THE NATURE AND RELATIONSHIPS OF THE TERTIARY BROWN COAL FLORA OF THE YALLOURN AREA IN VICTORIA, AUSTRALIA

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ABSTRACT

To date, sixteen taxa from the brown coal have been identified satisfactorily. Almost all of these had a wider distribution in Australia during the Tertiary period than they do at present, and only about half of them still occur in Victoria. A search for comparable modern floras shows that all sixteen taxa are still represented in New Guinea, with somewhat smaller numbers in New Caledonia, part of the eastern Australian coast and northern New Zealand. The nature of these modern floras and the climatic conditions under which they occur suggest that the brown coal vegetation consisted mainly of *Nothofagus* rain forests and gymnosperm or mixed gymnosperm-broadleaf forests, possibly with some overlap between these types, and that the rainfall was high and the temperatures were moderate.

Pollen analysis has shown that, with the exception of the Lauraceae and Oleaceae (the vertical distribution of which is not known) and the Restionaceae/Centrolepidaceae (which only occurs at the top of the coal), the taxa concerned occurred throughout the period of formation of the coal, but that their relative abundance varied considerably. *Nothofagus* pollen dominates the diagram as a whole, with values of up to 95%, and when the few low values for this genus are recorded the values for one or more of *Casuarina*, Myrtaceae and Gymnosperms are high. Complex changes in the diagram suggest a major change in environmental conditions at about the middle of the coal-forming period, with the possibility that conditions were much less stable during the second half of this period.

INTRODUCTION

YALLOURN lies in the south-eastern corner of the mainland of Australia, and the brown coal which occurs in this area is, according to Thomas & Baragwanath (1949), of Oligocene age. Research over a number of years has provided some useful information about the plant fossils in the brown coal, and in the present paper the results of this work are considered in an attempt to answer the following questions:

What plants grew in the area when the brown coal was forming?

Can this flora be related to any present-day communities?

What were the climatic conditions under which the plants grew?

Were there any major changes in climate or vegetation during the period of formation of the coal?

FLORA OF THE BROWN COAL

In discussing the plants which have been identified from the brown coal, only taxa which can be related to present-day ones are considered and identifications which are believed to be unsatisfactory are omitted. These omissions comprise:

1. A record by Chapman (1925a) of *Callitris* wood; this was not positively identified, and the illustration in the paper does not show the microscopic structure of the wood.
2. A record by the same author (CHAPMAN, 1925b) of a cycad seed; the identification was hesitant and the illustrations do not prove the case.
3. Records, based only on the external morphology of leaves, of *Dryandra*, *Lomatia*, *Cinnamomum* and ?*Tristania* by Deane (1925).

The uncertainty of identifications of the last-mentioned kind is well known, and both this point and the value of cuticular studies were emphasized during the course of work by the present author on lauraceous leaves from the brown coal. When this work was being carried out, one of the living plants believed to belong to the Lauraceae was known as *Cryptocarya graveolens* Bail.; this name was established on the basis of specimens without flowers, i.e. on fruit structure and the external morphology of the leaves. The cuticle of leaves of this species was found to be unique among Australian members of the family, and the subsequent discovery of flowers led to the transfer of the plant by Smith (1956) to the Myrtaceae, where the same type of cuticular structure is common. Cuticular studies of the fossil leaves in question confirmed the position in the Lauraceae suggested by their external morphology, but it was found that there is no combination of cuticular and morphological characters which can be used to identify such leaves at a generic level. Consequently, Deane's identification of *Cinnamomum* cannot be accepted, and his other identifications must be regarded as unproven.

Many of the fossils to be discussed in this paper are pollen grains which have been referred to modern taxa. While this practice is regarded with suspicion by many palynologists, who prefer to give purely descriptive names to Tertiary pollen grains, there seem to be sound reasons for accepting it here. The identification of some of the fossil pollen (e.g., the Araucariaceae) has been supported by evidence from wood and/or fruits and leaves with the cellular structure preserved; some of the pollen grains (e.g., *Nothofagus*) are of very distinctive types which are unknown in taxa other than the ones to which the fossils have been referred; with one exception, all the taxa concerned still occur in Australia, and many of them belong to families, such as the Myrtaceae and Proteaceae, which obviously have major centres of development in Australia and may be expected to have had a long evolutionary history here. Furthermore, it may be noted that the structure of a modern plant has in a sense been predicted by a study of fossil pollen which was referred to a modern genus; Cookson (1946) placed some fossil pollen of *Nothofagus* in a group which she assumed to be extinct, but she found later that these fossils could be matched by the pollen of the recently discovered species of this genus in New Guinea and New Caledonia (COOKSON, 1952).

