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Taxonomic notes in *Hypochoeris* L. (Asteraceae)

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Abstract

During the works for the treatment of the genus *Hypochoeris* in the Rio Grande do Sul State we verify that *H. rosengurtii* CABR. cannot be separated from *H. lutea* (VELL.) BRITTON. *H. rosengurtii* var. *pinnatifida* (SPEG.) CABR. and *H. microcephala* var. *albiflora* (OK.) CABR. are elevated to the category of species. Comments about the species are presented.

Kew words: *Hypochoeris*, Asteraceae, taxonomy. Brazil

Resumo

Durante os trabalhos para o tratamento do gênero *Hypochoeris* no Rio Grande do Sul, verificou-se que *H. rosengurtii* CABR. não ser pode separada de *H. lutea* (VELL.) BRITTON. *H. rosengurtii* var. *pinnatifida* (SPEG.) CABR. e *H. microcephala* var. *albiflora* (OK.) CABR. são elevados a categoria de espécie. Comentários sobre as espécies são apresentados.

Palavras chave: *Hypochoeris*, Asteraceae, taxonomia.

Introduction

The genus *Hypochoeris* L. comprises between 50 and 100 species (STEBBINS 1971, TOMB 1978, BREMER 1994). Its two principal areas of geographic distribution are the Mediterranean Region and South America (CABRERA 1963, CERBAH et al. 1998). Actually, this genus has 12 species referred to Brazil, but only 10 were found during the revision of the taxonomy of the genus in Rio Grande do Sul, the southernmost Brazilian State. The northern limit for Brazilian native species of *Hypochoeris* is the Minas Gerais State, in the Southeast region.

The genus is identified by the constancy of some characters, as the presence of paleae on the receptacle, all florets ligulate with 5-lobed apex, and plumose pappus (CABRERA

1976). In *Hypochoeris*, characters with taxonomic value in the species classification are the capitula size, stem ramification, ligule length, and presence or absence of beaks in the fruits (CABRERA 1976). This author considers that other characters, as leaf shape and pubescence, stem and involucre bract measurements, and plant size, has no or little taxonomic value.

During the taxonomic study of the genus *Hypochoeris* from the Rio Grande do Sul State, we analysed many collections of the herbaria from this State, as well as from other Brazilian herbaria. Photos and photocopies of type specimens were studied. With these analyses and observations, we can verify that *Hypochoeris rosenfurtii* CABR. cannot be separated from *H. lutea* (VELL.) BRITTON. On the other hand *H. rosenfurtii* var. *pinnatifida* (SPEG.) CABR. has diagnostic characters that permit the elevation of this taxon to the species rank. Similarly, *H. microcephala* var. *albiflora* (OK.) CABR. is also elevated to the species category.

1. *Hypochoeris lutea* (VELL.) BRITTON, Ann. New York Acad. Sci. 7:153. 1894.

Basionym: *Prenanthes lutea* VELLOZO, Flora Fluminensis: 350. 1825. Icones, 8: tab. 91. 1827 (1835). Typus: VELLOZO, Flora Fluminensis, Icones 8, tab. 91. 1827 (1835) (lectotype, designated here).

Synonym: *Achyrophorus trichocephalus* SCH. BIP., Pollichia 16–17: 57. 1859. *H. lutea* var. *trichocephala* (SCH. BIP.) CABR., Bol. Soc. Arg. Bot. 10: 182. 1963. Typus: Brazil, Santa Catarina, D'URVILLE 102^a, 1859 (P holotype, non vidi).

H. rosenfurtii CABR. var. *rosenfurtii*. Flora de la Provincia de Buenos Aires, parte VI, Compuestas: 150–153. 1963. Typus: Uruguay, Dept. Florida, Cerro Colorado, Estancia Santa Elvira, B. ROSENURTT 262, XII. 1936 (LP holotype; photocopy!), syn. nov.

CABRERA (1963a, b) refers to *H. lutea* as a Brazilian endemic species. The same author (CABRERA 1941) described *H. rosenfurtii* as a different species from Uruguay and Brazil. Our observations of specimens and type photos revealed that the differences between them (such as the presence of hairs in the first taxon cited, as well as the size of the stem leaves, and the capitula size) are inconsistent. Accordingly, we here propose that *H. rosenfurtii* var. *rosenfurtii* and *H. lutea* var. *trichocephala* are synonyms of *H. lutea*.

2. *Hypochoeris pinnatifida* (SPEG.) C. F. AZEVEDO-GONÇALVES & N. I. MATZENBACHER, comb. nov.

Basionym: *H. variegata* (LAM.) BAKER var. *pinnatifida* SPEGAZZINI, Contrib. Flora Sierra Ventana: 40. 1896. Type: Sierra de la Ventana, Nov. 1895, C. SPEGAZZINI (LP holotype, non vidi).

Synonyms: *H. rosenfurtii* CABR. var. *pinnatifida* (SPEG.) CABR., Rev. Mus. La Plata Sec. Bot. n. s. 4: 393. 1941.

Hypochaeris variegata (LAM.) BAKER var. *acutibracteata* SPEGAZZINI, Contrib. Flora Sierra Ventana: 39, 1896. Type: Sierra de la Ventana, Nov. 1895, C. SPEGAZZINI (LP holotype, non vidi).

In florets and cypselas *H. pinnatifida* is similar to *H. lutea*, and it is difficult to separate the two species on such characters. However, there are some good diagnostic characters: the involucre of *H. pinnatifida* is campanulate, while the involucre of *H. lutea* is campanulate to cylindrical-campanulate; the ligules of the first species are pale yellow, but dark yellow in the second. *H. lutea* presents a stem with more branches (up to 34) than *H. pinnatifida* (up to 7). The involucral bracts of *H. pinnatifida* are disposed in four to five series and are darkened from the apex to their middle. *H. lutea* has two to three series of imbricate involucral bracts with darkness along their whole extension. In vegetative aspects these species differ by the presence of pinnatifid leaves in *H. pinnatifida*, while the leaves of *H. lutea* are entire and linear-lanceolate, although some individuals of *H. lutea* have leaves with shortly toothed margins. Finally, *H. pinnatifida* attains 14 to 36 cm in height, while *H. lutea* is usually taller, 22 to 77 cm. Because of these differences, we elevate *H. pinnatifida* to species rank.

3. *Hypochaeris albiflora* (OK.) C. F. AZEVÊDO-GONÇALVES & N. I. MATZENBACHER, comb. nov.

Basionym: *H. brasiliensis* GRISEB. var. *albiflora* O. KUNTZE, Rev. Gen. Plant. III (2): 159. 1898. Type: Santa Fé, Ceres, OTTO KUNTZE, without date (F holotype; photo!).

Synonym: *H. microcephala* (SCH. BIP.) CABR. var. *albiflora* (OK.) CABR., Notas Mus. La Plata II: 201. 1937.

During the fieldwork we concluded that *H. microcephala* var. *microcephala* is in reality a hybrid between *H. chillensis* (H.B.K.) Hieron. and *H. albiflora*. This result is reported in a separate paper and is the motive for the elevation of var. *albiflora* to the species rank. *H. albiflora* was originally described as a variety of *H. brasiliensis* (LESS.) GRISEB. (= *H. chillensis* (H.B.K.) Hieron.) and later transferred by CABRERA (1937) to *H. microcephala*. The species *H. albiflora* exhibits great morphological variability, being easily confused with *H. chillensis* when exsiccated. This confusion is especially common when the collector does not refer to the flower color. In field observations the main difference between *H. albiflora* and *H. chillensis* is the white flowers of the former species. It is also distinct by the cylindrical or cylindrical-campanulate involucre (*H. chillensis* has a campanulate involucre), and by the branching system of its stem.

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A new species of *Aequatorium* (Asteraceae: Senecioneae) from Peru

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Abstract

Aequatorium pascoense (Asteraceae: Senecioneae) a new species is described from Peru with opposite leaves and quadrangular branches, with an illustration and a key to the opposite-leaved species of *Aequatorium*.

Resumen

Aequatorium pascoense (Asteraceae: Senecioneae) una especie nueva con hojas opuestas y tallos cuadrangulares es descrita e ilustrada para el Perú, se presenta una clave par las especies de *Aequatorium* con hojas opuestas.

Aequatorium pascoense H. BELTRÁN & H. ROB., sp. nov.

Type: PERU, Dpto. Pasco. Prov. Oxapampa. Rail to summit of Cordillera Yanachaga, via Río San Daniel, 75° 27' W, 10° 23' S, 2600 m, 18 Jul 1984. Primary high montane forest; quite moist, heavy epiphyte and bryophyte load on trunks, shrub 4 m, flowers yellow, D. N. SMITH & H. BOTIGER 7884 (Holotype: USM; isotypes: AMAZ, MO, US). – Fig. 1.

A speciebus congeneribus in foliis oppositis sessilibus base saepe subauriculatis distincta.

Shrub to small tree, laxly branched; stems strongly quadrangular, sulcate, glabrate, with nodes conspicuous. Leaves opposite, sessile; blades subcoriaceous, narrowly elliptic to oblanceolate, 15–21 cm long, 4.5–6.0 cm wide, slightly auriculate at base, slightly amplexicaul, sometimes slightly narrowed above base, margins with numerous minute denticulations, apex acute with a mucro (mucronulate), upper surface pale green, glabrate, lower surface sparsely pilose with short, slightly branched hairs; venation pinnate, veins ca. 10 spreading oblique (at 80° angles), arching and anastomosing. Inflorescence terminal on branches, 10–14 cm high, 13–16

cm wide; peduncles 2–4 mm long. Heads campanulate, radiate, 6–7 mm high, 3–4 mm wide; subinvolucral and calycular bracts 5 or 6, 5–6 mm long, 3.0–3.5 mm wide, apices acute, margins scarious. Ray florets 2 or 3; corollas yellow, glabrate, tube ca. 3 mm long, limb elliptical, ca. 4 mm long, 1.5 mm wide, wider above, apex tridentate. Disk florets 3; corollas yellow, 6–7 mm long, glabrous, tube 3–4 mm long, throat narrowly campanulate, ca. 1.5 mm long, lobes narrowly oblong, ca. 2 mm long, with apex acute; anther collar ca. 0.4 mm long; thecae ca. 2 mm long; apical appendage 0.4–0.5 mm long and 0.2 mm wide; style branches stigmatic on whole inner surface, sometimes depressed along middle, 1.8–2.0 mm long, 0.2–0.3 mm wide, tips acute with short apical pencil of hairs. Achenes submature, ca 1.8 mm long, glabrous; pappus 6–7 mm long, with bristles in 2 series.

Aequatorium pascoense is the third known member of the genus with consistently opposite leaves (NORDENSTAM 1997; ROBINSON & CUATRECASAS 1992). The other two species, *A. limonense* B. NORD. of Ecuador and *A. cajamarcense* H. ROB. & CUATREC. of Peru both have distinct petioles.

Distribution: Known only from the type locality.

Key to the species of *Aequatorium* with opposite leaves.

1. Leaves petiolate; branches only slightly quadrangular.
 2. Leaf blades elliptical, 6–12 cm long, base obtuse *A. cajamarcense*
 2. Leaf blades elliptical, 7–18 cm long, base cordate *A. limonense*
1. Leaves sessile, often slightly auriculate, branches distinctly quadrangular
 *A. pascoense*

Acknowledgement

We thank MARJORIE KNOWLES of the Botany Department, U.S. National Museum for repositioning part of the illustration.

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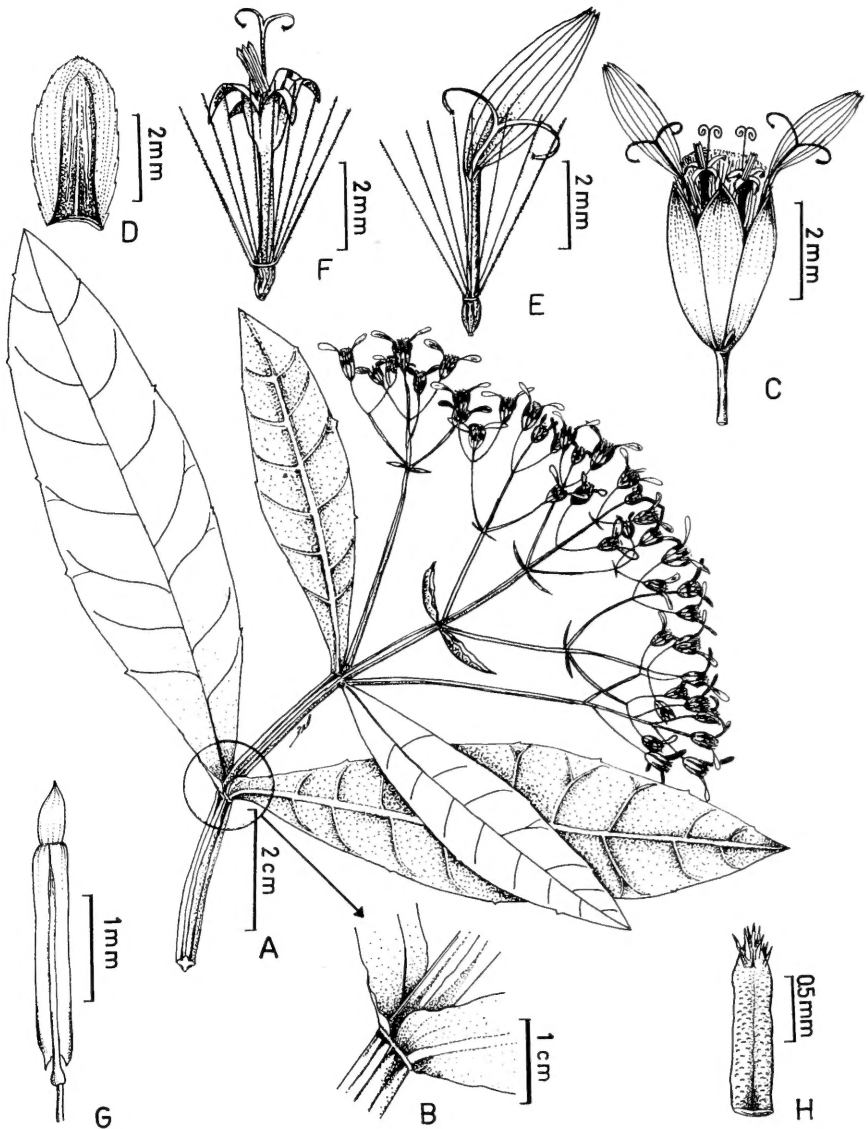


Fig.1. *Aequatorium pascoense* H. BELTRÁN & H. ROB.

A. Flowering branch. **B.** Enlarged leaf with slightly auriculate base. **C.** Capitulum. **D.** Involucral bract. **E.** Ray floret. **F.** Disk floret. **G.** Anther. **H.** Style branch.
 Drawn from D. N. SMITH & BOTIGER 7884 (USM).

A biosystematic evaluation of the relationship between three allopatric shrubby species of *Vernonia* SCHREB. (Asteraceae) in Nigeria

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Abstract

Biometric data and analyses of morphological attributes, reproductive biology and cytological traits of three allopatric shrubby species, *Vernonia tenoreana* OLIV., *V. stenostegia* (STAPF) HUTCH. & DALZ. and *V. kotschyana* SCH. BIP., are presented. The data were used to highlight the similarities and differences between the species with intent to enhance a biosystematic delimitation of the taxa.

Further details for the taxa delimitation are provided. There is evidence of character convergence as well as considerable degree of parallelism among the species. Morphological modifications are considered of adaptive significance and related to the environment of each species. They are, however, not viewed as sufficient for a change in nomenclature of the studied taxa or their generic relocation.

Introduction

HUTCHINSON & DALZIEL (1963) provided a taxonomic basis for the identification of *V. tenoreana* OLIV., *V. stenostegia* (STAPF) HUTCH. & DALZ. and *V. kotschyana* SCH. BIP. as separate species of *Vernonia* found in West Africa. However, a cursory collector of the materials from their natural habitats in Nigeria is most likely to misidentify them and hence group them as one and the same because of some obvious morphological similarities. AYODELE (1999) reported as a possible explanation that the delimitation might be influenced by some geographic habitat differences.

One tendency of a large size genus as *Vernonia* is the considerable variation among the species just as there is a considerable degree of convergence of attributes (JONES 1979). The tremendous diversity that has evolved in the genus *Vernonia* is demonstrated by the wide ecological preferences, the variable growth forms and the morphological traits that readily adapt the species to their accredited habitats (JONES 1979, AYODELE 2000).

A number of reports have highlighted the difficulty in the delimitation of taxonomic units in *Vernonia* (FAUST 1972, JONES 1979, ISAWUMI 1985). A need for a better understanding of the morphological variation in the group was long ago suggested (SMITH 1971). Commenting on the West African *Vernonia*, SMITH (1971) opined that the species were not clearly delimited, their delimitation having been based upon relatively few and poorly understood characters. For this reason, he in fact also declared the traditional sections of *Vernonia* as clearly artificial.

ISAWUMI (1985) noted the similarity between many West African *Vernonia* species and has since been consistent about this opinion (ISAWUMI 1993, 1995a & b), but allowed for a large number of taxa being transferred to another genus, *Baccharoides* (ISAWUMI et al. 1996). ISAWUMI (1995b) also reported that workers on the classification of *Vernonia* are not in total agreement as to the limits of the sections. These observations call for more information on parameters for species delimitation in the West African *Vernonia* group.

A better scientific understanding of species and their lineage is one major goal of biosystematics. This makes possible the comparative study of attributes, which can be interpreted in the light of evolutionary and genetic theory (ROSS 1974). Three attributes namely: the widespread distribution, the morphological variability and the ecological versatility of *Vernonia*, recommend the genus as highly suitable for biosystematic study (FAUST 1972, JONES 1979, AYODELE 2000).

The objective of this paper is to document the observed biometric variations in morphological, reproductive and cytological attributes within and among three shrubby species of *Vernonia* namely: *V. tenoreana*, *V. stenostegia*, and *V. kotschyana*. This is with a view to highlight any similarities and differences in morphological traits, reproductive biology and cytological attributes, that are germane for a biosystematic delimitation of the taxa.

Materials and Methods

Location Survey of the *Vernonia* Plants

Plant materials for investigations were obtained from field trips to different locations of high populations of the taxa as described in Table 1 for the various data collected.

Studies on the Morphological Characters

Observed morphological traits were measured and recorded from randomly sampled specimens at their natural habitats. These traits include plant height at flowering, and leaf, capitulum and fruit measurements by methods described by FAUST (1972) and modified by AYODELE (1997).

Studies on Reproductive Biology

The gross floral morphology and reproductive capacity of each species were studied through: plant branching traits, arrangement and number of capitula per branch or branchlet, number of florets per capitulum, morphological forms of phyllaries, flower maturation time, pollen morphology, fruit morphology, fruit production rate and fruit viability.

Cytological Studies

Karyomorphological studies were carried out on the species. Root tip cells were obtained from seedlings raised in the laboratory. Karyotype data based on average measurements of the chromosomes of 5–8 well-spaced metaphase plates for each species, were analysed and compared. Data included chromosome morphology i.e. absolute size, position of centromere (expressed as long arm/short arm ratio) and symmetry or asymmetry in arm length. Idiograms for each taxon were prepared, with all chromosomes arranged in order of decreasing length and assigned numbers.

Data Analysis

Means, standard deviations and ranges of all measurements taken, were determined for each species. The coefficients of variation (CV %) for the leaf, floral and fruit measurements, were computed to compare the variations in the attributes within each species. Statistical analysis of the data was done, employing analysis of variance and Duncan's Multiple Range Test.

All significant differences in the compared parameters measured were made by a -posteriori comparison (SOKAL & ROHLF 1969). Scatter diagrams of some morphological and reproductive attributes were constructed by means of the Genstat 5 Release 3.22 high-resolution graphics to highlight the relationships among the taxa.

Results

Morphological Variations Within and Between Accessions of *V. tenoreana*, *V. stenostegia* and *V. kotschyana*

Vernonia tenoreana, *V. stenostegia* and *V. kotschyana* are consistently erect shrubs in all their habitats (Tables 1 & 2). *Vernonia stenostegia* plants were heavily branched from the lower parts of the main stem. The stem and branches were very leafy during the vegetative growth phase. The branches were usually leafless at the lower parts during the peak of flowering of adult plants. In contrast, much of the broad leaves of *V. tenoreana* were retained even during the moisture stress period of the dry season. *Vernonia kotschyana* appears to be intermediate between these two extremes.

Variations in leaf measurements within and between taxa were quite obvious (Fig. 1a). There was no conspicuous difference in leaf shape of the three species (Table 5). The scatter diagram on leaf measurements (Fig. 2a) indicates that the three taxa belong to separate groups of leaf size. There is an overlap between *V. stenostegia* and *V. kotschyana*, both of which were distinct from *V. tenoreana* (Tables 2 & 3). Other records of morphological attributes of value in species delimitation can be found in Tables 2, 3 and 5.

Reproductive Attributes of *V. tenoreana*, *V. stenostegia* and *V. kotschyana*

Floral measurements show significant differences ($P = 0.05\%$) between *V. stenostegia* on one hand, and the other two species (Table 3, Fig. 2). The infraspecific variation in capitulum diameter was conspicuously smaller in both *V. tenoreana* and *V. kotschyana* (Fig. 1b). These two species also belong to the same capitulum-size group with heads larger than those of *V. stenostegia* (Fig. 2b). The florets (the corolla length in particular) of *V. stenostegia* were conspicuously smaller than those of the other two species. This was consistent for all accessions of the taxa from different habitats. There is no significant difference among the number of florets contained in the capitula of the three species (Tables 3 & 5). Other floral characters of value in delimitation can be found in Table 2 and Fig. 3. The differences in the phyllaries of the taxa are quite distinct with regard to shape, texture and number per capitulum (Table 2).

