

## Everywhere but Antarctica: Using a supertree to understand the diversity and distribution of the Compositae

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One of every 10 flowering plant species is in the family Compositae. With ca. 24,000-30,000 species in 1600-1700 genera and a distribution that is global except for Antarctica, it is the most diverse of all plant families. Although clearly monophyletic, there is a great deal of diversity among the members: habit varies from annual and perennial herbs to shrubs, vines, or trees, and species grow in nearly every type of habitat from lowland forests to the high alpine fell fields, though they are most common in open areas. Some are well-known weeds, but most species have restricted distributions, and members of this family are often important components of 'at risk' habitats as in the Cape Floral Kingdom or the Hawaiian Islands. The sub-familial classification and ideas about major patterns of evolution and diversification within the family remained largely unchanged from Bentham through Cronquist. Recently obtained data, both morphological and molecular, have allowed us to examine the distribution and evolution of the family in a way that was never before possible. It is now known that the tribe formerly thought to be ancestral (*Heliantheae s. l.*) is actually nested high in the phylogeny while one previously thought to be in a derived position (*Mutisieae s. l.*) is basal. Likewise, tribes previously thought to be closely related, *Eupatorieae* and *Vernonieae*, are now widely separated, and the *Cardueae* (thistles) are embedded in the African *Mutisieae* clade. The results of recent broad-scale molecular studies of the tribes, both published and unpublished, were used to produce a supertree formed by linking the respective trees together. By examining the distribution of the terminal taxa on the phylogeny using parsimony analysis with optimization and ancestral areas analysis, a biogeographic pattern emerges. Basal lineages of the family as well as the sister group *Calyceraceae*, are all South American and mostly southern South American, and it appears incontrovertible that the origin of extant members of the Compositae was in southern South America. Although numerous, these basal clades represent only a small percentage of the diversity in the family. A subsequent radiation in Africa gave rise to most of the tribes we know today. The African radiation was followed by the movement of individual clades into Asia and Eurasia as well as Australia. Finally, there was a North American origin and diversification of the *Heliantheae s. l.* that involved repeated incursions into Mexico and South America. The South American radiation followed by the African explosion might suggest a Gondwanan origin for the family, but the few data that exist from pollen records and geology seem to indicate a more recent origin for the family. The existence of the monotypic genus *Hecastocleis*, endemic to the mountains of Nevada and Death Valley, inserts a North American taxon in between the South American and African radiations which might indicate long distance dispersal, or a North American or even an Asian presence in

between South America and Africa. Also of interest is the geographic origin of the ancestor of the Heliantheae *s. l.* clade. The sister-group to the western hemisphere clade Heliantheae *s. l.* is the small tribe Athroismeae, a group of three genera from eastern tropical Africa, leaving a unknown area, possibly Asia, between Africa and western North America. This global picture of the Compositae provides a framework for studies in morphology and clearly indicates the need for future molecular and morphological studies.

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## Introduction

The Compositae (Asteraceae) contains the largest number of described species of any plant family, 24,000-30,000, distributed in 1600-1700 genera occurring on all continents except Antarctica. Estimates vary, but assuming that there are 200,000-300,000 species of flow-

ering plants, then one out of every 8-12 species of flowering plants is in the Compositae (about 10%). The family is monophyletic, characterized by florets arranged on a receptacle in centripetal heads and surrounded by bracts, by anthers fused in a ring with the pollen pushed or brushed out by the style and by the presence of achenes (cypselas) often with a pappus (Fig.

1). Although the family is well-defined, there is a great deal of variation among the members: the habit varies from annual and perennial herbs to shrubs, vines, or trees, although few are true epiphytes; the heads can have one to more than 1000 florets; chromosome numbers range from  $n=2$  to high level polyploidy with  $n=114$ ; and species grow in just about every type of habitat from forests to high elevation grasslands, however they are less common in tropical wet forests and more common in open areas. Most groups in the family contain some useful and some noxious species as well as common and rare taxa. They can be fragrant or foul, breathtakingly beautiful or nondescript. However, the general perception of this family as “weedy” is not correct. Certainly there are members that benefit from disturbance such as a few species of dandelions, goldenrods, and thistles, but most species have a restricted distribution, and just about every ‘at risk’ habitat in the world contains members of this family that are an important part of the flora. Fig. 2 is a grouping of photographs that show the diversity within the Compositae and also illustrate a number of the characters. Of particular interest are the bilabiate corollas of *Leucheria* (Fig. 2-16) characteristic of many taxa in the Mutisieae and the rolled actinomorphic corollas of *Stiffia* (Fig. 2-7; probably in the Mutisieae as well). The deeply divided corollas of many of the non-Asteroideae taxa are illustrated in Fig. 2-15. Corollas that are not deeply divided, and are often characteristic of the Asteroideae taxa, are shown in several photos (Fig. 2-9 to 11). *Acmella* is a good example of a paleaceous receptacle (Fig. 2-6). Many species in the family are woody, e.g., the species in *Montanoa* (Fig. 2-3) are shrubs or trees, and many species are herbaceous (Fig. 2-2), some are mat forming (Fig. 2-5), and others have unusual habits, such as the monocarpic *Wilkesia* (Fig. 2-1). Pollination mechanisms vary from birds to insects to wind. However, bird and Lepidoptera pollina-

tion seem to be more frequent near the base of the tree and these clades do have a lot of brightly colored flowers (Fig. 2-7, 2-8, 2-13 to 16). Throughout the family pollination is also facilitated by all types of insects, however in the more highly nested portions of the family there is less bird and Lepidoptera pollination and more bee, fly, *etc.* pollination and most flowers are yellow or white (with a few notable exceptions; Fig. 2-3, 2-5, 2-10, 2-11). When wind pollination occurs the heads can have a quite different appearance from most groups in the family (Fig. 2-12).

That the family is monophyletic has never been in question. Every early worker in plant classification recognized the Compositae as a group at some level. The distinctive inflorescence (centripetal head) often found in the striking ray/disk arrangement (Fig. 1, 2-2, 5, 10 & 11, 13 & 14) along with the fruit type (achene) and the development of the calyx into a pappus enabled everyone to accurately delimit this group (Bentham 1873a, b; Cassini 1818). In every type of analysis the results show that the family is monophyletic (*i. e.*, Bremer 1992; Hansen 1991a; Jansen & Palmer 1987; Small 1919). However, within the family things are less clear. From the beginning those who studied this family thought the ray and disk floret pattern (Fig. 1) represented the basic head structure in the family. In the classic illustration by Cassini (Fig. 3) the Heliantheae is at the center; the Vernoniaeae and Eupatorieae are at one end and the Mutisieae and Cichorieae (Lactuceae) at the other. This view persisted with some modification until the 1980’s. The treatment by Bentham (1873a) had 13 tribes (the most frequently used suprageneric rank) which remained more or less the same until the 1980’s although some of the concepts changed, especially in the Vernoniaeae, Liabeae, Senecioneae and Heliantheae-Helenieae. According to Bremer (1994), Bentham’s work was strongly influence by Cassini’s

writings, and, indeed, the 13 tribes of Bentham are a condensation of the 19-20 tribes of Cassini. Hoffmann's treatment of the Compositae (1890) essentially repeated the classification of Bentham (Bremer 1994; Turner 1977). Bentham (1873b), and more recently Cronquist (1955) and Turner (1977), all thought that the Heliantheae were the most primitive tribe of the family, and accordingly assumed that the ancestor was a perennial herb with opposite leaves and a yellow-flowered, radiate, capitula. In 1977 Cronquist allowed for a woody ancestor, as suggested by Carlquist (1966, 1976). Carlquist (1966) proposed changes to the system of Bentham but they were not adopted and the basic 13 tribes continued to be used into the 1980's. In 1975 a meeting on "The Biology and Chemistry of the Compositae" was held in Reading, England (Heywood *et al.* 1977). The proceedings from that meeting are very interesting in that the book used the Bentham system but several of the chapters made it clear that the data did not fit this scenario. A good example is the pollen paper by Skavarla (1977) where he mentions that the pollen structure of the Mutisieae is more like the closely related families and that the Heliantheae is very different. The chapter by Turner (1977) provides a good summary of the work of Bentham and Bremer's book (1994) discusses the work of Cassini.

At about the same time Wagenitz (1976) surveyed the distribution of certain characters and noted the existence of two very different groups of tribes (excluding the Lactuceae), this agreed with Carlquist's (1966) findings. In 1978 Jeffrey divided the Compositae into two subfamilies (as cited in Jeffrey 1993). The main differences among these three treatments is whether or not the Lactuceae (dandelions) is in a subfamily of its own and the placement of the Eupatorieae.

The biggest change in Composite systematics took place in the late 1980's and early

1990's and it was based on the molecular work by Jansen and Palmer (1987, 1988), Jansen *et al.* (1991a, b) and Jansen and Kim (1996). They literally turned the Compositae phylogeny upside down, showing that part of the Mutisieae was the basal branch of the family and that the tribe Heliantheae *s. l.* was nested far up in the tree. Furthermore, their work showed that the Vernonieae and Eupatorieae, long believed to be closely related, were actually in separate parts of the tree. When Bremer (1987) added the inversion character to his morphological data the base of the tree agreed with the molecular findings, however Bremer's analysis placed the Eupatorieae close to the Astereae and not the Heliantheae.

The task of understanding the phylogeny of the Compositae has come a long way since Jansen and Palmer's 1987 paper. The advent of new techniques and new markers has greatly increased the amount of sequence data available. Using a published tree for the family as a whole, and published and unpublished trees for individual clades we have constructed a supertree for the family, a tree of trees (Fig. 4, as a fould-out). It illustrates the current thinking about the relationships among the major tribes and subfamilies in the Compositae. The basal group, which is monophyletic and the sister-group to the rest of the family, is the distinctive subfamily Barnadesioideae which contains less than 1% of the species in the family. Also monophyletic is the highly nested subfamily Asteroideae, which contains ca. 65% of the species in the family. Within this subfamily a new classification system has been proposed for the large paraphyletic tribe Heliantheae *s. l.* (Baldwin *et al.* 2002). Intercalated between the two monophyletic subfamilies are groups that used to be included in the subfamily Cichorioideae (ca. 35% of the species in the family) and that vary in their morphological and molecular characters. Recently a new higher classification system has been proposed for the Cichorioideae

(Panero & Funk 2002). The Baldwin *et al.* (2002) and the Panero and Funk (2002) papers recognized new and previously described subfamilies and tribes so that now there are 10 and 35 respectively; it remains to be seen whether or not the new classification will be accepted by the Compositae community.

For such a large and interesting family, relatively little has been published on its geographic origin and diversification since Bentham (1873b). Bentham (1873b), Small (1919), Raven and Axelrod (1974), and Turner (1977) all believed that the Compositae had their origin in the northwest portion of South America, in the Andes. Rzedowski (1972) and Hu (1958) pointed out the increased diversity in the family in montane areas. Most recently Bremer (1992, 1994) developed a method called 'Ancestral Areas' analysis and came to the conclusion that the family originated in "South America and the Pacific" and Graham (1996) summarized the fossils for the family. Other than these efforts, little attention has been paid to this topic. Perhaps the size of the family and its global distribution has restricted attempts to understand its history.

