A PRELIMINARY ACCOUNT OF THE STRUCTURE OF THE CUTICLES OF *DICROIDIUM* (*THINNFELDIA*) FRONDS FROM THE MESOZOIC OF AUSTRALIA.*

By K. JACOB, *D.Sc., F.N.I., and* (MRS.) CHINNA JACOB, *M.Sc., Ph.D.*, *Geological Survey of India.*

(*Received 18th April, 1950.*)

CONTENTS.

I. INTRODUCTION.

A small collection of *Dicroidium* (*Thinnfeldia*) fronds from the Mesozoic of Australia was kindly lent to one of us in 1946 by Dr. A. B. Walkom, Director, Australian National Museum, Sydney, for a detailed study of their cuticles. All the specimens yielded satisfactory preparations after the usual chemical treatment. This is a preliminary note and briefly deals with the structure of the cuticles of eight species of *Dicroidium* studied by us. A detailed paper supported by photomicrographs will be published shortly.

According to the suggestion already made by Gothan (12) and Antevs (14), we refer these southern forms of *Thinnfeldia* fronds, characteristic of the Glossopteris province, to the genus *Dicroidium*, mainly based on their geographical distribution as was done in the case of *Noeggerathiopsis* (*Cordaites*) and *Gondwanidium* (*Neuropteridium*). Walkom (17, 21) and Du Toit (27), however, prefer to retain the generic name *Thinnfeldia* to include the southern fronds also, while Thomas (33) and Jones and de Jersey (47) suggest *Dicroidium* to accommodate the southern *Thinnfeldia*. The question of nomenclature will be fully discussed in the subsequent paper.

Based on megascopic features the following species may be recognized in the present collection:—

Alethopteroid fronds: pinnate—

(F 35803 *a*) *Dicroidium lancifolium* (Morris).
? *Dicroidium acuta* (Walkom).
(F 41810) *Dicroidium narrabeenensis* (Dun MS.).
(F 17822) *Dicroidium eskensis* (Walkom).
(F 35803 *b*) *Dicroidium* sp. *cf. D. talbragarensis* (Walkom).

* Published by permission of the Director, Geological Survey of India.

Odontopteroid fronds: bipinnate—

(F 408) *Dicroidium feistmanteli* (Johnston).

There are two other bipinnate fronds (Figs. 20, 25) which may be compared with Walkom's *D. feistmanteli* (1925, Pl. XXIV, fig. 7; Pl. XXV, fig. 1). But the cuticles of these two forms (Figs. 21–24; 26, 27) which are totally different from each other do not agree with those of typical *D. feistmanteli* (Figs. 17–19). Hence they are placed in two new species. We have great pleasure in naming the smaller frond (F 16391) shown in Fig. 25 as *D. walkomi* after Dr. A. B. Walkom who kindly made this collection available for our study. The larger frond (F 17832) shown in Fig. 20 is named *D. australis.*

Brief descriptions of the cuticular structure of the southern fronds, *Dicroidium odontopteroides* (Seward, 03 and Gothan, 12), *D. feistmanteli* (Antevs, 13, 14) and *D. lancifolium* (Walkom, 17) have previously appeared. Thomas (33) has made a detailed study of the cuticles of *Dicroidium* fronds as well as those of the male and female fructifications suspected to belong to the same type of plant. The cuticles of some species of the northern *Thinnfeldia* have also been studied by Gothan (12), Antevs (14), and Harris (37).

Jones and de Jersey (47) suggest that *D. odontopteroides, D. acuta, D. lancifolium, D. talbragarensis* and *D. feistmanteli* are probably con-specific. We are unable to agree with their suggestion. On the present evidence available to us from a cuticular study, we are inclined to consider that each one of the above species should be treated as distinct.

II. General Features of *Dicroidium* Cuticle.

The cuticles of all the species of *Dicroidium* examined by us, show appreciable differences from each other in their thickness, arrangement of the cells, their average size, shape cutinization, in the distribution of the stomata per unit area and in the nature of the subsidiary cells.

But they all show a striking similarity with each other in the presence of the stomata in the upper and lower cuticles of the lamina and rachis; and in the size, shape, structure and orientation of the stomata.

Lamina—Upper cuticle:

In the low power, an apparent linear arrangement of the cells parallel to the secondary veins is clearly discernible. In some of the alethopteroid forms where the frequency of stomata is less, this arrangement is more definite. In all the forms the cells over the veins are inclined to be arranged in rows, the stomata being fewer in number in that region.

The cells are polygonal, usually 4–6 sided. They may be straight-walled with sharp angles or rounded corners. Striations due to uneven thickening are observed in the cells of almost all the species, but the nature of these striations varies in the different species. The more thickened areas appear as ridges and the thinner areas as lacunae. The walls of the cells are undulated in some species and in others straight-walled. In addition to faint striations, irregular pitting is noticed in one or two species. The thickness of the cell wall may vary from 3–5μ. In a few species the cell walls are heavily cutinized.

Papillae or indications of them are seen in the cuticles of four species. In some they are raised; in one species they occur as flat structures present in most cells.

In the presence of irregularly oriented stomata both on the upper and lower cuticles and in the general shape, size and structure of the stomata, all the species agree. The distribution of stomatal groups in the areas between the forked veins is fairly noticeable in the alethopteroid fronds. Stomata may also be present over

the veins, but are few in number. In the odontopteroid fronds the number of stomata per unit area is greater than in the alethopteroid fronds. In the former the number per 1 mm. square area varies from 25–40, while in the latter it is only 5–20.

In their essential features, the structure of the stomata is similar in all the forms. They are more or less oval in shape with constrictions towards the poles, 40–45μ long and 16–22μ broad. The length of the pore varies from 16–23μ. The sides of the guard cells facing the lateral subsidiary cells are generally thickened (Fig. 3*d*). They possess characteristic transverse extensions towards the pore (Fig. 3*t*). These transverse extensions and the polar regions of the guard cells (Fig. 3*p*) usually remain unthickened; in *D. feistmanteli* (Fig. 18) the whole of the guard cell is thin. In a few species the stomata are sunken.

Though the subsidiary cells (Florin's *Nebenzellen*, 1931) vary in shape, size and number, they show a general similarity in all the forms. The common features found in one species may be the exception in the other. Stomata with two subsidiary cells occupying the whole dorsal side of the two guard cells are commonly found in the majority of the species. The subsidiary cells may be crescent-shaped, 40–50μ in length and 20–25μ in width in the broadest part (Fig. 8A, *l.s.* 1), or may be angular and as broad as 50μ (Fig. 8A, *l.s.* 2). Occasionally one or both the subsidiary cells may divide transversely (Fig. 3, *l.s.*1–*l.s.* 4), in which case the lateral subsidiary cells may (Fig. 3, *l.s.* 3) or may not extend to the polar regions (Fig. 3, *l.s.* 4). Separate polar subsidiary cells also are not uncommon (Fig. 2, *p.s.*). In *D. feistmanteli* every stoma has highly cutinized subsidiary cells both in the lateral and the polar regions (Figs. 17, 18, *l.s.*, *l.s.* 1, *p.s.*).

Encircling cells (Florin's *Krantzzellen*, 1931) also may be found occasionally for one (Fig. 3, *l.e.*) or both the lateral subsidiary cells. But in *D. feistmanteli* (Figs. 17, 18 *l.e.*, *l.e.* 1) every stoma has highly cutinized encircling cells adjoining the lateral and sometimes the polar subsidiary cells. Both subsidiary cells and encircling cells may be thicker or thinner than the ordinary cells. They also show striations in many of the species.

Midrib—Upper cuticle:

The cells are shorter and more rectangular than those of the lamina; their linear arrangement is more pronounced.

The stomata per unit area may be the same as in the lamina or somewhat less.

Lamina—Lower cuticle:

The lower cuticle does not show any appreciable difference from the upper in some of the species. In others, they are thinner, the cells are slightly larger and the frequency of stomata is less than in the upper.

Rachis—Upper cuticle:

The cuticle thicker than that of the lamina. Cells arranged in definite longitudinal rows, longer in the middle part of the rachis, gradually become shorter and irregular in shape near the attachment of the lamina. The cells are striated in almost all the species. The cell-walls are more cutinized; they may be smooth or crenate irrespective of those of the lamina.

Stomata per unit area less, orientation transverse or irregular; the size may or may not be the same as in those of the lamina; guard cells uniformly thickened all round; subsidiary cells not specialized in the stomata of the middle region; no encircling cells present.

Rachis—Lower cuticle:

The cells are shorter and broader than those of the upper cuticle of the rachis. Rows irregular; cells 4-5 sided, irregular in shape and size, larger than those of the lamina; stomata per unit area more than in the upper cuticle of the rachis; subsidiary cells specialized.

III. Description of Species.

Alethopteroid fronds—Pinnate:

Dicroidium lancifolium **(Morris).** Figs. 1-3

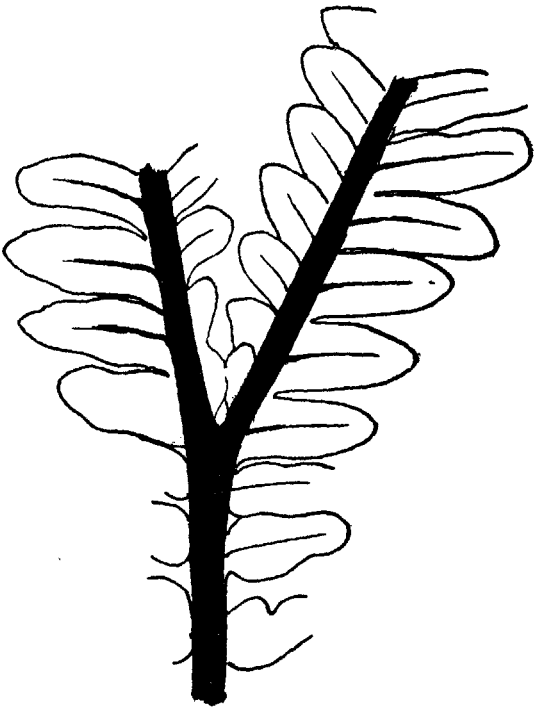


Fig. 1 x ca 1

Dicroidium lancifolium.

