FOSSIL BANKSIEAE FROM YALLOURN, VICTORIA, WITH NOTES ON THE MORPHOLOGY AND ANATOMY OF LIVING SPECIES

By ISABEL C. COOKSON* and SUZANNE L. DUIGAN*

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Summary

The morphological and anatomical features of six types of fossil leaves from brown coal at Yallourn, Victoria, have been described. Comparison with similar features of living species has shown that all are extinct members of the tribe Banksieae of the family Proteaceae. A new genus *Banksieaephyllum* has been instituted to include these fossil leaves. The suggestion has been made that the identification of fossil leaves with either *Banksia* or *Dryandra* is impracticable.

Fruiting cones of *Banksia* from Tertiary deposits are figured and described. The morphology and anatomy of a leaf, *Phyllites yallournensis*, have been investigated.

The chief anatomical features of the leaves of 53 species of *Banksia* and 51 species of *Dryandra* are considered.

I. INTRODUCTION

This paper is mainly concerned with the description of some Victorian Tertiary leaves, the morphological and anatomical features of which suggest affinities with the tribe Banksieae of the family Proteaceae. Previous identifications of fossil leaves with either *Banksia* or *Dryandra* (see Kausik 1943), the two closely allied genera that comprise this tribe, have not, as far as the authors are aware, been supported by anatomical investigations. The advantages of information from such a source, as well as the question of the reliability of morphological characters as guides to the identity of fossil Banksieae, will be discussed. The results of a detailed study of the cuticles of living Banksieae, made in an attempt to determine the affinities of the fossil types, have been presented in condensed form in Tables 1 and 2. The principal characters will be individually considered in the text.

II. MATERIAL AND METHODS

The leaves were collected from the brown coal deposits exposed in the Yallourn North and Yallourn open cuts in south-eastern Victoria. These deposits are being worked by the State Electricity Commission and one of the types was collected by Mr. A. J. H. Adams of that organization. Agreement as to the precise age of these beds has not been reached but it is generally believed to be Oligocene.

* Botany School, University of Melbourne.

The fossils are preserved as "mummies" and retain much of their original structure. Treatment with a 12 per cent. solution of sodium hypochlorite was found to be the most satisfactory method of maceration but the use of Schultze's solution was sometimes found advantageous. The cuticles thus freed and cleared were washed in water, stained with safranin, and mounted in glycerine jelly. Cuticular preparations of living species were obtained in the same way, but, when herbarium material was used, the leaves were boiled in water prior to immersion in the macerating solution.

Transverse sections, which provide instructive details regarding the internal anatomy of the leaves, were prepared by the use of the paraffin method.

III. General Morphology of Leaves of Banksieae

In 1925 Deane drew attention to the close similarity in external form that exists between leaves of *Banksia* and *Dryandra*. He pointed out that "the so-called *Dryandra* form of leaf, as usually understood, is not peculiar to that genus but occurs also in many species of *Banksia*." His illustrations give clear support to this statement. Referring to the identification of isolated fossil leaves from brown coal deposits at Morwell (the locality now known as Yallourn North) he remarked that "It may be that the fossil leaves with this character should be placed under *Banksia* and not under *Dryandra* at all . . . Following Professor Ettingshausen's lead, however, I have called the serrated leaves *Banksia* and those possessing more or less triangular pinnae *Dryandra*."

Since the results of the present investigation suggest that a revision of Deane's policy concerning the determination of fossil leaves of Banksioid form is desirable, it may not be out of place to elaborate further the difficulties of separating, on external form alone, the leaves of these two genera.

Species having simple leaves with entire margins are rare in *Dryandra* and more numerous in *Banksia*, but the long, narrow, linear leaves with entire margins of *B. tricuspis* have their counterpart in those of *D. speciosa*. As examples of broadly obovate, prickly-toothed leaves, those of *B. coccinea* and *D. cuneata*, or *B. goodii* and *D. praemorsa* may be cited. More deeply lobed leaves of essentially similar form, although of somewhat different size, are found in *B. victorieae* and *D. kippistiana*. Of the pinnate types, *B. speciosa* and *D. formosa*, also *B. dryandroides* and *D. baxteri*, have the same general form, again with the *Banksia* species as the larger. Furthermore, whilst the bipinnatifid character of the leaves of *D. bipinnatifida* cannot be exactly matched in any species of *Banksia*, it is approached to some extent by *B. repens*.

The venation is similar in both genera. The midrib and veins are usually conspicuous and always more so on the lower surface, but they may be obscured to some extent by the hairy covering. The secondary veins arise at a wide angle and run directly to the margin of the leaf, the larger ones passing to the tips of the serrations or pinnae when these are present.

IV. Cuticular Structure of Living Species of Banksieae

The close similarity between *Banksia* and *Dryandra** expressed in the external morphology of their leaves is further emphasized when their cuticles are compared. All the main characters and their variants occur in both genera, and a constant distinguishing feature has not been discovered.

(*a*) *Position of the Stomata*

The leaves of all members of the Banksieae are bifacial, the stomata being confined to the lower surface. In most species the stomata are situated on the sides and bases of small pits or depressions and are accompanied by numerous hairs which develop from the interstomatal epidermal cells. These stomatal pits early attracted the attention of botanists of whom, according to Jönsson (1878), Schleiden was the first.

The breadth and depth of the stomatal pits vary considerably from species to species, and have no constancy in the individual sections of either genus. In five of the species of *Banksia* (Table 1) belonging to the section Oncostylis (Bentham 1870) the stomata are diffusely arranged in longitudinal grooves one on either side of the midrib. In the remaining members of the same section the lamina between the margin and the midrib is wider and flatter, so that the stomata, as well as being diffuse, are superficially placed.

Three species of *Dryandra*, namely *D. kippistiana* of the series Floribundae and *D. serra* and *D. foliolata* of the series Concinnae (Bentham loc. cit., p. 564), also have their stomata superficially placed, but in none are stomatal grooves developed.

(*b*) *The Stomata*

The stomatal characters of *Banksia* and *Dryandra* were first investigated by von Mohl (1833) who found them to be in agreement with those of several other genera of the Proteaceae (Solereder 1908, p. 712).

In this basic type of stoma, from which the authors have found no deviation in the Banksieae, the two guard cells are accompanied by a pair of subsidiary cells arranged parallel to the pore. The guard cells are usually slightly raised above the epidermal cells and their cuticular ridges are prominent.

(*c*) *Hairy Covering*

The leaves are never completely devoid of hairs in any species of *Banksia* or *Dryandra*. Entire hairs may be either sparsely developed or completely absent from the upper surface of mature leaves. When the latter condition prevails, hair-bases, from which the hair proper has been shed during the development of the leaf, can be observed on detached cuticles of most species (Tables 1 and 2). On the lower surface, on the other hand, hairs, apart from those in the stomatal pits, are sometimes so plentiful that they form a thick woolly felt, as, for example, in *B. robur* and *D. concinna*.

The hairs of the Banksieae have been described and illustrated by several earlier writers (Engler 1889; Hamilton 1907; Haberlandt 1909). They are simple and bicellular. Typically each consists of a short, thick-walled basal cell

* Chattaway (1948*a*, 1948*b*) has shown that the woods of these genera are indistinguishable; the same also applies to the pollen grains.

connected with one or more epidermal cells and a terminal, thick-walled, pointed hair-cell. Variations in the shape and proportions of these two components have enabled the following types, illustrated in Figure 1, to be distinguished:

Type (*a*).—Consists of a cylindrical basal cell of variable length (up to 45 μ in *B. sceptrum* and *B. hookeriana*) with a diameter of 8-12 μ throughout, and a long, thick-walled, often spirally coiled terminal cell the diameter of which (5-6 μ) is generally considerably less than that of the basal cell.

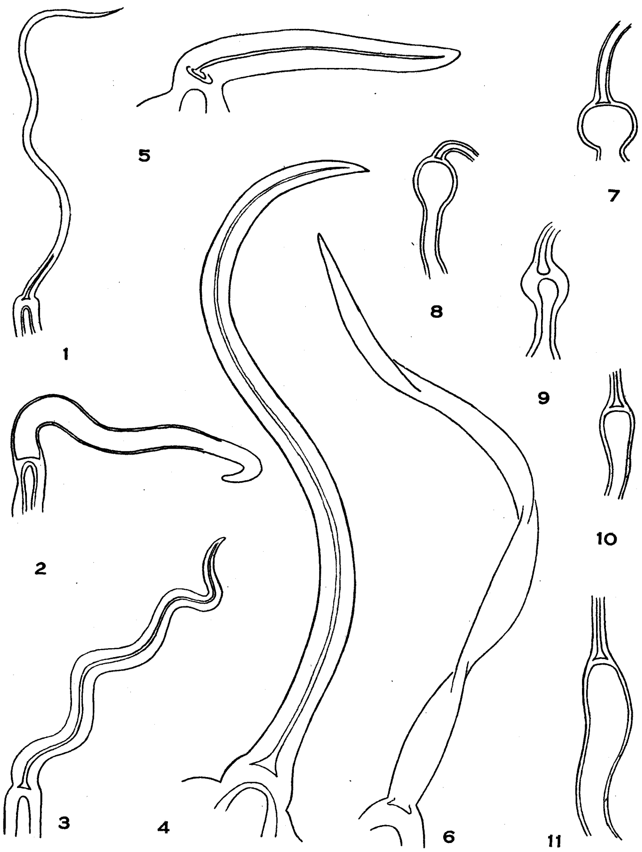


Fig. 1.—Types of hairs found in the tribe Banksieae. x 270. 1. Type *a*. *Banksia marginata*. 2. Type *b*. *Banksia goodii*. 3. Type *b*. *Dryandra quercifolia*. 4. Type *b*. *Banksia robur*. 5. Type *c*. *Dryandra praemorsa*. 6. Type *d*. *Banksia robur*. 7. Type *e*. *Banksia verticillata*. 8. Type *e*. *Banksia sphaerocarpa*. 9. Type *e*. *Banksia tricuspis*. 10. Type *f*. *Dryandra stupposa*. 11. Type *f*. *Banksia hookeriana*.

Type (*b*).—The basal cell is thick-walled, 10-20 μ wide throughout; occasionally, as in *B. robur*, measuring as much as 28 μ. The terminal cell is usually thick-walled, about 8-22 μ wide, of variable length, angularly bent, loosely coiled, or almost straight, the surface sometimes striated.

Type (*c*).—The basal cell, 19-60 μ wide, has a strongly thickened wall and a correspondingly reduced cavity; the terminal cell is short, straight or nearly so, and very thick-walled. This type is associated with the upper epidermis or midrib and is well seen in such species as *B. prionotes* and *D. bipinnatifida.*

Type (*d*).—The basal cell is short, 14-25 μ wide and thick-walled; the long terminal cell, about 12-15 μ wide, has a rather thin wall which is twisted in a loose spiral as in the hairs of *Gossypium.* Such hairs occur in *B. robur, D. ashbyi* etc.*

Type (*e*).—The basal cell of this type is differentiated into a globular "head," 10-36 μ in diameter, to the centre of which the terminal hair-cell is attached, and a more or less extended "stalk" approximately 8.5 μ wide. The total length of the basal cell varies from 25-56 μ and its wall is either thin or thickened to varying degrees. The terminal cell is narrow, usually thick-walled, and spirally coiled. Examples of this type are found in *B. verticillata* and *D. praemorsa.*

Type (*f*).—The basal cell is club-shaped, frequently thin-walled, and of variable length, ranging from 28 μ in *D. nobilis* to 90 μ in *B. hookeriana;* the terminal hair-cell, which is broadly attached, is thick-walled and spirally coiled.

(*d*) *Epidermal Papillae*

This term refers to conical extensions of the outer walls of epidermal cells into which the cell-lumen passes (Fig. 2; Plate 8, Fig. 58). Such papillae are developed in only a few species of *Banksia* and then are restricted to those

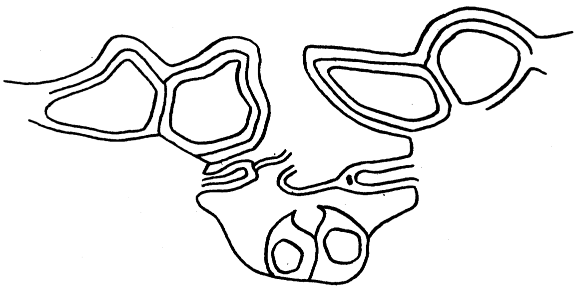


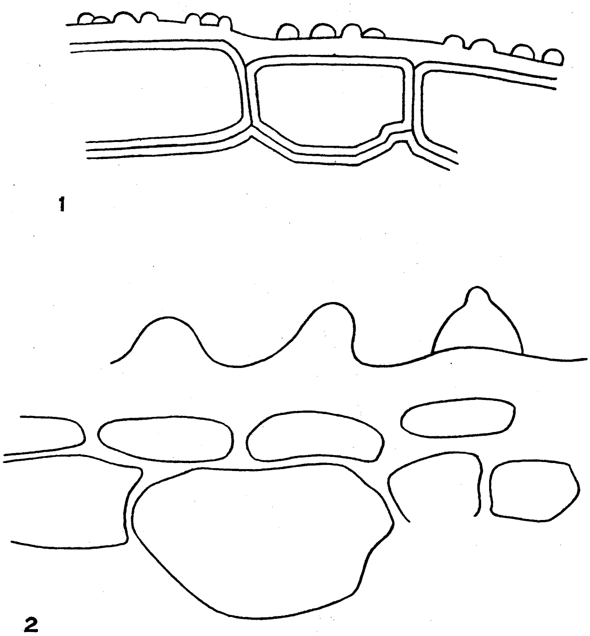
Fig. 2.—Epidermal papillae of *Banksia quercifolia.* x 400.

cells adjacent to or abutting on the stomatal pits (*B. quercifolia*) or grooves (*B. pulchella, B. meissneri*). Each cell has one centrally placed papilla. Epidermal papillae have not been observed in any species of *Dryandra,* but their infrequent occurrence in *Banksia* makes them of little systematic value. Epidermal papillae have been recorded by Jönsson (loc. cit., Table 3, Fig. 36) as present in the lower epidermis of *Embothrium coccineum* Forst., but in this species the whole outer wall is involved and not only the central portion of it, as in *Banksia* spp.

* Hairs of this type occur on the bracts of cones of *Banksia integrifolia* and *B. marginata.*

(*e*) *Cuticular Papillae*

These are verrucose thickenings of the outer cutinized layers of the epidermal cell walls (Fig. 3). They have been observed in 96 per cent. of the species of *Dryandra,* the two species from which they appear to be absent being *D. speciosa* and *D. conferta,* and in 38 per cent. of the species of *Banksia.* They may be distributed on both surfaces of the leaf, as in *B. baxteri* and *D. praemorsa,* but are usually only on one. If the number of papillate cells in the lower epidermis is small or the papillae are not clearly defined, their presence can usually be detected in the vicinity of the stomatal pits.



1

2

Fig. 3.—Cuticular papillae.
1. T.S. Upper epidermis of *Dryandra foliolata.* x 320.
2. T.S. Upper epidermis of *Banksia verticillata.* x 320.

The number of papillae per epidermal cell is generally proportional to their size and may vary from one (*B. hookeriana*) to thirty or even more (*D. squarrosa*). Their outline in surface view is also variable; they may be circular, oval, or in elongated cells, such as those covering the midrib and secondary veins, ridge- or streak-like. Usually cuticular papillae are restricted, as in *D. praemorsa* (Plate 8, Fig. 59), to those epidermal cells from which hair-bases are absent, but in heavily papillate forms such as *D. kippistiana* and *D. foliolata* (Plate 8, Fig. 60) they are also present on the cells supporting the hair-bases.

(*f*) *Epidermal Parenchyma*

(i) *Lower Epidermis.*—The parenchyma which lines the stomatal pits is usually different from that between the pits and covering the veins. The cells associated with the stomata have thin, slightly curved lateral walls with a large number of pits. The cells of the non-stomatiferous parenchyma, on the other hand, are less uniform, have thicker walls and in some forms, such as *B. attenuata* and *B. baueri,* are of two sizes, small cells which support hair bases and larger ones without hairs (Plate 8, Figs. 61, 62). Their lateral walls are generally straight or slightly curved, thin or as much as 8 μ thick, and pitted or unpitted according to the species.

