

TAXONOMY

The genus *Colchicum* L. redefined to include *Androcymbium* Willd. based on molecular evidenceJohn Manning¹, Felix Forest² & Annika Vinnersten³¹ *Compton Herbarium, South African National Biodiversity Institute, Kirstenbosch, Private Bag X7, Cape Town, 7735, South Africa. manning@sanbi.org (author for correspondence)*² *Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, U.K.*³ *Department of Systematic Botany, Evolutionary Biology Centre, Uppsala Universitet, Norbyvägen 18D, 752 36 Uppsala, Sweden*

A recent molecular analysis of the Colchicaceae has revealed that the genus *Androcymbium* is paraphyletic in relation to *Colchicum* and that the genus *Merendera* is polyphyletic. The implications of these results on the monophyly of the genera in this alliance are discussed. Two independent lineages within the paraphyletic *Androcymbium* are characterised by enlarged and brightly or contrastingly coloured bracts, which conceal the flowers. The tepals in these species are always cucullate. In the remaining lineages the flowers are more prominent and the tepals are mostly flat. No morphological characters can be identified that serve to diagnose the lineages in *Androcymbium* that are retrieved by the molecular analysis, and the only practical option is to include all species of *Androcymbium* within an expanded circumscription of *Colchicum*. The genus *Colchicum* in this expanded sense is defined by its short-stemmed or acaulescent habit, androecial nectaries, and 2–4-porate pollen. The necessary synonymy and new combinations are made.

KEYWORDS: *Androcymbium*, *Colchicum*, Mediterranean, South Africa, taxonomy

INTRODUCTION

The phylogeny and classification of the family Colchicaceae was recently investigated using DNA sequence data (Vinnersten & Reeves, 2003). This study established the monophyly of the family as defined by Nordenstam (1998) but indicated a need for a revision of the infrafamilial classification. It also suggested that several of the genera in the family are paraphyletic as currently circumscribed. The genera affected are in most cases very small and the nomenclatural implications of the changes in their circumscription that are required to render them monophyletic are readily done (Vinnersten & Manning, 2007). A significant exception concerns the two genera *Androcymbium* Willd. and *Colchicum* L. The molecular analysis of these genera (Vinnersten & Reeves, 2003) suggests that *Androcymbium* is paraphyletic in relation to *Colchicum*. This discovery and its implications are more fully dealt with here.

Androcymbium is a genus of ± 60 species from southern, eastern and northern Africa and the Mediterranean, with a marked centre of diversity in southern Africa (± 50 spp.), especially in the South African winter rainfall region, where some 32 species are recorded. The genus includes a diversity of species that are somewhat loosely linked by their more or less congested inflorescences (rarely solitary flowers) and often enlarged floral bracts (Table 1, Figure 1A–G). Although many of the species are

acaulescent, others have well developed aerial stems. The number of vegetative leaves in the majority of species is fixed at three, but may number as many as ten in some. In several species the floral bracts are highly differentiated from the foliage leaves in shape and coloration and conceal the flowers. These constitute the species typically accommodated in the genus and for which it was established by Willdenow (1808). The Mediterranean species, which have smaller bracts that do not conceal the flowers, were at first segregated as the genus *Erythrostictus* Schltld. but were subsequently relegated to a section of *Androcymbium* (*A. sect. Erythrostictus*) (Bentham & Hooker, 1883), a treatment that has been followed by all subsequent authors. The most recent review of the genus (Müller-Doblies & Müller-Doblies, 2002) divides it into five sections, distinguished primarily by the shape of the tepal blades and the degree of differentiation between the floral bracts and the foliage leaves (Table 2).

The genus *Colchicum* L. (± 90 spp.) is a moderately large genus of acaulescent, often hysteroanthous geophytes distributed from Portugal and North Africa eastwards through Europe and Asia as far as the Himalayas. It is centred in the Mediterranean basin. As originally conceived (Table 1, Fig. 1I), the genus included species with three separate styluli in which the tepals were fused below into a tube, while the genus *Bulbocodium* L. contained a single species with free tepals in which the styluli were joined

into a single three-branched style. The genus *Merendera* Ram. (Fig. 1H) was subsequently created for species with both free tepals and free styluli, and *Synsiphon* Regel for an aberrant *Colchicum* species in which the styluli were fused into a style (Table 1). Stefanoff (1926) was the first to include *Bulbocodium* and *Merendera* in *Colchicum*, and many contemporary authors follow this treatment, including all four genera within the circumscription of *Colchicum* (Dahlgren & al., 1985; Persson, 1993; Nordenstam, 1998).

