

# 8

## PHYTOCHEMISTRY

### 8.1 Introduction

The value of *Hypoxis* as a medicinal plant with potential anti-tumour properties was discussed in Chapter 3 on the Ethnobotany of the genus. Over the past decade considerable interest has been generated in the therapeutic properties of *Hypoxis* in treating prostatic hypertrophy and HIV/AIDS. From the review of the various chemical studies in the genus (included in Chapter 3), the following conclusions are drawn: a) a number of phenolic compounds namely acuminoside, hypoxoside, nyaside, nyasoside, nyasicoside and obtusaside were isolated from *Hypoxis*, b) the compound recognised as having anti-tumour activity is hypoxoside, c) *H. hemerocallidea* (earlier name *H. rooperi*), *H. angustifolia*, *H. nyasica* and *H. obtusa* were reported to contain hypoxoside, d) hypoxoside is concentrated in the rootstocks of the plants and e) hypoxoside has been shown to have activity on immune-related illnesses like cancer, HIV and inflammation.

As part of this project, a preliminary investigation of compounds in the rootstocks of 14 of the 28 southern African species of *Hypoxis* was undertaken. The aim of the study was to investigate the taxonomic value of hypoxoside and other phenolic compounds in rhizomes of southern African species. This chapter discusses the results obtain from thin layer and high performance liquid chromatography and reports on the taxonomic value of chemical patterns in species. Three main fingerprint types are recognised in *Hypoxis*: the *hemerocallidea*-, *filiformis* and *angustifolia* type. The *hemerocallidea* type is present in robust species with rhizomes yellow or orange internally and is the dominant type among the species sampled. Species with white rhizomes have the *filiformis*- or *angustifolia* type profile with hypoxoside absent or subtle in these species. The *angustifolia* type is restricted to *H. angustifolia* which has a unique compound, not present in any other species sampled. From the profiles, relationships of taxa are inferred and these largely confirm the grouping of species based on morphology.

### 8.2 Materials and method

The materials and methods used for thin layer and high pressure liquid chromatography are described in Chapter 4. The vouchers for the specimens cited in Tables and Figures are presented in Table 4.4 (page 48).

### 8.3 Results

The results of the thin layer chromatography (TLC) are presented in Figure 8.1 and those of the high performance liquid chromatography (HPLC) are summarised in Table 8.1 and illustrated by the profiles in Figures 8.2, 8.4 & 8.5. The TLC plate (Figure 8.1) gives an overview of the main phenolic compounds in the 20 samples investigated. Three main fingerprint types are evident:

- 1 The *hemerocallidea*-like type: this is the common pattern detected in 14 of the 20 samples analysed. Hypoxoside (Figure 8.1, arrow) is the main compound with several other minor compounds.
- 2 The *filiformis*-type: present in *H. argentea*, *H. filiformis*, *H. membranacea* and *H. parvula* (Figure 8.1, tracks 11, 15, 17 & 19). A characteristic unknown compound is noticed at  $R_f$  0.4 and  $R_f$  5.3 minutes (Figure 8.2A–D).
- 3 The *angustifolia*-type: with a unique combination of compounds. The marker compound is visible as a red spot at  $R_f$  0.4 and  $R_f$  11.3 (Figure 8.5).

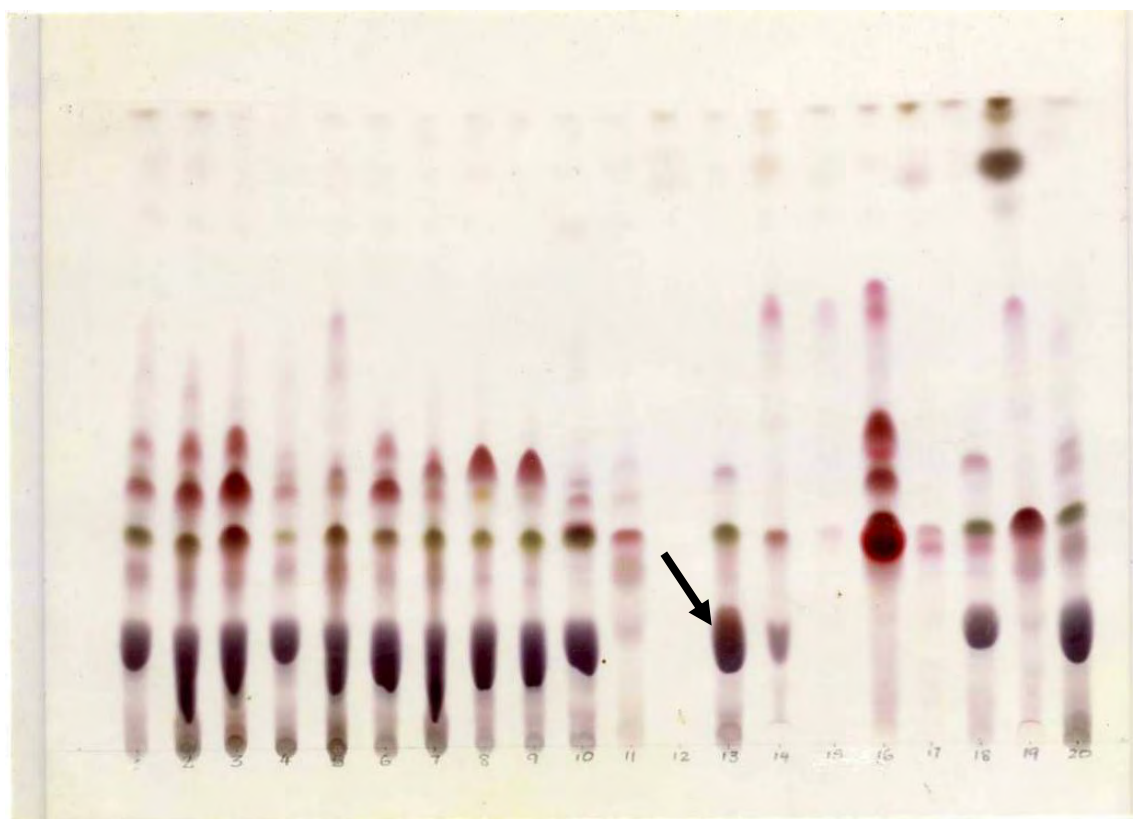


Figure 8.1.—TLC plate showing chemical profiles of 14 southern African species of *Hypoxis*. Species include 1 = *H. hemerocallidea*; 2 = *H. hemerocallidea*; 3 = *H. hemerocallidea*; 4 = *H. hemerocallidea*; 5 = *H. hemerocallidea*; 6 = *H. rigidula* var. *pilosissima*; 7 = *H. rigidula* var. *rigidula*; 8 = *H. colchicifolia*; 9 = *H. galpinii*; 10 = *H. obtusa*; 11 = *H. sobolifera* var. *pannosa*; 12 = *H. costata*; 13 = *H. multiceps* 14 = *H. parvula* var. *parvula*; 15 = *H. membranacea*; 16 = *H. angustifolia* 17 = *H. argentea* var. *argentea*; 18 = *H. acuminata*; 19 = *H. filiformis*; 20 = *H. rigidula* var. *rigidula*. The arrow indicates hypoxoside.

Table 8.1.—HPLC profiles for *Hypoxis*: Retention Time and UV Patterns  
 +, ++, +++ = relative to the quantity present , tr = trace amounts

	4.34	7.60	5.30	5.36	10.39	12.81	10.21	12.30	11.32	6.87	16.86	16.90	17.84	18.76	21.16	8.67	5.37	11.34	12.50	17.18	10.58	4.21	13.28	
<i>H. hemerocallidea</i> 1	+						tr						+++	+										
<i>H. hemerocallidea</i> 2																								
<i>H. hemerocallidea</i> 3																								
<i>H. hemerocallidea</i> 4	+	+					tr				+++		+	+										
<i>H. hemerocallidea</i> 5																								
<i>H. rigidula</i> var. <i>pilosissima</i>	tr										+++		+	+	+									
<i>H. rigidula</i> var. <i>rigidula</i> 1	++							+			+++		+	+	+									
<i>H. colchicifolia</i>	tr							++			+++			++	+									++
<i>H. galpinii</i>											+++		+		+								++	
<i>H. obtusa</i>							tr				+++				+					+++	++			
<i>H. membranacea</i>				+++						+++			+++											
<i>H. sobolifera</i> var. <i>pannosa</i>	+++			++									++											
<i>H. costata</i>	+++			+++									+++								+++			
<i>H. multiceps</i>	+				+++									+										
<i>H. parvula</i> var. <i>parvula</i>					++								+++			++	++	+++	+					
<i>H. angustifolia</i>	++																							
<i>H. argentea</i>	++																							
<i>H. acuminata</i>	tr			+++																				
<i>H. filiformis</i>	++																							
<i>H. rigidula</i> var. <i>rigidula</i> 2	++	+	+++																					

The HPLC profiles confirm relationships of *Hypoxis* species inferred from morphology. Species with delicate, white rhizomes have similar profiles and show a lack of or slight levels of hypoxoside (Figure 8.2A–D). The composition of compounds was found to be uniform among different populations of *H. hemerocallidea* (Figure 8.1, tracks 1 to 5 and Figure 8.3A–C). Similarity between populations was also noted in *H. rigidula* var. *rigidula* (Figure 8.1, tracks 7 and 20). Hypoxoside is the major compound among species with robust, yellow to orange rhizomes (Figure 8.1, tracks 1 to 10, 13, 18 and 20). Its presence is noted in the medicinally important species, *H. hemerocallidea* and *H. colchicifolia* (Figure 8.1, tracks 1–5, 8). The profile of *H. angustifolia* (Figure 8.4) is unique, although morphologically the rhizome in the species is similar to that in members of the *filiformis* type.

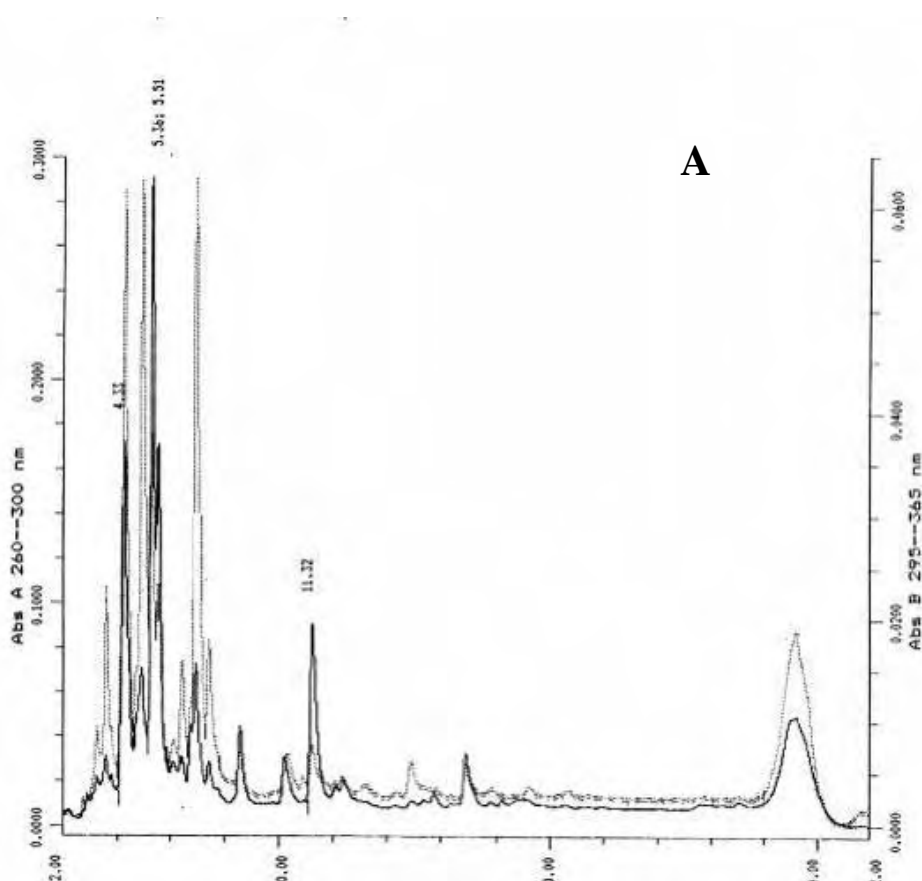


Figure 8.2.—HPLC profiles for species with *filiformis* type fingerprint. A, *H. argentea* var. *argentea*.

