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Towards a Classification of the African Acacias

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ABSTRACT

Some of the first attempts to subdivide the genus *Acacia* Mill. as a whole are discussed briefly. Bentham's work, in which the subdivisions of the genus were for the first time given names, is considered and his two series into which the African species fall are reproduced. The characters employed by various workers to divide the African species into two main groups are mentioned and the advantages of using each of these characters for the first dichotomy in a key are discussed. Recent work on pollen morphology and seedling morphology is correlated with general morphology. A proposal put forward by Guinet to divide *Acacia* into three large genera on the basis of pollen morphology is briefly discussed. Certain modifications to Bentham's series Vulgares and Gummiferae are suggested.

INTRODUCTION

Philip Miller (Gard. Dict. abridg. ed. 4, 1754) was the first author to employ the name *Acacia* in a generic sense subsequent to 1753 and is, therefore, regarded as the author of *Acacia*. Miller's generic description, which is based on the "Egyptian Thorn" [*A. nilotica* (L.) Willd. ex Del.], is as follows:

> "It hath a tubulous flower consisting of one leaf, with many stamina or threads, which are many of them collected into a kind of sphere or globe: the pointal of the flower afterwards becomes a pod in which are included several seeds, each of which is separated by transverse diaphragms, and are generally surrounded with a sweetish pulp."

Acacia Mill. is a large tropical or subtropical genus of about 850–900 species. The vast majority of species (± 620) are found in Australia, while many (± 115) occur in Africa, many in America, and fewer species in Asia. Europe is the only large geographical area which is devoid of the genus, while there are no indigenous species in New Zealand despite its close proximity to Australia.

EARLY GENERIC SUBDIVISIONS

Following his generic diagnosis, Miller (l.c.) enumerated and discussed 24 species under *Acacia* but made no attempt to divide the species into groups. As the generic limits of *Acacia* were very broad it is not surprising that a number of the species enumerated under *Acacia* are no longer referable to the genus as it is at present defined.

Lamarck, Encycl. 1: 8 (1783), listed 58 species under *Acacia* and divided the species into two groups depending upon whether or not the stipules were spinescent. The two groups were not prefaced by any indication of rank.

Willdenow, Sp. Pl. ed 4, 4: 1049 (1806), listed 102 species under *Acacia* and was among the first to attempt to draw up a system of classification of the *Acacia* species. Willdenow divided the species into seven groups on the basis of vegetative characters but, once again, the groups were not prefaced by any indication of rank.

De Candolle, Prodr. 2: 448 (1825), listed 258 species under *Acacia* and divided the species into four main Sections. His Sections, which were not named, were founded essentially on leaf characters with the nature of the stipules and of the inflorescences being employed to distinguish groups of species within the Sections.

Sprengel, Syst. Veg. 3: 133 (1826), listed only 188 species under *Acacia* and divided the species into three groups on the basis of leaf characters. His first group was subdivided on the nature of the inflorescence, the second was subdivided on whether or not the plants were armed, while the third group was subdivided on whether or not the plants were armed, and then on the nature of the inflorescence. Like the preceding generic subdivisions, Sprengel's groups were not prefaced by any indication of rank.

In 1842 Bentham published his notes on Acacieae in Hook. Lond. J. Bot. 1: 318–392. In his treatment of *Acacia*, Bentham (l.c.: 319) wrote:

> "A dry two-valved pod has been the character hitherto chiefly relied upon for the distinction of this extensive genus; but this has not only the great inconvenience that there are but few cases where the ripe pod can be observed, but also it is often even then very uncertain, and not at all consonant with general habit and other characters. Many species, precisely similar in almost every other respect, have very different pods, and the same pod may be found in two Mimoseae having scarcely any other point in common. I have, therefore, thought it better to derive the principal character from the flower, and by excluding all species with definite stamens, or with the filaments connected in a cylindrical tube, it has appeared to me that the genus *Acacia* becomes more natural than it could be made by any other limitations hitherto proposed, and certainly very much more clearly and easily defined. Even in the subdivision of the genus, imperfectly as a great number of the species are as yet known to us, it becomes necessary to rely more on foliage and habit than on the pod, however diversified may be the forms assumed by that organ."

Bentham divided *Acacia* into six Series, the Series being delimited primarily on foliage, on whether or not the plants were armed, and, if armed, upon whether or not the stipules were spinescent. The inflorescence played a far less important rôle in his division of the genus than the vegetative characters. For the first time the generic subdivisions were formally given names. It is perhaps surprising that Bentham only accorded his subdivisions the rank of Series and did not, for example, recognize them as subgenera. All of the African species fall into two of Bentham's Series, namely, Gummiferae and Vulgares.

