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An analysis of the African *Acacia* species: their distribution, possible origins and relationships

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ABSTRACT

The three subgenera recognized within the genus *Acacia* are outlined and the global distribution of each is indicated. The differences between the subgenera and the degree of relationship and levels of specialization are discussed briefly. It is suggested that the ancestral members of the genus were climbers or lianes. Past geological events considered likely to have influenced the distribution of the *Acacia* species in Africa are outlined. The number of species recorded from each African country is tabulated and the distribution and concentration of species within the genus *Acacia* as a whole and within each subgenus in Africa are illustrated. The highest concentrations of species within each subgenus occur in tropical east and south-east Africa. The distribution of species within some of the individual African countries and possible affinities are discussed and attention is drawn to the main centres of endemism. The distribution of the African species is correlated with the major phytogeographical regions recognized on the continent. The relationships between the African and the American, Madagascan, Indian and Australian *Acacia* species are discussed briefly.

RÉSUMÉ

*UNE ANALYSE DES ESPÈCES D'*ACACIA *AFRICAINS: LEUR DISTRIBUTION, ORIGINES EVENTUELLES ET RELATIONS*

Les trois sous-genres reconnus dans le genre Acacia *sont esquissé et la distribution globale de chacun est indiquée. Les différences entre les sous-genres et le degré de relation et niveaux de spécialisation sont brièvement discutés. Il est suggéré que les membres ancestraux du genre étaient des grimpants ou des lianes. Des évènements géologiques du passé considérés comme avoir vraisemblablement influencer la distribution des espèces d'*Acacia *en Afrique sont décrits. Le nombre des espèces enrégistrées dans chaque pays d'Afrique a été présenté sous forme de tables et la distribution ainsi que la concentration des espèces dans le genre* Acacia *dans son ensemble et dans chaque sous-genre d'Afrique sont illustrés. Les concentrations les plus élevées d'espèces dans chaque sous-genre surviennent en Afrique tropicale orientale et sud-orientale. La distribution des espèces dans certains pays africains individuels et les affinités possibles sont discutées et l'attention est attirée sur les centres principaux d'endémisme. La distribution des espèces africaines et des espèces d'*Acacia *américaines, malgaches, indiennes et australiennes est brièvement discutée.*

INTRODUCTION

The genus *Acacia* at present consists of about 1 100 species (perhaps as many as 1 200) which are widely dispersed in the Americas, the Carribbean and Pacific Islands, Africa, Madagascar and the Mascarenes, Asia, the Indo-Malesian region and Australia. Europe is the only large geographical area devoid of indigenous *Acacia* species, and there are no indigenous species in New Zealand despite its relative proximity to Australia. The fossil record indicates that the genus was previously more widely distributed having been present formerly in the Ukraine (Shchekina, 1965) and in New Zealand (Mildenhall, 1972, 1975). Most species of *Acacia* occur in regions where the rainfall is markedly seasonal or low, relatively few inhabiting rainforest areas, but even then the rainfall is usually unevenly distributed throughout the year and even in the wettest parts there is usually a short dry season. This does not imply that the genus originated in an arid or semi-arid region. On the contrary, it is considered probable that *Acacia* originated in the tropical lowlands and that most of the xerophytic features within the genus are secondary.

Much evidence has accumulated in recent years to support the contention that there have been large scale movements of continents during geological time and Raven & Axelrod (1974) summarized the biogeographic support for the theory of plate tectonics. Raven & Axelrod (*l.c.*) postulated that West Gondwanaland, combined Africa and South America, was a primary area of evolution for many major orders of angiosperms and perhaps the earliest angiosperms themselves, and that the initial radiation of the angiosperms occurred when direct migration was possible between South America, Africa, India, Antarctica and Australia, and via Africa to Laurasia. West Gondwanaland included vast arid to subhumid areas in tropical latitudes where the terrain and edaphic conditions were diverse and provided every opportunity for rapid evolution. Thorne (1977), on the other hand, favoured south-eastern Asia and associated archipelagoes as the primary centre of origin of the most primitive angiosperms and maintained that prior to its fragmentation West Gondwanaland was merely one of a number of important centres for the development of the tropical angiosperm flora.

In support of their contention Raven & Axelrod (*l.c.*) argued that West Gondwanaland was centrally located on routes of dispersal at the time when the primary evolutionary radiation of the angiosperms was taking place. The climatic changes associated with the fragmentation of Gondwanaland, which, according to Raven & Axelrod, commenced in the mid-Cretaceous approximately when the first angiosperms are encountered in the fossil record, probably had a profound influence on the evolution of the angiosperms and on the establishment of major lines within it. There is some disagreement over the timing of the fragmentation of Gondwanaland, an event of primary importance from a phytogeographic point of view. Melville (1975), for example, was of the opinion that Gondwanaland started to fragment earlier than indicated by Raven & Axelrod. In this paper I have followed Raven & Axelrod in assuming that

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Gondwanaland started to fragment in the mid-Cretaceous and that the angiosperms were already fairly widely distributed.

The opening of the South Atlantic 125–130 million years ago heralded the spread of more mesic climates over much of West Gondwanaland and is thought to have started the surge of angiosperms into the mesic lowland record about 110 million years ago (Raven & Axelrod, *l.c.*). The pattern of appearance of the angiosperms in the lowland record suggested to Raven & Axelrod that the primitive members of several extant orders and perhaps even a few families were already in existence by the close of the early Cretaceous 110 million years ago. Thorne (1978), however, maintained that few, if any, extant families, and certainly no extant genera, had evolved in West Gondwanaland before the final sundering of South America from Africa 100 million years ago.

Raven & Axelrod (*l.c.*) expressed the opinion that most modern angiosperm families were in existence in the Paleocene about 65 million years ago before the connection between Africa and Eurasia was severed. The family Leguminosae is thought to have originated or at least have undergone its primary radiation and differentiation into three subfamilies in West Gondwanaland and Raven & Axelrod expressed the view that Mimosoideae, Caesalpinioideae and perhaps Papilionoideae were in existence by the Paleocene. There are no reliable Cretaceous records of Caesalpinioideae or of the other two subfamilies. From what can be inferred about its history and present distribution patterns, Raven & Axelrod presume that Mimosoideae migrated between Africa and South America during or prior to the Paleocene. After the Paleocene (54 million years ago) the evidence suggests only limited migration between these two continents.

Vassal (1972) recognized three subgenera within *Acacia,* namely, subgenera *Acacia, Aculeiferum* and *Heterophyllum**, chiefly on the basis of characters of seeds and seedlings and on the occurrence of stipular spines and pollen characters. The three subgenera recognized by Vassal broadly correspond to groupings of Bentham's six series which is fortunate as most of the characters on which Vassal's classification are based are not obvious from the gross morphology of conventional herbarium specimens. The relationship between Bentham's series and Vassal's subgenera is as follows:

1. Subgenus Aculeiferum Vassal (= series *Vulgares* Benth. and series *Filicinae* Benth.)
2. Subgenus Heterophyllum Vassal (= series *Phyllodineae* Benth., series *Botryocephalae* Benth. and series *Pulchellae* Benth.)
3. Subgenus Acacia (= series *Gummiferae* Benth.)

The following sections within each subgenus were proposed by Vassal (1972) and Guinet & Vassal (1978) and the names are used in this paper:

1. Subgenus Aculeiferum (Sections *Aculeiferum, Monacanthea* and *Filicinae*)
2. Subgenus Heterophyllum (Sections *Heterophyllum, Uninervea* and *Pulchelloidea*)
3. Subgenus Acacia (Section *Acacia*)

GLOBAL DISTRIBUTION OF THE GENUS *ACACIA*

An indication of the global distribution of each subgenus is given in Figs 1–3.

The distributions of subgenera *Acacia* and *Aculeiferum* are very similar but subgenus *Acacia* apparently enjoys a slightly wider distributional range than subgenus *Aculeiferum.* Subgenus *Aculeiferum* has a more restricted distribution in Africa than subgenus *Acacia,* is present in New Guinea while subgenus *Acacia* is absent, and only just reaches Australia (in the vicinity of Coen in northern Queensland) where it is represented by a solitary species (*A. albizioides* Pedley) in contrast to subgenus *Acacia* which is widely distributed in northern Australia although represented by fewer than ten species. The vast majority of species in the genus belong to subgenus *Heterophyllum* which is fundamentally an Australian group (including Tasmania), while a further eighteen species (Pedley, 1975) occur in Madagascar and the Mascarenes, New Guinea, Formosa, the Philippines and the Pacific Islands to Hawaii. The genus reaches its southern limit of distribution in Tasmania. The position of *A. willardiana* Rose, which occurs on the west coast of North America (Mexico), is not clear (see later discussion) but if it is placed in subgenus *Heterophyllum* as advocated by Vassal & Guinet (1972) then the distribution of the subgenus shown in Fig. 3 should be extended eastwards from Hawaii to Mexico.

Guinet & Vassal (1978) are of the opinion that the three subgenera were differentiated by the Oligo-Miocene period (± 27 million years ago), and that no fundamental difference seems to exist between their geographical distribution then and the present. They pointed out that the apparent absence of the genus in the fossil record during the Paleocene is surprising, particularly if the genus is held to have had a monophyletic origin and if one considers that its distribution during the Neogene was what it is now.

ORIGIN AND POSSIBLE IDENTITY OF THE ANCESTRAL MEMBERS OF THE GENUS *ACACIA*

Like the origin of the angiosperms, the identity of the ancestral form of *Acacia* has been the subject of much speculation and disagreement, but recently a broad consensus appears to have been reached which contradicts the earlier views of Andrews (1914) and Atchison (1948). Andrews and Atchison considered the *Gummiferae* (subgenus *Acacia*) to be the ancestral form as its members contained the morphological characters of the genus that they considered to be primitive, namely, bipinnate leaves and persistent spinescent stipules. Atchison maintained that chromosome number variation, morphological uniformity and geographical distribution contributed toward establishing *Gummiferae* as the ancestral form of the genus pointing out, in support of this contention, that *Gummiferae* is the only section of the genus with a cosmopolitan distribution (this is not strictly correct). The other sections of the genus were held to have developed from the original forms in secondary centres where isolation through climatic or edaphic change was favourable to the survival of new types. Tindale & Roux (1975), on the basis of a limited sample, suggested that the chemical content of the South African species with non-spinescent stipules (subgenus *Aculeiferum*) is generally more advanced than that of the species with spinescent stipules (subgenus *Acacia*), a suggestion that supports the above view. However, most of the *Gummiferae* are polyploids and polyploidy is now held to

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*The subgeneric name *Phyllodineae* (DC.) Seringe has priority and will have to be adopted in place of *Heterophyllum* Vassal, but the name *Heterophyllum* is retained for the purpose of this paper.

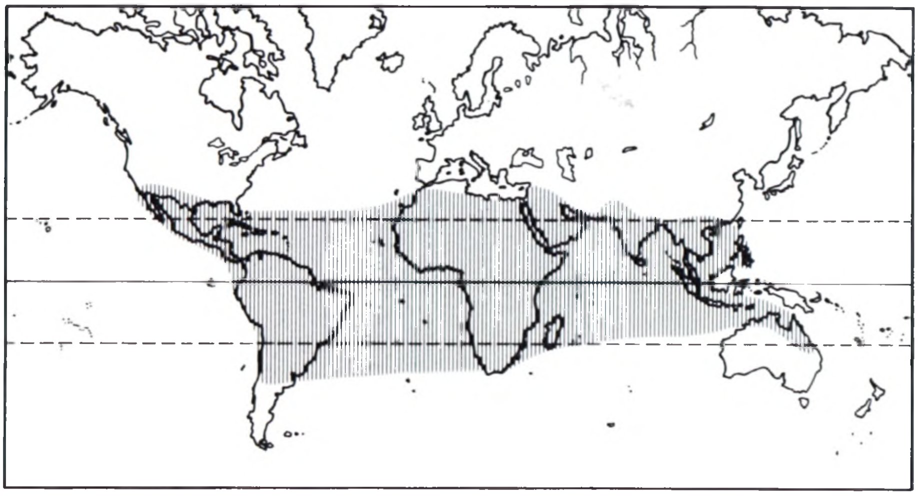

FIG. 1.—An indication of the global distribution of subgenus *Acacia* (excluding the distribution of *Acacia farnesiana* in Australia).

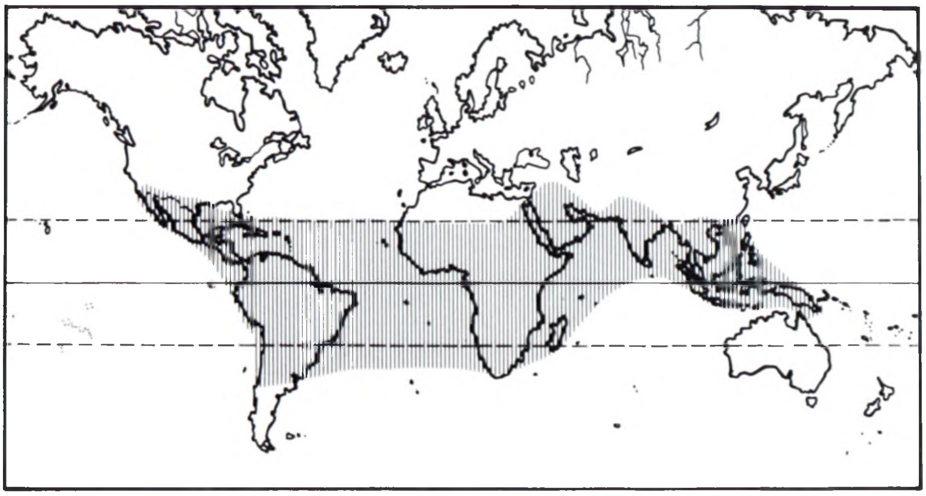

FIG. 2.—An indication of the global distribution of subgenus *Aculeiferum*.

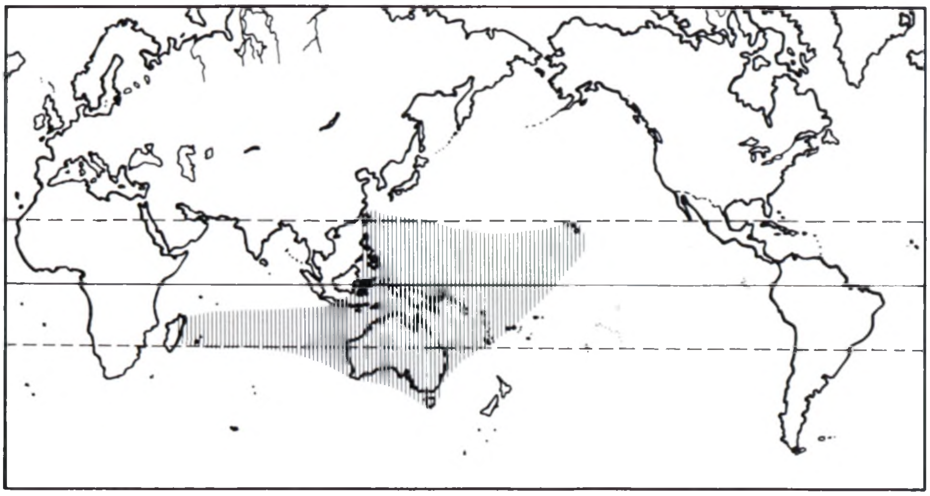

FIG. 3.—An indication of the global distribution of subgenus *Heterophyllum* (excluding *A. willardiana* which probably belongs in subgenus *Aculeiferum*).

correspond to a high degree of differentiation in the genus *Acacia*.