(ii) *Midrib.*—The cells covering the midrib are more or less elongated and have straight, moderately thickened lateral walls which may or may not be pitted.

(iii) *Upper Epidermis.*—In some species (*B. elderiana*) the cells of the upper epidermis are identical with those of the lower surface. More often there are small differences such as a greater uniformity, a somewhat larger size, more regular form, and, on the whole, thicker lateral walls which may be pitted or unpitted.

V. Internal Anatomy of the Leaves of Banksieae

In addition to symmetry, two structural features have been used by Jönsson (loc. cit., p. 49) to distinguish leaves of *Banksia* and *Dryandra* from those of other proteaceous genera. They are the frequent presence of a hypodermis and, in most species, the association of anastomosing plates of sclerenchyma with the vascular bundles of the leaf.

Hypodermis.—In the leaves of most species of *Banksia* and *Dryandra* there are one or two layers of cells between the epidermis and the mesophyll tissue. These may constitute a true hypodermis and the cells be either larger (*D. squarrosa*) or smaller (*D. ashbyi*) than those of the epidermis, or they may be fibrous in character and belong, as asserted by Jönsson, to the bast proper.

In three species of *Dryandra,* namely *D. kippistiana, D. concinna,* and *D. foliolata,* neither hypodermal nor fibrous layers are developed.

Sclerenchyma.—The leaves of most Banksieae are highly sclerenchymatous. This is partly the result of the rich development of fibrous cells around the vascular bundles of the midrib and lateral veins and partly the presence of characteristic "vertically transcurrent plates" of sclerenchyma which reach the hypodermis when one is present (Solereder 1908, p. 770). This sclerenchymatous network has been observed during the present investigation, in most species of *Banksia* and *Dryandra,* the only exceptions being those species of *Banksia* which comprise the section Oncostylis. Its absence from *B. pulchella* and *B. littoralis,* both members of this section, was recorded earlier by Jönsson (1878) who also showed that, with the exception of a few species of *Hakea* and *Synaphea,* it does not occur in other members of the Proteaceae. Taken in conjunction with other characteristics, therefore, this feature seems to be of value in the separation of the Banksieae from other tribes of this family, and has been used for this purpose in the section dealing with fossil species.

Outer walls of epidermal cells.—These are invariably thick and highly cutinized on both surfaces. This is particularly noticeable on the upper surface where the thickness is frequently considerable. Amongst species of *Banksia* a maximum thickness of 28 μ is seen in *B. media,* a minimum of 5.5 μ in *B. marginata, B. serratifolia, B. ornata, B. sphaerocarpa, B. spinulosa, B. meissneri,* and *B. pulchella.* In *Dryandra* a maximum thickness of 25 μ occurs in *D. preissii, D. pteridifolia,* and *D. plumosa,* while the minimum, 5.5 μ, occurs in *D. floribunda.* The material from which these figures have been derived came from natural habitats, so that there is no reason to think that the approximate measurements given are in any way abnormal.

VI. Salient Characters of Leaves of the Banksieae

The preceding survey of morphological and anatomical features of the leaves of living members of the tribe Banksieae has shown:

(1) That there is no feature by which leaves of *Banksia* can be safely distinguished from those of *Dryandra.*

(2) That some features are constant in the tribe:

- (*a*) A pair of subsidiary cells lies parallel to the pore of each stoma.
- (*b*) The stomata are always associated with small, bicellular hairs.
- (*c*) The epidermal cells in the stomatal areas have thin, pitted lateral walls.
- (*d*) The outer walls of the epidermal cells are thick and heavily cutinized.

(3) That some features are common, though not constant, in the tribe:

- (*a*) Prominent venation, with secondaries emerging at a wide angle from a conspicuous midrib.
- (*b*) The presence of hypodermal layers.
- (*c*) The occurrence of stomata in pits or grooves.
- (*d*) The development of cuticular papillae on at least one surface.
- (*e*) The subdivision of the mesophyll into quadrangular areas by vertically transcurrent plates of sclerenchyma.

While the exact systematic value of some of these characters may be doubtful, it does appear that a combined anatomical and morphological examination of the leaves of this tribe may successfully separate them both from the remainder of the family and from other families.

Tables 1 and 2 show features of leaves of *Banksia* and *Dryandra* which can be observed in cuticular preparations and transverse section. The general symbol "+" refers either to the presence of a particular character or to its agreement with the adjective used at the top of a column; "–" refers to the opposite condition, and "×" to an intermediate state.

In the column referring to the distribution of the stomata, "P" indicates that they are located in pits, "D" in depressions, "G" in grooves, and "S" that they are more or less superficial. There is no absolute dividing line between pits and depressions, although the two classes are usually quite distinct. The grooves are not actual cavities in the structure of the leaf, but are formed by the conspicuous curving of the margin towards the midrib of very narrow leaves.

The letters designating the type of hairs refer to the classes described in Section IV(*c*).

The columns referring to the epidermis between the stomatal areas are not filled in when the stomata are in grooves, as these grooves occupy all the lower epidermis, and the stomata are irregularly scattered over the whole surface. When the stomata are superficially placed, the epidermal characters are noted only when the stomata are restricted to definite areas. The epidermal cells of the actual stomatal areas always have thin, pitted walls, and cuticular papillae are never present.

The cells of the epidermis are only considered to be non-uniform when there is a very conspicuous difference in size between the cells – as, for example, in *Banksia baueri*. The number of papillae per cell is only approximate, and is included solely as a measure of their relative frequency.

Under the heading of hypodermal layers, "t" represents thin-walled cells and "f" thick-walled or fibrous ones; the figures indicate the number of layers present.

VII. Victorian Tertiary Banksieae

Six Tertiary leaf-types which possess positive characters connecting them with the Banksieae have now to be considered. Their shape (three have entire, one serrated, and two lobed margins), venation, and stomatal structure are quite consistent with such a determination. Moreover, cylindrical hair-bases of the type invariably found accompanying the stomata of living Banksieae also occur. In three of them the stomata are restricted to shallow pits; in the other three they are superficially situated.

Having reached satisfaction regarding the tribal affinities of the fossils, the question of a suitable name arose. Should von Ettingshausen (1888) and Deane (1925) be followed and the lobed types be associated with *Dryandra* and those having undivided or serrated leaf-blades with *Banksia*, or should a new genus be created to indicate relationship to the tribe rather than to either genus? In view of the inseparability of leaves of *Banksia* and *Dryandra*, demonstrated above, the latter course seems to be preferable. The authors therefore propose the name *Banksieaephyllum* for Australian Tertiary leaves, the form and structure of which conforms to those of living members of the Banksieae.

The present distribution favours this decision. *Banksia* is now widely distributed in Australia, where it is represented by forty-one western and ten eastern species. *Dryandra*, on the contrary, is confined to Western Australia. By referring fossil leaves from New South Wales and Victoria to *Dryandra*, von Ettingshausen (1888), and later Deane (1925), implied that this genus had a wider range in Tertiary times. This may have been the case, but their identifications, based as they were on leaf-form alone, are too uncertain to warrant such an assumption.

TABLE 1

CUTICULAR AND OTHER FEATURES OF *BANKSIA* LEAVES

BANKSIA	LOWER EPIDERMIS: Stomata: Distribution	LOWER EPIDERMIS: Stomata: Raised	LOWER EPIDERMIS: Margins of Stomatal Areas: Thickened	LOWER EPIDERMIS: Margins of Stomatal Areas: Epidermal Outgrowths	LOWER EPIDERMIS: Type of Hairs	LOWER EPIDERMIS: Epidermis between Stomatal Areas: Cuticle Granular	LOWER EPIDERMIS: Epidermis between Stomatal Areas: Cells Uniform	LOWER EPIDERMIS: Epidermis between Stomatal Areas: Lateral Walls Pitted	LOWER EPIDERMIS: Epidermis between Stomatal Areas: No. Papillae/Cell	LOWER EPIDERMIS: Epidermis between Stomatal Areas: Hair Bases: Present	LOWER EPIDERMIS: Epidermis between Stomatal Areas: Hair Bases: Large	LOWER EPIDERMIS: Epidermis between Stomatal Areas: Hair Bases: No. Cells/H.B.	MIDRIB: Lateral Walls Pitted	MIDRIB: Hair Bases	MIDRIB: Papillae	MIDRIB: Cuticular Ridges	MIDRIB: Epidermal Outgrowths	MIDRIB: Cells Uniform	UPPER EPIDERMIS: Cuticle Granular	UPPER EPIDERMIS: Lateral Walls Pitted	UPPER EPIDERMIS: Papillae	UPPER EPIDERMIS: Hair Bases: Present	UPPER EPIDERMIS: Hair Bases: Large	UPPER EPIDERMIS: Hair Bases: No. Cells/H.B.	UPPER EPIDERMIS: Hair Bases: Radial Cells around H.B.	Hypodermal Layers	Plates of Sclerenchyma
Sect. 1. Oncostylis																											
B. pulchella R.Br.	G	+	−	+	*a,e*								+	+	+	−	+	+	+	+	+	+	+	1-4	−	1t, 1f	−
B. meissneri Lehm	G	+	−	+	*a,e*								+	+	−	−	+	+	+	+	+	+	+	1-3	−	1t, 1f	−
B. nutans R.Br.	G	+	−	−	*a,e*								+	+	−	−	−	+	+	+	−	+	+	2-4	−	1f	−
B. sphaerocarpa R.Br.	G	+	−	−	*a,e*								+	+	−	−	−	+	+	+	−	+	+	1-2	−	1f	−
var. *violacea* C. A. Gard.	G	+	−	−	*a,f*								+	+	−	−	−	+	+	+	−	+	+	1-6	−	2f	−
B. tricuspis Meissn.	G	+	−	−	*a,e*								+	+	−	−	−	+	+	+	−	+	+	1-2	−	1t, 1f	−
B. occidentalis R.Br.	S	+	−	−	*a,b,e*								+	+	+	−	−	+	−	−	+	+	×	1	+	1t	−
B. littoralis R.Br.	S	+	−	−	*a,b,e*								+	+	−	−	−	+	−	+	+	−	−	—	−	1t	−
B. ericifolia Linn.	G	+	−	−	*a,e*								+	+	−	+	−	+	−	+	+	+	+	1-2	−	1t, 1f	−
B. spinulosa Sm.	S	+	−	−	*a,e*								+	+	−	−	−	−	−	+	+	+	+	1-4	−	1t	−
B. collina R.Br.	S	+	−	−	*a,e*								+	+	−	+	−	−	−	+	+	+	+	2-6	−	1t	−
B. verticillata R.Br.	S	+	−	−	*a,e*								+	+	−	−	−	−	+	+	+	+	+	1-4	−	2t	−
B. dryandroides Baxt.	S	+	−	−	*a,b,e*								+	+	−	−	−	+	−	+	−	+	+	1-2	×	1t, 1f	−
B. brownii Baxt.	G	+	−	−	*a,b,e*								+	+	+	−	−	+	+	−	+	+	×	1	−	1t	−
Sect. 2. Cyrtostylis																											
B. attenuata R.Br.	P	+	−	−	*a,f*	−	−	+	1-5	+	−	1	+	+	−	−	−	+	+	−	−	+	+,−	1-3	×	1t	+
B. media R.Br.	P	+	+	−	*a,b,f*	−	−	+	−	+	−	1	−	+	−	−	−	+	+	+	−	+	+	1-2	−	1t	+
B. solandri R.Br.	P	+	−	−	*a,b*	−	+	+	1-5	+	+,−	1-4	+	+	−	−	−	+	−	+	−	+	+	1-4	−	2t	+
B. goodii R.Br.	P	+	−	−	*b,f*	−	+	+	−	+	×	1	+	+	−	−	−	+	−	+	−	+	+	1-2	−	1t	+
B. petiolaris F.v.M.	P	+	−	−	*a,b,f*	+	+	+	−	+	×	1	+	+	−	−	−	−	−	+	−	+	+	1-3	−	1t	+
B. repens Labill.	P	+	−	−	*b,f*	+	+	+	−	+	−	1	−	+	−	−	−	+	−	+	−	+	+	1	−	1t	+
B. prostrata R.Br.	P	+	+	−	*b,f*	+	+	+	−	+	×	1	+	+	−	−	−	+	−	+	−	+	+	1	−	1t	+
B. grandis Willd.	P	+	+	−	*a,e,f*	+	+	+	−	+	×	1-3	+	+	−	−	−	+	−	−	−	+	−	1-3	−	1t	+
B. quercifolia R.Br.	P	+	−	+	*a,e*	−	+	+	−	−	−	—	+	+	−	−	−	+	+	+	−	−	−	−	−	1t, 1f	+
B. baueri R.Br.	P	+	+	−	*a,b,f*	+	−	+	1-10	+	−	1	+	+	−	+	−	−	−	+	−	+	−	1	−	1t	+
Sect. 3. Eubanksia																											
B. marginata Cav.	P	+	−	−	*a,e*	+	+	+	−	+	−	1	+	+	−	−	−	+	−	+	−	+	+	1-5	−	1t, 1f	+
B. integrifolia Linn.f.	P	+	−	−	*a,e*	+	+	+	−	+	−	1	+	+	−	−	−	+	−	+	−	+	+	1-2	−	1t, 1f	+
B. dentata Linn.f.	P	+	−	−	*a,e*	−	+	+	1-10	+	+,−	1	+	+	−	−	−	+	−	+	−	+	+	1	−	2f	+

TABLE 1 (*Continued*)

