

## PHYTOGEOGRAPHICAL PATTERNS IN THE TRIBE EUPATORIEAE (ASTERACEAE)

Por HAROLD ROBINSON AND ROBERT M. KING<sup>1</sup>

The Compositae Tribe Eupatorieae contains more than 2,000 species that are concentrated in the Neotropical Region. Fully half the tribe has been traditionally submerged in an artificial genus concept of *Eupatorium* which has been convenient for non-specialists, but useless for detailed comparison of structure, cytology, chemistry and phytogeography. The present authors in the last decade have furnished numerous revisions in the Eupatorieae detailing many structural and phyletic aspects unique to the tribe. While many of the features of the tribe are not applicable to other groups of plants, there is an inevitable resource in the geographic patterns within related groups that are now evident for the first time.

In the extensive revisions of the Eupatorieae by the authors, the phytogeographic aspect has been consistently noted, and the classic Arcto-Tertiary distribution of *Eupatorium sensu stricto* has been demonstrated (King & Robinson, 1970). Still, the distribution data derived from the recent revisions is mostly scattered in the numerous separate publications of taxonomic results. It is hoped that a review and discussion here of a number of the phytogeographic patterns of the Neotropical Eupatorieae based on the new phyletic concepts will be of general interest to other botanists.

Basic phytogeographic categories include (1) widely distributed taxa (2) taxa of restricted distribution and narrow endemics (3) groups with widely distributed weedy species (4) and taxa of erratic distribution.

<sup>1</sup> Department of Botany, Smithsonian Institution, Washington, D. C. 20560 U.S.A.

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## CATEGORY (1) WIDELY DISTRIBUTED TAXA

Of the widely distributed groups the most notable are those with natural extensions of range into the Eastern Hemisphere. The genus *Mikania* Willd., which occurs throughout the Neotropics is also found in Africa, southern Asia and in Indonesia. The species of the Paleotropical region include a few considered as endemic, but all belong to the closely related group that includes *M. scandens* (L) Willd., the only species of Eastern North America.

A second genus extending into the Paleotropical region is *Adenostemma* J. R. & G. Forster which possesses the most effective specialization for distribution in the tribe. In *Adenostemma* the achene bears knobs with viscid tips, obviously adapted for distribution by animals. At least 6 species occur in Africa, tropical Asia and the Pacific that are distinct from those of the Neotropics. Within the Neotropical region three species of *Adenostemma* show a series of parallel but non-overlapping distributions along the Andes (King & Robinson, 1974). The most restricted, *A. cuatrecasatii* K & R is at higher elevations in Colombia and adjacent Venezuela. At lower elevations, *A. fosbergii* K. & R. occurs in the intermontane area of El Valle in Colombia near the Pacific Coast and crosses to the Amazonian side of the Andes in Southern Colombia, Ecuador and northern Peru. The most widely distributed *A. platyphyllum* Cass. is also at low elevations along the Atlantic coasts of Costa Rica and Venezuela and along the Pacific Coasts of Colombia and Ecuador. The species crosses to the eastern side of the Andes in Peru and extends southward through Bolivia to northern Argentina. The distribution patterns seem particularly interesting considering the specialization of the genus for animal distribution. It is notable that the related genus *Sciadocephala* Mattfield which has somewhat similar viscid knobs on the achene does not have the same success at dispersal, consisting of five species each of limited distribution in Panama, Colombia, Ecuador and Guayania.

The subtribe Eupatoriinae contains the only other members of the tribe naturally occurring in the Eastern Hemisphere. The Arcto-Tertiary distribution of *Eupatorium* L. has been noted (King & Robinson, 1970) with entrance into Asia probably across the Bering Strait. It now seems likely that this occurred without the genus ever crossing to the west and south of the Rocky Mountains or the southern ranges in Alaska. The genus is not now known northwest of Alberta, Canada. In the south another genus, *Stomatanthes* King & Robinson of the same subtribe has entered the Eastern Hemisphere apparently by an entirely different route across the southern Atlantic. *Stomatanthes* is represented in Brazil by ca. 12 species (Robinson, 1970) while 3 species are endemic to tropical Africa (King & Robinson, 1975). A special capacity for long distance dispersal for mem-

bers of the subtribe might be suspected such as resistance to colder temperatures or desiccation.

