

A comparison of Australian tropical rainforest and Tertiary fossil leaf-beds

D. C. CHRISTOPHEL and D. R. GREENWOOD

Botany Department, University of Adelaide, G.P.O. Box 498, Adelaide, S.A. 5001

Abstract

The fossil record is revealing the nature of Australian vegetation prior to the Miocene contact between Australia and Asia. There are divergent views on whether fossil leaf beds always give an accurate picture of past vegetation. Leaf litter from sites in modern Australian tropical rainforests, however, reflect the physiognomic character of the surrounding forest. Complex Mesophyll (CMVF), Complex Notophyll (CNVF), and Simple Notophyll Vine Forests (SNVF) have characteristic foliar physiognomic signatures. The physiognomic signature of stream bed deposits of SNVF leaf litter was within the range of variation observed for forest floor leaf litter from SNVF.

These results suggest that Tertiary fossil leaf-beds can be used in some instances to reconstruct past vegetation based on the physiognomic characteristics of the fossil leaves and the overall representation of taxa where modern affinities can be determined. The physiognomic character of the Eocene leaf assemblages from Anglesea in Victoria appears to match tropical montane and sub-tropical rainforest (Simple Notophyll Vine Forest) from Australia in both physiognomic character and the presence of some taxa.

The Anglesea flora has many elements in common with the modern wet tropical flora of northern Queensland. The Podocarpaceae is represented by at least six species from five modern genera at Anglesea (Dacrycarpus, Decussocarpus, Falcatifolium, Podocarpus and Prumnopitys), whereas only two genera are present in the modern wet tropical forests of Australia (Podocarpus and Prumnopitys).

Many angiosperm taxa characteristic of the modern Australian wet tropical forests are also found as significant components of the Anglesea fossil flora, including Gymnostoma (Casuarinaceae), Musgravinaeanthus and Orites (Proteaceae), Austrodiospyros (Ebenaceae), Brachychiton (Sterculiaceae) and Quintinia (Escalloniaceae). In the case of Gymnostoma, and species of the Musgraveinae, the modern taxa are restricted to a small region in northern Queensland. The close match to the Anglesea Orites species is also restricted to the same region.

At Noah Creek in N.E. Queensland, the streamside vegetation is dominated by the only extant Australian species of Gymnostoma and an undescribed species of Orites which is highly similar to the Anglesea fossil species. Podocarpus and Prumnopitys are also present.

These facts, along with the rarity of some of the plant associations found at Anglesea and Noah Creek (e.g., the Gymnostoma/Orites/Musgraveinae association) suggest that Noah Creek may provide as good a comparative model as possible for the Anglesea flora.

The demonstration of the correlation between rainforest type and physiognomic analyses of leaf litter from modern Australian rainforests, coupled with the evidence that similar types of plant associations can be noted from the modern forests and the Eocene floras, suggests that a more accurate interpretation than previously expected of Australian vegetation prior to the Miocene may be possible. The existing evidence predicts that forests very similar to those found in the modern wet tropics of Australia were present in southern Australia in the Eocene, prior to Australia's contact with Asia.

Introduction

The widespread acceptance of the plate tectonics theory of continental drift has promoted the idea that much of the Australian flora has either been inherited from the pan-Gondwanan flora, or is autochthonous, evolving from the more labile members of the ancient Gondwanan flora. There is, however, debate as to the extent to which the composition of Australia's tropical rainforests reflect immigration by northern taxa into Australia (mainly from the extensive rainforest flora of the Malesian region), or the persistence of Gondwanan taxa (Barlow 1981; Whiffin & Hyland 1986).

The post-Miocene northern invasive flora corresponds largely to the "Indo-Malayan" element espoused by Burbidge (1960) and her predecessors, and is based on the observation that for many taxa found in the tropical rainforests of Australia, a much higher diversity is present in Malesia, often with only a single species present in Australia (Martin 1982; Whiffin & Hyland 1986).

There are contradictory views however. Webb *et al.* (1986) suggest that the integrated nature of tropical rainforest, with its highly interdependent synusia, makes the idea of individual rainforest taxa colonizing the Australian tropics *en masse* implausible.

An ever-growing catalogue of early Tertiary pollen records of taxa with affinities to modern genera in the Australian tropical rainforests is demonstrating that some so-called Indo-Malayan or Malesian taxa were present in Australia well before the establishment of the link between Asia and Australia (Martin 1977, 1982). Similar finds of plant megafossils [*Parafatsia*, (Blackburn 1982) and *Austrodiospyros*, (Basinger & Christophel 1985)] have reinforced the expectation amongst some botanists that analysis of early Tertiary vegetation may now be able to provide insight into the origins of the Australian tropical rainforest flora.

