Floral and macroecological evolution within *Cyrtanthus* (Amaryllidaceae): Inferences from combined analyses of plastid *ndhF* and nrDNA ITS sequences

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Abstract

One of the most diverse members of Amaryllidaceae is *Cyrtanthus* Aiton, a large, sub-Saharan Africa genus of approximately 55 species found mostly in South Africa. To investigate phylogenetic and biogeographic relationships within *Cyrtanthus*, sequence data from the plastid *ndhF* gene and the ITS nrDNA region for 41 species were analyzed with parsimony, maximum likelihood, and Bayesian-inference approaches. Various recombination detection algorithms were used to test for interspecific hybridization in the ITS alignment. The genus resolved as monophyletic, comprising three poorly to well-supported major lineages: a predominantly Afrotemperate lineage, largely restricted to seasonally moist sites in summer rainfall southern Africa, a subtropical lineage found mostly in nonseasonal rainfall regions, often in dry habitats, and a Cape Floristic Region-centered lineage in which most species are concentrated in the summer-dry to nonseasonal rainfall southwest. The ITS sequence alignment shows no evidence for reticulation between any of the species. Relationships inferred by the molecular data disagree with those derived from morphological data, but agree with previously published groupings based on karyotype morphology. Fitch optimization of selected floral characters on the combined gene tree reveals recurrent patterns of convergence. Ornithophilous floral forms occur in parallel among the three primary clades, putatively *Aeropetes tulbaghia* butterfly and inferred long-proboscid fly pollination syndromes are unique in the Cape lineage. Macroecological factors inferred to have influenced the evolution of *Cyrtanthus* are changes in rainfall seasonality, the advent of fire, and the availability of new habitats at high and low altitudes and in rock-free soils or rock crevices. This study gives greater clarity on relationships within the genus and enables its division into three informal infrageneric groups.

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1. Introduction

The genus *Cyrtanthus* Aiton is endemic to sub-Saharan Africa, with well over 90% of its species concentrated in South Africa (Dyer, 1939; Reid and Dyer, 1984). With about 55 species it is the largest genus of southern Africa’s Amaryllidaceae (Snijman and Archer, 2003) and one of the largest in the family overall. Within this ecologically diverse region *Cyrtanthus* extends from the summer-dry southwest to the summer rainfall northeast. A remarkable response of several species within fire-prone ecosystems is their dependence on fire to flower (Gordon-Gray and Wright, 1969; Le Maitre and Midgley, 1992; Keeley, 1993).

Traub (1963) placed *Cyrtanthus* in its own tribe, Cyrtantheae, a treatment maintained by Meerow and Snijman (1998), whereas Müller-Doblies and Müller-Doblies (1996) placed *Cyrtanthus* in the tribe Haemantheae, albeit as a monotypic subtribe, Cyrtanthinae, based on bulb morphology and chromosome number, a classification accepted by Dahlgren et al. (1985). Combined *rbcL* and plastid *trnL-F* sequences (Meerow et al., 1999) indicated a position for *Cyrtanthus* as sister to the remainder of Amaryllidaceae after the branching of the tribe Amaryllidaceae. Plastid *ndhF* sequences (Meerow and
Snijman, 2006), however, resolved *Cyrtanthus* as sister to a clade comprising Calostemmataceae and Haemanthaceae. An ITS alignment across the entire family (Meerow, unpubl. data) places *Cyrtanthus* as sister to Haemanthaceae, but until additional data are available the position of the genus relative to the rest of the family remains ambiguous.

The genus exhibits a high level of floral morphological diversity which is unparalleled in any other genus of the family. Conversely, the genus shows great consistency in chromosome number, with $2n=16$ characteristic of most, if not all, of the species (Wilsenach, 1963; Ising, 1970; Strydom et al., 2007). It is also the only African genus with the flattened, winged, phytomelanous seed, so common in the American clade of the family (Meerow and Snijman, 1998). Following Baker’s (1888) treatments of *Cyrtanthus*, Dyer (1939) provided a synoptic review of the genus and Nordal (1979) revised the two East African species. The most recent account is that of Reid and Dyer (1984); six new species have since been described (Hilliard and Burtt, 1986; Snijman and Van Jaarsveld, 1995; Snijman, 1999, 2001, 2003, 2007).

The showiness of the flowers in *Cyrtanthus* is comparable to those of Orchidaceae and Iridaceae in southern Africa, families for which extensive data on pollination systems are available (Goldblatt et al., 1995, 1998; Johnson et al., 1998; Linder and Kurzweil 1999; Goldblatt and Manning, 1999, 2000). These studies indicate that shifts in pollination systems occur frequently within groups of closely related species and have necessitated the revision of several genera formerly classified as sister to Haemantheae, but until additional *Cyrtanthus* and Kurzweil 1999; Goldblatt and Manning, 1999, 2000). Best fit models were evaluated using the corrected Akaike Information Criterion (AICc; Akaike, 1973; Shono, 2000) for ML and the Bayesian Information Criterion (BIC) with Akaike Information Criterion (AICc; Akaike, 1973; Shono, 2000). Best fit models were evaluated using the corrected Akaike Information Criterion (AICc; Akaike, 1973; Shono, 2000) for ML and the Bayesian Information Criterion (BIC) with significance determined by Chi-square analysis.

Parasimony tree searches were heuristic, conducted under the Fitch (equal) weights (Fitch, 1971) criterion with 2000 rounds of random addition sequence, saving no more than 20 minimum length trees per search for swapping using tree branch reconnection (TBR). Tree branches were collapsed if the
minimum length = 0. Gaps were coded as missing characters in all of the analyses, as there were no informative indels in either matrix. Before combining the ITS and \textit{ndhF} data sets, we performed an incongruence length difference test (ILD = partition homogeneity test in PAUP) on the matrices (Farris et al., 1994, 1995) to assess the degree of congruence between them. One thousand heuristic searches were conducted for the ILD, each with 10 random addition replicates, saving no more than 20 trees from each for TBR branch swapping. Internal support was determined by bootstrapping (BP; Felsenstein, 1985; 5000 heuristic replicates with simple addition, TBR branch swapping, saving 20 trees per replicate). For the combined analysis, partitioned Bremer (decay) indices (Bremer, 1988) using TreeRot v. 3.0 (Sorenson and Franzosa, 2007) were also calculated. The cut-off BP value was 50%. A BP value greater than 75% was designated moderate support, 65–75% was designated moderate support, and less than 65% as weak (Meerow and Snijman, 2001; Meerow et al., 2002; Meerow and Clayton, 2004). Five hundred
heuristic searches with random addition sequence were imple-
mented for each constraint statement postulated by TreeRot,
saving no more than 10 trees per search. A minimum DI=2 was
considered to represent good support for a clade (Meerow and
Snijman, 2001; Meerow et al., 2002; Meerow and Clayton, 2004).

