

NOTES ON SOME TASMANIAN PINES. I. SOME LOWER TERTIARY PODOCARPS

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(With two plates and 11 text figures.)

ABSTRACT

Podocarps from a new locality are described under the following names, *Podocarpus strzeleckianus* sp. nov. (Eupodocarpus), *P. tasmanicus* sp. nov. (Stachycarpus), *P. setiger* sp. nov. (Dacrycarpus), *P. goedei* sp. nov. and *P. acicularis* sp. nov. (of unknown Section), *Microstrobos sommervillae* sp. nov. and *Coronelia molinae* Florin. Of these *P. tasmanicus*, *P. strzeleckianus*, and *Coronelia molinae* represent sections or genera previously unknown in Tasmania, *M. sommervillae* represents the first fossil record of *Microstrobos*. Some features of the distribution of the Podocarpaceae are discussed.

INTRODUCTION

Conifers from the Tasmanian Tertiary were discussed by Florin (1940), and further studies (mostly of pollen) have since been undertaken by Cookson (1953), Cookson and Pike (1953, 1953a, 1954) and Cookson and Duigan (1951). There still are not many records of macrofossils. Lately Mr. Albert Goede, University of Tasmania, discovered a rich Lower Tertiary locality at Buckland, and with Mr. J. L. Davies, most generously turned the material over to me. I thank them for this courtesy. The following covers some of the Podocarpaceae, most of which belong to genera or sections already known from pollen, but some new records are included.

MATERIAL AND AGE

The Material. The material consists of detached leaves and fragments of leaves and shoots in a soft clay. At its best the clay is almost solid plant matter. The richest blocks were found loose in the bed of the Tea Tree Rivulet, and the possibility was considered that they might not belong with the strata on which they were resting. However, with Mr. Goede's help other material with, in part, the same flora, was found in situ. It is most likely that all comes from the same deposit.

The plant beds occur as lenses in lacustrine clays, and the material, is, presumably, the "sweepings" of the forest floor carried into a lake or other still water.

To isolate the plants the clay was soaked in dilute nitric acid (about 10% HNO₃), when it

broke down, and the plant material could be decanted off from the remaining clay. The fragments were then divided into sorts of leaf, and cuticles prepared from each sort. Although the final identification had to be done on the cuticle, after a while it became possible to determine the fragments unmacerated in about four cases out of five.

The locality of all species is: Bed of Tea Tree Rivulet, about two miles upstream from the Gatehouse Marsh causeway, Buckland, Tasmania.

For comparison, herbarium material and cuticles were examined from the following species: *Aemopyle pancheri*, *Dacrydium bifforme*, *D. colensoi*, *D. kirkii*, *D. franklinii*, *D. falciforme*, *D. taxoides*, *D. cupressinum*, *D. intermedium*, *D. elatum*, *Microstrobos niphophilus*, *M. fitzgeraldii*, *Microcachrys tetragona*, *Podocarpus andinus*, *P. montanus*, *P. spicatus*, *P. lalei*, *P. ferrugineus*, *P. ferruginoides*, *P. totara*, *P. lawrencei*, *P. acutifolius*, *P. hallii*, *P. nivalis*, *P. gnidioides*, *P. minor*, *P. vitiensis*, *P. dacrydoides*, *P. imbricatus*, *P. elatus*, *P. spinulosus*, *P. drouynianus*, *P. latifolius*, *P. henkelii*, *P. falcatus*, and *P. gracilior*.

Age.—Among the material are specimens of *Coronelia molinae* Florin. This species is only known from the Eocene Concepcion Coal Measures of Chile. Dr. S. Duigan kindly examined the pollen from one sample and found *Ephedra notensis* and *Triasaccites micropertus*, both only known so far from lower Tertiary or earlier localities. The evidence is not as strong as would be desirable, but a Lower Tertiary age seems most likely at present, possibly Eocene.

Nomenclature. The nomenclature of the fossils is unsatisfactory. Several species of podocarp pollen have been described (e.g. Couper 1960), and it is highly likely that some at least were produced by the same trees as produced the foliage here discussed. One is forced, however, to make a new name for the foliage, in absence of knowledge of the parent plant of the pollen. When the male cones are found, it is to be hoped that some of the names here suggested can be abandoned.

Throughout these notes type and figured material is referred to by its registration number in the collections of the Department of Geology, University of Tasmania, where it has been deposited.

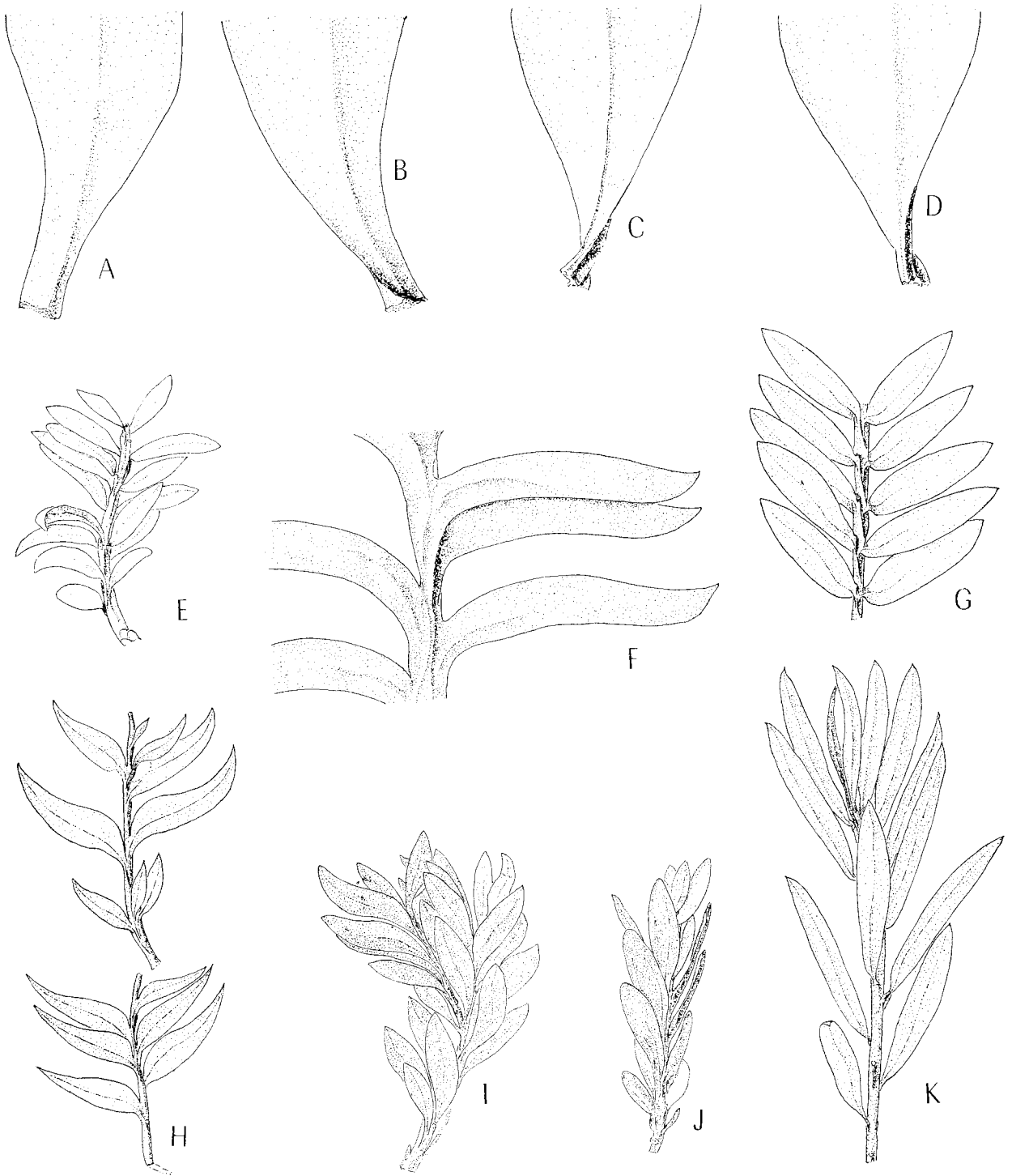


FIG. 1.—*Dacrydium taxoides*, A-D, I; *D. falciforme*, H; *Podocarpus ferrugineus* E; *P. dactydiodes*, F; *P. vitiensis*, G; *P. minor*, J; *P. falcatus*, K.

A-D: Leaf bases. A, B, of a leaf borne edge on to the shoot and scarcely twisted; C, D, borne flat on and strongly twisted $\times 15$.

E-K: Portions of shoots, to show leaf arrangement. F, note spirally inserted leaves flattened into one place with adjacent leaves pointing in the same direction.

E, G $\times 1.5$. I, J $\times 1$; H $\times 0.5$; K, 0.75; F $\times 10$.

DESCRIPTIONS

Family PODOCARPACEAE

Genus **PODOCARPUS** L'Herit

Section: *Eupodocarpus*, sub-section D Gray

PODOCARPUS STRZELECKIANUS sp. nov.

Pl. I C; Figs. 2 A, B, D, E, 6L-T.

Type specimen (Holotype): University of Tasmania, 81917 see Pl. I C.

Diagnosis. Leaf 2-3 mms. wide, about 1.5 cms. long, probably borne spirally on shoot and leaves not or only slightly twisted into two rows. Leaves monomorphic (as far as known). Leaves flat, of moderately thick substance, margins scarious, and showing small shoulders near the apex, but parallel sided over most of their length. Short petiole present, showing only slight twisting, more or less symmetrically inserted; leaf widening to full width within 1-3 mm. of petiole. Apex pointed, but not acuminate. Midrib projecting very slightly on stomatiferous side of leaf.

Cuticle 1.5-2 μ thick, but thinner over stomatal zones. Leaf hypostomatic, showing longitudinally orientated stomata close set in two narrow stomatal zones. Epidermal cells outside stomatal rows more or less elongated, 70 μ x 20 μ , outlines thin about 1.5 μ , nearly or quite straight. In stomatal bands cells about 50 μ x 20 μ , outlines thinner, and straight. Cells over scarious margin somewhat wider than over rest of leaf. Cuticle devoid of papillae or other ornament.

Stomata lying in rows about 12 (5-16) stomata high, stomatal zone showing 5-7 such rows across its width. Stomatal rows lying in 2-4 groups across width of a stomatal zone; within such a group laterally adjacent stomata having their lateral subsidiary cells touching; but having 1-3 rows of cells lying between any two such groups. Adjacent stomata in a row normally sharing a terminal subsidiary cell. Lateral subsidiary cells normally two, rarely three; stomata on edge of a stomatal group sometimes amphicyclic, other stomata rarely amphicyclic.

Stomatal aperture more or less rectangular, 20 μ x 10 μ , often distinctly elongated. Florin ring present. Surface of guard cells thinly cutinised, and scarcely thicker cutin present around the aperture.

Description. The material consists of broken leaves only no complete or attached leaf has been seen. The longest specimen is 1 cm. long (fig. 6 Q), and it is the basal part. By analogy with living conifers, it is likely that the presence of a petiole sometimes somewhat twisted (fig. 6, O, P.), indicates that the leaves were spirally borne and showed a slight tendency to be in two rows. In a good many hand specimens, the stomatal zones can clearly be seen, and between them the midrib projects very slightly (figs. 6, P, N); these specimens also show that the leaf was flat, or perhaps rarely slightly concave (fig. 6 R), and it appears not to have tapered towards the margin. The scarious margins, and its shoulders can be seen both on the intact specimen (figs. 6 L, M, S, T) and also on the cuticle as differently shaped cells.

No small leaves of this species were seen; it is probable, therefore that like e.g. *P. lawrencei*, *P. strzeleckianus* did not show a regular and prolonged series of small to large leaves in each year's increment.

Specimens from all parts of the leaf were available for maceration no stomata on the upper leaf surface were seen. The form of the stomatal zones is shown in pl. I. C, they were narrow, and sharply set off from the margins and midrib. They formed, however, a line of weakness in the cuticle, and were usually torn, often before manipulation. The arrangement of stomata within the zones is shown in figs. 2 A, D and given in the diagnosis. An important point is that the cell outlines were either straight, or only the slightly wavy (figs. 2 E). The Florin ring is visible on every stoma examined, but most plainly on the lateral margins of the stomatal pit (fig. 2 A, E).

Classification. *Podocarpus strzeleckianus* is believed to have small (1-2 cm.) leaves, probably spirally borne, petiolate with a scarious margin, hypostomatic with the stomata disposed in two well defined zones. This sort of leaf, according to Laubenfels (1953) is found chiefly in the Taxaceae, Pinaceae, Cephalotaxaceae and Podocarpaceae. The first three are unlikely, for *P. strzeleckianus* shows points of difference from all, e.g. it lacks the cuticular papillae of the Taxaceae (Florin 1931, 1953). They are also unlikely on geographical grounds (Florin 1963). On the other hand it agrees well with certain podocarps, especially those of the subsection D of section *Eu-podocarpus* (Gray 1956, see also Florin 1931; Wasscher 1941, Orr 1944). The other sections can be disposed of: *Dacrycarpus* has bilateral juvenile leaves and awl-like adult ones, *Microcarpus* scale leaves, *Nageia* several veins per leaf, *Polypodiopsis* a special leaf arrangement and nearly equally amphistomatic leaves, *Afrocarpus* has amphistomatic leaves, and *Sundacarpus* large leaves. The section *Stachycarpus* is a possibility, but in this section the hypostomatic species appear to have rather wide stomatal zones (Florin 1931 and cf. figs. 3 A, D) and strongly wavy cell outlines. Of the other subsections of *Eu-podocarpus*, sub-section B has no Florin ring (this subsection contains the mainland Australian species *P. spinulosus* *P. elatus* and others), while sub-section E (*P. rostratus*) has minute leaves. Sub-sections A and C appear to be characterised by having rather large leaves, that is 2 cms. or more long, and this makes them unlikely, though remaining perhaps a possibility. Sub-section F has large leaves and also no Florin ring (Bucholtz and Gray, Gray 1948, 1953, 1955, 1956, 1958).

