Cladode Anatomy and Leaf Trace Systems in New Zealand Brooms

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Summary

The anatomy of the stem of the New Zealand Leguminous genera *Carmichaelia, Corallospartium, Notospartium* and *Chordospartium* is described and figured. Special structures dealt with are the cortical parenchyma, secondary growth, cork and leaf trace systems A discussion on the relationships of the genera and species follows. It is shown that the primitive condition as seen in *Carmichaelia kirkii* is a round, non-flattened stem with leaf traces trilacunate. All other species possess flattened stems This flattening takes place at two points in the stem: (a) in the region of the stem between the lateral traces of successive nodes (in all flattened species), (b) in the region of the stem between the median traces and the lateral traces of the same node (in *Carmichaelella*). The primitive trilacunate leaf traces derive extra traces either interpolating or flanking, or both. Furrow development is associated with the fibre development of the leaf trace bundles. The interrelation of the four genera is shown on a chart (Fig. 10). From the subgenus *Kirkiella* arose an ancestral stock in which extra traces were added on the flanks. From this stock, within the genus *Carmichaelia,* came forms in which further flattening was accompanied by the interpolation of traces The subgenus *Huttonella* and *Corallospartium* have in common flanking trace systems and indehiscent pods. In *Notospartium* the stem is rounded, although its pith is distinctly flattened The anatomical evidence strongly favours the view that *Chordospartium* is derived from the hybridization of *Notospartium* and *Corallospartium.* In the adult stems of *Corallospartium* and *Chordospartium* a varying number of ridges is present

Introduction

The Leguminosae is poorly represented in New Zealand and of the eight genera, the brooms constitute four. Of these, *Notospartium* Hook. f., *Corallospartium* L. B. Armstrong, *Chordospartium* Cheeseman are endemic, and the fourth, *Carmichaelia* R. Brown, has but one out-lying species, *Carmichaelia exsul,* found in Lord Howe Island (Cheeseman, 1925; Cockayne, 1928)

This paper deals with the stem anatomy and morphology of these brooms, taking special notice of:

1. The development of flattening in the stems in all four genera.
2. The development of shallow grooving in many species of *Carmichaelia* and the deeper furrowing in *Chordospartium* and *Corallospartium.*
3. Changes in stem anatomy and particularly in the leaf trace systems that accompany the flattening.

Some investigators (Dormer, 1945, 1946; Sinnott, 1914) have shown that certain features of shoot structure have phylogenetic significance, and on this basis an attempt is made to interrelate the New Zealand genera Since many of the *Carmichaelia* species are difficult to identify, and also have localised distribution, the writer is much indebted to Mr G. Simpson, who, having recently revised the genus (1945), aided in supplying her with authentic material.

The writer wishes to express her thanks to Dr. G. T. S. Baylis for helpful advice and criticism.

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GENERAL DESCRIPTION

A. CARMICHAELIA R. Br.

This genus is the largest. Cheeseman (1925) divided it into the sections *Eucarmichaelia* (18 species) and *Huttonella* (4 species). Previously Kirk (1899) gave the *Huttonella* group generic rank. Simpson (1945) has now divided it into 8 subgenera, and while discarding some species listed by Cheeseman, he recognises 40 species* and 11 varieties. The subgenera are separated according to pod characters. Preliminary examination was made of all *Carmichaelia* species except five as indicated below. For further anatomical study at least one species from each subgenus was selected, and in *Carmichaeliella* four were chosen to show a sequence in the flattening of the stems within that subgenus. The selected species were:

A **Carmichaelia** R. Br.
1. THOMSONELLA Simpson—4 species.
   Ca. grandiflora Hook. f. (Pl. 28 E).
2. CARMICHAELIELLA Simpson—17 species (16 investigated).
   Ca. solandri Simpson.
   Ca. cunninghamii Raoul
   Ca. aligera Simpson
   Ca. williamsii Kirk (Pl. 27 A).
3. KIRKIELLA Simpson—1 species.
   Ca. kirkii Hook. f.
4. ENYSIELLA Simpson—2 species.
   Ca. enysii Kirk (Pl 27 D).
5 PETRIEA Simpson—3 species (2 investigated)
   Ca petriei Kirk (Pl. 28 F).
6 MONROELLA Simpson—3 species.
   Ca. hollowayi Simpson.
7. SUTERELLA Simpson—2 species.
   Ca. uniflora Kirk (Pl. 27 C).
8. HUTTONELLA Kirk—8 species (5 investigated)
   Ca. curta Petrie

B **Notospartium** Hook. f.—3 species.
   No. carmichaeliae Hook. f.

C. **Chordospartium** Cheeseman—1 species
   Ch. stevensoni Cheeseman.

D. **Corallospartium** J. B. Armstrong—1 species.
   Co. crassicaule J. B. Armstrong (Pl. 27 B).

Carmichaelia shows wide variety in the external form of the stem. Even in the mat-forming subgenera the stems vary considerably in texture and size. *Monroella* is the stoutest, and the branches may have one side convex and the other concave or almost flat. *Enysiella* is distinguished by its "cushion" form on a stocky main stem (Pl. 27 D), while *Suterella* with its more slender creeping underground stems, forms mats (Pl. 27 C). Of the erect shrubby subgenera, *Kirkiella* alone can be singled out as easily distinguished, this being the only species showing no trace of flattening in either young or old stems (Pl. 30 A, B). The rest of the subgenera have flattened young stems, even if at one year they have become rounded (Pl 30 C, D), but in several such as *C williamsii* (Pl. 27 A)

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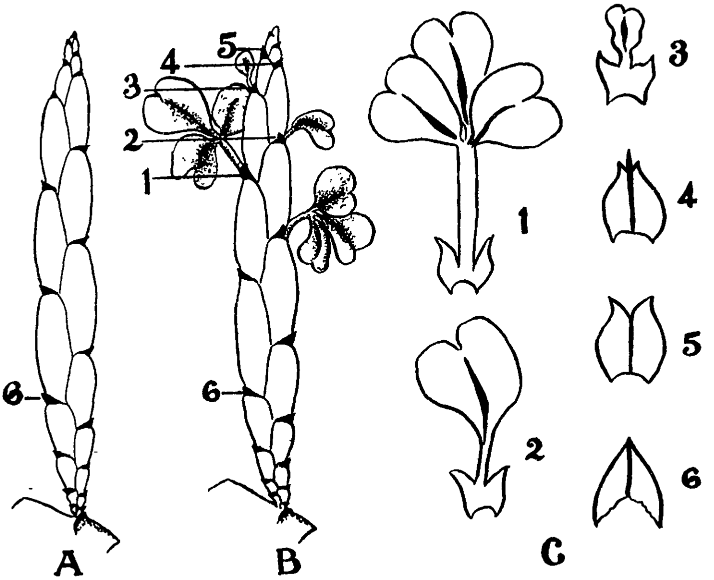
* Simpson lists 41 species, but *Ca. corymbosa* not specific rank.

the flattening always persists, except in the main stems of plants several years old. These extremely flattened forms are all members of *Carmichaeliella,* and a series of forms exists linking this condition with the terete *Kirkiella.* No *Carmichaelia* species have deeply furrowed stems, but many show grooving which internal examination proves to be associated with fibrous bands that run longitudinally in the cortex.

