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EDITORIAL NOTE

We were very happy to find that there is still a demand for the *Compositae Newsletter*, and we thank our readers for their kind response. We hope that you will help to keep the Newsletter alive by sending us material for publication. Notices of all kinds and short manuscripts are very welcome.

Our address is: *Compositae Newsletter*, Department of Phanerogamic Botany, Naturhistoriska Riksmuseet, P.O. Box 50007, S-104 05 Stockholm, Sweden.

The next issue of *Compositae Newsletter* will appear in May, 1989.

REQUESTS FOR MATERIAL

Dr. Harald Ohle, Quedlinburger Strasse 41, Gatersleben, DDR - 4325, is working on *Calendula*. His particular interests are the *C. suffruticosa*-group from Algeria, Morocco, and the Iberian peninsula as well as the *C. incana*-group from Portugal and Spain. He would appreciate obtaining specimens and viable seeds for study. Furthermore, Dr. Ohle would like to get in touch with colleagues for an exchange of literature concerning the flora (and fauna) of the Mediterranean countries.

Drs. Jansen, Palmer, and Michaels (cf. the first article in this issue of the Newsletter) would appreciate receiving seed or living material from the groups discussed in their contribution.

INVESTIGATIONS OF CHLOROPLAST DNA VARIATION IN THE ASTERACEAE

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During the past 30 years, six very different schemes of phylogenetic relationships among the subfamilies and tribes of Asteraceae have been proposed (Cronquist, 1955, 1977; Carlquist, 1976; Wagenitz, 1976; Jeffrey, 1978; Thorne, 1983; Bremer, 1987). Most of these recent classifications agree that two distinct subfamilies (Asteroideae and Cichorioideae) should be recognized; however, there is no consensus concerning the circumscription of the subfamilies, the number of monophyletic tribes, and the relationship among the tribes. Two reasons account for the lack of agreement on intrafamilial relationships in the Asteraceae. First, previous studies have relied almost completely on morphological characters, which have undergone repeated parallel and convergent evolution. Second, only the most recent reassessment of relationships (Bremer, 1987) has applied cladistic approaches to phylogeny reconstruction, and even that study is limited by high levels of homoplasy and a lack of statistical testing of alternative trees.

To provide new characters to aid in clarifying relationships in this complex family, we have been analyzing chloroplast DNA (cpDNA) variation within the Asteraceae and putatively related families. We have completed investigations using two approaches to the study of cpDNA evolution, the assessment of genome arrangement and comparative restriction site mapping, and recently initiated a comparative study of *rbcL* (large subunit of ribulose-1,5-biphosphate carboxylase) sequences.

Our studies have revealed two genome arrangements in the Asteraceae that differ by a single inversion (Jansen and Palmer, 1987a, b). Chloroplast DNAs from the subtribe Barnadesiinae (Mutisieae) are colinear with cpDNAs of most other land plants, including 10 families putatively related to the Asteraceae. All other Asteraceae examined (57 genera from 16 tribes) share a derived 22 kilobase-pair (kb) inversion. This rearrangement defines a basal evolutionary dichotomy within the family and has two important phylogenetic implications.

First, the Mutisieae are paraphyletic, as previously hypothesized on the basis of morphological evidence (Small, 1918; Wodehouse, 1928; Cabrera, 1977; Bremer, 1987). Second, the Barnadesiinae represent the sister group to the rest of the family, which resolves one of the most controversial systematic issues within the Asteraceae. Five different tribes - Cardueae, Heliantheae, Mutisieae, Senecioneae, and Vernoniae - have previously been suggested as the most primitive lineage (Cronquist, 1955, 1976, 1977; Carlquist, 1987; Wagenitz, 1976; Jeffrey, 1977). The identification of the earliest lineage provides indirect support for previous hypotheses concerning the place of origin of the Asteraceae in the Andes of northern South America (Raven and Axelrod, 1974; Turner, 1977) and the primitively woody habit and bilabiate flowers of the ancestors of the family (Carlquist, 1976; Jeffrey, 1977).