A difficulty might be that the cell outlines are usually (but not quite always) straight; *P. gnidioides* is nearly the same, however. It might be argued that the scarcely projecting midrib is a difficulty. I doubt this, for in a species such as *P. lawrencei* described as having a strongly projecting midrib, *living* material, or wet rotten leaves, do not show a projecting midrib; what happens is that as material dries, e.g. on an herbarium sheet, the tissue under the stomatal zones collapses.

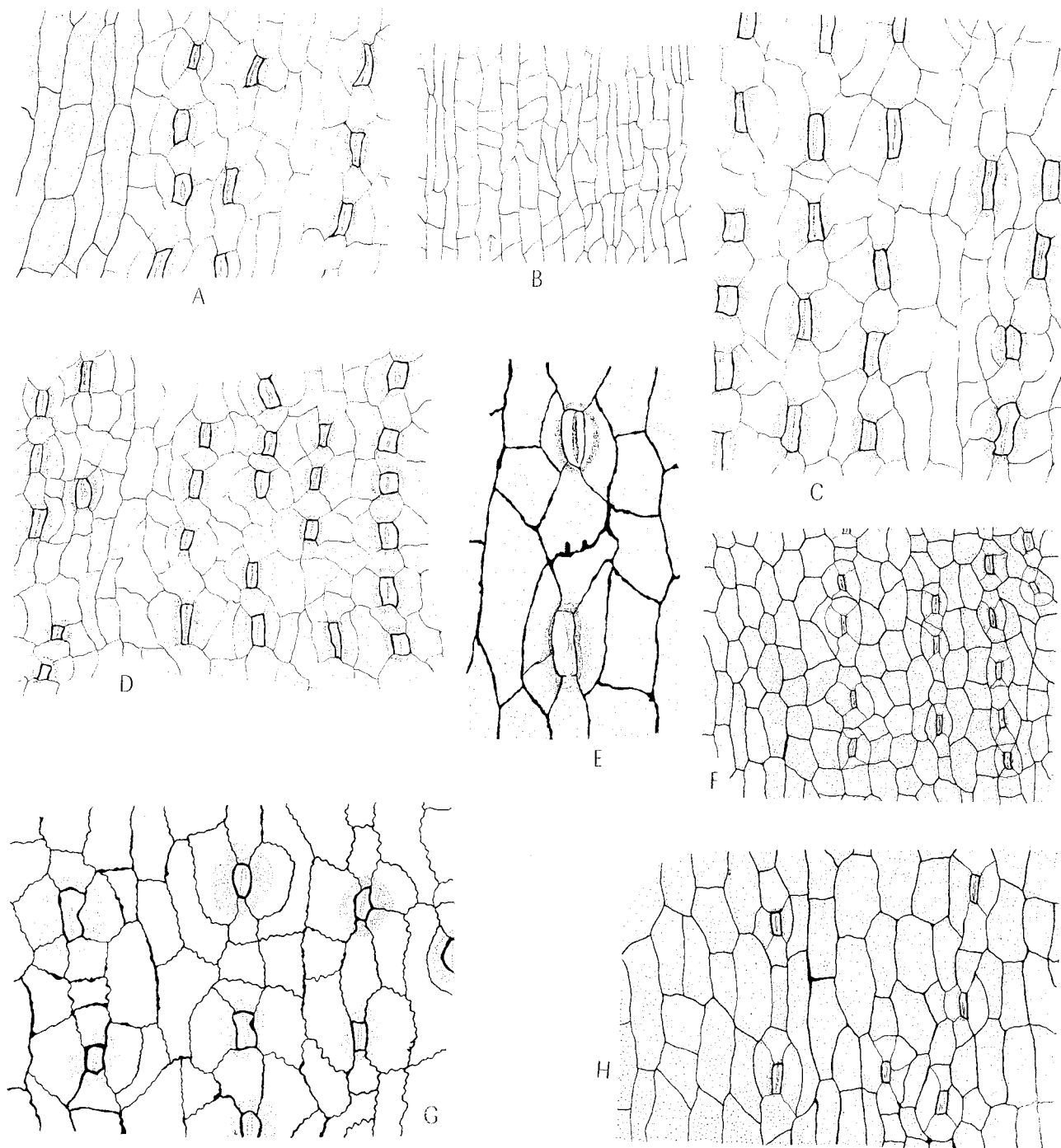


FIG. 2.—*Podocarpus strzeleckianus*, A, B, D, E; *P. gnidioides*, C; *P. tasmanicus*, F, H; *P. totara*, G.

A, D: Lower cuticle, with stomatal rows and (A, to left) margin. x 350. 81916.

B: Upper cuticle, margin marked by arrow, showing differently shaped cells. x 170. 81916.

C: Lower cuticle, note similarity to A and D. Herb. N.S.W. x 350.

E: Stomatal details and sinuosities of cell outlines. x 600. 81916.

F, H: Upper and lower cuticle, showing stomatal arrangement in stomatiferous zones. x 230. 81909.

G: Lower cuticle, showing stomatal arrangement and sinuosities on outlines. Herb. N.S.W. x 350.

It is not possible to compare *P. strzeleckianus* specially closely with any one of the species placed in sub-section D. In showing a scarious margin and a nearly flat leaf *P. strzeleckianus* resembles *P. totara* and is distinct from e.g. *P. laurencei*. The cuticles of sub-section D seem to show two intergrading sorts of stomatal arrangement in the zones; either the stomata are more or less evenly scattered, and without touching lateral subsidiary cells (*P. totara*, *P. hallii*, *P. laurencei*, *P. nivalis* fig. 2 G) or else the stomatal rows are grouped into sub-zones within which lateral subsidiary cells of adjacent stomata do (often) touch, each sub-zone being separated by a file one or two cells wide from its neighbours (figs. 2 C). This is the disposition most usually seen in *P. strzeleckianus* (fig. 2 D) and it is also seen in *P. gnidioides* and *P. acutifolius*.

Sub-section D has not been definitely reported fossil from the early Tertiary before. Florin (1940: 33) considered the *Elatocladus kerguelensis* Seward and Conway (1934) was probably of the group, close to *P. nivalis*, but in absence of microscopic detail did not make a firm identification. It would seem likely that this sub-section was already defined by the Tertiary, in at least one of the areas it now occupies, but it is very doubtful whether the species now extant were then in existence.

Section: *Stachycarpus* Endlicher, sub-section *Idioblastus* Bucholtz and Gray.

PODOCARPUS TASMANICUS sp. nov.

Pl. I A; Figs. 2 F, H; 3 A, D, E; 6 A-K; II A, B.

Type specimen (Holotype)—University of Tasmania No. 81905. See figs. 6 H, I.

Diagnosis. Leaves 2-3 mm. wide, about 1 cm. long. Almost certainly spirally borne, and larger leaves very probably twisted into two rows. Leaves dimorphic, size ranging from small oval leaves 2.5 x 1.5 mm. to size given. Leaves flat, of thick substance tapering to a thin, but not scarious nor inrolled, entire and even margin.

Petiole, or (at least) a basal contraction of the leaf present, up to 2 mm. long and in larger leaves asymmetrically inserted, leaf widening within 3 mm. to maximum width thereafter more or less parallel sided, or rarely bulging slightly. Apex pointed or blunt. Midrib obscurely visible on lower leaf surface.

Cuticle 2-2.5 μ thick more or less same thickness all over. Leaf unequally amphistomatic, showing on lower surface two wide stomatal zones separated by a distinct non-stomatiferous zone over the midrib. On upper surface, stomata up to about half as numerous as on lower surface, usually more or less scattered, especially numerous in the midrib region; distally, sometimes showing imperfect separation into two zones. Epidermal cells outside stomatal bands elongated longitudinally, 65 μ x 24 μ , outlines slightly wavy, or pierced by holes, or (most often) straight, 5 μ thick. Epidermal cells in stomatal zones about 38 μ x 30 μ , otherwise similar to the rest. Cuticle devoid of papillae or other ornament.

Stomata lying in rows about 15 (7-20) stomata high, and stomatal rows separated from one another by one or two rows of cells so that lateral subsidiary cells of adjacent stomata do not touch. Within rows stomata usually having their own terminal subsidiary cell, terminal encircling cell either absent or shared between adjacent stomata. Usually two lateral subsidiary cells, but three or four seen, stomata most often amphicyclic with respect to lateral subsidiary cells, or stomata in adjacent rows sharing a lateral encircling cell. Stomata on upper leaf surface as those on the lower.

Stomatal aperture rounded, or rectangular, 14 μ x 8 μ , sometimes almost square, Florin ring present, but sometimes indistinct. Guard cells feebly cutinised, even round the aperture.

Description. As with *P. strzeleckianus* attached leaves have not been seen, but again as in that species, the presence of a more or less strongly twisted petiole suggests a spiral leaf arrangement, in this case more definitely modified by twisting into two rows. There are a few complete probably small leaves (fig. 6 A, C, H) but more fragments; the leaf seems to have been a small one, however, i.e. less than 2 cms. long. There is a steady gradation between the small almost scale like leaves and the larger ones, and, except for size and the position of the petiole (or basal contraction) there is no difference between the different sorts of leaf (fig. 6 C, D). A similar gradation can be seen over the years increment in *Podocarpus ferrugineus*, *P. ladei* and *P. ferruginoides* and doubtless others (figs. 1 E, J). It is unlikely that *P. tasmanicus* was like e.g. *Sequoia sempervirens* in which the change over from small scale leaves to full sized ones tends to be abrupt.

In this case, as in *P. strzeleckianus*, I assume that the surface upon which the midrib projects, and upon which the majority of stomata lie is the lower; this seems to be only reasonable (Florin 1931, Laubenfels 1953).

In most leaves the margin shows one or two cell rows beneath which the substance is thin, almost to the point of forming a scarious margin (fig. 6 H, I). This feature is not accompanied by any difference in the epidermal cells, and I suggest it probably represents a tapering margin (e.g. *P. ferrugineus*) as against a thick one (e.g. *P. laurencei*).

The cuticle is somewhat variable, especially in the number of stomata on the upper leaf surface (Pl. I A and figs. 2 F, H). This feature however, is also variable in the material of living *Podocarpus* species, and I am inclined to disregard it, though it is always possible that the material is composite. On the under surface the non-stomatiferous zone over the midrib (fig. 11 A, B) appears to be constant and well marked. The cell outlines are shown in figs. 3 C. On the other hand the stomata were similar in all the material, the chief variation (which was not great) being in the shape of the stomatal pit (figs 3 A, D). The Florin ring was sometimes obscure, though I think probably always present, and of about the same size all round the stoma.

