

# Ten Things I learned on the way to the Mother Tree (i. e., Mother Ship)\*

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## Abstract

The completion of the recent book on the Compositae has answered some questions about evolution and biogeography of the family but it has also produced new and interesting areas for research. Ten such topics are discussed and some suggestions about future topics are made.

## Introduction

The Compositae (Asteraceae) family is nested high in the Angiosperm phylogeny in the Asterideae/Asterales. The family contains the largest number of described, accepted, species of any plant family, ca. 24,000, with estimates of the total number reaching 30,000. There are 1600–1700 known genera distributed around the globe except for Antarctica. That the family is monophyletic has never been in question. Every early worker in plant classification recognized the Compositae as a group at some level (e.g., TOURNEFORT 1700, BERKHEY 1760, VAILLANT 1719–1723) and in every type of analysis the family is monophyletic (e.g., SMALL 1919, BREMER 1987, JANSEN & PALMER 1987, HANSEN 1991a & b, MICHAELS et al. 1993, LUNDBERG & BREMER 2003). Possibly this is because morphologically the family is well characterized: flowers (florets) arranged on a receptacle in centripetal heads and surrounded by bracts, anther thecae fused at the margins to form a ring but the filaments are free, pollen pushed out by the style, calyx (when present) developed into a pappus, and the fruit is an achene (cypsela).

Family wide treatments are few, BREMER's 1994 cladistic analysis was the first revision of the whole family based on morphology since those of BENTHAM (1873a) and HOFFMANN (1890) and although he recognized many of the problem areas in the cladograms of the family, the morphology did not generate enough data to resolve many of the issues. Just over ten years later KADEREIT & JEFFREY (2007)

and their numerous co-workers reordered the genera, tribes, and subfamilies within the family based on recent morphology and molecular results and this work is now the standard reference for descriptions of the tribes and genera of the family.

From the beginning those who studied this family thought the ray and disk pattern represented the basic head structure. CASSINI in his famous 1816 diagram (FUNK et al. 2009a: Chapters 2, 6, 41) placed the Heliantheae at the center, the Vernoniaeae and Eupatorieae at one end, and the Mutisieae and Cichorieae (Lactuceae) at the other. CRONQUIST (1977) agreed and pointed out that BENTHAM thought the Heliantheae was most primitive (BENTHAM 1873b). CRONQUIST (1955, 1977) and TURNER (1977) also thought that the Heliantheae was the most primitive tribe of the family, and accordingly assumed that the ancestor was a perennial herb (or shrub) with opposite leaves and yellow-flowered, radiate capitula. BREMER and JANSEN and their colleagues (BREMER 1987, JANSEN & PALMER 1987, 1988, JANSEN et al. 1991a, 1991b, BREMER & JANSEN 1992, MICHAELS et al. 1993, JANSEN & KIM 1996, LUNDBERG & BREMER 2003) have used morphological and molecular data to change that view to one with a basal grade made up of members of the former Mutisieae (sensu CABRERA).

### **The Book and the ‘Mother Tree’**

The recent publication *Systematics, Evolution, and Biogeography of Compositae* (FUNK et al. 2009a) links the most recent molecular trees together in a metatree framework (FUNK & SPECHT 2007) and uses that tree to provide a basis for understanding the evolution and biogeography of the family. The basic structure of the tree was taken from PANERO & FUNK (2002, 2008) and BALDWIN (et al. 2002, 2009). The trees in PANERO & FUNK (2008) contained extensive sampling from the base of the tree, the Mutisieae (sensu CABRERA), 3–10 genera representing all other tribes, and many taxa that had been “hard to place” in previous studies. The phylogeny was based on data from 10 chloroplast gene regions (*ndhF*, *trnL-trnF*, *matK*, *ndhD*, *rbcL*, *rpoB*, *rpoCl*, *exon1*, *23S-trnI*, and *ndhI*). The Heliantheae Alliance portion of the base tree was taken from work by BALDWIN and his collaborators (BALDWIN et al. 2002, BALDWIN 2009) and is the result of nuclear rDNA of the ITS region. The phylogenies of the individual tribes are the work of many individuals (see the Acknowledgements) and a variety of types of molecular data, the most frequent being ITS and *ndhF* or *matK*. These molecular data have given us the opportunity to examine the history and morphology of the family in a way never before possible. The book (FUNK et al. 2009a, c) includes overview chapters and a chapter on each tribe; for more information on the book see the *The International Compositae Alliance* (TICA) website ([www.compositae.org](http://www.compositae.org)),

visit [www.YouTube.com](http://www.YouTube.com) (search *Compositae*), or email [compositaebok@gmail.com](mailto:compositaebok@gmail.com). All proceeds from the sale of the book go to the *International Association for Plant Taxonomy*.