Our restriction mapping study has been carried out in two stages. We first examined taxa primarily from the tribe Mutisieae (Jansen and Palmer, 1988) and then studied representatives of the entire family (Palmer et al., 1988; R. Jansen, H. Michaels, and J. Palmer, unpublished). Initially, cpDNAs from 13 genera of the Mutisieae, one genus from each of three other tribes, and four genera from two outgroup families were analyzed with 10 restriction enzymes. A total of 211 restriction site mutations were detected, 55 of which were phylogenetically informative. Wagner (Farris, 1970) and Dollo (Le Quesne, 1974; DeBry and Slade, 1985) parsimony trees constructed with these data were very similar; only the Wagner tree is discussed here. The Wagner parsimony analysis resulted in a single most parsimonious tree (Fig. 1, top) with 247 steps and 15% homoplasy. Four major phylogenetic relationships are depicted in this tree. The most significant is the initial dichotomy separating the subtribe Barnadesiinae (Mutisieae) from the rest of the Asteraceae, including the three other subtribes of the Mutisieae. This is the same dichotomy defined by the inversion described above. The robustness of this initial dichotomy has strong statistical support (98% confidence interval) by the bootstrap analysis of Felsenstein (1985). Furthermore, recent cladistic analysis (Bremer, 1987) based primarily on morphological data, but including the 22 kb inversion (Jansen and Palmer, 1987b), placed the Barnadesiinae at a basal position within the Asteraceae. Cladistic analyses of our preliminary rbcL sequence data (H. Michaels, R. Jansen, and J. Palmer, unpublished) indicate the same initial dichotomy in the Asteraceae (described below). Also in accord with the inversion result, the restriction site data indicate the Mutisieae as paraphyletic, since three of its four subtribes are more closely related to the three other examined tribes of the Asteraceae than the subtribe Barnadesiinae. The molecular phylogeny (Fig. 1, top) also provides support for the monophyly of three of the four currently recognized subtribes of the Mutisieae (*sensu* Cabrera, 1977). Only the morphologically diverse and geographically widespread subtribe Gochnatiinae is shown

to be paraphyletic, which is consistent with recent suggestions by Bremer (1987).

To clarify further relationships within the Mutisieae, a more extensive analysis was performed in which 12 of the 16 genera of Asteraceae examined above were analyzed using 19 restriction enzymes (Jansen and Palmer, 1988). A total of 390 restriction site mutations were detected, 117 of which were phylogenetically informative. Wagner and Dollo parsimony analyses again gave similar results. The Wagner analysis (Fig. 1, bottom) resulted in a single most parsimonious tree of 454 steps and 14% homoplasy. The tree provides further support for the relationships indicated by the 10 enzyme tree (Fig. 1, top). This is reflected in the higher confidence intervals for a number of monophyletic groups, including all taxa which share the cpDNA inversion, the three subtribes of the Mutisieae with the inversion, and the subtribes Mutisiinae and Nassauviinae. The 19 enzyme tree also indicates that the subtribe Gochnatiinae is paraphyletic.

Much broader phylogenetic comparisons were performed using 11 enzymes and 57 genera of the Asteraceae, representing all currently recognized tribes. A total of 926 restriction site mutations were mapped, 328 of which were phylogenetically informative. Wagner parsimony analyses using the global swapping option of PAUP (developed by D. Swofford) generated 12 equally parsimonious trees of 1 315 steps, all of which support the monophyly of the subfamily Asteroideae (sensu Thorne, 1983). Phylogenetic analysis of the data using the same options in PHYLIP (developed by J. Felsenstein) gave six equally parsimonious trees of 1316 steps, all of which support two monophyletic subfamilies (Asteroideae and Cichorioideae sensu Thorne, 1983). A bootstrap analysis (Felsenstein, 1985) produced a majority rule consensus tree (Fig. 2) with 1318 steps and 30% homoplasy. Although this tree is three steps longer than the most parsimonious tree, it is presented here because it shows the groups that are best supported statistically.

