

## Geography of Iridaceae in Africa

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### ABSTRACT

Iridaceae, a family of worldwide distribution, comprises some 1 500 species and 85 genera. It exhibits its greatest radiation in Sub-Saharan Africa, where over half the species and some 48 genera occur, 45 of which are endemic. All three major subfamilial taxa are represented in Africa, where Ixioideae are almost entirely restricted, with extensions into Eurasia. Areas of greatest concentration are either montane or in areas of winter rainfall. In southern Africa alone, there are some 850 species in 46 genera, making the family the fifth largest in the flora. In the Cape Floristic Region there are 620 species, and the family is the fourth largest in this area. All major infrafamilial groups occur in the Cape Region where most of the variability as well as generic radiation is encountered. The idea of a southern origin for Iridaceae in Africa is analysed systematically, and is correlated with the major climatic changes that occurred in Africa since the mid-Tertiary, and culminated in the seasonally dry climates along the west coast. The establishment of mediterranean climate in the southwest provided the stimulus for massive speciation and radiation of the family there. Plio-Pleistocene uplift along the eastern half of the African continent led to the establishment of substantial upland areas and allowed the spread of some genera, such as *Romulea*, *Gladiolus*, *Moraea*, and *Hesperantha* into tropical Africa. Short-distance dispersal probably accounts for the presence of genera such as *Gladiolus*, *Gynandriris* and *Romulea* in Eurasia.

### RÉSUMÉ

#### GÉOGRAPHIE DES IRIDACEAE EN AFRIQUE

Les Iridaceae, famille répandue dans le monde entier, comprend quelques 1500 espèces et 85 genres. Elle présente sa plus grande expansion en Afrique au sud du Sahara où plus de la moitié des espèces et quelques 48 genres sont présentes, 45 d'entre eux étant endémiques. Les trois sous-familles principales sont représentées en Afrique, où les Ixioideae s'y limitent presque entièrement avec des extensions en Eurasie. Les régions aux plus grandes concentrations sont soit montagnardes soit en région à pluies hivernales. En Afrique australe seule, il y a quelques 850 espèces et 46 genres, faisant de cette famille la cinquième plus grande de la flora. Dans la Région floristique du Cap, il y a 620 espèces et la famille est la quatrième en importance de cette région. Tous les groupes majeurs infra-familiaux existent dans la région du Cap où le plus de variabilité et radiation générique sont rencontrées. L'idée d'une origine australe pour les Iridaceae en Afrique est analysée systématiquement et est mise en corrélation avec les changements climatiques qui survinrent en Afrique depuis le milieu du Tertiaire et qui culminèrent dans le climats saisonnièrement secs, le long de la côte de l'Ouest. L'établissement d'un climat méditerranéen dans le Sud-Ouest a fourni le stimulus de la spéciation et de l'expansion massive de la famille à cet endroit. Le soulèvement Plio-Pleistocène le long de la moitié orientale du continent africain amena l'établissement de régions élevées assez importantes et permit la dissémination de certains genres tels que *Romulea*, *Gladiolus*, *Moraea* et *Hesperantha* en Afrique tropicale. Une dispersion à courte distance explique probablement la présence des genres tels que *Gladiolus*, *Gynandriris* et *Romulea* en Eurasie.

### INTRODUCTION

Iridaceae are a family of petaloid monocotyledons, of the order Liliales, comprising some 1 500 species in 85 genera, distributed throughout the world. The area of greatest concentration is Africa south of the Sahara, where ca. 48 genera and about 925 species occur. Explosive radiation has taken place in the extreme southwestern part of the continent, an area of mediterranean climate. In this Cape Floristic Region there are 620 species in 36 genera (Goldblatt, 1978). Iridaceae is the fifth largest family in southern Africa in terms of numbers of species and fourth largest in the Cape Region, a situation without parallel for a petaloid monocot group.

Outside the Cape Region and the immediately adjacent western Karoo and Namaqualand, significant numbers of species occur in the well watered coastal and mountain belts of eastern southern Africa. North of the Transvaal, species of Iridaceae are concentrated in the islands of Afromontane flora that extend northwards through Zimbabwe, Malawi, Tanzania and Kenya into Ethiopia. Smaller numbers

of species occur in savanna regions. Very few occur in lowland forest.