Methods of Comparing Fossil and Modern Vegetation

There are two main methods used to reconstruct past vegetation. The more traditional approach has been to identify the modern affinities of most of the fossil taxa from a deposit and infer from the ecological preferences of the closest modern relatives the nature of the palaeoenvironment. This method has given contrasting interpretations of the early Tertiary vegetation of southern Australia, with palynologists initially predicting a

cool to warm temperate vegetation dominated by *Nothofagus* and Podocarpaceae (Kemp 1981), whereas the megafossil record suggests a vegetation of sub-tropical to tropical character (Christophel 1981). This is explained by the fact that fossil pollen often reflects the regional flora with prolific producers such as *Nothofagus* swamping the samples, whereas fossil leaf beds generally reflect the local flora (Martin 1982).

Numerous studies on modern plant communities have demonstrated a link between leaf form and size, or physiognomy, and the environment (Dolph 1978; Davis & Taylor 1980; Givnish 1984). In Australia, Webb (1959, 1968) classified Australian rainforest on physiognomic criteria, primarily leaf size and margin type, using canopy leaves. These studies have given rise to the idea that the physiognomic characteristics of fossil leaf beds may yield significant palaeoecological information (Dolph & Dilcher 1979). This constitutes the second main method of reconstructing past vegetation and is usually referred to as leaf or foliar physiognomic analysis.

Foliar Physiognomic Analysis of Fossil and Modern Tropical Rainforest Leaf Beds

Previous attempts to apply leaf physiognomic analysis to Tertiary floras assumed a direct correspondence between the physiognomic characteristics of the forest community and the leaves found in a fossil deposit (Dolph & Dilcher 1979; Christophel 1981). This assumption has been questioned on the grounds that most of the studies on modern forest communities have dealt with regional floras (Roth & Dilcher 1978) or have been based exclusively on canopy leaves (Martin 1982). The physiognomic analysis of three Eocene floras by Christophel (1981) was further questioned by Nix (1982) who suggested that as southern Australia lay in high southern latitudes in the Eocene, a tropical (megathermal) or subtropical (mesothermal) climate was not possible for Anglesea, Nerriga, or Maslin Bay.

In order to further refine the foliar analysis of Australian Tertiary floras, a study of the physiognomic characteristics of leaf litter from the types of tropical rainforest recognized by Webb (1968) was initiated. Leaf litter on the forest floor represents the leaves of all the members of the plant community in the immediate vicinity, and not just a single stratum (Ferguson 1985), whereas most foliar physiognomic studies are based on either herbarium specimens or field collections of living leaves. The leaves in leaf litter better reflect a

fossil leaf bed than herbarium collections, as recent studies (Ferguson 1985) have found that leaves do not travel in air much further than the height of the parent tree, and that larger leaves tend to be screened out by intervening vegetation, producing a different physiognomic character than the original forest (Drake & Burrows 1980).

A fossil leaf bed is usually formed in a stream or lake where water flow was reduced to allow settling of both the leaves and a layer of sediment. Several studies have suggested that where the point of leaf deposition is some distance from the source of the leaves, such as in a lake where the leaves have been brought in by a stream, the resultant leaf bed will be dominated by the lakeside and streamside flora with the smaller, more coriaceous canopy leaves distorting the physiognomic interpretation (Roth & Dilcher 1978; Drake & Burrows 1980). These changes are the net result of the preferential destruction of larger, more fragile leaves from the interior of the forest due to hydrodynamic forces in the stream, and the low input of leaves from the interior of the forest due to the screening effect of the streamside and lakeside vegetation (Ferguson 1985). These same studies have also found that these effects become more pronounced with increasing distance from shore, and hence source.

When leaves are deposited directly into a potential fossil deposit, such as by forest on a flood plain with numerous ox-bow lakes or ephemeral channels in a braided stream system, the resultant leaf bed will closely resemble the leaf litter from the same forest. The study on modern leaf litter from Australian tropical rainforest has found that each of the three forest types examined has leaf litter with a characteristic physiognomic signature. The implication is that where fossil leaf beds come from situations like that described above, it is possible to make a direct comparison between the forest types and the fossil vegetation.

Three rainforest types were examined ranging from the tropical lowland (Complex Mesophyll Vine Forest or CMVF), to the montane tropical rainforest (Simple Notophyll Vine Forest or SNVF), and the forest physiognomically intermediate between these two (Complex Notophyll Vine Forest or CNVF). Samples were taken from several localities in north-east Queensland in the region of Cairns and Atherton (Fig. 1), with each sample representing all of the litter scraped from a square metre of ground. Approximately 200 leaves from each sample were measured for length, width (as a fraction of length), and the

position of maximum width (as a fraction of length). The type of margin and the taxonomic identity of each leaf was also recorded but will not be considered here. A frequency histogram of leaf length for the three forest types indicates the clear partitioning of the leaf litter from different forest types (Fig. 2). The mean value for each character for each sample has been plotted on a box diagram (Fig. 3) to illustrate the characteristic physiognomic signature of the three forest types from the region studied.