Although it seems reasonable to relate fossil pollen grains to modern genera, it is perhaps more doubtful whether they can be referred to particular subdivisions of such genera. Van Steenis (1953) concludes that pollen type is not a good criterion for taxonomic infrageneric distinction because, in the genus *Nothofagus*, both *fusca* and *menziesii* type pollen can occur in a single subsection. However, even in this case it should be possible to place *brassi* type pollen in a subsection, as it is restricted to and present in all species of one subsection, and subdivisions of some other genera are known to have equally distinctive pollen (e.g., section Dacrycarpus of *Podocarpus*, COOKSON & PIKE, 1953b). Although fossil *Nothofagus* pollen of neither *fusca* nor *menziesii* type can be referred to a particular subdivision of the genus, it seems more probable that fossil *fusca* pollen belongs to a species related to modern ones which produce *fusca* pollen rather than to those which have *menziesii* pollen, and vice versa.

The information available at present about the nature of the brown coal flora is summarized in the list below, which includes a record of the organs on which the identifications were based. All macroscopic remains cited showed details of cellular structure. Where two or more organs of one taxon have been described, they were not in organic connection unless this is specifically stated, but it is believed that evidence from several sources must strengthen the case for the identification in question. Only gymnosperms and angiosperms have been included in the list.

(A) GYMNOSPERMS

1. *Agathis* — wood (PATTON, 1958); leaves, male and female cones, pollen grains extracted from the male cones (COOKSON & DUIGAN, 1951).
2. *Araucaria* — leaves, male and female cones, pollen extracted from the male cones (COOKSON & DUIGAN, 1951).
3. *Dacrydium* — leaves, seeds (COOKSON & PIKE, 1953a); pollen (COOKSON & PIKE, 1953a; COOKSON, 1953, 1957).
4. *Phyllocladus* — leaves, pollen (COOKSON & PIKE, 1954a).
5. *Podocarpus*, section Dacrycarpus — pollen, leaves (COOKSON & PIKE, 1953b).

(B) ANGIOSPERMS

6. *Casuarina* — wood (PATTON, 1958); cone (PIKE, 1953); pollen (as *Casuarinidites*; COOKSON & PIKE, 1954b).
7. Ericales — pollen (DUIGGAN unpub.).
8. *Nothofagus* — pollen (COOKSON, 1946, 1959).
9. Lauraceae (broadleaved) — leaves (DUIGAN unpub.).
10. Myrtaceae — pollen (COOKSON & PIKE, 1954b). A wide variety of types, possibly including members of the tribe Eugeniinae.
11. Oleaceae — pollen, leaves (COOKSON, 1947).

12. Proteaceae — pollen of a number of types, including grains similar to, but not identified with certainty as, *Beauprea*, *Xylomelum* and *Symphyonema* (COOKSON, 1950). This group does not include *Banksia*.

13. *Banksia* — cones (COOKSON & DUIGAN, 1950; PIKE, 1953). Leaves (COOKSON & DUIGAN, 1950) and pollen (COOKSON, 1950) referred to the tribe Banksieae probably also represent this genus.

14. Restionaceae/Centrolepidaceae — pollen (DUIGAN, unpub.).

15. Tribe Cupaneae — pollen (COOKSON & PIKE, 1954b).

16. Winteraceae — pollen (DUIGAN, unpub.).

RELATIONSHIP OF BROWN COAL PLANT TO MODERN FLORAS

This list of 16 taxa includes 9 which still occur in Victoria; some of these grow in the dry sclerophyll eucalypt forests of the Yallourn area, but others, such as *Nothofagus* and the Oleaceae, are restricted to wetter localities in the state. The Cupaneae, the broad-leaved Lauraceae and all the gymnosperms are now absent from Victoria, and it is evident that a community of the kind suggested by the list is not found anywhere in the state at the present time. If it is accepted that climatic change led to the elimination of this community in Victoria, then this change may also have led to the migration of the community into an area where the climate is now similar to the one in which it developed, or to its contraction into such an area. This concept is in line with the ideas put forward by Burbidge (1960), who agrees with other authors that plant migration has been by the advance and retreat of communities, and who believes that, in the past as well as the present, climate has been the most important agent controlling the distribution of communities. If these views are accepted, then it is of interest to find out where a community comparable with that of the brown coal exists today and under what climatic conditions it occurs, as this should provide a guide to the climate in which the brown coal was formed. The authors cited in the list of plants have, of course, considered the relation between the past and present distribution of individual taxa, but it is hoped that a consideration of all these taxa together may lead to a more accurate interpretation of the facts. While the assumption that the distribution of plants in the past was governed by the same climatic conditions as those which control them today may not be true in individual cases, it is more likely to be valid if a number of taxa are taken into account.