Two parallel runs were performed in MrBayes, each con-
isting of four chains, one “cold” and three incrementally
heated. Five million Markov chain Monte Carlo (MCMC)
generations were run, with convergence diagnostics calculated
every 1000th generation for monitoring the stabilization of
log likelihood scores. Trees in each chain were sampled every
100th generation. A 50% majority rule consensus tree was
generated from the sampled trees after discarding the first 25%
(12,500 trees).

2.4. Morphological characters and macroecological parameters

We scored a set of 23 morphological characters (Appendix A)
and four ecological parameters (altitude, rainfall seasonality,
groundwater availability, and soil rockiness) (Appendix B) for
parsimony analyses (morphological only) as described above
and/or optimization on gene trees. Derived from live plants,
dried specimens at NBG and current literature (Dyer, 1939;
Gordon-Gray and Wright, 1969; Nordal, 1979; Reid and Dyer,
1984; Snijman and Van Jaarsveld, 1995; Snijman, 1999, 2001,
2003, 2007), the morphological data were treated as 13 binary
state characters and ten unordered multi-state characters. Fire-
dependence (character 23) was ascribed to species tightly keyed
to fire events and that flower over a relatively wide period
(several months) following a fire (Keeley, 1993). It was deter-
mined from herbarium records (BOL, NBG, and PRE), and
assigned to species which showed short discontinuous flowering
times scattered over a period of several months and very rarely
in successive years at any particular locality. These were not
confused with species occupying dry, fire-free areas with erratic
rainfall that also show long gaps between flowering periods.
Chromosome morphology was omitted from the analysis due to
an absence of data for many species.

Species’ distributions were obtained from locality data on
herbarium specimens (in BOL, NBG, PRE, and SAM) and
these were plotted onto the vegetation map of southern Africa
(Mucina and Rutherford, 2006) from which the associated data
on altitude and rainfall seasonality were derived. Data on soil
rockiness and groundwater availability were derived from field
studies and herbarium specimens. Although the macroecologi-
cal estimates are rough, similar parameters have given valuable
insights in other studies (Hardy and Linder, 2005; Linder and
Hardy, 2005; Linder et al., 2006). To accommodate ancestral
polymorphisms, the ecological parameters (Appendix B) were
coded as binary states: presence or absence (Hardy and Linder,
2005; Linder and Hardy, 2005). Both DELTRAN (delayed
transformation) and ACCTRAN (accelerated transformation)
optimizations, as implemented in MacClade 4.08 (Maddison
and Maddison, 2001), were used on one fully resolved tree,
following the method of Linder et al. (2006).

Floral morphology was used to hypothesize pollinators by
matching sets of floral features with those constituting flower
types as recognized by Faegri and Van der Pijl (1979), Johnson
and Bond (1994), and Goldblatt and Manning (2006). Although
important when inferring pollination syndromes, nectar data
are still absent for the genus. We identified four flower types
within Cyrtanthus and listed their inferred pollinators along-
side the species in the cladogram which traces the evolution
of macroecological habitats. Where the floral morphology of
a species could not be matched with any one of the classical
flower types the pollinators were regarded as equivocal. The
following sets of characters were sought: classic butterfly-
flowers: radially symmetrical, vividly coloured, including pure
red, nectar guides (if present) simple, rim generally flat, often
narrow (not allowing access of a bird’s bill) and not much
divided, odour weak, nectar well hidden in a tube; brush-type
butterfly-flowers: as above but stems long, projecting from a
funnel-shaped perianth; moth-flowers: pendent or held hori-
izontally, long-tubed with rim absent or bent back, mostly white
or drably coloured, strongly perfumed at night, landing sur-
face present in noctuid-type, but absent in sphenid-type; bird-
flowers: usually hanging, vividly coloured, odourless, deep-
tubed, with a hard wall, lip or margin curved back, filaments
stiff; long-proboscid fly-flowers: perianth white to pink with
dark markings towards throat, odourless, with a long cylindrical
tube (1.0–1.5 mm diameter).

2.5. Testing for interspecific hybridization

Tests of recombinant signal in the ITS alignment of Cyrtan-
thus were conducted with the program RDP3 (Martin et al.,
2005a). RDP3 (Recombination Detection Program version 3) is a
Windows 95/98/NT/XP program for detecting and analyzing
recombination signals in a set of aligned DNA sequences. In addition to its own RDP method (Martin and
Rybicki, 2000), RDP3 implements a Bootscanning method
(Salminen et al., 1995; Martin et al., 2005b), the GENECONV
method (Padidam et al., 1999), the Maximum Chi-Square
method (MaxChi; Maynard Smith, 1992; Posada and Crandall,
2001), the Chimaera method (Posada and Crandall, 2001),
the Sister Scanning Method (SiScan; Gibbs et al., 2000), the
3SEQ method (Boní et al., 2007), the Reticulate compatibility matrix
method (Jakobsen and Easteal, 1996) and the TOPAL DSS
method (McGuire and Wright, 1998, 2000). RDP3 also
functions as a Windows interface for other recombination
detection and analysis programs including LARD (Likeli-
hood Assisted Recombination Detection; Holmes et al.,
1999) and LDHAT (McVean et al., 2002, 2004). Breakpoint polishing
and checking for misalignment were options that were
invoked, and the matrix was analyzed both with and without
the requirement for phylogenetic evidence for recombination
signals. All tests were permuted by simulation 1000 times,
using SEQ-GEN (Rambaut and Grassy, 1997) parametric
simulations in order to generate simulated alignments with
approximately the same distribution of polymorphic sites as
the actual data matrix. Highest acceptable P value was set to
0.05 with Bonferroni correction applied. The full gamut of
tests was run five times.
3. Results and discussion

3.1. Phylogenetic analyses of molecular data

3.1.1. ndhF

The ndhF matrix consisted of 2040 characters, 129 of which were variable and 36 were parsimony informative. The heuristic search found 153 equally parsimonious trees that condensed to one (Fig. 1) when branches of minimum length=0 were collapsed. The tree was 147 steps in length, with consistency index (CI) = 0.898 (CI with informative characters only = 0.712) and retention index (RI) = 0.913. Branch lengths are short in the tree, with nine being the largest number of apomorphies (ancestral node of *C. labiatus* and *C. montanus*). The monophyly of *Cyrtanthus* is supported with BP = 99%, after which three distinct clades are resolved (Fig. 1), with weak BP. In Clade A (BP < 50%), the best supported group (BP = 84%) unites a large group of the narrow-leafed species, after a grade of three species is formed with little or no parsimony support.