CUTICULAR AND OTHER FEATURES OF *BANKSIA* LEAVES

BANKSIA	LOWER EPIDERMIS: Stomata: Distribution	LOWER EPIDERMIS: Stomata: Raised	LOWER EPIDERMIS: Margins of Stomatal Areas: Thickened	LOWER EPIDERMIS: Margins of Stomatal Areas: Epidermal Outgrowths	LOWER EPIDERMIS: Type of Hairs	LOWER EPIDERMIS: Epidermis between Stomatal Areas: Cuticle Granular	Cells Uniform	Lateral Walls Pitted	No. Papillae/Cell	Hair Bases: Present	Hair Bases: Large	Hair Bases: No. Cells/H.B.	MIDRIB: Lateral Walls Pitted	MIDRIB: Hair Bases	MIDRIB: Papillae	MIDRIB: Cuticular Ridges	MIDRIB: Epidermal Outgrowths	UPPER EPIDERMIS: Cells Uniform	UPPER EPIDERMIS: Cuticle Granular	UPPER EPIDERMIS: Lateral Walls Pitted	UPPER EPIDERMIS: Papillae	UPPER EPIDERMIS: Hair Bases: Present	Hair Bases: Large	Hair Bases: No. Cells/H.B.	Hair Bases: Radial Cells around H.B.	Hypodermal Layers	Plates of Sclerenchyma
Sect. 4. Orthostylis																											
B. robur Cav.	P	+	−	−	*a,b,d,e*	+	+	+	−	+	+,−	2-4	+	+	−	−	−	+	+	+	−	+	+	1-5	−	1t, 1f	+
var. *minor*	P	+	−	−	*a,b,e*	−	+	+	−	+	+,−	1-2	+	+	−	−	−	+	+	−	−	+	+	2-5	−	1t, 1f	+
B. serrata Linn.f.	P	+	+	−	*a,f*	+	+	+	−	+	+	1-3	+	+	−	−	−	+	+	−	−	+	×	1-4	−	1t	+
B. serratifolia Salisb.	P	+	−	−	*a,b,f*	−	+	−	−	+	×	1-4	−	+	−	−	−	+	+	−	−	+	×	1-4	−	1t	+
B. ornata F.v.M.	P	+	−	−	*a,b,f*	−	+	+	−	+	×,−	1-3	+	+	−	−	−	+	+	+	−	+	+	1-2	−	1t	+
B. coccinea R.Br.	P	+	−	−	*a,b,f*	−	+	+	1-10	+	×	1	+	+	−	−	−	+	−	+	+	+	×	1-3	−	1t	+
B. sceptrum Meissn.	P	+	−	−	*a,f*	−	+	−	1-6	+	−	1	+	+	−	−	−	+	−	−	−	+	−	1-2	−	1t	+
B. menziesii R.Br.	P	+	−	−	*a,b,f*	−	+	−	−	+	−	1	+	+	−	−	−	+	−	−	−	−	−	−	−	2t	+
B. laevigata Meissn.	P	+	+	−	*b,e,f*	+	−	−	−	+	+	1	+	+	−	−	−	+	+	−	−	+	+	1-8	×	1t	+
B. hookeriana Meissn.	P	+	−	−	*a,f*	+	+	+	1-10	+	−	1	+	+	−	−	−	+	+	+	−	+	×	1	−	1t	+
B. prionotes Lind.	P	+	+	−	*a,b,e,f*	−	+	+	−	+	×	1-2	+	+	−	−	−	+	+	−	−	+	−	1	−	1t	+
B. victoriae Meissn.	P	+	−	−	*a,b,f*	−	−	+	1-10	+	×	1-2	+	−	−	+	−	+	+	+	−	+	+	1-4	−	1t	+
B. speciosa R.Br.	P	+	+	−	*a,b,f*	−	+	+	1-10	+	−	1	+	+	−	−	−	+	+	+	−	+	+	1-2	−	1t	+
B. baxteri R.Br.	P	+	−	−	*b,e*	−	+	+	5-20	+	+	1	+	+	−	−	−	+	−	+	+	+	+	1-4	+	2t	+
B. marcescens R.Br.	P	+	+	−	*a,e,f*	+	+	+	−	+	×	1	+	+	−	−	−	+	+	−	−	+	+	1-2	×	1t	+
B. lemanniana Meissn.	P	+	+	−	*b*	−	−	−	−	+	−	1-4	−	−	−	−	−	+	−	−	−	+	−	1-4	−	1t	+
B. caleyi R.Br.	P	+	+	−	*a,f*	+	+	+	−	+	+	1-4	+	+	−	−	−	+	−	+	−	+	×	1-2	−	1t	+
B. lindleyana Meissn.	P	+	+	−	*a,b,f*	+	+	+	−	+	×	1	+	+	−	−	−	+	+	−	−	−	−	−	−	1t	+
B. elegans Meissn.	P	+	−	−	*a*	+	+	+	−	+	×	1-2	+	−	−	−	−	+	−	+	−	+	×	1-2	−	1t	+
B. candolleana Meissn.	P	+	−	−	*b,f*	+	+	+	−	+	−	1	+	+	−	−	−	+	−	+	−	+	+	1-4	−	2t	+
Sect. 5. Isostylis																											
B. ilicifolia R.Br.	P	+	−	−	*a,f*	+	+	−	−	−	−	—	+	−	−	−	−	+	+	−	−	−	−	—	−	2t	+
B. ashbyi Bak.f.	P	+	−	−	*a,f*	+	+	+	−	+	−	1	−	+	−	−	−	+	−	+	−	+	+	1-4	−	2t	+
B. audax C. A. Gard.	P	+	+	−	*b,f*	+	+	−	−	+	+	1-2	+	+	−	−	−	−	+	−	−	+	−	1-5	−	1t	+
B. benthamiana C.A.G. (M.S.)	P	+	−	−	*b,f*	+	−	−	−	+	−	1	+	+	−	−	−	−	+	−	−	+	−	1	×	1t	+
B. burdettii Bak.f.	P	+	+	−	*a,b,f*	+	+	+	−	+	×	1	+	+	−	−	−	+	+	−	−	−	−	−	−	1t	+
B. drummondiana C.A.G. (M.S.)	P	+	+	−	*a,b,f*	+	−	+	−	+	−	1	+	+	−	−	−	+	−	+	−	+	×	1	−	1t	+
B. elderiana F.v.M.	P	+	+	−	*a,b*	+	+	−	−	+	+	1	+	+	−	−	−	+	+	−	−	+	+	1	−	1t	+
B. paludosa R.Br.	P	+	−	−	*a,e*	−	+	+	1-5	+	−	1	+	+	−	−	−	+	+	+	+	+	+	1	−	1t, 1f	+

TABLE 2

CUTICULAR AND OTHER FEATURES OF *DRYANDRA* LEAVES

	LOWER EPIDERMIS													MIDRIB					UPPER EPIDERMIS								
	Stomata		Margins of Stomatal Areas			Epidermis between Stomatal Areas				Hair Bases												Hair Bases					
DRYANDRA	Distribution	Raised	Thickened	Epidermal Outgrowths	Type of Hairs	Cuticle Granular	Cells Uniform	Lateral Walls Pitted	No. Papillae/Cell	Present	Large	No. Cells/H.B.	Lateral Walls Pitted	Hair Bases	Papillae	Cuticular Ridges	Epidermal Outgrowths	Cells Uniform	Cuticle Granular	Lateral Walls Pitted	Papillae	Present	Large	No. Cells/H.B.	Radial Cells around H.B.	Hypodermal Layers	Plates of Sclerenchyma
Sect. 1. Eudryandra																											
Ser. 1. Armatae																											
D. quercifolia Meissn.	P	+	−	−	*a,b*	+	+	+	1-6	+	+	1-4	+	+	−	−	−	+	+	+	−	+	+	1-4	−	1t	+
D. praemorsa Meissn.	P	+	−	−	*a,b,e*	−	−	+	20-40	+	+,−	1-2	+	+	−	+	−	+	−	+	+	+	+	1-4	−	1t	+
D. cuneata R.Br.	P	+	−	−	*a,f*	+	+	+	5-15	+	+,−	1-4	+	+	−	−	−	−	+	+	+	+	−	1	−	1t, 1f	+
D. falcata R.Br.	P	+	−	−	*a,f*	+	+	+	2-15	+	+,−	1	+	+	+	+	−	+	+	+	+	+	+	1	−	1t	+
D. armata R.Br.	P	+	−	−	*a,f*	+	+	+	1-15	+	−	1	+	+	−	−	−	+	−	−	−	+	+,×	1-2	−	1f	+
D. longifolia R.Br.	P	+	+	−	*b,f*	−	+	+	1-15	+	+	1	+	+	+	−	−	+	−	−	−	−	−	1	−	1t	+
D. fraseri R.Br.	P	+	−	−	*a,f*	−	+	+	1-15	+	−	1	+	+	+	−	−	+	+	+	+	+	+	2-4	−	1f	+
Ser. 2. Floribundae																											
D. floribunda R.Br.	P	+	−	−	*a,b,f*	+	+	+	1-10	+	×	1	+	+	+	−	−	−	−	+	+	+	+	1-4	−	1t	+
D. carduacea Lindl.	P	+	−	−	*a,b,f*	−	+	+	1-20	+	−	1	+	+	−	−	−	+	+	+	−	+	×	1	−	1t	+
D. carlinoides Meissn.	P	+	−	−	*a,b,e*	−	−	+	10-40	+	−	1	+	+	+	−	−	−	+	+	+	+	+,×	1-5	×	1f	+
D. polycephala Benth.	P	+	−	−	*a,b*	+	+	+	10-30	+	−	1	+	+	+	−	−	+	−	+	−	+	×	1	−	1t	+
D. kippistiana Meissn.	S	−	−	−	*a,b*	+	−	−	10-30	+	−	1	+	+	−	−	−	+	+	−	+	−	−	1	−	−	+
Ser. 3. Concinnae																											
D. squarrosa R.Br.	P	+	−	−	*b,e,f*	+	+	+	10-40	+	−	1	−	+	+	−	−	−	+	+	−	+	+	1	−	1t	+
D. serra R.Br.	D	+	−	−	*a,b,e*	−	+	+	10-30	+	−	1	+	+	+	−	−	+	+	−	+	+	+,×	1-4	−	1t	+
D. concinna R.Br.	S	−	−	−	*a,b,f*	−	−	−	−	+	−	1	+	+	−	−	−	+	−	−	−	+	×	1	−	−	+
D. foliolata R.Br.	S	−	−	−	*a,b,f*	+	−	−	1-10	+	−	1	+	+	−	−	−	+	+	−	+	+	+	1-2	−	−	+
Ser. 4. Formosae																											
D. stupposa Lindl.	P	+	−	−	*a,b,f*	−	−	+	1-20	+	−	1	−	+	+	−	−	+	+	+	+	+	−	1	−	1t	+
D. nobilis Lindl.	D	+	−	−	*a,b,f*	+	−	+	10-20	+	−	1	+	+	−	−	−	−	+	−	+	+	+	1-2	−	1t	+
D. mucronulata R.Br.	D	+	−	−	*a,b,e,f*	−	−	+	10-30	+	−	1	+	+	+	−	−	+	+	+	+	+	+	1	×	1t	+
D. formosa R.Br.	D	+	−	−	*a,b,f*	+	−	+	10-30	+	−	1	+	+	+	−	−	+	−	+	+	+	+	1	−	1t	+
D. baxteri R.Br.	S	+	−	−	*a,b,f*	−	+	+	10-20	+	−	1	+	+	+	−	−	−	+	+	+	+	×	1	−	1t	+
Ser. 5. Niveae																											
D. nivea R.Br.	P	+	−	−	*a,f*	−	+	+	15-40	+	−	1	+	+	+	−	−	+	+	−	+	+	×	1	−	1t	+
D. arctotidis R.Br.	P	+	−	−	*a,f*	+	+	+	5-15	+	−	1	+	+	+	−	−	−	+	+	+	+	+	1-2	×	1t	+
D. nana Meissn.	P	+	+	−	*a,b,e*	−	+	+	1-10	+	−	1	+	+	−	−	−	+	−	+	−	+	+	1-5	−	1t	+
D. preissii Meissn.	P	+	−	−	*a,f*	−	+	+	20-40	+	−	1	+	+	+	−	−	+	+	+	+	+	+	1-4	−	1t	+

TABLE 2 (*Continued*)

CUTICULAR AND OTHER FEATURES OF *DRYANDRA* LEAVES

DRYANDRA	LOWER EPIDERMIS												MIDRIB					UPPER EPIDERMIS									
	Stomata		Margins of Stomatal Areas			Epidermis between Stomatal Areas				Hair Bases												Hair Bases					
	Distribution	Raised	Thickened	Epidermal Outgrowths	Type of Hairs	Cuticle Granular	Cells Uniform	Lateral Walls Pitted	No. Papillae/Cell	Present	Large	No. Cells/H.B.	Lateral Walls Pitted	Hair Bases	Papillae	Cuticular Ridges	Epidermal Outgrowths	Cells Uniform	Cuticle Granular	Lateral Walls Pitted	Papillae	Present	Large	No. Cells/H.B.	Radial Cells around H.B.	Hypodermal Layers	Plates of Sclerenchyma
Ser. 6. Obvallatae																											
D. sclerophylla Meissn.	D	+	−	−	*a,b,e*	+	+	+	−	+	−	1	+	+	−	+	−	+	−	−	+	+	+	1-3	−	1t	+
D. pulchella Meissn.	D	+	−	−	*a,b,e*	+	−	+	10-20	+	−	1	+	+	+	−	−	+	+	+	+	−	−	1-2	−	1t	+
D. plumosa R.Br.	D	+	−	−	*a,e,f*	+	−	+	10-20	+	×,−	1	+	+	−	−	−	+	+	+	−	+	+	1-4	−	1t	+
D. seneciifolia R.Br.	D	+	−	−	*a,f*	+	+	−	10-20	+	×,−	1	+	+	+	−	−	−	+	−	+	+	+,×	1-2	−	1f	+
D. vestita Kipp.	P	+	+	−	*a,b,e,f*	+	+	+	1-10	+	−	1	+	+	−	−	−	+	−	−	−	+	+	1-4	−	1f	+
D. cirsioides Meissn.	P	+	−	−	*a,e,f*	−	+	+	1-10	+	×,−	1-2	+	+	−	−	−	+	+	+	−	+	×	1-2	−	1f	+
D. hewardiana Meissn.	P	+	−	−	*a,b,f*	−	+	+	1-30	+	−	1	+	+	+	−	−	+	+	+	+	+	×	1	−	1t	+
D. patens Benth.	P	+	−	−	*a,b,f*	−	+	+	10-30	+	−	1	+	+	+	−	−	+	−	+	−	+	×	1	−	1t	+
D. conferta Benth.	P	+	−	−	*a,b*	+	−	+	−	+	×,−	1	+	+	−	−	−	−	+	+	−	+	+,×	1	−	1f	+
D. horrida Meissn.	P	+	−	−	*a,f*	+	+	+	1-10	+	−	1	+	+	+	−	−	+	−	+	−	+	×	1-2	−	1f	+
D. serratuloides Meissn.	P	+	−	−	*a,b,e*	−	+	−	1-10	+	×,−	1	+	+	+	−	−	+	+	−	−	+	+,×	1-2	−	1f	+
D. comosa Meissn.	P	+	−	−	*a,b,f*	+	+	−	1-10	+	−	1	+	+	−	−	−	+	+	−	−	+	+,×	1-2	−	1f	+
Ser. 7. Gymnocephalae																											
D. shuttleworthiana Meissn.	P	+	−	−	*a,e*	−	+	+	1-15	+	−	1	+	+	+	−	−	+	+	+	+	+	×	1	−	1f	+
D. speciosa Meissn.	P	+	−	−	*a,f*	−	−	+	−	+	−	1	+	+	−	−	−	+	−	+	−	+	×	1-2	−	1f	+
D. tridentata Meissn.	P	+	−	−	*a,e*	+	+	+	2-8	−	−	1	+	+	−	−	−	+	+	+	−	+	+	1-4	−	1t	+
Sect. 2. Aphragmia																											
D. tenuifolia R.Br.	D	+	−	−	*a,e*	−	+	+	1-10	+	−	1	+	+	−	−	−	+	+	−	−	+	−	1	−	1t	+
D. proteoides Lindl.	P	+	−	−	*a,b,f*	−	+	+	1-20	+	−	1	+	+	−	−	−	+	+	+	+	+	×	1-2	−	1t	+
D. runcinata Meissn.	P	+	−	−	*a,b,f*	+	+	+	10-30	+	−	1	+	+	−	−	−	+	−	+	−	+	×	1-2	−	1t	+
D. obtusa R.Br.	P	+	−	−	*a,b,e*	−	+	+	1-15	+	−	1	+	+	−	−	−	+	−	+	−	+	+,×	1-2	−	1t	+
D. bipinnatifida R.Br.	D	+	−	−	*a,b,e*	+	−	+	−	+	+,−	1	+	+	−	−	−	+	+	+	−	+	+	1-2	+	1f	+
D. pteridifolia R.Br.	P	+	−	−	*a,b,f*	−	+	+	1-10	+	×	1	+	+	−	−	−	+	−	+	−	+	+	1	−	1t, 1f	+
D. calophylla R.Br.	P	+	−	−	*a,b,e,f*	+	−	+	1-30	+	−	1	+	+	−	−	−	+	+	−	+	+	+,×	1-2	−	1t	+
D. ashbyi Burtt	D	+	−	−	*b,d,e*	−	+	+	1-15	+	−	1	+	+	+	−	−	+	+	+	+	+	×	1	−	1f	+
D. erythrocephala C.A.Gard.	P	+	−	−	*a,b,f*	+	+	+	1-15	+	−	1	+	+	+	−	−	+	+	+	+	+	+,×	1-4	−	1f	+
D. gilbertii S. Moore	P	+	−	−	*a,b,f*	+	−	+	1-10	+	×	1	−	+	−	−	−	+	+	−	−	+	×	1-4	−	1f	+
D. purdieana Diels	P	+	−	−	*a,b,f*	+	+	+	1-10	+	−	1	+	+	−	+	−	+	+	+	−	+	×	1-2	−	1f	+

VIII. Genus Banksieaephyllum n. gen.

Table 3

Leaves simple with entire, serrate, or lobed margins, or pinnate; bilateral. Stomata either superficial, or in pits or grooves, each with a pair of subsidiary cells placed parallel to the pore. Cells of the stomatiferous epidermis with thin, pitted, straight or slightly curved lateral walls, some with bicellular hairs. The basal cells of the hairs are either thick- or thin-walled, of even diameter throughout or expanded distally. Cylindrical hair-bases present on some or all cells of the non-stomatiferous epidermis. Cuticular papillae sometimes present.