The most significant implications of the cpDNA phylogeny concern the circumscription of tribes and subfamilies and the phylogenetic relationships among the tribes. There is strong support for the monophyly of the subfamily Asteroideae, which includes the eight tribes Tageteae, Heliantheae, Eupatorieae, Calenduleae, Senecioneae, Inuleae, Anthemideae, and Astereae. This group occurs in all most parsimonious trees generated by both PAUP and PHYLIP and has a high confidence interval of 86%. The remaining tribes do not form a monophyletic group, indicating that the Cichorioideae as circumscribed by most recent workers (Carlquist, 1976; Wagenitz, 1976; Jeffrey, 1978; Thorne, 1983) may not be a strictly natural group. This conclusion is consistent with Bremer's (1987) recent morphologically based cladistic study. The molecular phylogeny indicates that 11 of the 14 currently recognized tribes are monophyletic with the tribes Heliantheae, Mutisieae, and Tageteae being

paraphyletic. The cpDNA data (Fig. 3) reveal that the Liabeae and Vernoniaeae are a monophyletic group, which agrees with suggestions of their close affinity by Robinson (1977) and Bremer (1987). Relationships among the eight tribes in the subfamily Asteroideae are clearly resolved in some instances. The previously recognized tribes Cotuleae and Ursinieae (sensu Jeffrey, 1978; Robinson and Brettell, 1973) are very closely allied to the Anthemideae, which agrees with their placement in this tribe by Bremer and Humphries (in press). There is a strong affinity between the tribes Tageteae, Heliantheae, and Eupatorieae. The very close relationship between the Eupatorieae and Heliantheae does not agree with Bremer's (1987) placement of the former tribe close to the Astereae. Except for the relationship between the Calenduleae and Senecioneae, there is little resolution of tribal affinities for the remaining members of the Asteroideae. Further phylogenetic analyses using Dollo parsimony and a careful reassessment of character homology are underway to resolve more fully the relatedness of these tribes.

Our preliminary rbcL sequence data are very promising in terms of further resolving phylogenetic relationships of the Asteraceae. We have sequenced the entire gene (1431 basepairs) from eight species representing three putatively related families (Campanulaceae, Dipsacaceae, Valerianaceae) and four tribes of Asteraceae (Cichorieae, Heliantheae, Mutisieae, Senecioneae). Two phylogenetic relationships are indicated in trees generated for the sequence data. *Barnadesia* forms the sister group of the rest of the Asteraceae, in agreement with the phylogenies based on the cpDNA inversion and restriction site mutations. Of the three related families examined, the Campanulaceae is most closely related to the Asteraceae. We have already cloned and are beginning to sequence the rbcL gene from 24 additional taxa from the Asteraceae and putatively related families. One of our labs (JDP) is expanding the comparative sequencing study to include representatives from 45 families of the Asteridae. The other lab (RKJ) is performing restriction site mapping studies in the tribes Cichorieae, Heliantheae, Liabeae, Senecioneae, and Vernoniaeae. Both of these projects will require seed or living material of a diverse range of Asteraceae and Asteridae families. If you have material available for any of these groups please contact us.

