

# THE HISTORY OF LIFE IN NEW ZEALAND FORESTS

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The indigenous forests of New Zealand are ecosystems made up of several hundreds of different kinds of plants and animals, each of which is to some extent dependent on the others, to form a series of complex communities, their distribution controlled ultimately by physical conditions such as climate, slope, watertable and soil-forming substratum, but also by the historical events of the last few thousand years. Sometimes forest communities have been thought of as having an organic unity in themselves, as if each type of forest was itself an organism that had evolved through long geological time, with the component species interrelated and bound together like the parts or organs of a living body. But what we know of the past history of our forests from the study of fossils (summarised in Fleming, 1975a) leads us to conclude that each member of a forest community, be it tree or shrub or herb, or bird or insect or earthworm, has had its own history, never independent of its companions and surroundings but not rigidly dependent on their absolute stability. Despite their great age and seeming permanence on the time scale of human life, the forests have varied in their composition and structure, in their dominant species, and in their physiognomy or growth form, so that the inter-relationships and interdependence between the component members of the communities have changed through geological time.

## FOSSIL PLANTS

New Zealand has a good identifiable record of vegetation history for about 200 million years, thanks to the preservation of fossil pollen grains in coals and other deposits (Harris, 1951; Couper, 1953, 1960a, b; Mildenhall, 1970, 1972), supplemented by leaf imprints, fossil wood and seeds. But the record of fossil animals is almost lacking completely, so that very indirect arguments have to be used to build up an account of their history, which remains speculative in the extreme but none the less a legitimate interest of science.

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When we study the geological evidence we have on the history of New Zealand forests, we find that recognisable ancestors of some of their plants extend back in time to the Mesozoic or even the Late Paleozoic Era, some 250 million years ago. These ancient elements were joined by newcomers, either by immigration or by organic evolution throughout the course of later geological time. Some fell by the wayside, becoming extinct as a result of competition or by their inability to survive changes in the environment, especially climatic changes of various kinds. Finally, less than two million years ago the rather rapid and extreme alternations of cold and warm climate we call the Ice Age began. The forests retreated and advanced under the influence of successive glacial and interglacial phases and many of the more sensitive plants and animals went to the wall; yet forests survived, as they always have done so far, to become the dominant vegetation cover of New Zealand when man first set foot on her shores about a thousand years ago.

### PLATE TECTONICS

Recent advances in marine geophysics have led to widely supported theories of plate tectonics, a unifying model for earth history that has allowed general acceptance of the concept of "sea-floor spreading" as a mechanism for "continental drift" (Heirtzler, 1968). There are many variations and no unique interpretation of the history of the continents, and there will be for many years, but most geologists now support the view that southern lands were for long ages associated together as a super-continent known as Gondwanaland (Fig. 1). New Zealand's greywacke rocks, now forming our main ranges, were deposited in geosynclinal troughs, marginal to Gondwanaland (Fleming, 1971). During the Permian, some 250 million years ago, the chief plants were strange gymnosperms such as *Glossopteris* (Mildenhall, 1970), horse-tails, fern-like plants and early conifers, perhaps ancestors of kauri and podocarps.

### ANCIENT PLANTS AND ANIMALS

Gondwanaland continued through the Triassic and Jurassic Periods. Pollen grains and leaf impressions show that predecessors and probably ancestors of some modern podocarps, araucarians and lower plants, lycopods and ferns, including tree ferns, were present. The fossils include pollen grains like those of living podocarps — matai, miro, kahikatea, totara — and fossil foliage, for instance of a New Zealand Jurassic podocarp called *Mataia podocarpoida* (Townrow, 1967). In addition there were ginkgo and araucarians, the name given