Figure 1 is a summary tree of the metatree (taken from FUNK et al. 2009c) where each tribe or clade has been reduced to a branch (or visit [www.compositae.org](http://www.compositae.org) to see the ca. 900 taxon tree). Some of the biogeographic conclusions from the study include:

- 1) Extant members of the basal radiation are found in southern South America; the basal clades inhabit the oldest rocks in **South America** (Southern Andes, Guiana Shield, Brazilian Shield). The members of the basal radiation comprise ca. 5 % of the extant genera in the *Compositae*.
- 2) The central part of the area cladogram is a grade dominated by **African** based radiations with numerous movements into Eurasia and beyond. The members of these clades make up 66 % of the extant genera in the *Compositae*.
- 3) The origin of the extant core Heliantheae Alliance is **North America** and **Mexico** with numerous links to South America and back to Mexico and North America. This clade contains 29 % of the extant genera.
- 4) The **Northern Africa-Mediterranean** area and the **Asia-Eurasia-European** area played important roles in the history of the family especially in the radiation of the *Cardueae*, *Lactuceae*, *Anthemideae*, and *Senecioneae*.
- 5) Major radiations in **Hawaii**, **Australia**, and **New Zealand** are in more highly nested clades.
- 6) The north and northwest **Andes**, long thought to be the cradle of *Compositae* evolution, hold large numbers of taxa but all are highly nested.
- 7) Western **North America** and **Mexico** hold many clades from a variety of tribes but all are highly nested.

#### **What we don't know!**

- 1) What happened between the time of the **South American** radiation and the base of the African radiation?
- 2) What happened among the clades in the ambiguous areas of the phylogeny?
- 3) What happened between the *Inuleae* & *Athroismeae* clades, extant members of both originate in **Africa**, and the origin of the Heliantheae Alliance in **SW United States – NW Mexico**?

During the construction of the Compositae metatree we began to call it the 'Mother Tree' (i.e., the Mother Ship) because we liked the analogy of a large facility where smaller ships could dock. These smaller ships (trees of individual tribes) could leave and others could dock as information about individual tribes change and when the Mother Ship becomes outdated, a new one can take its place and the smaller ships can dock at the new facility. In the process of producing the metatree several things became apparent that seemed interesting to relate to others. I have organized them into ten things that I thought were worth mentioning. Certainly there are many other interesting things related to the book and I take full responsibility for selecting those I discuss.

## The Ten Things

### 1. Unrooted trees are important.

Trees can be rotated at the nodes and there is always a chance that personal bias will be reflected in the final shape of the tree. It is always a good idea to examine the results as an unrooted tree periodically during a project so that such bias can be removed. Figure 2 is an unrooted version of the summary tree (Figure 1). In The Book (FUNK et al. 2009a) the unrooted tree is printed on the back of the bookmark so it can be turned in any direction.

### 2. All tribes except one were monophyletic or easily modified to be so (=GOOD JOB!).

Most of the traditional 13 tribes were found to be monophyletic or could be made monophyletic with a few rearrangements (FUNK et al. 2009b). Tribes such as Cardueae, Vernonieae, Cichorieae, Senecioneae, Asteraeae, Anthemideae, etc. are all pretty much the same as they were from CASSINI to the 1977 volumes (HEYWOOD et al. 1977). A few adjustments were necessary, for instance the tribe Inuleae ended up being divided into two tribes that are not closely related (Gnaphalieae and Inuleae) and it is still unclear exactly what goes in the Arctotideae, but these rearrangements were easily accomplished or the subtribes were found to be good. Even the Heliantheae s. lat., which has been divided into 12 or 13 tribes (depending on acceptance of Feddeae), was a grade and monophyletic if one includes the Eupatorieae. In fact, it was the finding that the Eupatorieae were nested inside the rest of the Heliantheae s. lat. that resulted in the breakup of the group. However, it should be noted that only two of the newly recognized tribes in the Heliantheae Alliance had to be described as new, all of the others had been used previously.