Of the three species, *V. stenostegia* produced more capitulum-clusters in which there were a higher number of capitula. The mode of inflorescence branching clearly distinguishes the three species (Table 2). The differences in pollen and fruit characters were significant among the species (Tables 3, 4 & 5). The pappus bristles were different in length while their surface micro-characters were different in the number of multicellular spine-like projections at the top, middle and lower portions respectively.

Cytological Variations Among the Taxa

The three species have a diploid chromosome number of $2n = 20$ ($x = 10$). The karyotype of their chromosomes manifests varying morphology, the details of which are contained in Table 6. There were marked differences in the length of chromosomes and the absolute length of chromosome complements. *Vernonia kotschyana* had the shortest chromosome complements (Table 6 & Fig. 4). The CTL values were also highly variable among the species ($CV = 36.26\%$), the value being lowest in *V. kotschyana* (2.08 μm). The relative sizes of the chromosome complements (Fig. 4) in *V. tenoreana* and *V. stenostegia* appear rather more homogeneous than those in *V. kotschyana*.

The centromere positions in the three species were variable and heterogeneous (Fig. 4). Striking shifts of centromere were observed in chromosome pairs 6 and 10 of *V. tenoreana* and chromosome 7 in *V. kotschyana* (Fig. 5). The chromosomes of the

species clearly display a considerable degree of asymmetry in arm ratio values (Table 6, Fig. 5). The arm ratio values are high especially in those chromosomes with striking shifts of centromere positions. Generally, there is variation in the extent of heterogeneity in centromere positions and the number of chromosomes showing the heterogeneity.

Discussion

The leaf measurements (Fig. 2a and Tables 1 & 3) reveal the morphological association between *V. stenostegia* and *V. kotschyana*. However, *V. tenoreana*, the species with broader leaf, maintains its identity of a plant form growing in the more humid environment of the derived savanna in the rain forest zone. Of the three taxa, *V. stenostegia* has the narrowest ecological amplitude with the apparent restriction of its natural populations to the Guinea savanna zone only (AYODELE 2000). The other two species especially *V. tenoreana* are well distributed further from the savanna grassland into the rainforest zone.

The observed relatively narrower leaf especially of *V. stenostegia* is therefore, a manifestation of the property of plants growing in a moisture stress habitat. Usually the dry and exposed habitats have the highest proportion of plants with small leaves (STERN & ROCHE 1974, SANFORD & ISICHEI 1981). The convergence of the relatively small size leaf attribute in *V. stenostegia* and *V. kotschyana* (Fig. 2a) is thus a demonstration of the need for smaller size broad leaf shape, a moisture conservation strategy essential in a dry habitat where they are found. The high amplitude of intra-specific variation in leaf size of *V. tenoreana* collected across these vegetation zones corroborates this (Fig. 1a).

Certain floral attributes are very useful tools in plant taxonomy because of their consistency despite environmental factors (BURTT 1977). The capitula of *V. tenoreana* and *V. kotschyana* that are also morphologically associated (Fig. 2b) were grouped in the large size class (AYODELE 1995). Their sizes are apparently unaffected by changes in environmental fortunes. This is particularly true of *V. tenoreana* collected across varying vegetation habitats.

Similarly consistent for each taxon are the differences in their phyllaries with regard to shape, texture and number per capitulum (Table 2). This attribute clearly separates the taxa. So does also the corolla size especially in *V. stenostegia* (Fig. 3). The texture of the phyllaries and leaves in *V. stenostegia* is indicative of its xeric habitat. Other reproductive factors contributive to a clear delimitation of the taxa include the mode of inflorescence branching, the significant differences in pollen, and fruit features (Fig. 2c; Tables 2, 3, 4 & 5).

AYODELE (1995) reported the presence of multicellular spine-like projections on the otherwise smooth-looking pappus hairs on cypselas of 16 species of *Vernonia*. From his observation of inter-species variation in the quantity of these 'spines' at the top, middle and lower portions of a pappus hair respectively, he suggested the use of this character for delimitation of taxa among growth forms and for species within a growth form. The taxa under study can be delimited by the surface micro-characters of their pappus (Plate 1). This is in addition to the fact that they differ significantly in pappus length (Table 5).

The distinctive differences in cytological attributes among the taxa (Table 6, Figs. 4 & 5) suggest the possibility of a phenetic delimitation of the taxa confirmable with modern molecular genetics. A prominent problem in the taxonomy of *Vernonia* is the diversity of ecological preferences and the associated convergence of morphological attributes. This is made more complex by the observed adaptation strategies to differing environments that have brought about the diversity and ecological versatility.

Morphological attributes constitute the orthodox tool of the taxonomist because of their diagnostic value in taxonomic evaluation. It must however be borne in mind that the morphology of an organism is not simply an accident. It represents the result of a long evolution of successive adaptation of living things to their environment (BALDAUF 1965). JONES (1973) observed that morphological discontinuities in *Vernonia* are representative of the genetic differences caused by adaptation to differential climatic and edaphic conditions. It is in this purview that a holistic biosystematic approach is being suggested for analytical consideration of plant taxonomy adjustments or generic relocations. This will prevent a chaotic reclassification of plants upon every circumstantial morphological evidence, devoid of other equally important reasons for the observed similarities or dissimilarities in traits.

This call is necessary in view of suggestions for changes and corrections to names of Nigerian plants, which unite *V. tenoreana*, *V. stenostegia* and *V. kotschyana* under the name *Vernonia adoensis* (LOWE & SOLADOYE 1990). In a review of some of such united or renamed species, LOWE & SOLADOYE (1990) quoted floras and other taxonomic publications as their sources of information on the change of names. ISAWUMI (1995a & 1995b) also proposed a total relocation of the homonym and its constituent taxa to a 'resurrected' genus *Baccharoides*, followed later by numerous more transfers (ISAWUMI et al. 1996). This proposal was based on some discovered morphological attributes and in particular, floral micro-characters (ROBINSON 1990, ISAWUMI 1993, 1995a & b, ISAWUMI et al. 1996). Such re-classifications may result in the loss of appreciation of adaptation strategies developed over time by plant species to promote an individualistic identity.

Different workers display different emphasis in plant classification. Classification primarily, should be an information retrieval system that may also almost as a subsidiary feature, indicate evolutionary relationship. A correctly determined evolutionary relationship will produce a useful information retrieval system. It may therefore, be necessary to always investigate the genetic basis and adaptive significance of morphological features before they are propounded as sole reason for any form of nomenclature adjustments or re-classification of plants.

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Table 1. Population, location & collection data of *V. tenoreana*, *V. stenostegia* & *V. kotschyana*

Name & accession number of species	Location of collection	Description of location
<i>Vernonia tenoreana</i> OLIV. msa 040, 041, 043, 048 & 051	Routes: Ede/Awo, Osogbo/Ede, Osogbo/Ilesa, Olupona/Iwo, Oyo/Awe, Ilorin/Igbeti; Township: Ogbomoso/Igbeti	Guinea & Derived savanna grassland with sandy loam soil; uncultivated burnt forest vegetation, abandoned plots, and weedy roadsides
<i>Vernonia stenostegia</i> (STAPP) HUTCH. & DALZ. msa 061, 069, 070 & 076	Routes: Gimi/Jos, Jos/Akwanga, Jos/Kuru; Township: NIVR - Vom, & Jos.	Guinea & Plateau open rolling grassland with altitude cooling effect; fallow plot in sandy, sometimes rocky woody valleys in shallow soils
<i>Vernonia kotschyana</i> SCH. Bip. msa 071, 081 & 082	Routes: Jos/Bauchi; Township: Bayero University Kano & ABU premises Zaria	Guinea savanna grassland with sandy/gravelly soil; abandoned plots and weedy roadsides

Table 2. Morphological features of stem, leaf, flower and fruit of *V. tenoreana*, *V. stenostegia* & *V. kotschyana*

Morphological features					
Plant stem and leaf features		Flower head (capitulum) features			Fruit features
Species/stem & growth habit	Leaf shape (tip & base)	Phyllaries	Corolla (form & colour)	Type of inflorescence branching, Flowering & fruiting season	Cypselas shape, pubescence & ripe pappus colour
<i>V. tenoreana</i> Erect tall-growing (81-185 cm) woody shrub with few branches (3-5) & tuberous rootstock; leafy stem branches terminating in a few but large flower heads	Ovate	Herbaceous & polyseriate; inner layer lanceolate and interlocking	Fluted	Racemose arrangement	Terete with groove on fruit surface
	Acute-rounded, acute		Creamy white	May to December	Glabrous Buff
<i>V. stenostegia</i> Erect woody shrub (50-185 cm high), slender stem & many branches; stem leafless below but terminating in many heads at fruiting peaks	Obovate	Acicular, uniseriate, tomentose, woolly surface	Fluted	Racemose arrangement of cymes	Terete
	Acute, cuneate		Pale bluish to purple	September to March	Pubescent (sericeous) Light brown
<i>V. kotschyana</i> Erect short woody shrub (38-90 cm at flowering), sparsely branched with branches terminating in large corymbose heads	Obovate to oblong	Herbaceous & polyseriate; outer layer more or less curled bracts	Fluted	Racemose arrangement of umbels	Terete
	Acute, acute		Light purple tubular florets, creamy white at full bloom	September to December	Scabrid Buff

Table 3. Measurements of morphological characters of *V. tenoreana*, *V. stenostegia* & *V. kotschyana*

Length (cm)	Leaf			Floral (Capitulum)			Fruit (Cypsel)									
	Width (cm)		L/W ratio	Length (cm)		Diameter (cm)	# Florets/capitulum		Length (cm)		Width (cm)		Pappus length (mm)			
	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}		
<i>V. t.</i>	20.3 – 32.4	10.6	7.8 – 13.4	2.63	2.37 – 3.09	3.42	3.3 – 3.7	3.46	3.1 – 3.7	135.4	111 – 169	5.20	4.1 – 6.0	1.46	1.2 – 1.9	12.0 – 13.9
<i>V. s.</i>	11.9 – 14.8	5.0	4.1 – 6.2	2.72	2.16 – 3.15	2.64	2.4 – 3.0	2.41	1.7 – 2.8	131.6	112 – 160	3.32	2.7 – 4.4	1.27	1.0 – 1.6	6.8 – 8.7
<i>V. k.</i>	15.2 – 17.3	6.53	5.4 – 7.4	2.70	2.31 – 3.02	3.46	2.7 – 4.1	3.14	2.8 – 3.3	146.2	131 – 168	5.53	4.2 – 6.6	1.8	1.6 – 2.1	10.8 – 13.2

Key: *V. t.* = *Vernonia tenoreana*; *V. s.* & *V. stenostegia*; *V. k.* = *V. kotschyana*

Table 4. Summary data on some reproductive attributes of *V. tenoreana*, *V. stenostegia* & *V. kotschyana*

Species	Pollen				Flowering			Fruiting			Cumulative seed germination % (days after sowing)			
	Size (μ) (\bar{x} & Sd)	CV %*	Quantity index (\pm & Sd)	% Fertility	Initiation range **	Duration range ***	Fruit-set %	Wt of 10 fruits (mg) (\bar{x} & Sd)	0-7 days	7-14 days	14-21 days	%		
												0-7 days	7-14 days	
<i>V. tenoreana</i>	69.8 \pm 7.05	10.1	35.4 \pm 11.8	98.83	155–160	120–210	92.9	59.16 \pm 12.99	10.8	63.0	71.0	6.0	16.0	17.6
<i>V. stenostegia</i>	61.4 \pm 4.02	6.5	23.5 \pm 12.8	99.44	130–135	110–180	79.6	17.80 \pm 1.43	6.0	16.0	17.6	13.4	33.3	89.0
<i>V. kotschyana</i>	59.8 \pm 8.61	14.4	9.1 \pm 2.96	100.00	78–140	100–180	30.9	70.8 \pm 3.11	13.4	33.3	89.0			

* Intra-species pollen size coefficient of variation

** First appearance of flower buds in days after seed sowing

*** Period of continuous flowering in a season

Table 5. Summary ranking of scored values of morphological & reproductive attributes

		Duncan's Multiple Test Ranking & Score index		
S/N	Morphological/Reproductive attributes	<i>V. tenoreana</i>	<i>V. stenostegia</i>	<i>V. kotschyana</i>
1.	Leaf length (cm)	8a	5c	6b
2.	Leaf width (cm)	7a	5c	6b
3.	Leaf shape index *	6a	6a	6a
4.	Capitulum length (cm)	9a	8b	9a
5.	Capitulum diameter (cm)	9a	7c	8b
6.	# Florets/capitulum	7b	7b	8a
7.	Fruit length (cm)	8b	5c	9a
8.	Fruit width (cm)	8b	7c	9a
9.	Pappus length (cm)	9a	7c	8b
10.	# Branches/plant	5b	8a	4c
11.	# Terminal capitula clusters	4b	7a	1c
12.	# Capitula/terminal clusters *	7a	7a	7a
13.	Estimated seed production/plant	6b	8a	6b
14.	Plant height at flowering (cm)	5a	5a	3c
15.	Pollen size	9a	8b	8b
16.	Pollen quantity index	9a	7b	5c
17.	Pollen viability *	9a	9a	9a

Notes:

1. Species with the same letters have values not significantly different at 5 % level for the attribute.
2. * Major attribute convergence features among the taxa.

Table 6. Summary data on chromosome morphology of the three taxa

Species (Chromosome number $2n = 20$)	n	Number of chromosomes in each group			Size of chromosome complement		
		M	nm	nsm (-)	CTL* (μ)	TF% **	Coefficient of variation (CV %) in chromosome length
<i>V. tenoreana</i>	10	5	2	3	3.30	43.64	12.12
<i>V. stenostegia</i>	10	6	2	2	2.70	45.19	12.71
<i>V. kotschyana</i>	10	1	6	3	2.08	70.67	15.83

Notes:

- * Cumulative total length or the index of the volume of all chromosomes in set (after GRANT 1975).
- ** Total Chromosome Form Percentage calculated as:

$$\frac{\text{Total length of all short arms}}{\text{Total length of chromosome complement}} \times 100$$

Fig. 1a. Intraspecies variation in leaf measurements of the taxa

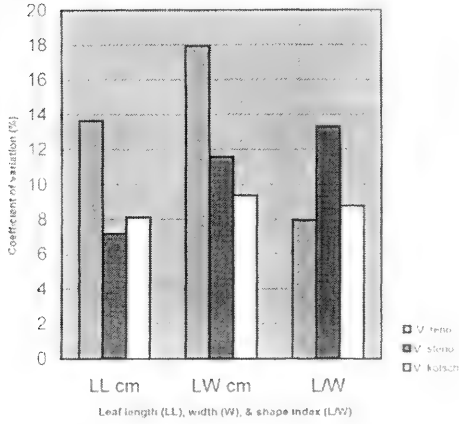


Fig. 1b. Intraspecies variation in capitulum measurements of the taxa

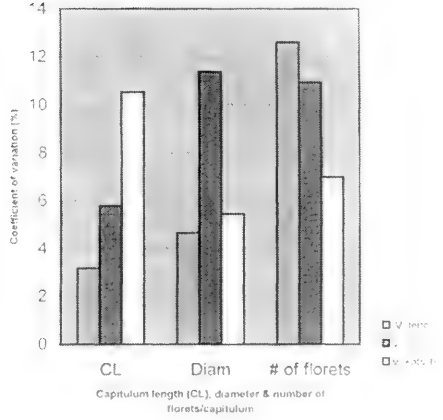


Fig. 1c. Intraspecies variation in fruit measurements of the taxa

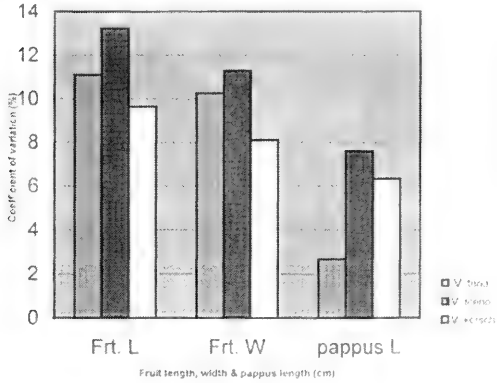


Fig. 1. Intraspecies variation in leaf, capitulum and fruit measurements

Fig. 2a. Scatter Diagram of Leaf Measurements

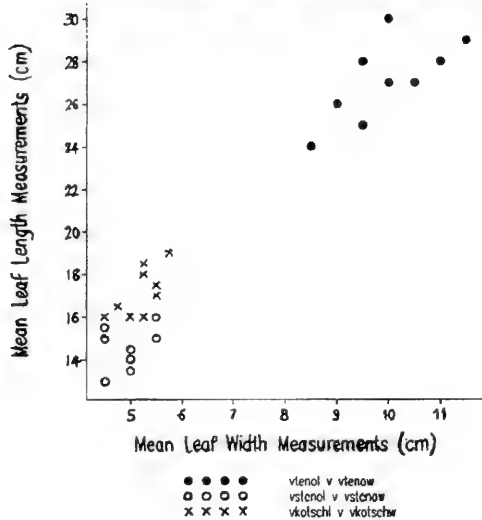


Fig. 2b. Capitulum Measurement of the Taxa

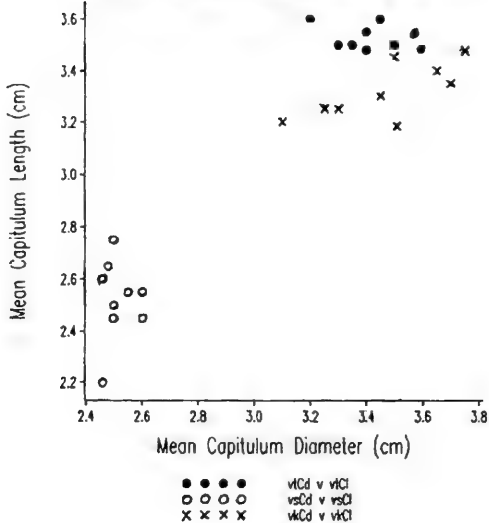


Fig. 2c. Scatter Diagram of Fruit Measurements (mm)

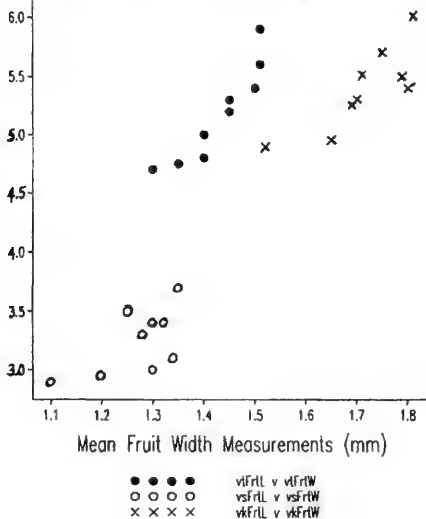


Fig. 2a. Scatter diagram of leaf measurements

Fig. 2b. Capitulum measurement of the taxa

Fig. 2c. Scatter diagram of fruit measurements (mm)

