

***Cymbonotus* (Compositae: Arctotideae, Arctotidinae): an endemic Australian genus embedded in a southern African clade**

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The Compositae (Asteraceae) is the largest flowering plant family if described, accepted taxa are considered. Recent revisions in the taxonomy of the family have resulted in the recognition of ten subfamilies and 35 tribes. The tribe Arctotideae is one of the smallest, with around 200 species; it contains two subtribes and several hard-to-place taxa. Previous work has shown that the subtribe Arctotidinae is well defined and is restricted to southern Africa, except for the Australian genus *Cymbonotus*. Molecular data from internal transcribed spacer (ITS), *ndhF*, and *trnL-F* sequences were used (24 previously published sequences; 47 new sequences) to determine the patterns of relationships within the subtribe. Twenty-three samples from the ingroup, including members of all genera and all three species of *Cymbonotus*, were included in the analysis, together with two outgroup taxa. *Cymbonotus* is monophyletic and deeply embedded in the subtribe; *Haplocarpha* is paraphyletic and basal in position; all other genera are monophyletic; however, *Arctotis* has over 60 species and only eight were sampled for this study, so additional work may prove otherwise. *Arctotis* is nested high in the tree and has short branch lengths; this may reflect recent radiation. By contrast, the species of the paraphyletic and basal *Haplocarpha* have long branches, which may indicate an older radiation and a shared ancestry with the remainder of the subtribe. The presence of *Cymbonotus* in Australia is most probably the result of long-distance dispersal. Journal compilation © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, 153, 1–8. No claim to original US government works

ADDITIONAL KEYWORDS: Asteraceae – Australia – chloroplast DNA – Cichorioideae – internal transcribed spacer (ITS) – sequence data – South Africa.

INTRODUCTION

The Compositae (Asteraceae) has the largest number of described and accepted species of any family of seed plants (23 000–30 000), a global distribution, and is found in temperate and tropical habitats. Bentham's (1873a, b) 13 tribes were commonly used until DNA sequence data from chloroplast and nuclear genomes altered the classification of Compositae. First, by identifying basal clades that turned the ideas about evolution within the family upside down (Jansen *et al.*, 1991; Kim & Jansen, 1995) and, more recently, by proposed revisions dividing the family into ten subfamilies and 35 tribes (Baldwin, Wessa & Panero, 2002;

Panero & Funk, 2002). The Arctotideae belongs to the redefined subfamily Cichorioideae s.s. (Panero & Funk, 2002), which contains seven tribes: the four traditional and larger tribes (Arctotideae, African daisies; Lactuceae, dandelions; Liabeae, Andean sunflowers; Vernonieae, ironweeds) and the three small tribes (Eremothamneae, Gundelieae, and Moquineae).

The tribe Arctotideae was first recognized by Cassini (1816); however, most modern treatments of the tribe are based on the work of Bentham (1873a, b), who recognized the Arctotideae with three subtribal groups: the Euarctotideae (now the Arctotidinae), Gorterieae (Gorteriinae), and Gundelieae (Gundelinae). Hoffmann (1890) used Bentham's subtribes; he interpreted *Arctotis* L. in the broad sense, encompassing most of the modern day genera of the subtribe. Nor-

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lindh (1977) accepted the three subtribes of Bentham; however, in the most recent classification of the Arctotideae, Bremer (1994) recognized only the two main subtribes: Arctotidinae and Gorteridinae.

Funk, Chan & Keeley (2004) summarized the morphology of the subtribe, pointing out that members of the Arctotidinae (*Arctotis*, *Arctotheca* J.C.Wendl., *Cymbonotus* Cass., *Dymondia* Compton, and *Haplocarpha* Less.) can be characterized by the absence of latex, involucre bracts that are free, outermost bracts that are foliaceous with a scarious apical lamina, a receptacle that is smooth or shallowly areolate–alveolate, ligulate florets that are four-veined and three-lobed (when lobes are present), fertile ligulate florets (except for *Arctotheca*), shallowly lobed corollas on the central or disc florets, anthers without tails (except for *Arctotis*), a style with a swollen portion below the branch point, sometimes with a ring of hairs, and achenes that have three to five abaxial, well-developed ribs or wings. In addition, many species are rosette-forming, perennial herbs. Most of these characters can be considered to be plesiomorphous, with the exception of the swollen portion of the style with the ring of sweeping hairs (also found in some members of the Cardueae) and the three to five well-developed ribs or wings on the achenes. The lack of latex is also most probably apomorphic, but it comes and goes across the subfamily and it is unclear at what level it is a useful character.