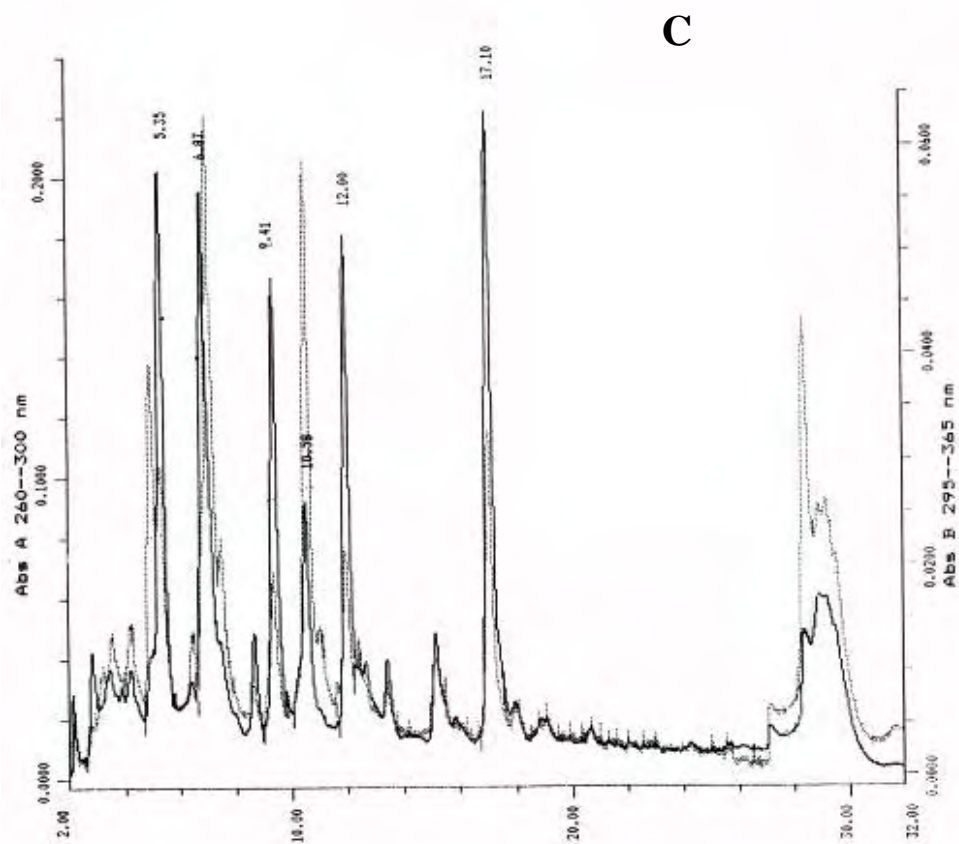
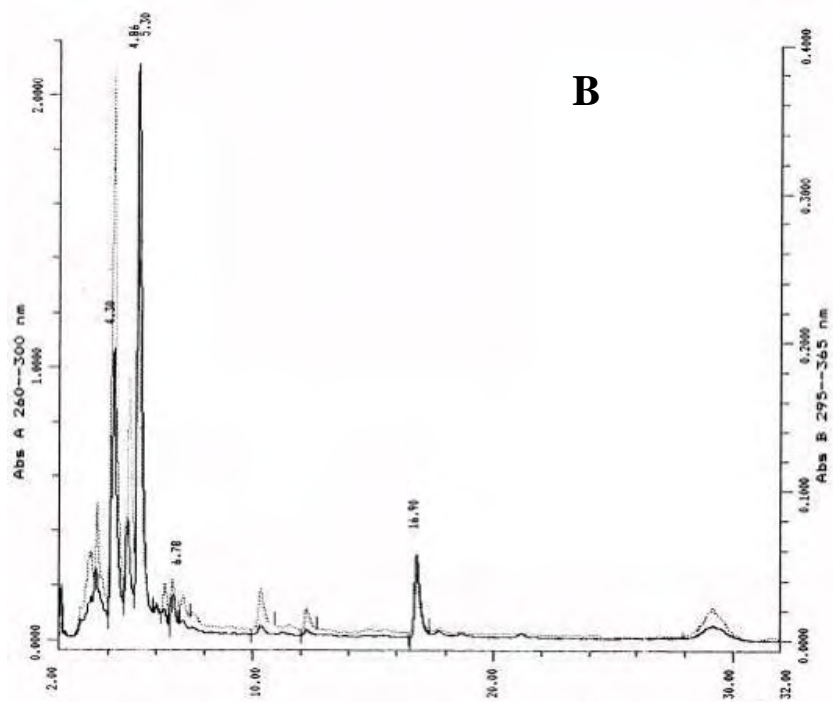


Figure 8.2 cont.—HPLC profiles for species with *filiformis* type fingerprint. B, *H. filiformis*;  
C, *H. membranacea*.

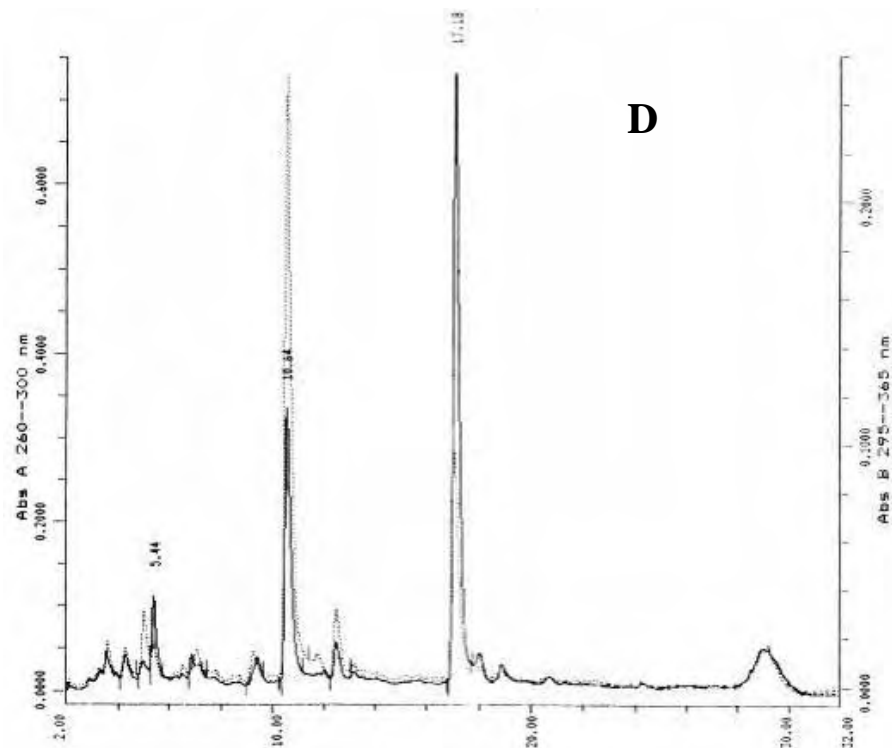


Figure 8.2 cont.—HPLC profiles for species with *filiformis* type fingerprint. D, *H. parvula*.

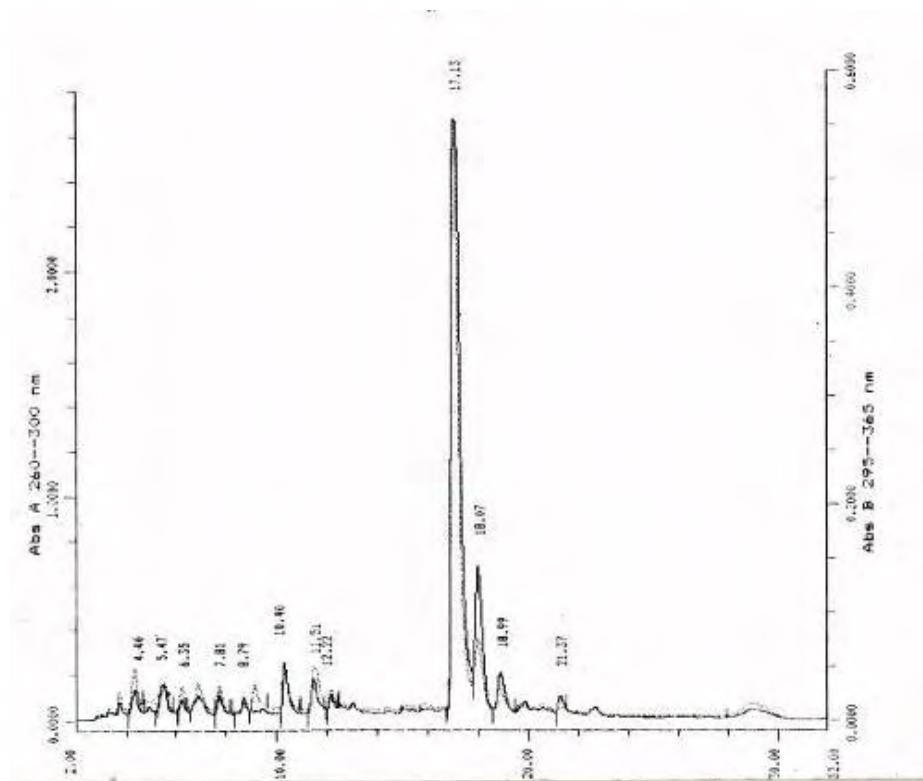


Figure 8.3.—HPLC profiles for three populations of *H. hemerocallidea* (samples 2, 3, 5) showing similarity.

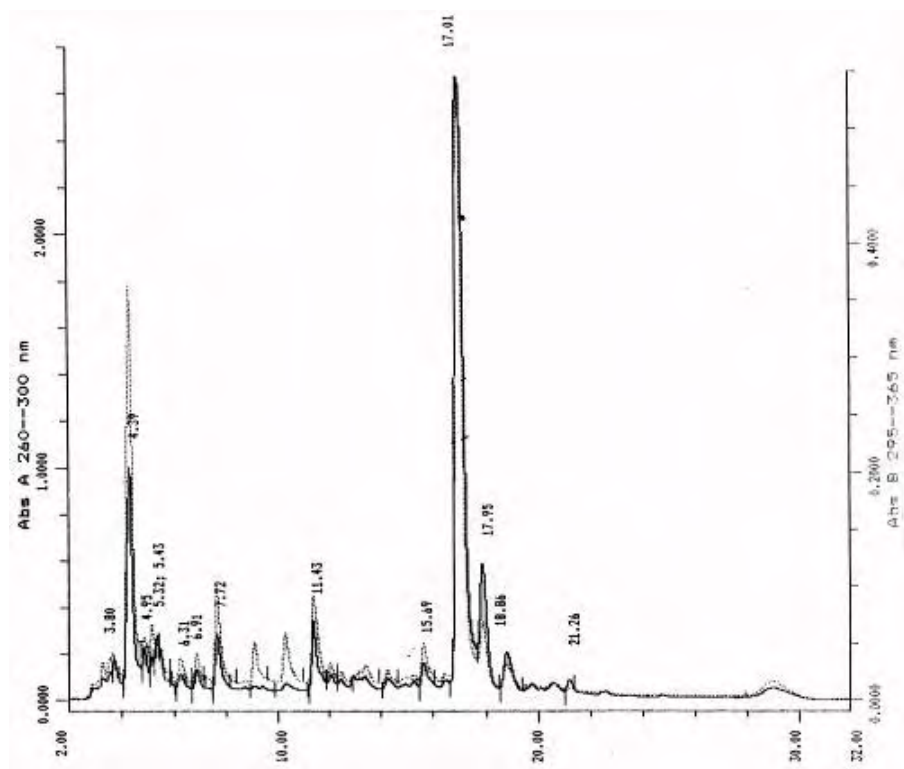
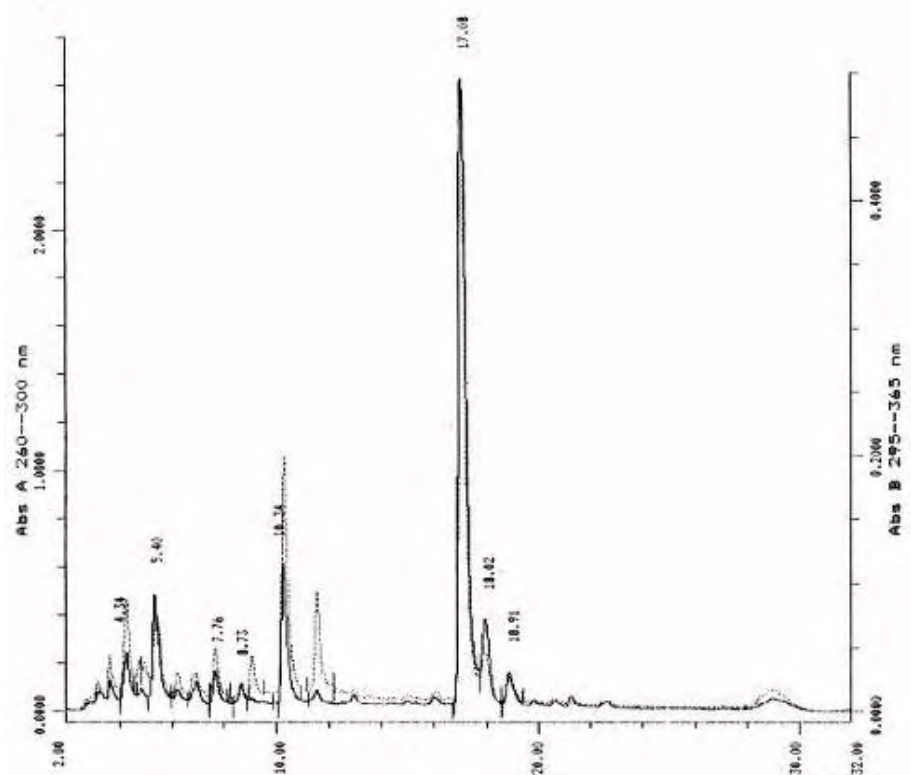


Figure 8.3 cont.—HPLC profiles for three populations of *H. hemerocallidea* (samples 2, 3, 5) showing similarity.

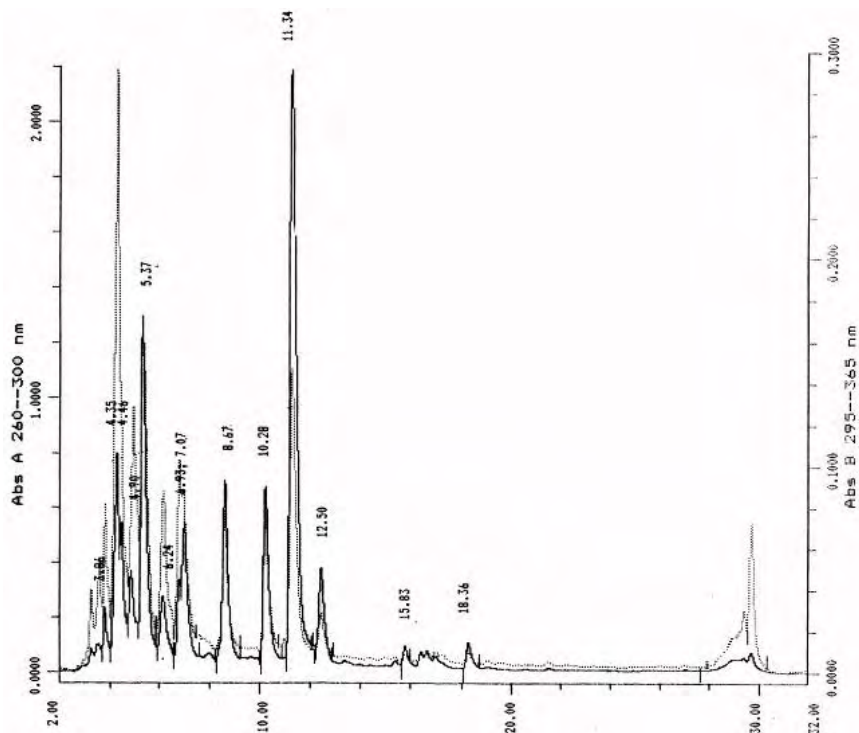


Figure 8.4.—HPLC profile of *H. angustifolia* showing a pattern different to that of the delicate, white rhizomes shown in Figure 8.2.