The general pattern of the distribution of Iridaceae suggests an explosive radiation in the Cape Region with secondary migration and dispersal from this area eastwards and then northwards; species numbers decreasing with latitude. This implies a southern (and thus Cape) origin for the family in Africa. The situation is, however, more complex and can only be interpreted from post-Cretaceous climatic changes that have occurred in Africa. Since the Eocene (55-38 m.y. ago), when the ancestors of the modern genera of Iridaceae were found in Africa and South America (and probably Australasia), the African continent has moved some 15° northwards (Axelrod & Raven, 1978). At the same time, climates became warmer, drier and more strongly seasonal. After the Miocene, dry zones began to develop, culminating in the establishment of a mediterranean climate along the southwest coast and desert to the north and east.

### ECOLOGY OF IRIDACEAE

Species of Iridaceae are almost exclusively herbaceous perennials; a few are annual or shrubby. The majority are adapted to climates with a

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substantial dry season. This is particularly so in Africa, where adaptations for seasonal climates such as deciduous habit, specialized underground organs, and reduced plant size are found in the majority of species, including all of the more advanced lines.

A few, mostly primitive and probably very old, genera occur either in association with evergreen forest (notably *Dietes* and *Aristea*), in grassland in areas of high rainfall (*Dierama*), or in favourable habitats in areas of apparently arid climate. Such habitats include stream sides, or sheltered valleys and ravines in mountainous areas, where dry season moisture is available through cloud condensation. Therefore, although the arid, summer-dry climate of the Cape Region is of comparatively recent origin, and much of the species richness is equally recent, local areas of moist climate here harbour species not at all drought adapted. Such species are often isolated relics (*Pillansia*, *Aristea* spp., and *Bobartia*). These genera, together with the few forest or moist grassland genera provide important clues to the origin and evolution of Iridaceae in Africa. Before analysing them further, however, the systematic classification of Iridaceae is outlined.

#### IRIDACEAE — OUTLINE OF CLASSIFICATION AND REVIEW OF MODERN DISTRIBUTIONS OF GENERA

Iridaceae are usually treated as comprising three major infrafamilial groups, which for convenience, are best regarded as subfamilies. These are the Ixioidae, Iridoideae and Sisyrinchioideae. There is some doubt about the status and circumscription of the latter, but it is useful for purpose of this paper to recognize it.

(a) *Sisyrinchioideae*. This predominantly New World subfamily is represented on all southern continents. It is fairly low on the evolutionary scale: representatives typically have unspecialized flowers and unmodified underground parts. There are five African genera (Table 1). *Aristea*, the largest, together with *Klattia*, *Witsenia* and *Nivenia* form one alliance, and *Bobartia* another. The less specialized species of *Aristea* occur in well watered grassland throughout Africa and Madagascar (Weimarck, 1940) and also in moist sites in the south-western Cape. More specialized species, belonging to several alliances are restricted to the Cape Floristic Region, where some recent radiation seems to have occurred. The peculiar shrubby genera, *Klattia*, *Witsenia* and *Nivenia* are found exclusively in the mountains of the Cape Region, mostly in more favoured situations. All are very specialized in their shrubby habit and also in their flowers. The group probably represents a unique trend in Iridaceae towards the shrubby growth form very common in the Cape Region, although rare in monocots.

*Bobartia*, distantly related, if at all, to the *Aristea* group, is usually regarded as most closely allied to the New World *Sisyrinchium*. If this is correct, the separation must be very ancient. The affinities of *Bobartia* are by no means satisfactorily understood and require investigation. *Bobartia* may possibly be an aberrant member of Iridoideae (Goldblatt, 1979) rather than a member of Sisyrinchioideae.

The genus consists of 15 species. Two, with a presumably primitive open branching pattern, occur at high altitudes in the mountains of the Cape Region. The 13 more specialized species, with clustered inflorescences and lacking branches, extend from the western Cape to southern Natal. They probably represent recent speciation in an old group.

