Raine (1974) estimates loss of material during preparation to be low, although he did not use the heavy-liquid separation technique. As no estimate of small losses was made, all values for pollen concentration must be regarded as minimum figures. However, as similar methods were used on all samples within the same core, these results should be consistent, even if not strictly comparable with results from other cores or pollen traps.

The technique adopted for the estimation of pollen concentration is a flexible one able to handle large variation in the pollen content of the sediment and at the same time allow full manipulation of grains for identification and recording. The method is not greatly time-consuming and yet appears sufficiently reliable to disclose moderate changes in pollen concentration. The confidence limits calculated provide a useful indication of the probable variation, although they may represent an underestimate for some samples due to the possible sources of error mentioned.

## *DETERMINATION OF CHARCOAL CONCENTRATION*

Carbonised plant fragments are frequently encountered in lake sediments, and their occurrence has been associated (e.g. Waddington, 1969, Swain, 1973) with natural or artificial fires within the catchment. Charcoal particles were noticed during initial sediment analyses from Lake Wanum, and, in view of the role of fire in the maintenance of present day grassland, some index of their past abundance was considered desirable.

Such carbonised fragments usually survive routine pollen analytical preparation treatments, and it is possible to record the occurrence of both charcoal and pollen from the same slide. If insufficient particles are found, or if greater precision is sought, separate slides may be prepared by treatment with hot concentrated nitric acid. However, Swain (1973) notes that both procedures produce closely similar results. In this study, all charcoal counts were made on the slides quantitatively prepared for pollen analysis.

Carbonised particles from Lake Wanum core LW II were tallied by their 'apparent surface area' as measured by an eyepiece micrometer. Three size classes were distinguished: 25 - 600 $\mu m^2$, 600 - 3 000 $\mu m^2$ and 3 000 - 6 000 $\mu m^2$. Particles smaller than 25 $\mu m^2$ were ignored, these being difficult to distinguish from mineral grains. Examination of the larger particles retained during sieving of samples revealed a general correlation between the abundance of the fragments in the sieve, and that of the smaller ones on the slide.

Estimates for charcoal concentration and deposition rate were derived in a similar manner to those for palynomorphs. However, as fewer transects were usually counted per slide, the carbonised particle results are probably less accurate. These estimates may be expressed in various ways. Although Waddington (1969) and Swain (1973) counted a large number of size classes, both subsequently summed the class totals to produce a single 'charcoal index', expressed as area of particles $cm^{-2}$ $yr^{-1}$. This procedure was initially adopted for the Lake Wanum samples. However it was clear that the three size classes did not always show parallel trends. More information is retained if each size class is shown individually as the number of carbonised particles $cm^{-2}$ $yr^{-1}$, as in Fig. 8.1.

A cruder index of charcoal abundance was used for the sediments of Yanamugi, where more rigorous sample treatment had been used. For each sample, numbers of carbonised fragments were counted (by J. Guppy) along two transects of a slide. The concentration of particles was calculated, and the results expressed as a percentage of the maximum concentration, occurring in the sample from 670 cm, (Fig. 8.6). This rapid method appears adequate to reveal major fluctuations in the carbonised particle content of the sediments, and is perhaps more appropriate where the chronology to derive annual deposition rates is lacking.

# CHAPTER 7

# CONTEMPORARY POLLEN DEPOSITION IN THE MARKHAM AREA

Pollen analysis as a tool of palaeoecology, rather than biostratigraphy, rests on a number of important assumptions concerning the production, dissemination and deposition of pollen grains and spores. In northern temperate regions studies on the dispersal of pollen grains under different conditions (e.g. Tauber, 1965, Andersen, 1973) have refined formerly intuitive models of pollen transfer. Further detailed work has elucidated the processes of pollen recruitment to lake sediments, and the mechanisms of deposition and redeposition (Davis and Brubaker, 1973, Davis *et al.*, 1973, and Bonny 1976, 1978).

Many empirical studies of regional contemporary pollen deposition have revealed facets of the relationship between pollen assemblages and the source vegetations crucial to the ecological interpretation of fossil palynological data. Recent approaches have employed multivariate statistical techniques to illuminate correlations between modern pollen spectra and vegetation composition (Kershaw 1973*a*, Webb, 1974, Davis and Webb, 1975, and Webb and McAndrews, 1976) or climate (Webb and Bryson, 1972).

A number of contemporary pollen deposition studies, reviewed by Flenley (1973), has been carried out in tropical regions, although the majority relate to predominantly upland or alpine, rather than lowland, areas. Of particular regional significance to lowland Papua New Guinea is the work of Hope (1973), Kershaw (1973*a*), Kershaw and Hyland (1975) and Morley (1976).

Despite these recent advances there still exists neither a sound theoretical basis for the interpretation of pollen analytical evidence from the tropical lowlands, nor a comprehensive regional study of contemporary pollen assemblages from any lowland tropical area. Investigations within the study area were therefore directed towards an understanding of the main aspects of pollen production and transfer, and of the nature of contemporary pollen assemblages in the environs of the Markham Valley.

## *SAMPLING CONTEMPORARY POLLEN DEPOSITION*

The lack of pollen preservation in many situations proved a major problem in sampling pollen deposition in the diverse vegetation of the Markham Valley. As Flenley (1973) notes, moss polsters, commonly employed for their natural pollen-trapping properties, are surprisingly rare in lowland tropical forest. Damp moss tussocks from 'hill' forest between 180 m and 1 000 m altitude contained abundant well preserved pollen and spores. In lower altitude forests adequate samples could sometimes be obtained from the thin moss cover of tree trunks or rocks, provided several samples within close proximity were amalgamated for analysis. Pollen is generally not well preserved in lowland tropical soils (Hedberg, 1954, Hamilton, 1972). Some periodically inundated litter and surface-soil samples yielded small quantities of pollen, although spores were more abundant, perhaps suggesting differential destruction of pollen grains. Sediments from perennially waterlogged swamps and lakes provided the most satisfactory natural traps for pollen and spores, although even here the concentration may be low due to rapid accumulation of the sediment. Such sites were unfortunately not widespread.

*TABLE 7.1. Contemporary pollen samples from the Markham Valley*

| Sample No. | Type | Location | Alt. (m) | Vegetation type | Local plant taxa |
|---|---|---|---|---|---|
| PT 1 | Pollen trap | Markham Point | 180 | Slightly disturbed 'hill' or 'ridge' forest | *Aporosa papuana*, *Melicope* (21144), *Gnetum gnemon*, *Lucinaea* (21146), *Urophyllum* (21149), *Endiandra* (21147), *Dysoxylum* (21148), Myristicaceae (21143) |
| PT 4 | Pollen trap | Lake Wanum eastern shore *c*. 500 m from water | 40 | Lowland closed forest on gentle slope | *Clerodendrum buchanii*, ?*Popowia* (21130), *Polyalthia* (21131), *Commelina* (21132), *Macaranga* *Alpinia* (21127), Meliaceae (21129) |
| PT 5 | Pollen trap | Lake Wanum, promontory at the western margin of north-east bay | 40 | Partially cleared, open forest | *Asplenium nidus*, *Rhaphidophora* (21108), *Alpinia* (21109), *Diplocyclos palmatus*, *Mukia maderaspatana*, *Passiflora foetida*, *Mezonevron* (21110), *Malaisia scandens*, ?*Ganophyllum* (21116), *Cissus* (21115), *Celtis* (21117), *Murraya paniculata* |
| PT 6 | Pollen trap | Lake Wanum, on floating raft in centre of north-east bay; 250 m from shore | 35 | Open water | None |
| SQ 35 | Litter and detritus, root mat | Lake Wanum, western margin of north-east bay, vegetation quadrat 35 | 35 | Deep water floating root-mat (Group A) swamp vegetation | *Nephrolepis hirsutula*, *Hypolytrum nemorum*, *Stenochlaena palustris*, *Microsorium* (21067) |
| SQ 40 | Lake sediment surface detritus | Lake Wanum, south swamp, vegetation quadrat 40 | 35 | *Hypolytrum nemorum* association (Group B) swamp vegetation | *H. nemorum*, *Cyclosorus* (21050), *Ceratophyllum demersum* |
| SQ 50 | Lake sediment surface detritus | Lake Wanum, south swamp, vegetation quadrat 50 | 35 | *Nelumbo nucifera* association (Group E) swamp vegetation | *N. nucifera*, *Leersia hexandra* |
| SQ 51 | Surface detritus and litter from root-mat | Lake Wanum, south swamp, vegetation quadrat 51 | 35 | *Leersia hexandra* floating mat (Group D) swamp vegetation | *L. hexandra*, *Phragmites karka*, *Nelumbo nucifera*, *Stenochlaena palustris*, *Hypolytrum nemorum* |
| SS 13-15 | Thin moss cover from dead tree trunks (3 samples, a few metres apart | Forest plot vicinity of lower Sankwep River | ?50 | Rain-forest | *Homalium*, *Pometia*, *Artocarpus*, *Dysoxylum*, *Horsfieldia*, *Sterculia*, *Cryptocarya*, *Pangium*, *Antiaris*, *Gmelina*, *Gnetum*, *Gastonia*, (identifications by R.J. Johns) |

*TABLE 7.1. (Cont.)*

| Sample No. | Type | Location | Alt. (m) | Vegetation type | Local plant taxa |
|---|---|---|---|---|---|
| SS 18 | Leaf litter and surface soil | Markham river flood plain, about 0.5 km south of Markham bridge | ?20 | 'Alluvium' forest; periodically inundated | *Antidesma* (21155), *Psychotria* (21156), *Voacanga papuana*, *Alpinia* (21154) |
| SS 20 | Moss polster | Foothills of Hertzog ranges south of Gabensis | 970 | Tall 'hill' forest | *Acronychia trifoliolata*, *Aporosa papuana*, *Maesa* (21161) in area |
| SS 22 | Moss polster | Foothills of Herzog ranges south of Gabensis | 790 | Tall 'hill' forest disturbed by logging | as above |
| SS 23 | Organic detritus from swamp margin | Redhill swamp, eastern margin | 35 | Swamp margin vegetation under 20 cm of water | *Alyxia ?floribunda*, *Coleus scutellarioides*, *Dysophylla verticillata* |
| SS 27 + 28 | Dry moss from tree roots and limestone boulders (2 samples, 100 metres apart) | 50 m west of lake, Yanamugi | 175 | Semi-deciduous forest on thin soil on slope | - |
| LWMC 3 SS | Organic detritus and surface sediments | Short core LWMC 3, western margin of north-east bay, Lake Wanum | 35 | Open water | none |
| YANMC 1 SS | Calcareous surface mud | Short core YANMC 1, southern end of Yanamugi lake | 170 | Open water | none |

Artificial pollen traps proved well suited to the collection of pollen and spores under a variety of conditions. Facilities were not available for the exclusive use of these devices, nor for monitoring rain-gauge catches, another alternative. Therefore both natural and artificial trapping methods were employed. A random collection scheme was thus not feasible, and most samples derive from either swamp or forest vegetation, leaving other dry land vegetation largely unrepresented. Open grassland areas remain unsampled, as the dry soil preserved no pollen, and placement of traps would have been futile in the annually fired vegetation.

The locations of the 16 samples analysed, four from pollen traps and 12 from surficial sediments or moss polsters, are given in Table 7.1. With the exception of four samples from swamp vegetation quadrats, no ecological measurements were made on the vegetation at these sites, although many plants from the vicinity of the samples were collected and identified.

### *Estimation of annual pollen deposition rates*

In order to obtain estimates of annual pollen and spore deposition (PDR) rates under various conditions, pollen traps of the Tauber (1974) design were deployed. These consist of a PVC cylinder 10.1 cm internal diameter by 58.5 cm high, sealed at the base and with a circular aerodynamic lid having a 5 cm diameter orifice. The traps were stationed for 511 to 519 days between December 1974 and April/May 1976, and were not subsampled within this period.

Of six Tauber traps set, only four were recovered. One (PT 1) was located in 'hill' forest at an altitude of *c.* 180 m at Markham Point. The forest canopy, initially closed, was opened up by the natural fall of a large tree immediately adjacent to the pollen trap prior to the recovery date. Three traps were situated in the vicinity of Lake Wanum, two on land and the third on an anchored raft. Trap PT 4 was located in closed forest at the base of Mount Misantum, about 500 m from the eastern shore of the lake. Open forest surrounded trap PT 5 on the narrow promontory west of the north-east bay. This site had been extensively cleared by 1976. All forest traps were located at ground level, with the trap lid about 30 cm above the forest floor. The floating trap (PT 6) was positioned in the centre of the north-east bay, at least 250 m from land, although it appeared to have drifted slightly by 1976.

On recovery the traps were sealed and shipped to Canberra intact. The entire contents were then consolidated by centrifugation and pollen slides prepared using the volumetric technique described previously.

A number of uncertainties are associated with the use of such pollen trapping methods. Human interference may be implicated in the disappearance of two of the traps, and might have affected the results from others, especially the highly conspicuous floating trap. In theory, a full year is the most appropriate sampling period, rather than 16 months. However, as the climate, and presumably flowering, is relatively aseasonal in this part of the valley, a reasonable estimation of annual PDR should be possible. The traps could accommodate up to 2390 mm of rainfall, equivalent to an annual precipitation of 1700 mm assuming zero evaporation. This figure is substantially lower than the actual rainfall over the whole area, and one trap (PT 1) was found full, and another (PT 4) nearly so. Estimates of PDR from these sites must therefore represent minimum values. The two traps PT 5 and PT 6 from more exposed situations contained considerably less water, presumably due to greater evaporation, and had probably not overflowed.

Recently Krzywinski (1977) has questioned the utility of Tauber's pollen trap design, suggesting that inflated influx values may be produced due to rain-splash redeposition of pollen from the lid. The trap is however regarded as an inefficient collector in conditions of high wind speed (Peck, 1973). The size of errors is unknown, but can be presumed to be essentially similar for all traps in this study. In several cases the aerodynamic properties of the lid had been altered either by detrital twigs and leaves, or, in the floating trap, by bird excreta.

Estimates of total pollen content and annual PDR values are given for each of the trap sites in Table 7.2. Very great variations in PDR between traps are apparent. The two traps from closed forest sites, PT 1 and PT 4, give almost similar estimates of annual pollen and spore deposition at 132 000 and 102 000 $cm^{-2}$ respectively. Figures for pollen alone are even closer, as the wetter site (PT 1) records over five times as many pteridophyte spores as the drier.

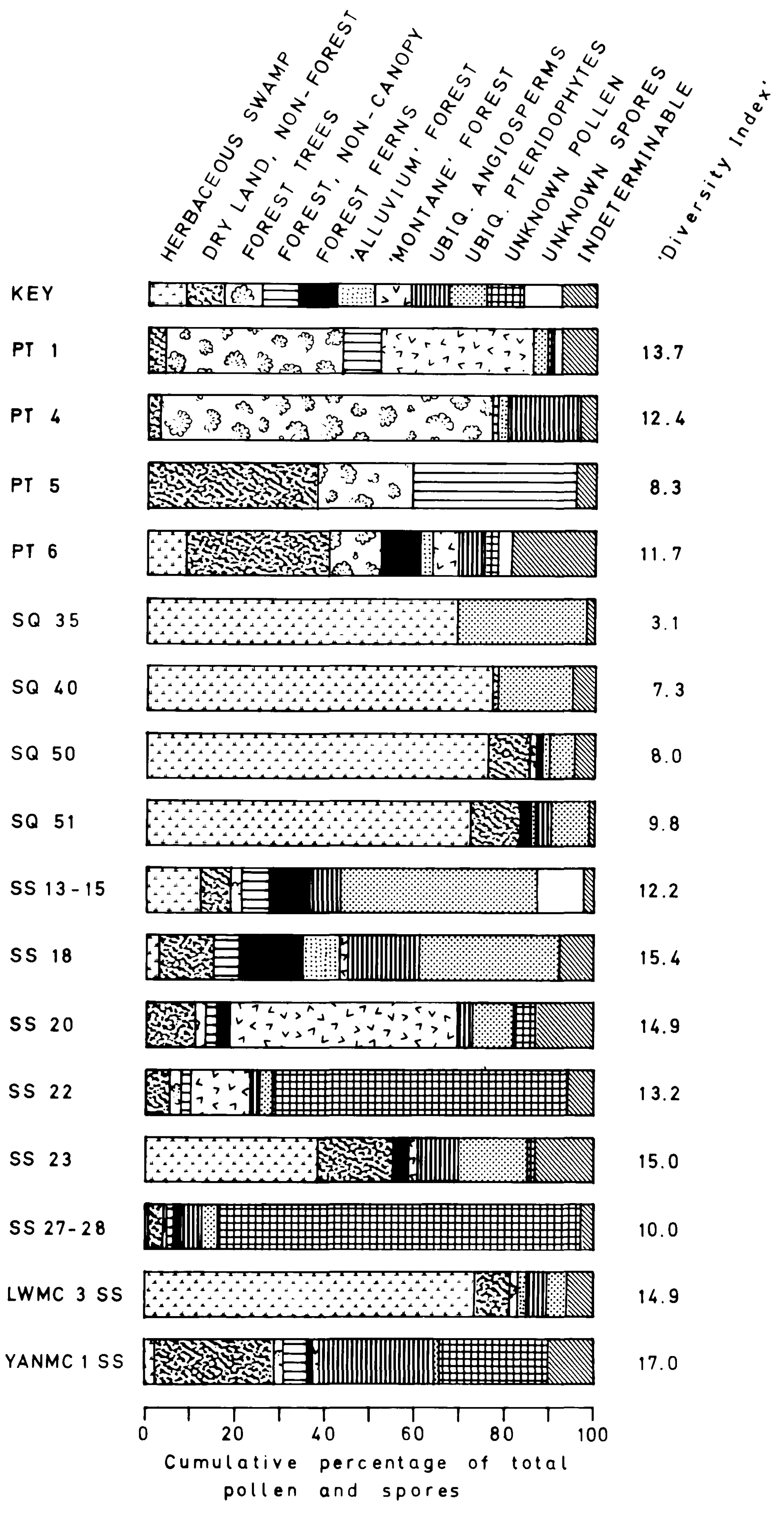
The highest influx estimates come from PT 5, the disturbed forest site west of the north-east bay. Here the annual PDR apparently exceeds 400 000, a figure that may have been inflated by the action of red ants, found infesting the trap, in importing appreciable quantities of pollen.

In contrast, the floating trap (PT 6) records a pollen influx one thousand times smaller than that of PT 5. Spores represent a higher proportion of the total catch in the floating trap, with an influx only 25 times lower than for the land trap. Despite the vulnerability of the raft trap, there was no evidence of overt

TABLE 7.2. *Annual pollen and spore deposition rates estimated from pollen traps*

| Pollen trap no. | Location | Pollen and spores per trap | Spores cm$^{-2}$ yr$^{-1}$ | Pollen cm$^{-2}$ yr$^{-1}$ | Pollen and spores cm$^{-2}$ yr$^{-1}$ |
|---|---|---|---|---|---|
| PT 1 | Hill Forest, Markham Point | 3 638 568 ± 249 751 | 6 835 ± 2 061 | 125 056 ± 8 815 | 131 892 ± 9 053 |
| PT 4 | Closed forest, east shore, Lake Wanum | 2 845 711 ± 220 870 | 1 228 ± 868 | 100 696 ± 7 830 | 101 924 ± 7 911 |
| PT 5 | Disturbed forest, promontory, Lake Wanum | 11 046 433 ± 688 054 | 1 945 ± 1 739 | 399 042 ± 24 915 | 400 986 ± 24 976 |
| PT 6 | Open water, north-east bay, Lake Wanum | 10 057 ± 3 400 | 73 ± 55 | 293 ± 111 | 366 ± 124 |

*FIGURE 7.1. Major ecological groups represented in contemporary pollen samples*



tampering and no reason to suspect that these figures do not represent a valid estimate of airborne pollen and spore deposition in the central area of the north-east bay of Lake Wanum.

## *CONTEMPORARY POLLEN ASSEMBLAGES*

Pollen assemblages from all traps and surface samples are summarised in Fig. 7.1. Pollen and spore taxa are grouped[1] into tentative ecological classes, based on known plant distributions (Table II.1).

Herbaceous swamp taxa comprise over 70% of the total count from all Lake Wanum swamp sites, with the exception of the floating pollen trap where they represent only 9%. These taxa also contribute 40% of the catch to the swamp marginal sample at Redhill. Small percentages recorded from the 'alluvium forest' (SS 18) and wet forest at Sankwep (SS 13-15) sites reflect the presence of *Nephrolepis*, *Stenochlaena palustris* (SS 18) and *Uncaria* T. (SS 13-15). Although these three taxa are included in the herbaceous swamp category, their sources are obviously not restricted to this vegetation type.

The dry land non-forest category is harder to define. Taxa included are those frequently represented in such situations, although many show a more widespread distribution, either within the single species or in other plant taxa contributing to the pollen taxon. The group is represented to some extent in almost all surface assemblages, being understandably more abundant in disturbed forest and non-forest sites. Good representation occurs in open lake catches also, e.g. pollen trap PT 6 and the surface

---

[1] Lists of taxa comprising each group may be found in Table II.2

sediments from short cores, but not where samples are overwhelmed by taxa from locally growing herbaceous swamp vegetation.

Included in the forest trees category are a number of genera more common in the canopy of lowland forest, although again many show a much wider distribution. This group of taxa appears to reflect best the composition of the forest in the vicinity of Lake Wanum, and is well represented in all pollen traps. The high values of the group in PT 1 are primarily due to the inclusion of *Aporosa*, a genus with a wide altitudinal range, and *Macaranga ovatifolia* T. the source and range of which is unknown.

'Alluvium' forest is a group of taxa frequently found in riparian, floodplain and mangrove environments, although many constituent plants possess a much less restricted distribution than this. The group is not particularly diagnostic as even at the 'alluvium' forest site (SS 18) its taxa make up less than 10% of the total catch. The representation in open sites at Lake Wanum may derive from nearby sources in the Markham and Oomsis valleys.

Non-canopy forest taxa include those trees restricted to, or more common in, the understorey together with shrubs, palms and vines. Components of the group are represented in all samples from forest sites. A small but distinct group of taxa comprises the forest ferns, although many such plants must also contribute to the 'ubiquitous pteridophytes' class. The highest proportions of these spore taxa occur in the wetter lowland (SS 13-15) and 'alluvium' forest (SS 18) samples.

Pollen taxa from plants not occurring in the lowest altitude vegetation are included in the 'montane' forest category. Some taxa, such as *Lithocarpus*, extend down to altitudes of 180 m and lower, and *Castanopsis* T. pollen is found in trap PT 1 from 'hill' forest. Other taxa are more common above the 1 000 m altitude of the highest site sampled, but contribute to pollen assemblages at lower elevations.

The ubiquitous angiosperm and pteridophyte classes include pollen and spore taxa the sources of which are either undetermined, or cannot be assigned with confidence to any ecological category. Some such taxa embrace many plant genera or families, e.g. Urticaceae/Moraceae pollen, or psilate monolete fern spores. In other cases the pollen or spore taxon is identifiable to the generic, or even specific level, but the plant occupies a wide variety of different habitats. The ubiquitous pteridophytes appear most common in the wetter forest types and in herbaceous swamp samples where many spores from locally abundant ferns, especially *Nephrolepis*, lose their diagnostic perisporia.

Pollen or spores not assignable to any lower level taxonomic unit are included in the 'unknown' classes. The only significant values are encountered in the two samples from Yanamugi, where pollen type UK 194 is abundant, and in the 'hill' forest site SS 22, where pollen type UK 106 dominates the assemblage. Both taxa almost certainly derive from the local flora at each site.

Most of the ecologically defined groups of pollen and spores appear to characterise the vegetation type to some extent, even though few taxa are restricted to a single habitat. Minor refinements of the group allotment of taxa could be proposed, but few would substantially alter the overall results.

*Diversity of contemporary pollen assemblages*

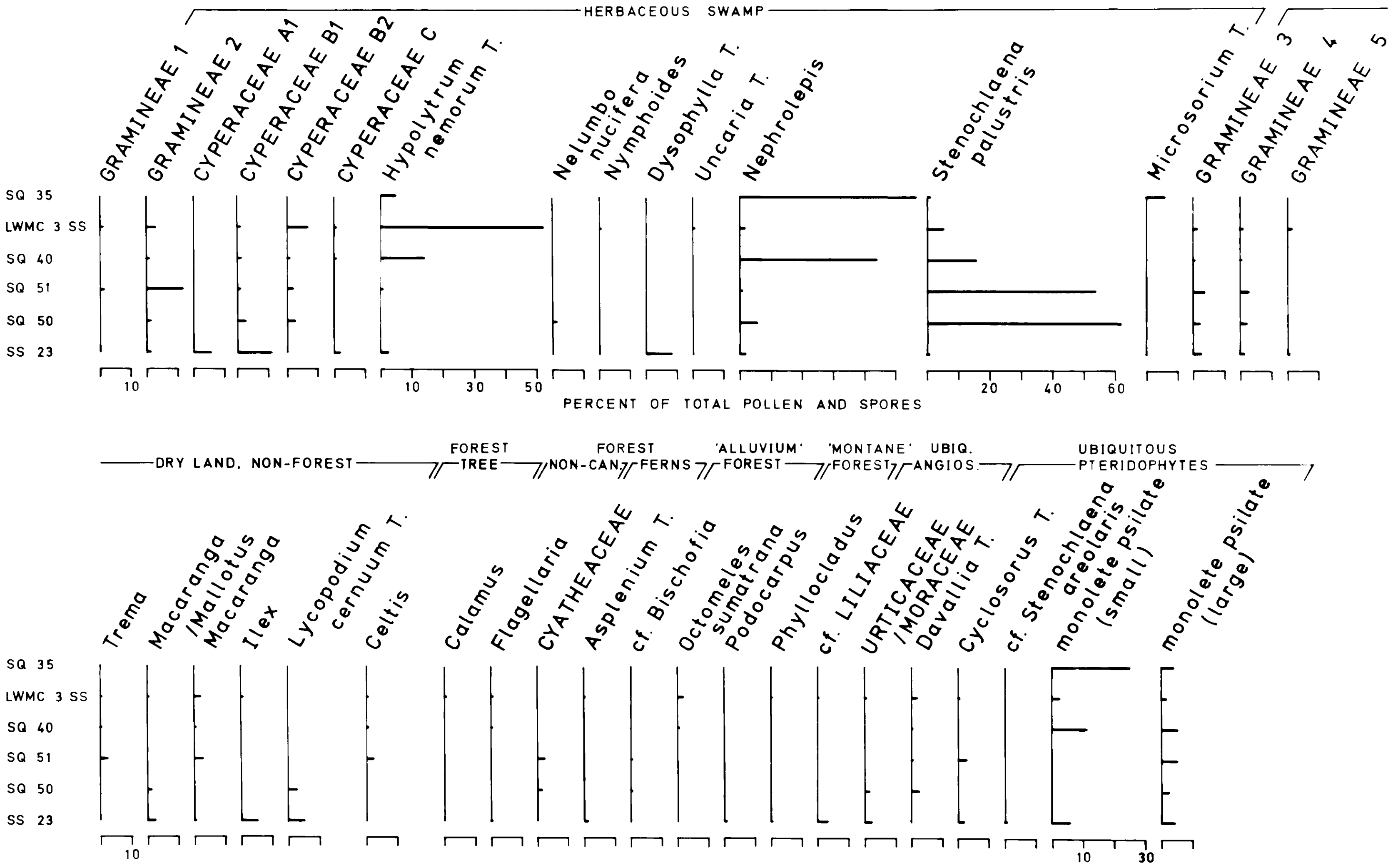
Diversity, or the relationship between numbers of taxa and individuals is a difficult measure to define for pollen spectra. The often non-specific composition of pollen and spore taxa and the vagaries of pollen dispersal render improbable a correlation between the diversity of a pollen assemblage, and that of the vegetation from which it derives. However, in some cases such a relationship does exist. Using Williams' (1964) index of diversity, Birks (1973) showed such a correlation in alpine and sub-alpine vegetation types of western Scotland. Williams' index is appropriate only where the assemblage contains a large number of taxa whose abundance follows a logarithmic series. As the number of taxa was limited for some of the Markham Valley samples a cruder index was calculated by

$$\frac{\text{no. of pollen and spore taxa}}{\text{log. total no. of individuals}}$$

to give relative measures of the diversity of catch in the contemporary pollen assemblages.

The lowest diversity values shown in Fig. 7.1 are recorded from herbaceous swamp sites where the number of local plant species is also low. A low value is also obtained from the disturbed forest site, PT 5. Highest indices of diversity are produced by samples from within forest vegetation, or from those open sites that might be expected to collect pollen and spores from a number of different vegetation types. Although no diversity measures for the vegetation exist for comparison, intuitively the diversity of the pollen assemblages appears to reflect, to some degree,

FIGURE 7.2. Contemporary pollen spectra (selected taxa) from herbaceous swamp sites



vegetation diversity, except where a pollen spectrum derives from a number of different vegetation types.

### *Herbaceous swamp site assemblages*

The herbaceous swamp vegetation of the Lake Wanum area is one of the vegetation types better defined by its pollen spectra, although at Yanamugi there is poorer representation of the much less extensive swamp community. It is fortunate that 12 out of 37 plant taxa recorded in the vegetation quadrats at Lake Wanum and 7 out of 8 designated 'common' taxa produce recognisable and preservable pollen or spores. As herbaceous swamp vegetation associations have been previously described, it may be possible to characterise these by their pollen assemblages. Selected taxa recorded from surface spectra at Lake Wanum and Redhill are shown in Fig. 7.2 as percentages of the total pollen and spore count.

Samples SQ 35 and LWMC 3 SS both come from the western margin of the north-east bay of Lake Wanum. The first comprises surface litter from floating root-mat of Group A vegetation, whilst the second is surface detritus from a short core in open water, 15 m to the east. Both assemblages are dominated by the pollen and spores of herbaceous swamp taxa. The assemblage from SQ 35 consists almost exclusively of the four species dominating the root-mat vegetation: *Nephrolepis, Hypolytrum nemorum* T., *Stenochlaena palustris,* and *Microsorium* T. *Nephrolepis* is by far the most abundant, even more so if a proportion of the monolete fern spores lacking a perisporium is included. In contrast, the core surface sample reveals a very different pollen and spore assemblage despite its proximity to the same vegetation type. *Hypolytrum nemorum* T.

pollen dominates the count, with *Stenochlaena palustris* and *Nephrolepis* well represented. Also present is a number of pollen and spore taxa from other local swamp plants, including Gramineae 1 and 2 (probably *Leersia hexandra*), several Cyperaceae types and *Nymphoides*.

The root-mat litter sample is obviously dominated by extremely local taxa to a greater extent than the core sample that probably receives water-borne pollen and spores from a wider area. *Nephrolepis hirsutula* is found in the lower level of the root-mat vegetation and appears an abundant spore producer. In contrast *Hypolytrum nemorum* produces flowers above the general height of the dense vegetation mat, and was not observed in flower during 1974 when the litter sample was gathered. Profuse flowering did occur during 1976, when the short core was collected. These factors alone could account for observed differences in the two assemblages. It is also possible that the litter sample records a shorter time span than the surface detritus from the core and may thus be unduly influenced by temporary patterns of pollen and spore accumulation.

Four samples come from vegetation quadrats in the south swamp area of Lake Wanum. *Hypolytrum nemorum* dominates the (Group B) vegetation at the site of SQ 40. *H. nemorum* T. is well represented in the surface assemblage, but *Stenochlaena palustris* is equally so and the count is dominated by *Nephrolepis* spores although neither fern occurs in the quadrat. Pollen of grasses and of other sedges occurs in small proportions.

Vegetation of Group D (*Leersia hexandra* floating mat) occupies the site of sample SQ 51. *Stenochlaena palustris* spores dominate the count of litter from the root-mat. *Leersia hexandra* is probably well represented in the Gramineae 1 and 2 grains, and *Phragmites karka* could account for a proportion of the larger grass pollen classes. *Nephrolepis* and various sedges are also represented despite their absence from the quadrat. No pollen of *Nelumbo nucifera* was encountered although the species occurs locally. *Nelumbo nucifera* and *Leersia hexandra* are the only species growing at the site of SQ 50, a quadrat of the Group E open water association. Both taxa are represented in the pollen assemblage, although the count is dominated by *Stenochlaena palustris* with *Nephrolepis* spores and various Cyperaceae pollen also present.

A sample of fine organic detritus from the margin of Redhill swamp (SS 23) contains herbaceous swamp taxa as 40% of the pollen assemblage. *Hypolytrum nemorum* T., *Nephrolepis* and *Stenochlaena palustris*, all components of the swamp vegetation, are represented together with a relatively high proportion of other Cyperaceae pollen. The small aquatic herb *Dysophylla verticillata* is abundant in the vicinity of the sample site and presumably contributes the proportion of *Dysophylla* T. pollen.

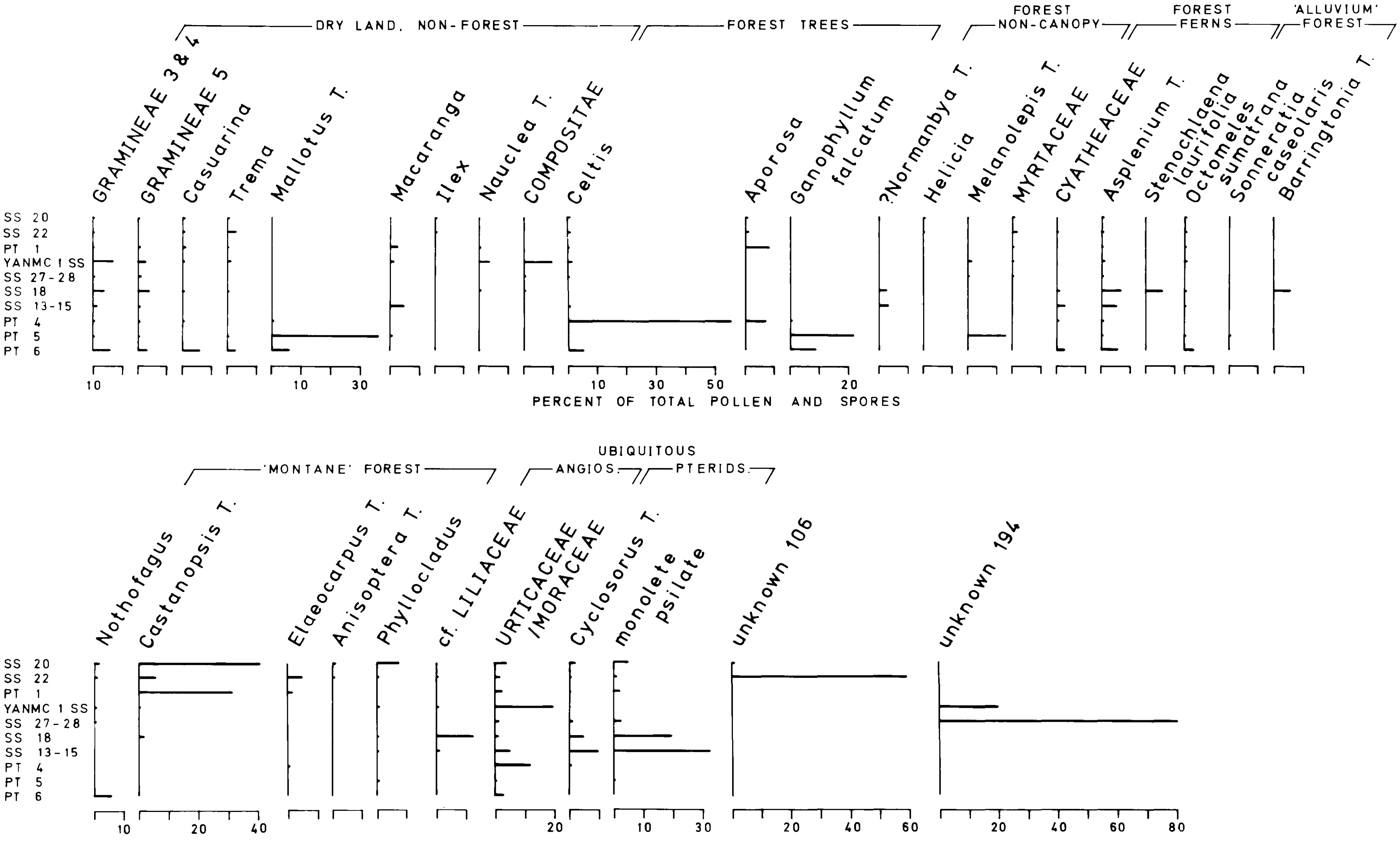
Surface pollen assemblages from swamp sites do reflect, to a limited extent, the herbaceous swamp vegetation associations described previously. Correlation between the floristics of the vegetation and of the pollen spectrum appears better where the sample analysed consists of litter or detritus from a floating mat. In the case of samples derived from the underlying sediment surface a number of factors may explain the less satisfactory correlation. The pollen assemblage is less dominated by very localised pollen and spore sources, and may also collect pollen from a larger area containing different vegetation types. A higher proportion of water-borne pollen may also become incorporated into the sediment samples. The sediments may integrate several years' deposition, during which time the floristic composition of the adjacent vegetation may well have changed.

The surface pollen assemblages from swamp sites contain varying proportions of non-swamp taxa. In the sample from Redhill (SS 23), that with the highest proportion of non-swamp and ubiquitous taxa, a number of these taxa probably emanate from periodically inundated vegetation e.g. *Lycopodium cernuum* T., cf. Liliaceae, *Ilex, Cyclosorus* T., and *Asplenium* T.

The short core surface sample from Lake Wanum (LWMC 3 SS) shows the greatest diversity of pollen and spore taxa, despite consisting of over 50% of *Stenochlaena palustris* spores. Notable is the representation of sub-canopy components of the nearby forest, namely *Flagellaria, Asplenium* T. and probably *Davallia* T. Pollen assemblages from samples SQ 50 and SQ 51 reflect the influence of riparian and swamp forest along Oomsis Creek in the proportions of cf. *Bischofia* pollen and Cyatheaceae spores. The percentages of larger Gramineae pollen in these two samples may reflect the proximity of grassland. However, there are no patterned grains larger than 30 µm (Gramineae 5) typical of *Themeda australis*, the major dry land grass species in the area. In SQ 51 at least, the grass pollen may represent the local occurrence of *Phragmites karka*.

The remaining swamp site pollen assemblages contain few non-swamp taxa. This may be due either to the large distance from dry land vegetation (SQ 40) or to the intensely local representation and low total count (SQ 35).

*FIGURE 7.3. Contemporary pollen spectra (selected taxa) from non-swamp sites*



*Non-swamp site assemblages*

The composition of pollen assemblages from sites not dominated by herbaceous swamp taxa is very varied, as might be expected given the wide range of vegetation types encompassed. Selected taxa represented in these samples are shown, as percentages of the total pollen and spore count, in Fig. 7.3.

Many spectra, especially those from within forest, are dominated by one or more highly abundant taxa. In pollen trap PT 5, 80% of grains are from three taxa (*Hypserpa, Mallotus* T. and *Ganophyllum falcatum*), whilst *Celtis* comprises 54% of the catch in PT 4. Both samples from Yanamugi are dominated by the unidentified pollen type UK 194. In samples from higher altitudes *Castanopsis* T. is strongly represented with 31% in PT 1 and 41% in SS 20. The unidentified pollen taxon UK 106 accounts for 64% of the total in sample SS 22, also from high altitude 'hill' forest. Two extreme lowland forest sites (SS 13-15 and SS 18) are dominated by fern spores and other understorey components, such as cf. Liliaceae, rather than arboreal pollen.

In contrast to the forest and herbaceous swamp samples, non-forest site assemblages appear less dominated by a few locally occurring taxa. These samples include the floating pollen trap PT 6, the surficial sediment from Yanamugi, and the samples LWMC 3 SS and SS 23 that, although swamp dominated, include a wide variety of dry-land taxa also.

Few pollen or spore taxa are present in all dry-land assemblages. Those with the widest occurrence tend to be taxa such as Gramineae, Urticaceae/Moraceae, or monolete fern spores that represent a large group of plants from many ecological situations.

Nor are many taxa restricted to a single, well defined community, although a few such possible 'indicator' taxa may be identified. One group termed 'montane' (at least with respect to the present study) includes *Nothofagus, Podocarpus* and *Phyllocladus*. These three genera of trees are more common above 1 000 m, although all have been recorded growing at lower elevations. Both *Nothofagus* and *Phyllocladus* pollen are well represented in the higher altitude 'hill' forest samples SS 20 and SS 22, although neither tree appears to grow in the local forest. These taxa are also found in pollen spectra from much lower altitudes. *Nothofagus* occurs in both contemporary assemblages from Yanamugi and from the floating pollen trap PT 6, at Lake Wanum, whilst *Phyllocladus* is even more widespread occurring in over half the low altitude samples. *Podocarpus* pollen is represented by two grains from the swamp margin sample SS 23 at Redhill.

The designation of taxa restricted to lowland environments is more difficult. Two predominantly mangrove genera, *Sonneratia* and *Rhizophora* are sufficiently restricted to coastal habitats. The occurrence of considerable *Sonneratia caseolaris* pollen in trap PT 5 may be attributable to the action of red ants, although wind-borne influx cannot be excluded. The species does not grow at Lake Wanum today although it may occur nearby in the Markham Valley. The closest definite source is east of Labu, 13 km distant. A single occurrence of *Rhizophora apiculata* T. pollen from sample SS 20 at an altitude of 970 m is unlikely to be a misidentification as the genus is quite distinctive (Anderson and Muller, 1975). Although contamination cannot be ruled out, Muller and Caratini (1977) also report finding pollen of *Rhizophora* from a *Sphagnum* polster from 870 m altitude on Mount Santabong, West

Sarawak. *Octomeles sumatrana*, a species of large tree particularly common along lowland river channels, is also represented in the high altitude 'hill' forest pollen assemblages, although its pollen is less distinctive than the aforementioned taxa.

## *POLLEN PRODUCTION AND DISPERSAL IN THE MARKHAM VALLEY*

Data presented above are too fragmentary to allow construction of an integrated model of contemporary pollen deposition in the area. They do however illustrate various aspects of pollen production and transfer in the lowland tropics that may be compared instructively with similar studies from other tropical and temperate regions.

### *Pollen production rates*

The PDR estimates from the three pollen traps within arboreal vegetation suggest a high level of pollen production for at least some taxa. The maximum PDR for a single taxon is 143 000 grains $cm^{-2}$ $yr^{-1}$ for *Mallotus* T. in trap PT 5 although this value may have been inflated by insect activity. Estimates from undisturbed, although possibly overloaded, traps include 55 000 grains $cm^{-2}$ $yr^{-1}$ for *Celtis* in PT 4, and an annual deposition rate of 41 000 grains $cm^{-2}$ in PT 1 for *Castanopsis* T.

The total PDR estimates from these three traps range between 100 000 and 400 000 grains $cm^{-2}$ $yr^{-1}$. These figures are much higher than estimates from pollen trapping studies in a variety of other climatic and vegetation types (Table 7.3) although few of the tabulated samples derive from unroofed traps within forest. Intermediate PDR estimates have been calculated for lake sediments from deciduous forest sites in North America (Davis, *et al.*, 1973).

*TABLE 7.3. Comparative airborne pollen and spore deposition rates from other areas*

| Author | Vegetation | Trap type and location | PDR, Pollen and spores $\mathrm{cm}^{-2}\ \mathrm{yr}^{-1}$ |
|---|---|---|---|
| Flenley (1973) | Tropical rain-forest, Selangor, Malaysia | Oldfield traps | |
| | | Canopy | 800 |
| | | Ground | 1 100 - 2 020 |
| Kershaw and Hyland (1975) | Tropical rain-forest margin, Atherton Tableland, Qld, Australia | Tauber traps floating on small lake | |
| | | Roofed | 90 - 124[a] |
| | | Unroofed | 129 - 250[a] |
| Hope (1973) | Alpine and sub-alpine forest and non-forest, Mt. Wilhelm, Papua New Guinea | Tauber traps | |
| | | Roofed | 40 - 710 |
| | | Unroofed | 750 - 6 450 |
| | | Floating unroofed | 750 - 900 |
| Flenley (1973) | Montane forest, Papua New Guinea | Rain gauge sample | 1 130 |
| Hope (1968) | Forest and non-forest vegetation, Wilson's Promontory Vic., Australia | Tauber traps | |
| | | Unroofed | 1 300 - 14 500 |
| Tauber (1967) | Temperate broad-leaved forest, Zealand, Denmark | Tauber traps | |
| | | Unroofed floating on lake | 2 850 - 6 600[b] |
| | | Roofed within forest | 788 - 825[b] |
| Berglund (1973) | Temperate forest and non-forest, Blekinge, south-eastern Sweden | Tauber traps floating on four lakes | 2 000 - 4 400[c] |

[a] Excludes aquatic, weed, and grass pollen

[b] Collection period March - November only

[c] Mean of roofed and unroofed traps. Unroofed traps collected 10 - 40% more pollen than roofed

Investigations within Malaysian lowland forest (Flenley, 1973) produced PDR estimates of 1 100 and 2 020 grains $cm^{-2}$ $yr^{-1}$ from ground level traps. Although pollen traps of different design were employed, this factor alone is unlikely to explain the great difference between these figures and the values obtained in the current study. Estimates of contemporary PDR for Papua New Guinea highland areas (Hope, 1973, Flenley, 1973) indicate values in the range of 750 to 6 400 grains $cm^{-2}$ $yr^{-1}$, only slightly lower than comparable northern European and temperate Australian situations (Tauber, 1967, Berglund, 1973, Hope, 1968).

### *Pollen dispersal*

It is evident from the PDR results that pollen dispersal within the study area is a highly localised process. The very low annual influx values obtained from the isolated floating trap PT 6, one thousand times smaller than the maximum forest PDR estimates, can be explained only by an extremely low efficiency of aerial pollen transport. Values of a similar order of magnitude (hundreds of grains $cm^{-2}$ $yr^{-1}$) are reported from floating pollen traps at other tropical sites (Hope, 1973, Kershaw and Hyland, 1975) and the canopy level trap of Flenley (1973). In contrast, from Blelham Tarn, a small lake in north-west England, Bonny (1978) reports an annual pollen influx rate to floating traps only twenty times less than the rate recorded from adjacent forest or lake-marginal sites.

A proportion of the pollen in the floating trap at Lake Wanum derives from vegetation types not immediately adjacent to the lake. A similar component is identifiable in surface assemblages from non-forested sites not overwhelmingly dominated by local herbaceous swamp taxa. Within the forest, a high proportion of taxa derive from plants growing in the understorey. This situation is analogous with Tauber's three-component model of pollen transfer (Tauber, 1965). A 'trunk space' component is recognisable in forest sites, and a more regional 'rainout component' becomes significant in open sites where the pollen and spore influx from local vegetation is not overwhelming. Identification of an 'above the canopy' forest component is less satisfactory, as many canopy taxa are also common in the 'trunk space' component. Proportions of taxa thought to represent both of these components are found in open depositional sites adjacent to the forest and in the isolated floating pollen trap.

In a study of pollen transfer at sites in West Malesia Morley (1976) found that pollen from larger trees dominated assemblages in forest, although there was a substantial representation of trunk space taxa. Herbaceous swamp pollen was also found to predominate over forest pollen in swamp sites, although less so in open water. Unlike the situation in the Markham Valley there was little transfer of trunk space pollen and spores to swamp depositional sites, possibly due to the denser nature of the forest margin. Morley also found transport of *Trema* pollen above the altitudinal limit of the genus, but no evidence for downslope dispersal of any pollen taxa.

At Lake Euramoo, in north-east Queensland, Kershaw and Hyland (1975) identify a small 'rainout' component, with the 'above the canopy' component dominating pollen fallout onto the central lake surface. At Yanamugi, slightly smaller than Euramoo, the surface sediment assemblage contains some non-canopy forest taxa and a high proportion of non-forest taxa. The open nature of the semi-deciduous forest around the site could allow for significant transfer of 'trunk space' pollen and spores.

*Pollen representation*

Pollen 'representation' is an ill-defined concept depending as it does on the net outcome of pollen production, dispersal and preservation. In certain cases it may be feasible to compare frequencies of pollen in a modern assemblage with the proportions of source taxa in the surrounding vegetation (e.g. Davis and Goodlett, 1960). In the absence of comprehensive data on vegetation composition and floristics any such estimates here are highly subjective.

In the lowland tropical situation it could be argued that any pollen or spore taxa consistently encountered in sediments are 'over-represented'. Perhaps the majority of species hardly ever contribute to the pollen assemblage either because their pollen production is very low, maybe coupled with zoophilous pollination mechanisms, or because their wind-borne pollen is poorly dispersed or easily degraded by soil organisms. Nevertheless, certain pollen taxa possess a combination of production and dispersal abilities that enable them to be deposited well beyond the borders of the parent population. In tropical montane pollen studies these 'high relative export' taxa (*sensu* Flenley, 1973) are usually those found above the altitudinal limit of the source vegetation. In the present study pollen taxa similarly 'over-represented' are identified as those found either above or below the altitudinal limits of their source, or as pollen taxa much more widespread than the corresponding vegetation. Most noticeable are *Rhizophora apiculata* T. and *Octomeles sumatrana* (above alt. limit), *Nothofagus, Phyllocladus* and *Podocarpus* (below alt. limit) and *Trema* and *Casuarina* (generally widespread). With the exception of *O. sumatrana*, all taxa have been cited by other authors as showing a similarly high relative export capacity (Hafsten, 1960, Hamilton, 1972, Flenley, 1973, Hope, 1973, Morley, 1976, Colinvaux and Schofield, 1976*a*, Caratini *et al.*, 1973 and Muller and Caratini, 1977).

Many other taxa show a locally very high representation in the vegetation type in which the source plant occurs. Conversely some pollen taxa occur as very small proportions of the total even when the source plants are abundant and close to the sampling site. The best evidence comes from the herbaceous swamp assemblages, from which comprehensive ecological data are also available. Here taxa considered 'under-represented' include Cyperaceae (excepting *Hypolytrum nemorum* T.), *Nelumbo nucifera*, *Nymphoides*, and Gramineae. Hope (1973) and Colinvaux and Schofield (1976*a*) also comment on the apparently poor dispersal properties of grass pollen. It should be emphasised that these taxa remain 'over-represented' in relation to the large number of plants 'non-represented' in contemporary and fossil pollen assemblages.

## *POLLEN TRANSFER IN THE LOWLAND TROPICS*

Flenley (1973) concludes that there appears to be no fundamental difference between tropical and temperate pollen 'rain'. Whilst this is true,the current study reveals great differences in the degree of influence of various factors. Pollen and spore production, at least in forest conditions, is shown to be very high, whereas preservation and aerial dispersal are of a very low order. At forest and herbaceous swamp vegetation sites the great majority of the pollen appears to be derived from the local vegetation within tens of metres. In more open sites the proportion of taxa from increasingly distant sources is much greater.

Pollen is carried both upslope and downslope. Although downslope transport appears more significant, this may be due only to the number of distinctive taxa involved. With the steep altitudinal gradients of Papua New Guinea this process could produce considerable mixing of pollen from a wide range of vegetation types. Such a 'regional' component is nevertheless a much lower proportion of the total PDR than it appears to be in higher altitude sites (Hope, 1973).

Because of the generally low efficiency of aerial pollen dispersal, other routes for the incorporation of pollen into sediments may be important. Extensive water-borne influx of pollen has been demonstrated for temperate lakes (Bonny, 1976, 1978, Peck, 1973) and may be proportionally more important in the tropics (Germeraad *et al.*, 1968). Although neither lake in this study possesses a permanent inflow stream, the effect of slopewash and periodic flooding on pollen transfer is unknown. Landslips and other natural or artificial erosional events could release large quantities of freshly deposited pollen from the soil surface into lakes or watercourses. These agents surely require investigation for a better understanding of pollen transfer and deposition in the tropical lowland environment.

# CHAPTER 8

# INTERPRETATION OF VEGETATION CHANGE FROM POLLEN ANALYTICAL DATA

The interpretation of vegetation change from palynological evidence involves:

( i) the recognition of sequential trends in the plant microfossil record not explicable by random or non-biological factors,

( ii) the equation of such pollen assemblages with existing or hypothetical vegetation communities to reveal the nature of the ecological change involved and

(iii) the identification of causal mechanisms for any vegetation changes found.

This chapter attempts to recognise and explain the nature of changes in the palynological record of the two Markham Valley lake sites. In so doing possible causes are necessarily invoked. However, these are discussed in a broader context in the succeeding chapter.

## *THE NATURE OF THE DATA*

The form of the palynological data dictates their potential usefulness and manner of interpretation. In comparison with most temperate regions, pollen assemblages from the lowland tropics are comprised characteristically of few relatively abundant taxa and a large number of much less frequently encountered types. Unless very many grains are counted, statistical confidence limits on the occurrence of most taxa are very wide. Thus, referring to the formula for the estimation of pollen concentration (Chapter 6), it can be seen that where four or less grains of a taxon are encountered in a sample the 95% confidence limit is equal to, or greater than, the actual count. Confidence limits can be reduced only by counting a larger proportion of the sample, or by amalgamation of the counts for co-varying taxa. Confidence limits should also be applied to relative pollen frequency data (Mosimann, 1965, Maher, 1972).

The coexistence of pollen concentration estimates and a sound chronology allows calculation of estimates for annual pollen and spore deposition rates (PDR) for a sedimentary sequence. Liberating pollen data from the constraints of relative frequency calculation, PDR figures provide a greater potential for the interpretation of the spectral results. Truly quantitative changes in pollen deposition are open for study, and fluctuations in the frequency of selected taxa may be investigated independently of changes in the rest of the assemblage. This is especially useful when the knowledge of ecological status, and even the identification of many pollen taxa, is incomplete or obscure.

Despite the availability of PDR estimates, it is recognised that the palynological data in this study require cautious interpretation. Sufficiently narrow confidence limits can be assigned to only the most commonly occurring taxa, or groups of taxa. A large number of pollen or spore types are represented in a sample by one or two grains only. In view of the large confidence interval associated with such occurrences it make little difference to the interpretation whether these minor taxa are expressed as PDR values or as relative frequencies.

### *METHODS OF INTERPRETATION*

The most convincing method of recognising vegetational analogues of sub-fossil pollen spectra is through the medium of contemporary pollen assemblages. Subjective comparisons may suggest similarities between modern and ancient pollen assemblages and thus infer some similarity between vegetation types. Conversely, lack of correlation may eliminate a certain vegetation type from consideration as a modern analogue of past communities. The most accurate results are to be expected where a large number of widespread contemporary assemblages are available for comparison. In such cases statistical techniques may be used to equate subfossil spectra with extant vegetation communities (e.g. Kershaw, 1973*b*).

Once periods of similarity are identified, the pollen sequence may be divided into temporal 'pollen assemblage zones' thought to reflect a vegetation unit of either local or regional importance (West, 1970). Alternatively a zone may be defined as a period of consistent directional change in the sequence. Samples showing relative homogeneity can be united to form pollen assemblage zones either subjectively, or by means of probability statistics such as chi-square values (Kershaw, 1970). Use of more complex multivariate techniques has also been explored (e.g. Dale and Walker, 1970, Gordon and Birks, 1972). However, as Walker (1971) reminds us, statistical comparison between the pollen assemblages of neighbouring samples is legitimate only if the variation within each sample is first taken into account. This is rarely undertaken, since it involves counting numbers of replicate subsamples from each horizon.

Whilst pollen assemblage zones have a demonstrated utility in delimiting periods dominated by few abundant pollen taxa, their efficacy may be questioned where most samples are comprised of a large number of infrequently found taxa. Neither is there any theoretical reason to presume synchronous change in different vegetation associations contributing to the pollen assemblage, unless perhaps as a result of overwhelming regional environmental change. In relative frequency pollen diagrams the fluctuations of one interdependent taxon lead to corresponding changes in other taxa thus reinforcing the impression of synchronous events. Such statistical artefacts are taken into account during subjective interpretation, but become more difficult to assess as the number of taxa involved increases. One major advantage of the PDR diagram in this respect is in allowing for the examination of individual taxa or groups of taxa independently of others. Separate zonations can be applied with greater confidence to groups of ecologically similar taxa. In addition, the temporal representation of single taxa can be described, or analysed statistically (Walker and Wilson, 1978).

## *INTERPRETATION OF POLLEN SEQUENCES FROM THE MARKHAM VALLEY*

A variety of approaches was taken in the description and interpretation of the sub-fossil pollen records from the two Markham Valley lake sites. A solid radiocarbon chronology for Lake Wanum allows the estimation of PDR figures. At Yanamugi the tentative chronology based on radiocarbon, stratigraphic and palaeomagnetic evidence is too unsound for systematic calculation of such rates. However, comparable figures are derived for some of the more reliably dated sections of the core. Confidence intervals are shown only on summary PDR diagrams where a number of taxa are grouped together. Corresponding confidence limits for individual taxa are proportionally greater. The 95% confidence interval for *counting error* on other PDR and pollen concentration figures may be calculated using the data in Appendix III.

In describing the pollen sequences, the representation of the more important taxa is first considered in relation to their supposed vegetational source. The array of taxa, or selected components thereof, is then divided into pollen assemblage zones. These zones are defined as periods of similarity or consistent trends in the PDR or relative abundance of taxa. The ecological implication of trends shown by individual taxa and groups of taxa is sought, as far as possible, by reference to contemporary pollen assemblages. The pollen data are not considered sufficiently robust to allow comprehensive use of statistical techniques either for erection of assemblage zones or comparison with contemporary spectra.

## *THE POLLEN RECORD FROM LAKE WANUM*

Twenty-eight samples were analysed from the 13.81 m long core LW II, the most ancient sediments retrieved during 1974. The sampling interval varied between 13 cm and 119 cm, being closest in the more slowly sedimented sections of the core. The approximate age difference between neighbouring samples is typically 350 years. A suite of radiocarbon dates (Chapter 3) provides an excellent chronology for the core. Sediment accumulation rate 'C' (Fig. 3.11c) derived from these determinations enables calculation of PDR estimates for the whole sequence. The total PDR, and sub-totals for herbaceous swamp taxa and dry land taxa are plotted against the inferred radiocarbon age in Fig. 8.1. Also shown are the sediment accumulation rates for 'organic' and 'inorganic' fractions (from Fig. 3.13) and the incidence of carbonised particles in each of three size classes.

Considerable variation in total PDR exists between samples. Values estimated range from less than 1 000 grains $cm^{-2}$ $yr^{-1}$ to a maximum of over 40 000 grains $cm^{-2}$ $yr^{-1}$. Before accepting these figures as representative of the true PDR, possible causes of error are briefly considered.

The 95% confidence interval for counting error shown on these curves may represent an underestimate of this error in some circumstances.

The radiocarbon-based sedimentation rate employed obviously influences the PDR results. Sediment accumulation rate 'C' is chosen as the most acceptable for the core as a whole. However, this takes no account of known secular variations in atmospheric radiocarbon as does rate 'B' (see Chapter 3). Use of the latter curve as the basis for PDR calculations would lead to a slight reduction in total PDR estimates between the radiocarbon ages of 2000 BP and 4300 BP. Even after such adjustment, these PDR values would remain amongst the highest encountered in the sequence.