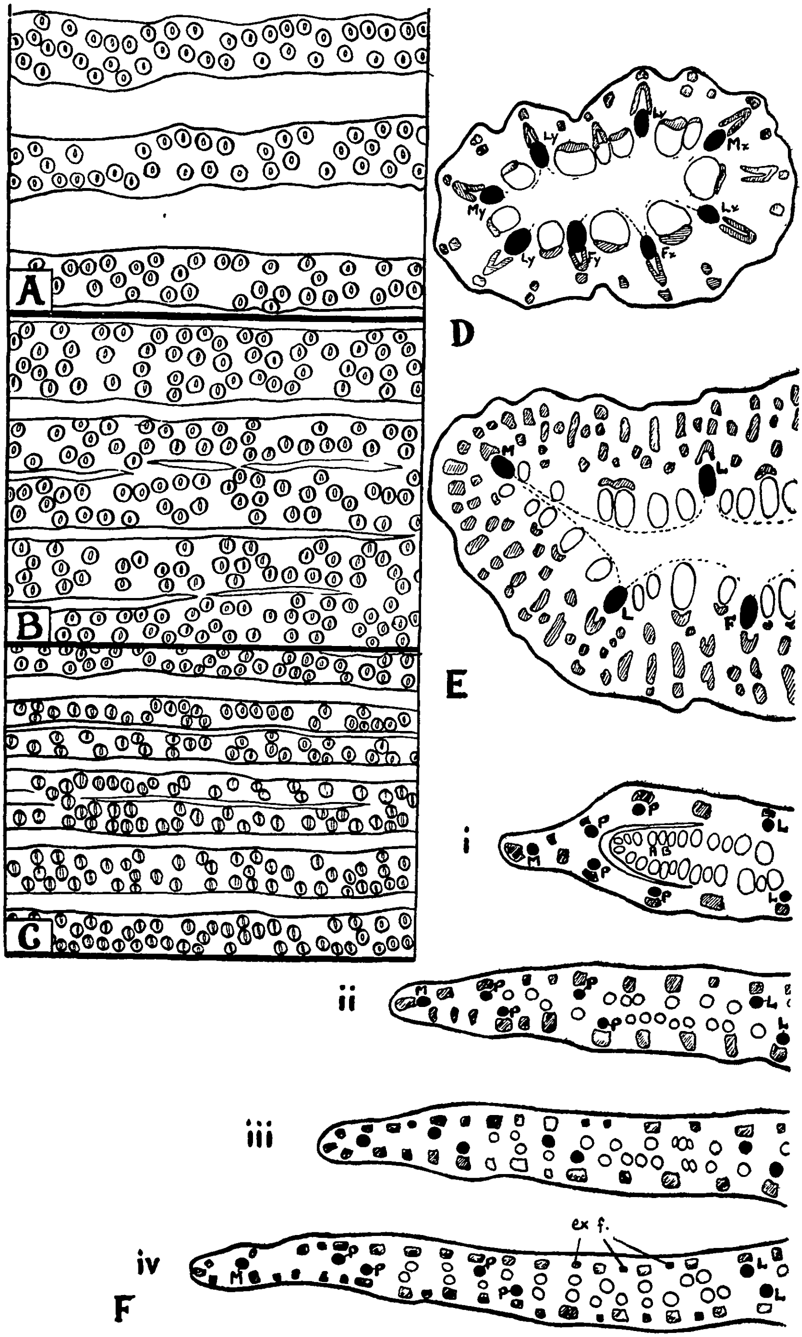
The stems of *Notospartium* are smooth and not dissimilar from those of the slender-stemmed species of *Carmichaelia,* but its longer branches give the plant a semi-weeping habit. Of the two genera with furrowed stems *Chordospartium* has the weeping habit of *Notospartium,* while *Corallospartium* (Pl. 27 B) is strongly contrasted in habit, having thick, slightly flattened stems.

Phyllotaxy of all New Zealand brooms is one half. Seedlings of all genera bear foliate leaves with 1–7 leaflets Adult plants usually produce scale leaves (Text-fig. 1 A), but they may produce small foliate ones (3–7 leaflets) at the height of each growing season. This recurrent foliage is a pronounced feature of some Carmichaelias (e.g., *C grandiflora*—Pl. 28 E), but is insignificant in *Chordospartium* and *Corallospartium,* where such leaves are few and unifoliate, and absent altogether in *Notospartium.* Apart from this normal retention of a leafy habit in those adults usually producing only scale leaves, there may be a development of reversion shoots which are entirely leafy (Text-fig. 1 B), but these also have not been seen in *Notospartium.*



TEXT-FIG 1—*Ca williamsii.* A Normal spring shoot (× 1) B. Shoot with reversion foliage. (× 1). C Leaves 1–6 from shoot B Leaves 1–2. × 2 Leaves 3–6, × 4

When a laminate leaf is shed, its stipules persist as a scale, and from plants which are changing from production of laminate to production of scale leaves, it is possible to obtain a series of intermediate forms which show that the scale leaf itself is composed of more or less coalesced stipules, the rest of the leaf having failed to develop (Text-fig. 1 C, 1–6).



TEXT-FIG. 2—A. Epidermal strip of *Ca. grandiflora* stem (× 30). B. Epidermal strip of *Ca. hollowayi* stem (× 30) C. Epidermal strip of *Ca. williamsii* stem (× 30). D. T.S. stem *Ca grandiflora* (× 15). E. T.S. half stem *Ca. hollowayi* (× 30). F. I–IV, T.S.'s half stems *Ca. williamsii* from nodal to internodal regions (× 15) M,Mx, median traces, L,Lx, lateral traces; F,Fx, flanking traces; P,Px, interpolated traces, A.B., axillary bud, ex.f., extra cortical fibre.

GENERAL STEM ANATOMY

Epidermis

In all genera a thick cuticle is present. In the furrowed ones this is accentuated on the ridges (Text-fig. 3, Pl 29 C). In the furrows, are heavily cutinised unicellular hairs characteristic of the Leguminosae (Solereder, 1908). Stomata are arranged in longitudinal areas even in the smooth or slightly grooved stems, e.g. *Ca. grandiflora, Notospartium.* The epidermal strips devoid of stomata are underlaid by bands of cortical fibre (Text-fig. 2 A and D). In a few species, such as those of *Monroella* subgenus and *Ca. williamsii,* the distribution of this fibre is more diffuse (Text-fig. 2 E and F) and the stomatal areas less well defined (Text-fig. 2 B and C). Successive developmental stages of *Corallospartium* stems show that the stomatal areas (Text-fig. 2 A) are the forerunners of stomatal furrows. As the initially smooth seedling develops, fibre increases to form ridges and the stomatal areas are sunken to form the furrows (Pl. 29 C). *Chordospartium* (Pl. 29 B) resembles *Corallospartium.* Stomata in all species are orientated transversely.

Cortical Parenchyma

All cortical parenchyma is photosynthetic except the layer adjacent to the fibres, which forms colourless sheaths (Text-fig. 3). In seedlings and in summer leafy species such as *Ca. kirkii* and *Ca. grandiflora* (Pl. 28 A), the cortex is composed of chains or small plates of cells with large air spaces between. This condition along with the leafiness is an indication of a more mesophytic nature. Progressive reduction of the air spaces is shown by *Notospartium* (Pl. 28 B) and *Corallospartium* (Pl. 28 C). The majority of Carmichaelias are similar to *Notospartium,* while *Chordospartium* again resembles *Corallospartium.* The very narrow flattened stems of *Ca. williamsii* depart from the usual *Carmichaelia* condition in having both pith and cortex greatly reduced (Pl. 29 D).

Endodermis

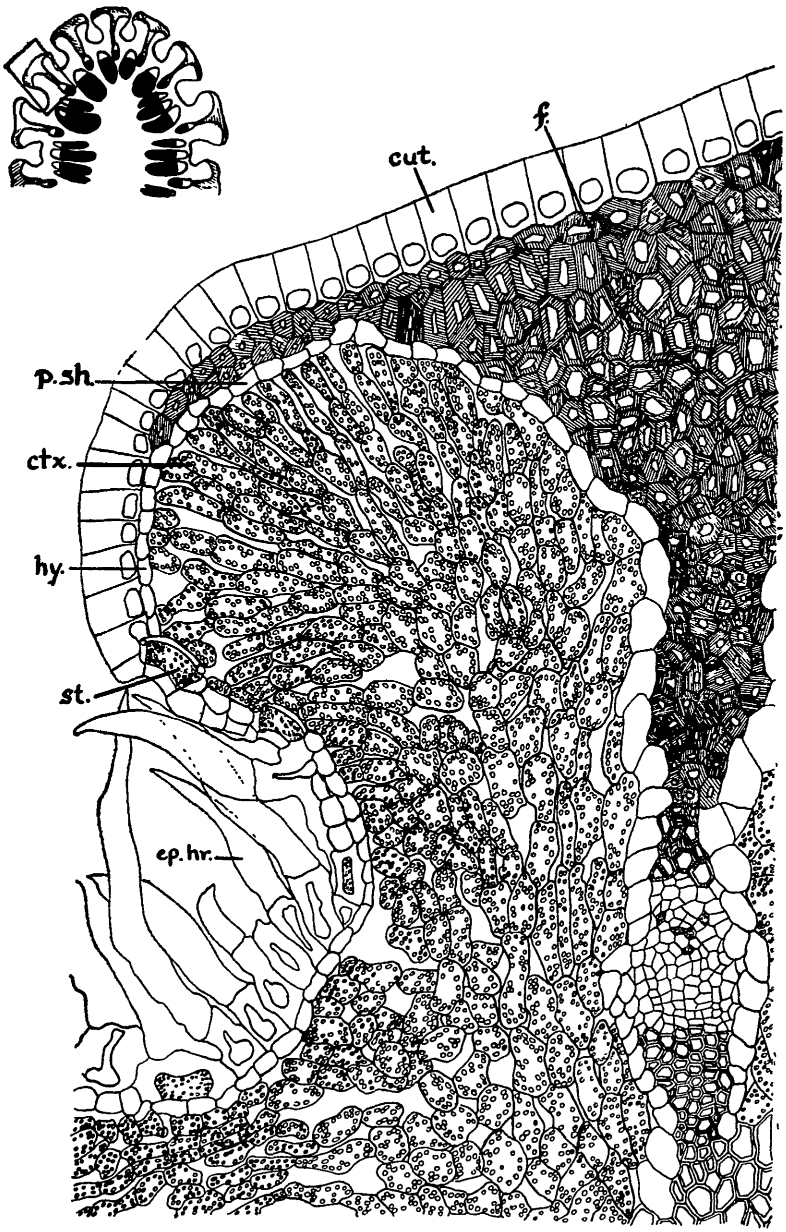
Normally this is a colourless layer that delimits the cortex from the stele. Adjacent to the fibre caps of the bundles it may, however, be obliterated as the fibre cap unites with the adjacent patch of cortical fibre. The interfasicular sections of the endodermis then link with the parenchymatous fibre sheath and this with the hypodermis, so that a continuous line of colourless cells is seen surrounding the photosynthetic cortex (Text-fig. 3).

