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A preliminary analysis of distribution patterns in a large, pantropical genus, *Barleria* L. (Acanthaceae)

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Abstract. *Barleria* L. (Acanthaceae) is a large, polymorphic, widespread genus of herbs and shrubs comprising about 300 species, occurring mainly in Africa and Asia but with one species, *Barleria oenotheroides* Dum.Cours., extending to the New World tropics. Recent completion of a monographic infra-generic classification of the genus (in which seven sections are recognised, and the names of four of these validated in this paper—see Appendix 1), has facilitated a comprehensive analysis of distribution patterns on a global scale. The richest representation of *Barleria* is in Africa where there are two centres of diversity, one in tropical East Africa (about eighty species) and the other in southern Africa (about seventy species). The number of species tails off rapidly to both the Far East and the West. *Barleria* shows a marked trans-Atlantic disjunction between West Africa and the Neotropics, with *B. oenotheroides* shared by these two regions. This type of disjunction, which is known in other genera of the family, cannot be adequately explained in *Barleria* on the basis of long-distance dispersal or past continental movements. There is a high degree of regional endemism (e.g. 75% for the Indian subcontinent) at both the species and sectional levels within this genus. The degree of similarity between regions is correspondingly low. The endemics in each region tend to belong to only one or a few of the sections. There are few truly widespread taxa within the genus. East and West Africa are the only regions in which all sections are represented. Sections *Barleria* and *Prionitis* C.B. Cl. are the most widespread in the genus; Sections *Somalia* (Oliv.) Lindau, *Fissimura* M. Balkwill and *Stellatohirtae* M. Balkwill are mainly restricted to Africa and Sections *Chrysothrix* M. Balkwill and *Cavirostrata* M. Balkwill are the most restricted, occurring mainly in India and Sri Lanka. On a local scale, many of the species show highly restricted, clumped distributions; this is apparently related to particular soil types and possibly to the short-distance, ballistic mode of seed dispersal. This account of the biogeography of *Barleria* is to be regarded as preliminary, as much taxonomic work at the species level remains to be done before a full-scale cladistic biogeographic account can be undertaken. Particular areas worthy of future investigation include establishing the centre of origin of the genus and investigating the basis for the high degree of endemism shown by many of the species.

Key words. Acanthaceae, *Barleria*, distribution, disjunction, endemism, phylogeny.

INTRODUCTION

This paper has two main purposes: the first is to bring attention to hitherto unknown distribution patterns within a pantropical genus, *Barleria* L. (Acanthaceae), and the second is to raise a number of important biogeographical questions based on these distribution patterns. A third, much more minor aim, is to draw attention to a recent monographic infra-generic classification that has been formulated for the genus (Balkwill & Balkwill, 1997), as it is this that has facilitated an analysis of the distribution patterns. To date, very little biogeographical work has been published for the Acanthaceae; many of the genera within the family are large and widespread and few recent monographic accounts of these large genera have been undertaken. Most accounts that have been published are regional in nature and form components of regional floras, in which distribution patterns have only been discussed at a local scale. It is hoped that this paper, which analyses distribution patterns within *Barleria* on a global scale, will stimulate further interest in monographic work and biogeographical studies within the Acanthaceae.

Barleria is a large, polymorphic, widespread genus of herbs, shrubs and rarely climbers comprising, at a conservative estimate, some 300 species worldwide. Members of the genus occur from Japan in the Far East, through southern Asia, India, Arabia, Africa, Madagascar to as far west as Central America and Mexico. *Barleria* is, however, predominantly an Old World genus, with its greatest centre of species diversity in east tropical Africa followed by southern Africa. The number of species in other regions of the world tails off rapidly towards both the east and west with nine species in the Far East and only one in the New World tropics.

An analysis of distribution patterns in *Barleria* has not

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TABLE 1. Total number of species, number of endemics and number of representatives of each infra-generic taxon in each major region of the world in which *Barleria* occurs. Abbreviations: Bia = Section *Barleria*; Chry = Section *Chrysothrix*; Cavi = Section *Cavirostrata*; Fiss = Section *Fissimura*; Stel = Section *Stellatohirta*; Som1 = Section *Somalia*, species with spotty corollas; Som2 = Section *Somalia*, species without spotty corollas; Prio = Section *Prionitis*. NS = species not seen (those names of which herbarium material could not be traced).

Region	Total no. of species	Number of endemics	Numbers of species from different sections in each major region								
			Bia	Chry	Cavi	Fiss	Stel	Som1	Som2	Prio	NS
Far East	9	6	2	1	—	—	—	—	—	1	5
India	32	24	10	8	5	—	—	1	1	3	4
Sri Lanka	4	1	1	3	—	—	—	—	—	—	1
Arabia	16	6	4	—	—	1	1	4	—	3	3
North Africa	12	2	4	—	—	2	—	2	1	2	1
East Africa	77	43	13	2	1	18	4	6	3	16	14
Uganda	9	—	1	—	—	7	—	1	—	—	—
West Africa	25	18	4	2	1	8	3	—	2	1	4
Flora Zam.* region	49	15	24	—	—	1	5	—	10	7	5
Angola	25	13	5	—	—	2	5	—	10	—	3
Southern Africa	69	45	32	3	—	1	3	—	17	8	2
Central America	1	—	—	—	1	—	—	—	—	—	—
Madagascar	28	27	7	—	—	1	—	—	5	11	4
Socotra	4	3	1	—	—	—	—	1	1	1	—
S.E. Asia	3	—	—	—	—	—	—	—	—	3	—

* Flora Zam. = *Flora Zambesiaca.*

TABLE 2. Symbols used to denote major areas of the world in which *Barleria* occurs, and the countries included in each area.

Symbol used	Area denoted	Countries included in area
a	Central Americas	Mexico, Panama, Guatemala
b	West Africa	Senegal, Sierra Leone, Liberia, Togo, Ivory Coast, Ghana, Nigeria, Cameroon, Congo
c	North Africa	Egypt, Sudan
d	East Africa	Ethiopia, Somalia, Djibouti, Tanzania, Kenya
e	Angola	Angola
f	Uganda	Uganda, Rwanda, Birundi, Zaire
g	*Flora Zambesiaca* regions	Malawi, Zimbabwe, Mozambique, Zambia
h	Southern Africa	Namibia, Botswana, South Africa, Swaziland
i	Madagascar	Madagascar and the Mascarene Islands
j	Arabia	Saudi Arabia, Yemen, Oman
k	Socotra	Socotra
l	India	India, Bhutan
m	Sri Lanka	Sri Lanka
n	Malaya	Malayan Peninsula, Malayan Islands
o	Phillipines	Phillipines and associated Islands
p	Far East	Japan, China, Thailand

been possible before because of the absence of any recent, monographic account of the genus. The circumscription and subdivision of *Barleria* has received attention from a number of authors (Nees, 1847; Oersted, 1854; Anderson, 1863; Bentham, 1876; Clarke, 1885, 1899, 1901; Lindau, 1895; Burkill & Clarke, 1899; Ridley, 1931; Obermeijer, 1933; Benoist, 1967). The genus is clearly defined though highly variable and this has made it the subject of considerable taxonomic interest. It is readily distinguished from other genera in the Acanthaceae by a combination of three features: a four-partite calyx with two large outer segments and two smaller inner ones; globose, honeycombed pollen, and the predominance of double cystoliths (calcium oxalate crystals) in the epidermal cells. The only previous accounts of this genus that have been undertaken on monographic scale are those of Nees (1847) and Lindau (1895). All other accounts have been regional in nature and so have not adequately solved the problem of a satisfactory subdivision of this large genus into natural groups and also have not facilitated a comprehensive analysis of distribution patterns on a global scale.

We recently undertook a reassessment of the delimitation and subdivision of *Barleria* on a global scale and have proposed a new classification of the genus (Appendix 1). In this classification seven sections placed in two subgenera are recognized. Four of these sections are newly described and the names of these are validated in this paper (see Appendix 1). Detailed descriptions of the taxa and a full discussion of the new classification of the genus will be published separately (Balkwill & Balkwill, 1997). The production of this monographic treatment of the genus has facilitated an analysis of the distribution patterns of the infra-generic taxa, and it is the preliminary results of this analysis that form the main substance of this paper.

APPROACH

Our reassessment of the subdivision of *Barleria* concentrated on the production of a new infra-generic classification of

TABLE 3. Matrix of similarity indices showing similarity (as a percentage) between different areas in terms of species of *Barleria* present. Symbols used to denote regions are the same as those given in Table 2. Regions 'n' and 'o' have been omitted from this table due to the very small numbers of species occurring in them.