The accumulation rate used for calculation of PDR assumes a constant sedimentation rate between radiocarbon samples. No account is thus taken of fluctuations of shorter periodicity. As such variations in sedimentation are more effectively averaged during periods of slow accumulation they may become significant when the accumulation rate is high, e.g. between 3400 BP and 4300 BP. Large fluctuations in PDR are indeed found during this period and this factor may remain the largest unaccountable source of error affecting the PDR estimates.

FIGURE 8.1. Lake Wanum core LW II: Pollen deposition rates (PDR) for major groups (± 95% confidence limits), carbonised particle and sediment accumulation rates

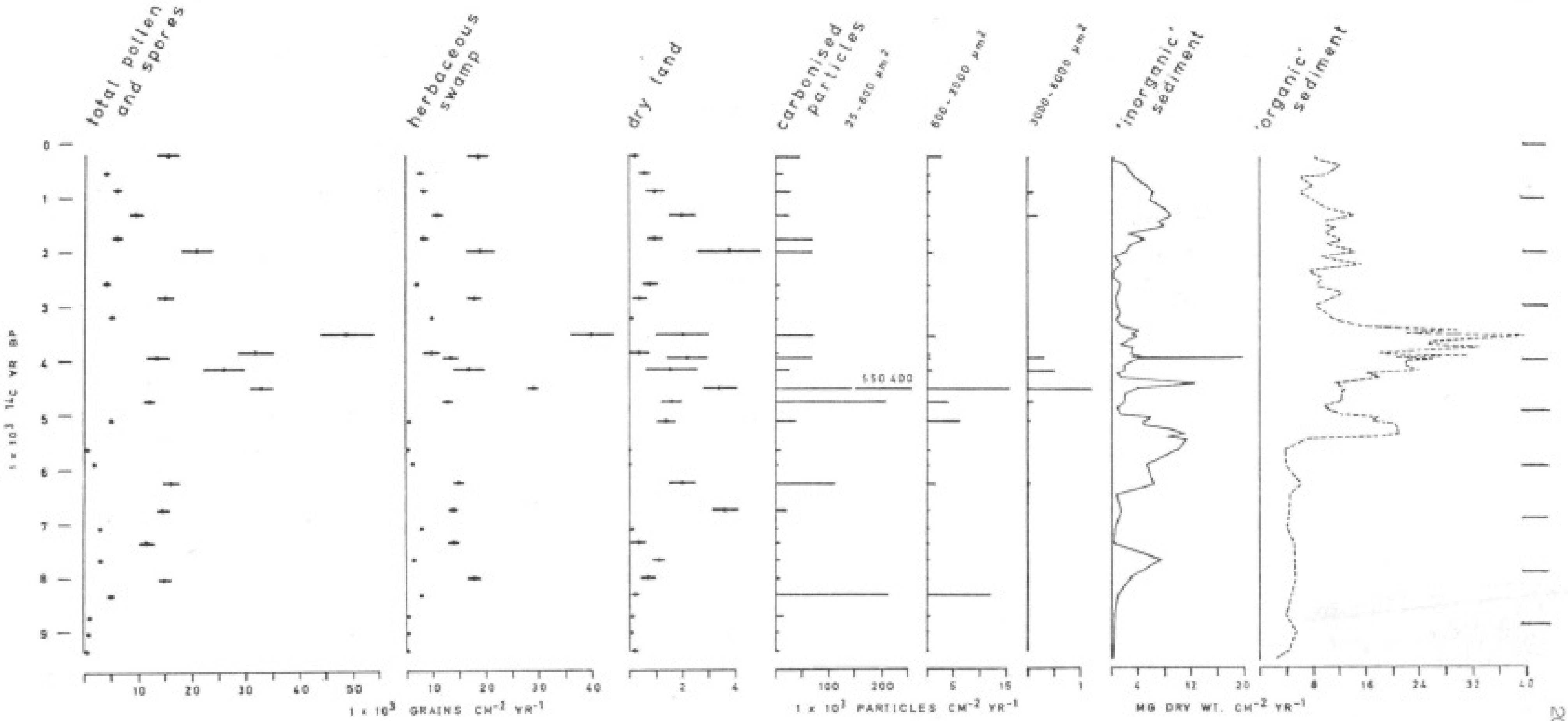


*FIGURE 8.2. Lake Wanum core LW II: PDR for herbaceous swamp pollen and spore taxa*

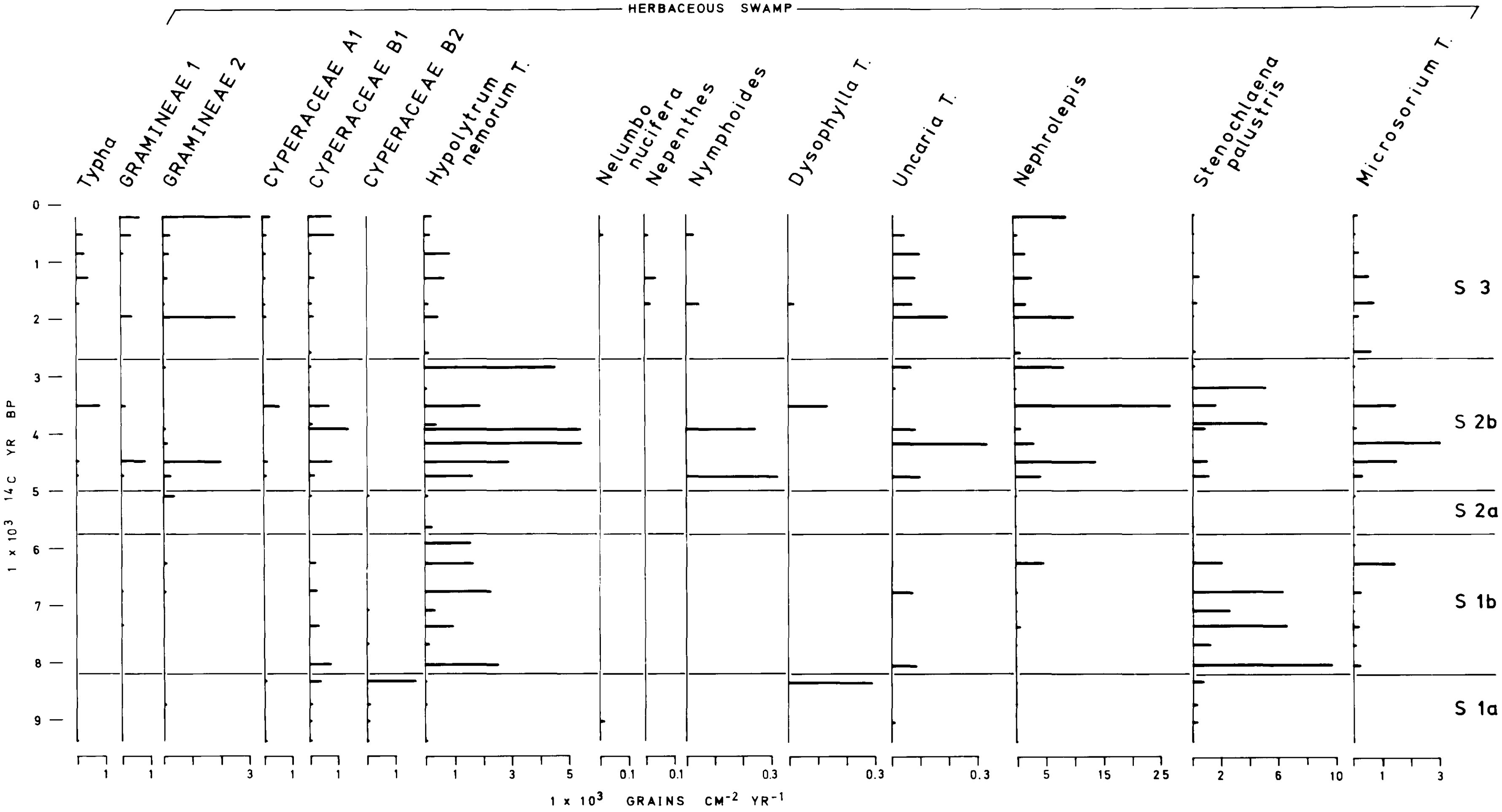
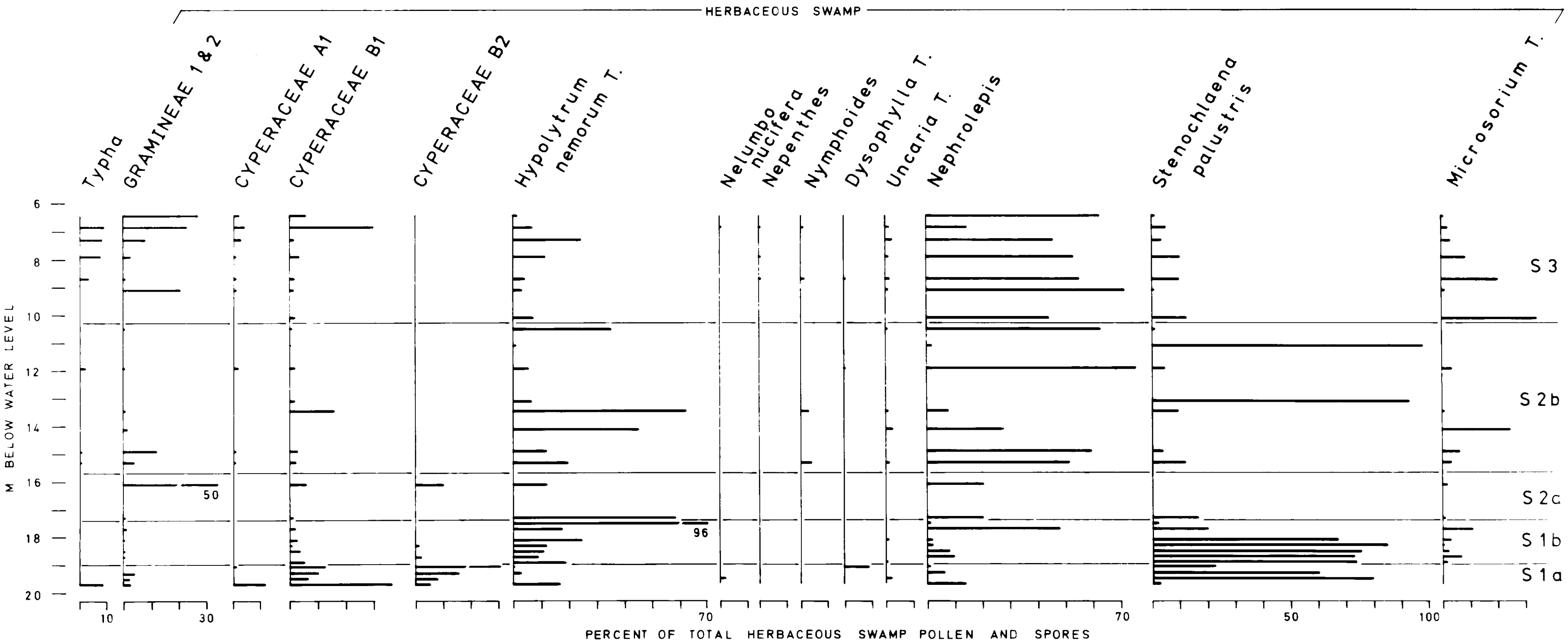


*FIGURE 8.3. Lake Wanum core LW II: Relative frequency diagram for herbaceous swamp pollen and spore taxa*



Post-depositional destruction of pollen or spores, either selectively or *in toto* is a problem in some depositional environments. This possibility should be considered where stratigraphic evidence reveals oxidising conditions or where the PDR appears abnormally low.

## *EVIDENCE FOR CHANGES IN HERBACEOUS SWAMP VEGETATION AT LAKE WANUM*

As shown in Fig. 8.1 the herbaceous swamp pollen and spore taxa dominate the majority of pollen assemblages from core LW II. The relatively few structural and floristic dominants of the swamp vegetation are well represented in the sub-fossil record. Of equal importance, the main features of the ecology and, to a lesser extent, the contemporary pollen deposition are known. The palynological evidence for vegetation change within the swamp environment is therefore considered first, separately from the pollen record of the less well represented dry-land vegetation.

The estimated PDR of individual herbaceous swamp taxa are shown on an age axis in Fig. 8.2. Relative frequencies of the same taxa are plotted in Fig. 8.3 against stratigraphic depth. The latter diagram allows comparison with the contemporary pollen assemblages, also calculated on a relative frequency basis.

### *The palynological record of herbaceous swamp taxa*

*Hypolytrum nemorum* T. pollen is recorded from all but one (1950 cm) of the core samples. Although poorly represented in sediments older than 8200 BP it becomes abundant between 8200 BP and 5800 BP and reaches its highest PDR from 5000 BP to 2700 BP. The taxon is an important component of the pollen assemblage from 2700 BP to the top of the core, although the PDR are lower than during the previous 2000 years. The species appears an obligate hydrophyte, although it is occasionally found in only periodically inundated swamp localities. Although contemporary observations show *H. nemorum* to be an erratic pollen producer, the record suggests that the large sedge has been a significant component of the vegetation of the north-east bay since at least 8200 BP.

*Stenochlaena palustris* spores are also well represented throughout the sequence, comprising a very high proportion of the total swamp taxa prior to 7200 BP (Fig. 8.3). However, this abundance may be largely an artefact of low total PDR as the PDR of the spore increases to its highest values around 8200 BP, and continues at a generally high level until approximately 3000 BP. At this time the representation of *S. palustris* decreases to fairly constant, though lower, PDR values.

*Nephrolepis hirsutula* is probably the species represented by the great majority of *Nephrolepis* spores, although *N. biserrata* may contribute to the spore taxon in non-swamp locations. Whilst *Nephrolepis* spores are present throughout the core, their representation increases considerably subsequent to 5000 BP.

Occurrence of grass pollen smaller than 20 µm (Gramineae 1) associated with a larger proportion of Gramineae 2 (max. dimension 20-25 µm) may indicate presence of the swamp grass *Leersia hexandra*. Substantial PDR figures for both size classes are found between 5000 and 4000 BP and from about 2000 BP to the present.

Pollen of Cyperaceae other than *Hypolytrum nemorum* occurs throughout the deposit. Differences in the representation of the several pollen morphological classes must be interpretated with caution. The morphology of only the more common species has been studied, and many fall into more than one category. A wider range of cyperaceous pollen classes may be seen in the sediments prior to 8200 BP. Categories B1 and B2 are the most common, A1 and A2 being present in some samples. Since 8200 BP the grains most frequently found belong to the smaller size classes, in particular B1, although Cyperaceae A1 become more common subsequent to 5000 BP. *Cyperus platystylis* and *C. polystachos* are the only common species contributing to class A1, and their pollen forms a large proportion of class B1 also.

*Microsorium* T. spores first appear in the sequence around 8200 BP but show their greatest abundance since 5000 BP. Although a species of *Microsorium* is a component of floating root-mat vegetation at the present time, it is unlikely that the spore taxon is unique to this species.

*Nepenthes* pollen is confined to the most recent 2000 years of the sequence and is thought to represent *N. mirabilis*. This species is found in well developed floating root-mat vegetation although it also occurs in periodically inundated or otherwise damp grassland localities. *Uncaria gambir* is also a component of floating root-mat vegetation and contributes a proportion of *Uncaria* T. pollen. This taxon occurs throughout the core, but becomes more abundant subsequent to 5000 BP.

Neither *Nelumbo nucifera* pollen, nor *Nymphoides* pollen (almost certainly from *N. indica*) are common in the deposits. However both are obligate aquatics and useful indicators of water depth. Two *N. nucifera* grains are recorded from the sample at 1950 cm showing the species' presence by at least 9100 BP. In contrast, *Nymphoides* pollen is not found until about 4800 BP.

*Typha* pollen occurs in small quantities in a number of samples, and reaches a fairly high PDR within the last 2000 years, although it is absent from the most recent sample. Neither

*Typha,* nor *Sparganium antipodum* T., represented by a single pollen grain, appears to grow in the vicinity of Lake Wanum today.

*Herbaceous swamp pollen assemblage zones*

Zone S1a: 9500-8200 BP (1970-1900 cm)

During the period of 1300 years represented by the four oldest pollen analysed samples, sediment accumulation rates are very slow. Estimated PDR figures, both for swamp and non-swamp taxa, are low although they show a general increase towards the top of the zone.

The most abundant taxa encountered are *Stenochlaena palustris* spores, and Cyperaceae pollen of morphological classes A1, B1 and B2. Minor quantities of other herbaceous swamp taxa, *Typha, Sparganium antipodum* T., cf. *Colocasia, Nelumbo nucifera* and *Nephrolepis* are also represented. A peak of *Dysophylla* T. pollen occurs at the top of the zone in conjunction with an increase in Cyperaceae class B2 pollen and a general rise in PDR. Grass pollen is present throughout the zone, although none falls into the smallest size class (Gramineae 1) suggesting that *Leersia hexandra* may have been absent from the site.

Comparison of relative frequency pollen assemblages from this zone with contemporary spectra reveals no direct parallel. Sample SS 23 from the swamp marginal vegetation at Redhill shows the closest similarity, containing high proportions of Cyperaceae and larger grass pollen classes, *Hypolytrum nemorum* T., and spores of *Nephrolepis*. Most significant is the large representation of *Dysophylla* T. pollen matching that found at the top of zone S1a.

The proportion of *Stenochlaena palustris* spores, however, is considerably lower in the contemporary assemblage than in the core. Although not particularly common in the swamp marginal vegetation at Redhill, *S. palustris* can be found in such habitats and is reported to be exceedingly common in open swamp forest throughout the Malayan peninsula (Holttum, 1932).

Zone S1b: 8200-5750 BP (1900-1740 cm)

Organic sediment accumulation rates in this zone remain similar to those of the preceding period, although inorganic accumulation shows a slight peak at about 7700 BP. In contrast, estimates both of total PDR and herbaceous swamp PDR, although fluctuating, show large increases over rates for the previous zone, S1a.

The highest sustained PDR figures for *Stenochlaena palustris* spores, up to 9 500 $cm^{-2}$ $yr^{-1}$, are found in this zone, and the species comprises 70% to 90% of the herbaceous swamp pollen and spore sum. *Hypolytrum nemorum* T. pollen is well represented with higher PDR figures becoming more common in the upper part of the zone. Spores of *Nephrolepis* are recorded from all samples. Cyperaceae pollen of class B1 occurs throughout although PDR values show a decline towards the end of the zone.

Zone S1b sees the first occurrence, albeit in small quantities, of other herbaceous swamp taxa. *Microsorium* T. spores are present in all samples and grass pollen of the smallest size category (Gramineae 1) may indicate the presence of *Leersia hexandra*.

Again, no direct parallel exists between the pollen spectra of this zone and any modern assemblage. No contemporary sample adequately reflects the predominance of *Stenochlaena palustris* in association with substantial frequencies of *Hypolytrum nemorum* T. and a low proportion of *Nephrolepis* and *Microsorium* T. spores. Although samples SQ 51 (*Leersia hexandra* root-mat vegetation) and SQ 50 (open water *Nelumbo nucifera* association) show similarly high values for *S. palustris*, they contain few or no *Nephrolepis* spores and none of *Microsorium* T. Towards the top of zone S1b the proportion of *S. palustris* declines and that of *Nephrolepis* increases. These spectra more closely resemble the contemporary sample SQ 40, taken from the rooted *Hypolytrum nemorum* vegetation association.

Lack of a direct modern analogue for the pollen assemblages of this zone makes characterisation of the probable swamp vegetation difficult. The relative dominance of *Stenochlaena palustris* spores appears, by analogy with contemporary spectra, to be associated with sparse vegetation cover or open water conditions. Alternatively, it may reflect the proximity of open swamp forest or swamp marginal vegetation rich in *S. palustris*, as proposed for zone S1a. In either case the herbaceous swamp vegetation of zone S1b could resemble the present day rooted *Hypolytrum nemorum* association of shallow water. This association also contains *S. palustris* but little or no *Nephrolepis hirsutula.* The increased incidence of *Nephrolepis* spores during the latter part of zone may reflect the proximity of floating root-mat vegetation as appears the case in contemporary samples.

Zone S2a: 5750-5000 BP (1740-1570 cm)

A greater than five-fold increase in the rate of organic sedimentation occurring at about 5500 BP is maintained until *c.* 5000 BP. Inorganic influx also increases substantially, reaching the highest sustained rates in the core between about 5700-5200 BP. The two pollen analysed samples from the zone are characterised by very low PDR values both for herbaceous swamp and dry-land taxa.

*Hypolytrum nemorum* T. pollen and *Nephrolepis* spores are recorded from both samples, whilst *Stenochlaena palustris* is present only in the lower. The upper sample of the zone shows various other cyperaceous pollen and a substantial proportion of Gramineae 2. However, no grass pollen of the smallest size class indicative of *Leersia hexandra* was found.

The taxonomic composition of zone S2a appears similar to that of the previous zone, but with an increase in the proportion of Cyperaceae B1 and B2, and a substantial decrease in that of *S. palustris*. The cause of the dramatic decline in PDR to figures similar to those of zone S1a remains enigmatic. Revertance to the marginal swamp conditions of the earlier zone appears unlikely in view of the continued presence of *H. nemorum* T., and lack of pollen indicative of marginal conditions. Reduced pollen deposition could result from a decrease in the cover of swamp vegetation, possibly caused by a rise in water level. A rapid influx of inorganic sediment such as occurs at this time may have had an effect on the vegetation. However, a hypothesis of reduced swamp vegetation is hard to reconcile with the increase in the organic sediment accumulation rate during the later part of the zone.

Zone S2b: 5000-2700 BP (1570-1030 cm)

Organic sedimentation rates and the PDR of herbaceous swamp taxa reach their highest values during the earlier part of zone S2b. Although *Nephrolepis*, *Stenochlaena palustris* and *Hypolytrum nemorum* T. are the most abundant, the zone shows the greatest diversity of herbaceous swamp taxa encountered in the whole sequence. Pollen of various Cyperaceae, Gramineae 1 and 2, *Uncaria* T., *Typha* and even *Dysophylla* T. are present, as are *Microsorium* T. spores. *Nymphoides* pollen first occurs at the base of the zone.

Comparison of the pollen spectra of zone S2b with contemporary assemblages suggests similarities with a range of herbaceous swamp vegetation types. The high proportion of *Hypolytrum nemorum* T. pollen in the earlier part of the zone parallels that of sample SQ 40 from the rooted *H. nemorum* vegetation association. The considerable proportion of *Nephrolepis* spores recorded in the sub-fossil assemblages suggest the presence of floating root-mat vegetation such as that represented by the contemporary sample SQ 35. The wide range of pollen taxa recorded may reflect a variety of vegetation associations contributing to the palynological record of the zone. It is quite possible that herbaceous swamp vegetation during zone S2b consisted of a mosaic of associations with floristic composition essentially similar to those occupying the south swamp area of Lake Wanum at the present day.

Zone S3: 2700 BP to present (1030-640 cm)

In this most recent pollen assemblage zone the organic sedimentation rate, although fluctuating, declines to values intermediate between those of zone S2b and of the lower zones. Herbaceous swamp PDR also shows a decline to values between 5 000 and 20 000 grains $cm^{-2}$ $yr^{-1}$.

By far the most abundant taxon throughout the zone is *Nephrolepis*. A considerable decline in the PDR of *Hypolytrum nemorum* T. is seen, but the sedge remains consistently represented. *Stenochlaena palustris* spores also occur in all samples although less abundantly than in zone S2b. *Microsorium* T. is represented throughout and shows a relative increase in abundance over the previous zone. Pollen of *Nepenthes* and *Uncaria* T. is found in a number of samples. Cyperaceae pollen of classes A1 and B1 become more frequent towards the top of the zone, as does that of *Typha* and of the two smallest size classes of Gramineae. Isolated grains of *Nymphoides, Nelumbo nucifera* and *Dysophylla* T. also occur.

There is close correlation between the proportions of major taxa represented in zone S3 and two contemporary assemblages associated with floating root-mat vegetation. Sample SQ 35 exhibits a very high proportion of *Nephrolepis* spores and a substantial number of *Microsorium* T. Sub-fossil spectra with a higher ratio of *Hypolytrum nemorum* T. to *Nephrolepis* resemble more closely the surficial sample from short core LWMC 3. This assemblage also contains a variety of other sedge and smaller grass pollen classes as do the later samples of zone S3.

It is therefore suggested that the dominant vegetation type throughout zone S3 has been a well developed floating root-mat vegetation of floristic composition similar to that of the

'Group A' association (Chapter 5). Pollen indicative of *Leersia hexandra* mat, various sedges and *Nymphoides indica* completes the parallel between the pollen spectra of this zone and those from the mosaic of largely floating vegetation seen in the north-east bay of Lake Wanum at the present day.

*Constraints on the use of contemporary assemblages*

Comparison of contemporary herbaceous swamp pollen spectra with sub-fossil assemblages is shown to be an effective means for reconstruction of past vegetation associations. In cases where the zonal pollen assemblages do not resemble closely any modern pollen spectrum (zones S1a, S1b) it is possible that they represent vegetation associations not extant today.

Most sub-fossil assemblages do however resemble one or more contemporary spectra to some extent, and the lack of exact correlation is probably due to other factors. Most core samples integrate several years' pollen deposition. In the more slowly accumulating sediments they may represent 15 years or more, during which time the local vegetation may have changed.

Comparisons between assemblages from different areas may be misleading. The south swamp of Lake Wanum is a large area of fairly uniform water depth whereas at the margin of the north-east bay water depth increases sharply offshore. In the latter situation one might expect a closer juxtaposition of vegetation associations characteristic of different water depths. Thus assemblages might incorporate pollen and spores from a wider selection of taxa.

## *THE DEVELOPMENT OF SWAMP VEGETATION IN THE NORTH-EAST BAY OF LAKE WANUM*

The pollen record of the last 9500 years can be interpreted largely by analogy with the present herbaceous swamp associations of the Lake Wanum area.

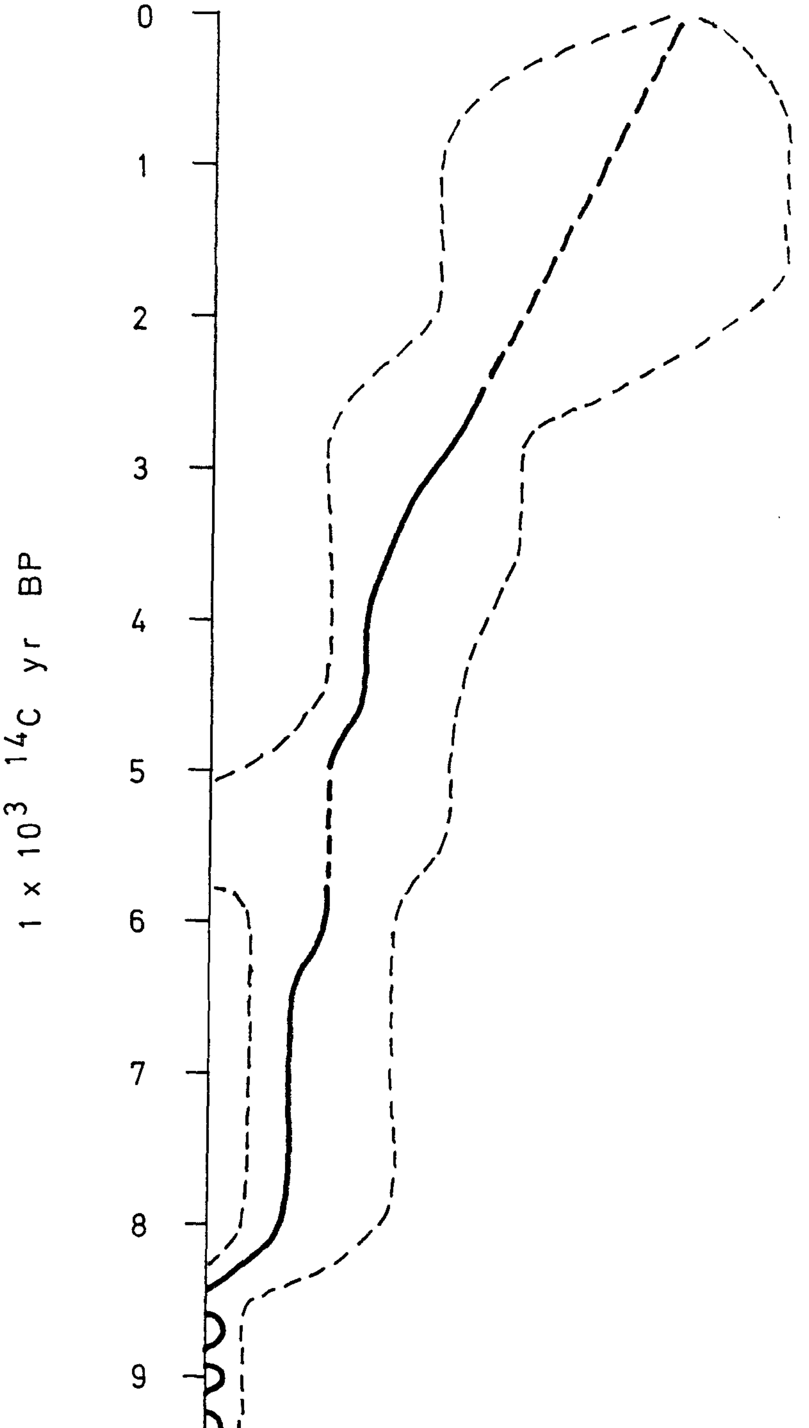
The oldest period of 1300 years (zone S1a) is thought to represent periodically inundated or marginal swamp conditions. A change to a permanent, though shallow water, swamp environment takes place at around 8200 BP at the onset of zone S1b. This vegetation, probably dominated by rooted *Hypolytrum nemorum* association persisted for approximately 2500 years. A subsequent period of up to 750 years (zone S2a) records very low PDR figures coincident with high influx rates of inorganic sediment.

From 5000 BP, the beginning of zone S2b, the herbaceous swamp flora appears to diversify. There is suggestion of both rooted and open water vegetation associations. With the increase in the PDR of *Nephrolepis* spores, free-floating root-mat vegetation appears important for the first time. Conditions during this zone may resemble the swamp vegetation mosaic of the Lake Wanum south swamp today.

At some time between 3000 and 2000 BP the vegetation becomes dominated by the floating root-mat vegetation characteristic of the latter part of zone S3, an association essentially similar with that found at the coring site today. *Leersia hexandra* root-mat may have become somewhat more abundant in the most recent millennium.

The preceding synopsis suggests an increase in the absolute water level and a general trend to increased effective water depth at the core site during the past 9500 years. This

*FIGURE 8.4. Schematic Holocene water depth record for the site of core LW II*



conclusion is in agreement with the stratigraphic record of relatively shallow water swamp deposits rather than deeper water limnic sediments.

### *A WATER LEVEL RECORD FOR LAKE WANUM*

Knowledge of the ecology of the contemporary herbaceous swamp vegetation allows tentative reconstruction of a more detailed water depth record. This interpretation relies both on the records of individual taxa possessing known water depth tolerances, and on analogy between the habitat of modern vegetation associations and those reconstructed from the palynological record. Several important assumptions are thus implicit:

( i) that water depth tolerances for both individual taxa and vegetation associations have remained constant throughout the Holocene,

( ii) that all ancient swamp vegetation associations are broadly analogous with the extant associations surveyed and

(iii) that the area of vegetation reflected in each sediment pollen assemblage is largely known.

The water depth ranges for species and associations have probably remained constant. Although the vegetation of zones Sla and Slb cannot be equated directly with any contemporary association, it is considered broadly similar to an existing herbaceous swamp association. The area contributing to sub-fossil pollen assemblages is almost certainly influenced by inconstant factors such as local bathymetry and vegetation structure.

A schematic construction of trends in the effective water depth at the site of core LW II is shown in Fig. 8.4. The central curve represents the proposed path of general water depth during the

Holocene. The broader limits indicate the maximum and minimum water depths considered probable, assuming most sub-fossil assemblages to reflect the vegetation in the close vicinity (perhaps less than 10 m) of the coring site.

From 9500 to 8500 BP a fluctuating water level with a maximum depth of 20 cm to 30 cm is suggested. Standing water is indicated by *Nelumbo nucifera* pollen but may have been intermittent, becoming permanent only after 8500 BP when pollen of the aquatic herb *Dysophylla verticillata* is abundant. From 8200 BP to about 5750 BP (zone S1b) the swamp vegetation is thought to consist at least in part of a rooted *Hypolytrum nemorum* association. By inference, the water depth remained fairly constant at 1.0 m to 1.5 m during this period. The decline in the PDR of *Stenochlaena palustris* spores could be interpreted as a retreat of the swamp margin perhaps due to increasing water depth.

Any changes in water depth during the 750 years of zone S2a remain enigmatic. By the start of zone S2b (5000 BP) the water was probably 1.5 m to 2.0 m deep, although the suggested coexistence of rooted and floating vegetation communities makes accurate assessment difficult. A further increase to a depth of 3.0 m to 3.5 m by 2700 BP is indicated by the predominance of floating root-mat vegetation. This rise may have started at around 4000 BP, or may have taken place more rapidly at a later date. With the onset, in zone S3, of floating vegetation insensitive to rising water level the assessment of effective depth becomes impossible. It is virtually certain that the water depth has not fallen below 3.5 m to 4.0 m during the last 2500 years. A steady rise to the present depth of 6.25 m is assumed for this period. However the current water depth may have been achieved or even exceeded earlier in zone S3.

The trend of water level at the site of core LW II over the Holocene shows a general rise in excess of that accountable solely due to infilling of the lake basin. The greater part of the increase in water level and effective water depth has taken place during the past 5000 years. No prolonged decline in water level is apparently recorded although minor fluctuations of short periodicity, such as shown by the present lake level, may also have occurred in the past.

### *Absolute rise in lake level*

Whilst the effective water depth curve (Fig. 8.4) appears valid for the western margin of the north-east bay, trends may have differed in other areas of lake.

The absolute lake surface level relative to the 1974 datum may be calculated for any date by subtracting the estimated effective water depth at site LW II (Fig. 8.4) from the radiocarbon age/depth curve of Fig. 3.10a. This procedure takes no account of any post-deposition compaction of the sediments. Using the absolute lake surface level calculated in this way, some estimates of effective water depth at the site of core LW I can be derived. At 2070 BP the lake level lay perhaps 5 m below the 1974 datum, when the sediment/water interface was 9.3 m below datum at LW II, and 12.3 m at LW I. The effective water depth at LW I was thus at least 3 m, and probably closer to 8 m. The present effective depth at LW I is 2 m, and at LW II 6.25 m. There thus appears to have been a decrease in water depth at the site of LW I over the past 2000 years in contrast to the trend seen at LW II. However, lack of a comprehensive series of radiocarbon dates from core LW I precludes the construction of a comparable effective water depth curve.

## *HERBACEOUS SWAMP VEGETATION AND ORGANIC ACCUMULATION*

The greater proportion of the organic sediment in marginal areas appears to be detritus derived from aquatic macrophytes. Water depth is shown to be the major control on the distribution of this herbaceous swamp vegetation. It may be hypothesised that water depth, through its effect on vegetation, influences organic deposition. Comparison of the effective water depth curve (Fig. 8.4) with the organic sediment accumulation rate (Fig. 8.1) may therefore be instructive.

In a periodically inundated or static shallow water swamp environment (zones S1a and S1b) little organic detritus accumulates. When a rise in water level occurs only those rooted associations that can accommodate the increased water depth by virtue of fast detrital sediment accumulation can persist. This could be the case for the *Hypolytrum nemorum* association in zones S2a and S2b. If the water level increases dramatically, rooted vegetation is excluded, and only free floating root-mat associations can continue to occupy the area. This process may have taken place within zone S3. Floating root-mat vegetation, due to its relative stability and insular distribution, possibly contributes less organic detritus to the sediment surface.

## *EVIDENCE FOR CHANGES IN DRY-LAND VEGETATION AT LAKE WANUM*

The pollen analytical record of dry-land vegetation is much more fragmentary than that available for the herbaceous swamp. In most samples from core LW II, dry-land taxa constitute only a small proportion of the total pollen and spore count. Even so, the number of different dry-land taxa encountered frequently exceeds that of swamp taxa. With many taxa poorly represented, it becomes difficult to recognise statistically significant variations in pollen frequencies. In addition, the identity of many dry-land pollen and spore types is uncertain, and data on their ecological status limited (see Table II.1).

Due to this paucity of data the pollen record of dry-land vegetation requires circumspect interpretation. Comparison of subfossil assemblages with contemporary spectra is found to be of limited interpretative use. Nevertheless changes are recognised in the pollen records of a number of taxa that appear to possess ecological significance. Estimated PDR for selected taxa from various ecologically defined groups are plotted against age in Fig. 8.5.

*The palynological record of dry-land taxa*

*Non-forest pollen:* Although grasses are represented throughout the sequence, few Gramineae grains attributable to dry-land species are present prior to 6300 BP, and do not become abundant until 5100 BP. Patterned grass grains larger than 30 µm (Gramineae 5), perhaps deriving from *Themeda australis*, first occur at about 6800 BP, and are consistently represented only in the sediments of the last 3000 years.

Few other dry-land taxa show continuous representation throughout the sequence. *Trema* pollen is first recorded at about 8050 BP but is best represented subsequent to 5350 BP. The highest PDR values (up to 350 grains $cm^{-2}$ $yr^{-1}$) are achieved between 5100 BP and 4500 BP, and from 2000 BP to the present.

Similar trends are apparent for *Macaranga* pollen. Although present from almost the base of the core, the PDR increases sharply between 6700 BP and 6200 BP and after 5350 BP. Maximum PDR estimates for *Macaranga* reach 750 grains $cm^{-2}$ $yr^{-1}$.

*FIGURE 8.5. Lake Wanum core LW II: PDR of selected dry land pollen and spore taxa*

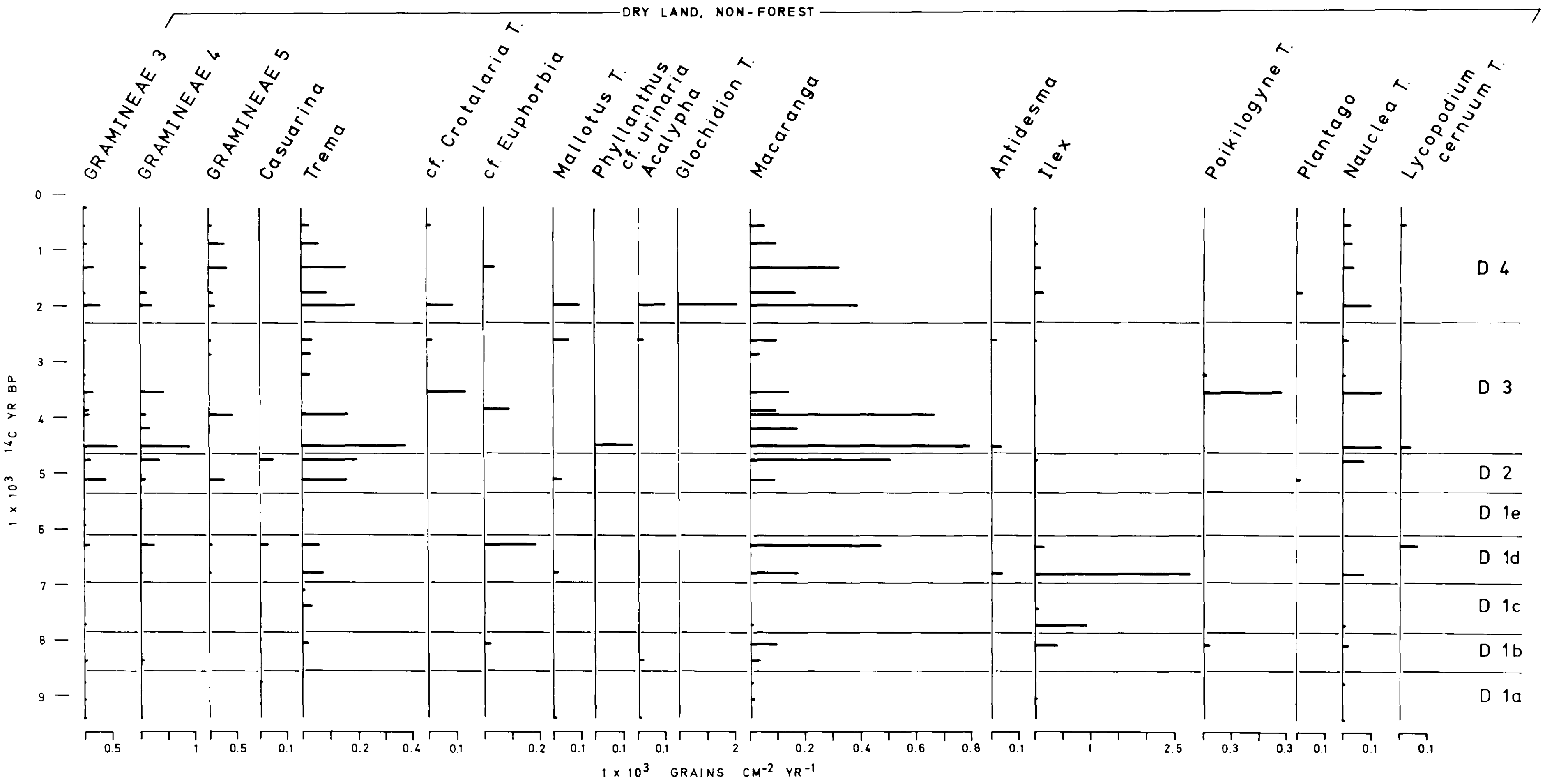


*FIGURE 8.5 (Cont.). Lake Wanum core LW II: PDR of selected dry land pollen and spore taxa*

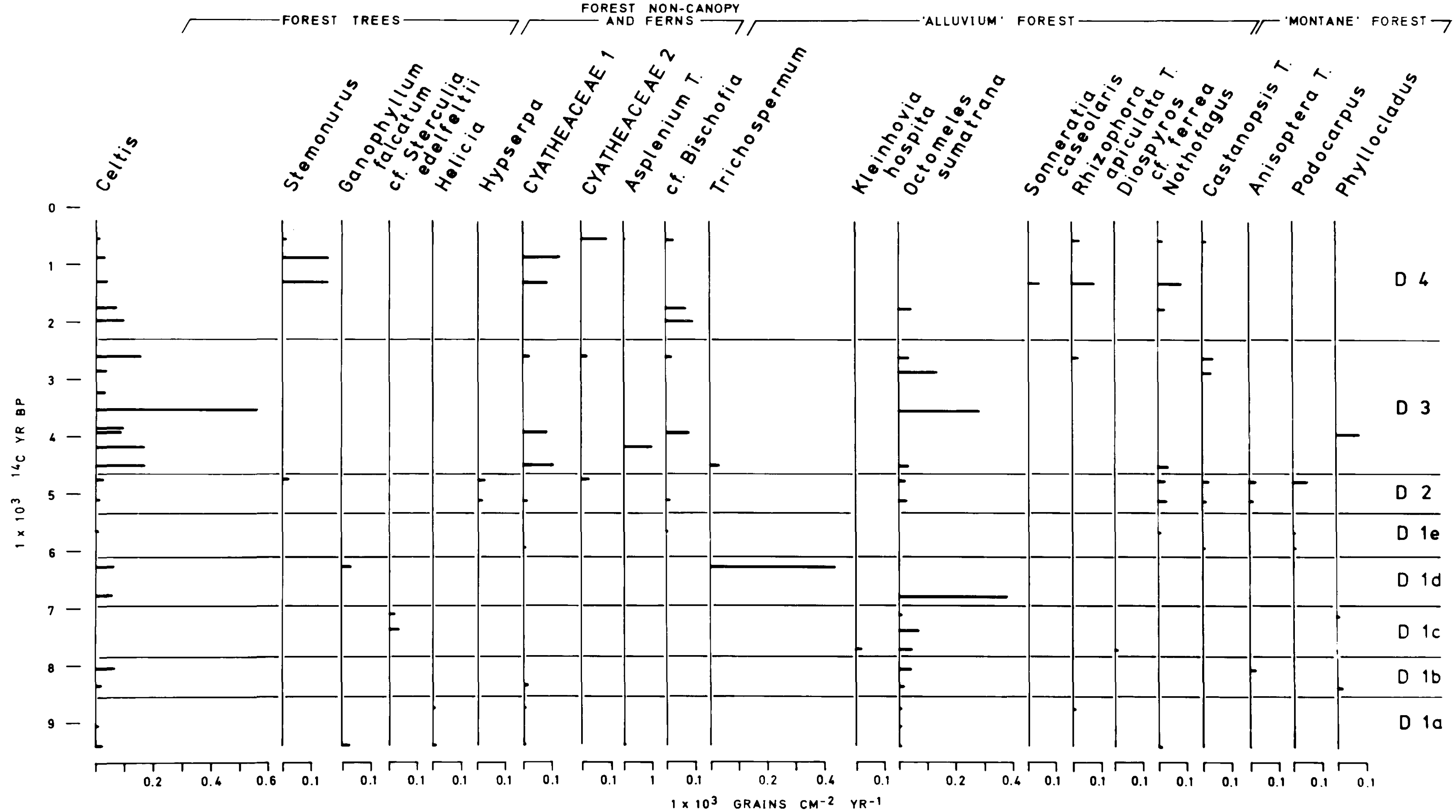
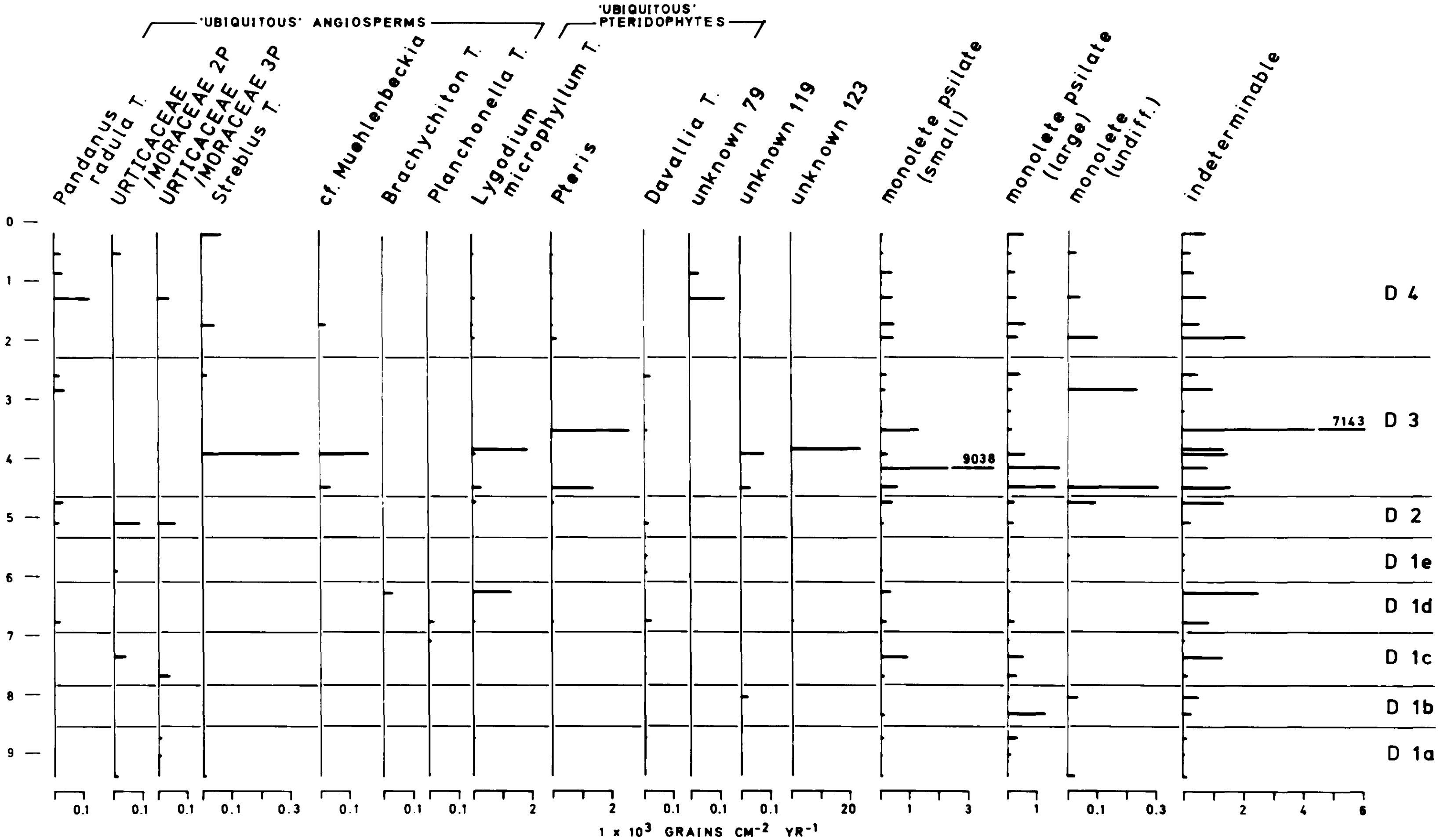


FIGURE 8.5 (Cont.). Lake Wanum core LW II: PDR of selected dry land pollen and spore taxa



*Nauclea* T. pollen is intermittently represented throughout the core, with highest PDR values being found between 5350 BP and 1800 BP.

Many dry-land forest taxa occur in the pollen record only occasionally, and in small quantity. Although *Mallotus* T. and *Acalypha* are present throughout the core they show an increased PDR around 3000 BP to 2000 BP. Pollen of cf. *Crotalaria* T. occurs first at about 3600 BP. Several representatives of woody shrub or herb taxa, *Phyllanthus* cf. *urinaria, Glochidion* T. and *Poikilogyne* T., show isolated but high peaks in PDR since 4700 BP.

The pollen record of *Ilex* contrasts with the trend shown by most non-forest taxa. This taxon reaches very large PDR values, up to 2 700 grains $cm^{-2}$ $yr^{-1}$, between 8050 and 6250 BP. It is almost unrepresented from this date until 2600 BP when it reappears, although with much lesser abundance.

*Forest trees:* *Celtis* is the only commonly occurring pollen taxon in the category and is present throughout most of the core. Small peaks in abundance are seen around 8500 BP to 8100 BP and 6800 BP to 6250 BP, whilst a major increase in PDR occurs between 4600 BP and 3500 BP. From about 2700 BP the PDR of *Celtis* declines constantly.

Only minor occurrences of other tree taxa in this category are found. *Ganophyllum falcatum,* cf. *Sterculia edelfeltii* and *Olea* pollen occur in the lower sections of the core whilst *Spiraeopsis* T. and *Stemonurus* are found in the sediments of the last 1500 years.

*Non-canopy forest pollen, and forest ferns:* Both categories are poorly represented in the pollen record from core LW II. *Helicia* occurs sparsely prior to 8750 BP. Myrtaceae pollen is found intermittently throughout the sequence with a slight increase in PDR around 4600 BP to 4000 BP. Other taxa, *Hypserpa,* Cyatheaceae and *Asplenium* T. appear more common since 5350 BP.

*'Alluvium' forest:* *Octomeles sumatrana* is the most abundant taxon in this ecological category, and occurs throughout the core. The tree is consistently represented during the oldest 3000 years of the sequence, its PDR increasing to a peak of nearly 4 000 grains $cm^{-2}$ $yr^{-1}$ around 6800 BP. *Kleinhovia hospita* and *Diospyros* cf. *ferrea* occur at about 7800 BP, and a large peak in the PDR of *Trichospermum* is seen at 6300 BP. Pollen of cf. *Bischofia* is more abundant between 5700 BP and 1500 BP, whilst most occurrences of *Rhizophora apiculata* T. pollen are recorded in the last 3000 years of the core.

*'Montane' forest:* *Nothofagus* and *Castanopsis* T. show the greatest occurrence, other taxa, *Podocarpus, Phyllocladus, Elaeocarpus* T., *Anisoptera* T. and cf. *Engelhardia* being found only very infrequently. Although the ecological category appears better represented subsequent to 5100 BP, this may be an artefact of the faster deposition rate as no more than two grains of a single taxon are found in any sample.

*Ubiquitous pollen and spores:* A few taxa whose ecological status is unclear show consistent trends of possible significance. *Pandanus radula* T. pollen occurs sparsely since 7000 BP and appears more common in the last 1300 years. Undifferentiated Urticaceae/ Moraceae pollen are more abundant prior to 5000 BP, whereas *Streblus* T. largely occurs subsequent to 4600 BP as does cf. *Muehlenbeckia*. Sparse representation of *Brachychiton* T. and *Planchonella* T., possibly from 'alluvium' forest trees, occurs around 7000 BP.

Spores of *Lygodium microphyllum* T. are found throughout the sequence with very high PDR values in samples around 6300 BP and 3900 BP. *Pteris* spores also show very high PDR from 4600 BP until 3500 BP and are also frequent in the sediments of the last 2000 years.

The majority of monolete psilate spores undoubtedly derive from ferns of the herbaceous swamp vegetation, in particular from *Nephrolepis hirsutula* and *Microsorium*. Their PDR closely reflects that of the swamp ferns.

### *Dry-land pollen assemblage zones*

The pollen record of dry-land taxa is divided into assemblage zones largely on the basis of changes in the most abundant ecological category, that of non-forest pollen. The representation of other ecologically defined groups is too low to allow separate zonation.

### Zone D1: 9500-5350 BP (1970-1670 cm)

Pollen representative of 'alluvium' forest is present from the base of the core until about 6100 BP. *Octomeles sumatrana* predominates, although *Kleinhovia hospita* and *Diospyros* cf. *ferrea* are also recorded. The presence of *Brachychiton* T. and *Planchonella* T. grains around 7000 BP to 6100 BP could also be associated with 'alluvium' or riparian forest, as might *Antidesma*. The PDR of *O. sumatrana* increases to a peak at 6800 BP but the taxon is absent from the remainder of the zone. A subsequent peak in *Trichospermum* pollen is seen but 'alluvium' forest taxa are generally unrepresented between 6100 and 5350 BP.

Zone D1 may be subdivided on the basis of the representation of various non-forest taxa. Two phases of increased PDR for this ecological category are recorded. The first, zone D1b, occurs between 8550 and 7850 BP (1920 cm to 1880 cm). During this episode, PDR values for *Macaranga* increase substantially and *Trema* pollen first appears in the sequence. There is also a slight increase in the representation of grass pollen, although not in the Gramineae 5 class. Several possible pollen indicators of herbs and shrubs are recorded, including cf. *Euphorbia, Acalypha* and *Poikilogyne* T.

The second episode, zone D1d (6940 to 6100 BP, 1820 cm to 1760 cm), is similar in character. Increases in the PDR of the non-forest taxa are even more marked. *Trema* and, in particular, *Macaranga* pollen show dramatic increase, and Gramineae class 5 pollen occurs for the first time. An increase in the PDR of other dry-land grass pollen classes is seen. *Casuarina,* cf. *Euphorbia, Mallotus* T. and *Lygodium microphyllum* T., possibly a component of the dry-land non-forest vegetation, are also encountered.

The pollen records of two well represented non-forest trees, *Nauclea* T. and *Ilex* do not follow this pattern of episodic increase. The very high PDR of *Ilex* between 8050 BP and 6250 BP is likely to be derived locally, possibly from *Ilex arnhemensis*.

This shrubby tree occurs today in grassland bordering Redhill swamp and its pollen is abundant in contemporary assemblage SS 23 from the site. *Nauclea* T. is present from the base of the sequence until about 6700 BP. A larger number of ecologically diverse genera of the sub-family Naucleae contribute to the *Nauclea* T. pollen taxon (Table II.1). *Nauclea orientalis* is commonly found in riparian or lake marginal situations in the Lake Wanum vicinity.

With the exception of the mentioned 'alluvium' forest taxa the PDR of forest pollen is very low during zone Dl. *Celtis* is the most abundant taxon represented throughout the period. During both zones Dlb and Dld the representation of *Celtis* pollen increases synchronously with the non-forest pollen taxa.

The three zones not dominated by pollen of non-forest taxa, although difficult to characterise by their pollen assemblages, include a number of forest taxa. In zone Dla (9500 BP to 8550 BP, 1970 cm to 1920 cm) the forest tree taxa *Ganophyllum falcatum* and *Olea* occur, with various vines and understorey taxa; *Calamus, Helicia,* Cyatheaceae and *Asplenium* T. A proportion of the undifferentiated Urticaceae/Moraceae pollen may also derive from forest species. Zone Dlc (7850 BP to 6950 BP, 1880 cm to 1820 cm) records pollen of cf. *Sterculia edelfeltii,* Myrtaceae and Urticaceae/Moraceae.

Very low PDR estimates are shown for zone Dle (6100 BP to 5350 BP, 1760 cm to 1670 cm). An assemblage of non-forest and forest taxa is seen, including Gramineae, *Trema, Antidesma, Celtis,* Cyatheaceae, cf. *Bischofia* and Urticaceae/Moraceae.

Zone D2: 5350-4650 BP (1670-1510 cm)

During this period the pollen assemblage is dominated by a few non-forest taxa. Substantial increases are seen in the PDR of the grasses, *Trema,* and *Macaranga*. *Casuarina, Mallotus* T., *Plantago* and *Nauclea* T. are also present. The PDR of forest pollen is low, although *Celtis* is found. 'Alluvium' forest is represented by pollen of *Octomeles sumatrana* and cf. *Bischofia*.

Zone D3: 4650-2300 BP (1510-960 cm)

Although PDR values for the major non-forest taxa remain as high or higher than for zone D2 during the first 1000 years of zone D3, a declining trend is evident. Notable is the representation of some forest taxa. The PDR of *Celtis* increases to the highest figures seen in the core (nearly 600 grains $cm^{-2}$ $yr^{-1}$). Myrtaceae pollen, possibly from subcanopy trees, increases in representation as do the forest ferns Cyatheaceae and *Asplenium* T. Of the ecologically 'ubiquitous' taxa *Streblus* T., cf. *Muehlenbeckia*, *Lygodium microphyllum* T. and *Pteris* also show peaks in occurrence during this period.

From about 3600 BP, the PDR of most taxa decline, although that of *Celtis* less so than the non-forest representatives. In contrast, *Octomeles sumatrana*, present throughout the zone, records a large increase in PDR.

Zone D4: 2300 BP to Present (960-640 cm)

A renewed increase in the PDR of many non-forest taxa begins by 2000 BP. Although rates for individual pollen types are generally slightly less than for zone D2 and the lower part of zone D3, a larger number of taxa show increased representation. Grass pollen, especially Gramineae 5, *Trema* and *Macaranga* record the greatest increase in PDR. Pollen characteristic of herbs and shrubs, cf. *Crotalaria* T., cf. *Euphorbia, Euphorbia hirta* T., *Plantago* and *Acalypha*, is well represented in the zone. A large peak of *Glochidion* T. pollen occurs in the initial sample of the zone at about 2000 BP. *Nauclea* T. shows a fairly constant PDR throughout the period.