Except for *Cymbonotus*, all members of the tribe Arctotideae are confined to southern Africa, and there has been some discussion amongst Australian botanists that the genus may be a recent introduction from South Africa (A. Holland, pers. comm.). *Cymbonotus* clearly belongs to the Arctotidinae, and this subtribe has strong support from both molecular and morphological data, although support for the monophyly of the entire tribe Arctotideae is weak (Funk *et al.*, 2004). A recent revision of *Cymbonotus* (Holland & Funk 2006) has indicated that the genus has three species. However, previous molecular studies used only a few taxa and only one species of *Cymbonotus*, and so the position of *Cymbonotus* within the Arctotidinae and the relationships among the five genera of the subtribe and that of the three species of *Cymbonotus* have not been investigated. A recent paper on achene morphology (McKenzie *et al.*, 2005) has indicated that the genus *Arctotis* may not be monophyletic. The goal of this study was to examine, at the species level, the systematics of the subtribe Arctotidinae, and to determine whether or not *Cymbonotus* is indeed an endemic genus from Australia.

MATERIAL AND METHODS

The study group included all species of *Cymbonotus* (three) and *Dymondia* (one), representative species of

the other genera of the Arctotidinae, and two outgroup species from two sister taxa of the Arctotidinae. A previous study (Funk *et al.*, 2004) has clearly identified the Arctotidinae as monophyletic.

DNA amplification and sequencing were performed by the junior author (R. Chan) using the methods described in Funk *et al.* (2004). The primer sequences used for polymerase chain reaction (PCR) and cycle sequencing are given in Table 1. All sequences were available for all taxa except one (*Haplocarpha ruepellii* Beauverd is missing *ndhF*), including 24 previously published sequences and 47 new sequences (see Table 2 for voucher information, species authorities, and GenBank numbers). According to Funk *et al.* (2004), the Arctotidinae has five genera; we used two species of *Arctotheca* (four species), nine samples from eight species of *Arctotis* (64 species), four samples, including all three species, of *Cymbonotus*, one sample from the monotypic *Dymondia*, and six samples from four species of *Haplocarpha* (see Table 2).

Twenty-two ingroup and two outgroup samples were used for the combined data analysis [*trnL-F*, *ndhF*, internal transcribed spacer (ITS)]. The outgroup taxa, *Didelta* L'Her. and *Hoplophyllum* DC., were determined on the basis of a tribal survey by Funk *et al.* (2004). All sequences were aligned visually, with the insertion of gaps where necessary. Maximum parsimony analysis, parsimony bootstrap [with 1000 replicate runs, each with ten random taxon additions, tree bisection–reconnection (TBR) branch swapping, and MULPARS in effect], and likelihood were performed on the aligned *trnL-F*, *ndhF*, and ITS sequences (with and without the outgroups) for each marker and for the cpDNA data and the combined data sets via full heuristic searches with PAUP* (Swofford, 2002). No weighting was used. The bootstrap runs employed 1000 replicates with branch-and-bound searches. The likelihood ratio tests were performed using the 'Tree Scores' function in PAUP* under the likelihood criterion, the Hasegawa–Kishino–Yano model of sequence evolution, and a gamma distribution of rate variation amongst sites (with the shape parameter estimated and with four

Table 1. Primer sequences used for polymerase chain reaction (PCR) and cycle sequencing