The SNVF leaf litter was characterized by microphylls (< 75 mm length) with an average width of 30-40% of length (narrow elliptic), and were generally symmetric about the midpoint of the leaf. The CNVF leaf litter was composed of a mixture of microphylls and notophylls (75-125 mm length) with an average width of 40-45% of length and distinctly ovate (position of maximum

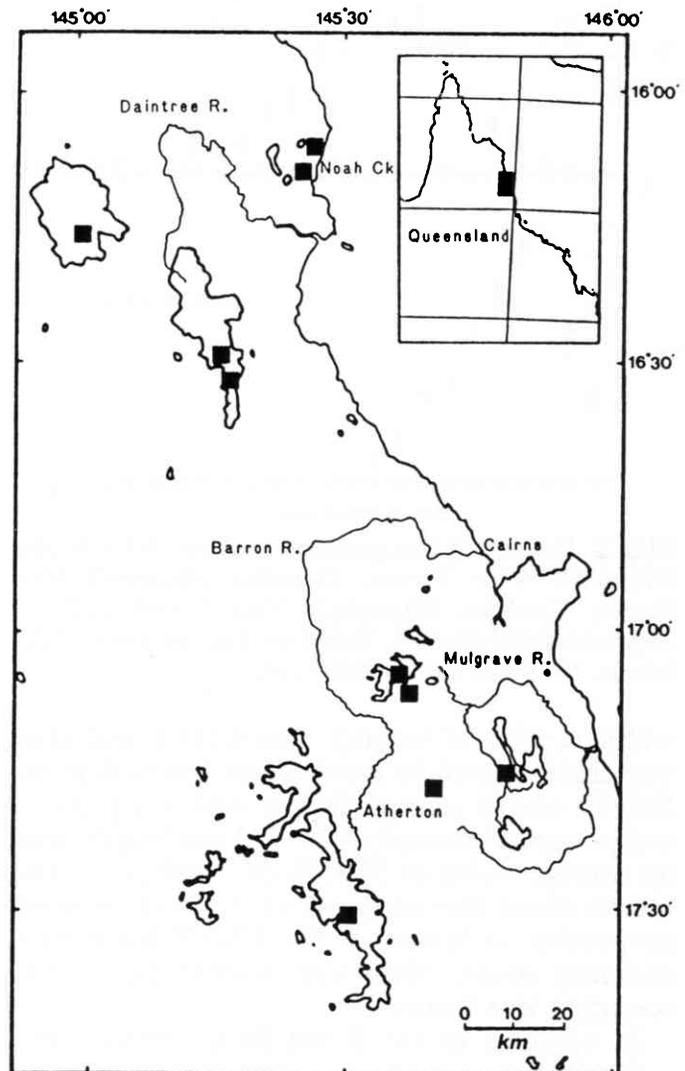


FIG. 1. Location of leaf litter collection sites (black squares). 1 000 metre contour indicated.

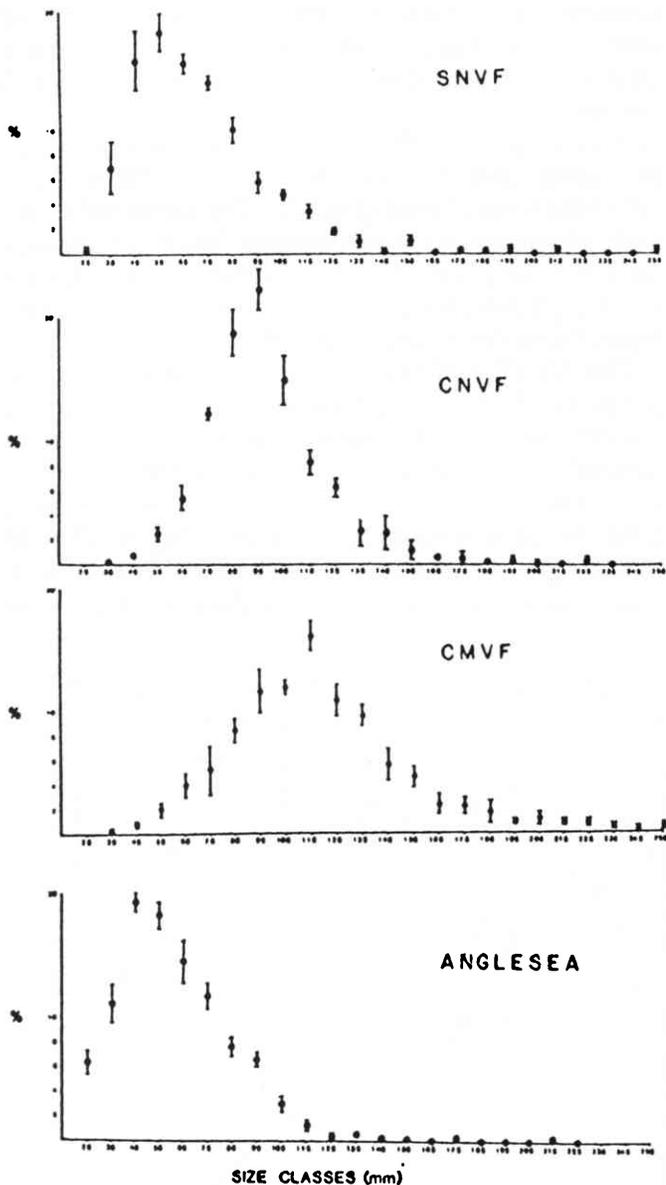


FIG. 2. Frequency histograms of leaf length for Simple Notophyll Vine Forest, Complex Notophyll Vine Forest, Complex Mesophyll Vine Forest and the Anglesea fossil deposit. Based on four samples of 224 leaves, Standard Errors indicated.

