

# Eupatorieae

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## INTRODUCTION

The majority of the taxonomic history of the non-radiate, non-yellow-flowered Eupatorieae (Figs. 43.1–43.3) has depended on broad generic concepts such as those in Bentham (1873), Hoffmann (1890–1894), and B.L. Robinson (1913). Some rather well-defined genera were recognized such as *Brickellia* Elliot, *Mikania* Willd. and *Stevia* Cav., but the core of the tribe consisted of a broad concept of *Eupatorium* L. and many artificial segregates based on variations in pappus and anther appendages. Redefinition of the core group into reasonably phyletic units was the aim of studies by King and Robinson summarized in the treatment of 1987.

## PHYLOGENY

The present study takes the biosystematic, phenetic study of Eupatorieae by King and Robinson (1987), based on morphology, anatomy, cytology, and secondary metabolite chemistry, and compares it with preliminary results of DNA sequencing, a method not available for the 1987 study. The DNA sequence results presented here are derived mostly from the work of Schilling et al. (1999), Schmidt and Schilling (2000), and Ito et al. (2000a, b). Two phyletic trees are presented here, one an extract from the big tree made available for the Barcelona Symposium, and a second tree derived through the efforts of Dr. Funk and Dr. Chan including additional generic data available from GenBank. Some problems in the latter effort arise from different sites that have been examined by different

workers: Ito et al. (2000a, b) use nrDNA ITS regions and cpDNA RFLP, Schmidt and Schilling (2000) use nuclear ITS sequence data, and Schilling et al. (1999) use chloroplast DNA restriction site data. Though genera sampled are limited, some generalizations on phylogeny can be made.

As seen in the Eupatorian part of Helianthodae in the Big Tree (Fig. 43.4), Eupatorieae are not the most plesiomorphic group in the Helianthian relationship (supertribe Helianthodae) as suggested in King and Robinson (1987). Structurally, the tribe could already be seen as highly derived in its enlarged styler appendages and its tendency for reduced and hollow apical anther appendages.

The genera of Eupatorieae come out as a natural group among the various elements of the supertribe Helianthodae, nested within groups that have been traditionally treated as Helenieae (Bentham 1873; Hoffmann 1890–1894). On the basis of structure, particularly hairs on the style base, closest relatives outside of the tribe would be *Arnica* L., *Chaenactis* DC., and *Chamaechaenactis* Rydb. of Chaenactidinae (Robinson 1981). Closest relative on the basis of secondary metabolite chemistry could be *Arnica* L., which shares the presence of pyrrolizidine alkaloids with Eupatorieae (C. Jeffrey, oral statement at Kew Symposium, 1994). The most closely related group to Eupatorieae according to DNA sequencing, based on ITS regions, is Peritylinae (Fig. 43.4). Structurally the two groups are not close. The most plesiomorphic elements of Eupatorieae, Hofmeisteriinae and Oaxacaniinae, already show highly subimbricated, graduated involucre, no ray florets, lack of yellow pigmented corollas, 5-merous florets, and

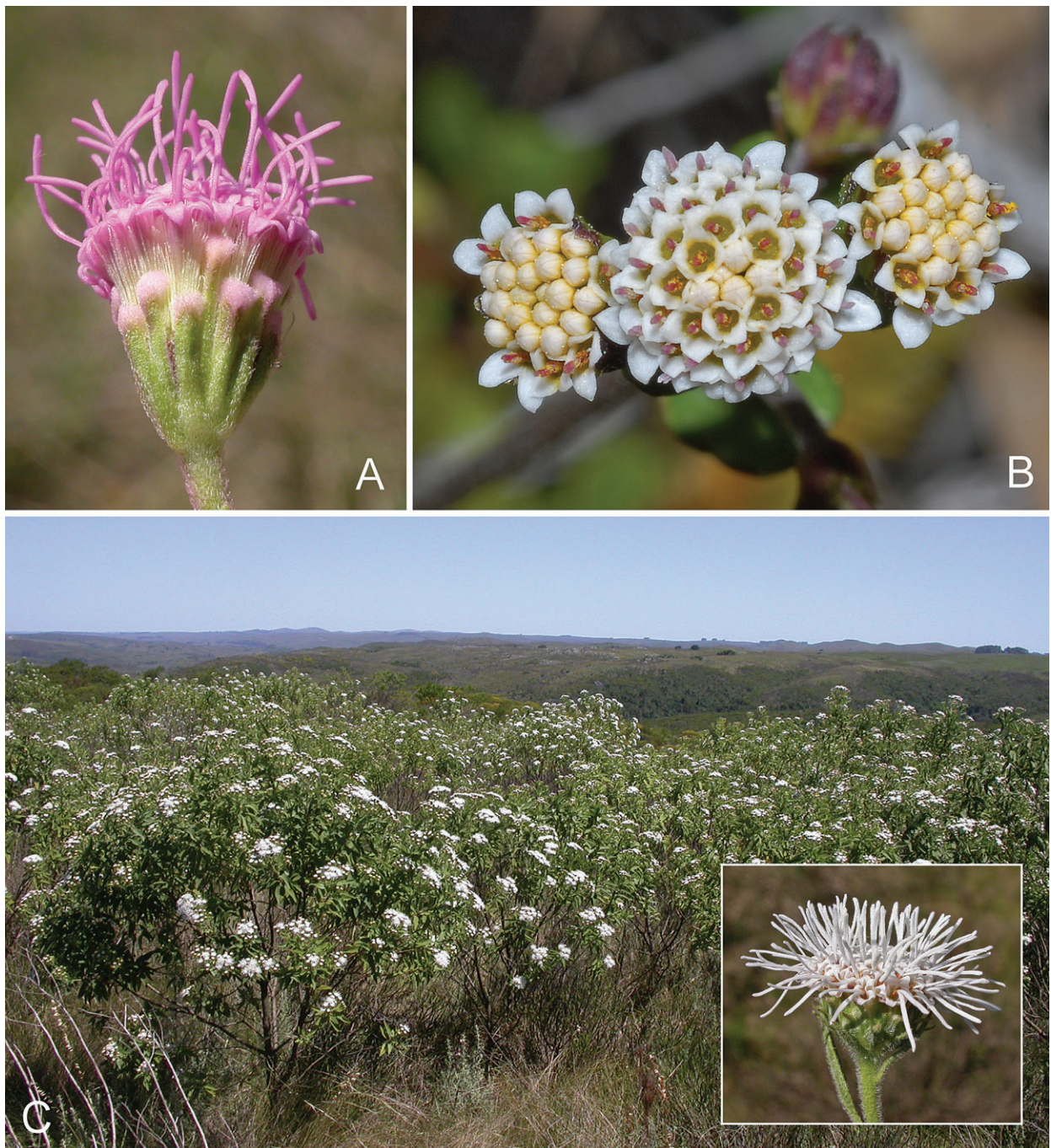


**Fig. 43.1.** Eupatorieae: Disynaphiinae and Adenostemmatinae. **A** *Disynaphia calyculata* (Hook. & Arn.) R.M. King & H. Rob., Uruguay; **B** *Acanthostyles buniifolius* (Hook. & Arn.) R.M. King & H. Rob., Uruguay; note style appendages; **C** *Grazielia brevipetiolata* R.M. King & H. Rob., Uruguay; **D** *Gymnocoronis spilanthoides* (D. Don.) DC., Argentina. [Photographs and plate preparation, J.M Bonifacino.]

well-developed style appendages, differing from the few subequal involucre bracts, presence of rays, commonly yellow pigmented corollas, 4-merous florets, and unexpanded style appendages in Peritylinae.