The greatest number of the 16 listed taxa are found in the following areas:

New Guinea	16
Australia	15
Malaysia (excluding New Guinea)	13
New Caledonia	13
New Zealand	12

Consequently, it is to be expected that communities comparable with those associated with the brown coal are most likely to be found in these areas, and they will be considered in turn.

Although all of the taxa recorded from the brown coal still grow in New Guinea, a perfect match for the brown coal flora cannot be found there because one of the species of *Dacrydium* recorded from the coal (*D. mawsonii*) has pollen which resembles only that of the living Tasmanian species of the genus, and none of the New Guinea species of *Nothofagus* produce either *fusca* or *menziesii* pollen, both of which occur in the coal. However, it is of interest that by far the most abundant *Nothofagus* pollen in the coal is of the *brassi* type characteristic of modern species of the genus in New Guinea and New Caledonia.

According to Robbins (1961), the classification of vegetation types in New Guinea is far from complete, and there is a considerable overlap in the altitudinal ranges of the different communities which have been recognized there. However, it appears that the type of vegetation classed by Robbins as the lower montane rain forest formation corresponds very closely with the flora which formed the brown coal, and it is possible to gain a general idea of the altitudinal range of this type of forest. Robbins' subdivisions, together with an attempt to correlate these with the vegetation types described by other authors, are given below in Table 1, and the discussion which follows is based on the information provided by the four papers cited.

With the exception of *Banksia* and the Restionaceae/Centrolepidaceae, all of the brown coal taxa have been recorded in one or other of the communities noted above,

TABLE 1 — VEGETATION TYPES IN NEW GUINEA AS DESCRIBED BY VARIOUS AUTHORS

Robbins (1961)	Lane-Poole (1925)	Brass (1941)	Womersley and McAdam (1952)
Lower montane rain forest formation			Montane forests
Broadleaf-gymnosperm alliance			? Conifer forests
Fagaceous forest alliance			
Nothofagus spp. association		Beech forest	*Nothofagus* forests
			Submontane rain forests
Castanopsis-*Quercus* spp. association	Mid-mountain forest	Mid-mountain forest	*Castanopsis* forests
			Araucaria forests

at least 11 of them occur in the *Nothofagus* forests. The *Nothofagus* forests range from about 3,000-10,000 ft., but the main belts lie between about 6,000-9000 ft. In these forests, up to three species of *Nothofagus* occur together, and they may make up more than 75% of the canopy. In describing such forests, Womersley and McAdam (1952) state that associated trees include species of *Podocarpus* (section Dacrycarpus), *Dacrydium* and *Phyllocladus*, that members of the Myrtaceae are common and the broad-leaved Lauraceae locally so, and that the Proteaceae is well represented among the subcanopy species. Robbins observes that *Nothofagus* forests may form an ecotone with mixed broad-leaf gymnosperm forests, and that here *Nothofagus* is scattered throughout but may dominate on the ridges. These mixed forests occur at approximately the same altitudes as the main belt of *Nothofagus* forests, and they include at least 10 of the brown coal taxa. The trees in these forests belong mainly to the genera *Podocarpus*, *Phyllocladus*, *Dacrydium* and *Papuacedrus* and the dicot families Cunoniaceae, Eleaocarpaceae and Lauraceae.

Araucaria and *Casuarina* are not recorded for the forest types already mentioned, but occur in association with the oak (*Quercus*-*Castanopsis*) forests at rather lower levels (below 7,500 ft.). *Casuarina* is reported by Brass to be a subseral dominant which does not occur in the climax oak forests, but he notes the presence of this genus up to 4,000 ft. in an area where *Nothofagus* forests occur and the remnants of an original forest which included *Casuarina* at over 5,000 ft.; otherwise, *Casuarina* appears to be mainly a coastal plant in New Guinea, although Lam (1945) recorded a mountain form above the treeline on Doormantop in western New Guinea. *Araucaria* is often an important constituent of the oak forests, and Womersley and McAdam state that *Araucaria* forests occur below the *Nothofagus* forests at altitudes of about 2,000-6,000 ft. These *Araucaria* forests are said to occur on sloping to steep topography which ensures adequate drainage. While *Agathis* may occur in the *Nothofagus* forests, it seems to be restricted to the lower end of their range; Brass describes a particular locality at about 3,000 ft. where *Agathis* occurs as scattered trees protruding through the *Nothofagus* canopy but dominates the forests on broad swampy or ill-drained ridges nearby. Brass also comments that, in this area, both *Agathis* and *Casuarina* range up the slopes to about 4,000 ft. Gibbs (1917) records *Agathis* at about 5,000 ft. in western New Guinea.

