A TAXONOMIC ANALYSIS OF A MIDDLE CRETACEOUS MEGAFOSIL PLANT ASSEMBLAGE FROM QUEENSLAND, AUSTRALIA

by

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ABSTRACT

This thesis is a taxonomic analysis of a recently discovered megafossil flora from the middle Cretaceous of central Queensland, now called the Winton Fossil Plant Assemblage. Representation of Australian (or indeed world) floras of this age is extremely poor.

The fossil material consists of silicified wood, shoots, cones, fruits and seeds, embedded in matrices of variable composition. Specimens in silica-matrix rocks have been anatomically studied by means of thin-sectioning techniques. Plant organs embedded within carbonate-matrix rocks have been removed intact by dissolution of the matrix in acid.

As wood forms a significant part of the deposit, a first consideration was an assessment of the value of wood anatomy in taxonomy. It is concluded that incomplete description and illustration of fossil woods leads to erroneous interpretations. Of the 5 wood taxa identified in the Assemblage, 4 show positive familial affiliations, all to the anatomically conservative Araucariaceae. This family is the best represented of the predominantly coniferous flora, the most common single taxon, Araucaria microcarpa sp. nov. being an atypically small but mature ovulate strobilus from the generic Section Eutacta. The only other fossil member of this section to provide any detailed anatomical data is from the Jurassic of Yorkshire.

The Podocarpaceae is also common in the deposit. The female cone Pecundistrobus gen. nov. is most closely allied to the extinct Mehtaia from the Indian Jurassic. Lepidothamnus australis sp. nov. is the first fossil or extant member of this living genus to be found in Australia.

The now predominantly Northern Hemisphere family, the Taxodiaceae, is represented by 2 common taxa of female strobili in the Winton Assemblage. Austrosequoia wintonensis Peters and Christophel, and Wintonia gen. nov. appear to be distinctive new members of the family from the Southern Hemisphere. Surprisingly, the Cupressaceae, now populous in Australia, has only one taxon in the Assemblage - a new species of Callitris, the oldest member of the genus to be found in Australia.

The angiosperms are predictably rare in the Assemblage, with occasional leaf fragments and one taxon of primitive fruits. Other rare groups in the flora include foliage structures related possibly to the Gingkoales, pteridosperms and ferns.

A total of 33 taxa are described from the deposit, which appears to represent a unique and therefore significant component of the Australian palaeoenvironment. It provides megafossil support for a period, which up until now, has almost solely been interpreted by microfloral evidence.
DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University. To the best of my knowledge and belief this thesis contains no material previously published or written by another person except where due reference is made in the text.

Mark D. Peters.
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CHAPTER 1

GENERAL INTRODUCTION

The value of fossils in determining the biological, geographical and geological history of an area has long been appreciated. Our increasing knowledge of the variations and distributions of past life-forms has contributed to an understanding of the ways in which mechanisms of evolution and dispersal have produced the current biological array over the earth.

The Cretaceous is a particularly important Period in the evolutionary history of the earth's flora. In what seems an inordinately short time, the angiosperms began to flourish, the bennettitaleans disappeared, and the pteridosperms rapidly dwindled. Unfortunately, information about the biological history of Australian Cretaceous floras has been principally supplied by microfloral rather than megafloral evidence. An exception is the extensive Late Cretaceous Waare Flora of Victoria (Douglas, 1969). As surface exposures and subsurface sections of Cretaceous sediments occur over almost one-third of Australia, this lack of megafossil support for the supposed land floras is disappointing.

The problem of the scarcity of middle-Cretaceous plant assemblages was alleviated in part in the 1970s with the discovery by Mr. M. Elliott of Lovelle Downs Station, near Winton, Queensland, that some rocks in one of his grazing paddocks contained minor veins of opal. A request of evaluation was directed to Dr. M. Wade, palaeontologist of the Queensland Museum, who was, at that time, searching for dinosaur remains in the area. It was found that although
the opal was worthless, the surrounding rock was rich in petrified plant structures.

Dr. D. Christophel, head of the Palaeobotanical Laboratory of the University of Adelaide, was notified of the discovery, and subsequently conducted a major collecting trip to the site in 1976. The deposit was found to be a lens-shaped assemblage of surface-scattered quartz rock. Field examinations showed that wood, leaves, fruits and cones existed as three-dimensional silica replacements with excellent morphological preservation. The site was apparently the result of the deposition of litter from a prehistoric forest.

The first taxonomic work on the deposit was done by me, as part of an Honours Degree (Peters, 1977). My thesis was based on a particularly common taxon of ovulate taxodiaceous cones. This cone, subsequently described as Austrosequoia wintonensis (Peters and Christophel, 1978) represents the first discovery of such a close relative to Sequoia in the Southern Hemisphere.

This thesis is a taxonomic analysis of the other plant structures found in the deposit, to be known as the Winton Fossil Plant Assemblage. Evidence will be presented that the material was laid down in the Albian-Cenomanian Stages of the Cretaceous Period, about 100 million years ago. Very few megafossil plant assemblages of this age have been described from Australia. This description of the Winton deposit therefore makes a significant addition to our knowledge of the history of the Australian land flora. Although information about the vegetation of central Queensland during the middle-Cretaceous has been gained by studies of microfossil assemblages (Dettmann, 1963; Dettmann and Playford, 1969; Playford et al., 1975), co-evidence from
megafossils of the same age can be very important in forming an accurate and complete picture of a fossil flora, as it is known that microfossils may not accurately reflect the diversity and frequency of their megafossil counterparts.

A petrified fossil assemblage is particularly valuable, in that frequently both morphological and anatomical information can be assessed. The Winton Fossil Plant Assemblage is unusual in not having any trace of the original organic content. Much of the fossilized material occurs as silicifications in a carbonate matrix (see Section 2.4.3.) A major task on beginning research into the assemblage was therefore the development of methods which would isolate the different fossilized structures and thus enable their close study. These techniques are discussed in Chapter 3.

Petrified wood is the most obvious morphological type in the Winton Fossil Plant Assemblage. I therefore began my taxonomic analysis with these fossils. I believed that their good cellular preservation would allow me to make some fundamental conclusions about the primary species which made up the ancient Winton forests. However, the study of wood anatomy has escalated rapidly during this century, probably to the point that its value in taxonomy has been abused and misunderstood. I have consequently devoted part of this thesis to reviewing the current state of knowledge in this field.

Throughout this thesis I stress the importance of making conservative taxonomic assertions based on accurate description and comparison, rather than making optimistic or premature classifications based on characters of questionable taxonomic value. Taxonomic classification of fossil material is certainly more reliable when it is
based on the conservative diagnostic features of reproductive structures. The Winton Fossil Plant Assemblage contains numerous reproductive organs from four families of conifers: Araucariaceae, Cupressaceae, Podocarpaceae and Taxodiaceae. These are described thoroughly in Chapter 4. Prior to the systematic descriptions of the individual taxa found within each family, there is a brief discussion concerning the taxonomy of extant genera and the important fossil representatives which have been ascribed to these families.

The only reproductive structure of the Angiospermeae to be found as yet in the Winton Fossil Plant Assemblage is a single taxon of fruit. This exhibits excellent anatomical preservation, but cannot be confidently assigned to any extant or fossil family. It is hoped however, that its description and illustration here may assist in some future determination.

Foliage shoots and detached leaves are very common morphological types in the deposit. These structures are known to be rather plastic and susceptible to major environmental modification. More conservative cuticular characters are helpful in leaf diagnoses, but these could not be fully assessed in the Winton fossils due to poor epidermal preservation. Consequently, the shoots are divided into their distinctive foliage types, each of which is compared if possible with natural taxonomic groups.

In Chapter 5, I compare the results of the taxonomic determinations from the Winton Fossil Plant Assemblage with evidence of other Cretaceous megafossil and microfossil floras from Australia and elsewhere.
2.1. General Geography

The Winton Fossil Plant Assemblage is found in a grazing paddock on Lovelle Downs Station, 48km west-north-west of the town of Winton, and 8km east of the Diamantina River in central Queensland (Fig. 1)(22° 12' 00" S, 142° 31' 30" E, altitude 180 metres, Winton Map Sheet SF/54-12, International Index). The area is generally without topographic relief, being a mature erosional landform of gently undulating grassland. Non-conformable Tertiary mesas are scattered over the plains. The water courses have little gradient and form a well-developed braided system which slowly drains floodwaters toward salt lakes in north-eastern South Australia.

2.2. Geological History of the Area

The fossil locality lies in the Winton Formation of the Eromanga Basin, the largest and deepest depositional sequence of the Great Artesian Basin (Fig. 2). The history of the Eromanga Basin has been reviewed by various workers, including Whitehouse (1954), Day and Tweedale (1960), Vine et al. (1967), Day (1969), Senior et al. (1975), Exxon and Senior (1976) and Smart and Senior (1980). The nomenclature of Vine et al. and Senior et al. is in current use (Table 1).

The conformable sediments of the Eromanga Basin begin with the Middle Jurassic Westbourne Formation, which is overlain by the Middle/Late Jurassic to Early Neocomian Hooray Sandstone. These latter sediments are predominantly non-marine stream deposits which contain aquifers fed by marginal outcrops to form the artesian system of the Great Artesian Basin. (Non-conformable Permian and Triassic sediments
Table 1. Present Nomenclature of the Eromanga Basin

<table>
<thead>
<tr>
<th>AGE</th>
<th>NOMENCLATURE (Vine et al., 1967)</th>
<th>NOMENCLATURE (Senior et al., 1975)</th>
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<tbody>
<tr>
<td>Cenomanian</td>
<td>Winton Formation</td>
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<td></td>
<td>Mackunda Formation</td>
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<td>Allaru Mudstone</td>
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<td></td>
<td>Toolebuc Formation</td>
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<td>Wallumbilla Formation</td>
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<td></td>
<td>Ranmoor Member</td>
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<td></td>
<td>Coreena Member</td>
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<td></td>
<td>Jones Valley Member</td>
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<td></td>
<td>Doncaster Member</td>
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<tr>
<td></td>
<td>Wyandra Sandstone Member</td>
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<tr>
<td>Aptian</td>
<td>Cadna-owie Formation</td>
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<tr>
<td>Neocomian</td>
<td>Hooray Sandstone</td>
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<tr>
<td>Middle and Late Jurassic</td>
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<tr>
<td></td>
<td>Westbourne Formation</td>
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</tbody>
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also yield some of this groundwater (Exon and Senior, 1976)].

During the Late Neocomian and Early Aptian, a shallow sea began to cover most of the Eromanga Basin, a feature of a world-wide Cretaceous marine transgression (Smart and Senior, 1980). About 60 metres of stream-deposited sandstone, siltstone and mudstone, known as the Cadna-owie Formation, was formed before and during this transgression. Part of the Cadna-owie Formation is overlain by medium to coarse sandstone called the Wyandra Sandstone Member. Exon and Senior (1976) believe these sediments may be beach deposits representing a transgressing sea. The marine transgression reached a peak by the Late Aptian, when much of north-eastern Australia was inundated (Smart and Senior, 1980). The Carpentaria, Eromanga and Surat Basins were united by these seas. Impermeable marine clays of the Wallumbilla Formation were laid down at this time, which served as the cap-rock for the aquifer system of the Great Artesian Basin. (The Wallumbilla Formation represents the first depositional event of the Rolling Downs Group). Marine fauna found in the clays indicate that cold water conditions occurred in the Aptian (Day, 1969).

Conditions altered radically in the Early Albian, when the marine environment was replaced by a warmer fresh-water system (Day, 1969). This quickly reverted in the early part of the Late Albian, when a shallow sea returned to the Eromanga Basin from the north. The first sediments of this transgression were laid down as the Toolebuc Formation. When the transgression again reached its peak, much of the Eromanga Basin was covered by up to 270 metres of marine muds, known as the Allaru Mudstone.

The sea began to withdraw northward during the latest Albian, leaving 100 metres to 300 metres of feldspathic and lithic sand, silt
and mud, as the Mackunda Formation. Smart and Senior (1980) have hypothesized that these sediments were originally deposited as detritus from an Albian andesitic volcanic mountain chain which extended for several hundred kilometres from north of Brisbane in Queensland. The Mackunda Formation has a paucity of planktonic organisms, which Exon and Senior (1976) have taken to indicate a shallowing and regression of the Albian seas.

This withdrawal of the sea from the Great Artesian Basin during the Late Albian permitted an extensive northward flowing river system to develop, which deposited the Winton Formation (Brown et al., 1968). Vine (1966) has suggested that the Winton sediments were laid down in an area of very low relief, with many sluggish streams, wide river flats and local development of short-lived lakes and swamps. The complete lack of marine fossils, and the presence of intraformational conglomerate and peat led Exon and Senior (1976) to believe that it was deposited on a broad coastal plain as the sea withdrew.

Sediments of the Winton Formation have been dated into the Cenomanian (Playford et al., 1975), but as its eroded surface now outcrops over much of the Eromanga Basin, younger deposits could have been lost. The stream-deposited Tertiary Werite Beds are separated from the Winton Formation by this unconformity, and outcrop in the scattered mesas and hills. Superficial Quaternary alluvium completes the Eromanga sequence.

The site of the Winton Fossil Plant Assemblage existed at a latitude of about 57° S during the middle Cretaceous (see Irving, 1964). Palynological studies (Dettmann and Playford, 1969), together with macropalaeontological evidence (Day, 1969) and oxygen isotope
evidence (Dorman and Gill, 1959) indicate that in general, the Cretaceous sediments of the Eromanga Basin were deposited in cool temperate climates.

2.3. Structure of the Winton Formation

The Winton Formation is the youngest Cretaceous unit preserved in the Great Artesian Basin, except for some Late Cretaceous sediments at Mt. Howie in the north-east of South Australia (Brown et al., 1968). The Formation outcrops over much of central and south-west Queensland (Fig. 3). Its maximum thickness is 1100 metres near Winton, with an average thickness of 500 metres. The Winton Formation has no direct relationship with any other rock unit of Late Albian-Cenomanian age.

The Lovelle Downs No. 1 Well was drilled 1.5km west of the Winton Fossil Plant Assemblage. The thickness of the Winton Formation at that site is 293 metres, and is underlain by 262 metres of Mackunda Formation, 294 metres of Allaru Mudstone, 32 metres of Toolebuc Formation and 237 metres of Wallumbilla Formation (Mines Administration Pty. Ltd., 1973). The Winton Formation was found to be made up of fresh-water deposits of interbedded blue-grey sandstone and mudstone in about equal proportions. The sandstone is feldspato-lithic, medium- to fine-grained, commonly calcareous and concretionary. The mudstone is thick-bedded to massive. Thin beds of conglomerate are common and locally abundant. Minor coal seams up to 2 metres thick have been recorded (Casey, 1966). Locally found cross-bedded sandstones, channel fill and lenticular beds are indicative of the short-lived lakes, swamps and sluggish streams which laid down the Winton unit.
2.4. The Winton Fossil Plant Assemblage

2.4.1. Locality

The fossil deposit occurs as a lenticular body on a slight rise, 100 metres long and 40 metres wide, oriented and striking in a north-south direction (Fig.4). The fossil material consists of a scattered layer of broken and weathered rocks, of variable size up to 30cm in diameter. Preservation is by silicification, with the petrified plant material embedded and exposed in a varied matrix of silica, limestone and dolostone (see Section 3.1.).

2.4.2. Age of the Locality

Evidence was presented by Peters and Christophel (1978) for the Winton Fossil Plant Assemblage being part of the Winton Formation, despite the lack of a pollen date or lithological correlation. This evidence included the facts that:
- The locality lies directly on identifiable sediments of the Winton Formation.
- The physiography of the Winton Formation (described by Vine (1964)) accords well with the fossil site.
- Surrounding marine Tertiary sediments (in mesas) are not conformable with the Winton Formation and fossil locality.
- The strikes of both the fossil lens and the surrounding outcrop of the Winton Formation are consistent.
- Some fossiliferous rocks at the margin of the locality grade conformably into non-fossiliferous feldspathic sandstones which are typical of those in the Winton Formation.
Sediments of the Winton Formation have chiefly been dated by palynological methods (Dettmann and Playford, 1969, Playford et al., 1975). Despite numerous early attempts by me and other workers, no palynomorphs could be extracted from rocks of the Winton Fossil Plant Assemblage. This is hardly surprising, due to the complete chemical replacement of all the original plant matter.

I more recently found, however, that one particular rock type in the deposit contained "in situ" silicified spores in a transparent rock matrix. These could be isolated and photographed from thin sections. The palynomorphs are poorly preserved, and their examination, identification and photography was made difficult by the enclosing quartz matrix. In many cases, identification of the microfossils must be tentative, as apertures and sculpturing of the spore and pollen exines are obscured or eroded.

Seventeen separate microfossil forms were found in the rocks. These are illustrated in Figures 5 - 27. The palynomorphs isolated are as follows.

1. Lycopodiumsporites? Thiergart ex Delcourt and Sprumont 1955 (Fig. 5)
   Six species are known to occur commonly in the Upper Mesozoic of south-eastern Australia (Dettmann, 1963).

2. Podocarpidites Cookson ex Couper 1953 cf. P. ellipticus (Fig. 6, 7)
   P. ellipticus is a common microspore from the Australian Mesozoic (Dettmann, 1963).

3. Liliacidites Couper 1953 (Fig. 8)
   Species of this genus have been recorded from the Eocene of south-eastern Australia (Harris, 1970, Stover and Partridge, 1973).

4. Laevigatosporites? Ibrahim 1933 (Fig. 9)
   A single species, L. ovatus is confined to the Wallumbilla to
Winton Formation (Albian to Cenomanian) of the Eromanga Basin (Dettmann, 1963).

5. *Alisporites similis* Balme (Fig. 10)

Two species are found in the Upper Mesozoic of south-eastern Australia. *A. grandis* is common, though *A. similis* has not been found in the Winton Formation (Dettmann, 1963).

6. *Podosporites* Rao 1943 (Fig. 11)

A single species, *P. microsaccatus* ranges from the Lower Cretaceous to the Miocene of eastern Australia (Harris, 1970). Cookson and Pike (1954) related this species to the extant genus *Phyllocladus*. Another species, *Podosporites rotundis*, has been ascribed to the Upper Eocene of south-eastern Australia (Harris, 1970).

7. *Crybelosporites* Dettmann 1963 (Figs. 12,13)

These spores are similar to those of extant *Marsilea*. Three species are known, all from the Upper Mesozoic sediments of the Eromanga Basin. One species, *C. striatus*, extends into the Winton Formation (Dettmann, 1963).

8. *Microthyriacites*? Cookson 1947 (Fig. 14)

Cookson (1947) erected this genus after finding these fossil fruiting bodies in Tertiary deposits from Australia and New Zealand. Microthyriageous fungi are common ascomycete saprophytes found on a variety of megafossils (see van Geel, 1978).

9. *Schizosporis reticulatus* Cookson and Dettmann 1959 (Fig. 15)

This algal spore, possibly chlorophycean (Brenner, 1963), is widely distributed in the Upper Mesozoic of eastern Australia (Dettmann, 1963).

10. *Contignisporites*? Dettmann 1963 (Fig. 16)

Four species are known, all from the Upper Mesozoic sediments of
the Eromanga Basin (Dettmann, 1963).

11. *Microcachrydites antarcticus* Cookson 1953 (Figs. 17 - 20)

This species is common in the Upper Mesozoic, extending into the Oligocene of eastern Australia (Dettmann, 1963).

12. *Stereisporites?* Pflug 1953 (Fig. 21)

One species, *S. antiquaesporites*, is found in the Winton Formation (Dettmann, 1963). The spore resembles those of *Sphagnum*.

13. *Araucariacites?* Cookson ex Couper 1953 (Fig. 22)

A single species, *A. australis*, is widely distributed in the Upper Mesozoic of south-eastern Australia (Dettmann, 1963).

14. Tricolpate pollen grains (Figs. 23 - 25)

These are probably angiospermous, but of indeterminate affinity.

15. Algal or bryophyte spore? (Fig. 26)

16. Septate fungal spores (Fig. 27)

17. Bisaccate taxodiaceous grains? (not illustrated)

A count of 500 individual microfossils was made, giving the following proportions of palynomorphs.

- **Microcachrydites**: 60%
- **Podocarpidites, Alisporites, Podosporites**: 27%
- **Araucariacites**: 5%
- **Crybelosporites**: 4%
- Tricolpate angiosperm(?) pollen: 3%
- Other types: 1%

On the basis of the forms identified, this assemblage of microfossils seems consistent with those of Albian or Cenomanian age (Dettmann, pers. comm.). If *Crybelosporites, Laevigatosporites* and

*Dr. M.E. Dettmann, Dept. Geology and Mineralogy, University of Queensland, St. Lucia, Queensland.*
Stereisporites are in fact present, the deposit can be assigned to the Winton Formation.

Three microfloral zones are recognized from the Winton Formation of the Eromanga Basin (Dettmann and Playford, 1969). The earliest Coptospora paradoxa Zone (Upper Aptian to Upper Albian) is found from the basal Winton Formation. The Tricolpites pannosus Zone and the Appendicisporites distocarinatus Zone have both been dated as Upper Albian – ?Cenomanian. Unfortunately, the Winton Fossil Plant Assemblage has, as yet, not been found to contain any of the indicator species used to denote these zones. Further evidence is therefore required to substantiate its age from palynological data.

The fossil assemblage lies on sediments of the Winton Formation, so that it must be at least Late Albian to Cenomanian in age. The very low number of angiospermous grains present, compared to the high proportion of coniferous grains (particularly Microcachry tidites and Podocarpidites) points to the deposit being older than Senonian, when angiosperm pollen was dominant (Dettmann and Playford, 1969). Triporate pollen grains first appeared in the Cenomanian of eastern Australia. This form has not been identified from the fossil assemblage. The rare angiosperm grains in the assemblage are all simple tricolpate types, which first appeared in the Albian of eastern Australia (Dettmann and Playford, 1969).

An extended analysis of the suitable rock matrices in the deposit might yield pollen types which could substantiate the age, but from the above evidence, a Late Albian-Cenomanian age is most likely. As will be seen in Chapter 4, the megafossil flora is nearly all gymnospermous, the only angiosperm remains being occasional leaves and fruits. The deposit seems certain to have formed before the domination of the
angiosperms in the Late Cretaceous.

2.4.3. Petrology

X-ray diffraction has shown that the Winton fossils are made entirely of silica, with no trace of the original organic content. The general term for such compact siliceous sediments is chert, which may be composed of a variety of silicas, including quartz, chalcedony and opal. The Winton fossils have a high concentration of chalcedony, a typically fibrous variety of cryptocrystalline silica, distinguishable by using electron microscopy. Quartz, in the form of minute crystals, has been identified in fossil rock crevices. Common opal is occasionally seen to fill cracks and fissures in some specimens, but this is probably due to a more recent infilling of the weathered rock.

Complete three-dimensional permineralization of plant matter, particularly wood, is a well known form of fossilization. The precise mechanism of this mineral replacement, however, is very poorly understood. Oehler and Schopf (1971) artificially silicified extant wood by subjecting specimens, in the presence of dissolved silica, to high temperatures and pressures. While this may explain the abundance of silicified wood in the fossil record, it does not adequately explain the undistorted petrification of relatively delicate tissues such as those from Winton. Scurfield et al. (1974) believe that most silicification occurs in surface conditions of relatively normal temperature and pressure.

The usual fate of plant litter is to decompose by oxidation and by the saprophytic activity of organisms such as bacteria and fungi. If however, the litter falls into a stagnant pool which is low in
dissolved oxygen, oxidizing conditions are replaced by reducing conditions, which, in addition to the activity of anaerobic organisms, release molecules of carbon dioxide and water. The plant tissue therefore becomes progressively concentrated in carbon to form peat. With the chance introduction of a high concentration of dissolved silica, mineral replacement of the plant matter may occur. (Ordinarily, continued deposition without silica replacement would supply the high temperature and pressure conditions which convert peat to coal).

Dissolved silica may come from several sources. Some of the silica found in surface waters is known to be derived from volcanic emanations. Soluble silica is also a breakdown product of the weathering of complex silicates, including feldspars and other volcanically derived siliceous sediments. Volcanic activity is not known to have occurred during the Cretaceous of central Queensland, however, siliceous sediments such as feldspathic sands, which constitute the Winton Formation, are thought to have been deposited in the Albian as detritus from coastal volcanoes (Smart and Senior, 1980). Weathering of these sediments could well have supplied the dissolved silica. Tropical or sub-tropical conditions increase the mobility of silica in the soil, especially in areas of low relief (Dunbar and Rodgers, 1957). It has already been stated that the Winton Formation was probably deposited in temperate conditions, however, hot mineral springs feed the surface over much of the Great Artesian Basin, and these could have assisted in the breakdown and transport of soil silicates.

Several theories have been advanced to explain the way in which dissolved silica replaces organic matter. A problem exists in determining how the soluble silica precipitates to the solid form.
Initial concentration may occur by evaporation of silica-rich pools. Correns (1950) has shown that a change in pH from 9 to 5 will result in the precipitation of two-thirds of dissolved silicates from a concentrated solution. The slow decomposition of organic matter in anaerobic ponds usually produces acidic conditions which could therefore assist in the precipitation of silica. Scurfield et al. (1974) pointed to the probability of silification occurring under acidic conditions due to the frequent association of silica with iron oxide. Iron and manganese oxides exist in the Winton fossils as natural stains.

It is believed that the process of silification begins with the impregnation of the plant cell walls by the silica in solution. (Sigleo (1978) has proposed a way in which this chemical bonding occurs.) This must be accompanied or preceded by dissolution of the organic compounds (lignin, cellulose) which make up the cell walls. The fate of these compounds is unknown, but microbial action is probably involved. Scurfield et al. (1974) have recognized fungal hyphae and possibly bacteria in permineralized wood. The Winton fossils have a rich fungal content within the silicified tissues, which may explain the complete absence of organic matter. (Incomplete permineralization of the cell walls is common in other fossil deposits, which usually allows study of the fossils by taking cellulose-acetate peels). The next stage of silification is a secondary deposition of silica in the cell lumina and intercellular spaces. Permineralization is completed with the loss of all water from the sediment, either by evaporation or compaction.

The silicified fossils from the Winton assemblage are usually cemented together by a compact matrix of opaque or transparent chert. The cohesion between this matrix and the fossils leads me to believe
that both formed at about the same time. Many of the fossilized plants are cemented together with limestone and dolostone. These fossils are usually poorly preserved. The manganese and iron oxide stain appears to have leached out, leaving the fossils as bleached, often translucent specimens. I would assume that this has arisen from the weathering of part of the initial or primary silica matrix and the partial hydration of the permineralized plants. The matrix was then replaced by limestone and dolostone (limestone with a magnesium carbonate constituent), which is readily transported in groundwater. This replacement probably coincided with the weathering of the primary matrix, as breakdown of the silica fossils is minimal. Some fossils have a partial secondary matrix of lithified clay, which was probably also transported and deposited by groundwater.

At the edge of the lens, occasional fossiliferous specimens were found which consist of an earthy haematite matrix enclosing poorly preserved pyrite-replaced fossils. Both haematite and pyrite are transported by groundwater, pyrite being a mineral which may often chemically replace silicas. These specimens were of no taxonomic value.

2.4.4. A Model for the Formation of the Assemblage

The postulated Albian-Cenomanian landscape of central Queensland, with its wide river flats, sluggish streams and short-lived swamps is an ideal situation for the accumulation and preservation of plant matter in anaerobic ponds. This is indicated by the high frequency of thin coal seams in the Winton Formation.

The Winton Fossil Plant Assemblage probably formed in the actual area where its constituent plants grew. Three lines of evidence point
to this being the case.

1. The absence of clastic sediments such as sand and "in situ" clay within the fossiliferous rocks indicates that minimal erosion of surrounding sediments was occurring.

2. The presence of undamaged and delicate plant tissues within the assemblage means that little transport of plant litter would have occurred.

3. The mixture of these fine tissues with other large plant organs indicates that no size-sorting by moving water would have occurred.

The generally good preservation of the fossil assemblage, especially the replacement of fine leaf tissues, means that silicification would have been very rapid. This might have occurred if the plant litter was deposited directly into a spring-fed pool, which was rich in dissolved silica weathered from underlying feldspathic sediments. As the plant material began to decay in the anaerobic pond, the resultant acidic conditions would have promoted the precipitation of silica from solution. Saprophytic water fungi and bacteria would have broken down the organic plant matter, with the concurrent replacement by silica.

The assemblage is now an erosion surface, so that it cannot be postulated how thick the original fossil lens was, or what period of deposition it represents. It may be that the fossil deposit is the resultant deposition of just several day's plant litter.

Following silicification, the depositional environment of the area may have changed, capping the deposit in further sediments. More recent erosion could have exposed the top of the fossil assemblage to weathering and erosion of a less stable silica matrix which enclosed the fossils. This was possibly replaced quite rapidly by the secondary
cementation of limestone and dolostone, followed by further deposition of sediments above the deposit.

In recent history, the assemblage was again exposed, so that now it exists as a broken and weathered surface layer capping a slight rise. This elevation, accompanied by the complete exposure of the lens, means that the physical and chemical weathering which is now acting on the fossils, will destroy the deposit in the near future.

The complete absence of other known fossil assemblages of this nature in the Winton Formation leaves the above hypothesis in some doubt. However, fossilization by petrification is at any time a rarely encountered phenomenon and depends on a chance series of events which severely limits the probability of preservation of an original flora. In addition, the ephemeral nature of the deposit on exposure to surface conditions means that should other assemblages be exposed through time, they might rapidly be weathered and eroded. Other such localized assemblages could be quite common in the Eromanga sediments, but have not been found by natural exposure or random exploration.
3.1. Materials

The first significant collection from the newly discovered Winton Fossil Plant Assemblage was made by D.C. Christophel and D.T. Blackburn from the Palaeobotanical Laboratory of the University of Adelaide in 1976. Specimens were selected for the presence of well preserved or interesting plant structures on the rock surfaces. A second extensive collection was made in 1979 by C.A. Peters and me. The locality was systematically covered to collect the better preserved specimens. Based on the development of new techniques of fossil extraction, a third collection was made in 1981 by D.C. Christophel, L. Hickey and me to collect rocks which might yield good fossil material within them (see Section 3.2.). The total collection stands at some 600 rock specimens, now housed in the Palaeobotanical Laboratory of the University of Adelaide. Type specimens are to be permanently housed in the Queensland Museum.

I would reasonably assert that all common taxa and most of the less common or rare taxa are represented in the collection, so that the fossils described in this study represent a fair and substantial range of the plant variation within the locality.

The petrology and mechanism of deposition and preservation of the fossil material have been outlined in Chapter 2. As described there, the material consists of several rock types which vary somewhat in their mode of lithification. The actual plant remains are all preserved
as silica, and the differences between rock specimens lie in the type of matrix in which the fossils are embedded. It was suggested in Chapter 2 that the original matrix was siliceous and that the limestone, dolostone and clay matrices in many rocks are due to a secondary cementation following weathering and erosion, or chemical replacement of the original matrix.

3.2. Methods

The variety of matrix types and the associated effects on the permineralized plant material meant that different methods of study were needed. Most of the plant taxa described in the following chapter were found exposed on the surfaces of rocks with limestone, dolostone or clay matrices. Following the erosion of protective upper layers which would have covered the locality, these relatively soft matrices have begun to weather away from the previously enclosed siliceous fossils. Many exposed fossils show excellent preservation of their gross morphology, frequently with at least half a cone or shoot left in relief on the rock surface. Distortion of the plant structures is usually minimal, allowing accurate descriptions to be formulated. Photographs were taken with a Leitz Aristophot 4" x 5" plate camera. Unfortunately, most of these exposed fossils have been superficially pitted during weathering, so that there is little or no preservation of epidermal features. These specimens were also found to have generally poor preservation of internal tissues, due to hydrolyzation of the silica during the secondary replacement which is postulated to have formed the soft matrices.

Those specimens consisting of silicified plants embedded in a
primary matrix of unweathered silica probably originated in the lower part of the fossil lens where secondary replacement did not occur. Some of the larger rock specimens contain a silica matrix which grades into a crust of softer matrix, and may have come from the boundary between the primary and secondary replacement zones. The silica-matrix rocks rarely show three-dimensional plant structures on the rock surfaces, however, this rock type usually yields good anatomical preservation of the most delicate plant tissues.

The 200 or so rock specimens of this type were systematically sectioned into slabs with a 30cm diamond saw. Each slab was cut to a thickness of about 1cm. From a good knowledge of the taxa present on rock surfaces, it was usually possible to recognize these structures on the cut surfaces within the rocks. Some rocks were rich in particular taxa, and these were more completely searched. Specimens of interest were cut from the 1cm slabs, usually in a plane parallel or perpendicular to the specimen axis. The cut blocks were hand smoothed on a lapidary wheel through a sequence of carborundum powders of grit size 200, 400, 500, and then polished on a high speed lapidary machine with carborundum impregnated paper of grit size 1000. (A counterpart of the specimen usually existed on the adjacent cut slab and this too was polished). The polished specimens were then mounted on glass microscope slides with thermal plastic, and thin sections were cut using a diamond saw fitted with a thin-sectioning attachment.

The thin sections were ground down by hand through the same sequence of carborundum powders until the specimens were translucent. Examination of the slides was done through a water or glycerine mount. (Permanent mounting media like "Xam" were found to render the sections somewhat transparent). The natural manganese and iron oxide staining of
the silica was usually sufficient for microscopic examination, although some slightly porous specimens could be artificially stained by immersing the slides in a 5% aqueous solution of malachite green for 60 seconds (Bartholomew et al., 1970).

As discussed in Chapter 2, the degree of preservation of the plant material is extremely variable, due not only to the degree of decay prior to silicification or to weathering of the fossils, but also to irregularities in natural staining. When differences in plant tissues were not reflected in different degrees or colours of natural stain, it was found that phase contrast and Nomarski microscopy could often distinguish the tissues according to the slight variation in refractive indices of the silica. Microscopic examination and photography was done with a Reichert Univar microscope with 35mm or 4" x 5" plate camera, or a Wild stereomicroscope with 35mm or 4" x 5" plate camera. All photographs were taken with Ilford FP4 film and printed on Ilfospeed Grade 3 and Grade 4 photographic paper.

Thin sectioning in this way meant that a 1.5mm – 2.0mm thick slice of rock was cut and ground down to produce each mounted section. Larger plant structures allowed a series of sections to be made in either a transverse or longitudinal plane. This technique was not suitable for a complete study of smaller structures, or when greater three-dimensional detail was required. Therefore, specimens of this type were serially ground down. Every 100μ, a photograph was taken of a highly polished surface using the reflected light of a high intensity fibre-optic light source. The detail seen in polished surfaces was usually inferior to that of thin sections, so that particularly important structures were thin sectioned, giving a permanent record of
the actual material.

During mass sectioning of the material I quickly became aware of the subtle distinctions between rock types. Those with an opaque grey silica matrix containing cream or pale brown fossils usually showed superior preservation, while clear or translucent silica matrices (and dolostone, limestone and clay matrices) invariably contained fossils with little or no preservation of plant cells. However, an advantage of the clear matrix rocks was that some were later found to be rich in silicified pollen grains, which, although poorly preserved, allowed some taxonomic identifications to be made which assisted in dating the deposit (see Section 2.4.2.).

The discovery that soft secondary matrices surrounded closely spaced silica fossils allowed techniques to be developed to extract the three-dimensional plant structures from the rocks. Limestone and dolostone could be dissolved with acid. Blocks or slabs of rock with these matrix types were added to large beakers containing 50% hydrochloric acid. (Dolostone was more soluble in a hot acid solution). Depending on the concentration of calcium carbonate, the matrices would dissolve over a period of several weeks without harming the silica fossils. Unfortunately, the fossils were usually held tightly together by insoluble clay or granular silica. It was found that some of this matrix could be removed by decanting off the acid and replacing it with a 25% solution of sodium bicarbonate, which immediately reacted with the acid remaining in the pore spaces, causing violent effervescence and an associated dislodging of matrix particles.

Many siliceous plant fragments could be sieved from the sediment in the beakers, but most of the fossils lay exposed and partly buried.
in the rock surfaces. By placing these rocks under a stereomicroscope, it was possible to extract many useful fossils by carefully scratching out the clay or weathered silica with needles. Occasionally, much of the matrix could be removed by blasting the rock with a powerful and fine stream from a water gun. The extracted specimens were usually found to be coated with a fine layer of clay or soft silica. This could be removed by boiling the fossils in a 30% solution of hydrogen peroxide into which was added 10% by weight sodium pyrophosphate crystals to act as a detergent. Gentle brushing usually removed remaining debris.

Anatomically, these fossils were poorly preserved, the silica being transparent and possibly hydrated during the secondary matrix replacement earlier postulated. However, it was found that the dissolved-out plant remains had retained many epidermal features including stomata and epidermal cells. (This bolsters the argument that the secondary replacement by dolostone, clay and limestone must have occurred without exposure of the lens). Specimens under study were mounted on stubs for examination with a scanning electron microscope, which allowed easy comparison of epidermal structures with extant plants. Seeds, leaves, shoots and cones were all extracted from the soft matrix rocks. The excellent morphological preservation of many of these fossils allowed accurate descriptions of taxa to be formulated.
CHAPTER 4

SYSTEMATICS

The fossils isolated from the Winton Fossil Plant Assemblage can be divided into three categories, according to the type of plant organ. Fossil woods are dealt with first, followed by reproductive organs and finally foliage organs. The section on reproductive organs is subdivided taxonomically into families. An introduction to the taxonomy of extant and fossil taxa is given.

4.1. WOOD

A significant component of the Winton fossil plant assemblage is represented by fossil woods, deposited chiefly on the southern edge of the lens. The silicified specimens vary greatly in size and quality.

4.1.1. Value of Xylotomy in Taxonomy

Arguments concerning the value of fossil woods as identifiable botanical specimens have occurred since the creation of the science of palaeoxylotomy by Witham in 1833, who first studied fossil woods from thin sections. Prior to this, petrified woods were generally placed under the artificial genus, Lithoxylon, created by Luidius in 1699 (Ward, 1885). Following Witham’s pioneering work, there appeared in the literature a string of organ-genera to cover fossil woods resembling modern genera, including Araucarioxylon (Kraus, 1870), Taxodiocxylon (Felix, 1886) and Piceoxylon (Gothan, 1905). Angiospermous fossil woods were usually ignored by the early workers, who undoubtedly
despaired at the thousands of modern genera with which to compare their fossils. Most of the original organ-genera have now been abandoned following more detailed research into the nature of wood.

Many of the earlier twentieth century anatomists, including Record (1931,1934), Rendle (1936), Chalk (1937) and Metcalfe (1943) envisioned xylotomy as a means of substantiating and revising plant systematics, natural relationships being supposedly expressed in the highly specialized structure of secondary wood. Classical taxonomists have maintained that floral structure is the most indicative feature of natural groups, as climatic and edaphic influences usually do not affect floral morphology in a species, whereas vegetative and vascular structures may alter appreciably in different environments. As Bailey (1924) suggested, however, foliar and cauline structures may merely respond more readily to climatic and edaphic selection, producing a genetically distinct form of foliage and/or wood.