A close relationship between *Colchicum* and the genus *Androcymbium* was first demonstrated by Buxbaum (1925) on morphological, anatomical and palynological evidence, and since then the two have invariably been allied in the tribe *Colchiceae* (Buxbaum, 1936; Nordenstam, 1982; Vinnersten & Manning, 2007). The genera *Colchicum* and *Androcymbium* share several significant synapomorphies. Both are unique in Colchiceae in their 2(–4)-porate pollen, and in their androecial nectaries, which are situated at the base of the filaments rather than on the blade or claw of the tepals themselves as in other genera in the family. All species of *Colchicum* and many species of *Androcymbium* are acaulescent. Although both genera have diversified primarily in mediterranean-type climates, *Colchicum* is found strictly in the northern hemi-

sphere, whereas the majority of *Androcymbium* species are found in southern Africa, with a few species in North Africa and the Mediterranean, thus linking temperate South Africa with temperate Europe. In its modern circumscription *Colchicum* is separated from *Androcymbium* by its acaulescent habit, radical leaves and subterranean ovary, although only the latter is strictly diagnostic. These three characteristics comprise a suite of character states that are often linked (Burt, 1970) and are best thought of as an adaptive syndrome rather than as independent characters.

MATERIALS AND METHODS

Details of the materials and methods used in the analysis are as in Vinnersten & Reeves (2003) and Fig. 2 is derived from this study. Species of *Androcymbium* were selected to encompass the complete range of morphological variation in the genus, and for *Colchicum* all available material was used. The sampling includes representatives from all five sections and eleven series recognised in the most recent survey of the genus *Androcymbium* (Müller-Doblies & Müller-Doblies, 2002). Morphological char-

Table 1. Diagnostic characters of *Androcymbium* and the segregate genera of *Colchicum*.

Character	<i>Androcymbium</i>	<i>Erythrostictus</i>	<i>Bulbocodium</i>	<i>Colchicum</i>	<i>Merendera</i>	<i>Synsiphon</i>
Stem	Subterranean or aerial	Subterranean	Subterranean	Subterranean	Subterranean	Subterranean
Leaves	Radical or cauline	Radical	Radical	Radical	Radical	Radical
Bracts	Enlarged and concealing flowers or not	Not concealing	Not concealing	Not concealing	Not concealing	Not concealing
Tepals	Free	Free	Free	Fused into a tube	Free	Fused into a tube
Ovary	Aerial or at ground level	Aerial	Subterranean	Subterranean	Subterranean	Subterranean
Styluli	Free	Free	Fused below	Free	Free	Fused below

Table 2. Diagnostic characters of the sections of *Androcymbium* recognised by Müller-Doblies & Müller-Doblies (2002).

Character	Section of <i>Androcymbium</i>				
	<i>Erythrostictus</i>	<i>Dregeocymbium</i>	<i>Marlothiocymbium</i>	<i>Kunkeliocymbium</i>	<i>Androcymbium</i>
Leaf number	6–10	3–6	3–5	2–6	3
Floral bracts	Not differentiated from leaves	Not differentiated from leaves	Not differentiated from leaves	Differentiated from leaves in size and shape	Differentiated from leaves in size, shape, margins and colour
Tepals	White or pink, blades plane	Green, blades plane	White, blades plane	Whitish/greenish, cucullate	Whitish/greenish, cucullate or rarely plane
Filaments	> 2 mm	< 2 mm	> 2 mm	> 2 mm	> 2 mm
Styluli	< 11 mm	1.4–3.3 mm	11–17 mm	4–13 mm	4–20 mm