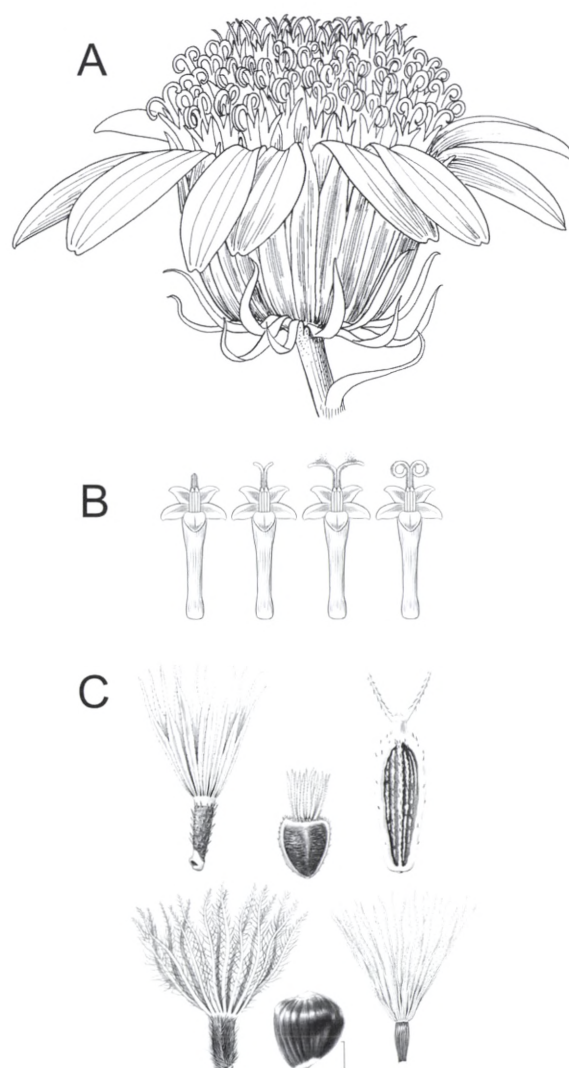
The goal of this paper is to use the most recent molecular phylogenies that are available, either from the literature or contributed by the authors as unpublished trees, to produce a supertree showing the overall phylogeny of the Compositae. The supertree makes it possible to look at the family as a whole and to try to discern its origin and his-

tory. It is also an excellent method for determining critical areas of the tree for future work.

## Materials and methods

### *Construction of the supertree*

The supertree for the Compositae was developed using a compilation of trees. Perhaps it would be best to call this type of tree a 'meta-



**Fig. 1.** Characters of the Compositae. A. The head with ray florets arranged around the perimeter, disc florets in the center, and involucre bracts surrounding the outer florets. B. The pollen is released via the style pushing out through the anthers which are fused at the margins. C. A few of the achene (cypsela) and pappus types found in the Compositae. The scale bar in C is 1 mm in length. Drawings by Alice Tangerini (US).



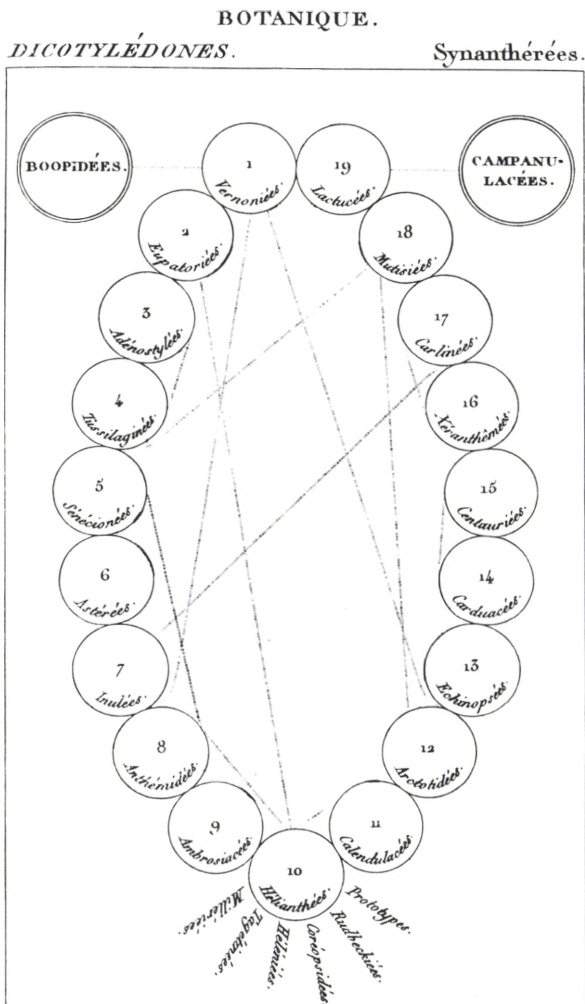
tree' rather than a supertree because it is a "tree of trees" rather than a tree produced by an analysis based on single or multiple data matrices or by analyzing tree structure. The two methods are sometimes referred to as 'supertree' and 'supermatrix'. There has been some recent discussion on the pros and cons of the two methods (Steel *et al.* 2000; Gatesy *et al.* 2002; Bininda-Emonds *et al.* 2003). Currently the supermatrix method is not a viable option for the Compositae because of the size of the family and the lack molecular markers for which we have comprehensive (or even substantial) coverage. The supertree was constructed in the following manner:

1. A 'backbone' or 'base tree' was constructed using Panero and Funk (2002) and modified slightly by Bayer (unpublished) and Funk *et al.* (in press). This tree was reduced to a matrix using Brooks Parsimony Analysis (BPA; Brooks 1982; Brooks & McLennan 2002) wherein any branching diagram can be reduced to a series of zeros and ones in a data matrix (we used MacClade; Maddison & Maddison 2001). The data matrix can then be run in a tree program (we used PAUP 4.0b10; Swofford 2002) and it will produce an exact replica of the original tree.
2. The most recent and available tree for each clade (see below) on the "backbone" tree was reduced to a matrix (using BPA) and
3. The distributions were mapped on the supertree using the Farris double pass method (1970). The results of the mapping were checked using the PAUP 'Acctran' option (Swofford 2002) and the MacClade 'Trace' option (Maddison & Maddison 2001). These techniques provided the hypothesized distributions of the deep branches and nodes. The final supertree was moved into Photoshop and each taxon branch and internode was colored as to its distribution. In essence, Fig. 4 is an 'area supertree' as opposed to an 'area cladogram'.
4. An 'Ancestral Areas' analysis, according to Bremer (1992, 1994), was performed. In an ancestral areas analysis the terminal taxa are

←

1	2	3		
4	5	6		
7	8	9	10	11
				12
13	14	15	16	

**Fig. 2.** Photographs of some members of the Compositae illustrating various characters: 1. *Wilkesia* (Madieae; Hawaii; photo by G. D. Carr), 2. *Xerochrysum* (Gnaphalieae; Australia; photo by R. J. Bayer), 3. *Montanoa* (Heliantheae; Mexico; photo by V. A. Funk), 4. *Solidago* (Astereae; USA; photo by G. D. Carr), 5. *Xenophyllum* (Senecioneae; Ecuador; photo by V. A. Funk), 6. *Acmella* (Heliantheae; photo by G. D. Carr), 7. *Stiffia* (Mutisieae *s. l.*; Ecuador; photo by G. Lewis), 8. *Stemacantha* (Cardueae; Australia; photo by V. A. Funk), 9. *Erechtites* (Senecioneae; photo by G. D. Carr), 10. *Helenium* (Helenieae; USA; photo by B. G. Baldwin), 11. *Helenium* (Helenieae; USA; photo by B. G. Baldwin), 12. *Artemisia* (Anthemideae; photo by G. D. Carr), 13. *Gazania* (Arctoteae; South Africa; photo by V. A. Funk), 14. *Philoglossa* (Liabeae; Ecuador; photo by V. A. Funk), 15. *Lychnophora* (Vernonieae; Brazil; photo by V. A. Funk), 16. *Leucheria* (Mutisieae; Argentina; photo by M. Bonifacino).



**Fig. 3.** Tribes of the Compositae and their affinities according to Cassini (1818). Note the position of the Boopidées (now Calyceraceae). [The following figure, Fig. 4, the supertree for the Compositae, is included as a separate foldout].

replaced by their distribution. The necessary gains (dispersals) and losses (extinctions) of each area on the cladogram are calculated (see Bremer 1992 for details). Bremer (1992, p. 439) states that "... if there are more losses than gains then ... the area is excluded from the ancestral area." and, "... if there are more gains than losses ... the

area is assumed to be part of the ancestral area." Appendix 1 is a list of the areas and the gains and losses for each assumption. For instance, if one assumes Brazil to be an ancestral area it would have to have been 'lost' six times. The gains are divided by the losses for a ratio and the ratio is standardized by dividing it by the largest gain/loss (2.4) to give a scale from 0 to 1(AA). A high G/L value is an indication that the area is part of the ancestral area.

### Sources of the trees.

General references for this study were Bremer (1994), Heywood (1993), Heywood *et al.* (1977), and Hind (1996).

### The Backbone or base tree

The basic structure (backbone) of the tree was taken from Panero and Funk (2002) and modified slightly based on work by Funk *et al.* (2004) and Bayer (unpublished). The tree in Panero and Funk (2002) was taken from two unpublished analyses. The overall analysis (Panero & Funk unpublished) contained extensive sampling from the base of the tree, the Mutisioideae *s. l.*, 3-10 genera representing all other tribes (including Heliantheae *s. l.*), and many taxa that had been "hard to place" in previous studies (including *Hecastocleis*, *Gymnarrhena*, and *Corymbium*). The data included DNA sequences of *ndhF*, *trnL-trnF*, *matK*, *ndhD*, *rbcl*, *rpoB*, *rpoCl*, *exon1*, *23S-trnI*, and *ndhI* for an approximate total data matrix of 13,380 bp. The analysis produced 42 trees that had only minor differences. The Heliantheae *s. l.* portion of the backbone comes from a study by Panero *et al.* (2001a, b, c, unpublished) that resulted in one tree.

**Goodeniaceae:** The second outgroup of the Compositae and the first branch on the supertree is the Goodeniaceae, a moderate sized family (14 genera, over 400 species) of herbs and some shrubs. The family is largely confined to Australia, particularly Western Aus-



tralia, with only a few species extending elsewhere, mostly in the Pacific area. A recent study (Howarth *et al.* 2003) has shown that the base of the phylogeny of the Goodeniaceae is in Australia with dispersals by members of *Scaevola* into the Pacific area, coastal areas in southern Asia and Africa, and the east coast of the Americas. The relationship between the Goodeniaceae and the Compositae is supported by recent work in both molecular (Gustafsson *et al.* 1996) and morphological (Gustafsson *et al.* 1997; Lammers 1992; Takhtajan 1987) studies.

**Calyceraceae:** The first outgroup of the Compositae, and therefore its sister-group, is the Calyceraceae, a small family (six genera, ca. 52 species) of annual and perennial herbs. The family is entirely South American, being most abundant in the Andes south from Bolivia, extending eastwards through Paraguay to Uruguay and southern Brazil and down through Argentina to southern Patagonia (Heywood 1993). The suggestion that the Calyceraceae is closely related to the Compositae was first mentioned by Cassini (1818) as reflected by Fig. 3 (Boopidées). The position of Calyceraceae as the first outgroup has been supported by both molecular (Olmstead *et al.* 2000) and morphological (Lammers 1992; Skavarla 1977; Turner 1977) studies.

**Barnadesioideae:** The subfamily Barnadesioideae is the basal group in the Compositae phylogeny. This has been known since the seminal papers by Jansen and Palmer (1987, 1988) established the presence of a chloroplast DNA inversion shared by the rest of the family, but not by the Barnadesioideae or other flowering plants. The tree for the Barnadesioideae was taken from Gustafsson *et al.* (2001) which used many terminal taxa and included eight of the nine genera found in this subfamily. All genera were monophyletic except for one disjunct species of *Dasyphyllum*; missing was the genus *Duseniella*. Gustafsson *et al.* (2001) used *trnL*

and ITS sequence data to produce a single most parsimonious tree.

