

The genus *Acacia* in South Africa. IV. The morphology of the mature pod

P. J. ROBBERTSE*

ABSTRACT

The external morphology and the anatomy of the pods of all the South African *Acacia* species are discussed. It was found that the South African *Acacia* species can be grouped into a number of distinct categories on the basis of the anatomy of their pods. There is quite a marked difference in the anatomy of the pod of the series *Vulgares* and that of the series *Gummiferae*.

INTRODUCTION

Most authors who provide keys to the South African and other African *Acacia* species (Oliver, 1871; Benthams, 1875; Harvey, 1862; Keay, 1958; Baker, 1930; Burtt Davy, 1932; Young, 1955; Verdoorn, 1957; Brenan, 1959 and Von Breitenbach, 1965) use the shape and external structure of the pod as taxonomically important characters. No previous instance is known where the anatomy of the pod was used as a taxonomic character to distinguish between *Acacia* species. Kraus (1866), Hildebrandt (1873-1874) and Majewsky (1873) made a general study of the anatomy of the pod, and Fahn and Zohary (1955) devised a scheme according to which they classified the pods of a number of Leguminosae genera on an anatomical basis.

In the course of this study the external morphology and anatomy of the pods of all South African *Acacia* species were examined. Only mature preserved and

dried pods were used. For the external and anatomical examinations at least 10 pods of each species derived from two or more localities were intensively studied, and general observations were made in the field and on samples from the National Herbarium in Pretoria. For the anatomical examination, microtome sections were made of one pod of each species as well as hand sections of at least two other pods per species.

EXTERNAL MORPHOLOGY OF THE POD

The pods of South African *Acacia* species vary considerably in form and texture. They may be linear, elongated, straight, crescent-shaped or curled into a spiral, flattened, round, sometimes constricted (Fig. 1). They have a membranous, leathery or woody texture and the surface may be smooth, hairy or covered with glands. The texture of the valves is a character determined by the anatomy of the pods. This character is accordingly discussed under anatomy.



FIG. 1.—Pods of some southern African *Acacia* species. 1, *A. albida*; 2, *A. schweinfurthii*; 3, *A. ataxacantha*; 4, *A. here- roensis*; 5, *A. caffra*; 6, *A. senegal* var. *rostrata*; 7, *A. senegal* var. *leiorhachis*; 8, *A. mellifera* subsp. *detinens*; 9, *A. erubescens*; 10, *A. galpinii*; 11, *A. nigrescens*; 12, *A. burkei*; 13, *A. montis-usti*; 14, *A. erioloba*; 15, *A. haematoxylon*; 16, *A. sieberana* var. *woodii*; 17, *A. robusta* subsp. *clavigera*; 18, *A. luederitzii* var. *retinens*; 19, *A. reficiens*; 20, *A. hebeclada* subsp. *hebeclada*; 21, *A. hebeclada* subsp. *chobiensis*; 22, *A. stuhlmannii*; 23, *A. rehmanniana*; 24, *A. grandicornuta*; 25, *A. tortilis* subsp. *spirocarpa*; 26, *A. tortilis* subsp. *heteracantha*; 27, *A. kirkii*; 28, *A. nilotica* subsp. *kraussiana*; 29, *A. gerrardii* var. *gerrardii*; 30, *A. xanthophloea*; 31, *A. arenaria*; 32, *A. davyi*; 33, *A. karroo*; 34, *A. tenuispina*; 35, *A. exuvialis*; 36, *A. borleae*; 37, *A. nebrownii*; 38, *A. permixta*; 39, *A. swazica*.

* Department of General Botany, University of Pretoria.

Most species are characterized by dehiscent pods, but the pods of *A. schweinfurthii*, *A. kraussiana*, *A. albida*, *A. erioloba* (= *A. giraffae sensu auct. mult. fide* Ross, 1975), *A. haematoxylon*, *A. stuhlmannii*, *A. xanthophloea* and *A. nilotica* do not normally open. *A. hebeclada* pods usually open along one side, whereas *A. sieberana* and *A. tortilis* pods are sluggish in opening and usually remain closed. According to Fahn and Zohary (1955) the ability of a pod to dehisce is determined by its anatomy and by the fibrils in the fibre walls.

Pods exhibit three types of epidermal appendages: hairs, multicellular glands and minute, reddish-brown, multicellular organs. The hairs are unicellular and their length varies from a few millimetres in *A. stuhlmannii* to papilliform hairs in *A. tortilis* subsp. *heteracantha*. Species with hairy ovaries do not necessarily bear hairy pods, e.g. *A. xanthophloea* and *A. reficiens*. The same applies to species with gland-covered pods. *A. karroo*, like *A. nebrownii*, *A. borleae*, *A. tenuispina*, *A. swazica*, *A. exuvialis* and *A. permixta*, has glands on the ovaries but the mature pods of *A. karroo* possess few or no glands whereas the mature pods of a species such as *A. permixta* are covered with glands. In respect of the number of glands on the mature pod, *A. exuvialis* lies between *A. karroo* and *A. permixta* and the other species between *A. exuvialis* and *A. permixta* (see also Verdoorn, 1957 and Ross, 1972).

All the species with glands on the mature pods are shrub-like. *A. borleae* and *A. exuvialis* can grow to some 3 m in favourable conditions, but most of these shrubs vary from 1 to 2 m. A dwarfed form of *A. karroo* is also found on the Springbok Flats and near Rustenburg. These variations of *A. karroo* require intensive study and the problem will have to be passed over here for lack of further data.

