TERTIARY ARAUCARIACEAE FROM SOUTH-EASTERN AUSTRALIA, WITH NOTES ON LIVING SPECIES

By Isabel C. Cookson* and Suzanne L. Duigan*

[*Manuscript received June* 28, 1951]

Summary

The foliage shoots, male cones, and female cone-scales of a new Tertiary species of *Araucaria,* section Eutacta, from the brown coal at Yallourn, Victoria, have been described; leaves and male and female cones possessing the general features that characterize species of *Agathis* have been identified. Leaves of a second species of *Agathis* have been distinguished in a bed associated with the brown coal at Bacchus Marsh, near Melbourne, Vic.

Pollen grains from fossil male cones of *Araucaria* and *Agathis* have been recognized and the exine structure of a recent species of *Araucaria* has been considered. Fossil pollen grains of araucarian type have also been recorded from several deposits in south-eastern Australia and Tasmania.

The morphological and cuticular features of the leaves, male cones, and female cone-scales of recent species of *Araucaria,* section Eutacta, and *Agathis* have been investigated.

The present and past southern distribution of both genera have been discussed.

I. Introduction

There is not a great deal of reliable information available regarding the exact identity of Australian Tertiary conifers. The comprehensive review of southern Mesozoic and Tertiary conifers published by Florin in 1940 includes all Australian records existing at that date, and indicates the author's views on the accuracy of their identification. More recently Krausel (1949) revised the determinations of fossil coniferous woods, and drew up a key for their separation.

About half of the recorded Australian species apparently belong to the family Podocarpaceae, most of the remainder being members of the Araucariaceae or Cupressaceae. However, many of these determinations are open to question, particularly those based on leaf morphology. Much of the confusion surrounding species identified from wood fragments has been eliminated by Krausel, who at the same time has considerably reduced the number of distinct Australian species. Few cones or seeds have been recorded, and the accuracy of the identification of some of these has been questioned by Florin.

As a result of visits to the Yallourn open cut during the last few years, a collection of coniferous remains has been built up. This consists of reproductive organs and leaves sufficiently well preserved to show microscopic features.

* Botany School, University of Melbourne.

It is hoped that this material will supply more details than have hitherto been available, and thus permit more precise identifications. Supporting evidence obtained from the palynological examination of Tertiary deposits is also being collected, and it is proposed to publish the results of these combined studies as opportunity offers. The present communication, which is concerned with the Araucariaceae, provides conclusive proof of the presence of the genera *Agathis* and *Araucaria* in Victoria during the Tertiary period.

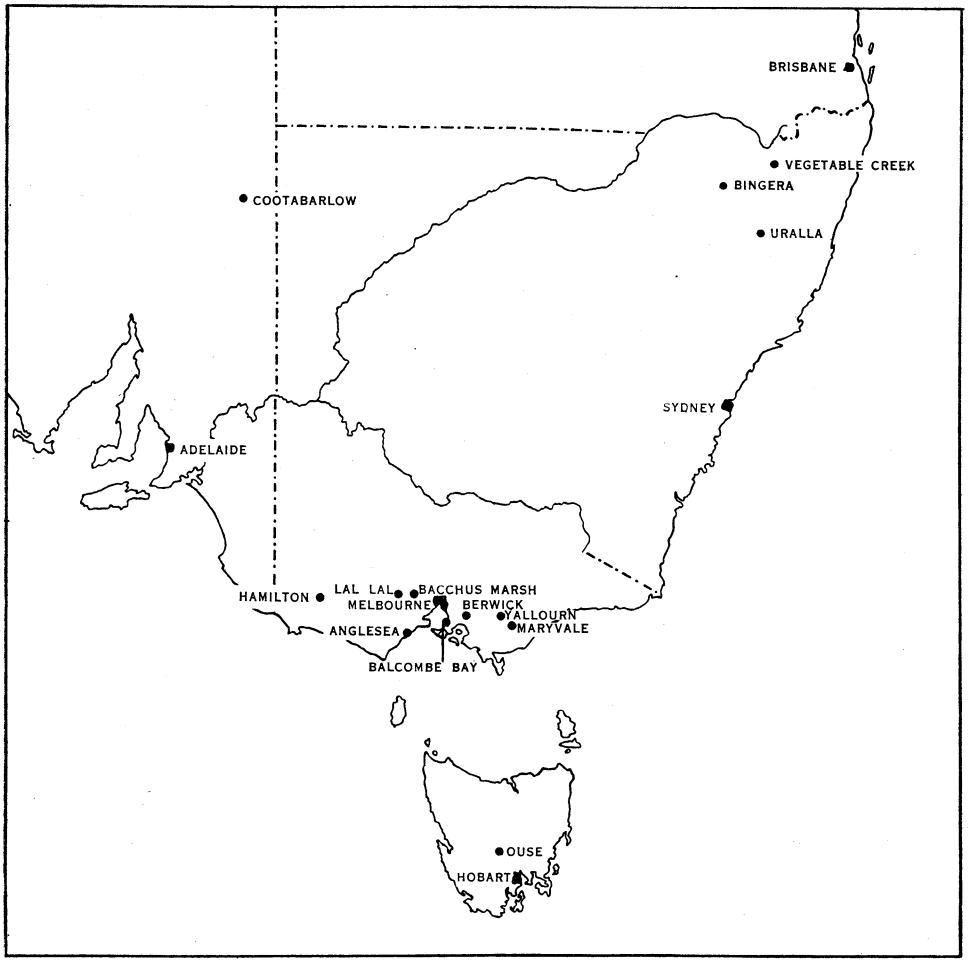


Fig. 1.—Map of south-eastern Australia, showing the locations in which Tertiary members of the Araucariaceae occurred (prepared by the Geological Survey of Victoria).

II. Scope of the Investigation

Most of the specimens to be considered here were collected from the State Electricity Commission's open cut at Yallourn, Vic. A small number from a sandy leaf-bed above the coal at the Lucifer Colliery near Bacchus Marsh, Vic., and from other Australian deposits (see Fig. 1), will also be discussed.

The fossils include:

(*a*) Leafy shoots, detached male cones with pollen grains, and isolated female cone-scales typical of *Araucaria* (section Eutacta).

(*b*) Leaves of two species of *Agathis*; one detached male cone with pollen grains and two female cones which are also believed to have belonged to *Agathis*.

(*c*) Pollen grains of araucarian type from Tertiary sediments in south-eastern Australia.

A detailed study of the leaves, male cones, pollen grains, and female cone-scales of living species of *Araucaria* and *Agathis* has been undertaken with a view to establishing the generic identity and specific affinities of the plant remains listed above. This has shown that a number of small variations exist between the species of both genera. Unfortunately it has not been possible, from the limited amount of authentic material available, to determine the constancy of the individual variations. However, while realizing that a more comprehensive examination may necessitate future modifications in some directions, it has been decided to publish the observations made in this connection. These are shown in Tables 1-5.

III. Location and Age of the Deposits

The location of the sediments in which pollen grains of the Araucariaceae have been observed is shown in Figure 1. Most of these deposits have been mentioned previously (Cookson 1946, 1947, 1950). New localities are:

Bingera, New South Wales. Pink mudstone, Australian Museum. Probably Oligocene (Singleton 1941).

Berwick, Vic. Ligneous clay underlying the older basalt at Wilson's Quarry. Probably Oligocene.

Hamilton, Vic. Ligneous clay on the north side of Grange Creek. Military map grid reference Hamilton sheet 496,346. This deposit underlies the newer basalt, and Mr. E. D. Gill, Palaeontologist to the National Museum of Victoria, has personally expressed the view that its age is Upper Pliocene.

Ouse, Tasmania. Lignitic seam in the Ouse River, about 400 yards upstream from the Bridge hotel, Ouse. ? Oligocene-Miocene.

The age of the brown coal deposits in south-eastern Australia has been the subject of considerable discussion. The latest statement is that of Thomas and Baragwanath (1949), who accept the view that the brown coals are mainly of Oligocene age.

IV. Methods

For the removal of cuticles from leaves and sporophylls of both fossil and recent types, treatments either with nitric acid and potassium chlorate followed by ammonia, or with a 12 per cent. solution of sodium hypochlorite were used.

Pollen grains were obtained after maceration of portions of the male cones by sodium hypochlorite or by Erdtman's (1948) chlorination-acetolysis-alkali

method. For the recovery of pollen grains from ligneous clays and shales, the latter method, after a pretreatment with hydrofluoric acid, proved to be most satisfactory.

V. Araucaria, Section Eutacta

Portions of leafy shoots of a species of *Araucaria* (Section Eutacta) were relatively abundant in a bed exposed during 1950 at the third level of the Yallourn open cut, the coordinates of which were 7160S. and 1050E. and the reduced level 92. With them were disconnected male cones and detached female cone-scales which also resemble those of members of the section Eutacta. Although no organic connection between the three types of fossil has been observed, their relative abundance and close proximity in this particular zone make it seem likely that they represent different organs of one species. As such they are viewed here, where all three are included in the new Tertiary species *A. lignitici* now to be described.

(*a*) *Leaves*

Araucaria lignitici n.sp.

(i) *External Characters* (Plate 1, Figs. 1-4)

The leaves (presumed to be adult) are arranged on the slender axes in a rather close spiral. They are from 3 to 8 mm. long and from 1 to 1.5 mm. broad, usually narrow-triangular with an acute apex, falcate, and prominently carinate. In the small fragment shown in Plate 1, Figure 3, the leaves are shorter and relatively broader.

(ii) *Cuticular Structure* (Plate 1, Figs. 5, 7)

Stomata.—The leaves are amphistomatic, but the arrangement of the stomata differs on the two surfaces. The stomata are relatively large, the average polar diameter of the guard cells being 55 μ and the range 47-60 μ. The guard cells are surmounted by from four to six rather inconspicuous subsidiary cells, one or two of which are frequently polar, and a similar number of large, clearly defined, encircling cells. Usually the stomata are separated from one another by ordinary epidermal cells, but sometimes the encircling cells of neighbouring stomata abut on one another. The majority of the stomata are obliquely oriented.

Lower epidermis.—The epidermal cells are square, quadrangular, polygonal, or irregular, with their major axis in a longitudinal direction. Their lateral walls are straight or curved, 2.5-3 μ thick, and pitted, often inconspicuously so.

The stomata are arranged in more or less well-defined longitudinal rows situated in two roughly triangular areas, which are separated from one another by a wide central zone completely devoid of stomata. Two lateral zones without stomata also occur.

The stomatal rows, which at the base are about 12 in number, become gradually reduced to one on either side towards the middle of the leaf. Soon

afterwards the two remaining rows are discontinued, to recommence at varying distances from the apex, where they are represented by from 6 to 20 stomata. This arrangement (type *B*2, Fig. 2), shown in Plate 1, Figure 5, has been observed in a considerable number of leaves, and appears to be the one typical of the species. Slight variations have been noted in the extent of the gap between the proximal and distal rows, which in some examples may be quite small. An exception to this arrangement was seen in a leaf removed from the specimen with shorter, broader leaves shown in Plate 1, Figure 3. In it the stomata appeared to be restricted to two proximal groups as in type *C*, Figure 2. More material of this type will be necessary before the significance of this exception can be determined.

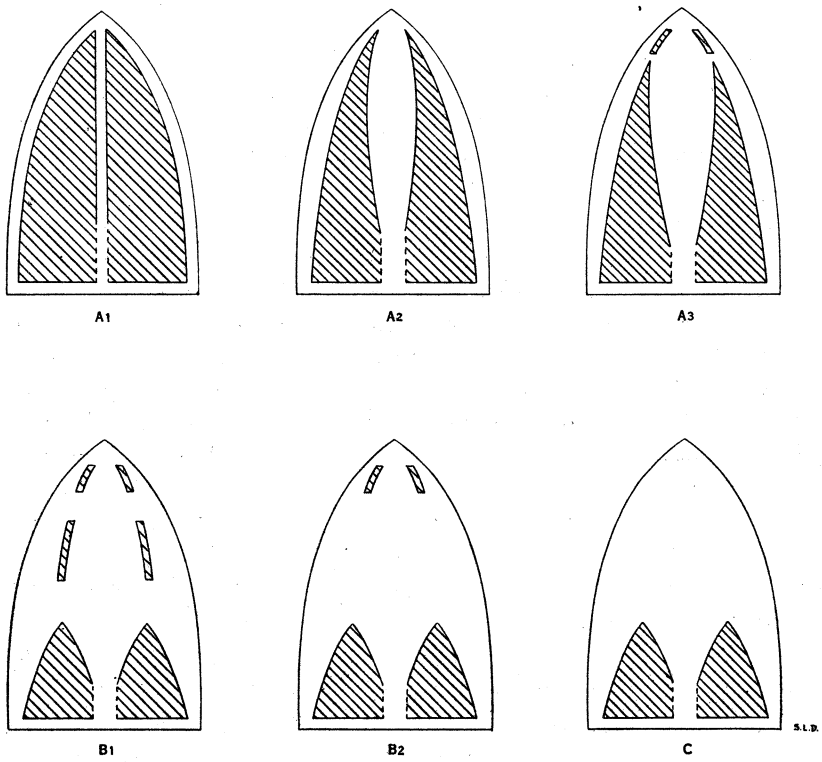


Fig. 2.—Diagrammatic representation of the types of stomatal arrangement found in recent species of *Araucaria*, section Eutacta.

Upper epidermis.—The stomata are more closely placed than on the lower epidermis. They occur in longitudinal rows. Towards the base of the leaf there are usually from six to eight rows on either side of a wide, central, stomata-free zone. The number of stomatal rows becomes gradually reduced distally, but the few that remain extend without appreciable interruption from base to apex. Two lateral zones without stomata occur.

The epidermal cells are similar in all respects to those of the lower epidermis.

(iii) *Internal Anatomy* (Plate 1, Fig. 6)

The internal tissues are rather compressed, and only the gross features can be distinguished. The mesophyll is differentiated into spongy and palisade tissues, and branched sclereids and resin canals occur.

The cells of the epidermal layer are small, square to quadrangular in cross section, and have thick (5 μ), cutinized outer walls. Beneath it on both surfaces is a hypodermal layer composed of thick-walled fibres interrupted only at the stomata. The guard cells (Plate 1, Fig. 6) are deeply sunken, their outer walls extremely thick (7.5 μ), and their cavities considerably reduced. They are almost completely covered by the subsidiary cells, which themselves lie vertically beneath the encircling cells, so that a funnel-like outer chamber is formed.

Recent Species

Of the conifers still living in Australasia and the south Pacific islands, only *Athrotaxis selaginoides* Don, and certain species of *Dacrydium* and *Araucaria* show any morphological resemblance to *Araucaria lignitici.* Comparisons with a view to the establishment of the affinity of this fossil have, therefore, been restricted to these particular types.

The similarity between *A. lignitici* and *Athrotaxis,* apparent as regards external morphology, does not extend to the cuticle. In *Athrotaxis* the stomata are irregularly arranged and are restricted to the upper surface of the leaf, whereas in *Araucaria lignitici* they are arranged in rows and occur on both surfaces of the lamina. Moreover, the stomatal apparatus is different in the two forms, that of *Athrotaxis* being without the encircling cells that are a conspicuous feature in *Araucaria.* The leaves of such species as *Dacrydium araucarioides, D. balansae,* and *D. lycopodioides* can be distinguished from those of *A. lignitici* by their cuticular structure. In these forms (group *B,* Florin 1931, p. 248) the stomata are always longitudinally oriented and the walls of the subsidiary and encircling cells associated with them are more or less conspicuously ribbed.

On the other hand, the evidence of general morphology, cuticular structure, and internal anatomy indicates a close affinity with the genus *Araucaria.*

Two sections are recognized within this genus, namely Colymbea and Eutacta. The species included in the section Colymbea need not be considered further, because of their relatively large leaves and the distinctive cuticular features, such as the predominantly longitudinal orientation of the stomata, that characterize them. Moreover, comparative work has clearly demonstrated that the shoot of *A. lignitici* is very similar to those of certain species of the section Eutacta — *A. balansae, A. beccarii, A. cunninghamii,* and *A. excelsa.* Confirmation of such a taxonomical position has been obtained from a comparative study of 11 species of this section. The observations made, together with information provided by Bertrand (1874), Thomson (1905), Seward and Ford (1906), Florin (1931), and Dallimore and Jackson (1948) are contained in the summary and discussion which follow, and in Table 1.

