Early Tertiary Podocarpaceae: Megafossils from the Eocene Anglesea Locality, Victoria, Australia

D. R. Greenwood

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

Abstract

The nomenclature of some Tertiary fossil Podocarpaceae is reviewed. Fossil Podocarpaceae from the Eocene Anglesea locality in Victoria are described and assigned to six species from five modern genera using cuticular and other vegetative morphology. *Falcatifolium australis* D. R. Greenwood is the first record for this genus in Australia. *Dacrycarpus eocenica* D. R. Greenwood, *Podocarpus platyphyllum* D. R. Greenwood and *Prumnopitys lanceolata* D. R. Greenwood are new species. *Decussocarpus brownei* (Selling) D. R. Greenwood and *Prumnopitys* aff. *Pr. tasmanica* (Townrow) D. R. Greenwood have previously been recorded as megafossils from the Australian Tertiary. The diversity of Podocarpaceae recorded from Anglesea is far greater than in any modern Australian forests.

Introduction

The modern Australian flora has a lower diversity of Podocarpaceae than New Guinea, New Caledonia or New Zealand and with the exception of the alpine shrub vegetation of Tasmania the Podocarpaceae are not conspicuous in the modern vegetation of Australia. Podocarpaceae megafossils, however, are common in Australian Tertiary deposits (e.g. Cookson and Pike 1953; Florin 1963; Townrow 1965; Blackburn 1981; Hill and Macphail 1983).

The modern genera of Podocarpaceae can be defined by their vegetative morphology (de Laubenfels 1969, 1972, 1978, 1985; Quinn 1982) which allows confident comparison of Tertiary Podocarpaceae to modern species. In many cases fossil vegetative material can be placed into modern genera (sens. de Laubenfels 1969) and in some cases sections of genera (e.g. Blackburn 1981). Many of the Podocarpaceae megafossils from Australian Tertiary deposits assigned to *Podocarpus* s.l. can be referred to de Laubenfels' genera based on the systematic treatment they were given in their original or subsequent treatments (see Appendix 1). Other fossil species have not been identified to sectional level; however, some of these can be assessed by their morphology and will be discussed at a later date.

The Eocene megafossil locality in the Alcoa open-cut coal mine at Anglesea, Victoria (38°25'S., 144°11'E.; Fig. 1) is a rich source of information on Eocene vegetation (Christophel 1981, 1984). This paper reports on fossil Podocarpaceae from this locality, including the first Australian record of *Falcatifolium*. The diversity of Podocarpaceae at Anglesea in the Eocene is higher than in any modern Australian vegetation type, and includes genera now absent from the Australian flora, i.e. *Dacrycarpus*, *Decussocarpus* and *Falcatifolium*, and genera of restricted distribution, i.e. *Prumnopitys* which, within Australia, is restricted to montane rainforest in NE. Queensland.

In the course of identifying the Anglesea Podocarpaceae the cuticular morphology of modern Podocarpaceae was surveyed. The segregate genera of de Laubenfels were most fully covered in the survey as gross features of vegetative anatomy of the fossils suggested affinity with these taxa. Detailed accounts of the vegetative morphology which define the modern genera of Podocarpaceae were given by de Laubenfels (1969, 1978, 1985) and Quinn (1982). An example of each of the segregate genera is illustrated (Figs 2–5 and 7).
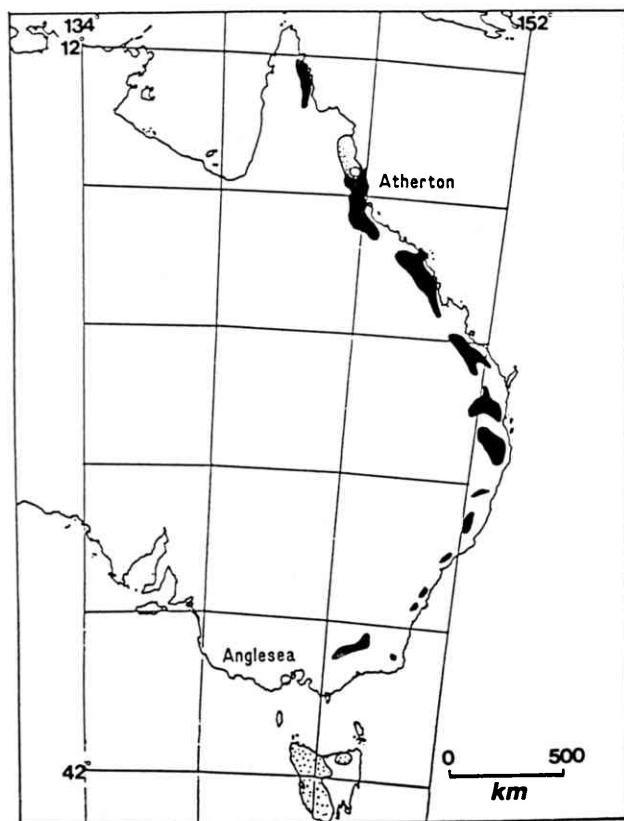
Fig. 1. The distribution of modern Podocarpaceae in Australia (excluding *Podocarpus drouynianus* in Western Australia). Black areas indicate only *Podocarpus* s. str. In the stippled area near Atherton, *Prumnopitys* (2 spp.) is also present and four other genera in addition to *Podocarpus* s. str. are in Tasmania. The Alcoa Anglesea fossil locality is also indicated.

Cuticular morphology has often been used in the classification of the modern Podocarpaceae. The orientation of paratetracytic or, rarely, amphicyclic stomata parallel to the long axis of the leaf is considered diagnostic of the family, although not exclusive to it (Florin 1931; Dilcher 1969; Blackburn 1981). Florin (1931) and Buchholz and Gray (1948) considered stomatal distribution diagnostic in some taxa in the Podocarpaceae. De Laubenfels (1985) also used stomatal features to separate his two subgenera of *Podocarpus*. The characteristic cuticular morphology of some genera will be discussed here as will the range of variation in these and other cuticular characters used in taxonomic treatments of the Podocarpaceae.

Locality

Blocks of leaf-bearing clay and mudstone from the overburden of the Alcoa Anglesea open-cut coal mine in Victoria (38°25′S., 144°11′E.;   Fig. 1) were collected from the south face of the new workings (site II) at Anglesea in 1983 from two laterally extensive

lenses in the mudstones and unconsolidated sands unconformably overlying the brown coal of the Eastern View Formation (Christophel *et al.* 1987). The two lenses, *c.* 70 m below the ground surface, consist of fine mudstone and clay rich in mummified leaves and probably represent deposition in cut-off branches of a meandering river system (Christophel *et al.* 1986). The smaller of the two lenses is a lateral extension of the lens from which *Musgraveinanthus alcoensis* Christophel was reported (Christophel 1984).

These sediments represent the Anglesea member of the Demon Bluff Formation (Abele *et al.* 1976) and, in a personal communication quoted by Christophel (1984), Partridge placed the lenses in the upper subzonule of Stover and Partridge's (1973) lower *Nothofagidites aspersus* Zone, middle to late Eocene. Some of the fossil species described here were also found in the old workings where *Austrodiospyros* flowers and leaves were reported (Basinger and Christophel 1985).
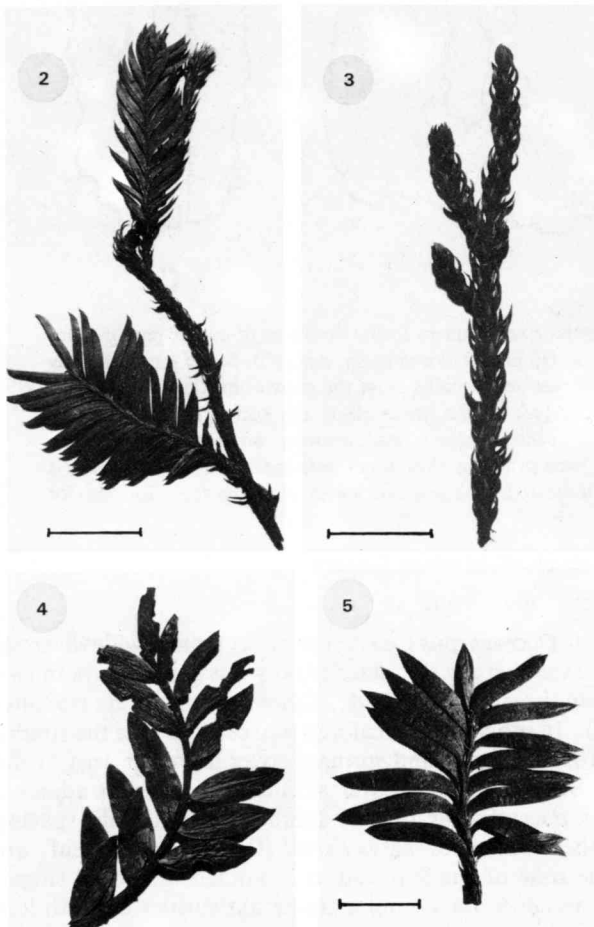
Fig. 2. Twig from *Dacrycarpus imbricatus* var. *robustus* Laubenf. showing dimorphic foliage. Scale: 1 cm.
Fig. 3. Uniform foliage of *D. compactus*. Scale: 1 cm.
**Fig. 4.** Twig from *Decussocarpus rospigliosii*.
Fig. 5. Twig from *Falcatifolium papuanum*. Scale: 1 cm (also applies to Fig. 4).

Materials and Methods

The fossil material was extracted from the clays by disaggregation of the inorganic matrix in a 3% w/v soln of hydrogen peroxide (H_2O_2). Some material was further cleaned in 40% hydrofluoric acid (HF). Slices of representative leaves of several specimens of each taxon were treated in heated H_2O_2 of *c.* 30% w/v. The clean cuticle sheaths were stained with crystal violet and mounted in phenol glycerine jelly for microscopic examination. Pollen was extracted from fossil cones by heating in 30% w/v H_2O_2.