Name	Sequence (5' to 3')
ITS5a	GGAAGGAGAAGTCGTAACAAGG
ITS4	TCCTCCGCTTATTGATATGC
<i>trnL-F</i> C	CGAAATCGGTAGACGCTACG
<i>trnL-F</i> F	ATTTGAACTGGTGACACGAG
<i>ndhF</i> 1603	CCTYATGAATCGGACAATACTATGC
<i>ndhF</i> +607	ACCAAGTTCAATGYTAGCGAGATTAGTC

Table 2. Source of sequence data and GenBank numbers. Twenty-four sequences were reported in a previous study (Funk *et al.*, 2004) and are already listed in GenBank; 47 sequences are newly reported (in bold)

Sample no.	Genus	Species	Authority	Locality	Collector	No.	Herb	ITS	trnL	ndhF
Ingroup										
3	<i>Arctotheca</i>	<i>calendula</i>	(L.) Levyns	South Africa, NW Cape	Trinder-Smith	143	US	DQ889629	DQ889645	DQ889661
95	<i>Arctotheca</i>	sp.		South Africa, E Cape	Funk & Koekemoer	12266	US	AY504703	AY504785	AY504745
11	<i>Arctotis</i>	<i>acaulis</i>	L.	South Africa, N Cape	Koekemoer & Funk	1948	PRE, US	DQ889632	DQ889648	DQ889664
97	<i>Arctotis</i>	<i>angustifolia</i>	Jacq.	South Africa, W Cape	Koekemoer	2024	PRE, US	DQ889636	DQ889652	DQ889668
8	<i>Arctotis</i>	<i>bellidifolia</i>	Berg.	South Africa, W Cape	Koekemoer & Funk	1926	PRE, US	AY504704	AY504786	AY504746
12	<i>Arctotis</i>	<i>crispata</i>	Hutchinson	South Africa, NW Cape	Trinder-Smith	56	US	DQ889633	DQ889649	DQ889665
10	<i>Arctotis</i>	<i>cuprea</i>	Jacq.	South Africa, W Cape	Koekemoer & Funk	1939	PRE, US	DQ889631	DQ889647	DQ889663
14	<i>Arctotis</i>	<i>fastuosa</i>	Jacq.	South Africa, NW Cape	Trinder-Smith	238	US	AY504705	AY504787	AY504747
7	<i>Arctotis</i>	<i>laevis</i>	Thunb.	South Africa, W Cape	Koekemoer & Funk	1922	PRE, US	DQ889630	DQ889646	DQ889662
15	<i>Arctotis</i>	<i>laevis</i>	Thunb.	South Africa, NW Cape	Trinder-Smith	342	US	DQ889635	DQ889651	DQ889667