Few data are available on the presence of the gland-like bodies (Fig. 2A) found in some *Acacia* species. Brenan (1959) writes in connection with *A. brevispica* of the "... reddish or dark glands with which the inflorescence-axes are sprinkled, ..." The same type of gland-like bodies are found on the pods of *A. erioloba*, *A. stuhlmannii*, *A. sieberana*, *A. haematoxylon* and *A. nilotica*, all belonging to the series Gummiferae, and *A. schweinfurthii*, *A. polyacantha*, *A. hereroensis*, *A. fleckii* and *A. senegal* of the series Vulgares. The number of glands per surface unit not only varies considerably according to species, but also within the same species. Fig. 2B shows young pods of *A. erioloba* from two different trees growing close to the Pienaars River. The dark colour of the three pods is caused by a dense concentration of glandular bodies; the concentration on the light coloured pod is less dense. All the pods on one tree have the same colour and the colour difference in the pods from the two trees is conspicuous, even at a distance of 80 m. The glands can also occur on the vegetative parts, e.g. in the seedlings of *A. erioloba*, where they occur in the axils of leaves and cotyledons.

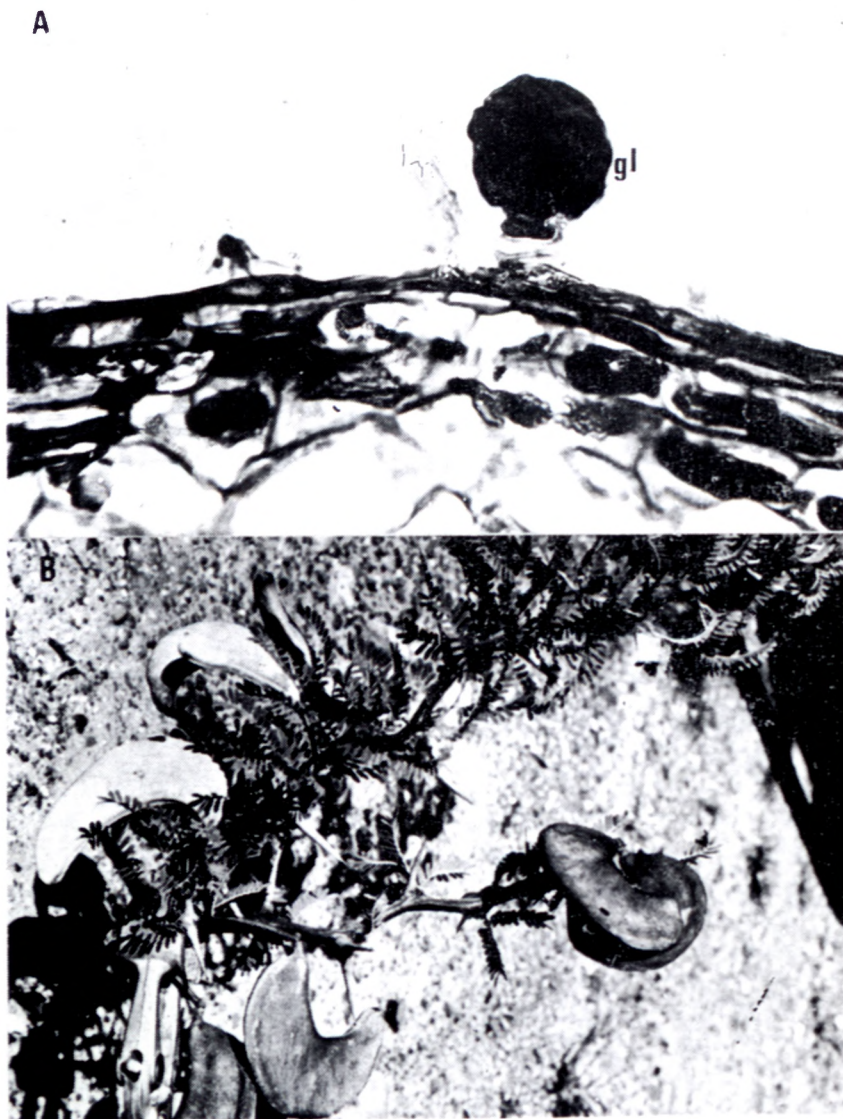


FIG. 2.—A, gland-like body on part of section through *Acacia erioloba* pod; B, twigs and pods of *A. erioloba* with dark pods crowded with gland-like bodies. gl, gland-like body.

These minute, reddish-brown, gland-like bodies consist of epidermal cells with the walls thickened and permeated with tannin. The epidermal cells enclose a number of thin-walled packing cells. These organs with their elongated stalks and incrassate cellular walls are very similar to the sporangium of a fern, but their function is unknown. Their presence may be of taxonomic importance, but too little is known on the subject at present for any comment to be possible.

ANATOMY OF THE POD

The abaxial epidermis (outer epidermis)

In the discussion of the external morphology reference was made to the structure of the abaxial or outer epidermis of the pod and the glands characteristic of certain species. These glands are shield-shaped, with a diameter of approximately

0,5 mm. They are solid while young, but as soon as they enlarge, a hypodermal cavity is formed at the tip. The cavity is formed schizogenously, since the cells do not disintegrate but merely separate (Fig. 3A). The gland cavity is filled with a glutinous fluid which is secreted immediately the epidermal cells are mechanically damaged, or else through a glandular aperture which is schizogenously formed. This glandular secretion appears to be a good nourishing medium for certain fungi (unidentified), since older glands are constantly infected with them. The glandular stalks vary from species to species. *A. exuvialis* and *A. nebrownii* have thin stalks (some 3 to 5 cells in diameter), whereas *A. permixta* has a considerably thicker stalk (10 cells or more in diameter). The glands on *A. borleae* pods are slightly submerged below the pod surface, whereas those of *A. permixta* are usually found on a protrusion.