Banksieaephyllum angustum n. sp.

Plate 1, Figs. 1-10

(a) *External Characters*

The description of this type has been derived from a large number of leaf-fragments amongst which, however, neither a complete leaf nor a leaf-apex has been seen, and only exceptionally is the extended petiolar region preserved. The shape of the leaf of *B. angustum* is best shown by the large specimen illustrated in Plate 1, Figure 1. It is narrow-linear and gradually narrows towards both apex and base. The total length preserved in this example is 15 cm. but, allowing for the missing portions, its total length must have approached 20 cm.

The lamina is divided about half-way to the midrib into numerous small, triangular lobes, each with a prominent, forwardly directed mucro (Plate 1, Fig. 3). These segments are frequently opposite but may alternate slightly on either side of the midrib. The leaves, in their central region, are 3-4 mm. wide, the lobes themselves having a depth of about 0.75 mm. Towards the petiole the lobing becomes decreasingly evident until it is represented only by slight crenulations on either side of the midrib (Plate 1, Fig. 4). The margins are strongly revolute.

The midrib is a conspicuous feature of the under surface and has a width of 0.75-1 mm. (Plate 1, Fig. 3). The secondary veins are prominent and arise from the midrib at right angles. One secondary vein terminates in the apex of each lobe and one at each sinus (Plate 1, Fig. 5), two slightly less prominent veins being situated between them. Anastomoses occur between the finer secondary veins, with the result that the lower surface under a low magnification is clearly aereolate (Plate 1, Fig. 5).

(b) *Cuticular Structure*

(i) *Lower Epidermis* (Plate 1, Fig. 10).—The stomata occur in rather large shallow depressions which occupy the meshes of the vascular network. These areas measure 120-470 μ across and are separated from one another by the several rows of parenchyma which cover the veins. The stomata are raised above the level of the surrounding epidermis and each is accompanied by a pair of subsidiary cells placed parallel to the pore. The epidermal cells are

TABLE 3

CUTICULAR AND OTHER FEATURES OF *BANKSIEAEPHYLLUM* LEAVES

	LOWER EPIDERMIS												MIDRIB					UPPER EPIDERMIS									
	Stomata		Margins of Stomatal Areas			Epidermis between Stomatal Areas				Hair Bases												Hair Bases					
BANKSIEAEPHYLLUM	Distribution	Raised	Thickened	Epidermal Outgrowths	Type of Hairs	Cuticle Granular	Cells Uniform	Lateral Walls Pitted	No. Papillae/Cell	Present	Large	No. Cells/H.B.	Lateral Walls Pitted	Hair Bases	Papillae	Cuticular Ridges	Epidermal Outgrowths	Cells Uniform	Cuticle Granular	Lateral Walls Pitted	Papillae	Present	Large	No. Cells/H.B.	Radial Cells around H.B.	Hypodermal Layers	Plates of Sclerenchyma
B. angustum	P	+	–	–	*a,f*	–	+	+	–	+	–	1	+	+	–	–	–	+	+	–	–	–	–	1	–	2t	+
B. acuminatum	P	+	–	–	*a,e*	–	+	+	–	+	–	1	+	+	–	–	–	+	+	+	–	+	+	1	–	2t	+
B. laeve	S	+	–	–	*a,?*	–	+	+	–	+	+,–	1-4	+	+	–	–	–	+	–	–	+	–	–	1-3	–	–	+
B. obovatum	S	+	–	–	?	+	–	–	10-20	+	–	1							–	–	–	–	–	1	–	–	+
B. pinnatum	S	+	–	–	?	+	–	–	–	+	–	1	+	+	–	–	–	–	+	–	–	–	–	1	–	–	+
B. fastigatum	D	–	–	–	?	+	–	+	–	+	–	1	–	+	–	+	–	–	+	–	–	+	–	1	–		

small, with diameters of about 14-28 μ and vary considerably in shape; their lateral walls are thin, 1.5 μ, straight to slightly curved, and rather strongly pitted. At least 90 per cent. of the cells support thin-walled cylindrical hair-bases. These have basal diameters of about 6-11 μ with either a uniform diameter throughout (cf. type (*a*)) or are gradually expanded distally as in type (*f*) of the Banksieae.

(ii) *Midrib*.—The cells are quadrangular and their lateral walls thick and pitted. Hair-bases 11-14 μ wide are numerous near the edges.

(iii) *Upper Epidermis* (Plate 1, Fig. 9).—The cells form a uniform parenchyma; they are small, 16-28 μ in diameter, five- to six-sided, and without hair-bases. Their lateral walls are straight or curved, about 3 μ thick, and unpitted. The cuticle is granular. Hair-bases are present only on the elongated cells which cover the midrib.

(*c*) *Internal Anatomy*

Plate 1, Figs. 7, 8

The cells of the upper epidermis, as seen in transverse section, are small and cubical; their outer walls, which are about 14 μ thick, are highly cutinized, the cutinization extending into the lateral walls. Between the epidermis and palisade parenchyma are two layers of hypodermis, the cells of which are larger than those of the epidermis. The mesophyll is crossed at intervals by vertical plates of fibres which, as in living Banksieae, pass from the vascular bundles to the hypodermis on either surface. The outer walls of the lower epidermal cells are about 8 μ thick.

Occurrence: Brown coal, Yallourn and Yallourn North, Victoria.

Localities: Shovel face, east side, Yallourn open cut, near pole 70, 9.xi.49. No. 2 coal face, east side, below pole 70, 24.xi.49.

Banksieaephyllum acuminatum n. sp.

Plate 2, Figs. 11-19

(*a*) *External Characters*

The specimens of *B. acuminatum* do not include a complete leaf, but the preservation in some of the fragments of either the basal or terminal regions allows a fairly accurate picture to be reconstructed. The leaves are broadly linear and taper gradually towards the base and sharply towards the short, pointed apex. The basal region was apparently long, the example shown in Plate 2, Figure 13, measuring 4.5 cm. without showing any appreciable expansion of the lamina. The width of the middle region ranges from 5 to 9 mm. and portions with straight sides of up to 5 cm. are preserved. It seems probable, therefore, that some of the leaves of this species were considerably longer than 10 cm. The leaf margin is entire and strongly recurved.

The midrib, 1-2 mm. wide, and the vascular network are both strongly marked on the under surface (Plate 2, Fig. 14). The secondary veins arise from the midrib at a wide angle and run out parallel to one another. They are not equally prominent; the stronger laterals 1.5-2 mm. apart bifurcate a short distance from the margin, the branches curving back to join those from the weaker and shorter laterals on either side.

(*b*) *Cuticular Structure*

(i) *Lower Epidermis* (Plate 2, Figs. 15, 18, 19).—The raised stomata and their accompanying subsidiary cells placed parallel to the pore are restricted to the parenchyma lining rather large pits. The diameter of these pits ranges from 380 to 500 μ. The epidermal cells are small, four- to six-sided, and have diameters of approximately 14-28 μ; their lateral walls are thin, about 1.5 μ, straight or slightly curved and strongly pitted. Practically all cells, both inside and outside the pits, support hair-bases. These are from 8.5 to 11 μ wide, and are moderately thick-walled. Some hairs have straight sides, and are similar to type (*a*); others, resembling type (*e*), have a distal expansion of up to 28 μ with the hair-cell occupying the central portion of the hair-base. The short lengths of the hair-cells retained in some cases suggest that they were probably about 5-6 μ wide (Plate 2, Fig. 19). A few larger hair-bases, 16-22 μ wide, occur on the larger secondary veins.

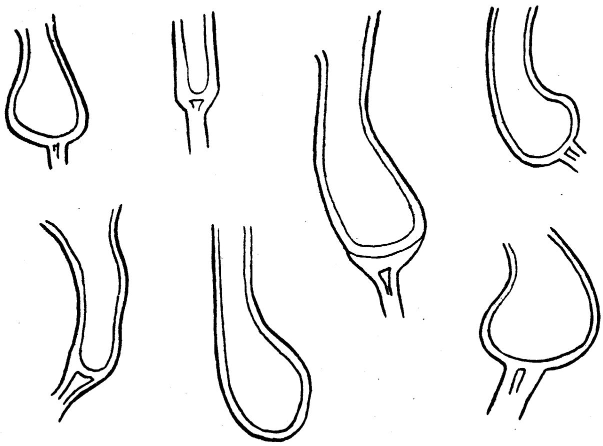


Fig. 4.—Hairs of *Banksieaephyllum acuminatum*. x 535.

(ii) *Midrib*.—The cells covering the midrib are square to quadrangular, their walls are thin and the cross-walls pitted. Short, thin-walled hair-bases 24-25 μ wide are numerous at the edges but sparsely developed or absent from the central region.

(iii) *Upper Epidermis* (Plate 2, Fig. 17).—The parenchyma is uniformly composed of four- to six-sided cells with maximum diameters of 16-36 μ. Their lateral walls are occasionally heavily thickened, 4-8.5 μ wide, straight, and pitted. Large hair-bases are sometimes sparingly present. The cuticle is granular.

(*c*) *Internal Anatomy*

Plate 2, Fig. 16

The upper epidermal cells are cubical with much thickened (16 μ), highly cutinized outer walls. They are separated from the palisade parenchyma by a two-layered hypodermis, the cells of which are larger than those of the epidermis. Vertical plates of fibres occur at frequent intervals in the palisade tissue. The cells of the lower epidermis have cutinized outer walls about 8 μ thick.

Occurrence: Brown coal, probably from S.E.C. open cut, Yallourn North.

BANKSIEAEPHYLLUM LAEVE n. sp.

Plate 3, Figs. 20-26

The reference of the fragmentary remains of this type to a distinct species of *Banksieaephyllum* is substantiated by their perfectly preserved cuticles. The specific name has been chosen on account of the smooth under surface, due to the inconspicuousness of the veins, a feature in which this form differs from both the previous species.

(*a*) *External Characters*

No information regarding the shape of the complete leaf is available but one fragment (Plate 3, Fig. 21) shows that the width of the blade was not uniform. The largest fragment is 4 mm. wide and 1.6 cm. long. The margin is entire, slightly thickened, but not recurved as in *B. angustum* and *B. acuminatum*. A wide midrib (1 mm.) is conspicuous underneath; the fine secondaries, visible on upper surface only, arise from the midrib at a wide angle and run parallel to one another towards the margins of the leaf.

(*b*) *Cuticular Structure*

(i) *Lower Epidermis.*—The raised stomata are numerous, superficially situated, and each is accompanied by two rather large subsidiary cells placed parallel to the pore. The interstomatal parenchyma is composed of small cells with thin (1 μ), straight or somewhat curved, pitted walls and about 90 per cent. support hair-bases. These are rather thin-walled and of two sizes, small ones with straight sides and diameters of 5-8.5 μ (cf. type (*a*)) and large ones 14-28 μ across, which are associated with from one to four epidermal cells.

The position of the veinlets is indicated by one to three rows of cells with long axes parallel to the course of the veins; most of these cells carry hair-bases similar to those of the interstomatal parenchyma.

(ii) *Midrib.*—The cells are square to quadrangular and thick-walled, the cross-walls being pitted; hair-bases are present.

(iii) *Upper Epidermis.*—The parenchyma is uniform; its cells are small (Plate 3, Fig. 26), five- to six-sided with straight, unpitted, lateral walls about 2 μ thick. The cuticle appears to be indistinctly papillate. Hair-bases are absent.

(*c*) *Internal Structure*

Transverse sections (Plate 3, Fig. 24) show that this leaf was much thinner (approximately 140 μ in the fossilized condition) than leaves of *B. angustum* and *B. acuminatum*. This is largely due to the development of only one layer of small palisade cells and the absence of hypodermal layers. The upper epidermal cells are small, cubical and the outer walls, though cutinized, are relatively thin (3 μ). Slender vertical strands of fibres cross the mesophyll at intervals.

Occurrence: Yallourn, Victoria.

Locality: Open cut, No. 1 batter, east side.

BANKSIEAEPHYLLUM OBOVATUM n. sp.

Plate 4, Figs. 27-34

(*a*) *External Characters*

These have been derived from the sole specimen available, shown at natural size in Plate 4, Figure 27. The leaf, which is incomplete, measures 7.2 cm. and its maximum width is 12 mm. It is obovate-oblong with an entire, slightly recurved margin and it narrows towards the base. The midrib is relatively broad (1 mm.) on the under surface but the secondary veins are not visible; their position and general direction, however, are indicated on the upper surface by delicate grooves which run from the midrib at right angles.

(*b*) *Cuticular Structure*

(i) *Lower Epidermis* (Plate 4, Figs. 30-33).—The stomata are superficially situated in clearly defined areas marked out by the several layers of parenchyma cells which cover the veinlets. The guard-cells, which are slightly raised, are accompanied by a pair of inconspicuous subsidiary cells lying parallel to the pore, and the whole stomatal apparatus is surrounded by three or four encircling cells which are smaller and stain more deeply than the general epidermal cells.

The cells of the epidermal parenchyma are of two conspicuously distinct forms, firstly very small, three-, four-, or five-sided cells 5-8 μ in diameter which support thick-walled cylindrical hair-bases of about the same width, and secondly, medium-sized cells of various shapes without hair-bases which have thin, unpitted, curved lateral walls. The cuticle of most of the epidermal cells, including that of the encircling cells of the stomata, is papillate. There are approximately 10 to 20 small papillae per cell (Plate 4, Fig. 31).

(ii) *Upper Epidermis* (Plate 4, Fig. 29).—The cells above the veins are smaller and slightly thicker-walled than those of the areas enclosed by them. All have straight, unpitted walls. Neither hair-bases nor cuticular papillae occur.

(*c*) *Internal Anatomy*

Plate 4, Fig. 34

The upper epidermal cells are cubical with relatively thin, but highly cutinized, outer walls (3 μ). Hypodermal layers are absent but a well-defined sclerenchymatous network is present.

Occurrence: Brown coal, Yallourn, Victoria.

Locality: Yallourn open cut, No 1 coal face, east side, below pole 30, 9.xi.49.

BANKSIEAEPHYLLUM PINNATUM n. sp.

Plate 5, Figs. 37-42

(*a*) *External Characters*

Plate 5, Figs. 35, 37

As the sole specimen available was a portion of a leaf about 2 cm. long, no conclusions regarding size or shape can be drawn. The leaf is divided to the midrib into flat, entire, broadly-falcate, obtuse segments 3-4 mm. long and 4-5 mm. broad.

The midrib is very narrow above, 1 mm. broad below. The secondary veins are at right angles to the midrib and run directly to the margin, the most conspicuous being those passing to the tips of the segments; they are seen only on the upper surface.

(*b*) *Cuticular Structure*

(i) *Lower Epidermis* (Plate 5, Figs. 40, 42).—The stomata occur in slightly depressed areas delimited by the ultimate branches of the veins. They are accompanied by pairs of subsidiary cells lying parallel to the pore and are raised above the surrounding epidermis. The subsidiary cells in this type, however, are often difficult to see and are never prominent.

The epidermal parenchyma is composed of cells of two sizes, moderately large cells with exceedingly thin (1 μ), straight, pitted walls, and very small cells (5.5 μ) situated at the junctions of several of the large ones, which support thick-walled cylindrical hair-bases with diameters approximately equal to their own.

(ii) *Midrib*.—The cells are somewhat elongated, and have thin, slightly pitted walls. Small hair-bases are present at the junctions of some of the cells.

(iii) *Upper Epidermis* (Plate 5, Fig. 39).—The cuticle of the upper surface is divided into approximately equal areas by small, thick-walled cells which lie above the veins. The cells become larger and their walls thinner towards the centres of these areas. The lateral walls are unpitted. Hair-bases are absent.