13	<i>Arctotis</i>	<i>scullyi</i>	Dummer	South Africa, NW Cape	Trinder-Smith	205	US	DQ889634	DQ889650	DQ889666
45	<i>Cymbonotus</i>	<i>lawsonianus</i>	Gaudich.	Australia, Qld	Holland & Fechner	1336	QLD, US	AY504706	AY504788	AY504748
46	<i>Cymbonotus</i>	<i>maidenii</i>	(G.Beauv.) A. Holland	Australia, Qld	Holland & Fechner	1339	QLD, US	DQ889637	DQ889653	DQ889669
145	<i>Cymbonotus</i>	<i>maidenii</i>	(G.Beauv.) A. Holland & V.A. Funk	Australia, Qld	Holland & Funk	1413	QLD	DQ889638	DQ889654	DQ889670
146	<i>Cymbonotus</i>	<i>preissianus</i>	Steetz	Australia, Qld	Holland & Funk	1414	QLD	DQ889639	DQ889655	DQ889671
53	<i>Dymondia</i>	<i>margaretae</i>	Compton	South Africa	Trinder-Smith	197	US	AY504707	AY504789	AY504749
100	<i>Haplocarpha</i>	<i>lanata</i>	Less.	South Africa, W Cape	Koekemoer & Funk	1941	PRE, US	DQ889641	DQ889657	DQ889672
139	<i>Haplocarpha</i>	<i>nervosa</i>	(Thunb.) Beauverd	Lesotho	Funk & Koekemoer	12417	PRE, US	DQ889643	DQ889659	DQ889674
76	<i>Haplocarpha</i>	<i>ruepellii</i>	Beauverd	Kenya: Meru	Robertson <i>et al.</i>	3960	MO	DQ889640	DQ889656	None
77	<i>Haplocarpha</i>	<i>scaposa</i>	Harv.	Lesotho	Trinder-Smith	191	US	AY504708	AY504790	AY504750
138	<i>Haplocarpha</i>	<i>scaposa</i>	Harv.	South Africa, Free State	Funk & Koekemoer	12401	PRE, US	DQ889642	DQ889658	DQ889673
140	<i>Haplocarpha</i>	<i>scaposa</i>	Harv.	South Africa, Free State	Funk & Koekemoer	12406	PRE, US	DQ889644	DQ889660	DQ889675
Outgroup										
109	<i>Hoplophyllum</i>	<i>spinosum</i>	DC.	South Africa, W Cape	Koekemoer	2045	PRE	AY190607	AY504784	AY504744
51	<i>Didelta</i>	<i>spinosa</i>	Aiton	South Africa	Trinder-Smith	142	US	AY504717	AY504799	AY504759