The concentrated supernatant was left unstained and mounted in glycerine jelly. All of the type material is housed in the State Herbarium of South Australia.

Voucher samples of vegetative material of modern species from both herbarium and field-collected specimens were used in the survey of cuticular features. Leaf slices from these specimens were heated in a wet Schulze's solution and the clean cuticle sheath stained in crystal violet and mounted in phenol glycerine jelly on glass microscope slides for light microscopy. The species used for a direct comparison with the fossil species in this study are listed in Appendix 2.

A   **B**   **C**
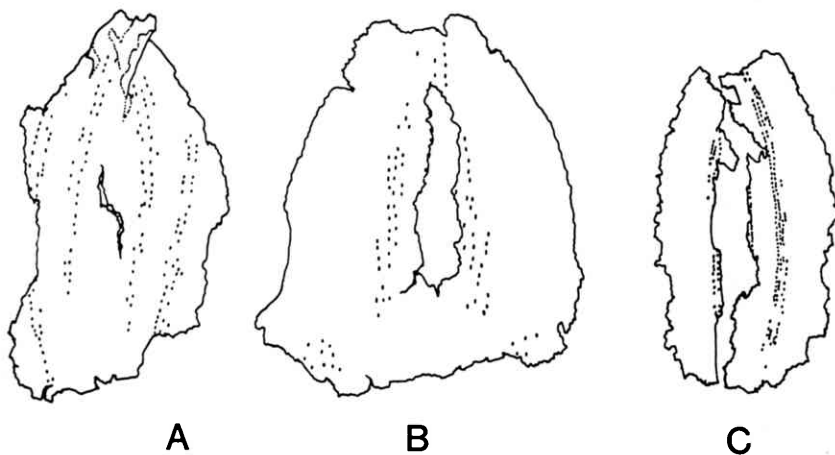
Fig. 6. Stomatal distribution in *Dacrycarpus*. Camera lucida drawings of cuticle preparations of *D. dacrydioides (A)*, *D. compactus (B)* and *D. eocenica* sp. nov. *(C)*. Scale: 1 mm. During preparation the keeled leaves of *Dacrycarpus* usually cause the cuticle sheaths to split along the midline of the abaxial (lower) surface of the leaves along the keel. Consequently, the adaxial (upper) surface appears as the centre region of each drawing, and the abaxial surface as the outer edge on both sides of each drawing. Prominent dots indicate stomata. There is no stippling but folded cuticle is indicated. The apex of leaves is to the top. See text for explanation.

Vegetative and Cuticular Morphology of Modern Genera

Dacrycarpus (Endl.) de Laubenfels. (Figs 2 and 3)

There are nine modern species of *Dacrycarpus* (see Appendix 2) from a wide diversity of moist habitats. The cuticle of *Dacrycarpus* characteristically has the stomata in two narrow irregular bands, two (rarely three) stomata wide, either side of a wide stomate-free zone over the midvein (Fig. 6). In other needle-leaf and narrow-leaf taxa the stomatal bands are much wider than in *Dacrycarpus* and stomata cover a greater area of the leaf. The stomata in *Dacrycarpus* usually share polar subsidiary cells with adjacent stomata and are elongated in *D. dacrydioides* (Rich.) Laubenf., with wide spacing between stomata; by contrast, the stomata of *D. viellardii* (Parlatore) Laubenf. are packed close together towards the base of the leaf and are rounded in overall shape. *Dacrycarpus dacrydioides* and *D. viellardii* have similar stomatal densities on both leaf surfaces, whereas *D. compactus* (Wasscher) Laubenf. has only two small patches of stomata at the base of one surface (Fig. 6).

Decussocarpus de Laubenfels. (Fig. 4)

There are nine species and three sections in *Decussocarpus* (de Laubenfels 1969). The stomata occur in wide bands in long regular uniseriate rows on both surfaces with usually a stomate-free zone over the midvein of both surfaces, although this zone may be absent and the rows less regular on the upper surface of some species. The anticlinal

walls of epidermal cells in section *Dammaroides* of *Decussocarpus* are strongly buttressed whereas those of the other two sections are usually smooth or only slightly irregular as found in *Podocarpus* and *Dacrycarpus*. In *Decussocarpus* the lateral subsidiary cells are often obscure. The modern species of *Decussocarpus* are uniformly amphistomatic, although the pattern of distribution and density of stomata vary slightly between surfaces in some species, e.g. *D. vitiensis* (Seeman) Laubenf.

Falcatifolium de Laubenfels. (Fig. 5)

Falcatifolium was segregated from *Dacrydium* s.l. by de Laubenfels (1969) on the basis of the 'strikingly different foliage morphology' of the taxon. There are five species. *Falcatifolium* is also separable on the basis of cuticular morphology (Florin 1931; as 'group C' of *Dacrydium*). The stomata of the Podocarpaceae are generally fairly uniform, although *Dacrydium* (sens. de Laubenfels, 1969) and *Falcatifolium* present a characteristic circular arrangement that is better described as amphicyclic than paratetracytic. This occurs because the polar subsidiary cells do not project beyond the outer border of the lateral subsidiary cells. The lateral subsidiary cells are often bisected. The majority of stomata on the leaves of some species of *Falcatifolium* may not be of this form, although amphicyclic stomata are present. The modern species of *Falcatifolium* are amphistomatic; however, some species have fewer stomata on the upper surface (*F. papuanum* Laubenf.) whereas others are isofacial (*F. falciforme* (Parlatore) Laubenf.).
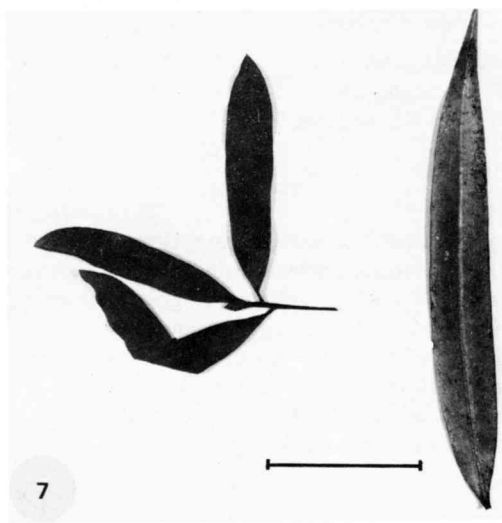

Fig. 7. Dimorphism in leaf size between adult (*left*) and juvenile (*right*) *Podocarpus smithii*. Scale: 5 cm.

Podocarpus L'Hérit. ex Pers. (Fig. 7)

De Laubenfels divided *Podocarpus* into two subgena with 95 species across 18 sections. *Podocarpus* is considered hypostomatic (Florin 1931; Buchholz and Gray 1948; Quinn 1982); however, many species have rare scattered stomata on the so-called non-stomatiferous surface and *P. elongatus* (Aiton) L'Hérit. ex Pers. often has many short rows of stomata on the upper surface (Florin 1931; de Laubenfels 1985). The stomata are in two wide bands in regular to irregular rows either side of a (usually) wide stomate-free zone over the midvein. The small-leafed species have much narrower stomatal bands, although not as narrow as found in *Dacrycarpus*, and the stomata are closely packed in very regular rows. Subgenus *Podocarpus* of *Podocarpus* is distinguished from subgenus *Foliolatus* by the association of 'Florin rings' with the stomata (de Laubenfels 1985).

Prumnopitys Phillipi

There are 10 species and 2 sections in *Prumnopitys* (de Laubenfels 1978). The cuticle of *Prumnopitys* is characterised by strongly sinuous or sculptured anticlinal walls of the epidermal cells (not so in *P. ladei* (Bailey) Laubenf.). Half the modern species of *Prumnopitys* are hypostomatic [e.g. *P. amara* (Blume) Laubenf., and *P. taxifolia* (Solander ex D. Don)]; one, *P. ferruginea* (D. Don) Laubenf., is variable (Townrow 1965), and the remainder are amphistomatic (e.g. *P. ferruginoides* (Compton) Laubenf., *P. ladei*). A prominent Florin ring is a feature of the stomata of the hypostomatic species of *Prumnopitys*, but it is poorly developed in the amphistomatic species.

Comparison of the Genera

In *Dacrycarpus*, *Decussocarpus* and *Prumnopitys* the lateral subsidiary cells abut and surround the base of the polar subsidiary cells whereas in *Podocarpus* the lateral subsidiary cells usually touch only at the apices of the respective cells. The stomata of *Falcatifolium* may be of the form seen in *Decussocarpus*, although the polar subsidiary cells never project to the same extent and the stomata are more typically amphicyclic. The anticlinal walls of the epidermal cells of most *Prumnopitys* are strongly sinuous whereas those of some species of *Decussocarpus* and *Podocarpus* may be buttressed or beaded but are never sinuous. The walls of *Dacrycarpus* and *Falcatifolium* are smooth.

Taxonomic Description of Fossil Species from Anglesea

Order Coniferales
Family Podocarpaceae
Dacrycarpus (Endl.) de Laubenfels 1969

Dacrycarpus eocenica D. R. Greenwood, sp. nov.

Figs 6*C*, 8, 9, 14, 15

Diagnosis. Foliage dimorphic; distichous leaves bilateral, falcate, decurrent, loosely imbricate leaves strongly keeled, hypostomatic, stomata paratetracytic, in orderly rows, non-stomatal cells rectangular, length : width (L : W) of cells never greater than 1 : 3.

Type material and locality. *Holotype*: 2351 and 2350 (upper and lower parts of fragmented whole twig, Figs 8 and 9). Clay lens 70 m below ground level in the Demons Bluff Formation, 25 m above coal surface, south face of the new workings (1983) of the Alcoa Anglesea open-cut (Eastern View Coal measures) Victoria, Australia.

Etymology. The specific epithet refers to the age of the deposit.

Description

Architectural features. Foliage dimorphic, early leaves distichous (Fig. 8), bilateral, sessile, base falcate, leaf blade upward-pointing, 6–8 mm long, 1–1·2 mm wide, tip acuminate to mucronate, transition to later foliage abrupt, ultimate leaves loosely imbricate awl-shaped needles (Fig. 9), strongly keeled by midvein, pungent.