#### 8.4 Discussion

Earlier phytochemical analyses in the Hypoxidaceae dealt with isolating and identifying active compounds in particular species (Table 2.1). Seven compounds were isolated from members of *Hypoxis* (Table 8.2), mostly from the rhizomes. These studies showed that hypoxoside occurs in *H. hemerocallidea*, the most commercially utilised species, as well as its closest relative, *H. obtusa*. This study confirms that hypoxoside is a major constituent of the rhizomes of many *Hypoxis* species with robust rhizomes that are yellow to orange within. Hypoxoside is a glycoside which on hydrolysis gives an aglycone with the trivial name rooperol (Figure 8.5) [Drewes 1984, Drewes & Khan 2004].

Due to the high degree of uniformity in floral characters, infrageneric classification in *Hypoxis* depends largely on vegetative characters. In Chapter 7, it was reported that the identification of species in the group is best achieved by combining leaf characters with inflorescence types. Rhizome size and internal colour are also useful in classifying species into two broad groups. Stigma shape is either pyramidal or spherical in the genus and is useful in separating the species with membranous leaves. However, both stigma types, more commonly pyramidal stigmas are found in *H. angustifolia*, a species found to have a unique combination of chemical compounds. Among the species included in this study, *H. angustifolia*, *H. argentea*, *H. filiformis*,



Table 8.2.—Selected compounds isolated in *Hypoxis*

Authors	Year	Compound	Species	Organ
Marini-Bettolo <i>et al.</i>	1982	hypoxoside	<i>H. obtusa</i>	rhizome
Drewes <i>et al.</i>	1984	hypoxoside	<i>H. hemerocallidea</i> ( <i>H. rooperi</i> )	rhizome
Marini-Bettolo <i>et al.</i>	1985	hypoxoside nyasoside	<i>H. nyasica</i>	rhizome
Galeffi <i>et al.</i>	1987	nyasicoside	<i>H. nyasica</i>	rhizome
Drewes <i>et al.</i>	1989	hypoxoside	<i>H. hemerocallidea</i> ( <i>H. rooperi</i> )	Rhizome
Galeff <i>et al.</i>	1989	nyaside	<i>H. nyasica</i>	rhizome
Msonthi <i>et al.</i>	1990	acuminoside hypoxoside obtusaside nyasoside	<i>H. obtusa</i>	whole fresh plant
Sibanda <i>et al.</i>	1990	nyasol nyasoside nyaside mononyasine A and B	<i>H. angustifolia</i>	rhizome

*H. membranacea* and *H. parvula* are related in having delicate rhizomes that are white internally. Further, in these species the tepals are linear in shape and the inner and outer tepals appear about equal in width to the naked eye. In the remaining species, rhizomes are robust and are distinctly

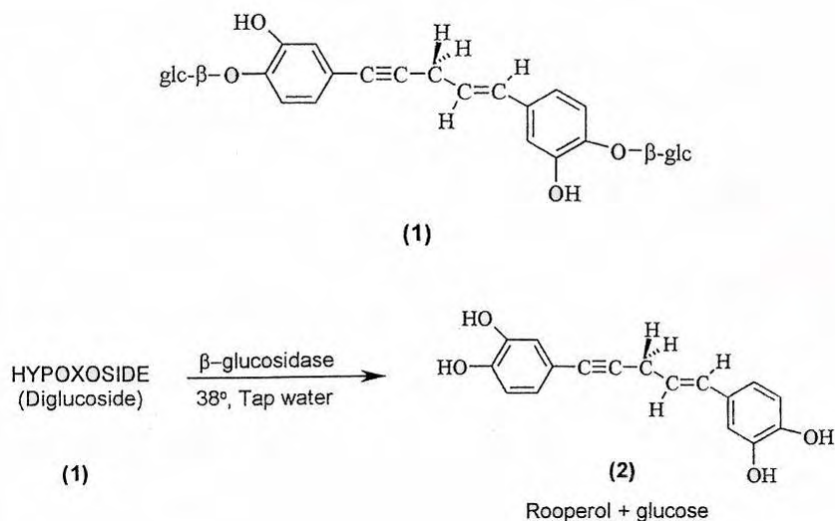


Figure 8.5.—Structure of hypoxoside and its aglycone, rooperol (from Drewes &amp; Khan 2004).

yellow or orange internally. In these species, the inner tepals are broadly ovate and about twice as broad as the outer tepals which are linear or linear-acuminate. The *hemerocallidea*-type chemical profile is present in all species with yellow or orange rhizomes except *H. sobolifera* var. *pannosa*. It

is the dominant type in southern African members of *Hypoxis*. Species with soft, white rhizomes have *filiformis*- and *angustifolia*-type profiles with hypoxoside significantly reduced or absent in these species. *H. sobolifera* var. *pannosa* (Figure 8.1, track 11) has the *filiformis* type profile but the rhizomes of the species are white or yellow internally. The species is however related to the other species with this profile by the shape of its tepals. *H. angustifolia* (Figure 8.1, track 16; Figure 8.5) also has white rhizomes but the species has a unique combination of compounds. The distinctive red spot at  $R_f$  0.4 and  $R_f$  11.3 in *H. angustifolia*, is not visible in the *filiformis* type fingerprint. A flow diagram (Figure 8.6) was constructed to indicate relationships among the 14 species of *Hypoxis* used in the study. The grouping of species in the diagram is based on morphology and chemical data was superimposed onto the groups. As depicted in the diagram, chemical evidence from this study largely confirms the grouping of species based on morphology.

It is noteworthy that there is chemical congruence between morphologically similar species, e.g. *H. colchicifolia* and *H. galpinii*, and *H. hemerocallidea* and *H. obtusa*. *H. sobolifera* var. *pannosa* has the *filiformis*-type profile and this correlates with the flowers having inner and outer tepals about the same width but rhizomes in the species are white or pale yellow internally. The TLC plate (Figure 8.1) shows remarkable uniformity among different populations of *H. hemerocallidea* which is the main commercialised species. This uniformity is also seen in the HPLC profiles (Figure 8.4). Since the medicinal activity of *Hypoxis* is ascribed to the presence of phytosterols, the presence of these medicinally important antioxidants were investigated further using TLC (Figure 8.3). The presence of  $\beta$ -sistosterol and/or stigmasterol is shown in all the *H. hemerocallidea* samples and also in the remainder of the species studied.

## 8.5 Conclusions

This preliminary chemical evaluation showed that the *hemerocallidea* type profile is present in all species with hard rhizomes that are yellow or orange internally and with hypoxoside as a dominant constituent. Species with soft, white rootstocks have *filiformis*- or *angustifolia* type profiles and hypoxoside significantly absent or reduced in these types. The phenolic compounds show considerable promise as chemotaxonomic characters in the genus, and a detailed survey will be worthwhile in view of the ease at which the compounds can be studied in the genus.

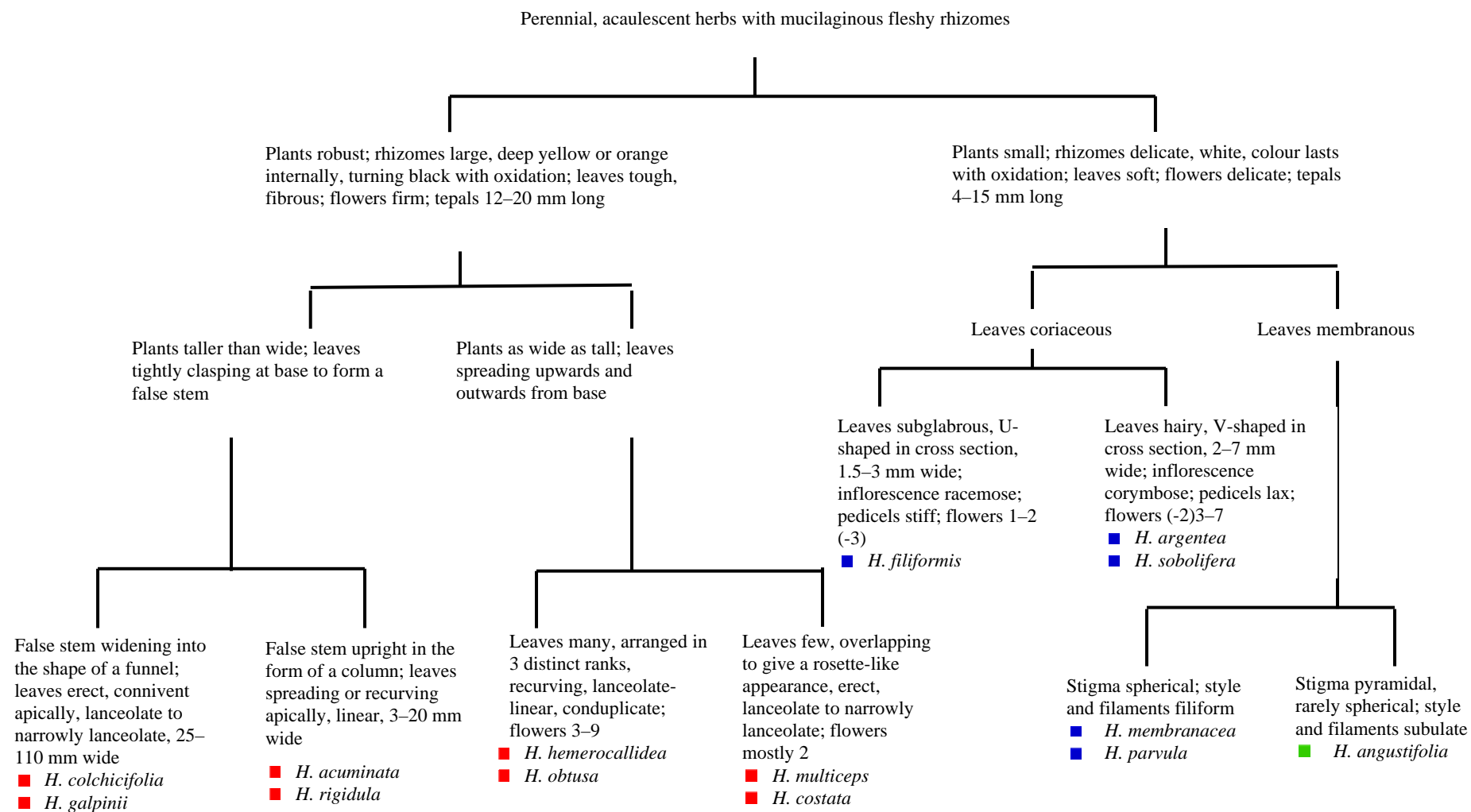


Figure 8.6.—Morphological grouping of *Hypoxis* species used in the study. The main phenolic profiles are superimposed on the diagram.

■ *hemerocallidea* type      ■ *filiformis* type      ■ *angustifolia* type

# 9

## GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

### 9.1 Introduction

The Hypoxidaceae is a predominantly African family with seven of the ten genera represented on the continent. The family is most diverse in southern Africa with six genera (*Empodium*, *Hypoxis*, *Pauridia*, *Rhodohypoxis*, *Saniella* and *Spiloxene*), comprising about 75 species, occurring in the area covered by the Flora of southern Africa [FSA] region (South Africa, Namibia, Botswana, Swaziland and Lesotho). Except *Hypoxis* and *Spiloxene*, all these genera are endemic to southern Africa. *Hypoxis* is widespread in Africa, mainly in the sub-Saharan region and also occurs in the New World, Australasia and some island archipelagoes, e.g. the Antilles and Galápagos. With about 30 species, of which 20 are endemic, southern Africa [FSA region] is the main centre of diversity and endemism for the genus. A secondary centre is located in tropical Africa in the Rift Valley where there are about 24 species, nine of which are endemic to the region. Smaller centres of diversity exist in the southeastern United States of America, Mexico (14 species) and Australia (six species), close to the coast. In Africa, *Hypoxis* is a typical floristic element of the afro-montane phytochorion of White (1981, 1983). It occurs mainly in the Grassland Biome and extends into the associated Savanna, Albany Thicket, Indian Ocean Coastal Belt Biomes. Four taxa (the minority) are semi-shade dwellers, being restricted to open areas in forest, particularly cliff faces. This Chapter is a descriptive account of the geographical distribution patterns and habitat affinities of *Hypoxis* in Africa with emphasis on southern Africa. Its primary aim is to report on species richness and endemism for the genus in sub-Saharan Africa, and to correlate these to phytochoria and biome types. The distributions of species are discussed in terms of their ecological requirements. See Chapter 12 for the distribution of individual species in southern Africa. As biome preferences may influence pollination and seed dispersal strategies in the group, a short discussion on these aspects is also offered. The Chapter concludes with a discussion on the possible evolution of *Hypoxis* on the continent. As a member of the core monocots, the Hypoxidaceae probably has its origins in southern Gondwana (South America, Australasia and Antarctica) and diversified by the Early Tertiary (about 65.5–33.9 Ma) following break-up of the supercontinent and associated transitions in climate, geomorphology and vegetation patterns Bremer & Janssen (2006). It is proposed that orogenic events due to continental uplift in the mid-Tertiary (Oligocene-Miocene epochs, 33.9–5.332 Ma) gave rise to grasslands that fragmented the extensive forest vegetation in Africa (Scotese *et al.* 1988), and this change coupled with the ecological requirements of *Hypoxis* are the main

causes of its speciation and high species richness and endemism on the continent. Speciation in the genus is also driven by evolutionary processes involving hybridisation, polyploidy and apomixis and these are discussed in Chapter 12.