Fig. 1. Morphological variation in *Androcymbium* and *Colchicum*. A, *Androcymbium ciliolatum*; B, *A. latifolium* subsp. *latifolium*; C, *A. asteroides*; D, *A. longipes*; E, *A. striatum*; F, *A. dregei*; G, *A. cuspidatum*; H, *Merendera trigyna*; I, *Colchicum saviczii*. Photographs: John Manning.

acters were observed in living and herbarium material (NBG, SAM, S) and taken from the literature (Brickell, 1980; Heywood, 1980; Valdés, 1980; Valentine, 1980; Nordenstam, 1998; Müller-Doblies & Müller-Doblies, 1984, 1990, 1998, 2002; Pedrola-Monfort & Caujapé-Castells, 1998; Membrives & al., 2003). The areas of distribution are modified from Membrives & al. (2002).

RESULTS AND DISCUSSION

Results from the molecular study. — The phylogenetic analysis of Colchicaceae by Vinnersten & Reeves (2003) retrieved a well supported (100% jackknife support;

JS) clade comprising the two genera *Androcymbium* and *Colchicum*. Two well-supported branches (A and B in Fig. 2, with 95% and 92% JS respectively), are resolved within this clade. Branch A resolves into a further two well supported groups (both with 98% JS). One of these comprises the four South African taxa *A. ciliolatum*, *A. circinatum*, *A. scabromarginatum*, and *A. latifolium* subsp. *latifolium* (all *A. sect. Androcymbium*) (Fig. 1A, B). This clade is characterised by the consistent occurrence of just three vegetative leaves per plant and enlarged and often highly differentiated floral bracts, which may be brightly coloured or marked. The second clade comprises a trichotomy of *A. asteroides* (*A. sect. Erythrosticktus*), *A. eucomoides* (*A. sect. Androcymbium*) and a clade compris-

