STUDIES IN THE INDIAN MIDDLE GONDWANA FLORA: 1. ON *DICROIDIUM* FROM THE SOUTH REWA GONDWANA BASIN

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ABSTRACT

The structure of the epidermal cells of three species of *Dicroidium*, viz. *D. odontopteroides* (Morr.), *D.* sp. cf. *D. feistmanteli* (Johnston) and *D. hughesi* (Feist.) is for the first time described from the Triassic (Mid. Gondwana) rocks of the South Rewa Gondwana basin. Of these, *D.* sp. cf. *D. feistmanteli* is a new record. The epidermal structure, as far as known, favours the view that the two genera *Dicroidium* and *Thinnfeldia* are distinguishable. The epidermal structure of *D. hughesi* now conclusively proves that the generic name *Danaeopsis* originally used by Feistmantel for these fronds is unwarranted. The evidence as a whole strongly suggests that like the other Gondwanaland components, the Triasso-Rhaetic Gondwanas of India contain what should be recognized as a *Dicroidium* flora. It is further suggested that this flora, with *Dicroidium* as its characteristic genus, constitutes the Indian Middle Gondwana flora.

INTRODUCTION

THE fossil plants described in this paper comprise two collections from the South Rewa Gondwana basin, one made by the author during 1952-54 and a part of the other by N. K. N. Aiyengar of the Geological Survey of India in 1929. The latter was sent to the Late Professor Sahni for indentification, along with geological notes, a list of fossils and maps showing fossiliferous localities. The map represented in Text-fig. 1 shows all the hitherto known or newly discovered fossiliferous localities which I am inclined to regard as Triassic (Middle Gondwana) in age on geological and palaeobotanical evidence (this evidence will be separately discussed elsewhere).

The localities which have yielded most of the *Dicroidium* material are:

Parsora (Locality 10, *see* map) — About five and a half miles N. E. of Pali village (Birshingpur Rly. Station; Katni-Bilaspur line), on the east bank of Ghorari Nala, N.W. of the deserted site of the South Parsora village (Ref. Topo sheet No. 64E/3 of the Survey of India). From this well-known spot I have already described certain hitherto unrecorded plant remains (LELE, 1953, 1955).

Barnauda (Locality 11) — From a small exposure in the Patparia Nala, about half a mile South of Barnauda village or about a mile west of the deserted site of Parsora. This spot is new.

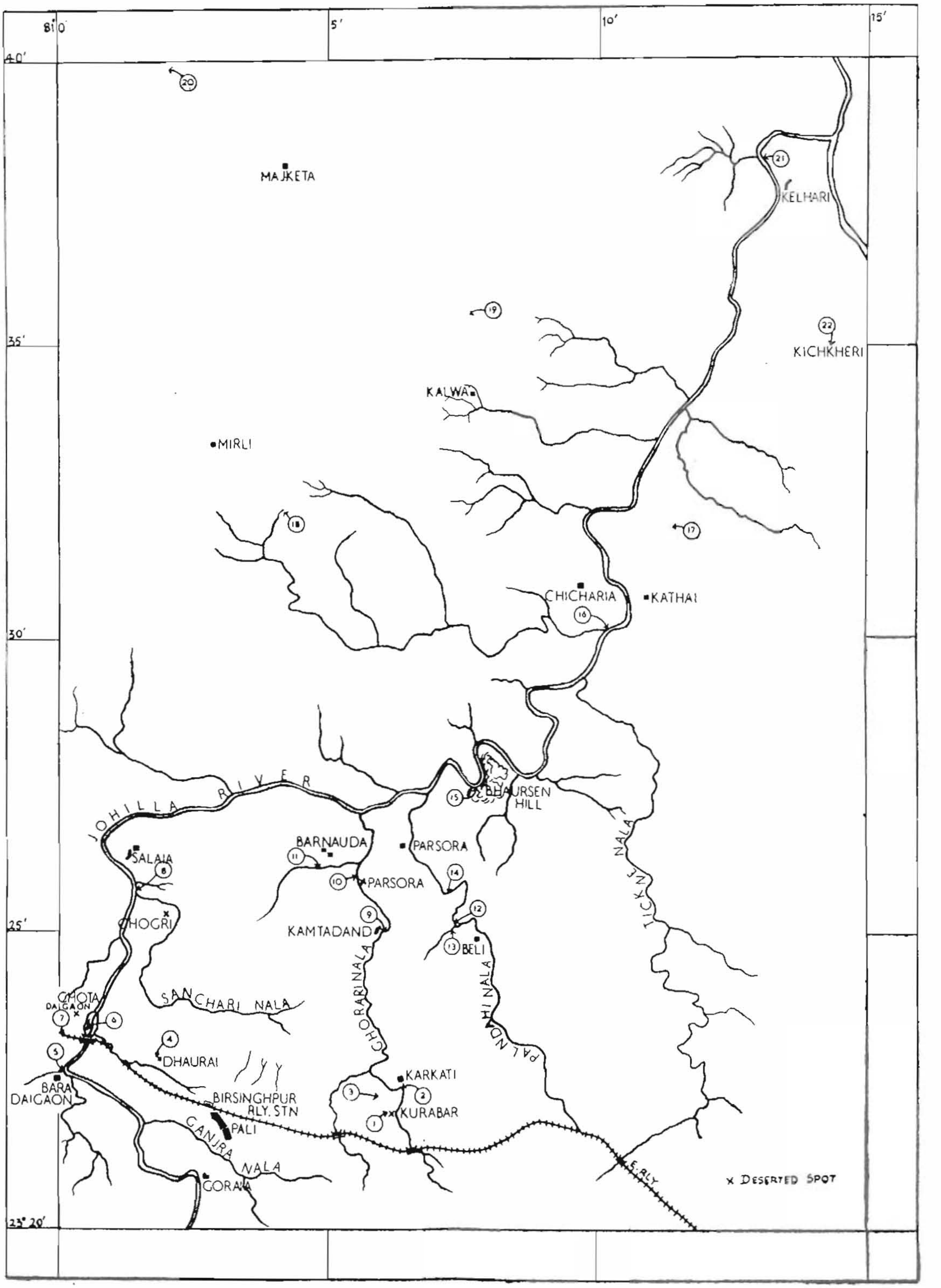
Bhaursen (Locality 15) — On the south bank of Johilla river, in the foothill exposures of Bhaursen hill. Spot new.

Chicharia (Locality 16) — Exposures along the Johilla river, east of Chicharia village (AIYENGAR COLL. 1929).

MATERIAL AND METHOD

The material comprises mostly of impressions or partly compressions (casts) which are preserved in ferruginous red-brown or yellowish argillaceous or arenaceous sandstones. The rock usually appears like a shale but frequently it is not well-bedded and exhibits variations in texture. Preservation of the fossils is obviously comparatively better in the fine-grained type of rock. More often the remains are fragmentary and stained by ferruginous substances.

The fossils are devoid of any trace of carbon and cuticular preparations by conventional methods are, therefore, not possible. However, in a number of cases, it is found that the epidermal structure is preserved as imprints on an almost opaque, black, non-carbonaceous (probably ferruginous) epidermal cast which appears to be the result of some process akin to mineralization. The epidermal cells occur in small patches in the form of a thin but distinct crust. In fact, it is occasionally observed that a fragmentary specimen which is too imperfectly preserved to reveal its form or venation is yet found to possess distinct epidermal cell imprints on the cast. Such crust-bearing fossils in the form of casts could be directly studied under strong incident light which reveals the epidermal structure. However, this method is



TEXT-FIG. 1 — Map showing all the known or new fossil localities of the area investigated (South Rewa Gondwana basin). (Scale 1″ = ca. 3 miles) cumbersome and would permit the study of only one surface (which is exposed to view) of the cast. Attempts were, therefore, made to remove small pieces of the crust under a binocular, thus making it possible to turn it and study the other surface. Several preparations including exposed and unexposed sides of the casts were thus made in Canada balsam and studied under strong incident light. It is true that epidermal cells are not as favourably preserved as to distinctly reveal certain finer details such as the sculpturing of the cell walls, undulations in cell outlines, papillae, and particularly the cutinization in the walls of the guard-cells and the different degree of sinking of the stomatal apparatus. However, the information revealed of the epidermal cells by the present material is, in any case, very useful for the identification of species.

DESCRIPTION

Genus : *Dicroidium* Gothan

Ever since Gothan (1912) instituted the genus *Dicroidium* to incorporate certain forms which, according to him, were wrongly placed in the genus *Thinnfeldia* Ettingshausen 1852, opinions have remained divided regarding the choice between the two genera. While Seward (1903), Walkom (1917), Arber (1917), du Toit (1927), and Jones & de Jersey (1947) have preferred to use the name *Thinnfeldia* more or less in a comprehensive sense, others such as Antevs (1913, 1914), Halle (1927, pp. 116, 117, footnote), Frenguelli (1943), Jacob & Jacob (1950) have had their own reasons for regarding *Dicroidium* as separate from *Thinnfeldia*. It appears now that the general consensus of opinion has lately grown more and more in favour of distinguishing the two genera (SEWARD, 1932; THOMAS, 1933; SAHNI, 1938; HARRIS, 1931, 1937, 1947). A recent contribution by Townrow (1957) has thrown fresh light on this problem and is a useful advance on the original ideas of Gothan. A number of points regarding the diagnostic characters of *Dicroidium* and *Thinnfeldia* have become more clear; at the same time certain discrepancies, which in the past had largely led to more confusion, have been corrected. As for example, certain different and more *Thinnfeldia*-like leaves, previously placed by Antevs (1914) in *Dicroidium*, have now been removed by Townrow (1957, p. 22, 47) to a new genus *Hoegia* and certain fertile fragments described by Walkom (1917, pp. 21-23, pp. 17-19) as fertile leaves of *Thinnfeldia* have now been shown (TOWNROW, 1957, p. 22) to belong to an entirely different plant, *Asterotheca*.

According to Townrow (l.c., p. 28) the two genera *Dicroidium* and *Thinnfeldia* can be distinguished by the following characters:

Dicroidium (TYPE: *D. odontopteroides*)	***Thinnfeldia*** (TYPE: *T. rhomboidalis*)
1. Almost always forked.	1. Never forked.
2. Leaf amphistomatic; stomata scattered, subsidiary cells not forming a regular ring and commonly only four, common wall of guard cells and lateral subsidiary cells strongly cutinized, at least in those species having sunken stomata.	2. Leaf hypostomatic, stomata mostly in interveinal bands, stomatal pit rounded and surrounded by a regular ring of fairly numerous subsidiary cells; wall between the guard cells and lateral subsidiary cells only weekly cutinized.
3. Cell outlines sinuous or with processes; a papilla on each epidermal cell normally present.	3. Cell outlines straight; cuticle surface smooth.