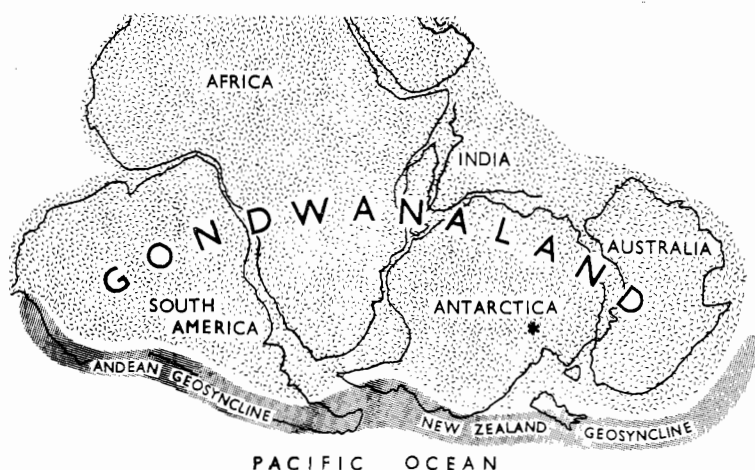


FIG. 1: A reconstruction of Gondwanaland and its marginal geosynclines in the Permian. The Lower Permian position of the South Pole is shown by an asterisk.

to relations of the kauri, like the Queensland hoop pine and bunya bunya and the Norfolk pine no longer surviving here, but recognised by fossils (Florin, 1940). The Jurassic fossil forest at Curio Bay, Southland, impressive even by production forest standards, consists of conifers of these types.

No fossil land animals are known from the Jurassic, but on theoretical grounds it seems likely that the tuatara, the native frog, and many primitive and conservative invertebrate animals may have reached New Zealand at this early date, about 150 million years ago. Possibly the Paryphantid snails are in this category. New Zealand was still part of Gondwanaland. Its forests and the life they supported must in general have been common to all the other segments of that "jigsaw continent" — Antarctica, Australia, Africa, India and South America — so that the present differences between them have developed after they drifted apart in contrasting climatic conditions, partly by differences in the survival of these old elements, partly by differences in the number and source of immigrants.

#### CONTINENTS IN DISPERSAL

The break-up of the South-west Pacific segments of Gondwanaland began in the Cretaceous Period, a time of rapid change in New Zealand's structure and geography. The Tasman Sea and Southern Ocean opened up as splits between Australia and New Zealand and Antarctica (Hayes and Ringis,

1973) as shown in a series of reconstructions by Suggate (1972). New Zealand was twisted, broken and uplifted to form a mini-continent, as it began to drift away from other segments of the old continent (Fleming, 1970).

### CRISIS IN LIFE HISTORY

A revolution in the history of the world's vegetation also took place in the Cretaceous, with the evolution and rapid proliferation and spread of the angiosperms or flowering plants throughout the world in the latter half of the Period, while at the end of the Cretaceous, throughout the world, occurred the most catastrophic extinction (or severe reduction) of dominant organisms characteristic of Mesozoic life — dinosaurs and other giant reptiles, ammonites, belemnites and many other marine invertebrates, and some of the fern-like plants and gymnosperms. There was an overall decline in generic diversity of about 50% (Russell, 1977). The three phenomena (continental drift, angiosperm development, massive extinctions), whether independent or causally related, overlapped in time, so that New Zealand drifted into isolation after the first angiosperms had dispersed and before the climax of extinction. This mysterious biological crisis, subject of much research and enquiry, has been termed a watershed of Earth history, and from the survivors, "the debris from the age of reptiles" (Lemieux, 1977), has sprung all the diversity of modern life.

### GONDWANALAND HERITAGE

Ancestors of southern beech trees, *Nothofagus*, were distributed at this time, apparently before the Gondwana continent dispersed. With the Proteaceae, similarly distributed, and *Casuarina*, the she-oak (now mainly Australian), they joined the conifers and at times dominated the forest vegetation. At various times there were at least 20 kinds of Proteaceae, although only two, the rewarewa and toru, persist in New Zealand today. About 60 to 70 million years ago podocarps still dominated New Zealand forests, including two types that no longer persist here but still live in Tasmania, *Microcachrys* and *Dacrydium franklini*; but the angiosperms, especially beeches, Proteaceae in abundance, and *Casuarina*, were increasingly prominent, these groups all including extinct forms. For instance, *Nothofagus* included members of the *brassi* group which still live in New Caledonia and the highlands of New Guinea (Couper, 1960a).