Of the forest pollen taxa, *Celtis* is present at the base of the zone, but its PDR subsequently declines sharply. *Stemonurus* is abundant between 1500 BP and 600 BP and Myrtaceae pollen and spores of Cyatheaceae also occur in the zone.

*Octomeles sumatrana* is not well represented after 1750 BP although there are isolated occurrences of the predominantly mangrove taxa, *Sonneratia caseolaris* and *Rhizophora apiculata* T.

Ecologically 'ubiquitous' taxa represented include *Pandanus radula* T., *Streblus* T., and spores of *Pteris* and *Lygodium microphyllum* T.

The inferred age of the uppermost sample analysed from core LW II is 225 BP. However there appears to be little significant difference between this pollen assemblage, and one from the surficial sediments of the nearby short-core, LWMC 3. Comparison of relative pollen frequencies for both samples shows a slight increase in Gramineae and *Macaranga* pollen in the more recent sediment. The proportions of *Trema* and *Celtis* are similar in both samples although those of *Octomeles sumatrana* and Urticaceae/ Moraceae are greater in the contemporary assemblage. However no major changes are reflected in the pollen record of the last 250 years.

## *DRY-LAND VEGETATION CHANGE IN THE LAKE WANUM VICINITY*

The pollen evidence comprises the combined records of individual taxa that are frequently ambiguous or obscure. Despite these limitations, clear trends are shown in the dry-land taxa pollen diagrams. These trends may be tentatively interpolated to produce a fragmentary picture of changes in the ecology of nearby dry-land vegetation.

Most of the pollen and spore taxa recorded from the core can be found in contemporary assemblages from the near vicinity of the lake. Conversely, none of the modern assemblages from higher altitudes (180 m to 1 000 m) show any close counterpart in the sub-fossil record. Small quantities of 'montane' forest tree pollen, in particular *Nothofagus*, *Phyllocladus* and *Podocarpus*, are recorded throughout the core. However, pollen of these taxa is seen to be efficiently transported into contemporary low altitude spectra, and there is no suggestion that these genera were formerly more abundant in the vicinity than today.

'Alluvium' or riparian forest, characterised chiefly by *Octomeles sumatrana* pollen appears better represented in the early Holocene, prior to about 6500 BP. The high PDR values for *Ilex* between 8050 BP and 6250 BP are interpreted as possibly indicative of woody swamp-marginal vegetation. Subsequently, the pollen representation of both taxa declines considerably although *O. sumatrana* reappears after 5350 BP and again achieves a high PDR between 3700 BP and 2700 BP. It is interesting to compare the representation of these two taxa with the reconstructed swamp vegetation communities and the water depth curve for the LW II site (Fig. 8.4). Although both taxa occur during the initial 1300 years of the sequence (swamp zone S1a), an increase in relative frequency and PDR is seen between 8200 BP and 6250 BP, in the initial phase of zone S1b. The rise in water level postulated for about 8200 BP may have led to the increased importance of 'alluvium' forest and *Ilex* within the vicinity. As suggested previously, high PDR values for *Stenochlaena palustris* spores at this time could possibly have been associated with 'alluvium' or riparian forest rather than with herbaceous swamp vegetation. Further rise in water level, such as may have occurred at about 6500 BP, could explain the apparent recession of 'alluvium' forest and swamp marginal vegetation from the immediate vicinity of the coring site.

Whilst this hypothesis may explain the sequence of development during the first 3000 years of the swamp's history, it does not adequately account for increased representation of *Octomeles sumatrana* later in the core, at a time of postulated deeper water conditions.

The most evident trend in the dry-land pollen sequence is the increasing representation in the later Holocene of certain non-forest taxa. The most abundant of these are the grasses, and the tree genera *Trema* and *Macaranga*. Also showing the same pattern are other woody and herbaceous taxa, including various Euphorbiaceae, cf. *Crotalaria* T. and *Poikilogyne* T. Many of these pollen taxa can be identified with light-demanding species of forest regeneration or grassland communities. In Papua New Guinea highland pollen records *Trema* and *Macaranga* in particular often appear to be associated with human induced forest disturbance or clearance (Powell *et al.*, 1975, Walker and Flenley, in press) and Morley (1976) postulates a similar association for lowland sites in Malesia. Although circumstantial, several lines of evidence suggest human disturbance to be the primary cause of the expansion of non-forest vegetation in the Lake Wanum area also.

The relationship between pollen of the forest tree genus *Celtis* and that of the non-forest taxa is of especial interest. During zone D1b, increase in the PDR of the non-forest taxa is matched by similar increase in the PDR of *Celtis*. In zone D1d *Celtis* pollen shows an increased PDR, but it is much less than the increase in the selected 'disturbance' taxa, particularly *Macaranga*.

The onset of zone D2 at 5350 BP sees a large increase in the PDR of non-forest pollen. During this period *Celtis* registers only a very slight increase in PDR. Much higher values for *Celtis* pollen are seen in the initial part of the succeeding zone (D3) in association with similarly high PDR of Gramineae, *Macaranga*, and to a lesser extent *Trema*. Although the PDR of most taxa decline in the latter part of the zone, the decrease in *Celtis* is less marked. The tree pollen thus becomes proportionally more abundant during this time, accounting for up to 15% of the dry-land pollen sum.

The most recent 2300 years (zone D4) sees a renewed increase in the PDR of grasses, *Trema, Macaranga,* and a number of other non-forest pollen taxa. The PDR values for *Celtis*, however, decline during this zone. The taxon represents only 1.5% of the dry-land pollen seen in the surficial sediment from core LWMC 3. *Celtis* pollen is absent from PT 5, the closest trap to the coring site, even though it dominates the count from PT 4, in forest to the east of Lake Wanum.

The pollen record thus appears to suggest that *Celtis* is promoted during the initial two 'disturbance' phases, prior to 5350 BP. After this date, however, the *Celtis* PDR is inversely correlated with that of the major non-forest taxa. It is possible that the apparent synchroneity in the lower sediments is due only to the averaging effect of the slower sedimentation rate.

The second major change seen in succeeding 'disturbance' zones is in the representation of pollen thought to derive from dry-land grass species. The PDR values for such grass pollen are very low in zone Dlb, and only slightly higher in zone Dld. The latter zone sees the first occurrence of Gramineae class 5 grains, some of which may be associated with the main grassland species today, *Themeda australis*. The grass PDR tends to increase synchronously with other dry-land taxa, but Gramineae pollen becomes proportionally more important in the later zones. The representation of Gramineae 5 is significantly higher in zone D4.

Of especial interest is the close correlation between the PDR of the 'disturbance' taxa, and the estimated influx of carbonised plant fragments (Fig. 8.1). These charcoal particles are presumably produced as the result of fire in the dry-land vegetation. The first large peak in carbonised particles occurs in the lower sample of zone Dlb, and increased influx is also seen during the second 'disturbance' episode, zone Dld. The major peak in carbonised particle influx is recorded in zone D2, and the early part of zone D3, where PDR values for 'disturbance' taxa, especially *Macaranga*, are also very high. The incidence of carbonised particles is low for the latter part of zone D3, but increases, although still at a fairly low level, at the start of zone D4. The charcoal particles are assigned to three size classes, each showing a generally similar pattern of representation. The largest fragments are, however, almost absent from the earliest zones, and become most abundant in the initial part of zone D3. Many of these large particles can be identified as fragments of monocotyledonous cuticle, possibly from grasses.

Thus it seems likely that the increased representation of non-forest pollen in the sequence at least partially reflects anthropogenic impact on the vegetation. The early 'disturbance' zones, prior to 5350 BP appear to favour increased representation of secondary forest trees, such as *Celtis*, and other woody taxa. It is possible that the preponderance of *Celtis* in the forest to east of Lake Wanum today reflects a history of human impact. As vegetation disturbance becomes perhaps more frequent, or intense, woody taxa such as *Trema* and *Macaranga* are favoured. This appears the case during zone D2, and the earlier part of zone D3. In zone D3, and especially from the start of zone D4 (2300 BP), a greater proportion of the pollen of dry-land grasses and of grassland herbs is found.

### *The extent of grassland and non-forest vegetation*

Some estimate of the areal extent of the vegetation contributing to the pollen assemblages is crucial in the reconstruction of past communities. This is especially true when attempting to assess the extent, and thus any extension, of the non-forest and grassland vegetation previously recognised in the pollen record.

Some insight can be gained from the comparison of PDR figures. The PDR estimates in the LW II core for total dry-land pollen and spores (including 'ubiquitous' angiosperm taxa, but not 'ubiquitous' spores as many are produced by herbaceous swamp ferns) range from 30 grains $cm^{-2}$ $yr^{-1}$ to 3 800 grains $cm^{-2}$ $yr^{-1}$. In contrast, estimated annual aerial influx rates to the three pollen traps in the Lake Wanum area for this group of taxa were 377 800 grains $cm^{-2}$ for PT 4 in disturbed forest, 98 000 grains $cm^{-2}$ for PT 4 in *Celtis* dominated forest and 240 grains $cm^{-2}$ for the floating trap, PT 6. As can be seen, PDR estimates from the sediments fall into the lower end of this range. A few values are even lower than those shown in the isolated floating trap, but in no sample do the PDR estimates for dry-land taxa approach those recorded by the two traps located within forest.

Assuming that PDR estimates from sediments may be compared with the solely aerial pollen influx of the traps, several conclusions are suggested. At no time was dry-land vegetation growing on the site of core LW II as sediment PDR values do not approach the high influx rates found in the pollen traps. However, dry-land vegetation may have been closer to the site in the past than its distance (*c.* 50 m) today. In zone D1d, D2 and the early part of zone D3, PDR values for non-forest 'disturbance' taxa are considerably higher than those for the most recent period. Pollen assemblages of these earlier zones may thus record events that are either different in character, more extensive, or closer to the coring site, than those seen in the younger sediments. None of these possibilities can be certainly excluded. Qualitative differences between succeeding zones have been shown, and the lower water level especially prior to about 3500 BP could have allowed dry-land vegetation closer to the site. It is thus not admissible to equate the increased PDR values for 'disturbance' taxa with a general extension of non-forest or grassland vegetation.

Dry-land PDR estimates in the core are, for the most part, greater than those from the centre of the north-east bay today (PT 6). The pollen assemblages of the core may therefore reflect, to some extent, more localised events. Very low PDR values for *Celtis*, a taxon with abundant sources within the lake's catchment, occur in the upper samples of the core and in all contemporary spectra but PT 4. This also suggests that the majority of the dry-land pollen contributing to the core assemblages originates in the fairly local area, certainly within several hundred metres, and possibly much less. Conversely, a small 'regional' or long-distance component, is reflected in the occurrence of pollen of taxa restricted to higher altitudes.

Further circumstantial evidence as to the extent of the 'disturbance' events may be suggested by the carbonised particle data (Fig. 8.1). It is probable that only a small proportion of the charcoal produced by a fire is aerially dispersed (Corlett, unpubl.) and that most enters the lake via slopewash (Swain, 1973). Assuming, perhaps unrealistically, that charcoal is not carried far once in the lake, the proportion of carbonised particles to pollen of 'disturbance' taxa may indicate the proximity of the fires. Thus zone D1b shows a high proportion of carbonised particles to pollen, perhaps reflecting a local event. The proportion of charcoal is lower during the later zones, especially in zone D4, perhaps indicating that the 'disturbance' events occurred further away from the coring site.

## *VEGETATION DISTURBANCE AND INORGANIC SEDIMENTATION*

The sedimentary record (Figs. 8.1 and 3.6) shows discrete phases of inorganic influx that appear restricted to the western margin of the north-east bay of Lake Wanum. As the vegetation 'disturbance' also appears predominantly local, comparison with these allochthonous horizons may be profitable.

The first inorganic deposition peak in the LW II core occurs at about 7700 BP in zone D1c, although a slight rise in deposition rate is seen towards the end of the previous 'disturbance' zone D1b. The longest sustained phase of inorganic sediment deposition is found from about 6300 BP to 5250 BP. This horizon, although apparently initiated during zone D1d, reaches its greatest influx in zone D1e, a section of the core with very low PDR values for both swamp and dry-land taxa.

The inorganic sediments of these early zones are composed of orange- or grey-brown gritty sand (*Grana arenosa*) with lesser proportion of grey clay (*Argilla steatodes*). However, the composition of the influx phases subsequent to 5000 BP is qualitatively different. Grey clay (*As*) predominates, whilst *Grana arenosa* is absent. Narrow clay bands occur within zone D3 at about 4400 BP and 3900 BP. Both are synchronous with increases in the PDR of 'disturbance' taxa. The most recent phase of sustained inorganic sediment influx occurs during zone D4. Here too the peak in clay deposition is approximately contemporaneous with increased PDR values for 'disturbance' taxa.

There is thus some circumstantial evidence to link increased pollen representation of disturbed vegetation and grassland with deposition of grey clay during the last 5000 years. Prior to this, the peaks in inorganic influx are different in nature and do not appear to be correlated with pollen or charcoal evidence for vegetation disturbance. Even in the upper part of the sequence there is no simple correlation between phases of disturbance and grey clay deposition. Zone D2 shows the highest PDR values for many 'disturbance' taxa and a large number of carbonised particles, yet lacks any influx of grey clay, although a narrow peak is shown shortly after, in zone D3.

Inorganic sedimentation is influenced to a large extent by the depositionary environment of the site. Increases in water depth and in distance from shore that have taken place particularly since 5000 BP may be the prime cause of the change in the inorganic sediments subsequent to this date.

## *THE POLLEN RECORD FROM YANAMUGI*

The 10.38 m long core YAN 2, collected from the margin of the sago swamp at Yanamugi, was selected for pollen analysis. Twenty-three samples were taken, most at intervals of 40 cm, although in some upper sections of the core the interval was increased to 80 cm.

The basal age of core YAN 2 probably lies between 1000 BP and 2000 BP. The core thus possesses a much shorter pollen record than that available from Lake Wanum. The temporal interval between samples is in the order of decades, rather than hundreds of years. The sequence therefore may thus be useful for the finer resolution of short term vegetational events.

The chronology of the sediments is not firmly established. A correlation between the relative chronologies of cores YAN 2 and YAN 1 has been suggested (Fig. 4.9b, Table 4.4) but this is not sufficiently reliable to allow general calculation of annual pollen deposition rates. The pollen data for Yanamugi core YAN 2 are therefore presented as pollen concentrations for the major ecological groups (Fig. 8.6), whilst selected individual taxa are shown in Fig. 8.7 as percentages of the total pollen sum. The total pollen and spore concentration is seen to fluctuate considerably. Some of the lowest values occur between 450 cm and 600 cm, partially coinciding with the section of suggested rapid clay influx between 450 cm and 800 cm. Pollen concentrations in samples between 600 cm and 800 cm are generally higher, although some lesser values are recorded. An increase in pollen concentration is seen in the uppermost sediments, between 240 cm and 120 cm. In the lower part of the core, below 1035 cm, the inferred sedimentation rate drops substantially. This decline is not reflected by consistently higher pollen concentrations, however.

Adjustment of the pollen concentration values for the inferred sedimentation rate (Table 4.4) produces a wide range of PDR estimates. The least, 420 grains cm$^{-2}$ yr$^{-1}$ occurs in the basal sample of the core, whilst the greatest, over 44 000 grains cm$^{-2}$ yr$^{-1}$, is from the sample at 670 cm, due to the assumption of an extremely rapid sediment accumulation at this time. Many PDR values, including those from the better dated top metre of the core, occur within the range of 2 500 to 7 000 grains cm$^{-2}$ yr$^{-1}$. These values are similar to those found for the non-swamp component of many spectra in the Lake Wanum core LW II.

*The pollen record of individual taxa*

*Herbaceous swamp taxa:* The most common taxa represented are the various grass pollen classes. Few Gramineae 1, possibly indicative of *Leesia hexandra,* occur. The main swamp grass at Yanamugi today is *Phragmites karka*. Most pollen from this species falls into classes 3 and 4 (not included in the herbaceous swamp category) and into Gramineae 2. These three categories of grass pollen show an increase above about 400 cm, although all are present throughout the core.

*FIGURE 8.6. Yanamugi core YAN 2: Pollen concentration of major ecological groups, and frequency of carbonised particles*

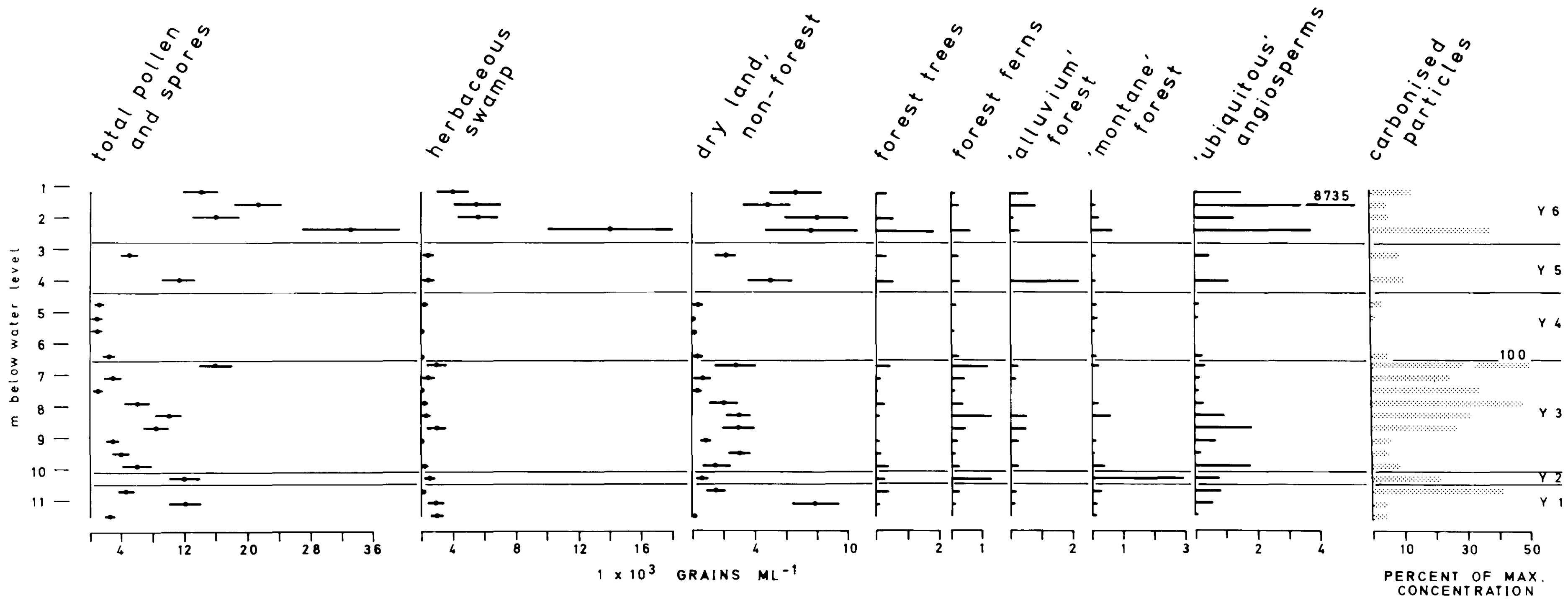


FIGURE 8.7. *Yanamugi core YAN 2: Relative frequency diagram for selected pollen and spore taxa*

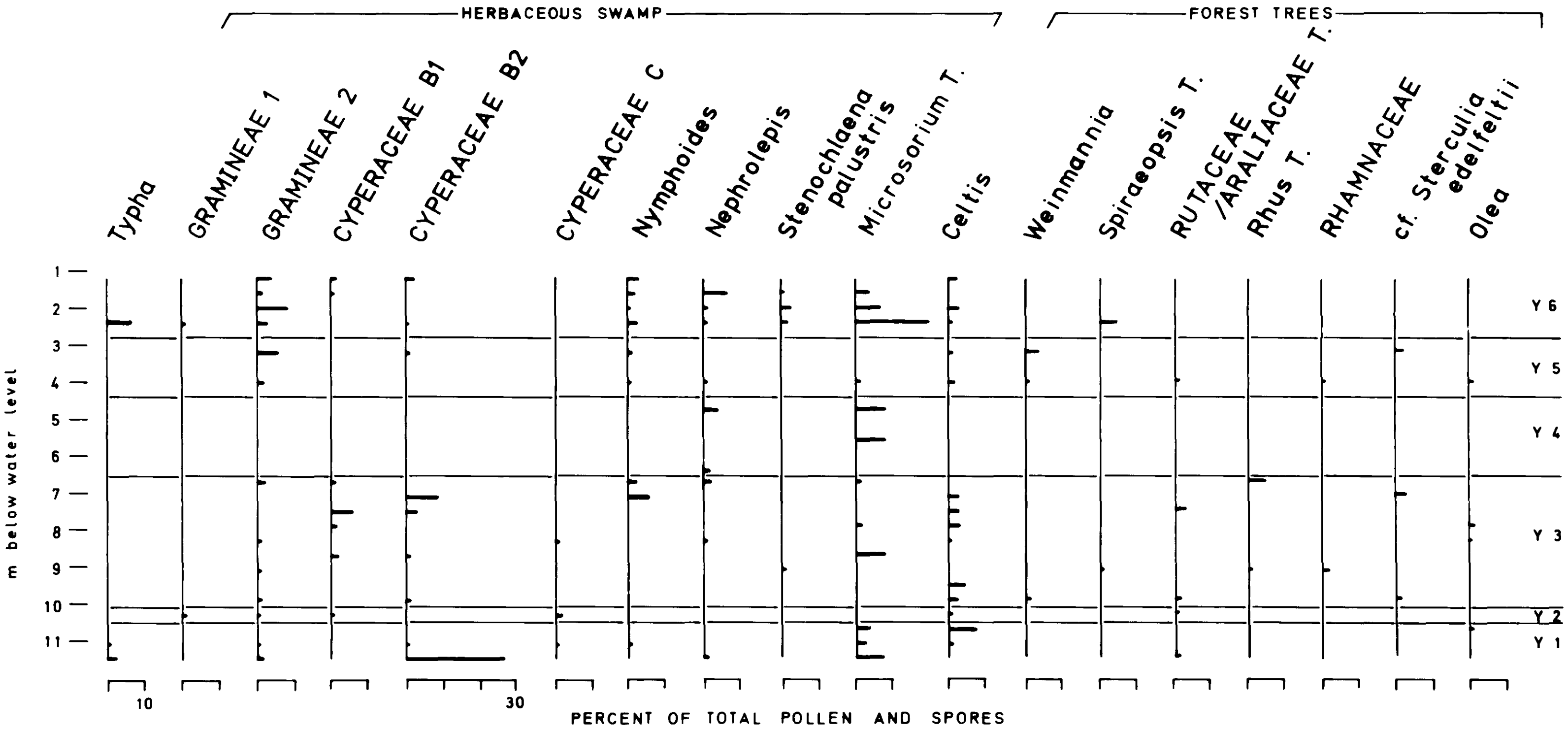


FIGURE 8.7 (Cont.). *Yanamugi core YAN 2: Relative frequency diagram for selected pollen and spore taxa*

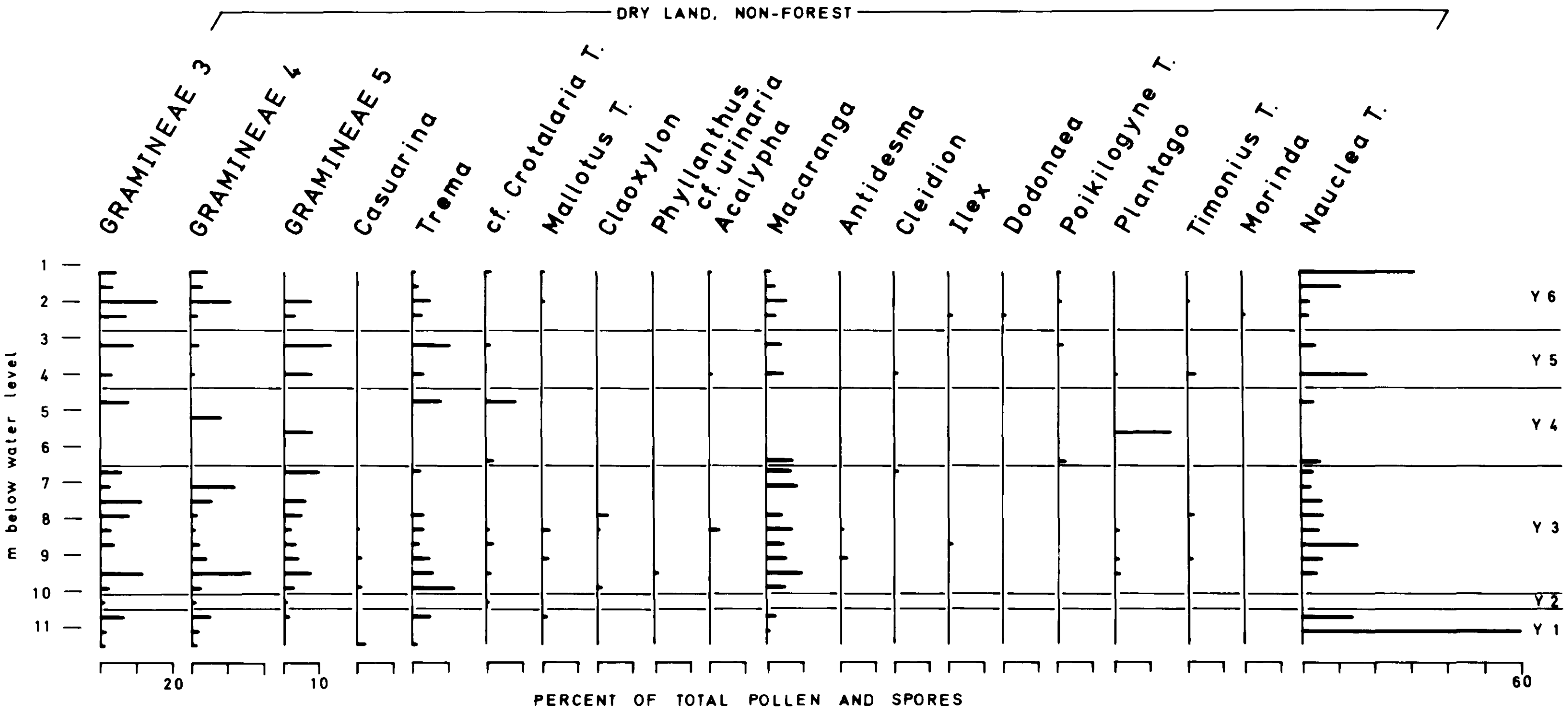


*FIGURE 8.7 (Cont.). Yanamugi core YAN 2: Relative frequency diagram for selected pollen and spore taxa*

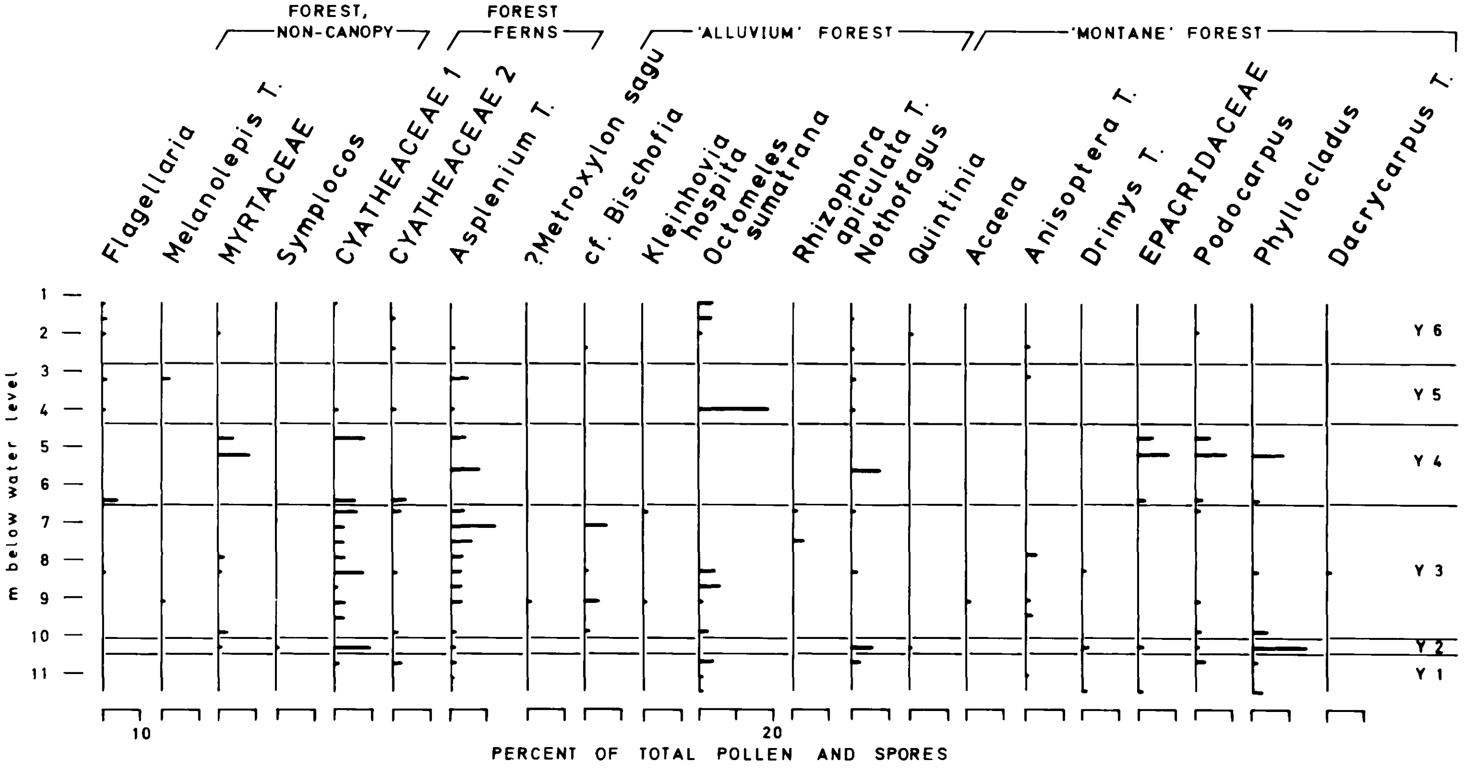
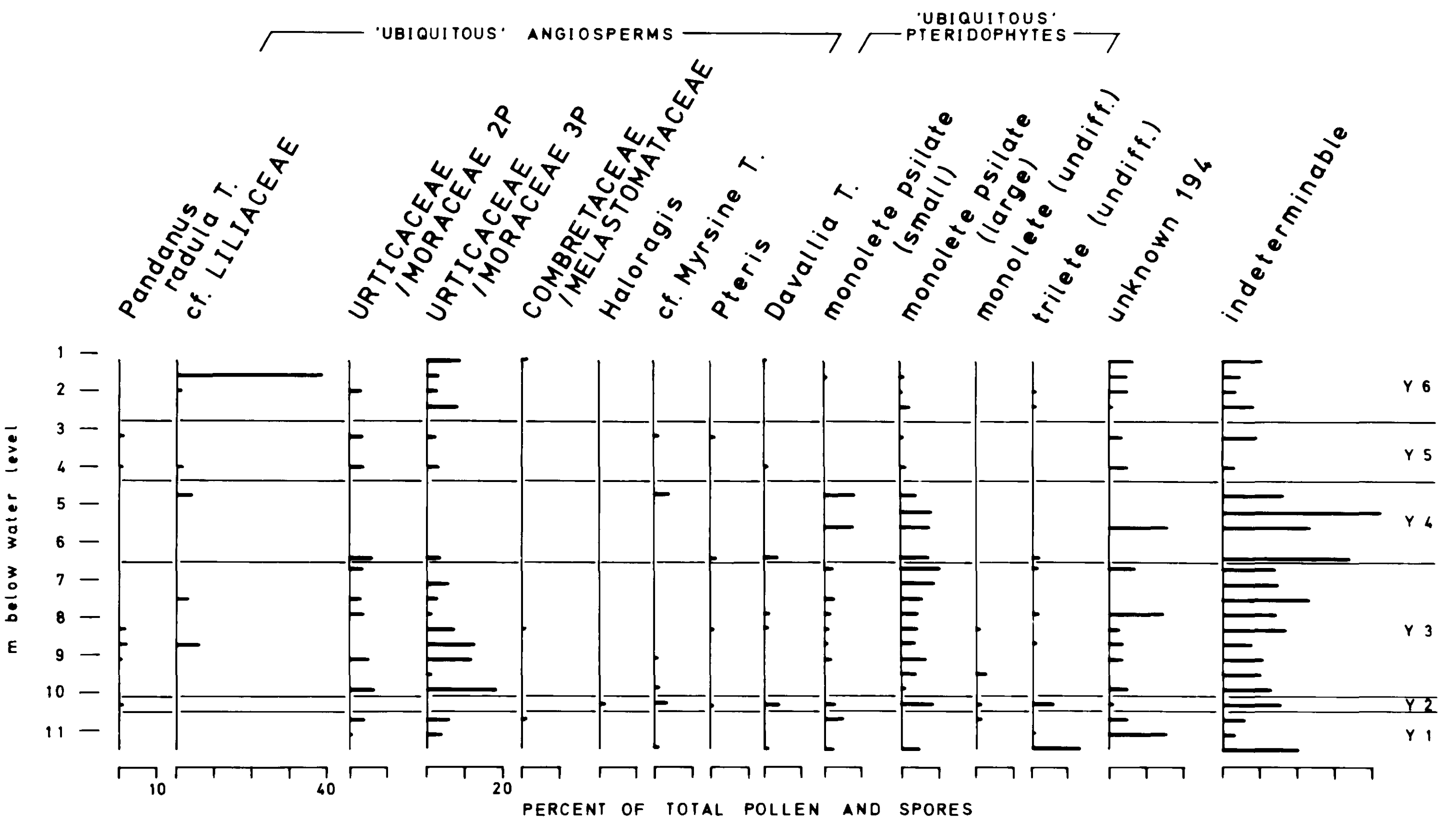


FIGURE 8.7 (Cont.). Yanamugi core YAN 2: Relative frequency diagram for selected pollen and spore taxa



Sedge pollen also occurs throughout the sequence. Cyperaceae B2 comprises a large proportion of the basal sample assemblage. It is present in lesser quantity between 700 cm to 775 cm, and above 320 cm. Pollen of Cyperaceae class Bl shows a similar distribution apart from its absence from the basal sample. Some grains attributed to Cyperaceae class C are found in the lower sediments.

*Nymphoides* pollen is the only indicator of floating leaved aquatic vegetation. Scattered occurrences are found throughout the core, but the taxon is consistently represented only in samples from 400 cm and above.

Lake marginal plants, or shallow water floating vegetation, are probably represented by the taxa *Uncaria* T., *Nephrolepis*, *Stenochlaena palustris*, and *Microsorium* T. All show increased abundance above 300 cm in the core although *Microsorium* T., *Uncaria* T., and to a lesser extent *Nephrolepis* are found throughout the sequence.

*Metroxylon sagu* is a major component of the contemporary lake marginal and swamp vegetation at Yanamugi. Only one grain tentatively attributed to the palm was found (at 910 cm).

*Dry-land, non-forest taxa:* Grass pollen is the most abundant component of this ecological category also, although as suggested above a proportion may derive from swamp species. Gramineae class 5 is less abundant below 990 cm, and is absent from the two most recent samples.

*Macaranga* and *Trema* are well represented throughout the sequence. Their occurrence follows a pattern similar to that shown by the dry-land grasses, both being less abundant below 990 cm.

Various taxa possibly representative of non-forest shrub and herb species are found although none is common. Those most frequently encountered are cf. *Crotalaria* T., *Mallotus* T., *Claoxylon, Acalypha, Poikilogyne* T. and *Timonius* T. *Casuarina* pollen occurs only below 800 cm and *Plantago* also appears more frequent in the lower part of the core.

Pollen of *Nauclea* T. is present in abundance throughout much of the core. The taxon shows greater fluctuation in representation than do the grasses, *Trema* or *Macaranga*. It forms a large proportion of the pollen sum in samples from 1160 cm, 160 cm and 120 cm. The most likely source of this pollen may be the riparian forest associated with Sina Creek, although there are many trees of Naucleae species, e.g. *Nauclea orientalis,* in the grasslands of the Markham Valley floor.

*Forest tree taxa:* *Celtis* pollen shows a pattern of representation similar to that of *Trema* and *Macaranga,* although it is proportionally slightly more abundant in the lower sediments. A number of other forest tree taxa are infrequently found. Of these, *Weinmannia* T., Rutaceae/Araliaceae, cf. *Sterculia edelfeltii* and *Olea* are the most common. The unidentified pollen taxon UK 194, present throughout the core, may also derive from a forest tree species as it dominates the contemporary pollen assemblage of the local forest.

*Non-canopy forest taxa:* Pollen of the vine *Flagellaria* is distinctly more frequent in the samples from 400 cm and above. Myrtaceae pollen occurs in small quantities throughout the sequence.

The spores of forest ferns, predominantly Cyatheaceae and *Asplenium* T. are much more abundant in the sediments below 440 cm. Both show much reduced percentages in the more recent samples and contemporary assemblages.

*'Alluvium' forest taxa:* *Octomeles sumatrana* is the most abundant taxon in this category, occurring consistently below 800 cm but also substantially represented in the sample at 400 cm. A slight increase in abundance is also seen in the most recent three samples. Pollen of cf. *Bischofia* shows a similar distribution and *Kleinhovia hospita* occurs infrequently in the lower part of the core. The presence of two grains of *Rhizophora apiculata* T. may be attributed to long-distance transport from the lower Markham Valley.

*'Montane' forest taxa:* A much larger number of 'montane' taxa are recorded in the Yanamugi sediments than at Lake Wanum. The most abundant are *Nothofagus* and *Anisoptera* T., found throughout the core, and Epacridaceae, *Phyllocladus* and *Podocarpus,* restricted, or almost so, to the sediments below 440 cm. The pollen concentration figures for the total of this ecological category remain fairly constant, with the exception of a large peak in the sample from 1030 cm.

*'Ubiquitous' angiosperm taxa:* Undifferentiated pollen of Urticaceae/ Moraceae is the most abundant taxon in this category. Diporate and triporate grains of the taxon occur throughout the core and constitute nearly 20% of the contemporary assemblage from core YANMC 1. Forest trees, such as *Pipturus,* probably contribute to the taxon, but the majority of the pollen may derive from non-forest urticaceous genera. Pollen of cf. Liliaceae is first represented at 870 cm. The taxon generally occurs in small

proportions, but accounts for nearly 45% of the pollen sum in the sample at 160 cm. It is possible that the source is a lake marginal or swamp taxon. *Pandanus radula* T. pollen is sparsely represented throughout the sequence. That of cf. *Myrsine* T. is more abundant in the lower core, especially in the sample from 1030 cm, and may be associated with the 'montane' group of taxa.

*'Ubiquitous' pteridophyte taxa:* Almost all 'ubiquitous' spore taxa are absent, or less abundant above 440 cm. The pattern of representation is thus similar to that of the forest ferns, and 'montane' forest categories. Most abundant above 440 cm are the large monolete psilate spores, possibly deriving from *Microsorium* or *Asplenium* species.

### *Pollen assemblage zones*

Zone Y1: 1150-1050 cm

In the deepest sample from core YAN 2, the pollen concentration is low, and the assemblage is dominated by herbaceous swamp taxa. Pollen of Cyperaceae class B2 possibly reflects the presence of *Eleocharis dulcis*. *Typha* pollen occurs and Gramineae 2 pollen and *Microsorium* T. spores may derive from herbaceous swamp vegetation. The high proportion of swamp pollen taxa in this sample may be associated with the band of compact organic detritus from 1152-1153 cm at the base of the core. This horizon is thought to represent redeposited detritus, possibly from lake marginal vegetation.

Swamp taxa are little represented in the two succeeding samples, the predominant pollen taxon being *Nauclea* T. Proportions of other dry-land non-forest taxa are low, although *Trema*, *Macaranga*, and various Gramineae occur. Forest trees are represented by pollen of *Celtis*, Rutaceae/Araliaceae, *Olea*, and possibly by the unidentified pollen taxon UK 194. *Octomeles sumatrana* occurs in the zone, and undifferentiated Urticaceae/ Moraceae grains are also present.

Zone Y2: 1050-1010 cm

This zone consists of a single sample (1030 cm to 1031 cm) from the proximity of the dark gritty horizon at 1032 cm to 1037 cm. The sample is uniquely characterised by the high proportion and pollen concentration of taxa assigned to the 'montane' forest category. *Phyllocladus* pollen is best represented, but pollen of *Nothofagus, Quintinia, Drimys* T., Epacridaceae and *Podocarpus* also occur. The 'ubiquitous' pollen taxa cf. *Mysine* T. and *Haloragis* present in the sample may also derive from 'montane' vegetation. Many spore taxa are also better represented in this zone. A rise in the proportion of the forest fern Cyatheaceae occurs, although not in the values for *Asplenium* T. Increases are seen in the concentrations of 'ubiquitous' pteridophytes, especially of monolete psilate spores, and various unidentified spore taxa.

Zone Y3: 1010-655 cm

The pollen concentration of the sediments of this zone fluctuates, but does not generally reach values as high as in some samples of the preceding zones.

Swamp vegetation is only sparsely represented. There is increasing occurrence of Cyperaceae pollen towards the top of the zone, and *Nymphoides* and ?*Metroxylon sagu* are also found.

A large number of dry-land pollen taxa contribute to the pollen spectra of the zone, non-forest taxa being particularly abundant. An increase in the occurrence of the larger grass pollen grains, especially of the Gramineae 5 class, is seen. *Macaranga* and *Nauclea* T. are well represented by fairly constant percentages throughout the zone. *Trema* is also abundant, although a slight decline occurs towards the top of the zone. Amongst other non-forest taxa represented are *Casuarina,* cf. *Crotalaria* T., *Mallotus* T., *Antidesma,* and *Plantago.*

*Celtis* is the best represented of the forest trees, occurring in most samples. Rutaceae/Araliaceae, *Rhus* T., cf. *Sterculia edelfeltii* and *Olea* are also recorded. Myrtaceae pollen, possibly from understorey trees, is found in several samples.

The forest ferns, Cyatheaceae and *Asplenium* T. show their greatest abundance in zone Y3. The frequency of Cyatheaceae spores (mainly Cyatheaceae 1, those without a perisporium) is fairly constant. Percentages of *Asplenium* T. increase towards the top of the zone. The 'ubiquitous' monolete psilate fern spores are also abundant throughout.

'Alluvium' forest is represented in the earlier part of the zone by *Octomeles sumatrana* pollen. *Kleinhovia hospita* and cf. *Bischofia* also occur, and *Rhizophora apiculata* T. pollen is found in the upper section of the zone.

Most of the 'montane' taxa present in zone Y2 continue to occur, although at lower frequencies, in zone Y3. In addition, isolated grains of cf. *Engelhardtia, Acaena, Anisoptera* T., *Rapanaea* cf. *achradaefolia* T. and *Dacrycarpus* T. are found.

Undifferentiated pollen of Urticaceae/Moraceae is fairly abundant and the unidentified pollen type UK 194 is also present.

Zone Y4: 655-440 cm

This zone coincides with stratigraphic evidence for very rapid sediment deposition. Plant detritus accumulation occurs between 640 cm and 540 cm and a rapid influx of clay from 540 cm to 420 cm is suggested by the inferred chronology. As a consequence, very low pollen concentrations are recorded in the four samples of zone Y4. The total pollen sum is also small, ranging from 12 to 53 grains. Dry-land non-forest pollen is present, but a larger proportion of the count comprises 'montane' forest taxa and 'ubiquitous' fern spores.

Zone Y5: 440-280 cm

Zone Y5 sees a return to a more moderate sedimentation rate, and increased pollen concentrations. In many respects the pollen spectra of this zone and zone Y3 are very similar.

*Nymphoides* is present in the upper part of Y3, and throughout Y5, although there is a drop in the proportion of Cyperaceae pollen.

The pollen concentration of dry-land taxa shows an increase over zone Y3, and the category comprises nearly 50% of the pollen sum. Grass pollen representation also rises, especially in the Gramineae 2 and Gramineae 5 classes. *Trema, Macaranga* and *Nauclea* T. are the most abundant taxa.

Forest trees are represented by essentially the same taxa as in zone Y3, *Celtis* and *Weinmannia* T. being the most common. Pollen of the vine *Flagellaria* occurs in both samples from the zone. A large peak of *Octomeles sumatrana* pollen is seen at 400 cm, but other 'alluvium' forest taxa are absent.

Of the 'ubiquitous' pollen taxa, Urticaceae/Moraceae remain represented, and *Pandanus radula* T. is also present. The unidentified taxon UK 194 comprises about 5% of the pollen sum during the zone.

The major difference between the pollen assemblages of zone Y5 and the previous zones lies in the markedly decreased representation of 'montane' forest and various pteridophyte taxa. A few grains of *Nothofagus* and *Anisoptera* T. occur but spores of Cyatheaceae and the small monolete psilate class are almost absent.

Zone Y6: 280-120 cm

The most recent pollen assemblage zone of the YAN 2 core sees a general increase in pollen concentration. Herbaceous swamp taxa show proportionally the largest increases. The representation of *Nymphoides* pollen increases to about 2% of the sum throughout the zone, and *Typha* and Cyperaceae B1 and B2 pollen also occur. Increases in Gramineae classes 3 and 4, and to a lesser extent class 2, may suggest the presence of *Phragmites karka* near the site. Most other taxa included in the herbaceous swamp category probably represent lake marginal vegetation. *Uncaria* T., *Nephrolepis*, *Stenochlaena palustris* and *Microsorium* T. fall into this category, as may cf. Liliaceae pollen. All these taxa show increased representation in zone Y6. There is little open swamp today at Yanamugi, although some floating root-mat associations exist close to shore. It is suggested that the swamp and aquatic vegetation of this period probably resembles that observable at the present time both in floristic structure and general distribution.

The dry-land pollen assemblages remain similar to those of the previous zone with grasses, *Trema* and *Macaranga* well represented. *Nauclea* T. also occurs, showing a large increase in frequency in the two uppermost samples of the zone. Forest trees continue to be represented by *Celtis* pollen, and *Flagellaria* occurs consistently. The proportion of *Octomeles sumatrana* increases towards the top of the zone. Very few pollen taxa of 'montane' forest are represented, and values for forest fern and other pteridophyte spores are also low. Urticaceae/Moraceae pollen show a slight increase in representation over zone Y5, and the unidentified UK 194 pollen taxon remains present.

The pollen spectra from zone Y6 are thus very similar to the contemporary pollen assemblages from Yanamugi. Particularly close correlation is found with the surficial sediment assemblage from core YANMC 1. Less similarity exists with the moss polster, SS 27-28, from within the neighbouring forest, as this sample is dominated (80%) by the unidentified pollen taxon UK 194. The proportion of herbaceous swamp taxa is generally lower in the surficial sediment, presumably due to the greater distance from the lake margin. Cyperaceae, Gramineae 4 and 5, *Nymphoides* and *Microsorium* T. all record lower frequencies, whilst *Nephrolepis* and *Stenochlaena palustris* are absent from the modern assemblage.

The percentages of dry-land taxa in zone Y6 and the contemporary assemblage are fairly similar. Urticaceae/Moraceae pollen, especially diporate grains, are more abundant in the surficial sample. Less well represented than at the top of core YAN 2 are *Octomeles sumatrana* and *Nauclea* T. pollen. The pollen taxon

UK 194, presumably originating in the local forest, accounts for 20% of the pollen sum in the surficial sediment sample.

A number of taxa not found in the sub-fossil assemblages occur in the contemporary spectra. Notable are *Calamus, Streblus* T., *Tinospora, Macaranga ovatifolia* T., cf. *Sterculia* and cf. *Palaquium*. Most significant, however, is pollen of Compositae (Tubuliflorae). This taxon comprises 9% of the pollen sum in the YANMC 1 surface sample and is also found in the forest moss polster SS 27-28. Compositae pollen also occurs in the contemporary sample SS 18 from roadside 'alluvium' forest in the lower Markham Valley, but has not been identified from any sub-fossil assemblage. Herbaceous composite species are widespread post-cultivation or vegetation disturbance ruderals in the area today, but it appears that they have achieved this status only recently.

## *VEGETATION CHANGE IN THE VICINITY OF YANAMUGI*

Swamp vegetation is represented in the pollen record of Yanamugi by fewer, generally less abundant, taxa than at Lake Wanum. Two important species are either almost absent (*Metroxylon sagu*) or impossible to distinguish (*Phragmites karka*). Despite these limitations, certain trends can be discerned in the swamp pollen record.

There is no evidence of substantial floristic change in the swamp community. Most taxa are represented to some extent throughout the sequence. The only possible exceptions are Cyperaceae class C, that occur only in the lower core, and *Stenochlaena palustris*, only sparsely represented in the sediments below 240 cm. Except for the basal sample of the core, where a high percentage of Cyperaceae B2 occurs, the proportion of herbaceous swamp taxa is low until the onset of the most recent zone, Y6. At this time both the pollen concentration and proportion of herbaceous swamp taxa increase, comprising 40% of the pollen sum. Within this zone, spores of *Nephrolepis*, *Microsorium* T. and *Stenochlaena palustris* become more abundant. *Nymphoides* and Cyperaceae pollen show an increase over the previous zone, and pollen of Gramineae 2, 3 and 4 become more common.

The sequence is interpreted as reflecting the migration to the coring site of emergent aquatic vegetation (*Nymphoides indica*) probably by the beginning of zone Y5. Subsequently, in zone 6, herbaceous swamp vegetation comprising various ferns, Cyperaceae and perhaps *Phragmites karka* occupies the site. Floristically similar vegetation is found at the lake today. The cause of encroachment by swamp vegetation probably lies in a decrease in the effective water depth along the northern margin of the lake, presumably resulting from the accelerated clay deposition recorded in core YAN 2 between 640 cm and 420 cm.

Few consistent trends exist in the dry-land pollen record of core YAN 2 that can be interpreted in terms of vegetation change. Perhaps the most striking feature of the Yanamugi pollen diagrams is the abundance, below 440 cm, of pollen and spore taxa thought to originate from higher altitude vegetation. These include not only identifiable 'montane' forest genera, but also a wide variety of other pollen taxa and pteridophyte spores. Above 440 cm in the core their representation decreases markedly. However, it seems unlikely that this clear change in pollen assemblage reflects a change in vegetation.

It is improbable that many of the 'montane' forest tree taxa grew in close proximity to the lake at any time in the recent past, given their current altitudinal preferences (Table II.1). Many are effective pollen distributors and would be expected to dominate the pollen spectra of the core if located at, or very near, the site. Downslope aerial dispersal of *Nothofagus, Phyllocladus,* and *Podocarpus* pollen has already been demonstrated for the Lake Wanum area. Yanamugi is higher in altitude than Lake Wanum and is also closer to the mountain ranges south of the valley. Increased representation of higher altitude pollen might therefore be expected. However, it seems unlikely that entomophilous taxa such as Epacridaceae, or large spores of Cyatheaceae could be aerially transported in the quantities found in the sediments of the YAN 2 core. Fluvial transport, e.g. Sina Creek, seems to be the most likely dispersal agent for these taxa. The close association of the maximum concentration of the 'montane' taxa with a distinct horizon in the core adds further circumstantial evidence for this interpretation.

The possibility of actual reduction in the area of 'montane' forest within the vicinity of Yanamugi cannot be excluded, as grassland now extends to 1 000 m altitude on some local ranges. However, the decrease in the representation of 'montane' taxa within the last two pollen assemblage zones coincides with a reduced influx of allochthonous clay, also perhaps fluvial in origin. With a considerable increase in the pollen concentration of other ecological categories, these factors alone are probably sufficient to explain the pattern of occurrence of the 'montane' taxa.

Little consistent change is revealed in the dry-land vegetation surrounding the lake. Essentially the same taxa found in contemporary assemblages occur throughout the sediments. As the composition of the local forest is largely unknown, few taxa are identifiable as originating from forest tree species. In the record of non-forest taxa there appears an inverse relationship between *Nauclea* T. and pollen of the 'disturbance' taxa: mainly Gramineae, *Trema* and *Macaranga*. Without reliable PDR estimates, however, it is difficult to say whether this trend is an artefact of the relative frequency calculation. There is some coincidence between the representation of *Nauclea* T. and *Octomeles sumatrana* pollen.

As at Lake Wanum a group of pollen taxa possibly representative of vegetation 'disturbance' may be identified. Pollen of dry-land grasses are the most abundant. *Trema, Macaranga* and various herb and shrub representatives, particularly genera of Euphorbiaceae, are also included. At Yanamugi also there is some correlation between the occurrence of these taxa, especially Gramineae pollen, and the incidence of carbonised particles (Fig. 8.6). Charcoal fragments are most abundant in the zone (Y3) that records the greatest variety of non-forest pollen taxa. The representation of *Celtis* follows closely that of the 'disturbance' taxa, and there is no sustained trend towards increased proportions of grassland pollen in the sequence.

In summary, apart from the localised encroachment of swamp vegetation, few indications of vegetation change are recognised in the pollen record of core YAN 2. Fluctuations in the frequency of some higher altitude taxa are considered to reflect primarily the effect of fluvial inwash into the lake, the source of which is not identified. Only minor changes occur in the pollen record of local forest and non-forest associations, and all presently extant vegetation types appear to be represented throughout the sequence. Pollen taxa attributable to grassland and 'disturbance' vegetation occur throughout, but show no marked changes in frequency. It is suggested that little substantial alteration in the composition or distribution of the dry-land plant communities around Yanamugi has occurred within the past 1000 to 2000 years.

### *CONCLUSIONS*

Although the palynological data present a very partial record of the vegetation, it is possible to demonstrate ecological change in certain plant communities. The most precise vegetation reconstruction comes from the herbaceous swamp associations of Lake Wanum where the contemporary ecology and pollen dispersal are best known. Changes in local hydrology during the Holocene may be surmised from the known habitat preferences of herbaceous swamp associations and individual taxa. The pollen representation of 'alluvium' forest at Lake Wanum appears to reflect, to some extent, similar environmental trends.

Except for taxa of the 'alluvium' category, there is a sparse record of forest tree pollen. This is primarily due to the lack of information on the floristic composition of the local forest at both sites. The major taxon at Lake Wanum, *Celtis*, appears to be favoured by some degree of vegetation disturbance.

No pollen indisputably from cultivated plants is found although circumstantial evidence of human impact on the vegetation is available from both Lake Wanum and Yanamugi. Increased influx of carbonised particles and non-forest pollen is first seen at 8500 BP in Lake Wanum, and the presence of substantial non-forest and grassland vegetation is indicated throughout the sediments of Yanamugi. At neither site is it possible to identify any sequence indicative of an individual cycle of forest clearance, cultivation, and secondary regrowth.

Estimates of annual pollen deposition rates allow a much more precise interpretation of vegetational change than do relative frequency figures. The few comparable PDR values available suggest that the influx of dry-land pollen to the marginal sediments of both lakes is fairly similar. The PDR of herbaceous swamp taxa, however, is much greater at Lake Wanum. Pollen assemblages from Yanamugi show the greater taxonomic diversity.

The vegetational interpretation of the pollen assemblages in this study relies on the relatively few taxa whose affinity and ecological preferences are better known. Increased ecological and pollen morphological data would undoubtedly allow the recognition of more subtle changes in the palynological record.

# CHAPTER 9

# HOLOCENE VEGETATION AND ENVIRONMENTAL CHANGE IN THE MARKHAM VALLEY AND OTHER TROPICAL REGIONS

Palynological and stratigraphic evidence from the two lake sites studied reveals significant changes in both vegetation and sedimentary regime during the Holocene period.

Organic accumulation at the margin of the north-east bay of Lake Wanum commenced at about 9600 BP. The subsequent development of swamp vegetation in this area is interpreted as showing a general increase in water depth throughout the course of the Holocene. At Yanamugi, encroachment of swamp vegetation has taken place within the last few hundred years. The pollen sequence of dry-land taxa from Lake Wanum records the increasing influence of non-forest and grassland vegetation from about 8500 BP. Synchronous influx to the sediments of carbonised particles suggests that fire may play a role in the establishment or maintenance of such vegetation. Non-forest and grassland pollen taxa are present throughout the much younger deposits of Yanamugi.

## *DETERMINANTS OF ENVIRONMENTAL AND VEGETATIONAL CHANGE*

It is apparent that most of these changes cannot have occurred under static environmental conditions. The evidence in favour of specific determinants of environmental changes is largely circumstantial, it being particularly difficult to discriminate between local causes and those of more widespread significance on the basis of the record of a single site. Only the pollen record from Lake Wanum core LW II covers the period from 9500 BP to *c.* 1500 BP. The poorly known chronology of the deposits at Yanamugi hinders correlation for the period when both sites preserve a pollen record. Although the most recent 250 years is the best dated section at Yanamugi, no comparable pollen record exists for this time from Lake Wanum.

Environmental factors likely to produce vegetational changes fall into three major groups: geomorphic and hydrologic, climatic and anthropogenic. These determinants are almost never discrete, but impinge on each other in complex interaction. The positive identification of a single cause for any event is thus almost impossible. Probable determinants and their influence may, however, be evaluated in relation to evidence from the Markham Valley and other areas of New Guinea and tropical Australia.

### *Geomorphology and hydrology*

Regional geological events, such as seismicity, or sea level fluctuation may influence local hydrology and thus lacustrine sedimentation. The study area is known to be tectonically active, the southern side of the Markham Valley less so than the Saruwaged Ranges to the north. Chappell (1973) has suggested that lakes and swamps in the vicinity of Lake Wanum may be fault impounded, but the extent of any movement during the Holocene remains speculative.

Of more direct impact on the sedimentation is the behaviour of local watercourses. At both Lake Wanum and Yanamugi influx of allochthonous grey clay is attributed, at least in part, to fluvial activity. Oomsis Creek directly affects the sedimentary regime of the southern and central sections of Lake Wanum. Given a lower water level, this influence may have extended to the northern margin of the basin also. Alluvial sediment is considered to be partially responsible for impounding of swamps and lakes adjoining the creek. At Yanamugi, an unidentified source, possibly Sina

Creek, appears to contribute to the influx of pollen, spores, and perhaps other detritus, from higher elevations into the lake. It thus becomes important to explore the causes and effects of probable changes in the morphology of these streams in relation to the sedimentary history of the two sites.

