THE BRACHYPHYLLUM CRASSUM COMPLEX OF FOSSIL CONIFERS

By

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(With one plate and 11 text figures.)

ABSTRACT

The holotype of *Brachyphyllum crassum* Tenison Woods, is re-examined, and this species reclassified as *Araucaria crassa* (Tenison Woods) com. nov.; it is probably Tertiary in age. Of shoots referred to *A. crassa* one belongs to the Taxodiaceae, *Athrotaxus tasmanica* com. nov. also almost certainly Tertiary; while the other, Jurassic in age, is referred to *Pagiophyllum feistmanteli* Halle, which is redescribed. Another group of shoots sometimes confused with *A. crassa* is described as *Allocladus* gen. nov., with three species *Al. rajmahalense* (Feistmantel) com. nov. *Al. milneanus* (Tenison Woods) com. nov. and *Al. cribbii* sp. nov. The supposed cone of *Al. milneanus* is examined, and doubt is thrown on its ascription to *Allocladus*. It is renamed *Conites tenison-woodsi* nom. nov.

INTRODUCTION

One of the earliest fossil conifers to be described from Australia was *Brachyphyllum crassum* (Tenison Woods 1883), but though the original description was a good one for its date, the species has never been adequately redefined. This is now attempted, from an examination of the holotype. From this it appears that this species is almost certainly a Tertiary *Araucaria* sect. Eutacta, close to *A. montana* Bgt. and Gris and *A. berneri* Bucholz. Of the various shoots confused with *A. crassa* (Tenison Woods), when microscopic detail is available, all prove to be very readily distinguishable. However, without this detail the shoots dealt with here are extremely difficult. Detail was not available to many of the earlier authors, and so it is quite impossible to be sure that specimens thought to be identical with one another really are. It is a case of making the best guess. For this reason few firm identifications are made, but comparable specimens are cited. Sometimes one specimen is comparable with more than one shoot; in these cases the reference appears twice.

Of the shoots confused with *Araucaria crassa*, one proves now to be another Tertiary species, of *Athrotaxis* Don, leaving a rather heterogeneous group of Mesozoic shoots. These Mesozoic species fall into the large *Brachyphyllum* Brongniart and *Pagiophyllum* Heer group of conifers. One is placed provisionally in *Pagiophyllum*, but the others are placed in a new genus. The reasons for this step are three: none of the shoots involved would fit comfortably into *Brachyphyllum* or *Pagiophyllum* as recently defined (Kendall 1947, 1948, Wesley 1956): to classify them into *Brachyphyllum* and *Pagiophyllum* would separate in an inconvenient way shoots that are very similar (*Allocladus milneanus* and *Al. cribbii*): in my view *Brachyphyllum* and *Pagiophyllum* are already too diverse for ease, and to add more badly fitting species would not make for convenience.

As regards the affinities of the Southern conifers considered here, nothing definite can be said. Florin (1940, 1963), having very imperfect evidence, considered they were araucarians. This may well prove to be so, but on present evidence they cannot be securely classified.

DESCRIPTIONS

Family ARAUCARIACEAE

Araucaria crassa (Tenison Woods) com. nov.
Pl. 1 H, Figs. 1A; 2A, C; 3B-E, H; 4A, B.

1883 *Brachyphyllum australe* var. or n.s. *crassum* Tenison Woods, p. 159-160, pl. 5. Type specimen described.

1892 *Brachyphyllum crassum* Tenison Woods in part: Jack and Etheridge, p. 385. Tenison Wood's description quoted, figs. on pls. 17 and 18 are distinct.

1917 *Brachyphyllum crassum* Walkom non Tenison Woods, p. 25. Tenison Wood's description quoted but applied to pl. 9 fig. I, which is distinct.

Holotype: No. 137 Macleay Museum, University of Sydney; Fig. 1A.

Age: Probably Tertiary from the Booval Group, Queensland. Locality unknown.

Diagnosis emended: Shoots with more or less pinnate branching of the penultimate branches; ultimate branches at least 11 cms. long and 0.5-0.75 cms. thick, curved (possibly pendulous or curved upwards in life). Shoots covered with leaves of one sort, spirally arranged, four visible in one turn of the spiral, close set and imbricated; 3-4.5 mms. long and the same or slightly less in greatest width. Leaves arising from a rhomboidal, only slightly decurrent cushion, upper margin of cushion nearly horizontal, leaves thick 2-2.5 mms. at base, free parts of leaf directed forward usually strongly curved inwards but rarely tightly appressed: lower surface more or less strongly keeled, upper surface slightly keeled, apex obtuse, margins sharp, but not scarious or scalloped. Leaf triangular, near base margin showing ear-like projections.

Leaf (in all probability) supplied by two (or three) vascular bundles, derived by branching in the cortex of a single trace.

FIG. 1.—*Araucaria crassa* A; *Allocladus cribbii*, B-F; *Pagiophyllum feistmanteli*, G; *Athrotaxis tasmanica*, H; *Al. milneanus* I, J. A-I, Shoots, showing forming of branching and general appearance, all x 1. A, H, I, MacLeay Museum, 137, 41; B-F; Univ. Queensland F5075-50759; G, H, Queensland Geol. Survey, 705 and 711.

Cuticle of different thickness on two sides, below about 7μ above about 3μ. Leaf amphistomatic, on lower surface stomata grouped in two areas flanking a central " midrib ", devoid, or almost devoid, of stomata, the areas reaching about to leaf apex; on upper surface stomata at least 50% more numerous, lying in similar areas flanking the " midrib ". On both surfaces stomata set more or less regularly in long rows, running from leaf base to within 3-5 cells of the margin: orientation of stomatal pore irregular in the rows. Epidermal cells away from stomata more or less rectangular, in rows, becoming irregular at leaf base.

Epidermal cell outlines thick, 8-12μ, straight, or showing sinuous projections down the anticlinal epidermal cell walls, surface generally smooth, rarely ornamented with low but hollow papillae about 30μ across, papillae seen on both surfaces, near " midrib " only. Cells about 60μ x 50μ. Stomata dicyclic, on lower leaf surface normally separated by one or more epidermal cells, on upper surface adjacent stomata in the rows either sharing an encircling cell, or (about as often) having the encircling cells in contact, but only very rarely encircling cell missing. Guard cells sunken in a pit, concave (as seen from above), sides of pit formed by subsidiary cells, either vertical or overhanging, but subsidiary cells' dorsal surface more or less flat, and not papillate. Subsidiary and encircling cells together forming further pit, with sloping or vertical sides, encircling cells rarely overlapping mouth of pit. Wall between subsidiary and encircling cells heavily cutinised. Hypodermis not cutinised. Stomatal rows not sunken.

Description and Discussion: The material examined consists of Tenison-Woods' Type, shown in Fig. 1A. The specimen is now less complete than when first figured. It is not much compressed. The largest shoots show the pinnate sort of branching seen in *Araucaria* Juss. sect. Eutacta Endl. From the curving of the ultimate branchlets it seems likely, as from their size relative to the penultimate shoot, that they were pendulous, though they may have curved up, as in *A. excelsa* (Lamb.) R. Br. ex Ait. It is not quite true that the ultimate branches are the same thickness as the penultimate, and they do taper slightly (about 1 mm. in 10 cms.).

The leaves are all of the same sort, varying only in size, and degree to which they are appressed (Figs. 2A, C). When they stand out, the leaf base is seen and here too the keel on the upper surface of the leaf can be seen. Wherever the presentation allows it, a keel can be seen on the lower leaf surface, and I can find no case where it has been obliterated by pressure (Jack and Etheridge, 1892, p. 385), and in fact the shoot is only compressed to about half its original thickness, supposing it to have been round.

In one shoot, some leaves were broken in such a way that the leaf base was seen, more or less in tangential longitudinal section (the earlier authors noticed this). The clearest is shown in Fig. 2A. In the centre of the broken surface there is a more or less triangular area, not flat, but sloping so that its base lies deeper into the cortex than its top. Over part of this central area there are striae, about 50μ apart (shown diagramatically by vertical lines), forming a Y shaped pattern. There is no proof (such as pitting) that these striae are tracheid walls, but they are of the right size and in the right position for the leaf traces, which in the living species of *Araucaria* sect. Autacta emerge as a single trace from the stem stele, then divide in the outer cortex or leaf base into two or three (Fig. 6E *A. cunninghamii* Ait.). In *A. crassa* it is not clear whether there are two or three traces, but it is clear that, if these marks are tracheids, there were at least two traces in the leaf.

The cuticle is not well preserved, and brittle. The fossil is covered with a layer of mud that clings to it firmly, and large silica grains, which may have formed on the plant, locally destroying the cuticle in the process (Pl. 1 H). The pieces for maceration were first cleaned in HF. The distribution of stomata, as put together from several pieces is shown in Figs. 3 B, C, and in general, it is extremely like a living *Araucaria* (Florin 1931). The stomatal rows run vertically, so that they would impinge on the margin; they stop short, however some five cells away from the margin. The margin itself is shown in Fig. 3D and Pl. 1H, and, as in *A. cunninghamii*, appears to have been thin, (also showing ear-like projections at the base, Fig. 6F), but is definitely not scarious.

The stomatal details are given in Figs. 3H, 4B. For the most part the stomata were sunken in a pit formed by the subsidiary cells, overtopped by but rarely, overhung by, the encircling cells; there is variation however, the stomata on the upper leaf surface being rather less overhung (Fig. 3H). The cell outlines are shown in Fig. 3E, a leaf base, where compression presents them partly in section. The sinuous downward extensions are seen in *A. cunninghamii* (and others), but are larger in the living species, making the whole outlines sinuous.

Comparisons. The nomenclature of *A. crassa* is badly confused. This arises from two circumstances: the species was thought to be Triassic (or at least lower Mesozoic, a mistake heightened by the original rather misleading comparison with *Brachyphyllum mammillare* Brgt.), so it was left out of account in discussions of Tertiary species of *Araucaria*: and even more, several authors (e.g. Walkom 1917) quote the original description, mistakes and all, and apply it to specimens to which it does not fit. The Jurassic specimens to which the name *B. crassum* was applied are readily distinguishable.

In addition, the combination *Brachyphyllum crassum* was proposed in 1883 both by Tenison Woods and Lesquereux (see Seward 1919, pp. 324-325), however, contrary to Seward's statement, Tenison Woods did figure his Type, it is in his pl. 5. Lesquereux did not publish figures till 1891, and his material became entangled with another American species called originally *B. macrocarpum* Hollick and Jeffrey. As regards the Australian material, the confusion over the American species is immaterial: Tenison Woods' name was validly published (originally as a variety) and has priority, while the transference of his species to *Araucaria* avoids the difficulty caused by one binomial being given to two different species.

At every available point the specimen agrees with species of *Araucaria* sect. Eutacta. The branching, including possibly pendulous habit sometimes seen

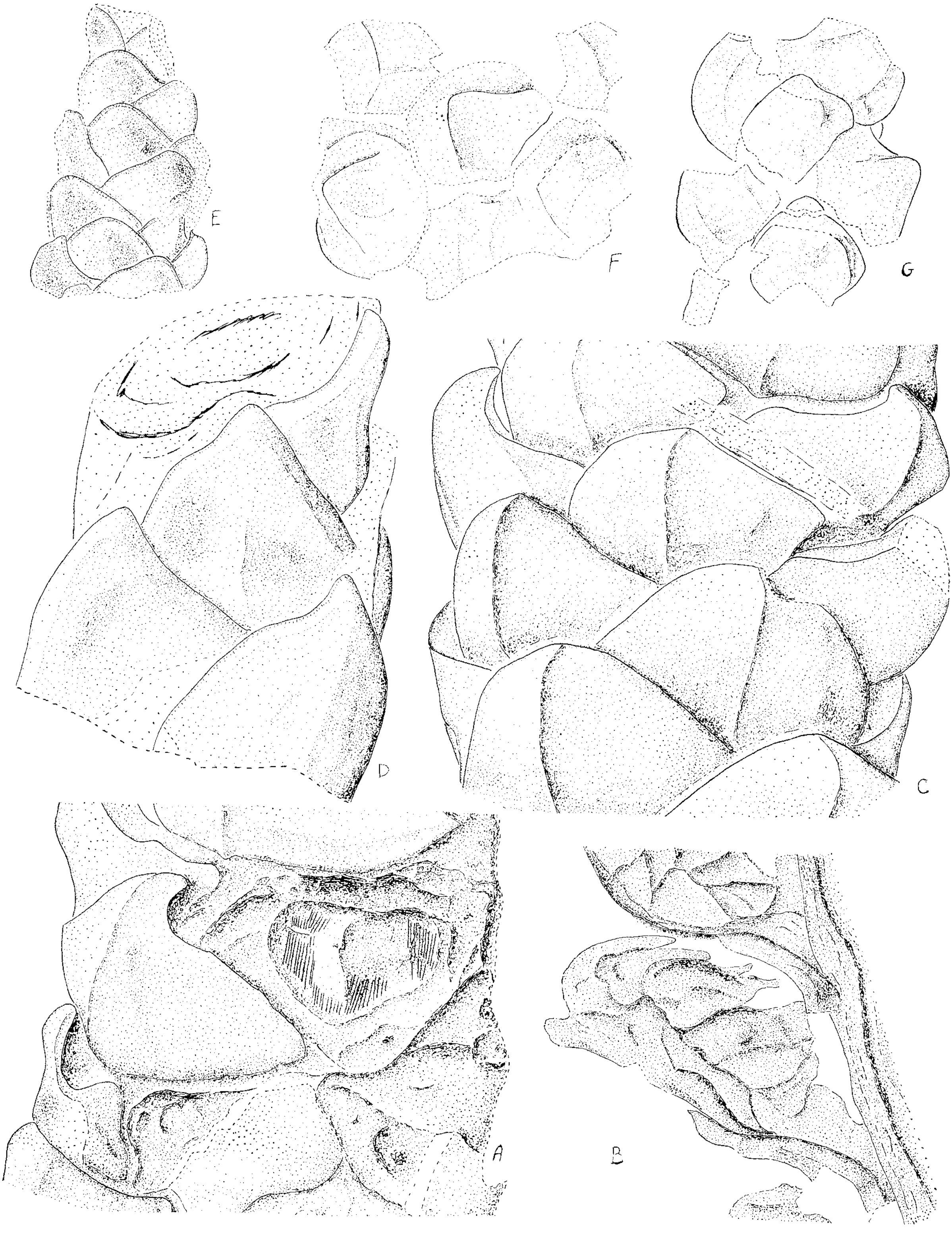

FIG. 2.—*Araucaria crassa* A, C; *Conites tenison-woodsii* B; *Athrotaxis tasmanica* D, E; *Pagiophyllum feistmanteli*, F, G. A. Part of a shoot showing broken leaves and traces within the leaf base believed to be of tracheids (vertical lines). x 7, MacLeay Museum 137. C-G. Parts of shoots to show differences in leaf shape, all x 7. C, MacLeay Museum 137; D-G, Queensland Geol. Survey, 705, 753 and 711. B. A unit of structure showing its double nature, and adaxial objects, possibly seeds. x 7. MacLeay Mus. 102.