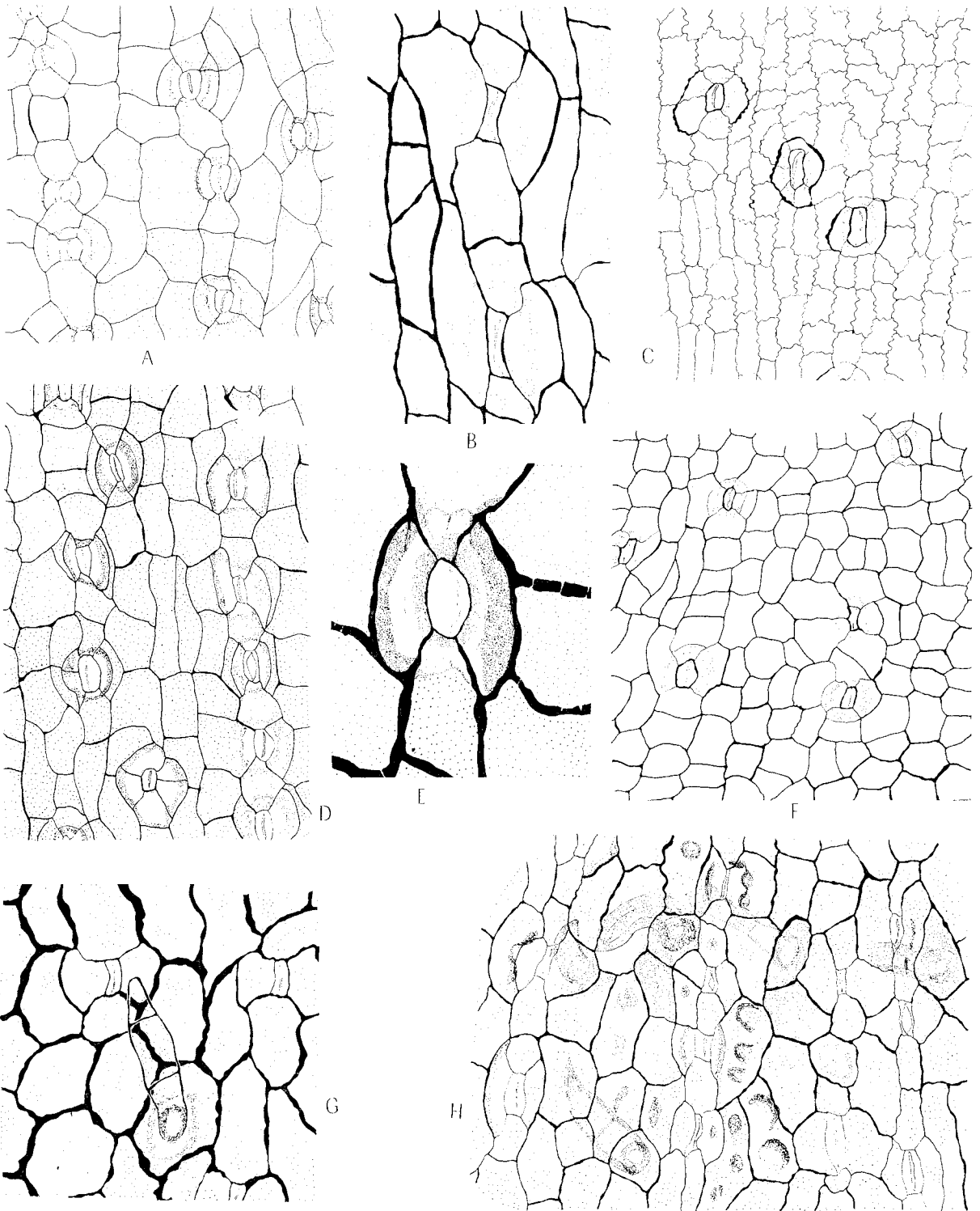


FIG. 3.—*Podocarpus tasmanicus*, A, D, E; *P. acicularis*, B; *P. andinus*, C; *P. ferrugineus*, F; *Coronelia molinae*, G, H.
 A, D: Cuticle from large and small leaf respectively, showing varying appearance of stomata and epidermal cells. x 430.
 A, 81911. D, E, 81912.
 B: Somatal details and subsidiary cells. x 600. 81925.
 E. Stomatal details, showing Florin ring, and holes in the cell outlines. x 600.
 C, F: Upper cuticle showing stomata; note straight cell outlines in F. C. Bot. Gdn., Hobart; F. Herb., N.S.W. x 230.
 G: Stomata, cell outlines and a large hair. The cells scarcely are papillate. x 430. 81898.
 H: The same, note large papillae on some cells. x 430. 81898.

P. tasmanicus and *P. strzeleckianus* superficially are similar, but can fairly readily be told apart, on the hand specimen by the form of the margin, and by the appearance of the stomatal bands, which are scarcely visible in *P. tasmanicus*. The cuticles separate them without difficulty, there is, indeed scarcely a feature in which confusion could arise.

Classification. *Podocarpus tasmanicus* is believed to have had spirally disposed leaves, probably twisted into two rows, and grading over gradually from small to large leaves but all more or less of the same sort. The leaves were small (1-2 cm.) flat, petiolate, unequally amphistomatic, with stomata lying in two wide rows on the under surface, but more scattered above, and all longitudinally oriented. It seems to me that this combination of characters again indicates the Podocarpaceae, genus *Podocarpus*. Following the argument given for *P. strzeleckianus*, I suggest that *P. tasmanicus* is likely to belong to the Section Stachycarpus.

It is possible that these leaves might be the juvenile leaves of a *Dacrydium species*, but this is I think unlikely. There are fewer stomata on the upper leaf surface than appears to be usual in *Dacrydium* juvenile leaves, and there is evidence that the leaves were twisted into two rows. The stomatal zones are also more definite than appears to be usual in *Dacrydium*.

Section Stachycarpus has been divided into two sub-sections by Bucholtz and Gray (1952) as follows:—

Idioblastus—with idioblasts, and an unequally amphistomatic leaf (*P. ladei*, *P. ferruginoides* and (originally) *P. distichus*).

Eu-prumnopitys—without idioblasts, and hypostomatic, except *P. andinus* and *P. ferrugineus* (described as hypostomatic, but see p. 7).

The fundamental character is the presence of idioblasts. These would be difficult to demonstrate in fossil material, though they might be visible in partly macerated leaves (cf. Harris 1958). In fact I have been unable to see anything that could be called an idioblast, but this is not conclusive.

As regards stomatal distribution there is difficulty, *P. tasmanicus* approaches *P. ladei* in number of stomata on the upper leaf surface, and like *P. ladei* shows a definite non stomatiferous zone over the midrib, though more definite than *P. ladei* (fig. 10 A, F). There are still not nearly as many stomata on the upper surface in *P. tasmanicus* as *P. ladei*. *P. tasmanicus* shows more stomata on the upper leaf surface than *P. ferruginoides* and *P. distichus*, and differs further from these leaves in showing a definite non-stomatiferous zone over the midrib (figs. 11 E). It resembles *P. ferrugineus* in this (fig. 11 C) though having more stomata on the upper leaf surface. *P. ferrugineus* also may show, like *P. tasmanicus*, nearly straight cell outlines, unlike *P. ferruginoides*, but again like *P. ladei*. The leaf margin is also believed to have been tapering as in *P. ferrugineus*.

On the whole I think comparison is closest with *P. ladei*, and *P. tasmanicus* is accordingly placed in sub-section Idioblastus. It is interesting that *P.*

ladei has the smallest idioblasts of the three species of the sub-section. It is also interesting that there is the uncertainty in classification (there is not in dealing with the cuticles of the living species, so far as I have seen them): it might suggest that in the early Tertiary the difference between the two sub-sections was not so great as at present. At present *P. ladei* grows in a small area near Atherton (Queensland) *P. ferruginoides* and *P. distichus* in New Caledonia, and *P. ferrugineus* is confined to New Zealand.

Note on the leaf anatomy of *Podocarpus ferrugineus* Don.

Podocarpus ferrugineus is usually stated to be amphistomatic in the juvenile leaves, but hypostomatic later (see e.g. Griffin 1908, Florin 1931: 362-363, Bucholtz and Gray 1951: 351). In the material available to me this is not entirely so. I have seen only one specimen that was hypostomatic, coming from the Botanical Gardens, Melbourne; and it showed on the small leaves starting the years increment, a very few (1-5) stomata on the upper surface. This specimen was unusually small leaved, and also showed unusually tightly packed stomata in the stomatal rows. The remaining material always showed some stomata on the upper surface, sometimes quite numerous at the apex, (fig. 11 C, D) down to only a very few. For the most part the stomata reached less than a quarter the way down the leaf, but in one specimen (from Upper Hutt) they reached about three quarters way down the leaf, and this specimen also showed a band of elongated cells over the midrib. In general, where there were stomata on the upper leaf surface the cell outlines were very nearly straight (fig. 3 F). The stomata were mostly in the region of the midrib, and in details, like those on the lower surface (see Florin 1931: pl. 21 fig. 6).

It would seem better to describe the stomatal arrangement of this tree as "unequally amphistomatic, but sometimes hypostomatic; stomata on upper surface few, lying towards apex, rarely seen more than a third way down the leaf". In its stomatal arrangements *P. ferrugineus* comes very close to the sub-section Idioblastus e.g. *P. ferruginoides*. It differs from *P. ferruginoides* and *P. distichus* in showing (normally) a distinct non stomatiferous zone over the midrib. Such a zone is also present in *P. ladei*, but possibly less pronounced than in *P. ferrugineus*. (Figs. 11 C-F). The absence of idioblasts is ultimately the only reason for placing *P. ferrugineus* in sub-section Euprumnopitys.

Material Examined.

- (1) Geological Survey of New Zealand: exact locality not given.
- (2) National Herbarium, New South Wales:
 - (a) from Upper Hutt,
 - (b) from Huia near Auckland,
 - (c) tree growing in Melbourne Botanic Gardens,
 - (d) no locality beyond New Zealand,
 - (e) no locality beyond New Zealand.

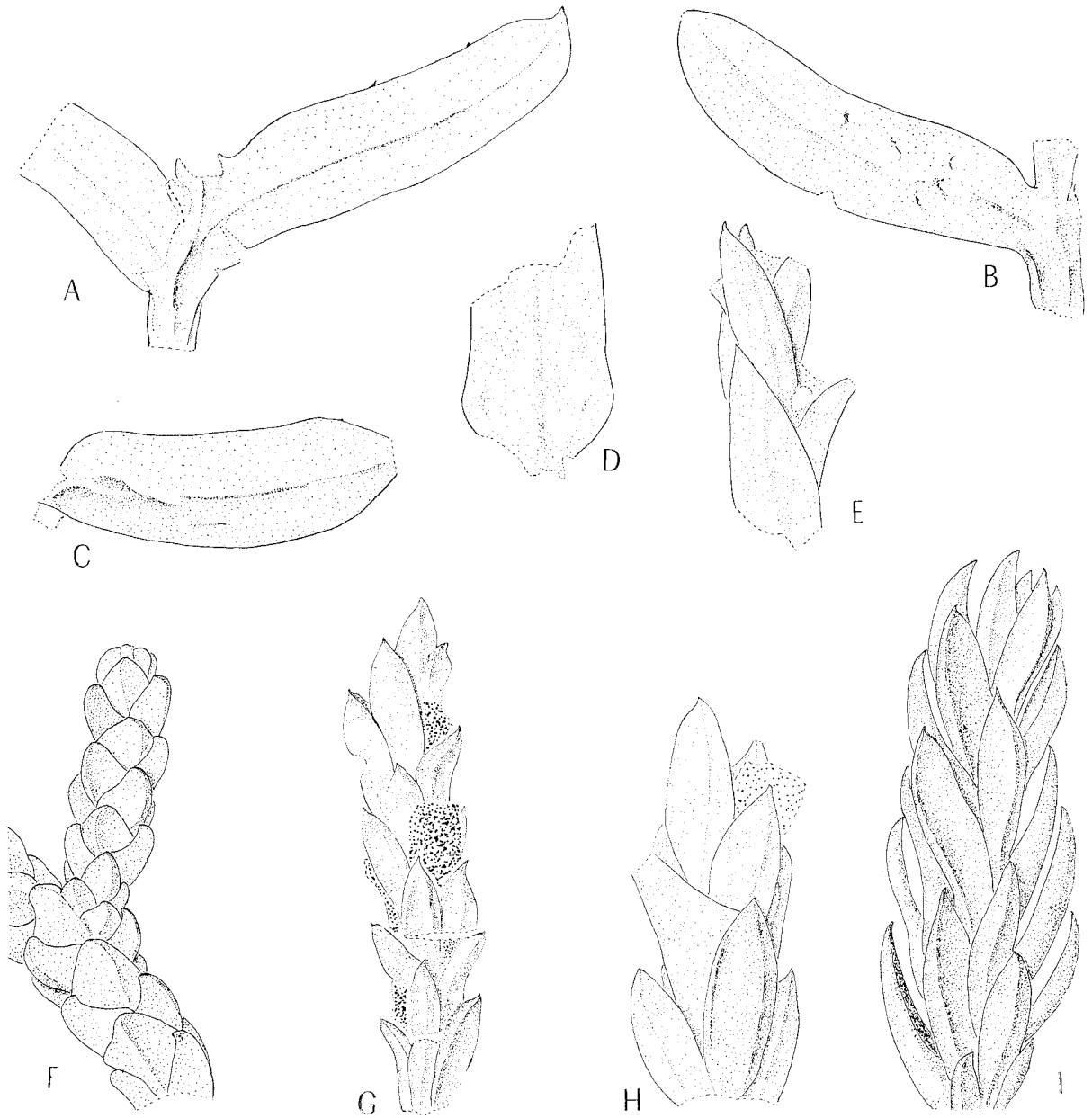


FIG. 4.—*Podocarpus setiger*, A, B, C; *Coronelia molinae*, D; *Microstrobos somervilleae*, E, G, H; *M. niphophilus*, F; *M. fitzgeraldii*, I.

A, B: Parts of two leafy shoots. x 10. 81918, 81919.

C: A rather short leaf, apex broken off. x 10. 81921.

D: A leaf base, note widest part of leaf very near base. x 10. 81899.

E, K: Lengths of shoot, with leaves of varying size. Heavy stipple marks where leaves are missing, all x 15. E, 81902; G, 81900; H, 81903; F and K, Herb. Univ. Tas.

- (3) Arnold Arboretum, Cambridge, Mass. (annotated by late Prof. J. Bucholtz):
- (a) Longwood Range, New Zealand Cockayne, 9096,
 - (b) Bay of Island, New Zealand,
 - (c) New Zealand, Wilson S.N. 2/28/21.
- (4) Botanic Gardens, Dunedin: in cultivation.

Section: *Dacrycarpus* Endlicher.

PODOCARPUS SETIGER sp. nov.

Pl. 2 A; Figs. 4 A, B, C; 5 B, E; 7 F; 10 A, B.

Type specimen (Holotype); University of Tasmania. No. 81908 see Fig. 4 A.

Diagnosis. Bilateral leaves only known; these about 6 mm. long (4-8 mm.) and 2 mm. wide (1-2.5 mm.); straight or slightly falcate, apex acute to mucronate, mucro forming angle of about 60° with axis. Base contracted, leaf at base about 1.5 mm. wide, contraction seen only on upper leaf edge, leaf as a whole decurrent, and probably borne in two ranks on the axis. Midrib prominent, asymmetrical, lying nearer lower leaf edge, substance of leaf bulging somewhat over midrib, but leaf otherwise flat and (probably) thin in life. Edges entire, showing about 10 stiff cutinised unicellular bristles along their length.

