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The genus Acacia Miller in South Africa — 6. The morphology of the leaf

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SUMMARY

The author has studied the morphology and anatomy of the heterophyllous (proximal and distal) leaves of South African *Acacia* species. The pinnules have been found to be anatomically different in the *Vulgares* and in the *Gummiferae*. From a morphological point of view, *A. albida* differs from the other species and merits to be treated as being a separate, monotypic genus, *Faidherbia*.

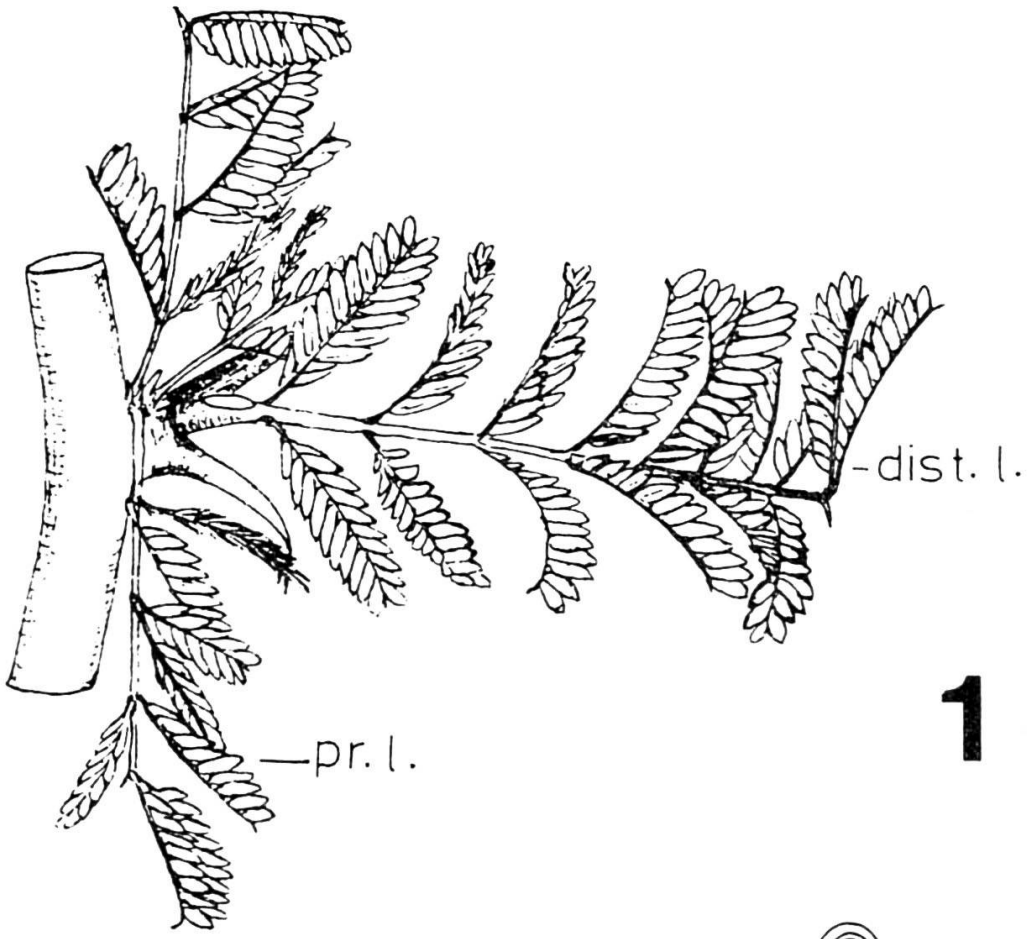
RÉSUMÉ

L'auteur a étudié l'anatomie et la morphologie des feuilles hétérophylles (proximales et distales) des espèces sud-africaines d'*Acacia*. Une différence anatomique des pennes a été constatée entre les *Vulgares* et les *Gummiferae*. Du point de vue morphologique, *Acacia albida* se distingue des autres espèces et devrait être considéré comme représentant d'un genre monotypique distinct, *Faidherbia*.