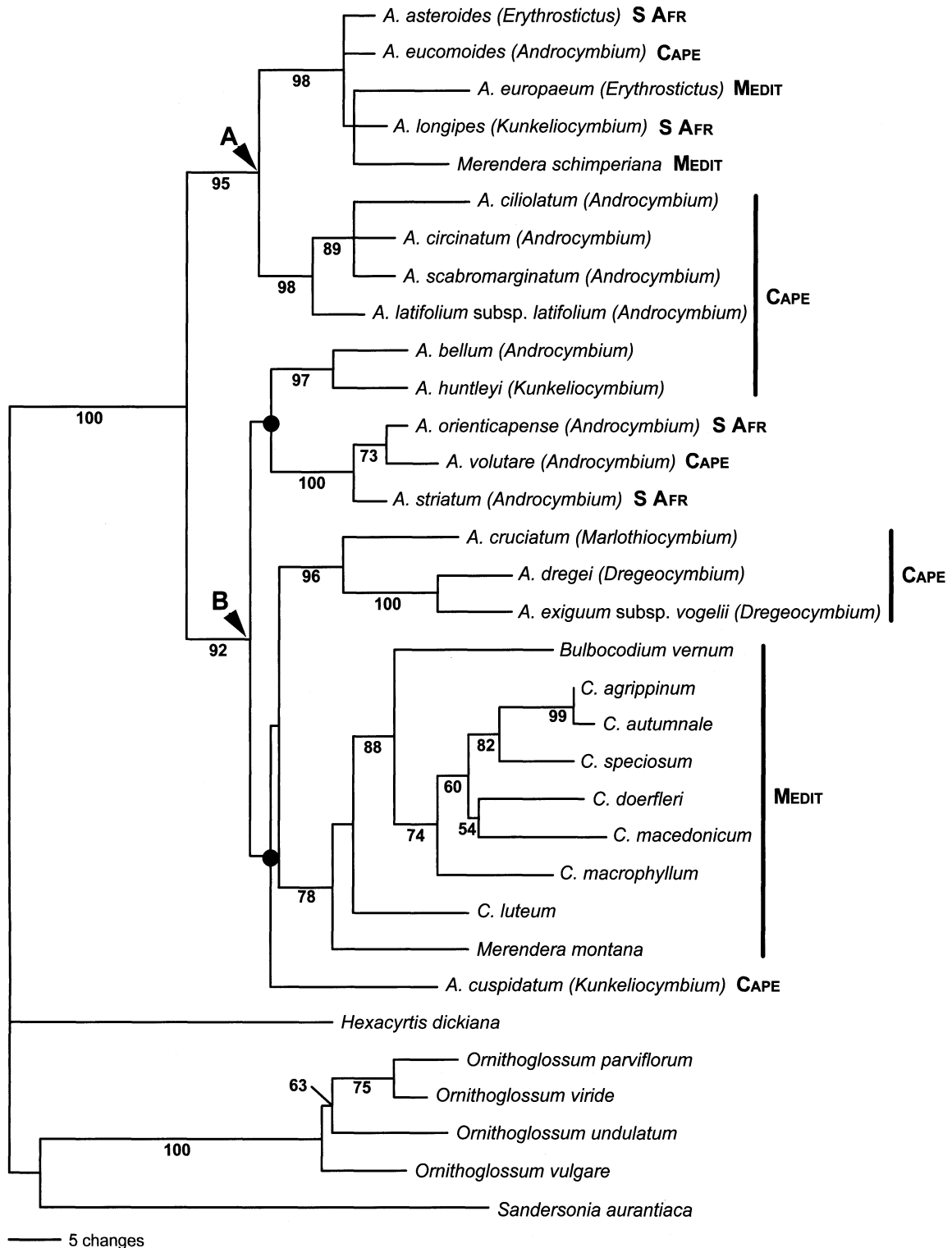


Fig. 2. Phylogram of one of the 24 most parsimonious trees resulting from the phylogenetic analysis of *Androcymbium*, *Colchicum* and related genera based on DNA sequences from the *rps16* intron, the *atpB-rbcL* spacer and the *trnL-F* region. Jackknife support percentages are shown below branches. The old generic names *Bulbocodium* and *Merendera* have been kept to facilitate the recognition of their placement in the tree. For *Androcymbium*, sections are indicated by including the epithet in brackets. Distributions are indicated on the right of the phylogram: Cape (Greater Cape Floral Region), S Afr (subtropical sub-Saharan Africa), MEDIT (Sahel, North Africa and Eurasia). Dots indicate nodes that are collapsed in the strict consensus.

ing *A. europaeum* (*A. sect. Erythrostictus*; the only European species of *Androcymbium* included in this analysis), *A. longipes* (*A. sect. Kunkeliocymbium*), and *Merendera schimperiana*. This clade is characterised by foliage leaves that grade into the floral bracts without significant differentiation between the two apart from the reduction in size. *Merendera schimperiana* and *A. longipes* are morphologically very close and the decision by Stefanoff (1926) to include *M. schimperiana* within *Androcymbium* near *A. gramineum* is in hindsight a lot more prescient than was generally supposed (Greuter, 1967). Stefanoff based his decision on the occurrence in this species of idioblasts containing sulphur-mucopolysaccharides (which dry reddish) in the tepals. These inclusions suggested the generic name *Erythrostictus*, which was applied originally to the Mediterranean species but they now appear to characterise most or all species of *Androcymbium* (Membrives & al., 2003). The similarity between *Merendera schimperiana* and single-flowered plants of *A. gramineum* is striking and there is little incongruence in accepting a close relationship between *M. schimperiana* and the Mediterranean species of *Androcymbium*. Furthermore, the species of *A. sect. Erythrostictus* (the closely allied species-pair *A. asteroides* and *A. roseum* from sub-Saharan Africa plus the European species) share numerous (6–10) foliage leaves and exposed, conspicuous flowers with plane rather than cucullate tepal limbs. The distribution of leaf number and tepal shape across the phylogenetic tree suggests that 3 or 4 foliage leaves and cucullate tepals represent the plesiomorphic state for the *Androcymbium-Colchicum* group. The numerous leaves and plane tepals that characterise the *Erythrostictus* clade may thus constitute synapomorphies defining the group. A less predictable relationship is the association between this group and the two South African species *A. longipes* (*A. sect. Kunkeliocymbium*) and *A. eucoides* (*A. sect. Androcymbium*), both of which have cucullate tepals. However the relationships in this clade are poorly supported (> 50% JS) and further data may reveal a closer relationship between *A. asteroides* and the Northern Hemisphere members of *A. sect. Erythrostictus*.