The large flightless birds grouped as ratites have not left a satisfactory fossil record of their history, but there are good

reasons to conclude that they were dispersed over Gondwanaland in the Cretaceous, before it disintegrated, and subsequently differentiated by differential survival and evolution within the separate segments. The moas, no longer living, and the kiwis, still fortunately with us, have every right to be considered the most ancient of New Zealand birds known to us.

### CONTINUED IMMIGRATION

Despite the increasing distance between New Zealand and other lands as the continental segments drifted apart, immigrants have continued to arrive, presumably across the seas, carried by currents of air or water to increase the diversity of the biota. Figure 2 shows diagrammatically the first appearance in the fossil record of land and freshwater organisms, many of them part of our forest communities. They came mainly from Australia and from the Malayo-Pacific Region to the north, a few from other southern lands. For instance, *Leptospermum* (the manuka and kanuka) probably came from Australia, *Fuchsia* (konini) from South America and the kohekohe, kiekie, tawa and mistletoe from the tropics. When they were dispersed is suggested by the first appearance of distinctive pollen grains in the rocks, but how they dispersed is controversial. There were no more land connections, so that transport of succulent fruit in birds' stomachs is seriously suggested for plants like *Fuchsia*. We must remember that vegetation persisted on the shores of Antarctica until overwhelmed by glaciation, so that Antarctica provided a large stepping-stone for dispersal of southern organisms like *Fuchsia*, which has since reached the oceanic Society Islands from New Zealand. Wherever they came from, successful newcomers found a niche and diversified the forests, so that *Elytranthe* mistletoe from South-east Asia is found perched on *Nothofagus* beeches of southern origin.

In parenthesis, it is worth noting that neither *Metrosideros* (the genus that includes ratas) nor *Fuchsia* now lives in Australia. They are favourite foods of the browsing Australian opossum, which is eliminating rata and *Fuchsia* from many (but not all) New Zealand forests (Meads, 1976), and their absence from Australia may be due to the presence of browsing mammals like the opossum. Likewise the persistence of ratas suggests an absence of such browsers in New Zealand in the past.

Early Tertiary forests lacked the two major groups of angiosperms that were the last to evolve: the grasses and the Compositae. Until Oligocene-Miocene times, therefore, our forests lacked the toetoe and other grasses locally so characteristic today of clearings, stream banks and rock faces, and the