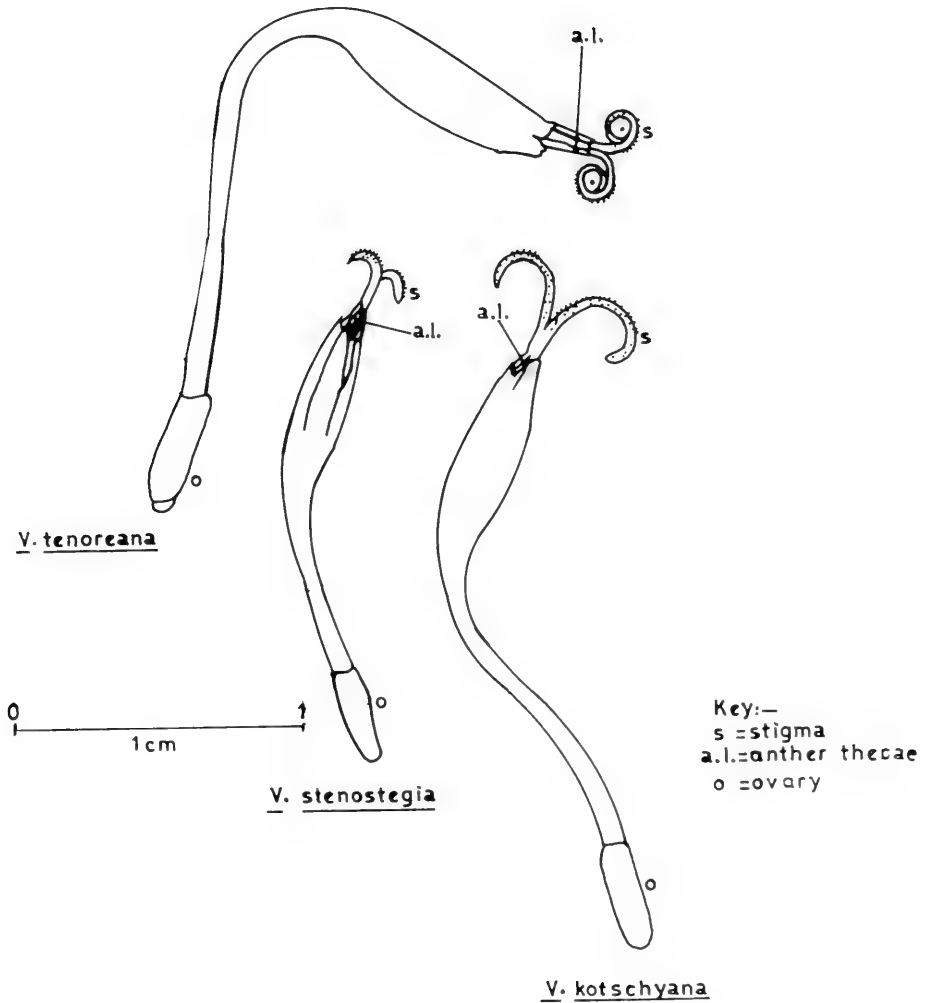


Fig. 3. Drawing of shapes and types of florets of the taxa

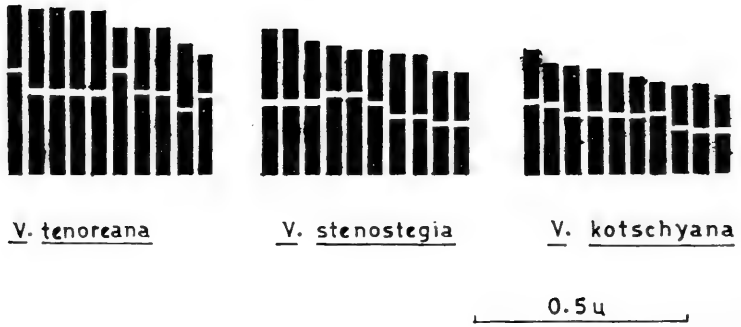


Fig. 4. Idiograms of *V. tenoreana*, *V. stenostegia* and *V. kotschyana*

Fig. 5. Arm ratios r (l/s) of the component chromosomes of the taxa

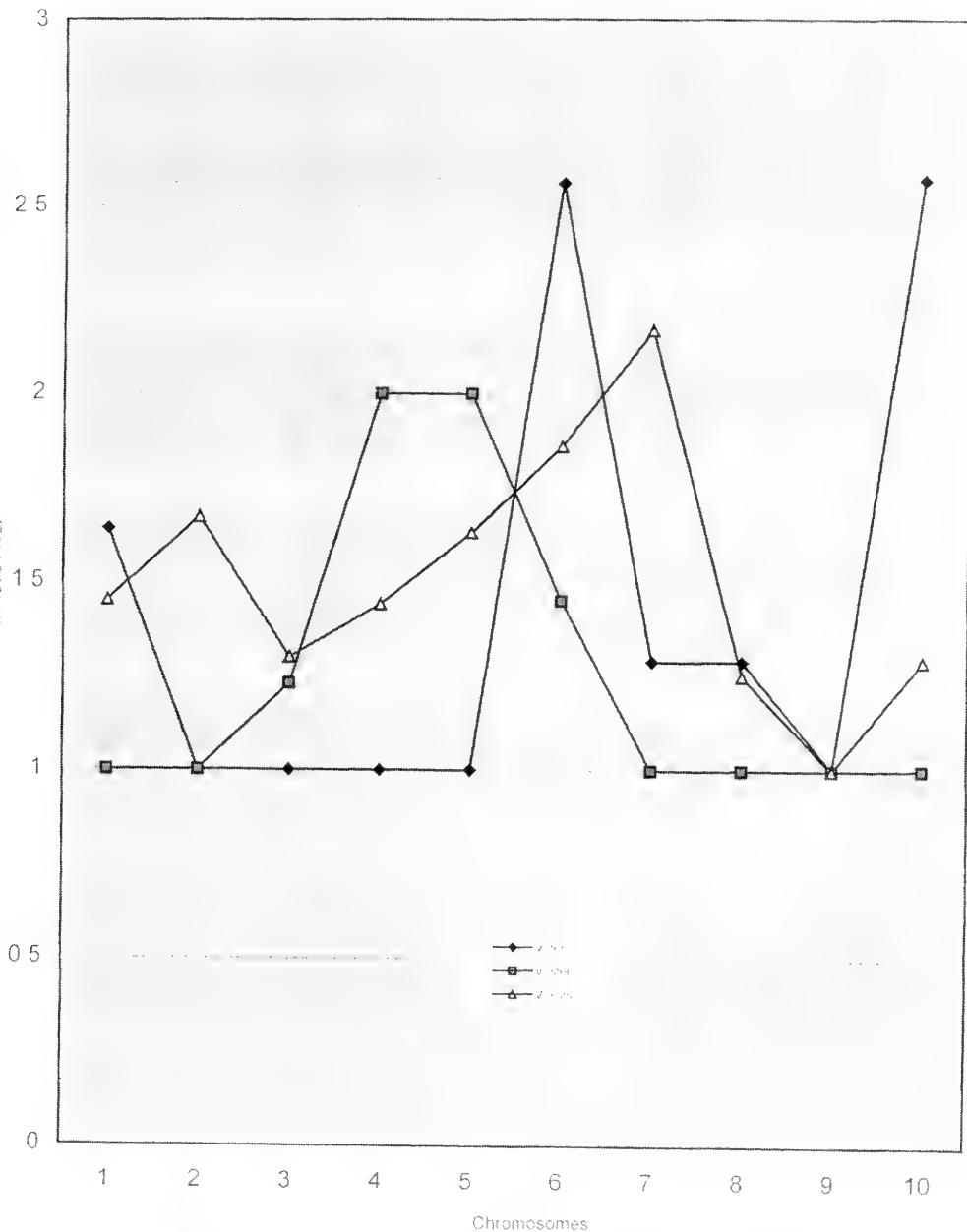


Fig. 5. Arm ratios r (l/s) of the component chromosomes of the taxa

A new species of *Amblysperma* (Asteraceae: Mutisieae)

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Abstract

Amblysperma minor G. J. KEIGHERY (Asteraceae-Mutisieae), a new species from Western Australia, is described and illustrated.

Introduction

Amblysperma has had a complicated generic history. The sole species was originally described in DE CANDOLLE (1836) as *Celmisia spathulata*, a predominantly New Zealand genus. BENTHAM independently created the monotypic genus *Amblysperma* BENTH. several months later by naming *Amblysperma scapigera* in ENDLICHER et al. (1837). BENTHAM (1866) retained this nomenclature; however, MUELLER (1882) transferred the species to *Trichocline* as *T. scapigera* (BENTH.) F. MUELL. *Trichocline* is a predominantly South American genus of Asteraceae, comprising about 25 species, now with one very disjunct species in Western Australia.

WILLIS (1967) made the correct combination of the earliest available name as *Trichocline spathulata* (DC.) WILLIS. He also noted that “No other member of this tribe (Mutisieae) is indigenous to the Australian Commonwealth, indeed our *Trichocline* has close affinities with *Gerbera* and might well be regarded as the “gerbera” counterpart on this side of the Indian Ocean - just as *Cymbonotus* is the Australian analogue of *Arctotheca* (Capeweed).” HIND (2001) considered that the Australian species was not congeneric with *Trichocline* and combined the earliest name into *Amblysperma* as *A. scapigera* (DC.) HIND. I concur with BENTHAM and HIND in recognizing this poorly placed group as a separate Australian endemic genus *Amblysperma*.

The vascular plant flora of the Mediterranean region of Western Australia is highly diverse and still relatively poorly known. Currently all populations of *Amblysperma* in Western Australia are considered part of the widespread species *Amblysperma spathulata*. Because the plants often present their inflorescence after the leaves have

completely withered, current herbarium material often lacks detailed taxonomically critical information on habit, floret colour, root characters and leaf morphology.

Over the past decade the Western Australian Department of Conservation and Land Management has undertaken intensive floristic and reserve surveys of the Swan Coastal Plain (GIBSON et al. 1994, KEIGHERY 1999). One new taxon uncovered during these surveys was a distinctive undescribed species of *Amblysperma*. This paper forms part of a continuing series (KEIGHERY 1997, 1998, 2001a,b) documenting the taxonomic outcome of these surveys.

Taxonomy

Amblysperma minor G.J. KEIGHERY, sp. nov. - Fig.1.

Type: Western Australia. Tuart Forest, SW Ludlow, 33° 37'S 115° 33'E, 13.XII.1994, G. J. KEIGHERY 13247 (PERTH 04122852, holotype).

Amblysperma minor G.J. KEIGHERY, sp. nov., differt a *A. scapigera* (DC.) HIND statura minore, foliis glabris erectis lanceolatis vel oblanceolatis.

Perennial caespitose herb from an abbreviated stem covered in the fibrous remains of older petioles, dying back to the rootstock in late summer. Tuberos roots, 10–30, light brown, linear, slender, terete, uniform along length, 2–3 mm wide, 5–15 cm long; tubers perennial but added to each year; some non-tuberos adventitious roots produced from the apex of old tubers. Leaves all radical, 5–15, erect, lanceolate to oblanceolate, 5–12 cm long, petiolate, narrowly obovate, glabrous except for long hairs at the base; blade 3–5 cm long, 5–10 mm wide; margins undulate, sinuate and broadly lobed; apex blunt, acute. Scape solitary, erect, 10–30 cm tall, slender, 1–2 mm wide, reddish, mostly glabrous except for silky hairs at base and cottony indumentum just below head; scape bracts 2–8, linear, acuminate, 4–7 mm long. Heads solitary. Involucre 10–15 mm diameter, narrowly hemispherical; involucre bracts narrowly ovate to linear-obovate, imbricate, 7–9 mm long, cottony pubescent, greenish; apex brown, long acute; outer involucre bracts shorter and more ovate. Marginal florets 11–15, white inside, pink-red outside; lower lip narrowly ovate, 23–25 mm long, c. 3 mm wide, apex shortly 3-lobed.

Flowering Period. From late spring (November) to January in summer.

Distribution. The species occurs on either side of the forest regions of southern Western Australia, where *Amblysperma scapigera* is found (Fig.2).

Habitat. This species grows in shallow fresh water claypans that fill with rain in winter and dry in early summer (the Western Australian equivalent of Vernal Pools). Leaves are produced when the pans are filled or drying, senescing as the pans dry. Flowering

commences after the pans have dried.

Conservation Status. The species is represented in several small and large nature reserves.

Other specimens examined. Western Australia: Lake Muir Nature Reserve, 11.XII.1997, G.J. KEIGHERY 15434 (PERTH); Yamup Nature Reserve, 25.X.1997, G.J. KEIGHERY & N. GIBSON 2638 (PERTH); Cobertup Nature Reserve, 10.XII.1997, G.J. KEIGHERY 15214 (PERTH); Gracetown, 14.XII.1994, G.J. KEIGHERY 14767 (PERTH); Brickwood Reserve, Byford, 29.XII.1992, G.J. KEIGHERY 12724 (PERTH); 9 km from Boyanup to Capel, 33°31' S 115° 38' E, 16.XI.1984, G.J. KEIGHERY 7417 (PERTH); Ironstone Gully, Treeton Forest Block, 33° 49' S 115° 13' E, 11.XI.1993, B.J. KEIGHERY & N. GIBSON 564 (PERTH); 2 km north of Waroona, 22.VIII.1993, G.J. KEIGHERY 13507 (PERTH); Capel Nature Reserve, 13.XII.1994, G.J. KEIGHERY 13251 (PERTH); Recreation Reserve, Scott National Park, 34° 16' S 115° 16' E, 29.XII.1990, G.J. KEIGHERY 12257 (PERTH); Qualen Reserve, west of York, 31° 54' S 116° 47' E. B. SALTER & R. BETJAMAN 10 (PERTH); Beaufort River Reserve, 14.XI. 2003, G.J. KEIGHERY 16569 (PERTH), Waterloo, 21.XII.2003, B.J. KEIGHERY 3193 (PERTH).

The new species is smaller in nearly all aspects compared to *Amblyserma scapigera*. It is characterised when vegetative by the erect, glabrous, lanceolate-oblancolate leaves compared to the large spreading, obovate-ovate, broadly lobed to almost lyrate, abaxially white cottony hairy leaves of *A. scapigera*. The peduncle of *A. scapigera* is stouter; cottony hairy with larger scape bracts and up to 50 cm tall, compared to the shorter, slender and largely glabrous peduncle of *A. minor*.

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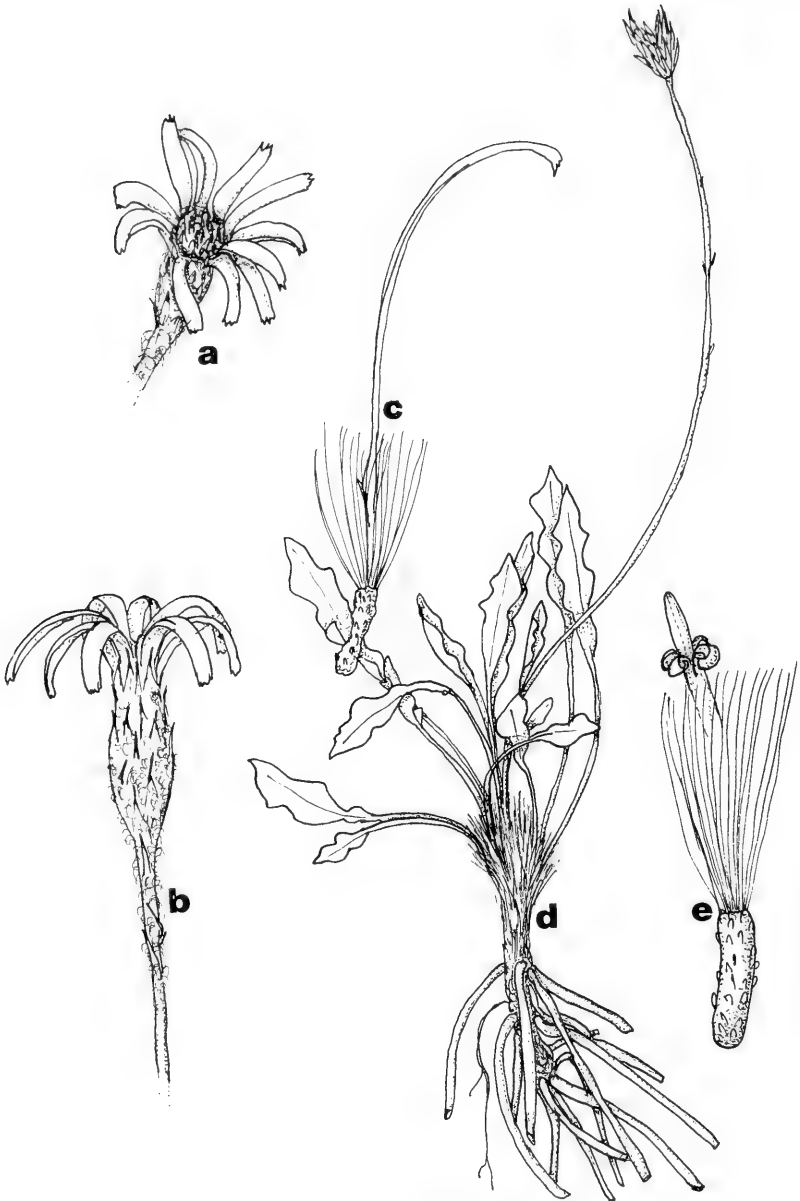


Fig. 1. *Amblysperma minor* G. J. KEIGHERY

a: Inflorescence, $\times 1/2$

b: Side view of inflorescence, $\times 1/2$

c: Ray floret, $\times 2$

d: Habit, $\times 1/2$

e: Disc floret, $\times 2$

(a, b, c, e: B. J. KEIGHERY 3193, PERTH; d: G. J. KEIGHERY 16569, PERTH).

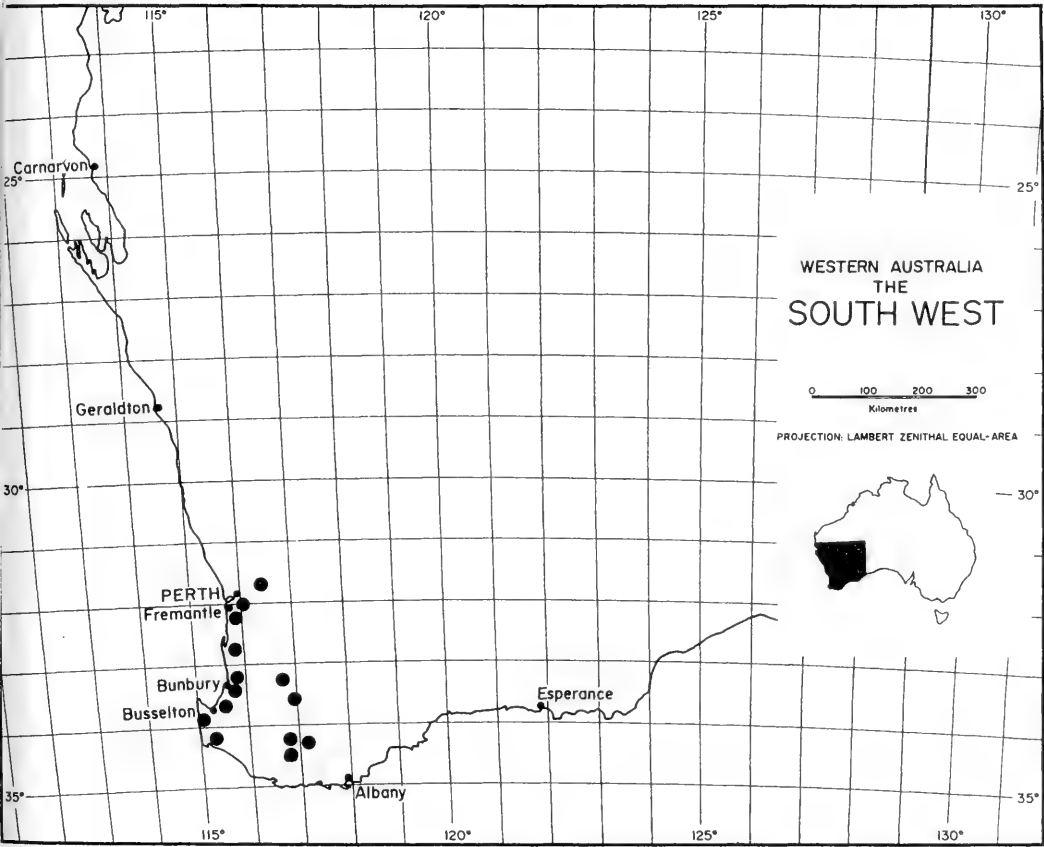


Fig. 2. Distribution of *Amblyperma minor* G. J. KEIGHERY

Nomenclatural notes on *Cyclachaena* (Compositae: Heliantheae), resurrection and lectotypification of *Iva* sect. *Picrotus*, and report of *Iva* (syn. *Cyclachaena*) as new to Armenia

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Abstract

The native New World genus *Iva* is reported as new to Armenia based on a recent collection of *Iva xanthiifolia* (marsh-elder). *Cyclachaena* is treated as a synonym of the newly resurrected *Iva* sect. *Picrotus*, which is treated as containing a single species. *Iva* sect. *Picrotus* is lectotypified by *Iva paniculata*. *Iva xanthiifolia* and *Cyclachaena xanthiifolia* are treated as taxonomic synonyms, and not nomenclatural synonyms. Therefore, *Cyclachaena* is typified by *Cyclachaena xanthiifolia*. *Iva*, *Ambrosia*, and *Xanthium* as traditionally defined may not be monophyletic, but in lieu of published combined nuclear and chloroplast DNA analyses of the genera of Ambrosiinae, are recognized in the traditional sense, rather than lumped or split.

Introduction

A collection under the name *Ambrosia* L. (Heliantheae: Ambrosiinae) made recently in Armenia and not matched by ELEONORA GABRIELIAN (of the Institute of Botany, ERE, in Yerevan, Armenia) was given to me for identification. While this collection is similar in gross appearance to *Ambrosia* (which has unisexual capitula and cypselae of the pistillate florets wholly enveloped by the subtending phyllaries), the plant in front of me differs by having bisexual capitula with cypselae free from the phyllaries.

This collection from Armenia is identified here as *Iva xanthiifolia* NUTT. *Iva xanthiifolia* is native to the Americas, but JACKSON (1960) and TUTIN et al. (1976) each note that it is widely naturalized in Europe. This same species [sub *Cyclachaena xanthiifolia* "(NUTT.) FRESEN."] was noted by SMOLJANINOVA (1959) as naturalized in the former Soviet Union in the Ukraine and adjacent areas. SMOLJANINOVA (1959) did not cite this species in the region south of the Caucasus Mountains. Neither *Iva* L. nor *Cyclachaena* FRESEN. were listed in the treatments of Compositae in the floras of Armenia (TAKHTAJAN 1995) and Turkey (DAVIS 1975). Thus, the documentation herein

of *Iva xanthiifolia* from the Shirak region represents a new generic record for the flora of Armenia.

Nomenclatural history of marsh-elder

The marsh-elder (*Iva xanthiifolia* NUTT.) was described in 1818 and includes *Cyclachaena xanthiifolia* FRESEN. as a taxonomic synonym. *Cyclachaena*, described in 1836, has been variously treated nomenclaturally since its inception. The protologue was not seen by the compilers of *Index Nominum Genericorum* (FARR et al. 1979), who listed the genus as “*Cyclachaena* FRESENIUS ex SCHLECHTENDAL, Linnaea 12 (Litt.): 78. 1838” and the type “non designatus.” The protologue of *Cyclachaena* shows that the author of the genus is FRESENIUS, that *Cyclachaena xanthiifolia* is the generitype, and that *Cyclachaena xanthiifolia* FRESEN. was not based on *Iva xanthiifolia* NUTT.

The first infrageneric use of *Cyclachaena* was as *Iva* subgen. *Cyclachaena* (FRESEN.) A. GRAY, into which was placed *Iva xanthiifolia*. This subgeneric combination was mistakenly attributed by JACKSON (1960) as a sectional combination, whereas BRIZICKY (1969) and K. GANDHI (pers. comm.) noted that in the preface to GRAY’S *Synoptical Flora* the substantive infrageneric names are said to be treated as subgenera. HOFFMANN (1890–1894) appears to have been the first to treat *Cyclachaena* at the sectional rank within *Iva*.