width < 35% of length). The CMVF leaf litter was characterized by much larger leaves than the SNVF, mainly notophylls but with a significant component of mesophylls (> 125 mm length) with an average width of 30-35% of length, and symmetric about the midpoint of the leaf. A small proportion of leaves in the CMVF litter were distinctly ovate, often with hastate bases, representing vine leaves.

In addition to the forest floor samples, two collections were made from two successive pools in a stream flowing through Simple Notophyll Vine Forest on the Windsor Tableland. The results suggest that these two samples have similar

physiognomic characteristics to leaf litter from the surrounding forest type. Based on this data, it is suggested that where leaves have been deposited with little transport after leaf fall, the physiognomic characteristics (the physiognomic signature) can be used to compare leaf populations from unknown forest type to leaf populations from known forest types. On this premise, collections of fossil leaves from two Eocene localities from southern Australia, Anglesea in Victoria, and a newly discovered deposit near Golden Grove in South Australia (Fig. 4a), were measured in the same manner as the leaf litter. These results are also plotted on the box diagram (Fig. 3).

The Anglesea samples were characterized by microphylls with an average width of 30-35% of length (narrow elliptic), and the position of maximum width was on average 40-45% of length, reflecting a small group of ovate leaves in some samples. This situation is to a lesser extent found in some SNVF litter samples. Overall, the