rate categories). Additional information on the methods used is given in Funk *et al.* (2004).

RESULTS

The results of the analyses for all three markers and for the combined data set were similar; most of the differences were the result of poor resolution rather than conflict. Figures 1–3 show the results of the combined analysis.

trnL-F

There were 24 parsimony informative (PI) characters that resulted in 22 trees [length (*L*), 58; consistency index (CI), 0.897; retention index (RI), 0.932]. The consensus tree did not conflict with Figure 1, but it was less resolved. All of the genera except *Haplocarpha* were monophyletic. *Dymondia*, *Arctotheca*, *Cymbonotus*, *Arctotis*, and one species of *Haplocarpha* formed a polytomy. There was no resolution amongst the species of either *Arctotis* or *Cymbonotus*.

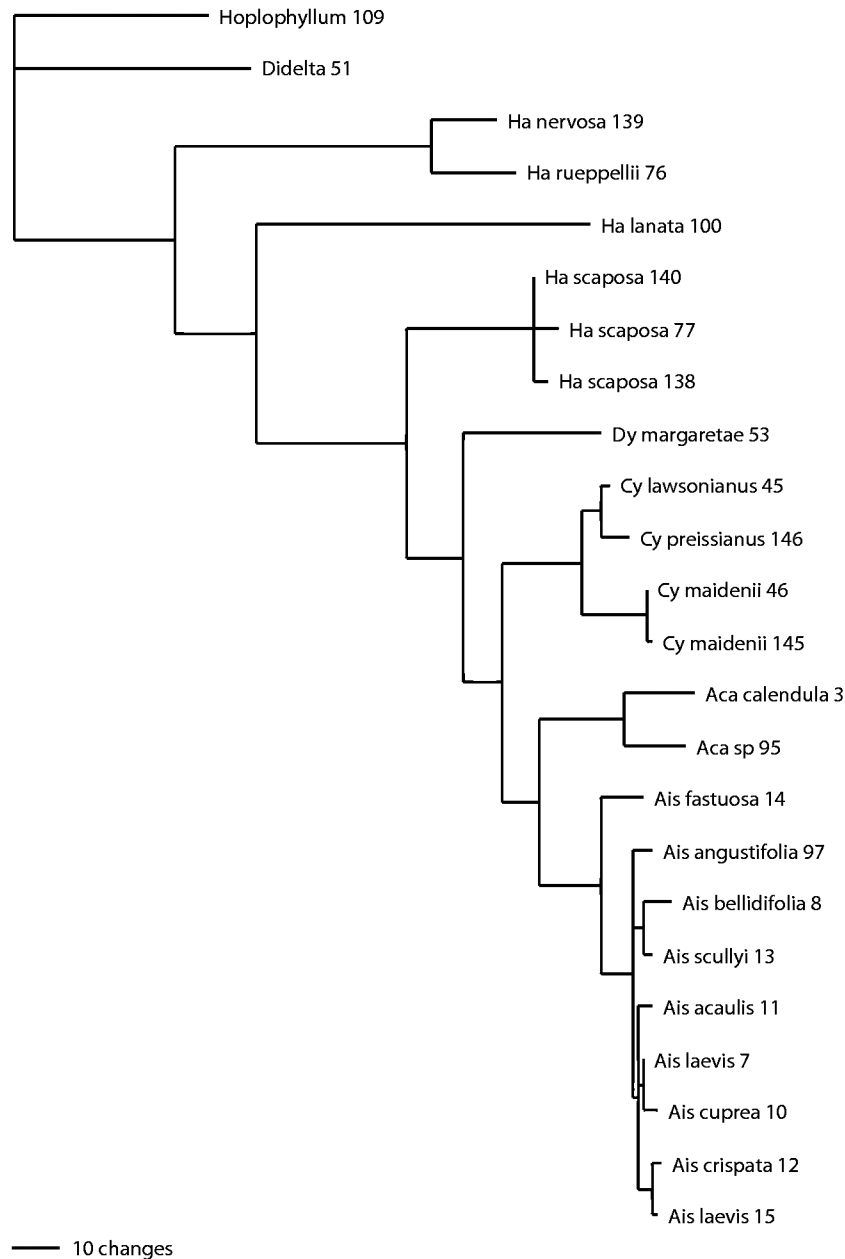


Figure 1. One of six equally parsimonious trees of the subtribe Arctotidinae based on data from internal transcribed spacer (ITS), *trnL-F*, and *ndhF* sequences. *Hoplophyllum* and *Didelta* are outgroups. *Aca*, *Arctotheca*; *Ais*, *Arctotis*; *Cy*, *Cymbonotus*; *Dy*, *Dymondia*; *Ha*, *Haplocarpha*.