in *A. excelsa* and more often in *A. columnaris* Hook., the sort of leaf, the cuticle and (in all probability) the leaf vascular supply, can all be matched. There are some difficulties; the leaves are shorter and wider than is common, but the living *A. bernieri* Bucholtz (1949) has leaves of similar size and shape (see Table I in Cookson and Duigan 1952). *A. biramulata* Bucholtz (*loc cit.*) is also similar, as Selling (1950 p. 557) remarks. The cell outlines are straight, only rarely showing sinuous projections, but the projections are of the same sort as in several living species, and the fossil *A. lignitica* Cookson and Duigan has cell outlines looking very similar, though sometimes obscurely pitted. The stomata may be overhung more than is usual, but again *A. lignitica* (a species known from cones as well as shoots) provides a parallel. These difficulties are fairly small, the living species seem to show the same sort of variation among themselves (Florin 1931, p. 232, Cookson and Duigan, 1952, p. 422), and there seems no good reason for keeping *A. crassa* out of *Araucaria*. In gross form (as in cuticle) it is like *A. bernieri* or *A. montana* Bgt. and Gris, but since it does not correspond exactly with any living species, it is worthy of specific rank.

Among fossil *Araucaria* species, comparison is close with *A. fletcheri* Selling (1950). This species, whose holotype I have examined, has leaves of similar size, 2-4 mm. long and 3 mm. wide, but which stand out from the stem more than the leaves of *A. crassa*, though the difference is not large, and might have been caused by different preservation. The two species are separable on their stomatal distribution. Whereas *A. crassa* shows stomata more or less all over the lower leaf surface, except for a narrow and somewhat ill defined midrib. *A. fletcheri* shows them only at the leaf base and in two small groups. On Cookson and Duigan's (1952) fig. 2, *A. crassa* falls with *A. montana* or *A. bernieri* (type A1 or A2) while A. fletcheri goes with A. columnaris (type C), as Selling (*loc. cit.*) indicated. On the upper leaf surface, the stomata are much more closely packed in *A. fletcheri* than in *A. crassa*, Density H.P. field 18:3, Stomatal Index 7:18. However, in stomatal details the two species are much alike, and also, in *A. crassa* there is wide variation in the number of stomata on the lower leaf surface, from leaves much like *A. fletcheri* to leaves showing about twice the number of stomata of the leaf shown in Pl. 1H. All these leaves come from a single shoot. Similar variation, though not so wide, is seen in such material of *A. excelsa, A. cunninghamii* and *A. columnaris* as I have had access to.

It will be best to keep *A. crassa* and *A. fletcheri* separate, but they are still decidedly similar. There do not appear to be other species with which serious confusion is likely.

I have not seen any material from the Triassic at Ipswich preserved like *A. crassa*, but do not know the flora well. On the other hand, *Athrotaxis tasmanica* (below), a Tertiary species, is preserved in the same way as *A. crassa*. Also, *A. crassa* is more like a Tertiary fossil or living species than anything known yet from the Triassic. For these reasons *A. crassa* is dated as Tertiary. It probably comes from the Booval Group (Hill and Denmead) 1960), but the locality is unknown.

Family TAXODIACEAE

Genus **ATHROTAXIS** Don

ATHROTAXIS TASMANICA nom. nov.

Figs. 1H; 2D, E; 3A, F, G; 6G.

1892 *Brachyphyllum crassum* Jack and Etheridge non Tenison Woods, pp. 385-386, pl. 17, figs. 11, 12 (F705); pl. 18, fig. 3. (F753), fig. 2 indeterminable. Material from Queensland.

1917 *Brachyphyllum crassum* Walkom non Tenison Woods, p. 25, pl. 9, fig. 1. Earlier material refigured.

1965 *Athrotaxis ungeri* Townrow non Halle, pp. 109-112, figs. 1 A-G and 2 A-G. Material from Tasmania

Holotype: F705 Queensland Geological Survey, see Fig. 1H.

Age: Probably Booval Group, Lower Tertiary.

Diagnosis emended. Shoots showing alternate to nearly opposite branches, coming off at various angles round main shoot. Shoots 2-5 mm. in diameter, showing more or less closely appressed, spirally arranged leaves, and rounded ends not much narrower than older parts of branch. Usually one complete leaf and parts of two or three others seen on each surface of shoot. Leaves more or less triangular, with rounded apex, about 3 mm. long and 2.5 mm. wide (extremes 4 x 3 mm. and 2.0 x 1.0 mm.) widest part about 0.75 mm. from leaf base, and leaf contracted slightly towards leaf base, contracting steadily above. Leaves thick, 1.5 mm. (compressed sideways) not keeled, showing general thick area, tapering rapidly in about 0.2 mm. to margin. Upper leaf surface flat, consisting of a portion over the midrib about 0.75 mm. long, and two flanking areas, tapering to widest part of leaf.

Cuticle on lower surface 2-5μ thick, on upper surface 1-2μ thick. Leaf amphistomatic, stomata lying on lower surface in two zones of indefinite outline, and set near leaf margin, separated by side non stomatiferous zone. On upper surface, two similar zones not reaching apex. Stomata showing no regular orientation or arrangement, many orientated longitudinally. Epidermal cells away from stomata in indistinct longitudinal rows; on lower surface cells equidimensional or wider than long, about 40μ x 35μ, on upper surface cells more or less rectangular 38μ x 20μ. Cell outlines more or less thick, up to 7μ, mostly straight but sometimes showing lateral small projections of cutin, and sometimes pierced by holes.

Stomata monocyclic (very rarely incompletely dicyclic), subsidiary cells more or less equidimensional, quite unspecialised, forming a ring of 5 (4-8) round the stomatal pit, not divisible into lateral and polar members. Guard cells feebly cutinised, sunk in a pit; pit overhung by a collar of cutin borne on the subsidiary cells. Collar 5μ-10μ wide, total width of more or less round stomatal pit 20μ-50μ.

Leaf margin scarious, formed of long finger like cutinised cells, often transversely divided, up to 0.2 mm. long, joined to one another below. Scarious margin longest near leaf apex, but extending all round leaf.

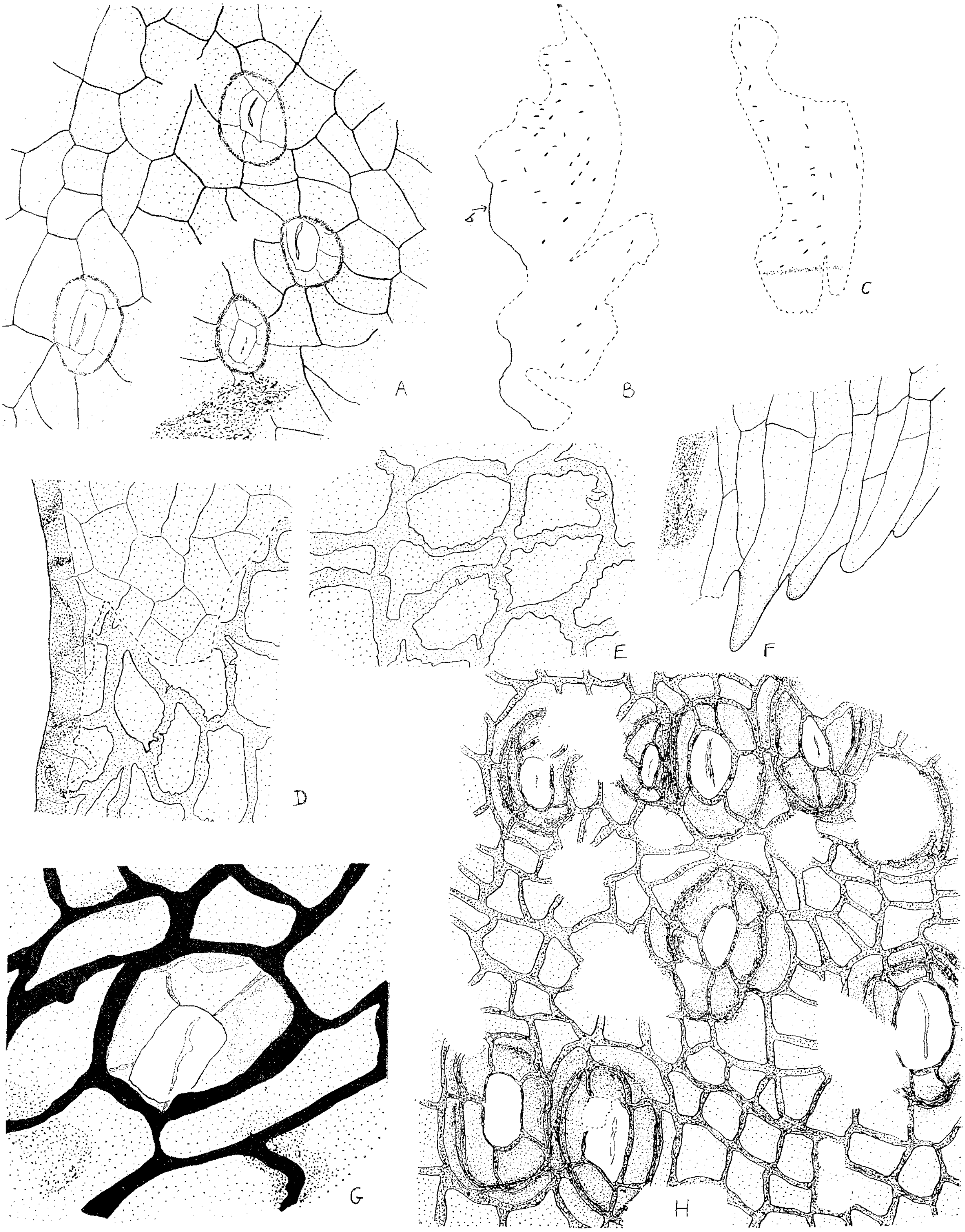

FIG. 3.—*Athrotaxis tasmanica* A, F, G; *Araucaria crassa* B-E, H. A, Part of the upper cuticle showing stomata, x 200. Queensland Geol. Survey, 705. B, C. Parts of the cuticle from the lower leaf surface, showing number and arrangement of stomata *b* = leaf base x 20. D, the leaf margin. Upper surface cuticle fine lines, x 500. MacLeay Mus. 137. E. Sinuous cell outline, x 800. F. part of leaf margin, x 200. G. A stoma. x 600. Queensland Geol. Survey, 705. H. Part of the cuticle of the upper leaf surface. Note holes left by *in situ* growth of silica. x 200. MacLeay Mus. 137.

Description: The Queensland material consists of two specimens collected many years ago, F705 from "Walloon" (a designation by itself of uncertain meaning, when used by the early collectors) and F753 from Rosewood near Ipswich, in ash beds, according to Jack and Etheridge (1892, p. 385). F.705 is covered with the muddy deposit already mentioned for *A. crassa* (p. 151), and F753 shows no cuticle but does show the external form of the leaves very plainly. Both specimens are little compressed, F753 is still nearly round in section. To obtain details from F.705, two small lengths were removed from the specimen and treated with HF; they were afterwards macerated.

F.705 is shown in Fig. 1H, where the branching consists of more or less, but not completely opposite pairs of branches, and each pair comes off at an angle of 45°-90° to the pair below. One branch is complete, it is 2.5 mms. long and tapers from 4 mm. to 2 mm., the apex being rounded. As covered by the mud the details of the leaves are entirely obscured; on removing this, the leaves are seen to lack a keel, but to be thick, and raised over the whole lower surface of the leaf, except where it thins suddenly to the markedly scarious margin (Figs. 2D, E). The leaves differ in size, but usually show a somewhat curved margin (Figs. 2D, E). In F753 the leaves are large, but what is important, show the scarious margin, even though no plant material remains. In this specimen a very faint keel can be seen in places.

The cuticle is badly preserved, and could only be obtained in small pieces, but these are numerous, and come from all over the leaf, so that though stomatal distribution (for example) cannot be determined, the details of cells, stomata and margin can be made out.

The cuticle is of two thicknesses, the thinner one presumably the upper. On both, the form of the cells is given in the diagnosis (see Figs. 3A, G; 6G).

