STUDIES ON TRIASSIC FOSSIL PLANTS FROM ARGENTINA. IV.

THE LEAF GENUS *DICROIDIUM* AND ITS POSSIBLE RELATION TO *RHEXOXYLON* STEMS

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ABSTRACT. The cuticle of four species of the genus *Dicroidium* is described. The material has been found in close association with *Rhexoxylon* stems in the locality of Ischigualasto, San Juan Province, Argentina. Two new combinations are proposed: *Dicroidium zuberi* (Szajnocha) and *Dicroidium elongatum* (Carruthers). It is proposed that *Dicroidium* leaves are related to *Rhexoxylon* stems (*a*) because they are associated in four Triassic localities of South Africa and Argentina, and (*b*) because there is a structural relation of both organs with the Palaeozoic pteridosperms.

THIS paper reports the very striking association of *Rhexoxylon* petrifactions with *Dicroidium* compressions and impressions in two localities in Argentina, and (though with less clear information) in South Africa.

The Ischigualasto Formation (of NW. Argentina) has yielded abundant petrifactions of *Rhexoxylon* stems (Archangelsky and Brett 1961, Brett 1968). The stems can be about 10 m. high and about 1 m. in diameter near the base. Most of the petrifactions observed in the field belong to this genus. In the same beds, pockets of loose sandstone with many leaves were also found. Some of these pockets include stems covered by compact masses of cuticles, and the stems are sometimes further surrounded by a thick layer of gypsum in which similar cuticles are embedded. The leaves are fragments consisting of cuticles with only a little internal substance. Four lots of material collected at different times, have been studied. The Archangelsky and Brett collection (1961) and the Romer collection (1964–5) belong to the La Plata Museum Palaeobotanical Collection (LP–PB), while the Archangelsky (1958) and Herbst (1960) material, belongs to the Lillo Institute Collection of Tucumán University (LIL–PB). In the same formation, and in the same area, a very rich vertebrate fauna has been found. Some of the skeletons are also covered by compact masses of cutinized leaves (Romer 1962).

Four species of leaves were found in Ischigualasto, associated with *Rhexoxylon*, and I refer them, on the ground of size and shape of pinnae, and cuticular structure, to the following species of *Dicroidium*:

Dicroidium zuberi (Szajnocha) comb. nov.
Dicroidium elongatum (Carruthers) comb. nov.
Dicroidium coriaceum (Johnson) Townrow
Dicroidium sp.

Only the first three species may be considered as abundant; the fourth is rare and difficult to determine precisely.

The second Argentine locality which has yielded *Rhexoxylon* petrifactions and

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Dicroidium impressions is Barreal, San Juan Province. This association is here reported for the first time; the petrifactions are now being studied by Dr. Bonetti (Buenos Aires Natural History Museum) who has already published the study of the leaf impressions (1963).

From the literature (Du Toit 1954, Walton 1956) it seems that the *Rhexoxylon–Dicroidium* association is also present in the Triassic of South Africa.

On independent grounds, both *Rhexoxylon* and *Dicroidium* (together with their known male and female fructifications, *Pteruchus* and *Umkomasia* respectively) may be derived from Palaeozoic pteridosperms.

DESCRIPTION OF THE MATERIAL

Genus DICROIDIUM Gothan 1912 emend. Townrow 1957

1943 *Dicroidiopsis* Frenguelli
1943 *Diplasiophyllum* Frenguelli
1943 *Zuberia* Frenguelli
1943 *Xylopteris* Frenguelli
1957 *Hoegia* Townrow

Discussion. Townrow (1957) emended the original diagnosis of *Dicroidium* (Gothan 1912), making a clear definition of its morphological and anatomical characters. I accept here this definition with the exception of two characters: (*a*) the cuticle may be thicker than 3 μ and (*b*) the stomata may be imperfectly dicyclic as well as dicyclic. In the emended diagnosis of *Dicroidium*, there is no statement of the shape of the pinnules. As *Xylopteris* is here included in *Dicroidium*, pinnules of the genus may be rhomboidal, elongated or linear, with one or several veins in them.

The thickness of a cuticle is of no generic value; it may even vary in one species. Also, the stomata may be variable (from mono- to di-cyclic) in one species of a genus; when the cycles of subsidiary cells are constant, the character may be regarded as specific rather than generic. Accepting these two emendations, the genus *Hoegia* (Townrow 1957) is a synonym of *Dicroidium*. (The forking of the main rachis of the frond was not observed by Townrow in his *Hoegia* specimens, probably because he dealt with small fragments of pinnae. Large fronds of *Dicroidium* are commonly found broken and it is not easy to find the main rachis with its fork.)