External morphology

In taxonomic descriptions of South African *Acacia* species very little is said about the heteromorphic leaves. Ross (1966) mentions that the leaf form of *A. albida* can vary on the same branch, while Gerstner (1938) uses the terms "primary" and "secondary" leaves in his description of *A. grandicornuta*. The latter terms are regarded as inadequate by the author and the terms "distal" and "proximal" leaves will be used instead.

The heterophyllous condition is far better developed in the *Gummiferae* species than in the *Vulgares*. The leaf types of both series are bipinnate with the proximal leaves usually having a lesser number of pinnae than the distal leaves. A petiolar gland is usually present on the distal leaves but is lacking on the proximal leaves (Fig. 1). In the *Gummiferae* species the stipular spines of the distal leaves are much more pronounced than those of the proximal leaves which might be reduced to small bracts. The distal leaves can be regarded as "Hochblätter" (Troll, 1967) and occur on actively growing twigs and coppice shoots. The proximal leaves, which are found on axillary short shoots and at the base of long shoots, can be regarded as transition leaves between the cataphylls and the distal leaves.



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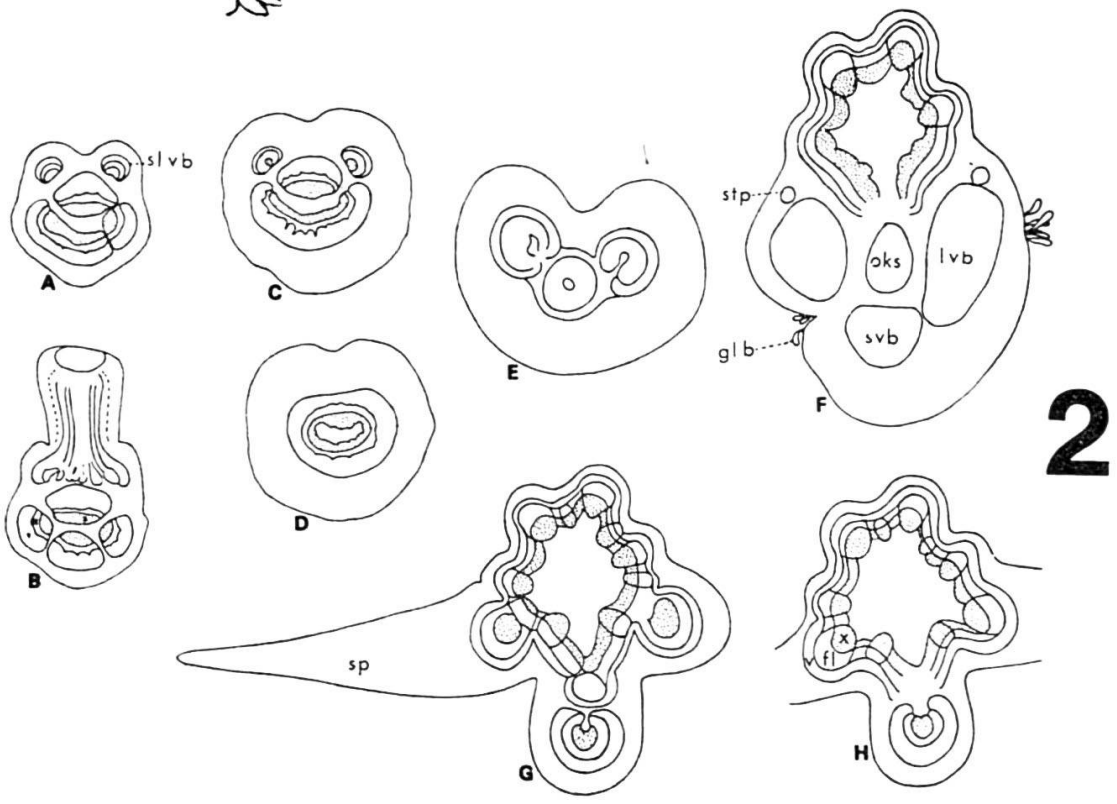

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In Table 1, the details of distal and proximal leaves of a few specimens taken at random are compared.