Robbertse (1974) outlined the possible evolution of the inflorescence and flowering system in the South African acacias and considered subgenus *Acacia* (*Gummiferae*) to be more advanced than subgenus *Aculeiferum* (*Vulgares*), a view which is supported by the detailed studies of Guinet & Vassal (1978). Robbertse considered it probable that the paniculate flowering system, spicate inflorescence, pedicellate flowers, presence of a cup-shaped disc and a pedicellate ovary, all of which are found in subgenus *Aculeiferum*, are primitive characters.

Guinet & Vassal (1978) evaluated the degree of relationship and specialization of the major subdivisions recognized within the genus on the basis of pollen, chromosome, seed, pod, inflorescence and vegetative characters. Each character was divided into three states, namely, unspecialized, specialized and highly specialized, and that section of the genus displaying the characters considered to be highly specialized was itself considered to be highly specialized. The division of some characters, for example seed size, into somewhat arbitrary size classes is questionable, especially as it was not disclosed why the range of continuous variation in seed size was divided in such a manner or what criteria were employed to established the degree of specialization of each size class. For example, seed were divided into the following size classes, small (less than 5 mm long), medium (5–10 mm long) and large (more than 10 mm long). Small seed were regarded as unspecialized but it is quite conceivable that in some instances small seed may be specialized. In addition, the range of variation in seed size in many species obscures the limits of Guinet & Vassal's size classes.

Guinet & Vassal (*l.c.*) concluded that:

1. On the basis of pollen morphology subgenus *Acacia* is the most specialized of the three subgenera and subgenus *Aculeiferum* the least specialized. Although the pollen of subgenus *Heterophyllum* is generally more specialized than that of subgenus *Aculeiferum,* the two subgenera share important characters, for example, the absence of columellae and the presence of simple apertures.

2. Subgenus *Acacia* is clearly distinguished from the other two subgenera by the high level of specialization of the chromosome characters (chromosome numbers and the degree of homogeneity of the karyotype). Subgenera *Aculeiferum* and *Heterophyllum* are more homogeneous and have similar levels of differentiation of chromosome characters. On the basis of chromosome characters, subgenus *Aculeiferum* is the least specialized and subgenus *Acacia* the most specialized.

3. The characters of the seeds of subgenus *Acacia* are often highly specialized, and the levels of specialization in the series *Filicinae* and *Monacanthea* of subgenus *Aculeiferum* are fairly close.

4. The cotyledonary and adult foliar characters selected did not appear to be specialized in subgenera *Aculeiferum* and *Acacia* except in a few rare cases, while many specializations occurred in subgenus *Heterophyllum* except in the development of spinescence. Section *Filicinae* of subgenus *Aculeiferum* shows no specialized characters.

5. The characters of the inflorescence and pod selected indicated that certain characters in subgenus *Acacia* are infrequently encountered in the other subgenera.

Guinet & Vassal attempted to estimate the total levels of specialization within each subgenus (and within the sections within each subgenus) and concluded that:

1. On the basis of their average level of specialization subgenus *Acacia* is the most specialized subgenus and *Aculeiferum* the least specialized.

2. Section *Filicinae* of subgenus *Aculeiferum* is characterized by a preponderance of unspecialized characters and shows the least diversity of all series in the genus.

3. Section *Monacanthea* of subgenus *Aculeiferum* contains more possible primitive states than section *Aculeiferum* and appears to be less advanced than the latter.

4. The *Phyllodineae* are more specialized than the *Botryocephalae* and the *Pulchellae* in subgenus *Heterophyllum* but the persistence of unspecialized states occurs to a similar degree in the three series.

Guinet & Vassal (*l.c.*) stressed that if the correlation of the characters selected reflects a true relationship between the major subdivisions of the genus, then subgenera *Aculeiferum* and *Heterophyllum* are more closely related to one another despite the fact that they occupy basically different geographical areas which show relatively little overlap, than are subgenera *Aculeiferum* and *Acacia* which share a common geographical area.

Guinet & Vassal favoured the concept that *Acacia* originated in West Gondwanaland in an area that approximates to the area presently occupied by Central America (from Mexico to Bolivia). In support of this contention Guinet & Vassal pointed out that characters which are absent in the genus *Acacia* itself in America are nevertheless found in indirectly related genera. For example, the fundamentally Australian extraporate pollen type (subgenus *Heterophyllum*) exists in some South American genera closely related to *Piptadenia,* and phyllodes are present in some South American species of *Mimosa.* These occurrences were regarded by Guinet & Vassal as evidence that the American continent contains most of the evolutionary potential for the characters now found in the genus *Acacia* and accords with Guinet's (1969) earlier suggestion that phyllodes and the pollen type commonly found in subgenus *Heterophyllum* may have originated in South America and that Australia was a secondary centre of development and differentiation. However, because of the occurrence in Australia of phyllodes and the pollen type alluded to, it can equally well be argued that Australia also contains most of the evolutionary potential for the characters now found in the genus *Acacia* and that these characters originated in Australia. Guinet & Vassal are of the opinion that section *Filicinae* of subgenus *Aculeiferum* preserves the morphological characters closest to those postulated as being ancestral in the genus. Section *Filicinae* is poorly known and much more information is required.

The rainforest areas of the world were previously much more extensive and during the Paleogene humid forests stretched through much of America, Africa, Arabia, India, Malaysia and Australia. *Acacia* species are not well represented in rainforest areas at the present time and it is thought that this is probably due to their general intolerance of low light intensities. In the absence of any indications to the contrary, it seems reasonable to assume that members of the genus have always been similarly intolerant of low light intensities. The *Acacia* species which are currently the most successful in rainforest areas are the climbers and it appears as though the climbing habit has enabled species to exploit situations in forests where light penetrates to the ground, for example in clearings, on the banks of streams or on forests margins, and reach and maintain an emergent position in the canopy. If, as is considered likely, *Acacia* originated in lowland forests, it is suggested that the ancestral members were climbers or lianes and, this being the case, members of proto-*Aculeiferum* which were similar in some respects to some members of subgenus *Aculeiferum.*

Taking the African species as an example, a number of the members of section *Monacanthea* subgenus *Aculeiferum* appear to be obligate climbers (*A. lujae* De Wild., *A. kraussiana* Meisn. ex Benth.) while others (*A. brevispica* Harms, *A. ataxacantha* DC.) occur as climbers in forested areas or as scandent shrubs or even large spreading shrubs in neighbouring woodland or grassland areas. *A. ataxacantha* occurs as a climber in forests and on forest margins, as a scandent shrub or non-scandent spreading shrub in woodland or grassland, but on occasions it grows as a substantial single-stemmed tree up to 10 m high in southern Africa. *A. ataxacantha* apparently exhibits the evolutionary potential that would have been necessary for a forest-dwelling climber to adapt and exploit the new habitats created in surrounding grassland and woodland areas as the forests retreated.

A. ataxacantha and the other climbers are invariably armed with scattered recurved non-stipular prickles but occasional plants are entirely or almost entirely unarmed. Some species [*A. caffra* Thunb.) Willd., *A. galpinii* Burt Davy, *A. polyacantha* Willd.] in section *Aculeiferum* of subgenus *Aculeiferum* which are typically armed with prickles in pairs at the nodes are likewise sometimes unarmed. In some species (*A. caffra*) in section *Aculeiferum* occasional specimens are found where a few irregularly scattered prickles occur *in addition* to the paired prickles at the nodes. This illustrates the apparent ease with which scattered or paired prickles can be lost and how scattered prickles could give rise to paired or solitary prickles at the nodes or vice versa. Once again, the evolutionary potential for such change is still apparently present. Members of the American section *Filicinae* which Guinet & Vassal consider to be ancestral are typically unarmed but prickles could have been lost as indicated.

Although subgenera *Acacia* and *Aculeiferum* share a common geographical area there are fundamental differences between them, as indicated by Guinet & Vassal, and they do not appear to be closely related which suggests that subgenus *Acacia* did not arise directly from subgenus *Aculeiferum* or vice versa. For example, the colporate pollen of subgenus *Acacia* with columellae is considered unlikely to have developed from the porate type without columellae. It seems more likely, therefore, that subgenus *Acacia* was derived from proto-*Aculeiferum* rather than from subgenus *Aculeiferum* itself. Subgenus *Heterophyllum* was possibly derived directly from subgenus *Aculeiferum* or, failing that, from proto-*Aculeiferum*.

It is difficult to speculate on the identity of the ancestral proto-*Aculeiferum* except very generally. It is suggested that the ancestral members were climbers or lianes, either unarmed or armed with prickles, with many-jugate bipinnate leaves. Robbertse's (1974) findings suggest that they would have possessed a paniculate flowering system and that the flowers were pedicellate. The transition from capitate to spicate inflorescences and vice versa appears to have occurred several times during the development of the genus and there is no certainty as to which condition might be considered unspecialized.

OUTLINE OF THE CRETACEOUS–QUATERNARY HISTORY OF AFRICA

The present distribution patterns in *Acacia* in Africa have been determined by events that lie deep in the past but it is difficult to assess, except very generally, the effects of past geological events on the flora of a continent. Unfortunately the plant fossil record in Africa is generally poor from the Jurassic until the Quaternary (Plumstead, 1969), largely because of the uplift of the continent following the break-up of Gondwanaland and the limited extent of lowland basins in which fossils were preserved. Consequently little information is available during the time that the angiosperms evolved and became dominant during the Cretaceous. According to Axelrod & Raven (1978), who provided an excellent survey of the late Cretaceous and Tertiary in Africa, the vegetation of Africa since the middle Cretaceous has been shaped by diverse physical factors, and in its broadest features the vegetation history in Africa has paralleled that of other austral continents which have remained relatively stable in latitude since the Cretaceous. A summary follows of the more important features of the Cretaceous–Quaternary history of Africa, largely as outlined by Axelrod & Raven.

During the late Cretaceous and Paleocene (75–55 million years ago) Africa lay 15–18° further south than at present. Relief was relatively low and a lowland rainforest stretched from coast to coast clothing nearly all of Africa except perhaps for the southern tip; the late Cretaceous and Paleocene rainforest covered much of North Africa which was then situated near the equator and what is now the Sahara desert. This was a period of benevolence during which rains were reliable and the widespread forests flourished, although even at this time isolated pockets of aridity are likely to have existed at the edge of the tropics because of high pressure cells and in edaphically dry sites in both tropical and temperate zones (Axelrod, 1972). The southern part of the continent, which came under the influence of the westerlies, probably had a cool wet climate (Goldblatt, 1979). At this time all of the temperate austral lands were covered with a dense *Podocarpus–Nothofagus*-evergreen dicot temperate forest and consequently it is inferred that a forest flora of the *Podocarpus–Nothofagus* type (*Nothofagus* was not necessarily present) probably covered the southern tip of southern Africa. The inferred distribution of vegetation in Africa during the late Cretaceous–Paleocene is illustrated by Axelrod & Raven, Fig. 6 (1978) along with that during the late Oligocene–early Miocene, middle–late Miocene and Recent.

By the close of the Cretaceous, Africa was isolated from South America and India-Madagascar and was surrounded by ocean. Although direct migration of plants to and from Africa was restricted after the mid-Cretaceous, direct interchange with South America was much easier than at present as the Atlantic was relatively shallow and numerous islands provided stepping stones between the two continents (Raven & Axelrod, 1974).

By the close of the Oligocene, the African plate had moved north to virtually its present position. During the late Oligocene–early Miocene (30–25 million years ago) the low relief in Africa was altered by uplift accompanied by warping (King, 1967), especially along the east coast, and the present landscape of the continent started to take shape. Volcanic activity started on a major scale and the East African rift valleys were initiated. Uplift brought a cooler drier climate and the development and spread of dry climate over tropical Africa probably began near the close of the Oligocene about 27 million years ago (Axelrod, 1972) and has continued to the present as the rift valleys continue to grow (Raven & Axelrod, 1974). The formation of a volcanic field from Ethiopia southwards down the rift valleys during the Miocene increased the development of rainshadows which in turn brought greater drought and temperature extremes.

As a result of the Neogene trend to a drier climate brought on by the general uplift of the continent, changes in circulation, and the resultant decrease in moisture, savanna started to spread at the expense of rainforest and the African rainforest was progressively impoverished. The development of rainshadows in the rift valleys favoured the spread of savanna and then grassland, at first locally in small patches but then more extensively as the rainshadow effect increased. By the mid Miocene lowland rainforest is thought to have had only a patchy distribution along the northern parts of the east coast, and it seems probable that a temporary dry season during which little or no rain fell was already evident in the Miocene.

By the close of the Oligocene–early Miocene the vegetation of Africa had assumed a near-modern aspect although the composition and distribution of vegetation differed in many important respects from that of today (see Axelrod & Raven, Fig. 6, 1978).

A further major factor that affected the African flora was the development of the cold Benguella current. By the early Miocene Antarctica had moved to its present position and glaciation had been initiated. When glaciation commenced in Antarctica cold water started to bathe the west coast of Africa bringing to it a drier colder climate. A full ice sheet did not appear until the Pliocene about 5 million years ago and it waxed and waned for 2–3 million years. As the major ice sheet spread the Benguella current increased in strength and became progressively colder bringing with it increased drought to the west coast of tropical Africa. The extensive Pliocene ice sheet would have brought a much drier climate not only to the coast of west tropical Africa but it may possibly also account for the dry global climate in the mid Pliocene (Raven & Axelrod, 1974).

As aridity spread and a seasonally dry climate became established, particularly during the Pliocene as the Antarctic ice cap developed, the African rainforest continued to be more and more restricted in distribution and impoverished and the taxa comprising the forests became progressively more discontinuous. The strengthening high pressure systems brought a drier climate to the interior of Africa and the spreading drought tended to disrupt and impoverish the African flora, the recurring aridity in the tropics during successive periods of 'ice-age aridity' resulting in increased selection pressure for drought resistant taxa. As a consequence, rainforest areas were replaced by savanna and grassland, savanna and grassland by dry thorn scrub and dry thorn scrub by semidesert and desert vegetation.

The later phases of this trend in the Pliocene probably resulted in the appearance of local areas of semidesert, but widespread regional semideserts and deserts are apparently the consequence of later phases of 'ice-age aridity'. According to Quezel (1979), a desert climate was probably initiated in the major part of the Sahara, at least in the lower altitudinal zones, during the Pliocene.

Throughout the Tertiary there was a symmetrical distribution of climate and vegetation in the central tropical belt. The present African vegetation shows much greater asymmetry than that of the early to late Tertiary (see Axelrod & Raven, Fig. 6, 1978). White (1965) discussed the marked differences that exist at present between the Sudanian and Zambezian floristic domains. The Sudanian Domain is much drier than the Zambezian and its greater aridity has been largely responsible for the impoverishment of its flora.

The close of the Pliocene and the early Pleistocene were characterized by major uplifting which raised the interior plateaux by over 1 700 metres. The altitude of parts of eastern Africa has increased by over 2 000 metres above that of the Miocene and has brought to it a drier climate. The Pliocene–Pleistocene uplifting and associated climatic fluctuations favoured local speciation.

Fluctuations in the Quaternary climate also had a significant effect on the tropical African rainforest flora, with the drier periods being times of extinction of taxa requiring more or less continuously wet conditions. Rainforest expanded during the humid interglacial periods and contracted again during the dry glacial periods. Wild (1968) reconstructed tentative vegetation maps of Zimbabwe showing how the vegetation would have differed from that of today if rainfall decreased by 50% or increased by about 150% above present levels. Wild demonstrated that if rainfall increased by 150% above present levels, Zimbabwean forests that are now isolated would have been sufficiently widespread to have been in contact with the main forest areas of Zaire and West Africa which would explain why some species in isolated Zimbabwean forests have west African affinities. Wild suggested that Quaternary pluvials of only 50% higher rainfall would probably have resulted in more or less continuous forest at lower altitudes through much of tropical Africa, but Axelrod & Raven (1978) considered this unlikely unless a considerable amount of rain fell during the present dry winter season so that the rainfall was fairly evenly distributed throughout the year, a situation which was itself considered unlikely because of the strength of the then prevailing anticyclonic circulatory systems. Axelrod & Raven suggested that the present links in forest taxa between the Zaire-West Africa and the relic forest patches in Zimbabwe may date from the early Miocene.