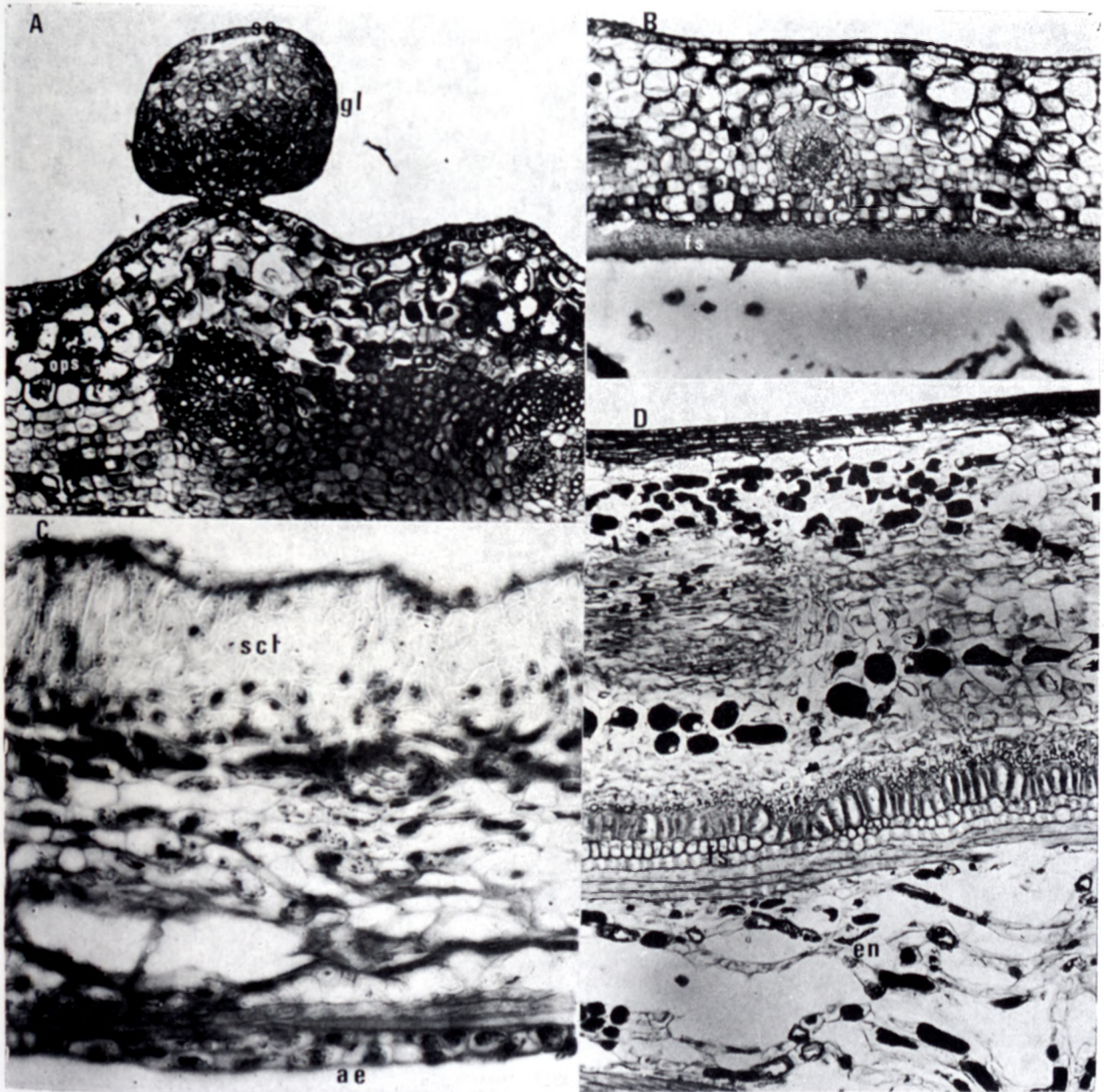


FIG. 3.—Segments of cross sections through the pericarp. A, B, *Acacia swazica*; C, *A. schweinfurthii*; D, *A. polycantha*. ae, adaxial epidermis; en, endocarp; fs, fibre stratum; gl, gland; ops, outer parenchyma stratum; sc, schizogenous cavity; scl, sclereid stratum.

The adaxial epidermis (inner epidermis)

The adaxial epidermis of the pods is usually only one cell layer thick. Fig. 3C shows local periclinal divisions in the epidermal cells of *A. schweinfurthii* to form more layers of cells. In certain species the epidermal cells may grow out to form multicellular hairs, as shown by Fahn and Zohary (1955). Several species, e.g. *A. nilotica* and *A. rehmanniana*, form a spongy tissue around the seeds: in a cross-section of the pod this tissue resembles chains of thin-walled intertwined parenchymatous cells (Fig. 3D). The cell walls of adjacent cellular chains fuse to form a pseudo-parenchymatous tissue.

To trace the origins of this pseudo-parenchymatous tissue, an ontogenetical study of the pods was necessary. Only the pods of *A. karroo* of the series Gummiferae and *A. caffra* of the series Vulgares were used for this study. The young ovaries of both types have papilliform epidermal cells around the base of the funiculus ("transmitting tissue", Fahn, 1967). These papillaceous epidermal cells (Fig. 4) are most conspicuous and grow out to form multicellular hairs, which grow into the loculus, early in the development of the pod—apparently immediately after fertilization. These multicellular hairs or cellular chains are largely responsible for the formation of the pseudo-parenchyma in *A. karroo* and *A. caffra* and there is reason to believe that this is the case with most other species. Further discussion will refer to the pseudo-parenchymatous tissue as a *spongy endocarp* to distinguish it from the outer portion of the pericarp and the fibre stratum of the endocarp. In *A. caffra* the pseudo-parenchymatous tissue occupies only a small portion of the loculus near the placenta: the rest of the epidermis consists of one layer, occasionally of two layers of cells.