(i) *External Characters.*—The leaves of living species of Eutacta are small (*A. muelleri* excepted), sessile, either lanceolate, triangular, or ovate, and have acute or obtuse apices. They are usually four-angled except when considerably flattened, spirally and imbricately inserted, and upwardly and inwardly curved.

(ii) *Cuticular Structure.*—Stomata occur on both sides of the leaf. On the upper surface they are arranged in rows that form two triangular areas extending from the base, where they may join, to a position just behind the apex. These areas are separated by a median zone of variable width devoid of stomata.

The stomata are less closely placed on the lower surface, and the size of the triangular areas is more variable. Three main types of stomatal arrangement can be distinguished (Fig. 2).

(*A*) The stomata occupy two triangular areas, which extend to, or nearly to, the apex.

(*A*1) The areas are separated only by a very narrow zone of epidermal cells.

(*A*2) The width of the stomatal areas decreases very considerably towards the apex, and they are separated by a relatively wide zone of epidermal cells.

(*A*3) As for *A*2, but there is a short gap between the stomata at the apex and those just behind it.

(*B*) The stomata are mainly concentrated in two triangular areas in the proximal region of the leaf, but isolated groups occur at or near the apex.

(*B*1) Isolated groups of stomata occur between the apical and basal groups.

(*B*2) The apical and basal groups are completely separate.

(*C*) The stomata are confined to two basal, triangular areas.

These types of stomatal arrangement, although described as being separate, actually form a continuous series. It has been found that, while the stomatal arrangement of a species may not always conform to one particular type, variations from it in either direction are only slight.

The stomata are usually obliquely oriented and have polar diameters of from 44 to 72 μ. Each consists of two deeply sunken guard cells surrounded and surmounted by from four to six subsidiary cells and an equal number of encircling cells. The walls that separate the subsidiary cells from the encircling cells are particularly strongly cutinized. The outer respiratory cavity is either oval or rectangular in surface view.

The epidermal cells are more or less elongated in a longitudinal direction. Their lateral walls are straight, curved, or sinuous, and are usually pitted.

(iii) *Internal Anatomy.*—The leaves are from flat to elliptical or more or less tetragonal in cross section. The outer walls of the epidermal cells are considerably thickened and a cryptocrystalline zone, consisting of minute grains of calcium oxalate, is present beneath the cuticle. The guard cells of the stomata

TABLE 1

MORPHOLOGICAL AND CUTICULAR CHARACTERS* OF THE LEAVES OF RECENT AND FOSSIL SPECIES OF *ARAUCARIA*, SECTION EUTACTA

Species	Leaf				Cuticle						
					Cell Walls				Stomata		
					Sinuous		Pitted				
	Size (mm.)		Shape Ovate-Lanceolate	Apex Acute	Upper Surface	Lower Surface	Upper Surface	Lower Surface	Group (See Section V(*a*)(iv))	Polar Diameter (μ)	
	Length	Width								Av.	Range
A. balansae Brongn. et Gris.	4-6	2-4	+	+	—	—	+	+	*B*1, *B*2	55	50-61
A. beccarii Warb.	*c.* 10	*c.* 3	+	+	+	+	+	+	*A*2, *A*3	50	45-55
A. bernieri Buchh.	*c.* 3.5	*c.* 2	—	+	—	—	+	+	*B*1, *B*2	60	54-68
A. biramulata Buchh.	8-9	4-6	+	+	—	—	+	+	*A*2, *A*3	58	54-67
A. columnaris (Forst.) Hook.	5-6	*c.* 4	—	—	—	×	+	+	*C*	51	48-57
A. cunninghami Ait.	*c.* 6	*c.* 4	+	+	+	+	+	+	*A*3, *B*1, *B*2	48	45-55
A. excelsa (Lamb.) R. Br.	*c.* 6		+,—	—	—	—	+	+	*B*2, *C*	47	44-49
A. humboldtensis Buchh.	6-7	4-5	—	—	—	+	+	+	*C*	64	54-72
A. intermedia Vieill.†	*c.* 13	*c.* 6	+	+	—	+	+	+	*B*2, *C*	62	52-70
A. montana Brongn. et Gris.	*c.* 7	*c.* 5	—	—	+	×	—	—	*B*2	54	45-59
A. muelleri Brongn. et Gris.	25-30	12-15	—	+	—	—,+	+	+	*A*1	63	56-68
A. rulei F.v.M.‡	12-26	6-8	—	—	—	—	+	+	*A*1	54	45-68
			—	—	—	+	+	+	*B*2		
A. lignitici	3-8	1-1.5	+	+	—	—	+	+	*B*1, *B*2, ?*C*	55	47-60
A. balcombensis Selling	*c.* 32	*c.* 16	—	+	—	—	?	?	?	?	?
A. derwentensis Selling	*c.* 7	*c.* 5	—	—	?	?	?	?	?	?	?
A. fletcheri Selling	*c.* 4.5	*c.* 3	+	+	—	—	—	—	?	?	?
A. ruei Seward and Conway	*c.* 12	*c.* 7	+	×	—	—	—	—	?	?	?

* In Tables 1-5, + and — are used to indicate presence or absence of the character listed at the top of any particular column, and × to denote an intermediate condition. Most of the figures relating to the size of leaves and cones have been taken from Seward and Ford (1906), Bailey and White (1916), Dallimore and Jackson (1948), and Buchholz (1949). Measurements from actual specimens have been used only when figures from such sources have not been available. The cell walls referred to in the tables are the lateral walls of the epidermal cells. They are regarded as being sinuous only when the undulations are conspicuous, of a narrow amplitude, and closely placed. The walls are classed as thick when they are of the order of 5 μ, thin if about 2 μ.

†, ‡ see page 423.

TABLE 4

MORPHOLOGICAL AND ANATOMICAL CHARACTERS* OF THE LEAVES OF RECENT AND FOSSIL SPECIES OF *AGATHIS*

Species	External Features				Internal Structure						Cuticle																	
											Lower Surface												Upper Surface Epidermal Cells††					
															Stomata**									Walls			
	Size (cm.)				Sclereids			S.C.‡			Epidermal Cell Walls				Polar Diameter (μ)												
	Length	Width	Shape Lanceolate†	Apex Acute	Numerous	In Palisade	In Sp.Mes.	In Palisade	In Sp.Mes.	Fibres Numerous§	Thick	Sinuous	Pitted	In Rows	Aver.	Range	Transverse (%)	Oblique (%)	Longitudinal (%)	Group	In Rows	Elongated and Parallel	Thick	Sinuous	Pitted	Thickened Corners
A. alba (Rumph.) Warb.	5-12.5	1-5	±	±	+	+	+	–	+	–	–	–	+	+	53	39-57	44(30-52)	55(47-69)	1(0-2)	*A*	+	–	–	–	+	–
A. australis Salisb.	1.5-5	1-2	–	–	+	–	+	–	+	+	–		+	+	52	48-53	13(4-19)	78(73-85)	9(4-11)	*B*	+	–	–	×, –	+	–
A. brownii (Lemaire) L. H. Bail.	5-15	2.5-6	±	±	×	+	+	–	+	×	–	–		±	51	44-57	34(30-38)	63(60-67)	3(2-5)	*A*	×	–	+	–	+	–
A. celebica Warb.	*c.* 4.5	*c.* 2.5	+ –	–	–	+	+	–	+	+	–	–	–		52	47-57	49(42-55)	50(44-56)	1(1-2)	*A*	–	–	–	–	+	+
A. flavescens Ridl.	5-6.5	1-2.5	–	–	+	+	+	+		×	–	–	–		50	45-53	40(33-48)	58(50-65)	2(1-3)	*A*	–	–	+	–	+	+
A. lanceolata (Panch.) Warb.	4-12.5	0.5-1.5	±	+	–	+	–	–	+	–	+	–	+	+	53	49-60	7(2-9)	80(78-91)	13(7-17)	*B*	–	–	+	–	+	+
A. microstachya J. F. Bailey and C. T. White	3-5	1.2	+	–	×	–	+	+	+	–	–	–	+	–	57	55-62	15(12-17)	84(82-85)	1(1-3)	*B*	–	–	+	–	+	–
A. moorei (Lindl.) Mast.	6-13	1-4	±	–	–	+	–	–	+	–	–	–	+	+	47	44-52	20(15-26)	76(69-82)	4(2-5)	*B*	+	+	+	●	+	–
A. obtusa (Lindl.) Morrison	12	3	–	–	+	+	+	–	+	–	–	–	+	+	44	40-51	43(33-55)	57(44-67)	0(0-1)	*A*	+	+	–	–	+	–
A. ovata Warb.	7.5-11.5	1.5-3	–	–	+	+	+	+	+	–	+	–	+	×	54	51-59	17(8-28)	70(67-84)	13(1-24)	*B*	–	–	+	–	+	–
A. palmerstoni F.v.M.	5-10	1-2	±	–	+	+	+	–	+	+	–	–	+	±	54	47-57	12(7-19)	75(64-82)	13(5-29)	*B*	–	–	+	–	+	–
A. philippinensis Warb.	7.5	1-2.5	+	±	–	–	+	+	+	+	+	–	+	–	47	44-49	18(13-24)	75(68-80)	7(4-9)	*B*	–	–	+	–	+	–
A. regia Warb.	7.5-9	*c.* 3	+	–	–	–	+	+	+	+	–	–	+	×	56	53-61	33(30-38)	64(61-66)	3(1-4)	*A*	–	–	+	–	+	–
A. vitiensis Benth. and Hook.	5-15	0.5-4.5	–	–	–	–	+	–	+	+	–	–	+	+	51	45-53	34(32-36)	64(63-65)	2(1-3)	*A*	–	–	+	–	+	–
A. parwanensis	?	?	?	?	–	?	+	+	+	+	–	–	+	+	50	44-55	41(32-50)	56(48-62)	3(2-6)	*A*	+	+	–	–	+	–
A. yallournensis	*c.* 9.5	1-2	+	–	–	+		+	+	+	–	–	+	–	60	52-65	8(3-16)	79(67-88)	13(6-24)	*B*	–	–	–	–	+	–

* See footnote to Table 1.

† In deciding whether a leaf should be classed as lanceolate, all variations, such as ovate-lanceolate, oblong-lanceolate, etc., have been included in this term.

‡ S.C. = secretory canals; Sp.Mes. = spongy mesophyll.

§ The fibres referred to in the table are those lying immediately beneath the upper epidermis.

** In all species, at least some of the stomata are in rows, but they are classed as such only when the majority are in long, clearly defined rows. The range given in brackets after the percentage orientation of each species is that of averages taken from separate counts (usually of about 500 stomata) on different leaves and on different parts of one leaf. The group refers to the distribution of the variously oriented stomata as described in the text.

†† The cells of the upper epidermis always show some degree of regularity in their arrangement, but it is only in a few species that the rows are long and clearly defined and the cells almost uniformly elongated in a direction parallel with that of the axis of the leaf. The column headed 'thickened' refers to a thickening which is sometimes present at the junctions of the lateral walls of the epidermal cells.

are deeply sunk beneath the surface of the epidermis. A fibrous hypodermal layer is present. The palisade and spongy mesophyll form two distinct layers and the latter is characterized by the presence of numerous thick-walled, branched sclereids. Resin canals are either scattered irregularly or may occur below each vein; in those leaves that are tetragonal in section there is frequently a canal at each angle.

Comparison of Araucaria lignitici *with Recent and Fossil Species*

Recent species.—In external form, the leaves of *A. lignitici* resemble most closely those of *A. balansae, A. beccarii, A. cunninghamii,* and *A. excelsa,* those of the remaining species differing from them either in size or shape. The type of stomatal arrangement usually found on the lower surface of the leaves of *A. lignitici* (Fig. 2, *B*2) appears to be typical of *A. balansae,** *A. bernieri,* and *A. montana,* and has also been observed in *A. cunninghamii, A. excelsa, A. intermedia,* and *A. rulei.** A somewhat similar type (Fig. 2, *A*3) has been recorded in *A. beccarii* and *A. biramulata,* but in these species the main stomatal areas extend much nearer to the apex than they do in *A. lignitici.* The distribution of the stomata on the leaves of *A. columnaris* (type *C*), *A. humboldtensis* (type *C*), and *A. muelleri* (type *A*1) appears to be quite distinct from that of *A. lignitici.*

In size, the stomata of *A. lignitici* approximate closely to those of recent species (Table 1), the average polar diameter of the guard cells being well within the range of averages (44-72 μ) obtained for the stomata of living representatives. The stomata of *A. excelsa,* which are consistently smaller, and those of *A. humboldtensis, A. intermedia,* and *A. muelleri,* which are usually larger, are the farthest removed in this respect.

Another feature that may prove useful for comparative purposes is the nature of the lateral walls of the epidermal cells. These are straight or curved on both surfaces of *A. lignitici, A. balansae, A. bernieri, A. biramulata, A. excelsa, A. muelleri,* and most specimens of *A. rulei,* but are sinuous on at least one surface of the material of *A. rulei* ex Kew and of the remaining species.

From the above discussion and the details shown in Table 1, it can be seen that the leaves of *A. lignitici* have more features in common with the leaves of *A. balansae* than with those of any other recent species. Whether this resemblance of foliar characters indicates a close relationship cannot be determined from the present evidence.

* According to Dallimore and Jackson (1948), the stomata of *A. balansae* and *A. rulei* are confined to the upper surface of the leaf. In all the material examined, stomata have always been present on both surfaces of both species.

† The cuticular characters of a single leaf of *A. intermedia* Vieill. No. 1276 ex Kew are included here although Dallimore and Jackson's mention of a "Var. *intermedia* Intermediate in foliage between *A. rulei* and *A. columnaris*" seems to imply their intentions to reduce this form to varietal rank.

‡ Two sets of information regarding the cuticular characters of *A. rulei* appear in this table. The upper one refers to material from all sources (Appendix I) except the Royal Botanic Gardens, Kew, the lower one refers to the specimen received from that institution.

Fossil species.—Four reliable species of the section Eutacta* have previously been described from Tertiary deposits in the Southern Hemisphere. They are *Araucarites ruei,* described by Seward and Conway (1934) from shoots and cone-scales found at the Kerguelen Archipelago, and the three species, *Araucaria derwentensis* from Tasmania, *A. balcombensis* from Victoria, and *A. fletcheri* from New South Wales described by Selling (1950) from sterile shoots and isolated leaves.

As many comparative features as possible have been extracted from the original descriptions and included in Table 1. These show that each of the southern fossil species is distinct from *A. lignitici* in more than one feature.

Possibly *A. lignitici* resembles *A. fletcheri* more closely than it does any of the other three species, but its leaves are narrower, its epidermal cells have pitted instead of unpitted lateral walls, and its stomata are not "closely packed" as they are said to be in *A. fletcheri.*

(*b*) *Male Cones*

Araucaria lignitici

(i) *External Characters* (Plate 2, Figs. 8-11)

Portions of detached male cones resembling those of recent species of *Araucaria,* section Eutacta, were relatively numerous in the particular locality at Yallourn that yielded shoots of *A. lignitici.*

As already indicated, none of the male cones of *A. lignitici* is complete, and most are considerably compressed. They appear to have been cylindrical, with a length of about 2 cm. and a width of approximately 0.5 cm.

The sporophylls are numerous, small, rather larger towards the base of the cone, and spirally arranged. Each consists of a stalk and a thin, flat, rhomboidal, vertically directed free portion, or lamina, with an acute or acuminate apex. There are several pollen-sacs per sporophyll, but the exact number has not been discernible.

The base of the cone is surrounded by a number of sterile bracts (Plate 2, Fig. 9), about 3-4 mm. long and 0.5 mm. broad, that are slightly carinate and somewhat falcate.

(ii) *Cuticular Structure of the Lamina of the Sporophyll* (Plate 2, Fig. 13)

Lower epidermis.—The epidermal cells are square, quadrangular, polygonal, or irregular, and elongated in a longitudinal direction. Their lateral walls are curved or slightly sinuous, 2.5-4 μ thick, and strongly pitted.

The number and arrangement of the stomata vary according to the position of the sporophyll on the cone, being few and widely spaced on, or absent from, the smaller terminal sporophylls, and more numerous, with a tendency to form short, longitudinal rows, in the central areas of the larger basal sporophylls.