Even during the past 20 000 years there have been major climatic changes over much of Africa (Van Zinderen Bakker, 1974) emphasizing that continued existence is not possible without continuous change. The tropical African rainforests continue to contract rapidly as a consequence of human activities and probably to a lesser extent because of climatic changes.

It is against this background of continuous change that the present distribution of the *Acacia* species must be seen. Just as the present distributions differ from those of the past, so too will those of the future differ from those of the present. Indeed, the present conservation status of a number of species is uncertain, especially of some of the endemic species with restricted distributions in the Horn of Africa.

ANALYSIS OF THE AFRICAN *ACACIA* SPECIES

The number of species recorded from each country in Africa is indicated in Table 1, the countries corresponding with the usual political boundaries except that, for the sake of convenience, the territory of the Afars and Issars has been included with Somalia. Table 1 was compiled from data contained in a conspectus of the African species (Ross, 1979) which was itself based on an examination of specimens in several African, British and European herbaria and on information contained in the regional African floras. The African *Acacia* species remain incompletely known and numerous taxonomic problems await elucidation, especially in north-east tropical Africa. For the purpose of Table 1 and in the discussion which follows the 115 species accepted by Ross (1979) have been taken as the number of species for the continent (this figure excludes *A. macrothyrsa* Harms which is now considered (Hunde, 1979) to be a synonym of *A. amythethophylla* A. Steud. ex A. Rich.). Taxa such as *A. farnesiana* (L.) Willd., which is not thought to be indigenous, and *A. schlechteri* Harms and *A. andongensis* Welw. ex Hiern, about whose precise taxonomic status there is some doubt, have been excluded as have the *A. erioloba* E. Mey × *A. haematoxylon* Willd. hybrid and other hybrids, *A. purpurea* Bolle, *A. mauroceana* DC. and *A. callicoma* Meisn., which are names of uncertain application, and *A.* sp. near *senegal, A.* sp. near *somalensis* and others which are insufficiently known. The 115 species recognized by no means represent the final total number of species for the continent but this figure does serve as a basis, imperfect as it is, for an analysis of the African species. Because of the variation in the size of individual countries and because no country has species evenly distributed throughout it, the number of species per country is of somewhat limited value alone. Furthermore, the distribution of species within countries in tropical east, south-east and southern Africa is far better documented than in a number of countries in other areas of the continent. However, despite these limitations and, although perhaps the figures provided in Table 1 are incorrect in some details and likely to need alteration in the light of additional information, it is believed that the overall patterns that emerge are sufficiently accurate to be of value.

Examination of Table 1 reveals, not surprisingly, that the highest concentrations of species occur in countries in tropical north-east, east and south-east Africa. The figures suggest that there is a tendency in most countries in tropical north-east, east, south-east, southern and south-west Africa for subgenus *Acacia* to be proportionately better represented than subgenus *Aculeiferum,* although Mozambique is an obvious exception to this generalization, while in Zaire and in countries to the north-west subgenus *Aculeiferum* is often numerically as important as or

TABLE 1.—The representation of the *Acacia* species within each African country

Country	No. of species in subgenus *Acacia*	No. of species in subgenus *Aculeiferum*	Total no. of species
Morocco	2	0	2
Algeria	5	1	6
Tunisia	0	0	0
Libya	3	0	3
Egypt	7	3	10
Western Sahara	1	0	1
Mauritania	3	2	5
Senegal	5	4	9
Gambia	2	3	5
Guinea-Bissau	3	2	5
Guinea Republic	1	2	3
Sierra Leone	0	4	4
Mali	7	7	14
Liberia	0	2	2
Ivory Coast	5	8	13
Ghana	6	6	12
Togo	3	1	4
Benin (Dahomey)	3	5	8
Upper Volta	4	3	7
Nigeria	8	10	18
Niger	6	6	12
Cameroon (British)	3	3	6
Cameroun (French)	2	3	5
Chad	3	2	5
Central African Republic	4	1	5
Sudan	19	12	31
Ethiopia	28	43	15
Somalia	18	14	32
Equatorial Guinea	0	1	1
Gabon	0	1	1
Congo Brazzaville	1	1	2
Cabinda	0	1	1
Zaire	11	13	24
Rwanda	6	3	9
Burundi	4	2	6
Uganda	18	9	27
Kenya	27	15	42
Tanzania	31	19	50
Angola	14	11	25
South West Africa/Namibia	14	9	23
Zambia	16	13	29
Malawi	13	8	21
Mozambique	20	20	40
Botswana	18	12	30
Zimbabwe	22	16	38
South Africa:			
Transvaal	21	14	35
Orange Free State	4	2	6
Natal	13	8	21
Cape Province	8	3	11
Swaziland	12	6	18
Lesotho	1	0	1
Transkei	2	3	5

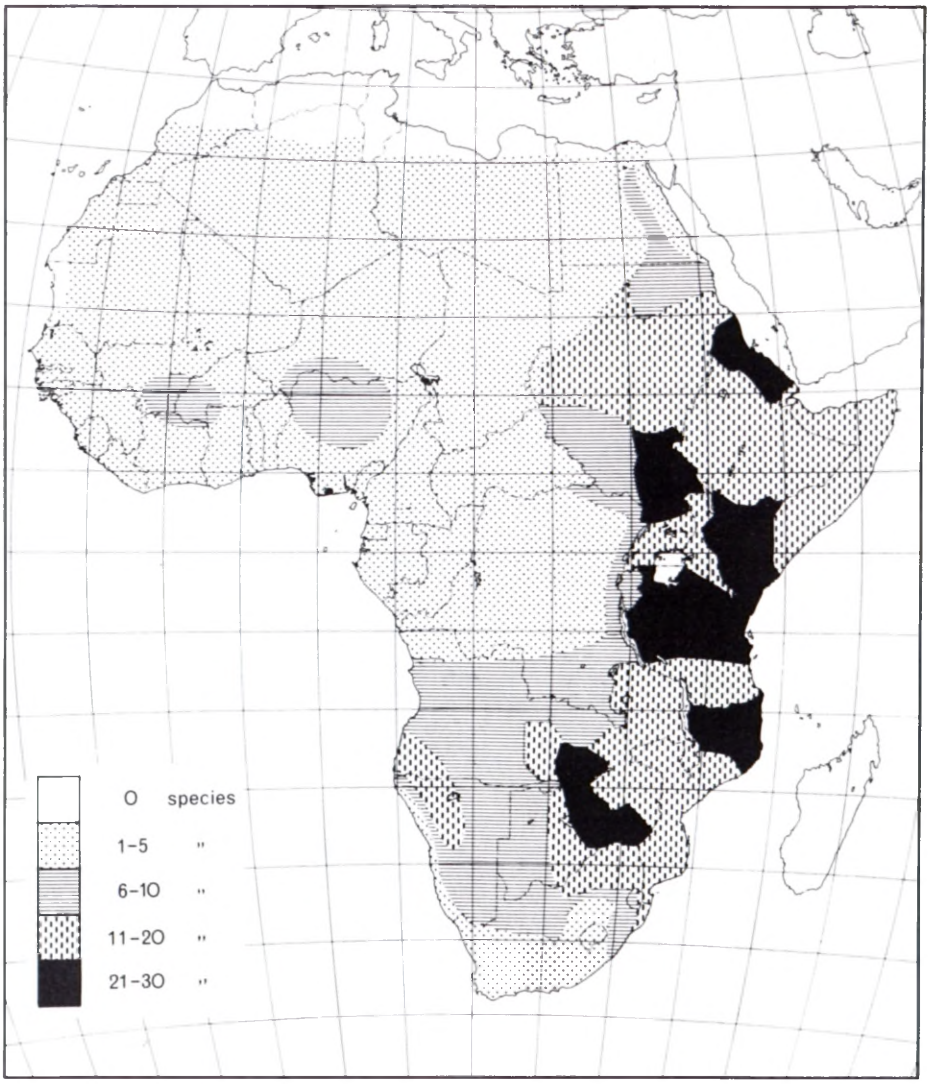

FIG. 4.—The general distribution of the *Acacia* species in Africa and an indication of the concentration of species over the distributional range of the genus.

even proportionately more important than subgenus *Acacia* although once again there are a number of exceptions. This apparent proportional preponderance of subgenus *Aculeiferum* in Zaire and parts of tropical west Africa may possibly be due to the presence of extensive forested areas which climbing species in subgenus *Aculeiferum* have been able to colonize but from which subgenus *Acacia* has been largely excluded.

The general distribution of the genus *Acacia* in Africa and an indication of the concentration of species over the distributional range is shown in Fig. 4. As in the case of the information in Table 1, Fig. 4 is more accurate in some areas than in others and this uneven treatment is a reflection of the uneven knowledge of the genus over its range of distribution.

The genus is widely distributed over the continent being absent only from the extreme northern portion of north Africa, part of Mauritania and western Sahara in West Africa, the vicinity of Cape Town in the extreme south-western tip of the continent and from parts of the west coast in South West Africa.* Tunisia is the only political entity on the continent in which no indigenous *Acacia* species are found. The greatest concentration of species occurs in tropical east and south-east Africa and, as one would expect, fewest species occur in desert regions to the north and south and in the rainforest areas, particularly in Zaire and in parts of tropical west Africa. Although the genus is so widespread and forms such a conspicuous feature of the landscape over much of the continent, the number of species found in Africa is lower than one might expect and represents less then one-sixth of the number of species found in Australia.

Having noted the distribution of the genus as a whole in Africa, the distributions of subgenus *Acacia* and of subgenus *Aculeiferum* are now examined (see Figs 5 & 6). Of the 115 species accepted for Africa, 52 belong to subgenus *Aculeiferum* and 63 to subgenus *Acacia*.

It is at once apparent that there are significant differences in the distributional ranges of the two subgenera. Subgenus *Acacia* extends far further north than subgenus *Aculeiferum* being found for the most part as far north as 30° N latitude except in Algeria and Morocco where the subgenus occurs even further north and in the Nile valley in Egypt where a species occurs in the Nile delta. Subgenus *Aculeiferum*, on the other hand, does not occur much north of 20° N latitude except in Egypt and more particularly in the Nile Valley. In the extreme south of the continent subgenus *Acacia* occurs to within 100 km of Cape Town while subgenus *Aculeiferum* has not succeeded in penetrating the south-west tip of the Cape Province and is also absent from the high country in Lesotho and the eastern Orange Free State. Both subgenera are absent from parts of the west coast of

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*Namibia

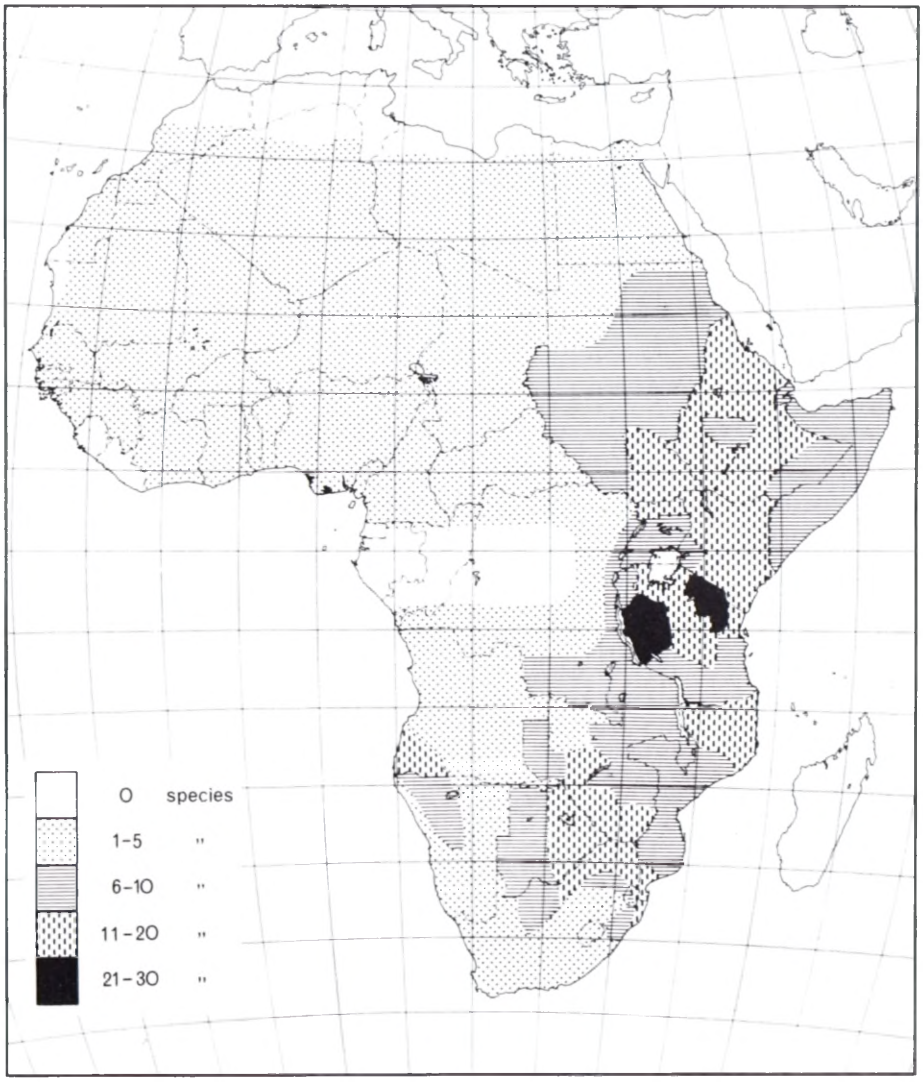

FIG. 5.—The general distribution of subgenus *Acacia* in Africa and an indication of the concentration of species over the distributional range of the subgenus.

South West Africa bordering the Atlantic Ocean and from part of western Mauritania. Although the range of distribution of some individual species in subgenus *Aculeiferum,* for example *A. ataxacantha,* is almost as extensive as that of some of the more widespread species in subgenus *Acacia* such as *A. sieberana* DC. (see Fig. 7), the total distributional range of subgenus *Acacia* greatly exceeds that of subgenus *Aculeiferum.* The fact that subgenus *Acacia* enjoys a wider range of distribution on the continent than does subgenus *Aculeiferum* suggests that the former has been able to occupy habitats, particularly the harsh habitats in the central Sahara and the high country of Lesotho, from which subgenus *Aculeiferum* has been excluded. Most (? all) members of subgenus *Acacia* are polyploid while those of subgenus *Aculeiferum* are diploid and the possibility exists that polyploidy has conferred greater genetic plasticity on subgenus *Acacia* which has enabled members of the subgenus to successfully occupy a greater diversity of habitats. On the other hand, however, some of the climbing species in subgenus *Aculeiferum* have been successful in the forested areas of the continent, particularly in Zaire and in parts of tropical west Africa, in which subgenus *Acacia* is not represented. It would appear that the climbing habit, which is unknown in subgenus *Acacia,* has enabled members of subgenus *Aculeiferum* to exploit situations in forested areas where light penetrates to the ground. Subgenus *Acacia* is apparently absent from Liberia, Sierra Leone, Gabon, Equatorial Guinea and the densely forested areas in Zaire.

Apart from the exceptions noted above, the distribution of species in subgenera *Acacia* and *Aculeiferum* over the remainder of the continent is roughly similar although the number of species in individual areas within each subgenus varies. The highest concentration of species in both subgenera occurs in tropical east and south-east Africa.