Area	a	b	c	d	e	f	g	h	i	j	k	l	m	p
a	—	0	0	0	0	0	0	0	0	0	0	0	0	0
b		—	16.2	5.8	12	11.7	5.4	2.1	0	4.8	0	0	0	5.4
c			—	20.2	5.4	28.5	3.2	2.1	0	28.5	0	9.0	0	9.5
d				—	3.9	18.6	15.8	6.8	1.9	21.5	2.4	2.7	0	2.5
e					—	0	13.5	6.3	0	0	0	0	0	0
f						—	0	0	0	16	15	0	0	11.1
g							—	44	2.5	0	0	0	0	3.4
h								—	2.0	0	0	1.9	0	2.5
i									—	0	0	3.3	0	5.0
j										—	0	11.1	0	0
k											—	0	0	0
l												—	16.6	14.6
m													—	0
p														1

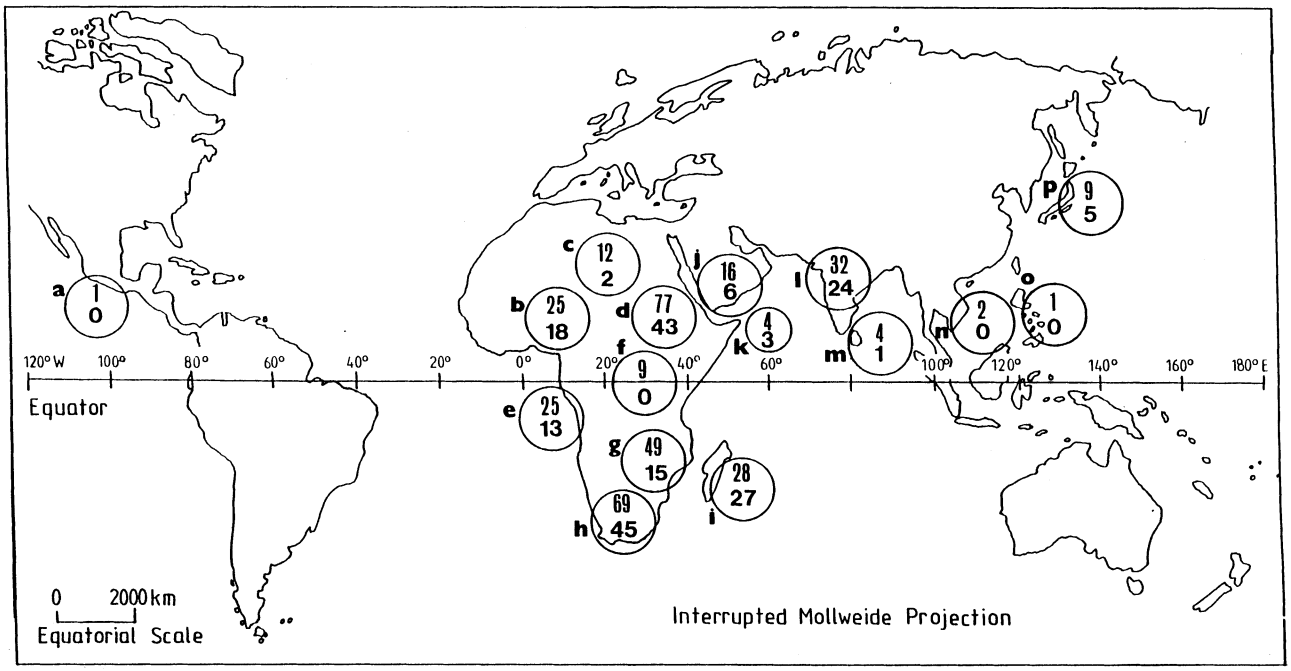

FIG. 1. Map showing global distribution of *Barleria* and the numbers of species occurring in different parts of the world. Lettered circles represent the major areas of the world in which *Barleria* occurs: the region denoted by each letter, and the countries included in it, are specified in Table 2. Within each circle the upper figure represents the total number of species of *Barleria* in the region and the lower (bold) figure represents the number of those species that are endemic to the region.

the genus on monographic scale. It did not deal in detail with the many problems that exist with species circumscription and nomenclature. Accurate distribution records, based on a study of herbarium specimens in numerous major herbaria (including The Natural History Museum, London (BM); Edinburgh (E); East Africa (EA); Firenze, Florence (FT); Kew, London (K); Missouri (MO); Pretoria (PRE); Harare (SRGH); Windhoek (WIND) and several other southern African herbaria), were ascertained for all taxa of which herbarium material was seen (approximately 240 of 300 described taxa, and approximately 8000 specimens). For the remaining taxa of which material could not be traced (and the true taxonomic status of which is unclear), it was necessary to rely on distribution reports documented in the literature. As many of these records are possibly incomplete, the figures used in this paper must, at this stage, be regarded as provisional. However, they are the most accurate and comprehensive figures available and do indicate interesting trends that could be tested more rigorously in future investigations.

Table 1 shows the number of species of *Barleria* recorded in each of the major areas in which the genus occurs. The

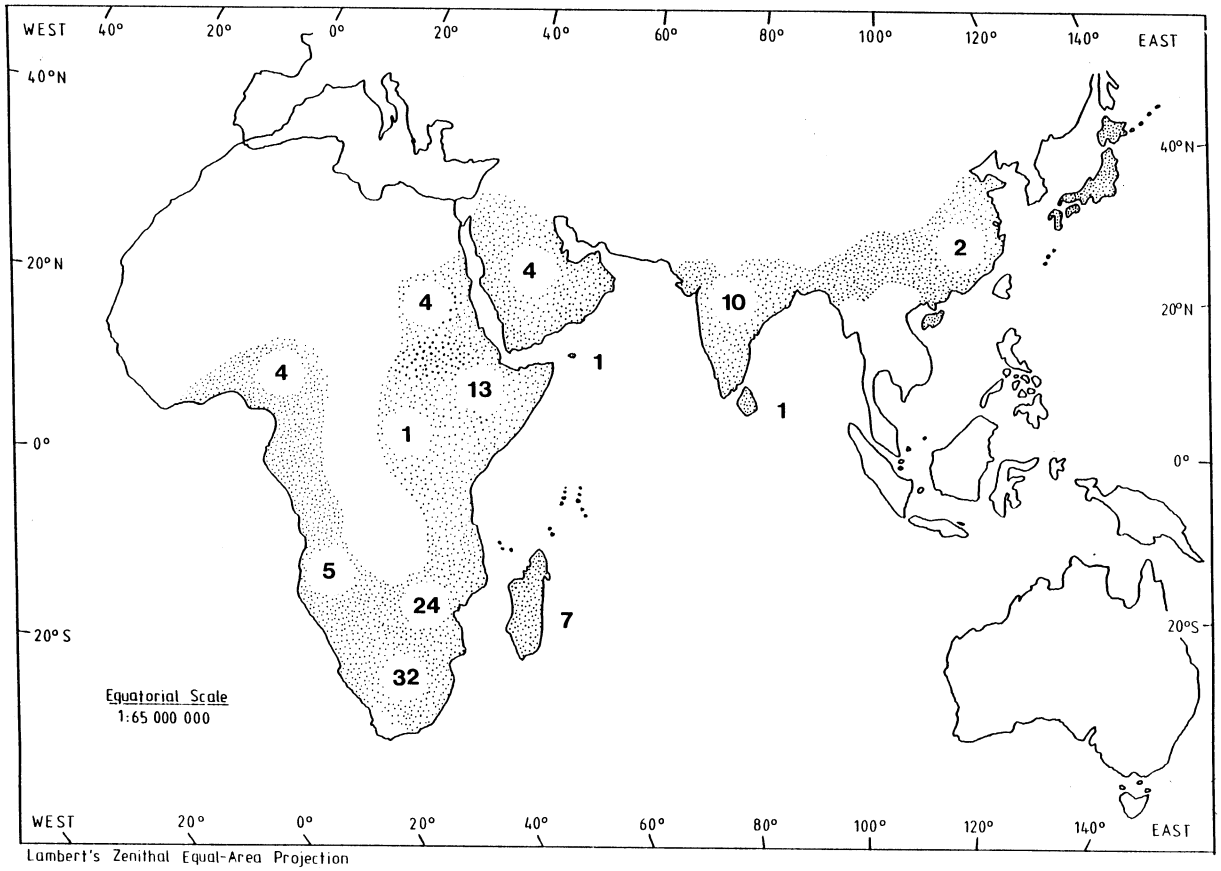

FIG. 2. Distribution of species of Section *Barleria*. Stippled areas represent those parts of the world in which members of Section *Barleria* occur and numbers indicate the number of species occurring in each part of the distributional range.

regions represented in the distribution maps and referred to throughout this paper were chosen to correspond with the major areas for which floras exist or are being written. They also correspond closely with major phytogeographic zones recognized in Africa (White, 1983); it would have been preferable to use the phytogeographic regions determined by White (*l.c.*) for Africa, but the distribution data for some of the species was not adequately detailed to do so, and comparable regions (determined in the same way) do not exist for other parts of the world. A key to the notation used to designate each area in the figures and tables is provided in Table 2. An index of the similarity between two different regions was obtained by dividing the total number of species in those regions being compared into the number they held in common and multiplying by 100 in order to obtain a percentage (see Table 3). Maps showing the known distribution of numbers of species in different parts of the world are given in Figs 1, 2, 4, 6, 7, 9, 11 and 13 while Figs 3, 5, 8, 10 and 12 show typical representatives of each of the infra-generic taxa recognized. For distributions at the worldscale, Mollweide's Equal Area Projection (Stott, 1981) has been used, and for distributions centred on Africa, Lambert's Equatorial Zenithal Equal-Area Projection (Bartholomew, 1977) has been used as it is thought to give the best representation for Africa (Stott, 1981).

RESULTS AND DISCUSSION

Broad-scale distribution patterns and numbers of species

The number of species occurring in different regions of the world is shown in Fig. 1 and Table 1. The richest representation of the genus occurs in Africa where there are two centres of species diversity, one in the north east and one in the south (Fig. 1). The largest number of species (approximately eighty) occurs in east Tropical Africa (including Somalia, Ethiopia, Kenya and Tanzania) with a second centre of diversity (approximately seventy species) in southern Africa (including South Africa, Lesotho, Swaziland, Namibia and Botswana). The next highest number of species occurring in any one area is in the *Flora Zambesiaca* region (forty-nine species) followed by the Indian subcontinent (thirty-two species) and Madagascar (twenty-eight species; Fig. 1). The number of species per region then tails off dramatically towards the Far East, with only three species occurring in the Malesian region and nine in Japan. Only one naturally occurring species, *Barleria oenotheroides* Dum. Cours., occurs in the New World (Fig. 1), where it is found from Mexico in the north, through the Central Americas and some of the Caribbean Islands, to Guatemala in the south.