Within Eupatorieae, the overall sequence of subtribes in King and Robinson (1987), and the implied phylogeny prove completely inverted on the basis of DNA sequence

data. In the 1987 work, the wide-spread  $x = 10$  was regarded as basic to the tribe, and the genera with higher numbers were considered derived. According to the DNA sequence data (Schilling et al. 1999), the large element of the tribe with stabilized chromosome base numbers of  $x = 10$  is apparently derived. It is the groups with higher basic chromosome numbers that are more plesiomorphic,



**Fig. 43.2.** Eupatorieae: Gyptidinae and Ageratinae. **A** *Gyptis pinmatifida* Cass., Uruguay; **B** *Iltisia repens* S.F. Blake, Costa Rica, note 4-lobed corollas; **C** *Radlkoferotoma cistifolia* (Less.) Kuntze, Uruguay. [Photographs and plate preparation, J.M. Bonifacino.]



**Fig. 43.3.** Eupatoriaceae: Eupatoriinae and Ageratinae. **A** *Eupatorium hyssopifolium* L.; **B** *Conoclinium coelestinum* (L.) DC., eastern United States. [Photographs, E.E. Schilling; plate preparation, J.M. Bonifacino.]

a situation seen also in several genera of Heliantheae and Helenieae (Robinson et al. 1981). The polyploid origin of the tribe is confirmed by Ito et al. (2000b).

DNA studies have provided some additional results. Schilling et al. (1999) have shown that *Eupatorium* must be interpreted much more narrowly than the traditional view (Benth. 1873). DNA studies by Schmidt and Schilling (2000) and Ito et al. (2000a) provide more concentrated surveys of *Eupatorium* in the strict sense with its closest relatives.

The intent of the King and Robinson (1987) study was to stabilize generic concepts, and generic concepts have not been altered by DNA data presently available. This is in spite of the fact that some generic elements are, and were then, seen as slightly paraphyletic. Definability of concepts is not sacrificed here to minor concerns about paraphyly. Excessively paraphyletic elements, those defined only by what they are *not*, rather than by what they *are*, have been rejected.

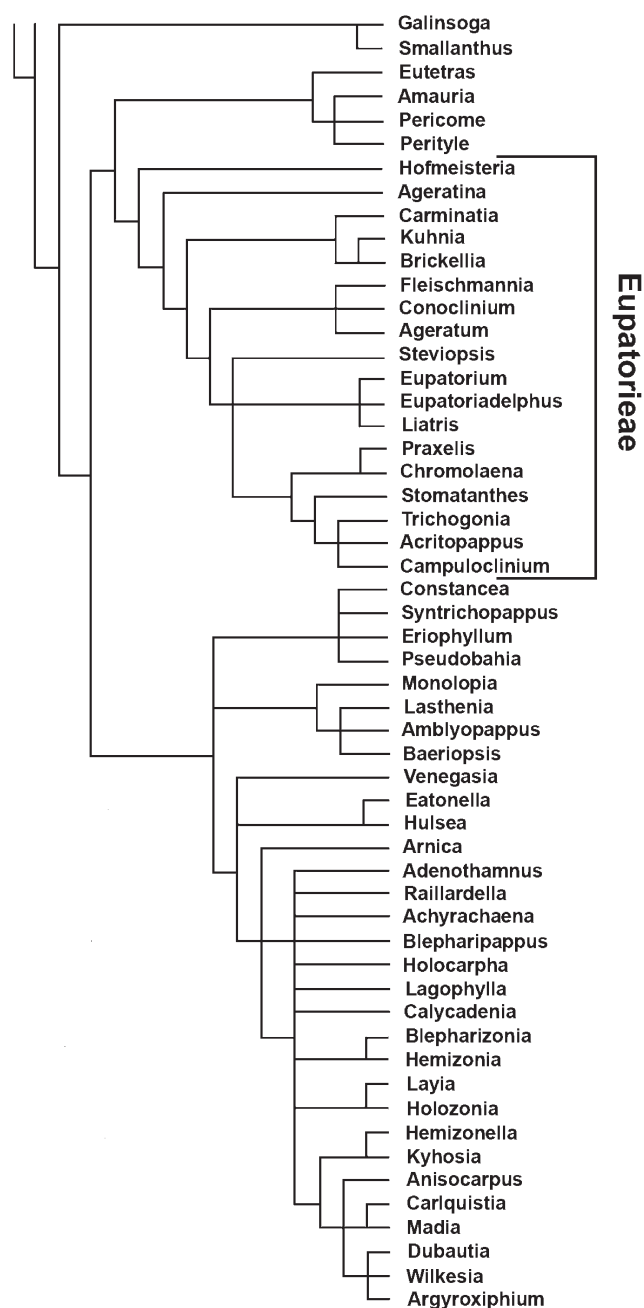
#### SUBTRIBAL CLASSIFICATION

The major taxonomic changes in Eupatorieae that can be anticipated from DNA data involve the sequence of the subtribes. There are also some evident alterations in the limits of the subtribes, as might be expected where limits tend to depend on one character or even lack of specialized characters. In contrast to the sequence given in King and Robinson (1987) beginning with Adenostemmatinae and Eupatoriinae, the subtribes are treated below in the order suggested by the available DNA (Figs. 43.5–43.10). Subtribes without known DNA sequences are included in the sequence on the basis of structural or cytological data.

**Oaxacaniinae.** —  $x = 18$ . Two genera, *Oaxacania* B.L. Rob. & Greenm. and *Carterothamnus* R.M. King & H. Rob. No DNA reports are available, but proximity to Hofmeisteriinae seems certain. Both groups are primarily Mexican. The most significant difference from Hofmeisteriinae is the paleaceous receptacles of the present group.

**Hofmeisteriinae.** — (Fig. 43.6).  $x = 17?, 18, 19$ . The subtribe is basal in Eupatorieae among the groups for which DNA has been sequenced. The epaleaceous receptacles, the pseudowhorled leaves subtending the peduncles, and the sometimes shortened apical appendages of the anthers are distinctive. The pollen of the subtribe is the most nearly smooth of any in Eupatorieae (King and Robinson 1966).

**Neomirandeeinae.** — (Fig. 43.6).  $x = 17, 20, 24, 25$ . DNA sequence data place the subtribe in a cluster that includes Oxylobinae and Trichocoroninae. Higher chromosome numbers in the group seem to be plesiomorphic. Previous assumptions of close relation to Critoniinae



**Fig. 43.4.** Segment of “Big Tree” showing Eupatorieae (*Hofmeisteria*–*Campuloclinium*) as a well-defined group within the supertribe Helianthodea. Position of Eupatorieae shown as closest to Peritylinae within various elements of the old tribe Helenieae. Tree derived from ITS data in GenBank.

seem incorrect based on data from *Critonia*. Relation to the subtribe Hebecliniinae remains in question, since DNA sequence data are not available for the latter. The most obvious difference between Neomirandeeinae and Hebecliniinae is the specialization for epiphytism and highly organic soils in the former and the presence of

