ON RISSIKIA AND MATAIA PODOCARPACEOUS CONIFERS FROM THE LOWER MESOZOIC OF SOUTHERN LANDS

By

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(With two plates and 15 text figures.)

ABSTRACT

The genus *Rissikia* gen. nov. consisting of leafy shoots and detached pollen and seed cones is described, with two species, *R. media* (Tenison Woods) com. nov. and *R. apiculata* sp. nov. Also described is *Mataia* gen. nov. with one species *M. podocarpoides* (Ettinghausen) com. nov. These are all ascribed to the Podocarpaceae, and the evolution of the Family, particularly of the epimatium is discussed.

INTRODUCTION

The two conifer shoots included in the following description are believed to be podocarpaceous, and indeed to throw light on the history of some organs in the Podocarpaceae, in particular, the nature of the epimatium. It has for long been considered (e.g. Gibbs 1912 and Florin 1944) that the epimatium is a modified seed scale complex but how it was modified has remained somewhat obscure. The fossils discussed herein offer one explanation. Much however, is left aside for the present: for example, the relationship of the earliest podocarps to the *Voltzia* group of conifers; the evolution in the non-epimatial cone; and the nature of the male fertile branch. These questions I hope to take up with the aid of other conifers both older and younger than those considered here.

Material is referred to under its numbers in Museum collection, by whoever it was collected.

DESCRIPTIONS

Family PODOCARPACEAE

Genus RISSIKIA nov.

Type species: *R. media* herein.

Diagnosis. Coniferous plant bearing regularly abscissed (? deciduous) foliar spurs. Spurs about 6 cms. long and of strictly limited growth, bearing small scale leaves at the base, and thirty or more large adult leaves. All leaves spirally inserted; either projecting spirally or in two lateral ranks. Leaves thick, rhombic in section or bilaterally flattened, about 0.75 cms. wide; bases decurrent but not or scarcely contracted, apices acute, sometimes assymetrical and terete. Cuticle thin (0.5μ—2μ), showing similar cellular pattern over the whole leaf. Cells more or less rectangular, set in regular longitudinal rows, and sometimes papillate, cell outlines sometimes sinuous, or pierced by small holes. Stomata in four diffuse zones, a zone per flank. Stomata lying in one to three rows per zone, separated from one another at least by a shared encircling cell, usually by more cells; most often monocyclic with four subsidiary cells, two lateral and two terminal, unmodified except by position. Stomatal pit rectangular, shallow, usually overhung by two to four solid or hollow cutin projections borne on surface of subsidiary cells. Guard cell surface slightly concave inwards, feebly cutinised, aperture about two thirds as long as pit.

Pollen cone rounded in outline, about 1 cm. long and 0.5 cm. wide in the middle, borne on a stout curving stalk about 2 mms. in diameter, showing remains of scale leaves. Cone consisting of (estimated) 25 units, each unit consisting of connective, peltate scale, and two pollen sacs. Connective about 0.75 cm. wide, inserted on to peltate scale a little below mid point of the scale, and bearing the two pollen sacs along its whole length, attached to under surface of connective. Peltate scale not radially symmetrical, rounded or slightly triangular in outline, about 1.5 mm. wide and 2 mm. high. Pollen sacs of thick wall, not attached to the scale. Outward surface of scale and pollen sac cutinised, probably also connective and cone axis, (cuticle always thin 0.5μ or less). On scale cells nearly equidimensional, set in rather irregular longitudinal rows, and with a few longitudinally orientated stomata, like stomata on leaves, but only very rarely with cutin projections over stomatal pit. On pollen sac, connective and cone axis cells elongated, in rows, stoma absent.

Pollen disaccate, striate, leptomatous, of total width about 50μ with rather thin extine. Corpus rounded in polar views, sacci slightly displaced distally. Striae showing as three to ten, mostly four to six, clefts with (presumed) intextine becoming visible. separated by bars of thickened exoextine. Clefts mostly narrow (about 2μ), but up to 10μ wide, when narrow occasionally forked. Thickened bars about 5μ (4-10μ) wide, surface more or less smooth, or showing minute pitted ornament. Striae concentrated on the cappa. Corpus about 35μ in diameter, about 30μ deep, widest part lying near the proximal surface. Sacci with proximal roots inserted at (or to either side of) widest part of corpus, as deep as corpus, and about 10μ high; rarely nearly continuous round corpus in equatorial plane. Ornament on sacci reticulate, brochi sometimes elongated at right angles to cappula long axis; brochi about 5μ long and 3μ wide. Form of ornament as in living conifers.
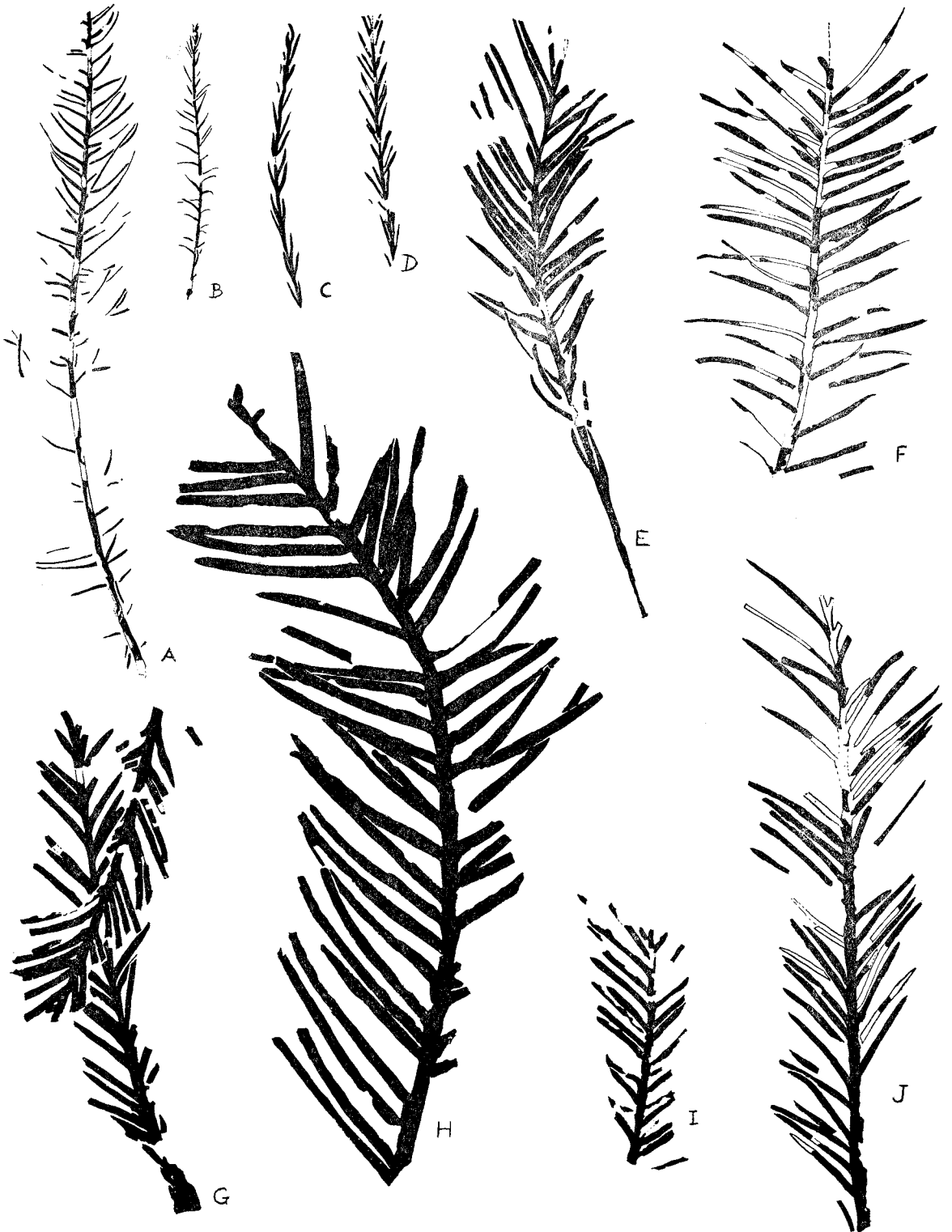
FIG. 1.—*Rissikia apiculata*, A-D: *R. media*, E-J.

A-J: Foliar spurs, all x 1.
A: 13036, Univ. Sydney.
B-J: Australian Museum, F51981, 51957, 59980, 51964, 51975, 51961, 51968, 51963.

Seed cones terminal on leafy branches; branches up to 1.5 cms. long (total length unknown) leaves on branches rhombic in section, up to 4 mm. long and 1 mm. wide, grading into bract scales. Whole cone spike-like in form, about 3 cms. long, bearing 15-25 units spirally arranged. Each unit consisting of bract subtending the cone scale and the stalked seeds (axillary short shoot, flower or seed scale complex). Bract trifid, with denticulate margin. about half as long as cone scale. Cone scale (seed scale complex, or flower in other terminologies) consisting of short axis, thick, possibly round in section, about 0.5 mm. long; axis produced into three lobes, rounded, denticulate, or produced into a long pointed apex. On abaxial surface, lobes showing two longitudinal ridges, possibly with vascular tissue. Seeds (ovules) inverted, borne at end of stalk 0.75 mm. long, and 0.2 mm. in diameter, round in section. Stalk inserted towards base of seed scale lobes, but otherwise free from lobe. Two to six seeds per cone unit, but probably only one or two reaching maturity. Seeds about 0.75 mm. long, 0.5 mm. in diameter, round in section.

Cuticle of bract about 1μ thick on abaxial surface, thinner on adaxial, showing elongated rectangular cells in rows, but no stomata. On lobes of cone scale, abaxial cuticle, 1μ-1.5μ thick, showing more or less equidimensional cells in rows, but over ridges, cells longer and narrower. Stomata few, as on the leaf, with or without cutin projections, cell outlines as on leaf. Abaxial surface with extremely thin cuticle, showing rows of more or less rectangular cells and no stomata. Cuticle of seed stalk showing obscure elongated cells. Cuticles of seeds consisting of cutinised integument, and projecting possibly hollow cutinised nucellar beak at micropylar end. Nucellus probably free from integument to its base. Further detail unknown.

Description and Discussion. (1) *Origin of material.* The material comes from Burnera Waterfall, Upper Umkomaas, Natal. This locality falls within the Molteno, the lowest member of the Stomberg Series. The Molteno has been considered Middle Triassic, but the discovery of sauropods in it (Dr. J. Cosgriff pers. comm.) places it in the Upper Triassic. A very few shoots, including the holotype of *R. media* come from other places e.g. the shoot shown in Pl. 2F, and Fig. 1A.

(2) *Ascription of organs to each other at the generic level.* *Rissikia* is represented by two suites of fossils at Burnera. *R. media* consists of 30 foliar spurs, four seed cones and probably two pollen cones: *R. apiculata* has 15 foliar spurs, two seed cones and no pollen cones. The corresponding organs of the two species are so similar that I think it is almost certain that we are dealing with two species of a single genus. In my collection there are no other conifer macrofossils (out of over 500 specimens). Even at Burnera therefore, *Rissikia* is still an uncommon fossil.

The conclusion that the separate organs belong together is reinforced by the resemblance between the cuticles of the separate organs. Though there is uncertainty at the specific level, taken as a group, the form of the cell outlines, papillae and especially, stomata is the same in all. Though most of the rather few stomata on the cones show no cutin projection over the stomatal pit, in this

matching a large minority of leaf stomata, some do show projections, agreeing exactly with some of those found on the leaf (Pl. 2B and Fig. 6F).

The stoma of *Xylopteris elongata* (Carruthers) Frenguelli is slightly like the stoma of *Rissikia* (see Jones and de Jersey 1947: Pl. 3 Fig 1, and Townrow 1962 b: Fig. 2) but can be easily told apart, for it is dicylcic and the stomata do not lie in more or less regular rows.

(3) *The foliage.* Eight foliar spurs of *R. media* are complete, or show the base, and two of R. *apiculata*. All these show a clean break at the base, with what looks like an abscission scar (Fig. 4A, B, D. G). There is no specimen of a foliar spur showing an eroded base. At the apex the leaves overlap the apex, and a bud cannot be seen (Figs. 4C, H), but one specimen which may have grown on is shown in Pl. 2H. These appearances can be matched in, *Metasequoia glyptostroboides* Cheng and Hu or *Podocarpus imbricatus* Blume, (juvenile form) and indicate that the fossils are foliar spurs, and of strictly limited growth (cf. Fig. 2G *P. imbricatus*). Hence, even though the long shoots are unknown, we can with some assurance, reconstruct the *Rissikia* branching pattern. The ultimate shoots of the tree were presumably like the young shoots of *Podocarpus* Section Dacrycarpus.

It is not clear whether the shoots were shed annually, as in *Metasequoia* or at longer intervals as in *Podocarpus imbricatus*. The very thin cuticle and scarcely sunken stomata recall *Metasequoia* (Figs. 10G, H), and suggest that *Rissikia* may have been deciduous also.

The shoot base itself is swollen and the scar heart-shaped as if was in two parts (Figs. 4A, F). It has not, however, been possible to make out the vascular supply. On this swollen portion there are three to six small flat scale leaves, attached in the manner of bifacial leaves, and about 0.5 mm. long, they pass rapidly but continuously into the adult sort of leaves. Such small leaves again can be matched in *Metasequioa* and *Podocarpus* species (Section Dacrycarpus) (Fig. 2G) and were, in the fossil, presumably a sort of bud scale. They are also seen in *Acmopyle* Bgt. and Gris. It appears therefore, that unlike some podocarps, (Wardle 1962), *Rissikia* had some definite structures protecting the spur bud, though not many of them. The leaves are spirally inserted, strongly decurrent but are dealt with in detail under the species. Towards the shoot base the spur axis is (now) more or less flat, but at the top distinctly angled, because of the large decurrent leaf bases (Fig. 3G). On some of the largest shoots the axis shows transverse ribs; these are wholly internal, and of unknown nature.

The cuticle is always thin, but often of about the same thickness all over the leaf, and in both species shows cells in longitudinal rows (Pls. 2A, C; Fig. 5). Judging from small pieces of cuticle only, the stomata density is about the same on both surfaces, or pairs of flanks, of the leaf. Figs. 5A-E show the disposition of the stomata in the zones, and Pd. 2B a stoma with cutin projections. In only about one stoma out of a hundred are the lateral subsidiary cells divided. Encircling cells are normally absent. The stomatal pit is rather

FIG. 2.—*Rissikia media* A, B; *Elatocladus planus*, C. D; *E. australis*, E; *Podocarpus lawrencei*, F; *P. imbricatus* (juvenile) G;
P. dacrydioides H.

A: The holotype, x1, MacLeay Mus. 102.
B: Foliar spurs from Gilgandra, N.S.W., x 1, Australian Museum 42354.
C, D: Parts of two foliar spurs, x 1, University of Tasmania.
F: The holotype, x 0.5 drawn over Kew Negative 6192, by courtesy of the Director, Kew Botanical Gardens.
G: A shoot system showing long and short shoots, x 0-5 Fiji Forestry Service.
H: Part of a shoot showing pinnate branching and variable leaves, x 0-5.

constant in shape, but the projections overhanging it vary. In general, they are best developed on the thicker cuticles, and are missing altogether on some leaves, especially some with a very thin cuticle. This may be the explanation for their absence on the extremely thin cuticles on the cones. The projections are dealt with in detail under the species, but they form in *R. media* solid cutin lappets, and in *R. apiculata* hollow papillae. In structure the stomata approach rather closely to the (somewhat unusual) stomata seen in *Microstrobos* Garden and Johnston and *Microcachrys* Hook f. (Florin 1931), and especially so, when lappets on the terminal subsidiary cells are missing (Fig. 5D). They also resemble the stomata of *Saxegothea* Lindl. (Fig. 13B). The guard cells are very thinly cutinised, but sometimes cutinisation of the dorsal guard cell surface under the subsidiary cell can be seen (Fig. 6D).

(4) *The pollen cone.* The pollen cone is represented by only two specimens each having part and counterpart. As discussed below (p. 119) the cone is thought to belong with *Rissikia media*. The incomplete curving stalk is about 2 mm. wide at the base (i.e. about the width of a foliar axis above the basal swelling), but is seen only in short length on one cone (Fig. 8B). On the pedicel there are more or less broken fragments of tissue (Fig. 8B) which look like the remains of small flat leaves, as on the foliar spur and at the base of the cone there are two (possibly three) larger leaves about 1.5 x 0.25 mms., more like a cone unit, but sterile (Figs. 7C, 8B, cf. Fig. 8A of *Dacrydium franklinii* Hook f.). The cone axis is about 1.5 cms. wide about half way up the cone, and counting the scars on it, and the visible units gives the estimated 25 units per cone. The connective, like the cone axis, is somewhat wrinkled (Fig. 7E), suggesting it may have been thick; it shows strong cellular striae, agreeing with the cells seen on some cuticles, but it was not possible to obtain a preparation of cone axis or connective only. At the end, the connective flattens out into a triangular structure, as seen from above (Fig. 7E), and is attached to the peltate scale rather nearer the base of the scale than the top. Seen from outside (Figs. 7D, E) the scale shows, in the appropriate position, a depressed area, interpreted as the area of attachment, diamond shaped, about 1 mm. long and 0.5 mm. high. No scale is complete, Figs. 7D, E shows parts of several scales in various views. The surface shows cellular striae, and at the top edge a slightly ragged appearance, caused, apparently, by rows of elongated cells, much as in many living conifers. Each scale overlaps about half the one above (Pl. 2I). There are almost certainly only two pollen sacs. In several places two can be seen at different levels (Fig. 7E), but not more than two. The base of the scale overlaps the pollen sacs, but, unlike living podocarps, the scale and pollen sacs do not seem to be joined: for there is a distinct gap, sometimes containing mud, between scale and pollen sac. This situation is seen in various fossil conifers, and in *Dacrydium laxifolium* Hook. f., there is an approach: a small flap of tissue partly overlaps the pollen sacs (Fig. 7F). I do not know how many cell layers compose the pollen sac wall, but it is probably several in the two specimens seen.

The cuticle is described in the diagnosis and shown in Figs. 6C, 10F). The details, and stomata, are like those on a thinly cutinised leaf of *R. media*.

(5) *Pollen.* The pollen appeared mostly as single grains or groups, sticking to pieces of cuticle prepared from the pollen cones. One preparation, however, showed a fragment of pollen sac, still full of pollen. There are many other sorts of pollen in the preparation. The sort described is thought to belong with the cone because (1) the full pollen sac contained grains of this sort and (2) the grains regarded as strangers were fewer in number, and appeared only as single grains, not groups. Only one grain showed what might be a colpus, but it was, I think, a tear: the grains are therefore described as leptomatous, especially since lateral longitudinal views showed an intact cappula (Fig. 9B). The striae are not very striking, and before staining, scarcely to be seen, but they are present with such regularity that I have no doubt they are genuine. I do not have a grain (out of about 80) compressed in such a way as to show the striae in optical section (cf. e.g. Leshik 1955, pl. 8 figs. 4 and 5), but in polar and lateral longitudinal views they look so like other striate grains that they are described in the same terms. There is, however, much variability. Five grains showed no striae at all (Fig. 9C). Most showed four to six bars of thickening, separated by more or less narrow clefts, and some 20 grains showed more or less wide clefts (cf. Pl. 1H and Figs. 9E, D), and about the same number showed up to 10 very narrow and sometimes forking clefts (Pl. 1F, Fig. 9A). In any case, the central two to four bars of thickening were the most stained—i.e. the thickest.

In polar view the corpus was always more or less round, but varied in lateral longitudinal views (Figs. 9B, D and Pl. 1F, H), as did the insertion of the sacci, though this was always close to the widest part of the corpus. The extine is probably thin (about 3μ) as seen in folds, and the saccus roots clearly visible. The other features are given in the diagnosis, and L.O. analysis shows the ornament to be of the usual conifer sort. A small number of grains show a crack (or very thin place) in the extine on the proximal surface, about in the middle (Fig. 9C). The feature is, however, variable in form. It is, I imagine, of the same nature as the similar looking crack shown by Klaus (1963 e.g. pl. 13) in his striate grains. Klaus regards it as a monolete mark, indicating that the pollen grains were produced in a planar tetrad, and I am inclined to agree (cf. also Balme 1963). However, I am not quite convinced, in *Rissikia*, that the crack is original, it is too seldom seen and too variable (there is also variation in Klaus' specimens); it might be a result of compression, or of Schultze's maceration.