The post-glacial sea level rise is likely to have affected the drainage of the lower Markham area. At the last glacial maximum (*c.* 18 000 BP) the oceans surrounding the New Guinea region lay perhaps 140 m to 150 below their present level (Chappell, 1976). Due to isostatic effects, the lesser figure appears more applicable to areas such as the Huon Gulf that lack a broad submarine shelf. Subsequent rise in sea level is thought (Chappell and Thom, 1977) to follow a trend between that reconstructed for south-east Australia (Thom and Chappell, 1975) and for Micronesia (Bloom, 1970). The exact course in relation to any specific coast is modified by local tectonic movement as well as global isostatic and glacio-eustatic effects. Chappell (1976) estimates the regional eustatic sea level to be 40 m to 50 m below present at 10 000 BP. The smoothed sea level curve for south-east Australia (Chappell and Thom, 1977) shows a fairly constant rate of rise to about -18 m at 8500 BP. The rate then slows slightly until 7500 BP when sea level stood at about -10 m, the present level being reached by 6000 BP. Data from north-western Australia (Jennings, 1975) also suggest sea level to be within a few metres of its present position by 7400 BP to 6000 BP. In the oceanic islands of Micronesia sea level stood at around -5 m at 6000 BP slowly rising to the current level within the last few millennia (Bloom, 1970). The course of sea level relative to the Huon Gulf coast may parallel these estimates, although the local tectonic component is uncertain.

Rivers such as the Sepik, with steep offshore submarine contours and slight gradients, have been most affected by the rising sea level (Löffler, 1977). The Markham also has a nearshore submarine canyon although the river's gradient is relatively steep. The rapid rate of alluvial deposition in the valley may have prevented any substantial marine transgression. Aggradation of the river profile may have kept pace with the up to 20 mm $yr^{-1}$ rise in sea level. Such aggradation would also have influenced the tributaries of the lower Markham, particularly those to the south of the valley where river gradients are less steep, such as the Wampit and Watut rivers. Oomsis Creek, a tributary of the Wampit River, may also have aggraded along its lower course and disrupted the drainage of the Lake Wanum basin. Initiation of organic accumulation in the basin occurred by 9600 BP against the background of a rapidly rising sea level. The rise in the water level of Lake Wanum between 9500 and about 7000 BP followed by a fairly static period until 5500 BP also parallels the trend of sea level. However, the most rapid increases in lake level, seen after this date, require an alternative explanation.

Geomorphic changes of a local nature include such phenomena as stream meandering, landslips, and floods. No major change in the course of Oomsis Creek is envisaged, as its valley is largely circumscribed by the topography of the surrounding granodiorite hills. The suspected fluvial influx at Yanamugi may, however, be due to changes in local hydrology. The channel of Sina Creek runs along the southern margin of the Markham floodplain and may be susceptible to the influence of movements in the major river. As the hydrology of the area is poorly known, this hypothesis is purely speculative.

*Climatic change*

The record of the earliest sediments at Lake Wanum coincides with the final phases of the global post-glacial amelioration of climate. Proxy data based on the evidence of glacial geomorphology and pollen analysis in the New Guinea highlands (reviewed by Bowler *et al.*, 1976) and the thermal implications of past marine planktonic assemblages (CLIMAP project members, 1976) provide a basis for reconstruction of the regional climate. Ambiguity exists in the interpretation of these data, although the major trends appear well defined.

Considerable refrigeration was experienced in the New Guinea highlands during the last glacial maximum, not only in the ice covered mountains above 3 400 m or 3 650 m, but as low as Sirunki (alt. 2 500 m). Lowering of the snow-line by 900 m to 1 200 m implies a mean annual temperature at least 6 °C lower than today, whilst pollen analytical data from Mt. Wilhelm and Sirunki suggest a temperature reduction at 17 000 BP of between 7 °C and 10 °C (Bowler *et al.*, 1976).

The refrigeration at sea level is likely to have been less dramatic. Nix and Kalma (1972) consider that the lapse rate of the drier, cooler air may have attenuated the temperature reduction to -3 °C or -4 °C. The CLIMAP reconstruction for 18 000 BP proposes a sea-surface temperature (SST) of 26 °C for the area, only 2 °C lower than present. Webster and Streten (1978) argue that the widely different temperature estimates from the marine and highland data are incompatible with even the most extreme probable lapse rates. If the highlands data are correct, these authors argue, then the SST of the western Pacific should be some 5 °C cooler than the CLIMAP estimate. The difference would be less if the reduction in freezing levels in the highlands were accomplished, in part, by increased equatorward incursions of cold air from higher latitudes. However, this effect is considered unlikely to account for the demonstrated depression of the tree-line to below 2 500 m.

By 10 000 BP to 9000 BP, temperatures in the highlands ameliorated to within -1 °C to -2.5 °C below present (Bowler *et al.*, 1976). Temperature fluctuations later in the Holocene are likely to have been slight. Webster and Streten (1978) consider a 'hypsithermal' interval (*sensu* Deevey and Flint, 1957) to be 'well defined' by the palynological data from the New Guinea highlands and estimate temperature between 7000 BP and 4000 BP at between 1 °C and 1.5 °C higher than present. The pollen analytical evidence for such a thermal maximum comes from two areas. A number of organic deposits, some with discontinuous pollen records, have been studied from Mt. Carstensz, Irian Jaya by Hope and Peterson (1976) who consider too little to be yet known to infer temperature change over the period 10 000 BP to 3500 BP. Better understood are the pollen records of four sites on Mt. Wilhelm (Hope, 1976*a*). Here the period from about 8600 BP to 5000 BP is characterised by the highest extension of the tree-line, and the greatest development of forest and alpine shrubland seen in the post-glacial sequence. However, no substantial change in vegetation is observed during this period at the lowest altitude site on Mt. Wilhelm, Komanimambuno Mire, (2 740 m) or at Sirunki (Bowler *et al.*, 1976). The most cautious appraisal of high altitude vegetational evidence in favour of mid- and late-Holocene temperature fluctuations is thus required. As Hope (1976*a*) concludes,

> 'although climates probably induced changes in vegetation distribution until 8 500 yr BP the minor changes since that time are as likely to be due to human activity or other ecological factors as to climate, even though climatic change is known to have occurred.'

Thus, although the first millennium of sediment accumulation at Lake Wanum coincides with the final phase of climatic amelioration, the mean temperature at sea level is unlikely to have been significantly below that of today. Even allowing extrapolation at the current Lae lapse rate from the most extreme highland temperature estimates the decrease would be less than 1 °C in the lowlands at 10 000 BP. Minor thermal fluctuations since 8500 BP may be demonstrable in some montane areas, however their effect on lowland mean temperatures was probably negligible.

Palaeoclimatic inferences from New Guinea highlands data are usually couched in terms of thermal change, as temperature is the main control on vegetation in the highlands where rainfall is not usually limiting. As demonstrated, temperature fluctuations in the lowlands, especially during the Holocene, are likely to have been less intense than at higher altitudes. However, regional climatic change is also expressed by variation in both actual and effective precipitation. These effects are most likely to have been felt in areas, such as the Markham Valley, that now experience relatively low rainfall.

A theoretical reconstruction of the Australasian climate at the last glacial maximum (Nix and Kalma, 1972) suggests reduced precipitation due to the lesser area of warm oceanic-shelf water and lower SST. With rising temperatures from 14 000 BP, evaporation increases and dry conditions become accentuated. After the major sea level rise, but before Torres Strait flooded, temperature and rainfall higher than present are hypothesised, although evaporation remains similar to that of today. Nix and Kalma (1972) date this phase at 8000 BP, although using the data of Chappell and Thom (1977) their suggested sea level for this phase (-30 m) would reflect conditions closer to 9000 BP.

The rainfall component at least of this reconstruction is supported by pollen analytic and stratigraphic evidence from the Atherton Tableland, north-east Queensland (Kershaw, 1975). The progressive onset of organic accumulation at three sites (Bromfield Swamp, Lake Euramoo, and Quincan Crater) indicates increase in available moisture over the period from about 11 000 BP to 7000 BP. A change from sclerophyll vegetation to rainforest is recorded at these sites and in the deposits from Lynch's Crater (Kershaw, 1976) occurring across the tableland between 9500 BP and 6000 BP. The sequence of initiation of swamp conditions and transition to rainforest appears related to a precipitation threshold that parallels the present rainfall gradient across the area. Only the most humid site today (Lynch's Crater) shows organic accumulation during the late Pleistocene.

In view of these data it may be admissible to formulate a conservative climatic interpretation of sedimentological and ecological changes at Lake Wanum. Ignoring for the moment the effects of basin morphometry and swamp vegetation on absolute water level and evaporation, postulated fluctuations in water depth (Fig. 8.4) may be viewed as a response to climatic factors.

The onset of organic accumulation at 9600 BP in the north-east bay may reflect a climate favourable for the initiation of swamp conditions. It appears that only a slight excess of moisture was available until 8500 BP or 8200 BP, when permanent standing water may have become first established. This sequence suggests the possibility of an absolute increase in rainfall, especially so if temperatures were at all reduced during the beginning of the Holocene.

Since about 8200 BP a positive water balance has been maintained. The effective water depth apparently remained fairly static from about 8000 BP until a substantial rise at around 5000 BP. An increase in precipitation at this time cannot be ruled out, but is considered unlikely, unless the final flooding of Torres Strait produced an effect on the climate greater than is generally assumed. At Yanamugi, encroachment of swamp vegetation within the last few centuries is interpreted as due to increased local sedimentation, rather than a drop in the water level of the lake.

In contrast to the reconstructed swamp environment, the dry-land vegetation of Lake Wanum reveals no suggestion of climatic fluctuation. Even a 1 °C reduction in temperature for the basal sections of the pollen sequence might be reflected by increased representation by forest taxa, such as perhaps *Lithocarpus*, found 150 m above the site today. The increasing influence of non-forest and grassland vegetation in the pollen sequence and the evidence for fire frequency, if having any climatic significance, might suggest relative aridity or at least seasonality. Such an interpretation would run contrary to the evidence of the water depth record, were the latter climatically determined.

Thus the tentative climatic implications of evidence from Lake Wanum parallel those from the Atherton Tableland sites in identifying an increase in effective precipitation from at least 9600 BP to perhaps 8000 BP. However, no significant decrease in the effective precipitation is recorded at either Markham Valley site within the last few millennia, contrary to the suggestion by Kershaw (1974) for Lynch's Crater. Apart from the evidence of early Holocene aridity, climatic inferences from Lake Wanum are ambiguous.

*Human impact*

Man's occupation of the greater Australian region probably dates to at least 50 000 BP (White and O'Connell, 1979). The most ancient reliable evidence of human presence is a 33 000 BP radiocarbon date from the Mungo lunette, south-western New South Wales (Bowler *et al.*, 1972). The first indication of man in New Guinea comes from Kosipe swamp, at 2 000 m in the Owen Stanley Ranges, and is dated at 26 000 years ago (White *et al.*, 1970). Continent-wide occupation is shown by a number of sites within the period 20 000 BP to 30 000 BP (White and O'Connell, 1979).

The first evidence for agriculture in New Guinea is found at Kuk swamp (alt. 1 550 m) in the upper Wahgi Valley of the Western Highlands. Here phases of cultivation are implied by a series of artificial channels, presumably created for the purpose of water control. The oldest are dated (Golson, 1977*a*) at *c.* 9000 BP ('Phase 1') and 6000 BP to 5500 BP ('Phase 2'). Both agricultural episodes are short-lived and evidence for an intensive drainage system and prolonged use of the site is not found until 4000 BP. Pollen analysed sequences are available from two swamps in this area: Manton's (alt. 1 590 m) across the Wahgi Valley and Draepi, situated at 1 890 m at the base of Mt. Hagen (Powell *et al.*, 1975). Both indicate substantial forest clearance by 5200 BP, although this represents a minimum date as deposits of preceding millennia are absent.

Pollen analyses from contemporaneous deposits at higher elevations are less equivocal in showing human influence on the vegetation. These sites undoubtably lie well above the altitudinal limit of extensive cultivation prior to the introduction of the sweet potato. Vegetation disturbance may account for the expansion of forest ephemerals, and non-forest shrubs, herbs and grasses around Sirunki (2 500 m) from 4500 BP (Walker, 1970). Circumstantial evidence for human activity at even higher altitudes on the Saruwaged Plateau is given by Costin *et al.* (1977). Fossil leaf remains from Lake Mamsim (3 500 m) indicate local presence at 5700 BP of podocarp forest now found 500 m below the site. Human activity is invoked as the most probable cause of the subsequent deforestation, although minor climatic deterioration is also suggested.

Evidence for intensified forest clearance and cultivation is recorded at sites above 2 500 m within the last 1000 to 1500 years and particularly from about 300 BP (Hope, 1976*a*) possibly in response to the introduction of the sweet potato (*Ipomoea batatas*) into the New Guinea highlands by the later date.

The dry-land pollen record of both Markham Valley sites is strongly suggestive of human impact on the vegetation, even though there is no clear indication of reduced forest area. Whilst it is not permissible to equate increased PDR of certain non-forest taxa with a decrease in the forest cover, qualitative changes suggest that grassland has become more predominant during the upper Holocene. Corroborative, if circumstantial, evidence is provided by the record of carbonised particles that correlates closely with that of certain non-forest pollen taxa.

The first indication of, possibly anthropogenic, disturbance of the vegetation at Lake Wanum is seen between 8550 BP and 7850 BP in increased values for woody non-forest pollen taxa and influx of carbonised fragments. The occurrence of natural fires must be considered, although this period is supposed to be more humid than the preceding millennium, during which time no such evidence is found. The second phase of vegetation disturbance, from 6950 BP to 6100 BP, is fairly similar in character to the earlier. From about 5350 BP, the dry-land pollen assemblages from Lake Wanum become dominated by woody non-forest and grassland taxa. A slight recovery of forest pollen taxa occurs from 3600 BP until 2300 BP, when a renewed phase of vegetation disturbance, continuing to the present day, is initiated. The dry-land pollen record of Yanamugi indicates presence of non-forest and grassland vegetation throughout the 1500 to 2000 year history of the sequence. Notably absent from either site is any indication of intensified agricultural activity several hundred years ago, such as is recorded in higher altitude sites. This period is, however, hardly represented in the Lake Wanum core LW II, although it is one of the better dated periods in Yanamugi's sedimentary history. It is unlikely that the introduction of the sweet potato had as great an effect on lowland agriculture, where it is not the staple crop today, as it did on the ceiling of cultivation in the highlands.

There is no clear evidence at either site for direct human impact on swamp vegetation. At Yanamugi it is possible that the sequence of clay and macrophytic detritus from 469 cm to 578 cm in core YAN 2 may reflect exploitation of the sago swamp, although this resource is not utilised today. Phases of considerable clay influx are recorded in the stratigraphy of both sites, some perhaps reflecting man-induced erosional events. A major clay band deposited between 6500 BP and 5000 BP at Lake Wanum overlaps two phases of suggested vegetation disturbance. It also precedes an increase in water level and diversification of the herbaceous swamp vegetation. It is possible to speculate that this horizon might reflect the erosional consequence of man's activity either in the lake basin, or in the catchment of Oomsis Creek. A similar hypothesis, of indirect human impact on local hydrology, is proposed by Powell *et al.* (1975) to account for the initiation of organic accumulation at the Manton site and to explain clay deposition at nearby Draepi swamp. Later disturbance phases at Lake Wanum possibly associated with clearance activity appear synchronous with narrow clay bands, but as discussed in Chapter 8, no general correlation exists.

The interpretation of the pollen records of the Markham Valley sites as reflecting a substantial degree of human influence on the dry-land vegetation accords with the available palynological and archaeological evidence from the New Guinea highlands. With the proposal of complex agriculture at Kuk 9000 years ago (Golson, 1977*b*), the lack of unequivocal evidence for forest clearance at mid-altitude (1 500 m to 2 000 m) sites prior to 5000 BP appears due only to the absence of deposits suitable for analysis.

The most convincing evidence for vegetation disturbance and firing at Lake Wanum dates from 5350 BP although two distinct phases of increase in woody non-forest pollen taxa occur earlier in the sequence. Accepting the inference of human involvement, the episode commencing at 8550 BP represents the earliest pollen analytical evidence for vegetation clearance in New Guinea, although it is younger than the 'Phase 1' drainage channels at Kuk. In view of the suggested antiquity of highlands agriculture it is quite probable that cultivation in the lowlands pre-dates the base of the Lake Wanum core LW II ( *c.* 9500 BP).

## *DETERMINANTS OF ENVIRONMENTAL AND VEGETATIONAL CHANGE IN THE MARKHAM VALLEY DURING THE HOLOCENE*

With only one stratigraphic sequence spanning most of the Holocene period, the identification of regional changes and their causes is highly tentative and will undoubtably be modified by future work.

The onset of swamp conditions in the north-east bay of Lake Wanum was probably facilitated by an increase in absolute precipitation during the period from 9600 BP to about 8000 BP. Increased humidity may reflect the progressive flooding of the Arafura Sea but is thought more likely due to more widespread changes concomitant with the global post-glacial climatic amelioration. The air masses of either the 'south-east' or 'north-west' circulations could have become more moist as increased rainfall from both would affect the Lake Wanum area. Local changes in hydrology as an indirect consequence of the rapidly rising sea level may also have had an influence on the water level of Lake Wanum during this period.

It is difficult to interpret the considerable increase in effective water depth in Lake Wanum subsequent to 8000 BP as a response to variation in precipitation. A period of clay influx from 6500 BP to 5000 BP may be associated with drainage disruption and an increase in the water depth of the lake. The clay deposition may result from local geomorphic change or might even have been triggered by man-induced erosion. A possibly analagous phase of clay influx at Yanamugi in more recent times may be anthropogenically caused, although again, natural hydrologic factors cannot be excluded.

No substantial desiccation is seen within the last 8000 years, although such an event would be recorded at Lake Wanum only if very severe. None of the palaeoecological evidence requires thermal change for its interpretation. If, as suggested by data from the New Guinea highlands, the mean temperature was lower during the early Holocene, this had a minimal effect on conditions at sea level.

Whilst the determinants of lake levels remain ambiguous, human impact can be identified as the major cause of changes in dry-land vegetation.

A Holocene vegetation history of the Markham region may be outlined thus. The altitudinal depression of montane vegetation associations influenced the lowland vegetation little, or at least, by 9000 BP, its effect was no longer felt. 'Alluvium' forest may have been more widespread in the vicinity of Lake Wanum during the early Holocene. Nix and Kalma (1972) postulate the Markham area to be too arid to support closed forest during the period 17 000 BP to 14 000 BP. It is suggested here that relative aridity was possibly maintained over much of the valley until about 8500 BP or 8200 BP. Taking into account the active geomorphic nature and poor soils of the valley floor it seems unlikely, therefore, that closed forest was much more widespread than present over the central valley prior to *c*. 8000 BP. Increased representation of 'alluvium' forest in the pollen record between 8000 BP and 6500 BP may reflect local conditions to the south of Lake Wanum, or of the lower Markham Valley. Although by perhaps 8000 BP the onset of more humid conditions is indicated, increasing human impact on the vegetation from this date may have contained the expansion of closed forest in the valley floor. Much of this area may have been occupied by non-forest or open forest vegetation although, initially, open grassland was probably less widespread than today.

In contrast to the valley floor, the vegetation of the now grassed areas of the foothill slopes is likely to have resulted primarily from human activity. Rainfall is higher around the valley margin and soils are generally better developed and not susceptible to the unstable conditions of the valley floor. It is nonetheless notable that the larger tracts of grassland have developed on the thinner soils of the granodiorite and limestone areas. If the Lake Wanum area be typical of the valley margin, forest clearance may have started by 8500 BP, with a resulting expansion in grassland area. A pattern of vegetation distribution fairly similar to that found today had probably become established by 1500 to 2000 years ago.

## *LATE QUATERNARY ENVIRONMENTS OF THE TROPICAL LOWLANDS*

Pan-continental correlations based on meagre and ambiguous data almost invariably prove in error. Bearing in mind Livingstone's admonition to 'beware of facile explanations not supported by evidence' (Livingstone, 1975) some wider implications of the present study may be sought by comparison with other tropical lowland areas.

The last glacial maximum is now generally considered a period of relative aridity in many tropical and sub-tropical areas (Rognon and Williams, 1977, Bowler, 1977). From about 11 000 BP to 8500 BP lake levels and vegetation in many regions reflect a change from arid to relatively humid conditions.

Morley (1976) reports the onset of organic accumulation at Danau Padang (alt. 950 m), Kerinci, Sumatra by 9800 BP. A transition from forest of an upper-montane to lower- or sub-montane affinity between 8600 BP and 8300 BP in interpreted as a response to a general increase in mean temperatures.

The considerable evidence for lake level fluctuations in Africa is summarised by Butzer *et al.* (1972) and Rognon and Williams (1977), whilst the course of climatic change is assessed by Livingstone (1975). A large number of dated sites, predominantly in east Africa, suggest progressively increasing humidity, particularly in the equatorial areas, from 12 000 BP to perhaps 7000 BP. The most informative sequence comes from Lake Victoria,on the equator at an altitude of 1 134 m. The lake level stood at 75 m below present 14 000 years ago (Livingstone, 1975). Kendall (1969) shows that the basin remained closed until 12 000 BP, indicating a climate drier than has prevailed since. From this date water level rises, although with a slight reversal at around 10 000 BP. Pollen analysis reveals a change from savanna vegetation to evergreen forest over the same period, the forest reaching its maximum extent by 8000 BP.

In Central America the onset of accumulation at the available lake sites is influenced either directly by rising sea-level, such as in the Gatun Basin of Panama (Bartlett and Barghoorn, 1973) or indirectly by the rising water-table as in the limestone area of the Yucatan peninsula (Deevey, 1978). Sedimentation in the Gatun Basin began around 11 300 BP, following an unconformity of over 20 000 years. Bartlett and Barghoorn (1973) interpret the pollen sequence from these sediments as indicating a temperature reduction of 2.5 °C at this time, ameliorating to the present temperature by 8500 BP to 7300 BP.

The Lago de Valencia in Venezuela was essentially dry and surrounded by semi-arid vegetation from the base of a 13 000 year old sediment core until about 11 000 BP (Leyden and Whitehead, 1979). Between 9500 BP and 8500 BP the lake achieved its maximum Holocene level, and the modern pollen flora became established. Wijmstra and van der Hammen (1966) investigated lake deposits in present savanna areas of Guyana. Lake Moriru (alt. 110 m) in the Rupununi savanna records a change from mixed savanna woodland, dry-forest and open savanna to a less open vegetation of closed dry-forest or savanna woodland. The authors place this transition at about 10 000 BP, although only two younger radiocarbon dates support the chronology. Subsequent increase in open savanna vegetation dates from perhaps 7500 BP.

The last glacial maximum was arid not only in the continental tropical lowlands. The Galapagos islands, on the equator in the eastern Pacific, were also drier. A core from El Junco lake at *c*. 700 m on San Cristobal island (Colinvaux and Schofield, 1976*a*,*b*) spans over 48 000 years. Only the sediments of the last 10 000 years are lacustrine, the underlying strata having been deposited in an arid climate. The pollen record of the upper core (Colinvaux and Schofield, 1976*a*) shows the present vegetation to have become established early in the Holocene, with only minor change since that time.

No general synthesis of climatic fluctuations is possible for the latter part of the Holocene. It is clear that in most tropical lowland regions any such effects are expressed in terms of rainfall, rather than temperature. The influence of most changes has been minor, compared to the events of the early Holocene. In many regions it becomes impossible to isolate the effects of minor climatic fluctuation from those of the progressively insistent human modification of the natural vegetation.

In Sumatra, Morley (1976) recognises two phases of vegetation disturbance. The first, interpreted as showing forest clearance, occurs between 4000 BP and 2500 BP, and is reflected by increase in the proportions of *Macaranga* and *Trema* pollen in the sediments. From 2500 BP until the present, higher frequencies of pollen of *Trema* and grasses apparently reflect sedentary agriculture.

Reduction in the PDR of forest trees in the pollen diagram from Lake Victoria is seen within the last 3000 to 3500 years, and may be attributed to human activity (Kendall, 1969).

Agriculture is well established by 3000 BP in the Yucatan lowlands, and forest clearance may date to 5000 BP (Deevey, 1978). Bartlett and Barghoorn (1973) identify maize pollen from sediments from the Gatun Basin dated at 6230 BP to 7300 BP, and increasing frequency of herb pollen and almost total disappearance of tree pollen is recorded within the last few millennia. Extension of the already extant Rupununi Savanna within the last 3000 years is attributed by Wijmstra and van der Hammen (1966) to man's activities.

Thus, the interpretation of the palaeoecological evidence from the Markham Valley accords, in broad detail with evidence from other tropical lowland or lower montane regions. Relative aridity during the late glacial period appears almost universal although the timing and regional expression of the early Holocene increase in humidity varies considerably. Many pollen records show the influence of human impact on the vegetation dating from 4000 BP or 5000

BP. At Lake Wanum, such effects appear well established by this date. Particularly interesting is comparison with the evidence from Sumatra (Morley, 1976). The palynological expression of human activity is very similar at Danau Padang and the Markham Valley sites. Man's destructive effect is however recorded at a much earlier date in Papua New Guinea lowlands.

In conclusion, the vegetation pattern of the Markham Valley has demonstrably not remained static during the Holocene. Both natural and anthropogenic environmental changes have been met by the ecological response of the plant communities.

## *PROSPECT*

Despite its limitations the pollen analytical method is one of the most informative sources of evidence for vegetational and environmental change in the tropical lowlands. The expression of pollen occurrence in terms of annual depositional rates circumvents many of the inherent problems of dealing with the diverse pollen flora although calculation of such estimates requires a sound, independently derived, chronology that many sites cannot provide. Due to the relatively local nature of pollen deposition, no single site is likely to produce a vegetational history applicable to a wide area. Prospective palaeoecological study sites must therefore be chosen with specific aims in mind. It appears that lowland sites in New Guinea currently experiencing less than perhaps 1 800 mm rainfall per annum did not accumulate organic sediment during the late Pleistocene and early Holocene. Fuller Quaternary sequences undoubtedly exist in wetter or more elevated areas. Sites at altitudes of 800 m to 1 200 m may better reflect post-glacial thermal fluctuations, In addition areas less disturbed by man remain to be investigated.

This study thus barely scratches the surface of the polliniferous mud. Palynology's contribution to our comprehension of the complex tropical lowland rainforest ecosystem has hardly begun.

# APPENDIX I

## IDENTIFICATION AND DESCRIPTION OF POLLEN AND SPORE TAXA RECORDED FROM MARKHAM VALLEY CORES AND SURFACE SAMPLES

Morphological descriptions and photographs of all identified pollen and spore types and the more common or distinctive unknown types are contained in this appendix. All were recorded on Kodak Panatomic-X film using a Carl Zeiss automatic photomicroscope equipped with X 40 and X 100 planapochromatic oil-immersion objectives.

The identification of unknown types was achieved by comparison with the Dept of Biogeography and Geomorphology's collection of nearly 15 000 reference slides of pollen and spores. The matching of unknown grains with the reference material was aided by the use of photographs and punched-card descriptions of sections of the collection, and also by the computer assisted retrieval system for morphological details of nearly 3 000 of the slides, described by Walker *et al.* (1968) and Guppy *et al.* (1973).

Despite its large size, the reference collection tends predominantly to represent material from the New Guinea highlands and temperate Australia. Although this bias was to a small extent rectified during the course of the project, there still remained a lack of adequate representation from the area under study in particular, and from tropical lowlands in general. For this reason many of the identifications set out below remain tentative only, a few relying solely on published accounts, whilst the general level of identification is certainly not as critical as perhaps could otherwise have been achieved.

The degree of certainty of an identification is indicated by the following conventions:

> The suffix 'T.' ('type') indicates that the fossil taxon is identical with the named taxonomic unit although not always uniquely so, other taxa also producing grains or spores that are morphologically indistinguishable from the named type.
>
> The prefix 'cf.' signifies that the type is closely similar, but not identical in every respect with the named taxon or taxa.
>
> The prefix '?' indicates a very tentative identification. The unknown type possibly lies within the group or groups of taxa mentioned, but the allocation is by no means certain.

### *MORPHOLOGICAL DESCRIPTIONS*

The pollen types are grouped into the morphological classes of Faegri and Iversen (1964), except that the sections Polyplicate, Trichotomocolpate, Dicolporate, Fenestrate, Dyad, and Polyad have been omitted as no grains of these categories were found during the course of the investigation. For convenience, all Cyperaceae grains have been included as a subsection of the Monoporate category, although many possess more than one pore. In addition to the pollen morphological groups, two classes (Monolete and Trilete) are used to encompass pteridophyte and allied spores. The complete groups and their representation are shown in Table I.1

The terms used in the morphological description of pollen grains are, except where stated, those defined by Faegri and Iversen (1964), whilst terms relating to pteridophyte spore morphology adhere to the usage of Harris (1955). The term 'exine' is used *sensu* Erdtman (1952) to describe the entire outer sporoderm of both pollen and pteridophyte spores. The perisporium, or perine, is defined as the outermost layer of some spores, whether or not it is supposed part of the exine, or extra exinous. The descriptions employ the minimum number of terms required to describe a taxon uniquely. Except where statistical parameters are given, size measurements are 'typical' rather than results based on a number of systematic measurements.

*TABLE I.1. Pollen- and spore-morphological groups recognised and their representation*

| Number | Morphological category | Number of types recognised<br>Identified | <br>Unidentified |
|---|---|---|---|
| 1. | Vesiculate | 3 | - |
| 2. | Inaperturate | 4 | 1 |
| 3. | Monocolpate | 4 | 1 |
| 4. | Monoporate & Cyperaceae | 15 | 1 |
| 5. | Dicolpate | 2 | - |
| 6. | Tricolpate | 7 | 3 |
| 7. | Stephanocolpate | 2 | - |
| 8. | Tricolporate | 53 | 17 |
| 9. | Stephanocolporate | 5 | 2 |
| 10. | Pericolpate/colporate | 2 | - |
| 11. | Diporate | 7 | 2 |
| 12. | Triporate | 13 | 2 |
| 13. | Stephanoporate | 1 | 1 |
| 14. | Periporate | 2 | 1 |
| 15. | Syncolpate/colporate | 5 | - |
| 16. | Heterocolporate | 2 | - |
| 17. | Tetrad | 4 | - |
| 18. | Monolete | 15 | 2 |
| 19. | Trilete | 9 | 4 |

## 1. VESICULATE

*Phyllocladus* (Podocarpaceae) (Plate I.1, 1)
128 PHYLO

Bisaccate grain, oval to rectangular in shape in polar view with narrow, flat, bladders. Size variable, max. dimension 30-40 µm.

*Podocarpus* (Podocarpaceae) (Plate I.1, 2,3)
127 PODOC

Bisaccate grain with large reticulate bladders. Size variable, max. dimension usually between 40-80 µm.

*Dacrycarpus* T. (Podocarpaceae) (Plate I.1, 4)
129 DACRY

Trisaccate ± spherical grain. Diameter *c.* 60 µm. This type also includes some *Podocarpus* spp., notably *P. imbricatus*, *P. compactus*, *P. papuanus*, and *P. cinctus*.

## 2. INAPERTURATE

cf. *Cananga odorata* (Annonaceae) (Plate I.1, 5)
41 CANAN

Grain flattened, ± oval in ?polar view. Exine thin, sculpturing ± psilate, but variable. Size very variable, typically 50-90 µm max. dimension.

cf. *Gnetum* (Gnetaceae) (Plate I.1, 6)
130 GNETU

Grain spheroidal, diameter *c.* 15 µm. Exine covered with regularly distributed micro-echinae less than 1 µm in length. Pattern appears almost foveolate at low focus.

*Pandanus radula* T. (Pandanaceae) (Plate I.1, 7)
2 PANDA

Grain a flattened sphere, maximum dimension *c.* 17 µm. Sculpturing consists of irregularly distributed micro-echinae less than 1 µm in length. A faint porus may be visible. Similar types probably occur in many other *Pandanus* spp.

cf. *Colocasia* (Araceae) (Plate I.1, 8)
20 COLOC

Grain ± spherical with regularly distributed, broad-based echinae, at least 2 μm in length.

Unknown 274 (Plate I.1, 9)
135 UK274

Grain with thick, heavily sculptured gemmate exine. Gemmae *c.* 3 μm in length.

## 3. MONOCOLPATE

?*Normanbya* T. (Palmae) (Plate I.1, 10)
18 NORMA

A plano-convex grain in equatorial view, with a long colpus. Exine psilate or faintly scabrate. Slightly similar to several Palmae including *Normanbya* and *Archontophoenix*.

cf. Liliaceae (Plate I.1, 11)
22 LILIA

Grain typically 26 x 22 μm. Exine reticulate, with two distinct layers. Generic affinity unknown. Some Palmae, such as *Caryota* have slightly similar pollen.

?Palmae (Plate I.2, 12)
15 PALMA

Grain *c.* 18 x 12 μm, faintly reticulate. Exine not visibly more than single layered.

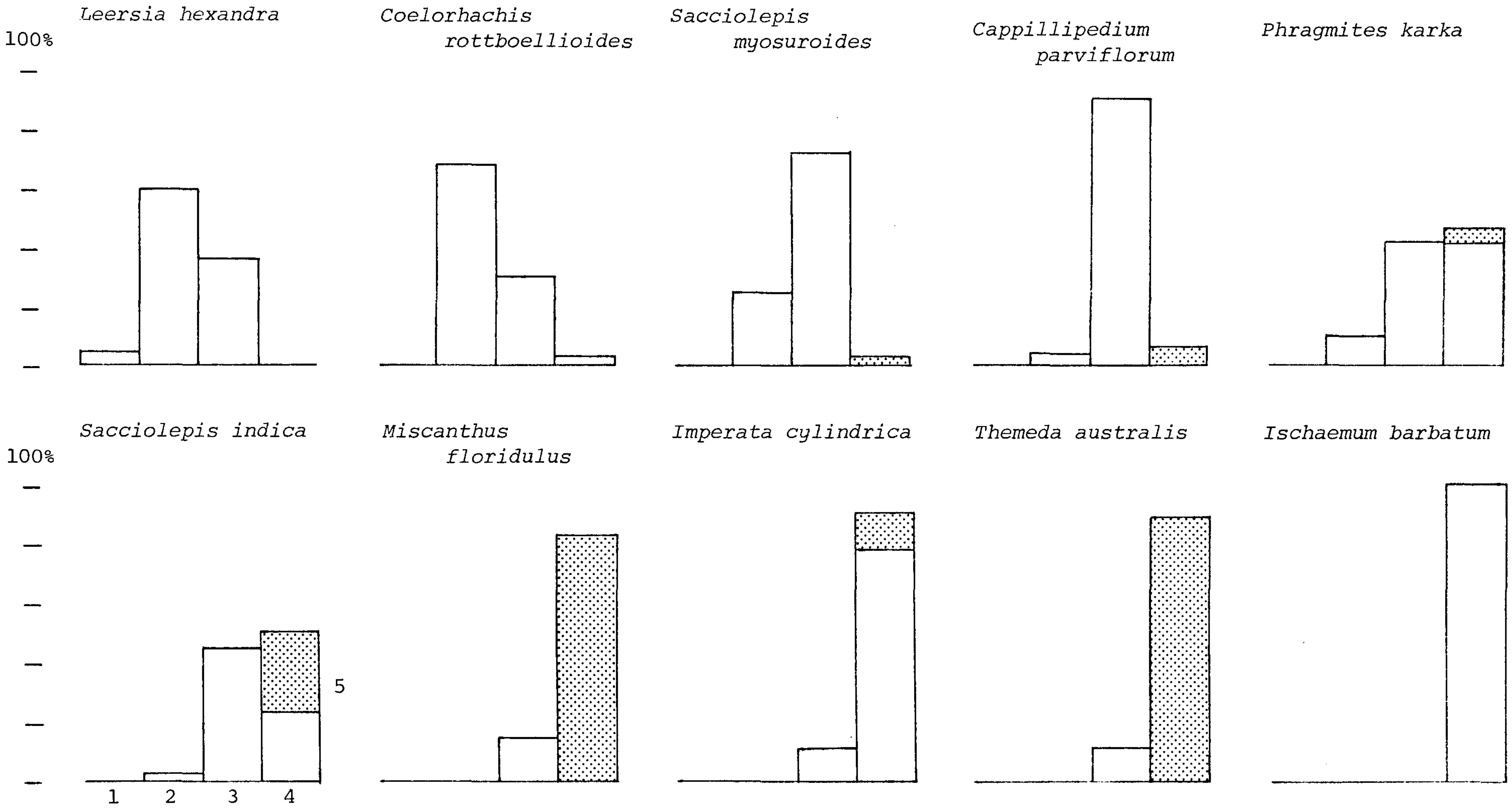
cf. *Arenga* (Palmae) (Plate I.2, 13)
19 ARENG

Grain circular in polar view, oval in equatorial view. Exine echinate, colpus indistinct.

Unknown 156 (Plate I.2, 14)
136 UK156

Plano-convex grain in equatorial view, with thick exine. Sparsely covered with small verrucae.

FIGURE I.1. Size-class distribution of pollen grains from some common grass species



## 4. MONOPORATE AND CYPERACEAE

### 4A. Monoporate

Gramineae 1
4 GRAM1

Max. dimension less than 20 µm.

Gramineae 2
5 GRAM2

Max. dimension 20-25 µm.

Gramineae 3 (Plate I.2, 15)
6 GRAM3

Max. dimension 25-30 µm.

Gramineae 4
7 GRAM4

Max. dimension larger than 30 µm.

Gramineae 5 (Plate 1.2, 16)
8 GRAM5

Grain with distinct areolate or coarse scabrate pattern, max. dimension greater than 30 µm. The distribution of the morphological types amongst the more common Markham Valley grasses is shown in Fig. I.1.

*Flagellaria* (Flagellariaceae) (Plate I.2, 17)
21 FLAGE

Grain ± spherical, *c*. 16 µm in diameter. Exine reticulate in high focus, becoming almost foveolate in low focus. Porus circular, with annulus, slightly protruding.

*Sparganium antipodum* T. (Sparganiaceae) (Plate I.2, 18)
3 SPARG

Grain ± spherical. Exine finely reticulate. Porus circular, unpatterned, without annulus.

*Typha* (Typhaceae) (Plate I.2, 19)
1 TYPHA

Grain oval to rectangular in either polar or equatorial aspect. Exine thick with reticulate sculpturing. Porus uneven in shape, sometimes indistinct. Grains frequently found clumped, or in tetrads.

Unknown 292 (Plate I.2, 20)
137 UK292

Grain ± spherical, exine scabrate. Porus diffuse with ragged edges, no annulus. *Cyrtospermum* (Araceae) is slightly similar, but larger.

Monoporate (undifferentiated)
138 MONPU

## 4B Cyperaceae

*Hypolytrum nemorum* T. (Cyperaceae) (Plate I.2, 21)
14 HYPOL

Grain ± spherical, diameter 16 µm. Exine scabrate. Porus unevenly circular or rectangular with distinct, but ragged edge; no annulus. *H. compactum* is similar to *H. nemorum*. Other *Hypolytrum* spp. differ in their pollen morphology.

Cyperaceae A1 (Plate I.2, 22)
9 CYPA1

Heteropolar 'pear-shaped' grains less than 30 µm maximum diameter. This type includes *c.* 8% of two common *Cyperus* spp., *C. platystylis* and *C. polystachos*.

Cyperaceae A2
10 CYPA2

Heteropolar 'pear-shaped' grain, max. dimension larger than 30 µm. Includes minor proportions of the grains from *Eleocharis dulcis*, *Scirpus grossus*, *Fuirena ciliaris*, and *c.* 20% of *Carex sarawaketensis* grains.

Cyperaceae B1
11 CYPB1

Grains rectangular to oval from either aspect, max. dimension less than 30 µm. Includes over 90% of *Cyperus polystachos*, *C. platystylis*, *Fimbristylis tenuinervia* and some *Fuirena ciliaris* grains.

Cyperaceae B2 (Plate I.2, 23)
12 CYPB2

Grains rectangular to oval in either aspect, max. dimension larger than 30 µm. Includes a large majority of *Eleocharis dulcis*, *Fuirena ciliaris*, *Fimbristylis dichotoma* and *Carex sarawaketensis* grains.

Cyperaceae C
13 CYPCI

Spherical cyperaceous grains (excluding *Hypolytrum nemorum* T.). About 15% of *Fimbristylis dichotoma* grains belong to this group.

## 5. DICOLPATE

*Calamus* (Palmae) (Plate I.2, 24)
17 CALAM

Grain oval in polar view. Scabrate-reticulate, or verrucate sculpturing. Colpus margin ragged.

?*Metroxylon sagu* (Palmae) (Plate I.2, 25)
16 METRO

Tentative identification based on description and illustration in Thanikaimoni (1970). Psilate grain with uneven colpus margins. Size *c*. 32 x 23 µm.

## 6. TRICOLPATE

*Anisoptera* T. (Dipterocarpaceae) (Plate I.3, 26,27)
93 ANISO

Grain ± spherical, diameter *c.* 17 µm, or oblate (split colpi). Exine regularly scabrate or per-reticulate. In polar optical section colpus edges appear rounded; only one layer distinguishable in exine. This type also includes *Vatica*. Most *Hopea* grains are 4- or 6-colpate.

*Dysophylla* T. (Labiatae) (Plate I.3, 28,29)
119 DYSOP

Grain ± spherical, diameter *c.* 18 µm, or oblate (split colpi). Exine reticulate with two distinct layers. In polar optical section, colpus edges appear pointed. Similar pollen grains also occur in other families including Hammamelidaceae and Verbenaceae. Many other Labiatae genera produce pollen that is stephanocolpate or tricolpate and psilate.

cf. Verbenaceae/Bignoniaceae (Plate I.3, 30)
117 VERBI

Grains spherical, or oblate (split colpi). Size *c.* 35 x 25 µm. Exine thick, reticulate. Two distinct layers sometimes visible in exine. This type is found in *Gmelina* and *Callicarpa* (Verbenaceae) and *Haussemanianthes* (Bignoniaceae).

*Timonius* T. (Rubiaceae) (Plate I.3, 31)
121 TIMON

Grain ± spherical, sometimes appearing inaperturate. Thick exine, with visible columellae. Sculpturing consists of a large-scale reticulum, diameter of lumina *c.* 3 µm. Muri become 'bead-like' in low focus. *Antirhea* produces similar pollen grains.

*Nelumbo nucifera* (Nymphaceae) (Plate I.3, 32)
37 NELUM

Grain ± spherical, although usually found oblate with split colpi. Diameter variable, typically *c.* 60 µm. Exine *c.* 4 µm in thickness, semitectate, dense columellae becoming ± fused in surface focus, discrete in low focus.

*Ilex* (Aquifoliaceae) (Plate I.4, 33,34)
76 ILEXA

Grain prolate to oblate, size variable, diameter typically 18 µm. Exine clavate, clavae becoming smaller towards the psilate colpus. A small circular porus is sometimes visible within the colpus.

*Endospermum* (Euphorbiaceae) (Plate I.4, 35)
72 ENDOS

Grain oblate, size variable. Exine thick, sculpturing consists of verrucae or gemmae that appear angular in optical section. Maximum diameter of elements is 2 µm, becoming smaller towards the colpi.

Unknown 235 (Plate I.4, 36)
139 UK235

Grain prolate, lobate in polar view, size *c.* 43 x 24 µm. Sculpturing reticulate, columellae clearly visible in exine optical section.

Unknown 293 (Plate I.4, 37)
140 UK293

Grain ± circular in equatorial view, inter-hexagonal in polar view. Diameter *c.* 31 µm. Sculpturing reticulate, scale becoming smaller towards poles. Maximum exine thickness *c.* 4 µm.

Tricolporate (undifferentiated)
141 TRICU

## 7. STEPHANOCOLPATE

cf. *Myrsine* T. (Myrsinaceae) (Plate I.4, 38,39)
107 MYRSI

Grain prolate to slightly oblate. Three to five colpi, often not parallel to polar axis. Colpus ± straight, with ragged margin. Exine scabrate or faintly microreticulate. Diameter *c.* 20 µm. Pollen grains of this type from various species of *Myrsine* have been described by Morley (1976) and Selling (1974). Some *Rapanea* spp. appear to produce similar grains (van der Hammen *et al.* 1973).

*Nothofagus* (Fagaceae) (Plate I.4, 40)
25 NOTHO

Grain ± hexagonal, depressed oval shape in equatorial view. Colpus short; sculpturing composed of regularly arranged minute baculae. All grains encountered fall within the '*brassii*' pollen subtype.

## 8. TRICOLPORATE

### 8A. Tricolporate - max. diameter smaller than 15 μm

*Elaeocarpus* T. (Elaeocarpaceae) (Plate I.4, 41)
85 ELAEO

Grain oblate to prolate, usually inter-sub-angular. Max. dimension 7 - 10 μm. Exine psilate. Meridional colpus interrupted at equator, although no distinct transverse aperture usually distinguishable.

*Octomeles sumatrana* (Datiscaceae) (Plate I.4, 42)
96 OCTOM

Grain oblate, ± sub-angular, typically 9.5 x 11 μm. Sculpturing faintly scabrate. Exine Max. thickness greater than 1 μm, becoming thinner towards the colpi. Polar area small, colpus long, unpatterned, although often indistinct. Porus small, ± circular, indistinct especially in surface focus.

*Macaranga ovatifolia* T. (Euphorbiaceae) (Plate I.4, 43)
67 MACOV

Grain ± spherical, diameter less than 10 μm. Faintly but distinctly scabrate. Transverse colpus almost slit-like, patterned in surface focus. Apart from the shape and patterning of the transverse colpus, this pollen type is almost identical to that produced by some *Aceratium* spp. (Elaeocarpaceae). A proportion of grains from other *Macaranga* spp., in particular *M. fimbriata*, may be included in this category.

*Macaranga* (Euphorbiaceae) (Plate I.4, 44,45)
66 MACAR

Grains prolate or oblate, semi-angular, or inter-sub-angular, maximum diameter usually less than *c.* 13 μm. Exine scabrate to microreticulate, appearing thickened around the colpi in polar view. Transverse colpus rectangular or slit-like, patterned in surface focus only.

*Macaranga/Mallotus* (Euphorbiaceae)
61 MACMA

Pollen grains of *Macaranga* or *Mallotus* configuration that cannot be assigned with certainty to either genus. Size range *c.* 13 to 18 µm max. dimension.

Rhamnaceae (Plate I.4, 46,47)
84 RHAMN

Grains usually oblate to circular in equatorial view, ± angular in polar view. Size variable, max. diameter usually less than 15 µm. Sculpturing psilate to faintly scabrate. Colpus long, transverse porus ± circular, with partial annulus. This type probably includes many rhamnaceous genera with predominantly small pollen grains, such as *Ventilago* and *Gouania*, and a minor proportion of the pollen of others, such as *Zizyphus*, and *Alphitonia*.

*Spiraeopsis* T. (Cunoniaceae) (Plate I.5, 48)
47 SPIRA

Grains ± spherical, very small, diameter *c.* 8 µm. Sculpturing faintly reticulate, columellae visible in exine optical section. Transverse porus ± circular, although small and indistinct especially in surface focus. This type also includes a large proportion of grains from the genera *Pullea, Aistopetalum, Opocunonia, Spiraeanthemum* and *Ackama*.

*Weinmannia* T. (Cunoniaceae) (Plate I.5, 49)
46 WEINM

Grain oblate, semi-angular or sub-angular, *c.* 10 x 11 µm. Sculpturing faintly reticulate, columellae visible in exine section. Transverse colpus ± rectangular, slightly constricted by the meridional colpus. This type may include a small proportion of grains from other tricolporate genera of Cunoniaceae.

*Hypserpa* (Menispermaceae) (Plate I.5, 50)
39 HYPSE

Grain oblate to prolate, polar axis *c.* 12 to 15 µm. Exine distinctly two-layered, sculpturing reticulate or microreticulate. Transverse porus ± circular, patterned in surface focus, sometimes indistinct.

*Uncaria* T. (Rubiaceae) (Plate I.5, 51,52)
125 UNCAR

Grain oblate to prolate, maximum diameter usually less than 11 µm. Morphologically similar to *Neonauclea*, although sculpturing less distinct, usually microreticulate or faintly scabrate, and porus smaller. A small proportion of *Neonauclea* grains may be included in this type.

*Nauclea* T. (Rubiaceae) (Plate I.5, 53)
124 NAUCL

Grains usually oblate, equatorial diameter 11 - 15 µm. Exine up to 1.5µm in thickness, columellae visible in optical section. Sculpturing finely reticulate. Meridional colpus distinct with thickened margo. Porus circular with thickened annulus. The type is also found in *Neonauclea, Sarcocephalus* and *Anthocephalus*. Pollen of these genera tends to be smaller with less pronounced sculpturing than that of *Nauclea*, although ranges overlap. This is perhaps to be expected given the complex generic synonymy of the Naucleae (Ridsdale, 1970). A small proportion of *Uncaria* grains may also be represented in this category.

*Tetracera* T. (Dilleniaceae) (Plate I.5, 54)
92 TETRA

Grain oblate to prolate. Exine visibly two-layered, sculpturing clearly reticulate. Size and shape very variable. Colpus usually splits, enclosing a large ± oval porus, unpatterned, with ragged edges. This pollen type also occurs in some species of *Hibbertia*.

*Olea* (Oleaceae) (Plate I.5, 55)
112 OLEAS

Grain oblate, or ± spherical, diameter *c*. 14 µm. Exine thick, distinctly two layered, columellae visible. Sculpturing reticulate in surface focus, discrete columellae visible at low focus. Porus indistinct.

*Rapanea* cf. *achradaefolia* T. (Myrsinaceae) (Plate I.5, 56)
106 RAPAN

Grain prolate, circular to inter-semi-angular in polar view. Sculpturing regularly scabrate, polar area small. Colpus unpatterned with slightly thickened margo, constricted at equator although no clear transverse aperture visible.

Unknown 194 (Plate I.5, 57)
142 UK194

Grain prolate, ± sub-angular, size variable, typically 12 x 10 µm. Exine relatively thick *c.* 1 µm, sculpturing psilate to faintly scabrate. Meridional colpus interrupted at equator, although transverse aperture not clearly visible.

Unknown 109 (Plate I.5, 58)
143 UK109

Grain ± spherical, diameter *c.* 12 µm. Exine distinctly two layered; sculpturing scabrate. Meridional colpus narrow; transverse colpus large, rectangular to oval, unpatterned. This type bears a slight similarity to some grains from the genus *Ternstroemia* (Theaceae).

Unknown 104 (Plate I.5, 59)
144 UK104

Grain oblate, almost apiculate in equatorial view, angular in polar view. Diameter *c.* 12 µm. Max. exine thickness *c.* 1.5 µm. Sculpturing psilate, or faintly scabrate. Transverse colpus protruding, constricted by meridional colpus, unpatterned.

Unknown 60 (Plate I.5, 60)
145 UK060

Grain ± spherical, diameter *c.* 14 µm. Sculpturing consists of a fine reticulum of isodiametric elements. Columellae clearly visible in exine optical section. Meridional colpus narrow, unpatterned; transverse colpus rectangular, patterned in surface focus. This type bears a superficial resemblance to the pollen produced by some genera of Sterculiaceae, Euphorbiaceae and Flacourtiaceae.)

Tricolporate, Section A, (undifferentiated)
146 3CPAU

8B. Tricolporate, max. diameter larger than 15 µm sculpturing scabrate or psilate, grain prolate

*Castanopsis* T. (Fagaceae) (Plate I.5, 61,62)
26 CASTA

Grains prolate, polar axis usually 14 - 20 µm, although may be larger. Inter-semi-angular or inter-semi-lobate in polar view. Sculpturing usually psilate or faintly scabrate, a few species coarsely scabrate. Transverse colpus rectangular or slit-like.

*Lithocarpus* spp. are generally more prolate, and larger than those of *Castanopsis*, however ranges of size and morphology overlap considerably.

*Rhizophora apiculata* T. (Rhizophoraceae) (Plate I.5, 63)
99 RHIZO

Grain prolate, size variable, polar axis usually 17 - 25 µm. Exine thick, evenly scabrate. Columellae sometimes visible. Distinct equatorial colpus is faintly patterned in surface focus.

cf. *Crotalaria* T. (Leguminosae) (Plate I.5, 64)
53 CROTA

A very variable type, both in size and morphology. Usually prolate, inter-semi-lobate *c.* 20 x 13 µm. Sculpturing evenly scabrate, or faintly microreticulate. Meridional colpus long, with slightly thickened margo, usually asymmetrically constricted at equator. Transverse colpus oval, patterned in surface focus. This pollen type is produced by some genera of Papilionatae, including *Crotalaria*, and by several species of *Cassia* (Caesalpinioideae).

?Leguminosae (Papilionatae) B (Plate I.5, 65)
50 LEGPB

Grains prolate, inter-sub-angular, or inter-semi-lobate. Sculpturing psilate or faintly scabrate. Colpus long, interrupted at equator by large indistinct, sometimes oval, transverse aperture.

cf. *Bischofia* (Euphorbiaceae) (Plate I.5, 66,67)
71 BISCH

Grain circular or prolate in equatorial view, ± circular in polar view. Size variable, polar axis *c.* 14 - 18 µm. Sculpturing microreticulate or regularly scabrate. Distinct columellae visible in exine section. Transverse colpus rectangular, patterned in surface focus, often slit-like. Meridional colpus narrow, unpatterned at any level.

*Antidesma* (Euphorbiaceae) (Plate I.6, 68,69)
68 ANTID

Grain prolate, often lobate. Size variable, typically 18 x 12 µm. Transverse colpus rectangular, bordered by distinct, parallel costae.

*Euphorbia hirta* T. (Euphorbiaceae) (Plate I.6, 70)
59 EUPHI

Grain prolate, inter-semi-lobate, *c*.24 x 16 µm. Exine thick, up to 3 µm, with distinct columellae; sculpturing coarsely scabrate, or almost microreticulate. Exine becomes thinner around the psilate colpus area. Transverse colpus ± oval or rectangular. This type is also found in other *Euphorbia* spp. including *E. velutina*.

cf. *Euphorbia* (Euphorbiaceae) (Plate I.6, 71)
58 EUPHA

Grains prolate *c*. 25 x 20 µm, with small polar area. Sculpturing coarsely scabrate to unevenly reticulate. Exine thick, two layers visible. Type found in some *Euphorbia* spp. and may also include representatives from other genera of the family, such as *Sapium*.

*Rhus* T. (Anacardiaceae) (Plate I.6, 72)
75 RHUST

Grain prolate, sub-angular, or semi-angular. Sculpturing scabrate to microreticulate. Transverse colpus rectangular, very equatorially elongated, edges ragged. This type closely resembles *Rhus taitensis* and similar forms occur in other genera of Anacardiaceae.

*Diospyros* cf. *ferrea* (Ebenceae) (Plate I.6, 73)
110 DIOSP

Grain prolate, inter-hexagonal to semi-lobate. Exine faintly scabrate to psilate. Meridional colpus faint in surface focus, transverse colpus ± circular, with indistinct edges.

*Planchonella* T. (Sapotaceae) (Plate I.6, 74,75)
108 PLANC

Grain prolate, size variable but polar axis usually larger than 30 µm. Colpus long and narrow. Porus well defined, circular or oval, unpatterned, without thickened annulus; often protruding. This type also includes *Chrysophyllum* and *Pouteria*. Most other genera of Sapotaceae produce 4-colporate pollen predominantly.

cf. *Palaquium* (Sapotaceae) (Plate I.6, 76)
109 PALAQ

Grain prolate, sub-angular, *c*. 31 x 26 µm. Sculpturing evenly scabrate or faintly microreticulate. Faint columellae visible in exine optical section. Transverse colpus oval, equatorially elongated. This type resembles a proportion of grains from the genus *Palaquium* but differs from *Planchonella* T. only in the sculpturing pattern and transverse colpus morphology.

Unknown 79 (Plate I.6, 77,78)
147 UK079

Grain prolate, inter-semi-angular size *c*. 18 x 12 µm. Sculpturing psilate or faintly scabrate. Colpus long and narrow, polar area small. Transverse aperture small, shape indistinct. Thickened costae visible around aperture especially in optical section.

Unknown 119 (Plate I.6, 79)
148 UK119

Grain prolate, inter-sub-angular, size *c*. 18 x 11 µm. Sculpturing scabrate. Exine max. thickness *c*. 2.5 µm. Meridional colpus long, polar area small. Transverse colpus wide, slit-like, patterned, with distinct thickened costae.

Unknown 174 (Plate I.6, 80)
149 UK174

Grain prolate, apiculate in equatorial view, sub-angular in polar view. Sculpturing coarsely scabrate to microreticulate. Polar area small. Transverse aperture indistinct.

Tricolporate, Section B, (undifferentiated)
150 3CPBU

8C. Tricolporate, larger than 15 µm, sculpturing scabrate or psilate, grain spherical to oblate

cf. Euphorbiaceae (Plate I.6, 81)
56 EUPHT

Grain oblate *c*. 14 x 15.5 µm. Sculpturing scabrate, meridional colpus narrow, polar area small. Transverse colpus patterned in surface focus; faint costae present.

*Mallotus* T. (Euphorbiaceae) (Plate I.6, 82)
60 MALLO

Grain spherical to oblate, max. diameter larger than 17 µm. Two broad types may be distinguished:
*M. philippinensis* T. with very short colpi, ± circular in polar view.
*M. paniculata* T. with longer colpi, semi-angular or almost inter-hexagonal in polar view. (Includes *M. ricinoides*).

*Cleidion* T. (Euphorbiaceae) (Plate I.6, 83)
73 CLEID

Grain inter-semi-lobate, ± circular in equatorial view. Max. diameter *c.* 17 - 20 µm. Transverse colpus wide, patterned in surface focus.

cf. *Muehlenbeckia* (Polygonaceae) (Plate I.6, 84)
36 MUEHL

Grain spherical to prolate, diameter *c.* 18 µm. Exine coarsely scabrate. Polar area small. Transverse colpus rectangular to oval, equatorially elongated.

cf. *Rumex brownii* (Polygonaceae) (Plate I.7, 85)
35 RUMEX

Grain inter-sub-angular, oblate, *c.* 20 x 22 µm. Sculpturing scabrate to unevenly reticulate. Porus ± circular, with slightly thickened annulus. Heteropolar, with arci linking colpi at one pole.

*Dodonaea* (Sapindaceae) (Plate I.7, 86)
81 DODON

Grain ± spherical, size variable. Colpus narrow and long, polar area small. Porus circular to slightly oval, equatorially elongated, and protruding. This type is characteristic of some New Guinea and North Queensland *Dodonaea* spp.

*Acaena* (Rosaceae) (Plate I.8, 87)
48 ACAEN

Grain spherical, or oblate, max. diameter *c.* 27 µm. Sculpturing coarsely scabrate. Meridional colpus short, often indistinct. Transverse colpus ± oval, equatorially elongated, with thin protruding operculum.

?*Parinari* (Rosaceae) (Plate I.7, 88)
49 PARIN

Grain oblate to prolate, semi-angular. Size variable. Sculpturing coarsely scabrate. Polar area small. Meridional colpus with slightly thickened margo. Transverse colpus indistinct. This type slightly resembles pollen from some species of *Thea* and *Gordonia* (Theaceae), *Indigofera* (Leguminosae).