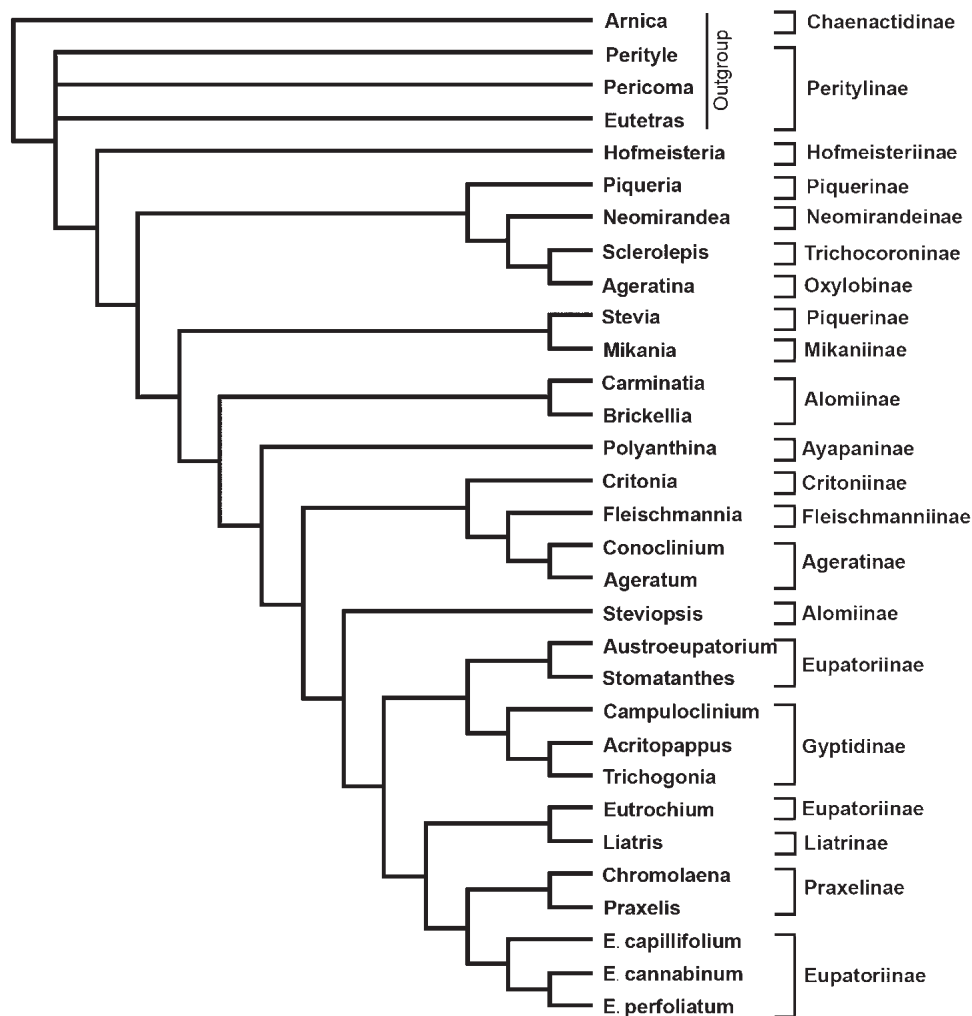
both  $x = 10$  and  $x = 16$  chromosome base numbers in the latter. Receptacles and inner surfaces of the corollas in Neomirandaeinae are often pubescent as in some Hebecliniinae and a few Critoniinae.

The subtribe is credited with one genus, but two clear subgroups can be seen. Typical *Neomirandea* includes both the epiphytic *N. araliifolia* (Less.) R.M. King & H. Rob. and its close relatives with the habit of a Strangler Fig, plus the terrestrial forms. The strictly epiphytic *Neomirandea eximia* (B.L. Rob.) R.M. King & H. Rob. and its relatives are distinct, having no hairs on the receptacle or on the inner corolla surfaces and no enlarged style bases.

**Trichocoroninae.** — (Fig. 43.6).  $x =$  ca. 15. In this group of three genera, *Trichocoronis* A. Gray, *Sclerolepis* Cass., and *Shinnersia* R.M. King & H. Rob., DNA

sequences are only published for *Sclerolepis* (Ito et al. 2000b). The group is notable for its aquatic and semi-aquatic nature and rather distinctive chromosome number. Structurally, the subtribe might seem a reduced close relative of Ageratinae, but sequence data indicate that relationship is remote. Distribution is in Mexico and the eastern United States.

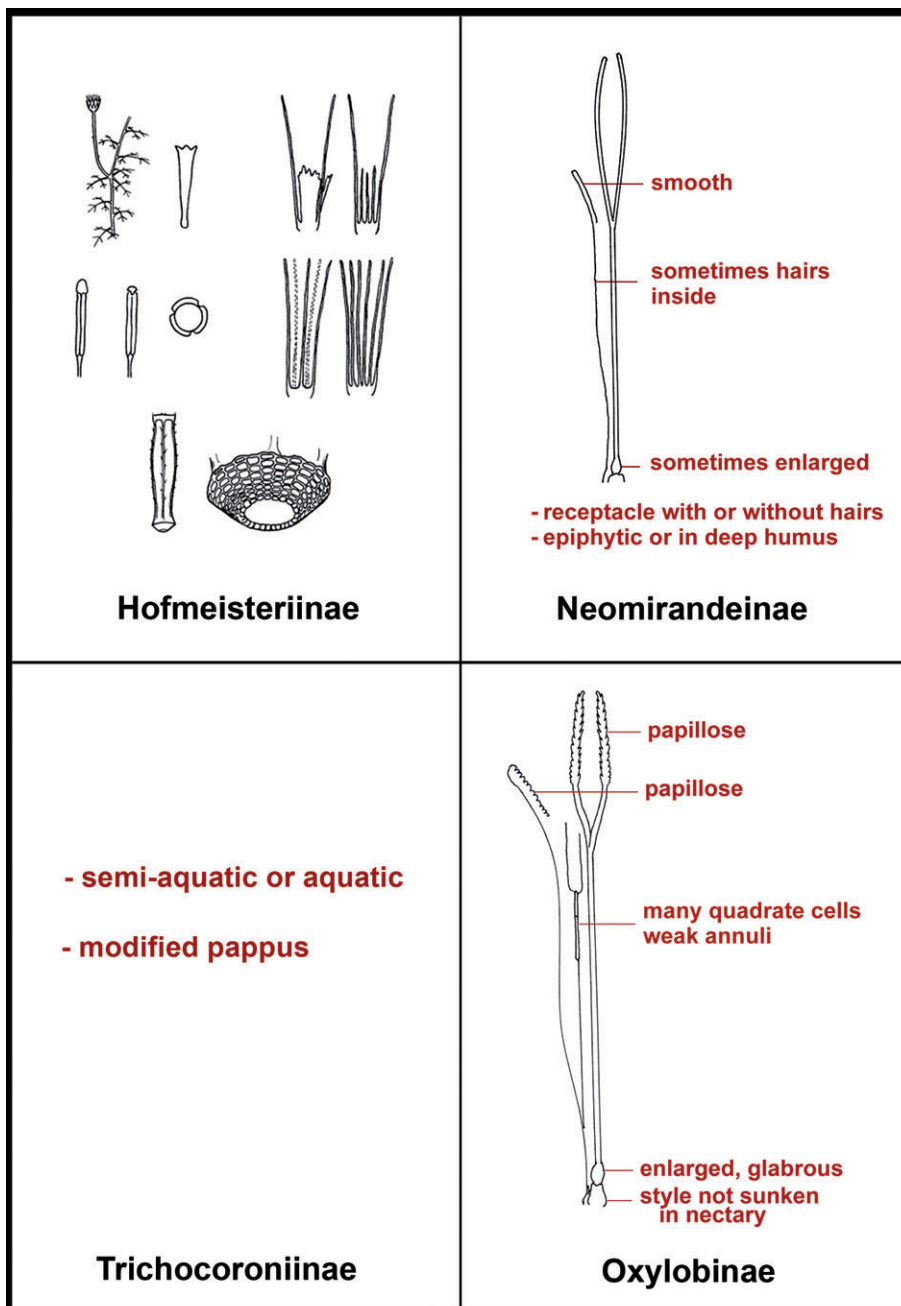
**Oxylobinae.** — (Fig. 43.6).  $x = 16, 17$ , ca. 40. DNA has been sequenced for the largest genus, *Ageratina* Spach, with well over 200 species (Robinson 2006b). From limited DNA results, the subtribe is in a group with Neomirandaeinae and Trichocoroninae. The group appears variously coequal with or basal to Mikaniinae. In the latter case it appears basal to the rest of the tribe above Hofmeisteriinae. This reinforces the conclusion