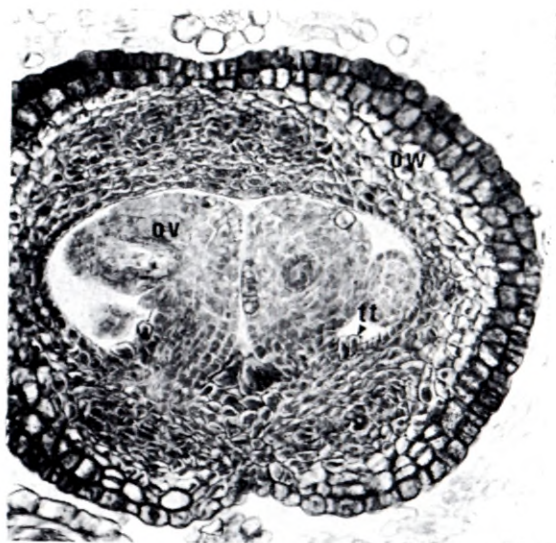


FIG. 4.—Part of cross section through the flower of *Acacia karroo* to show the structure of the ovary wall. ov, ovule; ow, ovary wall; tt, transmitting tissue.

In species such as *A. fleckii* it is difficult to determine to what extent the rest of the adaxial epidermal cells, away from the placenta, contribute to the formation of pseudo-parenchymatous tissue, since the walls of the cellular chains derived from the placenta will also merge with cell walls of other epidermal cells. It is clear, however, that the adaxial epidermal cells can grow out into multi-cellular hairs in various places.

In *A. erioloba* and *A. haematoxylon* virtually all the adaxial epidermal cells grow out to become part of the spongy pseudo-parenchyma, and no original

epidermal cells can be observed in the mature pod. In *A. haematoxylon* even subepidermal tissues may contribute to the formation of the spongy endocarp, but since there is no sclerenchymatous stratum (Fahn and Zohary, 1955) in this case, it is impossible to determine the boundaries of the epidermis in the mature pod. In the other species which do possess a sclerenchymatous zone, it extends to adjoin the adaxial epidermis.

The mesophyll of the pericarp

According to Fahn and Zohary (1955) the mesophyll of the pericarp is divided into an outer parenchymatous stratum and an inner sclerenchymatous stratum. The parenchymatous stratum extends from the abaxial epidermis up to the sclerenchymatous stratum and includes the vascular bundles and the various sclereid layers. The sclerenchymatous stratum adjoins the adaxial epidermis and consists of longitudinal and latitudinal fibres and sclereid layers (Fig. 5E) but one, two or all three of these layers may be partially or completely absent (Fig. 5A, H and I). This classification of the pericarp is useful for anatomical purposes, but is not ontogenetically correct.

The wall of the ovary, as in *A. karroo*, consists of two clearly distinguishable strata (Fig. 4A). The outer stratum consists of the abaxial epidermis and a hypodermal layer. The cells of both these layers contain a secretion-like substance, and the hypodermal layer is responsible for the formation of a portion of the parenchymatous stratum outside the vascular bundles (Fig. 6A—C). The other stratum of the ovary wall extends from the hypodermis up to the adaxial epidermis and consists of smaller, colourless cells. The vascular bundles, sclerenchymatous stratum and sclereid cells originate in this layer.

For the purpose of this discussion, the classification of the pericarp made by Fahn and Zohary (1955) will not be used, since it makes no provision for a clear delimitation of the sclereid layers. Instead, the terms used will be *parenchymatous stratum* which includes the vascular bundles with their sclerenchyma caps (fibre caps) a *fibre stratum* adjacent to the adaxial epidermis and consisting of longitudinal or else of longitudinal and latitudinal fibres, and a *sclereid stratum* which may be situated in the parenchymatous or next to the fibre stratum.

Using the data collated during this study, a key can be drawn up for the identification of the pods of South African *Acacia* species based on the anatomy of the pod (Fig. 5). For this classification, the arrangement of pericarpal tissues is schematically shown for each of the eleven groups (Fig. 5). Pods of the series Gummifera (sensu Rob.*) and series Vulgares (sensu Benth.) can be distinguished by the fact that the fibre stratum of the Gummiferae consists of longitudinal fibres only (Fig. 5H, J and K) or is absent (Fig. 5G and I), whereas those of the Vulgares consists of longitudinal and latitudinal fibres. In some Vulgares species, too, sclereid cells may be found on top of the fibre stratum (Fig. 5E and F). According to this classification, *A. albida* belongs to the series Vulgares (sensu Benth.), since the pericarp of the latter taxon also contains longitudinal as well as latitudinal fibres.

Fahn and Zohary (1955) made an anatomical study of the pods of 78 species of 54 genera of the Leguminosae and were able, on the basis of this study, to show developmental tendencies amongst certain groups. They showed, for instance, that from the Mimosoideae through the Caesalpinioideae to the

* Gummiferae sensu Benth., excluding *A. albida*.