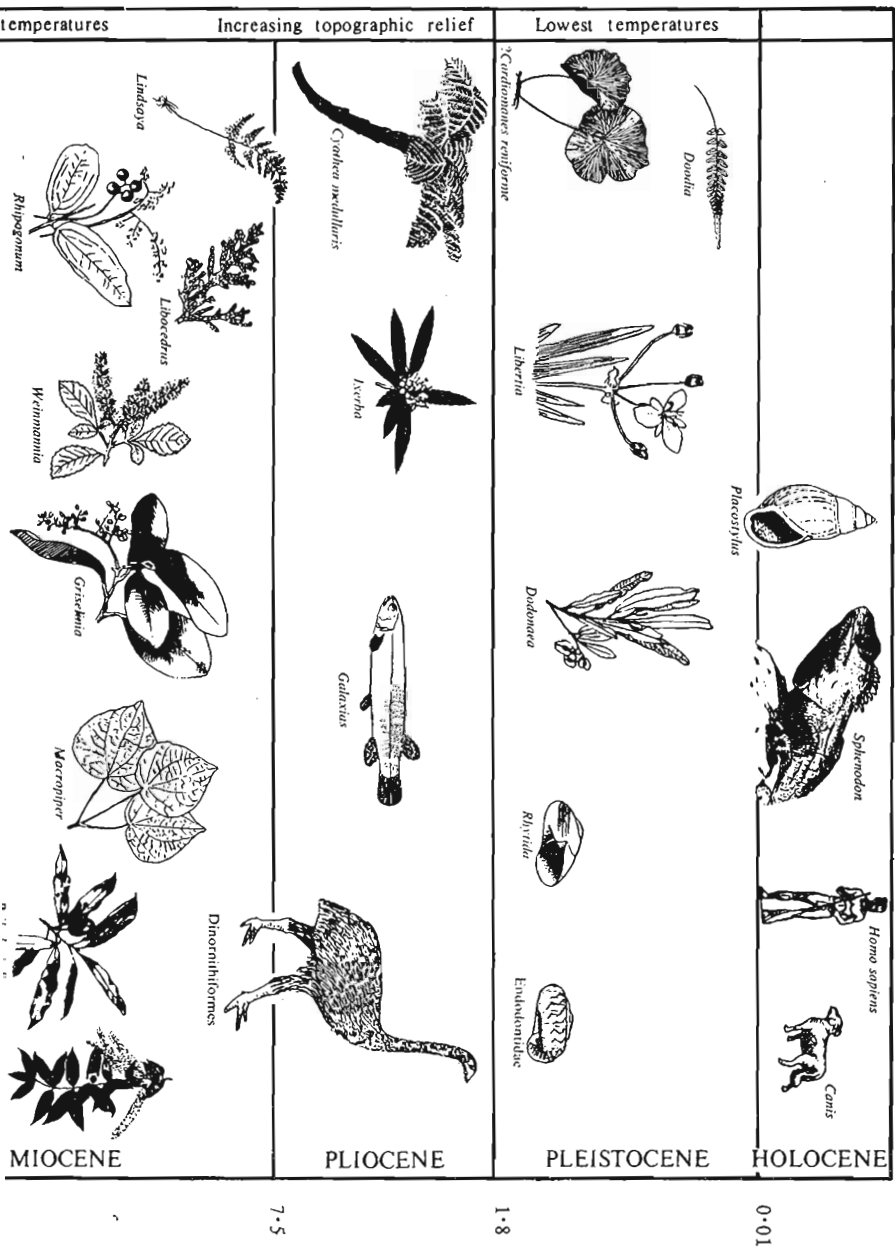




FIG. 2: First appearance in the New Zealand fossil record of members of the land and fresh-water biota, illustrated by living (or recently extinct) species shown at the dates in the geological time scale when the taxa to which they belong are first recorded by fossil predecessors in New Zealand. The panels for geological periods are not proportionate to their absolute duration.

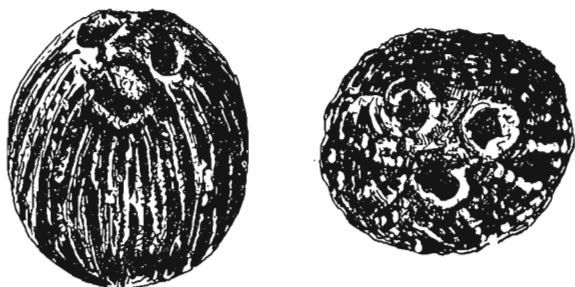


FIG. 3: *The New Zealand Miocene coconut Cocos zeylanica* Berry ( $\frac{3}{4}$  natural size).

tree daisies, *Olearia* and *Senecio*, like the heketara so conspicuous in some modern forests, and the many other composites of forest floor and margins.

All through the Tertiary sequence, new types of pollen appear, suggesting migration across the sea, for instance, of the ancestors of kohekohe and pukatea in the Paleocene, matipo, horopito and *Astelia* in the Oligocene, cabbage tree, titoki, wineberry, tutu, kamahi and kawakawa in the Miocene, mamaku tree-fern in the Pliocene, akeake and *Libertia* in the Quaternary.