**Fig. 43.5.** Phyletic tree of the tribe Eupatorieae with selected outgroups based on ITS data from GenBank with additional genera intercolated on the basis of their positions in the cpDNA RFLP results of Ito et al. (2000b). Tree prepared by V.A. Funk and R. Chan. Excluded here, but included in the text, members of the subtribes Adenostemmatinae, Disynaphiinae, Hebecliniinae, and Oaxacaniinae, for which no DNA data are available. A biogeographic tree of Compositae can be found in Chapter 44.

that higher chromosome numbers are plesiomorphic in Eupatorieae. There is no particular close resemblance between Mikaniinae and Oxylobinae except their higher chromosome numbers and great number of species. Oxylobinae more closely resemble the members of the tribe that follow Mikaniinae in this sequence. The group is geographically concentrated in the western parts of North and South America with a few intrusions into eastern North America and the West Indies. A number of the species seem to be apomicts, speciating like *Taraxacum* Weber in F.H. Wigg. and *Hieracium* L. in Cichorieae.

**Piqueriinae.** — (Fig. 43.7). *Stevia/Piqueria* group.  $x = 11, 12, 13$ . DNA sequences place the group among the basal subtribes of Eupatorieae, and the chromosome numbers fall outside of the stabilized  $x = 10$  that is widespread in the remainder of the tribe. Some features are the often reduced number of 3–5 florets and involucre bracts that equal each other in number, and the totally reduced or obovate and irregularly-margined apical appendages of the anthers. In the most complete DNA sequence results used here, *Piqueria* Cav. and *Stevia* Cav. are separated, the former closer to *Ageratina* Spach and the latter closer



**Fig. 43.6.** Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Hofmeisteriinae, Neomirandeinae, Trichocroniinae, Oxylobinae.

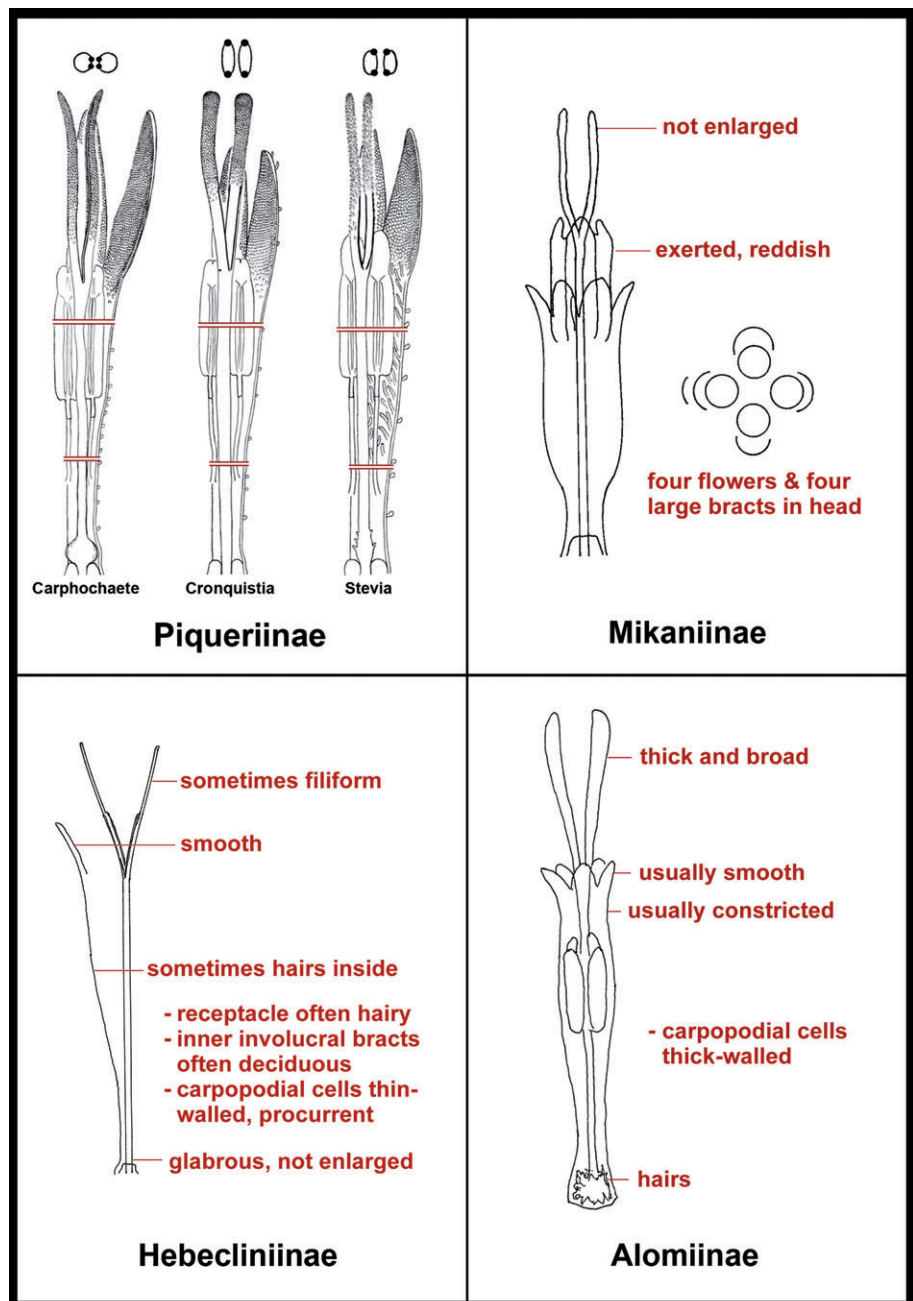
to *Mikania* Willd. Nevertheless, structure suggests that *Piqueria* and *Stevia* are closely related to each other, and more complete DNA results are expected to confirm that. Existing data using different sites, is not regarded as sufficient basis for contrary conclusions. Probably closely related are *Microspermum* Lag. and *Iltisia* S.F. Blake that have more florets in the heads. They also have a chromosome number of  $x = 12$ .

These genera were placed by King and Robinson (1987) in the subtribe Ageratinae with *Ageratum* L. on the basis of the usually papillose corolla lobes, modified

apical anther appendages, modified or absent pappus, and mostly non-Brazilian distribution. The present more restricted group is mostly Mexican and Central American with *Stevia* extending northward into the United States and southward into South America. A number of species of *Stevia* consist of both apomictic and non-apomictic populations (King and Robinson 1967). Some species of *Stevia* and most of the *Microspermum* group have zygomorphic peripheral corollas.

**Mikaniinae.** — (Fig. 43.7).  $x = 16, 17, 18, 19, 20$ . DNA sequences place the subtribe variously basal to everything

**Fig. 43.7.** Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Piqueriinae, Mikaniinae, Hebecliniinae, Alomiinae.





in the tribe above Hofmeisteriinae or basal to everything above the Oxyllobinae/Neomirandeiinae/Trichocoroninae group. The high chromosome number, the distinctive heads with four involucre bracts and four florets, exerted stamens, and an often pubescent style shaft of the single genus suggest a comparatively isolated position. *Mikania* Willd., with ca. 450 species, can be easily recognized, and does not seem closely related to any other. Species of *Litothamnus* R.M. King & H. Rob., in maritime Brazil, and a few species of *Ophryosporus* Meyen, with short apical anther appendages and usually broadened style tips, are only superficially similar to *Mikania*, but without close relationship. The distribution of the genus is throughout the moist temperate and tropical parts of America with one element that is pantropical. Most, but not all of the species are vines, and they occur frequently in forested areas such as the Amazon basin where other Eupatorieae are rare.