* *Araucaria imbricatiformis* R. M. Johnston is omitted because of the disagreement existing regarding its sectional position. Johnston (1888) and Florin (1940) relate it to the section Colymbea, but Selling (1950) writes: "It seems to come closest to the recent *A. muelleri,* a species of Eutacta restricted to the higher elevations in New Caledonia."

The stomata are identical with those of the leaves of *A. lignitici.* Each is associated with the usual number of subsidiary and encircling cells. Their orientation is variable.

Upper epidermis.—The epidermal cells are rather more regular and elongated than those of the lower surface, and their lateral walls are thinner and less strongly pitted. Stomata are absent.

Margin.—The margin of the lamina is minutely crenulate. Most of the marginal cells develop bluntly pointed, frequently recurved, cylindrical denticulations, the walls of which are about 2 μ thick.

(iii) *Cuticular Structure of the Bract* (Plate 2, Fig. 12)

Lower epidermis.—The epidermal cells are usually six-sided and longitudinally elongated; they have thin (about 2.5 μ), straight, strongly pitted lateral walls. Stomata appear to have been almost completely absent, only a single short row having been observed at the proximal end.

Upper epidermis.—The epidermal cells are similar to those of the lower surface, but their walls are less strongly pitted. Stomata of the normal type occur in two more or less unbroken rows, which extend from the base to the apex of the bract. These rows are separated from one another by a wide, central, stomata-free zone, and from the margin by two narrower zones in which stomata do not occur.

Margin.—Some of the cells at the junction of the upper and lower epidermis are prolonged into short, unicellular denticulations similar to those of the sporophylls.

Comments.—The distribution of the stomata on the lower surface of the bract as compared with that of the foliage leaves and sporophylls is of interest. The stomata on the lower surface of the foliage leaf are mainly in the proximal half of the leaf, with a few short rows at the apex. The same surface of the bract is almost devoid of stomata, only one or two occurring towards the base. In the sporophyll, however, the distribution of the stomata is reversed, a moderate number usually being scattered over the central area of the lower surface of the lamina, while there are none on the upper surface.

The development of minute denticulations from some of the marginal cells indicates the transitional character of the bracts. Marginal denticulations are numerous in the laminae of the male sporophylls, less numerous in the bracts, and undeveloped in the foliage leaves of *A. lignitici.*

(iv) *Pollen Grains* (Plate 2, Figs. 14, 15)

Pollen grains of araucarian type have been recovered from the male cones of *A. lignitici,* both after chlorination-acetolysis and treatment with sodium hypochlorite. The morphological features of the grains are equally clearly shown in both cases, but the measurements given have been taken from acetolysed grains.

The pollen grains of *A. lignitici* are non-aperturate and, when fully expanded, circular in outline. The average diameter is 59 μ, and the range 52-68 μ.

The exine is approximately 2 μ thick, and is clearly differentiated into nexine and sexine layers (Erdtman 1948) of almost equal thickness. The sexine is composed of numerous, densely arranged, oval granules or pilae about 1 μ long. Each terminates in a minute spine.

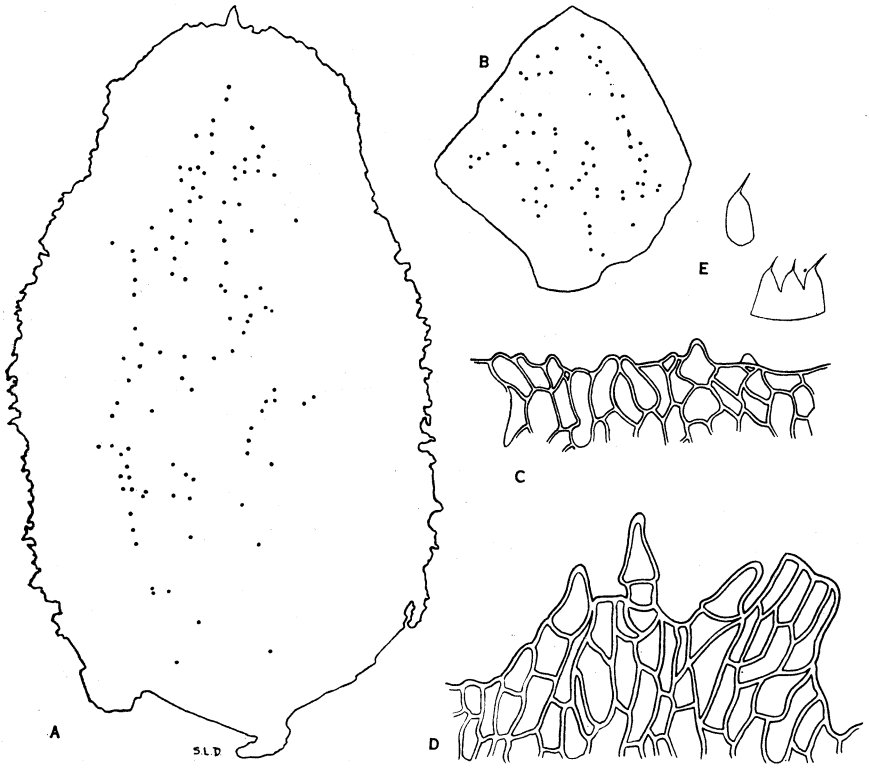


Fig. 3.—Portions of the male cones of recent species of *Araucaria,* section Eutacta.

A. A. montana. Sporophyll, showing the shape, apex, and the distribution of the stomata. x15.

B. A. beccarii. Sporophyll, showing the shape, apex, and the distribution of the stomata. x15.

C. A. rulei. Portion of the sporophyll, showing unicellular, ungrouped projections. x150.

D. A. columnaris. Portion of the sporophyll, showing multicellular, grouped projections. x150.

E. A. columnaris. Sexinous granules of the pollen grain. x10,000.

Recent Species

The recovery from the male cones of *A. lignitici* of large, spherical, non-aperturate, finely granular pollen grains identical with those of the family

Araucariaceae clearly indicates a connection with this family. However, since the pollen grains of *Agathis* and *Araucaria* are indistinguishable from one another, they provide no indication of the generic identity of the cones. It is only when detailed comparisons are made between the cones of *A. lignitici* and those of recent types that a greater resemblance to *Araucaria* becomes apparent.

The male cones of the two sections of *Araucaria* differ from one another both as regards their size and the arrangement of the sporophylls. Cones of the section Colymbea range from 7.5 to 17.5 cm. in length and the sporophylls are arranged in verticils (Seward and Ford 1906, p. 318), whereas those of the section Eutacta are smaller, ranging from 2.5 to 8 cm. (except *A. muelleri*), and the sporophylls are spirally arranged. In both respects, the agreement of the fossil cones is with those of the section Eutacta rather than Colymbea. As this similarity is further emphasized by the occurrence of a similar transition from sporophylls to foliage leaves and the detailed structure of the lamina of the sporophyll, the possibility of a connection with the section Colymbea will not be considered further.

The male cones of the section Eutacta are dense, cylindrical structures consisting of numerous spirally arranged sporophylls. The lamina of the sporophyll is usually relatively small and either rhomboidal or oval to oblong in shape (Fig. 3*b*, 3*a*). The apex may be acute or obtuse; sometimes a minute mucro is present (Fig. 3*a*). The margins are either entire or minutely crenulate, and the marginal cells of all species, except *A. muelleri*, are prolonged into bluntly pointed unicellular or multicellular denticulations of varying length (Fig. 3*c*, 3*d*), which towards the base of the lamina are frequently recurved. Their outer walls are sometimes strongly thickened. The cells of the outer epidermis are usually irregular in shape, but are often elongated in a longitudinal direction. Their lateral walls vary in thickness; they are always pitted and are either curved or sinuous. The stomata, which are moderately numerous, are usually restricted to the central portion of the lamina. Only those of *A. muelleri* and *A. rulei* are arranged in long longitudinal rows.

The cells of the upper epidermis are usually narrower and more elongated than those of the lower surface. Their lateral walls are thin, pitted or unpitted, and straight or sinuous. Stomata are absent, sparsely scattered or, as in *A. muelleri* and *A. rulei*, relatively numerous and arranged in rows.

The large, spherical, non-aperturate form of the pollen grains of the Araucariaceae is well known but no systematic account of the pollen grains of recent species has been given. Measurements of acetolysed pollen grains of the section Eutacta, made during the present investigation, have therefore been included in Table 2.

The disagreement existing regarding the sculpture of the exine has necessitated a more detailed examination of this layer. Thibout (1896), using pollen of *Araucaria columnaris*, and Cookson (1947*b*), using pollen of *Araucaria bidwillii* Hook. and *Agathis brownii*, have classed the exine as granular, whereas

Wodehouse (1935), from pollen grains of *Araucaria araucana* (Mol.) K.Koch and *Agathis philippinensis*, and Cranwell (1941), from *Araucaria excelsa*, have concluded that the exine is pitted.

From sections of acetolysed exines of *Araucaria columnaris*, it has been possible to determine that the sexine is composed of numerous closely placed, oval granules (pilae), and that each of these terminates in a short spine (Fig. 3; Plate 2, Fig. 16). The granules are of slightly different sizes (Plate 2, Figs. 17 and 18), but their length approximates fairly closely to 1 μ. As the sexine can be detached from the nexine as a complete layer, it seems probable that the bases of the pilae are loosely connected to one another. Isolated granules have been observed in the preparations.

Comparison of Araucaria lignitici *with Recent and Fossil Species*

Recent species.—Reference to the previous section and to Table 2 shows that the male cone and pollen grains of *A. lignitici*, while falling within the generalized description of those of living members of the genus *Araucaria*, section Eutacta, cannot be exactly matched with any particular living species. The cone appears to have been smaller than most of these, but the incompleteness of the available samples precludes satisfactory comparison on a size basis.

As regards the size and shape of the lamina of the sporophyll, it can be said that they are so distinct from those of *A. columnaris*, *A. excelsa*, and *A. montana* (Fig. 3) as to make it appear unlikely that the parent of the fossil cone was closely related to any of these species. On these and other grounds, it appears probable that the closest connection is with *A. beccarii*, *A. bernieri*, *A. cunninghamii*, and perhaps with *A. balansae* and *A. biramulata*.

Fossil species.—There have been no previous records of the male cones of *Araucaria* from Tertiary strata in Australia. In fact the only other fossil male cone of araucarian type ever recorded is that of *Brachyphyllum mammilare* Brongn., which was described by Kendall (1949). This species occurred in the mid-Jurassic estuarine series of north Yorkshire. Its general conformation is in agreement with that of *Araucaria lignitici*, but the pollen grains are quite distinct.

(*c*) *Female Cone-Scales*

Araucaria lignitici

(i) *External Characters* (Plate 3, Figs. 19-21)

The cone-scales are broadly cuneate, with a length of 11-18 mm. and a breadth at the distal end of 9-11 mm. A slightly thickened central area marks the position of the seed, and there are two well-defined lateral wings. The broad distal portion of the scale is prolonged into a flat, narrow spine about 4 mm. long . A broad (about 4 mm.), shallow ligule is inserted on the upper surface of the scale a short distance beyond the distal limit of the seed.

(ii) *Cuticular Structure* (Plate 3, Figs. 22-24)

The epidermal cells, which are essentially similar on both surfaces, vary in size and shape according to their position on the scale.

Distal region.—The cells of this area, including those of the terminal spine, are smaller and more regular than those of other regions, being frequently square to quadrangular. A tendency to form rows is evident, especially in and near the spine. Stomata occur on both surfaces. They are arranged in rows that become more clearly defined towards the spine. It is not known how far the stomatal rows extend, as no preparation has shown the complete length of the spine.

Epidermis covering the seed (Plate 3, Fig. 23).—The epidermal cells of this region are always longer than broad (65-166 × 13-27 μ), and those situated towards the periphery are somewhat larger than those of the centre. They are irregularly shaped and variously oriented. Occasionally, groups of similarly oriented cells lie either obliquely or at right angles to neighbouring groups, but the formation of such groups of "sister cells" (Kendall 1949) is not a conspicuous feature of the scales of this species. Stomata are absent from both surfaces.

Wings (Plate 3, Fig. 24).—The epidermal cells are similar to, but somewhat larger than, those covering the seed. Stomata are absent.

Ligule (Plate 3, Fig. 22).—Most of the cells are irregular in shape, but some degree of elongation and parallelism is evident in the centre and at the base near the margins. The cell walls are pitted, straight or curved, and thicker at the apex. Stomata are absent.

Recent Species

The attribution of the fossil cone-scales to a species of *Araucaria* is supported by the presence of an embedded seed, a ligule, and a prominent terminal spine. The section Eutacta is indicated by the lateral wings, the broadly cuneate shape of the scale, and its general cuticular characters.

The external form of the cone-scales of the section Eutacta is very uniform, and this uniformity extends to the cuticle. Cuticular characters that appear to be constant are:

The occurrence of amphicyclic stomata, which tend to form short rows, on both surfaces of the distal region.

The occurrence of epidermal cells oriented around the encircling cells of many of the stomata of the distal region.

The absence of stomata from the upper epidermis covering the seed and ligule.

The presence of smaller and usually more regularly arranged epidermal cells in the distal region.

The narrow-elongate form of the epidermal cells of the proximal region (the type of cell present in three living species is shown in Plate 3, Figs. 25-27).

The more or less frequent occurrence of groups of similarly oriented "sister cells" (Plate 3, Fig. 2*b*).

The presence of small unicellular or multicellular denticulations on the margin of the ligule.

Comparison of Araucaria lignitici *with Recent and Fossil Species*

Recent species.—It has not been possible to obtain large numbers of specimens of female cone-scales of living species, and consequently the determination of features likely to be of value in separating them has been, in many cases, incomplete. There have also been practical difficulties in the preparation of cuticular mounts of both recent and fossil species.

The cuticular features that appear to vary between the species are set out in Table 3. From these, and from a study of the external characters, it can be seen that the cone-scales of *A. lignitici* do not exactly correspond with those of any of the living species studied. It is possible that the closest resemblance lies with *A. beccarii* and *A. cunninghamii,* but there is not enough evidence available either to confirm this suggestion or to completely exclude other species.

Fossil species.—There are only two previous records of the female reproductive organs of *Araucaria* in Tertiary deposits of the Southern Hemisphere. In 1883, Mueller described the female cone of *A. johnstonii,* which was found as an impression in the travertine of Geilston Bay, Tasmania. As no individual scales were discovered, it is difficult to compare this fossil with scales of *A. lignitici.* However, if the cone of *A. johnstonii* was even approaching maturity, the scales must have been considerably smaller than those of *A. lignitici.* As, in addition, the terminal spine is either absent or differently shaped in the Tasmanian specimen, there appears to be little reason for regarding the two forms as belonging to one species. It is not possible to confirm this view by reference to the leaves, as both Florin (1940) and Selling (1950) agree that the shoot attributed to *A. johnstonii* does not, in fact, belong to *Araucaria.*

Female cone-scales of *Araucarites ruei,* from the Kerguelen Archipelago, were described and illustrated by Seward and Conway (1934). These scales are somewhat similar to those of *Araucaria lignitici,* although the terminal spine is relatively much longer. As mentioned previously, the leaves are different in the two forms, and it seems probable that the cone-scales also belonged to separate species. The great distance of the Kerguelen Archipelago from Victoria also points to the same conclusion.