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Bentham's paper was a most significant and important contribution because, for the first time, the generic limits of *Acacia* were clearly defined and those species which did not belong in it were excluded. Prior to 1842 the generic limits of *Acacia* were so vague and ill-defined that a rather heterogeneous assemblage of plants was included under *Acacia*. The early subdivisions of the genus, therefore, all suffered from the same deficiency in that they had to make provision for too many species which were actually not referable to *Acacia*. Indeed, the generic limits of *Acacia* have not been seriously in doubt since Bentham's work in 1842. His subsequent work in Flora Australiensis 2: 301–421 (1864), in Genera Plantarum 1: 594 (1865) and in his "Revision of the Suborder Mimoseae" in Trans. Linn. Soc. Lond. 30: 336–664 (1875), served to clarify the genus further.

The generic subdivisions of *Acacia* in Bentham's revision in Trans. Linn. Soc. Lond. 30 (1875) were based on his earlier treatment in 1842 but there are a number of significant alterations. Bentham (l.c. 444, 1875) wrote:

> "I have not either been able, in this my third careful revision of the species, to divide it into sections founded upon any character derived from the flowers or fruits; I therefore here repeat the series, based upon habit, inflorescence and geographical distribution, which are given in the Genera Plantarum, subdividing them into subseries and minor groups still less definitely limited, but of which the following may be taken as the chief characters, neglecting minor exceptions."

Because of the relevance of Bentham's Series Gummiferae and Vulgares to the following discussion they are reproduced below:

Series 4.—GUMMIFERAE. *Arbores v. frutices non scandentes nec aculeati. Folia bipinnata. Stipulae nonnullae v. omnes spinescentes. Capitula globosa v. spicae cylindraceae, ad axillas v. in racemo terminali brevi pedunculata, rarius paniculata. Tropicae v. subtropicae utrinsque orbis.*

Subseries 1.—*Summibracteatae*. Involucellum annulare sub capitulo ipso v. ab eo parum distans. Capitula globosa. Legumen crassum, turgidum v. rarius planum, non v. vix dehiscens, intus inter semina farctum. Americanae v. Africanae, una cosmopolitana.

Subseries 2.—*Medibracteatae*. Involucellum in medio pedunculo v. paullo altius v. inferius situm, rarius O. Capitula globosa. Legumen bivalve.

A.—*Heteracanthae*. Spinae minores recurvae, auctae rectae. Legumen demum turgidum v. subteres.—Species gerontogeae.

B.—*Moniliformes*. Spinae omnes rectae, v. minores recurvae. Legumen planum, saepe crassum, inter semina regulariter constrictum v. depressum. Species gerontogeae.

C.—*Thyrsiflorae*. Spinae omnes rectae. Inflorescentia terminalis, subaphylla, simplex. Legumen planum, continuum. Species Africanae.

D.—*Pubiflorae*. Spinae rectae. Pedunculi axillares. Flores pubescentes. Legumen planum, continuum. Species gerontogeae.

E.—*Normales*. Spinae rectae. Pedunculi axillares. Flores glabri v. parce puberuli. Legumen saepius planum, valvis tenuibus. Pleraeque Africanae; paucae Indicae, Australicae v. Mexicano-Texanae.

F.—*Paniculatae*. Spinae rectae. Panicula terminalis, subaphylla. Species Asiaticae.

Subseries 3.—*Basibracteatae*. Involucellum nullum nisi ad basin pedunculi. Spicae cylindraceae v. elongatae, v. in una specie (*A. sphaerocephala*) globosa. Americanae, Africanae v. Asiaticae.

Series 5.—VULGARES. *Arbores v. frutices interdum scandentes. Stipulae non spinescentes. Aculei infrastipulares sparsi v. O. Folia bipinnata, petiolo saepissime glandulifero.*

Subseries 1.—*Gerontogeae spiciflorae*.

A.—*Triacanthae*. Aculei terni, infrastipulares cum infrafoliaceo.

B.—*Diacanthae*. Aculei gemini, infrastipulares.

C.—*Ataxacanthae*. Aculei sparsi.

Subseries 2.—*Americanae spiciflorae*. Aculei sparsi v. O.

Subseries 3.—*Americanae capitulatae*.

Subseries 4.—*Gerontogeae capitulatae*.