**Mutisieae s. l. and Tarchonantheae:** The tribe Mutisieae s. l. has 84 genera and ca. 900 species. Its paraphyly has been suggested by morphological studies (Cabrera 1977; Hansen 1991b) and supported by the first molecular studies of the family. First the sub-tribe Barnadesiinae was recognized as being basal to the family and the sister-group to the rest of the family (Jansen & Palmer 1987, 1988), and then it was elevated to the rank of sub-family (Bremer & Jansen 1992). Later, Kim and Jansen (1995) and Kim *et al.* (2002) made apparent that there were several clades in the remainder of the tribe. Most recently Panero and Funk (2002) published a new phylogeny that confirmed that the Mutisieae was paraphyletic and elevated several groups within the tribe to sub-family and tribal levels; subfamilies Gochnatioideae, Hecastocleioideae, Pertyoideae, and Gymnarrhenoideae were described along with the tribe Dicomeae which is placed, along with the genus *Oldenburgia* and the previously described tribe Tarchonantheae, in the sub-family Carduoideae. The remaining clades of the Mutisieae s. s. may still be paraphyletic, for while it is likely that the *Mutisia* clade and the *Nassauvia* clade form a monophyletic group it remains to be seen whether or not the *Stiffitia* clade will need to be recognized at the subfamily level. The branching sequence of the clades and individual genera of the Mutisieae were taken from the multi-gene study by Panero and Funk (2002) and the relationships among the taxa within each clade were taken from the *ndhF* studies of Kim *et al.* (2002). The 34 genera on the tree represent 40% of the generic diversity in the tribe.

**Cardueae:** The Cardueae (thistles; 74 genera, ca. 2,500 species) are now known to be nested within the paraphyletic Mutisieae s. l. This tribe is the sister-group to the Tarchonantheae and/or the genus *Oldenburgia* (Kim *et*

*al.* 2002; Panero & Funk 2002). The tribes Cardueae, Tarchonantheae and Dicomeae along with the genus *Oldenburgia* are a monophyletic group. The Cardueae tree used for the supertree was taken primarily from Garcia-Jacas *et al.* (2002) but also from Garcia-Jacas *et al.* (2001) and Garcia-Jacas *et al.* (unpublished). Their work has shown the tribe to be monophyletic and it has provided a well-supported overall phylogeny. The original analyses were based on ITS and matK sequence data from many taxa representing ca. 56 genera, or approximately 75% of the generic diversity in the tribe. Thirty genera (41%) were included in the supertree with sampling coming mostly from the basal areas of the tree (Garcia-Jacas *et al.* 2002). More recently Garcia-Jacas *et al.* (unpublished) have added additional taxa and used new information to change the outgroup used in the study. The changing of the outgroups has rearranged the base of the tree to some extent and this new basal rearrangement is included in the supertree.

**Cichorieae (Lactuceae) and Gundelieae:** The phylogeny of the dandelion tribe Cichorieae (Lactuceae) has long presented a problem. In 1995 Whitton *et al.* did a preliminary phylogeny of the Lactuceae and more recently, Lee *et al.* (2003) worked on the North American members. Now a two gene phylogeny of the whole tribe is nearing completion (Gemeinholzer pers. comm.). The Lactuceae tree used in this study was provided by Gemeinholzer (Gemeinholzer & Bachmann 2003, submitted, unpublished) and was based on ITS data. The position of *Gundelia* (Gundelieae) as basal to the Lactuceae was suggested by Karis *et al.* (2001) based on *ndhF* data, and the position of *Warionia* as the sister taxon to *Gundelia* was suggested by Panero and Funk (2002); the positions of *Gundelia* and *Warionia* at the base of the Lactuceae were confirmed by Funk *et al.* (2004). Sixteen genera are included in the tree representing 16% of

the generic diversity. Lee *et al.* (2003) showed that the tribal name Cichorieae has priority over Lactuceae, however because we discuss the subfamily Cichorioideae several times it seemed less confusing to use the more common name Lactuceae for the tribe in the discussion section of this paper.

**Arctoteae (Arctotideae) and Eremothamneae:** The tribe Arctoteae (African Daisies) is a diverse and interesting group with a primarily southern African distribution (ca. 15 genera, 160 species). The closely related tribe, Eremothamneae (2 genera, 3 species) is also a part of this clade. These two tribes are especially important in that most of the species are found in the Cape Flora Kingdom, the smallest floral kingdom, which is the subject of intense conservation interest. The tree for this study was taken from a recent paper by Funk *et al.* (2004) where the tree is based on *ndhF*, *trnL-trnF* and ITS sequence data. The Eremothamneae is monophyletic and confined to southern Africa (Karis 1992). The Arctoteae is only weakly supported as monophyletic but the subtribes are strongly supported as clades. Because all of the basal taxa in each subtribe are in southern Africa, the monophyly of the Arctoteae does not affect the biogeographic outcome of our study. All 17 genera were covered in the paper but only nine have been included in this study representing 53% of the generic diversity. Current investigations seem to indicate that the name Arctotideae has priority over the more commonly used Arctoteae but this is not yet confirmed.

**Liabeae:** The Liabeae is a monophyletic Neotropical tribe containing approximately 180 species distributed in 16 genera and occupying a wide variety of habitats throughout Mexico, Central America, the West Indies, and the Andes. The greatest diversity in the tribe is found in Peru, where no fewer than 13 genera and over 70 species are represented. After a long history of moving from tribe to tribe, the

current members were brought together by Robinson (1983). A previous morphological analysis resolved a northwestern Andes origin (Funk *et al.* 1996). The tree for our study was based on Kim *et al.* (2003) and Funk (unpublished) and contains eight genera representing 50% of the generic diversity.

**Vernonieae:** The tribe Vernonieae with 98 genera and 1300 species has until recently had most of its species in the large and complicated genus *Vernonia* (Jones 1977). However, the tribe has been the subject of recent revisions that concentrated on the breaking up of *Vernonia* (e.g., Robinson 1999), first in the Americas and more recently in Africa. Sometimes referred to as the “evil tribe” by those who try to work with its members, using either molecular data or morphology, it is finally being examined using multiple molecular markers (Keeley & Chan unpublished). The tree used for this study was provided by Keeley and Chan (unpublished) and is based on *ndhF*, *trnL-trnF*, and ITS sequence data. The study has shown that the tribe is clearly monophyletic. This study includes 36 taxa but the number of genera in the tribe is in flux at the moment, and it is impossible to accurately estimate the percentage of coverage.

**Senecioneae:** The Senecioneae is the largest tribe with over 3000 species (Nordenstam 2003a) and it proved to be the most difficult clade tree to produce. There are seven phylogenies based on molecular data involving various parts of the tribe, each with a scattering of taxa from elsewhere in the tribe (Bain & Golden 2000; Coleman *et al.* 2003; Kadereit & Jeffrey 1996; Knox 1996; Knox & Palmer 1995; Pelsner *et al.* 2002; Swenson & Manns 2003). The number of taxa common to all phylogenies was very small so the trees were compared two at a time in various combinations until a pattern developed. This pattern agreed with the overall pattern in most of the studies. *Blennosperma* of the Blennospermatinae,

believed to be the basal group in the tribe, is always used as the outgroup. Its position has been tested only in a small study with two species of the Senecioneae (Swenson & Bremer 1999), so its location at the base has not been confirmed. One genus, *Blennosperma* has been included in several studies using *ndhF* (Kim & Jansen 1995; Swenson & Bremer 1999) and it comes out at the base of the Senecioneae, but the sample size within the tribe is small. Highly nested in the phylogeny is the largest clade, the Senecionoid group. It is monophyletic and contains most of the genera and species. Between these two groups is a mostly unresolved grade that includes some members of the Tussilaginoideae assemblage. Since most of these papers are based, at least partially, on ITS sequence data the trees are all more resolved at the end clades than at the base. Because the taxa at the base of the tree are from many parts of the world and because the relationships among them are not resolved, the base of the Senecioneae is indicated as unresolved. However, the unresolved nature of the base of the Senecioneae does not affect the family-wide biogeographic pattern. The tribe has 138 genera according to Nordenstam (2003a); the final tree contained 33 taxa, several of which were species in the large genus *Senecio*.

**Gnaphalieae:** The tribe Gnaphalieae has about 187 genera and 1250 species which have their greatest diversity in Southern Africa, Australia, and South America. The tree for this study was provided by Bayer (unpublished). It is based on three cpDNA sequences (*matK*, *trnL* intron, and the *trnL-trnF* spacer). A total of 88 genera were available for this study (47% of the generic diversity) but only 32 (18%) were used. Most of the genera not used were from members of a large monophyletic radiation in Australia.

**Calenduleae:** Sister to the Gnaphalieae is the Calenduleae with eight genera, seven of which

have distinct centers in South Africa; most of the species occur in the Cape flora area (Nordstrom 2003b). One genus, *Calendula*, is in North Africa and the Mediterranean north to central Europe and east into Iran and Turkey. Three genera (33% of the generic diversity) were sequenced by Bayer (unpublished) in order to establish an outgroup for the Gnaphalieae.

**Anthemideae:** The members of the tribe Anthemideae are mainly north temperate and Old World. The tribe has 109 genera and ca. 1740 species. Molecular work using *ndhF* (Watson *et al.* 2000) and ITS (Watson *et al.* 2002) and summarized by Watson (2003, unpublished) have provided a phylogeny that can be used for the supertree. There are 39 genera (36% of the generic diversity) in the supertree; many more genera are available in Watson's work but we did not use all members of the large radiations in East Asia and the Mediterranean.

**Astereae:** With 170 genera, ca. 3000 species, and a worldwide distribution, the Astereae is the second largest tribe after the Senecioneae. It has centers of diversity in southwestern North America, the Andes, South Africa, Australia and New Zealand. In 1996 Lane *et al.* published a preliminary analysis of the North American members of the tribe using chloroplast DNA restriction site data. Two recent studies for the tribe exist (Noyes & Rieseberg 1999; Cross *et al.* 2002) both based on ITS sequence data. The first paper focused on North American members of the tribe with seven outgroup taxa. The second focused on the Pacific genus *Olearia* and it had 23 other genera represented in the analysis. There was some overlap in taxa and a consensus tree was constructed of the two trees. The consensus tree contains 22 taxa representing 18 genera (ca. 10% of the generic diversity); some genera are polyphyletic.

**Inuleae and Plucheeae:** The Plucheeae has

28 genera and 220 species and is pantropical; the Inuleae has 38 genera and 480 species and is found in the Old World, mainly Eurasia. It is now known that the members of the Plucheeae, although monophyletic, are nested within the Inuleae. Because the two are treated in the same clade they are addressed together under the tribe name Inuleae. The tree for this study was provided by Bayer (unpublished) and is based on three cpDNA regions (*matK*, *trnL* intron, and the *trnL-trnF* spacer). A total of nine genera were used in this study, 14% of the generic diversity of the two tribes.

