THE GEOGRAPHICAL DISTRIBUTION OF COMPOSITAE NATIVE TO NATAL

O. M. HILLIARD*

ABSTRACT. The geographical distributions of 537 of the 551 species of Compositae native to Natal are analysed. In the consideration of endemism Natal is treated as a biological area with somewhat more extended boundaries than the political province. Twelve groups (or patterns) with four subgroups are recognized. The largest (group 1) is that of the Drakensberg endemics numbering 111, and there are 56 species endemic to other parts of Natal (group 3). The remaining groups are based on patterns of distribution both inside and outside Natal.

The high endemism of Compositae in Natal is discussed and the validity of some of the small groups recognized is supported by reference to other families. The relationship of the patterns described to some of the major phytochoria recognized in Africa is briefly considered. The high mountain endemic flora of Natal seems to be largely autochthonous, and links to the Afro-montane region are, at least at the level of species, rather slender.

Compositae in Natal outnumber any other family of flowering plants: 637 species in 113 genera, about 200 more species than either the legumes or the grasses, the other major constituents of the flora. Native species number 551, in 79 genera (and discoveries are still being made). Table 1 indicates the world-wide distribution of the 13 classical tribes of Compositae, the approximate number of genera in each, and the number of genera and species occurring naturally in Natal.

The following analysis of the geographical distribution of these species is based upon a recent account of the family in Natal (Hilliard 1977, where all the taxonomic references will be found).

Natal covers only a small area of some 90,000 sq. km, about the size of Portugal, but it contains 5000 species of flowering plants. It is a very rugged province, only c. 100 to 250 km wide, but rising rapidly from sea level to over 3000 m in a series of great "steps" very roughly parallel to the coast. These are deeply dissected by numerous rivers flowing from west to east, often in deep gorges. The 31° meridian and 29° parallel quarter the country. Latitude allied to rapid elevation inland engender climates ranging from tropical to subtropical along the coast to temperate and montane on the highlands and mountains. The east-west orientation of the ridges and valleys creates hot dry N-facing slopes and cooler, moister S-facing ones. There is thus considerable variation in altitude, aspect, rainfall, soils and climate. Most of the rain falls in summer, between October and March, when the days are warm to hot. Winters are cool to cold, and usually very dry; although the days may be warm, night frosts are common above an altitude of c. 600 m. The vegetation is richly diversified, and has both tropical and temperate affinities.

Natal can be roughly divided into three main regions: a coastal region from sea level to 600 m; a midlands region from 600–1500 m; and an uplands region above 1500 m. The coastal region can be further subdivided into the sandy seashore, a narrow zone of coast forest now largely cleared, many deep river valleys and gorges particularly south of the Tugela, and a sandy coastal

* Dept. of Botany, University of Natal, Pietermaritzburg, South Africa.

TABLE 1

The world-wide distribution of the 13 classical tribes of Compositae, the approximate number of genera in each tribe, and the number of genera and species native in Natal.

	Distribution	*Approx. total no. of genera*	*No. of genera native in Natal*	*No. of species native in Natal*
Vernonieae	Pantropical and subtropical	50	2	27
Eupatorieae	Most species American	50	2	3
Astereae	World-wide, mostly temperate & montane	110	10	44
Inuleae	World-wide	200	26	184 (125 *Helichrysum*)
Heliantheae	Mostly American	170	7 (including 2 pantropical weeds)	9
Helenieae	American	60	—	—
Anthemideae	Mostly extratropical Old World, particularly Mediterranean & S Africa	60	9	34
Senecioneae	World-wide	80	6	165 (126 *Senecio*)
Calenduleae	Old World, particularly Mediterranean & S Africa	10	3	14
Arctoteae	Old World, chiefly S Africa	16	7	44 (30 *Berkheya*)
Cardueae	Mostly Eurasian	50	—	—
Mutiseae	Mostly S hemisphere, particularly in the Andes	70	2	12
Lactuceae	Mostly N hemisphere	65	5	15
		—	—	—
			79	551
			—	—

plain broadest in the north where it continues into Moçambique and pinching out near Mtunzini, north of Durban. This coastal plain, the Tongaland plain, is largely covered in more or less open woodland; forest or woodland also fills the major river valleys elsewhere and therefore penetrates far inland.

The midlands region, intersected by the many deep, warmer river valleys, is mostly rolling grass-covered hills with relict forest patches on the southerly slopes. Wet mists are frequent in summer along the edges of rising ground facing SE to SW.

The midlands merge into the foothills of the Drakensberg escarpment. These foothills are very broken, with innumerable valleys and slopes banded with outcropping rock. Some of this (roughly between 1900 and 2300 m) is

FIG. 1. Map of southern Africa showing localities referred to in the text. Contours are at approx. 350, 1400 and 1800 m; land above 1800m shown black.

1, Zoutpansberg; 2, Waterberg; 3, Magaliesberg; 4, Transvaal Drakensberg; 5, Natal Drakensberg; 6, East Griqualand; 7, Cape Drakensberg; 8, Witteberg; 9, Pondoland; 10, Stormberg; 11, Great Winterberg and Amatola Mts.; 12, Sneeuwberg and Koudeveldberg; 13, Nieuweveld Mts.

Cave Sandstone, which weathers into the overhangs that give this formation its name. The slopes are largely grass-covered, with scrub and forest patches mainly in the valleys. The main face of the high Drakensberg is a rugged scarp of black basalt, where grass and scrub give way to sheer cliffs. The summit plateau at a general altitude of 2700–3000 m, bleak in winter, storm-swept in summer, is covered in grass and dwarf shrub communities.

This is a gross oversimplification of a very complex topographical and vegetational pattern as it is seen today. The land forms have changed considerably during the existence of the Angiosperms (see King 1972) and the vegetation patterns have changed in historic times (see Acocks 1975, maps 1 and 2).

Natal cannot of course be viewed in isolation. To the south lie East Griqualand (presently part of Cape Province) and the Transkei, similar in topography, climate and vegetation; to the west, mountainous Lesotho, part of the Drakensberg area; to the north-west and north, the Highveld of the Orange Free State, Transvaal and western Swaziland, which has affinity with northern Natal. The highlands of the eastern Transvaal and western Swaziland fall sharply away to wooded lowlands and so to the broad tree-covered tropical Moçambique (Tongaland) coastal plain (see fig. 1).

It is clear then that the political boundaries of Natal do not mark off a biological region. Therefore "Natal", as a distributional area, is here conceived in the somewhat wider sense explained below (group 1 and group 3). However, this analysis is based on the species that occur naturally in the political province of Natal, these being the only species for which the necessary distributional data are available. Thus the number of species occurring in, say, the extended Drakensberg centre or the Tongaland plain (which reaches to Delagoa Bay) will be higher than that analysed here. Nevertheless, available knowledge of the adjacent areas suggests that the overall picture presented will not be greatly altered.

In analysing the distribution of Compositae in Natal, a number of patterns emerged, though of course many species cover only part of the range of a pattern, and there are always exceptional ones, difficult to place. Because of taxonomic and other difficulties, a few species have been omitted, e.g. *Amphidoxa adscendens*, *A. filaginea*, *Gnaphalium drakensbergense*. Within the more widely ranging species there may be geographical patterns of variation that will become of interest when more fully analysed, e.g. *Gnaphalium declinatum* (see Hilliard & Burtt 1973, pp. 335–6), and *Senecio erubescens*.

