THE BRACHYPHYLLUM CRASSUM COMPLEX OF FOSSIL CONIFERS

By

JOHN A. TOWNROW

Botany Department, University of Tasmania.

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, Allocladium gen. nov., also almost certainly Tertiary: while the other, Jurassic in age, is referred to Pagophyllum feistmanteli Halle, which is described. Another group of shoots sometimes confused with A. crassa is described as Allocladium gen. nov., with three species A. crassum, A. cribbii, and A. milneanus (Tenison Woods) com. nov., also almost certainly Tertiary. The supposed cone of A. milneanus is examined, and doubt is thrown on its ascription to Allocladium. It is renamed Conites tenisoniwoodsii 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. Eutecta, 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 Bronnliart and Pagophyllum Heer group of conifers. One is placed provisionally in Pagophyllum, 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 Pagophyllum as recently defined (Kendall 1947, 1948, Waley 1956): to classify them into Brachyphyllum and Pagophyllum would separate in an inconvenient way shoots that are very similar (Allocladium milneanus and A. cribbii); in my view Brachyphyllum and Pagophyllum 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, 1953), 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.

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.
THE BRACHYPHYLLUM CRASSUM COMPLEX OF FOSSIL CONIFERS

FIG. 1.—Araucaria crassa A; Allocasuarina cribrilii, B-F; Pagiophyllum foliatumeli, 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 epidermal cell walls, surface generally smooth, rarely ornamented with low but hollow papillae about 30μ across, papillae seen on both surfaces, not only on anticlinal but also on 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 branchlet stems there is variation however, 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 the degree to which they are depressed (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 are, about 50μ apart (shown diagramatically by vertical lines), forming a Y shaped pattern, are 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. Eutacta emerge as a single trace from the stem just above 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 badly (Pl. i H). The processes for two circumstances 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 dicyclic, on upper surface stomata, at least near midrib, only. 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. i H, and, as in A. cunninghamii, is not scarious. It is not quite true that, if these marks 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 dicyclic, on upper surface stomata, at least near midrib, only. 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. i H, and, as in A. cunninghamii, is not scarious.

Comparisons. The nomenclature of A. crassa is distinct. It is immaterial: Tenison Woods' statement, the species was thought to be Triassic (or at least lower Mesozoic, a mistake heightened by the original rather misleading comparison with Brachypodium mammillare Brnth.), 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 Brachypodium crassum was proposed in 1883 both by Tenison Woods and Lesquereux (see Seward 1919, pp. 324-329), 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.
Diagram 2.—Araucaria craS8a A, C; Conites tenison-woodsi B; Athrotaxi tasmanica D, E; Pagophyllum jeistmanteli, 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. 192.
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* Bucholz (1949) has leaves of similar size and shape (see Table 1 in Cookson and Duigan 1952). *A. bimaculata* Bucholz (*loc. cit.*) is also similar, as *Selling* (1956 p. 557) remarks. The cell outlines are straight, only rarely showing sinusous 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 (Plink 1931, p. 232, Cookson and Duigan, 1952, p. 462) and there seems no good reason for keeping them separate. *A. linearis* and *A. montana* (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 separate 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 stomatical 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 detail 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 PI. III. All these leaves come from a single shoot. Similar variation, though not so wide, is seen in such material as *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. These 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 1950), but the locality is unknown.

**Family Taxodiaceae**

**Genus ATHROTAXIS** Don

**ATHROTAXIS TASMANICA** nom. nov.

*Plias. 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.


**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 or 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 2-5x thick, on upper surface 1-2x 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 40 x 35μ, on upper surface cells more or less rectangular 38 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 unscupied, 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.
The Brachyphyllum Crassum Complex of Fossil Conifers

Fig. 3.—Athrotaxia 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. 187. E. Sinuous cell outline, x 600. 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. 187.
Description: The Queensland material consists of two specimens collected many years ago, F705 from 'Walloon' (a designation by itself of uncertain meaning, the early collectors) and F753 from Rosewood near Ipswich, in ash beds, according to Jack and Etheridge (1892, p. 385). F705 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 F705, two small lengths were removed from the specimen and treated with HF; they were afterwards macerated.

