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Botany Profile

150 Years of Thistles, Daisies, and Sunflowers

By Vicki A. Funk

The US National Herbarium has an active research and collecting program in the flowering plant family Compositae (Asteraceae). Recent accomplishments include the Helianthae treatment for *Flora of Ecuador*, a supertree for the entire family, a new international organization and website, and the near completion of the monograph on the Espeletiinae by José Cuatrecasas.

The Compositae (Asteraceae) contains the largest number of described species of any plant family, 24,000—with estimates of total species ranging up to 35,000—distributed in 1,600 – 2,000 genera occurring on all continents except Antarctica. Estimates vary, but assuming that there are 200,000 – 300,000 species of flowering plants, then one out of every 8 – 12 species of flowering plants is in the Compositae (about 10 percent). The family is monophyletic, characterized by florets arranged on a receptacle in centripetal heads and surrounded by bracts, by anthers fused in a ring with the pollen pushed or brushed out by the style, and by the presence of achenes (cypselas) often with a pappus (see figure on Page 9). Although the family is well-defined, there is a great deal of variation among the members: the habit varies from annual and perennial herbs to shrubs, vines, or trees, although few are true epiphytes; the heads can have one to more than 1,000 florets; chromosome numbers range from $n = 2$ to high level polyploidy with $n = 114$; and species grow in just about every type of habitat

from forests to high elevation grasslands, however they are less common in tropical wet forests and more common in open areas.

The general perception of this family as “weedy” is only partially correct. Certainly there are members that benefit from disturbance but most species have a restricted distribution, and just about every “at risk” habitat in the world contains members of this family that are an important part of the flora. In fact, the *1997 IUCN Red List of Threatened Plants* (Walter and Gillett 1997) has 2,553 species of Compositae on its list.

It is an important family not only because it is pervasive in many ecosystems but also because members of the family dominate our gardens (about 260 species in the U.S.), provide a number of invasive species (i.e., *Chromolaena*, *Cirsium*, *Taraxicum*), produce secondary plant products that are used in traditional and homeopathic medicines (ca. 500 in China alone) and in pesticides, and provide food (i.e., dandelions, sunflowers, artichokes, lettuce).

The US National Herbarium houses approximately 500,000 specimens of Compositae and 8,500 recorded types and although it has global representation it is strongest in the Neotropical Compositae, perhaps the best in the world. There are no doubt many specimens in the general herbarium that should be in the type collection but have not yet been identified as such or they are duplicate material that was, until recently, kept in the main herbarium. This large collection was assembled over the history

of the herbarium but mostly during the last 100 years. A series of synantherologists (see photos on Page 10) have enhanced the herbarium by their collecting efforts and their willingness to identify Compositae from throughout the world. I think it is safe to say that anyone wanting to work in Neotropical Compositae must visit or borrow the collections at US.

The first people who made major contributions to the Compositae collection were Asa Gray and Benjamin L. Robinson, both synantherologists from Harvard. Gray identified the plants housed in the U.S. National Herbarium that were collected during early U.S. expeditions, *Plantae wrightianae texano-neo-mexicanae*, the boundary survey, published in *Smithsonian Contributions to Knowledge* 3, Art. 5. 1852 and 5 (Art 6). 1853 and the United States Exploring Expedition under the command of Charles Wilkes, published 1854 and 1856. Likewise, Robinson identified many specimens from US including the material from Hitchcock, Killip and Smith, Pringle, A.C. Smith, and Rose.

Sidney Fay Blake, a student of Robinson, was one of the foremost Compositae workers of the 20th century. In between his master’s and his Ph.D. he was perhaps one of our first “interns” because he spent the summer of 1913 arranging plants at the Smithsonian. Upon the completion of his Ph.D. Blake was offered jobs at both the Smithsonian and the Department of Agriculture. He took the USDA job because the pay

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Profile

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at the Smithsonian was “inadequate;” however, he spent a great deal of time working with material from US and doing field work. A search on IPNI finds his name associated with 4,159 plant names, about 3,000 of which are in the Compositae. He worked in the DC area from 1917-1959 and he added many specimens to the US collection. It is to Blake we owe the wonderful collection of photos of types from Europe that we all enjoy. He spent 42 years of his life producing 300 botanical papers, mostly on the sunflowers and mostly in his spare time and he died at his desk on 31 December 1959 (age 67). After his death, his personal herbarium and library were purchased by Lundell and ended up at the University of Texas Plant Resource Center in Austin.