(b) *Iridoideae*. All African Iridoideae belong to the Old World tribe Irideae, the sister group of the New World Tigridaeae. The most primitive genus of Irideae is *Dietes* (Goldblatt, 1981), with six species. Five occur in Africa, from Kenya to the southern Cape, and one is restricted to Lord Howe Island (Australasia). All species occur in forest or streamside habitats, are evergreen, and have unspecialized flowers for the tribe. *Dietes* or something very like it, probably gave rise to the two important lines of the Old World Irideae, *Iris*, *Hermodactylis*, *Pardanthopsis*, *Belamcanda*, etc. (Iridinae) in Eurasia (*Iris* extending to North America) and *Moraea*, its allies (Homeriinae) and *Ferraria* (Ferrariinae) in Africa. Most African members of Irideae are strongly drought adapted, are deciduous, have cormous rootstocks and with the exception of the isolated *Ferraria*, have an unusual bifacial type of leaf (Goldblatt, 1976).

The group has radiated considerably in the Cape region (Table 1) and adjacent Namaqualand, where several genera are endemic. *Moraea*, the largest genus extends into tropical Africa, where two specialized subgenera have become established, and *Ferraria*, mainly West Coast, has its most primitive species in central Africa. One specialized offshoot of *Moraea*, *Gynandriris* (Goldblatt, 1980) is centred in southern Africa, but two species are endemic in Eurasia, both polyploid and probably of recent origin there.

(c) *Ixioidae*. This subfamily, the largest in the family in Africa, consists of several separate lines, the relationships of which are not understood (Goldblatt, 1971). It is predominantly African. All 34 genera, except *Crocus*, occur in Africa south of the Sahara, and only *Gladiolus* and *Romulea*, both centred in the Cape Region, occur north of the Sahara.

Only three genera of significance do not occur at all in the Cape Region. Two, *Savannosiphon* (1 sp.) (Goldblatt & Marais, 1979) and *Zygotritonia* (2 spp.) are apparently isolated taxonomically, and possibly relictual, but seem fairly specialized. The third *Dierama* (ca. 15 spp.) is centred in the well watered coastal and montane grassland of eastern southern Africa. It extends north to Ethiopia (Cufodontis, 1974), occurring only in mountain areas. Most species are evergreen, and all have unspecialized actinomorphic flowers. Lewis (1962) regarded the predominantly Cape genus *Ixia* as closely allied to *Dierama*, but differing mainly in being deciduous, and having seasonally produced corms.

Apart from this example (and possibly also the *Crocsmia-Tritonia* alliance) all Ixioid lines are centred in the Cape Region. This is where most



TABLE 1.—Genera of African Iridaceae occurring south of the Sahara, with number of species in parentheses, and range. Notable disjunctions are highlighted in italics

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Sisyrinchioideae
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Aristea (50) SW Cape–Ethiopia incl. Madagascar
Klattia (2) southern Cape mts
Witsenia (1) southern Cape–marshes
Nivenia (8) Cape, mainly montane
Bobartia (15) Cape–S Natal

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Iridoideae
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Dietes (6) Africa, S Cape–Kenya and <i>Lord Howe Island</i>
Moraea (ca. 102) Africa, Cape–Ethiopia
Homeria (31) Cape–Namaqualand and Karoo to E Transvaal
Ferraria (10) SW Cape and Namaqualand– <i>Katanga</i>
Barnardiella (1) Namaqualand
Gynandriris (9) Cape–Karoo and <i>Eurasia</i> (2)
Roggeveldia (1) W Karoo
Rheome (2) W Cape
Hexaglottis (5) Cape–Namaqualand
Galaxia (13) Cape–Namaqualand

