



## Molecular phylogenetics of Hypoxidaceae – Evidence from plastid DNA data and inferences on morphology and biogeography

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### ABSTRACT

Phylogenetic relationships of the monocot family Hypoxidaceae (Asparagales), which occurs mainly in the Southern Hemisphere, were reconstructed using four plastid DNA regions (*rbcl*, *trnL* intron, *trnL-F* intergenic spacer, and *trnS-G* intergenic spacer) for 56 ingroup taxa including all currently accepted genera and seven species of the closely related families Asteliaceae, Blandfordiaceae, and Lanariaceae. Data were analyzed by applying parsimony, maximum likelihood and Bayesian methods. The intergenic spacer *trnS-G* – only rarely used in monocot research – contributed a substantial number of potentially parsimony informative characters. Hypoxidaceae consist of three well-supported major clades, but their interrelationships remain unresolved. Our data indicate that in the *Pauridia* clade one long-distance dispersal event occurred from southern Africa to Australia. Long-distance dispersal scenarios may also be likely for the current distribution of *Hypoxis*, which occurs on four continents. In the *Curculigo* clade, the present distribution of *Curculigo* s.s. on four continents could support a Gondwanan origin, but the level of divergence is too low for this hypothesis to be likely. The main clades correspond well with some floral characters, habit and palynological data, whereas chromosomal data exhibit plasticity and probably result from polyploidization and subsequent dysploidy and/or aneuploidy. Evolutionary flexibility is also suggested by the number of reported pollination syndromes: melittophily, myophily, sapromyophily, and cantharophily. Based on our phylogenetic results, we suggest cautious nomenclatural reorganization to generate monophyly at the generic level.

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### 1. Introduction

The monocot family Hypoxidaceae occurs mostly in the Southern Hemisphere with only a few species in the Northern Hemisphere (Table 1). In temperate southern Africa, Hypoxidaceae are important elements of spring- and summer-flowering bulb floras, and in Southeast Asia they can be the dominant herbs in secondary tropical forests. The family consists of nine genera and ca. 155 species, of which the largest is *Hypoxis* with up to 90 species (Nordal, 1998). The plants are herbaceous and mostly 20 cm or less tall, although a few reach a meter or more, all with a tuberous or elongated rhizome or corm (Fig. 1). Flowers of Hypoxidaceae are usually less than 2 cm in diameter and yellow, white, pink, or

rarely orange. They are mostly scentless and offer pollen as a reward. A genus endemic to the Seychelles, *Hypoxidia*, has large red-brown<sup>1</sup> fetid flowers (Fig. 1E). General flower structure follows the “typical” lily-like monocot pattern with three sepals, three petals, six stamens, and a trimerous gynoeceum (Remizowa et al., 2010). However, two remarkable exceptions exist: *Pauridia* from South Africa has only three functional stamens with the three stamens of the outer staminal whorl reduced to staminodes that terminate in minutely papillate hooks, and *Curculigo racemosa* from Borneo can be polyandrous, often combined with a variable number of carpels (Thompson, 1978; Burt, 2000; Rudall and Bateman, 2002; Kocyan, 2007). Hypoxidaceae are one of 12 families (Asteliaceae, Blandfordiaceae, Boryaceae, Doryanthaceae, Iridaceae, Ixioliriaceae, Lanariaceae, Orchidaceae, Tecophilaeaceae, Xanthorrhoeaceae s.l.,

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<sup>1</sup> For interpretation of color in Fig. 1, the reader is referred to the web version of this article.

**Table 1**  
Genera currently included in Hypoxidaceae R.Br. with their species numbers and geographic range.

Genera	No. of described species	Distribution
<i>Curculigo</i> Gaertn. <sup>a</sup>	±6	Africa, Asia, Australia, South-Central America, Seychelles
<i>Empodium</i> Salisb.	7	Southern Africa
<i>Hypoxidia</i> F. Friedmann	2	Seychelles
<i>Hypoxis</i> L.	±90	Africa, Asia, Australia, Americas
<i>Molineria</i> Colla	±10	Asia
<i>Pauridia</i> Harv.	2	Southern Africa
<i>Rhodohypoxis</i> Nel	6	Southern Africa
<i>Saniella</i> Hilliard & B.L.Burt	2	Southern Africa
<i>Spiloxene</i> Salisb.	±30	Southern Africa

Information of species numbers gathered from the following sources: Nordal (1998), Snijman (2000), Snijman and Singh (2003), Singh (2006, 2007), and World Checklist of Selected Plant Families, 2010.

<sup>a</sup> Ravenna (2003) separated the genus *Heliacme*, which includes solely the Latin American *Heliacme scorzonifolia* (formerly *Curculigo scorzonifolia*), from *Curculigo* stating that *Heliacme* is different in having an unilocular ovary, dry capsulate fruit, non-sagittate anthers and a one-flowered inflorescence. Unfortunately, Ravenna did not illustrate his result with line drawings or photographs, which would allow a verification of these characters. The first author of the present article has seen herbarium sheets with individuals of *Curculigo scorzonifolia* that have several flowered racemes. Also there are clearly sagittate anthers visible on line drawings of *Curculigo scorzonifolia* in floristic literature. Literature is non consistent about dry or succulent fruits in *Curculigo*. J. Dutilh reports fruits that are not dry (pers. comm.). Whether an ovary is unilocular or 3-locular can only be decided by detailed morphological studies and so far we are unaware of any publication on this subject, given that the ovary is very small. However, the authors prefer to keep the *Heliacme* in *Curculigo* for this study.

