

1

INTRODUCTION

1.1 Background

With about 70 species, *Hypoxis* L. is the largest genus in the small family Hypoxidaceae R. Br. within the ‘asteloid’ clade of the monophyletic order Asparagales (Rudall *et al.* 1998; Fay *et al.* 2000). Nine other genera namely *Curculigo* Gaertner, *Hypoxidia* Friedman, *Molineria* Colla, *Empodium* Salisb., *Heliacme* Ravenna; *Pauridia* Harvey, *Rhodohypoxis* Nel, *Saniella* Hilliard & Burt and *Spiloxene* Salisb. are included in the family (Nordal 1998). The family is most diverse in the Flora of southern Africa (FSA)¹ region with six genera, *Empodium*, *Hypoxis*, *Pauridia*, *Rhodohypoxis*, *Saniella* and *Spiloxene* (Figure 1.1) comprising about 75 species. All these genera, except *Hypoxis* and *Spiloxene* are endemic to southern Africa. *Hypoxis* occurs in warm parts of all continents except Europe. The genus is widespread in Africa, mainly in the sub-Saharan region and its main centre of diversity and high endemism is in the eastern region of southern Africa, with a smaller centre in tropical Africa. *Hypoxis* is distinguished from the other southern African genera in its combination of hairy leaves, mostly yellow flowers and free tepals that are hairy on the undersurface.

1.2 Geographical range of *Hypoxis*

About 50 species of *Hypoxis* occur in sub-Saharan Africa and its range on the continent is from the Western Cape in South Africa, through central Africa and further north into west Africa and also in Ethiopia, Eritrea and Egypt. With about 30 species, 22 being endemic, southern Africa is the main centre of diversity and high endemism for *Hypoxis*. In southern Africa, the genus is concentrated in the eastern region of South Africa, in the Eastern Cape and KwaZulu-Natal. A secondary centre of diversity and endemism is located in tropical Africa. One species, *H. angustifolia* occurs in Madagascar, Mauritius and Réunion (West Indian Ocean Islands).

Outside of Africa, 14 species of *Hypoxis* occur in the New World, concentrated mainly in south-eastern United States of America and Mexico, and six species occur in Australia. Three species, *H. breviscapa* H.B.K. *H. decumbens* L. and *H. domingensis* Urb. are recorded from South America.

¹ The FSA region includes South Africa, Botswana, Lesotho, Namibia and Swaziland and is referred to as southern Africa in the dissertation.



Figure 1.—Southern African genera of Hypoxidaceae. A, *Empodium* (with narrow leaves, do not confuse with broad-leaved plant in background); B, *Hypoxis*; C, *Pauridia*; D, *Rhodohypoxis*; E, *Saniella*; F, G, *Spiloxene*. Photographs C, E, F, G: Colin Paterson-Jones.

H. decumbens is listed as one of 12 weed species with seeds ending up in forage crops in Brazil (Groth 1988). It has also been recorded as naturalised at three sites in the midlands of KwaZulu-Natal (Hilliard & Burt 1979). A single species, *H. aurea* Lour. is widespread in southern Asia.

In Africa, *Hypoxis* is a typical component of the afro-montane flora. Majority of the species are

prevalent in the grassland biome and extend into the neighbouring subtropical dune thickets, savanna or forest biomes. A few taxa are semi-shade dwellers, being restricted to open areas in forest, particularly cliff faces. Within southern Africa, species may be widespread across the region or endemic to a province in South Africa. While some species are spread across habitats from well-drained to moist grassy slopes, forest margins and dune banks, others are restricted to one particular habitat like open grasslands, forest margins or cliff faces.

1.3 Generic nomenclature

Hypoxis was established by Linnaeus in 1759 and the name is derived from the Greek words *hypo* (beneath) and *oxys* (sharp) alluding to the elongated base of the capsule. The word *oxys* could also infer 'sharp' to refer to the somewhat bitter taste of the underground rhizome and roots as opposed to the sweet scented roots of *Acorus* L., as Linnaeus placed *Hypoxis* next to *Acorus* in edition 10 of his *Systema* (Henderson 1987).

1.4 Hypoxidaceae and its classification

The Hypoxidaceae has in the past been treated as a tribe of the family Amaryllidaceae. Hutchinson (1934) was the first to recognise that Hypoxidaceae should be excluded from the Amaryllidaceae and re-established as the family Hypoxidaceae. Hutchinson (1934) also proposed the Hypoxidaceae as a potential sister group to Orchidaceae. It is now widely accepted that the Hypoxidaceae represent the African branch of the Asparagales, with a close affinity to Asteliaceae Dumortier as proposed by Huber (1969) and this is supported by nucleotide analyses (Rudall *et al.* 1997). The generic circumscription in Hypoxidaceae has also varied considerably. Baker (1878b) recognised four genera in Hypoxidaceae; within *Hypoxis*, he distinguished two subgenera, *Euhypoxis* and *Ianthe* based on presence or absence of hairs, anthers basifixed or versatile, and stigma discrete or concrete. Nel (1914) recognised six genera in the Amaryllidaceae-Hypoxidaceae. He raised subgenus *Ianthe* of Baker (1878b) to genus as *Janthe*. He also removed the plants with pink and red flowers from subgenus *Euhypoxis* and placed them in a newly described genus *Rhodohypoxis* Nel. Within *Hypoxis*, Nel (1914) recognised 11 formal sections and 83 species in Africa. Early results of this study agree that species in *Hypoxis* can be broadly classified into groups (Singh 2004) as proposed by Nel (1914), however no formal sections were presented due to the study being restricted to the southern African region.

1.5 Economic significance

A few members of the southern African *Hypoxis* are of economic importance. *H. hemerocallidea* Fisch., C.A.Mey. & Avé-Lall. (earlier name *H. rooperi* T. Moore) commonly known as the ‘African potato’ has become one of the best known medicinal plants in South Africa. Rhizomes of *Hypoxis* are known to the Zulus as ‘inkomfe’ or ‘ilabetheka’ and have been used for many generations to treat headaches, dizziness, abdominal pains and mental disorders (Hutchings 1996). Aqueous extracts of rhizomes of *H. hemerocallidea* were used by white farmers in southern Africa to treat symptoms of prostate cancer (Van Staden 1981) and this gave rise to pharmacological interest in the species. These rhizomes are a rich source of hypoxoside (Drewes *et al.* 1984, Bayley and Van Staden (1990), a phenolic glycoside that hydrolyses to form its aglycone called rooperol which is active in inhibiting the growth of cancer cells (Drewes & Khan 2004). The popularity of the genus as an alternative remedy has resulted in unsustainable harvesting of rhizomes from the wild. Exploitation of rhizomes of target and related species has also expedited the need for correct species names and data on species.