If further analysis of the DNA data corroborate present reports, and Mikaniinae and Piqueriinae are close, it would mean that the genera with number of involucre bracts characteristically equaling the number of florets are all rather closely related.

**Hebecliniinae.** — (Fig. 43.7).  $x = 10, 16$ . No DNA sequences are available, and the position assigned here is in serious doubt. Relationship was considered close to Critoniinae by King and Robinson (1987). Specializations include the usually domed receptacle, often with many prominent hairs, procurrent carpodial extensions on the lower ribs of the achenes, very deciduous inner bracts of the involucre, and sometimes extremely filiform appendages of the style branches. The  $x = 10$  chromosome numbers in the subtribe suggest a more Critoniine relation, and, if so, the  $x = 16$  chromosome numbers of the more typical genera may be derived within the subtribe. The genera are concentrated in Central America with extensions into South America. One genus, *Guayana* R.M. King & H. Rob., is concentrated in the Guayana Highlands.

**Alomiinae.** — (Fig. 43.7).  $x = 9$ . The three elements for which DNA has been sequenced, *Brickellia* Elliot, nom. cons., *Kuhnia* L. (which is part of *Brickellia*), and *Carminatia* Mocino ex DC. were all treated as members of Alomiinae in King and Robinson (1987). Included are representatives of *Brickellia* and its relatives with upwardly constricted corollas, style branches expanded in both width and thickness, flattened outer surfaces of the pappus bristles, and densely pubescent style bases, and *Carminatia* with less constricted corollas, narrow style branches, scarcely flattened outer surfaces of the pappus bristles, and glabrous style bases. Plumose pappus bristles have evolved twice in the subtribe, in the *Kuhnia* element of *Brickellia* and in *Carminatia*. A unique form of papillosity is found on the corolla lobes and style appendages in one genus, *Phanerostylus* (A. Gray) R.M. King & H. Rob. On the basis of structure, this mostly western North American and Mexican subtribe

has many relatives in the eastern parts of South America and a few relatives in the Andes, the southernmost being *Helogyne* Nutt., but the latter relationships need confirmation from DNA analysis.

DNA indicates that at least one genus, *Steviopsis* R.M. King & H. Rob., placed in Alomiinae by King and Robinson (1987), is of questionable position in that subtribe. In the “Big Tree” based on ITS sampling of a more limited selection of genera (Fig. 43.4), *Steviopsis* is separated from Alomiinae with an intervening Fleischmanniinae/Ageratinae clade. In the more complete phylogeny using ITS and information from cpDNA (Fig. 43.5), *Steviopsis* falls directly between Alomiinae and closely related Ayapaninae in a clinal series. The Fleischmanniinae/Ageratinae clade and other subtribes are further derived in the same cline. The latter phylogeny, placing Alomiinae, *Steviopsis* and Ayapaninae next to each other, seems closer to the truth, but structure would suggest that the three would be together on a side-clade, not in a cline leading to other subtribes. For structural evidence see below under Ayapaninae.

**Ayapaninae.** — (Fig. 43.8).  $x = 10$ . Available DNA sequences place the subtribe somewhat apart from Alomiinae. However, the persistent subimbricate bracts of the involucre, the cells of the corolla lobes not differentiated from those of the throat, the thick cell walls of the carpodium, the usually enlarged pubescent base of the style, and the sometimes both broadened and thickened branches of the style indicate Alomiinae and Ayapaninae are very close. Carpodia of Ayapaninae are sometimes very specialized in having a very enlarged basal row of cells. The subtribe is mostly South American with extensions north into Central America as far as Mexico. A few members are very small ephemerals, similar in size and habit to some of the better known small, annuals or short-lived perennial genera in the *Ageratum* group, but the latter tend to have differentiated and often papillose cells in the corolla lobes.

**Adenostemmatinae.** — (Fig. 43.8).  $x = 10$ . No DNA sequences are available, and no structural feature shows particularly close resemblance to other members of the tribe. The placement here is based on the chromosome number, the  $x = 10$  that is essentially consistent for the remainder of the tribe. Distinctive features are the uniquely unsclerified interstices of the receptacle, which allows for changes of shape during maturation, and the pappus in the form of glanduliferous and often sticky knobs in two of the three genera, *Adenostemma* J.R. & G. Forster, and *Sciadocephala* Mattf. The presumed effective distribution mechanism of the sticky knobs has resulted in a pantropical distribution for *Adenostemma*.

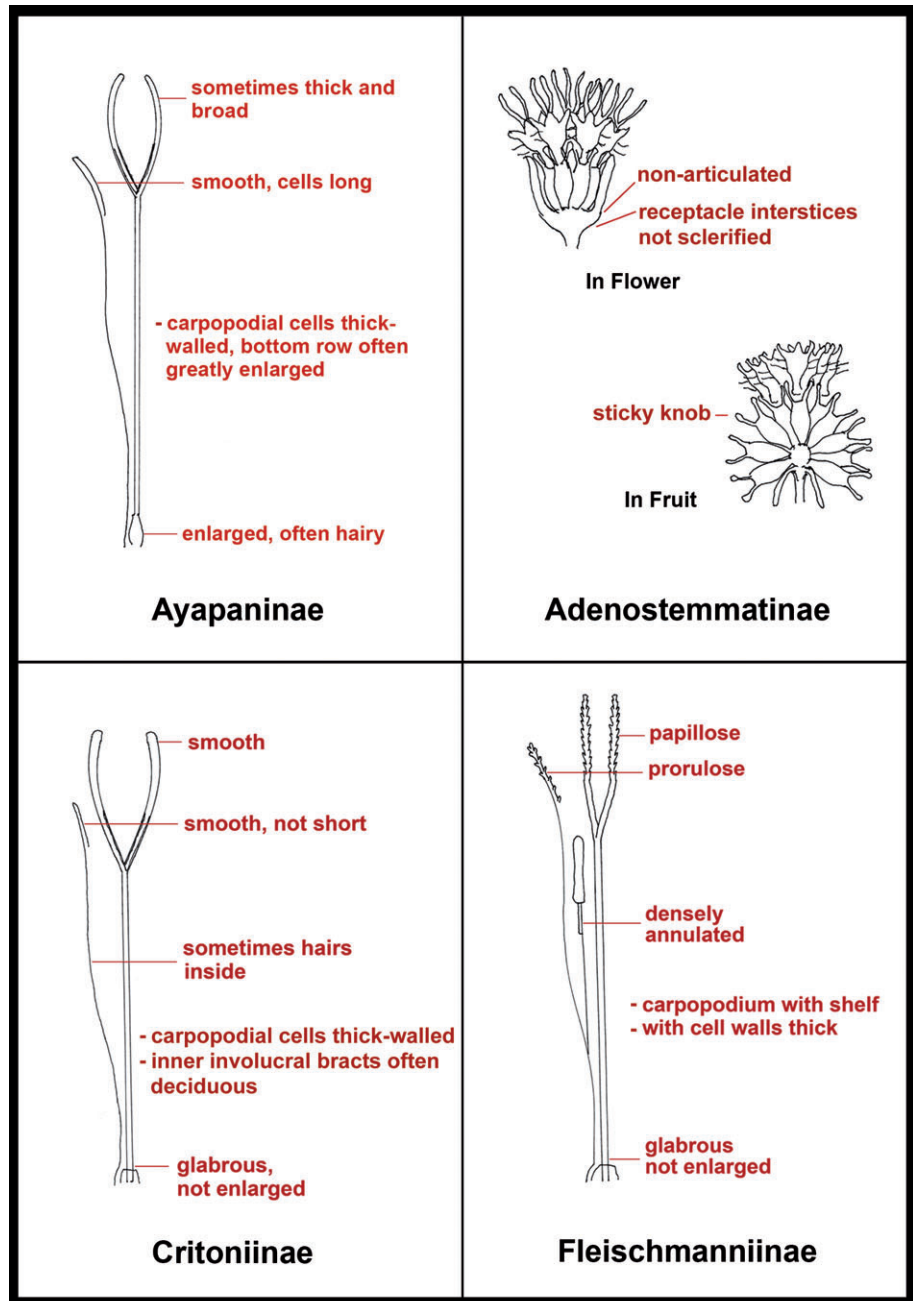
**Critoniinae.** — (Fig. 43.8).  $x = 10$ . Available DNA results place *Critonia* P. Br. basal to the *Fleischmannia*/*Ageratum* branch of the tribe. As delimited by King and