(6) *The seed cone.* The seed cones are spike-like in general outline (Pl. 1A, B, Figs. 8C, D, E) having 12-25 units (bract plus cone scale) disposed up a long axis, and though the units do overlap, they are well separated unlike, e.g. *Pinus* L. or *Cupressus* L., where the units are crowded together. The basic structure is as for all conifers, namely, an axis bearing leaves (the bract scale) in the axis of which arises short shoots with seeds (cone scale; or the seed scale complex or flower in
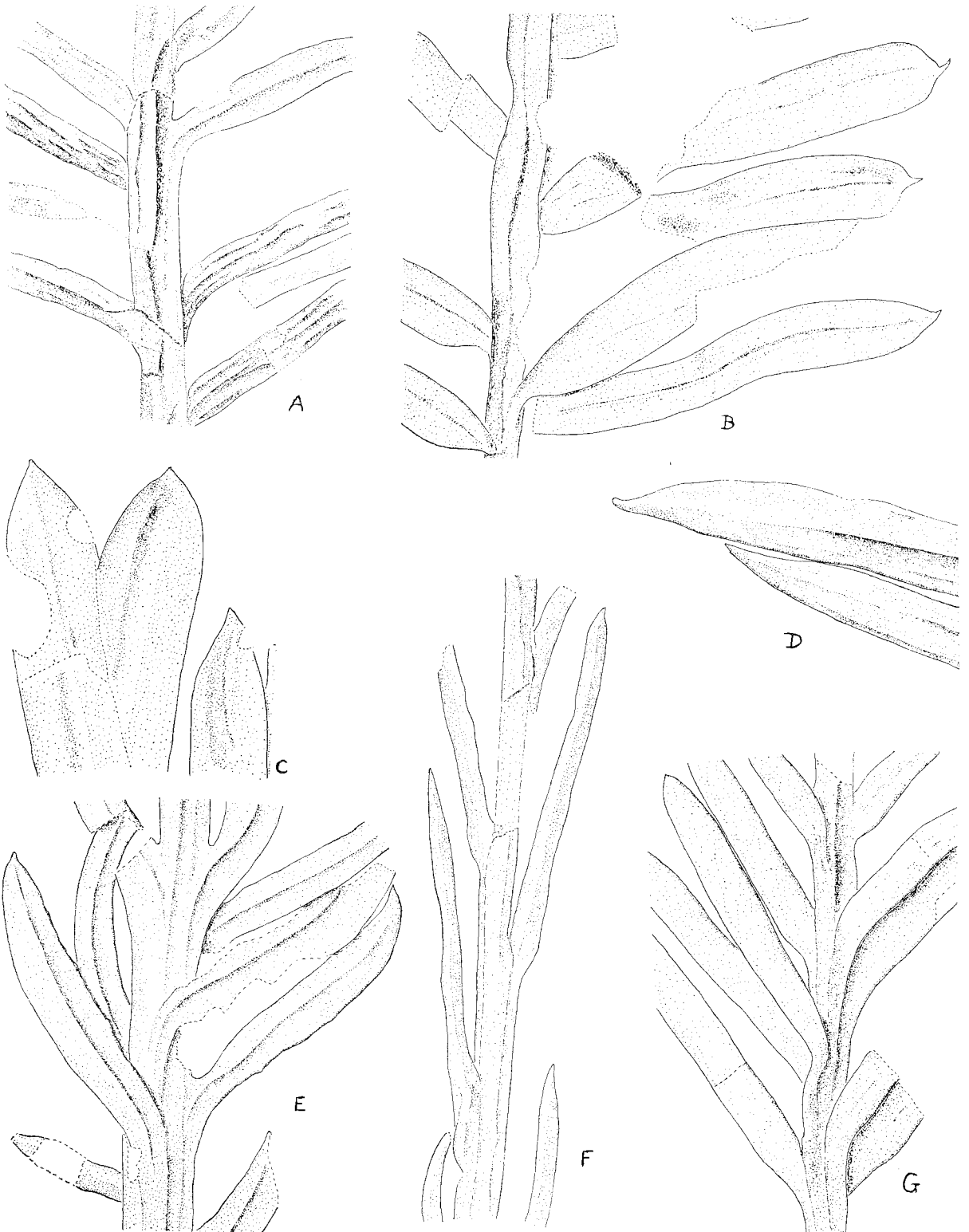
Fig. 3.—*Rissikia media*, A, D, E, G; *R. apiculata* F; *Elatocladus australis* B; *E. planus*, C.

A, B, E-G: Parts of foliar spurs, showing insertion of leaves and their variation in form, all x 7. B, Australian Museum 50192; A, E, F, G, Australian Museum, F 51965, 51964, 51976, 51967; C, D: Leaf apices x 14, C University Tasmania; D, Australian Museum, E 51960.

Florin's terminology). In both species the cone is terminal on a more or less short length of leafy axis, broken off unevenly below, unlike the foliar spurs (Figs. 8C-E), and hence presumably not abscissed. The greatest length of shoot seen was 1.25 cms. (Fig. 8C) and by analogy with several fossil and recent conifers, I imagine that it was probably not much longer originally. The leaves on this axis are nowhere seen really plainly, Fig. 8C shows the best specimen, and on it the leaves are rhombic in section, appearing thick about the middle, tailing away to a narrow margin and apex. They were, thus much like small closely appressed leaves of *R. apiculata* foliar spur. I could not see where they became trifid like the bracts.

(7) *The cone unit*. It was difficult to obtain satisfactory transfers of the bract scale. Fig. 8H shows the best, and from it the bract is seen to be trifid. Other specimens (Figs. 14D, E) are less clear, but in the better of these, three parts of the bract can be seen.

The cone scale with its subtending bract is sometimes presented face on to the observer (Figs. 8F, G), more often it is curved round the axis, and presumably this was its form in life (Figs. 8I). When seen face on, the cone scale is also seen to be trifid. It consists of three lobes joined below, but not always quite at the same level (Fig. 8F). one, often the central one, slightly overlapping the others. These lobes are of thick substance, and are themselves either slightly crenulate (Figs. 8F) or entire (Fig. 8G) sometimes produced to a long point (Pl. 1D, Figs. 14D, E). Seen compressed laterally (Fig. 8I) the common stalk of the three lobes, was only a little less thick than it was wide when compressed vertically. Presumably, therefore it was more or less terete.

The seeds (or ovules, *seeds* is used to cover both) lie on the adaxial surface of the lobes, appearing as raised areas (Figs. 7F, G, H). From the lower end of the seeds, a low ridge runs towards, and finally merges with the stalk of the lobe (Fig. 7G). This is interpreted as a seed stalk. In some specimens (Pl. 1D and Fig. 8G) the seed and its stalk could be broken up from the lobe surface revealing a very fine layer of mud between the two. Furthermore, although it proved impossible to obtain cuticles of an entire lobe with its seeds, some seeds, on maceration, showed a broken tube of cuticle emerging from one end (Pl. 1G and Figs. 9H-J) and another specimen (Fig. 10D) shows the adaxial surface of a lobe, and lying on it (actually adhering to it) is a tube of cuticle. This tube is shown to be separate from the lobe surface by a large spore, lodged between tube and lobe surface. This means that the seeds were borne on their own little stalks, not adnate to the cone scale. These stalks are all one can call a megasporophyll.

The seeds are minute, some 1.75-1 mm. long and 0.25-0.5 mm. wide, their stalks being about 0.2 mms. wide. Cuticle preparations show the micropylar apparatus at the same end of the seed stalk (Figs. 9A, H-J), hence the seeds were inverted. There are one or two seeds per lobe of the cone scale, but it is not unusual to see only one large seed (or its impression in the matrix) per cone unit, so that it is probable that not all the seeds

ripened, or were pollinated. Nothing is known directly of the internal structure of the cone scale. However, the abaxial surface of each lobe of the cone scale is raised in two ridges (Figs. 8I, 13D), and on the cuticle these ridges correspond to rows of more or less elongated cells (Fig. 9K). These features, in a leaf, mark the position of veins, and it is therefore possible that each lobe contained two vascular traces.

(8) *Cuticles*. As with the pollen cone, cuticle could only be prepared in small pieces, though as far as possible (which was not far) different organs were macerated separately. All parts are cutinised, but stomata are extremely rare, only eleven were seen altogether. By analogy with living plants, it is probable that the cone was not actively photosynthetic, or we might expect more stomata.

The bract shows a cuticle essentially similar on both surfaces (Fig. 10A), though the adaxial cuticle is extremely thin. The cells on the bract were elongated and, mostly, in fairly definite rows. Very few stomata at all were seen here and no differences in cell size could be seen distinctly. On the lobes of the cone scale the cells were different. The abaxial surface in both species was fairly thick (1μ or more) and showed cells distinctly and very rare stomata. The adaxial cuticle was so thin that by transmitted light it was invisible before staining, probably 0.5μ or even less. No stomata were seen on it, (Figs. 6C, F, 10D).

A feature of both species is a halo of staining material forming, as it were, a margin to the cell outline. This was not always present (Fig. 10B), and I suspect it is a result of slight under-maceration. In *R. media* the cell outlines were pierced by small holes, such as in some living conifers, e.g. *Microstrobos* (see also Florin 1931).

The seed cuticles were not seen satisfactorily. Despite repeated efforts with rather scanty material, I failed to obtain a seed with cuticles intact; by the time the internal substance was macerated, the very delicate cuticles were destroyed. The best specimens as shown in Figs. 9H-J. Another unfortunate fact is that no pollen could be seen clearly though there are objects that may be pollen in the micropyles. On maceration a great quantity of material dissolved out from the integument region. Possibly therefore the integument was thick, though whether woody or not, is not known.

Within the seed, several layers could be seen. The most disinct lay well inside and away from the micropyle (Fig. 9H) it presumably is the megaspore membrane. In two seeds (Fig. 9I, the other, Pl. 1G was unfortunately damaged) a further line outside the megaspore membrane could be seen, extending from the end of the nucellar beak (see below) to the seed base. This I take to be the outer edge of the nucellus, and since it can be seen so far, it probably indicates that the nucellus was free to the base (cf. Harris 1931). At the micropyle itself four seeds (representing both species) showed a similar appearance. The cutinised outer surface of the integument ends as a sort of collar, and from within this collar there is a further tube of cutin, which, as just noted is continuous with a line lying between the outside edge of the seed and megaspore membrane (Figs. 9H-J). The simplest explanation is that this is a nucellar beak, pro-
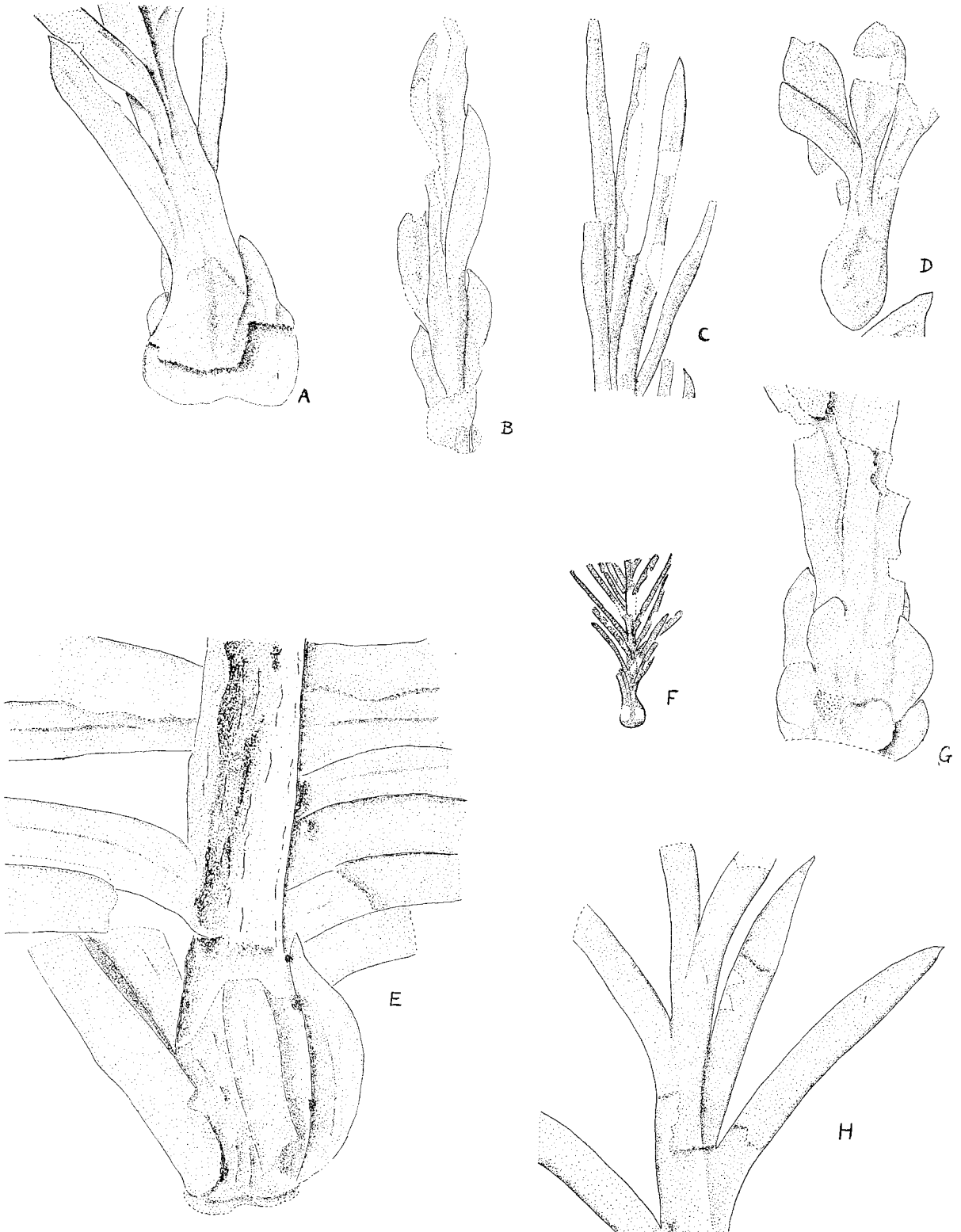
FIG. 4.—*Rissikia media,* A, D, F-H; *R. apiculata,* B. C.; *Elatocladus planus* E. A, B, E-G: Bases of foliar spurs, showing swelling, and small leaves not bilaterally flattened, x 7, F x 2 Australian Museum, F51960, 51976, 51969, 51961; D: A young foliar spur enclosed within the small protective leaves, x 10, Australian Museum F 51976. C, H: Apices of two foliar spurs, no bud to be seen, so growth presumably limited, x 7. C, Australian Museum F51976; H, F51961.

jecting out from inside the micropyle. The beak is now seen as a tube of cutin, and I suspect it was hollow in life, but in default of pollen inside it, or a cutin lining, cannot prove this point. The seeds were about the same width whether compressed dorsi-ventrally (Figs. 9H) or laterally (Pl. 1G). This indicates that they were round in section.

Unlike some conifers, such as *Voltziopsis* Potonié isolated cone units do not seem to occur; at any rate at all frequently. Probably the cone was shed as a unit, and did not disarticulate. This is what happens in *Podocarpus andinus* if the ovules are not pollinated.

The name is for Mr. and Mrs. U. Rissik, Johannesburg and Vergelegen, to whom I am indebted for much hospitality.

Rissikia media (Tenison Woods) com. nov.

Pls. 1A, B, E. F. H; 2A-C. Figs. 1E-J; 2A, B; 3A, D, E, G; 4A, D, F-H; 5A, B; 6A-D; 7C-E; 8B, C, E-J; 9A-E, H, I, K; 10A, C, D, F; 15A, B.

1883 *Taxites medius* Tenison Woods, p. 160-161, pl. 9, fig. 3. Impressions, localised as " Ipswich ".

1927 *Voltzia* cf. *liebiana* duToit non Goeppert, p. 393, pl. 21, fig. 3. Imperfect specimen from the Molteno.

1935 *Voltzia* cf. *heterophylla* Carpentier non Brongniart, pl. 4, fig. 4 (good complete shoot), ?pl. I, figs. 6, pl. 4, fig. 5. Lower Triassic of Madagascar.

?1935 *Voltzia* cf. *heterophylla* Carpentier, pl. 5, fig. 8. Imperfect specimen.

(I have not had access to the works of Geinitz or Szajnocha referred to by Florin 1940 p. 33).

Holotype. MacLeay Museum No. 102: see Tenison Woods 1883 pl. 9, fig. 3, and Fig. 2A.

Locus typicus. Burnera Waterfall, Upper Umkomaas, Natal: Molteno, Upper Triassic.

Diagnosis emended: Plant with foliar spurs about 8 cms. (3-11 cms.) long bearing thirty or more bilaterally flattened leaves of thick substance, about 1 cm. long (0.3-2.5 cms.) and 3 mms. (1.0-5 mms.) wide, twisted into two rows up the shoot. Leaf apex sometimes asymmetrical. Leaves 0.2-0.5 cms. apart. Cuticle of leaf often thicker on one pair of flanks than the other, cell outlines straight, about 1.5μ 1.0μ-2.5μ) thick, rather rarely pierced by small holes. Stomata in rows, separated by terminal subsidiary cells, and up to five other cells, and by at least two cell rows and the lateral subsidiary cells. Guard cells slightly sunken, normally overhung by solid cutin lappets on the subsidiary cells, but lappets sometimes absent. Pollen cone 1 cm. long and 0.5 cms. wide (see generic diagnosis), cell outlines pierced with holes at least on outward surface of scale. Seed cone, 2.5-6 cms. long with 15 to 20 units per cone, units about 0.3 cms. apart. Trifid bract scale about 3 mm. long, cone scale about 6 mm. Lobes of cone scale blunt, thick, sometimes showing shoulders. Two seeds per lobe of cone scale. Seed about 0.75 mms. long and 0.5 mms. wide (0.3-1 mms. x 0.2-0.75 mms), egg-shaped, narrow. Epidermal cells of bract scale somewhat elongated, about 40μ x 60μ; on cone scale more or less equidimensional on both surfaces, about 50μ. Cell outlines rather narrow, 1.0μ or more thick, pierced by holes. Stomata slightly sunken, and surface of guard cells convex inwards.

Description and discussion (1) *General.* The Waterfall specimens are finely preserved, but difficult to transfer. On treatment in HF, the matrix goes to a cheesy mass, tougher than the plant substance, that has to be carefully brushed off. The plant material sticks hard to the rock, and is difficult to remove to obtain cuticles.

As with all the thick organs considered here, the cones split more or less down the middle. This is most important. It means that to see the outside of the cone, a transfer must be made. It also means that to obtain an idea of the whole fossil, part and transfer of counter-part must be put together. Further, there is the danger of overlooking features when only part or counterpart is available.

The leaves are spirally inserted (possibly 3/8) but like many conifers are modified into two lateral rows, apparently by twisting, that is, unequal growth of the leaf base. The leaves, however, are flattened so that they are edge on to the shoot, just as in *Podocarpus imbricatus* (cf. Figs. 3A, E, G). Thus they are bilateral, each apparent surface being morphologically, half the upper and half the lower surface. The leaves, are, however, thicker than seems to be normal in living podocarps with bilateral leaves, some (Fig. 3A) showing several ridges, presumably caused by compression of a thick structure, along their length. At their apices the leaves are probably terete (Fig. 3D). However, in the middle part, even these thick leaves are flattened. The disposition of stomata in four zones, two on each pair of flanks, also agrees with the stomatal distribution in living bilaterally leaved conifers, though the zones are more diffuse than is common (see Florin 1931). The cuticle also shows wrinkling along the margins, supporting the idea that the leaf was thick (Figs. 5A, B). In some of the thickest cuticles, a few papillae on the epidermal cells can be seen (cf. Fig. 5D). These leaves with thick cuticle also show the largest lappets over the stomatal pit.

We only know one kind of pollen cone, and it has been already described (p. 107).

The seed cones are represented by four specimens, two with part and counterpart. To see the outside surface it is necessary to make a transfer of either part or counterpart. Some of these show the trifid bract, (Fig. 8H), and the whole surface of the bract is covered with cellular striae, but no veins can be made out. As already noted, the base of the cone scale was probably thick, perhaps terete, while Fig. 8F shows one cone in which the three lobes are not quite at the same level. Fig. 8G shows another cone scale, which indicates that the three lobes are all part of one structure, since they all spring from one common stalk. Two seeds is the normal number per lobe (Figs. 8F, G) but these may be of different sizes, there may rarely be only one, and, as already discussed, it is likely that only one or two seeds per unit came to maturity, rather as in *Dacrydium franklinii* Hook., where there may be ten or more seeds per cone, but only one or two ripen. Around the apex of each lobe there may be thickening rather like the ornament

FIG. 5.—*Rissikia media*, A, B; *R. apiculata*, C. D; *Elatocladus planus*, E.