Only two taxa seem out of place when the brown coal flora is compared with the lower montane rain forests of New Guinea. The Restionaceae/Centrolepidaceae is recorded by Brass and Robbins only from the very high level grasslands which occur above, and frequently very much above, 9,000 ft. However, Gibbs notes *Centrolepis* in a marsh beside an *Araucaria* forest, so the Centrolepidaceae at least can occur in the vicinity of forests of the type discussed. On the other hand, the distribution of

Banksia seems quite anomalous; Brass notes its occurrence in semi-arid savanna and savanna forest, and a similar distribution is described by Sleumer (1955).

With the one exception noted above, the picture presented by the brown coal flora bears a striking resemblance to the lower montane forests of New Guinea. The map drawn up by Lam (1934) shows that *Agathis* is almost entirely restricted to the western half of New Guinea, and hence it is in this part of the island that the most exact replica of the brown coal flora may be expected to occur. The distribution of *Agathis*, *Araucaria* and *Casuarina* suggest that altitudes towards the lower end of the range of the *Nothofagus* forests — say of the order of 4,000-7,000 ft. — may provide climatic conditions similar to those which prevailed during the formation of the brown coal.

Unfortunately, it is impossible to obtain details of the climate in which these modern forests occur. However, it is obvious that the rainfall is high, and the bulk of these forests have been classed as rain forests by the authors cited. An example of the possible rainfall is given by the rainfall map of the eastern half of New Guinea published by the Ministry of National Development (1951); the notes accompanying this map state that it includes a considerable amount of estimation, but it shows that the highlands covered by Robbins' survey have an annual rainfall of more than 100 inches, and the Kubor Range, on the northern slopes of which Robbins notes that *Nothofagus* occurs extensively, is shown as having a rainfall of more than 200 inches/annum. Hounam (1951) considers that, in eastern New Guinea, the year can be roughly divided into a wet and a relatively dry season, although these occur at varying times of the year in different parts of the island. Only the most general ideas regarding temperature are available; Hounam believes that even in the uplands the month to month changes in temperature are small; and he gives approximations of mean annual temperature in the eastern half of New Guinea as 81°F at sea-level, 69° at 3,000 ft., 61° at 6,000 ft. and 53° at 9,000 ft.

Some of the brown coal taxa drop out progressively in a north-westerly direction from New Guinea and, as it seems that, of the Malaysian area as a whole, New Guinea provides the closest counterpart of the brown coal flora, the other parts of this area are not considered further.

New Caledonia is of particular interest because of the presence of the endemic genus *Beauprea*, which Cookson suggested may be represented in the brown coal. However, it lacks *Phyllocladus*, *Banksia* and the Restionaceae/Centrolepidaceae. Furthermore, none of the species of *Dacrydium* produce pollen of the *mawsonii* type, and the *Nothofagus* species produce only pollen of the *brassi* type. The communities which appear to be closest to those associated with the brown coal are the ones classified by Sarlin (1954) as middle altitude forests (c. 1,300-3,250 ft.) and dry conifer forests (c. 3,250 5,400 ft.). The middle altitude forests form a very variable group, and seem to be predominantly dicotyledonous or of mixed dicots and gymnosperms. Hürlimann (1962) considers that the term 'dry' should not be used in relation to the conifer forests, and both forest types are classed as rain forest by Dawson (1963).

Ten of the brown coal taxa are recorded for these forests, and it is probable that all of the 13 taxa which occur in New Caledonia grow there. The relatively recent identification of *Nothofagus* in New Caledonia makes it difficult to discover its exact distribution there, but Dawson concludes that it occurs in the rain forests and may be dominant on the ridges, and Virot (1956) remarks that it is quite common on the summit region of Mt. Mou at about 4,000 ft. Hürlimann, whose main studies concerned the vegetation classed by Virot as vallicol-mésophile and oro-néphéliphile (in which either *Araucaria* or *Agathis* are important trees), found that *Nothofagus* formed the dominant stratum in some parts of the mountains, and noted the occurrence of *Araucaria*, *Agathis*, Epacridaceae, Myrtaceae and Cupaneae in these *Nothofagus* forests.