Frenguelli (1943, 1944) defined the genus *Zuberia* on external morphology of pinnae; there are no obvious reasons, however, to differentiate this genus from *Dicroidium*, as the shape of pinnules and venation are identical. Townrow (1957) believes that *Zuberia feistmanteli* sensu Frenguelli is in fact *Dicroidium*. Bonetti (1966) goes further and places all four species of Frenguelli's *Zuberia* in *Dicroidium feistmanteli*, but I unite them as a separate species, *Dicroidium zuberi*.

The genera *Dicroidiopsis* (Frenguelli 1943) and *Diplasiophyllum* (Frenguelli 1943) are also placed in *Dicroidium* by Townrow and by Bonetti; I agree with these authors.

Xylopteris (Frenguelli 1943) is here considered as belonging also to *Dicroidium*. Although not expressed in synonymy both Townrow (1962*a*) and Bonetti (1966) have already recorded this opinion. The cuticular structure of *X. elongata* for instance, in particular the stomatal apparatus, is similar to the cuticular structure of *Dicroidium* *coriaceum* (formerly known as *Johnstonia coriacea*). The forking of the main rachis in *Xylopteris* agrees with all known species of *Dicroidium*. The shape of the pinnules, which are linear, is here considered as a character of specific rank.

Dicroidium zuberi (Szajnocha) comb. nov.

Plate 98, figs. 1, 2; text-figs. 1*a*, 2*d*, *e*

1888 *Cardiopteris zuberi* Szajnocha, p. 233, pl. 2, fig. 1.
1943 *Zuberia zuberi* (Szajnocha) Frenguelli, p. 300.
1944 *Zuberia zuberi* (Szajnocha) Frenguelli; Frenguelli, p. 9, pl. iv–xi, pl. xii, figs. 1, 2.
1944 *Zuberia feistmanteli* (Johnston) Frenguelli; Frenguelli, p. 3, pl. i–iii.
1944 *Zuberia barrealensis* Frenguelli, p. 20, pl. ix, figs. 1, 3; pl. xiii.
1944 *Zuberia sahnii* Frenguelli, p. 23, pl. xii, fig. 3.
1957 *Hoegia papillata* Townrow, p. 49, pl. ii C, iii B, text-figs. 8 B–D, G, K; 10 C–J; 11 A–C.
?1957 *Hoegia antevsiana* Townrow, p. 50, pl. iii C, text-figs. 8 E; 9 L; 10 K; 11 D.

Description. This is the most frequent species in several beds of the Ischigualasto Formation. It is also present in association with all *Rhexoxylon* stems. The better fragments show the forking of the main rachis (Frenguelli 1944, pl. iv, pl. vii, 1), but since the whole leaf is large, small specimens appear bipinnate or simply pinnate. The size, and especially the shape of the pinnules are the most important characters of the species; usually the pinnules are rhomboidal or somewhat square, with slightly contracted bases and the distal margin may be entire or irregularly lobed. The pinnules of one row may overlap or be separated. Elongated pinnules do occur, but they are not common, their shape being slightly falcate. Venation is also characteristic; one or more groups of veins arise at the base of the pinnule from the rachis, each vein forking usually once or twice and curving slightly towards the lateral margins. Commonly the veins tend to concentrate all in one basiscopic point. Our specimens are in complete agreement in size, shape, and venation with the material described by Frenguelli as *Zuberia zuberi* and also with Townrow's *Hoegia papillata*. By transparency a distinct border is seen along the margins of the pinnules, devoid of venation and inner coaly substance.

One cuticle is slightly thicker than the other; both are very thick (about 8 μ). Epidermal cells on both cuticles are typically isodiametric and polygonal, with straight walls, about 50–60 μ. Cuticular projections from anticlinal walls present; they are most irregular in their thickness. Short, round papillae are commonly found on the cell surface (more frequent on the thicker cuticle). The stomata are indistinctly orientated, present on both cuticles and evenly distributed, rarely with subsidiary cells in contact. There are about 70–110 stomata per square millimetre. The stomatal apparatus is typically monocyclic, circular to oval. The guard cells are sunken in a pit formed by 4–6 subsidiary cells which coalesce around the mouth of the pit, forming usually a strong rim of cutine. Subsidiary cells normally not papillate (but sometimes they are).