Distal leaves are more abundant on young, actively growing trees than on old trees where proximal leaves are more abundant. There is a clear need, therefore, to differentiate between distal and proximal leaves when describing subtaxa in the genus *Acacia*.

Distal leaves have pulvini at the leaf base and at the bases of the pinnae and pinnules. Pulvini usually do not occur at the bases of proximal leaves. The anatomy of the pulvinus has been described by Robbertse (1972).

Petiolar glands are present on almost all distal leaves of most species used in this investigation (see Appendix to Robbertse, In print). The only species where they are usually lacking on the distal leaves are those with glandular glutinous pods, namely *A. borleae*, *A. exuvialis*, *A. nebrownii*, *A. permixta*, *A. swazica* and *A. tenuispina*. Ross (1966) and Wickens (1969) report an absence of petiolar glands in *A. albida*, although glands do occur between the pinna pairs. In some specimens of *A. albida*, however, the first of these glands is situated basally to the junction of the first pinna pair and could here be regarded as a petiolar gland.

The structure of the petiolar gland is not always very uniform, although it tends to be disc-like in the *Gummiferae* species and more spherical to slightly cylindrical in the *Vulgares* species.

Glands may also be present on the rhachis between the bases of all pinna pairs or between the bases of the upper or lower one or more pinna pairs only.

Anatomy

Petiole

The vascular supply of the leaf base and petiole of distal leaves was studied by means of serial sections of the node, leaf base and petiole of *A. caffra* (Fig. 2). A schematic reconstruction of the node is presented in Figure 3.

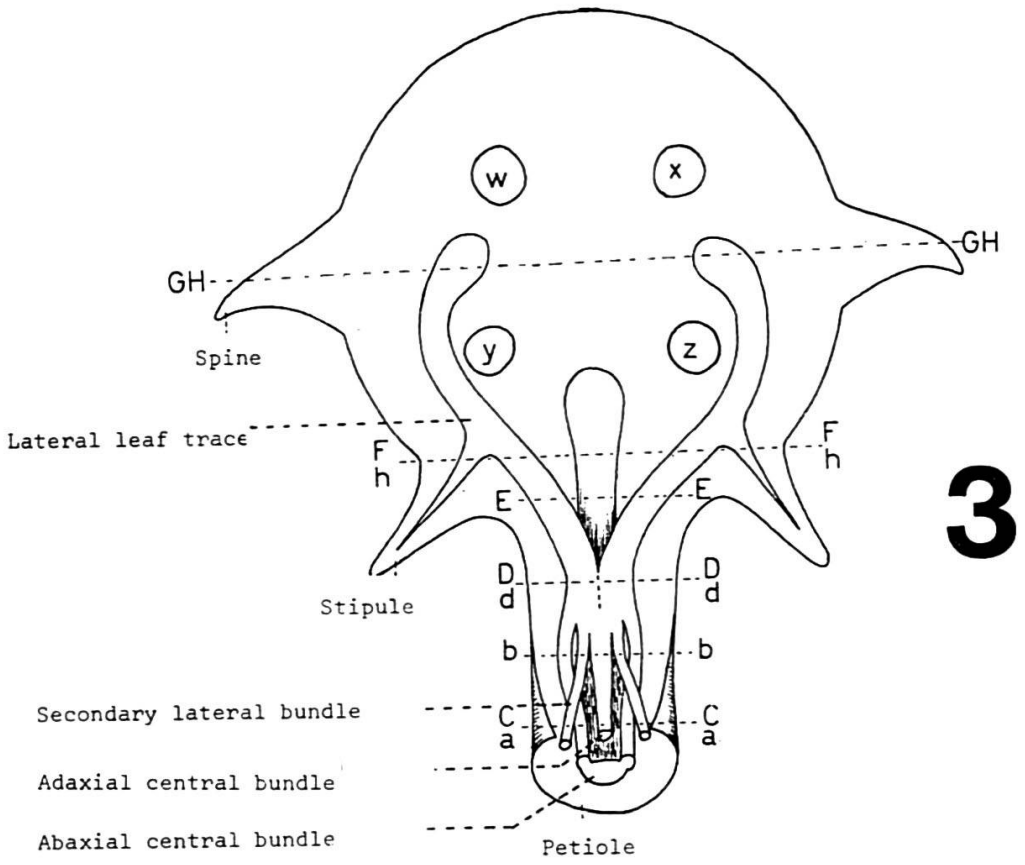
The nodes are trilacunar. Each lateral leaf trace gives rise to a vascular bundle entering a stipule (Fig. 2F). In the pulvinus the three leaf traces fuse to form a closed cylinder (Fig. 2D) which then breaks up into one abaxial central bundle, one adaxial central bundle and two secondary lateral vascular bundles (Figs. 2C, 3).

