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THE GENUS ACACIA MILLER IN SOUTH AFRICA — 5.

(WITH SPECIAL REFERENCE TO THE SEEDLING STRUCTURE AS A TAXONOMIC CHARACTERISTIC)

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INTRODUCTION

It is common knowledge for taxonomists working with the Mimosaceae that BENTHAM (1875) divided the genus *Acacia* in 5 subgenera or series and of these only the Vulgares and Gummiferae are represented in South Africa.

According to BENTHAM's classification, *A. albida* belongs to the Gummiferae, but the inflorescence of the Gummiferae is a capitulum and that of *A. albida* is a racemous spike like that of most of the Vulgares. The inflorescences of *A. schweinfurthii*, *A. kraussiana* and *A. brevispica* are all capituli, but according to BENTHAM's grouping they belong to the Vulgares.

To solve these ambiquities and to look for other taxonomic characteristics in the genus that could possibly be used for clearing up certain problems, a morphologic study on all the S. A. species was started.

Four papers have been written by the author on various aspects of this investigation. One dealt with the morphology of the spines and stipules (ROBBERTSE[1]) and the following facts were pointed out:

a) The stipules and recurved spines are not homologous organs;

b) Spinescent stipules are present in the Gummiferae and no hooked spines occur on the nodes or internodes.

c) In the Vulgares there appear, apart from the membranous stipules, also hooked spines on the nodes and sometimes also on the internodes.

Another paper was written on the morphology of the flowers and inflorescences (ROBBERTSE[2]). The following conclusions were made:

a) The flowers of the Gummiferae and Vulgares are markedly distinguishable from one another.

b) The inflorescences of the Vulgares are spikes or racemous spikes and that of the Gummiferae are capituli with involucral bracts on the peduncle.

c) Using the results of the two papers combined as a criterium for separating the S. A. species in two groups or subgenera it was found that *A. albida*, *A. schweinfurthii*, *A. kraussiana* and *A. brevispica* could not be grouped in either the Vulgares or the Gummiferae.

In the third and fourth papers dealing with the morphology of the seed (ROBBERTSE[3]) and the legume (ROBBERTSE[4]) the following facts were stated:
a) There are distinct differences in the anatomy of the pod between the Vulgares and Gummiferae.
b) The seeds of *A. albida, A. schweinfurthii, A. kraussiana* and *A. brevispica* contain starch grains where as no starch grains are found in the cotyledons of the Vulgares of Gummiferae.
c) On account of facts gained from the above mentioned papers, it was decided to group *A. albida, A. schweinfurthii, A. kraussiana* and *A. brevispica* together in a separate suborder called the Farinosae.

In this paper it was endeavoured to find other taxonomic characteristics by means of which this new grouping could be further justified.

MATERIAL AND METHODS

A list of the names and localities of samples that were used for this work is to be found in the first paper of this series (ROBBERTSE[1]). For each species, ten seeds per sample, taken at random from samples from at least two different localities were germinated in petri dishes on moist filter paper. After the tap roots had appeared the young seedlings were transplanted into black polythene bags filled with soil made up of one part compost, two parts of top soil and three parts of coarse sand. Observations were made with intervals over a period of one year.

RESULTS AND DISCUSSION

The results are given in Table 1, but to get an over all view of the morphology of the seedlings of the whole genus, the results obtained by CAMBAGE (1915—1928) and VASSAL (1965—1967) mainly on Australian and American *Acacia* species, were summarized and included in Table 1.

According to Table 1, the seedlings of the genus can be divided in two major categories, namely those of which the cotyledons are sessile as illustrated by groups 1—4 and those with petioled cotyledons (groups 5—10).

In group 1 (Table 1) both the first and second leaves are pinnate and subopposite to more or less opposite. The third leaf is alternate and bipinnate, with two jugae. This group is occupied by seedlings of the Phyllodinae and Pulchellae but no South African species are found with this type of seedling structure. VASSAL (1965) called this type of seedling structure "Mode 1" and included 2 species of the Gummiferae an 1 species of the Vulgares in his grouping of the seedlings.

Seedlings of group 2 (Table 1) differ from those of group 1 in having only one pinnate leaf with the second leaf already bipinnate. According to information obtained from CAMBAGE (1915—1926) and VASSAL (1965—1967) seedlings of the Bothryocephalae and some of the Phyllodinae belong to this group, but no South African species were found with seedlings of this type.