Epidermal features. Early leaves hypostomatic with the stomata restricted to two narrow bands either side of the midvein (Fig. 6*C*), stomate-free area 15–18 cells wide, stomata in ordered uniseriate rows, some rows discontinuous or merging with others, rows typically separated by 2–3 epidermal cells; stomata absent near leaf margin, sparse at leaf base becoming more frequent towards leaf tip (Fig. 14). Stomata paratetracytic (Fig. 15), rarely appearing amphicyclic; polar subsidiary cells typically shared between adjacent stomata of row, square to rectangular with smooth anticlinal walls, lateral subsidiary cells crescentic with a thicker band of cuticle adjacent to the guard cell, stomatal apparatus appearing circular. Epidermal cells adjacent to the stomata square

to rectangular. Cuticle over polar subsidiary thicker than over adjacent cells. Stomatal pore rectangular, orientation parallel to long axis of the leaf, 13 μm $\times$ 5 μm, lateral subsidiary cells 28 μm $\times$ 15 μm, polar subsidiary cells 10–13 μm $\times$ 15–18 μm. Epidermal cells in non-stomatiferous areas long rectangular, 13–18 μm $\times$ 40–60 μm, with smooth anticlinal walls; epidermal cells on margin convergent, becoming oblique.
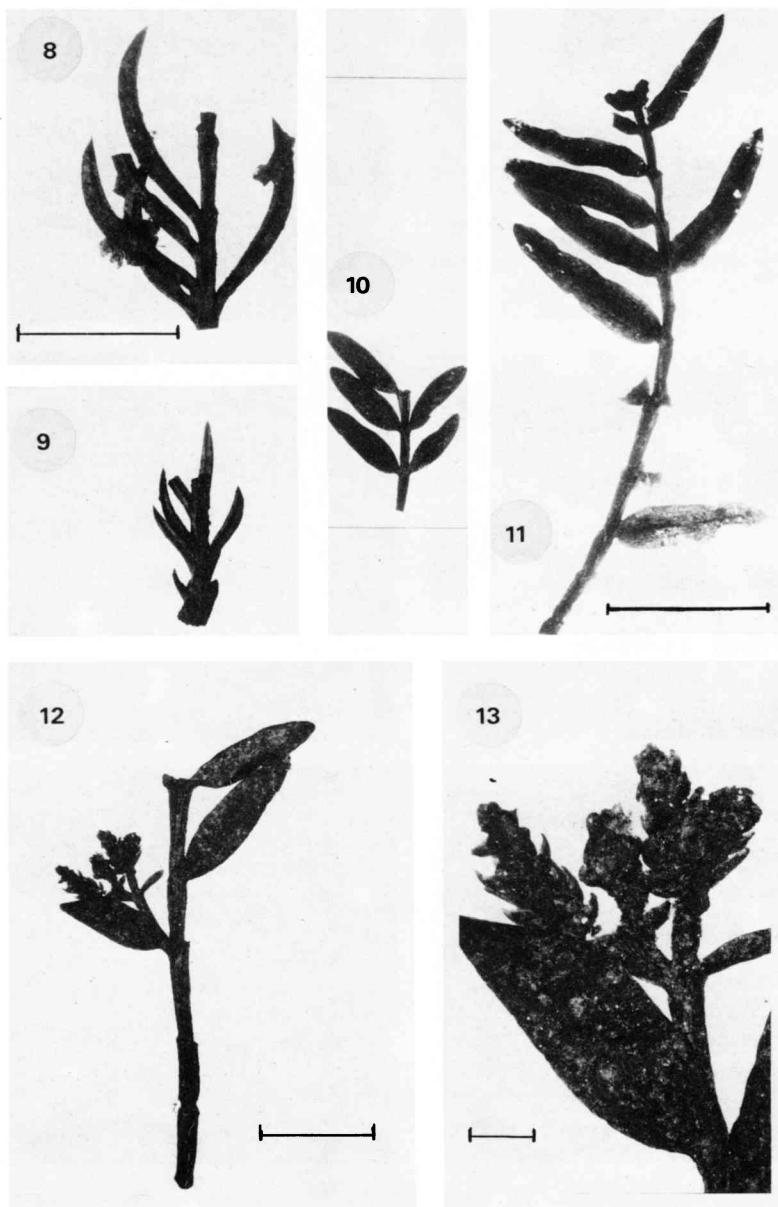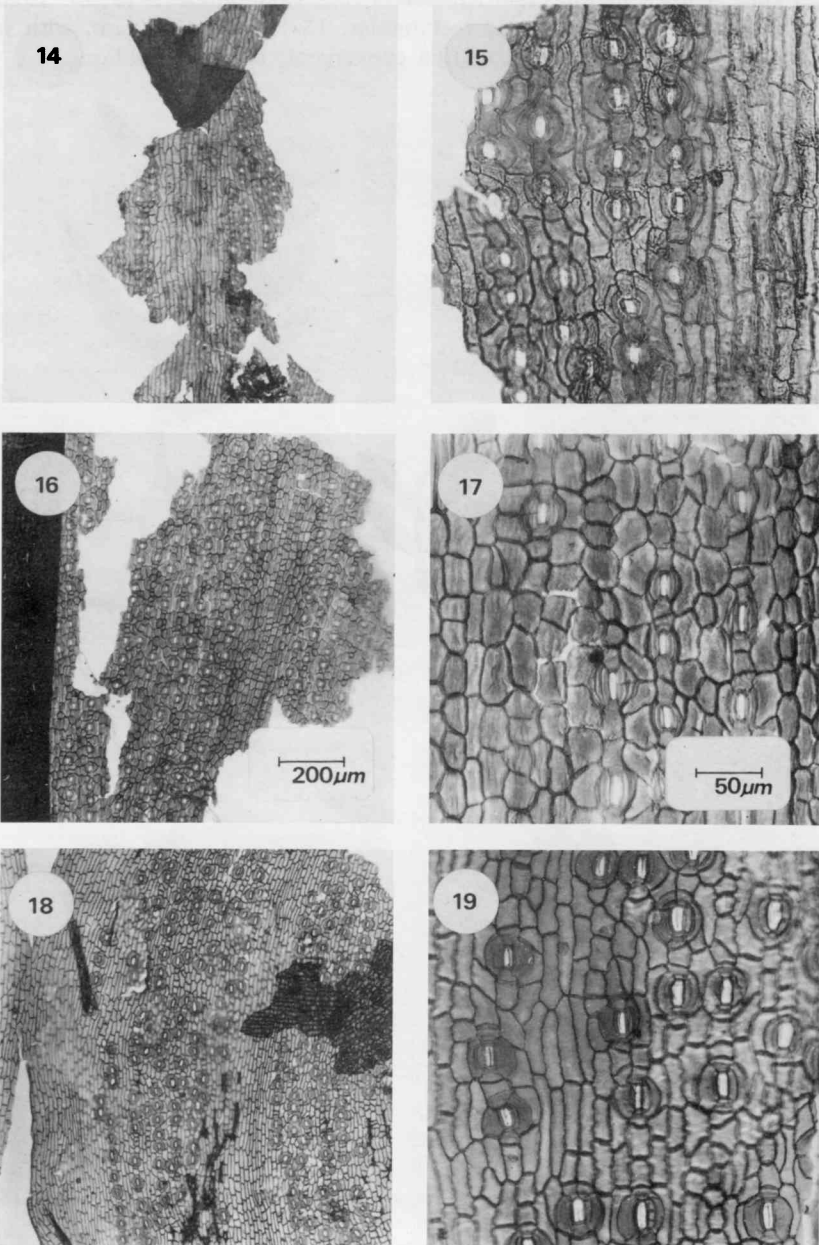

Figs 8 and 9. Upper and lower portions of *Dacrycarpus eocenica* sp. nov., holotype 2351 and 2350. Scale 1 cm.
Figs 10 and 11. Paratypes of *Decussocarpus brownei* (Selling) Laubenf. emend. Greenwood, 2353 and 2346. Scale: 1 cm.
Fig. 12. Paratype of *D. brownei*, 2345, with pollen cones. Scale: 1 cm.
Fig. 13. Detail of pollen cones from 2345. Scale: 2 mm.

Figs 14 and 15. Cuticle of *Dacrycarpus eocenica* sp. nov. showing a stomatal field (Fig. 14) and detail of the stomata (Fig. 15).
Figs 16 and 17. Cuticle of *Decussocarpus brownei* showing a stomatal field (Fig. 16), and detail of the stomata (Fig. 17). Scale in Fig. 16 applies to Figs 14, 16 and 18. Scale in Fig. 17 applies to Figs 15, 17 and 19.
Figs 18 and 19. Cuticle of *Falcatifolium australis* sp. nov. showing stomatal field (Fig. 18) and detail of the stomata (Fig. 19).

Decussocarpus section *Decussocarpus* de Laubenfels 1969

Decussocarpus brownei (Selling) D. R. Greenwood, diagnos. emend.

Podocarpus brownei O. H. Selling 1950

Figs 10–13, 16, 17

Emended Diagnosis. Leaves bilateral, narrowly ovate to broadly lanceolate, 5·7–11·0 mm long, 1·5–2·5 mm wide, subpetiolate to sessile, decurrent, unequally amphistomatic, stomata paratetracytic, lateral subsidiary cells poorly defined from other cells, polar subsidiary cells square, anticlinal walls of cells smooth.

Type material and locality. Paratypes: 2345 (Fig. 12, cone-bearing shoot, cuticle preparation and pollen extracted from the cones all bear the same number), 2346, 2352, and 2353 (leafy shoots, Figs 10 and 11). Clay lens 70 m below ground level in the Demons Bluff Formation, 25 m above coal surface, south face of the new workings (1983) of the Alcoa Anglesea open-cut (Eastern View coal measures), Victoria, Australia.