## 9.2 Global distribution of *Hypoxis*

*Hypoxis* occurs in the warm parts of all continents except Europe (Figure 9.1). Of a total of approximately 85 species, some 50 species occur in sub-Saharan Africa, most of these being concentrated in South Africa where 28 species are recognised. A secondary centre of diversity with 24 species is located in tropical Africa. In the latter region, *Hypoxis* is often associated with mountainous regions, especially the Eastern Arc Mountains in Tanzania (mainly) and Kenya, as well as the Katanga Highlands in the Democratic Republic of Congo (DRC). The two centres of high diversity for the genus in Africa correspond to the South Africa and Rift Valley Centres of Diversity (Figure 9.2) recognised by White (1978). A fuller discussion on the physiognomy of these centres is covered below under Centres of Diversity.

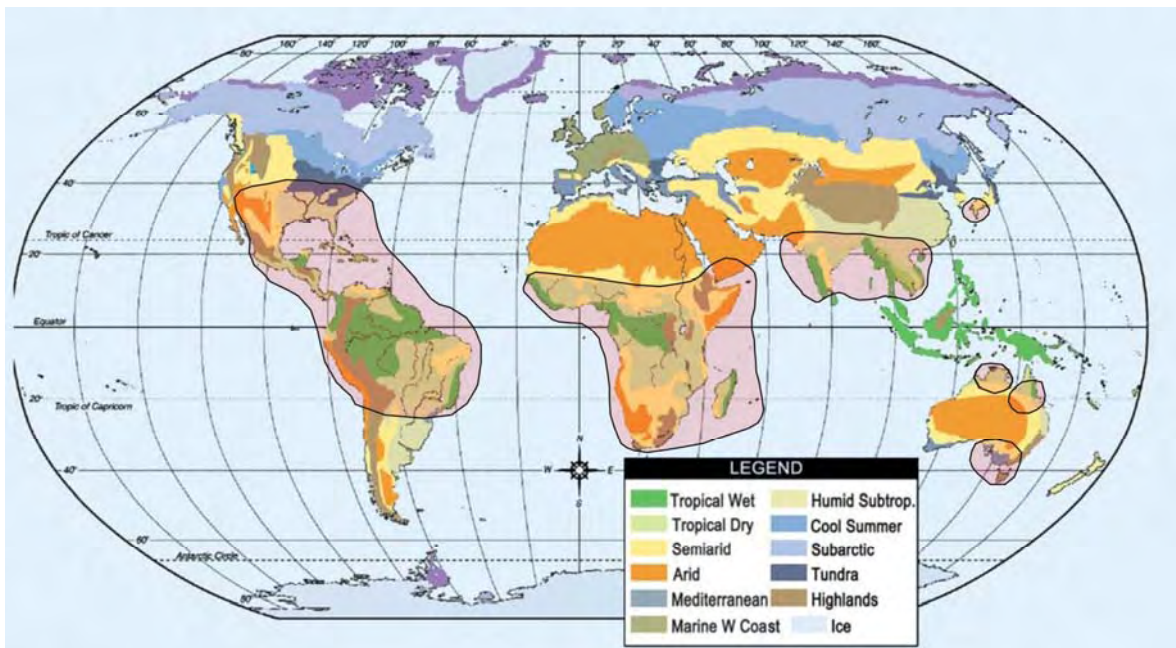


Figure 9.1.—Approximate global distribution of *Hypoxis* showing its occurrence in the warmer parts of the world. Base map from [www.theodora/maps](http://www.theodora/maps).

In the New World, 14 species occur from the southern provinces in Canada through the United States of America (USA), Meso- and Central America to South America with a southernmost occurrence at Buenos Aires (Argentina). In Mexico alone, there are nine species of which four are endemic to the country. Among the group of Mexican species, a few have a wide range. *H. hirsuta* (L.) Coville is widespread in the USA and is the only species that extends into the southern

provinces of Canada, while *H. mexicana* Schultes & Schultes f. ranges into Arizona (USA) and *H. wrightii* (Baker) Brackett also occurs in the USA, Cuba and the Bahamas. South America has three species, *H. breviscapa* Kunth, *H. decumbens* L. and *H. humilus* Tharp. *H. brevicarpa* is known from Bolivia, Argentina and Cojedes, Venezuela. *H. humilus* ranges across Mesoamerica, from Mexico in the north through eastern Brazil to the northern part of Argentina. *H. decumbens* has a similar distribution range but is also present in the Caribbean, the Galápagos and possibly in Tonga. The species is variable in fruit length and Nesom (1993) recognised the form with long fruits as a distinctive variety which he described as *H. decumbens* var. *dolichocarpa* G.L. Nesom.

*Hypoxis decumbens* was noted by Hilliard & Burt (1979) as being introduced in the Lion's River District in the midlands of KwaZulu-Natal in South Africa. The species can be confused with *H. angustifolia* on vegetative morphology but differs in having long, slender ovaries and lanceolate capsules that are mostly indehiscent, the persistent tepals are about  $\frac{1}{3}$  to  $\frac{1}{2}$  the length of the capsules (Wood 179, s.n. in NU, Moll 2860 in PRE). In *H. angustifolia*, the capsules are broadly ovate, dehiscent and the persistent tepals are equal to or longer than the length of the capsule. Seeds in Wood's specimens are black, either shiny or dull. Similar capsules were observed in *Chevalier* 9485 (BR) collected in Baguirmi, Chad, which is also the ex type of *Curculigo baguirmiensis* A. Chev. Seeds in this specimen are distinctly brown. See paragraph in next section for a discussion on seed colouration in *H. angustifolia*. During this study, localities of *H. decumbens* were not specifically traced as the focus was on resolving the status of indigenous taxa. Therefore, field work is required to assess the extent of the KwaZulu-Natal populations of *H. decumbens* and to determine whether they have any reproductive influence on indigenous species in the area. *H. domingensis* Urb. appears to be restricted to the West Indies and is not known from the South American mainland.

In Australia, there are six species of *Hypoxis* are found mostly in southern Queensland and New South Wales and northern Western Australia, as well as in Tasmania. A few specimens are known from the northern part of Queensland. In Asia, the single species, *H. aurea* Lour. has a wide distribution. It ranges from western India across the Himalayas into south China through to the southeast Asian islands of Hong Kong and Taiwan, and into Japan. The species is superficially similar to *H. angustifolia* and *H. decumbens* in its soft leaves and inflorescences but is closer to the latter taxon in its fruit morphology, the crown of persistent tepals being shorter in length than the capsule.

Despite the fewer numbers of species, the taxonomy of the American or Australian members is by no means less notorious than in Africa. Controversial views are seen in the demarcation of

species in these different centres. Based on seed characters, the American *H. potosina*, *H. fibrata* and *H. rugosperma* were recognised as separate species by Brackett (1923), whereas recently McVaugh (1989) and Serna & López-Ferrari (1996) considered them to represent a single species. Variation patterns noted in *H. decumbens* is analogous to the African *H. angustifolia*; both species pose problems for determining character and taxon limits. A comparable challenge is likely once specimens of *H. aurea* across its entire range in Asia are studied. Among the Australian species, the difficulties in dealing with morphological variation are evident in the varieties created for 50% of the species (Henderson 1987).

### 9.3 Distribution of *Hypoxis* in Africa

#### 9.3.1 Continental distribution

As modern revisions for the various floras in Africa emerge, they help resolve the basic taxonomy of *Hypoxis* and provide a more accurate account of the numbers and distribution of species. In Africa, *Hypoxis* ranges from the Western Cape, South Africa, through central Africa into western Africa, and into the horn of the continent. Clearly, eastern southern Africa is the most species-rich region and the number of species decreases northwards in tropical Africa up to the 10°S latitude (Figure 9.2). Species numbers increase again in Central and East Africa along the Rift Valley, approximately between the 10°S and 5°N latitudes. The high number of species in the Rift Valley is associated with the Eastern Arc Mountains of Tanzania and Kenya and the Katanga Highlands in the DRC, and this constitutes a secondary centre of diversity for the genus. A few species in the Rift Valley are endemic to the Katanga Highlands, mainly the Kendulungu Mountains (Table 9.1). Seven species were described by Wiland-Szymańska (2001) as new and are found to be restricted to this range. In south-central Africa (mainly Angola, Zambia, Zimbabwe and Mozambique) there are about 17 species of *Hypoxis*, five common with southern Africa (Table 9.1), nine found in Eastern and Central Tropical Africa (Table 9.2) and five species are widely distributed in Africa. The region has no endemic species. Beyond the 5°N latitude, a single taxon, *H. angustifolia* var. *luzuloides*, occurs in most countries, or it is occasionally found with one or two other species.

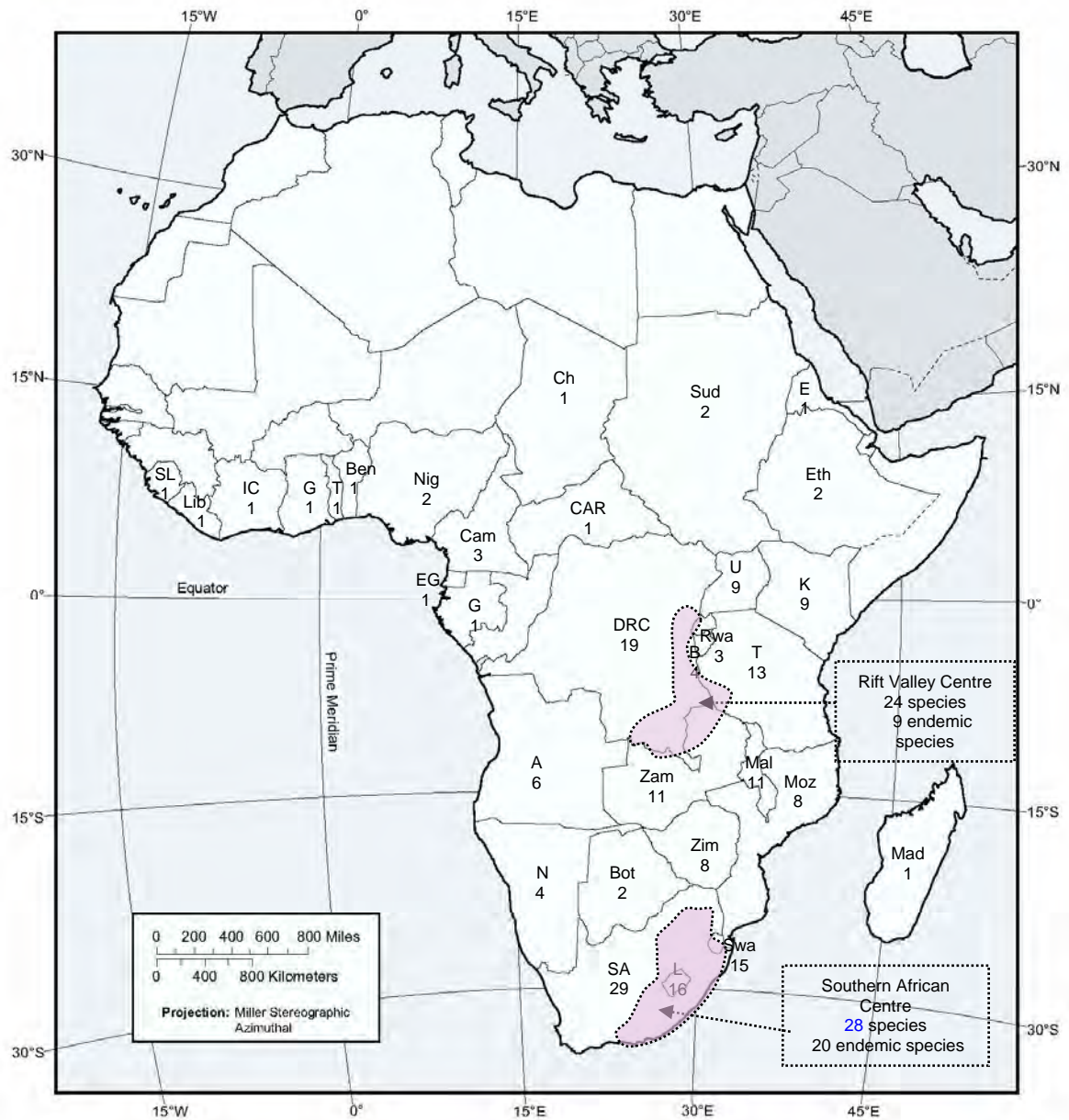





Figure 9.2.—Estimated number of species and endemics per country and the two Centres of high diversity and endemism (pink shade) in Africa. (Base map reproduced with permission from T. Dorschied, Arizona State University<sup>©</sup>).



Table 9.1.—Occurrence of southern African species of *Hypoxis* and their presence in countries in tropical Africa

Data for extra South African countries extracted from Hutchinson & Dalziel (1931), Hepper (1968), Nordal & Zimudzi (2001), Wiland-Szymańska & Adamski (2002), Wiland-Szymańska & Nordal (2006).