The cell outlines are often damaged, at first sight looking sinuous, but in a few places they really are sinuous, by reason of small cutin projections, pointing partly downwards into the leaf, a feature also seen in *Athrotaxis cupressoides* Hook. The stomata are also often damaged. Figs. 2A, G, show some of the better ones, and these show the walls of the pit, appearing as a dark line, within which arises the cutin collar, showing the outlines of the subsidiary cells. The margin is shown in Fig 3F.

Comparison: The specimens differ from *A. crassa* in size, branching, leaf shape and cuticular features, and cannot be identified with it. In branching and leaf shape they agree with *Athrotaxis*, and come near to *A. cupressoides* (see Florin 1931, pl. 11, fig. 8), but differ in showing a large scarious margin (*A. cupressoides* has only a small one) and in lacking a keel to the leaves, but as already noted, this can be largely an effect of drying. In cuticle, the details of the cells and stomata agree with *Athrotaxis*.

At the specific level, the material is identified with some specimens from the Tasmanian Tertiary (Townrow 1965). The Tasmanian specimens consisted of only short lengths of shoot, but in showing a large scarious margin, and in leaf shape the two agree. The Tasmanian material had an excellent cuticle, clearly showing stomatal distribution and the Queensland material is identified with it because, though less clearly it shows the same features. There is, however, one difficulty. Sinuosities were not at first seen on the Tasmanian leaves, on re-examination a few were seen, but they are smaller than on F.705. Both sets of specimens show the unusually wide cutin collar over the stomatal pit.

Earlier (1965) I identified the Tasmanian material, though with much hesitation, with *Athrotaxis ungeri* (Halle) Florin, (Florin 1960), from the Lower Cretaceous of Patagonia, the recent revision of this species by Archangelsky (1963), not being to hand. The identification was certainly incorrect. The leaves of *A. ungeri* are smaller than of the present species. (2 mm. long 1 mm. broad) and though they have a margin (Archangelsky *loc. cit.* pp. 83-86, pl. 10, fig. 68) it may be smaller than in these specimens. Also, there are many more stomata on the lower surface on *A. tasmanica* than *A. ungeri;* and the cutin collar round each stomatal pit is absent (or very small) in *A. ungeri.*

Various other Australian fossil species of *Athrotaxis* are compared elsewhere (Townrow 1965 p. 112); in gross form *A. tasmanica* comes nearest to the living *A. cupressoides,* but in cuticle to *A. laxifolia.* No living species shows so large a scarious margin and cutin collar over the stomatal pit.

CONIFERALES INCERTAE SEDIS

ALLOCLADUS gen. nov.

Type species *Al. rajmahalense* (Feistmantel)

Diagnosis: Conifer shoots, showing sparse irregular branching of the penultimate shoot system, and similar leaves all over. Leaves close set, spirally arranged, phyllotaxis probably 2/5 and/or 3/8. Leaves arising from a decurrent base, overlapping the next leaf above, and with free parts directed forward, parallel with, or nearly parallel with, the shoot long axis. Length of the free part of the leaf about as great as or greater than its width.

Leaves more or less triangular in outline, with apex acute, 2-8 mm long, with angular margin showing scarious projections. Leaves thick, strongly convex on lower surface but more or less strongly concave on upper surface. Leave base cushions concealed, probably more or less rhomboidal. (Venation unknown).

Leaf epistomatic, (rarely in one species with a few stomata on the lower leaf surface). Stomata either set in two zones, near the leaf margins, coalescing at leaf apex, or in one mass over central part of leaf upper surface, obscurely separating into two zones towards leaf base. In zones stomata either scattered, or showing a weak tendency to be in vague longitudinal rows; orientation of guard cells various. Ordinary epidermal cells square or slightly elongated, outside stomatal zones lying in rows converging on the apex, sometimes papillate, Hypodermis sometimes cutinised, consisting of narrow strongly elongated cells. Cuticle thick (5μ or more).

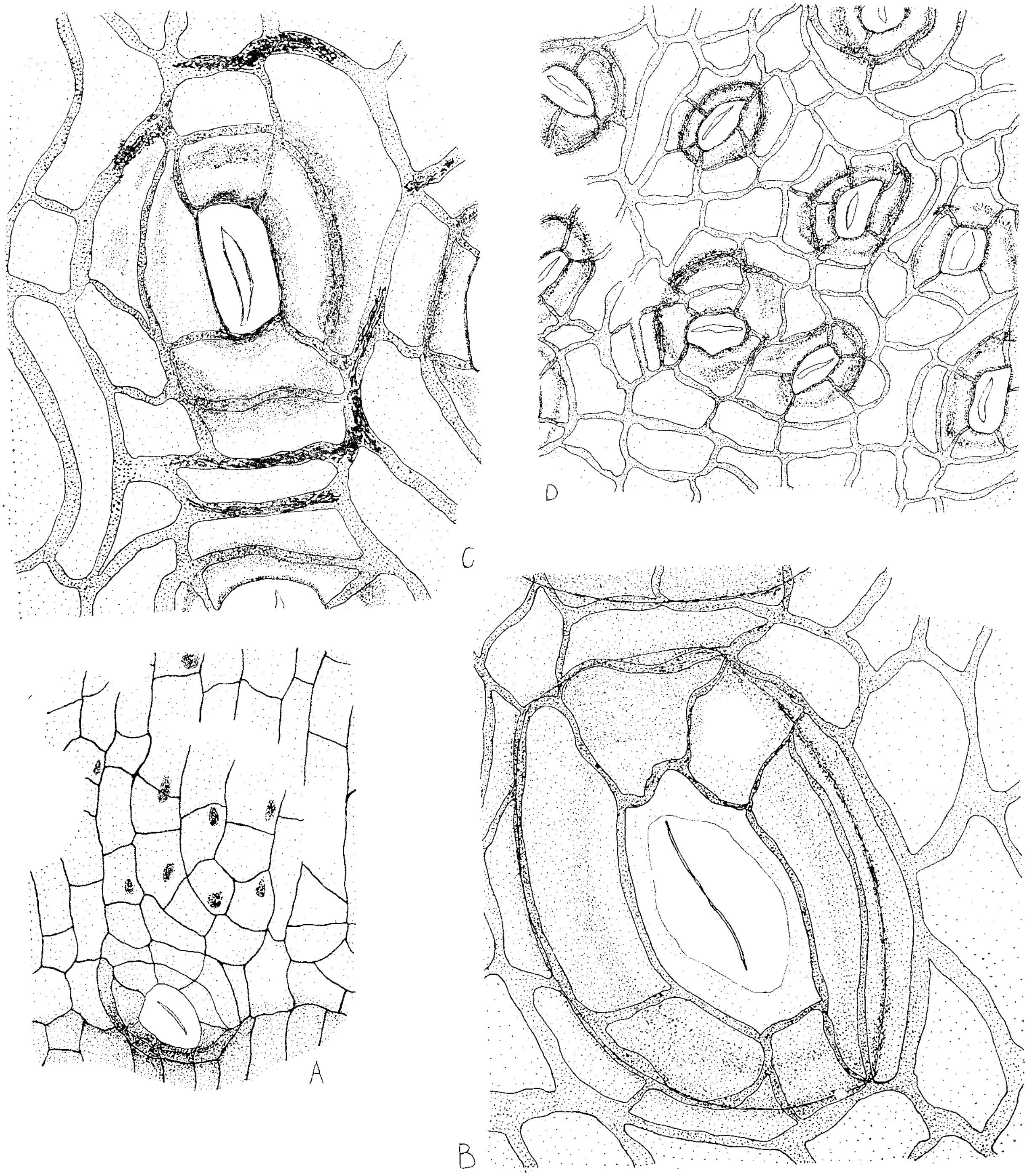

FIG. 4.—*Araucaria crassa* A, B; *Allocladus cribbii*, C. D. A. Stoma near the leaf base, and cells with papillae. x 150. **B.** A stoma, from upper leaf surface, x 600 MacLeay Museum 137. C. A stoma from about middle of the leaf x 600. D. Part of the upper leaf surface cuticle, x 200. Queensland Univ. F50756, F50758.

Stomatal zones not sunken, but individual stomata sunken, and usually dicyclic, 3-6 subsidiary cells forming a ring. Wall of pit formed by subsidiary and encircling cells together, and encircling cells sometimes overhanging the mouth of the pit. Dorsal surface of subsidiary cells more or less flat, bearing only minute cutin thickening overhanging the guard cells, or such thickening absent. Adjacent stomata usually separated by an ordinary epidermal cell, but sometimes encirling cells in contact, very rarely encircling cell shared between adjacent stomata.

Discussion: The shoots now segregated into *Allocladus* shows the general form of some species of *Araucaria*, sect. *Eutacta*, especially of *A. cunninghamii*, or of *Athrotaxis*, especially *A. sellaginoides*, and of some shoots referred to the form genus *Pagiopyhllum* Heer. They have more or less short leaves, the same over the whole shoot (as far as known), forwardly directed, and emerging all round the shoot (pl. 1B, D, Figs. 1, 7, 10). Only one specimen of the material available to me shows the branching pattern, (cf. the specimen of Walkom's (1921, p. 13, fig. 2) if correctly identified), and branching would seem to have been sparse and irregular. It is possible that the specimens consist of ultimate shoots, shed intact (again as in *A. cunninghamii*) but there is no evidence that this is so.

The form of the leaf base is uncertain, because each leaf covers the base of the one above (e.g. Fig. 7A, B), but in the lower parts of the shoot of *Al. milneanus*, the leaves spread out, and the one shown in Fig. 7B, is near the leaf base, which was probably of the normal decurrent sort.

The lower surface of the leaf shows no signs of a keel, but in *Al. milneanus* there are two angles at the leaf base (Fig. 7B), suggesting that on this surface the leaf was thick, rounded and convex, and either thinned suddenly towards the margins, or (*Al. cribbii*) was rounded, thinning more gradually towards the margins. The upper leaf surface was concave especially in *Al. cribbii*, and this is interpreted to mean that in life the upper leaf surface was concave, and, having impressed its shape onto the mud during fossilisation, has collapsed on to the mould so formed (Walton 1936).

The cuticles of all species are thick, and easily prepared. It was surprising to find that the leaves showed stomata only on the upper surface, and preparations were made of whole leaves, and large pieces of known orientation (on the basis of the leaf shape just set out) to confirm this. However, in one species *Al rajmahlensa*, some leaves, probably less than a tenth, show a few stomata on the lower leaf surface (p. 159). This exception, being rather minute, is ignored in the following discussion. The stomata are regularly dicyclic, and their arrangement has already been given in the diagnosis (see Figs. 4, 5, 11). As interpreted, the whole subsidiary cell ring is sunken, and the wall (or most of it) of the stomatal pit is formed by the encircling cells. The evidence for this is best seen in *Al. milneanus*, and is as follows. Viewed from the inner surface focussing shows first the guard cells with the stomatal aperture, and then, at only a slightly different level, the whole of the subsidiary cell surface. Finally, cell outlines continuous with those of the subsidiary cells, can be seen, and these pass *over* a thick mass of cutin representing the lips of the stomatal pit, being continuous with the outlines of the encircling cells as seen on the general surface of the cuticle (Figs. 5C, G). The whole appearance comes close to that seen in *Cycas revoluta* L. and presumably is to be interpreted the same way.

The hypodermis, where present, underlies the encircling cells, but, so far as can be seen, the dorsal wall of the subsidiary cells, which they share with the encircling cells, is not specially heavily cutinised—indeed it is often hard to make out. (Fig. 5A).

The margin of the leaf is modified. In *Al. cribbii* (in which no hypodermis can be seen) groups of epidermal cells turn and run out into short finger like processes along the edge of the leaf, similar to those seen in *Microstrobos*, and many other conifers. In *Al. milneanus* these scallopings are up to 1 mm. high, and consist of whole groups of epidermal cells, with their hypodermal cells, which turn outwards to form almost shovel-like projections (Fig. 5B). *Al. rajmahalense* is intermediate.

Comparisons: Twigs of *Allocladus* look rather like those of certain species of *Araucaria* or *Dacrydium* Sol. or *Athrotaxis*, but the difference in cuticle precludes referring *Allocladus* to any of those genera. It is more difficult to distinguish from *Brachyphyllum* and *Pagiophyllum* (Kendall 1947, 1948, Wesley 1956), as they are defined broadly, separated arbitrarily from one another, and probably artificial. *Allocladus* would however, make exceptional species, for no *Brachyphyllum* or *Pagiophyllum* is epistomatic, none have a scalloped margin, and in most (not all) the stomata run in rather well involved longitudinal rows.

It is difficult to discuss the possible relationship of *Allocladus* with *Brachyphyllum* and *Pagiophyllum*, since *Brachyphyllum* contains definite Araucariaceae (*B. mammillae*, see Kendall 1919a), and at least one species, *B. expansum* definitely not Araucarian (Kendall 1950). Perhaps it is fair to say that there are no features which particularly suggest relationship between the genera.

Cheirolepidium muensteri (Schenck) Takhtajan, (Florin 1944, (further references given), Harris 1957, Lewarne and Pallot 1957, Woods 1961, Challoner 1962) consists of shoots and cones, but only the shoots will be considered here since the *Allocladus* cone is unknown. The leaves vary considerably in length, but are generally from 2 mm.-5 mm. long and 1.25-3 mm. wide, and more or less appressed to the stem. They show a concave upper surface and, as noticed by Lewarne and Pallot, may show a scarious margin. The margin even when scarious is unscalloped. The cuticle is thick, (5μ or more) and shows stomata in irregular files on both surfaces and rows of little elongated cells. The cell outlines are straight. The stomata are generally described as monocyclic, but some at least are, as some authors have noticed, incompletely dicyclic (e.g. Lewarne and Pallot 1957 fig. 1B). Papillae have not been reported, though the subsidiary cell surface may be thickened. A hypodermis is sometimes to be seen.