Unknown 123 (Plate I.7, 89)
151 UK123

Grain oblate to prolate, inter-semi-angular. Max. diameter *c*. 16 µm. Sculpturing microreticulate, elements less than 1 µm in diameter. Columellae clearly visible in exine section. Meridional colpus constricted at equator although clear transverse aperture not visible in surface focus.

Unknown 221 (Plate I.7, 90)
152 UK221

Grain oblate, ± sub-angular, *c*. 15 x 17 µm. Sculpturing coarsely scabrate, colpus area psilate. Polar area small. Porus ± oval, equatorially elongated, extending to the margin of the meridional colpus.

Unknown 218 (Plate I.7, 91)
153 UK218

Grain oblate, *c*. 18 x 14 µm. Exine scabrate. Meridional colpus wide, unpatterned. In polar view exine becomes thinner towards colpus. Meridional colpus constricted at equator. Transverse colpus patterned in surface focus.

Tricolporate, Section C (undifferentiated)
154 3CPCU

### 8D. Tricolporate, larger than 15 µm, sculpturing reticulate

*Vandasia* T. (Leguminosae) (Plate I.7, 92)
52 VANDA

Grain ± circular in equatorial view, semi-angular in polar view. Max. diameter *c.* 16 µm. Sculpturing a small scale reticulum, with a psilate margo around the meridional colpus. Transverse colpus rectangular to oval, unpatterned. Morphologically similar grains occur in other genera of the Papilionatae, including *Pterocarpus, Pueraria,* and *Tephrosia*, and in some species of *Ternstroemia* (Theaceae).

cf. *Sterculia edelfeltii* (Sterculiaceae) (Plate I.7, 93,94)
91 STERE

Grain ± spherical, diameter *c.* 18 µm. Reticulate sculpturing consisting of elongated elements of variable size. Transverse colpus ± rectangular, patterned in surface focus.

*Platea excelsa* (Icacinaceae) (Plate I.7, 95)
80 PLATE

Grain ± spherical. Exine *c.* 2.5 µm thick, two layered, with clearly visible columellae. Reticulum breaks up into separate columellae in low focus. Transverse colpus ± rectangular, indistinct in surface focus.

*Melanolepis* T. (Euphorbiaceae) (Plate I.7, 96,97,98)
70 MELAN

Grain spherical to oblate, diameter *c.* 25 µm. Exine thick, sculpturing reticulate. Transverse colpus ± rectangular, patterned in surface focus only. This type is found also in *Bridelia* and *Cleistanthus*, although the grains are usually slightly smaller. In some *Bridelia* spp., the muri are aligned to form 'pseudostriations' *sensu* Punt (1962), whereas in *Cleistanthus,* the reticulum is less distinct.

*Boerlagiodendron* (Araliaceae) (Plate I.7, 99,100)
104 BOERL

Grain angular to sub-angular, oblate. Sculpturing dimorphic: microreticulate around colpi and porae, and disjunctly reticulate between the colpi.

*Morinda* (Rubiaceae) (Plate I.7, 101)
123 MORIN

Oblate to spherical grain, size variable. Sculpturing reticulate, colpus area psilate. Porus large, ± circular with heavily thickened annulus.

*Echium* cf. *plantagineum* (Boraginaceae) (Plate I.8, 102)
116 ECHIP

Grain heteropolar, 'pear-shaped' *c.* 22 x 15 µm. Exine microreticulate. Porus oval, with slightly thickened annulus.

*Evodia* T. (Rutaceae) (Plate I.8, 103,104)
55 EVODI

Grain prolate *c.* 18 x 13 µm. Exine two-layered, evenly reticulate. Transverse colpus rectangular, unpatterned. This type includes *E. xanthoxyloides* and other *Evodia* spp., and some species of *Melicope*.

*Aporosa* (Euphorbiaceae) (Plate I.8, 105,106)
69 APORO

Grain inter-sub-angular, prolate to circular in equatorial view, size *c.* 18 x 14 µm. Exine finely reticulate. Transverse colpus narrow, slit-like, *c.* 6 µm in length.

?Leguminosae (Papilionatae) D (Plate I.8, 107,108)
51 LEGPD

Grains prolate, inter-sub-angular or inter-semi-lobate. Max. diameter 18-25 µm. Sculpturing distinctly microreticulate. Meridional colpus, long, constricted or distorted at equator by the transverse aperture. This type is found in genera of the Papilionatae such as *Pueraria*, and *Gompholobium* and in several species of *Hypericum* (Guttiferae).

*Brachychiton* T. (Sterculiaceae) (Plate I.8, 109)
88 BRACH

Grain prolate, size variable. Exine two layered; sculpturing reticulate; max. diameter of luminae *c.* 2 µm, smaller towards colpi. Meridional colpus unpatterned, sharply defined. Transverse aperture oval or rectangular. Grains of this type occur in some *Brachychiton, Argyrodendron, Pterocymbium*, and *Sterculia* species.

*Microcos* T. (Tiliaceae) (Plate I.8, 110)
86 MICRO

Grain prolate to spherical, typically 21 x 14 µm. Reticulum similar to *Trichospermum*, but smaller scale, and more uniform in size. Transverse colpus wide but indistinct. Similar grains are produced by *Columbia*, and *Grewia paniculata*.

*Trichospermum* (Tiliaceae) (Plate I.8, 111)
87 TRICO

Grain prolate *c*. 30 x 18 µm. Exine reticulate, largest diameter of lumenae *c*. 2.5 µm, decreasing in size towards the colpi.

Rutaceae/Araliaceae T. (Plate I.8, 112,113)
54 RUTAR

Grains prolate, usually 20 - 30 µm polar axis. Exine ± reticulate, often distinctly two layered. Meridional colpus clearly interrupted by transverse aperture, usually rectangular, which may be patterned in surface focus. A diverse type found in many genera including *Evodiella, Acronychia* and *Flindersia* (Rutaceae), and *Schefflera* and *Harmsiopanax* (Araliaceae).

Unknown 309 (Plate I.8, 114)
155 UK309

Grain slightly oblate, semi-angular, size *c*. 20 x 22 µm. Sculpturing finely reticulate, colpus area psilate. Porus oval, meridionally elongated, unpatterned.

Unknown 310 (Plate I.8, 115)
156 UK310

Grain ± spherical, diameter *c*. 40 µm. Max. exine thickness *c*. 2.5 µm. Sculpturing a reticulum consisting of ± circular elements. Colpus area psilate. Porus unpatterned, ± circular, without annulus, fully enclosed by colpus. Polar area small.

Tricolporate, Section D, (undifferentiated)
157 3CPDU

8E. Tricolporate, larger than 15 µm. Other sculpturing configurations.

Anacardiaceae (Plate I.8, 116,117)
74 ANACA

Grains ± spherical with long meridional colpus and distinct ± rectangular transverse colpus. Sculpturing faintly striate. Pollen similar to this type is produced by several genera of Anacardiaceae, including *Euroschinus* and *Semecarpus*.

cf. *Vitex acuminata* (Verbenaceae) (Plate I.9, 118)
118 VITEX

Grain prolate, inter-sub-angular, size *c.* 18 x 12 µm. Exine thick with strongly striate sculpturing. Transverse colpus ± oval to rectangular. This type is very similar to *V. acuminata,* although is generally slightly smaller, and has more pronounced sculpturing. Slightly similar striate grains are found in several genera of the Anacardiaceae.

*Ganophyllum falcatum* (Sapindaceae) (Plate I.9, 119,120)
82 GANOP

Grain ± spherical to prolate. Size variable, polar axis *c.* 12 - 16 µm. Exine sparsely covered with minute verrucate or baculate elements less than 1 µm in height. Porus ± circular, patterned in surface focus.

*Trichadenia philippinensis* (Flacourtiaceae) (Plate I.9, 121)
95 TRICA

Grain spherical to prolate, *c.* 23 x 20 µm, size variable. Sculpturing dimorphic; ± regularly arranged gemmae, *c.* 2 - 3 µm in width interspersed with smaller (less than 1 µm) gemmate elements.

Compositae (Tubuliflorae) (Plate I.9, 122)
126 COMPT

Grains usually oblate to spherical, size variable. Exine thick, with echinate sculpturing of variable size and density. An unpatterned, usually circular, porus may be visible. This type includes the majority of genera in the Tubuliflorae sub-family.

Tricolporate, Section E, (undifferentiated)
158 3CPEU

## 9. STEPHANOCOLPORATE

*Acalypha* (Euphorbiaceae) (Plate I.9, 123)
64 ACALY

Grain circular to oblate, 3- or 4-colporate. Colpus very short, often indistinct. Exine scabrate. Porus ± circular, with irregular annulus, slightly protruding in polar view.

*Quintinia* (Saxifragaceae) (Plate I.9, 124,125)
44 QUINT

Grain prolate, 5-colporate, *c.* 15 x 13 µm. Exine thick, psilate to slightly scabrate. Colpus interrupted at equator, although clear porus not always visible in surface focus.

*Claoxylon* (Euphorbiaceae) (Plate I.9, 126)
62 CLAOX

Grain prolate, 4- or 3-colporate. Exine faintly reticulate, transverse colpus indistinct.

*Phyllanthus* cf. *urinaria* (Euphorbiaceae) (Plate I.9, 127,128)
63 PHYLA

Grain prolate, 21 x 14 µm, 5-colporate, or 3-colporate. Exine thick, *c.* 2.5 µm, columellae visible in optical section, strongly reticulate. Colpus straight, porus small, circular, patterned in top focus only. This type closely resembles *Phyllanthus urinaria* although the slide in the ANU collection has predominantly 4-colporate grains. Punt and Rentrop (1973) describe a similar 5-colporate morphology for *P. caroliniensis*.

*Glochidion* T. (Euphorbiaceae) (Plate I.9, 129)
65 GLOCH

Grain 4-colporate or 4-colpate, usually prolate, circular in polar view. Exine *c.* 3 µm thick, with reticulate sculpturing; diameter of luminae up to 2 µm. Colpus straight, very distinct, small circular porus sometimes visible. Closely similar types are found in some *Phyllanthus* spp.

Unknown 106 (Plate I.9, 130)
159 UK106

Grain ± circular, angular in polar view, diameter *c.* 18 - 24 µm, 4-colporate. Sculpturing coarsely scabrate. Colpus narrow and short, length not more than twice the diameter of the transverse porus. Exine thickened around the protruding porus. Two or more of the porae may be connected by an equatorial arcus. This type superficially resembles some *Dysoxylum* spp. (Meliaceae) although the latter are psilate, and larger than 30 µm.

Stephanocolporate (undifferentiated)
160 STCPU

## 10. PERICOLPATE/COLPORATE

?*Evolvulus* (Convolvulaceae) (Plate I.9, 131)
115 EVOLV

Grain ± spherical, diameter *c.* 21 µm, with six short colpi. Exine minutely baculate in surface focus, becoming scabrate to reticulate in low focus. Colpus patterned in surface focus. This type slightly resembles *Evolvulus*, and some *Merremia* spp. (Convolvulaceae), although these are generally larger than 30 µm in diameter, and have a less complex exine pattern.

?Euphorbiaceae (Plate I.9, 132)
57 EUPHO

Grain 5- or 6-colporate, reticulate. Transverse colpus and sculpturing similar to some euphorbiaceous taxa such as *Claoxylon*.

## 11. DIPORATE

Urticaceae/Moraceae (diporate) (Plate I.9, 133)
30 URMO2

Grain ± circular in polar view, oval in equatorial view. Psilate or scabrate. Porus small with thickened annulus. Includes the genera *Elatostema, Debregeasia, Laportia* and *Cypholophus* (Urticaceae) and *Maclura* and *Malaisia* (Moraceae).

*Pilea* T. (Urticaceae) (Plate I.9, 134)
33 PILEA

Grain oval in both polar and equatorial view. Psilate or faintly scabrate. Small, circular porus with annulus. Small proportions of this type are produced by other genera of Urticaceae.

*Streblus* T. (Moraceae) (Plate I.9, 135)
32 STREB

Grain oval in polar view. Exine scabrate, porus circular without annulus. This type also includes *Antiaris*.

*Trema* (Ulmaceae) (Plate I.9, 136)
28 TREMA

Grain circular or oval in polar view. Sculpturing unevenly scabrate, with columellae visible in optical cross-section. Porus circular with slightly thickened annulus.

*Sphenostemon* cf. *papuanum* (Aquifoliaceae) (Plate I.9, 137)
77 SPHEN

Grain diporate or triporate; depressed oval shape in equatorial view. Exine reticulate with two distinct layers. Porus unpatterned, circular, without annulus.

*Polyporandra scandens* (Icacinaceae) (Plate I.9, 138)
78 POLYP

Oblate grain with sparse echinae. Porus circular with thickened annulus. Size *c*. 16 x 18 μm.

*Alyxia* (Apocynaceae) (Plate I.10, 139)
114 ALYXI

Asymmetrical plano-convex grain. Exine reticulate; porus circular, very large.

Unknown 279 (Plate I.10, 140)
161 UK279

Reticulate grain with distinctly two-layered exine. Porus circular with annulus.

Diporate (undifferentiated)
162 DIPOU

## 12. TRIPORATE

Urticaceae/Moraceae (Triporate) (Plate I.10, 141)
31 URMO3

Grain circular in polar view. Exine psilate or scabrate, porus small with thickened annulus. Type includes *Elatostema, Pipturus,* and *Pouzolzia* (Urticaceae) and *Morus* and *Malaisia* (Moraceae).

*Stemonurus* (Icacinaceae) (Plate I.10, 142)
79 STEMO

Oblate semi-angular grain, psilate or faintly scabrate. Exine thickened around edge of porus in optical section. Equatorial diameter *c.* 12 µm.

*Helicia* (Proteaceae) (Plate I.10, 143)
34 HELIC

Oblate angular grain with protruding vestibulate porae. Sculpturing scabrate; size 10 x 19 µm.

*Celtis* (Ulmaceae) (Plate I.10, 144)
27 CELTI

Grain ± circular in polar view, oblate. Sculpturing coarsely scabrate, columellae distinctly visible in optical cross-section. Porus circular with thickened annulus, sometimes slightly protruding. Max. diameter typically 15 - 17 µm.

cf. *Engelhardtia* (Juglandaceae) (Plate I.10, 145)
24 ENGEL

Grain oblate ± circular in polar view with scabrate to faintly microreticulate sculpturing. Porus indistinct, not protruding. Equatorial diameter *c.* 18 µm.

*Casuarina* (Casuarinaceae) (Plate I.10, 146)
23 CASUA

Spherical, or oblate grain with protruding porae. Exine generally ± scabrate. Equatorial diameter typically 25 µm, and not usually less than 20 µm.

*Haloragis* (Haloragaceae) (Plate I.10, 147)
103 HALOR

Oblate grain, circular in polar view. Oval or slit-like porus (or colpus), protruding. The *Haloragis* spp. in the ANU reference collection are predominantly 4- or 5-stephanoporate or colpate.

*Polyosma* (Saxifragaceae) (Plate I.10, 148,149)
45 POLYO

Oblate ± circular grain with protruding porae. Exine psilate or faintly scabrate, except around porus where it is unevenly reticulate and thickened. Porus ± round, with diffuse margin.

*Sonneratia caseolaris* (Sonneratiaceae) (Plate I.10, 150,151, 152)
97 SONNE

Prolate grain with protruding porae and dimorphic sculpturing. An equatorial band is finely verrucate, whilst the polar caps are psilate or scabrate. This type corresponds to several of the *S. caseolaris* sub-types proposed by Muller (1969), but is considerably smaller than any, with a polar axis 32 -38 µm in length. The pollen is identical in morphology and size to that of Havel and Kairo's collection from Labu Swamp (NGF 17198).

*Stephania japonica* T. (Menispermaceae) (Plate I.10, 153)
38 STEPJ

Oblate, semi-angular grain with a thick reticulate exine. Porus not very distinct in equatorial view. Size typically 11 x 13 µm. This type includes *S. hernandifolia*. *S. erecta* is 4-porate.

*Kleinhovia hospita* (Sterculiaceae) (Plate I.11, 154)
89 KLEIN

Semi-angular, oblate grain, typically 7 x 18 µm in size. Distinctly or faintly reticulate sculpturing, with columellae visible in exine optical section. Porus sometimes protruding, or almost vestibulate.

cf. *Sterculia* (Sterculiaceae) (Plate I.11, 155)
90 STERC

Grain ± circular, oblate, max. diameter *c*. 17 - 20 µm. Exine thick, sculpturing reticulate, with luminae of varying size and shape, often elongated. Porus ± circular, indistinct in surface focus, without annulus. This type is very similar to the pollen of a *Sterculia* sp. (Craven and Schodde coll. no. 1388) from Morobe Province.

*Symplocos* (Symplocaceae) (Plate I.11, 156)
111 SYMPL

Semi-angular, oblate grain with slightly protruding porae. Exine sculpturing sparsely echinate. Similar to New Guinea *Symplocos* spp.

Unknown 147 (Plate I.11, 157)
163 UK147

Spherical to oblate grain with thick reticulate exine. Porus ± circular with thickened annulus.

Triporate (undifferentiated)
164 TRIPU

## 13. STEPHANOPORATE

cf. *Aphananthe* (Ulmaceae) (Plate I.11, 158)
29 APHAN

Oblate grain *c*. 20 x 26 µm. Exine faintly scabrate. Four small, circular porae, unpatterned, with slight annulus.

Stephanoporate (undifferentiated)
165 STEPU

## 14. PERIPORATE

*Plantago* (Plantaginaceae) (Plate I.11, 159,160)
120 PLANT

Spherical grain with 8 to 13 porae. Scabrate to faintly reticulate sculpturing. Porus circular, unpatterned, with a narrow annulus.

cf. *Trimenia* (Monimiaceae) (Plate I.11, 161)
42 TRIME

Grain with about 8 porae. Exine thick, coarsely scabrate. Porus ± circular, unpatterned, without annulus.

Unknown 290 (Plate I.11, 162)
166 UK290

Grain *c*. 15 - 18 µm in diameter, with 5 to 7 porae. Exine coarsely scabrate.

## 15. SYNCOLPATE AND SYNCOLPORATE

### 15A. Syncolpate

*Tinospora* (Menispermaceae) (Plate I.11, 163)
40 TINOS

Inter-sub-angular grain with thick, reticulate exine. Circular to prolate in equatorial view, diameter *c*. 20 µm.

*Barringtonia* T. (Barringtoniaceae) (Plate I.11, 164)
98 BARRI

Grain with thick ± psilate exine, often becoming reticulate towards the colpi. Circular to prolate in equatorial view, size variable, typically 40 x 30 µm. *Planchonia* is similar.

*Nymphoides* (Gentianaceae) (Plate I.11, 165,166)
113 NYMPH

Oblate semi-angular grain, sparsely scabrate, with distinct 'island' at pole. Size variable, typically 20 x 28 µm.

## 15B. Syncolporate

*Tristiropsis* T. (Sapindaceae) (Plate I.11, 167)
83 TRIST

Oblate semi-lobate grain. Scabrate or microreticulate with distinct, patterned 'island' at pole. Grain oval in equatorial view, with colpi appearing arcate. Large circular porus.

Myrtaceae (Plate I.11, 168,169)
101 MYRTA

Grains oblate; semi-angular, semi-lobate, or sub-angular. Depressed oval shape in equatorial view. Small transverse colpus. Size and sculpturing very variable.

## 16. HETEROCOLPORATE

*Poikilogyne* T. (Melastomataceae) (Plate I.12, 170,171)
102 POIKI

Grain spherical to slightly prolate. Tricolporate with three intervening, less indented 'pseudo-colpi'. Sculpturing psilate to scabrate. Porus ± rectangular, although not very distinct. This type also includes *Beccarianthus, Medinella, Everettia, Sonerila, Marumia,* and probably other melastomataceous genera.

Combretaceae/Melastomataceae (Plate I.12, 172,173)
100 COMEL

Grain prolate, tricolporate with intervening 'pseudo-colpi' as indented as the compound colpi. Porus usually distinct ± rectangular. Sculpturing psilate to scabrate. This type includes *Combretum* and *Terminalia* (Combretaceae) and also some genera or species of Melastomataceae, notably *Melastoma affine,* and some *Osbeckia* grains.

## 17. TETRAD

*Gardenia* (Rubiaceae) (Plate I.12, 174)
122 GARDE

Psilate grain with tetrad diameter of *c.* 40 µm. Porus circular with thickened annulus.

Epacridaceae (Plate I.12, 175)
105 EPACR

Exine sculpturing psilate to scabrate. Tetrad diameter usually less than 40 µm. This type may include some genera of Ericaceae such as *Vaccinium* and *Diplocosia*.

*Drimys* T. (Winteraceae) (Plate I.12, 176)
94 DRIMY

Compact tetrad with a diameter of 20 - 30 µm. Exine thick, with large reticulate sculpturing. *Bubbia* is similar.

*Nepenthes* (Nepenthaceae) (Plate I.12, 177)
43 NEPEN

Tetrad of sparsely echinate spheroidal monads.

## 18. MONOLETE SPORES

Monolete psilate spore (smaller than 30 µm)
189 MONLS

Spores without perisporium, or psilate or only faintly sculptured, less than 30 µm in length. This type is found in many Polypodiaceae *sensu lato*, including *Nephrolepis*, *Cystodium* , *Cyclosorus*, *Thelypteris*, *Asplenium*, *Lastreopsis*, *Tectaria* and *Blechnum*.

Monolete psilate spore (larger than 30 µm) (Plate I.12, 178)
190 MONLL

Similar to previous type, but with a max. dimension exceeding 30 µm. Many genera fall into this group, some of the more common being *Hypolepis*, *Nephrolepis*, *Arthropteris*, *Gleichenia*, *Cyclosorus*, *Athyrium*, *Stenolepis*, *Lomariopsis* and *Blechnum*.

*Microsorium* T. (Polypodiaceae) (Plate I.12, 179)
188 MICSO

Concavo-convex spore with thick exine. Sculpturing is scabrate to faintly reticulate. Size measurements (ANU 21014)
Equatorial: Range 34-54 µm, Mean 44.8 µm, S.D. 4 µm
Polar: Range 20 - 38.5 µm, Mean 28.5 µm, S.D. 3.8 µm.

*Nephrolepis* (Oleandraceae) (Plate I.13, 180)
176 NEPHR

Slightly concavo-convex, or plano-convex. Thick exine, sculpturing punctate to unevenly reticulate. Size measurements (ANU 21015)
Equatorial: Range 27 - 36.5 µm, Mean 31.5 µm, S.D. 2 µm
Polar: Range 13.5 - 21 µm, Mean 16.5 µm, S.D. 1.7 µm.

*Cyclosorus* T. (Thelypteridaceae) (Plate I.13, 181)
181 CYCLO

Plano-convex to slightly concavo-convex spore. Max. dimension 35-50 µm. Perisporium sculpturing coarsely scabrate, or verrucate. Similar spores occur in some *Athyrium* spp.

*Histiopteris incisa* T. (Dennstaedtiaceae) (Plate I.13, 182)
174 HISTI

Plano-convex or concavo-convex spore with large scale, unevenly distributed verrucate sculpturing. Size typically 35 x 25 µm. *Belvisia* is similar, but larger.

*Davallia* T. (Davalliaceae) (Plate I.13, 183)
175 DAVAL

Large plano- or concavo-convex spore. Thick exine with rounded, discrete, and regularly distributed verrucae. This type includes other Davalliaceae such as *Scyphularia* and *Humata*.

*Stenochlaena palustris* (Blechnaceae) (Plate I.13, 184)
187 STENO

Biconvex or plano-convex spore. Distinctive sculpturing of sparse, rounded triangular verrucae. Size measurements (ANU 21045)
Equatorial: Range 36 - 47 µm, Mean 42 µm, S.D. 2.5 µm
Polar: Range 20.5 - 30 µm, Mean 25 µm, S.D. 2.2 µm.

cf. *Tectaria* (Aspidaceae) (Plate I.13, 185)
184 TECTA

Small spore, *c.* 31 x 20 µm. Thick perisporium with verrucate ridges.

*Stenochlaena laurifolia* (Blechnaceae) (Plate I.13, 186)
186 STENL

Distinctive plano-convex or concavo-convex spore *c.* 45 x 28 µm. Sculpturing of large verrucae aligned in ridges, ± parallel to the equatorial axis.

*Asplenium* T. (Aspleniaceae) (Plate I.13, 187)
183 ASPLE

Spores with a distinct, thin, folded or lightly sculptured perisporium. A large and diverse type including, as well as Aspleniaceae, many Dennstaedtiaceae, Aspidaceae, and Blechnaceae.

?*Arthropteris* cf. *tenella* (Oleandraceae) (Plate I.14, 188)
177 ARTHR

Spore with thin perisporium formed into long (15 µm) echinate projections. This type may also occur in other families, in particular Aspleniaceae.

cf. *Cyclosorus archboldiana* T. (Thelypteridaceae) (Plate I.14, 189)
180 CYCLA

Concavo-convex spore. Perisporium covered with sparse echinae, *c.* 3 µm in length. Similar echinate types occur in *C. unitus, Drynaria,* and baculate types in *Drynaria* and *Selliguea*.

*Cyclosorus truncatus* T. (Thelypteridaceae) (Plate I.14, 190)
182 CYCLT

Spore with dense, curved triangular echinae. Slightly similar types occur in other *Cyclosorus* spp.

cf. *Stenochlaena areolaris* (Blechnaceae) (Plate I.14, 191)
185 STENA

Identification based on descriptions by Holttum (1932) and Anderson and Muller (1975). Large spore 80 x 45 µm, with sparse echinae up to 12 µm in length.

Unknown 19 (Plate I.14, 192)
192 UK019

Spore of *Pteris*-like morphology, but bilateral rather than tetrahedral in shape. Both Lugardon (1963) and Devi (1974) report the occurrence of monolete *Pteris* spores.

Monolete spores (undifferentiated)
193 MONLU

## 19. TRILETE SPORES

cf. *Adiantum diaphanum* T. (Adiantaceae) (Plate I.14, 193)
173 ADIAN

Spore with distinct, but faint, reticulate pattern, and wide, unthickened tri-radiate scar. Max. dimension *c*. 32 µm. Many other genera produce morphologically very similar spores.

Cyatheaceae 1 (Plate I.14, 194)
178 CYAT1

Psilate spore of diverse shape, thick unpatterned exine. Perisporium absent, or psilate. Equatorial diameter *c*. 35 - 40 µm.

Cyatheaceae 2 (Plate I.15, 195,196)
179 CYAT2

Psilate spore with loose, patterned perisporium. Sculpturing often papillate or striate, and denser on the distal surface. Size similar to psilate Cyatheaceae. Spores of this morphology are not well represented in the ANU reference collection, but have been described by Harris (1955), Tindale (1956), and Murillo and Bless (1974).

*Lycopodium cernuum* T. (Lycopodiaceae) (Plate I.15, 197)
167 LYCOC

Small spore *c*. 25 x 10 µm. Thin tri-radiate scar. Rugulate sculpturing on distal surface.

*Lycopodium squarrosum* T. (Lycopodiaceae) (Plate I.15, 198)
169 LYCOS

Spore *c*. 45 µm equatorial diameter with thin trilete scar. Thick unpatterned exine, psilate on proximal surface, sparsely foveolate on distal surface. Similar spores occur in *L. macgregorii* and *L. apiculata*.

*Lycopodium* cf. *volubile* T. (Lycopodiaceae) (Plate I.15, 199)
168 LYCOV

Spore circular in polar view. Loose, reticulate perisporium. Similar types are found in other *Lycopodium* spp., including *L. fastigatum* and *L. complanatum*.

*Pteris* (Pteridaceae) (Plate I.15, 200)
172 PTERI

Spore triangular in polar view, with thick (*c*. 5 µm) exine. Thickened trilete scar. Psilate on proximal surface, some degree of verrucate patterning on the distal surface. The type occurs in many New Guinea *Pteris* spp., although not in *P. molluccana*.

cf. *Anemia hirsuta* (Schizeaceae) (Plate I.15, 201,202)
171 ANEMI

A very large spore, equatorial diameter *c*. 100 µm. Thick striations or ridges parallel the scar and the equatorial axis.

*Lygodium microphyllum* T. (Schizeaceae) (Plate I.16, 203)
170 LYGOD

Spore triangular to circular in polar view, with distinctive foveo-reticulate exine. Size variable, equatorial diameter *c*. 55 - 90 µm.

Unknown 312 (Plate I.16, 204)
194 UK312

Spore triangular in polar view with sparsely verrucate perisporium. Long, thin trilete scar. Equatorial diameter *c*. 28 µm.

Unknown 170 (Plate I.16, 205)
195 UK170

Spore triangular in polar view. Perisporium foveo-reticulate. Equatorial diameter *c*. 25 µm.

Unknown 172 (Plate I.16, 206)
196 UK172

Large spore, triangular in polar view with loose, faintly reticulate perisporium.

Trilete ferns (undifferentiated)
197 TRILU

UNCATAGORISED PALYNOMORPHS
198 UNCAT

Palynomorphs unable to be assigned with certainty to any of the above 19 morphological categories.

INDETERMINABLE PALYNOMORPHS
199 INDET

Pollen or spores too corroded or degraded (*sensu* Cushing, 1964) to describe adequately the morphological features, or those too crumpled, fragmented or obscured by immovable debris to identify.

## *NOTES ON THE PHOTOMICROGRAPHS*

All photomicrographs of pollen and spore taxa are reproduced at a magnification of X 1000. The scale at the foot of each plate represents 50 μm. As all photographs are of subfossil specimens, or those from contemporary surface samples, extraneous debris is occasionally visible. Each number represents a different grain, whilst views of the same individual are indicated by the suffix a,b, etc. Also indicated is the sample from which the illustrated grain was recovered.

## *PLATE I.1*

| | | |
|---|---|---|
| 1a,b | *Phyllocladus* (Podocarpaceae) | YAN 2, 990 cm |
| 2,3 | *Podocarpus* (Podocarpaceae) | YAN 2, 476 cm |
| 4 | *Dacrycarpus* T. (Podocarpaceae) | YAN 2, 830 cm |
| 5 | cf. *Cananga odorata* (Annonaceae) | SS 18 |
| 6a,b,c | cf. *Gnetum* (Gnetaceae) | SS 13-15 |
| 7a,b,c | *Pandanus radula* T. (Pandanaceae) | YAN 2, 1030 cm |
| 8a,b | cf. *Colocasia* (Araceae) | LW II, 1930 cm |
| 9 | Unknown 274 | PT 4 |
| 10 | ?*Normanbya* T. (Palmae) | SS 18 |
| 11a,b | cf. Liliaceae | YAN 2, 160 cm |

PLATE I.1

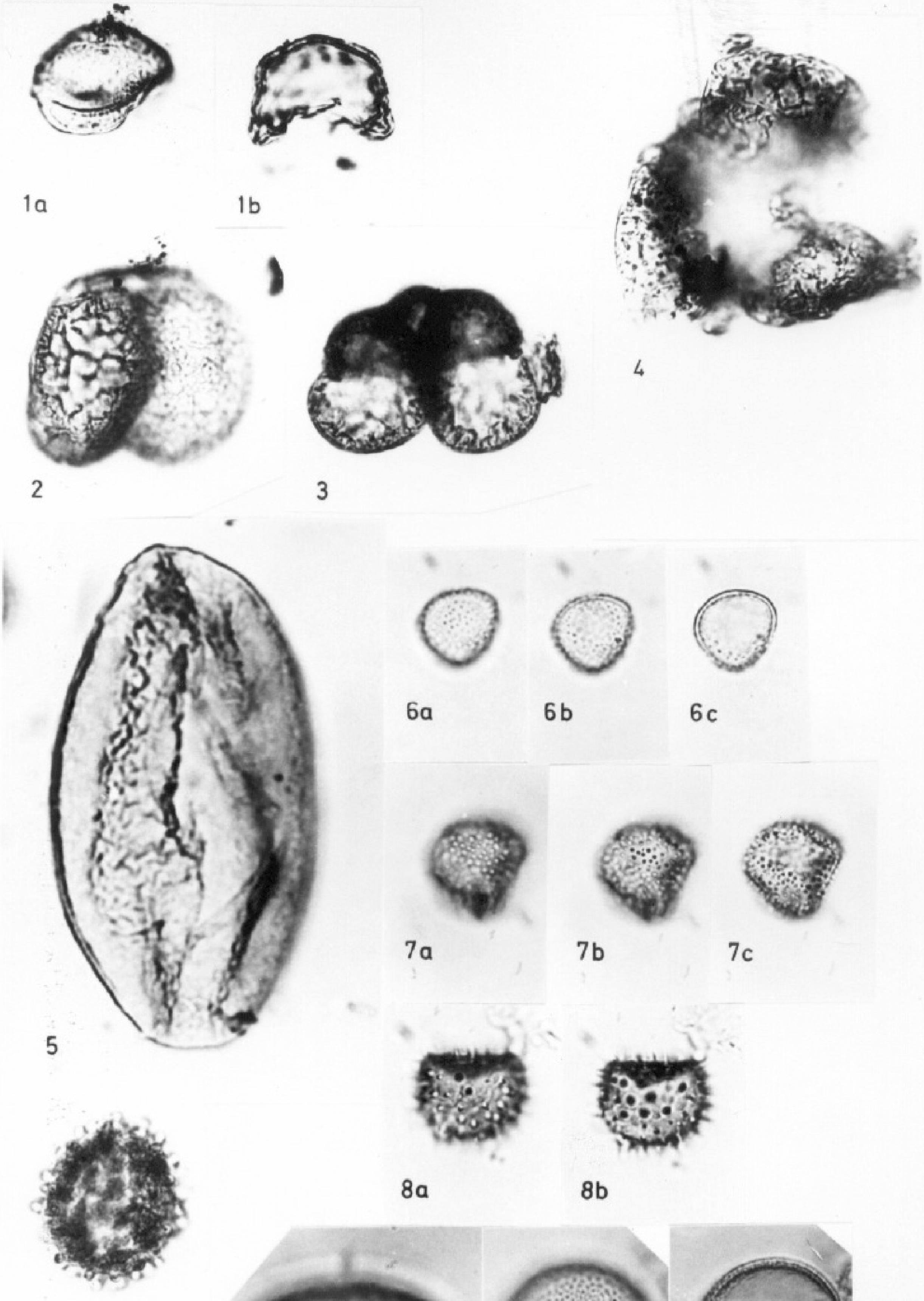


*PLATE I.2*

| | | |
|---|---|---|
| 12a,b | ?Palmae | PT 4 |
| 13a,b | cf. *Arenga* (Palmae) | PT 4 |
| 14a,b | Unknown 156 | YAN 2, 1150 cm |
| 15a,b | Gramineae 3 | |
| 16a,b | Gramineae 5 | LW II, 1490 cm |
| 17a,b | *Flagellaria* (Flagellariaceae) | YAN 2, 160 cm |
| 18a,b,c | *Sparganium antipodum* T. (Sparganiaceae) | LW II, 1970 cm |
| 19 | *Typha* (Typhaceae) | LW II, 730 cm |
| 20a,b | Unknown 292 | PT 1 |
| 21a,b,c | *Hypolytrum nemorum* T. (Cyperaceae) | LW II, 1346 cm |
| 22 | Cyperaceae A1 | SS 23 |
| 23 | Cyperaceae B2 | YAN 2, 870 cm |
| 24a,b | *Calamus* (Palmae) | YANMC 1 SS |
| 25a,b | ?*Metroxylon sagu* (Palmae) | YAN 2, 920 cm |

PLATE I.2

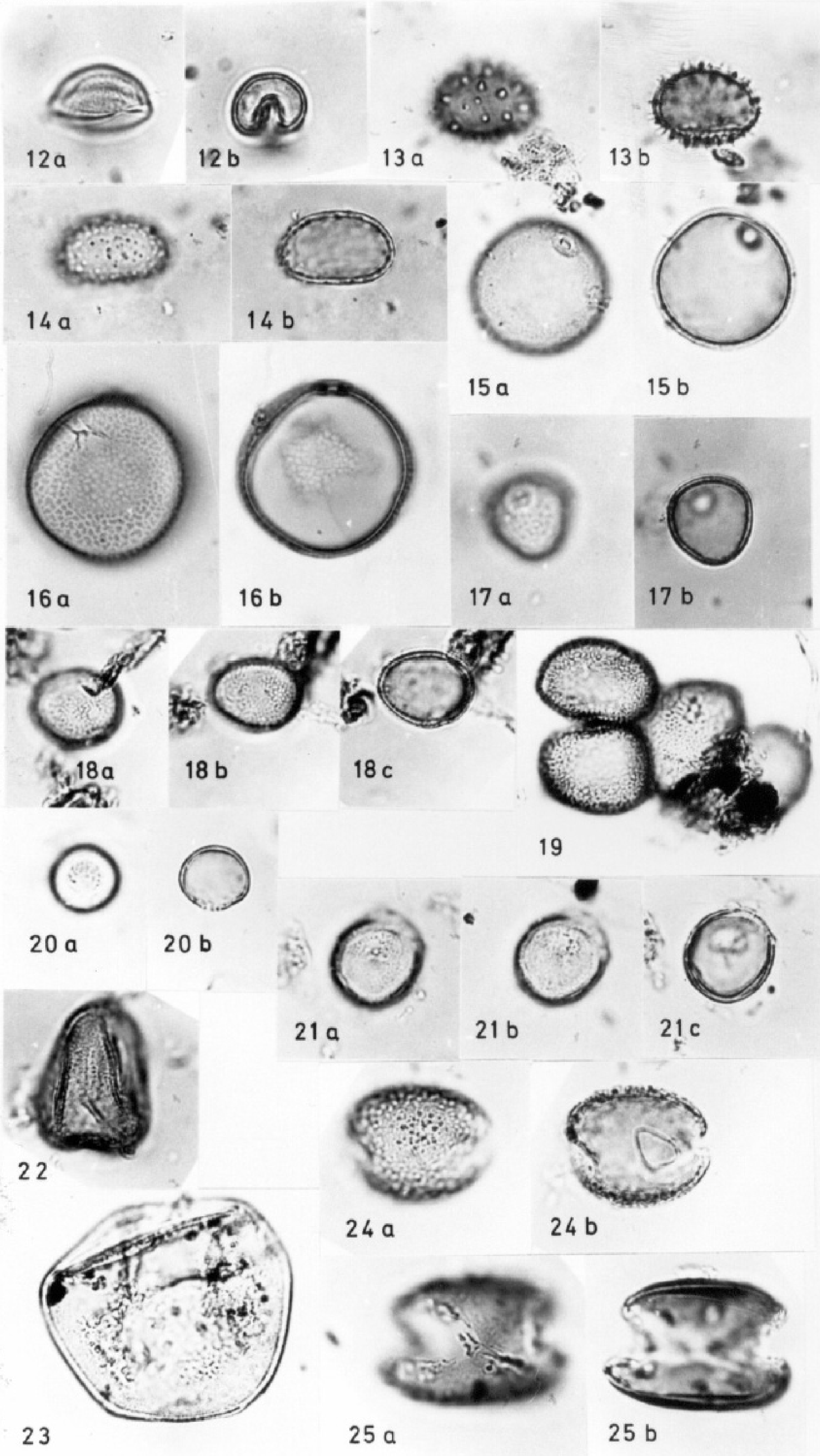
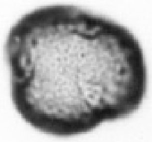

12a
12b
13a
13b
14a
14b
15a
15b
16a
16b
17a
17b
18a
18b
18c
19
20a
20b
21a
21b
21c
22
24a
24b
23
25a
25b

*PLATE I.3*

| | | |
|---|---|---|
| 26a,b | *Anisoptera* T. (Dipterocarpaceae) | YAN 2, 320 cm |
| 27a,b | *Anisoptera* T. (Dipterocarpaceae) | LW II, 1890 cm |
| 28a,b | *Dysophylla* T. (Labiatae) | SS 23 |
| 29 | *Dysophylla* T. (Labiatae) | LW II, 1907 cm |
| 30a,b,c | cf. Verbenaceae/Bignoniaceae | YAN 2, 200 cm |
| 31a,b,c | *Timonius* T. (Rubiaceae) | YAN 2, 910 cm |
| 32a,b | *Nelumbo nucifera* (Nymphaceae) | LW II, 685 cm |

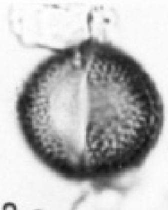
PLATE I.3

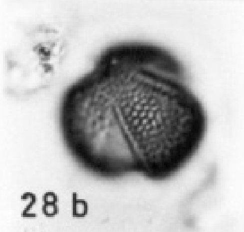

26a


26b

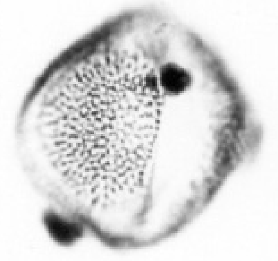

27a

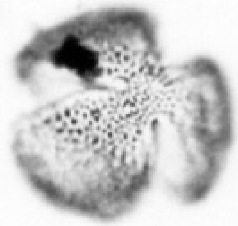

27b


28 a


28 b

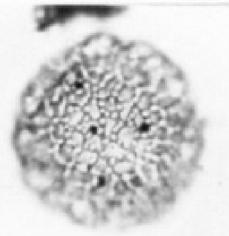

29

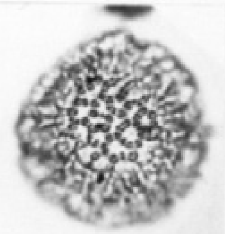

30 a

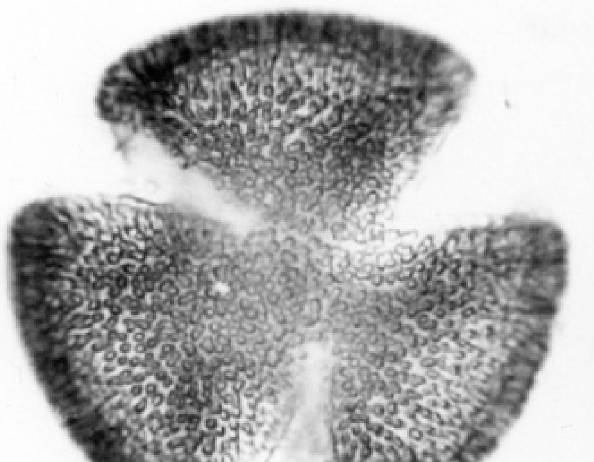

30 b


30 c


31 a


31 b


31 c


32 a

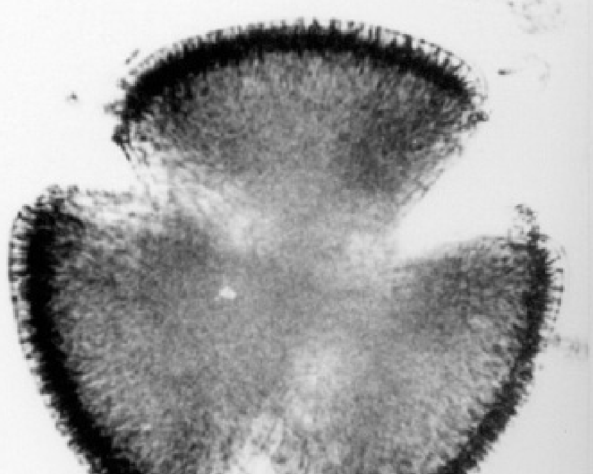

32 b

*PLATE I.4*

| | | |
|---|---|---|
| 33a,b,c,<br>34a,b | *Ilex* (Aquifoliaceae) | LW II, 1530 cm |
| 35a,b | *Endospermum* (Euphorbiaceae) | PT 4 |
| 36a,b | Unknown 235 | YAN 2, 670 cm |
| 37a,b | Unknown 293 | PT 1 |
| 38a,b | cf. *Myrsine* T. (Myrsinaceae) | SQ 40 |
| 39 | cf. *Myrsine* T. (Myrsinaceae) | YAN 2, 1030 cm |
| 40a,b,c | *Nothofagus* (Fagaceae) | YAN 2, 1030 cm |
| 41a,b,c | *Elaeocarpus* T. (Elaeocarpaceae) | PT 1 |
| 42a,b,c,d | *Octomeles sumatrana* (Datiscaceae) | LW II, 1980 cm |
| 43a,b,c | *Macaranga ovatifolia* T. (Euphorbiaceae) | PT 1 |
| 44a,b,c,d | *Macaranga* (Euphorbiaceae) | LW II, 1490 cm |
| 45a,b | *Macaranga* (Euphorbiaceae) | LW II, 730 cm |
| 46a,b | Rhamnaceae | YAN 2, 400 cm |
| 47a,b | Rhamnaceae | YAN 2, 910 cm |

PLATE I.4

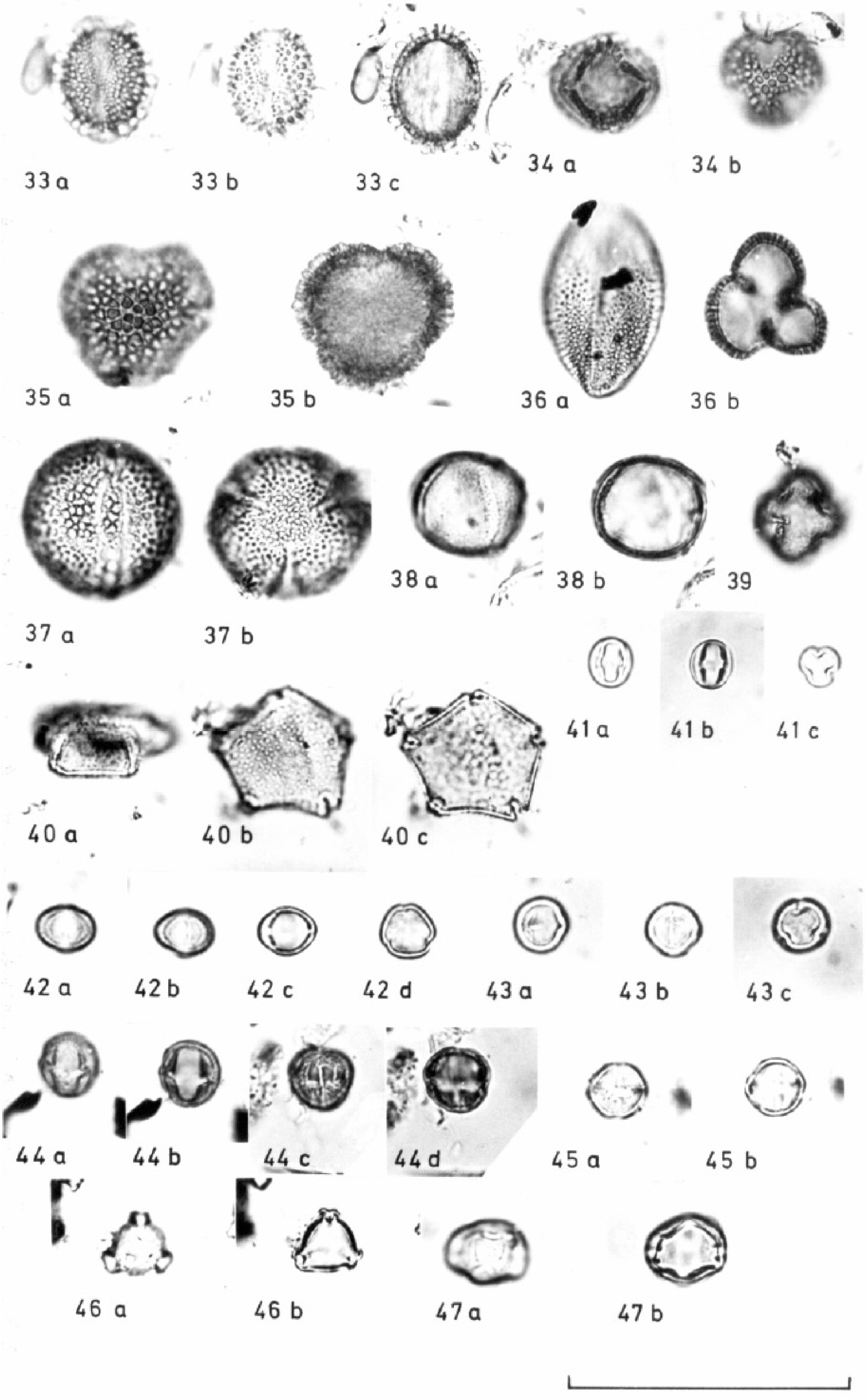

33 a
33 b
33 c
34 a
34 b
35 a
35 b
36 a
36 b
37 a
37 b
38 a
38 b
39
41 a
41 b
41 c
40 a
40 b
40 c
42 a
42 b
42 c
42 d
43 a
43 b
43 c
44 a
44 b
44 c
44 d
45 a
45 b
46 a
46 b
47 a
47 b

*PLATE I.5*

| | | |
|---|---|---|
| 48a,b,c | *Spiraeopsis* T. (Cunoniaceae) | LW II, 685 cm |
| 49a,b | *Weinmannia* T. (Cunoniaceae) | PT 1 |
| 50a,b,c | *Hypserpa* (Menispermaceae) | LW II, 1610 cm |
| 51 | *Uncaria* T. (Rubiaceae) | LW II, 1530 cm |
| 52 | *Uncaria* T. (Rubiaceae) | SQ 40 |
| 53a,b,c | *Nauclea* T. (Rubiaceae) | LW II, 1490 cm |
| 54a,b,c | *Tetracera* T. (Dilleniaceae) | PT 1 |
| 55a,b,c,d | *Olea* (Oleaceae) | YAN 2, 1070 cm |
| 56 | *Rapanea* cf. *achradaefolia* T. (Myrsinaceae) | YAN 2, 830 cm |
| 57a,b | Unknown 194 | YAN 2, 160 cm |
| 58 | Unknown 109 | LW II, 1970 cm |
| 59a,b | Unknown 104 | LW II, 1970 cm |
| 60a,b,c,d | Unknown 60 | LW II, 1770 cm |
| 61a,b, 62 | *Castanopsis* T. (Fagaceae) | PT 1 |
| 63a,b,c | *Rhizophora apiculata* T. (Rhizophoraceae) | LW II, 790 cm |
| 64a,b,c | cf. *Crotalaria* T. (Leguminosae) | LW II, 685 cm |
| 65a,b | ?Leguminosae (Papilionatae) B | YAN 2, 240 cm |
| 66a,b,c,d,e | cf. *Bischofia* (Euphorbiaceae) | LW II, 685 cm |
| 67 | cf. *Bischofia* (Euphorbiaceae) | YAN 2, 990 cm |

PLATE I.5

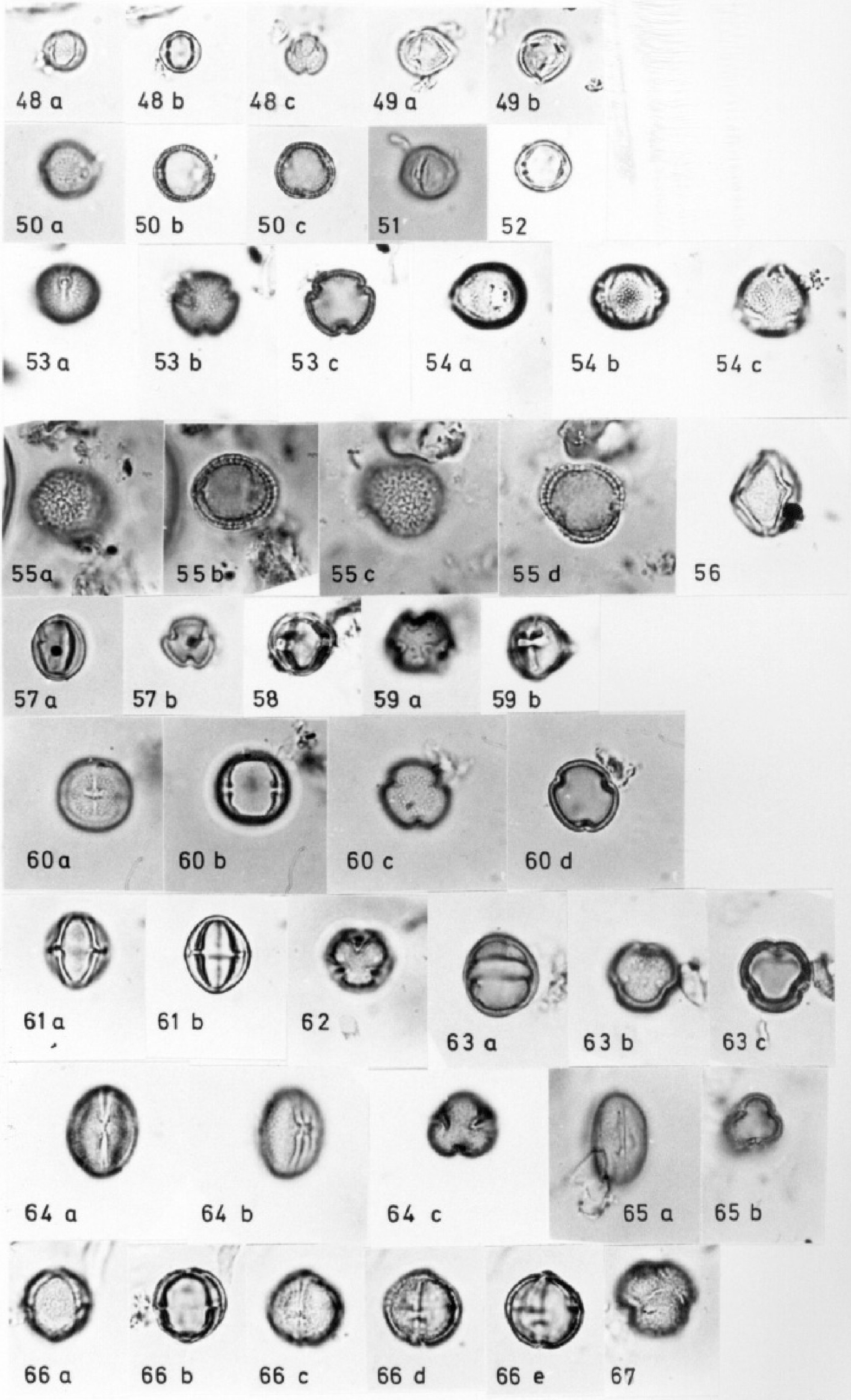
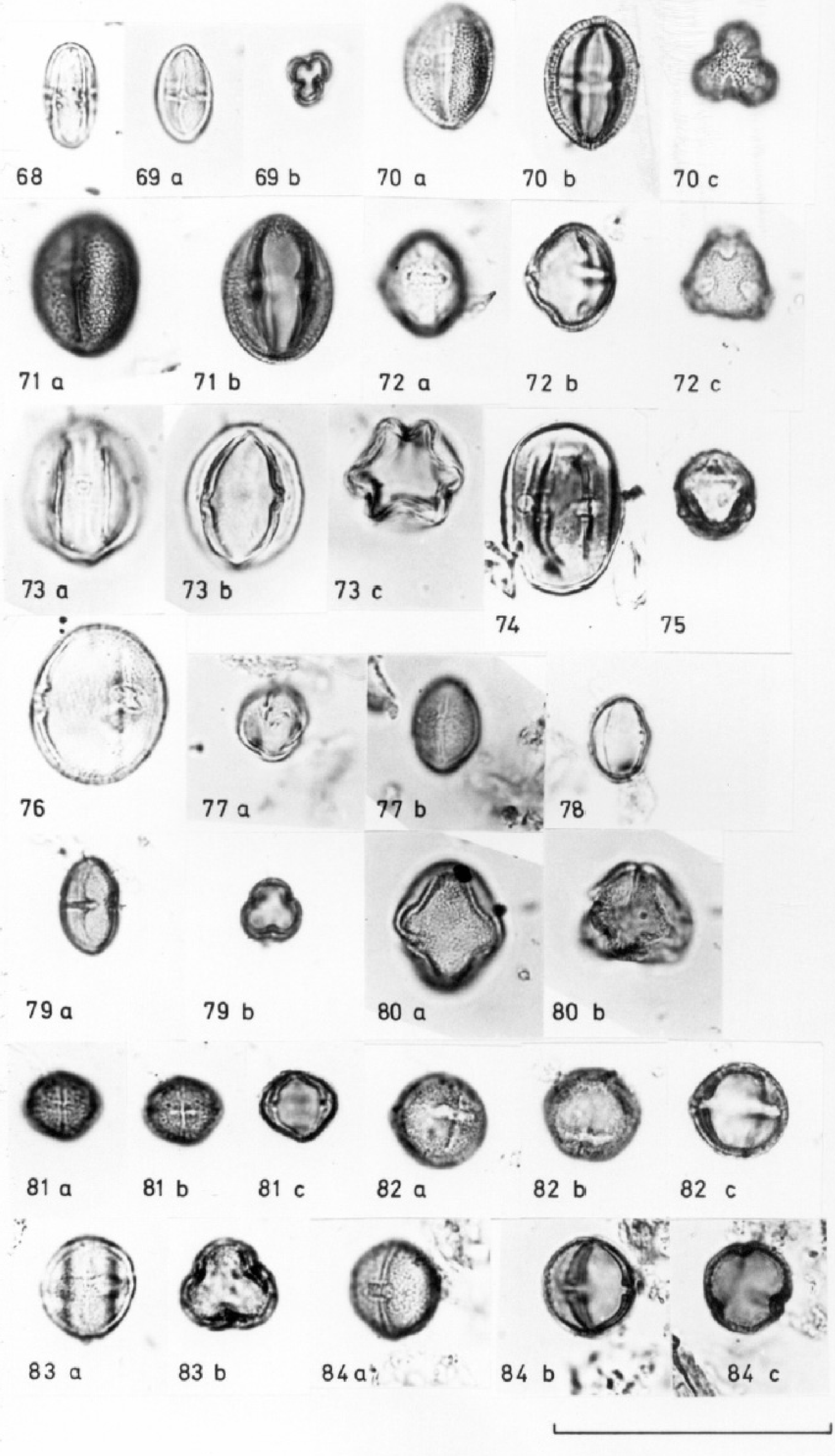

48 a
48 b
48 c
49 a
49 b
50 a
50 b
50 c
51
52
53 a
53 b
53 c
54 a
54 b
54 c
55a
55 b
55 c
55 d
56
57 a
57 b
58
59 a
59 b
60 a
60 b
60 c
60 d
61 a
61 b
62
63 a
63 b
63 c
64 a
64 b
64 c
65 a
65 b
66 a
66 b
66 c
66 d
66 e
67