There have subsequently been many criticisms of Bentham's classification. For example, Newman in J. Linn. Soc. Bot. 49: 133–143 (1933), considered Bentham's classification to be too static in concept. However, it must be borne in mind that almost a century has elapsed since Bentham produced his final classification in 1875, and that the number of species now included in the genus is double the number that he made provision for. Bentham was well aware of many of the deficiencies, but many of his decisions were, of necessity, based on specimens which, by modern standards, would be considered quite inadequate. Despite the criticism there has been no comprehensive account of the genus as a whole, nor any attempt to subdivide the entire genus since 1875. Indeed, Bentham's major subdivisions of the genus have stood the test of time and evidence will be led later in support of their retention.

Britton and Rose, N. Amer. Fl. 23, 2: 84 (1928), divided the American Acacieae into a number of genera on the basis of pod characters, but posterity has rejected most of these new genera. Newman (l.c. 137) drew up a phylogenetic classification to the acacias, mostly the Australian species, based primarily on the inflorescence. Each of the three groups thus formed was subdivided on flower-group and then on the foliar types. However, this classification has not found favour either.

As the vast majority of the species occur in Australia and are not of immediate concern to a study of the African species, the general subdivisions of the genus as a whole will not be considered further. The methods employed to subdivide the African species will now be considered.

SUBDIVISIONS OF THE AFRICAN SPECIES

A. Richard, Tent. Fl. Abyss. 1: 237 (1847), divided the *Acacia* species into two groups on the basis of whether or not the stipules were spinescent. Although the two groups were not prefaced by any indication of rank, they correspond to Bentham's Gummiferae and Vulgares.

Harvey in Fl. Cap. 2: 279 (1862) used Bentham's subdivisions of 1842, the species being placed either in Gummiferae or in Vulgares. The nature of the inflorescence was employed to subdivide the species within each of these series. Engler in Bot. Jahrb. 10: 16 (1888), Taubert in Engl. Pflanzenfam. 3, 3: 108 (1891) and Glover in Ann. Bolus Herb. 1: 143 (1915) also followed Bentham's classification.

Oliver in Fl. Trop. Afr. 2: 337 (1871) did not follow Bentham, but based his primary division of the species on the nature of the inflorescence. Two broad groups were recognized, namely, those species with spicate inflorescences and those with capitate inflorescences. The second dichotomy within each group was based upon whether or not the stipules were spinescent. This appears to have been the first departure from Bentham's classification for the African species and it was in time to be followed by the authors of nearly all of the major regional African floras. Similar keys to the species using the inflorescence for the first dichotomy were used by Hutchinson & Dalziel in Fl. W. Trop. Afr. 1 (2): 359 (1928); Burtt Davy, Fl. Transv. 2: 333 (1932); Torre in Consp. Fl. Angol. 2: 269 (1956); Keay in Fl. W. Trop. Afr. 1 (2), ed. 2: 496 (1958); Brenan in Fl. Trop. E. Afr. Legum.—Mimos.: 49 (1959);

in Fl. Zamb. 3 (1): 53 (1970); F. White, For. Fl. N. Rhod.: 78 (1962) and Schreiber in Fl. S.W. Afr. 58: 2 (1967). Gilbert & Boutique in Fl. Congo Belg. 3: 146 (1952) alone in recent years have used stipular spines versus prickles for the first dichotomy in a key.

E. G. Baker in his Leguminosae of Tropical Africa 3: 815 (1930) also used the inflorescence for dividing the species into two main groups. The species in the group with spicate inflorescences were divided according to whether or not the stipules were spinescent. Those species with prickles were then subdivided into four series depending upon whether the prickles were in threes at the nodes, in pairs at the nodes, solitary, or scattered along the internodes. The group with capitate inflorescences was divided according to whether or not the stipules were spinescent, and then on the type of pods. Eighteen series in all were recognized by Baker.

The African species, therefore, have been divided in the past by various authors into two main groups on the basis of two different characters. Some authors have given preference to whether or not the stipules are spinescent as the primary character in separating the two groups, while other authors have employed the inflorescence. What then are the advantages offered by each of these characters, and which provides a more natural systematic arrangement of the species?