During the 60 million years of the Tertiary Epoch, the forests varied in their dominant trees as age succeeded age, probably in response to changing climates (McQueen *et al.*, 1968). The Paleocene forests had dominant podocarps, the Eocene began with diverse forests including she-oak communities, continuing with *fusca*-group *Nothofagus* forests, changing to forests with dominant *brassi*-group *Nothofagus*, which persist into the Oligocene. There was evidence of warmth then from pollens representing palms and tropical plants no longer with us, such as *Cupania* and *Bombax* (kapoc family). We can have only a vague idea what some of these forests looked like. For instance, judged by the diversity of ferns, the she-oak forests of New Zealand were not desert or savanna vegetation like many Australian communities with *Casuarina*. The Miocene began with a more complex pattern of forests, to judge from the pollens, suggesting local differentiation; but the *brassi* beeches became dominant again at the peak of the Miocene warm period, best shown by marine fossils. At that time coconut palms grew in the North Island, probably in coastal forest belts (Fig. 3).

By the Late Miocene, earth movements were raising mountains for the first time since the Cretaceous, and thereafter lowland and upland forests probably differed in their dominant beech types.



## DIVERSITY THROUGH GLACIATION

As the early Ice Ages gripped the land, the *brassi* beeches and several other warmth loving plants became extinct. We lost *Casuarina*, the kapoc, *Cupania*, coconuts, many of the Protea family; while both New Zealand and mainland Australia had already lost the two podocarps now confined to Tasmania. The Alps rose until parts lay above the bush-line; and at each glacial age the climate zones descended so as to push out forests from at least the southern South Island, and sometimes (geologists conclude) from the southern half of the North Island.

In certain districts, for instance, near the present Pohangina valley on the west of the Ruahine Range, species of *Acacia* (wattles) from Australia successfully colonised when cool savanna conditions temporarily prevailed (Mildenhall, 1972). They did not persist, however, once closed-canopy forests again became ubiquitous.

At each glaciation, as water was locked up in the world's ice caps and snowfields, sea level fell, linking the islands of New Zealand in an extended land that was broken up into a number of isolated ecological islands by glaciers and barren unstable outwash plains of rivers. This favoured speciation of isolated populations in relict areas of scrubby vegetation, so that locally endemic plants may have evolved in north-west Nelson and elsewhere at such times. Similarly, when sea level rose in interglacial ages, the sea formed barrier straits between islands on which speciation occurred, and montane organisms became isolated on mountain tops by lowland valleys they could not cross. The distribution patterns of *Rhytida* snails and stag beetles of Northland, and the *Paryphanta* snails of Nelson show these effects.

The forests also played their part in the peopling of the alpine zone as can be illustrated by the derivation of the kea and rock wren from their forest ancestors, the kaka and bush wren. Similarly, forest insects, such as wetas, and lowland plants of many kinds, invaded the new habitats. When the last Ice Age ended, the pollen record, studied especially by Moar (1971) in the South Island, shows how subalpine grasslands gave way to scrub, then generally to podocarp forests easily dispersed by birds that eat their succulent fruits, followed later by slower-moving *Nothofagus*, which failed to reach Foveaux Strait before the rising Post-glacial sea cut off its access to Stewart Island. Although evolved in Tertiary lowlands, New Zealand forest ecosystems have been able to clothe the young mountains in Post-glacial times to serve as protection forests except where handicapped by the interference of man, his fires, and his introduced animals.

## FOREST SANCTUARIES FOR ANCIENT LIFE

As a result of the mountain building movements and the ice ages, New Zealand today is much more diverse in its vegetation than it was for the previous 100 million years, when forests clothed the whole land. On the whole, therefore, the forests and forest margins supported the most ancient and distinctive New Zealand animals: the tuatara (in its original state) and the endemic geckos, the native *Leiopelma* frogs of forest stream banks, the nocturnal or crepuscular kiwi and kakapo, the wattlebirds, the short-tailed bat, the ancient peripatus and many other distinctive invertebrates such as the giraffe weevil. In the absence of mammals (other than bats) some of the ecological niches used by rodents in other lands are occupied by the wingless crickets we call wetas, which browse on foliage by night and retreat by day to holes and crevices like mice, even producing similar droppings.