F705 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 mm. 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. Similarities were not at first seen on the Tasmanian leaves, on re-examination a few were seen, but they are smaller than on F705. 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 in these specimens. Also, there are many more stomata on the lower surface, even in st. 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. laziolota. 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 or lateral 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).
THE BRACHYPHYLLUM CRASSUM COMPLEX OF FOSSIL CONIFERS

FIG. 1.—Araucaria. A, B; Allocadus cribris. 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 127. 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 encircling cells in contact, very rarely encircling cell shared between adjacent stomata.

Discussion: The shoots now segregated into Allocadus shows the general form of some species of Araucaria, sect. Eutacta, especially of A. cunninghamii, or of Athrotaxis, especially A. selaginoides, and of some shoots referred to the form genus Pagiothyllum Hemsley. 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, 16). Only one specimen of the material available to me shows the branching pattern, (cf. the specimen of Walton'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. milneanmus, 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. milneanmus 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 1938).

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. rajmahalense, 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 diagnoses (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. milneanmus, 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, D). The whole appearance comes close to that seen in Cyclic 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 Microstrobus, and many other conifers. In Al. milneanmus these scalloping are up to 1 mm. high, and consist of whole groups of epidermal cells, with their hypodermal cells, which turn upwards to form almost shovel-like projections (Fig. 5B). Al. rajmahalense is intermediate.

Comparisons: Twigs of Allocadus look rather like those of certain species of Araucaria or Dacrydium Sol. or Athrotaxis, but the difference in cuticle precludes referring Allocadus to any of these genera. It is more difficult to distinguish from Brachypodium and Pagiothyllum (Kendall 1947, 1948, Wesley 1956), as they are defined broadly, separated arbitrarily from one another, and probably artificial. Allocadus would however, make exceptional species for no Brachypodium or Pagiothyllum is epistomatic, none have a scalloped margin, and in most the stomata run in rather well involved longitudinal rows.

It is difficult to discuss the possible relationship of Allocadus with Brachypodium and Pagiothyllum, since Brachypodium contains definite Araucariaceae (B. mammillea, see Kendall 1919a), and at least one species, B. expansum definitely not Araucarian (Kendall 1956). Perhaps it is fair to say that there are no features which particularly suggest relationship between the genera.

Cheiroplepidium muensleri (Sechenov) Takhtajan, (Florin 1944, further references given), Harris 1957, Lewarne and Pallot 1957, Woods 1961, Chaloner 1962) consists of shoots and cones, but only the shoots will be considered here since the Allocadus 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 searious 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. 8.—Allocladus minutus A-C, E-G; A1. 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. cribbi. 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 stromatous, but Cheirolepidium amphistomatic. (i) Allocladus has a scapulated leaf margin but Cheirolepidium does not, (ii) Allocladus has regular dicyclic stomata, with the subsidiary cells sunk in the leaf, whereas Cheirolepidium is only irregularly dicyclic or monocyclic with only slightly sunk 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.

**ALLOCADUS RAJMAHALENSE** (Feistmantel) com. nov.

Pl. 1D. Figs. 8C, D, E; 10; 11A–D. 1877 *Echinostrobus rajmahalensis* Feistmantel, p. 90, pl. 65, figs. 3, 3a. Small branching shoot, from "Bindabrum, Amrapora, Burlo, &c." 1928 *Brachyphyllum mammillare* Sahni non Brongniart, p. 18, pl. 2, figs. 18, 20 only. Feistmantel's specimen retigured.

**Comparable Specimens.** Oldham and Morris 1863, pl. 32, fig. 8 (very obscure fragments) : Feistmantel 1887, pl. 42, fig. 2; 1879, pl. 19, figs. 2a; 1877, pl. 13, figs. 2, 2a, and the whole list given under Allocladus.

**Holotype:** Feistmantel 1877, pl. 65, fig. 3. 283. 4/525, Geol Survey, India.

**Locality:** Binduram, 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 in transverse section of obtuse apex. Maximal width 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 oriented, 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 papillae at leaf base on lower cuticle only, papillae as for Al. cribbi. Cell outlines thin, about 3μ sometimes bordered.