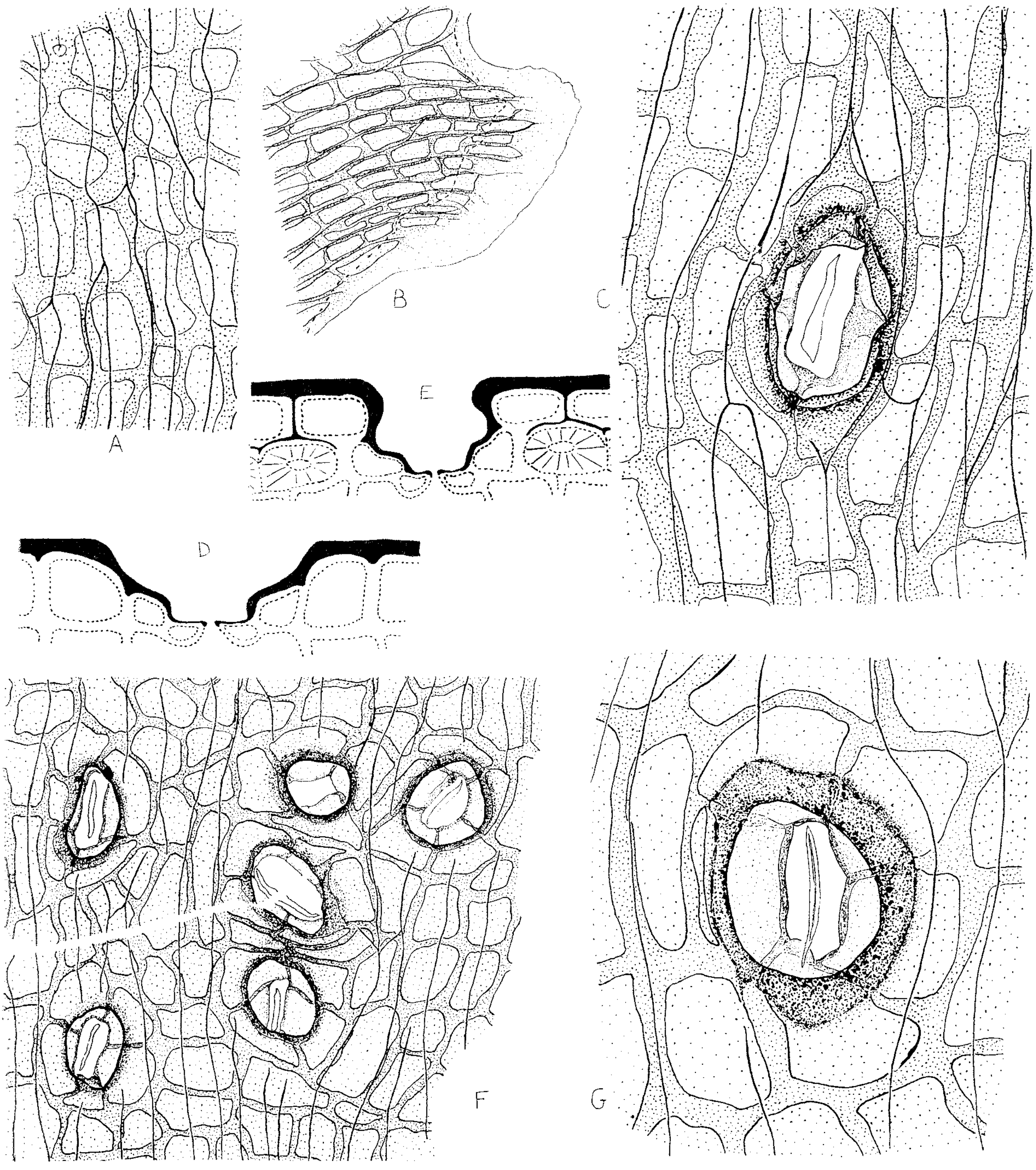

FIG. 5.—*Allocladus milneanus* A-C, E-G; *Al. cribbii* D. A. Cells, epidermal and hypodermal, of the lower leaf surface x 200. B. A marginal projection, with its epidermal and hypodermal cells. x 100. C, G. Stomata, seen from outside in (C) and from inside out (G), to show forms of the pit. x 600. F. Cells of the upper leaf surface x 200. All MacLeay Mus. 41. D, E, Reconstructed transverse section through a stoma. x ca. 600.

Thanks to the kindness of Dr. W. G. Challoner (University College London,) I have been able to examine material of *C. muensteri* from Schnaittach. In addition to the points mentioned above, the cuticle of *C. muensteri* does rather rarely show low papillae to a point at which it compares with *Al. cribbii*. Also, in at least half of the stomata examined a difference in level can be detected between the subsidiary cells and their neighbours (cf. Wood 1962, fig. 2). The possibility was considered that this might be merely a compression fold, but first, it is found in parts of the leaf compressed vertically, i.e. where no other folding exists, and second it extends all the way round the stomatal apparatus, whereas a compression fold would be expected on one side only.

Cheirolepidium and *Allocladus* show some very interesting similarities. The leaf outline, and shape in section, is similar or the same, the branching is irregular, not pinnate, the cuticle is thick, the cells not much elongated, and the stomata variously orientated. The cells of *Cheirolepidium* may rarely be papillate. *Cheirolepidium* may have a scarious margin. *Al. milneana* has a cutinised hypodermis, as *Cheirolepidium* sometimes has.

They differ, however, in that (1) *Allocladus* is epistomatic, but *Cheirolepidium* amphistomatic, (ii) *Allocladus* has a scalloped leaf margin but *Cheirolepidium* does not, (iii) *Allocladus* has regularly dicyclic stomata, with the subsidiary cells sunken, but *Cheirolepidium* is only irregularly dicyclic or monocyclic with only slightly sunken subsidiary cells. These differences are enough to make a useful generic separation between the two.

Haiburnia Harris (1952), Florin (1958) has a leaf crescentic in section like *Allocladus*, and with a scarious margin, and in *H. blackii* Harris the stomata are dicyclic. However, the leaves are amphistomatic, though with more stomata on the upper surface in *H. blackii*, the stomata are scattered all over the leaf, and the stomatal details differ (see Harris 1952, figs. 3B, D). *Haiburnia* definitely has only one vein in its leaves.

ALLOCLADUS RAJMAHALENSE (Feistmantel) com. nov.

Pl. 1D. Figs. 8C, D, E; 10; 11A-D.

1877 *Echinostrobus rajmahalense* Feistmantel, p. 90, pl. 65, figs. 3, 3a. Small branching shoot, from " Bindabrum, Amrapora, Burio, &c."

1928 *Brachyphyllum mammilare* Sahni non Brongniart, p. 18, pl. 2, figs. 19, 20 only. Feistmantel's specimen refigured.

Comparable Specimens. Oldham and Morris 1863, pl. 32, fig. 8 (very obscure fragments): Feistmantel 1887, pl. 42, fig. 2; 1879, pl. 19, figs. 2, 2a; 1879, pl. 12, figs. 2, 2a, *and* the whole list given under *Al. cribbii.*

Holotype: Feistmantel 1877, pl. 65, fig. 3. 283. 4/532, Geol Survey, India.

Locality: Bindarum, Rajmahal Hills; Middle Jurassic.

Diagnosis emended. Leaves very closely appressed, so whole shoot appearing circular in section and about 3 mm. in diameter. Leaves about 2 mm. long and same or slightly less at widest point seen, triangular, of obtuse apex, making an angle of less than 20° to axis of shoot, about 1.5 mm. thick at base (when compressed laterally). Leaf under surfaces somewhat convex, not keeled and without angles towards leaf margin, upper surface somewhat concave. Branching irregular.

Cuticle of markedly different thickness on two sides of the leaf, on lower side about 5μ, on upper 1-2μ. Stomata probably in two vague zones towards leaf base, zones coalescing towards leaf apex; within zones stomata more or less longitudinally orientated, more or less in rows, but many out of their rows. A very few stomata rarely present on lower leaf surface near leaf margin. Stomata irregularly dicyclic, usually with encircling cells in contact but not shared. Ordinary epidermal cells more or less rectangular on both leaf surfaces; on lower cells about 50μ x 40μ, on upper more elongated, about 60μ x 40μ. Cells papillate at leaf base on lower cuticle only, papillae as for *Al. cribbii*. Cell outlines thin, about 3μ sometimes bordered.

Stomata sunken in a pit, walls formed wholly or mainly by subsidiary cells, encircling cells not overhanging pit. Subsidiary cells numbering 3-6.

Margin scarious, scalloped (as *Al. cribbii*) only at leaf base, cutinised hypodermis not seen.

Description and Discussion. The material consists of one large shoot and five smaller pieces collected by Mr. R. Gould at I at Tannymorel Colliery, and it is well preserved. This is the only species in which the branching pattern is seen clearly, and it is irregular (Pl. 1D). The branches come off at various angles in all three planes, and it often happens that both parent shoot and branch are about the same size (dichotomous of Feistmantel 1877). The shoot apex is shown in Fig. 8C; and one short branch tapered from 2 mm. diameter to 1.5 mm. in 5 mm.

The leaves are closely appressed, more so even than *A. cribbi* (Figs. 8C-E), and overlap one another, so that the leaf base is not seen. One and part of two other leaves, or two half leaves are seen in one side of the spiral. The upper (adaxial) leaf surface is not well seen, but in one or two places (Fig. 8E), where matrix has got between the leaves the whole leaf is convex towards the observer, suggesting that the leaf was concave above (see below *Al. cribbii*). Parts of shoots, when macerated and then dissected apart also show a more or less concave upper surface. The lower (abaxial) surface is rounded and, usually (Figs. 8C, D), not very convex.

It proved very difficult to obtain good cuticle preparations of the upper leaf surface, and I have not seen a leaf in which it was complete. Fig. 4B shows one in which a good deal of the cuticle remains, and it appears from it that the upper cuticle extended as two more or less narrow strips about to the widest part of the leaf, but was probably not extensive at the leaf apex. The stomata are often in one mass at the leaf apex, but another specimen (Fig. 4B) shows some near the leaf margin, but towards the midrib there are somewhat elongated cells but no stomata. In two leaves, out of some 15 macerated, there was a group of 3 or 4 stomata, extending laterally from the leaf margin

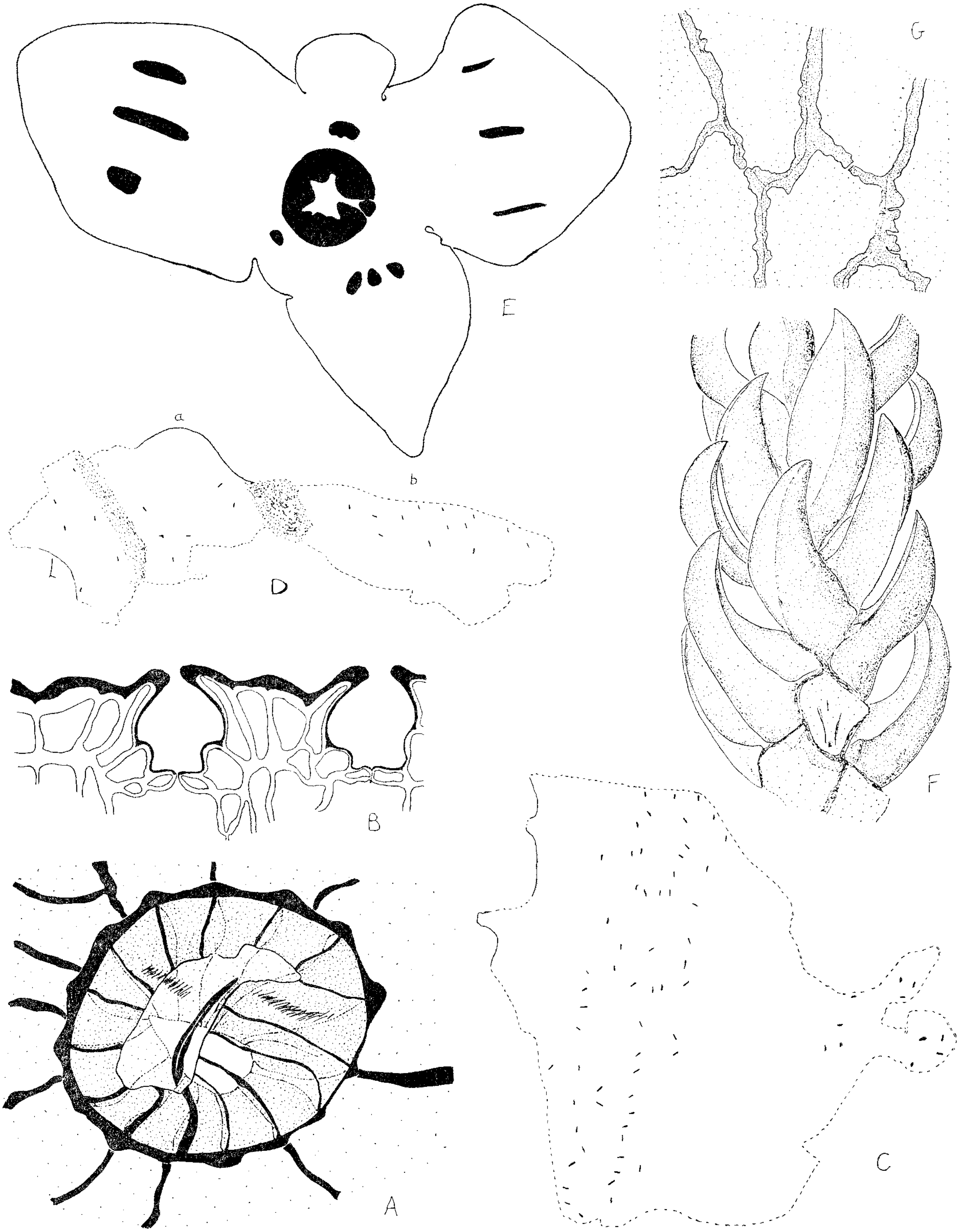

FIG. 6.—*Cycas revoluta* A, B; *Allocladus milneanus* C; *Pagiophyllum feistmanteli* D; *Araucaria cunninghamii* E, F; ***Athrotaxis tasmanica***, G. A. Stoma in surface view, viewed from inside out x 600. B. Section of two stomata. x 400. **C, D., Part** of the upper (C) or lower (D) surface of a leaf, showing number and arrangement of stomata, x 20. MacLeay Mus. 41: Queensland Geo. Surv. 711. E. Section through leaf bases, vascular tissue black, x 15. F. Part of a shoot, lower leaves broken off to show vascular tissue in one (Cf. Fig. 2A) x 7. G. Cell outlines from the lower leaf surface cuticle. x 800. Queensland Geol. Surv. 705.