Two species, *H. hemerocallidea* and *H. angustifolia* Lam. are largely used as garden ornamentals in the summer rainfall regions in South Africa. Species like *H. obtusa* Ker Gawl. and *H. sobolifera* Jacq., although floriferous are not widely used in horticulture. *H. stellipilis* would also be an excellent ornamental. The leaves of this species are neatly arranged in three ranks, are dark green above and white on the undersurface, making the species unique and attractive.

1.6 Taxonomic difficulties

The taxonomy of *Hypoxis* offers an extraordinary challenge to systematists. *Hypoxis* plants are easily recognised by their geophytic, erect habit, usually hairy leaves, star-shaped, yellow flowers (white in a few taxa), free tepals and anthers and tepals with hairy backs. However, it is difficult to distinguish between species due to the lack of diagnostic morphological characters. The fairly uniform flower structure in the genus means that greater emphasis is placed on vegetative characters, mainly the leaves, and often these characters overlap between closely related species. Separation of species is also hampered by the changing appearance of leaves during the growing season; younger flowering plants often appear very different to mature plants and may not match the descriptions. The main reason for the complex taxonomy is polymorphism caused by genetic abnormalities arising from hybridization, polyploidization and apomixis. Hybrids, polyploids and apomicts derived through these processes end up with variable chromosome sets that cause morphological variation. The derived character sets of these forms start to obscure species limits

and the forms no longer align with the original parent species. Variation in morphology makes it difficult for taxonomists to construct workable keys for *Hypoxis* and species identification usually requires the expertise of a specialist familiar with the group.

The present state of knowledge on biology, ecology and phytogeography for species of *Hypoxis* is inadequate. New species are sometimes described based on an understanding of the morphology of the species in a particular region, and without critical assessment of its morphological variation and distribution range. Such studies, including the current one are often based on attempts at regional floras. From the time of Nel (1914), descriptions of new species have led to a large number of synonyms being in current use. In fact, *Hypoxis* phenotypes are either lumped into a single taxon or split into distinct taxonomic units. Geerinck (1971) for instance, reduced four species to synonymy under *H. angustifolia* in Central Africa, which Wiland (1997a) more recently resurrected as distinct species, the morphological species concept being applied by both authors. Based on a survey of morphological characters, Nordal *et al.* (1985) and Zimudzi (1996) adopted the approach of creating species complexes for the Floras of Tropical East Africa and Zambesiaca regions. On the whole, the genus still appears to be evolving and the predicament that taxonomists face is how to deal with individuals that show morphological variation within a species concept: to create synonymy, or to recognise distinct species or species complexes?

1.7 Study objectives

The aims of this study were

- to undertake a survey of macromorphological characters, determine their absence, presence and infraspecific variation in southern African *Hypoxis* and evaluate their diagnostic value in delimiting species and infraspecific taxa.
- to provide a taxonomic revision of the genus *Hypoxis* in southern Africa based on the morphological (character-based) species concept and combine these with geographical distribution patterns in an identification key to the species.
- to use data from leaf anatomy, preliminary phytochemical studies of rhizomes and seed micromorphology to comment on the possible phylogenetic relationships of species surmised mainly from macromorphology.
- to highlight southern African members of *Hypoxis* of uncertain taxonomic status and in need of further study.

1.8 Lay-out of thesis

The information in the thesis is presented as Chapters, with each chapter addressing a discipline investigated. The thesis starts with a review of the historical circumscription of the family Hypoxidaceae and the genus *Hypoxis* in Chapter 2. A summary of nucleotide analyses by botanists working on the phylogenetics of the Asparagales and Orchidaceae over the past 12 years is included in this chapter. In Chapter 3, the medicinal, horticultural and magical properties of *Hypoxis* are described. As the focus of this study is to clarify the taxonomy of *Hypoxis*, it merely offers a synthesis of information on the ethnobotanical uses of the Hypoxidaceae that already exists in published literature. The materials and methods used in accumulating data on macromorphology, leaf anatomy, phytochemistry and phytogeography are consolidated and presented in Chapter 4. As part of the study, diagnostic characters for species were recorded from field work in South Africa and plants kept in cultivation as well as from the study of numerous herbarium specimens. Vegetative, flower and fruit characters and their value in classifying species are discussed in Chapters 5 and 7 respectively. The anatomy of most species of *Hypoxis* in southern Africa was studied by examining transverse sections of leaves and additional information was gathered from leaf surface scans. Chapter 6 provides an illustrated account of the anatomy of leaves for the genus. A preliminary investigation of the phytochemical compounds in rhizomes of 15 species of *Hypoxis* was undertaken. The results from the investigation are reported in Chapter 8. Chapter 9 discusses the geographical distribution and ecology of *Hypoxis* in southern African biomes. An integration of morphology, vegetative anatomy and ecological data has led to a better understanding of the phylogeny of species and this data is synthesised in Chapter 10. Also in this chapter, a discussion is offered on the grouping of species and the possible driving forces behind the evolutionary diversification of species in southern Africa. Conclusions drawn from the discussion are summarised in Chapter 11. The thesis is concluded by a taxonomic treatment of *Hypoxis* (Chapter 12) in the format of *Bothalia* where a key to species based on macromorphology and distribution patterns is presented. Finally, publications emanating from this study are included as Appendices 1 and 2.