The whole question regarding the relative conservatism of different plant organs in revealing inherited features is no longer a strong issue in plant systematics. As Bailey and Howard (1941) pointed out, rates of evolution in different plant organs need not be equal, just as different organs are differentially affected by their environment. It is no longer justifiable to regard any one organ or part of a plant as more conservative or reliable than any other part. With the increasing application of various branches of botany in the phylogenetic placement of plants, including the use of chemical, numerical and physiological techniques, more natural and objective systems of classification are being achieved.
In contrast to Moll and Janssonius (1906) who believed that any specimen may be taxonomically placed on the basis of its wood structure alone, many notable xylotomists, including Record (1931), Vestal (1940), Tippo (1946) and Bailey (1957) have strongly urged that all plant organs be examined to assess their worth as phylogenetic indicators, after realizing the futility of using any single plant part.

Following intensive investigations into the anatomy of woody tissue by Sanio (1872) and Janssonius (1906), many workers undertook laborious surveys of the xylotomy of numerous large and varied plant groups. This resulted in the premature reorganization and reclassification of species which have since been found to be unjustified. Disturbed at the bad impression being given by such work, xylotomists began to question the validity of the application of wood anatomy in taxonomy. As pointed out by Bancroft (1932), Jane (1934) and Rendle and Clarke (1934), too little was known of the minute structure of wood and its exact significance in distinguishing which characters were of systematic importance. Rather than supporting the continuation of superficial or inadequate descriptions, research by various anatomists concentrated on determining how xylotomy could effectively be used in taxonomy. The International Association of Wood Anatomists was set up to make an organized effort in the collection and distribution of authenticated wood specimens, and to fix international standards of terminology and description. An international glossary of terms to be used in wood anatomy was published by the Committee on Nomenclature in 1933, and was revised in 1957.
The major problem for the systematic xylotomist is that of the variability of wood. The problem of variation involves every character that is now or may be used for diagnostic purposes. Anatomical characters can legitimately be used only if the degree of variation is duly recognized and taken into account. The wood anatomist must search for characters which are inherent and relatively constant within a group. Failure to realize the degree of variation which might exist within wood has led to publications based on insufficient material. The extensive work of Greguss (1955), in which he describes the wood anatomy of most species of extant gymnosperms is typically deficient in this respect. Many species are described from a single wood specimen, which can hardly take into account the variation which might exist in different parts of the tree, or in different trees from different habitats. Unfortunately, the misunderstanding of the taxonomic significance of variability still exists.

A great deal of research has been done to determine which anatomical features of secondary wood show a range of variation which is small enough to be accurately and reliably descriptive of a given family, genus or species. Any parallelism between wood anatomy and pre-existing taxonomy tends to disappear in taxonomic groups larger than the family (Chalk, 1937). A major difficulty in assessing the significance of variation is in the identification of those wood structures which can be classed as being inherently different in the individuals of a single species.

Many botanists have made use of the dimensions of the various xylem elements in the classification and description of secondary wood. The variation in this character within a single tree has received the
most attention in studies of wood variability. The first work of this kind was done by Sanio (1872), who investigated the tracheid variation in different parts of \textit{Pinus sylvestris}. Subsequent workers found that the trends discovered by Sanio generally hold true for all trees, and they became known as the Laws of Sanio. In summary, the Laws state:

1. Tracheids in the stem and branches generally increase in size from the inside toward the outside through a number of annual rings, until a definite size is reached, which then remains constant.

2. In any one annual ring, the final size of the tracheids in the stem increases from the base toward the top of the tree; at a definite height it reaches a maximum and then decreases toward the crown.

3. The final size of the tracheids in the branches is less than in the stem, but depends upon the latter, in that those branches which arise at such a stem-height that the stem tracheids are larger, themselves have larger cells than do those branches which arise at a stem-height where the constant cell size is less.

4. In the branches, the constant cell size increases in the outer rings towards the tip, and then falls again.

5. In the root, the width of the cells first increases through the cross-sectional area, then falls, and then rises again until the constant size is reached. Also, toward the end of the root, an increasing size is found.

More recently, Anderson (1951) found that in four coniferous trees, the relationship between tracheid length and distance from the pith could be expressed mathematically for each tree, regardless of age or level in the trunk, provided that the portion of the tree up to 60cm
from the ground was eliminated.

Clarke's anatomical investigation of the elm tree in 1930, was the first study to look at the variations in the dimensions of vessel elements. His results confirmed that vessels conform at least to the first two Laws of Sanio. Research by Desch (1932) on Alnus, Betula and Fagus, and by Bisset and Dadswell (1949) on fibre length in Eucalyptus regnans, similarly showed the adherence of wood fibres to Sanio's Laws.

More specific investigations by Bisset, Dadswell and Amos (1950) and by Bisset and Dadswell (1950) into the variation in cell length in angiosperms and gymnosperms, showed further differences in cell size within a single growth ring. In angiosperms with distinct growth rings, an increase of up to 200% in fibre length was observed from the first formed early-wood to the last formed late-wood. In species without definite growth rings, little or no variation in fibre length was observed over a radial distance covering several years. In the gymnosperms, a slight increase (up to 12%) in tracheid length from the early- to the late-wood was noted in most cases. Swamy et al. (1960) looked at the variation in vessel length within one growth ring in arborescent angiosperms, and found that late-wood vessel elements are also larger than those of the early-wood. Chalk and Chattaway (1935) also found that in ring porous woods, the vessels of the early-wood are consistently shorter than those of the late-wood. Handokey (1936) determined that the length of vessel elements is dependent on whether the wood is ring porous or diffuse porous. It has also been found that distorted tissues and regions of mechanical stress commonly possess shorter vascular cells (Bailey and Faull, 1934).

There is disagreement as to whether tracheid length is correlated

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with growth ring width. Shepard and Bailey (1914) could find no correlation. Bisset, Dadswell and Wardrop (1951) demonstrated that in general, within a conifer stem, a wider growth ring has a low average tracheid length compared to a narrow growth ring. One would assume that vessel elements and fibres follow a similar pattern.

Cell diameter is another character commonly used by xylotomists. Desch (1932) found that the radial diameter of vessels show a closer correlation with annual increment than the tangential diameter. Where cell size is used for the purpose of identification, tangential diameter is therefore a preferable measurement. In Bannan's (1965) investigation into cell length of conifer tracheids, he determined that the length to width ratio (measuring tangential tracheid width) correlates positively with tracheid length and tree height. On the other hand, increased radial growth in mature trees is accompanied by a reduction in cell length and a lowering of the tracheid length to width ratio.

In their study of the factors affecting dimensional variations of vessel elements, Chalk and Chattaway (1935) concluded that wood descriptions should include the type of perforation plate with the length and diameter of the vessels. These three characters determine the length of the vessel element tail and the height of the perforation plate, so that the latter features are not likely to be of diagnostic value when the others fail.

To understand the significance of dimensional variations in the vascular elements in different parts of the same tree, it is necessary to look at the growth factors which control cell development. The explanation by Bailey and Tupper (1919), that cell length is governed
by the retarding effect of the roots and stems has been discounted by Spurr and Hyvarinen (1954). They see cell size as a function of both organization and growth. Apart from the major effect on cell size of position in the tree, they discovered that the fibre lengths in successive annual layers of wood follow the normal growth curve of the tree. In early years, when the tree is growing rapidly, the cells quickly lengthen. During the steady growth of a mature tree, fibre length remains fairly constant. Finally, in very old trees, fibre length decreases as does growth. These trends were found to hold true for differing trees, growth rates and growth sites.

Bailey (1920) found that the size of the cells in the secondary xylem is also determined by the size of the cambial initials. In the Coniferae the length of the initials closely resembles that of the tracheids of the last formed growth layer. For most angiosperms, on the other hand, these meristematic cells are shorter than the fibre-tracheids, but are of approximately the same length as the vessel elements. The cambial initials vary in size in different parts of the plant, being relatively short near the young shoots, and increase in size during subsequent growth until a maximum length is reached. Bailey (1957) found that in different parts of the conifer Pseudotsuga, the cambial initials vary between 900µ and 6000µ, while in the angiosperm Robinia, the initials vary only between 150µ and 190µ.

Chalk (1943) believed that the significance of the length of tracheary elements and cambial initials would prove to be the greatest contribution to wood anatomy. More recently, it has been shown using statistics that tracheid length is inherited and therefore of taxonomic value. These works include Echols (1955) for Pinus elliotii, Hartley (1960) for Pinus radiata, Wellwood (1960) for Tsuga heterophylla, and
Boycie and Kaeber(1961) for *Populus deltoides*. According to Sterne and Green (1958), vessel element length and diameter also possess phylogenetic significance.

Taking into account the obvious variation which occurs in the dimensions of vascular elements, there is a great need for care in selecting material for measurements, which may only be significant if compared with those secured from an homologous region in a tree grown under similar conditions. It is no longer acceptable to randomly choose a single timber specimen on which to base a specific description. Cell dimensions quoted in the literature can only be taken as approximations. Rendle and Clarke (1934) calculated that an accurate timber description must be based on at least 25 measurements from 5 samples from each of 4 trees. Unless the mean sizes of an element in two species differ by at least 3.5 times the standard deviation of the individual elements in any one sample, they believe it is unsound to use this feature diagnostically. In describing the xylem structure of a species, it also becomes necessary to refer to the actual material used, its position within the tree, the age and height of the tree, and the environmental conditions in which the tree was growing. Despite suggestions of this sort being made by xylotomists for the past 50 years, anatomists are still comparing tracheary dimensions without applying adequate statistical tests to assess the significance of variations which are known to exist.

The characteristics of growth ring structure of secondary wood have also received attention in studies of wood variability. While many wood descriptions merely refer to the presence or absence of obvious annual layers, others include such subjective and vague terms as
"growth rings fairly distinct" or "growth rings almost indistinct". Attempts at greater detail are occasionally made by giving the relative proportions of late-wood to early-wood in any one annual growth layer.

It is recognized that plants showing a yearly growth pattern in their wood do so in response to climatic periodicity, which promotes then retards xylem production, giving early-wood and late-wood respectively. This has been explained by Zahner (1963) in terms of tree hormone levels. During crown elongation when soil moisture levels are high, increased auxin production stimulates early-wood formation. As the moisture level decreases and the production of auxin is reduced, the radial enlargement of the wood slows down, causing the xylem elements to live longer. The cell walls are then able to thicken with lignin deposits, giving the typical appearance of late-wood.

Most temperate zone plants develop growth rings, while the constant climatic conditions of the tropics do not markedly alter secondary growth. It is known, however, that many tropical plants will not produce rings even if grown in a temperate environment (Douglas, 1919, and Anteves, 1925). Genetically, they are unable to respond to climatic change. Similarly, temperate species normally without growth rings are not affected by climatic periodicity due to some inherent factor.

Climatically induced variability in growth rings within a single tree can be quite marked. Bailey and Faull (1934) found that the growth layers in _Sequoiadendron_ may vary considerably in width and in the ratio of early-wood to late-wood. The branches and roots have narrower growth rings than those of the stem of comparable age. Schultze-Dewitz (1960) and Kennedy (1961) observed that increased soil moisture levels also produce broad annual rings and reduced late-wood. Trees growing in
highly fertile soil tend to develop wider growth rings compared to those growing in poor soil (de Zeeuw, 1965).

It seems pointless for anatomists to compare the structure of growth rings, when the environmental effects may be so pronounced. Growth ring morphology is more accurate in determining the climatic history of an individual tree, and unless wood samples are compared from identical regions of trees growing in identical environmental conditions, growth ring morphology cannot be validly used in plant systematics.

Despite Jeffrey's (1917) feeling that "...no feature is more subject to variability within the limits of a single sub-tribe, and hence is less available for comprehensive conclusions in regard to evolutionary sequence", the size and form of xylem rays in secondary wood are always included in xylotomical descriptions. This character is expressed in terms of ray height and width (in number of cells) and whether or not the ray-parenchyma cells are all of one type (ray homogeneous) or of different types (ray heterogeneous).

Essner (1886), Fisher (1903) and Jaccard (1915) were among the first workers to investigate the variability of wood rays. They independently concluded that rays may differ in size and in the number present per unit area, not only within different parts of a single tree, but also within different parts of a single growth ring. Bailey and Faull (1934), in their study of the wood variability in *Sequoia*, showed that the rays are smaller and more numerous in the innermost rings, and increase in size and number towards the periphery. An increase in ray height and width along a single radius was confirmed in other species by de Bruyne (1952) and Sébastine (1955). Despite this
general increase in ray size with age, Bailey and Faull (1934) noticed that the size of the rays may not remain constant even in the outer growth rings of roots, branches and stems. Barghoorn (1941) has shown that rays may also change in structure between homogeneous and heterogeneous types at various distances from the pith.

The causes of variation in ray structure are unknown. Clarke (1930) believed that total ray volume is closely related to the environment, where conditions allowing greater metabolism demand greater ray volumes for storage purposes. This does not explain the correlation between ray volume and age. It is known that ray cells are produced independently in the cambium layer by the ray initials, so that their size and structure are not directly influenced by the fusiform initials. Bailey and Faull (1934) made measurements of single ray cells in Sequoia, and found that the cell dimensions also vary markedly in different parts of the tree. They tend to be larger in the early-wood, in wide growth rings, and in the outer growth layers of the plant.

The type, size, shape and arrangement of the vascular pitting in the tracheids of gymnosperms and the vessel elements of angiosperms are considered to be an integral part of wood descriptions. Research by Bailey and Faull (1934) on the tracheary pitting in Sequoia showed that these characters display a degree of variation within an individual tree to make their taxonomic value questionable. Unfortunately, no significant work has been done on the pitting in angiospermous plants.

In Sequoia, the bordered pits become larger and more numerous as the tracheids increase in radial diameter. Within a growth ring, however, they decrease in size and number passing from the early-wood
to the late-wood tracheids. The pits also tend to be more numerous in relatively narrow rings than in unusually wide growth rings. Furthermore, pits are commonly more frequent toward the overlapping ends of the tracheids and in those portions of the radial walls which are in contact with the terminal portions of adjoining tracheids.

Bailey and Faull (1934) found that the pits in *Sequoia* may be uniseriate to multiseriate, with a spaced, opposite or alternate arrangement. They vary in size between 5μ and 25μ, and may be circular, oval, or transversely elongated, with circular, oval, lenticular, or slit-like pit apertures. In comparing the pitting characteristics of different species, or individuals of a species, it is not only necessary to compare homologous parts of the growth ring, but also equivalent areas of the cell walls.

The cross-field pits, which connect ray-parenchyma cells with adjacent xylem elements are described in terms of their size, shape, number and arrangement in the cross-field. In *Sequoia*, Bailey and Faull (1934) found that they may vary between 1 and 20 pits per cross-field, and can be less than 5μ and greater than 15μ in diameter. They may be arranged irregularly, or in horizontal, diagonal or vertical rows. The pit apertures vary between a narrow slit to a circular opening. Presumably, a range of variation similar to this occurs in many other conifers and angiosperms.

Bailey (1933) did some work on the diagnostic value of vestured pits in dicotyledons. These special structures are bordered pits with the pit cavity wholly or partially lined with projections from the tertiary cell wall layer. Bailey found that true vestured pits are either present throughout the secondary xylem of a species or genus, or
are entirely absent. This constancy in the presence or absence of these structures exists in most families of dicotyledons. Vestured pits may therefore be of value in the systematic study of woods. Unfortunately, xylotomists rarely refer to them.

Bailey and Faull (1934) found that the abundance and distribution of wood parenchyma in *Sequoia*, as in many other Coniferae, varies greatly in different parts of a single tree. It may be abundant and diffuse, or aggregated into zones. The wood parenchyma tends to be more developed in the inner rather than in the narrow outer growth rings of stems and roots. Many species lack any significant parenchyma.

The individual parenchyma cells vary in length and in tangential diameter as do the surrounding tracheary elements. This is because both cell types are derived from the same fusiform initials in the vascular cambium.

A wood character which is occasionally used by those workers striving for detail is the concentration of xylem elements in a given unit area of timber. This feature is rather superfluous in the elements of gymnosperms, as tracheid concentration is directly correlated to cell size. Foresters do use tracheid concentration, however, as a useful indicator of wood texture and density.

The concentration of the sparser vessel elements is often used in systematic comparisons of angiosperm woods. The only detailed research into the variation of this character was done by Desch (1932), who found statistically significant correlations between vessel concentration and growth ring width. Predictably, the total number of vessels in an annual ring increases with an increase in ring width, but the increase is not directly proportional. The number of vessels per
unit area increases very considerably with a decrease in ring width. Desch believed that these differences were related to seasonal variation.

Apart from the correlations of vessel concentration with growth ring width, there are several reasons for not regarding this character as an essential part of a wood description. It is only applicable to those timbers with a fairly even distribution of vessel elements. The extreme variation between different timbers in respect to the number of vessels is so wide, that it is impracticable to fix any one unit of area as the standard for diagnostic purposes.

A wood character often used by foresters, but seldom by xylotomists, is specific gravity. Desch (1932) studied the variation of specific gravity within trees of several species of deciduous angiosperms, and found that at a given height, specific gravity tended to be low at the tree centre and to increase outwards for a period, then to decrease towards the periphery. More recently, Spurr and Hsiung (1954) and Göhre (1955) and Zobel et al. (1959) found that in conifer stems, the specific gravity also increases from the pith outward and decreases from the base upward. While the core of wood near the pith has a low specific gravity and is essentially uniform at all heights in the tree (Zobel et al., 1953), Desch (1932) found that variation in specific gravity in the same annual ring showed differences between individual trees. Research by Cech et al. (1960) on Populus trichocarpa and by Zobel (1956) on Pinus taeda has determined specific gravity to be a genetically controlled property of wood, which further explains variations between individuals.
The organization and composition of the cell walls in secondary wood are generally not referred to in wood descriptions, due possibly to the difficult and precise examinations required. Nevertheless, research by a small number of workers has revealed that the fine structure of cell walls may well prove to be of taxonomic value.

These characters are also subject to variation, which needs to be considered before their value can be assessed. Wardrop and Preston (1950) and Pillow et al. (1953) found that the orientation of the microfibrils within the layers of the cell wall is related to the position in the tree. From the pith outward, microfibrillar angle approaches more closely the cell axis. Wardrop and Dadswell (1957) also studied the variability of these cell wall layers, in terms of the proportionate amount of different layers present in the cells within the tree and between species. They determined that the presence of reaction wood within a stem is one of the most marked causes of variability in cell wall layering.

Within a growth ring, it was found by Ritter and Fleck (1926) that the cellulose content increases in the late-wood, with a corresponding decrease in lignin content. There is also a significant increase in cellulose from the pith outward, and a decrease from the tree base to the crown (Hale and Clermont, 1963).

A final wood character which has received attention in studies of wood variability is spiral wood grain. Although this character does not normally feature in formal wood descriptions, it provides a good example of the unexpected variations which may occur in a single plant specimen.

It has been noticed that the orientation of cells in a stem is
seldom parallel to a plane through the pith. Moskowiak (1963) concluded that in conifers, the cells spiral to the left during the first ten years of growth. In older trees, the spiral decreases to zero and then the grain angle increases in the right-hand direction. In different trees, the angle may vary markedly, even between the early-wood and late-wood of a single growth ring. The spiral grain in angiosperms is too complex to be accurately defined (de Zeeuw, 1965).

In 1941, Tippo published a list of diagnostic characters to be used in descriptions of dicotyledonous woods. These can be summarized as follows:

I. Growth Rings - presence or absence

II. Tracheids and Fibres
   A. Type
   B. Wall Thickness, Sculpturing, Cell Length

III. Vessels
   A. Frequency and Distribution
   B. Vessel Element Shape, Wall Thickness, Size
   C. Perforation Plate Type, End-wall Orientation
   D. Intervascular and Cross-Field Pitting - Size, Shape, Arrangement
   E. Other Features eg. Tyloses

IV. Rays
   A. Type
   B. Abundance
   C. Size
   D. Pitting
E. Specialized Cells and their Contents

V. Axial Parenchyma
  A. Distribution
  B. Pitting
  C. Specialized Types

VI. Other Minor Features
  A. Storied Structure
  B. Crystals
  C. Intercellular Canals
  D. Included Phloem
  E. Vestured Pits
  F. Fibriiform Vessel Elements
  G. Disjunctive Tracheids
  H. Disjunctive Parenchyma

(With the lack of vessels, the relatively uniform structure of gymnosperms is more easily expressed).

To this list can be added further characters which are occasionally used by other xylotomists: specific gravity, tracheid and/or vessel concentration, cell wall composition and cell wall organization.

Within a single tree, and even in a single wood specimen, it is apparent that most of these listed features exhibit a range of variation to make their common use in wood descriptions questionable. Due to a lack of understanding of wood variation or the reluctance of xylotomists to sufficiently assess the variation within a species, most of the wood descriptions published would not accurately or adequately define a species. To survey the range of characters used in description
would involve an inordinate amount of time. Even if the degree of variation were known, the cause and significance of anatomical differences is often unknown, which further complicates any systematic assessments.

It may be that xylotomists have overlooked wood characters which are in fact constant within a species or genus, and which are not subject to environmental fluctuation. Less obvious features of cellular ultrastructure are now receiving more attention, and these may prove to be more reliable taxonomic indicators.

Despite the limitations of most commonly used wood characters, it is generally assumed that many species, genera and families of both gymnosperms and angiosperms are successfully delimited on the sole basis of distinctive combinations of wood features. To classify an unknown plant on the basis of its wood anatomy, it then becomes a process of elimination, to find a set of characters which most closely approximates that usually found in a known species. This lack of precision and subjective deduction, combined with a misunderstanding of the variability and significance of wood features, naturally leads to debatable taxonomic conclusions in many instances.

The whole system of wood taxonomy as it exists is in need of revision, so that uniform methods of description can be adopted. Further studies on the variation of wood features in a variety of species should be carried out to gain more knowledge of the causes and significance of these differences. In the meantime, xylotomists must use greater caution in describing woods. Sections should be studied from all regions of plants growing in a variety of habitats, and the description should accurately portray the degree of variation observed.
Barefoot and Hankins (1982), in their study of the identification of modern and Tertiary woods, have independently reached this conclusion. Formal descriptions should also be accompanied by detailed photomicrographs showing all the features referred to. Taxonomic interpretations based on those features which are known to vary greatly within a single plant must be conservative or tentative.

4.1.2. Palaeoxylotomy

The tough, resistant properties of secondary wood allow it to be preserved much more readily than other more fragile plant tissues. Fossil wood is therefore a common component of prehistoric plant deposits. The cellular structure of wood may be preserved in several ways. In conditions of high temperature and pressure caused by overlying sediment, the original cellulose and lignin composition may alter to relatively pure carbon-containing coal. Petrification of wood results from the replacement by dissolved mineral salts, usually phosphates, carbonates and most commonly silicates. Although the process of petrification is still poorly understood, it is generally believed that silification of plant matter occurs as a result of precipitation and absorption of dissolved silicates in a body of water (Scurfield et al., 1974). The possible genesis of the Winton Fossil Plant Assemblage is detailed in Section 2.4.4.

The accurate interpretation of fossil woods is dependent on a thorough knowledge of the structure and significance of modern wood types. The deficiencies of extant wood taxonomy have therefore been expressed repeatedly as erroneous identifications of fossil taxa. The
palaeoxylotomist is disadvantaged in usually having fragmentary fossil remains of variable quality. It is not generally known which part of the plant a fossil specimen was derived from, or whether a number of specimens found together are from one or more individuals. Unless identifiable foliar and reproductive structures are associated with the wood in a fossil deposit, the describer is given no clues as to the possible identity of the wood.

In view of the problems of variability encountered in the description and classification of living woods, it may be suggested that the identification of inadequate and imperfectly preserved fossil woods should not be attempted. The more responsible workers make it clear that their interpretations are tentative and may be subject to revision or correction on the discovery of more reliable information. With the scarcity of all fossil material, and our lack of knowledge of phylogenetic and evolutionary pathways, it can only be advantageous to record and affiliate all reasonable material discovered. As Bailey (1924) expressed, undescribed specimens tend to deteriorate rapidly through neglect, with the loss of necessary collateral data. The description of fossil material not only facilitates its preservation, but leads to the accumulation of detailed information in the form of descriptions and figures, which may eventually form the basis of important generalizations. An additional argument for not deferring the description of preserved woods arises from the fact that, even if of uncertain genetic relationship, they afford reliable clues concerning palaeoclimates and ancient habitats, and may serve as useful stratigraphic indicators.
The occasional procedure of referring wood petrifications to extant or extinct genera is somewhat deceptive. Unless diagnostic floral and foliar structures are associated with the wood, it is undesirable to place fossil woods in natural genera, especially when our knowledge of the taxonomic significance of wood features is still incomplete. Fossil woods are usually placed in artificial form-genera of organ-genera, with no implications of affinity to natural groups. Some fossil woods, particularly conifers, which have remained relatively unchanged since the Mesozoic, have been given artificial generic names which include the names of the modern genera they most closely resemble, for example Araucarioxylon and Piceoxylon. A major problem with this type of nomenclature is that subsequent workers may justifiably assume that these generic names mean the inclusion of the types possessing them in a modern family. It must also be emphasized that the specific epithets of form- and organ-genera refer merely to the specimens described from given localities. The failure to recognize this fact may lead to much confusion and to numerous misleading generalizations.

In describing a fossil wood from a new locality, it is most important to realize that the degree of variation that exists in the species will be much greater than in the sample examined. Evolutionary interpretations and taxonomic conclusions must therefore be conservative, while the description of the wood specimen must be sufficiently complete to accurately express the characteristics of the individual sample.
4.1.3. *Araucarioxylon* Kraus 1870

Vegetative shoots and reproductive cones assignable to the genus *Araucaria* are common in the Winton Fossil Plant Assemblage. As expected, a high proportion of the petrified woods have a typical araucarian structure, but in the absence of leaves and cones joined to the wood, they must be placed in the form-genus *Araucarioxylon* Kraus 1870. While this name in principle disregards natural affinity to the modern genus, it is reasonable to assume that the *Araucarioxylon* from Winton is in fact araucarian.

The definition of the *Araucarioxylon* type has been disputed by many workers, so that clarification of its structure and status is necessary. The type species is *Araucarioxylon carbonaceum* (Witham) Kraus from the Carboniferous of England. The genus comprises over 50 species found in all continents (Lepekhina, 1972). *Araucarioxylon* has been recorded from the Lower Carboniferous well into the Tertiary (Miller, 1977).

The structure of the genus has been discussed by various workers, however the interpretation by Lepekhina (1972) is in accordance with the original diagnosis of *Araucarioxylon* Kraus in Schimper (1872, pp. 380-1) and reads as follows:

"Growth rings more or less distinct or are absent. Polygonal or round tracheid pits in uniseriate or multiseriate araucarioid arrangement, spiral thickenings not present. Cross-field pits are cupressoid and numerous. Wood parenchyma, ray tracheids and ducts are absent. Rays, as a rule, are uni- to biseriate, rarely up to five-seriate, of various height from low (up to 10 cells) to rather high (50 - 60 cells). Horizontal and ray walls smooth, unpitted."

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Many other form-genera have been confused with *Araucarioxylon*, to the degree that an unwieldy synonymy exists. *Dadoxylon* Endlicher 1847 has the same secondary wood structure as *Araucarioxylon*. As it infers no affinity with the Araucariaceae, the noted workers Gothan (1905), Seward (1919) and Scott (1920-23) preferred the name *Dadoxylon*. However, the two genera can be separated by the distinctive pith and primary xylem present in *Dadoxylon*, both of which are absent in *Araucarioxylon*. Lepekhina's diagnosis of *Dadoxylon* (which follows the original description by Endlicher (1847) is as follows:


Greguss (1967) and Maheshwari (1972) prefer to separate *Araucarioxylon* and *Dadoxylon* on the basis of growth ring width, after noting that many species of *Dadoxylon* have multiseriate rays, compared with the mostly uniseriate rays of *Araucarioxylon*. This distinction is not acceptable, as the character of growth ring width is known to be extremely variable within a single species. Torrey (1923) distinguished *Dadoxylon* by its lack of resin canals and wood parenchyma, which he said were present in *Araucarioxylon*. However, this disagrees with the original diagnosis. Other workers, including Seward and Ford (1906) and Jeffrey (1912) agree that these structures are absent in both genera. Felix (1887) and Arber (1905) suggested that *Araucarioxylon* should be used for Mesozoic species, while *Dadoxylon* should be used for Palaeozoic species, but distinctions based on age are misleading.
It is now generally accepted that *Dadoxylon* is in fact the wood of *Cordaites*, a genus common in the late Palaeozoic and thought to be ancestral to modern conifer families (Miller, 1977). Although *Cordaisxylon* Grand’Eury 1877 is also used for *Cordaites* wood, it can be separated from *Dadoxylon* by its possession of a septate pith (Lepekhina, 1972). The importance of this character in taxonomy is not understood, but it is known that the structure of the pith and primary xylem alters within a single trunk from the base to the apex (Lepekhina, 1972). It is therefore reasonable that *Dadoxylon* and *Cordaisxylon* should be closely related.

The identical structure of the secondary xylem in *Araucarioxylon* and *Dadoxylon* (and *Cordaisxylon*) pose problems in the identification of samples which consist only of secondary tissue. In these cases, the specimens must by definition be placed in *Araucarioxylon*. Obviously, many Palaeozoic species of *Araucarioxylon* are in reality the cordaitean *Dadoxylon* with pith and primary tissues missing. Similarly, Mesozoic and Tertiary species of *Dadoxylon*, like those referred to by Lakhanpal et al. (1975) cannot be cordaitean. It is therefore dangerous to classify fossil woods which are not associated with specimens which are indicative of true affinity.

It is also important that descriptions of new fossil wood species should include information about the following characters:

1. Growth ring structure
2. Tracheid pitting
3. Cross-field pitting
4. Porosity of horizontal and tangential ray cell walls
5. Width and height of rays
6. Wood parenchyma
7. Resin ducts

8. Presence of spirals in tracheids

According to Lepekina (1972), incomplete descriptions have rendered half the species of Araucarioxylon useless. This is particularly true of most of the Australian species described by Carruthers (1880), Shirley (1898), Chapman (1903) and Sahni and Singh (1926).

4.1.4. Winton Fossil Woods

(Figs. 28 - 83)

Twenty-one of the better specimens of fossil wood from the Winton assemblage were sectioned for examination. They were all found to be coniferous, however, only 12 specimens showed a sufficient degree of preservation to enable their accurate description. The form-genus Araucarioxylon (8 samples) was divided into 4 parataxa, and proved to be the predominant wood type. Presumably, araucarians were a major feature of the original forest.

One other parataxon was described from 4 samples, but these immature woods lacked sufficient distinctive features to systematically place them. They most closely resemble the woods of the Podocarpaceae and Taxodiaceae, both of which are common families in the fossil deposit.

While studying the techniques and procedures used in classifying woods (Section 4.1.1.), it became apparent that the degree of variation within a single species may be enough to cover the known variation in most families of conifers. Only the primitive Araucariaceae really shows a uniqueness in its woods which allows quick identification to
the family level. For this reason, I cannot justify describing any of the Winton woods which lack the diagnostic features listed earlier. The descriptions which follow are necessarily complete so that the same or similar species may readily be identified. The classifications I make are tentative, and I readily accept that the diagnoses may need to be modified if specimens are found in the future which stretch the species’ range of variability beyond that which I have described.

**Specimen W300** (Figs. 28 - 33)

Growth rings distinct. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 58μ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, occasionally biseriate in places, from 3 - 30 cells in height, average height 12 cells. Ray cells smooth-walled, barrel-shaped, small, 23μ x 11μ. Tacheidal pits simple-bordered, oval, uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Pit diameter averages 25μ. Cross-field pits large, 21μ, cupressoid, usually 2 and arranged vertically, rarely one which occupies most of the cross-field. Bars of Sanio absent. Spiral thickening on tracheids absent.

**Specimen W279** (Figs. 34 - 39)

Growth rings distinct. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 65μ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, occasionally biseriate in places, from 2 - 25 cells in height, average height 11 cells. Ray cells smooth-walled, barrel-shaped, small, 23μ x 13μ. Tacheidal pits simple-bordered, oval, uniseriate and contiguous, occasionally biseriate and alternating,
giving the pits a polygonal outline. Pit diameter averages 27μ. Cross-field pits large, 23μ, cupressoid, usually 2 in number and arranged vertically, rarely one, which occupies most of the cross-field. Bars of Sanio absent. Spiral thickening on tracheids absent.

Specimen W134 (Figs. 40 - 45)

Growth rings distinct, but distorted transversely during preservation. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 63μ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, occasionally biseriate in places, from 2 - 28 cells in height, average height 11 cells. Ray cells smooth-walled, barrel-shaped, small, 21μ x 12μ. Tracheidal pits simple-bordered, oval, uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Commonly, the alternately arranged pits are not closely contiguous, so that the pit borders have a circular to oval outline. Pit diameter averages 25μ. Cross-field pits large, 18μ - 35μ, average 25μ, cupressoid and dacrydioid, 1 to 3 in number, occupying most of the cross-field. Bars of Sanio absent. Spiral thickening on tracheids absent.

Specimen W197 (Figs. 46 - 50)

Growth rings indistinct, very distorted during preservation. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 28μ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, from 3 - 12 cells in height, average height 6 cells. Ray cells smooth-walled, barrel-shaped, 26μ x 18μ, often infilled with chemically replaced resins or tannins.
Tracheidal pits simple-bordered, oval, mainly uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Pit diameter averages 13µ. Cross-field pits small, 7µ, cupressoid, 2 to 5 per cross-field, mainly 2 and arranged diagonally, or 4 and spaced evenly in the cross-field. Bars of Sanio absent. Spiral thickening on the tracheids absent.

**Specimen W147** (Figs. 51 - 53)

Growth rings indistinct. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 31µ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, occasionally biseriate in places, from 1 - 9 cells in height, average height 4 cells. Ray cells smooth-walled, barrel-shaped, 28µ x 18µ. Tracheid pits simple-bordered, oval, mainly uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Pit diameter averages 17µ. Cross-field pits small, 7µ, cupressoid, 1 to 5 in number, arranged irregularly in the cross-field. Bars of Sanio absent. Spiral thickening on the tracheids absent.

**Specimen W154** (Figs. 54 - 57)

Growth rings indistinct, distorted slightly during preservation. Early-wood composed of thin-walled, squarish tracheids arranged in radial rows, average radial diameter of tracheids 35µ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, from 3 - 17 cells in height, average height 9 cells. Ray cells smooth-walled, barrel-shaped, 22µ x 16µ. Tracheid pits simple-bordered, oval, mainly uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Pit diameter averages 13µ.
Cross-field pits small, 7μ, cupressoid, 1 to 4 in number, arranged irregularly in the cross-field. Bars of Sanio absent. Spiral thickening on the tracheids absent.

Specimen W170 (Figs. 58 - 63)

Growth rings distinct. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 41μ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, from 2 - 6 cells in height, average height 4 cells. Ray cells smooth-walled, barrel-shaped, 19μ x 15μ. Tracheid pits simple-bordered, oval, usually uniseriate and contiguous, sometimes spaced, occasionally biseriate and alternating, rarely triseriate and alternating, usually giving the pits a polygonal outline. Pit diameter averages 18μ. Cross-field pits large, 15μ, cupressoid, usually 1, sometimes 2, arranged vertically in the cross-field. Bars of Sanio absent. Spiral thickening on tracheids absent.

Specimen W211 (Figs. 64 - 68)

Growth rings fairly distinct, but badly distorted during preservation. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 36μ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, from 1 - 26 cells in height, average height 9 cells. Ray cells smooth-walled, barrel-shaped, small, 23μ x 14μ, often infilled with tannins or resins. Tracheidal pits simple-bordered, oval, uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Pit diameter averages 26μ. Cross-field pits small, average 5μ, cupressoid, 2 to 8 in number, usually 2 and arranged diagonally in the cross-field, 4 and spaced in the crossfield, or 8 and crowded. Bars of
Sanio absent. Spiral thickening on tracheids absent.

**Specimen W165** (Figs. 69 - 74)

Growth rings fairly indistinct. Early-wood composed of thin-walled rounded tracheids, average radial diameter of tracheids 19µ. Axial wood parenchyma and resin canals absent. Xylem rays numerous, 1 - 7 cells in height, average height 3 cells, uniseriate. Ray cells smooth-walled, rounded, 26µ x 18µ, end cells usually elongate. Tracheidal pits simple-bordered, circular, occasionally contiguous, but usually separate. Pit diameter averages 12µ, pit aperture occupying half of the pit diameter. Cross-field pits small, cupressoid, 5µ in diameter, usually 4 spaced evenly in the cross-field. Bars of Sanio absent. Spiral thickening present faintly on some tracheids.

**Specimen W105** (Figs. 75 - 78)

Growth rings fairly distinct. Early-wood composed of thin-walled, rounded tracheids, average radial diameter of tracheids 23µ. Axial wood parenchyma and resin canals absent. Xylem rays numerous, 1 - 15 cells in height, average height 4 cells, uniseriate. Ray cells smooth-walled, rounded, average size 23µ x 16µ, end cells usually elongate. Tracheidal pits simple-bordered, circular, uniseriate, occasionally contiguous, usually separate. Pit diameter averages 12µ, pit aperture large, occupying half of the pit diameter. Cross-field pits small, cupressoid, 5µ in diameter, usually 4 and spaced evenly in the cross-field. Bars of Sanio absent. Spiral thickening on tracheids absent.

**Specimen W280** (Figs. 79,80)

Growth rings fairly distinct. Early-wood composed of thin-walled rounded tracheids, average radial diameter of tracheids 18µ. Axial wood
parenchyma and resin canals absent. Xylem rays uniseriate, 1 - 6 cells in height, average height 3 cells. Ray cells smooth-walled, rounded, average size 19μ x 14μ, end cells usually elongate. Tracheidal pits simple-bordered, circular, uniseriate, occasionally contiguous, usually separate. Pit diameter averages 13μ, pit aperture large, occupying half of the pit diameter. No cross-field pits preserved. Bars of Sanio absent. Spiral thickening on tracheids absent.

**Specimen W350** (Figs. 81 - 83)

Growth rings fairly distinct. Early-wood composed of thin-walled rounded tracheids, average radial diameter of tracheids 21μ. Axial wood parenchyma and resin canals absent. Xylem rays numerous, uniseriate, 1 - 6 cells in height, average height 3 cells. Ray cells smooth-walled, rounded, often infilled with chemically replaced resinous or tanniniferous contents, average size 19μ x 14μ, end cells usually elongate. Tracheidal pits rarely preserved, simple-bordered, circular, uniseriate, occasionally contiguous, usually separate. Pit diameter averages 15μ. No cross-field pits preserved. Bars of Sanio absent. Spiral thickening on tracheids absent.

It may be seen from the wood descriptions that the specimens may be divided into several groups, each containing woods with similar combinations of characters. Given the proven variability of wood anatomy, they are here designated as parataxa.

Specimens W300, W279, and W134 are very similar in most respects, except for the possession of some dacrydioid cross-field pits in W134. It is interesting that these three specimens have an almost identical external morphology, all being oblong pieces of regularly fractured,
lightly-stained, dull silica. These specimens are probably derived from
the same species, perhaps the same individual. Considering the range of
variability found in the cross-field pits of extant Sequoia by Bailey
and Faull (1934), I would place little emphasis on the possession of
dacrydioid pits by specimen W134. I suspect the dacrydioid pitting to
be merely air spaces in the highly resinous parenchyma cells of some
axial rays.