A. Cuticle showing cells and stomata in irregular rows, with some wrinkling over the midrib (to left), x 400. Australian Museum AM 6409; B: cuticle near margin (to left) showing cells and stomata x 200, Australian Museum AM 6409; C. D: Cuticle showing stomata, possibly in single row on each flank, and margin (right and central). x 200, Australian Museum, AM 6405, 6406. E. imprint of (probably) epidermal cells and stomata x 100. University Tasmania.

put on the pastry round a pie. (Fig. 8F). The nature of this is unknown. On one cone scale (Fig. 8G) the lobes seem to be raised into a tongue-shaped flap of tissue pointing down over the seeds. The nature of this is unknown, though it is just possible that it might be the first sign of the enveloping epimatium (cf. Pl. 1J).

(c) *The type specimen and synonomy*. *Rissikia media* does not seem to be a common fossil. The original specimen consists of a single block (No. 102, Macleay Museum) showing parts of three shoots, the longest of which is designated as Holotype. The material is badly preserved, but of the right size, and as Tenison Woods (1883) observed the leaves show the impression of a pronounced ridge over the midrib. They are scarcely or not at all contracted at the base, and the apex is pointed, the tip being acute and symmetrically placed (Fig. 2A). The stem also shows the impression of pronounced angles, formed by decurrent leaf bases (cf. Fig. 39). Thus, in the available features, Tenison Woods' specimens agree with the better preserved ones, and is identified with them. His name has priority.

The original locality label reads merely "Ipswich" In Tenison Woods' day it was not fully realised that some of the rocks round Ipswich are Tertiary, unconformable on the Triassic coal measures, so some material labelled simply "Ipswich" is Triassic, and some Tertiary. The holotype of *R. media* is Triassic, for there is a specimen of *Dicroidium odontopteroides* on the block. Since the locality of the holotype is unknown, I suggest, that Burnera Waterfall is considered the *locus typicus*.

Voltzia cf. *liebiana* of du Toit (1927 p. 393, pl. 21, fig. 3) is another badly preserved specimen, from the Molteno. It shows no distinct differences from my material, and is probably identical with it. As Florin (1940) has clearly pointed out, the specimen is not a *Voltzia* and the specific name is wrong. This specimen, therefore, does not affect the nomenclature.

Carpentier's (1935) material from Madagascar is extremely interesting. His pl. 4, fig. 4, shows a complete shoot, with swollen base, that corresponds at every available point with *R. media*, and is therefore identified though we do not know its cuticle. The ascription to *Voltzia* was always uncertain. Carpentier's flora is almost certainly Lower Triassic, and this gives a range for *R. media* from Lower to Middle and possibly upper Triassic (see above p. 105). This is long, but not impossibly so.

Rissikia apiculata sp. nov.

Pl. 1C, D; 2D.   Figs. 1 E-J; 3F; 4B, C; 5C, D; 6E, F, H, I; 7A, B; 8D; 9J; 10B; 14D, E.

Comparable specimens:

1935 *Phyllotheca* sp. Carpentier, pl. 5, fig. 2. Imperfect shoot, agreeing in general appearance.

Derivatio nominis: the pointed apices of the seed scale lobes.

Holotype: Australian Museum F; Pl. 2D. Locality as for *R. media*.

Diagnosis: Plant bearing foliar spurs 5-8 cms. long, spurs bearing twenty to forty leaves, rhombic in section, of more or less thick substance, about 5

mm. (4 mm.-10 mm.) long, not or only vaguely twisted into two rows up the shoot, and sometimes more or less appressed to shoot. Leaves about 5 mm. apart. Cuticle of leaf often thicker on one pair of flanks, showing cell outlines usually somewhat wavy, or else, if straight, very thin, (less than 1μ), outlines not pierced by holes. Stomata probably in 4 zones, each zone sometimes only one stoma wide, stomata separated by shared terminal encircling cell, or more than one terminal encircling cell. Guard cells only slightly sunken, surface about flat. Subsidiary cells bearing hollow cutin papillae, over-hanging, or not, the stomatal pit, sometimes only some subsidiary cells with papillae. Epidermal cells sometimes ornamented with solid cutin papillae.

Seed cone about 3 mms. long, probably with 12-15 units about 0.25 mm. apart. Bract about 1.5 mm. long and cone scale about 2.5 mm. Lobes of cone scale produced into a long point; the central lobe probably longer than the laterals. One seed only per lobe of cone scale.   Seed about 0.5 mm. long at 0.25 mm. wide, more or less oval. Epidermal cells on bract, rectangular, about 30μ x 50μ; on cone scale cells elongated, about 40μ x 60μ; cell outlines thin, or minutely wavy, not pierced by holes, 0.5μ or less thick. Stomata not convex inwards, sometimes showing cutin papillae on subsidiary cells. Other epidermal cells very rarely papillate.

Description and discussion. (1) *General*. The leaves are always spirally inserted, but there is a good deal of variation in the way in which they are borne. Most commonly the leaves are borne all round the stem (Pl. 2D, Fig. 3F); however, in specimens with larger leaves there is a distinct tendency for the leaves to fall into two rows (Fig. 7B). It is interesting also that such shoots with larger leaves, in two rows, also tend to have slightly flattened leaves, in this grading into the normal situation in *R. media* (Fig. 7A). The correlation between larger leaves, borne in two rows and flattened has exceptions; Fig. 7B shows a specimen with long leaves, but (almost certainly) rhombic in section. The leaves are described as rhombic in section when they show a ridge down the (apparent) middle.   The apices are generally pointed, and symmetrical (Fig. 4C).

The cuticle could only be prepared in small pieces, but certain of the larger fragmenst (e.g. Fig. 5D) show wrinkling both at the margins of the leaf, and down the middle. These wrinklings are (presumably) caused by compression, so their position supports the suggestion that the leaf was thick and rhombic in section. As in *R. media* the stomata are rather spread out, but there is the strong suggestion that they are in rows (Figs. 5C, D) apparently set in four zones, near to the margins, and thicker portion of the leaf over the midrib. However, in some of the smaller specimens each zone probably only consists of a single row of stomata, and their placing is not nearly so regular as in *Dacrydium elatum*, which has rather similar leaves. The cell outlines vary considerably. On the thinner cuticles they are straight, or nearly so, on the thicker cuticles, however, wavy (Figs. 6H), not because of cutin projection, but because the whole wall including the middle lamella is sinuous. Holes, such as are seen in *R. media* are very rare
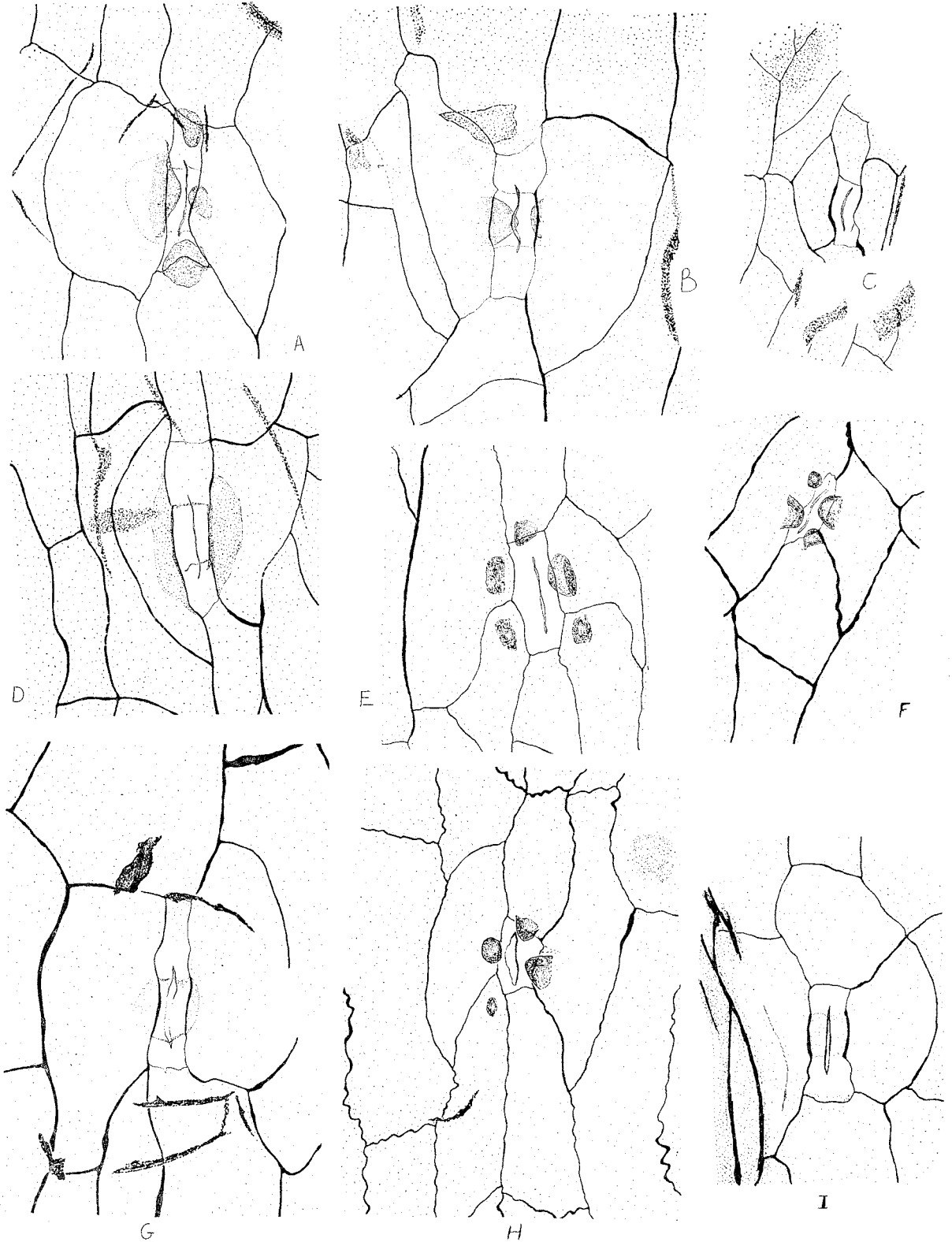
FIG. 6.—*Rissikia media*, A-D, G; *R. apiculata*, E, F, H, I.

A, B, Stomata from the leaf, with surrounding cutin lappets, and subsidiary cells, Australian Museum, A.M. 6408, 6409; C. Stoma from the scale of a pollen cone, Australian Museum AM 6412; D: stoma from leaf, without ornament around it. Australian Museum F51962; E, F, H, stomata from leaf or seed cone (F), showing hollow cutin papillae around stomata pit, Australian Museum F51978, AM 6404, 6468. I: Stoma from leaf without surrounding ornament, Australian Museum F51976 all x 600.

indeed. Around the stomata, on the thicker cuticles, there are hollow papillae, often one per subsidiary cell. These are seen to be hollow because, unlike the lappets of *R. media*, a wall and lighter coloured, and therefore hollow interior can be made out (Figs. 6H). On the thinner cuticles the size and number of the papillae decreases, and some stomata show none (Fig. 6I). Papillae, but solid, also occur on the surface of the epidermal cells.

The female cone material consists of two incomplete specimens. One (Fig. 8D) shows a leafy stalk, on which the cone was terminal, fretted away at the base, indicating that the cone was not abscissed. The interpretation of the specimens depends much upon the interpretation placed on the *R. media* cone. The bract scale was certainly deeply lobed, and in Fig. 14D, a cone unit laterally compressed shows on one side two lobes to the bract scale, and on the other tissue which, from its level and position, is most likely a third lobe of the bract scale. As in *R. media* the cone scale consists of three lobes. In Fig. 14E they are seen adaxial surface towards the observer, and elsewhere, three stalks, joined below (Fig. 14D) which indicates that the three lobes, as in *R. media* were joined to one common axis below. So far as can be seen, the central lobe may have been larger than the two lateral ones. However, there seems to have been only one seed per lobe, though this observation is based upon only three units, two of which are shown in Pl. 1D and Fig. 14E. Some lobes, indeed show no sign of a seed, and it may be that sometimes there were less than 3 per unit. The lobes are only of moderately thick substance, and end in a long point (Fig. 14E, Pl. 1D). The seeds themselves, to judge from only two examples, were like those of *R. media*, though perhaps more elongated (see the imprint in Fig. 14E). One lobe, (Fig. 14D top right) shows the two ridged appearance already discussed, and interpreted as perhaps indicating the presence of two vascular strands.

The position and general appearance of the cuticles is as in *R. media* and again, for the most part, the cuticles are extremely thin. In one unit, however, the abaxial surface of a seed scale lobe was thicker than usual, and showed slightly sinuous cell outlines, and hollow papillae over three or four stomata. On the thin cuticles, however, only two stomata were seen; in them the guard cell surface appeared to be quite flat.

COMPARISON OF THE GENUS

(1) *Comparison of macrofossils.* No conifer comes very close to *Rissikia*, the following are moderately similar. *Voltzia* Bgt Florin (see Florin 1938-1935; 492-492, pl. 181/182). The young cone is not spike-like, but the cone does elongate as it grows older. The cone unit consists of a simple bract scale, and five scales, three associated with seeds, which form the cone scale. *Voltziopsis* Potonié (Florin 1944) has a cone unit showing a forked bract and five lobes to the cone scale, each bearing an inverted seed on the end of an adnate stalk. *Pseudovoltzia* Florin (Florin *loc. cit.* p. 479-484, pls. 179 and 180 and Schweitzer 1963). The cone is ellipsoidal in outline, and the cone unit consists of undivided bract scale, subtending an axis, produced into three lobes associate with two

(or ? 3) inverted seeds, and two sterile lobes behind them.

Tricanolepis Roselt (1958) consists of three species *T. hoerensis* (Antevs), *T. frischmannii* and *T. monosperma*. In *T. monosperma* the seed cone is an elongated spike-like structure. The units in all species consist of a three pointed cone scale, borne on a somewhat elongated stalk, and divided for only about a quarter of its length. In all the bract appears to be adnate on to the cone scale. In *T. hoerensis* (e.g. Florin 1944, pl. 81-82, figs. 19, 20) and *T. frischmannii* there are three seeds, one per lobe of the cone scale, but in *T. monosperma* only one. Cuticular details are unavailable, though Roselt describes an embryo, so comparison with *Rissikia* is on general form only. And it is close. The chief difference is that in *Rissikia* the bract is free. Lesser differences are that the lobes of the cone scale are more deeply divided in *Rissikia*, though *T. hoerensis* comes close; and that in *R. media* all six seeds are borne at the same level, while the same is (probably) true of *R. apiculata*, whereas in *T. frischmannii* the seeds lie at different levels. However, in *T. hoerensis* the seeds lie at one level. Both genera display a trimerous arrangement of parts (or with reduction of the seed to one), a point discussed below.

I doubt whether any other of the fairly numerous fossil conifer cones is close enough to cause confusion, though several show one or two points of similarity, for example *Cheirolepidium muensteri* (Schenck) Takhtajan has peltate but not radially symmetrical scales on its pollen cone, like *Rissikia* (see Harris 1957) but is otherwise quite dissimilar. None of the foregoing genera have bilaterally flattened leaves. *Cycadocarpidium* Wieland has tripartite units to its seed cones, but the appearance of the parts is quite different (Frenguelli 1944c, Florin 1944).

The three Southern Permian conifers are also distinct; they show irregular branching, and the leaves and stomatal arrangements are also different (see Florin *loc. cit.* pls. 161-162 and 165-166 for *Buriadia* and *Paranocladus* and 1940 for *Walkomiella*) though the stomata of *Buriadia* and *Paranocladus* may resemble slightly those of *Rissikia*. *Walkomiella* also differs in its seed (see Surange and Prem Singh 1952).

Lebachia, and *Ernestiodendron*, the "walchias", though possibly foreshadowing the sort of structure shown by *Rissikia*, especially in branching pattern are distinct, at the generic level. The bilateral leaves of *R. media* separate it, at least from most Mesozoic conifers.

Genoites Feruglio (1942) looks at first much like the shoots of *Rissikia*, but may be distinguished by its leaves, which are divided into two over most of their length. Dr. S. Archangelsky tells me that this material is Permian not Liassic: with this age it looks similar to *Buriadia* Seward and Sahni.

(2) *Comparison of the pollen.* The striate disaccate pollens are very numerous and difficult. Somewhat arbitrarily, two groups are taken, very similar to *Rissikia*, and similar but distinguishable, and the large remainder, with which confusion is not very likely is ignored.

FIG. 7.—*Rissikia apiculata*, A, B; *R. media* C-E; *Dacrydium laxifolium*, F.

A, B: Parts of two shoots showing somewhat flattened leaves not much twisted into two rows (A), and thick leaves more or less strongly flattened into two rows (B) x 7. Australian Museum F51977, 51981, 40. C. Base of the cone, showing stalk and sterile units; D, E: Part of the cone showing scales from outside and seen laterally, and pollen sacs, all x 7, Australian Museum F51970, 51971 (cone). F: A cone unit showing two pollen sacs, and scale with tiny projection downwards, not attached to the pollen sacs. x 7. *P* = pollen sacs.

The very similar group consists of *Taeniaesporite krauselii* Leshik and also *T. noviaulensis* Leshik and a group of species centred about it. *T. krauselii* Leshik (1955 pl. 8, figs. 1-6) shows a rounder corpus than *Rissikia,* and fewer striae, but there is much overlap (Leshik fig. 2 and Fig. 9E, and Leshik fig. 3, and Fig. 9A), and I can see no character that separates the pollen grains satisfactorily. It might therefore be that one should use the specific name *krauselii* for *Rissikia media* but in ignorance of the plant producing *T. krauselii* pollen this would be unwise.

The grains centred about *T. noviaulensis* are difficult; they are taken here to be: *T. noviaulensis* (Leshik 1956, pl. 22, figs. 1 and 2); *T. cf. noviaulensis* Balme (1936, pl. 6, figs. 4-6): *T. novimundi* Jansonius (1962, pl. 13, figs. 19-25, except figs. 22 and 23: *T. interruptus* Jansonius (1962, pl. 13, figs. 26 and 27): *Striatites samoilovichi* Jansonius (1962 pl. 14, figs. 9-11): *S. samoilovich-pantii* Jansonius (1962 pl. 14, figs. 14 and 15: and *S. samoilovich-pantii* Jansonius) Klaus 1963, pl. 14, figs. 71-72): *T. ortisei* Klaus (1963, pl. 14, figs. 67-70): *T. labdacus* Klaus (pl. 13, figs. 65 and 66). In general these species differ from *Rissikia* in having sacii bulging beyond the corpus (polar views) and separated on the distal surface by a germination area more than half as wide as the whole corpus. Certain of them differ in number and sort of striae, or other ornament, but this is so variable in *Rissikia* that I place no reliance on it. The use of Schultze's mixture also introduces a variability that cannot easily be measured (Townrow 1962).

Another pair of rather similar grains is *Taeniaesporites alatus* Klaus (1963, pl. 13, figs. 62-62) and *Stratites marginalis* Klaus (1963, pl. 17, figs. 80 and 81). These two species differ from *Rissikia* in having (like *T. noviaulensis*) a wide germination area, and (unlike *T. noviaulensis*) sacci that do not bulge beyond the end of the corpus.

Certain of the species just discussed show the (possible) monolete mark, also rather rarely shown by *Rissikia.* Klaus (1963) was the first to give attention to this structure, and, for the present I do not utilise it as a character of taxonomic value (see p. 107).

The grains mentioned above are so similar to one another, and to *Rissikia,* that, with Balme (1963: 37), I think it likely that they form a "natural group" whether genus or group of genera one cannot say. For example, to take an argument by analogy, the pollen of four species of *Pteruchus* Thomas (see Townrow 1962a) and *Pteroma* Harris (1964) all placed in the Corystospermaceae, show a similar range of variation. So does the pollen of very similar group of species forming the sub section D. of Eupodocarpus (Gray 1956). These grains are non striate. *Arberiella* Pant (see below) has two species but there are not clear analogies to argue from among striate pollen. However the range of variation in *Rissikia* ties together the isolated grains just compared with it, into one group. If indeed these pollens form a natural group, its range is Upper Permian to Upper Triassic in the Northern Hemisphere, and perhaps basal Triassic into the Jurassic in the Gondwana region (Balme 1963).

The group of similar but distinguishable grains falls into several smaller groups; these are (as here taken):

(a) *Taeniaesporites albertae, T. gracilis, T. hexagonalis* and *Striatites rugosus* all of Jansonius (1962), with *Luekisporites multistriatus* Balme and Hennelly (1955, pl. 2, figs. 16-20), form a closely allied group, differing from *Rissikia* in having a corpus up to half as wide again as deep, instead of more or less round, and sometimes bluntly angled. As in *T. noviaulensis* the germination area is more than half as wide as the corpus.