Countries classified into flora regions and are abbreviated alphabetically as: A = Angola; B = Burundi; Bot = Botswana; Cam = Cameroon; CAR = Central African Republic; Ch = Chad; DRC = Democratic Republic of Congo; E = Eritrea; Eth = Ethiopia; G = Gabon; Gu = Guinea; IC = Ivory Coast; K = Kenya; L = Lesotho; Lib = Liberia; Mad = Madagascar; Mal = Malawi; Mau = Mauritius; Moz = Mozambique; N = Namibia; Nig = Nigeria; R $\grave{e}$  = R $\acute{e}$ union; Rwa = Rwanda; SL = Sierra Le $\acute{o}$ n; SA = South Africa; Swa = Swaziland; Sud = Sudan; T = Tanzania; U = Uganda; Zam = Zambia; Zim = Zimbabwe. Note countries making up the West Africa Flora region that do not have *Hypoxis* are not included.  = presence of a species  = possible presence of taxon  = endemic taxon


































































SPECIES OR INFRA-SPECIFIC TAXON	Southern Africa				South-central Africa					Central Africa			Tropical East Africa			Ethiopia and Eritrea		Tropical West Africa										West Indian Ocean Islands										
	S A	L	S w a	N	B o t	M o z	M a l	Z a m	Z i m	A	R w a	D R C	B	U	K	T	E	E t h	G	G u	L i b	I C	S u d	N i g	C a m	C h	S L	C A R	M a d	M a u	R $\acute{e}$							
<i>acuminata</i>																																						
<i>angustifolia</i>																																						
var. <i>angustifolia</i>																																						
var. <i>buchananii</i>																																						
var. <i>madagascariensis</i>																																						
var. <i>luzuloides</i>																																						
<i>argentea</i>																																						
var. <i>argentea</i>																																						
var. <i>sericea</i>																																						
<i>colchicifolia</i>																																						
<i>costata</i>																																						
<i>filiformis</i>																																						
<i>flanaganii</i>																																						
<i>floccosa</i>																																						
<i>galpini</i>																																						
<i>gerardii</i>																																						
<i>hemerocallidea</i>																																						
<i>interjecta</i>																																						

Table 9.1.—cont.

SPECIES	Southern Africa					Zambesiaca					Central Africa			Tropical East Africa			Ehiopia and Eritrea		Tropical West Africa										West Indian Ocean Islands											
	S A	L	S w a	N	B o t	M o z	M a l	Z a m	Z i m	A	R w a	D R C	B	U	K	T	E	E t h	G	G u	L I b	I C	S u d	N i g	C a m	C H	S L	C A R	M a d	M a u	R è									
<i>kraussiana</i>																																								
<i>longifolia</i>																																								
<i>ludwigii</i>																																								
<i>membranacea</i>																																								
<i>multiceps</i>																																								
<i>nivea</i>	•																																							
<i>obliqua</i>																																								
<i>obtusa</i>																																								
<i>parvifolia</i>																																								
<i>parvula</i>																																								
var. <i>albiflora</i>	•																																							
var. <i>parvula</i>																																								
<i>rigidula</i>																																								
var. <i>pilosissima</i>																																								
var. <i>rigidula</i>																																								
<i>sobolifera</i>																																								
var. <i>pannosa</i>	•																																							
var. <i>sobolifera</i>	•																																							
<i>stellipilis</i>	•																																							
<i>tetramera</i>																																								
<i>villosa</i>	•																																							
<i>zeyheri</i>	•																																							

Table 9.2.—Occurrence of Tropical African species of *Hypoxis*

Data for extra South African countries extracted from Hutchinson & Dalziel (1931), Hepper (1968), Nordal & Zimudzi (2001), Wiland-Szymańska & Nordal (2006). Country abbreviations as in Table 9.1.

◻ = presence of a species    ◯ = possible presence of taxon    ● = endemic taxon

SPECIES	Southern Africa					Zambesiaca					Central Africa			Tropical East Africa			Ethiopia and Eritrea		Tropical West Africa								West Indian Ocean Islands						
	S A	L	S w a	N	B o t	M o z	M a l	Z a m	Z i m	A	R w a	D R C	B	U	K	T	E	E t h	G	G u	L I b	I C	S u d	N i g	C a m	C H	S L	C A R	M a d	M a u	R è		
<i>angustifolia</i>										◯												◯											
<i>bampsiana</i>																																	
<i>canaliculata</i>																																	
<i>fischeri</i>																																	
var. <i>fischeri</i>																																	
var. <i>colliculata</i>																																	
var. <i>katangensis</i>																																	
var. <i>hockii</i>																																	
var. <i>zemyi</i>																																	
<i>goetzei</i>																																	
<i>gregoriana</i>																																	
<i>kilimanjarica</i>																																	
subsp. <i>kilimanjarica</i>																																	
subsp. <i>prostrata</i>																◯																	
<i>lejolyana</i>																																	
<i>lusalensis</i>																	●																
<i>malaissei</i>																																	
<i>monanthos</i>																																	
<i>muhilensis</i>																																	
subsp. <i>muhilensis</i>																	●																
subsp. <i>kansimbensis</i>																	●																
<i>nyasica</i>																																	
<i>polystachya</i>																																	
<i>robusta</i>																	●																
<i>schimperi</i>																																	
<i>suffruticosa</i>																																	
<i>symoensiana</i>																																	
<i>upembensis</i>																	●																
<i>urceolata</i>																																	

*Hypoxis angustifolia* is the most widespread species in Africa, ranging from southern Africa far north into Ethiopia and Eritrea and westwards into Cameroon, Nigeria, Guinea and Sierra Leone. The species also occurs in Madagascar, Mauritius and the R union. Recently, Wiland-Szymańska & Nordal (2006) recorded its presence in Yemen in southern Arabia. *H. angustifolia* is also the most variable species and in dealing with the variation, Baker (1878b) created two varieties, namely var. *angustifolia* and var. *buchananii*. Subsequently Wiland-Szymańska & Adamski (2002) added a further two varieties, var. *luzuloides* (Robyns & Tournay) Wiland and var. *madagascariensis* Wiland. The variety of *H. angustifolia* that is widespread in topical Africa, namely var. *luzuloides*, is considered absent or extremely rare in southern Africa while var. *buchananii* Baker is restricted to South Africa, Lesotho and Swaziland (Table 9.2). The separation of *H. angustifolia* var. *luzuloides* is on its brown seeds and Wiland-Szymańska & Adamski (2002) cite two specimens from South Africa (*Schlieben* 7345 in BR; *Acocks* 10832 in BR, PRE) as examples of the variety in the region. Unfortunately, the specimen of *Schlieben* at BR could not be studied and the duplicate specimen of *Acocks* collected in Weenen in KwaZulu-Natal housed at PRE is a poor specimen; it lacks flowers and fruit. Brown seeds in specimens were observed to be distinct under a stereomicroscope and these are seen in specimens from Mozambique (*Schlechter* 11659 in GRA), Zambia (*Mulligan s.n.* in GRA), Chad (*Chevalier* 9485 in BR) and Uganda (*Dummer* 2437a in SAM), and the ‘brown’ is associated with the discoloration of the ‘white’ cuticular folds on the seed surfaces, in these specimens. *H. angustifolia* in the Flora Zambesiaca region (Zambia, Zimbabwe, Malawi, Mozambique and Botswana) is reported as having dark brown seeds (Nordal & Zimudzi 2001). Also, according to current opinion (Wiland-Szymańska & Adamski 2002), the typical variety is restricted to Mauritius and R union. However, plants in southern Africa closely resemble var. *angustifolia* in morphology and have variable seed types including that recorded in the typical variety (Singh & Van Wyk, Appendix 1.5), all with a black testa. In the present study, both varieties recognised by Baker (1896) for South Africa are upheld and the typical variety is considered to be present in southern Africa as well.

A few other southern African species extend into Tropical Africa (Tables 9.2 & 9.3). *H. hemerocallidea* and *H. parvifolia* range into the Flora Zambesiaca region, while the distribution range for *H. filiformis*, *H. galpinii*, *H. obtusa* and *H. rigidula* var. *rigidula* extends further north into tropical East Africa, being present in Tanzania and/or Kenya and Uganda (Table 9.1). It is suspected that *H. argentea* var. *sericea* (including *H. dinteri*) also occurs in Zambia and the DRC. This needs to be confirmed by comparison of material from these regions. *H. longifolia* also extends from southern Africa northwards into Mozambique.

### 9.3.2 Distribution of species in southern Africa

Within southern Africa, four taxa, *H. argentea* var. *sericea* (including *H. dinteri*), *H. ludwigii*, *H. obtusa* and *H. rigidula* var. *rigidula* occur in Namibia and two species (*H. hemerocallidea* and *H. obtusa*) occur in Botswana. The rest of the species are concentrated in South Africa, Swaziland and Lesotho (Table 9.4, Figure 9.3), most being associated with the grassland biome. Eight species are restricted to the latter three countries, while a further eight species occur in South Africa and either Lesotho or Swaziland. All southern African species occur in South Africa (Table 9.4), 13 being endemic to the country. In South Africa, *Hypoxis* is most prevalent in summer rainfall grasslands, especially those along the eastern seaboard (Figure 9.3). About 26 species occur in KwaZulu-Natal and Eastern Cape, 22 being common to these two provinces. Mpumalanga, Free State, Gauteng and Limpopo Provinces have between 13 and 17 species and similar numbers are noted for Lesotho and Swaziland. Fewer species are present in the Northern Cape, Namibia and Botswana, here mainly associated with arid Kalahari Basin Savanna and Nama-Karoo vegetation. The dynamics of the Nama-Karoo Biome namely the varying rainfall pattern, low winter temperatures and dry summers combined with the lime-rich, weakly developed soil over rock and insufficient fires do not favour *Hypoxis*. In fact, Mucina *et al.* (2006) point out that by comparison, the Nama-Karoo is not species rich, and that the dominance of asteraceous shrubs might indicate a young biome, but this statement is debatable.

Numbers of *Hypoxis* species also diminish in the Fynbos Biome of the Cape Floristic Region. The biome has a Mediterranean-type climate in part, experiencing winter rainfall and is dominated by fynbos, renosterveld and strandveld vegetation (Rebello *et al.* 2006). Eight taxa, *H. argentea* var. *sericea*, *H. flanaganii*, *H. floccosa*, *H. longifolia*, *H. sobolifera* var. *sobolifera*, *H. stellipilis*, *H. villosa* and *H. zeyheri* occur in fynbos vegetation. *H. floccosa* and *H. villosa* are known from more sites in the Fynbos Biome than from the adjacent Albany Thicket and Grassland Biomes of the Eastern Cape; the other species being more common in the latter biomes.

In Chapter 12, the distribution of individual species of *Hypoxis* in southern African biomes as proposed by Rutherford *et al.* (2006), is presented. These maps indicate that although most members of *Hypoxis* are common in grassland in southern Africa, they are by no means endemic to this particular biome. They also occur in four other biomes namely the Indian Ocean Coastal Belt, Savanna, Albany Thicket and Fynbos, being more frequent in the former two types. After grassland, the higher frequency of *Hypoxis* in Indian Ocean Coastal Belt and Savanna is supported by the presence, at the local scale, of enclaves of grassland in these biomes. The Indian Ocean Coastal Belt is a mosaic of forest and grassland (Figure 9.4A) and most savanna has an herbaceous

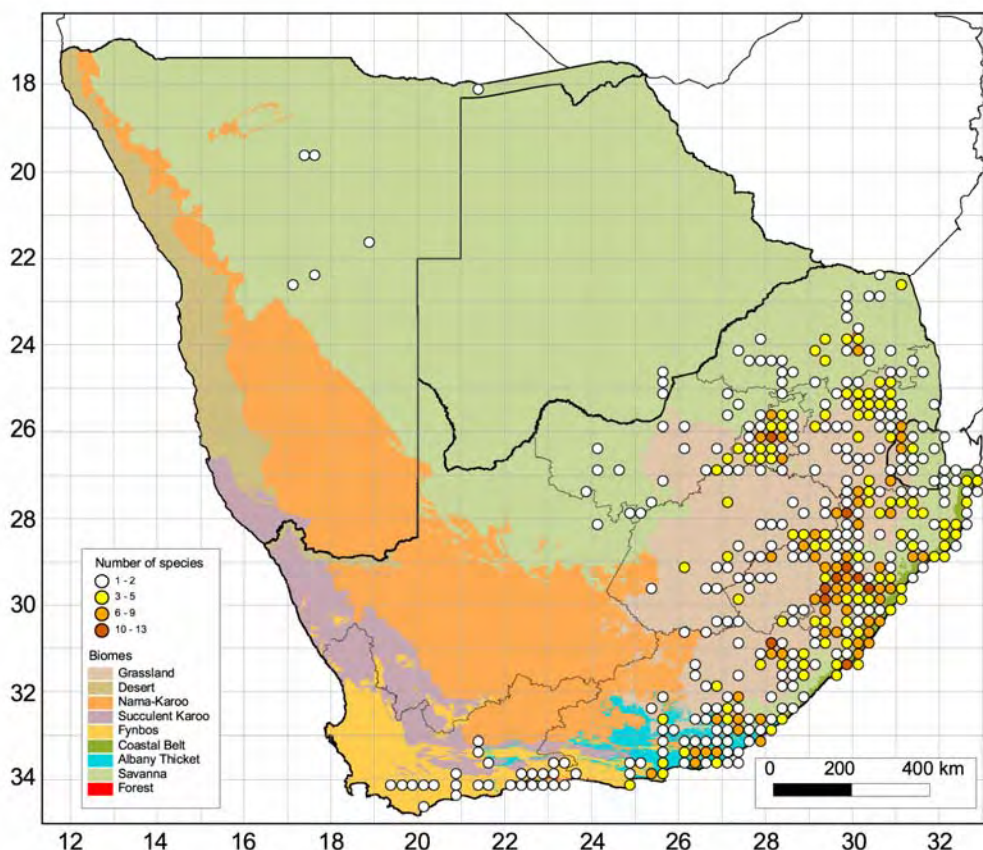


Figure 9.3.—Distribution of *Hypoxis* in southern Africa (South Africa, Lesotho, Botswana and Namibia) plotted against the biomes of the region.

layer dominated by grasses and an open tree layer (Rutherford *et al.* 2006). Mucina *et al.* (2006) explained that the Coastal Belt's tropical character makes it different from the Savanna Biome. It is dominated by trees, lianas and epiphytes and lacks an absolute rain-free period. Savannas, on the other hand, have strong seasonal rainfall and within the biome, trees and shrubs or grasses will dominate depending on the levels of rainfall (Rutherford *et al.* 2006). These authors describe savanna (Figure 9.4C) as being widespread in Africa from South Africa to Somalia and Ethiopia in East Africa and into West Africa reaching Senegal. They also mention its presence on other continents, coinciding mostly with the warmer areas and these contain many of the dominant grass genera that occur in southern African savannas.