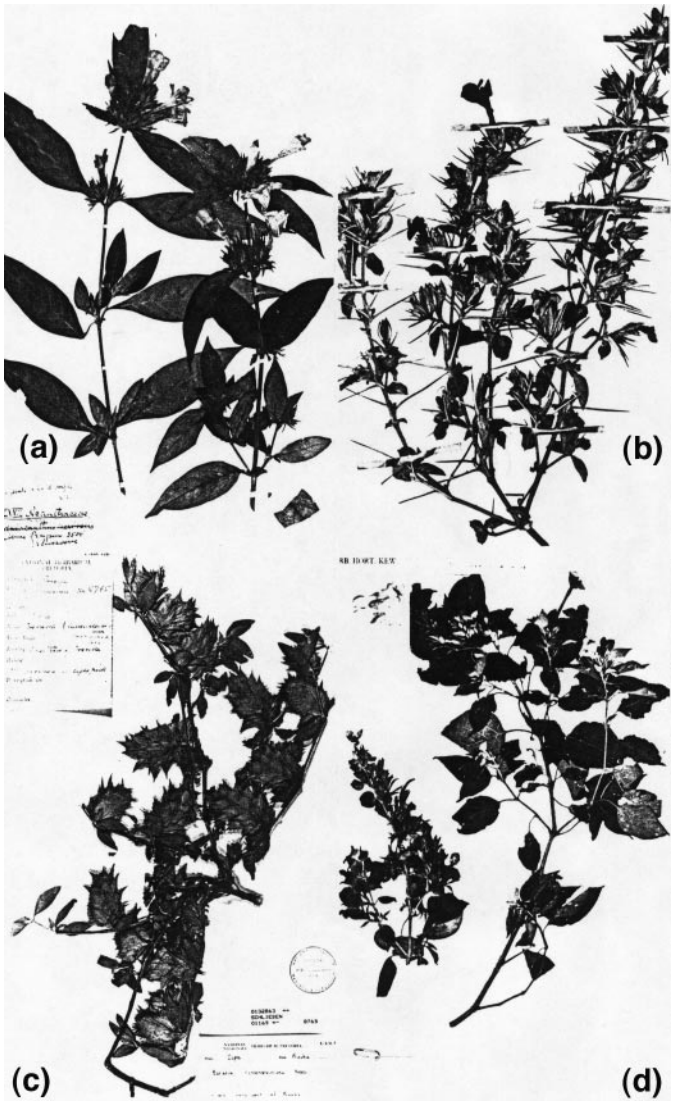

FIG. 3. Typical representatives of Section *Barleria*: (a) *B. cristata* L., from India and South East Asia, voucher: *Anderson 73* (E); (b) *B. bremekampii* Oberm., from Southern Africa, voucher: *Meeuse 9331* (K); (c) *B. lichtensteiniana* Nees, from Southern Africa, voucher: *Schlieben 8765* (PRE); (d) *B. longiflora* Linn. f. from India, voucher: *Borne 1677* (K).

Disjunction between West Africa and the New World Tropics

The disjunct distribution of *Barleria*, in which only one species of an essentially Old World genus occurs in the New World tropics, has not been extensively documented in the literature on Acanthaceae, although the same pattern has recently been published for a much smaller genus, *Phaulopsis* (Manktelow, 1996). This kind of disjunction is also interesting because the single species present in the New World, *B. oenotheroides*, also occurs in West Africa (Daniel, 1995). This distribution pattern has been discussed by Daniel (1995), but we feel that a few additional comments are necessary here.

Within the Acanthaceae, the larger, widespread genera tend to show one of three main types of distribution pattern: (i) fully pantropical with reasonably large numbers of species occurring in the tropical, subtropical and even temperate regions of both the New and Old World (e.g. *Justicia* L., with about 600 species world-wide); (ii) exclusively New World tropics (e.g. *Aphelandra* R. Br., which has approximately 175 species in tropical Americas), and (iii) exlusively Old World tropics, e.g. *Strobilanthes* Blume with about 250 species in Asia or *Thunbergia* L. with about 150 species in Africa (including Madagascar) and Asia (K. Vollesen, pers. comm.). The relationships among African and American Acanthaceae have been shown to be closer than believed previously (Daniel, 1995) with a number of genera, such as *Oplonia* Raf., *Mendoncia* Vell. ex Vand. (Daniel, 1995), *Phaulopsis* Willd. (Manktelow, 1996) and *Ecbolium* S. Kurz (K. Vollesen, pers. comm.) showing amphi-Atlantic disjunctions. In many cases, however, these disjunctions were previously masked by the tendency of identical taxa to occur under different names in Africa and South America (Gentry, 1993; Daniel, 1995).

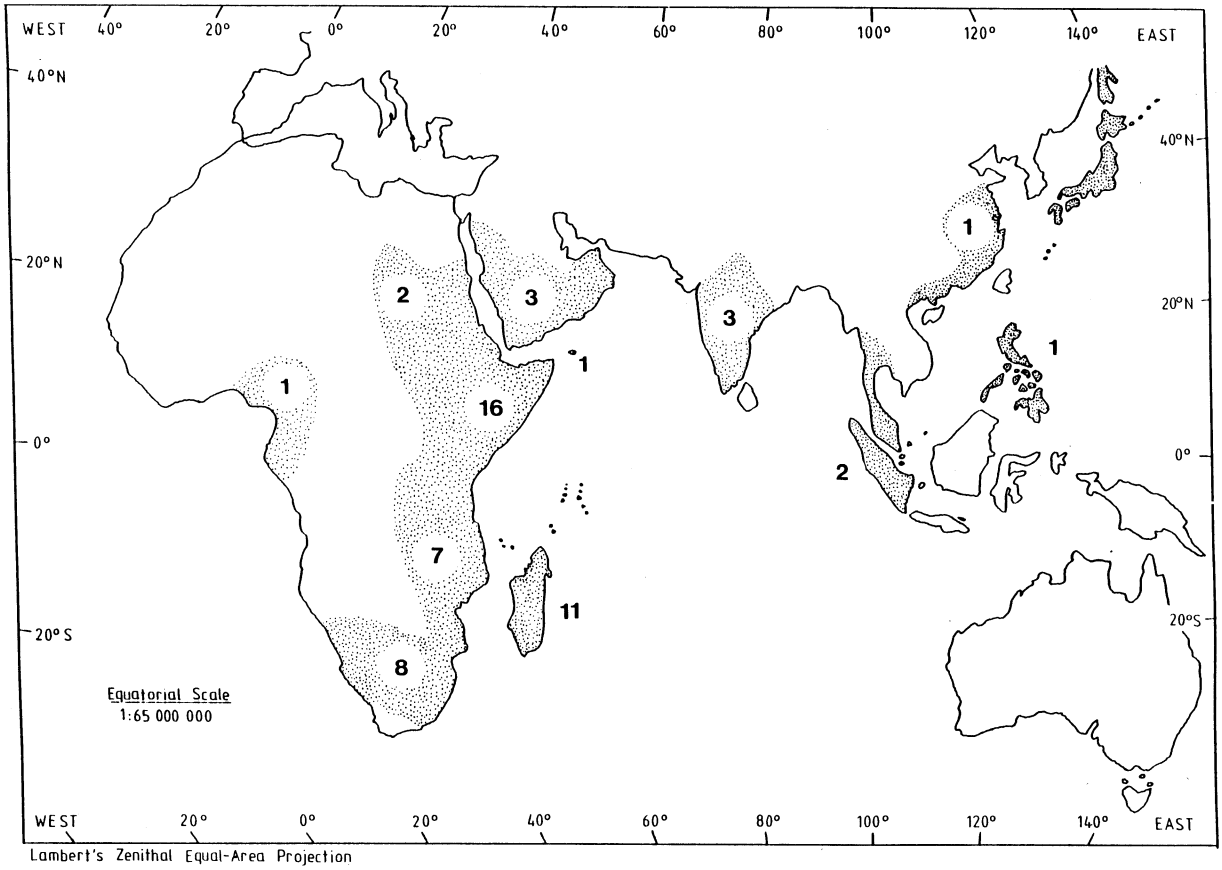

FIG. 4. Distribution of species of Section *Prionitis*. Stippled areas represent parts of the world in which Section *Prionitis* occurs and numbers indicate the number of species occurring in each part of the distributional range.

The role of long-distance dispersal

In a more general context, amphi-Atlantic connections are known in several plant groups (Brenan, 1973) and the biological relationships between the tropical biota of the Americas and Africa have been the subject of considerable biogeographic and systematic research (Meggers, Ayensu & Duckworth, 1973; Goldblatt, 1993). Most of the published disjunctions between Africa and the Americas (particularly South America) occur at the familial or generic levels (Brenan, 1973; Thorne, 1973) with the most often-cited cases including those of the Cactaceae, Bromeliaceae and Humiriaceae (Thorne, 1973; Stott, 1981) and some tropical leguminous trees of the subfamily Caesalpinioideae such as *Guibourtia* Benn. and *Cynometra* L. (Langenheim, 1973). Most of these disjunctions are explained on the grounds of occasional long-distance dispersal rather than convergence or past geography (Thorne, 1973), and many of the taxa involved are known to have fruits or seeds that are suitably adapted for long-distance water transport (Ayensu, 1973; Thorne, 1973), or are eaten by birds. Indeed, the consensus of most authors working at the familial and generic levels is that the similarities between the floras of tropical West Africa and South America can be adequately explained by occasional long-distance dispersal events (Gentry, 1993) either by the evolution of vagile disseminules, or through the activities of migratory birds (Hepper, 1965) or the movements of man (Manktelow, 1996). If the floras of the two regions are compared at the level of local communities, a high level of similarity is apparent and Gentry (1993) suggests that these similarities are a result of common origin rather than the product of chance migrations.