(b) *Taeniasporites transversundatus* Jansonius (1962), *Striatites nubilus* Leshik (1956, pl. 21, fig. 14, also Jansonius 1962 pl. 14, fig. 20), *T. obex* Balme (1963) and *Luekisporites cancellatus* Balme and Hennelly (1955, pl. 12, figs. 11-15) differ from *Rissikia* in having a small round corpus, overlapped in the *Platysaccus* Naumova manner, by the sacci. *L. cancellatus* looks colpate in the figures, the rest are leptomatous.

(c) *Strotersporites richeri* Klaus (1963, pl. 15, fig. 76-66), *S. jansonii* Klaus (1963, pl. 15, fig. 74 and pl. 16, fig. 78) *S. wilsoni* Klaus (1963, pl. 16, fig. 77) with *Striatites jacobii* Jansonius (1962, pl. 14, figs. 16 and 17, Klaus 1963, pl. 16, fig. 79). *Taeniaesporites antinquus* Leshik (1956, pl. 22, figs. 4 and 5), *T. cf. antiquus* Balme (1963, pl. 16, fig. 13), and *Striatites dussenii* Jansonius (1962, pl. 14, fig. 13 only), form a group differing from *Rissikia* in being about twice as large.

Those referred by Klaus (1963) to *Strotersporites* Wilson show a monolete mark of the sort already mentioned, but while in *Rissikia* this mark (where present) is about a quarter as long as the corpus is wide, in Klaus' grains it traverses about the whole corpus.

It is beyond the scope of this note to discuss the extremely difficult and complex taxonomy of triate pollens, a subject discussed at length by Samoilovitch (1953), Makjavkina (1953), Potonie (1958), (Wilson (1962), Jansonius (1962), and Hart (1964, 1965). Now that some striate grains are ascribed to a parent plant, some points arise however.

It is now known that *Arberiella* Pant (possibly a glossopterid), and the conifer *Rissikia media* had striate grains. It is therefore clear that the habit arose at least twice, independently.

When one considers *all* available charactrs, striae, siz, corpus and saccus shape, and germination area, the two sorts of striate grain known to belong to different plants, are fairly easily distinguishable. However, the grains whose parent organ is known (both striate and non striate) suggest that efforts to draw generic boundaries using only some features, e.g. striae are ill-founded. Thus grains from one pollen sac of *Rissikia media* would fall into both *Striatites* Pant and *Taeniaesporites* Leshik as e.g. Jansonius (1962) defines those genera. If my earlier assessment is correct, one species of *Arberiella* was striate, the other was not (Townrow 1962).

Examination of grains much like *Striatites sewardii* (Virkki) Pant, now *Protohaploxypinus* Hart (1964), suggest that it is colpate. Virkki's (1937) fig. 2A and 3A shows, I believe, a colpate grain presented

FIG. 8.—*Dacrydium franklinii*, A; *Rissikia media*, B, C, E-J; *R. apiculata*, D.

A, A pollen cone, showing sterile units at base (to left and right). x 7. B, Base of pollen cone, stalk with remains of leaves, and sterile units at cone base x 10. Australian Museum F51970 51971; C, D, E: Seed cones, showing parts of the leafy stalks on which the cone is terminal. All x 3, F, Apex of a cone, unit seen face on to observer. G: Cone unit, face on to observer; H: Part of a cone unit, seen from abaxial side, showing bract and part of unit in lateral view; I. Cone units seen in lateral view, wrapping round cone axis (left) and in abaxial view, showing two ridges (left). J. lower part of a cone, and leaves on cone branch, all x 7. C, G. H, Australian Museum F51974: E, F, J, I, Australian Museum F51975: D. Australian Museum F51983.

in a somewhat rotated proximal polar view (not a lateral longitudinal view as Potonie's (1958) copy might suggest). Pl. 1I and Fig. 10E show a closely similar grain in similar views. Hart (*loc. cit.*) has utilised this feature, though probably misinterpreting it as a keel, but it may be of wider use when looked for.

Finally, to compare *Rissikia* pollen at the specific level, one has to combine several species into groups, (above), and I imagine that, if isolated, the grains of *Rissikia* would be disposed in four to eight species. There seems to be little object in making the species limits as narrow in isolated grains as seems to be usual. Balme (1963) who took a wider view of a species, is, I think, more likely to be right, (cf. the grains of *Pteruchus* and *Caytonanthus* (Harris, 1964, Townrow, 1962).

DISCUSSION OF THE GENUS

(1) *Ascription of the organs at the specific level.* Since both species are known in fair number only from the Waterfall locality, ascription of cones to foliage rests on anatomical resemblances only, i.e. upon rather minute and sometimes variable features. Also the cuticles of the cones are usually thin, and as already noted, when thin, even the leaf cuticles become difficult if not impossible to separate. The most widespread character is the nature of the cell outlines. In all organs named *R. media* the cell outlines are not sinuous, but are pierced with holes (though these may be few) and tend to be thick and of slightly indefinite margin. The cone named *R. apiculata* shows, at least sometimes, sinuous cell outlines, the outlines are not pierced with holes, and are very thin but of definite margin (Fig. 10B). This sort of difference has less taxonomic value than those based on stomata, but it can be used to separate, for example, the two species of *Microstrobos* Garden and Johnston. However, as noted, a few stomata of *R. apiculata* cone do show the hollow papillae characteristic of the leaf. This tends to tie that leaf and cone together; by elimination, the other sort of cone belongs with the *R. media* foliage. This generalisation is based upon less than 12 stomata all told on both cones.

(2) *Shoots similar to Rissikia, and comparison of the whole group of shoots.* From rocks of Jurassic and Triassic age there are other shoots, closely similar to *Rissikia*, the whole forming a somewhat easily recognised assemblage.

They are—

(*a*) unbranched, possibly deciduous, short shoots; i.e. a long shoot/short shoot system;

(*b*) long (1-8 cms.) narrow (0.25-2 mm.) bilateral leaves, more or less strongly flattened into one plane;

(*c*) the base of the shoot either leafless, or showing some leaves rhomboidal in section passing into bilaterally flattened leaves. (*R. apiculata* flattening slight or none);

(*d*) stomata, where known, disposed in four wide rows, and about equally numerous all over the leaf;

(*e*) stomata monocyclic, subsidiary cells few, not touching in adjacent stomata.

At the specific level separating the shoots is difficult, largely because microscopic detail is unavailable for many specimens. For the present, it will probably be best to define the species rather widely, frankly recognising that this procedure is unsatisfactory, but inevitable. On this basis, two species can be usefully separated.

Elatocladus planus (Feistmantel) Seward
Figs. 2C, D; 3C; 4E.

Selected references:—

1879 *Taxites planus* Feistmantel, p. 31, pl. 13, figs. 1, 2-8. pl. 14, figs. 1-5, pl. 15, fig. 2. Good Indian Jurassic material.

1882 *Taxites planus* Feistmantel, pp. 48-49, pl. 2, figs. 7-11. Upper Jurassic.

1902 *Palissya gracilis* Shirley, p. 8, pl. 2. From Stanwell, Queensland. Jurassic or Cretaceous: see Hill and Denmead 1960, p. 333.

?1913 *Elatocladus* sp. Halle, pl. 9, fig. 7, Hope Bay, Antarctica, Jurassic.

1917 *Taxites planus* Feistmantel, Walkom, p. 25-26, pl. 9, fig. 4. From Stanwell, (correlated with Walloon, but species has not been recorded in the Walloon of the type area).

?1917 *Elatrocladus* sp. Arber, pl. 13, fig. 9; Waikawa, New Zealand, Jurassic.

1918 *Elatocladus plana* Feistmantel, Seward, p. 432, fig. 802. Change of name.

1919 *Cycadites* sp. Walkom, p. 187-188, pl. 7, fig. 5. Part of leaf, Bexhill near Lismore, Jurassic.

1921 *Elatocladus planus* Feistmantel: Walkom, p. 14-15, pls. 4, figs. 1-4, pl. 5, figs. 1-3. From Talbragar, New South Wales, locality dated as lower Jurassic on its fish fauna.

1928 *Elatocladus planus* Feistmantel: Sahni, pp. 11-12, pl. 1, fig. 9, Good leaf base.

1928 *Elatocladus tenerrima* Feistmantel pars. Sahni. p. 11. Revision of Indian material.

1940 *Elatocladus planus* Feistmantel: Florin, pp. 43, 51-53, 59-66. Extended discussion, no new material.

Indeterminable, probably distinct.

1919 *Elatocladus planus Walkom,* ?non Feistmantel, pp. 43-44, pl. 2, figs. 4, 5. Lower Cretaceous, Burram, Queensland. Fragments showing probably bifacial not bilateral leaves.

Holotype: Feistmantel 1879, pl. 13, figs. 1, 1a.

Locus typicus: Venaravum, near Madras.

Description and Discussion. Material examined comes from Talbragar, Bexhill near Lismore and Bugaldie in New South Wales (where the shoot appears to be widespread), also there is a shoot from Stanwell, Queensland, and two from the Rajmahal Hills, India. This material is in the collection of the Australian Museum.

The foliar spurs are large, 8-15 cms. long, and show numerous leaves, which are generally close set, sometimes so that their margins touch, and like most of the group, the leaves are strongly
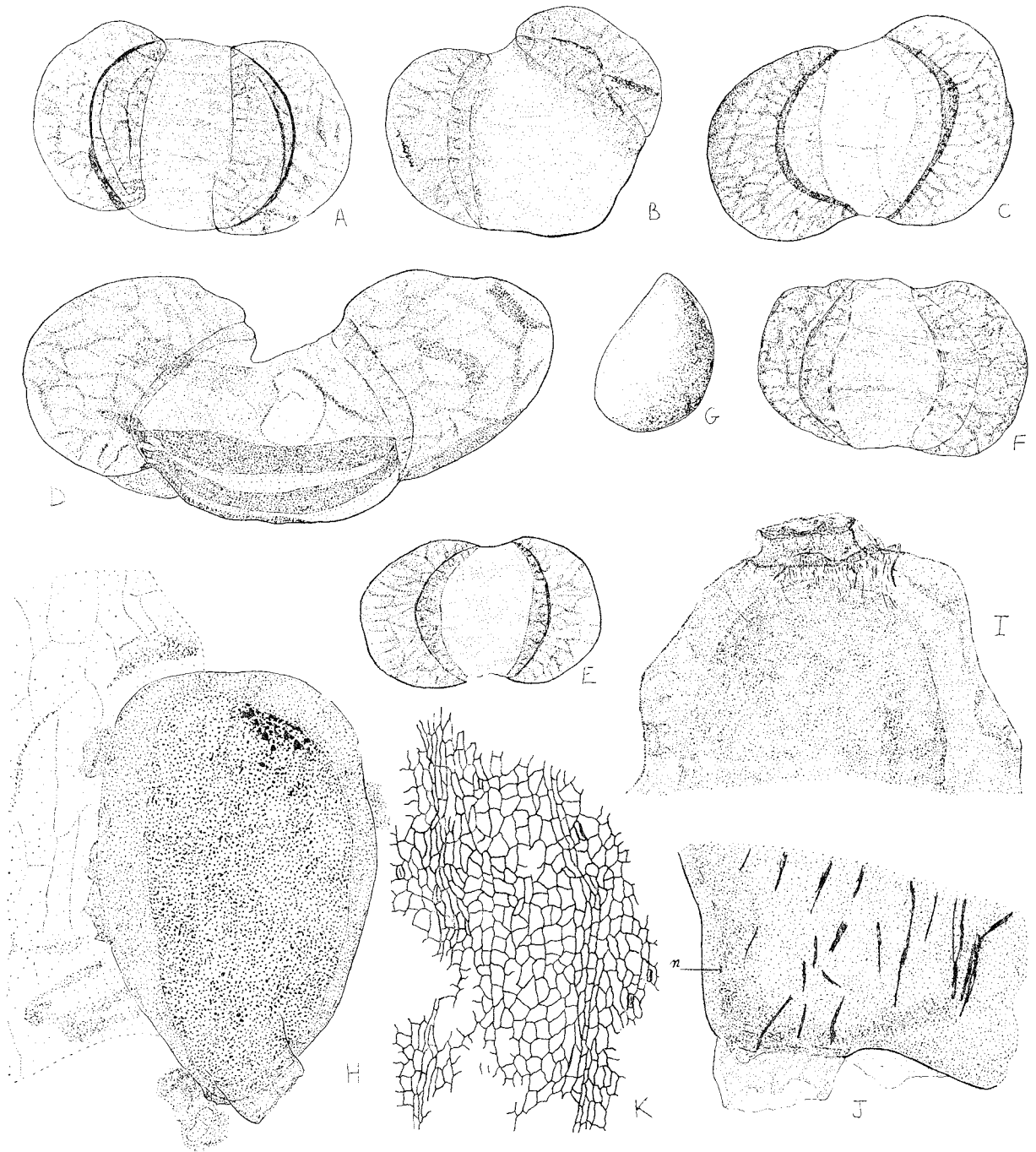
FIG. 9.—*Rissikia media*, A-E, H, I, K; *R. apiculata*, J, cf. *Luckisporites multistriatus* of Balme and Hennelly (1955), F; *Mataia podocarpoides* G. A, C, E: Pollen grains in polar view, with many striae (A), with none but a small crack or (?) monolete mark (C), or with few striae (E). B, D, grains in lateral longitudinal view, showing intact cappula, and variation in striae. F: Grain in proximal polar view, all x 600, except D, x 1,000. Australian Museum AM 6412: F Liveringa Frm. W. Australia, prep. Dr. B. E. Balme. G. A seed, similar to the seeds found in the cone, x 10 Canterbury Mus. 2517. H: A seed, partially macerated, showing seed stalk (curving to lower right), behind it micropylar regions and ? pollen. x 50. Australian Museum, F 51974. I: Micropylar region of a seed, showing broken end of seed stalk covering integument and supposed nucellar projection x 70, Australian Museum, AM 6408. J: As I, showing line *n* believed to represent the edge of the nucellus, free from integument (heavy lines = cracks). x 70 Australian Museum F 51983. K: Cuticle from abaxial surface of seed scale complex showing lines of elongated cells (? over veins) and stomata. x 100. Australian Museum AM 6408.

flattened in one plane. The leaves are bilaterally flattened, and show parallel margins, tapering only at the extreme end, and uncontracted at the base (see Walkom 1925, pl. 4, figs. 2 and 4, and Figs. 3C, 4E, Walkom's pl. 4, fig. 2 appears to be mounted upside down). The apex is pointed, the apiculus being set more or less symmetrically (Fig. 3C).

In most figures and some material (e.g. Talbragar) the leaf looks flat and of thin substance, but other shoots otherwise similar show a strongly projecting midrib (e.g. from Bexhill). In one or two specimens from Talbragar, e.g. that shown in Fig. 2C, the plant material has been replaced by some siliceous mineral, giving, with the impression, the contour of the leaf. The leaf appears to have been strongly flattened, but substantial, and to have shown a distinctly projecting, but narrow midrib.

For the most part the replacing mineral shows rows of more or less equidimensional honey-comb like " cells " whose shape may have nothing to do with the cells of the plant, but in a few places, the outermost surface of the mineral shows a different pattern, elongated prints of cells, certain of which are set in an arrangement interpreted as the imprints of stomata (Pl. 2E, Fig. 5E). On this evidence, the stomata lay in two wide vaguely defined zones, and were well separated within these zones. The stomata are monocyclic and seem to show four subsidiary cells, as a general rule, but this sort of detail is extremely difficult to make out.

On one specimen (F. 38830, 38831, Australian Museum) there are two indistinct objects that might be parts of the seed cone, but they, like the various objects figured by Walkom (1921a), are too obscure to yield definite information about their nature.

The information is not enough to delimit the species satisfactorily and in fact it almost certainly will prove to be composite. The figured Indian specimens, and those from Stanwell, seem to show a smaller shoot with narrower leaves than the shoots from Talbragar. However, without more material and microscopic detail, I think an attempt to divide up the species would be premature.

As here understood, E. planus appears at the base of the Jurassic (Talbragar), and extends into the Upper Jurassic (Jabalpur series), being found in India, Australia, and probably New Zealand and Antarctica. Walkom's (1919) record from the Burrum (Lower Cretaceous) is probably distinct, but indeterminable.

E. planus can be separated from Rissikia media because it is a larger shoot, has flatter and (often) closer set leaves, and also on its base, which shows only few (2-4) leaves rhomboidal in section (Fig. 2C). There is, however, a good deal of overlap.

Elatocladus australis Frenguelli

Figs. 2E, 3B.

1944 *Elatocladus australis* Frenguelli, pp. 300-303, pl. 1, figs. 1-3. Holotype: Frenguelli loc. cit. pl. fig. 1.

Locus typicus: Cerro Bayo de Potrerillos, Mendoza, Argentine.

Description and Discussion. The only material I have seen consists of F. 50190-50193 in the Australian museum, originally from the Geological Survey of New South Wales. There is no information on the locality of the specimens.

The shoot is small (about 4 cms.) and shows rather well separated short (1 cm. or less) leaves. The leaves are bilaterally flattened, and strongly contracted at the base (Fig. 3B). The margins are not parallel, but bulge out slightly, a feature well seen in Frenguelli's material. The apex is obtuse, but shows a small, often curved apiculus, set usually a little nearer the basiscopic edge of the leaf (Fig. 3B and see Frenguelli pl., fig. 2, leaves 6, 8, and 9 on right).

Frenguelli's specimens have some plant material left, and in the figures the leaves look strongly flattened. In my material there is no plant material but the impression shows, much as in *E. planus*, a substantial but flat leaf, with a narrow distinct ridge over the midrib (Fig. 3B). The iron-stained impression shows the honeycomb-like pattern of the replacing mineral of *E. planus*, and also, but much more obscurely, the prints of epidermal cells and possibly, stomata, much as in *E. planus*.

The identification of my material with Frenguelli's is not certain, but the shoots agree in available features, and differ from the others of the group in the same way. These differences are definite enough, I think, to make it desirable to recognise a species, and they are: from *R. apiculata*, which in leaf size and spacing *E. australis* resembles, the leaves are flattened; and from *R. media* and *E. planus*, the shoot is smaller, (but there is overlap), the leaf base contracted, the leaf margins not parallel, and the apex obtuse, but with the apiculus not symmetrically set (compare Figs. 2E, 3A). Bonetti (1963, p. 38) compares *E. australis* with *E. conferta* (here renamed *Mataia podocarpoides* (Ett.)), but to judge from the figures the two shoots differ widely, for *E. australis* has bilateral leaves, but *M. podocarpoides* bifacial ones.

As noted in the preceding section, the two species of *Rissikia* and the two of *Elatocladus* considered are closely similar. I hesitate, however, to place them all in *Rissikia* until the cuticular detail of the *Elatocladus* species is properly understood. Probably, however, when more fully known, these four species will be disposed in one genus.

Table I sets out a comparison between the four species. As between the cuticles of the two *Rissikia* species the most constant difference, but not the easiest, is in the presence or not of holes through the cell outlines. An easier distinction, where present, is between solid or hollow papillae on the subsidiary cells. Thin cuticles, however, whether of cone or leaf, are scarcely distinguishable.