The rainfall of the areas in which the forests discussed above grow is high; Sarlin considers that the middle altitude forests occur where the annual rainfall is about 80-120 inches, and it appears that the so-called 'dry' conifer forests may grow where the annual rainfall is more than 120 inches. However, Sarlin believes that the climate is drier than these figures suggest because the rainfall is so variable. The mean annual temperature is high at sea-level (74°F at Noumea), but Sarlin suggests that it decreases to 57° at about 3,500 ft. The seasons are not strongly marked.

Australia as a whole lacks only *Podocarpus* section Dacrycarpus out of the list of brown coal taxa, but none of the *Nothofagus* species produce *brassi* type pollen and the 15 taxa do not grow together in any one area. *Phyllocladus* and *Dacrydium* are restricted to Tasmania and, while the Tasmanian *D. franklinii* Hook.f. is the only living conifer with pollen like that of the fossil *D. mawsonii*, there are no other extant species of *Dacrydium* on the island to match the brown coal *D. florinii*. The only Australian species of *Nothofagus* to produce *fusca* type pollen is a Tasmanian endemic, and a species characterized by *menziesii* pollen also grows in Tasmania. *Phyllocladus* and *Dacrydium* occur in what are variously classified as cool temperate (FORESTRY & TIMBER BUREAU CURTIS, 1962) or temperate (CURTIS, 1956) rain forests; the first of these publications gives the mean annual temperature as 50°F and the rainfall as 40-100 inches/annum in the areas where these trees grow. While both *Phyllocladus* and *Dacrydium* are commonly associated with *Nothofagus* and other brown coal taxa, the Cupaneae, the broadleaved Lauraceae, *Agathis* and *Araucaria* are all absent from the island, and on the whole it appears that the Tasmanian communities are less like the brown coal flora than are some of the mainland rain forests of New South Wales and Queensland.

All the brown coal taxa still represented on the mainland occur in the area on or near the coast of northern New South Wales and southern Queensland which Burbidge (1960) calls the Macleay-MacPherson Overlap. Two of the taxa do not occur together because the northern limit of *Nothofagus* in Australia is further south than the southern limit of *Agathis*. Forests of a type similar to those of the Overlap (but without *Agathis* and *Araucaria*) extend southwards along the coast of New South Wales, and comparable ones (without *Nothofagus*) stretch northwards into the area termed North-East Queensland by Burbidge. Within the Overlap, all of the surviving mainland taxa except *Agathis* occur on the MacPherson Ranges (on the border of Queensland and New South Wales). Here the *Nothofagus* forests (which are classed by Bauer (1957) as temperate rain forests) occur above about 3,000 ft., and Bauer's subtropical rain forests (which include *Araucaria*, Myrtaceae, Proteaceae, broad-leaved Lauraceae, etc.) are found below this level. In the Dave's Creek country of the MacPherson Ranges, which is described by Jones (1964), a number of different communities occur near subtropical rain forest and *Nothofagus* forest. These communities include mallee, heath and wet sclerophyll forest, in which taxa such as *Casuarina*, *Banksia*, *Eucalyptus* and members of the Epacridaceae, which are usually rare or absent from Australian rain forests, form an important part of the vegetation. The height of the Dave's Creek country is 2,800 ft. and the annual rainfall is about 60 inches, with a fairly even distribution throughout the year but with a late winter minimum and a summer maximum. However, the map produced by Coaldrake and Bryan (1957) shows that parts of the MacPherson Range receive more than 100 inches/annum. Mt. Tamborine (2,000 ft. and some 15 miles to the north), with an average daily mean temperature of 69°F, is the nearest place to the Dave's Creek area for which temperature records are available, but Jones considers that this area would have temperatures rather below those of Mt. Tamborine.

New Zealand lacks *Araucaria*, *Banksia*, *Casuarina* and the Cupaneae. None of the *Nothofagus* species produces *brassi* type pollen, and the pollen of the *Dacrydium* species is not of the *mawsonii* type. The flora of the area defined by Cockayne (1928) as the Thames District appears to be the one which, in New Zealand, shows the closest resemblance to the brown coal flora. This district is situated immediately to the north of lat. 38°S (the parallel which marks the southern limit of *Agathis*), and Cockayne states that the northern limits of *Nothofagus* forests (as opposed to trees which are isolated or in small groups) lie in the Thames District. All 12 of the brown coal taxa still represented in New Zealand occur in the area, and the *Nothofagus* forests include species which produce *fusca* type pollen as well as one characterized by *menziesii* pollen (CRANWELL, 1939). The district has examples of the four main New Zealand forest types (ROBBINS, 1962), each of which is commonly dominated by a brown coal taxon — by *Agathis*, by podocarps (principally *Dacrydium*), by *Nothofagus* or by dicots other than *Nothofagus* (often Lauraceae). Cockayne classes the bulk of these forests as rain forests, the *Nothofagus* forests being regarded as subantarctic rain forests and the remainder as subtropical rain forests, but Chapman (1958) disagrees with the use of the term 'subtropical' in this context.