## FOREST CICADAS

In recent studies of New Zealand cicadas (Dugdale and Fleming, 1969; Fleming, 1973, 1975b) some of the most distinctive species, least like those of other countries, were found to be primarily inhabitants of the forests; and since North Island forests have been more persistent through the ice ages than the South Island forests, these distinctive forest elements may be solely North Island in distribution, because they did not spread south fast enough to cross before Cook Strait was formed by the rise of sea level. Such, for example, are the two shade singing species *Kikihia scutellaris* and *Kikihia cauta*. Several bright green foliage cicadas are also characteristic of North Island forest edges. More widespread in both islands is the large New Zealand cicada *Amphipsalta zelandica*, primarily a forest species but adapted to plantations and gardens. *Amphipsalta* is the only cicada genus in the world which supplements its tymbal song with wing clapping. Its original song station was probably the sunny aspect of emergent podocarp boles, for which wooden or concrete power poles are a modern substitute.

## FOREST BIRDS

In the absence of fossil birds in New Zealand, speculation on the history of forest birds is based on indirect evidence and guided by knowledge of fossils overseas. By comparing New Zealand birds with their nearest relations overseas, and noting the degree of distinction, we can get a rough idea of the time since their colonisation; unreliable but useful in default of better evidence (Fleming, 1962, 1974). The ratites almost certainly evolved in the Mesozoic Era and the endemic

suborders, moas and kiwis, unable to cross ocean barriers, can hardly have reached New Zealand later than the Cretaceous — some 70 million years ago — when New Zealand began to separate from Antarctica and Australia. Subsequently they proliferated on the New Zealand Archipelago, the separation of genera and species dating from Tertiary times when New Zealand's geography as a mobile archipelago changed rapidly.

The kiwis became highly specialised for nocturnal life, foraging for worms, arthropods, snails and berries on rain forest floors; and the moas too were probably forest browsers exploiting foliage, seeds and fruits at different heights above the forest floor. Greenwood and Atkinson (1977) have attributed to moa browsing the development of divaricate or twiggy juvenile plants in many New Zealand trees. H. W. Wellman (unpublished) suggested that the pole podocarp stands were established when the competing broad-leafed shrubs (which were more palatable) were kept closely browsed by moas, before the arrival of man led to their reduction and finally to their extermination.

#### DIFFERENCES IN AGE AND ENDEMISM

Next to the ratites, the most ancient forest birds are the three endemic families of New Zealand thrushes, wrens (including rifleman) and wattlebirds (kokako, huia and saddleback) whose overseas relatives are not known with certainty. Probably their ancestors came in the Early Tertiary. Next to the kiwis they are the most distinctive and biologically precious of New Zealand birds, already reduced from eight species to four by man's effect on the New Zealand environment. The endemic genera range from well-differentiated forms of obscure affinity, such as the bush canaries, *Nestor* parrots (sometimes given family rank), and the blue duck, to forms clearly related to the parent genus, such as bellbird and stitchbird to Australian honeyeaters or the weka to the banded rail. These genera seem likely to be the result of later Tertiary colonisations. Somewhat younger are the endemic species of overseas genera, including the cuckoos, grey warbler, robins and tits. These probably arrived during the Pleistocene ice ages and interglacials of the last million years, together with open-country and water birds, some of them occupying new habitats only then for the first time available; or Northern Hemisphere birds induced to spread from the Northern Hemisphere by the changes in climate the world was suffering (South Island pied oystercatcher, scaup, merganser).

Seventeen species of land or fresh-water birds are distinct New Zealand subspecies of Australian species, including the

fantails, kingfisher and banded rail. Since we know that many well-marked subspecies have developed since Cook Strait last became a barrier some 10 000 years ago, and since the formerly glaciated Auckland Islands were reclothed in forest at about the same date, there seems no reason to assume any New Zealand subspecies of an Australian species is much older than that. Finally, we have had later colonists from Australia that did not differentiate from the parent stock; some prehistoric, others in our own time; but only one of them, the silver-eye, includes forest in its wide range of habitats.