Description

Architectural features. Leaves narrowly ovate to broadly lanceolate (Fig. 10), straight, 5·7–12·0 (9·7, $n = 14$) mm long, 1·5–3·4 (2·0, $n = 14$) mm wide at the broadest point, length : width 3·7–7·3 (4·9, $n = 7$). Leaves borne in pairs, opposite decussate with leaves twisted at the base into a distichous arrangement with opposite surfaces uppermost on either side of the stem. Leaf margin entire, apex narrowly rounded to acute, base decurrent subpetiolate to sessile. Midvein not discernible on holotype (Figs 12 and 13), single central trace present in paratypes. Microsporangiate cones borne on a small branching axillary shoot in pairs subtended by a pair of small lanceolate bracts, 1·4–1·7 mm long and 0·4 mm wide. The arrangement of the cones suggests a fifth, terminal cone may have been present.

Epidermal features. Leaf unequally amphistomatic, stomata singly in poorly to well defined discontinuous rows (Fig. 16), rarely solitary, rows typically separated by 1–4 epidermal cells, reducing to 1–2 cells at leaf tip, rows indeterminate towards leaf base. Stomata absent over midvein of both surfaces, midvein 14–16 cells wide on morphologically lower surface (stomatiferous surface). Stomata paratetracytic (Fig. 17), lateral subsidiary cells narrow rectangular to irregular oblong, poorly differentiated from adjacent epidermal cells, 23–31 μm long with smooth anticlinal walls, polar subsidiary cells square, rarely isodiametric, indistinct from other epidermal cells, 13–18 μm across. Stomatal pore rectangular with thicker cuticle on outer ledge, oriented parallel to long axis of leaf, 13–20 μm $\times$ 5 μm. Cuticle of uneven thickness (uneven staining), more so on stomatiferous surface. Cuticle of even thickness over guard cells. Non-stomatal cells isodiametric to irregular or wedge-shaped near stomata, becoming more rectangular over midvein, more typically rectangular on morphological upper surface (i.e. surface with lower density of stomata), anticlinal walls smooth. Upper surface with fewer stomata in discontinuous rows with some stomate-free areas, rows separated by 4–12 epidermal cells.

Pollen grains. Pollen free, anisopolar, bisaccate, bilateral. Body of grain subcircular in polar view, total breadth 27–43 (34·0, $n = 6$) μm, breadth of body 18–23 (20·7) μm, depth of body 17–23 (20·0) μm, breadth of sacci 12–18 (14·7) μm, depth of sacci 17–26 (20·6) μm, breadth of sulcus (polar view) 3–6 (5·0) μm. The grains may have been immature as they were essentially featureless.
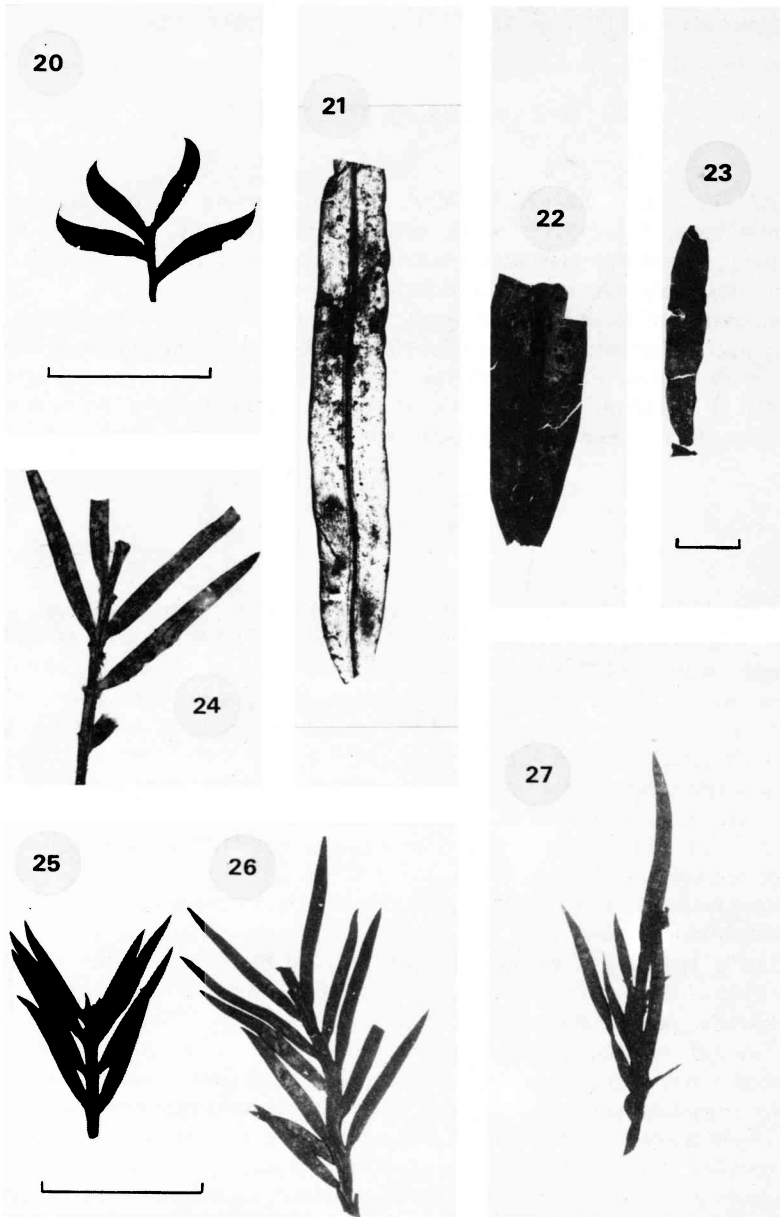
Fig. 20. Holotype of *Falcatifolium australis* sp. nov., 2349. Scale: 1 cm.

Fig. 21. Holotype of *Podocarpus platyphyllum* sp. nov., 1816.

Figs 22 and 23. Paratypes of *P. platyphyllum* sp. nov., 2362 and 2363. Scale: 1 cm (also applies to Figs 21–23).

Fig. 24. *Prumnopitys* aff. *P. tasmanica* (Townrow) Laubenf., 2347.

Figs 25 and 26. Paratype (Fig. 25) and holotype (Fig. 26) of *Prumnopitys lanceolata* sp. nov., 2357 and 2356.

Fig. 27. *Prumnopitys* aff. *P. tasmanica*, 2348. Scale: 1 cm (also applies to Figs 24–27).

Falcatifolium de Laubenfels 1969

Falcatifolium australis D. R. Greenwood, sp. nov.

Figs 18–20

Diagnosis. Leaves bilateral, falcate with a raised midrib, leaf apices mucronate, base curving away from stem, sessile, imperfectly hypostomatic, stomata with a ring of 4–5 subsidiary cells, stomatal rows discontinuous, anticlinal walls of epidermal cells smooth.

Type material and locality. Holotype: 2349 (leafy shoot and cuticle preparation, Figs 18–20). *Paratypes*: 2360, 2361 (leafy shoots). Clay lens 70 m below ground level in the Demons Bluff Formation, 25 m above coal surface, south face of the new workings (1983) of the Alcoa Anglesea open-cut brown coal mine (Eastern View coal measures), Victoria, Australia.

Etymology. The specific epithet refers to the fossil being the most southerly example described from the genus.

Description

Architectural features. Leaves bilaterally flattened, spreading distichously, falcate, leaf apex mucronate, base curving away from stem, sessile, decurrent (Fig. 20), single midvein prominent, leaves 6–12 mm long, 1–2 mm wide at the broadest point, length : width of leaves 4–7, stem 0·4 mm wide.

Epidermal features. Leaf imperfectly hypostomatic with rare scattered stomata on upper surface, stomata on stomatiferous surface in two distinct regions on both sides of the midvein in uniseriate rows (Fig. 18), rows discontinuous and becoming indiscernible towards the leaf tip. Epidermal cells over midvein rectangular, becoming much more long than wide towards the centre, anticlinal walls smooth to moderately irregular, cuticle generally of even thickness, cells 6–13 μm wide, 31–60 μm long. Stomatal rows separated by 2–4 epidermal cells, stomata paratetracytic more rarely amphicyclic (Fig. 19), lateral subsidiary cells reniform to crescentic, occasionally with one cell bisected, cells 28–40 μm long with smooth anticlinal walls, polar subsidiary cells square, rarely becoming more wedge-shaped, smaller than epidermal cells, 12–14 μm across, not projecting beyond lateral subsidiary cells, producing a ring effect around the stomatal pore, cuticle thicker over guard cells. Non-stomatal cells amongst stomata isodiametric to irregular, more rarely rectangular, 8–13 μm wide, 13–26 μm long with square end walls; where longer than broad, anticlinal walls smooth. Stomatal pore rectangular to narrowly barrel-shaped with thickened outer ledge, 13–16 μm long, oriented parallel to the long axis of the leaf. Epidermal cells of upper surface square in rows or more commonly rectangular in rows parallel to the long axis of the leaf, cells much longer over the midvein and near the leaf margin.

Podocarpus L'Hérit. ex Pers. subgenus *Podocarpus* de Laubenfels 1969

Podocarpus platyphyllum D. R. Greenwood, sp. nov.

Figs 21–23, 28, 29

Diagnosis. Leaves hypostomatic, bilateral, uninerved, entire-margined, not appearing to taper, dimorphic; large leaves 7–9·5 ($n = 2$) cm long, 1·2–1·4 cm wide, narrowly oblong, base cuneate, apex mucronate, other leaves 4–5 cm long, 1·2–1·4 cm wide, apex not seen. Anticlinal walls of epidermal cells slightly beaded, more so on smaller leaves.

Type material and locality. Holotype: 1816 (single incomplete leaf with matching cuticle preparation, Figs 21, 28 and 29). *Paratypes*: 2354, 2362, 2363 and 2364 (single leaves, Figs 22 and 23). Clay lens 70 m below ground surface in the Demons Bluff Formation, 25 m above coal surface, south face of the new workings (1983) of the Alcoa Anglesea open-cut brown coal mine (Eastern View coal measures), Victoria, Australia.