The highest concentration of *Hypoxis* species occurs in the Grassland Biome followed by the Indian Ocean Coastal Belt and Savanna Biomes (Figure 9.3). Within the coastal belt, species prefer the grassland to forest. Two species with membranous leaves, *H. membranacea* and *H. nivea*, are restricted to open forests which form a typical component of the Coastal Belt along the eastern seaboard of South Africa. These species grow on forest cliff faces, in partial shade and have white

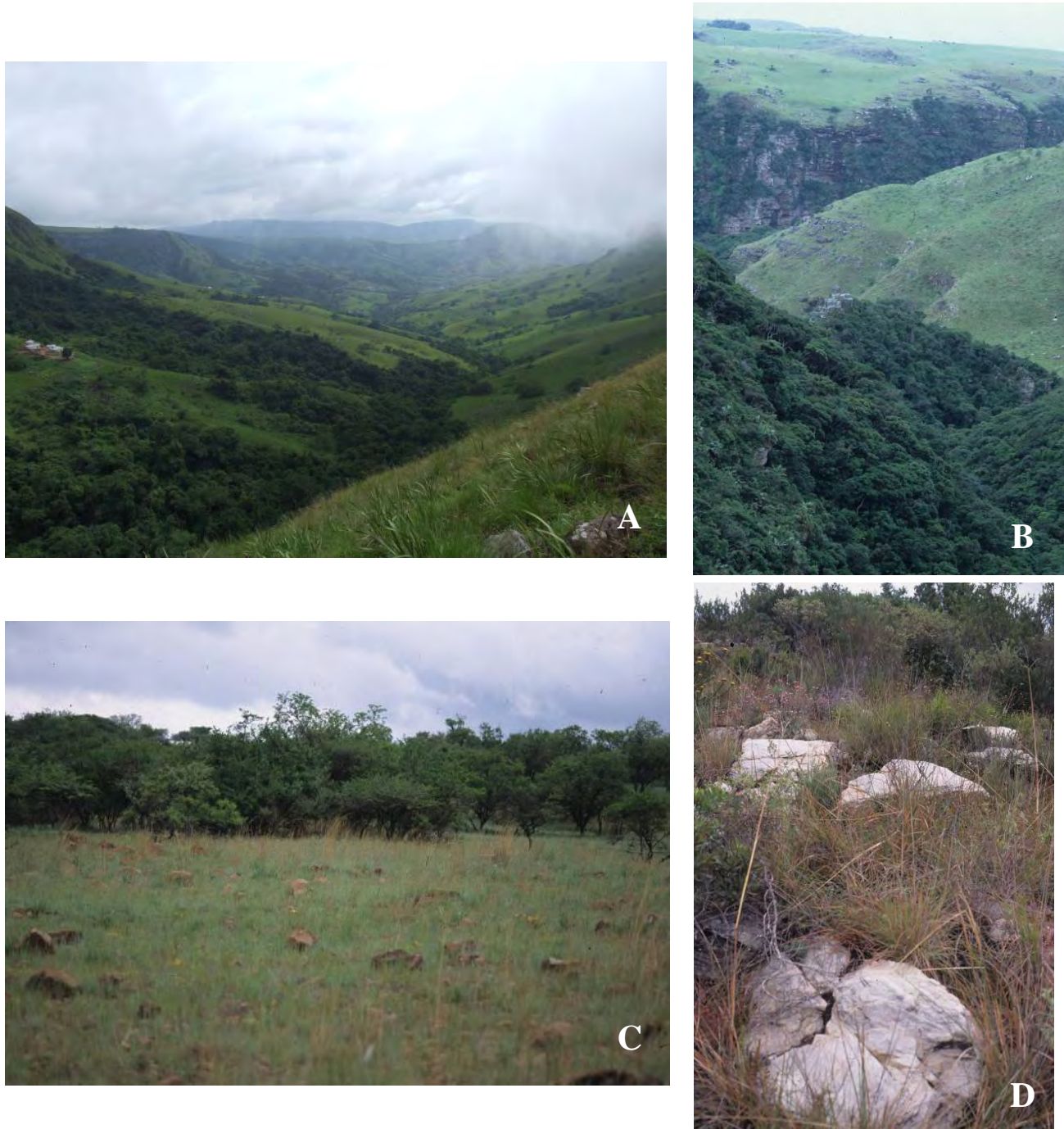


Figure 9.4.—Three of five biomes in southern Africa containing *Hypoxis* species, A, B, Indian Ocean Coastal Belt; C, Savanna; D, Albany Thicket.

Table 9.3.—Distribution of *Hypoxis* in southern Africa, including provinces in South Africa

Provinces in South Africa are abbreviated alphabetically as EC = Eastern Cape; FS = Free State; G = Gauteng; KZN = KwaZulu-Natal; LIM = Limpopo; M = Mpumalanga; NW = North West; NC = Northern Cape and WC = Western Cape. Countries outside South Africa are listed alphabetically as B = Botswana = L = Lesotho; N = Namibia and Swa = Swaziland. Light grey shade in column 1 indicates species with membranous leaves.

■ = presence of a species.

Species or infraspecific taxon	K Z N	E C	M	F S	G	L I M	N W	W C	N C	L	S w a	N	B o t
<i>obtusa</i>	■												
<i>hemerocallidea</i>													
<i>rigidula</i> var. <i>pilosissima</i>													
<i>rigidula</i> var. <i>rigidula</i>													
<i>longifolia</i>													
<i>acuminata</i>													
<i>multiceps</i>													
<i>filiformis</i>													
<i>galpinii</i>													
<i>costata</i>													
<i>interjecta</i>													
<i>parvifolia</i>													
<i>ludwigii</i>													
<i>obliqua</i>													
<i>colchicifolia</i>													
<i>kraussiana</i>													
<i>argentea</i> var. <i>argentea</i>													
<i>argentea</i> var. <i>sericea</i>													
<i>gerardii</i>													
<i>tetramera</i>													
<i>sobolifera</i> var. <i>pannosa</i>													
<i>sobolifera</i> var. <i>sobolifera</i>													
<i>flanaganii</i>													
<i>villosa</i>													
<i>stellipilis</i>													
<i>floccosa</i>													
<i>uniflorata</i>													
<i>zeyheri</i>													
<i>angustifolia</i> var. <i>angustifolia</i>													
<i>angustifolia</i> var. <i>buchananii</i>													
<i>parvula</i> var. <i>parvula</i>													
<i>parvula</i> var. <i>albiflora</i>													
<i>membranacea</i>													
<i>nivea</i>													



flowers. Seeing that this habitat preference is unusual for *Hypoxis*, Singh *et al.* (2007) [Appendix 1.4] discussed in detail the ecology of one of the forest species, *H. nivea*. According to Mucina & Geldenhuys (2006), the forest realm represents an archipelago of forest islands present in Fynbos, Albany Thicket, Grassland and Savanna, and its patchy occurrence is indicative of its relict-like character. This suggests that the forest species of *Hypoxis* may be relictual and were possibly widely distributed when forest cover was more extensive in the past. It is possible that species have adapted to grassland conditions and diversified following the shrinkage of the forests. Further discussion on this is provided under ‘origin and radiation of *Hypoxis* in Africa’.

In South Africa, the Grassland Biome covers mainly the high central plateau (Highveld), the inland areas of the eastern seaboard, the mountainous areas of KwaZulu-Natal and central parts of the Eastern Cape (Mucina *et al.* 2006), and the core distribution and diversity of *Hypoxis* correspond with these areas. According to Mucina *et al.* (2006), the grassland may represent a modern biome together with the Nama-Karoo and Fynbos. They also indicate that development of the Grassland Biome is possibly through global cooling and continental uplift in the Late Tertiary and the uplift moved a considerable area to high altitudes which are colder and more suitable for grassland than savanna vegetation. The diversity and taxonomic patterns in *Hypoxis* indicate that species with coriaceous leaves have either a thick waxy cuticle or an indumentum as possible adaptation to the grassland habitat. These exclude species with membranous leaves (*H. membranacea* and *H. nivea*) and those with slender leaves (3–4 mm wide) (*H. filiformis*, *H. flanaganii* and *H. tetramera*). *H. parvula* and *H. angustifolia* occur in forest and grassland and when in grassland, the species is associated with seasonally marshy patches and crannies among boulders.

The majority of the species prefer damp grassy patches or rock crannies where they often form stands. Many of the robust species, *H. acuminata*, *H. costata*, *H. galpinii*, *H. hemerocallidea*, *H. longifolia*, *H. multiceps*, *H. obtusa* and *H. rigidula*, defined by their coriaceous, firm leaves and racemose inflorescences, have a wide distribution in the eastern region of South Africa, extending in range from Savanna in Limpopo and Mpumalanga across Grassland/Coastal Belt region and reaching the Albany Thicket in the Eastern Cape. Smaller species (*H. argentea*, *H. flanaganii*, *H. sobolifera*, *H. stellipilis*, *H. villosa* and *H. zeyheri*) characterised by soft textured leaves and corymbose inflorescences, occur in Grassland, Savanna and the Albany Thicket. The Albany Thicket (Figure 9.4C) is floristically heterogeneous, having succulent elements from the Nama-Karoo as well as woody members from the subtropical vegetation, and have rainfall at any time of the year (Hoare *et al.* 2006). *H. stellipilis*, a morphologically distinct species (see Appendix 1.5 for

discussion on morphology of the species) is markedly an Albany Thicket element that enters into the adjacent Fynbos. In this species, hairs form a tomentose cover on the lower surface of the leaves, suggesting an ecological adaptation towards water retention under relatively arid conditions.

#### 9.4 Centres of diversity

*Hypoxis* species richness for tropical Africa was calculated from distribution data in Wiland-Szymańska (2001), Nordal & Zimudzi (2001), Wiland-Szymańska & Nordal (2006) and Hepper (1968) at a quarter degree square resolution. For southern African species, distribution data from the PRECIS database were used and built on by adding missing grids from collections obtained on loan from various herbaria. Grid references per species were entered into a matrix and from this the number of species per degree was calculated. Species frequencies per degree confirmed that *Hypoxis* has its core area of diversity in the eastern region of South Africa (Figure 9.5), that corresponds with the Afromontane Archipelago-like regional centre of endemism recognised in White (1993). Species frequencies also suggest a secondary centre located in the Zambesian Centre of endemism and Guinea-Congolia/Zambezia regional transition zone demarcated by White (1993). The highest number of species in Africa, between 10 and 12 are found in 6 grids, all in southern Africa and between 5 and 9 species occur in about 30 grids in southern African and the Sudano-Zambesian region. Most grids have between 1 and 4 species. In southern Africa, *H. argentea*, *H. hemerocallidea*, *H. obtusa* and *H. rigidula* are known from the largest number of quarter degree grids, between 40 and 50. Seven taxa are known from less than 10 grids in the region (Table 9.4). It should be noted that the distribution presented in Figure 9.5 is an estimate based on specimens cited in literature and is likely to change when the grid data are worked of specimens.

Table 9.4.—Taxa known from less than 10 quarter degree square grids

Taxon	Number of grids	Grids
<i>H. nivea</i>	9	2930BD, 2930DD, 3030CC, 3030CD, 3128DC, 3129BD, 3130AA, 3228AD, 3228BC
<i>H. interjecta</i>	9	2528CA, 2528CC, 2529BB, 2529CB, 2627BB, 2628AA, 2729DD, 2929BA, 2929BC
<i>H. sobolifera</i> var. <i>pannosa</i>	7	3129BC, 3225DA, 3227CD, 3325CA, 3325DA, 3326AD, 3326BC
<i>H. stellipilis</i>	7	3323CA, 3324DD, 3325CD, 3325DA, 3325DC, 3326BA, 3326CB
<i>H. kraussiana</i>	6	2730CB, 2730CC, 2731CB, 2829DD, 2930CB, 2930DD
<i>H. floccosa</i>	5	3227CB, 3419AB, 3419BA, 3420AB, 3420CA, 3421AB
<i>H. tetramera</i>	5	2730AC, 2730AD, 2929CB, 2929CC, 2929CD