The distinctive and characteristic possession of typical
araucarian pitting on the radial walls of the tracheids within this
group allows their placement within the form-genus Araucarioxylon.
However, their possession of one or two large cross-field pits is not
in accordance with the original description of the Araucarioxylon type,
which describes the cross-field pits as "numerous". In view of the
possession by some araucarians of only one or two large cross-field
pits (Greguss, 1955), and the possession of similar features in known
species of Araucarioxylon (Lakhanpal et al., 1975), little systematic
importance need be placed on this feature.

On comparison with other species of Araucarioxylon, these three
Winton woods show a distinct combination of features and hence are
described here as Parataxon 1 within Araucarioxylon.

4.1.4.1. Araucarioxylon Parataxon 1 (Figs. 28 - 45)

Diagnosis: Growth rings distinct. Early-wood composed of thin-walled
squirish tracheids arranged in radial rows, mean diameter of tracheids
between 58μ and 63μ. Axial wood parenchyma and resin canals absent.
Xylem rays uniseriate, occasionally biseriate in places, from 2 - 30
cells in height, average height 11 cells. Ray cells smooth-walled,
barrel-shaped, small, 21μ - 23μ high x 11μ - 13μ wide. Tracheidal pits simple-bordered, oval, uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Biseriate pits may sometimes be loosely contiguous, giving them a circular to oval outline. Mean pit diameter 25μ - 27μ. Bars of Sanio absent. Cross-field pits large, 21μ - 25μ, cupressoid, occasionally dacrydioid, 1 to 3 in number, usually two and arranged vertically, rarely one which occupies most of the cross-field. Spiral thickening on tracheids absent.

Specimens examined: W134, W279, W300

Locality: 50km north-west of Winton, Queensland. 22° 12' 00''S and 142° 31' 30''E.

Specimens W147, W154 and W197 can also be grouped into a separate parataxon within Araucarioxylon. They show more typical features of the classical Araucarioxylon type by their possession of up to five small, cupressoid, cross-field pits. It is also interesting to note that their external appearance reflects their anatomical similarities, in that the three specimens are all bulky, irregularly fractured, darkly-stained segments of branches or trunks, with deeply furrowed, lightly-stained bark. Single parataxa appear to follow similar patterns of mineralization and weathering, due perhaps to their uniform organic and physical nature.

4.1.4.2. Araucarioxylon Parataxon 2 (Figs. 46 - 57)

Diagnosis: Growth rings indistinct. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, mean radial diameter of
tracheids 28µ - 35µ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, rarely biseriate in places, from 1 - 17 cells in height, average height 4 - 9 cells. Ray cells smooth-walled, barrel-shaped, 22µ - 28µ high x 16µ - 18µ wide. Tracheidal pits simple-bordered, oval, mainly uniseriate and contiguous, occasionally biseriate or triseriate and alternating, giving the pits a polygonal outline. Mean pit diameter 13µ - 17µ. Bars of Sanio absent. Cross-field pits small, 7µ, cupressoid, 1 to 5 in number and spaced evenly or irregularly in the cross-field. Spiral thickening on tracheids absent.

Specimens examined: W147, W154, W197

Locality: 50km north-west of Winton, Queensland. 22° 12' 00''S and 142° 31' 30''E.

Specimens W170 and W211 both belong to the form-genus Araucarioxylon, but are sufficiently distinct from Paratax a 1 and 2 for them both to be classified as separate paratax a.

4.1.4.3. Araucarioxylon Parataxon 3 (Figs. 58 - 63)

Diagnosis: Growth rings distinct. Early-wood composed of thin-walled squarish tracheids arranged in radial rows, average radial diameter of tracheids 41µ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, 2 - 6 cells in height, average height 4 cells. Ray cells smooth-walled, barrel-shaped, 19µ x 15µ. Tracheidal pits simple-bordered, oval, uniseriate and contiguous, sometimes spaced, occasionally biseriate and alternating, rarely triseriate and alternating, usually giving the pits a polygonal outline. Pit diameter averages 18µ. Cross-field pits large, 15µ, cupressoid, usually one,
sometimes two, arranged vertically in the cross-field. Bars of Sanio absent. Spiral thickening on tracheids absent.

Specimen examined: W170

Locality: 50km north-west of Winton, Queensland. 22° 12′ 00″S and 142° 31′ 30″E.

4.1.4.4. Araucarioxylon Parataxon 4 (Figs. 64-68)

Diagnosis: Growth rings fairly indistinct, but badly distorted during preservation. Early-wood composed of thin-walled, squarish tracheids arranged in radial rows, average radial diameter of tracheids 36μ. Axial wood parenchyma and resin canals absent. Xylem rays uniseriate, 1 - 26 cells in height, average height 9 cells. Ray cells smooth-walled, barrel-shaped, small, 23μ x 14μ, often infilled with chemically replaced tannins or resins. Tracheidal pits simple-bordered, oval, uniseriate and contiguous, occasionally biseriate and alternating, giving the pits a polygonal outline. Pit diameter averages 26μ. Cross-field pits small, average diameter 5μ, cupressoid, 2 to 8 in number, usually 2 and arranged diagonally in the cross-field, 4 and spaced in the cross-field, or 8 and crowded. Bars of Sanio absent. Spiral thickening on tracheids absent.

Specimen examined: W211

Locality: 50km north-west of Winton, Queensland. 22° 12′ 00″S and 142° 31′ 30″E.

Another group of woods which can be assigned to a single parataxon are represented by specimens W105, W165, W280 and W350. The
last two specimens show incomplete preservation in that no evidence of
cross-field pitting was found, but based on all other characters, it is
apparent that the four specimens may be derived from the same species.
The external appearance of the wood is again similar, all being small
branch segments less than 5cm in diameter, with darkly stained matrices
showing clear evidence of growth ring structure.

4.1.4.5. Coniferae-Incertae sedis Parataxon 1 (Figs. 69 - 83)

Diagnosis: Growth rings usually distinct. Early-wood composed of
thin-walled, rounded tracheids, mean radial diameter of tracheids 18µ -
23µ. Axial wood parenchyma and resin canals absent. Xylem rays
numerous, uniseriate, 1 - 15 cells in height, average height 3 cells.
Ray cells smooth-walled, rounded, 19µ - 26µ high x 14µ - 18µ wide.
Tracheidal pits simple-bordered, circular, uniseriate and separate,
ocasionally touching. Mean pit diameter 12µ - 15µ. Bars of Sanio
absent. Cross-field pits small, cupressoid, 5µ in diameter, usually 4
in number and spaced evenly in the cross-field. Spiral thickening on
tracheids usually absent.

Specimens examined: W105, W165, W280 and W350
Locality: 50km north-west of Winton, Queensland. 22° 12'00'' S and
142° 31' 30'' E.

The combination of characters possessed by this parataxon lack
sufficient definition to accurately place it within a particular
form-genus. The type of tracheidal pitting excludes it from the family
Araucariaceae, while its lack of resin canals excludes it from the
Pinaceae. It most closely resembles the wood of the Podocarpaceae and
Taxodiaceae, both of which are well represented by leaf and fruit
fossils in the deposit. The wood parataxon shows equal similarity to both these families.

It is probable that the characters would have become more definitive during maturation of the wood, as the four specimens are from immature regions of the original trees, possessing typically small cells and tracheidal pits. These four woods illustrate some of the deficiencies in palaeoxylotomy, when random specimens are described as representatives of a whole species, and cannot account for the variation of characters which is known to occur within a species or individual plant.
4.2. Reproductive Structures

4.2.1. Araucariaceae

4.2.1.1. Introduction - Extant Species and Taxonomy

The Araucariaceae is a small relict family of conifers, currently restricted to the Southern Hemisphere (Fig. 84). Its members are tall, evergreen trees with characteristic woody seed cones which are deciduous at maturity.

The family contains two genera, Agathis Salisbury and Araucaria de Jussieu. Agathis can be distinguished from Araucaria by its possession of a winged seed which is free from the cone-scale. In Araucaria, the seed is not winged, but united with or enclosed within the cone-scale. Agathis leaves are petiolate with blunt apices, while in Araucaria, the leaves are not petiolate and have acute apices (Peters, 1983).

Agathis has recently been revised by Whitmore (1980), who recognized 13 species native to Borneo, Malaya, Indonesia, Philippines, New Guinea, Queensland, Fiji, New Caledonia and New Zealand. The Australian species, numbering 3, were earlier revised by Hyland (1977), who established a new species, Agathis atropurpurea Hyland. A. palmerstonii F. Muell. was placed in synonymy with A. robusta (C. Moore ex F. Muell.) F.M. Bail., while A. microstachya J.F. Bail. et. C.T. White was conserved.

Extant species of Araucaria are represented in temperate South America (Brazil, Argentina, Chile), eastern Australia, New Guinea, New Caledonia, New Hebrides and Norfolk Island. Relationships within the genus have never been clear, despite 5 taxonomic revisions of the group as a whole (see Table 2). Seward and Ford (1906) recognized 11 species, 4 belonging to the section Columbea Endlicher 1842 (incorrectly spelt
Table 2. The Extant Species of Araucaria de Jussieu, according to various authors

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*note incorrect spelling of Colymbes
The bracketed species are considered to be the correct synonyms in the present classification.
"Colymsa" by Seward and Ford), and 7 species in section Eutacta
Endlicher 1842. Wilde and Eames (1952) established a new section,
Bunya, into which they transferred *Araucaria bidwillii* from Colymbsa,
and recognized White's (1947) erection of a new section Intermedia,
which comprised 3 species from New Guinea: *A. hunsteinii* (removed from
Colymbsa) and 2 new species, *A. schumanniana* Warb. and *A. klinkii
Lauterb. (both also from Colymbsa). The original diagnosis of section
Colymbsa was therefore emended by Wilde and Eames. To the section
Eutacta, these authors added *A. humboldtensis*, *A. biramulate*, and *A.
berneri*, 3 new species from New Caledonia, described by Buchholz
(1949). Florin (1963) in his major review of the distribution of fossil
and extant conifers, recognized the new taxonomic system of Wilde and
Eames.

Dallimore and Jackson (1966) restored *A. bidwillii* to the section
Colymbsa, thus discarding Bunya. They placed *A. hunsteinii* and *A.
schumanniana* in synonymy with *A. klinkii* in section Intermedia. In the
section Eutacta, Dallimore and Jackson included a new species,
*Araucaria beccarii* Warburg. 1900 from New Guinea, which was previously
used as a synonym of *A. cunninghamii*, while *A. montana* Brongniart et
Gris 1870-1871 was omitted from the section.

Gaussen (1970) followed Dallimore and Jackson in placing *A.
bidwillii* in section Colymbsa, but recognized the 3 species in
Intermedia used in the classification of Wilde and Eames. Gaussen
returned *A. montana* to Eutacta and added 5 new species from New
Caledonia: *Araucaria laubenfelsii* Corbasson 1968, *A. luxurians*
(Brongniart et Gris) de Laubenfels 1969, *A. scopulorum* de Laubenfels
1969, *A. schmiedii* de Laubenfels 1969, and *A. nemorosa* de Laubenfels
1969. Gaussen adopted a New Guinean species *A. heineana* Schlechter in

65
section Eutacta.

De Laubenfels (1972) agreed with Gaussee and Dallimore and Jackson in eradicating section Bunya, but also discarded section Columbea in favour of a new section called Araucaria, into which he placed A. bidwillii. Similarly, de Laubenfels did not recognize the section Intermedia, and placed a single (undesignated) species representing Intermedia into section Araucaria. Fifteen species are placed in section Eutacta in de Laubenfels' listing. A. beccarii and A. heineana (both accepted by Gaussee (1970)) are placed in synonymy with A. cunninghamii, while A. balansae Brongniart et Gris 1870-1871 is made synonymous with A. subulata Vieill. 1861, which must receive priority.

Unfortunately, no list of the species of Araucaria includes all valid species in their accepted sections. This has led to inconsistencies in discussions of the genus, causing problems to the palaeosystematist. For example, in the study by Stockey (1982) on the evolution of the Araucariaceae, the author stated that according to de Laubenfels (1972), Araucaria contained 18 species, when in fact, de Laubenfels included 19 species. Stockey went on to list 21 species in the genus, by including the 3 species of section Intermedia proposed by White (1947), thus inferring that the grouping of A. klinkii, A. hunsteinii and A. schumanniace by de Laubenfels was not justified. When erecting the new section Intermedia, White recognized the possibility that these 3 species might all represent forms of one variable species. This has since been determined to be the case (Hall et al., 1970; Havel, 1975; Howcroft, pers. comm.)*. A. schumanniace Warb. 1900, and A. klinkii Lauterb. 1913 are now used in synonymy with A. hunsteinii K.

* Mr. N. Howcroft. Forest Research Station, Bulolo, Papua New Guinea.
Schum. 1889 (klinki pine). For reasons of priority, *A. hunsteinii* must therefore be recognized as the valid species to represent the section Intermedia. Unfortunately, although he recognized the synonymy, de Laubenfels (1972) did not indicate which species is valid.

The division of *Araucaria* into four sections by Wilde and Eames (1952) has received general acceptance by the taxonomists working with the genus, including Calder (1953), Stockey (1975) and Clifford and Constantine (1980). It is recognized that the genus is a relict group. Species assignable to each section have been found in the fossil record (Stockey, 1982), which supports the reasoning that each section can be clearly defined and is thus a separate taxonomic entity. The sections outlined and described by Wilde and Eames (1952) are as follows:

Section Butacta Endlicher 1842

Leaves reduced, thick and often keeled, imbricating and usually erect. Male cones terminal, solitary; female cones on long peduncles. Ovulate cone-scales samara-like, thinly winged, indehiscent, the seed retained on the scale at shedding; vascular supply of bract-scale unit single at source. Germination epigeal. Cotyledons subsessile, freed from seed at germination. Seedling not fleshy.

Section Columbea Endlicher emend. Wilde and Eames 1952

Leaves large, generally thin, flat. Male cones axillary, usually two to several on foliaceous branches. Ovulate cone-scales nut-like, wings absent, indehiscent, the seed retained on the scale at shedding; vascular supply of bract-scale unit single at source. Germination hypogeal. Cotyledons long, stalked in germination, retained in seed coats, stalks not fused. Seedling fleshy, without a long subterranean dormant period.
Section Intermedia White 1947

Leaves large, generally thin, flat, spreading, sometimes slightly imbricate; juvenile leaves needle-like, flat, small. Male cones axillary, female cones axillary. Ovulate cone-scales samara-like, with broad thin wings, indehiscent; seed retained on the scale at shedding. Germination epigeal. Cotyledons subsessile, freed from seed coats at germination. Seedling not fleshy.

Section Bunya Wilde and Eames 1952

Leaves large, flat, spreading or slightly imbricate. Male cones axillary; female cones subsessile or on short (to 2cm long) peduncles. Ovulate cone-scales large, heavy, with woody wings; dehiscent, the large "seed" shed from the scale at maturity; vascular supply of bract-scale unit double at source. Germination hypogeal. Cotyledons long, stalked in germination, retained within seed coats, the stalks fused into a hollow cylinder. Seedling fleshy, with a long subterranean dormant period.

The following list of the 19 true and extant members of Araucaria in their respective generic sections has not been seen before (see also Table 2).

Araucaria de Jussieu

Section Columbea Endlicher, Emend. Wilde and Eames 1952

Araucaria araucana (Molina) K. Koch

Chile, Argentina

A. angustifolia (Bertoloni) O. Kuntze

Brazil, Argentina

Section Bunya Wilde and Eames 1952

Araucaria bidwillii Hooker

Queensland

68
Section Intermedia White 1947

*Araucaria hunsteinii* K. Schumann. New Guinea

Section Eutacta Endlicher 1842

*Araucaria cunninghamii* Aiton ex Lambert New Guinea, north-east Australia

*A. heterophylla* (Salisbury) Franco Norfolk Island

*A. columnaris* (Forster) Hooker New Caledonia

*A. rulei* Mueller New Caledonia

*A. subulata* Vieillard New Caledonia

*A. muelleri* (Carrière) Brongniart et Gris New Caledonia

*A. montana* Brongniart et Gris New Caledonia

*A. humboldtensis* Buchholz New Caledonia

*A. piramulata* Buchholz New Caledonia

*A. bernieri* Buchholz New Caledonia

*A. laubenfelsii* Corbasson New Caledonia

*A. luxurians* (Brongniart et Gris) de Laubenfels New Caledonia

*A. scopulorum* de Laubenfels New Caledonia

*A. schmidii* de Laubenfels New Caledonia

*A. nemorosa* de Laubenfels New Caledonia

The only key including all currently recognized species of *Araucaria* was compiled in French by Gaussen (1970), and includes separated species now reduced to synonymy. The Appendix features an English key to the extant species just listed, which I have adapted from Gaussen.
4.2.1.2. Fossil Araucariaceae

The origin and evolutionary history of the modern conifer families has traditionally sparked interest and argument from palaeobotanists. The most accepted hypothesis was proposed by Florin (1951) who, after extensive analysis of fossil conifers, concluded that the present families arose from the Palaeozoic Lebachiaceae via the Voltziaceae of the Mesozoic. (After reviewing the reproductive structures of fossil and extant Taxaceae, (1954, 1958) Florin decided that this family had a separate ancestry from other modern conifers). Recently, Miller (1982) re-examined Florin’s hypothesis using two separate numerical analyses of the character states of 14 characters found in 48 taxa of fossil and modern conifers. The results of both analyses support Florin’s hypothesis.

The specific ancestors of the extant conifer families remain unknown. The Araucariaceae was a considerably larger and more diverse family during the Mesozoic. It is first found in the fossil record in the Late Triassic (Bock, 1954, 1969; Florin, 1963) and became very common in both hemispheres during the Jurassic. (Recent work by Cornet has shown that the genus Primarauarca from the Triassic of Virginia may not in fact be gymnospermous (Stockey, 1982)). By the end of the Cretaceous, the family began to diminish and became constricted to the Southern Hemisphere.

Araucarian wood (Araucarioxylon) is common throughout the fossil record and was discussed in Sections 4.1.3. and 4.1.4. Fossil leaves assignable to the Araucariaceae include species of the artificial form-genera Brachyphyllum Lindley et Hutton and Pagiophyllum Heer.
Unless cuticle is preserved, the true araucarian affinity of many species of these genera remains in doubt. The female cones can provide best evidence of natural relationships within the Araucariaceae.

Few araucarian male strobili have been described from the fossil record, particularly those found in association with identifiable araucarian foliage and pollen. The male cones borne on the shoots of *Brachyphyllum mamillare* (Kendall, 1949) and the cones found with leaves of *Araucaria lignitici* (Cookson and Duigan, 1951) are both typical of extant strobili of *Araucaria* section Eutacta. The only obvious distinguishing feature of the male cones between the species of *Araucaria* is the generally smaller cones seen in species of section Eutacta. The conservative nature of the microstrobili means that these structures are of minor value in determining evolutionary strategies of the genus.

Stockey (1982) recently reviewed the evolutionary history of the family by considering fossil evidence elucidated this century. The modern genus *Agathis* has a sparse fossil record, being found only from the Tertiary of the Southern Hemisphere. [*Agathis jurassica* White (= *Podozamites lanceolatus* Lindley et Hutton), a coniferous twig from the Jurassic Talbragar Fish Bed Flora in New South Wales (White, 1981) lacks diagnostic cuticular features, and is associated with cone-scales showing close similarity to those of *Araucaria* section Eutacta (Stockey, 1982)]. Definite *Agathis* fossils occurred in the Oligocene and Miocene sediments of New South Wales, Victoria (Cookson and Duigan, 1951), New Zealand (Cookson and Duigan, 1963) and the Eocene of South Australia (Blackburn, pers. comm.*). These late discoveries of the genus must infer a relatively recent evolution within the family.

* Dr. D.T. Blackburn, C/- Dept. of Botany, University of Adelaide, Adelaide, South Australia.
Miller (1977) noted the similarity between cone-scales of *Agathis* and those of the fossil araucarian genus *Doliostrobous* Marion, which is associated with leaves similar to those of section Eutacta. Miller suggested this to be support for the possible evolution of *Agathis* from *Araucaria* in the Late Jurassic to Early Cretaceous.

Knowledge of the evolutionary history of *Araucaria* and its closely related genera is more complete. The modern genus *Araucaria* is known from both hemispheres since the middle Jurassic. In view of Stockey's (1982) work on the family, it would serve little purpose in this thesis to reiterate in detail the significant araucarian fossils already discussed by that author. These fossils, with several additions, are listed in Table 3.

The only fossils in Table 3 which can be placed with certainty into the section Eutacta of *Araucaria* are the cone-scales, *Araucarites cutchensis* and seed-scale complexes of *Araucarites phillipsii* and its associated leafy shoots called *Brachyphyllum mammillare* (Stockey, 1982). Based on the cuticular preservation of *Araucaria lignitici*, this species may also be placed into Eutacta (Cookson and Duigan, 1951). The *Araucarites* cone described by Mildenhall and Johnston (1971) needs to be re-examined before placement into section Eutacta (Stockey, 1982).

The cuticular features of the fossil leaves named *Araucaria nathorstii* show close affinity to the modern species *Araucaria araucana* of section Columba (Stockey, 1982). Section Intermedia is only represented in the fossil record by the leaves *Araucaria baestii* (Bose, 1975).

The now monospecific section Bunya is the best represented group of fossil *Araucaria*. Wieland (1935), Calder (1953), and Stockey (1975,
Table 3. Significant Fossil Species of Araucaria and Related Genera

<table>
<thead>
<tr>
<th>Species and Reference</th>
<th>Age and Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachyphyllum mamillare (Kendall, 1949)</td>
<td>Jurassic, Yorkshire</td>
</tr>
<tr>
<td>Araucarites phillipsi (Kendall, 1949)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>Araucarites nipaniensis (Singh, 1957)</td>
<td>&quot; , India</td>
</tr>
<tr>
<td>unnamed (Sharma and Bohra, 1977)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>unnamed (Bose and Jain, 1964)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>Araucaria brownii (Stockey, 1980a)</td>
<td>&quot; , Dorset</td>
</tr>
<tr>
<td>Araucaria mirabilis (Wieland, 1935; Calder, 1953; Stockey, 1975, 1978)</td>
<td>&quot; , Patagonia</td>
</tr>
<tr>
<td>Araucarites bindabuncensis (Vishnu-Mitte, 1954)</td>
<td>&quot; , India</td>
</tr>
<tr>
<td>Araucarites cribii (Townrow, 1969)</td>
<td>&quot; , Australia</td>
</tr>
<tr>
<td>Araucaria sphaerocarpa (Stockey, 1980b)</td>
<td>Middle Jurassic, Britain</td>
</tr>
<tr>
<td>Conites araucarioides (Gothan, 1927)</td>
<td>Upper Jurassic, Tanzania</td>
</tr>
<tr>
<td>Araucarites seharaensis (Bose &amp; Maheshwari, 1973)</td>
<td>&quot; , India</td>
</tr>
<tr>
<td>Araucarites minutus (Bose &amp; Maheshwari, 1973)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>Araucaria indica (Sukh-Dev &amp; Zeba-Bano, 1978)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>Araucaria pantiana (Bose &amp; Maheshwari, 1973)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>Araucarites rogersii (Brown, 1977)</td>
<td>Lower Cretaceous, South Africa</td>
</tr>
<tr>
<td>Araucarites cutchensis (Pant &amp; Srivastava, 1968)</td>
<td>&quot; , India</td>
</tr>
<tr>
<td>&quot; (Halle, 1913)</td>
<td>&quot; , Antarctica</td>
</tr>
<tr>
<td>Araucarites wyomingensis (Seward, 1919)</td>
<td>&quot; , Black Hills U.S.A.</td>
</tr>
<tr>
<td>Araucarites baqueroensis (Archangelsky, 1966)</td>
<td>&quot; , Argentina</td>
</tr>
<tr>
<td>Araucarites minimus (Archangelsky, 1966)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>Araucarites fibrosa (Sukh-Dev &amp; Bose, 1974)</td>
<td>&quot; , India</td>
</tr>
<tr>
<td>Araucarites sp. (Mildenhall &amp; Johnston, 1971)</td>
<td>&quot; , New Zealand</td>
</tr>
<tr>
<td>Araucariostrobus creutzbergii (Huertas, 1970)</td>
<td>Middle Cretaceous, Colombia</td>
</tr>
<tr>
<td>Araucariostrobus camargo (Huertas, 1970)</td>
<td>&quot; , &quot;</td>
</tr>
<tr>
<td>Araucaria haastii (Bose, 1975)</td>
<td>Upper Cretaceous, New Zealand</td>
</tr>
<tr>
<td>Araucaria nathirstii (Menendez &amp; Carcavari, 1966)</td>
<td>Tertiary, Argentina</td>
</tr>
<tr>
<td>Araucaria lignitici (Gookson &amp; Duigan, 1951)</td>
<td>Oligocene, Victoria, Australia</td>
</tr>
</tbody>
</table>
shoot resembling section Columba (Florin, 1940)), *Araucaria derwentensis* (leaves) and *Araucaria balcombensis* (leaves) from Tasmania (Selling, 1950), two unnamed Eutacta-like species from Queensland (Bose, 1955), *Araucaria fletcheri* from New South Wales (Selling, 1950), and specimens recently identified by Blackburn (pers. comm.) from the Eocene of South Australia.

There is a great need for the original specimens of the above-mentioned species to be re-examined. Most of the leaves lack cuticular features, while the cones and scales lack definitive cuticular and anatomical features, so that their presence in the fossil record must be treated with caution.

Seven new taxa of araucarian reproductive organs have been isolated from the Winton Assemblage, and descriptions of these now follow.

4.2.1.2.1. *Araucaria microcarpa* sp. nov.

(Figs. 85 - 176)

**Systematic Description**

Order Coniferales

Family Araucariaceae

Genus *Araucaria* de Jussieu 1789

Section Eutacta Endlicher 1842

*Araucaria microcarpa* sp. nov.

**Diagnosis**: Ovulate cone, ellipsoidal in shape, 9.5mm – 14mm long, 6.3mm – 8.7mm wide. Cone-scales 2mm wide, 1.3mm high, 2mm – 3mm in
length, wingless. Ovule single on adaxial surface of cone-scale, variable in size, 765μ - 2000μ long, 550μ - 1200μ wide, 400μ - 950μ high, deeply embedded in cone-scale tissue to depth of 300μ. Prominent ridges, 170μ wide, often extending along middle of lateral sides of ovule from micropyle to the ligule. Cone axis 900μ - 1600μ wide, pith 700μ wide, cortical resin canals present. Vascular supply to cone-scale complex single at origin. Ovuliferous scale fused to bract scale for most of its length. Nucellus free from enclosing integuments except at chalazal region, where it is fused to integumentary layer, appearing stalked. Nucellar tissue not cellularized. Cells of megagametophyte isodiametric, 40μ - 50μ in diameter. Apex of gametophyte often eroded near micropyle. Cells of embryo 10μ - 25μ long, 15μ wide. Cotyledons 2. Leaves of reproductive shoot attached to cone are small, simple, spirally inserted, decurrent, with bifacial, spreading and incurved blades, length 2.3mm - 3mm, width 1.3mm - 1.9mm. Leaf surface keeled or ridged. Stomates only on adaxial leaf surface, closely spaced, length 60μ, width 35μ, longitudinally orientated.

Etymology: The specific epithet refers to the unusually small size of the ovulate cone.

Holotype: W171 (Fig. 103)

Type Locality: 50km north-west of Winton, Queensland. 22° 12' 00" S and 142° 31' 30" E.

Description: From 13 specimens, the average cone length is 12.3mm ± 1.3mm (range 9.5mm - 14mm); cone width from 32 specimens is 7.4mm ± 0.5mm (range 6.3mm - 8.7mm). The cones are invariably ellipsoidal in shape (Figs. 85 - 108) The cone-scales are densely packed, 100 - 150 in number, transversely rhomboidal in dorsal view, occasionally with the upper lateral edges (i.e. scale apex) concave rather than straight. Apart from the cone-scales at the cone base and apex, all are of a similar size on the one cone, 2mm ± 0.2mm wide (n=15), 1.3mm ± 0.2mm high (n=15). The scales are arranged spirally about the cone axis at a pitch angle of 58.4° ± 2° (n=7) from the longitudinal axis of the cone in a right-hand direction. The dorsal scale surface is convex, occasionally with a slight to distinct keel running vertically to the obtuse scale apex. A mucro is occasionally present on the scale apex, and may be deciduous.

In transverse view, the cone-scales are narrowly winged, obtangular to widely obdeltate in shape, 0.75mm wide adjacent to the cone axis, increasing gradually to a width of 2mm at the distal end of the scale (Figs. 109, 110). The cone-scale is 2mm - 3mm long, the apex strongly reflexed perpendicular to the horizontal plane of the scale (Fig. 111). The lateral wings of the scale are thin, increasing toward the centre due to the thick, embedded ovule, which is solitary and positioned on the adaxial surface of the cone-scale (Fig. 119). The ovule is a slightly flattened ellipsoid (Figs. 112 - 118), occasionally spheroid to ovoid, of variable size; average length 1540µ ± 200µ (n=56, min. 765µ, max. 2000µ), width 890µ ± 140µ (n=30, min. 550µ, max. 1200µ),
height $620 \pm 130\mu$ (n=26, min. 400\mu, max. 950\mu). The smaller ovules are usually placed to one side of the cone-scale (Fig. 109), indicating a possibility of 2 ovules per cone-scale. Although not yet seen in *A. microcarpa*, this phenomenon is known in *Araucaria* (Mitra, 1927). The normal sized ovules are borne at the centre of the cone-scale, deeply embedded in the scale tissue to a depth of 300\mu. Around the lateral sides of the ovule, from the micropyle to the ligule, prominent ridges may occur, of width 170\mu (Figs. 113, 114).

The ligule is small but distinct, shallowly triangular in transverse view with a rounded apex, 275\mu - 300\mu long, 625\mu - 675\mu wide (Figs. 112, 115, 116, 160 - 162). In side view, the ligule appears as a thin, upturned scale tip (Fig. 116).

The epidermal cells of the abaxial and adaxial cone-scale surfaces are square to rectangular in outline, 25\mu - 50\mu long, 25\mu wide, arranged in rows parallel to the long axis of the scale (Figs. 115 - 118, 120). Stomates are absent. The cells of the epidermis covering the ovule (sarcotesta) are much longer than broad, 50\mu - 130\mu long, 10\mu - 15\mu wide, linear in shape, arranged parallel to the long axis of the ovule (Figs. 116, 118, 121). Stomates are absent. The epidermal cells of the ligule have the same shape and orientation as those of the bract, but are slightly shorter, 30\mu long and 20\mu wide (Figs. 116, 118). Stomates are absent.

The general internal structure of the cones is illustrated in Figures 122 - 156. The cone axis is $1360\mu \pm 220\mu$ wide (n=12, min. 900\mu, max. 1600\mu). The parenchymatous pith is 700\mu wide. 11 - 25 resin canals (Figs. 138 - 143) are present in the cortex of the axis, often in 2 concentric rings. The resin canal diameter is $138\mu \pm 23\mu$ (n=100, min. 100\mu, max. 180\mu). No resin canals are present in the ligule. A large
canal, up to 250μ in diameter, runs along the centre of the adaxial surface of the bract scale towards the apex (Figs. 157 - 159). Up to 10 smaller resin canals run along the abaxial surface of the bract (Fig. 158).

The xylem forms a continuous ring around the cortex, and is 100μ - 150μ thick. The vascular supply to the cone-scale complex is single at its origin (Figs. 163 - 165, 167). Below the base of the ovule, the vascular supply divides, one branch entering the ligule, the other continuing into the bract-scale before dividing again (Fig. 166). Of this latter division, one strand follows the adaxial, the other follows the abaxial surface of the bract. The vascular supply entering the ligule divides at the base of the ovule, one strand entering the ovuliferous tissues at the chalaza, the other continuing into the short ligular tip (Figs. 166, 168).

The ovuliferous scale is fused to the bract for most of its length (Fig. 166). The ligular sulcus is shallow, 400μ - 500μ deep. The tissues of the cone-scale complex are very sclerotic (Fig. 167).

The sclerotesta is 20μ thick, visible in only well preserved ovules (Figs. 169, 170). The nucellus is free from the enclosing integuments except at the chalazal region, where it is fused to the integumentary layer, thus appearing stalked (Figs. 171, 172). The nucellar tissue is not cellularized, but is thin and often wavy, sometimes continuing into the narrow micropyle (Fig. 173). When the megagametophyte is preserved, it fills most of the nucellar cavity (Figs. 169, 174). The megaspore membrane is not preserved. Cells of the megagametophyte are isodiametric, 40μ - 50μ in diameter. The apex of the gametophyte is often eroded near the micropyle (Figs. 169, 171, 173), presumably due to the action of the pollen tubes (Eames, 1913).
The embryo, seen relatively clearly in 2 specimens (Figs. 170, 174), may have been rarely formed or preserved. (It is known that the cell walls of the araucarian embryo are very delicate, as shown in the preservation of *Araucaria mirabilis* (Stockey, 1975). The embryo is 580μ - 680μ long and 140μ - 200μ high, and is composed of very small, square to rectangular cells, 10μ - 25μ long, 15μ wide. Two cotyledons can be seen. There is no preservation of other embryonic regions.

The cones are frequently attached to unbranched reproductive shoots of varying length up to 11mm, and a width of 3.5mm - 5mm. The leaves are small, simple, spirally inserted and decurrent, consisting of a broad adnate base and a bifacial, spreading and incurved blade which overlaps subsequent leaves (Figs. 85, 87, 91 - 93, 97, 98, 103, 108). The ratio of the adnate base to the blade is 1:1.6 - 1:2. The adnate leaf base is obtriangular, 1.4mm - 1.8mm long, (n=2), 1.51mm ± 0.22mm wide (n=9, min. 1.26mm, max. 1.9mm).

When the abaxial leaf base surface is visible, it is keeled or flattened, with an entire margin. The basal angle is acute, 48° - 72° (n=8). The leaf blade is triangular to narrowly triangular, length 2.59mm ± 0.24mm (n=13, min. 2.26mm, max. 2.95mm), breadth 1.51mm ± 0.22mm (n=9, min. 1.26mm, max. 1.9mm). The blade is occasionally constricted at the point of insertion. The abaxial leaf surface is keeled or ridged; when ridged, the keel is acute, while the lateral faces are steeply sloping and slightly planar, with a ridged or convex adaxial surface at the insertion point. The leaf blade is flattened or slightly keeled with entire margins, and an acute, incurved and occasionally cuspidate apex (apical angle 63° ± 5°, n=9).

The leaves are thick, and unguiform in lateral view. The epidermal cells of both leaf surfaces are similar in size and shape, up
to 100μ long, 10μ wide, rectangular in outline, in rows parallel to the long axis of the leaf. Stomates are absent from the abaxial surface, but are common on the adaxial surface. They are sunken, in definite rows, closely spaced and longitudinally orientated (Figs. 175, 176). Stomatal length is 60μ, width 35μ. When the adaxial surface is keeled, the stomates are arranged in distinct bands, 180μ wide on each side of the keel. When the adaxial surface is flattened, the stomates are evenly distributed over the leaf blade.

Discussion

Structural and developmental studies of female Araucarian cones are few, with only several extant species having been looked at in detail. These include Agathis australis (Eames, 1913), Agathis brownii (Rastogi, 1964), Araucaria bidwillii (Wilde and Eames, 1948, 1952; Berg, 1950) and Araucaria araucana (Favre-Ducharte, 1960; Hodcent, 1967; Montaldo, 1971). (General studies on the anatomy of female conifer cones include Thomson (1940) and Florin (1954). Maheshwari and Singh (1967) have studied the structure and development of the female gametophyte in gymnosperms generally). Sections Eutacta and Intermedia in Araucaria have not been looked at in any detail. As Seward and Ford (1906) pointed out long ago, our knowledge of the embryogeny of the Araucariaceae is far from complete.

The large number of well preserved female cones of Araucaria mirabilis section Bunya (from the Jurassic of Patagonia), have allowed thorough studies of its structure and development (Stockey, 1975, 1978). Three other petrified members of section Bunya which have yielded much information on internal anatomy are Araucaria brownii (in Stockey, 1980a) and Araucaria sphaerocarpa (in Stockey, 1980b,) and
Araucarites bindrabunensis (in Vishnu-Mittre, 1954). The only fossil member of the section Eutacta to provide useful anatomical information is Araucarites phillipsii (in Kendall, 1949) from the Yorkshire Jurassic. Anatomical studies of fossil seed cones from sections Intermedia and Columbea are lacking. Only generalized and limited comparisons between fossil and extant species are possible until this gap in the literature can be filled.

Cones of the Araucariaceae are characterized by their large size, spheroid to ovoid shape, helically arranged cone-scales, large pith in the cone axis, cortical resin canals and the presence of one seed per ovuliferous scale. The presence of a ligular sulcus (space between the ovuliferous scale tip and the bract) and wingless seeds are characteristic of the cones of the genus Araucaria.

The inordinately small size of Araucaria microcarpa cones, together of course with all their contained structures, distinguishes this new species from all fossil and extant species at the same stage of development. A. microcarpa cones are all of approximately equal size, averaging 12.3mm long by 7.4mm wide. They possess several features indicating that they are at a stage approaching maturity, and therefore are close to their maximum size. These can be listed as follows:

1. the large size of the ovules compared to the cone size
2. the presence of a well developed vascular system throughout the cone
3. the presence of cellular megagametophytes and occasionally embryos
4. a shallow ligular sulcus
5. differentiation of integumentary layers around the ovule

Eames (1913) thoroughly investigated the development of the
female cone of *Agathis australis*, which at maturity reaches a typical araucariacean size of 7cm long by 7cm wide (viz. *Araucaria bidwillii*, with cones up to 30cm long). When young *Agathis* cones break from the bud scales, they are about 1cm in diameter (already larger than cones of *Araucaria microcarpa*). Ovular growth has not yet begun. After about 12 months, pollination occurs, and the cone has reached 2cm in diameter. By this time, the ovules have developed a general form, but are still comparatively small with no differentiation of integuments or megaspore tissue. After a further 13 months, fertilization occurs, by which time the cones have expanded to 6cm in diameter, almost their maximum size. The ovules now resemble the ripe seed in their form and size, being about 12mm long. (In *Araucaria bidwillii*, the mature ovule may be up to 4cm long (Wilde and Eames, 1948), while in the fossil *A. mirabilis* (also section Bunya) mature ovules are 8mm - 13mm long in cones 6cm in diameter). At the post-fertilization stage, ovules are usually about half the length of the cone-scale complex. Although the ovules in *Araucaria microcarpa* are only about 1mm long, they take up half the length of the cone-scale. They are deeply embedded in the cone-scale tissue, with little room for expansion. It cannot be said with certainty how long *A. microcarpa* cones take to mature, but owing to their small size and the lack of visible growth rings in the cone axis, it seems likely to be within a year.

The vascular system in *Araucaria microcarpa* is extensive, with clear vascular traces entering the fine tissues of the ovule and ligule.