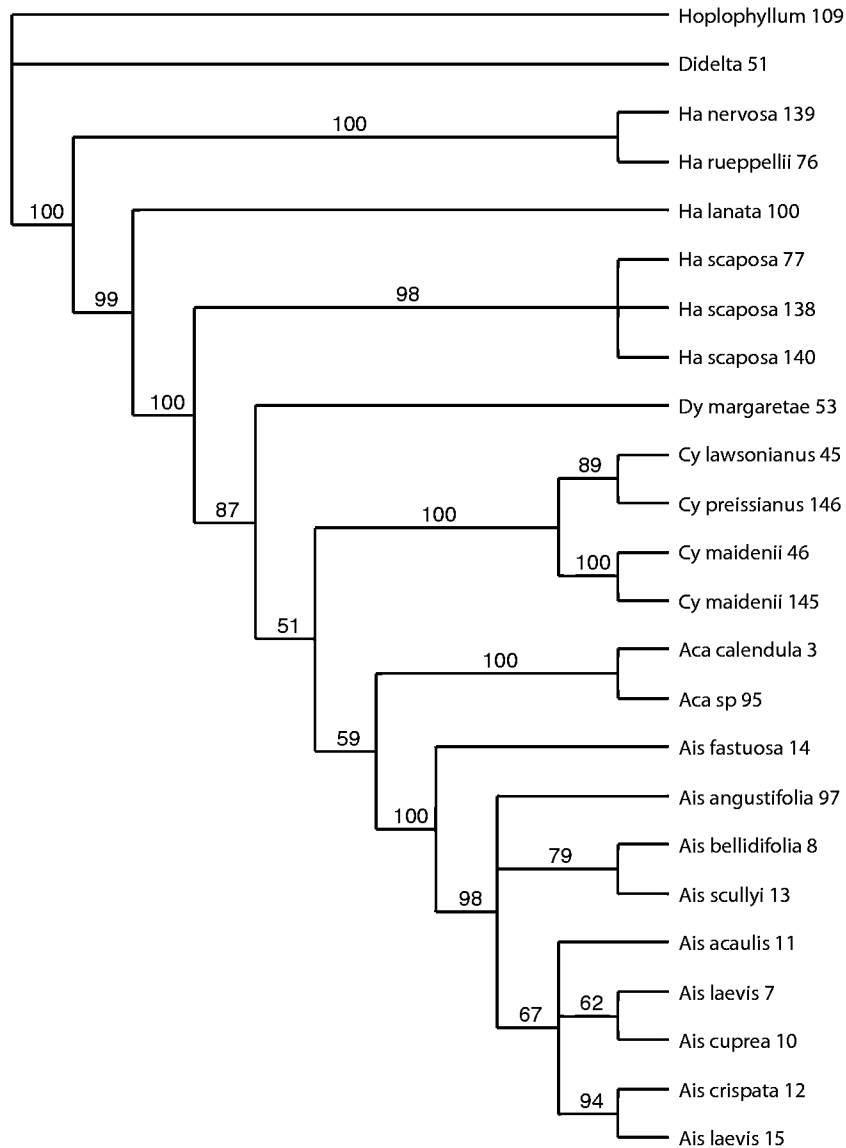


Figure 2. The strict consensus tree of the subtribe Arctotidinae (with bootstrap values) based on data from internal transcribed spacer (ITS), *trnL-F*, and *ndhF* sequences. *Hoplophyllum* and *Didelta* are outgroups. *Aca*, *Arctotheca*; *Ais*, *Arctotis*; *Cy*, *Cymbonotus*; *Dy*, *Dymondia*; *Ha*, *Haplocarpha*.

NDHF

There were 22 PI characters that resulted in one tree (L , 48; CI, 0.898; RI, 0.939). The tree differed little from Figure 1. All genera except *Haplocarpha* were monophyletic. *Dymondia*, *Arctotheca*, *Cymbonotus*, and *Arctotis* formed an unresolved group, inside of which *Dymondia* and *Arctotheca* were grouped, and there was no resolution amongst the species within either *Arctotis* or *Cymbonotus*.

CHLOROPLAST DATA SET

Neither of the chloroplast data sets contained sufficient information to fully resolve the trees. For addi-

tional resolution, the two data sets were combined to produce a larger number (46) of PI characters. The combined chloroplast analysis resulted in six trees (L , 107; CI, 0.907; RI, 0.929). The strict consensus tree and the bootstrap consensus tree were identical. All of the genera were monophyletic except *Haplocarpha*. The monophyletic group consisted of three branches: *Arctotis*, *Cymbonotus*, and the *Dymondia* and *Arctotheca* clade.

ITS

The ITS data set contained more PI characters (170) than the combined chloroplast data set and was much