towards the midrib, set on thin cuticle, passing smoothly into thick cuticle like that of most of the lower leaf surface (Fig. 4C). It appears therefore that in this species there were, somewhat rarely, a very few (perhaps 8 or 10) stomata on the lower surface of certain leaves, at the base. However, at least 8 leaves definitely had no stomata on the lower surface. The whole leaf, on this information is reconstructed like the leaf of *Diselma archeri* Hook. (See Florin 1931, pl. 45, fig. 5), only in *Diselma* the leaf is regularly amphistomatic. The cells and stomata are shown in Figs. 10, 11. The stomata are often, but not always, dicyclic, and when massed closely together, the subsidiary cells may be in contact. When dicyclic there is a band of darkly staining cutin adjacent to the outline between the subsidiary and encircling cell (Fig. 11A, C). This is interpreted as the compressed wall of the stomatal pit, and if the stoma is monocyclic, it lies on the subsidiary cells (Fig. 11D). The stomatal pit is therefore supposed to be formed partly by subsidiary and encircling cells together, or sometimes by the subsidiary cells only. The stomata of *Al. rajmahalense* are rather more often longitudinally orientated than in the other species.

As with many identifications, it is impossible to have any assurance that Feistmantel's specimens (1877 pl. 65, fig. 3) and mine are identical, while Sahni (1928 pl. 2, figs. 19, 20) provides a new photograph but no more information than Feistmantel. The shoots agree in manner of branching, in size, and in leaf shape and size, except only that some leaves on Feistmantel's shoot may have a slightly more acute tip than is normal in mine, though they can be matched. These similarities are held to justify identification. The new information makes it plain that this species is not identical with *Brachyphyllum mammillare* (see Kendall 1947, 1950), as Sahni thought, which differs in having many stomata on the lower leaf surface. The stomatal distribution indeed separates *Al. rajmahalense* from other *Brachyphyllum* species known in detail (e.g. Kendall *loc. cit.*, Wesley 1956, Archangelsky 1963). It is, I think, most improbable that *Al. rajmahalense* is identical with the younger shoots from Jabalpur called by Feistmantel and Sahni *Brachyphyllum mammillare* (almost certainly incorrectly, Florin 1940), but these shoots are not yet known in detail to settle the matter.

Brachyphyllum spiroxylon Bose (1952) is much like *Al. rajmahalense* in general form, but differs in its epidermis having more or less equally amphistomatic leaves, with scattered stomata (scarcely organised into lines or rows) hardly sunken at all and only irregularly dicyclic. It is still possible (in my view) that Feistmantel's specimen is really to be identified with *B. spiroxylon*, though Bose rejects this.

Al. rajmahalense is a Middle Jurassic species (Krishnan 1954, de Jersey and Paten 1965).

ALLOCLADUS MILNEANUS (Tenison Woods) com. nov.

Pl. 1A, G; Figs. 1I, J, 5, (not 5D), 6C, 7B.

1883 *Walchia milneana* Tenison Woods, P. 163-164, pl. 2, fig. 3 and pl. 6, fig. 7. (The supposed cone is excluded).

From the ? Lower Jurassic of Ballimore, New South Wales.

1921 *Pagiophyllum peregrinum* Walkon, non Lindley and Hutton, pp. 15-16, pl. 3, fig. 2. Talbragar Fish Bed, Lower Jurassic.

1928 ? *Brachyphyllum expansum* Sahni non Sternberg, pl. 2, figs. 28, 29, Golapilli, near Ellore, ? Lower Jurassic.

Comparable specimens. Feistmantel 1887, pl. 44, figs. 5, 5a; 1877a, pl. 8, fig. 8; 1879, pl. 16, fig. 10; Halle, 1913, pl. 8, figs. 15, 16; Sahni, 1928, pl. 2, figs. 21, 22; Feruglio, 1934, pp. 20-21, pl. 1, figs. 1-6; Jones and de Jersey, 1947a, figs. 15-17.

Holotype. McLeay Museum, No. 136, Pl. 1A.

Locality. Talbragar River near Ballimore (spelt Ballinore) ? Lower Jurassic.

Diagnosis emended. Leaves appressed or spreading about 8 mm. long (6-9 mms), widest about at junction of upper surface to the stem, about 3 mms. wide (2-4 mms.) at widest. Leaves directed forwards, falcate, making angle of up to 30° with shoot axis, 2.5-5 mms. thick (measured when compressed laterally). Leaf under surface not keeled, showing towards base two angles near the margin, upper surface only slightly concave. Leaf apex acute. (Branching pattern unknown).

Cuticle fairly thick (5μ), of about same thickness on each surface. Stomata in two zones, coalescing near leaf apex, and lying in short rows of 2-5, rows more or less longitudinal, but up to half stomata not in a row. Stomata strictly dicyclic, encircling cells of adjacent stomata almost never in contact. Ordinary epidermal cells about square or slightly elongated, 50μ x 30μ, not papillate, walls straight and indistinct, but thick, about 8μ. Stomata deeply sunken in a pit (depth not known), 3-6 subsidiary and encircling cells. Encirling cells forming much (if not most) of wall pit, and overhanging its upper edge.

Margins showing shovel-like scallopings, about 0.1 mm. high and 0.5 mms. apart; scallopings containing both epidermal and hypodermal tissue. Hypodermis cutinised.

Description and Discussion. The material available to me consists of the single block figured by Tenison Woods (1883), pl. 2, fig. 3. This shows fragments of three shoots, the longest of which (Pl. 1A) is taken as the holotype.

The angle which the leaves make with the stem varies: at the apex (Fig. 1J) they are appressed, though still falcate, on the larger (? older) shoots (Pl. 1A) they are more widely spread out, and the interstices between them filled with mud. The leaf base is not clearly seen, because of the way in which the leaves overlap one another, but I suspect that in the leaves in Fig. 7B we are near it, and it appears to have been of the normal decurrent sort.

The cuticle is easily prepared. Even after staining the wide cell outlines are somewhat indistinct, but the hypodermis (which must have been very strongly cutinised) shows up most clearly. In this species, as with the others, one was surprised to find that the leaves were epistomatic, and tried to check on this by observing the leaves throughout maceration, and by macerating leaves known way up. However, it seems clear that the leaves are epistomatic (see Pl. 1G, Fig. 5F).

FIG. 7.—*Allocladus cribbii* A; *Al. milneanus* B; *Pagiophyllum feistmanteli* C, D. A. B. Parts of shoots to show form, especially of margins. x 7. Univ. Queensland F50756 and MacLeay Mus. 41. C, D. Parts of shoots with large leaves and leaves of medium size, showing variation in form of the free part of the leaf. x 7. Univ. Queensland, F50769.

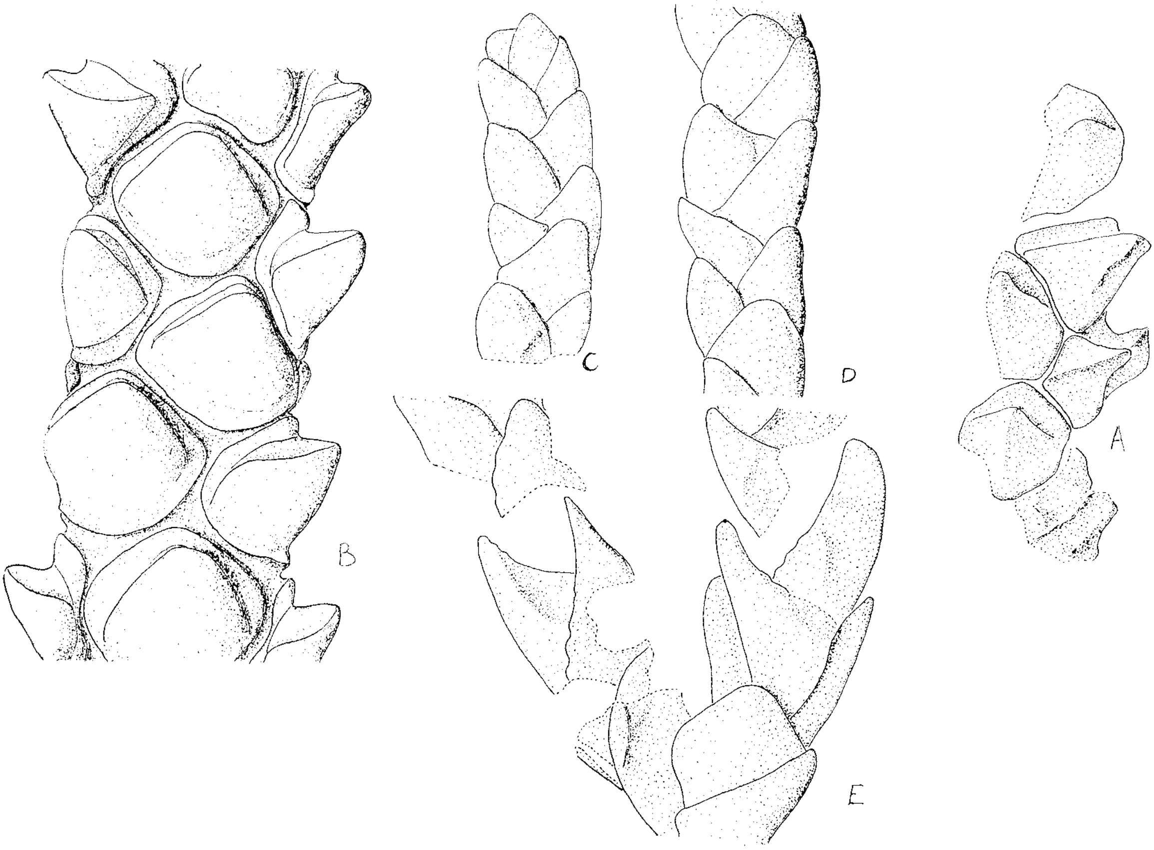

FIG. 8.—*Pagiophyllum feistmanteli*, A, B; *Alloccladus rajmahalensis*, C, D. E. A. Shoot with small leaves x 7. Univ. Queensland, F50769. B, Reconstruction of a shoot with small leaves x ca. 9. C-E. Parts of shoots showing variation in leaf form, and an apex (C), all x 7, Univ. Queensland, F50766-50768.

At the base on the lower surface the cuticle becomes thinner, and the cells become somewhat irregular. The same happens in the other species.

In this species there is some approach to rows of stomata; but it is not very clear. Rather, there are groups of stomata, two to five stomata in each, in which the stomata are very close set (Pl. 1G, Fig. 5F, B). These groups may be (but are not always) longitudinally orientated. Many stomata lie outside this arrangement. There are not rows such as are found, e.g. in *P. connivens* (of which I have examined Yorkshire material) or e.g. *Araucaria cunninghamii*.

At first sight the stomata look like those of *P. maculosum* Kendall (1948) but in detail their structure is believed to be different, and has been discussed above. The simplest interpretation is that expressed in the reconstruction in Figure 5E.

The hypodermal cells underlie the encircling cells, but so far as I could see, the inner wall of the subsidiary cells is not cutinised (Figs. 5C, G), unlike most species of *Brachyphyllum* and *Pagiophyllum*. The shovel like scalloping on the margins are shown in Figs. 5B. Cuticle preparations show whole files of epidermal cells turning out into them. They also contained hypodermis almost to their extreme edge.

Comparisons. Tenison Woods' description, considering its date (1883) is a good one, but *Al. milneanus* has since almost vanished from view. Walkoms' (1921) shoot is poorly preserved, but is identified as it shows the same leaf shape, is the right size, and comes from rocks of the right age. It is definitely distinct from *Pagiophyllum peregrinum* L. and H. (see Kendall 1948), and Walkom did not refer to Tenison Woods' work at all. My shoot is also probably distinct from *P. peregrinum* of Walkom (1919), from the Cretaceaous Burrum Series, but the conifer remains from the Burrum need further study before they can be discussed usefully.

Feruglios' (1934) material named *Elatocladus patagonicus* Fer. is stated to come from the Liassic of Patagonia, but Dr. S. Archangelsky tells me that it is really Permian. It agrees with *Al. milneana* in general form, no detail is known.