Pith

In all genera the pith of the first internode of the seedling is cylindrical, but only in *Ca. kirkii* is this form retained throughout life (Pl. 30 A and B). In all other species the pith flattens in the course of development (Pl. 30 C) and in the extremely flattened Carmichaelias (Text-fig. 2 F, iv) it is almost obliterated. The pith of internodes normally forms ridges where leaf trace bundles have withdrawn, but this does not occur in very flat stems nor in *Notospartium,* since in both these, bundles do not move out of alignment with the rest before reaching the node.

Vascular Bundles and Fibre Strands

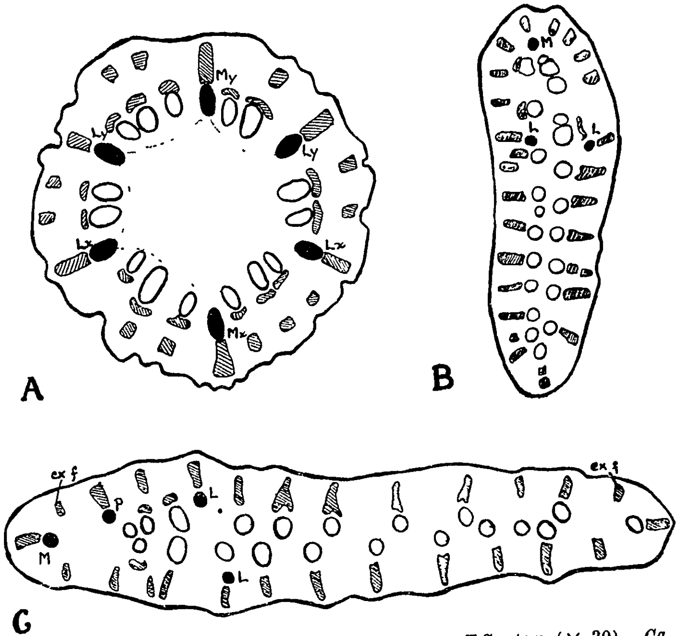
In stems of adult plants vascular bundles are arranged in a ring in *Ca. kirkii* (Text-fig. 4 A), in roughly an oval form in *Notospartium* (Pl. 29 A), *Chordospartium* (Pl. 29 B), *Corallospartium* (Pl. 29 C), and the majority of Carmichaelias (Pl. 30 C), and in a zig-zag or double line in the extremely flattened Carmichaelias (Text-fig. 2 F, IV, and Text-fig. 4 C). Except in *Notospartium*



Text-fig. 3—T.S. *Corallospartium* stem (× 308). Portion of a ridge and intervening furrow with one of the trace bundles and its associated fibre The fibre is sheathed by a clear parenchymatous sheath continuous with the hypodermis on the outside and the endodermis inside. cut, cuticle; ctx, cortex; ep hi, epidermal hair, f, fibre, hy, hypoderma; p.sh, parenchymatous sheath, st, stoma

the "ring" and "oval" types have from six to seventeen of the bundles situated a little out of alignment. These are the leaf trace bundles (Text-fig. 4 A and Text-fig. 2 D and E). In *Corallospartium* and *Chordospartium* they occupy the cortical ridges (Pl. 29 C).

Fibrous tissue occurs mainly in association with the vascular bundles, and in all species [except *Monroella* and the extremely flattened *Carmichaeliella* (Text-fig. 2 E and F)] the leaf trace bundles are usually accompanied by more fibre than the stem bundles. In *Ca. grandiflora* every bundle is accompanied by two distinct fibre strands, the outer of cortical fibre and the inner the fibre cap of the bundle (Text-fig. 2 D). In other species and genera cortical and bundle fibre commonly unite, crushing a portion of the colourless endodermis and parenchymatous sheaths to form a continuous fibrous band extending from the phloem to the epidermis or to the hypodermis, depending upon whether or not the latter also is crushed as the fibre develops. In *Notospartium* actual union of the fibre masses is rare, but they lie close together and the intervening tissue is entirely colourless. In *Ca. kirkii* only the fibre groups accompanying leaf-trace bundles coalesce. When *Ca. kirkii* is compared with other Carmichaelias it is apparent that flattening involves an increase in the circumference of the stem and its stele. In flattened species the stem bundles divide and some of these (as well as the leaf-trace bundles) develop fibrous bands traversing the cortex. In the very flattened species (Text-fig 2 F, iv), fibre of almost every bundle extends across the cortex. A converse development is seen in *Chordospartium* and *Corallospartium*. In the furrows of their stems the entire cortex is photosynthetic, the only fibre being in the bundle-caps. Each ridge is largely formed by the fibre-cap of a leaf-trace bundle united with a mass of cortical fibre.

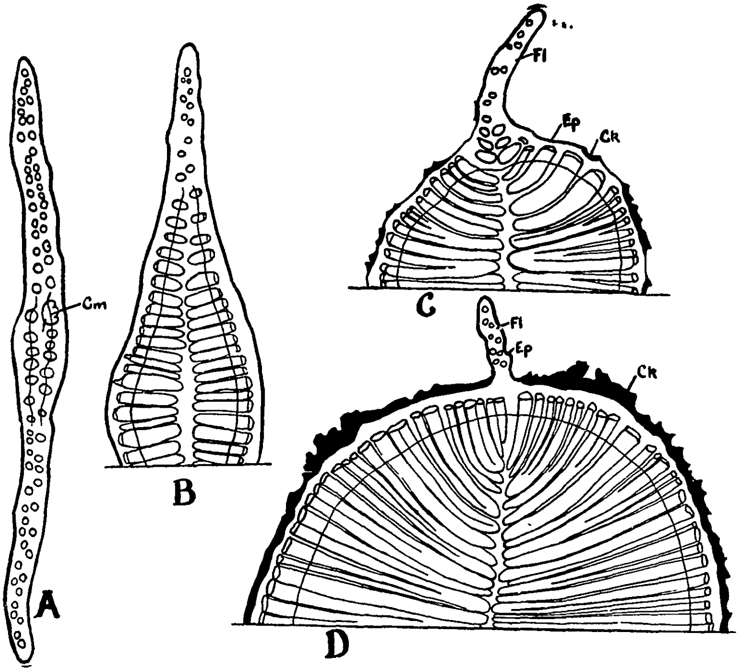


TEXT-FIG. 4—A. *Ca. kirkii*. T.S. stem (× 30). B. *Ca. enysii*. T.S. stem (× 30). *Ca. corrugata*. T..S stem (× 30). All sections are to show the distribution of fibre in the cortex and the leaf-trace bundles. Mx,My, median traces, Lx,Ly, lateral traces, P, interpolated traces; ex.f, extra cortical **fibre.**

In *Enysiella* and *Suterella* (Text-fig. 4 B and C) there are a few extra cortical fibre strands not associated with vascular bundles. Comparable strands occur also in *C. williamsii*. They are not present at the nodes, appearing only as the bundles diverge in the broadening internodes. External examination shows them as fine colourless lines. The most prominent run the whole length of the internode, those less well marked run for successively smaller distances (Text-fig. 2 F, i–iv). In *Monroella* there is much scattered fibre arranged without definite relation to the bundles (Text-fig. 2 E). In old stems of all species (Pl. 29 D–F) stone cells may occur in a similar irregular manner.