**Athroismeae, Heliantheae s. l., and Eupatorieae:** The newly described tribe Athroismeae is the sister group to the large and diverse clade that contains the Heliantheae s. l. and Eupatorieae. The three genera (two were included in the supertree) in the Athroismeae are centered in eastern tropical Africa and were in the Inuleae until moved to the Helenieae (Eriksson 1991). The tribe Eupatorieae is nested in the Heliantheae s. l., and as a result the Heliantheae has recently undergone a dissection into 12 tribes (Baldwin *et al.* 2002; Panero & Funk 2002). Bremer (1994) divided this part of the family phylogeny into three groups, Helenieae (including Athroismeae; 110 genera, ca. 800 species), Heliantheae (189 genera, ca. 2500 species), and Eupatorieae (170 genera, 2400 species) but recognized that the groups would need to be re-arranged once additional information was available. Both the Helenieae and Heliantheae of Bremer proved to be non-monophyletic and Baldwin *et al.* (2002) and Panero and Funk (2002) described additional tribes. The Eupatorieae was maintained as a separate tribe. The tree for this large section of the family has 120 genera out of 459 and so represents 26% of the generic diversity of this group. The tree for this clade in the supertree was formed by using the backbone of Panero and Funk (2002) for the relationships among the tribes; the branching

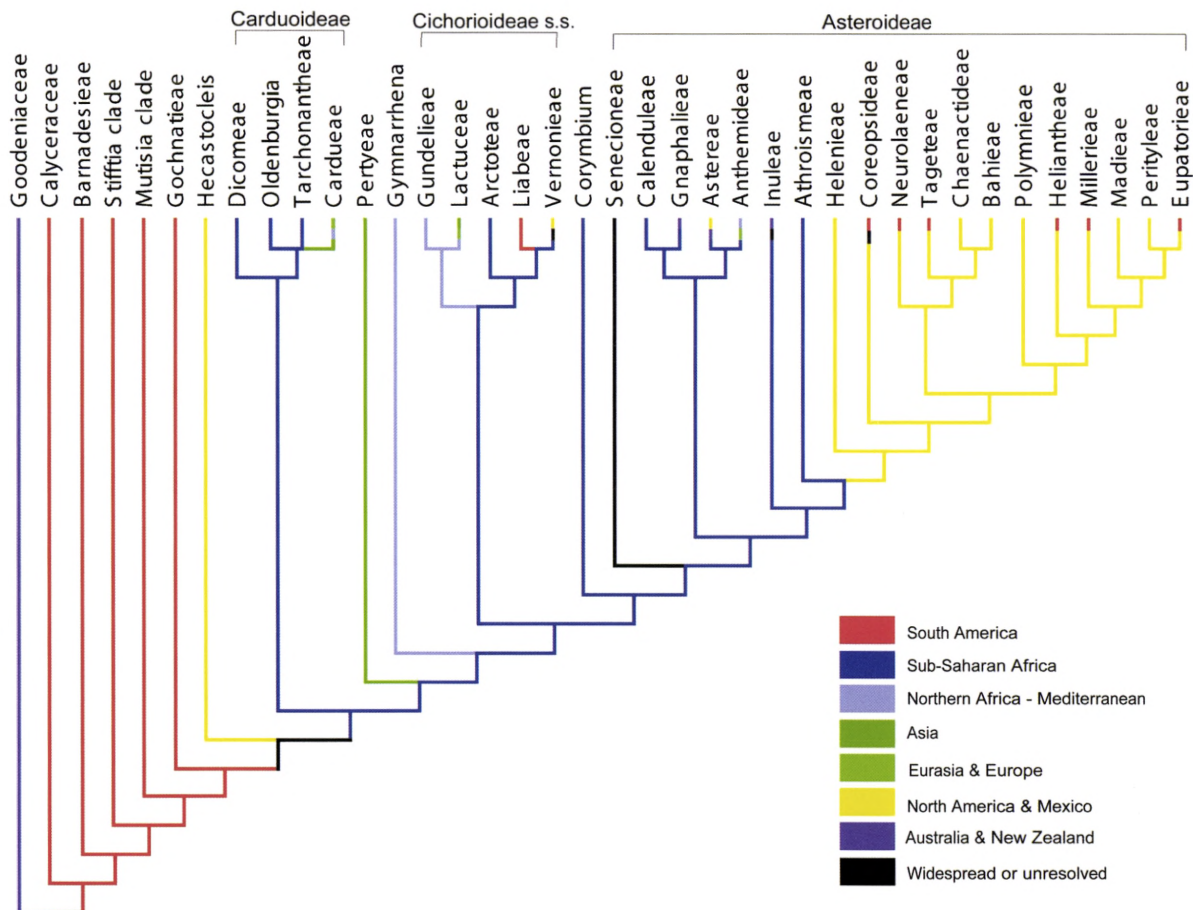
within each tribe of the former Heliantheae *s. l.* was taken from Baldwin *et al.* (2002). The branching within the Eupatorieae was taken from Schmidt and Schilling (2000) and Schilling (unpublished), and is congruent with results published by Ito *et al.* (2000a, b) for the tribe. Baldwin *et al.* (2002) focused on the members of the former tribe Helenieae and their study was, therefore, less representative of the paleaceous members from the former Heliantheae, although every attempt was made to cover the diversity. Because the members of the Helenieae form the basal grade, the under-

representation of the paleaceous members does not present an obstacle to the biogeographic analysis.

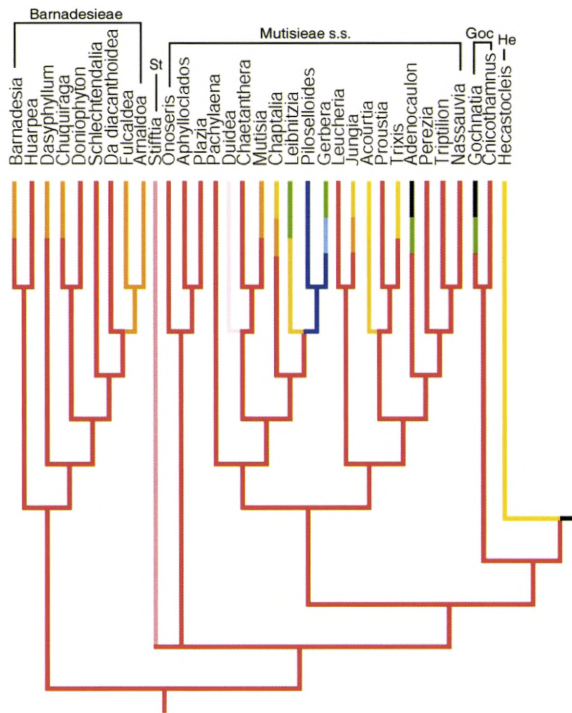
## Results and discussion

### *Parsimony Optimization Analysis*

The distribution of each terminal taxon is indicated on Fig. 4 by the color of the branch; taxa that span more than one area have multiple colors. The internodes were colored using the double pass method of Farris (1970), the ACC-TRAN routine from PAUP (Swofford 2002)



**Fig. 5.** The supertree (Fig. 4, as separate foldout) has been reduced in size by having tribes as terminal taxa. Also, the number of biogeographic areas has been reduced by combining areas.



**Fig. 6.** The supertree (Fig. 4) has been broken up into three grades and a clade. The reduced version of the supertree (Fig. 5) is used to show the positions of these Grades and Clade.

Shown in this figure is Grade 1 which forms the base of the tree from the Barnadesoideae through the genus *Hecastocleis* (the internodes have been compressed). Most of the members of this grade have a southern South American distribution but note that *Hecastocleis* is from North America. St = *Stiffia* clade, Goc = Gochnatieae, He = Hecastocleidae.

and the “Trace” routine from MacClade (Maddison & Maddison 2001). Most areas of the cladogram could be resolved with one or all three of these methods, but two areas in particular could not and were left black. A reduced tree (Fig. 5) was produced with fewer biogeographic categories and with only one branch for each major clade or important taxon.

In order to more easily discuss the tree it has been broken into parts. Grade 1 (Fig. 6), which is primarily southern South American, forms the base from just above the outgroups to just past the genus *Hecastocleis*. Grade 2 (Fig. 4), is an African grade with repeated radiations into Asia, Eurasia, Europe, *etc.* It begins above *Hecastocleis* and covers the central part of the supertree up through the tropical east African group, the *Athroisma* clade. This is a very large grade, and in order to examine it in better detail it has been divided into two subgrades. Grade 2a (Fig. 7) begins with the African Mutisieae and thistle clade (*Carduoideae*) and ends after *Corymbium*. Grade 2b (Fig. 8) begins with *Senecioneae* and ends after *Athroismaeae*. Clade 3 is North American, Mexican and South American and encompasses all of the *Heliantheae s. l.*, including the *Helenieae* and *Eupatorieae*.

#### *Grade 1 (Fig. 6):*

The sister group of the *Compositae* (Fig. 4 & 5) and the first outgroup, the *Calyceraceae*, is from southern South America. The basal branch of the *Compositae* is the subfamily *Barnadesioideae* (Fig. 6). Gustafsson *et al.* (2001) examined the biogeography and concluded that their analyses showed “... unambiguously that the *Barnadesioideae* as a whole are originally southern Andean ...” Our analysis agrees with Gustafsson *et al.* (2001). The next clade is the *Stiffia* clade which is in southern South America and Brazil. The large *Mutisieae* clade (including the *Nassauvia* clade) contains mostly southern South American taxa, however, it also contains *Gerbera* and *Piloselloides* from Africa, taxa that are in North America (*e.g.*, *Acourtia*), and *Leibnitzia* which is in China and Mexico. The final clade is the newly described tribe *Gochnatieae* (Panero & Funk 2002) which contains genera mainly from southern South America and Brazil. It is clear from the optimization that the extant taxa in

Grade 1, which form the base of the Compositae supertree, have their origin in southern South America. The last taxon in Grade 1 is the monotypic North American (Nevada and Death Valley) genus *Hecastocleis* which will be discussed in more detail below. The internode between the southern South American grade and the African middle of the tree (Grade 2) is unresolved as to origin because there are no areas shared among the three (South American Mutisieae, African base of Grade 2, and North American *Hecastocleis*). A species level analysis of the new tribe Gochnatieae (4-5 genera) and its relationships to *Hecastocleis* may provide some insight into the problem because one of the genera (*Gochnatia*) is found in South, Central and North America as well as having two species in Asia.

#### *Grade 2a (Fig. 7):*

The basal clade in this area of the supertree is the African Mutisieae-thistle clade (Carduoideae). The African Mutisieae consist of *Dicoma* and its relatives which form one subclade that is basal. The genus *Oldenburgia*, and the small tribe Tarchonantheae (*Tarchonanthus* and *Brachylaena*) are in a trichotomy with the Cardueae (thistles). *Gerbera*, which is from Africa as well as Asia, is not in this group, it is nested in the South American Mutisieae near the base of the tree. The thistle tree has a base that can be resolved as Asian with a significant presence in Northern Africa and Eurasia and, to a lesser extent, Europe. Many of the genera are found in two or more of these areas. So, this clade has an African base with a large radiation beginning in Asia followed by radiations into North Africa, Eurasia, and Europe.

The next clade on the supertree is the Asian Mutisieae (recently described as the tribe Pertyeae; Panero & Funk 2002); the taxa are found in Asia from Afghanistan through India to China, Korea and Japan. All Asian Mutisieae (genera that are restricted to Asia) are found

in this clade except *Nouelia* and *Leucomeris* which are sister-taxa in the Mutisieae *s. s.* near the base of the tree (Panero & Funk 2002).

Just after the Pertyeae is the monotypic genus *Gymnarrhena* (North Africa to the Middle East) which stands by itself.

The final clade in this grade is the Cichorioideae *s. s.* This large clade contains six tribes: the Gundelieae and Cichorieae (Lactuceae) are sister taxa and form a clade; the Arctoteae and Eremothamneae (the latter is nested within the former) are a second clade; and finally the Liabeae and Vernonieae are sister taxa and form a clade. The Liabeae-Vernonieae are the sister group of the Arctoteae-Eremothamneae. The Cichorioideae *s. s.* is a strongly supported group but the three major clades within it are not particularly close to one another, and all are on rather long branches (Funk *et al.* 2004). The Gundelieae (*Gundelia* and *Warionia*) is from northern Africa-Mediterranean-southern Europe, and the basal taxa from the Lactuceae are likewise from that area. From this northern African-Mediterranean base, the Lactuceae repeatedly spread into Eurasia, Asia and Europe. Nested in the Lactuceae is a monophyletic radiation in North America. In fact, Lee *et al.* (2003) state that all 23 genera of Lactuceae with centers of diversity in North America (and *Picrosia* from South America) represent a single, major radiation based in North America. This radiation is represented on the tree by *Microseris* and *Uropappus* (Fig. 7). The Arctoteae (including Eremothamneae) is almost wholly southern African and according to Funk *et al.* (2004) and all others who have worked on the tribe, the extant taxa have a southern African origin. The tribe Liabeae is believed to have an origin in northern Peru with a few separate small incursions into Central America and one clade each in Mexico (*Sinclairia*) and the Caribbean (*Liabum*) (Funk *et al.* 1996). The sister taxon of the Liabeae is the Vernonieae and it has a trop-

ical African base (including a significant presence in Madagascar) with a monophyletic new world radiation, first into Brazil and on into other parts of South America and then a monophyletic radiation into North America (Keeley & Chan unpublished). The unusual North American genus *Stokesia* is not in this main North American clade and its position is unresolved. With the exception of the Liabeae, every clade in the Cichorioideae s. s. has its origins in Africa, either north, tropical or southern, in effect covering the whole continent. The final resolution of the clade was a southern African base because of its close proximity to other branches from southern Africa. However, this resolution is somewhat weak and so it is drawn on the supertree as either Southern African or Northern African. Once the reduced area cladogram was produced (Fig. 5) with all of sub-saharan Africa a single area, there was no question that the origin of this subfamily was African.