Robinson (1987), the subtribe Critoniinae is a large, mostly Central American, West Indian, and northern South American group. Structure is of limited help since the group mostly lacks specializations such as cells of the corolla lobes shaped differently from those of the throat, ornate anther collars, or pubescence on the style, and few have highly reduced anther appendages. The cells of the carpodia tend to have thick walls and the inner bracts of the involucre are often deciduous. As such, the subtribe may be highly artificial. It is *Critonia* for which the DNA data are available, and the subtribe is listed here on

that basis. Other genera that have been placed in the subtribe may or may not be closely related, sharing a lack of specialized characteristics, and having a generally tropical aspect. Some of the features used to define the subtribe in King and Robinson (1987) are those shared by members of Neomirandinae, Hebecliniinae, and Praxelinae, to which some of the genera may prove to be related.

**Fleischmanniinae.** — (Fig. 43.8).  $x = 4, 10$ . DNA sequences place this almost monogeneric subtribe close to *Ageratum* L. to which it bears no particularly close resemblance. It is difficult to see close relationship for

**Fig. 43.8.** Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Ayapaninae, Adenostemmatinae, Critoniinae, Fleischmanniinae.



Fleischmanniinae with thick-walled cells in the carpodia to *Ageratum* and *Conoclinium* DC. and their closest relatives, which have thin-walled cells in their carpodia. There may be some superficial resemblance between the genera in the field, since many *Fleischmannia* specimens have been labeled in the field as *Ageratum*. Distinctions of Fleischmanniinae include the uniquely prurulose cells of both surfaces of the corolla lobes, the slender anther collars with cell walls obscured by annular thickenings, and carpodia with projecting upper rims in addition to their thick-walled cells. The style shafts are simple and glabrous except in the monotypic *Sartorina* R.M. King & H. Rob. The pappus is capillary, usually with many bristles, sometimes with only five or ten. The  $n = 4$  chromosome number in *Fleischmannia microstemon* Cass. (Baker 1967) is the result of dysploidy. The subtribe is primarily Mexican and Andean in South America, the Mexican part of the distribution overlapping closely with that of most species of *Ageratum*.

**Ageratinae.** — (Fig. 43.9).  $x = 10, 15$ . DNA sequences link the mostly Mexican *Ageratum* L. with the North American and Mexican *Conoclinium* DC., both with conical receptacles. Conical receptacles are also found in such genera as *Barrosoa* R.M. King & H. Rob., *Dasycondylus* R.M. King & H. Rob., and *Campuloclinium* DC. placed in Gyptidinae by King and Robinson (1987). DNA is available for *Campuloclinium*, which shows it is remote from Ageratinae. *Ageratum* is known mostly from highly weedy *A. conyzoides* L. and the widely planted *A. houstonianum* Mill., which have a pappus of five awns, but most of the species have no pappus or a coroniform pappus. The genus is concentrated in Mexico and Central America. *Conoclinium* of the United States and Mexico was placed in Gyptidinae by King and Robinson (1987). It differs from *Ageratum* by its pappus of numerous capillary bristles. The similarity between *Ageratum* and *Conoclinium* in their ITS DNA sequences includes both the alignments of nucleotides that are present and an almost identical large gap where nucleotides are missing.

Structural evidence seems to conflict with the DNA evidence for both the distance of Ageratinae from Gyptidinae and the closeness to Fleischmanniinae.

A close relative of *Ageratum* is *Phania* DC. of the West Indies, which has pappus squamae with sinuous cell walls. Some other South American genera placed in the subtribe by King and Robinson (1987) such as *Phalacraea* DC. are probably related. It remains to be seen whether *Piqueriopsis* R.M. King, *Ferreyrella* S.F. Blake, *Guevaria* R.M. King & H. Rob., and *Ellenbergia* Cuatrec., among various small, mostly rather ephemeral Eupatorieae, that usually have many-flowered heads, should be retained in Ageratinae or placed elsewhere.

Excluded here are Piqueriinae (*Stevia*/*Piqueria* group (see above) on the basis of the higher chromosome num-

bers and the reduced number of florets in the heads with matching numbers of florets and involucre bracts. Ageratinae have carpodia with thin or beaded cell walls, sometimes reduced anther appendages, and anther collars with annular thickenings. The thickenings of the anther collars are not as dense as in Fleischmanniinae and do not obscure the cellular structure.

**Gyptidinae.** — (Fig. 43.9).  $x = 10$ . The tribe is notable for a variety of habits, from large shrubs such as *Litothamnus* R.M. King & H. Rob., and *Bahianthus* R.M. King & H. Rob. to rosulate herbs such as *Bishopiella* R.M. King & H. Rob. Limits of the subtribe seem to be in need of revision. DNA sequences show close relationship between *Trichogonia* (DC.) Gardn. and *Campuloclinium* DC., which have been placed in the subtribe by King and Robinson (1987), but DNA also puts into the group two genera from other subtribes, *Acritopappus* R.M. King & H. Rob. from Ageratinae with a reduced pappus, and *Stomatanthes* from Eupatoriinae. The latter adds to the genera already known in the subtribe with hairs on the base or shaft of the style. All four sequenced genera are concentrated in Brazil, and relationship to each other is easily acceptable. Excluded according to DNA is the North American and Mexican *Conoclinium*, discussed above under Ageratinae.

Gyptidinae are notable for the differentiated cells of the corolla lobes, the usually thin-walled cells of the carpodium, and the usually large number of florets in the heads. Trends within the diverse subtribe include many genera with stipitate bases on the achenes and another series of genera with closely spirally inserted alternate leaves. Two genera reaching the Andes are *Neocuatreccasia* R.M. King & H. Rob. of Bolivia and Peru, which is most certainly a member of the subtribe, and *Lourteigia* R.M. King & H. Rob. of Colombia and Venezuela, which has a unique deep constriction in the callus under the pappus that causes the pappus and callus to come off as a unit. This is not the kind of dehiscence from the achenial body that is characteristic of *Symphyopappus* Turcz. in Disynaphiinae. Sequencing of *Lourteigia* would be particularly helpful.