In both groups 1 and 2 (Table 1) the stipules on the seedlings as well as

Table 2. The chromosome numbers of certain *Acacia* species according to the classification of Bentham (1875) and information obtained from Darlington & Wylie (1945)

Phyllodinae 1—277		Bothryocephalae 278—287		Gummiferae 296—355		Vulgaris 356—430		Filicinae 431—432	
A. viscosa	26	*A. dealbata*	26	*A. aroma*	26	*A. bonoriensis*	26	*A. villosa*	26
A. alata	26	*A. decurrens*	26	*A. cavenia*	26	*A. tenuifolia*	26		
A. armota	26			*A. choriophylla*	26	*A. albida*	26		
A. auriculaeformis				*A. giraffae**	26	*A. catechu*	26		
				A. macracantha	26	*A. detinens*	26		
A. baileyana	26			*A. tortuosa*	26	*A. mellifera*	26		
A. calamifdia	26			*A. arabica*	52	*A. modesta*	26		
A. cultriformis	26			*A. eburnea*	52	*A. senegal*	26		
A. cyanophylla	26			*A. horrida*	52	*A. suma*	26		
A. dermatophylla	26			*(= A. karroo)*		*A. sundra*	26		
A. falcata	26			*A. laeta*	52				
A. glaucoptera	26			*A. nilotica*	52				
A. graveolens	26			*A. scorpioides*	52				
A. longifolia	26			*A. seyal*	52				
A. melanoxylon	26			*A. spirocarpa*	52				
A. mollissima	26			*A. xanthophloea*	52				
A. penninerris	26								
A. podalyrifolia	26								
A. retinodes	26								
A. richei	26								
A. rubida	26								
A. saligna	26								
A. verticillata	26								
A. xylocarpa	26								
A. koa	52								

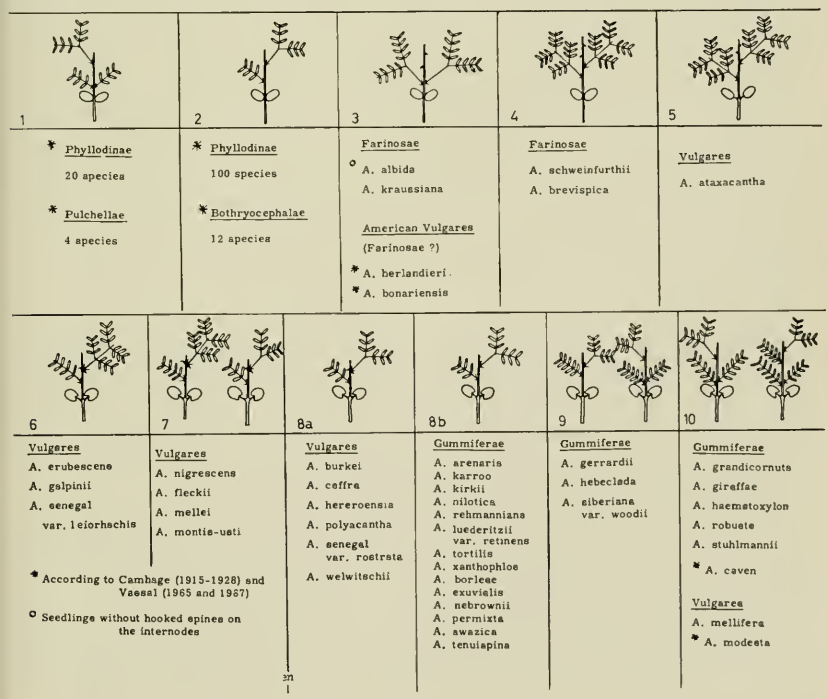
* Robbertse (unpublished)

on the adult plants are membranous and no spines are to be found on the stems (Robbertse[1]). Seedlings of all the remaining groups either have spinescent hooks on the internodes, like groups 3, 4 and 5, on the nodes like groups 6, 7 and 8a or the stipules may be spinescent like groups 8b, 9 and 10.