(d) Conclusion

It can be seen from the foregoing section that a complete description is now available of the leaves, male cones, and female cone-scales of a Tertiary conifer, the morphological and anatomical features of which agree with those characteristic of living species of the genus *Araucaria,* section Eutacta. While the generic identity of *A. lignitici* is regarded as being proved, its specific affinities remain uncertain. Although its leaves appear to be closest to those of *A. balansae,* they do not greatly differ from those of *A. cunninghamii.* The fact that both the male cones and female cone-scales resemble those of *A. beccarii* and *A. cunninghamii* (which according to Dallimore and Jackson are closely allied) suggests that *A. lignitici* may be related to the recent Australian species *A. cunninghamii.*

TABLE 3

MORPHOLOGICAL AND CUTICULAR CHARACTERS* OF THE FEMALE CONE-SCALES OF RECENT AND FOSSIL SPECIES OF *ARAUCARIA*, SECTION EUTACTA

Species	External Features: Size (cm.) Length	Width	Ligule Longer than Broad†	Epidermis: Terminal Spine: Lower Surface: Cell Walls Thick	Cell Walls Sinuous	Cell Walls Conspicuously Pitted	Terminal Spine: Upper Surface: Cell Walls Thick	Cell Walls Sinuous	Cell Walls Conspicuously Pitted	Covering Seed: Lower Surface: Cell Walls Thick	Cell Walls Sinuous	Cell Walls Conspicuously Pitted	Covering Seed: Upper Surface: Cell Walls Thick‡	Cell Walls Sinuous	Cell Walls Conspicuously Pitted	Sister Cells Frequent§	Length of Cells (μ)
A. balansae	*c.* 2.5	*c.* 3	—	+	—	+	+	—	+	*u*	—	+	*u*	—	+	×	80-390
A. beccarii	*c.* 2	*c.* 1.5	—	—	+	—	—	+	—	—	—	—	—	—	—	—	110-650
A. bernieri	*c.* 3	2.5-2.8	—	+	—	+	+	—	+	*u*	—	+	*u*	—	+	—	40-580
A. biramulata	*c.* 3	*c.* 2.2	—	+	—	+	+	—	+	*u*	—	+	*u*	—	+	—	50-330
A. columnaris	2.5-4.5	2-4.5	+	×	+	—	×	+	—	—	—	—	*u*	—	+	×	80-490
A. cunninghamii	*c.* 2	*c.* 3	—	+	+	—	+	+,—	—	—	—	—	—	—	—	+	40-330
A. excelsa	2-4	2-3	+	×	+,—	+	×	+,—	+	—	—	—	—	—	—	+	50-470
A. humboldtensis	*c.* 2.5	*c.* 2	—	+	+	+	+	+	+	—	×	+	—	—	+	—	110-490
A. muelleri	*c.* 3	*c.* 2	?	+	—	+	+	—	+	—	—	—	—	—	×	—	140-760
A. rulei	*c.* 3	*c.* 2	?	+	—	+	?	?	?	*u*	—	+	*u*	—	+	—	130-560
A. lignitici	1.1-1.8	0.9-1.1	—	+	—	+	×	—	+	—	—	+	×	—	+	—	40-270

* See footnote to Table 1.

† The ligules classed as being longer than broad are not very much longer, and the length and width may even be approximately equal; however, they do appear to be distinct from the remainder, in which the breadth is considerably greater than the length.

‡ The letter *u* in the columns referring to the thickness of the epidermal cell walls indicates that they are thickened unequally (Plate 3, Fig. 27).

§ The sister cells mentioned are discussed in the text.

TABLE 4

MORPHOLOGICAL AND ANATOMICAL CHARACTERS* OF THE LEAVES OF RECENT AND FOSSIL SPECIES OF *AGATHIS*

Species	External Features				Internal Structure						Cuticle																		
											Lower Surface													Upper Surface Epidermal Cells††						
					Sclereids			S.C.‡			Epidermal Cell Walls			Stomata**												Walls			
	Size (cm.)														Polar Diameter (μ)														
	Length	Width	Shape Lanceolate†	Apex Acute	Numerous	In Palisade	In Sp.Mes.	In Palisade	In Sp.Mes.	Fibres Numerous§	Thick	Sinuous	Pitted	In Rows	Aver.	Range	Transverse (%)	Oblique (%)	Longitudinal (%)	Group	In Rows	Elongated and Parallel	Thick	Sinuous	Pitted	Thickened Corners
A. alba (Rumph.) Warb.	5-12.5	1-5	±	±	+	+	+	−	+	−	−	−	+	+	53	39-57	44(30-52)	55(47-69)	1(0-2)	*A*	+	−	−	−	+	−
A. australis Salisb.	1.5-5	1-2	−	−	+	−	+	−	+	+	−		+	+	52	48-53	13(4-19)	78(73-85)	9(4-11)	*B*	+	−	−	×, −	+	−
A. brownii (Lemaire) L. H. Bail.	5-15	2.5-6	±	±	×	+	+	−	+	×	−	−		±	51	44-57	34(30-38)	63(60-67)	3(2-5)	*A*	×	−	+	−	+	−
A. celebica Warb.	*c.* 4.5	*c.* 2.5	+ −	−	−	+	+	−	+	+	−	−	−		52	47-57	49(42-55)	50(44-56)	1(1-2)	*A*	−	−	−	−	+	+
A. flavescens Ridl.	5-6.5	1-2.5	−	−	+	+	+	+		×	−	−	−		50	45-53	40(33-48)	58(50-65)	2(1-3)	*A*	−	−	+	−	+	+
A. lanceolata (Panch.) Warb.	4-12.5	0.5-1.5	±	+	−	+	−	−	+	−	+	−	+	+	53	49-60	7(2-9)	80(78-91)	13(7-17)	*B*	−	−	+	−	+	+
A. microstachya J. F. Bailey and C. T. White	3-5	1.2	+	−	×	−	+	+	+	−	−	−	+	−	57	55-62	15(12-17)	84(82-85)	1(1-3)	*B*	−	−	+	−	+	−
A. moorei (Lindl.) Mast.	6-13	1-4	±	−	−	+	−	−	+	−	−	−	+	+	47	44-52	20(15-26)	76(69-82)	4(2-5)	*B*	+	+	+	●	+	−
A. obtusa (Lindl.) Morrison	12	3	−	−	+	+	+	−	+	−	−	−	+	+	44	40-51	43(33-55)	57(44-67)	0(0-1)	*A*	+	+	−	−	+	−
A. ovata Warb.	7.5-11.5	1.5-3	−	−	+	+	+	+	+	−	+	−	+	×	54	51-59	17(8-28)	70(67-84)	13(1-24)	*B*	−	−	+	−	+	−
A. palmerstoni F.v.M.	5-10	1-2	±	−	+	+	+	−	+	+	−	−	+	±	54	47-57	12(7-19)	75(64-82)	13(5-29)	*B*	−	−	+	−	+	−
A. philippinensis Warb.	7.5	1-2.5	+	±	−	−	+	+	+	+	+	−	+	−	47	44-49	18(13-24)	75(68-80)	7(4-9)	*B*	−	−	+	−	+	−
A. regia Warb.	7.5-9	*c.* 3	+	−	−	−	+	+	+	+	−	−	+	×	56	53-61	33(30-38)	64(61-66)	3(1-4)	*A*	−	−	+	−	+	−
A. vitiensis Benth. and Hook.	5-15	0.5-4.5	−	−	−	−	+	−	+	+	−	−	+	+	51	45-53	34(32-36)	64(63-65)	2(1-3)	*A*	−	−	+	−	+	−
A. parwanensis	?	?	?	?	−	?	+	+	+	+	−	−	+	+	50	44-55	41(32-50)	56(48-62)	3(2-6)	*A*	+	+	−	−	+	−
A. yallournensis	*c.* 9.5	1-2	+	−	−	+		+	+	+	−	−	+	−	60	52-65	8(3-16)	79(67-88)	13(6-24)	*B*	−	−	−	−	+	−

* See footnote to Table 1.

† In deciding whether a leaf should be classed as lanceolate, all variations, such as ovate-lanceolate, oblong-lanceolate, etc., have been included in this term.

‡ S.C. = secretory canals; Sp.Mes. = spongy mesophyll.

§ The fibres referred to in the table are those lying immediately beneath the upper epidermis.

** In all species, at least some of the stomata are in rows, but they are classed as such only when the majority are in long, clearly defined rows. The range given in brackets after the percentage orientation of each species is that of averages taken from separate counts (usually of about 500 stomata) on different leaves and on different parts of one leaf. The group refers to the distribution of the variously oriented stomata as described in the text.

†† The cells of the upper epidermis always show some degree of regularity in their arrangement, but it is only in a few species that the rows are long and clearly defined and the cells almost uniformly elongated in a direction parallel with that of the axis of the leaf. The column headed 'thickened' refers to a thickening which is sometimes present at the junctions of the lateral walls of the epidermal cells.

TABLE 5

MORPHOLOGICAL AND CUTICULAR CHARACTERS* OF THE MALE CONES OF RECENT AND FOSSIL SPECIES OF *AGATHIS*

Species	Cone		Lamina of the Sporophyll†														Pollen‡	
					Marginal Denticulations				Lower Epidermis					Upper Epidermis					
									Cell Walls			Stomata		Cell Walls					
	Length (cm.)	Width (cm.)	Length (mm.)	Width (mm.)	Numerous	Long	Thick-walled	Mucro Present	Sinuous	Thick	Pitted	Present	Numerous	Sinuous	Thick	Pitted	Stomata Present	Average Diameter (μ)	Range (μ)
A. alba	5.0-7.5	1.5-2.5	4-6	5-7	+	+	−	−	−	+	+	+	−	−	+	+	−	54	52-57
A. australis	2.5-4.0	0.5-1.5	*c.* 2.5	2-3	−	−	+	+	−	+	+	+	−	−	+	−	−	55	44-60
A. brownii	2.5-10	*c.* 0.8	*c.* 1.5	*c.* 1	+	−	+	−	−	−	+	+	−	−	−	−	−	50	47-52
A. lanceolata	*c.* 2.5	*c.* 0.8	1-1.5	1-1.5	+	−	+	−	−	+	−	+	×	−	−	−	−	44	39-49
A. microstachya §	0.4-0.6	?	0.7-1.0	*c.* 1.0	−	−	+	−	−	+	+	+	−	−	−	+	−	50	36-60
A. moorei	*c.* 1.5**	*c.* 0.8**	1.5-2.5	1.5-2.0	+	++	+	+	−	−	+	+	×	−	−	+	−	46	39-50
A. obtusa	*c.* 2	*c.* 1	*c.* 2	*c.* 2	×	+,−	+	−	−	+	+	+	×	−	×	+	−	?	?
A. ovata	2.5-6.5	1-2	2.5-3.5	2.5-4.0	×	−	+	−	+,−	+	+	+	−	−	−	+	−	?	?
A. palmerstoni	2-5.5	1.0	1-1.5	1-1.5	−	−	+	−	−	−	+	+	+	−	−	−	−	44	34-49
A. philippinensis	2.5-4.0		1-1.5	*c.* 2	+		−	−	−	+	+	+	×	−	−	+	+	?	?
A. vitiensis	2.5-3.0	*c.* 1	1-2	1-1.5	−	×	+	−	−	−	+	+	×	−	−	+	−	47	39-55
A. yallournensis	*c.* 3.2	*c.* 0.8	1-2	1-2	+	−	−	−	−	−	+	+	+	−	−	−	+	46	34-62

* See footnote to Table 1.

† The figures for the length and breadth of the lamina of the sporophyll have been taken from measurements of herbarium specimens. The mucro refers to the same terminal prominence mentioned in *Araucaria*.

‡ The measurements of pollen grains have been taken from acetolysed material.

§ According to Mr. Lindsay Smith of Brisbane, the length of the male cones of A. *microstachya* considerably exceeds the figures given by Bailey and White (1916). Mature cones of this species kindly forwarded by him for examination are 2 cm. long and 0.6 cm. wide.

** Cones from Sydney, details of which are recorded here, were much larger.

VI. Agathis

Leaves of a species of *Agathis* to be described here, under the name *Agathis yallournensis* were collected from various levels in the Yallourn open cut. They were particularly abundant in the layer from which specimens of *Araucaria lignitici* were obtained. Two female cones of *Agathis* were also found at the latter horizon. Although there is no proof that they belonged to the same species as the leaves, the absence of any evidence indicative of a second species is regarded as sufficient justification for including them in the description of *Agathis yallournensis.*

Fragments of leaves referable to *Agathis* were also collected from a leaf-bed which, in 1947, overlay the brown coal on the north side of the Lucifer Colliery, Bacchus Marsh, Vic. These leaves appear to differ from those of *A. yallournensis* in certain well-defined and apparently constant cuticular features, and there is little doubt that they represent another species. Although the remains are so fragmentary that a complete description of the external form cannot be obtained, the fact that the identification of this species would, even if complete leaves were available, probably depend on cuticular characters, is sufficient reason for naming it specifically. It will be described as *Agathis parwanensis,* the specific name referring to the Parwan valley in which the coal seam lies.

(*a*) *Leaves*

Agathis yallournensis n. sp.

(= *Agathis intermedia* (Ett.) Chapman and Crespin in part)

(i) *External Characters* (Plate 4, Figs. 28-32)

With the exception of the small example shown in Plate 4, Figure 32, which is only 3.5 cm. long, all the leaves have been incomplete. They are narrow- to broad-lanceolate, with an obtuse apex and a petiolar region about 1.5 mm. wide. The greatest length observed has been 9.5 cm. without the proximal region. The width of the lamina ranges from 1 to 2 cm. The margin is entire, flat, and not appreciably thickened. The veins are numerous, parallel, and frequently inconspicuous.

(ii) *Cuticular Structure* (Plate 4, Figs. 33-36)

Lower epidermis.—The stomata are arranged either irregularly or in short longitudinal rows; their orientation is variable, the polar axis of the majority being oblique (Table 4). They are large, their polar diameters ranging from 52 to 65 μ, and amphicyclic, with from four to six small, thick-walled subsidiary cells, one or two of which are frequently polar, and a corresponding number of encircling cells. The outer stomatal chamber is wide and elliptical, square, or polygonal in shape.

The epidermal cells between the stomata vary considerably both in size and shape. They are either square, quadrangular, or irregular in surface view, with their long axes parallel to the length of the leaf. Their lateral walls are straight or slightly curved, about 2.5 μ thick, and inconspicuously pitted. From

one to several rows of narrow, elongated cells without stomata occur at intervals and extend for some distance in a longitudinal direction. Two narrow zones without stomata also occur at the margins.

Upper epidermis.—The cells are from four- to six-sided, or irregular, with straight, pitted lateral walls approximately 3 μ thick. They are sometimes arranged in longitudinal rows. A few stomata may be present.

(iii) *Internal Anatomy* (Plate 5, Figs. 37-39)

The internal structure of the leaves of *A. yallournensis* has been studied from sections prepared by the paraffin method. The mesophyll, especially the central zone, is frequently compressed.

The cells of the upper epidermis are from square to quadrangular in transverse section. Their outer walls are very thick (10.5 μ) and highly cutinized. A cryptocrystalline zone is conspicuous. Beneath the upper epidermis there is a one-layered hypodermis composed of isolated, thick-walled fibres, which are most numerous at the edges of the leaves, and of thinner-walled, more or less square cells. A similar layer, although less strongly developed, is present on the under surface. The lower epidermis is broken at intervals by the stomata. The guard cells are depressed below the surface and overarched by projections of the subsidiary cells, which in turn are partially covered by the encircling cells. The walls of the guard cells, especially the outer ones, are considerably thickened.

The mesophyll is differentiated into palisade and spongy parenchyma. Secretory canals, which alternate with the veins, run through both tissues. They are sharply delimited by a layer of small, rather thick-walled supporting cells; sometimes the remains of the secretory layer itself are also evident.

Large, thick-walled, branched sclereids occur in the spongy mesophyll and, less frequently, in the palisade parenchyma. Occasionally minute crystals can be detected on the arms of the sclereids. In spite of their thickened walls, the sclereids are frequently compressed, so that it is difficult to estimate their frequency; they appear to have been moderately numerous. A few fibres occur above and below the vascular bundles. Transfusion tracheids have not been distinguished with certainty.

Recent Species

The similarity that exists between the external form of the leaves of *A. yallournensis* and those of recent species of *Agathis* is also shown in the cuticle and the internal tissues, and consequently comprehensive comparisons of the fossil with living species have been limited to this genus. The only other coniferous leaves that resemble those of *Agathis* in external form belong to certain species of *Podocarpus,* but according to Florin (1931, 1951) they differ from *Agathis* in having longitudinally oriented stomata and in other cuticular features. A study of 14 recent species of *Agathis* has been made, and the resulting details, together with relevant information from Bertrand (1874), Thomson (1905), Seward and Ford (1906), Florin (1931), and Dallimore and Jackson (1948), are recorded in Table 4.

The following features, which can all be compared with those of the fossil leaves of *Agathis* described in this paper, are common to the leaves of the recent species studied:

They are flat, moderately large, and have numerous fine, parallel veins.

The stomata are amphicyclic. The sunken guard cells are overarched by from four to six subsidiary cells, which are themselves partly covered by a corresponding number of encircling cells. The stomata occur chiefly on the lower surface, but a few may also be present on the upper surface. They are arranged in more or less regular longitudinal rows, separated by bands of elongated epidermal cells that may overlie the veins or be irregularly placed, and are obliquely, transversely, or longitudinally oriented.