Fig. 1. Part of frond, F 35803*a*, × ca. 1.

'Frond divides dichotomously into two linear pinnae which are inclined to one another at an acute angle. Pinnules vary in form with their position; the majority are elongate, tapering, with a rather acute tip, and have a distinct midrib which does not usually persist to the tip of the pinnule. The pinnules on the inner sides of the branches become smaller as the point of branching is approached, and gradually change from elongate acute to a rather ovate semi-circular or more or less rhomboidal shape, without a midrib, the veins arising directly from the rachis. The pinnules on the rachis below the junction may be of either type. The venation is alethopteroid, the secondary veins being given off from the midrib at a rather acute angle. In the basal portion of the pinnules some of the veins come directly from the rachis; the pinnules are decurrent and are connected by a narrow lamina along the rachis.' (Walkom, 17.)

The details of the frond shown in Fig. 1 tally with the description given by Walkom. It can also be compared closely with *D. lancifolium* figured by him in 1925 (Pl. XXVI, Fig. 2).

The cuticle of *D. lancifolium* is very briefly described by Walkom (25). As the details are not indicated either in his description or in the figures, attempt is not made here to compare our cuticle with those figured by Walkom.

Lamina—Upper cuticle (Figs. 2, 3):

Cuticle comparatively thick; general linear arrangement of the cells discernible; over the veins the cells are in rows; cells polygonal, varying in shape and size, faintly striated, striations parallel to the length of the cells. Average cell $65\mu \times 40\mu$, walls straight, 2-3μ thick. Raised papillae observed (Fig. 2, *p.a.*) in a few cells, 10–16μ long.

Stomata 15–18 per 1 mm. square area, irregularly oriented, 40–45μ long, 20–25μ broad. Pore 16–20μ long. Thickened lateral walls of the guard cells measure 7–9μ. In a few stomata their free margin can be seen as in Bennettitalean stomata (Fig. 3, *d*). Transverse extensions present (Fig. 3, *t*). Polar regions not thickened (Fig. 3, *p*). Stomata appear sunken.

Subsidiary cells usually two (Fig. 2), lateral; may be crescent-shaped or angular; 3 or 4 also fairly common (Figs. 2, 3, *l.s.*1–*l.s.*4). Polar subsidiary cells also present in some (Fig. 2, *p.s.*). Encircling cells rare (Fig. 3, *l.e.*). Both subsidiary cells and encircling cells thinner than ordinary cells; striations parallel to the length of the cells.

Rachis—Upper cuticle: Not preserved.

Rachis—Lower cuticle:

Arrangement of cells more or less in rows, rectangular, very thickly cutinized, slightly smaller than those of the lamina; striations present; stomata irregularly oriented, 10–15 per 1 mm. square area.

Locality and Horizon: Triassic shales, Benelong, N.S. Wales.

***Dicroidium acuta* (Walkom).** Figs. 4–6

'Frond divides dichotomously into two linear pinnae; rachis strong. Pinnules some distance apart, long, narrow, tapering gradually to an acute tip, attached by the whole base, decurrent, joined by a narrow lamina along rachis. Venation alethopteroid, midrib prominent and persisting to the tip; secondary veins make an acute angle with the midrib. A few pinnules in the fork between the two branches are modified in shape on account of their position.' (Walkom, 17).

The frond shown in Fig. 4, though badly preserved, reveals the characteristic features of *D. acuta*. The midrib and veins are not clearly discernible.

Lamina—Upper cuticle (Figs. 5, 6):

Cuticle thick; the general linear arrangement of cells not well pronounced. However, the cells over the veins are in rows. They are of varying shape and size, polygonal; average cells $80\mu \times 65\mu$ in size, striated; striations forming short meshes; striations in one cell may or may not be parallel to those in the adjacent cells. Cell wall straight, no undulation, 3-4μ thick; papillae not observed.

Stomata 10–15 per 1 mm. square area, irregularly oriented; average stoma $40\mu \times 20\mu$; pore 18μ in length. Structure of the stomata more or less as in other species. The thickened lateral walls of the guard cells may measure 9μ (Fig. 6, *d*). Transverse extensions (Fig. 6, *t*) may or may not be prominent. Polar regions (Fig. 6, *p*) unthickened. The lateral subsidiary cells are not differentiated from the ordinary cells either in cutinization or in the presence of striations (Fig. 6, *l.s.*); but they are smaller than ordinary cells, the corners more angular than rounded;

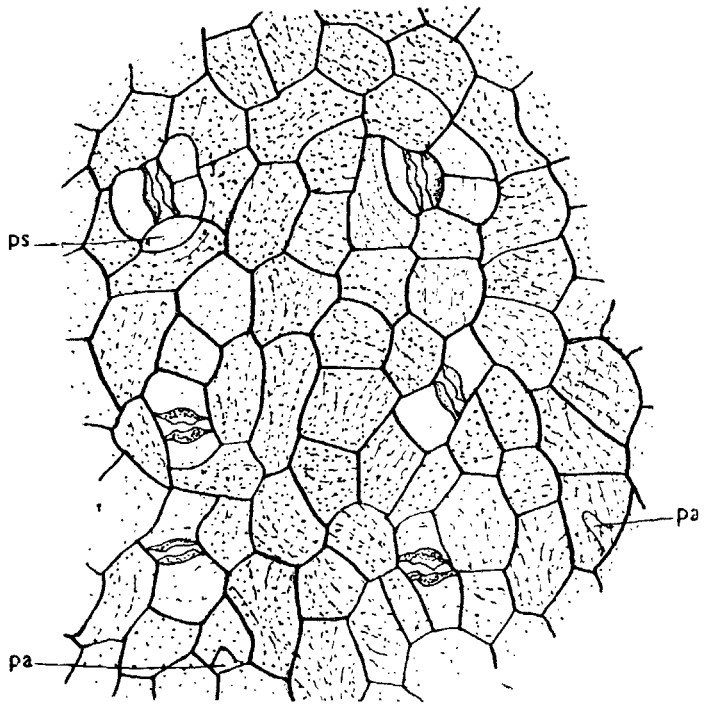


Fig. 2 x 190

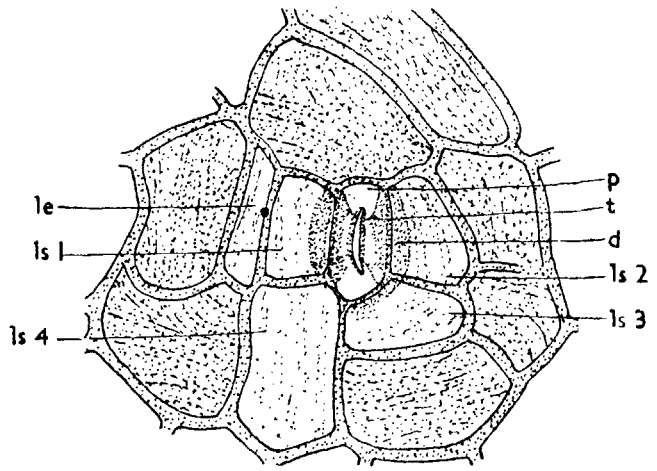
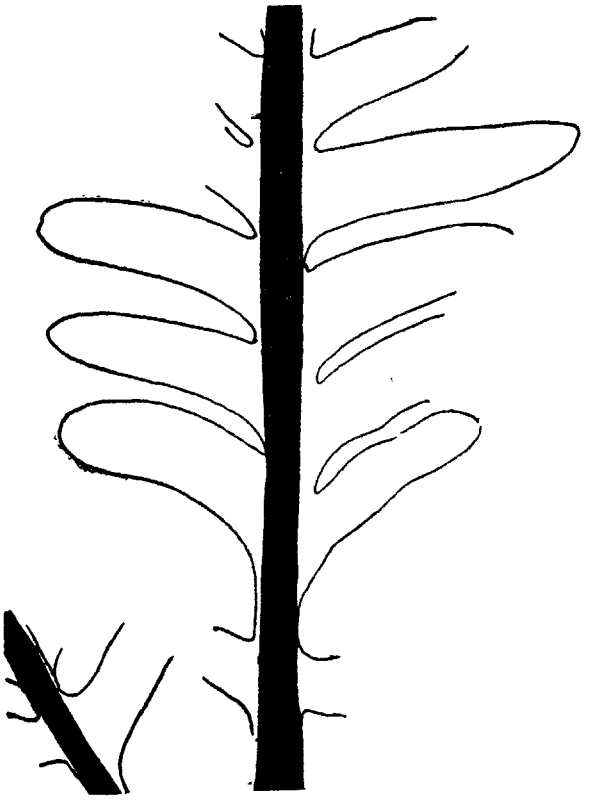


Fig. 3 x 430

Dicroidium lancifolium.