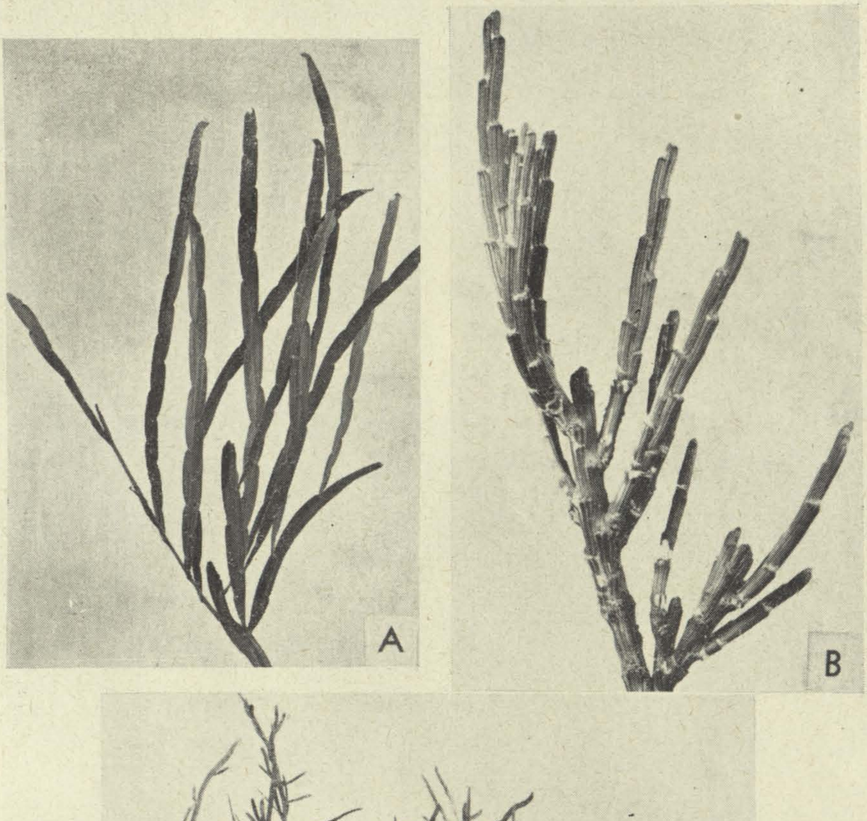
SECONDARY GROWTH IN THE OLDER STEMS AND FORMATION OF CORK

In *Ca. kirkii* the cambial activity results in the stem increasing more or less evenly in girth (Pl. 30 A, B), but in some species, e.g. *Ca. petriei,* the old stems are round, while young stems are distinctly flattened (Pl. 30 C, D). This rounding off is due to greater cambial activity on the two flattened sides of the stem. The flattened pith remains as an indication that flattening originally occurred in the stem (cf. C and D, Pl 30) Most of the woody shrub Carmichaelias resemble *Ca. petriei,* except the excessively flattened ones (*Ca williamsii*). In these the cambium never adds substantially to the bundles on the edges of the cladode so that these regions persist as flanges after the median portion of the stem has rounded into a cylinder (Text-fig. 5 A–D).



TEXT-FIG. 5—A–D: A series of stems of *Ca williamsii* of varying ages to show successive stages in the cambial activity and cork formation. Persistent flanges are present in C and D (× 8). ck, cork, cm, cambium, ep, epidermis; fl, flange

Cork formation is initiated only where there is mechanical rupturing of the epidermis and the outer soft cortical tissues, by stelar growth (Pl. 29 D). Isolated patches of wound cork form (Text-fig. 5 C), eventually uniting to form a continuous layer of cork (Text-fig 5 D) There is never any cork formation in persisting flanges since there is no stelar thickening in these to cause an initiating rupture; nor is there ever any supercession of the original cork-forming layers by a deeper cork cambium unless the original layers are somehow damaged. In *Corallospartium* and *Chordospartium* the weakest areas of the cortex are in the furrows Splitting and cork formation first occurs here (Pl. 29 E), but the

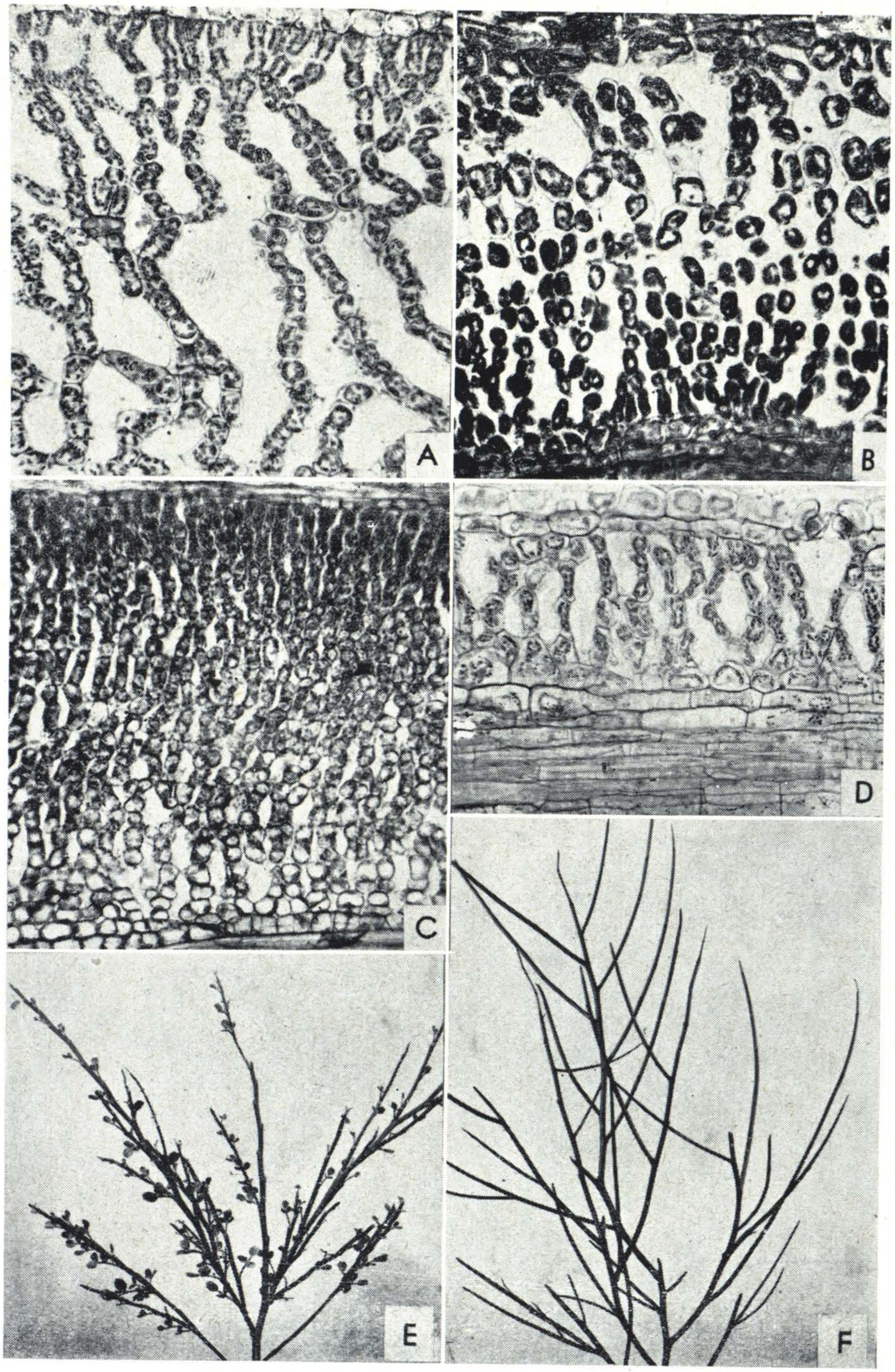


(A) *Carmichaelia williamsii.* × 2/9 approx.

(B) *Corallospartium crassicaule.* × $\frac{2}{5}$ approx.

(C) *Carmichaelia uniflora.* × $\frac{3}{7}$ approx.