Surprisingly, the two subspecies of *C. mackenii* do not resolve as sister taxa, probably an artefact of the overall short branch lengths (the two subspecies differ by only two base substitutions across the entire ndhF alignment). The second clade, B (BP = 70%), was largely unresolved internally except for strong to moderately supported sister relationships between *C. carneus*–*C. herrei* (BP = 81%), *C. collinus*–*C. ventricosus* (BP = 83%), and *C. labiatus*–*C. montanus* (BP = 96%). The third weakly supported (BP = 53%) clade C contains two well-supported groups that are weakly united (BP = 57%), then form a polytomy with *C. eucallus*, *C. galpinii* and *C. obliquus*.

The transversional model with gamma distributed rate heterogeneity (TVM + G) was the best fit for the ndhF alignment. The ML tree, with a likelihood score $= −3747.7$, was very similar to the parsimony topology with a few exceptions (Fig. 1). Clade B was resolved as sister to Clade A with weak (59%) BP. There was an additional sister species relationships resolved in Clade A: *C. brachyscyphus* with *C. mackenii* subsp. *cooperi* (63% BP). In Clade B, *C. leptosiphon* resolved as sister to *C. labiatus* – *C. montanus* clade with ML (98% bootstrap).

![Fig. 1. Single tree found by parsimony analysis of the ndhF sequence alignment across 42 Cyrtanthus taxa. Numbers above branches are branch lengths. Numbers below branches are parsimony (italic) and ML (underline) bootstrap percentages.](image-url)
to the *C. labiatus–C. montanus* clade (98% BP). Overall, bootstrap support tended to be higher with ML than parsimony, and several branches received BP > 50% with ML that did not in the parsimony analysis (Fig. 1).

### 3.1.2. ITS

The ITS matrix had a total of 661 characters, of which 121 were parsimony informative. Fifty-three equally most parsimonious trees were found, which condensed to four when branches of minimum length = 0 were collapsed. The trees were 379 steps long with consistency index (CI) = 0.784 (CI with informative characters only = 0.650) and retention index (RI) = 0.804. *Cyrtanthus* resolves as monophyletic with 100% BP (Fig. 2). Three clades in the genus are resolved, labelled A, B and C (Fig. 2). Clade A has 64% BP, and contains exactly the same taxa as Clade A with *ndhF* (Fig. 1), albeit with greater resolution and some differences in the terminal relationships of several taxa. The subspecies of *C. mackenii* are sisters with 81% BP, while *C. tuckii* var. *transvaalensis* forms a well-supported clade with *C. angustifolius* and *C. aureolinus*, but its sister in the *ndhF* tree (Fig. 1), *C. stenanthus*, is part of a different subclade that is sister to *C. macowanii* (BP = 93%). Clade B with ITS also contains the same species as its equivalent with *ndhF* with one exception: *C. ventricosus* is unresolved between Clades B and C. Clade B has 50% BP with ITS, even though it resolved in all four trees. Clade C with ITS is also similar to that resolved with *ndhF* except *C. falcatus* joins *C. obliquus* and *C. ventricosus* in a polytomy with both Clades B and C in the ITS trees (Fig. 2). Bootstrap support for Clade C is 68%. Two spiral-leaved species, *C. helictus* and *C. smithiae*, are sisters with 97% BP support, and, as in the *ndhF* tree, are included in a subclade with *C. flammosus*, *C. loddigesianus*, and *C. wellandii*. Absent from this grouping, however, is *C. spiralis*, which with *ndhF* formed a weakly supported subclade with the other two spiral-leaved species, *C. loddigesianus* and *C. wellandii* (Fig. 1), and *C. sp.* which instead is sister to *C. sanguineus* with 72% BP (Fig. 2). With *ndhF*, *C. sanguineus* formed a well-supported (94% BP) polytomy with *C. contractus* and *C. macmasteri* (Fig. 1).

Of the available models of molecular evolution, the best model fit to the ITS alignment was the general time reversible with gamma distributed rate heterogeneity (GTR + G). The ML tree log likelihood score was −2944.738. Major differences with the parsimony trees were few. Clade A received 95% BP with ML versus 64% with parsimony. In Clade B, *C. collinus* was sister to *C. debilis–C. elatus* with BP = 70%. *Cyrtanthus ventricosus*, which with parsimony was unresolved between Clades B and C, was sister to Clade B (BP = 67%) with ML. In

Fig. 2. Strict consensus tree of four most equally parsimonious trees found by cladistic analysis of the ITS sequence alignment across 42 *Cyrtanthus* taxa. Numbers below branches are parsimony (italic) and ML (underline) bootstrap percentages.
Clade C, \textit{C. contractus} was sister to the rest of the clade (BP=69\%) in the ML topology, and \textit{C. eucallus} and \textit{C. galpinii} were sister at BP=60\%.

The null hypothesis that interspecific hybridization had not figured in the evolution of \textit{Cyrtanthus} species was accepted. None of the recombination detection algorithms used by RDP found any sequence evidence for reticulation between any \textit{Cyrtanthus} species.

\subsection*{3.1.3. Combined loci}

The ILD resulted in the rejection of the null hypothesis that the \textit{ndhF} and ITS alignments were congruent ($P=0.01$), but in fact, the same main clades are resolved by both topologies (Figs. 1 and 2), with most differences concentrated in the terminal resolutions within each of the three. Partitioned decay indices indicate congruent support for Clades A and B (Fig. 3). The accuracy of the ILD as an arbiter of combinability has declined steadily since Farris et al. (1994, 1995) first recommended a $P$ value of 0.05 as the threshold for determining non-combinability. Numerous studies have concluded that $P$ values $<0.05$, and even as low as 0.001, should not preclude data set combination (Sullivan, 1996; Cunningham, 1997a,b; DeSalle and Brower, 1997; Sidall, 1997; Davis et al., 1998; Flynn and Nedbal, 1998; Messenger and McGuire, 1998; Yoder et al., 2001). This along with the main clade congruence between the two trees justified a combined analysis. For ML and Bayesian analyses, a mixed model, retaining each partition’s best fit nucleotide substitution model, was applied.