The pattern of distribution exhibited by *A. sieberana* (see Fig. 7) is fairly representative of that shown by a number of widespread species in both subgenera, extending from Senegal in the west to the Sudan or Ethiopia in the north-east and down tropical east Africa through Kenya, Uganda and Tanzania skirting around the forested areas of central Zaire with one arm swinging westwards through Zambia, south-east Zaire, Zimbabwe and Botswana to Angola and northern South West Africa and another arm continuing southwards through Mozambique, the Transvaal and Swaziland into Natal. The two arms of distribution approximate roughly to the temperature and rainfall belts.

The distribution of species within some of the individual countries is now considered in more detail.

Two species, both members of subgenus *Acacia,* have been recorded from southern Morocco in the extreme north-west of the continent, namely, *A.*

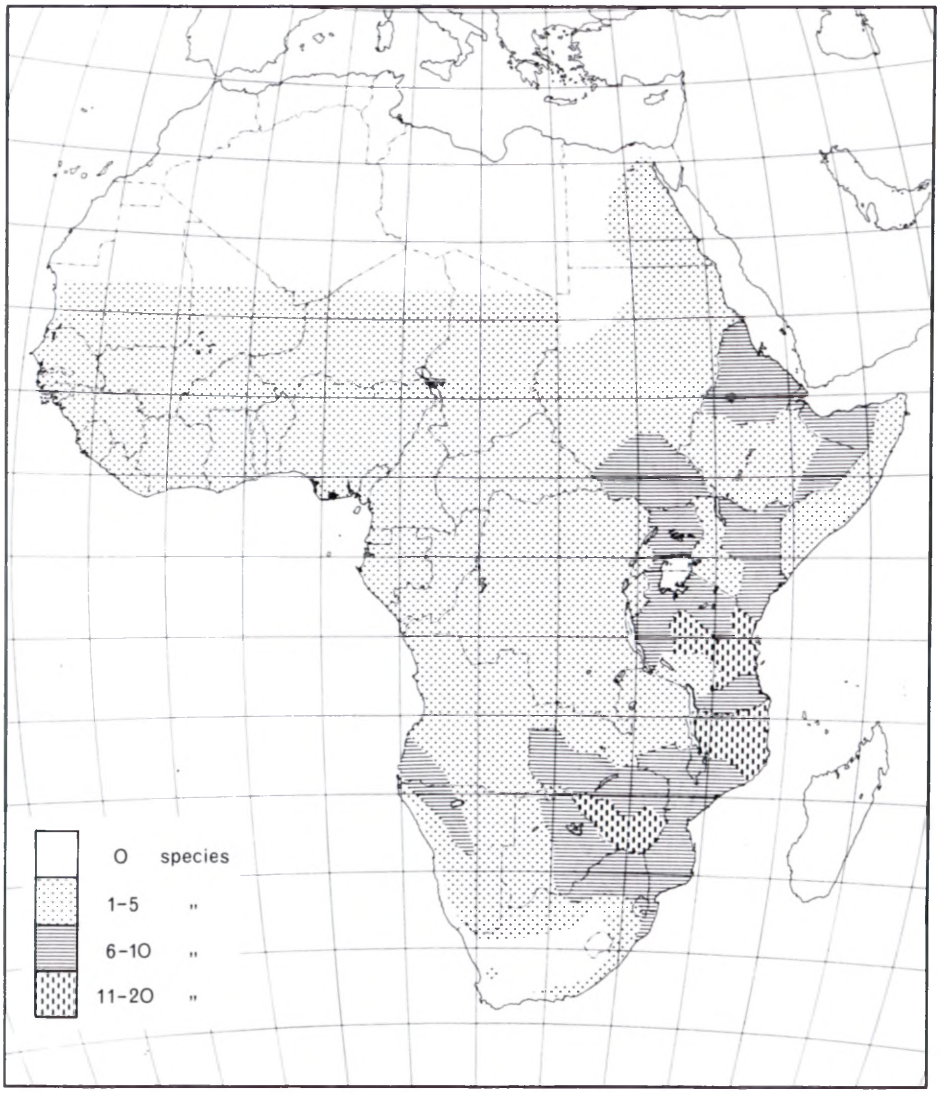

FIG. 6.—The general distribution of subgenus *Aculeiferum* in Africa and an indication of the concentration of species over the distributional range of the subgenus.

seyal Del. and *A. gummifera* Willd. While *A. seyal* is widely distributed in Africa, *A. gummifera* is endemic in Morocco and has a very restricted distribution within the country. Morocco is the only country in north or west Africa, which has an endemic *Acacia* species. Although *A. gummifera* is adapted to a Mediterranean climate Quezel (1979) considered it to be of tropical origin and represent a 'differentiated vestige' which has been 'in situ' since the Pleistocene. *A. gummifera* is most closely allied to the tropical and widespread *A. nilotica* (L.) Willd. ex Del. and possibly arose from *A. nilotica* stock that became isolated as a result of climatic vicissitudes which have largely eliminated the tropical element from Mediterranean Africa.

The northern limit of *Acacia* in Libya and Algeria corresponds with the northern limit of distribution of *A. tortilis* (Forssk.) Hayne subsp. *raddiana* (Savi) Brenan. The Sahara is inhabited by very few *Acacia* species and, according to Quezel (1979), the evidence indicates that they penetrated into the Sahara only at the end of the last pluvial, probably after several previous phases of extension, but did not reach the Mediterranean regions because of their thermal demands.

In Egypt most species occur in a zone along the Nile River with fewer species occurring in the adjacent desert areas. *A. nilotica* follows the course of the Nile into the delta itself.

Thirty-one species, none of which is endemic, occur in the Sudan. The highest concentration of species occurs in the south-east where the territory adjoins Ethiopia, Kenya and Uganda, and the numbers decrease quite sharply in the south-west, central and northern areas. The genus is very poorly represented in the north-western portion of the country.

Ethiopia, with its diversified topography, has 43 species, the second highest number among the African countries. In addition to being rich in species, Ethiopia is an important area of speciation for *Acacia*, each subgenus having three endemic species. Among the endemics are *A. walwalensis* Gilliland and *A. pseudonigrescens* Brenan & J. H. Ross, two very distinctive species confined to the Ogaden. The highest number of species occurs in the north-east adjacent to the Red Sea, but the Harar Province and Ogaden are also rich in species. *A. reficiens* Wawra has a very disjunct distribution (see Fig. 8) : subsp. *misera* (Vatke) Brenan occurring in north-eastern Uganda, south-eastern Sudan, Kenya, eastern Ethiopia and Somalia and subsp. *reficiens* occurring in south-western Angola and northern South West Africa, the species providing a good example of the well known distributional discontinuity between the more arid areas of South West Africa and the north-east Horn of Africa. Verdcourt (1969) and De Winter (1971) provided examples of disjunctions in other

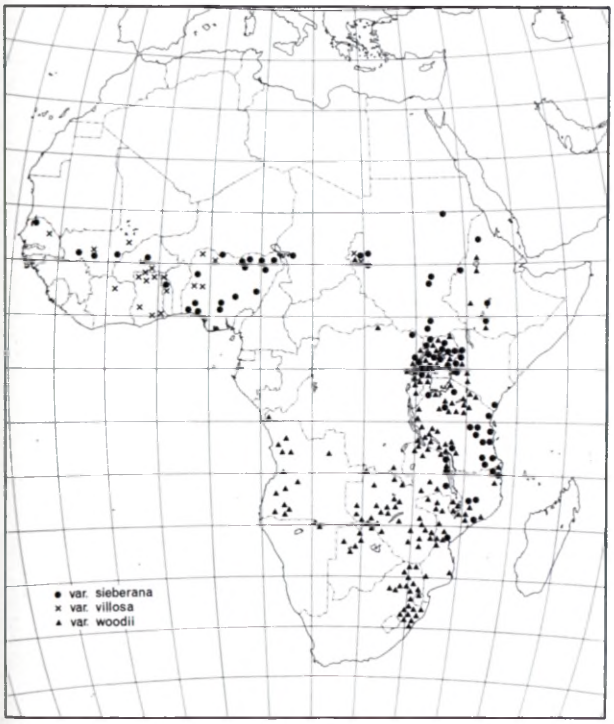

FIG. 7.—The known distribution of *Acacia sieberana*.

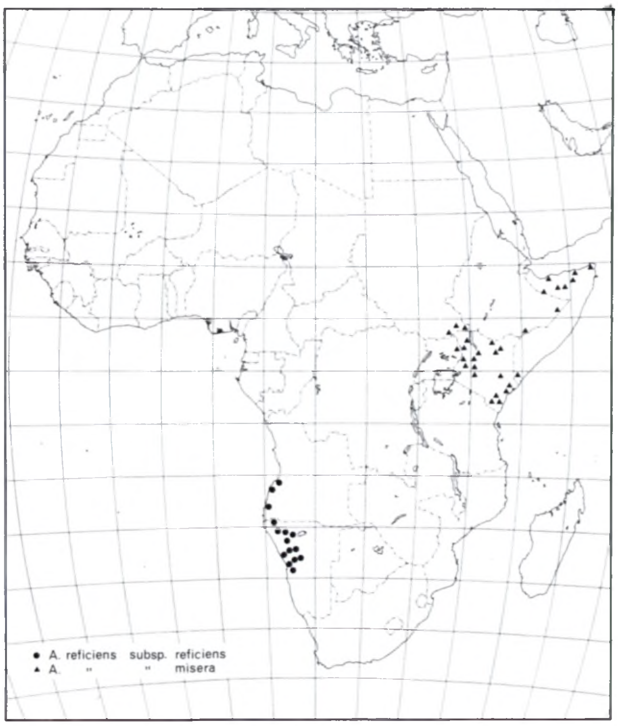

FIG. 8.—The known distribution of *Acacia reficiens*.

genera and families which furnish evidence of a former arid corridor across the continent from the north-east to the south-west. Conditions for direct migration were probably best when arid phases of the Pleistocene were at a maximum and distances between the arid zones were least or possibly when a continuous arid belt extended across Africa from the north-east to the south-east. The distribution of *A. stuhlmannii* Taub. provides a less extreme example of the disjunct distribution illustrated by *A. reficiens,* while some species have a more or less continuous distribution from the north-east to the south-west.

Somalia has a remarkable flora and the *Acacia* species are no exception. Although only 32 *Acacia* species have been recorded from Somalia, nine are endemic (seven in subgenus *Aculeiferum* and two in subgenus *Acacia*). Somalia has been an important centre of speciation in the '*A. senegal* (L.) Willd. complex' where six very distinctive endemic taxa have arisen, namely, *A. ankokib* Chiov., *A. caraniana* Chiov., *A. cheilanthifolia* Chiov., *A. ogadensis* Chiov., *A. somalensis* Vatke and *A.* sp. near *A. somalensis. A. zizyphispina* Chiov., another member of the '*A. senegal* complex', although not endemic in Somalia itself, has a very restricted distribution in southern Somalia and in the Ogaden in Ethiopia. *A. bricchettiana* Chiov. (subgenus *Acacia*) is similarly confined to the Ogaden region in Somalia and Ethiopia. Several other species, for example *A. condyloclada* Chiov., yet another member of the '*A. senegal* complex', and *A. edgeworthii* T. Anders. (subgenus *Acacia*) are confined to Ethiopia, Somalia and the Northern Frontier Province of Kenya (*A. edgeworthii* also occurs on Socotra), while *A. turnbulliana* Brenan is confined to Somalia and the Northern Frontier Province of Kenya. *A. leucospira* Brenan, another endemic, is a very distinctive species with minute laterally compressed leaflets which are reminiscent of those of *A. haematoxylon* in southern Africa (see Fig. 9). Small laterally compressed leaflets are unknown elsewhere amongst the African species but *A. leucospira* and *A. haematoxylon* are not closely related. The Horn of Africa has been an important centre of speciation in *Acacia.*

Kenya, with 42 species, has only one endemic species, namely, *A. thomasii* Harms, a member of the '*A. senegal* complex', while *A. paolii* Chiov. subsp. *paucijuga* Brenan is endemic in the north-west of the country. The poverty of endemism in Kenya is in marked contrast to Tanzania. The distribution of *Acacia* in Kenya according to the provinces recognized in the Flora of Tropical East Africa is as follows: K1, Northern Frontier : 26 species; K2,

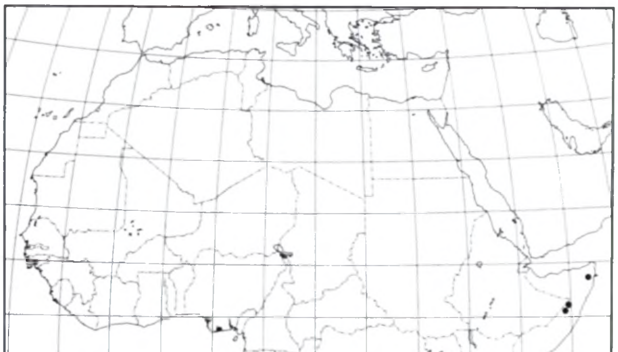

FIG. 9.—The known distributions of *Acacia leucospira* and *A. haematoxylon*.

Turkana : 18 species; K3, Rift Valley : 15 species; K4, Central : 23 species; K5, Nyanza : 12 species; K6, Masai : 19 species; K7, Coast : 23 species. These figures illustrate the richness of the Northern Frontier Province, mainly because of the presence there of the Somali element, the central and Coastal Provinces, and the relative poverty of western Kenya.

Uganda, with 27 species, has far fewer species than either Kenya or Tanzania and the relative poverty evident in western Kenya is again evident over much of Uganda. The distribution of *Acacia* in Uganda according to the provinces recognized in the Flora of Tropical East Africa is as follows: U1, Northern : 24 species; U2, Western : 11 species; U3, Eastern : 16 species; U4, Buganda : 13 species. The Northern Province which is well watered in the west is by far the richest province.

Tanzania, with 50 species, has significantly more species than any other country and both subgenera *Acacia* and *Aculeiferum* are best represented in Tanzania. In addition, ten of the species, three in subgenus *Aculeiferum* and seven in subgenus *Acacia,* are endemic in Tanzania. The distribution of *Acacia* in Tanzania according to the provinces in the Flora of Tropical East Africa is as follows: T1, Lake : 23 species; T2, Northern : 28 species; T3, Tanga : 28 species; T4, Western : 29 species; T5, Central : 27 species; T6, Eastern : 21 species; T7, Southern Highlands : 14 species; T8, Southern : 16 species. These figures illustrate the relative poverty of *Acacia* species in the Southern Highlands and Southern Province in contrast to the remainder of the country over which the species are fairly evenly spread. Tanzania has been an important centre of speciation in the '*A. drepanolobium* Harms ex Sjöstedt complex', a complex of species with characteristically enlarged stipular spines ('ant-galls'). In addition to the widespread *A. drepanolobium,* six species with enlarged stipular spines, namely *A. bullockii* Brenan, *A. burttii* Bak. f., *A. erythrophloea* Brenan, *A. malacocephala* Harms, *A. mbuluënsis* Brenan and *A. pseudofistula* Harms, are endemic in Tanzania and two of them, *A. bullockii* and *A. erythrophloea,* are endemic in the Western Province. The Western Province is outstanding on account of the number of endemics found within it: seven of the ten endemic *Acacia* species in Tanzania are found within the Western Province although only the above two species are confined to it. *A. taylorii* Brenan & Exell, a member of the '*A. pennata* complex' with scattered recurved prickles, is endemic along the coast in the Southern Province towards the Mozambique border, *A. tephrodermis* Brenan in the same complex is endemic in the Eastern Province and *A. latistipulata* Harms, yet another member of the complex, occurs from central Tanzania to central Mozambique. *A. ancistroclada* Brenan, although not endemic in Tanzanzia itself, has a restricted distribution in north-east Tanzania and south-east Kenya. *A. stuhlmannii* has a discontinuous distribution being recorded from Ethiopia, Somalia, Kenya and northern and central Tanzania in the north and from Zimbabwe, Botswana and the Transvaal in the south.