1. *The inflorescence*

The inflorescence is a very convenient character to employ for dividing the *Acacia* species into two main groups. It is usually far easier to decide whether the inflorescence is capitate or spicate than it is to decide whether or not the stipules are spinescent because in many species the stipules are very small and rapidly deciduous. However, despite the convenience of capitate versus spicate inflorescences, there are some difficulties as there is no absolute distinction between the two groups. For example, Brenan in F.T.E.A. Legum.-Mimos.: 80 (1959) points out that *A. dolichocephala* Harms "seems to bridge the gap between the capitate- and spicate-flowered groups of Acacias". In *A. mellifera* (Vahl) Benth. subsp. *mellifera* from tropical Africa the inflorescence is spicate while in subsp. *detinens* (Burch.) Brenan from southern Africa the flowers are in subglobose or ellipsoid heads and superficially are easily mistaken for those of a capitate-flowered species.

Several characters lend support to the contention that the two groups, obtained by using the inflorescence for dividing the species, may be natural. These are:

a. Almost all of the African species with spicate inflorescences are armed with recurved prickles while nearly all of the species with capitate inflorescences are armed with stipular spines. The exceptional species with stipular spines among the spicate-flowered species and the species with recurved prickles among the capitate-flowered species are readily and conveniently separated from the bulk of the species within each of these two main groups.

b. All of the species with spicate inflorescences have pale yellowish-white flowers (except for *A. persiciflora* Pax and *A. galpinii* Burtt Davy which have red or purplish calyces and corollas). Most of the species with capitate inflorescences have deep- or golden-yellow flowers, relatively few species having pale yellowish-white, white or rarely pinkish or purple flowers.

c. Further support derives from pollen-morphology (Coetzee in S. Afr. J. Sci. 52: 23, 1955) although admittedly only a small proportion of the species have been investigated. Coetzee examined 25 southern African species and found that the species with capitate inflorescences had pollen grains provided with furrows whereas the species with spicate inflorescences had pollen grains without furrows. Two exceptions were found, namely, *A. detinens* and *A. pennata* which "have a capitate inflorescence and have pollen in which no furrows occur". *A. detinens* (*A. mellifera* subsp. *detinens*) is not really an exception because the inflorescence is ellipsoid and the species belongs to the group with spicate inflorescences. However, the anomalous pollen-morphology of *A. pennata* cannot be explained on the basis of capitate versus spicate inflorescences. It must be mentioned here that all of the species with spicate inflorescences examined by Coetzee are armed with recurved prickles and that none has stipular spines.

Van Zinderen Bakker and Coetzee (South African Pollen Grains 3: 115, 1959) furnish the results of an investigation into the pollen-morphology of 28 species. Once again all of the species with spicate inflorescences (except for *A. pennata*) had pollen grains without furrows while all of the species with capitate inflorescences had pollen grains with furrows.

d. Although the chromosomes of only a relatively small number of species have been investigated, the results do suggest certain tendencies. Darlington and Wylie, Chromosome Atlas of Flowering Plants: 151 (1955), record that all species with spicate inflorescences investigated have a diploid chromosome number of 26 (except for *A. laeta* R. Br. ex Benth. in which $2n = 52$) whereas in the capitate-flowered species $2n = 52$. It has been suggested (Brenan l.c. 83, 1959) that *A. laeta* may be the outcome of hybridization and this could perhaps account for this chromosome number.

e. The seeds also provide support for using the inflorescence for the first dichotomy in dividing the species into two main groups. The seed of all *Acacia* species show on each face an area, usually more or less elliptic or oblong in shape, bounded by a fine line which frequently appears as a fissure in the testa. The size and shape of this area, termed the areole (Brenan l.c. 1, 1959), are often important taxonomically. The line is usually broken opposite the micropyle although in some species the line is almost continuous. Areole shape often provides a useful means of distinguishing between the seed of capitate- and spicate-flowered species. In spicate-flowered species the areole is typically horse-shoe shaped, fairly small, and occupies the central area of the seed. In the capitate-flowered species the areole is larger and conforms to the outline of the seed. *A. albida* is anomalous among the spicate-flowered species in having a large subcircular-lenticular areole as in the capitate-flowered species.

2. *The stipules*

The presence of spinescent stipules or of non-spinescent stipules provides a useful means of dividing the African species into two main groups. As each species is armed either with stipular spines, or with non-stipular prickles, the distinction between the two groups is absolute. A key in which the first dichotomy is based on stipular spines versus non-stipular prickles has the advantage that it can be used for flowering, fruiting, or even sterile specimens. Only very rarely, and in very few species, is an entire plant unarmed.