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Ixioidaeae
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Pillansia (1) SW Cape
Watsonia (70) SW Cape–eastern Transvaal Mts
Micranthus (3) SW Cape
Therianthus (7) SW Cape
Lapeirousia (28) SW Cape–Namaqualand–Ethiopia
Savannosiphon (1) SE tropical African plateau
Romulea (ca. 90) Cape and Namaqualand eastwards through Drakensberg and East African Highlands to Ethiopia (ca. 80) and <i>Mediterranean, Canary Islands</i> (ca. 15)
Syringodea (8) Cape–Karoo
Anomatheca (5) Cape and Namaqualand through E Cape to southern Tanzania
Freesia (11) Cape and Karoo (to southern Transkei)
Dierama (ca. 15) E Cape–Kenya, montane grassland, coastal in south
Ixia (45) SW Cape to Namaqualand
Sparaxis (6) W Cape
Synnotia (6) W Cape
Tritonia (ca. 30) SW Cape and Namaqualand through E Cape to Zimbabwe
Crocoshmia (6) E Cape–Tanzania
Chasmanthe (3) SW Cape
Duthieastrum (1) N Cape–W Transvaal
Gladiolus (160) SW Cape and Namaqualand, throughout tropical Africa and Madagascar in mountains and savannas (145) also in <i>Eurasia</i> (15)
Homoglossum (10) SW Cape
Anomalesia (3) SW Cape to Namibia
Radinosophon (?) E Transvaal to Zambia, along the escarpment
Oenostachys (?) South tropical Africa to Ethiopia, mainly high mountains
Hesperantha (50) SW Cape and Namaqualand through E Cape to Ethiopia
Schizostylis (1) Transkei to Zimbabwe
Geissorhiza (70) SW Cape and Namaqualand
Engysiphon (8) SW Cape (to Geissorhiza)
Melasphaerula (1) SW Cape and Namaqualand
Tritoniopsis (14) SW Cape
Anapalina (7) SW Cape–Transkei
Babiana (63) SW Cape and Namaqualand, Karoo to Zimbabwe (62) and <i>Socotra</i> (1)
Antholyza (2) SW Cape and Namaqualand
Zygotritonia (2) tropical African savannas

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variation occurs, the most primitive and presumably basal stocks are found, and much of the radiation and speciation has taken place. As in *Moraea* (Iridoideae), some genera have extended their range eastwards to some extent (*Anapalina*, *Watsonia*) into the well watered parts of southern Africa, or even into tropical Africa (*Gladiolus*, *Romulea*, *Hesperantha*), again mostly confined to mountain belts (Table 2). *Gladiolus* is exceptional in occurring in drier savannas as well, and it has spread, probably by short distance dispersal, into Eurasia, as has *Romulea*.

A few genera, also apparently centred, or at least well represented in the Cape Region, but adapted to drier habitats appear to have spread not eastwards through grassland, but northwards along the West Coast into the dry savanna and steppe of the Karoo-Namib zone. *Lapeirousia* is an outstanding example. Species of the *L. erythrantha* complex extend as far north as Nigeria and *L. abyssinica* and *L. schimperi* occur in Ethiopia (Cufodontis, 1974). The pattern in *Babiana* is similar, but most species occur in Namaqualand and the Karoo. Only *B. hypogea* reaches Zimbabwe and Namibia, and *B. socotrana* is disjunct on Socotra (Lewis, 1959). This disjunction seems unusual, but has parallels in several African plant families (De Winter, 1971).

Among the remaining non-Cape Ixioid genera are *Oenostachys*, *Schizostylis* and *Duthieastrum*. *Oenostachys* is a minor and possibly heterogeneous assemblage segregated from *Gladiolus*; *Schizostylis*

is a semi-aquatic and possibly secondarily rhizomatous segregate of *Hesperantha* (Goldblatt, 1971); and *Duthieastrum*, monotypic, is probably a close ally of *Tritonia* found in the north-western Cape and western Transvaal.

#### DISCUSSION

The patterns of distribution for African genera of Iridaceae, as outlined, fall into four broad categories:

1. Occurrence of unspecialized genera in forests, forest margins and other well watered habitats (*Aristea*, *Dietes*, *Dierama*).
2. Restriction of unspecialized or moderately specialized small genera, mainly taxonomically isolated, to moist sites in the Cape Region (*Bobartia*, *Pillansia*).
3. Explosive radiation and speciation in moderately to highly specialized genera within the Cape Region (e.g. *Gladiolus*, *Geissorhiza*, *Ixia*, *Homeria*; also of derived species of some unspecialized genera) and the evolution of a few small specialized, bird pollinated genera here (*Homoglossum*, *Antholyza*, *Anapalina*).
4. Dispersal of representatives of some specialized Cape genera either northeast into well watered and climatically mild parts of south tropical and east tropical Africa along mountain belts (*Gladiolus*, *Moraea*, *Hesperantha*) or northwest into the arid, climatically extreme Karoo-Namib and thence into tropical central Africa (*Babiana*, *Lapeirousia*).