The vascular supply of a distal leaf, up to the point where the petiolar gland is situated (as described above), is basically representative of all South African species although, in most *Gummiferae* species, two instead of one central adaxial bundle occur.

Fig. 1. — Distal (dist. 1.) and proximal (pr. 1.) leaves of *A. hebeclada* subsp. *hebeclada*.

Fig. 2. — Serial sections through the node and petiole of *A. caffra*.

A, cross section of distal part of petiole; *B*, section through petiolar gland; *C*, cross section of proximal part of petiole; *D* & *E*, cross sections of pulvinus; *F*, *G* & *H*, cross sections of node. f1, phloem; glb, glandular body; lvb, lateral leaf trace; oks, procambium of axillary bud; sp, stipular spine; stp, vascular branch of stipule; svb, central leaf trace; sl vb, secondary lateral bundle; v, fibres; x, xylem.


w
x
GH
GH
Spine
y
z
Lateral leaf trace
F
h
F
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E
D
d
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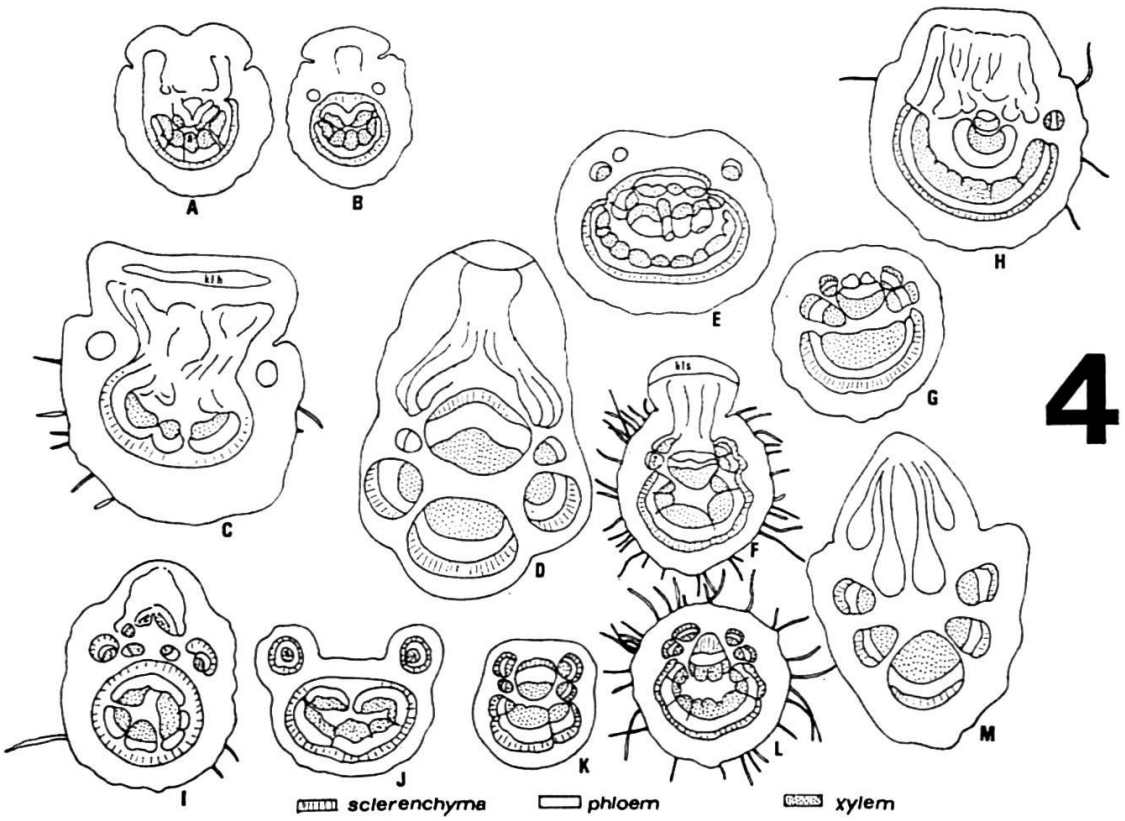
Stipule
Secondary lateral bundle
C
a
C
a
Adaxial central bundle
Abaxial central bundle
Petiole