The epidermal cells have more or less straight, pitted lateral walls. The outer walls of the epidermal cells are from 10 to 18 μ thick, and heavily cutinized; they contain more or less closely contiguous layers of minute crystals of calcium oxalate.

A hypodermis composed of irregularly shaped, thin-walled cells and a varying proportion of fibres is present on both surfaces, but is less strongly developed on the lower one.

The mesophyll is differentiated into palisade and spongy tissues. Thick-walled, branched sclereids occur in the mesophyll. Their arms are studded with crystals of calcium oxalate.

Secretory canals, which alternate with the vascular bundles, are present in the mesophyll. The vascular bundles are accompanied by thick-walled fibres.

Comparison of Agathis yallournensis *with Recent and Fossil Species*

Recent species.—It is difficult to compare the leaves of *A. yallournensis* with those of any particular living species because of the great similarity in external form throughout the genus, and the fact that the minor variations of internal and cuticular structure are of uncertain constancy within a species. The leaves of *A. yallournensis* were apparently longer than those of *A. australis, A. celebica, A. flavescens,* and *A. philippinensis,* but the variations in shape between the living species are of little value for comparative purposes.

There is little difference in the general appearance of the cuticle of the recent species, and the stomata are of almost uniform size, the average polar diameter of the guard cells ranging only from 44 to 56 μ. However, the orientation of the stomata may prove to be of diagnostic value, as on this basis it appears to be possible to divide the species into the two following groups:

(*A*) Species in which 30 per cent. or more of the stomata are placed transversely.* The number of longitudinal stomata is very small—5 per cent. or less, and frequently only 1 or 2 per cent.—and the number of oblique ones is less than 70 per cent.

(*B*) Species in which less than 30 per cent. of the stomata are transversely placed. The number of longitudinal stomata is variable, but tends to be

* In calculating the percentage of transversely and longitudinally oriented stomata, only those exactly at right angles to, or parallel with, the axis of the leaf are regarded as being transverse or longitudinal; all others are classed as oblique.

greater than in group (*A*), and may be up to 30 per cent. Oblique stomata are usually more frequent than in group (*A*), and may be up to 91 per cent.

Examination of Table 4, which gives the percentages of variously oriented stomata in all the living species examined, shows that there is a gradation between species such as *A. celebica,* which have a very high proportion of transversely placed stomata, and those such as *A. lanceolata,* with a very low one. The percentage (30) taken as the dividing line between groups (*A*) and (*B*), is therefore purely arbitrary, and in some cases it is even difficult to determine, with certainty, the group into which a given species should be placed. However, those species with either very low or very high proportions of transversely placed stomata do appear to be clearly and constantly distinct.

Agathis yallournensis belongs to group (*B*) and is thus similar to *A. australis, A. lanceolata, A. moorei, A palmerstoni,* and *A. philippinensis* as regards stomatal orientation. As the leaves of *A. australis* and *A. philippinensis* are smaller than those of *A. yallournensis,* the fossil leaves appear to be more like those of *A. lanceolata, A. moorei,* and *A. palmerstoni.* A consideration of the characters set out in Table 4 suggests that, of these three species, *A. palmerstoni* is the one most similar to *A. yallournensis.* However, this suggestion is only tentative, although the presence of *A. palmerstoni* in Australia at the present time makes this view not unreasonable.

Fossil species.—The only Australian Tertiary fossil leaves previously referred to *Agathis* are those of *A. intermedia* (Ett.) Chapman and Crespin, and *Dammara podozamioides* Ett., now to be called *Agathis podozamioides.* These leaves were first discovered as impressions in Tertiary mudstones from Vegetable Creek, New South Wales, and were described by Ettingshausen (1888). Deane (1925) attributed to *A. intermedia* certain leaf fragments from the Morwell brown coal mine, now known as the Yallourn North open cut, and Chapman and Crespin (1934) recorded *A.* cf. *intermedia* from Miocene beds at Cape Riche, Western Australia.

As far as external features are concerned, the leaves of *A. yallournensis* appear to be somewhat different from both *A. intermedia* and *A. podozamioides* as they were originally described by Ettingshausen. The petiole of *A. podozamioides* is considerably wider than those of the leaves from Victoria, and the leaves of *A. intermedia* appear to be relatively wider and to taper more sharply towards the apex. Perhaps the closer resemblance lies with *A. intermedia,* but the differences that exist, and the fact that no information is available regarding the leaf structure of that species, appear to justify the creation of a new species.

The leaves referred by Deane to *A. intermedia* are regarded as being identical with those of *A. yallournensis.* Fragments of cuticle removed from one of Deane's (1925, Fig. 12) specimens agree in all features with the cuticles from *A. yallournensis.*

The record of *Agathis* by Chapman and Crespin referred to above, is open to considerable doubt. The specimen on which these authors based their

determination has been available for re-examination, and, since it was not figured by them, is illustrated in Plate 5, Figure 44. The fossil is only a portion of a larger impression that apparently lay obliquely in the stone. Owing to its fragmentary nature, only the left-hand margin is intact, and a true estimate of its original shape cannot be formed. The surface of the impression is covered by a light brown film of mineral, and is distinctly marked by regularly arranged, longitudinal ridges separated by a corresponding number of narrow grooves, of which there are 12 in the widest part. While Chapman and Crespin's identification as *Agathis* cf. *intermedia* may be partially or wholly correct, the specimen does not seem to be adequate for a generic determination. Much clearer evidence than it provides is necessary before *Agathis* can be regarded as a component of the Tertiary flora of Western Australia. It is not possible to compare this very incomplete specimen with *A. yallournensis.*

Agathis parwanensis n. sp.

(i) *External Characters* (Plate 6, Fig. 45)

The example figured is the best of a small collection of this type. The leaf fragment is 2.8 cm. long, and in that length widens gradually from 0.4 to 0.9 cm. Its surface is marked by 12 parallel veins, and its margin is entire. As none of the remaining specimens exceeds 1 cm. in width, it is probable that the leaf of this species was a rather narrow one.

(ii) *Cuticular Structure* (Plate 6, Figs. 46, 47)

Lower epidermis.—The leaves are amphistomatic. The stomata are rather regularly arranged in longitudinal rows that extend for varying distances, the rows being separated by longitudinally elongated epidermal cells. Associated with the stomata are four, rarely five or six, subsidiary cells, two of which are frequently polar, and an equal number of encircling cells. Usually each stomatal group has its full complement of encircling cells, but sometimes two groups have an encircling cell in common, and in a few instances subsidiary cells of adjacent groups have been observed to abut on one another. The average polar diameter of the guard cells is 50 μ and the range from 44 to 55 μ. Their orientation is variable, but as many as 50 per cent. have been observed to be transversely oriented.

The epidermal cells are square, quadrangular, or somewhat irregular in shape, the long axis frequently lying in a longitudinal direction. The lateral walls are straight or curved, about 2.5 μ thick, and rather strongly pitted.

Upper epidermis.—The epidermal cells, which are usually square to quadrangular in shape, tend to be arranged in longitudinal rows. Their lateral walls are straight, about 2.5 μ thick, and fairly strongly pitted. Stomata have not been observed.

(iii) *Internal Anatomy*

It has not been possible to prepare very satisfactory sections of the leaves of *A. parwanensis,* and consequently the following description of the internal

anatomy may require modification if further material is obtained. The state of preservation of the internal tissues is not good, but sufficiently so to indicate structural affinity with leaves of recent species of *Agathis*.

The cells of the upper epidermis are rectangular in cross section, with outer walls from 9 to 11 μ thick. A cryptocrystalline zone is present beneath the cuticle. The hypodermis is composed chiefly of fibres, which form an almost continuous layer. The cells of the lower epidermis are similar to those of the upper surface, but the outer walls are thinner, being only from 4.5 to 5.5 μ thick. Isolated fibres lie beneath the lower epidermis. It has not been possible to observe the exact nature of the subsidiary and encircling cells of the stomatal apparatus, but the guard cells can be seen to be thick-walled and deeply sunken. The outer walls are particularly thick.

The mesophyll is differentiated into spongy parenchyma and a palisade layer that is two cells thick. Secretory canals are present, but they appear to have become partially disintegrated and, unless some contents are preserved, are considerably compressed. They occur in both the palisade and spongy parenchyma. A few indistinct cell remains have been interpreted as sclereids.

The vascular tissues are very much compressed, and hence the details of their structure are obscure. Fibres may have been associated with the bundles, but they cannot be recognized with certainty.

Comparison of Agathis parwanensis *with Recent and Fossil Species*

Recent species.—The incompleteness of the specimens available precludes satisfactory comparison with recent species on the basis of their external features.

In having a stomatal orientation of group (*A*), leaves of *A. parwanensis* resemble those of *A. alba, A. brownii, A. celebica, A. flavescens, A. obtusa, A. regia,* and *A. vitiensis.* When other cuticular and anatomical features are taken into consideration, the closer agreement between *A. parwanensis, A. alba,* and *A. brownii* becomes evident. However, the meaning of this apparent resemblance is rather uncertain, particularly as the leaves of both living species are usually much wider than any so far recorded for *A. parwanensis.* It is perhaps of interest to note in this connection that *A. brownii* occurs in southern Queensland.

Fossil species.—It is impossible to compare *A. parwanensis* with either of the previously recorded Australian Tertiary species of *Agathis,* as the descriptions of these were based on external form alone.

A. parwanensis differs from *A. yallournensis* as regards stomatal orientation, stomatal size, the arrangement of the epidermal cells of both surfaces, and the relative abundance of hypodermal fibres (Table 4). There seems to be little doubt that the leaves from Bacchus Marsh and Yallourn represent two distinct species, but it is unfortunate that the complete leaves and male and female cones of *A. parwanensis* are not available so that the question could be settled with certainty.

(*b*) *Male Cones*

Agathis yallournensis

The specimen illustrated in Plate 5, Fig. 40, is the only one of its kind in the present collection. It was discovered by Mr. H. A. Adams on June 4, 1950, in a sample of leafy coal taken from the Yallourn open cut at a locality the coordinates of which he estimated to be 1900E. and 6800S. and the reduced level 60.

Pollen grains recovered from this fossil show conclusively that it is a male cone of a member of the family Araucariaceae, but do not indicate whether it belonged to a species of *Agathis* or *Araucaria*. Agreement regarding the external form of the cone and the microscopic features of the laminae of the sporophylls, as well as the smaller size of its pollen grains, however, suggest a connection with *Agathis* rather than *Araucaria*. The occurrence of leaf fragments of *Agathis yallournensis* on the same coal sample is additional evidence supporting such a relationship. As *A. yallournensis* is the only representative of the genus as yet recognized at Yallourn, it seems reasonable that the cone under consideration should be specifically associated with the leaves of this type.

(i) *External Characters* (Plate 5, Fig. 40)

The specimen consists of a short length of a woody axis 3 mm. wide and a terminal cone. The cone is cylindrical, with an obtuse apex, and is 0.8 cm. broad at its widest part and 3.2 cm. long. It contains a large number of small sporophylls arranged in a close spiral. The laminae of the sporophylls are small, approximately 1.5 × 1.3 mm., and are thick and roughly oval in shape, those towards the base being slightly larger and more hemispherical. Bracts are not indicated.

(ii) *Cuticular Structure of the Lamina of the Sporophyll* (Plate 5, Fig. 41)

Lower epidermis.—The epidermal cells are irregular in shape and arrangement, and have straight or curved, inconspicuously pitted lateral walls about 2.5 μ thick. Stomata of araucarian type are relatively numerous and are scattered over the whole surface.

Upper epidermis.—The cells tend to be elongated in a longitudinal direction and to be arranged in rows. The cell walls are thinner than those of the lower surface, straight or curved, and unpitted. Stomata occur infrequently.

Margin.—The margin is even, but many of the marginal cells are produced into blunt, thin-walled denticulations.

(iii) *Pollen Grains* (Plate 5, Figs. 42, 43)

Pollen grains have been recovered in abundance from the cone of *A. yallournensis*. They are usually flattened and frequently crumpled and fragmentary, but in favourable examples the spherical form is discernible. The pollen grains are non-aperturate and very variable in size. The average diameter of 72 acetolysed grains was 46 μ and their range from 34 to 62 μ. The exine is

two-layered and approximately 2 μ thick. The sexine is composed of small, rather closely arranged granules, each of which terminates in a minute spine.

Recent Species

In some instances, it is rather difficult to distinguish between the male cones of recent species of *Agathis* and those of *Araucaria*. The cones of *Agathis* are usually smaller than those of *Araucaria,* but the measurements of a few species may overlap. However, the laminae of the sporophylls of the two genera appear to be morphologically and structurally dissimilar in some respects. The laminae of *Agathis* are oval to hemispherical in shape and the cells of the lower epidermis are irregularly arranged; those of *Araucaria,* on the other hand, are more frequently rhomboidal, with acute apices, and the cells of the lower epidermis are somewhat elongated and regularly arranged. It has been the recognition of similar differences in the fossil cones from Yallourn that has led to the reference of one of them to *Agathis* and the remainder to *Araucaria.*

In other respects, both the external form of the male cone and the structure of the lamina of the sporophyll of *Agathis* are similar to those of *Araucaria,* which were discussed earlier in this paper.

The pollen grains of six species of *Agathis* have been examined. All conform to the type described for *Araucaria* (see Section V(*b*) (iv)) but the average diameters have been consistently smaller. They range from 40 to 56 μ, whereas those of *Araucaria* range from 59 to 81 μ.

Comparison of Agathis yallournensis *with Recent and Fossil Species*

Recent species.—The male cone of *A. yallournensis* agrees with the general morphological and structural features of those of the genus *Agathis,* but does not appear to be identical with the cones of any of the living species studied.

As shown in Table 5, the size and shape of the cone and of the lamina of the sporophyll of *A. yallournensis* resemble those of *A. brownii* and *A. palmerstoni* most closely, and this resemblance is also evident in the cuticular features of the lamina.

Fossil species.—There are no previous records of the male cones of Tertiary species of *Agathis* in Australia.

(c) Female Cones

Agathis yallournensis

The two specimens of the female cone, here associated with *Agathis yallournensis,* were found at the third level of the Yallourn open cut in the bed that included remains of both *Araucaria lignitici* and *Agathis yallournensis.* The general features of the cone and the occurrence of stomata of araucarian type in the epidermis of the cone-scales suggest that it belonged to a species of the family Araucariaceae. More detailed comparisons of both macroscopic and cuticular characters indicate that its affinity is with *Agathis* rather than with *Araucaria.*

(i) *External Characters* (Plate 6, Figs. 48-52)

Both cones appear to be immature and to be laterally compressed. Each has a roughly circular outline and it seems probable that the original cones had a spherical form. The smaller of the two, shown in Plate 6, Figures 48-51, measures 1.6 cm. across, the larger 2 × 2 cm. Both cones are alike, but since the smaller one is more favourably exposed it has been selected as the type specimen.

The cone is composed of a number of individual cone-scales which are spirally inserted on a rather slender axis (2 mm. wide) and imbricately arranged. In the portion of the specimen that is transversely exposed and can be viewed from beneath, the outlines of several entire sporophylls are evident (Plate 6, Fig. 50). Each consists of a broad, sub-acute, somewhat reflexed distal expansion and a proximal portion with straight sides, which narrow considerably towards the axis of the cone. The cone-scales are approximately 7 mm. long and in their widest part 7-9 mm. across. Because of the unsatisfactory state of preservation of the proximal seed-bearing portion of the scale it has not been possible to remove a complete scale for the description of its upper surface. The distal margin of the cone-scale is crenulate. The under surface of the distal expansion is finely ridged.

(ii) *Cuticular Structure of Distal Portion of a Cone-Scale* (Plate 6, Figs. 53, 54)

Lower epidermis.—The cells are square, quadrangular, or irregular, with the long axis parallel to the length of the scale, and tend to be arranged in rows. The cell walls are about 3-4 μ thick and very strongly pitted. Stomata are numerous, becoming sparser towards the distal margin.

Upper epidermis.—The cells are larger than those of the lower epidermis. They are mostly quadrangular, with the long axis parallel to the length of the scale, and rather regularly arranged. Their lateral walls are thin (about 2.5 μ) and very strongly pitted. Stomata are absent.