TABLE 2. — Genera of Iridaceae with a pronounced centre in the Cape Region

1. Endemics or near endemics (locally extending into the western Karoo, Namaqualand or E Cape)		
Klattia	Pillansia	Homoglossum
Witsenia	Micranthus	Geissorhiza
Nivenia	Thereianthus	Engysiphon
Roggeveldia	Ixia	Melasphaerula
Hexaglottis	Sparaxis	Tritoniopsis
Rheome	Synnotia	Antholyza
Galaxia	Chasmanthe	
2. Genera with significant representation northeastwards (as far as Ethiopia, or Eurasia)		
Bobartia (to Natal)		Tritonia-Crocasmia (to Ethiopia)
Moraea (to Ethiopia)		Gladiolus (to Eurasia)
Watsonia (to Transvaal)		Hesperantha (to Ethiopia)
Romulea (to Eurasia)		Anapalina (to Transkei)
Anomatheca (to Tanzania)		
3. Genera with representatives extending north or west into arid zones (secondarily in tropical East Africa or Eurasia)		
Gynandriris (to Karoo and Transvaal, and Eurasia)		
Anomalesia (to Namibia through W Karoo and Namaqualand)		
Babiana (to south central Africa and Socotra)		

*Note:* *Lapeirousia*, though more diverse in the Cape area (Goldblatt 1972), has radiated in Namaqualand-Namibia, and as well in tropical Africa, and it cannot be regarded as a Cape genus. More information on primitive and advanced characters in *Lapeirousia* is needed before properly assessing its relationships and geography.

*Ferraria* has most of its species along the W Coast from the Cape, north to S Namibia, but the most primitive species is in central southern Africa and it is not, in a strict sense, a Cape genus.



The first pattern represents the most ancient one for African Iridaceae, and probably dates back to the Eocene, when lowland evergreen forest covered much of southern Africa (Axelrod & Raven, 1978), then lying some 12–15° S of its present position. Iridaceae presumably occurred either in open, rocky sites or on the forest floor much as *Dietes* and some species of *Aristea* do today. The single non-African *Dietes*, *D. robinsoniana*, occurs on the equable Lord Howe Island, a continental fragment lying between New Zealand and Australia, also in forested habitats. The significance of this distribution pattern is unclear (Goldblatt, 1981), but is most likely very old, although it probably does not predate the separation of Australia-Antarctica from Africa and therefore may represent long distance dispersal, perhaps across a narrow Indian Ocean via India when this lay between Africa and Australasia in the Eocene (Axelrod & Raven, 1978).

The first important climatic change in Africa during the Tertiary took place in the late Eocene (38 m.y. ago) when Antarctica became partly glaciated and substantial sea-ice began to form (Axelrod, 1981). As the bottom water temperature dropped and upwelling began, a drier climate began to spread over the middle latitudes. During the Oligocene the separation of Antarctica and Australia occurred, the circum-Antarctic current was initiated, and seasonal aridity spread. In Africa this trend was strengthened as coastal uplift, most notable along the eastern coast, broke the pattern of low relief of the continent (Axelrod & Raven, 1978). The establishment of open, seasonally dry habitats that these climatic changes imply, created a new adaptive zone for plants. Such open dry conditions would have favoured adaptations towards geophytism and deciduousness.

Corm-bearing and partly deciduous Iridaceae probably evolved from evergreen, rhizomatous ancestors at this time in such open or semi-forested habitats, probably in what is now central Africa, but which then lay some 10° to the south. Southern Africa then had a cool, wet climate and was heavily forested (Axelrod & Raven, 1978; Coetzee, 1978).

In the Miocene (26–5 m.y. ago) as the African plate moved northwards comparatively rapidly (Axelrod, 1981), the East African rift valley systems began to develop. Antarctic glaciation increased and the ocean off the west coast as a result became substantially cooler so that the western part of the subcontinent became drier than the east which was elevated and so cooler and wetter. The lines leading to the modern generic groups in Ixioidae and Iridoideae must then have differentiated in the general area of southeast central Africa.