Cuticle amphistomatic, stomata much more numerous on one pair of flanks than on the other, and borne in four extremely distinct narrow zones. Cells outside stomatal zones elongated, forming parallelograms or sometimes rather wider at the ends than in the middle, about 140 μ x 40 μ . Outlines distinct, pierced but not wavy. Within stomatal zones cells less elongated, about 50 μ x 30 μ , outlines finer. Characters of cells maintained in stomatal zones whether stomata present or not. Stomata lying in narrow rows, 20 or more stomata long, and stomatal zone at any point 3-7 (mainly 4 or 5) stomata wide. One pair of flanks showing fewer stomata, stomata mostly present near apex; cells looking like guard cell and subsidiary mother cells forming most of the cells in the zones. Stomata unequally amphicyclic, or two adjacent stomata showing a common encircling cell; adjacent stomata in a row normally showing a common terminal subsidiary cell. Lateral subsidiary cells most often two, rarely 3 or 4. Stomatal pit rectangular, about 20 μ x 7 μ , guard cells feebly cutinised even next to aperture. Surface of subsidiary cells flat.

Margin showing a few (up to 12) bristles along its length. Bristles arising from a single cell, unicellular, about 70 μ long, thickly cutinised except at base, which is hollow, orientated same way, pointing towards leaf apex.

Description. Three specimens showed leaves still attached to the parent shoot, indicating that they were bilateral (figs. 4 A, B). The leaf seems to have been rather uniform in its external morphology, the upturned apical point is sometimes missing, however. There is variation in the extent to which the base is contracted, if it is, the contraction takes place in that part of the leaf above the midrib (figs 4 A-C). There is no sign of wrinkling over the midrib, so I suppose the leaf

was flat in life, as it is now in the fossil. The cuticle is highly characteristic. The chief features are: (1) the highly distinct stomatal zones, containing several stomatal rows, (2) the tendency for most stomata to lie on one pair of flanks, but the existence of the stomatal rows, only devoid of stomata, on the other pair of flanks (fig. 10 B, pl. 2 A), and (3) the bristles. The tendency for the stomata to lie on one pair of flanks might perhaps indicate that the leaves were borne at an angle to, and not parallel with, the illumination. The features of the stomata are given in figs. 5 B, E; 7 F; 10 A, B.

Classification. The leaves of *P. setiger* are clearly bilateral, and of living groups showing bilateral leaves, the stomatal arrangement and form agree only with *Podocarpus* sect. *Dacrycarpus*. I have not, however, succeeded in finding the bifacial foliage that one might expect also to occur. Perhaps as in *P. imbricatus*, most of the leaves were bilateral, borne on foliar spurs.

Pollen of the section *Dacrycarpus* is known from several Tertiary localities (Cookson and Pike 1953, Couper 1960), and *Podocarpus praecupressinus* and *Podocarpus* sect. *Dacrycarpus* sp. (Selling 1950) have been described. Cookson and Pike (1953) emphasize the difficulty of distinguishing vegetative shoots of the section *Dacrycarpus*, but while acknowledging the uncertainty, I think comparison can be pressed further than they are willing to go.

P. setiger differs from *P. praecupressinus* Ett. in that (1) its bilateral leaves are about twice as big, (2) it has stomatal zones 4 or 5 stomata wide, as against only 1 or 2 (rarely 4, see pl. 2 fig. 20), (3) the stomatal pit is more nearly rectangular, and (4) it has bristles along the margin, lacking in *P. praecupressinus*. Among living species, none (so far as I can discover) show the bristles on the margin. However *P. javanicus* comes close in stomatal arrangement (Florin 1931, pl. 29 fig. 10) showing dense massed stomata in zones, as opposed to rather well separated rows in the zones. *P. imbricatus*, however, links the two situations. These two species are sometimes identified.

P. praecupressinus seems to me to be very close to the New Zealand species *P. dacrydioides* and exceedingly close to (if not identical with) *P. inopinatus* (compare Florin 1931 pl. 2; pl. 15 fig. 8; pl. 18 fig 4, 1940: pls. 5 and 6; and Cookson and Pike 1953 pl. 1 figs. 2, 3; pl. 2 figs 20, 24); but *P. setiger* compares with the more tropical *P. javanicus*. As shown by others (e.g. Selling 1950) the early Tertiary seems to have contained (in part) a mixture of forms now either in the tropics or in temperate regions.

Genus *Podocarpus* l'Herit. (Section unknown)

PODOCARPUS GOEDEI sp. nov.

Pl. 1 B. Figs. 8 C-I; 9 J-T; 10 C.

Type specimen (Holotype); University of Tasmania Nos. 81928a. see Figs. 8, 9, H.

Diagnosis. Leaves bilateral, but (probably) borne in opposite or nearly opposite pairs. Leaf bases usually contracted to an angular petiole, sometimes twisted one pair of flanks over the other, so that

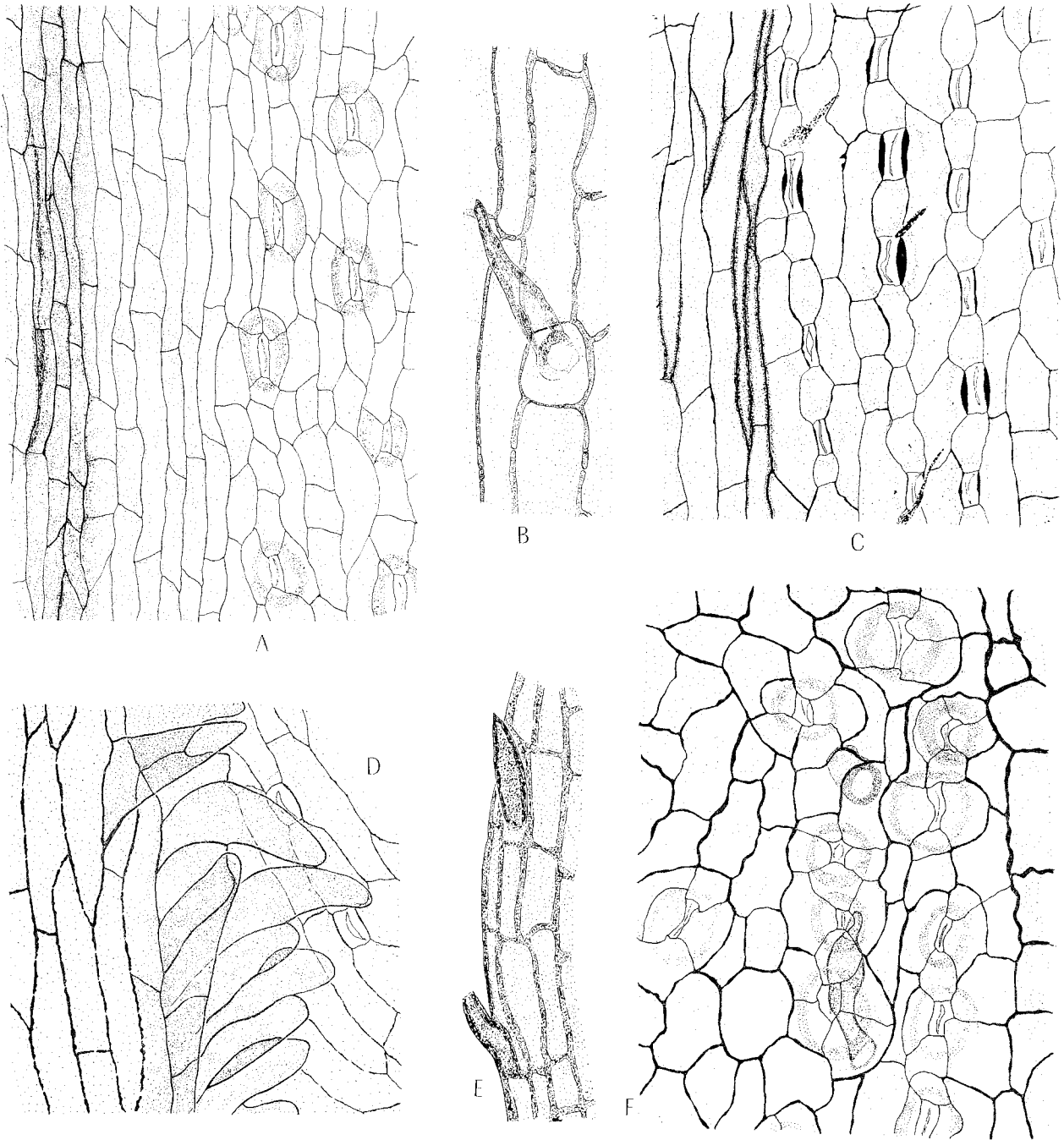


FIG. 5.—*Podocarpus acicularis*, A; *P. setiger*, B, E; *Microstrobis sommervilleae*, C, D; *Coronelia molinae*, F.
 A: Cuticle showing stomatal arrangement and marginal zone. $\times 350$. 81926.
 B, E: Hairs from leaf margin, small (un-macerated) and, B, larger (cuticle only). B $\times 230$, 81922; E $\times 430$. 81918.
 C: Cuticle upper surface, stomata and marginal zone. $\times 650$.
 D: Margin with processes, lower cuticle (left), note pierced cell outlines. $\times 650$.
 F: Cuticle, with closely massed stomata, with Florin ring. $\times 430$.

leaves (probably) sometimes showed one pair of flanks pointing upwards, the other pair down. Leaves flat, thick, midrib obscurely visible on one surface only, often falcate. Margins even, parallel over most of the length of the leaf, contracting gradually at base, but more or less suddenly to acute apex. Leaves 6-15 mm. long and 1.5-3 mm. wide.

Cuticle about 3 μ thick, amphistomatic, two surfaces almost indistinguishable, stomata distributed in long vague rows, or in short groups of 2 or 3 within rows, over the whole surface except a band at each margin, midrib not visible on cuticle. Over most of leaf cells about 50 μ x 30 μ , in marginal bands elongated, about 50 μ x 18 μ , cells rectangular more or less in rows, cuticle surface flat, or, especially along margins, showing small thickenings, several to a cell. Cell outlines distinct, straight or very slightly undulating, devoid of perforations or projections. Stomatal rows irregularly placed, 3-20 (usually 10-15) stomata high, stomata orientated longitudinally. In a row adjacent stomata often sharing common terminal encircling cell, or encircling cell absent, rarely sharing a common terminal subsidiary cell. Most often two lateral subsidiary cells, encircling cells usually present. Florin ring present and distinct. Stomatal μ t overhung by subsidiary cells, aperture rounded or slightly elongated; guard cell surface fairly strongly cutinised.

Description. The manner in which the leaves were borne is left over for discussion with *P. acicularis* (p. 11). The leaf contracts to an angled petiole, but the transition is gradual (fig. 9 Q, R) suggesting that the leaf may have been thick. By analogy with living conifers the obscure midrib and the absence of a non-stomatiferous band in the cuticle over the midrib also suggest a thick leaf (pl. 1 B, figs. 11 G). The cuticle from the two surfaces of the leaf is nearly indistinguishable; the only difference I can see is that one (presumably the lower) may be slightly thinner. This seems to be unusual, normally some difference is discernible (pls. 1 A, C; 2 B and see Florin 1931). At the apex and base there is an obscure suggestion that the stomata lie in four zones, (cf. fig. 11 H), but elsewhere on the leaf, no midrib region can be made out; there may be short lengths in which there does seem to be a non-stomatiferous zone, but they do not last. The details of the stomata are given in the diagnosis and in pl. 1 B and fig. 10 C. They were rather uniform. Some specimens have a rather thick cuticle, but no other regular difference from the rest; I have disregarded this difference and called all specimens the one species.

PODOCARPUS ACICULARIS sp. nov.

Figs. 3 B; 5 A; 8 A, B; 9 A-I; 11 H.

Type specimen (Holotype) University of Tasmania No. 81923 see Fig. 8 B.

Diagnosis: Leaves bilateral, probably spirally borne, normally contracting to an angular petiole, often twisted one pair of flanks over the other. Leaves flat or sometimes probably needle-like in section. Leaves 4-8 mm. long and 0.5-1 mm. wide.

Cuticle about 3 μ thick, amphistomatic, two surfaces only differing very slightly in stomatal density, or not at all; stomata lying well separated in long rows or in groups of two (rarely 3) over entire leaf surface except margins. At apex and base stomata grouped into four more or less definite rows. Cells and cell outlines as for *P. goebei*; 62 μ x 20 μ , in stomatiferous areas cuticle surface always flat. Stomata usually amphicyclic, with distinct terminal encircling cells, but terminal encircling cell sometimes shared between adjacent stomata; where two stomata lying in a group, terminal subsidiary cell often shared, Florin ring distinct, stomatal aperture more or less strongly elongated.

Description. There are only some half a dozen specimens in which the leave of *P. goebei* and *P. acicularis* are attached to their parent shoot. In *P. goebei*, the leaves in the available material come off from opposite sides of the shoot and at, or nearly at, the same level (figs. 8 D-H). In this species it is supposed that the leaves were borne in opposite pairs. On the other hand in *P. acicularis* one clear specimen shows two adjacent leaves pointing over on to one side of the shoot, the base of a third points in the opposite direction and it is at a different level (fig. 8 A). This appearance is like that in *P. dactyloides* (fig. 1 F) which has spirally borne bilateral juvenile leaves: *P. acicularis* is therefore described as having spirally arranged leaves.

The leaves of both species are described as bilateral because of (1) their insertion (cf. figs. 8 and figs. 1 F, H) and (2) the form of the apex (cf. figs. 8 B, 9 D, E, J, K) and (3) the stomatal distribution in *P. acicularis*, showing four stomatal zones (fig. 11 H). In both species the leaf is usually contracted to an angled petiole, which is sometimes twisted so as to bring one pair of flanks directly over the other. Sometimes the petiole is untwisted (figs. 9 G, I, M-T). This situation finds a parallel, among bilaterally leaved conifers, in *Dacrydium taxoides*, where the petiolate leaf base is twisted, or not, in a very similar way (figs. 1 A-D). From this parallel a suggestion can be made as to the manner in which the leaves were arranged.