The final taxon in Grade 2a is the genus *Corymbium* which is restricted to southern Africa and forms a very important anchor for the next section of the supertree.

*Grade 2b (Fig. 8):*

This section begins the Asteroideae, the largest subfamily in the Compositae. It is distinctive with its capillary pappus and true rays and was recognized by Cassini (1818) and Bentham (1873a). The basal branch for this section of the supertree is the Senecioneae. The Senecioneae tree that was used for Fig. 4 was a consensus tree from seven different studies most of which had different taxa near the base and so in the supertree the base of the Senecioneae is unresolved. Also, all the studies used part of the Senecioneae (usually *Blennosperma*) as the outgroup, so the actual base of the Senecioneae has not been firmly established. The two major groups within the Senecioneae, the subtribe Tussilaginatae

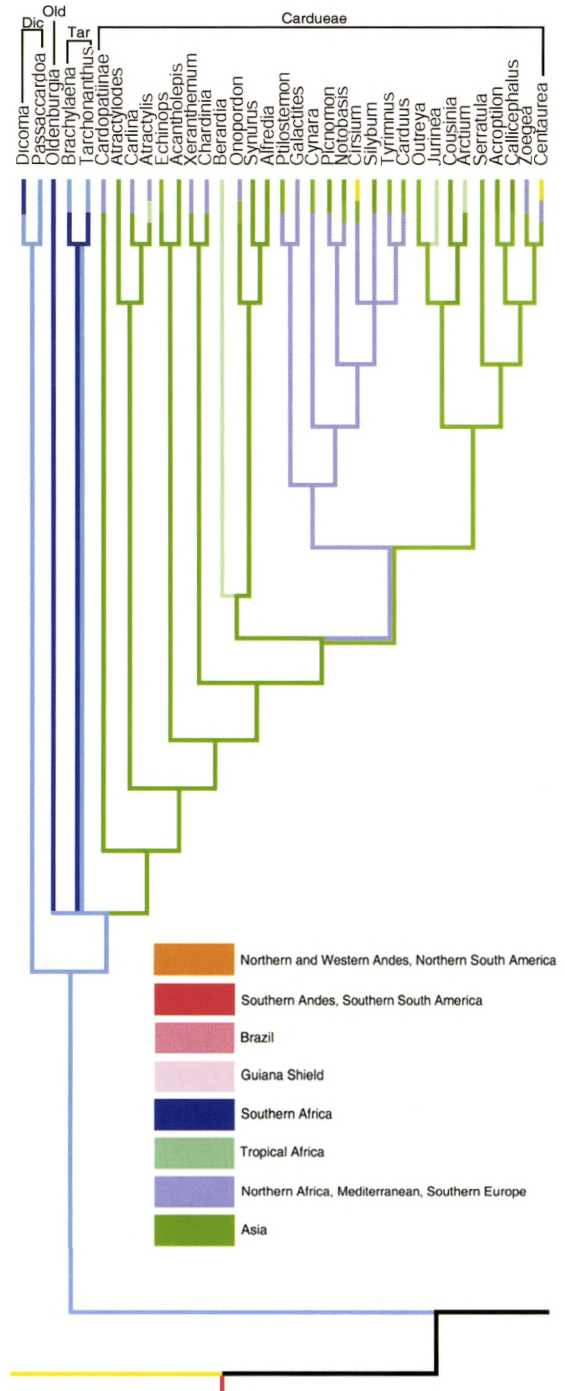
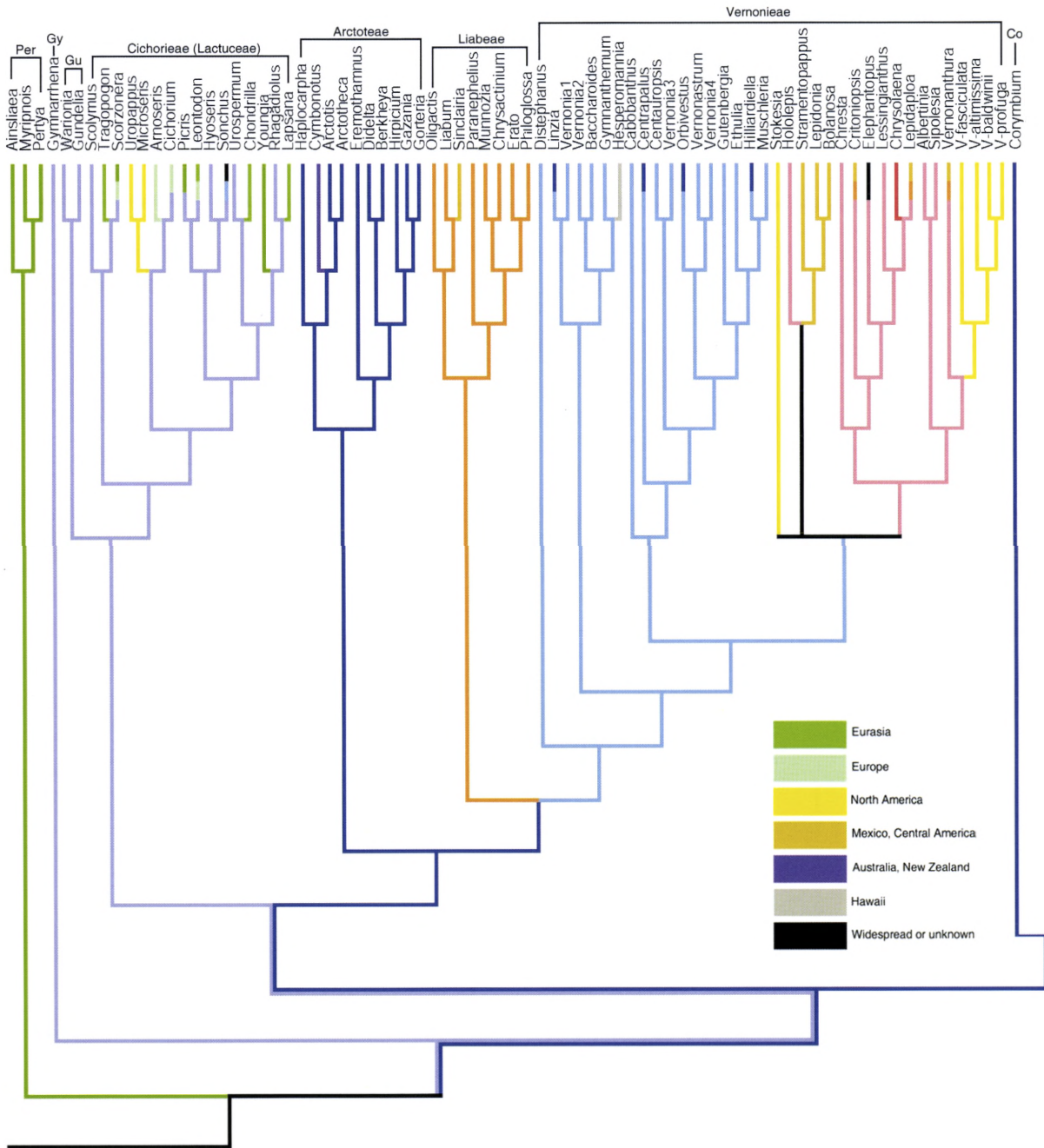


Fig. 7 (left hand part) – For legend, see opposite page.





**Fig. 7 (right hand part).** The supertree (Fig. 4) has been broken up into three parts. Grade 2 is an African grade with repeated radiations into Asia, Eurasia, Europe, *etc.* Its size has made it necessary to further divide it into two sub-grades. Shown in this Figure is Grade2a which begins with the African Mutisieae and thistle clade (Carduoideae) and ends after the Cichorioideae *s. s.* and the stem genus *Corymbium* (the internodes have been compressed). Dic = Dicoemeae, Old = Oldenburgia, Tar = Tarconantheae, Per = Pertyeae, Gy = Gymnarrheneae, Gu = Gundelieae, Co = Corymbieae.