Zaire illustrates very well the point made earlier that *Acacia* species are not spread uniformly throughout a country. Twenty-four species are recorded from Zaire but the great majority are confined to the mainly wooded grasslands of the Ubangi-Uele, Lac Albert, Lacs Edouard et Kivu, Bas-Katanga and Haut-Katanga regions (phytogeographical regions used in Flore du Congo, du Rwanda et du Burundi) in the north, north-east, east and south-east respectively. Only four species, *A. kamerunensis* Gandoger, *A. ciliolata* Brenan & Exell, *A. pentagona* (Schumach.) Hook. f. and *A. lujae,* all climbing species in subgenus *Aculeiferum,* occur in the Forestier Central region. *A. lujae* is the only endemic *Acacia* species in Zaire. *A. lujae* seems more closely related to *A. kraussiana,* which is endemic along the coast in southern Mozambique and Natal and from which it is separated by a wide interval, than it is to any members of the '*A. pennata* complex' (see Fig. 10).

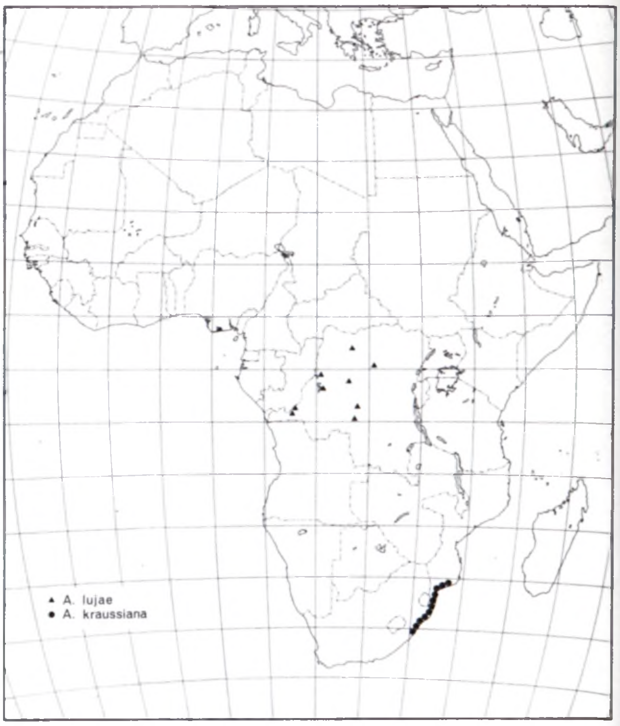

FIG. 10.—The known distributions of *Acacia lujae* and *A. kraussiana.*

Acacia is very poorly represented in Congo Brazzaville, Cabinda, Gabon and Equatorial Guinea, the sole member of the genus in each of the last three countries being a climbing member of subgenus *Aculeiferum.* In contrast to tropical east Africa, the genus is generally poorly represented in tropical west Africa.

Mozambique, with 40 species, has only one endemic species, namely *A. torrei* Brenan, a member of the complex with glandular glutinous pods which is centred on the Transvaal in South Africa. Although not endemic in Mozambique itself, a number of other species occurring in Mozambique have restricted distributions outside the country. *A. latistipulata* and *A. kraussiana* have already been alluded to but another example is *A. eriocarpa* Brenan whose distribution extends from Mozambique into eastern Zambia and central and western Zimbabwe. It is not clear whether or not *A. rovumae* Oliv. occurs in Mozambique as there are no definite records of the species from the territory. The type locality of *A. rovumae* was given as 'Rovuma Bay' without any indication of whether it was collected from the north or south side, crucial information as the Rovuma river forms the boundary between Mozambique and Tanzania. The absence of any definite records of the species from Mozambique suggests that it does not occur in the territory. The distribution of *Acacia* in Mozambique according to the provinces recognized in Flora

Zambesiaca is as follows: Niassa : 22 species; Zambezia : 16 species; Tete : 21 species; Manica e Sofala : 20 species; Sul do Save : 17 species; Lourenco Marques : 23 species. The highest numbers of species occur in the extreme north and south of the country and in the Tete province.

Of the 38 species occurring in Zimbabwe only *A. chariessa* Milne-Redhead, which is almost always found on serpentine soils, is endemic. Vegetation growing on serpentine soils often shows stunting or depauperation (Wild, 1974) and *A. chariessa* often looks superficially like a diminutive form of the widespread *A. ataxacantha,* although differing from it in several significant respects. The distribution of *Acacia* species in Zimbabwe according to the provinces recognized in Flora Zambesiaca is as follows: North : 19 species; East : 17 species; Central : 15 species; West : 27 species; South : 27 species. The greatest numbers of species occur in the south and west, the numbers there being increased by the presence of several members of the complex with glandular glutinous pods, namely *A. borleae* Burtt Davy, *A. exuvialis* Verdoorn, *A. nebrownii* Burtt Davy and *A. permixta* Burtt Davy, and species such as *A. erioloba* E. Mey. and *A. luederitzii* Engl. which favour dry woodland and often occur on the Kalahari sands.

No endemic species occur in Zambia, Malawi or Botswana. The southern province of Zambia, which to some extent represents a northern extension of the western province of Zimbabwe, is by far the richest province, while the western province with only six species is the poorest. The north and south-east provinces of Botswana each have 23 species but the genus is poorly represented in the arid south-west province where only 9 species occur.

The highest number of species in South West Africa occurs in the north-west and the highest number in Angola in the south-west in the Huila, Mossamedes and Benguela Districts. Two of the 23 species in South West Africa, namely *A. montis-usti* Merxm. & Schreiber and *A. robynsiana* Merxm. & Schreiber, are endemic in the north-west and two of the 25 species in Angola, *A. antunesii* Harms and *A. quintanilhae* Torre, are endemic in the south-west. While both endemics in South West Africa are members of subgenus *Aculeiferum,* the endemics in Angola both belong to subgenus *Acacia.* In addition to these endemics with narrow distributional ranges, *A. hebeclada DC.* subsp. *tristis* Schreiber is confined to much the same area in north-western South West Africa and south-western Angola. Reference has already been made to the discontinuous distribution shown by *A. reficiens* but *A. mellifera* (Vahl) Benth. subsp. *mellifera* also has a disjunct distribution occurring in northern South West Africa and south-western Angola (Mossamedes and Benguela Districts) in the south and in Tanzania and territories to the north. The number of *Acacia* species in Angola falls away from the south-west to the north and east particularly towards the forested areas in the north although *A. welwitschii* Oliv. subsp. *welwitschii* is endemic in northern Angola. South-western Angola and north-western South West Africa (with the exception of a narrow strip along the coast from which the genus is absent) appear to be one of the more important centres of speciation in *Acacia* in southern tropical Africa.

The southern limit of distribution of the genus in Africa occurs in the Cape Province in South Africa and, as one would expect, the number of species in South Africa declines rapidly to the south particularly along the east coast. Twenty-one species, all of which occur in Zululand and Tongaland in the north, are recorded from Natal. However, impoverishment to the south in Natal is fairly rapid as a number of species reach their southern limit of distribution in Natal. Of the twenty-one species which occur in Tongaland and Zululand in the north, only thirteen occur south of the Tugela River, and of these thirteen only five species extend south of the Umtamvuna river into Transkei. The number of species in Natal also falls away fairly rapidly with increasing altitude towards the interior and the widespread *A. karroo* Hayne is the only species in Lesotho. The majority of species in Swaziland occur in the lowveld in the east with fewer species in the higher areas. The Transvaal, with 35 species, has the highest number of species of all of the provinces in South Africa. Once again, the majority of species occur in the lowveld in the east and in the north with fewer species occurring in the highveld region with its colder winters. A number of species favouring sandy soils occur in the western portion of the province. The complex of species with glandular glutinous pods appears to be centred in the Transvaal where six of the seven species within the complex are found. Only *A. torrei,* which is endemic in Mozambique, is absent. Eleven species occur in the Cape Province one of which, *A. redacta* J. H. Ross, is endemic. *A. redacta* is an extremely interesting species in many respects showing no close affinity with any other species and the possibility exists that it is not an *Acacia* at all but is referable to a new monotypic genus. Although not confined to the northern Cape, *A. haematoxylon* has a restricted distribution outside the province occurring in the extreme south-west of Botswana and in the eastern portion of South West Africa, while the *A. erioloba* × *A. haematoxylon* hybrid is confined to the northern Cape. *Acacia* is best represented in the northern Cape on the Kalahari sands and only *A. karroo* is common over much of the southern and western portion of the province.

TABLE 2.—The countries within which endemic *Acacia* species occur and the number of endemic species within each country

Country	No. of species in subgenus *Acacia*	No. of species in subgenus *Aculeiferum*	Total no. of species
Morocco	1	0	1
Ethiopia	3	3	6
Somalia	2	7	9
Zaire	0	1	1
Kenya	0	1	1
Tanzania	7	3	10
Angola	2	0	2
South West Africa/Namibia	0	2	2
Mozambique	1	0	1
Zimbabwe	0	1	1
South Africa-Cape Province	1	0	1

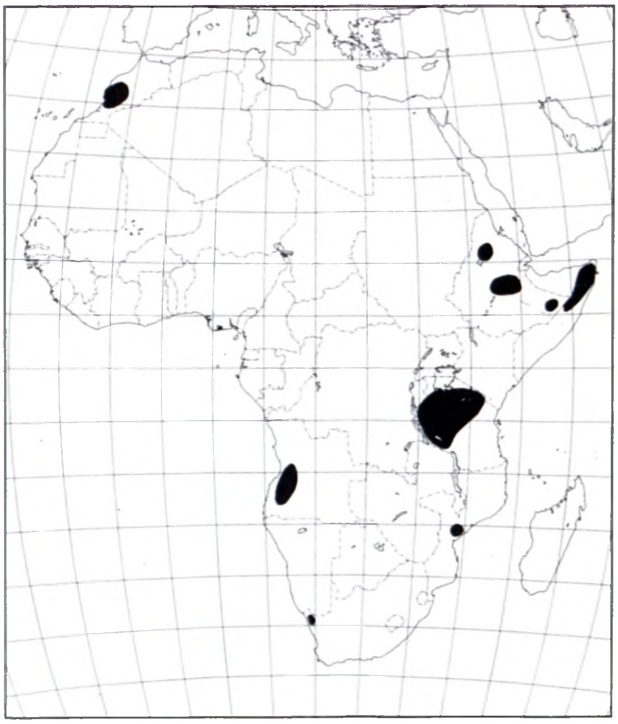

FIG. 11.—The distribution of the narrow endemics within subgenus *Acacia* referred to in Table 2.

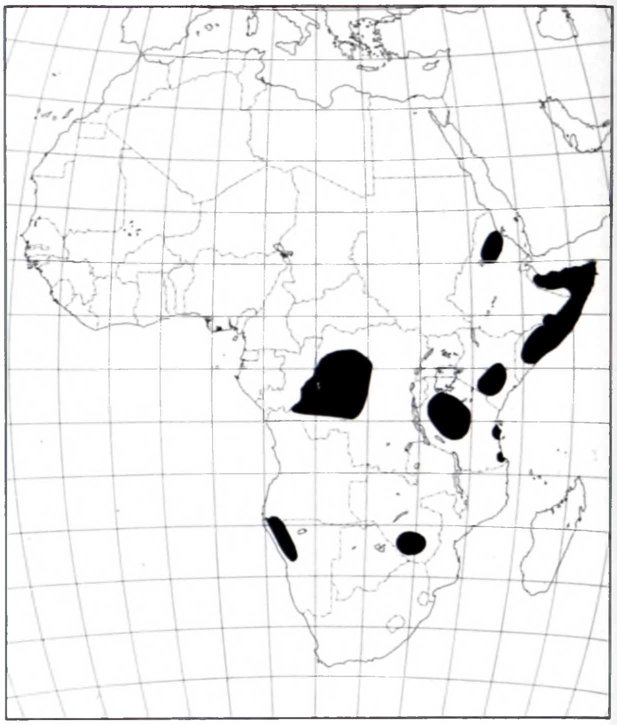

FIG. 12.—The distribution of the narrow endemics within subgenus *Aculeiferum* referred to in Table 2.

The countries in which endemic species occur and the number of endemics recorded within each are given in Table 2.

Because of the variation in the size of individual countries and because no country has an even spread of endemism, the number of endemic species per country is of limited value alone. For example, Tanzania with ten endemic species out of a total of fifty species has a greater number of endemics than Somalia with nine endemics out of a total of 32 species, but the proportion of endemics in Somalia is greater. However, despite the limitations, the information in Table 2 is nevertheless fairly instructive.

Table 2 shows that the highest numbers of endemic species occur in Tanzania, Somalia and Ethiopia in tropical east and north-east Africa. Interestingly, the highest number of endemic species in subgenus *Acacia* occur in Tanzania while the highest number of endemics in subgenus *Aculeiferum* occur in Somalia. Morocco is the only country in north or west Africa which has an endemic species. Although the Sudan has one more species than Somalia, the Sudan has no endemic species while Somalia has nine, and Ethiopia with one more species than Kenya has six endemics and Kenya only one. The distribution of the narrow endemics within each subgenus referred to in Table 2 are illustrated in Figs 11 and 12.

The endemism in the genus *Acacia* in Africa is shown in Table 3.

The high proportion of species endemic in one country in contrast to the much lower figures for those species endemic in two or three countries emphasizes the prevalence of species with narrow ranges.

It is instructive to briefly compare the distribution of the African *Acacia* species in Fig. 4 with the phytogeographical regions of Africa (see Fig. 13). Fig. 13 is a slightly simplified version adapted from the scheme accepted by Brenan (1979) which was itself based on the earlier works of Wickens (1976), White (1965) and Chapman & White (1970). Wickens (*l.c.*) recognized eight Regions in Africa, three of which were themselves divided into domains.

The Sudano-Zambezian Region, which is characterized by a strong seasonal climate, corresponds to the tropical savanna and is by far the largest Region in Africa extending north and south of the equator but physically continuous by a relatively narrow connection in east Africa. To the north it is bounded by the deserts and semideserts of the Sahara, in the centre it circumscribes the limits of the forests of the Guineo-Congo Region, and in the south it extends to the deserts and semideserts of the Karoo Namib Region and the Cape Region. As is to be expected, the majority of *Acacia* species occur within this region.