The new suborder Farinosea (Robbertse[3]) occupies groups 3 and 4 in Table 1. In both groups the first and the second leaves on the seedlings are bipinnate. In group 3 they are both 2-jugate and in group 4 they are both 4-jugate. The same type of seedling is found in *A. berlandieri* (Cambage 1915—1928) and *A. bonariensis* (Vassal 1965), but like *A. albida* they do not contain spinescent hooks on the internodes. Group 3 (Table 1) can therefore be divided into two subgroups of which *A. kraussiana* represents the subgroup with spinescent hooks on the stem and *A. albida* together with the American species *A. berlandieri* and *A. bonariensis* are representing the subgroup without spinescent hooks on the internodes.

A. ataxacantha has seedlings with both the first two leaves bipinnate, two jugate and spinescent hooks are present on the internodes. In these respects they are very much like the seedlings of *A. schweinfurthii* of the Farinosae but differ from them as far as the petioled cotyledons are concerned.

Table 1. A grouping of some species of the genus *Acacia* according to the external morphology of the seedlings



The close relationship between *A. ataxacantha* and the Farinosae was demonstrated in the fact that the cotyledons of seeds of *A. ataxacantha* also contain very small particles which, like the starch grain in the seeds of the Farinosae, also stain blue with Iodine (Robbertse[3]).

The rest of the Vulgares and all the Gummiferae have seedlings with petioled cotyledons as is shown in groups 6—10 (Table 1). Seedlings of these two subgenera can only be separated from one another on account of the spinescent hooks that are present on the Vulgares seedlings, situated on the nodes from the second or third leaves upwards together with the membranous stipules. In the Gummiferae the stipules are usually becoming spinescent from the second leaf upwards although even the cotyledons may sometimes have spinescent stipules as in the case of *A. giraffae.*

In all these seedlings the first leaves are pinnate with the second leaves varying from pinnate (groups 9 and 10) bipinnate with two jugae (groups 7, 8 and 9) to bipinnate with four jugae (groups 6 and 7). A certain amount of variation does occur in each species but the majority of seedlings from a given species belong to the corresponding type indicated in Table 1.

In all the Vulgares seedlings the second leaf is either bipinnate, two jugate or bipinnate, four jugate. According to the leaf structure the species mentioned in group 7 (Table 1) are transitional between groups 6 and 8a as they contain seedlings of both types. Judging on the structure and appearance of hooked spines on the internodes and the structure of the pods however, *A. hereroensis* and *A. caffra* are more closely related to *A. ataxacantha* than any of the species of from group 6. (Hooked spines often appear on the internodes of older seedlings of *A. hereroensis* and on sprouting shoots of *A. caffra).* This probably shows that the two-jugateness or four-jugateness of the second leaf of the seedling is not as important as the fact that the leaves are bipinnate and not pinnate. The same applies to the Farinosae. The S. A. Vulgares can therefore be regarded as a more or less homogenous group with a few aberrations showing relationships with other subgenera.

The Gummiferae seedlings can be classified in two main groups (groups 8b and 10 of Table 1) with a few intermediate species (group 9). In group 8b, like 8a of the Vulgares, the second leaf is bipinnate and two-jugate. Samples tested from the species mentioned in this group never produced seedlings other than the type figured. This is therefore a more or less homogenous group and most of the species show close relationships with *A. karroo,* the most widely distributed species in Southern Africa.

In the species mention in group 10 (Table 1) both the first and the second leaves of the seedlings are pinnate and very often the third leaf is also pinnate. In certain lots of *A. giraffae, A. haematoxylon* and *A. grandicornuta,* up to 50% of the seedlings had three pinnate leaves.

A. mellifera and *A. modesta* are two Vulgares species with the same type of seedling structure as the Gummiferae species in group 10. The inflorescence of *A. mellifera* is a reduced racemous spike and partly resembles the

capitate inflorescens of the Gummiferae. These two characteristics are indications of a possible relationship between *A. mellifera* and the Gummiferae although the pedicellated flowers of this species reminds one of the Farinosae.

Vassal (1967) made a study on the seedlings of *A. caven* and stated that seedlings with three pinnate leaves probably represent a more original type than the possible ancestral type with two opposite pinnate leaves suggested by Cambage (1915) and Newman (1933). He also stated that the seedling type like group 8b (Table 1) is probably a more recent type than that of group 10 (Table 1).