There are other supposedly bilaterally leaved conifers, but of Jurassic age, and these are comparable with *Rissikia*. They are *Elatocladus heterophylla* Halle (1913) and *E. tennerrima* of Sahni (1928). *E. tennerrima* (and *E. heterophylla*) is a branched shoot system, like an older shoot of *Podocarpus dacrydoides* (Fig. 2H), without clear separation into long and short shoots, and the stomata, though present all over the leaf, are much more abundant on one pair of flanks, and they are close set in rather regular rows (Sahni 1928, Florin 1940). *Retinsporites indica* Holden is extremely close to *Acmopyle* (see Florin 1940), and confusion with *Rissikia* is unlikely.
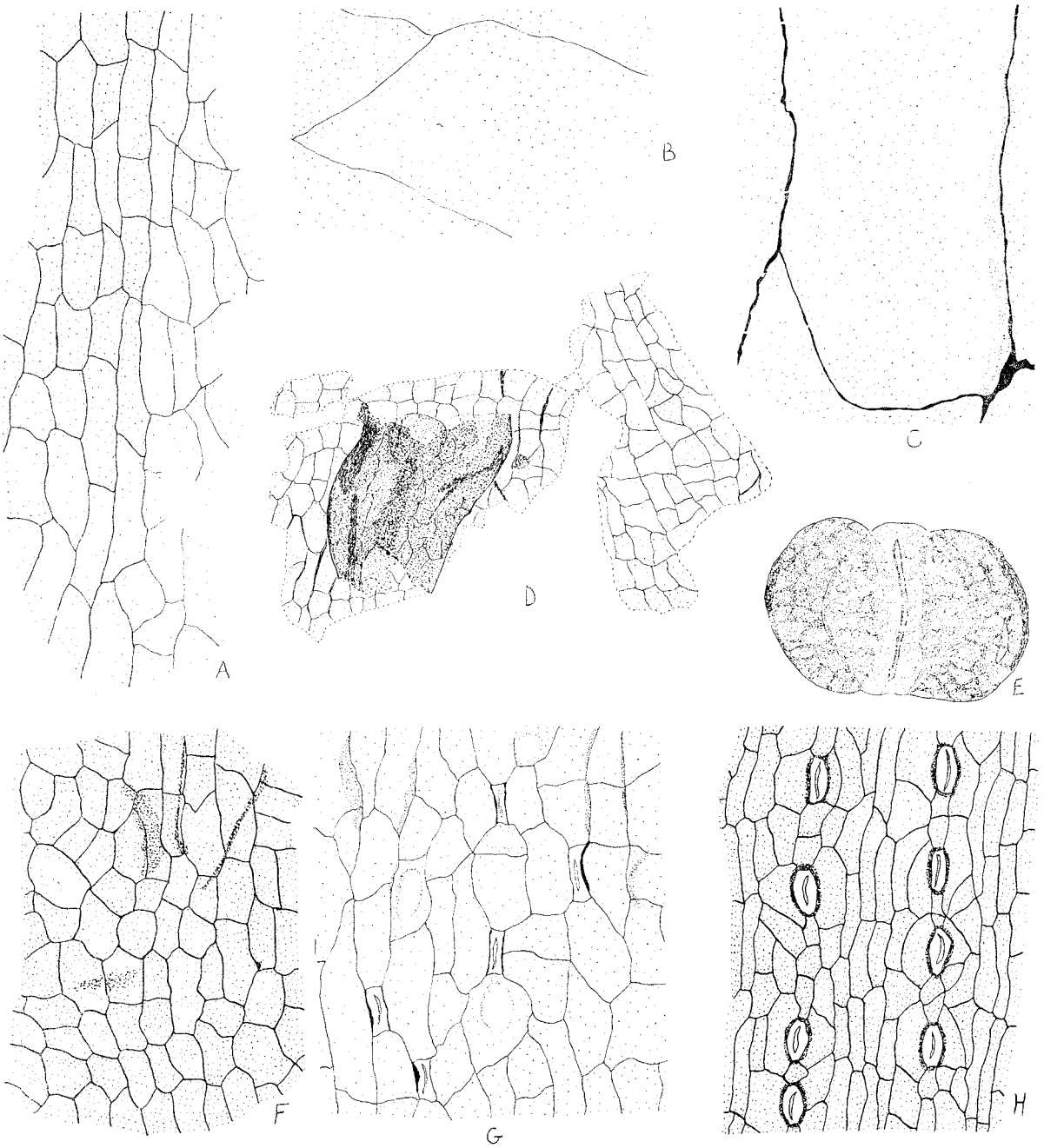
FIG. 10.—*Rissikia media*. A, C, D, F; *R. apiculata*, B; *Striatites sewardii* of Pant, E: *Metasequoia glyptostroboides*. G: *Podocarpus imbricatus*, H. A: Cuticle from cone scale, lower surface to left. x 200. Australian Museum AM 6408; B. C: Cells from seed cone showing slight difference in form of the cell outlines x 1000, Australian Museum AM 6407, 6408; D: Adaxial surface of cone scale, showing cuticle, and tube of cutin (seed stalk) lying over cutin but shown to be separate by large spore between tube and cutin. x 100 Australian Museum AM 6408; E: Grain in proximal polar view x 500, Liveringa Frm. W. Australia. Prep. Dr. B. E. Balme; F: epidermal cells from outward surface of cone unit x 100, Australian Museum AM 6412; G, H: Cuticle of species shedding leaves annually (G) or at a longer interval (H) x 200.

TABLE

SPECIES OF *RISSIKIA* AND *ELATOCLADUS* COMPARED.

|	Shoot	Leaf	Leaf Cuticle	Seed Scales	Cone Cuticles
RISSIKIA MEDIA	Shoot about 7 cms. long (3-12 cms.)	Leaf thick but bilaterally flattened, margins parallel, not contracted at the base, apex symmetrical. Leaves about 3 mm. apart, 1 cm. long, and 2 mm. wide.	Outlines straight with holes, stomata with solid cutin lappets. Epidermal cells smooth.	Lobes obtusely pointed, sometimes dentate with two seeds per lobe. Lobes all about same size.	Cells—equidimensional on seed scale; stomata without cutin ornament. (Otherwise as per leaf).
RISSIKIA APICULATA	Shoot about 7 cms. long (3-16 cms.)	Leaves rhomboidal in T.S., margins parallel, not contracted at base, apex symmetrical. Leaves 3-5 mm. or less apart, 0.5 cm. long, and 1 mm. wide.	Outlines sinuous or (rarely) straight without holes, stomata with hollow papillae. Epidermal cells with solid papillae sometimes.	Lobes sharply pointed, not dentate, one seed per lobe, and central lobe larger than lateral ones.	Cells more or less strongly elongated on seed scale. Few stomata with hollow papillae (otherwise as for leaf).
ELATOCLADUS PLANUS	Shoot about 12 cms. long (5-18 cms.)	Leaves thick, but strongly flattened, margins parallel, not contracted at the base, apex symmetrical. Leaves 2 mm. or less apart, 2 cms. or more long, 204 mm. wide.	No information.	No information.	No information.
ELATOCLADUS AUSTRALIS	Shoot about 4 cms. long (3-5 cms.)	Leaves thick but strongly flattened, margins not quite parallel, leaf contracted at base, apex not symmetrical. Leaves about 3 mm. apart, 1 cm. long, 2 mm. wide.	No information.	No information.	No information.

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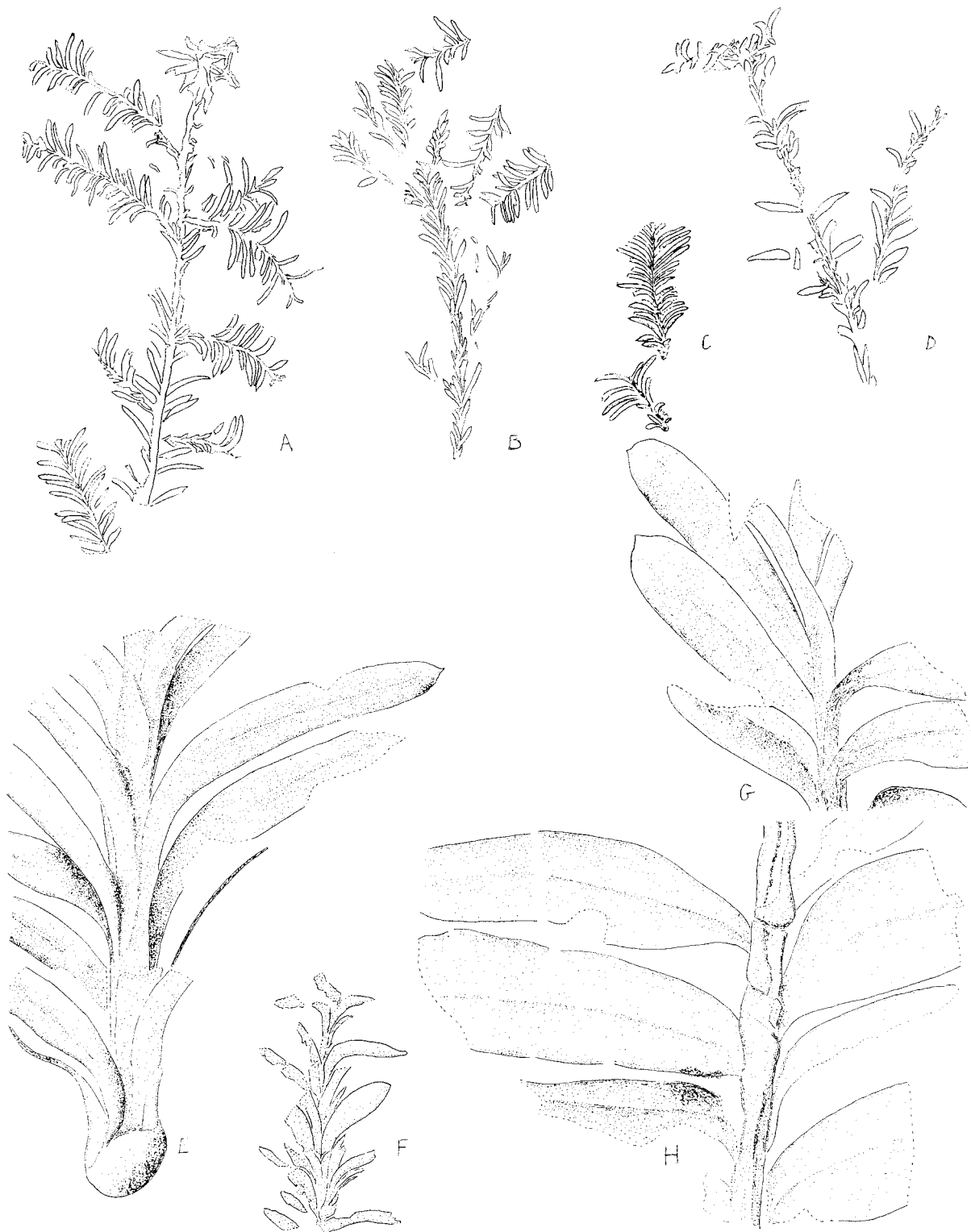
FIG. 11.—*Mataia podocarpoides.* A-D, F: portion of foliage showing branching all x 1. A, B-D Canterbury Museum z P 185, z P 231, C zP 189, C, E, Australian Museum F51956; F, University Queensland F50768, E, G, H Parts of shoots showing form of leaves, H from Malvern Hills, all x 7, Canterbury Museum G 2; F, 231; H, 15.

(3) *Taxonomic Position*: *Rissikia* shows several points of approach to the " Walchias ", but the seed cone indicates that it is quite separate from them. Likewise it shows an approach, in the unit of the seed cone, to certain Mesozoic conifers, especially *Voltzia* (see above p. 115). However, there are even greater differences. It seems to me that *Voltzia*, or *Pseudovoltzia* (see Schweitzer, 1963) and *Rissikia* are at the same level or organisation (or evolution), and perhaps in the Palaeozoic shared a common ancestor, but they are too different to group in the same Family.

Among living conifers, *Metasequoia* and *Taxodium distinchum* (L.) Rich in the Taxodiaceae, *Pinus, Larix* Mill and *Cedrus* L. in the Pinaceae, and *Acmopyle*, with *Podocarpus* Sections Davrycarpus Endl. and perhaps *Polypodiopsis* Bert. in the Podocarpaceae, show an unmodified system of long and short shoots. As for the leaves, bilateral leaves are found today *only* in the Podocarpaceae where they are associated with a long shoot: and short shoot branching pattern in *Acmopyle* and Section Dacrycarpus. Leaves rhombic in section on short shoots are seen in the (un-named) podocarp represented by Bower 199 and Schodde 1204 (C.S.I.-R.O.). The very thin leaves with four stomatal zones each only one stoma wide can be seen in young *Dacrydium novoguineense* Gibbs. The stomatal details of *Rissikia*, as noted, recall *Saxegothea* Lindl. and *Microstrobos* especially; these genera fall in the Podocarpaceae. Comparison is possible with *Metasequoia*, however (Fig. 10G).

The male cone is interpreted as showing two pollen sacs, and disaccate pollen. These features are found with regularity in the Podocarpaceae and Pinaceae only. The corpus and saccus shape and ornamentation seem to me to come close to *Dacrydium*, e.g. *D. laxifolium* Hook f. Striae are not known in any living conifer. It is true that *Ullmannia* Goepp. among Mesozoic conifers has only two pollen sacs per unit (Florin 1944), but this conifer differs in so many other respects from *Rissikia* that I disregard this similarity.

A spike-like seed cone is seen in the podocarps *Dacrydium franklinii* with *Podocarpus spicatus* and *P. andinus* (Wilde 1945). Other families have cone-like cones, or reduced cones, as *Juniperus* L. Trifid scales in which the lateral points are small are seen in *Pseudotsuga* Carr. and *Larix* Mill. (Pinacea) but no podocarp clearly shows this feature. However, in *P. andinus* (judging from three trees in the Hobart Botanical Garden) in the larger flowers on a cone, the bract may show small lateral points, as well as the slightly pointed apex (Fig. 14F) ; and this feature can be interpreted as a much modified trifid structure.

The cone scale in *Rissikia* is basically 3 partite, each lobe possibly having a double vascular trace. *Dacrydium franklinii* shows a cone scale often (if not normally) produced into three points; *Michrocachrys* is similar (Fig. 14H), and so is *Saxegothea* The cone scale in all these is a small non vascular structure. In *P. spicatus*, and *P. andinus*, *two* vascular traces proceed past the chalaza into the further part of the epimatium (Sinnott 1913). It thus seems to me that these podocarps (also resembling *Rissikia* in having several seeds per cone, not one as is normal among podocarps) are

explicable rather easily in terms of the *Rissikia* cone unit: *D. franklinii, Microcachrys*, and *Saxegothea* retaining all three lobes of the cone scale, though they are much reduced: while the double trace of *P. spicatus* epimatium recalls the (supposed) double trace in one lobe of the cone scale in *Rissikia*.

Another point is that *Rissikia* is linked to the living podocarps by *Mataia* (see below, p. 133), which falls nearly exactly halfway between *Rissikia* and *Podocarpus* sect. Stachycarpus or *Rissikia* and some *Dacrydium* species. Moreover,*Mataia* is also intermediate in age (p. 129).

Other conifer families show evidence for derivation from a complicated seed scale complex (Florin 1950 for summary), but none, it seems, is clearly characterised by a tripartite arrangement of parts in the seed scale complex. Rather, two, five or seven appear to be indicated, as well as one, through some genera (*Cunninghamia*, rarely *Athrotaxis*) seem to have a tripartite symmetry. If, as I think was the case, the nucellus of *Rissikia* projected beyond the integument, we have an unusual situation shared by *Saxegothea* alone (see Tison 1909 for example). However, in *Saxegothea* the nucellar projection is solid and acts like an Angiosperm stigma, whereas any nucellar projection in *Rissikia* may have been hollow.

Rissikia has more than one seed per unit, the Podocarpaceae one only. However, as seen on p. 115, there is reduction in the genus, *R. media* showing two per lobe, *R. apiculata* one only, and possibly also having some sterile lobes. There is also evidence that not every ovule reached maturity. The gap in this respect, is not very wide, it is again partly bridged by *Mataia*.

Taking all the above points into consideration, it seems to me that *Rissikia* falls with the Podocarpaceae, and with no other Family. The only Family that otherwise enters the picture is the Pinaceae, and this is very interesting, for others (e.g. Van Campo-Duplan (1950)) have suspected a connection between the Podocarpaceae and the Pinaceae.

For the present, I refer *Rissikia* to the Podocarpaceae, even though this does involve a slight widening of the limits of the Family (see Pilger and Melchior 1954, p. 357). Confusion is unlikely, for the modification needed is small. The alternative would be a new Family, and there seems no object in this.

Genus **MATAIA** nov.

Type species: *M. podocarpoides* (Ett.) see below..

Diagnosis. Woody conifer, showing main shoots bearing laterals in groups, possibly false whorls, at intervals. Leaves bifacial, small, 1.5 cms. long or less, borne spirally but twisted more or less distinctly into two rows. Shoot bases showing a few (about 6) small scale-like leaves, not twisted. Leaves more or less strongly concave, on the lower surface, with projecting midrib on lower surface, contracted at base, but not showing distinct petiole, leaf widening rather gradually; at apex leaf contracting abruptly to an often acute apex. Leaf margin same thickness on rest of leaf, not scarious. Leaf substance thin and fragile.
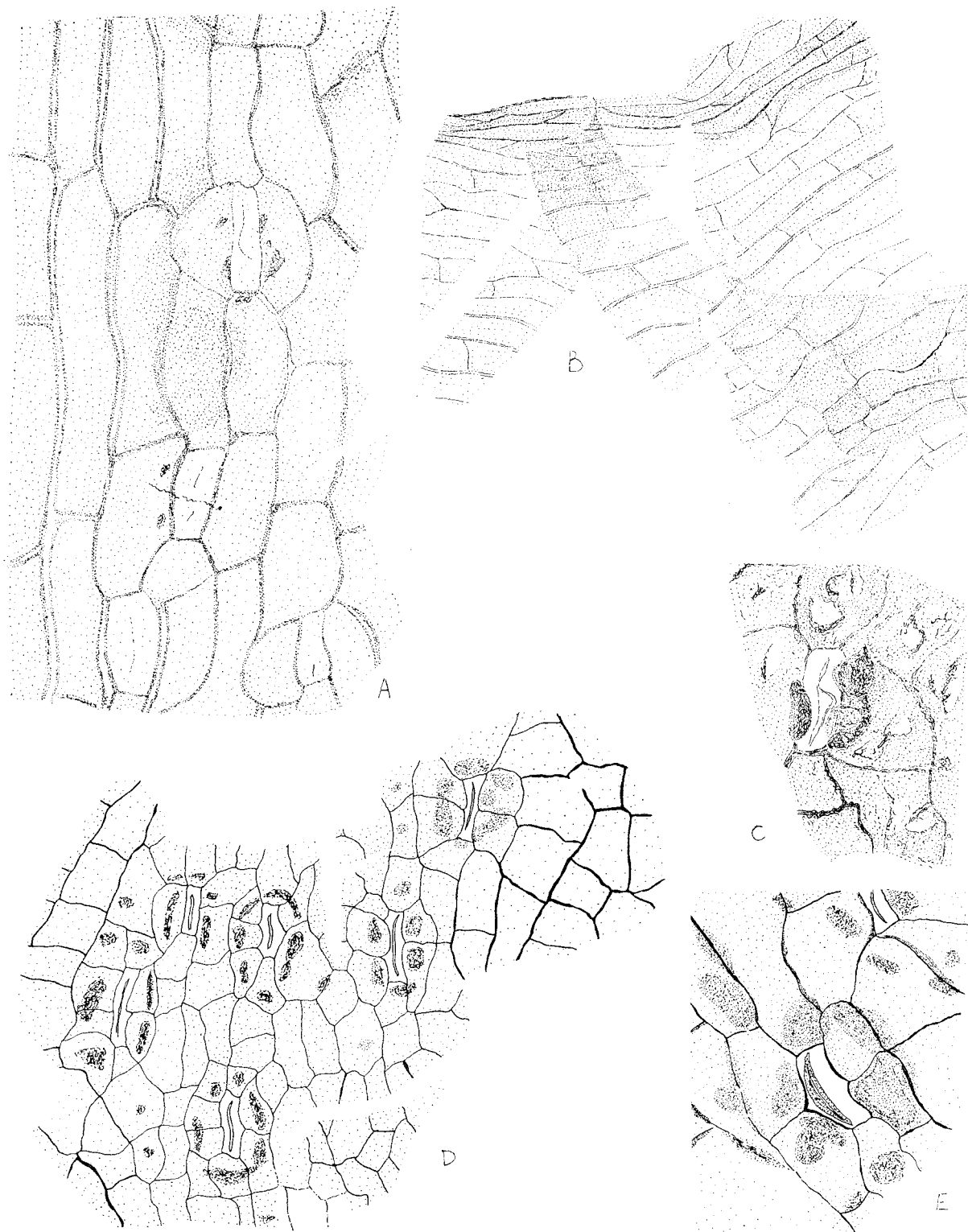
FIG 12.—*Mataia podocarpoides*. A: Cuticle (supposed under surface) and stomata x 400; B: Two layers of cuticle along leaf margin (heavy stipple) x 200; C: A stoma showing solid papillae round stomatal pit x 600, Canterbury Mus. ZF 15: D: Cuticle of under surface of the leaf x 200; E: stoma, 600, University of Queensland F50769.

Cuticle thin, about 1μ on (supposed) upper leaf surface, and slightly less on the other leaf surface, showing rectangular cells in more or less regular rows. Leaf either hypostomatic or very unequally amphistomatic; longitudinally orientated stomata lying in rows on one (presumably lower) leaf surface in two zones. Cell outlines slightly sinuous or pierced by small holes, or both, cuticle surface smooth. Stomata monocyclic, in often irregular rows, sometimes having touching subsidiary cells, or very rarely shared subsidiary cells, more usually stomata more distant from each other. Subsidiary cells 4-6 unspecialised. Stomatal pit rectangular, normally overhung with separate or somewhat concrescent papillae; continuous ring of thickened cutin round stomatal pit (Florin Ring) absent. Cell outlines sometimes appearing double.