1. The Sahelian Domain extends from Mauritania and Senegal on the Atlantic in the west to the Red Sea

TABLE 3.—Endemism in the genus *Acacia* in Africa

Region	No. of species	% of the total
Endemic in 1 country	35	30.43
Endemic in 2 countries	10	8.69
Endemic in 3 countries	8	6.95
Occurs in more than 3 countries but endemic in continental Africa	46	40.00
Distribution extends beyond the confines of continental Africa	16	13.92

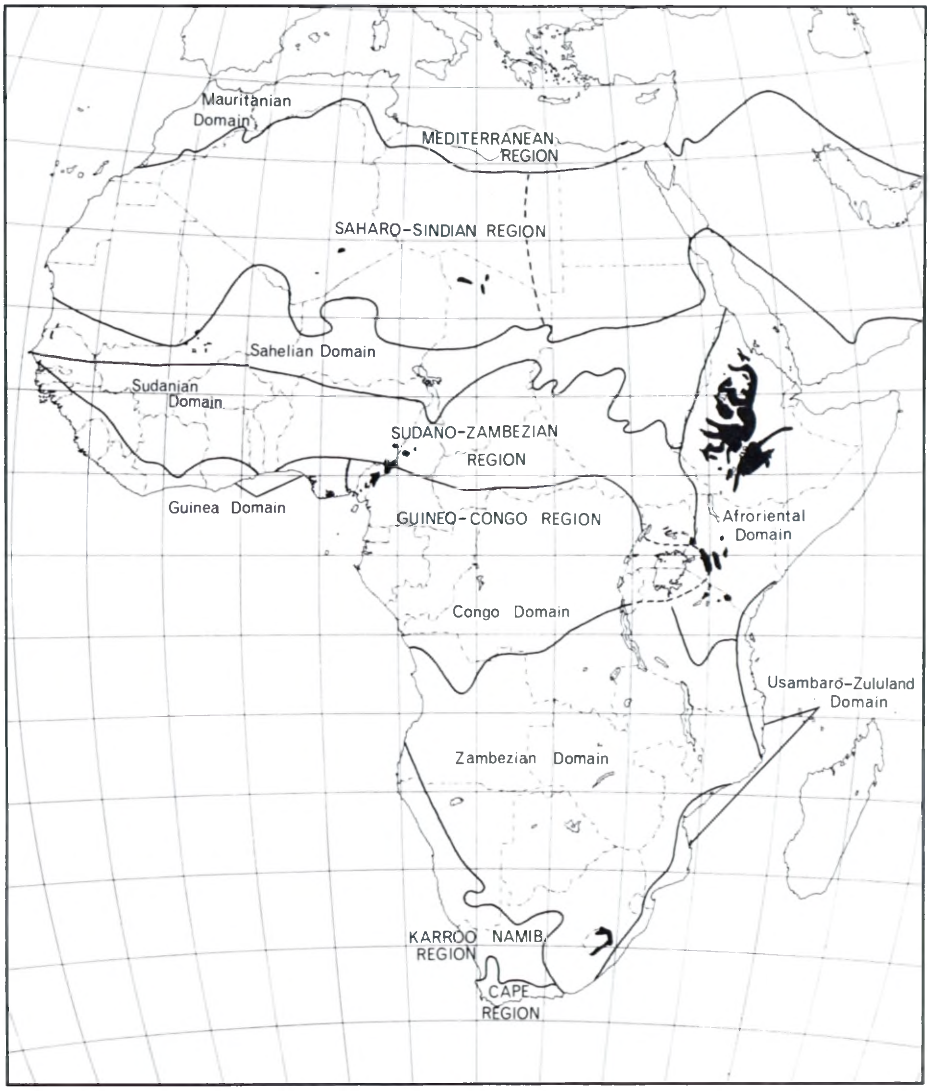

FIG. 13.—The phytogeographical regions and domains of Africa (After Brenan, 1979).

coast of the Sudan in the east forming a narrow belt bounded on the north by the Saharo-Sindian Region. The domain thus separates the desert flora of the Sahara from the deciduous woodlands and other communities of the Sudanian domain. The southern boundary of the Sahelian domain largely corresponds to the southernmost extent of the Pleistocene sand invasion (Wickens, 1976). A number of widespread species such as *A. tortilis, A. seyal, A. ehrenbergiana* Hayne and *A. nubica* Benth. are characteristic of this domain but no endemic species occur within it.

2. The Sudanian Domain extends from Senegal to the eastern border of the Sudan and forms a wide belt bounded to the north by the former domain and to the south by the Guineo-Congo Region. *Acacia* is well represented within the deciduous woodlands and savannas of this domain, most of the species occurring within it being fairly widespread in tropical Africa and some extending to Asia. The Sudanian domain is much drier than the Zambezian domain and its greater aridity has been largely responsible for the marked differences between the two domains, the impoverishment of the flora of the former, and the asymmetrical distribution of savanna-type vegetation north and south of the equator (White, 1965).

3. The Afro-oriental Domain, which includes the 'Horn of Africa' and extends southwards into Tanzania, contains by far the greatest number of *Acacia* species and the greatest number of endemics illustrating the importance of this area for speciation in *Acacia*.

4. The Zambezian Domain consists of the remainder of the Sudano-Zambezian Region lying to the south of the Afro-oriental domain and is also rich in species and endemics. The main centre of endemism within this domain is north-western Tanzania while a secondary centre occurs in the area occupied by Zimbabwe, Botswana, south-western Mozambique and the northern Transvaal.

The Guineo-Congo Region represents the main evergreen or partly evergreen forests of Africa extending from Senegal in the west, southwards to Angola and eastwards to Ruwenzori. The climate is characteristically one of high even temperatures and rainfall more or less throughout the year. As is to be expected of a genus which is intolerant of low light intensities, *Acacia* species are not very well represented within this region tending to occupy forest margins or clearings where openings in the canopy permit light to penetrate. The climbing species in subgenus *Aculeiferum* tend to be better represented in the forested region than the trees and shrubs of subgenus *Acacia*. Three domains are recognized within the region, namely, the Guinea, Congo and Usambaro-Zululand domains. The Usambaro-Zululand domain, which consists of the scattered relics of rainforest along or near the east coast of Africa, has the highest number of species of the three domains and five endemics, all members of subgenus *Aculeiferum,* occur within it. One of the endemics, *A. kraussiana* occurring in Natal and southern Mozambique, seems closely related to *A. lujae,* the only endemic species in the Congo domain. Neither the Congo nor the Guinea domain is very rich in *Acacia* species which is not surprising as these are the best forested domains in the region.

Acacia is absent from the Afromontane Region which corresponds to the Montane Forest and Ericaceous belts of the tropical mountain regions and from the Afroalpine Region which is the zone above the Ericaceous belt of the former Region.

The Saharo-Sindian Region is a region of desert and semidesert to the north of the Sahelian domain extending from western Sahara, Mauritania and southern Morocco eastwards across Sinai to India. The climate is characterized by high temperatures, often with extreme diurnal fluctuations, and low and often irregular rainfall. A few widespread species such as *A. tortilis, A. seyal, A. ehrenbergiana* and *A. nilotica* occur in parts of the region and there is a local concentration of species in the Nile valley. According to Quezel (1979), the Sahelian species penetrated into the Sahara only at the end of the last pluvial but did not reach the Mediterranean Region because of their thermal demands.

The Mediterranean Region, characterized by hot dry summers with mild winters during which much of the rain falls, is the northernmost fringe of Africa bounded in the south by the Saharo-Sindian Region and in the north by the Mediterranean. *A. gummifera* is endemic in Morocco and a few species occur in the Nile valley but, apart from these, *A. tortilis* is possibly the only other species to occur in parts of the Region.

The Cape Region, dealt with in detail by Goldblatt (1979), occupies the extreme south-west of the continent and has a Mediterranean type climate in which the genus *Acacia* is unimportant and represented by only a few species. *A. karroo* and *A. caffra* are the most widespread species within the Region.

The Karoo-Namib Region occupies the interior of the Cape Province, the western portion of South West Africa and extends into south-western Angola. Except for the southern portion of the Cape Province and isolated pockets along the Atlantic coast, *Acacia* is fairly well represented throughout the area, particularly in northern South West Africa and south-western Angola. *A. erioloba, A. hereroensis* Engl., *A. karroo, A. tortilis* and *A. mellifera* are characteristic of many areas. Four endemic species occur in northern South West Africa and south-western Angola, an important local centre of speciation in *Acacia.*

RELATIONSHIP BETWEEN THE AFRICAN AND AMERICAN SPECIES

The currently accepted sequence of events which marked the begining of the fragmentation of West Gondwanaland and the separation of the African and South American plates was outlined by Raven & Axelrod (1974) and is summarized briefly here. Separation of the African and South American plates started about 127 million years ago with the final marine connection between the North and South Atlantic occurring about 100 million years ago. The two continents remained in close proximity with only a narrow strait separating the present Gabon from north-eastern Brazil for another 10 million years. By the end of the Cretaceous, about 65 million years ago, the two continents are thought to have been separated at their closest points by about 800 km although they are said to have been linked by numerous volcanic islands. South America moved away from Africa and gradually converged with North America becoming equidistant between the two early in the Eocene about 50 million years ago. South America subsequently became more isolated from Africa and closer to North America until a direct land connection between North and South America occurred in the Pliocene 7–5 million years ago. This sets the background against which the African and American species must be seen.

There is no evidence and it seems unlikely that *Acacia* or its prototype had differentiated when Africa separated from South America about 100 million years ago, and it is not clear whether the genus crossed the Atlantic in the late Cretaceous about 65 million years ago (by which time the three subfamilies of Leguminosae are known to have been differentiated) when the two continents were separated but thought to have been linked by numerous volcanic islands, or whether the genus was carried over the Atlantic in Paleocene or Eocene time. From what is known or can be inferred about its history and present distribution patterns Raven & Axelrod (1974) presume that Mimosoideae migrated between Africa and South America during or prior to the Paleocene when the Atlantic was much narrower than at present, while Thorne (1978) is of the opinion that migration could have occurred in the late Cretaceous, Paleocene or Eocene. The evidence suggests that only limited migration occurred between these continents after the Paleocene.

Both subgenera *Acacia* and *Aculeiferum* are present in Africa and in America. However, the representation of subgenus *Aculeiferum* in each continent is different: sections *Monacanthea* and *Aculeiferum* occurring in Africa and sections *Monacanthea* and *Filicinae* in America, i.e. *Filicinae* is absent from Africa and *Aculeiferum* is absent from America. The position of *A. willardiana* Rose, which has a horizontally flattened petiole and is endemic to the west coast of North America (Mexico), is uncertain and opinions differ as to whether it should be referred to subgenus *Aculeiferum* or subgenus *Heterophyllum.* Vassal & Guinet (1972) included *A. willardiana* in subgenus *Heterophyllum* while Pedley (1975) argued that the species could be accommodated without difficulty in subgenus *Aculeiferum* as it showed relationships to American species of the subgenus. In support of their earlier contention that *A. willardiana* belonged to subgenus *Heterophyllum* Guinet & Vassal (1978) pointed out that the seed of *A. willardiana* contains the amino-acid 'willardine' (Gmelin, 1959) which has also been recorded from the Australian species *A. podalyriifolia* A. Cunn. ex G. Don and *A. dealbata* Link both of which are members of subgenus *Heterophyllum.* However, 'willardine' is also present in the Asian *A. modesta* Wall., a member of subgenus *Aculeiferum* (Evans *et al,* 1977). The available evidence suggests that *A. willardiana* is in fact referable to subgenus *Aculeiferum.*

No species in section *Monacanthea* is common to Africa and the Americas although some tropical species on each continent show close similarities, for example, *A. brevispica* Harms, *A. schweinfurthii* Brenan & Exell, *A. pentagona* (Schumach.) Hook. f. and allies in Africa and *A. riparia* H. B. K. and *A.*

paniculata Willd. in tropical America and the West Indies.

Although subgenus *Acacia* is well represented in both Africa and America no species is common to Africa and America; *A. farnesiana* is not indigenous in Africa having been introduced and subsequently become naturalized in some areas. *A. sieberana* in Africa shows some relationship to the American *A. macrantha* Humb. & Bonpl. ex Willd., an observation noted by Bentham (1875).

A feature shared by some species of subgenus *Acacia* in central America and in Africa is the production of swollen stipular spines and a mutualistic association of these spines with several species of ants, but the degree of mutualism in each continent differs. Some of the neotropical acacias with swollen spines, commonly referred to as swollen thorn acacias or 'bulls-horn acacias', have spicate inflorescences and others capitate inflorescences and the species do not appear to constitute a close phyletic unit, yet they share many adaptive ecological and morphological traits and, according to Janzen (1974), provide outstanding examples of evolutionary convergence. Janzen (*l.c.*) observed that the species of obligate acacia-ants in the New World are not specific to a swollen-thorn *Acacia* species, but rather to its life form. As an example he cited *A. collinsii* Safford, which has at least eight species of obligate acacia-ants living in it over its range from Mexico to Columbia, all of which also live in other swollen-thorn acacias.

The acacias with swollen spines in central America do not appear to occur south of Venezuela or Columbia (Janzen, 1966). The mutualistic interaction between ants and acacias in central America has been detailed in a series of papers by Janzen (1966, 1967a, 1967b) and subsequently summarized (Janzen, 1969a). Janzen (1969a) noted that the central American acacias with swollen stipular spines differ from the other *Acacia* species in the area in having:

1. partially hollow spines which are occupied by ants.
2. modified leaflet tips called Beltian bodies which constitute the primary source of protein and oil for the ant colony.
3. greatly enlarged foliar nectaries which supply the sugar requirements for the ant colony.
4. all-year-round leaf production on most individuals which provides a relatively constant source of food for the ants.
5. an absence of chemical and structural traits that protect other acacias from most herbivores in the environment. The ants are functionally analagous to the chemicals released by some plants in their competitive interactions with other plants; like these chemicals the ants are 'produced'at a metabolic cost to the plant (Janzen 1969b). Janzen (1966) expressed the view that the swollen-thorn acacias of central America have lost, apparently through evolutionary change, their ability to withstand the phytophagous insect damage and competitive pressure of neighbouring plants without the protection of the obligate acacia-ants.

Janzen concluded that those *Acacia* species with ants do not normally duplicate their defence systems and thus do not make toxic compounds such as cyanogenic glycosides in quantity. One exception he noted was *A. chiapensis* Safford which possesses both types of defence systems. Janzen (1974) concluded that *A. chiapensis* is a marginal host for obligate acacia-ants and in many features of growth and habit resembles non-ant acacias (Rehr *et al.,* 1973). However, Siegler *et al.* (1978) found specimens of *A. hindsii* Benth., a species inhabited by an obligate acacia-ant, in Oaxaca and Jalisco to be strongly cyanogenic which is another exception to Janzen's earlier observation.

The swollen-thorn acacias occur in the wettest areas of tropical central America. As the drier areas are approached the acacia cannot retain its leaves long enough to keep the ant colony alive and the unoccupied shoot does not survive to maturity because of insect damage. In cooler areas the growth of the acacia is slower and the ants are apparently insufficiently active in cool weather to deter the phytophagous insects and vertebrate browsers adapted to cool weather and thus the acacia receives more damage than it can tolerate and the ant colony starves to death owing to a lack of leaf products.

All of the central American swollen-thorn acacias have a sweet pulp around the seeds and the seeds are dispersed by birds. Janzen (1969a) noted that there appeared to be 'a selective pressure acting on all the swollen-thorn acacias that favours bird-dispersal of seeds'. The species of swollen-thorn acacia with the widest distributions are those whose seeds are most readily removed by birds while those with seeds that are less easily removed have more restricted distributions. The birds begin dispersal of seeds as soon as the pods are ripe which is important to plants that lose 60–100% of a particular seed crop through the predations of the larvae of Bruchidae. As the initial infestation usually destroys 40–80% of the seeds and all seeds remaining on a tree have usually been killed within two months of seed maturation, the rapid removal of the seeds by birds is possibly critical to the survival of the *Acacia* species.

Like the central American species, the African species with swollen stipular spines, commonly called 'ant-galls', do not consist of a group of closely related species. Most of the African 'ant-gall' acacias have white or pale yellowish white flowers in capitate heads but some have deep yellow flowers and two species have spicate inflorescences. The African *Acacia* species with swollen spines vary from those which are apparently partially ant-dependent to those which have no regular mutualistic association with ants.

Hocking (1970) investigated the East African swollen-thorn acacias and, although he worked on several different species, concentrated on *A. drepanolobium* Harms ex Sjöstedt which is probably the most ant-dependent African species. Hocking found that while *A. drepanolobium* can be grown to at least flowering stage in the absence of ants and probably the ants can be raised without the *Acacia,* in nature the association is essentially an obligate one as the ants and *A. drepanolobium* seldom persist independently. No more than 1% of the *A. drepanolobium* plants in the study area were found to be without ant associates. It follows that advantage must accrue to both parties so that these associations are also mutualistic as in the case of the New World *A. cornigera* L. (Janzen 1966, 1967b). However, although converging on the central American system, the association between *A. drepanolobium* and the ants has not reached the same degree of development as that in the neotropics.