Etymology. The specific epithet refers to the broad lamina of the leaves.

Description

Architectural features. Leaves narrowly oblong (Fig. 21), bilateral, arrangement on stem unknown, base cuneate, tip rounded, lamina not tapering, prominent single midvein, margin entire, leaf typically 8–9·5 cm long but some specimens 4–5 cm in length, 1·2–1·4 cm wide, upper and lower surfaces distinct.

Epidermal features. Leaf hypostomatic, stomata in uniseriate rows parallel to long axis of leaf (Fig. 28), rarely with two stomata parallel in the same row, some rows discontinuous more rarely as islands between other rows, typically separated by 9 epidermal cells, up to 36 where stomatal rows become discontinuous, stomata absent near margin. Stomata paratetracytic (Fig. 29), lateral subsidiary cells crescentic to reniform, 26 μm long with smooth anticlinal walls; polar subsidiary cells square to rectangular, rarely wedge-shaped, 8–14 μm across, often projecting beyond the boundary of the lateral cells. Stomatal pore rectangular, parallel to long axis of leaf, 13–16 μm long, Florin ring present, cuticle thin around guard cells. Non-stomatal cells associated with rows less regular in shape and smaller than interrow epidermal cells, often isodiametric, distorting to accommodate the stomata, 13–16 μm wide, 26–32 μm long. Inter-row epidermal cells rectangular, parallel to stomatal rows, 8–15 μm wide, 30–50 μm long with square end walls, anticlinal walls straight and slightly beaded to smooth. Non-stomatal surface homogeneous, epidermal cells square to rectangular, rarely wedge-shaped, aligned parallel to long axis of leaf, 8–15 μm wide, 20–40 μm long with square end walls, anticlinal walls slightly beaded to smooth, cuticle of uniform thickness. Epidermal cells on leaf margin square, anticlinal walls thicker than on other cells.

Prumnopitys Phillipi (de Laubenfels 1978) section *Prumnopitys* de Laubenfels 1978

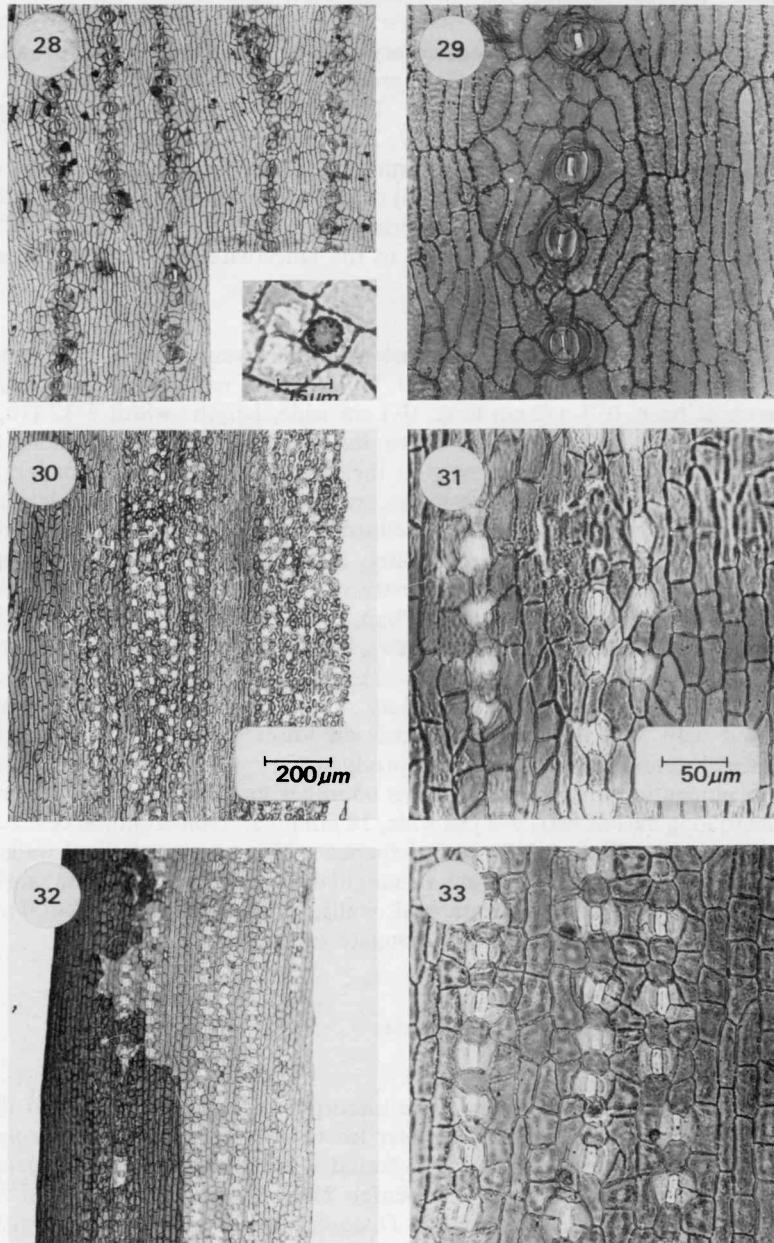**Prumnopitys** aff. ***P. tasmanica*** (Townrow) Greenwood

Figs 24, 27, 30, 31

Material and locality. Specimens 2347 and 2348 (leafy shoots and cuticle preparation, Figs 24, 27, 30, 31). Clay lens from the Demons Bluff Formation, south face of the new workings (1983) of the Alcoa Anglesea open-cut (Eastern View coal measures) Victoria, Australia. The lens is *c.* 25 m above the coal surface.

Description

Architectural features. Leaves narrowly lanceolate to linear (Fig. 24), arranged spirally on the stem, becoming more distichous on some specimens through a twist of the leaf base (Fig. 27), leaves becoming broader towards the base but attenuating prior to insertion into the stem, decurrent, gradually more rarely abruptly narrowing to a point at the leaf tip. Midvein not visible on specimens examined, leaves 0·7–1·5 cm long, 0·1 cm wide, length : width 7–15 (10·8, $n = 5$), stem 0·1 cm wide.

Epidermal features. Leaf amphistomatic, stomata on lower surface restricted to two narrow parallel bands either side of a stomate-free area over the midvein, 7–14 cells wide (Fig. 30). Stomata solitary in indistinct rows, rows rarely interrupted, separated by 2–3 epidermal cells, outer rows discontinuing before leaf tip. Upper surface with stomata more or less scattered though in poorly defined lines with little or no decrease in frequency over midvein. Stomata weakly paratetracytic, although most seem to lack distinct subsidiary cells (Fig. 31). Stomatal pore rectangular, parallel to long axis of leaf, 18–26 μm long, 5–8 μm wide. Non-stomatal cells isodiametric to rarely rectangular, 18–23 μm wide, 26–50 μm long with smooth to barely beaded anticlinal walls. Epidermal cells in stomate-free areas more often rectangular, becoming square on the leaf margin, stomata totally restricted to mid-region of both leaf surfaces.

Figs 28 and 29. Cuticle of *Podocarpus platyphyllum* sp. nov. showing stomatal field and fungal structure (inset) (Fig. 28) and detail of stomata (Fig. 29).
Figs 30 and 31. Cuticle of *Prumnopitys* aff. *P. tasmanica* (Townrow) Laubenf. showing stomatal field (Fig. 30) and detail of stomata (Fig. 31).
Figs 32 and 33. Cuticle of *Prumnopitys lanceolata* sp. nov. showing stomatal field (Fig. 32) and detail of stomata (Fig. 33).

Prumnopitys lanceolata D. R. Greenwood, sp. nov.

Figs 25, 26, 32, 33

Diagnosis. Leaves bilateral, narrowly lanceolate, base slightly narrowed, attached spirally but twisted in a distichous manner. Leaves 0·7–1·2 cm long, 0·1 cm wide, unequally amphistomatic, lateral subsidiary cells much longer than broad, clearly defined, polar subsidiary cells typically shared.

Type material and locality. *Holotype*: 2355 (leafy shoot and cuticle preparation, Figs 26, 32 and 33). *Paratypes*: 2356, 2357, 2358 and 2359 (leafy shoots, Fig. 25). Clay lens 70 m below ground surface in the Demons Bluff Formation, 25 m above coal surface, south face of the new workings (1983) of the Alcoa Anglesea open-cut brown coal mine (Eastern View coal measures), Victoria, Australia.

Etymology. The specific epithet refers to the lanceolate form of the leaves.

Description

Architectural features. Leaves spirally attached, decurrent, most leaves twisted at the base into a distichous arrangement (Figs 25 and 26), narrowly lanceolate, slightly inflated towards base, 0·7–1·2 cm long, 0·1 cm wide, length : width 7–12 (10, $n = 10$), single midvein, base attenuating prior to insertion of leaf, tip acuminate. Stem 0·1–0·2 cm wide, smaller leaves present at the base of some branches of larger twigs.

Epidermal features. Leaf amphistomatic, stomata on lower surface restricted to two bands either side of the midvein in well defined uniseriate rows (Fig. 32), stomate-free area over midvein, 5–10 cells wide, rows rarely interrupted, separated by 1–3 epidermal cells, typically 4 rows in each band, stomata on upper surface in less ordered rows, becoming scattered, more widely spaced than on lower surface, typically only 2 rows in each band, stomate-free area over midvein, 14–20 cells wide. Stomata paratetracytic (Fig. 33), polar subsidiary cells wedge-shaped to square, becoming rectangular on upper surface and projecting beyond the boundary of the lateral subsidiary cells and commonly shared with adjacent stomata in row on lower surface, not shared on upper surface; lateral subsidiary cells inflated, producing a butterfly appearance, becoming narrower by elongation of stomatal complex on upper surface. Stomatal pore rectangular, parallel to long axis of leaf, 5–8 μm wide, 18 μm long. Non-stomatal cells associated with stomatal rows isodiametric to wedge-shaped with smooth anticlinal walls, epidermal cells in stomate-free areas generally rectangular, becoming greatly elongate in centre of midvein with square or oblique end walls, 13–20 μm wide, 29–100 μm long. Epidermal cells on leaf margin greatly elongate rectangular.