2

TAXONOMIC HISTORY

2.1 Introduction

Family placement of the Hypoxidaceae fluctuated from being part of the Amaryllidaceae or Liliaceae s.l. to being treated as a family on its own depending upon the author and the context in which they were working. In the mid-1980s, it became widely accepted that the Hypoxidaceae is a natural family within the order Asparagales, a relationship that was proposed earlier by Huber (1969). This agreement is possibly due to a number of publications after 1970 on angiosperm classification by Dahlgren (1975, 1980, 1983) and on monocotyledon evolution by Dahlgren & Rasmussen (1983) and Dahlgren *et al.* (1985). Hutchinson (1934) considered the Hypoxidaceae to be a sister group to the Orchidaceae. Chase *et al.* (1993) found that the Hypoxidaceae forms a monophyletic group positioned near the base of the Asparagales. Further nucleotide sequencing in the Asparagales (Rudall *et al.* 1997; Pires *et al.* 2006) satisfactorily resolved that the Hypoxidaceae represent the African branch of Asparagales with a close relationship to Asteliaceae as proposed by Huber (1969). Recent *rbcL* nucleotide sequence studies in the Asparagales (Rudall *et al.* 1997; Pires *et al.* 2006) and Orchidaceae (Chase *et al.* 1995a; Cameron *et al.* 1999) confirm this. Generic delimitation within the Hypoxidaceae has also varied considerably over the years, the most recent treatment is offered by Nordal (1998). While the history of the family dates back to 1814 when it was first described as Hypoxidae by Robert Brown, the history of the genus *Hypoxis* goes back even earlier to 1759. In his *Species Plantarum*, Linnaeus (1759) established the genus *Hypoxis* and in it he placed three species, all described by himself. This chapter traces the phyletic placement of the Hypoxidaceae and gives an account of the history of *Hypoxis* from Linnean times to the modern molecular period.

2.2 Taxonomic position of the Hypoxidaceae

The Hypoxidaceae was described by Robert Brown in 1814 and has often been treated as a subfamily or tribe within the Amaryllidaceae on account of its inferior ovary. Earlier, Brown (1810) established the Amaryllideae in which he placed *Hypoxis* and *Curculigo*. According to Brackett (1923), Brown wrote in his *General Remarks on the Botany of Australia* (1814) that it is better to consider *Hypoxis* and *Curculigo* in a family separate from Amaryllidaceae and he proposed the name Hypoxidae. Sixty four years later, Baker (1878b) prepared the first synopsis of

Hypoxidaceae, where he detailed differences between Hypoxidaceae and Amaryllidaceae, and presented a description for Hypoxidaceae. Bentham & Mueller (1873) treated the family as tribe Hypoxideae of the family Amaryllidaceae. This delimitation was adopted by Bentham & Hooker (1883), Baillon (1895), Baker (1896, 1898), Nel (1914), Phillips (1926) and Hilliard & Burt (1978). Pax (1889) raised the tribe to subfamily level as Hypoxidoideae and divided the subfamily into 4 tribes: Alstroemerieae, Conanthereae, Conostylideae and the Hypoxideae. Bessey (1915), Pax & Hoffman (1930) and Emberger (1960) followed Pax's arrangement for the Hypoxideae. Hutchinson (1934) demarcated 14 orders in Division II, Corolliferae of the subphylum Monocotyledons. Among the orders, he included the Liliales with six families, Amaryllidales with only the typical family and the Haemodorales with six families including the Hypoxidaceae. The families included in these orders and the characters used by Hutchinson (1934) to define the orders are summarised in Table 2.1. The Orchidales which also belongs to Corolliferae is included in the comparison as Hutchinson (1934) considered the Orchidaceae to have evolved from the Hypoxidaceae through *Curculigo*.

Table 2.1.—Summary of families and characters used by Hutchinson (1934) to define the orders Liliales, Amaryllidales, Haemodorales and Orchidales

| Liliales | Amaryllidales | Haemodorales | Orchidales |
|---|---|--|---|
| Liliaceae Tecophilaceae Trillaceae Pontederiaceae Smilacaceae Ruscaceae | Amaryllidaceae | Haemodoraceae Hypoxidaceae Velloziaceae Apostasiaceae Taccaceae Philydraceae | Orchidaceae |
| Herbs with rhizomes, corms or bulbs, rarely climbing | Scapigerous herbs with bulbous rootstock and radical leaves | Rootstock a rhizome or rarely a corm | Terrestrial, epiphytic or saprophyti |
| Perianth corolla-like, the two series similar and often fusing together into one tube | Flowers showy in 1 to many umbels, subtended by one or more spatheaceous bracts; corona often present | Perianth-segments becoming valvate | Flowers strongly zygomorphic; perianth segments in 2 whorls, usually petaloid, variously modified |
| Stamens often 6 | Stamens 6 | Stamens numerous to 6; free or in bundles | Stamens 2 or 1; pollen from granular to waxy and in masses |
| Ovary superior or rarely semi-inferior | Ovary superior or inferior | Ovary superior to inferior; 3-celled with axile, or 1-celled with parietal placentas | Ovary inferior |
| Fruit | Not recorded | Not recorded | Fruit usually a capsule, mostly opening laterally by 3 or 6 longitudinal slits |
| Seeds with copious endosperm | Endosperm present | Seeds mostly numerous | Very numerous and minute, without endosperm |

More recently, Geerinck (1968) also considered Hypoxidaceae to be distinct from Amaryllidaceae, a view based on leaf and floral characters. Regardless of Baker's (1878b) and Geerinck's (1968) contributions, some authors still preferred to place the Hypoxidaceae as a subfamily or tribe in Amaryllidaceae or even as part of the Liliaceae s.l. Taxonomists like Bentham & Hooker (1862–1883) and Heywood (1993) have treated it as part of Amaryllidaceae while Cronquist (1981) and Thorne (1983) retained it in the Liliaceae. Hypoxidaceae was included in the order Haemodiales by Hutchinson (1959, 1973), Liliiflorae by Engler (1887–1909), Liliales by Takhtajan (1969) and Asparagales by Dahlgren (1975, 1983). Heywood *et al.* (2007) recognised the Hypoxidaceae as part of the Asparagales based on the Angiosperm Phylogeny Group II System, that is in turn based on analyses in Chase *et al.* (2000) and Fay *et al.* (2000). A table with comparison between the orders Asparagales and Liliales is provided by Dahlgren *et al.* (1985) who largely follow Huber (1969) in listing the differences as well as in the grouping of families in the orders. These authors further offered the view that the Asparagales forms a large fairly homogeneous complex of families that may have evolved in parallel to the Liliales and Dioscoreales.