Iva sect. *Picrotus* was circumscribed by NUTTALL (1840–1841) as containing two species (*I. xanthiifolia* and *I. paniculata* NUTT.), neither species name being designated by NUTTALL as the type. Because the NUTTALL holotype of *I. xanthiifolia* was not located, I must choose *Iva paniculata* as the lectotype of *Iva* sect. *Picrotus*. GRAY (1884) treated both NUTTALL species names as taxonomic synonyms of *I. xanthiifolia*, and one of the three subgenera recognized by GRAY (1884) was the newly combined *Iva* subgen. *Cyclachaena* (FRESEN.) A. GRAY. AS treated by GRAY (1884), *Iva* subgen. *Cyclachaena* contained both NUTTALL species, *Cyclachaena xanthiifolia*, as well as *Iva* sect. *Picrotus*. At the sectional rank, however, *Iva* sect. *Picrotus* has priority over *Iva* sect. *Cyclachaena*.

Although *Cyclachaena xanthiifolia* and *Iva xanthiifolia* have commonly been treated as homotypic (e.g., JACKSON 1960, CRONQUIST 1994, SMOLJANINOVA 1959, STROTHER 2000), FRESENIUS (1836) neither directly nor indirectly referred to *Iva xanthiifolia* or to THOMAS NUTTALL. While CRONQUIST (1994) noted that *Cyclachaena xanthiifolia* and *Iva xanthiifolia* might not be homotypic, he ultimately treated them as homotypic. The protologue of each species cited localities along the Missouri River, the *Iva* being described from material collected near “Fort Mandan,” whereas FRESENIUS cited a MAXIMILIAN collection from “Fort Union.” The original site of Fort

Mandan, which may now be underwater in the middle of the present Mississippi riverbed (ROBERTS 1988), is near Stanton, North Dakota, about 60 km NNW of the City of Mandan, North Dakota. Fort Union is some 210 km upriver from Stanton, near the border between the states of North Dakota and Montana.

The species names of NUTTALL and FRESENIUS are independent nomenclatural entities and are from moderately distant localities. There is no direct or indirect nomenclatural link between these two names, albeit taxonomically synonymous as treated by GRAY (1884), JACKSON (1960), and CRONQUIST (1994). Consequently, the generic name *Cyclachaena* is typified by *C. xanthiifolia* FRESEN., not by *Iva xanthiifolia* NUTT. The correct name for the marsh-elder in the genus *Iva* is *I. xanthiifolia* NUTT. 1818, whereas if treated as the genus *Cyclachaena* the correct name of the plant is *C. xanthiifolia* FRESEN. 1836, the nomenclatural transfer of NUTTALL's epithet being blocked in *Cyclachaena* by the later heterotypic FRESENIUS binomial.

Taxonomic treatment

Iva (Heliantheae: Ambrosiinae) was revised by JACKSON (1960) who recognized three sections (including sect. *Cyclachaena*) and 15 mostly temperate North American species. Here I treat *Iva* in the broad sense, albeit containing only 14 species as I do not herein formally return *Hedosyne ambrosiifolia* (A. GRAY) STROTHER (2000) to *Iva* s.l. The genus is known also in tropical Mexico and the West Indies, but not in South America (JACKSON 1960). GRAY (1884), HOFFMANN (1890-1894), BRITTON & BROWN (1913), JACKSON (1960), CORRELL & JOHNSTON (1970), TUTIN et al. (1976), CRONQUIST (1980), GLEASON & CRONQUIST (1991), and CRONQUIST (1994) are among the standard references that treated *Iva* as including the synonymous *Cyclachaena* (albeit sometimes indirectly sub the name *Iva xanthiifolia*), whereas TORREY & GRAY (1841-1843), BENTHAM & HOOKER (1873), RYDBERG (1922), BOLICK (1985), SMOLIANINOVA (1959), and STROTHER (2000) recognized unispecific *Cyclachaena* as distinct from *Iva*.

Iva sect. *Cyclachaena* sensu JACKSON (1960) differs from *Iva* sect. *Iva* and sect. *Linearibracteata* R. JACKSON by having dissected (vs. entire) leaves, by ebracteate (vs. bracteate) capitulescences, by non-connate phyllaries in two series, and by minute (vs. small) corollas of the pistillate florets. These differences are taken here as sectional differences, and not as important at the generic rank. While the features (e.g., bisexual or unisexual capitula) used to distinguish *Iva* from traditionally related genera of Ambrosiinae (e.g. *Ambrosia* and *Xanthium*) may not be phylogenetically significant, the morphological features used to separate *Cyclachaena* from *Iva* are admittedly slight.

KARIS (1993) in his Heliantheae overview noted that *Iva dealbata* of *Iva* sect. *Cyclachaena* (sensu JACKSON 1960) "corresponds well to other examined *Iva* species"

and BREMER (1994) treated *Iva* in the sense of JACKSON. However, the cladogram of KARIS (1995: pp. 50–51) shows that as currently circumscribed *Ambrosia*, *Iva* and *Xanthium* may not be monophyletic. The cladogram in KARIS (1995) shows *Hymenoclea* and *Xanthium* are nested within a traditionally circumscribed *Ambrosia*, and that this subclade in turn is nested within the *Iva-Euphrosyne-Ambrosia-Xanthium-Hymenoclea* clade. KARIS (1995) recommended recognition of *Cyclachaena* at the generic rank, yet maintained a paraphyletic *Ambrosia* pending further investigation. MIAO et al. (1995a) showed that by chloroplast DNA features *Iva* sect. *Cyclachaena* (sensu JACKSON, 1960) may be polyphyletic and MIAO et al. (1995b) showed that the genus *Parthenium* appears sister to the remaining taxa of Ambrosiinae. In the Ambrosiinae subclade sister to *Parthenium*, STROTHER & BALDWIN (2002) reduced *Hymenoclea* to *Ambrosia*, but retained *Iva* and *Xanthium*.

Cladistically (see cladogram in KARIS 1995: pp. 50–51), cases could be made for either (1) a single broadly defined genus including *Ambrosia*, *Cyclachaena*, *Iva*, *Xanthium* etc. or (2) recognizing many genera within the *Iva-Euphrosyne-Ambrosia-Xanthium-Hymenoclea* clade. Similarly, the cladogram in MIAO et al. (1995b) supports cases for either (1) treating *Iva*, *Ambrosia*, *Xanthium*, etc. as congeneric and sister to *Parthenium* or (2) splintering traditionally defined *Iva*, *Ambrosia*, *Xanthium*, etc. into microgenera. Moreover, it is conceivable that nuclear DNA analysis of subtribe Ambrosiinae (not known to me to have been published) would group taxa differently than KARIS (1995) and MIAO et al. (1995b).

In lieu of published combined nuclear and chloroplast DNA analysis of the genera of Ambrosiinae, however, I defer modification (be it lumping or splitting) of the traditionally accepted circumscriptions of *Ambrosia*, *Iva*, *Xanthium*, etc. Nevertheless, I recognize solely *Iva xanthiifolia* within *Iva* sect. *Picrotus* (syn. *Iva* sect. *Cyclachaena*), yet it is not my aim here to make sectional combinations in *Iva* for the four additional species of *Iva* sect. *Cyclachaena* (sensu JACKSON) excluded herein from *Iva* sect. *Picrotus*, nor to formally reduce *Hedosyne* STROTHER to synonymy under *Iva* s.l.

Here, I simply provide treatments of *Iva*, *Iva* sect. *Picrotus*, and *I. xanthiifolia*, which may be inserted in the Flora of Armenia (TAKHTAJAN 1995) between the treatments by AVETISJAN (1995) of *Ambrosia* (genus 70) and *Xanthium* L. (genus 71), and numbered as genus 70.1. The voucher documenting this species in Armenia is also listed.

***IVA* L., Sp. Pl. 988, 1753. Lectotype (chosen by BRITTON & BROWN 1913: 338): *Iva annua* L.**

Denira ADANS., Fam. Pl. 2: 118, 549, 1763. Type: *Iva frutescens* L.

Cyclachaena FRESEN., Index Sem. (Frankfurt) 4, 1836. *Iva* subgen. *Cyclachaena* (FRESEN.) A. GRAY, Syn. Fl. N. Amer. 1(2): 245, 1884 (as “§”). *Iva* sect. *Cyclachaena*

(FRESEN.) O. HOFFM. in ENGL. & PRANTL, Nat. Pflanzenfam. 4(5): 221. 1890. Type: *Cyclachaena xanthiifolia* FRESEN. [= *Iva xanthiifolia* NUTT.]

Oxytenia NUTT., Proc. Acad. Nat. Sci. Philadelphia 4: 20. 1848. Type: *Oxytenia acerosa* NUTT. [= *Iva acerosa* (NUTT.) R. C. JACKS.]

Iva subgen. *Chorisiva* A. GRAY, Syn. Fl. N. Amer. 1(2): 247. 1884 (as “§”). *Iva* sect. *Chorisiva* (A. GRAY) O. HOFFM. in ENGL. & PRANTL, Nat. Pflanzenfam. 4(5): 221. 1890. *Chorisiva* (A. GRAY) RYDB., N. Amer. Fl. 33: 8. 1922. Type: *Iva nevadensis* M. E. JONES.

Leuciva RYDB., N. Amer. Fl. 33: 8. 1922. Type: *Iva dealbata* A. GRAY.

Erect annual herbs to shrubs, glabrous or pubescent. *Leaves* opposite or sometimes alternate distally, entire to pinnately dissected; sessile to long-petiolate. *Capitulescence* many headed, bracteate or ebracteate. *Capitula* heterogamous, disciform or obscurely radiate, 4–30-flowered, often nodding, sessile or subsessile; involucre turbinate to hemispherical; phyllaries 3–9, imbricate, subequal, uniseriate or biseriate, mostly herbaceous, sometimes connate proximally when uniseriate, often pubescent; receptacle very reduced, obscurely paleate. *Marginal unisexual florets* pistillate, 1–9; corolla short, tubular, or sometimes nearly obsolete and represented merely by a small bit of tissue on top of the cypselae. *Disk florets* functionally staminate, 3–21, corolla tubular, shortly 5-lobed, often glandular; filaments shorter than thecae, thecae merely connivent to weakly connate; style undivided, ovary vestigial or lacking. *Cypselae* marginal, slightly obcompressed, thickened, obovoid, tapered basally, rounded apically, black, glabrous, glandular, or pubescent, surface muricate or smooth, margins not corky, cypselae shed singly, not with adjacent paleae; pappus none.

Iva sect. *Picrotus* NUTT., Trans. Amer. Philos. Soc., n.s. 7: 346. 1840 (as “§”). Lectotype (designated here): *Iva paniculata* NUTT.

Cyclachaena FRESEN., Index Sem. (Frankfurt) 4, 1836. *Iva* subgen. *Cyclachaena* (FRESEN.) A. GRAY, Syn. Fl. N. Amer. 1(2): 245. 1884 (as “§”). *Iva* sect. *Cyclachaena* (FRESEN.) O. HOFFM. in ENGL. & PRANTL, Nat. Pflanzenfam. 4(5): 221. 1890. Type: *Cyclachaena xanthiifolia* FRESEN. [= *Iva xanthiifolia* NUTT.]

Oxytenia NUTT., Proc. Acad. Nat. Sci. Philadelphia 4: 20. 1848. Type: *Oxytenia acerosa* NUTT. [= *Iva acerosa* (NUTT.) R. C. JACKS.].

Iva subgen. *Chorisiva* A. GRAY, Syn. Fl. N. Amer. 1(2): 247. 1884 (as “§”). *Iva* sect. *Chorisiva* (A. GRAY) O. HOFFM. in ENGL. & PRANTL, Nat. Pflanzenfam. 4(5): 221. 1890. Type: *Iva nevadensis* M. E. JONES.

Leuciva RYDB., N. Amer. Fl. 33: 8. 1922. Type: *Iva dealbata* A. GRAY.

Iva sect. *Picrotus* was described (NUTTALL 1840–1841) based on *Iva xanthiifolia* and

Iva paniculata. ASA GRAY (1884) placed *Iva* sect. *Picrotus* in synonymy of *Iva* subgen. *Cyclachaena*. HOFFMANN (1890–1894) reduced GRAY's subgenus to the sectional rank as *Iva* sect. *Cyclachaena*. More recently, JACKSON (1960) misattributed GRAY's subgenus as a section, treated *Iva xanthiifolia* as including both original elements of *Iva* sect. *Picrotus*, as well as the generitype of *Cyclachaena*, but did not cite *Iva* sect. *Picrotus*. I designate *Iva paniculata* as the lectotype of *Iva* sect. *Picrotus*. This lectotypification, coupled with JACKSON's species synonymy, renders *Iva* sect. *Cyclachaena* as synonymous with the earlier *Iva* sect. *Picrotus*.

The sole species included here in *Iva* sect. *Picrotus* is *Iva xanthiifolia* NUTT. JACKSON (1960) placed the following five species within *Iva* sect. *Cyclachaena*: *Iva acerosa* (NUTT.) R. C. JACKS., *Iva ambrosiifolia* (A. GRAY) A. GRAY, *Iva dealbata* A. GRAY, *Iva nevadensis* M. E. JONES, and *Iva xanthiifolia* NUTT. As noted above, however, *Iva* sect. *Cyclachaena* (sensu JACKSON) is not monophyletic (cf. BOLICK 1985, KARIS 1995, MIAO et al. 1995a, 1995b, STROTHER 2000), but monophyly is achieved here by treating the section as containing but a single species.

Iva xanthiifolia NUTT., Gen. N. Amer. Pl. 2: 185. 1818, as “*xanthiifolia*.” Type: United States: North Dakota: On the banks of the Missouri River, near Fort Mandan, s.d., NUTTALL s.n. (holotype: BM? or PH?). CHARLIE JARVIS (pers. comm.) was unable to locate a NUTTALL collection labelled with the basionym in the British Museum. Similarly, a NUTTALL collection of this name was not found in PH (JAMES MACKLIN, pers. comm.). Nevertheless, it seems likely that the NUTTALL collection is in either BM or PH, albeit not located.

Cyclachaena xanthiifolia FRESEN., Index Sem. (Frankfurt) 1, 4. 1836, as “*xanthiifolia*.” *Euphrosyne xanthiifolia* (FRESEN.) A. GRAY, Pl. Wright. 2: 85. 1853 [Smithsonian Contr. Knowl. 5(6): 85. 1853], as “*xanthiifolia*.” Type: United States: North Dakota or Montana: In sylvis prope Fort Union allisque locis Missouri superioris, 1832–1834, MAXIMILIAN s.n. (holotype: FR?). The original set of MAXIMILIAN's North American collections is at W, whereas FRESENIUS worked at FR. BRUNO WALLNÖFER (pers. comm.) was unable to find a MAXIMILIAN collection with this basionym in Vienna; thus the herbarium in Frankfurt may hold the holotype material. Fort Union is in North Dakota, only a few km east of Montana. It is located on the Missouri River just upstream from the confluence with Yellowstone River. The type locality, however, cannot be attributed with certainty to either state. *Cyclachaena* was described on the fourth (all unnumbered) page of this seed catalogue, but the binomial of the generitype appears only on the first page. Both pages must be consulted for validation of this species name.

Iva paniculata NUTT., Trans. Amer. Philos. Soc., n. s. 7: 347. 1840. Type: United States: Rocky Mountains, by streams, in alluvial places, s.d., NUTTALL s.n. (holotype: BM n.v., digital image!). ROBIN KENNEDY (pers. comm.), during a trip to London in 2001, found a

NUTTALL collection labelled with the basionym in the British Museum. Similarly, this year CHARLIE JARVIS (pers. comm.) located this same NUTTALL collection in the British Museum. A NUTTALL collection of this name was not found in PH (JAMES MACKLIN, pers. comm.), thus I consider the NUTTALL collection in BM to be the holotype. The NUTTALL collection in BM is marked with an asterisk (see fig. 1) typical of NUTTALL novelties, thus there is no doubt of the authenticity of this specimen.

Cyclachaena pedicellata RYDB., Fl. N. Amer. Fl. 33: 10. 1922. *Iva pedicellata* (RYDB.) CORY, Rhodora 38: 407. 1936. *Iva xanthiifolia* var. *pedicellata* (RYDB.) KITTELL, Fl. Ariz. N. Mex. 425. 1941. Type: United States. New Mexico: Santa Fé, 14 Sep 1895, MULFORD 1284 (holotype: NY!).

Annual tap-rooted herbs, 0.25–1.5 (2.4) m tall. *Stem* mostly simple, subterete, striate, glabrous, sometimes distally pilose or branching. *Leaves* opposite or distally alternate, long-petiolate; petiole (1) 2–9 (25) cm long, thin; blade simple or less commonly leaves of proximal nodes with blades trilobed, generally ovate to broadly so, distal leaves often narrowly elliptic, lanceolate, or oblanceolate, (2.5) 4–12 (21) cm long, (0.7) 1.5–11 (23) cm wide, chartaceous, trinerved from base or nearly so, reticulate, the adaxial surface scabridulous, sometimes lightly glandular, green, the abaxial surface hirsute, glandular, light green, base acute to truncate, apex acute to attenuate, margins irregularly serrate. *Capitulescence* terminal and axillary, thyrsoid-paniculate, many-headed, ebracteate, to 30 cm or more tall, ultimate branches ascending or less commonly spreading, mostly less than 15 cm long, these spicate with several to many essentially sessile capitula. *Capitula* 13–17 (25)-flowered, ca. 3 mm tall; involucre hemispherical 1.5–3 mm tall, 3–4.5 mm wide; phyllaries persistent, ca. 10, biseriata, broadly ovate, abaxially pubescent, the outer phyllaries herbaceous, opposite the inner series, the inner phyllaries scarious, oblong, cucullate, as broad as, subtending, and closely appressed to weakly enfolding the outer surface of the associated cypselae; receptacle weakly paleate, pales linear, ca. 0.3 mm long, glabrous or glandular. *Marginal florets* ca. 5; corolla tubular, nearly obsolete, ca. 0.1 mm long; style to 0.4–0.6 mm long, branches 0.2–0.3 mm long, spreading. *Disk florets* 8–13 (20), ca. 1.5 mm long; corolla funnelform, yellowish or cream-coloured, glandular; ovary vestigial, linear. *Cypselae* 2–2.5 mm long, commonly lightly hispidulous or glandular; chromosome number $2n = 36$ (CRONQUIST 1994, MIZIANTY et al. 1983).

Specimen examined: Armenia. Shirak Region, near Arax River, vil. Jrapy, 1450 m, 30 June 2003, H. STEPHANJAN s.n. (ERE n.v., MO!).

Distribution and Ecology: This summer- to fall-flowering annual herb is generally found in moist areas in a variety of disturbed habitats in north temperate zones. *Iva xanthiifolia* is apparently native to western North America (CORRELL & JOHNSTON 1970, CRONQUIST 1994, JACKSON 1960), but does not occur southwards near the Mexican border, nor does it occur in California (HICKMAN 1993). It is introduced to

eastern North America, where it may be found in the northern United States and adjacent Canada (BRITTON & BROWN 1913, GLEASON & CRONQUIST 1991, JACKSON 1960). It is found in the more temperate zones of the southern United States (CRONQUIST 1980), but not in the Gulf Coast subtropical zone.

Iva xanthiifolia is listed as a noxious weed by the Federal Government of the United States, causes contact dermatitis (pers. obs., JACKSON 1960), and its pollen is a known agent of hay fever (JACKSON 1960). That this species causes hay fever may be inferred from its common name of “false ragweed,” although its most frequent common name (marsh-elder) and some of its other common names (e.g., burweed, horseweed, sumpweed) perhaps do not indicate this.

In Europe, it is an occasional weed, typically on roadways and railroad lines, occurring from France to Poland, southeast into Macedonia and Bulgaria, and thence around the areas north of the Black Sea. The report of *Iva xanthiifolia* in Armenia is the first report of the plant occurring in Eurasia south of the Caucasus Mountains. In Armenia, it occurs in mountainous desert steppe near the Arax River at an elevation of about 1450 meters. While the plant produces seed in great abundance, it is not known to have invaded cultivated areas of the region. It is not known to me to have spread to eastern Asia, nor to the southern hemisphere.

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May 5. + Cyclachena
~~Iva~~ ~~sp.~~
 var. paniculata?
 var. fredericus
 Hb. Nuttall.
 R. Mtg
 Cyclachena
 Iva xanthifolia, Nutt.

Fig. 1. Label of the holotype of *Iva paniculata* Nutt. (BM).

New chromosome counts for some Lactuceae (Compositae)

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Abstract

Somatic chromosome numbers of 44 species in 19 genera of Lactuceae were counted. Chromosome counts of five species, *Cicerbita tianschanica* (REGEL & SCHMALH.) BEAUVERD, *Chondrilla canescens* KAR. & KIR., *Rhagadiolus angulosus* (JAUB. & SPACH) KUPICHA, *Leontodon muelleri* (SCHULTZ BIP.) FIORI, *Scorzonera taurica* BIEB., have not been reported before, while one or only few chromosome counts are published yet for *Picris sprengerana* (L.) POIR., *Crepis leontodontoides* ALL., *Rhagadiolus stellatus* var. *edulis* DC., *Scolymus hispanicus* L., and *Tragopogon pterocarpus* DC.

Introduction

According to BREMER (1994), the Lactuceae comprise 98 genera and more than 1550 species. As part of a study of the systematics of the tribe we counted chromosome numbers for 44 different species of 19 genera.

Material and Method

Seeds were obtained through the international seed exchange and were grown in the greenhouse, determined, and voucher specimens were taken. Vouchers for all counts are deposited at the Herbarium Gatersleben (GAT). Root tips were collected early in the morning, rinsed in water and placed for one hour in Paradichlorbenzol, following the protocol of FUKUI (1996) and then fixed in ethanol-acetic acid (3:1). Before staining the root tips were transferred into HCl for 7–8 min at 37°C, then stained with 45 % aceto-carmine for at least 30 min and analysed by the squash method. Photos of the chromosomes can be obtained from the first author upon request.