To go deeper into this problem it was necessary to have a look at the chromosome numbers of the *Acacia* species which is summerized in Table 2. From this it is quite clear that all the species of Bentham's Phyllodinae, Bothrycophalae, Pulchellae, Filicinae and Vulgares of which the chromosome numbers are known, have 26 chromosomes in the somatic cells. The Gummiferae corresponding with group 8b (Table 1) and of which the chromosome numbers are known have 52 chromosomes in the somatic cells. Certain other species of the Gummiferae also contain 26 chromosomes and at least one of them *A. caven*, is known to belong to group 10 (Table 1) while the seedling structure of the others has not yet been investigated. *A. giraffae* from group 10 (Table 1) also contains 26 chromosomes (Robbertse, unpublished). From the information gained from the chromosome numbers, Vassal's statement that the seedling type 8b (Table 1) is more advanced than type 10 (Table 1) (Vassal 1967) is quite feasible and it can further be stated that the S. A. Gummiferae can be divided into more or less two distinct groups. The one group has seedlings of the type figured in Table 1, 8b and the chromosome number is probably 52. In the other group the chromosome number of some species is probably 26 and the seedling structure is that figured in Table 1, 10. A few intermediate species exist where seedlings of both types 8b and type 10 can be obtained, but the chromosome numbers are still unknown.

Both categories (groups 1—4 and 6—10 of Table 1) previously referred to in this paper, contain species in which the first two foliar leaves are pinnate and according to Cambage (1915) this leaf structure could be representative of the original parent stock of the genus. If this theory of Cambage (1915) and Newman (1933) is accepted, ist must also be accepted that the separation of the two mentioned categories must have taken place at a very early stage in the evolution of the genus and that their further development probably took place along two more or less parrallel lines.

Vassal (1967) demonstrated how the bipinnate second leaf on the seedlings developed from a second pinnate leaf. This line of development is found in both mentioned categories. Using this characteristic as a criterium the *Farinosae* seedlings must be regarded as the most advanced. On the other hand, however, the Farinosae contain overies with extremely long pedicels (Robbertse[2]). Pedicellated ovaries are also found in the Vulgares but in most of the species the pedicels are comparatively shorter. The Phyllodinae and Gummiferae contain sessile ovaries. This characteristic, together with the

possible evolution of the inflorescence in the genus as a whole (ROBBERTSE[2]) refers to a possible original structure. These facts also make the Farinosae to qualify as possible ancestral representatives of the genus. This possibility was already mentioned by BENTHAM (1875) when he regarded *A. pennata* WILLD. (= *A. schweinfurthii* pro parte) as one of the possible original forms, based on its wide geographical distribution.

CONCLUSION

To bring the results of this paper in line with previous work that had been done on the genus *Acacia* the following possible phylogenetic lines can be suggested for the genus *Acacia* in South Africa:

1. A primitive ancestor probably existed which must have had a diploid number of 26 chromosomes, spicate inflorescences (ROBBERTSE[2]), non dehiscent pods (ROBBERTSE[3]), seeds containing starch grains (ROBBERTSE[3]), no endosperm in the seed, seedlings with two or more pinnate or two bipinnate juvenile leaves and sessile cotyledons.

2. From this hypothetical primitive stock several different lines of development conceivably occurred. The South African *Acacias* probably developed from two of these lines

a) The Vulgares could have developed via the Farinosae. Relicts of primitive characteristics are still found among a few species such as the starch-like particles in the seed of *A. ataxacantha,* two pinnate juvenile leaves on the seedlings of *A. mellifera,* longly pedicellated flowers and a short inflorescence in *A. mellifera,* long pedicellated ovaries in *A. ataxacantha* and *A. robynsiana.*

b) The Gummiferae reveal several advanced characteristics such as the spinescent stipules the absence of a disc in the flower and sessile ovaries which indicate a divergence from the Vulgares. The evolution of the inflorescence (ROBERTSE[2]) and the structure and succession of the juvenile leaves on the seedlings, however, reminds one of the relavent conditions prevailing in the Vulgares and therefore propose the descendence from the same parental stock but along a different line of development.

This paper is not supposed to give a full account of the history of the genus *Acacia* as a whole but it only tries to suggest possible phylogenetic lines that can be visualised from work done on South African material and a meagre knowledge of a few other species out of this enormous genus.

Much more work is still to be done before it will be possible to get any idea of the true phylogenetic history of the whole taxon.

SUMMARY

1. In this paper a summary is given of a series of papers written by the senior author on different aspects of this investigation.
2. According to the seedling structure two main categories in the genus is suggested.
3. Different lines of phylogenetic development for the South African Vulgares and Gummiferae are suggested.

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