The phylogenetic associations of the Hypoxidaceae within the Asparagales have also been clarified over the past 15 years. Both Hutchinson (1959) and Takhtajan (1969) placed the Hypoxidaceae close to the Orchidaceae. Based on seed anatomy in *Curculigo* and *Hypoxis*, Huber (1969) considered the Hypoxidaceae to represent the African branch of Asparagales, close to the Asteliaceae. Dahlgren & Clifford (1982) pointed out that the phytomelan crusts of the seeds in Hypoxidaceae did not support its close relationship to the Orchidaceae, although there were a few notable similarities (epigyny, lack of septal nectaries and rarely nuclear endosperm formation) between the families. However, the association of Hypoxidaceae with Asteliaceae by Huber (1969) and Blandfordiaceae Dahlgren & Clifford is supported by *rbcL* data on Asparagales (Chase *et al.* 1995a; Rudall *et al.* 1997). Rudall *et al.* (1998) explained the phylogenetic associations in the asteloids that comprise the families Hypoxidaceae, Asteliaceae, Lanariaceae and Blandfordiaceae and considered the asteloid group as the first-branching clade of the Asparagales. Recent *rbcL* analyses of the Liliales (Chase *et al.* 1995a) and Orchidaceae (Cameron *et al.* 1999) further support Huber's (1969) association of the Hypoxidaceae to the Asteliaceae. These authors also discussed the affinities of the Boryaceae, Blandfordiaceae Asteliaceae and Hypoxidaceae as outgroups to the Orchidaceae. In proposing an orchid ancestor, Cameron (1999) suggested a plant with most characters from different genera in the Hypoxidaceae combined with simultaneous microsporogenesis as in Asteliaceae. A useful summary of the position of the Hypoxidaceae within

the Aparagales based on research by various groups is also provided by Judd (2000) in his treatment of the Hypoxidaceae in southeastern United States. In this publication, Judd annotated the findings reported in literature in the references. Evidence from nucleotide sequences may assist in resolving the phylogeny of genera in Hypoxidaceae, and its relation to the Orchidaceae. Such a study is presently being led by Alec Kocyan based at the Jodrell Laboratory, Royal Botanic Gardens, Kew. The study will hopefully clarify the generic limits in Hypoxidaceae using morphology, anatomy and *rbcL* techniques.

2.3 History of *Hypoxis*

Linnaeus established the genus *Hypoxis* in 1759 and in it he placed three species, *H. erecta* L., *H. decumbens* L. and *H. fascicularis* L. *Hypoxis erecta* [= *H. hirsuta* (L.) Coville] and *H. decumbens* L. are retained in the genus while *H. fascicularis* is a synonym of *Colchicum montanum* L. (Family Colchicaceae). The type species of the genus is the American *H. hirsuta* (L.) Coville (= *H. erecta* L., an illegitimate name based on the type of *Ornithogalum hirsutum* L.). Following Linnaeus (1759), eleven years later, *H. villosa* was the first southern African species to be described by the younger Linnaeus (1781). Table 2.2 summarises the authors of species and the year in which southern African and west Indian ocean islands taxa were described. The remaining African taxa are included in a list provided by Singh (2006) [Appendix 1.1]. Taxonomic treatments of *Hypoxis* were prepared by Baker (1878b) and Nel (1914) in their synopses of Hypoxidaceae. Between 1874 and 1904, Baker described 38 species of *Hypoxis* in Africa, 21 being endemic to southern Africa. Based on herbarium studies, Nel described 45 new species of *Hypoxis* in Africa, 13 from southern Africa. Only one of Nel's species, *H. interjecta* is upheld in this study and the species, *H. exaltata* and *H. sagittata* remain ambiguous due to the paucity of specimens. Baker (1896) offers the last published key to all known species in South Africa, where he recognised 41 species including nine belonging to *Spiloxene* and two to *Rhodohypoxis*.

Taxonomic work done on *Hypoxis* in southern Africa since Baker's (1896) account in *Flora Capensis* is fragmentary. Noteworthy contributions on the genus were made by Wood (1976) on *Hypoxis* in Natal (now KwaZulu-Natal) and Heideman (1979) studied *Hypoxis* on the Witwatersrand (part of the South African Highveld, covering much of the present-day Gauteng Province) and both these studies exist as unpublished masters theses. In 1995, Bruce-Miller presented a preliminary study on *Hypoxis* in the Eastern Cape Province based on herbarium material at GRA, as a project for her BSc. degree. Apart from Heideman's (1983, 1987) list of species on the Witwatersrand and contribution to the Hypoxidaceae in the Flora of the

Table 2.2.—Summary of names proposed for the southern Africa and west Indian ocean islands taxa in *Hypoxis* (Accepted species names are in **bold**, synonyms in *italics* and and insufficiently known species in normal font).

| Taxon | Author | Year described |
|---|-----------------------------|------------------|
| | | 1781–1799 |
| villosa | L.f. | 1781 |
| angustifolia | Lam. | 1789 |
| <i>decumbens</i> = villosa | Lam. | 1789 |
| <i>tomentosa</i> = villosa | Lam. | 1789 |
| obliqua | Jacq. | 1796 |
| sobolifera | Jacq. | 1796 |
| | | 1800–1899 |
| obtusa | Burch. ex Ker Gawl. | 1816 |
| stellipilis | Ker Gawl. | 1822 |
| <i>scabra</i> = villosa | Lodd. | 1824 |
| <i>filifolia</i> = longifolia | Eckl. | 1827 |
| hemerocallidea | Fisch., C.A.Mey. & Avé-Lall | 1842 |
| <i>abyssinica</i> = villosa | Hochst | 1844 |
| <i>simensis</i> = villosa | Hochst. | 1844 |
| multiceps | Buchinger | 1845 |
| <i>canescens</i> = sobolifera var. sobolifera | Fisch. | 1845 |
| <i>microsperma</i> = villosa | Lallem.in Fischer & Meyer | 1845 |
| <i>krebsii</i> = sobolifera var. sobolifera | Fisch. | 1846 |
| <i>petitiana</i> = villosa | A. Rich. | 1851 |
| <i>rooperi</i> = hemerocallidea | T.Moore | 1852 |
| <i>latifolia</i> = colchicifolia | Hook. | 1855 |
| <i>elata</i> = hemerocallidea | Hook.f. | 1868 |
| longifolia | Baker ex Hook.f | 1873 |
| <i>pannosa</i> = sobolifera var. pannosa | Baker | 1874 |
| <i>biflora</i> = angustifolia | Baker | 1876 |
| ludwigii | Baker | 1876 |
| <i>arnottii</i> = rigidula var. pilosissima | Baker | 1877 |
| angustifolia var. angustifolia | Baker | 1878b |
| angustifolia var. buchananii | Baker | 1878b |
| argentea var. argentea | Harv. ex Baker | 1878b |
| argentea var. sericea | Baker | 1878b |
| costata | Baker | 1878b |
| <i>decumbens</i> β & γ = sobolifera | Thunb. ex Baker | 1878b |
| filiformis | Baker | 1878b |
| gerarrdii | Baker | 1878b |
| <i>iridifolia</i> = obtusa | Baker | 1878b |
| <i>jacquinii</i> | Baker | 1878b |
| kraussiana | Buchinger ex Baker | 1878b |
| <i>longifolia</i> var. <i>thunbergii</i> = longifolia | Baker | 1878b |
| membranacea | Baker | 1878b |
| <i>pannosa</i> = sobolifera var. pannosa | Baker | 1878b |
| parvula | Baker | 1878b |
| rigidula | Baker | 1878b |
| rigidula var. pilosissima | Baker | 1878b |
| rigidula var. rigidula | Baker | 1878b |
| <i>rooperi</i> var. <i>forbesii</i> = hemerocallidea | Baker | 1878b |
| <i>sericea</i> = argentea var. sericea | Baker | 1878b |
| <i>sericea</i> var. <i>dregei</i> = argentea var. sericea | Baker | 1878b |
| <i>sericea</i> var. <i>dregei</i> = filiformis | Baker | 1878b |
| <i>sericea</i> var. <i>flaccida</i> = argentea var. sericea | Baker | 1878b |
| setosa | Baker | 1878b |