Results and Discussion

The chromosome numbers of the species reported here (Table 1) range from $2n=6-32$, with only one species being polyploid (*Sonchus oleraceus*). Chromosome counts for *Cicerbita tianschanica*, *Chondrilla canescens*, *Rhagadiolus angulosus*, *Leontodon muelleri* and *Scorzonera taurica* have never been reported before, while 23 chromosome counts confirm the data of earlier studies unambiguously (*Arnoseris minima*, *Catananche caerulea*, *Crepis alpina*, *C. dioscoridis*, *C. foetida*, *C. leontodontoides*, *C. neglecta*, *C. setosa*, *C. sibirica*, *C. tectorum*, *Hyoseris radiata*, *H. scabra*, *Lactuca perennis*, *L. saligna*, *L. sativa*, *L. viminea*, *L. virosa*, *Leontodon hispidus* subsp. *glabratus*, *Picris hieracioides*, *Prenanthes purpurea*, *Rhagadiolus stellatus* var. *edulis*, *Tolpis barbata*, *Tragopogon dubius*, *T. orientalis*, *T. porrifolius* subsp. *australis*, and *T. pterocarpus*; see BABCOCK 1947, BABCOCK & JENKINS 1943, GOLDBLATT 1981, 1984, 1985, 1988, GOLDBLATT & JOHNSON 1990, 1991, 1994, 1996, 1998, 2000, and references therein). The counts for *Crepis aurea* reported by earlier workers (see above) are $2n=10$, 14 or 20, the variation in numbers pointing to a heterogeneous assemblage. This also accounts for the reported chromosome numbers of *Koelpinia linearis*, $2n=14$, 40, 42, 56, *Sonchus oleraceus*, $2n=32$, 36, 64, and *Tragopogon dubius*, $2n=12$, 24, 36. For six species also surveyed here two different chromosome numbers have been reported, *Crepis pulchra*, $2n=8$, 18, *C. rubra* "Alba", $2n=10$, 12, *C. sancta*, $2n=10-12$, *Hypochoeris maculata*, $2n=10$, 20, *Lapsana communis*, $2n=14$, 16, and *Scolymus hispanicus*, $2n=10$, 20. In all these cases, our findings confirm earlier counts.

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Table 1. Chromosome nos. (2n) in taxa of Lactuceae

No.	Plants	Counts
bg73	<i>Arnoseris minima</i> (L.) SCHWEIGGER & KOERTE	18
bg54	<i>Catananche caerulea</i> L.	18
bg19	<i>Chondrilla canescens</i> KAR. & KIR.	16
bg259	<i>Cicerbita tianschanica</i> (REGEL & SCHMALH.) BEAUVERD	18
bg222	<i>Crepis alpina</i> L.	10
bg221	<i>Crepis aurea</i> (L.) CASS.	10
bg225	<i>Crepis conyzifolia</i> (GOUAN) A. KERNER	8
bg232	<i>Crepis conyzifolia</i> (GOUAN) A. KERNER	10
bg226	<i>Crepis dioscoridis</i> L.	8
bg227	<i>Crepis foetida</i> L.	10
bg252	<i>Crepis leontodontoides</i> ALL.	10
bg228	<i>Crepis neglecta</i> L.	8
bg231	<i>Crepis pulchra</i> L.	8
bg229	<i>Crepis pulchra</i> L.	8
bg22	<i>Crepis rubra</i> "Alba" L.	10
bg253	<i>Crepis sancta</i> (L.) BABC.	10
bg254	<i>Crepis setosa</i> HALLER F.	8
bg255	<i>Crepis setosa</i> HALLER F.	8
bg224	<i>Crepis sibirica</i> L.	10
bg177	<i>Crepis tectorum</i> L.	8
bg257	<i>Crepis vesicaria</i> subsp. <i>haenselevi</i> (BOISS.) SELL	8
bg62	<i>Hyoseris radiata</i> L.	16
bg39	<i>Hyoseris scabra</i> L.	16
bg238	<i>Hypochaeris maculata</i> L.	10

bg42	<i>Koelpinia linearis</i> PALL.	42
bg179	<i>Lactuca perennis</i> L.	18
bg182	<i>Lactuca saligna</i> L.	18
bg207	<i>Lactuca sativa</i> L.	18
bg180	<i>Lactuca viminea</i> (L.) J. PRESL & C. PRESL	18
bg181	<i>Lactuca virosa</i> L.	18
bg124	<i>Lapsana communis</i> L.	14
bg60	<i>Leontodon hispidus</i> (L.) subsp. <i>glabratus</i> (KOCH) HAYEK	14
bg55	<i>Leontodon muelleri</i> (SCHULTZ BIP.) FIORI	8
bg206	<i>Picris hieracioides</i> L.	10
bg8	<i>Picris sprengerana</i> (L.) POIR.	10
bg209	<i>Prenanthes purpurea</i> L.	18
bg 9	<i>Rhagadiolus angulosus</i> (JAUB. & SPACH) KUPICHA	10
bg10	<i>Rhagadiolus stellatus</i> var. <i>edulis</i> DC.	10
bg31	<i>Scolymus hispanicus</i> L.	20
bg269	<i>Scorzonera taurica</i> BIEB.	14
bg117	<i>Sonchus oleraceus</i> L.	32
bg58	<i>Tolpis barbata</i> (L.) GAERTNER	18
bg216	<i>Tragopogon dubius</i> SCOP.	12
bg235	<i>Tragopogon minor</i> MILLER	12
bg220	<i>Tragopogon orientalis</i> L.	12
bg234	<i>Tragopogon orientalis</i> L.	12
bg219	<i>Tragopogon porrifolius</i> subsp. <i>australis</i> (JORDAN) NYMAN	12
bg217	<i>Tragopogon pterocarpus</i> DC.	12

Ethnobotanical survey and conservation of medicinal Compositae species in Benin Kingdom, Nigeria

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Abstract

A combination of social survey and direct field observation was used to identify members of Compositae species valued for medicine in Benin Kingdom, Nigeria. A total of 23 Compositae species were identified as being used ethnomedicinally. Most of these species occurred naturally in the forests, which presently serve as the primary source of these species to the local residents. Over 70% of the species were found to be rare on the abundance scale, which indicates the need for conservation. Strategies toward the attainment of their conservation are proposed.

Introduction

The Benin Kingdom is located in the rainforest zone of Nigeria which is widely reputed for its species richness in both flora and fauna. At present over 70% of the human population living within the kingdom are engaged in agriculture (NYSC 2000) and live in the rural areas of the kingdom.

The dependency of the rural dwellers on plants for the amelioration and/or curing of diseases cannot be over-emphasized (WHO 1976) as the greater part of the traditional therapy involves the use of plant extracts or their active principles (WHO-IUCN-WWF 1993). Apart from their ready availability, native plants offer cheap and sustainable methods of health maintenance to the rural dwellers.

Currently, the natural vegetation of Benin Kingdom, like other parts of the rainforest zone of Nigeria, is disappearing or being altered at alarming rate. Thus, there is the urgent need for ethnobotanical survey of the flora species in the kingdom to provide information necessary for conservation of those with ethnopharmacological potentials. The study reported here focused on Compositae possessing such potentials within the kingdom.

Materials and methods

A combination of social surveys and direct field observations (after LIPP 1989 and KAYODE 2002) was used in this study. Five rural communities tagged A, B, C, D and E, which were far from urban influence, were selected within 40 km radius from Benin-City, the traditional headquarter of Benin Kingdom. Twenty-five rural dwellers were randomly selected and interviewed in each village. The interviews were conducted with a fairly open framework that allowed for focused, conversational, two-way communication.

Voucher specimens of plant species identified as being used as medicines by the villagers were collected and identified. Information on the parts of such plants used and the source(s) where the plants were collected were documented. The relative abundance of the medicinal plants in a 10m² land area within the areas of collection were defined using the abundance scale of BONGERS et al. (1998) as reported in KAYODE (1999). Also the index of similarity (IS) between the sampling communities was determined as defined by KAYODE (1999).

Results and discussion

A total of twenty-three Compositae species were found to be valued for medicine by the respondents in the study areas. This constitutes over 50% of the total number of species valued for medicinal use in the study area (Table 1). The index of similarity in the occurrence of the Compositae medicinal species (Table 2) revealed that most of the species were common to all communities used in this study. *Chromolaena odorata* was the most abundant of the Compositae in all the five communities used in this study. KAYODE (1999) had earlier enumerated the factors responsible for the ecological dominance of this species in the rainforest zone of Nigeria. The timing of this study, which was conducted in the rainy season, further constitutes an added advantage to the dominance of this species.

The relative abundance of each of the species, the parts used and their medicinal usage are shown in Table 3. The ailments cured by these species ranged from malaria, the most prominent disease in Africa, fever, cough, ulcer, tuberculosis, dysentery, gonorrhoea, lumbago etc. to dressing of wounds.

The primary source of most of these medicinal Compositae species is the forest, while the respondents' secondary sources were individuals' farms (Table 4). This tends to confirm the forest as not only a repository of genetic diversity but also as a reservoir that is accessible to the rural dwellers and resource-poor individuals in urban centers. Unfortunately, the Nigeria forest is being removed at an alarming rate of 300000 ha. annually (REPETTO 1988, KAYODE 1994). At present, a lot of plant species are

endangered in the country (NCF 1986) yet afforestation and reforestation rates are less than 5% of the rate of deforestation (ODEBIYI 1990). Over 70% of the medicinal Compositae species were found to be rare on the abundance scale (Table 5). This tends to suggest that these species are now grossly endangered. The loss of some of them is imminent, as their present scarcity suggests that they may be near extinction.

In conclusion, the survey revealed that there is an urgent need for the conservation of these medicinal Compositae species in the study area. Strategies toward achieving this goal might include an understanding of the ecology of these species, the domestication of some of them, public enlightenment, as well as intensification of and community participation in the conservation efforts.

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Table 1. Demographic features of the medicinal Compositae species in Benin Kingdom, Nigeria

	Features	Communities					Average
		A	B	C	D	E	Total
(a)	Number of medicinal plant species identified by respondents	45	38	42	40	39	45
(b)	Number of medicinal Compositae species among (a)	22	20	19	21	18	23
(c)	% composition of (b) to (a)	49	53	45	53	46	51
(d)	Most abundant of the Compositae in each community	<i>C. odorata</i>	<i>C. odorata</i>	<i>C. odorata</i>	<i>C. odorata</i>	<i>C. odorata</i>	
(e)	Relative dominance of (d) in 25 m ² land area of the community *	VA	VA	VA	VA	VA	
(f)	Primary source of (d) in each community **	CA	CA	CA	CA	CA	

*VA: Very abundant

** CA: Common area

Table 2. Index of similarity (IS) in the occurrence of medicinal Compositae species in the five sampled communities in Benin Kingdom, Nigeria

Communities	IS(%)
A and B	85.71
A and C	78.05
A and D	83.72
A and E	75.00
B and C	82.05
B and D	82.93
B and E	73.68
C and E	81.08
D and C	75.01
E and D	71.79

Table 3. Compositae species used for medicine by respondents in Benin Kingdom, Nigeria

S/N	Species	Sources *		Abundance **	Parts Used ***	Medicinal Usage
		1	2			
1	<i>Acanthospermum hispidum</i>	FR	F	R	L	Yellow fever Tuberculosis
2	<i>Ageratum conyzoides</i>	CA	F	R	WP, L, S	Ulcer, Inflammation Redness of eyes Dressing of wound
3	<i>Albizia adianthifolia</i>	FR	F	R	B	Coughs, Colds, Purgative
4	<i>Albizia ferruginea</i>	FR	F	R	L, B, R	Dysentery Dressing of wounds Constipation
5	<i>Albizia lebbek</i>	FR	F	R	L, B, S	Piles, Dysentery Diarrhoea, Gonorrhoea
6	<i>Aspilia africana</i>	CA	F	F	L, R	Lumbago, Headache Stomach trouble Dressing of wound
7	<i>Bidens pilosa</i>	CA	F	A	F, L, R	Diarrhoea, Rheumatism
8	<i>Blumea aurita</i>	FR	F	R	WP	Antipyretic Intestinal problems
9	<i>Calendula officinalis</i>	FR	F	R	L	Ulcer
10	<i>Chromolaena odorata</i>	CA	F	VA	L	Malaria fever, Headache Toothache, Dysentery
11	<i>Chrysanthemum cinerariifolium</i>	FR	F	R	L	Fever
12	<i>Dicoma tomentosa</i>	FR	F	R	WP	Cuts, Wounds, Sore, Ulcers
13	<i>Eclipta alba</i>	FR	F	R	R, L	Liver ailments, Elephantiasis, Skin disease, Fever
14	<i>Elephantopus scaber</i>	FR	F	R	L, R	Fever, Cough, Inflammation of uterus and ovaries
15	<i>Helianthus annuus</i>	CA	F	F	S, L	Malaria, Bronchial and pulmonary troubles
16	<i>Launaea taraxacifolia</i>	CA	F	O	L	Yaws
17	<i>Microglossa afzelii</i>	FR	F	R	L, S	Cough, Cold, Sore throat, Tuberculosis
18	<i>Microglossa pyrifolia</i>	FR	F	R	L, R	Headache, Fever, Purgative
19	<i>Mikania scandens</i>	FR	F	R	WP	Cough, Ringworm, Insect bite
20	<i>Sphaeranthus senegalensis</i>	FR	F	R	WP	Stomach ache
21	<i>Spilanthes africana</i>	FR	F	R	WP	Tooth ache
22	<i>Spilanthes filicaulis</i>	FR	F	R	L	Laxative
23	<i>Vernonia amygdalina</i>	CA	F	O	L, R, S	Stomach ache, Ringworm, Diabetes

* 1: Primary source 2: Secondary source

FR: Forest CA: Common area F: Household farm

** R: Rare O: Occasional F: Frequent A: Abundant VA: Very abundant

*** B: Bark L: Leaf S: Shoot R: Root WP: Whole plant

Table 4. Respondents source of the medicinal species in Benin Kingdom, Nigeria

Description of source	Proportion of species/source *		
	FR	CA	F
Primary	61	39	-
Secondary	-	-	100

* FR: Forest

CA: Common area

F: Household farm

Table 5. Relative abundance of the medicinal Compositae species in Benin Kingdom, Nigeria

Relative abundance*	Proportion of species
R	74
O	9
F	9
A	4
VA	4

*R: Rare O: Occasional F: Frequent A: Abundant VA: Very abundant

Biogeography of Cuban Asteraceae

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Abstract

Native Cuban Asteraceae have their origin and distribution patterns restricted to America although the original source of a basal taxon (*Gochnatia*) is related to the Pacific basin. Centers of origin can be summarized as follows: Gondwanian (Cichorioideae) and Laurasic and Gondwanian (Asteroideae). This seems to indicate that a gondwanian-centered invasion took place first, followed by a later laurasic-centered invasion. Being close to Laurasia since the Upper Eocene, Cuba has received a flow of laurasic taxa that have also invaded the Caribbean.

Keywords: Asteraceae, biogeography, Cuba

Biological, Ecological and Geological Background

Compared to the Cretaceous dispersal of angiosperms the invasion of the Caribbean by Asteraceae is a recent event. The Caribbean, however, has had a complicated geological history. Like the Indomalayan region, the Caribbean (southern Mexico, Central America, northern South America and the West Indies) has a mixed origin since at least 5 different areas are involved: 1) southern Mexico and northern (nuclear) Central America (GENTRY 1995) both Laurasian and dating back to the Cretaceous (GRAHAM 1995); 2) northern South America (Gondwanian but with terrane accretion from other sources); 3) the Greater Antilles and the Panama-Costa Rica arc both related to independent plates; 4) one (or several?) terranes (TAYLOR 1995) that collided with northwestern South America; and 5) the Lesser Antilles arc.

The first fossil records of Asteraceae date back to the Oligocene (CRONQUIST 1981, BREMER 1994) but a taxonomic group can exist long before it appears in the fossil record (BREMER 1994). Distributions of several basal genera (e. g., *Gochnatia*) suggest a Lower Eocene origin when a mild climate favoring dispersal of both Laurasian and Gondwanian taxa prevailed in northern Laurasia (GRAHAM 1995). A Cretacic origin is highly improbable (FUNK et al. 1995).

The Cuban species of *Gochmatia* confirm that basal Cuban Asteraceae prefer open ecotopes at low or middle altitudes (CRONQUIST 1994). Taking into account that many South American Asteraceae (both basal and derived) thrive at high altitudes (GENTRY 1995) where open vegetation is dominant, the current distribution of Asteraceae can be regarded as a successful attempt to escape from dense forests rather than from high temperatures.

Cuba is the result of a very intense folding and uplifting (involving rocks from the oceanic crust, two volcanic archipelagos and several non volcanic islands) that began in the Late Cretaceous and ended in Late Eocene times when the archipelago reached its current position lying on the Bahamas shelf and where it has stayed ever since (ITURRALDE-VINENT 1988). Accordingly, a great melange of soils and rocks was the obvious consequence of this process. Therefore, soils play a leading role in Cuba and secondly, niche specialization and geographic subdivision of populations (intra-island and inter-island gaps). Being a tropical lowland country, the climatic factor of equability (WEBSTER 1995, YOUNG 1995) is linked to almost all Cuban ecotopes and makes mountain climatic belts unimportant in most mountain ranges. In addition, it is obvious that the historic factor has to be taken into account as it happens in all floras.

During the Oligocene, Cuba already had bare limestone and serpentine rocks, red and brown serpentine soils, riverbank grasslands and swamps to offer to newcomers in sharp contrast to the dense forests that are usually avoided by Asteraceae, so the first Asteraceae pioneers could have arrived in the Upper Eocene-Oligocene. The Cayman, Beata and Aves mountain ranges were probably involved in the dispersal of Greater Antillean Asteraceae from continental sources.

Three quarters of the Cuban archipelago are lowlands, and this is a radical difference when compared to Hispaniola, Puerto Rico and Jamaica. There are four mountain ranges: 1) Guaniguanico in western Cuba (highest altitude: 699 m), 2) Guamuhaia in Central Cuba (1140 m), 3) Sierra Maestra in southeastern Cuba (1972 m) and 4) Nipe-Baracoa in northeastern Cuba (1231 m). It is obvious that Cuba had little to offer to montane austrotropical taxa since three out of four mountain ranges are premontane (BURGER 1995), their highest altitudes being below or little over 1000 m. However, serpentine barrens and bare limestone rocks were a good option for newcomers adapted to open ecotopes.

Results

Origin and distribution of alien taxa

Three tribes have been introduced with or without intention: Anthemideae (*Achillea*, *Leucanthemum*, *Matricaria*), Cardueae (*Cirsium*) and Lactuceae (*Launaea*, *Sonchus*, *Taraxacum*, *Youngia*). In addition, 36 genera (30 % of the Cuban genera of

Asteraceae) and 76 species have been added to the Cuban flora. Most of them have become naturalized and are now scattered all over the archipelago (HERRERA & VENTOSA 2005). A few do not persist under Cuban climatic conditions but many are weeds. Being adapted to ruderal ecotopes and cultivated fields and due to deforestation they currently prevail in the Cuban landscape.

Sources of origin of alien species are diverse: tropical America (from southern Mexico and Florida to Paraguay and Argentina, and also West Indies), Central America (Guatemala to Panama), continental Caribbean (southern Mexico, Florida and sometimes even Texas to Colombia and Venezuela, in some occasions including the Guyanas and northeastern Brazil), tropical and subtropical North America (including northern and central Mexico), temperate Eurasia (including the Mediterranean) and tropical East Asia (not only the continental part but also the islands). Some species were intentionally introduced but many came as weeds. Some others could be introduced in the future. General distribution is often pan(sub)tropical or even cosmopolitan but only a few species occur in temperate countries.

The composition of the Cuban Asteraceae is summarized in Table 1. The proportions of native (pre-Columbian) and alien taxa are as follows.

Pre-Columbian	2 subfamilies	10 tribes	81 genera	300-330 species
Alien	0 subfamilies	3 tribes	36 genera	76 species
Current (=total)	2 subfamilies	13 tribes	117 genera	400 species

Origin and distribution of native taxa

Subfamily 1. Cichorioideae

Tribe 1. Mutisieae

4 genera (*Chaptalia*, *Gochnatia*, *Proustia*, *Trixis*).

Gochnatia is a basal, crucial but paraphyletic taxon and allied to the archaic South American *Stenopadus* group (BREMER 1994). Current distribution of *Gochnatia* seems to be a relict of a wider distribution along the Pacific basin during the Lower-Middle Eocene involving Beringia (GRAHAM 1995). *Gochnatia* has over 68 species in the southern United States, Central and South America, continental southeast Asia, Cuba, Hispaniola and Bahamas. According to CABRERA (1971), the genus is divided in six sections. A cladistic analysis of the distribution of the species of *Gochnatia* in the northern Caribbean (PÉREZ CAMACHO & VENTOSA 2002) reveals that the 35 species (38 taxa) of section *Gochnatia* occur in: southeastern Brazil (1 species), southern Bolivia and northwestern Argentina (1), Bolivia (2), Peru (4), Hispaniola (7), Bahamas (1), Bahamas and Cuba (1) and Cuba (18). There is a wide gap in the distribution (Greater Antilles, central Andes, and southeastern Brazil) and therefore, no logic explanation

exists for the high endemism and diversification of this basal genus in the Greater Antilles. Other genera having a similar pattern are more derived (e.g., *Vernonia* s. l., *Koanophyllon*) although they are also paraphyletic and usually avoid the Pacific basin. The continental species of *Gochnatia* are in accordance with a montane austrotropical pattern of distribution but the Cuban species are not, suggesting that the group was less adapted to high altitudes in the past. However, sources of the other three genera of Mutisieae are montane austrotropical.