The age of *Al. milneana* is not satisfactorily settled. The New South Wales material and Sahni's specimen (pl. 2, figs. 28, 29) from India are Lower Jurassic. However, the comparable material of Halle (see p. 161) is probably Middle Jurassic. I do not think any record comes from definitely Triassic rocks. Provisionally, the age could be given Lower to Middle Jurassic.

ALLOCLADUS CRIBBII sp. nov.

Pl. 1E, Figs. 1B-F, 4C, D, 5E, 7A, 11F, G.

? 1928 *Pagiophyllum peregrinum* Sahni, non Lindley and Hutton, p. 23-24, pl. 3, figs. 43-45, (shoots), 46, 47 (cuticle). Sher River, Satpura, Upper Jurassic.

Comparable specimens. Oldham and Morris, 1863, pl. 32, figs. 8,8a; Feistmantel 1877, pl. 42, fig. 2; McCoy in Stirling, 1900, pl. 2, figs. 1, 2, 5, pl. 3, figs. 10-16; Chapman, 1908, pl. 35, figs. 3 and ? 2; Halle 1913, pl. 8, figs. 42, 42a, pl. 9, figs. 3, 4; Arber, 1917, pl. 13, figs. 1, 8, 10; Walkom, 1921, pl. 3, figs. 4, 5; Sahni, 1928, pl. 2, fig. 20; Medwell, 1954, pl. 6, fig. 26.

Holotype. No. F5075. University of Queensland, Pl. 1H, Fig. 12M.

Locality. No. 5. Caledonia Colliery, Walloon Coal Measures, Lower Jurassic.

Diagnosis. Leaves closely appressed, whole shoot about 5 mm. in diameter, about 5 (2-6 mm.) long, (free part only) and 5 mms. (2-7 mm.) wide at widest, free part triangular. Leaves directed forwards, sometimes slightly falcate, making an angle of 20° or less with the shoot axis, 2.5-5 mm. thick (measured when compressed laterally). Leaf under surface convex, and keeled, lacking angles towards leaf margin; upper surface strongly concave. Leaf apex blunt. Branching feebly pinnate.

Cuticle of different thicknesses on two surfaces of the leaf, about 6μ below, about 3μ or less above. Stomata entirely scattered within their zones, showing no discernible arrangement into rows or groups except for two obscure zones at leaf base. Stomata dicyclic, but in about 30% of the stomata the encircling cells lying in contact, and in about 5% an encircling cell shared between two stomata. Ordinary epidermal cells square, often wider than long, 40μ x 50μ, often papillate, papillae mostly lying over the cell outlines, solid, about 10μ high, tending to point forward. Cell outlines distinct, thick, about 5μ, sometimes slightly bulging into the neighbouring cells. Stomata sunken in a rather open pit formed by 3-6 subsidiary cells, and encircling cells outside them; encircling cells not overhanging the pit.

Margin showing small scallopings, about 100μ high, and rather irregular, scallopings formed of 3-6 epidermal cells. Hypodermis not cutinised.

Description and Discussion. The material examined consists of a number of shoots collected by Mr. Harold Cribb (Geological Survey, Queensland) and myself at the No. 5 Caledonia Colliery, near Walloon, Queensland.

Only one branching specimen has been figured: if the specimen from Talbragar (Walkom 1921, pl. 3, fig. 4) is rightly identified, the branching is weakly pinnate to irregular. The angle the leaves made with the stem varies (Figs. 1B-F), but they are always close set, a fact which makes cuticle preparations somewhat difficult to obtain, for the cuticles tend to stick together. The leaf base is not clearly seen, but appears to be of the normal cushion-like sort (Fig. 7A). The leaf, like many living conifers, shows an obscure angle or keel down the lower (abaxial) leaf surface. This is present in those leaves compressed partly laterally, and so is original, not caused by collapse into a mould.

The cuticle though thick is somewhat brittle, especially the upper, making it difficult to see the whole surface, however, Pl. 1E, shows one of the more complete preparations, and Fig. 11F the stomatal arrangement in a less complete piece. The papillae usually are prominent, especially after staining, and are sometimes visible on the hand specimen, giving the leaf an attractive appearance rather like morocco leather. The stomata are less sunken than those of *Al. milneanus* (Figs. 4C, D), comparing with the stomata of e.g. *P. ordinatum* Kendall (1948). There is variation, however, and some stomata approach *Al milneanus* a great deal more closely than the usual sort reconstructed in Fig. 5E. The stoma is interpreted therefore, as being of the same essential sort as *Al. milneanus* and not like e.g. *P. insigne* Kendall (1948) in which the deep stomatal pit is formed by the subsidiary cells.

The scallopings on the margin are much smaller than in *Al. milneana*, resembling those seen e.g. in *Athrotaxis cupressoides* Hook f. or *Microstrobos niphophilus* Garden and Johnson; however, in some leaves at least groups of epidermal cells run into a scalloping, as in Fig. 5B.

Comparisons. Sahni's (1928) material had cuticle, on which the stomata were grouped only on one side, which so far as can be judged from the small figure, agree with those from my Queensland material. The leaves on Sahni's shoots are, however, longer than mine, but this is a variable character, and I set it on one side. Sahni's shoot is certainly not *Pagiophyllum peregrinum* which is amongst other things, amphistomatic.

The Victorian material of McCoy (1900) Chapman (1908) and Medwell (1954) known as *Brachyphyllum gippslandicum* McCoy resembles other material ascribed to *Al. cribbii* in its irregular branching (a point of difference between it and some *Brachyphyllum* species) and leaf outline. It is impossible to go further than this. The flora was originally thought to be Jurassic (e.g. Seward 1904, Medwell 1954) but it was discovered that at least some plant bearing beds are conformably overlain by marine strata with Middle Cretaceous fossils and it is now known that the Victorian " Jurassic " floras are in fact Lower Cretaceous (see Dettmann 1963 for full discussion).

Most of the records of *Al. cribbii* come from rocks of Middle Jurassic age, though some may be lower Jurassic. The Walloon Coal Measures were dated by de Jersey (1959) as Lower Jurassic, but later (de Jersey and Paten 1964) a Middle Jurassic age has been suggested.

TABLE I.

THE SPECIES OF *ALLOCLADUS* COMPARED

	Leaves.	*Margin*	*Upper Surface*	*Stomatal distribution and Cuticles*	*Stomatal details*	*Hypodermis*
Al. rajmahalense	Closely appressed, shoot like a cat's tail, diameter, ca. 2.5 mm. Leaves triangular, apex obtuse, about 2 mm. long and 2 mm. wide at widest.	Scalloped only at base, 100μ, otherwise scarious	Only slightly concave	In rows, running up to leaf apex, (probably) in separate zones towards leaf base. Orientation more or less longitudinal. Two cuticles of very different thickness: 7μ : 1μ.	Somewhat sunken in a pit whose top may (about one in 10) overhang	None seen
Al. cribbii	More or less closely appressed, shoot like a cat's tail, diameter 5 mm. or more, leaves triangular, apex obtuse, about 5 mm. long and 3 mm. wide at widest.	Scalloped, or not, along whole margin, 100μ, otherwise scarious	Strongly concave	In a mass, obscurely separating below in two zones. Stomata not in rows, orientation irregular. Two cuticles of different thicknesses: 5μ : 1-2μ.	Slightly sunken in a rather open pit	None seen
Al. milneanus	Standing out from shoot, shoot not like a cat's tail. Leaves triangular, apex acute, 8 mm. long 3 mm. wide at widest.	Strongly scalloped along whole margin, 1 mm. or more	Only slightly concave	In two indistinct zones along whole length of leaf. Stomata tending to be in rows, orientation irregular. Cuticles of about same thickness, (5-7μ).	Strongly sunken in a pit whose top may overhang	Cutinised

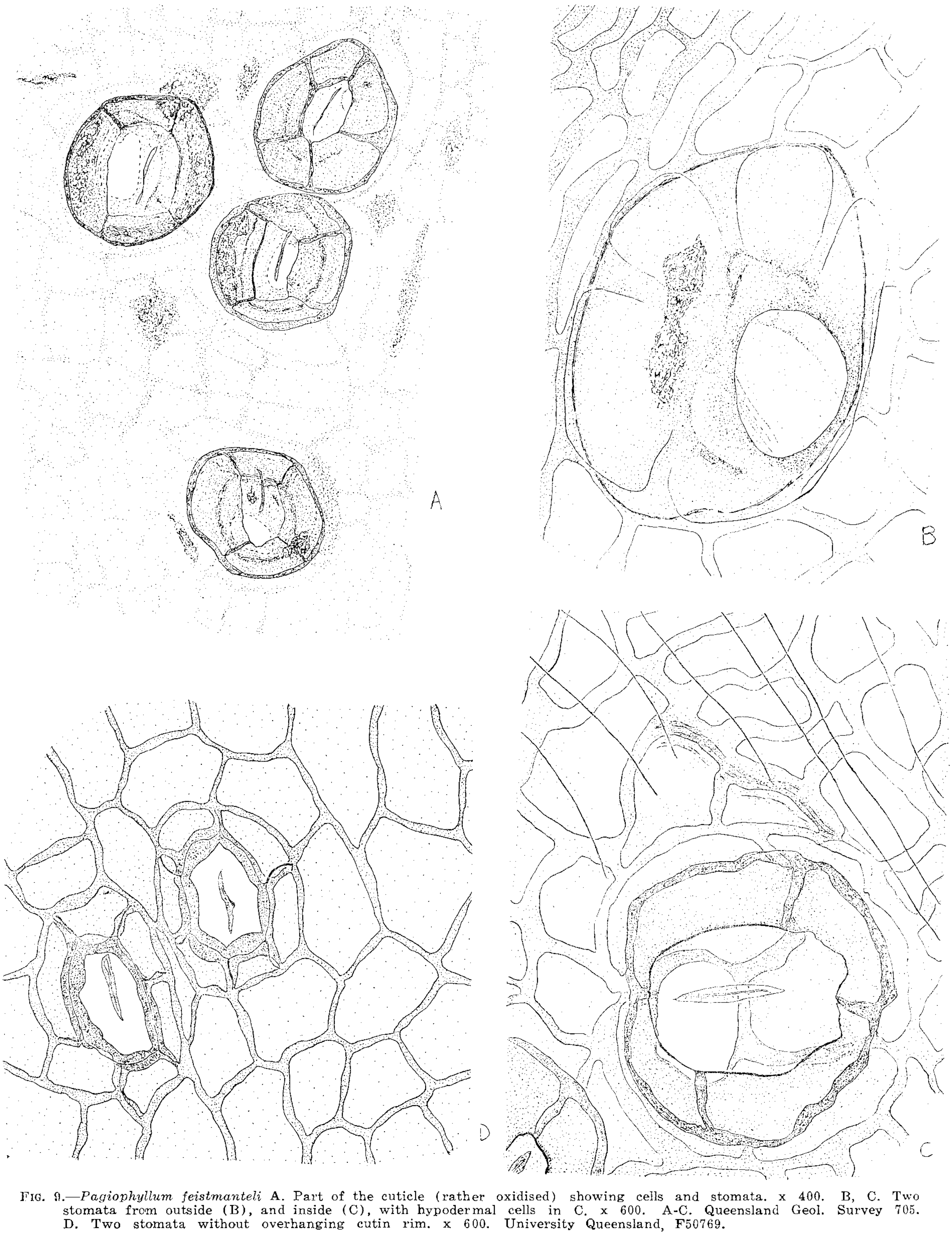

FIG. 9.—*Pagiophyllum feistmanteli* A. Part of the cuticle (rather oxidised) showing cells and stomata. x 400. B, C. Two stomata from outside (B), and inside (C), with hypodermal cells in C. x 600. A-C. Queensland Geol. Survey 705. D. Two stomata without overhanging cutin rim. x 600. University Queensland, F50769.

PAGIOPHYLLUM Heer

Pagiophyllum feistmanteli Halle

Pl. 1C, F, Figs. 1G, 2F, G, 7D, 7C, D, 8A, B9, 11E.

1879 *Pachyphyllum peregrinum* Feistmantel non Schimper, p. 28, pl. 12, figs. 3 and 9. Jurassic of Madras Coast, Vemavaram district. Pl. 11, fig. 5 distinct.

1892 *Brachyphyllum crassum* Jack and Etheridge non Tenison Woods, p. 385, pl. 18, Walloon, specimen here re-examined.

1913 *Pagiophyllum feistmanteli* Halle, pp. 76-78, pl. 9, figs. 17-17B, text figs. 17A-D. Large shoots, Jurassic of Antarctica.

1917 *Brachyphyllum crassum* Walkom non Tenison Woods, p. 92. Cited in a locality list.

1928 *Pagiophyllum feistmanteli* Halle: Sahni, p. 19-20, pl. 2, fig. 27. Feistmantel's holotype refigured.

1940 *Pagiophyllum feistmanteli* Halle: Florin, pp. 30, 63. Discussion.

1963 *Pagiophyllum feistmanteli* Halle: Bonetti, p. 39, pl. 7, fig. 3. Argentinian Middle Jurassic.

Comparable specimens. Feistmantel 1879, pl. 12, figs. 2, 2a; Halle, 1913, pl. 9, figs. 14, 14a.

Holotype. Feistmantel 1879, pl. 12, fig. 3.

Locality. Vemavaram, near Madras; Jurassic ? Middle Jurassic.