Fig. 2. Upper cuticle of lamina; *pa.* = papilla; *p.s.* = polar subsidiary cell; ×190.
Fig. 3. Single stoma; *d.* = thickened lateral part of guard cell; *p.* = polar region of guard cell; *t.* = transverse extension of cuticle of guard cell; *l.s.* 1–*l.s.* 4 = lateral subsidiary cells; *l.e.* = encircling cell; ×430.



Dicroidium acuta.

FIG. 4. Part of frond, ×ca. 1.

crescent-shaped subsidiary cells are also common; average lateral subsidiary cell 50μ × 25μ in size.

Midrib—Upper cuticle:

Cells over the midrib arranged in regular rows parallel to the midrib, cells rectangular; stomata fewer in number.

Rachis—cuticle: Under study.

Locality and Horizon: ? Triassic shales, ? Narrabeen, near Sydney, N.S. Wales.

***Dicroidium narrabeenensis* (Dun MS.).** Figs. 7–9

'Frond large, pinnate, dichotomous. Rachis strong, pinnules large, elongate, obtusely pointed, opposite or sub-opposite, with margins usually entire, occasionally broadly lobed. In the basal portion of the frond the pinnules are modified, being reniform to triangular and somewhat contracted at the base. The elongate pinnules have a prominent midrib, with secondary veins close, slightly curved, and branching. The basal pinnules have venation of the odontopteroid type.' (Walkom, 25).

Only a part of the frond is shown in Fig. 7. The basal portion is, however, not preserved.

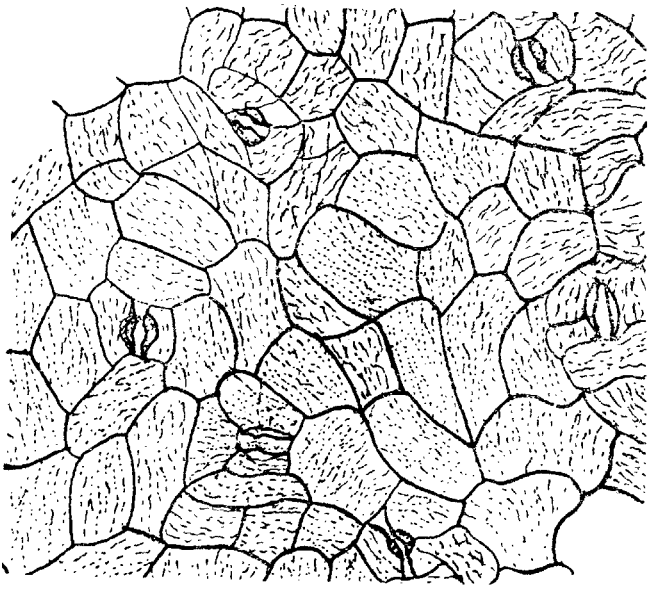


Fig. 5 x 190

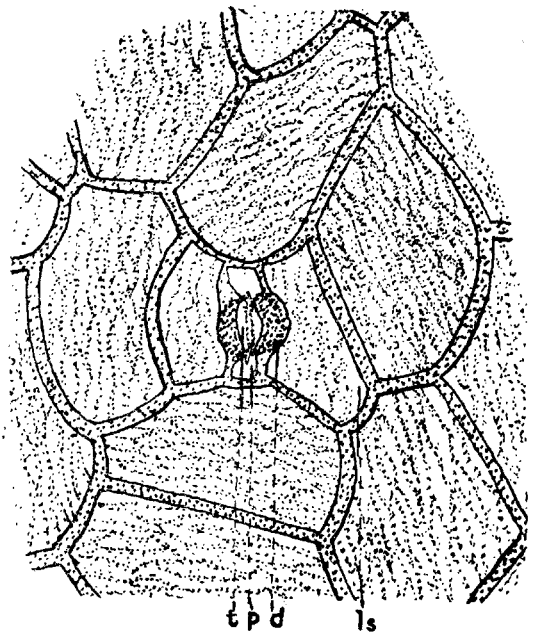


Fig. 6 x 430

Dicroidium acuta.

FIG. 5. Upper cuticle of lamina, ×190.
FIG. 6. Single stoma; *d.* = thickened lateral part of guard cell; *p.* = polar region of guard cell; *t.* = transverse extension; *l.s.* = subsidiary cell; ×430.

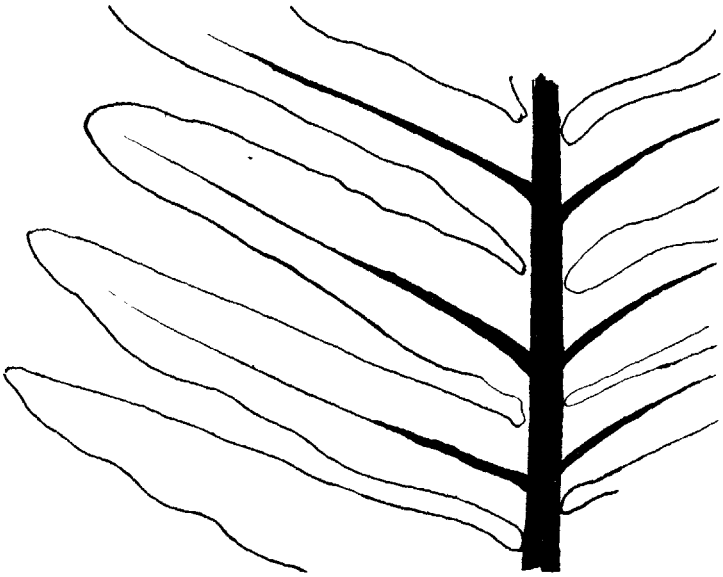


Fig. 7 x ca 1

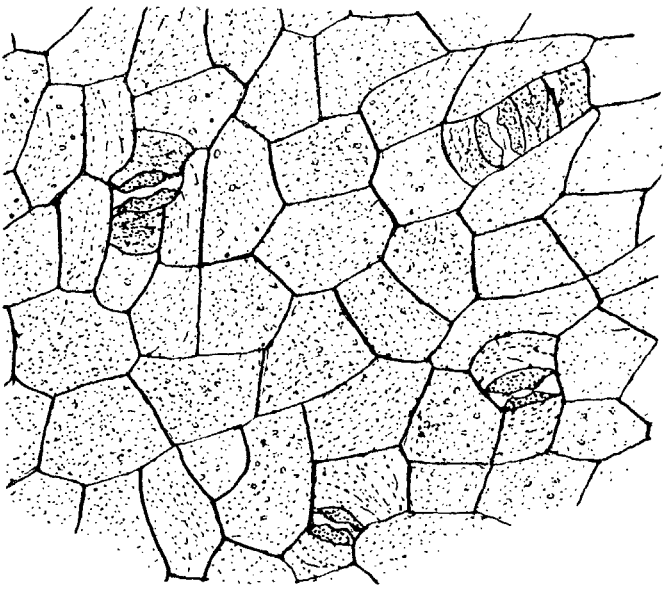


Fig. 8 x 190

Dicroidium narrabeenensis.

FIG. 7. Part of frond, F 41810, × ca. 1.

FIG. 8. Upper cuticle of lamina, ×190.

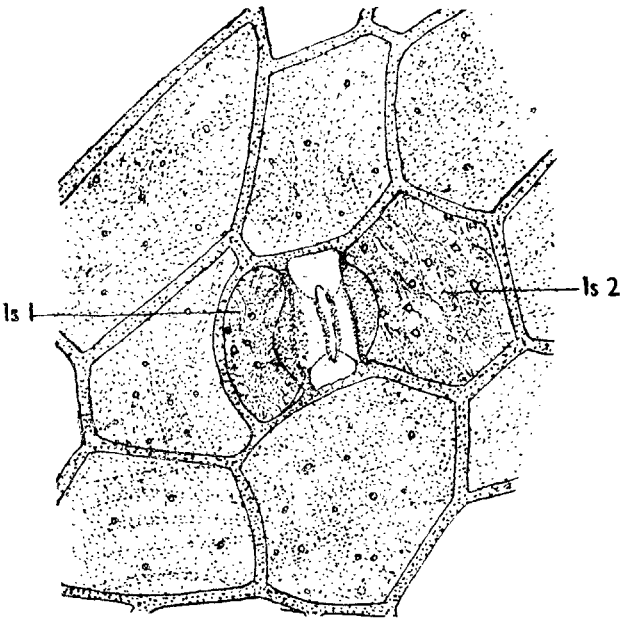


Fig. 8A x 430

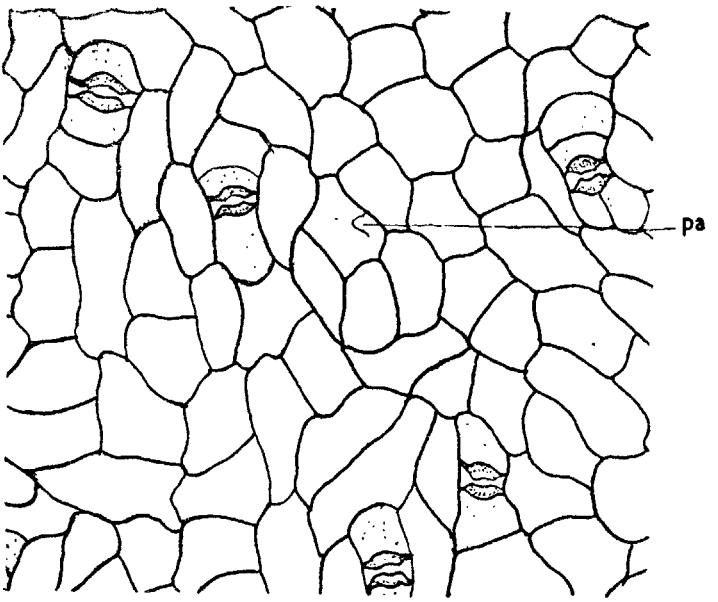


Fig. 9 x 190

Dicroidium narrabeenensis.