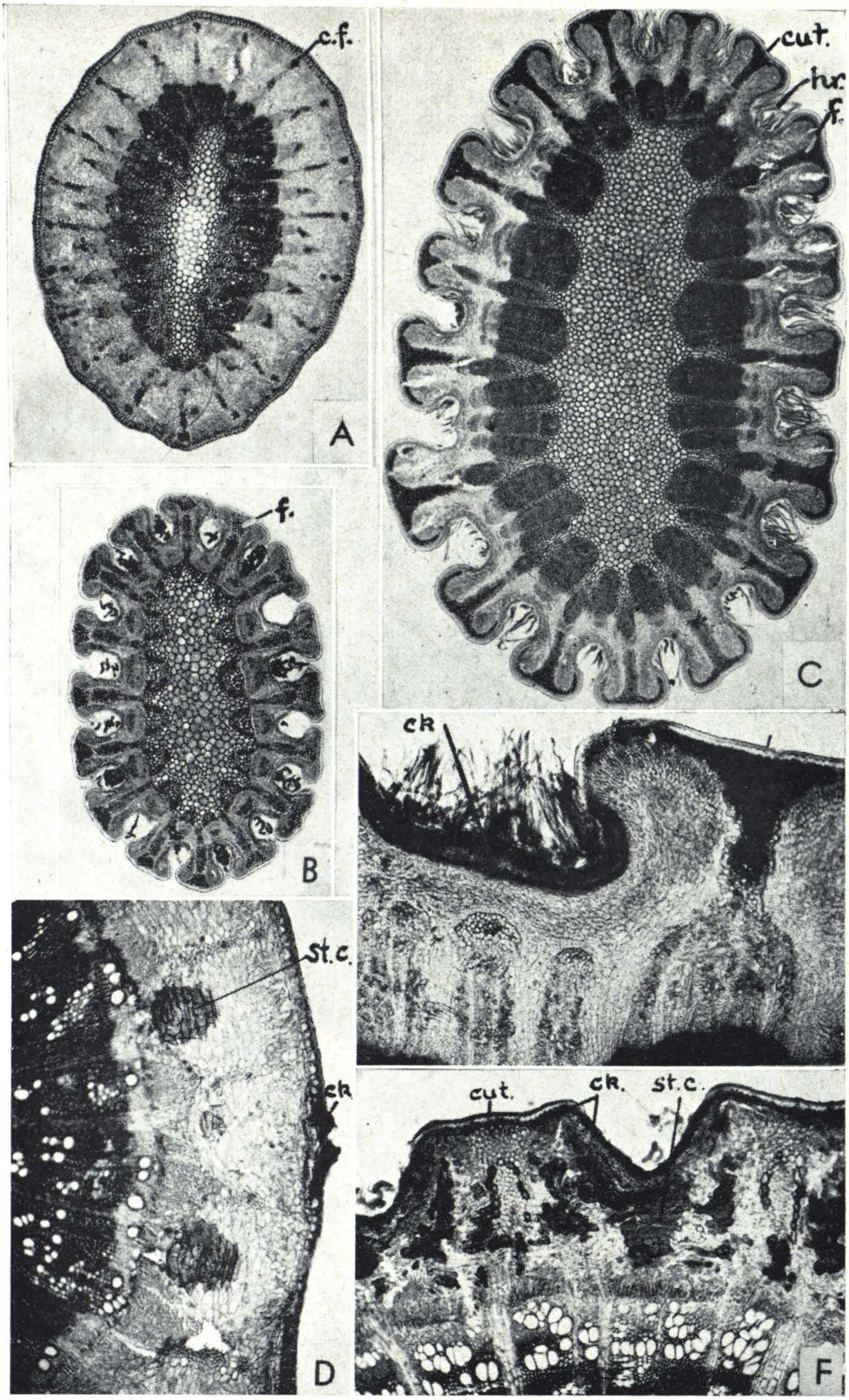
(D) *Carmichaelia enysii.* × $\frac{3}{4}$ approx.



(A) *Ca. grandiflora.* (B) *No. carmichaeliae.* (C) *Corallospartium.* (D) *Ca. williamsii.*

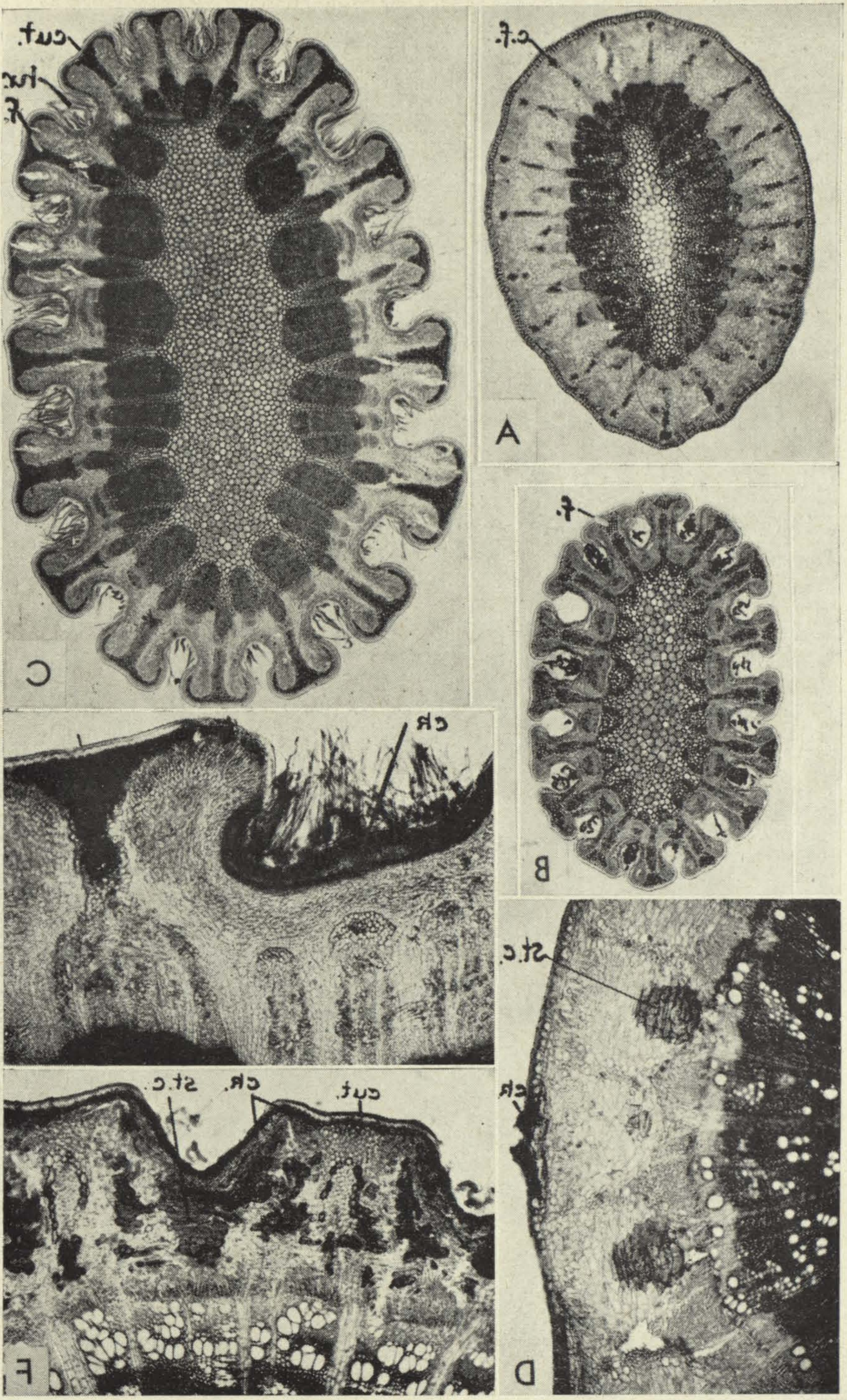
A—D (× 50). Longitudinal sections through cortex of these species to show the gradual reduction in the air spaces in the first three, and the decrease in width of cortex in the last,

(E) *Ca. grandiflora,* $\times \frac{1}{5}$. (F) *C. petriei.* $\times \frac{1}{5}$.



(A) *Notospartium*. (B) *Chordospartium*. (C) *Corallospartium*. A—C (× 16). Photomicrographs of young stems of approximately the same age. *Notospartium* and *Chordospartium* exhibit similar stem dimensions, but furrow development occurs in *Chordospartium* and *Corallospartium*. (D) *Notospartium*. (E) *Corallospartium*. (F) *Chordospartium*. D—F (× 50). T.S. of older stems of *Notospartium* and *Chordospartium* to show the masses of stone cells in the cortex. The initial cork formation is shown in the non-furrowed *Notospartium*, as well as two stages of cork cambial activity in the furrowed species.

f and cf, cortical fibre; hr, stomatal hairs; ck, cork; cut, cuticle; st.c, stone cells.