The papillae are sometimes almost absent on a whole cuticle; or they may vary greatly in concentration over the same cuticle. It seems that this is a variable character. The papillae are usually small and solid.

Material studied. San Juan Province, Ischigualasto Basin. Bed 1: LP 7449, 7450, 7453; LIL 2768, 2769. Bed 2: LP 7451, 7454; LIL 2770. Bed 3: LP 7439, 7440–3; LIL 2767, 2772. Bed 4: LP 7430–4,

TEXT-FIG. 1. Compressions of *Dicroidium* leaves, $\times \frac{2}{3}$. *a*, *D. zuberi* (Frenguelli) Archangelsky; slide LP 425, fragmentary pinnae. *b*, *D. elongatum* (Carruthers) comb. nov. (the four central linear pinnae), and *D. coriaceum* (Johnston) Townrow; slide LP 427 shows extreme types and transitional forms between the two species. *c*, *Dicroidium* sp.; slide LP 428, fragmentary pinnae.

7436–8, 7441, 7448; LIL 2765, 2776. Bed 7: LP 7452. Slides LP 417, 424, 425; LIL 504–8. Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. Frenguelli (1944) described four species of his previously established genus *Zuberia*. Two of the species, *Z. sahnii* and *Z. barrealensis*, based on very fragmentary material. *Z. zuberi* and *Z. feistmanteli*, as far as the Argentinian material is concerned, are very similar and there are no important characters differentiating them. *D. feistmanteli* (Johnston) Gothan, is distinguished by the entire margins of its pinnules, less crowded veins, much thinner cuticle and fewer stomata (25 against 70–100 per mm. in *D. zuberi*).

The Ischigualasto specimens, though fragmentary, are identified with Frenguelli's material (which I have examined in the La Plata Museum Collection) because they agree in size, shape, and venation of pinnules. Moreover, Frenguelli's four species integrate in these respects and for this reason I have merged them all in *D. zuberi*.

The original specimen (type) of *Zuberia zuberi* is the one that Szajnocha described as *Cardiopteris zuberi* (from Argentina) and Frenguelli combined in his genus *Zuberia*. This specimen should therefore be the holotype, but I do not know where it is located, and Szajnocha gave no collection reference or numbers in his paper (1888). I select a neotype, LP 9520, a large leaf with a main bifurcate rachis (figured by Frenguelli 1944, pl. iv).

Our material also coincides in morphology and cuticular structure with that described as *Hoegia papillata* by Townrow. As *D. zuberi* has a forked main rachis of leaves, there is no reason to keep a different species for pinnate fragments, which are too small to show the main rachis of the whole leaf.

Some specimens (particularly those found in Bed 2) present a very thick cell border of the pinnules, resembling in this respect *Hoegia antevsiana* Townrow. I suggest that Townrow's species might be regarded as a mere variation of *D. zuberi*, because they coincide in stomatal structure and the size of epidermal cells.

Dicroidium elongatum (Carruthers) comb. nov.

Plate 97, figs. 1, 3; Plate 98, fig. 4; text-fig. 1*b*, 2*a*

1872 *Sphenopteris elongata* Carruthers, p. 355, pl. 27, fig. 1.
1943 *Xylopteris elongata* (Carruthers) Frenguelli, p. 318, text-figs. A, B.
1962 *Xylopteris elongata* (Carruthers) Frenguelli; Townrow 1962, p. 123.

Description. The Ischigualasto material is comparable in shape and size with the lectoparatype figured and described by Townrow (1962*b*), having very elongated segments which sometimes fork dichotomously. The segments are almost parallel-sided and taper very gradually to a short but rounded apex. The best specimens are fairly