Diagnosis emended. Shoots more or less pinnately, but probably basically spirally branched. Ultimate shoots arising at nearly 90° from main shoot, from 6-12 mm. wide. Leaf bases rounded, sometimes slightly rhomboidal, about 3 mm. wide (2-5 mm.) and 4 mm. high (3-7 mm.). Free part of leaf forming chisel like or bluntly pointed projection, standing out at about 90° from the stem, or more when large, 1-4 mm. long. Junction of upper edge of free part of leaf and leaf base abrupt, at high angle and at about 0.5 mm. from upper margin of leaf base. Free part of leaf more or less rhomboidal in section, but lower surface more strongly keeled.

Cuticle thick, at least 3μ, or more or less same thickness all over the leaf. Stomata lying in two distinct zones, zones extending from basiscopic margin of leaf base towards acroscopic margin, but dying away towards acroscopic margin, and extending laterally from margin of leaf base onto flanks of free parts of the leaf. Upper surface of free part of leaf, and upper margin of leaf base free of stomata. Stomatal rows more or less regular, 8 (3-10) stomata high, two to five rows on leaf base with a few stomata not in the zones at the leaf base. Epidermal cells more or less square in irregular longitudinal rows of side 40μ, outlines 8-12μ thick, surface smooth.

Stomata dicyclic to irregularly tricyclic. Guard cells strongly cutinised round the stomatal pore, deeply sunken into the leaf, and themselves weakly concave. Stomatal pore of irregular orientation. Subsidiary cells four to six, often only four, two lateral and two polar members, forming a more or less rectangular pit over the guard cells. Cutinisation between subsidiary and encircling cells no stronger than between other cells of the leaf. Encircling cells of the first rank forming a chimney over guard and subsidiary cells, and walls of encircling cells often continued into a cutin collar, projecting up above general epidermal level. Encircling cells of second rank (when present) lying on general epidermal level, and unspecialised. Whole stomatal apparatus about 80μ in diameter, opening of chimney over stoma about 20μ, depth of pit about 50μ (?). Hypodermis sometimes cutinised, showing elongated cells. Venation unknown.

Description. The material available is specimen F711 Queensland Geological Survey, and I thank Mr. A. K. Denmead, Chief Government Geologist, most warmly for lending me the specimen, and a second larger specimen (Pl. 1C), from Tannymorel Colliery, near Warwick. No. 711 is the same one as that mentioned by Jack and Etheridge (1892) and Walkom (1917) and comes from the Clifton Colliery in the Walloon Coal Measures. The specimen is shown in Fig. 1G. The diagnosis is drawn also on Halle's (1913) account, for he had larger (though uncutinised) shoots.

As shown in Halle's figures and Pl. 1C, the branching is more or less pinnate and in Pl. 1C the four branchings visible all seemed to be lateral, rather than spiral twisted into one plane. However, from the way the material permeates the rock it is clear that branching is not rigorously in one plane. A useful model might be *Araucaria cunninghamii* Ait. in which the ultimate branching is also mostly but not all pinnate (the penultimate is definitely spiral).

Over most of F711 the plant material has vanished, but the second specimen is well preserved. On that part of 711 where the plant material has gone the leaf bases show a rounded depression, and the free parts a still deeper, somewhat angular depression not touching the margin of the leaf base impression (see Feistmantel 1879, Sahni, 1928, pl. 2, fig. 27 and Fig. 19). A somewhat similar appearance is shown by Yorkshire specimens of *Brachyphyllum mammillare*, but *Pagiophyllum feistmanteli*, and similar shoots, differs in that the junction of the upper surface of the free part of the leaf, and of the leaf base, lies somewhat below the upper margin of the leaf base, and is angular (see Figs. 2F, G, 7C, D, reconstruction in Fig. 8B, and cf. Kendall 1949 fig. 2C, and above). Moreover, the free parts of the leaf of my material occupied only part of the leaf base regardless of whether they were large or small, and Halle's and Bonetti's figures show the same. In *B. mammillare*, on the other hand, the larger leaves occupy the whole leaf base. The angle at which the free parts of the leaf projects varies, the angle being greater (up to or over 90°) in the larger leaves, and on these larger leaves with a strongly projecting free part, the rhomboidal section of the leaf is more marked (cf. Figs. 7C and see Halle 1913, fig. 17), whereas in the small leaves the upper surface of the free part is merely slightly convex. The cuticle at the edge of the leaf bases (marked by elongated cells) is folded, and the edge is marked by a trench in one or two places on the specimen (Fig. 8A): the whole leaf base was therefore swollen. An extremely similar apearance is seen in juvenile foliage of *A. cunninghamii* and *A. araucana* where the awl-like (or flat, *A. araucana*) leaf springs from near the centre of a rhomboidal swollen leaf base. As the branch increases in size the leaf base expands, the free part coming to occupy less and less of the leaf base, exactly as in my shoots. Furthermore, the older leaves, like the larger leaves of *P. feistmanteli* tend to project backwards. However, the leaf in *A. cunninghamii* is always longer than in *P. feistmanteli,* and (perhaps connected with this), stomata are present on the upper leaf surface, and along the acroscopic leaf base margin. *A. excelsa* (juvenile) is also similar (see Florin 1931).

The cuticle is brittle, despite its thickness, and it was not possible to obtain a complete leaf, and the stomatal distribution is deduced from pieces, of known origin (Pl. 1F and Fig. 6D). The cuticle from the upper surface of the free part of the leaf adjacent parts of the leaf base is sometimes thinner than the rest. In 711 the cuticle is not well preserved, (Fig. 9A), but in as much as can be seen, particularly in the stomata, it agrees with F50769. The hypodermis is, however, never clearly seen, appearing as a layer of cells under the cuticle (Fig. 9C), or as masses of delicate but distorted cuticle.

The stomata are often the most distinct feature of the cuticle, appearing like miniature cartwheels with four to seven spokes. Their structure is difficult to make out. The following is the easiest interpretation. Focussing showed the stomatal pore, and (viewed from inside) the subsidiary cells at a slightly different focus. Their radial walls continued up as the walls of the encircling cells (Figs. 9B, C, D, 11E). The wall between subsidiary cells is not especially cutinised, and the possibility was considered that the stomata were in fact monocyclic (cf. *Pinus thunbergii* Parl. Florin 1931, and *Pagiophyllum maculosum* Kendall (1949). However, stomata compressed a little on one side show a cell wall which is not present in the monocyclic conifers with a deep stomatal pit. Also, comparison is closer, in respect of cells though not of the pit, between *A. feistmanteli* and the dicyclic *Abies,* in which both subsidiary and encircling cells contribute to form the pit, than between *A. feistmanteli* and the *Pinus* species with a deep pit. I have examined *Abies pinsapo* Boiss, *A. nordmanniana* (Steven) Link., *P. contorta* Dougl. and *P. densiflora* Sieb et Zucc. The most similar stoma I have seen is that of *Cycas revoluta* (cf. Figs. 14, L. M), and the *Cycas* stomata in 14M, would probably do as a reconstruction of the *P. feistmanteli* stoma. To refer again to *Araucaria cunninghamii,* here the stomatal pit in the juvenile leaf is formed from both subsidiary and encircling cells, and occasionally stomata looking like *P. feistmanteli* can be found. Generally, however, the encirling cells do not overhang the pit. *Pagiophyllum maculosum* Kendall looks rather similar, but the chimney over the stomata is formed by the subsidiary cells. A further possibility was that the stomatal chimney was formed of three tiers of cells. However, observed from above (Fig. 9B) the encircling cells join onto the other epidermal cells, while the line that might have been the cell outline, corresponds to the line between the subsidiary cells and the collar of cutin over the stomatal pit of *Athrotaxis* Don (Florin 1931, Townrow 1965). Presumably, as in *Athrotaxis,* the cutin collar is in origin fused papillae, borne in *P. feistmanteli* on the encircling cells. The collar is not always present, however.

As noted, the cuticle at the junction between leaf bases shows elongated cells, some of which are shown in Fig. 9B top right. Some hypodermal cells are shown in Fig. 9C.

Discussion. There are probably no fully described fossil species with which *P. feistmanteli* can be confused. The form of the leaves has already been compared with *B. mammillare,* which may look similar, while in *B. desnoyersii* Saporta (see Kendall 1947) the leaves stand out from the shoot, but form a small pyramid, the whole leaf vase being involved.

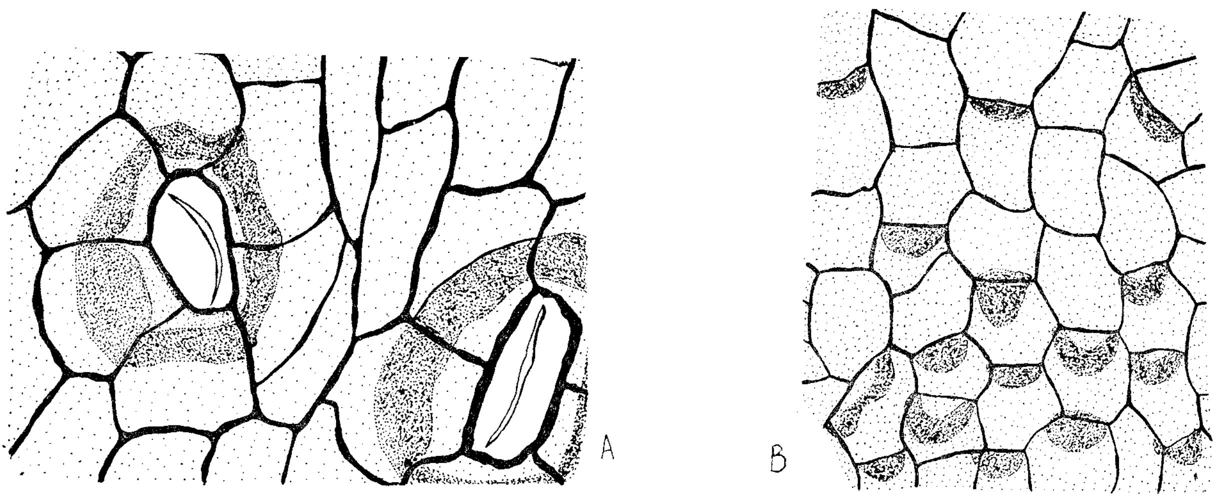

FIG. 10.—*Allocladus rajmahalense.* A. Two stomata, from lower surface of leaf. x 600. B. Cuticle of lower surface of leaf, near leaf base, showing papillae. x 400. Univ. Queensland, 50767.

In cuticle also *P. feistmanteli* differs from other described *Brachyphyllum* and *Pagiophyllum* species (Kendall 1947-1952, Wesley 1956, Archangelsky 1963), which mostly have dicyclic but rather open stomata, or else papillae on the subsidiary cells. *P. maculosum*, which could be confused has been dealt with above.

In the Indian Mesozoic there are several shoots, all incompletely known, looking rather like *P. feistmanteli.*

(*a*) *Echinostrobus expansus* of Holden (1915, see also *Feistmanteli* 1876 pl. 9, figs. 6-9, pl. 10, figs. 3, 4; 1879b, pl. 11, figs. 5, 5a; Sahni 1928, pl. 3, fig. 38), consists of a small shoot system showing pinnate branching, apparently opposite (but probably spiral) leaves which agree with my material in showing a tiny chisel like point arising some way below the upper margin of the rounded swollen leaf base. Further, the cuticle shows more or less the same disposition of stomata as *P. feistmanteli,* including a non stomatiferous " midrib " but differs in showing less regular stomatal rows. The stomata, judging from the figures and descriptions (especially Holden pl. 11, fig. 6) are like those of *P. feistmanteli.* The epidermal cells, however, are shown as differently shaped. The description would doubtless be reworded to-day, and the figures drawn larger, but it seems to me that Holden's material differs from *P. feistmanteli* only in details and proportions and stands with it, when being compared with other *Brachyphyllum* and *Pagiophyllum* species.

Sahni (1928 p. 33, pl. 39, figs. 41 and 42) placed Holden's material with another cutinised shoot in his *Brachyphyllum expansum* var. *indicum,* but judging from the small figures, this material differs from Holden's in leaf shape, stomatal distribution (noted by Sahni) and stomatal details. I here identify Sahni's shoot with quite a different plant (see above). Still another shoot named *B. expansum* is shown by Feistmantel (1887b, pl. 11, figs. 4, 4a, and Sahni, 1928, pl. 3, fig. 39 (Feistmantel's pl. 11, fig. 4, refigured) and 40). Feistmantel shows this shoot having small points to leaf bases, much like Holden's *B. expansum,* and Sahni's cuticle preparation (fig. 40) though far too small to show detail is comparable with Holden's. The shoots differ, though not widely in the shape of their leaves, Holden's being rounded in outline, and in branching, which is regularly pinnate in Feistmantel's shoot. The shoot may be identical with either Holden's shoot or *P. feistmanteli,* or might be specifically different, I cannot decide on the information available. It would seem clearly to belong to the same group.

(*b*) *Echinostrobus rhombicus.* Feistmantel (1887a, pl. 11, figs. 6-11; 1879, p. 30, pl. 12, figs. 2, 2a, 10, 10a; Halle 1913, pl. 9, figs. 15-16a; Sahni 1928, pl. 1, figs. 23-25, to which some of the specimens cited on p. 167 as comparable with *P. feistmanteli* may belong), consists of long sparingly branched shoots with very regular rhomboidal leaf bases. In some figures (see especially Sahni 1928, pl. 2, fig. 25) there appears to be free part to the leaf looking like the free part of *P. feistmanteli,* though smaller. No cuticle is known.