Several characters lend support to the contention that the two groups, obtained by using the nature of the stipules for the first dichotomy, may be natural. These are:

a. Nearly all of the species armed with prickles have spicate inflorescences (except for a group of climbers with recurved prickles scattered along the internodes) while nearly all of the species armed with stipular spines have capitate inflorescences.

b. All of the species armed with prickles have pale yellowish-white flowers (except for *A. galpinii* and *A. persiciflora* which have red or purplish calyces and corollas). Most of the species armed with stipular spines have deep- or golden-yellow flowers, relatively few species having pale yellowish-white, white or rarely pinkish or purple flowers. There is a slightly better correlation between flower colour and the nature of the stipules than there is between flower colour and the type of inflorescence.

c. If Coetzee's pollen-morphology studies are correlated with the nature of the stipules, it is found that all the species armed with stipular spines have pollen grains with furrows whereas the species armed with prickles have pollen grains without furrows. On this basis, the position of *A. pennata* is no longer anomalous as its pollen structure is then the same as that of all the other species armed with prickles. However, Van Zinderen Bakker and Coetzee (l.c.) studied a larger number of species including *A. albida.* When their results are correlated with the nature of the stipules it is found, once more, that all of the species armed with prickles have pollen grains without furrows while all of the species with stipular spines (except for *A. albida*) have pollen grains with furrows. The position of *A. albida* within the genus, which is anomalous in several respects, will be considered later in more detail.

Studies on pollen-morphology by Guinet (Inst. Fr. Pondichery, Trav. Sec. Sci. Tech. 9, 1969) also provide evidence in support of the division of the African acacias on the basis of spinescent stipules versus non-spinescent stipules. Guinet found a definite correlation between the nature of the stipules and the pollen-morphology in *Acacia*, *Dichrostachys* and *Prosopis:* in these genera it was found that stipular spines are correlated with a high degree of differentiation in the pollen grains (for example, the presence of furrows in the exine). Conversely, in species of *Acacia* without spinescent stipules a low degree of differentiation in the pollen grains was found. It should be emphasized here that there is no similar correlation between pollen morphology and the type of inflorescence.

d. When the chromosome numbers recorded by Darlington and Wylie are correlated with the nature of the stipules it is found that in all of the species armed with stipular spines $2n = 52$ (except for *A. albida* in which $2n = 26$) while in all of the species armed with prickles $2n = 26$ (except for *A. laeta* in which $2n = 52$).

Presumably the higher chromosome complement of the species with spinescent stipules has given these species greater genetic plasticity and the ability to exploit new habitats. Could this be the reason for the preponderance of species armed with stipular spines in Africa? There is no real evidence that the species with spinescent stipules are more widespread in Africa than species with non-spinescent stipules. For example, *A. ataxacantha* DC. and *A. senegal* (L.) Willd. are probably as widespread in Africa as any of the species with stipular spines. Endemics are found among species armed with spinescent stipules and among species with non-spinescent stipules. However, there is a suggestion that some of the species with spinescent stipules are able to occupy more adverse habitats than species with non-spinescent stipules.

e. If areole shape is correlated with the nature of the stipules, it is found that nearly all of the species with non-spinescent stipules (except for those species with prickles scattered irregularly along the internodes) have small horse-shoe shaped areoles, while nearly all of the species armed with spinescent stipules have large subcircular-lenticular or quadrate areoles conforming to the shape of the seed.

f. There is a tendency in the species armed with prickles for the veins to run transversely across the pods while in the species armed with stipular spines the veins tend to run longitudinally. In many species, for example in *A. nilotica* (L.) Willd. ex Del. and *A. giraffae* Willd., no distinct venation is visible on the pods, but in those species where the venation is conspicuous there is a tendency for the above distinctions to prevail. The species with prickles scattered irregularly along the internodes have transversely venose pods irrespective of whether the inflorescences are spicate or capitate.

g. The development of secondary leaves (Ross, The Acacia species of Natal: 6, 1971) seems to be almost restricted to the species armed with stipular spines. The secondary leaves are fascicular and arise from dwarf lateral shoots at the nodes. These secondary leaves are thought to be an adaptation which enables a plant to produce new leaves, particularly in an unfavourable season, without first having to draw on its reserves to produce new branchlets to carry primary leaves. Even most of the spicate-flowered species armed with spines produce secondary leaves.

h. A study of the seedling morphology of some of the African acacias by Vassal (Trav. Lab. For. Toulouse, Tome 1, Vol. 8, 3, 1969) revealed differences between those species armed with stipular spines and those species armed with prickles. Once again, these results support the division of the species on the nature of the stipules rather than on the type of inflorescence.