(*c*) *Internal Anatomy*

Plate 5, Fig. 41

In transverse section the cells of the upper epidermis above the veins appear radially elongated and convergent towards the strands of fibres which cross the mesophyll at rather frequent intervals. The epidermal cells between the veins are square in section. All have cutinized outer walls about 11 μ thick. The outer walls of the under epidermis are thinner (5.5 μ). A hypodermis is not developed.

Occurrence: Open cut, Yallourn, Victoria.

BANKSIEAEPHYLLUM FASTIGATUM (Deane) n. comb.

Plate 6, Figs. 43-47

The leaf-type from the brown coal deposit at Yallourn North described by Deane (loc. cit.) under the name *Banksia fastigata* was recently collected at the open cut at Yallourn. This new material, from which the specimen shown in Plate 6, Figure 44, was obtained, agrees so closely with Deane's description and figures of *B. fastigata* that there is little doubt of its identity with that species. Satisfactory cuticular preparations were obtained from it, the study of which has led to the conclusion that *B. fastigata* Deane is allied to the species of *Banksieaephyllum* described above. Since the use of the generic name *Banksia* for fossil types has been shown to be misleading, the authors suggest as a suitable alternative the combination *Banksieaephyllum fastigatum.*

(*a*) *External Characters*

Plate 6, Figs. 43, 44

The following is Deane's specific description. "Leaves rather long and tapering both at base and apex. The name is given as descriptive of this character. Width, about 3/5 inch, regularly toothed, the lobes turned towards the apex, sinuses often one-third of the distance from midrib to tip of tooth, lateral veins curved, one terminating each tooth and one each sinus."

(*b*) *Cuticular Structure*

(i) *Lower Epidermis* (Plate 6, Figs. 47, 48).—The stomata are situated in slight depressions, the long axes of which tend to be oriented in one direction. The individual stomata appear to be slightly sunk below the surface of the surrounding epidermis. Lying parallel to the pore of each stoma are two inconspicuous subsidiary cells, over which the neighbouring epidermal cells may project slightly. The stomatal apparatus is surrounded by from three to six narrow cells which stain deeply.

The epidermal parenchyma is not uniform. Most of its cells are of medium size with, in the stomatal areas, straight or curved, very thin and pitted walls, and above the veins similar but somewhat thicker walls. Amongst them are scattered exceptionally small cells, 4-6 μ in diameter, which support hair-bases of similar size.

(ii) *Midrib*.—The cells are small, square to quadrangular, with moderately thick, unpitted walls; small hair-bases are sparsely developed. The cuticle is longitudinally ridged.

(iii) *Upper Epidermis*.—The cells above the veins are somewhat smaller than those of the areas enclosed by them. All have rather thin, unpitted, straight or slightly curved walls.

Occurrence: Brown coal, Yallourn and Yallourn North, Victoria.

IX. Discussion

The six species of *Banksieaephyllum,* while agreeing in general form and structure with living members of the Banksieae, cannot be identified with any particular species of this tribe.

In view of the present restriction to Western Australia of species of *Banksia* having pinnate leaves or simple leaves with deeply lobed margins, it is of interest to note the occurrence in eastern Australia of fossil Banksieae possessing these features. In *Banksieaephyllum angustum* the lamina is divided about half-way to the midrib into triangular segments, while in the leaf of *B. pinnatum* the subdivision extends to the midrib. The fossil leaf of *Dryandra urniformis* Deane from Yallourn North is also pinnate but since the authors have been unable to examine the structure of this species further comment is not made.

Deane (1925, p. 494) has already referred to the broad apex typical of leaves of living species and contrasted it with the tapering tip of his species *B. fastigata* (here referred to as *Banksieaephyllum fastigatum*). The leaf of *B. acuminatum* also has an acute apex. The apex of *B. obovatum,* on the other hand, is obtuse and the general form of the leaf closely approaches that of the Victorian species *Banksia integrifolia.*

The leaves of the species of *Banksieaephyllum* show the same variations in the disposition of the stomata as those of living Banksieae. In *B. acuminatum* and *B. angustum* the stomata line the epidermis of distinct pits. In *B. pinnatum, B. obovatum,* and *B. fastigatum* they are superficially placed in distinct areas marked out by the cells covering the veins. In *B. laeve* they are diffusely arranged as in *Dryandra kippistiana.*

When considered collectively, the species of *Banksieaephyllum* appear to fall naturally into two groups according to the character of the parenchyma of the upper and lower surfaces and the degree of hairiness of the latter. The parenchyma of the under surface of *B. angustum, B. acuminatum,* and *B. laeve* is uniform and strongly hairy, the hair-bases approximating closely to those of some species of *Banksia* and *Dryandra.* In *B. pinnatum, B. obovatum,* and *B. fastigatum,* however, hair-bases are sparsely developed and the parenchyma is not uniform, with a marked difference in size and shape between the small cells which support the hair-bases and those of the larger ones of the general epidermis. The epidermal parenchyma of several species of *Banksia* and *Dryandra* is similarly differentiated, sometimes on the upper as well as the lower surface, e.g. *B. benthamiana* (Plate 8, Fig. 61). They also show the same pronounced difference in size, but in none are the cells with hair-bases as small as they are in the fossil species, where the diameter is only about 5.5 μ.

The upper epidermis of *Banksieaephyllum angustum, B. acuminatum,* and *B. laeve* is composed of uniform straight-sided cells with thick lateral walls. Hair-bases, as in a few living Banksieae (Tables 1, 2) are usually entirely absent, but occur, occasionally, in *B. acuminatum.* In *B. obovatum, B. pinnatum,* and *B. fastigatum* the upper epidermis has a patterned appearance due to the different size and shape of the cells covering the veins from those of the areas enclosed by them.

The hair-bases of the fossils are, on the whole, thinner-walled than those of the living species, where the walls usually attain a considerable thickness. In only one species—*B. laeve*—are large and small hair-bases associated together as they are, for example, in *Banksia robur*. The occurrence in *B. angustum* and *B. acuminatum* of hair-bases closely similar to those of types (*e*) and (*f*) of living forms is of interest.

The development of cuticular papillae in *Banksieaephyllum laeve* and *B. obovatum* provides a close link with living Banksieae, in which they are frequently present. In *B. laeve* the papillae, which are only faintly defined, are restricted to the cuticle of the upper epidermis. In *B. obovatum* they are more clearly outlined and occur on all the cells of the lower epidermis without hair-bases.

As far as the internal structure of the fossil leaves is concerned, that of *B. acuminatum* and *B. angustum* approaches most closely to the structure typical of leaves of *Banksia* and *Dryandra*. The outer walls of the upper epidermal cells are considerably thicker than those of the other fossil species; there is a two-layered hypodermis in both types and the anastomosing sclerenchymatous strands are numerous and prominent. In contrast to this the outer walls of the upper epidermal cells of *B. laeve* and *B. obovatum* are thinner than those of any living species. In both species, as well as in *B. pinnatum*, a hypodermis is not developed. This structure is absent only from the leaves of *Dryandra kippistiana*, *D. serra*, and *D. concinna*.

X. Fruiting Cones of Banksia sp.

Plate 7, Figs. 49-56

Evidence of the presence of *Banksia* in beds regarded by early Victorian geologists as of older Pliocene age was provided by the discovery of fruiting cones and wood during gold mining operations almost a century ago. The age of the Victorian older deep leads is still in doubt but Mr. W. Baragwanath and Dr. D. Thomas of the Victorian Mines Department believe that they are probably pre-Pliocene.

The earliest record of the occurrence of *Banksia* appeared in a paper by Redeway (1858) on the gold diggings of Creswick Creek and Ballarat, in which he remarked "The cones of the 'honeysuckle' or *Banksia* have been found not unfrequently in this drift. These are very brittle, but the wood is often well preserved." In a footnote the author stated that some of the cones "were submitted by Sir R. Murchison to the late Dr. R. Brown, who identified them as belonging to *Banksia*."

Several later references occur in the Reports of Progress of the Geological Survey of Victoria. Smyth in 1873 stated that "In the leads at Chiltern and at Creswick the cones of the *Banksia*, scarcely to be distinguished from those gathered now in the forest, are associated with rich auriferous gravels." In 1875 he wrote further that "Cones of *Banksia* (like *Banksia ericifolia*) are found in some leads."

Since fossil fruiting cones of *Banksia* have not hitherto been illustrated, a photograph has been included (Plate 7, Fig. 49) of a specimen belonging to the Geological Survey Museum from the deep leads at Eldorado, Victoria. It contains a high proportion of mature fruits, in a few of which the valves are widely separated.

Banksia cones occur also in lignite from an unspecified locality at Yallourn, thus confirming other evidence of the presence of the genus in early Tertiary times. Two specimens have been available for examination, and both are figured in Plate 7. The one shown in Plate 7, Figure 50, is a small cone 4.5 cm. long and about 2 cm. wide. On its exposed surface bracts and bracteoles can be clearly distinguished, but no fruits are evident. This cone may have been sparingly fertile or even infertile, a condition often met with in living species.

The second cone has been split longitudinally, and the apical region, shown enlarged in Plate 7, Figure 52, completely detached. Its impression, however, can be seen in the half illustrated in Plate 7, Figure 51. This cone is 5.5 cm. long and 3 cm. wide and its woody axis measures 5 mm. across. A large number of bracts and bracteoles, whose radial measurement is about 2 mm., are crowded on the axis and amongst them are suggestions of possible fruit valves. The bracts can be removed from the axis and preparations made of the matted hairs with which they are invested. These hairs (Plate 7, Fig. 55) are long, about 22 μ wide, and have moderately thick, spirally twisted walls similar to those of type (*d*) of the living Banksieae (Fig. 1). Cuticles detached from the bracts show that the basal cells of these hairs are thin-walled and about 22 μ wide throughout. Hairs showing features similar to these occur on bracts of *Banksia integrifolia* and *B. marginata* (Plate 7, Fig. 56).

Occurrence: Deep leads, Eldorado, Victoria. Brown coal, probably from the open cut at Yallourn North, Victoria.

XI. Records of Leaves of the Banksieae from Australian Tertiary Deposits

In order to complete the account of the fossil Banksieae, a list is included of all Australian records which have been validly published (Table 4). Fossil leaves which have been identified as members of this tribe have been found in Tasmania, Victoria, New South Wales, Queensland, South Australia, and Central Australia. Although *Banksia* and *Dryandra* have reached their greatest present-day development in Western Australia, no fossil species has been recorded from that State. This is doubtless partly due to the paucity of Tertiary deposits there, and to the fact that little palaeobotanical research has been carried out in connection with these deposits.

A total of 19 species has been previously recorded. However, much of the material on which these determinations have been based is fragmentary, and thus descriptions and illustrations are frequently inadequate. Without other evidence, it is impossible to decide whether all these species are really distinct, or to confirm their affinities with the tribe Banksieae or even the family Proteaceae. Because of these difficulties, no attempt has been made to include these fossils in the genus *Banksieaephyllum* unless type specimens have been available.

TABLE 4

AUSTRALIAN RECORDS OF FOSSIL BANKSIEAE AND MYRICACEAE

Species	Tas.	Vic.	N.S.W.	Qld.	Cent. Aust.
Banksieae					
Banksia adunca Deane (1925)		x			
B. blaxlandi Ett. (1888)			x		
B. campbelli Ett. (1888)			x		
B. crenata Ett. (1894)				x	
B. cretacea Ett. (1894)				x	
B. fastigata Deane (1925)		x			
B. hovelli Ett. (1888)				x	
B. lancifolia Ett. (1888)	x		x		
B. lawsoni Ett. (1888)			x		
B. myricaefolia Ett. (1888)			x		
B. plagioneura Ett. (1894)				x	
B. poolii Ett. (1888)			x		
B. praegrandis Chap. (1937)					x
B. sub-longifolia Ett. (1894)				x	
B. cf. *marginata* Cav. Chap. (1937)					x
Dryandra benthami Ett. (1888)				x	
D. praeformosa Ett. (1888)				x	
D. urniformis Deane (1925)		x			
Dryandroides johnstonii Ett. (1888)	x				
Myricaceae					
Myrica eyrei Ett. (1888)	x				
M. konincki Ett. (1888)			x		
M. pseudo-lignitum Ett. (1894)				x	
M. pseudo-salix Ett. (1888)			x		
M. subsalicina Shirley (1898)				x	
Myricophyllum longepetiolatum Ett. (1894)				x	

Deane (1900) points out that there is frequently a strong resemblance between the leaves of some *Banksia* and *Dryandra* species and those of certain species of *Myrica*. The similarity between these forms, coupled with the facts of their present-day distribution, tend to suggest that Australian fossil representatives of the genus *Myrica* may have been incorrectly identified. If this is so, it is possible that they should be placed in the tribe Banksieae. Table 4 includes the species of *Myrica* described from Australian Tertiary deposits, although it is impossible to voice an opinion as to their true affinity until further material is available.

XII. Palaeoecological Considerations

The six species of *Banksieaephyllum* described in the present paper exhibit various degrees of xeromorphism, this phenomenon being particularly evident in *B. angustum* and *B. acuminatum*. It is of interest, therefore, to consider the plants with which they may have been associated and the climatic conditions under which they may have lived.

The first published work on fossil plants from the lignites at Yallourn and the Latrobe valley generally appeared in 1922 when Miss Nobes described the wood of four conifers. No definite assertions were made, however, regarding their relationship with living genera.

In 1925, Chapman published two papers dealing with material from the same area. In one he noted wood fragments which he considered were derived from trees allied to *Callitris* and *Casuarina*, in the other a seed resembling those of modern cycads. In the same year Deane described and illustrated leaves which he identified as belonging to species of *Banksia, Lomatia, Dammara* (now *Agathis*), *Ginkgo, Phyllocladus, Cinnamomum*, and *Tristania*.

In 1945, Cookson reported the occurrence of pollen grains of the Podocarpaceae, *Casuarina*, and *Nothofagus* in the lignites of eastern Victoria and in 1946 recognized the pollen grains of three distinct species of *Nothofagus* from this Yallourn deposit; a leaf believed to have belonged to an oleaceous plant was described in 1947 (Cookson 1947*a*).

The association of xeromorphic Banksieae with *Nothofagus* and other rain-forest types appears incompatible until it is realized that a similar association of divergent ecological types exists in the present flora of certain parts of Australia. In the Dave's Creek area of the Lamington Plateau, southern Queensland, for example, *B. serratifolia* occurs in close proximity to a luxuriant rain-forest in which are found conifers such as *Podocarpus* and *Araucaria*, and species of *Cinnamomum, Lomatia, Tristania, and Casuarina.* On Mount Hobwe, only eight miles away, is a forest dominated by *Nothofagus moorei* (F. Muell.) Maiden. Cycads also occur in southern Queensland.

It will be seen, therefore, that species present in the rain-forest areas of warm-temperate Queensland include some that are closely allied to forms identified from the Yallourn deposits. This fact was noticed by Deane, who tentatively inferred that "the general temperature of the southern part of Australia when the brown coal of Morwell was deposited was higher than it is at the present day, that warmth and moisture abounded, and that hot dry winds did not occur, or at least were a rarity." Patton (1933) and Crocker and Wood (1947) have expressed similar opinions.

That the air was moist at this time is also suggested by the discovery of a variety of epiphyllous fungi on leaves preserved in the brown coal (Cookson 1947*b*).

It is more difficult to deduce the thermal conditions prevailing from the evidence of the plants which existed during this period, particularly as the true identity of these plants is frequently uncertain. In some instances, the problem of distribution is complicated by the influence of ecological factors other than climate. Also, as Seward (1931) points out, closely related plants often occur in a wide variety of habitats and hence are useless as indicators of climate. It is even possible, as Seward suggests, that plants of the Tertiary period may have tolerated wider ranges of temperature and rainfall than those of the present day.

However, if the distribution of a fossil flora as a whole, rather than that of individual genera and species is considered, these difficulties may be of reduced importance. A number of fossil plants in the Yallourn brown coal have not yet been identified and it is possible that further work may produce more definite evidence regarding the Tertiary climate of south-eastern Victoria.