Probably by the end of the Miocene (5 m.y. ago) most of the genera found today were in existence. These Iridaceae probably could not survive in the tropical areas that were becoming rapidly drier and were displaced southwards. The family probably reached the Cape at this time, which by now was north of the main zone of westerlies, but had a more equable climate than the plains of south central Africa.

During the Pliocene-Quaternary the climate became more extreme and at this period a winter rainfall pattern probably became established in south-western Southern Africa. The high plains to the north became extremely seasonal and dry and cold in the winter. These changes resulted in the opening of a major adaptive zone in southern Africa and one into which geophytes including Iridaceae were supremely preadapted. The genera must have undergone explosive radiation in this new climate zone, as the older, more mesic flora contracted into small pockets of more equable climate or was eliminated.

The sporadic uplift round the southern African coasts most likely meant that mountains existed here since at least the late Miocene. The quartzitic sandstones of the Cape system are particularly resistant to erosion and elevated sandstone areas must have been present for long periods, with perhaps greater or smaller height differentials from time to time.

The presence of elevated areas with accompanying higher rainfall, suggest that even as the climate deteriorated and became more extreme some sites remained available to plants not adapted to seasonally dry conditions. It seems likely that such unspecialized genera as *Bobartia* and *Aristea* (Sisyrrhynchoideae) *Pillansia* (Ixioidae) are essentially relics which survived as a result. In both *Bobartia* and *Aristea* some radiation subsequently occurred and both have species well adapted to the mediterranean type climate that prevails in the Cape today, but significantly, both are poorly represented in the more extreme west than in the south where summer precipitation is not uncommon and the temperatures lower.

The extraordinary radiation in genera like *Gladiolus*, *Moraea*, *Geissorhiza*, *Ixia*, *Romulea*, *Homeria*, to mention only some, is probably a phenomenon of the recent past, when a true mediterranean climate had become established. Part of the richness is due to the varied environments found in the mountainous Cape Region, with its differences in climate, soil and rainfall forming a complex mosaic throughout the area. The richness of species is well known for areas of mediterranean climate (Raven & Axelrod, 1978), but the Cape Region is substantially richer than comparable areas. The reasons for this are not clear (Goldblatt, 1978). Axelrod (pers. comm.) has suggested that the fluctuating climates of the Pleistocene, well documented in the south-western Cape (Schalke, 1973), perhaps acted as a species pump and that with each major climate shift new species evolved, while those already in existence migrated locally into sites suitable for their survival.

The evolution of bird-pollinated species and genera is most likely very recent. Floral modifications for bird pollination which include a long wide perianth tube, red to orange coloration and anthers held above the tepals, represent the highest degree of specialization in Iridaceae. They have evolved independently in several lines: within *Watsonia*; in *Antholyza*, an offshoot of *Babiana*; in *Chasmanthe*, related to the *Tritonia-Crococsmia* alliance; in



*Anapalina*, related to *Tritoniopsis*; and in *Anomaleisia* and *Homoglossum*, both allied to *Gladiolus*. All are southern African and largely restricted to the south-western and southern Cape.

The geography of the Iridaceae in the Cape Region is complex. The pattern most often observed in Cape taxa is for a species concentration peak in the Caledon district with decreasing representation north and east. This is true only for a few of several genera of Iridaceae for which there are detailed treatments. *Ixia* (Lewis, 1962) and *Tritonia* conform to this pattern, but in *Moraea* (Goldblatt, 1976) the peak is shifted northwards into the Worcester-Tulbagh District, and in *Homeria* (Goldblatt, in press) the highest number of species occurs in the Cold Bokkeveld-Cedarberg Mountain belt. *Babiana* (Lewis, 1959) and *Lapeirousia* are centred along the west coast and species concentration falls rapidly east of the Caledon District.

A pattern therefore emerges of the concentration of species in the more specialized genera, being shifted to the west, along the coast and in the mountains running north-south, parallel to the coast. This area has a more extreme climate than the southern coast and southern mountains, with reduced rainfall and typically very little or no summer precipitation. The vegetation is shorter and more open, and it seems that this has allowed far greater radiation than along the moister, more heavily vegetated southern parts of the Cape Floristic Region.

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