3


A
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4

The petiolar gland is also supplied with vascular tissue from the petiole and therefore has a marked influence on the anatomy of the latter. The petiolar anatomy of different species was compared in sections through the petiolar gland or, where petiolar glands were absent, halfway between the leaf base and the first pinna pair. Diagrams of a few sections are shown in Figure 4.

In the *Gummiferae* species three basic petiolar types can be distinguished. Type B (Fig. 5B) is typical of the *Gummiferae* species where there is one large abaxial bundle and two adaxial bundles which branch into the gland. Two secondary lateral vascular bundles arising between the adaxial and abaxial bundles run parallel to the former and can also form branches to the gland. *Acacia polyacantha* is the only *Vulgares* species with this petiolar type, but is also the only *Vulgares* species in which the rhachis turns upwards during nocturnal movements (Robbertse, 1972).

The other *Gummiferae* types are type C (Fig. 5C) where petiolar glands are absent and type A (Fig. 5A) where either a single concave adaxial bundle is present or a closed cylinder is formed.

The typical *Vulgares* petiolar type (Fig. 5D) has a single adaxial bundle with one or two pairs of lateral vascular bundles. Of these lateral bundles one or both pairs may form branches to the gland. *Acacia albida*, unlike any other *Acacia* species, has two adaxial bundles on top of each other with two pairs of lateral bundles leading to the first gland on the rhachis (Fig. 5E).

In *A. brevispica*, *A. kraussiana* and *A. schweinfurthii*, the abaxial "bundle" is pentafid (Fig. 5F) while the adaxial bundles are the same as in the typical *Gummiferae* type.

Pinnules

Pinnules were studied in transverse sections of distal leaves only. The sections were stained in safranin and fast green.

The epidermis in most species is covered with a relatively thick cuticle. In the species with glandular glutinous pods the cuticle has an uneven surface (Pl. I, A). The stomata have very distinct outer and inner cuticular ridges on the guard cells (Pl. I, B). The pinnules are amphistomatic although in some species they tend to be hypostomatic.

Pinnules of *A. borleae* can be distinguished from those of all the other South African species on the basis of the presence of glands on the epidermis (Pl. I, A).

Since palisade parenchyma is present both ab- and adaxially, the pinnules should be regarded as equifacial or isobilateral. The palisade cells are multiseriate with those on the adaxial side usually longer and better defined than the cells on the abaxial side.

Fig. 3. — Schematic reconstruction of the path of the primary vascular tissue in the node and leaf base of *A. caffra*. Capital letters refer to Fig. 2 and small letters refer to Robbertse (In print), Fig. 1.

Fig. 4. — Cross sections of petioles of different South African *Acacia* species.

A & B, A. giraffæ × *A. haematoxylon; C, A. gerrardii; D, A. galpinii; E & H, A. albida* (*E* proximally to and *H* through the petiolar gland); *F & L, A. burkei* (*L* proximally to and *F* through the petiolar gland); *G, A. nigrescens; I, A. stuhlmannii; J, A. borleae; K, A. robynsiana; M, A. kraussiana.* kls, glandular cells; klh, glandular cavity.