Fifty-three equally most parsimonious trees were found (Fig. 3), which condensed to 20 when branches of minimum length=0 were collapsed. The trees were 544 steps long with consistency index (CI)=0.789 (CI with informative characters only=0.622) and retention index (RI)=0.806. Clades A, B and C were resolved with 84, 75 and 72\% BP (DI=3, 2, 1, respectively). \textit{Cyrtanthus falcatus} and \textit{C. obliquus} formed a polytomy with Clade C at 59\% BP (DI=1). Clades B and C were sister groups with 65\% BP (DI=1). In Clade C, a sister relationship between \textit{C. contractus} and \textit{C. sanguineus} received weak BP=53\%; as did a sister relationship of \textit{C. galpinii} to the single well-resolved subclade (BP=53\%), unresolved in the strict consensus (Fig. 3).

The ML tree had a log likelihood = $-2944.7$. Clades A and B were almost identical to their resolution with parsimony. In Clade A, a few subclades received weak bootstrap support with
ML, vs. <50% with parsimony (Fig. 3). In Clade B, C. collinus and C. ventricosus were sister species (BP=69%). Clade C has the most disparate internal resolution between the two methods of analysis. In the ML tree, C. galpinii and C. eucallus were sisters at 79% BP. Cyrtanthus contractus, C. macmasteri, and C. sanguineus formed a clade with 90% BP. All of these species were unresolved within Clade C with parsimony.

All stabilization diagnostics indicated that the log likelihood scores in the Bayesian analysis converged before 500,000 iterations, thus our 50% majority consensus (Fig. 4) of trees sampled from the latter 3.75 million generations is a conservative estimate of clade credibility (CC). Clades A, B and C had CC=1, 1, and 0.99, respectively, and the same species resolution as the parsimony and ML trees for A and B. Sister relationship of C. collinus and C. ventricosus, resolved by ML but not parsimony, received a CC=0.85. There is weak and polytomous subclade resolution (CC=0.55) in Clade B for these two species with C. debilis–C. elatus, C. labiatus–C. montanus and C. odorus. The level of support for Clade C in the Bayesian tree (Fig. 4) is significantly more robust than with either parsimony or ML (Fig. 3). The well-supported ML clade (BP=90%) of C. contractus, C. macmasteri and C. sanguineus in Clade C was also resolved by Bayesian analysis (CC=1.00), as was the sister relationship of C. eucallus and C. galpinii (CC=0.92). As with the parsimony and ML analyses, C. falcatus and C. obliquus occupy unresolved positions in Clade C in the Bayesian topology.

3.2. Phylogenetic analyses of morphological data

Heuristic search found 2276 equally most parsimonious trees with the morphological data set. Trees were 126 steps long, with CI=0.278, and RI=0.664. The homoplasy index was a high 0.838. The trees were very poorly resolved (not shown). In the strict consensus of all trees, ten of the 14 species placed in Clade C of the combined gene tree formed a monophyletic group, but with <50% BP. The six morphological synapomorphies at the ancestral node were leaves distinctly narrowed towards the base, perigone tube more-or-less abruptly inflated from near the base into a bell-shaped tube, tube less than twice the length of the segments, flowers with dark stripes leading into the throat, anthers just exserted from the perigone throat, and stigma minutely 3-lobed. Within this clade, C. helictus, C. smithiae and C. loddigesianus formed a clade with 63% BP, a monophyletic group that was also resolved in the ITS and combined analyses (Figs. 2 and 3). The four morphological

![Fig. 4. Fifty percent majority rule consensus tree of 37,500 trees sampled after burn-in from Bayesian analysis of the combined ndhF and ITS sequence matrices across 42 Cyrtanthus taxa. Numbers at nodes represent clade credibility scores (as proportion of trees in which that clade was resolved).](image-url)
synapomorphies for this small clade were solitary bulbs; cream-coloured, pale lemon or white flower colour; red, pink or green stripes on the backs of segments and outside of tube; and strongly biseriate stamens.

Combining the morphological data with the sequence matrices yielded 45 trees of length=775 steps, CI=0.662 and RI=0.695 (not shown). Clade A, and most of Clades B and C were resolved as in the combined gene tree, but a fourth clade was formed consisting of *C. carneus* and *C. herrei* (Clade B in Fig. 3) and *C. falcatus* and *C. obliquus* (Clade C in Fig. 3). The two morphological synapomorphies supporting this subclade were clump-forming bulbs, as large as 65–100 mm in diameter at maturity.

We concluded that the morphological data matrix was not very informative from the perspective of phylogenetic analysis, and then traced the evolution of selected floral characters through the optimization of their states on the combined gene tree using MacClade v4.08 (Maddison and Maddison, 2001).

3.3. Biogeography and macroecology

The three major lineages generated in our analyses show different biogeographic affinities although their distributions overlap to some extent for a few extant species.

Clade A encompasses taxa concentrated in southern Africa’s Grassland Biome together with a few outlying species in the Savanna Biome to the east and north, the Indian Ocean Coastal Belt Biome in the extreme east and the Fynbos Biome in the south (Fig. 5a). As such, it falls mostly in the Afrotemperate Phyto-geographical Region (Galley et al., 2007), made up of the Afromontane phytochorion (White, 1983) in the north and the Cape Floristic Region in the south. Apart from *C. tuckii* var. *transvaalensis*, which is found in grassland of the Highveld in the northern parts of South Africa, most other extant species in this ‘Afrotemperate’ lineage (*C. attenuatus*, *C. epiphyticus*, *C. huttonii*, *C. mackenii* subsp. *cooperi*, *C. macmestersi*, *C. macowanii*, *C. stenanthus* var. *stenanthus*, *C. suaveolens*), including the earliest diverging species (*C. flanaganii*), are endemic to or occur in the present-day southeastern African temperate grasslands. The few species that presently occur outside this grassland area may therefore best be interpreted as instances of secondary range expansion. These are: *C. angustifolius*, *C. fergusoniae* and *C. aureolimus* in the Cape Region and *C. mackenii* subsp. *mackenii* and *C. brachyscyphus* that occupy drainage lines on the subtropical Indian Ocean Coastal Belt, the youngest biome in South Africa (Mucina and Rutherford, 2006). Likewise, southern Africa appears to be the source area for the widespread *C. breviflorus* which extends northwards in a series of disjunct populations along mountain corridors to East Africa and Angola.

The extent species of Clade B are almost entirely restricted to the Fynbos and Succulent Karoo Biomes which constitute the Greater Cape Region (Jürgens, 1991; Born et al., 2007), hereafter referred to as ‘the Cape’ (Fig. 5b, d). Two species, *C. labiatus* and *C. montanus* from the Baviaanskloof Mountains, Eastern Cape, are found at the interface of the Fynbos and Albany Thicket Biomes. One species, the Richtersveld endemic *C. herrei*, occurs in the semi-arid Succulent Karoo. *Cyrtanthus herrei* is one of several other known outliers found outside the core Cape Region (sensu Goldblatt and Manning, 2002) in the Richtersveld: *Amaryllis paradisicola* is sister to the Western Cape *A. belladonna* (Snijman and Williamson, 1998), *Moreaea gariepensis*, is sister to the Cape-centered *M. ramosissima* (Goldblatt et al., 2002), and *Trachyandra adamsonii* (Manning, 1990) and *Walleria gracilis* have disjunct populations in the Richtersveld and Western Cape (Manning et al., 2001). The disjunction between *C. herrei* and its sister species, the southwestern Cape *C. carneus*, therefore suggests vicariance, probably corresponding with phases of range expansion and contraction during climatic oscillations of the Pleistocene (Midgley et al., 2001, 2005).