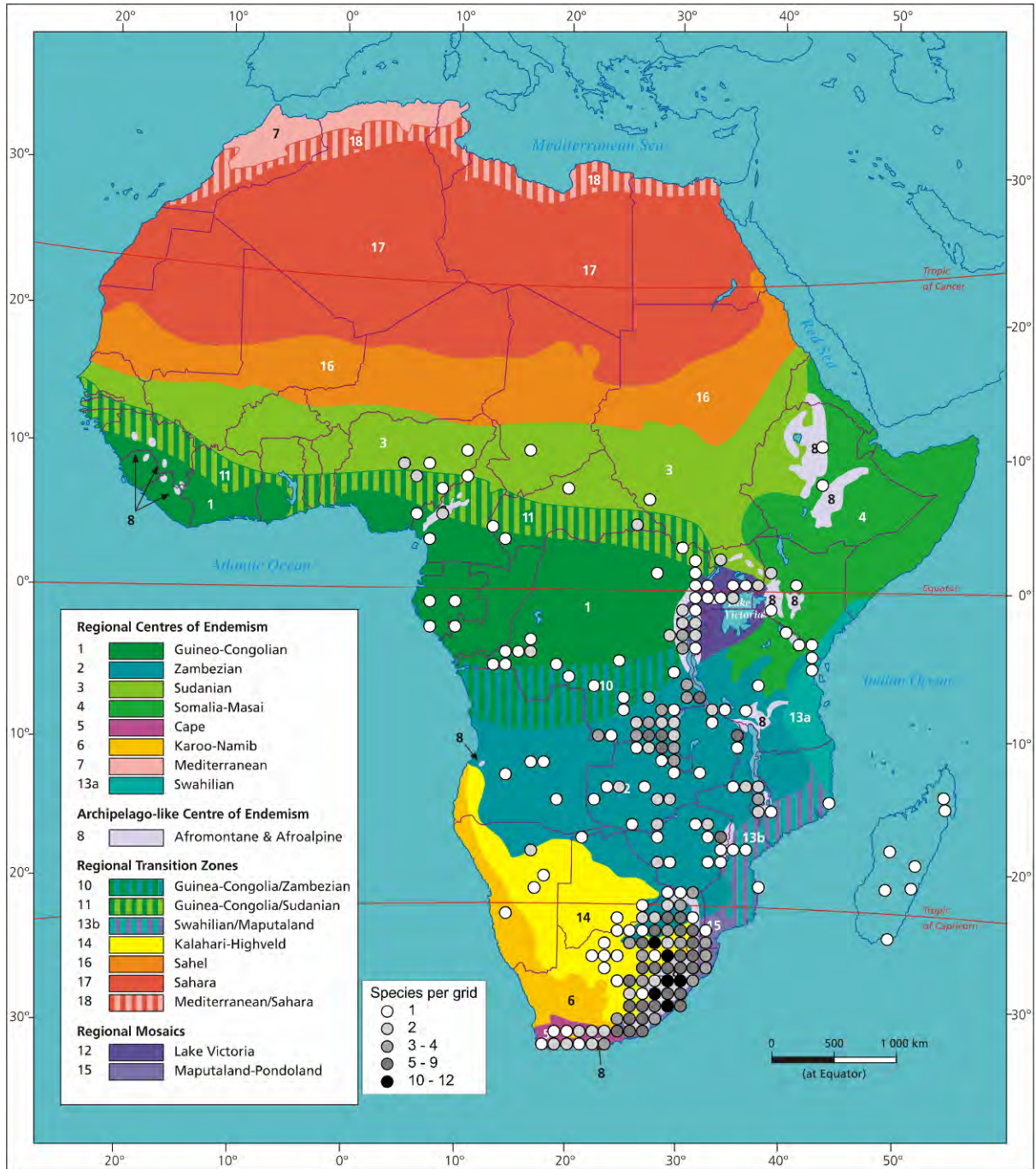


Figure 9.5.—*Hypoxis* diversity in sub-saharan Africa. Grid size is 1 by 1 degree. (Base map reproduced with permission from Van Wyk & Smith<sup>©</sup> 2001). Although *Hypoxis* occurs in Sierra Lorne, Liberia, Ivory Coast, Ghana, Tunisia, Benin and Ethiopia (see Figure 5.2), localities to trace grid references were not available for these countries. Further, for tropical Africa, grid data is based on records cited in literature and this distribution is likely to change when grids are added from specimen data.

In writing about *H. sobolifera* as an example of a widespread grassland species and *H. nivea* as a narrow forest endemic in southern Africa, Singh *et al.* (2007) [Appendices 7 & 8] indicated that *Hypoxis* is of special biogeographical significance as it is a predominantly grassland element with a few species restricted to forest habitats. These authors surmised that the range for the genus reflects a temperate rather than tropical affinity for the genus in Africa, its occurrence shows a strong Afromontane affinity and that its core diversity coincides with two Hotspots on the continent– the Eastern Afromontane (Brooks *et al.* 2004) and Maputaland-Pondoland-Albany (Steenkamp *et al.* 2004). See Singh *et al.* (2007a) [Appendix 1.3] for a general discussion on the biogeography of *Hypoxis* in Africa. This varies from the distribution and centre of diversity in Tropical Africa presented in Figure 9.5. However, the high numbers of endemic species of *Hypoxis* in Tropical Africa, occur in Centraland Tropical East Africa, located in the Eastern Afromontane Hotspot.

In the Eastern Afromontane Hotspot, *Hypoxis* is associated with the Uluguru and Usambara Mountains of the Eastern Arc (Wiland-Szymańska & Nordal 2006) and the High Katanga (Wiland 1997a, 2001) of the DRC. The Eastern Arc is a series of mountain blocks ranging in southern Kenya and Tanzania that peak to altitudes of 2000 to 2500 m. Concerning the origin of the Eastern Arc Mountains in East Africa, Griffiths (1993) explains that ‘the individual mountain blocks have been uplifted along ancient faults dating back to the breakup of Gondwana (more than 180 million years ago), with some uplift events occurring at least since the Miocene (about 30 million years ago), and especially over the last seven million years, associated with the development of the Rift Valley system’. The mountains receive an annual rainfall of mostly above 1500 mm, and as high as 3000 mm is recorded for the Ulugurus (Burgess *et al.* 2004).

Like the Coastal Belt in southern Africa, the Eastern Arc is a forest-grassland mosaic of Afromontane affinity. The mountain slopes are covered in tropical forests that grade into grassland and heathland plant communities with temperate affinities on the plateau (Lovett, 1990). This vegetation is nourished by moisture-laden winds from the Indian Ocean (Burgess *et al.* 2004), and Lovett & Wasser (1993) claim that the climatic regime of the region is maintained by the Indian Ocean climate that is believed to have been stable over millions of years.

The topography of the High Katanga (Central Africa) and the Zambesian region is mainly Savanna (=miombo woodlands). The mountainous margins of Lake Malawi (Nyasa) and the Mulanje Massif in southern Malawi form part of the Southern Rift, which is not under the stable Indian Ocean climatic regime and is biologically poorer (Burgess *et al.* 2004) in comparison to the Eastern Rift.

Outside of Africa, smaller centres of diversity are recorded in the USA-Mexico region, with high endemism of species recorded in the Mesoamerican Mountains. Australia represents the smallest centre of diversity. In general, *Hypoxis* on all continents is associated with the grasslands and savanna woodlands, and rarely open forests.

## 9.5 Ecology

*Hypoxis* species-richness in southern Africa is clearly centred in Grassland with predominantly summer rainfall. The genus, in general, prefers direct sunlight. The majority of species grow in open grassland and may continue into adjoining dune and savanna vegetation provided sites offer sufficient light. Species with membranous leaves, *H. angustifolia*, *H. parvula*, *H. membranacea*, and *H. nivea* grow in Coastal Belt Forest, on cliff ledges in partial shade and the latter two species are restricted to this habitat.

Most species of *Hypoxis* in southern Africa are either widespread and have a range from coast to the interior, reaching high altitudes of 2400 m above sea level (Snijman & Singh 2003) [Figure 9.6]. Species may be restricted either to the coast or to high altitudes in the interior, particularly the Drakensberg Mountains. Five species, *H. flanaganii*, *H. floccosa*, *H. nivea*, *H. stellipilis* and *H. villosa* have a coastal distribution. *H. sobolifera* occurs mainly along the coast and forms prolific masses along the rocky coastline (Figure 9.7) in the salt spray zone from Swellendam in the Western Cape to Port Edward in KwaZulu-Natal, but there are also rare inland collections of the taxon from the foothills of the Drakensberg Mountains in KwaZulu-Natal. A few species are endemic to the Drakensberg Mountains, the range of which forms part of the Great Escarpment and extends from the Eastern Cape through KwaZulu-Natal, Lesotho, Free State and reclines in Gauteng and Limpopo. Grasslands of the Drakensberg receive rainfall mainly in the form of thunderstorms, about 1000–2000 mm per annum, but orographic mist is also an important contributor to precipitation of the area. *H. tetramera* is restricted to high altitudes (1800–2400 m) and is an element of the Drakensberg Alpine Centre [DAC]. The DAC is recognised as a distinct local centre of floristic endemism by Van Wyk & Smith (2001). It has a temperate climate with summer rainfall, and mist is common throughout the year. However, these DAC endemic species do not reach the alpine belt, the region above 2800 m that endures severe changes in weather with cold to freezing winter temperatures (Van Wyk & Smith 2001). *H. parvifolia* occurs at a lower

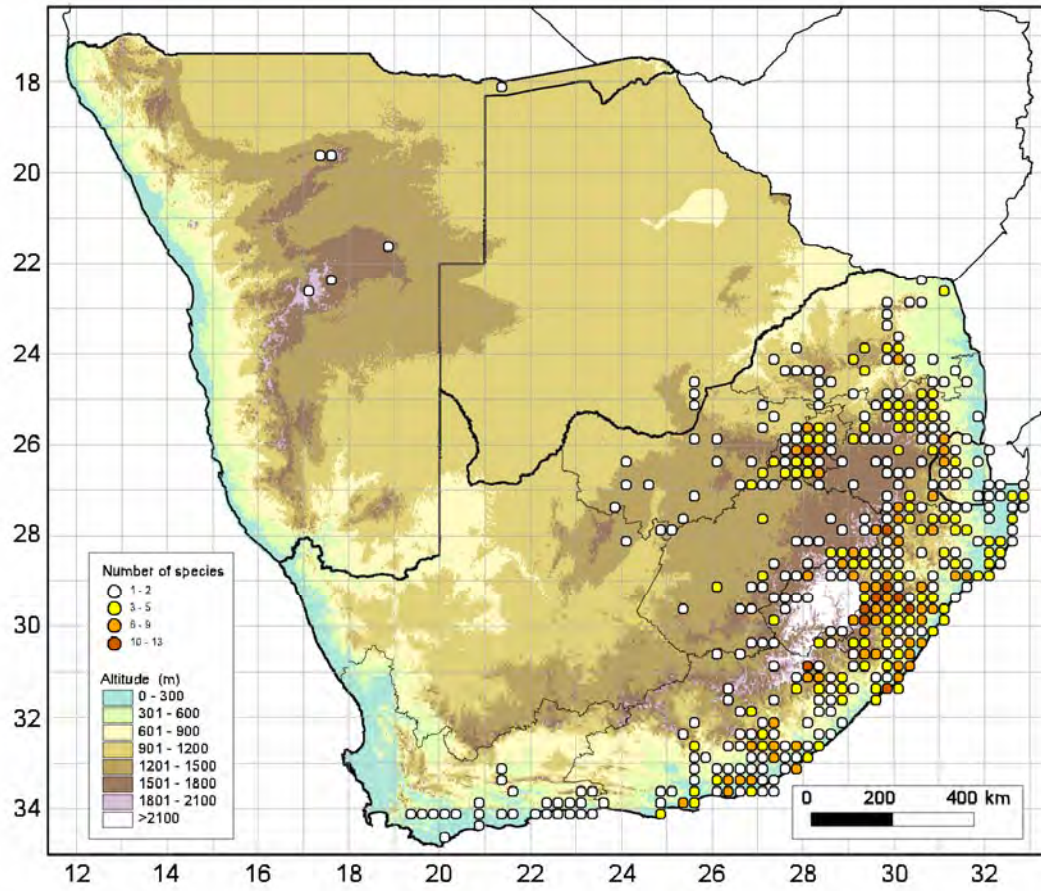


Figure 9.6.—Distribution of *Hypoxis* in southern Africa plotted against altitude.



Figure 9.7.—Mass of *H. sobolifera* along coast in East London, Eastern Cape.

altitude of 1200 m. *H. parvula* shows a disjunct distribution across biomes and altitudes. In the Coastal Belt, *H. parvula* occurs in forest but when in grassland, the species is restricted to high altitudes (1200–2400 m), reaching the DAC. In the DAC, it is often found growing with *Rhodohypoxis* (also Hypoxidaceae) among short grass. Hilliard & Burt (1988) report on an association of flower colour with altitude and exposure in *H. parvula* in the Drakensberg Mountain and its outliers. They found that the white-flowered plants (var. *albiflora*) occur at lower altitudes (c. 1500–1850 m) and usually on thinner drier grassland of the northwestern slope. Plants with yellow flowers (var. *parvula*) on the other hand, usually grow at slightly higher altitudes (c. 1900–2200 m) in damp grass of the southeasterly slopes. *H. angustifolia* is widespread in forest and grassland from close to sea level and reaches an altitude of 1800 m in the Drakensberg.

Shade and moist habitats presumably facilitate water retention in species with membranous leaves (*H. angustifolia*, *H. membranacea*, *H. nivea* and *H. parvula*) and those with slender leaves, between 3–4 mm wide (*H. filiformis*, *H. flanaganii* and *H. tetramera*). In grassland, these species are largely confined to damp grassy slopes, seasonally marshy depressions and seepage or shade spots among boulders. Other species grow mostly in drier conditions and show structural adaptation presumably to reduce transpiration in having coriaceous (non-membranous) leaves either with a thick, waxy cuticle or a dense indumentum. Species with glabrous laminae (hairs completely absent or restricted to margins and veins), *H. colchicifolia*, *H. longifolia*, *H. obtusa*, *H. kraussiana*, *H. ludwigii*, *H. obliqua* and *H. rigidula* var. *rigidula* have a thick, waxy cuticle that probably reduces transpiration. Leaves in the remaining species are covered in hairs, usually more densely on the lower surface. The presence of hairs in *Hypoxis* is interpreted as an adaptation to drier conditions. It is known that hairs lessen air movement at the leaf surface by forming a zone of still air through which water vapour diffuses from the leaf interior to the relatively dry air surrounding the atmosphere (Woolley 1964). Hairs may also indirectly influence the water economy of plants by lowering leaf temperature (Fahn & Cutler 1992). The layer of hairs increases leaf reflectance substantially for all wavelengths of solar radiation between 400 and 3000 nm and reduces radiation absorption which results in reduced heat load, reducing transpiration (Ehleringer 1984). Similarly, cuticular waxes also reflect light and have been shown to regulate leaf temperature and reduce transpiration. Fahn & Cutler (1992) indicate that it is possible to find members of a family or even a genus, with dense indumentum on both or one surface growing in the same habitat. Varying densities of leaf hairs were observed in *H. argentea*, *H. acuminata*, *H. rigidula*, *H. sobolifera*, *H. villosa*, *H. flanaganii*, *H. floccosa* and *H. gerrardii*, often among plants in the same population.