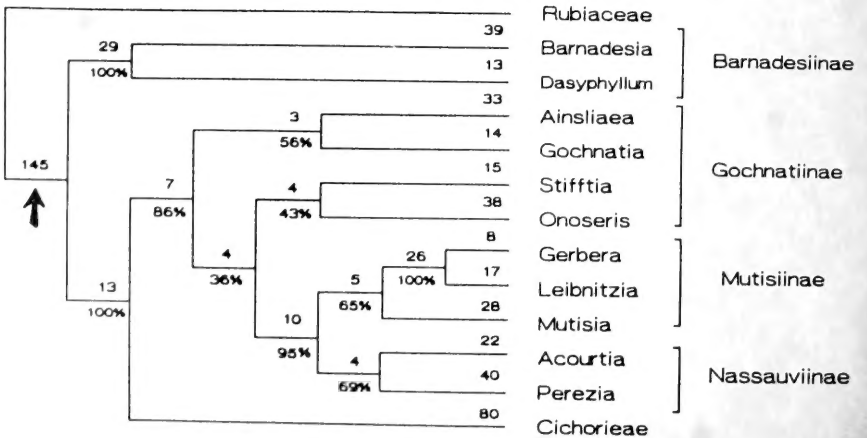
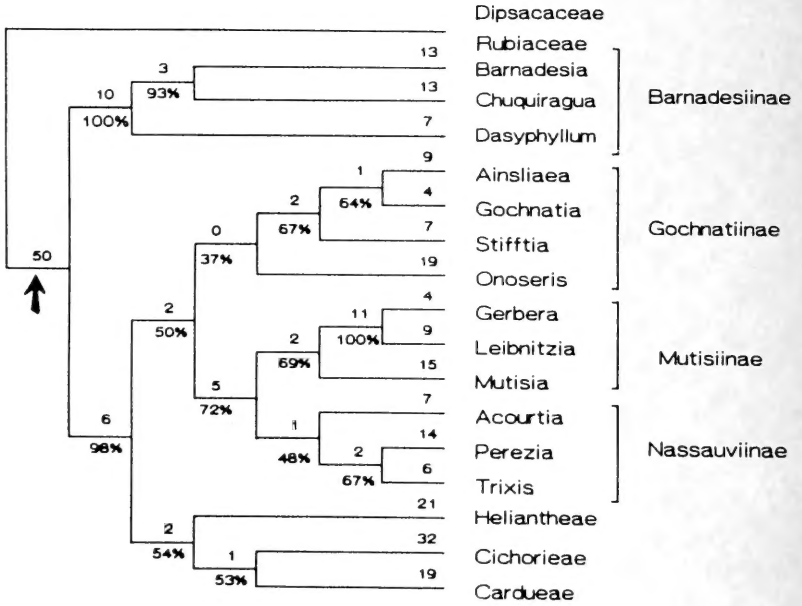


Fig. 1.

Wagner parsimony trees of genera in the Mutisaceae and other Asteraceae. The numbers at each node and along each lineage indicate the number of site mutations. The percentages indicate the number of times that a monophyletic group occurred in 100 bootstrap samples (Felsenstein, 1985). The arrows indicate the occurrence of a 22 kb cpDNA inversion (Jansen and Palmer, 1987b). A single species was examined from each genus, which are as shown for the Mutisaceae, and for the other taxa are: Dipsacaceae, *Cephalaria* and *Dipsacus*; Rubiaceae, *Pentas* and *Psychotria*; Heliantheae, *Helianthus*; Cichorieae, *Lactuca*; Cardueae, *Carthamnus* (Top). Single most parsimonious tree for 16 species of Asteraceae using 211 cpDNA restriction site mutations identified with 10 enzymes. The tree has 247 steps and 15% homoplasy, including 27 parallel losses, two parallel gains, five gains/losses, and two losses/gains. (Bottom) Single most parsimonious tree for 12 species of Asteraceae using 390 cpDNA restriction site mutations. The tree has 454 steps and 14% homoplasy, including 41 parallel losses, six parallel gains, nine gains/losses, and eight losses/gains.