The first major clade within *Androcymbium* (A in Fig. 2) thus includes two species of *A. sect. Erythrostictus*, five species of *A. sect. Androcymbium*, and one species of *A. sect. Kunkeliocymbium*. *Androcymbium* sections *Androcymbium* and *Kunkeliocymbium* appear to be paraphyletic in relation to *A. sect. Erythrostictus*, which further investigation may reveal to be monophyletic.

The second major clade (B in Fig. 2) resolves into a polytomy in the strict consensus comprising four lineages. Two of these lineages are well supported. The first strongly supported clade (97% JS) comprises *A. bellum* and *A. huntleyi* (*A. sections Androcymbium* and *Kunkeliocymbium* respectively). *Androcymbium bellum* is a curious species with a solitary, exposed flower in which the tepals are

enlarged, plane and truncate. The plane tepals led Krause (1921) to place it in *A. sect. Erythrostictus* but it was recently moved to a monotypic series in *A. sect. Androcymbium* (Müller-Doblies & Müller-Doblies, 2002). *Androcymbium bellum* and *A. huntleyi* are vegetatively very similar, sharing rather attenuate, glaucous leaves and relatively short, pale bracts. The second strongly supported clade (100% JS), comprising *A. orienticapense*, *A. volutare*, and *A. striatum* (*A. sect. Androcymbium*), is characterised by enlarged floral bracts that conceal the flowers and which are longitudinally striped with pale green or whitish between the veins, and often an increased number of foliage leaves. It is plausible to interpret the enlarged bracts as a shift associated with pollinator attraction. The third branch is poorly supported (> 50% JS) and comprises *A. cruciatum* (*A. sect. Marlothiocymbium*) sister to *A. dregei* and *A. exiguum* (*A. sect. Dregeocymbium*), together sister to a moderately supported clade (78% JS) comprising the genus *Colchicum* and the species *Merendera montana* and *Bulbocodium vernum*. The species in the *A. cruciatum* clade, like *A. bellum* and those of *A. sect. Erythrostictus*, have smaller bracts, exposed flowers and flattened tepal blades. *Androcymbium sect. Dregeocymbium* includes probably the most atypical species of the genus, characterised by their linear-lanceolate leaves and exposed flowers with very short filaments, and unusually large pollen grains with regulate exine (Membrives & al., 2002). The position of *A. cruciatum* is uncertain and it forms the fourth lineage of this polytomy. It is a stemless species with solitary white or pink flowers and long filiform styluli, features strongly reminiscent of *Merendera* species.

The genus *Merendera* is clearly polyphyletic in the molecular study, with species in each of the two major clades (A and B in Fig. 2). Accepting *Merendera schimperiana* as a species of *Androcymbium* would result in a monophyletic *Colchicum* provided that it includes the rest of *Merendera*. Analysis of further *Merendera* species is required to assess this.

More significantly, however, the genus *Androcymbium* emerges as paraphyletic in relation to *Colchicum*. Within *Androcymbium*, only section *Dregeocymbium* was retrieved as monophyletic (*A. sect. Marlothiocymbium* is monospecific), although *A. sect. Erythrostictus* may be shown to be monophyletic with further data. *Androcymbium* sections *Kunkeliocymbium* and *Androcymbium*, however, are evidently polyphyletic.

Within *Androcymbium*, the clades that are retrieved in the molecular analysis tend to coincide with adaptive trends that can be identified in the genus. The *A. asteroides-A. europaeum* clade (*A. sect. Erythrostictus*), the *A. cruciatum* clade (*A. sect. Marlothiocymbium*), and the *Colchicum* clade represent trends in which the flower is maximised as the attractive organ in the inflorescence through enlargement of the tepals, flattening of the limbs

and often pink floral pigmentation. In contrast, the *A. latifolium* subsp. *latifolium* clade and the *A. striatum* clade (both *A. sect. Androcymbium*) seem to have independently shifted the role of floral attraction to the vegetative organs, developing enlarged and often coloured or contrastingly marked bracts that conceal the flowers themselves. This strategy is almost certainly associated with novel pollination systems, including rodent-pollination. The winged or cucullate tepals of many species appear to function as nectar reservoirs (pers. obs., J. Manning) and are thus also related to the pollination biology.