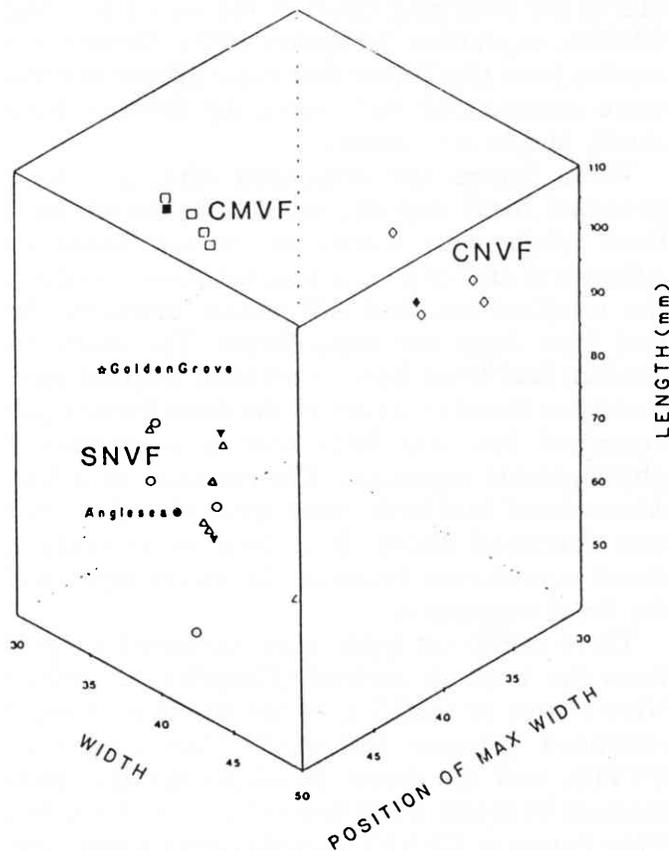
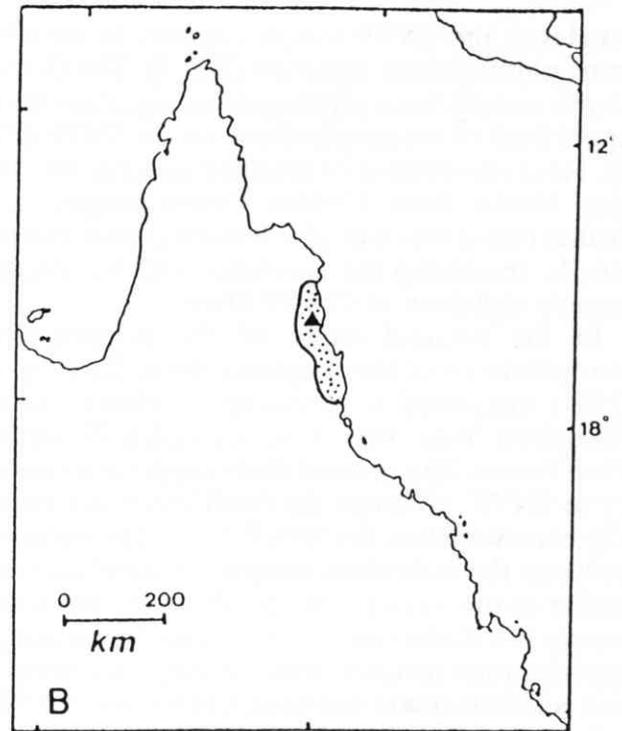
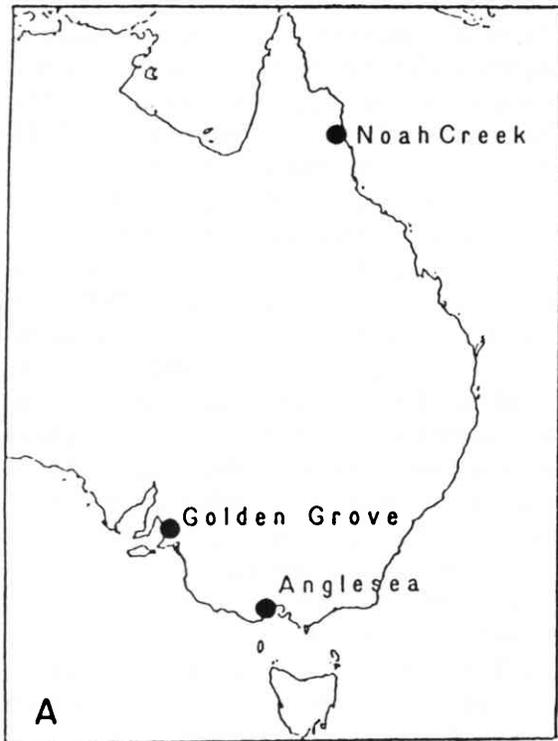
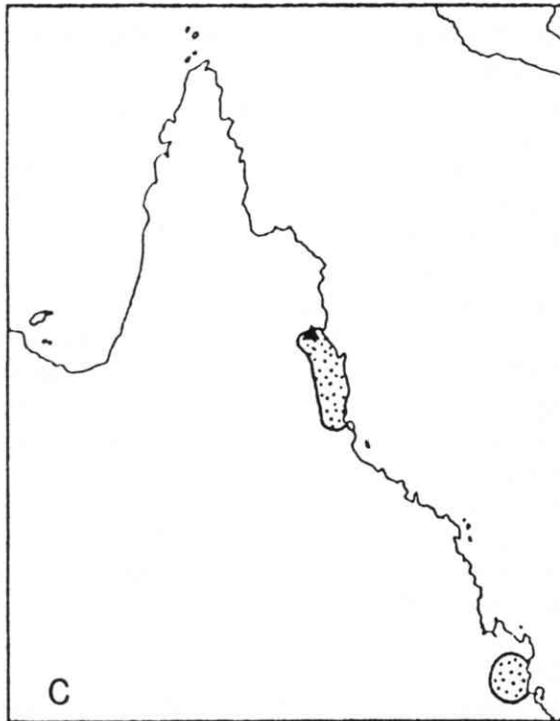


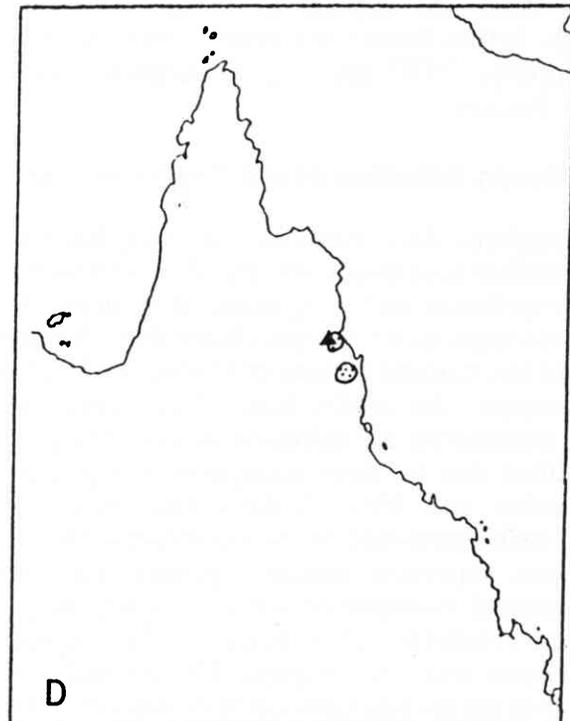
FIG. 3. 'Box Diagram' displaying the physiognomic signatures of SNVF (open Δ), CNVF (open \diamond), CMVF (open \square) the Anglesea flora (open \circ) and the Golden Grove flora (\blacktriangledown). The stream samples of SNVF are indicated by the inverted solid \blacktriangledown 's. Means of each are indicated by solid symbols.