In *D. jalciforme*, and also in *Podocarpus dactyloides* and *P. imbricatus*, the leaves are arranged in two rows, though spirally inserted (figs. 1 F, H). However, in *D. taxoides* this is not always so. Some decurrent leaf bases are twisted to bring these leaves into two rows up the shoot, but the orientation of the leaf relative to the shoot itself is unaltered; the leaf is set "edge on" to the shoot. These leaves are not, or only slightly, twisted in the petiole or lower blade (fig. 1 I). Other leaves, however, are not much twisted in the leaf base, but are twisted in the petiole or lower blade (fig. 1 A-4 I). The effect of this is to rotate the leaf so that one pair of flanks faces upwards (i.e. into the sky), and the other pair downwards (i.e. to the ground). Such a leaf is thus "flat on" to the shoot and simulates a normal bifacial leaf.

The similarity in the twisted leaf bases and petioles of the fossils and *D. taxoides* leads to the suggestion that in the fossils also some leaves were born "flat on".

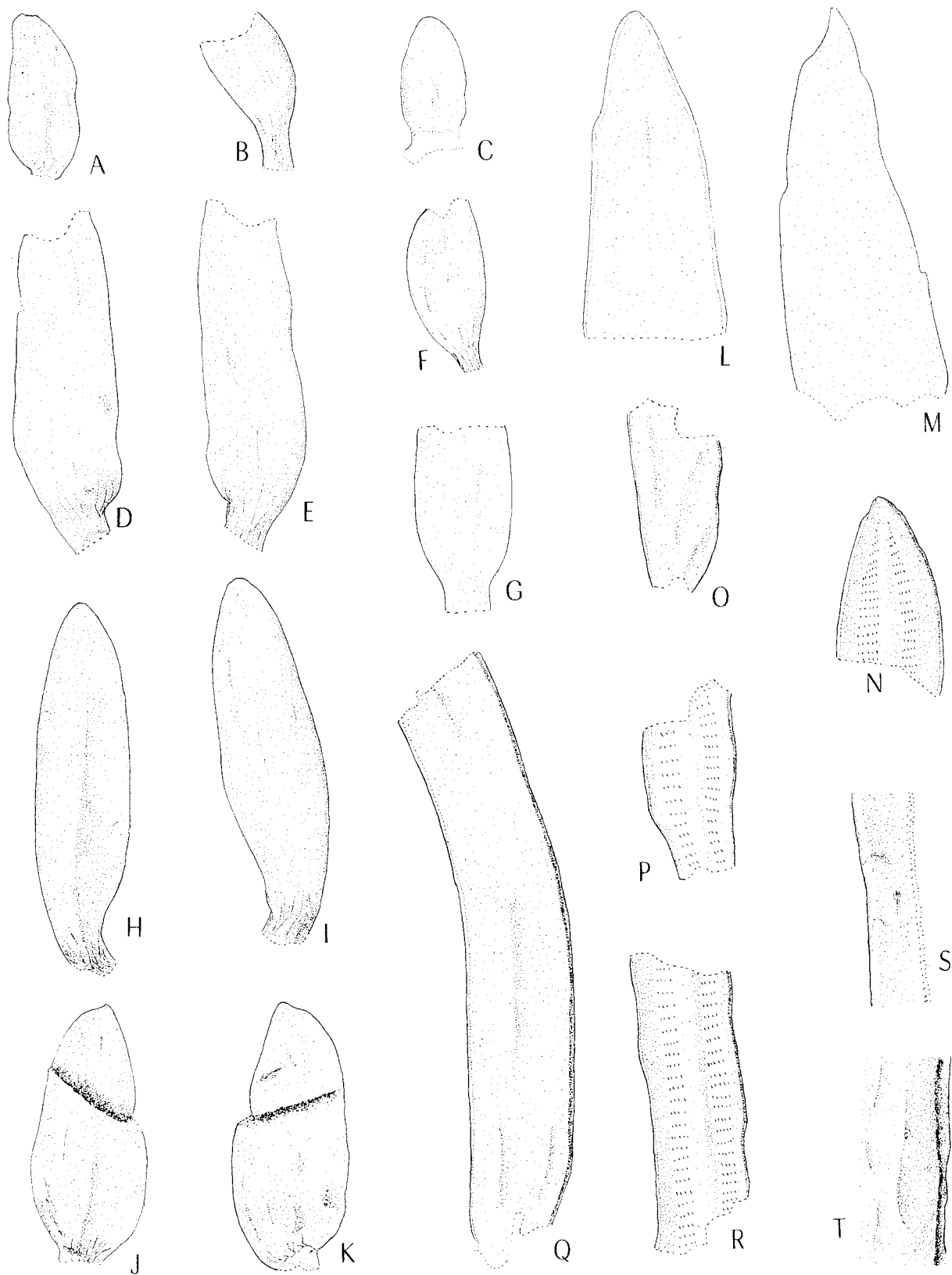


FIG. 6.—*Podocarpus tasmanicus*. A-K; *P. strzdeckianus*, L-T.

A-K: Leaves and leaf bases, small scale-like leaves (A, C, F), twisted bases (D, E, H, I), straight leaf bases (F, G) and small broad leaf (J, K). All x 10. 81905-81907.

L-N: Leaf apex, with shoulders. L, M x 15. 81915. N x 10. 81914.

O, P: A leaf base, Q, R, parts of leaves (note stomatal band, shown by oblique lines) x 10. 81915.

S, T: Scarious margin, both sides of same leaf (S, lower). x 36. 81913.

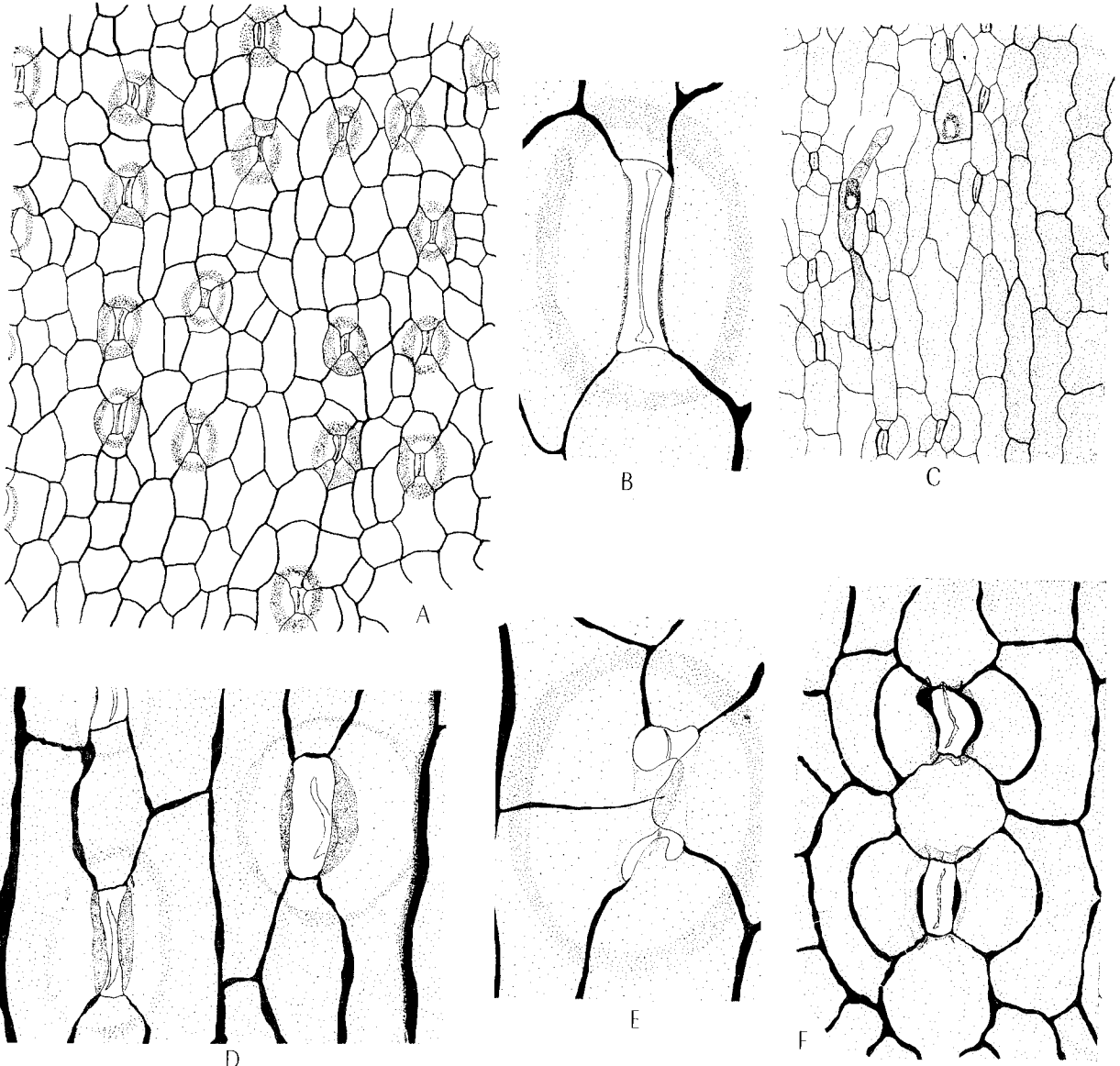


FIG. 7.—*Podocarpus minor*, A; *Microstrobos fitzgeraldii*, B; *M. sommervillae*, D; *M. niphophilus*, E; *Podocarpus setiger*, F; *Coronelia molinae*, C.

A: Upper cuticle, to show arrangement of stomata. Herb. N.S.W. x 330.

B, D, E: Stomata, and surrounding cells and cutin lappets. B, E, Herb. Univ. Tas., D, 81903, x 1,500.

C: Lower cuticle, stomatal rows and margin (right). x 230. 81898.

F: Two stomata and their surrounding cells. x 600. 81922.

A further interesting, perhaps significant, point is that in *D. taxoides* there are stomata over the midrib, as in the fossils, whereas in *D. falciforme*, bearing its leaves edge on, there is a distinct non-stomatiferous zone flanking the midrib.

Some specimens of *P. acicularis* show rather a prominent ridge over the midrib on both sides: these may have been needle-like in cross section. In this species, unlike *P. goedei*, there may be a difference in stomatal numbers on each surface of the leaf, down to about twice as many stomata on one side as the other. The stomatal details are shown in figs. 3 B, 5 A.

Podocarpus goedei and *P. acicularis* are much alike, the differences are in their size (about 10 mm. versus about 6 mm.), in the leaf shape, which may be needle-like in *P. acicularis* and in the form of the stomatal pit. These differences seem to me sufficient to make it convenient to separate the two as distinct species.

Classification. The leaves of *P. goedei* and *P. acicularis* are basically bilateral, and bilateral leaves are taken to indicate the Podocarpaceae. *Acmopyle*, *Dacrydium taxoides*, *D. falciforme* and *Podocarpus* section *Dacrycarpus* show bilateral leaves. *Acmopyle* I rule out for it has a different stomatal distribution, and the subsidiary cells are flat (Florin 1931). The *Dacrydiums* also differ in stomatal details, for they have long but scattered rows of stomata, adjacent stomata showing a common encircling or subsidiary cell (Florin 1931). However, *D. taxoides* has a strongly contracted leaf base (called here petiolate). *Dacrycarpus* often shows an uncontracted leaf base (e.g. fig. 1 R), the stomata lie in four zones, one on each flank, not scattered all over the leaf and the subsidiary cells are flat. Thus the two fossils do not fall easily into any living group with bilateral leaves.

On the other hand they show considerable resemblance to *Podocarpus minor* (section *Polypodiopsis*). The leaves are thick, with an obscure, or even invisible midrib; the stomata are scattered in short rows all over both surfaces of the leaf (except a marginal band) sometimes in nearly equal numbers on both surfaces (*P. minor* usually has more stomata below, however); the stomatal rows are long, but somewhat vague, and within a row there may be groups of 2 to 5 closely set stomata (figs 5 A, 7 A, 10 C): and the number, arrangement and form of the subsidiary cells is similar, especially in that both fossils and *P. minor* have the Florin ring. (Figs. 10 C, 4).

The difference is that the leaves are bilateral in the fossils and bifacial (approaching equifacial) in *P. minor*.

The fossils are placed in *Podocarpus*, but they will not fit into an existing section.

The evolution of the Polypodiopsis sort of foliage.

It has been concluded that both *P. goedei* and *P. acicularis* bore bilateral leaves, some of which were twisted so that one pair of flanks pointed upwards, the other pair down. It has also been deduced that while the leaf arrangement in *P. acicularis* may have been spiral, in *P. goedei* the leaves may have been opposite and decussate (fig. 8 D). Also, a similarity has been noticed between these fossils and *P. minor*.

P. minor (fig. 1 J) has opposite and decussate more or less equifacial leaves arranged so that in each pair the adaxial surface faces the axis. It seems to me that a series of forms can be traced through the fossils to *P. minor*. That is from a shoot with bilateral, spirally inserted leaves, some borne "flat on". (*P. acicularis*); to a shoot with opposite and decussate, but still bilateral, leaves (*P. goedei*); to, finally, more or less equifacial leaves (*P. minor*). That is, the *Polypodiopsis* sort of leaf insertion and form can be derived, with the fossils as models, from a bilateral leaf.