Seed cone spike-like, about 3 cms. long, having a few leaves like the foliage leaves at its base, followed by a leafless portion up to 3 mm. long, and 8-12 well separated spirally arranged units. Each unit consisting of small, entire more or less triangular subtending bract and axillary cone scale. Cone scale consisting of thick (probably nearly round) stalk, expanding into an entire broadly hastate scale, of overall length about 3 mms., about half as wide as long, and showing apical third to quarter turned back over the adaxial scale surface. Two stalked seeds borne on adaxial surface of scale; seed stalks arising about at distal end of cone scale stalk, lying over, but (in all probability) free from scale margin. Seeds (or ovules) round in section, inverted, partly covered by overfolded portion of scale, about 1 mm. x 0.75 mm., free from the scale. Pollen cone and microscopic details of seed cone unknown.

DESCRIPTION AND DISCUSSION

(1) *Use of one name.* On the holotype, the base of the cone is probably seen (Fig. 13A). This shows a number of leaves, of shape much like (but not entirely like) the foliage leaves. The resemblance extends to their convex shape and projecting midrib, but cuticle is not available. This is a sort of organic connection, and is the chief ground for using one name for both foliage and cone.

There is also the evidence from association at one, just possibly two, localities. At the Clent Hills the only conifer known so far is *M. podocarpoides* (foliage): it is common, and has already been tentatively compared with *Podocarpus* (e.g. Florin 1940). The cone, also *Podocarpus*-like is found lying with shoots.

In the Malvern Hills, from which *M. podocarpoides* foliage is known, I have found seeds, in size and gross shape indistinguishable from those in the cone from the Clents but again lacking cuticle (Fig. 9G). However, there are two floras in the Malvern Hills, one with Angiosperms, and I am not certain which my small seeds belonged to.

The Clent Hills material is somewhat metamorphosed, and no cuticle is available. Essentially, however, the plants are finely preserved. Examined dry, the material often is disappointing, but when covered with kerosene (or better, xylol) a great deal of detail previously invisible comes to view.

(2) *General form.* In the material now called *M. podocarpoides* the branching is irregular. In some shoots (Figs. 9A, D) there appeared to be

groups of side shoots, which may be false whorls, set at intervals; Bonetti's (1963) shoot shows this excellently. In the living *Podocarpus lawrencei* Hook f., as in some similar trees, the branching shows similar groups of laterals (Fig. 2F), but again as in *M. podocarpoides,* the laterals are not of limited growth, but themselves grow on to produce further groups of laterals of the second order. In the living species the groups of branches arise more or less annually, and where the annual increment is small (as in the mountain top habitat of *P. lawrencei*) the branching pattern becomes obscure. This sort of branching grades into the modified pinnate sort seen in *P. spicatus* but generally they are distinguishable.

The leaves of the New Zealand material available to me are not thick. They appear so, but when they are seen compressed lower surface downwards (as judged from comparison of part and counterpart), the fossilised leaf is seen to be strongly convex, the midrib being supported by the raised matrix of the impression beneath the leaf, (Figs. 11 E, G, H). On Walton's compression theory, this means that in life the leaf was thin and concave. The midrib projects downwards in the fossil, appearing as a trench on the impression.

The cuticle will be discussed in the specific description.

(3) *Seed cone.* The general outline of the cone is shown in Pl. 2G. The length of the leafless stalk is not known, in the most complete specimens it is 2 mms. long (in *P. spicatus* the stalk may be 1 cm. long, also without large leaves).

The evidence for the form of the base of the cone comes from the holotype. This specimen (probably collected by Haast) is not well preserved, and has lost much of its plant material, leaving one to judge the form of the organ from differences in level in the rock. The base of the cone swells into a little knob (like some shoots), and also like *Podocarpus andinus* in which the abortive cones are shed entire, and possibly the fossils represent abortive cones. On either side, there are three impressions, apparently attached spirally, interpreted in Fig. 12A as leaves, though they are obscure. The uppermost on each side, and the lowermost of the right hand side still have, however, some plant material, showing the midrib and what looks like a concave lower leaf surface. In showing leaves set a little way up the cone base, *M. podocarpoides* recalls the living *Podocarpus standlei* Bucholtz and Gray (1950), of section Stachycarpus.

The bract was seen complete (or nearly so) in three units only (Figs. 13 A, C, B), in all it was single and entire. The stalk of the cone scale appears about the same thickness whether compressed ventrally or laterally (Figs. 13C, D): it must therefore have been nearly round in section. Without a cuticle, it is not possible to be certain that the apex of the scale is turned over, but the circumstantial evidence is strong. On all the units there is a line of carbon (i.e. tissue) crossing over the chalazal end of the seed, and traceable back to the margin of the scale, (Figs. 13B, C, D), while in those units compressed dorsi-ventrally the same line can be seen, here often associated with a difference in rock level, coming to a point
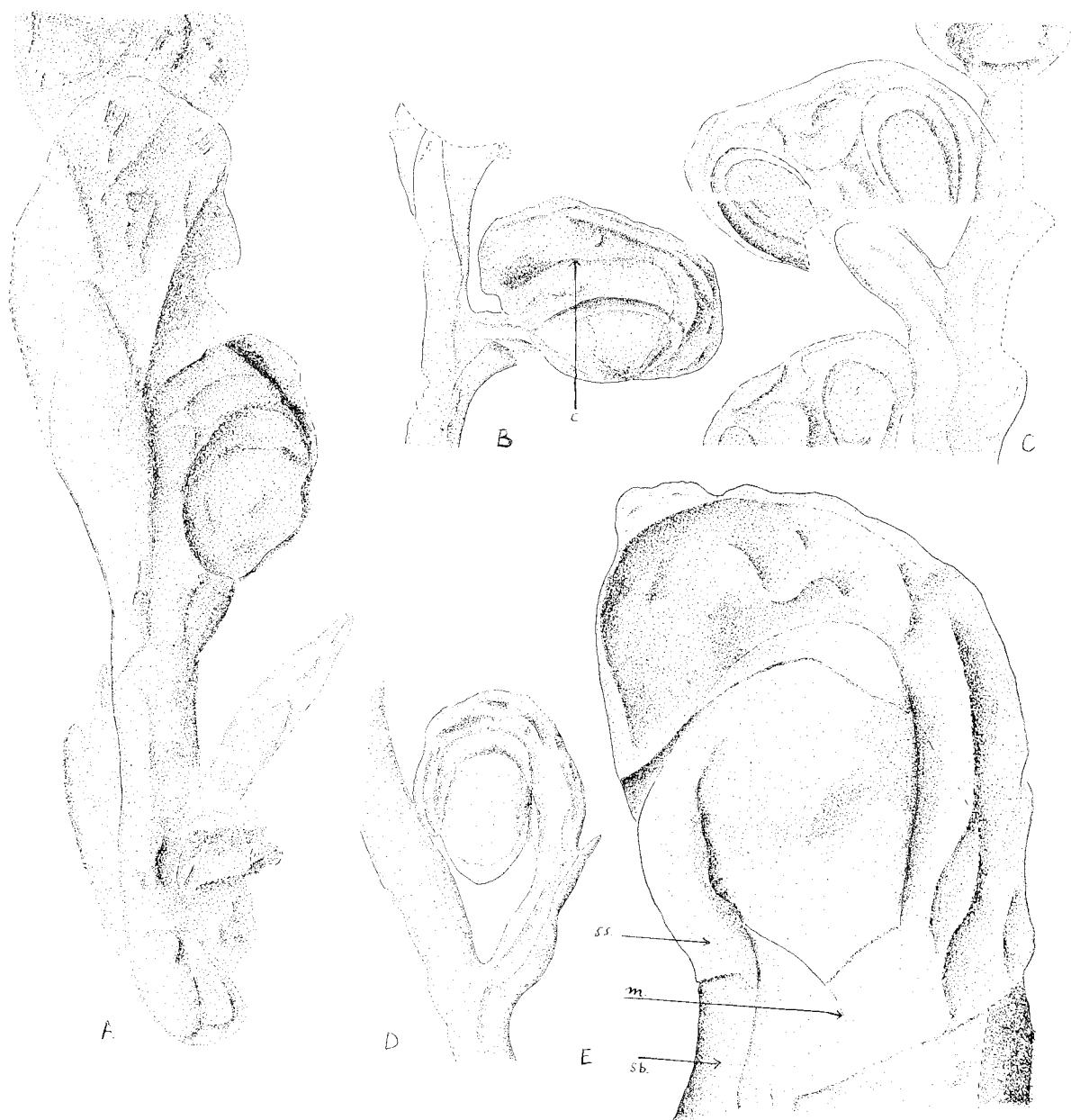
FIG. 13.—*Mataia podocarpoides*. A: Lower part of the holotype, base of cone, leaves at cone base, and two units, lower right compressed laterally, upper abaxial surface seen, note ridges on cone scale. x 7, Canterbury Museum z P 190; B: Flower (or cone unit) with only one seed, compressed laterally; C: Counterpart of unit shown in Plate 1 J, seeds and bract; D: Unit compressed laterally; E: Unit compressed partly laterally, partly dorsi-ventrally x 14, rest all x 7.   New Zealand Geological Survey 581/519. *ss* = seed stalk, *sb* = position of seed stalk which is broken up off the seed scale, *m* = micropyle, *c* = edge of the unfolded part of the seed scale.

(Pl 1J). The other possible explanation, that the adaxial scale surface is raised in a lump, is very unlikely because the tissue is smoothly continuous over the overfolded portion (as it is here interpreted), on to the abaxial scale surface (Pl. 1J, Fig. 13G, D). Accepting the first view, the cone scale was a simple, bluntly pointed structure: to judge from the wrinkling in the fossil, it was probably also thick, As noted in the diagnosis the over-folded portion of the scale overlaps parts of the seeds, and may have been in contact with them, since mud is not found between seed and scale at this point.

In these cone units compressed more or less laterally, there is a bar of thick material running from the seed to the scale stalk (Figs. 13B, E). Towards its distal end this bar can be broken off the underlying plant material, and in one unit (shown in Fig. 13E) there is a layer of mud between it and the scale. This is interpreted as a seed stalk, which must have been free from the scale at least for part of its length. The stalk lies at the edge of the scale; it is not clear whether it was lateral or adaxial to the scale, but probably it was adaxial. It joins on to the distal end of the seed showing that the seed was inverted.

Nothing in the seeds can be made out except that since they are the same thickness however compressed, they must have been round in section. The narrow end (micropyle) shows no sign of a projecting nucellus.

The name is from Matai, Maori for *Podocarpus spicatus* R.Br.

Mataia podocarpoides (Ettinghausen) com. nov.

Pls. 1J, 2G; Figs. 9G, 10A-D, F, 11, 12, 13, 14A, 15C, D.

1891 *Palissya podapoides* Ettinghausen, p. 31. Nomen nudum. Material here re-examined.

1917 *Elatocladus conferta* Arber non Oldham and Morris, pp. 9 and 58-59; pl. 1, figs. 1-3; pl. 6, fig. 4; pl. 13, fig. 11 and pl. 8, fig. 6. Various New Zealand localities.

1963 *Elatocladus conferta* Bonetti non Oldham and Morris, pp. 37-39, pl. 7, figs. 1 and 3. Middle Jurassic, the Argentine.

Comparable material: Palissya australis McCoy (Sterling 1900, p. 6 pl. 3, figs. 8, 9).

Holotype: Fig. 13A, of No. Z.P. 190 Canterbury Museum; Ettinghausen's specimen.

Locus typicus: The Clent Hill, Jurassic (? Middle Jurassic).

Diagnosis emended: Sprays of foliage showing spirally inserted difacial leaves, twisted into two rows except at the leaf base. Spreading leaves 0.5-1.5 cms. long, strongly decurrent, leaf margin contracting somewhat gradually to decurrent base, apex usually acute, leaf 0.2-0.4 cms. wide. Leaf more or less concave, midrib usually distinct.

Cuticle 1μ or less thick, of different thickness on each side of the leaf. Cuticle of (presumed) upper surface showing rectangular cells, about 60μ x 30μ, with wide cell outlines appearing double; outlines up to 3μ thick, and these cells not usually pierced by holes. On lower cuticle, non stomatiferous margin at least 10 cells wide, stomatal zones containing 8-10 rows of stomata, cell sizes as

for upper leaf surface. In zones cells about 40μ x 30μ, and cell outlines pierced. Stomatal pit, more or less rectangular, usually 5 subsidiary cells (one lateral divided); showing either one low solid papilla each, or terminal subsidiary cells lacking a papilla, or papillae more or less concrescent. Pit about 30μ x 10μ length of pore about 20μ.

Seed cone over 2 cms. long, leafless pedicel 0.25 cms. long (total length unknown). Bract about 2 mms. long, 1 mm. wide at the base, somewhat rounded. Scale about 4 cms. long, including over-folded portion 0.5-1 mm. long, and 2-4 mms. wide. Apex bluntly pointed, margin of scale entire. Seeds about 1.5 mm. long, 1.0 mm. in diameter, lying at an angle of about 60° to one another; seed stalks about 0.25 wide.

DESCRIPTION AND DISCUSSION

(1) *Form and general.* Most material comes from the Clent Hills, Canterbury, New Zealand, and was either in the collection of the Canterbury Museum, or was collected by Mr. G. Grindley and given to me, or (most) was collected by Mr. Allan Beck, New Zealand Geological Survey, and I. One specimen comes from the Malvern Hills (Fig. 9G) and one from Caledonia No. 5 Colliery near Walloon, Queensland (Fig. 11F).

Only the Malvern Hills and Caledonian specimens have cuticles. Both are, however, indistinguishable in gross form from the Clent Hills twigs. The Caledonian specimen, represents the first record, having form and microscopic detail of *M. podocarpoides* in Australia.

The branching and leaf form have already been discussed. There is a good deal of variation, even in one twig, in the leaf size and shape (Figs. 11 A-D): in general the smaller leaves tend to be wider in proportion to their length. Also, the apex may be merely acute, and may contract less sharply than is usual (Fig. 11E). However, these differences are, in the Clent Hills material at least, rather minute; all share the thin leaf substance, concave shape and narrow projecting midrib.

The cuticle is difficult to study and the interpretation given, though it appears to be the simplest, is not the only one possible. On maceration the material broke up into small rhombs, but these covered all parts of the leaf. The cuticle pieces fall into two groups, a thicker group entirely, without stomata, and a thinner group which showed all the stomata seen. This suggests that the leaf was hypostomatic, but it remains possible that it was very unequally amphistomatic, like *P. andinus.* The margin shows unmodified, but wrinkled cells (Fig. 12B), indicating that the margin was thick and not scarious. The stomata lie in rows and on the fragments are confined to strips of cuticle (Fig. 12A, D), indicating that they lay in zones. In the zones the rows are not entirely regular, rather as is *Podocarpus ferrugineus,* and they are not as closely packed as in, say, *Saxegothea* (Fig. 14B). A Florin ring could not be seen, but the stomata showed low solid papillae, like *Rissikia,* and these were sometimes concrescent. The sinuosities on the outlines are very small and often absent, and it is not possible to be certain that the middle lamella was sinuous or not; I think it
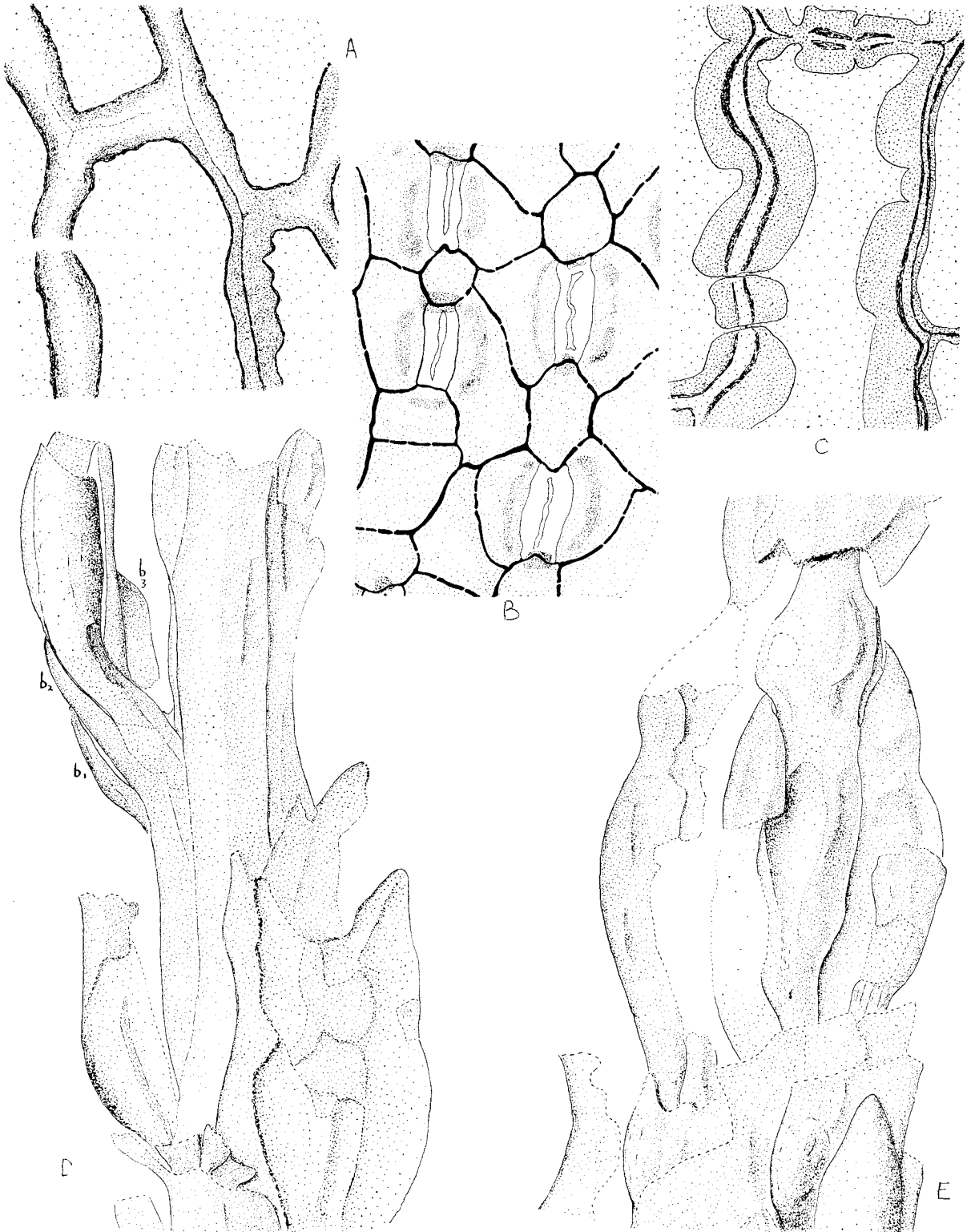
FIG. 14.—*Mataia podocarpoides* A; *Saxegothea conspicua* B, C; *Rissikia apiculata* D, E.

A, C: Cell outlines compared, showing apparently double appearance grading into outline with more deeply penetrating "middle lamella" region. x 1000, A, University Queensland F50769, B and C, Nat. Herb. Melb. Buchtien 1903. B: Lower cuticle with stomata x 400; D: Part of a seed cone, showing broken bases of three lobes of seed scale complex (lower left), three parts of bract, (b1, b2, b3), seed scale in abaxial view (top right) and tip of lobe of cone scale (bottom right) x 14; E: Part of seed cone, showing imprint and part of single seed associated with two of the three lobes of cone scale x 14. Australian Museum F51983.

sometimes was (Fig. 12C), so that the sinuosities compare with the small ones seen in *Podocarpus gnidioides* Carriere. The outlines are also occasionally pierced by small holes. In the thicker cuticle the cell outlines were wide, and the central part stained very feebly, giving the outline the appearance of being double. This appearance is only seen in the wider outlines, and there is a series from outlines with a clear central portion, to ones in which the central portion is quite absent (Figs. 12A, 14A). A slightly similar effect may be seen rather rarely in *Saxegothea* (Fig. 14C). Here the central portion is bordered, and penetrates some way down into the leaf. However, it sometimes does not stain very fully, and then the outline appears double. Presumably the fossil is similar. Incidentally, in *Saxegothea* the papillae round the stoma discussed by Florin (1931, see also Fig. 14B) are not always present.

The cones have split more or less through the middle, so that structures on the outside, such as bracts, are only seldom seen intact. The one in Fig. 13C was bared by dissecting away the rock and plant material over it. The scanty material cannot give a proper idea of the range of variation in the cone, but the number of seeds (or seeds reaching maturity) is variable. Mostly it is two, but in the uppermost and lowermost complete cone units it is only one (Fig. 13B). In one cone unit (Pl. 1J) one seed is compressed more or less exactly dorsi-ventrally, the second partly laterally. This means, I take it, that the rather wide scales were curved round the axis. On one unit, (Fig. 13A, the lower one) two ridges ascend the abaxial side of the seed scale complex. *Rissikia* showed a similar appearance and it was suspected there that the ridges contained veins (p. 109), possibly they do in *Mataia*.