There have been few investigations into the vasculature of the female cones of extant araucarians, so that most species still need to be examined. Strasburger (1879) and Worsdell (1899) pioneered much of
this work. After reviewing and further examining the vascular arrangement of the cone-scale complex of *Araucaria*, Eames (1913) found that three groups could be set up on the basis of separate vascular patterns. *Araucaria bidwillii*, representing section Bunya, falls in one group (Fig. 177), where the vascular supply to the cone-scale is double at its origin, so that the bundles leading into the bract scale and fused ovuliferous scale arise separately from the central vascular cylinder. *Araucaria heterophylla*, *A. cunninghamii*, *A. rulei* and *A. columnaris* belong to the second group (Fig. 178) (all in section Eutacta), where a single bundle leaves the cone axis and divides into two series in the cortex of the axis, both of which enter the cone-scale complex. The upper series supplies the ovule and sometimes the ligule, while the lower series supplies the bract scale. Nase (1915) found that *A. subulata* (section Eutacta) shows the same basic pattern. The third group (Fig. 179) comprises both species of section Columbea, *Araucaria angustifolia* and *A. araucana*. Here a single bundle enters the cone-scale complex from the cone axis. An upper vascular series is not developed, the ovular supply being derived from the lower series near the ovule base.

Eames (1913) also thoroughly investigated the vascular pattern in *Agathis australis* and several other species within the genus, all of which have similar reduced vascular systems. A single bundle leaves the cone axis and enters the cone-scale complex. Near the base of the scale, a weak upper branch departs from the main bundle to enter the base of the ovule. The lower main bundle continues into the bract tissues (Fig. 180).

The vascular patterns described above refer only to branching in the longitudinal plane and ignore the complex system of transverse
branching, which may further separate different species. (Although appearing similar to that of *Araucaria* section Columbea, the vascular pattern of *Agathis* is in fact almost identical to that seen in *Cunninghamia* and *Athrotaxis selaginoides* of the Taxodiaceae (Eames, 1913)). The interruption by the comparatively large, embedded ovule in the cone-scales of *Araucaria microcarpa* has not made it possible to view the transverse vascular patterns. In comparing the longitudinal arrangement of the bundles, *A. microcarpa* (Fig. 181) shows a similar cone-scale vascularization to extant *Agathis* and *Araucaria* section Columbea, in that a single vascular bundle departs from the cone axis, and then divides longitudinally deep in the cone-scale complex. It resembles the *Araucaria* type more closely as the branch leading into the ovule arises at the base of the ovule rather than mid-way beneath it. The very thin and compressed scale tissue beneath the embedded ovule in *Araucaria microcarpa* means that if two vascular series were in fact present (as in section Eutacta), they could not be seen discreetly. *A. microcarpa* shows vascularization of the ligule, which is seen only in some species of section Eutacta and in section Bunya.

The internal ovular tissue of *Araucaria microcarpa* is commonly not preserved, the ovular contents having been replaced by clear or opaque silica with distinctive crystallization patterns. It can be assumed that the cones remained floating in water for some period during fossilization, so that the delicate ovules would have been obliterated. When the preservation is good, megagametophytes and occasionally dicotyledonous embryos can be seen. Two cotyledons are usual in araucarian embryos, with only several species from section Eutacta of *Araucaria* possessing four cotyledons. The megagametophytes are made up of the typical isodiamic cells of gymnospermous ovules.
(Miller and Brown, 1973), while the embryonic cells are small and elongate. It is known that the megagametophyte becomes cellularized well after pollination (Chamberlain, 1935) and that embryos are found in cones of approximate full size, as stated previously. The cones of *A. microcarpa* containing megagametophytes are the same size as those containing embryos, so that these structures should be close to their mature size.

A single ovule was only ever found on each cone-scale of *Araucaria microcarpa*. It was noted however, that occasionally a small ovule was positioned to one side of the cone-scale surface, leading to an assumption that there may sometimes be two ovules per scale. This has been found in extant species of *Araucaria montana* and *A. rulei* (Mitra, 1927) and *A. bidwillii* (Wilde and Eames, 1948). In these species, cone-scale complexes at the base of the cone were occasionally found to have two ligules and two aborted ovules. Both Mitra (1927) and Florin (1944) have concluded that the present one-seeded condition is a derived feature. Florin has presented evidence of the possible derivation of the araucarian cone-scale from the three-sided scale of *Schizolepis* from the Upper Palaeozoic. The small ovules in *A. microcarpa* were not found to be restricted to the cone base, nor is it known whether or not they were fertile, but from their size and positioning, it appears that two small ovules per scale may sometimes have occurred.

The cuticular features of extant cone-scales from section Butacta was discussed by Cookson and Duigan (1951). The shape and arrangement of epidermal cells in *Araucaria microcarpa* follow closely that seen in the extant species, with the exception that stomates which are absent from the distal scale region in *A. microcarpa* are present in the other
species. More species need to be examined to allow further comparison.

Possession of a ligule is a feature absent from *Agathis* but present in *Araucaria*. The degree of fusion between the ligule and the bract can give some indication of the maturity of the cone. In *Araucaria rulei* and *A. subulate*, the greater portion of the ligule is free in the young strobilus. In the mature strobilus, the ligule is free only at its tip (Aase, 1915). This is also true in *Araucaria bidwillii* (Wilde and Eames, 1948). Stockey (1975, 1978) has used evidence of the depth of the ligular sulcus in *Araucaria mirabilis* to ascertain the maturity of various cones. The ligular sulcus in *A. microcarpa* is also shallow with respect to the length of the cone-scale. The ligule shows a degree of fusion and basic morphology comparable to mature araucarian cones.

The structure of the cone-scales of *A. microcarpa* is typical of that found in fossil and extant members of the section Eutacta. Of the fossil species, only *Araucarites phillipseii* shows significant preservation of scale tissues, which follow the general pattern of that seen in *Araucaria microcarpa*. The fossil Australian species, *Araucaria lignitici*, consisting of isolated cone-scales (without ovules), has been compared with the scales of extant *A. cunninghamii* (Cookson and Duigan, 1951).

Apart from the obvious difference in cone size, *Araucaria microcarpa* has a comparable cone morphology to the species of *Araucaria* in section Eutacta. The most similar extant species are *A. subulate* and *A. cunninghamii* (Figs. 182, 183).

In the absence of attached and distinctive reproductive structures, the identification of coniferous shoots to the generic or
sometimes familial level is often not possible. This was made plain by de Laubenfels (1953) who attempted to classify all coniferous leaf types on the basis of general morphology. The only subsequent worker to comprehensively study the morphology of coniferous shoots was Offler (1969, 1984), who carefully examined and described the shoots of the conifers of Australia and New Guinea with a view to determining the taxonomic value of shoot morphology. After consideration of the necessary characters to diagnose shoot types, Offler formulated a key to these conifers based entirely on external vegetative features. This degree of precision was adopted in describing the foliage of Araucaria microcarpa.

Offler found that certain shoot types, even from different families, could not be separated on the basis of their morphology. The mature foliage of the extant species Araucaria cunninghamii cannot be separated, according to Offler’s system, from Dacrydium elatum, D. novo-guineense and Dacrycarpus, while three Australian species of Agathis together cannot be differentiated from the leaves of Podocarpus blumei. Indeed, it may be difficult to separate araucarian foliage from members of the Taxodiaceae. (De Laubenfels (1972) has produced a key to the New Caledonian species of Araucaria on the basis of leaf morphology, but few species can be clearly set apart).

Using Offler’s key, the foliage of A. microcarpa keys out with A. cunninghamii (together with the previously mentioned species of Dacrydium and Dacrycarpus). Offler only considered the two extant Australian species of Araucaria. However, A. microcarpa has foliage typical of species from section Eutacta, particularly A. subulata from New Caledonia, A. heterophylla from Norfolk Island and A. cunninghamii from eastern Australia. The leaves of A. microcarpa may be
distinguished from these extant species due to their much smaller size and more rhombic shape.

A general similarity occurs between *A. microcarpa* and the foliage of the fossil species *Araucaria lignitici* and *Brachyphyllum mamillare*. *A. lignitici* has a more similar shoot morphology (see Cookson and Duigan, 1951), although the leaves of this species may be up to 3 times longer than those of *A. microcarpa*. *A. lignitici* leaves have also been likened to those of *A. cunninghamii*, *A. subulate* and *A. heterophylla* (Cookson and Duigan, 1951).

Scanning electron microscopy has revealed the size and arrangement of stomates on the leaves of *Araucaria microcarpa*, which follow the general pattern seen in most araucarian species. Stockey and Taylor (1978a, 1978b, 1981) have examined the cuticles of some species of *Araucaria* and *Agathis* to determine the taxonomic significance of cuticular structures in these genera. Features of the cuticular organization can be successfully used to separate leaves at the sectional level in *Araucaria* (Stockey and Taylor, 1978b). The use of cuticular features has similarly been effective in the identification of fossil araucarians, including *Brachyphyllum mamillare* (Kendall, 1949), *Araucaria lignitici*, *Agathis vallournensis*, and *Agathis parvianensis* (Cookson and Duigan, 1951) and *Araucaria haastii* (Bose, 1975). Unfortunately, the delicate epidermal features necessary to assign leaves to the sections of *Araucaria* have not been preserved in *A. microcarpa*.

The specialized features which allow *Araucaria microcarpa* to be assigned to the modern genus *Araucaria* are its non-petiolate leaves with acute apices, and the occurrence of a free ligule in the
cone-scale complex. The reduced, keeled, imbricate and erect leaves, together with the narrowly winged cone-scales with a single vascular source allow *A. microcarpa* to be placed in the section Eutacta. Apart from its atypically small cone size, the fossil is sufficiently similar to the recent and living members of the genus for it to be placed in the modern genus. Similarly, the special combination of features previously described for this species separate it from all other members of the genus. *Araucaria microcarpa* is, therefore, the most completely described fossil representative of the section Eutacta.
4.2.1.2.2. Araucariaceae Incertae sedis 1
(Figs. 184 - 193)

Description: (Specimen W016) This specimen represents the largest single reproductive organ in the Winton fossil deposit. The degree of compression, fragmentation and weathering, together with poor anatomical preservation due to a secondary carbonate replacement, mean that natural affinities cannot be proven. On the basis of gross morphology, however, the specimen shows the typical structure of a female australarian cone.

The cone is bilaterally flattened to a maximum thickness of 4cm (Fig. 184), while the cone width reaches 14.5cm. The base of the cone is intact, however the cone apex is missing. Considering the even symmetry of the specimen, it seems likely that about one-third of the strobilus fragmented away, the remaining portion having a length of 10.8cm (Fig. 185, 186). If it can be assumed that the cone originally had a circular circumference about its centre, the actual diameter can be roughly calculated by running a tape around the widest part of the flattened cone and dividing this measured circumference by the value pi. The living cone might therefore have had a diameter of about 11cm. If the top third of the cone is missing, the original length might have been about 15cm. These dimensions fall within the normal size range of Agathis and Araucaria strobili.

The cone-scales are numerous (possibly up to 600 in the complete cone), spirally arranged and transversely rhombic in shape (Fig. 187). The scale width is 9.5mm - 14.4mm, while the scale height is 4.8mm - 5mm. The apex of most scales has been broken or eroded away, but in complete scales, the apex is recurved, acute pointed and imbricate with the adjacent scales. Scanning electron microscopy of the cone-scale
surfaces did not reveal any preservation of epidermal structure.

The internal structure of the cone is poorly preserved. In longitudinal section, a thick cone axis is revealed (Fig. 188). It was hoped that araucarian pitting within vascular tissue might be found which would help to indicate natural affinity, but extensive compression and poor mineral replacement have obliterated this cellular detail.

Figure 189 shows a radial longitudinal thin section adjacent to the cone axis revealing divergent cone-scales with heavily convoluted and folded scale bases. Between some scales, ovate structures may be seen, up to 1.3mm in length. Similar but more elongate structures occur at the cone apex (Fig 190). These possibly represent ovules, although integuments and ovular tissue are not apparent. If the cone is araucarian, ovules of this size would be very immature, and therefore gametophytic tissue and integuments are not likely to have been developed.

The only preservation of internal tissues was found in the distal portions of some cone-scales. The scales are heavily sclerotic with numerous resin canals (up to 400μ in diameter) running along their length. These are visible in polished tangential rock surfaces and thin sections (Figs. 191,192). About 10 large canals run along the adaxial side of the scale, while several series of smaller ducts are scattered along the abaxial side of the scale. Occasionally a single series of small ducts runs along the adaxial scale surface, above the large canals.

Vascular tissue is not clearly visible in the cone-scales. In ground thin-sections, a dark region of small cells is present immediately above the large resin canals (Fig. 193) These cells may be

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xylem tracheids. They are positioned in an arrangement consistent with that found in species of *Araucaria* and *Agathis* (Aase, 1915).

**Discussion**: In general appearance, the cone resembles many extant species of *Agathis* and *Araucaria* section Buteacta. Until better preserved specimens are found, its natural generic affinities must remain in doubt.

4.2.1.2.3. Araucariaceae **Incertae sedis 2**

(Figs. 194 - 197)

**Description**: (Specimen W065) This three-dimensional, petrified specimen was extracted from the soft, carbonate rock matrix described in Chapter 2. The fossil is a conifer strobilus, perhaps ovulate, with a short attachment or peduncle (Fig. 194). The cone is flattened to some degree, to give a length of 5.7mm, a maximum width of 4.5mm and a maximum thickness of 2.7mm. The measured circumference at its central girth is 13.7mm. If it can be assumed that the cone was originally rounded, the calculated original cone diameter is approximately 4.4mm. The cone is covered in about 50 elongate, heavily imbricate and recurved scales, narrowly triangular in shape, of average length 2.6mm and average breadth 0.7mm at the scale base. The scale apices are acute pointed. On the dorsal (abaxial) surfaces, the cone-scales are convex, or occasionally slightly keeled. Stomates are absent. The ventral (adaxial) scale surfaces are sometimes planar but more often keeled along their middle (Fig. 195). The scales are concave either side of the keel. Stomates, 35μ - 45μ long by 25μ - 30μ wide, run in parallel bands along the concave surfaces for the entire scale length (Figs.
196,197). The stomates are usually orientated parallel to the direction of the scale, but are occasionally perpendicular. No seeds or sporangial structures are present between the cone-scales.

The cone attachment (peduncle) is short, 4mm long by 1.8mm wide (Fig. 194). A single complete leaf remains attached to the peduncle, the remainder having broken off at the point of insertion. The leaf is strongly decurrent, with a narrowly elliptical, bifacial, spreading and incurved blade, 2.5mm long by 0.75mm broad. The dorsal leaf surface is slightly ridged. The adnate leaf bases have equal dimensions to the blade, and are broadly ridged by the median vein, with convex or planar faces on either side of the ridge. The leaf bases are entire and slightly involute. Phyllotaxis is spiral. Stomates have not been found on the leaves.

Discussion: The lack of formation or preservation of diagnostic reproductive structures means that the cone cannot be placed in any natural genus. A close similarity exists between the fossil and very immature araucarian cones, particularly the extant New Caledonian species, Araucaria rulei (Fig. 198), but the fossil possesses an inordinately small number of cone-scales. A superficial resemblance also occurs between the fossil and the cones of the extant taxodiaceous species Athrotaxis selaginoides from Tasmania (Fig. 199). This species however, has peltate rather than bifacially flattened cone-scales.

The cone attachment is typically araucarian (section Eutacta), but a likeness to the Taxodiaceae and Podocarpaceae cannot be discounted.

The cone is preserved as brittle silicate, due probably to weathering during the secondary carbonate replacement, so that no
anatomical structure has been preserved.

4.2.1.2.4. Araucariaceae Incertae sedis 3
(Fig. 200)

Description: (Specimen W328) This fossil occurs as a cone fragment visible on the surface of a weathered rock (Fig. 200). There is no preservation of the internal cone structure. The cone diameter is 11.3mm; cone length is unknown with only 10mm exposed. The nearly parallel sides of the strobilus may indicate a fairly elongate shape. Forty-five scales are visible, each being quadrato-rhombic in shape, 2mm wide by 1.9mm high. The dorsal (distal) scale surface is convex. Phyllotaxis is spiral with a symmetrical angle of divergence of about 45° in both directions. There is no preservation of epidermal cells on the weathered scale surfaces.

Discussion: The cone size, and the shape and orientation of the cone-scales are consistent with the male strobili of the Araucariaceae. The petiolate appearance and rhomboidal scale shape is more consistent with cones of the genus *Araucaria* than those of *Agathis*.

Figure 201 shows the male cone of the extant New Caledonian species, *Araucaria muelleri* which closely resembles the fossil in its size and morphology.

Walkom (1919) attributed a fossil cone from the Upper Mesozoic of Queensland to *Araucarites polycarpe* Tenison-Woods 1884. This cone (Fig. 202) shows a markedly similar morphology to the Winton fossil. Although named as a female cone, no reproductive structures were preserved to indicate this. Based on its morphology, the specimen is probably a male
strobilus.

4.2.1.2.5. Araucariaceae *Incertae sedis* 4  
(Figs. 203 - 205)

**Description**: (Specimen W191) This specimen was extracted from a carbonate-matrix rock, and probably represents a portion of a male araucarian strobilus (Figs. 203 - 205). The preservation is poor, due to distortion, compression and weathering of the cone surface. The maximum diameter of the specimen is 11mm, while the visible length is 11.5mm. The cone-scales are small, 1mm wide by 0.75mm high, spirally arranged (angle of divergence indeterminate) and roughly rhomboidal to hexagonal in shape.

**Discussion**: The scales are much smaller than those of *Incertae sedis* 3, despite the similar cone diameter, so that the specimen possibly belongs to a separate taxon. Its lack of definitive features means that it cannot be classified at the generic level, however the cone size and scale shape is typical of the genus *Araucaria*.

4.2.1.2.6. Araucariaceae *Incertae sedis* 5  
(Figs. 206 - 211)

**Description**: (Specimen W106) This specimen probably represents a large male araucariacean cone, as do *Incertae sedis* 3 and *Incertae sedis* 4, but shows the best preservation of structure (Figs. 206 - 211). The rounded cone apex is complete, but the cone base has fractured away. The strobilus is elongate, with a visible length of 34mm and a maximum
diameter of 10.5mm. The cone-scales are typically araucarian, small, 1mm in height and breadth, rhomboidal to hexagonal in shape and arranged spirally around the cone axis at an angle of divergence of about 45°. The scale apices are peltate. A shallow groove running around the edge of the scale apices suggests that terminal spines may have originally extended from them, which have weathered or broken away (Fig. 207).

The internal structure of the cone is poorly preserved, but a wide central axis, 4.3mm across, is apparent (Fig. 208). A tangential longitudinal section through the sporophyll shows that 3 resin canals run horizontally to the scale apex, each canal about 110μ in diameter (Fig. 209). A radial longitudinal thin section (Fig. 210) shows the wide cone axis, and the divergence of the microsporophylls. No vascular tissue is preserved. It is probable that the dark structures illustrated in Figure 211 represent microsporangia. The number of sporangia per sporophyll is indeterminate. Some sporangia appear to be split longitudinally. This is the usual method of dehiscence seen in araucarians (Burlingame, 1913). No spores were observed in thin sections, indicating that the sporangia had probably dehisced prior to fossilization.

4.2.1.2.7. Araucariaceae Incertae sedis 6
(Figs. 212 - 216)

This cone taxon is represented by 4 specimens, which, although varying somewhat in their degree of preservation, all show a clearly similar morphology. Specimens W089 (Figs. 212, 213) and Specimen W094 (Fig. 214) were both extracted from carbonate rock matrices. The
complete cone and an attached peduncle are found in Specimen W089. Most of the basal cone-scales have been broken away from the cone axis in Specimen W094. Epidermal structure was only found to be present in these two specimens. The remaining cones were all exposed longitudinally on the external surfaces of rocks. The cones have suffered from weathering, with few of the cone-scales showing good preservation. Specimens W369 and W471 (Figs. 215, 216) have well preserved peduncles attached.

**Description:** (Specimens W089, W094, W369, W471) The cones are narrowly ellipsoidal in shape. The two complete strobili are 11.5mm and 12.5mm in length, but based on fractured specimens, the cones may exceed 15.8mm in length. Cone diameter varies between 3.0mm and 4.5mm. The cone-scales are numerous (98 scales were counted on the completely exposed specimen). The scales are arranged spirally about the cone axis at an angle of divergence of about 30°. The distal ends of the cone-scales are imbricate, roughly trullate in shape, with a broad base 0.9mm - 1.3mm wide, and a vertically upturned scale apex 0.9mm - 1.4mm in height. The sides of the apices are straight to concave, slightly crenulate along the margin, leading to an acute (about 45°) pointed apex. The dorsal scale surface is slightly convex, made up of square to rectangular epidermal cells, up to 60μ long by 15μ wide, arranged in a longitudinal direction. Stomates are found only on the adaxial cone-scale surface, where they are few in number, 50μ long by 20μ wide, arranged parallel to the longitudinal plane of the scale. The internal cone structure is not preserved.

A short, leafy peduncle, up to 6.6mm long and 3.7mm wide, is attached to the base of some cones. The leaves are spirally arranged,
consisting of a broad, obtriangular, decurrent leaf base, 1.3mm - 1.4mm wide and 0.7mm - 1.0mm long, and a divergent and recurved, narrowly triangular leaf blade, 1.3mm - 1.4mm wide at the base and 2.2mm - 2.8mm long. The dorsal leaf surface has a distinct keel running from the base to the acute (65°) leaf apex. The leaf blade is flattened to concave on either side of the keel, with an entire leaf margin. No epidermal cells or stomates are preserved on the leaf surfaces.

Discussion: Despite the lack of internal structure and the absence of pollen within the cones, this taxon shows the typical morphology of microsporangiate cones of the Araucariaceae. The male cones of Agathis and Araucaria are rather difficult to distinguish, but the distal ends of the sporophylls of these two genera appear to be morphologically and structurally dissimilar in some respects (Cookson and Duigan, 1951). The scales of Agathis are usually oval to hemispherical in shape and the adaxial epidermal cells are irregularly arranged. The scales of the fossil cones are more like those of Araucaria, which are usually rhomboidal with acute apices, and with regularly arranged and somewhat elongate cells of the adaxial epidermis.

The microsporophylls of most species within section Eutacta of Araucaria are vertically upturned and imbricate. The other generic sections commonly have less imbricate and more peltate scales. Combined with the very small cone size, this may indicate that the fossil belongs to Eutacta.

The leaves of the peduncle are also like those of Eutacta. Apart from an insignificantly shorter leaf base, the fossil leaves described above are indistinguishable from those of the peduncle of the ovulate cones described earlier as Araucaria microcarpa. While this is
insufficient proof that these male cones represent the sexual
counterpart of *Araucaria microcarpa*, this is possibly the case. The
small size of the microsporangiate cones agrees well with the smallness
of *A. microcarpa* strobili.

The comparative rarity of the male cones may be explained by the
fact that male araucarian cones shed their pollen well before
fertilization of the female cones. At the time of fossilization of the
deposit, it is therefore unlikely that both male and female araucarian
cones were commonly present together.
4.2.2. **Podocarpaceae**

4.2.2.1. **Taxonomy of Extant Genera**

The Podocarpaceae, consisting of 150 species, is the largest and most widespread conifer family in the Southern Hemisphere. It is found in south-east Asia, South and Central America, southern Africa, eastern Australia, Malesia, Melanesia and New Zealand (see Fig. 217).

The largest genus, **Podocarpus** L'Herit. ex Pers., was systematically revised by Buchholz and Gray (1948a, 1948b, 1948c, 1951), Gray and Buchholz (1948, 1951) and Gray (1953a, 1953b, 1955, 1956, 1958, 1960, 1962), who split the genus into 8 sections (see Buchholz and Gray, 1948a). The taxonomic differences between some of these sections was thought by de Laubenfels (1969a, 1969b) to be as great as those which separate most other genera. In his revision of the Malesian conifers, de Laubenfels (1969a, 1969b) divided Podocarpus into 4 genera, by erecting **Dacrycarpus** (11 species) and **Decussocarpus** (12 species), retaining Podocarpus (78 species) and reinstating the genus **Prumnopitys** (9 species). De Laubenfels footnoted his intention of elevating the monospecific Podocarpus section Microcarpus to the generic level. This was done in 1972, however section Microcarpus was elevated to a new genus which de Laubenfels named **Parasitaxus** (1 species).

The validity of the other large podocarp genus, **Dacrydium** Soland. ex G. Forst., has been questioned by several workers, including Hair (1963) and Quinn (1970). In 1931, Florin divided the genus into three sections A, B and C. Section A was subsequently raised to generic status as **Falcatifolium** de Laub. (4 species)(de Laubenfels, 1969a). Quinn
(1982) has since revised Dacrydium so that the species of section C are now represented in three separate genera, Lepidothamnus Phil., Lagarostrobus Quinn and Halocarpus Quinn. Dacrydium Sol. ex Laub. (16 species) has been retained for the species in section B only.

Lepidothamnus was originally submerged into Dacrydium by Bentham and Hooker (1880). This genus contains three closely related species, one endemic to southern Chile and the other two to New Zealand. The new genus Lagarostrobus includes one species endemic to Tasmania and one to New Zealand. Halocarpus comprises three closely related species, all endemic to New Zealand.

One specimen from the Winton Fossil Plant Assemblage can be placed in the extant genus Lepidothamnus, and represents the only fossil to be described from the genus. Indeed, the only fossil reproductive structures assigned to Dacrydium are isolated seeds found in association with D. rhomboideum (Australian Tertiary), which have been assigned to section B of Florin's (1931) sectional treatment of the genus (Cookson and Pike, 1953). Thus, according to Quinn's revision, D. rhomboideum truly belongs to Dacrydium.

The smaller genera of the Podocarpaceae have been generally accepted, with the possible exception of Phyllocladus L.C. and A. Rich. (5 species), which some workers treat as a separate family (see Keng, 1973, and Clifford and Constantine, 1980. Acmopyle Pilger, containing 2 species, closely resembles Podocarpus, and is restricted to the Pacific Islands of New Caledonia and Fiji. The remaining 3 genera all contain small plants from cool, mountainous areas: Saxegothaea Lindl. (1 species from Chile and Patagonia), Microcachrys Hook. f. (1 species from Tasmania) and Microstrobus Gard. and Johns. (1 species from Tasmania and 1 species from New South Wales).
Since 1969, the number of extant genera within the Podocarpaceae has increased from 7 to 15. A key to these genera is found in Quinn (1982).

4.2.2.2. Fossil Podocarpaceae

The Podocarpaceae made its appearance in the Lower Triassic with the occurrence of Risaikea Townrow, a primitive podocarp which inhabited South Africa, Madagascar, Australia and Antarctica until the Upper Triassic (Townrow, 1969). The Palaeozoic ancestor of the family is unknown, but like the Araucariaceae and Pinaceae, the Podocarpaceae is thought to have evolved from the Voltziaceae (Florin, 1951; Miller, 1982).

A number of now extinct podocarp genera existed throughout the Mesozoic. These have been summarized by Miller (1977), and are listed in Table 4. To this list can be added certain species assigned to the extinct artificial genus Elatocladus, with leaves and shoots showing typical podocarpaceous features (see Halle, 1913b; Florin, 1940; Vishnu-Mittre, 1958). Two more podocarps restricted to the Mesozoic are Dicrydites Marik and Podocarpites Andra (Miller, 1977). The fossil woods Podocarposyllum and Phyllocladoxylon have been described from the Mesozoic of the Northern Hemisphere, however their true relationships are uncertain (Florin, 1940).

The Mesozoic genera listed show a strictly southern distribution. This reflects Florin’s (1958) hypothesis that the Podocarpaceae originated in the Southern Hemisphere. Although the modern genera have a similar distribution, Podocarpus is reported to have grown in the Early and Late Cretaceous of Russia (Krassilov, 1974) and up to the
<table>
<thead>
<tr>
<th>Genus and Reference</th>
<th>Fossil Type</th>
<th>Locality</th>
<th>Age</th>
</tr>
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<tbody>
<tr>
<td><em>Niovisia</em> (Townrow, 1967a, 1969)</td>
<td>foliage, male &amp; female cones</td>
<td>South Africa, Madagascar, Australia Antarctica</td>
<td>Lower to Upper Jurassic</td>
</tr>
<tr>
<td><em>Mataia</em> (Townrow, 1967a, 1969)</td>
<td>foliage, female cones</td>
<td>New Zealand, Australia</td>
<td>Jurassic</td>
</tr>
<tr>
<td><em>Nutholacium</em> (Townrow, 1967b)</td>
<td>female cones</td>
<td>Antarctica</td>
<td>Jurassic</td>
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<tr>
<td><em>Mehnaia</em> (Vishnu-Mittre, 1958)</td>
<td>female cones</td>
<td>India</td>
<td>Jurassic</td>
</tr>
<tr>
<td><em>Nipponiostrobus</em> (Vishnu-Mittre, 1958)</td>
<td>female cones</td>
<td>India</td>
<td>Jurassic</td>
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<tr>
<td><em>Sitholeya</em> (Vishnu-Mittre, 1958)</td>
<td>female cones</td>
<td>India</td>
<td>Jurassic</td>
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<tr>
<td><em>Podostrobus</em> (Rao and Bose, 1970)</td>
<td>male cones</td>
<td>India, Antarctica</td>
<td>Jurassic</td>
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<tr>
<td><em>Bullarines</em> (Florin, 1952)</td>
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<td>Australia</td>
<td>Jurassic</td>
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<td><em>Indophyllum</em> (Vishnu-Mittre, 1958)</td>
<td>foliage</td>
<td>India</td>
<td>Jurassic</td>
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<tr>
<td><em>Trisacciodus</em> (Archangelsky, 1966)</td>
<td>foliage, male &amp; female cones</td>
<td>Argentina</td>
<td>Lower Cretaceous</td>
</tr>
<tr>
<td><em>Aperocladus</em> (Archangelsky, 1966)</td>
<td>foliage, male cones</td>
<td>Argentina</td>
<td>Lower Cretaceous</td>
</tr>
</tbody>
</table>
Eocene in North America (Dilcher, 1969).

Florin (1940, 1963) has summarized the discoveries of most modern podocarpaceous genera in the fossil record. The occurrences of these macrofossils may be listed as follows:

**Phyllocladus**
- Oligocene to Miocene of New Zealand
- Oligocene of Victoria, New South Wales

**Dacrydium**
- Tertiary of Kerguelen Archipelago
- Oligocene of Victoria, New South Wales

**Dacrycarpus**
- Middle Jurassic of western Antarctica
- Late Cretaceous of southern Patagonia
- Pliocene, Pleistocene of New Zealand
- Oligocene of eastern and south-eastern Australia
- Eocene, Oligocene of southern Chile, Patagonia
- Paleogene of eastern Australia, Tasmania

**Decussocarpus**
- Eocene of southern Chile
- Oligocene to Miocene? of New Zealand
- Tertiary (Paleogene?) of Tasmania, New South Wales

**Prynopitys**
- unknown in fossil state

**Parasitaxus**
- unknown in fossil state

**Podocarpus**
- since the Jurassic of Indonesia, eastern Australia, New Zealand, Antarctica, South America
- Early and Late Cretaceous of Russia
- Eocene of North America
Acnopyle  Eocene of western Antarctica, northern Patagonia

Saxegothaee  Oligocene? of Tierra del Fuego
Upper Cretaceous of northern Patagonia

Microcachrys  unknown in fossil state

Microstrobus  Lower Tertiary (Eocene?) of Tasmania

Fossil pollen resembling extant Phyllocladus, Dacrydium, Podocarpus, Dacrycarpus and Microcachrys has been identified from principally Tertiary strata of Australia, New Zealand and Antarctica (see Cookson and Pike, 1953a, 1953b, 1954; Couper, 1953, 1960a, 1960b).

In 1970, Rao and Bose erected the new organ genus Podostrobus to include male strobili of fossil podocarps. Initially, several species of Masculostrobus Seward were placed in Podostrobus which were subsequently found to contain saccate pollen, whereas the original specimens Seward (1911) used to describe Masculostrobus were found by Barnard (1968) to be non-saccate. Species of Podostrobus are characterized by their closely spiral sporophylls which are distally upturned and overlapping. The sporangia are positioned on the abaxial scale surface, and bear bi- and tri- saccate pollen grains. The genus has previously been recorded from the Jurassic of India and Antarctica (Rao and Bose, 1970).

Five taxa of reproductive structures assignable to the Podocarpaceae have been isolated from the Winton Fossil Plant Assemblage, descriptions of which now follow.
4.2.2.2.1. **Fecundistrobus** gen. nov.

**Systematic Description** (Figs. 218 - 228, 231 - 236)

Order: Coniferales

Family: Podocarpaceae

Genus: **Fecundistrobus** gen. nov.

**Diagnosis**: Ovulate cone narrowly ellipsoidal to ellipsoidal. Cone-scales 23 - 32 in number, imbricate, elliptic to ovate in dorsal view, arranged helically about cone axis. Fertile scales numerous, one ovule per cone-scale, erect, attached to adaxial scale surface. Epimatium absent. Integument single. Immature ovules with large, recurved micropyle, concealed by cone-scale. Mature ovules ovoid, extending beyond scale apex. Stomates on adaxial surface of scale, each stomate 50μ long, 30μ wide. Epidermal cells square to rectangular, arranged in longitudinal rows.

**Etymology**: The name was chosen from the Latin words "fecundus" meaning fruitful, and "strobus" meaning cone, illustrating the large number of ovules produced by each strobilus, a feature uncommon in other genera of the Podocarpaceae.

Type Species: **Fecundistrobus hamusites** Peters

**Fecundistrobus hamusites** sp. nov. **Systematic Description**

Order: Coniferales

Family: Podocarpaceae

Genus: **Fecundistrobus** Peters

**Fecundistrobus hamusites** sp. nov.
Diagnosis: Ellipsoidal to narrowly ellipsoidal ovulate cone, length 5.9mm ± 1mm (n=18, min. 4.4mm, max. 8.2mm), width 2.6mm ± 0.3mm (n=18, min. 2mm, max. 3.1mm). Cone-scales densely packed, imbricate, 30 ± 3 per cone, (n=12, min. 23, max. 32,) each scale consisting of a decurrent, obtangular scale base, adnate to cone axis, 1.3mm ± 0.2mm long (n=6, min. 1.2mm, max. 1.6mm), 0.8mm ± 0.1mm wide (n=39, min. 0.7mm, max. 1.0mm), (Scale base usually concealed by surrounding scales) and a free portion of the cone-scale, elliptic to ovate in dorsal view, 1.3mm ± 0.1mm long (n=47, min. 1.3mm, max. 1.7mm), 0.8mm ± 0.1mm wide (n=39, min 0.7mm, max 1.0mm). Scale radially divergent from cone axis, then recurved so that the apex faces cone axis. Scale apex rounded. Dorsal scale surface convex, occasionally with slight keel running down its centre from apex to the adnate base. Scale phyllotaxis spiral, pitch angle 54° ± 10° (n=6) from the vertical. Cone-scales usually possess a single ovule on adaxial surface, at various stages of development in any one cone. Mature ovules erect, basally attached to free portion of cone-scale about 400µ above point of insertion of scale with axis. Cone-scales obscure immature ovules from dorsal view.

At apex of ovule, a large, recurved micropyle hooks back to face cone axis. Micropyle substantial in young ovule, one quarter to one third its total length. Mature ovules 1.9mm - 2.4mm long, extending well beyond bract, 1.4mm wide, 1.1mm - 1.4mm thick, ovoid in shape with rounded and slightly bifacial apex. Distinct ridges along lateral edges of anterior half of ovule. Micropyyle still present in mature ovule, small in comparison to that of immature ovule.

No ovuliferous scale or epimatium present, integument single. Stomates arranged in longitudinal rows along adaxial cone-scale surface. Each stomate 50µ long, 30µ wide. Epidermal cells of abaxial
cone-scale surface square to rectangular, arranged in longitudinal rows. Epidermal cells of adnate scale base smaller, 15µ - 45µ long, 15µ wide, square to rectangular, arranged in longitudinal rows. Epidermal cells of immature ovules elongate, 10µ wide, length indeterminate. Cellular detail of mature ovules poor.

**Etymology**: The specific epithet is taken from the Latin "hamulus" meaning a small hook, referring to the hooked micropyle of the ovule.

**Holotype**: W702 (Fig. 220)

**Paratypes**: W700, W701, W703 - W712

**Type Locality**: 50 km northwest of Winton, Queensland, 22°12' 00"S and 142°31' 30"E.

**Discussion**: The female reproductive structures of the Podocarpaceae show a wide variation among the genera, but all can be characterized by the single ovule per sporophyll and the fleshy seeds. Those genera with several or many sporophylls have them arranged in small strobili. The genera can be separated on the basis of their general strobilus morphology, positioning and orientation of their ovules, and the possession and arrangement of sterile scale tissue.

A collection of *Fecundistrobus* cones is illustrated in Figures 218 - 228. This new genus shares characteristics of its female strobilus with various extant podocarpaceous genera. The total combination of features seen in the fossil, however, separates it clearly from the living taxa.

Only *Microcachrys* (Fig. 229) and *Saxegothaea* (Fig. 230) have
similarly well defined female cones. \textit{Microcachrys} has a unique phyllotaxis for the family, with the cone-scales arranged in alternate whorls of four. The other extant genera have reduced cones, as in \textit{Microstrobus} and \textit{Phyllocladus}, or the sporophylls are single, as in \textit{Podocarpus}, or few in number and arranged in reduced spikes (eg. \textit{Acnopyle}, \textit{Lagarostrobus}, \textit{Halocarpus}).

Both \textit{Microcachrys} and \textit{Saxegothaee} usually have sterile scales at the cone base and fertile scales above. \textit{Phyllocladus}, however, has sterile scales only at the cone apex. The ovules are distributed evenly in the cones of \textit{Fecundistrobus}.

The erect orientation of the ovules of \textit{Fecundistrobus} (Fig. 231) is also found in \textit{Microstrobus}, \textit{Phyllocladus}, \textit{Lepidothammus} and mature strobili of \textit{Lagarostrobus}. The ovules of \textit{Microcachrys} are erect in the immature cones, but reflex during maturation. The other podocarpaceous genera possess reflexed ovules (eg. \textit{Podocarpus}, \textit{Saxegothaee} and mature \textit{Microcachrys}) or semi-erect ovules (\textit{Dacrydium}). Of the four extant genera with erect ovules, \textit{Lepidothammus}, \textit{Phyllocladus} and \textit{Microstrobus} have the ovules attached at the scale axil. \textit{Lagarostrobus} and \textit{Fecundistrobus} have their ovules attached to the cone-scale above the axil. The erect ovules of immature \textit{Microcachrys} cones arise from a median position on the sporophyll, rather than in the scale axil.

With the exception of \textit{Microstrobus} with its single integument, the other extant genera all have sterile tissue around the ovule to some degree, either enclosing the seed, as in \textit{Saxegothaee} and \textit{Podocarpus}, or forming a basal epimatium as in \textit{Dacrydium}, \textit{Phyllocladus}, and \textit{Microcachrys}. \textit{Fecundistrobus} has a single integument and no epimatium.

The sharply reflexed micropyle of the ovules in \textit{Fecundistrobus}
(Fig. 232) is a feature not found in extant podocarps, with the exception of the three species of *Lepidothamnus*, particularly *L. laxifolius* (Fig. 248).

Figures 233 - 236 illustrate the epidermal features of the cone-scales and ovules of *Fecundistrobus hamusites*. A description of these characteristics has been included in the generic and specific diagnoses to completely portray the features observed. Epidermal characters are not generally used as taxonomic indicators in the family.

In summarizing the comparisons made between the fossil and extant genera, *Fecundistrobus* shares a compound cone structure with *Microcachrya* and *Saxegothaea*: perpetually erect ovules with *Microstrobus*, *Phyllocladus* and *Lepidothamnus*: a single ovule integument with *Microstrobus*: a non-axillary ovule position with *Microcachrya* and *Lagarostrobus*: and a hooked micropyle with *Lepidothamnus*.