In addition to the above criteria, Townrow regards that the two genera are separable on the grounds of their stratigraphical as well as geographical distribution, *Dicroidium* being essentially a Southern genus, characteristic of the Triassic rocks, while *Thinnfeldia* is essentially a Northern genus occurring in rocks of the Rhaetic and the Lower Liassic Age (mostly Lower Liassic)

Despite the rather unfavourable state of preservation of the present fossil material, the epidermal structures as far as known have answered very well to almost every character on which *Dicroidium* is based. I am, therefore, inclined to regard the scheme proposed by Townrow as a useful and reasonable approach towards the understanding of the two genera *Dicroidium* and *Thinnfeldia*.

1. *Dicroidium odontopteroides* (Morr.) Gothan

Pl. 1, Figs. 1-7; Text-figs. 2-4

Complete fronds are rare. Incomplete ones do not always show epidermal details which makes their identification more difficult. The following description is based on only those specimens which reveal sufficient data regarding the epidermal structure for their identification.

The small specimen (Pl. 1, Fig. 1; Text-fig. 2A) comes from Chicharia while the other one (Pl. 1, Fig. 2; Text-fig. 2B) is from Parsora. In both cases, a few obtuse pinnules are attached by their whole base (slightly decurrent) to the pinna-rachis. Venation is not discernible, but in the Chicharia specimen (Pl. 1, Fig. 1) it seems to be like *D. odontopteroides*. The epidermal crust on these leaves is shown in black in Text-figs. 2A, B. The third specimen (Pl. 1, Fig. 3; Text-fig. 2C), collected from Chicharia is fairly big, measuring 20 × 7 cm. The two rachises are preserved in circumstances which suggest that they belong to a forked frond. The rachises bear mostly lanceolate pinnae with somewhat obtusely pointed apices and slightly decurrent broad bases. A midrib, clear for most part except near the apex, gives out forked secondary veins at acute angles. The pinnae within the fork above the point of dichotomy are modified in shape, short, more or less ovate and without any distinct midrib. Similarly, pinnae in the apical region of the frond also tend to become shorter. The rachis terminates in a single compound lobe as is evident from the two other specimens (Text-figs. 2D, E) from the same locality.

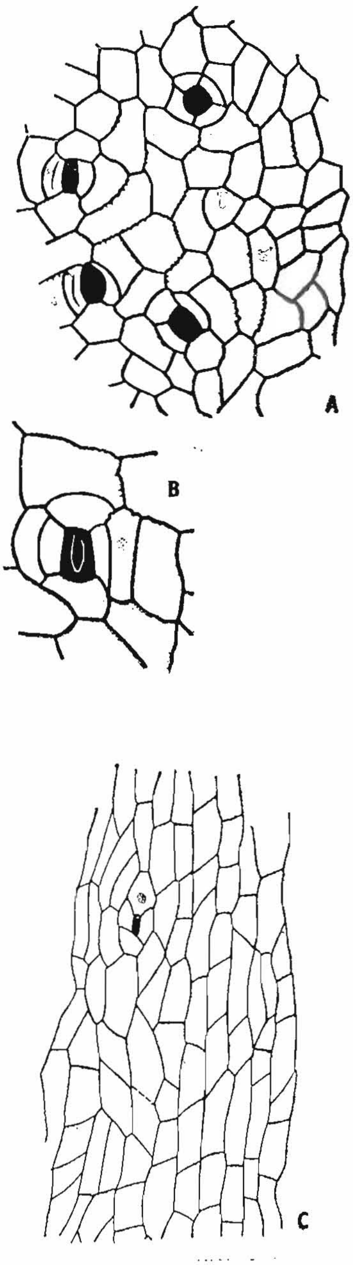
The three specimens (Pl. 1, Fig. 3; Text-figs. 2C, D, E) mentioned above are quite similar to those hitherto described as *Dicroidium lancifolium* by several authors. Townrow (1957, p. 37) has, however, shown that *D. lancifolium* represents merely one extreme of a continuous range of varying leaves belonging to *D. odontopteroides*, and that there is no difference in the cuticle of the two. The epidermal structure of the Chicharia specimens, as far as known, seems to support Townrow's contention. I have, therefore, included these forms with alethopteroid venation and lanceolate pinnae under *D. odontopteroides*.

Epidermal Structure — In the Chicharia specimen (Pl. 1, Fig. 1) the epidermal cells of both the surfaces are more or less similar in their shape and size. They are ± isodiametric, polygonal, irregularly distributed and measure 40-84 × 25-73 μ (Pl. 1, Fig. 4; Text-fig. 3A). The cell wall is about 2 μ thick. The cell outlines show minute undulations or projections (Pl. 1, Fig. 4) under high magnification. Impressions left by the papillae are seen on the cells here and there. Cells on the veins and near the margins of the pinnules are more elongated and in the former case they are usually in apparent rows.

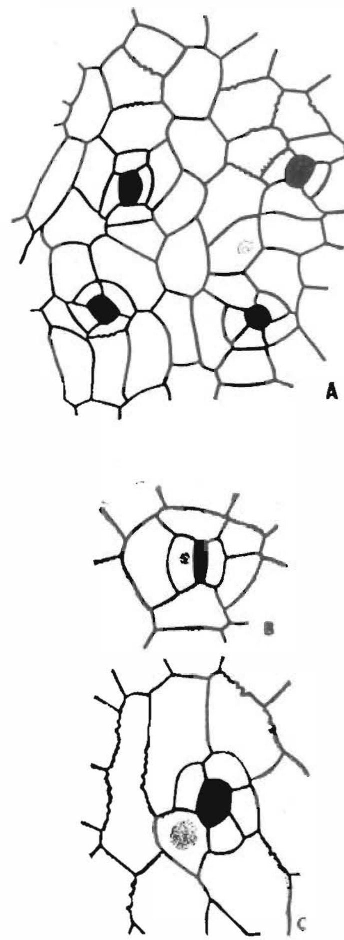
The leaf is amphistomatic, stomata being scattered and without any preferred orientation. They are also present on veins, but appear to be less frequent. Stomatal density is not known. It is, however, noticed that on one of the surfaces (which is probably the lower) the stomata are comparatively more in number. On both the surfaces they do not show any difference in respect of their size, shape or orientation (Text-fig. 3A). The stomatal apparatus consists of commonly four subsidiary cells surrounding the guard cells (Pl. 1, Fig. 4, *st.*; Text-fig. 3B). Frequently two of the subsidiary cells are polar in position while the rest two are lateral. Occasionally five subsidiary cells are present (Pl. 1, Fig. 5, *st.*). Faint remains of what appears like a papilla are sometimes seen on some of the subsidiary cells. In certain cases the lateral subsidiary cells show the presence of a narrow elongated strip (S) running parallel to the longer axis of the cell (Text-fig. 3A). It is normally difficult to make out the guard cells which appear to be more or less sunken inside a ± rectangular pit. Sometimes with better illumination and in deeper focus two long strips are seen which may represent the boundary wall of the pore (Text-fig. 3B). Noted range in size of the stomata[1] is 41-90 × 34-67 μ, the visible area of the pit being 11-33 × 10-23 μ.

1. The size of the stomata, whenever mentioned, is inclusive of the subsidiary cells.

TEXT-FIG. 2 — *Dicroidium odontopteroides* (Morr.) A, enlarged drawing of the specimen in Pl. 1, Fig. 1; black areas indicate the cuticular crust. × 1·5. B, enlarged drawing of the specimen in Pl. 1, Fig. 2. × 1·5. C, drawing of the specimen in Pl. 1, Fig.3. × 0·64. D, E, two specimens representing the terminal part of a frond such as in Text-fig. 2C. The venation is alethopteroid. × 1·5.



TEXT-FIG. 3.—*Dicroidium odontopteroides* (Morr.) Specimen K25/563. A, epidermis of the lamina (? upper surface) showing epidermal cells, stomata and a few papilla remains (*p*). As the guard cells are frequently not visible, the whole area of the pit is shown in black. Some of the lateral subsidiary cells show longitudinal strips (*s*). × 200. B, a stoma from the lamina (? upper surface); a slit (white lines) is faintly seen in deeper focus. × 250. C, epidermis of pinna-rachis (? upper surface). × 100.



TEXT-FIG. 4 — *Dicroidium odontopteroides* (Morr.) specimen 8753. A, epidermis of the lamina (? lower surface). × 200. B, C, two stomata from the lamina (? upper surface); one of them (B) appears to be less sunken than the other (C). Faint remains of papillae are seen on the subsidiary cells. × 200.

The epidermal cells on the pinna-rachis are polygonal, elongate and arranged in linear rows (PL. 1, FIG. 7; TEXT-FIG. 3C). They measure 44-98 × 22-44 μ in size and show the presence of similar stomata.

The epidermal structure of the Parsora specimen (PL. 1, FIG. 2) is represented in Pl. 1, FIGS. 5, 6 and Text-figs. 4A, B, C. It agrees in every respect with that of the Chicharia specimen described above.

Remarks — Feistmantel (1881, 1882) has recorded certain fragmentary specimens as *Thinnfeldia odontopteroides* from the Triassic sediments of Ramkola coalfield and Parsora beds (South Rewa Gondwana basin). Among these, his Parsora specimens are forked and can be referred to *Dicroidium*. The Ramkola specimen as well as a few others from the Jurassic strata (FEISTMANTEL, 1879; *see* also ANTEVS, 1914, p. 55 — Synonymy) may belong to this species, but further material — particularly such as could reveal epidermal data — is necessary to confirm these records. Similarly a specimen earlier described by me (LELE, 1955, p. 25) as *Thinnfeldia odontopteroides* may require revision.

2. *Dicroidium* sp. cf. *D. feistmanteli* (Johnston) Gothan

Pl. 2, Figs. 8-13; Text-fig. 5

There are two specimens which are compared with *D. feistmanteli* on the basis of their external features and epidermal structure. The first specimen (PL. 2, FIG. 8; TEXT-FIG. 5A) comes from near Bhaursen (locality 15), while the other one (PL. 2, FIG. 9; TEXT-FIG. 5D) is from Chicharia (Locality 16). Of these two, my specimen from Bhaursen (PL. 2, FIG. 8; TEXT-FIG. 5A) is a complete, forked frond about 20 cm. in length. The rachis is fairly stout, and measures about 7 mm. in width below the point of dichotomy. Above the fork the two rachises are about 4-5 mm. wide. Small lumps or striae are visible on the rachis as in *D. feistmanteli* (cf. TOWNROW, 1957, p. 41). The other specimen (PL. 2, FIG. 9) also shows this feature on its rachis.