### TRENDS IN EVOLUTION

New Zealand birds, in a land with few predators and reduced competition, have shown a tendency to evolve by increase in size, by becoming partly or entirely flightless, with short rounded wings, their legs becoming stouter. Several independently have developed melanistic forms under relaxation of the selection pressures that normally maintain cryptic colour patterns and camouflage. The black fantail is the only melanistic form in the mainland forests, but there are black tits and robins on the Snares and Chatham Islands. This is not the place to emphasize the vulnerability of our forest life to the effects of human occupation in both Maori and European colonisations; suffice it to say there is enough left to be worth saving.

### CUSTODIANS FOR THE WORLD

Let me try to summarise. The oldest life in New Zealand forests goes back more than a hundred million years to Gondwanaland. Other southern lands started with a similar heritage, but have differentiated owing to their reduced isolation from the Northern Hemisphere (South America and Africa), or the Late Tertiary desiccation that triggered off the evolution of savannas, of eucalypts in Australia and the veldt of Africa, both of which countries retained more Proteaceae than New Zealand. As a result New Zealand forests are most like the Mesozoic forests of Gondwanaland, and are so regarded by Northern Hemisphere biologists who visit them in pilgrimage. We are the custodians of a New Zealand heritage of world interest.

In Britain and in Canada, the forests had to be established afresh after the last ice age wiped the slate clean less than twenty thousand years ago. There, nothing is old in the same sense that our kauri, podocarp and beech forests are old. If we look at our forests with the eye of a biologist, and a geologist's sense of time, we must admit that the kauri forests of

Northland (especially if they also have kiwis and native frogs), the great podocarp-tawa forests of the central North Island (especially if they have kokako and kaka), and the kahikatea forests of swamps (if seldom with as much zoological interest) have somewhat greater biological interest than the montane beech forests of steeper slopes (protection forests), which, however, are now the main habitat of the rifleman (endemic family).

Development of our national culture demands the retention, in all districts, of those skylines of native forest that represent the mystery and adventure of the unknown to every youngster in farm and suburban homes. The intellectual value of the indigenous forests, their long history, and the relationships of their component species, enhance the recreational and aesthetic values that the environmental movement has emphasised when urging their preservation on behalf of future generations of New Zealanders.

#### ACKNOWLEDGEMENTS

The data on the fossil occurrences of the pollen grains and spores of New Zealand forest plants cited in this paper are based on the pioneer work of Dr R. Ashley Couper (1953, 1960), which has been supplemented by the work of younger palynologists, for the most part unpublished. I am particularly grateful to D. C. Mildenhall and Dr J. I. Raine for much data and for comments on the manuscript. Students of fossil pollen use distinctive generic names, for objectivity, such as *Haloragacidites* for the pollen attributed to *Casuarina*, but I must take the responsibility for using the botanical names of the inferred source plants, in order to present an account that can be understood by forest botanists.

#### REFERENCES

- Couper, R. A., 1953. New Zealand Mesozoic and Cainozoic spores and pollen grains. *N.Z. Geol. Surv. Paleontol. Bull.*, 22, 77 pp., 9 pl.
- 1960a. Southern Hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and their palaeogeographic significance. *Proc. Roy. Soc. London B*, 152 (949): 491-500.
- 1960b. New Zealand Mesozoic and Cainozoic plant microfossils. *N.Z. Geol. Surv. Paleontol. Bull.* 32, 87 pp., 12 pl.
- Dugdale, J. S.; Fleming, C. A., 1969. Two New Zealand cicadas collected on Cook's Endeavour voyage, with description of a new genus. *N.Z. Jl Sci.*, 12 (4): 929-57.
- Fleming, C. A., 1962. History of the New Zealand land bird fauna. *Notornis*, 9 (8): 270-4.
- 1970. The Mesozoic of New Zealand: Chapters in the history of the circum-Pacific mobile belt. *Q. J. Geol. Soc. London*, 125 (2): 125-70.