The *Colchicum*-clade is essentially diagnosed by a subterranean ovary. The degree to which the ovary is buried in the various species of *Colchicum* appears to be variable and the character state is thus a qualitative one. The evolution of a subterranean ovary and associated floral characters of this syndrome has occurred several times in the Liliales and Asparagales (Burt, 1970), primarily as a solution affording greater protection from cold to the ripening seeds. An origin of *Colchicum* from within *Androcymbium* was actually suggested by Burt (1970), who pointed to the occurrence of species of *Merendera* in North Africa as a possible link to *Androcymbium* in southern Africa. He also highlighted the fact that the species of *Colchicum* from the southern Mediterranean, and thus nearest the ancestral area for the group, were simple diploids and by implication less derived than the polyploids from further north.

In conclusion, therefore, some of the lineages in *Androcymbium-Colchicum* that are identified by the molecular analysis appear to represent adaptive strategies, some of which might be diagnosable by their associated morphological features. Scattered among these lineages, however, are other species with diverse morphologies.

Biogeographical discussion. — The molecular analysis of Vinnersten & Reeves (2003) suggests that the monospecific *Hexacyrtis* is sister to the *Androcymbium-Colchicum* clade, although this relationship is only moderately well supported (63% JS), and it is possible that further data may associate *Hexacyrtis* with the *Sandersonia-Ornithoglossum* clade. *Hexacyrtis* is restricted to southern Namibia and the Richtersveld in the Northern Cape Province of South Africa. This is an arid, strictly winter-rainfall region. The remaining genera of the tribe Colchiceae as circumscribed by Vinnersten & Manning (2007) are distributed throughout southern Africa, including the winter-rainfall Cape region (*Ornithoglossum*), and through temperate, tropical and east Africa (*Sandersonia* and *Gloriosa* including *Littonia*). Of the ± 50 southern African species of *Androcymbium*, 38 are endemic to South Africa, with 32 confined to the mainly winter-rainfall Northern and/or Western Cape provinces of South Africa (Müller-Doblies & Müller-Doblies, 2002). This implies an origin of the *Androcymbium-Colchicum* clade in

the northern and western parts of South Africa, followed by several independent invasions of eastern Africa. An origin for the genus in western South Africa was proposed by Margeli & al. (1999) and Caujapé-Castells & al. (1999, 2001) based on karyology and cpDNA RFLPs, and this hypothesis is supported by molecular phylogeny.

Lineages that appear to have moved northwards into the summer-rainfall regions of the continent include the *A. asteroides-A. europaeum* group (*A. sect. Erythrostictus*), the *A. striatum-A. orienticapense* group, and the *Colchicum* group. The Northern Hemisphere species appear to have arrived in the Mediterranean basin through two separate invasions. The track by which the *A. europaeum* clade arrived is readily traced from North Africa (*M. schimperiana*) down the temperate eastern southern African corridor (*A. longipes*) to the semi-arid parts of southern Africa (*A. eucomoides* and *A. asteroides/A. roseum*). The European species of *Androcymbium* exhibit lower levels of morphological and molecular variation than the southern African species (Caujapé-Castells & al., 1999), which is consistent with a relatively recent diversification from a single ancestral introduction. The track by which *Colchicum* reached the Mediterranean, however, is less easy to discern. There is no significant support identifying any of the *Androcymbium* species included in the analysis as the sister to the *Colchicum*-clade, although it is quite clear that its relationships lie within the genus, and more particularly among species from the winter-rainfall part of southwestern Africa. On morphological grounds it is not unlikely that the lineage shared a common ancestry with *A. cruciatum*. In any event, the relationships of *Colchicum* do not lie with the species of *Androcymbium* from North Africa and the Mediterranean. On current sampling, therefore, it appears that the *Colchicum*-clade originated by long-distance dispersal from an ancestor in the northern and western parts of South Africa. A similar scenario is proposed for the origin of the genus *Crocus* (Iridaceae), which is sister to *Afrocrocus*, a genus endemic to southwestern South Africa (Goldblatt & Manning, in press). *Crocus* and *Colchicum* are remarkably similar in gross morphology, sharing a subterranean stem, long-tubed flowers with subterranean ovary, and hysteranthous leaves. The origin of the *Colchicum*-clade near the base of the *Androcymbium* group suggests that this dispersal event took place early in the history of the group.