Blake overlapped with José Cuatrecasas who worked in the US herbarium until a few days before his death at the age of 93. His career extended from his studies in Barcelona and Madrid (1924-1931), graduate work in Berlin (1930-31) where he knew Adolph Engler, Directorship of the Sección de Flora Tropical del Jardín Botánico de Madrid (1933-39), the years in Colombia (1939-47), in Chicago (1947-1955) to his 41 years in Washington (1955-1996). Although Cuatrecasas (1903-1996) worked on many families his concentration was on the Compositae of the northern Andes. He did a large amount of field work, mostly in Colombia. He was an author or coauthor of two subtribes and over 20 genera in five tribes. A quick check of IPNI shows that 1,307 records from Cuatrecasas are in the Compositae. At the time of a 1985 festschrift, Cuatrecasas was listed with Robinson, Blake, Angel L. Cabrera, and Hermann Merxmüller, as individuals who had made truly constructive and insightful contributions to the study of the Compositae in the first three quarters of the 20th century: three of the top five synantherologists had worked at or with the collections from US. Cuatrecasas’ specimens, research materials and photographs remain at the Smithsonian Institution; his library is in Barcelona.

Kitty Parker (1910-1994), a student of Lyman Benson in Arizona, came to the

Washington area in 1953 and was a professor at George Washington University. She worked in the Helenieae and did many identifications especially in the years immediately following the death of Blake. She was the advisor of two taxonomists that were eventually hired at US.

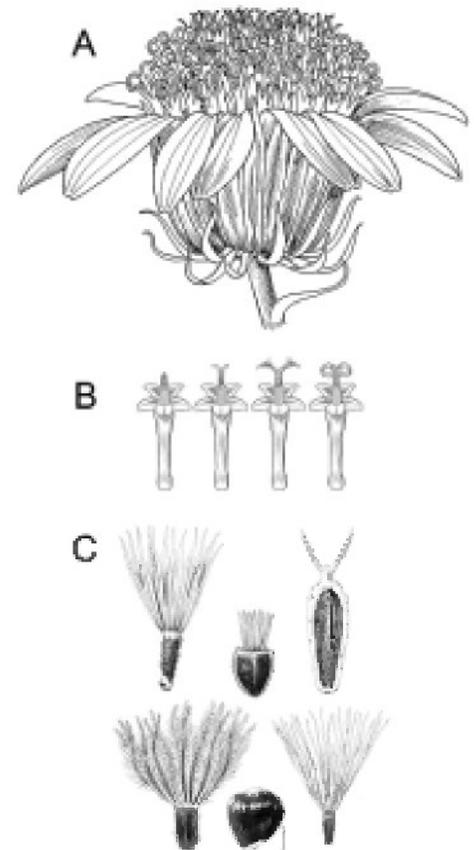
Robert M. King (1929-), a professor at Catonsville Community College, came to the Washington area in 1962. During his time in the DC area he made many field trips that resulted in numerous collections for US. He collaborated with Harold Robinson in the work on the Eupatorieae. King left the Washington area in 1997. One of King’s major contributions to Compositae systematics was introducing Harold Robinson to the family.

Harold Robinson came to US in 1962 as a bryologist and moved over to working on the Compositae in 1964, applying bryological techniques to a group that had previously had inadequate anatomical study. Although he has rarely collected in the family, he has identified more than 30,000 specimens that he has received as a “gift for determination” and is the author or coauthor on over 600 papers dealing with the family. His most recent accomplishments include the Heliantheae for the *Flora of Ecuador*. He is currently finishing the monograph on the Espeletinae by Cuatrecasas.