The subtribe Eupatoriinae is more phytogeographically significant as one of a related group of three subtribes which might be referred to as the "Eastern Complex" of the Eupatorieae. That subtribe with the related *Gyptis* (Cass.) Cass. and *Disynaphia* Hook. & Arn. ex DC groups are concentrated in eastern South America and eastern North America with minor representation in the Andes, Mexico and western North America. This phytogeographic bond between the eastern portions of the two continents stands in sharp contrast to the distribution of two other large genera of the tribe, *Ageratina* Spach. and *Fleischmannia*. Schultz-Bipontinus. Both of the latter genera, having similar general aspect but not being closely related, are concentrated in Mexico, Central America and in the Andes of South America. Representation in eastern parts of North and South America is minimal. The latter distribution pattern is the more explicable being essentially continuous. The former pattern is completely discontinuous in most of the intervening West Indian region.

Another subtribe of the Eupatorieae tends to show in another way the extent of the barrier between eastern and western parts of South America. The Alomiinae containing the genus *Brickellia* Elliott and its relatives is common in Mexico and the Southwestern United States. Though not generally recognized as such, many genera of Brazil such as *Dissothrix* A. Gray, *Leptoclinium* Benth., *Planaltoa* Taubert, *Austrobrickellia* King & Robinson, are of this relationship. Some of the Brazilian genera are comparatively closely related to those of Mexico. With the exception of one widely distributed weedy species, *Brickellia diffusa* (Vahl) A. Gray, it is only the most divergent element of the subtribe, *Helogyne* Nutt. that crosses the Andes extending from northern Argentina and Bolivia into Peru and Chile.

#### CATEGORY (2) TAXA OF RESTRICTED DISTRIBUTION AND NARROW ENDEMICS

While genera such as *Stevia* Cavanilles, *Mikania*, *Brickellia*, *Fleischmannia*, *Ageratum* L. and *Ageratina* are notable for wide distribution, other genera of equal distinction are, as a result of more recent origin or greater specialization, more restricted. Perhaps the most extreme example is the genus *Standleyanthus* King & Robinson known from one stem collected in 1924 in Costa Rica. The genus has not been recollected and may be extinct. The genus was a weak shrub in a wet forest area that is now mostly destroyed.

Another genus, *Neomirandea*, King & Robinson, is mostly specialized for wet forest areas from Mexico southward to Ecuador with

the greatest concentration of species in Costa Rica and western Panama. Many of the species are epiphytes, a specialization that is comparatively rare in the Asteraceae. An unusually high percentage of the ca. 25 species, more than half, have been uncollected until the last 15 years. Also an epiphyte is the monotypic genus *Gongrostylus* K. & R. The species described from eastern Costa Rica was for many years known only from there and western Ecuador. Recent collecting in the Atlantic slopes in Panama have revealed two new localities. A third genus of the Eupatorieae *Tuberstyles* Steetz is an epiphyte on Mangroves along the Pacific coast from eastern Panama, through Colombia to northern Ecuador. None of the three epiphytic genera are particularly closely related to each other.

At higher elevations in central Mexico is the genus *Microspermum* Lag. having 7 species (Rzedowski, 1970, 1972). The genus is a specialized member of the tribe with ray-like peripheral flowers. The most closely related genus is the monotypic *Iltisia* Blake of high elevations on the Sierra de la Muerte in Costa Rica, which lacks the distinctive ray-like flowers.

In Central Mexico are the genera *Dyscritogyne* K. & R. with 2 species and *Erythradenia* (B. L. Robinson) K. & R. *Mexianthus* B. L. Robinson and *Neohintonia* K. & R. with 1 species each. The latter two genera are notable for having only one flower per head. To the north are *Verieckia* K. & R. and *Brickelliastum* K. & R. each with one species, *Phanerostylis* (Gray) K. & R. with 3 species and *Flyriella* K. & R. with 4 species, all sufficiently distinct to suggest they are relicts of groups more widely distributed in pre-glacial times. Similar relict status is suspected for members of the *Liatris* groups to the east in Florida including *Liatris* J. K. Small (1 sp.), *Trilisa* (Cass.) Cass. (2 sp.), *Garberia* A. Gray (1 sp.) and *Hartwrightia* A. Gray ex Watson (1 sp.).