Table 2.2.—cont.

| Taxon | Author | Year described |
|--|-----------------|------------------|
| <i>villosa</i> L.f. var. <i>scabra</i> = villosa | (Lodd.) Baker | 1878b |
| <i>villosa</i> var. <i>canescens</i> = sobolifera var. sobolifera | (Fisch.) Baker | 1878b |
| <i>villosa</i> var. <i>obliqua</i> = obliqua | (Jacq.) Baker | 1878b |
| <i>villosa</i> var. <i>pannosa</i> = sobolifera var. pannosa | Baker | 1878b |
| <i>villosa</i> var. <i>sobolifera</i> = sobolifera var. sobolifera | (Jacq.) Baker | 1878b |
| <i>villosa</i> var. δ = longifolia | Thunb. ex Baker | 1878b |
| zeyheri | Baker | 1878b |
| acuminata | Baker | 1889 |
| colchicifolia | Baker | 1889 |
| <i>oligotricha</i> = colchicifolia | Baker | 1889 |
| <i>woodii</i> = angustifolia var. buchananii | Baker | 1889 |
| floccosa | Baker | 1894 |
| <i>villosa</i> var. <i>schweinfurthii</i> = sobolifera | Harms | 1895 |
| <i>brevifolia</i> = parvula var. parvula | Baker | 1896 |
| flanagani | Baker | 1896 |
| galpinii | Baker | 1896 |
| parvifolia | Baker | 1896 |
| | | 1900–1999 |
| <i>caespitosa</i> = filiformis | Baker | 1901 |
| <i>ecklonii</i> = floccosa | Baker | 1901 |
| <i>junodii</i> = gerardii | Baker | 1901 |
| <i>longifolia</i> (nom. illeg.) = rigidula var. rigidula | Baker | 1904 |
| <i>longipes</i> | Baker | 1904 |
| <i>mollis</i> | Baker | 1904 |
| <i>nigricans</i> | Baker | 1904 |
| <i>beyrichii</i> | Nel | 1914 |
| <i>cordata</i> = rigidula var. rigidula | Nel | 1914 |
| <i>dinteri</i> = argentea var. sericea | Nel | 1914 |
| <i>distachya</i> = colchicifolia | Nel | 1914 |
| <i>dregei</i> = argentea var. sericea | (Baker) Nel | 1914 |
| <i>elliptica</i> = rigidula var. rigidula | Nel | 1914 |
| <i>exaltata</i> | Nel | 1914 |
| <i>gilgiana</i> = colchicifolia | Nel | 1914 |
| interjecta | Nel | 1914 |
| <i>lata</i> = angustifolia | Nel | 1914 |
| <i>obconica</i> = hemerocallidea | Nel | 1914 |
| <i>obliqua</i> Jacq. var. <i>woodii</i> = angustifolia var. buchananii | (Baker) Nel | 1914 |
| <i>oblonga</i> = rigidula | Nel | 1914 |
| <i>obtusa</i> var. <i>chrysotricha</i> = obtusa | Nel | 1914 |
| <i>patula</i> = hemerocallidea | Nel | 1914 |
| <i>sagittata</i> | Nel | 1914 |
| <i>sobolifera</i> var. <i>accedens</i> = sobolifera var. sobolifera | Nel | 1914 |
| sobolifera var. pannosa | (Baker) Nel | 1914 |
| sobolifera var. sobolifera | (Jacq.) Nel | 1914 |
| <i>stricta</i> = galpinii | Nel | 1914 |
| <i>villosa</i> var. <i>fimbriata</i> = villosa | Nel | 1914 |
| <i>neliana</i> = kraussiana | Schinz | 1926 |
| <i>uniflora</i> | Markötter | 1930 |
| <i>volkmanniae</i> = rigidula var. rigidula | Dinter | 1931 |

Table 2.2.—cont.

| Taxon | Author | Year described |
|--|---------------------------|----------------|
| <i>nitida</i> = obtusa | I. Verd | 1949 |
| <i>obtusa</i> var. <i>nitida</i> = obtusa | (I. Verd.) Heideman | 1983 |
| tetramera | O.M.Hilliard & B.L.Burt | 1983 |
| <i>limicola</i> = parvula var. parvula | B.L.Burt | 1988 |
| parvula var. albiflora | B.L.Burt | 1988 |
| angustifolia var. luzuloides | (Robyns & Tournay) Wiland | 2002 |
| angustifolia var. madagascariensis | Wiland | 2002 |
| nivea | Y. Singh | 2007 |

Witwatersrand, no other taxonomic treatment on southern African *Hypoxis* has been published since Baker's (1896) revision. Burt (1986, 1988) and Hilliard & Burt (1983) through their extensive field work mainly in the Drakensberg (Ukhhlamba) Mountains updated much of the taxonomy and nomenclature of individual species. In a recent conspectus of the Cape Flora, Snijman (2000) reviewed Hypoxidaceae, in which she records seven species of *Hypoxis* for the Cape winter-rainfall region of South Africa. Snijman & Singh (2003) and Snijman & Singh (2006) offered lists of species of Hypoxidaceae in southern Africa and South Africa respectively. As part of this study, Singh (2006) [Appendix 1.1] presented a list of species and infraspecific names in *Hypoxis*, including manuscript names. A useful key to infrageneric taxa in *Hypoxis* is offered by Compton (1976) for the Flora of Swaziland where he recognises 12 species, all of which also occur in South Africa. Compton applied macromorphological characters that are easily observable in the field such as habit, leaf shape and width, abundance of flowers on the inflorescence and density of hairs on the leaves. In this communication, he also indicated that it is impossible to construct a simple key to *Hypoxis* and that his key may fail in practice, thus emphasising the difficulty in applying suitable diagnostic characters in keys to members of the group.