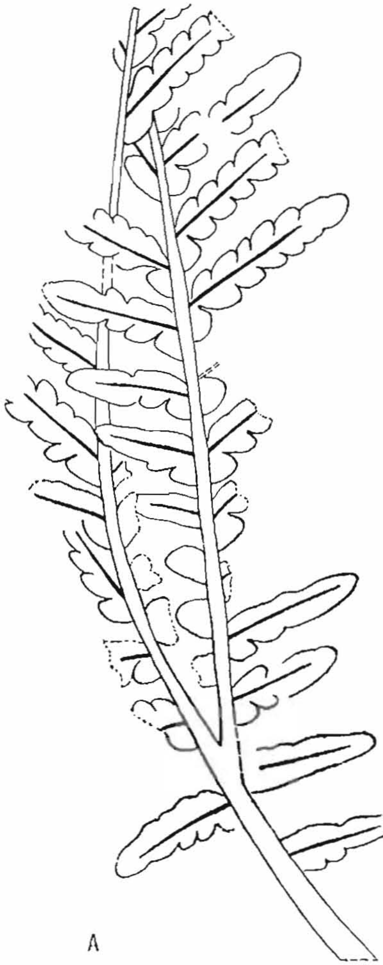
The two rachises are inclined at an acute angle and bear pinnate leaves. The pinnae are opposite to alternate, with a midrib distinct for most part except near apex where it fades out. The pinnae are longest in the middle of the frond and tend to become shorter towards both the ends. The longest pinna measures 4×1 cm. Pinnae in between the fork are short, orbicular and gradually increase in length upwards. In the lower part of the frond the pinnules are not so well-marked, often appearing like lobes but higher up they become more distinct, rhomboidal and give to the rachis a definite bipinnate appearance. Near the apex of the pinnae, their margins become entire or very slightly uneven and terminate into a roundly acute point. The basal-most pinnule (on the lower side of the pinna) is almost invariably expanded, is somewhat bigger in size than the rest and is largely borne directly on the rachis (cf. FRENGUELLI, 1944, PL. 3, FIG. 6). This feature seems to attain greater prominence from base upwards in the frond. The venation is not preserved, but at one or two places appears to be odontopteroid type.

The other specimen (PL. 2, FIG. 9; TEXT-FIG. 5D) is incomplete. It shows long pinnae (in one case 2·1 cm.), with roundly acute apices and ± contracted and slightly decurrent bases. While a few lower pinnae are simple with almost entire margin, those higher up have wavy margins giving lobed appearance to the pinna. A midrib which fades out near apex gives rise to secondary veins which fork more than once. This specimen does not show any clear expansion of the basalmost pinnule as in the previous specimen.

Epidermal Structure — In the specimen in Fig. 8 the epidermal cells of the lamina on both the surfaces are essentially similar, although they appear to be somewhat bigger on one of the surfaces (presumably the upper). The cells are polygonal, ± isodiametric, scattered and measure about 37-95 ×25-57 μ (mean 66×42 μ) on the (?) upper surface (PL. 2, FIG. 10; TEXT-FIG. 5B) and about 25-77×17-37 μ (mean 40×30 μ) on the (?) lower surface (PL. 2, FIG. 11; TEXT-FIG. 5C). Cell wall is little more than 1 μ thick. Cell outlines show minute sinuosities or projections (only seen under higher magnification). Stomata are present on both the surfaces but probably more on one of them (? Lower). They are scattered without any orientation. Normally, 4 subsidiary cells enclose a rectangular pit (PL. 2, FIG. 11, *st.*; TEXT-FIG. 5C). Occurrence of 5 subsidiary cells is also noted. Stomata appear to show different degree of sinking. The cells of the rachis are not well-preserved, they are elongate and arranged in rows.

The structure of the epidermis in the other specimen (FIG. 9; TEXT-FIG. 5D) is shown in Pl. 2, Figs. 12, 13 and Text-figs. 5E, F. Often the cells show large and heavy scars which may represent remains of papillae (PL. 2, FIG. 13, *p.*) On the whole the epidermal structure is essentially similar to that described above.

Comparison — The present specimens offer some difficulty in assigning them to *D. feistmanteli* with certainty. This is chiefly because the typical characters of the fronds of *D. feistmanteli* and its type are not present



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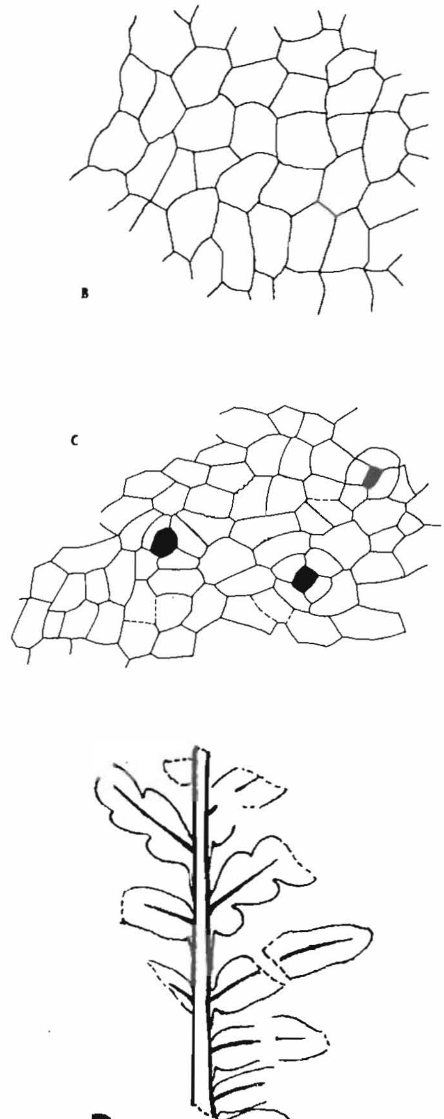
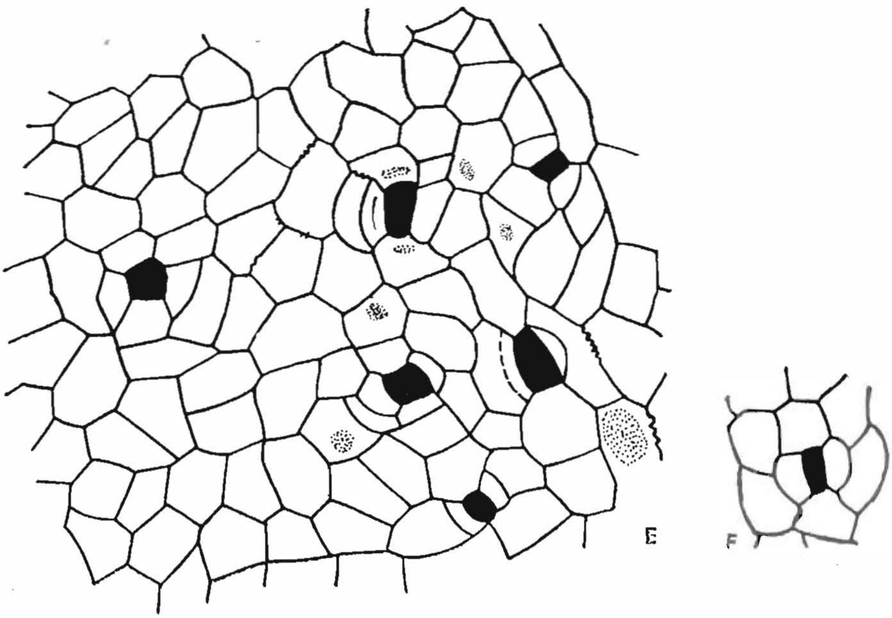
TEXT-FIG. 5A — *Dicroidium* sp. cf. *D. feistmanteli* (Johnston). A, drawing of the specimen in Pl. 2, Fig. 8. × ⅔.



TEXT-FIG. 5B-D — *Dicroidium* sp. cf. *D. feistmanteli* (Johnston). B, epidermis of the lamina (? upper surface). × 133. C, epidermis of the lamina (? lower surface). × 133. D, drawing of specimen in Pl. 2, Fig. 9. × Nat. size.

in my specimens. Unlike *D. feistmanteli* the present specimen (FIG. 8) is comparatively much smaller and shows small pinnae whose segmentation into pinnules is ill-defined for a large part of the frond except near its apex. The termination of the pinnae in my case is also not similar (although may be comparable to a degree) to that of *D. feistmanteli* (cf. TOWNROW, 1957, p. 40, FIG. 7A; FRENGUELLI, 1944, PL. 3, FIG. 5; THOMAS, 1933, p. 248, FIG. 50).

It is, however, interesting to point out that Seward (1908, TEXT-FIG. 3B; TEXT-FIG. 4) has described certain specimens as *D. odontopteroides* which according to him ' demonstrate the passage, from linear segments with a midrib giving off clusters of forked veins and with a lamina showing different degree of lobing to pinnae with short and broad ultimate segments '. Seward's Text-fig. 3B compares well with the Chicharia specimen (FIG. 9) while his Text-fig. 4 shows a frond



TEXT-FIG. 5E-F — *Dicroidium* sp. cf. *D. feistmanteli* (Johnston). E, epidermis of lamina (? lower surface) of specimen in Text-fig. 5D. × 200. F, a stoma from the lamina (? lower surface) of the specimen as above. × 200.

which has certain features common with the Bhaursen specimen (FIG. 8), especially the termination of the pinnae and the much less demarcated pinnules.

It is evident that like my specimens, those of Seward also show a certain deviation from the typical fronds of *D. feistmanteli* and its type. It is, however, remarkable that Seward's specimens were regarded by Antevs (*see* DU TOIT, p. 336) as young fronds of *D. feistmanteli* and Townrow (1957, p. 39) has now included them under the same. Similarly certain specimens described by Jacob & Jacob (1950, p. 119) as *Dicroidium australis*, which according to those authors are different from typical *D. feistmanteli*, also show a good deal of resemblance with my specimen. These are also regarded as *D. feistmanteli* by Townrow (1957, p. 39) on cuticular grounds. My specimen, especially that in Fig. 8, is also comparable with that of Thomas (1933, p. 248, FIG. 50) described as *D.* sp. cf. *D. feistmanteli*.

If Townrow is justified in placing the above mentioned variation under *D. feistmanteli*; I think, it would be better to provisionally place the present specimens also near *D. feistmanteli*. It may be that my specimen (FIG. 8) represents a smaller young frond like that of Seward. The epidermal structure of the specimens described above also does not show any marked difference from that of *D. feistmanteli*. It would, therefore, seem more appropriate, at least for the present, to treat these fronds as a species only comparable to *D. feistmanteli*. More and better preserved material in future may throw light whether they belong to this species or have to be placed elsewhere.