DISCUSSION AND CONCLUSIONS

It is apparent from the above that the division of the African species into two main groups on the basis of the inflorescence has certain advantages, while a division of the species into two groups on the nature of the stipules likewise has certain advantages. Some characters are better correlated with the type of inflorescence than with the nature of the stipules, and vice versa. The anomalous species recorded when the species are divided on the basis of the inflorescence are often explained away when the species are divided on the basis of the stipules, although such a division in turn usually creates a further set of anomalous species. For example, when Van Zinderen Bakker and Coetzee's pollen-morphology studies are correlated with the type of inflorescence, it is found that all of the species with pollen grains without furrows have spicate inflorescences (except for *A. pennata*) and all of the species with pollen grains with furrows have capitate inflorescences. However, when their studies are correlated with the nature of the stipules it is found that all of the species with prickles (including *A. pennata*) have pollen grains without furrows while all of the species armed with stipular spines (except for *A. albida*) have pollen with furrows.

If the African acacias are divided according to the type of inflorescence, within each of the groups thus formed some of the species are armed with stipular spines and some of the species are armed with non-stipular prickles. Conversely, if the species are divided on the nature of the stipules, within each group some of the species have spicate inflorescences and some of the species have capitate inflorescences. In other words, if the division of the species on the basis of the inflorescences is considered a natural one, then spinescent and non-spinescent stipules must have developed within each group, whereas if the division on the nature of the stipules is considered a natural one, then capitate and spicate inflorescences must have developed within each group. Apparently, therefore, certain characters must have evolved at least twice during the development of the African acacias.

For use in regional African floras the inflorescence is a very convenient character to employ for the primary division of the species into two main artificial groups. However, when a more natural systematic division is sought, it is clear that it is the nature of the stipules that must be employed for separating the two main groups of species. This view is in agreement with the work of Bentham and the two groups thus obtained correspond to his series Gummiferae and Vulgares. Certain modifications within each of Bentham's series are, however, desirable.

At this stage it is not intended to formally propose a system of classification of the African species, but rather to put forward some tentative suggestions. In any event the taxonomy of many of the species, particularly in north-east tropical Africa, is still confused so it seems desirable to wait until these problems are resolved so that all of the species can be accurately placed within the framework of a classification. Furthermore, it seems pointless to draw up a classification of the African species in isolation without taking into account the species in other areas of distribution, particularly those in Australia which, after all, constitute the vast majority of the genus. A classification of the African species must fit within the framework of a classification of the genus as a whole. The Australian species are currently being investigated, but the American and Asian species are badly in need of attention. It is clear, therefore, that a considerable amount of basic work is still required throughout the distributional range of the genus.

The present attempt to arrive at a classification of the African species must be seen in the light of the important work on pollen-morphology by Guinet (l.c.). On the basis of the number, position, complexity and size of the apertures, the number of cells in the polyads, the sculpturing of the exine and the position of the furrows, Guinet has proposed that:

1. *A. albida* should be removed from the genus *Acacia* and that the genus *Faidherbia* A. Chev. should be resuscitated. Guinet and Vassal (l.c.) agree that *Faidherbia* is a good genus.

2. *A. farnesiana* (L.) Willd., *A. giraffae* Willd. and *A. caven* (Mol.) Mol. constitute a good group within Bentham's Series Gummiferae and should be referred to the genus *Vachellia*.

3. The existing genus *Acacia* should be subdivided into three large genera (see Guinet fig. 19). The Gummiferae would constitute one genus. As the type species of *Acacia*, *A. nilotica*, is a member of Gummiferae, the species in Gummiferae would remain under *Acacia*. Bentham's series Vulgares and Filicinae would constitute a second genus, and the Phyllodineae, Pulchellae and Botryocephalae the third. New generic names would be required for the last two groups.

In Africa, therefore, *A. albida* would be referred to *Faidherbia*, *A. giraffae* to *Vachellia*, the remaining species armed with stipular spines would remain in *Acacia*, and the species with non-spinescent stipules would be referred to yet another genus. All four of these genera would occur in southern Africa.

As discussed elsewhere (Ross in Bol. Soc. Brot., sér 2, 40: 188, 1966), *A. albida* exhibits a number of unusual characters, some of which are peculiar to this species alone amongst the African acacias. It differs in having leaves with eglandular petioles but a gland on the rhachis at the point of attachment of each pinnae pair, stamen filaments which are shortly connate basally (also in *A. eriocarpa* Brenan and in *A. ogadensis* Chiov.) and large anthers which are eglandular even when in bud. Eglandular petioles do occur in certain other African species although not consistently while eglandular anthers are found in most of the extra-African species of the genus. The pollen of *A. albida* forms polyads of 30 cells whereas in all of the other African species investigated the polyads have only 16 cells, except for *A. giraffae* with 26 to 48 cells (van Zinderen Bakker and Coetzee, l.c.). Vassal (Bull. Soc. Hist. Nat. Toulouse 103: 583, 1967) found from a study of seedling development that the ontogeny of the leaf in *A. albida* differed from all other members of the Gummiferae studied in producing bipinnate leaves from the outset.