*Fecundistrobus* therefore exhibits a unique compliment of features so that its position as a separate genus can be justified. The endemic Australian genus, *Microstrobus* (Fig. 237), shows the greatest similarity to the fossil, but as discussed above, significant differences exist between them.

Unfortunately, most of the modern podocarp genera are only represented in the fossil record by sterile foliage (including one species of *Microstrobus*, *M. sommervillae* (Townrow 1967b). The discovery of *Fecundistrobus* is therefore most important in elucidating the structure of a Cretaceous podocarp which possesses an array of features not seen in modern genera. Its presence in the fossil record supports the idea that the extant genera of the Podocarpaceae represent relict groups of a more restricted nature than those present in the Mesozoic.

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It is the first recorded discovery of a Cretaceous podocarp megastrobilus from Australia.

Only two extinct genera of podocarps have been described from Australia: *Rissikia* from the Triassic and *Mataia* from the Jurassic (Townrow, 1967a). Both had long, spike-like female cones with well separated bract-scale complexes (15 - 25 in *Rissikia*, 8 - 12 in *Mataia*). The more primitive *Rissikia* possessed one or two inverted seeds on each of the three lobes of the ovuliferous scale (Fig. 238), while *Mataia* had a pair of round, inverted, stalked seeds, partly covered by each folded cone-scale (Fig. 239).

The only extinct podocarp genus showing a close morphology to *Pecundistrobus* is *Mehtaia* from the Rajmahal Series of the Indian Jurassic (Vishnu-Mittre, 1958). The female cones of this genus are compact or loose. The spirally arranged cone-scales bear a single erect ovule, up to 1.5mm long, borne from a median position on the scale. Each ovule has a single integument, and a curved micropyle faces the cone axis. No epimatium or sterile scale tissue is present. Three species have been described. The cones of *Mehtaia rajmahalensis* are oblong, 10mm by 5mm, with compactly arranged cone-scales, keeled on the abaxial surfaces. From the base of the cone to the apex, there is a gradual change in the orientation of the ovule from a horizontal to an erect position (Fig. 240). *M. nipaniensis* has a cylindrical cone, 8mm by 4mm, with loosely arranged, fleshy cone-scales. The ovules are narrowly oval with a strongly recurved micropyle (Fig. 241). The cones of *M. santalensis* (Fig. 242) are compact and conical, 5mm - 6mm long by 5mm wide, with ovules only present in the apical region. Based on the cone structure, together with the morphology of accompanying foliage, Vishnu-Mittre (1958) has also likened *Mehtaia* to *Microstrobus*.  

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Fecundistrobus shares many features with Mehtaia. The compact cone of *H. rajmahalensis* places it close to Fecundistrobus, however the loose, fleshy cone of *H. nipaniensis* has the more erect ovules with strongly recurved micropyles seen in the Australian genus. The conical, few-seeded cones of *H. santalensis* make this species quite distinct. Fecundistrobus can be separated from Mehtaia by its smaller, more elongate cones and much larger ovules. Unfortunately, Fecundistrobus has not been found with attached foliage, nor has any vascular structure been preserved within the cones, as have been found in Mehtaia. The discovery of Fecundistrobus however, has increased the range of this type of podocarp into the Australian region.

4.2.2.2.2. *Lepidothammus australis* sp. nov.

**Systematic Description** (Figs. 243 – 247)

Order : Coniferales

Family : Podocarpaceae

Genus : *Lepidothammus* Phil.

*Lepidothammus australis* sp. nov.

**Diagnosis** : Fragmented female reproductive shoot, consisting of single, elliptic ovule, 2.9mm long, 1.8mm wide, arising from axil of sporophyll. Ovule fully erect, with recurved apical micropyle, 0.3mm high. Thin, asymmetrical sheath encircles ovule base, maximum height 0.5mm. Sporophyll consisting of an adnate obtriangular base, 1.2mm long, and an acute pointed, triangular blade, 0.7mm high, 0.9mm wide at the base. Widely elliptic stomates, 40μ by 35μ arranged longitudinally on dorsal surface of sporophyll.
Etymology: The specific epithet indicates the Australian distribution of this new species.

Holotype: W145 (Figs 243–248)

Type Locality: 50km northwest of Winton, Qld., 22°12′00″S and 142°31′30″E

Description: A single, erect, silicified ovule is positioned in the axil of a terminal sporophyll of a fragmented reproductive axis (Figs. 243 – 245). A second, incomplete sporophyll is located opposite and slightly above the other.

The ovule is elliptic in shape, 2.9mm long, 1.8mm wide and 1.4mm thick. The longitudinal axis of the ovule is in line with the attached sporophylls. A strongly recurved micropyle (0.3mm high) is positioned at the apex of the ovule facing the shoot apex. A slight convex ridge, continuous with the micropyle, runs down the median face of the ovule to its base. A thin, asymmetrical sheath of maximum height 0.5mm encircles the base of the ovule.

The sporophyll subtending the ovule consists of an obtriangular, adnate base, 1.2mm long, and a triangular, free blade, 0.7mm high and 0.9mm wide at its base, with an acute, pointed scale apex. The dorsal sporophyll surface is made up of poorly preserved, elongate epidermal cells of indeterminate size (Fig. 246). Small, widely elliptic stomates are present, 40μ long and 35μ wide, arranged longitudinally along the axis of the sporophyll.

The ovule epidermis is composed of regular, square to rectangular cells, 30μ - 60μ long by 30μ wide, arranged in longitudinal rows (Fig. 247). Stomates are absent. There is no preservation of epidermal cells
on the basal ovular sheath.

**Discussion**: This fossil was extracted as a three-dimensional petrification from a carbonate rock-matrix. The degree of preservation is good, with only slight compression of the ovule. Unfortunately, the silica is soft and powdery, so that internal structural investigations were not possible.

In producing a single ovule on the adaxial surface of the sporophyll, the specimen shows the typical arrangement seen in the Podocarpaceae. The only genera possessing a single, erect ovule on a terminal sporophyll are *Lepidothamnus* and *Lagarostrobus*. Ovules of *Dacrydium* are partially inverted when first formed, becoming partially erect when mature. *Halocarpus* has distinctly reflexed ovules. All other podocarp genera have either small, reflexed or erect ovules arranged in cones (e.g. *Microstrobos*, *Saxegothaea*) or the ovules are terminal, single, and reflexed (e.g. *Podocarpus*, *Acropyle*).

Only *Lepidothamnus* has its erect ovule borne in the axil of a sporophyll, as occurs in the fossil. The ovule of *Lagarostrobus* is obliquely inclined toward the cone axis when young, becoming erect at maturity. In this genus, the ovule is borne in a median position of the surface of the fertile bract (Quinn, 1982).

*Lepidothamnus* has 3–5 sporophylls, of which one or two are fertile. The peculiarly spreading sporophylls of *Lagarostrobus* number 5–10, and are each separated by distinct internodes. While only the top two sporophylls remain in the fossil, they show the same size, form and arrangement seen in extant *Lepidothamnus*, with its elongated sporophyll bases, and the fertile sporophyll positioned opposite and and slightly lower than another sterile scale. *Dacrydium cupressinum*, which,
although appearing similar to *Lepidothamnus* in general form, has a semi-erect ovule borne on the median surface of a single, fertile sporophyll.

*Lepidothamnus*, *Lagarostrobus* and *Decrydium* all possess a sheath around the base of the seed. This sheath is formed from the epimatium (the sterile part of the seed-scale complex). Quinn (1982) has described the sheath of *Lepidothamnus* as membranous and asymmetrical, less than one-quarter the height of the seed. That of *Lagarostrobus* is fleshy and asymmetrical, extending to half the seed height. The basal sheath of *Decrydium* is submembranous and asymmetrical, less than one-third the height of the seed. In the previously described fossil, the epimatium has formed a very asymmetrical, membranous sheath, extending to one-fifth the height of the seed. In this respect, it significantly resembles the condition seen in the extant species of *Lepidothamnus*.

Of all the extant podocarp genera, only *Lepidothamnus* possesses ovules with a recurved micropyle. (Fossil genera with this feature include *Mehtaia* Vishnu-Mitre and *Fercundistrobus* Peters gen. nov.. The strongly reflexed micropyle of the fossil is identical to that of the extant species *Lepidothamnus laxifolius* from New Zealand (Fig. 248). The only characteristics which separate *Lepidothamnus australis* sp. nov. from *L. laxifolius* are its slightly smaller ovule and its more asymmetrical and less extensive basal sheath.

*Lepidothamnus australis* is the first member of the genus to be described from the Australian continent. With extant species occurring in Chile and New Zealand, *L. australis* further indicates that the genus was probably widely distributed across the southern Gondwana regions from at least the Late Mesozoic.
4.2.2.2.3. *Podostrobus eromanga* sp. nov.

**Systematic Description** (Figs. 249 - 262)

Order: Coniferales
Family: Podocarpaceae
Genus: *Podostrobus* Rao et Bose 1970

*Podostrobus eromanga* sp. nov.

**Diagnosis**: Narrowly ellipsoidal microstrobilus, min. length 10.7mm, max. diameter 4.7mm, comprising numerous, spirally arranged microsporophylls, angle of pitch 30° - 32°. Dorsal sporophyll surface roughly triangular to quadrate-rhombic in shape, convex, 1mm wide and 1mm high, with a rounded apex. Sporophylls imbricate, peltate, with 2 microsporangia positioned on abaxial surface of each sporophyll. Microsporangia narrowly ellipsoidal to ellipsoidal in shape, thin-walled, 1.0mm - 1.3mm long, 0.3mm - 0.5mm wide, 0.5mm - 0.7mm high, filled with numerous, incompletely developed tri-saccate microspores, 23μ - 30μ in diameter. Cone axis 1.2mm - 1.6mm across, containing 1 or 2 rings of resin ducts, 15 - 20 in number, arranged about perimeter of axis. Each duct 50μ in diameter. Single vascular strand enters the thin lamina of each sporophyll. Several bract-like, upturned, recurved leaves, 2.2mm - 2.8mm long, are attached to cone peduncle.

**Etymology**: The specific epithet is taken from "Eromanga Basin", the depositional basin containing the Winton Fossil Plant Assemblage.

**Holotype**: W579 (Figs 250, 254-256, 258, 259, 262)
Paratypes : W168, W198, W562

Type Locality : 50km north-west of Winton, Queensland. 22° 12' 00''S and 142° 31' 30''E.

Description : Podostrobus eromanga is represented by four specimens. W562 and W579 are longitudinally exposed cones which give detail of the external cone morphology (Figs. 249, 250). W198 and W168 (Figs. 251, 252) were both embedded in a solid quartz matrix, showing excellent preservation of internal anatomy. Only W562 showed poor replacement of its internal structure.

The cone bases had fragmented away from all the specimens, so that a minimum cone length of 10.7mm was measured. The maximum cone diameter was 4.7mm. The microsporophylls are spirally arranged, with a pitch angle of 30° - 32°, imbricate with triangular to quadrate-rhombic dorsal scale surfaces. The sporophylls measure 1mm broad and 1mm high, with a rounded scale apex, and convex distal surface. In a radial longitudinal section, the cone-scales are distinctly peltate, with narrow laminae and thin distal surfaces (Figs. 252 - 255). A single vascular strand enters each sporophyll (Fig. 255).

Two closely spaced microsporangia are attached to the abaxial surface of each microsporophyll (Fig. 256). Each sporangium is narrowly ellipsoidal to ellipsoidal in shape, 1.0mm - 1.3mm long, 0.3mm - 0.5mm wide and 0.5mm - 0.7mm high. The sporangia are packed with mostly immature spores (Fig. 258 - 261). The more mature spores are tri-saccate, 23μ - 30μ in diameter.

The cone axis is wide, 1.2mm - 1.6mm in diameter. The preservation of internal tissue is poor. One, sometimes two rings of
small resin ducts, 15 - 20 in number, are found around the perimeter of the cone axis (Fig. 257).

Several, small, bract-like leaves, 2.2mm - 2.8mm long, are attached to the cone peduncle of W579 (Fig. 262). Each leaf is upturned and slightly recurved. There is no preservation of epidermal cells.

Discussion: *Podostrobus eromanga* sp. nov. differs from previously described species of the genus in its slightly larger strobili and proportionally larger sporangia. Nevertheless, according to the generic diagnosis by Rao and Bose (1970), it can clearly be placed in *Podostrobus* (see Fig. 263).

The tri-saccate microspores enclosed within the sporangia of *P. eromanga* are of a similar size and shape as *Microcachrydites antarcticus*, a common palynomorph in the deposit (Figs. 17 - 20). The fossil strobili can be distinguished from those of extant *Microcachryus*, however, in several respects. Microcachrean cones have a distinctive cavity between the two sporangia beneath the sporophyll (Stiles, 1912), whereas the sporangia are almost fused together in *Podostrobus eromanga*. Resin canals are absent from the cone axis in *Microcachryus*, but are present in *P. eromanga*. Tri-saccate pollen is found in at least two other genera of extant podocarps, including *Microstrobus* and *Dacrycarpus*, so that despite the prevalence of *Microcachrydites* in the deposit, and possibly within *Podostrobus*, the fossil pollen cones cannot be assigned to an extant genus.
4.2.2.4. **Podostrobus major** sp. nov.

**Systematic Description** (Figs. 264 - 266)

**Order**: Coniferales

**Family**: Podocarpaceae

**Genus**: **Podostrobus** Rao et Bose 1970

**Podostrobus major** sp. nov.

**Diagnosis**: Large, elongate microstrobilus, min. length 16.3mm, max. diameter 7.5mm, comprising numerous spirally arranged microsporophylls, pitch angle 31°. Distal sporophyll surface triangular in shape, 1mm wide, 1mm high with an acute, upturned and incurved scale apex. Sporophylls imbricate, peltate, with 2 ellipsoidal microsporangia attached to abaxial surface. Sporangia 2mm long, 0.8mm wide. 0.8mm high, filled with numerous, tri-saccate microspores, 25µ - 30µ in diameter. Cone axis wide, 2.5mm in diameter, pith 1.2mm across, vascular cylinder 500µ thick. No resin canals present.

**Etymology**: The specific epithet refers to the characteristically large size of the strobilus.

**Holotype**: W433 (Figs 264-266)

**Type Locality**: 50km north-west of Winton, Queensland. 22° 12' 00''s and 142° 31' 30''E.

**Description**: This species is represented by a single specimen, found embedded longitudinally in a quartz-matrix rock. After transverse and radial sectioning, the maximum cone thickness was found to be 7.5mm, while the minimum length is 16.3mm. Many of the sporophylls on the exposed cone surface have been broken. Figure 264 shows the spirally
arranged cone-scales, of pitch angle 31°, with their triangular scales, 1mm high and 1mm wide. The scale apices are acute, vertically upturned and incurved.

Two large, closely-spaced and ellipsoidal microsporangia are attached to the abaxial surface of each sporophyll (Fig. 265). The sporangia measure 2mm long, 0.8mm wide and 0.8mm high, and are filled with numerous, tri-saccate microspores, 25μ - 30μ in diameter (Fig. 266).

The cone axis is quite well preserved, with a large central pith, 1.2mm across, and a vascular cylinder 500μ thick around the circumference of the axis (Fig. 265). Resin canals are absent from the axis.

Discussion: *Podostrobus major* is the largest microstrobius that has been assigned to this organ genus. The original species described by Rao and Bose (1970) measure only 3.5mm - 7.0mm in length, with sporangia less than half the length of those of *P. major*. The cones of *P. eromanga* have a maximum measured length of 10.7mm. The size of the male cones of the Podocarpaceae vary greatly, and variation in this character is not a criterion used in diagnosing *Podostrobus*.

The acute, pointed, incurved cone-scales of *P. major* are also distinguishable from the more rhombic scales and rounded scale apices of *P. eromanga*.

Although containing pollen of the *Microcachryditea* type, *Podostrobus major* also differs from the male strobili of *Microcachryys* in its adnate sporangia. The absence of resin ducts in the cone axis of the Winton fossil, however, is a feature seen in *Microcachryys* cones. One is left with the assumption that either Cretaceous microcachreon
male strobili were larger and more varied than the extant species, or Podostrobus eromanga and P. major are the microstrobili of extinct podocarps with microspores closely allied to Microcachrys.

4.2.2.5. Podostrobus bisaccata sp. nov.

Systematic Description (Figs. 267 - 270)

Order : Coniferales
Family : Podocarpaceae
Genus : Podostrobus Rao et Bose 1970
Podostrobus bisaccata sp. nov.

Diagnosis : Ovoid microstrobilus, 4.2mm long, 2mm wide. Cone axis slender, widest near base, 550μ across, tapering slightly toward cone apex. Sporophylls spirally arranged, distal part of each sporophyll upturned and imbricate. Sporangia ovoid, abaxially placed, thin-walled, mostly ruptured, 400μ long, 200μ high. A single vascular strand enters each microsporophyll. Microspores bisaccate, 35μ - 45μ by 25μ - 30μ, bilaterally symmetrical, sacchi hemispherical.

Etymology : The specific epithet refers to the bisaccate nature of the microspores.

Holotype : W008 (Figs 267-270)

Type Locality : 50km north-west of Winton, Queensland. 22° 12′ 00′′S and 142° 31′ 30′′E.

Description : The cone was found longitudinally exposed during sectioning of a quartz-matrix rock. External scale features are not
visible. The cone is ovoid in shape, 4.2mm long and 2mm wide near the base (Figs. 267, 268). The sporophylls are narrow and imbricate, spirally arranged about the cone axis. A single vascular strand enters each sporophyll (Fig. 269). The cone axis is slender, 550μ across near its base, tapering gently toward the cone apex (Fig. 268). There is no clear preservation of the pith or cortical tissue. The microsporangia are positioned on the abaxial surfaces of the sporophylls. Most of the sporangia were preserved during the process of dehiscing, with their thin walls ruptured (Fig. 267). The sporangia are ovate, 400μ long and 200μ high. Bisaccate microspores are concentrated within and around the sporangia. The spores are bilaterally symmetrical, 35μ - 45μ wide and 25μ - 30μ high, with hemispherical sacci (Fig. 270).

Discussion: The small, ovoid cone and bisaccate microspores of this species separates it from the other Winton species of Podostrobus. The most similar species within the genus is P. rajmahalensis from the Upper Jurassic of India (Rao and Bose, 1970), which differs only in its slightly larger cones and spores (Fig. 263).

The microspores in Podostrobus bisaccata can be assigned to Podocarpidites Cookson ex Couper 1953, a relatively common palynomorph in the deposit (see Figs. 6, 7). The presence of these well preserved, dehisced spores demonstrates the very immediate fossilization which must have occurred in calm, non-oxidizing conditions.
4.2.3. *Taxodiaceae*

4.2.3.1. *Taxonomy of Extant Genera*

The *Taxodiaceae*, consisting of just 15 species in 10 genera, are a truly relic family of conifers. Their present distribution (Fig. 271), with no genus native to more than one continent, indicates a rapid retreat from wider Late Mesozoic and Tertiary environments (Florin, 1963).

The family is characterized by its spirally arranged foliage and cone-scales (opposite in *Metasequoia*) and globose cones which bear persistent scales, fused to the bracts. Between 2 and 6 erect or inverted seeds are positioned on each scale.

The relative uniqueness of each genus has meant that little taxonomic revision at the generic level has been necessary since Pilger (1926) erected the family. The marked segregation of the genera in fact led Hayata (1931, 1932) to divide 5 separate families from the *Taxodiaceae*, viz. *Sciadopityaceae*, *Limnopityaceae* (including *Taxodium* and *Glyptostrobus*), *Cryptomeriaceae*, *Taiwaniaceae* and *Cunninghamiaaceae*. Of these segregates, only *Sciadopityaceae* has received acceptance by subsequent authors, including Gauasen (1966) and Christophel (1973).

The only modern genus to be recently erected is *Sequoiadendron*, split from *Sequoia* by Buchholz (1939). *Metasequoia* Miki was described as a fossil genus in 1941, and was subsequently discovered to have an extant representative in central China. Hu and Cheng (1948) assigned this species, *Metasequoia glyptostroboidea* to a monotypic *Metasequoicaceae* because of its possession of decussate phyllotaxis, an
arrangement atypical in the Taxodiaceae. It has since been shown, however that *Metasequoia* is truly taxodiaceous with a close relationship to *Sequoia* and *Sequoiadendron* (Gaussen, 1966).

Eckenwalder (1976) proposed that the Taxodiaceae be merged into the Cupressaceae, based on his calculated similarities in measured characters between the families. In particular, Eckenwalder reasoned that his observed close affiliation between *Cupressus* and *Callitris* (both Cupressaceae) and *Sequoia, Sequoiadendron* and *Metasequoia*, and the equally close affiliation between these taxodiaceous genera and the other taxodioids, give reason for the taxonomic merger to occur. I do not believe that such an assumption is valid before more extensive intergeneric comparisons are made. Miller (1977) has compared the taxodiaceous genera with Late Triassic remains of the Cupressaceae reported by Lemoigne (1967), and suggested the two families may have had a common ancestor resembling *Pseudovoltzia*. Eckenwalder confirmed that fossil taxonomic evidence pointing to the evolutionary development of both the Cupressaceae and Taxodiaceae is lacking. Until such evidence appears, it is well enough to recognize the traditional distinctions of the taxodioids so far accepted by conifer taxonomists.

The following list gives the extant species of the Taxodiaceae, together with their natural areas of distribution (also see Fig. 271)

*Athrotaxis cupressoides* Don.  
Tasmania

*A. laxifolia* Hooker  
"

*A. selaginoides* Don.  
"

*Cryptomeria japonica* (Linn. fil.) Don.  
Japan
Cunninghamia lanceolata (Lambert) Hook. fil. south-east China

C. konishii Hayata Japan

Glyptostrobus lineatus (Poiret) Druce south China

Metasequoia glyptostroboides Hu et Cheng central China

Sequoia sempervirens (D. Don) Endl. western U.S.A.

Sequoiaadendron giganteum (Lindl.) Buchholz western U.S.A.

Taiwania cryptomerioides Hayata central China, Burma, Taiwan

Taxodium ascendens Brongniart south U.S.A.

T. distichum (L.) Richard " "

T. mucronatum Tenore Mexico

Only the 3 species of Athrotaxis are native to the southern hemisphere, and are restricted to dwindling habitats in the mountainous regions of Tasmania. It has been suggested that the intermediate appearance of A. laxifolia might be due to hybridization between the other 2 species, but this is not supported by cytological evidence (Gulline, 1952).

4.2.3.2. Fossil Taxodiaceae

Mesozoic fossils assignable to the Taxodiaceae have been discussed by Miller (1977), who holds the general view that the modern genera are representative of long lines of specialization of groups more abundant in the past.

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The family can be traced back to the Jurassic, with the appearance of several genera of seed cones with clear taxodiaceous affinity: Pararaucaria Wieland and Romeroites Spengazzini from Argentina, and Elatides williamsonii Brongniart from England. Less reliable remains from the Jurassic include Cunninghamamites Presl., Elatocladus, Sewardiodendron, Farndalea, Sciadopitytes and Sciadopityoxylon (see Miller, 1977). Sequoia is the only modern genus with supposed Jurassic species, including imprints of leafy shoots called S. jeholensis from Manchuria (Endo, 1951) and a seed cone species from France (Jongmans and Dijkstra, 1972).

The family showed greater diversity in the Cretaceous, with the appearance of the remaining modern genera (with the exception of Sequoiadendron). The foliage forms of the Cretaceous species were similar to their corresponding extant species, so that the family has changed little since the Late Mesozoic (Eckenwalder, 1976; Miller, 1977). Table 5 gives the significant Cretaceous fossil representatives of the modern genera, and closely related extinct genera within the Taxodiaceae.

Apart from the recently described genus Austrosequoia from the Winton Fossil Plant Assemblage (Peters and Christophel, 1978), Athrotaxis is the only taxodiaceous genus known to have existed in the southern hemisphere, which is strong evidence for the northern origin of the Taxodiaceae. The other modern genera had a generally wide distribution over Europe, Asia and North America during the Tertiary before retreating to their current habitats (see Florin, 1963).

The geographical separation of Athrotaxis has not been adequately explained by palaeobotanists, particularly in light of the supposed
<table>
<thead>
<tr>
<th>CLADO &amp; REFERENCE</th>
<th>FOSSIL TYPE</th>
<th>LOCALITY</th>
<th>AGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Athrotaxis (Hdl, 1936)</td>
<td>leafy twig &amp; female cones</td>
<td>Canada</td>
<td>Early Cretaceous</td>
</tr>
<tr>
<td>Athrotaxis (Aranghelinsky, 1936)</td>
<td>leafy twig</td>
<td>Argentina</td>
<td>Early Cretaceous</td>
</tr>
<tr>
<td>&quot; (Hdl, 1937b)</td>
<td>leafy twig &amp; female cones</td>
<td>Patagonia</td>
<td>Lower Cretaceous</td>
</tr>
<tr>
<td>Athrotaxiscepaea (Fontaine, 1889)</td>
<td>foliage &amp; cones</td>
<td>eastern U.S.A.</td>
<td>Early Cretaceous</td>
</tr>
<tr>
<td>Cryptomeria (Joungmans &amp; Dijkstra, 1972)</td>
<td>leafy twig</td>
<td>Russia</td>
<td>Cretaceous</td>
</tr>
<tr>
<td>Cryptomeriopsis (Stopes and Fujii, 1910)</td>
<td>foliage</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Cunninghamia (Matsuo, 1966, 1970)</td>
<td>foliage, cones</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Joungmans &amp; Dijkstra, 1972)</td>
<td>foliage, cones</td>
<td>Bohemia</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Cunninghamiostrobis (Ogura, 1930)</td>
<td>cones</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Miller, 1975)</td>
<td>foliage, cones</td>
<td>California</td>
<td>Early Cretaceous</td>
</tr>
<tr>
<td>Glyptostrobus (Hollick &amp; Martin, 1930)</td>
<td>foliage</td>
<td>Alaska</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Matsuo, 1930)</td>
<td>foliage</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Rouse, 1967)</td>
<td>cones &amp; pollen</td>
<td>British Columbia</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Schweizer, 1974)</td>
<td>foliage, seeds</td>
<td>Spitzbergen</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Metasequoia (Rouse, 1967)</td>
<td>foliage</td>
<td>British Columbia</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Matsuo, 1970)</td>
<td>foliage</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Shermacher, 1966)</td>
<td>foliage</td>
<td>U.S.A.</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Sciadopitys (Durov &amp; Sveshnikova, 1959)</td>
<td>foliage</td>
<td>Russia</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Ogura, 1932)</td>
<td>foliage</td>
<td>Japan</td>
<td>Late Cretaceous (cont.)</td>
</tr>
<tr>
<td>GENUS &amp; REFERENCE</td>
<td>FOSSIL TYPE</td>
<td>LOCALITY</td>
<td>AGE</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>----------------</td>
<td>----------</td>
<td>----------------</td>
</tr>
<tr>
<td>Sciadopitys (Florin, 1961)</td>
<td>foliage</td>
<td>Spain</td>
<td>Early Cretaceous</td>
</tr>
<tr>
<td>Sciadopitysophyllum (Christophel, 1973)</td>
<td>foliage</td>
<td>Canada</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Sequoia (Hollick &amp; Jeffrey, 1909)</td>
<td>foliage</td>
<td>New York</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Matuo, 1970)</td>
<td>foliage</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Shoemaker, 1966)</td>
<td>foliage</td>
<td>Montana</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Schweitzer, 1974)</td>
<td>foliage</td>
<td>Spitzbergen</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Austrosequoia (Peters &amp; Christophel, 1978)</td>
<td>foliage and female cones</td>
<td>Queensland</td>
<td>middle Cretaceous</td>
</tr>
<tr>
<td>Sequoiadendron (Florin, 1963)</td>
<td>foliage</td>
<td>western Europe</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Florin, 1963)</td>
<td>foliage</td>
<td>U.S.A.</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Florin, 1963)</td>
<td>foliage</td>
<td>Greenland</td>
<td>Early Cretaceous</td>
</tr>
<tr>
<td>Taiwania (Matuo, 1970)</td>
<td>foliage, pollen cones</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Taxodium (Matuo, 1962)</td>
<td>foliage</td>
<td>Japan</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>&quot; (Schweitzer, 1974)</td>
<td>foliage, male cones</td>
<td>Spitzbergen</td>
<td>Late Cretaceous</td>
</tr>
<tr>
<td>Paratassodium (Florin, 1963)</td>
<td>foliage</td>
<td>Alaska</td>
<td>Cretaceous</td>
</tr>
</tbody>
</table>
appearance of the genus in the Early Cretaceous of Canada (Bell, 1956), which had by that time been long separated from the Gondwana flora. Bell closely compared the Canadian species *A. berryi* with *Athrotaxites ungeri* from the Lower Cretaceous of Patagonia (Halle, 1913b), and reasoned that because Florin (1940) believed the latter species to be a true *Athrotaxis*, that there is justification for the Canadian species to be assigned to the modern genus. Although this argument is by its nature unsound, the well preserved specimens of *A. berryi* do in fact seem to be well assigned. On the other hand, the poorly preserved *Athrotaxis* fossils described by Bose (1955) lack the necessary features for generic classification. The peltate scales of *A. sellingii* from the Oligocene(?) of Queensland more closely resemble those of *Austrosequoia* rather than the typically upturned scales of *Athrotaxis*.

Florin (1963) hypothesized that *Athrotaxis* originated in eastern Asia and migrated southward in the Jurassic via fold belts into the southern Australian region, and then spread by way of Antarctica to South America in the Late Jurassic or Early Cretaceous. This theory cannot hold true, as the position of Asia relative to Australia in the Jurassic would not have allowed this migration via land masses. Dietz and Holden (1970) and McKenzie and Slater (1973) gave no evidence for the presence of fold belts ever occurring between Asia and Australia. In the Jurassic, this region was only occupied by deep oceanic floor.

*Austrosequoia wintonensis* is as yet the only published fossil from the Winton Fossil Plant Assemblage (Peters and Christophel, 1978). This genus represents a group of taxodiaceous ovulate cones and attached foliage which shows a very close similarity to fossil and extant *Sequoia*. Contrary to Florin’s (1963) belief that *Sequoia* had not crossed into the Southern Hemisphere, the existence of *Austrosequoia*
provides evidence that this had probably occurred. The equally perplexing presence of fossil *Athrotaxis* in Canada may indicate a previous dispersal of taxodiaceous plants between the Australian and North American continents by some undetermined route.

Most specimens of *Austrosequoia* occur as buried petrifications partially exposed on rock surfaces, where weathering has obliterated much of the cone-scale morphology. The buried portions of the cones have needed to be sectioned for internal examination. A problem exists where the variably stained silica matrix camouflages much of the internal cone morphology. A more recent collection from the type locality has revealed some specimens which are totally or partially embedded in a carbonate matrix, so that complete cones could be extracted (see Chapter 3). These new specimens show superior preservation of cone-scale surfaces. Whole scales could be removed from the cone axis to show the precise nature of the ovules. The original diagnosis of *Austrosequoia wintonensis* has therefore been emended.

4.2.3.2.1. *Austrosequoia wintonensis* Peters and Christophel

**Emended Systematic Description** (Figs. 272 - 290)

Order : Coniferales

Family : Taxodiaceae

Genus : *Austrosequoia* Peters and Christophel

**Emended Diagnosis** : Ovulate cone ellipsoidal. Cone scales 29 - 49 in number, peltate, transversely rhomboidal to hexagonal in dorsal view, arranged helically about cone axis. Bract scale and ovuliferous scale united, with a broad, upturned spine or ridge with sunken base on
dorsal surface of each scale, or absent leaving median transverse groove. Cone-scales with resin duct running in transverse direction on the abaxial and adaxial side relative to the cone axis. Cone axis slender, with large pith, rarely dissected by vascular traces leading to cone-scales; uniseriate parenchyma present, growth rings not discernible. Vascular traces leading to cone-scales diverge from vascular cylinder as single unit, splitting into two traces on entry into cone-scale, and diverging abaxially and adaxially. Ovules arranged in single crescentic row on adaxial side of cone-scale. Leaves on cone-bearing stems scale-like, slightly imbricate, incurved and appressed against shoot. Scale outline simple and entire. Phyllotaxis spiral.

**Type Species**: Austrosequoia wintonensis Peters and Christophel

**Emended Diagnosis**: Ellipsoidal ovulate cone, 9mm - 16mm long, 6mm - 11mm wide. Cone-scales 29 – 49 in number, 2.5mm – 4.5mm wide, 1.5mm – 2.5mm high, arranged spirally at pitch angle of 53° - 58° from longitudinal axis of cone. Broad, median upturned spine or ridge on bract-ovuliferous scale, or spine absent, leaving median transverse groove with plications radiating to outer edges. Cone axis slender with pith 0.75mm – 1.1mm across, composed of thick-walled parenchyma cells, circular in cross section, tabulate in profile, with horizontal cross walls, few intercellular spaces. Resin canals, sclereids and fibres all absent from pith. Tracheids regular in radial strands. Ovules 4 – 7, reflexed, ellipsoidal, 600µ long, 200µ wide, dehisced from mature cones. Leaves on stems bearing cones, spiral with pitch angle of 48° - 52° from the vertical. Leaves rhomboidal in dorsal plane, 1.2mm wide. Scale apex acute to acuminate, incurved. Leaves rounded on dorsal
surface, with keel running from leaf apex to base. Pith of shoot small, with several strands of tissue radiating to edge of vascular cylinder.

Discussion: The paratype number F9512 was found to be partially embedded in a carbonate-rich rock matrix (Fig. 272). When the carbonate was dissolved, it revealed greater detail of the specimen (Fig. 273). Figures 274 - 281 illustrate a collection of cones of *Austrosequoia wintonensis* completely extracted from carbonate matrices. The dorsal cone-scale spine is only present in smaller, presumably younger cones (Figs. 274 - 276, 282) and further associates *Austrosequoia* with *Sequoia* and *Sequoiadendron*, which also possess scale spines which dehisce at maturity. The Australian taxodioid *Athrotaxis* has a distinctly different scale morphology, with fine pointed, upturned rather than peltate scales. Figure 282 shows an electron micrograph of the cone-scale surface of *Austrosequoia*. The abaxial side of the spine shows good preservation of epidermal cells. No stomates were found.

In the published diagnosis of *Austrosequoia wintonensis*, it was not certain whether the ovules were reflexed or erect. Figures 283 and 284 show a single mature ovule still attached to the scale surface, indicating clearly that the ovules are reflexed, typical of other taxodioids. Preservation of the integuments is poor and cannot be further defined. Very few cones were found to contain any ovules, and it can now be hypothesized that most cones discovered were mature, and had shed their fertilized seeds prior to fossilization. Figures 285 and 286 show a typical adaxial scale surface. The site of vascular attachment between the scale and the seed can be seen. Unfortunately, cones containing ovules have shown poor preservation of the ovulate tissue, and hence the diagnosis only refers to the size, shape and
arrangement of the ovules. Two poorly preserved cones have been found possessing some ovules/seeds in their scales. Shrivelled gametophytes or embryos can be seen in Figures 287 to 290. (Small cells of the integument are also visible). The chalazal end of the ovule is directed away from the cone axis, reflecting the inverted nature of the ovules. A small, pointed ovuliferous scale (200μ - 300μ long) radiates from the abaxial side of the ovule (Figs. 288, 290).

Holotype : F9509

Paratypes : WA1 - WA9, W152, W276, W334, W553, F9512

Type Locality : 50 km northwest of Winton, Queensland, 22° 12′ 00″S and 142° 31′ 30″E.

More recent investigations of the Winton fossil collection have revealed a small number of immature ovulate cones, which are probably those of Austrosequoia wintonensis. Until they are found attached to indisputable specimens of Austrosequoia, they cannot be included in the diagnoses. In view of their potential importance, I have informally described the specimens in this section.

Description : Immature ovulate cones cf. Austrosequoia wintonensis

(Specimens W188, W335, W358, W450, W576, W577, W655, W666)

This fossil type is represented by a collection of 9 specimens of variable quality. Six cones were found partially exposed on rock surfaces (Figs 291 - 296). One cone was discovered following dissolution of carbonate-matrix rocks (Fig. 297), while two cones were encountered during random thin-sectioning of silica-matrix rocks (Figs
The cones are ellipsoidal, 6.5mm - 9.5mm long, 2.5mm - 4.7mm wide, with approximately 40 - 60 cone-scales arranged spirally about the cone axis. Good preservation of external cone-scale morphology is only seen in W666 (Fig. 297). A short, upturned and appressed spine or ridge is present on the dorsal scale surface (Fig. 298), or the spine may be absent. W666 shows preservation of some stomates, 30u long, on the abaxial scale surface (Fig 299). The cone-scales are peltate, rhomboidal to hexagonal in shape, 0.8mm - 1.7mm wide and 0.8mm - 1.7mm high. The bract scale and ovuliferous scale are fused. A single row of 3 - 5 reflexed ovules, ellipsoidal in shape, are positioned on the adaxial surface of most cone-scales (Figs. 301 - 308). The ovules are small, 0.5mm long, 0.25mm wide. There appears to be no development of gametophytic tissue or separate integuments. The cone axis is comparatively wide, up to 2mm across. A single major vascular bundle leaves the vascular cylinder in the axis and enters each cone-scale complex (Figs. 301,302). Resin canals are common in the cone-scales (Fig. 305).

Cones W577 (Fig. 296) and W335 (Fig. 291) are attached to the apices of short foliage twigs, each bearing small, rhomboidal, spirally arranged scale leaves, 1.3mm high and 0.8mm wide. The leaves are appressed to the stem, acute-pointed with a ridge running vertically down the dorsal surface.

While in general these immature cones lack sufficient cellular detail for complete anatomical description, their basic similarity to Austrosequoia wintonensis is quite apparent. The only major difference between them is in size. In all other respects, this fossil type fits in well with the expected juvenile cone of Austrosequoia.
4.2.3.2.2. *Wintonia peltata* gen. et sp. nov.

**Systematic Description** (Figs. 309 - 341)

Order: Coniferales

Family: Taxodiaceae

*Wintonia* gen. nov.

**Diagnosis**: Ovulate cone spheroidal. Cone-scales 65 - 100 in number, peltate, rhomboidal to polygonal in dorsal view, arranged helically about cone axis. Bract scale and ovuliferous scale united, dorsal surface of scale convex. Ovule inverted, single on cone-scale. Leaves on stems bearing cones scale-like, adnate base narrowly triangular, free portion triangular with acute apex. Phyllotaxis spiral.

**Etymology**: The name was chosen to illustrate the occurrence of the genus within the Winton Formation.

**Type Species**: *Wintonia peltata* Peters

*Wintonia peltata* sp. nov.

**Diagnosis**: Spheroidal, ovulate cone, 10mm - 16mm in length, 6.3mm - 20mm wide. Cone-scales 65 - 100 in number, 1mm - 4.5mm across, arranged spirally around cone axis. Scales crowded, peltate, with convex dorsal surface, usually raised in central region with indentioned centre. Resin canals common in distal portions of cone-scales. Ovules inverted, spheroidal to ellipsoidal, 0.9mm - 2mm long, 1mm - 1.5mm wide. Ovuliferous scale with 3 short projections at distal end in line with
base of ovule. Leaves on stems bearing cones spirally arranged, appressed against stem. Adnate leaf base 1.9mm long, 1.3mm wide. Free portion 1.1mm long, with convex to slightly ridged dorsal surface.