3. *Dicroidium hughesi* (Feistmantel) Gothan

Pl. 3, Figs. 14-22; Pl. 4, Figs. 23-28; Text-figs. 6, 7

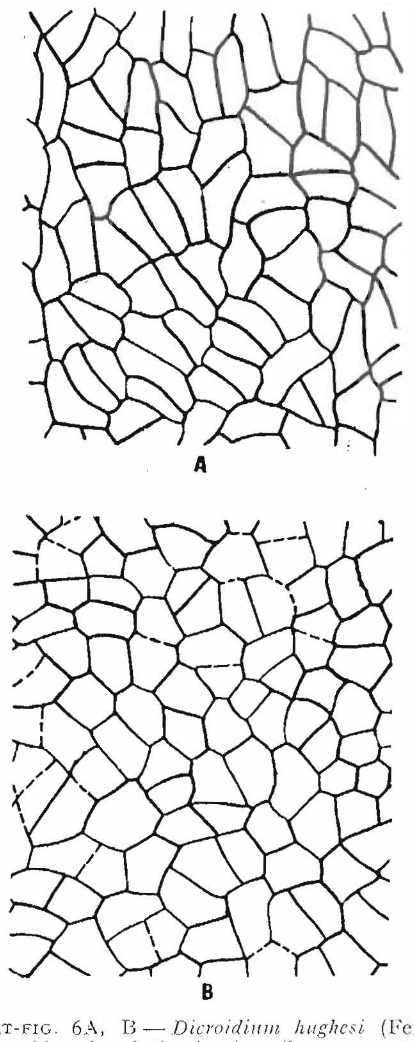
The occurrence of *Dicroidium hughesi* is well known from the Parsora beds (Locality 10) ever since it was first described with several illustrations by Feistmantel (1882, p. 25) under *Danaeopsis hughesi*. The fronds, some of them considerably large in size, now collected by me from Parsora show the same features as described earlier. The two specimens from Parsora reproduced here are shown on (PL. 3, FIGS. 14, 15). Of these the one in Fig. 14 shows two rachises which originally belonged to a forked frond. In its incomplete state, it measures 30 × 38 cm.

Epidermal Structure — A preliminary attempt to describe the epidermal structure of these fronds was first made by me (LELE, 1955). The leaves were then attributed to *Thinnfeldia* — using that term in a comprehensive sense. Further work on these interesting and much disputed leaves has subsequently yielded sufficient data which strongly favours the view that these fronds belong to *Dicroidium*. The structure of the epidermal cells is revealed by three specimens, two of which are figured here.

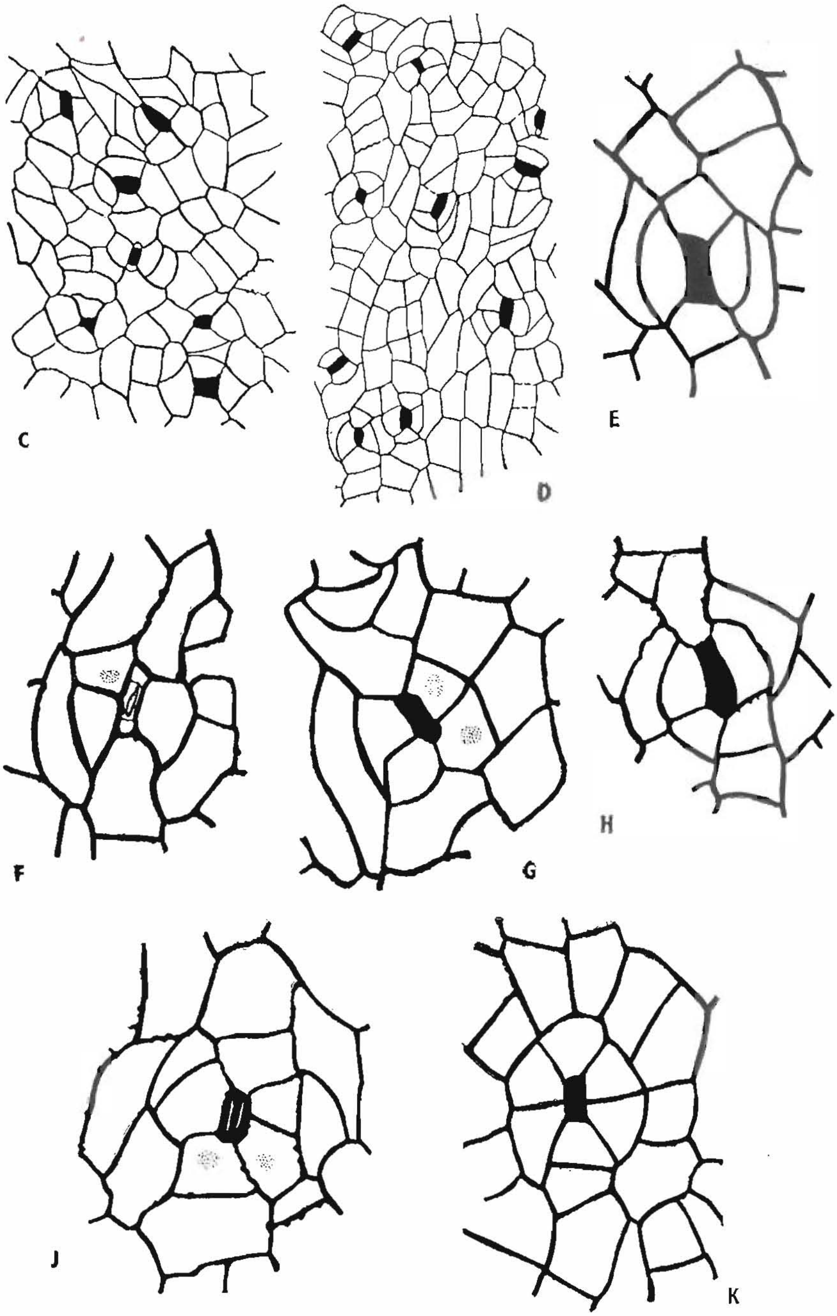
The (?) upper surface of the lamina has polygonal cells which are usually somewhat longer than broad, with rounded corners and sometimes gently curved walls (PL. 3, FIG. 16; TEXT-FIG. 6A). Deviations from these are also seen where the cells are ± isodiametric and with pointed corners (PL. 3, FIG. 17; TEXT-FIG. 6B). The epidermal cells show a range in size from 45-127 × 25-80 μ (mean 85 × 54 μ). They are scattered, except on veins, where they show linear arrangement. The cell wall is ± 4 μ thick and in better preserved cases the cell outlines show minute undulations or processes (under high magnification). In the centre of certain cells a rounded scar or elevation is sometimes seen which represents a papilla. However, the papillae are not always clearly visible.

The (?) lower surface of the lamina has also polygonal cells (PL. 3, FIG. 18; TEXT-FIG. 6C), ± isodiametric, irregular in arrangement except on veins. These cells are on the whole somewhat smaller than those of the other surface and appear to be more angular. They show a range in size from 25 to 105 × 15-72 μ (mean 74 × 44 μ). The cell wall is about 2-3 μ thick. Minute sinuocities or projections in the cell outlines are better seen on this side. A papilla on each cell is sometimes fairly clear (PL. 3, FIG. 19, *p*).

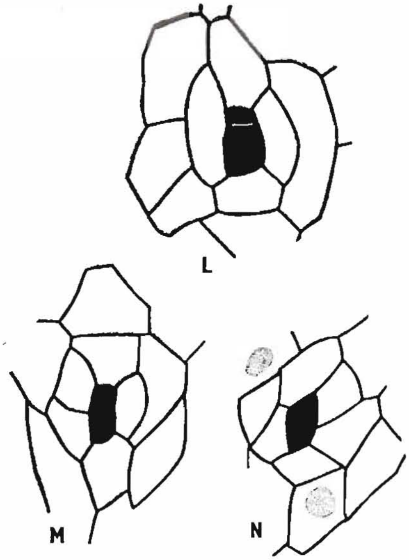
Stomata occur on both the surfaces but they are abundant on one of them (? lower) while rare on the other (? upper). In Pl. 3, Fig. 18 (? lower surface) stomatal density is about 20/sq. mm. They are scattered, without any orientation (TEXT-FIG. 6C). They also seem to be present on what appears to be region of the vein (TEXT-FIG. 6D). The stomatal apparatus is of the *Dicroidium* type, consisting commonly of four subsidiary cells (PL. 3, FIGS. 20, 21; TEXT-FIG. 6E) forming an irregular ring and enclosing a rectangular to somewhat broadly elliptical pit. The subsidiary cells may divide to give rise to five (TEXT-FIGS. 6, F, J) or rarely six subsidiary cells (TEXT-FIG. 6K). Polar subsidiary cells are not uncommon. Fairly often, and especially in cases with 4 subsidiary cells, the lateral subsidiary cells may be as long as the guard cells. Encircling cells are also seen. Presence of papillae is sometimes seen on some of the subsidiary cells. Occasionally the stomata may be close apart but, as far as known, do not share common subsidiary cells. The guard-cells are usually not decipherable. They seem to show different degrees of sinking. In some cases, where the apparatus is more or less exposed, the



TEXT-FIG. 6A, B — *Dicroidium hughesi* (Feist.). A, B, epidermis of the lamina (? upper surface) showing variations in the shape and outlines of the cells. 8742 & 5112. × 100.



TEXT-FIG. 6C-K — *Dicroidium hughesi* (Feist.). C, epidermis of the lamina (? lower surface) showing epidermal cells and stomata. 8742. × 100. D, epidermis of the lamina (? lower surface) on a probable vein region. 8742. × 100. E-J, stomata from lamina (? lower surface) showing variations in their shape, size and number of subsidiary cells. The stoma in F shows a pore and what appears like poles of the guard cells. Stoma in J also shows indication of a pore in deeper focus. Other stomata are probably much more sunken. Occasionally remains of papillae are indistinctly seen on the subsidiary cells. 8742. × 200. K, a stoma from lamina (? lower surface) with 6 subsidiary cells. Apparatus sunken. 5112. × 200.



TEXT-FIG. 6L-N — *Dicroidium hughesi* (Feist.) L, a stoma from the lamina (? upper surface) in the close vicinity of the midrib. 8694. × 200. M, N, two stomata on the midrib (? upper surface) of leaf. Both are orientated oblique to the midrib direction. 8694. × 200.

guard cells and a narrow elongated pore are faintly visible (PL. 3, FIGS. 20, 21; TEXT-FIG. 6, F, J). Cutinization in the wall of the guard cells cannot be ascertained. Noted range in size of the stoma is 62-216 × 47-113 μ (mean 113 × 67 μ). The entire visible area of the pit (shown in black) ranges in size from 25-44 × 11-35 μ (mean 35 × 15 μ).

The (?) upper surface, as far as known, seems to have comparatively very few stomata. In most cases, the bits scratched from the lamina did not show stomata. In one favourable case, however, a few stomata were seen on the lamina in the close neighbourhood of the midrib (TEXT-FIG. 6L). In this case also, stomata were not seen in regions farther away from the midrib. I am, therefore, led to believe that the upper surface has very few stomata and they probably occur mostly in the vicinity of the midrib.