Chevalier (Rev. Bot. Appl. 4: 876, 1934) considered *A. albida* to be sufficiently distinct from all of the other species to transfer it to the monotypic genus *Faidherbia*. *A. albida* is not closely related to any of the other African species and there are the above characters to suggest that the species would be better placed in *Faidherbia*. However, although *A. albida* differs from the other African acacias it

does nevertheless share many characters in common with them. In deciding whether or not the species should be excluded from *Acacia*, it depends upon whether one is more influenced by the similarities or by the differences. Despite the somewhat anomalous position of *A. albida*, the species is being left in *Acacia* for the account of Mimosoideae which is currently being prepared for the Flora of Southern Africa, although clearly it may ultimately be found better to place the species in *Faidherbia*.

A. giraffae shares so many common characters with other species in the Gummiferae that I would be extremely reluctant to see it split off *Acacia* and placed in another genus. It is unfortunate that Guinet has not yet investigated the pollen-morphology of *A. haematoxylon* Willd. as *A. giraffae* and *A. haematoxylon* hybridize. Consequently, it would be interesting to know whether *A. haematoxylon* has pollen similar to that of *A. giraffae*.

One important result of Guinet's studies is that they confirm Bentham's broad subdivisions of the genus for, as mentioned above, Guinet's three proposed genera may be arrived at by amalgamating certain of Bentham's series. I am opposed to the idea of fragmenting *Acacia* into three large genera because, despite the differences in pollen-morphology enumerated by Guinet, the species share so many other characters in common. What would really be achieved by giving the three groups generic status? The three genera thus recognised would still be more closely related to one another than to any other genera. Surely a more satisfactory solution would be to accord each of the three proposed genera subgeneric rank within *Acacia*.

Irrespective of whether or not *Acacia* is fragmented into three large genera, it would still be necessary for each of the groups to be subdivided. A system of subdividing the African Vulgares and Gummiferae (this name would have to fall into disuse in any new system of classification as the group contains the type species of *Acacia*) would still be required. Nearly all of the classifications to date have been based on gross morphology alone but it is clear that other characters, for example, pollen-morphology and seedling-morphology yield valuable information. It seems most desirable to correlate information of this nature with gross morphology in any new attempt to draw up a classification. Hopefully it will not be too long before this is possible. Meanwhile, some suggestions are advanced for subdividing the Vulgares and Gummiferae.

I. *Vulgares*

Bentham recognized four subseries within the Vulgares. In doing so he relied to a certain extent on geographical distribution, dividing the series into the capitate- and the spicate-flowered species of the Old World, and the capitate- and the spicate-flowered species of the New World. Despite the convenience, it no longer seems desirable to segregate the Old World and the New World species.

All of the species with prickles in pairs near the nodes (Diacanthae) or prickles in threes (Triacanthae) have spicate inflorescences. It is only among the species armed with irregularly scattered prickles that capitate- and spicate-flowered species occur. Consequently, there is no need to draw upon the nature of the inflorescence to provide the major subdivisions within the Vulgares as the subdivisions can be arrived at by using the arrangement of the prickles. The envisaged subdivisions within Vulgares would then be as follows (Bentham's ranks and names have been retained here purely for convenience although clearly they are no longer appropriate):

Series Vulgares

Subseries 1. Triacanthae
Subseries 2. Diacanthae
Subseries 3. Ataxacanthae
A. Spiciflorae
B. Capitulatae

The Ataxacanthae, when delimited as above, would contain all of the species with prickles scattered irregularly along the internodes. These species appear to form a far more convenient group than is apparent from Bentham's subdivision of the Vulgares. However, the division of Ataxacanthae into those species with capitate inflorescences and those species with spicate inflorescences is desirable because, although the species share many characters in common, there are also some notable differences. Guinet's division of the Vulgares on the basis of pollen-morphology indicates that the pollen in the capitate- and in the spicate-flowered species with irregularly scattered prickles is different. This is also supported by Vassal's studies on seedling morphology. Vassal maintains that the "*A. pennata*" group and *A. ataxacantha* (unfortunately no other species with scattered prickles and spicate inflorescences were investigated), although sharing some characters in common, should nevertheless be separated because of differences in seedling morphology.