The 1873 treatment by George Bentham divided the family into 13 tribes (the most frequently used suprageneric rank) which remained more or less the same until the 1980s. Many of the tribes had a large genus that provided the central focus for the tribe: *Senecio* of the Senecioneae, *Eupatorium* of the Eupatorieae, *Aster* of the Astereae, and *Vernonia* of the Vernonieae. These genera remained largely unchanged having only a few satellite genera removed from them. Beginning with his work on the Eupatorieae, Robinson has tackled one large genera after another. While his Eupatorieae work was done with King, subsequent work has been done by himself or with others. His detailed work resulted in the break up of several of these large genera. Each time the work was resisted because others liked the convenience of a very few generic names that could be used for most specimens without concern for relationships or the identity of thousands

of species concepts that were included. Time and subsequent molecular work, however, have largely supported Robinson’s work. Robinson has done generic level revisions of the Eupatorieae (with King), Liabeae, Heliantheae, and Vernonieae. More recently he has helped implement the presentation of a similar work of Guy Nesom in the Astereae. He has revised tribal limits and described new tribes and subtribes. The Liabeae had traditionally been recognized as one unnatural core genus with three other genera, all in separate tribes, Senecioneae, Heliantheae, Helenieae and Mutisieae. The Eupatorieae and Vernonieae, traditionally placed together, were shown to be only distantly related. It can safely be said that the work of H. Robinson has changed the way we do Compositae systematics. One particular series of results was the dismissal of the Cronquist view that the Rubiaceae were the closest relatives of the Compositae and that the Heliantheae were the primitive core

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A. Head showing ray and disc florets, **B.** Disc floret showing pollen presentation, **C.** Achene (cypsela) showing pappus. (Drawings by Alice Tangerini)

Compositae

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group, a concept referred to by Robinson as the “Heliocentric Theory of the Compositae.”

In 1980 the newest member of the Compositae crew joined the Smithsonian. Vicki A. Funk currently specializes in some of the tribes near the base or mid-level of the phylogeny of the family: Mutisieceae, Liabeae, and Arctoteae. She has an interest in phylogenetics and biogeography and coordinates the supertree of the family. She does identifications in her areas of interest and has collected extensively in Mexico, the Andes, and South Africa.

Through the years a number of synantherologists have passed through the herbarium and the collections have benefited from their stay. Some have stayed long enough or visited often enough to annotate a number of specimens, including Walter Holmes, Rogers McVaugh, John Pruski, and Gisela Sancho. In addition, some curators at US, such as Conrad Morton and Warren L. Wagner, have shown an interest in the family even though it was not their area of specialization.