Shade and moisture are also responsible for a fair amount of phenotypic plasticity in members of the genus. Leaves in species growing in partial shade provided by trees or rocks are usually about twice as large as those in direct sunlight. Singh *et al.* (2007a & b) described the variation in leaves recorded in plants of *H. sobolifera* [Appendix 1.3] and the similar effect of deeper shade on plants of *H. nivea* [Appendix 1.4]. Plants of *H. angustifolia* and *H. parvula* in forest habitats are almost glabrous in comparison to plants from grassland, denoting the possible role of hairs to reduce transpiration in warmer open habitats.

In southern Africa, flowering of *Hypoxis* is often associated with areas burned in winter/early spring and spring rains. The genus is noticeable in burnt fields (Figure 9.8A) due to their prolific flowering in the absence of above-ground growth and leaf litter. Their presence in unburnt fields is not only obscured by tall grasses (Figure 9.9), but flowering is also less prolific (Figure 9.8B). Figure 9.10 shows *Hypoxis* plants in unburnt grassland during the dormant season. Flowering in *Hypoxis* is clearly stimulated by periodic burning, but fire is not essential for this purpose (Figure 9.8B) and the plants cannot be regarded as obligate pyrophytes. The genus survives fires by a perennial rhizome, an adaptation possibly established during the Tertiary (Burgoyne *et al.* 2005). Burgoyne *et al.* (2005) emphasised that fire is an integral natural factor of the climate in Africa and that grassland and savanna biomes are fire-dependent for the maintenance of their structure and biodiversity as well as their proper functioning. Herndon (1988) studied the effect of fire on the reproductive activity of *H. sessilis* and *H. wrightii* in southern Florida. He concluded that fire acts as a strong flowering stimulus and flowering in these species peaks in the first three months after a burn. Flowering peaks occur in a similar time frame in southern African *Hypoxis*. In the summer-rainfall region, peak flowering in the grassland species coincides with burning during the dormant season (mainly May–July) and with the onset of the spring rains in September or later. Burning probably stimulates flowering in petaloid monocots by reducing competition from woody members (Goldblatt 1991), but this probably only applies to the Fynbos Biome. In the Grassland and Savanna Biomes, associated woody plants are usually dormant during flowering of *Hypoxis*. Herndon (1988) explains the effect of fire and rain on the herbaceous layer. Firstly, fire removes the litter layer and reduces the hardwood leaf area giving the herb layer access to increased light levels, and this stimulates reproductive activity. Secondly, there is a brief increase in soil fertility as nutrients mineralised by fire from the leaf litter enter the soil with the first rains and thirdly, more soil water and nutrient reserves become available to the herbs that re-sprout at a faster rate





Figure 9.8.—Impact of burning on *Hypoxis* growth. A, *Hypoxis obtusa* in burnt grassland in KwaZulu-Natal, Estcourt; B, *H. hemerocallidea* not noticeable in unbrunt grassland, KwaZulu-Natal, Durban.



Figure 9.9.—Winter dormant, summer rainfall grassland, Gauteng, Suikerbosrand (May-July).



Figure 9.10.—*Hypoxis* plants during winter dormancy. A, *Hypoxis rigidula*, past season's leaves (arrow); B, *H. obtusa*, past season's leaves (arrows).

than woody members, after a fire. Moreover, smoke from veld fires is known to stimulate seed germination (Brown & Van Staden 1997). Indications are that smoke may similarly stimulate flowering in some Grassland and Savanna Biomes species, but this requires further experimental study.

The nutrient rich soil, rainy season and absence of dominant vegetation also provide a favourable habitat for seed germination. Several species of *Hypoxis* belong to a unique group of perennial resprouters known as pre-rain flowers and is defined by Van Wyk (2004) as a group that flower and set seed before the first spring rains after the dormant season and especially following a fire. Production of flowers early in the season, in the absence of competitive vegetation is believed to promote pollination and seed set in the genus. Herndon's (1988) studies showed that by growing and reproducing quickly after a fire, *Hypoxis* species are able to disperse their seed in a habitat that supports germination. The temporary absence of a complete ground cover may be important for seedling establishment, as suggested for the Iridaceae by Goldblatt (1991). Recent studies (Brown *et al.* 2003 and Van Staden *et al.* 2004) showed that smoke from burning plant material contains a chemical compound that triggers seed germination. The compound presumably enters the soil with the nutrients and seeds of *Hypoxis* may depend on it as a germination trigger. Seeds of *Hypoxis* should be sown immediately after harvesting and seedlings develop between four to six weeks later as reported for *H. hemerocallidea* by Gillmer & Symmonds (1999). Poor germination rates were recorded for seeds of the same species stored for two to eight months (Hammerton & Van Staden 1988). Due to lack of competition (and probably more frequent watering), cultivated plants of *H. hemerocallidea*, *H. sobolifera* and certain forms of *H. angustifolia* remain evergreen for most of the year. Cutting back the browning leaves of the earlier season in these plants, stimulates new growth and flowering.

## 9.6 Pollination and seed dispersal

Except for white flowers in *H. membranacea*, *H. nivea* and *H. parvula* var. *albiflora*, flowers in *Hypoxis* are yellow. The anthers and pollen in the white flowers are yellow (Figure 7.7) and the stigma although white is dry and papillate like the rest of the members in the genus. In these white-flowered species, the stigma is oblong to spherical and is held on a filiform style. Yellow-flowered species of *Hypoxis*, on the other hand, have pyramidal stigmas on subulate styles, except in *H. parvula* that has a spherical stigma and filiform style, and *H. angustifolia* in which the shape of the stigma varies between pyramidal and spherical and the ratio of style to stigma length varies (Nordal *et al.* 1985; Wiland-Szymańska & Adamski 2002). The functional significance of flower colour and stigma types is most probably associated with different pollination strategies. Yellow-flowered

species are pollinated by bees, mainly the common honeybee (*Apis mellifera scutellata*) [Figure 7.9] and solitary bees. Open flowers, free tepals, and lack of nectar and scent imply bee pollination for the genus. No pollinators were observed in populations of the white-flowered taxa during daylight hours. This has led Singh *et al.* (2007b) to suggest primitive pollen-eating moths as potential pollinators for the white-flowered *H. nivea*. Flowers in *Hypoxis* open for a few hours only. On sunny days they open after sunrise, between 6:30 and 7:00 and close around midday, following pollination. On cloudy and rainy days when bee activity is low, flower opening and closing is delayed till late afternoon. Usually, only one to three flowers per inflorescence open each day, the lower ones on the inflorescence opening first. In *H. acuminata*, *H. hemerocallidea*, *H. obtusa*, *H. galpinii*, *H. ludwigii* and *H. sobolifera* flowers on many inflorescences open at the same time and the flowers in these species are large and of a thicker texture, revealing their floriferous status. Rogers (2006) points out that duration of the flower is species specific and carefully tailored to its ecological requirements. She suggests three reasons for flowers closing after pollination: firstly the flower is a substantial sink on the plant's resources, and it is energetically expensive to maintain beyond its useful life, secondly, it prevents pathogens that exploit the stigma as a point of entry and thirdly, it removes them from the population and reduces competition for pollinators. These reasons may also, singly or in combination, hold for *Hypoxis*, but the duration of flowers in the genus corresponds with the time of day when bee activity is highest. Further, closing of flowers after pollination must trigger the physiology for seed set, as there is an ecological need in the genus for seeds to be set swiftly.

From a study on seed surfaces in *Hypoxis* in southern Africa (Singh & Van Wyk, Appendix 1.5), it is estimated that close to 85% of the species have papillate seeds. In this contribution, the authors indicate that the ecological significance of papillations or its absence in *Hypoxis* seeds is unclear, but may relate to uptake of water. Of further interest is the water droplet that collects over dehiscent capsules of *H. parvula* var. *parvula* (Figure 7.11). This suggests a possible dependence on water for seed dispersal, at least in the delicate species with lax, drooping inflorescences.

## 9.6 Origin and radiation of *Hypoxis* in Africa

Naturally, the origins and radiation of any group should be dealt with at family level to fully understand specialisation of members and radiation patterns. In this section, data from literature on historical biogeography and age of monocot groups were synthesised to propose a generalised view on the possible origin of Hypoxidaceae (Asparagales) in Africa, and the possible radiation of *Hypoxis* on the continent, a genus present on all Gondwana fragments, and North America. However, in the absence of a robust phylogenetic hypothesis for *Hypoxis*, evolution at generic and

species level must be seen as highly speculative at the moment. Moreover, the conventional view that Afromontane grassland is a relatively young vegetation type in Africa (compared to Afromontane forest) rests also on questionable assumptions. For example, the high levels of local plant endemism in Afromontane grassland compared to the low plant endemism of the associated Afromontane forest suggest a considerable age for these temperate grasslands (Van Wyk & Smith 2001).

From a combined biogeographical and geological history analysis, Bremer & Janssen (2006) inferred a South Gondwana (South America, Antarctica and Australasia) origin for commelinids, and core monocots Asparagales and Liliales. According to these authors, Africa and North America were presumably not parts of the ancestral area for these plant groups. They suggest that the Asparagales, with its many small families, has a Southern Hemisphere distribution, especially in Australasia, thus suggesting an originally Australasian distribution for the order. From Janssen & Bremer's (2004) age estimates for families and orders of monocots, all orders are older than 100 Mya (except the Zingiberales) and Hypoxidaceae has a crown node age of 78 Mya while that for the Asparagales is 119 Mya. These authors indicate that most monocot families diverged between 100 and 65 Mya and this timing coincides with the Late Cretaceous (97.5–65 Mya). By this period Africa had separated from South America (in the Mid-Cretaceous, around 100 Mya according to Scotese *et al.* 1988) but South America remained connected to Australia via Antarctica until the Eocene epoch (55.8–33.9 Mya) of the Tertiary (Bremer & Janssen 2006). Raven and Axelrod (1972) mention that although gymnosperms seemed to have reached Africa overland from the south, distribution patterns of angiosperms agree with a Tertiary origin for most genera.

Patterns of distribution indicate a conglomeration of genera (six of ten) in the Hypoxidaceae in southern Africa. *Curculigo*, *Hypoxidia*, *Heliacme* and *Molineria* are absent from southern Africa, but occur in areas that were also part of Gondwana. *Curculigo* occurs in Tropical Africa and Asia, *Molineria* is found in Asia and *Hypoxidia* is restricted to the Seychelles. The breakup of Gondwana caused vicariant division of its ancestral biota that is reflected in the biogeography of the Southern Hemisphere (Raven & Axelrod 1972). Likewise, the Hypoxidaceae probably has an austral affinity described by Raven & Axelrod (1972) as the time when Africa was joined with Antarctica, and its disjunct distribution may be due to vicariance. However, long distance dispersal cannot be dismissed as a cause of disjunction in the Hypoxidaceae, as Sanmartín & Ronquist (2004) maintain that land link and recent dispersal is a likely explanation for the biogeographical relationships in the southeastern tropics. The southeastern tropics include Africa, Madagascar, India, Southeast

Asia/Southwest Pacific, northern Australia and New Guinea. In the absence of fossil pollen for the Hypoxidaceae, distribution by vicariance remains speculative.

The genus *Hypoxis* is best developed in Africa at two centres, South Africa and the Rift Valley. Its ancestors were most likely similar to the extant fragile, almost glabrous species found in forests. These fragile members have small delicate rhizomes, membranous leaves, few, lax corymbose inflorescences with not many flowers (1–3, less often 5). Species with these characters are fewer in number and are found in Africa, South America, Australia and Asia. On the continent of Africa, the diversification of geophytic monocots has been linked to uplift events in southern and East Africa. These events are believed to have caused the extensive forest cover in Africa to fragment in the Tertiary. Fragmentation created open areas which with climate change gave rise to Afromontane grassland that further supported the development of an extensive herbaceous flora (Goldblatt 1991). Although the ancestors of Hypoxidaceae are considered to be ancient (80–90 Mya or earlier), diversification of the family on the continent is hypothesized to be recent, as species are found mainly in grassland, that are recognised as a modern biome by some authors. Burgoyne *et al.* (2005) mentioned findings by Rayner *et al.* (1991) that suggest the climate of Botswana in the Mid-Cretaceous was temperate, seasonal and wet and the surrounding area was forested. This presumably implies that forest-dwellers, if they existed at the time, were widespread in southern Africa. It may also mean that species of both forest and grassland habitats were also widely distributed in forests, but with uplift events in Africa in the Miocene (23.03–5.332 Ma) and consequential fragmenting of forests, forest species descendents, such as *H. parvula*, have become restricted to forests and cooler alpine grasslands, while grassland-forest species, such as the extant *H. angustifolia*, retained a wide range, but migrated to wetter areas in open grasslands. *H. angustifolia* is very variable in morphology and probably represents the image of those ancestral species with transitional adaptation from forest to grassland habitats in Africa, especially in also having both stigma types.

All other species of *Hypoxis* show adaptation to grassland in having acquired a coriaceous leaf texture or a strong indumentum or both. Increase in grassland areas in Africa, meant that plants were subjected to regular burning and the development of a robust underground storage in *Hypoxis* can be interpreted as a modification to survive fires. Another possible adaptation to fire is the change from corymbose, few-flowered inflorescences and small, thin-textured flowers in fragile species to racemose, many flowered inflorescences and larger, firm-textured flowers in grassland species of robust stature. The increase in number of flowers possibly indicates enhanced reproductive vigour as a result of the extra resources available in the enlarged rhizomes.

## 9.7 Conclusions

There is a clear assemblage of genera of the Hypoxidaceae in southern Africa. Data presented in this Chapter confirmed that the genus *Hypoxis* is also centred in the region and that a secondary centre of diversity is located in Tropical Africa. Members of the genus are dominant in Afromontane grassland that is considered by some authors to be of modern origin. Essentially, the development of grasslands due to climate changes on the continent is recognised as one of the main reasons for speciation of *Hypoxis*, as for the herbaceous flora in general. Speciation in the group may also have been driven by evolutionary events involving polyploidy, hybridisation and apomixis (discussed on Chapter 12) and these factors contribute towards the group's complex taxonomy.