The role of past continental movements

In the Palmae, similar disjunctions to the kind seen in *Barleria* (i.e. at the species level) are known, but these can most often be plausibly explained on the basis of past continental movements (Uhl & Dransfield, 1987). The palms were already fairly diverse during the Cretaceous and so were in existence early enough that their present distribution has been greatly influenced by the break-up of Gondwanaland (Uhl & Dransfield, 1987). Even though the present-day distribution of *Barleria oenotheroides* is suggestive of Gondwanan ancestry, it seems unlikely that past continental movements can account for its distributional disjunction. There is no fossil evidence to suggest that the Acanthaceae were differentiated in the Americas during the Cretaceous (Romero, 1993; Daniel, 1995) when the African and South American landmasses were still in direct contact, let alone that differentiation had occurred at the species level in *Barleria*. Fossil pollen does indicate that the Acanthaceae formed a characteristic

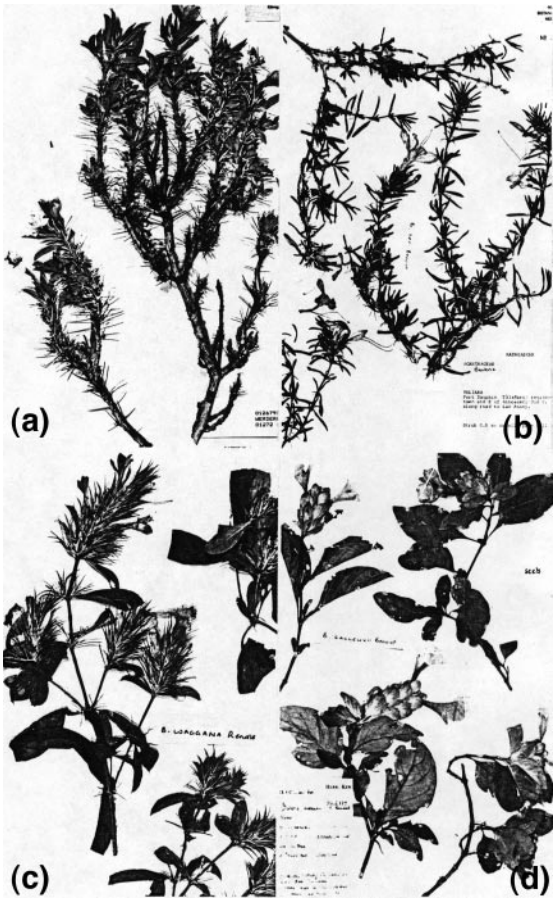

FIG. 5. Typical representatives of Section *Prionitis*. (a) *B. prionitis* L., from south western Africa, voucher: *Werdemann and Oberdieck 2427* (PRE); (b) *B. her* Benoist, from Madagascar, voucher: *McPherson & Pigeon 14 955* (MO); (c) *B. waggana* Rendle, from Ethiopia, voucher: *Thulin & Abdi Dahir 7589* (K); (d) *B. sacleuxii* Benoist from Tanzania, voucher: *Faulkner 2337* (K).

element of the palaeoflora of South America during the Miocene (25 million years ago), long after Africa and South America had split at the end of the Albian (Goldblatt, 1993; Pitman *et al.*, 1993).

The role of man

True disjunctions at the species level are uncommon (Brenan, 1973), except for some obvious trans-Atlantic introductions (Heiser, 1973) and those occasional instances where barriers to long-distance dispersal have been overcome (Ayensu, 1973). In *Phaulopsis* only one species, *P. talbotii* S. Moore, occurs in the New World and it is shared with West Africa. Manktelow (1996) concludes that this distribution has come about through unintentional anthropochoric dispersal related to the slave trade. In the case of *Barleria oenotheroides*, long-distance dispersal by means of floating on water is unlikely and past continental movements do not seem an adequate explanation for the intercontinental disjunction shown by this species. Daniel (1995) has concluded that *Barleria oenotheroides* arrived in the New World in fairly recent geological time, especially as this species occurs in some weedy habitats.

However, not all the localities at which it occurs (particularly in the southernmost parts of its Noetropical range), are disturbed and before simply inferring anthropochoric dispersal, it would be worth investigating more thoroughly, as suggested by Hepper (1965) in a more general context, the possible role of birds in determining this kind of distribution pattern.

Regional endemism

A particularly interesting aspect of the distribution patterns in *Barleria* is the relatively high level of endemism in most of the major regions in which the genus is represented (see Fig. 1). All but one species in Madagascar is endemic to the island. This, in itself, may not seem remarkable as high levels of endemism are known in many other plant and animal groups on this island (Uhl & Dransfield, 1987). What is especially interesting, however, is the high degree of endemism in other regions such as the Indian subcontinent (75% endemism), West Africa (72%), Southern Africa (65%) and East Africa (55.8%). In general, species of endemic or regionally localized distribution are relatively few in tropical Africa, with many species exhibiting widespread, if discontinuous, distributional ranges (Richards, 1973). This general trend is not upheld at any taxonomic level in African *Barleria* and certainly is not true for other large genera of the Acanthaceae, such as *Blepharis*, *Justicia* and *Thunbergia*, which also have fairly large numbers of localized endemics (K. Vollesen, pers. comm.).

The data presented in Table 1 show that the members of the different sections of *Barleria* tend to be concentrated in certain geographic regions, a pattern also known to occur in *Blepharis* (K. Vollesen, pers. comm.). Furthermore, many of the endemics in the different regions belong predominantly to only one or two of the sections. East and West Africa are the only regions of the world in which all sections of *Barleria* are represented. Southern Africa has representatives of all the sections with the exception of only Section *Cavirostrata*. The *Barleria* flora of the East African region is dominated by Sections *Fissimura* (eighteen species) and *Prionitis* (sixteen species), followed by Section *Barleria* (thirteen species) and smaller numbers of species from each of the other sections (see Table 1). Most of the endemics in the East African region are from Sections *Fissimura* (e.g. *B. boehmii* Lindau, *B. lukafuensis* Wildem., Fig. 12) and *Prionitis* (e.g. *B. waggana* Rendle, Fig. 5) with fewer numbers of endemics from sections *Somalia* (e.g. *B. glandulifera* Lindau, *B. angustiloba* Lindau, Fig. 10) and *Stellatohirta* (e.g. *B. splendens* E.A.Bruce, Fig. 12). The neighbouring Ugandan region is also dominated by members of Section *Fissimura*, with all but two of the species belonging to this section. The only other sections represented in this region are *Barleria* and *Somalia*.

The North African and Arabian regions are similar in that the Sections *Barleria, Prionitis* and *Fissimura* are more or less equally well represented. Neither of these regions has any members of Sections *Chrysothrix* and *Cavirostrata*. A point of difference between these two regions is that Section *Somalia* (which has only one species in North Africa) is represented by four species in Arabia, and Section

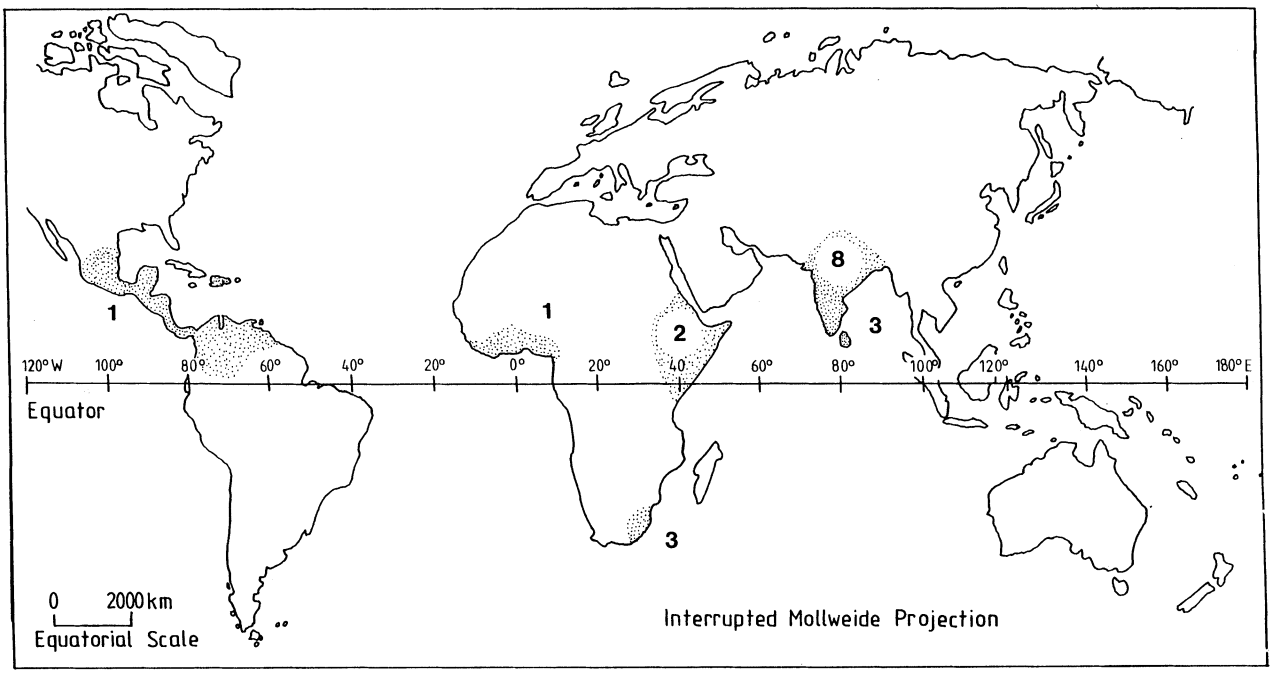

FIG. 6. Distribution of species of Section *Chrysothrix*. Stippled areas represent parts of the world in which members of Section *Chrysothrix* occur and numbers indicate the number of species occurring in each part of the distributional range.