For Tropical Africa, small contributions to the taxonomy of *Hypoxis* were made between 1930 and 1990 mainly through Flora work. These were based on the morphological species concept. Hutchinson & Dalziel (1931) presented a treatment of the genus for the Flora of West Tropical Africa where they recognised five species. Hepper (1968) updated the Hypoxidaceae for the Flora of West Africa and provides a key to three species for the region. He commented that several species described by Nel can hardly be maintained as distinct in this confusing genus. He noted that the appearance of the plants change as the leaves develop and further suggested that field workers should note variation within populations and this will help to determine the taxonomic worth of characters. Geerinck (1971) writing on the Flora of Congo, Rwanda and Burundi, upheld two species in Central Africa namely *H. angustifolia* and *H. subspicata* Pax. Champluvier (1987)

recognised three species, *H. angustifolia*, *H. kilimanjarica* Baker and *H. obtusa* in the Flora of Rwanda. The first comprehensive work on *Hypoxis* in tropical Africa was provided by Nordal *et al.* (1985) for the Flora of Tropical East Africa. The authors offered a general discussion on the morphology and complex cytology of the genus. For the sub-region, they recognised five species and one species complex and used seed and leaf characters to delimit taxa. This was followed by a revision of Hypoxidaceae for the Flora of Cameroon by Nordal & Iversen (1987) where four species were recognised in *Hypoxis*.

More recently, taxonomic initiatives in *Hypoxis* in tropical Africa has led to an improved understanding of the genus on the continent and its taxonomy is slowly becoming settled. Zimudzi (1993) presented a doctoral thesis on his studies on the family Hypoxidaceae (*Hypoxis* and *Curculigo*) in South Central Africa with emphasis on variation patterns in the genus. The study contributed to a synopsis of the family in the *Flora Zambesiaca* region (Zimudzi 1996) and to the publication of a treatment of the family by Nordal & Zimudzi (2001) for the region. In the former publication, eight species were upheld and in the latter treatment, the authors recognised 14 species, seven of which also occur in southern Africa. In 1998, Wiland completed a doctoral thesis on *Hypoxis* and *Curculigo* in Central Africa (Zaire, Rwanda and Burundi) in Polish. Following on from her studies, Wiland (1997a & b) published seven new species of *Hypoxis* for the region. In 2001, she published a treatment of the genus in Central Africa recognising 20 species, three in Rwanda, five in Burundi and 19 in Congo-Kinshasa, seven being endemic to the region. In the treatment, Wiland-Szymańska (2001) provided scanning electron micrographs of seed surfaces for most species. This was followed by Wiland-Szymańska & Adamski's (2002) contribution to the taxonomy and morphology of *H. angustifolia* from Africa and the West Indian Ocean Islands. Wiland-Szymańska & Nordal (2006) provided a much needed treatment for the diverse Flora of Tropical East Africa region, where they recognised 15 species. Five southern African species namely *H. angustifolia*, *H. filiformis*, *H. galpinii*, *H. obtusa* and *H. rigidula* are recorded as being present in East Africa.

Zimudzi (1996), Nordal & Zimudzi (2001), Wiland (1997a & b) Wiland-Szymańska (2001) and Wiland-Szymańska & Adamski (2002) used macromorphological characters of the leaf, inflorescence and seed character to delimit *Hypoxis* species in Africa. Their contributions are largely revisionary and based on the morphological species concept.

Outside Africa, *Hypoxis* has received attention from Henderson (1987) for the Flora of

Australia where he recognised two sections, *Hypoxis* with six species and *Ianthe* with four species. According to Manning *et al.* (2002) consider species in *Ianthe* to be closely allied to the southern African *Spiloxene* and proposed their transfer to *Spiloxene*. Henderson (1987) placed *H. marginata* R.Br., *H. nervosa* R. Henderson, *H. arillacea* R. Henderson, *H. exilis* R. Henderson, *H. hygrometrica* Labill. (3 varieties) and *H. pratensis* R. Br. (2 varieties) in Section *Hypoxis*. He used a combination of characters namely pubescence, venation, seed morphology, rhizome length and shape and number of flowers per inflorescence to separate species.

The American members of *Hypoxis* were first studied by Brackett (1923) who recognised 15 species and her key is based primarily on seed morphology. Later, Britt (1967) provided a revision of *Hypoxis* in the United States and Canada as a doctoral thesis in which he proposed a single polymorphic species, *H. hirsuta* (L.) Coville with four varieties for all *Hypoxis* plants in the region. He reduced most species to the typical variety. Herndon (1992b) produced a treatment of *Hypoxis* found in Florida where he recognised five species namely *H. juncea* Sm., *H. leptocarpa* (Engelmann & Gray) Small, *H. rigida* Chapman, *H. sessilis* L. and *H. wrightii* (Baker) Brackett. His treatment includes distribution and ecological observations for each species. Herndon (1992b) found density of leaf hairs, leaf cross-sectional shape and width, texture, pedicel relative to bract and flower length, anther and ‘sepal’ lengths as well as seed colour and ornamentation to be useful for species separation. More recently, Judd (2000) prepared an account of Hypoxidaceae for the Generic Flora of the southeastern United States in which he traced the generic circumscriptions by various authors based on morphology, anatomy and *rbcL* sequences. He also provided a comprehensive description of *Hypoxis* and recognised seven species in the United States of America and Canada. These include *H. curtissii* Rose, *H. juncea*, *H. hirsuta*, *H. mexicana* Schultes & Schultes f., *H. rigida*, *H. sessilis* and *H. wrightii*. Judd’s delimitation of species is along the lines of Brackett (1923) and Herndon (1988, 1992a, 1992b) where he adopts the distinguishing characters suggested mainly by these authors.