*PLATE I.6*

| | | |
|---|---|---|
| 68 | *Antidesma* (Euphorbiaceae) | LWMC 3 SS |
| 69a,b | *Antidesma* (Euphorbiaceae) | YAN 2, 910 cm |
| 70a,b,c | *Euphorbia hirta* T. (Euphorbiaceae) | LW II, 730 cm |
| 71a,b | cf. *Euphorbia* (Euphorbiaceae) | LW II, 790 cm |
| 72a,b,c | *Rhus* T. (Anacardiaceae) | YAN 2, 670 cm |
| 73a,b,c | *Diospyros* cf. *ferrea* (Ebenaceae) | SS 18 |
| 74 | *Planchonella* T. (Sapotaceae) | LW II, 1810 cm |
| 75 | *Planchonella* T. (Sapotaceae) | PT 4 |
| 76 | cf. *Palaquim* (Sapotaceae) | YANMC 1 SS |
| 77a,b | Unknown 79 | LW II, 790 cm |
| 78 | Unknown 79 | LW II, 730 cm |
| 79a,b | Unknown 119 | LW II, 1346 cm |
| 80a,b | Unknown 174 | YAN 2, 1030 cm |
| 81a,b,c | cf. Euphorbiaceae | LW II, 1930 cm |
| 82a,b,c | *Mallotus* T. (Euphorbiaceae) | LW II, 790 cm |
| 83a,b | *Cleidion* T. (Euphorbiaceae) | YAN 2, 670 cm |
| 84a,b,c | cf. *Muehlenbeckia* (Polygonaceae) | LW II, 1346 cm |

PLATE I.6


68
69 a
69 b
70 a
70 b
70 c
71 a
71 b
72 a
72 b
72 c
73 a
73 b
73 c
74
75
76
77 a
77 b
78
79 a
79 b
80 a
80 b
81 a
81 b
81 c
82 a
82 b
82 c
83 a
83 b
84 a
84 b
84 c

## *PLATE I.7*

| | | |
|---|---|---|
| 85a,b,c | cf. *Rumex brownii* (Polygonaceae) | YAN 2 830 cm |
| 86 | *Dodonaea* (Sapindaceae) | YAN 2, 240 cm |
| 87a,b | *Acaena* (Rosaceae) | YAN 2, 910 cm |
| 88a,b | ?*Parinari* (Rosaceae) | PT 1 |
| 89a,b,c | Unknown 123 | LW II, 1310 cm |
| 90a,b | Unknown 221 | YAN 2, 400 cm |
| 91a,b | Unknown 218 | YAN 2, 400 cm |
| 92a,b,c | *Vandasia* T. (Leguminosae) | PT 5 |
| 93 | cf. *Sterculia edelfeltii* (Sterculiaceae) | YAN 2, 1030 cm |
| 94a,b | cf. *Sterculia edelfeltii* (Sterculiaceae) | YAN 2, 320 cm |
| 95a,b,c | *Platea excelsa* (Icacinaceae) | PT 1 |
| 96a,b,c | *Melanolepis* T. (Euphorbiaceae) | PT 5 |
| 97 | *Melanolepis* T. (Euphorbiaceae) | YAN 2, 320 cm |
| 98 | *Melanalepis* T. (Euphorbiaceae) | PT 5 |
| 99a,b | *Boerlagiodendron* (Araliaceae) | YAN 2, 910 cm |
| 100 | *Boerlagiodendron* (Araliaceae) | YAN 2, 670 cm |
| 101a,b | *Morinda* (Rubiaceae) | YAN 2, 240 cm |

PLATE I.7

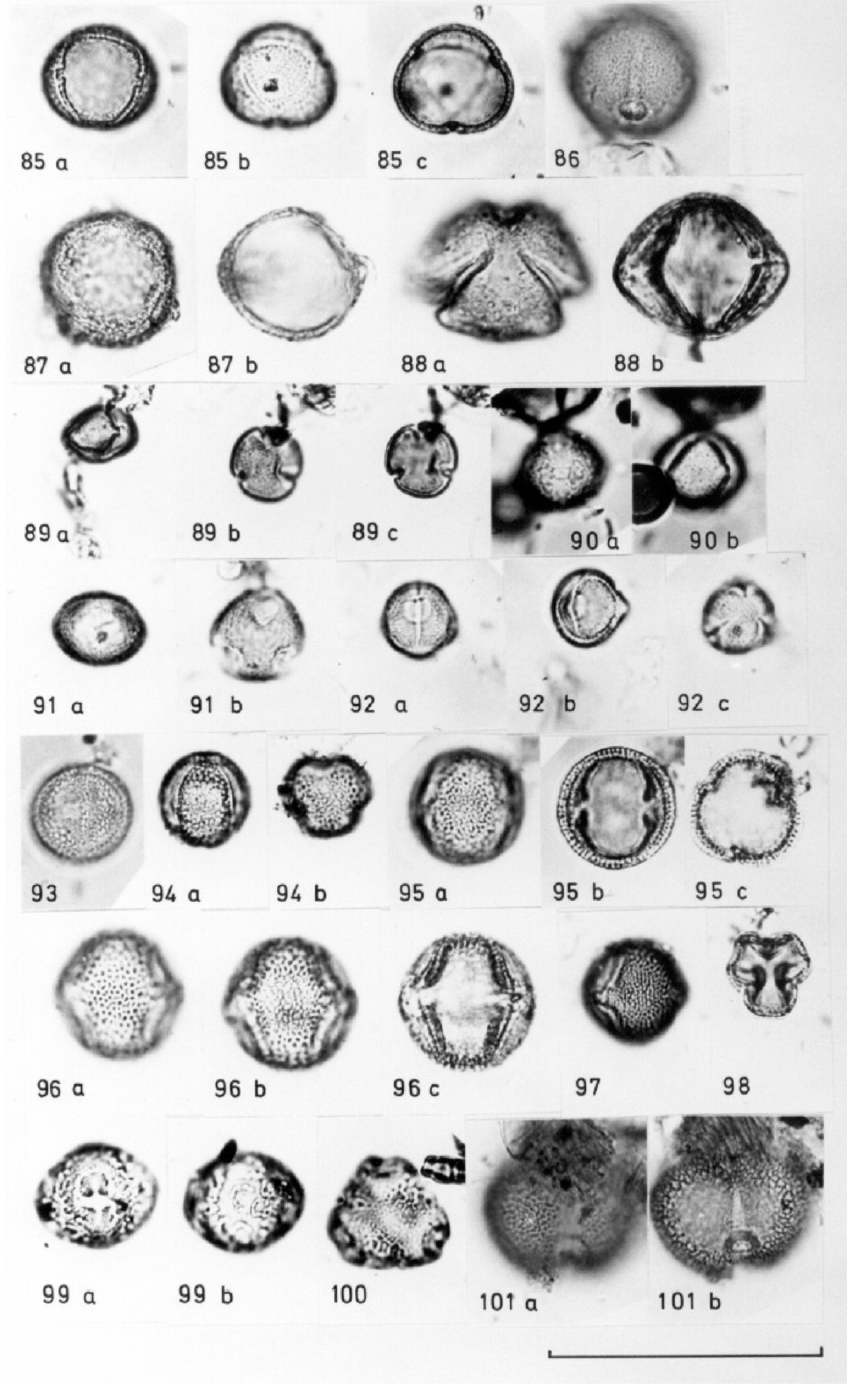
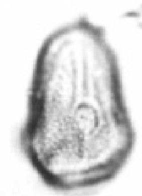
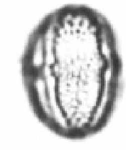

85 a
85 b
85 c
86
87 a
87 b
88 a
88 b
89 a
89 b
89 c
90 a
90 b
91 a
91 b
92 a
92 b
92 c
93
94 a
94 b
95 a
95 b
95 c
96 a
96 b
96 c
97
98
99 a
99 b
100
101 a
101 b

*PLATE I.8*

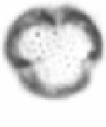
| | | |
|---|---|---|
| 102 | *Echium* cf. *plantagineum* (Boraginaceae) | YAN 2, 476 cm |
| 103a,b | *Evodia* T. (Rutaceae) | YAN 2, 870 cm |
| 104a,b | *Evodia* T. (Rutaceae) | SS 20 |
| 105 | *Aporosa* (Euphorbiaceae) | PT 4 |
| 106a,b | *Aporosa* (Euphorbiaceae) | PT 1 |
| 107 | ?Leguminosae (Papilionatae) D | LW II, 1730 cm |
| 108a,b | ?Leguminosae (Papilionatae) D | YAN 2, 1030 cm |
| 109a, b | *Brachychiton* T. (Sterculiaceae) | LW II, 1770 cm |
| 110 | *Microcos* T. (Tiliaceae) | LW II, 1770 cm |
| 111a,b,c | *Trichospermum* (Tiliaceae) | LW II, 1730 cm |
| 112 | Rutaceae/Araliaceae T. | YAN 2, 400 cm |
| 113a,b | Rutaceae/Araliaceae T. | YAN 2, 1150 cm |
| 114a,b,c | Unknown 309 | YANMC 1 SS |
| 115a,b | Unknown 310 | YANMC 1 SS |
| 116 | Anacardiaceae | YAN 2, 1030 cm |
| 117 | Anacardiaceae | PT 1 |

PLATE I.8


102


103 a


103 b


104 a

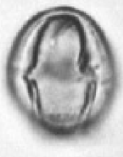

104 b

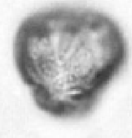

105


106 a


106 b

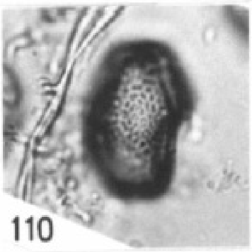

107

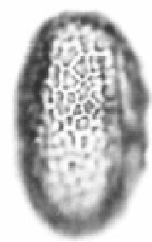

108 a

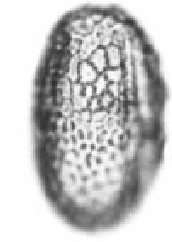

108 b

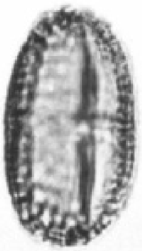

109 a


109 b

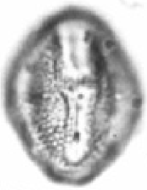

110


111 a

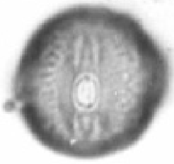

111 b

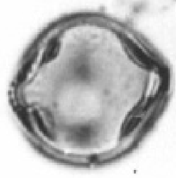

111 c


112

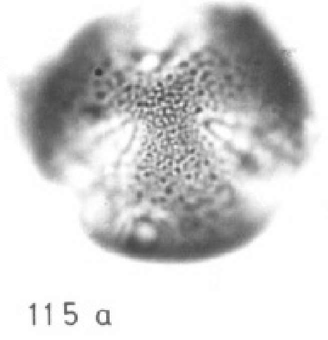

113 a

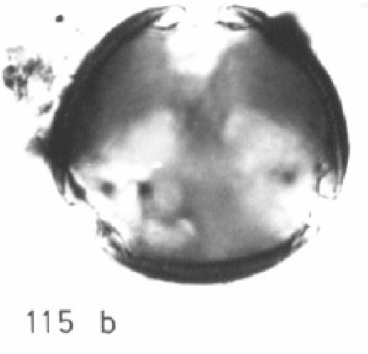

113 b

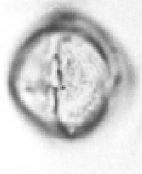

114 a


114 b


114 c


115 a


115 b


116

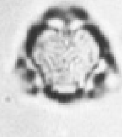

117

*PLATE I.9*

| | | |
|---|---|---|
| 118a,b,c | cf. *Vitex acuminata* (Verbenaceae) | LW II, 685 cm |
| 119a,b | *Ganophyllum falcatum* (Sapindaceae) | PT 4 |
| 120 | *Ganophyllum falcatum* (Sapindaceae) | PT 5 |
| 121a,b,c | *Trichadenia philippinensis* (Flacourtiaceae) | LW II, 1610 cm |
| 122a,b | Compositae (Tubuliflorae) | LW II, 910 cm |
| 123a,b | *Acalypha* (Euphorbiaceae) | LW II, 910 cm |
| 124 | *Quintinia* (Saxifragaceae) | YAN 2, 200 cm |
| 125 | *Quintinia* (Saxifragaceae) | YAN 2, 1030 cm |
| 126a,b | *Claoxylon* (Euphorbiaceae) | YAN 2, 790 cm |
| 127a,b | *Phyllanthus* cf. *urinaria* (Euphorbiaceae) | LW II, 1490 cm |
| 128 | *Phyllanthus* cf. *urinaria* (Euphorbiaceae) | LW II, 1490 cm |
| 129a,b,c | *Glochidion* T. (Euphorbiaceae) | LW II, 910 cm |
| 130a,b,c | Unknown 106 | SS 22 |
| 131a,b | ?*Evolvulus* (Convolvulaceae) | YANMC 1 SS |
| 132 | ?Euphorbiaceae | YAN 2, 870 cm |
| 133 | Urticaceae/Moraceae (diporate) | YAN 2, 120 cm |
| 134 | *Pilea* T. (Urticaceae) | SS 18 |
| 135a,b | *Streblus* T. (Moraceae) | LW II, 1970 cm |
| 136a,b | *Trema* (Ulmaceae) | LW II, 1490 cm |
| 137a,b | *Sphenostemon* cf. *papuanum* (Aquifoliaceae) | SS 22 |
| 138a,b | *Polyporandra scandens* (Icacinaceae) | SS 20 |

PLATE I.9

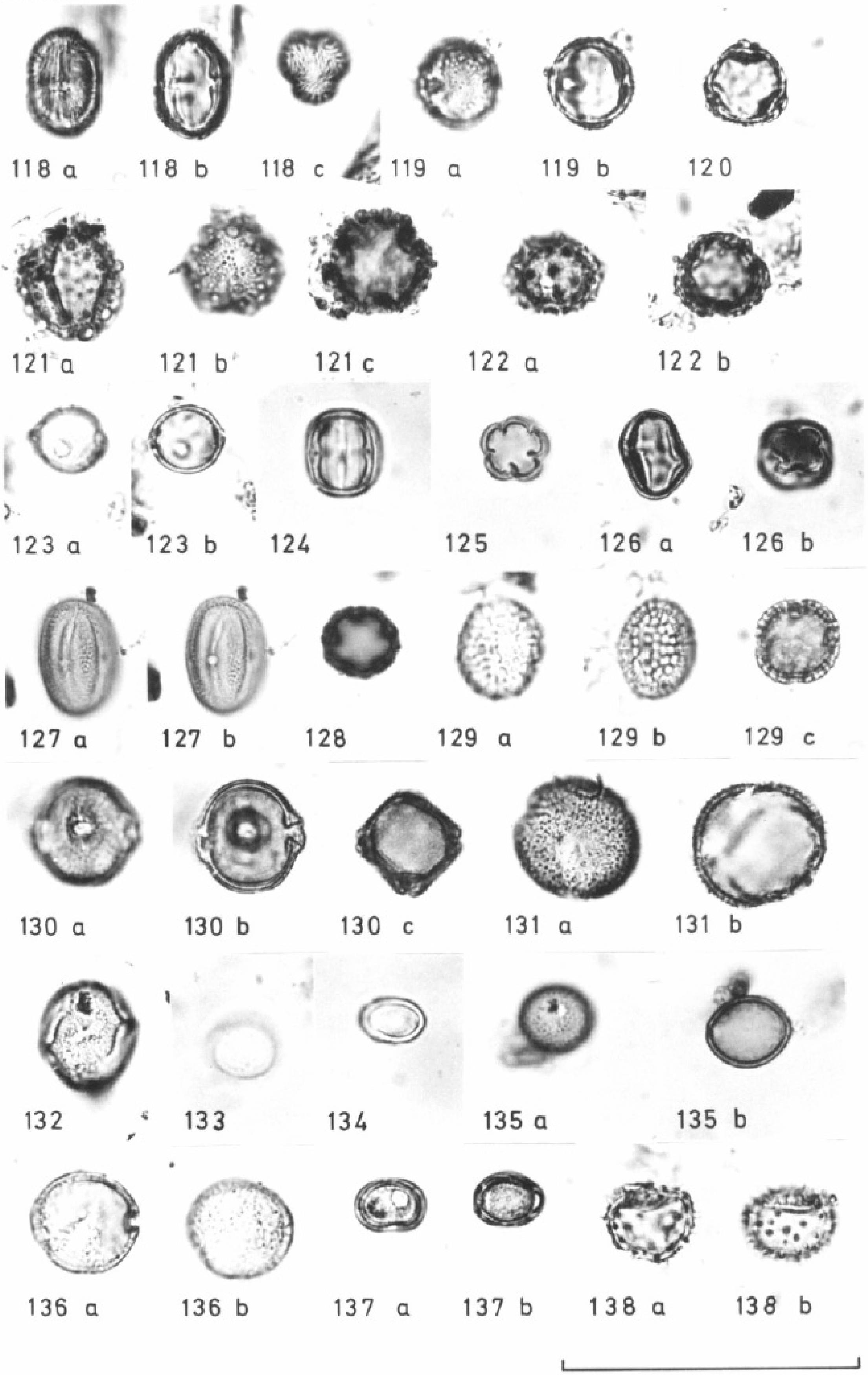
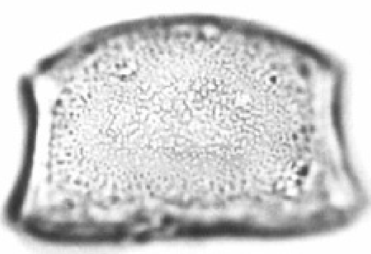
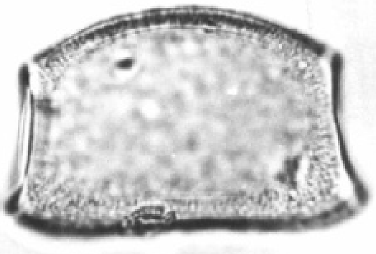

118 a
118 b
118 c
119 a
119 b
120
121 a
121 b
121 c
122 a
122 b
123 a
123 b
124
125
126 a
126 b
127 a
127 b
128
129 a
129 b
129 c
130 a
130 b
130 c
131 a
131 b
132
133
134
135 a
135 b
136 a
136 b
137 a
137 b
138 a
138 b

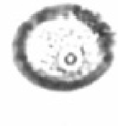
*PLATE I.10*

| | | |
|---|---|---|
| 139a,b | *Alyxia* (Apocynaceae) | PT 1 |
| 140a,b,c | Unknown 279 | PT 5 |
| 141 | Urticaceae/Moraceae (triporate) | PT 5 |
| 142a,b | *Stemonurus* (Icacinaceae) | PT 1 |
| 143a,b | *Helicia* (Proteaceae) | SS 20 |
| 144a,b | *Celtis* (Ulmaceae) | YAN 2, 950 cm |
| 145a,b | cf. *Engelhardtia* (Juglandaceae) | LW II, 1010 cm |
| 146 | *Casuarina* (Casuarinaceae) | PT 1 |
| 147a,b | *Haloragis* (Haloragaceae) | YAN 2, 1030 cm |
| 148 | *Polyosma* (Saxifragaceae) | PT 1 |
| 149 | *Polyosma* (Saxifragaceae) | PT 1 |
| 150 | *Sonneratia caseolaris* (Sonneratiaceae) | LW II, 1980 cm |
| 151 | *Sonneratia caseolaris* (Sonneratiaceae) | LW II, 790 cm |
| 152 | *Sonneratia caseolaris* (Sonneratiaceae) | PT 5 |
| 153a,b,c | *Stephania japonica* (Menispermaceae) | PT 4 |

# PLATE I.10


139 a


139 b


140 a


140 b

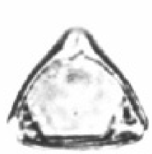

140 c


141

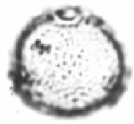

142 a


142 b

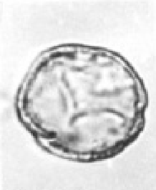

143 a


143 b

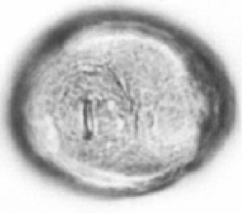

144 a

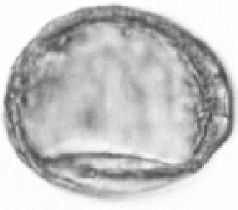

144 b

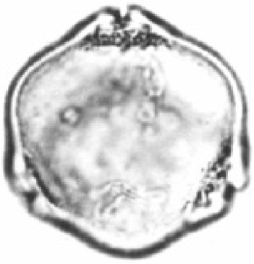

145 a

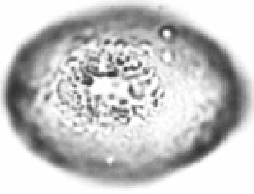

145 b

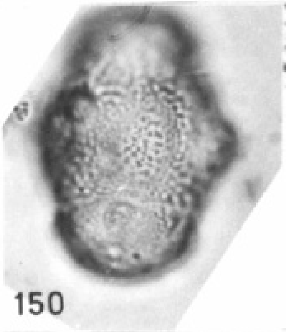

146


147 a

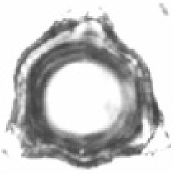

147 b

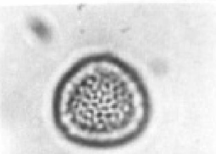

148

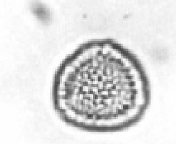

149


150


151


152


153 a


153 b


153 c

*PLATE I.11*

| | | |
|---|---|---|
| 154a,b,c | *Kleinhovia hospita* (Sterculiaceae) | PT 4 |
| 155a,b | cf. *Sterculia* (Sterculiaceae) | PT 5 |
| 156a,b | *Symplocos* (Symplocaceae) | YAN 2, 1030 cm |
| 157a,b | Unknown 147 | YAN 2, 240 cm |
| 158a,b | cf. *Aphananthe* (Ulmaceae) | YAN 2, 990 cm |
| 159 | *Plantago* (Plantaginaceae) | YAN 2, 560 cm |
| 160 | *Plantago* (Plantaginaceae) | LW II, 870 cm |
| 161a,b | cf. *Trimenia* (Monimiaceae) | LWMC 3 SS |
| 162 | Unknown 290 | PT 1 |
| 163a,b,c | *Tinospora* (Menispermaceae) | PT 4 |
| 164a,b | *Barringtonia* T. (Barringtoniaceae) | SS 18 |
| 165 | *Nymphoides* (Gentianaceae) | LW II, 1530 cm |
| 166a,b | *Nymphoides* (Gentianaceae) | LW II, 1530 cm |
| 167a,b | *Tristiropsis* T. (Sapindaceae) | PT 4 |
| 168 | Myrtaceae | LW II, 1490 cm |
| 169a,b | Myrtaceae | YAN 2, 990 cm |

PLATE I.11

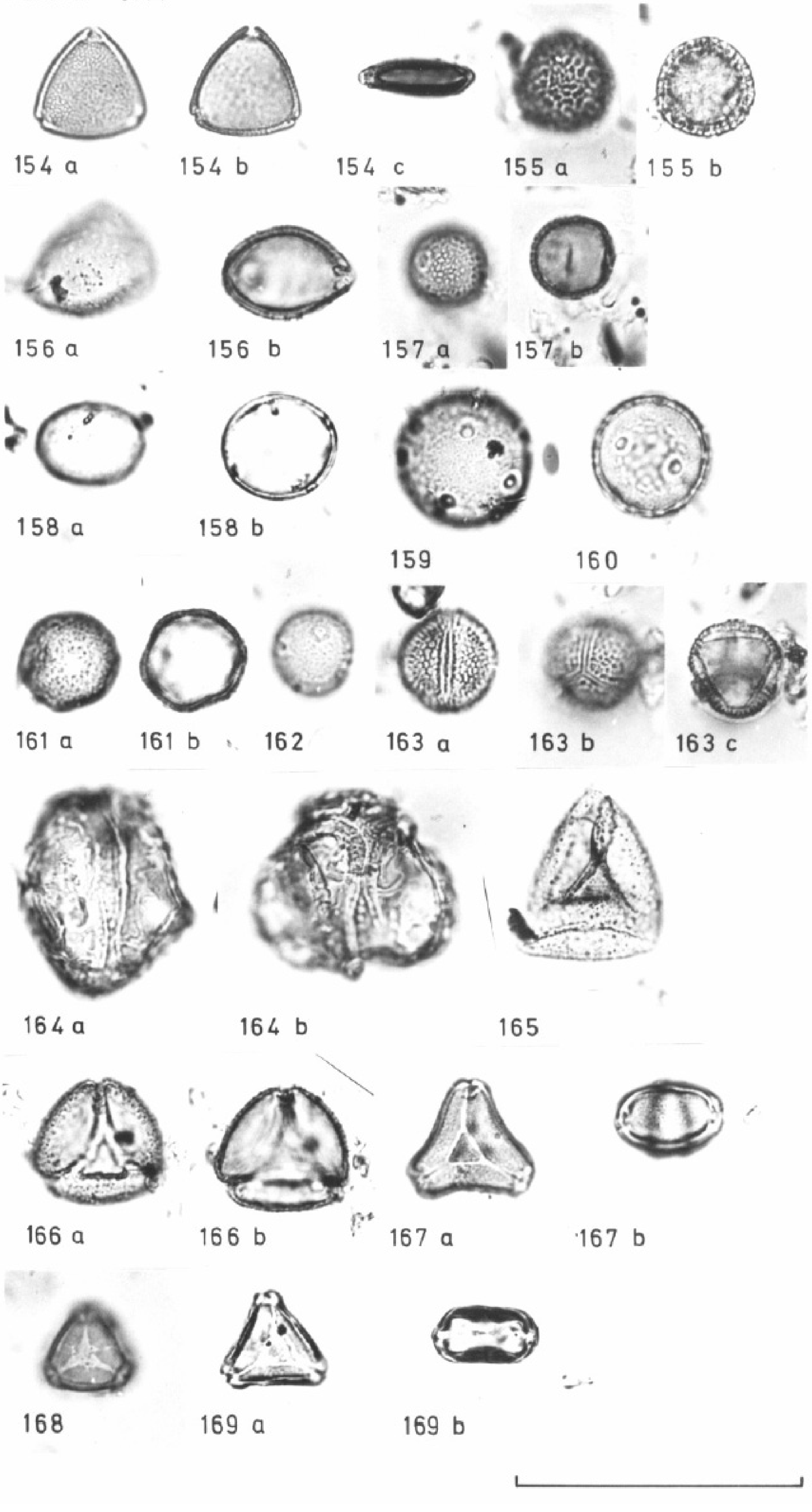

154 a
154 b
154 c
155 a
155 b
156 a
156 b
157 a
157 b
158 a
158 b
159
160
161 a
161 b
162
163 a
163 b
163 c
164 a
164 b
165
166 a
166 b
167 a
167 b
168
169 a
169 b

*PLATE I.12*

| | | |
|---|---|---|
| 170 | *Poikilogyne* T. (Melastomataceae) | LW II, 1191 cm |
| 171a,b | *Poikilogyne* T. (Melastomataceae) | YAN 2, 120 cm |
| 172a,b | Combretaceae/Melastomataceae | SQ 40 |
| 173a,b | Combretaceae/Melastomataceae | YAN 2, 120 cm |
| 174a,b | *Gardenia* (Rubiaceae) | SS 13-15 |
| 175a,b | Epacridaceae | YAN 2, 1030 cm |
| 176a,b,c | *Drimys* T. (Winteraceae) | YAN 2, 1030 cm |
| 177a,b | *Nepenthes* (Nepenthaceae) | LW II, 870 cm |
| 178 | Monolete psilate spore,<br>larger than 30 um | SS 13-15 |
| 179 | *Microsorium* T. (Polypodiaceae) | LW II, 790 cm |

PLATE I.12


170

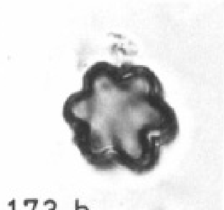

171 a


171 b


172 a

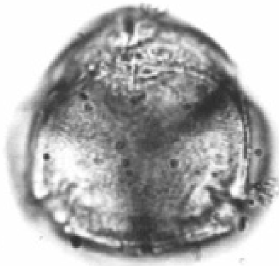

172 b

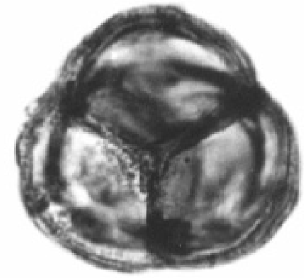

173 a

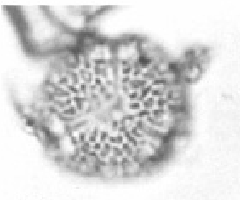

173 b


174 a


174 b


175 a


175 b


176 a


176 b


176 c


177 a


177 b


178

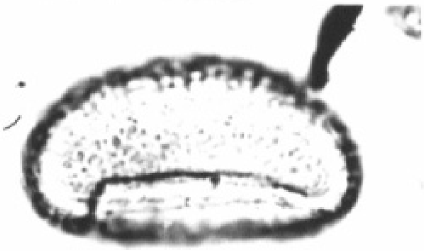
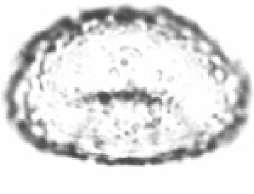
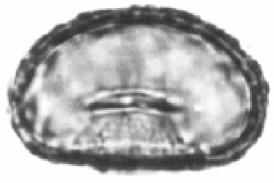

179

*PLATE I.13*

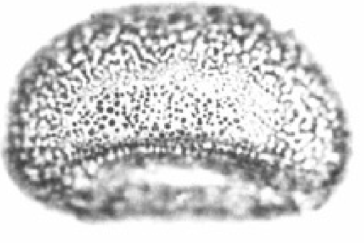
| | | |
|---|---|---|
| 180a,b | *Nephrolepis* (Oleandraceae) | LW II, 1110 cm |
| 181a,b | *Cyclosorus* T. (Thelypteridaceae) | PT 1 |
| 182 | *Histiopteris incisa* T. (Dennstaedtiaceae) | LW II, 1810 cm |
| 183 | *Davallia* T. (Davalliaceae) | LW II, 1730 cm |
| 184a,b | *Stenochaena palustris* (Blechnaceae) | LW II, 1890 cm |
| 185a,b | cf. *Tectaria* (Aspidaceae) | YAN 2, 1030 cm |
| 186a,b | *Stenochlaena laurifolia* (Blechnaceae) | SS 18 |
| 187a,b | *Asplenium* T. (Aspleniaceae) | YAN 2, 710 cm |

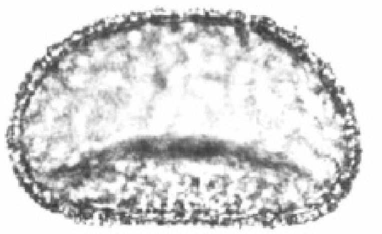
PLATE I.13

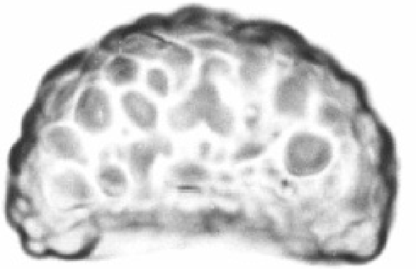

180 a

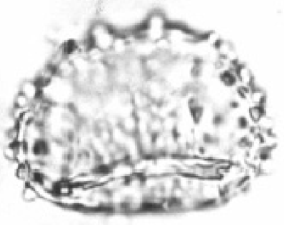

180 b

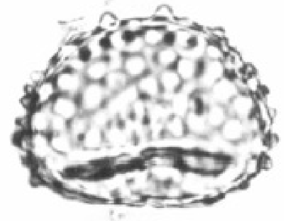

182

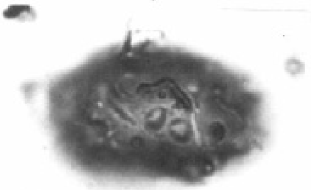

181 a

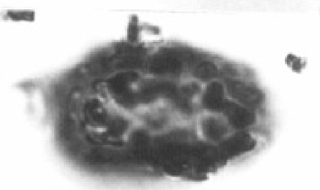

181 b

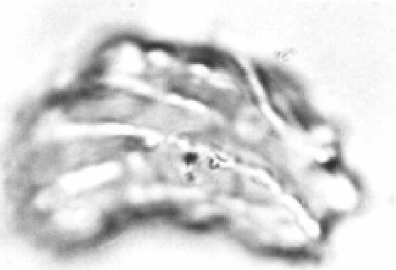

183


184 a


184 b


185 a


185 b


186 a


186 b


187 a

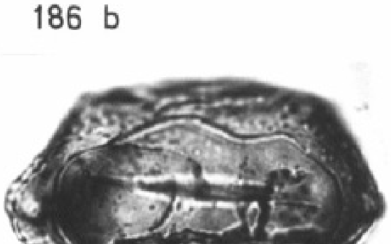
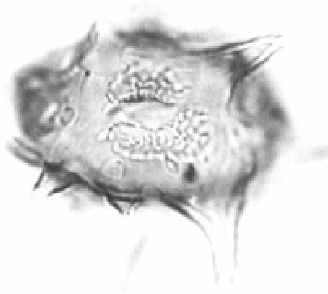

187 b

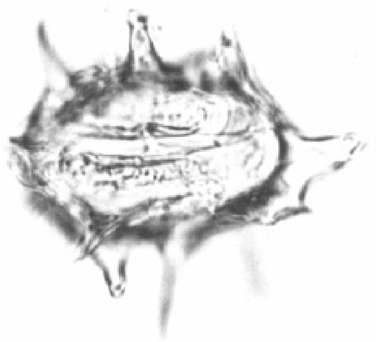
*PLATE I.14*

| | | |
|---|---|---|
| 188a,b | ?*Arthropteris* cf. *tenella*<br>(Oleandraceae) | SS 18 |
| 189a,b | cf. *Cyclosorus archboldiana* T.<br>(Thelypteridaceae) | YANMC 1 SS |
| 190a,b | *Cyclosorus truncatus* T.<br>(Thelypteridaceae) | YAN 2, 1030 cm |
| 191 | cf. *Stenochlaena areolaris*<br>(Blechnaceae) | SS 23 |
| 192 | Unknown 19 | LW II, 1490 cm |
| 193 | cf. *Adiantum diaphanum* T.<br>(Adiantaceae) | PT 4 |
| 194 | Cyatheaceae 1 | LW II, 1490 cm |

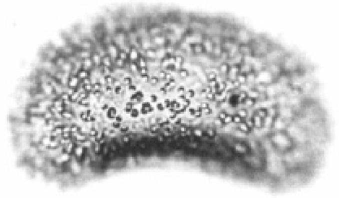
# PLATE I.14



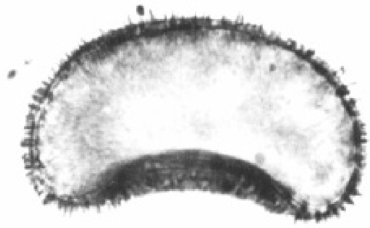
188 a



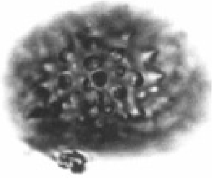
188 b



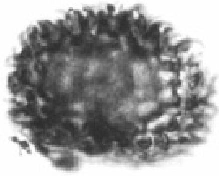
189 a



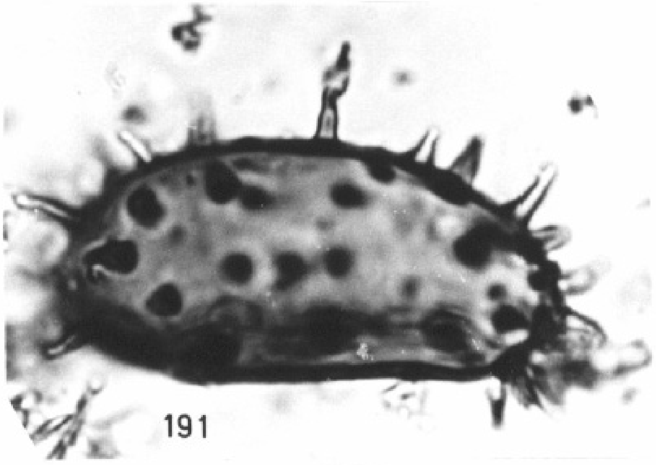
189 b



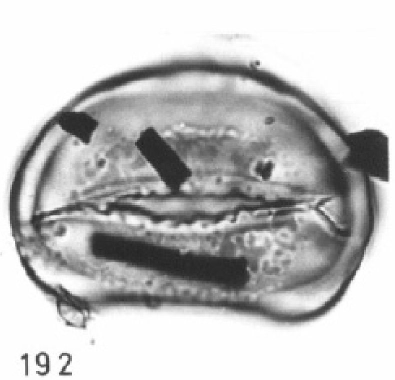
190 a



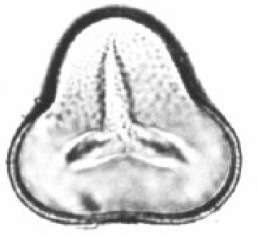
190 b



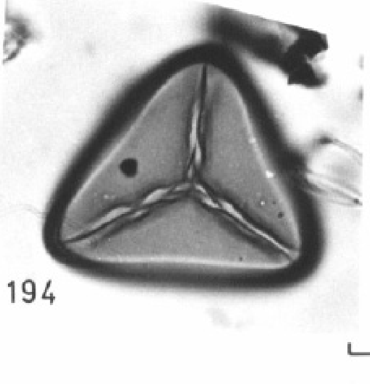
191



192



193

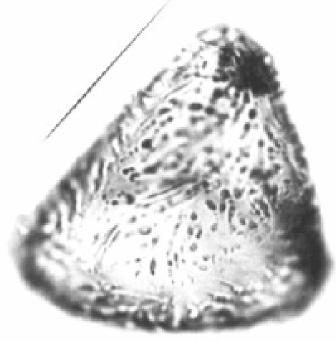


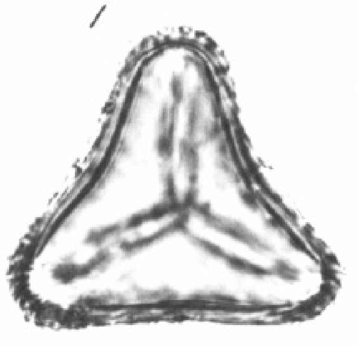
194

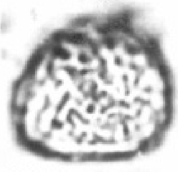
*PLATE I.15*

| | | |
|---|---|---|
| 195 | Cyatheaceae 2 | LW II, 685 cm |
| 196 | Cyatheaceae 2 | YAN 2, 670 cm |
| 197a,b | *Lycopodium cernuum* T. (Lycopodiaceae) | PT 1 |
| 198 | *Lycopodium squarrosum* T. (Lycopodiaceae) | YAN 2, 870 cm |
| 199 | *Lycopodium* cf. *volubile* T. (Lycopodiaceae) | YAN 2, 1030 cm |
| 200, 201 | *Pteris* (Pteridaceae) | LW II, 1191 cm |
| 202 | cf. *Anemia hirsuta* (Schizeaceae) (fragment) | LW II, 1870 cm |

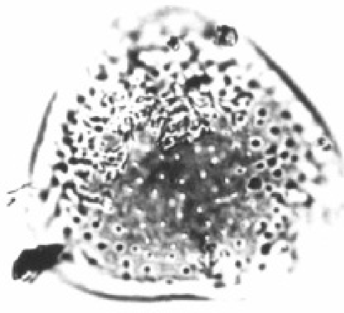
PLATE I.15

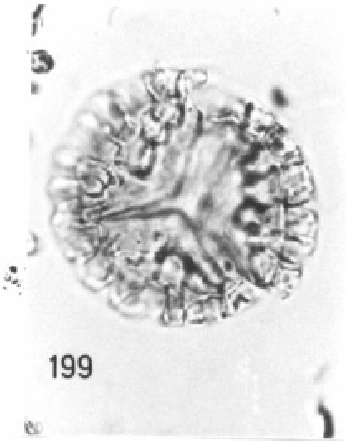

195

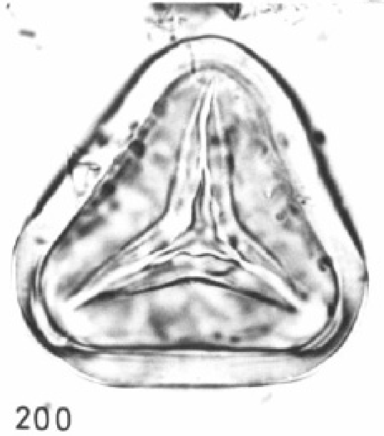

196

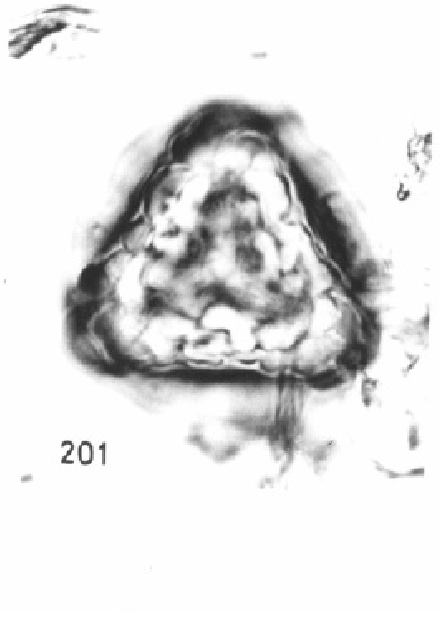

197 a


197 b


198


199


200

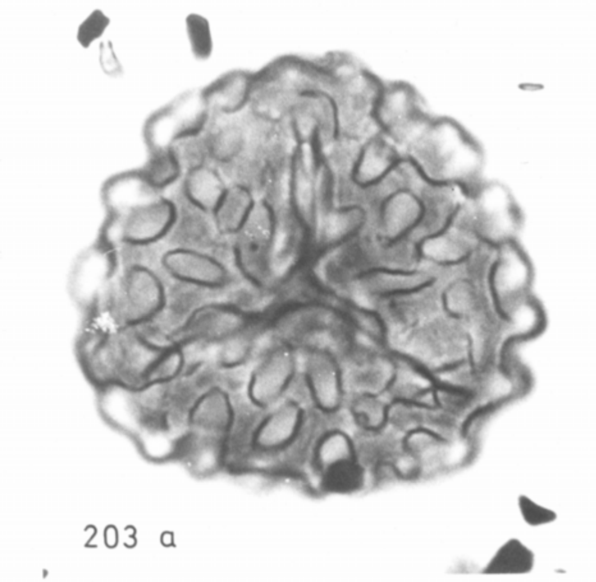

201

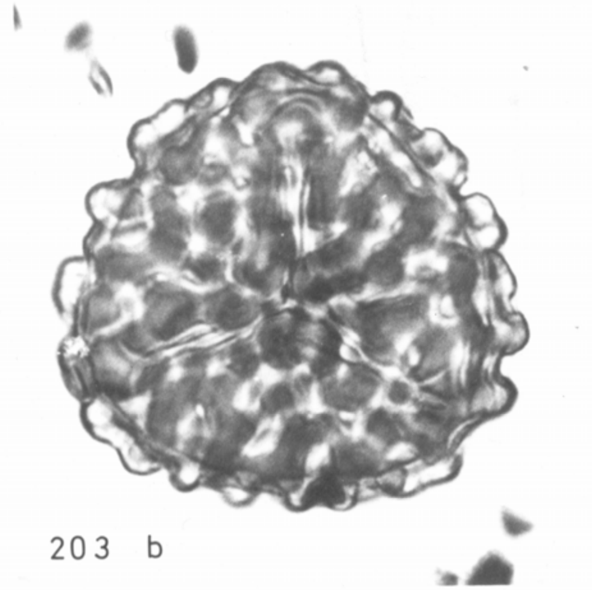

202

*PLATE I.16*

| | | |
|---|---|---|
| 203a,b | *Lygodium microphyllum* T. | LW II, 1490 cm |
| 204 | Unknown 312 | SS 27 and 28 |
| 205 | Unknown 170 | YAN 2, 1030 cm |
| 206 | Unknown 172 | YAN 2, 790 cm |

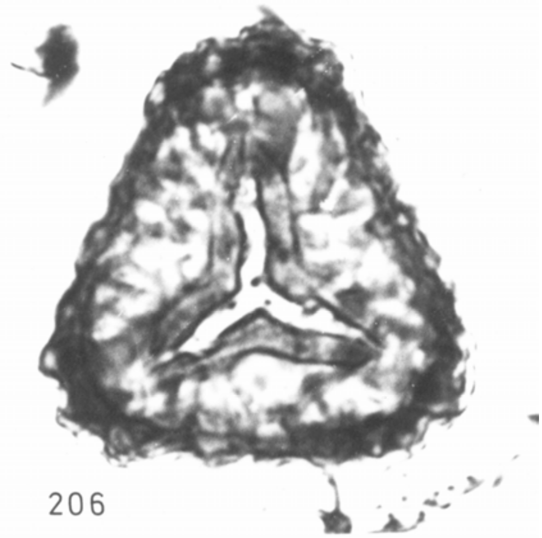
PLATE I.16


203 a


203 b


204


205


206

# APPENDIX II

## THE ALLOCATION OF POLLEN AND SPORE TAXA TO ECOLOGICAL GROUPS

This appendix is comprised of two sections. Table II.1 represents a collation of available information concerning the habit, ecology, and altitudinal and geographical distribution of plant taxa probably represented by the identified pollen and spore taxa. Table II.2 shows all pollen and spore taxa actually included in each of the groups plotted on the pollen diagrams in Chapters 7 and 8.

With the exception of observations by the author on predominantly swamp and non-forest taxa, the data in Table II.1 are based on secondary sources. These fall into three main categories: results of ecological studies in the Markham Valley and environs, botanical collections from this area, and ecological and botanical information either of a more general or regional nature, or pertaining to locations outside the present study area.

The only systematic ecological sampling work from the area is that of Johns (unpubl. *a*) for seventeen forest plots within the Oomsis-Gabensis region, and of Gillison (1970) who investigated the composition of the forest-grassland transition along transects at three localities near Oomsis. In addition, Holloway *et al.* (1973) have described and mapped the major vegetation alliances of the Markham Valley floor, as far east as the Erap River.

Extensive botanical collections have been made in the Oomsis-Gabensis area, and along the Wampit and lower Markham valleys. Johns (unpubl. *b,c.*) presents preliminary check-lists of plant collections relating to the Herzog Ranges and adjacent areas. Lane-Poole (1925) lists some of the major tree species found in the forest of the valley floor at Yalu. Other collections noted in the records of the Herbarium of the Botany Division, Lae, include a great many by staff of the Division and also comprehensive series by L.J. Brass and T.G. Hartley.

No Flora of Papua New Guinea yet exists although some of the more common forest tree species are briefly described in publications of the Botany Division (van Royen, 1964, Coode, 1969, and Foreman 1971) and of the Forestry College (Johns, 1975). A large quantity of plant ecological data from Papua New Guinea has also been gathered by the CSIRO Division of Land Use Research, and much of this is summarised by Paijmans (1975, 1976).

The *Flora Malesiana* provides information on the known distribution and ecology of many New Guinean representatives of families so far revised for the series, as do the *Flora of Java* (Backer and Backhuisen van der Brink, 1963-1968) and the *Tree Flora of Malaya* (Whitmore, 1972, 1973).

The data presented in Table II.1 have thus been gleaned from a variety of sources of differing emphasis and accuracy, ranging from individual botanists' field descriptions through forestry manuals, to detailed scientific, but primarily taxonomic, works. Much of the information derives from observations made outside the study area, and the extent of its applicability to the Markham region is largely unknown. However, in many cases this represents the only data available on which to base an interpretation of the plant's ecology.

The uncertainty both in the identification of some pollen and spore taxa, and in the ecological affinities of these and other taxa is reflected in Table II.2. Many of the palynomorph taxa may therefore be placed in more than one ecological group, depending on the criteria used for the construction of each category.

*TABLE II.1. The ecology of plants contributing to the pollen and spore taxa.*

| Computer Identifier | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|
| 1 TYPHA | 1-1- | *Typha* | Swamp herbs | *T. angustifolia* is a tall erect herb of swamp and shallow fresh or brackish water situations found particularly where the substrate is predominantly inorganic. Not recorded from the Markham area. |
| 2 PANDA | 2-1-6 | *Pandanus radula* T. | Small trees 'pandans' | *Pandanus* spp. are common in swamp and swamp forest vegetation; also in wet grassland areas and around lake shores, particularly at Lake Wanum. A frequent understorey component of lowland forest. |
| 3 SPARG | 3-1-2 | *Sparganium antipodum* T. | Swamp or aquatic herb | Erect herb of swamp or shallow water. Not recorded from the Markham area. |
| 4 GRAM1 | 11- | Gramineae 1 | Swamp grass | *Leersia hexandra* grows in swamp margin situations, and as an almost monospecific stand on some floating root-mats. |
| 5 GRAM2 | 11- | Gramineae 2 | Grasses | Represents predominantly swamp grasses, *Leersia, Sacciolepis,* and *Phragmites.* |
| 6 GRAM3 | 11- | Gramineae 3 | Grasses | Genera from swamp, wet grassland, and dry grassland situations. |
| 7 GRAM4 | 11- | Gramineae 4 | Grasses | This taxon includes a proportion of swamp genera, and a majority of the grains of *Imperata cylindrica* and *Ischaemum barbatum.* |
| 8 GRAM5 | 11- | Gramineae 5 | Grasses | Small proportion of swamp genera, large proportion of land grasses, including *Themeda australis,* and *Miscanthus floridulus.* |
| 9 CYPA1 | 12- | Cyperaceae A1 | Swamp herbs | Mainly representative of swamp and floating root-mat taxa. |
| 10 CYPA2 | 12- | Cyperaceae A2 | Erect herbs | Includes swamp and wet grassland taxa. |
| 11 CYPB1 | 12- | Cyperaceae B1 | Erect herbs | Includes swamp and wet grassland taxa. |
| 12 CYPB2 | 12- | Cyperaceae B2 | Erect herbs | Includes swamp and wet grassland taxa. |
| 13 CYPC1 | 12- | Cyperaceae C | Erect herbs | Includes swamp and wet grassland taxa. |
| 14 HYPOL | 12-19-2 | *Hypolytrum nemorum* T. | Swamp herb | *H. nemorum* is the dominant taxon in much of the herbaceous swamp vegetation at Lake Wanum and Redhill Swamp. It occurs rooted in the substrate in up to 1.5 m of water, and forms part of the floating root-mat vegetation in areas of greater water depth. |
| 15 PALMA | 13- | ?Palmae | Understorey trees or vines | Many genera of Palmae are found in lowland forests as sub-canopy or understorey trees, and vines. Some are also cultivated in gardens. |
| 16 METRO | 13- | ?*Metroxylon sagu* | Swamp palm | *Metroxylon* is very common in open swamp, swamp forest and alluvium forest in the lower Markham Valley, and also occurs around Yanamugi lake. |
| 17 CALAM | 13-3- | *Calamus* | Vines | Abundant in lowland forests. |
| 18 NORMA | 13-27- | ?*Normanbya* T. | Trees | Probably occur in the subcanopy component of lowland forest. |
| 19 ARENG | 13-48 | cf. *Arenga* | Small trees | Occur as understorey in lowland forest and also in swamp forest. Some species are cultivated. |

*TABLE II.1 (Cont.)*

| Computer Identifier | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|
| 20 COLOC | 15-6-1 | cf. *Colocasia* | Fleshy herbs | Species of *Colocasia* occur in swamp margin and floating root-mat vegetation at Lake Wanum. The cultivated *C. esculenta* (taro) is commonly grown in gardens fringing the lake. |
| 21 FLAGE | 17-1- | *Flagellaria* | Vines | *F. indica* is abundant in forests of seasonally drier areas but is also widespread in lowland forest up to 1 500 m, and in coastal scrub. |
| 22 LILIA | 32- | cf. Liliaceae | Shrubs, herbs, and vines | Widespread in lowland forest; some genera occur in regrowth or swamp vegetation. |
| 23 CASUA | 45-1- | *Casuarina* | Small trees | Generally restricted, in the Markham area, to village and garden sites. |
| 24 ENGEL | 55-4- | cf. *Engelhardtia* | Canopy trees | More common in ridge-top and lower montane forest between *c.* 1 000-2 000 m, although also present in the lowlands particularly along watercourses. Not found on limestone. |
| 25 NOTHO | 59-3- | *Nothofagus* | Canopy trees | Known to occur between 750-3 100 m on the New Guinea mainland but could be present at slightly lower altitudes. Assumes dominance in many areas between 1 500-3 000 m. |
| 26 CASTA | 59-4-1 | *Castanopsis* T. | Canopy trees | Alt. range of *Castanopsis/Lithocarpus* spp. descends to sea-level. The genera become domínent in many ridge-top and lower montane forests between *c.* 1 000-1 500 m. *Castanopsis* is not found on limestone soils. |
| 27 CELTI | 60-1- | *Celtis* | Tall canopy trees | Common in primary and secondary lowland and lower montane forests, particularly below *c.* 1 100 m altitude. |
| 28 TREMA | 60-2- | *Trema* | Trees | Common and abundant in secondary regrowth. |
| 29 APHAN | 60-4- | cf. *Aphananthe* | Trees or shrubs | - |
| 30 URMO2 | 61-/62- | Urticaceae/ Moraceae (diporate) | 1.Herbs, shrubs or trees (Urticaceae)<br>2.Shrubs or trees (Moraceae) | Widespread; herbs in wetter grassland, shrubs and trees in forest and regrowth communities. |
| 31 URMO3 | 61-/62- | Urticaceae/ Moraceae (triporate) | as above | as above |
| 32 STREB | 61-4- | *Streblus* T. | Trees or shrubs | *Streblus* is altitudinally widespread. *Antiaris toxicaria* is a large tree of 'alluvium' forest below *c.* 600 m. |
| 33 PILEA | 62-2- | *Pilea* T. | Herbs | Ground cover in forest and secondary vegetation. |
| 34 HELIC | 63-15- | *Helicia* | Sub-canopy trees and shrubs | The many species of *Helicia* occupy a wide altitudinal range, although representatives of the genus are more common above *c.* 500 m. *H. latifolia* is recorded from the Gabensis area. |
| 35 RUMEX | 75-1-3 | cf. *Rumex brownii* | Herb | - |
| 36 MUEHL | 75-11- | cf. *Muehlenbeckia* | Scandent shrubs or vines | - |

*TABLE II.1 (Cont.)*

| Computer Identifier | | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|---|
| 37 | NELUM | 85-6-1 | *Nelumbo nucifera* | Aquatic herb | Occurs at Lake Wanum in wet swamp and open water less than 4 m in depth. Dominant in open water shallower than 2 m, particularly where the substrate is predominantly inorganic. |
| 38 | STEPJ | 92-2-2 | *Stephania japonica* T. | Vine | In lowland forest. Collected from the Oomsis area. |
| 39 | HYPSE | 92-4- | *Hypserpa* | Vines | *H. polyandra* has been recorded from Lake Wanum. |
| 40 | TINOS | 92-6- | *Tinospora* | Woody vines | Fairly common especially in seasonally drier areas. |
| 41 | CANAN | 96-1-1 | cf. *Cananga odorata* | Canopy tree | Common in lowlands, particularly in secondary 'alluvium' and swamp forests. |
| 42 | TRIME | 100-5- | cf. *Trimenia* | Trees or shrubs | - |
| 43 | NEPEN | 110-1- | *Nepenthes* | Herbaceous creepers | *N. mirabilis* occurs commonly in wet grassland or swamp margin communities, and also occasionally in well developed floating root-mat vegetation. |
| 44 | QUINT | 117-3- | *Quintinia* | Canopy trees | More common in montane forest than at lower altitudes. |
| 45 | POLYO | 117-7- | *Polyosoma* | Canopy or sub-canopy trees | More common in montane forest, but recorded from lower altitudes in the Oomsis Creek area. |
| 46 | WEINM | 120-3- | *Weinmannia* T. | Canopy or sub-canopy trees | Occur in lowland and montane forest communities especially along the forest margin. |
| 47 | SPIRA | 120-15- | *Spiraeopsis* T. | Canopy and sub-canopy trees | Lowland and montane forests |
| 48 | ACAEN | 127-4- | *Acaena* | Herbs | More common in alpine and sub-alpine non-forest communities, although may be present at lower altitudes. |
| 49 | PARIN | 127-16- | ?*Parinari* | Canopy or sub-canopy trees | In lowland and lower montane forests, particularly in areas of lower rainfall. |
| 50 | LEGPB | 129- | ?Leguminosae (Papilionatae) B | Trees, shrubs, herbs, climbing herbs, or vines | Widespread in lowland forest and non-forest vegetation. |
| 51 | LEGPD | 129- | ?Leguminosae (Papilionatae) D | as above | as above |
| 52 | VANDA | 129-1- | *Vandasia* T. | 1.Climbing herbs or shrubs<br>2.large trees (*Pterocarpus*) | 1. Found in non-forest vegetation<br>2. *Pterocarpus indicus* occurs in lowland forest below 700 m altitude. |

*TABLE II.1 (Cont.)*

| Computer Identifier | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|
| 53 CROTA | 129-23- | cf. *Crotalaria* T. | Herbs or small shrubs | Commonly found in non-forest vegetation particularly on disturbed or cultivated ground. |
| 54 RUTAR | 139-/231- | Rutaceae/ Araliaceae T. | Trees | Mostly canopy or sub-canopy forest trees. |
| 55 EVODI | 139-9- | *Evodia* T. | Canopy or sub-canopy trees | In primary forest, but more common in secondary regrowth communities. Some species occur in swamp forest. |
| 56 EUPHT | 149- | cf. Euphorbiaceae | Herbs, shrubs or small trees | More commonly genera of non-forest or secondary forest vegetation rather than rainforest. |
| 57 EUPHO | 149- | ?Euphorbiaceae | as above | as above |
| 58 EUPHA | 149-1- | cf. *Euphorbia* | 1.Herbs or small shrubs<br>2.Small trees or shrubs (*Sapium*) | *Euphorbia* spp. are common in grassland, and in the early stages of regrowth after cultivation. *S. indicum* is found in 'alluvium' forest. |
| 59 EUPHI | 149-1-41 | *Euphorbia hirta* T. | Herb | Common in grassland and early stages of regrowth. |
| 60 MALLO | 149-3- | *Mallotus* T. | Small trees | Sub-canopy trees in lowland forest, particularly at margins. Also fairly common in disturbed forest and post-cultivation regrowth associations. |
| 61 MACMA | 149-3/-19 | *Macaranga/ Mallotus* | Small trees | In forest, regrowth, or grassland. |
| 62 CLAOX | 149-7- | *Claoxylon* | Small trees or shrubs | Present in the sub-canopy of the forest, or in secondary vegetation communities. |
| 63 PHYLA | 149-8-18 | *Phyllanthus* cf. *urinaria* | Herbs, shrubs or small trees | *P. urinaria* is a widespread erect herb of open ground. Other *Phyllanthus* spp. also occur in disturbed areas and grassland. |
| 64 ACALY | 149-9- | *Acalypha* | Herbs, shrubs or small trees | In shrubby grassland and regrowth communities; sometimes in the forest understorey. |
| 65 GLOCH | 149-17- | *Glochidion* T. | sub-canopy tree or shrub | Farily common sub-canopy tree in open forest, particularly where disturbed. Also occur as isolated small trees or shrubs in grassland. |
| 66 MACAR | 149-19- | *Macaranga* | Trees or shrubs | Very common in regrowth communities in areas of disturbed vegetation. *Macaranga* spp. frequently occur as solitary trees in grassland, and in the forest understorey. |
| 67 MACOV | 149-19-17 | *Macaranga ovatifolia* T. | small tree | - |
| 68 ANTID | 149-36- | *Antidesma* | Small trees or shrubs | Fire-tolerant trees of *A. ghaesembilla* occur frequently in grassland areas. *Antidesma* spp. are also found as sub-canopy trees in 'alluvium' forest. |
| 69 APORO | 149-61- | *Aporosa* | Sub-canopy trees | Small trees occurring commonly in lowland and lower montane forests. |

