Compositae metatrees: the next generation

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INTRODUCTION

Constructing a large combined tree of Compositae, a 'metatree' (also called 'meta-supertree' by Funk and Specht 2007 and 'megatree' by R. Ree, pers. comm.) allows one to examine the overall phylogenetic and bio-geographic patterns of the family. The first modern attempts to understand the family were by the authors in Heywood et al. (1977) plus the paper by Cronquist (1977), which was initially intended to be in the Heywood publication. Literature prior to 1977 has been discussed in detail in other chapters (for the early literature, see Chapter 1). In Cronquist's 1977 paper he reaffirmed his agreement with Bentham's 13-tribe classification of the family and the concept that Heliantheae s.l. were the primitive members (Cronquist 1955; Bentham 1873a, b). Cronquist (1977) pointed out that the Heywood et al.

volumes listed the tribes mostly in the order of Bentham 1873a rather than beginning with Heliantheae, which Bentham thought was most primitive (Bentham 1873b). The papers in the 1977 volumes did accept some changes such as the recognition of Liabeae and the conclusion that Helenieae were not a 'good' group, both more or less accepted by Cronquist in 1977. However, most proposed changes such as the new tribe Coreopsideae, etc. were not accepted by the synantherological community.

Cronquist (1977) believed that the primitive characters of the family were as follows (slightly modified): shrubby; leaves opposite; inflorescence cymose; heads few, each with many florets; involucre leafy, several-seriate; receptacle chaffy; ray florets present and fertile; disk florets perfect and fertile; lobes of the disk corollas with well developed mid-vein; pappus chaffy, of five members; and anthers connate, not tailed. Cronquist stated that the

presence of ray florets may have predated the origin of Compositae, so that even discoid tribes might have had a radiate ancestry.

The acceptance of the modified Bentham system was not universal. There were at least two papers in the Heywood et al. volumes (Jeffrey 1977; Skvarla 1977) and two individuals who published elsewhere (Carlquist 1966, 1976; Robinson 1981) who had reservations about the concept of "13 tribes rooted in the Heliantheae". All of these dissenting authors observed that the data they were generating did not support all of the above-listed characteristics as primitive in the family. However, for the most part, the synantherological community continued to use the Bentham classification.

Not too long after 1977, opinions began to change with the advent of cladistic methodology and molecular data. Jansen and Bremer and their collaborators (Bremer 1987, 1992, 1994; Jansen and Palmer 1987, 1988; Hansen 1991a, b; Jansen et al. 1991a, b; Bremer and Jansen 1992; Jansen and Kim 1996; Bremer and Gustafsson 1997) reordered Compositae by placing Barnadesiinae as the sister group of the family and placing Heliantheae (including Eupatorieae) highly nested in the phylogeny of the family.

Bremer's cladistic analysis (1994) was the first revision of the whole family based on morphology since Bentham, and he recognized many of the problem areas in the cladograms of the family and tribes, but the morphology did not generate enough data to resolve many of the issues. Over ten years later Kadereit and Jeffrey (2007) reordered the genera, tribes, and subfamilies within the family based on morphology and molecular results, and this work is now the standard reference for descriptions of the tribes and genera of the family.

This chapter seeks to link the most recent molecular trees together in a metatree framework (Funk and Specht 2007) and to use that tree to provide a basis for understanding the systematics, evolution, and biogeography of the family.

MATERIALS AND METHODS

Construction of the metatree

The metatree for Compositae was developed using a compilation of trees. The name metatree was adopted for this type of tree because it is a "tree of trees", one that is based on a fixed 'base tree' topology (Funk and Specht 2007). This type of tree has also been called a meta-supertree or megatree (R. Ree, pers. comm.), and some authors refer to it as a supertree. It is, however, neither a tree produced by a combined analysis of coded cladograms obtained from individual datasets (classic 'supertrees') nor is it the result of analyzing a dataset in which data from multiple datasets have been combined ('supermatrix' trees). There

has been some discussion on the pros and cons of the 'supertree' and 'supermatrix' methods (Steel et al. 2000; Gatesy et al. 2002; Bininda-Emonds et al. 2003), and both methods are compared with the metatree approach by Funk and Specht (2007). The metatree for this analysis was constructed in the following manner:

1. A 'base tree' was formed from the phylogeny of Panero and Funk (2008) with a few alterations. The most important change was the addition of taxa from the Heliantheae Alliance. The Heliantheae Alliance section of the Panero and Funk tree (which had only a few taxa) was replaced with the branching pattern of the Heliantheae Alliance from Baldwin (Baldwin et al. 2002; Chapter 41). Also, some refinements were made using the work of Ortiz (Chapters 18 and 19) and Ortiz et al. (Chapter 17) for Carduoideae, and Funk and Chan (Chapter 23) for Cichorioideae. The base tree was reduced to a matrix using Brooks Parsimony Analysis (BPA; Brooks 1982; Brooks and McLennan 2002), wherein any branching diagram can be reduced to a series of zeros and ones in a data matrix. We used MacClade to generate the data matrix (Maddison and Maddison 2001). The data matrix was run in a tree program (PAUP 4.0b10; Swofford 2002) to check for errors. All trees have been "ladderized to the right" for consistency, although anyone familiar with cladistics will understand that the tree can be "rotated" at any node. This feature is amply demonstrated by comparing the rooted tree (Fig. 44.1) and the unrooted tree (Fig. 44.2).

2. The most recent (and available) tree for each clade (see below) was reduced to a matrix (as above) and these matrices were added to the original matrix. Each time a new clade tree was added, the overall analysis was re-run to insure an accurate replication of the newly added tree, as well as to confirm that the addition did not result in topological changes elsewhere in the metatree. It should be noted that when a phylogeny for a tribe contained many taxa from the same area in a monophyletic group or a grade, these were often pruned to decrease the size of the tree without subtracting any biogeographical information. For instance, the phylogeny of Gnaphalieae contained a clade of 58 terminal taxa all endemic to Australia; this clade was reduced to 25 taxa.

3. A summary tree (Fig. 44.1) was produced in which each major clade was reduced to a single branch. This tree also shows the phylogenetic position of critically placed taxa and is displayed as an unrooted tree in Fig. 44.2.

See the section on optimization for an explanation of the biogeographic areas and how they were assigned.

Sources of the trees

General references for this study were Bremer (1994), Heywood (1993), Heywood et al., (1977), Hind (1996), and Kadereit and Jeffrey (2007). Below, the origin of each phylogeny on the metatree is discussed.

Outgroups

Lundberg (Chapter 10) examined the relationships among the families now contained in Asterales, including Compositae. His work indicated that Calyceraceae were the sister group of Compositae (1st outgroup) and that Goodeniaceae (2nd outgroup) were the sister group of the Calyceraceae + Compositae clade. The next most closely related family is Menyanthaceae, and it is followed by a clade containing Stylidiaceae, Alseuosmiaceae, Phellinaceae, and Argophyllaceae. The distribution of these eight families (Fig. 44.1) shows that the Compositae + Calyceraceae clade is nested in a grade of Australasian taxa (Australia, New Guinea, New Caledonia, and New Zealand). Each of these families is discussed below (listed in reverse order of relatedness to Compositae).

Argophyllaceae. — Two genera with ca. twenty species that are distributed on Australia, Lord Howe Island, New Caledonia, New Zealand, and Rapa Island.

Phellinaceae. — One genus with eleven species, all of which are found on New Caledonia.

Alseuosmiaceae. — Five genera and ten species all located on Australia, New Caledonia, New Guinea, and New Zealand.

Stylidiaceae. — Six genera with 245 species found in Australia and New Zealand with a few species in East Asia and South America.

Menyanthaceae. — Five genera with sixty species having an almost cosmopolitan distribution; however, four of the five genera are found in Australia, and because the closely related taxa are found in the Australia–New Zealand–New Guinea–New Caledonia area, this family is treated as having an Australasian distribution at its base.

Goodeniaceae. — The second outgroup of Compositae is a moderate-sized family of herbs and some shrubs: Goodeniaceae (fourteen genera, over 400 species). The family is largely confined to Australia, particularly western Australia, with only a few species extending elsewhere, mostly in the Pacific area (Gustafsson et al. 1996, 1997). A recent study (Howarth et al. 2003) has shown that the base of the phylogeny of 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.

Calyceraceae. — The first outgroup of Compositae, and therefore its sister group, is Calyceraceae, a small family (six genera, ca. sixty 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).

Cassini, in his famous 1816 diagram (Chapter 41: Fig. 41.1), showed Calyceraceae and Campanulaceae to be closely related to Compositae. Even though he did not have it in the diagram, he also thought Goodeniaceae were close (see Chapter 1).

Compositae

The base tree. — The basic structure of the tree was taken from Panero and Funk (2002, 2008) and Baldwin (Baldwin et al. 2002; Chapter 41); see above for details. The trees in Panero and Funk (2008) contained extensive sampling from the base of the tree, Mutisieae (sensu Cabrera), three to ten genera representing all other tribes (including the Heliantheae Alliance), and many taxa that had been "hard to place" in previous studies (including *Hecastocleis*, *Gymnarrhena*, and *Corymbium*). The Panero and Funk phylogeny was based on data from ten chloroplast gene regions (*ndhF*, *trnL-trnF*, *matK*, *ndhD*, *rbcL*, *rpoB*, *rpoC1*, *exon1*, *23S-trnI*, and *ndhI*). Relationships within tribes of the Heliantheae Alliance were taken from Baldwin et al. (2002) and Chapter 41 and were based on data from the ITS region of rDNA. Modifications were made in Cichorioideae (based on Chapter 23) and in Carduoideae (based on Ortiz, Chapters 18 and 19; and Ortiz et al. (Chapter 17).

Mutisieae s.l. sensu Cabrera (Chapter 12)**.** — The tribe Mutisieae (sensu Cabrera) has 84 genera and ca. 900 species. The paraphyly of Mutisieae (sensu Cabrera) was suggested by morphological studies (Cabrera 1977; Hansen 1991b) as well as the first molecular studies of the family. The subtribe Barnadesiinae was recognized as being the sister group to the rest of the family (Jansen and Palmer 1987, 1988; Bremer 1994; Kim and Jansen 1995). Kim et al. (2002) showed that the remainder of the tribe (sensu Cabrera) could not be supported as a monophyletic group. Most recently, Panero and Funk (2002, 2008) published phylogenies based on molecular data from ten chloroplast regions that *(1)* confirmed that Mutisieae (sensu Cabrera) were paraphyletic, *(2)* identified additional clades, and *(3)* elevated several groups to tribal and subfamily levels. Except for Barnadesieae, the phylogeny of Panero and Funk (2008) formed the base tree for Mutisieae (sensu Cabrera) with a few additions from Kim et al. (2002) and Katinas et al. (2007).

Barnadesieae (Chapter 13)**.** — The subfamily Barnadesioideae (nine genera; 91 species) has one tribe, and it is the sister group for the rest of Compositae. 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 Barnadesieae or other flowering plants. The
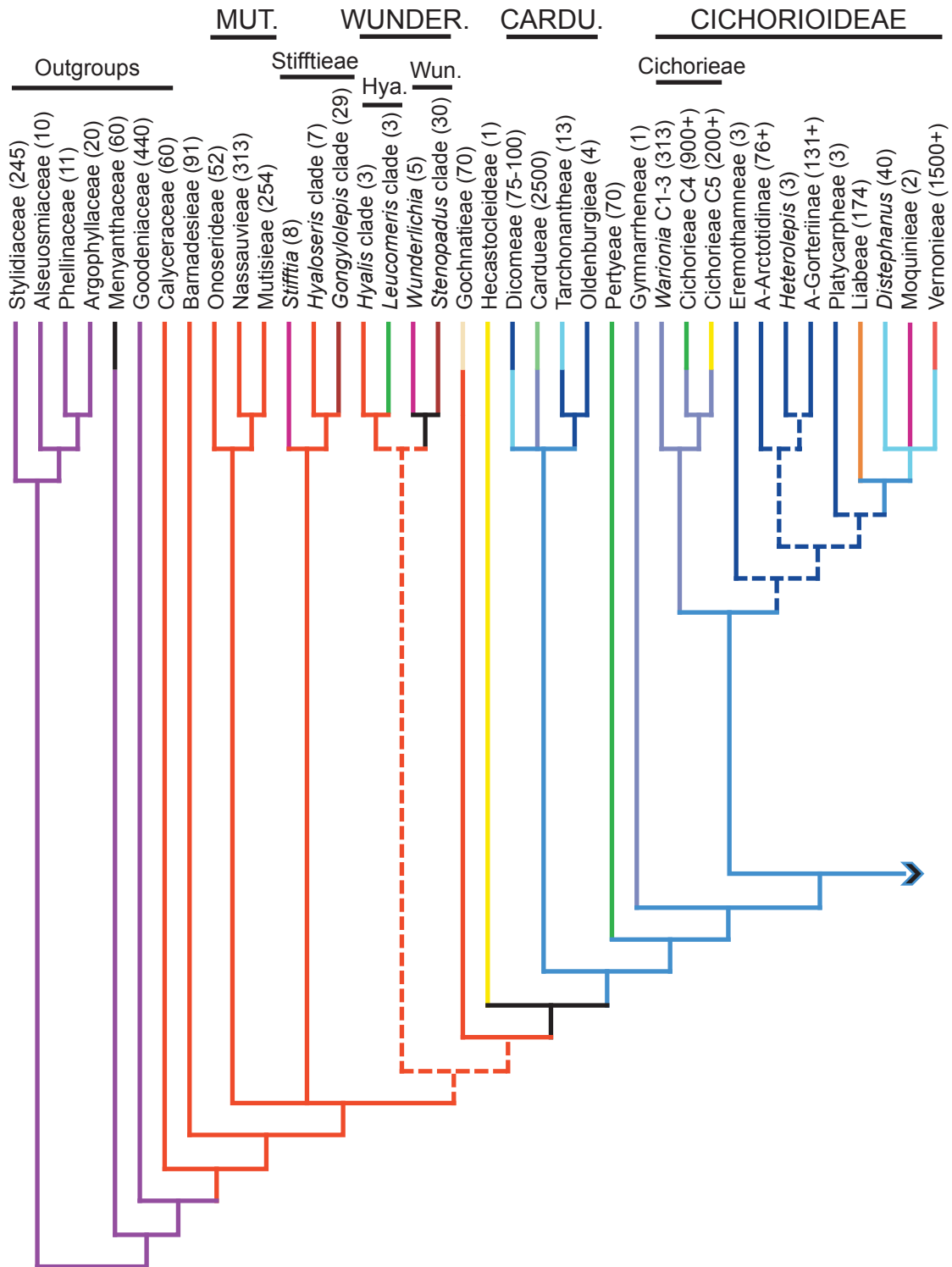
Fig. 44.1. A summary tree based on the metatree (Figs. 44.3–44.7). The tribes or clades have been represented by one to four-branches. The branches and internodes were colored according to the distribution of the taxon or the optimization of those distributions. The numbers by the terminal taxa reflect the number of species in that clade. Note that some areas have been combined (e.g., Mexico and North America) and that the red color in Vernonieae represents Tropical America. Subfamilies that have more than one tribe are indicated on the summary tree in capital letters (see Chapter 11 for details). A = Arctotideae; CARDU. = Carduoideae; Hya. = Hyalideae; MUT. = Mutisioideae; S = Senecioneae; Wun. = Wunderlichieae; WUNDER. = Wunderlichioideae.
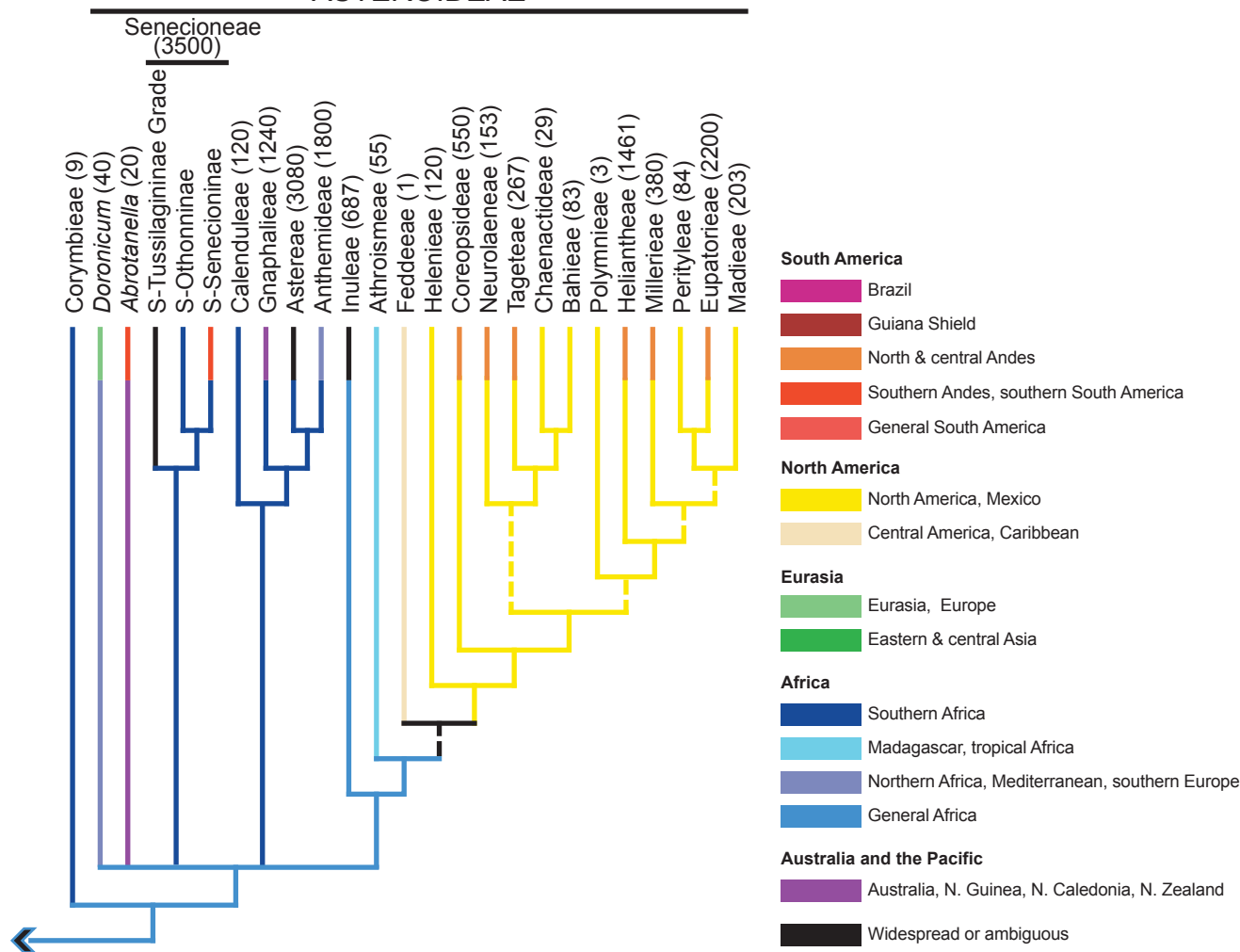
first phylogeny of this tribe was done by Gustafsson et al. (2001), but it was not completely resolved. The phylogeny for the tribe was taken from Gruenstaeudl et al. (2009). It was based on DNA sequence data of nine chloroplast gene regions (*atpI-atpH* IGS, *matK*, *psbA-trnH* IGS, *rbcL*, partial *rpoC1* gene+intron, *rps16-trnK* IGS, partial *trnK* intron, *trnL* intron, *trnL-trnF* IGS), the nuclear ribosomal ITS region (ITS1, 5.8S, ITS2), recoded DNA insertions/deletions, and selected morphological characters from previous investigations. In their analysis all genera were monophyletic except for *Dasyphyllum*, which fell into two groups reflecting the subgenera and their respective distributions "east of the Andes" and "west of the Andes". There are two possible positions for *Schlechtendalia*, one of which is basal for the tribe, and the other is more highly nested. The ambiguity of the position of *Schlechtendalia* does not affect the biogeographic hypothesis for this tribe.