Robbins notes that there are gradations between all the forest types which he recognizes, and it is impossible to select any one site in the Thames District as having a vegetation which corresponds most clearly with that of the brown coal. However, some idea of the altitude which may give conditions comparable with those of the brown coal period may be obtained by examining the distribution of the *Agathis* and *Nothofagus* forests in the area. Cockayne considers that *Agathis* forests are associations of the lowlands and lower hills, extending up to about 2,000 ft. but usually occurring below 1,500 ft., but Cranwell and Moore (1936) describe *Agathis* forests up to about 2,600 ft. in a part of the Thames District which is otherwise occupied mainly by *Dacrydium* forests. In general, the *Nothofagus* forests lie at higher altitudes than the *Agathis* forests, and Cranwell (1939) observes that the only New Zealand species of *Nothofagus* to produce *menziesii* type pollen never occurs below 2,500 ft. Cockayne notes *Nothofagus* forests at about 3,000 ft. in one part of the Thames District, but the genus may still form an important constituent of the forests at lower levels, as Mason & Preest (1953-54) record the occurrence of mixed *Agathis*-*Nothofagus* forests between about 800-1,800 ft. in another area, and state that *Nothofagus*, together with *Phyllocladus* and members of the Proteaceae, Myrtaceae and broad-leaved Lauraceae, is a subdominant in an *Agathis* forest which descends to sea-level in this part of the district. Altitudes of about 1,000-3,000 ft. appear to cover the part of the flora of the Thames District which most nearly resembles that of the brown coal.

Cockayne considers that the mountainous character of the Thames District leads to various local climatic differences, but a general idea of the temperatures can be gained from the map provided by Kidson (1950), this shows that almost all of the area lies between the 56-58°F annual isotherms. This data is reduced to sea-level, the correction being 2.74° per 1,000 ft. of altitude. Kidson also shows that most of the area receives an annual rainfall of 50-80 inches, with a small part exceeding 80 inches and another receiving less than 50 inches. The area has a summer minimum and winter maximum of rainfall, but the difference between the mean monthly temperatures is small.

Although it is clear that more facts about both fossil and living plants are required before any definite conclusions can be drawn about the nature and relationships of the brown coal flora and the conditions under which it grew, the points discussed above provide some information about these matters. The greatest number of brown coal taxa which exist together, or at least within reasonable proximity to one another, at the present day occur in localities where the environment permits the growth of both *Agathis* and *Nothofagus*. The modern vegetation which is most like that of the brown coal consists in some cases of a single forest type which includes a mixture of most of the brown coal taxa, but more often it is divided into two or more communities, a *Nothofagus* forest (usually the community at the highest altitude) and forests dominated by gymnosperms and/or dicots other than *Nothofagus*. This suggests that forests of the latter kind may have been responsible for the formation of the Yallourn brown coal (the alleged overwhelming preponderence of gymnosperm wood in the coal supports the idea of a gymnosperm-dominated forest), while *Nothofagus* forests may have occupied any high ground in the vicinity of the basin in which the coal was formed. The climate at the time when the coal was forming would be expected to match that of the boundary between the modern *Nothofagus* forests and the other forest types discussed — i.e., the climate prevailing at an altitude of the order of 4,000-7,000 ft. in New Guinea and at somewhat lower levels in the areas further to the south. These localities share a high rainfall, probably at least 60 inches/annum and in many cases much higher, and there is usually some seasonal variation in the rainfall. Mean annual temperatures are more difficult to obtain and show an appreciable variation between the different localities, but in general they appear to lie between about 55°-65°F. There is not a very great seasonal variation in temperature. These, then, are the climatic conditions under which the brown coal flora may have existed.