A difficulty, however, is that the leaves of *P. minor* are not twisted at the base, but on the suggestion just made, one would perhaps expect them to be twisted. Further developments in Sect. *Polypodiopsis* are to increase the torsion in the internodes and also twisting the leaf blade as in *P. rospigliosii* or *P. vittensis* (see Florin 1931: 192-194, also fig. 1 G, Gray 1962). Since species of *Polypodiopsis* resembling *P. rospigliosii* and *P. vittensis* were already evolved in the lower Tertiary, they are *P. araucoensis* and *P. brownii*, *P. goedei* and *P. aciculosus* are most unlikely to represent evolutionary sequence.

Section *Afrocarpus* also has equifacial leaves, lying more or less in two rows up the shoot, but the leaves of *P. falcatus* and *P. gracilior* (at any rate) in this section are spirally inserted, and twisted in the leaf base, essentially as in *Taxus* or *Sequoia* (fig. 1 K). I think it is unlikely that *Polypodiopsis* and *Afrocarpus* are especially close to one another (Gray 1953). Section *Nageia* also has decussate leaves, but these are multiveined.

Family **PODOCARPACEAE**

Genus **MICROSTROBUS** Garden and Johnston *MICROSTROBUS SOMMERVILLAE* sp. nov.

Pl. 2 B; Figs. 4 E, G, H; 5 C, D; 7 D.

Type (Holotype): University of Tasmania No. 81900, see Fig. 4 G.

Diagnosis. Ultimate leafy shoots 1-2 mm. in diameter bearing spirally arranged leaves, probably about 5 leaves in one turn of the spiral. Leaves 2-3 mm. long, 1.5-2 mm. wide at widest, decurrent, and showing cutinised upper surface about 1.5 mm. long. Leaves pointed, or acuminate, diverging from shoot at angle of 10°-20°, widest part near base of leaf. Abaxial leaf surface strongly keeled, adaxial leaf surface somewhat keeled. Depth of leaf (when compressed laterally) 1-1.5 mm.

Cuticle epistomatic, stomata borne in two zones, separated proximally by a triangular non-stomatiferous zone, but coalescing near leaf apex. Cells of under surface similar all over, in rows, rectangular or forming parallelograms, about 60 μ x 15 μ . Cell outlines much pierced by holes, between holes swelling out laterally to give sinuous appearance to outline. Cells of upper surface forming the margins and non-stomatiferous zone similar to cells of under surface, but outlines more delicate and less sinuous; 70 μ x 12 μ . Stomata lying in rows 4-6 stomata high, the zones 4-6 stomatal rows wide, one or two stomatal rows lying at apical end of the non-stomatiferous zone. Stomata sharing

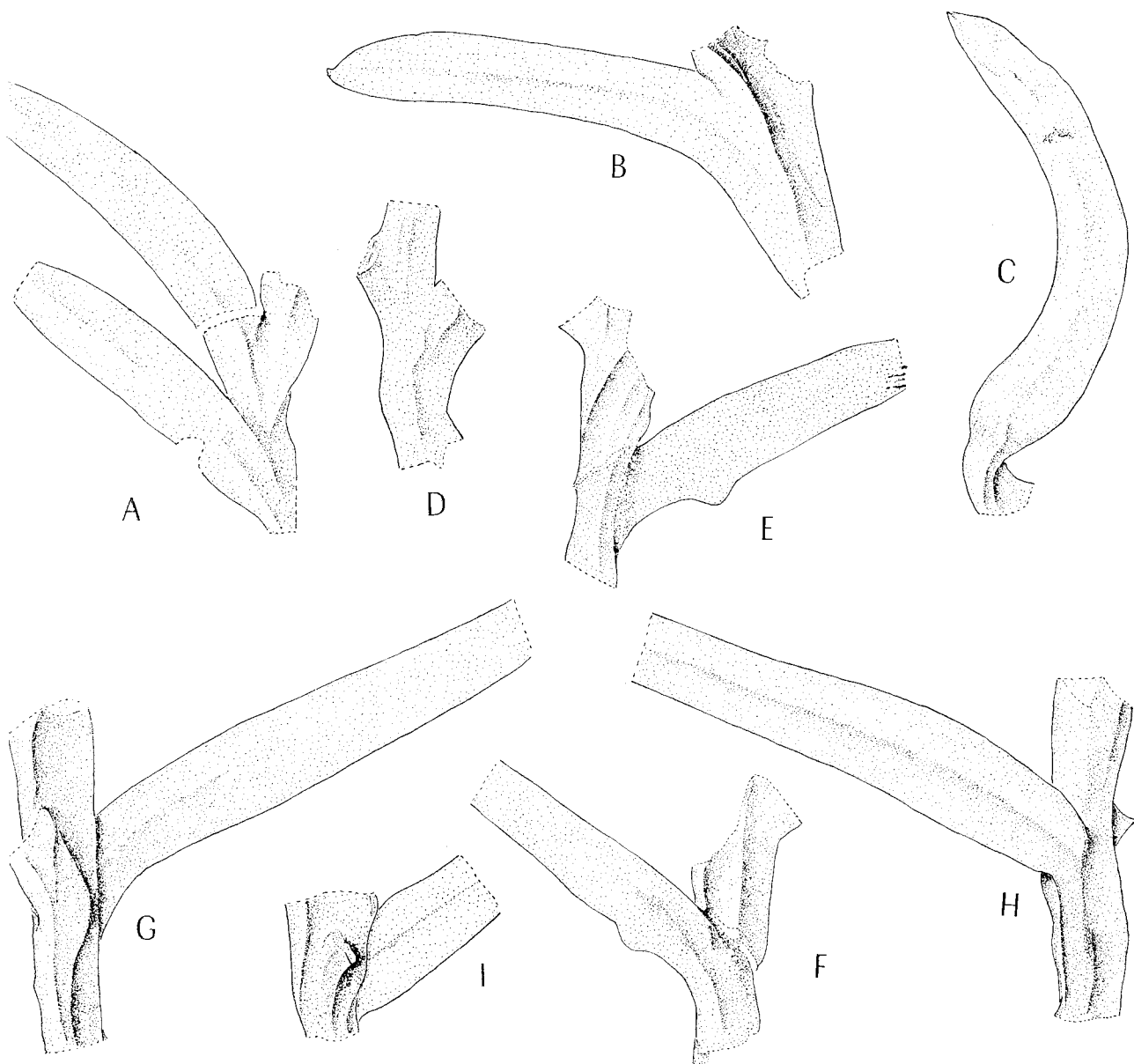


FIG. 8.—*Podocarpus acicularis*, A, B; *P. geodei*, C-I.

- A: Shoot, two adjacent leaves pointing the same way, and a broken leaf base to right. x 15. 81923.
 B: Complete (small) leaf, untwisted at base. x 15. 81923.
 C: Falcate leaf with twisted base. x 10. 81929.
 D: Leaf bases, pointing in opposite directions, and nearly on same level. x 10. 81931.
 E, F: Two opposite leaves, nearly at the same level. x 10. 81932.
 G, H, I: Opposite and decussate leaves. x 10. 81931.



FIG. 9.—*Podocarpus acicularis*, A-I; 81927 a, b. *P. goodei*, J-T. 81928 a-c, 81930.

A, G, F: Twisted leaf bases. $\times 15$.

C, I: Untwisted leaf bases. $\times 15$.

B, D, E, H, J, K, L: Leaves with apices, or leaf apices. B, D, E, H $\times 15$; J, K, L $\times 10$.

M, N, O, P: Two bases with twisted bases, both sides drawn. $\times 10$.

Q, R: Leaf with long angled petiole. $\times 10$.

S, T: Leaf bases, untwisted. $\times 10$.

terminal subsidiary cells, lateral subsidiary cells of adjacent stomata touching, or sometimes one subsidiary cell shared between two adjacent stomata. Usually two lateral subsidiary cells, rarely three or four. Stomatal pit overhung by upward projection borne on all the subsidiary cells, aperture of the pit usually rectangular, about $14 \mu \times 5 \mu$, rarely partly occluded by the upward projection, or by cutin extension (lappett) of it; projection and lappetts (if present) not very large. Junction of ad, and abaxial leaf surfaces marked by cutinised processes. Processes finger-like more or less independent of one another near leaf base, and lying in one or two rows, becoming concrescent and forming single crest towards leaf apex.

Discussion and Classification. This species is represented only by half a dozen or so small shoot fragments, extensive enough, however to show that the leaves are spirally borne, not opposite (figs. 4 E, G, H). Though decurrent the leaves are free over most of their length, to judge from the extent of cutinisation on the upper leaf surface; and on the hand specimens show a strong keel on the under side, and some sign of a keel on the upper also (figs. 4 G, H). This is confirmed from the cuticle, which on the upper leaf surface, at the edges of the non-stomatiferous zone is a little folded (fig. 5 C). The leaf shape is somewhat variable, one specimen (fig. 4 H) showing longer leaves than usual, the leaves also being slightly falcate. The cuticle, however, is similar in all the material seen (Pl. 2 B, figs. 5 C, D; 7 D).

The fossils show small, almost scale like leaves, epistomatic and spirally borne. This narrows the field for comparison very greatly. According to Florin (1931, 1958) several genera, e.g. *Microcachrys* (Podocarpaceae), *Callitris*, some *Juniperus* species and others among the Cupressaceae show, or may show, scale-like epistomatic leaves, but these genera have opposite, and opposite and decussate, or whorled leaves. This leaves *Microstrobos* (*Athrotaxis selaginoides* differs in its much larger leaves and in its stomata). In addition to the above points, the form and cuticle of the fossil agrees extremely well with *Microstrobos*.

Microstrobos has two species *M. niphophilus* (earlier known as *Pherosphaera hookeriana*) and *M. fitzgeraldii*. *M. sommervilleae* comes nearly exactly intermediate between them. In gross form it is more like *M. fitzgeraldii* (figs. 4 F, I), in stomatal distribution, cell outlines and marginal fringe, very close to *M. niphophilus* (Florin 1931, pl. 17, fig. 1, pl. 26, fig. 7, also pl. 2 B fig. 5 D), but in detailed construction of the stomatal pit again it recalls *M. fitzgeraldii* (figs. 7 B, D and Florin 1931, pl. 18, fig. 8). Incidentally, in the fairly abundant material of the Tasmanian endemic *M. niphophilus* the stomatal pit is rather often more occluded (fig. 7 C) than is suggested by Florin's figure (1931, pl. 18, fig. 8). The stomata of *M. sommervilleae* are rather more open than either living species, and the finger-like processes forming the marginal fringe more distinct. A further point is that the projection over the stomatal pit (Florin 1931, fig. 68 A, B) is smaller (or rather, less distinctly seen) in the cuticle of *M. sommervilleae* than in either living species (figs. 7 B, D, E).

The specific name is suggested in acknowledgement of much help received from Miss Janet Sommerville, University of Tasmania.

As far as I know, *Microstrobos* has not been found fossil before. The genus evidently was clearly recognisable, at least its foliage was, in the early Tertiary. A further point of great interest is that it is found fossil in one of the only two places where is now growth. In this *Microstrobos* contrasts with *Microcachrys*, now a Tasmanian monotypic endemic, but judging from pollen grains, widespread in Tasmania and elsewhere in the past (see p. 19).

? PODOCARPACEAE.

Coronelia molinae Florin

Pl. 2 C. Figs. 3 G, H; 4 D, 5 F, 7 C.

1940 *Coronelia molinae* Florin, 20-22: Pl. 3, Figs. 3-10; Pl. 4, Figs. 1-8; Pl. 5, Figs. 1-4. Description of Type from Chile.

Description and discussion. The material consists of four leaves, but is identified because it agrees almost exactly with the type, and with nothing else.

One complete leaf is 12 mm. long and 2.5 wide at the widest, another is 3 mm. wide at the widest (versus 15-16 mm. x 3 mm. given by Florin); and two specimens show the base, sharply contracted to a short petiole; and from the widest point, very near the base, the leaf tapers gradually till very near the apex, when it contracts suddenly to an acuminate point, (Pl. 2 C, and fig. 4 D cf. Florin 1940 pl. 3 fig. 10). The minute marginal teeth are seen in pl. 2 C.

The leaves are hypostomatic, with the stomata lying in two bands separated by a rather indefinite (and sometimes indiscernible) non-stomatiferous zone over the midrib, which does not extend to the leaf apex (pl. 2 C). The Chilean material had a non-stomatiferous zone over the midrib, but in the figures (e.g. pl. 3 figs. 3, 6) it is seen to be indefinite, as in the Tasmanian leaves. The papillae on the encircling and subsidiary cells are most variable, usually faint (fig. 3 G) sometimes invisible, but sometimes strong (fig. 3 H), stomata with strong papillae tending to appear in groups; the papillae on one leaf show a gradation from separate papillae to a distinct Florin ring (figs. 3 H, 5 F). In the Chilean material the papillae are stronger, but still distinctly variable and only seen sometimes (Florin 1940 pl. 4 figs. 3, 4, 8). In the papillae found a little away from the stomatal apparatus agreement is complete (fig. 3 H cf. Florin pl. 3 fig. 5).

The stomatal details are shown in figs. 3 G, H; the stomata lying rather separate from one another in sparse rows within the stomatal zones (fig. 7 C) and the stomata themselves are dicyclic with (usually) two lateral subsidiary cells, but sometimes three or four (fig. 5 F). In these respects agreement is complete between Florin's material and mine (cf. pl. 3, figs. 5, 6; pl. 4, figs. 3, 4).