2.4 Generic affinities in Hypoxidaceae

Generic circumscription in Hypoxidaceae has varied over the years and it is now generally accepted that the family comprises ten genera, nine as proposed by Nordal (1998) and *Heliacme* described by Ravenna (2003). In his synopsis, Baker (1878b) recognised four genera in Hypoxidaceae namely *Hypoxis*, *Molineria*, *Curculigo* and *Pauridia* (Table 2.3). He divided *Hypoxis* into two subgenera, *Ianthe* Salisb. and *Hypoxis* Baker and described the *Ianthe* as having plants totally glabrous, anthers linear, basifixed and stigma about discrete. In contrast, plants of

Table 2.3.—Summary of genera and subgenera in Hypoxidaceae in four different classifications

| Baker (1878b) | Nel (1914) | Hilliard & Burt (1978) | Nordal (1998) |
|---|---------------------------------------|-----------------------------------|----------------------|
| <i>Hypoxis</i> subgenus <i>Hypoxis</i> subgenus <i>Ianthe</i> | <i>Hypoxis</i> | <i>Hypoxis</i> | <i>Hypoxis</i> |
| <i>Molineria</i> | <i>Molineria</i> | <i>Molineria</i> | <i>Molineria</i> |
| <i>Curculigo</i> | <i>Curculigo</i> | <i>Curculigo</i> | <i>Curculigo</i> |
| <i>Pauridia</i> | | <i>Pauridia</i> | <i>Pauridia</i> |
| | <i>Rhodohypoxis</i> | <i>Rhodohypoxis</i> | <i>Rhodohypoxis</i> |
| | Forbesia (= <i>Empodium</i>) | <i>Empodium</i> | <i>Empodium</i> |
| | Janthe (Ianthe) (= <i>Spiloxene</i>) | <i>Spiloxene</i> | <i>Spiloxene</i> |
| | | <i>Saniella</i> | <i>Saniella</i> |
| | | | <i>Hypoxidia</i> |

subgenus *Hypoxis* are hairy, the ovary is nearly always covered in setose, dense hairs and the leaves are pilose. In these species, the anthers are nearly always versatile with the base sagittate and the stigma is ‘concrete’ (Nel 1914).

Nel (1914) recognised six genera in the tribe Hypoxideae in Amaryllidaceae, among these were *Hypoxis* and *Curculigo* as in Baker (1878b). To these genera, he added *Forbesia* Eckl. with six species. He revived *Ianthe* Salisb. (as *Janthe*, a German transliteration misspelling) including *Spiloxene* Salisb. as distinct from *Hypoxis*. Further, he removed two species with pink or red flowers from Baker’s subgenus *Hypoxis* and placed them in a new genus, *Rhodohypoxis* Nel, retaining the yellow-flowered species in *Hypoxis*. Within *Hypoxis*, Nel (1914) classified 83 African species into 11 sections based on morphology mainly the anther apex, leaf dimensions, style to stigma ratio, leaf venation and inflorescence type.

Following Nel’s (1914) treatment, five species of *Forbesia* were transferred to *Empodium* (Hilliard & Burt 1973) while one species was transferred to *Saniella* (Burt 2000). The use of the generic names *Ianthe* and *Spiloxene* also fluctuated. Previously, Baker (1878b) and Williams (1901) regarded members of the *Ianthe* as different from *Hypoxis* in being glabrous. Fourcade (1934) pointed out that *Ianthe* and *Spiloxene* are congeneric and recognised *Ianthe* as a synonym of *Spiloxene* into which he transferred four species. Garside (1936) accepted this view and transferred a further 16 species from *Ianthe* and *Hypoxis* to *Spiloxene*.

Hilliard & Burt (1973) helped to clarify the differences between *Curculigo* and *Empodium*, both genera are characterised by the presence of a long beak to the ovary. These authors also discussed floral and fruit differences within *Rhodohypoxis* in the same paper. A few years later,

Hilliard & Burt (1978) presented a taxonomic treatment of *Rhodohypoxis* and described a new genus called *Saniella*. Burt (2000) elaborated upon the interrelations of *Saniella*, *Spiloxene*, *Empodium* and *Pauridia* and purported that these genera should be maintained until further study. He pointed out that *Spiloxene* needs critical analysis to give a fuller understanding of the genus in addition to Thompson's (1976, 1978) studies. Dr Dee Snijman, based at SANBI's Compton Herbarium is presently revising the genus. In their publication of 1978, Hilliard & Burt also presented a key to eight genera of Hypoxidaceae. The most recent treatment of the family was by Nordal (1998), who recognised the eight genera of Hilliard & Burt (1978) and *Hypoxidia* of Friedman (1984) as the ninth genus. In 2003, a tenth genus *Heliacme* Ravenna based on *Hypoxis scorzonerifolia* Lam. (= *Heliacme scorzonerifolia* (Lam.) Ravenna) was added to the family. Morphological differences between the currently accepted genera are tabulated in Table 2.4 and the data is based mainly on the above mentioned studies.

Stamen characters were found to be useful at generic and specific level in the Hypoxidaceae. Nel (1914) resolved that in *Spiloxene* (*Ianthe*), the length of the anthers is uneven between the inner and outer stamens whereas in *Hypoxis*, it is the length of the filaments that are unequal, the outer stamens having longer filaments than the inner ones. Geerinck (1969) pointed out that the terminology used by Nel to describe the attachment of the anther to filament in *Hypoxis* is confusing. Hilliard & Burt (1978) found the stamens to provide important taxonomic characters at generic level and they illustrated differences in stamen features for seven genera. They broadly classified the stamens into two types based on the point at which the anther is attached to the filament and whether the inner and outer faces of the anther are similar or different. In their classification, *Empodium*, *Molineria*, *Rhodohypoxis* and *Saniella* have stamens where the anther joins the filament low down on the outer surface and the inner and outer anther faces are different, while in *Curculigo*, *Hypoxis*, *Pauridia* and *Spiloxene* the filaments join the anther at midway in the sinus between the basal lobes. In the first group, the cross-section of the anther is asymmetrical and in the second group it is symmetrical. Their grouping is similar to that proposed by Nel (1914) but differs in interchanging the positions of *Rhodohypoxis* and *Spiloxene* between the groups. However, Hilliard & Burt (1978) cautioned that these characters alone are insufficient to reflect generic affinities. They indicate for instance *Rhodohypoxis* and *Hypoxis* have different stamen types, yet they are closely related, and similarly, the stamens of *Empodium* and *Molineria* are both asymmetrical in cross section, yet the two genera are obviously not closely related.