FIG. 8A. Single stoma; *l.s.* 1 = crescent-shaped subsidiary cell; *l.s.* 2 = broad subsidiary cell; ×430.

FIG. 9. Lower cuticle; *pa.* = papilla; ×190.

Lamina—Upper cuticle (Figs. 8, 8A):

Cuticle moderately thick, cells arranged in apparent linear rows running parallel to the secondary veins. Cells 4–6 sided, irregular in size and shape, 50–100$\mu \times$ 25–40μ in size. Both parallel striations and fine pitting present. Short papillae preserved in a few cells.

Frequency of stomata 10–15 per 1 mm. square area, irregularly oriented and mostly confined to areas between the veins, 40–45$\mu \times$ 16–25μ in size; pore 16–22μ long; thickened part of the guard cells 7–9μ broad. Transverse extensions present. Polar regions unthickened.

Subsidiary cells usually two, lateral, crescent-shaped (Figs. 8, 8A, *l.s.* 1), 40$\mu \times$ 20μ in size. Stomata, with broader subsidiary cells (Figs. 8, 8A, *l.s.* 2) which may be 40$\mu \times$ 50μ in size, are also common. Occasionally 3 or 4 subsidiary cells are observed; polar cells also met with in certain cases. Encircling cells occasionally present. The subsidiary and encircling cells slightly more cutinized than the ordinary cells; striations which may form meshes are more prominent than in the ordinary cells.

Midrib—Upper cuticle:

Cells shorter, 65$\mu \times$ 50μ in size, more or less rectangular, arranged in rows parallel to the midrib. Frequency of stomata 10–12 per 1 mm. square area.

Lamina—Lower cuticle (Fig. 9):

Much thinner, cells elongated and rounded at corners as in *D. eskensis*. Striations very faint; pits present. Raised papillae in a few cells (Fig. 9, *pa.*). Subsidiary cells striated.

Rachis:

Cuticle not preserved.

The lower cuticle of the lamina of this species shows striking similarity with those of *D. eskensis* and *Dicroidium* sp. *cf. D. talbragarensis* in the general appearance, the apparent linear arrangement of the cells, and in the shape of the subsidiary cells.

Locality and Horizon: Triassic shales, Narrabeen, near Sydney, N.S. Wales.

***Dicroidium eskensis* (Walkom).** Figs. 10–12

'Frond large, with strong, striated rachis. Pinnules large, robust, gradually tapering to rounded acute apex; upper half of lamina contracting at base, lower half broadening slightly and somewhat decurrent; midrib prominent becoming evanescent near apex; secondary veins make an acute angle (20°–50°) with midrib and divide, usually only once; a small number of veins at the base of the pinnule spring direct from the rachis.' (Walkom, 28).

The dichotomizing pinnate frond shown in Fig. 10 is typical of *D. eskensis*.

Lamina—Upper cuticle (Figs. 11, 12):

Cuticle thin. Linear arrangement of cells more pronounced; cells longer; corners rounded, striations not observed; irregular pits or fine pits present, size of cells 70–120$\mu \times$ 40–50μ; cell walls straight, 3–5μ thick.

Stomata only 5–8 per 1 mm. square area. Some appear in uninseriate bands; orientation irregular; 40–50μ long and 20–30μ broad; thickened area of the guard cells about 9μ broad (Fig. 12, *d*).

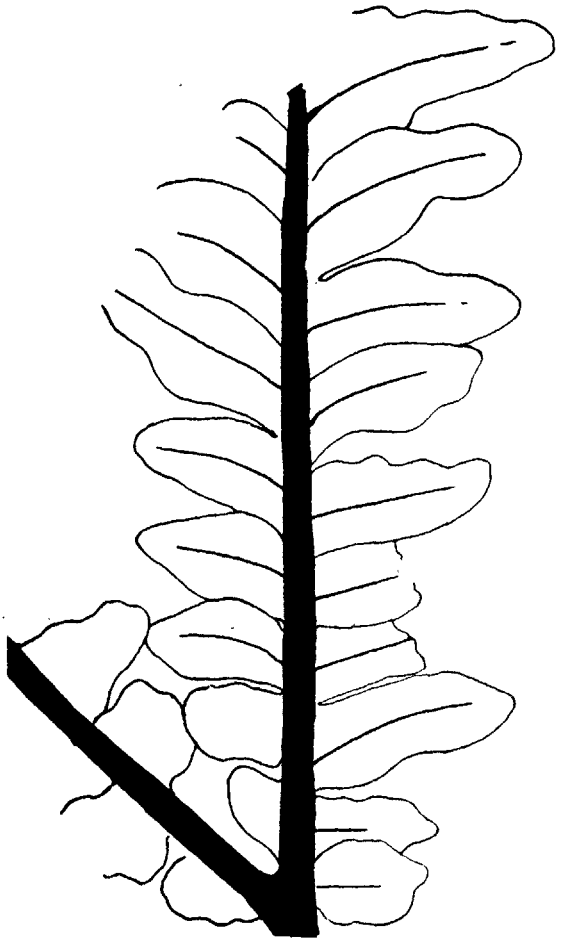


Fig. 10 x ca 1

Dicroidium eskensis.

FIG. 10. Part of frond, F 17822, ×ca. 1.

Subsidiary cells more cutinized than the ordinary cells, usually two, lateral (Figs. 11, 12, *l.s.*), with the longer axis transverse to the length of the pore, average size $40\mu \times 50\mu$, striations not present; polar subsidiary cells rare. Encircling cells (Fig. 12, *l.e.*) occasionally present.

Midrib—Upper cuticle:

Cells more or less rectangular, arranged in rows parallel to the midrib, $90\mu \times 50\mu$, shorter than those of ordinary cells, corners not rounded.

Stomata 3–5 per 1 mm. square area.

Midrib—Lower cuticle:

Cells still smaller, $65\mu \times 50\mu$; stomata 5–8 per 1 mm. square area.

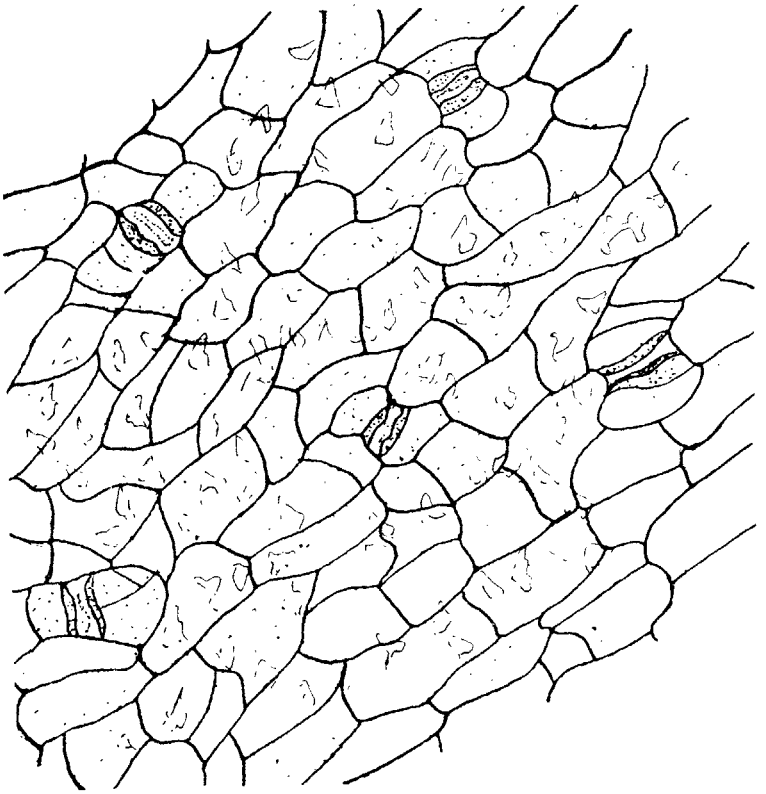


Fig. 11 x 190

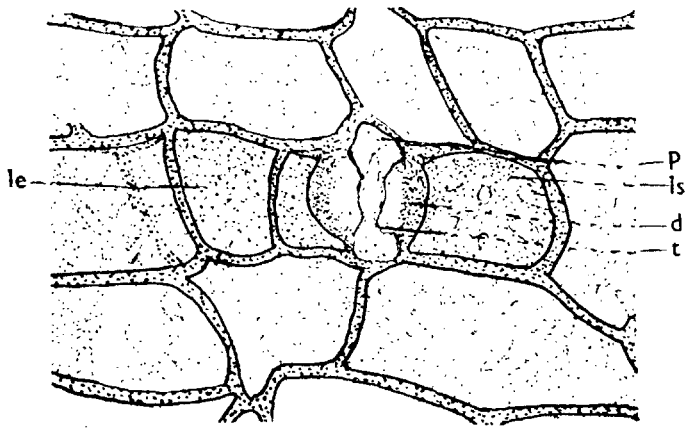


Fig. 12 x 430

Dicroidium eskensis.

FIG. 11. Upper cuticle of lamina, ×190.
FIG. 12. Single stoma; *d.* = thickened lateral part of guard cell; *p.* = polar region of guard cell; *t.* = transverse extension; *l.s.* = broad subsidiary cell; *l.e.* = encircling cell; ×430.