CASSINI, in his famous 1816 diagram (reproduced in BALDWIN 2009), showed the Calyceraceae and Campanulaceae to be closely related to the Compositae and even though he did not have it in the diagram the text indicates that he also thought

the Goodeniaceae was close. He has turned out to be correct about this as well.

So, if the previous tribes were so good, why do we have 42-43 tribes now instead of the traditional 13? The breakup of the Heliantheae s. lat. increased the number as did the breakup of the Mutisieae (sensu CABRERA; see #3 below) and several anomalous taxa did not fall into any group and were recognized as separate tribes. As we continue to examine the family the total number of tribes will likely continue to be in flux. However, the original 13 tribes described by our predecessors were, for the most part, good, and it is important that we acknowledge the latter for their insight.

### **3. The big exception is (as is usual) the basal grade.**

Frequently the base of a phylogeny is occupied by a basal grade. At the level of the Compositae family, the basal grade involves members of the Mutisieae (sensu CABRERA 1977). The group is largely paraphyletic but does have disjunct clades that make it polyphyletic. Unlike the Heliantheae there was no easy solution concerning the taxonomy and most of the clades had not been recognized at the tribal level before. The Mutisieae of CABRERA are now placed into 14 tribes (18 clades; Figure 1). In the Compositae Book (FUNK et al. 2009a) and here the use of the taxon “Mutisieae (sensu CABRERA)” is meant to represent the historic circumscription of the tribe as defined by CABRERA (1977). This is in no way meant as a negative reflection on the many contributions of CABRERA (see BONIFACINO et al. 2009). In fact, his work is the foundation for all modern work in the tribe (ORTIZ et al. 2009) and within his 1977 paper he mentions groups of taxa that have a direct correlation to the results of the molecular analyses. Also, unlike the Heliantheae Alliance, the relationships between the morphological and molecular treatments are not always clear (ORTIZ et al. 2009) and there is no universal agreement on the taxonomic solutions. The creation of the metatree has been the impetus for most of the taxonomists studying these groups to get together to find out more about the morphology of the various taxa.

Another contrast between the Heliantheae Alliance and the Mutisieae (sensu CABRERA) is that until KATINAS et al. (2008), CABRERA’S treatment (1977) was the only one for the tribe in modern times while members of the Heliantheae Alliance had been studied by many individuals. As a result most of the clades within the Heliantheae Alliance already had tribal names that had been proposed while the Mutisieae had very few.

### **4. Chloroplast and nuclear data don’t usually agree.**

Chloroplast data appear to be more conservative and provide estimates of relationship for bigger picture questions such as the base tree for the family and relationships among tribes. Nuclear data such as ITS and ETS appear to

change more rapidly and are commonly used to provide species and generic level relationships; sometimes they can also be used at the tribal level. When examining the relationships among clades at the 'generic' and 'groups of genera' level both types of molecular data can be used. It seems to be the case that at this level one often finds different arrangements of the groups in question. In addition, the attachment of outgroups can be quite different in the two types of data. For instance, repeated analyses of the tribes within the subfamily Cichorioideae (FUNK & CHAN 2009) show big differences in the placement of the tribes and unplaced taxa in the subfamily.

BARKER et al. (2008) have indicated that there is a paleopolyploidization event at the base of the Compositae. This could help explain the discrepancy between the types of data and we may be in a position of always having different trees for different types of molecular data. We will have to be careful to select the type of data that will best answer the questions we are asking. In addition PENNISI (2008) mentions that data sets will have to be reanalyzed with different methods in order to determine the best tree and that the latter is not necessarily guaranteed by more data.

### **5. What about morphology; a lot of it is missing!**

It is imperative that we include morphology in our studies. Otherwise we will never understand evolution in the family. Unfortunately, much of the necessary work has yet to be done. Often characters are discussed only if they are informative within a certain group and that means we are missing information across the family. It is now incumbent on the community to organize and try to fill in the missing information. Two TICA projects have been started, a preliminary checklist of the species in the family including distribution (CHRISTINA FLANN is in charge of this project - christinaflann@gmail.com) and a virtual key to the species in the family starting with the USA (J. MAURICIO BONIFACINO is in charge of this project - mbonifa@gmail.com). It is hoped that these two projects will help provide some of the missing data. In addition, many of the tribes now have working groups that are making great strides in our understanding of the morphology.