African Mutisieae (Chapters 17–19). — With the exception of *Gerbera* and the closely related and sometimes congeneric *Perdicium*, which are found in Africa and to a lesser extent in Asia, all Mutisieae (sensu Cabrera) from Africa are no longer part of Mutisioideae (sensu Panero and Funk) and are now in Carduoideae. Using ITS and *ndhF* sequence data, Ortiz and his collaborators (Chapters 17–19) have shown that these segregate African Mutisieae form three (or four) distinct groups that are separated by striking morphological as well as molecular differences. Currently, there are three tribes: Dicomeae, Oldenburgieae, and Tarchonantheae. However, it is possible, but not yet certain, that the tribe Dicomeae may fall into two distinct groups that are not sister taxa. In addition, there is still some ambiguity as to the relationships among some of the tribes.

The tribe Dicomeae contains seven African genera (ca. 75–100 species) occurring in tropical and southern Africa and Madagascar with a minor presence in the Arabian Peninsula, India, and Pakistan. The tribe Tarchonantheae contains two African genera (13 species) occurring
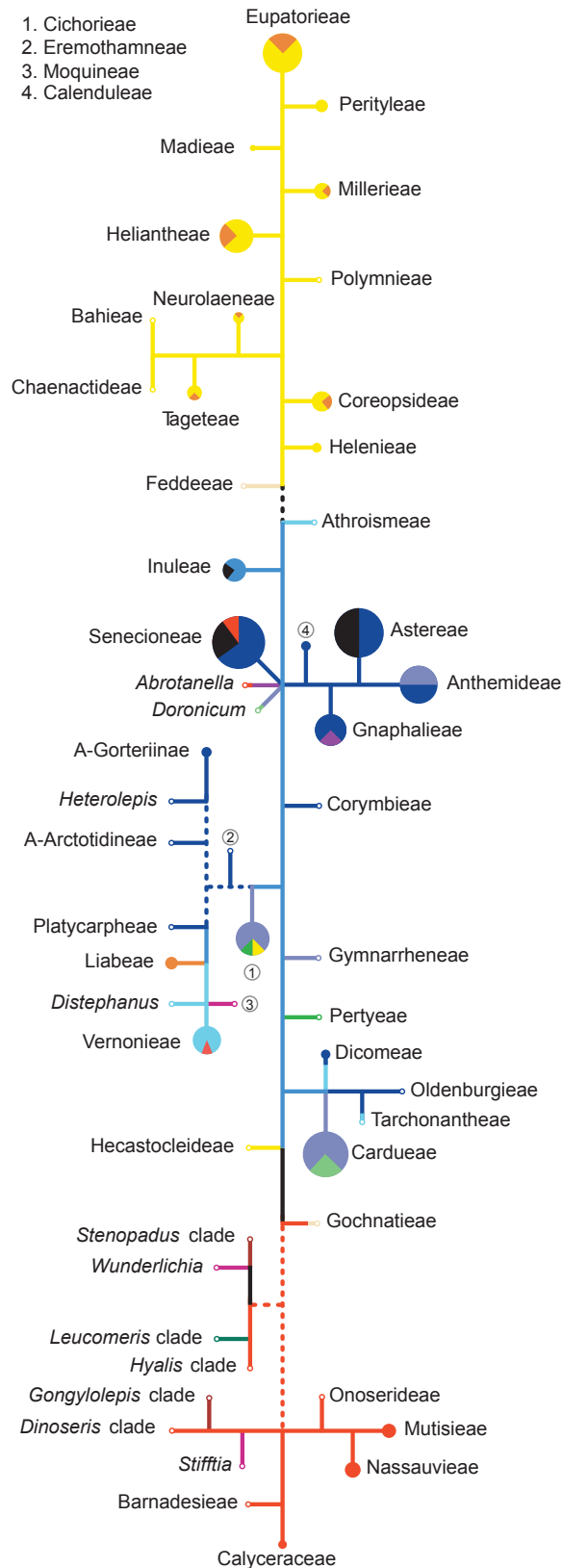
1. Cichorieae
2. Eremothamneae
3. Moquineae
4. Calenduleae

Fig. 44.2. An unrooted representation of the summary tree. The size of the circle indicates the number of species found in that clade. Colors are the same as in Fig. 44.1.

mainly in tropical and southern Africa, and Madagascar, but it is also present on the Arabian Peninsula. The tribe Oldenburgieae has only the genus *Oldenburgia* (4 species), which is endemic to the Cape Floristic Region of South Africa.

Cardueae (Chapter 20). — Cardueae (thistles; 73 genera, ca. 2500 species) are now known to be nested within a paraphyletic Mutisieae (sensu Cabrera). This tribe is the sister group of the African Mutisieae clades. The tribes Cardueae, Tarchonantheae, Oldenburgieae, and Dicomeae form a monophyletic group that is now the subfamily Carduoideae. The Cardueae tree used for the metatree is based on *matK*, *trnL-F*, and ITS sequence data (Susanna et al. 2006).

Cichorieae (Lactuceae; Chapter 24). — The phylogeny of the mainly north temperate dandelion tribe Cichorieae (Lactuceae) has long been problematic. It has 93 genera arranged in eleven subtribes, but the number of species varies depending on one's species concept. If one excludes the problematic genera *Hieracium*, *Pilosella*, and *Taraxacum*, there are about 1400 species (Kilian et al., Chapter 24). The Cichorieae tree used in this study was provided by Gemeinholzer and her collaborators based on recent molecular analyses of a large ITS dataset (428 taxa of 83 genera; Gemeinholzer and Bachmann 2003; Kilian et al., Chapter 24; Gemeinholzer et al., unpub.). The analyses revealed the existence of five major clades, with a total of eleven subclades, within the tribe.

The position of *Gundelia* (Gundelieae) as basal within Cichorieae was suggested by Karis et al. (2001) based on *ndhF* data, and this was supported by Panero and Funk (2008), who also found *Warionia* to be at the base. However, the current studies of Gemeinholzer and her collaborators comprising more basally branching taxa place the Northern African genus *Warionia* at the base of Cichorieae with the Mediterranean *Gundelia* slightly more highly nested. Since both are from the same biogeographic area, the two different placements of *Gundelia* and *Warionia* do not affect the biogeographic analysis.

Arctotideae, Eremothamneae, Platycarpheae, and Heterolepis (Chapters 25, 26, 29, 31). — The tribe Arctotideae (African Daisies) is a diverse and interesting group (18 genera, 215 species). Recent molecular studies are ambiguous as to the monophyly of this tribe, and some former members have been moved out of the tribe based on morphology and/or molecular data. The positions of *Heterolepis* (Funk and Karis, Chapter 31) and the tribe Eremothamneae (2 genera, 3 species; Robinson and Funk, Chapter 26) vary depending on the data used in the analysis, and the new tribe Platycarpheae (2 genera and 3 species) is most likely closely related to the Liabeae + Vernonieae clade (Funk et al., Chapter 29). Although Arctotideae cannot be unambiguously diagnosed, the two core subtribes are distinctive based on morphology as well as molecular data (Funk et

al. 2004; Karis et al., Chapter 25). Recently published phylogenies using both chloroplast and nuclear DNA and representing all of the genera (some with many species) provided the structure for the trees (Funk and Chan 2008; McKenzie and Barker 2008) and the relationships among the clades was taken from Funk et al. 2004 and Funk and Chan, Chapter 23).

Liabeae (Chapter 27). **—** Liabeae are a monophyletic Neotropical tribe containing approximately 174 species distributed in 17 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 14 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 Andean origin (Funk et al. 1996). The tree for our study was based on Dillon et al. (Chapter 27) and contains all the genera of the tribe except the monotypic *Bishopanthus*, which is only known from the type. Although the type was relatively recently collected, it is just a small piece of the original collection, most of which was destroyed by one of the collectors.

Vernonieae and Moquinieae (Chapters 28, 30). **—** The tribe Vernonieae with 126 genera and 1500 species has until recently had most of its species placed in the large and complicated genus *Vernonia* (ca. 1000; Jones 1977; Keeley and Robinson, Chapter 28). The tribe is widely distributed with centers of diversity in tropical Africa and Madagascar, Brazil, and North America. However, it has been the subject of recent revisions that concentrated on recognizing monophyletic genera from within the 1000 species of the core genus *Vernonia* s.l. (e.g., Robinson 1999), first in the Americas and more recently in Africa and Asia. Vernonieae have recently been examined by Keeley et al. (2007; Keeley and Robinson, Chapter 28) based on *ndhF*, *trnL-trnF*, and ITS sequence data. Their work supports the monophyly of the tribe and the non-monophyly of *Vernonia*. However, in the analysis of the subfamily Cichorioideae (Funk and Chan, Chapter 23), *Distephanus* had alternative placements: as the sister group to the rest of Vernonieae, or unresolved at the base with the tribe Moquinieae (Robinson, Chapter 30).

Senecioneae (Chapter 34). **—** Senecioneae are the largest tribe with over 150 genera containing 3500 species (Nordenstam 2007a) and they have a global distribution. Pelser et al. (2007), recently published a phylogenetic analysis of the tribe based on ITS data that, while unresolved at the base, showed several well supported clades. The genus *Senecio*, which contained the majority of the species of the tribe, was shown to be non-monophyletic, and the authors indicated that revisions of the generic boundaries that are needed to achieve monophyletic groups are completed or in progress.

The relationship of Senecioneae to other clades is uncertain. The tribe is variously positioned as *(1)* the sister group to the rest of Asteroideae, *(2)* the sister group to the Calenduleae + Gnaphalieae + Astereae + Anthemideae clade, or, in the least likely scenario, *(3)* the sister group to the Inuleae + Athroismeae + Heliantheae Alliance clade. The support for its inclusion is strongest for option 1, but the relatively short branches make its placement there tentative (see Pelser and Watson, Chapter 33). This ambiguity will not be resolved until more taxa and characters from both plastid and nuclear markers are included in a tribal-level study of the subfamily. At this time we are following the resolution favored by Panero and Funk (2008), which shows the Senecioneae in a polytomy with the clade formed by the Inuleae + Athroismeae + Heliantheae Alliance and the clade containing Calenduleae + Gnaphalieae + Astereae + Anthemideae. *Doronicum* and *Abrotanella*, the two additional taxa in this polytomy, are Senecioneae genera that have been hard to place and may have to be excluded from the tribe (Pelser et al. 2007).

Calenduleae (Chapter 35). **—** The placement of Calenduleae as the sister taxon to the Gnaphalieae + Anthemideae + Astereae clade is based on the Panero and Funk (2008) analysis as well as those by Kim and Jansen (1995) and Eldenäs et al. (1999). The sister group relationship of Calenduleae to the other three tribes is strongly supported in the Panero and Funk (2008) study, even though the number of taxa sampled is small. The tribe Calenduleae has 12 genera with 120 species (Nordenstam 2007b), and most genera have distinct centers of distribution in southern Africa; most of the species occur in the Cape Floristic Region. However, one genus, *Calendula*, is found in northern Africa and the Mediterranean north to Central Europe and east into Turkey, Iraq, and Iran; but it is nested in the higher portion of the tree and so does not affect the biogeographic pattern.