The genera, and number of species in each, actually analysed are shown in Table 2.

Distributional groups

Twelve groups, or patterns, are recognized, together with 4 subgroups. Drakensberg endemics comprise group 1 (111 species) and other Natal endemics group 3 (56 species); groups 2, 4, 4a and 5 are montane or sub-montane extending beyond Natal (106 species in all), while 6, 6a and 7 show different patterns of penetration from the central plateau lying to the north and west. Group 8 (55 species) has a wide altitudinal range in Natal and a wide range north and south, being montane northwards. Groups 9 and 10

TABLE 2

Genera, and number of species in each, analysed.

Adenanthemum	1	*Enydra*	1	*Microglossa*	1
Adenostemma	2	*Epaltes*	1	*Mikania*	1
Anisochaeta	1	*Ethulia*	1	*Nidorella*	7
Anisopappus	1	*Eumorphia*	2	*Nolletia*	3
Arctotheca	1	*Euryops*	13	*Osteospermum*	7
Arctotis	1	*Felicia*	12	*Othonna*	3
Artemisia	1	*Garuleum*	3	*Pegolettia*	2
Aspilia	2	*Gazania*	3	*Pentzia*	1
Aster	7	*Geigeria*	4	*Platycarpha*	1
Athanasia	12	*Gerbera*	7	*Pluchea*	1
Athrixia	7	*Gnaphalium*	4	*Printzia*	3
Berkheya	30	*Grangea*	1	*Pulicaria*	1
Bidens	1	*Gymnopentzia*	1	*Relhania*	3
Blumea	3	*Haplocarpha*	2	(incl. *Nestlera*)	
Brachylaena	5	*Helichrysum*	121	*Rhynea*	1
Callilepis	1	(+ 2 subspecies, 1 var.)		*Schistostephium*	5
Calostephane	1	*Heteromma*	3	*Senecio*	118
Chrysanthemoides	1	*Hirpicium*	1	(+ 1 var.)	
Chrysocoma	1	*Lactuca*	3	*Sonchus*	6
Cineraria	14	*Laggera*	1	*Sphaeranthus*	1
Conyza	8	*Launaea*	3	*Spilanthes*	1
Cotula	8	*Leontonyx*	1	*Stoebe*	1
Crassocephalum	4	*Lopholaena*	4	*Tarchonanthus*	2
Crepis	1	*Macowania*	7	*Tolpis*	1
Denekia	1	*Matricaria*	2	*Ursinia*	5
Dichrocephala	1	*Melanthera*	2	*Vernonia*	26
Dicoma	5	*Metalasia*	1	(+ 1 var.)	
Disparago	1				

(50 species in all) are basically coastal in distribution; group 11 embraces those species (44) with a really wide distribution and group 12 (41 species) comprises the tropical elements. It may be noted that the smaller groups, which may even seem too small to deserve recognition, have their justification in reflecting patterns better represented in families other than Compositae. Thumb-nail sketch maps roughly indicating the patterns of distribution are given in figs. 2 and 3.

Group 1. Drakensberg endemics, "Drakensberg" embracing the foothills of the Natal Drakensberg as well as the heights (roughly 1800 m to 3300 m, but some of the species may descend to c. 1500 m), outliers such as the Biggarsberg and Ngeli Mt with heights over 2000 m, the Cape Drakensberg and neighbouring Witteberg, with outliers on some of the high Transkeian mountains such as Baziya, Insikeni, Insizwa and Tabankulu, the high Lesotho mountains, and the mountainous NE corner of the Orange Free State (Witzieshoek, Golden Gate, Platberg).

CONTENT: 111 species in 23 genera, 20% of the total species number; *Helichrysum* 34, *Senecio* 19, *Athanasia*, *Berkheya*, *Euryops* and *Macowania*, 6, *Cotula* 5, *Felicia* 4, *Aster* and *Heteromma*, 3, *Athrixia*, *Eumorphia*, *Relhania* and *Ursinia*, 2, *Cineraria*, *Garuleum*, *Gerbera*, *Gnaphalium*, *Hirpicium*, *Nidorella*, *Osteospermum*, *Othonna*, *Printzia* and *Vernonia*, 1.