Species	Author's collection numbers	Distal leaves					Proximal leaves				
		Length of petiole in mm	Petiolar gland present (+) or absent (−)	Length of rhachis in mm	Number of pinnae	Number of pinnules	Length of petiole in mm	Petiolar gland present (+) or absent (−)	Length of rhachis in mm	Number of pinnae	Number of pinnules
A. gerrardii	242	8-10	+	60-80	12-18	24-34	3-5	—	5-15	4-6	12-24
A. grandicornuta	256	5-8	+	10-15	4-8	24-30	10-20	—	0-10	2-4	14-20
A. hebeclada subsp. *tristis*	324	5	+	40	16	18-24	5-7	—	15-20	2-8	14-18
A. nilotica	391	5-8	+	20-30	16-20	40-50	3-8	small or —	0-10	2-10	20-36
A. reficiens	249	2-3	+	12-15	8-10	20-30	4-7	—	15-60	4-12	22-32
A. tortilis	293	2-3	+	10-15	12-20	20-34	5-8	—	3-5	2-8	14-30
A. stuhlmannii	240	3-5	+	50-80	24-34	22-28	3-5	—	10-20	6-12	12-18
A. exuvialis	278	8-10	+	18-35	6-14	8	5-8	—	0	2	6
A. permixta	205	3-5	+	8-10	4-8	10-16	3-8	—	0-5	2-4	6-8
A. robusta subsp. *clavigera*	873	8-12	+	50-60	10-16	30-40	15-30	—	30-40	6-10	34-40

Table 1. — Differences between proximal and distal leaves of a few *Gummiferae* species.

In the *Vulgares* species the adaxial and abaxial palisade cells are separated from each other between adjacent vascular bundles by one or more layers of well-defined spongy mesophyll cells (Pl. I, C). In this respect, the pinnules of the *Vulgares* species differ distinctly from those of the *Gummiferae* species where there is no separating layer of spongy mesophyll between the ad- and abaxial palisade cells (Pl. I, D). This phenomenon is not only seen in pinnules of mature plants but also in pinnules of seedlings (Pl. II, A and B).

Discussion

Some work has been done by Buscalioni & Catalano (1924), Peters (1925) and Boke (1940) on the anatomy of phyllodes of *Acacia* species but very little is known about the leaf anatomy of the South African species. Also, very little has been written about the dimorphous leaves in *Gummiferae* (sensu Bentham, 1875) species. This study indicates that future descriptions should contain more details about the two leaf types.

There is a distinct anatomical difference between the petioles of the *Vulgares* and those of the *Gummiferae* species. Although the petiolar anatomy of *A. albida* resembles that of *A. giraffae* most closely, the anatomy of the pinnules corresponds to that of the *Vulgares* species. *Acacia albida* cannot, therefore, be included in either of these two series. Considering the morphology of the seed (Robbertse, 1973a), the pollen (Robbertse, 1973b) and the stipules, the author must agree with Vassal (1972) that the taxon *Acacia albida* Del. is best regarded as being a separate, monotypic genus, *Faidherbia* A. Chev.