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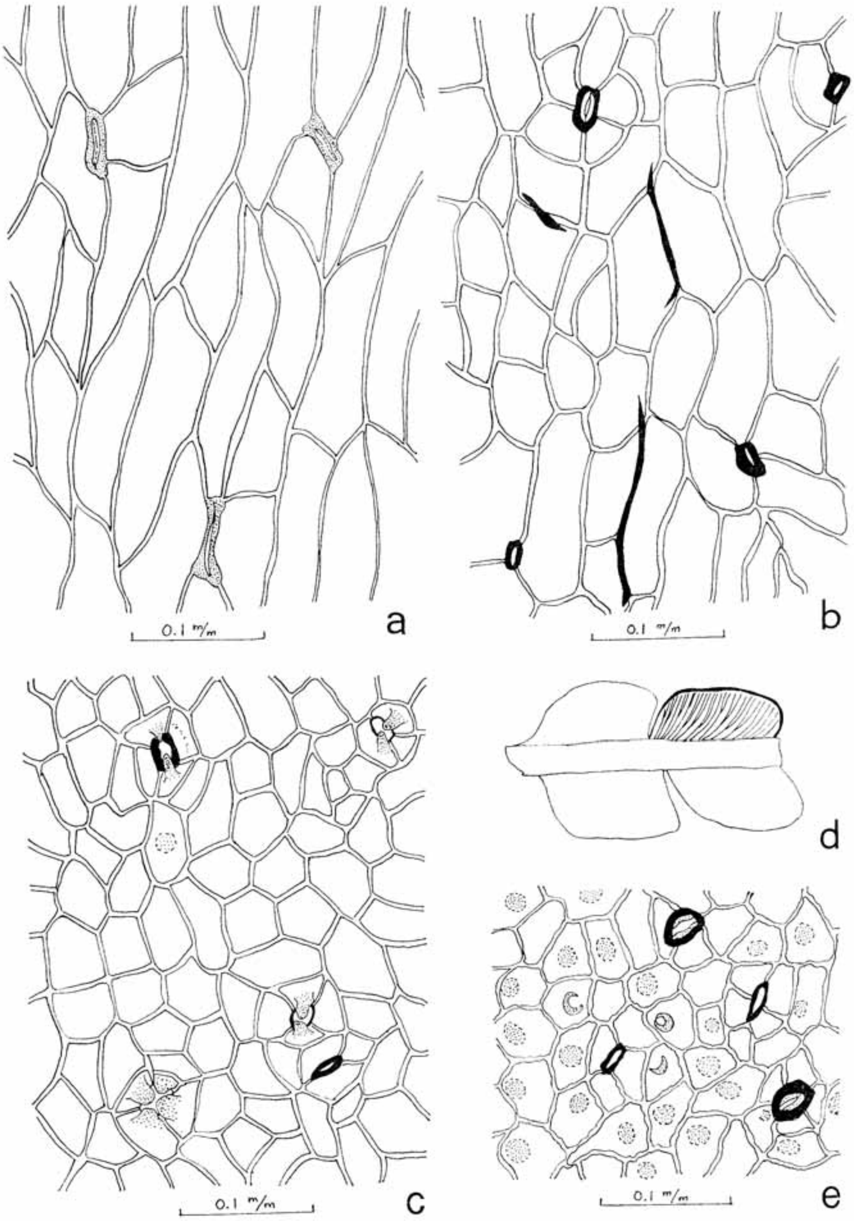
EXPLANATION OF PLATE 97

Figs. 1, 3. *Dicroidium elongatum* (Carruthers) comb. nov. 1, Specimen showing bifurcation of the main rachis; LP 7456, × 1. 3, Two stomata; LP 416, × 300.

Figs. 2, 5. *D. coriaceum* (Johnston) Townrow. 2, Fragment of leaf showing bifurcate rachis; LP 7457, × 1. 5, Two stomata; LP 437, × 300.

Fig. 4. *D.* sp., a few stomata showing papillae overhanging the mouth of the pit; LP 432, × 300.



TEXT-FIG. 2. Drawings of *Dicroidium* leaves. *a*, *D. elongatum* (Carruthers) comb. nov.; epidermis showing three stomata, slide LP 14. *b*, *D. coriaceum* (Johnston) Townrow; epidermis showing stomata and cuticular ridges, slide LP 437. *c*, *D.* sp.; epidermis showing stomata and papillae overhanging the mouth of the pit, slide LP 432. *d*, *D. zuberi* (Szajnocha) comb. nov.; outline of pinnules showing venation, slide LP 425; × 1·5. *e*, As last, epidermis showing stomata and papillae on cells, slide LP 418.

complete, and they are preserved as impressions; compressions are usually very fragmentary, represented by only the single linear segments. Though a midrib is not at first visible in these segments, a suggestion of one is visible when the fossil (consisting of little more than cuticles) is cleared as a transparency. Also by transparency a clear marginal zone may be seen, with no coaly substance in it. Some fragments of pinnae seem to have wider segments, showing what may be an incipient marginal lobing. Such fragments show, by transparency, a clear median vein.