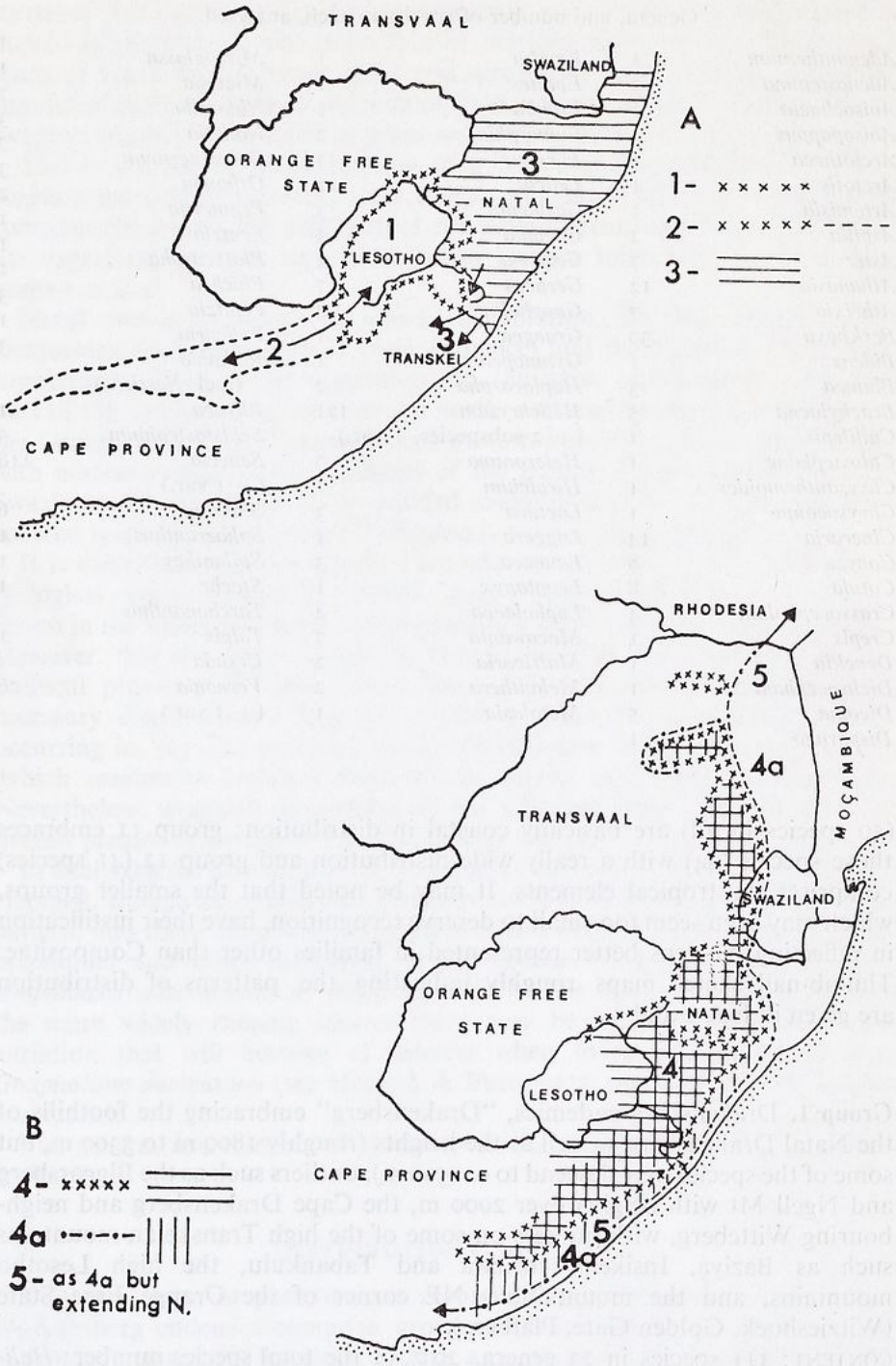

FIG. 2. Maps to show distribution patterns: A, groups 1 to 3; B, groups 4, 4a and 5.

Thirty-nine percent of the Composites recorded in the Natal Drakensberg are endemic. It is important to remember that this figure relates only to those Composites recorded from Natal itself. The Drakensberg area as a whole extends far beyond Natal's political boundaries and little of the floristically rich summit plateau falls within the province (fig. 1). Also, the flora of the Drakensberg area as a whole is ill-collected and poorly known. Therefore the figure given above will not be correct for the whole Drakensberg centre when the full data are available.

Of the 111 Composites endemic in the Drakensberg, 32 grow only at altitudes greater than 2300 m. This means that they are more or less confined to igneous rock (mainly basalt), but this may be fortuitous: the stratification is horizontal, and climate rather than rock type may be the controlling factor. A further 44 species are recorded only above 1800 m. Some of these are more or less confined to Cave Sandstone, the predominant rock at this altitude, but 27 of them also occur above 2300 m, on the basalt. The remaining 35 species may descend lower than 1800 m, but half of them also range higher than 2300 m, some reaching the summit plateau itself.

Of the species recorded only above c. 2300 m, *Helichrysum* numbers 14, *Senecio* 5, *Cotula* 4, *Euryops* 3, *Felicia* 2, *Aster*, *Athanasia*, *Berkheya* and *Eumorphia*, 1. Nearly all these species of *Helichrysum* are either taxonomically isolated or are related only among themselves or to other Drakensberg species. One of them (*H. pagophilum*) forms a rock-hard cushion pressed against rock surfaces; *H. haygarthii*, *H. praecurrens*, *H. retortoides*, *H. milfordiae* and *H. marginatum* are mat-forming; *H. witbergense* and *H. glaciale* are dwarf shrubs; the others are small tufted perennials, *H. basalticum* having prostrate branches. All five Senecios are taxonomically isolated; 4 are small perennial herbs, but *Senecio macrospermus* is a large handsome plant that, although stemless, is reminiscent of some of the giant Senecios of tropical Africa. All the Cotulas are mat-forming perennials related among themselves and to two somewhat wider-ranging species; otherwise they are without close allies. *Felicia uliginosa* and *F. drakensbergensis* are dwarf shrubs, also without close allies. The three species of *Euryops* too are small or dwarf shrubs; *E. acraeus* shows relationship only to *E. brownei* S. Moore from the high Kenyan mountains (Nordenstam, 1968, p. 129); *E. brevipes* and *E. decumbens* are allied to each other and to *E. montanus*, which may grow with them, but also descends to slightly lower altitudes.

The content of the group occurring at middle altitudes (1800 m and above) is: *Helichrysum* 10, *Senecio* 9, *Macowania* 5, *Berkheya* 3, *Heteromma* and *Relhania*, 2, *Aster*, *Athanasia*, *Athrixia*, *Cotula*, *Eumorphia*, *Euryops*, *Felicia*, *Gerbera*, *Gnaphalium*, *Osteospermum*, *Othonna*, *Printzia* and *Ursinia*, 1. Again, most (32) of the species are either taxonomically isolated, or they belong to groups of species or genera that are either themselves endemic to the Drakensberg or are distinctly centred there. The plants are mostly small or dwarf shrubs or cushion plants (20 species) or mat-forming (7). The remainder are tufted perennials, with one biennial.

The species growing at lower altitudes comprise: *Helichrysum* 10, *Senecio* 5, *Athanasia* 4, *Berkheya* and *Euryops*, 2, *Aster*, *Athrixia*, *Cineraria*, *Felicia*, *Garuleum*, *Heteromma*, *Hirpicium*, *Macowania*, *Nidorella*, *Osteospermum*, *Ursinia* and *Vernonia*, 1.

Group 2. Drakensberg-Sneeuwberg species, which occur mainly above 1200 m in Natal and range west from the Drakensberg region across the Stormberg to the Sneeuwberg, Koudeveldberg and occasionally the Nieuweveld Mts, all N of the Great Karroo; or sometimes absent from the main face of the Natal Drakensberg but ranging from the highlands of N Natal to the southern Transvaal Highveld, through the eastern Orange Free State and western Lesotho and so to the Cape Drakensberg and further west.
CONTENT: 15 species in 6 genera; *Helichrysum* 7, *Senecio* 3, *Cineraria* 2, *Felicia*, *Osteospermum* and *Pentzia*, 1.

Half the species in this group occur only above c. 1800 m in the Natal Drakensberg and range south-westwards to the Cape Drakensberg, Witteberg, Stormberg, Sneeuwberg and Koudeveldberg (*Helichrysum* 3, *Cineraria*, *Felicia*, *Senecio*, *Pentzia*, 1). Some of these high altitude plants (*Cineraria mollis*, *Felicia petiolata*, *Pentzia cooperi*, *Senecio tanacetopsis*) are rare in Natal, and obviously at the limit of their eastern range there. Others, with the same range south-westwards, are also known from only two or three records, but at lower altitudes (*Helichrysum dregeanum*, *Cineraria aspera*, *Senecio arabidifolius*) and have weed propensities. A few (*Helichrysum chionosphaerum*, *Senecio harveianus*, *Osteospermum caulescens*) have a wide range, from at least the Stormberg to the southern or eastern Transvaal, and are common in Natal above c. 1500 m.

Group 3. Natal endemics not confined to the Drakensberg, "Natal" here embracing neighbouring, similar, parts of the Transkei and East Griqualand, and occasionally the NE corner of the Orange Free State around Harrismith. The altitudinal range may be wide (sea level to c. 2300 m), or it may be restricted; those endemics found *only* above c. 1500 m are deemed Drakensberg endemics (group 1).
CONTENT: 56 species in 17 genera, 10% of the total species number; *Senecio* 19, *Helichrysum* 10, *Cineraria* 5, *Berkheya* 4, *Athanasia*, *Dicoma*, *Lopholaena*, *Nidorella* and *Vernonia*, 2, *Aster*, *Euryops*, *Garuleum*, *Gerbera*, *Matricaria*, *Othonna*, *Sonchus*, *Tarchonanthus*, 1.