Several species in the '*A. drepanolobium* complex' are associated with ants to a lesser extent. At the other extreme are a number of species with swollen spines, for example *A. luederitzii* Engl. var. *retinens*

(Sim) J. H. Ross & Brenan, which have no mutualistic association with ants, the ants and other insects merely taking advantage of the hollow spines as suitable domatia. The hollow spines in *A. luederitzii* var. *retinens* and in several other species are frequently unoccupied and often entire plants lack any enlarged spines.

The African acacias with swollen spines differ from the American swollen-thorn species in the following respects:

1. they lack Beltian bodies at the tips of the leaflets. Hocking (*l.c.*) suggested that the occurrence of Beltian bodies at the tips of the leaflets in the New World *Acacia* species may ensure a more uniform distribution of ants on the foliage and be an adaptation to an environment in which phytophagous insects are a relatively greater threat than browsing herbivores.
2. they lack all-year-round leaf production.
3. they are not confined to the wettest areas. On the contrary, in Africa they occupy areas which experience a pronounced dry season. Hocking (*l.c.*) suggested that the establishment of ants on the African acacias may improve their adaptation to a dry environment through the pruning out, by the ants, of the axillary buds of the swollen stipules.
4. the extra-floral nectaries do not appear to be developed to the same extent.
5. the seeds are not surrounded by sweet pulp.
6. the seeds are not distributed by birds. In Africa some of the large herbivorous mammals rapidly disperse the seed of certain *Acacia* species, for example *A. tortilis* (Forssk.) Hayne, away from the parent plant and in so doing play a similar rôle to that played by birds in central America.

It is not known whether or not the African species lack the chemical and structural traits that protect the American acacias from most herbivores in the environment and the matter needs investigation.

The genera of ants involved in the mutualistic association with species of *Acacia* in Africa and in America differs as one might expect. *Pseudomyrmex* is the important ant genus in America while *Crematogaster* is the most important genus in Africa. The development of swollen spines and the mutualistic association with ants in Africa and in America appears to have taken place independently in each continent and represent an example of convergent evolution.

RELATIONSHIP BETWEEN THE AFRICAN AND THE MADAGASCAN AND MASCARENE SPECIES

Madagascar was connected with Africa into the mid-Cretaceous when it was situated against Tanzania-Kenya about 15° N of its presenty position (Axelrod & Raven, 1978). Madagascar then formed part of the now largely submerged Mascarene Plateau which joined India in the east into the late Cretaceous. Precisely when Madagascar-India separated from Africa is still not certain but it could have occurred at any time between the mid- and late Cretaceous. India separated from the Madagascar-Mascarene subcontinent early in the Paleocene about 65 million years ago and moved north to meet the Asian land mass by the middle Eocene about 45 million years ago (Axelrod & Raven, 1978).

Both subgenera *Acacia* and *Aculeiferum* are present in Africa and in Madagascar but, in addition, subgenus *Heterophyllum* occurs in Madagascar and the Mascarenes. Subgenus *Heterophyllum* is essentially Australian so the occurrence of *A. xiphoclada* Bak. in Madagascar and *A. heterophylla* (Lam.) Willd. in the Mascarenes is of considerable phytogeographic interest. As species with phyllodes do not occur on the mainland of any other continent it is probably reasonable to assume that any species of *Acacia* with phyllodes now occurring outside of Australia must either have come from the Australian region or have been derived from species which have (Pedley, 1975). Bell & Evans (1978) found that the seed of *A. heterophylla* and all of the Australian species analysed showed a single characteristic amino acid pattern which led them to suggest that Australia and the Mascarene Islands once formed part of the same land mass and that the seed chemistry of subgenus *Heterophyllum* is the seed chemistry that characterized the ancestral species of Gondwanaland. *A. heterophylla* is superficially very similar to *A. koa* A. Gray which is endemic in the Hawaiian Islands some 15 000 kilometres away but differs in characters of the corolla, pod, seed and seedlings (Vassal, 1969). Carlquist (1965) postulated that *A. koa* and *A. heterophylla* are probably descendants of seeds which floated from Australia into the Pacific and Indian Oceans respectively. While this may be true, both species are, however, tetraploid and probably not primitive.

Despite the close proximity of Madagascar to Africa, as far as is known only one indigenous species in subgenus *Aculeiferum*, namely *A. rovumae* Oliv., is common to both Africa and Madagascar. In tropical east Africa *A. rovumae* occurs on or near the coast and the appearance of the pods suggests that they are indehiscent and water-borne. If the pods are indeed dispersed by water this may possibly account for the occurrence of the species in Africa and in Madagascar and it seems reasonable to assume that migration of the species between the two areas took place in geologically recent time. There is a very doubtful and unlikely record of *A. pervillei* Benth., a Madagascan species, from Delagoa Bay, Mozambique, but the most likely explanation is that the label does not belong with the specimen (Ross, 1973). Bentham (1875) was of the opinion that *A. pervillei* was more closely allied to the South American *A. lacerans* Benth. than it is to any other Old World species. There is no recent taxonomic revision of the Madagascan species and several of the species are insufficiently known.

RELATIONSHIP BETWEEN THE AFRICAN AND INDIAN SPECIES

There are far fewer *Acacia* species in India than in Africa but both subgenera *Acacia* and *Aculeiferum* are present in Africa and in India and, moreover, two species in each subgenus are common to each land mass which provides clear evidence of a close relationship between the Indian and African acacias. Although migration between Africa and India is now extremely difficult or perhaps impossible because of the intervening arid areas, in former times the two areas were connected by a belt of tropical forest and savanna and direct migration was possible. The fact that a number of the acacias in India and in Africa, in areas that are now widely separated, cannot be distinguished at specific level suggests that their separation is geologically relatively recent and was attained when direct migration was possible between India and Africa and not when India 'rafted' north-

TABLE 4.—Species common to Africa and India and the infraspecific taxa recorded within each species

Africa	India
A. horrida (L.) Willd. subsp. *benadirensis* (Chiov.) Hillcoat & Brenan	*A. horrida* subsp. *horrida*
A. nilotica (L.) Willd. ex Del. subsp. *nilotica*	*A. nilotica* subsp. *indica* (Benth.) Brenan
subsp. *tomentosa* (Benth.) Brenan	[subsp. *hemispherica* Ali & Faruqi and subsp. *cupressiformis* (J. L. Stewart) Ali & Faruqi occur in Pakistan]
subsp. *adstringens* (Schumach. & Thonn.) Roberty	
subsp. *subalata* (Vatke) Brenan	
subsp. *kraussiana* (Benth.) Brenan	
subsp. *leiocarpa* Brenan	
A. polyacantha Willd. subsp. *campylacantha* (Hochst. ex A. Rich.) Brenan	*A. polyacantha* subsp. *polyacantha*
A. senegal (L.) Willd. var. *senegal*	*A. senegal* var. *senegal*
var. *kerensis* Schweinf.	
var. *leiorhachis* Brenan	
var. *rostrata* Brenan	

wards after breaking from Africa with Madagascar about 100 million years ago (Raven & Axelrod, 1974) or perhaps earlier (Schuster, 1976) otherwise one would have expected greater morphological diversification to have occurred. The morphological differences between the species common to Africa and India are mostly slight but the differences, taken together with the geographical discontinuity between the African and Indian populations, have been considered sufficiently significant to warrant the populations being regarded as subspecifically or varietally distinct (see Table 4).

In addition to these species which are common to both Africa and India, the Indian *A. pennata* (L.) Willd., one of the climbers with scattered recurved prickles in subgenus *Aculeiferum*, is extremely closely related to a number of African species such as *A. brevispica*, *A. schweinfurthii*, *A. pentagona* and allies. Once again, the degree of similarity between *A. pennata* and the African species suggests that their separation is geologically relatively recent. It is clear that there is a much closer affinity between the African and Indian species than there is between the African and South American species.

Although not present in India, *A. tortilis*, a member of subgenus *Acacia* which is widespread in Africa where it is represented by a number of subspecies, extends into Arabia as do several other African species. *A. gerrardii* Benth. is represented in the Negev Desert by subsp. *negevensis* Zohary, this subspecies being separated from all of the other variants in Africa by a wide geographical discontinuity.

The Indian species *A. ferruginea* (Roxb.) DC., a member of subgenus *Aculeiferum*, has some pollen characteristics which are specific to the Australian subgenus *Heterophyllum*, while at least twenty-six species in subgenus *Heterophyllum* have a porate type of pollen with simple appertures which is characteristic of subgenus *Aculeiferum* (Guinet & Vassal, 1978) illustrating the apparent close relationship between subgenera *Aculeiferum* and *Heterophyllum*.

RELATIONSHIP BETWEEN THE AFRICAN AND AUSTRALIAN SPECIES

The vast majority of the *Acacia* species (830 species fide Hopper & Maslin, 1978) occur in Australia where considerable morphological diversity has occurred. *Acacia* is represented in Africa by subgenera *Acacia* and *Aculeiferum* and in Australia by subgenera *Acacia*, *Aculeiferum* and *Heterophyllum*. Most of the Australian species (over 800) belong to subgenus *Heterophyllum*, which is basically Australian (including Tasmania and New Guinea) although a few representatives also occur in Madagascar and the Mascarenes, the Pacific Islands and Hawaii. Although subgenera *Acacia* and *Aculeiferum* occur in Australia they are poorly represented on the continent, subgenus *Acacia* being represented by fewer than ten indigenous species mainly in the more northern parts of the continent (see Fig. 14) and subgenus *Aculeiferum* by the recently described endemic species (*A. albizioides* Pedley) which occurs in the vicinity of Coen in northern Queensland (see Fig. 15). The only species in subgenus *Acacia* common to Africa and Australia is *A. farnesiana* (apart from *A. nilotica*, *A. karroo* and *A. albida* Del. which are fairly recent introductions into Australia) but, as already indicated, *A. farnesiana* was almost certainly introduced into Africa. Bentham (1864) stated that *A. farnesiana* had every appearance of being indigenous in Australia but doubt has been expressed from time to time (Pedley, 1979) as to whether or not the species is in fact indigenous. *A. farnesiana* has an extensive distribution in Australia covering over 5 million square kilometres (N. Hall, pers. comm.) which greatly exceeds that of any other member of subgenus *Acacia* in Australia or the distribution of all of the other members of the subgenus collectively (see Fig. 16). If *A. farnesiana* is not indigenous in Australia then presumably it must have been introduced prior to European settlement as the species was encountered in the inland areas of Australia by early explorers.

The Australian members of subgenera *Acacia* and *Aculeiferum* are not particularly well known; some members of subgenus *Acacia* are not yet described although the subgenus is currently being revised. Except for the pantropical *A. farnesiana* which has a diploid chromosome number of 52 and the naturalized *A. nilotica* subsp. *indica* (Benth.) Brenan in which $2n = 44, 52, 104$ (Vassal, 1974), there are no chromosome data available for other Australian

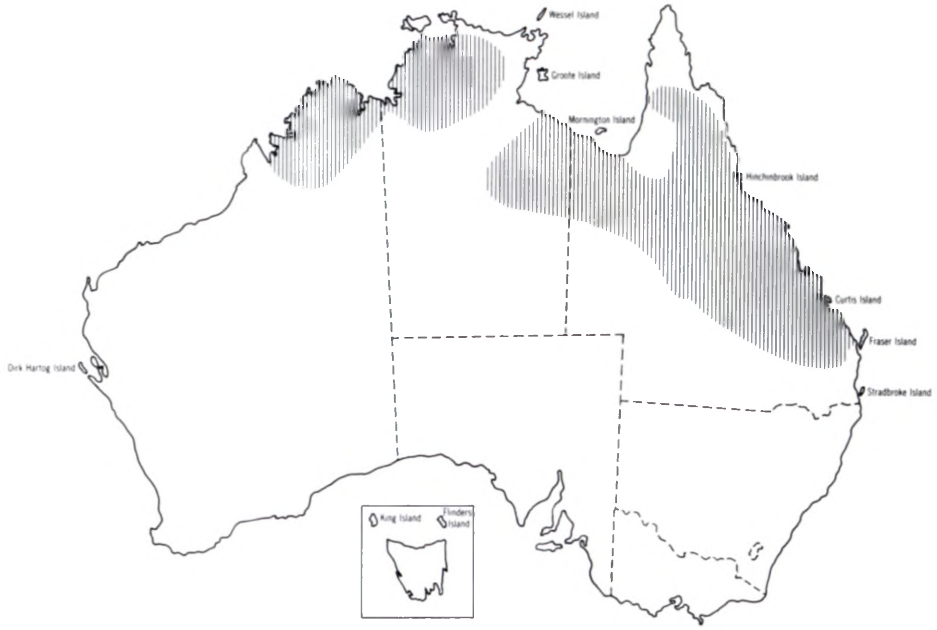

FIG. 14.—An indication of the general distribution of subgenus *Acacia* in Australia (excluding *A. farnesiana*).

FIG. 15.—An indication of the distribution of subgenus *Aculeiferum* in Australia.

FIG. 16.—An indication of the general distribution of *Acacia farnesiana* in Australia.

members of subgenus *Acacia* and none for the solitary representative of subgenus *Aculeiferum*.

The contemporary Australian *Acacia* species appear to present a contradiction. On the one hand the majority of the Australian species (members of subgenus *Heterophyllum*) are unique and differ significantly from all of the other species in other regions (except for the few outliers discussed by Pedley, 1975) which suggests that they have evolved in isolation, while on the other hand this uniqueness is contradicted by the presence of a handful of species in subgenus *Acacia* and the solitary representative of subgenus *Aculeiferum* which share a number of the characters found in members of the respective subgenera elsewhere. This would seem to suggest that *Acacia* may have entered Australia on more than one occasion. For example, it would appear that the solitary member of subgenus *Aculeiferum* has entered Australia from New Guinea in geologically recent time, perhaps before the separation of Australia and New Guinea in the late Pleistocene. The other alternative is that the species is a relic. The important questions to which answers will have to be found are, firstly, when did *Acacia* first enter the Australian region and, secondly, from where.

There would appear to be two possibilities, namely, either the ancestors of *Acacia* must have been present in the Australian region at the time of the fragmentation of Gondwanaland although there is no evidence that the ancestors had differentiated at this stage or else the genus entered the region during the Tertiary. According to Raven & Axelrod (1974) geological evidence suggests the possibility of more or less direct migration between West Gondwanaland, combined Africa and South America, and East Gondwanaland, combined Australasia and Antarctica, up until the close of the early Cretaceous about 110 million years ago (± 10 million years). When the connection between Africa and Australasia was severed is not clear, but it is possible that Madagascar and India served as a subtropical route of migration, perhaps somewhat interrupted, to Australasia into the late Cretaceous. Once the migration of tropical alliances by this route was no longer possible, Australasia was connected with the rest of the world by a cool-temperate pathway to South America via Antarctica up until about 45 million years ago. However, the present mainly tropical and subtropical global distribution of *Acacia*, the absence of species from the southern portion of South America and the few species in the southern tip of South Africa and in Tasmania, suggests that *Acacia* did not enter Australia from the south via this cool-temperate route as some other genera such as *Nothofagus* appear to have done. In general, the ease of migration to Australasia is believed to have decreased during the late Cretaceous to Paleogene only to increase again in the Neogene as the Australian plate neared Asia. Nevertheless, according to Raven & Axelrod (*l.c.*), migration between Australasia and Africa via India and Madagascar was probably relatively direct, but with fairly long steps over water, after the start of the Tertiary 65 million years ago.

The first recorded appearance of *Acacia* pollen in the Australian fossil record is in mid-Miocene deposits (± 16 million years ago) in southern Victoria (Cookson, 1954). To explain the apparent absence of *Acacia* pollen from Paleogene beds Cookson concluded that either the genus *Acacia* was not represented in the *Nothofagus*–conifer forests which are known to have covered large areas of Australia during the early Tertiary period or else the genus did not become an integral part of the Australian flora as a whole until after the Lower Miocene period (25 million years ago). Although the evidence was not conclusive, Cookson favoured the latter possibility.