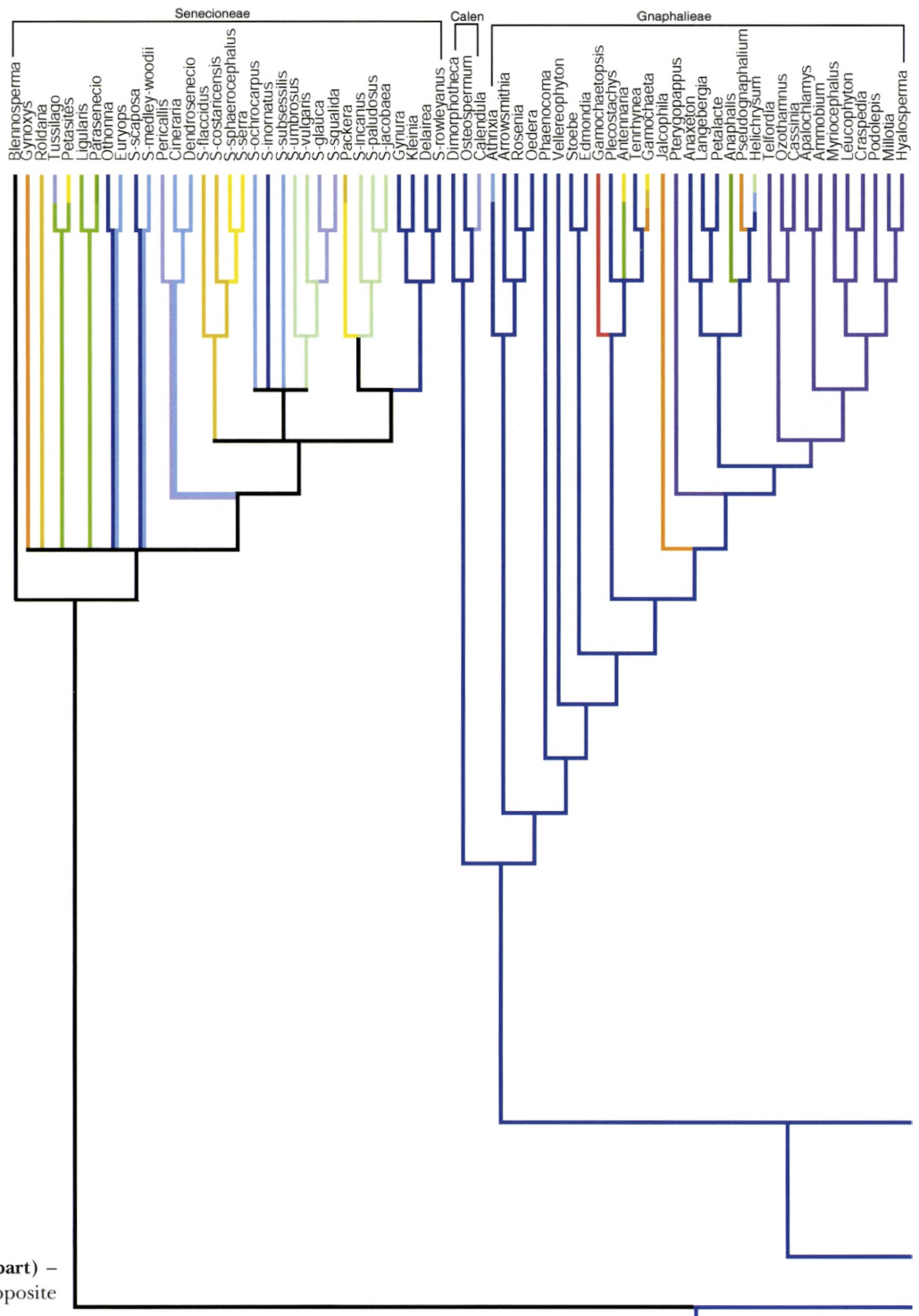
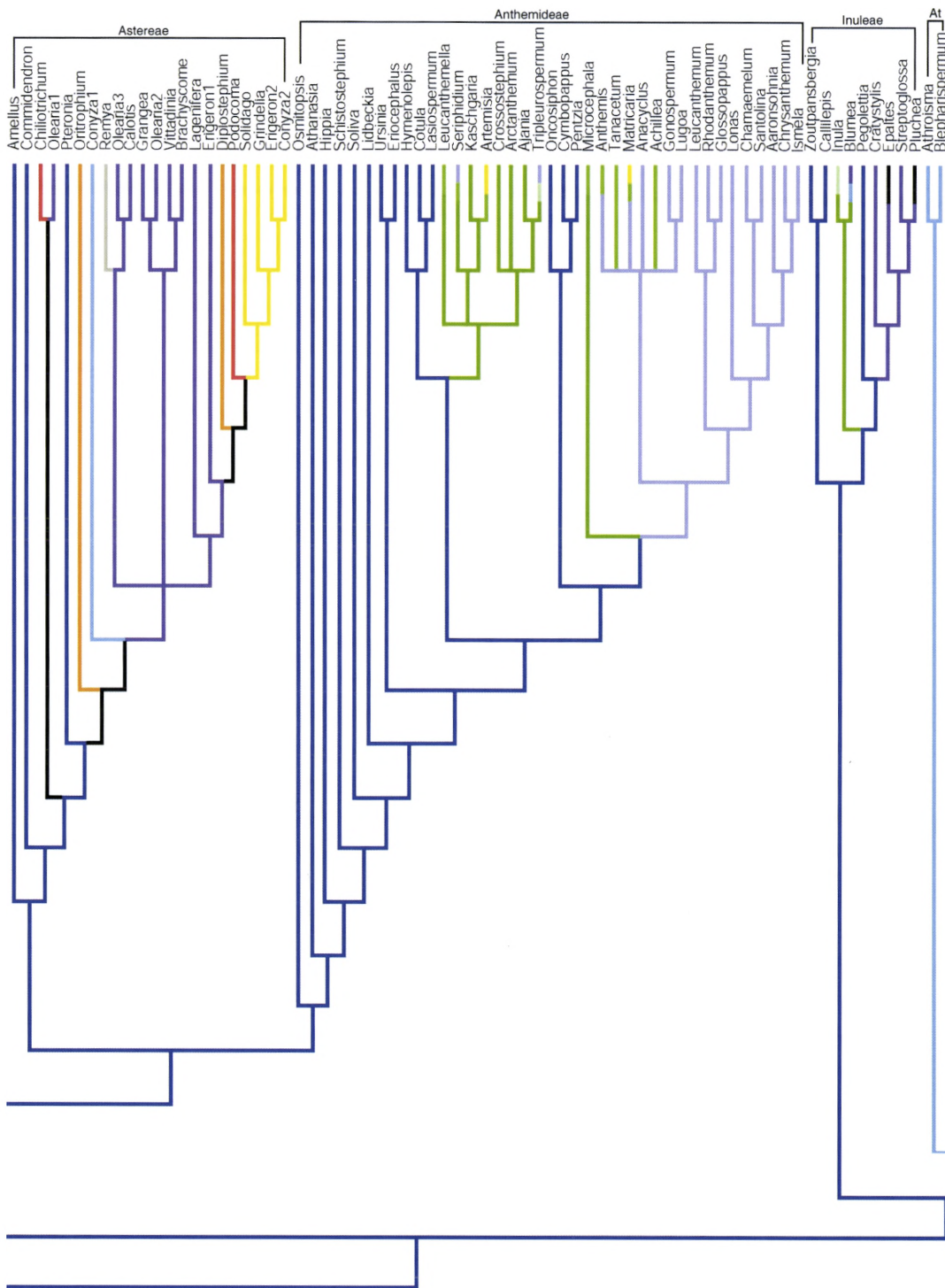


Fig. 8 (left hand part) –  
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**Fig. 8 (right hand part).** The supertree (Fig. 4) has been broken up into three parts. Grade 2 is an African grade with repeated radiations into Asia, Eurasia, Europe, *etc.* Its size has made it necessary to further divide it into two sub-grades. This figure is Grade 2b which begins with Senecioneae and ends after the Athroismeae (the internodes have been compressed). Calen = Calenduleae, At = Atroismeae.

(probably a basal grade) and the Senecioninae (a clade) are consistently found in all studies. The Tussilagininae has an African core and the Senecioninae has an African base with monophyletic radiations in South Africa, Europe, North America, and the Mediterranean. The subtribe Blennospermatinae is primarily Pacific but also North and South American. Because of the clades surrounding it, the Senecioneae probably had an African base, but it is the weakest part of the supertree. Nordenstam, Kadereit, and Watson are collaborating on sequencing projects with a tribal perspective, and it is hoped a better resolution will be available for the next version of the Compositae Supertree.

A major clade containing four tribes, three of which are large, follows the Senecioneae. The small tribe Calenduleae is southern African in origin and is the sister taxon of the Gnaphalieae, which has a southern African grade at the base of its tree. Included in this tree are the genera of the Gnaphalieae from the African basal groups, members of the subtribes Angianthinae, Cassiniinae, Gnaphaliinae, Loricariinae, and Relhaniinae, and African and Australian representatives from the large Old World genus *Helichrysum* s. l. The Relhaniinae, which are restricted to Africa, are not a monophyletic group as presently circumscribed, nor are the Cassiniinae and Gnaphaliinae (Bayer *et al.* 2000, 2002). Results also indicate that the primarily Australian subtribes Angianthinae and Cassiniinae are non-monophyletic as currently circumscribed. In most trees the Relhaniinae s. s. and some of the basal taxa comprise a clade that is sister to the remainder of the tribe Gnaphalieae. Sister to the Relhaniinae are clades of African, South American, North American, and European taxa that are primarily woody perennials often found at montane to high alpine elevations. Sister to these clades is a large clade representing the major radiation of Australian, primarily

herbaceous, annual taxa mainly from the subtribe Angianthinae. Therefore, these two tribes, Calenduleae and Gnaphalieae, have a solid southern African origin.

Sister to the above pair of tribes are the Astereae and Anthemideae. After the Senecioneae, the Astereae is the least well-understood tribe. Lane *et al.* (1996) covered only North American taxa which were also the subject of one of the more recent papers (Noyes & Rieseberg 1999); we used the more recent results in this study. The two recent studies available for the Astereae (Cross *et al.* 2002; Noyes & Rieseberg 1999) used substantially different sets of taxa. The consensus tree, based on the trees for the two recent studies, has an African base, an Australia-New Zealand grade in the middle, and a monophyletic radiation into North America. There are several separate disparate locations of South American taxa. Noyes and Rieseberg (1999) showed that "... all North American Astereae are members of a strongly supported clade, and that a diverse group of predominantly woody taxa from Africa, Australia, and South America are basal Astereae." Several taxa (*e.g.*, the southern African genus *Felicia*) had to be left out of the tree because they had conflicting positions. Also, Cross *et al.* (2002), although they focused on Pacific taxa, used a large assortment of genera in the tribe and showed that several large genera are non-monophyletic (*Olearia*, *Conyza*, *Erigeron*). Clearly, the Astereae is in serious need of attention, and several groups of researchers are working on it. As with the Senecioneae, it is hoped that by the time of the next version of the Compositae supertree some of these issues will be resolved.

Sister to the Astereae is the Anthemideae. Watson and her collaborators (Watson *et al.* 2000, 2002, 2003) have shown that the tribe has a southern African grade at the base as well as an Asian clade, a Eurasian clade, and a large Mediterranean radiation. There are also clades

in Asia and the Mediterranean. The Calenduleae and Gnaphaleae have a southern African base; the Astereae has an African base, with a southern African taxon at the very base, and the Anthemideae a southern African base. The result is a southern African base for the four tribes that form this major clade of the supertree.

The next clade on the supertree (Fig. 4) is the Inuleae (including the Plucheeae). Basal in this clade are two southern African genera formerly thought to be part of the Gnaphalieae. Within the Inuleae there is an Asian clade and a pantropical clade (Plucheeae represented here by *Pluchea*, *Streptoglossa*, and *Epaltes*). Interestingly the Australian genus *Cratystylis*, which has often been difficult to place (Bremer 1994), is sister to the Plucheeae (Bayer & Cross 2003).

The final clade in this section of the supertree (Fig. 4) is the new tribe Athroismeae which includes a few genera from tropical east Africa. This small clade is sister to the large Heliantheae *s. l.* clade that follows.

#### *Clade 3 (Fig. 9):*

The Heliantheae *s. l.* (including the Eupatorieae and Helenieae) has recently been broken up into 12 tribes (Baldwin *et al.* 2002; Panero & Funk 2002), some new and some described in the past. This large clade contains over 25% of the genera in the family and is predominantly American, with a large representation in western North America and Mexico. The supertree (Fig. 9) shows clearly that the base of the tree is North American; however, what it does not show is that approximately 50% of the genera in the basal clade (now the tribe Helenieae) have a distribution of southwest US and northern Mexico. This agrees with Baldwin *et al.* (2002) who said, "... the most recent common ancestor of taxa referable to Helenieae *s. l.* (and to Heliantheae *s. l.* + Eupatorieae) ... probably occurred in southwestern North

America (including northern Mexico)." Baldwin *et al.* (2002) also point out that the endemic California diversity in this tribe is mostly confined to one clade, the Madieae. Within the Heliantheae *s. l.* clade there are many different incursions into South America, especially in the northwestern Andes, and there are even more than indicated in this supertree because the work of Baldwin *et al.* (2002) focused on the Helenieae *s. l.*, which is a North American group. The concentration of taxa in the Heliantheae *s. l.* in the northwestern Andes played an important role in early estimates of the origin and diversification of the Compositae (summarized by Turner 1977). However, it is clear that the origin of this large and important clade is centered in western North America. The sister group to the Heliantheae *s. l.* is the Athroismeae, which is the last branch from the African portion of the supertree (Fig. 4). What happened between Africa and North America is not known but since the base of the Heliantheae is in western USA and northwest Mexico one could speculate that it might have come to North America via Asia.

The reduced tree (Fig. 5) shows the results of the mapping of the distributions. In this tree several areas were combined: tropical Africa and southern Africa were combined into one area, Sub-Saharan Africa (blue); all South American areas were combined into one area (red); and North America and Mexico were combined (yellow). In this reduced tree it is even more evident that the extant Compositae had a South American base with an African diversification and radiation into Asia, Eurasia, Europe, Australia, *etc.* followed by the burst of diversity in North America.