The epidermal cells on the (?) upper surface of the midrib (TEXT-FIG. 6P) are usually more or less isodiametric, (occasionally elongated) polygonal and appear to be arranged in rows. They measure 52-105 × 35-70 μ (mean 73 × 51 μ). The cells on the (?) lower surface (TEXT-FIG. 6Q), on the other hand, are more elongated in shape and also show better linear arrangement. They measure 52-145 × 30-57 μ (mean 94 × 41 μ). A few stomata (TEXT-FIG. 6, M, N), mostly orientated oblique to the midrib, are also seen on the upper surface. Often the apparatus is sunken (TEXT-FIG. 6P).

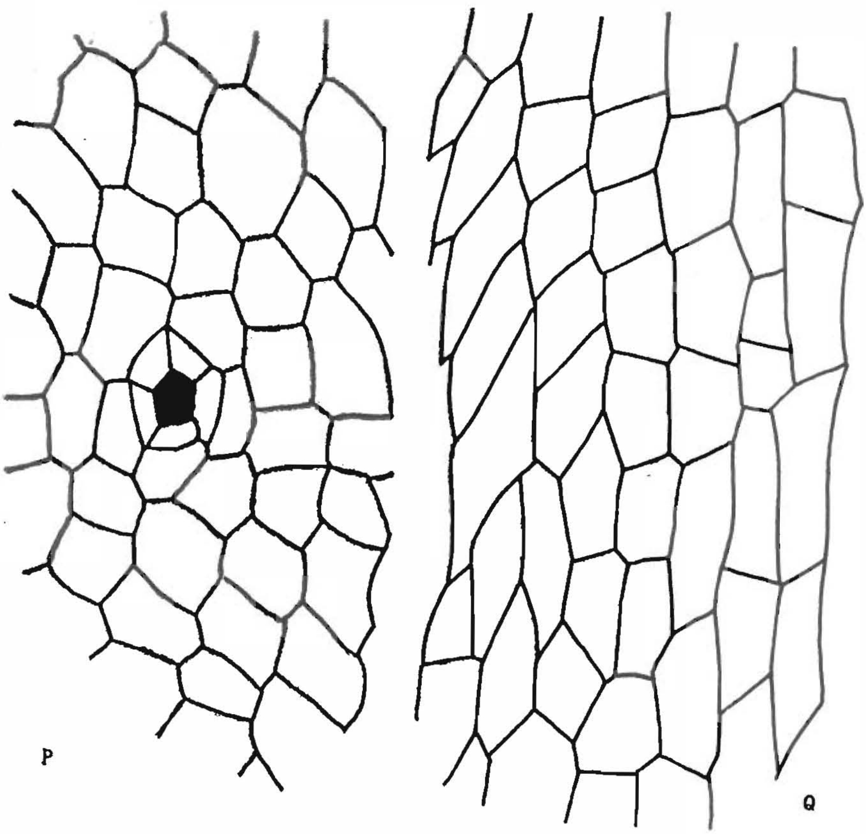
The epidermis of the rachis is usually not well-preserved. The cells on both the surfaces seem to be arranged in rows. A few cells from the lower surface are shown in Pl. 3, Fig. 22. In my previous paper (LELE, 1955, p. 25; TEXT-FIG. 1) a few cells from the lower surface of the rachis have already been figured. These measure approximately 43-101 × 30-43 μ in size.

SOME DETACHED LEAVES REFERABLE TO *D. HUGHESI*

From another locality, viz. Barnauda (Locality 11) which is only a few miles west of Parsora, a small collection was made. This includes 5 incomplete leaves whose form and venation is closely comparable to that of *D. hughesi*. Two of these specimens are figured (PL. 4, FIGS. 23, 24). In most of these fragments the leaves show oblique folds, or are rolled to some extent. The rock containing these fragments is also very irregularly laminated and is variable in texture. Complete fronds are totally absent, the incomplete ones also preserved in very oblique planes. All these circumstances perhaps suggest that the sediments were laid down under somewhat disturbed conditions of deposition.

Although these leaves are too incomplete for their identification, they possess a very well-preserved epidermal structure which is like *D. hughesi*. The (?) upper surface shows epidermal cells (PL. 4, FIG. 25; TEXT-FIG. 7A) which could be matched with those of *D. hughesi* shown in Pl. 3, Fig. 16; Text-Fig. 6A. On the veins the epidermal cells are arranged in rows and measure 36-87 × 18-51 μ. Stomata are not seen on this surface in spite of good preservation. The region near the midrib, where one would expect the stomata, is unfortunately badly crushed which renders any observation difficult.

The cells of the (?) lower surface of the lamina are shown in Pl. 4, Fig. 26 & Text-Fig. 7B. They have essentially the same characters as noted for *D. hughesi*. This surface also has a large number of stomata. The stomatal apparatus (PL. 4, FIG. 27; TEXT-FIG. 7B) is also like *D. hughesi*. The



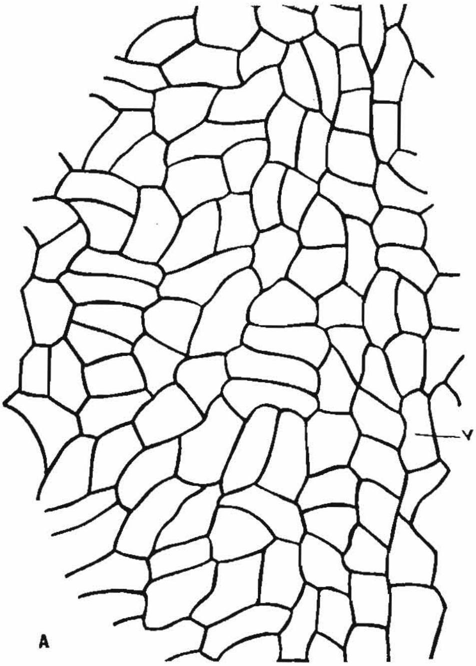
TEXT-FIG. 6P, Q — *Dicroidium hughesi* P, epidermis of the leaf midrib (? upper surface). A much sunken stoma is seen. 8694. × 200. Q, epidermis of the leaf midrib (? lower surface). 8694. × 200.

epidermal cells of the (?) upper surface of the midrib are shown in Pl. 3, Fig. 28. Their elongated appearance is also partly because of lateral compression they have undergone during preservation.

The above specimens serve to illustrate that it may be sometimes possible to identify small fragments, if their epidermal structure is critically studied. This is important especially because, such fragmentary specimens often form a large part of the Triassic fossil material from the South Rewa Gondwanas.

Discussion — The generic name *Danaeopsis* was instituted by Heer in 1876 for a Rhaetic species which is known in both fertile and sterile state. It was attributed to the Marattiaceae of the filicales on that evidence. Feistmantel described the Indian fronds as *Danaeopsis hughesi* because of their close similarity with *Danaeopsis* and its type *D. marantacea*. Gothan (in POTONIÉ & GOTHAN, 1921, p. 60), however, pointed out that the Indian leaves were in all probability not ferns and had no claim to *Danaeopsis*. Halle (1921, 1927, p. 131) also ruled out the possibility of using *Danaeopsis* for the Indian leaves which he accommodated in the genus *Protoblechnum* Lesq. together with his unforked Chinese specimens.

Because of the lack of any evidence regarding the fructifications or cuticular structure of these leaves, several authors continued to use, although with hesitation, the term *Danaeopsis* (ARBER, 1917; WALKOM, 1917, 1925; SEWARD & SAHNI, 1920; DU TOIT, 1927; JONES & DE JERSEY, 1947; P'AN, 1936) A few others, on the other hand, made new designations to accommodate *Danaeopsis hughesi*, e.g. *Supaia* White (1929) and *Desplasiophyllum* Frenguelli (1943). However, these designations have not been consistently used.



TEXT-FIG. 7A — Cf. *Dicroidium hughesi* (Feist.) A, epidermis of the lamina (? upper surface). A vein region (*v*) is indicated on the extreme right. The cells are fairly comparable with those of *D. hughesi* shown in Text-fig. 6A. 9084. × 133.

Sahni (1922, p. cliii) remarked that *Danaeopsis hughesi* appeared like a giant *Thinnfeldia*. Subsequently Seward (1932, p. 238) strongly emphasized that the name *Danaeopsis* must be abandoned for the Indian fronds as they did not provide any evidence whatsoever of relationship to *Danaea* or other Marattaceous ferns, nor could they be included in *Danaeopsis* as represented by the type species *D. marantacea*. He favoured the name *Thinnfeldia* for the leaves previously known as *Danaeopsis hughesi*.

Jones & de Jersey (1947, pp. 17, 18) further pointed out the differences between the Northern Hemisphere fronds placed under *Danaeopsis* and those of the Southern Hemisphere. They shared the views of Sahni (1922) and Seward (1932).

In fact, despite the lack of cuticular data, the general consensus of opinion had grown in recent years more and more in favour of regarding *Danaeopsis hughesi* as a *Thinnfeldia* or *Dicroidium* (HARRIS, 1931, p. 145; GOTHAN & WEYLAND, 1954, p. 113).