Rachis—Upper cuticle:

Cells in definite rows, majority short, 30–150μ long and 50μ broad. Heavily cutinized cell wall 10μ thick.

Stomata 2-3, irregularly oriented, guard cells thick all round. Specialized subsidiary cells as in lamina may or may not be present, more cutinized.

Rachis—Lower cuticle:

Cells shorter and polygonal, arranged in irregular rows; stomata 5–10 per 1 mm. square area.

The upper cuticle of this species can be compared with the lower of *D. narrabeenensis* in its general appearance, the apparent linear arrangement of the cells in rows, the shape of the cells, the somewhat indefinite differentiation of the stomatal and non-stomatal bands, the fewer number of stomata per unit area and in the shape and size of the subsidiary cells.

Locality and Horizon: Triassic shales, Narrabeen, near Sydney, N.S. Wales.

***Dicroidium* sp. *cf. D. talbragarensis* (Walkom).** Figs. 13–15.

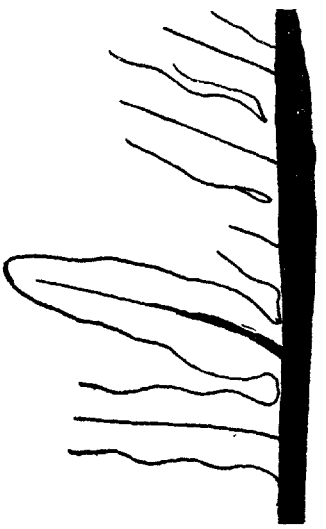


Fig. 13 x ca 1

Dicroidium sp. *cf. D. talbragarensis.*

FIG. 13. Small part of frond, F 35803*b*, ×ca. 1.

'Frond bipinnate, pinnae variable—some of the same type as *T. lancifolia,* some with markedly wavy margins, and others with the lamina distinctly divided after the manner of *T. feistmanteli.* Pinnae narrow at base and attached to rachis only by narrow portion. The venation in the simple pinnae is alethopteroid, while in those pinnae resembling *T. feistmanteli,* the pinnules have the typical odontopteroid venation.' (Walkom, 21).

Walkom created this species to accommodate two markedly different types of fronds; one, pinnate with alethopteroid venation and the other bipinnate with odontopteroid venation.

The frond (Fig. 13) may be compared to the pinnate forms of the above species except in the absence of the extremely constricted base.

Fig. 14 x 190

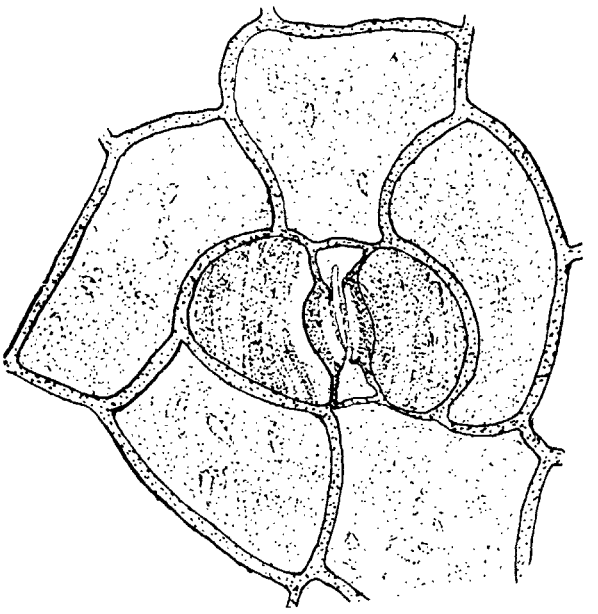


Fig. 15 x 430

Dicroidium sp. *cf. D. talbragarensis.*

FIG. 14. Upper cuticle of lamina, ×190.
FIG. 15. Single stoma, ×430.

Lamina—Upper cuticle (Figs. 14, 15):

Cuticle moderately thick; arrangement of cells in fairly pronounced rows; shape of cells similar to those in *D. eskensis*, but striations present, pits more or less oval, average size of cell $100\mu \times 50\mu$.

Stomata 15–20 per 1 mm. square area, orientation, size and shape of the stomata as in other species; 2, 3 or 4 subsidiary cells fairly common. Encircling cells also present; both striated as in *D. narrabeenensis*.

Though this cuticle resembles those of *D. narrabeenensis* and *D. eskensis* in some respects, it cannot be closely compared with either of them. It appears to be a form intermediate between the above two.

Locality and Horizon : Triassic shales, Benelong, N.S. Wales.

***Dicroidium feistmanteli* (Johnston).** Figs. 16–19

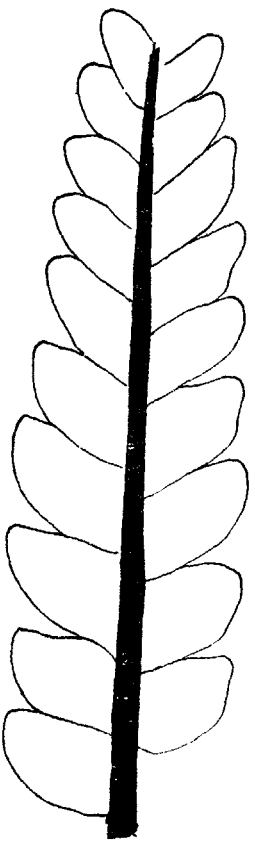


Fig. 16 x ca 1

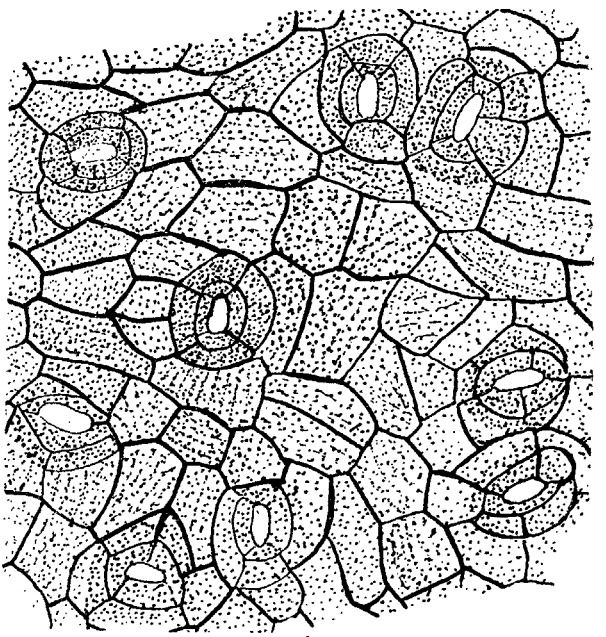


Fig 17 x 190

Dicroidium feistmanteli.

FIG. 16. Part of a pinna, F 408, ×ca. 1.
FIG. 17. Upper cuticle of lamina, × 190.

'Frond bipinnate, paripinnate with a dichotomous rachis; apex is formed by a dichotomous branching of the rachis. Pinnae elongate, gradually tapering, alternate or opposite. Pinnules

rhombic, ovate or semicircular, thick, attached by whole of base and connected by very narrow lamina along the rachis. Venation odontopteroid, the veins springing directly from the rachis and dividing once or twice before reaching the pinnae, but in this position they may be slightly contracted at the base.' (Walkom, 17).

In our specimen (Fig. 16) only one pinna is preserved. In its external features it shows the characteristics of a pinna of *D. feistmanteli.* It is paripinnate; the basal pinnules on either side of the midrib are similar and are larger than those above indicating that it is most probably not a branch of the dichotomizing frond of *D. odontopteroides.* Further, its cuticle closely resembles that of *D. feistmanteli* described by Antevs (13, 14) except in the absence of papillae.

Lamina—Upper cuticle (Figs. 17, 18):

Cuticle more heavily cutinized than in any other species described. Arrangement of cells irregular; cells polygonal, of varying shape and size, 60–80μ long and about 50μ broad, parallel striations clearly seen in most of the cells; in others, faint or absent. Walls straight, 3–5μ thick, strongly cutinized. Papillae or indications of them not observed.

Distribution of stomata, 35–40 per 1 mm. square, irregularly oriented. Stomata 40–45μ long and 20–23μ broad; pore 16–20μ long; guard cells (Fig. 18, *g*) unique in being uniformly thin unlike those in the other forms where their lateral sides are much thickened. However, the outline of the guard cells with their transverse extensions (Fig. 18, *t*) can be clearly made out.

According to Antevs (13), 'they are surrounded by 4–7 "Wallzellen", whose outer walls form a thick circle. The inner walls as well as the radial ones are, on the contrary, thin and lie a little immersed. The guard cells are not preserved.' The guard cells in our preparations are seen preserved in all the stomata (Figs. 17, 18, *g*); but due to their extreme thinness, they are very inconspicuous inside the ring of the heavily cutinized subsidiary and encircling cells. In this species the stomata are much sunken.

The stoma of this species is unique in yet another respect in having two rings of highly cutinized specialized cells. The inner ring (6–9μ broad) consists of 4–6 (4 being more common) subsidiary cells; the two laterals may be 65$\mu\times$8μ in size and the polars 25$\mu\times$8μ, if their encircling cells are present; otherwise (*p.s.*), 25$\mu\times$20μ in size. Or the laterals may divide transversely forming four cells (Fig. 18, *l.s.–l.s.* 1), some of which may extend to the polar region (Fig. 18, *l.s.* 1). The laterals also are broader in case they have no encircling cells. The outer, inner and radial walls of these cells are apparently thinner than those of the ordinary cells; the cells are more heavily cutinized; striations transverse.