**Disynaphiinae.** — (Fig. 43.9).  $x = 10$ . No DNA sequences are available. The placement here is based on some possibly superficial resemblance to Eupatoriinae. The two subtribes share a tendency toward reduced numbers of florets in the heads, undifferentiated cells in the corolla lobes, and thin-walled cells in the carpodium when the carpodium is not vestigial. In Disynaphiinae, the floret number is five in all but one species (Robinson 2006a). Disynaphiinae differ from Eupatoriinae by being basically woody, having simple and glabrous style shafts, and having pitting of the phytomelanin in the achene walls in regular transverse rows. The leaves of *Disynaphia* Hook. & Arn. are spirally inserted, whereas most other genera have opposite leaves. The leaves of *Campovassouria*

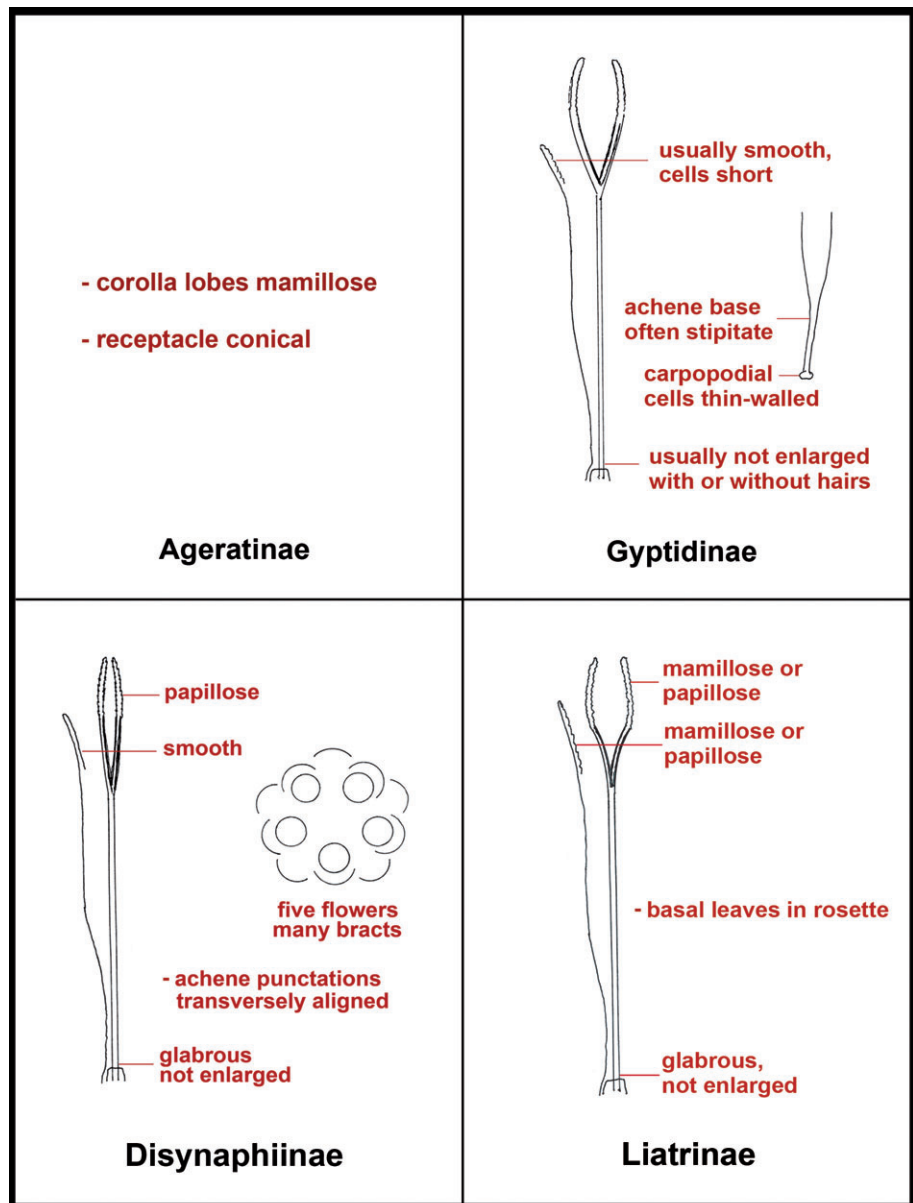
R.M. King & H. Rob. are alternate or opposite. The unity of the members of Disynaphiinae is not considered to be in question. All but one species have a well-developed capillary pappus and persistent involucre bracts. The group is almost entirely Brazilian with a few species reaching as far as Peru.

**Liatrinae.** — (Fig. 43.9).  $x = 10$ . DNA sequencing places this almost exclusively eastern United States group of genera close to Eupatoriinae. Both subtribes are strongly North American, but do not seem particularly close on the basis of structure. Liatrinae have glabrous style bases and at least the young leaves are in a rosette. The spiciform cymes of most species of *Liatris* Gaertn. ex Schreb. seem unique in Asteraceae.

**Praxelinae.** — (Fig. 43.10).  $x = 10, 20$ , polyploids. DNA confirms close relationship between *Chromolaena* DC. and *Praxelis* Cass. The sequences also place the subtribe close to the subtribe Gyptidinae. The most notable character is the totally deciduous involucre, usually leaving a bare receptacle after anthesis. Characteristically the bracts do not spread as they mature or dry, they dehisce. The subtribe extends mostly from the Gulf Coast of the United States south to Argentina, but the concentration of genera and species is in Brazil the same as Gyptidinae.

Members of the subtribe include the extremely weedy *Chromolaena odorata* (L.) R.M. King & H. Rob. and potential weeds such as *Praxelis clematidea* R.M. King & H. Rob. The most exceptional member of the subtribe is

**Fig. 43.9.** Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Ageratinae, Gyptidinae, Disynaphiinae, Liatrinae.



*Praxeliopsis* G.M. Barroso, which was seemingly rare and occurring sparsely, but apparently occurs instead in large turfs as seen in Bolivian collections. It has the anthers mounted at the mouth of the zygomorphic corollas, and the style base is unique in the subtribe by being enlarged. Polyploidy and apomixis seem common in the subtribe, the best example being *Praxelis capillaris* (DC.) Sch.Bip.

The subtribe contains the only genera in the tribe with tangentially spreading style branches, most notably *Praxelis* Cass., *Eitenia* R.M. King & H. Rob. and *Eupatoriopsis* Hieron. (Robinson 1984). Corollas of the subtribe also sometimes have prominent colored resin ducts along the veins of the throat.

In the West Indies are found members of Eupatorieae that show unquestionable traits of Praxelinae combined with unquestionable traits of *Koanophyllon* Arruda de Camara of Critoniinae. This apparent intersubtribal hybridization seems to have produced many healthy offspring and should be examined more carefully (King & Robinson 1987, example *Osmiopsis* R.M. King & H. Rob.).

**Eupatoriinae.** — (Fig. 43.10).  $x = 10$ . This is one of the most completely studied subtribes of the tribe Eupatorieae, distributed as it is mostly in the north temperate zone. DNA sequences are available for *Eupatorium* L. and the subgroup of *Eupatorium* that has been known as *Eupatoriadelphus* R.M. King & H. Rob. or *Eutrochium* Raf. The genera have a north temperate distribution concentrated in North America.