- 1971. Continents in dispersion. Pp. 12-13, 16-21 in Knox, R. (editor), *New Zealand's Heritage*, 1 (1). Hamlyn, Wellington.
- 1973. The Kermadec Islands cicada and its relatives (Hemiptera: Homoptera). *N.Z. Jl Sci.*, 16: 315-32.
- 1974. The Coming of the Birds. Pp. 61-8 (12 fig.) in Knox, R. (editor), *New Zealand's Nature Heritage*, 1 (3). Hamlyn, Wellington.
- 1975a. The geological history of New Zealand and its biota. Pp. 1-87 in Kuschel, G. (editor), "Biogeography and Ecology in New Zealand". *Monographiae Biologicae* 27. W. Junk, The Hague.
- 1975b. Adaptive radiation in New Zealand cicadas. *Proc. Am. Phil. Soc.*, 119 (4): 298-306.
- Florin, R., 1940. The Tertiary fossil conifers of South Chile and their phytogeographical significance; with a review of the fossil conifers of southern lands. *K. Svenska Vetenskapsakademien. Handlingar*, 19 (2): 1-107.
- Greenwood, R. M.; Atkinson, I. A. E., 1977. Evolution of divaricating plants in New Zealand in relation to Moa browsing. *Proc. N.Z. Ecol. Soc.*, 24: 21-9.
- Harris, W. F., 1951. New Zealand plants and their story: Clues to the past. *N.Z. Sci. Rev.*, 9 (1-2): 3-7.
- Hayes, D. E.; Ringis, J., 1973. The early opening of the Tasman Sea. P. 338 in Fraser, R. (editor), *Oceanography of the South Pacific*. N.Z. National Commission for Unesco. 524 pp.
- Heirtzler, J. R., 1968. Sea floor spreading. *Sci. Am.*, 219 (6): 60-70.
- Lemieux, L., 1977. Preface, p. 4, in Cretaceous-Tertiary extinctions and possible terrestrial and extra-terrestrial causes. *Syllogeus No. 14*.
- McQueen, D. R.; Mildenhall, D. C.; Bell, C. J. E., 1968. Paleobotanical evidence for changes in the Tertiary climates of New Zealand. *Tuatara*, 16 (1): 49-56.
- Meads, M. J., 1976. Effects of opossum browsing on northern rata trees in the Orongorongo Valley, Wellington, New Zealand. *N.Z. Jl Zool.*, 3 (2): 127-39.
- Mildenhall, D. C., 1970. Discovery of a New Zealand member of the Permian Glossopteris flora. *Aust. J. Sci.*, 32 (12): 474.
- 1972. Fossil pollen of *Acacia* type from New Zealand. *N.Z. Jl Bot.*, 10 (3): 485-94.
- Mildenhall, D. C.; Harris, W. F., 1971. Status of *Haloragacidites* (al. *Triorites*) *harrisii* (Couper) Harris comb. nov. and *Haloragacidites trioratus* Couper, 1953. *N.Z. Jl Bot.*, 9 (2): 297-306.
- Moar, N. T., 1971. Contribution to the Quaternary history of the New Zealand flora 6: Aranuiian pollen diagrams from Canterbury, Nelson and North Westland, South Island. *N.Z. Jl Bot.*, 9 (1): 80-145.
- Russell, D. A., 1977. The biotic crisis at the end of the Cretaceous Period. Pp. 11-23, in Cretaceous-Tertiary extinctions and possible terrestrial and extra-terrestrial causes. *Syllogeus No. 14*.
- Suggate, R. P., 1972. Mesozoic-Cenozoic development of the New Zealand region. *Pacific Geol.*, 4: 113-20.
- Townrow, J. A., 1967. On *Rissikia* and *Mataia*, podocarpaceous conifers from the Lower Mesozoic of southern lands. *Proc. Roy. Soc. Tasmania*, 101: 103-36.