Most species in the ‘Cape’ lineage are presently concentrated on the summer-dry, southwest coast forelands (west of 21°E), with only half this number in the Fynbos of the nonseasonal rainfall Eastern Cape (Fig. 5b). This pattern corresponds with species richness in the Cape flora as a whole (Cowling and Lombard, 2002; Linder, 2003). Most of the species (*C. carneus*, *C. elatus*, *C. guthriaceae*, *C. labiatus*, *C. leptosiphon*, *C. leucanthus*, *C. montanus*, and *C. odoros*) are range-restricted habitat specialists confined to specific vegetation types and/or soils. Only two species (*C. collinus* and *C. ventricosus*) are widespread, occupying the same soils and aspect in habitats on the continuous Cape Fold mountain ranges. *Cyrtanthus collinus* is found on the coastal and inland mountains of the southern Cape and *C. ventricosus* extends from the Cape Peninsula into the Eastern Cape.

Most species of Clade C are located in the eastern lowlands and midlands of southern Africa (Fig. 5c, d), where they are concentrated in the subtropical biomes: Albany Thicket and Savanna (Cowling et al., 2005; Mucina and Rutherford, 2006). Nested in this lineage are *C. flamosus* and *C. spiralis* which are narrowly endemic to the Albany Thicket Biome and confined to the Savanna Biome are *C. eucalus* and *C. galpinii* in the Lowveld. Other species straddle the Albany Thicket and Savanna Biomes: the Eastern Cape *C. helicus* and, extending northwards from the Albany region through South Africa, Zimbabwe, western Mozambique and East Africa into Sudan, is *C. sanguineus* (Nordal, 1979). Only one species, *C. contractus*, extends beyond the Savanna Biome into the Sub-Escarpment and Highveld grasslands (Fig. 5d), which suggests that this is a later radiation into the temperate grasslands of the high-lying interior. Two representatives extend beyond the Albany Thicket Biome to the eastern Fynbos Biome: *C. obliquus*, adapted to nutrient-poor soils, occupies rocky habitats in east–west tending valleys, whereas the narrowly distributed *C. loddigesianus* extends south westwards along fixed coastal dunes that were probably exposed after the retreat of the sea level to its current position, an event dated at two to three million years ago (Siesser and Dingle, 1981). Only *C. wellandii*, in the Humansdorp district, is strictly endemic to the Fynbos Biome. Despite several species belonging to the semi-arid Albany Thicket Biome being arid-adapted, only *C. smithiae* extends beyond this Biome along valleys into the southern parts of the Nama Karoo. Essentially, the transitional nature of the distribution ranges evident in this lineage reflects the complexity...
of the Albany Thicket Biome itself which is hypothesized to have incorporated many lineages from adjacent vegetation formations while it was contracting during climatic deterioration in the past (Cowling et al., 2005).

Habitats in the Albany Thicket Biome are fire-free, but most in the Fynbos, Grassland and Savanna Biomes are fire-prone (Mucina and Rutherford, 2006) and the latter are home to the fire-specialists (*C. angustifolius*, *C. breviflorus*, *C. contractus*, *C. tuckii* var. *transvaalensis* and *C. ventricosus*), the most widespread extant species of the genus.

Although the ‘Cape’ lineage of *Cyrtanthus* displays geographical patterns similar to many of the taxa regarded as ‘core’ Cape groups as defined by Linder (2003), it is nevertheless nested within extra-Cape clades that are essentially Afrotemperate and subtropical in nature, suggesting that the evolutionary history of *Cyrtanthus* is strongly tied to the subcontinent’s southeastern region. Incomplete sampling at the base of a tree is known to affect ancestral analyses (Bremer, 1992), but our sample of species from the Cape lacks only *C. ochroleucus* (Herb.) Burch. ex Steud., previously treated as a close ally of *C. mackenii* and *C. aureolinus* (Snijman, 2007) but considered here to be a close relative of *C. odorus*, *C. staadensis* Schönland which is believed to be closely allied to *C. contractus* but often confused with *C. collinus* (Snijman, 1999), and the poorly known *C. inaequalis* O’Brien. So their omission is unlikely to alter the tree topology.

To date, few attempts have been made to reconstruct the evolution of lineages with broad distributions in southern Africa.

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Fig. 5. *Cyrtanthus* in southern Africa: (a–c) species richness per one geographical degree square for Clade A, Clade B and Clade C respectively within the major biomes; (d) distribution outlines for Clades A, B and C relative to altitude above sea level.
Major ecological factors that have been implicated in the lineage diversification of *Zaluzianskya*, *Brassicaceae*, *Melianthus* and *Arctotidinae* within southern Africa are past shifts in annual precipitation and rainfall seasonality, and changes in altitude (Archibald et al., 2005; Mummenhoff et al., 2005; Linder et al., 2006; McKenzie and Barker, 2008). Our reconstruction of the ecological evolution of *Cyrtanthus* (Fig. 6) suggests that stony, well-drained uplands (300–1500 m) were the ancestral niche. The earliest rainfall seasonality of the lineage remains ambiguous but subsequent divergence is clearly evident among the major lineages. The occupation of summer-wet conditions and seasonally moist sites is concentrated in the ‘Afrotemperate’ clade (Clade A) and appears to have been accompanied by a contemporaneous shift (with ACCTRAN) or later shift (with DELTRAN) to highlands (1500–3000 m), followed, however, by the exploitation by several species of upland and lowland habitats and nonseasonal rainfall conditions. The only instance of adaptation to strictly summer-dry conditions is in the ‘Cape’ clade (Clade B). ACCTRAN infers that adaptation to a summer-dry climate is the most recent state. DELTRAN, however, resolved summer-dry habitats at the base of the clade with a reversal to nonseasonal habitats. This suggests that lineages which receive not just winter rainfall but summer moisture from clouds formed on the south coast forelands off the warm Agulhas current as well, are recently derived, as has been suggested for *Thamnochortus* (Hardy and Linder, 2005). Our use of summer-dry conditions encompasses climates on mountains in the northwest as well as on coastal lowlands in the southwest, hence summer drought may be a compound ecological attribute. The former habitat may represent long-term, relatively stable inland refugia, whereas the southwestern Cape lowlands may have provided