(A) *Notospartium*. (B) *Chordospartium*. (C) *Corallospartium*. A—C (× 16). Photomicrographs of young stems of approximately the same age. *Notospartium* and *Chordospartium* exhibit similar stem dimensions, but furrow development occurs in *Chordospartium* and *Corallospartium*. (D) *Notospartium*. (E) *Corallospartium*. (F) *Chordospartium*. D—F (× 50). T.S. of older stems of *Notospartium* and *Chordospartium* to show the masses of stone cells in the cortex. The initial cork formation is shown in the non-furrowed *Notospartium*, as well as two stages of cork cambial activity in the furrowed species.

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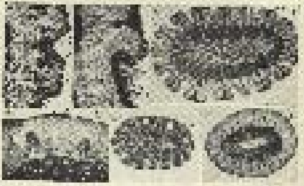

heavily cutinised epidermis on their ridges may persist for a considerable time as vertical lines on old stems, although cork cambium has extended across the ridges (Pl. 29 F).

LEAF TRACE SYSTEMS

1. *Relationship of Shoot Structure to Taxonomy and Phylogeny*

Sinnott (1914) by comparative anatomical study showed the node with three leaf gaps in the stele (trilacunate) to be primitive. He showed the unilacunate node with one leaf gap to have been derived from the trilacunate condition either by gradual movement of the two lateral traces into the same position as the central one, or by the lateral traces disappearing, only the central trace persisting. Multilacunate nodes with more than three leaf gaps have been derived from the trilacunate node by one of two methods. In some, supernumerary traces have been added on the flanks of the original trilacunate insertion (i.e flanking traces), while in others there appeared to be a diversion into the leaf of some of the traces normally destined to serve the axillary branch (interpolating traces). Neither Sinnott (1914) nor Dormer (1945) mentioned multilacunate nodes in which both flanking and interpolating traces were present, but this paper will describe nodes in which the additional traces are of both types. Sinnott (1914) found that the seedling of the unilacunate and multilacunate forms often showed the primitive trilacunate condition. The Leguminosae he studied are tri- or penta-lacunate. Dormer, although principally investigating the taxonomic value of the shoot structure in the Leguminosae, also showed the same principles to extend to many other families. In the following table he listed criteria that could be applied to problems of phylogeny

Primitive Characters	*Advanced Characters*
1. Spiral phyllotaxy	1 Phyllotaxy verticillate, + or distichous with two vertical rows.
*2. Woody habit.	2. Herbaceous habit.
*3. "Open" bundle system.	3. "Closed" bundle system.
4 Leaf trace insertions in contact.	*4. Leaf trace insertions separated or interlocked.
5 Leaf highly compound.	*5. Leaf less compound
*6. Stipules present and free.	6. Stipules absent or * adnate to the petiole.
*7. Leaf with three traces.	*7. Leaf with more or less than 3 traces.
*8 Pulvinus present.	8 No general foliar pulvinus.

"Closed" bundle systems are those in which nodal anastomoses connect bundles of the vascular system tangentially so that there is no necessity for a continuous cylinder of secondary tissues for tangential continuity. They are always present in plants of extreme herbaceous habit. No such anastomoses are present in the "open" systems, which are always associated with secondary growth Insertions of leaves in "contact" are those with extreme lateral traces of successive leaves arising vertically above one another or adjacent to one another Those "interlocked" have points of origin overlapping. The trilacunate condition is the most common in the Leguminosae and departures from this are not found in the highly standardised "closed" bundle system (Sinnott, 1914). On the other hand, multilacunate nodes have been found to be frequent in "open" bundle systems and it will be seen that the New Zealand broom genera provide further examples of this.

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* Features present in one or other New Zealand broom species,

2. *Carmichaelia Leaf-trace Systems*

A. *Trilacunate.* Apart from two very reduced forms which are mentioned later, only the round-stemmed *Kirkiella* (Text-fig. 4 A) is consistently trilacunate, but usually the other subgenera are trilacunate at the first seedling internode and often at every branch base where flattening is at a minimum, e.g., Text-fig. 6 A, C, E.

B. *Types with Additional Traces "Flanking"—Hultonella, Monroella, Petriea.* The flattening in these groups arises by the division of the stem bundles between the original lateral traces of two successive nodes (between Lx and Ly, Text-fig. 4 A). If these bundles divide at an equal rate on each side of the stem, then the flanking traces are added in pairs to form pentalacunate nodes (Text-fig. 6 F) On the other hand, if the division is greater on one side than upon the other, so that the stem becomes flat or slightly concave on one surface while convex on the other, the flanking traces may only occur on this convex side of the stem. Such a node is tetralacunate and asymmetrical, the median trace being distinguishable by the fact that it is at the edge of the cladode (Text-fig. 2 E).

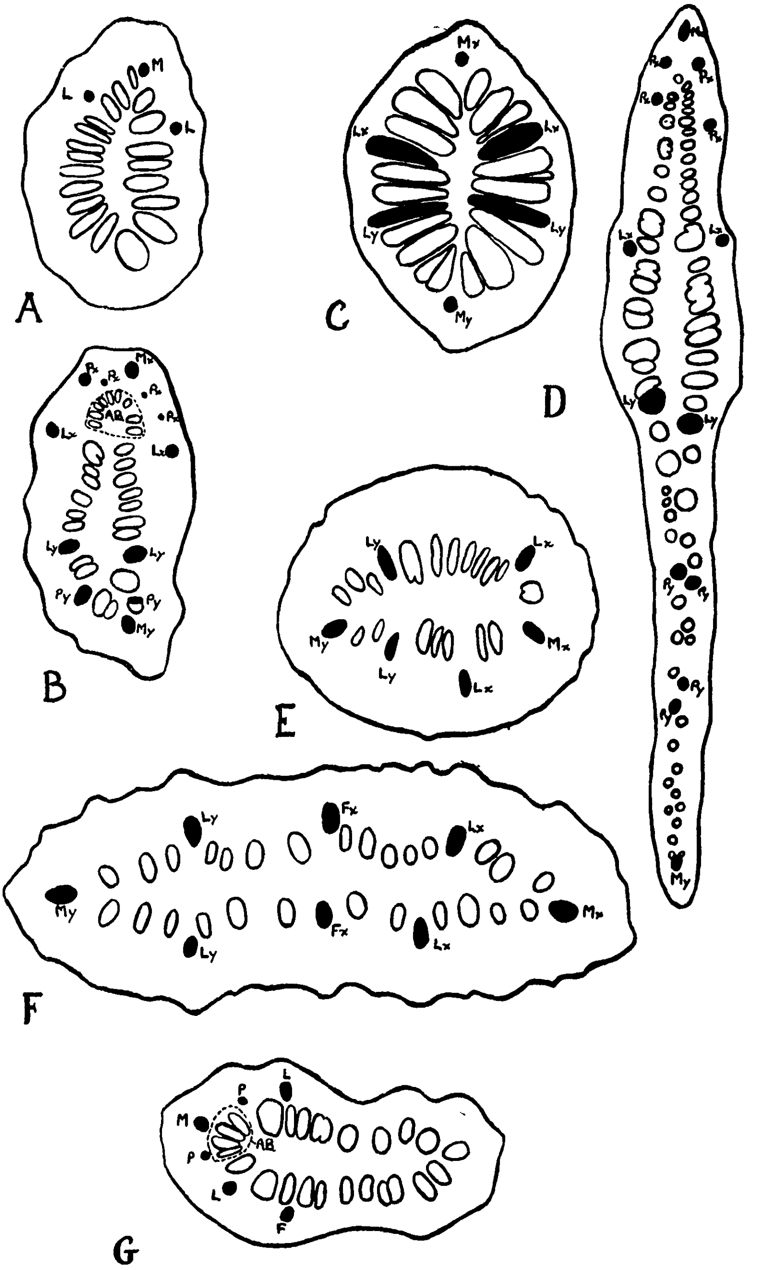
C. *Types with Additional Traces "Interpolating."* These are found only in the extremely flattened species of *Carmichaeliella*, the rest of the subgenus having the nodal structure discussed under Section D. The initial flattening in these species is also by the division of stem bundles between the lateral traces of two successive nodes, but this is superseded by more intensive division of the bundles that normally supply the axillary bud. This division of axillary bud bundles does not take place at the lowest nodes of branches which are almost round, but at successively higher internodes division and spacing of the bundles increases until the stem attains maximum width. It is constricted, however, at each node, and it is when the bundles are thus congested that the interpolating traces withdraw into the cortex (Text-fig. 6 D). The trilacunate node of the branch base becomes pentalacunate as the stem flattens, and finally septalacunate. But there may be asymmetrical nodes where interpolating traces only depart on one side.