Tribe 2. Vernonieae

7 genera (*Ekmania*, *Elephantopus*, *Lachnorhiza*, *Pacourina*, *Struchium*, *Trichospira*, *Vernonia* s. l.).

In general, the forebearers of the Cuban species of Vernonieae had their original source in a low to medium altitude center in South America, probably in Brazil (BREMER 1994). This center is a very old shield (Pre-Cambrian) and several angiosperm taxa have their center of diversification there. Catinga and serrado vegetation units could be involved in the evolution of at least part of the neotropical members of the tribe. From a phylogenetic standpoint, Vernonieae was also the first tribe to colonize Cuban humid ecotopes. However, the fact that the current phylogenetic system (BREMER 1994) does not necessarily reflect the chronology of events should not be overlooked when considering Vernonieae as a relatively old group in Cuba. In addition, *Vernonia* s. l. is paraphyletic.

Tribe 3. Liabeae

1 genus (*Liabum*).

Austrotropical montane following an Andean-Mesoamerican-Greater Antilles route. A very homogeneous tribe in Cuba and therefore unique. Possibly a newcomer (Pliocene-Pleistocene-Holocene).

Subfamily 2. Asteroideae

Tribe 4. Plucheae

6 genera (*Epaltes*, *Pluchea*, *Pseudoconyza*, *Pterocaulon*, *Sachsia*, *Rhodogeron*).

Most taxa are aquatic, semi-aquatic or thrive in wet ecotopes and therefore they show a great deal of contradiction in their distributions, being readily dispersed by birds. There is a native group of genera in primary vegetation units in western and central Cuba coming from pantropical and North American sources, e.g., the semi-aquatic species of *Pluchea* from North America and *Sachsia* and *Rhodogeron* from the Greater Antilles, Bahamas and southeastern North America. On the other hand, alien species (*Pluchea carolinensis*, *Pseudoconyza lyrata* and perhaps *Pterocaulon*) had their origin in confusing pantropical and Australian centers. Man was (and is)

possibly involved in the dispersal of these species.

Tribe 5. Gnaphalieae

1 genus (*Gnaphalium*).

Being highly polyphyletic (BREMER 1994), *Gnaphalium* is puzzling. This genus is a somewhat weedy and montane newcomer and has been little investigated in Cuba. Some of the species could belong to the Central American genera that are currently being segregated from *Gnaphalium*. The tribe is scattered throughout the Caribbean (Mexico, Central America and northern South America) but is also well represented in North and South America so the center of origin is obscure. Man probably was involved in the dispersal of some of the species and one or two could have been introduced, though some thrive at high altitudes being native beyond any doubt. Summing up, some of the species seem montane boreotropical and others recent introductions.

Tribe 6. Astereae

6 genera (*Aster*, *Baccharis*, *Egletes*, *Erigeron*, *Gundlachia*, *Solidago*).

Scattered and well represented in the West Indies and North America. However, *Egletes* likely followed a South America-Lesser Antilles and/or South America-Central America-Greater Antilles route. All genera occur in North America except the Antillean genus *Gundlachia*. Most Cuban species are endemic, Antillean or North American.

Tribe 7. Senecioneae

4 genera (*Senecio* s. l., *Pentacalia* s. l., *Oldfeltia*, *Shafera*).

A Gondwanian group from South America (Andean-Mesoamerican-Macroantillean) and so far with two endemic genera (*Oldfeltia*, *Shafera*) though the number of endemic genera will increase in the near future due to current research (B. NORDENSTAM, pers. comm.). The taxonomic position of the monotypic genus *Shafera* is in doubt (JEFFREY 1992, BREMER 1994). In Cuba the tribe is strongly restricted to serpentine barrens and pine forests in ecotopes at medium altitudes (500-1200 m). Two species also occur in Hispaniola, the rest are endemics. Colonization of young mountains (Late Tertiary) is almost lacking and white sand savannas are totally avoided. Therefore the tribe behaves in a similar way to Mutisieae-*Gochmatia* and we believe it was the second group to arrive in Cuba. It could also be a newcomer with strong trends towards extreme ecotopes but this seems highly unlikely. As a rule, the Cuban Senecioneae avoid bare limestone rocks and only a few species have entered the orophilous series (=mountain floor ecotopes) on non-serpentine soils.

Tribe 8. Helenieae

7 genera (*Flaveria*, *Harnackia*, *Helenium*, *Lebetina*, *Lescaillea*, *Pectis*, *Thymopsis*).

The Cuban species are also found in the northern Caribbean (Mexico, Florida, Bahamas, Greater Antilles) and in the Lesser Antilles. The tribe evolved in the continental Caribbean (Mexico, Central America, northern South America and Florida) probably from a North American stock (Mexico and southwestern United States).

Tribe 9. Heliantheae

21 genera (*Acmella*, *Ambrosia*, *Ancistrophora*, *Bidens*, *Borrchia*, *Clibadium*, *Enydra*, *Heptanthus*, *Iva*, *Koehneola*, *Lantanopsis*, *Melanthera*, *Neurolaena*, *Pinillosia*, *Salmea*, *Sphagneticola*, *Spilanthes*, *Tetraperone*, *Verbesina*, *Viguiera*, *Wedelia*).

A group that is basically laurasic, probably derived from Mexican and nuclear Central American forebearers. Many species occur in the continent especially in the continental Caribbean, North America (76 %) and tropical America (24 %).

Tribe 10. Eupatorieae

19 genera (*Adenostemma*, *Ageratina*, *Ageratum*, *Antillia*, *Brickellia*, *Chromolaena*, *Ciceronia*, *Conoclinium*, *Critonia*, *Eupatorium*, *Grisebachianthus*, *Hebeclinium*, *Isocarpha*, *Koanophyllon*, *Lepidesmia*, *Mikania*, *Phania*, *Spaniopappus*, *Urbananthus*).

Similar to Heliantheae in having a laurasic origin derived from Mexican and nuclear Central American forebearers (GENTRY 1995). Many species also occur in North America and the Caribbean (71 %) and to a lesser extent in tropical America (29 %). They are often restricted to old ecotopes (serpentine barrens, limestone cliffs and sierras) but are also found in swamps and young mountains.

Discussion

Biogeographical patterns of the native tribes of Cuban Asteraceae

Tribe Mutisieae. Pacific basin and montane austrotropical centered. Although *Gochnatia* is a circumpacific genus, it probably evolved in South America and reached North America (before the emergence of the Isthmus of Panama) and East Asia following a Beringian rather than a North Atlantic route. *Gochnatia* section *Gochnatia* is restricted to the Greater Antilles, central Andes and southeastern Brazil. The South American members of this section are montane austrotropical, but their Greater Antillean counterparts are low to medium altitude dwellers (premontane). In addition, the section does not occur in the northern Andes, which are very young (FUNK et al. 1995), and one species is not only found in Cuba but also in Hispaniola. This dates back to the Oligocene-Miocene since these islands were united until the Miocene. Probably, the genus was not as clearly montane austrotropical in the Middle

Tertiary as it currently is, and therefore further secondary specialization in extreme ecotopes and rare soils in the Greater Antilles and at high altitudes in South America led to the current, remarkable pattern. The rest of Cuban Mutisieae are newcomers (Pliocene-Pleistocene-Holocene). Being scapose herbs, it is quite likely that the species of *Chaptalia* had more opportunities for a fast evolution. Nevertheless, no evolution yielding endemic genera has occurred but speciation (29 species) in ecological islands has been the most intense after Eupatorieae and Vernonieae.

Tribe Vernonieae. Centered in old Brazilian shields. According to current standpoints in synantherology the forebearers of *Vernonia* were African, further dispersal in South America and colonization of the Greater Antilles being later events. There are two endemic genera (*Ekmania*, *Lachnorhiza*) not having much in common in their habit, habitat and morphology and restricted to ecological islands. Some taxa come from wetland centers in South America not previously accounted for in literature. These wetlands seem to have no relation whatsoever with similar swamp areas of North America (Louisiana bayous, Everglades). A slight influence from North America probably involving man is also evident. Speciation has been intense and in this aspect Vernonieae is second only to Eupatorieae.

Tribe Liabeae. Montane austrotropical centered. Consequently, the tribe is poorly developed in Cuba where mountains above 1000 m are scarce. No endemic genera occur and there is a single endemic species (25 %) in an edaphic-altitudinal ecological island.

Tribe Plucheeae. Centered in Laurasia (Florida, wetlands of southeastern United States and Bahamas but also the Greater Antilles). However, several taxa have a pantropical distribution and therefore their centers of origin are obscure. A single endemic genus, *Rhodogeron* (one species) thriving in an edaphic-ecological island and related to *Sachsia* (northern Caribbean, three species). Speciation in these two genera and, as a rule in most Cuban endemic genera of Asteraceae, is highly restricted in number.

Tribe Gnaphalieae. Laurasic centered with primary sources in Mexico and northern (nuclear) Central America. More oriented towards the orophilous series (500-1972 m) than Plucheeae. The only Cuban tribe that so far has no endemic genera or species.

Tribe Astereae. Laurasic centered (southeastern United States wetlands), with a secondary dispersal into the continental Caribbean and West Indies. According to the distribution of many Cuban angiosperm taxa there was an intense exchange among these three areas in the Late Tertiary. Endemic genera are lacking but there is a strong speciation (19 species).

Tribe Senecioneae. Montane austrotropical centered. Splitting of the core genus *Senecio* has become necessary for understanding the tribe. Being restricted to old

serpentine and limestone ecological islands the taxa are quite like Mutisieae-*Gochnatia* in this respect, but Cuban Senecioneae genera are not found in East Asia, and both groups differ from Liabeae in being seemingly older. The Cuban taxa of the tribe have evolved in pine forests, scrub barrens and sclerophyllous mountain rainforest, all these vegetation units occurring on serpentine at low to medium altitude. Evolution towards endemic genera (*Shafera*, *Oldfeltia*, and some more in the near future according to B. NORDENSTAM, pers. comm.) has been more intense than in Mutisieae and speciation is similar to that of Astereae (19 species).

Tribe Helenieae. Laurasian centered. *Pectis* is the only genus reaching South America. Two endemic genera in pine forest on serpentine (*Lescaillea*, *Harnackia*) and 10 endemic species.

Tribe Heliantheae. Laurasic centered with notable extensions to South America including lowlands in that continent. This tribe in Cuba is similar to Eupatorieae in number of endemic genera (4), but concerning speciation it is more like Astereae and Senecioneae (20 species).

Tribe Eupatorieae. Due to rapid evolution and dispersal, origins are complicated and confusing. There is a mixture of eastern United States, eastern South America, Central American and Andean centers involving laurasic lowlands, laurasic medium to high altitudes, nuclear Central America (which is in fact a part of North America), the Andes and the Brazilian and Guyana shields. KING & ROBINSON (1987) arrived to interesting conclusions in this species-rich tribe. Undoubtedly, the most intense evolution towards endemic genera in Cuba, together with Heliantheae and also the greatest speciation together with Vernonieae.

General considerations on the biogeography of Cuban Asteraceae, according to current paleobiogeographical information

Reproduction in modern Asteraceae has high rates, but the Cuban species of *Gochnatia* though free-flowering exhibit low rates. Data on behaviour of South American Barnadesioideae and Mutisieae in this respect seem to be lacking. However, the following hypothesis can be considered.

Asteraceae arrived in successive waves during the Late Paleogene and/or the Early Neogene. Taking into account that its species are now distributed in accordance with an archipelago-like or ecological island pattern and have not colonized the young mountains of eastern Cuba, *Gochnatia* section *Gochnatia* (a basal relict) was the first or one of the first to arrive in the Upper Eocene-Upper Oligocene. According to FUNK et al. (1995) "the high northern Andes have opened for invasion by many members of the Compositae comparatively recently and the more consistently elevated Central Andes, Mexico and parts of Central America have been among the principal sources". This would explain the lack of species of *Gochnatia* section *Gochnatia* in the

northern Andes and the possible existence in Late Paleogene times of lowland taxa of *Gochnatia* section *Gochnatia* in northern South America (GRAHAM 1995) which underwent a strong diversification in the Greater Antilles, even stronger than in South America. Cuba, Hispaniola and Jamaica split apart in the Miocene due to the opening of the Cayman Hoya and this led to further speciation and specialization in rare soils and open ecotopes in the Greater Antilles while diversification at high altitudes in South America was taking place. Since there is one species of *Gochnatia* shared by Cuba and Hispaniola, *Gochnatia* was already living in both islands at least in the Oligocene-Miocene though the arrival to either of the two islands could have taken place much later by means of bird dispersal or any other factor.

After entering eastern Cuba via Cayman, Aves or Beata, Asteraceae colonized the large (2500 km²) area in the Nipe-Cristal-Moa-Toa-Baracoa low altitude serpentine mountains and the rocky coasts and limestone sierras undergoing speciation as it moved towards the west. Endemic genera began to appear but not in Mutisieae and Liabeae (Cichorioideae) nor in Gnaphalieae and Astereae (Asteroideae).

Serpentine dwellers followed the serpentine backbone extending from east to west (Holguín-Habana). Some sections of this backbone, however, have been under the influence of marine transgressions on several occasions and consequently most of the species restricted to this area are either relicts or new taxa. Two tribes (Heliantheae and Eupatorieae) have no endemic genera or species in the serpentine backbone. However, two species of *Gochnatia* and *Rhodogeron* (Plucheeae), a monotypic and endemic genus are restricted to the serpentine backbone, though some of the species restricted to the serpentine Nipe-Cristal-Moa-Toa-Baracoa region (up to 11 species of *Gochnatia*, 58 %) can occasionally be found in the easternmost parts of this serpentine backbone.

On the other hand, white sand savannas are the result of recent geological events (Pleistocene-Holocene) but small areas should have existed in earlier times (Neogene, Paleogene?). Considering that many endemics (mostly scapose herbs) are partial to white sand savannas, they could be either neoendemics or paleoendemics. Their habit seems to point at the former.

Asteraceae have no endemic genera or species in the sandstone hills in western Cuba. Species occurring there are also found in all the Cuban territory.

The taxa of Asteraceae that arrived in western Cuba via Yucatan or southeastern United States-Bahamas were few in number as shown by the number of western endemics and non-endemics among native Asteraceae, even though the smaller size of serpentine areas in western Cuba and the recent origin of white sand savannas could have had some influence in the limited colonization of western Cuba.

The source-centers were primarily Gondwanian (Cichorioideae). Later on, North

America became an important center. Cayman, Nicaragua, Aves and Beata probably contributed to the dispersal from both subcontinents.

Conclusions

1. The sources of origin of alien species are: tropical America (indefinite), Central America, continental Caribbean, tropical and subtropical North America, temperate Eurasia including the Mediterranean, and East tropical Asia including its islands. Alien species are 1) weeds, 2) cultivated or 3) non persisting under Cuban climatic conditions. All are sun-loving and prefer open situations.
2. The main centers of origin of native Asteraceae are: Pacific basin (*Gochnatia*), montane austrotropical (Mutisieae, Liabeae, Senecioneae), old southern Brazilian shield (Vernonieae), and North America-nuclear Central America (Plucheeae, Gnaphalieae, Astereae, Helenieae, Heliantheae). The origin of Eupatorieae is confusing though it seems to have been originally laurasic. There are also a few puzzling taxa in the Plucheeae.
3. Gondwanian sources prevail in Cuban Cichorioideae. Laurasian centers prevail in Asteroideae though they are more complicated due to the derived nature of this subfamily.
4. An archaic dispersal from Gondwana seems to have existed (*Gochnatia*, *Senecio*?, Vernonieae) during the Middle Tertiary followed by a more "modern" wave in the Neogene-Quaternary but this is open to question since speciation has been similarly intense but endemic genera are lacking in Mutisieae.
5. Although the Greater Antilles were a single geological unit in the Cretaceous, their separation during the Neogene has had a definite influence on the Cuban flora since isolation favored endemism. This flora is related to the flora of the rest of the Greater Antilles but being a lowland country Cuba exhibits a sharp contrast with Hispaniola, Puerto Rico and Jamaica, to say nothing of the mainland. Wide occurrence of serpentine rocks and soils in Cuba is another isolating factor when Cuba is compared to the West Indies and the continent.
6. Laurasia has played an important role in some Cuban angiosperm families including Asteraceae. Lying on the Bahamas shelf and under the influence of the Cayman, Nicaragua, Beata and Aves mountain ranges which not only allowed the dispersal of Gondwanian elements but also the dispersal of laurasian elements from Mexico, nuclear Central America and the United States and being close to North America and consequently serving as stepping stone for migratory birds carrying propagules, Cuba has received a flow of laurasian taxa which are low to medium altitude dwellers unlike the laurasian taxa that have invaded South America. The

Caribbean is known to have been influenced by Gondwana, but Caribbean taxa centered in the West Indies or the continental Caribbean have been influenced and enriched by Laurasia and have had a definite importance for the Cuban archipelago.

7. The Sierra Maestra folding (1974 m) is a late Neogene event. Accordingly, the moderately high mountains of Cuba have been available for colonization only in recent geological times.

8. Seed dispersal by birds could be important in Cuban Asteraceae but data on long or short distance seed dispersal are lacking.

9. The number of primary and secondary centers of origin will be modified in the near future. There are some centers involved in the biogeography of Asteraceae that are not mentioned in current references.

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Table 1. Native subfamilies, tribes and genera of Cuban Asteraceae**Subfamily Cichorioideae**

Tribe Mutisieae (*Chaptalia*, *Gochnatia*, *Proustia*, *Trixis*).

Tribe Vernonieae (*Ekmania*, *Elephantopus*, *Lachnorhiza*, *Pacourina*, *Struchium*, *Trichospira*, *Vernonia* s. l.).

Tribe Liabeae (*Liabum*).

Subfamily Asteroideae

Tribe Plucheeae (*Epaltes*, *Pluchea*, *Pterocaulon*, *Sachsia*).

Tribe Gnaphalieae (*Gnaphalium*).

Tribe Astereae (*Aster*, *Baccharis*, *Egletes*, *Erigeron*, *Gundlachia*, *Solidago*).

Tribe Senecioneae (*Senecio* s. l., *Pentacalia* s. l., *Oldfeltia*, *Shafera*).

Tribe Helenieae (*Flaveria*, *Harnackia*, *Helenium*, *Lebetina*, *Lescaillea*, *Pectis*, *Porophyllum*, *Thymopsis*).

Tribe Heliantheae (*Acmella*, *Ambrosia*, *Ancistrophora*, *Bidens*, *Borrchia*, *Clibadium*, *Enydra*, *Heptanthus*, *Iva*, *Koehneola*, *Lantanopsis*, *Melanthera*, *Neurolaena*, *Pinillosia*, *Salmea*, *Sphagneticola*, *Spilanthes*, *Tetraperone*, *Verbesina*, *Viguiera*, *Wedelia*).

Tribe Eupatorieae (*Adenostemma*, *Ageratina*, *Ageratum*, *Antillia*, *Brickellia*, *Chromolaena*, *Ciceronia*, *Conoclinium*, *Critonia*, *Eupatorium*, *Grisebachianthus*, *Hebeclinium*, *Isocarpha*, *Koanophyllon*, *Lepidesmia*, *Mikania*, *Phania*, *Spaniopappus*, *Urbananthus*).

***Trichocline dealbata* (HOOK. & ARN.) BENTH. & HOOK. f. ex GRISEB. (Compositae: Mutisieae),
saved by ICBN Art. 33.2**

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Abstract

The combination *Trichocline dealbata* (HOOK. & ARN.) "BENTH. & HOOK. f. ex GRISEB." is valid, albeit GRISEBACH did not explicitly cite the basionym. The GRISEBACH and the HOOKER and ARNOTT names are thus homotypic (nomenclatural) synonyms, as allowed by application of the newly reworded ICBN Art 33.2. The combination *Trichocline dealbata* is thus not to be attributed to HIERONYMUS (as done in Index Kewensis, an interpretation under which the GRISEBACH name would block that of HIERONYMUS), and the senior synonym (*Chaetanthera parviflora*) does not need to be transferred to *Trichocline*.

Argentina

Introduction

Many "presumed" new combinations that do not explicitly cite a basionym are, nevertheless, to be taken as combinations as per the newly reworded ICBN Art 33.2 (GREUTER et al. 2000). The following example illustrates this point, specifically showing that there is a single legitimate (rather than two heterotypic names as) *Trichocline dealbata* (Compositae: Mutisieae).

In Index Kewensis, JACKSON (1895) treated *Chaetanthera dealbata* HOOK. & ARN. as the basis of "*Trichocline dealbata* BENTH. & HOOK. f. ex HIERON.," perhaps because there is no explicit citation of the valid basionym of *Chaetanthera dealbata* HOOK. & ARN. in the earlier GRISEBACH (1879). CABRERA (1971), however, cited the transfer of *Chaetanthera dealbata* HOOK. & ARN. to *Trichocline* CASS. as being effected by GRISEBACH (1879). This interpretation was followed by ZARDINI (1975) and MARTICORENA & QUEZADA (1985).

The names involved thereby are homotypic as allowed in ICBN 33.2 (GREUTER et al. 2000). Given the conspecific nature of LORENTZ 1310 and the type *Chaetanthera dealbata* HOOK. & ARN., the combination *Trichocline dealbata* is not to be attributed to HIERONYMUS (which would thus be blocked by the earlier GRISEBACH name), and the

senior synonym (*Chaetanthera parviflora*) does not need to be transferred to *Trichocline*. The name and author citation of this uncommon southern Andean composite remains “*Trichocline dealbata* (HOOK. & ARN.) BENTH. & HOOK. f. ex GRISEB.”