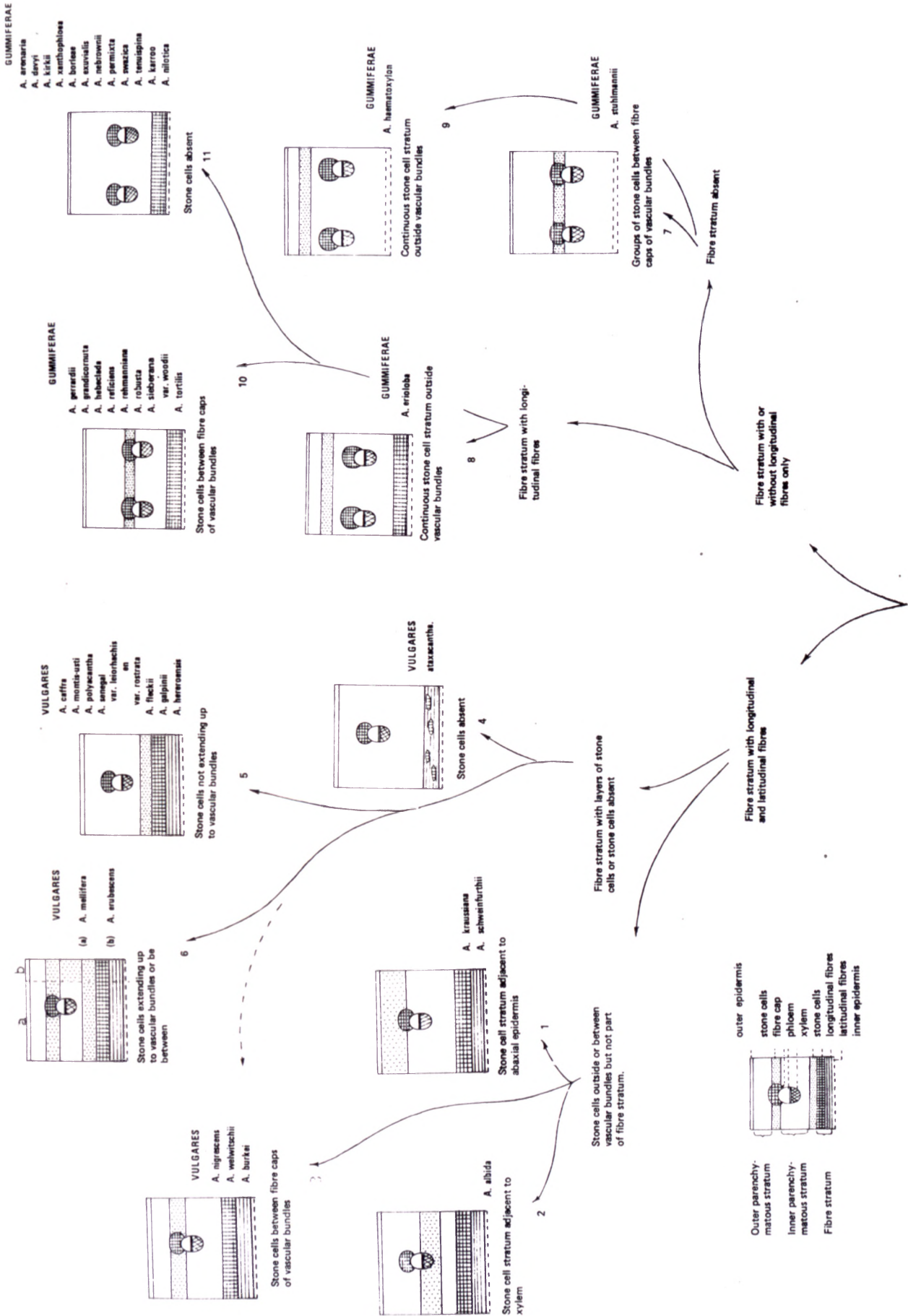


FIG. 5.—Key to the grouping of southern African *Acacia* species, based on the anatomy of the pod.



FIG. 6.—Parts of sections through the margins of *Acacia* pods. A, *A. kirkii*; B, *A. karroo*; C, *A. ataxacantha*. art, articulation; ops, outer parenchymatous stratum; fs fibre stratum.

Papilionoideae the sclerenchymatous stratum tends to diminish. According to this view the series Gummi-ferae is considered more advanced than the Vulgares, since the latter's fibre stratum consists of latitudinal as well as longitudinal fibres whereas in the Gummi-ferae it is reduced to longitudinal fibres only or is absent altogether.

Unfortunately Fahn and Zohary did not include many examples from the genus *Acacia* and come to

some faulty conclusions, such as the following: "Thus in the subfamily Mimosoideae, the most primitive subfamily of the Leguminosae, no species was found without any sclerenchymatous stratum", whereas this fibre stratum is absent in two South African *Acacia* species alone, viz. *A. haematoxylon* and *A. stuhlmannii*. In their description of their "*Acacia* type" pericarp they state that the sclerenchymatous stratum consists of latitudinal and longitudinal fibres. At the same

time they illustrate a cross-section of part of the pericarp of *A. raddiana* (= *A. tortilis* subsp. *raddiana*) in which only longitudinal fibres occur. They were, therefore, unable to distinguish between the two types of pericarpous composition shown in Fig. 5. The fact that *A. decurrens* and *A. neriifolia*, which they call "*Acacia types*", belong to the series Bothrycephalae and Phyllodinae respectively, stresses the relationship between the series Vulgares and the two above-mentioned subgenera. This relationship is discussed in greater detail in Robbertse (1973) and two papers still in press.

(a) *The parenchymatous and sclereid strata*

As already mentioned, the parenchymatous stratum is heterogeneous in origin. The portion between the vascular bundles and the abaxial epiderm consists of 5–10 cell layers and derive principally from the hypodermal layer of the ovary wall. This portion differentiates relatively early and does not change significantly. The cells are larger than those in the inner portion of the parenchymatous stratum and in most species it contains a secretion clearly visible in unstained preparations and very chromatic (Fig. 3D). In *A. tortilis* the outer portion of the parenchymatous stratum is collenchymatous and in *A. schweinfurthii* it is replaced by a sclereid zone.