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

**Margin scarious, scalloped (as Al. cribbi) 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 Tarnymore Colliery, and it is well preserved. This is the only species in which the branching pattern is seen clearly, and it is irregular (Pl. ID). 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–D), 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. 8F), 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. cribbi). 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 narrow, 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 25. 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 represented by 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 pi. 2, figs. 19, 20) has compared them. The shoots agree in manner of branching, in size, and in leaf shape and size, except only that some leaves do not have a slightly more acute tip than 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 spirizylon 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 (scarcey 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. spirizylon, 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. 11, J, 5, (not 5D), 6C, 7B.

1883 Walchia milneana Tenison Woods, P. 163-164, pl. 2, fig. 3 and pl. 6, fig. 1. (The supposed cone is excluded).

R.S.—12

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, pi. 44, figs. 5, 5A; 1877a, pl. 8, fig. 8; 1879, pl. 16, fig. 10; Halle, 1913, pl. 9, figs. 15, 16; Sahni, 1928, pl. 2, figs. 21, 22; Feruglio, 1934, pp. 260-261, pi. 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 Ballimore) ? Lower Jurassic.

Diagnosis emended. Leaves appressed or spreading about 2-5 mms. 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, 2.5-3 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, 50 x 30μ, not papillate, walls straight and indistinct, but thick, about 4μ. Stomata deeply sunken in a pit (depth not known), 3-6 subsidiary and encircling cells. Encircling 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; *A. milneanus* B; *Papiophyllum 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. F50749.
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. Warkoms’ (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 Warkom did not refer to Tenison Woods’ work at all. My shoot is also probably distinct from *P. peregrinum* of Warkom (1919), from the Cretaceous Burrum Series, but the conifer remains from the Burrum need further study before they can be discussed usefully.

Feruglio’s (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. 55, figs. 2, 3; Halle 1919, pl. 2, figs. 42, 42a, pl. 3, figs. 3, 4; Araya 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 mm's. (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, 4μ x 5μ, often 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 neighboring cells. Stomata sunken in 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 10μ 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 slightly 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* Kendal (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. insignae* Kendal (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 *Atroraxis 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. 5E.

**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 and Medwell (1954), known as *Brachyphylum gippslandicum* McCoy resembles other material ascribed to *Al. cribbi* 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. cribbi* come from rocks of Middle Jurassic age, though some may be Lower Jurassic. The Walloon Coal Measures were dated by de Jersey (1958) as Lower Jurassic, but later (de Jersey and Paten 1964) a Middle Jurassic age has been suggested.

**THE BRACHYPHYLLUM CRASSUM COMPLEX OF FOSSIL CONIFERS**
### Table I.

**THE SPECIES OF *ALLOCLADUS* COMPARED**

<table>
<thead>
<tr>
<th></th>
<th>Leaves.</th>
<th>Margin</th>
<th>Upper Surface</th>
<th>Stomatal distribution and Cuticles</th>
<th>Stomatal details</th>
<th>Hypodermis</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Al. rajmahalense</em></td>
<td>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.</td>
<td>Scalped only at base, 100μ, otherwise scarious</td>
<td>Only slightly concave</td>
<td>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.</td>
<td>Somewhat sunken in a pit whose top may (about one in 10) overhang</td>
<td>None seen</td>
</tr>
<tr>
<td><em>Al. cribbi</em></td>
<td>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.</td>
<td>Scalloped, or not, along whole margin, 100μ, otherwise scarious</td>
<td>Strongly concave</td>
<td>In a mass, obscurely separating below in two zones. Stomata not in rows, orientation irregular. Two cuticles of different thicknesses: 5μ : 1-2μ.</td>
<td>Slightly sunken in a rather open pit</td>
<td>None seen</td>
</tr>
<tr>
<td><em>Al. milneanus</em></td>
<td>Standing out from shoot, shoot not like a cat’s tail. Leaves triangular, apex acute, 8 mm. long 3 mm. wide at widest.</td>
<td>Strongly scalloped along whole margin, 1 mm. or more</td>
<td>Only slightly concave</td>
<td>In two indistinct zones along whole length of leaf. Stomata tending to be in rows, orientation irregular. Cuticles of about same thickness, (5-7μ).</td>
<td>Strongly sunken in a pit whose top may overhang</td>
<td>Cutinised</td>
</tr>
</tbody>
</table>
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, F50763.
**PIAGIOPHYLLUM** 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. 13, 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.