▲ *Gymnostoma*
 :: *Musgraveinae*



▲ *Orites* sp. nov.
 :: *Bowenia*



▲ *Prumnopitys ladei*
 :: *Podocarpus smithii*

FIG. 4. Maps showing location of fossil localities, Noah Creek and distribution of selected taxa. (a) Fossil localities and Noah Creek. (b) Distribution of extant *Gymnostoma* and *Musgraveinae*. (c) Distribution of extant *Orites* sp. nov. and *Bowenia*. (d) Distribution of *Prumnopitys ladei* and *Podocarpus smithii*.

Anglesea and SNVF samples appear to have the same physiognomic signature (Fig. 3). The Golden Grove sample has a physiognomic signature at the upper limit of the length character for SNVF (Fig. 3). Field observation of oxidized material on fresh clay blocks from Golden Grove suggest that further collections may give a much greater average length, increasing the similarity with the physiognomic signature of CMVF litter.

In the original study of the physiognomic characteristics of the Anglesea flora, Christophel (1981) suggested a similarity to either Simple Notophyll Vine Forest or Complex Notophyll Vine Forest. The present study supports a similarity to SNVF, although the fossil leaves are generally narrower than the SNVF litter. The variation between the individual samples of fossil leaves is similar to that seen for the SNVF litter, which represents two distinct sites. The Golden Grove sample appears quite distinct from the Anglesea samples and is intermediate between CMVF and SNVF.

It is clear that some fossil samples are not close matches to the suggested analogous modern forest types; however, given the high southern latitude of Australia in the Eocene, some differences must be expected. What is apparent though, is that there were forests very like SNVF and perhaps CNVF growing in southern Australia in the Eocene.

Taxonomic Affinities of the Anglesea Flora

The Anglesea flora, while incompletely known, is nevertheless revealing a wealth of detail about the past vegetation and suggesting that many taxa now restricted to north-east Queensland formerly grew in the Eocene forests of southern Australia. For example, the conifer family Podocarpaceae is often considered an indicator of cool temperate conditions due to their conspicuous presence in Tasmanian and New Zealand rainforests. The megafossils attributed to the Podocarpaceae from Anglesea represent modern genera associated with tropical montane or less commonly, tropical lowland rainforest (*Dacrycarpus*, *Falcatifolium*, *Podocarpus* and *Prumnopitys*; Greenwood 1987). A total of six species have been described to date, including a species of *Podocarpus* which is closely related to *P. smithii*, a species of restricted occurrence in north-east Queensland which grows in Simple Notophyll Vine Forest. *Prumnopitys* in Australia is also restricted to the same area (Fig. 4b). The *Decussocarpus* species described has also been found at a new Eocene deposit at Golden Grove, South Australia.

Several angiosperm taxa described from Anglesea also have their closest extant relatives growing in the north Queensland rainforests. *Musgraveinanthus* (Christophel 1984) has affinities with the Musgraveinae (Proteaceae), all of which have a distribution restricted to north-eastern Queensland (Fig. 4b). Remains of *Gymnostoma* (Casuarinaceae) have also been described from Anglesea (Christophel 1980). Only one species of *Gymnostoma* occurs in Australia, and it is also restricted to this same region (Fig. 4b). A lobed Proteaceae leaf type is frequently encountered in some lenses of the Anglesea locality, and this fossil has been found to be most similar to an extant species of *Orites* from north-eastern Queensland which is as yet undescribed (Figs. 4c, 5d). This extant species has an auriculate, clasping leaf base which is also found in the fossil and is unique within the tribe.

Hill (1978) described two species of fossil *Bowenia*. One species from Anglesea has since been collected as a complete pinnule (Fig. 5a). The restricted distribution of extant *Bowenia* is shown in Fig. 4.

Using the positive identification of five of the taxa described above from Anglesea — *Podocarpus*, *Bowenia*, *Gymnostoma*, *Musgraveinanthus* and *Orites* — and considering the restricted distributions of their extant counterparts, a very small region remains within which to look for a modern analogue of the Anglesea vegetation. In so doing, however, it must be stressed that the basic realities of shifting continents, changing climates and natural selection over 40 million years guarantee that exact equivalent floras would not exist. Nonetheless, modern communities which demonstrate strong taxonomic and physiognomic similarities to the Anglesea fossil flora might well be helpful in further interpreting the as yet unknown elements of that and other fossil floras.

One such possible direct comparison for the Anglesea flora was found in an area of rainforest near Noah Creek (16°07'S, 145°26'E), a small river north of the Daintree River, draining Thornton Peak on the north-eastern coast of Queensland (Fig. 4a). This locality and its similarity to Anglesea have been described in detail by Christophel *et al.* (1987). It is worth noting, however, that at one point along Noah Creek the streamside vegetation is dominated by one of the rare populations of *Gymnostoma* in the region, and by the undescribed species of *Orites*. Several hundred metres downstream from this spot, the vegetation is a typical lowland tropical forest