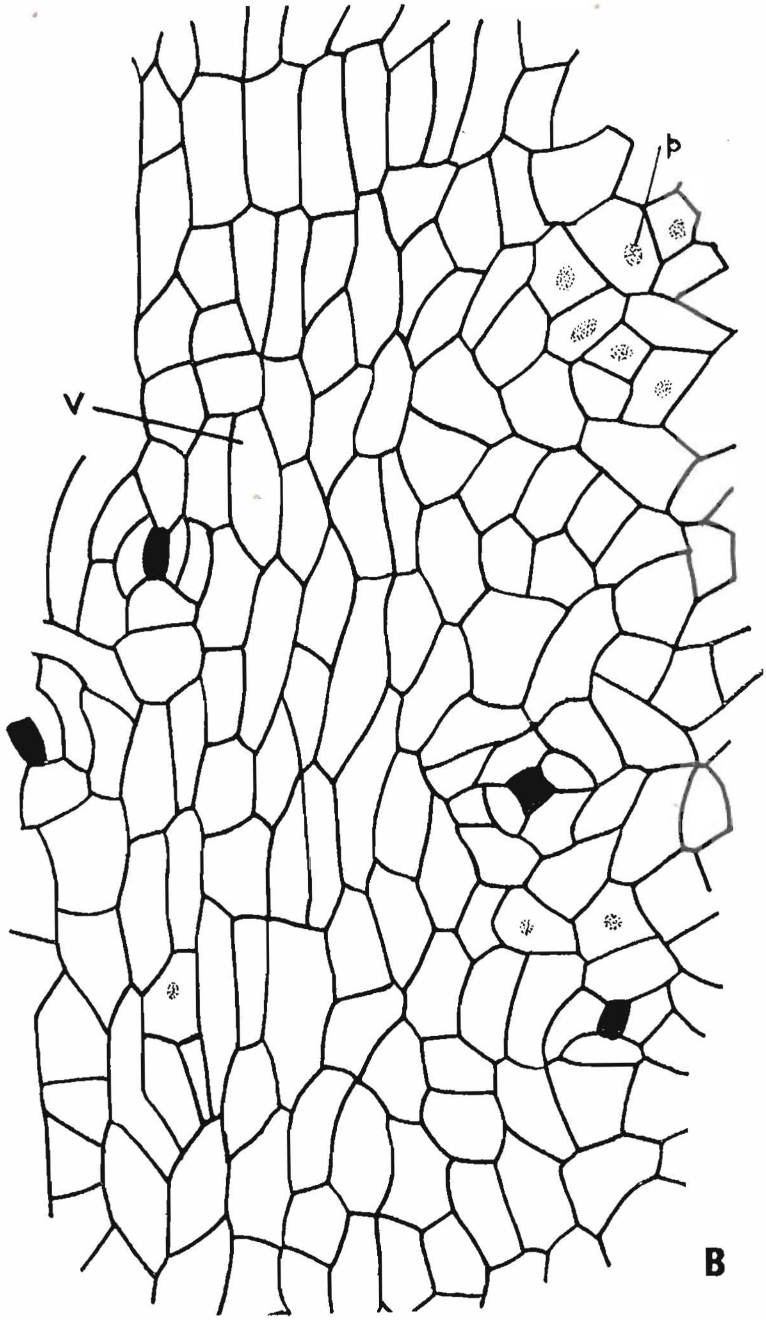
The characteristic forking habit of these leaves and the epidermal structure now described are in complete agreement with those of the genus *Dicroidium*. This evidence is now sufficient to conclusively prove that *Danaeopsis hughesi* must be placed under *Dicroidium*. Certain leaves originally described as *Thinnfeldia narrabeenensis* (WALKOM, 1925; DU TOIT, 1927) show close resemblance with *D. hughesi* both in regard to their external form and habit. Their cuticle is described by Jacob & Jacob (1950) which justifies their inclusion under *Dicroidium* (*see* also TOWNROW, 1957, p. 39). The fronds of *D. narrabeenensis* are, however, much smaller in size and their cuticle is distinguishable from that of *D. hughesi*.

The occurrence of certain incomplete fronds described as *Danaeopsis hughesi* is already known from China (KRASSER, 1900; P'AN, 1936), Tonkin (ZEILLER, 1903) Australia (WALKOM, 1917; ARBER, 1917; JONES & DE JERSEY, 1947) and West Kazakstan (BRICK, 1952). It would be worthwhile reinvestigating this material from cuticular standpoint in order to ascertain its reference to *Dicroidium*. Similarly the Indian Jurassic species *Danaeopsis rajmahalensis*, which according to Feistmantel shows close resemblance with *Dicroidium hughesi*, has not yet been found in forked state. A reinvestigation of this Jurassic species, particularly its cuticle, would therefore, prove significant. Lastly, it may be pointed out that Halle (1927) and Sze (1955, 1956, p. 148) have included the Indian forked leaves of *D. hughesi* under *Protoblechnum* because of its close agreement with the Chinese fronds. Now that the Indian forked leaves are proved to belong to *Dicroidium*, a question arises as to the nature of the Chinese fronds. It may be remarked that the genus *Protoblechnum* was originally created by Lesquereux (1880, p. 188) to include simple unforked fronds of Upper Carboniferous age. While Halle's specimens were all unforked, Sze (1955) has now discovered forked leaves which he refers to *Protoblechnum*. It would be most interesting, in my opinion, to critically investigate the Chinese fronds for their epidermal structure which might give some important clues to their generic position.

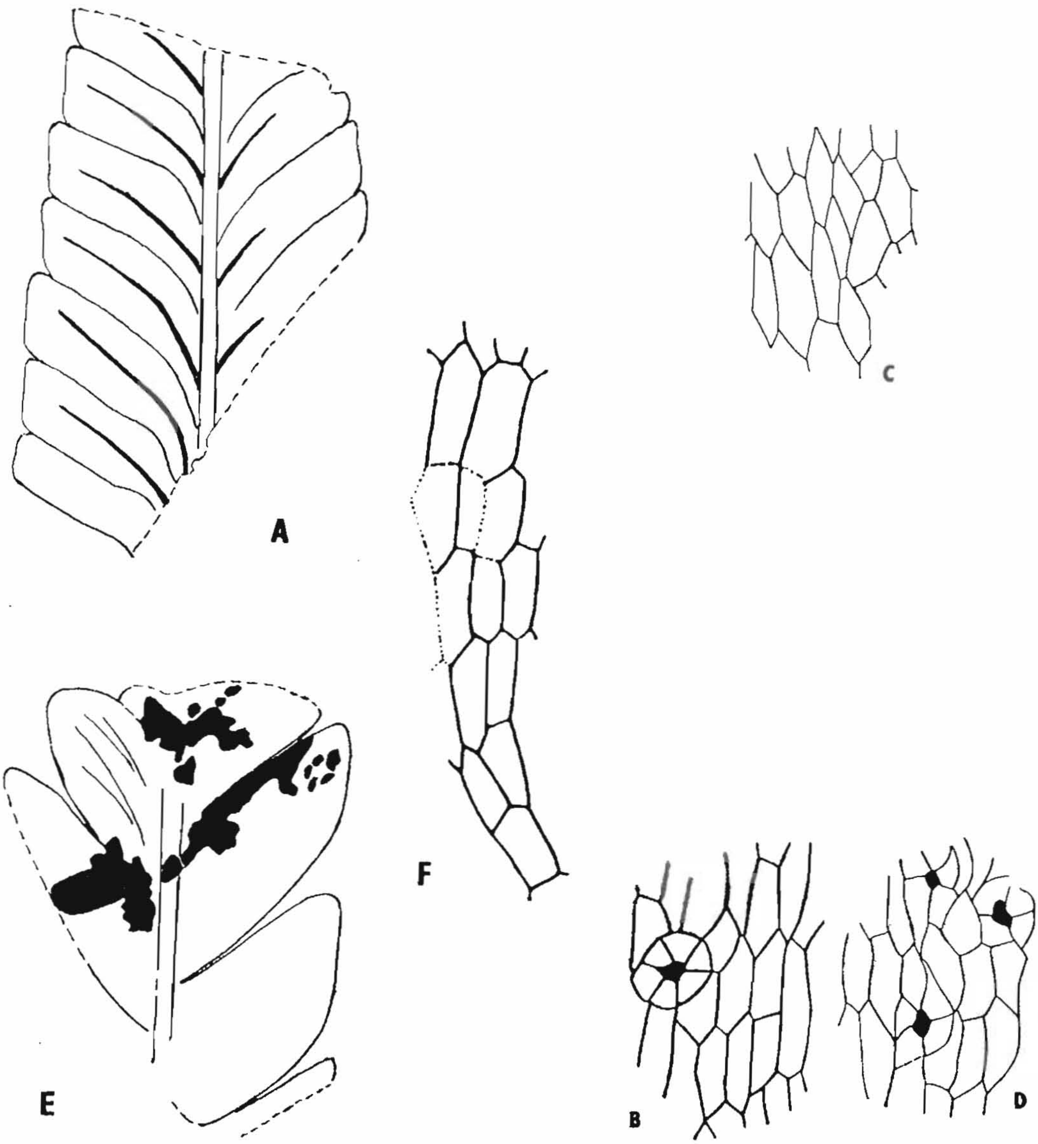
4. *Dicroidium* sp.

Pl. 4, Figs. 29-33; Text-fig. 8

There are two incomplete specimens from *Daigaon* (Locality 7) which are referred to *Dicroidium*.



TEXT-FIG. 7B — Cf. *Dicroidium hughesi* (Feist.). B, epidermis of the lamina (? lower surface). A vein region (*v*) is clearly distinguishable by the linear arrangement of cells, while in the remaining part the cells are scattered and ± isodiametric. Stomata are also present on the vein. A few cells show papillae (*p*). 9084. × 266.



TEXT-FIG. 8 — *Dicroidium* sp. A, enlarged drawing of specimen in Pl. 4, Fig. 29. × 6. B, epidermis of lamina (? upper surface) from the above specimen. A stoma is seen. × 200. C, D, epidermis of lamina (? lower surface) showing cells and stomata. Specimen as above. × 200. E, enlarged drawing of specimen in Pl. 4, Fig. 32. × 6. F, epidermis of lamina (? upper surface) from the above specimen. × 200.

The first specimen shown in Pl. 4, Fig. 29; Text-fig. 8A measures 1 cm. × 7 mm. It shows a slender rachis bearing a number of ± rhomboidal, opposite, contiguous pinnules which are coherent for the most part except near the apex. One of the pinnules measures 4×1 mm. The base of the pinnules is somewhat narrowed. A midrib is distinct for most part except near apex and curves down near its emergence. The substance of the pinnules appears to have been originally thick. Small patches of the epidermal cells are preserved here and there but are mostly in the close vicinity of the midrib. The epidermal cells on the exposed side (? upper) show linear arrangement. The cells (PL. 4, FIG. 30; TEXT-FIG. 8B) are elongated, polygonal, measuring about 43-94 × 16-25 μ.

The epidermal cells on the other side (? Lower) are similar (TEXT-FIG. 8C) to the upper. Stomata occur on both the surfaces, but may be more on the lower side. They appear like somewhat rounded structures with 4-5 subsidiary cells, enclosing a pit (PL. 4, FIG. 31*st*; TEXT-FIGS. 8B, D). In some cases, the subsidiary cells seem to slightly project in the pit. However, this may also be partly due to preservation. The guard cells are sunken. On the whole the stomatal apparatus is of the *Dicroidium* type.

The other specimen is shown in Pl. 4, Fig. 32; Text-fig. 8E. It measures 1·8 cm. × 8 mm. and shows a few ± rhomboidal, obtuse pinnules attached by their whole base, recalling *Dicroidium odontopteroides*. One of the pinnules measures about 5 × 2 mm. Veins are not distinct. The epidermal cells are badly preserved on the pinnules (shown in black in TEXT-FIG. 8E), which reveal polygonal, somewhat elongated cells at some places (PL. 4, FIG. 33; TEXT-FIG. 8F).

Remarks — The above two specimens are fragmentary and may represent terminal portions. They are, however, important inasmuch as they reveal the presence of a cuticular crust with impressions of epidermal cells. Of these two, the one in Fig. 29 has yielded sufficient information about the epidermal structure which leaves no doubt as to its inclusion under *Dicroidium*. The other specimen (FIG. 32) is less clearly known regarding its epidermis. However, the shape of the pinnules and their attachment, together with the presence of an epidermal crust, is in itself suggestive of its close resemblance with *Dicroidium*. As the material is rather imperfect, it would seem more appropriate to describe them as *Dicroidium* sp. for the present. It may be that the two specimens represent different species.