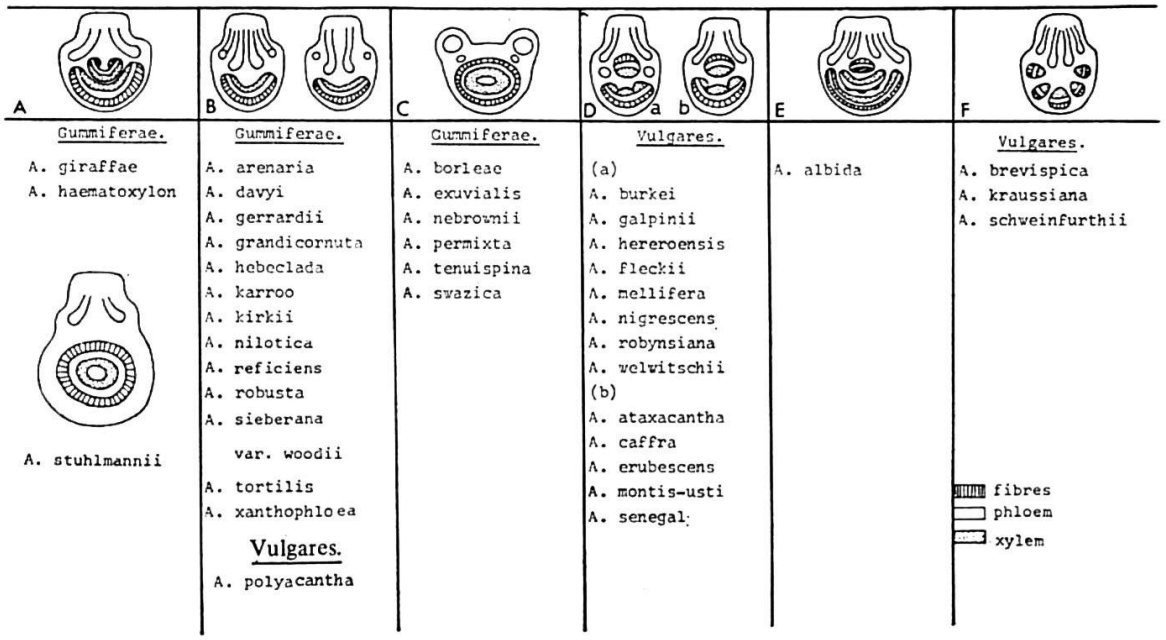

Fig. 5. — Grouping of South African *Acacia* species based on the anatomy of the petiole.