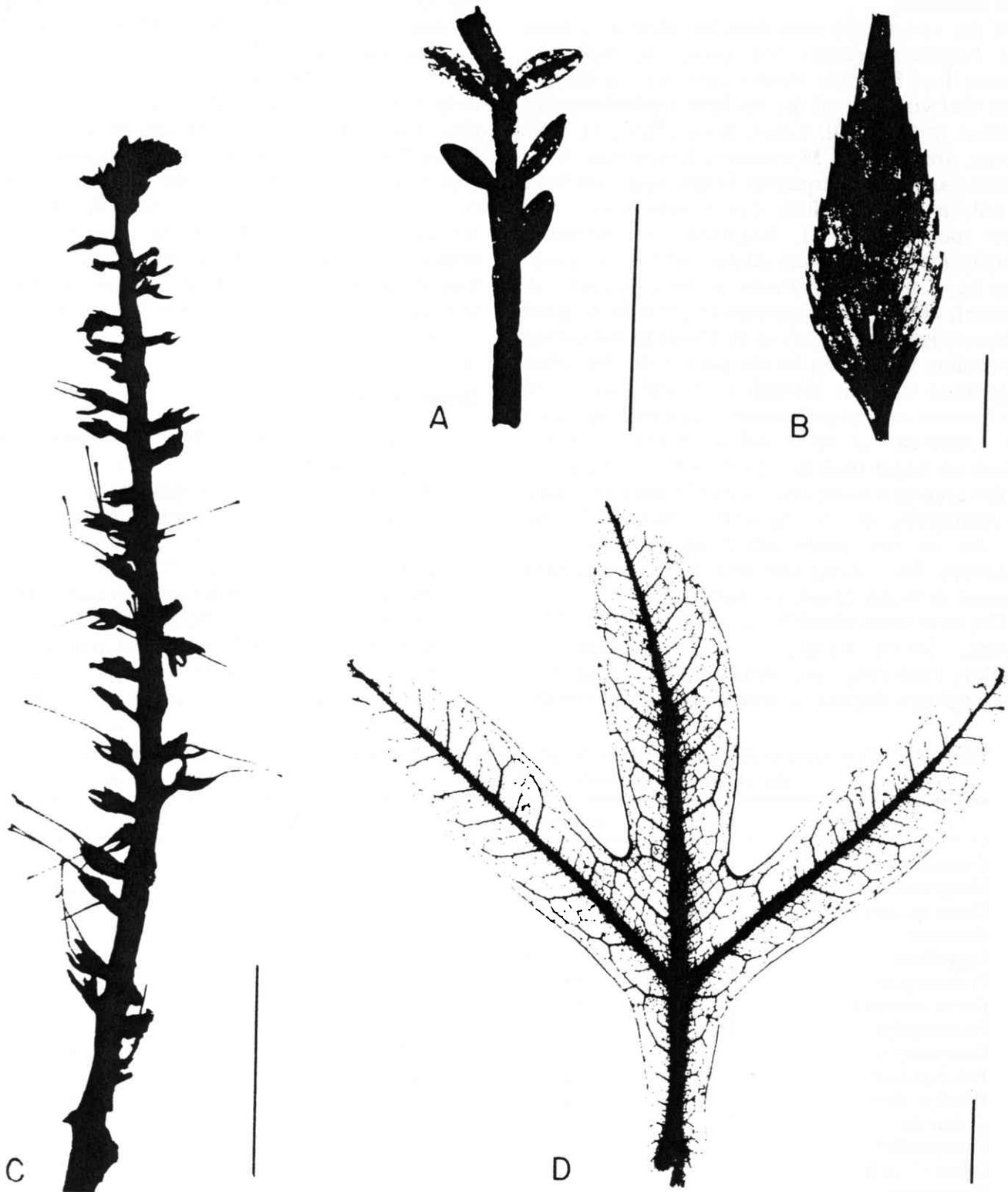


FIG. 5. Fossil and extant rainforest taxa. (a) Fossil *Decussocarpus* — Specimen GG124 from Golden Grove, South Australia. Scale bar = 1 cm. (b) *Bowenia eocenica* Hill 1978 from Anglesea, Victoria — Specimen A2249. Scale bar = 1 cm. (c) *Musgraveinanthus* — Specimen GG144 from Golden Grove, South Australia. Scale bar = 1 cm. (d) *Orites* sp — Juvenile leaf of undescribed species from Noah Creek, Queensland. Scale bar = 2 cm.

(CMVF) whose component taxa include two of the three described species of the Musgraveinae, and *Bowenia*.

If the rest of the taxa thus far identified from the Anglesea locality are compared with the known flora from the Noah Creek area, it may be seen that virtually all the modern equivalents are present in the Noah Creek flora (Table 1). The strong presence of Myrtaceae, Lauraceae, Proteaceae and Elaeocarpaceae in the Anglesea flora is reflected in the Noah Creek vegetation. The rarer occurrences at Anglesea of *Quintinia*, *Brachychiton*, *Lygodium* and possibly *Linospadix* also have their equivalents at Noah Creek. In general, Noah Creek appears to provide as good a comparison as is likely to be found in the extant Australian vegetation for the part of the Anglesea vegetation thus far identified. In addition, all of the floristic and physiognomic variation recorded for Anglesea can be found in an area at Noah Creek no larger than the fossil locality. The utility of the area as a comparative model may be tested by attempting to determine the affinities of some of the as yet unidentified elements of the Anglesea flora using the rest of the plant taxa present at Noah Creek as starting points.