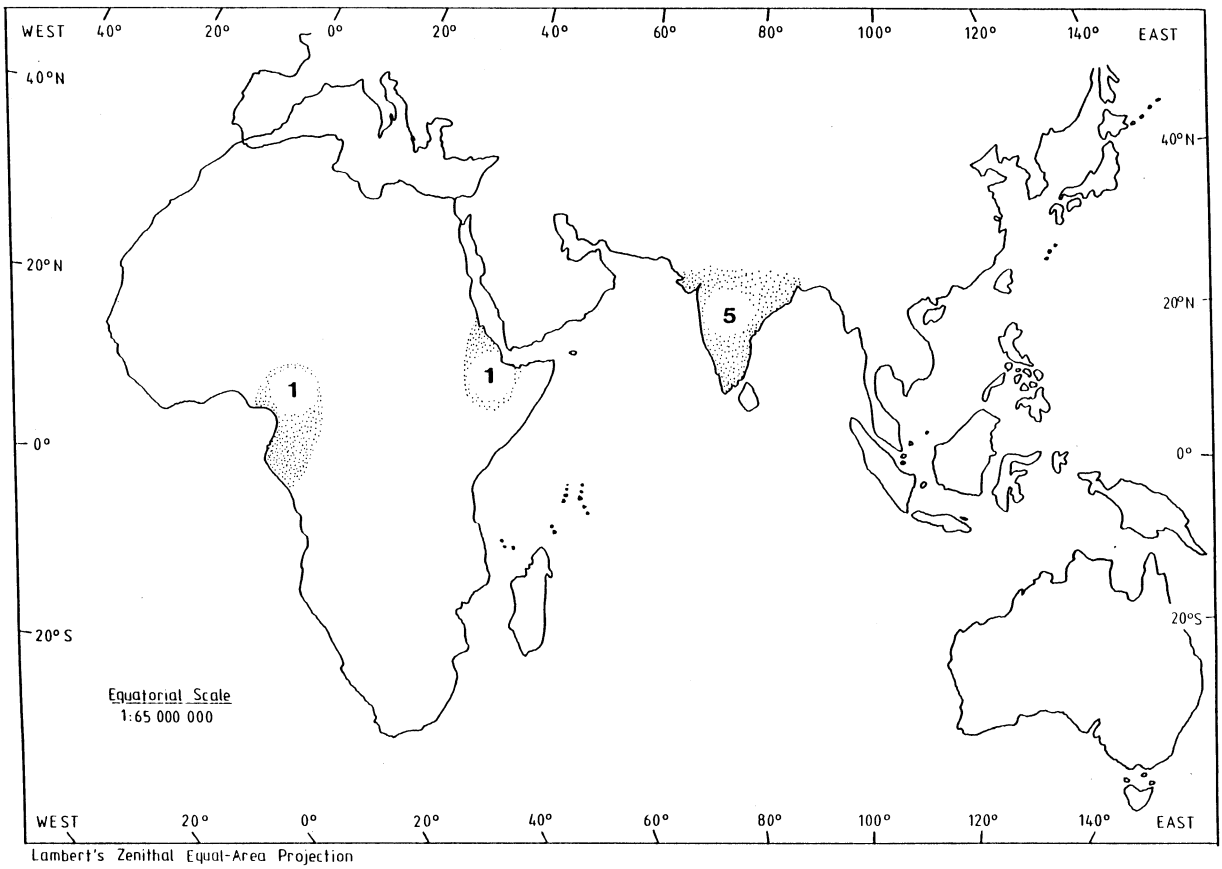

FIG. 7. Distribution of species of Section *Cavirostrata*. Stippled areas represent parts of the world in which members of Section *Cavirostrata* occur and numbers indicate the number of species occurring in each part of the distributional range.

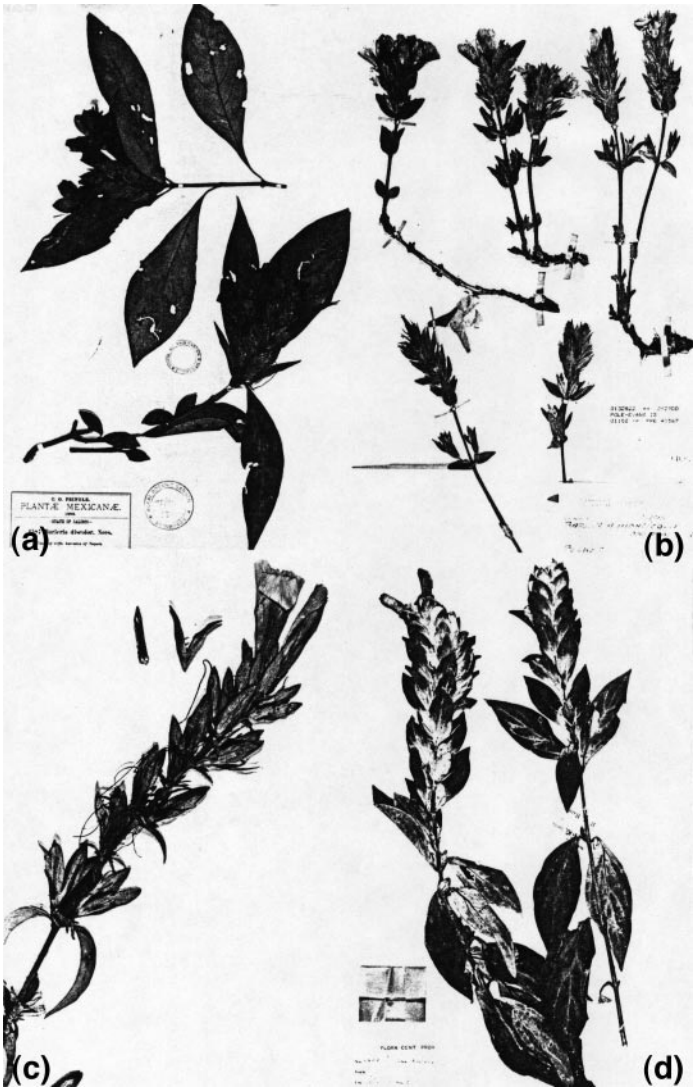

FIG. 8. Typical representatives of Sections *Chrysothrix* and *Cavirostrata*. (a) *B. oenotheroides* Dum. Cours, from Mexico, voucher: *Pringle 4587* (MO); (b) *B. monticola* Oberm., from southern Africa, voucher: *Pole Evans 40567* (PRE); (c) *B. grandis* Nees, from Ethiopia, voucher: *Friis 4526* (K); (d) *B. gibsonii* Dalz., from India, voucher: *Haines 2406* (K).

Stellatohirta (which is absent from North Africa) has one species, *B. hildebrandtii* S.Moore, in Arabia.

All of the sections are represented in West Africa, but about one third of the species in this area belong to section *Fissimura*; the remaining two thirds of the species fall mainly into Section *Barleria*, with only one or two representatives from each of the other sections (Table 1). Members of the 'typical' group of Section *Somalia* are present in West Africa, but there are no representatives from the other parts of the section in this region. The endemics in this region belong mainly to section *Fissimura* (e.g. *B. talbotii* S. Moore) and Section *Stellatohirta* (e.g. *B. argenteo-calycina* De Willd.).

The *Flora Zambesiaca* and southern African regions are both dominated (at least half the number of species in each case) by members of Section *Barleria.* Section *Somalia* is also well represented in these two regions, especially in southern Africa where seventeen of the forty-two species of the section occur. The degree of endemism in this region is high (65%) with the majority of endemics contributed by members of Sections *Barleria* and *Somalia*. Section *Somalia* can be divided into two groups, based on differences in corolla morphology and pubescence. The 'typical' group is characterized by the presence of biramous hairs on vegetative parts, bracts and calyces and the possession of spotty corollas, both considered to represent derived character states. Most of the members of Section *Somalia* that occur in southern Africa belong to the 'atypical' group within the section (e.g. *B. lancifolia* S.Moore), with only one species (currently undescribed) from the 'typical' group occurring in this region. Conversely, most of the members of Section *Somalia* in East Africa belong to the more typical group with biramous hairs and spotty corollas.

The Angolan region is dominated by members of Section *Somalia*, the second most highly derived taxon in the genus, accounting for about ten of the twenty-five species in the region. There are approximately equal proportions of