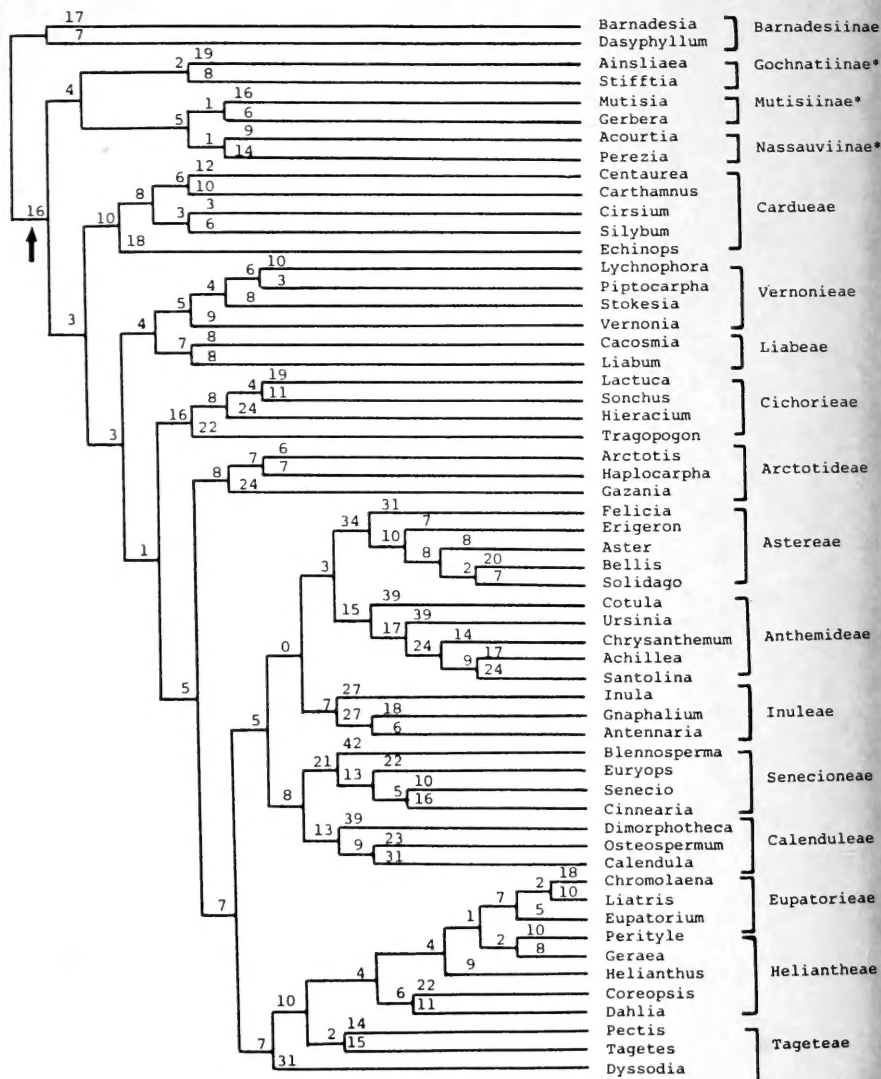


Fig. 2.

Molecular phylogeny of the Asteraceae. Shown in the majority rule consensus tree of generated by the boot option of PHYLIP using 926 restriction site mutations. The numbers at each node and along each lineage indicate the number of site mutations. The tree has a total of 1318 ssteps and 30% homoplasy and rooted relative to the Barnadesiinae. Brackets show the current circumscription of the 13 tribes, while the four subtribes of the Mutisieae are indicated with asterisks. The arrow indicates the occurrence of a 22 kb cpDNA inversion (Jansen and Palmer, 1987b). Unpublished data of R. Jansen, H. Michaels, and J. Palmer.

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A NEW COROLLA TYPE FROM THE ASTERACEAE-ARCTOTIDEAE

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In Asteraceae the common type of peripheral florets with expanded limbs are called rays. Generally the limb is minutely 3-lobed apically and provided with four main veins, joined at the sinuses of the lobes, although this basic structure may be secondarily modified, for example by fusion or reduction of the apical lobes and by multiplication of the veins. In contrast to other tribes, the Lactuceae have ligulate florets with 5-lobed limbs and six main veins. They are often called ligules, in order to distinguish them from the rays.

The Asteraceae are currently divided into two subfamilies, Asteroideae and Cichorioideae (Carlquist 1976, Wagenitz 1976). Rays are common in the tribes of the subfamily Asteroideae, for example in the Inuleae, Astereae, Senecioneae, Calenduleae, Anthemideae, and Heliantheae (they are absent in the discoid tribe Eupatorieae), whereas they are rare in the subfamily Cichorioideae: they are absent in the Cardueae, Lactuceae, and Vernonieae, very rare in the Mutisieae, and commonly present only in the small tribes Arctotideae and Liabeae.

Carlquist (1976) placed the Arctotideae within the Cichorioideae and observed that the only character discordant with that placement "would be if the peripheral flowers of arctoid heads are ray flowers rather than ligulate-type flowers". He suggested that Arctotideae peripheral florets are ligules rather than rays and cited Hoffmann (1890), who had an illustration of the arctoid genus *Didelta*. The illustration (Fig. 1) shows peripheral florets with a varying number of apical lobes, five as in ligules but also four, or three as in rays. The artist certainly did not perceive the significance of the lobe number and probably he did not count them very carefully.