Relationships of the Anglesea Fossil Species

Dacrycarpus eocenica

Dacrycarpus eocenica sp. nov. has the dimorphic foliage with flattened distichous early growth and spreading awl-shaped later leaves characteristic of *Dacrycarpus* (Figs 2, 3, 6, 8, 9). Foliage dimorphism is also found in some other modern genera but the distichous foliage type is absent (de Laubenfels 1969; Quinn 1982). In gross vegetative morphology *D. eocenica* closely resembles *D. compactus* of New Guinea (Fig. 3), which also has loosely imbricate ultimate leaves; however, this modern species is unusual in that the adult foliage is not dimorphic and the distichous foliage phase is absent. In all the specimens of *D. eocenica* seen, the transition from the early distichous phase to the imbricate phase was observed, as found in the other modern species.

Dacrycarpus eocenica is hypostomatic whereas the modern species are considered amphistomatic (Florin 1931; Townrow 1965). However, given the much reduced presence of stomata on the lower surface of *D. compactus* (Fig. 6), it is plausible that

stomatal distribution may have exhibited more plasticity within the genus in the past. This is in contrast to Florin's view that amphistomatic leaves were in part characteristic of *Dacrycarpus* (Florin 1931). Buchholz and Gray (1948) also used this feature to define their section *Dacrycarpus*.

Other features of the cuticle of *D. eocenica* are, however, well within the range of variation of the modern species and match those seen in both *D. compactus* and *D. viellardii* where the stomatal rows are more regular and the stomata closer together than in *D. dacrydioides* or *D. imbricatus*. The stomata of *D. eocenica* (Fig. 15), *D. viellardii* and *D. compactus* are circular, in contrast to the elongate stomata of *D. dacrydioides*. The 'early Tertiary' species *D. setiger* (Townrow) Greenwood, also has these features but differs from *D. eocenica* by possessing bristles on the leaf margin, more inflated lateral subsidiary cells and stomata on both leaf surfaces. The Tertiary species *D. praecupressinus* (Ett.) Greenwood has a vegetative morphology closer to *D. dacrydioides* (Cookson and Pike 1953), with very few stomata in very narrow bands with very elongate polar subsidiary cells, and is unlikely to have been closely related to *D. eocenica*.

Table 1. Comparison of modern and fossil (F) species of section *Decussocarpus*

e, Estimates only based on the range

Taxon	Leaf length (mm)	Leaf width (mm)	L : W	Source
D. comptonii	0·6–1·5	0·25–0·4	2·4–3·8e	de Laubenfels (1969)
D. minor	0·7–2·0	0·25–0·5	2·8–4·0e	de Laubenfels (1969)
D. rospigliosii	1·1–1·4	0·3–0·5	2·6–4·3	Specimens
D. vitiensis	1·5–5·0	0·3–0·5	5·0–10·0e	de Laubenfels (1969)
D. araucoensis (F)	0·6–1·1	0·2–0·3	3·0–3·7e	Florin (1940)
D. brownei (F)	0·57–1·1	0·15–0·25	3·7–7·3	Specimens and Selling (1950)
D. maslinensis (F)	1·7–3·3	0·25–0·5	4·4–8·6	Blackburn (1981)

Decussocarpus brownei (Selling) Greenwood

Selling, in the original description of *Decussocarpus brownei*, did not discuss its relationship with other species, either fossil or modern, due to the lack of epidermal detail (Selling 1950). *Decussocarpus* section *Decussocarpus*, to which *D. brownei* belongs, has four modern species (see Appendix 2) and two other Tertiary megafossil species, *D. maslinensis* Blackburn from South Australia (Eocene, Blackburn 1981) and *D. araucoensis* (Berry) Greenwood from Chile (Eocene, Florin 1940). A third fossil species, *Podocarpus goedei* Townrow, from the early Tertiary (Townrow 1965) may also be related to *D. brownei*.

Townrow considered *P. goedei* to be related to members of section *Decussocarpus* (as section *Polypodiopsis*, Buchholz and Gray 1948) but considered that section *Decussocarpus* had evolved from plants with similar morphology to *P. goedei*. *Decussocarpus brownei* has broader leaves than *P. goedei* and an unequally amphistomatic cuticle whereas *P. goedei* has an isofacial cuticle. *Podocarpus goedei* also lacks the distichous leaf arrangement characteristic of *D. brownei* (Fig. 10) and the other members of section *Decussocarpus*. However, the overall appearance of the cuticle of *P. goedei* is similar to *D. brownei*. The poorly defined subsidiary cells, well defined very regular stomatal rows and the opposite decussate leaf arrangement of both species are characteristic of the three modern sections of *Decussocarpus*, and perhaps *P. goedei* should be considered a member of a now extinct section of *Decussocarpus*.

The two Eocene species, *D. araucoensis* and *D. maslinensis*, have very similar vegetative morphologies to *D. brownei* (Selling 1950; Blackburn 1981), although the leaves of *D. maslinensis* are much larger than those of *D. brownei* or *D. araucoensis* (Table 1). All three species can be separated by cuticular features. *Decussocarpus araucoensis* has an isofacial cuticle, in contrast to *D. brownei* and *D. maslinensis*. The last species is characterised by a strongly developed beading or buttressing of the anticlinal walls of epidermal cells (Blackburn 1981). According to Florin (1931) and my observations, this feature also characterises modern members of section *Dammaroides* of *Decussocarpus*, and is not seen in either *D. araucoensis* or *D. brownei*. Section *Dammaroides* is distinguished from the other extant sections of *Decussocarpus* by the presence of multiple veins in the leaves (de Laubenfels 1969).

The vegetative morphology of *Decussocarpus brownei* (Fig. 10) most closely resembles two modern species, *D. rospigliosii* (Pilger) Laubenf. (Fig. 4) and *D. vitiensis* (Seemann) Laubenf.; however, the latter species generally has much larger leaves than either *D. brownei* or *D. rospigliosii* (Table 1). The cuticle of *D. vitiensis* is very similar to that of *D. brownei*, both exhibiting differences in stomatal distribution and frequency between the two leaf surfaces, whereas *D. rospigliosii* is perfectly amphistomatic and isofacial. *Decussocarpus brownei* is intermediate between *D. rospigliosii* and *D. vitiensis*, bearing similarities and differences to both, and these species together with *D. araucoensis* form a closely related group. The arrangement of the microsporangiate cones in the Anglesea specimens of *D. brownei* supports this view.

One of the Anglesea specimens of *D. brownei* has cones on a short axillary shoot (Figs 12 and 13). In *D. vitiensis* microsporangiate cones are typically borne terminally on normal leafy shoots and are solitary. *Decussocarpus rospigliosii* may have a terminal cone borne on a short axillary shoot with 2–3 lateral sessile cones (Florin 1940; de Laubenfels 1969), as found in the Anglesea specimen of *D. brownei*. This condition is also found in *D. minor* (Carrière) Laubenfels.

Table 2. Comparison of modern and fossil (F) species of *Falcatifolium*

Taxon	Leaf length (mm)	Leaf width (mm)	Source
F. angustum	*c.* 7·0	1·2	de Laubenfels (1969)
F. falciforme	2·0–6·5	0·5–0·7	de Laubenfels (1969) and specimens
F. papuanum	1·1–1·7	0·2–0·35	de Laubenfels (1969) and specimens
F. taxoides	1·5–2·0	1·5	de Laubenfels (1969, 1972) and specimens
F. australis (F)	0·6–1·2	0·1–0·2	Specimens

Falcatifolium australis

The distichous bilaterally flattened falcate leaves of *F. australis* (Fig. 20) place it in *Falcatifolium*, as bilaterally flattened leaves do not occur in *Dacrydium* (de Laubenfels 1969). According to de Laubenfels, the five modern species of *Falcatifolium* can be separated on leaf form. The survey of the cuticles of three of the modern species (see Appendix 2) found that this also was an effective means of separating species. The leaf form of *F. australis* is different from *F. angustum* Laubenf., which has narrow-keeled leaves, but is close to those of *F. falciforme* and *F. papuanum* (Fig. 5), and less so to *F. taxoides* (Brogn. & Gris) de Laubenfels. The specimens of *F. australis* had smaller leaves than the typical sizes for both *F. falciforme* and *F. taxoides*, although their size ranges do overlap (Table 2). However, the leaves of *F. falciforme*, *F. papuanum*, and *F. taxoides* are amphistomatic whereas *F. australis* has only scattered rare stomata on the upper surface of the leaf.

The stomata of *F. australis* have a distinctive circular appearance (Fig. 19) as the polar subsidiary cells do not project beyond the boundary of the lateral subsidiary cells, matching the situation seen in *F. papuanum*. In both *F. falciforme* and *F. taxoides* the polar subsidiary cells project beyond the lateral cells and are often shared with adjacent stomata in the same row. Occasional isolated stomata in these species are of the same form as found in *F. australis* and *F. papuanum*.

On the basis of vegetative morphology, *F. australis* is closest to *F. falciforme*. However, on the basis of cuticular morphology, it is closer to *F. papuanum*, which differs mainly in the greater numbers of stomata on the upper surface and their more regular arrangement. It should be noted that there is a newly described fifth modern species of *Falcatifolium* (D. J. de Laubenfels, personal communication) and that it was not available for comparison. No fossil species of *Falcatifolium* have been described previously, although Zastawniak (1981) reported *Falcatifolium* foliage from the Antarctic Peninsula (?Miocene).