### **6. Details of the distribution and morphology don't matter to the big questions; but they are interesting.**

One of the most difficult aspects of the metatree project is trying to maintain the correct scale. Close enough that we would maintain the information we needed for the analyses but distant enough that we do not get lost in the details. An example from the distribution is the radiations within the Gnaphalieae in New Zealand and Australia. These are large and important radiations and we must examine them to achieve an understanding of the evolution within the tribe, however, that does not change the fact that the base of the tribe is in Africa and for family

wide biogeographic purposes we use that rooting. In morphology there are many examples, one is the ligulate corolla that is characteristic of the tribe Cichorieae but similar corollas are also found in several other taxa, *Stokesia* (Vernonieae), *Dinoseris* and *Hyaloseris* (*Hyaloseris* Clade; Stiffiteae) and *Catamixis* (an anomalous taxon now tentatively placed in the Pertyeae). The evolution of a ligulate corolla in several isolated taxa does not diminish the utility of the character in the Cichorieae. A common expression is “Don’t throw out the baby with the bath water.”

### **7. Extinction is important & fossils would be nice or dates for the Compositae are difficult.**

Considering the size and importance of the family little has been published about its possible age. One reason may be the lack of any reliable macrofossils from the early diversification of the family. Without such fossils it is impossible to discount ideas of radiation followed by extinction that would drastically change the pattern produced by the extant taxa. There have been various estimates but several recent ones center on an origin of 41–50 Ma (see discussion in FUNK et al. 2009c) based on largely circumstantial evidence. 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). Other dates of tribes or small clades have been proposed; many of these are just speculation. What is needed is a detailed analysis of pollen cores from the Antarctic, Australia, and southern South America to determine when the Calyceraceae + Compositae clade separated from the ancestors of the Goodeniaceae. It is likely that this will involve the ultra-structure of the grains since the external appearance of the grains of the base of the Compositae and its related families is similar.

### **8. The Biogeography makes a fairly complete story.**

I have been asked repeatedly why the biogeographic pattern is relatively clear in the Compositae but not so obvious in other families. One possible reason is that the family is relatively young and extinction has not wreaked havoc on its distributions. There are exceptions, of course, but in general it is pretty good. Of course, one can turn this around and say that this pattern may be the result of extinction!

### **9. Some things just don’t make sense.**

What in the world is *Hecastocleis* doing between the basal radiation and the jump to the old world? How did the huge radiation of the Heliantheae Alliance get from Africa to western North America and is it possible that such an event happened only once? Why in the world are *Stiffitia*, the *Gongylolepis* clade, and the *Hyaloseris* clade grouping together? Why is the Asian *Leucomeris* clade

grouping with the Brazilian and tepui Wunderlichieae? There are many such questions which illustrate that a good research project generates more questions than it answers.

### **10. The Real fun starts now!**

Now that we have the metatree what do we do with it? There are many things that can be investigated: the history of family through time, vicariance versus dispersal hypotheses, origin of floras in natural areas, character evolution, adaptive radiations on islands, convergent evolution, evolution of pollination systems, coevolution, characteristics of invasive species, and the evolution of unusual structure such as secondary heads, are just a few of the topics that come to mind. Each of these could be a separate paper(s). Truly, there are many interesting things to investigate.

This project is a good example of the power of phylogenies in our quest to understand the history and evolution of life. Without such an overall organizing principle we will continue to look at small pieces of the puzzle and have no way to put them together.