The cuticles may be of equal thickness, or one (which Townrow regards as the lower) is rather thinner. The epidermal cells on both cuticles are alike, usually rectangular or elongated, with their longitudinal axis parallel to the long axis of the segments. They form ill-defined rows. Isodiametric epidermal cells also do occur. Long cutin ridges are present on both cuticles, and they are also longitudinally orientated, although oblique and transversely orientated stomata have been observed. They are widely separated and rarely have subsidiary cells in contact. I have counted about 10–15 stomata per square millimetre. Epidermal cells are 100–150 μ long × 20–40 μ wide (and 50–70 μ when isodiametric). Their outline is straight, showing small sinuosities due to different thickness of the anticlinal walls. Papillae are rarely seen. The stomatal apparatus is oval, typically monocyclic. The guard cells are feebly cutinized and are sunken in a pit formed by 4–6 unspecialized subsidiary cells. The mouth of the pit usually has a distinct cutin border, sometimes forming a continuous rim. The poles of the guard cells are sometimes exposed on the surface. Occasionally, a circular stomatal apparatus was seen, with strongly sunken guard cells. In the apical parts of the segments, the epidermal cells tend to be more isodiametric.

Material studied. San Juan Province, Ischigualasto Basin. Bed 2: LP 7451; Bed 4: LP 7429, 7438; LIL 2766. Bed 6: LP 7418–28; LIL 2763, 2764, 2771. Bed 7: LP 7452, 7456, 7463, 7464, 7466. Slides LP 412–16, 426, 427; LIL 501–3. Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. Our material agrees in all respects with the type material of *D. elongatum* as described by Townrow (1962*b*), in the shape and size of the segments and in the cuticular structure.

In Ischigualasto, *D. coriaceum* and *D. elongatum* occur together in some beds, while *D. elongatum* is found alone in some others (Beds 4 and 7).

In the Barreal region (San Juan Province) three plant beds have been recognized (Bonetti 1963). *D. elongatum* does occur together with *D. coariaceum* in Bed I, but in Bed II, *D. elongatum* occurs alone.

In some other Triassic localities in Argentina, *Xylopteris* species have been described, but there is no mention of the *Johnstonia* type of leaves (Neuquen, Santa Cruz, etc.).

All these additional references seem to indicate that *D. coriaceum* and *D. elongatum* are probably two different species, although they have some morphological similarities.

Dicroidium coriaceum (Johnston) Townrow

Plate 97, figs. 2, 5; Plate 98, fig. 3; text-figs. 1*b*, 2*b*

Description. The leaf is very variable. The less-lobed segments (pinnae) are somewhat similar to the *D. elongatum* linear segments, although they are wider. The lobing of the segments (differentiation of the pinnules) may be just incipient, or it may be quite developed; in such a case, the resulting pinnules may be again similar to unlobed pinnae. All three degrees of variation have been observed in the abundant material. The size and the shape of the Australian material described by Townrow (1957) may be matched in our specimens. The pinnules of the well-developed pinnae are linear and have rounded apices. The segments are bordered by a rim of cutin, clearly seen by transparency. One vein penetrates each segment, and it may fork once or twice (veins were seen by transparency).

Both cuticles are of a similar thickness. The epidermal cells are of two kinds: elongated (more than 100 μ long × 40 μ wide) and isodiametric (50–70 μ in diameter). Low cuticular papillae, one per cell, are sometimes seen. The stomata are usually longitudinally orientated, sometimes obliquely or transversely. The walls of epidermal cells are straight, sometimes with irregular cutinization of anticlinal walls. Strong longitudinal ridges of cutin are also present. The stomata are irregularly disposed, separated and never with subsidiary cells in contact. There are about 30 stomata per square millimetre. The stomatal apparatus is typically imperfectly dicyclic, with feebly cutinized guard cells, little or not at all sunken. There are 4–6 subsidiary cells, the polar usually differentiated from the lateral. Subsidiary cells often having papillae. When the guard cells are little sunken, the subsidiary cells (usually the lateral) form a rim of cutin at the opening of the epistomatal chamber.

Material studied. San Juan Province, Ischigualasto Basin. Bed 6: LP 7424, 7425, 7428; LIL 2764, 2771. Material Romer, LP 7457, 7458, 7460–2, 7465. Slides, LP 426, 427, 436, 437 (Bed 2); LIL 515. Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. Our material seems to have more variation in cuticular structure than that described by Townrow. However, Australian specimens are very fragmentary, while our material presents a wide variety of leaves and different segment types. I believe that epidermal cells tend, in this species as a rule, to be longitudinally orientated in long pinnae or pinnules. Townrow's material shows only short, not fully developed pinnules, where the epidermal cells are usually more isodiametric. The papillae may be fairly common or may be lacking in large sectors of leaves; it is also a very variable character.