2.5 Conclusions

This account traced the development of the treatment of Hypoxidaceae and confirmation of its relationships with evidence from macromorphology, anatomy and nucleotide sequencing that is becoming available. It also traced the addition of new species in the genus *Hypoxis* from the time of Linneaus (1759) to the present. As various studies on hypoxid genera for the Flora of Southern Africa region are concluded, generic delimitation in Hypoxidaceae will be further clarified. There is no doubt that an integration of characters from morphology, anatomy, phytochemistry and molecular data will benefit the phylogenetic placement of the nine genera in Hypoxidaceae as is being applied for the family by studies at Royal Botanic Gardens, Kew.

Table 2.4.—Summary of morphological characters of currently accepted genera in Hypoxidaceae based on Hilliard & Burt (1978), Thompson (1979), Nordal (1998), Burt (2000), Snijman (2000) and Ravenna (2003). Data not shown could not be sourced.

| | <i>Hypoxis</i> | <i>Rhodohypoxis</i> | <i>Saniella</i> | <i>Empodium</i> | <i>Spiloxene</i> | <i>Pauridia</i> | <i>Curculigo</i> | <i>Molineria</i> | <i>Hypoxidia</i> | <i>Heliacme</i> |
|-------------------------|-----------------------------------|--|--------------------------------------|-----------------|---|--------------------------------------|--------------------------|------------------|--------------------------------------|--------------------------------------|
| Underground stem | perennial | perennial | annual | annual | annual | annual | perennial | perennial | perennial | perennial |
| Duration | | | | | | | | | | |
| Morphology | rhizome | rhizome | corm | corm | corm | corm | rhizome | rhizome | rhizome | rhizome |
| Plants | | | | | | | | | | |
| Vestiture | hairy | hairy | glabrous | hairy | glabrous/ hairy | hairy | hairy | hairy | hairy | glabrous/ hairy |
| Hair type | simple, bifurcate, stellate | bifurcate or stellate | | simple | | | bifurcate or stellate | | | simple |
| Flowers | | | | | | | | | | |
| per nflorescence | 1-22 | 1-2 | 1 | 1 | 1-7 | 1-2 | 1-few | 10 or more | 2-5 | 1 |
| | bisexual | bisexual | bisexual | bisexual | bisexual | bisexual | unisexual | bisexual | bisexual | |
| Tepals | | | | | | | | | | |
| Number | 3+3 (rarely 2+2) | 3+3 | 3+3 | 3+3 | 3+3 (-2+2) | 3+3 | 3+3 | 3+3 | 3+3 | 3+3 |
| Fusion | free | united at base into a tube | united at the base into a tube | free | free | united at the base into a tube | free | free | united at the base into a tube | united at the base into a tube |
| | | clawed, inflexed above base and closing mouth of perigone | | | | | | | | |
| Colour | yellow (rarely white) | red, pink or white | whitish, pale yellow at base | yellow | orange, yellow, white (rarely pink) tinged with red or green | white to pale pink | yellow | yellow | red-brown yellowish pink | yellow |
| Stamens | | | | | | | | | | |
| Number | 6 (rarely 3, 4, 5) | 6 | 6 | 6 | 6 | 3 | 6 | 6 | 6 | 6 |
| | uniseriate | biseriate | uniseriate | uniseriate | uniseriate | uniseriate | uniseriate | uniseriate | biseriate | biseriate |

Table 2.4.—cont.

| | <i>Hypoxis</i> | <i>Rhodohypoxis</i> | <i>Saniella</i> | <i>Empodium</i> | <i>Spiloxene</i> | <i>Pauridia</i> | <i>Curculigo</i> | <i>Molineria</i> | <i>Hypoxidia</i> | <i>Heliacme</i> |
|-------------------------------|---|---|---|---|---|---|---|---|---|-----------------|
| Anthers | | | | | | | | | | |
| Attachment | filament joins anther medianly in basal sinus | filament joins anther low down on the outer surface | filament joins anther low down on the outer surface | filament joins anther low down on the outer surface | filament joins anther medianly in basal sinus | filament joins anther medianly in basal sinus | filament joins anther medianly in basal sinus | filament joins anther low down on the outer surface | filament joins anther low down on the outer surface | |
| In cross section | symmetric | asymmetric | asymmetric | asymmetric | symmetric | symmetric | symmetric | asymmetric | asymmetric | |
| Apical appendages | absent | absent | absent | present | absent | absent | absent | Absent | present | |
| Pollen grains | monosulcate | | | | | bisulcate | | | | |
| Dehiscence | latrorse | introrse | latrorse | latrorse | latrorse | latrorse | latrorse | latrorse or introrse | latrorse | Introrse |
| Style length | usually short rarely long | lacking or short | short | short or long | short | | | | | |
| Stigmatic lobes Number | 3 | 3 | 3 | 3 | 3 | 6 | 3 | 3 | 3 | 3 |
| Ovary | | | | | | | | | | |
| Epigynous beak | absent | present | present | present | absent | absent | present | present or absent | absent | |
| Locule number | 3 | 3 | 3 | 1 | 3 (rarely 1) | 3 | 3 | 3 | 3 (incompletely) | 1 |
| Placentation | axile | axile | axile | parietal | axile | axile (rarely parietal) | axile | axile | axile | parietal |
| Capsules | thin-walled | thin-walled | thin-walled | | thin-walled | thin-walled | | | | |
| Dehiscence | dehiscent, circumscissile longitudinal or indehiscent | dehiscent, circumscissile or rupturing irregularly | dehiscent, rupturing irregularly | indehiscent | dehiscent, circumscissile or indehiscent | indehiscent | indehiscent | indehiscent | indehiscent | indehiscent |
| Position | aerial | aerial or subterranean | subterranean | aerial or subterranean | aerial | aerial | aerial or subterranean | aerial | aerial | |
| Seeds | | | | | | | | | | |
| Strophiole | absent | absent | absent | present | absent | present | absent | absent | absent | |
| Testa | smooth or papillate | | | | | | smooth | | | papillate |