Of the 14 African species in this group with scattered prickles, only four have spicate inflorescences. However, all of the species, irrespective of whether the inflorescence is capitate or spicate, have the following characters in common:

1. Pale yellowish-white flowers.

2. Stipitate ovaries.

3. Pubescent ovaries (except for *A. lujae* De Wild.). Pubescent ovaries are, of course, found in several other species of African acacias but it seems of some significance that nearly all of the species in this group have this character and one wonders whether there is possibly some evolutionary involvement.

4. Almost all of the species are climbers or scandent shrubs. *A. ataxacantha* and *A. brevispica* Harms sometimes grow as trees while *A. eriocarpa* apparently always grows as a small tree.

5. They all lack secondary leaves. As mentioned earlier, secondary leaves are thought of as an adaptation for the production of new leaves without necessitating the formation of new branchlets. However, climbers must continue to grow in order to compete for light otherwise they face the possibility of being shaded out by the surrounding vegetation. The possession of secondary leaves may, therefore, not confer any significant benefit to a climber.

6. The pods of all species are essentially similar in being $\pm$ umbonate over the seeds and in having a fairly conspicuous transverse venation.

Within this group of 14 species, the species with spicate inflorescences differ from those with capitate inflorescences in the following respects:

1. The size of the apertures of the pollen grains. Guinet records that in the spicate-flowered species the diameter of the apertures is 3–5μ whereas in the capitate-flowered species the diameter is 1,2–2,9μ.

2. Seedling morphology.

3. Areole shape. In the species with spicate inflorescences the areole is small and typically horseshoe shaped (in *A. ataxacantha* it is a small central depression) while in the capitate-flowered species the areoles tend to be larger and conform in shape to the outline of the seeds.

II *Gummiferae*

The subdivision of the series Gummiferae presents far greater difficulty. Bentham subdivided Gummiferae into three main groups primarily on the position of the involucel on the peduncle, namely, Summibracteatae, Medibracteatae and Basibracteatae. The position of the involucel in many species varies within far wider limits than previously realized so that this character is no longer suitable for delimiting major groups within the Gummiferae. The character is, however, important in certain small groups of species for distinguishing between closely related species. Some new character or combination of characters must, therefore, be employed to subdivide Gummiferae.

The obvious character for dividing Gummiferae is the nature of the inflorescence but the result is very disappointing because the vast majority of species have capitate inflorescences. In Africa only five species have a spicate inflorescence, namely, *A. albida*, *A. lahai* Steud. & Hochst. ex Benth., *A. horrida* (L.) Willd., *A. bussei* Harms ex Sjostedt and, doubtfully, *A. dolichocephala*. *A. albida* differs from the other four species in several respects so it would have to be split off from the rest, if not placed in *Faidherbia*.

Flower colour is important taxonomically and could be employed to distinguish two broad groups within the capitate-flowered species. The two main colour groups found are white to pale yellowish-white (or occasionally pale pink or rarely purple in *A. xanthophloea* Benth. in tropical east Africa) and bright- or golden-yellow. *A. xanthophloea* has bright-yellow flowers throughout most of its range but, apart from the anomalous behaviour of this species, all of the other species can be satisfactorily placed in one or the other colour group.

The species within each of these groups could be subdivided on the basis of the stipular spines, a character employed by Bentham. The stipular spines are usually either straight or almost so, or else they are strongly recurved, while in certain species a mixture of long straight and short hooked spines occur together. The latter group of species corresponds to Bentham's "Heteracanthae".

The pods are useful for breaking down the groups further into those species with indehiscent pods and those species with dehiscent pods. The species with indehiscent pods could be divided according to whether the valves are thin or whether they are markedly thickened, woody or pulpy. Pod shape, that is falcate as opposed to straight or almost so, often varies within a single species and it is felt that this is not a suitable character to employ for further subdividing major groups of species with dehiscent pods.

These above gross morphological characters, when considered together with pollen and seedling morphology, should enable the Gummiferae to be divided satisfactorily.

Despite the need for a classification of the African species, there is, however, an even greater need to resolve numerous basic taxonomic problems, particularly those in north-east tropical Africa. The last fairly comprehensive account of the species was by E. G. Baker in his Leguminosae of Tropical Africa (1930), but unfortunately this treatment of the genus is now quite out of date. The regional floras have contributed greatly to our knowledge of the African species, but many problems await elucidation.