(2) *Specific identities and comparison with Elatocladus conferta Oldham and Morris and E. jabalpurense Feistmantel.*

As with *Elatocladus* species resembling *Rissikia*, the species resembling *M. podocarpoides* are not well known, and a satisfactory scheme is impossible. Florin (1940) discussed these shoots at length, but my suggestions differ somewhat from his.

Elatocladus confertus Oldham and Morris (1862, pl. 32, fig. 10). See also Feistmantel 1877, pp. 85-86, pl. 45, figs. 4-8a; 1877a pp. 183-184, pl. 5, fig. 3, pl. 8, figs. 1-6; Halle 1913, pp. 86-87, pl. 8, figs. 26-40; Sahni 1928, pl. 1, figs. 4-8; consists of shoot systems showing a more or less pinnate habit of branching. This is not seen in Oldham and Morris' original figure (a fragment only), and in Halle's figure (1913, pl. 8, fig. 26) it is possible that the branching is not pinnate, but in most material it is plainly pinnate. The leaves are short (0.5-1.5 cms.), twisted into two rows, and, where well seen (e.g. Halle 1913, pl. 8, fig. 32 or Feistmantel 1887, pl. 45, figs. 9, 9a,) contract more or less sharply at the base to a distinct petiole (not always seen, e.g. Feistmantel 1877, pl. 45, fig. 8a). On the other hand the leaf apex contracts only rather gradually to a more or less sharp apex. The leaves are said to be thick, but I doubt this, they might be concave. *Elatocladus jabalpurensis.* Feistmantel (1877a, p. 16, pl. 9, pl. 10, fig. 1: 1879, pl. 12, fig. 4: Sahni 1928, pl. 5, figs. 71-75), consists of

pinnately branched shoots, with leaves about 1.5-2.5 cms. long twisted into two rows, and contracted rapidly to a distinct petiole. The apex tapers slowly to an acute tip but over most of the length of the leaf the margins are parallel. I do not know whether the leaf is concave or not. Sahni (1928) describes a cone associated with the foliage. No detail is available, but the general form of this cone, is similar to *Mataia* (see pl. 5, fig. 72, extreme right, and others). It is not placed in *Mataia* because I have not examined material and the details are not clear, but from the figures it appears to have only one large seed per cone unit, and so to come closer to *Podocarpus* Section Stachycarpus than *Mataia*. Arber's (1917) specimens and mine do not show pinnate branching (see also Bonetti 1963) though their branching pattern grades into that of *E. confertus* and, at least in most shoots, the leaf shape differs. From *E. jabalpurensis*, *M. podocarpoides* differs in leaf shape. Two records, *E. confertus* of Edwards (1934) and *E. jabalpurensis* of Sahni (1928, p. 12; *E. conferta* of Feistmentel 1882 pl. 2, figs. 10, 10a) show bilaterally flattened leaves, and so differ from any of the other specimens discussed here.

These differences between *M. podocarpoides*, E. *confertus* and *E. jabalpurensis* are admittedly small, but they do enable the material to be split up. A new name is needed for the New Zealand material, and Ettinghausen's (1881) *Palissya podocarpoides*, originally published without figure, is revived and his specimen figured, as the holotype. I express no opinion as to whether the three species discussed are as closely related as Florin (1940) suggested.

DISCUSSION OF THE GENUS

(1) *Generic comparisons.* The spike-like cone of *Mataia*, and the construction of the individual units, as here interpreted, probably remove it from close comparison with any known fossil conifer. *Callipitys Harris* (1935: 110-111) might perhaps be confused, but it differs in having no separate bract (i.e. the cone scale is simple, see p. 111), and in the orientation of the seeds (ovules) which are directed upwards and unstalked, whereas in *Mataia* the seeds are inverted and stalked (it is admitted that cuticle is needed to prove both statements about *Mataia*).

Among living Families the Podocarpaceae seems to me to be the only one in view. Superficially the cone recalls the cone of *P. spicatus* or *P. andinus*, but differs from these, indeed any living podocarp, in often or usually having two seeds per cone unit. The form of the scale removes *Mataia* from any living podocarp genus, though in *Microcachrys* and also *Saxegothea* (Figs. 15H), whose cones are otherwise quite different, the seed scale folds over the seed in a similar way.

However, though different from any extant genus, I place *Mataia* in the Podocarpaceae, primarily on the form of the seed cone. The difficulty about there being more seeds than just one per cone unit, I do not think is important, in some units of the present material there is only one seed. The foliage offers confirmatory evidence. In gross form and cuticle (so far as known) it is much like *Podocarpus*.
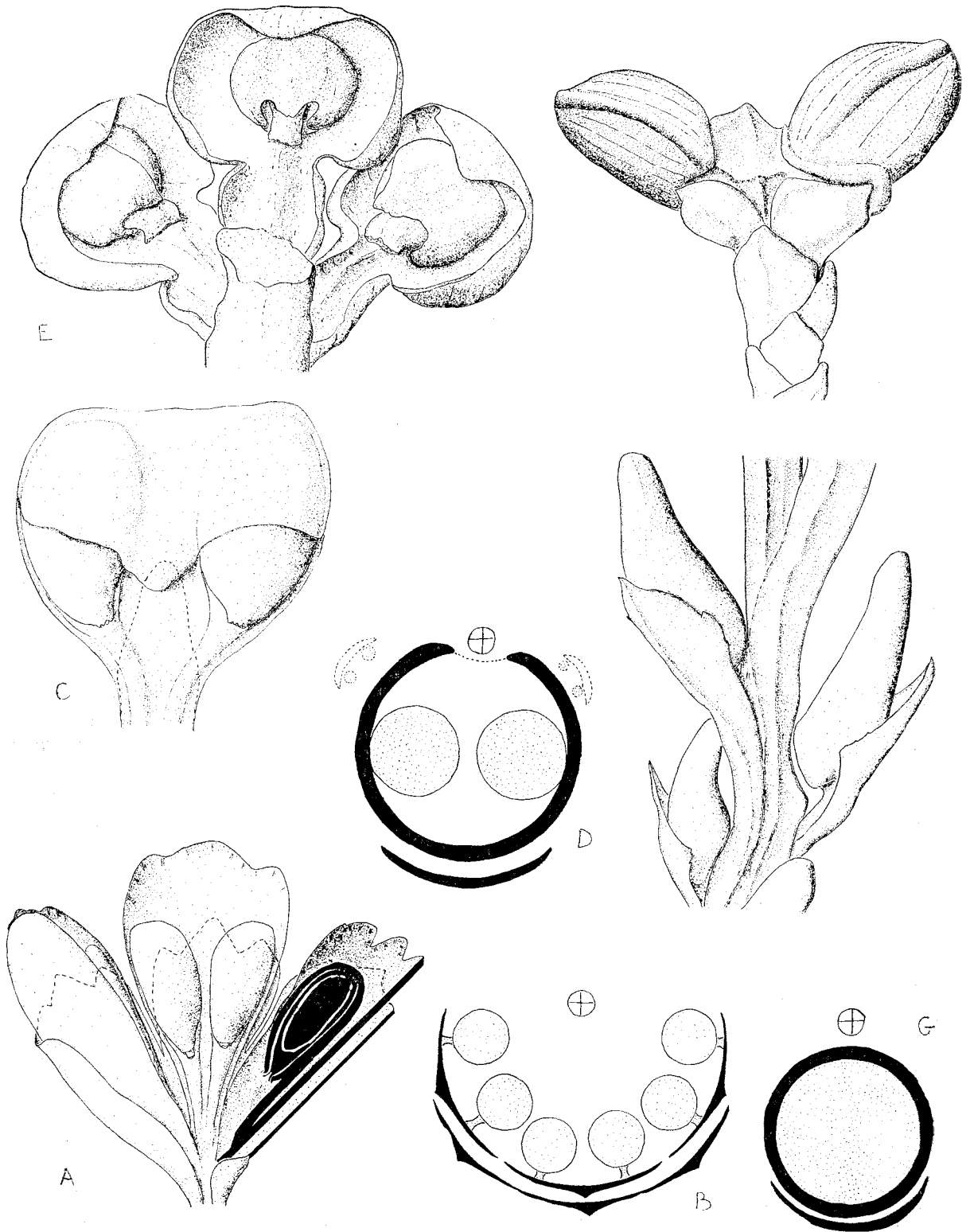
FIG. 15.—*Rissikia media* (reconstruction), A, B: *Mataia podocarpoides* (reconstruction), C. D; *Podocarpus andinus,* E, G; *Dacrydium bidwillii,* F; *Microcachrys tetragona,* H.

A: Reconstruction of a cone unit, seen abaxial surface facing observer, bract dotted, cut tissue solid black, x ca. 10; B: Floral diagram (Florin's terminology) of one cone unit; C: Reconstruction of cone unit, as A, x ca. 10; D: Floral diagram. E, F. H The cone, or parts of the cone, showing (E, F) two sorts of epimatial seed, and H, three of a whorl of four, showing large bract, and three-pointed seed scale, all x 7. G. floral diagram of E.

NOTE.—
  (i) The seeds are stippled in B, D and G; parts missing as between B and D, dotted in D.
  (ii) The diagrams are drawn as the units are, i.e. as dorsiventrally flattened. These diagrams are therefore not entirely comparable with those of Florin (1944), which interpret several conifer flowers in their supposed primitive radially symmetrical form.

There is uncertainty as to which section or genus *Mataia* resembles most. In *Podocarpus* Section Stachycarpus the branching may be more or less pinnate, but the laterals are not of limited growth, nor very numerous, so that the distinction between the main (penultimate) and side (ultimate) shoots is blurred. In Section Eupodocarpus Sub-sect. D. (Gray 1956) the branching is not strictly pinnate (Fig. 2F) but as in *Mataia*. In leaf shape, a concave leaf is found widely in Section Stachycarpus (e.g. *P. spicatus, P. ferrugineus* and *P. andinus*), but though it does occur in *P. totara* for example (Sub-Sect. D) in other species, e.g., *P. lawrencei* with which Florin (1940) especially compared his *E. confertus,* the leaf is usually thick.

The cuticle recalls both Stachycarpus and Sub-section D if it is hypostomatic, but Stachycarpus only if it is unequally amphistomatic, while the close-set stomata in a narrow rectangular pit, perhaps are most like *P. totara* or *P. gniodiodes* of Subsection D, but comparison with species of Stachycarpus is certainly possible. It differs from both lacking the Florin ring.

The two pollen cone specimens referred to *E. confertus* do not belong with the shoots now separated as *M. podocarpoides*. They are seen in Halle (1913, pl. 8, fig. 31) and Sahni (1928, pl. figs. 5-7), and have been compared with the cones of *P. lawrencei* or *P. nivalis*. This can be maintained; so could a comparison with *P. ferrugineus* (for figs. see Wilde 1945). To me the pollen cones appear different from either group. Unluckily Sahni's figure of the pollen is too small to be of use.

The seed cone is in gross form similar to Stachycarpus, but in details, it is different from either that section or Eupodocarpus sub-section D.

However, though *Mataia* cannot be compared very closely with either group, it does share a number of features with them, and differs more widely from any other living genus or section. Perhaps *Mataia* preceded the evolution of Stachycarpus or of Sub-section D.

A further very interesting fact is that in a few features *Mataia* recalls *Saxegothea*. *Saxegothea* may show the same sort of false whorled branching (cf. Fig. 2F) the leaf is concave and hypostomatic; while the stomata of *Mataia* approach those of *Saxegothea* more closely than do any other podocarp figured, especially in the form of the papillae round the pit (Fig. 14B). In *Saxegothea* also the outlines may be pierced by holes (Fig. 14C) and may appear double. However, the stomata are closer packed in *Saxegothea* than they are in *Mataia* and the difference in cone structure is great.

(2) *The morphology of the seed cone.* In *Rissikia media* the cone scale (short shoot or seed scale complex) consisted of three lobes, joined below into a thick stalk. From the extreme base of each lobe two (in most cases, sometimes only one) stalked inverted seeds took their origin (Fig. 8G). In *Mataia* there are two stalked seeds in a similar position, but only one lobe on its (still thick) stalk. I think the easiest interpretation is that in *Mataia* we have one presumably the central one, of the three lobes of *Rissikia*, and the other two have vanished. (Fig. 14D).

On the other side, it is fairly easy to interpret the cone scale of *P. spicatus* and *P. andinus* in terms of *Mataia*. One seed has been lost, as sometimes is seen in *Mataia*, and the folded-over seed scale (epimatium) now envelopes the whole seed.

There may be some confirmatory evidence. No clear evidence can be seen of the bundles in *Mataia*, but as in *Rissikia* there is reason to think that each lobe contained two. In *P. spicatus* (Sinnott 1913) and *P. andinus* two bundles enter the base of the cone scale, which branch at the level of the chalaza; two passing to the chalaza, and two passing down into the (morphologically) distal parts of the epimatium (*P. spicatus*), or into its end beyond the seed (*P. andinus*). I regard the two bundles supplying the epimatium only as equivalent to the two (supposed) bundles in the lobes of the *Rissikia* cone scale.

There are difficulties about this interpretation The interpretation of the bundle course is not everywhere easy. Apparently normally in *Podocarpus* (though not very many species seem to have been examined) and in *Dacrydium biduillii* two bundles supply the seed; and in *P. dacrydoides* and *P. lawrencei* for example, no others are present ascribable to the cone scale or seed. But in other species such as *P. totara* (Sub-section D, like *P. lawrencei*) and *P. elatus* (Eupodocarpus Sub-section B) the bundles perform a set of fairly complex evolutions between the levels of the micropyle and chalaza. In those genera and species in the case of *Dacrydium* without an epimatium, only one bundle supplies the seed (see Sinnott 1913, Florin 1950).

If the epimatium of *Podocarpus* is simply folded over the end of the cone scale, one might expect to see some sort of suture at the base of the whole cone scale or along the sides of the epimatium but one does not, at least in *P. spicatus* and *P. andinus*, the species chiefly concerned. In *Dacrydium bidwillii*, which here goes with *Podocarpus*, there are two lateral ridges, which could represent the position of the expected sutures, but, though these ridges contain various lacunae, the tissue between the ad- and abaxial sides of the seed is continuous through them.

Despite these uncertainties, in what follows the cone scale of *Mataia*, and of *Podocarpus* is regarded as equivalent to one of the three lobes seen in the flower of *Rissikia*. After all, this seems to be the simplest view.

GENERAL DISCUSSION

If *Rissikia* and *Mataia* belong to the Podocarpacaea, they raise a number of questions about the Family. The first is, where did it come from? The Southern Hemisphere Permian conifers seem unlikely. *Walkomiella* (Florin 1940, Surange and Prem Singh 1952) is different at every known feature. *Buriadia* Seward and Sahni (Florin 1944) and *Paranocladus* remain possible while only the shoot and cuticle is known. In neither feature do they especially recall *Rissikia*. Similarly, though the later Permian and Triassic conifers (*Voltzia* and its allies) are rather like *Rissikia* in the general organisation of their cones, the differences are considerable, and I doubt whether any direct

descent is likely either on morphological or stratigraphical grounds (but see Schweitzer 1963 for another view).

It seems to me one must consider the earliest conifers, *Lebachia* and especially *Ernestiodendron* (Florin 1938-1945). These conifers had pinnate, though probably unlimited, ultimate branches; they had leaves, rhomboidal in section, as in *R. apiculata,* and in some instances (Florin 1938-45, pl. 141/2, Fig. 17, pl. 133/4, Fig. 2: pl. 145/6, Figs. 7, 8) they seem to show a weak tendency towards flattening in one plane. The pollen cone of *Rissikia* is closely similar to the pollen cone of these conifers though the pollen differs. *Ernestiodendron* had a long spike-like cone, (Florin *loc. cit.* e.g. pl. 149/50, figs. 1, 5, 9) like *Rissikia.* The cuticle of these earliest conifers were not in general like the cuticle of *Rissikia* (but see *E. filiciforme* var. *gracile* Florin *loc. cit.* pl. 111/112, figs. 18, 19). Their cone scales also were not like those of *Rissikia,* though some could perhaps be considered similar, and in the *Ernestiodendron* group there is considerable variability (see e.g. *Walchiostrobus* sp. Florin *loc. cit.* pl. 163/164, figs. 3, 4, text fig. 34).

The matter remains open, though perhaps an origin in the complex of very early conifers from which *Lebachia* and *Ernestiodendron* sprang is the most likely.

As for evolution of organs in the *Podocarpaceae,* it now appears as Wilde (1945) visualised, that a richly branched habit, of the sort seen in *Podocarpus* Section Dacrycarpus (juvenile Fig. 2G), is a primitive feature. Whether all early Podocarpaceae had this form of branching in uncertain. Again, the bilaterally flattened leaf is seen to be extremely ancient, and considering the morphological (probably not phylogenetic) series *Ernestiodendron—Rissikia apiculata—R. media,* would seem to have evolved from the leaf rhomboidal in section, without reference to the bifacial leaf. For this reason, I, following Florin 1931, Gray 1962, and Hair 1963, doubt whether *Podocarpus* Section Dacrycarpus is rightly placed in *Podocarpus.* The features of the pollen cones seem to have changed very little. The scale has been reduced, and that is about all. We now know that within the Podocarapaceae, the disaccate pollen grain is very ancient, and most probably the primitive form.

In the seed cone, the special cone branch would appear (see Wilde 1945) to be retained, though often strongly reduced. I express no opinion on the details of Wilde's scheme however.

The chief contribution of the present fossils is to suggest, in a fairly direct way, that the single unit (i.e., bract plus cone scale with its seeds) of the *Podocarpus* cone can be regarded as equivalent to one of the lobes of the *Rissikia* cone scale (Fig. 15). That is, that the epimatium is a single but bivascular structure, not two univascular ones fused laterally as has sometimes been supposed (e.g. Florin 1950 for discussion of the point). However, the epimatial structures of the Podocarpaceae are varied. There is no suggestion that the method visualised here is the only means of attaining the epimatial state. Still less do I suggest that this process has happened only once.

In certain non-epimatial genera (e.g. *Microcachrys, Saxegothea* and *Dacrydium franklinii*) the cone scale is a trifid (non vascular) structure with one seed. It is possible to derive this from *R. apiculata* assuming the loss of two seeds (Fig. 15).

If this is so a trimerous symmetry would seem to characterize the Podocarpaceae. On these grounds, I would suggest that *Tricanolepis* Roselt (1958) should be reclassified under the Podocarpaceae, and not as he did, with the Taxodiaceae. Roselt largely relied upon the fact that in *Athrotaxis* three points to the cone scale may be found. This is true, but it is not the normal arrangement; which is for there to be four or five vascular bundles in the cone scale, and only one point. *Cunninghamia* (Taxodiaceae) also has three points to the cone scale. However, in other genera, notably in *Cryptomeria,* supposed to be very primitive, five lobes to the cone scale are present, or else five (or more) vascular bundles. The comparison of *Tricanolepis* with members of the Taxodiaceae is therefore with abnormalities; the comparison with the Podocarpaceae is between the normal situations. The distribution of *Rissikia* and a *Tricanolepis* is not a serious difficulty. *Rissikia* pollen belongs to a group that appeared first in the Upper Permian of Europe, Asia and America (e.g. Saarschmidt 1963, Jansonius 1962) and extended in those areas till the end of the Triassic. There is thus other independent evidence for the Podocarpaceae in the Northern Triassic.

On the pollen evidence, as on the comparison with the *Lebachia* group of conifers above, it seems possible that the Podocarpaceae were northern in origin reaching gondwana areas at the base of the Triassic (Balme 1963).

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REFERENCES

ARBER, E. A. N., 1917.—The Older Mesozoic floras of New Zealand. *N.Z. Geol. Surv., Pal. Bull.* 6: 1-80.
ARCHANGELSKY, S., 1963.—A new Mesozoic flora from Tico, Santa Cruz province, Argentina. *Bull. Brit. Mus. (Nat. Hist.) Geol.,* 8: 47-92.
BALME, B. E., 1957.—Spores and pollen grains from the Mesozoic of Western Australia. *C.S.I.R.O. Fuel Res. Nat. Coal. Res. T.C.* 25: 1-48.
———— 1963.—Plant microfossils from the Lower Triassic of Western Australia. *Palaeontology* 6: 12-40.
————, and HENNELLEY, J. P. F., 1955.—Bisaccate sporomorphs from Australian Permian coals. *Austr. J. Bot.,* 3: 89-99.
BONNETTI, M. I. R., 1963.—Florula mesojurassica de la zona de Taquetren (Canadon del Zaino), Chubut. *Rev. Mus. Sci. Nat. Argentina,* 1 (2): 1-43.
BUCHOLZ, J. and GRAY, N. E., 1948.—A taxonomic revision of *Podocarpus I.* The sections of the genus. *J. Arnold Arbor.,* 29: 49-63.
————, and ————, 1948a.—A taxonomic revision of *Podocarpus II.* The Americal species of *Podocarpus* Section Stachycarpus. *ibid.* 29: 64-76.