**Etymology**: The specific epithet refers to the typically peltate nature of the cone-scales.

**Holotype**: W398 (Fig. 516)


**Type Locality**: 50 km northwest of Winton, Queensland, 22° 12′ 00″S and 142° 31′ 30″E.

**Description**: *Wintonia peltata* is the largest ovulate conifer strobilus from the fossil assemblage, other than *Incetrae sedis* 1 in the Araucariaceae (Section 4.2.1.2.2.). The new genus is represented by a collection of 19 specimens, 11 of which were found exposed on rock surfaces (Figs. 309 - 319), while 7 specimens were extracted from carbonate-matrix rocks (Figs. 320 - 326). One cone was found completely enclosed within a rock matrix (Figs. 331,332).

Unfortunately, there is no preservation of epidermal cells on the cones or leafy attachments. Only 4 specimens (W022, W027, W169, W386) showed preservation of ovules. The remaining cones either showed no preservation of delicate ovular tissues, or were small and presumably juvenile.

The ovules were found to vary greatly in size within a single cone. A solitary ovule was found to occupy most of the adaxial surface of the cone-scale, and is therefore comparatively large (Figs. 327 -
Several scales have a small ovule positioned to one side of the scale (Fig. 338), and it therefore seems possible that if more than one ovule is originally borne on the cone-scale, only one matures, displacing other ovules during development. The larger ovules are interpreted as mature, due to the presence of a well defined integumentary layer (Figs. 334 - 337). Figure 335 shows a thin nucellus, free from the enclosing integuments. Within are the remains of either gametophytic or embryonic tissue attached to a chalaza. Cells of the ovular stalk are preserved in some specimens (Figs. 333, 334).

The ovuliferous scale is almost covered by the large ovule. The 3 short projections at the distal end of the ovuliferous scale (Figs. 333 - 335) can be likened to those possessed by the extant taxodioid, Cryptomeria. However, these projections protrude past the bract scale in Cryptomeria and are visible at the cone surface. The ovuliferous scale of Wintonia in Figure 336 shows only one rounded or distorted projection, and probably represents a longitudinal rather than transverse section.

None of the specimens show any preservation of vascular tissue, or tissue of the cone axis. A large resin canal runs through to the distal part of the cone-scale (Figs. 339, 340). Only one specimen showed good preservation of a cone-bearing stem (Figs. 316, 341).

Discussion: Wintonia peltata possesses the features common to the Taxodiaceae, including numerous spirally arranged scales, globose cones, inverted ovules and fused bract and ovuliferous scales. While the cones bear a resemblance to the ovulate strobili of Taxodium distichum (Fig. 342), many of the diagnostic features which are necessary for accurate comparison have not been found. I anticipate
that new, better preserved specimens will supply such necessary information as vascular patterns and ovule development. It is apparent however, that the particular combination of morphological features found in this new genus is unique, and further indicates that the representation of the Taxodiaceae within the Australian vegetation of the Late Mesozoic is far greater than has been previously thought.
4.2.4. Cupressaceae

4.2.4.1. Extant and Fossil Genera

The Cupressaceae is a large conifer family, consisting of 137 extant species in 18 genera, and is distributed principally throughout the Northern Hemisphere (see Fig. 343). The family is characterized by its whorled, scale leaves and small, few-scaled ovulate cones with erect ovules. The following list gives the number of living species and the distribution of each modern genus in the family.

<table>
<thead>
<tr>
<th>Genus</th>
<th>No. of Species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juniperus L.</td>
<td>60</td>
<td>North America, Mexico, West Indies, North Africa, east tropical Africa, Himalaya, China, Taiwan</td>
</tr>
<tr>
<td>Cupressus L.</td>
<td>21</td>
<td>west U.S.A., Mexico, Mediterranean region, China, Himalaya</td>
</tr>
<tr>
<td>Callitris Vent.</td>
<td>16</td>
<td>Australia, New Caledonia</td>
</tr>
<tr>
<td>Thuja L.</td>
<td>6</td>
<td>China, Japan, Taiwan, North America</td>
</tr>
<tr>
<td>Chamaecyparis Spach</td>
<td>6</td>
<td>North America, Japan, Taiwan</td>
</tr>
<tr>
<td>Libocedrus Endl.</td>
<td>5</td>
<td>New Zealand, New Caledonia</td>
</tr>
<tr>
<td>Widdringtonia Endl.</td>
<td>5</td>
<td>southern and tropical Africa</td>
</tr>
</tbody>
</table>
Actinostrobus Miq.  3  Western Australia
Calocedrus Kurz  3  western U.S.A., Taiwan, China, Burma
Papuacedrus Li  3  New Guinea
Pokienia Henry & Thomas  2  eastern China
Austrocedrus Florin & Boutelje  1  Chile, Argentina
Diselma Hook f.  1  Tasmania
Fitzroya Hook f.  1  Chile, Argentina
Neocalitropsis Florin  1  New Caledonia
Pilgerodendron Florin  1  southern Chile
Tetraclinia Masters  1  North Africa, Spain
Thujopsis Siebold & Zuccarini  1  Japan

The three largest genera, Juniperus, Cupressus and Callitris all show wide distributions and are thought to be in an active evolutionary state (Miller, 1977). The remaining genera are small and somewhat relictual. Australian genera include Callitris (recently revised by Venning (1979)), Actinostrobus and Diselma.

Most fossil members of the Cupressaceae are represented only by vegetative structures, which has opened many taxonomic interpretations to question (Florin, 1963). However, an analysis of fossilized cones and twigs from France confirms that the family has existed since the Late Triassic (Lemoigne, 1967).

The Mesozoic and Tertiary representatives of the Cupressaceae
have been briefly reviewed by Miller (1977) and Florin (1963) respectively. The modern genera *Widdringtonia*, *Fitzroya*, *Thuja*, *Juniperus* and possibly *Callitris* and *Chamaecyparis* have been identified from Cretaceous sediments (see Miller, 1977). *Cupressus*, *Chamaecyparis*, *Thuja* and *Widdringtonia* were dispersed principally over their current range during the Tertiary (Florin, 1963). Only a few other genera in the family have been identified from Tertiary sediments. *Juniperus* has been found in the Palaeocene of Greenland and in the Miocene of Poland (Florin, 1963). The only Australian genus to be found in the fossil record is *Callitris*. A seed cone from the Early Cretaceous of the Potomac Flora was tentatively assigned to the extant genus by Fontaine (1889), while Florin (1963) mentions specimens of *Callitris* from the Cretaceous (?) of Queensland and the Oligocene of New South Wales. Blackburn (1980) has recently reported *Callitris* foliage from the Miocene of Victoria. The cuticles of his specimens were found to be identical to those of extant species.

A single cupressaceous form has been found in the Winton Fossil Plant Assemblage. The taxon is represented by 6 specimens, 4 of which were exposed on rock surfaces (Figs. 344 - 346), while 2 were dissolved from carbonate rock matrices (Figs 347, 348). Unfortunately, preservation is poor, with no detail of fine epidermal or anatomical structure.
4.2.4.1.1. *Callitris octothamna* sp. nov.

**Systematic Description** (Figs. 344 - 349).

Order : Coniferales

Family : Cupressaceae

Genus : *Callitris* Ventanat 1808

*Callitris octothamna* sp. nov.

**Diagnosis** : Undehisced fruiting cones, oblate spheroid to spheroid in shape, 6.7mm - 8.8mm long, 7.2mm - 7.8mm wide. Cone-scales 8 in number, whorled, valvate, with alternating major and minor scales broadly united at base. Free portion of scales triangular in shape, 2.75mm - 3.7mm long, 2.1mm - 2.6mm wide at base, minor scales generally 2/3 the size of major scales. Lateral edges of major scales slightly overlap minor scales. Cone-scales adnate along their length, dorsal surfaces smooth, convex, incurved toward rounded cone apex. Scale apices blunt to acute. Immature seeds present on adaxial surfaces of cone-scales, more than 30 per cone, flattened in shape, 400μ wide. Cone peduncle occasionally present, up to 8mm long, 1.4mm wide, very broad at cone base. Peduncle leaves sparse, whorled in groups of 3, decurrent, each consisting of a long, adnate base, and a short, triangular and divergent free portion, 1mm long, 1mm wide.

**Etymology** : The specific epithet refers to the presence of 8 cone-scales in the cone.

**Holotype** : W605 (Fig. 346)
Paratypes: W177, W225, WC0, WC1

Type Locality: 50 km northwest of Winton, Queensland. 22° 12' 00'' S and 142° 31' 30'' E.

Discussion: This new species possesses all the features typical of Callitris, including valvate scales which enclose a large number of flattened seeds (Fig. 349), and whorled foliage in groups of 3. While most extant species of Callitris invariably possess 6 cone-scales, several species are known to occasionally have 8 scales, including C. macleayana and C. oblonga (on juvenile branches) (Venning, 1979). Callitris octothamna most closely resembles C. oblonga (Fig. 350), an extant species endemic to Tasmania. The fossil cones however, are much smaller and lack dorsal scale points.

Unfortunately, further diagnostic characters such as features of the columella and epidermis are not preserved in the fossil, but in view of the excellent preservation of general cone morphology with atypical scale number, I believe the fossils warrant separate specific status. The poor fossil record of Callitris increases the importance of a specific diagnosis. As Florin (1963) questioned the age of a Cretaceous Queensland specimen of Callitris, C. octothamna may represent the earliest defined member of the genus so far found in Australia.

Detached foliage assignable to the genus (apart from that found attached to the cones) has not been discovered elsewhere in the deposit, so that Callitris octothamna represents a very minor component of the Winton flora.
4.2.5. Angiospermae

Angiosperm fossils form a very minor component of the Winton Fossil Plant Assemblage, which is not surprising given the supposed Albian - Cenomanian age of the deposit. (Angiospermous megafossils and pollen first appeared in Australian sediments during the Albian (Gould, 1975)). The other major Australian Late Cretaceous megafossil flora, the Waare Flora of Victoria, also has a minor angiosperm content (Douglas, 1969).

One taxon of reproductive structures from the Winton Assemblage is assignable to the Angiospermae (Foliage structures are discussed in Section 4.3.2.1.). It lacks sufficient definitive characters to be confidently placed in any fossil or extant family and is hence described under **Incertae sedis**.

4.2.5.1. Angiospermae **Incertae sedis** (Figs. 351 - 362).

**Description**: (Specimen numbers W188, W188A, W188C, W324, W334, WC3). This taxon is represented by 5 separate fruits. Four of these were found exposed on rock surfaces (Figs. 351 - 353) while one was extracted from a carbonate-matrix rock (Fig. 354). The fruits are pome- or hip-like in structure, spheroidal to oblate-spheroidal in shape, 12mm - 16mm in width and 11mm - 15mm in height, composed of a large bulbous base (without peduncle) and a minor apical bulge (Figs. 351, 354). The apex is composed of up to 15 triangular and appressed appendages (perianth parts), reflecting a perigynous floral arrangement (Fig. 354). The bulbous base is a thick-walled hypanthium, containing up to 50 single-seeded, unfused carpels, attached to a basal receptacle (Figs. 355 - 362). Each carpel is ovoid in shape, consisting of a stalk
and a fleshy wall (Fig. 358) surrounding a basally attached ovoid seed (Fig. 362), 1mm - 2mm long and 1mm wide. The seed contains a large embryo (Figs. 357, 358).

Discussion: The above-described fruit is not totally representative of any recognizable extant plant family. The angiosperm taxonomist, J. Veldkamp*, has suggested to me that the fruit may possibly be allied to the Eupomatiaceae (Magnoliales) or the Idiospermaceae (Laurales). Modern representatives of the Eupomatiaceae have bi-ovulate carpels with small embryos, while the fruits of the Idiospermaceae have only one to two stalkless carpels. Veldkamp and P.F. Stevens** have independently suggested that the fruit may be a fossil representative of the Monimiaceae (Laurales) while the floral anatomist Van Heel* and his colleagues suggest the Calycanthaceae (Laurales). The Monimiaceae and Calycanthaceae are closely related, and both may have numerous, single-chambered, unfused carpels, as does the Winton fruit. These suggested families are all thought to be primitive members of the Angiospermae. Flowers of the Calycanthaceae, for example, are known to be beetle-pollinated (Sporne, 1974), butterflies, bees and wasps not having appeared until the Tertiary. The sinking of the carpels in an hypanthium is thought to have given the flowers extra protection from pollinating beetles and birds.

It is hoped that further collections from the Winton Fossil Plant Assemblage may perhaps yield the flowers which develop into these fruits, so that they may be more positively classified.

* J. Veldkamp, M.Van Heel, Rijksherbarium, Leiden.
** P.F.Stevens, Herbarium, Harvard University.
4.3. **Isolated Foliage Structures**

4.3.1. **Conifers**

Coniferous branchlets are the most common type of fossil in the Winton deposit. Small twigs with attached leaves can be seen partially exposed on most rock surfaces where the softer limestone or dolostone matrix has eroded away from the siliceous fossils. Weathering of these exposed fossils has destroyed much of the finer morphological and epidermal details, but an extensive collection of several hundred well preserved foliage shoots was made by dissolving the rock matrices in acid (see 3.2.).

Offler (1969, 1984), in her studies of the morphology of Australian fossil and extant conifer shoots, pointed out the difficulty classification of this type of structure according to traditional descriptive techniques without additional reproductive characters. Offler formulated a comprehensive character set for the accurate description of coniferous foliage. A necessary criterion for accurate description is a complete and detailed study of a large number of specimens, so that natural variation within a foliage form can be considered in its definition. The large sample size of Winton specimens meant that this was possible. From photographs and actual specimens, a usually statistically significant number of measurements were made of the length and breadth of the leaf bases and leaf blades, and the apical and basal angles of the leaves. Detailed examinations and descriptions of leaf shape and surface features of both leaf faces could be done by carefully detaching the leaves from the twigs. (Stomatal characters and epidermal features were not used by Offler, but their value in systematics is now well known among taxonomists). Unfortunately, none of the foliage types showed anatomical preservation
of their leaf tissues.

It will be seen that this form of detailed analysis reveals many characters which may be used to separate the 7 major foliage forms described. A simple dichotomous key to the foliage types is included following their description.

4.3.1.1. Foliage Type I

(Figs. 363 - 368)

Description: Foliage twigs with small, simple, spirally inserted and decurrent leaves, consisting of a broad adnate base and a bifacial, spreading and incurved blade which overlaps subsequent leaves. Ratio of adnate base to blade 1:1.8. Adnate leaf base obtriangular, 1.6mm±0.4mm long (n=17), min. 0.85mm, max. 2.25mm, 1.7mm±0.3mm wide (n=69), min. 1.2mm, max. 2.3mm. Abaxial surface of leaf base keeled or flattened, with entire margin. Basal angle bluntly acute. Leaf blade triangular to narrowly triangular, length 2.9mm±0.5mm (n=85), min. 2mm, max. 4.4mm, breadth 1.7mm±0.3mm (n=69) min. 1.2mm, max. 2.3mm. Blade occasionally constricted at point of insertion. Abaxial leaf surface keeled or ridged, when keeled, keel acute, while lateral faces are steeply sloping and slightly concave. When ridged, lateral faces convex or almost planar. Adaxial surface convex at point of insertion, concave to flattened along blade. Blade with entire margins.

Apex acute, incurved and occasionally cuspidate, apical angle 66° ± 11.5° (n=32), min. 43°, max. 83° on either side of the leaf centre. Stomata individually sunken, in vertical rows, oriented parallel to long axis of leaf. Stomate 45μ long, 40μ wide, with a circular to oval aperture, 20μ in diameter. Subsidiary cells indistinct in preservation. Epidermal cells rectangular, 40μ long, 15μ wide,
parallel to long axis of leaf.

Discussion: Using Offler's key to the vegetative shoots of the extant Australian and New Guinean Coniferales, Type I can be grouped with the mature foliage of *Araucaria cunninghamii*, *Dacrydium elatum*, *D. novoguineense* and *Dacrycarpus*. However, the fossil shoots are sufficiently similar to those found attached to the cones of *Araucaria microcarpa* for them to be regarded as conspecific (see Section 4.2.1.2.1.). The frequency of this foliage form also matches the abundance of *Araucaria microcarpa* cones.

4.3.1.2. Foliage Type II
(Figs. 369, 370)

Description: Foliage twigs with small, simple, spirally inserted and decurrent leaves, consisting of a broad adnate base and a bifacial, spreading and incurved blade which overlaps subsequent leaves. Ratio of adnate base to blade 1:1.3. Adnate leaf base narrowly triangular, 1.1mm ± 0.3mm long (n=11), min. 0.8mm, max. 1.5mm, 0.6mm ± 0.1mm wide (n=13), min. 0.4mm, max. 0.8mm. Abaxial surface of leaf base keeled or flattened, with entire margin. Basal angle acute. Leaf blade narrowly triangular, length 1.3mm ± 0.2mm (n=30), min. 1mm, max. 1.8mm, breadth 0.6mm ± 0.1mm (n=13), min. 0.4mm, max. 0.8mm. Abaxial leaf surface keeled or ridged, adaxial surface concave, occasionally ridged. Blade with entire margins. Apex acute, incurved and occasionally acuminate, apical angle 40° ± 10° (n=14), min. 26° , max. 59° . Leaves thick, unguiform in lateral view. Stomata on adaxial leaf surface only, either scattered along the midrib region of leaf, or more commonly arranged in several vertical rows. Guard cells raised well above
epidermal cells, oriented parallel to long axis of leaf. Stomate 40μ long, 25μ wide, with oval aperture, 20μ long. Subsidiary cells indistinct in preservation. Epidermal cells rectangular, small, 35μ long, 12μ wide, arranged parallel to long axis of leaf.

Discussion: While superficially resembling a smaller form of Foliage Type I, Type II possesses a number of distinctive characters which may easily separate it. This indicates the necessity of a thorough analysis of a large number of leaf characters. In comparing Type II with Type I, the former has smaller and comparatively narrower leaves with more acute apices. The leaves are more divergent from the shoot axis, and the stomates are raised rather than sunken. Offler's vegetative key would group Foliage Type II with the mature foliage of Microstrobos fitzgeraldi. Pseudostrobos hamusites (Podocarpaceae), from the Winton Assemblage, has cones with structural affinities to extant Microstrobos cones. Unfortunately, no foliage was found attached to the fossil cones. It should be included that Foliage Type II may represent immature foliage, which can frequently differ markedly from adult leaves (de Laubenfels, 1953). The immature foliage of Araucaria is usually smaller and narrower than mature foliage, so that Type II may be the young leaves of Araucaria microcarpa from the same deposit. At present, no conclusive taxonomic affiliations can be demonstrated, but there is justification to assert that Foliage Type II represents a distinctive vegetation form in the deposit.
4.3.1.3. **Foliage Type III**  
(Figs. 371 - 374)

**Description**: Foliage twigs with small, simple, spirally inserted and decurrent leaves, each consisting of a narrow adnate base and a bifacial, spreading, straight blade which overlaps subsequent leaves. Ratio of adnate base to blade 1:1.1. Adnate leaf base cuneate, 3.2mm±0.9mm long (n=17), min. 2mm, max. 5.3mm; breadth 1.1mm±0.1mm (n=43), min. 0.8mm, max. 1.3mm. Abaxial surface, when visible, slightly convex or flattened, margin entire, basal angle acute. Leaf blade narrowly triangular to linear, length 3.6mm±1.0mm (n=49), min. 2mm, max. 6.1mm, width 1.1mm±0.1mm (n=43), min. 0.75mm, max. 1.3mm. Abaxial surface rounded to slightly ridged, when ridged, lateral faces convex. Adaxial surface convex or flattened, margins entire, apex rounded, sometimes acute, occasionally mucronate. Apical angle 82.7°±12° (n=20), min. 62°, max. 106°. Leaves thick, in lateral view, spreading. Stomata on adaxial leaf surface only, numerous, distributed evenly over leaf in closely spaced vertical rows. Stomata slightly sunken, oriented parallel to long axis of leaf, each stomate round, 40μ in diameter with a round to oval aperture up to 25μ. Subsidiary and epidermal cells indistinctly preserved.

**Discussion**: Foliage Type III can generally be characterized by its long, spreading blades with convex leaf surfaces and rounded leaf apices. These features are not displayed collectively by any of the wide variety of foliage types of extant Australian conifers. Interestingly, the foliage can be classified into a group of fossil foliage forms described by Offler (1969) from the Oligocene/Miocene of central South Australia.
4.3.1.4. **Foliage Type IV**

(Figs. 375 - 379)

**Description**: Vegetative twigs occasionally bearing simple leaves, spirally inserted, sometimes pseudowhorled. Leaves decurrent, consisting of a distinct adnate base and a bifacially flattened, spreading blade, blade often missing. Adnate base irregular and variable in length, depending on internodal distance, average length 4.7mm $\pm$ 1.9mm (n=17), min. 2.1mm, max. 8.8mm. Abaxial surface of adnate base broadly ridged by median vein, lateral faces convex or planar, margins entire and slightly involute. Leaf blade narrowly elliptical, length 4.4mm $\pm$ 1.2mm (n=10), min. 2.8mm, max. 7.3mm, width 0.9mm $\pm$ 0.1mm (n=10), min. 0.6mm, max. 1.2mm. Leaf twisted at point of insertion, both surfaces planar or slightly convex, median vein occasionally expressed as a slight ridge visible on both leaf surfaces for entire leaf length, margins entire, usually slightly thickened. Apex acute, occasionally cuspidate, apical angle 58° $\pm$ 13° (n=6), min. 42°, max. 76°. Stomata scattered evenly over adaxial and abaxial leaf surfaces, less common toward leaf margin and over midrib. Stomata scarcely sunken, large, 60μ long, 40μ wide, oriented perpendicular to long axis of leaf. Stomatal aperture circular to commonly oval, up to 20μ in diameter. Subsidiary cells and epidermal cells indistinctly preserved.

**Discussion**: The linear, bifacially flattened and spirally arranged leaves of Foliage Type IV are the same as those found within the large genus *Podocarpus*. Buchholz and Gray (1948), in their subdivision of the genus into 8 sections, used both reproductive and anatomical
characters, which cannot be applied to the fossil form. Nevertheless, Offler's (1969, 1984) key to the vegetative shoots of Australian conifers would place Foliage Type IV with a group of species all belonging to Section *Podocarpus* of the genus. (Two sections with similar foliage, *Stachyocarpus* and *Sundacarpus*, both differ from the fossil in not having their adaxial leaf surfaces ridged by the median vein for their full length). The Australian species *Podocarpus alpinus* (Section *Podocarpus*) characteristically loses its leaf blades, so that the foliage twigs remain clothed in the adnate bases. This is also typical of Foliage Type IV.

Although the morphology of Foliage Type IV is characteristic of many podocarps, it must be noted that juvenile leaves of some species in *Araucaria*, *Agathis*, *Dacrydium* and *Phyllocladus* may share all the features described, so that definite taxonomic affiliation of this Winton foliage is neither practical nor advisable at this stage.

4.3.1.5. **Foliage Type V**

(Figs. 380 - 382)

**Description**: Branched and unbranched vegetative twigs bearing small, scale-like, spirally inserted leaves. Branching not restricted to a single plane. Leaves decurrent and appressed, consisting of an adnate base and a free portion (equivalent to a blade). Free portion slightly overlapping the bases of subsequent leaves. Leaf shape rhombic, length 2.1mm - 0.4mm (n=25), min. 1.1mm, max. 2.6mm, width 1.4mm - 0.4mm (n=25), min. 0.9mm, max. 2mm, widest portion of leaf at the axil. Leaves thick, convex in cross-section, sometimes keeled on the abaxial surface. Keel rounded to acute, lateral faces usually convex. Leaf margin entire, basal angle usually obscured by preceding leaves, when visible, acute.
Leaf apex acute, often incurved, apical angle 65°±10° (n=27), min. 41°, max. 82°. Leaves uniform in lateral view. Epidermal features of adaxial leaf surface not preserved. Abaxial surface without stomata, epidermal cells square to rectangular in shape, 25µ - 60µ long, 25µ wide, arranged in rows parallel to long axis of leaf.

Discussion: The small, rhombic, spirally arranged leaves of Foliage Type V are identical to those found on twigs attached to the taxodiaceous cones, *Austrosequoia wintonensis* from the same deposit (see Section 4.2.3.2.1.)(The high frequency of both fossil types may also point to them belonging to the same plants). Other conifer taxa have a similar shoot morphology, including *Dacrydium elatum* and *D. novoequineense*, but Foliage Type V can be individually characterized by its leaf dimensions.

4.3.1.6. Foliage Type VI
(Figs. 383 - 387)

Description: Branched and unbranched vegetative shoots bearing simple, scale-like, spirally inserted leaves. Branching not restricted to a single plane. Leaves decurrent and usually appressed, occasionally divergent and slightly recurved, consisting of an adnate base and a free portion (equivalent to a blade); free portion overlapping the bases of subsequent leaves, but usually only slightly, mostly flattened onto the bases of subsequent leaves. Leaf shape variable, even on the same branchlet, from rhombic to very narrowly rhombic, length 3.7mm±1.7mm (n=34), min. 1.5mm, max. 8mm, breadth 1.2mm±0.3mm (n=31), min. 0.8mm, max. 1.8mm, with the widest portion at the axil. Leaves thick,
convex in cross-section, sometimes keeled on the abaxial surface, keel rounded to acute, lateral faces usually convex. Leaf margins entire, basal angle usually obscured by preceding leaves, when visible, acute. Leaf apex acute to obtuse, occasionally incurved, apical angle 56° ± 20° (n=37), min. 19°, max 106°. In lateral view, leaves uncifrom, occasionally unguiform. Stomates usually restricted to adaxial surface of leaf blade on either side of medial line, frequently oriented perpendicular to long axis of leaf in uneven rows. Stomates oval in outline, 50µ long, 30µ wide, not sunken. Subsidiary cells and epidermal cells poorly preserved. Abaxial surface of adnate leaf base with well preserved epidermal cells square to rectangular in outline, occasionally polygonal, 50µ - 70µ long, 15µ - 40µ wide. Stomates occasionally found on lateral edges of leaf, interspersed with few to many leaf hair bases, 65µ in diameter.

Discussion: Leaves of Foliage Type VI vary significantly in size and form, even on the same twig. This polymorphism has been observed in many conifers (Offler, 1969). Foliage Type VI shares many characters with Foliage Type V, but can usually be distinguished by the leaf variety and occasionally divergent leaf blades. Hair bases and stomata which are oriented perpendicular to the long axis of the leaves have only been seen in Foliage Type VI. This Type also resembles a twig found attached to a cone ascribed to Wintonia peltata gen. et sp. nov. from the same deposit (see Section 4.2.3.2.2.). However, with such variety of form observed, no confident assertion can be made. Several extant taxa may also possess foliage barely distinguishable from Foliage Type VI, including some specimens of Decrytium elatum, D. novo-guineense, and species of Decrycarpus. (Note that these species of
Dacrydium also share characteristics with Foliage Type V).

4.3.1.7. Foliage Type VII
(Figs. 388, 389)

Description: Vegetative shoots bearing small, simple leaves, spirally inserted, but appearing distichous. Leaves decurrent, consisting of an adnate base and a spreading, bilaterally flattened blade, slightly incurved distally. Adnate base linear-obtriangular in shape, length 4.2 mm, width 0.8 mm, bilaterally flattened faces sloping at a constant gradient, margins entire, basal angle acute. Leaf blade linear in shape, apex acute to rounded, length 5.7 mm, width 1 mm, not constricted or twisted at point of insertion. Blade tetragonal in cross-section. Epidermal features not preserved.

Discussion: Foliage Type VII has the characteristic bilaterally flattened, linear leaf blades of Dacrycarpus (formerly in Podocarpus). The lack of epidermal features in the fossil unfortunately prevents its insertion in Dacrycarpus. Foliage Type VII is rare in the fossil deposit and presumably reflects a low frequency of this fossil taxon in the Winton flora.

4.3.1.8. Key to Coniferous Foliage Types

A. Leaves usually spreading from axes of branchlets...B.
A' Leaves usually appressed against branchlets........F.

B. Leaf blades flattened..........................C.
B' Leaf blades not flattened........................D.
C. Leaf blades bifacially flattened....................Foliage Type IV
C' Leaf blades bilaterally flattened....................Foliage Type VII
D. Leaf blades spreading and incurved................E.
D' Leaf blades spreading and straight....................Foliage Type III
E. Stomata raised on leaf blades, average length
   of leaf blades less then 1.5mm....................Foliage Type II
E' Stomata sunken in leaf blades, average length
   of leaf blades greater then 2.5mm....................Foliage Type I
F. Stomata found on abaxial surface of leaf blades,
   leaves of variable length, 1.5mm - 8mm............Foliage Type VI
F' Stomata not found on abaxial surface of leaf
   blades, leaves of fairly constant length,
   1.1mm - 2.6mm.............................................Foliage Type V

4.3.2. Non-Coniferous Foliage

4.3.2.1. Non-Angiosperma

Ginkophytes and possible pteridosperms, ferns, or
bennettitaleans are occasionally found in the Winton Fossil Plant
Assemblage. Unfortunately, the specimens have only been found as
partial leaf imprints or surface leaf petrifications, without
preservation of anatomical structure or epidermal features. No
reproductive structures have been found, either attached to leaves or
separate in the assemblage. Accompanied by a lack of distinct leaf
preservation, this makes direct diagnosis impossible. It should be stressed here that the rarity of these plants in the deposit may be due to lack of silicification of their thin, delicate tissues, rather than a general uncommonness in the original flora.

Four separate non-coniferous, non-angiospermous foliage types have been recognized.

Foliage Type I (Figs. 390 - 394)

*Description*: (Specimen numbers W077, W116, W141, W173, W526) Five specimens of incomplete laminae and leaf bases, up to 2.5cm in width. No margins preserved. Leaves appear fan-shaped, non-digitate, without a midrib. Venation dichotomous, sub-parallel.

Foliage Type II (Fig. 395)

*Description*: (Specimen number W033) One specimen of a terminal leaf portion with three attached pinnules, one terminal and two lateral and sub-opposite. Each pinnule about 6mm wide. Leaf margin uneven or not preserved. Veins sub-parallel.

Foliage Type III (Figs. 396, 397)

*Description*: (Specimen numbers W359, W449) Two specimens of single leaves or detached pinnules, both 12mm long, 8.5mm and 9.5mm wide, ovate in shape. Leaf margin uneven, apex rounded. Venation dichotomous, no midrib.

Foliage Type IV (Fig. 398)

*Description*: (Specimen number F9514) Single specimen, 16mm long, 8mm wide, of leaf portion with sunken rachis and five oppositely attached pinnules. Each pinnule roughly square to rectangular in shape, up to 7mm long, 5.5mm wide, apex right-angled. Venation dichotomous,
subparallel.

**Discussion**: Foliage Type I has the typical morphology of ginkgophyte leaves. Members of the Ginkgoales have commonly been found in other Australian Cretaceous floras, including the Late Cretaceous Waare Flora of Victoria (Douglas, 1969), the Neocomian-Aptian Blythesdale Formation Flora of Queensland (Day, 1964), and the Albian Flora of the Burrum and Styx Coal Measures of Queensland (Walkom, 1915). It is therefore quite reasonable that the order be represented in the Albian-Cenomanian Winton Formation. However, without the preservation of diagnostic cuticular features, Foliage Type I cannot be formally assigned to the Ginkgoales.

Foliage Types II, III, and IV have indeterminate relationships with other taxa. They all bear superficial resemblances to *Thinnefeldia* (pteridosperm), *Otozamites* (bennettitalean) and *Adiantum* (extant fern). *Otozamites* and *Thinnefeldia* have both been discovered in the Waare Flora (Douglas, 1969). *Otozamites* was also found in the Burrum and Styx Coal Measures (Walkom, 1915). It is hoped that future collections from the Winton fossil assemblage may supply more determinate material.

4.3.2.2. **Angiosperms**

Silicified fragments of angiospermous leaves are present in small numbers throughout the Winton fossils. No major leaf portions have been encountered. Some fragments show a midrib and secondary veins (Fig. 399). Specimens extracted from carbonate-matrix rocks show well-preserved reticulate venation. Scanning electron microscopy has failed to reveal preservation of epidermal cells, and hence no further taxonomic classification of the leaves can be made.
CHAPTER 5

GENERAL DISCUSSION

This thesis features descriptions of 33 taxa from the mid-Cretaceous Winton Fossil Plant Assemblage. Nine taxa of reproductive structures were found to be sufficiently identifiable to be given generic and specific status. The remaining 24 taxa, mostly foliage structures, have less determinate affinities, some being described under *Incertae sedis* within specific families.

Both megafossil and microfossil evidence point to the assemblage being dominated by conifers, with a very minor angiosperm and pteridosperm (possibly bennettitalean and/or cryptogam) component. This is the typical structure of a mid-Cretaceous flora, prior to the expansion and diversification of the flowering plants in the Late Cretaceous.

Members of the Araucariaceae dominate the Winton Assemblage, with wood, male and female cones and probably araucarian foliage being common fossil types. Interestingly, spores assignable to the family are rare (if present at all). Three of the four male araucarian cones described show no preservation of sporangial tissue, while one cone was found to possess empty sporangia, indicating that spore dispersal might have occurred prior to fossilization.

The small female cone, *Araucaria microcarpa* sp. nov., is the most common reproductive taxon in the deposit. Many cones show excellent preservation of their internal structure, which allows the fossil to be placed in Section Eutacta. *A. microcarpa* is the most completely described fossil representative of this section. Some cones have typical Eutacta-like foliage attached to them. This foliage matches the
description of Coniferous Foliage Type I (Section 4.4.1.1.), the second most common form of conifer shoot in the assemblage. Some of the male araucarian cones were also attached to foliage of this type, so that Araucaria microcarpa, Foliage Type I and these male cones may all be derived from the same species. Whether or not the araucarian trees were as correspondingly small as the leaves and cones is of course indeterminate.

Two other taxa of female araucariacean strobili were placed under Incertae sedis, each represented by a single specimen (Sections 4.2.1.2.2. and 4.2.1.2.3.). Both lack the necessary anatomical detail for a more complete analysis.

The Podocarpaceae is another commonly represented family in the Winton flora. Podocarpaceous spores form 87% of the microfloral component. Although Microcachrydites antarcticus accounts for 60% of the total number of palynomorphs, male cones of Microcachryde have not been found in the deposit. These spores possess three bladders which function in dispersal, so that the parent plants may have been some distance from the fossil locality. However, two podocarpaceous male cones, Podostrobus eromanga sp. nov. and P. major sp. nov. were found to contain trisaccate grains resembling Microcachrydites, so that these may be the microspore source. Another male cone, Podostrobus bissaccata sp. nov. contains spores assignable to Podocarpidites, a relatively common palynomorph in the assemblage.

Two important taxa of female podocarpaceous strobili are described from the Winton flora. Fecundistrobus gen. nov. (Section 4.2.2.2.1.) is represented by numerous fruiting cones which share a similar morphology to the extinct genus Mehtaia from the Indian Jurassic (Vishnu-Mittle, 1958). Fecundistrobus can be compared with
several extant podocarps, particularly the Australian genus *Microstrobos*, but it has a unique combination of characters which substantiates its new generic status. A single species, *P. hamusites* sp. nov., has been identified.

*Lepidothamnus*, with 3 extant species, has recently been separated from *Dacrydium* by Quinn (1982). A solitary species, *Lepidothamnus australis* sp. nov. is described from the Winton Fossil Plant Assemblage (Section 4.2.2.2.2.). This species is the only fossil member of the genus, and represents the first recording of *Lepidothamnus* from the Australian continent. Extant species are now found only in New Zealand and Chile, so that *L. australis* extends the distribution of the genus further across the Gondwana region.

No podocarpaceous cones were found to be attached to foliage, however several of the described coniferous Foliage Types may be considered to be podocarpaceous in general form. Foliage Types IV and VII (Section 4.4.1.4. and 4.4.1.7.) have the typical bifacially and bilaterally flattened leaves of *Podocarpus* and *Dacrycarpus* respectively. Further cuticular evidence will be necessary before assigning these foliage types to the Podocarpaceae. Foliage Type VI shares a morphology with representatives from the Podocarpaceae and the Taxodiaceae.

Two megafossil taxa from the Winton assemblage have been ascribed to the Taxodiaceae. *Austrosequoia wintonensis*, a female cone related closely to *Sequoia*, has already been published (Peters and Christophel, 1978). Additional structural information from more recently collected material has allowed me to expand and emend the original diagnosis (Section 4.2.3.2.1.). In addition, a small collection of immature cones are described which possibly represent younger specimens of
**Austrosequoia.**

A second taxon of female taxodiaceous cones, *Wintonia peltata* gen. et sp. nov. is described in Section 4.2.3.2.2. While typically taxodiaceous in general form, it shows no close resemblance to any other taxodioid genus and is thus deserving of new generic status.

The shoots attached to *Austrosequoia* cones are of the same morphological type described as Foliage Type V, which forms the major component of foliage shoots in the deposit. The leaves of Foliage Type VI have been likened to those found attached to one of the female cones of *Wintonia peltata*.

The Cupressaceae has only a single female cone taxon in the Winton Fossil Plant Assemblage. *Callitris octothamna* sp. nov., described from 6 specimens, has characteristically 8 cone-scales, while 6 are normal for most members of the genus. One cone was found attached to a short twig bearing typically cupressaceous whorled leaves. No separate foliage of this type was found in the deposit, which may be indicative of the comparative rarity of *Callitris* in the original forest vegetation. Apart from a specimen of disputably Cretaceous age from Queensland, referred to by Florin (1963), *Callitris octothamna* is the earliest recording of the genus from Australia.

A very minor component of the foliar remains of the Winton Fossil Plant Assemblage can be regarded as non-coniferous. These include forms similar to the Gingkophytes, pteridosperms and Bennettitaleans. Unfortunately, the diagnostic features of the leaf epidermis have not been preserved.
Angiospermous fossils are a rare feature of the Winton Assemblage, which is an acceptable fact given that their first appearance in Australian sediments was in the Albian (Gould, 1975). One taxon of angiosperm fruits is described, which has possible affinities to the primitive families Calycanthaceae and Monimiaceae. Several angiospermous pollen grains were isolated from the Winton rocks, but these cannot be further classified.

Many of the described taxa from the Winton Assemblage confirm the view expressed earlier that the Winton Formation was laid down in temperate conditions. If indeed Austrosequoia is so closely related to Sequoia, the temperate conditions favoured by the extant genus indicate a cool environment. The presence of Microcachrydites in the deposit may infer the proximity of a stand of Microcachryx trees, the genus being now confined to the alpine regions of Tasmania. The wood specimens from the fossil deposit were nearly all observed to possess distinct growth rings, which must indicate a seasonal fluctuation in temperatures, and therefore a non-tropical environment.

The Winton Fossil Plant Assemblage is the first flora of megafossils to be described from the Winton Formation. The composition of the flora conforms well with our present knowledge of the succession of Cretaceous floras in Australia.