The outer ring (10–12μ broad) consists of the encircling cells (Fig. 18, *l.e.*, *l.e.* 1) of the lateral subsidiary cells and the broad polar subsidiary cells, if the latter have no encircling cells; for, only occasionally we find encircling cells for one or both the polar subsidiary cells. In the case of the lateral subsidiaries, however, only occasionally they are found devoid of encircling cells; the walls are not thicker than those of the ordinary cells, but they are heavily cutinized. The breadth of these cells are slightly more than their subsidiary cells.

Rachis—Upper cuticle (Fig. 19):

Cells arranged in longitudinal rows, 60$\mu\times$70μ long and 40$\mu\times$45μ broad. Striations are prominent. Walls different from those of the lamina in their crenate appearance; 6–8 irregularly oriented stomata per 1 mm. square area, smaller than those of the lamina; subsidiary cells similar to ordinary cells; encircling cells absent; towards the lamina where the frequency of stomata (8–15) is higher, a ring of subsidiary cells present.

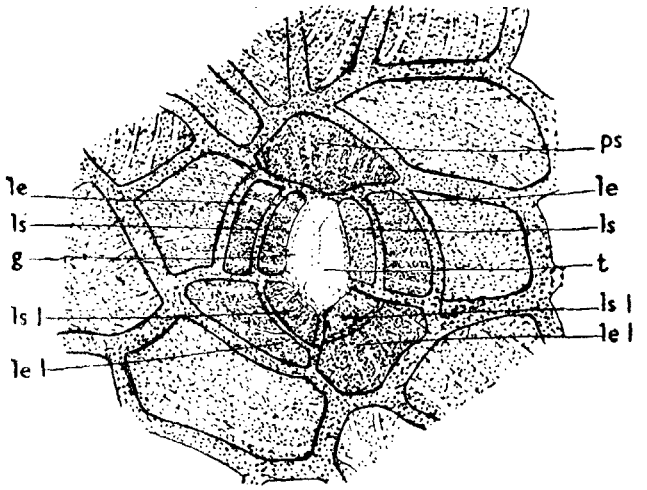


Fig. 18 x 430

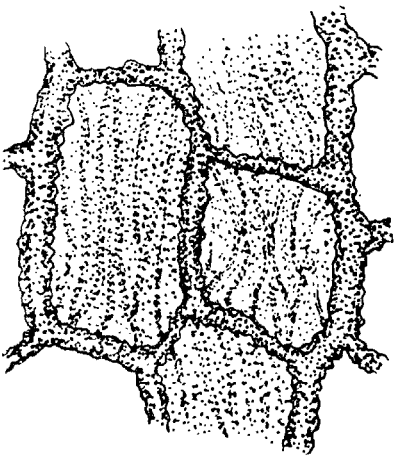


Fig. 19 x 430

Dicroidium feistmanteli.

FIG. 18. Single stoma; *g.* = guard cell; *t.* = transverse extension; *l.s.*—*l.s.* 1 = lateral subsidiary cells; *l.e.*—*l.e.* 1 = lateral encircling cells; *p.s.* = broad polar subsidiary cell which has no encircling cell; ×430.

FIG. 19. A few rectangular striated cells of the upper cuticle of rachis showing crenate wall; ×430.

Rachis—Lower cuticle :

Cells shorter and broader; frequency of stomata higher (10–15); regular rings of subsidiary and encircling cells.

The cells of the rachis of this species show a slight resemblance to those of the lamina in *D. australis* (Fig. 21) in their undulating cell-walls and striated cells. But the similarity ends there.

Locality and Horizon : Wianamatta shales, McDonald Town, N.S. Wales.

***Dicroidium australis* sp. nov.** Figs. 20–24.

The frond shown in Fig. 20 is only partly preserved. The basal and apical portions of the rachis, the region of forking and the terminal regions of the larger pinnae are not preserved. However, it can be made out that it is a large bipinnate frond. The simple pinnae between the forked branches are 2 cm. long and 1·5 cm. broad. They have constricted bases and pointed apices. The margin is entire. The venation is essentially of the odontopteroid type; but an indication of midrib is vaguely visible just at the base of the pinnae.

Though the tip of none of the larger pinnae is preserved, it can be made out that originally they were at least as long as 10 cm., and about 2 cm. broad at the base. The basal parts are deeply lobed into ovate segments, the latter becoming smaller towards the apex; the upper part is simple with wavy margin. The pinnae have thick prominent midrib; veins odontopteroid in the ultimate segments; the basal lobes receive veins both from the midrib and the rachis.

On a casual examination the frond shows a close resemblance with *D. feistmanteli* figured by Walkom in 1925 (Pl. XXIV, Fig. 7). However, it varies from the typical fronds of *D. feistmanteli* in having only lobes instead of pinnules. Further, the upper part of the pinnae is simple with crenate and wavy margin. The cuticular structure is also different from that of *D. feistmanteli* (Figs. 16–19). Hence this frond is placed in a new species, *D. australis*.

Diagnosis :

Frond bipinnate, rachis dichotomizing. Pinnae between the forked region simple, 2 cm. long and 1·5 cm. broad; margin entire, base constricted; venation odontopteroid; vague indication of a midrib just at the base; longer pinnae alternate or opposite, about 10 cm. long and 2 cm. broad at the base; basal part deeply lobed into ovate segments; apical region not lobed, wavy to entire. Pinnae with a definite midrib; venation odontopteroid in the ultimate segments; veins to the basal lobes arise both from the rachis and the midrib. Structure of the lower and upper cuticle of the lamina essentially the same; cuticle thick, cells polygonal, varying in shape and size; average cell $80\mu \times 50\mu$, striated; striations converge to the middle of the cells in most cases and at the point of convergence, a single papilla is present. In cells where striations run parallel, no papillae observed. Walls undulating. Stomata *Dicroidium* type, 20–25 per 1 mm. square area. Cells of the upper cuticle of rachis in longitudinal rows; striated, striations parallel to the length of the cells, undulations faint; stomata fewer in number. Cells of the lower cuticle of rachis polygonal, in irregular rows.

Lamina—Upper cuticle (Figs. 21–24):

Cuticle moderately thick. Cells irregularly arranged, polygonal, not uniform in shape and size, $60–80\mu \times 40–60\mu$. Cell wall appears undulating due to uneven thickening. Wall $2–3\mu$ thick. Cells striated; in many the striations converge to the centre where a single papilla is observed above the point of convergence (Figs. 21–23). In cells where the striations do not converge but run more or less parallel from wall to wall, papillae are absent (Figs. 21, 24).

Stomata about 20–25 per 1 mm. square, irregularly oriented, $40–45\mu$ long and $20–23\mu$ broad. Pore $16–20\mu$ long. Thickened dorsal side of the guard cells $4–6\mu$ (Fig. 24, *d*); polar region unthickened (*p.*); transverse extension present (*t.*).

Many stomata have two lateral subsidiary cells (Figs. 21, 22, 24, *l.s.*), $40\mu \times 25–30\mu$ in size; 3-4 subsidiary cells also very common, more or less extending to the

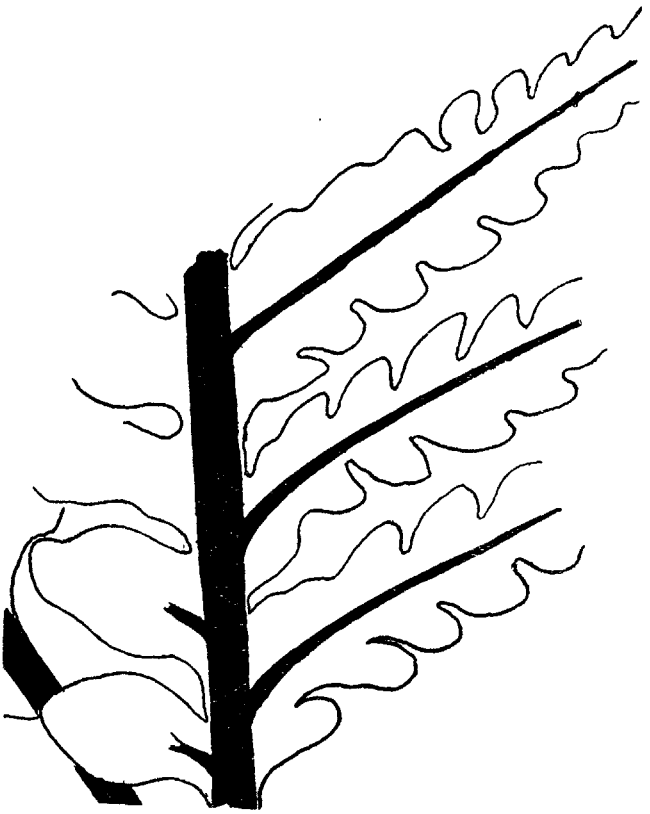


Fig. 20 x ca 1

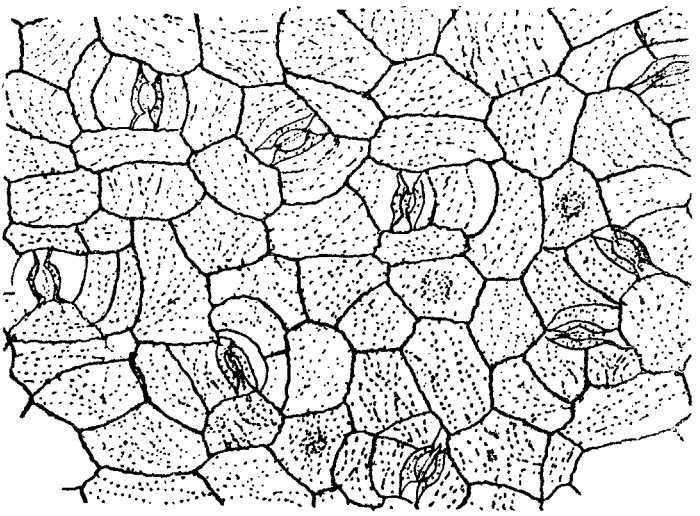


Fig. 21 x 190

Dicroidium australis sp. nov.