D. *Types with Additional Traces both Interpolating and Flanking.* The species of *Carmichaeliella* (other than those of division C above)), *Thomsonella*, and most members of the subgenera *Enysiella* and *Suterella*, have extra traces of both types. In a few species nodes may have only extra traces flanking but usually there are a varying number of interpolating traces as well (Text-fig. 6 G), and nodes with interpolating traces only are very common. They have been found in *Ca. solandri, Ca. arborea, Ca. flagelliformis, Ca. hookeri* (*Carmichaeliella*); *Ca. grandiflora* (*Thomsonella*); *Ca. corrugata* (*Suterella*) (Text-fig. 4 C and Text-fig 6 B). However, Group D do not exhibit such well-developed flanges as stems of Group C. It seems fairly obvious that such stems show an intermediate stage between the two types of stem flattening described under B and C, and between their corresponding nodal structure.

Of the six nodes of *Ca. enysii* that were examined, all were trilacunate (Text-fig. 4 B). *Ca. uniflora*, the smaller stemmed species of *Suterella*, was also trilacunate. As both these species are small reduced forms (Pl. 27 C and D), it is unlikely that the trilacunate node is phylogenetically significant in them. Further investigation of nodal anatomy may reveal that extra traces may sometimes be present, though the small stem dimensions make this unlikely.

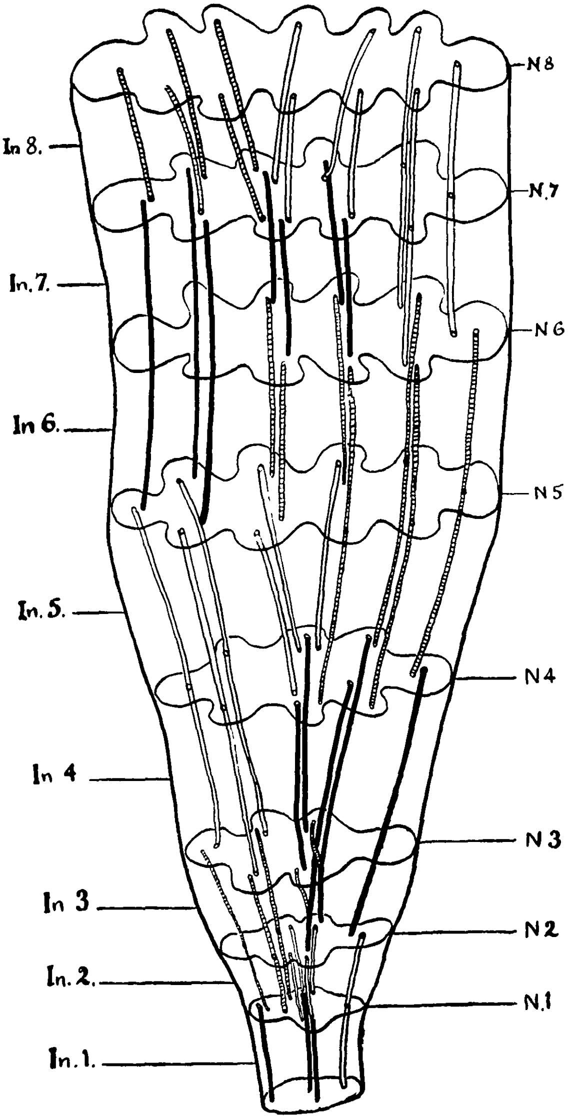
3. *Corallospartium and Chordospartium Leaf-trace Systems*

In *Corallospartium* and *Chordospartium* extra traces are exclusively flanking and added progressively as the stem flattens by the division of the stem bundles



TEXT-FIG. 6—A. T.S. branch *Ca. solandri* at the base (× 16). B. T.S. branch *Ca. solandri* several nodes above the base (× 16). C. T.S. branch *Ca. williamsii* at the base (× 16). D. T.S. branch *Ca. williamsii* several nodes above the base (× 16). E. T.S. branch *Ca hollowayi* at the base (× 40). F. T.S. branch *Ca. hollowayi* several nodes above the base (× 40). G. T.S. branch *Ca. grandiflora* several nodes above the base (× 16). These are selected examples to show the various types of leaf trace that are found in *Carmichaeliella, Thomsonella, Monroella* Abbreviations as Text-fig. 2.

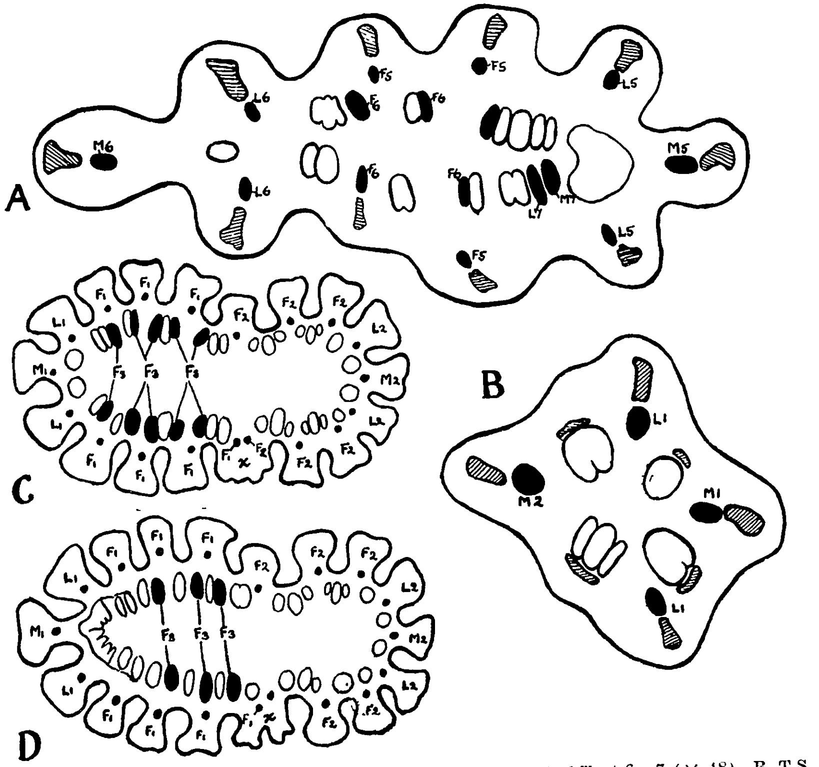
between the lateral traces of two successive nodes. Text-fig. 7 is a diagram illustrating the leaf-trace system of a seedling of *Corallospartium*. The first internode (Text-fig. 8 B) shows the stem isodiametric and with four corners associated



TEXT-FIG. 7—Diagram of the leaf trace system of a *Corallospartium* seedling. Stem bundles are not shown. N1–N8, Nodes 1–8. In1–In8, Internodes 1–8. For explanation see text.

with four leaf traces. At higher internodes the number of ridges increases, along with an increase in the number of flanking traces (Text-fig 8 A). The median trace always runs through two internodes before departing to a leaf, but lateral traces may arise only one internode before supplying the leaf (Text-fig. 8).