BUCHOLZ, J. and GRAY, N. E., 1951.—A taxonomic revision of *Podocarpus II.* The South Pacific species of the Section Stachycarpus *ibid.* **32**: 82-97.

CARPENTIER, A., 1935.—Etude paléobotanique sur le groupe de la Sakoa et le groupe de la Sakmena (Madagascar) *Ann. Geol. Serv. Mins. Gouvt. Gen. Madagascar*, **5**: 7-32.

————, 1936.—Additions a l'étude de la flora de groupe de la Sakmena. *ibid.* **6**: 7-11.

DUTOIT, A. L., 1927.—The fossil flora of the Upper Karroo beds. *Ann. S. Afr. Mus.* **22**: 284-420.

ETTINGHAUSEN, C. VON, 1890.—Contributions to the knowledge of the fossil flora of New Zealand. *Trans. Proc. N.Z. Inst.* **23**: 7-85 (translation of 1887 *Denkschr. K.K. Akad. Wissen*, Wien, **53**: 143 et seq.).

FEISTMANTEL, O., 1877.—Jnrassic (Liassic) Flora of the Rajmahal Group in the Rajmahal Hills. *Pal. Indica. (Mem. Geol. Surv. Ind.)* (2) **1**: 1-110.

————, 1877a.—Jurassic (Liassic) Flora of the Rajmahal Group from Golapili (near Ellore), South Godavari District *ibid.*, (2) **1** (3): 163-190.

————, 1879.—Flora of the Jabalpur Group in the Son Narbada region. *ibid.* (11) **2** (2): 81-106.

————, 1879a.—The fossil floras of the upper Gondwanas. Outliers on the Madras Coast. *ibid*, 2, **1** (4): 1-34.

————, 1882.—The fossil flora of the Gondwana System. Pt. 1. The fossil flora of the South Rewah Gondwana Basin. *ibid.* **12**: 52 ii.

FERUGLIO, E., 1934.—Fossil liassic della Valle del rio Genua (Patagonia). *Giorn. Geol., Ann. R. Mus. Geol. Bologna*, (2) **9**: 1-64.

————, 1942.—La flora liasica del Valle Rio Genoa (Patagonia), Ginkgoineae et Gymnospermae *incertae sedis. Nat. Mus. la Plata.* **7**: 93-110.

FLORIN, R., 1931.—Untersuchungen über die Stammesgeschichte der Coniferales and Condaitales. *K. Svensk. Vet.—Akad. Handl.*, (12) **3**: 1-25.

————, 1937-1945.—Die Koniferen des Oberkarbons und unteren Perms. *Palaeontographica*, **85** B: 1-727 (special parts, 1-8).

————, 1940.—On *Walkomia (Walkomiella)* n. gen. a genus of Upper Palaeozoic conifers from Gondwana lands. *K. Svensk. Vet. -Akad. Handl.*, (3) **18** (5): 1-23.

————, 1950.—Evolution in the Cordiates and Conifers. *Act. Hort. Bergian.* **15**: 285-288.

FRENGUELLI, J., 1940.—Contributions al conocimiento de la flora del Gondwana superior en la Argentina XXIX. *Elatocladus australis. Nat. Mus. La Plata*, **9**: 543-548.

————, 1944a.—Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. XXXI. *Cycadocarpidium majus y C. minus* (Weil.). *ibid.* **9**: 557-568.

GIBBS, L. S., 1912.—On the development of the female strobilus in the Podocarpaceae. *Ann. Bot.* **26**: 515-571.

GRAY, N. E., 1956.—A taxonomic revision of *Podocarpus* X. South Pacific species of *Podocarpus* Section Eupodocarpus sub-section D. *J. Arnold Arbor.*, **37**: 160-172.

————, 1962.—A taxonomic revision of *Podocarpus* XIII Section Polypodiopsis in the South Pacific. *ibid.*, **43**: 67-79.

HALLE, T. G., 1913.—The Mesozoic flora of Graham Land. *Schwed. Sud. -Pol. Exped.* 1901-1903. *wiss-ergeb.* **3** (14): 1-123.

HARRIS, T. M., 1931.—The fossil flora of Scoresby Sound, East Greenland. Part II. Seed plants *incertae sedis. Medd. Gronland*, 85 (3): 1-112.

————, 1935.—The fossil flora of Scoresby Sound, East Greenland. Part IV. Ginkgoales, Coniferales and isolated fructifications. *ibid.*, 112 (1): 1-176.

————, 1957.—A Rhaeto-Liassic flora in South Wales. *Proc. Roy. Soc. Lond.*, B147: 289-308.

————, 1964.—*The Yorkshire Jurassic Flora II Caytoniales and Cycadales* Brit. Mus. (Nat. Hist.) viii + 191 London.

HART, G. F., 1964.—A review of the classification and Distribution of the Permian miospores. *Disaccate Striatiti. Compte Rend. 6th Cong. Int. Strat. Carb*, 1171-1199.

————, 1965.—*The systematics and distribution of Permian Miospores.* 252, Johannesburg.

JANSONIUS, J., 1962.—Palynology of Permian and Triassic sediments, Peace River area, Western Canada. *Palaeontographica*, **110B**: 35-98.

KLAUS, W., 1953.—Uber die Sporendiagnose des deutschen Zechstein-salzes und des alpinen Salzgebirges *Z Deutsch. Geol. Gess.*, **105**: 776-788.

————, 1963.—Sporen aus dem Südalpinen Perm. *Jb. Geol. B.A.*, **106**: 229-363.

LELE, K. M., 1955.—Plant fossils from Parsora in the South Rewa Gondwana Basin, India. *Palaeobotanist*, **4**: 23-34.

LESHIK, G. 1955.—Die Keuperflora von Neuewelt bei Basel, II. Die iso—und Mikrosporen *Schweiz Paliont.* Abhandl., **72**: 1-67.

————, 1956.—Sporen aus dem Salzston des Zechsteins von Neuhof bei Fulda. *Palaeontigraphica*, **100B**: 122-142.

MALJAVKINA, V. S., 1953.—Verkhnetriasovye, niznejurskie i serednejurskie sporovo-pyl'tsevye kompleksy vostochnogo i zapadnogo Priural'ya *VNIGRI*, ns. **75**: 93-147.

OLDHAM, T. and MORRIS, J., 1863.—Fossil flora of the Rajmahal Series, Rajmahal Hills. *Pal. Indica (Mem. Geol. Surv. Ind.)* (2) **1** (1): 1-52.

PANT, D. D., 1955.—On two new disaccate spores from Australia. *Ann. Mag. Nat. Hist.* (12) **8**: 757-765.

PILGER, R. and MELCHIOR, H., 1954.—Gymnospermae in MELCHIOR, H., and WERDEMANN, E., A. Englers *Syllabus der Pflanzenfamilien* 12 Ed. **1**: 312-344.

POTONIE, H., 1958.—Synopsis der Gattungen der Sporae Dispersae. II Teil. *Geol. Jb. Beih* **31**: 1-114.

ROSELT, G., 1958.—Neue Koniferen aus dem Unteren Keuper und ihre Beziehungen zu verwandten fossilen und rezenten. *Wiss. Z Univ. Jena. K. Math-Nat.* **4/5**: 387-409.

SAARSCHMIDT, F., 1963.—Sporen und Hystrichosphaerideen aus dem Zechstein von Budingen in der Wetterau. *Palaeontographica*, **113B**: 38-91.

SAHNI, B., 1928.—Revision of Indian fossil plants. Part I. Coniferales. (a) Impressions and incrustations. *Pal. Indica n.s.* **11**: 1-49.

SAMOYLOVICH, S. R., 1953.—Pyl'tsa i spory iz Permskich otlozhenii Cherdinskogo Aktyabinskogo Priural'ya, *VNIGRI*, n.s. **75**: 5-51.

SCHWEITZER, H. J., 1963.—Der weibliche Zapfen von *Pseudovoltzia liebiana* und seine Bedeutung für die Phylogenie der Koniferen. *Palaentographica*, **113B**: 1-29.

SEWARD, A. C., 1918.—*Fossil plants* (iv) xvi + 543. Cambridge.

SHIRLEY, J., 1902.—Fossil plants from Duaringa, Ipswich, Dawson River and Stanwell. *Geol. Surv. Qd. Bull.* **18**: 1-16.

SINNOTT, E. W., 1913.—The morphology of the reproductive structures in the Podocarpinae. *Ann. Bot.* **28**: 39.82.

STILES, W., 1908.—The anatomy of *Saxegothea conspicua* Lindl. *New Phyt.* **7**: 209-222.

STIRLING, J., 1900.—Notes on the fossil flora of the South Gippsland Jurassic Beds. *Rep. Vict. Coalfield Dep. Mins. Vict.*, **7**: 1-25.

SURANGE, K. and PREM SINGH, 1953.—The female dwarf shoot of *Walkomiella indica*—a conifer from the lower Gondwanas of India. *Palaeobotanist*, **3**: 5-8.

TENISON WOODS, J. E., 1883.—On the fossil flora of the coal deposits of Australia. *Proc. Linn. Soc. N.S.W.*, **8**: 23-167.

TISON, A., 1909.—Sur le *Saxegothea conspicua* Lindl. *Bull. Linn. Soc. Norm.* **23**: 139-158.

TOWNROW, J. A., 1962.—On some disaccate pollen grains of Permian to Middle Jurassic age. *Grana Palynol.* **3**: 13-44.

————, 1962a.—On *Pteruchus*, a microsporophyll of the Corystospermaceae. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, **6**: 289-320.

————, 1962b.—Note on the type material of *Xylopteris elongata* (Carruthers) Frenguelli *Proc. Roy. Soc. Qd.* **72**: 123-127.

VAN CAMPO-DULPAN, M., 1950.—Researches sur la phylogenie des Abietinées l'apres leurs grains de pollen. *Trav. Lab. For. Toulouse* **4**: 1-180.

VIRKKI, C., 1937.—On the occurrence of two winged spores in the Lower Gondwana rocks of India and Australia. *Ind. Acad. Sci. Proc.* **6B**: 428-431.

WALKOM, A. B., 1917.—Mesozoic floras of Queensland: Part I concluded. The flora of the Ipswich Series d) Ginkgoales e) Cycadophyta f) Coniferales. *Qd. Geol. Surv. Publ.* **259**: 1-30.

——————, 1919.—Mesozoic floras of Queensland, Parts III and IV. The floras of the Burrum and Styx River Series. *Qd. Geol. Surv. Publ.* **263**: 76 iv.

——————, 1919a.—On a collection of Jurassic plants from Bexhill, near Lismore, N.S.W. *Proc. Linn. Soc. N.S.W.,* **44**: 180-190.

WALKOM, A. B., 1921.—Mesozoic floras of New South Wales Part I. Fossil plants from Cockabutta Mountain and Talbragar. *Mem. Geol. Surv. N.S.W., Pal.* **12**: 21 u.

WARDLE, P., 1963.—Growth habits of New Zealand sub alpine shrubs and trees. *N.Z. J. Bot.* **1**: 18-47.

WILDE, M. H., 1945.—A new interpretation of the coniferous cone. I Podocarpaceae (*Podocarpus*) *Ann. Bot.* n.s. **8**: 1-41.

WILSON, L. R., 1962.—Permian microfossils from the Flowerpat Formation, Green Country, Oklahoma. *Oklah. Geol. Surv. Circular* **49**: 1-50.
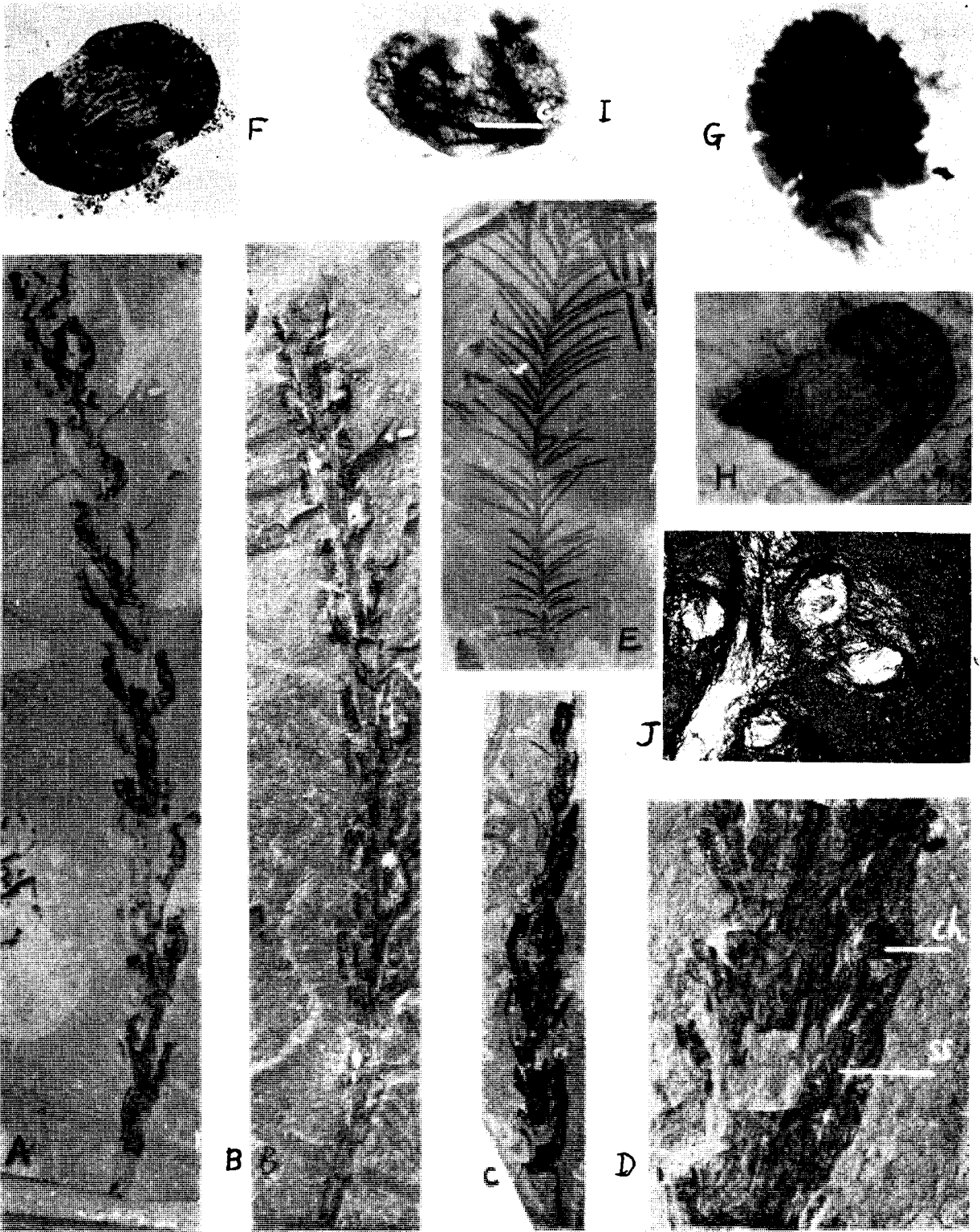
PLATE 1.—*Rissikia media*, A, B, E-H; *R. apiculata* C, D. *Mataia podocarpoides*, J; *Striatites sewardii* of Pant 1.

A, B. Part of the seed cone, under kerosene (A) and dry (B). x 2. Australian Museum F51972, 51973. C. A seed cone, taken under kerosene x 2. D, lower right part of cone, showing chalaza of seed (*ch*), seed stalk *ss*, and form of lobe of cone scale. x 6. Australian Museum F51983. E. A complete foliar spur x 1, Australian Museum F51960. F. Pollen grain with many striae. H. pollen grain with few striae, x 500. Australian Museum AM 6413. G. Seed somewhat compressed and crushed. Micropyle shown by black speck to right (cf. Fig. 9 J), and seed stalk on bottom left x 10, Australian Museum AM 6407. I. striate grain in slightly rotated proximal polar view, colpus 𝑐 x 300. Liveringa Frm. W. Australia prep. Dr. B. E. Balme. J. Cone unit with two seeds and overfolded portion. x 3. N.Z. Geol. Surv. 581-591.
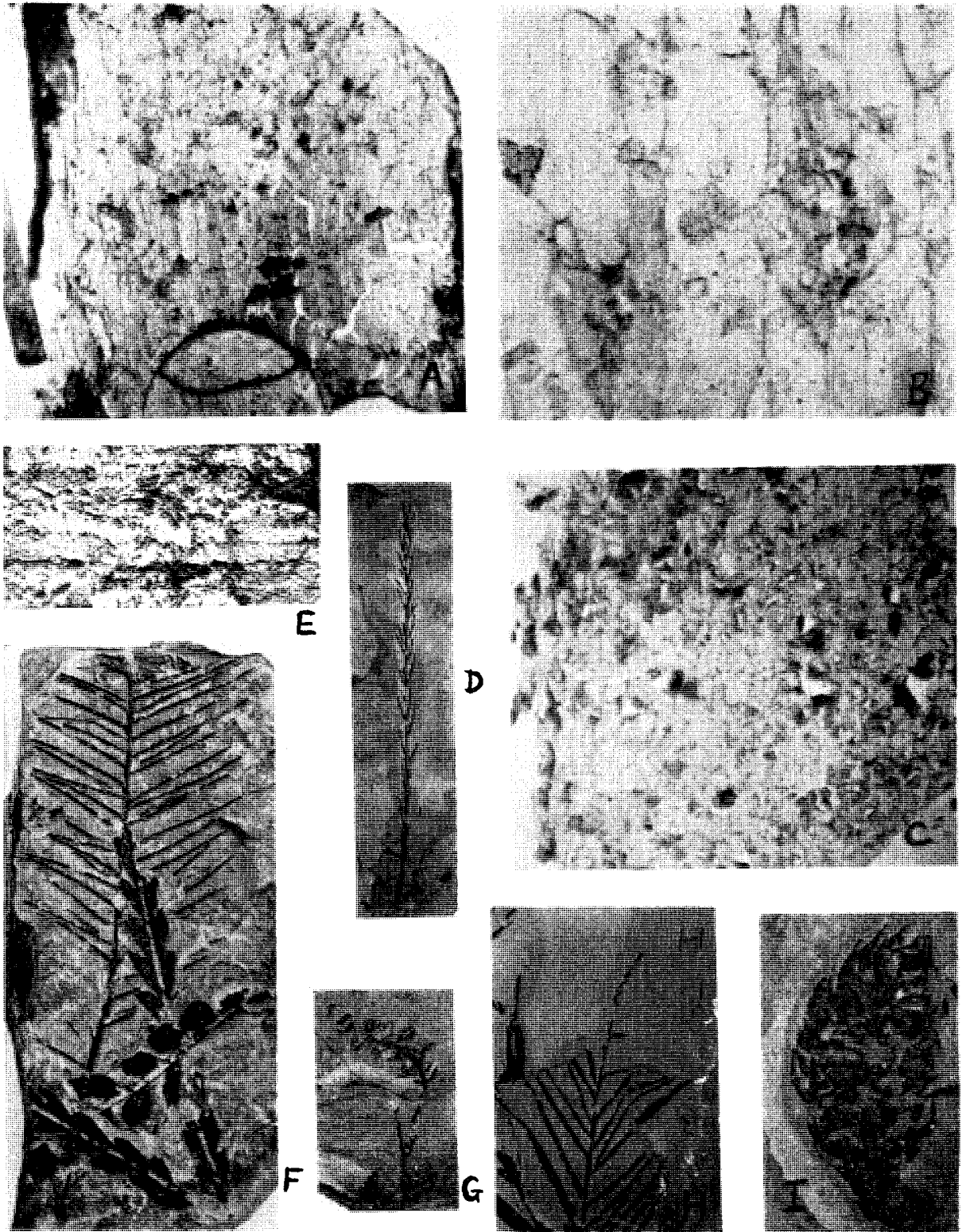
PLATE II.—*Rissikia media* A-C, F, H, I: *R. apiculata* D (holotype): *Elatocladus planus* E; *Mataia podocarpoides* G.

A, C: cuticle from two pairs of flanks of one leaf x 50, Australian Museum AM 6409. B: Two stomata with surrounding lappets x 250, Australian Museum AM 6404. D. A foliar spur, x 1, Australian Museum F51976. E: parts of two leaves showing "cells" of replacing mineral x 20. University Tasmania. F, a foliar spur x 1 from Mt. Bumstead, E. Antarctica, Lat. 82° S. New Zealand Geol. Survey B 822. G. A seed cone x 1, New Zealand Geol. Survey B 913. H, the apex of a foliar spur, just possibly growing on, i.e. not limited in growth x 1 Australian Museum F51966, I. The pollen cone x 2. Australian Museum F51972.