The treatments of GRISEBACH (1879) and HIERONYMUS (1882a, 1882b) for this species are as follows:

GRISEBACH (1879: 215):

1310. *T. dealbata*. BENTH. HOOK. ex descr.- Syn. *Bichenia* DON. Involucri squamae rub3seriales [sic! sphalm. for ‘sub3seriales’], exteriores breves, omnes acuminatae; ligulae radii 4nerves. Nom. vernac. Contrayerba. - Ct. (“Mendoza”).

The collector in GRISEBACH (1879), except where stated otherwise, is LORENTZ, and “Ct.” refers to Prov. Catamarca. The generic name *Trichocline* appears with the first species on page 214, but is then abbreviated on pages 214–215.

HIERONYMUS (1882a: 359; 1882b: 165):

Trichocline dealbata (sec. BENTH. HOOK. gen. II, p. 497), syn. *Chaetanthera dealbata* (HOOK. et ARN. comp. I, p. 104). N.v. yerba del corro, yerba corro. M. Ct. (cordilleras).

GRISEBACH (1879) attributed the name *T. dealbata* to BENTHAM & HOOKER, but did not explicitly cite a valid binomial as the basis of *T. dealbata*. GRISEBACH cited only “*Bichenia* DON,” perhaps in reference to the invalid manuscript name “*Bichenia dealbata* DON” cited by HOOKER & ARNOTT (1835). BENTHAM & HOOKER (1873) treated *Bichenia* as a synonym of *Trichocline*, but mentioned neither *Chaetanthera dealbata* nor *Trichocline dealbata*.

HIERONYMUS (1882a, b) was the first to explicitly cite *Chaetanthera dealbata* as the basionym of *Trichocline dealbata*. If, however, HIERONYMUS (1882a, b) is taken as the place of the first valid combination for *Chaetanthera dealbata* HOOK. & ARN. in *Trichocline*, the earlier GRISEBACH name would need to be taken as an independent heterotypic novelty typified by LORENTZ 1310 (GOET) from Catamarca, Argentina. [As an aside, LORENTZ 1310 from Catamarca, Argentina is not listed in HUNZIKER (1960), but is not expected to be in HUNZIKER’s list of types at CORD]. In this scenario, an earlier and heterotypic *Trichocline dealbata* of GRISEBACH (1879) would preempt the illegitimate (later homonym) name of HIERONYMUS (1882a, b), and the plant now known as *Trichocline dealbata* would be left without a legitimate name in *Trichocline*. Thankfully, as discussed below, this is not the case.

ICBN Art. 33.2 (GREUTER et al. 2000) allows GRISEBACH’s use of the epithet “*dealbata*” and his description, coupled with the taxonomic synonymy of CABRERA (1971) and ZARDINI (1975), for GRISEBACH’s *Trichocline dealbata* to be treated as a new combination based on *Chaetanthera dealbata* HOOK. & ARN. Specifically, ICBN Art.

33.2 in GREUTER et al. (2000) reads “If, for a presumed new combination, no reference to a basionym is given but the epithet of a previously and validly published name that applies to the same taxon is adopted, the new combination is validly published as such if, and only if, it would otherwise be validly published as the name of a new taxon.”

CABRERA (1971), ZARDINI (1975), and MARTICORENA & QUEZADA (1985) each recognized *Trichocline dealbata* “(HOOK. & ARN.) BENTH. & HOOK. f. ex GRISEB.” Additionally, CABRERA (1971) and ZARDINI (1975) each treated *Chaetanthera parviflora* PHIL. as a synonym of *Trichocline dealbata*. Neither CABRERA (1971) nor ZARDINI (1975) use the author citation of *Trichocline dealbata* as given by JACKSON (1895).

I agree with the treatments in CABRERA (1971) and ZARDINI (1975) for this species, and that the GRISEBACH name is a new combination based on *Chaetanthera dealbata* HOOK. & ARN. The citation of *Trichocline dealbata* in HIERONYMUS (1882a, b) is taken simply as that in a floristic treatment, and not as a nomenclatural innovation. The taxonomy and nomenclature of *Trichocline dealbata* follows.

Taxonomy and Nomenclature

Trichocline dealbata (HOOK. & ARN.) BENTH. & HOOK. f. ex GRISEB., Abh. Königl. Ges. Wiss. Göttingen 24: 215. 1879. Basionym: *Chaetanthera dealbata* HOOK. & ARN., Companion Bot. Mag. 1: 104. 1835. Lectotype (chosen from among syntypes by ZARDINI 1975): Argentina. Mendoza: Ascent to Los Pequeños, Andes, GILLIES s.n. (lectotype: K).

Chaetanthera parviflora PHIL., Anales Univ. Chile 27: 335. 1865, as “*parviflor.*” Type: Argentina. Mendoza. Cordillera entre Santiago i Mendoza, al otro lado del rio Tunuyán, prope la Guardia, Jan 1865, LANDBECK s.n. (holotype: SGO; isotype: SGO). SGO herbarium sheets #43758 & #64696 were cited by MUÑOZ (1960).

Gerbera pulvinata KUNTZE, Revis. Gen. Pl. 3(3): 149. 1898. *Trichocline cineraria* var. *pulvinata* (KUNTZE) HAUMAN, Anales Soc. Ci. Argent. 86: 337. 1918. Type: Argentina. Paso Cruz, Cordillera, 3000 m, KUNTZE 104 (holotype: NY!).

Scapose perennial herbs to ca. 8 cm tall; caudex and rhizome woody, simple or few-branched. *Leaves* simple, alternate, petiolate, to ca. 3.2 cm long, clustered at tips of caudex branches; petiole 0.6–1.2 cm long; blade spatulate to oblong, slightly ca. 5-pinnatilobed, 1.3–2 cm long, 0.3–0.6 cm wide, subcoriaceous, venation obscurely pinnate, base attenuate, apex obtuse, margins crenate, the adaxial surface lanuginose to glabrescent, the abaxial surface white-tomentose (whence the epithet), sometimes glandular-punctate, veins glabrescent. *Capitulescence* monocephalous on each of the few caudex branches; peduncles stout, ebracteate or occasionally 1-bracteate, 2–6 cm long, lanuginose to glabrescent; receptacle weakly foveolate. *Capitula* ca. 12

mm high, heterogamous, florets bilabiate with heteromorphic corollas; involucre hemispherical, to ca. 10×10 –17 mm; phyllaries 3–5-seriate, imbricate, gradated, 2–10 mm long, 1–2 mm wide, apically acute, outer ones deltoid grading to inner ones lanceolate. *Marginal florets* ca. 15, pistillate with staminodia, uniseriate; corolla bilabiate, strongly exerted from the involucre, white or yellow, tube 2–4 mm long, outer lip an expanded limb, elliptic-lanceolate, 8–12 mm long, 1.5–2 mm wide, abaxially tomentose, apically bi- or tridentate, teeth minute, inner lip bifid, segments filiform, coiled; staminodia ca. 2 mm long. *Central florets* many, bisexual, multiseriate; corolla shortly bilabiate; tube 4.5–7 mm long, outer lip and inner bifid lip ca. 1 mm long; anthers to ca. 5 mm long, filaments papillose; style branches ca. 0.5 mm long, dorsally papillose. *Cypselae* oblong-elliptic, shortly pubescent, to ca. 4 mm long; pappus of many scabrid bristles, often apically barbellate, to ca. 9 mm long.

Distribution and Ecology. *Trichocline dealbata* is known only from Argentina and Chile, where it occurs at elevations of 2000–3800 meters. The species grows in the high Andes west of the city of Mendoza, Argentina to the frontier with Chile (Provs. Mendoza and Neuquén, Argentina; O'Higgins, Chile). *Trichocline dealbata* flowers in the summer months, from about December until April. The plant is illustrated in CABRERA (1971: fig. 315) and ZARDINI (1975: fig. 29).

Acknowledgements

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Dauresia and *Mesogramma*: one new and one resurrected genus of the Asteraceae-Senecioneae from Southern Africa

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Abstract

Dauresia B. NORD. & PELSER is described as a new genus of the Asteraceae-Senecioneae. A single species is recognized here, viz., *D. alliariifolia* (O. HOFFM.) B. NORD. & PELSER, restricted to Namibia. It is clearly distinguished from the core of *Senecio* on basis of morphological and molecular evidence. In a phylogeny based on ITS sequence data, *Dauresia* appears basal to *Senecio* s. str. and the 'synotoid group', which includes i. a. *Synotis* (C. B. CLARKE) C. JEFFREY & Y. L. CHEN and *Cissampelopsis* (DC.) MIQ. In floral morphology the new genus has some 'tussilaginoïd' traits such as discoid white-flowered capitula, an ecalyculate involucre and a polarized endothecium.

Another genus is resurrected as *Mesogramma* DC. with the single species *M. apiifolium* DC. It is an annual herb known from Namibia, Angola, Botswana, and the South African provinces Transvaal, Orange Free State, and the Cape. Although previously placed in *Senecio*, its closest affinities are with the *Cineraria* group of Southern African genera, especially with *Bolandia* G. V. CRON (CRON et al., in press).

Introduction

The Senecioneae constitute one of the largest tribes of the family Asteraceae, with a worldwide distribution, 150 genera and about 3,500 species (NORDENSTAM, submitted). The phylogeny of the tribe is not yet well understood, but now intensely studied by

a team consisting of JOACHIM KADEREIT (Mainz), BERTIL NORDENSTAM (Stockholm), LINDA WATSON and PIETER PELSER (Oxford, Ohio), and ILSE BREITWIESER and STEVE WAGSTAFF (Landcare Research, New Zealand). Our ambition is to cover all of the genera and most of the sections within *Senecio*, analysing nuclear and plastid DNA sequence data.

This paper is concerned with two taxa previously placed in *Senecio* L., as *S. allariifolius* O. HOFFM. and *S. apiifolius* (DC.) BENTH. & HOOK.f. ex O. HOFFM.

The distribution of the former species is restricted to Namibia, where material was studied and collected by the senior author in 1963 and 1974 (cf. NORDENSTAM 1974). It gave the impression of a singular taxon, because of the stems with white bark, white-woolly leaf-axils and long-petiolate, cordate, subcarnose, and palmately veined leaves. The involucre consists of five bracts in spiral arrangement and lacks a calyculus. The capitula are homogamous and discoid and usually white-flowered. Both the morphological and molecular data unequivocally suggest the recognition of a new genus.

The second species, i.e. *S. apiifolius*, also occurs in Namibia, but has a wider distribution and extends into Angola, Botswana, and several of the South African provinces. It was already described as the genus *Mesogramma* DC. by DE CANDOLLE (1838) and was later synonymized with *Senecio* by BENTHAM & HOOKER (1873, also ex HOFFMANN 1892) and since then remained in oblivion.

Material and methods

Both taxa have been studied in the field, and additional herbarium material mainly in Stockholm (S) has been examined. Distribution data from herbarium specimens in PRE, S and WIND (abbreviations according to HOLMGREN et al. 1990) were used to construct distribution maps using the ArcView program (cf. Acknowledgements). For micro-morphological observations using light-microscopy, floral parts were boiled in water and subsequently dissected and mounted in HOYER'S solution.

As part of our ongoing effort to reconstruct the evolutionary history of tribe Senecioneae, the phylogenetic position of *Dauresia* and *Mesogramma* in Senecioneae was explored with maximum parsimony analyses of an ITS sequence data set composed of 516 species of 108 genera of Senecioneae. These analyses were carried out with the parsimony ratchet method as implemented in PAUPRat v.1.0 (SIKES & LEWIS 2001) to find islands of shortest trees. The shortest trees found with this analysis were subsequently used as starting trees for TBR branch swapping in a heuristic search in PAUP* 4.0b10 (SWOFFORD 2001). Bootstrap support (FELSENSTEIN 1985) was estimated with 5,000 bootstrap replicates using fast stepwise addition. The studies performed to examine the position of *Dauresia* and *Mesogramma* are

preliminary, and the results of our molecular phylogenetic analyses will be more elaborately presented and discussed elsewhere in due time.

1) *Dauresia* B. NORD. & PELSNER, gen. nov.

Herba perennis aliquando suffruticosa ramosa glabra (praeter axillas foliorum plerumque albolanatas), cortice albo striato. Folia alterna petiolata, lamina ovato-rotundata vel cordata ad reniformi subcarnosa margine dentata. Capitula corymbosa homogama discoidea. Involucrum ecalyculatum sed interdum bracteis exterioribus una vel duabus involucro aequilongis; involucri bractee quinque subuniseriatae ovatae. Flosculi numerosi hermaphroditi, corolla tubulosa profunde quinquelobata. Antherae basi caudatae; cellulae endothecii parietibus horizontalibus solum noduliferis; collum filamenti subcylindricum. Styli rami intus areis stigmaticis separatis, apice subtruncati papillati. Cypselae dense papilloso-hirsutae madefactae mucosae. Pappi setae pluriseriatae minute barbellatae albae persistentes.

Type: *D. alliarifolia* (O. HOFFM.) B. NORD. & PELSNER.

***Dauresia alliarifolia* (O. HOFFM.) B. NORD. & PELSNER, comb. nov.**

Basionym: *Senecio alliarifolius* O. HOFFM. ("*alliariefolius*"), Bot. Jahrb. 10: 280 (1888). - Type: MARLOTH 1480, in saxosis inter convalles "Huseb" et "Dariep", Damara-land, 450 m, Jun. 1886 (B holotype†, PRE isotype!). In HOFFMANN op. cit. cited as "Hereroland, Dariep, in saxosis desertis, alt. 400 m, flor. Jun. 1886".

Suffrutescent herb or halfshrub 0.3–1 m high, branching, glabrous (except for leaf-axils). Stems and branches striate, with white bark. Leaves alternate, long petiolate (petioles –5 cm long); leaf-blade entire, thickish and subcarnose, cordate, rounded or reniform, 4–5 cm long and wide, grossly to shallowly dentate, palmately veined; upper leaves gradually smaller and transcending into lanceolate bracts; leaf-axils white-woolly. Capitula several in umbellate corymbs, homogamous, discoid, ca. 1 cm long and wide. Involucral bracts 5, subuniseriate, ovate, 5–10 mm long, 2–3.5 mm wide, with ca. 5 resiniferous veins, glabrous, obtuse; calyculus absent but subinvolucral bracts often present, 1–2, equally long as the involucral bracts or longer, but narrower, linear-lanceolate to narrowly spatulate, 7–10 mm long and 1.5–2.5 mm broad. Receptacle convex, alveolate, glabrous. Florets ca. 25–35, bisexual; corolla 7–8 mm long, white or yellowish, tubular and gradually widening above, deeply 5-lobed; lobes lanceolate, 3–3.5 mm long, ca. 0.6 mm wide, usually without midvein but with distinct marginal veins, apex cucullate with minute papillae, otherwise glabrous. Anthers ca. 3 mm long, shortly caudate; filament collar very short, subcylindrical and only slightly enlarged towards the base; endothelial tissue strictly polarized with numerous short cells having thickenings only on horizontal walls; apical appendage narrowly ovate, acute or shortly acuminate. Style branches linear, ca. 1.5 mm long, stigmatic areas distinctly

separated and extending a little on the dorsal side, apex slightly obtuse with a short cone and with short papilliform sweeping-hairs arranged in a median tuft and two lateral shorter tufts. Cypselas subterete, 3–4 mm long, somewhat constricted at the apex, densely papillate-hirsute with appressed short obtuse trichomes, mucilaginous when soaked, with ca. 5 low and broad indistinct ribs; carpodium short, indistinct. Pappus bristles numerous, pluriseriate, persistent, white, densely barbellate with fine acute lateral teeth. – Fig. 1.

Distribution: Only known from Namibia and mostly in the northwestern and central districts (Map, Fig. 2). Some collections from southernmost Namibia deviate in certain respects including floret colour (\pm yellow) and seem to represent a second taxon of the genus (NORDENSTAM, in prep.)

Dauresia is not yet recorded outside Namibia, but may very well be found in southern Angola and the northwestern Cape Province (Little Namaqualand), South Africa, since the genus occurs rather close to the borders of these countries.

Selected specimens examined:

(district abbreviations as in MERXMÜLLER 1967)

NAMIBIA. **Distr. SW:** 61 km NE of Swakopmund on Usakos road, gravelly desert, 13.VII.1974, NORDENSTAM & LUNDGREN 777 (PRE, S); near the junction of Khan and Swakop Rivers, at 'Tsawichab', along Swakop, gorge from the Namib plain, II.1963, KERS 697 (S). **Distr. OM (Nb):** Brandberg, upper Tsisab Valley, on rocks, 6.V.1963, NORDENSTAM 2566 (S); Brandberg, SE side, c. 8 km S of Tsisabschlucht, 20.VI.1961, W. GIESS 3700 (S, WIND). **Distr. OM:** 2 miles S of Ugab River bridge on road from Welwitschia to Omaruru, red granite koppie, 2.IV.1963, DE WINTER & HARDY 8207 (PRE, S).

The generic name is derived from an indigenous name of the Brandberg, highest mountain of Namibia. The Damara name *Dâures* means 'Burning Mountain' (KINAHAN 2000).

HOFFMANN (1888) noted the singularity of this species and commented: "Species habitu peculiari, involucri squamis latis oligophyllo et pappi setis barbellatis insigne, qui characteres etiam in specie tasmanica, *S. centropappo*, observatur". Our preliminary results of phylogenetic studies using ITS sequence data indicate that the Australian *Senecio centropappus* F. MUELL. (syn. *Centropappus brunonis* HOOK. fil., *Brachyglottis brunonis* (HOOK. fil.) B. NORD.; NORDENSTAM 1978) is only distantly related. It groups with other Australian taxa in and around *Brachyglottis* J. R. FORST. & G. FORST. in a clade with a basal position in the 'tussilaginoïd' alliance.

However, the singularity of *Dauresia alliariifolia* observed by HOFFMANN remains undisputed. Some features were mentioned in the introduction and additional

comments should be made. The involucre has five broad phyllaries which are spirally arranged with basally partly overlapping margins. The arrangement can be called subuniseriate. Although here regarded as ecalyculate, the involucre often has one or two subtending bracts equalling the phyllaries in length. The homogamous and usually white-flowered ecalyculate capitula suggest a 'tussilaginoïd' affinity, as do additional floral characters. Thus the endothecial tissue of the anthers is strictly polarized as in most 'tussilaginoïd' genera, in contrast to the generally radial endothecium of 'senecioid' genera (NORDENSTAM 1978). Also, the filament collar is not distinctly balusterform, but subcylindrical and only slightly dilated basally. On the other hand, the styles have separated stigmatic areas as in many of the 'senecioid' genera. Tailed anthers are not acceptable in *Senecio* s. str. but are a general feature of the 'synotoid' group (JEFFREY 1992). This is a group of Central and East Asiatic genera (e.g., *Synotis* (C. B. CLARKE) C. JEFFREY & Y. L. CHEN, *Cissampelopsis* (DC.) MIQ.) and African-Malagassy-Mascarene genera (e.g., *Mikaniopsis* MILNE-REDH., *Humbertacalia* C. JEFFREY, *Hubertia* BORY) with truly 'senecioid' style and anther morphology including a radial endothecium. In spite of this, *Dauresia* may be allied to this group, with which it shares the caudate anthers and often palmately veined leaves.

It should be noted, however, that several 'tussilaginoïd' genera also have caudate anthers (BREMER 1994, NORDENSTAM, submitted) and not seldom palmately veined leaves. Morphologically *Dauresia* takes a somewhat intermediate position between the 'senecioid' and 'tussilaginoïd' groups and thus obliterates the distinction between the traditionally distinguished two subtribes Senecionineae and Tussilaginoïdineae. However, molecular data place the genus clearly in a 'senecioid' context (cf. below).

The pollen morphology of *Dauresia* has not yet been investigated, but the exine of the pollen grains appears to be unusually smooth with only minute spinulae. Further palynological studies are called for.

In conclusion, *Dauresia* is a monotypic (or bispecific) genus with an isolated position in the tribe. Although the ITS phylogeny indicates a basal position to the core of *Senecio*, some floral characters indicate an affinity to the 'tussilaginoïd' complex, which is otherwise not well represented in Africa.

2) *Mesogramma* DC.

Monotypic: *M. apiifolium* DC., Prodr. 6: 304 (1838); DC. in DELESSERT, Icones selectae 4, t. 58 (1838).

Syn.: *Senecio apiifolius* (DC.) BENTH. & HOOK. fil. ex O. HOFFM., Nat. Pflanzenfam. IV(5): 298 (1892), comb. non rite publ.; *S. apiifolius* (DC.) BENTH. & HOOK. fil. ex

MENDONCA, Contrib. Conhec. Fl. Angola, I. Compos. 119 (1943). – Type: Ufern des Gariép, DRÈGE 2823 (G-DC lectotype, selected here; S isolectotype).

Further syn.: *Senecio peculiaris* DINTER, Fedde, Repert. 30: 94 (1932). – Type: DINTER 4252, Garius bei Warmbad, im Rivier an dauernd feuchten Stellen des “Wasserfalles”, 30.XI.1922 (B†).

The genus *Mesogramma* DC. is here resurrected as a monotypic genus in the Asteraceae-Senecioneae on morphological and molecular (ITS) evidence. The single species *M. apiifolium* DC. is an annual herb distributed in Namibia, Angola, Botswana and several provinces of South Africa (Map, Fig. 4).

When DE CANDOLLE described *Mesogramma*, he included a single species, *M. apiifolium* DC. with a reference to the same species as “DC. in Delessert, Ic. Sel. 4 t. 58”. However, the *Icones selectae* were published in February 1838, whereas the *Prodromus* vol. 6 was published in early January 1838 (STAFLEU & COWAN 1976), and accordingly the latter publication has priority.