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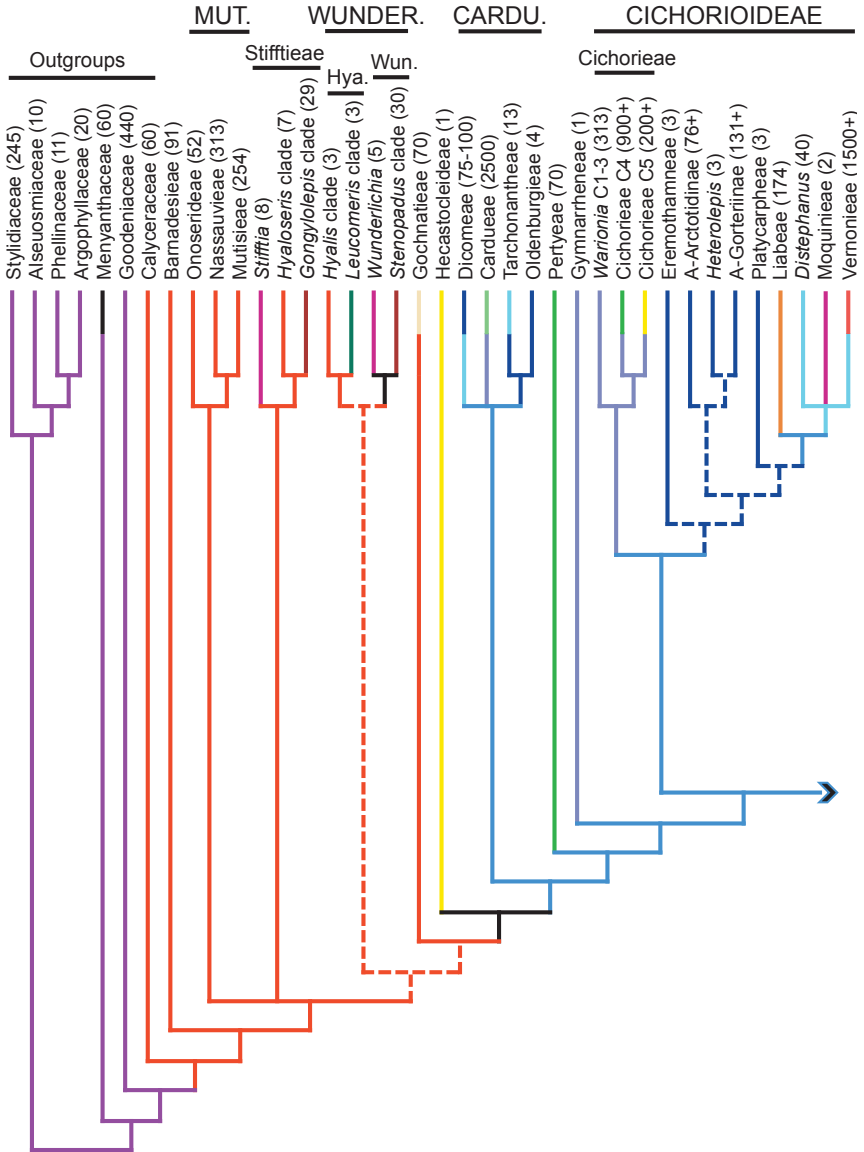