Extreme types of *D. elongatum* and *D. coriaceum* are quite distinct in shape. Intermediate forms can, however, be confused, and their determination becomes more or less arbitrary. The cuticles of both species are alike. The elongation of epidermal cells depends on the shape of segments and pinnules. Similar segments of both species have similar epidermal cells. Papillae are more abundant in *D. coriaceum*, but they are also present, though rarely, in *D. elongatum*. Stomata are similarly orientated in both species, and their concentration is alike. The structure of the stomatal apparatus is similar, though in *D. elongatum* guard cells seem to be more sunken. Differentiation of polar and lateral subsidiary cells is more clear in *D. coriaceum*.

It is difficult and may even be arbitrary to distinguish these species, for there are intermediate types. The cuticular structure is of no particular help in this respect. It seems, however, wise to have the two forms separated into two species. Certainly there are no firm grounds for the use of separate genera.

Dicroidium sp.

Plate 97, fig. 4; text-figs. 1*c*, 2*c*

Discussion. Although there is a lack of certain characters, particularly the gross morphology of the fronds, this species is described here in order to complete the presentation of all the taxa which are found in association with the petrified *Rhexoxylon* stems. The only exception is *Neocalamites*, which is found with these compressions but which cannot be related to either *Dicroidium* or *Rhexoxylon*.

Description. This species is the least frequent in Ischigualasto. The size and the shape of pinnules and pinnae coincides with *Dicroidium superbum* (Shirley), as described by Townrow (1957). Pinnules are usually longer than wider, and their margins are sinuous or lobed. One complete pinna shows a narrow acute apex. Usually one decurrent vein was seen by transparency, running up to near the apex of the pinnule. Forking of veins was not clearly seen, but it may be possible in larger pinnules. By transparency the pinnules show a clear border of cutin without coaly substance.

Both cuticles are of an even thickness. Epidermal cells are usually isodiametric, except on the rachis and on the main vein, where they tend to be rectangular or elongated. Anticlinal walls are straight. On the surface, single round papillae are sometimes seen; one, rarely two, per cell. The stomata are irregularly orientated and distributed, sometimes with subsidiary cells in contact. The stomatal apparatus is usually oval, sometimes subcircular, imperfectly dicyclic. The guard cells are cutinized and sunken in a pit formed by 4–7 subsidiary cells, which can be wedge-shaped or of irregular shape. Subsidiary cells each bearing characteristically one round or slightly elongate papilla. Papillae usually overhanging mouth of pit, almost closing it. Guard cells slightly thickened near the aperture. Polar and lateral subsidiary cells not differentiated.

A few large pinnules are included in this species. In gross morphology they resemble *D. zuberi*, but they differ in their stomatal structure, and in the presence of strongly developed papillae and unicellular hairs. The cuticle of these pinnules is thick, up to 10 μ (one of the two is slightly thinner); the epidermal cells are isodiametric, often square or rectangular, forming definite longitudinal rows for a variable distance, about 40–50 μ in diameter, when elongated up to 60 μ long × 20–30 μ wide. Epidermal cells as a rule bear one strong, usually hollow, papilla; towards the margins papillae becoming high, in some cases resembling unicellular hairs up to 50 μ long. Cell walls with a uniform thick border. Stomata present on both cuticles, up to 60 per square millimetre. Stomata slightly sunken, surrounded by 4–5 subsidiary cells. Mouth of pit square, rectangular sometimes oval. Normally, subsidiary cells with strongly developed papillae overhanging the mouth of the pit, sometimes almost closing it. Epidermal cells on rachis, elongated and bearing papillae. Longitudinal cutin ridges also present.

EXPLANATION OF PLATE 98

Figs. 1, 2. *Dicroidium zuberi* (Szajnocha) comb. nov., LP 418. 1, Epidermis showing distribution of stomata, × 120. 2, Epidermal cells with papillae and two stomata, × 300.

Fig. 3. *D. coriaceum* (Johnston) Townrow, LP 437; epidermis with thickened bands of cutin, × 120.

Fig. 4. *D. elongatum* (Carruthers) comb. nov., LP 416; epidermis, × 120.

There are variations: some pinnules although having stomata with protective papillae, have no papillae on ordinary epidermal cells. Sometimes, most stomata are devoid of protective papillae, but after careful search, a few are found to be present.

It is difficult to establish whether these specimens are merely ecological varieties of *D. zuberi* or if they do belong to another species.