#### *Ancestral Areas Analysis*

Bremer (1992, 1994) performed an 'Ancestral Areas' analysis based on his cladogram for the Compositae. His cladogram focused on the

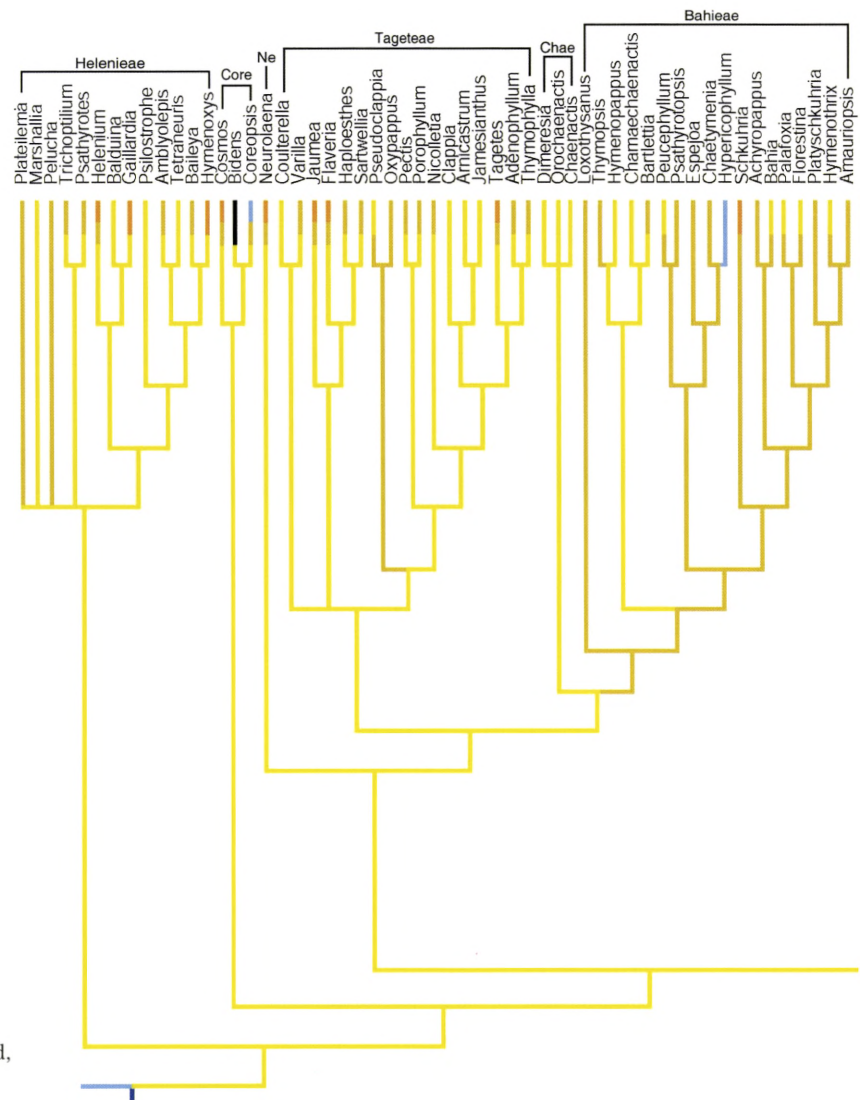
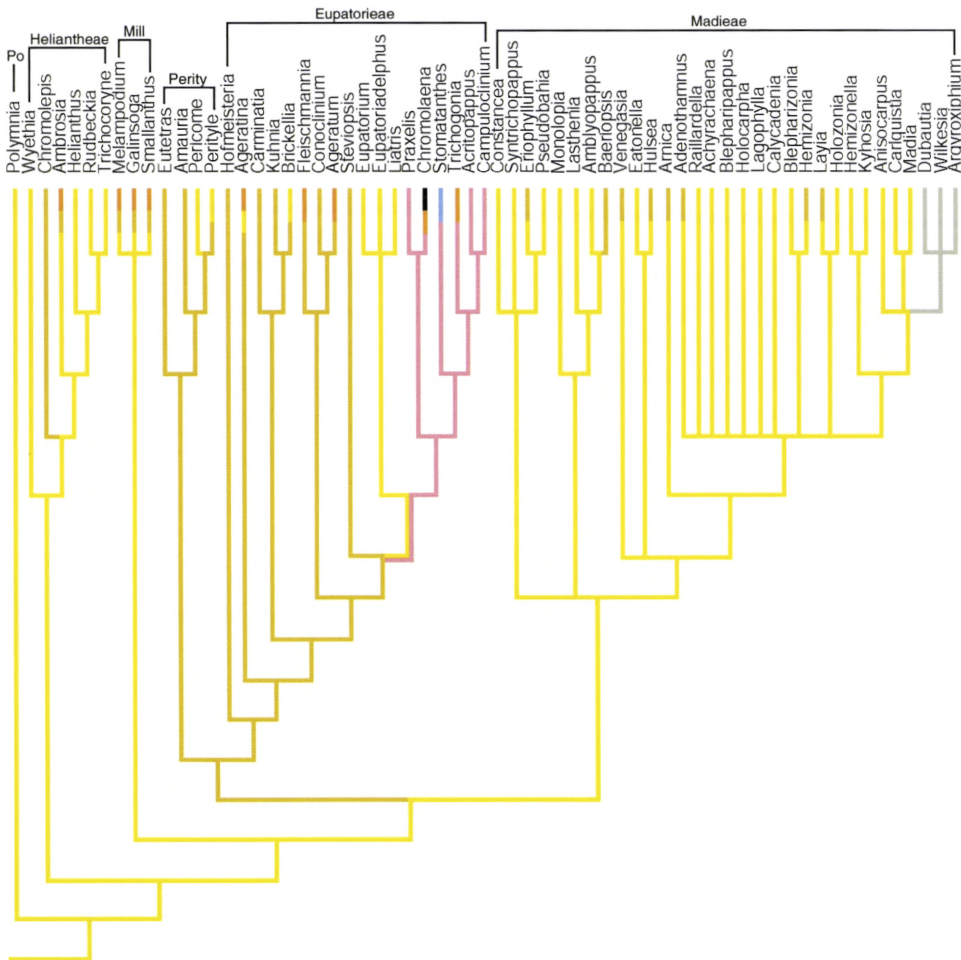


Fig. 9 (left hand part) – For legend, see opposite page.

base of the tree and was based on morphological data. In an ancestral areas analysis the terminal taxa are replaced by their distribution. The necessary gains (dispersals) and losses (extinctions) of each area on the cladogram are calculated (see Bremer 1992 for details). Bremer's results (1994) suggested that the most likely position of the ancestor was in southern Brazil, followed by a category designated the 'Andes, Patagonia, Guiana Shield,

and the Hawaiian Islands'. Other areas were deemed less likely. He concluded that the geographic origin of the Asteraceae probably involved South America and the Pacific. However, he was misled by several factors. First, *Hesperomannia* (endemic to Hawaii) was at that time thought to be in the Mutisieae; it is now known that it is nested higher up in the tree in the *Vernonieae* (Keeley & Chan unpublished, Kim *et al.* 1998). Second, the Mutisieae from



**Fig. 9 (right hand part).** The supertree (Fig. 4) has been broken up into three parts. This figure shows Clade 3 which is primarily in North America, Mexico and South America and encompasses all of the Heliantheae *s. l.*, including the Helenieae and Eupatorieae (the internodes have been compressed). Core = Coreopsidae, Ne = Neurolaeneae, Chae = Chaenactideae, Po = Polymineae, Mill = Millerieae, Perity = Perityleae.

the Guiana Shield are now known to be nested in two southern South American clades. Third, the molecular cladogram is somewhat different than Bremer's morphological one. Finally, in our study South America was broken up into more than one area. All these taken together predicted that the current 'ancestral areas analysis' would produce different results. Fig. 10 represents the base of the tree (following Bremer's method) with some taxa eliminated if

they provided no new information (see Fig. 4 & 6). Bremer (1992, p. 439) states that "... if there are more losses than gains then ... the area is excluded from the ancestral area." and "... if there are more gains than losses ... the area is assumed to be part of the ancestral area." Appendix 1 is a list of the areas and the gains and losses for each assumption. For instance, if one assumes Brazil to be an ancestral area there would have to have been eight

losses (extinctions). The gains are divided by the losses for a ratio, and the ratio is standardized by dividing it by the largest gain/loss (2.4) to give a scale from 0 to 1. A high G/L value is an indication that the area is part of the ancestral area. By all three criteria, southern South America is viewed as the most likely candidate for the position of the ancestral area. The tree used in the ancestral areas analysis was also run using the 'Trace' option of MacClade (Maddison & Maddison 2001) with the same result, southern South American was the estimated area for the base of the tree, indeed for the whole tree.

The 'Parsimony Optimization' and the 'Ancestral Areas' analysis provided the same answer to the question on the origin and diversification of the family; extant Compositae originated in southern South America.

#### *Odd Genera*

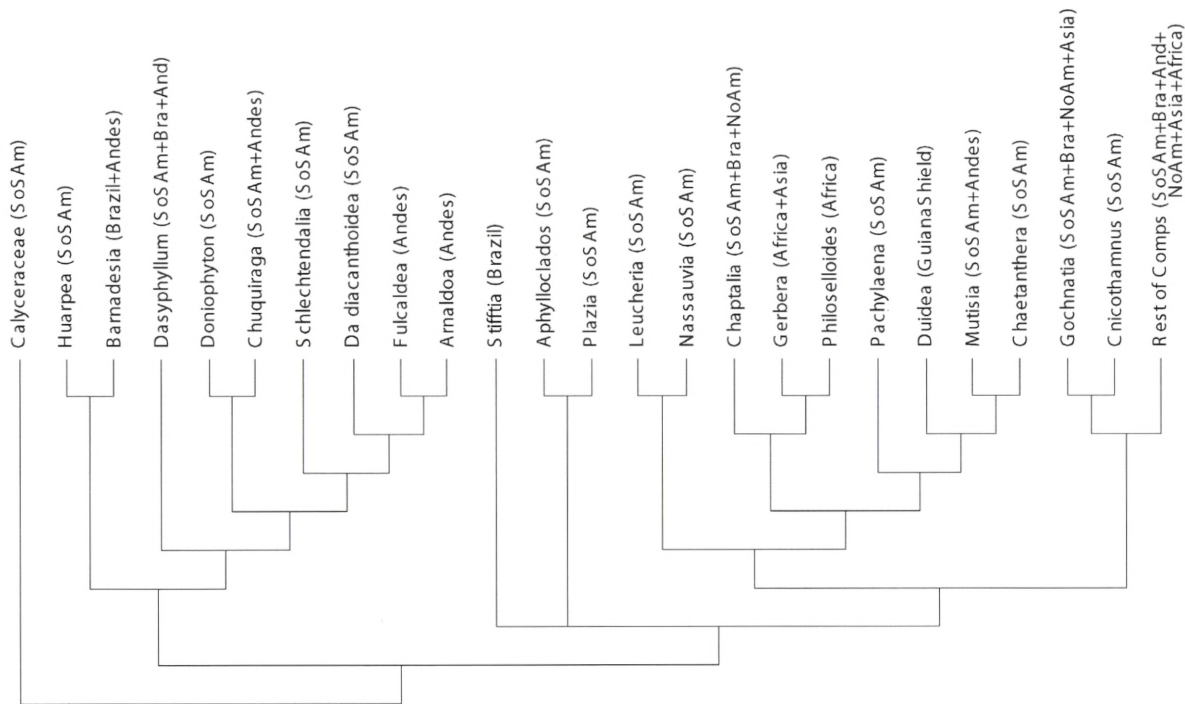
Throughout the history of the classification of the Compositae there have been a number of genera that are difficult to place. These genera were usually grouped with taxa that they were "less different from" than anything else. It is interesting to note that many of these 'odd' taxa have secondary or tertiary heads in that they have been reduced to one or a few florets per head and then re-aggregated onto another common receptacle. As a result they usually lack ray florets and do not have the common involucre and receptacle characters. The lack of basic characters has made it difficult to use morphology to place these taxa. The advent of molecular data has allowed us to determine the location of many of these taxa on the tree. Some that have relevance to the biogeography of the family are discussed here. Their positions have turned out to be among the more interesting aspects of this study because they are frequently at the base of large radiations: *Cratystylis* at the base of the Plucheeae, Athroismeae at the base of the Heliantheae *s. l.*, *Corym-*

*bium* at the base of the Asteroideae, *Gymnarhena* at the base of the Cichorioideae – Asteroideae, the African Mutisieae at the base of the thistles, and *Hecastocleis* at the base of the major radiation of the family. Each of these either reinforces or resolves the biogeographic hypothesis from that section of the tree except, of course, *Hecastocleis*. This same clarification also arose from the placement of other odd genera at the base of smaller radiations such as the location of *Gundelia* at the base of the Lactuceae. All of these have important positions for the biogeographic analysis because they anchor radiations and as a result show clearly that odd taxa should always be included in analyses at all levels.