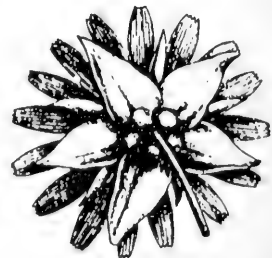


Fig. 1.

A capitulum of *Didelta carnosa*
(= *D. tomentosa*) as illustrated
in Hoffmann 1890 p. 310.

The subfamilial classification into Asteroideae and Cichorioideae is contrary to Cronquist's (1955) perception of tribal interrelationships. In a paper following that of Carlquist (1976), Cronquist (1977) discussed the peripheral florets and the systematic position of the Arctotideae. Cronquist examined species of *Didelta* and he found the peripheral florets to be minutely 4-lobed, seldom only 3-lobed.

In the arctotid genera *Arctotis* and *Gazania* Cronquist found the peripheral florets to be minutely 3-lobed or 2-lobed, or exceptionally 4-lobed. In contrast to Carlquist, Cronquist concluded that Arctotideae peripheral florets are rays rather than ligules and that the tribe forms "a link between the radiate and the discoid tribes", obscuring the distinction of the two subfamilies Asteroideae and Cichorioideae. However, Cronquist also noted that "the variation in number of apical teeth on the rays in this small genus *Didelta* is interesting and possibly significant".

Didelta as well as *Gazania* and six other genera belong to the subtribe Gorteriinae of the Arctotideae (Roessler 1959). *Arctotis* and four other genera belong to the subtribe Arctotidinae. Examination of *Didelta*, *Gazania*, and other Gorteriinae genera shows that the peripheral florets are 4-lobed with five main veins (Fig. 2). Occasionally, for example in *Gazania*, the two middle lobes are smaller or reduced so that the limb appears to be 2-3-lobed. Additional veins are frequently present.

In his revision of the Gorteriinae Roessler (1959) also clearly described the peripheral florets as generally 4-lobed. However, the importance of this observation has apparently not been appreciated. Gorteriinae peripheral florets are neither 3-lobed rays nor 5-lobed ligules, they are 4-lobed and 5-veined "Gorteriinae rays", not homologous with true rays or ligules. The type has hitherto not been described (cf. Jeffrey 1977). *Arctotis* and the other genera of the subtribe Arctotidinae do have true rays, 3-lobed with four main veins.

Fig. 2.

True rays (A-D) and Gorteriinae rays (E-F).

A: *Arctotis venusta*.

B: *Arctotheca calendula*.

C: *Heterolepis aliena*.

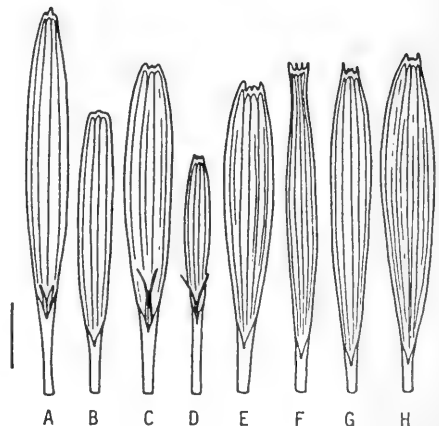
D: *Eremothamnus marlothianus*.

E: *Didelta carnosa*.

F: *Cullumia ciliaris*.

G: *Berkheya angustifolia*.

H: *Gazania krebsiana*.