Margin.—Most of the cells at the distal margin of the cone-scale are prolonged into blunt, unicellular denticulations similar to those present in the male sporophylls of both *Agathis* and *Araucaria.*

Recent Species

The female cones of members of the genus *Agathis* are roughly spherical or ellipsoidal in shape and are composed of numerous spirally arranged, imbricate cone-scales. These scales, the broad, thick, distal regions of which are reflexed in relation to the proximal portions, are without the lateral wings, terminal spine, ligule, and embedded seed characteristic of *Araucaria,* section Eutacta.

It is not possible to consider the cuticular features of the cone-scale as a whole, because the epidermis of the proximal portion is so lightly cutinized that it is destroyed by "macerating" fluids. However, this portion of the scale is not important for present comparative purposes since the same area is, probably for a similar reason, badly preserved in the cone of *Agathis yallournensis.*

The cuticle removed from the distal region of the cone-scales of the species examined (*A. australis, A. brownii, A. lanceolata, A. moorei, A. ovata, A. palmerstoni, A. philippinensis,* and *A. vitiensis*) is broadly triangular in shape; owing to an unequal degree of cutinization the portion of it derived from the lower surface is always longer than that from the upper surface. The margin is minutely crenulate or, in immature scales at least, has some of its cells produced into small, unicellular denticulations similar to those observed in the fossil cone-scales. The cells of the lower epidermis are irregularly arranged and have thick, straight or curved, unpitted or inconspicuously pitted walls. Numerous stomata are present.

The structure of the cuticle of the upper surface is rather similar to that of the lower surface but the stomata are either sparse or absent and the cells are usually more regularly arranged and have thinner walls.

Comparison of Agathis yallournensis *with Recent and Fossil Species*

Recent species.—The female cones of *A. yallournensis* cannot be reliably compared with those of any particular living species. Their compressed condition and probable immaturity precludes any comparison on the basis of size and shape. They are distinct from cones of all the living species listed above in the conspicuous pitting that characterizes the lateral walls of their epidermal cells.

Fossil species.—Female cones of *Agathis* have not previously been recorded from rocks in the Southern Hemisphere. Impressions of isolated cone-scales of *Agathis* type were mentioned by Ettingshausen (1888, Plate VIII, Fig. 36) and associated by him with leaves of *Agathis intermedia.* The example figured appears to represent a mature cone-scale and is thus not comparable with the cones of *A. yallournensis.*

(*d*) *Conclusion*

A reasonably complete description of an undoubted member of the genus *Agathis* has been obtained from leaves and cones found at Yallourn, Victoria. Because the leaves and male cones of *A. yallournensis* both resemble those of the living Australian species *A. palmerstoni* and the female cone, as far as is known, is not dissimilar, it seems possible that the affinities of the fossil lie with this species.

Leaves of a second species, *Agathis parwanensis,* have been distinguished in a deposit near Bacchus Marsh, Vic. The specimens of this type, however, are too incomplete to allow its closer relationships to be determined.

VII. Fossil Pollen Grains of the Araucariaceae

Large spherical, non-aperturate pollen grains with granular exines have been recovered in small numbers from brown coal, ligneous clays, and mudstones in south-eastern Australia and Tasmania (Fig. 1). These agree in all respects with the pollen grains of recent species of *Araucaria* and *Agathis* and

the fossil pollen grains of *Araucaria lignitici* and *Agathis yallournensis.* They are also indistinguishable from the pollen grains preserved in the ligneous deposit at the Kerguelen Archipelago, upon which the sporomorph *Araucariacites australis* Cookson (1947*b*) was based.

As was mentioned earlier, the pollen grains of *Agathis* are generally smaller than those of *Araucaria,* but the fact that the maximum size in *Agathis* may overlap the minimum size in *Araucaria* precludes the reliable separation of isolated pollen grains on this basis. The pollen grains recovered from the Australian deposits are therefore referred to the sporomorph *Araucariacites australis,* without implying more than a family connection with those from the Kerguelen deposits.

TABLE 6

DIAMETERS OF *ARAUCARIACITES AUSTRALIS* FROM AUSTRALIAN DEPOSITS

Location		Range in Diameter (μ)
N.S.W.		
	Vegetable Creek. Eh.192. Aust. Mus.	34-86
	Bingera. Aust. Mus.	40-73
Vic.		
	Yallourn. 'Pollen' coal, 3rd Level, Open Cut	60-80
	Berwick. Nat. Mus. Vic.	52-83
	Lal Lal. Lig. Clay Bore 55. 238 ft.	44-50
	Bore 51. 398 ft.	37-59
	Bore 60. 189 ft.	35-57
	Anglesea	45-65
	Hamilton	47-65
S.A.		
	Cootabarlow. Bore 1. 493-515 ft.	52-86
	Bore 1. 537-538 ft.	43-53
Tas.		
	Ouse	52-68

Table 6 gives the location of the deposits at which pollen grains of araucarian type have been found, and records the sizes observed.

VIII. DISTRIBUTION OF ARAUCARIA (SECTION EUTACTA) AND AGATHIS IN AUSTRALIA AND TASMANIA

(*a*) *Present Distribution*

(i) *Araucaria* (see McArthur 1949).—*Araucaria cunninghamii* is the only representative of the section Eutacta still existing in Australia. This species extends from the moist mountain forests of New Guinea, where the annual rainfall is in the vicinity of 142 in. and the average temperature for the coldest month 64°F., to the coastal rain forests of Queensland and north-eastern New South Wales. In the latter state *A. cunninghamii* has been recorded from a number of localities on the Northern Tableland (Baker and Smith 1910). The

most southerly of these is Nambucca Heads, at a latitude of 30° 36′S., where the average rainfall is 51.26 in. and the average temperature of the coldest month 54.5°F. The most westerly record in this area for *A. cunninghamii* is near Tenterfield (152° 1′E.) where the average rainfall is 31.78 in. and the average temperature of the coldest month is 54.2°F.

Araucaria excelsa is the only other member of the section that is a native of a subtropical area. At Norfolk Island, however, in spite of its latitude (29° 3′S., 167° 56′E.), tropical conditions prevail; the rainfall is high (53.27 in.), and the average temperature of the coldest month is 60.9°F.

All the remaining species are tropical.

(ii) *Agathis.*—Of the two Australian species, *A. brownii* has a restricted distribution in the coastal scrub of southern Queensland (Francis 1929). Its range is from Tewantin (20° 32′S.), where the annual rainfall is 67.09 in. and the mean temperature of the coldest month 58.8°F., to within 60 miles of Maryborough (25° 32′S.), where the rainfall is 46.05 in. and the average temperature of the coldest month 59.3°F.

Agathis palmerstoni, the northern species, is, according to Swain (1928) "common on the highlands of the Cairns-Ravenshoe tableland at 2,000 to 3,000 feet elevation." In this area the mean temperature of the coldest month is 59.5°F. and the annual rainfall 65.69 in. Swain further remarks that "The Kauri Pines are trees of the regions of 50 to 80 in. annual average rainfall having little or no seasonal drought. The mean temperature of their habitat varies from 59 to 65 deg. F."

The southern limit of the New Zealand kauri, *Agathis australis,* is near Auckland (36° 51′S.) where the annual rainfall is 43.95 in. and the average temperature for the coldest month is 51.7°F.

All the remaining species are tropical.

It is evident from these data that both *Araucaria* and *Agathis* flourish in regions with a relatively high degree of humidity and with at least a moderately warm temperature.

(*b*) *Tertiary Distribution*

The Tertiary records indicate that both genera extended further south than they do at present.

(i) *Araucaria,* Section Eutacta.—The occurrence of shoots of *Araucaria derwentensis* and a female cone of *A. johnstonii* near Hobart shows that the section Eutacta was represented at least as far south as 45° 43′. It has not, as yet, been recorded further north than Uralla (30° 36′S.), the area from which Selling (1950) described *Araucaria fletcheri.* In Victoria, two distinct species have been distinguished, *A. balcombensis,* a large-leaved species from Balcombe Bay, near Melbourne, and *A. lignitici,* the smaller and narrower-leaved species from Yallourn.

(ii) *Agathis*.—The only valid Tertiary records of *Agathis* are *A. intermedia* from beds near Vegetable Creek in north-eastern New South Wales (lat. 29° 24'S.), *A. yallournensis* from Yallourn, and *A. parwanensis* from Bacchus Marsh, both situated in Victoria at approximately 38°S. latitude. The uncertainty regarding the record of *Agathis* from Western Australia has already been referred to.

(iii) *Araucariaceae*.—The recognition of pollen grains of araucarian type in ligneous clays at Cootabarlow, near Lake Frome in South Australia (140°E.), has established a wider westerly limit for the family than now exists. At present neither *Agathis* nor *Araucaria* occur much more than 100 miles from the east coast, whereas on the evidence of pollen grains, over 700 miles must have separated the occurrences of the Araucariaceae in north-eastern New South Wales from those at Cootabarlow.

The recovery of araucarian pollen grains from ligneous clay at Hamilton extends the time range for the family in Victoria to the Early Pliocene period.

The inclusion of *Agathis* and *Araucaria* in the Tertiary flora of south-eastern Australia and Tasmania, as well as the frequent presence on their leaves of the epiphyllous fungus *Asterothyrites ostiolatus* Cookson (1947*a*), is compatible with the view, expressed by palaeontologists and palaeobotanists, that the climate during this period was warmer and more humid than it is at present.

IX. Acknowledgments

The authors wish to acknowledge their indebtedness for material of recent species to Sir Edward Salisbury, Royal Botanic Gardens, Kew; Dr. G. Taylor, British Museum (Natural History); the late Professor J. T. Buchholz; Professor R. Holttum, University of Malaya; Le Chef du Service des Eaux et Forêts, New Caledonia; Mr. J. H. Willis and Mr. P. F. Morris, National Herbarium of Victoria; Mr. R. H. Anderson and Mr. K. Mair, Botanic Gardens, Sydney; the late Mr. C. T. White, Mr. W. D. Francis, and Mr. L. Smith, Botanic Gardens, Brisbane; and Mr. R. Cooper, Auckland Institute and Museum.

Thanks are due also to Dr. D. Thomas, Chief Government Geologist, Victoria; Dr. A. B. Edwards, C.S.I.R.O., Melbourne; Mr. E. D. Gill, National Museum, Melbourne, for information regarding localities; to Mr. H. O. Fletcher, Australian Museum, Sydney, and Mr. J. C. McMath, Geological Survey of Western Australia, for the loan of specimens for comparative purposes; to Mr. J. W. Lillywhite, Commonwealth Meteorological Branch, Melbourne, for climatological data, and to Dr. B. Lundblad, Riksmuseet, Stockholm, for help with literature.

The former general superintendent, Mr. W. Morrison, and the following officers of the State Electricity Commission of Victoria—Mr. G. F. Rusden, Mr. H. W. Lynch, Mr. A. J. H. Adams, and Mr. K. A. Lamin—have generously provided facilities for the collection of material from the open cut at Yallourn.

This work was made possible by considerable financial assistance from the State Electricity Commission of Victoria and the Commonwealth Scientific and Industrial Research Organization.

X. References

Bailey, J. F., and White, C. T. (1916).—Dep. Agric. Stock, Brisbane, Botany Bull. No. 18. 16 pp.

Baker, R. T., and Smith, H. G. (1910).—"A Research on the Pines of Australia." (Dep. Publ. Instruction, N.S.W. Tech. Education Ser. No. 16, 452 pp.)

Bertrand, C. (1874).—*Ann. Sci. Nat.* **5**: 20.

Buchholz, J. T. (1949).—*Bull. Mus. Hist. Nat. Paris* (2) **21**: 279.

Chapman, F., and Crespin, I. (1934).—*J. Roy. Soc. W. Aust.* **20**: 103.

Cookson, I. C. (1946).—*Proc. Linn. Soc. N.S.W.* **71**: 49.

Cookson, I. C. (1947*a*).—*Proc. Linn. Soc. N.S.W.* **72**: 207.

Cookson, I. C. (1947*b*).—*Rep. Brit., Aust., N.Z. Antarctic Res. Exped.* A **2**: 127.

Cookson, I. C. (1950).—*Aust. J. Sci. Res.* B **3**: 166.

Cranwell, L. (1941).—*N.Z. J. Sci. Tech.* **22**: 1B.

Dallimore, W., and Jackson, A. B. (1948).—"Handbook of Coniferae." (Edward Arnold & Co.: London.)

Deane, H. (1925).—*Rec. Geol. Surv. Vict.* **4**: 492.

Erdtman, G. (1948).—*Geol. Fören Stockh. Förh.* **70**: 265.

von Ettingshausen, C. (1888).—*Mem. Geol. Surv. N.S.W.* Palaeontol. No. 2. 189 pp.

Florin, R. (1931).—*K. Svenska VetenskAkad. Handl.* (3) **10**: 1-588.

Florin, R. (1940).—*K. Svenska VetenskAkad. Handl.* (3) **19** (2): 1-107.

Florin, R. (1951).—*Acta Hort. Berg.* **15** (11): 285.

Francis, W. D. (1929).—"Australian Rain-Forest Trees." 347 pp. (Government Printer: Brisbane.)

Johnston, R. M. (1888).—"A Systematic Account of the Geology of Tasmania." (Hobart.)

Kendall, M. W. (1949).—*Ann. Bot.* **13**: 151.

Krausel, R. (1949).—*Palaeontographica* B **89**: 83.

McArthur, W. M. (1949).—Res. Rep. Geog. Lab. Univ. W. Aust. No. 5.

von Mueller, F. (1883).—"Observations on New Vegetable Fossils of the Auriferous Drifts," 2nd Decade, Melbourne. (Geol. Surv. Vict.)

Selling, O. H. (1950).—*Svensk Bot. Tidskr.* **44**: 551.

Seward, A. C., and Conway, V. (1934).—*Ann. Bot.* **48**: 715.

Seward, A. C., and Ford, S. O. (1906).—*Philos. Trans.* B **198**: 365.

Singleton, F. A. (1941).—*Proc. Roy. Soc. Vict.* **53** (1): 1.

Swain, E. H. F. (1928).—"The Timbers and Forest Products of Queensland." 500 pp. (Government Printer: Brisbane.)

Thibout, E. (1896).—"Recherches sur l'appareil mâle des Gymnospermes." (Lille.)

Thomas, D. E., and Baragwanath, W. (1949).—*Min. Geol. J. Melb.* **3**: 28.

Thomson, R. B. (1905).—*Science* **22**: 88.

Wodehouse, R. (1935).—"Pollen Grains." (New York.)

Explanation of Plates 1-6

The photographs are the work of I. Cookson and all figures are from untouched negatives. The letters N.M.V. before a specimen number refer to the collection of the National Museum of Victoria. Duplicate specimens, where available, will be deposited in the Geological Department, British Museum (Natural History).

Plate 1

Araucaria lignitici n.sp.

Fig. 1.—Portion of a shoot. Natural size. (N.M.V. P.15254.)

Fig. 2.—Portions of two shoots. Natural size. (N.M.V. P. 15265.)

Fig. 3.—Small fragment of a shoot with shorter, broader leaves. x2 (N.M.V. P. 15256.)

Fig. 4.—Portion of a shoot. x1¾. (N.M.V. P. 15255.)
Fig. 5.—Entire cuticle of a leaf opened out to show the distribution of stomata on the upper and lower surfaces. x17.
Fig. 6.—A stoma with its associated subsidiary and encircling cells, in transverse section. x400.
Fig. 7.—Cuticle of upper surface of a leaf. x200.

PLATE 2

Fig. 8.—*Araucaria lignitici.* Portion of a male cone. Natural size. (N.M.V. P. 18266.)
Fig. 9.—*A. lignitici.* The same cone. x3.
Fig. 10.—*A. lignitici.* Portions of another male cone. x2. (N.M.V. P. 15258.)
Fig. 11.—*A. lignitici.* Portions of a male cone. x2½. (N.M.V. P. 15259.)
Fig. 12.—*A. lignitici.* Cuticle of a bract opened out. x15.
Fig. 13.—*A. lignitici.* Lower cuticle of the lamina of a male sporophyll. x40.
Fig. 14.—*A. lignitici.* Pollen grain from a male cone. x500.
Fig. 15.—*A. lignitici.* Another pollen grain from a male cone. x500.
Fig. 16.—*Araucaria columnaris.* An oblique section through the exine of an acetolysed pollen grain. x1220.
Fig. 17.—*A. columnaris.* Surface view of exine at a high focus. x1200.
Fig. 18.—*A. columnaris.* The same area at a low focus. x1200.