**Fig. 6.** Macroecological attributes mapped onto a fully resolved consensus tree of *Cyrtanthus* and a list of inferred primary pollinators. Abbreviations: ACCTRAN underlined, DELTRAN in italics, non-italics and not underlined reflect agreement between ACCTRAN and DELTRAN, altitude (up = uplands, hl = highlands, and ll = lowlands), rainfall (ns = nonseasonal, ms = moderately seasonal, sw = summer-wet/winter-dry, and sd = summer-dry/winter-wet), groundwater (wd = well-drained and ss = streams or seepages), soil rockiness (st = stony, bd = bedrock, and rf = rock-free).
less stable environments in which the winter-rainfall patterns were more transient during sea-level changes of the Quaternary (Siesser and Dingle, 1981; Deacon et al., 1992), particularly when the seashore on the Agulhas Bank was almost 200 km distant from the present one (Dingle and Rogers, 1972). Apart from this ambiguity, the late occupation of lowland coastal sites is inferred from all three lineages. This is thought to be a general feature of the Cape flora (Linder and Hardy, 2005) and our reconstruction for Cyrtanthus suggests this is true of extra-Cape areas as well, and may correspond with the extensive fluvial reconstruction for the primary clades, most often in the Afrotemperate clade (Fig. 7a). This latter state is shared by at least seven species.

In effect, Cyrtanthus shows greater evolutionary lability in floral symmetry and colour than any other genus of Amaryllidaceae. Changes in floral symmetry are known in the Amaryllidaceae as a whole, which led Meirer et al. (1999) to suggest that it is likely under simple genetic control. Zygomorphy (with one plane of symmetry both vertically and face on) in Cyrtanthus, however, is associated with both sternotribic and nototribic flowers. Interestingly, nototribic flowers are unknown in any other African genus of Amaryllidaceae and both states have not yet been noted in any other single genus of the family. Zygomorphy in Cyrtanthus is associated with the flowers being directed sideways through the curvature of the floral tube. This predisposes the stamens and style to further bending which changes their orientation in the mouth. From the cladogram we infer that the evolution of pronounced zygomorphy in Cyrtanthus progressed after a slight widening and marked lengthening of the perigone tube in the ancestral lineage (Fig. 8c, d). At first zygomorphy appears to have been weak but, probably through co-evolution with increasingly specialized insect visitors, sternotribic or nototribic flowers evolved. Increased zygomorphy in Cyrtanthus also appears to have been associated with the evolution of enhanced visual patterns, such as dark bands and stripes in the floral throat that are particularly characteristic of the ‘subtropical’ lineage and to a lesser extent the ‘Cape’ lineage. Fundamental to the elaboration of all these characteristics, however, was the increase in the length of the floral tube which shows recurrent development of increased floral robustness, sufficient to accommodate visits by birds.

The cladogram also points to the shift from weak zygomorphy to floral actinomorphy which is considered to be the derived state in Amaryllidaceae (Snijman, 1992). In the Cape, the large showy red flowers of C. guthrieae, C. elatus and C. montanus retain several plesiomorphic characters: a straight floral tube, no floral markings, a truncate stigma, and equally long stamens exserted from the throat, but importantly the position of the flower switched from the plesiomorphic horizontal state to an apomorphic suberect one (Fig. 8b). The erect floral position is associated with increased size and showiness, leading to perfect actinomorphy in C. guthrieae and C. montanus. The only other change towards near perfect radial floral symmetry is evident in species from the moist upland grasslands of southern Africa: in the funnel-form flowers of C. breviflorus and in the secondarily narrowed and much elongated perigone tube of C. attenuatus and C. stenanthus. Unlike the Cape species, the stamens of C. attenuatus and C. stenanthus form two distinct whorls, the derived state for Cyrtanthus (Fig. 7b).

Published observations on pollinators and inferred pollination systems based on flower types reveal that the tubular floral form in Cyrtanthus favours sunbirds and insects with long mouthparts, mainly butterflies and moths, and less often long-proboscid flies (Fig. 6). Moreover, with similar floral forms found repeatedly among the primary clades, many distantly related species appear to share the same class of pollinators,
particularly of sunbirds and butterflies. A few floral forms are, nevertheless, unique to a particular clade which possibly indicates that the selective environment for each lineage is slightly different.

Ornithophily involving sunbirds (family Nectariniidae) is inferred to have evolved one or more times in each major lineage: in the tubular, red-flowered *C. angustifolius*, *C. collinus* (Vogel, 1954), *C. contractus* (Vogel, 1954), *C. huttonii* (Vogel, 1954), *C. parviflorus* (Vogel, 1954), *C. spiralis* and *C. tuckii* (Vogel, 1954); in the tubular, red-to-dusky pink-flowered *C. carneus* (Vogel, 1954) and *C. ventricosus*; in the bilabiate, red-flowered *C. fergusoniae*...
Vogel, 1954) and C. labiatus; as well as in the orange and red-flowered C. herrei (Snijman, pers obs.) and C. obliquus (Vogel, 1954). C. herrei with its specialized laterally winged filaments has the firmest flowers of the putative ornithophilous species, and C. falcatus, which is also considered to be bird-pollinated, has a unique sharply recurved scape topped with pendulous, reddish flowers.

The high-altitude grassland species (C. attenuatus, C. stenanthus var. stenanthus and C. suaveolens) in the ‘Afrotropical’ clade have the longest and most slender floral tubes, the shortest tepals, and the most concealed stamens in the entire genus, which together with scent and pale or dull colours (sweet in C. stenanthus var. stenanthus and clove-scented in C. suaveolens), is typical of sphingid moth pollination (Vogel, 1954). The concentration of
putative sphingophilous *Cyrtanthus* species in the grasslands of southern Africa, particularly in seasonally moist habitats, follows the pattern for all southern African Amaryllidaceae (Manning and Snijman, 2002) as well as for *Satyrium* (Van der Niet, 2006). Floral scent and narrow perigone tubes have also evolved independently in two species of the ‘Cape’ clade. The cream-flowered *C. leucanthus* is inferred to be sphingophilous (Vogel, 1954), whereas the dull red-flowered *C. odorans* is regarded as noctuid moth-pollinated (Manning and Snijman, 2002).