Podocarpus platyphyllum

Podocarpus (sens. de Laubenfels) is generally characterised by fairly broad (1–3 cm) and in juvenile plants often long leaves (up to 30 cm, see Fig. 7), although species with small leaves (1 × 0·3 cm) are known from section *Australis* of subgenus *Podocarpus*, e.g. *P. alpinus* R.Br. ex Hook. f., of alpine and subalpine habitats in south-eastern Australia and Tasmania. The monotypic section *Sundacarpus* of *Prumnopitys* (*P. amara*) is also broad-leafed, but the distinctive stomata and the highly sinuous anticlinal walls of the epidermal cells characteristic of *Prumnopitys* distinguish it from *Podocarpus*.

The association of Florin rings with the stomata of *Podocarpus platyphyllum* places it in subgenus *Podocarpus* (de Laubenfels 1985). *Podocarpus platyphyllum* had the closest similarity to the restricted north-eastern Queensland endemic *P. smithii* Laubenf. (subgenus *Podocarpus*), but surprisingly was superficially similar to *P. polystachyus* from subgenus *Foliolatus*. The epidermal cells of *P. platyphyllum* have almost smooth anticlinal walls (Figs 28 and 29) whereas those of *P. smithii* have a distinctive beading. This feature is poorly developed on some smaller specimens of *P. platyphyllum*, and may be under environmental or ontogenetic control.

The leaves of *P. platyphyllum* fall into two size classes (Figs 21–23), reflecting the situation seen in some Australian species of *Podocarpus* (e.g. *P. grayii* Laubenf. and *P. smithii* Laubenf., Fig. 7) where the leaves of juvenile trees are much longer than the leaves of the adult trees. This transition is reflected in the cuticle with (in *P. smithii*) the beading of the anticlinal walls less prominently developed in the juvenile leaves than in the adult leaves. Probably the two leaf sizes of *P. platyphyllum* reflect the input of both juvenile and adult foliage into the fossil deposit.

The 18 sections of *Podocarpus* are separated by bud and fertile shoot characters (de Laubenfels 1985). In the absence of more information about the fossil it is not possible to definitively place *P. platyphyllum* in a section, although it probably belongs in section *Crassigemmis* for which *P. smithii* is the sole modern species. This section is distinctive within *Podocarpus* as the epimatium is poorly developed and the seed has a prominent ridge or crest. *Podocarpus smithii* is restricted to montane rainforest in north-eastern Queensland. The fossil species is the first record of a broad-leafed *Podocarpus* from an Australian Tertiary locality.

Prumnopitys tasmanica (Townrow) Greenwood

The Anglesea material referred to *Prumnopitys tasmanica* has much larger leaves than Townrow's (1965) Tasmanian specimens (Figs 24 and 27) but otherwise is a close

match. It is possible that either the two populations represent different ecotypes of the one species or the Tasmanian specimens represent a subspecies or perhaps stunted individuals of the same species. Further work is needed to clarify the status of the Anglesea specimens.

Prumnopitys lanceolata

The spiral phyllotaxy and linear to lanceolate leaves twisted into a distichous arrangement (Figs 25 and 26) place *Prumnopitys lanceolata* into section *Prumnopitys* of *Prumnopitys* (de Laubenfels 1978). *Prumnopitys lanceolata* is different from the other *Prumnopitys* species at Anglesea as it has a well developed distichous leaf arrangement (Figs 25–27) similar to that of the modern New Zealand species *P. taxifolia*. The modern species *P. ladei* is also strongly distichous and amphistomatic but, unlike *P. lanceolata*, it has oblong mucronate leaves. The linear, acuminate leaves of *P. lanceolata* are closer in form to the Chilean *P. andina*, the two New Zealand species *P. ferruginea* and *P. taxifolia* and the New Caledonian *P. ferruginoides*. The size range of the fossil leaves is also comparable with these species (Table 3). However, unlike *P. lanceolata* both *P. andina* and *P. taxifolia* are hypostomatic, although *P. ferruginea* is variable in cultivation (Townrow 1965).

Table 3. Comparison of the modern and fossil (F) species of *Prumnopitys*

H, hypostomatic; A, amphistomatic

Taxon	Leaf length (mm)	Leaf width (mm)	Source
P. amara, H	4·5–13·5	0·8–1·4	Specimens
P. andina, H	3·1	0·4	Specimens
P. ferruginea, H / A	1·9–3·1	0·2	Specimens
P. ferruginoides, A	0·9–1·8	0·2–0·35	Specimens and de Laubenfels (1972)
P. harmsiana, H	1·0–3·1	0·1–0·3	Specimens
P. ladei, A	1·3	0·2–0·4	Specimens
P. montana, H	1·0–2·0	0·2–0·3	Specimens
P. taxifolia, H	0·6–1·2	0·1	Specimens
P. lanceolata, (F), A	0·7–1·2	0·1	Specimens
P. tasmanica (F), A	0·25–1·0	0·15–0·3	Townrow (1965)
P. aff. *P. tasmanica* (F), A	0·7–1·5	0·1	Specimens

The characteristic strongly sinuous or sculptured anticlinal epidermal cell wall of most of the modern species of *Prumnopitys* is absent in *P. ladei* and *P. lanceolata* (Fig. 33) and is erratically developed in *P. amara* and *P. montana* (Humb. & Bonpl. ex Willd.) de Laubenfels. *Prumnopitys montana* has a subsidiary cell pattern very similar to that in *P. lanceolata*.

Prumnopitys lanceolata is perhaps most closely allied to *P. ladei* and *P. ferruginoides*, based on their common amphistomatic state and other features of their cuticles, and perhaps more distantly to *P. montana*. Both *P. ladei* and *P. lanceolata* lack a well developed Florin ring, suggesting a closer affinity than other features would indicate as this character is well developed in the majority of the modern species.

Discussion

Some important trends in the evolution of the foliage of the Podocarpaceae into the forms characteristic of the modern genera can be detected in the Tertiary fossils. Townrow (1965) suggested that *Podocarpus acicularis* and *P. goedei* might represent the

type of foliage from which the '*Polypodiopsis*-foliage type' evolved, i.e. the decussate, secondarily distichous foliage of section *Decussocarpus* of *Decussocarpus*. *Podocarpus acicularis* and *P. goedei* were contemporaries of the Eocene species *D. brownei* and *D. araucoensis* (and now also, *D. maslinensis*), so cannot be considered ancestral to section *Decussocarpus*, but may represent a now extinct more primitive or at least divergent section within *Decussocarpus*.

Dacrycarpus eocenica sp. nov. differs from the modern species of *Dacrycarpus* in having hypostomatic rather than amphistomatic leaves. While Florin (1931) and Buchholz and Gray (1948) considered stomatal distribution to be an important diagnostic feature, it is variable in several genera. In *Prumnopitys*, half the modern species are hypostomatic and half amphistomatic to varying degrees. One species, *P. ferruginea*, is variable, *Podocarpus* s. str., however, is generally considered to be strictly hypostomatic, although rare isolated stomata may be seen on most species and one, *P. elongatus*, is amphistomatic. The condition seen in *D. compactus* therefore, suggests that the possession of stomata on both surfaces may also have been variable in *Dacrycarpus* in the past. A similar situation can be argued for both *Falcatifolium* and *Prumnopitys* as the Anglesea fossil species represent the extremes of the variation seen in stomatal distribution for the modern species of these genera (Tables 2 and 3).

Dacrycarpus is much reduced in occurrence since the Tertiary, having occurred formerly in South America and Australia (Florin 1940; Cookson and Pike 1956) and is now represented only by single species in both New Caledonia and New Zealand. It seems to have radiated in Malesia, however, where five species now occur in a variety of circumstances from alpine shrub vegetation to lowland swamp forests and montane rainforests (de Laubenfels 1969). *Falcatifolium* and *Prumnopitys* (section *Prumnopitys*) have undergone similar reductions in range but are today found only in subtropical or tropical montane forests (de Laubenfels 1969, 1978). The greater diversity of form found in *Dacrycarpus*, *Falcatifolium* and *Prumnopitys* in the past and the relic nature of these genera today suggest that a broader concept of some of the genera of the Podocarpaceae is therefore appropriate when dealing with Tertiary material.

Some other Australian Tertiary fossil Podocarpaceae, e.g. *Podocarpus goedei* and *P. acicularis*, differed enough from modern species for Townrow (1965) to suggest that they did not belong to a modern subgeneric group. Other taxa, e.g. *Coronelia* Florin, while clearly belonging to Podocarpaceae, were considered to differ too greatly from modern species to be placed in modern genera (Florin 1940; Townrow 1965).

The variability seen in stomatal distribution, however, reflects a level of deviation too small to warrant the erection of new genera or sections. I suggest that the taxa present in the Eocene represented a more diverse and larger assemblage of Podocarpaceae, from which the modern representatives (at least in some taxa) are only a poor and perhaps specialised remnant.

The wider distribution and morphological variation may also indicate wider ecological preferences for some genera. Palaeoclimatic interpretations based on the modern ecological preferences of relic genera such as *Dacrycarpus* or *Falcatifolium* are therefore limited.

Recent debate has centred on palaeoenvironmental reconstructions, and some authors have questioned the 'tropical' nature of southern Australian Eocene vegetation. The high diversity of Podocarpaceae at Anglesea in the Eocene represented by these megafossils is greater than in any comparable vegetation type of modern Australia. Similar mixes of genera can be found in modern New Guinea and New Caledonia in tropical montane rainforests, but not to my knowledge with all five genera together. The tropical montane rainforests of north-eastern Queensland formerly supported a higher diversity of Podocarpaceae (Kershaw 1976; Kershaw and Sluiter 1982), and still contain *Podocarpus* (*P. smithii*) and *Prumnopitys* (*P. ladei*), suggesting a possible similarity to the Anglesea flora.

Acknowledgments

References

Abele, C., Gloe, C. S., Hocking, J. B., Holdgate, G., Kenley, P. R., Lawrence, C. R., Ripper, D., and Threlfall, W. F. (1976). Tertiary. *In* 'Geology of Victoria'. (Eds J. G. Douglas and J. A. Ferguson.) pp. 177-274. Geol. Soc. Aust. Spec. Publ. 5.