There appear to be a number of possible reasons for the absence of certain brown coal taxa in the areas discussed. Present day climates in the parts of New Zealand and Tasmania concerned are somewhat colder than those of the areas further to the north, and it may be that, in the south, only that part of the brown coal flora which had an appreciable tolerance to cold survived the cold periods of the Pleistocene and persisted in the present climate there. The absence of *Araucaria*, the Cupaneae, *Agathis* and the broad-leaved Lauraceae from Tasmania and of the first two taxa from New Zealand may be due to such a cause, as it is conceivable that the areas further to the north were less affected by the glacial periods and that comparable floras there had a greater opportunity of migrating to lower altitudes when cold conditions occurred. This is assuming that these taxa did in fact grow in these southern areas during the Tertiary period; this appears to be true in some cases (e.g., the Araucariaceae in Tasmania), but the past distribution of the other taxa is less well known. It is also clear that, in some cases, brown coal taxa are missing from present day floras in certain areas because they have never occurred there. Thus Couper (1960) has shown that *Dacrydium* with *mawsonii* type pollen and *Nothofagus* with *fusca* and *menziesii* pollen have never occurred in New Guinea. The absence of *Dacrydium* with *mawsonii* type pollen from the mainland of Australia (where it had a very wide distribution in the past) is more difficult to explain; its climatic tolerances may have been inadequate for survival in warm periods in the past, or present day environmental conditions may not provide an exact match for those of Yallourn when the coal was forming, or the climatic requirements of the fossil may in fact have differed from those of what is assumed to be its nearest living relative.

Couper has shown that some of the brown coal taxa are comparatively recent immigrants to New Guinea; *Phyllocladus* and *Podocarpus* section Dacrycarpus, for example, are not found in New Guinea Tertiary deposits. This indicates that, in some instances, at least part of the brown coal flora migrated into present day areas after the formation of the coal. There is also evidence to show that present day areas can be relics — i.e., that the brown coal flora contracted into these areas. In Australia, while the past distribution of the brown coal flora as a whole is not known, it is clear that some of the constituent taxa had a far wider distribution in the past than they do at present. This is illustrated below in Table 2, where distribution is shown in terms of the number of Australian states for which the taxa are recorded; the Northern Territory is omitted because of the lack of described fossil plants there.

TABLE 2 — PAST AND PRESENT DISTRIBUTION OF SOME TAXA INCLUDED IN THE BROWN COAL FLORA

Taxon	Tasmania	Western Australia	South Australia	Victoria	New South Wales	Queensland
Araucariaceae	●	●	●	●	● ○	● ○
Dacrydium	● ○	●	●	●	●	●
Phyllocladus	● ○		●	●	●	
Cupaneae	●	●	●	●	● ○	● ○
Nothofagus	● ○	●	●	● ○	● ○	● ○

○ — Occurs at the present day
● — Recorded from Tertiary deposits

CHANGES IN THE FLORA AS THE BROWN COAL FORMED

In the early part of this paper, it has tacitly been assumed that all of the 16 taxa discussed occurred together throughout the whole of the period of formation of the coal and that the climate remained uniform throughout this period. Recent pollen analytical work (Duigan unpub.) suggests that both these assumptions need some modification. The analysis in question is concerned with a bore through brown coal and lignitic clay from 42-713 ft., most of the samples being at intervals of 5 ft. Because interest has been focussed on the taxa already discussed, the pollen sum is retricted almost entirely to these taxa; the only other pollen included is that of undescribed gymnosperms and a few undescribed but readily recognizeable angiosperm pollen grains. Values for other unknown (i.e., undescribed) pollen grains were calculated separately; they usually make up only a relatively small proportion of the total pollen content of the coal. Spores were also calculated separately.

The most obvious feature of the pollen diagram is the dominance of *Nothofagus* pollen, the values for which are usually high and may reach more than 90%. However, there is a marked difference between the *Nothofagus* curves in the lower and upper parts of the diagram, the change corresponding with a depth of 307 ft. In the lower part, the values are almost invariably high, whereas there are a series of wide oscillations in the upper part. The rises in the values of other pollen types which correspond with the low points on the *Nothofagus* curve affect different taxa at different times, but the gymnosperms, Myrtaceae and *Casuarina* are the ones most directly concerned.

It is not easy to interpret these differences between the lower and upper parts of the diagram, but it appears that some feature of the habitat fluctuated during the second half of the coal-forming period. The local change most likely to alter the components of the forests would be a change in the drainage patterns, but the fact that the coal still formed in the latter part of the period suggests that no major change in drainage occurred, and a series of climatic fluctuations during the second half of the period seems a more probable explanation for the changes in the vegetation. This is assuming, of course, that the change shown in the present bore also occurs in other parts of the coal. Climatic fluctuations of the kind envisaged could lead to periodic reductions in the extent of the *Nothofagus* forests (or the *Nothofagus* constituents of other forests) or to their migration away from the area, and also to a change in other taxa or in the relative proportions of such taxa.