XIII. Records of Extra-Australian Banksieae

A number of isolated leaves from extra-Australian deposits have been referred to *Banksia* and *Dryandra* (Kausik 1943) but some, at least, of the identifications seem extremely doubtful. Since the authors have seen only Australian material this matter is not discussed further; at the same time, however, they desire to reiterate their belief that misleading conclusions may be drawn when detached leaves are attributed to either genus.

Two examples from the present study may be cited in support of this statement. The Victorian fossil leaf *Banksieaephyllum obovatum* is very similar in shape to that of the living species *Banksia integrifolia* but the cuticular and internal structure of the two species, as can be seen in Tables 1 and 3, are completely different. To mention only one of the distinctions, the stomata of *B. integrifolia* occur in well-defined pits (Plate 8, Fig. 57) whereas those of *B. obovatum* are superficially placed (Plate 4, Fig. 30). A second example is afforded by the fossil leaf *B. pinnatum*, which externally is closely similar to that of *Dryandra formosa*, but structurally is quite distinct from that species. Moreover, there is no reason for associating the fossil with *Dryandra* rather than with *Banksia*. With such facts in mind, it is difficult not to question the authenticity of the assignment by Berry (1916) of an American leaf to *Banksia lennifolia* and the tentative suggestion put forward that it is most like *Banksia spinulosa*, a New South Wales species. As none of the Victorian fossil leaves discussed in this paper can be satisfactorily identified with living Australian species, it seems extremely doubtful whether extra-Australian types, should they exist, would closely approach living Australian forms.

Kirchheimer (1937) expressed doubts as to whether leaves from European deposits referred by Viniklar and other authors to *Banksia* and *Dryandra* are correctly placed and reiterated earlier suggestions that they may have belonged to myricaceous plants.

Professor T. G. Halle (1940) referred briefly to this question and the following paragraph (translated by Dr. Britta Lundblad) presents his considered opinion.

Earlier authors describe a great number of remains supposed to be referable to the Proteaceae from Europe and North America, but their determinations are probably all misinterpretations, the remains concerned belonging to several different families. Recently, a few data considered to be of a more reliable kind have been added, viz. the report of several species of leaves and a young inflorescence from the Upper Cretaceous of Bohemia, and an infructescence from the Eocene of England. In addition, a species of *Banksia* from the Eocene of southern U.S.A. is considered by Berry to be correctly determined. The question of the early appearance of the Proteaceae in Europe is still under discussion, however.

XIV. Phyllites yallournensis n. sp.

A rather common leaf in the Yallourn seam is the one described below under the name of *Phyllites yallournensis* (Plate 9). It is included in this paper because it shows a superficial likeness to leaves of certain Banksieae and as an illustration of the unreliability of assuming affinity with this tribe on similarity of leaf form alone. Apart from their smaller size, the resemblance of leaves of *P. yallournensis* to those of *Dryandra calophylla* is particularly strong. When, however, the cuticular characters of the two species are compared it becomes evident that they are distinct and unrelated. *P. yallournensis* possesses none of those characteristics which, as has been shown, belong to the Banksieae. Moreover, there seems no reason to think that it belonged to the Proteaceae at all.

The leaves of two extra-Australian plants, both native of North America, whose shape approaches that of the leaves of *P. yallournensis* must be mentioned. They are *Lyonothamus floribundus* Gray var. *asplenifolium* Brand, of which individual pinnae bear comparison, and *Comptonia peregrina* Coulter, where the leaf is simply pinnate. An examination of the cuticles of these species has shown, however, that the structure is quite distinct from that of *P. yallournensis* and suggests that the Australian fossil leaf is unrelated to either. The affinity of *P. yallournensis* thus remains obscure. Although it probably belonged to a dicotyledonous plant, it appears preferable to place it in the form genus *Phyllites* until more information becomes available.

(*a*) *External Characters*

Plate 9, Figs. 64-6

The specimens, though numerous, are fragmentary, the longest piece being 4 cm. The leaf is pinnate, the segments becoming smaller towards the base. The pinnae are numerous, 2-7 mm. long and 1.5-4 mm. broad, oblong-obtuse or slightly narrowed towards the apex, broadly attached and contiguous at the base, opposite or slightly alternate on either side of the midrib, the margin entire, not revolute. The midrib is relatively wide (about 1 mm.) underneath; the secondary veins are inconspicuous, parallel, arising at a wide angle, and frequently converging towards the apex of the segments.

(*b*) *Cuticular Structure*

(i) *Lower Epidermis* (Plate 9, Figs. 68, 69).—The stomata are superficial and irregularly oriented in large areas marked out by the cells covering the veins. They are oval to isodiametric, the long axes of the oval ones ranging from 16 to 28 μ; the poral rim has a narrow cutinized edge, and the dorsal wall is delicate. The stomata are usually surrounded by three or four rather small cells which may be of the nature of subsidiary cells. These are irregular in shape and their position in relation to the guard cells varies considerably.

The interstomatal epidermal cells are small with rather thin, straight or curved, pitted lateral walls. The cells covering the veins have slightly thicker, sparingly pitted walls and their long axes are parallel to the course of the veins. Hair-bases are absent.

(ii) *Midrib.*—Cells small, square, quadrangular or triangular, with straight, moderately thick, pitted walls. Small hair-bases sparsely distributed.

(iii) *Upper Epidermis.*—The cells of the epidermal parenchyma are small, 14-25 μ in diameter, with thin, straight or slightly curved, unpitted lateral walls; those above the veins are smaller and thicker-walled than those situated in the areas they delimit. The cuticle is granular. Hairs are not developed.

(*c*) *Internal Structure*

The tissues of the leaves available are rather crushed and distorted, but in small areas of transverse sections, such as the one shown in Plate 9, Figure 70, the differentiation of the mesophyll is reasonably clear. The cells of the upper epidermis are square in section and the outer walls, 3 μ thick, are cutinized. There are no hypodermal layers. Beneath the epidermis is a single layer of palisade parenchyma. The under epidermal cells are similar to those of the upper surface. The vertical strands of parenchyma which cross the mesophyll in the Banksieae appear to be absent from the leaves of *P. yallournensis*.

Occurrence: Brown coal, Yallourn, Victoria.

Locality: Yallourn open cut, No. 1 coal face, east side, below pole 30, 9.xi.49.

XV. Acknowledgments

The authors wish to express gratitude to Mr. A. W. Jessep, National Herbarium of Victoria; Mr. C. A. Gardner, Department of Agriculture, Western Australia; Mr. C. T. White, Botanic Gardens, Brisbane; and Mr. J. Ramsbottom, British Museum (Natural History), for kindly supplying leaves of *Banksia* and *Dryandra* from the collections in their charge. Thanks are due also to Mr. R. T. M. Pescott, National Museum, Melbourne, and Dr. D. Thomas, Chief Government Geologist, for the loan of fossil specimens and to Mr. W. Baragwanath for information regarding literature and localities.

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Explanation of Plates 1-9

The photographs are the work of I. Cookson except those in Figures 28, 37, 44, and 65 which were taken by Mr. E. Matthaei and those in Figures 20, 21, 22, 51, and 69 which were taken by Miss M. Johnson. 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.

PLATE 1

Banksieaephyllum angustum n.sp.

Fig. 1.—An almost complete leaf 3/5 natural size. (N.M.V. No. 14734.)
Fig. 2.—Upper surface of a small leaf fragment. Natural size. (N.M.V. No. 14848.)
Fig. 3.—A small leaf fragment showing prominent venation on the under surface. x 4.
Fig. 4.—Proximal region with lamina narrowing towards the petiole. Natural size. (N.M.V. No. 14735.)
Fig. 5.—A piece of cuticle showing the course of the secondary veins and the presence of stomatal pits on the lower surface. x 24.
Fig. 6.—Cuticle of lower surface with stomatal pits and numerous hair-bases. x 50.
Fig. 7.—Transverse section of leaf showing revolute margin and subdivision of mesophyll by vertical plates of sclerenchyma. x 100.
Fig. 8.—Transverse section showing upper epidermis, two-layered hypodermis, and palisade parenchyma. x 250.
Fig. 9.—Cuticle of upper surface. x 300.
Fig. 10.—Cuticle of lower surface showing stomata and hair-bases. x 300.

PLATE 2

Banksieaephyllum acuminatum n.sp.

Fig. 11.—Leaves with acuminate apices viewed from above. Natural size. (N.M.V. No. 14736.)
Fig. 12.—Portion of a leaf showing narrowing of lamina. Natural size. (N.M.V. No. 14737.)
Fig. 13.—Proximal portion of a leaf with slender petiole. Natural size. (N.M.V. No. 14737.)
Fig. 14.—Under surface of leaf to show inrolled margin, wide midrib, and prominent venation. x 4½. (N.M.V. No. 14738.)
Fig. 15.—Cuticle of lower epidermis showing anastomosing veins and stomatal pits. x 50.
Fig. 16.—Transverse section of leaf showing upper epidermis, two-layered hypodermis, palisade parenchyma, sclerenchyma, lower epidermis. x100.
Fig. 17.—Cuticle of upper epidermis; l.h.b., large hair base. x 300.
Fig. 18.—Cuticle of interstomatal epidermis with stomata and hair-bases. x 300.
Fig. 19.—Cuticle of interstomatal epidermis showing bicellular hairs. x 300.

PLATE 3

Banksieaephyllum laeve n.sp.

Fig. 20.—Portion of a leaf from above. x 3. (N.M.V. No. 14739.)
Fig. 21.—A fragment showing narrowing of lamina. x 6. (N.M.V. No. 14740.)
Fig. 22.—Leaf from below, showing smooth surface, prominent midrib, and entire, flat margin. x 5. (N.M.V. No. 14741.)
Fig. 23.—Cuticle of lower epidermis with diffusely arranged stomata. x 100.
Fig. 24.—Transverse section of leaf showing upper epidermis, palisade parenchyma, under epidermis with hair-bases, and sclerenchymatous strand cut longitudinally. x 250.
Fig. 25.—Cuticle of lower epidermis showing stomata with subsidiary cells, and hair-bases of two sizes. x 350.
Fig. 26.—Cuticle of upper epidermis showing cells with cuticular papillae. x 300.

PLATE 4

Banksieaephyllum obovatum n.sp.

Fig. 27.—Type specimen from above. Natural size. (N.M.V. No. 14741.)
Fig. 28.—A small portion of the type from below showing wide midrib and smooth surface. x 5.
Fig. 29.—Cuticle of upper epidermis. x 100.
Fig. 30.—Cuticle of lower epidermis showing superficial stomata. x 100.
Fig. 31.—Lower cuticle showing small cells with hair-bases and larger cells with cuticular papillae. x 350.

Fig. 32.—Lower cuticle showing presence of cuticular papillae on encircling cells of stomata. x 550.

Fig. 33.—Lower cuticle, the stoma in the lower right-hand corner focused to show a pair of subsidiary cells lying parallel to the pore.

Fig. 34.—Transverse section of leaf showing two vertical strands of fibres—the one to the right being cut obliquely. x 250.

PLATE 5

Banksieaephyllum pinnatum n.sp.

Figs. 35 and 36.—Type specimen. Natural size and x 3. (This specimen was destroyed to obtain its cuticle.)

Fig. 37.—Portion of the lower surface of the same specimen. x 5.

Fig. 38.—Cuticle of the lower epidermis showing stomatal areas and cells of two sizes. x 100.

Fig. 39.—Cuticle of upper epidermis. x 100.

Fig. 40.—Cuticle of lower epidermis with stomata and their subsidiary cells. x 300.

Fig. 41.—Transverse section of the leaf showing mesophyll crossed by two vertical strands of fibres, and thick outer walls of epidermal cells. x 250.

Fig. 42.—Cuticle of lower epidermis. Small cells with hair-bases can be distinguished from larger ones without hairs; subsidiary cells related to two stomata can be seen in the lower right-hand corner. x 350.

PLATE 6

Banksieaephyllum fastigatum (Deane) n.comb.

Fig. 43.—The specimen of *Banksia fastigata* illustrated by Deane in Plate 61, Figure 4, of his paper (1925). x 2.8.

Fig. 44.—A small leaf-fragment. x 4. (N.M.V. No. 14780.)

Fig. 45.—Cuticle of upper epidermis. x 100.

Fig. 46.—Cuticle of lower epidermis. x 100.

Figs. 47, 48.—Cuticle of lower epidermis showing small cells with hair-bases, stomata with subsidiary cells, and elongate cells covering the veins. x 350.

PLATE 7

Fruiting cones of *Banksia* sp.

Fig. 49.—Fertile cone of *Banksia* from Eldorado, Victoria. Natural size. (Geol. Surv. Mus. No. 50750.)

Fig. 50.—A cone from Yallourn. Natural size. (N.M.V. No. 14742.)

Fig. 51.—Median longitudinal view of a cone from Yallourn, showing central axis, bracts, a possible fruit on left-hand side, and the impression of the apex of the cone. Natural size. (N.M.V. No. 14743.)

Fig. 52.—Surface view of counterpart of apical region of the previous specimen showing bracts and bracteoles. x 4. (N.M.V. No. 14775.)

Fig. 53.—Transverse view of second half of the same specimen showing bracts covered with matted hairs. x 2. (N.M.V. No. 14776.)

Fig. 54.—Cuticle of a bract showing hair-bases. x 300.

Fig. 55.—Hairs from a bract of No. 14776. x 100.

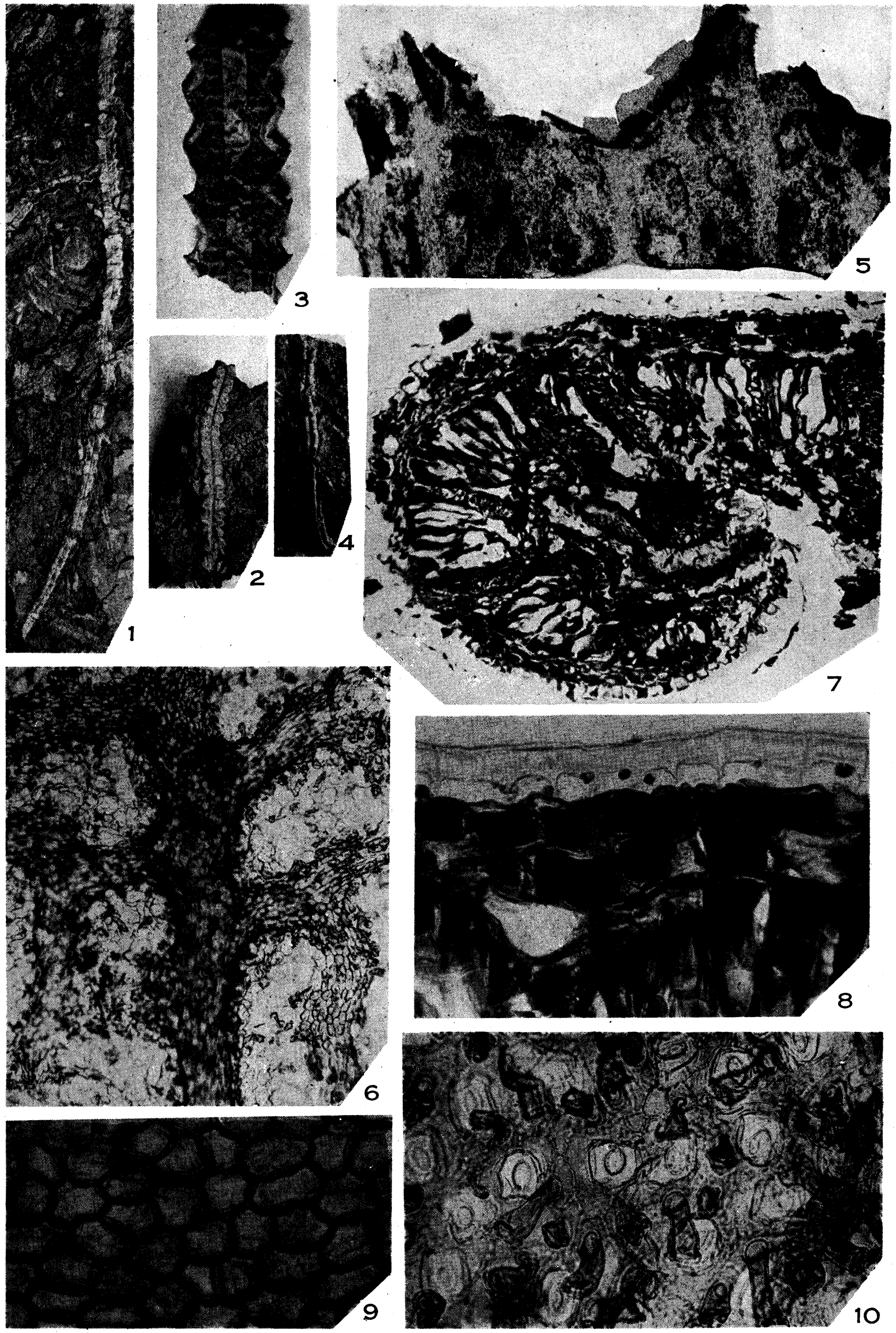
Fig. 56.—A hair from a bract of *Banksia marginata.* x 100.