and Xeronomataceae) that together constitute the 'lower asparagoid' grade of the order Asparagales. These asparagoid lilies are characterized by predominantly simultaneous microsporogenesis and an inferior ovary (Rudall et al., 1997). Within this grade, four families (Asteliaceae, Blandfordiaceae, Hypoxidaceae and Lanariaceae) form a well-supported clade (Chase et al., 2006). Boryaceae also have been found to belong to this clade (Graham et al., 2006; Pires et al., 2006). Monophyly of Hypoxidaceae, confirmed by cladistic analyses of *rbcl* DNA sequences (Rudall et al., 1998), is supported by several micro-morphological characters. Synapomorphies that unite Hypoxidaceae are the presence of bulliform cells in leaves, successive microsporogenesis, and tenuinucellate ovules. Two other characteristic features, mucilage canals in a wide range of organs and branched trichomes on leaves, occur within the family, but these two are also shared with Asteliaceae.

Although hypotheses of the systematic position of the family have been consistent in molecular analyses, only a modest set of information has been gathered on the intrafamilial relationships of Hypoxidaceae. Rudall et al. (1998) included seven of the nine genera, but did not analyse multiple species from most of these (see below). Nordal (1998) proposed some clades based on geographical and basic morphological information. She suggested two primary groupings: (1) *Curculigo*, *Hypoxidia* and *Molineria* centered around the Indian Ocean and (2) *Empodium*, *Pauridia*, *Rhodohypoxis*, *Saniella*, *Spiloxene* and *Hypoxis* focused mainly in southern Africa; *Hypoxis* was regarded as sister to the southern African genera because of its much wider distribution (more or less cosmopolitan, except Europe). Earlier, Thompson (1978) separated the southern African genera still further, placing *Hypoxis* and *Rhodohypoxis* in one group and *Empodium*, *Spiloxene* and *Pauridia* in another.

According to Rudall et al. (1998; Fig. 2), who analyzed *rbcl* DNA sequences and morphological data, the family is divided into two major clades. In contrast with Nordal's (1998) proposal, *Molineria* (based on *Molineria capitulata*, but with the voucher referred to as a species of *Curculigo*), *Empodium* and *Hypoxidia* formed one clade. The second clade consisted of two subclades, of which the first contained *H. leptocarpa* (= *H. curtissii*) and *Rhodohypoxis*, and the second contained *Hypoxis glabella*, *Spiloxene* and *Pauridia*. This indicated that *Hypoxis* is polyphyletic, an unexpected finding; *H. leptocarpa* (= *H. curtissii*) occurs in North America, whereas *H. glabella* is from Australia. All other members of this clade (*Pauridia*, *Rhodohypoxis*, *Spiloxene*) are from southern Africa. Thus far, no *Hypoxis* species from Africa – the center of diversity for *Hypoxis* – have been analyzed in a phylogenetic context at the family level. All

other genera in the Rudall et al. (1998) study were represented by only a single species.

Generic limits in Hypoxidaceae have always been problematic. *Hypoxis* has been variously treated by several authors (Baker, 1878; Nel, 1914b; Garside, 1936; Geerinck, 1969), whereas separation of *Pauridia* from *Spiloxene* has remained uncertain (Burt, 2000). Ongoing taxonomic confusion also surrounds the identity of *Curculigo* and *Molineria*, and often the species of the latter have been treated as *Curculigo* (e.g. Geerinck, 1969, 1993). Henderson (1987) stated that differences exist in each organ, such as stem system, flowers, fruit and seeds, that warranted keeping the two genera distinct. This ambiguity was partly caused by the somewhat overlapping diagnostic characters for the two genera. Nel (1914a) distinguished them on the presence of beaked (*Curculigo*) or unbeaked (*Molineria*) fruits. However, the beak character is not consistent because several species placed in *Molineria* are clearly beaked (Fig. 1K and L). A more consistent but difficult to observe diagnostic character was proposed by Hilliard and Burt (1978), who studied stamen morphology in detail and showed that the anthers in transverse section are asymmetrical in *Molineria* and symmetrical in *Curculigo*. However, observations by Kocyan and Endress (2001b) and Kocyan (2007) indicated that *Molineria* has asymmetrical as well as symmetrical anthers (*Molineria* was treated there as *Curculigo* for *C. capitulata* and *C. latifolia*). At present, the only clear morphological distinction between the two genera is the presence in *Curculigo* of prominently beaked seeds, in which the funicle has an expanded end and the seed surface is usually striately ornamented (Henderson, 1987; Wiland, 1997; Nordal, 1998). In contrast, the seeds of *Molineria* are unbeaked, generally smaller than *Curculigo* seeds, and the surface is striate or not with a subtle tessellate ornamentation (pers. obs., Kocyan). The overlapping distributions of the two genera have added to the confusion; *Curculigo* occurs throughout the tropics and subtropics, whereas *Molineria* occurs naturally only from southern Asia to northern Australia.

Hypoxidaceae have been proposed as a potential sister family of Orchidaceae (e.g. Garay, 1960, 1972; Hutchinson, 1973) based on morphological features. *Curculigo* and *Molineria* show some similarity in leaf characters with the two genera of Apostasioideae, which are sister to the rest of Orchidaceae: both genera are herbs with plicate palm-like leaves found in forests in Southeast Asia. Moreover, *Apostasia* and *Molineria* (= *Curculigo*) *capitulata* both have *Solanum*-type flowers with united stamens, most probably exhibiting a buzz-pollination syndrome (Kocyan and Endress, 2001a, b). A further similarity with orchids is found in the small hypoxid genus

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