Perhaps the most prominent feature of the cuticle is the hairs, which lie in the stomatal zones, and all point more or less in the same

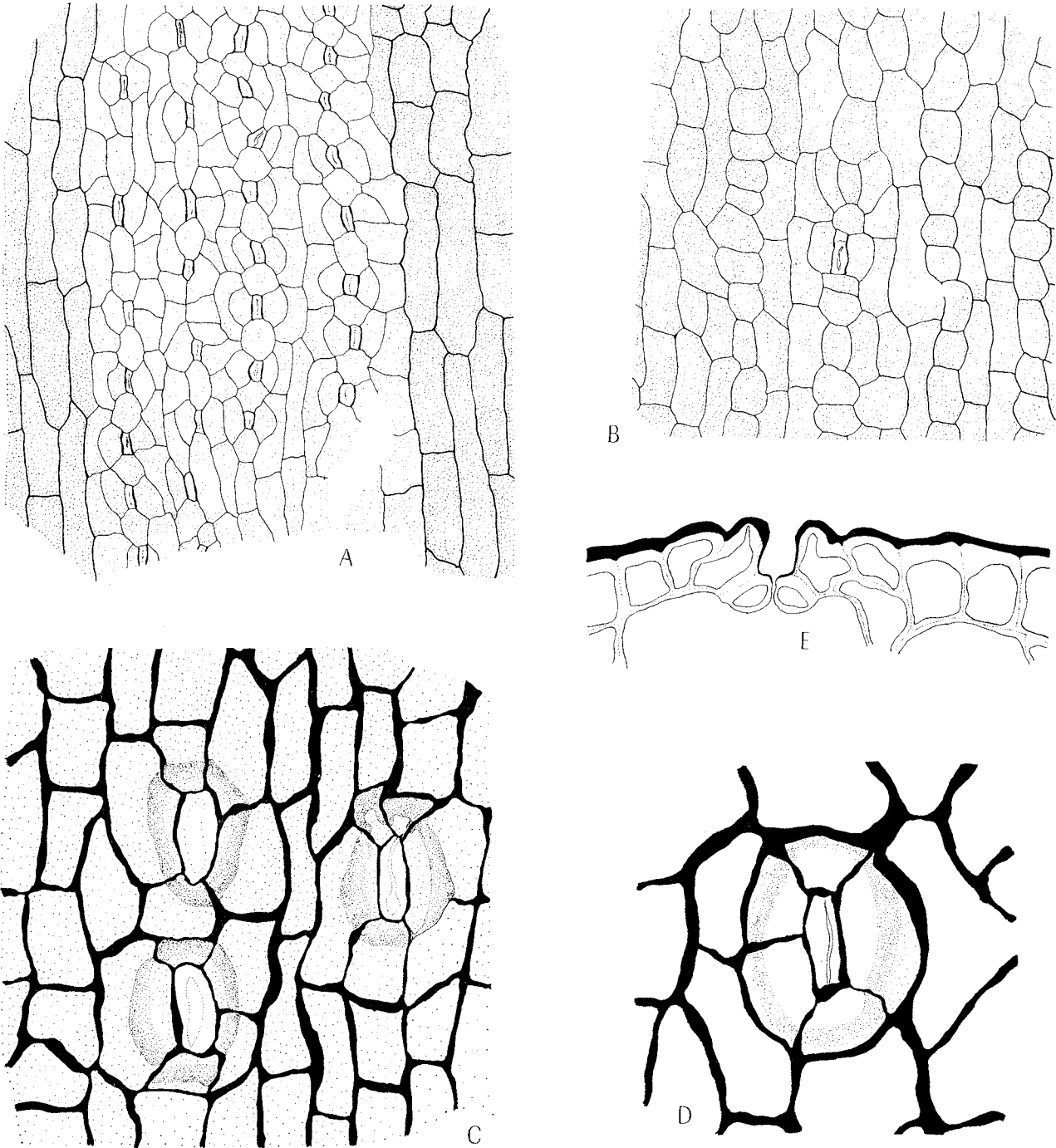


FIG. 10.—*Podocarpus setiger*, A, B; *P. goedei*, C; *P. minor*, D, E.

A: Cuticle from one flank, compact stomatal zone. x 230.

B: Cuticle from another flank, a stoma, and (presumably) incompletely developed stomata above and below it. x 230.

A and B, 81922.

C: Stomata, and surrounding cells. x 600. 81933.

D, E: Stomata in surface view and transverse section. Herb. N.S.W. x 600.

direction (pl. 2 C). These arise from a single cell, or more often the terminal cell of a short row and are multicellular, or unicellular when small, (fig. 3 G, H). Thus far they agree with those shown by Florin (pl. 3, figs. 5, 6, 9; pl. 4, fig. 5, 7). The difference lies in their form. In my material the larger hairs are mostly broken off (figs. 5 F, 7 C), the smaller ones are pointed (fig. 3 H): in Florin's material, however, though most figured examples are broken off, the end cell in some is swollen (e.g. pl. 3, fig. 8). This is the only definite difference between the Tasmanian and Chilean leaves.

I am inclined to explain it away. If the terminal cell swelled up at maturity it might become weak and be broken off before preservation. One example (pl. 3, fig. 5, to left) in Florin's material appears to be pointed, and it is a small hair. The multicellular hairs were stated by Florin to be an unusual feature: to some extent, however, they can be matched (when small) by the *marginal* hairs of *Podocarpus setiger* (P. 9 figs. 5 B, E) which are, however, normally unicellular, though whether this similarity is of significance I doubt. The larger papillae are hollow (fig. A H), and may look like very small hairs. Possibly the two organs are ultimately of the same nature.

The material adds very little to our knowledge of the affinities of *Coronelia*; its main interest is stratigraphic and geographical. As noted, the Tasmanian and Chilean leaves correspond at nearly every point, and I think they almost certainly belong to the same species. This is important, for it suggests a lower Tertiary age for the Buckland flora, though not indubitably, since the range of *Coronelia* is unknown. It also adds another small point of similarity between the Chilean and Australian Tertiary floras.

GENERAL DISCUSSION

It is known, mainly from pollen studies, that in the early Tertiary there was a forest flora, in which the Podocarpaceae were prominent, extending over New Zealand, southern Australia, Chile and southwards to the Antarctic. (e.g. Cookson 1953, Cookson and Pike 1953, 1953a, 1954, Couper 1960, 1960a, Selling 1950, Florin 1940, 1963). The present species fall into this flora. Sections *Dacrycarpus* and *Polypodiopsis* were already known to occur in Tasmania, (neither are now found in Australia). *Eu-podocarpus* Section D, *Stachycarpus* (not now in Tasmania, *P. ladei* in N. E. Queensland) and *Microstrobos* are new. It is surprising not to have found *Dacrydium*, for this genus (in its sections B and C) is also known to have occurred in Tasmania in the early Tertiary, as did *Phyllocladus* and *Microcachrys*. They will doubtless turn up in time.

Florin (1963) has argued strongly that the present sections and sub-sections of the Podocarpaceae, especially of *Podocarpus*, originated

well to the South of the present chief density of sections and species in the New Caledonia, Fiji, Indonesian region. In this he differs from Bucholtz and Gray (1948) who ignored the fossil record. Gray (1962), however, has since partly accepted Florin's views.

The present material supports Florin with two examples of foliage which, as it is interpreted, lie somewhat intermediate between sections or sub-sections, but which are found well to the South of the present range of the most similar species. *P. tasmanicus* (p. 7) is believed to lie close to *P. ladei* (sub-section *Idioblastus*) now found in the Atherton region of Queensland. But it can also be compared with *P. ferruginus* (*Euprumpitys*) of New Zealand. The two species *P. goedei* and *P. acicularis* (pp. 11-13) are believed to show features recalling both *Polypodiopsis* (New Caledonia, New Guinea, Fiji, Equador) and *Dacrycarpus* (New Zealand, also New Guinea to Burma).

With the exception of *P. goedei* and *P. acicularis* the species described here fall easily into sections or genera. This supports the view, also derived from pollen studies, that by the Tertiary the genera, usually sections and sometimes sub-sections, of the Podocarpaceae were already in existence. The species, however, do not seem to have been evolved.

While the present distribution of some groups (e.g. the Araucariaceae Cookson and Duigan 1951) can rather easily be interpreted in terms of a simple retreat northwards under the influence of increasing cold, leading to the Pleistocene glaciations others have stayed put. Examples are *Eu-podocarpus* sub-section D, *Stachycarpus*, sub-section *Euprumpitys*, *Dacrycarpus*, and also *Microstrobos*, *Phyllocladus* and *Dacrydium* of groups B and C. Simple refrigeration will not explain their distribution. It seems likely here that desiccation was equally important, but I hope to elaborate on this elsewhere.

ACKNOWLEDGMENTS

I am very grateful indeed to the following, who have helped me with material of living conifers for comparison: Dr. R. H. Anderson, Sydney; Dr. N. T. Burbridge, Canberra; Mrs. N. Gray, Decatur, Georgia, U.S.A.; Dr. J. B. Hair, D.S.I.R., New Zealand; Professor R. Howard, Arnold Arboretum; Mr. F. W. James, British Museum, (Natural History); Professor J. Rylands, Kirstenbosch, South Africa; Dr. B. Slade, Otago University, New Zealand; Mr. G. Watkins, Forestry Department, Fiji; Mr. J. H. Willis, Melbourne. I must also thank Professor H. N. Barber, F.R.S., University of New South Wales, and Dr. W. D. Jackson, University of Tasmania, for help and criticism during the course of this work.

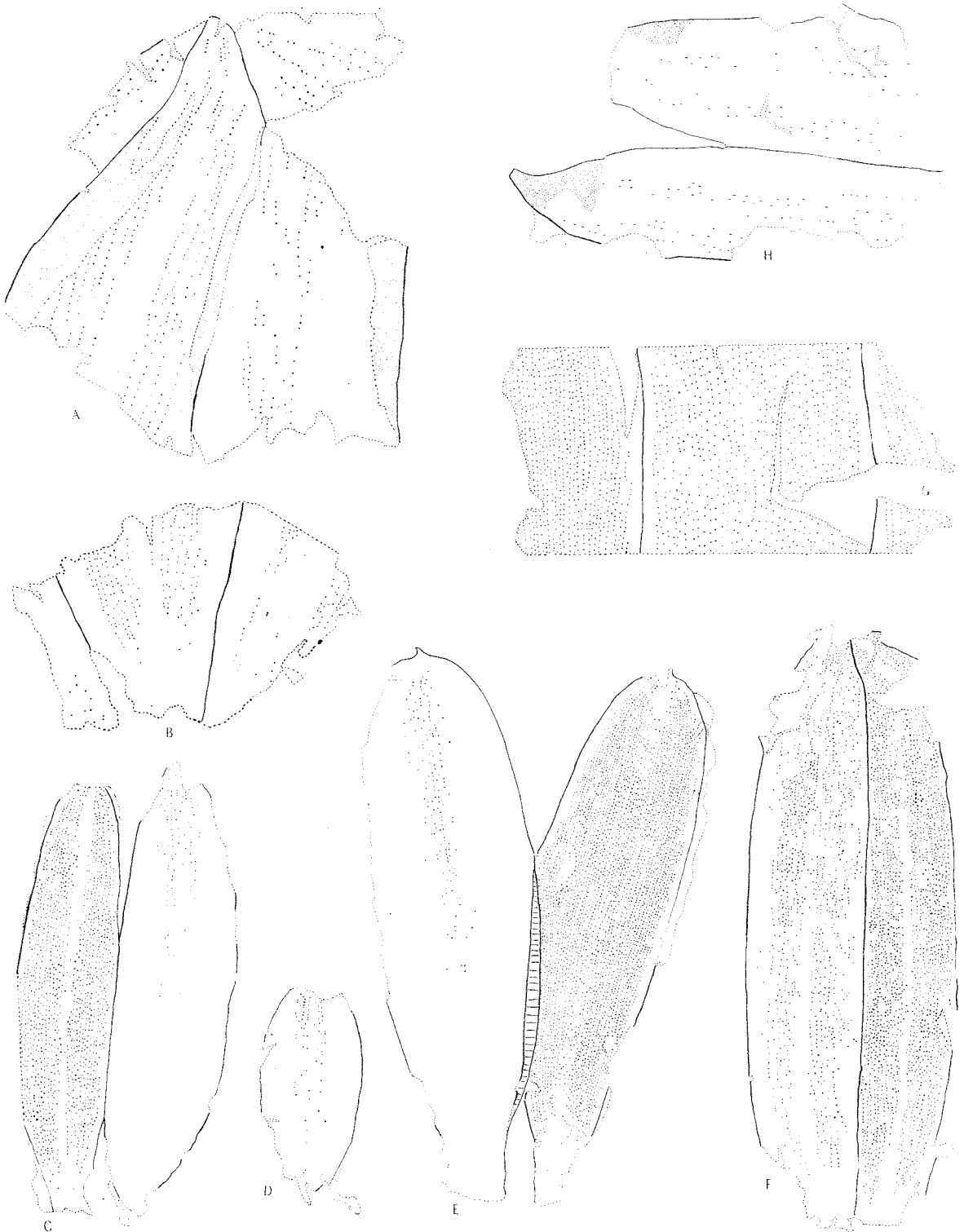
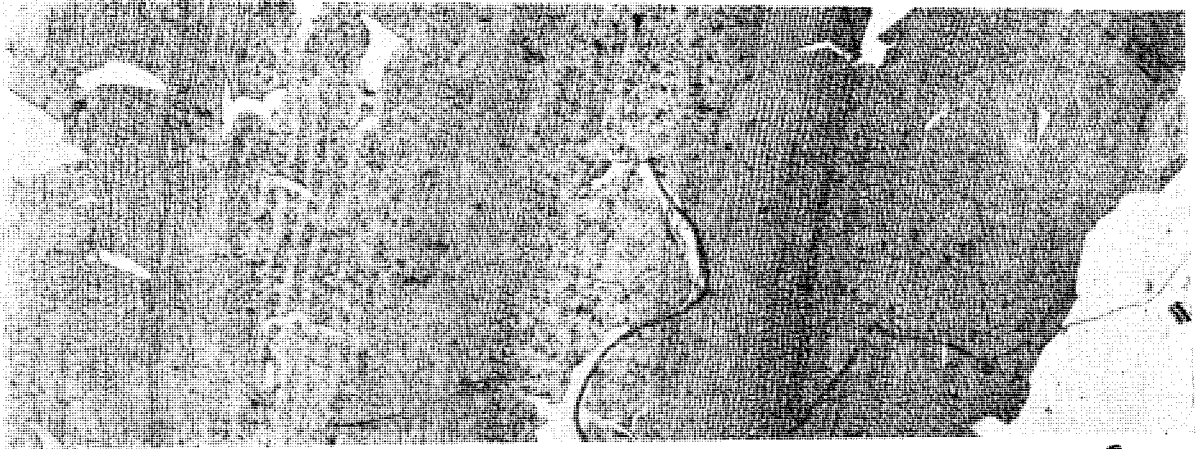