PLATE 8

Structural features of living Banksieae

Fig. 57.—Lower cuticle of *Banksia integrifolia* showing stomatal pits and prominent veins. x 40.

Fig. 58.—Lower cuticle of *Banksia quercifolia* showing epidermal papillae around and near the pits. x 100.



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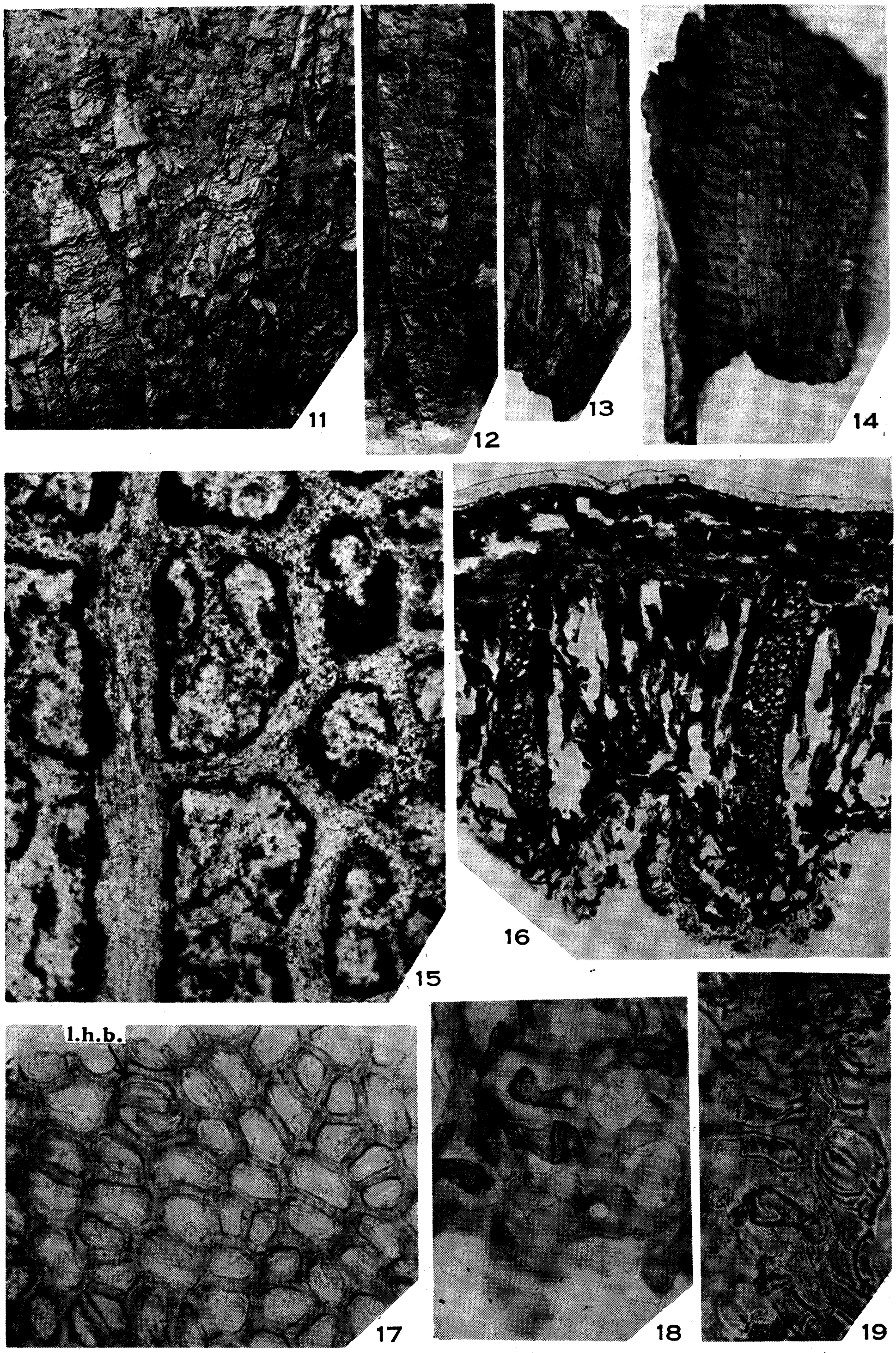

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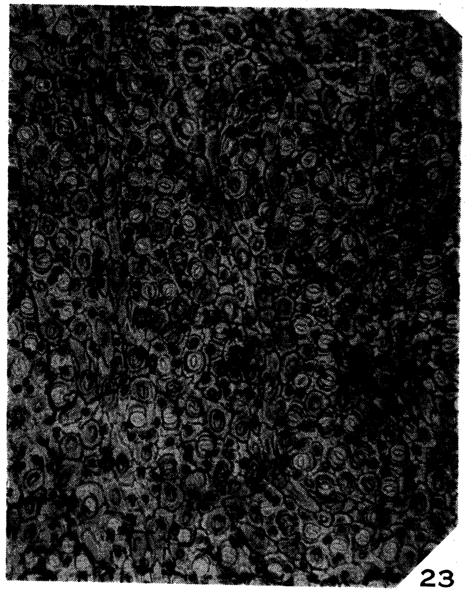
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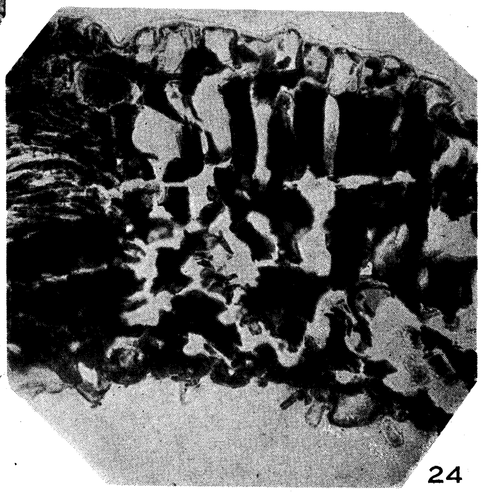
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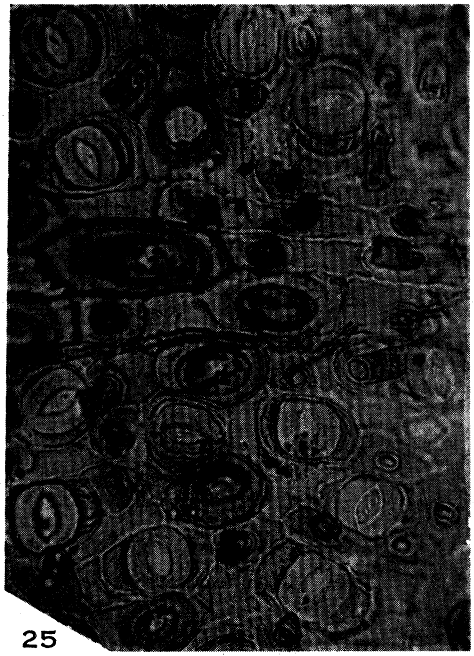
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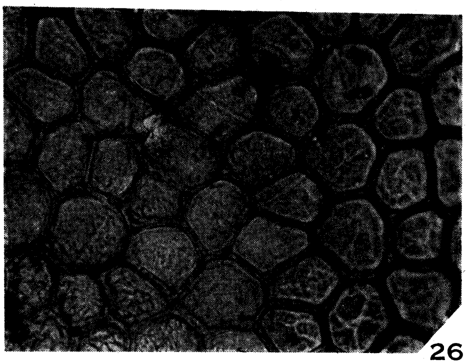
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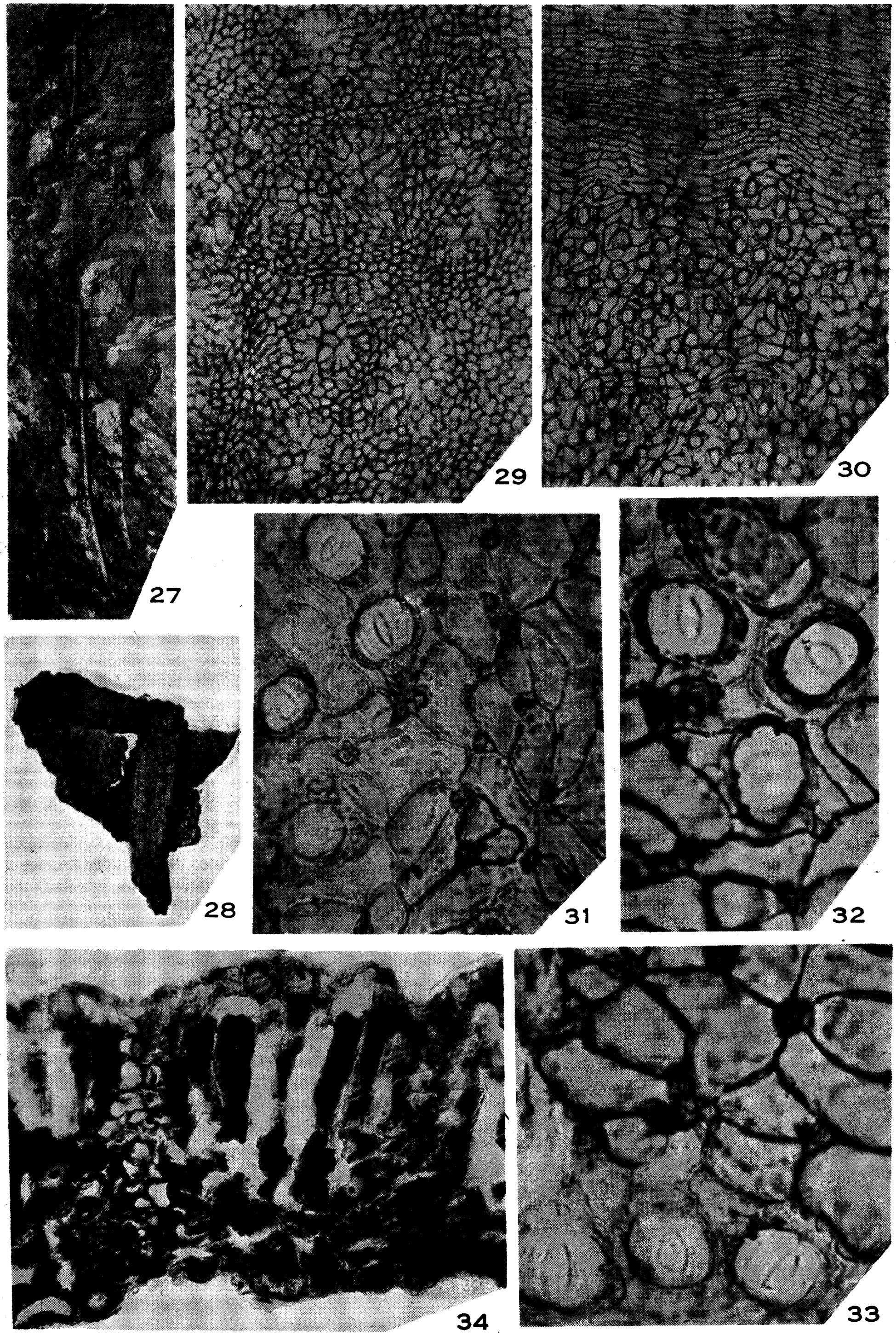

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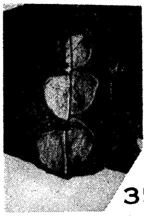
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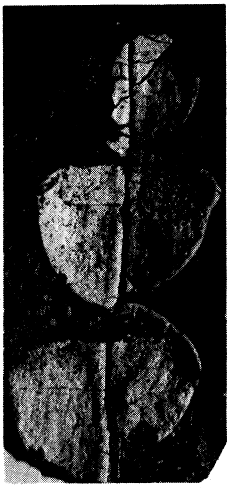
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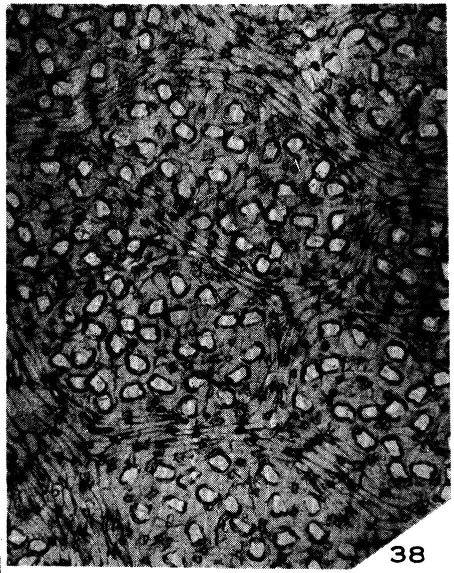
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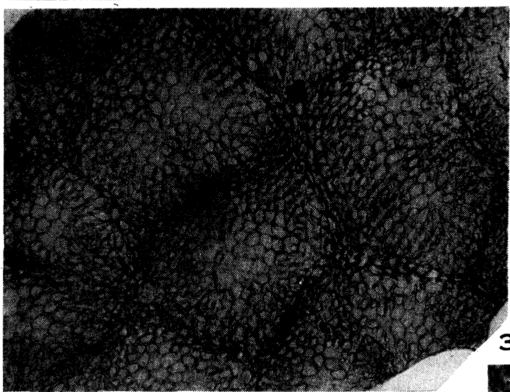
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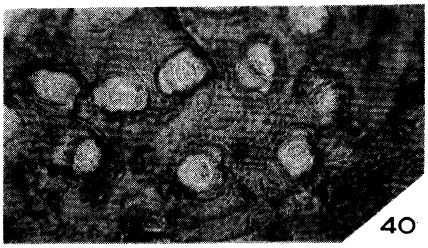
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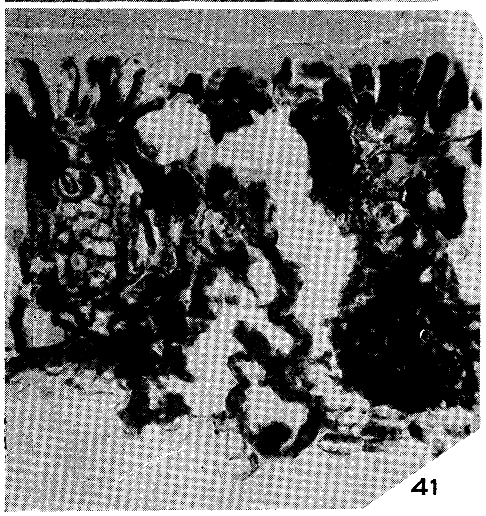
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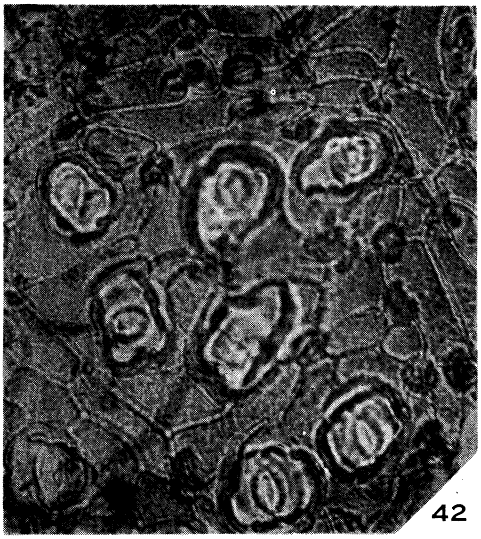
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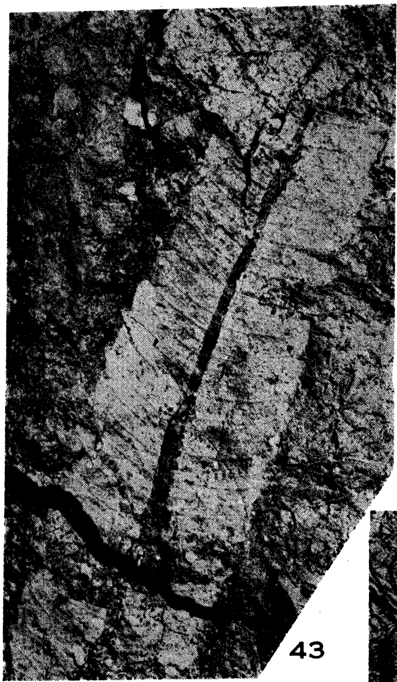