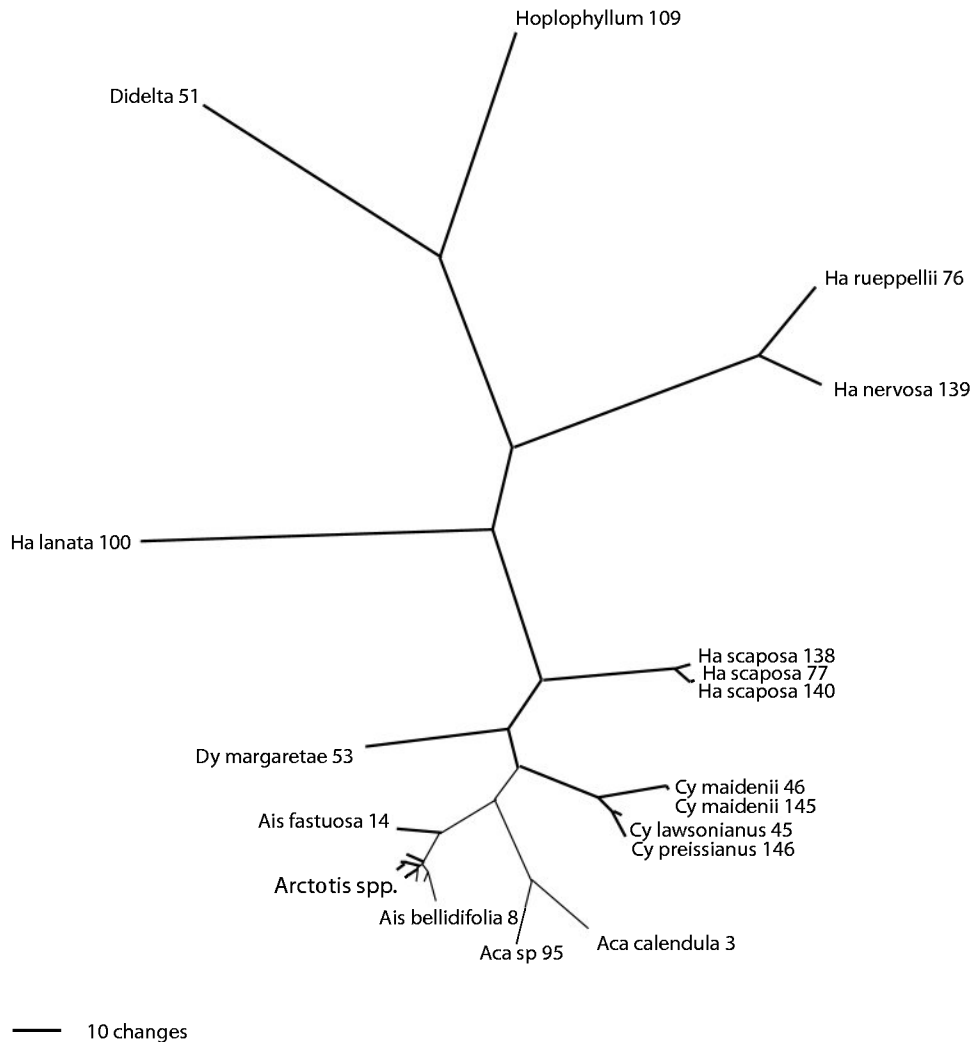


Figure 3. An unrooted phylogram of the subtribe Arctotidinae based on data from internal transcribed spacer (ITS), *trnL-F*, and *ndhF* sequences. *Hoplophyllum* and *Didelta* are outgroups. *Aca*, *Arctotheca*; *Ais*, *Arctotis*; *Cy*, *Cymbonotus*; *Dy*, *Dymondia*; *Ha*, *Haplocarpha*.

better resolved. The analysis resulted in two trees (L , 483; CI, 0.754; RI, 0.776). The results were nearly the same as shown in Figure 2 with a small difference in the placement of one species of *Arctotis*. The only conflict between the ITS trees and the chloroplast trees was that, in the ITS trees, *Dymondia* did not group with *Arctotheca*, as it did in the *ndhF* data set.

COMBINED ANALYSIS

The parsimony analysis resulted in six trees (L , 591; PI characters, 216; CI, 0.780; RI, 0.807). The six trees differed only in the relationship among the species of *Arctotis*. The maximum likelihood tree (6580.1923) was virtually identical to the strict consensus tree and is not shown. Figure 1 shows a phylogram of one of the

six equally parsimonious trees. It should be noted that the species of *Haplocarpha* form a ladder-like progression at the base of the phylogeny. Figure 2 shows a strict consensus tree with the bootstrap values (1000 replicates), and Figure 3 shows an unrooted phylogram that highlights the branch lengths and the insertion points for the outgroups. An identical ingroup phylogeny was produced when each outgroup was used separately and without outgroups.

It should be kept in mind that *Arctotis* has more than 60 species and this study contains only eight representatives; therefore, it is possible that *Arctotis* may not be monophyletic (Funk *et al.*, 2004). Recent work by McKenzie and collaborators on *Arctotis*, presented at the 2006 Meeting of TICA (The International Compositae Alliance), indicated that, although a large

number of the species of *Arctotis* are monophyletic, there are several species that are located elsewhere in the subtribe (R. J. McKenzie, pers. comm.).