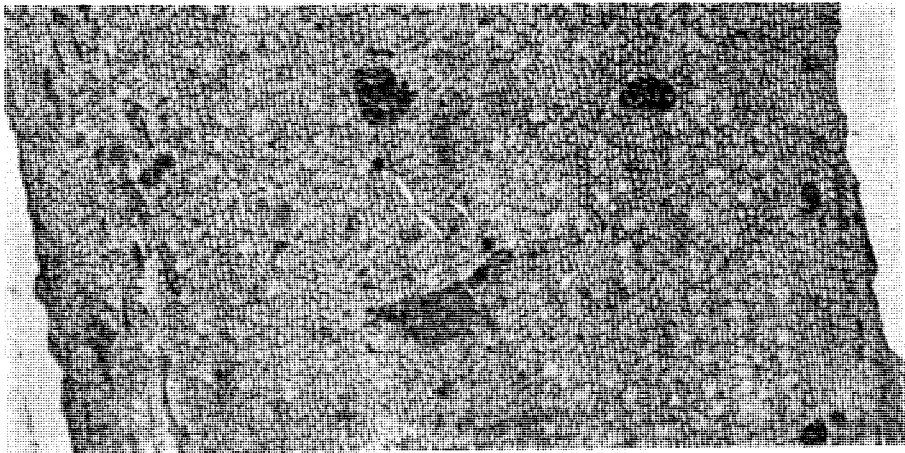
FIG 11.—*Podocarpus tasmanidus*, A, B; *P. ferrugineus*, C, D; *P. ferruginoides*, E; *P. ladci*, F; *P. minor*, G; *P. acicularis*, H.
 A, B: Apex and base of a leaf, showing stomatal distribution. x 12. 81910.
 C-F: Stomatal distribution in members of Sect. *Stachycarpus*, all x 8.
 K: Part of a leaf, upper cuticle in centre. x 8.
 H: Apex showing form and four rows of stomata, one on each flank. x 12. 81920.

REFERENCES

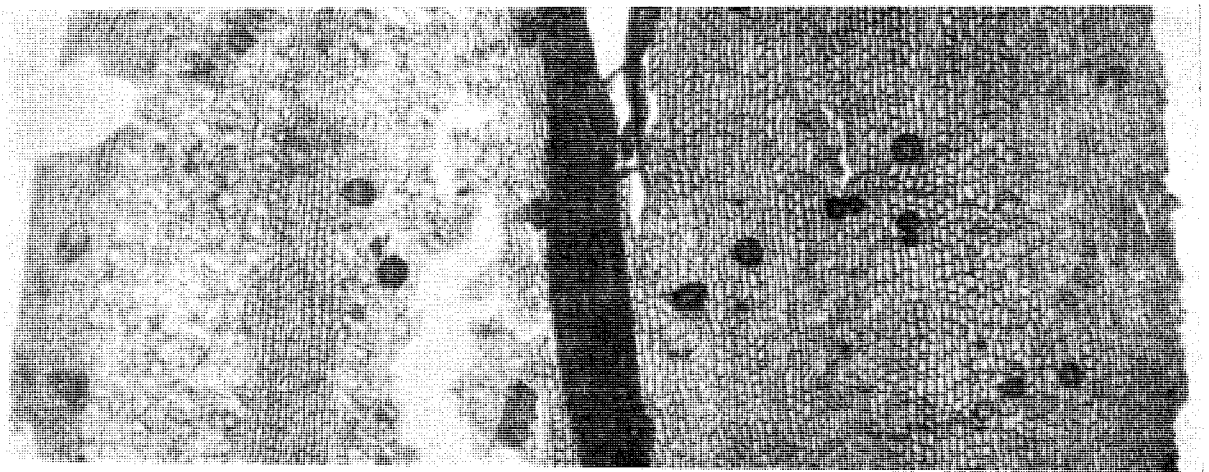
- BUCHOLTZ, J. AND GRAY, N., 1948.—Taxonomic review of *Podocarpus* I. *J. Arnold Arbor.*, **29**: 49-63.
- , 1951.—Taxonomic revision of *Podocarpus* V. South Pacific species of the Section *Stachycarpus*. *ibid.*, **32**: 82-105.
- COOKSON, I. C., 1953.—The identification of the sporomorph *Phyllocladites* and *Dacrydium* and its distribution in southern Tertiary deposits. *Aus. J. Bot.*, **1**: 64-70.
- , AND DUGAN, S. L., 1951.—Tertiary Araucariaceae from South-Eastern Australia with notes on living species. *Aust. J. Sci. Res.*, **B4**: 415-449.
- , AND PIKE, K. M., 1953.—The Tertiary occurrence of *Podocarpus* (Section *Dacrycarpus*) in Australia and Tasmania. *Aust. J. Bot.*, **1**: 71-82.
- , 1953a.—A contribution to the Tertiary occurrence of *Dacrydium* in the Australian region. *ibid.*, **1**: 474-484.
- , 1954.—Fossil occurrence of *Phyllocladus* and two other Podocarpaceous types in Australia. *ibid.*, **2**: 60-68.
- COUPER, R. A., 1960.—New Zealand Mesozoic and Cainozoic Plant microfossils. *N.Z. Geol. Surv.: Pal. Bull.*, **32**: 1-87.
- , 1960a.—Southern Hemisphere Mesozoic and Tertiary Fagaceae and Podocarpaceae and their palaeogeographic significance. *Proc. Roy. Soc. Lond.*, **B152**: 491-500.
- FLORIN, R., 1931.—Untersuchungen zur Stammesgeschichte der Coniferales under Cordaitales. Erste Teil. *K. svensk. Vet.-Akad. Handl.*, (3) **10** (1): 1-588.
- , 1940.—The Tertiary conifers of Southern Chile and their phyto-geographical significance. *ibid.*, (3) **19** (2): 1-107.
- FLORIN, R., 1958.—On Jurassic Taxads and Conifers from North-Western Europe and Greenland. *Act. Hort. Berg.*, **17** (10): 257-402.
- , 1963.—The distribution of conifer and taxad genera in time and space. *ibid.*, **20** (4): 121-312.
- GRAY, N. E., 1953.—A taxonomic revision of *Podocarpus* VII. The African species of *Podocarpus*: Section *Afrocarpus*. *J. Arnold Arbor.*, **34**: 67-76.
- , 1956.—Taxonomic revision of *Podocarpus*. Part X. South Pacific species of the section *Eu-podocarpus* subsection D. *ibid.*, **37**: 160-172.
- , 1962.—Taxonomic revision of *Podocarpus*, XIII. Section *Polypodiopsis* in the South Pacific. *ibid.*, **43**: 67-79.
- GRIFFIN, E. M., 1907.—Conifer leaves with regard to trans-fusion tissue and to adaptation to environment. *Trans. N.Z. Inst.*, **40**: 43-72.
- HARRIS, T. M., 1958.—The seed of *Caytonia*. *Palaeobot.*, **8**: 18-27.
- LAUBENFELS, D. J. de., 1953.—The external morphology of conifer leaves. *Phytomorph.*, **3**: 1-20.
- ORR, M. Y., 1944.—The leaf anatomy of *Podocarpus*. *Trans. Proc. Bot. Soc. Edin.*, **34**: 1-54.
- PILGER, R.—Coniferae in ENGLER, A., 1926. *Die natürlichen Pflanzenfamilien*. 2nd Ed. 13: 1-324.
- SELLING, O., 1950.—Some Tertiary plants from Australia. *Svensk. Bot. Tidskr.*, **44**: 551-560.
- SEWARD, A. C. AND CONWAY, V., 1934.—A phytogeographical problem: fossil plants from the Kerguelen Archipelago. *Ann. Bot.*, **48**: 715-741.
- WASSCHER, J., 1941.—The genus *Podocarpus* in the Netherlands Indies. *Blumea*, **9**: 359-481.



C



B



A

PLATE 1.—*Podocarpus tasmanicus*, A; *P. goedei*, B; *P. strzeleckianus*, C. All x 50.
Portions of the leaves to show margins, midrib region and stomatal distribution. 81908, 81934, 81917.

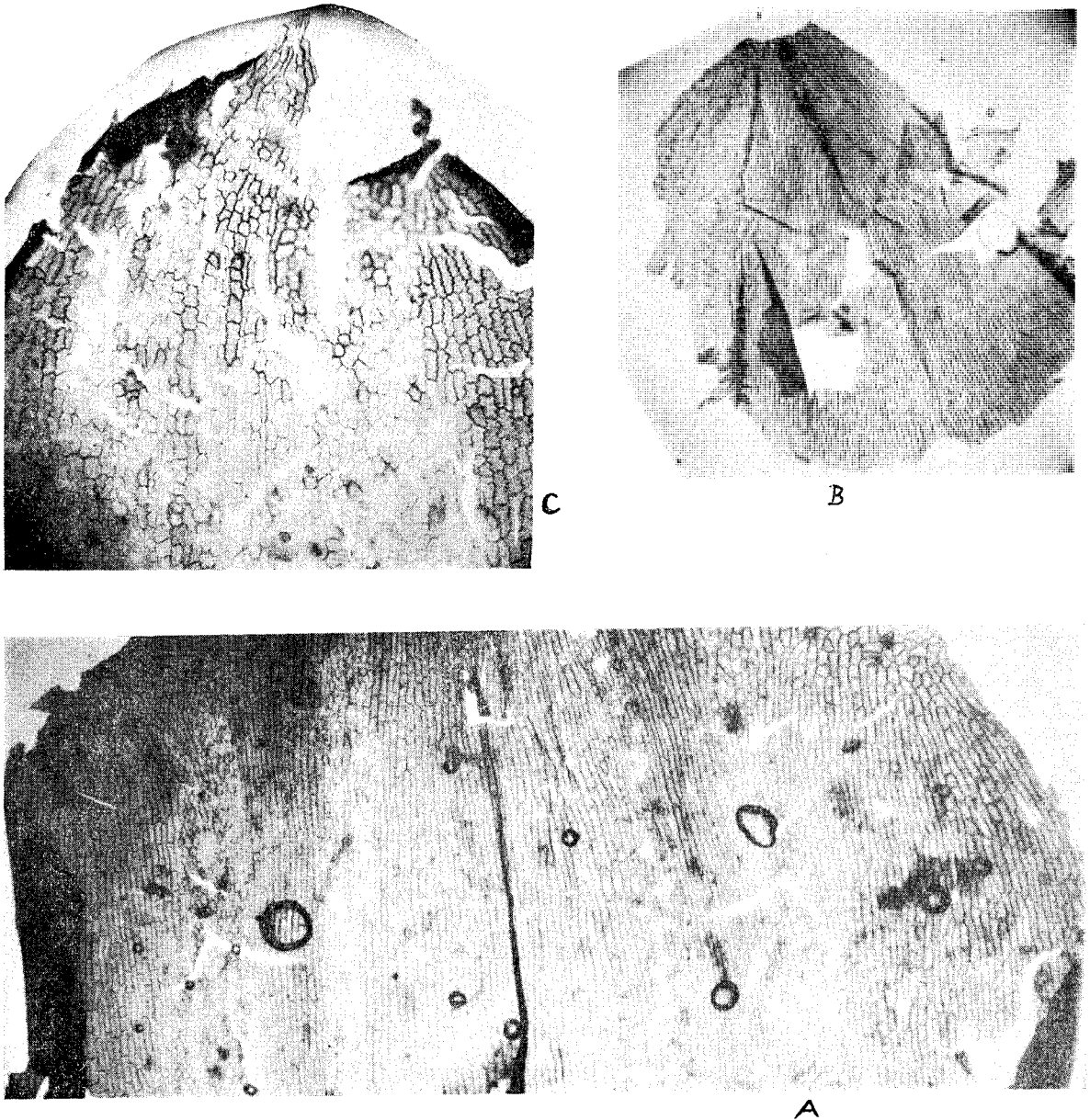


PLATE 2.—*Podocarpus setiger*, A; *Microstrobus sommervillae*, B; *Coronelia molinae*, C. All x 50.

A: Portions of both pairs of flanks, showing stomatal rows. 81920.

B: Both leaf surfaces, showing stomatal distribution and marginal wing. 81904.

C: Apex of the lower cuticle of a leaf. 81898.