*TABLE II.1 (Cont.)*

| Computer Identifier | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|
| 70 MELAN | 149-73- | *Melanolepis* | Small trees or shrubs | *Melanolepis* is found in the understorey of secondary forest; *Bridelia* is a sub-canopy forest tree. |
| 71 BISCH | 149-79- | cf. *Bischofia* | Large canopy trees | Widespread and common in 'alluvium' forest and secondary forest with soils of high moisture content. Also occur in lower montane forest. |
| 72 ENDOS | 149-42- | *Endospermum* | Emergent forest tree | Some species occur as emergent trees in lowland rainforest and 'alluvium' forest. The genus is also common in long-established secondary forest. Characteristically a fast-growing opportunist tree. |
| 73 CLEID | 149-83- | *Cleidion* T. | Small trees or shrubs | Reported from lowland forest and limestone areas in Malaya. Probably not common. |
| 74 ANACA | 155- | Anacardiaceae | Forest trees | *Euroschinus* and *Semecarpus* are commonly found in swamp and 'alluvium' forest, but also occur in lowland and hill forest, and in secondary forest. |
| 75 RHUST | 155-1- | *Rhus* T. | Small trees | *R. taitensis* is very common in many lowland secondary forests. |
| 76 ILEXA | 159-1- | *Ilex* | Small trees | *I. arnhemensis* is common in wet scrub-grassland around Redhill Swamp. Other species occur as canopy or sub-canopy trees in lowland and montane forest. |
| 77 SPHEN | 159-2-1 | *Sphenostemon* cf. *papuanum* | Forest tree or shrub | Probably more common in montane forest than at lower altitudes. |
| 78 POLYP | 165-4-1 | *Polyporandra scandens* | Woody vine or scandent shrub | Present in lowland forest up to *c.* 700 m altitude. |
| 79 STEMO | 165-15- | *Stemonurus* | Canopy tree | The only representative of the genus in New Guinea is *S. monticolus* which occurs in lowland forest on slopes, up to *c.* 750 m altitude. Locally common. |
| 80 PLATE | 165-16-1 | *Platea excelsa* | Canopy or sub-canopy tree | Found in lowland and montane forests. |
| 81 DODON | 168-5- | *Dodonaea* | Shrub or small tree | *D. viscosa* is a pioneer plant of disturbed ground over a wide altitudinal range. |
| 82 GANOP | 168-18-1 | *Ganophyllum falcatum* | Canopy or sub-canopy tree | Restricted to lowland forest, frequently on the better drained soils. |
| 83 TRIST | 168-22- | *Tristiropsis* T. | Tall canopy trees | Lowland forest, especially in valleys, and 'alluvium' or swamp forest. |
| 84 RHAMN | 172- | Rhamnaceae | Shrubs or trees | *Gouania* and *Ventilago* are climbing shrubs; *Alphitonia* and *Zizyphus* are trees of lowland rainforest. |
| 85 ELAEO | 174-1- | *Elaeocarpus* T. | Canopy trees | Widespread in lowland and lower montane forests. |
| 86 MICRO | 177-4- | *Microcos* T. | Trees or shrubs | Occur commonly as understorey in lowland hill forest and 'alluvium' forest. |

*TABLE II.1 (Cont.)*

| Computer Identifier | | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|---|
| 87 | TRICO | 177-9- | *Trichospermum* | Trees | May be locally common along river banks and similar localities. |
| 88 | BRACH | 180-1- | *Brachychiton* T. | Trees | *B. carruthersii* is a deciduous species occurring in lowland forest, particularly 'alluvium' forest, below *c.* 550 m. However, it is not common in New Guinea and has not been reported from the Markham area. *Agyrodendron* is also rare. *Pterocymbium* is a common lowland tree, sometimes deciduous, often found on alluvial or swampy soils, and on ridges. Many *Sterculia* spp. are also common in lowland forests. |
| 89 | KLEIN | 180-6-1 | *Kleinhovia hospita* | Understorey tree | Common in lowland forest regrowth, especially in areas of seasonal rainfall, and in'alluvium' forest particularly in the early stages of colonisation of river margins. |
| 90 | STERC | 180-11-4 | cf. *Sterculia* | Small trees or shrubs | Many species occur in New Guinea. Widespread in lowland and lower montane forests, particularly in secondary forest. Sometimes deciduous. |
| 91 | STERE | 180-11-7 | cf. *Sterculia edelfeltii* | Small tree | Recorded from hill forest in the Oomsis area. |
| 92 | TETRA | 182-5- | *Tetracera* T. | Vines or scandent shrubs | Particularly in lowland forest-margin situations. |
| 93 | ANISO | 190-1- | *Anisoptera* T. | Tall canopy trees | *A. polyandra* is a common species of ridge crest and hill forest in the Oomsis area. The species is frequently deciduous. *Vatica* is a common tree, particularly in parts of Papua, growing both in swamp and hill forest situations. It has not been recorded from the Markham area. |
| 94 | DRIMY | 198-1 | *Drimys* T. | Shrubs or understorey trees | *Drimys* is a widely distributed component of upper-montane or sub-alpine forest, although it has also been reported growing as low as 1 600 m. *Bubbia* has been collected in the Morobe Province at Mt. Kiandi, and Gurakor (640 m). |
| 95 | TRICA | 200-7-1 | *Trichadenia philippinensis* | Canopy trees | Widespread, but not common, lowland tree of primary or secondary rainforest (up to *c.* 500 m altitude). Never in periodically inundated localities. |
| 96 | OCTOM | 208-1-1 | *Octomeles sumatrana* | Tall canopy tree | Massive tree up to 75 m in height. Common near rivers and in 'alluvium' forest, often in almost uniform stands. Fast growing pioneer species on abandoned river channels and levees. |
| 97 | SONNE | 218-1-1 | *Sonneratia caseolaris* | Shrub or tree | A pioneer species of the coastal mangrove vegetation, although generally growing in areas less saline than those occupied by *S. alba*. |
| 98 | BARRI | 220-1- | *Barringtonia* T. | Canopy or sub-canopy trees | *Barringtonia* spp. occur in coastal forest, 'alluvium' forest and some swamp forest. *Planchonia* is also found in littoral and 'alluvium' forest. |

*TABLE II.1 (Cont.)*

| Computer Identifier | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|
| 99 RHIZO | 221-1- | *Rhizophora apiculata* T. | Tree | *R. apiculata* is widespread and common mangrove species, although it is more tolerant of freshwater conditions than the two other New Guinean members of the genus. |
| 100 COMEL | 224-/226- | Combretaceae/ Melastomataceae | 1. Canopy trees or shrubs (Combretaceae)<br>2. Herbs or shrubs (Melastomataceae) | 1. The many species of *Terminalia* occupy a wide range of habitats. The genus is common in lowland 'alluvium' forest although may occur up to *c.* 2 000 m altitude. Most are deciduous. *Combretum* is an understorey shrub or vine.<br>2. *Melastoma affine* is a small shrub found in established tall grassland. *Osbeckia* is an erect herb which often grows on bare ground within grassland. |
| 101 MYRTA | 225-1- | Myrtaceae | Canopy or sub-canopy trees or shrubs | Main representatives are probably the many *Syzygium* spp. These occur in a wide variety of forest habitats including littoral forest and swamp forest. The genus is also common as an understorey component of lowland hill forest. |
| 102 POIKI | 226-1- | *Poikilogyne* T. | Herbs and scandent shrubs | - |
| 103 HALOR | 228-2- | *Haloragis* | 1. Herb (*H. chinensis*)<br>2. Shrub (*H. halconensis*) | 1. On open ground in grassland, especially on poor soils or river banks. Recorded growing close to the Markham River.<br>2. More common in montane forest, or as a garden weed in the highlands. Also possibly occurs in drier swamp situations. |
| 104 BOERL | 231-9- | *Boerlagiodendron* | Tree or erect shrub | Occurs in swamp forest at Oomsis. |
| 105 EPACR | 238- | Epacridaceae | Shrubs | The many genera occupy a wide altitudinal range, although are more common in montane forest and sub-alpine vegetation. |
| 106 RAPAN | 241-1-7 | *Rapanea* cf. *achradaefolia* T. | Small tree or shrub | More common in montane forest than at lower altitudes. |
| 107 MYRSI | 241-4- | cf. *Myrsine* T. | Small tree or shrubs | - |
| 108 PLANC | 244-2- | *Planchonella* T. | Canopy tree | *Planchonella* is widespread in lowland and lower montane forest, and 'alluvium' forests. *Pouteria* and *Chrysophyllum* tend to occur on well drained ridge sites. |
| 109 PALAQ | 244-7- | cf. *Palaquium* | Tall canopy tree | Lowland rainforest, coastal or swamp forests. |
| 110 DIOSP | 245-1-4 | *Diospyros* cf. *ferrea* | Sub-canopy tree | Found in 'alluvium' and swamp forests, and lowland hill forest. Occurs at Yanamugi in forest bordering the lake. |
| 111 SYMPL | 246-1- | *Symplocos* | Small sub-canopy tree | Commonly occurs as an understorey genus in montane forest, but also recorded from the Oomsis Creek area. |
| 112 OLEAS | 248-3- | *Olea* | Canopy trees | - |
| 113 NYMPH | 250-2- | *Nymphoides* | Aquatic herb | *N. indica* is a common species at both Lake Wanum and Yanamugi, occurring in open water up to *c.* 4 m in depth. |

TABLE II.1 (Cont.)

| Computer Identifier | ANU Ref. Collection No. | Pollen taxon | Habit | Ecology and distribution of plants probably included in the pollen taxon |
|---|---|---|---|---|
| 114 ALYXI | 251-2- | *Alyxia* | Vines or shrubs | In lowland forest, or swamp marginal vegetation. |
| 115 EVOLV | 254-9- | ?*Evolvulus* | Herbs or shrubs | - |
| 116 ECHIP | 257-1-1 | *Echium* cf. *plantagineum* | Herb | An exotic European weed, not recorded from New Guinea, but naturalised in southern Australia. |
| 117 VERBI | 258-/263- | cf. Verbenaceae/ Bignoniaceae | Herbs and vines | Predominantly genera of forest or secondary vegetation. |
| 118 VITEX | 258-14-1 | cf. *Vitex acuminata* | Canopy tree | Some *Vitex* spp. are found in lowland 'alluvium' and swamp forest. |
| 119 DYSOP | 259-7- | *Dysophylla* T. | Swamp herb | *D. verticillata* is an erect herb common in swamp margin situations. It may be found growing in up to *c*. 15 cm of water, and is particularly predominant at Redhill Swamp. |
| 120 PLANT | 271-1- | *Plantago* | Herbs | Several *Plantago* spp, are found in sub-alpine herb-fields, Exotic species have become introduced to the Eastern Highlands Province, although there is no record of these from the Markham area. |
| 121 TIMON | 275-7- | *Timonius* T. | Small tree | *T. timon* is a bushy fire tolerant tree often found in shrubby grassland. It is particularly common around the margin of Redhill Swamp. Other species occur in 'alluvium' or swamp forest. |
| 122 GARDE | 275-11- | *Gardenia* | Understorey tree | In lowland forest, especially along the forest margin. |
| 123 MORIN | 275-20- | *Morinda* | Shrubs or vines | *M. citrifolia* and *M. hirtella* are large shrubs occurring fairly commonly in forest-margin situations. *Morinda* is present around the lake at Yanamugi, and has been collected from many locations in the Markham Valley and Oomsis areas. |
| 124 NAUCL | 275-35- | *Nauclea* T. | Trees or shrubs | Some *Nauclea* spp. are found in swampy grassland or mixed swamp forest. *N. orientalis* is a common tree in the 'savanna' grassland areas of the Markham Valley. It is fire tolerant, yet also thrives in water-logged or swampy soils, occurring at the water's edge around Lake Wanum. It is also a common and vigorous pioneer on the steep piedmont fans of the northern side of the valley. *Anthocephalus* is a tree or shrub of 'alluvium' or swamp forest and possesses exceptional capacity for regeneration in such situations. Many *Neonauclea* spp. are shrubs or small trees found in 'alluvium' forest or along watercourses, although others are trees of montane forest up to 2 000 m in altitude. |
| 125 UNCAR | 275-78- | *Uncaria* T. | Herbaceous creeper or climber | *U. gambir* is found in the dense herbaceous swamp vegetation at Lake Wanum. |
| 126 COMPT | 286- | Compositae (Tubuliflorae) | Erect herbs | Many genera represented. Composites commonly occur on disturbed ground, in short grassland, and as weeds in cultivated gardens. |
| 127 PODOC | 305-1- | *Podocarpus* | Canopy trees | A dominant genus of much montane forest above *c*. 2 400 m, although *P. amarus* may be found as low as 600 m altitude. |

*TABLE II.1 (Cont.)*

| Computer Identifier | ANU Ref. Collection No. | Pollen or Spore taxon | Habit | Ecology and distribution of plants probably included in the pollen or spore taxon |
|---|---|---|---|---|
| 128 PHYLO | 305-4- | *Phyllocladus* | Canopy tree | More common in upper-montane forest, although has been recorded as low as 900 m altitude. |
| 129 DACRY | 305-7- | *Dacrycarpus* T. | Canopy tree | Generally restricted to montane vegetation above *c*. 2 600 m. |
| 130 GNETU | 311-1- | cf. *Gnetum* | Trees, shrubs or woody vines | *G. gnemon* is a common understorey tree of hill forest. It is often cultivated, and is present on old garden sites around the shores of L. Wanum. Other species may occur as vines in lowland forest. |
| 167 LYCOC | 401-1-17 | *Lycopodium cernuum* T. | Ground creeper | Commonly found on areas of disturbed ground, especially on landslips and in gullies. |
| 168 LYCOV | 401-1-18 | *Lycopodium* cf. *volubile* T. | Ground creeper | Found in wet grassland |
| 169 LYCOS | 401-1-19 | *Lycopodium squarrosum* T. | Epiphyte | In lowland forest. |
| 170 LYGOD | 407-1-1-3 | *Lygodium microphyllum* T. | Scandent fern | Grows on trees particularly at the forest margin of secondary communities. In areas with a pronounced dry season the species may also occur in swamp communities. Other species are ground creepers of grassland, or old garden sites. Restricted to lowlands below *c*. 1 300 m altitude. |
| 171 ANEMI | 407-1-2-1 | cf. *Anemia hirsuta* | Ground fern or vine | - |
| 172 PTERI | 407-2-1- | *Pteris* | Fern | - |
| 173 ADIAN | 407-8-1-6 | cf. *Adiantum diaphanum* T. | Fern | - |
| 174 HISTI | 407-11-3-1 | *Histiopteris incisa* T. | Fern | - |
| 175 DAVAL | 407-13-1- | *Davallia* T. | Epiphytic ferns | - |
| 176 NEPHR | 407-14-1- | *Nephrolepis* | Swamp ferns, ground ferns and epiphytes | *N. hirsutula* is a very common species in the floating root-mat vegetation at Lake Wanum *N. biserrata* is a ground fern, occurring particularly along creeks. |
| 177 ARTHR | 407-14-2- | ?*Arthropteris* cf. *tenella* | fern | - |
| 178 CYAT1 | 407-18- | Cyatheaceae 1 (psilate) | tree ferns | In forest, especially near creeks. All lowland *Cyathea* spp. are more or less shade-demanding and are not found in grassland. |
| 179 CYAT2 | 407-18- | Cyatheaceae 2 (patterned perisporium) | Tree ferns | as above |
| 180 CYCLA | 407-20-1-5 | cf. *Cyclosorus archboldiana* T. | Ground ferns | *Cyclosorus* spp. are common in the ground cover of swamp forest. At least one species occurs in the floating root-mat vegetation at Lake Wanum, but is not common. |

*TABLE II.1 (Cont.)*

| Computer Identifier | ANU Ref. Collection No. | Pollen or Spore taxon | Habit | Ecology and distribution of plants probably included in the pollen or spore taxon |
|---|---|---|---|---|
| 181 CYCLO | 407-20-1-11 | *Cyclosorus* T. | Ground fern | as above |
| 182 CYCLT | 407-20-1-12 | *Cyclosorus truncatus* T. | Ground fern | as above |
| 183 ASPLE | 407-21-1- | *Asplenium* T. | Epiphytic or ground ferns | In forest |
| 184 TECTA | 407-23-9- | cf. *Tectaria* | Fern | - |
| 185 STENA | 407-25-3- | cf. *Stenochlaena areolaris* | Scandent epiphytic fern | Occurs in New Guinea growing often on *Pandanus*. |
| 186 STENL | 407-25-3-1 | *Stenochlaena laurifolia* | Fern | In 'alluvium' forest |
| 187 STENO | 407-25-3-2 | *Stenochlaena palustris* | Scandent swamp fern | Abundant in open swamp forest and lake marginal vegetation, and as a component of floating root-mat vegetation. |
| 188 MICSO | 407-29-2 | *Microsorium* T. | Swamp or ground ferns | One *Microsorium* sp. is fairly common in established floating root-mat vegetation at Lake Wanum. Others occur in lowland forest. |

*TABLE II.2. Identified pollen and spore taxa included in ecological groups*

HERBACEOUS SWAMP

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 1 | TYPHA | 20 | COLOC |
| 3 | SPARG | 37 | NELUM |
| 4 | GRAM1 | 43 | NEPEN |
| 5 | GRAM2 | 113 | NYMPH |
| 9 | CYPA1 | 119 | DYSOP |
| 10 | CYPA2 | 125 | UNCAR |
| 11 | CYPB1 | 176 | NEPHR |
| 12 | CYPB2 | 187 | STENO |
| 13 | CYPCI | 188 | MICSO |
| 14 | HYPOL | | |

DRY LAND, NON-FOREST

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 6 | GRAM3 | 66 | MACAR |
| 7 | GRAM4 | 68 | ANTID |
| 8 | GRAM5 | 73 | CLEID |
| 23 | CASUA | 76 | ILEXA |
| 28 | TREMA | 81 | DODON |
| 42 | TRIME | 102 | POIKI |
| 53 | CROTA | 114 | ALYXI |
| 56 | EUPHT | 115 | EVOLV |
| 57 | EUPHO | 117 | VERBI |
| 58 | EUPHA | 120 | PLANT |
| 59 | EUPHI | 121 | TIMON |
| 60 | MALLO | 123 | MORIN |
| 61 | MACMA | 124 | NAUCL |
| 62 | CLAOX | 126 | COMPT |
| 63 | PHYLA | 167 | LYCOC |
| 64 | ACALY | 168 | LYCOV |
| 65 | GLOCH | | |

FOREST TREES

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 27 | CELTI | 79 | STEMO |
| 46 | WEINM | 80 | PLATE |
| 47 | SPIRA | 82 | GANOP |
| 49 | PARIN | 83 | TRIST |
| 54 | RUTAR | 84 | RHAMN |
| 67 | MACOV | 91 | STERE |
| 69 | APORO | 95 | TRICA |
| 74 | ANACA | 112 | OLEAS |
| 75 | RHUST | 122 | GARDE |

*TABLE II.2. (Cont.)*

FOREST, NON-CANOPY

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 15 | PALMA | 40 | TINOS |
| 17 | CALAM | 70 | MELAN |
| 18 | NORMA | 78 | POLYP |
| 21 | FLAGE | 92 | TETRA |
| 34 | HELIC | 101 | MYRTA |
| 38 | STEPJ | 111 | SYMPL |
| 39 | HYPSE | 130 | GNETU |

FOREST FERNS

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 169 | LYCOS | 183 | ASPLE |
| 178 | CYAT1 | 186 | STENL |
| 179 | CYAT2 | | |

'ALLUVIUM' FOREST

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 16 | METRO | 96 | OCTOM |
| 41 | CANAN | 97 | SONNE |
| 71 | BISCH | 98 | BARRI |
| 72 | ENDOS | 99 | RHIZO |
| 86 | MICRO | 104 | BOERL |
| 87 | TRICO | 110 | DIOSP |
| 89 | KLEIN | 118 | VITEX |

'MONTANE' FOREST

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 24 | ENGEL | 93 | ANISO |
| 25 | NOTHO | 94 | DRIMY |
| 26 | CASTA | 105 | EPACR |
| 44 | QUINT | 106 | RAPAN |
| 45 | POLYO | 127 | PODOC |
| 48 | ACAEN | 128 | PHYLO |
| 77 | SPHEN | 129 | DACRY |
| 85 | ELAEO | | |

*TABLE II.2. (Cont.)*

UBIQUITOUS ANGIOSPERMS

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 2 | PANDA | 51 | LEGPD |
| 19 | ARENG | 52 | VANDA |
| 22 | LILIA | 55 | EVODI |
| 29 | APHAN | 88 | BRACH |
| 30 | URMO2 | 90 | STERC |
| 31 | URMO3 | 100 | COMEL |
| 32 | STREB | 103 | HALOR |
| 33 | PILEA | 107 | MYRSI |
| 35 | RUMEX | 108 | PLANC |
| 36 | MUEHL | 109 | PALAQ |
| 50 | LEGPB | 116 | ECHIP |

UBIQUITOUS PTERIDOPHYTES

| Taxon No. | Taxon Identifier | Taxon No. | Taxon Identifier |
|---|---|---|---|
| 170 | LYGOD | 180 | CYCLA |
| 171 | ANEMI | 181 | CYCLO |
| 172 | PTERI | 182 | CYCLT |
| 173 | ADIAN | 184 | TECTA |
| 174 | HISTI | 185 | STENA |
| 175 | DAVAL | 189 | MONLS |
| 177 | ARTHR | 190 | MONLL |

# APPENDIX III

## POLLEN ANALYTICAL DATA

*TABLE III.1. Pollen and spore counts from contemporary surface samples*

| | TYPHA | PANDA | SPARG | GRAM1 | GRAM2 | GRAM3 | GRAM4 | GRAM5 | CYPA1 | CYPA2 | CYPB1 | CYPB2 | CYPCI | HYPOL | PALMA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| SQ 40 | 0 | 1 | 0 | 0 | 2 | 4 | 1 | 0 | 0 | 0 | 7 | 1 | 1 | 79 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 1 | 16 | 5 | 4 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 0 | 0 | 2 | 6 | 7 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| SS 20 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 22 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 2 | 7 | 2 | 1 | 14 | 0 | 29 | 0 | 5 | 6 | 0 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 0 | 6 | 0 | 1 | 12 | 7 | 5 | 7 | 0 | 0 | 4 | 34 | 1 | 260 | 0 |
| YANMC1 SS | 0 | 13 | 0 | 0 | 0 | 11 | 6 | 6 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |

| | METRO | CALAM | NORMA | ARENG | COLOC | FLAGE | LILIA | CASUA | ENGEL | NOTHO | CASTA | CELTI | TREMA | APHAN | URMO2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 |
| SS 13-15 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| SS 18 | 0 | 2 | 6 | 0 | 0 | 2 | 26 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| SS 20 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | 7 | 167 | 4 | 2 | 0 | 3 |
| SS 22 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 30 | 5 | 15 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 0 | 1 | 8 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| LWMC3 SS | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| YANMC1 SS | 0 | 3 | 0 | 0 | 0 | 5 | 1 | 1 | 0 | 1 | 1 | 4 | 3 | 0 | 13 |

| | URMO3 | STREP | PILEA | HELIC | RUMEX | MUEHL | NELUM | STEPJ | HYPSE | TINOS | CANAN | TRIME | NEPEN | QUINT | POLYO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| SS 20 | 10 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 22 | 7 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 11 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 27+28 | 4 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 11 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YANMC1 SS | 35 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |

| | WEINM | SPIRA | ACAEN | PARIN | LEGPB | LEGPD | VANDA | CROTA | RUTAR | EVODI | EUPHT | EUPHO | EUPHA | EUPHI | MALLO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 20 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 9 | 0 | 0 |
| SS 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 27+28 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YANMC1 SS | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.1. (Cont.)*

| | MACMA | CLAOX | PHYLA | ACALY | GLOCH | MACAR | MACOV | ANTID | APORO | MELAN | BISCH | ENDOS | CLEID | ANACA | RHUST |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 20 | 26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 22 | 10 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 6 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 1 | 0 | 0 | 0 | 0 | 10 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YANMC1 SS | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 |

| | ILEXA | SPHEN | POLYP | STEMO | PLATE | DODON | GANOP | TRIST | RHAMN | ELAEO | MICRO | TRICO | BRACH | KLEIN | STERC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| SS 20 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| SS 22 | 1 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 27 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| LWMC3 SS | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YANMC1 SS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | STERE | TETRA | ANISO | DRIMY | TRICA | OCTOM | SONNE | BARKI | RHIZO | COMEL | MYRTA | POIKI | HALOR | BOERL | EPACR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 11 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| SS 20 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| SS 22 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 9 | 0 | 0 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| YANMC1 SS | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

| | RAPAN | MYRSI | PLANC | PALAQ | DIOSP | SYMPL | OLEAS | NYMPH | ALYXI | EVOLV | ECHIP | VERBI | VITEX | DYSOP | PLANT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| SS 20 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 22 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 | 0 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| LWMC3 SS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YANMC1 SS | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |

| | TIMON | GARDE | MORIN | NAUCL | UNCAR | COMPT | PODOC | PHYLO | DACRY | GNETU | UK274 | UK156 | UK292 | MONPU | UK235 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 6 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 29 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 11 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YANMC1 SS | 0 | 0 | 0 | 8 | 0 | 23 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.1. (Cont.)*

| | UK293 | TRICU | UK194 | UK109 | UK104 | UK060 | 3CPAU | UK079 | UK119 | UK174 | 3CPBU | UK123 | UK221 | UK218 | 3CPCU |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| SS 27+28 | 0 | 0 | 250 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YANMC1 SS | 0 | 2 | 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | UK309 | UK310 | 3CPDU | 3CPEU | UK106 | STCPU | UK279 | DIPOU | UK147 | TRIPU | STEPU | UK290 | LYCOC | LYCOV | LYCOS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 20 | 0 | 0 | 15 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| SS 22 | 0 | 0 | 1 | 0 | 347 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 |
| SS 27+28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LWMC3 SS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YANMC1 SS | 1 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

| | LYGOD | ANEMI | PTERI | ADIAN | HISTI | DAVAL | NEPHR | ARTHR | CYAT1 | CYAT2 | CYCLA | CYCLO | CYCLT | ASPLE | TECTA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 0 | 0 | 0 | 0 | 48 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 40 | 0 | 0 | 0 | 0 | 0 | 1 | 247 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 50 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| SQ 51 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 |
| SS 13-15 | 0 | 0 | 0 | 0 | 0 | 2 | 17 | 0 | 2 | 4 | 0 | 16 | 0 | 8 | 0 |
| SS 18 | 0 | 0 | 2 | 0 | 7 | 0 | 3 | 5 | 4 | 2 | 0 | 10 | 0 | 13 | 0 |
| SS 20 | 0 | 0 | 0 | 0 | 3 | 8 | 0 | 0 | 9 | 0 | 0 | 8 | 1 | 2 | 0 |
| SS 22 | 0 | 0 | 0 | 4 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 0 |
| SS 23 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 5 | 0 | 0 | 5 | 0 | 3 | 0 |
| SS 27+28 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 0 |
| LWMC3 SS | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| YANMC1 SS | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 0 |

| | STENA | STENL | STENO | MICSO | MONLS | MONLL | UK019 | MONLU | UK312 | UK170 | UK172 | TRILU | UNCAT | INDET | SUMPS* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SQ 35 | 0 | 0 | 1 | 5 | 21 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 85 |
| SQ 40 | 0 | 1 | 88 | 0 | 61 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 | 559 |
| SQ 50 | 0 | 0 | 47 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 76 |
| SQ 51 | 0 | 0 | 75 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 139 |
| SS 13-15 | 0 | 0 | 0 | 1 | 15 | 38 | 0 | 1 | 16 | 0 | 0 | 0 | 0 | 4 | 165 |
| SS 18 | 0 | 11 | 2 | 0 | 4 | 38 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 20 | 215 |
| SS 20 | 0 | 0 | 0 | 0 | 9 | 8 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 55 | 411 |
| SS 22 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 32 | 539 |
| SS 23 | 1 | 0 | 2 | 0 | 15 | 16 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 33 | 249 |
| SS 27+28 | 0 | 0 | 2 | 0 | 3 | 4 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 11 | 314 |
| LWMC3 SS | 0 | 0 | 28 | 0 | 13 | 7 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 34 | 496 |
| YANMC1 SS | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 257 |

* SUMPS = sum total of counts for all pollen and spore taxa, including uncategorised and indeterminable palynomorphs.

*TABLE III.2. Pollen and spore counts from pollen traps*

| | TYPHA | PANDA | SPARG | GRAM1 | GRAM2 | GRAM3 | GRAM4 | GRAM5 | CYPA1 | CYPA2 | CYPB1 | CYPB2 | CYPCI | HYPOL | PALMA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 4 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | METRO | CALAM | NORMA | ARENG | COLOC | FLAGE | LILIA | CASUA | ENGEL | NOTHO | CASTA | CELTI | TREMA | APHAN | URMO2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 6 | 0 | 0 | 265 | 5 | 3 | 0 | 11 |
| PT 4 | 0 | 0 | 0 | 3 | 0 | 4 | 0 | 1 | 0 | 0 | 0 | 361 | 0 | 0 | 60 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 1 | 1 | 0 | 0 |

| | URMO3 | STREB | PILEA | HELIC | RUMEX | MUEHL | NELUM | STEPJ | HYPSE | TINOS | CANAN | TRIME | NEPEN | QUINT | POLYO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| PT 4 | 14 | 28 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| PT 5 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 235 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | WEINM | SPIRA | ACAEN | PARIN | LEGPB | LEGPD | VANDA | CROTA | RUTAR | EVODI | EUPHT | EUPHO | EUPHA | EUPHI | MALLO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| PT 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 368 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |

| | MACMA | CLAOX | PHYLA | ACALY | GLOCH | MACAR | MACOV | ANTID | APORO | MELAN | BISCH | ENDOS | CLEID | ANACA | RHUST |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 0 | 0 | 18 | 200 | 0 | 62 | 0 | 0 | 0 | 0 | 4 | 0 |
| PT 4 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 45 | 0 | 0 | 2 | 1 | 0 | 0 |
| PT 5 | 9 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 134 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | ILEXA | SPHEN | POLYP | STEMO | PLATE | DODON | GANOP | TRIST | RHAMN | ELAEO | MICRO | TRICO | PRACH | KLEIN | STERC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 1 | 49 | 0 | 0 | 0 | 1 | 13 | 0 | 0 | 0 | 0 | 0 |
| PT 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 72 | 0 | 1 | 0 | 0 | 0 | 11 | 0 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 0 | 218 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |

TABLE III.2. *(Cont.)*

| | STERF | TETRA | ANISO | DRIMY | TRICA | OCTOM | SONNE | PARRI | RHIZO | COMEL | MYRTA | POIKI | HALOR | ROFRL | EPACR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 60 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| PT 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | RAPAN | MYRSI | PLANC | PALAQ | DIOSP | SYMPL | OLEAS | NYMPH | ALYXI | EVOLV | ECHIP | VERBI | VITEX | DYSOP | PLANT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| PT 4 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | TIMON | GARDE | MORIN | NAUCL | UNCAR | COMPT | PODOC | PHYLO | DACRY | GNETU | UK274 | UK156 | UK292 | MONPU | UK235 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 |
| PT 4 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| PT 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | UK293 | TRICU | UK194 | UK109 | UK104 | UK060 | 3CPAU | UK079 | UK119 | UK174 | 3CPBU | UK123 | UK221 | UK218 | 3CPCU |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |

| | UK309 | UK310 | 3CPDU | 3CPEU | UK106 | STCPU | UK279 | DIPOU | UK147 | TRIPU | STEPU | UK290 | LYCOC | LYCOV | LYCOS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| PT 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | LYGOD | ANEMI | PTERI | ADIAN | HISTI | DAVAL | NEPHR | ARTHR | CYAT1 | CYAT2 | CYCLA | CYCLO | CYCLT | ASPLE | TECTA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 2 | 0 |
| PT 4 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 0 |
| PT 5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| PT 6 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 |

| | STENA | STENL | STENO | MICSO | MONLS | MONLL | UK019 | MONLU | UK312 | UK170 | UK172 | TRILU | UNCAT | INDET | SUMPS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PT 1 | 0 | 0 | 2 | 0 | 1 | 14 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 62 | 849 |
| PT 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 664 |
| PT 5 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 27 | 1031 |
| PT 6 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 7 | 35 |

*TABLE III.3. Pollen and spore counts from Yanamugi core YAN 2*

| | TYPHA | PANDA | SPARG | GRAM1 | GRAM2 | GRAM3 | GRAM4 | GRAM5 | CYPA1 | CYPA2 | CYPB1 | CYPB2 | CYPCI | HYPOL | PALMA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 5 | 6 | 6 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 3 | 7 | 6 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 12 | 22 | 15 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 240 | 7 | 0 | 0 | 1 | 3 | 8 | 2 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 320 | 0 | 1 | 0 | 0 | 5 | 8 | 2 | 11 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 400 | 0 | 1 | 0 | 0 | 2 | 4 | 1 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 2 | 5 | 0 | 8 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 3 | 0 | 0 | 2 | 5 | 1 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| YAN 2 870 | 0 | 2 | 0 | 0 | 0 | 4 | 2 | 3 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| YAN 2 910 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 8 | 11 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 2 | 0 | 2 | 1 | 2 | 2 | 1 | 0 | 0 | 2 | 0 | 4 | 0 | 0 |
| YAN 2 1070 | 0 | 0 | 0 | 0 | 0 | 5 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 1 | 0 | 0 | 0 | 1 | 3 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| YAN 2 1150 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 21 | 0 | 0 | 0 |

| | METRO | CALAM | NORMA | ARENG | COLOC | FLAGF | LILIA | CASUA | ENGEL | NOTHO | CASTA | CELTI | TREMA | APHAN | URMO2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 2 | 70 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 4 | 7 | 0 | 4 |
| YAN 2 240 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 3 | 0 | 0 |
| YAN 2 320 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 9 | 0 | 3 |
| YAN 2 400 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 2 | 4 | 0 | 4 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 3 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| YAN 2 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 2 |
| YAN 2 830 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 3 | 0 | 1 | 5 | 0 | 0 |
| YAN 2 870 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| YAN 2 910 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 5 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 0 | 0 |
| YAN 2 990 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 9 | 1 | 5 |
| YAN 2 1030 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 3 | 0 | 0 | 0 |
| YAN 2 1070 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 6 | 4 | 0 | 3 |
| YAN 2 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |

| | URMO3 | STREB | PILEA | HELIC | RUMEX | MUEHL | NELUM | STEPJ | HYPSE | TINOS | CANAN | TRIME | NEPEN | QUINT | POLYO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 240 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 710 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 13 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 870 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 910 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 950 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 1070 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.3. (Cont.)*

| | WEINM | SPIRA | ACAEN | PARIN | LEGPB | LEGPD | VANDA | CROTA | RUTAR | EVODI | EUPHT | EUPHO | EUPHA | EUPHI | MALLO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 240 | 0 | 5 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| YAN 2 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 910 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1070 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

| | MACMA | CLAOX | PHYLA | ACALY | GLOCH | MACAR | MACOV | ANTID | APORO | MELAN | BISCH | ENDOS | CLEID | ANACA | RHUST |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 240 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 0 | 0 | 0 | 1 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 1 | 0 | 5 | 0 | 13 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 870 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 910 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 2 | 0 | 1 | 4 | 0 | 0 | 0 | 1 |
| YAN 2 950 | 2 | 0 | 1 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 0 | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 1070 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | ILEXA | SPHEN | POLYP | STEMO | PLATE | DODON | GANOP | TRIST | RHAMN | ELAEO | MICRO | TRICO | BRACH | KLEIN | STERC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 240 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 870 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| YAN 2 990 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1070 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.3. (Cont.)*

| | STERE | TETRA | ANISO | DRIMY | TRICA | OCTOM | SONNF | BARRI | RHIZO | COMEL | MYRTA | POIKI | HALOR | BOERL | EPACR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| YAN 2 240 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 400 | 0 | 0 | 0 | 0 | 0 | 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 710 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 0 | 0 | 1 | 0 | 9 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 870 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 910 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 950 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 3 |
| YAN 2 1070 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

| | RAPAN | MYRSI | PLANC | PALAQ | DIOSP | SYMPL | OLEAS | NYMPH | ALYXI | EVOLV | ECHIP | VERBI | VITEX | DYSOP | PLANT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 240 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 476 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| YAN 2 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 910 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 990 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 7 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1070 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

| | TIMON | GARDE | MORIN | NAUCL | UNCAR | COMPT | PODOC | PHYLO | DACRY | GNETU | UK274 | UK156 | UK292 | MONPU | UK235 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 39 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 1 | 0 | 0 | 4 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 240 | 0 | 0 | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 3 | 0 | 0 | 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 710 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 0 | 0 | 9 | 1 | 0 | 0 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 870 | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 910 | 1 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 950 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 50 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 1070 | 0 | 0 | 0 | 11 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 0 | 0 | 0 | 102 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |

*TABLE III.3. (Cont.)*

| | UK293 | TRICU | UK194 | UK109 | UK104 | UK060 | 3CPAU | UK079 | UK119 | UK174 | 3CPBU | UK123 | UK221 | UK218 | 3CPCU |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 1 | 8 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 1 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 240 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 0 | 5 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 870 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| YAN 2 910 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1030 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 1070 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 0 | 0 | 26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | UK309 | UK310 | 3CPDU | 3CPEU | UK106 | STCPU | UK279 | DIPOU | UK147 | TRIPU | STEPU | UK290 | LYCOC | LYCOV | LYCOS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 240 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 320 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 400 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 640 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 750 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 790 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| YAN 2 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 950 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| YAN 2 1030 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 |
| YAN 2 1070 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.3. (Cont.)*

| | LYGOD | ANEMI | PTERI | ADIAN | HISTI | DAVAL | NEPHR | ARTHR | CYAT1 | CYAT2 | CYCLA | CYCLO | CYCLT | ASPLE | TECTA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 160 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 |
| YAN 2 200 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| YAN 2 240 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 320 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| YAN 2 400 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 |
| YAN 2 476 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 560 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 640 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 0 |
| YAN 2 670 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 5 | 2 | 0 | 0 | 0 | 3 | 0 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 0 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 |
| YAN 2 790 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 |
| YAN 2 830 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 14 | 2 | 4 | 2 | 0 | 5 | 0 |
| YAN 2 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 0 |
| YAN 2 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| YAN 2 990 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 1030 | 0 | 0 | 2 | 0 | 0 | 8 | 0 | 0 | 20 | 0 | 0 | 0 | 1 | 2 | 1 |
| YAN 2 1070 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 |
| YAN 2 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| YAN 2 1150 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | STENA | STENL | STENO | MICSO | MONLS | MONLL | UK019 | MONLU | UK312 | UK170 | UK172 | TRILU | UNCAT | INDET | SUMPS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| YAN 2 120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 124 |
| YAN 2 160 | 0 | 0 | 1 | 7 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 186 |
| YAN 2 200 | 0 | 0 | 4 | 9 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 139 |
| YAN 2 240 | 0 | 0 | 2 | 21 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 9 | 108 |
| YAN 2 320 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 86 |
| YAN 2 400 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 121 |
| YAN 2 476 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 25 |
| YAN 2 520 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 12 |
| YAN 2 560 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 13 |
| YAN 2 640 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 18 | 53 |
| YAN 2 670 | 0 | 0 | 0 | 1 | 2 | 9 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 12 | 85 |
| YAN 2 710 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 34 |
| YAN 2 750 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 35 |
| YAN 2 790 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 9 | 63 |
| YAN 2 830 | 0 | 0 | 0 | 0 | 2 | 8 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 30 | 179 |
| YAN 2 870 | 0 | 0 | 0 | 8 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 8 | 103 |
| YAN 2 910 | 0 | 0 | 1 | 0 | 2 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 | 102 |
| YAN 2 950 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 7 | 69 |
| YAN 2 990 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 77 |
| YAN 2 1030 | 0 | 0 | 0 | 0 | 6 | 18 | 0 | 2 | 0 | 2 | 1 | 12 | 1 | 32 | 209 |
| YAN 2 1070 | 0 | 0 | 0 | 3 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 80 |
| YAN 2 1110 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 6 | 171 |
| YAN 2 1150 | 0 | 0 | 0 | 6 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 16 | 80 |

*TABLE III.4. Pollen and spore counts from Lake Wanum Core LW II*

| | | | TYPHA | PANDA | SPARG | GRAM1 | GRAM2 | GRAM3 | GRAM4 | GRAM5 | CYPA1 | CYPA2 | CYPB1 | CYPB2 | CYPCI | HYPOL | PALMA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 10 | 46 | 1 | 0 | 0 | 4 | 0 | 12 | 0 | 0 | 4 | 0 |
| LW | II | 695 | 18 | 2 | 0 | 27 | 20 | 2 | 3 | 4 | 8 | 0 | 62 | 0 | 5 | 15 | 0 |
| LW | II | 730 | 9 | 1 | 0 | 2 | 7 | 2 | 2 | 9 | 3 | 0 | 2 | 0 | 1 | 28 | 0 |
| LW | II | 790 | 11 | 3 | 0 | 0 | 4 | 5 | 3 | 8 | 1 | 0 | 5 | 0 | 1 | 17 | 0 |
| LW | II | 870 | 5 | 0 | 0 | 0 | 1 | 1 | 5 | 3 | 1 | 0 | 3 | 0 | 0 | 7 | 0 |
| LW | II | 910 | 0 | 0 | 0 | 4 | 26 | 3 | 2 | 1 | 1 | 0 | 2 | 0 | 0 | 5 | 0 |
| LW | II | 1010 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 4 | 0 | 0 | 2 | 0 | 0 | 8 | 0 |
| LW | II | 1050 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 2 | 135 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 8 | 0 |
| LW | II | 1191 | 6 | 0 | 0 | 1 | 0 | 1 | 3 | 0 | 4 | 0 | 5 | 0 | 13 | 14 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 4 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 5 | 0 | 0 | 17 | 0 | 0 | 66 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 0 |
| LW | II | 1490 | 2 | 0 | 0 | 25 | 60 | 18 | 26 | 0 | 4 | 0 | 20 | 0 | 31 | 86 | 0 |
| LW | II | 1530 | 1 | 1 | 0 | 3 | 11 | 4 | 14 | 0 | 2 | 0 | 8 | 0 | 5 | 67 | 0 |
| LW | II | 1610 | 0 | 1 | 0 | 0 | 25 | 22 | 5 | 19 | 0 | 0 | 3 | 5 | 0 | 6 | 0 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 4 | 78 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 309 | 0 |
| LW | II | 1770 | 0 | 0 | 0 | 0 | 4 | 3 | 8 | 2 | 0 | 0 | 7 | 0 | 6 | 54 | 0 |
| LW | II | 1810 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 14 | 0 | 2 | 122 | 0 |
| LW | II | 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 0 | 38 | 0 |
| LW | II | 1850 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 28 | 0 |
| LW | II | 1870 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 16 | 0 |
| LW | II | 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 0 | 6 | 114 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 2 | 2 | 24 | 98 | 0 | 1 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 9 | 15 | 0 | 3 | 0 |
| LW | II | 1950 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 6 | 7 | 0 | 0 | 0 |
| LW | II | 1970 | 3 | 0 | 1 | 0 | 1 | 3 | 2 | 0 | 4 | 0 | 13 | 2 | 0 | 6 | 0 |

| | | | METRO | CALAM | NORMA | ARENG | COLOC | FLAGE | LILIA | CASUA | ENGEL | NOTHO | CASTA | CELTI | TREMA | APHAN | URMO2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 695 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 2 |
| LW | II | 730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| LW | II | 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 4 | 0 | 0 |
| LW | II | 870 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 3 | 4 | 0 | 0 |
| LW | II | 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| LW | II | 1010 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 8 | 2 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 4 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1490 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 11 | 0 | 0 |
| LW | II | 1530 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 8 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 11 | 0 | 6 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| LW | II | 1770 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 0 | 0 |
| LW | II | 1810 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 0 | 0 |
| LW | II | 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW | II | 1850 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| LW | II | 1870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 4 | 0 | 0 | 2 |

*TABLE III.4. (Cont.)*

| | URMO3 | STREB | PILEA | HELIC | RUMEX | MUEHL | NELUM | STEPJ | HYPSF | TINOS | CANAN | TRIME | NEPEN | QUINT | POLYO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW II 644 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 685 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW II 730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 790 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW II 870 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW II 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1010 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1346 | 0 | 4 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1490 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1530 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1610 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1770 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1810 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1850 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1870 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1907 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1930 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1950 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1970 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | WEINM | SPIRA | ACAEN | PARIN | LEGPB | LEGPD | VANDA | CROTA | RUTAR | EVODI | EUPHT | EUPHO | EUPHA | EUPHI | MALLO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW II 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 685 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| LW II 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW II 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| LW II 1010 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| LW II 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW II 1346 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1490 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1530 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1610 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| LW II 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1770 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 |
| LW II 1810 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| LW II 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1850 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW II 1907 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1930 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW II 1950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1970 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |

| | MACMA | CLAOX | PHYLA | ACALY | GLOCH | MACAP | MACOV | ANTID | APORO | MELAN | RISCH | ENDOS | CLEID | ANACA | RHUST |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW II 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 685 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| LW II 730 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 790 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 870 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| LW II 910 | 0 | 0 | 0 | 1 | 22 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW II 1010 | 0 | 0 | 0 | 1 | 0 | 5 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW II 1050 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1191 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1310 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1346 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW II 1410 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1490 | 0 | 0 | 4 | 0 | 0 | 23 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1530 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1610 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW II 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW II 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1770 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1810 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1850 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1870 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW II 1890 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1907 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1930 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1950 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW II 1970 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.4. (Cont.)*

| | | | ILEXA | SPHEN | POLYP | STEMO | PLATE | DODON | GANOP | TRIST | RHAMN | ELAEO | MICRO | TRICO | PRACH | KLEIN | STERC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 685 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 730 | 1 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 790 | 3 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 870 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1010 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1490 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1530 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1770 | 5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 14 | 1 | 0 | 0 |
| LW | II | 1810 | 148 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1850 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1870 | 96 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| LW | II | 1890 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | STERE | TETRA | ANISO | DRIMY | TRICA | OCTOM | SONNE | BARRI | RHIZO | COMEL | MYRTA | POIKI | HALOR | BOERL | EPACR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 685 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 790 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 870 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1010 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 1490 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 1530 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1770 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1810 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1830 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 1850 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1870 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 1890 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | RAPAN | MYRSI | PLANC | PALAQ | DIOSP | SYMPL | OLEAS | NYMPH | ALYXI | EVOLV | ECHIP | VERBI | VITEX | DYSOP | PLANT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 685 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW | II | 730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 1 | 1 |
| LW | II | 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1010 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1490 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1530 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1770 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1810 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1830 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1850 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1870 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.4. (Cont.)*

| | | | TIMON | GARDE | MORIN | NAUCL | UNCAR | COMPT | PODOC | PHYLO | DACRY | GNETU | UK274 | UK156 | UK292 | MONPU | UK235 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 685 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 730 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 790 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 870 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 910 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1010 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1490 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1530 | 0 | 0 | 0 | 3 | 4 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1770 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1810 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1850 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1870 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1890 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | UK293 | TRICU | UK194 | UK109 | UK104 | UK069 | 3CPAU | UK079 | UK119 | UK174 | 3CPBU | UK123 | UK221 | UK218 | 3CPCU |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 685 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1010 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 251 | 0 | 0 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1490 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1530 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1770 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1810 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 9 | 0 | 0 | 0 |
| LW | II | 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1850 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

| | | | UK309 | UK310 | 3CPDU | 3CPEU | UK106 | STCPU | UK279 | DIPOU | UK147 | TRIPU | STEPU | UK290 | LYCOC | LYCOV | LYCOS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 685 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| LW | II | 730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| LW | II | 790 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 910 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1010 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1310 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1346 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1490 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 |
| LW | II | 1530 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1770 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| LW | II | 1810 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1830 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1850 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1870 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1930 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*TABLE III.4. (Cont.)*

| | | | LYGOD | ANEMI | PTERI | ADIAN | HISTI | DAVAL | NEPHR | ARTHR | CYAT1 | CYAT2 | CYCLA | CYCLO | CYCLT | ASPLE | TECTA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 0 | 0 | 0 | 0 | 130 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 685 | 1 | 0 | 1 | 0 | 0 | 0 | 30 | 0 | 0 | 7 | 0 | 0 | 0 | 1 | 0 |
| LW | II | 730 | 0 | 0 | 1 | 0 | 0 | 0 | 52 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 790 | 3 | 0 | 1 | 0 | 0 | 0 | 77 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 870 | 1 | 0 | 1 | 0 | 0 | 0 | 85 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 910 | 1 | 0 | 2 | 0 | 0 | 0 | 104 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1010 | 0 | 0 | 0 | 0 | 0 | 1 | 46 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 |
| LW | II | 1050 | 0 | 0 | 0 | 0 | 0 | 0 | 239 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1110 | 0 | 0 | 0 | 0 | 0 | 1 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1191 | 0 | 0 | 19 | 0 | 0 | 0 | 192 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1310 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1346 | 1 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1410 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 1 | 0 | 0 | 6 | 0 |
| LW | II | 1490 | 9 | 0 | 42 | 0 | 0 | 0 | 415 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1530 | 3 | 0 | 1 | 0 | 0 | 0 | 171 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1610 | 0 | 0 | 0 | 0 | 0 | 1 | 10 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1730 | 0 | 0 | 0 | 0 | 0 | 1 | 27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1750 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1770 | 41 | 0 | 0 | 0 | 0 | 0 | 148 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1810 | 1 | 0 | 1 | 0 | 1 | 1 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1830 | 0 | 0 | 0 | 0 | 1 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1850 | 0 | 0 | 0 | 0 | 0 | 0 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1870 | 0 | 1 | 0 | 0 | 0 | 0 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1907 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| LW | II | 1930 | 1 | 0 | 0 | 0 | 0 | 1 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LW | II | 1970 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |

| | | | STENA | STENL | STENO | MICSO | MONLS | MONLL | UK019 | MONLU | UK312 | UK170 | UK172 | TRILU | UNCAT | INDET | SUMPS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LW | II | 644 | 0 | 0 | 3 | 2 | 1 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 235 |
| LW | II | 685 | 0 | 0 | 11 | 5 | 6 | 9 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 26 | 299 |
| LW | II | 730 | 0 | 0 | 4 | 4 | 12 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 184 |
| LW | II | 790 | 0 | 0 | 15 | 13 | 9 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 20 | 245 |
| LW | II | 870 | 0 | 0 | 15 | 32 | 20 | 24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 | 271 |
| LW | II | 910 | 0 | 0 | 1 | 2 | 4 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 22 | 220 |
| LW | II | 1010 | 0 | 0 | 13 | 36 | 11 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 29 | 212 |
| LW | II | 1050 | 0 | 0 | 5 | 1 | 4 | 4 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 32 | 445 |
| LW | II | 1110 | 0 | 0 | 656 | 1 | 2 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 712 |
| LW | II | 1191 | 0 | 0 | 12 | 10 | 9 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 52 | 357 |
| LW | II | 1310 | 0 | 0 | 54 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 350 |
| LW | II | 1346 | 0 | 0 | 10 | 1 | 4 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 | 166 |
| LW | II | 1410 | 0 | 0 | 0 | 18 | 55 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 157 |
| LW | II | 1490 | 0 | 0 | 26 | 46 | 15 | 49 | 1 | 9 | 0 | 0 | 0 | 0 | 0 | 49 | 993 |
| LW | II | 1530 | 0 | 0 | 40 | 12 | 16 | 8 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 55 | 493 |
| LW | II | 1610 | 0 | 0 | 0 | 1 | 4 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 175 |
| LW | II | 1730 | 0 | 0 | 22 | 1 | 0 | 12 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 18 | 176 |
| LW | II | 1750 | 0 | 0 | 6 | 1 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 342 |
| LW | II | 1770 | 0 | 0 | 61 | 34 | 9 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 82 | 517 |
| LW | II | 1810 | 0 | 0 | 327 | 15 | 9 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 49 | 777 |
| LW | II | 1830 | 0 | 0 | 266 | 1 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 337 |
| LW | II | 1850 | 0 | 0 | 191 | 6 | 25 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 37 | 344 |
| LW | II | 1870 | 0 | 0 | 126 | 12 | 13 | 29 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 350 |
| LW | II | 1890 | 0 | 0 | 437 | 11 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 23 | 665 |
| LW | II | 1907 | 0 | 0 | 42 | 0 | 5 | 73 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 296 |
| LW | II | 1930 | 0 | 0 | 57 | 0 | 13 | 59 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 207 |
| LW | II | 1950 | 0 | 0 | 69 | 0 | 1 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 118 |
| LW | II | 1970 | 0 | 0 | 1 | 0 | 4 | 3 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 21 | 102 |

*Calculation of pollen concentrations and pollen deposition rates*

Estimates for either pollen concentration (grains $ml^{-1}$) or pollen deposition rate (grains $cm^{-2}$ $yr^{-1}$) with 95% confidence limits for *counting* errors, may be calculated from the preceding pollen and spore counts by the formula:

$$T \times F \pm 2\sqrt{T} \times F$$

Where

T = the count for any taxon, or group of taxa in a sample,

F = the multiplicative factor for either pollen concentration or PDR for the appropriate sample, given in tables III.5 to III.7.

Due to the unreliable chronology, no PDR factors are shown for Yanamugi core YAN 2.

*TABLE III.5. Factors for pollen and spore counts from pollen traps*

| Trap | Factor for grains per trap | Factor for grains $cm^{-2}$ $yr^{-1}$ |
|---|---|---|
| PT 1 | 4285.71 | 155.35 |
| PT 4 | 4285.71 | 153.50 |
| PT 5 | 10714.29 | 388.93 |
| PT 6 | 287.35 | 10.45 |

*TABLE III.6. Factors for pollen and spore counts from Yanamugi Core YAN 2*

| cm below datum | Factor for grains $ml^{-1}$ of sediment |
|---|---|
| 120 | 114.94 |
| 160 | 114.94 |
| 200 | 114.94 |
| 240 | 306.12 |
| 320 | 57.47 |
| 400 | 95.79 |
| 476 | 57.47 |
| 520 | 57.47 |
| 560 | 57.47 |
| 640 | 47.89 |
| 670 | 114.94 |
| 710 | 82.10 |
| 750 | 27.37 |
| 790 | 95.79 |
| 830 | 57.47 |
| 870 | 82.10 |
| 910 | 28.74 |
| 950 | 57.47 |
| 990 | 82.10 |
| 1030 | 57.47 |
| 1070 | 57.47 |
| 1110 | 71.84 |
| 1150 | 32.81 |

*TABLE III.7. Factors for pollen and spore counts from Lake Wanum core LW II*

| cm below datum | Factor for grains $ml^{-1}$ of sediment | Factor for grains $cm^{-2}$ $yr^{-1}$ (assuming sediment accumulation rate 'C') |
|---|---|---|
| 644 | 357.14 | 65.77 |
| 685 | 102.02 | 13.27 |
| 730 | 238.10 | 30.96 |
| 790 | 214.29 | 39.18 |
| 870 | 122.95 | 22.48 |
| 910 | 535.71 | 94.94 |
| 1010 | 122.95 | 19.06 |
| 1050 | 214.29 | 33.22 |
| 1110 | 47.89 | 7.42 |
| 1191 | 357.14 | 137.36 |
| 1310 | 238.10 | 91.58 |
| 1346 | 238.10 | 81.26 |
| 1410 | 535.71 | 164.33 |
| 1490 | 194.81 | 33.42 |
| 1530 | 142.86 | 24.50 |
| 1610 | 47.89 | 14.51 |
| 1730 | 47.62 | 3.40 |
| 1750 | 71.84 | 5.14 |
| 1770 | 428.57 | 30.63 |
| 1810 | 285.71 | 18.59 |
| 1830 | 143.68 | 9.35 |
| 1850 | 535.71 | 34.85 |
| 1870 | 143.68 | 9.35 |
| 1890 | 357.14 | 22.13 |
| 1907 | 287.36 | 17.02 |
| 1930 | 95.79 | 5.66 |
| 1950 | 114.94 | 6.80 |
| 1970 | 100.00 | 5.91 |

# APPENDIX IV

## COMPUTER PROGRAMS

When handling the large array of unfamiliar pollen analytical data from tropical lowland samples, the utility of computer assistance becomes obvious. Different base sums for relative diagrams can be evaluated rapidly, as can the effect on PDR values of applying alternative sediment accumulation rates. This accuracy and flexibility should, in theory, allow for better interpretation of the available evidence.

Modified versions of two pre-existing FORTRAN V programs for manipulation of palynological data (Raine, 1974), run on the ANU UNIVAC 1100/42 computer, were used extensively in this study. The program sources are listed in full on following pages.

Program POLGRP checks the format of the raw data and produces tables of pollen counts, such as those in Appendix III. The program can also amalgamate any combination of samples and/or taxa and tabulate the results, or store them in the same format as the original data.

Program PLOTABS is an expanded version of Dodson's PLNSPRS and PLNGPS programs (Dodson, 1972) and incorporates many of their features. In addition, PLOTABS can handle 'absolute' pollen analytical data, and, using ANU library routine ANUPLOT, writes plotfiles for subsequent production on a CALCOMP 960 plotter. Using the raw data, or the output from POLGRP, program PLOTABS allows for amalgamation of taxa, calculation of relative frequencies in relation to any base sum, and multiplication of counts by a factor to produce values for pollen concentration or

PDR. With some manipulation, publication standard relative pollen diagrams can be drawn via the program. The pollen concentration or PDR diagrams are often less satisfactory due to the limited horizontal scaling available. All pollen diagrams in this thesis have been re-drawn from computer-generated plots. The PLOTABS program could be substantially improved by addition of more sophisticated plot-scaling, and sub-routines for the calculation of confidence limits on percentage and 'absolute' values.