Within each of the major subdivisions of the coal, there is evidence of at least one change in the vegetation. In the lower part, there is a band of lignitic clay from 520 to 560 ft., and this corresponds with a number of changes in the diagram. Here the values for *Nothofagus aspera* Cookson, Myrtaceae, gymnosperms, monocots with large pollen grains, some unknown pollen grains and the spores are appreciably higher, and those for *Casuarina* lower, than they are in the remainder of the lower half of the diagram. In the upper half of the diagram there is a zone at the top (42-77 ft.) which is marked by fluctuating but generally high values for Restionaceae/Centrolepidaceae (to 25%). Apart from a single high value (40%) at 157 ft., pollen of this type is absent or very sparse from 77 to 200 ft. and is not recorded at all below 200 ft.

The significance of these changes in the vegetation cannot be determined, but the appearance and rise of the Restionaceae/Centrolepidaceae seems to mark the onset of conditions under which the formation of coal eventually became impossible. Because *Centrolepis* is recorded at very high altitudes in New Guinea, it is tempting to suggest that the advent of pollen of this type in the coal indicates increasingly cold conditions. However, there is practically no grass pollen in the coal, and hence no possibility of the development of grasslands of the New Guinea type there. Furthermore, Bakker (1957) states that the Restionaceae in New Guinea occurs in swamp forests and savanna forests, so that the appearance and rise of the Restionaceae/Centrolepidaceae could equally well be associated with increasing dryness.

At the level of identification at which the 16 brown coal taxa were discussed earlier in this paper, the only one which has a restricted vertical distribution is the Restionaceae/Centrolepidaceae. The pollen of other taxa, particularly that of certain gymnosperms, is absent sporadically, but there are no long sequences in depth where such pollen is absent. On the other hand, individual species of some of the angiosperm families discussed (e.g., the Myrtaceae and Proteaceae) are present only at certain levels. Lauraceous pollen has not been recognized and, as the leaves which were identified came from one level, nothing is known about the vertical distribution of members of this family.

Because there is no detailed information about the pollen production of the taxa concerned, not a great deal can be deduced about the abundance of the different plants and their distribution in the Yallourn area when the coal was forming. Although *Nothofagus* produces large quantities of pollen, the extraordinarily high values for this genus in the pollen diagram suggest *Nothofagus* forests rather than merely a *Nothofagus* component of forests dominated by other trees. The fact that at least seven species are known to be represented in the coal recalls the observation of several species growing together in the New Guinea forests and making up more than three quarters of the canopy. If these *Nothofagus* forests occured on high ground rather than in the coal basin itself, it is unlikely that this high ground was very far from the basin. It seems probable that members of the Proteaceae and Myrtaceae actually grew in the basin, as insect-pollination is believed to be the rule in these families and hence the pollen would not be expected to be carried over long distances. Values for the proteaceous pollen are low throughout the diagram, seldom reaching 5 per cent and never exceeding 10 per cent, but this does not necessarily mean that members of the Proteaceae were poorly represented in the forests. The values for Myrtaceae in the upper part of the diagram are generally high and are sometimes very high (to 84%); if an appreciable proportion of this pollen came from trees, then members of this family must have dominated the forests forming the coal on some occasions. In view of the belief that nearly all the wood in the coal is coniferous, and the fact that gymnosperms are wind-pollinated, the values for gymnosperm pollen in the diagram are, in general, surprisingly low. These values vary considerably, but there is one section of 200 ft. in the lower part of the coal in which the values are below 10 per cent on all but one occasion and barely exceed it then. This may be due to over-representation of *Nothofagus* pollen, but even in the upper part of the diagram, where the *Nothofagus* values are no longer consistently high, the values for gymnosperms exceed 50 per cent only once and 25 per cent four times.

To sum up, it appears that, at the level of identification at which the taxa have been discussed, these taxa showed no major changes until the last part of the period of coal formation, when the Restionaceae/Centrolepidaceae came in. However, other changes affected the relative proportions of the taxa, and suggest that climatic conditions during the second half of the period were less stable than those of the first half. The pollen diagram is consistent with the view that *Nothofagus* forests occurred on high ground around the basin in which the coal formed, that gymnosperms, Myrtaceae and Proteaceae were constituents of the forests of the basin and that members of the Myrtaceae may have dominated these forests at some stage during the formation of the coal.

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