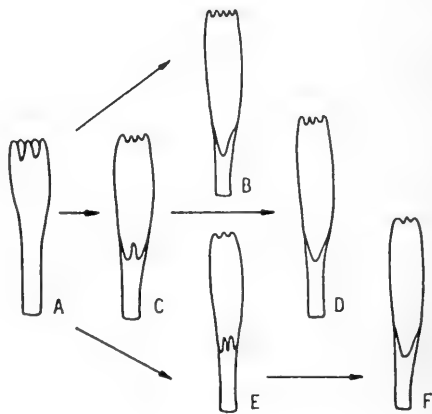
The Gorteriinae rays are a synapomorphy for the genera of this subtribe, corroborating its monophyly which is supported also by other characters. Likewise, the presence of true rays in the Arctotidinae may be a synapomorphy for the genera of that subtribe, if they were independently evolved in the Arctotideae compared to those of the radiate tribe Liabeae and the subfamily Asteroideae. Morphological data indicate that the whole tribe Arctotideae is most closely related to the discoid Cardueae, Carlineae, and Echinopsidae (Bremer 1987) and hence that the Arctotidinae rays are autapomorphic for the subtribe. However, data from chloroplast DNA restriction site mapping indicate that the Arctotideae are the sister group of the radiate Asteroideae (Jansen et al. 1988), implying that rays may be plesiomorphic in the Arctotideae. Independent origin of rays in the Arctotideae is therefore uncertain.

The Gorteriinae rays did not evolve from the ordinary type of 3-lobed rays or vice versa. The latter are usually considered to be derived from mutisoid bilabiate corollas with two ventral lobes and a 3-lobed limb, by reduction of the two ventral lobes (e. g. Jeffrey 1977). Gorteriinae rays presumably evolved from pseudobilabiate corollas, with a single ventral lobe and a 4-lobed limb, by reduction of the ventral lobe. Pseudobilabiate corollas are present within the Mutisieae-Barnadesiinae, but there is no close relationship between that group and the Arctotideae-Gorteriinae (Bremer 1987, Jansen et al. 1988). Bilabiate, pseudobilabiate and ligulate corollas presumably evolved independently from the actinomorphic corolla (Fig. 3).

Fig. 3.

Possible evolution of rays and ligules.

- A: Actinomorphic.
- B: Ligule.
- C: Pseudobilabiate
- D: Gorteriinae ray.
- E: Bilabiate
- F: True ray.



The distinction between true rays and Gorteriinae rays is significant for the classification of *Heterolepis* and *Eremothamnus*, two arctotid genera of uncertain position. *Heterolepis* was placed in subtribe Gorteriinae by Norlindh (1977), but it has 3-lobed rays, not Gorteriinae rays. The rays of *Heterolepis*

often have one or two small ventral lobes, so that several of them are actually bilabiate. *Eremothamnus*, by Norlinth classified in its own monotypic subtribe, has 3-lobed rays of the ordinary type. The tribal relationship of *Eremothamnus* is uncertain (Robinson and Brettell 1973, Bremer 1987). It could be related to other tribes than the Arctotideae.

The rays of *Heterolepis* and *Eremothamnus* reveal that those genera are not members of the Gorteriinae. Furthermore, I am reluctant to classify them in the Arctotidinae. Genera of the latter subtribe are all united by synapomorphies in style and other floral traits not shared by *Heterolepis* and *Eremothamnus*. The presence of rays in *Heterolepis*, *Eremothamnus* and the Arctotidinae could be a synapomorphy for them, but as explained above, rays may be plesiomorphic within the Arctotideae. For the moment I would leave *Heterolepis* and *Eremothamnus* unclassified as to subtribe, noting that *Heterolepis* is probably a member of the Arctotideae, whereas the placement of *Eremothamnus* in this tribe is open to question.

The unique nature of the Gorteriinae rays became apparent to me when examining the Arctotideae for my planned book on cladistics and systematics of the Asteraceae. I will return to the subtribal classification of the Arctotideae in that work.

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Compiled by Charles Jeffrey, Royal Botanic Gardens, Kew.

Now and as from 1 Jan. 1987, "The Kew Record of Taxonomic Literature" is being published quarterly, and those requiring information on works on *Compositae* published since that date and currently are referred to that publication.

Annual volumes of the "Kew Record" cover the years 1971-1982 inclusive. For the years 1983-1986, annual volumes are in preparation, but have not yet appeared. This series will be continued to cover the gap up to such time as the backlog volumes appear.

General

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