There appear to be two minor centres of endemism in Natal (in contrast to the major Drakensberg centre), one associated with the Table Mountain Sandstone (TMS) formations (about 4% of the Composites endemic), the other on the Tongaland plain from about Mtunzini north to Delagoa Bay in Moçambique and sometimes beyond. The latter is discussed under group 10.

Many of the spectacular gorges and cliffs of coastal Natal are carved out of Table Mountain Sandstone. This formation extends northwards to just beyond the Tugela river (Eshowe, Melmoth, Nkandla), but stretches southwards along the shores of the Transkei and so to the Cape of Good Hope and Table Mountain itself. The top of the TMS never lies much above 1000 m, often at about 600 m, in Natal. It is the lowest and oldest in the sequence of strata covering the basement, crystalline, rocks (King 1972) and appears to provide a migration route for certain plants.

These fretted sandstone cliffs and outcrops above the forested gorges harbour a number of Natal endemics: *Helichrysum populifolium*, a large spreading broad-leaved shrub quite unlike any of its South African congeners; the shrubby *Senecio medleywoodii*, also taxonomically isolated; *Tarchonanthus trilobus* var. *trilobus*, a small tree; *Lopholaena dregeana* and *Euryops leiocarpus*, two shrubby relatives of *Senecio*. *Helichrysum woodii*, a winter-flowering shrublet found on TMS cliffs in the environs of Durban, has affinity with Transvaal species. *Athanasia pinnatifida* and *A. villosa*, both of limited distribution on TMS soils in Natal, are allied to *A. acerosa*, a wide-ranging species (E Cape to E Transvaal). *Helichrysum pannosum* too seems to be confined to TMS soils from about Durban to Port St. Johns; it is without close allies.

Forest patches and bush clumps are still a conspicuous feature of the Natal scene, despite extensive clearance and erosion by grass fires and grazing. Undisturbed forest margin vegetation is rich in shrubby Composites and climbers. Many of these range widely, with the forests, but a few are restricted to Natal. These include *Aster pleiocephalus*, closely allied to the grassland species *A. bakeranus*, which, if a broad view is taken of species circumscription, crosses both the Limpopo and Zambezi intervals; *Helichrysum citricephalum*, known only from Ixopo, whose relationships lie with tropical rather than South African species; *Matricaria zuurbergensis*, a loosely branched scrambling stoloniferous shrub ranging from the mountains near Kokstad in East Griqualand to the Karkloof Range NNW of Pietermaritzburg, without allies, and undoubtedly misplaced in the genus (Nordenstam 1976, p. 163); and *Senecio tysonii*, which is also taxonomically isolated. *S. poseideonis*, a purple-flowered bushy perennial, often favours a more shaded habitat just within the forest, as does *Berkheya debilis*. *Garuleum latifolium*, recorded only from coastal Natal, is close to *G. sonchifolium*, which is found on forest margins at higher elevations and has a greater range (group 4.)

Many of the other Natal endemics are found in the grasslands that cover so much of the province; a few are without close affinity, but the majority are allied to more wide-ranging species.

Group 4. Species occurring mainly above 1200 m in Natal, sometimes as low as 600 m, and ranging south and west across the high ground to the Great Winterberg and Amatola Mountains of the E Cape, occasionally to Somerset East or Grahamstown; and north to the eastern highlands of the Transvaal and neighbouring Swaziland, sometimes also ranging westwards across the Magaliesberg, Waterberg and Zoutpansberg; sometimes in Lesotho and the eastern highlands of the Orange Free State. This group is a submontane extension of group 1, the Drakensberg endemics.

CONTENT: 59 species in 15 genera; *Senecio* 19, *Helichrysum* 17, *Berkheya* 4, *Cineraria* 3, *Athanasia*, *Athrixia*, *Felicia*, *Printzia* and *Schistostephium*, 2, *Cotula*, *Garuleum*, *Gerbera*, *Gymnopentzia*, *Lactuca* and *Nidorella*, 1.

A few of the species (*Felicia rosulata*, *Helichrysum bellidiastrum*, *Senecio hypochoerideus*, *S. gramineus*) are decidedly montane in Natal, growing only between 2000 and 3300 m above sea level, but they range south-west across the mountains to lower altitudes in the Amatola Mountains, the Great