Many other tubular-flowered species belonging to the ‘Afrotemperate’ clade are inferred to be butterfly-pollinated. They have a medium-sized floral throat (5–10 mm wide) with flowers arranged in a somewhat compact, one-sided cluster on which butterflies can settle and manoeuvre. Exclusive to four species of this primary clade is clear yellow floral colouring which butterflies can settle and manoeuvre. Exclusive to four flowers arranged in a somewhat compact, one-sided cluster on honey bees (‘features which match the brush-type syndrome (Johnson and Prosoeca ganglbauri the guild of late summer- and autumn-flowering species pollination including short-tongued bees. appears to be most suited to a variety of generalist insects, whereas the dull red-flowered *fly pollination (family Nemestrinidae) (Snijman, 1999). As yet as nectar guides that constitute the syndrome for long-proboscid these are the only *been reported for several red-flowered members of the *clade (‘syndrome is known to combine elements of both classical bird and butterfly *syndromes (Johnson and Bond, 1994) and this is reflected in the close association between the sunbird- and *A. tulbaghia butterfly-pollination syndromes in sister species of the Cape *Cytanthus. In addition, the pollination syndromes of the *A. tulbaghia butterfly, other Lepidoptera and long-proboscis flies (*Prosoeca spp.) appear to be closely linked. There is no evidence from any of the sister species pairs, however, to suggest that taxa with bird-pollinated flowers share a most recent common ancestor with those characterized by long-proboscid fly-flowers, thus morphological changes of this kind may be phylogenetically constrained in *Cytanthus.

4. Taxonomic conclusion

The difficulty of determining the species relationships in *Cytanthus* (Dyer, 1939; Reid and Dyer, 1984) is clearly a result of the evolutionary nature of the genus: one in which different lineages are inferred to have repeatedly converged on various suites of morphological characteristics, apparently as an adaptation to shared classes of pollinators. In particular, the similarity in the floral characters of the putatively bird-pollinated species that are segregated between different clades is actually greater than that among the members within each of the main lineages. Not surprisingly, there is strong incongruence between the evolutionary relationships indicated in our study and the current taxonomic treatment of *Cytanthus* (Dyer, 1939; Reid and Dyer, 1984), in which the species with bird-adapted flowers are arranged together, as are the large, red-flowered, butterfly-pollinated species. Despite greater clarity on the phylogeny of *Cytanthus*, the repeated reversals in floral morphology, however, complicate the morphological characterization of the primary clades.

Despite the lack of support by Strydom et al. (2007) for the value of chromosome morphology in identifying groups of species in *Cytanthus*, Ising’s (1970) groupings based on karyotypes correspond well with those generated by plastid *ndhF* and nrDNA ITS sequences. Ising’s groups one and two (*C. brachyscyphus, C. parviflorus, C. tuckii, C. mackenii, C. breviflorus, C. huttonii* and *C. epiphyticus and *C. stenanthus*), along with other unsampled species (*C. erubescens* Killick, *C. rotundifolius* N.E.Br., *C. obrini* Baker) correspond with members of the ‘Afrotemperate’ clade. Group three (*C. contractus, C. eucallus, C. sanguineus and *C. nutans* R.A.Dyer), which was erroneously called a form of *C. breviflorus*, falls within the ‘subtropical’ clade. Group four (*C. obliquus, C. herrei, C. falcatus and *C. flanaganii*), however, comprises elements from all three primary clades. Sharing a large habit and somewhat similar vegetative morphology, these four species resolve as sisters to the rest of the taxa in each of the primary clades to which they belong. *Cytanthus elatus* and
C. staadensis, the only Cape species in Ising’s study, were not allied to any of the above groups.

Further analysis of additional gene sequence data may strengthen support for the major clades resolved in this study, but since we consider the recognition of formal subgenera based on the present results to be premature, we propose the division of Cyrtanthus into three informal groupings, mainly as a framework for future taxonomic studies in the genus (Appendix C). Many of the species not sampled are doubtfully distinct from those included in this study, but some are undoubtedly distinct and their placement must be regarded as tentative.

Lastly, the phylogeny presented here should facilitate further critical studies on the range of pollination systems that appear to characterize the genus and thereby contribute to an understanding of the underlying processes involved in speciation.

Acknowledgements

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Appendix A

Morphological data matrix for Cyrtanthus. Characters and character states are: 1—Plants evergreen (0), deciduous (1). 2—Bulbs solitary (0), clumped (1). 3—Bulb 65–100 mm across (0), less than 60 mm across at maturity (1). 4—Leaves strap-shaped and parallel-sided (0), distinctly narrowed towards base (1), linear (2). 5—Leaf straight (0), twisted (1), spiralled (2). 6—Spathe valves 2 (0), 3 or 4 (1). 7—Flowers more or less erect at anthesis (0), deflexed sideways (1), pendulous (2). 8—Perigone tube not abruptly inflated from near the base, varying from tubular to somewhat trumpet-shaped (0), more or less abruptly inflated from near the base into a bell-shaped tube (1). 9—Perigone tube more or less straight (0), distinctly curved (1). 10—Perigone tube at least twice as long as segments (0), less than twice the length of segments (1). 11—Perigone throat 10–35 mm wide (0), 5–10 mm wide (1), 2–4 mm wide (2). 12—Perigone segments all connivent and more or less straight (0), all spreading more or less evenly (1); upper connivent and more or less hooded with lower spreading, thus somewhat bilabiate (2), all recurved and rolled back when fully mature (3). 13—Perigone segments longer than broad (0), approximately as long as broad (1). 14—Flowers red to salmon (0), pink (1), cream-coloured, pale lemon or white (2), clear yellow or greenish yellow (3). 15—Flowers not striped (0), with dark stripes leading into the throat (1), red-, pink- or green-striped on backs of segments and outside of the tube (2). 16—Flowers not scented (0), spicy or sweetly scented (1). 17—Anthers well exerted beyond perigone throat (0), just exerted from throat (1), included in throat (2). 18—Stamens weakly bisericrate to more or less uniseriate, i.e. outer anthers reaching above the base of inner anthers to both whorls almost perfectly aligned (0), strongly bisericrate, i.e. outer anthers falling short of inner anthers (1). 19—Filaments filiform (0), distinctly laterally winged towards base (1). 20—Filaments inserted in the upper half of tube (0), near the base of tube (1). 21—Style more or less regularly disposed in or from perigone tube (0), style deflected towards the upper segments (1), style curved down towards the lower segments (2). 22—Stigma minutely 3-lobed, at most 0.25 mm long (0), tricuspidate with short narrow branches, 0.5–2.0 mm long (1), tridal with long slender branches, 2.5–5.0 mm long, rarely up to 10.0 mm (2). 23—Flowering not keyed to fire (0), following fire at any time during a five-month fire season and in the absence of leaves or with leaves just emerging (1).