Ecologically the South African species of *Androcymbium* are adapted to two different climatic regions. Most species are endemic to the winter-rainfall climate region of the southwest, but some species are found only in a summer-rainfall climate in the south and east. The onset of the winter-rainfall climate is proposed to have taken place 5–8 mya (Deacon & al., 1992), which is substantially later than the dates proposed for the early speciation events in the genus (Vinnersten & Bremer, 2001; Caujapé-Castells

& al., 2002). Thus although the onset of a winter-rainfall climate may be correlated with later radiations in the genus, current evidence is insufficient to link it directly to the initial divergence in the genus.

Generic circumscription. — The topology provides two options for the taxonomic treatment of the taxa in the analysis in order to preserve the monophyly of the genera that can be recognised. Option 1 is to recognise a single large genus to accommodate all of the species today included in *Colchicum* and *Androcymbium*. Option 2 demands the subdivision of the genus *Androcymbium* into several smaller segregates. The type of *Androcymbium*, *A. melanthioides* Willd., which is morphologically very close to *A. striatum*, can be predicted to fall within the *A. striatum*-*A. orienticapense* group (B in Fig. 2). This cluster of species is distinguished by the enlarged bracts longitudinally streaked with white or green. Recognition of this clade as the genus *Androcymbium*, however, would exclude the great majority of species, and require the recognition of several further genera to accommodate them. Among these lineages are the species of *A. sect. Dregeocymbium* (*A. dregei* and *A. exiguum*), *A. cuspidatum*, *A. bellum*, and *A. huntleyi*. Of these, *A. only sect. Dregeocymbium* has been recognised as monophyletic on morphological grounds (Müller-Doblies & Müller-Doblies, 2002). The remaining three species are currently associated with unrelated species in the polyphyletic *A. sections Androcymbium and Kunkeliocymbium* (Müller-Doblies & Müller-Doblies, 2002). Morphologically, therefore, it is not possible to predict the relationships between many of the species of *Androcymbium* that are suggested by the molecular data. The species included in clade B comprise a heterogeneous assemblage that cannot be defined morphologically in relation to those species in clade A. It includes a mix of species in which the flowers are exposed and conspicuous, as well as others in which they are concealed among enlarged bracts, which appear to have assumed the role of pollinator attraction in some species.

The designations “*Cymbanthes* Salisb.” and “*C. foetida* Salisb.” appear in some publications, but these are not validly published names although they were intended to apply to *A. eucomioides* (Jacq.) Willd. The position of this species in the first major clade (A in Fig. 2) offers the possibility of publishing *Cymbanthes* as a new name for the entire clade. However, as with clade B, although well supported in the analysis, clade A lacks any good morphological characters defining it in its entirety. The genus *Erythrostictus*, which was described to accommodate some of the Mediterranean species with flat tepals, and flowers as the attractive organs, is available for the *A. asteroides*-*A. europaeum* clade. Retaining these two genera, in addition to the retention of *Colchicum* in its present circumscription, would necessitate the description of at least three new genera, one for the *A. latifolium*-

A. ciliolatum clade, one or two for the *A. bellum*-*A. striatum* clade, and another one or two to accommodate the species in the *A. cruciatum*-*A. dregei* clade.