GENERAL DISCUSSION

Our knowledge of the Indian Triassic forms of *Dicroidium* was hitherto limited to a few specimens without known epidermal structure. They are *D. odontopteroides* from the Trias of South Rewa Gondwana basin (FEISTMANTEL, 1882, p. 38) and Ramkola coalfield (FEISTMANTEL, 1881, p. 87), *D. hughesi* from the South Rewa basin (FEISTMANTEL, 1882, p. 25) and *D. sahnii* from the same basin (SEWARD, 1932, p. 235). The occurrence of *D.* sp. cf. *D. feistmanteli* is a new addition. The entire evidence now at hand shows that the Indian Triassic Gondwanas contain at least four recognizable species of *Dicroidium* and in all the cases their epidermal structure is now known. They are:

1. *D. odontopteroides* (MORR.)
2. *D.* sp. cf. *D. feistmanteli* (JOHNSTON)
3. *D. hughesi* (FEIST.)
4. *D. sahnii*[2] (SEW.)

The epidermal structure of the above forms now investigated fits in very well in the diagnosis of the genus *Dicroidium* as outlined by Townrow. This evidence not only lends support to the basis on which *Dicroidium* is defined, but also points out that cuticular characters are a valid criteria for distinguishing *Dicroidium* from *Thinnfeldia*.

To be able to resolve all such records from India and abroad, which are suspected *Dicroidium* or *Thinnfeldia*, it would now seem necessary to reinvestigate them especially from cuticular point of view. Of particular interest is the Indian early Jurassic record which contains the following forms —

1. *Dicroidium odontopteroides*: See Antevs, 1914, p. 55, Synonymy; Two specimens originally described by Feistmantel (1879, p. 13) as *Thinnfeldia subtrigona* and *Thinnfeldia* sp.; cuticle unknown.
2. *Danaeopsis rajmahalensis*: Feistmantel (1877, p. 53); This form is closely comparable to *Dicroidium hughesi*. Its cuticle is, however, unknown.
3. *Thinnfeldia indica*: Feistmantel (1877, p. 35); cuticle unknown.

2. This species which was originally described under *Thinnfeldia* has a *Dicroidium*-type of cuticle. The results will be published elsewhere.

TABLE 1 — *DICROIDIUM* SPECIES IN THE TRIASSIC OF INDIA AND THEIR DISTRIBUTION IN THE CONTEMPORARY DICROIDIUM FLORA OF OTHER GONDWANALAND COMPONENTS

GONDWANALAND COMPONENTS	*D. odontopteroides*	*D.* sp. Cf. *D. feistmanteli*	*D. hughesi*	*D. sahnii*	REMARKS
INDIA	+	+	+	+	Total 4 species
S. AFRICA	+	+	+	+	Total about 6 species (Seward 1908, du Toit, 1927, Thomas, 1933, Townrow, 1957)
AUSTRALIA	+	+	+		Total about 8 species (Walkom, 1917, 1921, 1924, 1925, 1925a, b; 1928; Jacob & Jacob, 1950; Townrow, 1957)
S. AMERICA	+	+	+		Total about 6 species (Frenguelli, 1941-1944, 1944a, Gordon & Brown, 1952, Townrow, 1957)
NEW ZEALAND	+	+			Total about 3 species (Arber, 1917, Townrow, 1957)
TASMANIA	+	+			Total about 5 species (Walkom, 1926a, b, Townrow, 1957).

4. *Thinnfeldia chunakhalensis*: Sah & Sukh-Dev (1957, p. 22); cuticle unknown.

The above list appears to suggest the presence of both *Thinnfeldia* and *Dicroidium* in the early Jurassic rocks of India. Although this cannot be taken for granted unless cuticular details are known in each case, the probability of a *Dicroidium-Thinnfeldia* association or at least an admixture would not be surprising. For, there are already a few suspected records of *Thinnfeldia* from the Southern Hemisphere and of *Dicroidium* from the Northern Hemisphere (TOWNROW, 1957, p. 33). Townrow (1957, p. 31) contends that *Dicroidium* (Triassic) is stratigraphically older than *Thinnfeldia* (Lower Jurassic), and that the end of the former overlaps the beginning of the latter. If this is true, a *Dicroidium-Thinnfeldia* admixture would be expected in rocks on the boundary between the Triassic and the Jurassic periods. Such an admixture, if really found existing, would also impart additional interest to the phytogeographical relationship of the essentially southern genus *Dicroidium* and the northern genus *Thinnfeldia*.

A close survey of the fossil floras of the Gondwanaland clearly points out that during the Permo-Triassic times the *Glossopteris* flora suffered a decline and gave way to a new flora poineered by *Dicroidium*. This is corroborated by the remarkable appearance of *Dicroidium* in the beginning of the Triassic period on the Gondwanaland and its greater preponderance and widespread distribution throughout the Triassic period (TABLE I). It is only apt, therefore, to call this flora as *Dicroidium* flora.

India, once a part of the Gondwanaland, also registered in its own way a similar transition. During the early part of the Triassic the Glossopteris flora began to dwindle and *Dicroidium* made its appearance along with a few new elements. The Panchet flora, although little known, bears this out. It is but natural that the two genera *Glossopteris* and *Dicroidium* or their associates overlapped for sometime during the Triassic which is exemplified by their admixture known from the Panchets of Ramkola coalfield (FEISTMANTEL, 1880, 1881, p. 87) and from Parsora beds (SAKSENA, 1952, LELE, 1953, 1955). A similar admixture of certain elements of the *Glossopteris* flora and the *Dicroidium* flora is also known from the Upper Beaufort and Molteno beds of South Africa (DU TOIT, 1954, p. 350) and the Narrabeen stage of Australia (WALKOM, 1925, pp. 214, 215). However, during the large part of the Triassic period, the genus *Dicroidium* appears to have predominated in India in a manner similar to that of other Gondwanaland components. This is strongly supported by the occurrence of at least four species of *Dicroidium* namely *D. odontopteroides*, *D.* sp. cf. *D. feistmanteli*, *D. hughesi* and *D. sahnii*. Of these four species, *D. odontopteroides* and *D. feistmanteli* are most widely-spread in the Gondwanaland Trias (*see* TABLE I). *D. hughesi* is known from Australia and Africa while *D. sahnii* is known from Argentina (FRENGUELLI, 1944, p. 23).

It is true that we have only begun to unravel the secrets of the Triasso-Rhaetic Gondwana flora of India[3]. Nevertheless, the evidence now available from the South Rewa basin strongly favours the contention that like other Gondwanaland components, the Triasso-Rhaetic sediments of India also bear testimony to the presence of what should be recognized as a *Dicroidium* flora. It seems now more probable that this flora with *Dicroidium* as its characteristic genus would constitute the Indian Middle Gondwana flora, much in the same way as the *Glossopteris* Flora and the *Ptilophyllum* Flora characterize the Lower and the Upper Gondwanas respectively.

3. Other fossil plants constituting this flora of the South Rewa basin would be described elsewhere.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

(*All photographs are from untouched negatives. The specimens and slides are preserved in the Birbal Sahni Institute.*)

PLATE 1

Dicroidium odontopteroides (Morr.) Gothan

1. Specimen No. K25/563, Aiyengar coll.; Chicharia (Loc. 16); × Nat. size.
2. Specimen No. 8753, B.S.I.P. Coll.; Parsora (Loc. 10). × Nat. size.
3. Specimen No. K25/567, Aiyengar coll; Chicharia (Loc. 16). × 1/2.
4. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 1 showing minute sinuosities or projections in the cell outlines and stoma (*st*); × 200.
5. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 2 showing similar features as in Fig. 4. One of the stoma (*st*) has 5 subsidiary cells. × 200.
6. Epidermal cells of the lamina (? lower surface) of specimen in Fig. 2. Stomata with 4 and 5 subsidiary cells are seen. × 200.
7. Epidermal cells of the pinna-rachis (? upper surface) of specimen in Fig. 1. × 100.

PLATE 2

Dicroidium sp. cf. *D. feistmanteli* (Jonston) Gothan

8. A complete forked frond. Specimen No. 9103, B.S.I.P. coll; Bhaursen (Loc. 15); × Nat. size.
9. Another specimen, No. K 25/567, Aiyengar coll; Chicharia (Loc. 16); × Nat. size.
10. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 8; × 200.
11. Epidermal cells of the lamina (? lower surface) of specimen in Fig. 8. Two stomata (*st*) are seen.
12. Epidermal cells of the lamina (? lower surface) of specimen in Fig. 9; × 200.
13. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 9; × 200.

PLATE 3

Dicroidium hughesi (Feist.) Gothan

14. A specimen showing leaves with clear venation. Specimen No. 8742, B.S.I.P. coll. × ½.
15. A large portion of an originally forked frond. Specimen No. 5112, B.S.I.P. coll. × 1/4.
16. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 14; × 100.
17. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 15; × 100.
18. Epidermal cells of the lamina (? lower surface) of specimen in Fig. 15. A number of stomata are present; × 75.
19. Epidermal cells of the lamina (? lower surface) of specimen in Fig. 14. Most of the cells show the presence of a rounded papilla base (p); × 100.
20. A single stoma (± exposed type) from the lamina (? lower surface) of specimen in Fig. 14. The apparatus shows 4 subsidiary cells. The guard cells and a pore are indistinctly visible. × .200
.21 Another stoma (exposed type) from same place as in above. The guard cells and a pore are also seen; × 200.
22. Epidermal cells of the main rachis (? lower surface) of specimen in Fig. 15; × 100.

PLATE 4

Cf. *Dicroidium hughesi* (Feist.) Gothan

23. A specimen with a concave depression; specimen No. 9084, B.S.I.P. coll., Barnauda (Loc. 11). × 2.
24. Another specimen rolled in a direction (shown by arrow mark) slightly oblique to the midrib. The venation is clearly seen. Specimen No. 9090, B.S.I.P. coll., Barnauda (Loc. 11); × 2.
25. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 23; × 100.
26. Epidermal cells of the lamina (? lower surface) of specimen in Fig. 23. A number of stomata are seen. On the vein region (*v*) cells are arranged in rows. Some of the cells also show remains of a papilla (*p*); × 75.
27. Two stomata (*St*) from the lamina (? lower surface) of specimen in Fig. 23 showing subsidiary cells enclosing a pit. The apparatus appears to be sunken. × 200.
28. Epidermal cells of the midrib (? upper surface) of specimen in Fig. 23. The midrib has undergone lateral compression along its length which has partly modified the shape of the cells, which may not be originally as long as they appear now. × 100.

Dicroidium sp.

29. A small specimen, probably representing a terminal part of a pinna; specimen No. K 25/722, Aiyengar coll., Daigaon (Loc. 7); × 3.
30. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 29. × 200.
31. A rounded stoma (*St*) from the lamina of specimen in Fig. 29 showing 5 subsidiary cells, enclosing a pit. × 200.
32. Another small specimen referred to *Dicroidium*. Specimen No. K 25/725, Aiyengar coll., Daigaon (Loc. 7); × 3.
33. Epidermal cells of the lamina (? upper surface) of specimen in Fig. 32; × 100.