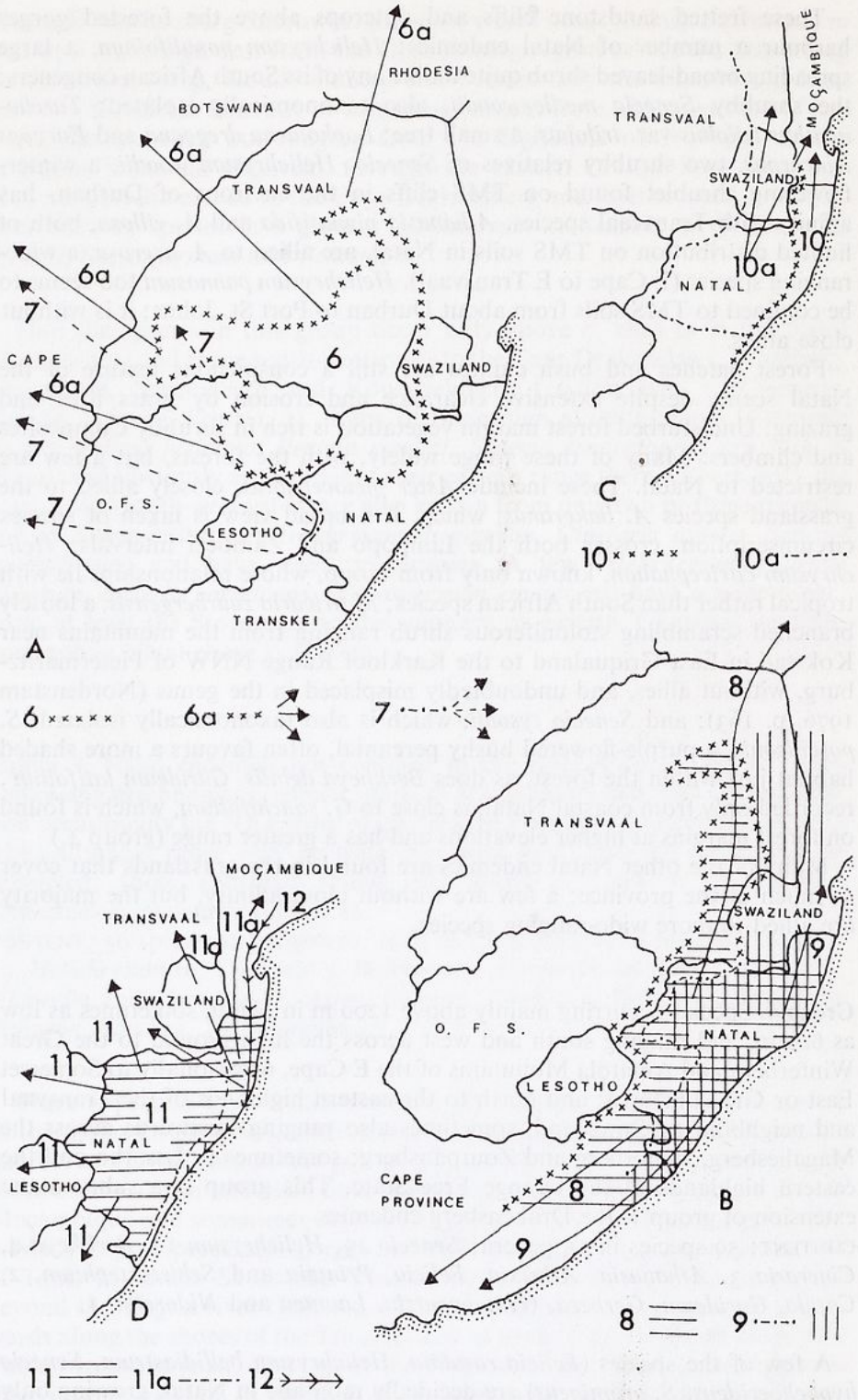

FIG. 3. Maps to show distribution patterns: A, groups 6, 6a and 7; B, groups 8 and 9; C, groups 10 and 10a (with arrows indicating extension N); D, groups 11 and 11a (with arrows indicating extension N and W) and group 12 (penetrating from the N).

Winterberg and the mountains near Somerset East, where higher latitude presumably compensates for lower altitude. Only one (*Felicia rosulata*) ranges north beyond the high Natal Drakensberg to the Transvaal Drakensberg.

The majority (39) range from the Natal Drakensberg or central Natal at least as far south-west as the Amatola Mountains, 14 reaching either (or both) the Somerset East and Grahamstown areas; 13 extend northwards to the Transvaal Drakensberg, and occasionally to the west-east-orientated Transvaal ranges. Half these species occur only above 1200 m in Natal, all but 3 above 600 m. The majority of species (14) are Senecios, with *Helichrysum* 9 and *Berkheya* 3.

There is a small group (14 species) scarcely known beyond Natal's southern border, except for a few records from some of the prominent mountains in the Transkei and East Griqualand, both of which regions are very poorly collected. All but one range north to the eastern highlands of the Transvaal, and usually western Swaziland too. They have an altitudinal range from at least 600 m to at least 2000 m. Here, the majority of species are *Helichrysum* (7), with *Senecio* 4, *Athanasia* 2, and *Gerbera natalensis*.

Subgroup 4a. Species ranging from the midlands and uplands of Natal (that is above c. 600 m), first south-west across the high ground, then west at lower altitudes to the coastal parts of the S or SW Cape; also north as in group 4.
CONTENT: 19 species in 8 genera; *Senecio* 7, *Helichrysum* 5, *Gnaphalium* 2, *Arctotis*, *Chrysocoma*, *Cineraria*, *Felicia* and *Metalasia*, 1.

The species in this subgroup differ from those in group 4 in their wider range to the coastal areas of the S or SW Cape. As in group 4, the majority are Senecios (7) and Helichrysums (5). Most of the remainder (*Chrysocoma tenuifolia*, *Felicia filifolia*, *Metalasia muricata*, *Arctotis arctotoides*) are members of predominantly Cape genera.

Group 5. Species mostly occurring above at least 600 m in Natal, ranging south and west across the mountains to the E, S or SW Cape and north along the mountains of the E Transvaal and E Rhodesia, sometimes reaching Ethiopia, sometimes also in Angola.
CONTENT: 13 species in 4 genera; *Helichrysum* and *Senecio*, 5, *Haplocarpha* 2, *Nidorella* 1.

This is the ultimate extension of groups 1, 2 and 4; it comprises a small number of species with an upland or montane distribution south and west to the Cape, where they may descend to lower elevations, and also northwards, bridging both the Limpopo and Zambezi intervals. Again, *Helichrysum* and *Senecio* predominate; *Haplocarpha* and *Nidorella* are both small genera endemic in sub-Saharan Africa.

Group 6. Species occurring mainly in northern Natal (occasionally extending to central or even southern Natal) above c. 1200 m, ranging northwards to the Transvaal Highveld and E highlands, western Swaziland, sometimes also in the eastern part of the Orange Free State and neighbouring Lesotho.

CONTENT: 43 species in 18 genera; *Senecio* 10, *Helichrysum* 6, *Berkheya* 5, *Euryops* and *Vernonia*, 3, *Athrixia*, *Geigeria* and *Lopholaena*, 2, *Adenanthemum*, *Anisopappus*, *Aster*, *Dicoma*, *Gerbera*, *Macowania*, *Nolleti'a*, *Pegolettia*, *Schistostephium* and *Ursinia*, 1.

The majority (30) of species have their main centre of distribution on the Transvaal and Swaziland Highveld and extend southwards into northern Natal. Others are distributed along the mountains of the eastern Transvaal, the low Drakensberg and neighbouring mountains of northern Natal, and the foothills of the high Drakensberg.

Subgroup 6a. Within Natal, confined to the northern districts (roughly at altitudes between 1200 and 1800 m) but ranging widely from the northern Cape Province and the Transvaal NE and W to S.W.A., Angola, Botswana, Rhodesia, Zambia and occasionally further north.
CONTENT: 5 species in 5 genera; *Dicoma*, *Felicia*, *Geigeria*, *Helichrysum* and *Osteospermum*.

The species may be widely distributed in sub-Saharan Africa, but in Natal are not known further south than the Tugela basin. *Helichrysum coriaceum* is a grassland species; all the others favour rather dry sandy or stony habitats, and may behave as weeds.

Group 7. Plants of the dry interior of the Cape Province, S.W.A., the Orange Free State, southern Transvaal and Lesotho, recorded mainly above 1500 m in Natal.
CONTENT: 9 species in 8 genera; *Berkheya* 2, *Cineraria*, *Conyza*, *Cotula*, *Geigeria*, *Helichrysum*, *Nolletia* and *Senecio*, 1.

The main centre of distribution is the arid and semi-arid parts of S.W.A. and South Africa. Records in Natal are few and nearly all from the foothills of the Drakensberg, usually in weed habitats.

Group 8. Species occurring from about sea level to c. 1200–2750 m in Natal, extending on a rather broad front south and west to the E or S Cape and north to the E Transvaal highlands and neighbouring Swaziland, sometimes to the high parts of the NE Orange Free State and nearby Lesotho, sometimes reaching the E highlands of Rhodesia or the highlands of Malawi and Zambia.
CONTENT: 55 species in 20 genera; *Senecio* 12, *Helichrysum* and *Vernonia*, 8, *Berkheya* 5, *Conyza* 4, *Euryops*, *Gazania* and *Schistostephium*, 2, *Athanasia*, *Athrixia*, *Callilepis*, *Chrysanthemoides*, *Gerbera*, *Leontonyx*, *Matricaria*, *Osteospermum*, *Othonna*, *Rhynea*, *Stoebe* and *Ursinia*, 1.