The inner portion of the parenchymatous stratum, i.e. the portion on the adaxial side (inside) of the vascular bundles, generally consists of smaller cells than the outer portion. The vascular bundles are embedded in the parenchymatous zone and are bounded on the abaxial side by fibre caps. In species such as *A. nilotica* and *A. montis-usti*, where the pericarp is succulent when young, only a few isolated fibres are found on the abaxial side of the widely spaced vascular bundles. In species with woody pods, such as *A. hebeclada*, *A. erioloba* and *A. robusta*, there are large groups of fibres and the vascular bundles lie close together. In certain species (Figs. 5C, F, G and J) there are sclereid cells between the fibre bands of adjacent vascular bundles. An interesting phenomenon here is that the parenchymatous cells directly adjacent to the fibre caps of the vascular bundles can become meristematic in order to give rise to new cells. Since the fibre caps, on account of their position, represent pericycle cells and since a pericycle is potentially meristematic (Esau, 1965), this phenomenon cannot be considered unusual. Young *A. hebeclada* pods have secondary parenchymatous pericycle cells adjacent to the fibre caps, and these later become sclereid cells. The meristematic activity of the pericycle cells is so pronounced in *A. erioloba* and *A. haematoxylon* pods that sclereid cells are forced from between the vascular bundles to form a sclereid zone around them (Fig. 5H and I). The latter can therefore be considered a derived type which may have originated from the type of structure found in *A. hebeclada* and other species (Fig. 5J). In species without any sclereid cells among the vascular bundles, (Fig. 5K) no meristematic activity has been noted in the pericycle.

The position of *A. albida* (Fig. 5B), where the sclereid cells are located adaxially with respect to the vascular bundles, is basically the same as for groups G and J (Fig. 5). The difference is that the cells of the outer portion of the parenchymatous stratum in *A. albida* are enlarged to form a more or less fleshy portion. The pericycle cells adjoining the outer parenchymatous stratum (= cortex) extend anticlinally to contribute to the fleshiness of this zone and this extension of the cells displaces the sclereid cells deeper into the parenchymatous stratum.

In the pods of certain species of the series Vulgares, the parenchymatous cells directly adjacent to the fibre zone become meristematic. The secondary cells formed in this way differentiate into sclereid cells, resulting in a sclereid layer on the abaxial edge of the fibre stratum, which may be confined to the median longitudinal axis of the valves or may reach to the edges. This is the structure found in group 6 (Fig. 5) of the series Vulgares. It is never found amongst the Gummiferae.

Compared with *A. ataxacantha* pods, *A. hereroensis* pods have more longitudinal fibres and even possess occasional single sclereid cells on top (i.e. at the abaxial edge) of the fibrous stratum. In *A. polyacantha*, *A. caffra* and *A. galpinii* there are also more sclereid cells on top of the fibre stratum, so that we have here a sclerenchymatous stratum consisting of fibres and sclereid cells.

The sclereid cells have conspicuously large nuclei and are therefore alive. Live sclerenchymatous elements have also been described by Van Vuuren (1970) in *Adenia*. The pods of *A. nigrescens*, *A. burkei* and *A. welwitschii* (Fig. 5C) have sclereid cells amongst the adjacent vascular bundles. The entire portion of the parenchymatous stratum between the sclereid cells linking the vascular bundles and the sclereid cells adjacent to the fibre stratum is temporarily meristematic. The secondary parenchymatous cells formed as a result of this meristematic activity also have conspicuous nuclei like the sclereid cells of *A. caffra*. Although some of the secondary parenchymatous cells differentiate into sclereid cells, most of them retain their thin walls. The notable meristematic activity of the adaxial portion of the parenchymatous stratum is similar to a phenomenon found in the pods of *A. erioloba* and *A. haematoxylon*.

The arrangement of tissue types in the pericarp of *A. erubescens* and *A. mellifera* (Fig. 5F) look like a combination of the arrangements shown in Fig. 5C and E.

The arrangement shown in Fig. 5Fa is found near the edges of the valves, whereas Fig. 5Fb shows the tissue arrangement along the median axis of the valves. The tissue organization found in *A. galpinii* (Fig. 5E) actually lies between types C and F, since the succession of the tissue layers at the sides of the valves corresponds with the arrangement shown in Fig. 5C.

It has already been pointed out that the sclereid cells found in the pericarp of *A. schweinfurthii* and *A. kraussiana* (Fig. 3C) are derived from hypodermal cortex tissue. These sclereid cells are therefore ontogenetically totally different from the other sclereid cells found amongst vascular bundles or at the abaxial edge of the fibre stratum. The latter two kinds of sclereid cells differ because those amongst the adjacent vascular bundles originate from the pericycle and those adjoining the fibre stratum from an inner tissue layer which may be considered homologous with a pith. In the ovary wall, however, 'pericycle' and 'pith' cells cannot yet be differentiated. Strictly speaking, the pods of the series Vulgares show sclereid cells of three different origins whereas the series Gummiferae possesses only one kind of sclereid cell—the kind originating from the pericycle.

At the edges of the valves, in most species, the fibre caps of adjacent vascular bundles merge lengthwise to form a continuous fibre layer (Fig. 6C). In some species such as *A. xanthophloea*, *A. kirkii* (Fig. 6A) and *A. stuhlmannii*, where the pods do not dehisce, the fibre layer extends well past the vascular bundles, imparting a characteristic edge structure to the pods.

Next to the fibre layers in the valve edges sclereid cells occur amongst the vascular bundles, so that the edge structure of these pods (e.g. *A. erubescens* and *A. mellifera* of the series *Vulgares* and *A. nilotica* and *A. xanthophloea* of the series *Gummiferae*) differs from the portion along the central longitudinal axis of the valves.