Basinger, J. F., and Christophel, D. C. (1985). Fossil flowers and leaves of the Ebenaceae from the Eocene of southern Australia. *Can. J. Bot.* **63**, 1825-43.

Blackburn, D. (1981). Tertiary megafossil flora of Maslin Bay, S. Aust.: numerical study of selected leaves. *Alcheringa* **5**, 9-28.

Buchholz, J. T., and Gray, N. E. (1948). A taxonomic revision of *Podocarpus*. 1. Sections of the genus and their subdivisions with special reference to leaf anatomy. *J. Arnold Arbor. (Harvard Univ.)* **29**, 49-63.

Christophel, D. C. (1981). Tertiary megafossil floras of Australia as indicators of floristic associations and palaeoclimate. *In* 'Ecological Biogeography of Australia'. (Ed. A. Keast.) pp. 379-90. (Junk: The Hague.)

Christophel, D. C. (1984). Early Tertiary Proteaceae: the first floral evidence for the Musgraveinae. *Aust. J. Bot.* **32**, 177-86.

Christophel, D. C., Harris, W. K., and Syber, A. K. (1987). The Eocene flora of the Anglesea locality, Victoria. *Alcheringa* (in press).

Cookson, I. C., and Pike, K. M. (1953). The Tertiary occurrence and distribution of *Podocarpus* (section *Dacrycarpus*) in Australia and Tasmania. *Aust. J. Bot.* **1**, 71-82.

Dilcher, D. (1969). *Podocarpus* from the Eocene of North America. *Science* **164**, 299-301.

Florin, R. (1931). Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. *Kungl. Svenska Vetenskapsakademiens Handligar B.* **10** (1), 1-588.

Florin, R. (1940). The Tertiary fossil conifers of South Chile and their phytogeographical significance (with a review of the fossil conifers of southern lands). *Kungl. Svenska Vetenskapsakademiens Handligar B.* **19** (2), 1-87.

Florin, R. (1963). The distribution of conifer and taxad genera in time and space. *Acta Horti. Bergiani* **20**, 121-402.

Hill, R. S., and Macphail, M. K. (1983). Reconstruction of the Oligocene vegetation at Pioneer, north-eastern Tasmania. *Alcheringa* **7**, 281-99.

Kershaw, A. P. (1976). A Late Pleistocene and Holocene pollen diagram from Lynch's Crater, north-eastern Queensland, Australia. *New Phytol.* **77**, 469-98.

Kershaw, A. P., and Sluiter, I. R. (1982). Late Cenozoic pollen spectra from the Atherton Tableland, north-eastern Australia. *Aust. J. Bot.* **30**, 279-95.

de Laubenfels, D. J. (1969). A revision of the Malaysian and Pacific rainforest conifers. 1. Podocarpaceae. *J. Arnold Arbor. (Harvard Univ.)* **50**, 274-369.

de Laubenfels, D. J. (1972). Gymnosperms. Flore de la Nouvelle Caledonie et Dépendences'. Vol. 4. (Ed. A. Aubreville.) (Musée National D'Histoire Naturelle: Paris.)

de Laubenfels, D. J. (1978). The genus *Prumnopitys* (Podocarpaceae) in Malesia. *Blumea* **24**, 189-90.

de Laubenfels, D. J. (1985). A taxonomic revision of the genus *Podocarpus*. *Blumea* **30**, 251-78.

Quinn, C. J. (1982). Taxonomy of *Dacrydium* Sol. ex Lamb. emend. de Laub. (Podocarpaceae). *Aust. J. Bot.* **30**, 311-20.

Selling, O. H. (1950). Some Tertiary plants from Australia. *Sversk. Bot. Tidskr.* **44**, 551-61.

Stover, L. E., and Partridge, A. D. (1973). Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, southeastern Australia. *Proc. R. Soc. Victoria* **85**, 237-86.

Stover, L. E., and Partridge, A. D. (1973). Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, southeastern Australia. *Proc. R. Soc. Victoria* **85**, 237–86.

Townrow, J. A. (1965). Notes on some Tasmanian pines. 1. Some lower Tertiary podocarps. *Pap. R. Soc. Tasmania* **99**, 87–107.

Zastawniak, E. (1981). Tertiary leaf flora from the Point Henniquin Group of King George Island (South Shetland Islands), Antarctica. Preliminary report. *Geologica Sudetica (Polska)* **72**, 97–108.

Appendix 1. Nomenclatural changes to Tertiary Podocarpaceae

Dacrycarpus Laubenfels 1969

Dacrycarpus praecupressinus (Ett.) Greenwood, comb. nov.

    Podocarpus praecupressinus Ett. (section *Dacrycarpus*) 1888, *Mem. Geol. Surv. N.S.W.* 2; Cookson and Pike 1953, *Aust. J. Bot.* **1**: 71–82.

Dacrycarpus setiger (Townrow) Greenwood, comb. nov.

    Podocarpus setiger Townrow (section *Dacrycarpus*) 1965, *Pap. Roy. Soc. Tas.* **99**: 87–107.

Decussocarpus Laubenfels 1969

Section *Decussocarpus*

Decussocarpus araucoensis (Berry) Greenwood, comb. nov.

    Araucaria araucoensis Berry 1922, *Johns Hopkins Univ. Stud. in Geol.* 4. Baltimore, Md.

    Podocarpus araucoensis (Berry) Florin (section *Polypodiopsis*) 1940, *Kungl. Svenska Vetenskapsakademiens Handligar B.* **19** (2), 1–87.

Decussocarpus brownei (Selling) Greenwood, comb. nov.

    Podocarpus brownei Selling (section *Polypodiopsis*) 1950, *Sversk. Bot. Tidskr.* **44** (a): 551–561.

Prumnopitys Laubenfels 1978

Section *Prumnopitys*

Prumnopitys tasmanica (Townrow) Greenwood, comb. nov.

    Podocarpus tasmanicus Townrow (section *Stachycarpus*) 1965, *Pap. Roy. Soc. Tas.* **99**: 87–107.

Podocarpus L'Hérit. ex Pers. emend. Laubenf. 1985

Subgenus *Podocarpus*

Section *Australis*

Podocarpus strzeleckianus Townrow (section *Eupodocarpus*, subsection D) 1965, *Pap. Roy. Soc. Tas.* **99**: 87–107.

Appendix 2. Modern species compared with the Anglesea Podocarpaceae

Dacrycarpus (9 modern spp., 7 examined)

D. cinctus	New Guinea
D. compactus	New Guinea
D. dacrydioides	New Zealand
D. expansus	Malesia
D. imbricatus	Malesia to Fiji
D. steupii	New Guinea
D. viellardii	New Caledonia

Decussocarpus (12 modern spp., 7 examined)

section *Afrocarpus*

D. falcatus	Africa
D. mannii	W. Africa

section *Dammaroides*

D. wallichianus	India, SE. Asia, Malesia

section *Decussocarpus*

D. comptonii	New Caledonia
D. minor	New Caledonia
D. rospigliosii	Venezuela, Colombia, Ecuador
D. vitiensis	New Guinea to Fiji

Falcatifolium (5 modern spp., 3 examined)
    F. falciforme   Borneo
    F. papuanum   New Guinea
    F. taxoides   New Caledonia

Podocarpus (95 modern spp., 49 examined)
subgenus *Podocarpus*
section *Australis*

P. alpinus	SE. Australia
P. cunninghamii	New Zealand
P. gnidioides	New Caledonia
P. lawrencii	New Zealand
P. nivalis	New Zealand
P. nubigenus	Chile
P. totara	New Zealand

section *Capitulatis*

P. glomeratus	Peru, Ecuador, Bolivia
P. parlatorei	Argentina
P. salignus	Chile
P. sellowii	Brazil
P. sprucei	Ecuador, N. Peru

section *Crassiformis*

P. smithii	NE. Queensland

section *Nemoralis*

P. brasiliensis	Brazil
P. celatus	Venezuela to Bolivia
P. magnifolius	Venezuela, Colombia, Peru, Brazil

section *Lanceolatis*

P. salicifolius	Venezuela

section *Podocarpus*

P. latifolius	South Africa

section *Pratensis*

P. oleifolius	Mexico, Central America, northern S. America
P. tepuiensis	Venezuela

section *Scytopodium*

P. henckelii	South Africa
P. madagascariensis	Madagascar

subgenus *Foliolatus*
section *Acuminatis*

P. dispermus	NE. Queensland
P. ledermannii	New Guinea and New Britain

section *Foliolatus*

P. insularis	Fiji
P. levis	New Caledonia
P. neriifolius	Malesia
P. novae-caledoniae	New Caledonia
P. rubens	Sumatra to Solomons
P. spathioides	Malesia to Solomons

section *Globulus*

P. lucienii	New Caledonia
P. sylvestris	New Caledonia
P. teysmannii	Malaya to Sumatra

section *Gracilis*

P. glaucus	Philippines to Solomons
P. pilgeri	China, Malesia to Solomons

section *Longifoliolatus*
 P. decumbens   New Caledonia
 P. longifoliolatus   New Caledonia
 P. polyspermus   New Caledonia
 P. pseudobracteatus   New Guinea
 P. salomonensis   Solomon Islands
section *Macrostachyus*
 P. crassigemmis   New Guinea
section *Polystachyus*
 P. chinensis   China
 P. elatus   E. Australia
 P. macrocarpus   Philippines
 P. polystachyus   Malesia (incl. New Guinea)
section *Rumphius*
 P. grayi   NE. Queensland
 P. rumphii   Malesia (incl. New Guinea)
section *Spinulosus*
 P. drouynianus   W. Australia
 P. spinulosus   E. Australia

Prumnopitys (10 modern spp., 7 examined)
section *Sundacarpus*
 P. amara   Malesia to NE. Queensland
section *Prumnopitys*
 P. andinus   northern S. America
 P. ferruginea   New Zealand
 P. ferruginoides   New Caledonia
 P. ladei   NE. Queensland
 P. montanus   Colombia
 P. taxifolia   New Zealand