All the species grow at or near sea level in Natal and range up to at least 1200 m above the sea: 31 reach 1800 to 2000 m; 8, 2500–3000 metres. Their range, south and west, and north, may also be great; 14 cross the Limpopo and Zambezi intervals. Nearly all are denizens of open grassland; a few favour the coarse herbage on forest margins, or climb there; one (*Matricaria nigellifolia*) is a marsh plant.

Group 9. Species ranging from about sea level to a maximum of c. 1500 m in Natal, often extending only south and west along the coast to the E, S, or SW Cape (30 spp.), or sometimes north as well to Moçambique (Delagoa Bay) and the Transvaal Lowveld and Swaziland (13 spp.), very rarely reaching Rhodesia or Madagascar.

CONTENT: 44 species in 16 genera; *Senecio* 11, *Helichrysum* 8, *Brachylaena* and *Osteospermum*, 4, *Berkheya* and *Vernonia*, 3, *Felicia* 2, *Anisochaeta*, *Arctotheca*, *Athanasia*, *Disparago*, *Euryops*, *Gazania*, *Microglossa*, *Platycarpha* and *Relhania*, 1.

About half the species have not been recorded above 600 m in Natal; all range south or north only through coastal or low-lying areas. Five are strand plants or are never far from the sea (*Arctotheca populifolia*, *Brachylaena discolor*, *Gazania rigens* var. *uniflora*, *Osteospermum fruticosum*, *Senecio skirrhodon*); these range from the southern Cape to Moçambique, sometimes reaching Madagascar. Several more are widely distributed in the Cape coastal districts and are at the northern limit of their distribution in southern Natal, mainly in mixed shrub-grassland communities. Such are *Felicia aethiopica*, *Helichrysum teretifolium*, *H. serpyllifolium*, *H. felinum*, *H. diffusum* (with a disjunction between the Hottentots Holland Mountains, near the Cape Peninsula, and the cliffs above the Umtamvuna on the Natal-Transkei border), *Disparago ericoides*, *Relhania pungens*, *Senecio lanceus*, *Euryops chrysanthemoides*, *Osteospermum herbaceum*. Others are constituents of coastal grasslands roughly between East London and Delagoa Bay (e.g. *Helichrysum decorum*, *H. longifolium*, *Senecio speciosus* sens. lat., *S. variabilis*). Some trees, shrubs or climbers are constituents of warm river valley woodland or coastal forest, and their ranges lie between the coastal forests of the southern Cape and the lowveld of Moçambique, Swaziland and the Transvaal e.g. *Brachylaena* spp., *Microglossa mespilifolia*, *Senecio brachypodus*, *S. macroglossus*, *Vernonia* spp. These, in contrast, may have tropical affinities, but their actual distribution patterns dictate their inclusion here.

Group 10. Species confined to the low coastal plain (0–150 m altitude) north of Durban and extending into Moçambique (viz. the Tongaland plain), rarely also in the Transvaal Lowveld. These could be termed Tongaland endemics.

CONTENT: 6 species in 5 genera; *Helichrysum* 2, *Cineraria*, *Gnaphalium*, *Senecio*, *Vernonia*, 1.

The low hot sandy coastal plain, the Tongaland plain, is of marine origin and is geologically recent. Both *Nidorella linifolia* and *N. tongensis* are known from only a few records between Durban and the Moçambique border, but almost certainly occur in Moçambique too. *Vernonia africana* can perhaps be mentioned here, though it is was not strictly a coastal plain plant, but one apparently restricted to grassland just north of Durban; this locality is now under sugarcane and the *Vernonia* probably extinct. It was so isolated taxonomically that Sonder created the monotypic genus *Vernonella* to accommodate it. These three species are enumerated in group 3, Natal endemics. *Vernonia centaurioides*, ranging from about the mouth of the

Zambezi to the Tugela, is a Moçambique-Tongaland endemic and is one of a group of closely related tropical species (see group 11a, *V. fastigiata*, *V. steetziana*).

The large genus *Helichrysum* has produced only one species (*H. silvaticum*) and one subspecies (*H. adenocarpum* subsp. *ammophilum*) endemic to Tongaland but in the allied genus *Gnaphalium* there is a very interesting and taxonomically isolated species, *G. septentrionale*, ranging from about Beira in Moçambique to St. Lucia in Zululand (Tongaland). *Senecio*, too, has only one endemic there, the purple-headed *S. ngoyanus*, a plant of marshy depressions, related to the wide-ranging *S. polyodon* that reaches Angola, Rhodesia and Zambia. No less than 5 of the 9 Tongaland endemics favour damp or even marshy habitats, which abound in this low-lying area.

Subgroup 10a. Species that are not recorded south of the Tugela basin, and usually at altitudes well below 1500 m, ranging northwards to the Transvaal and Swaziland Lowveld, usually lowland Moçambique, and sometimes the Rhodesian Lowveld.

CONTENT: 5 species in 3 genera; *Senecio* 3, *Nolletia* and *Helichrysum*, 1.

All five species favour hot dry sandy or rocky places. *Senecio barbertonicus* is a succulent-leaved, sometimes scandent, shrub with yellow discoid heads, found on rock outcrops or in sand forest. *S. viminalis* is similar in habit and habitat preference, but has white flowers and cone-tipped style branches; it is possibly misplaced in *Senecio*. *Senecio transvaalensis* too, with its lilac flowers, tailed style branches and peculiar achenes, is possibly better placed in the tropical genus, *Emilia*.

Group 11. Species occurring roughly between sea level and c. 1200 to 3000 m in Natal, ranging widely within South Africa, frequently reaching Angola, tropical Africa, Ethiopia, West Africa, sometimes Madagascar.

CONTENT: 44 species in 17 genera; *Helichrysum* 15, *Senecio* 6, *Sonchus* 5, *Aster*, *Gerbera*, *Launaea* and *Nidorella*, 2, *Artemisia*, *Crepis*, *Denekia*, *Dicoma*, *Felicia*, *Lactuca*, *Pulicaria*, *Tarchonanthus*, *Tolpis* and *Ursinia*, 1.

These are the really wide-ranging species, being widely distributed not only within Natal and often South Africa as a whole, but frequently bridging both the Limpopo and Zambezi intervals and sometimes with disjunctions to Angola (8 species), Ethiopia (7 species), West Africa (4 species) and Madagascar (5 species), occasionally even beyond Africa (*Gerbera piloselloides*, *Lactuca capensis*). Virtually all are plants of grassland or open woodland and belong to genera or sections of genera centred in southern Africa (*Aster*, *Felicia*, *Helichrysum*, *Nidorella*), while some may become weeds, though their native habitat is grassland (*Launaea*, *Sonchus*, *Felicia muricata*, *Lactuca capensis*, *Tolpis capensis*, *Ursinia nana*).

Subgroup 11a. Species confined to warm sandy places in coastal Natal, but ranging north and west to the warm dry parts of the Transvaal, N Cape Province, S.W.A., Angola and tropical Africa, occasionally in Madagascar.

CONTENT: 8 species in 4 genera; *Helichrysum* 3, *Senecio* and *Vernonia*, 2, *Blumea* 1.