FIG. 20. Part of frond, F 17832, × ca. 1.

FIG. 21. Upper cuticle of lamina; striations more or less parallel, majority without papillae; × 190.

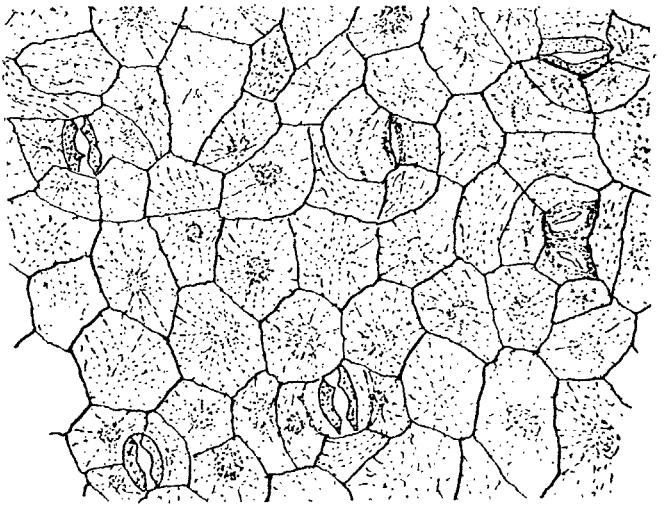


Fig. 22 x 190

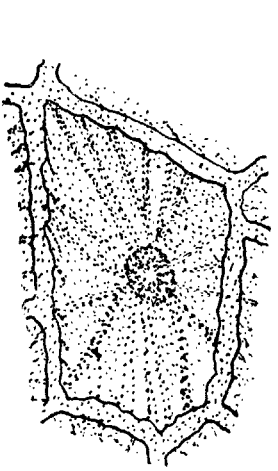


Fig. 23 x 430

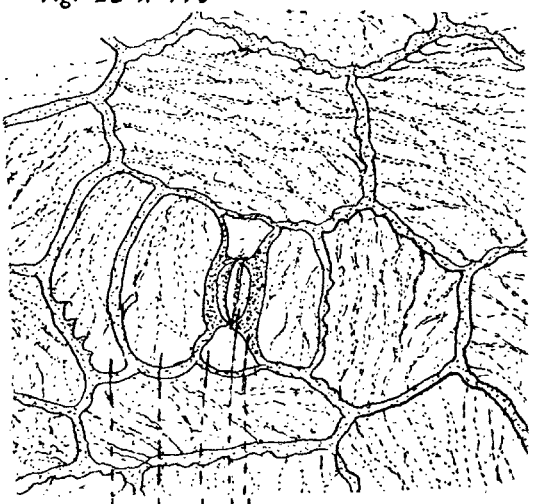


Fig. 24 x 430

Dicroidium australis sp. nov.

FIG. 22. Upper cuticle of lamina, striations converge to the centre of cell where a single papilla present; median papilla on subsidiary cell also; ×190.
FIG. 23. Single cell showing striations and papilla; ×430.
FIG. 24. Single stoma; *d* = thickened lateral part of guard cell; *p.* = polar region of guard cell; *t.* = transverse extension; *l.s.* = lateral subsidiary cell; *l.e.* = lateral encircling cell; ×430.

polar regions forming a ring round the stoma; occasionally stomata with clear polar subsidiary cells are observed.

Encircling cells are common (Fig. 24, *l.e.*). Both subsidiary cells and encircling cells are striated with undulating walls; median papillae observed in many (Fig. 22).

Rachis—Upper cuticle:

More thickened than those of the lamina, cells longer and arranged in longitudinal rows. Middle row of cells 110–112$\mu \times 25$–30μ. Towards either side, the cells shorter and broader. Cell walls only 2-3μ thick; undulations very faint or absent. Striations on cells quite prominent and run parallel to the length of the cells.

Stomata 3–5 per 1 mm. square area, smaller and irregularly oriented; guard cells heavily cutinized all round; transverse thickening not prominent. No specialized subsidiary cells.

Rachis—Lower cuticle:

Cells shorter and broader, irregular in shape and size; stomata of greater frequency than in the upper cuticle; guard cells uniformly cutinized all round. Ring of 4–6 unspecialized subsidiary cells, also heavily cutinized.

The cuticle obtained by Thomas (33, fig. 52 *b*) from the frond described by him as *Dicroidium* sp. *cf. D. feistmanteli* (33, fig. 50) shows identical features with those of *D. australis*. In our opinion Thomas' frond belongs to *D. australis*.

Locality and Horizon: Triassic shales, Narrabeen, near Sydney, N.S. Wales.

***Dicroidium walkomi* sp. nov.** Figs. 25–27.

The frond (Fig. 25) assigned to this new species also is partly preserved. One branch of the dichotomizing rachis is preserved with a few incomplete pinnae on either side.

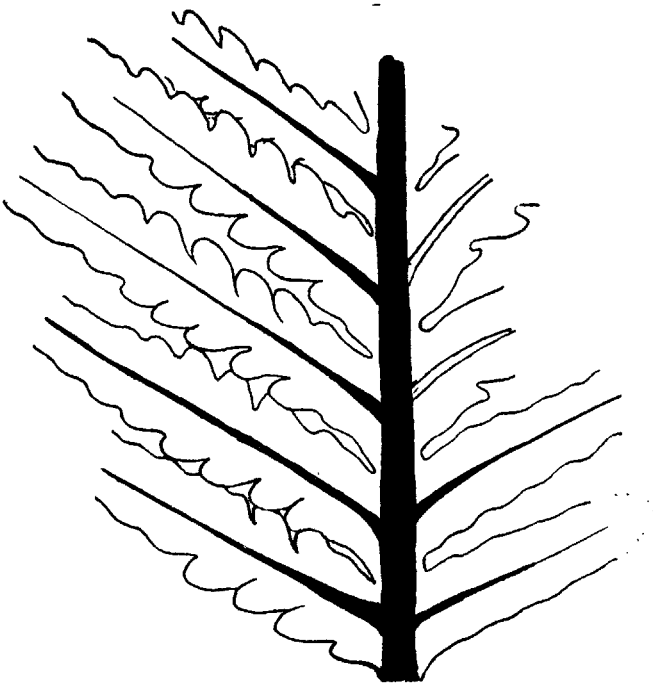


Fig. 25 x ca 1

Dicroidium walkomi sp. nov.

FIG. 25. Part of frond, F 16391, $\times$ca. 1.

The rachis is 3–4 mm. broad. Basal pinnules on one side are simple and smaller than those opposite, indicating that the simple pinnae occupy the position just above the forked region of the rachis. These simple pinnae, about 3–3·5 cm. long and 1 cm. broad, resemble those of *D. talbragarensis* in their shape, size and venation. The base is not constricted; margin wavy. There is a definite midrib, persisting to the apex and giving rise to forked secondary veins. The apex is not preserved.

The longer pinnae are sub-opposite 6 cm. long and 1–1·5 cm. broad at the base. The basal parts have ovate lobes. Towards the apex the lobes are less definite and nearer the apex the margin is wavy as in the case of *D. australis*. The midrib is strong. The venation of the lobes is odontopteroid.

Though this frond could be compared with Walkom's *D. feistmanteli* (1925, Pl. XXV, fig. 1) in megascopic features, it differs from typical *D. feistmanteli* in its smaller size, in the absence of definite pinnules with the lamina only incompletely divided gradually giving rise to wavy margins in the apical half of the longer pinnae, and further, in the alethopteroid venation of the simple pinnae in the region of forking.

From *D. australis* it differs in the smaller size of the frond and the alethopteroid venation of the simple pinna over the forked region.

The cuticle of both *D. feistmanteli* and *D. australis* are structurally different from that of *D. walkomi*.

For reasons given above, we suggest the institution of a new species, *D. walkomi*, to accommodate this form.

Diagnosis:

Frond bipinnate; rachis dichotomizing. Pinna above the forked region simple, 3–3·5 cm. long, 1 cm. broad; base broad without constriction, margin wavy or entire; venation alethopteroid. Longer pinnae sub-opposite, 6 cm. long and 1·5 cm. broad at the base, without constriction; basal region with definite ovate lobes, apical region showing wavy margin of the lamina. Midrib fairly thick; venation of lobes odontopteroid; cuticle thick, linear arrangement of cells less pronounced, walls straight. Stomata *Dicroidium* type, 25–30 per 1 mm. square area; subsidiary cells 2–4, very thin.

Lamina—Upper cuticle (Figs. 26, 27):

Cuticle thick, cells in irregular rows, short and broad, of varying shape, striated, size 30–50$\mu \times$30–50μ; walls straight, 2-3μ in thickness.

Stomata 25–30 per 1 mm. square area, 45–50$\mu \times$16–18μ in size; pore 20–24μ. Dorsal wall of the guard cells 4μ thick (Fig. 27, *d*); transverse thickening not very prominent (*t.*); polar regions unthickened (*p.*).