In the adult stems a varying number of ridges are present, depending upon the number of trace bundles per leaf, and whether or not the leaf insertions are overlapping. In young stems and tapering branch tips the most remote pair or pairs of flanking traces overlap (Text-fig. 8 A, F5 and F6 overlap). Sometimes a ridge is seen to be dividing, this being associated with the division of a trace bundle (Text-fig. 8 C and D at X), while on the other hand, the suppression or reduction of a trace bundle, particularly when the stem is narrowing towards



TEXT-FIG 8—A T.S. stem of *Corallospartium* seedling at node 5 of Text-fig. 7 (× 48). B. T.S. stem of *Corallospartium* seedling at node 1 of Text-fig 7 (× 48) C and D. T S 's through the node of an adult *Corallospartium* stem to show the division of one of the ridges at "x" associated with the division of the leaf-trace bundle (× 10). M, M1, M2, median traces, L, L1, L2, lateral traces; F, F1, F2, flanking traces

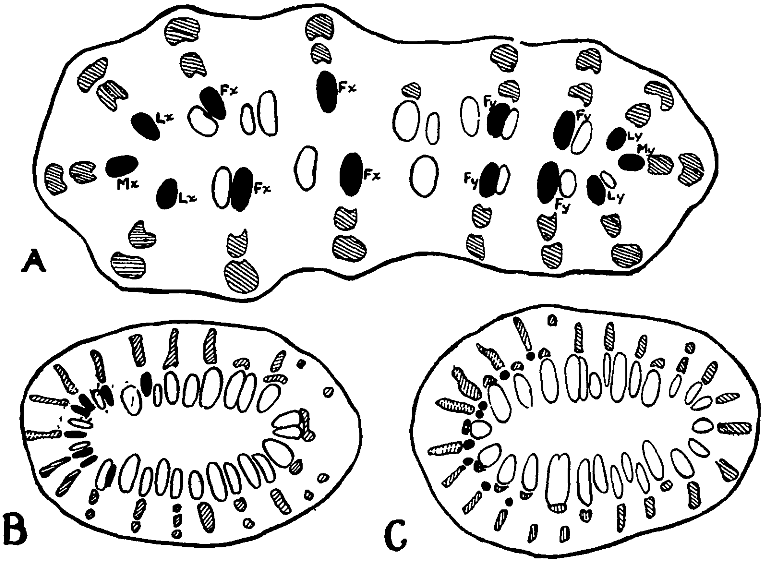
the distal nodes, is accompanied by a partially formed ridge. Such features show the close relationship between ridge and leaf-trace development.

Although *Corallospartium* has been investigated both from developmental anatomy as well as from the anatomy of the adult, and *Chordospartium* only from investigation of the adult, both genera seem remarkably similar, despite the fact that they are so different in habit and stem dimensions. *Chordospartium* sometimes has fewer ridges in its stems, but this is apparently connected with its smaller dimensions (Pl. 29, B).

4. *Notospartium Leaf-trace Systems*

The nodes of stems of seedlings of various ages show that the trilacunate node becomes pentalacunate and septalacunate by addition of flanking traces. Occasionally an asymmetrical tetralacunate node is developed. Insertions are initially in contact, but in branches of the older seedlings the stem bundles between the last pairs of flanking traces of two successive nodes (Text-fig. 9 A between Fx and Fy) increase in number so that insertions become separated. Older seedlings of *Carmichaelia* species were not available for similar investigation in that genus, but from comparison of leaf insertions in adults of both genera, a similar change appears to occur in *Carmichaelia*.

One difficulty arises in the adult *Notospartium* which is not met with elsewhere, this being the variability of the adult nodes both in number of trace

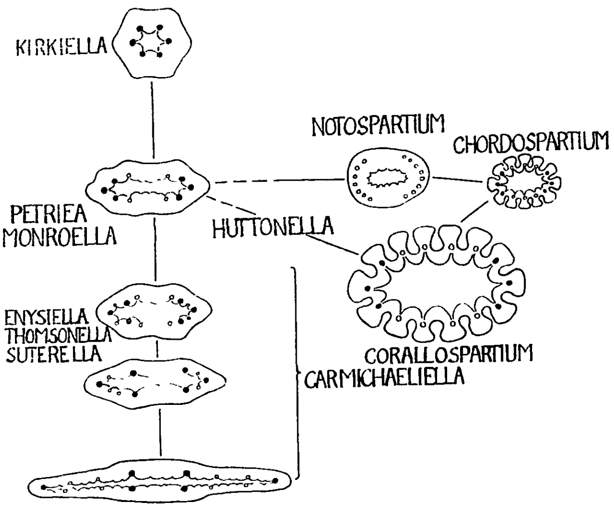


Text-fig. 9—A. T.S. stem of *Notospartium* seedling of one year (× 40). B and C. T.S. nodes of adult *Notospartium* (× 18). Abbreviations as for Text-fig. 2

bundles and in their arrangement and departure from the stele. Although the oldest seedlings available for this investigation showed a distinct edge to the cladode, the adult stems are more rounded and consequently median trace bundles are impossible to determine (Text-fig. 9 B, C), particularly in a trace consisting of an even number of bundles. Moreover, the trace bundles are usually very late in branching from the stem bundles, so that they may run as distinct leaf-trace bundles for only a very short distance in the internode. This feature was also often noticed in the seedling (Text-fig. 9 A). The other feature peculiar to this genus was that at some seedling nodes there was apparent movement of the original three traces to one edge of the stem, while the axillary bud bundles usually separating them tended to move further in (Text-fig. 9 A). Under such circumstances the median and original lateral traces would depart from one gap in the stele instead of from three, this being a similar change to one described by Sinnott (1914) for the origin of a unilacunate from a trilacunate node. A trace with three bundles departing from one gap was not observed in an adult node, but there were many gaps from which two departed. In view of what was observed in the seedling, these pairs may be two approximated traces rather than a divided trace. To sum up, it seems clear that in *Notospartium* initially flanking traces are added as the stem flattens, but subsequently various changes peculiar to the *Notospartium* genus take place, so that the interpretation of the structure of the adult is not possible until plants of intermediate age are available for stages between that of a one-year seedling and the adult.

DISCUSSION

Text-fig. 10 is an attempt to reconstruct the history of the New Zealand brooms using cladode structure as the principle guide. *Kirkiella* is chosen as the ancestral type because of its unflattened stem and trilacunate node. From *Kirkiella* arose an ancestral stock in which extra traces were added on the flanks. Its most direct derivatives to-day are the *Petriea, Monroella* and *Huttonella* subgenera. From this stock in turn came forms in which further flattening was accompanied by the interpolation of traces, a modification which as time went on tended to supersede the older supplementation by flanking traces. *Thomsonella* and some of the forms of *Carmichaeliella*, e.g. *Ca solandri*, occupy a primitive place in this series, the bulk of their nodes having added traces of both types, while the greatly flattened members of *Carmichaeliella* show complete replacement of the flanking by the interpolating traces They are connected with the *Ca. solandri* type by a complete series of intermediate forms. *Enysiella* and *Suterella* are linked to the ancestral *Carmichaeliella* stock in the belief that their trilacunate node is not primitive, but the result of elimination of both interpolating and flanking traces as the habit became reduced to a mat form. The fact that *Ca. corrugata* (Text-fig. 4 C), the wider-stemmed *Suterella* species, does frequently have extra interpolated traces, upholds this idea.



Text-fig. 10—Suggested evolution of the cladode types in the New Zealand brooms. Explanation in text

Corallospartium and *Huttonella* have in common flanking trace systems and indehiscent pods. The indehiscent pod distinguishes *Huttonella* from the other Carmichaelias. However, *Corallospartium* and *Huttonella* became separated when *Corallospartium*, becoming more flattened, added further traces so that its leaf insertions met or interlocked.

The structure of *Notospartium* seedlings indicates a close relationship between *Notospartium* and those *Carmichaelia* species in which extra traces are flanking. In *Notospartium* adult, however, there is much greater multiplication of stem bundles between the lateral traces of successive leaves, causing leaf insertions to be further apart. The adult stem is more rounded at its edges than in Carmichaelias, although its pith is distinctly flattened.

Chordospartium's connection with the other genera has for long been a problem. The anatomical evidence presented here indicates a close relationship with *Corallospartium*, the only other genus with furrowed stems. Trace systems are very similar (Pl. 29 B, C), and, as noted by Cheeseman (1925), pods are almost identical. However, the inflorescence, habit, and wiry stems of *Chordospartium* are reminiscent of *Notospartium* (Pl. 29, A, B) and quite unlike the rigid erect habit of *Corallospartium* (Pl 27 B, Pl. 29 C) Cheeseman, in fact, says that *Chordospartium* combined characters of both genera The pod structure is common also to the ***Huttonella*** section of *Carmichaelia*, a fact which has led Laing and Blackwell (1940) to suggest a possible hybrid ancestry of *Chordospartium* from *Notospartium* and *Carmichaelia*. The other possibility implied even in the similarities listed by Cheeseman is its derivation from the hybridisation of *Notospartium* and *Corallospartium*. The anatomical evidence strongly favours this alternative and in this case the few Carmichaelian features of *Chordospartium* could easily be derived from either parent, since both are probably descended from *Carmichaelia*.

The writer hopes to collect further evidence from wood histology and cytology to elucidate the relationship of these three genera.

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