Gnaphalieae (Chapter 36). **—** Gnaphalieae are a moderately large tribe whose members were traditionally included in the tribe Inuleae. It has only been recently that the tribe has been shown to be isolated from the remainder of "old" Inuleae (Anderberg 1989, 1991). The approximately 180–190 genera and ca. 1240 species of Gnaphalieae are most numerous in the southern hemisphere, with strong centers of diversity in southern Africa, Australia, and South America (Anderberg 1991; Bayer et al. 2007). The tree for this study was provided by Bayer and his collaborators (Ward et al., Chapter 36) and it is based on chloroplast DNA sequences for *matK*, the *trnL* intron, and the *trnL-trnF* intergenic spacer. The principal improvement of this tree over previously published DNA sequence phylogenies for Gnaphalieae is that it includes a broad sampling of genera from Africa and Australasia together with some from other continents.

Astereae (Chapter 37). — With 170 genera, ca. 3000 species, and a worldwide distribution, Astereae are the second largest tribe after Senecioneae. It has centers of diversity in southwestern North America, the Andes, South Africa, Australia, and New Zealand. The tree presented in this book (Brouillet et al., Chapter 37) is the first global, molecular phylogenetic analysis of the tribe. It is based on ITS sequence data and shows that interrelationships among genera are better reflected by geographic origin than by the current classification.

Anthemideae (Chapter 38). — The tribe Anthemideae is composed of 111 genera and ca. 1800 species with main concentrations of species in southern Africa, the Mediterranean region, and Central Asia. The phylogeny for the metatree was generated using data from two recent publications that used *ndhF* (Watson et al. 2000; Himmelreich et al. 2008) and one that used ITS (Oberprieler et al. 2007).

Inuleae and Plucheeae (Chapter 39). — Plucheeae are now known to be nested within Inuleae, and so they are recognized as a single tribe with about 66 genera and ca. 700 species (Anderberg and Eldenäs 2007). The tree for this study was provided by Anderberg and his collaborators (Anderberg et al. 2005) based on *ndhF* data. Inuleae are a mainly Eurasian and east and southern African tribe, but some genera (e.g., *Pluchea*) have a worldwide distribution.

Athroismeae (Chapter 40). — The tribe Athroismeae is the sister group to the rest of the large and diverse clade that is the Heliantheae Alliance. The five genera (only two were included in Panero and Funk 2008) and 55 species in Athroismeae are centered in eastern tropical Africa and were in Inuleae until moved to Heliantheae s.l. (Eriksson 1991).

Heliantheae Alliance (including Eupatorieae) (Chapters 41–43). — The tribe Eupatorieae is nested in the Heliantheae Alliance, and former Heliantheae s.l. have been reorganized into twelve tribes (Baldwin et al. 2002; Panero and Funk 2002; Cariaga et al. 2008). Bremer (1994) divided this part of the family into three groups, Helenieae (including Athroismeae), Heliantheae, and Eupatorieae, but recognized that the groups would need to be re-arranged once additional information was available. The studies of both Baldwin et al. (2002) and Panero and Funk (2002) showed Helenieae and Heliantheae of Bremer to be non-monophyletic, and they described additional tribes where needed. More recently, Cariaga et al. (2008) published a treatment of the problem genus *Feddea* based on *ndhF* sequence data. As part of their study the genus was placed in a new tribe by itself, Feddeeae, located as the sister group of the "rest" of the Heliantheae Alliance (minus Athroismeae). The inclusion of the tribes Feddeeae and Eupatorieae in the Heliantheae Alliance brings the total number of tribes in the Alliance to 13.

The tree for this clade in the metatree was formed by using the Baldwin treatment of the Heliantheae Alliance (Chapter 41), the Coreopsideae treatment of Crawford et al. (Chapter 42), and the Funk et al. paper (2005). The branching within Eupatorieae was taken from Robinson et al. (Chapter 43).

The tree for the Heliantheae Alliance section of the family contains 160 out of ca. 460 genera and so represents about 35% of the generic diversity of this clade. This is the lowest percentage for any clade on the metatree, however the poor representation is found primarily in three tribes, Eupatorieae (the tree has 25 genera represented out of a total of 182; there are 2200 species), Heliantheae (6 out of 113 genera were represented; there are 1461 species), and Millerieae (3 genera out of 36 were represented; there are 380 species). When totaled together, these three tribes are represented by only about 10% of the generic diversity within them. The other ten tribes in the Alliance are much better represented, some at or close to 100% (see below). Because the members of former Helenieae form the basal grade, the under-representation of three of the more highly nested groups does not present an obstacle to the biogeographic analysis, although it does give an under-estimate of the importance of the northern and central Andes.

The tribe Heliantheae s.l. was broken up by Baldwin et al. (2002) and by Panero and Funk (2002) when Eupatorieae were found to be nested within what is now referred to as the Heliantheae Alliance (Fig. 44.1). Most of the new tribes, however, were actually not new and had been described previously by others but not picked up by the synantherological community. In fact, only three of the tribes recognized by Baldwin needed to be described as new (Baldwin et al. 2002): Bahieae (17 out of 20 genera were represented in the analysis; there are 83 species), Chaenactideae (all 3 genera were represented; 29 species), and Perityleae (4 out of 7 genera were represented; 84 species) (see Funk et al., Chapter 11). Other tribes in the Heliantheae Alliance (not mentioned above) include: Coreopsideae (21 genera out of 30 were represented; 550 species), Helenieae (all 13 genera were represented; 120 species), Madieae (35 genera were represented out of 36; 203 species), Neurolaeneae (1 out of 5 genera was represented; 153 species), Polymnieae (the only genus was represented; 3 species), and Tageteae (17 out of 32 genera were represented; 267 species).

Area optimization analysis using parsimony

The terminal branches of the metatree were colored based on the distribution of each terminal taxon; taxa that span more than one area have multiple colors (Figs. 44.1–44.7). The internode distributions were mapped onto the metatree using the Farris double pass method (1970). The results of the mapping were checked using

the PAUP 'Acctran' option (Swofford 2002). These techniques provided the hypothesized distributions at deep branches and nodes.

Following the theory that bold hypotheses are better than weak ones (courtesy of Popper), equivocal situations were resolved when possible to present the most predictive estimate of the biogeographic history. In a few instances there were equivocal resolutions which were left black, or if the two areas were contained in a single continent, they were coded for that continent (e.g., general Africa). In essence, we created an 'area metatree' as opposed to an 'area cladogram'. In the summary tree and unrooted tree (Figs. 44.1, 44.2), some of the biogeographic areas were combined (e.g., North America was combined with Mexico).

RESULTS AND DISCUSSION

The first supertree (= metatree) for Compositae was published in 2005 (Funk et al.), and since then there has been considerable progress in the reconstruction of evolutionary relationships in many clades. In fact, we now have robust phylogenies for most of the clades in the family. Descriptions and diagnostic characters for all of the tribes and critical clades are found in Chapter 11. Without a doubt the most substantial progress has been made in the large and complicated Astereae, Cichorieae, Senecioneae, and Vernonieae tribes, all of which were problematic in the 2005 publication (Funk et al. 2005) but now have their first comprehensive molecular phylogenetic hypotheses (Keeley et al. 2007; Pelser et al. 2007; Brouillet et al., Chapter 37; Kilian et al., Chapter 24; and other references in the corresponding chapters). For the first time within these tribes we have a fairly good idea of what the basal groups are and where different clades are found, and we know that the large genera with global distributions are not monophyletic.

Considering the entire metatree, most of the traditional thirteen tribes were found to be monophyletic or could easily be made monophyletic with only a few rearrangements. The big exceptions to this are Mutisieae (sensu Cabrera) and the Heliantheae Alliance, both were broken up into many groups. The genera that were once placed in Mutisieae by Cabrera or others are now in fourteen tribes, Helenieae are in seven, and Heliantheae are in six (including Feddeeae).

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 Compositae had their origin in the northwest portion of South America, in the Andes. Rzedowski (1972) and Hu (1958) pointed out the high diversity of the family in montane areas. More recently, Bremer (1992, 1994) developed a method he called 'Ancestral Areas Analysis' and came to the conclusion that the family originated in "South America and the Pacific". DeVore and Stuessy (1995) suggested that the family originated in southern South America, which was re-emphasized by Bremer and Gustafsson (1997). Graham (1996) summarized the fossils for the family but had wide estimates of the age of some of the pollen. Other than these efforts, little attention has been paid to this topic. Perhaps the size of the family, its global distribution, the lack of macrofossils and paucity of discriminating characters in fossil pollen, and the lack of an agreed upon phylogeny have restricted attempts to understand its history.

The meta showing the overall phylogeny of Compositae allows us to use information from the most recent available molecular phylogenies to look at the family as a whole and to try to discern its origin and history. It is also an excellent method for determining critical areas of the tree for future work (Funk and Specht 2007).

The metatree and its sections
In order to more easily discuss the tree it has been broken into sections. Section 1 (Fig. 44.3) covers the Basal Grade, from the outgroups through monotypic Gymnarrheneae. Section 2 (Fig. 44.4) covers the large subfamily Cichorioideae. Section 3 (Fig. 44.5) covers Corymbieae, Senecioneae, Calenduleae, and Gnaphalieae; Section 4 (Fig. 44.6) Anthemideae and Astereae; and finally, Section 5 (Fig. 44.7) Inuleae, Athroismeae, and the Heliantheae Alliance (including the Eupatorieae). Figure 44.8 has some of the proposed ages of the clades and Figs. 44.9 and 44.10 show some of the morphological variation.

Since we have no macrofossil data, the following discussion is based on extant taxa.

Section 1, Basal Grade (Figs. 44.3, 44.9A–D). — Except for Calyceraceae (the sister group of Compositae), the most closely related families to Compositae are found in Australia, New Zealand, New Guinea, and New Caledonia (purple lines; Fig. 44.3). The members of Calyceraceae are from southern South America.

The first split within Compositae is between the subfamily Barnadesioideae and the remainder of the family (Fig. 44.3). Gustafsson et al. (2001) and Stuessy et al. (Chapter 13) examined the biogeography and concluded that the Barnadesioideae clade has its origin in southern South America; this is confirmed by our analysis. In the sister group of Barnadesioideae the relationships among the basal groups are largely unresolved and are shown as a trichotomy (Fig. 44.3). However, this part of the tree could have been shown as a polytomy containing four or even five clades because support for monophyly of the subfamily Wunderlichioideae is not consistently strong, nor is its phylogenetic position; this ambiguity is

Fig. 44.3. The metatree of Compositae has been broken up into five figures with two to three parts for each figure. The original trees are from the various chapters in this volume, but some taxa with redundant distributions have been pruned from the tree to save space. Figure 44.3 covers the Basal Grade of the family and includes the outgroups through Gymnarrheneae, including this-tles (some of the internodes have been compressed). All outgroups except for the sister group are Australasian. The extant taxa from the sister group of the family, Calyceraceae, along with those from the basal grade of Compositae have a southern South American origin. For subfamily groups see Chapter 11, for color chart see Fig. 44.7. Gy. = Gymnarrheneae; H. = Hecastocleideae; O. = Oldenburgieae; Onoser. = Onoserideae; Perty. = Pertyeae; Tar. = Tarchonantheae; Wund. = Wunderlichieae.

indicated in Fig. 44.3 by a dotted line. However, many of the main clades basal to the clade formed by *Hecastocleis* and its sister group are consistently resolved as having a southern South American origin, with the exception of the tribe Wunderlichieae whose members are found in the Guiana Shield and Brazil. The large Mutisioideae clade (composed of the tribes Mutisieae, Nassauvieae, and Onoserideae) contains mostly southern South American taxa, but it also contains *Gerbera* from tropical and southern Africa and Asia, North America taxa (e.g., *Acourtia*), and *Leibnitzia* from Asia and Mexico. Hyalideae have two clades, one from Asia and one from southern South America. Gochnatieae contain genera mainly from southern South America and Brazil, but there is also a radiation

in Cuba. It is clear from the optimization that the extant taxa at the base of the Compositae metatree have their origin in southern South America.

The internode between the southern South American grade and the beginning of the African radiation (labeled "General Africa" in Fig. 44.3) is left unresolved as to origin because there are no areas shared among the three (South American base, African radiation, and the North American genus *Hecastocleis*). A species level analysis of the tribe Gochnatieae (4–5 genera) is underway (Sancho et al., pers. comm.) and its relationships to *Hecastocleis* may provide some insight into the problem, because one of the genera (*Gochnatia*) is found in South America, the West Indies, and North America.
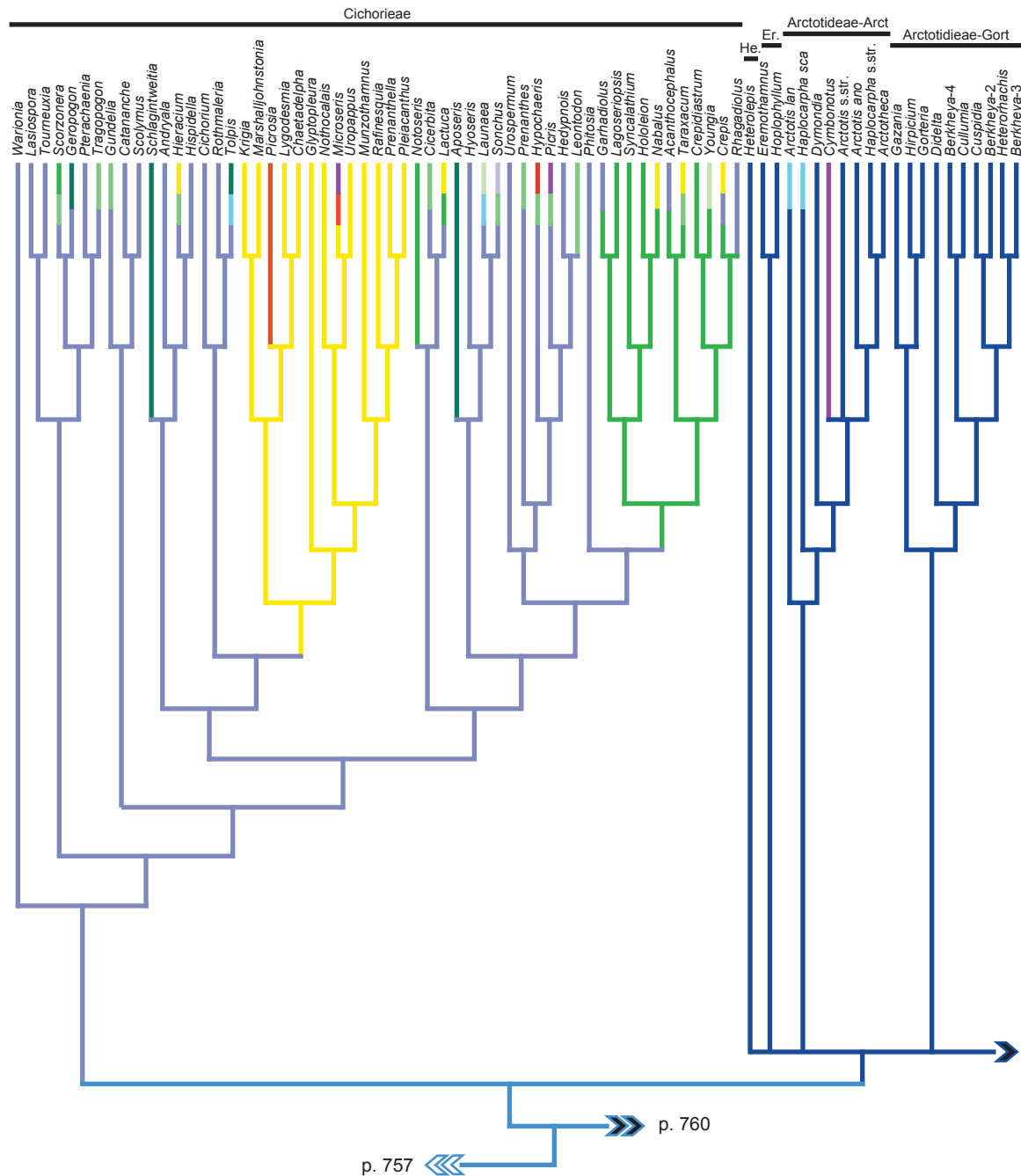
Fig. 44.4. Monotypic Cichorioideae (internodes have been compressed). For subfamily groups see Chapter 11, for color chart see Fig. 44.7. Di. = *Distephanus*; Er. = Eremothamneae; He. = *Hecastocleis*; Mo. = Moquinieae; Pl. = Platycarpheae.