*Program POLGRP*

```
C        PROGRAM POLGRP        VERSION 2,  4 AUG 1977
C        THIS PROGRAM TAKES RAW SPECTRA AND FORMS COUNTS FOR GROUP
C        AND FOR GROUPS OF SPECTRA ( LEVELS OF POLLEN DIAGRAM)
C
C        INPUT FORMAT IS 20F3.0 FOR DATA, UNIT 1
C        OUTPUT FORMAT IS 20F3.0 FOR DATA, UNIT 24
C
C        FIRST DATA CARD: NOTAX,NOSPEC,NGRPS,NLEV,NOUT
C        NOTAX IS NO OF TAXA    (MAX 200)
C        NOSPEC IS NO OF SPECTRA    (MAX 30)
C        NGRPS IS NO OF GROUPS TO BE MADE
C        NLEV IS NO OF LEVELS OF SPECTRA TO BE MADE
C        NOUT IS LOGICAL UNIT NO FOR OUTPUT OF FINAL TABLE
C        RAW DATA SET CARDS FOLLOW   (2013,7X,2A5,I3)
C        GROUP NAME CARDS ARE EACH FOLLOWED BY TAXON NO. CARDS
C        GROUP NAME CARD FORMAT (3X,A5)
C        TAXON NO. CARD FORMAT (I3)
C        A CARD WITH 999 IN COLS. 1-3 TERMINATES GROUP CARD SET
C        LEVEL NAME CARDS ARE EACH FOLLOWED BY SPECTRUM NO. CARDS
C        LEVEL NAME CARD FORMAT (3X,2A5)
C        SPECTRUM NO. CARD FORMAT (I3)
C        A CARD WITH 999 IN COLS. 1-3 TERMINATES LEVEL CARD SET
C
         DIMENSION NAMGRP(200),LEVEL(30),LCONT(30)
         INTEGER   FDATA(200,30),DATA(200,30),GDATA(200,30)
         EQUIVALENCE (DATA(1,1),GDATA(1,1))
C        READ CONTROL CARD
         READ(1,400)NOTAX,NOSPEC,NGRPS,NLEV,NOUT
  400    FORMAT()
C        READ IN DATA
         DO 30 J=1,NOSPEC
         READ(1,100) (DATA(I,J),I=1,NOTAX)
  100    FORMAT(20I3)
   30    READ(30,101) LEVEL(J),LCONT(J)
  101    FORMAT(67X,2A5,3X)
         NS=1
         NF=20
   40    IF(NOTAX-NF)41,41,1
```

*Program POLGRP (Cont.)*

```
C        PRINT OUT TABLE
   41   NF=NOTAX
    1   WRITE ( 3,110)
  110   FORMAT(1H1,/,1X,'LEVEL           TAXON NUMBER')
        WRITE ( 3,120) (I,I=NS,NF)
  120   FORMAT(14X,20(I3,1X),/,)
        DO 42 J=1,NOSPEC
   42   WRITE ( 3,130) (LEVEL(J),LCONT(J),(DATA(I,J),I=NS,NF))
  130   FORMAT(1X,2A5,3X,20(I3,1X))
        IF(NOTAX.EQ.NF) GO TO 50
        NS=NS+20
        NF=NF+20
        GO TO 41
   50   I=1
        DO 51 KJ=1,200
        DO 51 KI=1,30
   51   FDATA(KJ,KI)=0
        WRITE ( 3,270)
C       READ GROUP NAME & COMPOSITION CARDS & FORM GROUPS
  270   FORMAT(1H1)
        READ( 1,200)NAMGRP(I)
  200   FORMAT(3X,A5)
        WRITE( 3,200)NAMGRP(I)
    2   READ( 1,210) ICOLL
  210   FORMAT(I3)
        IF(ICOLL)91,5,3
    3   IF(ICOLL.EQ.999) GO TO 7
        WRITE( 3,260) ICOLL
  260   FORMAT(7X,I3)
        DO 4 J=1,NOSPEC
    4   FDATA(I,J)=FDATA(I,J)+DATA(ICOLL,J)
        GO TO 2
    5   I=I+1
        READ( 1,200)NAMGRP(I)
        WRITE (3,200) NAMGRP(I)
        GO TO 2
    7   IF(NGRPS.NE.I) GO TO 90
        J=1
        DO 71 KJ=1,200
        DO 71 KI=1,30
   71   DATA(KJ,KI)=0
        WRITE( 3,270)
```

*Program POLGRP (Cont.)*

```
C       READ LEVEL NAME & COMPOSITION CARDS & FORM GROUPS
        READ( 1,201)LEVEL(J),LCONT(J)
        WRITE( 3,201) LEVEL(J),LCONT(J)
   201  FORMAT(3X,2A5)
     8  READ ( 1,210) ICOLL
        IF(ICOLL)91,11,9
     9  IF(ICOLL.EQ.999) GO TO 13
        WRITE( 3,260) ICOLL
        DO 10 K=1,NGRPS
    10  GDATA(K,J)=GDATA(K,J)+FDATA(K,ICOLL)
        GO TO 8
    11  J=J+1
        READ( 1,201)LEVEL(J),LCONT(J)
        WRITE ( 3,201) LEVEL(J),LCONT(J)
        GO TO 8
    13  IF(J.NE.NLEV) GO TO 90
        NS=1
        NF=15
    14  IF(NGRPS-NF)15,15,16
    15  NF=NGRPS
C       PRINT OUT FINAL TABLE OF GROUPED SPECTRA
    16  WRITE( NOUT,300) (NAMGRP(I),I=NS,NF)
   300  FORMAT(1H1,//////,19X,15(A5,1X),/,)
        DO 18 J=1,NLEV
    18  WRITE( NOUT,310) (LEVEL(J),LCONT(J),(GDATA(I,J),I=NS,NF))
   310  FORMAT(7X,2A5,15(I5,1X))
        IF(NGRPS.EQ.NF) GO TO 17
        NS=NS+15
        NF=NF+15
        GO TO 14
    17  DO 20 J=1,NLEV
        K=1
        KK=20
C       SEND DATA IN 20I3 FORMAT TO LOGICAL UNIT 24
    21  WRITE(24,80) (GDATA(I,J),I=K,KK),LEVEL(J),LCONT(J)
    80  FORMAT(20I3,7X,2A5,3X)
        IF(NGRPS.LE.KK) GO TO 20
        K=K+20
        KK=KK+20
        GO TO 21
    20  CONTINUE
    91  STOP
    90  WRITE(3,240)
   240  FORMAT(2X,'NO. OF GROUPS OR LEVELS INCORRECT AT READ-IN')
        END
```

```
C     PROGRAM PLOTABS   VERSION 2,   SEPT.1977
C     CALCULATES AND LISTS PERCENTAGES AND ABSOLUTE VALUES OF
C     MICROFOSSIL TYPES AND WRITES THESE TO A PLOTFILE (LDEV 9).
C     INCLUDE LIB E8*ANUPLOT. IN MAP
C
C     FIRST CARD : CONTROL CARD
C     COL.  1-3 NO. OF DATA BATCHES (MAX = 80)
C     COL.  4-6 NO. OF MICROFOSSIL TYPES (MAX = 200)
C     COL.  7-8 NO. OF GROUPS TO BE USED AS BASE SUMS
C               (THESE ARE ARRANGED FIRST)
C     COL. 9-10 TOTAL NO. OF GROUPS  (MAX. 24)
C     COL     11        PUT  0  FOR A RELATIVE (PERCENTAGE) DIAGRAM
C                       PUT  1  FOR AN ABSOLUTE (LINEAR SCALE) DIAGRAM
C                       PUT  2  FOR AN ABSOLUTE (LOG. SCALE) DIAGRAM
C     COL.12-15 THE STARTING VALUE FOR THE DEPTH AXIS (I4)
C     COL.16-24 DIVISION FACTOR (F9.0) FOR PLOT IF COL. 11 = 1
C     COL.25-80 HEADING FOR SITE
C
C     HEADINGS FOR GROUPS IN 2A6 FORMAT (COLS.1-12).
C
C     BLANK CARD  IF LESS THAN 24 GROUPS ARE TO BE FORMED
C
C     DATA DECK IN 20I3 FORMAT (COLS.1-60), WITH DEPTHS IN I5
C     (COLS.68-72) AND DEPTH (I5) IN COLS. 73-77.
C     COLS. 78-80 ARE FOR CARD SEQUENCE
C     NUMBERS WHICH ARE NOT READ BY THE PROGRAM.
C
C     CARDS CONTAINING LIST OF MICROFOSSIL TYPES FOR EACH GROUP:
C     FORMAT MMMXNNN,1X WHERE    MMM IS 1ST TAXON ORDINAL NO.
C                                NNN IS 2ND TAXON ORDINAL NO.
C                                X=1 IF TAXA MMM & NNN TO BE ADDED
C                                X=2 IF TAXA MMM TO NNN TO BE ADDED
C     FURTHER GROUPINGS MMMXNNN,1X MAY FOLLOW THE FIRST,
C     UP TO A MAXIMUM OF 10 PER CARD.  ANY NO. OF ADDITIONAL
C     CARDS, IN THE SAME FORMAT,  MAY FOLLOW.
C     HOWEVER, IF  THE LAST CARD FOR A GROUP CONTAINS
C     10 GROUPINGS, A BLANK CARD MUST FOLLOW.
```

*Program PLOTABS (Cont.)*

```
C
C      CARDS WITH ABSOLUTE CORRECTION FACTORS IN F10.3 FORMAT,
C      ONE PER CARD IN COLS.1-10, IN ORDER OF INCREASING DEPTH.
C
C******************************************************************************
C
       DIMENSION ISITE(12), LEV(80), NEV(80), PERC(25,80),CORR(80)
       DIMENSION NGP(2 ,25)
       COMMON MPLN(200), ILK
       COMMON LIST(200,80)
       DIMENSION X(400),Y(400)
       CALL PLOTC(9,32,100.0,0)
       CALL PLOT(1.5,1.5,-3)
C      READ CONTROL INFORMATION
       READ(1,10)NUM,NPLN,KNT,MANYGP,JABS,ISTAR,FACTOR,(ISITE(I),I=1,14)
   10  FORMAT(I3,I3,I2,I2,I1,I4,F9.0,14A4)
       NABS=JABS
       WRITE(3,11) (ISITE(I), I=1,14)
   11  FORMAT(1H1,5HSITE ,14A4,///)
C      READ IN GROUP NAMES
       DO 13 I=1,MANYGP
   13  READ(1,14) (NGP(J,I), J=1,2 )
       IF(MANYGP.EQ.24) GO TO 15
       READ(1,14) (NGP(J,25), J=1,2 )
   14  FORMAT( 2A6)
C      READ IN CORE DATA
   15  DO 12  IBATCH=1,NUM
       NNPLN=NPLN-20
       MNPLN=NNPLN+1
       READ(1,20)(LIST(I,IBATCH),I=1,NNPLN)
   20  FORMAT(20I3)
       READ(1,999)(LIST(I,IBATCH),I=MNPLN,NPLN),LEV(IBATCH),NEV(IBATCH)
  999  FORMAT(20I3,7X,A5,I5,3X)
   12  CONTINUE
C      DO GROUPING AND PERCENTAGE CALCULATIONS
       JUMP = 1
       KOUNT = 0
   25  KOUNT = KOUNT + 1
       IF(KOUNT - KNT) 32,32,26
   32  CONTINUE
       IF(NABS)27,27,33
   27  WRITE(3,28)
   28  FORMAT(///,1X,21HFOR NEXT CALCULATIONS,/)
   30  WRITE(3,31) (NGP(J,KOUNT), J=1,2 )
   31  FORMAT(1X,27HTHE FOLLOWING = 100 PERCENT,5X,2A6 ,///)
   33  CONTINUE
```

*Program PLOTABS (Cont.)*

```
      GO TO (56,103), JUMP
   56 DO 55 INIT =1,NUM
      DO 55 IT=1,24
   55 PERC(IT,INIT) = 0.0
      DO 60 KA=1,MANYGP
      CALL UTLY (NPLN)
      DO 60  K=1,NUM
      DO 60  L=1,ILK
      NTT = MPLN(L)
   60 PERC(KA,K) = PERC(KA,K) +FLOAT( LIST(NTT,K))
      NANYGP=MANYGP
      IF(MANYGP - 23) 42,42,103
   42 MANYGP = MANYGP + 1
      DO 43 KA=MANYGP,24
      DO 43 K=1,2
   43 NGP(K,KA) = NGP(K,25)
      MANYGP = MANYGP - 1
  103 DO 104 LOT=1,NUM
  104 PERC(25,LOT)=PERC(KOUNT,LOT)
      IF(JABS.NE.0) GO TO 39
      DO 102 LOT=1,NUM
      DO 102 IPERC=1,24
      IF(PEPC(25,LOT)) 67,67,68
   67 PERC(IPERC,LOT)=9999.0
      GO TO 102
   68 PERC(IPERC,LOT)=PERC(IPERC,LOT)/PERC(25,LOT)*100.0
  102 CONTINUE
  803 IMANY = 1
      JMANY = 6
C     PRINT OUT PERCENTAGE TABLES
   38 WRITE(3,110) ((NGP(J,I), J=1,2 ), I=IMANY,JMANY)
  110 FORMAT(1H1,5(/),1X,5HLEVEL,9X,6(2A6,7X),/)
      WRITE(3,111)
  111 FORMAT(1X,129(1H=)/)
      DO 115 LOT=1,NUM
  115 WRITE(3,112) LEV(LOT), NEV(LOT), (PERC(N,LOT), N=IMANY,JMANY)
  112 FORMAT(1X,A5,1X,I5,6(2X,F10.2,7X)/)
      WRITE(3,111)
      IF(JMANY - MANYGP) 41,39,39
   41 IMANY = IMANY + 6
      JMANY = JMANY + 6
      GO TO 38
   39 JUMP = 2
      IF(JABS.EQ.0) GO TO 903
C     READ IN CORRECTION FACTORS & CORRECT  DATA
      READ(1,800)(CORR(I),I=1,NUM)
  800 FORMAT(F10.3)
```

*Program PLOTABS (Cont.)*

```
      DO 801 J=1,NUM
      DO 801 I=1,NANYGP
  801 PERC(I,J)=PERC(I,J)*CORR(J)
  805    WRITE(3,802)
  802 FORMAT(///,1X'ABSOLUTE COUNT FIGURES',///)
      JABS=0
      GO TO 803
C     SET UP PERC FOR LINEAR SCALE ABSOLUTE COUNTS
  903 NF=10
      IF(NABS-1)908,904,906
  904 DO 905 I=2,NANYGP
      DO 905 J=1,NUM
  905 PERC(I,J)=PERC(I,J)/FACTOR
      GO TO 908
  906 NF=1
      DO 907 I=2,NANYGP
      DO 907 J=1,NUM
      IF(PERC(I,J)-1.0)907,907,909
  909 PERC(I,J)=10*ALOG10(PERC(I,J))
  907 CONTINUE
C     SET UP PLOTTER INSTRUCTION FILE
  908 DO 900 I=2,NANYGP
      NO=1
      PMAX=0.
      DO 901 J=1,NUM
      IF(PERC(I,J).GT.PMAX)PMAX=PERC(I,J)
      X(NO)=NEV(J)-ISTAR
      Y(NO)=0.
      X(NO+1)=X(NO)
      Y(NO+1)=PERC(I,J)
      X(NO+2)=X(NO)+0.02
      Y(NO+2)=Y(NO+1)
      X(NO+3)=X(NO+2)
      Y(NO+3)=0.
      NO=NO+4
  901 CONTINUE
      X(NO)=0.
      Y(NO)=0.
      X(NO+1)=254.
      Y(NO+1)=25.
      NO=NO-1
      LNTH=PMAX
      IF(PMAX.LE.0.0)GO TO 900
      IF(LNTH.LT.4)LNTH=4
      LNTH=((LNTH/10)+1)
      ALNTH=FLOAT(LNTH*0.4)
      CALL PLOT(0.0,0.0,3)
      CALL PLOT(-0.3,0.0,-3)
      A=0.4
```

*Program PLOTABS (Cont.)*

```
      DO 902 J=1,LNTH
      B=FLOAT(J*NF)
      C=A-0.07
      CALL SYMBOL(0.,A,0.07,13,90.,-1)
      CALL NUMBER(-0.07,C,0.07,B,90.0,-1)
      A=A+0.4
  902 CONTINUE
      CALL PLOT(0.0,0.0,3)
      CALL PLOT(0.0,ALNTH,2)
      CALL PLOT(0.0,0.0,3)
      CALL SYMBOL(-0.03,0.03,0.14,NGP(1,I),120.0,12)
      CALL PLOT(0.3,0.0,-3)
      CALL PLOT(0.0,ALNTH,2)
      CALL PLOT(0.0,0.0,3)
      CALL LINE(X,Y,NO,1,0,0)
      CALL PLOT(0.0,0.0,2)
      CALL PLOT(0.0,ALNTH+0.4,-2)
  900 CONTINUE
      GO TO 25
   26 CALL PLOT(0.0,0.0,999)
C     GROUPING SUBROUTINE
      SUBROUTINE UTLY (NPLN)
      DIMENSION LOT1(10), IA(10), LOT2(10)
      COMMON MPLN(200),ILK
      KNUT = 1
   20 READ(1,1) (LOT1(I), IA(I), LOT2(I) ,I=1,10)
    1 FORMAT(10(I3,I1,I3,1X))
      II = 1
   30 IF(LOT1(II)) 9,9,4
    4 IF(IA(II).EQ.2) GO TO 5
      MPLN(KNUT) = LOT1(II)
      KNUT = KNUT + 1
      MPLN(KNUT) = LOT2(II)
      KNUT = KNUT + 1
      GO TO 8
    5 MPLN(KNUT) = LOT1(II)
    6 IF(LOT2(II) - LOT1(II))7, 7,50
   50 LOT1(II) = LOT1(II) + 1
      KNUT = KNUT + 1
      MPLN(KNUT) = LOT1(II)
      GO TO 6
    7 KNUT = KNUT + 1
    8 II = II + 1
      IF(II - 10) 30,30,20
    9 ILK = KNUT - 1
      WRITE(3,100)ILK,(MPLN(JJ),JJ=1,ILK)
  100 FORMAT(/ I4,' TAXA IN THIS GROUP'/10(20I4/))
      RETURN
      END
```

# BIBLIOGRAPHY

AABY, B. and H. TAUBER. 1975. Rates of peat formation in relation to degree of humification and local environment, as shown by studies of a raised bog in Denmark. *Boreas 4*:1-17.

ALLIED Geographical Section: Allied Forces south-west Pacific area 1941-1945. 1942. Locality study of Lae (revised) and the Lower Markham Valley. *Terrain Study 32*.

ALLIED Geographical Section: Allied Forces south-west Pacific area 1941-1945. 1943*a*. Area study of the Markham catchment (2 vols). *Terrain Study 49*.

ALLIED Geographical Section: Allied Forces south-west Pacific area 1941-1945. 1943*b*. The Markham River Valley. *Terrain Handbook 2*.

ALLIED Geographical Section: Allied Forces south-west Pacific area 1941-1945. 1943*c*. Lae and the lower Markham Valley. *Terrain Handbook 4*.

ANDERSEN, S.T. 1973. The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region. Pages 109-115 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology*. The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

ANDERSON, J.A.R. 1963. The flora of the peat swamp forests of Sarawak and Brunei, including a catalogue of all species of flowering plants, ferns, and fern allies. *Gardens Bulletin, Singapore 20*:131-228.

ANDERSON, J.A.R. and J. MULLER. 1975. Palynological study of a Holocene peat and a Miocene coal deposit from north west Borneo. *Review of Palaeobotany and Palynology 19*:291-351.

BACKER, C.A. and R.C. BAKHUIZEN van der BRINK. 1963-1968. *Flora of Java*. 3 Vols. Noordhoff, Groningen.

van BALGOOY, M.M.J. 1976. Phytogeography. Pages 1-22 *in* K. Paijmans, editor. *New Guinea Vegetation*. Australian National University Press, Canberra.

BALL, E.E. and R.W. JOHNSON. 1976. Volcanic history of Long Island, Papua New Guinea. Pages 133-147 *in* R.W. Johnson, editor. *Volcanism in Australasia*. Elsevier, Amsterdam.

BARTLETT, A.S. and E.S. BARGHOORN. 1973. Phytogeographic history of the Isthmus of Panama during the past 12 000 years (A history of vegetation, climate, and sea level change.) Pages 203-299 *in* A. Graham, editor. *Vegetation and Vegetational History of Northern Latin America*. Elsevier, New York.

BATTARBEE, R.W. 1973. A new method for the estimation of absolute microfossil numbers, with reference especially to diatoms. *Limnology and Oceanography 18*:647-653.

BATTARBEE, R.W. and M.E. McCALLAN. 1974. An evaporation tray technique for estimating absolute pollen numbers. *Pollen et Spores 16*:143-150.

BENNINGHOFF, W.S. 1962. Calculation of pollen and spores density by addition of exotic pollen in known quantities (Abstract). *Pollen et Spores 4*:332-333.

BERGLUND, B.E. 1973. Pollen dispersal and deposition in an area of southeastern Sweden - some preliminary results. Pages 117-129 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology*. The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

BIRKS, H.J.B. 1973. Modern pollen grain studies in some arctic and alpine environments. Pages 143-168 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology*. The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

BLONG, R.J. (in preparation). The time of darkness; legend and reality. Investigations of a volcanic eruption in Papua New Guinea *circa* 1700 AD.

BLOOM, A.L. 1970. Paludal stratigraphy of Truk, Ponape and Kusaie, eastern Caroline islands. *Bulletin of the Geological Society of America 81*:1895-1904.

BONNY, A.P. 1972. A method for determining absolute pollen frequencies in lake sediments. *New Phytologist 71*:391-403.

BONNY, A.P. 1976. Recruitment of pollen to the seston and sediment of some Lake District lakes. *Journal of Ecology 64*:859-887.

BONNY, A.P. 1978. The effect of pollen recruitment processes on pollen distribution over the sediment surface of a small lake in Cumbria. *Journal of Ecology 66*:385-416.

von der BORCH, C.C. 1972. Marine geology of the Huon Gulf region, Papua New Guinea. *Bulletin No. 127*. Australia. Bureau of Mineral Resources, Geology and Geophysics. Canberra.

BOWLER, J.M. 1977. Glacial age environments and aeolian episodes: some comparisons from Australian, African and Northern Hemisphere records. (Abstract). Tenth INQUA Congress, Birmingham. *Abstracts*, 50.

BOWLER, J.M., G.S. HOPE, J.N. JENNINGS, G. SINGH and D. WALKER. 1976. Late Quaternary climates of Australia and New Guinea. *Quaternary Research 6*:359-394.

BOWLER, J.M., A.G. THORNE and H.A. POLACH. 1972. Pleistocene man in Australia: Age and significance of the Mungo skeleton. *Nature 240*:48-50.

BRASS, L.J. 1964. Results of the Archbold Expeditions No. 86. Summary of the 6th Archbold Expedition to New Guinea, 1959. *Bulletin of the American Museum of Natural History 127*:145-216.

BROOKES, D. and K.W. THOMAS. 1967. The distribution of pollen grains on microscope slides. Part I. The non-randomness of the distribution. *Pollen et Spores 9*:621-629.

BROOKFIELD, H.C. 1964. The ecology of highland settlement: some suggestions. *American Anthropology Special Publication 66*:20-38.

BROOKFIELD, H.C. and D. HART. 1966. *Rainfall in the Tropical South West Pacific*. Publication G/3, Dept of Geography. A.N.U., Canberra.

BUTZER, K.W., G.L. ISAAC, J.C. RICHARDSON and C. WASHBOURN-KAMAU. 1972. Radiocarbon dating of East African lake levels. *Science 175*:1069-1076.

CARATINI, C., F. BLASCO and G. THANIKAIMONI. 1973. Relationship between the pollen spectra and the vegetation of a South Indian mangrove. *Pollen et Spores 15*:281-292.

CHAPPELL, J. 1973. *Geology of Coral Terraces on the Huon Peninsula, New Guinea*. Ph.D. thesis (unpubl.). Australian National University, Canberra.

CHAPPELL, J. 1976. Aspects of late Quaternary palaeogeography of the Australian-East Indonesian region. Pages 11-22 *in* R.L. Kirk and A.G. Thorne, editors. *The Origin of the Australians*. Australian Institute of Aboriginal Studies, Canberra.

CHAPPELL, J. and B.G. THOM. 1977. Sea levels and coasts. Pages 275-291 *in* J. Allen, J. Golson and R. Jones, editors. *Sunda and Sahul. Prehistoric Studies in Southeast Asia, Melanesia and Australia*. Academic Press, London.

CLARK, R.M. 1975. A calibration curve for Radiocarbon dates. *Antiquity 49*:251-266.

CLIMAP Project Members. 1976. The surface of the Ice-Age earth. *Science 191*:1131-1137.

COCHRAN, W.G. 1954. Some methods for strengthening the common $\chi^2$ tests. *Biometrics 10*:417-451.

COLINVAUX, P.A. and E.K. SCHOFIELD. 1976*a*. Historical ecology in the Galapagos Islands. 1. A Holocene pollen record from El Junco Lake, Isla San Cristobal. *Journal of Ecology 64*:989-1012.

COLINVAUX, P.S. and E.K. SCHOFIELD. 1976*b*. Historical ecology in the Galapagos Islands. II. A Holocene spore record from El Junco Lake, Isla San Cristobal. *Journal of Ecology* *64*:1013-1028.

COODE, M.J.E. 1969. *Manual of the Forest Trees of Papua and New Guinea. Part 1 (revised) - Combretaceae.* Territory of Papua New Guinea. Division of Botany. Dept of Forests, Lae.

CORLETT, R.T. (unpubl.). Carbonised Particle Analysis on Mt. Wilhelm. Unpublished Manuscript, 4 pages.

COSTIN, A.B., R.D. HOOGLAND and C. LENDON. 1977. Vegetation changes in the Lake Mamsin area, Saruwaged Plateau, New Guinea. *American Museum of Natural History Novitates* *2628*:1-9.

CRAIG, A.J. 1972. Pollen influx to laminated sediments: a pollen diagram from north eastern Minnesota. *Ecology 53*:46-57.

CUSHING, E.J. 1964. Redeposited pollen in Late-Wisconsin pollen spectra from east-central Minnesota. *American Journal of Science 262*:1075-1088.

DALE, M.B. and D. WALKER. 1970. Information analysis of pollen diagrams I. *Pollen et Spores 12*:21-37.

DAMON, P.E. 1970. Climatic versus magnetic perturbation of the atmospheric $C^{14}$ reservoir. Pages 571-593 *in* I.U. Olsson, editor. *Radiocarbon Variations and Absolute Chronology*. 12th Nobel Symposium, Uppsala, 1969. Almqvist and Wiksell, Stockholm.

DAMON, P.E., A. LONG and E.I. WALLICK. 1973. Dendrochronologic calibration of the carbon-14 timescale. Pages 44-59 *in* T.A. Rafter and T. Grant-Taylor, editors. *Proceedings of the 8th International Conference on Radiocarbon Dating*. Lower Hutt, 1972. Royal Society of New Zealand, Wellington.

DAVIS, M.B. 1965. A method for determination of absolute pollen frequencies. Pages 674-686 *in* B. Kummel and D. Raup, editors. *Handbook of Paleontological Techniques*. Freeman, San Francisco.

DAVIS, M.B. 1966. Determination of absolute pollen frequency. *Ecology 47*:310-311.

DAVIS, M.B. 1969. Climatic changes in southern Connecticut recorded by pollen deposition at Rogers Lake. *Ecology* *50*:409-422.

DAVIS, M.B. and L.B. BRUBAKER. 1973. Differential sedimentation of pollen grains in lakes. *Limnology and Oceanography* *18*:635-646.

DAVIS, M.B., L.B. BRUBAKER and T. WEBB. 1973. Calibration of absolute pollen influx. Pages 9-25 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology.* The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

DAVIS, M.B. and E.S. DEEVEY. 1964. Pollen accumulation rates: Estimates from late-glacial sediment of Rogers Lake. *Science 145*:1293-1295.

DAVIS, M.B. and J.C. GOODLETT. 1960. Comparison of the present vegetation with pollen-spectra in surface samples from Brownington Pond, Vermont. *Ecology 41*:316-357.

DAVIS, R.B. and T. WEBB. 1975. The contemporary distribution of pollen in Eastern North America: a comparison with the vegetation. *Quaternary Research 5*:395-434.

DEEVEY, E.S. 1978. Holocene forests and Maya disturbance near Quexil Lake, Peten, Guatemala. *Polskie Archiwum Hydrobiologii 25*:117-129.

DEEVEY, E.S. and R.F. FLINT. 1957. Postglacial hypsithermal interval. *Science 125*:182-184.

DEEVEY, E.S., M.S. GROSS, G.E. HUTCHINSON and H.L. KRAYBILL. 1954. The natural $C^{14}$ contents of materials from hard-water lakes. *Proceedings of the National Academy of Sciences 40*:285-288.

DEEVEY, E.S. and M. STUIVER. 1964. Distribution of natural isotopes of carbon in Linsley Pond and other New England lakes. *Limnology and Oceanography 9*:1-11.

DEVI, S. 1974. On the occurrence of bilateral spores in *Pteris longifolia* L. *Grana 14*:1-3.

DIGERFELDT, G. 1974. The post-glacial development of the Ranviken bay in Lake Immeln. I. The history of the regional vegetation. *Geologiska Foreningens i Stockholm Forhandlingar 96*:3-32.

DODSON, J.R. 1972. Computer programs for the pollen analyst. *Pollen et Spores 14*:455-465.

DONNER, R., H. JUNGNER and Y. VASARI. 1971. The hard-water effect on radiocarbon measurements of samples from Säynäjälampi, northeast Finland. *Commentationes Physico-Mathematicae 41*:307-310.

DOW, D.B., J.A.J. SMIT and R.W. PAGE. 1974. Wau, Papua New Guinea. Sheet SB/55-14 International Index. *1:250 000 Geological Series Explanatory Notes.* Australia. Bureau of Mineral Resources, Geology and Geophysics, Canberra.

DURKEE, L.V.H. 1964. A quantitative method for the study of pollen and spores in bog sediments. *Proceedings of the Iowa Academy of Sciences 71*:116-118.

EDEN, M.J. 1974. The origin and status of savannah and grassland in southern Papua. *Transactions of the Institute of British Geographers 63*:97-110.

ENGSTROM, D.R. and L.J. MAHER. 1972. A new technique for volumetric sampling of sediment cores for concentrations of pollen and other microfossils. *Review of Palaeobotany and Palynology 14*:353-357.

ERDTMAN, G. 1952. *Pollen Morphology and Plant Taxonomy - Angiosperms.* Almqvist and Wiksell, Stockholm.

FAEGRI, K. 1966. Some problems of representativity in pollen analysis. *Palaeobotanist 15*:135-140.

FAEGRI, K. and J. IVERSEN. 1964. *Textbook of Pollen Analysis.* Munksgaard, Copenhagen.

FERGUSON, C.W. 1970. Dendrochronology of bristlecone pine, *Pinus aristata.* Establishment of a 7484-year chronology in the White Mountains of eastern-central California, U.S.A. Pages 237-259 *in* I.U. Olsson, editor. *Radiocarbon Variations and Absolute Chronology.* 12th Nobel Symposium, Uppsala, 1969. Almqvist and Wiksell, Stockholm.

FLENLEY, J.R. 1972. Evidence of Quaternary vegetational change in New Guinea. Pages 99-108 *in* P. and M. Ashton, editors. *The Quaternary Era in Malesia.* Miscellaneous Series 13. Dept of Geography, University of Hull.

FLENLEY, J.R. 1973. The use of modern pollen rain samples in the study of the vegetational history of tropical regions. Pages 131-141 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology.* The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

de GEER, G. 1912. A Geochronology of the last 12,000 years. International Geological Congress, Stockholm. *Comptes Rendus 1*:241-258.

GERMERAAD, J.M., C.A. HOPPING and J. MULLER. 1968. Palynology of Tertiary sediments from tropical areas. *Review of Palaeobotany and Palynology 6*:189-348.

GILLISON, A.N. 1970. *Dynamics of Biotically Induced Grassland/ Forest Transitions in Papua New Guinea.* M.Sc. thesis (unpubl.). Australian National University, Canberra.

GODWIN, H. 1962. Half life of Radiocarbon. *Nature 195*:943-945.

GOLSON, J. 1977*a*. No room at the top: agricultural intensification in the New Guinea highlands. Pages 601-638 *in* J. Allen, J. Golson and R. Jones, editors. *Sunda and Sahul. Prehistoric Studies in Southeast Asia, Melanesia and Australia.* Academic Press, London.

GOLSON, J. 1977*b*. The making of the New Guinea highlands. Pages 45-56 *in* J.H. Winslow, editor. *The Melanesian Environment.* Australian National University Press, Canberra.

GORDON, A.D. and H.J.B. BIRKS. 1972. Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. *New Phytologist 71*:961-979.

GREGORY, S. 1968. *Statistical Methods and the Geographer.* 2nd edition. Longman, London.

GUPPY, J., P. MILNE, M. GLIKSON and H. MOORE. 1973. Further developments in computer assistance to pollen identification. *Geological Society of Australia Special Publication 4*:201-206.

HAANTGENS, A.H., J.A. MABBUTT and R. PULLEN. 1965. Environmental influences in the anthropogenic grasslands in the Sepik Plains, New Guinea. *Pacific Viewpoint 6*:215-219.

HAFSTEN, U. 1960. Pleistocene development of vegetation and climate in Tristan da Cunha and Gough Island. *Arbok for Universitetet i Bergen. Mat. - Naturv. Serie No. 20*:1-48.

HAMILTON, A.C. 1972. The interpretation of pollen diagrams from highland Uganda. *Palaeoecology of Africa, the Surrounding Islands and Antarctica 7*:45-149.

van der HAMMEN, T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography 1*:3-26.

van der HAMMEN, T., J.H. WERNER and H. van DOMMELEN. 1973. Palynological record of the upheaval of the Northern Andes: a study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera, and the early evolution of its High-Andean biota. *Review of Palaeobotany and Palynology 16*:1-122.

HARRIS, W.F. 1955. *A Manual of the Spores of New Zealand Pteridophyta.* Bulletin 116. New Zealand. Dept of Scientific and Industrial Research, Wellington.

HEDBERG, O. 1954. A pollen-analytical reconnaissance in tropical East Africa. *Oikos 5*:137-166.

HOLLOWAY, R.S., M.F.W. ZIJSVELT, M.J. KNIGHT, J.M. BRIGATTI, D. LEGGER, B.W. STRONG, F.P. ALAND, K.J. BLACKBURN and H.A. HOLZKNECHT. 1973. Land resources and agricultural potential of the Markham Valley. (10 parts). *Research Bulletin No. 14.* Papua New Guinea. Dept of Agriculture, Stock and Fisheries, Port Moresby.

HOLTTUM, R.E. 1932. On *Stenochlaena, Lomariopsis* and *Teratophyllum* in the Malayan region. *Gardens Bulletin, Straits Settlements* 5:245-313.

HOLZKNECHT, H.A. 1974. Report on anthropological research and associated findings in the Markham Valley of Papua New Guinea. *Research Bulletin No. 15*. Papua New Guinea. Dept of Agriculture, Stock and Fisheries, Port Moresby.

HOLZKNECHT, K.G. 1973. *Agi tafan gan nan gan fisa gin. (Our Ancestors' Stories)*. Summer Institute of Linguistics. Lae, Papua New Guinea.

HOOLEY, B.A. and K.A. McELHANON. 1970. Languages of the Morobe District - New Guinea. *Pacific Linguistics, Series C 13*:1065-1094.

HOPE, G.S. 1968. *Pollen Studies at Wilsons Promontory, Victoria*. M.Sc. thesis (unpubl.). University of Melbourne.

HOPE, G.S. 1973. *The Vegetation History of Mt. Wilhelm*. Ph.D. thesis (unpubl.). Australian National University, Canberra.

HOPE, G.S. 1976*a*. The vegetational history of Mt. Wilhelm, Papua New Guinea. *Journal of Ecology 64*:627-663.

HOPE, G.S. 1976*b*. Vegetation. Pages 113-172 *in* G.S. Hope, J.A. Peterson, U. Radok and I. Allison, editors. *The Equatorial Glaciers of New Guinea*. Balkema, Rotterdam.

HOPE, G.S. and J.A. PETERSON. 1976. Palaeoenvironments. Pages 173-205 *in* G.S. Hope, J.A. Peterson, I. Allison and U. Radok, editors. *The Equatorial Glaciers of New Guinea*. Balkema, Rotterdam.

JACOBSON, G. 1971. Preliminary appraisal of groundwater resources, Markham Valley, Papua New Guinea. *Note on Investigation No. 71-005*. Geological Survey of Papua New Guinea. Port Moresby.

JENNINGS, J.N. 1975. Desert dunes and estuarine fill in the Fitzroy estuary (north-western Australia). *Catena 2*:215-262.

JOHNS, R.J. 1975. *Common Forest Trees of Papua New Guinea*. Papua New Guinea Forestry College, Bulolo.

JOHNS, R.J. (unpubl.*a*). *Anisoptera* forests in Papua New Guinea - An example of the importance of historical factors in the vegetation patterns of the lowland tropics. Mimeo.

JOHNS, R.J. (unpubl.*b*). A preliminary check list of the species of the Herzog ranges. Mimeo.

JOHNS, R.J. (unpubl.*c*). A provisional check list of the species found in the Herzog range.

JØRGENSEN, S. 1967. A method of absolute pollen counting. *New Phytologist 66*:489-493.

KENDALL, R.L. 1969. An ecological history of the Lake Victoria basin. *Ecological Monographs 39*:121-176.

KERSHAW, A.P. 1970. A pollen diagram for Lake Euramoo, north east Queensland, Australia. *New Phytologist 69*:785-805.

KERSHAW, A.P. 1973*a*. The numerical analysis of modern pollen spectra from northeast Queensland rain-forest. *Geological Society of Australia, Special Publication 4*:191-199.

KERSHAW, A.P. 1973*b*. *Late Quaternary Vegetation of the Atherton Tableland, North East Queensland, Australia*. Ph.D. thesis (unpubl.). Australian National University, Canberra.

KERSHAW, A.P. 1974. A long continuous pollen sequence from north-eastern Australia. *Nature 251*:222-223.

KERSHAW, A.P. 1975. Late Quaternary vegetation and climate in northeastern Australia. *Royal Society of New Zealand Bulletin 13*. Wellington.

KERSHAW, A.P. 1976. A Late Pleistocene and Holocene pollen diagram from Lynch's Crater, northeastern Queensland, Australia. *New Phytologist 77*:469-498.

KERSHAW, A.P. 1978. The analysis of aquatic vegetation on the Atherton Tableland, north-east Queensland, Australia. *Australian Journal of Ecology 3*:23-42.

KERSHAW, A.P. and B.P.M. HYLAND. 1975. Pollen transfer and periodicity in a rain forest situation. *Review of Palaeobotany and Palynology 19*:129-138.

KIRKLAND, D.W. 1967. Method of calculating absolute spore and pollen frequency. *Oklahoma Geological Notes 27*:98-100.

KRZYWINSKI, K. 1977. The Tauber pollen trap, a discussion of its usefulness in pollen deposition studies. *Grana 16*:147-148.

LANE-POOLE, C.E. 1925. *The Forest Resources of the Territories of New Guinea and Papua*. Australian Parliamentary Paper No. 73. Melbourne.

LEYDEN, B.W. and D.R. WHITEHEAD. 1979. Paleoecological investigations of Late Pleistocene and Holocene sediments of Lago de Valencia, Venezuela. (Abstract). *Bulletin of the Ecological Society of America 60*:101-102.

LIBBY, W.F. 1949. *Radiocarbon Dating*. 2nd revised edition, 1962. University of Chicago Press.

LIVINGSTONE, D.A. 1975. Late Quaternary climatic change in Africa. *Annual Review of Ecology and Systematics 6*:249-280.

LIVINGSTONE, D.A. and A.M. ESTES. 1967. A carbon-dated pollen diagram from the Cape Breton Plateau, Nova Scotia. *Canadian Journal of Botany 45*:339-357.

LÖFFLER, E. 1977. *Geomorphology of Papua New Guinea*. Australian National University Press, Canberra.

LUGARDON, B. 1963. Les spores des pteridacees de France. *Pollen et Spores 5*:325-336.

MACKERETH, F.J.H. 1969. A short core sampler for sub-aqueous deposits. *Limnology and Oceanography 14*:145.

MAHER, L.J. 1972. Absolute pollen diagram of Redrock Lake, Boulder County, Colorado. *Quaternary Research 2*:531-553.

MAHER, L.J. 1976. The confidence limit is a necessary statistic for relative and absolute pollen data. Paper presented to the Fourth International Palynological Conference, Lucknow, India, 1976-1977.

MATTHEWS, J. 1969. The assessment of a method for the determination of absolute pollen frequencies. *New Phytologist 68*:161-166.

McALPINE, J.R. and K. SHORT. 1974. Water balance estimates for Papua New Guinea. *Division of Land Use Research Technical Memorandum 74/9*. Australia. Commonwealth Scientific and Industrial Research Organisation, Canberra.

MOLYNEUX, L., R. THOMPSON, F. OLDFIELD and M.E. McCALLAN. 1972. Rapid measurement of the remanent magnetization of long cores of sediment. *Nature (Physical Science) 237*:42-43.

MORLEY, R.J. 1976. *Vegetation Change in West Malesia During the Late Quaternary Period: A Palynological Study of Selected Lowland and Lower Montane Sites*. 2 Vols. Ph.D. thesis (unpubl.). University of Hull.

MOSIMANN, J.E. 1965. Statistical methods for the pollen analyst: Multinomial and negative multinomial techniques. Pages 636-673 *in* B. Kummel and D. Raup, editors. *Handbook of Paleontological Techniques*. Freeman, San Francisco.

MULLER, J. 1969. A palynological study of the genus *Sonneratia* (Sonneratiaceae). *Pollen et Spores 11*:223-298.

MULLER, J. and C. CARATINI. 1977. Pollen of *Rhizophora* (Rhizophoraceae) as a guide fossil. *Pollen et Spores 19*:361-390.

MURILLO, M.T. and M.J.M. BLESS. 1974. Spores of recent Colombian Pteridophyta. I. Trilete spores. *Review of Palaeobotany and Palynology 18*:223-270.

NIX, H.A. and J.D. KALMA. 1972. Climate as a dominant control in the biogeography of northern Australia and New Guinea. Pages 61-91 *in* D. Walker, editor. *Bridge and Barrier: the Natural and Cultural History of Torres Strait*. Publication BG/3, Dept Biogeography and Geomorphology. A.N.U., Canberra.

OGDEN, J.G. 1967. Radiocarbon determinations of sedimentation rates from hard and soft-water lakes in northeastern North America. Pages 175-183 *in* E.J. Cushing and H.E. Wright, editors. *Quaternary Paleoecology.* Yale University Press, New Haven.

OLDFIELD, F. 1977. Lake sediments and human activities in prehistoric Papua New Guinea. Pages 57-60 *in* J.H. Winslow, editor. *The Melanesian Environment.* Australian National University Press, Canberra.

OLDFIELD, F., J.A. DEARING, R. THOMPSON and S.E. GARRETT-JONES. 1978. Some magnetic properties of lake sediments and their possible links with erosion rates. *Polskie Archiwum Hydrobiologii 25*:321-331.

OLSSON, I.U. 1974. Some problems in connection with the evaluation of radiocarbon dates. *Geologiska Foreningens i Stockholm Forhandlingar 96*:311-320.

ORLOCI, L. 1975. *Multivariate Analysis in Vegetation Research.* Junk, Hague.

PAGE, R.W. 1971. *The Geochronology of Igneous Rocks in the New Guinea Region.* Ph.D. thesis (unpubl.). Australian National University, Canberra.

PAIJMANS, K. 1975. Explanatory notes to the vegetation map of Papua New Guinea. *Land Research Series No. 35.* Australia. Commonwealth Scientific and Industrial Research Organisation, Melbourne.

PAIJMANS, K. 1976. Vegetation. Pages 23-104 *in* K. Paijmans, editor. *New Guinea Vegetation.* Australian National University Press, Canberra.

PECK, R.M. 1973. Pollen budget studies in a small Yorkshire catchment. Pages 43-60 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology.* The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

PENNINGTON, W. 1973. Absolute pollen frequencies in the sediments of lakes of different morphometry. Pages 79-104 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology.* The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

PENNINGTON, W. and A.P. BONNY. 1970. Absolute pollen diagram from British Late Glacial. *Nature 226*:871-873.

PETTIFER, G.R. 1974. Markham Valley gravity survey, 1972. *Record 1975/65.* Australia. Bureau of Mineral Resources, Geology and Geophysics. Canberra.

POLACH, H.A. 1976. Radiocarbon dating as a research tool in archaeology - hopes and limitations. Pages 255-298 *in* N. Barnard, editor. *The Proceedings of a Symposium on Scientific Methods of Research in the Study of Ancient Chinese Bronzes and Southeast Asian Metal and other Archaeological artifacts.* National Gallery of Victoria. Melbourne, Australia.

POLACH, H.A. and J. GOLSON. 1966. *Collection of Specimens for Radiocarbon Dating and Interpretation of Results.* Manual 2. Australian Institute of Aboriginal Studies, Canberra.

von POST, L. 1918. Skogstradpollen i sydsvenska torfmosselagerfoljder. *Skandinaviske Naturforskermøte 1916. Forhandlingar 16*:432-465.

von POST, L. 1967. Forest tree pollen in south Swedish peat bog deposits. (Translation of von Post, 1918 by M.B. Davis and K. Faegri). *Pollen et Spores 9*:375-401.

POWELL, J.M. 1976. Ethnobotany. Pages 106-183 *in* K. Paijmans, editor. *New Guinea Vegetation.* Australian National University Press, Canberra.

POWELL, J.M. and G.S. HOPE. 1976. Vegetation history. Pages 101-104 *in* K. Paijmans, editor. *New Guinea Vegetation.* Australian National University Press, Canberra.

POWELL, J.M., A. KULUNGA, R. MOGE, C. PONO, F. ZIMIKE and J. GOLSON. 1975. *Agricultural traditions of the Mount Hagen area.* Occasional Paper No. 12. University of Papua New Guinea, Geography Department. Port Moresby.

PUNT, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. *Wentia 7*:1-116.

PUNT, W. and J. RENTROP. 1973. Pollen morphology of the *Phyllanthus* species occurring in the continental United States. *Review of Palaeobotany and Palynology 16*:243-262.

RAINE, J.I. 1974. *Pollen Sedimentation in Relation to the Quaternary Vegetation History of the Snowy Mountains of New South Wales.* Ph.D. thesis (unpubl.). Australian National University, Canberra.

RALPH, E.K., H.N. MICHAEL and M.C. HAN. 1973. Radiocarbon dates and reality. *Museum Applied Science Centre for Archaeology Newsletter 9*:1-20. University of Pennsylvania, Philadelphia.

RAVEN, P.H. and D.I. AXELROD. 1972. Plate tectonics and Australian paleobiogeography. *Science 176*:1379-1386.

REINER, E.J. and R.G. ROBBINS. 1964. The Middle Sepik Plains, New Guinea. *Geographical Review 54*:20-44.

RENFREW, C. and R.M. CLARK. 1974. Problems of the radiocarbon calendar and its calibration. *Archaeometry 16*:5-18.

RICHARDS, P.W. 1952. *The Tropical Rain Forest.* Cambridge.

RICHARDS, P.W. 1973. Africa, the 'odd man out'. Pages 21-26 *in* B.J. Meggers, E.S. Ayensu and W.D. Duckworth, editors. *Tropical Forest Ecosystems in Africa and South America: A Comparative Review.* Smithsonian Institution Press, Washington.

RIDSDALE, C.E. 1970. The arborescent Naucleae of New Guinea and Solomon Islands (Rubiaceae). *Gardens Bulletin, Singapore 25*:247-281.

ROBBINS, R.G. 1963*a*. The anthropogenic grasslands of Papua and New Guinea. Pages 313-330 *in Impact of Man on the Vegetation of the Humid Tropics.* UNESCO Symposium, Goroka, 1961. Government Printer, Canberra.

ROBBINS, R.G. 1963*b*. Correlation of plant patterns and population migration into the Australian New Guinea Highlands. Pages 45-59 *in* J. Barrau, editor. *Plants and the Migration of Pacific Peoples.* Symposium of the 10th Pacific Science Congress, 1961. B.P. Bishop Museum Press, Honolulu.

ROBINSON, G.P. 1974. Huon-Sag Sag, Papua New Guinea. Sheet SB/55-11 International Index. *1:250 000 Geological Series - Explanatory Notes.* Australia. Bureau of Mineral Resources, Geology and Geophysics, Canberra.

ROBINSON, G.P., A.L. JAQUES and C.M. BROWN. 1974. *Explanatory Notes on the Madang Geological Map.* Report 74/13. Geological Survey of Papua New Guinea, Port Moresby.

ROGNON, P. and M.A.J. WILLIAMS. 1977. Late Quaternary climatic changes in Australia and North Africa: A preliminary interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology 21*:285-327.

van ROYEN, P. 1964. *Manual of the Forest Trees of Papua and New Guinea. Parts 2-9.* Territory of Papua and New Guinea. Dept of Forests, Port Moresby.

SACK, P.G. 1976. *The Bloodthirsty Laewomba? Myth and History in Papua New Guinea.* Research School of Social Sciences, A.N.U., Canberra.

SEAVOY, R.E. 1975. The origin of tropical grasslands in Kalimantan, Indonesia. *Journal of Tropical Geography 40*:48-52.

SELLING, O.H. 1947. Studies in Hawaiian pollen statistics. Part I. The pollens of the Hawaiian phanerogams. *Bernice P. Bishop Museum Special Publication 38.* Honolulu.

SHOTTON, F.W. 1972. An example of hard-water error in radiocarbon dating of vegetable matter. *Nature 240*:460-461.

SIMS, R.E. 1973. The anthropogenic factor in East Anglian vegetational history: an approach using A.P.F. techniques. Pages 223-236 *in* H.J.B. Birks and R.G. West, editors. *Quaternary Plant Ecology*. The 14th symposium of the British Ecological Society, 1972. Blackwell Scientific Publications, Oxford.

SPECHT, J. and H. HOLZKNECHT. 1971. Some archaeological sites in the Upper Markham Valley, Morobe District. *Papua New Guinea Museum Records 2*:52-73.

STOCKMARR, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores 13*:615-621.

STUIVER, M. 1970. Long-term $C^{14}$ variations. Pages 197-213 *in* I.U. Olsson, editor. *Radiocarbon Variations and Absolute Chronology*. 12th Nobel Symposium, Uppsala, 1969. Almqvist and Wiksell, Stockholm.

SUESS, H.E. 1967. Bristlecone-pine calibration of the radiocarbon time scale from 4100 BC to 1500 BC. *Proceedings of the Symposium on Radioactive Dating Methods and Low-level Counting, Monaco*. 145-151. International Atomic Energy Authority, Vienna.

SUESS, H.E. 1970. Bristlecone-pine calibration of the radiocarbon time scale from 5200 BC to the present. Pages 303-311 *in* I.U. Olsson, editor. *Radiocarbon Variations and Absolute Chronology*. 12th Nobel Symposium, Uppsala, 1969. Almqvist and Wiksell, Stockholm.

SWAIN, A.M. 1973. A history of fire and vegetation in north east Minnesota, as recorded in lake sediments. *Quaternary Research 3*:383-396.

TAUBER, H. 1965. Differential pollen dispersion and the interpretation of pollen diagrams. *Danmarks Geologiske Undersøgelse. II. Raekke. No. 89.*

TAUBER, H. 1967. Investigations of the mode of pollen transfer in forested areas. *Review of Palaeobotany and Palynology 3*:277-286.

TAUBER, H. 1970. The Scandinavian varve chronology and $C^{14}$ dating. Pages 173-196 *in* I.U. Olsson, editor. *Radiocarbon Variations and Absolute Chronology*. 12th Nobel Symposium, Uppsala, 1969. Almqvist and Wiksell, Stockholm.

TAUBER, H. 1974. A static, non-overload pollen collector. *New Phytologist 73*:359-369.

TAYLOR, B.W. 1959. The classification of lowland swamp communities in north-eastern Papua. *Ecology 40*:703-711.

THANIKAIMONI, G. 1970. Les Palmiers: Palynologie et systematique. Institut Francais de Pondichery. *Travaux de la section scientifique et technique tome XI.*

THOM, B.G. and J. CHAPPELL, 1975. Holocene sea levels relative to Australia. *Search 6*:90-93.

THOMPSON, R. 1973. Palaeolimnology and palaeomagnetism. *Nature 242*:182-184.

THOMPSON, R., R.W. BATTARBEE, P.E. O'SULLIVAN and F. OLDFIELD. 1975. Magnetic susceptibility of lake sediments. *Limnology and Oceanography 20*:687-698.

TINDALE, M.D. 1956. The Cyatheaceae of Australia. *Contributions of the New South Wales National Herbarium 2*:327-361.

TINGEY, R.J. and D.J. GRAINGER. 1976. Markham, Papua New Guinea. Sheet SB/55-10 International Index. *1:250 000 Geological Series - Explanatory Notes.* Australia. Bureau of Mineral Resources, Geology and Geophysics, Canberra.

TROELS-SMITH, J. 1955. Karacterisering af løse jordater (Characterisation of unconsolidated deposits). *Danmarks Geologiske Undersøgelse IV Raekke 3. No. 10.*

VEEH, H.H. and J. CHAPPELL. 1970. Astronomical theory of climatic change - support from New Guinea. *Science 167*:862-865.

VOGEL, J.C. 1970. $C^{14}$ trends before 6000 BP. Pages 313-325 *in* I.U. Olsson, editor. *Radiocarbon Variations and Absolute Chronology.* 12th Nobel Symposium, Uppsala, 1969. Almqvist and Wiksell, Stockholm.

de VRIES, H. 1958. Variation in concentration of radiocarbon with time and location on earth. *Koninklijke Nederlandsche Akademie van Wetenschappen. Proceedings Series B 61:*94-102.

WADDINGTON, J.C.B. 1969. A stratigraphic record of the pollen influx to a lake in the Big Woods of Minnesota. *Geological Society of America Special Paper 123*:263-282.

WADE, L.K. and D.N. McVEAN. 1969. *Mount Wilhelm Studies I: The Alpine and Subalpine Vegetation.* Publication BG/1, Dept Biogeography and Geomorphology. A.N.U., Canberra.

WALKER, D. 1964. A modified Vallentyne mud sampler. *Ecology 45*:642-644.

WALKER, D. 1970. The changing vegetation of the montane tropics. *Search 1*:217-221.

WALKER, D. 1971. Quantification in historical plant ecology. *Quantifying Ecology. Ecological Society of Australia, Proceedings 6*:91-104.

WALKER, D. 1972*a*. Vegetation of the Lake Ipea region, New Guinea Highlands. II. Kayamunda Swamp. *Journal of Ecology 60*:479-504.

WALKER, D. 1972*b*. Bridge and Barrier. Pages 399-405 *in* D. Walker, editor. *Bridge and Barrier: the Natural and Cultural History of Torres Strait*. Publication BG/3, Dept of Biogeography and Geomorphology. A.N.U., Canberra.

WALKER, D. and J.R. FLENLEY. In press. Late Quaternary vegetational history of the Enga District of upland Papua New Guinea. *Royal Society of London. Philosophical Transactions B*.

WALKER, D. and D. GREGORY. 1965. The plant ecology of tropical freshwater lakes: A review. *Water Research Foundation of Australia, Report No. 18*.

WALKER, D. and J.C. GUPPY. 1976. Generic plant assemblages in the highland forests of Papua New Guinea. *Australian Journal of Ecology 1*:203-212.

WALKER, D., P. MILNE, J. GUPPY and J. WILLIAMS. 1968. The computer-assisted storage and retrieval of pollen morphological data. *Pollen et Spores 10*:251-262.

WALKER, D. and S.R. WILSON. 1978. A statistical alternative to the zoning of pollen diagrams. *Journal of Biogeography 5*:1-21.

WEBB, L.G., J.G. TRACEY and W.T. WILLIAMS. 1976. The value of structural features in tropical forest typology. *Australian Journal of Ecology 1*:3-28.

WEBB, T. 1974. Corresponding patterns of pollen and vegetation in lower Michigan: A comparison of quantitative data. *Ecology 55*:17-28.

WEBB, T. and R.A. BRYSON. 1972. Late and post glacial climatic change in the northern Midwest U.S.A. Quantitative estimates derived from fossil pollen spectra by multivariate statistical analysis. *Quaternary Research 2*:70-115.

WEBB, T. and J.H. McANDREWS. 1976. Corresponding patterns of contemporary pollen and vegetation in Central North America. *Geological Society of America Memoir 145*:267-299.

WEBSTER, P.J. and N.A. STRETEN. 1978. Late Quaternary ice age climates of tropical Australasia: Interpretations and reconstructions. *Quaternary Research 10*:279-309.

WELTEN, M. 1944. Pollenanalytische, stratigraphische und geochronologische Untersuchungen aus dem Faulenseemoos bei Spiez. *Ver Offenlichungen des Geobotanischen Institutes Rubel in Zurich 21*:1-201.

WEST, R.G. 1970. Pollen zones in the Pleistocene of Great Britain and their correlation. *New Phytologist 69*:1179-1183.

WHITE, J.P., K.A.W. CROOK and B.P. RUXTON. 1970. Kosipe: A late Pleistocene site in the Papuan highlands. *Proceedings of the Prehistoric Society 36*:152-170.

WHITE, J.P. and O'CONNELL. 1979. Australian prehistory: New aspects of antiquity. *Science 203*:21-28.

WHITMORE, T.C., editor. 1972. *Tree Flora of Malaya*. Vol. 1. Longman, London.

WHITMORE, T.C., editor. 1973. *Tree flora of Malaya*. Vol. 2. Longman, London.

WIJMSTRA, T.A. and T. van der HAMMEN. 1966. Palynological data on the history of tropical savannas in northern South America. *Leidse Geologische Mededelingen 38*:71-90.

WILLIAMS, C.B. 1964. *Patterns in the Balance of Nature and Related Problems in Quantitative Ecology*. Academic Press, London.

WILLIS, E.H., H. TAUBER and K.O. MUNNICH. 1960. Variations in the atmospheric radiocarbon concentration over the past 1300 years. *American Journal of Science, Radiocarbon Supplement 2*:1-4.

WILLIS, I. 1974. *Lae - Village and City*. Melbourne University Press.

WILLKOMM, H. and H. ERLENKEUSER. 1973. $C^{14}$ measurements on water, plants, and sediments of lakes. Pages 312-323 *in* T.A. Rafter and T. Grant-Taylor, editors. *Proceedings of the 8th International Conference on Radiocarbon Dating*. Lower Hutt, 1972. Royal Society of New Zealand, Wellington.

YANG, A.I.C. and A.W. FAIRHILL. 1973. Variations of natural radiocarbon during the last 11 millenia and geophysical mechanisms for producing them. Pages 60-73 *in* T.A. Rafter and T. Grant-Taylor, editors. *Proceedings of the 8th International Conference on Radiocarbon Dating*. Lower Hutt, 1972. Royal Society of New Zealand, Wellington.