| Taxon                        | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|------------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Amaryllis belladonna         | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |    |
| Calostemma luteum            | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |    |
| Clivia nobilis               | 0 | na | na | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |    |
| Cyrtanthus angustifolius     | 0/1 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| C. attenuatus                | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | ? | 2 | 1 | 0 | 0 | 0 | 1 |
| C. auriculatus               | 0/1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| C. brachyscyphus             | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 |
| C. breviflorus               | 0/1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| C. carnose                   | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| C. collins                   | 0/1 | 0 | 1 | 1 | 0 | 0 | 1 | 0/1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. contractus                | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| C. debilis                   | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| C. elatus                    | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| C. ephiphyticus              | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 |
| C. eucallus                  | 0/1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 |
| C. falcatus                  | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0/1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. fergusoniae               | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. flammosus                 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 |
| C. flanaganii                | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 0 |
| C. galpinii                  | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| C. guthrieae                 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
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Appendix B

Macroecological data matrix for Cyrtanthus optimized on combined ndhF and ITS gene trees. Characters and character states are:
1—Lowlands, 0–300 m: absent (0), present (1). 2—Uplands, 300–1500 m: absent (0), present (1). 3—Highlands, 1500–3000 m: absent (0), present (1). 4—Nonseasonal, wet in any month of year: absent (0), present (1). 5—Moderately seasonal, summer-wet/winter-moist: absent (0), present (1). 6—Strongly seasonal, summer-wet/winter-dry: absent (0), present (1). 7—Seasonal, summer-dry/winter-wet: absent (0), present (1). 8—Well-drained: absent (0), present (1). 9—Seepages and stream-sides: absent (0), present (1). 10—Rock-free: absent (0), present (1). 11—Stony: absent (0), present in (1). 12—Bedrock: absent (0), present in (1).

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### Appendix C

**Proposed informal groups within the genus *Cyrtanthus* based on the results of the analysis of combined *ndhF* and ITS sequence alignments shown in Figs. 3 and 4.** An asterisk indicates taxa not included in the phylogenetic analyses. In the absence of known synapomorphies or strong morphological markers for the groups, the placement of some unsampled taxa remains tentative.

#### A.1. Gastronema group

Leaves straight or spiralled, rarely twisted. *Spathe valves* 2, rarely 3 or 4. *Flowers* deflexed sideways, rarely pendulous or suberect, red, pink, cream-coloured, pale lemon or white, mostly with dark stripes leading into throat or running along backs of segments; tube more or less abruptly inflated from near base into a bell-shaped tube above, less to more than twice as long as segments; throat mostly broad (up to 35 mm); segments more or less evenly spreading, longer than broad. *Stamens* weakly to strongly biseriate; anthers mostly exserted, rarely included in the tube. *Style* more or less evenly disposed within tube or curved downwards to lower segments; stigma minutely 3-lobed to deeply divided into 3 branches up to 5 mm long.

17 species, mostly in southern Africa, with one species extending northwards into Sudan. Found in Albany Thicket, Savanna, Fynbos, Indian Ocean Coastal Belt and Grassland Biomes, in a variety of habitats.

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<td><em>C. wellandii</em></td>
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A.2. Monella group

Leaves straight, infrequently twisted. *Spathe valves* 2, rarely 3 or 4. *Flowers* deflexed sideways or erect, rarely pendulous, red, pink, cream-coloured or pale lemon, rarely with dark stripes in throat or on backs of segments; tube narrow or widening gradually to throat, at least twice as long as segments or seldom as long; throat approximately 5–10 mm wide; segments evenly spreading or upper three connivent and more or less hooded, longer than broad. *Stamens* weakly to strongly biseriate; anthers well exserted from throat. *Style* more or less evenly disposed within tube or deflected towards upper segments; stigma minutely tricuspidate or with 3 short branches up to 2 mm long.

14 species, nearly all endemic to the Greater Cape Floristic Region, southern Africa. Most common in the Fynbos Biome, with one species in the Succulent Karoo Biome, and two species located between the Fynbos and Albany Thicket Biomes. Often in stony or rocky habitats.

- *C. carneus* Lindl.
- *C. herrei* (F.M.Leight.) R.A.Dyer
- *C. collinus* Ker Gawl.
- *C. odorus* Ker Gawl.
- *C. ochroleucus* (Herb.) Burch. ex Steud.
- *C. ventricosus* Willd.
- *C. guthriae* L.Bolus
- *C. leptosiphon* Snijman
- *C. leucanthus* Schltr.
- *C. debilis* Snijman
- *C. elatus* (Jacq.) Traub
- *C. labiatus* R.A.Dyer
- *C. montanus* R.A.Dyer
- *C. inaequalis* O’Brien

A.3. Cyrtanthus group

Leaves straight, rarely twisted. *Spathe valves* 2. *Flowers* deflexed sideways, rarely pendulous or suberect, red, pink, cream-coloured or pale lemon, white or clear yellow, without contrasting stripes; tube narrow or widening gradually to throat, less to more than twice as long as segments; throat 2–10 mm wide; segments evenly spreading or rolled back, rarely all connivent, as long as or longer than broad. *Stamens* weakly to strongly biseriate; anthers included in tube to shortly or rarely well exserted from throat. *Style* regularly disposed in tube, only rarely deflexed towards upper segments; stigma with 3 branches 0.5–2.0 mm long, rarely shorter.

24 species, mostly southern African with a few reaching East Africa and Angola. Commonly found in the Grassland Biome, less so in Savanna, Indian Ocean Coastal Belt and Fynbos Biomes, often favouring seasonally moist habitats.

- *C. flanaganii* Baker
- *C. breviflorus* Harv.
- *C. bicolor* R.A.Dyer
- *C. brachysiphon* Hilliard & B.L.Burtt
- *C. erubescens* Killick
- *C. macowanii* Baker
- *C. rotundilobus* N.E.Br.
- *C. obrienii* Baker
- *C. suaveolens* Schönland
- *C. stenanthus* Baker var. *stenanthus*
- *C. stenanthus* var. *major* R.A.Dyer
- *C. epiphyticus* J.M.Wood
- *C. attenuatus* R.A.Dyer
- *C. huttonii* Baker
- *C. parviflorus* Baker
- *C. fergusoniae* L.Bolus
- *C. brachyscyphus* Baker
- *C. flavus* P.E.Barnes
- *C. mackenii* Hook.f. subsp. *mackenii*
- *C. mackenii* subsp. *cooperi* (Baker) Snijman
References


Cunningham, C.W., 1997b. Can three incongruence tests predict when data should be combined? Molecular Biology and Evolution 14, 733–740.