PLATE 3

Fig. 19.—*Araucaria lignitici.* A female cone-scale. Natural size. (N.M.V. P. 15261.)
Fig. 20.—*A. lignitici.* Another cone-scale. Natural size. (N.M.V. P. 15262.)
Fig. 21.—*A. lignitici.* A third example showing full length of the spinous process at the distal end of the scale. x3. (N.M.V. P. 15263.)
Fig. 22.—*A. lignitici.* Upper cuticle of distal region of cone-scale and ligule. x12.
Fig. 23.—Upper cuticle from above the seed. x70.
Fig. 24.—Cuticle of the lateral wing. x70.
Fig. 25.—*Araucaria beccarii.* Cuticle of the upper surface above the seed, showing long, narrow epidermal cells with thin, unpitted walls. x70.
Fig. 26.—*A. cunninghamii.* Cuticle of the upper surface above the seed, showing prominent groups of "sister cells." x70.
Fig. 27.—*A. columnaris.* Cuticle of the upper surface above the seed, showing unevenly thickened, strongly pitted cell walls. x140.

PLATE 4

Agathis yallournensis n.sp.

Fig. 28.—An almost complete leaf. Natural size. (N.M.V. P. 15266.)
Fig. 29.—Portion of another leaf. A small globule of resin is seen in transverse section on the right-hand margin of the leaf. Natural size. (N.M.V. P. 15267.)
Fig. 30.—Portion of a wide leaf. Natural size. (N.M.V. P. 15268.)
Fig. 31.—Another leaf showing an obtuse apex. Natural size. (N.M.V. P. 15269.)
Fig. 32.—A small complete leaf. Natural size. (N.M.V. P. 15270.)
Fig. 33.—Cuticle of upper epidermis. x100.
Fig. 34.—Cuticle of lower epidermis. x100.
Fig. 35.—Cells of upper epidermis showing pitted cell walls. x400.
Fig. 36.—Lower epidermis showing two stomatal groups. x400.

PLATE 5

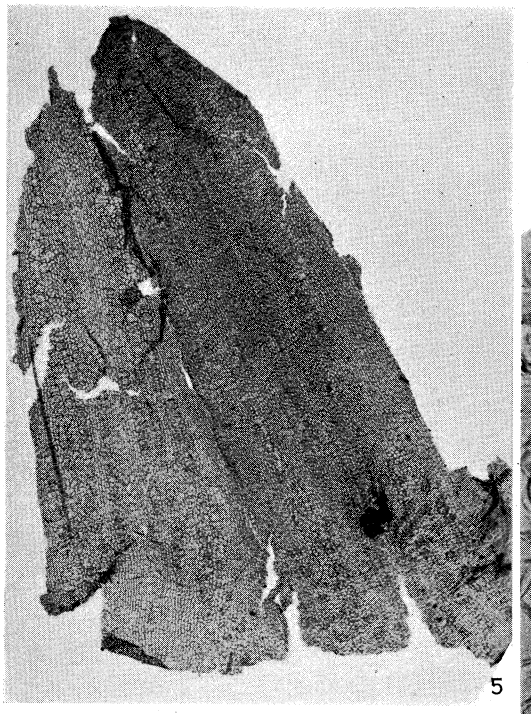
Fig. 37.—*Agathis yallournensis.* Transverse section of a leaf. x120.
Fig. 38.—*A. yallournensis.* Transverse section of a leaf showing a sclereid. x400.