Material studied. San Juan Province, Ischigualasto Basin. Slides LP 428–35; LIL 509–15 (Beds 1, 3, 4, 6). Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. The size and the shape of the small pinnae resemble *D. superbum* (Shirley) Townrow. However, the cuticle shows some differences, mainly in the stomatal apparatus. No papillae overhanging the stomatal pit are known in *D. superbum*. Such papillae are normal in *Lepidopteris* but for other reasons our leaves must be placed in *Dicroidium*. The rachis of our specimens is not covered by lumps; the shape of the pinnules is not alike (neither is the venation) and the stomatal apparatus is not circular as a rule but often tends to be oval. On the other hand, similar stomata have been reported and figured by Townrow for *D. odontopteroides* (1957, figs. 5D, 6M).

As our material is scanty, I prefer to make no specific assignation until better specimens become available from this and other Triassic localities.

ASSOCIATION OF *DICROIDIUM* LEAVES AND *RHEXOXYLON* STEMS

San Juan Province, Ischigualasto Basin.

The material described here was collected from about 10 lenses of plant-bearing sandstones, over a distance of about 4 km. There are also compressions of *Neocalamites* stems. No other compressions have so far been found in these particular beds, although in other strata of the formation there are different plant elements. There are several petrifactions in close association with the compressions; most of them belong to *Rhexoxylon*. One small petrifaction belongs to a Cycad-like stem, *Michelilloa waltonii* Arch. and Brett (1963), which is unlikely to have borne *Dicroidium*, because the leaf base scar is too small. Finally, one petrified Conifer was recently described as *Protojuniperoxylon ischigualastensis* Bonetti (1966), which is also unlikely to have borne *Dicroidium* leaves. The overwhelming abundance of *Rhexoxylon* as petrifaction, and *Dicroidium* as compression, provides strong support of probable relationship.

San Juan Province, Barreal

In the locality Quebrada de la Tinta, La Cortaderita Formation, Bed III. 36 (Bonetti 1963), also of Triassic age, some *Rhexoxylon* petrified stems have been found. They have not yet been described, but Dr. Bonetti who collected them, kindly showed the material to me. It undoubtedly belongs to *Rhexoxylon*, and possibly to the Ischigualasto species *R. piatnitzkyi*. In the same bed, Bonetti reports the following plant impressions: *Dicroidium lancifolium* and *D. feistmanteli* (which in her sense is equivalent to *Zuberia zuberi* of Frenguelli) and *Pseudoctenis ctenophylloides* as the most abundant; less abundantly are found *Cladophlebis mendozaensis*, *Dicroidium narrabeenense*, and *Pteruchus dubius*. Therefore, there are four of the six species belonging to the *Dicroidium* complex, two of them being dominant. *Cladophlebis*, being a fern, is not related to *Rhexoxylon*. Only *Pseudoctenis* could perhaps be related to the petrified stems, apart from *Dicroidium* species.

South Africa

In South Africa the evidence of association is less clear, the facts not being available to me. Species of *Rhexoxylon* certainly do occur in the same formations with *Dicroidium* leaves. The stratigraphic references as given by Walton (1956) and Du Toit (1954) indicate that *Rhexoxylon* is present in several localities; all findings of the stems are referred to the Triassic Molteno and Red Beds in the Cape Province, and to the Somabula Beds of Rhodesia. Both units are part of the Stormberg Series. In the Red Beds, only silicified woods of *Rhexoxylon* and *Dadoxylon* are known. In the Molteno Beds, a large number of leaf impressions are known, including several species of *Dicroidium*. But in the taphoflora of the Somabula Beds in Rhodesia, apart from *Rhexoxylon*, three species of *Dicroidium*, one of *Taeniopteris* and one of *Schizoneura* have been reported. So, again only two genera can be related to *Rhexoxylon*, and the more important of them, having several representatives, is *Dicroidium*.

Resuming all the facts, *Rhexoxylon* is always associated with *Dicroidium* in two localities of Argentina and in two of South Africa. In Ischigualasto, they are the only taxa which might be related. In two other localities (Barreal, Argentina and Rhodesia, South Africa) *Rhexoxylon* and *Dicroidium* are almost exclusive elements in association, apart from *Pseudoctenis* in one and *Taeniopteris* in the other. Therefore, all four plant associations from South Africa and Argentina are consistent with the idea that *Rhexoxylon* bore *Dicroidium* leaves.