(b) *The fibre stratum*

The fibre stratum originates directly underneath the adaxial epidermis but does not extend to the edge of the pod valves. In most *Vulgares* species the fibre stratum extends virtually up to the vascular bundles in the valve edges (Fig. 6C) whereas in most *Gummiferae* species it ends before the edge of the husk. In *A. karroo* and certain other species the fibre band is macroscopically visible as a leathery layer at the adaxial side of the valves. As already noted, the fibre stratum may consist of both longitudinal and latitudinal fibres. The latitudinal fibres directly adjoin the adaxial epidermis (Fig. 5A–F) and vary from one to approximately four layers. Longitudinal fibres occur in most South African *Acacia* species and are found on the abaxial side of the latitudinal fibres or, where these are absent as in the *Gummiferae* (Fig. 5H, J and K), against the adaxial epidermis.

The greatest variation in the layers of longitudinal fibres is found in species of the series *Gummifera*. In *A. karroo* it may consist of up to ten layers of fibres, whereas in *A. haematoxylon* and *A. stuhlmannii* it is completely absent (Fig. 5G and I). The fibre stratum in *A. erioloba* differs from that of the other species. In this species we find reduced vascular bundles with sclerenchymatous fibres on the adaxial side (inside) of the larger, outer vascular bundles. These reduced vascular bundles appear to be branches of the outer vascular bundles and where they are thickly clustered they form a fibre band which, though interrupted, occupies the same position as the fibre stratum found in species such as *A. karroo* (Fig. 5K).

THE RELATION BETWEEN THE DEHISCENCE OF PODS AND THE ANATOMY OF THE PERICARP

Pods which do not dehisce are found inter alia in *A. kraussiana*, *A. schweinfurthii*, *A. erioloba* and *A. haematoxylon*. In all these species there is a sclereid stratum in the abaxial portion of the parenchymatous stratum, a character found in no other South African species. *A. haematoxylon* and *A. stuhlmannii* were the only two species examined which had no fibre stratum and both possess non-dehiscent pods. This seems to show that the presence of a sclereid stratum in the abaxial part of the parenchymatous stratum and the absence of a fibre stratum are correlated with non-dehiscent pods.

Fahn and Zohary (1955) found that crossed fibres in the fibre stratum and a differentiating layer at the edge of the pod are prerequisites for the dehiscence of pods. In every taxon of the series *Vulgares* (sensu Rob.*) examined, crossed fibres occur in the fibre stratum and the pods dehisce, but in *A. kraussiana* and *A. schweinfurthii*, which have the same characteristic, the pods do not dehisce. It seems then that the presence of a hypodermal sclereid stratum (Fig. 3C) in this case is the dominant factor precluding the pods from dehiscing.

In species with pods that do dehisce, the articulation layer is usually well developed (Fig. 6B and C). However, an articulation layer is usually absent in the closed pods of *A. xanthophloea*, *A. kirkii* (Fig. 6A) and, to a lesser extent, *A. nilotica*. The latter three species belong to group K (Fig. 5) where the remaining species all have dehiscent pods although all the fibres are longitudinal.

To sum up, it can be stated that a well-developed fibre stratum and articulation layer are probably prerequisites for the dehiscence of *Acacia* pods and that the presence of a sclereid stratum in the abaxial portion of the parenchymatous stratum, the absence of a fibre stratum and an undeveloped articulation layer at the edge of the pod may be reasons why a pod does not dehisce.

THE ORIENTATION OF SEEDS IN THE PODS

In general, the pods of South African *Acacia* species have a single, unpartitioned loculus. As already noted in the discussion of the adaxial epidermis, some species exhibit a spongy endocarp which may fill up the loculus partially or entirely. In the species where an extensive spongy endocarp is found, as in *A. erioloba* and *A. haematoxylon*, pseudo-partitions are formed between the seeds, because the endocarp fills up all the open spaces in the husk not occupied by the seeds themselves.

In most species the seeds are arranged in a single row in the pod (Fig. 7A–C), but in *A. erioloba* a longitudinal section of the pod may show two or even three rows of seeds ranged one above the other. (Fig. 7D–F). This arrangement basically corresponds with that of *A. cavenia* (Mel.) Hook. & Arn. where two adjacent rows (one row in each valve) is found with a false septum of spongy tissue between the two rows of seeds (Fig. 7G).

In species with flattened pods, the seeds are also flattened and can be found in three different positions. In most of the *Vulgares* species (sensu Rob.) the hilum is aligned diagonally backwards (Fig. 7B), whereas in most of the *Gummiferae* species (sensu Rob.) with flattened pods the hilum points in the direction of the stylar end of the pod (Fig. 7A). The seeds in the pods of *A. schweinfurthii*, *A. kraussiana* and *A. albida* have the hilum pointing towards the placenta. In cases where the pods are thicker and more or less rounded, as in *A. haematoxylon*, *A. stuhlmannii* and *A. erioloba*, each seed (as against the location of seeds in Fig. 7A–C) is rotated against its own longitudinal axis through an angle of 90° so that the raphe-antiraphe (Robbertse 1973) is directed vertically to the valves (Fig. 7D and E). In *A. erioloba* the hilum of the seeds in the same pod can be oriented in different directions since the developing seeds crowd and displace one another.

It is difficult to assess the taxonomic value of the seed orientation in the pod, since the variation in South African species is too minute to warrant a conclusion. Brenan (1957) used this character to differentiate between *A. robusta* and *A. clavigera*, but the local material examined shows a transitional phase between the two orientations. It will be necessary, therefore, to examine species from all the genera of the subfamily Mimosoideae to determine whether the orientation of seeds in the pod is taxonomically significant or not.