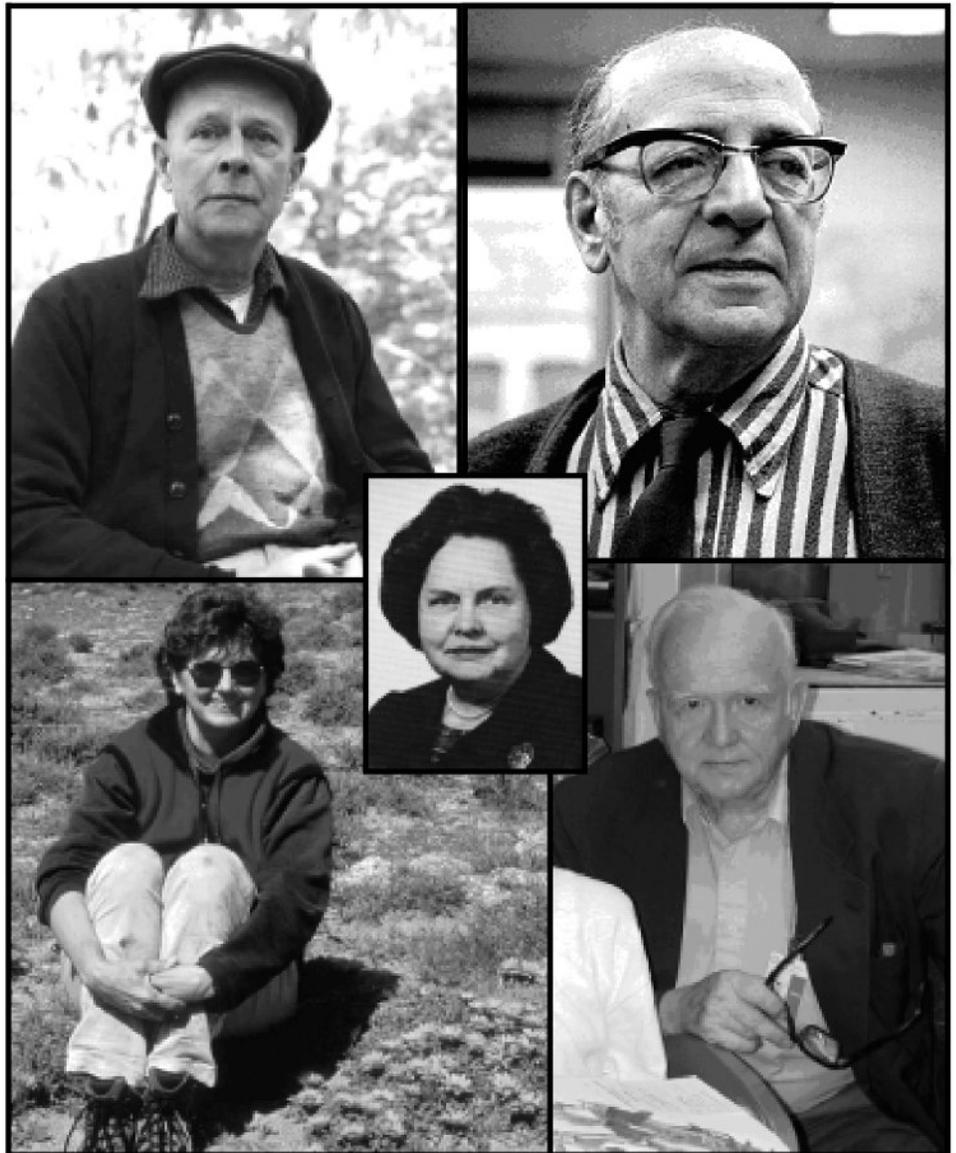
Molecular data came to Composite systematics in the late 1980s and early 1990s and it was based on the work by Robert Jansen (TEX) and his collaborators. These individuals have literally turned the Compositae phylogeny upside down, showing that elements previously placed in the Mutisieceae were a basal branch of the family and that the tribe Heliantheae *s.l.* was nested far up in the tree. Furthermore, their work confirmed that the Vernoniaceae and Eupatoriaceae were actually in separate parts of the tree. Bruce Baldwin (UC) and his collaborators have proposed new suprageneric ranks for the Heliantheae *s.l.* and Jose Panero (TEX) and Funk have done the same for the base of the tree. Harold Robinson has proposed two supertribes for the Asteroideae.

More recently Funk (along with 11 co-authors) has created a supertree for the family that includes approximately 500 genera. The authors used a published tree for the backbone or base tree of the family and grafted onto the base tree the