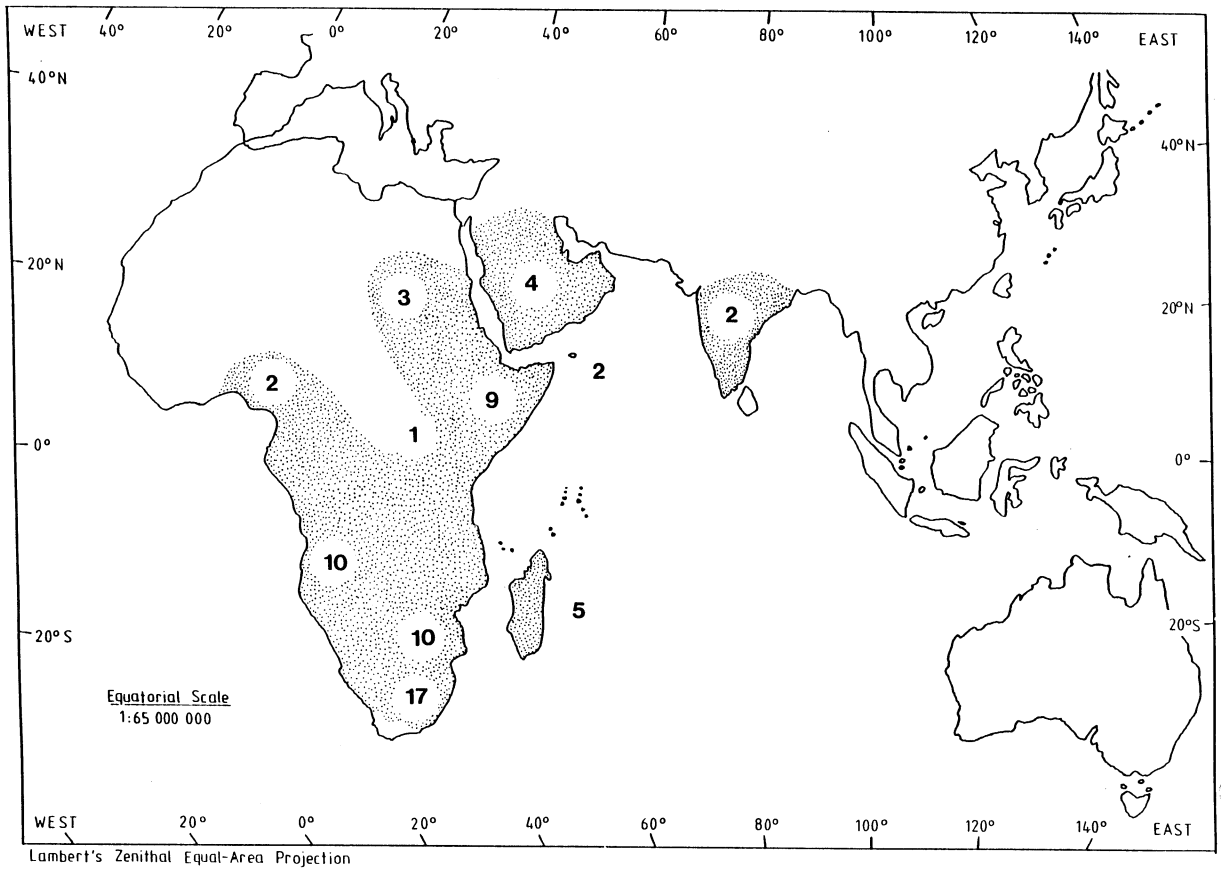

FIG. 9. Distribution of species of Section *Somalia* (Oliv.) Lindau. Stippled areas represent those parts of the world in which members of Section *Somalia* occur and numbers indicate the number of species occurring in each part of the distributional range.

Sections *Barleria* and *Stellatohirta* in the area, accounting for the bulk of the remaining species. Most of the thirteen endemic species in this region belong to Sections *Somalia* and *Stellatohirta* (e.g. *B. salicifolia* S. Moore and *B. buddleoides* S. Moore, Fig. 12). The *Flora Zambesiaca,* southern African and Angolan regions lack any members of Section *Cavirostrata*, and the only one of these three regions with any species from Section *Chrysothrix* is southern Africa.

In all other regions *Barleria* tends to have representatives from only a few of the sections. In Madagascar, for example, only Sections *Barleria, Prionitis, Somalia* and *Fissimura* are represented and in the Americas only Section *Chrysothrix* is present.

Degrees of similarity between regions

The relatively high levels of endemism shown in Table 1 and Fig. 1 are paralleled by correspondingly low degrees of similarity between the regions. The highest degree of similarity shown between any two regions is that of 44% between southern Africa and the countries of the *Flora Zambesiaca* region (Table 3). The latter region in turn shares 15.8% of its species with East Africa, a higher degree of similarity than it shows to Angola, which spans a similar latitude (Table 3). Approximately half of the species occurring in Angola are also endemic to it and the remaining species provide a link between southern Africa and the Guineo–Congolian region of West Africa. The index of similarity between southern Africa and East Africa is low (6.8%). Balkwill (1985) and Balkwill & Getliffe Norris (1989) found that a number of species of *Peristrophe* Nees and *Dicliptera* Juss. (Acanthaceae) occur in southern Africa (particularly the dry western parts) and East Africa with a distinct Arid Corridor (Balinsky, 1962) link. This pattern is not reflected in the distribution of species of *Barleria* as only a few species, notably *B. lugardii* C.B.Cl., *B. taitensis* S. Moore (= *B. rogersii* S. Moore) and *B. mackenii* Hook.f. from the Namibian region are shared with East Africa. The East African region shows a greater similarity to Arabia and North Africa than it does to any other region of Africa (Table 3). The number of species shared between North Africa and the central African region including Uganda, Rwanda and Burundi is greater than the number shared by this region and neighbouring East Africa. The degree of similarity shown between India and all other regions is generally low (less than 17%) as many of the taxa occurring in this region are endemic to it, but the affinities it does show lie more strongly with the Far East, Sri Lanka and Arabia than they do with any African region (see Table 3). The only African regions sharing any species with India are

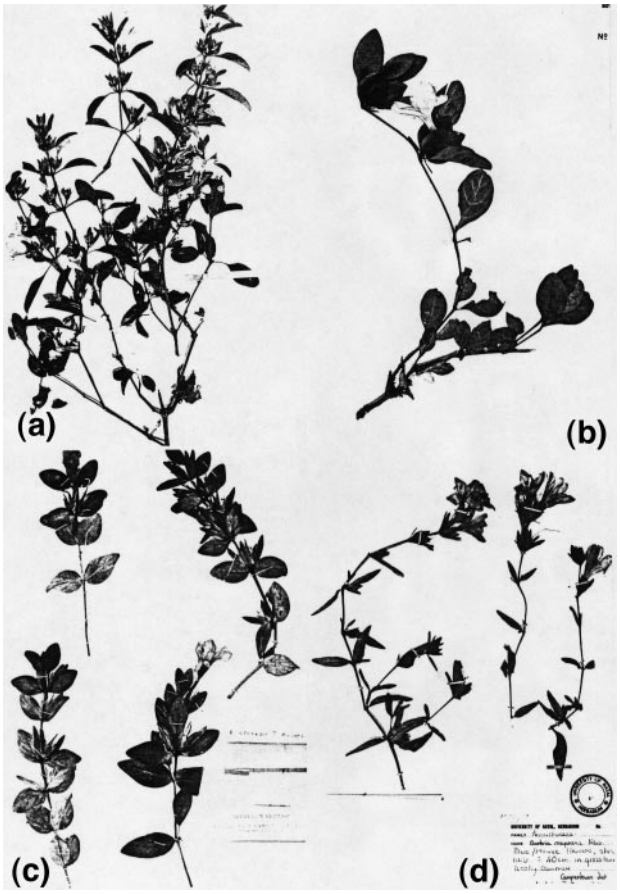

FIG. 10. Typical representatives of Section *Somalia*. (a) *B.* sp. aff. *glandulifera* Lindau, from Kenya, voucher: *Greenway 13534* (PRE); (b) *B. calophylloides* Lindau, from Malawi, voucher: *Pawek 10904* (MO); (c) *B. stocksii* T.Anders., from India, voucher: *Gamble 20438* (K); (d) *B. meyeriana* Nees, from southern Africa, voucher: *Edwards 25* (NU).

North Africa (similarity index of 9%), East Africa (2.7%) and southern Africa (1.9%).

Distribution trends within each section

Only two of the sections, *Barleria* and *Prionitis*, are widespread, all the others have restricted distributions. Sections *Fissimura*, *Stellatohirta* and *Somalia* are largely restricted to Africa and Sections *Chrysothrix* and *Cavisrostrata* occur mainly in India.

Widespread taxa

Section *Barleria* (typical members of which are illustrated in Fig. 3) is the most widespread, occurring almost throughout the entire distributional range of the genus (see Figs 1 and 2). It is absent only from the New World and is weakly represented in the Far East. Its greatest representation is in Africa where it is present in all regions, but it is especially abundant in the south eastern parts of the continent. Members of this section predominate in subtropical and temperate parts of the southern African and *Flora Zambesiaca* regions (Fig. 2), especially in hot, at least seasonally dry areas. Section *Barleria* accounts for half the total number of species occurring in the southern part of Africa, with its next greatest number of species in East Africa.

Section *Prionitis* is the most highly derived infra-generic taxon within *Barleria*. It occurs almost throughout the geographic range of the genus, being absent only from the Neotropics and from the Angolan and Ugandan regions of Africa(Fig. 4). It is weakly represented in West Africa (one species), southern Asia (two species) and the Far East (one species). This section has its greatest number of species in East Africa, particularly in Somalia, Ethiopia and Tanzania, with smaller centres of abundance in Madagascar, Southern Africa and the *Flora Zambesiaca* region (Fig. 4). If the number of species present relative to the area of the region is taken into consideration, then the greatest centre of diversity for this section would be in Madagascar, where Section *Prionitis* accounts for at least 40% of the total number of species of *Barleria*. It should be noted here, however, that there are a number of undescribed taxa in the East African region. When the species in this genus are next revised it is most likely that the number of species recognized in Section *Prionitis* will be considerably increased, thus making this section account for a greater proportion of the total number of species in the region. Some of the most widespread taxa in *Barleria*, such as *B. prionitis*, occur in this section. Typical representatives of Section *Prionitis* are illustrated in Fig. 5.

Taxa with restricted distributions

Sections *Chrysothrix* and *Cavirostrata*, which have the most restricted distributions within the genus, have their greatest representation in India and Sri Lanka (see Figs 6 and 7). Section *Chrysothrix* (Fig. 8) is closely related to Section *Barleria* and occurs mainly in India (eight species), with three species in southern Africa (all localized endemics) and one each in West Africa and the Caribbean–Central American region (Fig. 6).

Section *Cavirostrata* (Fig. 8), which is characterized by a number of unusual features, has the most restricted distribution of all the infra-generic taxa, with five of the seven species restricted to India (Fig. 7). The other two species of this group are known from relatively few collections and occur in Africa, one in the West and the other endemic to Ethiopia. Section *Cavirostrata* is relatively highly advanced and is most closely related to sections such as *Fissimura*, *Stellatohirta* and *Somalia*. It is interesting that most of the character reversals (such as glabrous seeds) that occur in Subgenus *Prionitis* occur in Section *Cavirostrata*.