There are unfortunately no apparent morphological characters that will retrieve the topology of option 2. The obvious lack of success in dividing the genus *Androcymbium* into morphologically recognisable, monophyletic, infrageneric taxa emphasises this difficulty. Contributing factors include the homoplasious nature of several of the distinctive morphological traits, among them the showy bracts, reduction of the inflorescence to a single flower, and the development of plane tepals. This makes it impossible to predict relationships between species based on morphology. The *Merendera*-type plant (acaulescent and single-flowered with long-clawed, flat, white tepals and filiform styluli), for instance, appears to have evolved independently at least three times in the group (once in clade A in the form of *M. schimperiana*, and twice in clade B as *A. cruciatum* and *M. montana*).

It is also clear that the morphologically more distinctive lineages are dispersed among other lineages, some of which comprise single, independently specialised species. The degree of sequence divergence at lower levels within the *Androcymbium*-*Colchicum* group is comparatively small, and recognition of these several lineages as mono- or oligotypic genera would obscure the obvious close relationship between all the species in the group. We accordingly prefer to adopt option 1. It is possible that the more distinctive lineages, such as *Colchicum* and *Erythrostictus*, which appear to represent particular adaptive radiations, could be recognised at some infrageneric level following more complete sampling of the species.

The genus *Colchicum* in this expanded circumscription is well-defined by its reduced or absent stem, erect sessile or subsessile flowers, androecial nectaries situated at the base of the filaments (secondarily lost in some species), 2–4-porate pollen, and occurrence of idioblasts containing sulphur-mucopolysaccharides. These idioblasts, which are distributed throughout the foliage and flowers of all *Androcymbium* species, appear to have been secondarily lost in the vegetative parts and perianth of *Colchicum* s.str. but are present in the fruits. The necessary transfers from *Androcymbium* to *Colchicum* are made below.

TAXONOMIC CONCLUSIONS

The *Merendera* and *Bulbocodium* species still not transferred to *Colchicum* will not be dealt with here as these groups are currently under study by Persson (in prep.).

***Colchicum* L.**, Sp. Pl.: 341. 1753 – Type (designated by Hitchcock, Prop. Brit. Bot. 148. Aug 1929): *C. autumnale* L.

- Bulbocodium* L., Sp. Pl.: 294. 1753 – Type (designated by Steudel, Nom. ed. 2. 1: 236. 1–8 Aug 1840): *B. vernum* L. (≡ *Colchicum vernum* (L.) Ker Gawl.)
- Merendera* Ramond in Bull. Sci. Soc. Philom. Paris 2: 178. 1801 – Type: *M. bulbocodium* Ramond, nom. illeg. (≡ *M. montana* (L.) Lange ≡ *Colchicum montanum* L.)
- Androcymbium* Willd. in Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 2: 21. 1808, **syn. nov.** – Type (designated by Müller-Doblies & Müller-Doblies in Feddes Repert. 109: 553. 1998): *A. melanthioides* Willd. (≡ *Colchicum melanthioides* (Willd.) J.C. Manning & Vinnersten) (see below).
- Erythrostictus* Schltld. in Linnaea 1: 90. 1826, **syn. nov.** – Type: *E. gramineus* (Cav.) Schltld. (≡ *Colchicum gramineum* (Cav.) J.C. Manning & Vinnersten) (see below).
- Synsiphon* Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada (Acta Horti Petropol.) 6: 490. 1879 – Type: *S. crociflorus* Regel (= *Colchicum crociflorum* (Regel) Regel).
- Colchicum albanense* (Schönl.) J.C. Manning & Vinnersten, **comb. nov.**; *Androcymbium albanense* Schönl. in Rec. Albany Mus. 1: 123. 1904.
- Colchicum albomarginatum* (Schinz) J.C. Manning & Vinnersten, **comb. nov.**; *Androcymbium albomarginatum* Schinz in Bull. Herb. Boiss. 4: 415. 1896.
- Colchicum amphigaripense* (U. Müll.-Doblies & al.) J.C. Manning & Vinnersten, **comb. nov.**; *Androcymbium amphigaripense* U. Müll.-Doblies, Weiglin, M. Gottlieb & D. Müll.-Doblies in Feddes Repert. 113: 569. 2002.
- Colchicum asteroides* (J.C. Manning & Goldblatt) J.C. Manning & Vinnersten, **comb. nov.**; *Androcymbium asteroides* J.C. Manning & Goldblatt in Bothalia 31: 203. 2001.
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