The largest clade of the basal grade contains the subfamily Carduoideae (Tarchonantheae, Oldenburgieae, Dicomeae, Cardueae; Fig. 44.3); this is followed on the metatree by the Pertyeae (Asia) and Gymnarrheneae (northern Africa). At the base of Carduoideae are several former members of Mutisieae from southern and tropical Africa (African Mutisieae). The relationships of these clades to one another are unresolved at this time, except for the sister group relationship between Oldenburgieae and Tarchonantheae. The thistles (Cardueae) are monophyletic and show a Mediterranean–northern African radiation with numerous incursions into Eurasia and Asia. The combination of the Mediterranean–northern African base of the thistles and the tropical and southern African Tarchonantheae, Oldenburgieae, and Dicomeae give a 'general Africa' base to this clade.
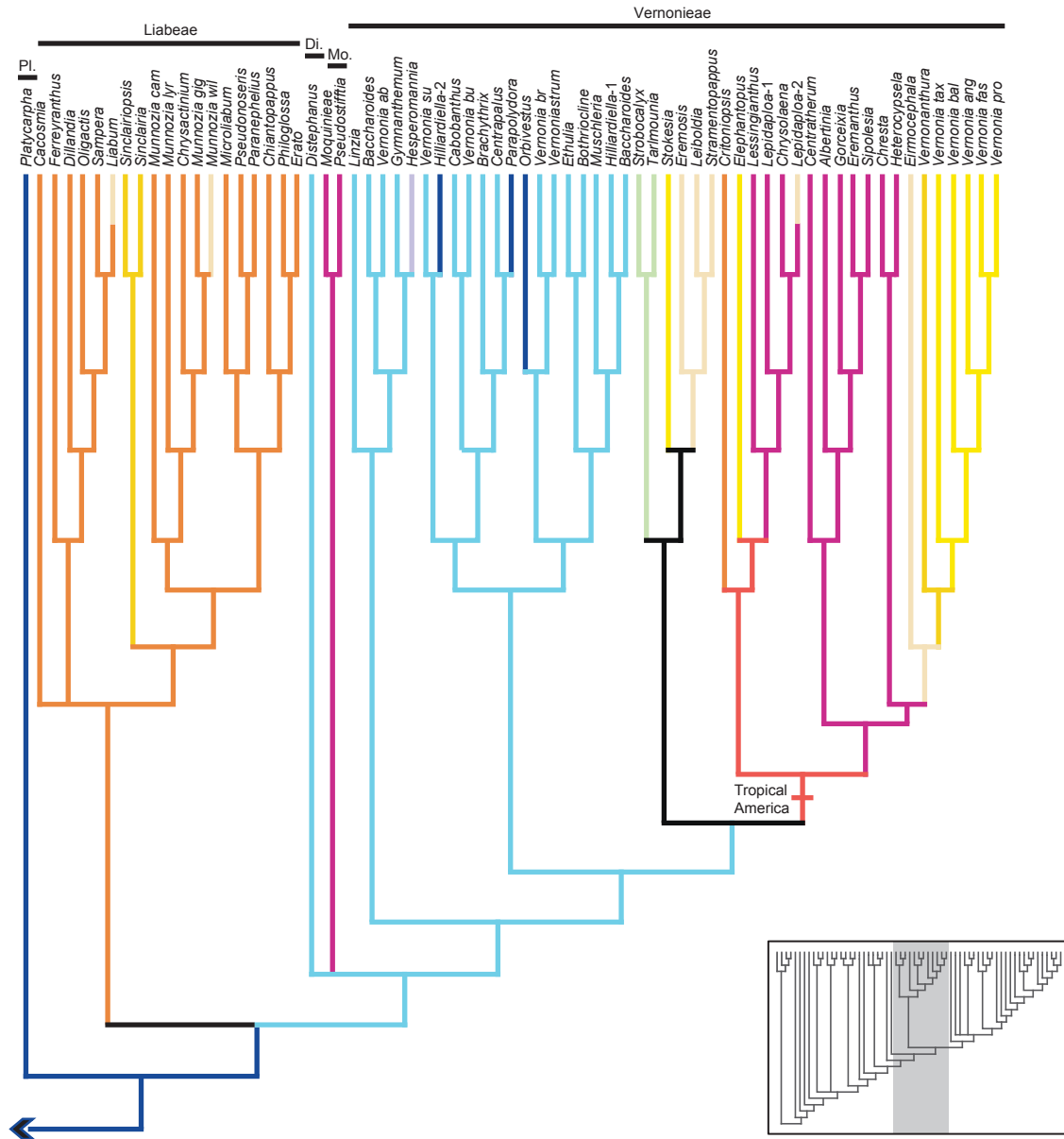
The sister group of Carduoideae is the remainder of the family (Pertyeae, Gymnarrheneae, Cichorioideae, Corymbieae, and Asteroideae) all of which, except for Pertyeae (Asia), presumably originated in Africa. The first group to split off is Pertyeae followed by Gymnarrheneae (Northern Africa) followed by Cichorioideae.

Section 2, subfamily Cichorioideae (Figs. 44.4, 44.9E, F). — This large clade contains six tribes: Cichorieae (Fig. 44.4; also referred to as Lactuceae) is the sister group to the remainder. This tribe has a Mediterranean–northern African base with independent radiations in North America and Asia. Interestingly, the main North American clade of Cichorieae is not nested within the Asian radiation as was predicted (Funk et al. 2005). In

that paper, it was thought that the biogeographic pathways of Cichorioideae would lead from the Mediterranean via Eurasia to Asia and across to North America but it seems that the Asian and North American taxa are separately derived from Mediterranean clades.

At the base of the rest of the subfamily Cichorioideae there are five clades containing members of the former Arctotideae: two are subtribes of that tribe (Arctotidinae and Gorteriinae), two are now recognized at the tribal level (Eremothamneae and Platycarpheae), and one is an unplaced genus (*Heterolepis*). All are from southern Africa (Fig. 44.4) and are prominent members of the Cape Floral Region, which is the subject of intense conservation in–terest. Because all of the basal taxa in each subtribe are in

Fig. 44.5. Corymbieae, Senecioneae, Calenduleae, and Gnaphalieae. For subfamily groups see Chapter 11, for color chart see Fig. 44.7. Co. = Corymbieae.

southern Africa, the lack of evidence for the monophyly of Arctotideae does not affect the biogeographic hypotheses produced in this study.

The tribe Platycarpheae (southern Africa) is the sister taxon of the Liabeae + Vernonieae clade (including *Distephanus* and Moquinieae) but without strong support. This clade is nested in a grade formed by the southern

African clades (Fig. 44.4). Liabeae are predominantly central Andean and the tribe is believed to have originated in northern Peru and southern Ecuador with small incursions into Central America and radiations in Mexico (*Sinclairia*) and the Caribbean (*Liabum*). The basal branches of Vernonieae are from the area we have designated as 'tropical Africa and Madagascar'. New to the analysis is

the small Brazilian tribe Moquinieae (*Pseudostifftia* and *Moquinia*). In some of the analyses the inclusion of this tribe results in *Distephanus* changing position from being the sister group of the rest of the tribe to being ambiguous at the base of the Vernonieae-Moquinieae clade (Keeley and Robinson, Chapter 28; Funk and Chan, Chapter 23). More highly nested members of Vernonieae are from Brazil and North America. In Vernonieae, the unusual North American genera *Stokesia* and *Elephantopus* are not in the main North American clade but rather represent two independent lineages (Fig. 44.4). With the exception of Liabeae, every tribe or subtribe in Cichorioideae s.str. has its origins in Africa, either north, tropical or

southern, in effect covering the whole continent. As a result the final biogeographic resolution of the subfamily is listed as 'General Africa'.

Sections 3–5 (Figs. 44.5–44.7) cover Corymbieae (Corymbioideae) and its sister group Asteroideae.

Section 3, tribes Corymbieae, Senecioneae, Calenduleae and Gnaphalieae (Figs. 44.5, 44.10)**. —** The tribe Corymbieae (Corymbioideae) consists of only one genus, *Corymbium*, and this distinctive group is restricted to southern South Africa (Nordenstam 2007c; Fig. 44.5).

Asteroideae encompass the remainder of the family phylogeny, and it is the largest subfamily. It was recognized by Cassini (1816) and Bentham (1873a) due to the
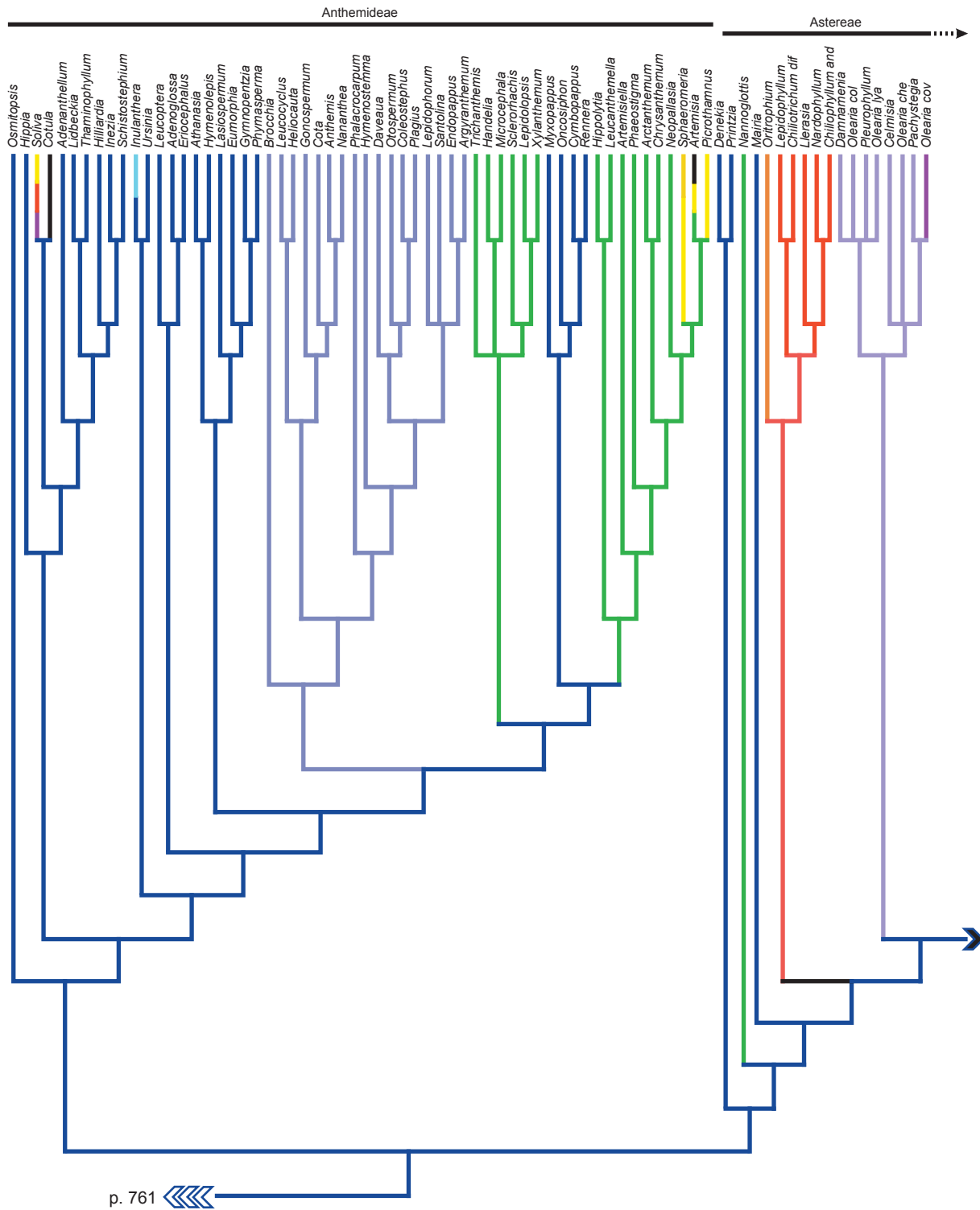
Fig. 44.6. Anthemideae and Astereae. All taxa are in the subfamily Asteroideae; see Fig. 44.7 for the color chart.