Fig. 1

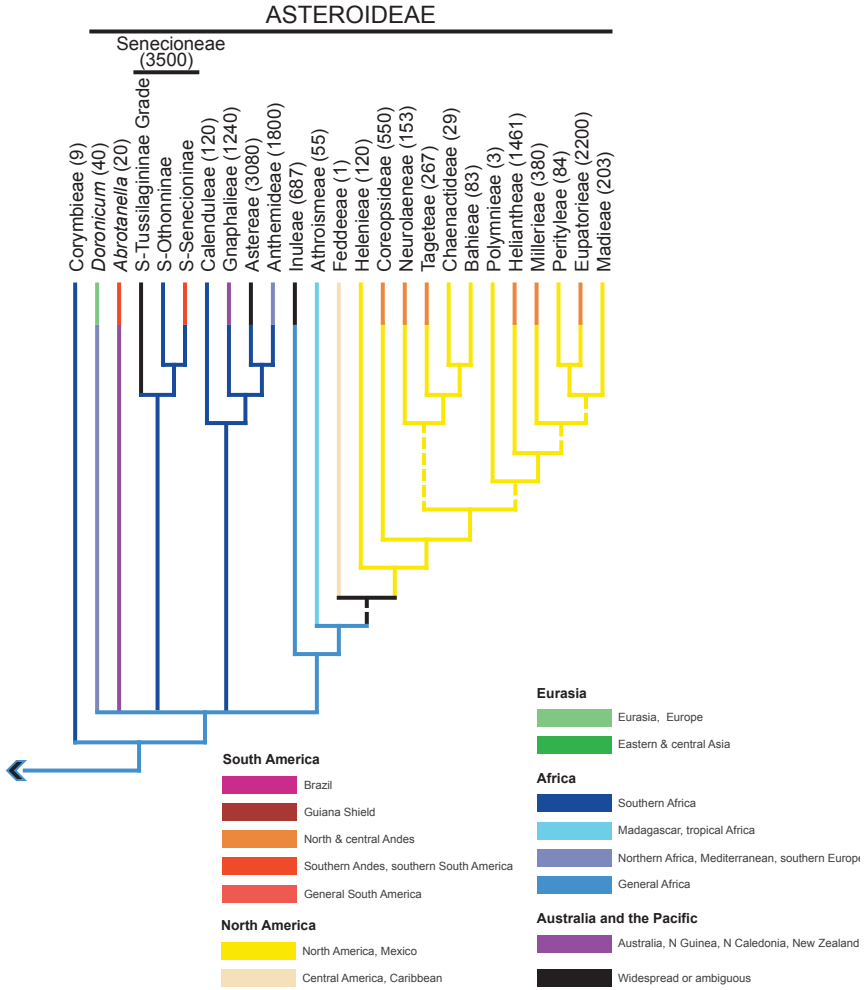


Fig. 1 (contd.)

### Figure Legends

Fig. 1. A summary tree based on the most recent supertree of the Compositae (Chapter 44), branches and internodes are colored according to the distribution of the terminal taxa or the optimization of those distributions. Some major radiations that are highly nested within the clade are show on the branches. [Hya. = Hyalideae; Wun. = Wunderlichieae; A-Arctotidinae = Arctotideae-Arctotidinae; A-Gorteriinae = Arctotideae-Gorteriinae]. Reproduced from FUNK et al. 2009b with permission from IAPT.

Fig. 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. 1.

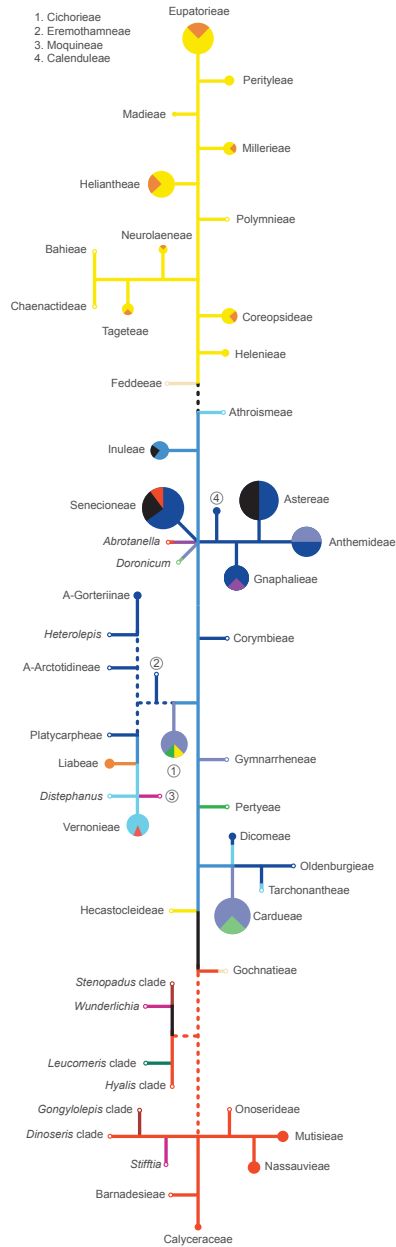


Fig. 2



# COMPOSITAE

## NEWSLETTER

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### CONTENTS

BREMER, K.: Personal reflections on a new Compositae book	1
FUNK, V. A.: Ten Things I learned on the way to the Mother Tree (i.e., Mother Ship)	6
MAITY, D. & G. G. MAITI: Taxonomic delimitation of the genus <i>Tibetoseris</i> SENNIKOV and the new genus <i>Pseudoyoungia</i> of the Compositae-Cichorieae from Eastern Himalaya	22
J. NOROOZI, Y. AJANI & B. NORDENSTAM: A new annual species of <i>Senecio</i> (Compositae-Senecioneae) from subnival zone of southern Iran with comments on phytogeographical aspects of the area	43
MUKHERJEE, S. K. & B. NORDENSTAM: Distribution of calcium oxalate crystals in the cypselar walls in some members of the Compositae and their taxonomic significance	63
ADEGBITE, A. E.: Pollen studies on some populations of <i>Aspilia</i> (Asteraceae) in Nigeria	89
New taxa and combinations published in this issue	102