The species included here may range widely within East Tropical Africa, but in southern Africa they are confined to warm, often sandy, areas and in Natal, to the coast. *Vernonia fastigiata*, *V. steetziana* and *Blumea gariepina* are all tropical in affinity; so are *Senecio fulgens* (possibly better placed in the tropical genus *Notonia*) and *S. pleistocephalus*. *Helichrysum argyrosphaerum*, *H. candolleanum* and *H. kraussii* too are more closely allied to tropical than to South African species.

Group 12. Tropical and subtropical species, mostly widespread in the warm parts of West, Central and East Africa, sometimes also extra-African, often at or near the southern limit of their distribution in coastal Natal, but sometimes getting as far south as Knysna in the S Cape.
CONTENT: 41 species in 26 genera; *Vernonia* 7, *Crassocephalum* 4, *Conyza* 3, *Adenostemma*, *Aspilia*, *Blumea* and *Melanthera*, 2, *Bidens*, *Berkheya*, *Brachylaena*, *Calostephane*, *Cotula*, *Dichrocephala*, *Enydra*, *Epaltes*, *Ethulia*, *Grangea*, *Lactuca*, *Laggera*, *Launaea*, *Mikania*, *Pegolettia*, *Pluchea*, *Senecio*, *Sphaeranthus* and *Spilanthes*, 1.

All the species have strong tropical affinities and are tropical or subtropical in their distribution. Half of them (22 out of 41) favour damp or marshy habitats, and 8 of these 22 species can behave as weeds. Of the remaining 19 species, 5 more will behave as weeds, 2 are strand plants, 5 are forest margin climbers.

In Natal, nearly all are confined to coastal areas; the exceptions (9 in number), which range up into the midlands, are either weeds or plants of damp situations, or both. Only 14 species cross the Umtamvuna river, Natal's southern boundary, and of these, only 5 get beyond the Kei River. No less than 12 of these 14 species favour marshy or at least damp habitats, and of those that cross the Kei, *Ethulia conyzoides*, *Dichrocephala integrifolia* and *Crassocephalum picridifolium* favour damp places, while *Launaea sarmentosa* is a strand pioneer, and *Mikania cordata* is a forest-margin climber that has strong weed propensities. Six of the 12 species that occur in Natal but range as far as Asia and Australia favour damp habitats, 2 more are strand plants; the other 4 behave as weeds.

ENDEMISM IN NATAL

The most striking facet of this analysis of Compositae in Natal is the surprising number of endemic species, 168 out of a total of 551, or 30%: surprising because Natal is part of a continental mass, and surprising even though "Natal" has been broadly defined.

By far the greatest number of endemic species, 111, is found in the Drakensberg. There are also several endemic genera or sections of genera (not necessarily formally recognized), as well as genera that achieve maximum development there. For example, *Heteromma*, with 3 species, is confined to the Natal and Cape Drakensberg and nearby Witteberg; *Macowania* has 6 of its 11 species confined to the Natal Drakensberg, 1 to the Cape Drakensberg and Witteberg, 1 to the Amatola Mountains and nearby, 1 to the Transvaal Highveld and Drakensberg, then a great disjunction to the two species in

Ethiopia and Yemen (see Hilliard & Burtt 1976, pp. 260–276); *Eumorphia* comprises 6 species confined to the Sneeuwberg and Cape, Natal and Transvaal Drakensberg. All three genera are taxonomically isolated. *Cotula* is a southern hemisphere genus with a rich representation in the Cape Province, mostly annual species; there are 6 perennial species with homogamous heads that are more closely related among themselves than to any other South African species; 5 of them are confined to the Drakensberg above c. 2200 m. *Athanasia*, a predominantly Cape genus of about 50 species, has 12 species in Natal. Three of them have affinity with section *Morysia*, which is otherwise confined to the Cape, but the other 9 could be regarded as constituting a fourth section of the genus (see Hilliard & Burtt 1973, p. 329); 6 of them are Drakensberg endemics, while another occurs there but also ranges further afield. A few endemic species of *Euryops* have been mentioned above; two sections of the genus reach maximum development in the Drakensberg Centre (Nordenstam 1969, p. 67).

The Drakensberg is also a rich centre of endemism for the big genera *Helichrysum* and *Senecio*, and many of these endemic species have little or no affinity outside the area. Indeed, taxonomic isolation of the high altitude endemics prevails in all the genera detailed above. But it is probably true to say that overall affinity of the Composite flora of the Drakensberg lies with the mesophytic flora of the Cape (cf group 1, generic list), and with the flora of Natal itself. Recent revisionary work in other families emphasises the importance of the Drakensberg centre: *Craterocapsa* (Campanulaceae) with 4 species (Hilliard & Burtt 1973, pp. 314–326), two genera in Scrophulariaceae, *Glumicalyx* with 6 species and the monotypic *Strobilopsis* (Hilliard & Burtt 1977, pp. 155–175), and two genera in Hypoxidaceae, *Rhodohypoxis* with 6 species and *Saniella* with one (Hilliard & Burtt 1978, pp. 43–76). Other examples would not be hard to find. However, only further collecting, further revisionary work, and of course consideration of the *whole* Drakensberg centre and its flora will reveal the true picture of this outstanding montane centre of speciation.

Mention has already been made of the TMS formations of the Natal south coast as a centre of endemism for Compositae (under group 3). There are other notable endemics that appear to be confined to TMS soils. These include the monotypic small tree genera *Pseudosalacia* (Celastraceae), known only from the coastal forests of southern Natal, and *Rhynchocalyx* (Lythraceae) confined to southernmost Natal. *Eriosemopsis* (Rubiaceae), a perennial herb recorded only from southern Natal and the E Cape border (Dyer, 1975) is also monotypic. Then there are a number of species from diverse genera that appear to be confined to the TMS formations of S Natal and nearby Pondoland; these include *Phylica natalensis* Pillans (Rhamnaceae), *Struthiola pondoensis* C. H. Wright and *Passerina vulgaris* Thoday (Thymelaeaceae), *Eugenia erythrophylla* Strey (Myrtaceae), *Streptocarpus porphyrostachys* Hilliard and *S. trabeculatus* Hilliard (Gesneriaceae).

Other elements in the Natal flora

The sandstone area about the gorges of the lower Umtamvuna river and its tributaries on Natal's southern border is not only notable for its endemics but is also well-known for its connexions with the Cape flora, Here for

instance are found the only representatives in Natal of such typically Cape plants as *Raspalia trigyna* (Schltr.) Dümmer (Bruniaceae), *Podalyria burchellii* DC. and *Rafnia elliptica* Thunberg (Leguminosae), *Leucadendron spissifolium* (Knight) Williams (Proteaceae) and *Disparago ericoides* (Compositae); all these genera are at the NE limit of their distribution in southernmost Natal, on TMS-derived soils. So are many Composite species (enumerated in the discussion under group 9).