Subsidiary cells may be two, lateral and crescent-shaped. 50$\mu \times$16μ in size; 3 or 4 subsidiary cells very common (Figs. 26, 27); occasionally polar subsidiary cells also present; subsidiary cells much thinner than the ordinary cells; encircling cells very rare. Striations not observed.

Midrib—Upper cuticle:

Cells very short and mostly rectangular in shape, smaller than those of the lamina; walls slightly more cutinized; stomata about 20 per 1 mm. square area.

Rachis—Upper cuticle:

Cells in the region of the midrib arranged in rows, rectangular to polygonal, 100$\mu \times$50μ in size; wall 10μ in thickness; towards the periphery the rows of cells

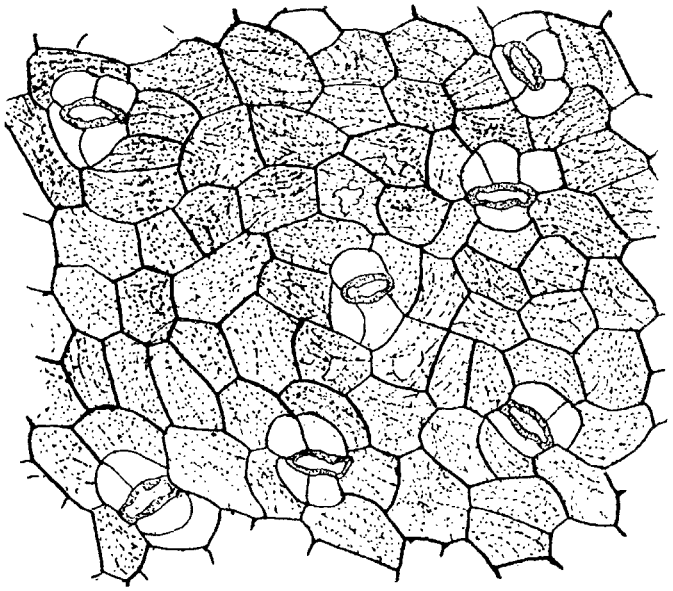


Fig. 26 x 190

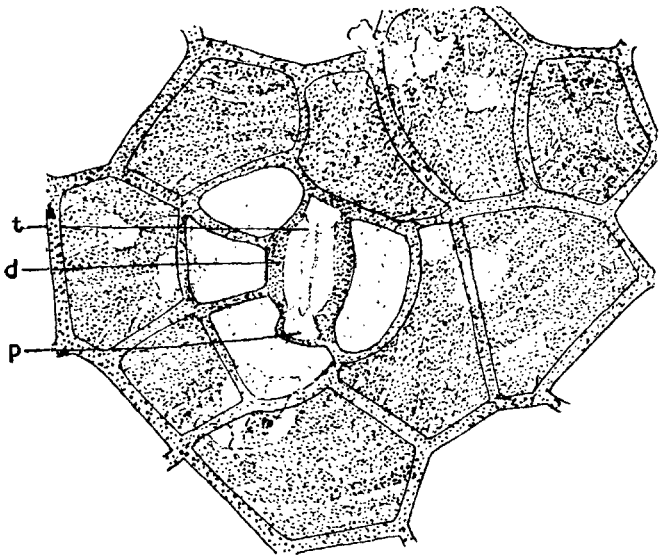


Fig. 27 x 430

Dicroidium walkomi sp. nov.

FIG. 26. Upper cuticle of lamina, ×190.
FIG. 27. Single stoma; *d.* = lateral part of guard cell; *p.* = polar region of guard cell; *t.* = transverse extension; ×430.

become irregular as also their shape and size; striations present. Stomata 10–12 per 1 mm. square area, usually larger, $60\mu \times 30\mu$; subsidiary cells thin.

Rachis—Lower cuticle :

Cells smaller in size than those of the upper cuticle, walls less thickened; striations not prominent.

Stomata 20–25 per 1 mm. square area, large as in the upper cuticle of the rachis.

Locality and Horizon : Triassic shales, Narrabeen, Manly, N.S. Wales.

Affinity

The earlier workers have included *Thinnfeldia* under the Filicales. Schenk (67) and Antevs (14) have raised this group to a position intermediate between the ferns and the gymnosperms. Seward (10, 31) was the first to include *Thinnfeldia* under the pteridosperms. But when Walkom (17) discovered fertile fronds of *Thinnfeldia* he instituted a new family the *Thinnfeldieae* the sporangia of which, according to him, showed affinities both with the Gleicheniaceae and the Marattiaceae. Du Toit (27) followed Walkom's suggestion and included *Thinnfeldia* fronds under the Filicales. Hamshaw Thomas (33), however, could prove with convincing evidence that *Dicroidium* (*Thinnfeldia*) belonged to Pteridospermae. He discovered also detached male and female fructifications lying in close association with *Dicroidium* and allied fronds from the Mesozoic of S. Africa. By their cuticular resemblance he has suggested that both the fructifications and the leaves belonged to the same type of plants.

It may be mentioned here that our study of the *Dicroidium* stoma has shown that it is typically gymnospermous. Although in certain respects it recalls some characteristics of the Bennettitalean stoma on the one hand, and the *Ctenis* group of the non-Bennettitalean fossil Cycadophyta on the other, it has been found to be distinct from those groups in many respects. The affinities of the *Dicroidium* stoma will be discussed in full in the detailed paper.

IV. Summary.

The following species of *Dicroidium* (*Thinnfeldia*) have been recognized in a small collection of fronds from the Mesozoic of Australia, kindly lent by Dr. A. B. Walkom, Director, Australian National Museum, Sydney:

D. lancifolium (Morris), *D. acuta* (Walkom), *D. narrabeenensis* (Dun), *D. eskensis* (Walkom), *Dicroidium* sp. *cf. D. talbragarensis* (Walkom), and *D. feistmanteli* (Johnston).

Two new species, *D. australis* and *D. walkomi*, have been instituted based mainly on their cuticular structure.

The cuticles of the above species are briefly described.

We are grateful to Dr. W. D. West, C.I.E, Director, Geological Survey of India, for giving us all facilities for palaeobotanical research and to Dr. A. B. Walkom, Director, Australian National Museum, Sydney, for kindly placing the material at our disposal.

V. Bibliography.

Antevs, E. (1913). Some Mesozoic plants. Results of Dr. E. Mjoberg's Swedish Scientific Expeditions to Australia, 1910–1913. *K. Svenska Vet. Akad. Handl.*, Bd. 52, No. 5, 1–6.

——— (1914). Die Gattungen Thinnfeldia Ett. und Dicroidium Goth. *K. Svenska Vet. Akad. Handl.*, Bd. 51, No. 6, 1–71.

Du Toit, A. L. (1927). The fossil flora of the Upper Karroo Beds. *Ann. S. Afr. Museum*, **22**, 328–340.

Feistmantel, O. (1890). Geological and Palaeontological relations of the Coal and Plant-bearing beds of Palaeozoic and Mesozoic age in Eastern Australia and Tasmania, with special reference to the fossil flora. *Mem. Geol. Surv. N.S.W., Pal.*, No. 3, 101–107.

Florin, R. (1931). Untersuchungen zur Stammesgeschicte der Coniferales und Cordaitales. *K. Svenska Vet. Akad. Handl.*, Bd. 10, No. 1, 11–24.

Gothan, W. (1912). Über die Gattung Thinnfeldia Ettingshausen. *Abh. Naturhist. Gesell. Nurnberg*, Bd. XIX, 2, 68–80.

Harris, T. M. (1932). The fossil flora of Scoresby Sound, East Greenland, Pt. 2: Description of seed plants *incertae sedis* together with a discussion of certain Cycadophyte cuticles. *Meddl. Grønland*, Bd. 85, Nr. 3, 71–94.

——— (1937). The fossil flora of Scoresby Sound, East Greenland, Pt. 5: Stratigraphic relations of the plant beds. *Meddl. Grønland*, Bd. 112, Nr. 2, 31–33.

Jones, O. A. and de Jersey, N. J. (1947). The flora of the Ipswich Coal Measures. Morphology and floral succession. *Univ. Q'land Papers, Dept. Geol.*, **3**, new series, Nos. 3, 4, 15–17.

Schenk, A. (1867). Die fossile Flora der Grenzschichten der Keupers und Lias Frankens, 111, *Wiesbaden*.

Seward, A. C. (1903). Fossil floras of Cape Colony. *Ann. S. Afr. Museum*, **4**, 50–57.

——— (1910). Fossil Plants, **2**, 538. *Cambridge*.

——— (1931). Plant life through the ages, 314–317. *Cambridge*.

Thomas, H. H. (1933). On some Pteridospermous plants from the Mesozoic rocks of South Africa. *Phil. Trans. Roy. Soc. London*, Ser. B. **222**, 193–265.

Walkom, A. B. (1917). Mesozoic floras of Queensland. Pt. I: The flora of the Ipswich and Walloon Series. *Q'land. Geol. Surv.*, Publ. No. 257, 12–24.

——— (1921). Mesozoic floras of New South Wales. Pt. 1—Fossil plants from Cockabutta Mountain and Talbragar. *Mem. Geol. Surv. N.S.W.*, Pal., No. 12, 1–21.

——— (1925). Fossil plants from the Narrabeen stage of the Hawksbury series. *Proc. Linn. Soc. N.S.W.*, **50**, pt. 3, 214–224.

——— (1928). Fossil plants from the Esk district, Queensland. *Proc. Linn. Soc. N.S.W.*, **53**, pt. 4, 459–461.