The new mummified Eocene flora from Golden Grove, South Australia, was discovered in January 1986 (Fig. 4a). While slightly older than the Anglesea deposit, it contains a number of the

key taxa found at Anglesea, and hence provides a possibility of studying the evolution of some of the taxa over reasonably short periods of time. As may be seen from Table 1, *Musgraveinanthus*, *Banksiaephyllum*, *Podocarpus* and *Lygodium* are found in both Eocene deposits. It is particularly interesting to note that both *Musgraveinanthus* and *Banksiaephyllum* are present in both floras, but neither leaves of the Musgraveinae nor reproductive structures of the Banksineae have been recovered at either locality. As these two are sub-tribes of the Banksieae, it is not beyond possibility that we could be dealing with an Eocene plant which combined features of the two sub-tribes. The Golden Grove *Musgraveinanthus* is shown in Fig. 5c.

Discussion

Several points emerge from the physiognomic and taxonomic data presented above.

- (1) By presenting the physiognomic data collected from the leaf litter from different sites in northern Queensland graphically (Figs. 2, 3) it is evident that the differences in canopy physiognomy which allowed Webb (1959) to define his Complex Notophyll Vine Forest, Simple Notophyll Vine Forest and Complex Mesophyll Vine Forest are reflected in litter samples from those forest types. This litter

TABLE 1. Comparison of identified megafossil taxa from Anglesea, Victoria and Golden Grove, S.A. with the vegetation at Noah Creek, Qld. (Species nos. in parentheses).

Taxa	Anglesea	Golden Grove	Noah Creek
<i>Gymnostoma</i>	(1)	—	(1)
<i>Musgraveinanthus</i>	(1)	(1)	(3)
<i>Orites</i> sp. nov.	(1)	—	(1)
<i>Bowenia</i>	(2)	—	(1)
<i>Lygodium</i>	(1)	(1)	(1)
<i>Podocarpus</i>	(1)	(1)	(2)
<i>Decussocarpus</i>	(1)	(1)	—
<i>Prumnopitys</i>	(2)	—	(1)
<i>Dacrycarpus</i>	(1)	—	—
<i>Falcatifolium</i>	(1)	—	—
<i>Brachychiton</i>	(1)	(1)	(1)
<i>Quintinia</i>	(1)	—	(1)
<i>Linospadix?</i>	(1)	—	(2)
Other Cycads	(1)	—	(1)
Ebenaceae	(1)	(1)	(2)
Elaeocarpaceae	(1)	(2)	(2)
Myrtaceae	(2)	(2)	(7)
Other Proteaceae	(2)	(3+)	(5)
Lauraceae	(5+)	(3+)	(9)
<i>Banksiaephyllum</i>	(1)	(1)	?
TOTAL DIVERSITY	(80+)	(40+)	(110+)

data can then be compared directly with physiognomic data collected from fossil leaf deposits, which are interpreted as being litter from fossil vegetation. This was done with the result that strong physiognomic similarities were shown between three Eocene deposits from southern Australia and Webb's three forest types mentioned above. This then provided one piece of evidence for the hypothesis that the Eocene floras of southern Australia were most similar to the wet tropical vegetation of northern Australia.

- (2) Examination of the taxa thus far identified from the Eocene Anglesea Locality showed that their nearest living relatives in Australia are found in these same wet tropical forests. Not only are specific (and rare) taxa such as members of the Musgraveinae, *Podocarpus smithii*, *Bowenia* and *Gymnostoma* found there, but the general floristic composition when examined at the family level is similar. A preliminary examination of the Golden Grove Eocene Flora suggests similar comparisons.
- (3) By examining closely one locality in north-eastern Queensland (Noah Creek) where the rarer extant relatives of the Anglesea flora are found, it can be seen that both floristically and physiognomically all tested elements of the Anglesea flora can be accounted for within a small area similar in size to the fossil deposit. This demonstrates the viability of direct comparisons between the southern Australian Eocene Floras and the Wet Tropical Forests of northern Australia.

This paper began with the question of the origin of the Australian Tropical Rainforests. We believe that the fossil evidence shows clearly that the ancient relatives of a growing number of extant Australian rainforest taxa were to be found in the Eocene forests of southern Australia. Not only were these taxa present, but they were in similar associations, were in forests of similar general composition, and represented vegetations with similar physiognomic signatures to those of modern day northern Australia. Although some extant rainforest taxa (e.g., *Ficus*, *Saurauia*) as yet have no Australian fossil record and may possibly be Malesian in origin, the majority of northern Australian rainforest taxa, and perhaps their associations, appear to be autochthonous.

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