The West Indian region possesses mostly members of the Eupatorieae that are related to the large genera *Critonia*, P. Browne *Koanophyllon* Arruda ex Koster and *Chromolaena* DC. However, three smaller genera of isolated relationship and geography are known; *Ciceronia* Urb. of Oriente in eastern Cuba, *Antillia* K. & R. of the Trinidad Mts. of central Cuba and *Eupatorina* K. & R. a caliphile of central Hispaniola.

In South America there are numerous genera of restricted distribution. Three genera, *Alomiella* K. & R., *Monogerion* Barroso and King and *Praxeliopsis* Barroso of Central Brazil each have a single species. The restricted genera of more interest are those with 2 or more species. *Radlkoferotoma* Kuntze of Southern Brazil and Uruguay has 2 species (Cabrera, 1957), *Neocabreria* K. & R. of southern Brazil and northern Argentina includes 3-4 species with the recent addition of *Eupatorium catharinense* Cabrera, *Macropodina* K. & R. of southern Brazil and Paraguay has 3 species, *Lomatozoma* Baker of



southern Brazil long considered monotypic now has 3 known species. There are numerous endemic Eupatorieae in eastern Brazil including *Agrianthus* Mart ex DC with 6 species, *Lasiolaena* K. & R. with 2 species, and *Stylotrichium* Mattf. with 2 species all of Bahia, and *Acritopappus* K. & R. with 5 species distributed from Ceara south to northern Minas Gerais. *Lorentzianthus* K. & R., a genus of only one species ranges from southern Bolivia to northern Argentina where it was until recently treated as separate unrelated species *E. viscidum* H. & A. in Argentina and *E. santacruzense* B. L. Robinson in Bolivia. *Amboroa* Cabrera described from central Bolivia has a second species in northern Peru (King & Robinson, 1975), *Neocuatrecasia* K. & R. includes 7 species at high elevations along the Amazonian side of the Andes in southeastern Peru and adjacent Bolivia, *Lourteigia* K. & R. with 7-8 species is restricted to the Paramos of Colombia and western Venezuela where it occurs with other Eupatorieae of widely distributed genus *Ageratina*, *Ascidiogyne* Cuatr. of northern Peru is now known to have 2 species (Cabrera, 1976) and also *Ferreyrella* Blake of the same area has 2 species (King & Robinson, 1973). The genus *Guayania* K. & R. with 7 species presently known is restricted to the Guayana Shield area of Venezuela and northern Brazil where it occurs around and on the Tepuis.

#### CATEGORY (3) GENERA WITH WIDELY DISTRIBUTED OR WEEDY SPECIES

Some genera such as *Mikania* and *Stevia* are widely distributed with 150-300 known species but they also contain individual species of wide distribution. In *Mikania* both of the closely related species *M. micranthera* HBK and *M. cordifolia* (L.) Willd. occur throughout the Neotropical region and the former is also found in India and the Indonesian region. In *Stevia* there are 4 species that have extensive ranges from Mexico southward into the Andean regions of South America, *S. lucida* Lag. *S. elatior* HBK, *S. ovata* Willd. and *S. serrata* Cav. In *Conocliniopsis* K. & R., the single species *C. prasiifolia* (DC) K. & R. long erroneously confused with the totally distinct *Lourteigia ballotaefolia* (HBK) K. & R., has an interrupted range. The species occurs in Colombia and Venezuela to the north and is common again in Brazil south of the Amazon basin. The range of the single species equals that of the entire closely related genus *Barrosoa* K. & R. containing 11 species.

In a number of genera widely distributed species can be traced to specific areas of origin. *Chromolaena* is most richly represented in the area of Central and southern Brazil with decreasing representation in more distant parts of South America. Also, all closely related genera are concentrated in Brazil. However, three species have attained distributions throughout Tropical America, *C. laevigata*

(Lam) K. & R., *C. ivaefolia* (L.) K. & R. and *C. odorata* (L.) K. & R. The latter two species extend their range into the southeastern United States. *Chromolaena odorata* has close relatives and variants in Guatemala and Chiapas which indicate origin or diversification in that area. The latter species has in recent times become widely adventive in the Eastern Hemisphere. *Brickellia diffusa* (Vahl) A. Gray is common in Mexico, Central America, the West Indies and South America, but a close relative is limited to south central Mexico, and the genus *Brickellia* is otherwise limited to North America south to Costa Rica. *Austroeupatorium* K. & R. is a genus concentrated in Brazil and Argentina but one species *A. inulaefolia* (HBK) K. & R. occurs throughout South America and into Panama and is now widely adventive in the Eastern Hemisphere. *Hebeclinium* DC is a genus with most species restricted to the northern Andes but one species *M. macrophyllum* (L.) DC has successfully extended its range throughout Tropical America.