Further evidence is needed for making a much better case of this association. We are not able at present to relate particular species of *Dicroidium* leaves with species of *Rhexoxylon*. Indeed, different species of *Rhexoxylon* may represent different stages of development of one stem. An organic connexion is therefore needed.

STRUCTURAL RELATION OF *DICROIDIUM* AND *RHEXOXYLON*

On general grounds *Rhexoxylon* may be related in its structure to some Palaeozoic pteridosperms (Medullosae; Archangelsky and Brett 1961). On the other hand, all other organs of *Dicroidium* (male and female fructifications) are also related to the Palaeozoic pteridosperms. The leaves are also related to the pteridosperms as they have a fern-like appearance, with dichotomous main rachis and a thick cuticle with specialized stomata. It may be added that there is agreement between the leaf base of *Dicroidium* and the scars on *Rhexoxylon*, but only in their similar size and shape, for we have no supporting evidence of the vascular bundles.

The geological and geographical distribution shows *Rhexoxylon* and *Dicroidium* confined to the Gondwana Palaeofloristic Region, during the Triassic Period. Therefore, the data so far available are not against considering these two taxa as belonging to the same plant. The peculiar structure of *Rhexoxylon* is not in favour of its abundant representation in the sediments.

CONCLUSION

This paper makes a strong suggestion that the *Dicroidium* leaf was borne on the *Rhexoxylon* stem, but I do not claim that the present evidence constitutes overwhelming proof. It is merely circumstantial evidence, each item no more than suggestive, but gaining greatly in weight by repetition. I publish this idea mainly in the hope that it will cause others to notice further evidence bearing on this question. On the assumption that the idea is right, I examine some of the taxonomic consequences.

The Corystosperms constitute an important stock of information. Several Mesozoic groups, such as the Peltaspermaceae and the Caytoniaceae may be linked with them in varying degree. The Corystosperms are obviously an evolutionary step forward from the Palaeozoic pteridosperms, and attention should be paid to them when new relationships are to be established with other Mesozoic pteridosperms. Dispersed information available at present, seems to indicate that the Mesozoic pteridosperms played an important role not only in a particular palaeogeographical area, but all over the world. The stems of *Hermanophyton* from the Jurassic of U.S.A., *Pteroma* and *Pachypteris* (Harris 1964) from the Jurassic of England, and even the Peltaspermaceae, clearly indicate the world-wide occurrence of plants whose allies are the Palaeozoic pteridosperms.

Finally, I believe that further research work with the Mesozoic pteridosperms is of utmost importance for Palaeobotany, not only to establish the real taxonomic status of the different groups, but also to look for further evidence in relation to the origin of the angiosperms, which are claimed as descendants of the pteridosperms.

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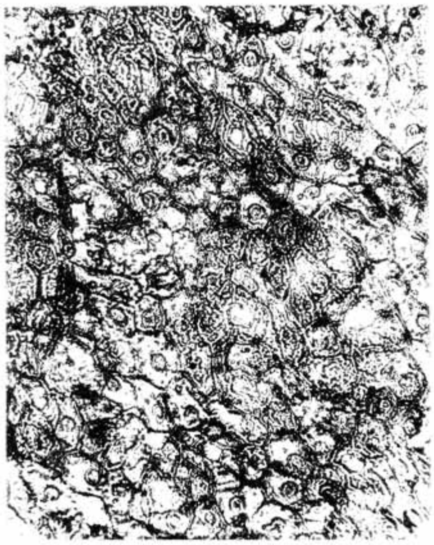
ARCHANGELSKY, Triassic *Dicroidium* leaves



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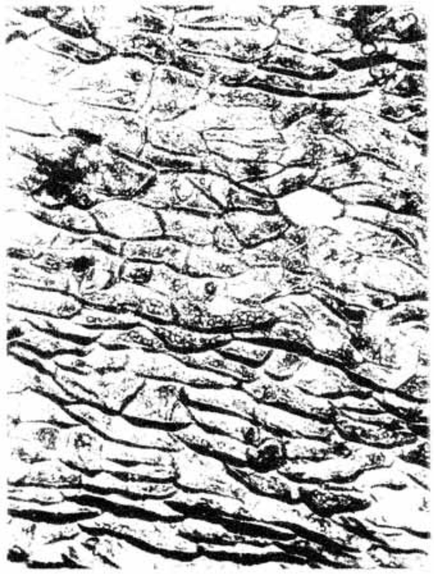

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ARCHANGELSKY, Triassic leaf cuticles