#### *Age of Origin*

Considering the size and importance of the Compositae, surprisingly little has been published about the possible area of its origin or its age since Bentham (1873a, b). Estimates of the time of origin of the Compositae vary from Miocene (20 Mya) to Cretaceous (100 Mya) or earlier (Turner 1977). It is probably safe to say that most authorities agree that based on pollen data (Germeraad *et al.* 1968; Muller 1970), most of the current tribes were in existence by the end of the Oligocene (22- 25 Mya; Muller 1981). An older date is given by Graham (1996) who dates *Ambrosia*-type pollen as late Eocene to early Oligocene (25-35 Mya). This was followed by an explosive evolution of species in the Miocene. By late Miocene (5 Mya) most of the current genera of Compositae were present (Raven & Axelrod 1974; Turner 1977). The comparatively recent origin and great diversity of the Compositae are indicative of the competitive success of the family. Turner (1977) felt that the family's "... rich secondary metabolite chemistry, often short life cycle, facultative pollination, and freedom from many co-evolutionary restraints may be responsible for this success." Turner



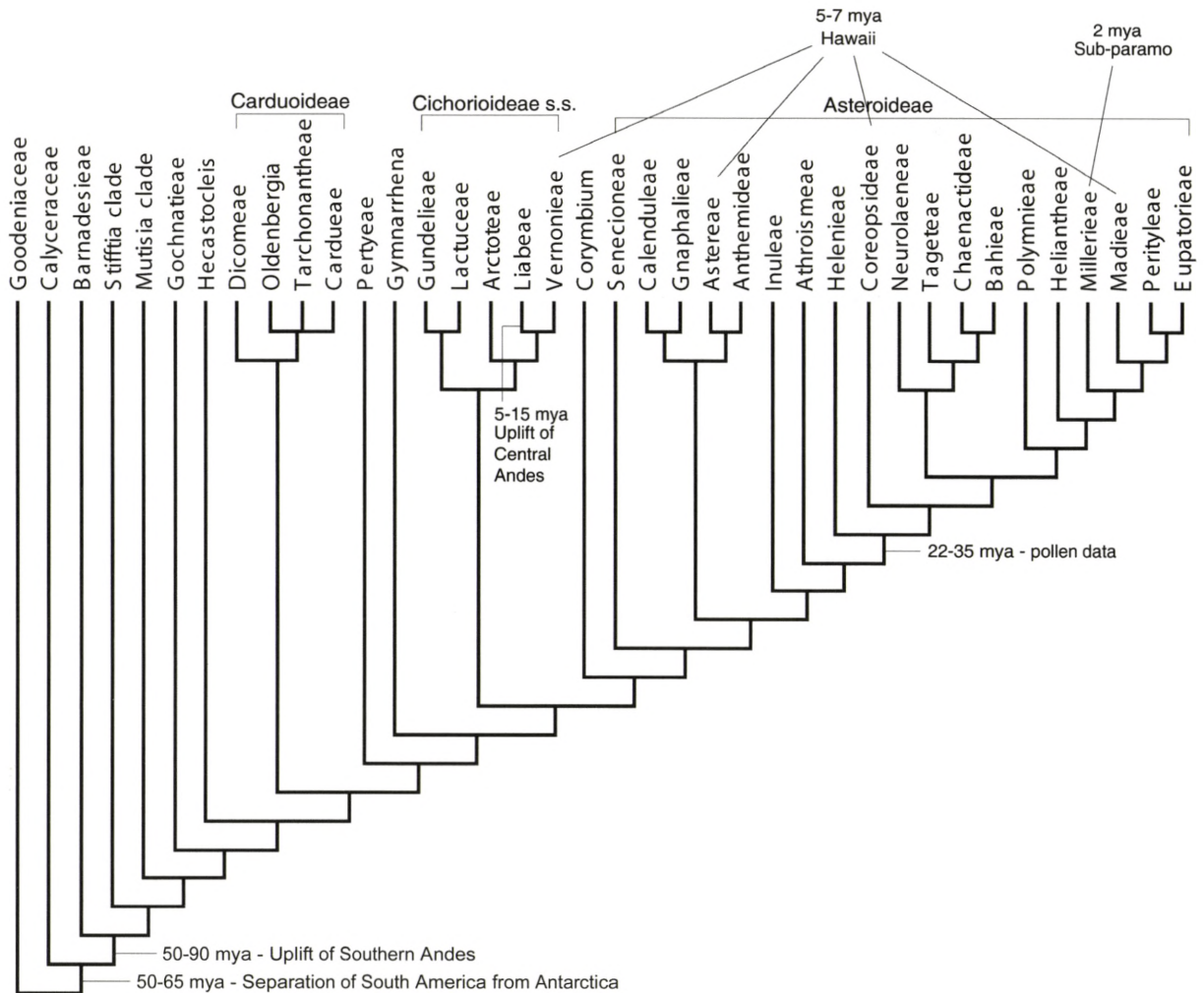


**Fig. 10.** The 'ancestral areas' analysis (sensu Bremer 1992) focuses on the base of the supertree with the areas of the terminal taxa indicated and it places the origin of the extant Compositae in southern South America.

(1977) also thought that the family originated in the mid-late Cretaceous possibly near the same time as the first upheaval of the Andes.

Using the supertree, some dates can be ascribed to different parts of the tree (Fig. 11). There are no reliable fossils from the early evolution of the family. However, some estimate of the age of the family can be obtained by examining the relationship of the Compositae to its two most closely related families. The first outgroup is the Calyceraceae whose members have the same distribution as the base of the Compositae, so we are really searching for the age of the ancestor of the Calyceraceae-Compositae clade. The sister-group to the Calyceraceae-Compositae clade is the Goodeniaceae whose members are found mainly in Australia. If one examines the distribution of these three families then one could hypothesize that the

ancestor of the three families had a Gondwanan origin, and the split between the ancestor of the Goodeniaceae and the ancestor of the Calyceraceae-Compositae took place when South America broke off from the Antarctica-Australia part of Gondwana. An examination of the dates given in various scenarios for the separation of South America from Australia and Antarctica, at the K/T boundary, results in dates of about 50-65 Mya (e.g., Scotese 2002). Another recent estimate of the age of the clade is 43-53 Mya from DeVore and Stuessy (1995; cited from Bremer & Gustafsson 1997). All these dates are based on the same vicariant event, the breaking away of South America; the discrepancy comes when one tries to determine when the two continents had separated far enough that they no longer shared a common flora. Additional support for this scenario



**Fig. 11.** There are few dates that can be placed on the phylogeny of the Compositae with any certainty. The separation of the lineage that led to the Goodeniaceae and the lineage that led to the Calyceraceae-Compositae may be placed at a time when Australia separated from Antarctica-South America (the flora is believed to have separated about 50 Mya) and the radiation at the base of the Compositae may be linked to uplift of the southern Andes (50-90 Mya). The occurrence of the Heliantheae *s. l.* can be placed by pollen records at 22-35 Mya.

comes from the fact that the oldest part of the Andes is the southern Andes and the uplift of this area began approximately 90 Mya and lasted until 50 Mya (another vicariant event). The mountains were high enough to cause a drying effect only late in this time period. So perhaps we can use the figure of 50 Mya for the

origin of the Calyceraceae-Compositae clade with the base of the Compositae radiating as the Andes developed. Since Africa drifted away from Gondwana quite some time before South America, it seems unlikely that the African continent had any influence on the base of the cladogram.

A few other dates for the Compositae can be estimated. According to Muller (1981) pollen data indicate that all major groups in the family were present 22-25 Mya. However, the date is extended further back by Graham (1996) who dates the earliest pollen from the Mutisieae as Eocene to middle Oligocene (25-50 mya), pollen from the Astereae-Heliantheae-Helenieae group as Eocene (35-50 Mya), and pollen of the *Ambrosia*-type (Heliantheae) from latest Eocene/early Oligocene (25-35 Mya) (Graham 1996). Since taxa with the *Ambrosia* type are nested high up in the tree we can use the date of 25-35 Mya for the base of the Heliantheae *s. l.* Across the top of Fig. 4 there are four Hawaiian taxa estimated to be 5-7 Mya; one radiation in the northern Andes (Espeletitineae) with an age of approximately 2 Mya in line with occurrence of the sub-paramo habitat, and the tribe Liabeae is a north-central Andean clade that can be dated 5-15 Mya when the central Andes were uplifted. Finally, there are taxa from near the base of the tree from the Guiana and Brazilian Shield; these plants inhabit areas where the rock is older than the family. On the Guiana Shield at least, the final uplift was probably in the Cretaceous, and so predates the origin of the Compositae and is no help in determining the ages of those clades.

### Concluding statements

The Calyceraceae-Compositae clade (as we know it today) may have originated in southern South America ca. 50 Mya and the diversification of the base of the family was in the same area. The diversification of the Calyceraceae was strikingly modest by comparison with that of the Compositae, which conquered the world. In the Compositae, following the southern South American radiation, there was an African explosion. Of the 1600-1700 genera in the Compositae today about 2/3 are in clades

with the basal branches in Africa, many in southern Africa. In fact, with the exception of the Mutisieae (*s. l.*) grade at the base and the highly nested Heliantheae *s. l.*, all of the major clades in the family appear to have an African origin. From this African origin came numerous movements into Asia, Eurasia, Europe, Australia, *etc.*, many of which have spawned substantial radiations (*e.g.*, Cardueae). The Heliantheae *s. l.* clade has a North American origin beginning by 22-35 Mya which coincides with the land bridge connection from Asia. The sister clade to the Heliantheae *s. l.* is found in tropical east Africa; it has a couple of species that are also in Asia. The ancestor of the Heliantheae *s. l.* could have come over the land bridge into western North America, down into Mexico with repeated incursions into Central America, and South America, especially in the northwestern Andes. The timing fits with many known migrations across the land bridge. But what about *Hecastocleis*? This monotypic North American genus from Nevada and Death Valley sits in-between the southern South American basal radiation and the African explosion. Were there two events of long distance dispersal, one from South America to North America and one from North America to Africa? Did a group of Compositae move into North America, then over to Europe and down into northern Africa followed by extensive extinction in the northern hemisphere? Or did this group of comps move into North America and then over into Asia and down into Africa followed by extensive extinction in the northern hemisphere? There is some evidence from other groups that show large-scale extinctions in the northern hemisphere, however, we do not have enough data to decide about this area of the Compositae supertree. It is possible that additional sequence data from more of the taxa in the Gochnatieae would provide a better estimation of the relationships. For now, that question

must remain unanswered. We have learned a great deal about the biogeography of this most interesting family but it is clear that we still have much to discover.

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**Appendix 1.** Estimation of ancestral area for the Compositae based on Figure 11. G=number of necessary gains, L = number of necessary losses, G/L = the ratio of gains to losses, AA = G/L quotients rescaled to a maximum value of 1 by dividing by the largest G/L.

Area	Gains	Losses	G/L	AA
Southern south America	12	5	2.40	1.00
Brazil	5	8	0.63	.26
Andes	6	13	0.46	.19
North America	3	8	0.38	.16
Asia	3	9	0.33	.14
Africa	2	8	0.25	.10
Guiana Shield	2	9	0.22	.09