The shoot called *Brachyphyllum divaricatum* by Feistmantel (1877a, p. 59, pl. 10, figs. 1, 1a; Sahni, 1928, p. 23, pl. 2, figs. 30, 31) differs from any of the above species, in that its thorn like leaves occupy the whole of the leaf base, and are longer and more acute than is, at least normal in the material otherwise compared with *P. feistmanteli.*

I suggest that possibly the three species *P. feistmanteli, " E. expansus "* of Holden and *B. rhombicum* form a group of *Brachyphyllum*-like conifers that could form one genus. However, not having seen material of the Indian shoots, I refrain from moving the Indian specimens at present. It would seem that this little group (if real) is Gondwanan, and not Northern. *P. feistmanteli* comes from floras usually given as Middle Jurassic (Halle 1913), (Sahni 1928, de Jersey 1963). *E. rhombicus* and *" B. expansum "* of Holden come from the Jabalpur Series, Upper Jurassic or Lower Cretaceous, and from other localities, probably Jurassic.

P. feistmanteli cannot be classified on its shoot alone, but, as with several other *Brachyphyllum* and *Pagiophyllum* species, there is a strong suspicion that it stands near *Araucaria* especially Sect. Eutacta. As noted, the rather unusual leaf shape is matched in *A. cunninghamii* juvenile foliage, while the stomata are similar, rarely very similar. The branching pattern of the ultimate shoots is also, in all probability, the same. The differences lie in stomatal distribution and leaf length.

Brachyphyllum differs from *Pagiophyllum* only in that the free part of its leaf is shorter than the leaf base cushion, not projecting beyond it (e.g. Wesley 1956). *P. feistmanteli* crosses this admittedly artificial boundary, but having been once put in *Pagiophyllum* I see no gain in moving it now. Its position in *Pagiophyllum* can in any case be merely provisional.

CONITES TENISON WOODSI nom. nov.
Pl. 1B, Fig. 2B.

1883 " Cone of *Walchia milneana* " Tenison Woods, pp. 164-165.

With the foliage called originally *Walchia milneana* (now *Allocladus milneanus*) Tenison Woods (1883, p. 164), described a structure he regarded as the male cone. The original is in the McLeay Museum, No. 36. It is neither of the specimens figures in Tenison Woods pl. 6, figs. 7 and 8, but the description refers to it.

The single specimen represents a more or less median longitudinal section, and except for minute cubes of carbon, no plant material is left. The specimen is a rather spike like infloresence (cone) containing at least 30 units, (Pl. 1B), each unit consisting of a bract and an axilliary structure, which, for simplicity, is termed the seed scale complex. The units are almost certainly spirally inserted, not in pairs, for passing up the cone, successive units appear in (approximate) saggital section, to a view which is almost certainly abaxial surface exposed. The appearance of paired units arises from the circumstances that the fossil is a longitudinal section. It is not clear whether the bract is separate from the seed scale complex, but from the difference in level between the two (Fig. 2B), I think it is. The complex consists of a supporting portion, curved in distally, on the

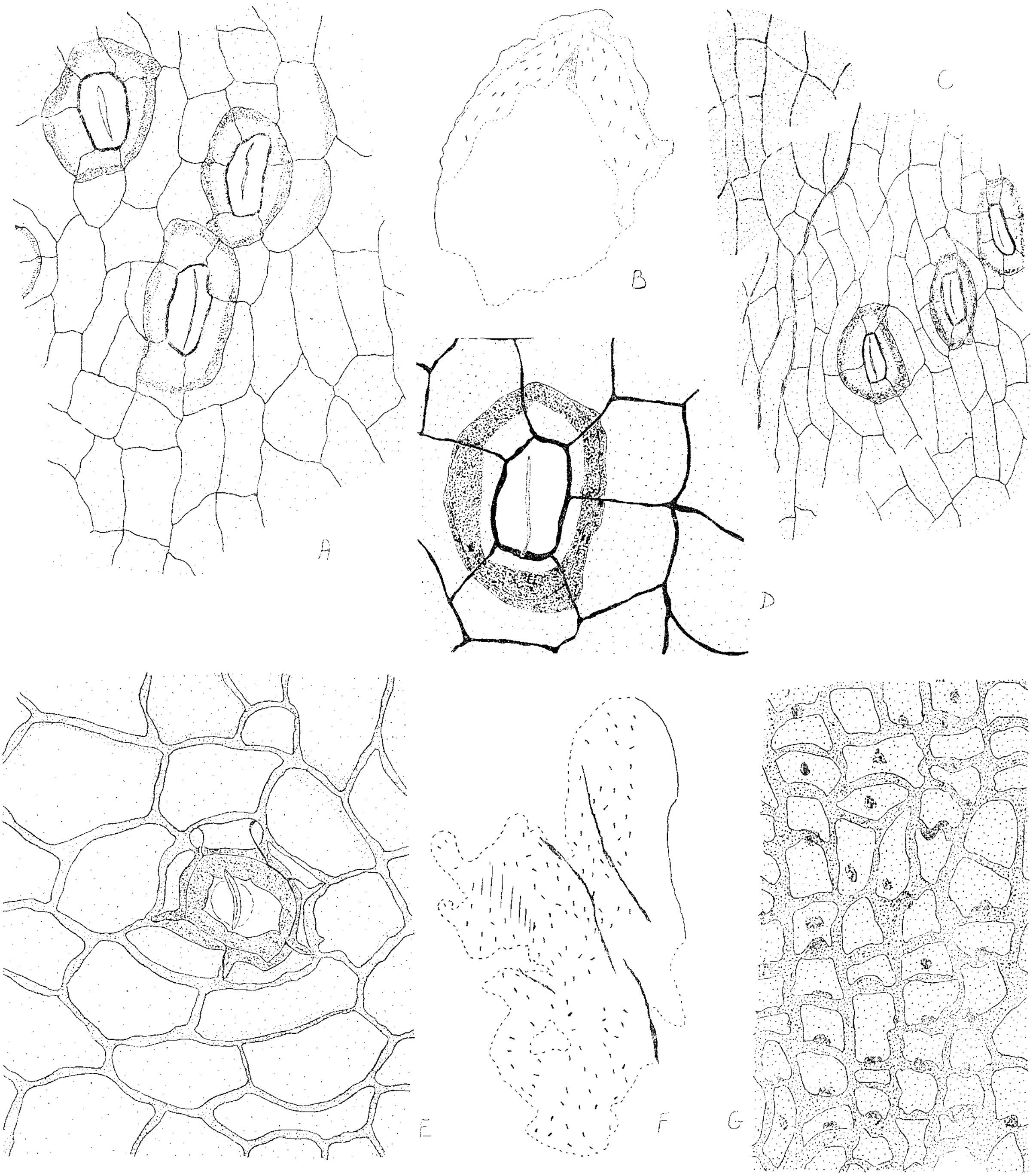

FIG. 11.—*Allocladus rajmahalense*, A-D; *Al. cribbii*, F, G; *Pagiophyllum feistmanteli* E. A. Cuticle from upper leaf surface x 400. B. A leaf, showing number and arrangement of stomata on upper leaf surface; close lines represent "midrib". Possibly not all stomata shown. x 10. C. Cuticle from lower leaf surface, with stomata, and thick cuticle (top left) x 300. D. A stoma from the upper leaf surface x 600. Univ. Queensland, F50766, F50767. E. Stoma with cutin rim forming chimney over stomatal pit, Univ. Queensland, F50769. F. Cuticle from upper surface of leaf with stomata, margin to right, vertical lines, folded area where stomata not visible. x 20. G. Cuticle from lower surface of leaf, showing papillae. x 400. Univ. Queensland, F50760.

adaxial surface of which there are three to five scale-like structures (as noticed by Tenison Woods). Without plant material it is impossible to say what these structures are. In places (Fig. 2B), there may be a micropyle seen, and my guess is that they are seeds. They could equally well, however, be a cupular investment of the seed, or projection of the main part of the complex, unconnected with the seed.

The only evidence that the shoot and this cone belong to the same plant is Tenison Wood's statement that they are associated in Ballimore district. The lithology of the matrix is, however, not identical for the cone and supposed shoot, and I doubt whether they come from the same locality.

There is far too little information to attempt an adequate comparison, however, the probability is that the cone belongs to the Coniferales. Within the conifers comparison seems possible with *Palissya* Bronn (see Florin 1944), but if the bract is indeed separate from the seed scale complex, it differs sharply from *Palissya,* and the resemblance may well be only superficial. A rather similar looking fossil is figured by Edwards (1934, pp. 100-102, pl. 3, figs. 5, 6) as *Palissya bartrumi,* from the Jurassic of New Zealand. I consider Tenison Woods' cone no further, except that if it does belong with the foliage called *Allocladus milneana,* it, even on present information, removes that plant from close comparison with any living conifer; also from *Lebachia* Florin (*Walchia* pars.). I doubt if the resemblance to *Ernestiodendrom* (*Walchia*) *filiciforme* (Sternberg) Florin is more than superficial.

The best way of dealing with this specimen would seem to be to transfer it to the non commital genus *Conites* till more can be found out about it.

Diagnosis. Spike-like fertile structure at least 7 cms. long and 1 cm. wide, consisting of about 30 units spirally arranged up the cone axis. Each unit double, with basiscopic (subtending) portion, and an acroscopic (axilliary) portion. These two probably separate. Acroscopic portion curved inwards distally, and having on its upper surface three to five more or less oval bodies, about 1.5 mm. high and 1 mm. wide, possibly seeds.

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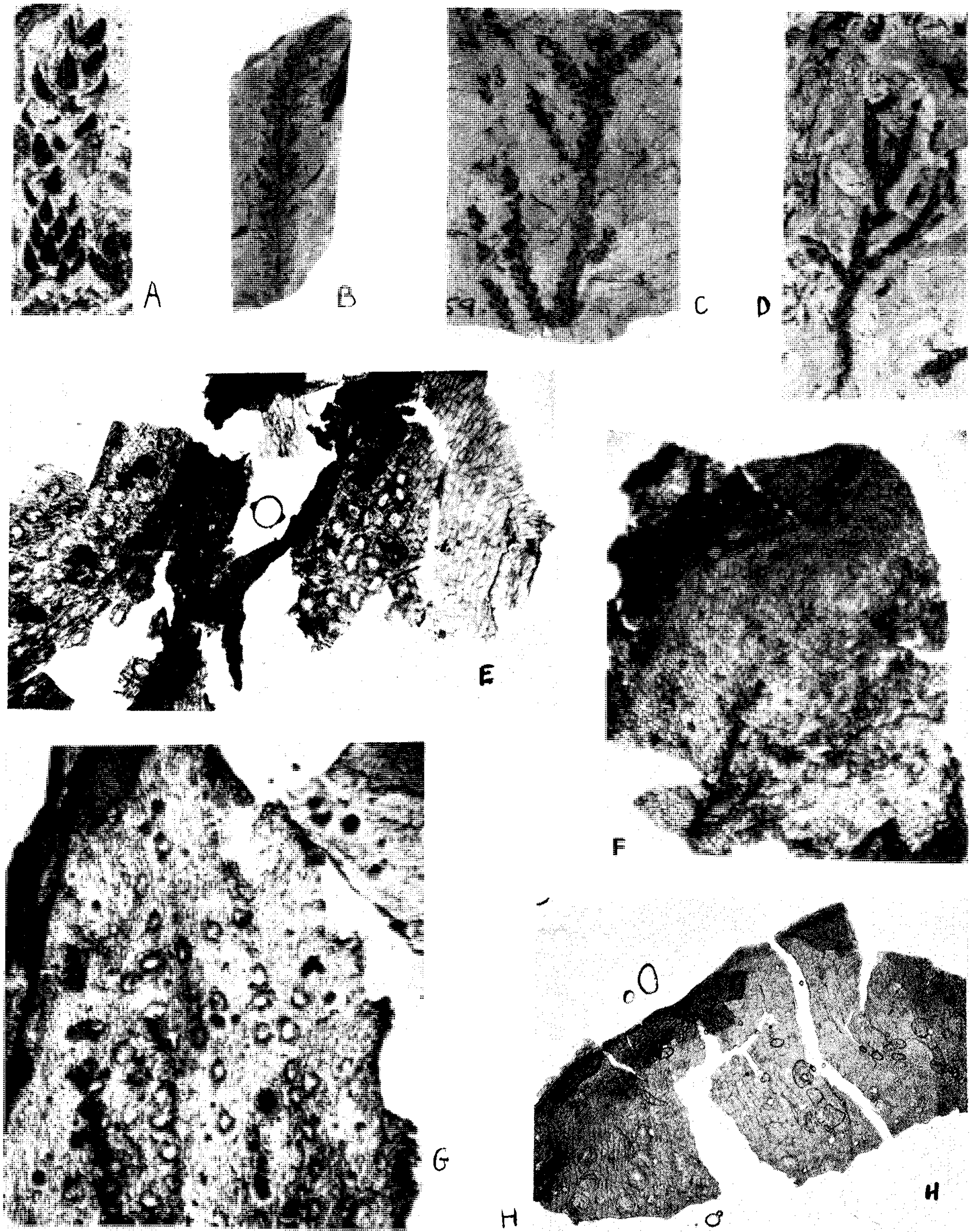

PLATE I.—A. *Allocladus milneanus*, holotype, x 1. MacLeay Museum 136. B. *Conites tenison woodsii;* the specimen x 1. MacLeay Museum 36. C. *Pagiophyllum feistmanteli*, branching specimens, x 1. F50769. E. *Al. cribbii*, upper cuticle, stomata and margin. x 25. F50761. F. *P. feistmanteli*, cuticle, a stomatal zone lower left (arrow) x 25. F. G. *Al. milneanus*, upper cuticle, stomata and margin. Macleay Museum 136. H. *Araucaria crassa*, lower cuticle, cells, stomata and margin x 25. MacLeay Mus. 137.

F.P.172