The remaining sections, *Somalia*, *Fissimura* and *Stellatohirta*, are essentially African in their distribution. Section *Somalia*, as a whole, is largely limited to Africa, although it has a few representatives in Arabia and India (Fig. 9). Different groups of species within this section tend to be concentrated in particular geographic regions. The species with spotty corollas and biramous hairs are concentrated in East Africa with only one representative occurring in South Africa. Conversely, the other species within this section occur mainly in eastern South Africa and Angola where they account for a large proportion of

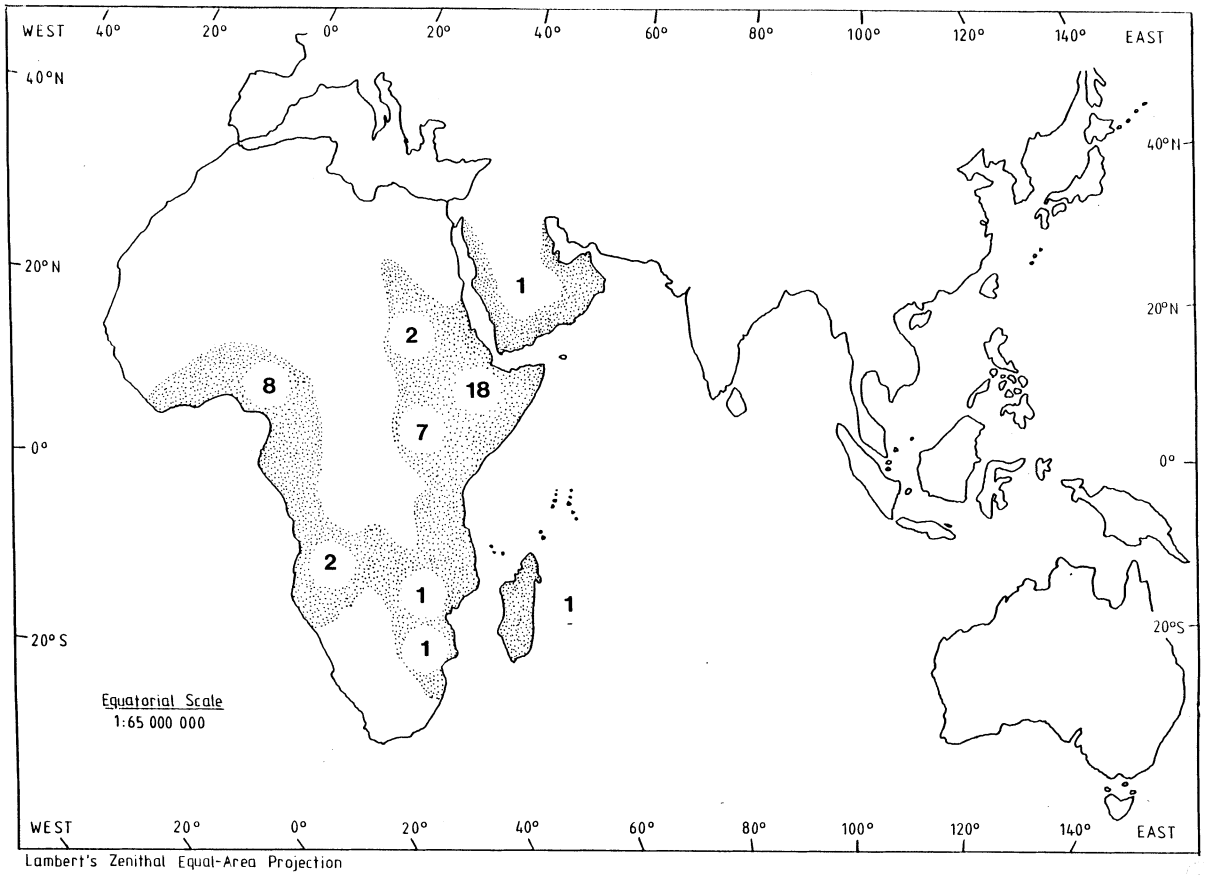

FIG. 11. Distribution of species of Section *Fissimura*. Stippled areas represent those parts of the world in which members of Section *Fissimura* occur and numbers indicate the number of species occurring in each part of the distributional range.

the endemic species. Section *Somalia*, typical representatives of which are illustrated in Fig. 10, is most closely related to Section *Prionitis*.

Section *Fissimura*, characterized by its unique fruit morphology, is almost entirely African with only one species in Madagascar (Fig. 11). The centre of diversity for this section is in East Africa (particularly Kenya and Tanzania), where eighteen of the twenty-one species occur. Members of this section also dominate the West African and Ugandan region, contributing many of the endemics in these regions. Most of the representatives of this section in East Africa are highly localized endemics, such as *Barleria lukafuensis* (Fig. 12), an unusual creeper with bird-pollinated flowers occurring only in the Uluguru Mountains of Tanzania. Only a few species occur in the southern parts of Africa (Fig. 11).

Section *Fissimura* is most closely related to Section *Stellatohirta*, which is also largely restricted to Africa (Fig. 13). Only one species from Section *Stellatohirta*, *B. hildebrandtii* S. Moore, occurs off the African continent in the Arabian Peninsula, but this species is also shared with North and East Africa. The centre of diversity of this section is in southern Central Africa with most species, several of which are endemics (e.g. *B. salicifolia* S.Moore, Fig. 12), occurring in the Angolan and *Flora Zambesiaca* areas (Fig. 13). Although the number of species from this section in West Africa is relatively small, all of them are localized endemics. Typical representatives of this group are illustrated in Fig. 12.

Relationship between soil type, seed dispersal and localized distribution patterns

There are few truly widespread species in *Barleria*. The most widespread species, occurring naturally in all parts of the distributional range except Central America, is *B. prionitis* L. (Section *Prionitis*). In Africa, the next most widespread species are *B. grandicalyx* Lindau (Section *Barleria*) and *B. ventricosa* Hochst. ex Nees (Section *Fissimura*) which occur in Arabia and throughout western, Central and East Africa. In southern Africa *B. obtusa* Nees (Section *Barleria*) and *B. lancifolia* T.Anders. (Section *Somalia*) are the most widespread, with the latter occurring throughout the southern African region and *B. obtusa* being widespread in the eastern parts of the region. Many species of *Barleria* (and other Acanthaceae), particularly the endemics, have very localized distributions; where these species occur, they tend to be very abundant, but in a broader context their distribution is very restricted. For example, *Barleria greenii* M. & K. Balkwill (Fig. 14), is known from only seven localities within the same degree square in the Estcourt region of the midlands of KwaZulu-Natal in South Africa.

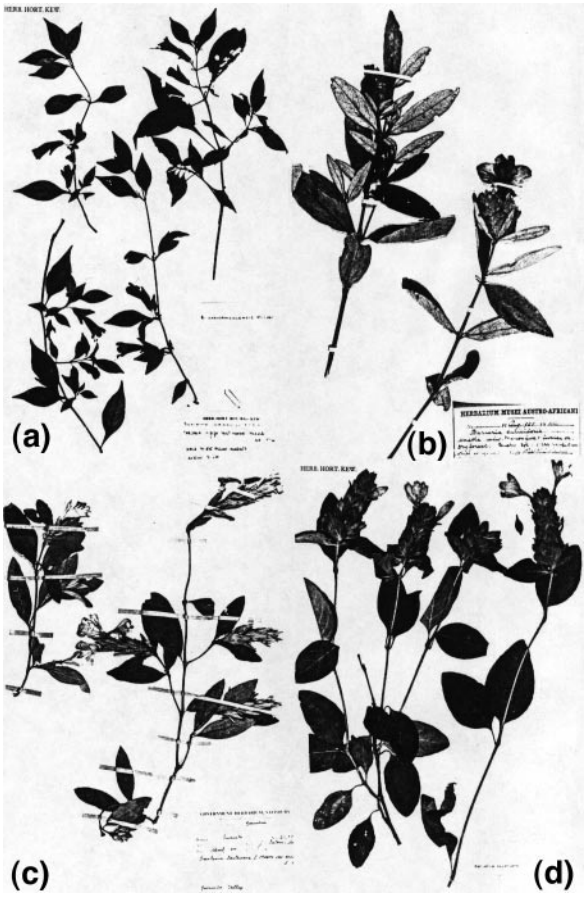

FIG. 12. Typical representatives of Section *Fissimura* (a) and Section *Stellatohirta* (b–d). (a) *B. lukafuensis* Wildem., from Tanzania, voucher: *Congdon 209* (K); (b) *B. salicifolia* S. Moore, from Angola, voucher: *Pocock 89145* (SAM); (c) *B. taitensis* from Zimbabwe, voucher: *Anton-Smith 211772* (SRGH); (d) *B. splendens* E.A.Bruce, from Tanzania, voucher: *Bidgood, Mwasumbi and Vollesen 1096* (K).

The plants, which can reach up to 2 m in height, form dense populations with very discrete boundaries. The populations of this species are only found at altitudes above 1200 m on heavy, black, shrink-swell clays within the region (Balkwill, Balkwill & Vincent, 1990). Similarly, *Barleria dolomiticola* M. & K. Balkwill (Fig. 14) occurs only in the Wolkberg mountain region of the Mpumalanga Province (former Eastern Transvaal) of South Africa and is restricted to outcrops of dolomite (Balkwill, Stalmans & Balkwill, 1992). In these and many other cases the distributions can be related to particular soil or rock types, but the manner in which the seeds are dispersed ballistically over short distances may also account for the clumped distribution of the populations of these species within a particular area.

GENERAL DISCUSSION AND CONCLUDING REMARKS

The distribution patterns in *Barleria* are notable in several respects, particularly within the Acanthaceae. The overall distribution of the genus is characterized by a disjunction between the tropics of the Old and New World (with only one of the 300 species occurring in the Neotropics). Other notable features of the distribution patterns in *Barleria* include high levels of regional endemism and strong geographic concentration of the species belonging to the infra-generic taxa. The *Barleria* floras of different regions of the world thus tend to be highly distinctive and are dominated by members of only a few (or even one) of the seven sections recognized within the genus. The highest degree of similarity between any two regions occurs between southern Africa and the Flora Zambesiaca region. The degree of similarity between these regions and others in Africa is relatively low. East Africa shows greater similarity to North Africa than to other parts of Africa. The *Barleria* flora of India is highly distinctive; it shows a greater degree of similarity to other Asian regions than to any region in Africa, although the eastern, northern and southern African regions do show low levels of similarity to the Indian subcontinent.