The earliest Australian Cretaceous land floras are poorly known from a fragmentary megafossil record. Rich microfloras, however, suggest that there was a diverse and widespread distribution of
gymnosperms (particularly podocarpaceous conifers and bennettitaleans) and cryptogams over Australia, which was little changed from latest Jurassic times (Dettmann, 1981). The Neocomian to Aptian floras of the Early Cretaceous are known in more detail. Microfloral evidence from eastern Australia (Dettmann, 1963; Dettmann and Playford, 1969; Evans, 1966a, 1966b; Burger, 1973a, 1973b, 1974, 1976; Haig and Barnbaum, 1978) and megafossil floras from Victoria (Douglas, 1969, 1973) and central South Australia (Glaessner and Rao, 1955) suggest that there were numerous Ginkgoales, pteridosperms, Bennettitales, conifers and cryptogams at that time. Unfortunately, the coniferous megafossils of Victoria have not yet been described, but palynological evidence points to an abundance of podocarpaceous and araucarian forms (Dettmann, 1981). The Early Cretaceous (to Neocomian) of Queensland features a poorly known megaflora from the Blythesdale Formation, with numerous conifers, ginkgophytes and pteridosperms (Day, 1964).

The middle Cretaceous, during which the Winton Formation was laid down, saw significant changes in the Australian flora. The angiosperms appeared in the early Albian, accompanied by qualitative changes in the gymnosperm and cryptogam elements. This information comes principally from widespread spore-pollen assemblages in eastern Australia (Dettmann, 1963; Dettmann and Playford, 1968, 1969; Burger, 1970, 1973b, 1975; Playford, Haig and Dettmann, 1975; Dettmann, 1981) and from the Perth and Eucla Basins of Western Australia (Balme, 1964; Ingram, 1968).

Prior to the discovery of the Winton Fossil Plant Assemblage, only several megafloras had been described from the mid-Cretaceous of Australia. The most complete of these is the rich Albian and poorer Cenomanian megafloras of Victoria, described by Douglas (1969, 1973).
As stated earlier, the coniferalean element of the Victorian Cretaceous floras remain undescribed, which precludes a complete taxonomic comparison of these deposits with the Winton Fossil Plant Assemblage. However, the mid-Cretaceous Victorian floras reveal that the conifers assumed an increasingly dominant role in the Albian and Cenomanian. Associated microfloras contain plentiful saccate podocarpaceous grains, including *Microcachrydites antarcticus* and *Podocarpidites*, while asaccate *Araucariacites* and *Cycadopites* were subordinate (Dettmann and Playford, 1969). From megafossil evidence from the Victorian mid-Cretaceous, it is known that the Bennetitales declined through the Albian to become virtually absent by the Cenomanian. The Ginkgoales persisted throughout the Albian. Angiospermous fruits and leaves were introduced into early Albian sediments (Douglas, 1969). Angiospermous pollen is never common in mid-Cretaceous sediments, although it increases in frequency and diversity with the introduction of sulcates and tricolpates in the Albian and tricolporates in the Cenomanian (Dettmann, 1981). The angiosperm grains from the Winton Fossil Plant Assemblage were found to be all tricolpate.

As in the Victorian flora, the Winton flora is dominated by conifers, principally podocarpaceous and araucariaceous forms. Both *Microcachrydites* and *Podocarpidites* are recorded from the Winton Assemblage, while there is a minor angiosperm and ginkgoalean component. Bennetitalean and/or seed-fern representatives are rare.

The poorly known mid-Cretaceous megafloras of the Burrum and Styx Coal Measures of eastern Queensland were described by Walkom (1919). Much of this material was incompletely described and inadequately illustrated, and is in need of re-evaluation. The Burrum Flora comprises 36 species, 12 of which are coniferalean, the remainder being
cycadalean, filicalean, equisetalean and ginkgoalean. The Styx Flora has just 14 species, only 3 of which are coniferous. Reproductive structures assignable to the Coniferales include just 2 species of Araucarites, A. polycarpe (cone impression) and A. arberi (detached cone-scales). Both these fossils lack sufficient definition to be closely compared to any of the Winton fossils. Douglas (1969) has determined some similarities between species of Brachyphyllum and Podozamites from Burrum and Victoria.

Rich microfloral evidence from the Great Artesian Basin indicates that the early to middle Albian gymnosperms were similar to those from the Albian of south-eastern Australia, however, the northern floras underwent some modification by the close of the Albian to produce a distinctive flora (Dettmann, 1981). Microcachrydites declined in importance, while Araucariacites increased in frequency (Balme, 1964). This shift to a high araucariaceous component is reflected in the Winton Fossil Plant Assemblage.

Information about Late Cretaceous Australian floras is based almost entirely on microfloral evidence from the Ottway and Gippsland Basins of Victoria. The gymnosperms remained dominant, with abundant spores of Microcachrydites, Phyllocladidites and araucariaceous pollen (Dettmann, 1981). The angiosperms became increasingly significant, with complex sculptured and apertured pollen like Nothofagus and Proteacidites becoming prevalent (Partridge, 1973). The absence of these angiospermous types and Phyllocladidites from the Winton Assemblage helps to confirm its mid-Cretaceous age.

Comparisons between the Cretaceous floras of Australia and other regions naturally show that the constituent countries of Gondwanaland
share most floral components. The well documented Belgian Wealden Flora and neighbouring Lower Cretaceous floras of Europe appear to differ greatly, for example, from Victorian species of the same age (Douglas, 1969). European and Victorian microfloras are also dissimilar (Dettmann, 1963). Douglas (1969) has concluded that the uppermost Gondwana beds in India (probably Lower Cretaceous) is the only overseas flora in which there is a whole group of plants (Bennettitales) with species anatomically similar to those of Victoria.

Up until the middle Cretaceous, Australia was united with Antarctica, India, New Zealand, New Caledonia, Lord Howe Island and Norfolk Island (Raven and Axelrod, 1972) and so it is not surprising that these regions should share many similar fossil and extant floras. Unfortunately, mid-Cretaceous floras are virtually unknown from southern regions of Gondwanaland other than in Australia and a largely microfloral component in New Zealand (Dettmann, 1981). This lack of mid-Cretaceous floras highlights the importance of the Winton Fossil Plant Assemblage in determining the megafloral elements of that time.

Australia was connected to South America via Antarctica up until Late Cretaceous times (Page and Clifford, 1981). A lack of migrational barriers would probably have allowed free dispersal of plant groups through these regions. Both South America and Australia share an extant component of species of Araucaria in their floras. Section Bunya of Araucaria, now with just one species endemic in Australia, has a well-determined member from the Jurassic of South America (Stockey, 1975). The Lower Cretaceous floras of Patagonia (Halle, 1913b) are known to have similar species to those of Victoria (Elatocladus, Podozamites) (Douglas, 1969), but too little is known of them to allow close comparison.

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The paths of migration also remain unclear between the floral (and faunal) components of the Northern and Southern Hemispheres. The presence of *Araucaria* in the Mesozoic of Europe for example (Stockey, 1980) seems anomalous when considering the strictly southern distribution of extant species, and rich Gondwana fossil element of the genus. It is known that connections between North and South America were absent until comparatively recently, so that migration probably occurred by way of Africa and Europe during the Cretaceous (Raven and Axelrod, 1972).

The Winton Fossil Plant Assemblage can shed no new light on migrational pathways, principally due to the lack of other Cretaceous megafossil assemblages in Gondwanaland. This new deposit, however, upholds the determinations of mid-Cretaceous floras in Australia previously determined by mainly microfossil assemblages. In particular, the Winton flora highlights the significance of the Coniferales in the mid-Cretaceous of Queensland. Many new taxa and fossil forms described in this thesis have not been previously recorded. (Further historical information about the conifers will be supplied when the Victorian Cretaceous members are described. A small Cenomanian flora from south-east Queensland with a coniferalean component also awaits description (Whitehouse, 1954)).

The plants described in this thesis are those identifiable in their three-dimensional form. Frequently, anatomical information has been gathered by sectioning fossils found embedded within rocks. Although this thesis serves to determine the diversity of the Winton flora, with detailed analyses of better preserved specimens, many unidentifiable plant pieces were encountered during rock sectioning.
The actual diversity of the flora is therefore somewhat greater than has been presented here. A similar pattern must occur with all fossil floras. It is consequently vital that continued research on this material be given a high priority. With Cretaceous plant assemblages relatively uncommon throughout the world, the Winton Fossil Plant Assemblage can be considered as one of the most significant and important floras discovered.

The fossil site is literally dissolving away from the face of the Queensland landscape. Although the best preserved specimens have already been collected, more collections must be made. A more extensive study of the material will require painstaking extraction of delicate and minute structures from carbonate rock, and the orderly sectioning of thousands of quartz specimens. Together, this will yield additional information to further elucidate plant development and evolution in the Australian Cretaceous.
BIBLIOGRAPHY


Bailey, I.W. (1957). --The potentialities and limitations of wood anatomy in the study of phylogeny and classification of


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Aust. 140: 27-44.


New Guinea Dept. of Forests.

Hayata, B. (1931). --The Sciadopityaceae represented by Sciadopitys 
verticillata Sieb. and Zucc., an endemic species of 

(Tokyo) 46: 24-27.

de l'Araucaria araucana aux derniers stages cenocytiques 
et lors de son passage a l'etat "alveolaire". C.R. Acad. 

Cretaceous plant remains commonly referred to the genera 

coniferous remains from Kreischerville, New York. New 


Metasequoiaceae and on Metasequoia glyptostroboides, 
a living species of the genus Metasequoia found in 
1: 153-159.


Acad. 48: 531-571.


II; Plantae, Pars 79-87, Gymnospermae. W. Junk, Gravenhage.


142-145.


Kraus, G. (1870). --Bois fossiles de conifères. In. Schimper’s

of eastern Asia and its bearing on the theory of conifer

fossil wood from the Deccan Intertrappean Beds of Mohgaon

Laubenfels, D.J. de (1953). --The external morphology of coniferous

Laubenfels, D.J. de (1969a). --A revision of the malesian and
pacific rainforest conifers I. Podocarpaceae, in part.


APPENDIX

A KEY. WITH ACCOMPANYING DESCRIPTIONS, TO THE EXTANT SPECIES OF ARAUCARIA JUSS. - (adapted from Gaussen, 1970, in French).

1.A. Mature leaves large and flat, female cone large, greater than 10cm in diameter, cotyledons 2, germination hypogeal...........2.

1.B. Mature leaves large and flat, not imbricate, juvenile leaves awl-shaped, seed terminal with a recurved point, germination epigeal........4.

1.C. Leaves imbricate, cone less than 15cm in diameter, cotyledons 4...........5.

2.A. Leaves large, densely imbricate and concealing the branch, bright green on both faces. Cone between 10cm and 18cm in diameter.

Branchlets - in opposite pairs, incurved towards the top, growing to as much as 20cm when mature.

Leaves - imbricate, persistent along the trunk, ovate-lanceolate, very stiff, coriaceous and strongly pointed, concave at the base, glossy green on both faces, the surface marked with longitudinal lines, stomates on both faces. Leaves remain for 10-15 years, then become brown; 3 - 5cm x 0.8 - 2.5cm (to the base) along the branches and 2.5cm long on the branchlets.

Longitudinal Section of Leaf - thick cuticle, endodermis containing a mass of fibres, palisade tissue on both faces, sclereids large and rare, resin canals numerous between the many vascular bundles,
transfusion tissue forms a complete arc.

**Dioecious or sometimes monoecious**

**Male Cones** - axillary, solitary or grouped, erect, yellowish brown, irregularly shaped, microsporophylls pointed, recurved, persistent for a long time after pollen shed, 16 - 20 pollen sacs per sporophyll, cone 7 - 15cm x 5cm; sporophylls 0.7 - 1cm. Pollen 80 - 88μ.

**Female Cones** - globose, dark brown at maturity, ripening after 2 or 3 years, disarticulating at maturity, 10 - 18cm x 8 - 15cm.

**Cone-scales** - numerous, terminated by long spines 2.5cm long.

**Seeds** - shiny brown, wingless or margins resembling a rudimentary wing, with a triangular, stiff, recurved ligule of 1 - 1.5cm x 0.5cm which has denticulate margin near the apex, seed 2.5 - 4cm x 0.7 - 1.5cm.

*Araucaria araucana* (Molina) K. Koch. Argentina and Chile

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B. Leaves not or only slightly imbricate, the wood still visible on the branches.........3.

3.A. Leaves stiff, a little narrow towards the base. Cone 20cm in length

**Branchlets** - strongly covered with leaves, but leaves spaced on sterile branchlets.

**Leaves** - erect on sterile branchlets, lanceolate, somewhat concave on upper surface, veins barely visible, often in pairs, green or glaucous, coriaceous, pointed, sometimes a little narrowed toward the base and somewhat decurrent, stomates on lower surface, leaves keeled beneath, 3
- 6cm long x 0.6cm. Leaves of the fertile branchlets densely arranged spirally and shorter, lateral nerves without relief.

**Longitudinal Leaf Section** - cuticle thick, endodermis between the stomates, palisade tissue on both surfaces, often lignified, sclereids rare. Resin canals in the 7 spaces between the 6 veins, little transfusion tissue.

**Male Cones** - dense, on short peduncles in the leaf axils, 10 - 18cm x 1.2 - 2.5cm, scales imbricate 0.8 - 1cm, thickened at the apex, 10 - 12 pollen sacs per scale in a line, pollen 64μ.

**Female Cone** - narrowing from the middle towards the apex, globular, 18 - 20cm long x 13cm diameter. Take 2 - 3 years to mature, colour chestnut brown.

**Cone-scales** - terminated by a strong, recurved spine.

**Seed** - shiny brown, more than 5 x 0.5 - 2cm. Their ability to germinate lasts for a maximum of 6 weeks.

*A. angustifolia* (Bertolini) O. Kuntze. Argentina and Brazil.

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3.B. Leaves less stiff, some narrowing towards the base, cone exceeding 27cm in length.

**Branchlets** - green

**Leaves** - spirally arranged, not imbricate, contracted at the base, lanceolate, dark green, thick at the entire margin, with a long point, stomates in regular lines beneath the leaves, irregular above. On the fertile and upper branchlets often much shorter, incurved, more dense, not keeled, often < 2.5cm long; on sterile branchlets 5 x 0.5 - 1cm.
Longitudinal Leaf Section - endodermis continuous across the adaxial face, palisade tissue on both surfaces, sclereids rare, resin canals central in the leaf and spaced, fibres independent, transfusion tissue in large bundles.

Generally dioecious, sometimes monoecious

Male Cones - 15 -17 (20) cm x 1.2cm, positioned near the summit of the branchlets at the top of the tree. On small branchlets, surrounded at the base by rigid bracts, microsporophylls imbricate, denticulate at the margin, 6 pollen sacs about 0.3cm long, pollen 88μ.

Female Cones - erect on upper branches, ellipsoidal or globular, exceeding 27 x 25cm, sometimes weighing up to 3kg.

Cone-scales - numerous, with a long recurved spine at the apex, 10 x 7.5cm.

Seeds - cone contains more than 150 seeds, pear-shaped, with rudimentary wings, enclosed in a very thick scale. Seed 4 - 7cm x 2.5cm at widest point.

*A. bidwillii* Hooker. Queensland.

4.A. Female cone large, up to 25cm in length, occasionally flattened and broader than long.

Leaves not or slightly imbricate, flattened, sometimes attenuate to a point, sometimes rounded at the summit, 5 - 10cm x 1cm, juvenile leaves awl-shaped.

Male cones - long, cylindrical, sessile or on a peduncle, 15 - 20cm x 1.8 - 2.5cm; microsporophylls numerous, lanceolate, pointed 0.7 x 0.3 -
0.4cm, margins sub-denticulate, membranous, recurved; pollen 70 - 80μ.

Longitudinal Leaf Section - epidermis and endodermis with fibres, stomates covering lower surface, only on lower third of the upper surface, resin canals spaced, sclereids rare, transfusion tissue with few cells, vascular bundles small.

Female Cones - large, often broader than long, 10 - 19cm long x 12 - 13cm broad, young cones cylindrical.

Cone-scales - 3 - 3.5cm x 4 - 4.5cm.

Seeds - triangular, 1.5cm x 0.8 - 1cm, occasionally with terminal recurved point.


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4.B. Not as above.......5.

5.A. Leaves densely imbricate, 0.6cm wide at the base, 3cm in diameter; female cone > 10cm wide.

Branchlets - pendulous, reaching 3cm in diameter.

Leaves - shiny, dark green, incurved, closely imbricate and concealing the stem; hard, coriaceous, variable in length, wide at the base, abruptly pointed at the apex, stomates small, rarely on the upper surface, leaves steel-grey on the upper surface, 1 - 2.5cm x 0.6 - 0.8cm. Juvenile leaves arched, sharp pointed.

Longitudinal Leaf Section - endodermis continuous through the lower face, discontinuous through the upper face, palisade tissue on both surfaces, sclereids numerous to few beneath the vascular bundles;
bundles 3 – 8, resin canals present.

**Male Cones** - terminal, 8 – 12cm x 3 – 4cm, 15 triseriate pollen sacs. Involucre present at the base of the bracts.

**Female Cone** - ellipsoidal, 10 – 15cm x 10 – 12cm.

**Cone-scales** - 3 – 3.5cm long, terminal spine 1.8cm long. perpendicular to the axis of the scale.

**Seed** - 0.8 x 0.45cm with narrow wings.

*A. rulei* Mueller. New Caledonia

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5.B. Branchlets 2cm in diameter, width of female cone < 10cm.

**Juvenile Leaves** - slender, adult leaves thick, ovate, obtuse at the apex, squamiform, concave to the cisible stomates, 1.2cm long x 0.8cm wide.

**Longitudinal Leaf Section** - diamond-shaped, cuticle thick, endodermis very thick, sclereids numerous, resin canals under the vascular bundles 5 in number, transfusion tissue in an arc.

**Male Cones** - cylindrical, 8 – 9cm x 2.5 – 3cm, 12 pollen sacs in 3 layers, 0.6 – 0.7 x 0.4 – 0.5cm, pollen 67μ.

**Female Cone** - ovate, 10 – 11cm x 8cm.

**Cone-scale** - atenuate to a raised spine of about 0.8cm length.

*A. montana* Brongniart et Gris. New Caledonia.

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5.C. Leaves less imbricate, more than 2cm long, male cones more than
20cm long.

**Juvenile Leaves** - almost linear, becoming progressively ovate, mature leaves thickened, coriaceous, slightly imbricate, strongly pointed, stomates on both faces; 2.25 - 3cm x 1.12 - 1.5cm.

**Longitudinal Leaf Section** - diamond shaped, endodermis thick, sclereids numerous, 2 - 3 resin canals surrounding the vascular bundles; bundles 4, transfusion tissue present.

**Male Cones** - terminal, reaching 25 x 3cm, involucre of leaves of 3cm length around cone base, microsporophylls 0.7 x 0.5cm, margin entire, 20 pollen sacs, pollen 85μ.

**Female Cone** - ovate, resembling an immature cone of *A. araucana*, the base tightly enclosed by leaves; cone 11 - 15cm x 9 - 10cm.

**Cone-scales** - abruptly attenuate at the point, with or without a keel, scales 3 - 4cm x 3 - 4cm.

**Seeds** - 2.25 x 0.8cm with slim and narrow wings.

*A. muelleri* Brongniart et Gris. New Caledonia.

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5.D. Male cones 12 - 15cm x 2.8cm. Branchlets leafy, thick, from 2 - 2.8cm in diameter (including leaves).

**Leaves** - spirally arranged, thick, imbricate, apex slightly recurved; juvenile leaves quadrangular; adult leaves keeled, 1.2 - 1.8 x 0.8 - 1cm, less thick on the smaller branches.

**Male Cones** - 12 - 15cm x 2.8cm, microsporophylls 1cm, apex triangular, pointed, 0.5 x 0.4cm.

**Female Cone** - ovate, about 14cm long.
A. laubefelsii Corbasson. New Caledonia.

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5.E. Not as above........6.

6.A. Branches often bifurcate, leaves mainly lanceolate, keeled, cone very distinct with its peduncle, 10cm x 9cm.

**Branchlets** - of variable length, about 30 - 40 x 1.2cm (including leaves).

**Leaves** - mainly awl-shaped or ovate-lanceolate, spirally arranged, strongly decurrent, dorsiventrally flattened, with or without a keel; stomates on both surfaces, leaves 0.8 - 1cm x 0.4 - 0.6cm at the base. Much larger beneath the cone.

**Longitudinal Leaf Section** - semi-elliptical, stomates on adaxial surface numerous, rare on abaxial surface, endodermis continuous around the stomates, palisade tissue in 2 layers around the periphery; sclereids numerous; one resin canal beneath the vascular bundle and 3 others spaced apart; transfusion tissue developed.

**Male Cones** - about 7 x 1.8cm at the summit of the branchlets, with imbricate bracts at their base. Microsporophylls spathulate, freely triangular at the apex 0.8 - 0.9cm long; 7 - 8 pollen sacs, pollen 75μ.

**Female Cones** - globose, prickly, cone separates abruptly from the peduncle; cone 10 x 9cm.

**Cone-scales** - roughly horizontal to the spine, which is recurved, apex of 3.5 - 4cm length.
**A. biramulata** Buchholz. New Caledonia.

6.B. Leaves pointed, flattened or very keeled on both surfaces, female cone 8 - 10cm x 6 - 8cm.

**Branchlets** - 2cm in diameter (including leaves).

**Leaves** - when on young sterile trees, spirally arranged on the lateral branchlets, margin entire, green or glaucous, very flattened laterally, may or may not be spreading from the branchlets, pointed, stomates on both faces; when on fertile, mature trees, leaves shorter, appressed along the branch forming a jacket, incurved, pointed, imbricate, bi-keeled, stomates on both faces, leaves 0.8 - 2cm long.

**Longitudinal Leaf Section** - triangular or diamond shaped, cuticle thick, endodermis discontinuous, 1 layer of palisade tissue, sclereids quite rare, about 8 resin canals, 3 vascular bundles (1 bundle in juvenile leaves), transfusion tissue developed.

**Male Cones** - cylindrical, terminal, 2 - 3cm x 0.5 - 0.7cm, involucre at base of cone with short, pointed leaves. Microsporophylls rhomboidal, obtuse, 0.4 - 0.6cm, pollen 60μ.

**Female Cone** - ovate, symmetrical, 8 - 10cm x 6 - 8cm.

**Cone-scales** - terminated by a long spine reflexed into an awl, 2 x 1.5cm, denticulate.

**Seeds** - with narrow wings on both sides, 1.5 x 0.6 - 0.7cm.

**A. cunninghamii** Aiton ex Lambert. New Guinea, Australia.

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6.C. Leaves pointed, quite loose, cone on a large peduncle, cone < 10cm long.

**Leaves** - on mature trees, oval, pointed, 0.6 x 0.4cm. Juvenile leaves linear-lanceolate, 0.5cm long. Leaves beneath the cone mainly ovate, loosely imbricate, finely denticulate, sub-keeled, resembling those of *A. columnaris*.

**Male Cones** - pollen 75µ.

**Female Cone** - subglobose or ovoid with a 2.5cm peduncle, cone 8 - 10cm x 9cm.

**Cone-scales** - progressively tapering to a point, reaching 3.5cm ioncluding the point. Ligule short, 0.1 x 0.3cm, slightly apiculate, appressed against the scale.

*A. humboldtensis* Buchholz. New Caledonia.

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6.D. Adult branchlets, leaves compressed, 0.6 - 0.9cm diameter, mature leaves 0.7 - 1cm x 0.15 - 0.2cm.

**Branchlets** - of juvenile trees, 1.2 - 2.5 cm in diameter, leaves compressed, adult branches 0.6 - 0.9cm diameter, leaves compressed.

**Leaves** - imbricate, keeled, lanceolate, pointed, 0.7 - 1 x 0.15 - 0.2cm, juvenile leaves more or less imbricate, lanceolate, keeled, sharp pointed, 1.8 x 0.15cm.
A. schmidii de Laubenfels. New Caledonia.

6.E. Mature leaves mucronate or obtuse, slightly keeled.
   Male cones < 8cm long............7.
   Male cones 8cm or >8cm long.......8.

7.A. Adult leaves forming a sleeve along the branch, < 0.5cm long.

**Branchlets** - on mature branchlets, leaves closely spaced.

**Leaves** - of 2 types: juvenile leaves and leaves on lateral branchlets awled, incurved, bright green, perpendicular to the branch, about 1.2cm long; leaves on adult branchlets shorter, forming a sleeve surrounding the branch, point incurved, leaf 0.4 - 0.5cm long.

**Longitudinal Leaf Section** - diamond shaped, cuticle thick, endodermis sometimes sclerified, 1 layer of palisade tissue, sclereids quite numerous, 3 vascular bundles, 4 - 6 resin canals in the leaf corners, transfusion tissue developed.

**Male Cones** - elongate, yellow or reddish brown, microsporophylls at the apex sometimes pointed, margins denticulate, ciliate, 10 - 12 pollen sacs in a single row, pollen 66μ.

**Female Cone** - large, sometimes wider than long, 12 - 15cm long, weight about 1kg, terminal on branchlets.

**Cone-scales** - terminated by a long, recurved spine, triangular, of size 1 - 1.2cm x 0.6cm.

**Seed** - strongly winged, 2.5 - 3cm x 1 - 2cm.

Many horticultural forms now exist.
A. heterophylla (Salisbury) Franco. Norfolk Island.

7.B. Juvenile leaves dense, perpendicular to the branch, adult leaves 0.6cm long; adult branchlets resembling a plaited rope of 0.8cm diameter and more than 20cm long. Seed >4cm long, cone >10cm long.

Branchlets - of about 0.8cm diameter (including leaves), foliage very compact.

Leaves - slightly decurrent on the juvenile shoots, triangular or lanceolate, exceeding 1.3cm in length, mucronate but without a terminal spine. On the mature shoots, leaves oval, 0.6 x 0.3cm, rigid, obtuse, closely imbricate and curved toward the axis.

Longitudinal Leaf Section - elongate or diamond shaped, according to age, stomates mainly on adaxial surface, endodermis continuous along the abaxial surface, palisade tissue in one layer, sclereids numerous, 1 - 5 resin canals beneath the vascular bundles, transfusion tissue developed, vascular bundles 1 - 9.

Male Cones - placed in a spaced arrangement between the leaves, 2 - 6 x 1 - 1.8cm. Pollen sacs 7 - 9, pollen 74 - 85μ.

Female Cone - ellipsoidal, 10 - 15 x 8 - 12 cm.

Cone-scales - almost laterally winged, terminated by a triangular spine which is slightly or not reflexed, fragile, 0.6cm long.

Seed - reddish brown, winged, 4 - 5 x 3 - 4 cm; each wing 1 - 2cm broad, terminal spine of 0.8cm length.

A. columnaris (Forster) Hooker. New Caledonia.

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7.C. Male cone 3 - 5cm long. Branchlet pinnate, 0.6 - 0.8cm diameter (including leaves).

Leaves - of secondary branchlets small, 0.1 - 0.2 x 0.1 - 0.15cm. Adult leaves flattened, incurved at the apex, imbricate, keeled, subulate, 0.3 - 0.4cm x 0.25 - 0.3cm.

Male Cones - 3 - 5 x 0.7 - 1.1cm, leaves at base of cone subulate, 0.6 x 0.2cm. Microsporophylls imbricate with triangular, pointed apex, 0.2 x 0.2cm, pollen sacs 6.

Female Cone - ovate, 7 x 5.5cm.

Cone-scales - appendiculate, 1.5 x 1.3cm, apex 0.7cm long.

Seeds - ovate-elongate, 0.8 x 0.4cm.

A. scopulorum de Laubenfels. New Caledonia.

7.D. Branchlets fine, about 18cm long, leaves curved, female cone 6 - 10cm long.

Branchlets - very fine and drooping, about 18cm long.

Leaves - juvenile leaves awl-shaped; adult leaves small, uniform, densely spaced and persistent for a number of years, obtuse, dark green, concave towards the centre, curved at the summit, stomates on the inner surface. Leaves 0.3 - 0.4 x 0.2cm, maintaining their breadth to the base.

Longitudinal Leaf Section - diamond-shaped, flattened, sclereids large, resin canals numerous, vascular bundles 3 - 4, transfusion tissue developed.
Male Cones - 5 - 7.5 x 1.8 - 2.3cm; involucre at the base, 10 pollen sacs in 3 rows, pollen 70µ.

Female Cone - ovate, at the summit of a short shoot, 6 - 10 x 5 - 6cm.
Cone-scales - terminated by a raised lanceolate spine of 0.3cm.

*A. subulata* Vieillard. New Caledonia.

7.E. Branchlets very fine to 30cm long. Female cone > 10cm long, male cone > 6cm long.

Branchlets - 30cm, on both sides of the branches.
Leaves - juvenile leaves much shorter than *A. subulata*, strongly keeled and not flattened. Adult leaves large, spirally arranged, triangular, curved at the apex like *A. subulata*, leaves 0.35 x 0.2cm, completely concealing the branchlet.

Longitudinal Leaf Section - elliptical, cuticle thick, endodermis discontinuous, palisade tissue on both faces, sclereids sparse, elongate, generally 3 resin canals, of which one is opposite the vascular bundles. Transfusion tissue developed.

Male Cones - 6.8 - 8 x 0.8cm, cylindrical, glaucous white. Microsporophylls 0.35 x 0.2 - 0.4cm, cone on a peduncle 0.25 - 0.3cm long. Pollen sacs 4-6.

Female Cone - cylindrical to ovate, blue-white glaucous, exceeding 10 x 7.5cm, rarely solitary, more often in groups of 2 - 3 or commonly 3 - 7.
Cone-scales - terminated by a fine spine bending towards the cone base, ligule ovato-triangular.
**A. bernieri** Buchholz. New Caledonia.

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8.A. Male cones < 10cm long, female cone 11 x 9cm, adult branchlets of diameter 0.9 - 1.1cm (including leaves).

**Branchlets** - with juvenile leaves dense.

**Leaves** - juvenile leaves flattened, falcate, keeled, obtuse, quadrangular, 0.4 - 0.8 x 0.08 - 0.12cm. Adult leaves flattened or more or less imbricate, falcate, keeled on the back, lanceolate, obtuse, 0.6 - 1 x 0.15 - 0.3cm.

**Male Cones** - 8 x 1.4cm, basal leaves narrow, 1 - 1.2 x 0.1cm, microsporophylls flattened toward the triangular apex, apex obtuse 0.3 x 0.2cm, 6 pollen sacs.

**Female Cone** - ovate, 11 x 9cm.

**Cone-scales** - appendiculate, flat, 1.2 - 2cm long.

**A. nemoropa** de Laubenfels. New Caledonia.

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8.B. Adult leaves < 0.9cm, male cone . 10cm long, similar to **A. columnaris**.

**Leaves** - mostly larger than 0.8 - 0.9cm long, oval rounded.

**Longitudinal Leaf Section** - resembling that of **A. columnaris**, but vascular bundles much more numerous.

**Male Cone** - 12cm long, mostly arched.

**Female Cone** - 7.5 x 11.5cm.
Cone-scales - with triangular of 1 x 0.4cm.

A. luxurians (Brongniart et Gris) de Laubenfels. New Caledonia.

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Figure 1:

Figure 2:
The Great Artesian Basin and its major sub-basin, the Eromanga Basin, which contains the Winton Fossil Plant Assemblage.
Figure 3:
Outcrop pattern and extrapolated subsurface range of the Winton Formation. (analysis and compilation by H. Apperley, Geology Dept., University of Adelaide).

Figure 4:
Site photograph of the Winton Fossil Plant Assemblage.
Figures 5 - 18:
Microfossils isolated from the Winton Fossil Plant Assemblage. (Scale bar: 10µ).

Figure 5: Lycopodiumsporites? Thiergart ex Delcourt & Sprumont
Figures 6, 7: Podocarpidites Cookson ex Couper cf. P. ellipticus
Figure 8: Liliacidites Couper
Figure 9: Laevigatosporites? Ibrahim
Figure 10: Alisporites similis? Balme
Figure 11: Podosporites Rao
Figures 12, 13: Crybelosporites Dettmann
Figure 14: Microthyriacites? Cookson
Figure 15: Schizosporis reticulatus Cookson and Dettmann
Figure 16: Contignisporites? Dettmann
Figures 17, 18: Microcachrydites antarcticus Cookson
Figures 19 - 27:

Microfossils isolated from the Winton Fossil Plant Assemblage (cont.).
(Scale bar: 10μ).

Figure 19: *Microcachrydites antarcticus* Cookson. This group of 4 grains may represent a newly dispersed tetrad.

Figure 20: *Microcachrydites antarcticus* Cookson. Polar view.

Figure 21: *Stereisporites*? Pflug

Figure 22: *Araucariacites*? Cookson ex Couper

Figures 23 - 25: Tricolpate grains, possibly angiospermous.

Figure 26: Algal or bryophytic spore?

Figure 27: Septate fungal spore.
Figures 28 - 33:

Araucarioxyylon Parataxon 1 (Specimen W300) (Scale bar: 100μ).

Figure 28: Transverse section, showing distinct growth rings.

Figure 29: Transverse section, showing shape and arrangement of tracheids.

Figure 30: Tangential longitudinal section, showing distribution of xylem rays.

Figure 31: Tangential longitudinal section, showing uniseriate xylem rays.

Figure 32: Radial longitudinal section, showing contiguous tracheidal pitting.

Figure 33: Radial longitudinal section, showing large, cupressoid, cross-field pits (arrowed).
Figures 34 - 39:

**Araucarioxylo**n Parataxon 1 (continued) (Specimen W279) (Scale bar: 100μ).

**Figure 34:** Transverse section, showing distinct growth rings.

**Figure 35:** Transverse section, showing shape and arrangement of tracheids.

**Figure 36:** Tangential longitudinal section, showing distribution of xylem rays.

**Figure 37:** Tangential longitudinal section, showing uniseriate xylem rays.

**Figure 38:** Radial longitudinal section, showing contiguous tracheidal pitting.

**Figure 39:** Radial longitudinal section, showing cupressoid, cross-field pits.
Figures 40 - 45:

Araucarioxyon Parataxon 1 (continued) (Specimen W134) (Scale bar: 100µ).

**Figure 40:** Transverse section, showing distinct growth rings.

**Figure 41:** Transverse section, showing shape and arrangement of tracheids.

**Figure 42:** Tangential longitudinal section, showing distribution of xylem rays.

**Figure 43:** Tangential longitudinal section, showing uniseriate xylem rays.

**Figure 44:** Radial longitudinal section, showing contiguous tracheidal pitting.

**Figure 45:** Radial longitudinal section, showing large cupressoid and dacydioid cross-field pits.
Figures 46 - 51:

_Araucarioxylon Parataxon_ 2 (Figs. 46 - 50, Specimen W197, Fig. 51, Specimen W147) (Scale bar: 100μ).

**Figure 46:** Transverse section, showing indistinct, distorted growth rings.

**Figure 47:** Tangential longitudinal section, showing distribution of uniseriate xylem rays.

**Figure 48:** Radial longitudinal section, showing contiguous tracheidal pitting.

**Figure 49:** Radial longitudinal section, showing contiguous tracheidal pitting and cross-fields.

**Figure 50:** Radial longitudinal pitting, showing small, cupressoid, cros-field pits.

**Figure 51:** Transverse section, showing indistinct growth rings.
Figures 52 - 57:

_Araucarioxylon Parataxon_ 2 (cont.) (Figs. 52 - 53, Specimen W147 cont., Figs. 54 - 57, Specimen W154) (Scale bar: 100μ).

**Figure 52:** Tangential longitudinal section, showing uniseriate xylem rays.

**Figure 53:** Radial longitudinal section, showing contiguous tracheidal pitting and small, cupressoid, cross-field pits.

**Figure 54:** Transverse section, showing indistinct growth rings.

**Figure 55:** Tangential longitudinal section, showing xylem rays.

**Figure 56:** Radial longitudinal section, showing contiguous tracheidal pitting and cupressoid cross-field pits.

**Figure 57:** Radial longitudinal section, showing biseriate, contiguous tracheidal pitting, and cross-field pits.
Figures 58 - 63:

_Araucarioxylon Parataxon_ 3 (Specimen W170) (Scale bar: 100μ)

**Figure 58:** Transverse section, showing distinct growth rings.

**Figure 59:** Transverse section, showing shape and arrangement of tracheids.

**Figure 60:** Tangential longitudinal section, showing uniseriate xylem rays.

**Figure 61:** Radial longitudinal section, showing contiguous tracheidal pitting.

**Figure 62:** Radial longitudinal section, showing contiguous tracheidal pitting.

**Figure 63:** Radial longitudinal section, showing cupressoid, cross-field pits.
Figures 64 - 69:

* Araucarioxylon Parataxon 4* (Figs. 64 - 68, Specimen W211) and * Incertae sedis Parataxon 1* (Fig. 69, Specimen W165) (Scale bar: 100μ).

**Figure 64:** Transverse section, showing fairly distinct growth rings.

**Figure 65:** Transverse section, showing shape and arrangement of tracheids.

**Figure 66:** Tangential longitudinal section, showing xylem rays.

**Figure 67:** Radial longitudinal section, showing contiguous tracheidal pitting.

**Figure 68:** Radial longitudinal section, showing small, cupressoid, cross-field pits.

**Figure 69:** * Incertae sedis Parataxon 1: * transverse section, showing fairly indistinct growth rings.
Figures 70 - 75:

**Incertae sedis Parataxon 1** (cont.) (Figs. 70 - 74, Specimen W165; Fig. 75, Specimen W105) (Scale bar: 100μ).

**Figure 70**: Transverse section, showing rounded tracheids.

**Figure 71**: Tangential longitudinal section, showing numerous, small xylem rays.

**Figure 72**: Tangential longitudinal section, showing uniseriate xylem rays.

**Figure 73**: Radial longitudinal section, showing separate and contiguous tracheidal pitting, and cupressoid cross-field pits.

**Figure 74**: Radial longitudinal section, showing separate tracheidal pitting and some cross-fields.

**Figure 75**: Transverse section, showing fairly distinct growth rings.
Figures 76 - 81:

Incertae sedis Parataxon 1 (cont.) (Figs. 76 - 78, Specimen W105 cont.; Figs. 79 - 80, Specimen W280; Fig. 81, Specimen W350) (Scale bar: 100μ).

Figure 76: Tangential longitudinal section, showing uniseriate xylem rays.

Figure 77: Radial longitudinal section, showing separate tracheidal pitting.

Figure 78: Radial longitudinal section, showing cupressoid, cross-field pits.

Figure 79: Transverse section, showing fairly distinct growth rings.

Figure 80: Tangential longitudinal section, showing uniseriate xylem rays.

Figure 81: Transverse section, showing fairly distinct growth rings.
Figures 82 - 83:

**Incertae sedis Parataxon 1** (cont.) (Specimen W350 cont.) (Scale bar: 100μ).

**Figure 82**: Tangential longitudinal section, showing uniseriate xylem rays.

**Figure 83**: Radial longitudinal section, showing separate tracheidal pitting.

**Figure 84**:
Map showing the global distribution of extant members of the Araucariaceae (shaded). Black dots represent localities of important fossil members of the extant genera (after Florin, 1963).
Figures 85 - 94:

*Araucaria microcarpa* sp. nov., showing external morphology of ovulate cones and subtending foliage. (Scale bar: 1mm).

*Figure 85:* Specimen W380B.

*Figure 86:* Specimen W380A.

*Figure 87:* Specimen W415.

*Figure 88:* Specimen W284.

*Figure 89:* Specimen W590B.

*Figure 90:* Specimen F9513.

*Figure 91:* Specimen W695.

*Figure 92:* Specimen W693.

*Figure 93:* Specimen W580.

*Figure 94:* Specimen W325.
**Figures 95 - 101:**

*Araucaria microcarpa* sp. nov., showing external morphology of ovulate cones and subtending foliage (cont.). (Scale bar: 1mm).