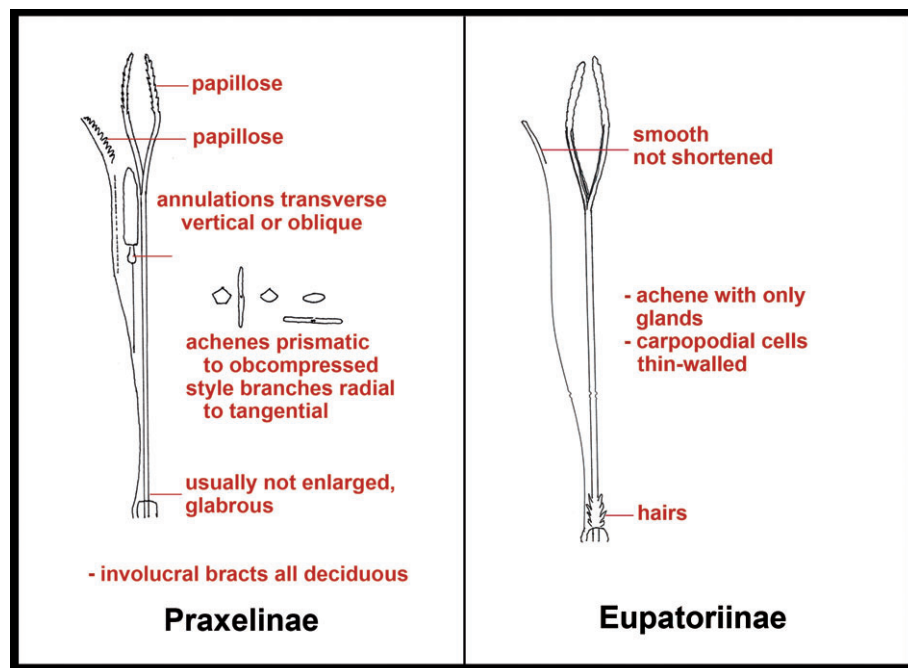
The structurally related *Austroeupatorium* R.M. King & H. Rob. is mostly South American and a weedy introduc-

tion to the paleotropics. The bases of the styles are characteristically hairy, and relationship with the northern Eupatoriinae seems close on the basis of structure. On the basis of nuclear DNA sequences, Ito et al. (2000a) place the genus closer to *Eupatorium* than *Fleischmannia* or *Chromolaena*, but outside of the *Eupatorium/Eupatorium* sect. *Traganthes/Eutrochium* group. The present reworked tree based on GenBank data places *Austroeupatorium* even more remote, within Gyptidinae with *Stomatantes*.

One of the genera placed here by King and Robinson (1987), *Stomatantes* R.M. King & H. Rob. of eastern South America and sub-Saharan Africa, has been placed by DNA sequencing in Gyptidinae, which is also mostly eastern South American. The most notable distinguishing features of the latter were the densely setuliferous achenes and the usually enlarged tips of the style branches, and such placement is not unreasonable. It remains to be seen where *Hatschbachiella* R.M. King & H. Rob. will fall, since it, too, is eastern South American and has setulae on the achenes.

## EVOLUTION

Hybridization seems to occur in a number of elements of Asteraceae. At the species level, as an obvious example, hybridization is seen in the Helianthean genus *Encelia* Adans. (Funk 1985), where its extent may be underestimated. Hybridization at higher levels may be rare, but could have marked effects, as in Coreopsidae (Panero 2007). On the basis of structural study, intersubtribal



**Fig. 43.10.** Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in text: Praxelinae, Eupatoriinae.

hybridization is particularly evident in Eupatorieae between Praxelinae and elements that have been placed by King and Robinson (1987) in Critoniinae. Notably, the areas of likely intersubtribal hybridization in Eupatorieae are between subtribes having a chromosome base of  $x = 10$ . These are also now seen to be the more recently evolved members of the tribe. Many of the more isolated and sharply defined genera of the tribe are ones with higher or lower chromosome base numbers. Previously, such higher numbers might have been considered a primary isolating mechanism for these latter genera, but the phylogeny based on DNA sequences might mean that these genera and subtribes are more isolated and resistant to hybridization primarily because of their greater evolutionary distance from each other.

## CONCLUSION

Further DNA sequences in Eupatorian genera will fill in many gaps. Sequences of Adenostemmatinae, *Critonia* P. Browne, *Hebeclinium* DC., and Disynaphiinae are particularly desirable. Positions of many individual genera from some of the more crudely circumscribed groups will also be helpful, for example *Ferreyrella* S.F. Blake, *Guevaria*

R.M. King & H. Rob., *Radlkoferotoma* Kuntze, and *Scherya* R.M. King & H. Rob., the latter having some aspects of both Gyptidinae and Ageratinae. Nevertheless, it seems unlikely that further changes as great as those shown above will be necessary. It is very reassuring that none of the changes suggested by known DNA sequences alter any of the groups circumscribed with certainty in King and Robinson (1987) having unique and well-defined characters.

The primary problem seen in the present study is the conflict between the sharp delimitation of the internally strongly cohesive Eupatorieae on the basis of non-DNA characters versus the DNA evidence of a position buried amidst a series of structurally very different and unlikely subtribes or tribes of the supertribe Helianthodae.

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## Literature cited

- Baker, H.G.** 1967. The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate. *Taxon* 16: 293–300.
- Bentham, G.** 1873. Compositae. Pp. 163–533 in: Bentham, G. & Hooker, J.D. (eds.), *Genera Plantarum*, vol. 2(1). Reeve, London.
- Funk, V.A.** 1985. Phylogenetic patterns and hybridization. *Annals of the Missouri Botanical Garden* 72: 681–715.
- Hoffmann, O.** 1890–1894. Compositae. Pp. 87–387 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, vol. 4(5). Engelmann, Leipzig.
- Ito, M., Watanabe, K., Kitai, Y., Kawahara, T., Crawford, D.J. & Yahara, T.** 2000a. Phylogeny and phytogeography of *Eupatorium* (Eupatorieae, Asteraceae): insights from sequence data of the nrDNA ITS regions and cpDNA RFLP. *Journal of Plant Research* 113: 79–89.
- Ito, M., Yahara, T., King, R.M., Watanabe, K., Oshita, S., Yokoyama, J. & Crawford, D.J.** 2000b. Molecular phylogeny of Eupatorieae (Asteraceae) estimated from cpDNA RFLP and its implication for the polyploid origin hypothesis of the tribe. *Journal of Plant Research* 113: 91–96.
- King, R.M. & Robinson, H.** 1966. Generic limitations in the *Hofmeisteria* complex (Compositae – Eupatorieae). *Phytologia* 12: 465–476.
- King, R.M. & Robinson, H.** 1967. Multiple pollen forms in two species of the genus *Stevia* (Compositae). *Sida* 3: 165–169.
- King, R.M. & Robinson, H.** 1987. *The Genera of the Eupatorieae (Asteraceae)*. Monographs in Systematic Botany from the Missouri Botanical Garden 22. Missouri Botanical Garden, St. Louis.
- Panero, J.L.** 2007 [2006]. Coreopsidae. Pp. 406–417 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales*. Springer, Berlin.
- Robinson, B.L.** 1913. A key to the genera of the Compositae – Eupatorieae. *Proceedings of the American Academy of Arts and Sciences* 49: 429–437.
- Robinson, H.** 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). *Smithsonian Contributions to Botany* 51: 1–102.
- Robinson, H.** 1984. Style rotation in the Asteraceae. *Taxon* 33: 400–404.
- Robinson, H.** 2006a. New species and new records in *Symphopappus* (Eupatorieae: Asteraceae). *Phytologia* 88: 129–135.
- Robinson, H.** 2006b. New species of *Ageratina* from andean South America (Eupatorieae: Asteraceae). *Phytologia* 88: 154–175.
- Robinson, H., Powell, A.M., King, R.M. & Weedon, J.F.** 1981. Chromosome numbers in Compositae, XII: Heliantheae. *Smithsonian Contributions to Botany* 52: 1–28.
- Schilling, E.E., Panero, J.L. & Cox, P.B.** 1999. Chloroplast DNA restriction site data support a narrowed interpretation of *Eupatorium* (Asteraceae). *Plant Systematics and Evolution* 219: 209–223.
- Schmidt, G.J. & Schilling, E.E.** 2000. Phylogeny and biogeography of *Eupatorium* (Asteraceae: Eupatorieae) based on nuclear ITS sequence data. *American Journal of Botany* 87: 716–726.