The Tongaland plain, mentioned above as only a minor centre of endemism in Compositae, is important in other groups as a centre of endemism, and it also plays a major role as a migration route from the north and north-west, especially for woody plants, as emphasized by Ross (1973, p. 106). There are a number of woody genera whose only known record in South Africa is from Tongaland. These include *Epinetrum* (Menispermaceae), *Newtonia* and *Sophora* (Leguminosae), *Pseudobersama* (Meliaceae), *Tapura* (Dichapetalaceae), *Cleistanthus* (Euphorbiaceae), *Haplocoelum* and *Blighia* (Sapindaceae), *Gossypioides* (Malvaceae), *Synaptolepis* (Thymelaeaceae), *Ceriops* (Rhizophoraceae), *Lumnitzera* (Combretaceae), *Inhambanella* (Sapotaceae), *Guettarda* and *Coffea* (Rubiaceae). The list could be extended to include herbaceous plants, also numerous tropical and subtropical genera and species, both woody and herbaceous, that are at their southern distributional limit in Tongaland; but the point has been made.

Parallels for many of the other groups are undoubtedly abundant in other families, but there are no published sources of distributional data apart from a few monographs and revisions. It was possible to extract some information on Tongaland and southern Natal endemics from Ross (1972), and it seems useful to add a few selected examples of Highveld elements (group 6) from personal knowledge. These include *Zantedeschia rehmannii* Engler (Araceae), *Wahlenbergia pinnata* Compton (Campanulaceae), *Cephalaria foliosa* Compton and *C. zeyherana* Szábo (Dipsacaceae), *Pearsonia aristata* (Schinz) Dümmer (Leguminosae), *Polycarena transvaalensis* Schlechter and *Selago transvaalensis* Rolfe (Scrophulariaceae), *Hermannia brachymalla* K. Schumann *vel. aff.* (Sterculiaceae), and *Peucedanum magalismontanum* Sonder (Umbelliferae).

Distributional patterns of Natal Compositae in relation to the major African phytochoria

The higher levels of the Drakensberg in Natal are remarkable for the number of endemic species; 32 of the 135 Composite species recorded above 2300 m are endemic. Taxonomic links to the high mountains of tropical Africa are extremely tenuous, the only one being *Euryops acraeus* to *E. brownei*, mentioned above. There *are* other links to the high mountains of E Africa, but the southern species at least are not always confined to high altitudes. For example, *Haplocarpha nervosa* (group 5) has a wide altitudinal range in Natal (1525–3050 m) and extends south to the Cape Peninsula as well as north to the E Transvaal and Inyanga in Rhodesia; it is allied to *H. schimperi* (Sch. Bip.) Beauverd in Ethiopia and *H. rueppellii* (Sch. Bip.) Beauverd from the high E African mountains and Ethiopia (Hilliard &

Burtt 1971, p. 13). *Macowania tenuifolia* (group 6) with an altitudinal range of c. 1500–2300 m in northern Natal and the Transvaal Highveld and E highlands is perhaps linked to *M. ericifolia* (Forsk.) Burtt & Grau, one of the Yemen-Ethiopia outliers of the genus (Hilliard & Burtt 1976, p. 275). *Stoebe vulgaris* (group 8) extends from Kingwilliamstown in the Cape to the high parts of the Transvaal and Swaziland and the E highlands of Rhodesia, with an altitudinal range in Natal from near sea level to 2200 m; it is allied to *S. kilimandscharica* O. Hoffmann from the high mountains of E Africa and the Nyika plateau in Malawi. *Helichrysum tenuiculum sens. lat.* (subgroup 4a) ranges from the mountains of the SW Cape to Natal, Lesotho, the Natal-Transvaal border and W Swaziland, ranging between 1300 and 2440 m in Natal. It is allied to *H. fruticosum* Vatke *sens. lat.*, widespread in the uplands of Yemen, and from Ethiopia to E and W tropical Africa, Malawi, Rhodesia and Angola (fide Hedberg 1957, p. 204). However, the taxonomy of both species is still confused. *Senecio baurii* (group 4), ranging from Stutterheim in the E Cape north to the southern Natal Drakensberg, where it is found between 1200–1800 m, appears to be closely allied to *S. gazensis* S. Moore from the E highlands of Rhodesia and *S. depauperata* Mattfeld from the mountains between Lakes Tanganyika and Malawi, while *S. hypochoerideus*, found between 2440 and 3200 m in the Natal Drakensberg and Lesotho, and extending SW to the mountains near Graaff Reinet, may be allied to *S. schweinfurthii* O. Hoffmann, endemic to the high mountains of E Africa.

The inclusion of the Drakensberg in a general (archipelagic) Afromontane centre of endemism (White 1976) is scarcely upheld by this analysis. In fact, in Compositae, as in some other groups that have been studied (*Craterocapsa*, *Glumicalyx*, *Rhodohypoxis*) the affinities of high level endemics, where they can be traced at all, is usually with species of lower altitudes. In other words, such evidence as there is suggests that the high level flora of Natal is almost entirely autochthonous. Furthermore, the submontane groups (e.g. 4 and 5) present extensions of the high level pattern consistent with the available habitats. There appears to be a common floristic background, which stretches down to c. 600 m, and sometimes lower. This is compatible with the geomorphic history of the province. It was part of the low Gondwanaland plain that, after the rifting apart of the supercontinent, underwent a series of mighty uplifts and tiltings; the last of these occurred in the late Pliocene and raised the Drakensberg and the high Lesotho plateau a further 600 m to their present levels (King 1972, pp. 41–44).

If Natal is to be split between major phytochoria it can be done only by the segregation of a coastal strip, relatively narrow in the south and broader in the north, associated with the lower ground of the major river valleys inland, corresponding to Acocks "Bushveld" vegetation type (Acocks 1975, map 2). The existence of a Highveld element in the northern part and of a Cape element in the extreme south are examples of phtogeographical penetrations and do not necessarily imply equivalent vegetation types on the ground.

References

Acocks, J. P. H. (1975). Veld types of South Africa, ed. 2. *Bot. Surv. S. Afr. Mem.* 40. Pretoria.

DYER, R. A. (1975). *The genera of South African flowering plants*, 1. *Dicotyledons*. Pretoria.

HEDBERG, O. (1957). Afro-alpine vascular plants. *Symb. Bot. Ups.* 15, 1. Uppsala.

HILLIARD, O. M. (1977). *Compositae in Natal*. Pietermaritzburg.

——& BURTT, B. L. (1971–78). Notes on some plants of southern Africa chiefly from Natal: II, *Notes R.B.G. Edinb.* 31:1–33 (1971); III, *l.c.* 32:303–387 (1973); V, *l.c.* 34:253–286 (1976); VI, *l.c.* 35:155–177 (1977); VII, *l.c.* 36:43–76 (1978).

KING, L. C. (1972). *The Natal monocline: explaining the origin and scenery of Natal, South Africa*. Geology Dept., Univ. of Natal, Durban.

NORDENSTAM, B. (1968). The Genus Euryops, I. *Opera Botanica* 20. Lund.

——(1969). Phytogeography of the genus Euryops (Compositae). *Opera Botanica* 23. Lund.

——(1976). Re-classification of Chrysanthemum L. in South Africa. *Bot. Not.* 129:137–165.

ROSS, J. H. (1972). The Flora of Natal. *Bot. Surv. S. Afr. Mem.* 39. Pretoria.

——(1973). An analysis of the flora of Natal. *Bothalia* 11:103–106.

WHITE, F. (1976). The vegetation map of Africa—the history of a completed project. *Boissiera* 24:659–666.