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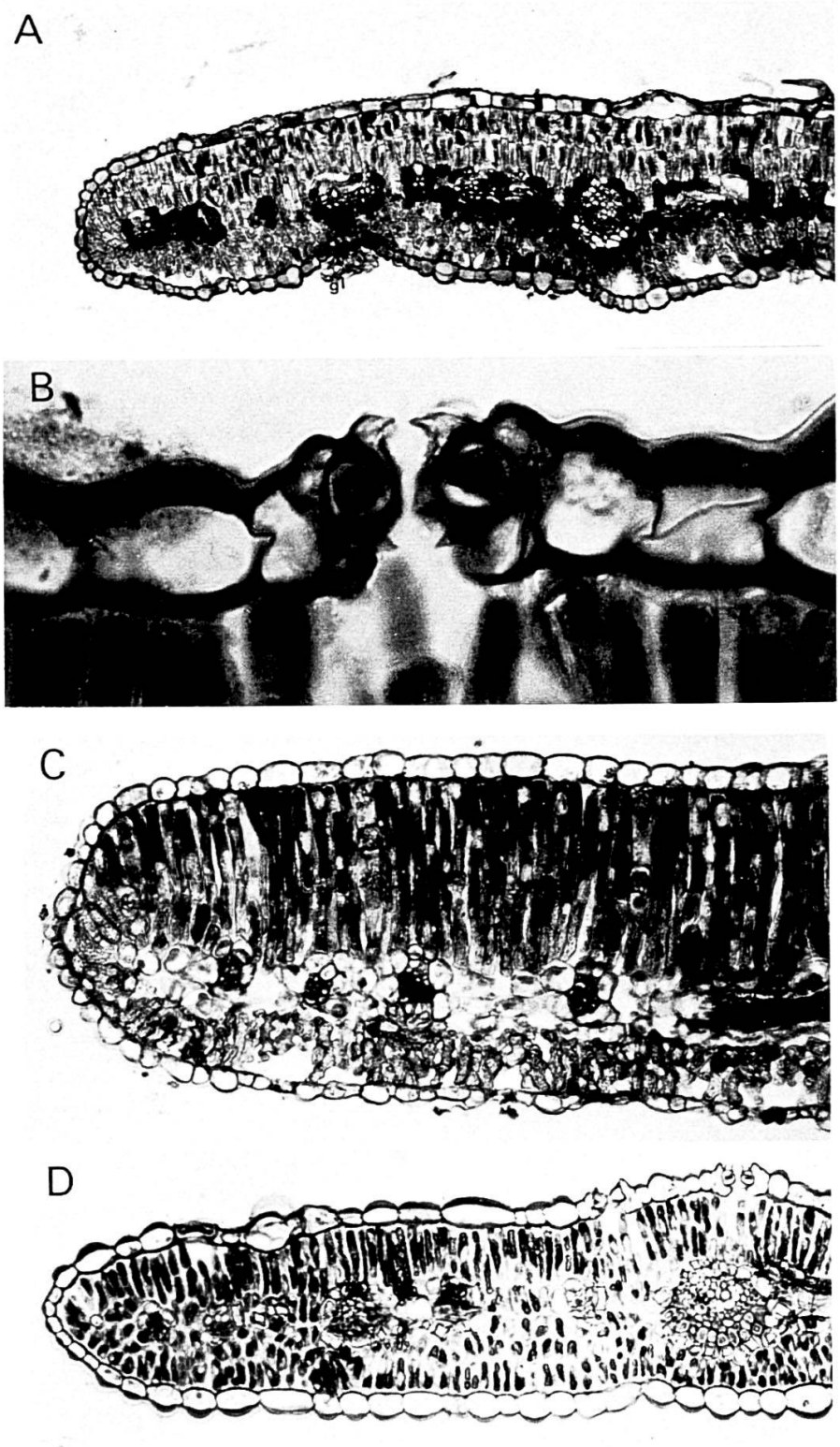
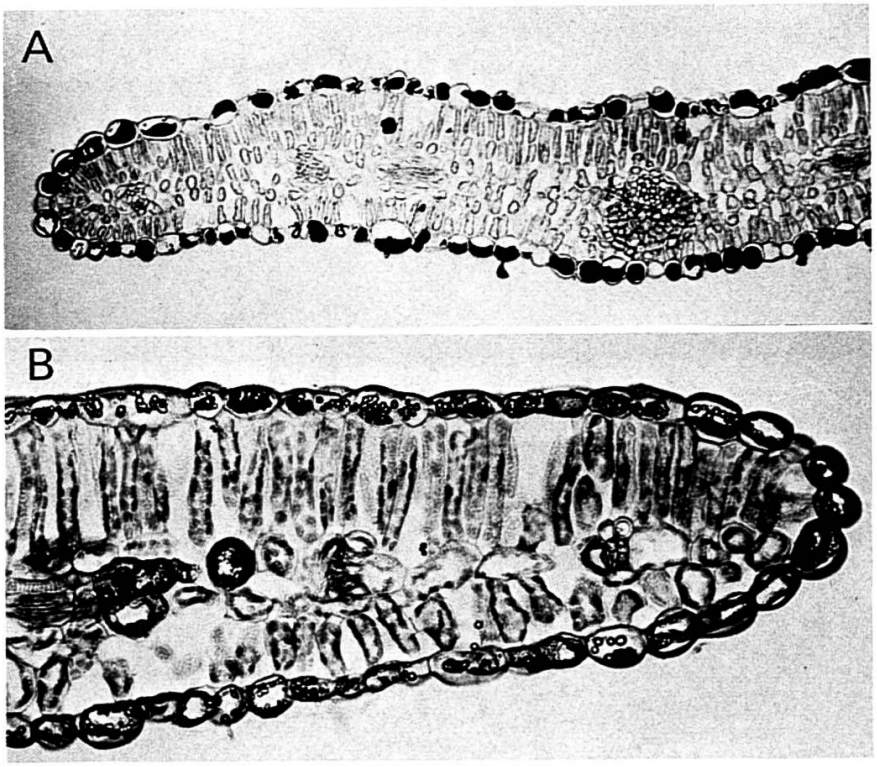


A, Cross section of a pinnule of *A. borleae* (*gl,* gland).
B, section through stomium cells.
C, D, cross sections of pinnules of leaves from mature trees. *C, A. polyacantha; D, A. hebeclada* subsp. *hebeclada.*



A, B, cross sections of pinnules of seedling leaves.
A, A. haematoxylon; B, A. caffra.