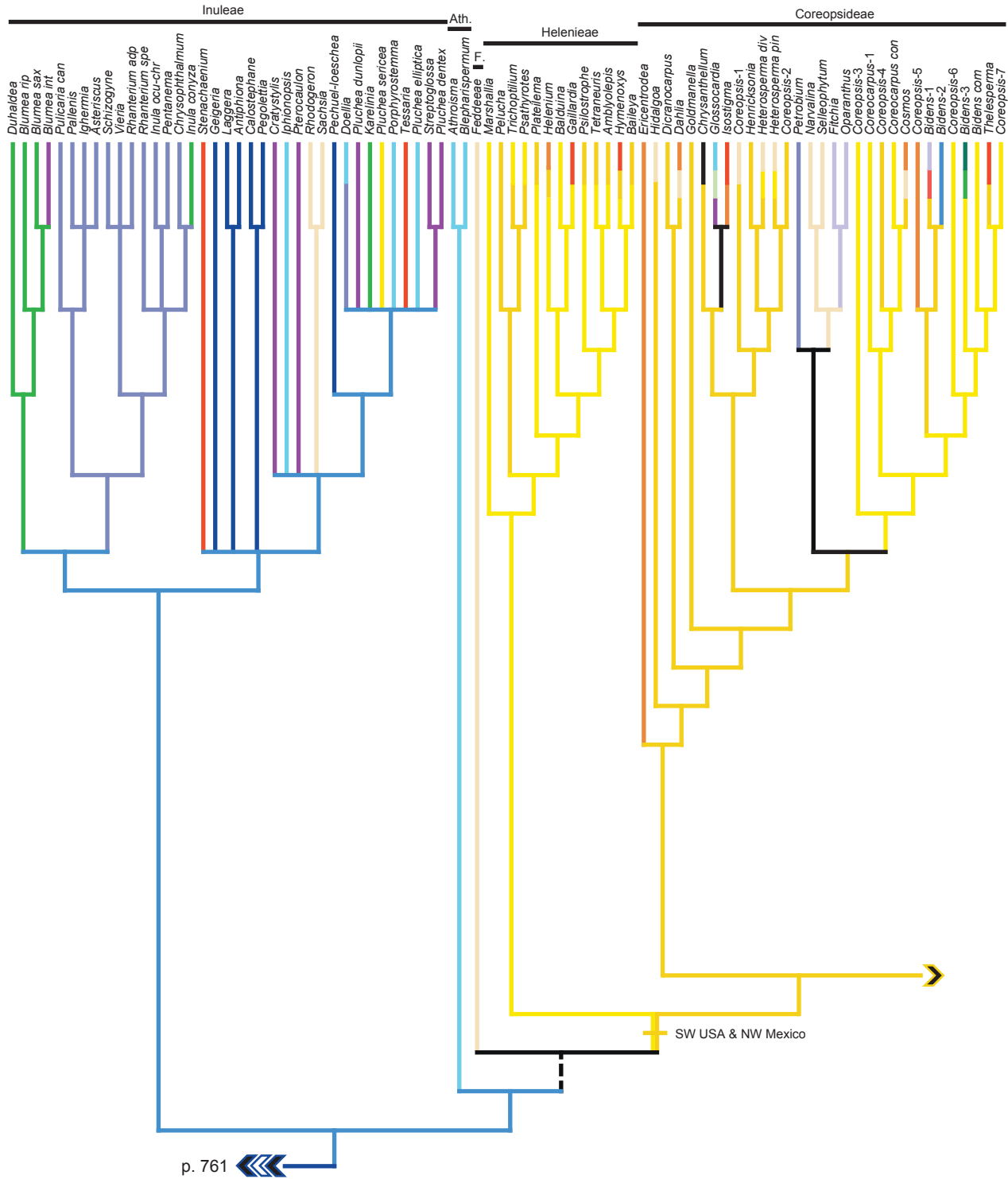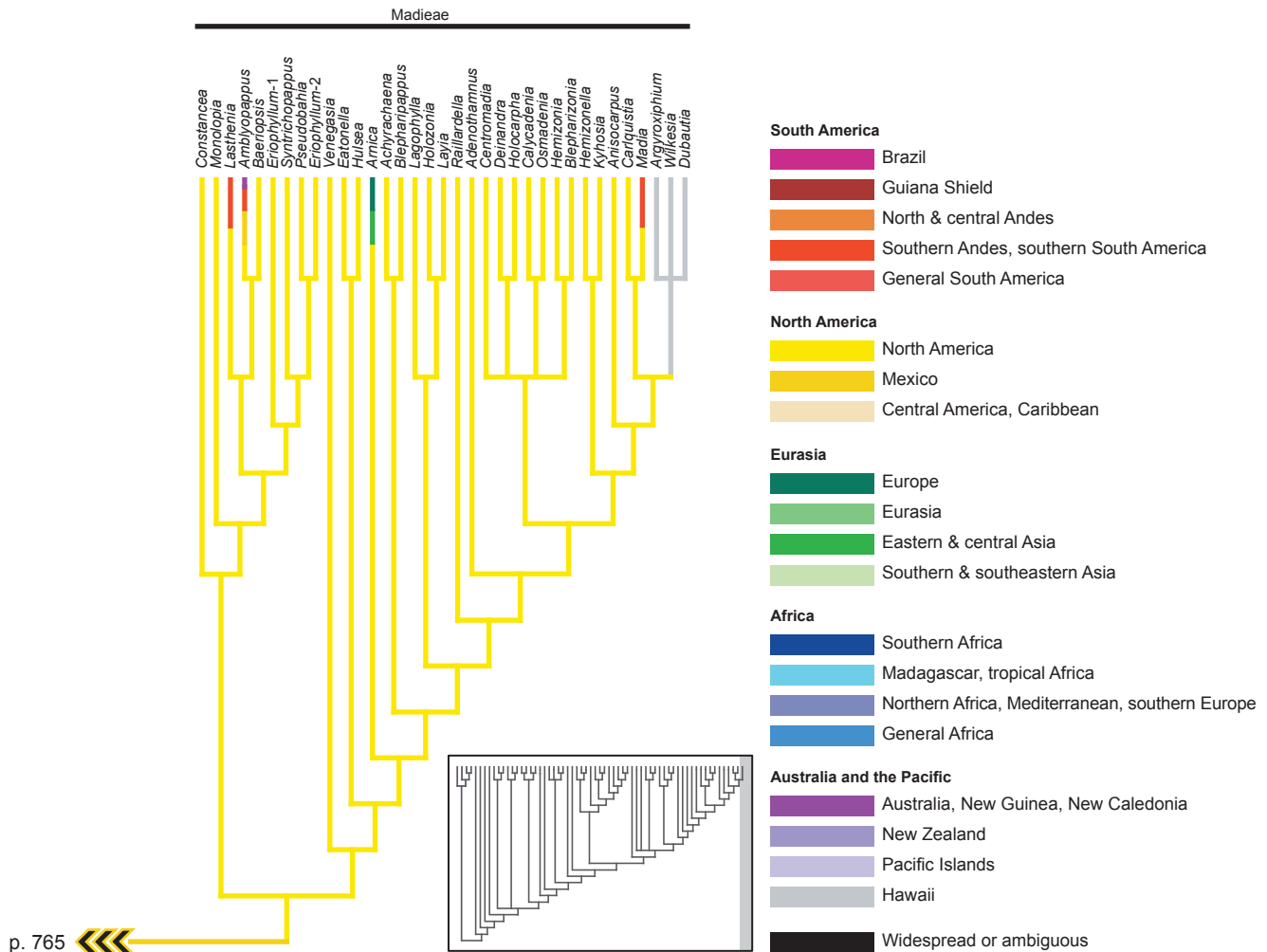combination of its capillary pappus, true rays, and a receptive area in two lines on the inside of the style branches.

Senecioneae have long been one of the largest and most difficult groups to understand; they are truly a global tribe with major radiations in sub-Saharan Africa, West and East Asia, Andean South America, and Mexico. Because of uncertainty about the phylogenetic positions of the core of Senecioneae and two of the genera usually assigned to this tribe, relationships among these taxa and the clade formed by the other Asteroideae tribes are presently unresolved.

Two genera of Senecioneae, *Doronicum* (Eurasia and northern Africa) and *Abrotanella* (Australasia and southern South America), "fall out" of monophyletic Senecioneae. Since there is a general problem of tribal relationships

among Senecioneae and its potential sister groups, there are not enough data to determine whether or not these two genera should stay in the tribe as subtribes or be moved to tribes of their own. The authors of the Senecioneae Chapter (Nordenstam et al., Chapter 34) have reserved final judgment on this matter until they have more information.

Within the core Senecioneae clade there are four clades that form a polytomy. One represents the bulk of the species, which are found in two monophyletic subtribes that are sister taxa (Othonninae + Senecioninae). This major clade has a sub-Saharan African base with highly nested groups of species from South America and Central America–Caribbean basin. The second clade, the core of subtribe Tussilagininae, has clades in Asia, Eurasia, North

Fig. 44.7. Inuleae, Athroismeae, and the Heliantheae Alliance. All taxa are in the subfamily Asteroideae. See p. 766 for color chart. Chaen. = Chaenactideae; F. = Feddeeae; Miller. = Millerieae; N. = Neurolaeneae; P. = Polymnieae; Perity. = Perityleae.

America, Mexico, and South America, but the relationships among these clades are not resolved. Two small clades complete Senecioneae. One is the South American genus *Chersodoma*, and the other is a clade composed of two groups: *(1)* an Australasian-Pacific subclade of nine genera, and *(2)* a subclade composed of a few succulent species from sub-Saharan Africa that were historically included in *Senecio* (*Senecio* m-w group, Fig. 44.5).

On the basis of the biogeographic patterns observed in the metatree, one can certainly propose a sub-Saharan origin for the Othonninae + Senecioninae clade and possibly a southern African origin for the tribe with radiations into other areas. The southern African origin

is reinforced by the fact that the most closely related clades in more basal and derived positions in the metatree have a southern African origin (i.e., Corymbieae and the clade made up by Calenduleae + Gnaphalieae + Astereae + Anthemideae).

The small tribe Calenduleae is found almost exclusively in Africa with its greatest diversity in southern Africa; the tropical and northern African groups are nested high in the tree. It is the sister taxon of Gnaphalieae + Anthemideae + Astereae clade (Figs. 44.5, 44.6).

The extant members of the Gnaphalieae had a major radiation in southern Africa early in their history with large radiations into Australia and New Zealand.

Although not reflected in this figure, this tribe also has large highly nested groups of taxa in South America and Asia indicating dispersal to these regions as well (Ward et al., Chapter 36).

Section 4, tribes Anthemideae and Astereae (Fig. 44.6, pp. 762, 763; Fig. 44.10C). — Sister to Gnaphalieae is the clade consisting of Anthemideae + Astereae (Fig. 44.6). The tribe Anthemideae has a southern African grade at the base followed by a Mediterranean–northern African clade as well as one or two Asian clades (Oberprieler et al. 2009, Chapter 38).

The phylogeny of the tribe Astereae (Fig. 44.6) is not as clearly based in southern Africa as are the other tribes in this clade: Calenduleae, Gnaphalieae, and Anthemideae. Nevertheless, this origin is the most parsimonious expla–nation for the basal grade of this tree. Although the tribe is nested among clades with a southern African origin, there are several taxa from other regions that are found in basal positions in the Astereae clade (e.g., *Nannoglottis* from south-central China, a clade from South America,

and one from New Zealand). More highly nested in the tribe are some tropical African and Asian groups as well a clade with representatives in South America, North America, and Australia, although their relationships to one another are somewhat unresolved.

The extant members of the large clade consisting of Calenduleae + Gnaphalieae + Anthemideae + Astereae, has an African origin, most likely sub-Saharan or south–ern Africa. As mentioned earlier it is possible that the Senecioneae are the sister group of this clade.

Section 5, tribes Inuleae, Athroismeae and the Heli-antheae alliance (Fig. 44.7, pp. 764–766; Fig. 44.10D–F). — The next clade on the metatree (Fig. 44.7) contains Inuleae (including Plucheeae). The tribe is divided into two subtribes, Plucheinae and Inulinae (Anderberg et al., Chapter 39). The Inulinae clade has a split between a Mediterranean–northern African clade and an Asian clade. The Plucheinae clade has a southern African basal polytomy (except for *Stenachaenium*) with a pantropical clade nested within (including southern Africa, tropical

Africa, and northern Africa). Given that one subtribe has the potential for being rooted in the Mediterranean–northern African area and the other in southern Africa and that the clades basal to Inuleae as well as Athroismeae are most likely rooted in sub-Saharan Africa or southern Africa, it seems likely that Inuleae have an African origin, and it is shown as 'General Africa' in origin in Fig. 44.7.

The tribe Athroismeae is the sister group of the Heliantheae Alliance and includes five genera from Africa, mostly from the tropical eastern region (Fig. 44.7). This clade marks the end of the African influence on the family and signals a dramatic shift to the Americas, most notably southwestern United States (SW USA) and northwestern Mexico (NW Mexico).

The recently described tribe Feddeeae is endemic to Cuba and is supported as being part of the Heliantheae Alliance (Cariaga et al. 2008). However, it may be the sister group to the rest of the Alliance, grouped near the base, or related to Athroismeae. For now it sits with some ambiguity at the base (Fig. 44.7).

The core Heliantheae Alliance begins with the tribe Helenieae and its sister group (Fig. 44.7). This clade has strong support. Many of the clades within the core Heliantheae Alliance are ambiguous as to whether they are rooted in Mexico or North America (north of Mexico). This is the result of the somewhat artificial political categories selected for the biogeographic portion of this analysis. Some of the clades of the Heliantheae Alliance are from both SW USA and NW Mexico and frequently switch from one location to the other or inhabit both. Other clades are more firmly affiliated with either Mexico or North America (north of Mexico). For instance, the tribe Madieae (Fig. 44.7) is almost totally in North America (north of Mexico) while Helenieae (Fig. 44.7A), Coreopsideae (Fig. 44.7), Tageteae (Fig. 44.7), and Bahieae (Fig. 44.7), are frequently found in both areas. For tribes such as Heliantheae (Fig. 44.7) and Millerieae (Fig. 44.7), there are too few taxa sampled to make a decision on the origin of these clades. These sampling concerns are minor since the root of the entire radiation is clearly in NW Mexico and the SW USA, with repeated incursions into Central America, the Andes, and back to North America. 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 pointed out that the endemic Californian diversity in the Heliantheae Alliance is mostly confined to one clade, Madieae.

Nested within the Heliantheae Alliance is the large and distinctive tribe Eupatorieae (Fig. 44.7), a large New World tribe with its base in Mexico and repeated dispersals to Brazil, South America, and North America.

What happened in the history of Compositae between the radiations in Africa and the Heliantheae Alliance in North America? Previously, Funk et al. (2005) speculated that since the base of the Heliantheae Alliance was in the SW USA and NW Mexico, the path from Africa to North America and Mexico might have been via Asia. However, if *Feddea* (Cuba) is the sister taxon of the core Heliantheae Alliance, then that proposition seems less likely. One possibility might be something like a peri-Tethyan dispersal, but these dates (late Triassic 6–2 Ma) would make the clade much younger than previously thought. Much depends on whether or not *Feddea* is ultimately supported as the sister group of the core Alliance.

The summary trees for the family (Figs. 44.1, 44.2) show the results of the parsimony mapping of the distributions. In this condensed tree it is even more evident that extant Compositae had a South American base with an African diversification and radiation into Asia, Eurasia, Europe, Australia, etc. followed by the burst of diversification in North America. The unrooted diagram provided greater clarity as to the biogeographic patterns of the phylogeny (Fig. 44.2).

Odd genera

Throughout the history of the classification of Compositae there have been a number of difficult-to-place genera. Funk et al. (2005) and Panero and Funk (2008) discussed how important these genera were to resolving biogeographic hypotheses for the family. These problem genera were traditionally grouped with taxa that they were "less different from" rather than groups with which they shared characters. It is interesting to note that many of these taxa have secondary or tertiary heads, with primary heads reduced to one or a few florets and then re-aggregated onto a common receptacle. As a result they usually lack ray florets and do not have the common involucral and receptacular characters, adding to the difficulty of assigning them to tribe.

The advent of molecular data has allowed us to determine the relationships of many of these odd genera. 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 relatively species-poor sister groups of large radiations: *Cratystylis*, in Plucheinae, Athroismeae, or even *Feddea*, as the sister group to the Heliantheae Alliance, *Corymbium* as the sister group to Asteroideae, *Platycarpha* as the sister group to the Vernonieae + Liabeae clade, *Gymnarrhena* as the sister group of Cichorioideae + Asteroideae, African Mutisieae at the base of the thistles, and *Hecastocleis* as the sister group to the major radiation of the family. All of these have important phylogenetic positions for the biogeographic analysis and

illustrate the fact that odd taxa should always be included in analyses at all levels (Funk et al. 2005; Funk and Chan, 2008; Panero and Funk 2008). Although, some of these taxa are on long branches and their position may be affected by 'long branch attraction'.