The most important weedy species of the tribe belong to the widely distributed genera *Ageratum* L. *Ageratina* Spach and *Fleischmannia* Sch-Bip. In *Ageratina* the species are all concentrated in Central America though some of the most diverse elements are in South America. It is two Mexican-Central American species *A. conyzoides* L. and *A. houstonianum* (Mill) that have become widely adventive throughout the tropics of both hemispheres. *Ageratina* has some widely distributed species such as *A. prunellaefolia* (HBK) K. & R. of Mexico, Central America and Ecuador. In the latter locality the species has usually been confused with the related *A. gracilis* (HBK) K. & R. of the northern Andes. The truly weedy members of the genus are two Mexican species *A. adenophora* (Spreng.) K. & R. and *A. riparia* (Regel) K. & R. that have become a nuisance in Australia, Hawaii and Ceylon among other places. The example of *A. riparia* is particularly interesting in view of its very restricted distribution in the country of origin, Mexico (Rose pers. communication).

The genus *Fleischmannia* has a number of widely distributed species such as *F. pratensis* (Klatt) K. & R. ranging from Mexico to the northern Andes. Most notable, however, is *F. microstemon* (Cass.) K. & R. of Central America, the West Indies and South America which is now also adventive in Africa and few other places in the Eastern Hemisphere. The species is sufficiently distinct that the exact relationship is not certain. Baker (1967) in analyzing the weedy specializations erroneously related the species to *F. sinclairii* Benth ex Oerst. of Central America, but origin in that general geographical area is still most likely.

## CATEGORY (4) GROUPS OF ERRATIC DISTRIBUTION

Examples of erratic distributions are not common in the Eupatorieae, but three examples are of particular interest. The genus *Guevaria* K. & R. is restricted to the Andes of Ecuador and Peru and the closely related genera *Ferreyrella* Blake and *Ellenbergia* Cuart. are endemic to Peru. It is unexpected, therefore, to find a closely related genus *Piqueriopsis* King in a totally remote locality in Michoacan, Mexico, and another close relative, *Piqueriella* K. & R. even farther away in the state of Ceara in eastern Brasil. Such a distribution would seem the result of long distance dispersal.

The genus *Steyermarkina* K. & R. includes 3 species in southern and central Brazil. A fourth species is restricted to an area draining into Lake Maracaibo in northwestern Venezuela. The specific differences are sufficient to rule out recent introduction but not sufficient to suggest long separation that might result from migration through suitable habitats to the west of the Amazon Basin. Long distance dispersal is the probable explanation.

The genus *Idiothamnus* K. & R. includes 4 species (King & Robinson, 1975), and relationships of three of the species were recognized by B. L. Robinson (1919, 1930) in spite of the scattered distributions. None of the species seem to be common in collections but a number of specimens have been seen of *I. lilloi* (BLR) K. & R. from the eastern slopes of the Argentine Andes from Salta and Tucumán. Two specimens have been seen of *I. pseudorgyalis* K. & R. from near Rio de Janeiro in Brazil. *Idiothamnus orgyaloides* (B. L. R.) K. & R. from near Tarapoto in northern Peru is known only from the type, and *I. clavisetus* (Badillo) K. & R. is represented by a few specimens from the northern coastal range in Venezuela. The disjunction of the species may be partly the result of inadequate collecting, but a severe habitat restriction might also play a role. The species all have a look commonly associated with shrubs of temperate forests and the general range of the genus seems to be entirely within the distribution of the more temperate forest zone in South America.

## CONCLUSIONS

Genera and groups of genera in the tribe Eupatorieae provide many examples for phytogeographic interpretation and correlation. Those cases cited are believed to be significant indicators of special floristic provinces habitats, or distribution phenomena. The results are only one of the biproducts of the recent taxonomic revisions in the tribe.

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