ACKNOWLEDGEMENTS

This work was supported by the Research and Publication Committee of the University of Pretoria and the C.S.I.R.

* *Vulgares* sensu Benth., excluding *A. kraussiana*, *A. brevispica* and *A. schweinfurthii*.

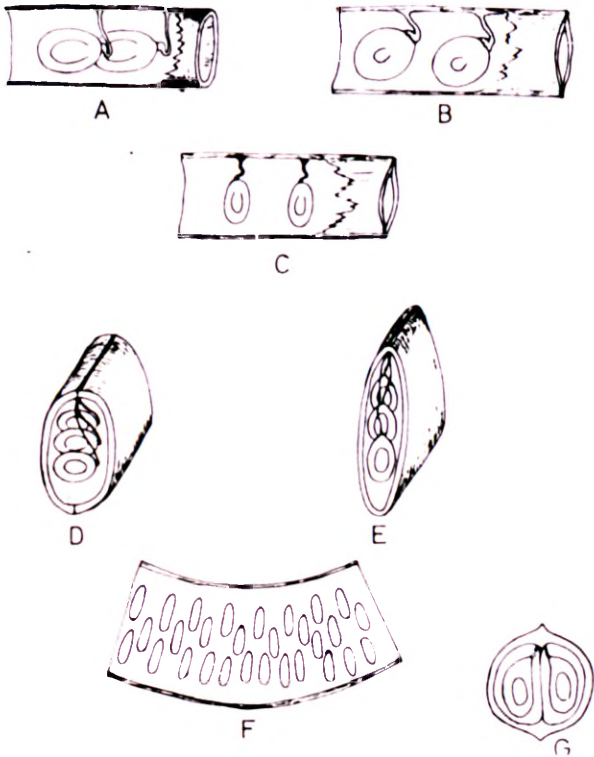


FIG. 7.—Diagram of seed arrangement in the pods of certain *Acacia* species. A, Gummiferae; B, Vulgares; C, *A. albida*, *A. schweinfurthii*, *A. kraussiana* and *A. brevispica*; D-F, *A. erioloba*; G, *A. cavenia*.

UITTREKSEL

Die uitwendige morfologie en anatomie van die peule van al die Suid-Afrikaanse *Acacia*-soorte word bespreek. Dit is gevind dat die Suid-Afrikaanse *Acacia*-soorte op grond van die anatomie van die peul in 'n aantal groepe verdeel kan word. Daar is opvallende verskille tussen die anatomie van die peule van die series *Vulgares* en *Gummiferae*.

REFERENCES

- BAKER, E. G., 1930. *Leguminosae of Tropical Africa*, 3. Ostend: Erasmus Press.
- BENTHAM, G., 1875. Revision of the suborder Mimosaceae. *Trans. Linn. Soc. Lond.* 30: 335-664.
- BRENNAN, J. P. M., 1957. Notes on Mimosoideae: IV. *Kew Bull.* 1957: 357-372.
- BRENNAN, J. P. M., 1959. Leguminosae, subfam. Mimosoideae. In C. E. Hubbard & E. Milne-Redhead, *Flora of Tropical East Africa*. London: Crown Agents.
- BURITT DAVY, J., 1932. *A manual of the flowering plants and ferns of the Transvaal with Swaziland, South Africa*. London: Longmans, Green.
- ESAU, K., 1965. *Plant anatomy*. New York: John Wiley.
- FAHN, A. & ZOHARY, M., 1955. On the pericarpial structure of the legumen, its evolution and relation to dehiscence. *Phytomorphology* 1: 99-111.
- FAHN, A., 1967. *Plant anatomy*. London: Pergamon.
- HARVEY, W. H., 1862. Leguminosae. In W. H. Harvey & O. W. Sonder, *Flora Capensis*, 2. Kent: Reeve.
- HILDEBRAND, F., 1873-1874. Die Schleuderfrüchte und ihr im anatomischen Bau begründeter Mechanismus. *Jahrb. Wiss. Bot.* 9: 235-276.
- KEAY, R. W. J., 1958. Mimosaceae. In J. Hutchinson & J. M. Dalziel, *Flora of West Tropical Africa*, ed. 2, 1, 2. London: Crown Agents.
- KRAUS, G., 1866. Über den Bau trockener Pericarpien. *Jahrb. Wiss. Bot.* 9: 235-276.
- MAJEWSKY, P., 1873. Kurtze Notiz. Über die gewebeartigen Plazenhaute. *Bot. Ztg.* 33: 24.
- OLIVER, D., 1871. Mimosaceae. In D. Oliver, *Flora of Tropical Africa*, 2. London: Reeve.
- ROBBERTSE, P. J., 1973. Die genus *Acacia* in Suid-Afrika—3 (met spesiale verwysing na die morfologie van die saad). *Tydskr. Natuurwet.* 13,2: 72-95.
- ROSS, J. H., 1972. The *Acacia* species with glandular glutinous pods in Southern Africa. *Bothalia* 10,2: 351-354.
- ROSS, J. H., 1975. Notes on African *Acacia* species. *Bothalia* 11: 443-447.
- VAN VUUREN, D. R. J., 1970. 'n Morfologiese studie van die stingels van die houtagtige verteenwoordigers van die genus *Adenia* Forsk. in Suid-Afrika. D.Sc.-verhandeling, Univ. van Pretoria.
- VERDOORN, I. C., 1957. South African species of *Acacia* with glandular glutinous pods. *Bothalia* 6: 153-413.
- VON BREITENBACH, F., 1965. *The indigenous trees of Southern Africa*, 2. Pretoria: Department of Forestry.
- YOUNG, R. G. N., 1955. The *Acacia* species with spicate inflorescence in the Transvaal. *Candollea* 15: 79-123.