Age of origin

Considering the size and importance of Compositae, surprisingly little has been published about the possible area of its origin or its age since Bentham (1873a, b). As mentioned before, one reason may be because of the absence of any reliable macrofossils from the early diversificaiton of the family. A few individuals have guessed at a possible age. Turner (1977) thought that the family originated in the mid–late Cretaceous (ca. 100 Ma), possibly near the time of the first upheaval of the Andes (ca. 90 Ma). Other recent estimates include 60 Ma (Zavada and de Villiers 2000), 53–43 Ma from DeVore and Stuessy (1995), and 38 Ma from Bremer and Gustafsson (1997). In the 2005 supertree paper (Funk et al.), an examination of the relationship of Compositae to its two most closely related families was used to suggest an age of around 50 Myr for the separation of Compositae + Calyceraceae (southern South America) from Goodeniaceae (Australia).

Lundberg's study (Chapter 10) included the whole of the order Asterales. In addition to Goodeniaceae, the other families of the order that are closely related to Compositae are all found in Australia, New Guinea, New Caledonia, and/or New Zealand (Fig. 44.3). As a result of these distribution patterns, one can hypothesize that the ancestor of these eight families of Asterales had a Gondwanan distribution, and that the split between the ancestor of Goodeniaceae and the ancestor of Calyceraceae + Compositae took place with the formation of the Drake Passage that separated South America and Australia from Antarctica. Estimations of when that passage was formed range from middle Eocene to Oligocene to early Miocene but recent evidence narrows it to 50–41 Ma (Ghiglione et al. 2008 and references cited therein). The earlier date reflects a spreading with low incursions of water and the younger time period reflects a deeper water passage. The question then becomes how deep and wide did the Drake Passage have to be to prevent easy dispersal of pollen and seeds? Other factors to consider include the fact that the oldest part of the Andes Mountains is the southern section, and the uplift of this area began ca. 90 Ma and lasted until ca. 50 Ma. The mountains were high enough to cause a drying effect only late in this time period; in fact, pollen records show that 53 Ma southern South America was forested. So, the earliest time of separation between the continents coincides with the final uplift of the southern mountains. Geological, climatic, and ecological considerations, therefore, can be used to suggest an origin of the Calyceraceae–Compositae clade at some time after 50 Ma

(perhaps as recent as 41 Ma), with the base of Compositae radiating as the Andes developed. Since Africa drifted away from Gondwana some time before South America and Australia each drifted away from Antarctica, it appears unlikely that the movement of the African continent had any influence on the base of the cladogram.

Within the family, 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 (25–22 Ma; Muller 1981). An older date is given by Graham (1996) who dates the earliest pollen from Mutisieae as Eocene to middle Oligocene (50–25 Ma), pollen from the Astereae-Heliantheae-Helenieae group as Eocene (50–35 Ma), and pollen of the *Ambrosia*-type (Heliantheae) from latest Eocene/early Oligocene (35–25 Ma). Given the phylogenetic position of taxa with the *Ambrosia*-type pollen, we can use the date of 35–25 Ma for the base of the Heliantheae Alliance (Fig. 44.8). There are four Hawaiian taxa estimated to have diverged 7–5 Ma nested high in the metatree. A radiation in the northern Andes (Espeletiinae), with an age of approximately 2 Myr, is in line with the occurrence of the sub-páramo habitat. The tribe Liabeae is a north-central Andean clade that can be dated 15–5 Ma when the central Andes were uplifted. Finally, there are taxa from the basal grade that are found on the Guiana and Brazilian Shields; these plants inhabit areas where the rock is older than the family. For instance, in the Guiana Shield area, the final uplift was probably in the Cretaceous (Gibbs and Barron 1993), and so predates the origin of Compositae and is of no help in determining the ages of those clades.

The authors of some of the chapters in this book have speculated as to the age of origin of their clades. The Barnadesieae clade, which is the sister group to the rest of the family, is estimated to be at least 23 Myr old (Stuessy et al., Chapter 13). A minimum age of 23–28 Myr (Late Oligocene) for fossil pollen related to the extant genera of Gochnatieae, and a minimum of 20–23 Myr (Early Miocene) for fossil pollen of Nassauvieae and Barnadesieae were reported (Katinas et al. 2007). On the basis of ITS divergence, Wang et al. (2007) suggested a date of 29–24 Ma for the separation of Cardueae from the African (former Mutisieae) tribes; and in Chapter 20, Susanna and Garcia-Jacas stated that Cardueae originated as part of the Tertiary flora and benefited extensively from the new habitats that were open during the deep climatic and geological changes during the Miocene (24–5 Ma), based on data from Cox and Moore (2004). In Cichorieae, Kilian et al. (Chapter 24) point out that the fossil record shows three different types of echinolophate pollen, i.e., the *Cichorium intybus* L. type (age 22–28.4 Myr; Hochuli 1978), the *Scorzonera hispanica* L. type (minimum age 3.4 Myr; Blackmore et al. 1986), and the *Sonchus oleraceus* type (minimum age 5.4 Myr; Blackmore et al. 1986),
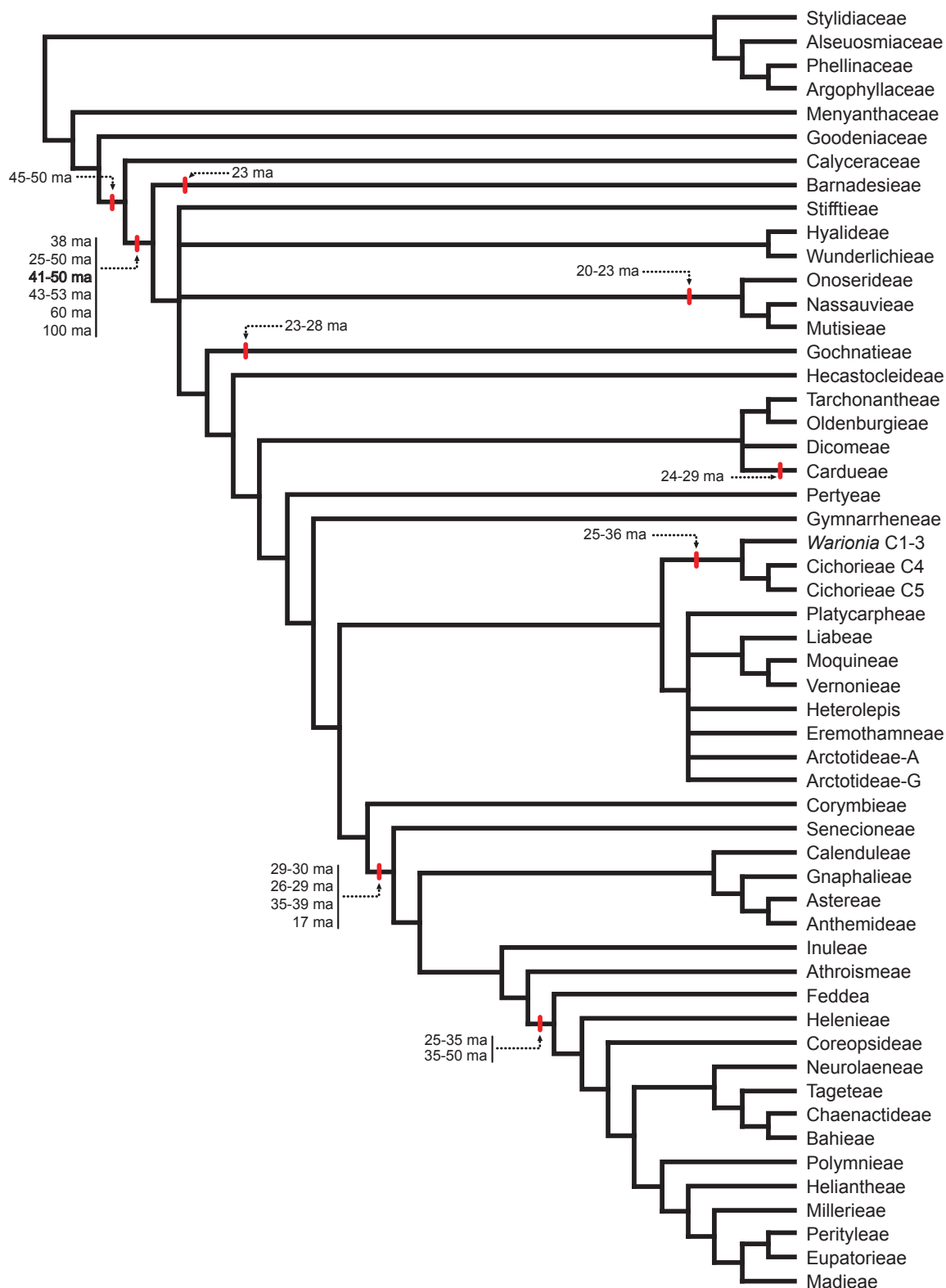
Fig. 44.8. There are few dates that can be placed on the phylogeny of Compositae with any certainty. The separation of the outgroup lineages from that of Calyceraceae–Compositae may be placed at a time when Australia separated from Antarctica– South America (the flora is believed to have separated about 50–41 Ma), and the radiation at the base of Compositae may be linked to uplift of the southern Andes.

that were used to calibrate the phylogenetic tree; and estimates were calculated by using an uncorrelated relaxed molecular clock approach (Drummond et al. 2006). The results indicated a most probable origin of the tribe in the Late Eocene or Oligocene (36.2–25.8 Ma; Tremetsberger et al., unpub. data) in North Africa.

Pelser and Watson (Chapter 33) discussed the age of the subfamily Asteroideae on the basis of age estimates in the recent literature. Hershkovitz et al. (2006) estimated the crown age of Asteroideae to be ca. 29–30 Myr. Kim et al. (2005) used nonparametric rate smoothing in their molecular dating study of *ndhF* data and *Cornus* as an internal calibration point and arrived at an estimate for the subfamily of 26–29 Myr. Their age estimate for Asteroideae derived from average synonymous nucleotide substitutions using the same dataset and substitution rates for Poaceae and Oleaceae was 35–39 Myr (Kim et al. 2005). These studies and unpublished data for Senecioneae (Pelser et al., in prep.) further indicate that the Heliantheae Alliance and all Asteroideae tribes outside of it are 17 Myr old or older and were the result of a family-wide, rapid Oligocene–Early Miocene diversification. These results are roughly in line with other molecular dating studies in Compositae (e.g., Wikström et al. 2001; Wagstaff et al. 2006) and with paleo-palynological data (e.g., Katinas et al. 2008), although the latter source of data generally results in somewhat lower age estimates for Asteraceae lineages.

Most of the dates discussed above are displayed on Fig. 44.8 and if we eliminate some of the outliers, we find that all of the tribes are proposed to have, more or less, the same age, around 25–35 Myr, and the age of the family seems to be 41–50 Myr. Initiation of all of the known major radiations of Compositae 35–25 Ma places their origins within the Oligocene, which is often considered an important time of transition, a link between "[the] archaic world of the tropical Eocene and the more modern ecosystems of the Miocene" (Scotese 2008). It makes ecological sense that a rapid expansion of the number of taxa in many groups of Compositae would have coincided with the regression of tropical broad-leaf forests to the equatorial belt and the expansion of open, drier areas.

The comparatively recent origin and great diversity of Compositae are likely indicative of the ecological success and evolutionary lability of the family (as is evidenced by their diverse appearance in Figs. 44.9 and 44.10), especially in drier environments. 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." It seems likely that the high seed set, dispersal ability, and ability to radiate into new habitats have helped as well.

Barker et al. (2008) examined gene duplication and retention in Compositae and found that there were at least three ancient whole genome duplications in the family resulting from paleopolyploidization events: at the base of the family just prior to its radiation, and near the base of tribes Mutisieae and the large Heliantheae Alliance. As one explanation for Compositae's evolutionary success, they suggest that retention of the resulting duplicates of *CYCLOIDEA* genes, which code for transcription factors associated with floral symmetry and branching patterns, were likely significant in the evolution of Compositae, because Chapman et al. (2008) observed that some copies have experienced positive selection and that the expression of *CYC* genes is subfunctionalized among the disk and ray florets of the composite inflorescence. Thus, ancient polyploidization may be, in part, responsible for the evolutionary success of the family.

CONCLUSIONS

The Calyceraceae-Compositae clade (as we know it today) may have originated in southern South America ca. 50–41 Ma, and the diversification of the family started in the same area. The diversification of Calyceraceae was modest by comparison with that of Compositae, which have traveled the globe. In Compositae, following the southern South American radiation, there was an African explosion. Of the 1600–1700 genera in Compositae today, about two-thirds are in clades with the basal branches in Africa, many in southern Africa. In fact, with the exception of the Mutisieae (sensu Cabrera) grade at the base and the highly nested Heliantheae Alliance, all of the major clades in the family appear to have an African origin or a major African presence near the base of their phylogenies. From this African origin came numerous movements into Asia, Eurasia, Europe, Australia, etc., many of which have spawned substantial radiations (e.g., Cardueae, Vernonieae, Anthemideae). The clade formed by the core Heliantheae Alliance has a North American (including NW Mexico) origin beginning by 35–22 Ma, which coincides with a land bridge connection from Asia. Previously (Funk et al. 2005) it was suggested that, because the sister clade to the Heliantheae Alliance is found in tropical eastern Africa, the ancestor of the Heliantheae Alliance could have come over the land bridge from Asia into western North America and down into Mexico. However, the position of the Cuban *Feddea* at the base of the American clade of the Heliantheae Alliance does not reinforce a land-bridge hypothesis. Given the success of a diversity of young lineages in the Heliantheae Alliance and long-distance dispersal to remote oceanic islands and between continents (see Baldwin 2009, Chapter 41), the possibility of a direct Old World to New World dispersal
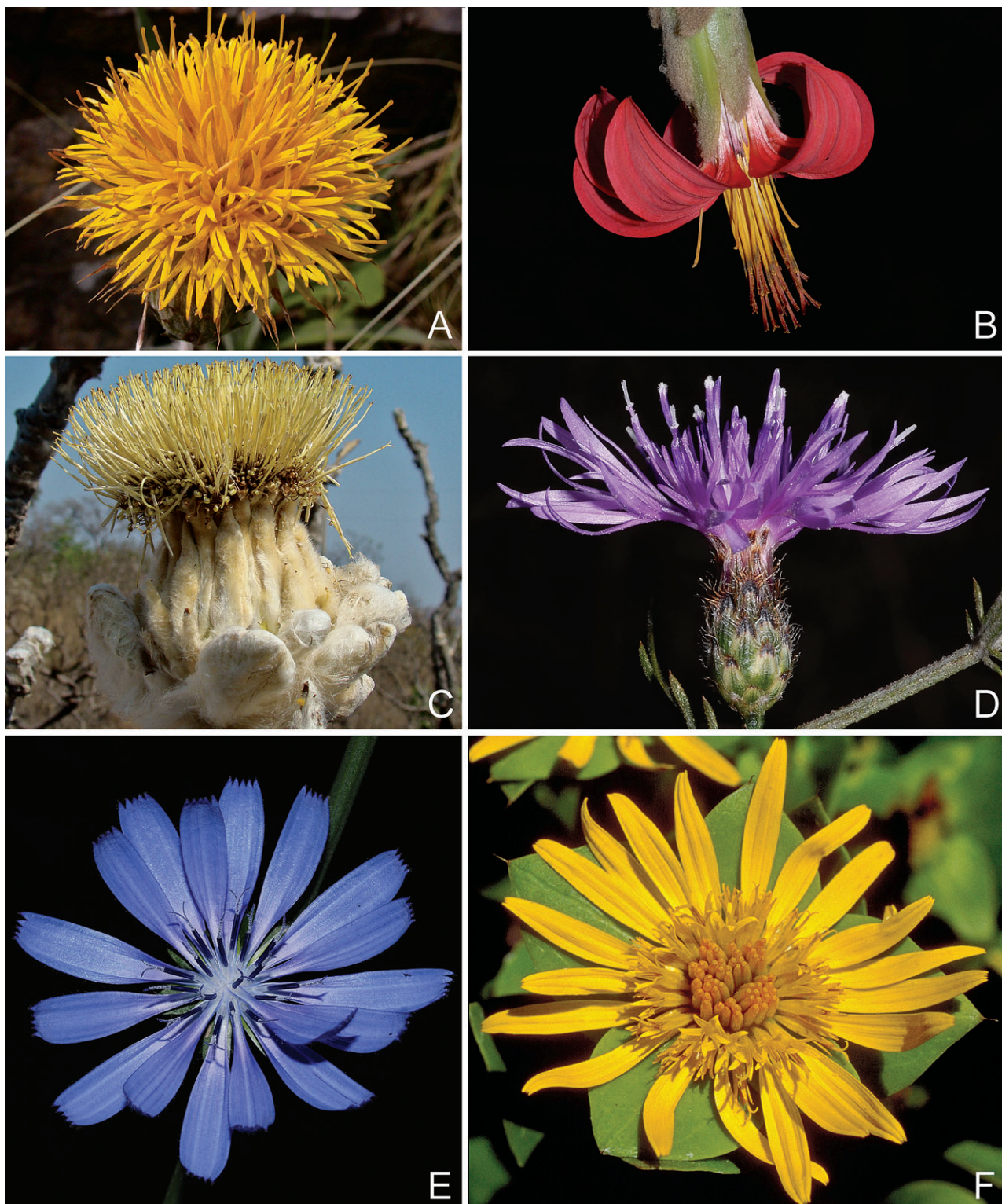
Fig. 44.9. Members of Compositae, subfamilies Barnadesioideae through Cichorioideae. **A** *Schlechtendalia luzulaefolia* Less. (Barnadesieae from Uruguay: Maldonado, Piriápolis, Cerro San Antonio); **B** *Mutisia clematis* L. (Mutisieae from Colombia: Cundinamarca, Finca "El Cerro"); **C** *Wunderlichia mirabilis* Riedel (Wunderlichieae from Brazil: Minas Gerais, Cerra do Cipó; *Roque 1622*); **D** *Centaurea stoebe* L. (Cardueae from USA: Virginia, Shenandoah National Park); **E** *Cichorium intybus* L. (Cichorieae from Uruguay: Montevideo); **F** *Didelta spinosa* Ait. (Arctotideae from South Africa, Northern Cape: *Funk and Koekemoer 12641*). [Photographs: A, B, D, E, J.M. Bonifacino; C, N. Roque; F, V.A. Funk]