**Figure 95:** Specimen W269. Part of the apical region is missing and several seeds are visible.

**Figure 96:** Specimen W418.

**Figure 97:** Specimen W424.

**Figure 98:** Specimen W345.

**Figure 99:** Specimen W088. Note exposed seeds at apical region.

**Figure 100:** Specimen W413. Note exposed seeds and spiral scars marking points of attachment of missing cone-scales on cone axis.

**Figure 101:** Specimen W379.
Figures 102 - 108:

*Araucaria microcarpa* sp. nov., showing external morphology of ovulate cones and subtending foliage (cont.). (Scale bar: 1mm).

**Figure 102:** Specimen W401.

**Figure 103:** Specimen W485.

**Figure 104:** Specimen W590A.

**Figure 105:** Specimen W491.

**Figure 106:** Specimen W572.

**Figure 107:** Specimen W686.

**Figure 108:** Specimen W171 (Holotype).
**Figures 109 - 116:**

* Araucaria microcarpa * sp. nov., showing cone-scales and attached ovules. (Scale bar: 100μ).

**Figure 109:** Specimen W695. Adaxial view of exposed cone-scales (also see Fig. 91), showing a single ovule on the winged scale-surface. At the bottom left of the figure, a small ovule is visible, positioned to one side of the cone-scale.

**Figure 110:** Specimen W695. Electronmicrograph of detached cone-scale, showing ovule on adaxial surface. Note the narrow scale wings on either side of the ovule.

**Figure 111:** Specimen W695. Lateral view of cone-scale (ovule absent), showing thin, lateral wing and upturned, distal region of scale.

**Figure 112:** Specimen W695: Electronmicrograph of small, possibly immature ovule (also see Fig. 109), showing small ligule at ovule base (L).

**Figures 113 and 114:** Specimen W695. Electronmicrographs of mature ovules, showing attachment of ovuliferous scale (0) and thin lateral wings of the cone-scale (W) surrounding the embedded ovule.

**Figure 115:** Specimen W695. Electronmicrograph of portion of cone-scale and ovule, showing reflexed scale tip and small ligule.

**Figure 116:** Specimen W695. Electronmicrograph of cone-scale, ovule and ligule, showing epidermal cells.
Figures 117 – 121:

_Araucaria microcarpa_ sp. nov. (Scale bar: 100μ).

**Figure 117:** Specimen W695. Adaxial view of cone-scale and attached ovule, with ligule visible at base of reflexed ovule.

**Figure 118:** Specimen W695. Enlarged electronmicrograph of ovule and ligule, showing epidermal cells.

**Figure 119:** Specimen W413. Electronmicrograph of shattered cone (adaxial view). The ovules are missing, revealing their previously sunken position in the cone-scales.

**Figure 120:** Specimen W381. Electronmicrograph of abaxial surfaces of cone-scales (distal ends), showing regular nature of epidermal cells.

**Figure 121:** Specimen W695. Electronmicrograph of ovule surface, showing elongate cells of the sarcotesta.
Figures 122 - 129:

Araucaria microcarpa sp. nov. Longitudinal sections through cones, showing general internal structure. (Figs. 122 - 126, Specimen W032; Figs. 127 - 128, Specimen W500Q2; Fig. 129, Specimen W500Q1). (Scale bar: 1mm).

Figure 122: Tangential longitudinal section, showing many ovules.

Figure 123: Tangential longitudinal section close to cone axis, showing ovules positioned on adaxial surfaces of scales.

Figure 124: Radial longitudinal section, showing ovules and cone axis. Several foliage scales are visible at cone base.

Figure 125: Tangential longitudinal section outside cone axis.

Figure 126: Tangential longitudinal section through distal portion of cone-scales. The large central resin canals are visible.

Figure 127: Radial longitudinal section (polished).

Figure 128: Ground thin section of same surface seen in Fig. 127. Note the wide cone axis and numerous ovules between the cone-scales.

Figure 129: Oblique longitudinal section. Ovules can be seen in both tangential and radial planes. Several foliage scales are attached to the cone base.
Figures 130 - 136:

*Araucaria microcarpa* sp. nov. Longitudinal sections through ovulate cones, showing general internal structure. (Scale bar: 1mm).

**Figure 130:** Specimen W500Q4. Tangential longitudinal section.

**Figure 131:** Specimen PS4. Radial longitudinal section. (Most of cone is missing).

**Figure 132:** Specimen W055. Radial longitudinal section.

**Figure 133:** Specimen PS1. Radial longitudinal section.

**Figure 134:** Specimen W500A1. Tangential longitudinal section.

**Figure 135:** Specimen W500C1. Tangential longitudinal section.

**Figure 136:** Specimen W500C. Radial longitudinal section.
Figures 137 - 144:

*Araucaria microcarpa* sp. nov. Specimen W500FG. (Scale bar: 1mm).

These figures show a series of polished transverse surfaces of the same cone, beginning near the cone apex (Figure 137) and going toward the cone base (Figure 144). Photographs were taken at intervals of 1mm. The entire cone is 11.5 mm in length. The cone axis is clearly visible, containing many resin ducts. Numerous well-preserved ovules are attached to the cone-scales.
Figures 145 - 150:

_Araucaria microcarpa_ sp. nov. Transverse sections through ovulate cones, showing general internal cone structure. (Scale bar: 1mm).

**Figure 145**: Specimen W500F1. Ground thin section.

**Figure 146**: Specimen W500F3. Ground thin section.

**Figure 147**: Specimen W500A3. Ground thin section.

**Figure 148**: Specimen W500A2. Ground thin section.

**Figure 149**: Specimen W500AB. Polished surface.

**Figure 150**: Specimen W500B. Ground thin section.
Figures 151 - 156:

_Araucaria microcarpa_ sp. nov. Transverse thin sections through ovulate cones, showing general internal cone structure (cont.). (Scale bar: 1mm).

**Figure 151:** Specimen W500P.

**Figure 152:** Specimen W500D. (Cone is very distorted).

**Figure 153:** Specimen W376. (Oblique transverse section).

**Figure 154:** Specimen W500P3.

**Figure 155:** Specimen W500G1.

**Figure 156:** Specimen W500S.
Figures 157 - 162:

_Araucaria microcarpa_ sp. nov. Thin sections through ovulate cones. (Scale bar: 500μ).

**Figure 157:** Specimen W500P1 (transverse section), showing bract scale extending to the right of an ovule. Note the large central resin canal in the distal part of the bract (arrowed).

**Figure 158:** Specimen W500S11. Tangential longitudinal section through distal region of bract-scale, showing numerous abaxial, and several adaxial resin canals (arrowed).

**Figure 159:** Specimen W500A2. Transverse section showing bract scale and attached, reflexed ovule. Note the large median resin canal in the bract (arrowed).

**Figure 160:** Specimen W500S11. Transverse section through ovuliferous/bract scale complex. The distal portion of the ovuliferous scale takes the form of an arrowhead (O). Note the vascularization entering the ovuliferous scale and bract scale (B).

**Figure 161:** Specimen W500A3. Transverse section through cone, showing pointed ovuliferous scale (arrowed). The dark areas inside the ovules are artefacts of permineralization.

**Figure 162:** Specimen W500A4. Transverse section through cone, showing ovuliferous scale (arrowed). The wings of the cone-scale can be seen on either side of the ovule.
Figures 163 - 168:

_Araucaria microcarpa_ sp. nov. Longitudinal thin sections through ovulate cones, showing vascularization of the cone-axis and cone-scales. (Scale bar: 500μ).

Figures 163 and 164: Specimen W500C. Radial sections showing the single vascular supply to the cone-scale complexes (arrowed). Note the woodiness of the cone axis. Large resin canals (R) run vertically along the lateral edges of the axis. Well preserved ovules (O) and embryos (E) can be seen.

Figure 165: Specimen W500Q2. Radial section showing wide cone axis and single vascular supply to each cone-scale complex (arrowed).

Figure 166: Specimen WPS5. The vascularization of the bract scale (B) and ligule (L) is visible. In the bract, one strand follows the abaxial, the other the adaxial scale surface. Note the entry of the vascular supply to the ligule (arrowed), where it soon divides, with one strand entering the ligular tip, and the other entering the chalazal end of the ovuliferous tissue. Note also the shallow ligular sulcus (S).

Figure 167: Specimen WPS5: Radial section, showing single strand of vascular tissue entering the cone-scale complex, and the sclerotic nature of the bract. Note the well formed ovuliferous tissue.

Figure 168: Specimen W500Q3. Tangential section, showing entry of vascular tissue (arrowed) from the bract scale (B) into the ovuliferous scale and ovule.
Figures 169 - 176: *Araucaria microcarpa* sp. nov.

Figures 169 - 174:

Longitudinal sections through ovuliferous regions of cone-scales, showing structure of ovules and integuments. (Scale bar: 500μ).

**Figure 169:** Specimen WPS5. Note the micropyle (M), poorly preserved gametophyte (G) and its eroded apex, shrunken nucellus (N) around the gametophyte and thick sclerotesta (S).

**Figure 170:** Specimen WPS4. The gametophyte is cellular and possibly contains an embryo (arrowed). Note also the thick sclerotesta and enclosing integuments (I), and the thin nucellus (N).

**Figure 171:** Specimen WPS5. Megagametophytes are present in each of two ovules. The lower one is cellular. Note the thin nucellus (N), large nucellar cavity (C) and eroded apex of gametophyte.

**Figure 172:** Specimen WPS5. Highly magnified section showing nucellus, gametophyte (G) and chalaza (C). Note also the small pointed ligule.

**Figure 173:** Specimen W500C. Note the micropyle (arrowed), eroded ovular apex and wavy nucellus (N).

**Figure 174:** Specimen W500C. Section through two ovules (chalazal end to the left). The upper ovule contains a well-formed embryo with 2 cotyledons. (The dark circle around it is an artefact of thin sectioning). Note the eroded ovular apex. The bottom ovule contains a large cellular megagametophyte.

**Figures 175 and 176:** Electronmicrographs of foliage scales taken from cone peduncle of *Araucaria microcarpa* (Specimen W181). Epidermal cells are visible on the scale surface (adaxial). Stomates are longitudinally orientated, sunken, and in rows (Scale bar: 100μ).

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Figures 177 - 181:
Drawings of the vascularization of cone-scale complexes in *Araucaria* and *Agathis* (after Eames, 1913). (Not to scale).

**Figure 177:** *Araucaria bidwillii* (Section Bunya), showing the double vascular supply to the scales.

**Figure 178:** *Araucaria subulata* (Section Eutacta). Note the single bundle leaving the cone axis, which divides into two series in the axial cortex.

**Figure 179:** *Araucaria angustifolia* (Section Columbea), showing the single vascular bundle entering the cone-scale.

**Figure 180:** *Agathis australis*, showing a single vascular bundle entering the cone-scale, which divides into two bundles near the base of the scale.

**Figure 181:** *Araucaria microcarpa* sp. nov. Note the similarities in vascularization to *Araucaria* Section Columbea and to *Agathis*. It resembles the araucarian type more closely, as the branch leading into the ovule arises at the ovule base, rather than mid-way beneath it. Vascularization of the ligule (present in *A. microcarpa*) is only seen in species of *Araucaria* Section Eutacta and Section Bunya. (*Agathis* does not possess a ligule).

Figures 182 and 183:
Drawings of mature ovulate cones of *Araucaria subulata* (Fig. 182) and *A. cunninghamii* (Fig. 183) (both Section Eutacta). Note the morphological similarity to the cones of *Araucaria microcarpa* (Figs. 85 - 108). (Scale bar: 1cm).
Figures 184 – 187:
Araucariaceae: Incertae sedis 1. Specimen W016. External cone morphology (Scale bar: 1cm).

**Figure 184:** Adaxial view of cone, showing strong bilateral compression. (Some of cone has been sectioned).

**Figure 185:** Lateral view of cone, showing numerous spirally arranged cone-scales.

**Figure 186:** Lateral view of cone (opposite side to that of Fig. 185).

**Figure 187:** Cone-scales, showing transversely rhombic and upturned distal regions.
Figures 188 - 193:
Araucariaceae: Incertae sedis 1 (cont.). Longitudinal sections through cone.

Figure 188: Radial longitudinal polished surface, showing wide cone axis and compressed lateral cone-scales (Scale bar: 1cm).

Figure 189: Radial longitudinal thin section, showing heavily convoluted diverging cone-scales. Ovate structures, possibly ovules, are present between some scales (arrowed). (Scale bar: 5mm).

Figure 190: Radial longitudinal polished surface of cone apex, showing compressed cone-scales and ovules (?) (arrowed). (Scale bar: 1mm).

Figure 191: Tangential longitudinal polished surface through the distal regions of cone-scales, showing numerous resin canals which appear as white dots. (Scale bar: 1mm).

Figure 192: Tangential longitudinal thin section through distal region of a cone-scale, showing lines of resin canals scattered along the abaxial and adaxial scale surfaces. (Scale bar: 1mm).

Figure 193: Tangential longitudinal thin section through distal region of a cone-scale, showing resin canals (R) and possible xylem bundles (X). (Scale bar: 1mm).
Figures 194 - 197:

**Figure 194:** Whole silicified cone with attached peduncle bearing a single foliage scale. (Scale bar: 1mm).

**Figures 195 - 197:**
Electronmicrographs of the adaxial cone-scale surface.

**Figure 195:** Central keel is visible with concave surfaces on either side. (Scale bar: 100μ).

**Figure 196:** Parallel bands of stomates occur on either side of the keel. (Scale bar: 100μ).

**Figure 197:** Stomates are usually orientated parallel to vertical scale axis, but may be perpendicular. Note the sunken position of the stomates. (Scale bar: 10μ).

**Figure 198:**
Drawing of immature ovulate cone of *Araucaria rulei* (Section Eutacta). (after de Laubenfels, 1969). Note similarity to Araucariaceae: *Incertae sedis* 2. (Scale bar: 1cm).

**Figure 199:**
Drawing of ovulate cone of *Atroraxis selaginoides* (Taxodiaceae). Note the superficial resemblance to Araucariaceae: *Incertae sedis* 2. (Scale bar: 1mm).
Figure 200:
Araucariaceae: *Incertae sedis* 3. Specimen W328. Cone portion is visible on the surface of a weathered rock. (Scale bar: 1mm).

Figure 201:
Staminate cone of *Araucaria muelleri* (Section Eutacta) (after de Laubenfels, 1969). Note the morphological resemblance to Araucariaceae *Incertae sedis* 3. (Scale bar: 1cm).

Figure 202:
*Araucarites* polycarpa Tenison-Woods from the Upper Mesozoic of Queensland (illustration after Walkom, 1919). This cone has a similar morphology to Araucariaceae *Incertae sedis* 3. (Scale bar: 2mm).

Figures 203 - 205:
Araucariaceae *Incertae sedis* 4. Specimen W191. (Scale bar: 1mm).

Figure 203: Lateral view of cone embedded longitudinally in rock matrix.

Figure 204: Adaxial view of cone, showing wide cone axis and radiating cone-scales.

Figure 205: Lateral view of cone after carbonate rock-matrix was dissolved, showing numerous, spirally arranged, peltate cone-scales.
Figures 206 - 211:
Araucariaceae Incertae sedis 5. Specimen W106.

Figure 206: General view of cone morphology, showing elongate strobilus. (Scale bar: 5mm).

Figure 207: Spirally arranged, peltate cone-scales. Note the shallow groove around the edges of the scales, which may mark the bases of dehisced or broken terminal scale spines. (Scale bar: 1mm).

Figure 208: Transverse polished surface through cone, showing wide cone axis and lateral scales. (Scale bar: 1mm).

Figure 209: Tangential longitudinal polished surface through distal region of cone-scales, showing 3 resin canals in each scale (arrowed). (Scale bar: 500 µ).

Figures 210 and 211: Radial longitudinal thin sections through cone, showing wide cone axis and diverging scales. The dark structures in Fig. 211 (arrowed) are probably microsporangia, which appear to have released spores through longitudinal slits. (Scale bar: 1mm).
Figures 212 - 216:
Araucariaceae Incertae sedis 6, showing general cone morphology. (Scale bar: 1mm).

Figures 212 and 213: Specimen W089. Note the single subtending foliage scale at cone base.

Figure 214: Specimen W094. Most of the basal cone-scales are missing, exposing the cone axis.

Figure 215: Specimen W369. Cone apex is missing. Several foliage scales subtend the cone at its base.

Figure 216: Specimen W471. Cone apex is missing. Foliage scales subtend the cone at its base.
Figure 217:
Map showing the global distribution of extant members of the Podocarpaceae (shaded). Black dots represent localities of the more important fossil members of the extant genera (after Florin, 1963).
Figures 218 - 226:

*Fecundistrobus hamusites* gen. et sp. nov. General morphology of ovulate cones. (Scale bar: 1mm).

**Figure 218:** Specimen W700.

**Figure 219:** Specimen W701. Note several large ovules at cone apex.

**Figure 220:** Specimen W702. Note 2 ovules on right side of cone. Holotype.

**Figure 221:** Specimen W703. Note 2 ovules at cone apex.

**Figure 222:** Specimen W704. Note large ovule on right side of cone.

**Figure 223:** Specimen W705. Note 2 large ovules.

**Figure 224:** Specimen W706.

**Figure 225:** Specimen W707. Note mature ovules at bottom left and top right of cone.

**Figure 226:** Specimen W708.
Figures 227 and 228:

_Fecundistrobus hamusites_ gen. et sp. nov. General morphology of ovulate cones (cont.). (Scale bar: 1mm).

**Figure 227:** Specimen W709. Note 2 ovules on left side of cone.

**Figure 228:** Specimen W710.

**Figure 229:**

Photograph of ovulate cone of _Microcachrys tetragona_. Note general similarity to _Fecundistrobus hamusites_. (Scale bar: 1mm).

**Figure 230:**

Drawing of ovulate cone of _Saxegothaea conspicua_. Note general similarity to _Fecundistrobus hamusites_. (Scale bar: 5mm).
Figures 231 - 236:

Fecundistrobus hamusites gen. et sp. nov. Morphological detail of ovulate cones. (Scale bar: 100μ).

Figure 231: Specimen W711. A pair of mature ovules detached from cone. Note the small cone-scales and the erect orientation of the ovoid ovules.

Figure 232: Specimen W712. Lateral view of immature ovule subtended by the protecting cone-scale. Note the sharply reflexed micropyle.

Figure 233: Specimen W705. Electronmicrograph of abaxial cone-scale surface (free portion), showing longitudinal rows of epidermal cells. Note the indistinct keel running along the scale.

Figure 234: Specimen W702. Electronmicrograph of abaxial cone-scale surface (basal portion), showing longitudinal rows of epidermal cells, which are smaller than those of the free portion.

Figure 235: Specimen W702. Electronmicrograph of cone-scale surfaces. The scale on the left contains typically large epidermal cells of the adaxial surface. The scale on the right features small epidermal cells of the basal portion of an abaxial scale surface.

Figure 236: Specimen W700. Electronmicrograph of adaxial cone-scale surface, showing longitudinal rows of stomates (arrowed).
Figure 237:
Drawing of ovulate cone of Microstrobos niphophilus. (Scale bar: 500μ).

Figure 238:
Drawing of ovulate cone of Rissikia (after Townrow, 1969).

Figure 239:
Drawing of ovulate cone of Mataia (after Townrow, 1969).

Figure 240:

Figure 241:

Figure 242:
Drawing of branchlet bearing ovulate cones of Mehtaia santalensis (after Vishnu-Mittre, 1958). (Scale bar: 1mm).
Figures 243 - 248:

Lepidothamnus australis sp. nov. Specimen W145. Holotype.

Figures 243 - 245:

General cone morphology. (Scale bar: 1mm).

Figure 243: Frontal view.

Figure 244: Left lateral view.

Figure 245: Right lateral view.

Figure 246: Electronmicrograph of abaxial cone-scale surface, showing poorly defined, elongate epidermal cells, and longitudinally arranged stomates. (Scale bar: 100μ).

Figure 247: Electronmicrograph of the ovule epidermis, showing regular cells arranged in longitudinal rows. (Scale bar: 100μ).

Figure 248: Electronmicrograph of ovulate cone of Lepidothamnus laxifolius (an extant species from New Zealand). Note the excellent morphological similarity to L. australis sp. nov. (Scale bar: 100μ).
Figure 249 - 254:

Podostrobus eromanga sp. nov. (Scale bar: 1mm).

Figure 249: Specimen W562.

Figure 250: Specimen W579. Holotype.

Figure 251: Specimen W198.

Figure 252: Specimen W168. Radial longitudinal polished surface. Only the left side of the cone is preserved.

Figure 253: Specimen W168. Radial longitudinal thin section (see also Fig. 252), showing peltate cone-scales with narrow laminae and thin distal surfaces.

Figure 254: Specimen W579. Radial longitudinal polished surface of cone base, showing wide cone axis and lateral scales. Holotype.
Figures 255 - 262:

*Podostrobus eromanga* sp. nov. (cont.).

**Figure 255:** Specimen W579. Enlarged view of radial longitudinal thin section, showing microsporangia attached to cone-scales, and the single vascular strand entering the cone-scales (arrowed). (Scale bar: 1mm). Holotype.

**Figure 256:** Specimen W579. Transverse polished surface. Note that each cone-scale has 2 microsporangia attached to it (arrowed). (Scale bar: 1mm). Holotype.

**Figure 257:** Specimen W198. Transverse polished surface. Note that 2 rings of resin ducts occur around the perimeter of the cone axis. (Scale bar: 1mm).

**Figures 258 - 261:**
Thin sections through microsporangia, showing immature and tri-saccate microspores (arrowed). (Scale bar: 10μ).

**Figures 258 and 259:** from Specimen W579. Holotype.

**Figure 260:** from Specimen W198.

**Figure 261:** from Specimen W168.

**Figure 262:** Specimen W579. Polished section through cone peduncle, showing the upturned and recurved scale leaves. (Scale bar: 1mm). Holotype.

**Figure 263:** Drawings of *Podostrobus podocarpoides* (a) and *P. rajmahalensis* (b) (after Vishnu-Mitte, 1958). Note the similarity to *P. eromanga*. (Scale bar: 1mm).
Figures 264 - 266:
*Podostrobus major* sp. nov. Specimen W433.

Figure 264: Radial longitudinal thin section through cone apex, showing upturned and incurved cone-scales. (Scale bar: 1mm).

Figure 265: Transverse thin section, showing wide cone axis and sporangia attached to cone-scales. (Scale bar: 1mm).

Figure 266: Thin section through microsporangia, showing poorly preserved tri-saccate microspores (arrowed). (Scale bar: 30μ).

Figures 267 - 270:
*Podostrobus bisaccata* sp. nov. Specimen W008. Holotype.

Figure 267: Radial polished section through cone, (Scale bar: 1mm).

Figure 268: Radial thin section through cone (same plane as Fig. 267). Note the wide cone axis and ruptured sporangia. (Scale bar: 1mm).

Figure 269: Enlarged view of cone axis and base of diverging cone-scale, showing vascular strand entering the scale (Scale bar: 200μ).

Figure 270: Thin section through sporangium, showing typical bisaccate microspores, which are assignable to *Podocarpidites*. (Scale bar: 30μ).
Figure 271:
Map showing the global distribution of extant members of the Taxodiaceae (shaded). Black dots represent localities of the more important fossil members of the extant genera (after Florin, 1963).

Figure 272:
*Austrosequoia wintonensis* Peters and Christophel. Specimen F9512. (Scale bar: 1mm).

Figure 273:
*Austrosequoia wintonensis* Peters and Christophel. Specimen F9512 (as in Fig. 272, but following treatment of the fossil in acid.) Note the more extensive exposure of the cone. (Scale bar: 1mm).
Figures 274 - 281:

Austrosequoia wintonensis Peters and Christophel. New Paratypes of isolated cones recovered after dissolution of carbonate rock-matrices. (Scale bar: 1mm).

Figure 274: Specimen WA1.

Figure 275: Specimen WA2.

Figure 276: Specimen WA3.

Figure 277: Specimen WA4.

Figure 278: Specimen WA5.

Figure 279: Specimen WA6.

Figure 280: Specimen WA7.

Figure 281: Specimen WA8.
**Figures 282 - 290:**

**Austrosequoia wintonensis** Peters and Christophel (cont.).

**Figure 282:** Specimen WA3. Electronmicrograph of cone-scale, showing scale spine and epidermal cells, which are well preserved on the abaxial side of the spine. (Scale bar: 250µ).

**Figures 283 and 284:** Specimen WA9. View of adaxial cone-scale surface, showing a single reflexed ovule. (Scale bar: 500µ (Fig. 283), 100µ (Fig. 284)).

**Figure 285:** Specimen W152. Adaxial cone-scale surface after dehiscence of seeds. Note the depressions in the scale indicating the prior positions of the seeds. (Scale bar: 1mm).

**Figure 286:** Enlargement of Fig. 285, showing the site of vascular attachment between the cone-scale and seed (arrowed). (Scale bar: 500µ).

**Figure 287:** Specimen W334. Transverse thin section through cone, showing wide cone axis and peltate (though distorted) cone-scales. (Scale bar: 200µ).

**Figure 288:** Specimen W334. Enlargement of Fig. 287, showing 3 ovules containing shrivelled gametophytes. Note the small, pointed, ovuliferous scales extending beyond the ovules. (Scale bar: 200µ).

**Figure 289:** Specimen W553. Transverse thin section through cone, showing peltate scales and several ovules. The cone axis is arrowed. (Scale bar: 200µ).

**Figure 290:** Specimen W553. Enlargement of Fig. 289, showing a single ovule. Note the shrivelled gametophyte (or embryo) and pointed ovuliferous scale (Scale bar: 100µ).
Figures 291 - 296:
Immature ovulate cones cf. *Austrosequoia wintonensis*, showing general morphology. All cones were found exposed on rock surfaces. (Scale bar: 1mm).

**Figure 291**: Specimen W335. Note foliage attachment bearing scale leaves.

**Figure 292**: Specimen W358.

**Figure 293**: Specimen W378.

**Figure 294**: Specimen W450.

**Figure 295**: Specimen W576.

**Figure 296**: Specimen W577. Note foliage attachment bearing scale leaves.
Figures 297 - 302:
Immature ovulate cones cf. *Austrosequoia wintonensis* (cont.).

**Figure 297**: Specimen W666. Whole cone extracted from carbonate-matrix rock. (Scale bar: 1mm).

**Figure 298**: Specimen W666. Electronmicrograph of cone surface, showing a short, upturned and appressed dorsal spine (arrowed). (Scale bar: 500µ).

**Figure 299**: Specimen W666. Electronmicrograph of abaxial surface of cone-scale, showing several small stomates (arrowed). (Scale bar: 100µ).

**Figure 300**: Specimen W655. Oblique longitudinal thin section through cone.

**Figure 301**: Specimen W655. Longitudinal thin section through one of the peltate cone-scales, showing several ovules on its adaxial surface. Note also the single vascular strand entering the scale. (Scale bar: 500µ).

**Figure 302**: Specimen W655. Longitudinal thin section through a cone-scale, showing the adaxially positioned, reflexed ovules. (Scale bar: 500µ).
Figures 303 - 308:

Immature ovulate cones cf. *Austrosequoia wintonensis* (cont.).

**Figure 303:** Specimen W188. Radial longitudinal polished surface through a cone. (Scale bar: 1mm).

**Figure 304:** Specimen W188. Enlargement of Fig. 303, showing peltate cone-scales, wide cone axis and several reflexed ovules on the adaxial surface of the cone-scales. (Scale bar: 500μ).

**Figure 305:** Specimen W188. Transverse thin section, showing cone-scales around the cone axis. Each scale bears up to 5 reflexed ovules. Note the large resin canals present in the distal part of the scales (arrowed). (Scale bar: 500μ).

**Figure 306:** Specimen W450. Radial longitudinal polished surface through cone (whole cone illustrated in Fig. 294). (Scale bar: 1mm).

**Figure 307:** Specimen W450: Transverse polished surface through cone, showing peltate cone-scales, wide cone axis and reflexed ovules. (Scale bar: 1mm).

**Figure 308:** Specimen W450. Enlargement of polished surface, showing 5 reflexed ovules. The area arrowed is the cone-scale stalk. (Scale bar: 500μ).
Figures 309 - 314:

*Wintonia peltata* Gen. et sp. nov. General cone morphology. (Scale bar: 1mm).

**Figure 309:** Specimen W022.

**Figure 310:** Specimen W027. Note several ovules exposed by weathering of fossil.

**Figure 311:** Specimen W169.

**Figure 312:** Specimen W205.

**Figure 313:** Specimen W297. This cone was extracted from acid-soluble rock matrix.

**Figure 314:** Specimen W326.
Wintonia peltata Gen. et sp. nov. General cone morphology (cont.)
(Scale bar: 1mm).

Figure 315: Specimen W369.

Figure 316: Specimen W398. Holotype. Note foliage attachment bearing scale leaves.

Figure 317: Specimen W417.

Figure 318: Specimen W538.

Figure 319: Specimen W564. Transverse view of cone. Note several large ovules exposed by weathering.

Figure 320: Specimen WA19. Cone isolated from rock matrix by acid treatment. Note the single, large ovule in the centre. Most of the cone is missing.
Wintonia peltata Gen. et sp. nov. General cone morphology (cont.). Cones were isolated from acid-soluble carbonate rock matrices. (Scale bar: 1mm).

Figure 321: Specimen WD3. Cone is laterally distorted.

Figure 322: Specimen W004. The dark area in the cone centre is its base.

Figure 323: Specimen W004. Other side of cone illustrated in Fig. 322, showing spiral arrangement of scales leading to the cone apex.

Figure 324: Specimen WD5.

Figure 325: Specimen WA20.

Figure 326: Specimen WD1.
Figures 327 - 332:

*Wintonia peltata* Gen. et sp. nov. (cont.). Sections through ovulate cones, showing their internal structure. (Scale bar: 1mm).

**Figure 327:** Specimen W022 (also see Fig. 309). Polished section showing large ovules. The white area around the cone edge represents a region of chemical weathering.

**Figure 328:** Specimen W022. Ground thin section of surface illustrated in Fig. 327. The weathered region now appears black. The cone axis is severely distorted and is hardly visible.

**Figure 329:** Specimen W027 (also see Fig. 310). Polished surface showing large ovules. There is no preservation of the cone axis or internal ovular tissue.

**Figure 330:** Specimen W169 (also see Fig. 311). Polished surface through cone. Again there is no preservation of the cone axis. Large ovules are visible.

**Figures 331 and 332:** Specimen W386. Ground thin section through cone. Note the large, pelate cone-scales in Fig. 331 and the large ovules in which integuments are visible. The cone axis is barely visible.
**Figures 333 - 336:**

*Wintonia peltata* Gen. et sp. nov. (cont.). Specimen W022. Ground thin sections through ovules. (Scale bar: 500μ).

The micropyle is directed downwards in each photograph. Note the well-defined integumentary layers in Fig. 334. The ovuliferous scale is seen to extend past the ovule with 3 short projections in Figs. 333 - 335. The scale in Fig. 336 is differently shaped and is probably a longitudinal rather than transverse view. Fig. 335 features an ovule containing a thin nucellus, free from the enclosing integuments. Within are the shrivelled remains of gametophytic or embryonic tissue, still attached to the chalaza. (These tissues are seen less clearly in the other figures).
Figures 337 - 341:

Wintonia peltata Gen. et sp. nov. (cont.).

Figure 337: Specimen W022. Ground thin section through ovule (micropyle at left). (Scale bar: 500µ).

Figure 338: Specimen W386. Ground thin section through part of cone (transverse view). Note the remains of a small ovule positioned to one side of the peltate scale (arrowed). (Scale bar: 500µ).

Figure 339: Specimen WD6. Polished tangential section through cone-scales, showing large central resin canals in the scales. (Scale bar: 1mm).

Figure 340: Specimen W297. Tangential longitudinal polished section showing rhombic cone-scales and large central resin canals. (Scale bar: 1mm).

Figure 341: Specimen W398 (also see Fig. 316). Foliage attachment at base of cone, showing the spirally arranged scale leaves. (Scale bar: 1mm). Holotype.

Figure 342:
Drawing of ovulate cone of Taxodium distichum. (Scale bar: 1cm).
Figure 343:
Map showing the global distribution of extant members of the Cupressaceae (shaded). Black dots represent localities of the more important fossil members of the extant genera (after Florin, 1963).

Figures 344 and 345:
Callitris octothamna sp. nov. (Scale bar: 1mm).

Figure 344: Specimen W177. The base of the cone is badly weathered.

Figure 345: Specimen W225.
Figures 346 - 349:

*Callitris octothamna* sp. nov. (cont.). (Scale bar: 1mm).

**Figure 346:** Specimen W605. Two ovulate cones are exposed on the surface of a single rock specimen. Both cones are attached to short peduncles, the upper one possessing a whorl of scale leaves. Holotype.

**Figure 347:** Specimen WC0. This cone was extracted whole from a carbonate matrix. Note the short peduncle bearing scale leaves.

**Figure 348:** Specimen WC1. This cone was also extracted from a carbonate matrix. There is obvious compression of the cone.

**Figure 349:** Specimen W177. (also see Fig. 344). A transverse polished surface through the cone, showing the cone-scales and numerous flattened seeds within.

**Figure 350:**

Drawing of ovulate cone of *Callitris oblonga*, an extant species endemic to Tasmania. (Scale bar: 2mm).
Figures 351 - 354:

Angiospermae Incertae sedis. Fruiting structures. (Scale bar: 1mm).

Figure 351: Specimen W188. Two fruits (W188A & W188B) are visible on the surface of a rock. Both may have been attached to a single stalk. The larger fruit (W188A) possesses an apical bulge, representing the perianth.

Figure 352: Specimen W324. Fruit exposed on rock surface. The base of the structure is visible. A scar is present which represents the site of dehiscence of the fruit from its peduncle.

Figure 353: Specimen W334. Fruit exposed on rock surface. There was possibly some decay of the fruit prior to preservation, as evidenced by the crinkly surface and holes in the fruit wall.

Figure 354: Specimen WC3. This fruit was extracted whole from carbonate-matrix rock. The fruit apex is at the top. Note the numerous triangular perianth parts.
Figures 355 - 358:

Angiospermae **Incertae sedis** (cont.). Specimen W188A. Transverse thin sections.

**Figure 355:** Section through base of fruit, showing numerous ovoid carpels attached by stalks. (Scale bar: 1mm).

**Figure 356:** Section through centre of fruit, showing large number of carpels. (Scale bar: 1mm).

**Figure 357:** Enlargement of Fig. 356, showing several carpels. Note the large embryos in each. (Scale bar: 500μ).

**Figure 358:** A single carpel. Note the fleshy wall and large embryo. (Scale bar: 500μ).
Figure 359 - 362:

Angiospermae *Incertae sedis* (cont.) (Scale bar: 1mm).

**Figure 359:** Specimen W188B. Transverse thin section near base of fruit, showing the large number of stalked carpels.

**Figure 360:** Specimen W188B. Enlarged view of polished surface near fruit base, showing large number of radiating carpels.

**Figure 361:** Specimen W324. Radial longitudinal thin section through fruit, showing stalked carpels radiating from base. Note the enlarged basal receptacle.

**Figure 362:** Specimen W324. Enlargement of radial section through a single carpel, showing ovoid seed (basally attached - see arrow) surrounded by a fleshy carpel wall.
**Figures 363 - 368:**
Conifer Foliage Type I.

**Figures 363 - 366:**
Selection of foliage shoots, showing general morphology, all isolated from carbonate-matrix rocks. (Scale bar: 5mm).

**Figure 367:** Electronmicrograph of adaxial leaf surface, showing the 2 bands of stomates on either side of the leaf midline (Scale bar: 100μ).

**Figure 368:** Electronmicrograph of adaxial leaf surface, showing vertical rows of stomates, orientated parallel to the long axis of the leaf. (Scale bar: 100μ).
Figures 369 - 370:
Conifer Foliage Type II.

Figure 369: Selection of foliage shoots showing general morphology. (Scale bar: 5mm).

Figure 370: Electronmicrograph of lateral view of leaf, showing a vertical row of stomates on the adaxial leaf surface. (Scale bar: 50μ).

Figures 371 - 374:
Conifer Foliage Type III.

Figures 371 - 373:
Selection of foliage shoots, showing general morphology. (Scale bar: 5mm).

Figure 374: Electronmicrograph of adaxial leaf surface, showing many vertical rows of stomates, orientated parallel to the long axis of the leaf. (Scale bar: 100μ).
Figures 375 - 379:

Conifer Foliage Type IV.

Figure 375: Selection of foliage shoots, showing general morphology. (Scale bar: 5mm).

Figure 376: Electronmicrograph of adaxial leaf surface, showing scattered rows of stomates arranged parallel to the long axis of the leaf. (Scale bar: 100μ).

Figure 377: Specimen W063. Rock surface, showing example of Foliage Type IV. (Scale bar: 5mm).

Figure 378: Electronmicrograph of a single shoot, showing the planar leaves which are twisted at the point of insertion. (Scale bar: 1mm).

Figure 379: Electronmicrograph of abaxial leaf surface, showing the arrangement of stomates (compare with Fig. 376). (Scale bar: 100μ).

Figure 380:

Conifer Foliage Type V. Selection of foliage shoots, showing general morphology. (Scale bar: 5mm).
Figures 381 - 382:
Conifer Foliage Type V (cont.).

Figure 381: Specimen W149. Rock surface, showing a collection of shoots of Foliage Type V. (Scale bar: 5mm).

Figure 382: Electronmicrograph of abaxial leaf surfaces. Note the regular and small epidermal cells. (Scale bar: 100μ).

Figures 383 - 384:
Conifer Foliage Type VI.

Figure 383: Selection of foliage shoots, showing general morphology. Note commonness of branching. (Scale bar: 5mm).

Figure 384: Specimen W283. Twig of Foliage Type VI on rock surface. Note that the scale leaves change in morphology halfway along the length of the shoot. (Scale bar: 5mm).
Figures 385 - 387:

Conifer Foliage Type VI (cont.).

**Figure 385:** Electronmicrograph of branching shoot, showing irregularly shaped scale leaves. (Scale bar: 1mm).

**Figure 386:** Electronmicrograph of adaxial leaf surface, showing stomates unusually orientated perpendicular to the long axis of the leaf on either side of the midline. (Scale bar: 100μ).

**Figure 387:** Electronmicrograph of abaxial surface of the adnate part of the leaf base, showing stomates and hair bases. (Scale bar: 100μ).

Figures 388 - 389:

Conifer Foliage Type VII. Selection of foliage shoots, showing general morphology. (Scale bar: 5mm).
Figures 390 - 395:
Non-coniferous / non-angiospermous foliage. (Scale bar: 5mm).

Figures 390 - 394:
Foliage Type 1.

Figure 390: Specimen W077.

Figure 391: Specimen W526.

Figure 392: Specimen W173.

Figure 393: Specimen W116.

Figure 394: Specimen W141.

Figure 395:
Foliage Type II. Specimen W033.
Figures 396 - 398:
Non-coniferous / non-angiospermous foliage. (Scale bar: 5mm).

Figures 396 - 397:
Foliage Type III.

Figure 396: Specimen W449.

Figure 397: Specimen W359.

Figure 398:
Foliage Type IV. Specimen F9514.

Figure 399:
Angiospermous foliage. Specimen F9515. Note midrib and secondary veins. (Scale bar: 5mm).