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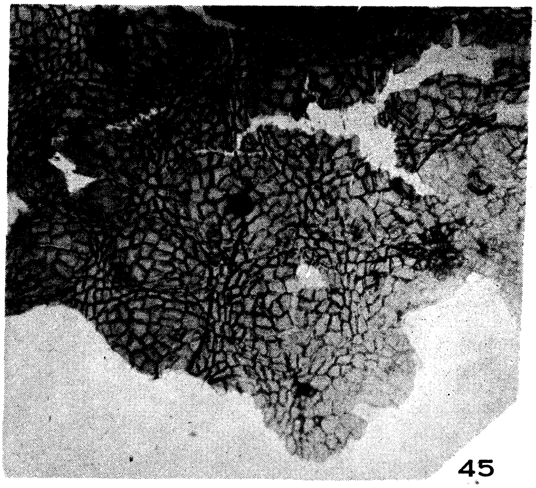

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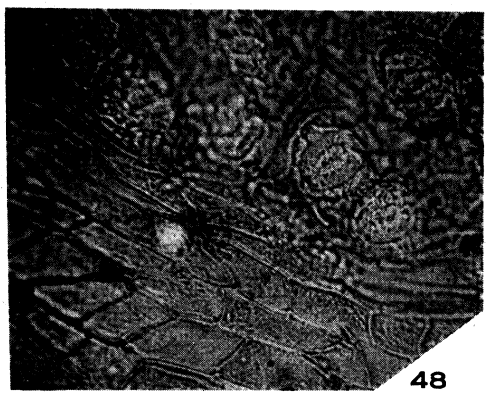

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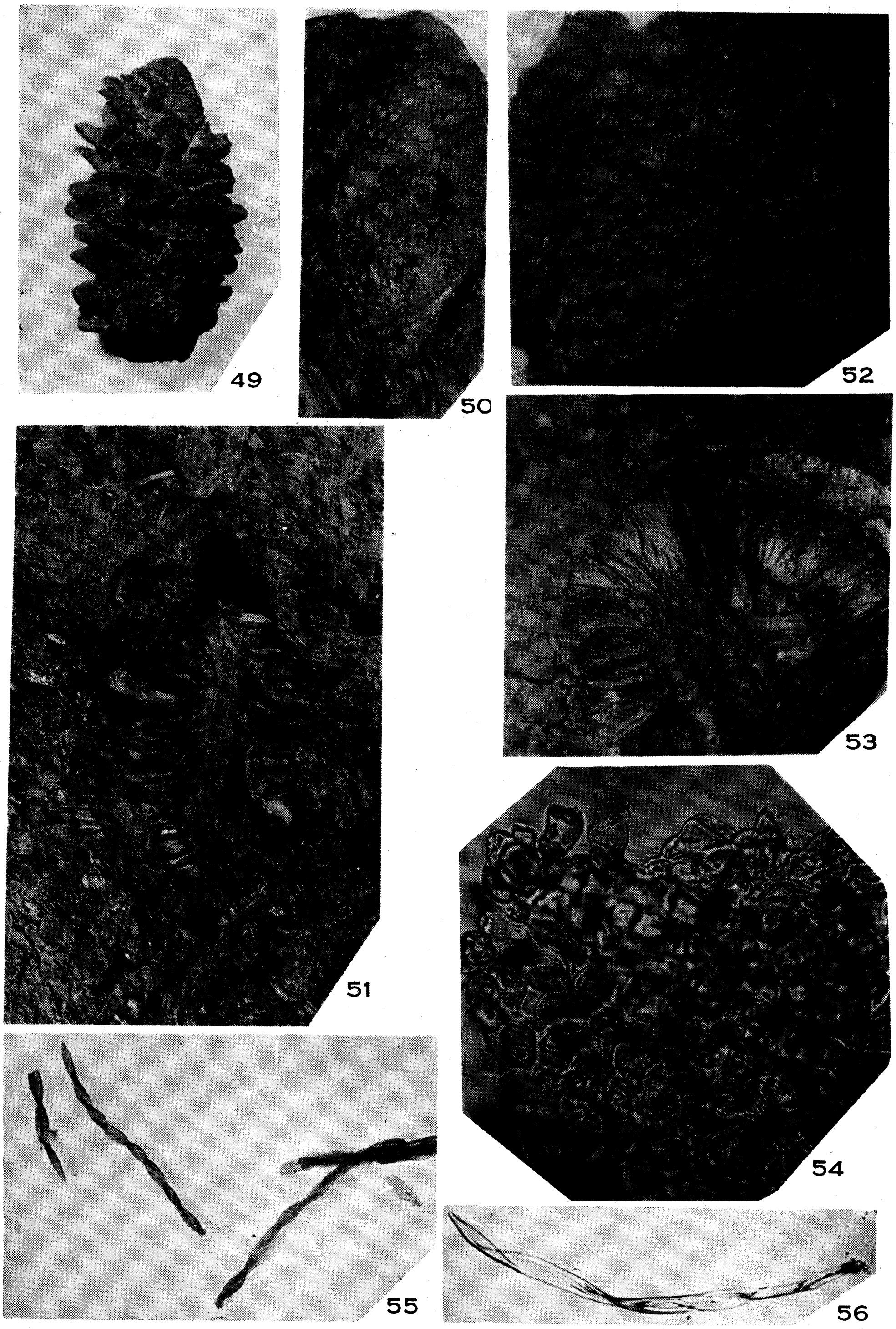
Cookson and Duigan.—Fossil Banksieae from Yallourn, Victoria



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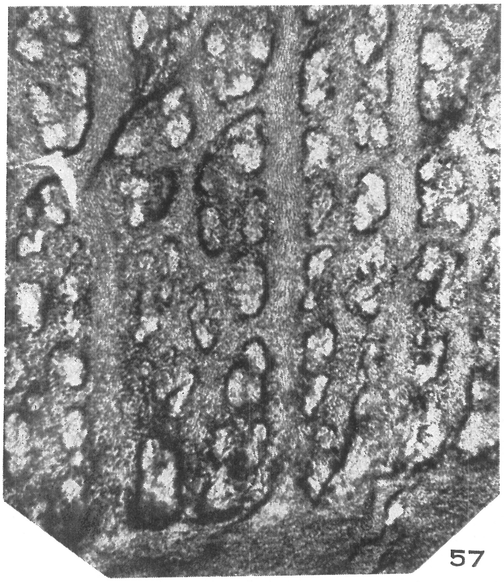

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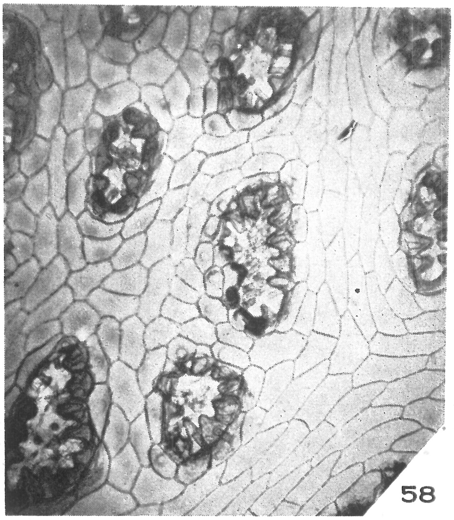

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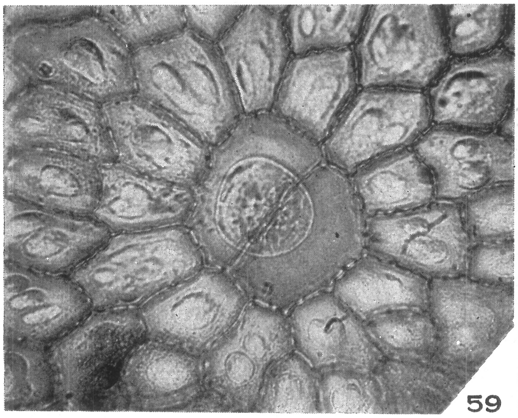

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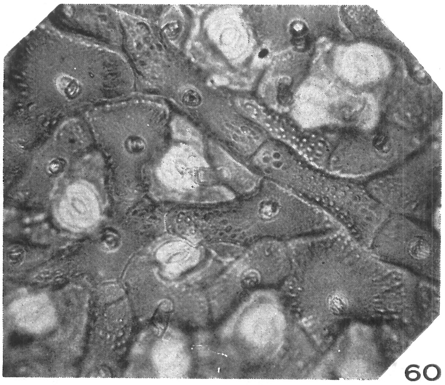

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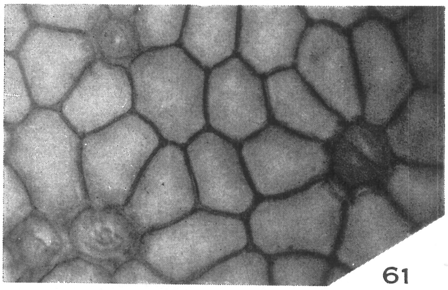

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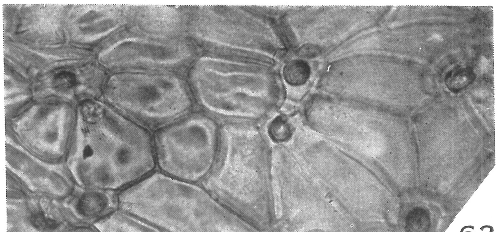

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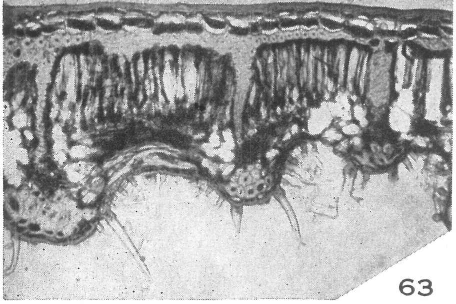
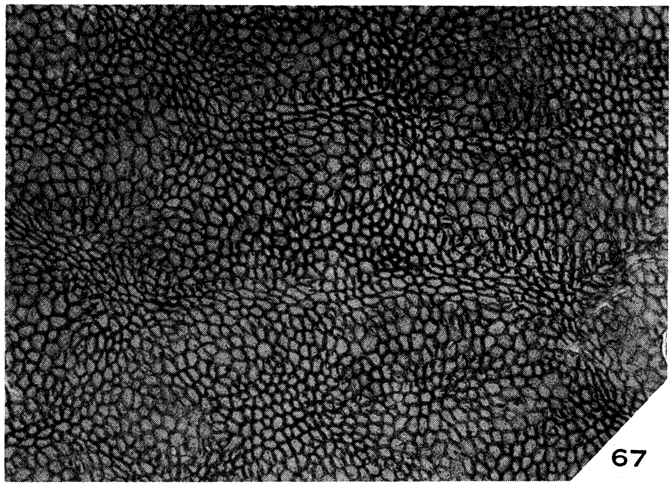


63

COOKSON AND DUIGAN.—FOSSIL BANKSIEAE FROM YALLOURN, VICTORIA


64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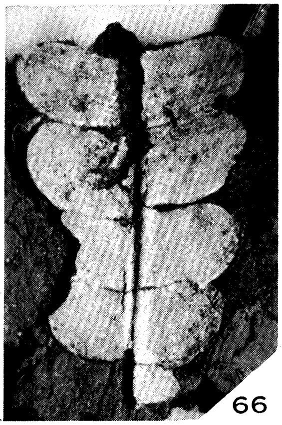
65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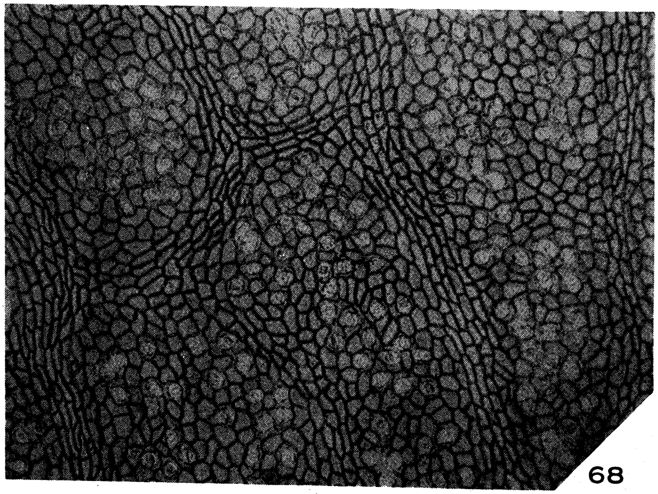
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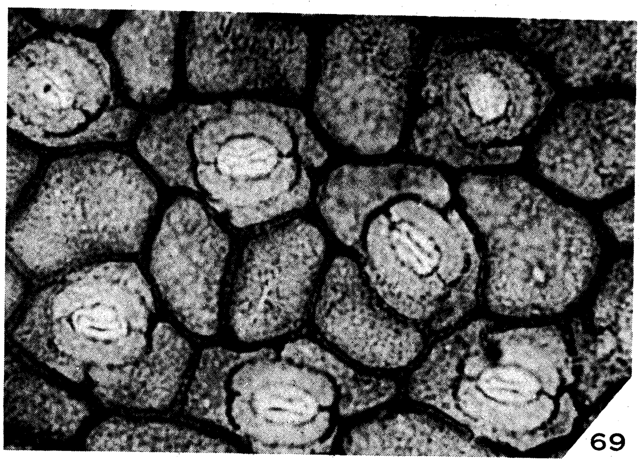
69

COOKSON AND DUIGAN.—FOSSIL BANKSIEAE FROM YALLOURN, VICTORIA

Fig. 59.—Cuticle of upper epidermis of *Dryandra floribunda* showing radial arrangement of epidermal cells around two cells supporting a large hair-base, their strongly pitted walls, and large cuticular papillae. x 325.

Fig. 60.—Cuticle of lower epidermis of *Dryandra kippistiana* showing numerous small cuticular papillae both on cells with and without hair-bases. x 230.

Fig. 61.—Cuticle of upper epidermis of *Banksia benthamiana* showing un-uniform, unpitted parenchyma cells and small hair-bases supported by one or two equally small cells. x 450.

Fig. 62.—Cuticle of upper epidermis of *Banksia baueri* showing the cells of two sizes which comprise the epidermal parenchyma. The small cells support small hair-bases. x 300.

Fig. 63.—Transverse section of *Banksia robur* showing two-layered hypoderm, vertical plates of sclerenchymatous fibres, stomatal pits, and hairs. x 60.

Plate 9

Phyllites yallournensis n.sp.

Fig. 64.—Basal portion of a leaf from above. Natural size. (N.M.V. No. 14777.)

Fig. 65.—Under surface of another fragment. (N.M.V. No. 14778.)

Fig. 66.—A leaf fragment from above. x 3. (N.M.V. No. 14779.)

Fig. 67.—Cuticle of upper epidermis. x 100.

Fig. 68.—Cuticle of lower epidermis. x 100.

Fig. 69.—Cuticle of lower epidermis. x 420.

Fig. 70.—Cross section of leaf. x 250.