Fig. 44.10. Members of Compositae subfamily Asteroideae. **A** *Senecio ceratophylloides* Griseb. (Senecioneae from Uruguay: Canelones); **B** *Dimorphotheca sinuata* DC. (Namibia); **C** *Bellis perennis* L. (Astereae from Argentina: Tierra del Fuego, close to Paso Garibaldi); **D** *Stenachaenium megapotamicum* (Spreng.) Baker in Mart. (Inuleae from Uruguay: Maldonado, Sierra de las Animas); **E** *Helianthus annuus* L. (Heliantheae s.str. from Uruguay: Río Negro, close to Fray Bentos); **F** *Gyptis pinnatifida* Cass. (Eupatorieae from Uruguay: Rivera, Arroyo Lunarejo). [Photographs: B, C.A. Mannheimer; A, C–F, J.M. Bonifacino.]

of the ancestor of the American clade of the Heliantheae Alliance must be taken seriously.

What about *Hecastocleis*? This monotypic North American genus from the mountains of Nevada and the Death Valley area sits between the southern South American basal radiation and the African diversification. In Funk et al. (2005) two possible scenarios were proposed (apart from errors and misidentifications). First, there could have been two events of long distance dispersal, one from South America to North America and one from North America to Africa. The second possibility is that Compositae moved into North America from South America, then over to Europe and down into northern Africa followed by extensive extinction in the northern hemisphere (Panero and Funk 2008). There are, no doubt, other explanations; however, we do not have sufficient data to favor one hypothesis over another. One key group, Gochnatieae, is located just below *Hecastocleis* on the metatree, and it is being studied at the species level using both molecular and morphological data in the hope of providing a better estimation of the early biogeographic history of Compositae (Sancho et al., pers. comm.).

Prior to the development of molecular techniques, most workers in the family followed the traditional concept of the family laid down by Bentham and elaborated upon in Cronquist (1955, 1977). Cronquist had detailed ideas about the characteristics of ancestral Compositae. He believed that the tribe Heliantheae, and more specifically core Heliantheae, were the cauldron out of which the rest of the tribes evolved. He thought that the ancestor might have been something like *Viguiera* (Heliantheae s.l.), but he pointed out that it was still "not exact" because the genus has neutral ray florets and only two principal pappus members (Cronquist 1977). Several scientists disagreed with Cronquist. Skvarla (1977) and Jeffrey (1977) pointed out that the characters were not consistent with the position that Heliantheae s.l. was the primitive group of the family. In publications outside the 1977 Heywood et al. volumes, Carlquist (1966, 1976) and Robinson (1981) tried to add additional tribes and to point out that the proposed direction of evolution did not make sense. These synantherologists thought that the pollen, anatomy, and morphology of Mutisieae were more like that of the related families, and that Heliantheae and other tribes had derived characters.

Acknowledging that extant lineages of Barnadesieae have been around for as long as the most highly nested branches of the family, it is wise to not put too much emphasis on the characteristics that are found in this basally diverging group but rather on characteristics that are shared by all early diverging branches and the outgroups. Many characters of Barnadesieae and Mutisioideae are variable (e.g., corolla morphology), but a few common

characteristics can probably be determined: the pollen was probably psilate (Skvarla 1977; Zao et al. 2006; Blackmore et al., Chapter 7); the basal chromosome number for the closely related families is $x = 9$ and that number has been proposed for Compositae with $x = 10$ as the apparent basal number for tribes of South African origin (Semple and Watanabe, Chapter 4); and secondary chemical compounds have developed from a small number of relatively simple flavonoids, polyacetylenes, coumarins, and triterpenes to a large number of complex compounds from many different chemical classes (Calabria et al., Chapter 5).

Bremer (1994) started the process of updating the characters attributed to a hypothetical ancestor and Lundberg (Chapter 11) has added to the list. Here we have refined some of the characters and added a few more. Here we offer a list of potential plesiomorphic characters for the extant members of Compositae (⋆ indicates that the character defines a larger clade than the Calyceraceae + Compositae clade; bold indicates a potential character unique to the ancestral members of Compositae):

❍ ⋆Shrubs or subshrubs; ⋆no internal secretory systems.

❍ **Inflorescence cyme-like.**

❍ ⋆Leaves alternate and spirally inserted.

❍ **Heads indeterminate;** few heads per plant, each with many flowers.

❍ **Involucral bracts in several series, imbricate without hyaline or scabrous margins.**

❍ **Receptacle naked.**

❍ Florets perfect and fertile, arranged in a head; ⋆parts in 5's; mostly one type of flower, **some differentiation in floral morphology in peripheral florets possible** but without true rays.

❍ Corolla white or possibly pink, yellow or blue; ⋆probably 5-lobed, lobes deeply divided and with much variation.

❍ ⋆Stamens alternate with the corolla lobes; **anthers fully connate at the margins with the filaments free** with upper part of filaments forming a filament collar; **thecae spurred (calcerate) and possibly tailed (caudate);** possibly without apical appendage; ⋆dehisce by longitudinal slits; pollen kit present.

❍ **Pollen grains 3-celled,** ⋆pollen prolate and psilate.

○ Styles slender, shortly bifid, without hairs; **solid band of stigmatic surface on inside of style branches; ovary consistently inferior with ovule in a basal position.**

○ **Pappus of capillary bristles.**

○ Fruit an indehiscent achene; ribbed.

○ ⋆Base chromosome number: $x = 9$.

○ Secondary chemistry simple and characterized by a small number of flavonoids, polyacetylenes, coumarins, and triterpenes.

○ Southern South American in distribution; probably growing in open dry habitats.

Finally, looking to the future, advances in genomics are changing the way we do research in systematics. Phylogenomics, the use of whole genomes for phylogenetic studies, is already occurring in many plant and animal groups and at ever increasing speeds (see brief overview in Pennisi 2008) and will no doubt become the standard of the future in Compositae systematics as costs decrease and technology becomes more widely available. Whole chloroplast genomes have already been sequenced for many plant groups and used in phylogenetic studies, particularly for establishing the position of basal angiosperms (Goremykin et al. 2004; Soltis et al. 2004). Phylogenomic studies in Compositae lag considerably behind those of the Angiosperm Phylogeny Group (APG) and that of many animals groups as well. Although the genomes of a number of Cichorioideae taxa are currently under study (Rieseberg, pers. comm.) only two economically important taxa, *Helianthus annuus* L. and *Lactuca sativa* L., are the subject of a coordinated, large scale effort. The Compositae Genome Project (CGP), headquartered at the UC Davis Genome Center, has a wide range of objectives for its studies of lettuce and sunflower (and presumably others in the future). The goal as given on the home page (http://compgenomics.ucdavis.edu/index.php) is to "integrate information at the genetic, physiological and population/evolutionary levels for a broad range of genes involved in evolution of cultivated plants and weeds, evaluate the relative importance of changes in gene sequence versus gene expression in phenotypic evolution, determine the genotypic consequences of parallel phenotypic evolution, and provide a basis for future functional analyses." For most systematists, however, the focus of whole genome sequencing will be on more accurately reconstructing the evolutionary history of a particular group of plants, most of which are not cultivated and for which the vast funding required to map genes and determine their functions will likely never be available.

As in all molecular studies, a cautionary note has been sounded relative to the resolving power of genomics for phylogenetic study (Soltis et al. 2004; Pennisi 2008). Data analysis of huge numbers of sequences is daunting and will probably still require collaboration with mathematicians and bioinformaticists. Another issue is lack of congruence, particularly with existing trees. Hervé Philippe (University of Montreal; cited in Pennisi 2008) stresses that datasets will have to be reanalyzed with different methods in order to determine the best tree. The latter is not necessarily guaranteed by more data. Additionally, taxon sampling will remain an issue. Lots of information from only a few taxa does not guarantee a sound phylogeny no matter how cutting-edge the sequencing or the analyses. Still, we can expect that genomes will be increasingly common tools in future phylogenetic studies. Hopefully, as the data accumulate there will be better resolution of taxonomic placements, particularly in the location of Senecioneae and at the base of the Compositae family tree where the position of some mutisioids and some enigmatic genera remain unclear.

Literature cited

Anderberg, A.A. 1989. Phylogeny and reclassification of the tribe Inuleae (Asteraceae). *Canadian Journal of Botany.* 67: 2277–2296.

Anderberg, A.A. 1991. Taxonomy and phylogeny of the tribe Inuleae (Asteraceae). *Plant Systematics and Evolution* 176: 75–123.

Anderberg, A.A. & Eldenäs, P. 2007 [2006]. Tribe Inuleae. Pp. 374–391 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales*. Springer, Berlin.

Anderberg, A.A., Eldenäs, P., Bayer, R.J. & Englund, M. 2005. Evolutionary relationships in the Asteraceae tribe Inuleae (incl. Plucheeae) evidenced by DNA sequences of *ndhF*; with notes on the systematic positions of some aberrant genera. *Organisms, Diversity and Evolution* 5: 135–146.

Baldwin, B.G., Wessa, B.L. & Panero, J.L. 2002. Nuclear rDNA evidence for major lineages of helenioid Heliantheae (Compositae). *Systematic Botany* 27: 161–198.

Barker, M.S., Kane, N.C., Matvienko, M., Kozik, A., Michelmore, R.W., Knapp, S.J. & Rieseberg, L.H.

2008. Multiple paleopolyploidizations during the evolution of the Compositae reveal parallel patterns of duplicate gene retention after millions of years. *Molecular Biology and Evolution* 25: 2445–2455.

Bayer, R.J., Breitwieser, I., Ward, J.M. & Puttock, C.F. 2007 [2006]. Gnaphalieae. Pp. 246–284 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales.* Springer, Berlin.

Bentham, G. 1873a. Compositae. Pp. 163–533 in: Bentham, G. & Hooker, J.D. (eds.), *Genera Plantarum*, vol. 2(1). Reeve, London.

Bentham, G. 1873b. Notes on the classification, history and geographical distribution of Compositae. *Journal of the Linnean Society, Botany* 13: 335–577.

Bininda-Emonds, O.R.P., Jones, K.E., Price, S.A., Grenyer, R., Cardillo, M., Habib, M., Purvis, A. & Gittleman, J.L. 2003. Supertrees are a necessary not-so-evil: a comment on Gatesy & al. *Systematic Biology* 52: 724–729.

Blackmore, S., Van Campo, E. & Crane, P.R. 1986. Lophate Compositae pollen from the Miocene and Pliocene of the Mediterranean region. *Pollen et Spores* 28: 391–402.

Bremer, K. 1987. Tribal interrelationships of the Asteraceae. *Cladistics* 3: 210–253.

Bremer, K. 1992. Ancestral areas—a cladistic reinterpretation of the center of origin concept. *Systematic Biology* 41: 436–445.

Bremer, K. 1994. *Asteraceae: Cladistics & Classification.* Timber Press, Portland.

Bremer, K. 1996. Major clades and grades of the Asteraceae. Pp. 1–7 in: Hind, D.J.N. & Beentje, H.J. (eds.), *Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1., *Compositae: Systematics.* Royal Botanic Gardens, Kew.

Bremer, K. & Gustafsson, M.H.G. 1997. East Gondwana ancestry of the sunflower alliance of families. *Proceedings of the National Academy of Sciences of the United States of America* 94: 9188–9190.

Bremer, K. & Jansen, R.K. 1992. A new subfamily of the Asteraceae. *Annals of the Missouri Botanical Garden* 79: 414–415.

Brooks, D.R. 1982. Hennig's parasitological method: a proposed solution. *Systematic Zoology* 30: 229–249.

Brooks, D.R. & McLennan, D.A. 2002. *The Nature of Diversity: An Evolutionary Voyage of Discovery.* University of Chicago Press, Chicago and London.

Cabrera, A.L. 1977. Mutisieae—systematic review. Pp. 1039–1066 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), *The Biology and Chemistry of the Compositae*, vol. 2. Academic Press, London.

Cariaga, K.A., Pruski, J.F., Oviedo, R., Anderberg, A.A., Lewis, C.E. & Francisco-Ortega, J. 2008. Phylogeny and systematic positon of *Feddea* (Asteraceae: Feddeeae): a taxonomically enigmatic and critically endangered genus endemic to Cuba. *Systematic Botany* 33: 193–202.

Carlquist, S. 1966. Wood anatomy of Compositae. A summary, with comments on factors controlling wood evolution. *Aliso* 6: 25–44.

Carlquist, S. 1976. Tribal interrelationships and phylogeny of the Asteraceae. *Aliso* 8: 465–492.

Cassini, H. 1816. Troisième mémoire sur les Synanthérées. *Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts* 82: 116–146.

Chapman, M.A., Leebens-Mack, J. & Burke, J. 2008. Positive selection and expression divergence following gene duplication in the sunflower *CYCLOIDEA* gene family. *Molecular Biology and Evolution* 25: 1260–1273.