DISCUSSION

The phylogeny based on the combined data set (Figs 1–3) is fairly stable. An examination of these figures reveals that *Cymbonotus* has 100% support for being a monophyletic group. Furthermore, it clearly belongs in Arctotidinae, is not part of the large radiation of core *Arctotis* or any other existing taxon, and is properly recognized as a separate genus. *Haplocarpha* is basal to the subtribe and is paraphyletic, but each species of this genus has 99–100% bootstrap support grouping it with its sister taxa. Figure 3 shows that the branch lengths on two of the *Haplocarpha* branches are quite long (indeed, they are as long as those of the two outgroup taxa) and that the outgroups are attached to the branch containing *Haplocarpha nervosa* (Thunb.) Beauverd and *H. rueppellii*. *Arctotheca*, *Arctotis*, *Dymondia*, and *Cymbonotus* are each monophyletic, and form a monophyletic group separate from *Haplocarpha*; however, the three samples of *H. scaposa* Harv. are more closely related to the rest of the subtribe than are the remaining *Haplocarpha* species. All of the genera have 100% support, except, of course, for *Haplocarpha*. Some relationships amongst the genera are not firm (Fig. 2); for instance, the combined analysis shows that *Arctotheca* and *Arctotis* are sister taxa, supported by a bootstrap value of 59, and the grouping of *Cymbonotus* with *Arctotheca* and *Arctotis* has a bootstrap value of 51. These groupings appeared in all of the trees and in the ITS analyses; therefore, we feel that it is best to use them until other data become available. Figure 3 is particularly informative because it makes no assumptions about directionality, and the relationships among the taxa are unbiased and more clearly apparent. This figure shows why *Haplocarpha* is paraphyletic, and illustrates that some of the species are on very long branches and well separated from the core genera of the subtribe.

Although the monophyly for the *Arctotis* species sampled here is strongly supported, some of the branches within the genus are short and not well supported, possibly indicating an older lineage with recent radiations. *Arctotis* is a large, variable genus with many difficult-to-distinguish species; therefore, it is not surprising that the branches within the genus are short and poorly supported. Recent work by McKenzie and coworkers (R. J. McKenzie, pers. comm.), involving many species of *Arctotis*, has indicated that, although a large core of *Arctotis* is monophyletic, there are species that group with other clades.

Given that the family is relatively young (less than 50 million years old; Funk *et al.*, 2005), it seems certain that *Cymbonotus* is the result of a long-distance dispersal event from southern Africa long after contact between the two continents ceased. This is particularly interesting for two reasons. On the practical side, it determines that *Cymbonotus* is, indeed, an endemic Australian genus and therefore can be protected. On the theoretical side, many biologists (Wagner & Funk, 1995; Carlquist, Baldwin & Carr, 2003; and references cited therein) have made much of the repeated long-distance dispersal events from western North America to the Hawaiian islands (the shortest distance is 2455 miles from Los Angeles to Hilo), but the distance from Cape Town, South Africa, to the closest point in Australia, Perth, is over twice that far (5437 miles). In a recent paper examining the Cape floral region, Galley & Linder (2006) proposed two instances of long-distance dispersal between southern Africa and Australia (Ehrharta and Restionaceae). Other claims of plant trans-Indian Ocean dispersals include Baum, Small & Wendel (1998) and Kadereit *et al.* (2005). Crisp (2006) has evaluated these proposed long-distance events with regard to the unitary view of biome assembly. All of these authors have come to a similar conclusion: long-distance dispersal is far more common than has been acknowledged for the last 20 years. It stands to reason that such documented evidence of extreme long-distance dispersal serves as a reminder that plants have the ability to travel over very long distances, and it should encourage others to find similar documented cases and so expand our knowledge of the history of biotic diversity on Earth.

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NOTE ADDED IN PROOF

A recent article has been published that is related to this topic.

McKenzie RJ, Muller EM, Skinner AKW, Karis PO, Barker NP. 2006. Phylogenetic relationships and generic delimitation in subtribe Arctotidinae (Asteraceae: Arctotideae) inferred by DNA sequence data from ITS and five chloroplast regions. *American Journal of Botany* **93**: 1222–1235.

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