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. 16-17B; Halle 1913, pl. 9, figs. 14, 14Aa.

**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 acrosopic margin, but dying away towards acrosopic 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 diacytic 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. Cutilisation 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 cuticular collar, projecting up above general epidermal level. Encircling cells of second rank (when present) lying on general epidermal level, and unspecialised. Whole stomatal apparatus apparently 80μ in diameter, opening of chimney over stoma about 20μ, depth of pit about 50μ (?). Hypodermis sometimes cutinised, showing elongated cells. Veneration 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 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 PI. 1C, and is typical of the material available. 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; shoot is basically 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 F711 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, 1926, 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 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 then continued into a more similar appearance 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* and *P. desnoyersii* Saporta (see Kendall 1947) the leaves stand out from the shoot, but form a small pyramid, the whole leaf base being involved.

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* Bois., *Abies nordmanniana* (Steven) Link., *P. contorta* Doug., 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 encircling 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 base being involved.
In cuticle also *P. feistmanteli* differs from other described *Brachyphyllum* and *Pagiophyllum* species (Kendall 1947-1952, Wesley 1956, Archangelsky 1965), which mostly have dyicic but rather open stomata, or else papilae on the subsidiary cells. *P. proussonii*, 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 Feistmantel 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 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. rhombicum* 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 admitted artificial boundary, but having been once put in *Pagiophyllum* I see no pain 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 minoreana" Tenison Woods, pp. 164-165.

With the foliage called originally *Walchia minoreana* (now *Allocadietus minoreanus*) Tenison Woods (1883, p. 164), described a structure he regarded as the male cone. The original is in the McLean Museum, No. 36. It is neither of the specimen 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 inflorescence (cone) containing at least 30 units, (Pl. 1B), each unit consisting of a bract and an axillary 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) sagittal 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.—Alloclados rajmahalensis, A-D; Al. cristabilii, F, G; Pugio phyllicum 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 400. Univ. Queensland, F50766, F50767. E. Stoma with cutin rim forming chimney over stomatal pit, Univ. Queensland, F50768. 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 micropyile seen, and my guess is that they are seeds. They could equally well, however, be a curiapal 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 Baltimore 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 *Archehryphylh (see cited) but if the bract is adequately comparison, however, the probability is that the cone belongs to the Coniferales. Within the conifers comparison seems possible with *Archehryphylph* (see cited) but if the bract is

**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 (axillary) 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.

**ACKNOWLEDGMENTS.**

I am most grateful to the Chief Geologist, Queensland Mines Department, the Curator, McLeay Museum, Sydney, and to Mr. H. Fletcher, Australian Museum for lending me material. I am also indebted to the Management and staff of Caledonia Colliery and Tannymorel Colliery for facilities to collect, as to Mr. H. Cribb, Mr. R. Gould and D. G. Playford for helping me with parts of the collecting. I must thank Professor T. M. Harris, F.R.S., Reading, for most valuable suggestions concerning the criticisms of the manuscript.

**REFERENCES.**


**JACK, R. L., and EDIEMIN, R., 1925.—The geology and palaeo-entology of Queensland and New Guinea, xxx and 795, atlas, Brisbane.


**LIAI, ibid. (12) 2: 229-297.

**LIAI, 1940.—On Brachythylphus caespitosis and its cone. Ibid. (12) 2: 308-320.


**LIAI, 1940.—On a new conifer from the Scottish Lias. ibid. (12) 2: 308-320.

**LIAI, 1940.—On Brachythylphus caespitosis and its cone. Ibid. (12) 2: 308-320.


**LIAI, 1940.—On a new conifer from the Scottish Lias. ibid. (12) 2: 308-320.

**LIAI, 1940.—On Brachythylphus caespitosis and its cone. Ibid. (12) 2: 308-320.


THE BRACHYPHYLLUM CRASSUM COMPLEX OF FOSSIL CONIFERS


1918.—Fossil Plants (iv), xvi + 543 Cambridge.