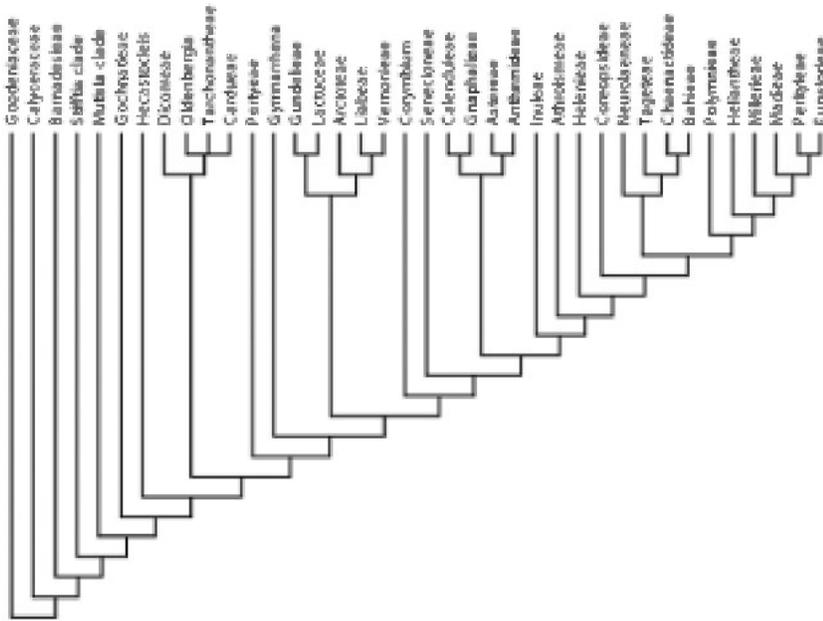
published and unpublished trees for individual clades (usually tribes). This type of a supertree is a meta-tree, a “tree of trees,” and it illustrates the current thinking about the relationships among the major tribes and subfamilies in the Compositae. The basal group, which is monophyletic and the sister-group to the rest of the family, is the distinctive subfamily Barnadesioideae which contains less than 1 percent of the species in the family. Also monophyletic is the highly nested subfamily Asteroideae, which contains ca. 65 percent of the species in the family. Between the two monophyl-

etic subfamilies are groups that used to be included in the now paraphyletic subfamily Cichorioideae (ca. 35 percent of the species in the family). The new classifications recognize 10 subfamilies and 35 tribes, some new and some previously described; it remains to be seen whether or not this new classification will be accepted by the Compositae community.

The supertree makes it possible to look at the family as a whole and to try to discern its origin and history as well as gain insights on character evolution (the figure below is a reduced version of the supertree). It is also an excellent method



Synantherologists at the US National Herbarium (clockwise from upper left): Sidney F. Blake (date unknown, photo from the Washington Biologists Field Club Archives); José Cuatrecasas (date unknown, photo from the Botany Department Archives); Kitty Parker (1973; photo from the NMNH Archives); Harold Robinson (2003; photo by M. Sangrey); Vicki Funk in Namaqualand, South Africa with *Gazania* (2002; photo by M. Koekemoer, PRE).



The reduced Compositae supertree showing tribes and a few other taxa.

for determining critical areas of the tree for future work. The creation of the supertree was an outgrowth of a new organization “The International Compositae Alliance” (TICA) that had its first international meeting in Pretoria, January 2003, and the second meeting is to be held in June 2006, in Barcelona, Spain (hosted by Alfonso Susanna and Nuria Garcia-Jacas). The organization is supported by its website <<http://www.compositae.org>>, hosted by Torsten Eriksson from Bergius Botanical Garden (Stockholm) and uses *The Compositae Newsletter* (edited by Bertil Nordenstam, S) as a venue for publishing abstracts, and other documents. The goal of the 2006 meeting is to produce a multi-volume work on the family. Scientists from around the world are expected to participate and contribute to the publication. TICA is run as an email society and anyone can join by sending a message to funkv@si.edu.

We are often asked, “Why is the Compositae so large and successful while its most closely related families, Calyceraceae and Goodeniaceae, are small with restricted distributions?” Well, it is most likely the same old story: the Comps are the new kid on the block. They are comparatively recently evolved (ca. 50 million years ago), overly big (with genera and species), opportunistic (often

growing in open areas), highly poisonous (in its chemistry), fecund (not picky about pollinators and have high seed set), and agile (adapt to new edaphic conditions rapidly). As a result they are disgustingly successful and have conquered the world. The size and complexity of the family often result in taxonomists avoiding them. They are often maligned by those who do not study them; but maybe those who study other plant families are just jealous.



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