The genus shows two centres of species richness, one in East Africa and a second, slightly lower one in southern Africa. Only two of the Sections, *Barleria* and *Prionitis*, are widespread, occurring in all parts of the distributional range except the Neotropics. The remaining five sections all have fairly restricted distributions, being more or less confined to Africa or to India. Species belonging to all of the sections occur in East Africa, which also has the greatest species richness and, using traditional criteria (Humphries & Parenti, 1986) would probably be designated as the centre of origin of the genus. The distribution patterns displayed by the species parallel those of the sections, with there being very few widespread species. Most of the species, but particularly the endemics, have very localized distributions.

This account of the biogeography of *Barleria* has to be regarded as preliminary; although we have proposed a new classification of *Barleria* (Balkwill & Balkwill, 1997), much taxonomic work remains to be completed at the species level and so exact numbers of species recognized in each region need to be revised. A cladistic biogeographic study has not been undertaken at this stage as it seems pointless to base a study of this kind on confused taxonomy at the species level. Hopefully, further research, and particularly expansion of the cladistic aspects of the work will cast further light on the biogeographic patterns within *Barleria*. Particular areas that are worthy of future investigation include: rigorous determination of the centre of origin of the genus, elucidation of patterns of migration and radiation and investigation of factors responsible for the high degrees of endemism displayed in the different regions in which *Barleria* occurs.

ACKNOWLEDGMENTS

This work formed part of a larger, monographic study of *Barleria* which was made possible by funding from the University of the Witwatersrand and Foundation for Research Development, South Africa. Dr Dick Brummitt and Dr Alan Radcliffe-Smith of the Herbarium, Royal Botanic Gardens, Kew, are thanked for nomenclatural advice and for checking the Latin diagnoses, and Dr Stuart

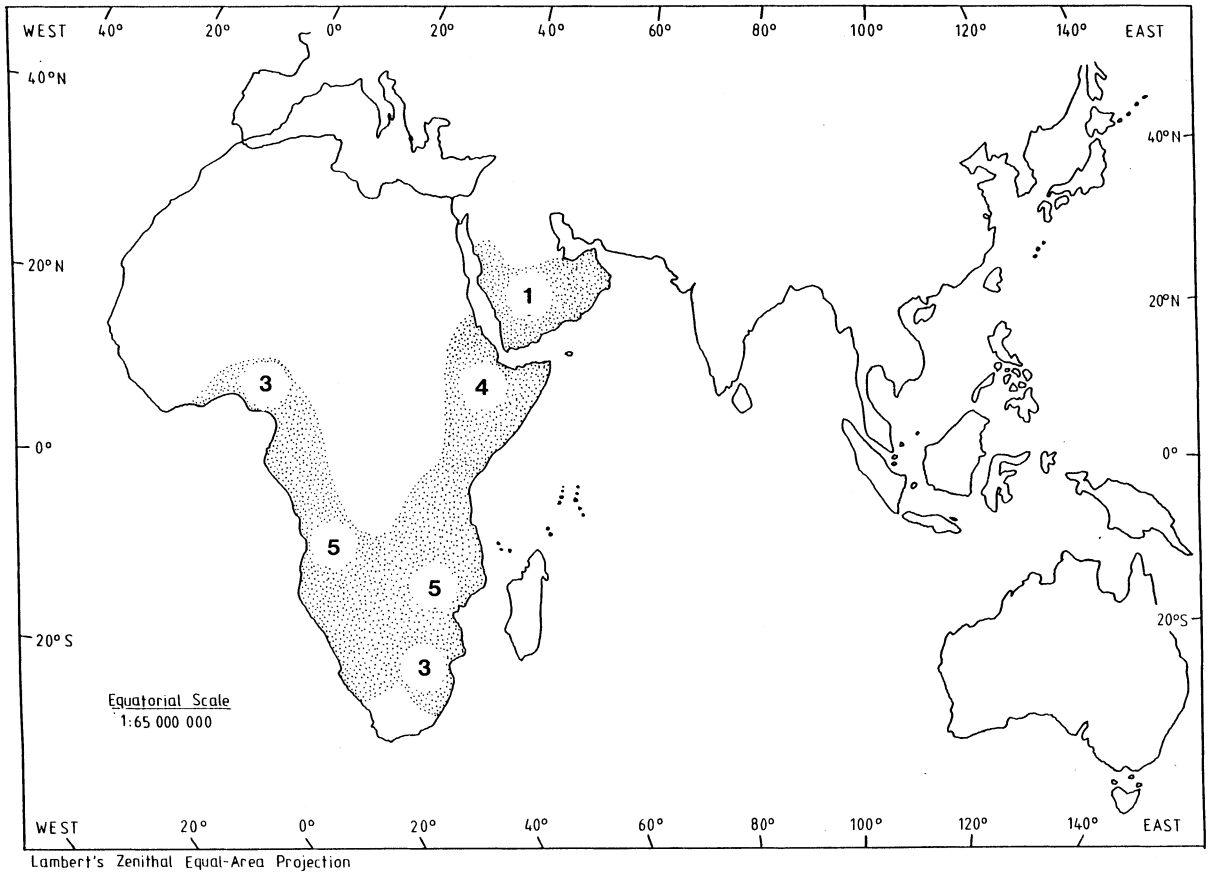

FIG. 13. Distribution of species of Section *Stellatohirta*. Stippled areas represent those parts of the world in which members of Section *Stellatohirta* occur and numbers indicate the number of species occurring in each part of the distributional range.

Sym (Department of Botany, University of the Witwatersrand) is thanked for initial help with the Latin diagnoses. Kaj Vollesen at the Herbarium, Royal Botanic Gardens, Kew, is thanked for his helpful input.

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FIG. 14. Regional endemics with highly restricted distributions: (a) *B. greenii* M. & K. Balkwill (Section *Barleria)*; (b) *B. dolomiticola* M. & K. Balkwill (Section *Somalia*). Drawn by M.-J. Balkwill.

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APPENDIX 1. Formal taxonomy and validation of sectional names.

Seven sections (*Barleria*, *Chrysothrix* M. Balkwill, *Cavirostrata* M. Balkwill, *Stellatohirta* M. Balkwill, *Fissimura* M. Balkwill, *Somalia* (Oliv.) Lindau and *Prionitis* (Nees) Lindau) within two subgenera (*Barleria* and *Prionitis* (Nees) C.B.Clarke) are recognized by us in *Barleria*. Three of the sections (*Barleria*, *Somalia* and *Prionitis*) are retained much as previously circumscribed in earlier classifications, but four are described anew or are formally accorded status as sections for the first time in this classification. It is thus necessary to validate and diagnose the names of the newly described taxa here. A full account of the nomenclature, synonymy and typification will be published separately (Balkwill & Balkwill, 1997).

New sections recognized within *Barleria*

1. Subgenus *Barleria*
   Type species: *B. cristata* L.

(i) Section *Chrysothrix* M.Balkwill, *sect. nov., ob capsulam 4-seminalem sine et rostro apicali et septo cum parte ad apicem angusta et membranacea, haec sectio Sectioni Barleria similissima est, sed proprie cum pilis adpressis et luteis et cum floribus in synflorescentiis terminalibus portatis; systemae spinarum axillares in hac turma destitutae.*
   Type species: *B. oenotheroides* Dum.Cours.

2. Subgenus *Prionitis* (Nees) C.B.Clarke
   Type species: *B. prionitis* L.

(i) Section *Stellatohirta* M. Balkwill, *sect. nov., haec sectio ob fructus 2-seminales sectionibus Somalia et Fissimura magnopere similis, sed pili tortuosis stellatis dendriticisque distinguibilis; Sectio Stellatohirta a sectione Somalia absentia rostri solidi et apicalis in capsulae et a sectione Fissimura absentia parietum findentium in fructu differt.*
   Type species: *B. albostellata* C.B.Cl.

(ii) Section *Fissimura* M. Balkwill, *sect. nov., ob capsulam compressum et 2-seminalem cum alis ligneis et septo submembranaceo distincta; haec sectio sectioni Stellatohirtae similis est sed per parietes findentes et absentiam pilorum tortuosorum distinguenda.*
   Type species: *B. ventricosa* Hochst. ex Nees.

(iii) Section *Cavirostrata* M. Balkwill, *sect. nov., haec sectio similissima est sectionibus Somalia et Stellatohirta sed ob et semina quattuor (non duo) et capsulam cum rostro cavo et apicali vice capsulis sine rostris (Sectio Stellatohirta) vel vice capsulis cum rostris solidis et apicalibus (Sectio Somalia) differt; species aliquot (plures) in hac turma seminibus glabris aut subglabris.*
   Type species: *B. grandis* Nees.

BIOSKETCHES

The latest research interest of the senior author has been the classification, phylogeny, taxonomy and biogeography of the genus Barleria (Acanthaceae). Current research is focussing on detailed investigation of the taxonomy and breeding biology of particular species complexes within the genus, especially those with restricted distributions. The author is also actively involved in a research programme investigating the taxonomy, biogeography and biosystematics of selected taxa growing on serpentine in the Barberton Greenstone Belt of South Africa, with particular emphasis on rare taxa or restricted endemics.

This author has been employed as a lecturer in botany since 1989 in the Department of Botany, University of the Witwatersrand, South Africa. Latest major publication: Delimitation and Infrageneric classification of Barleria (Acanthaceae) in *Kew Bulletin* 52 (3): 535–573.

The second author has been the Curator of the C.E. Moss Herbarium, University of the Witwatersrand, S.A. since 1989. His research has been centred on systematic studies in the Acanthaceae, Labiatae and Compositae and taxonomic, floristic and ecological studies of vegetation of serpentine areas in southern Africa