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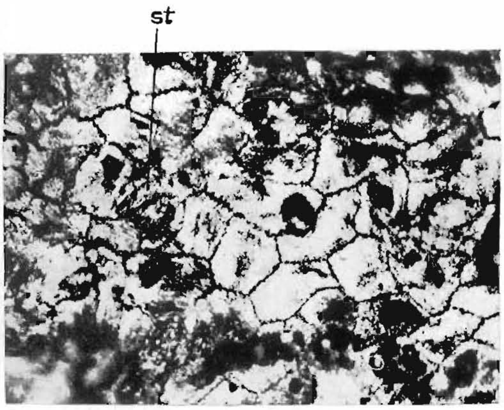

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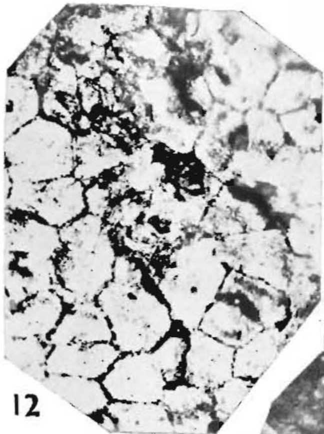

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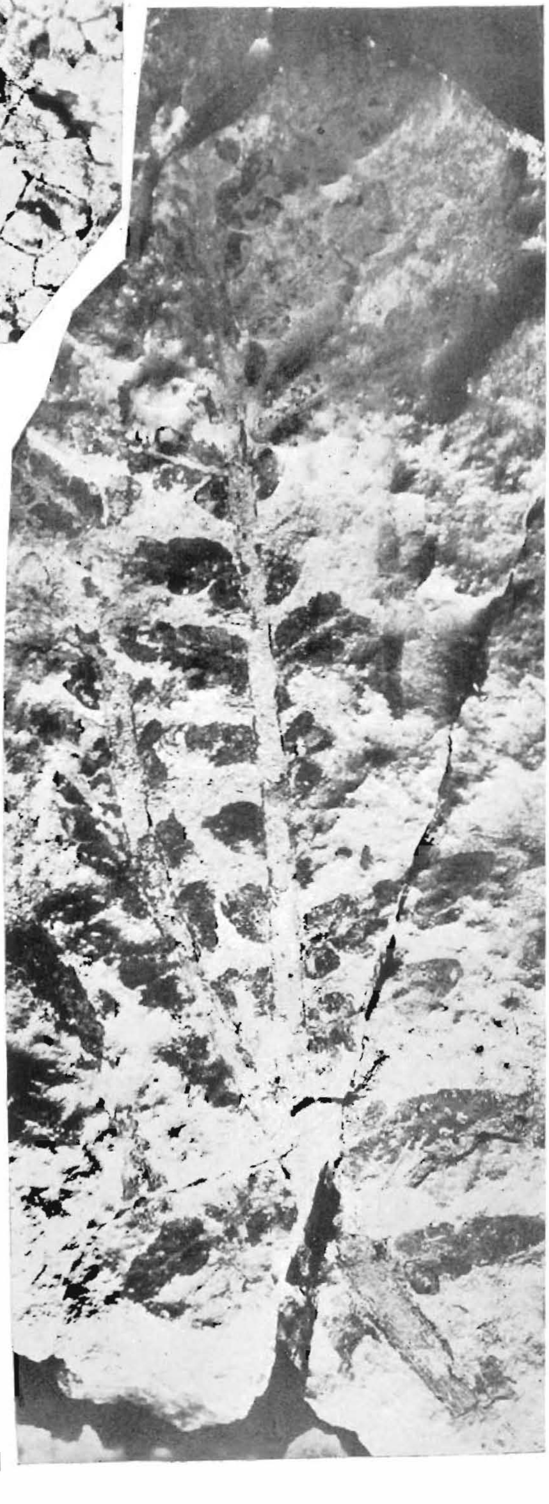

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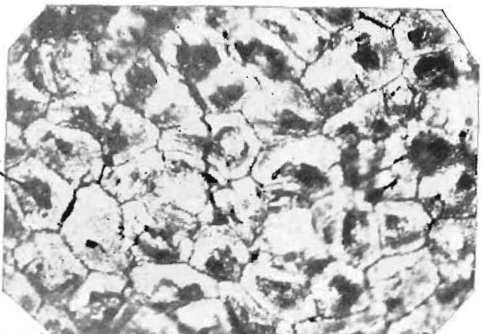

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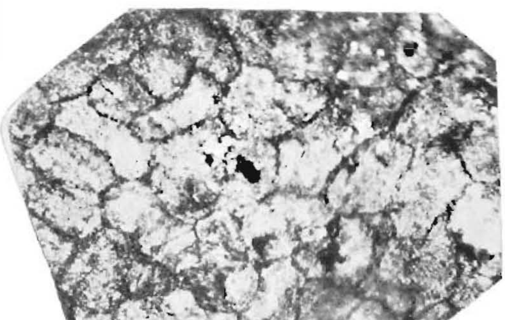

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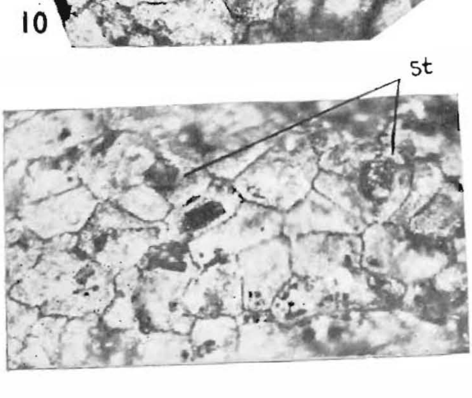

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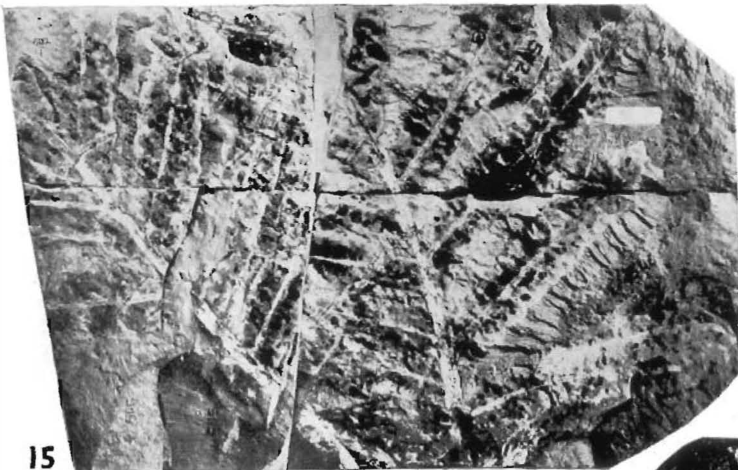
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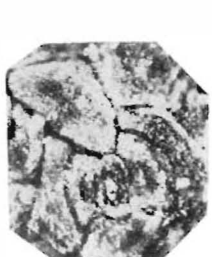
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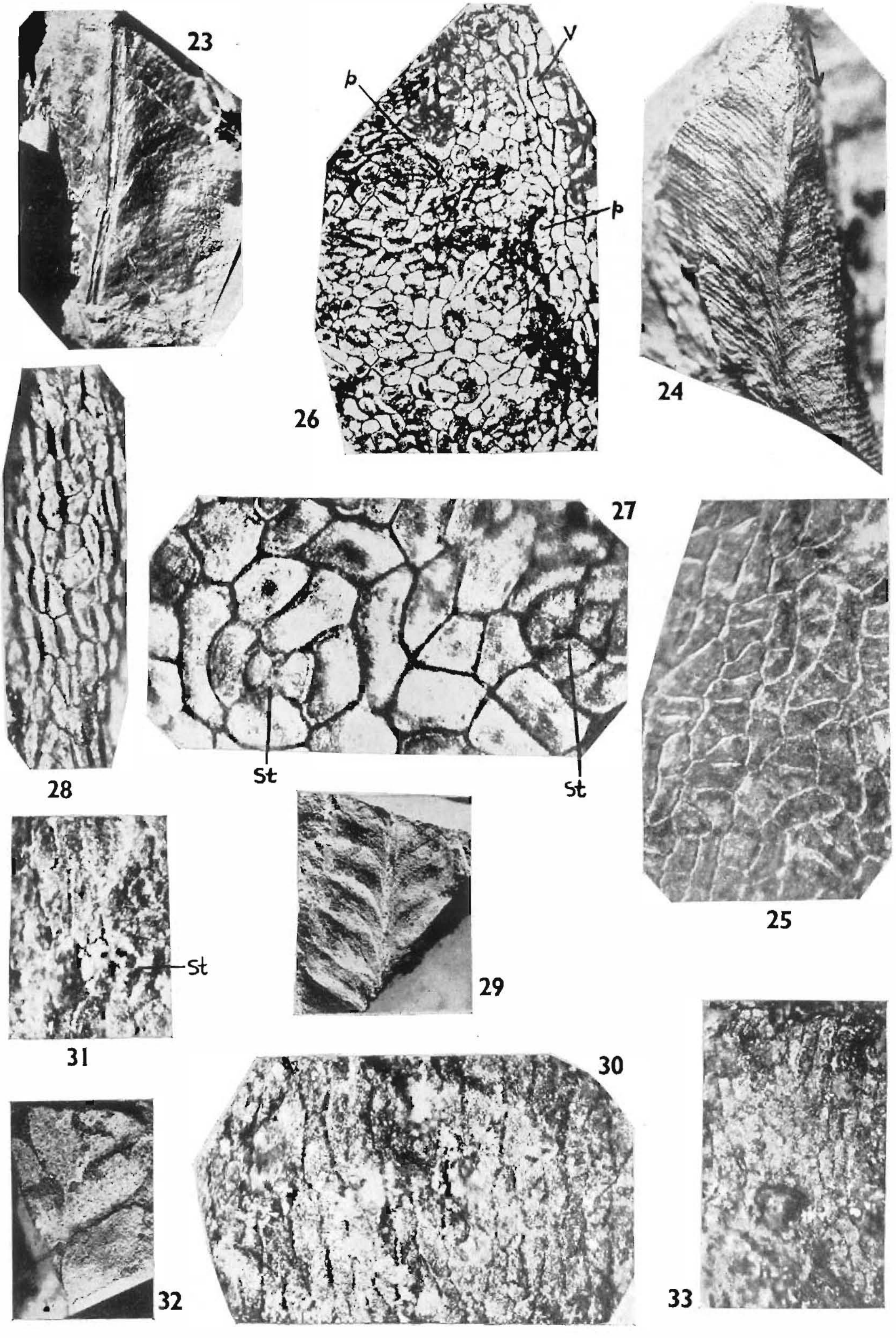
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