Cox, C.B. & Moore, P.D. 2004. *Biogeography. An Ecological and Evolutionary Approach.* Blackwell, Oxford.

Cronquist, A. 1955. Phylogeny and taxonomy of the Compositae. *American Midland Naturalist* 53: 478–511.

Cronquist, A. 1977. The Compositae revisited. *Brittonia* 29: 137–153.

DeVore, M.L. & Stuessy, T.F. 1995. The place and time of origin of the Asteraceae, with additional comments on the Calyceraceae and Goodeniaceae. Pp. 23–40 in: Hind, D.J.N., Jeffrey, C. & Pope, G.V. (eds.), *Advances in Compositae Systematics.* Royal Botanic Gardens, Kew.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* 4(5): e88 doi:10.1371/journal.pbio.0040088.

Eldenäs, P., Källersjö, M. & Anderberg, A.A. 1999. Phylogenetic placement and circumscription of tribes Inuleae s.str. and Plucheeae (Asteraceae): evidence from sequences of chloroplast gene *ndhF. Molecular Phylogenetics and Evolution* 13: 50–58.

Eriksson, T. 1991. The systematic position of the *Blepharispermum* group (Asteraceae, Heliantheae). *Taxon* 40: 33–39.

Farris, J.S. 1970. Methods of computing Wagner trees. *Systematic Zoology* 19: 83–92.

Funk, V.A., Bayer, R.J., Keeley, S., Chan, R., Watson, L., Gemeinholzer, B., Schilling, E., Panero, J.L., Baldwin, B.G., Garcia-Jacas, N., Susanna, A. & Jansen, R.K. 2005. Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. *Biologiske Skrifter* 55: 343–374.

Funk, V.A. & Chan, R. 2008. Phylogeny of the spiny African daisies (Compositae, tribe Arctotideae, subtribe Gorteriinae) based on *trnL-F, ndhF*, and ITS sequence data. *Molecular Phylogenetics and Evolution* 48: 47–60.

Funk, V.A., Chan, R. & Keeley, S.C. 2004. Insights into the evolution of the tribe Arctoteae (Compositae: subfamily Cichorioideae s.s.) using *trnL-F, ndhF*, and ITS. *Taxon* 53: 637–655.

Funk, V.A., Robinson, H. & Dillon, M.O. 1996. Liabeae: taxonomy, phylogeny and biogeography. Pp. 545–567 in: Hind, D.J.N. & Beentje, H.J. (eds.), *Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1, *Compositae: Systematics.* Royal Botanic Gardens, Kew.

Funk, V.A. & Specht, C. 2007. Meta-trees: grafting for a global perspective. *Proceedings of the Biological Society of Washington* 120: 232–240.

Gatesy, J., Matthee, C., DeSalle, R. & Hayashi, C. 2002. Resolution of a supertree/supermatrix paradox. *Systematic Biology* 51: 652–664.

Gemeinholzer, B. & Bachmann, K. 2003. Reconstruction of the phylogeny of the Lactuceae (Asteraceae) using the Internal Transcribed Spacer regions ITS 1+2. *Compositae Newsletter* 40: 15–16.

Germeraad, J.H., Hopping, C.A. & Muller, J. 1968. Palynology of Tertiary sediments from tropical areas. *Review of Palaeoboany and Palynology* 6: 189–348.

Ghiglione, M.C., Yagupsky, D., Ghidella, M. & Ramos, V.A. 2008. Continental stretching preceding the opening of the Drake Passage: evidence from Tierra del Fuego. *Geology* 36: 643–646.

Gibbs, A.K. & Barron, C.N. 1993. *The Geology of the Guiana Shield.* Oxford University Press, New York.

Goremykin, V.V., Hirsch-Ernst, K.I., Wolfl, S. & Hellwig, F.H. 2004. The chloroplast genome of *Nymphaea alba*: whole-genome analyses and the problem of identifying the

most basal angiosperm. *Molecular Biology and Evolution* 21: 1445–1454.

Graham, A. 1996. A contribution to the geologic history of the Compositae. Pp. 123–140 in: Hind, D.J.N. & Beentje, H.J. (eds.), *Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1, *Compositae: Systematics*. Royal Botanic Gardens, Kew.

Gruenstaeudl, M., Urtubey, E., Jansen, R.K., Samuel, R., Barfuss, M.H.J. & Stuessy, T.F. 2009. Phylogeny of Barnadesioideae (Asteraceae) inferred from DNA sequence data and morphology. *Molecular Phylogenetics and Evolution* 51: 572–587.

Gustafsson, M.H.G., Backlund, A. & Bremer, B. 1996. Phylogeny of the Asterales sensu lato based on *rbcL* sequences with particular reference to the Goodeniaceae. *Plant Systematics and Evolution* 199: 217–242.

Gustafsson, M.H.G., Grafström, E. & Nilsson, S. 1997. Pollen morphology of the Goodeniaceae and comparisons with related families. *Grana* 36: 185–207.

Gustafsson, M.H.G., Pepper, A.S.-R., Albert, V.A. & Källersjö, M. 2001. Molecular phylogeny of the Barnadesioideae (Asteraceae). *Nordic Journal of Botany* 21: 149–160.

Hansen, H.V. 1991a. Phylogenetic studies in Compositae tribe Mutisieae. *Opera Botanica* 109: 1–50.

Hansen, H.V. 1991b. SEM-studies and general comments on pollen in tribe Mutisieae (Compositae) sensu Cabrera. *Nordic Journal of Botany* 10: 607–623.

Hershkovitz, M.A., Arroyo, M.T.K., Bell, C. & Hinojosa, L.F. 2006. Phylogeny of *Chaetanthera* (Asteraceae; Mutisieae) reveals both ancient and recent origins of the high elevation lineages. *Molecular Phylogenetics and Evolution* 41: 594–605.

Heywood, V.H. (ed.). 1993. *Flowering Plants of the World.* Oxford University Press, New York.

Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.). 1977. *The Biology and Chemistry of the Compositae*, 2 vols. Academic Press, London.

Himmelreich, S., Källersjö, M., Eldenäs, P. & Oberprieler, C. 2008. Phylogeny of southern hemisphere Compositae-Anthemideae based on nrDNA ITS and cpDNA *ndhF* sequence information. *Plant Systematics and Evolution* 272: 131–153.

Hind, D.J.N. (ed.). 1996. *Proceedings of the International Compositae Conference, Kew, 1994*, 2 vols. Royal Botanic Gardens, Kew.

Hochuli, P.A. 1978. Palynologische Untersuchungen im Oligozän und Untermiozän der zentralen und westlichen Paratethys. *Beiträge zur Paläontologie von Österreich* 4: 1–132.

Howarth, D.G., Gustafsson, M.H.G., Baum, D. & Motley, T.J. 2003. Phylogenetics of the genus *Scaevola* (Goodeniaceae): implications for dispersal patterns across the Pacific basin and colonization of the Hawaiian Islands. *American Journal of Botany* 90: 915–923 and Supplementary Data from the *American Journal of Botany* website: Pp. 1–3.

Hu, S.Y. 1958. Statistics of Compositae in relation to the flora of China. *Journal of the Arnold Arboretum* 39: 347–419.

Jansen, R.K. & Kim, K.-J. 1996. Implications of chloroplast DNA data for the classification and phylogeny of the Asteraceae. Pp. 317–339 in: Hind, D.J.N. & Beentje, H.J. (eds.), *Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1, *Compositae: Systematics*. Royal Botanic Gardens, Kew.

Jansen, R.K., Michaels, H.J. & Palmer, J.D. 1991a. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. *Systematic Botany* 16: 98–115.

Jansen, R.K., Michaels, H.J., Wallace, R., Kim, K.-J., Keeley, S.C., Watson, L.E. & Palmer, J.D. 1991b. Chloroplast DNA variation in the Asteraceae: phylogenetic and evolutionary implications. Pp. 252–279 in: Soltis, D.E., Soltis, P.S. & Doyle, J.J. (eds.), *Molecular Systematics of Plants*. Chapman & Hall, New York.

Jansen, R.K. & Palmer, J.D. 1987. A chloroplast DNA inversion marks an ancient evolutionary split in the sunflower family (Asteraceae). *Proceedings of the National Academy of Sciences of the United States of America* 84: 5818–5822.

Jansen, R.K. & Palmer, J.D. 1988. Phylogenetic implications of chloroplast DNA restriction site variation in the Mutisieae (Asteraceae). *American Journal of Botany* 75: 753–766.

Jeffrey, C. 1977. Corolla forms in Compositae—some evolutionary and taxonomic speculations. Pp. 111–118 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), The Biology and Chemistry of the Compositae, vol. 1. Academic Press, London. Jones, S. 1977. Vernonieae. Pp. 503–521 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), *The Biology and Chemistry of the Compositae*, vol. 1. Academic Press, London.

Kadereit, J.W. & Jeffrey, C. (eds.). 2007 [2006]. *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales*. Springer, Berlin.

Katinas, L., Crisci, J.V., Jabaily, R.S., Williams, C., Walker, J., Drew, B., Bonifacino, J.M. & Sytsma, K. 2008. Evolution of secondary heads in Nassauviinae (Asteraceae, Mutisieae). *American Journal of Botany* 95: 229–240.

Katinas, L., Crisci, J.V., Tellería, M.C., Barreda, V. & Palazzesi, L. 2007. Early history of Asteraceae in Patagonia: evidence from fossil pollen grains. *New Zealand Journal of Botany* 45: 605–610.

Karis, P.O., Eldenäs, P. & Källersjö, M. 2001. New evidence for the systematic position of *Gundelia* L. with notes on delimitation of Arctoteae (Asteraceae). *Taxon* 50: 105–114.

Keeley, S.C., Forsman, A.H. & Chan, R. 2007. A phylogeny of the "evil tribe" (Vernonieae: Compositae) reveals Old/New World long distance dispersal: support from separate and combined congruent datasets (*trnL-F*, *ndhF*, ITS). *Molecular Phylogenetics and Evolution* 44: 89–103.

Kim, H.-G., Loockerman, D.J. & Jansen, R.K. 2002. Systematic implications of *ndhF* sequence variation in the Mutisieae (Asteraceae). *Systematic Botany* 27: 598–609.

Kim, K.-J., Choi, K.-S. & Jansen, R.K. 2005. Two chloroplast DNA inversions originated simultaneously during the early evolution of the sunflower family (Asteraceae). *Molecular Biology and Evolution* 22: 1783–1792.

Kim, K.-J. & Jansen, R.K. 1995. *ndhF* sequence evolution and the major clades in the sunflower family. *Proceedings of the National Academy of Sciences of the United States of America* 92: 10379–10383.

Maddison, D.R. & Maddison, W.P. 2001. *MacClade*, vers. 4.03. Sinauer, Sunderland.

McKenzie, R.J. & Barker, N.P. 2008. Radiation of southern African daisies: biogeographic inferences for subtribe Arctotidinae (Asteraceae: Arctotideae). *Molecular Phylogenetics and Evolution* 49: 1–16.

Muller, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biological Review* 45: 417–450.

Muller, J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1–142.

Nordenstam, B. 2007a [2006]. Senecioneae. Pp. 208–241 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales*. Springer, Berlin.

Nordenstam, B. 2007b [2006]. Calenduleae. Pp. 241–245 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales.* Springer, Berlin.

Nordenstam, B. 2007c [2006]. Corymbieae. Pp. 207–208 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales.* Springer, Berlin.

Oberprieler, C., Himmelreich, S. & Vogt, R. 2007. A new subtribal classification of the tribe Anthemideae (Compositae). *Willdenowia* 37: 89–114.

Panero, J.L. & Funk, V.A. 2002. Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae). *Proceedings of the Biological Society of Washington* 115: 909–922.

Panero, J.L. & Funk, V.A. 2008. The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution* 47: 757–782.

Pelser, P.B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.

Pennisi, E. 2008. Building the tree of life, genome by genome. *Science* 320: 1716–1717.

Raven, P.H. & Axelrod, D.I. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539–673.

Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). *Smithsonian Contributions to Botany* 51: 1–102.

Robinson, H. 1983. A generic review of the tribe Liabeae (Asteraceae). *Smithsonian Contributions to Botany* 54: 1–69.

Robinson, H. 1999. Generic and subtribal classification of American Vernonieae. *Smithsonian Contributions to Botany* 89: 1–116.

Rzedowski, J. 1972. Contribuciones a la fitogeografía florística e histórica de México. III Algunas tendencias en la distribución geográfica y ecológica de las Compositae mexicanas. *Ciencia (México)* 27: 123–132.

Scotese, C. R. 2008. PALEOMAP website (http://www.scotese.com).

Skvarla, J.J. 1977. Pollen morphology. Pp. 141–248 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), *The Biology and Chemistry of the Compositae*, vol. 1. Academic Press, London.

Soltis, D.E., Albert, V.A., Salvolainen, V., Hilu, K., Qiu, Y.-L., Chase, M.W., Farris, J.S., Stfanovic, S., Rice, D.W., Palmer, J.D. & Soltis, P.S. 2004. Genome-scale data, angiosperm relationships, and 'ending incongruence': a cautionary tale in phylogenetics. *Trends in Plant Science* 19: 477–483.

Small, J. 1919. *The Origin and Development of the Compositae.* New Phytologist, Reprint No. 11. Wesley & Son, London.

Steel, M., Dress, A.W.M. & Bocker, S. 2000. Simple but fundamental limitations on supertree and consensus tree methods. *Systematic Biology* 49: 363–368.

Susanna, A., Garcia-Jacas, N., Hidalgo, O., Vilatersana, R. & Garnatje, T. 2006. The Cardueae (Compositae) revisited: insights from ITS, *trnL-trnF*, and *matK* nuclear and chloroplast DNA analysis. *Annals of the Missouri Botanical Garden* 93: 150–171.

Swofford, D.L. 2002. *PAUP★, Phylogenetic Analysis Using Parsimony (★and Other Methods)*, vers. 4.0b10. Sinauer, Sunderland.

Turner, B.L. 1977. Fossil history and geography. Pp. 21–39 in: Heywood, V.H., Harborne, J.B. & Turner, B.L. (eds.), *The Biology and Chemistry of the Compositae*, vol. 1. Academic Press, London.

Wagstaff, S.J., Breitwieser, I. & Swenson, U. 2006. Origin and relationships of the austral genus *Abrotanella* (Asteraceae) inferred from DNA sequences. *Taxon* 55: 95–106.

Wang, Y.-J., Liu, J.-Q. & Miehe, G. 2007. Phylogenetic origins of the Himalayan endemic *Dolomiaea*, *Diplazoptilon* and *Xanthopappus* (Asteraceae: Cardueae) based on three DNA regions. *Annals of Botany (London)* 99: 311–322.

Watson, L.E., Evans, T.M. & Boluarte, T. 2000. Molecular phylogeny and biogeography of tribe Anthemideae (Asteraceae), based on chloroplast gene *ndhF*. *Molecular Phylogenetics and Evolution* 15: 59–69.

Wikström, N., Savolainen, V. & Chase, M.W. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 268: 2211–2220.

Zao, Z., Skvarla, J.J. & Jansen, R.K. 2006. Mutisieae (Asteraceae) pollen ultrastructure atlas. *Lundellia* 9: 51–76.

Zavada, M.S. & De Villiers, S.E. 2000. Pollen of the Asteraceae from the Paleocene-Eocene of South Africa. *Grana* 39: 39–45.