If Cookson's view that *Acacia* did not occur in Australia prior to the Lower Miocene is correct, then either subgenus *Heterophyllum* developed in Australia after the Lower Miocene, probably from subgenus *Aculeiferum* and possibly from a species such as the Indian *A. ferruginea* or its ancestors, or else subgenus *Heterophyllum* entered Australia after the Lower Miocene after developing elsewhere in an area where it has since become extinct except for isolated species such as *A. confusa* Merr., *A. koa*, *A. heterophylla* and *A. xiphoclada*. The occurrence of the same seed amino acid pattern in *A. confusa*, which occurs in the Pacific Islands and Taiwan, as that found in the seeds of African and Asian species suggested to Evans *et al.* (1977) that this species originated in Asia rather than in Australia.

Another possibility, however, is that the genus may have been established in Australia prior to the Lower Miocene but confined to the northern part of the continent. The suggestion that *Acacia* first became established on the northern part of the Australian plate and later spread to other parts of the continent when suitable conditions prevailed for it to do so was advanced by Andrews (1914) and supported by Pedley (1975). Vassal (1972), on the other hand, considered that the primitive section of subgenus *Heterophyllum* probably occupied the whole of the Australian continent at the beginning of the Tertiary.

Although the centre of present-day development of species in a subgenus need not necessarily reflect the centre of past development, the great diversity exhibited by subgenus *Heterophyllum* in Australia and the lack of close relatives on other continents suggests that subgenus *Heterophyllum* developed in Australia from which source a few species such as *A. confusa*, *A. koa* and *A. heterophylla* were subsequently dispersed to other areas and that the subgenus did not enter Australia after developing elsewhere. It is tempting to speculate that subgenus *Acacia* entered northern Australia where it has since largely remained in the mid-Tertiary (or perhaps even later) when Australia came into contact with the south-east Asian plate but it is difficult to account for the poor representation of subgenus *Aculeiferum* in Australia.

As Australia was separated from Africa and India by a considerable marine gap and was distant from any other tropical land mass for millions of years until late in the Oligocene when contact was made with the south-east Asian plate, Melville (1975) concluded that 'the characteristic Australian flora — excluding the Indo-Malaysian element of relatively recent origin — must have evolved *in situ* from ancestors of Permian age'. Melville (*l.c.*) continued that 'Acceptance of this conclusion implies that evolutionary trends in many families such as *Proteaceae, Restionaceae, Leguminosae* and *Compositae,* must have been initiated already in the Permian for the observed parallel evolution to have taken place subsequently on separated Gondwanic fragments'.

Irrespective of when the genus first became established in Australia and from where it came its development and subsequent spread over the continent have been influenced by past geological and climatic changes. During the period from the Triassic, until northward drift began in the Eocene, Australia was situated about 15° south of its present latitude (Jones, 1971).

The Australian Tertiary pollen record is largely that of rainforest which must have been widespread, though not necessarily continuous, over the southern part of the continent (Martin, 1978). The high content of gymnosperms in the Australian Paleocene assemblages is thought to indicate a cool temperate climate similar to present-day Tasmania (Martin, *l.c.*). The subsequent increase in Myrtaceae and other angiosperms is taken to indicate a relative increase in temperature to a warm temperate or subtropical climate. Temperatures reached the maximum for the Tertiary in the early Eocene and the dramatic increase in *Nothofagus* in the mid-Eocene marks the onset of a cooling trend although further fluctuations were experienced. The Oligocene to early Miocene was a period of an equable climate with very high rainfall and stable temperatures while the mid–late Miocene was a time of profound change when *Nothofagus* and many other taxa disappeared from the fossil record in south-eastern Australia (Martin, 1977). During the late Miocene and Pliocene a moderate rainfall and drier type of vegetation existed and it is thought that remnants of lower Tertiary flora existed in small refuge areas in the eastern highlands and migrated westwards when the climate became wetter for a relatively brief period in the late Pliocene (Martin, 1977). There is every indication that aridity increased subsequent to Pliocene time and the climate became more seasonal with a well-marked dry period and it is not until the Pleistocene that grasslands and/or savanna woodlands became prominent in south-eastern Australia. According to Gill (1975) it was only at this stage about two million years ago that the full opportunity for speciation in *Acacia* and *Eucalyptus* occurred. As aridity intensified closed forest would have been eliminated from all but locally favourable sites in north-eastern Australia.

In rainforest areas *Acacia* species are confined to marginal areas and clearings and it is only when the canopy is disturbed that the light requiring elements of the Australian flora become established (Burbidge, 1960). The retreat of closed forest with increasing aridity would have favoured the dispersal of *Acacia* species and the fossil finds discussed by Cookson (1954) possibly indicate an expansion in the distributional range of *Acacia* which coincided with the retreat of *Nothofagus*. Hopper & Maslin (1978) suggested that the recent speciation in *Acacia* in Western Australia has been promoted by recurrent migration, extinction and isolation of populations as a result of Pleistocene climatic fluctuations and their erosional consequences in climatically transitional areas. The possible dispersal of *Acacia* in Australia as a whole is dealt with by Pedley (1980).

Apart from the obvious differences such as the development of phyllodes in many members of subgenus *Heterophyllum* in Australia and the differences between the three subgenera in pollen, chromosomes, seeds, seedlings, inflorescences and pods alluded to by Guinet & Vassal (1978), there are other differential tendencies between subgenus *Heterophyllum* and the African representatives of subgenera *Acacia* and *Aculeiferum* which are briefly discussed here.

1. The African species (except *A. albida)* are invariably deciduous during the dry season, either regularly or irregularly so, while the Australian members of subgenus *Heterophyllum* are invariably evergreen. The only Australian species thought to be deciduous is *A. ditricha* Pedley, a member of subgenus *Acacia,* but it is possible that some other members of this subgenus are also deciduous.

2. The flattened spreading crowns which are so characteristic of some of the African species such as *A. tortilis* subsp. *heteracantha* (Burch.) Brenan and subsp. *spirocarpa* (Hochst. ex A. Rich.) Brenan, *A. sieberana* var. *woodii* (Burtt Davy) Keay & Brenan, *A. lahai* Steud. & Hochst. ex Benth. and *A. abyssinica* Hochst. ex Benth. subsp. *calophylla* Brenan are absent amongst the Australian species. One explanation advanced for the flattened crowns in Africa is that it is an adaptive response to browsing (Brown, 1960). Another suggestion that has been offered is that it is the result of insolation damaging the apical growing buds, but if this was the case it is strange that none of the Australian species has developed the same adaptive response where the effects of insolation are as great as they are in Africa. The African species in general 'look' different to most of the Australian members of subgenus *Heterophyllum.*

3. The stipules in all African members of subgenus *Acacia* are spinescent and invariably very prominent and in the Australian members of the subgenus the stipules are typically spinescent at least when young although they are usually small or occasionally absent. The stipules in subgenus *Heterophyllum* are, with few exceptions, small, inconspicuous and often deciduous. Many of the species are entirely unarmed but in others spinescence has arisen in various ways through the modification of phyllodes, branchlets and peduncles. *A. paradoxa* DC. and *A. victoriae* Benth. are exceptional in having stipular spines although those of the latter are sometimes reduced to blunt outgrowths, and stipular spines also occur in some of the Western Australian species (Pedley, 1978). Stipular spines are far better developed in the African species of subgenus *Acacia* than they are in the Australian members of subgenus *Acacia* or in subgenus *Heterophyllum.* Brown (1960) suggested that '*Acacia* in Australia passed through an earlier period in which spininess had little adaptive value, followed by a time in which selective pressures again arose favouring the development of spines *de novo* in shrubs of the forested country and in the lower shrubs of the open country'.

Brown (*l.c.*) attributed the lack of spinescence in many of the Australian *Acacia* species and in other dominant genera like *Eucalyptus* to the 'long-continued absence or scarcity of effective large browsers' until the recent introduction of domesticated animals. Large browsing herbivores are now or have recently been abundant in Africa and in tropical America in areas where spinescent acacias occur and certainly in Africa the acacias constitute an important source of food for many browsing mammals. However, the argument loses some validity as many species in other genera have survived browsing pressure without the aid of spines although admittedly they may have developed other deterrents such as offensive chemical attributes to discourage large browsers. No similar radiation of large browsers appears to have occurred in Australia, the endemic Australian mammal fauna consisting of marsupials, monotremes, rodents and bats. Of these, the kangaroo is the largest survivor but kangaroos are chiefly grazers and it seems reasonable to assume that the extinct giant kangaroos were also grazers. Brown (*l.c.*) considered the development of spininess in many of the smaller shrubby acacias, grasses and other shrubs of the closed forest understandable seeing that kangaroos, smaller marsupials and rodents feed on them.

None of the Australian members of subgenus *Acacia* has swollen stipular spines which are so characteristic of some of the African and American species and none of the Australian species has formed any mutualistic association with ants although the seeds of many Australian plants, including some *Acacia* species, are dispersed short distances by ants (Berg, 1975). The Australian continent is richly endowed with ants so the lack of a mutualistic association between acacias and ants cannot be due to a scarcity of ants. Hocking (1970) suggested that if the Australian members of subgenus *Acacia* ever had the tendency to produce swollen spines then presumably the expression of the character has been lost under reduced selection pressure from herbivorous animals. The extra-floral nectaries in the Australian members of subgenus *Acacia* are small.

4. A number of the Australian members of subgenus *Heterophyllum* flourish in a cold and wet environment in southern Victoria and Tasmania far further south than on any other continent and have occupied a habitat that is generally avoided by the indigenous African species. The African species tolerate hot and dry, hot and wet, and cold and dry habitats but where cold and wet conditions persist for any great period of the year acacias are usually infrequent in their occurrence or absent.

5. The African species invariably flower in spring or early summer and the inflorescences are usually produced with or before the young leaves. In contrast, the Australian members of subgenus *Heterophyllum* are evergreen and a number of species flower in winter.

6. The anthers of nearly all of the African species (except *A. albida* and *A. redacta*, neither of which it has been suggested is referable to *Acacia*, Robbertse & Von Teichman, 1979) are adorned with a small apical deciduous gland but none of the Australian members of subgenus *Heterophyllum* appear to have glands on the anthers. The function of the glands in the African species is not clear but Hocking (1970) suggested that the tissue filling the glands may contain useful amounts of nitrogenous material which may be utilised by phytophagous insects. *A. bidwillii* Benth. and *A. sutherlandii* (F. Muell.) F. Muell., both Australian members of subgenus *Acacia*, have anthers with small deciduous apical glands but I have not seen suitable material of other Australian members of the subgenus, except of *A. farnesiana* which lacks the glands, to establish whether they also have the deciduous glands. This needs further investigation.

7. Some of the Australian members of subgenus *Heterophyllum* have seed with conspicuous brightly coloured arils, whereas none of the African species does.

8. Bruchids are responsible for the destruction of vast quantities of seeds of some American and African species in subgenera *Acacia* and *Aculeiferum* whereas seeds of the Australian species are relatively unaffected by bruchids, probably because few indigenous species of bruchid occur in Australasia and the Pacific Islands (Southgate, 1978). A survey of the free non-protein amino acids in the seeds of 106 *Acacia* species by Evans *et al.* (1977) revealed that the genus can be divided into four biochemically different groups on the basis of their seed chemistry and Southgate (*l.c.*) suggested that one of the factors influencing the ability of bruchid larvae to survive within a seed may be the level of certain amino acids, notably pipecolic acid and some heteropolysaccharides. The amino acid composition of the seed of the Australian members of subgenus *Heterophyllum* differs from that of the seed of members of other subgenera, and a possible explanation for this may be that members of subgenus *Heterophyllum* have apparently evolved without the selection pressure of bruchid predation.

DISCUSSION

As a result of the multidisciplinary approach to *Acacia* in recent years much evidence has accumulated which indicates that fundamental differences exist between subgenera *Acacia* and *Aculeiferum*, and that subgenus *Aculeiferum* is more closely related to subgenus *Heterophyllum* despite the fact that they occupy basically different geographical areas which show relatively little overlap, than are subgenera *Acacia* and *Aculeiferum* which share a common geographical area. The differences between subgenera *Acacia* and *Aculeiferum* are such that it is considered unlikely that the one gave rise to the other directly but rather that they arose from a common or similar prototype. Many questions concerning the origin, evolution and dispersal of the genus and of the relationships within it remain to be answered to enable a better understanding to emerge.

Although the African *Acacia* species have received a considerable amount of attention during the last few decades they remain inadequately known and numerous taxonomic problems await elucidation. Despite the incompleteness of the information on the distribution of the African species the overall patterns that emerge are probably sufficiently accurate to be of value. Further collecting, especially in tropical north-east Africa and in west tropical Africa, will resolve some of the taxonomic problems and provide more accurate information on the distributions of many species.

Some species in subgenus *Aculeiferum* are almost as widespread in Africa as the most widespread members of subgenus *Acacia*, but the distribution of subgenus *Acacia* as a whole in Africa exceeds that of subgenus *Aculeiferum*. That subgenus *Acacia* enjoys a wider range of distribution than subgenus *Aculeiferum* suggests that the former has been able to occupy habitats from which the latter has been excluded and the possibility exists that it has been assisted in this by the greater genetic plasticity conferred on it as a consequence of its members being polyploid. On the other hand, climbing members of subgenus *Aculeiferum* have been successful in forested areas of the continent in which subgenus *Acacia* is not represented, the climbing habit, which is not known in subgenus *Acacia* in Africa, enabling species to take advantage of suitable sites in forested areas. The highest concentration of species in each subgenus occurs in tropical north-east, east and south-east Africa but different parts of the continent have been important areas of local speciation for each subgenus, the highest concentration of endemic species in subgenus *Acacia* occurring in Tanzania and the highest concentration of endemics in subgenus *Aculeiferum* in Somalia.

Despite the advances in our knowledge of the African species in recent decades, detailed population studies are required and information is needed on their biology and autecology. Only when such a reservoir of information is available will a better understanding of the African species emerge. And, what is true for the African species applies equally to those in other continents. It would be highly beneficial as a first step to have a conspectus of the *Acacia* species occurring on each continent reflecting the current state of taxonomic knowledge along the lines of that produced for the African species (Ross, 1979) or the more detailed revision of Queensland species (Pedley, 1978, 1979), and ultimately a conspectus of the genus as a whole. This is, of course, a fairly formidable task especially when one considers the Australian species but much valuable work has already been done on the Australian species. Hopefully, a conspectus of the Australian species will be prepared before too long. *Acacia* is a fascinating genus, which commends itself to further study.

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UITTREKSEL

Die drie subgenera wat in die genus Acacia *erken word, word in hooftrekke beskrywe en die globale verspreiding van elk word aangedui. Die verskille tussen die subgenera en die graad en verwantskap en vlakke van spesialisasie word kortliks bespreek. Die voorstel word gemaak dat die voorouers van die genus klim- of slingerplante was. Geologiese gebeure in die verlede wat 'n moontlik invloed op die verspreiding van* Acacia*-spesies in Afrika kon gehad het, word geskets. Die aantal spesies wat vir elke land in Afrika aangeteken is word getabuleer en die verspreiding en konsentrasie van spesies binne die genus* Acacia *as geheel en binne elke subgenus in Afrika word geïllustreer. Die hoogste konsentrasie van spesies binne elke subgenus kom in oos en suid-oos tropiese Afrika voor. Die verspreiding van spesies in sommige van die afsonderlike Afrika-lande en moontlike verwantskappe word bespreek en die aandag word op die hoofsentra van endemisme gevestig. Die verspreiding van die spesies van Afrika word met die hoof fito-geografiese streke wat op die vasteland erken word, in verband gebring. Die verwantskappe tussen die* Acacia *spesies van Afrika, Amerika, Malgassie, Indië en Australië word kortliks bespreek.*

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