1

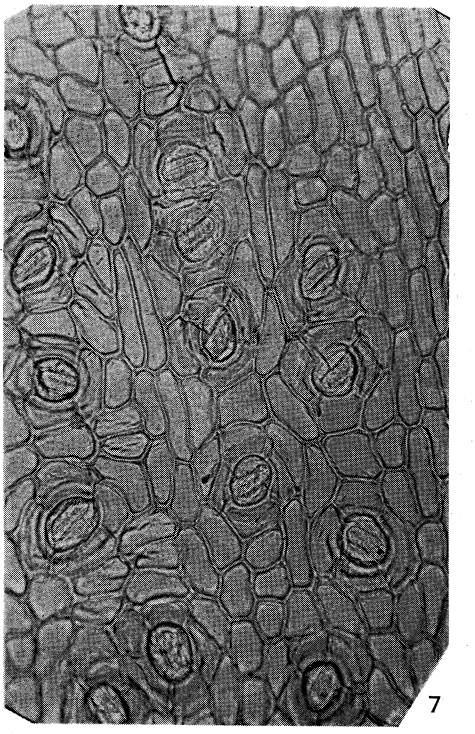

2

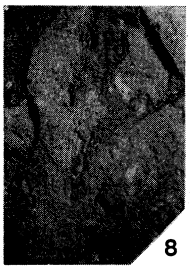

3


4

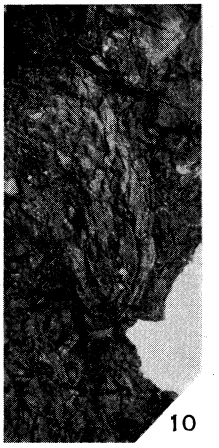

5

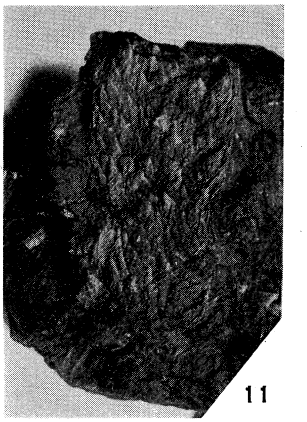

6


7

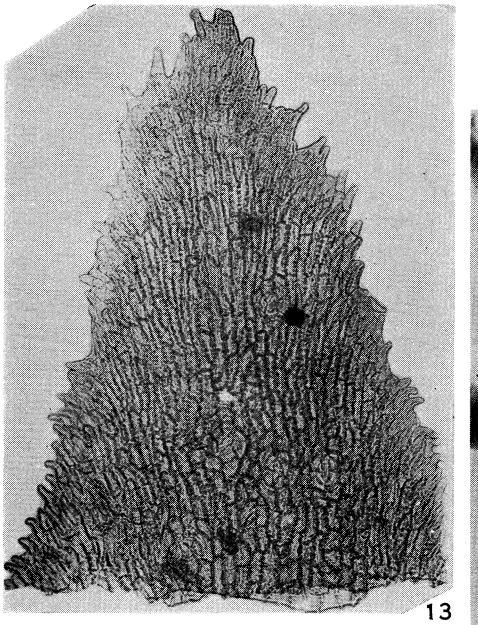

8

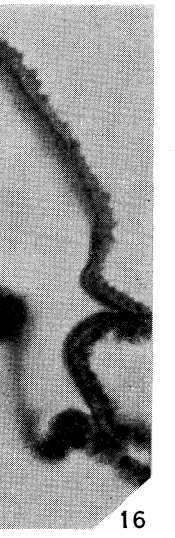

9

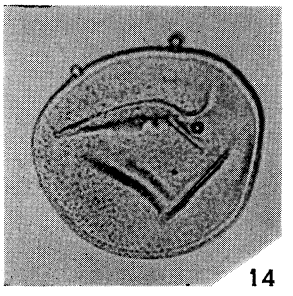

10

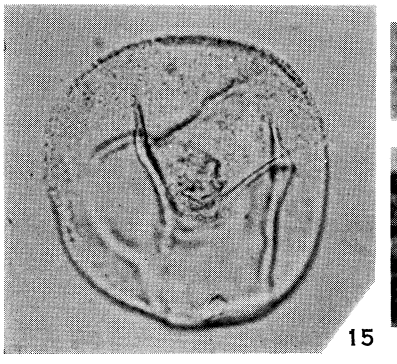

11

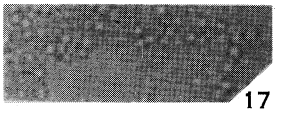

12

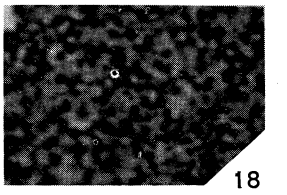

13

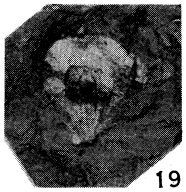

16

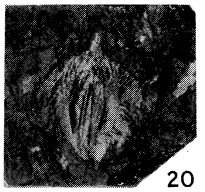

14

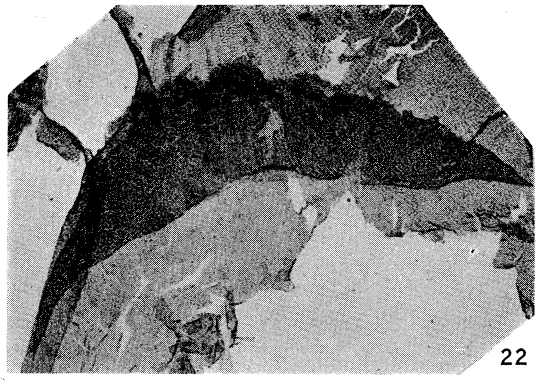

15

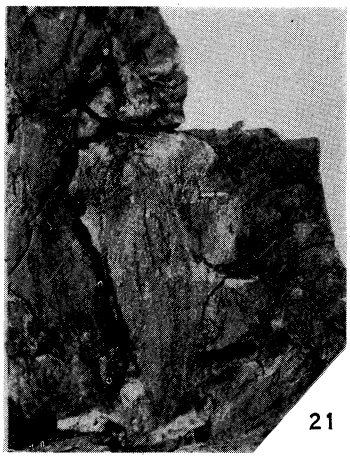

17


18

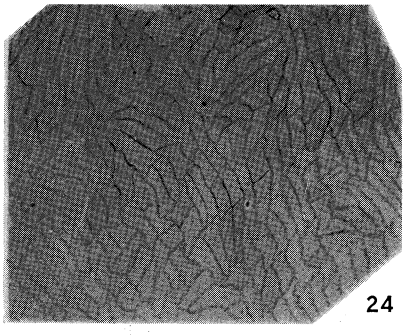

19

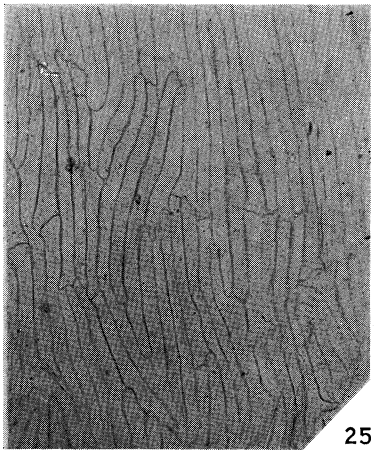

20

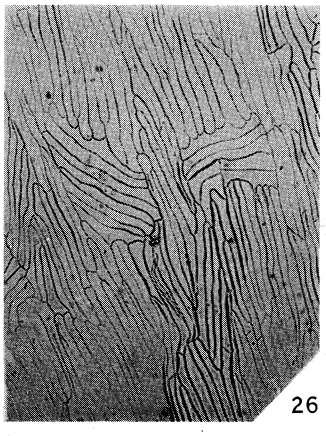

22

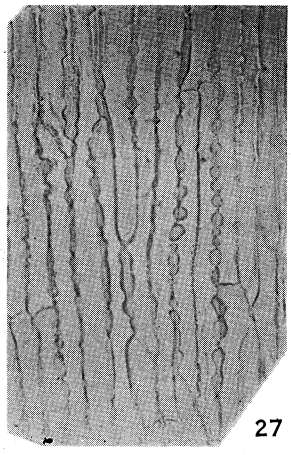

21

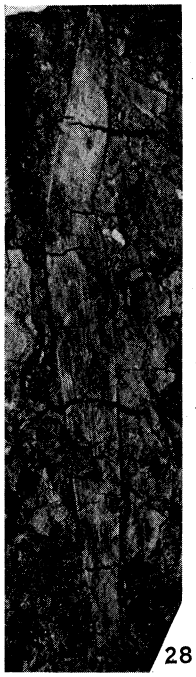

23


24

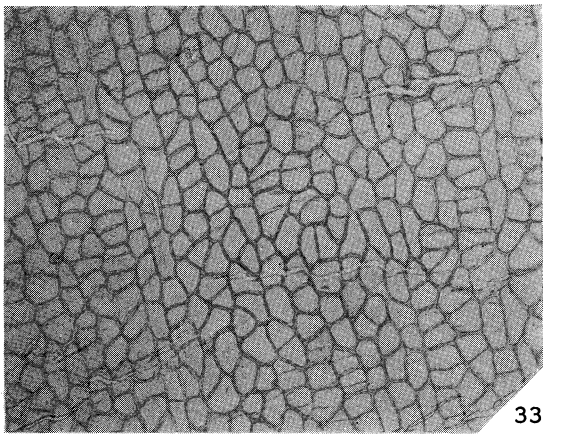

25


26


27


28

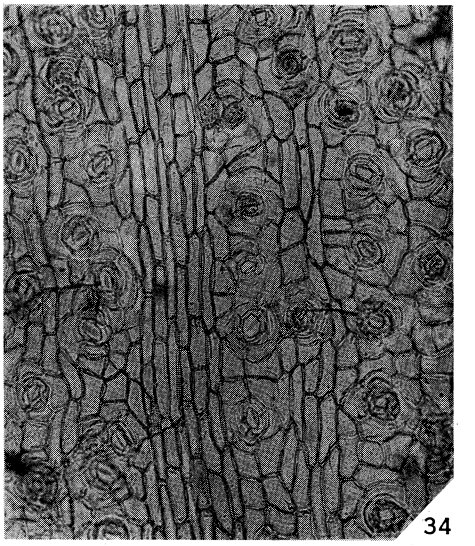

30

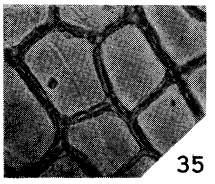

33

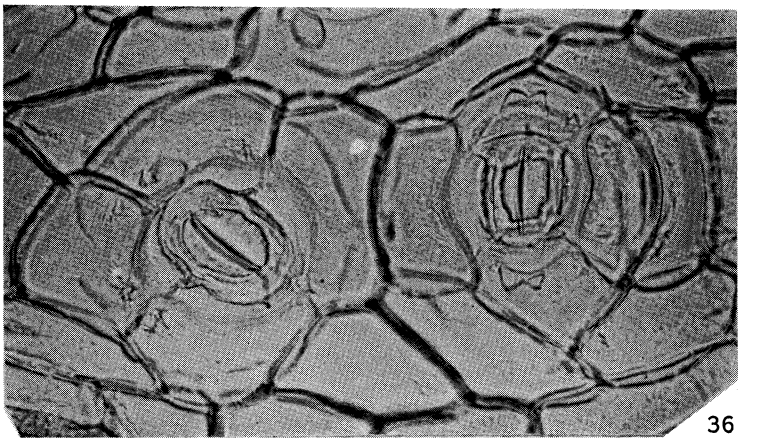

29


31

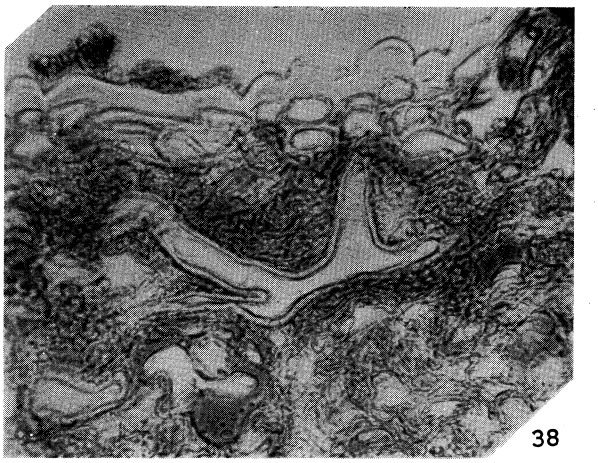

32

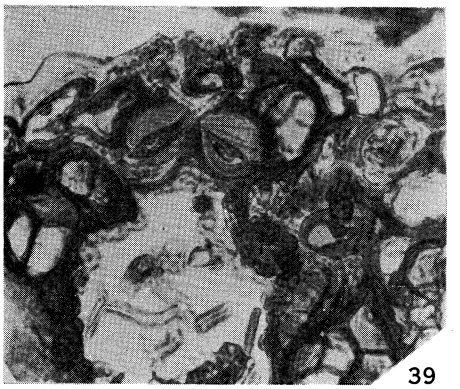

34

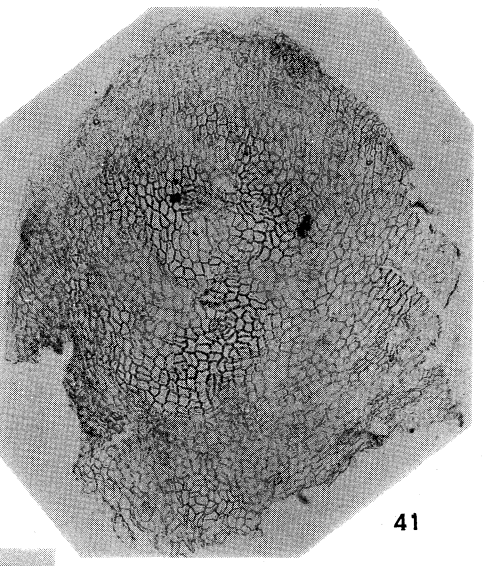

35


36

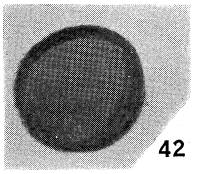

37

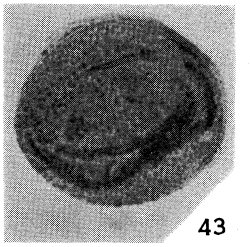

38

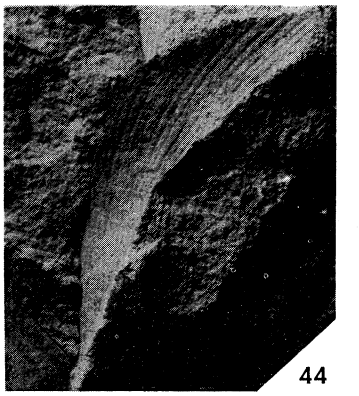

39


41

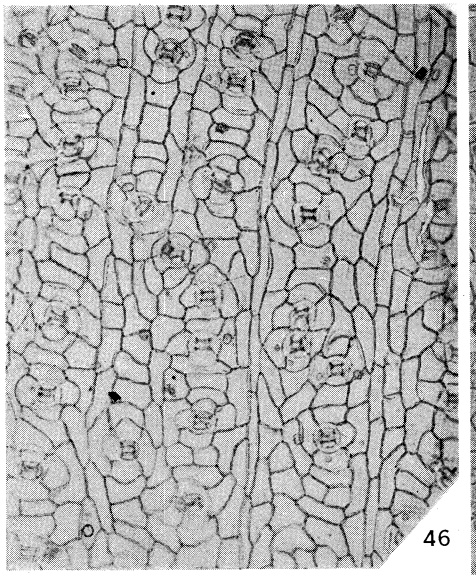

40

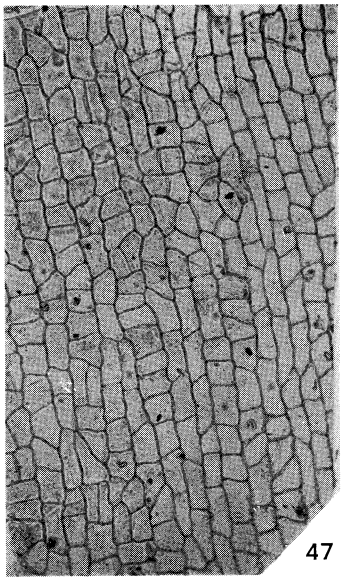

42

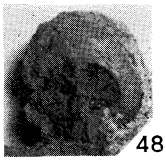

43

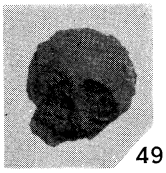

44

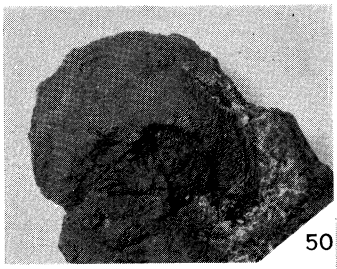

45

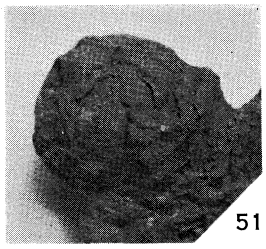

46

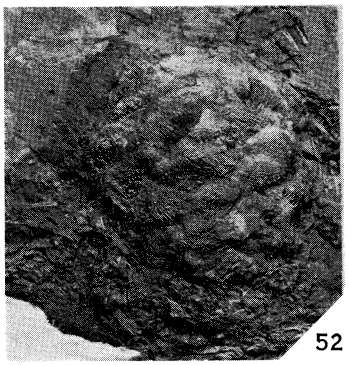

47

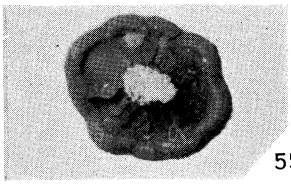

48

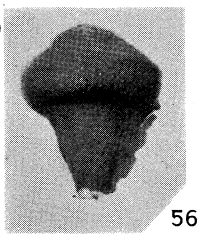

49

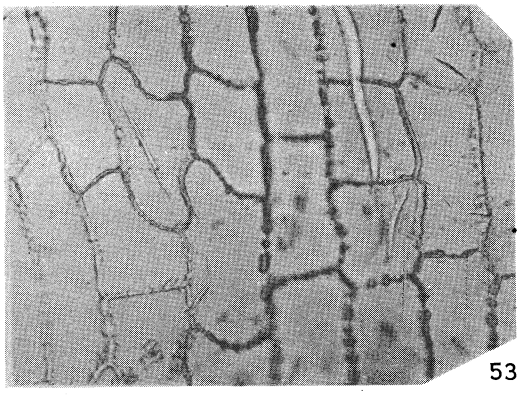

50


51


52


55


56


53

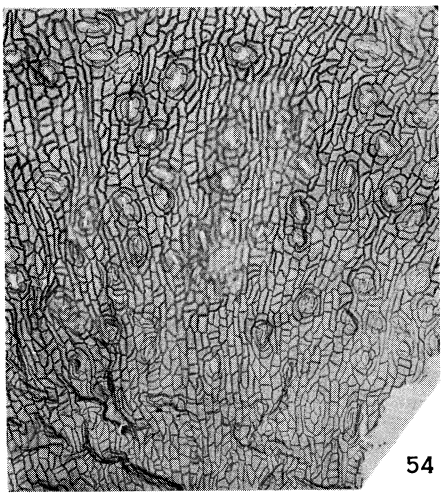

54

Fig. 39.—*A. yallournensis.* Transverse section of a leaf showing a stoma, the thick-walled guard-cells of which are overarched by subsidiary and encircling cells. x400.

Fig. 40.—*A. yallournensis.* A male cone. Natural size. (N.M.V. P. 15271.)

Fig. 41.—*A. yallournensis.* The lamina of a male sporophyll. x45.

Fig. 42.—*A. yallournensis.* A small pollen grain from the male cone shown in Figure 40. x500.

Fig. 43.—*A. yallournensis.* An average-sized pollen grain from the same cone. x500.

Fig. 44.—*Agathis* cf. *intermedia* Ett. Specimen from Cape Riche, Western Australia, identified as such by Chapman and Crespin. x2.

PLATE 6

Fig. 45.—*Agathis parwanensis.* A leaf fragment. Natural size. (N.M.V. P. 15272.)

Fig. 46.—*A. parwanensis.* Cuticle of lower epidermis. x100.

Fig. 47.—*A. parwanensis.* Cuticle of upper epidermis. x100.

Fig. 48.—*Agathis yallournensis.* Immature female cone from below showing the insertion of cone-scales on the axis of the cone. Natural size. (N.M.V. P. 15273.)

Fig. 49.—*A. yallournensis.* The same specimen more fully exposed as the result of the removal of a small piece of coaly matrix from the right-hand side. Slightly less than natural size.

Fig. 50.—*A. yallournensis.* The same view as in Figure 48. x2.

Fig. 51.—*A. yallournensis.* The reverse surface of the same specimen. x2.

Fig. 52.—*A. yallournensis.* Another female cone. x1½.

Fig. 53.—*A. yallournensis.* Upper cuticle of the distal region of a cone-scale. x280.

Fig. 54.—*A. yallournensis.* Lower cuticle of the same region. x70.

Fig. 55.—*A. australis.* Upper portion of young female cone, seen from below.

Fig. 56.—*A. australis.* Under surface of immature female cone-scale.

APPENDIX I

SOURCE OF MATERIAL OF LIVING SPECIES

ARAUCARIA	LEAVES
A. balansae	Colln. J. T. Buchholz, No. 1355. Plaine des Lacs, New Caledonia.
A. beccarii	Herb. Mus. Brit. No. 5749. L. S. Gibbs. Angi Lakes, Dutch NW. New Guinea.
A. bernieri	Colln. J. T. Buchholz, No. 1562. Plaine des Lacs, New Caledonia.
A. biramulata	Colln. J. T. Buchholz, No. 1691. Foret de Mai, Plaine des Lacs, New Caledonia.
A. columnaris	Colln. J. T. Buchholz, No. 1666. Isle of Pines. Nat. Herb. Victoria. New Caledonia. Melbourne Bot. Gard.
A. cunninghamii	Nat. Herb. Victoria. Queensland. Melbourne Bot. Gard. System garden, Bot. Dept., Univ. of Melbourne.
A. excelsa	Colln. J. T. Buchholz, No. 1599. Norfolk I. Melbourne Bot. Gard.
A. humboldtensis	Colln. J. T. Buchholz, No. 1686. Mt. Mou, New Caledonia.
A. intermedia	Kew Herb., No. 1276. Vieillard, New Caledonia.
A. montana	Colln. J. T. Buchholz, No. 1603. Mt. Ouli, N. of Table Mt., New Caledonia.
A. muelleri	Colln. J. T. Buchholz, No. 1207. New Caledonia.

APPENDIX I (*Continued*)

A. rulei	Colln. J. T. Buchholz, No. 1457. Mt. Mou, New Caledonia.
	Melbourne Bot. Gard.
	Kew Herb. Balansa. Kanala, New Caledonia.

MALE CONES

A. balansae	Queensland Herb., No. 2121. C. T. White. det. ver. A. Arb. Baie des Pirogues, New Caledonia.
	Service des Eaux et Forêts, New Caledonia.
A. beccarii	Queensland Herb., No. 11175. L. J. Brass and C. Versteigh. Balim River, Dutch New Guinea.
A. bernieri	Colln. J. T. Buchholz, No. 1562. Plaine des Lacs, New Caledonia.
A. biramulata	Colln. J. T. Buchholz. Foret du Mois de Mai, Plaine des Lacs, New Caledonia.
A. columnaris	Queensland Herb., No. 2290. C. T. White. Noumea (cult.).
	Herb. Brit. Mus., No. 1278. Vieillard. "Ad Tante Novae Caledoniae."
	Colln. J. T. Buchholz. Southern New Caledonia.
	Service des Eaux et Forêts, New Caledonia (pollen only).
A. cunninghamii	Queensland Herb., No. 6647. C. E. Hubbard and C. W. Winders. Magnetic I.
A. excelsa	Queensland Herb., No. 11091. C. T. White. Cleveland, Brisbane.
A. montana	Colln. J. T. Buchholz, No. 1603. Mt. Ouli, N. of Table Mt., New Caledonia.
A. muelleri	Kew Herb., No. 188. M. Balansa. New Caledonia.
A. rulei	Kew Herb., No. 2167. J. G. Veitch. New Caledonia.
	Colln. J. T. Buchholz. Mt. Mou, New Caledonia.

FEMALE CONE-SCALES

A. balansae	Colln. J. T. Buchholz, No. 1608. New Caledonia.
A. beccarii	Herb. Brit. Mus., No. 5749. L. S. Gibbs. Angi Lakes, Dutch NW. New Guinea.
A. bernieri	Colln. J. T. Buchholz. Plaine des Lacs, near Pirogues R., New Caledonia.
A. biramulata	Colln. J. T. Buchholz, No. 1691. Foret de Mai, Plaine des Lacs, New Caledonia.
A. columnaris	Colln. J. T. Buchholz, No. 1666. Isle of Pines.
	Nat. Herb. Victoria. New Caledonia.
	Museum, Bot. Dept., Univ. of Melbourne.
A. cunninghamii	System garden, Bot. Dept., Univ. of Melbourne.
A. excelsa	Museum, Bot. Dept., Univ. of Melbourne.
A. humboldtensis	Colln. J. T. Buchholz, No. 1206. Pic du Rocher, New Caledonia.
A. muelleri	Colln. J. T. Buchholz, No. 1207, New Caledonia.
A. rulei	Colln. J. T. Buchholz, No. 1457. Mt. Mou, New Caledonia.

AGATHIS	LEAVES
A. alba	Nat. Herb. Victoria. Java.
	Colln. R. Holttum. Penang Hill.
A. australis	Herb. Auckland Inst. and Mus., N.Z. L. M. Cranwell. Henderson, near Auckland, N.Z.

APPENDIX I (*Continued*)

A. brownii	Nat. Herb. Victoria. Wide Bay, N. of Gympie, Queensland (type area).
	Melbourne Bot. Gard.
	Sydney Bot. Gard.
	Brisbane Bot. Gard.
A. celebica	Neth. Ind. For. Serv., No. bb 31503. Manado, Posa, Bantjea.
A. flavescens	Colln. R. Holttum. Gunong Tahan.
A. lanceolata	Service des Eaux et Forêts, New Caledonia.
	Nat. Herb. Victoria.
A. microstachya	Queensland Herbarium, Atherton Tableland.
A. moorei	Nat. Herb. Victoria.
	Sydney Bot. Gard.
A. obtusa	Nat. Herb. Victoria.
A. ovata	Nat. Herb. Victoria.
	Colln. J. T. Buchholz, No. 1700. Plaine des Lacs, New Caledonia.
A. palmerstoni	Nat. Herb. Victoria. Mt. Bartlefrère, N. Queensland (type specimen and material from type area).
	Brisbane Herb., Mt. Molloy, N. Queensland; Parish of Barron, N. Queensland; Ravenshoe, N. Queensland; Atherton District, N. Queensland.
A. philippinensis	Neth. Ind. For. Serv., No. bb 28287. Boven Burveang, Pandok Bakarve.
A. regia	Neth. Ind. For. Serv., No. bb 24584. Molukken, Pilowe, Eil Morotai.
A. vitiensis	Nat. Herb. Victoria.

MALE CONES

A. alba	Colln. R. Holttum. Penang Hill.
A. australis	Herb. Auckland Inst. and Mus., N.Z. L. M. Cranwell. Henderson, near Auckland, N.Z.
A. brownii	Brisbane Bot. Gard.
A. lanceolata	Queensland Herb., No. 2064. C. T. White. Mt. Mou, New Caledonia.
	Arnold Arboretum. Baie des Pirogues, New Caledonia.
A. microstachya	Queensland Herb., Atherton Tableland.
A. moorei	Sydney Bot. Gard.
A. obtusa	Queensland Herbarium, No. 282. S. F. Kajewski. Nerndu, Dillon's Bay, Erromanga, New Hebrides.
A. ovata	Queensland Herb., No. 2284. C. T. White. Mountains near Dumbea, New Caledonia.
A. palmerstoni	Queensland Herb., No. 2421. L. J. Brass. Mt. Molloy, N. Queensland.
A. philippinensis	Kew Herb., No. 805. T. E. Borden. Lamas R., Mt. Meriveles, Bataan, Luzon.
A. vitiensis	Kew Herb., No. 15273. D. Degener. Viti Leva.

FEMALE CONE-SCALES

A. australis	Herb. Auckland Inst. and Mus., N.Z.
A. brownii	Melbourne Bot. Gard.
A. lanceolata	Colln. J. T. Buchholz, No. 1604. Near Canala, New Caledonia.
A. moorei	Sydney Bot. Gard.
A. ovata	Colln. J. T. Buchholz, No. 1700. Plaine des Lacs, New Caledonia.
A. palmerstoni	Nat. Herb. Victoria. Mt. Bartlefrère, N. Queensland (type locality).
A. philippinensis	Dist. A. E. Elmer. Philippine I.