The genus *Mesogramma* was included in *Senecio* by BENTHAM & HOOKER (1873), although they did not make the actual combination. This was done later by HOFFMANN (1892), who referred to it as *S. apiifolius* (DC.) BENTH. & HOOK. fil. This has been generally accepted as the valid combination under *Senecio* and the species has been cited frequently as *S. apiifolius* (DC.) BENTH. & HOOK. fil. ex O. HOFFM. (e.g., MERXMÜLLER 1967, ARNOLD & DE WET 1993). However, the Index Kewensis refers to another combining author by citing *S. apiifolius* BENTH. & HOOK. fil. ex MENDONCA, Contrib. Conhec. Fl. Angola, I. Compos. 119 (1943).

The generic status of this taxon has not been considered again until now. Although DE CANDOLLE did not explicitly state the characters that distinguish *Mesogramma* from *Senecio*, it can be gathered from his generic description that he emphasized the venation of the involucre bracts and the disc floret corollas. This is also reflected in his choice of generic name (from Gr. *mesos*, middle, and *gramma*, line or letter). He placed the genus closest to *Cineraria* L. (cf. discussion below).

The famous explorer of South West African flora, KURT DINTER, encountered the species and found it so special that he described it as *Senecio peculiaris* DINTER (1932) without realizing its identity with *S. apiifolius*. DINTER’s choice of epithet is not explained, but probably he was inspired by the strongly resiniferous phyllaries and the black papilla-lined cypselas, which he describes in some detail.

Description:

Annual glabrous erect herb, branching from the base. Leaves cauline, alternate, petiolate (petiole –3 cm long) to sessile (esp. upper leaves), leaf-blade ovate-lanceolate, grossly dentate or pinnatilobate with 5–6 lobes on each side, apically

mucronate, 3–7 cm long, 1–3 cm wide; upper leaves gradually smaller. Peduncles 3–8 cm long, nude except for 1–2 subulate bracts. Capitula 1–2 or up to 12 and laxly corymbose. Involucre calyculate; calyculus bracts 2–5, subulate, ca. 1 mm long. Involucral bracts 10–21, almost biseriata, lanceolate, 4–6 mm long, 0.8–1 mm wide, green with scarious margins, midribbed with a thin blackish resin vein and with two lateral blackish resin ducts; lateral resin stripes of inner bracts broad and glandular-dotted. Capitula radiate, yellow-flowered. Receptacle slightly convex, glabrous, minutely foveolate. Ray-florets 8–13, female, fertile; style bilobed; tube cylindrical, ca. 2 mm long; lamina oblong, 4–5 mm long, 1.5 mm wide, 4-veined. Disc-florets numerous (ca. 30–70), hermaphroditic. Corolla tubular, gradually widening above, 5-lobed, distinctly 5-veined with black veins from corolla tips down to the base of the tube; corolla lobes triangular-ovate, 0.5–0.7 mm long, with thin lateral veins in addition to the dark midvein. Anthers sagittate or minutely caudate; apical appendage narrowly ovate, obtuse; endothelial cells elongate, radial (but those of dehiscence zone shorter and polarized); filament collar distinctly balusterform. Style with dark resin vein branching into the style branches; base swollen, placed on a short stylopodium; style branches linear-oblong with separated stigmatic areas, apically truncate with rather long sweeping-hairs. Cypselas subtriquetrous or somewhat compressed, constricted apically and basally, ca. 1 mm long, black, with 3 lines of white papilliform obtuse duplex hairs, mucilaginous when soaked, and apically and basally with a crown of longer hairs with rounded tips; carpodium distinct with 4–6 rows of sclerified cells. Pappus bristles numerous (ca. 20), uniseriate, basally connate, ca. 3 mm long, white, barbellate with acute teeth, caducous. – Fig. 3.

Selected specimens examined:

(district abbreviations as in MERXMÜLLER 1967)

NAMIBIA. **Distr. GR:** Marienbrunn, 3.VIII.1974, O. H. VOLK 01370 (M, S), Farm Gaiikos (GR 729), 6.V.1974, O. H. VOLK 01106 (M, S). **Distr. OM:** Farm Etamba, NW corner of Erongo Mountains, 19.VII.1974, NORDENSTAM & LUNDGREN 925 (S, WIND). **Distr. KAR:** Ameib, S of Erongo, E of ‘Bull Party’, 11.VII.1974, NORDENSTAM & LUNDGREN 718 (PRE, S). **Distr. LUS:** At the ferry E of Sendlingsdrift, 21.IX.1972, MERXMÜLLER & GIESS 28649 (M, S). **Distr. BET:** Farm Daus (BET 27), 28.VI.1974, W. GIESS 13413 (S, WIND). **Distr. WAR:** Ai-Ais, Fish River riverbed, 26.VI.1974, NORDENSTAM & LUNDGREN 136 (S, WIND).

SOUTH AFRICA, CAPE. Kimberley, Rooivlakte, VIII.1936, M. WILMAN 3601 (PRE, S); L. Namaqualand, Gariiep, “*Mesogramma apifolium* DC.”, DRÈGE (S).

Some unusual morphological characteristics of *Mesogramma* were already noted by earlier authors. These include the arrangement and morphology of the involucral bracts, which are almost biseriata, with the inner ones partly overlapped by the margins of the outer ones. The inner phyllaries in *Mesogramma* are morphologically

different from the outer ones, most noticeably by the very distinct black resin ducts.

The cypselas of *Mesogramma* are also unusual in the tribe, being subtriquetrous and completely black, and provided with three lines of short white papilliform duplex hairs. In addition, the cypselas are both apically and basally constricted and provided with a crown or ring of longer papilliform trichomes.

The closest relative of *Mesogramma* is without doubt *Bolandia* G. V. CRON, a new genus of two species previously placed in *Cineraria* L. (CRON et al., in press). Characters in common between the two genera include the herbaceous habit, the presence of resin ducts e.g. in the involucre bracts and disc-floret corollas, and the black cypselas with short papilliform white duplex hairs becoming mucilaginous when wet.

Mesogramma differs from *Bolandia* by the absence of tomentum, the calyculate involucre, the branching (non-scapose) flowering stems, the glabrous (non-glandular) ray-floret tubes, the disc-floret styles lacking a central tuft of papillae, and the homomorphic cypselas with three lines of hairs. The distribution ranges of the two genera are vicariant, or allopatric, *Bolandia* occurring disjunctly in the Western and Eastern Cape and Lesotho, and *Mesogramma* having a larger range further north, mainly in the Orange Free State, Botswana and Namibia.

Molecular data

COLEMAN et al. (2003) included both *D. alliariifolia* and *M. apiifolium* (as *S. alliariifolius* and *S. apiifolius*, respectively) in their phylogenetic studies in *Senecio* sect. *Senecio* using ITS sequence data. In these analyses, both species formed a clade together with *Cineraria platycarpa* (misidentified as *Stilpnogyne bellidioides*, G. V. CRON, pers. comm.). This clade was found sister to a clade composed of *Senecio* species, *Crassocephalum crepidioides*, and *Erechtites hieraciifolia*. These findings indicated an isolated phylogenetic position of *S. apiifolius* and *S. alliariifolius* relative to other species of *Senecio* (Fig. 5).

Ongoing phylogenetic studies of a much larger ITS sequence data set (presently composed of 516 species of 108 genera of Senecioneae; PELSER et al., unpublished) confirm that both species are only distantly related to *Senecio* and to each other. In a preliminary maximum parsimony phylogeny of Senecioneae, *Dauresia* is placed sister to a clade composed of *Aetheolaena*, *Arrhenechthites*, *Cissampelopsis*, *Crassocephalum*, *Culcitium*, *Erechtites*, *Hasteola*, *Iocenes*, *Lasiocephalus*, *Robinsonia*, *Senecio* s.s., and *Synotis*. Although bootstrap support for this phylogenetic position of *Dauresia* is very low (< 50%), there is strong bootstrap support (99%) for the hypothesis that the genera *Aetheolaena*, *Culcitium*, *Hasteola*, *Iocenes*, *Lasiocephalus*, and *Robinsonia* are more closely related to *Senecio* s.s. than

Dauresia is (cf. Fig. 5).

In close agreement with the morphological evidence discussed above, *Mesogramma* is found most closely related to the new genus *Bolandia* (99% bootstrap support). This clade is in turn closely related to *Cineraria*, although this relationship is only weakly supported (56%).

Although these preliminary results need to be confirmed with more detailed analyses using both nuclear and plastid DNA sequence data for a larger taxon sampling, *S. apiifolius* and *S. allariifolius* are clearly quite distantly related to *Senecio* s.s. and have to be excluded from this genus to approach a monophyletic *Senecio* concept.

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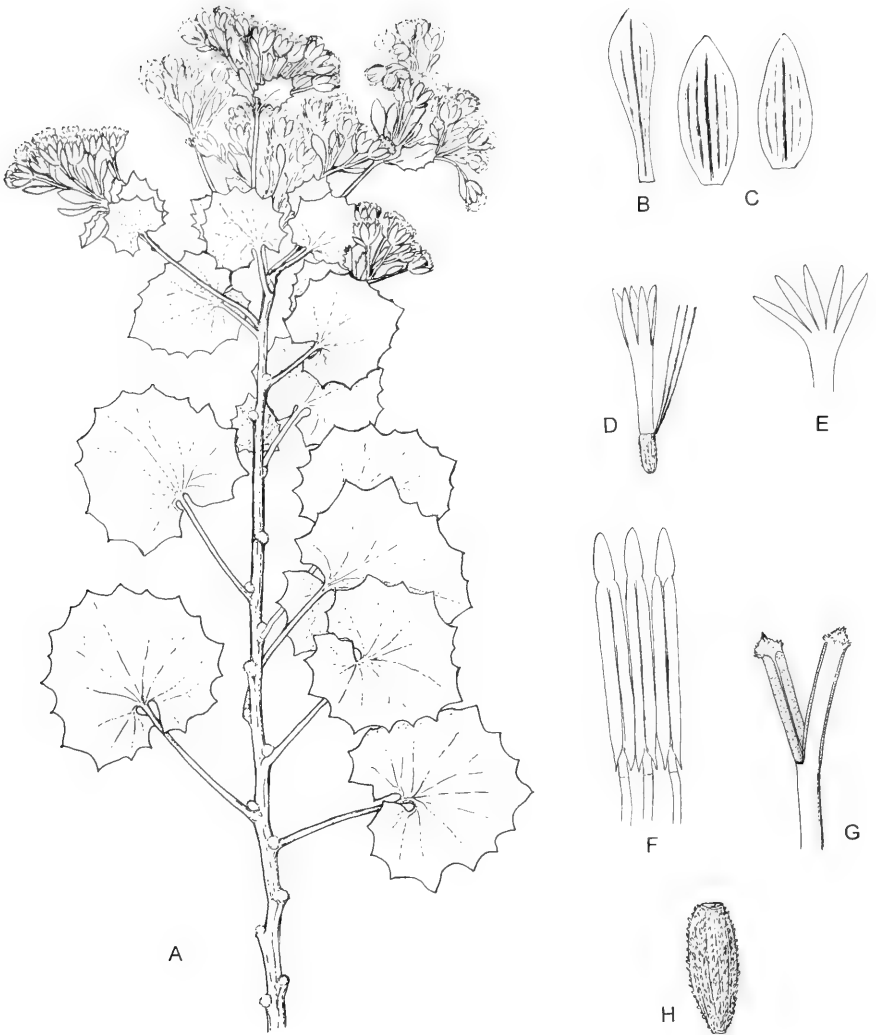
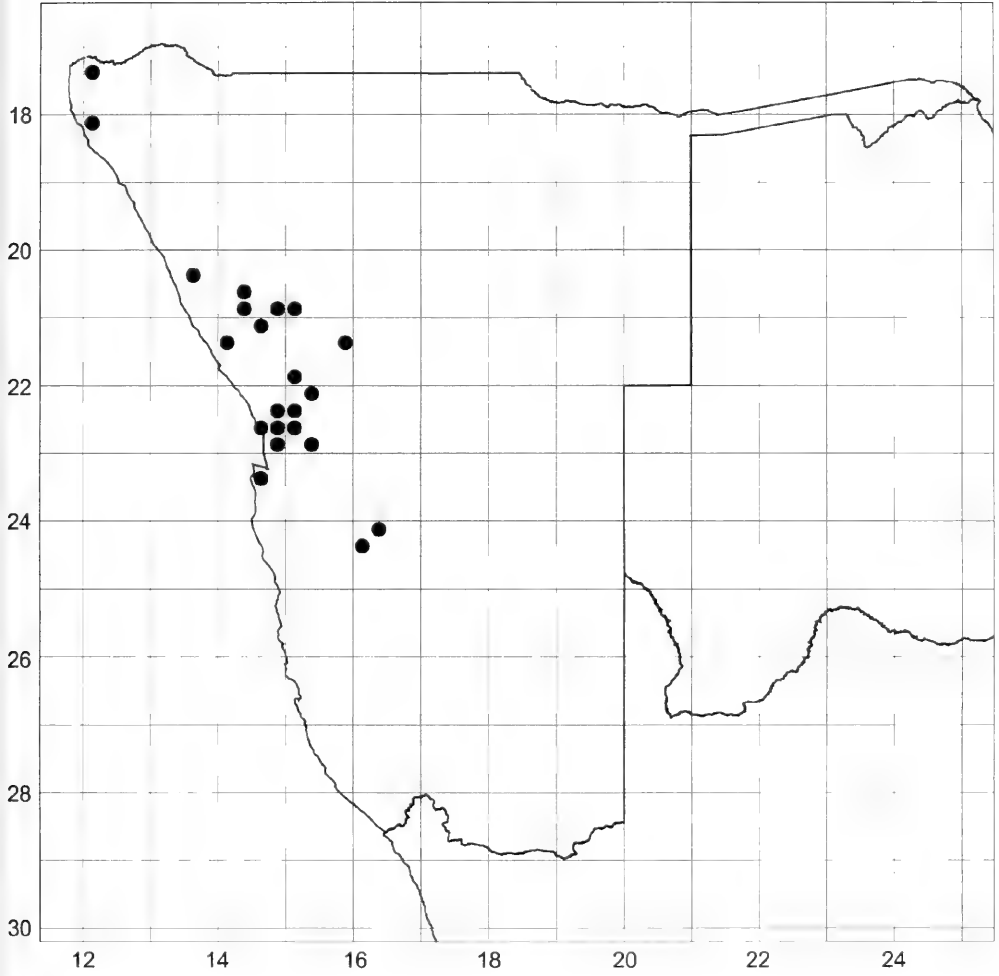


Fig. 1. *Dauresia alliariifolia* (O. Hoffm.) B. Nord. & Pelsner.

A Habit, $\times \frac{1}{2}$. B Subinvolucral bract, $\times 2.5$. C Outer and inner involucral bract, $\times 2.5$. D Floret, $\times 2.5$. E Corolla laid out, $\times 5$. F Anthers, $\times 10$. G Style branches, $\times 10$. H Cypsel, $\times 5$. A–G GIES 3700 (S); H KERS 697 (S). Del. B. NORDENSTAM.



Dauresia alliarifolia

Fig. 2. Distribution of *Dauresia alliarifolia* (O. HOFFM.) B. NORD. & PELSER.

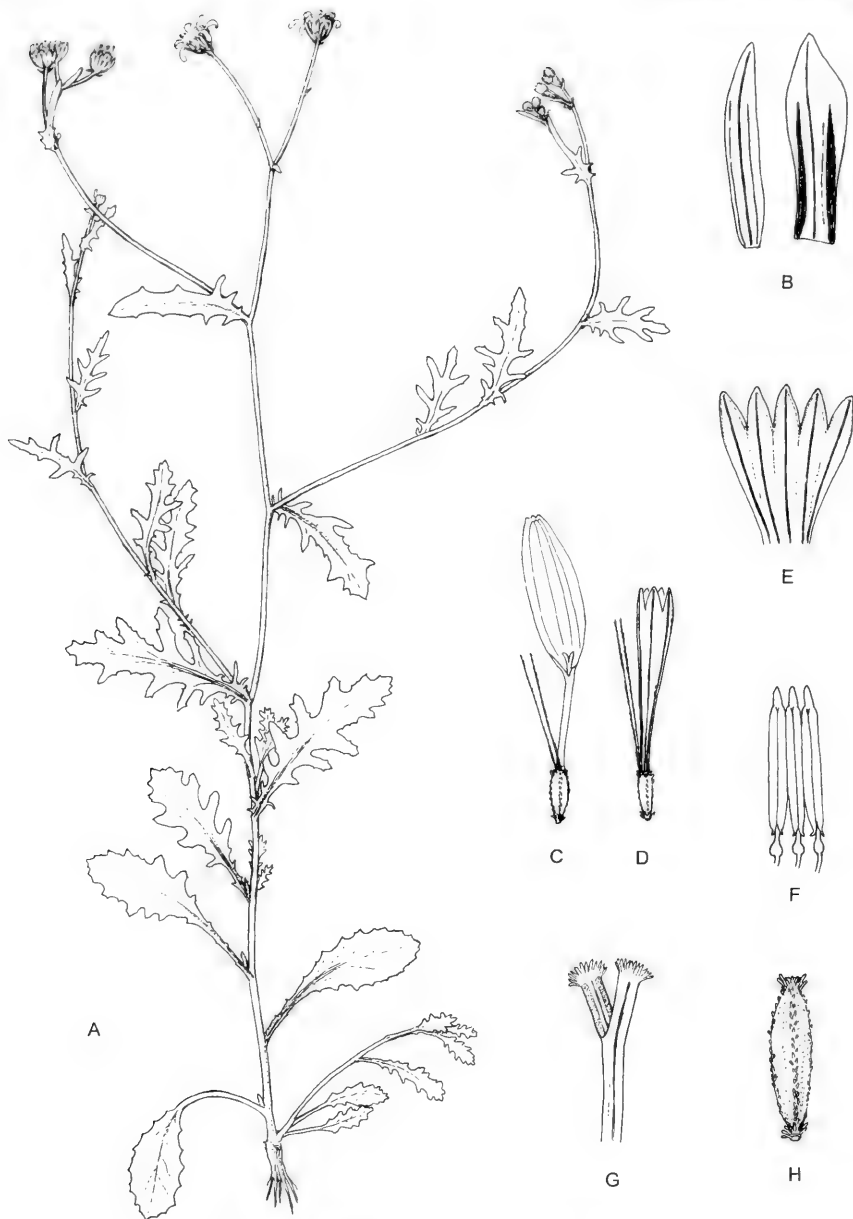
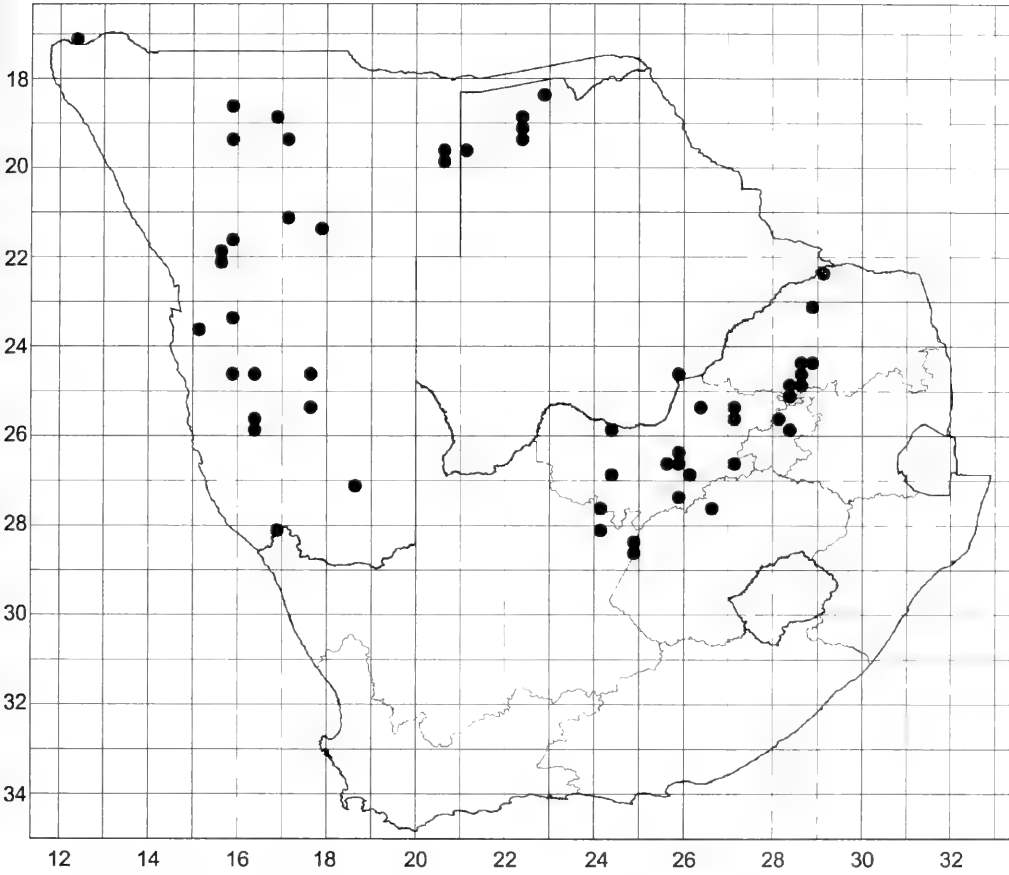


Fig. 3. *Mesogramma apiifolium* DC.

A Habit, $\times \frac{1}{2}$. B Outer and inner involucral bract, $\times 5$. C Ray-floret, $\times 5$. D Disc-floret, $\times 5$. E Corolla of disc-floret laid out, $\times 10$. F Anthers, $\times 10$. G Style branches of disc-floret, $\times 20$. H Cypsela of ray-floret, $\times 20$. NORDENSTAM 925 (S). Del. B. NORDENSTAM.



Senecio apiifolius (DC.) Benth. & Hook.f. ex O.Hoffm.

Fig. 4. Distribution of *Mesogramma apiifolium* DC.

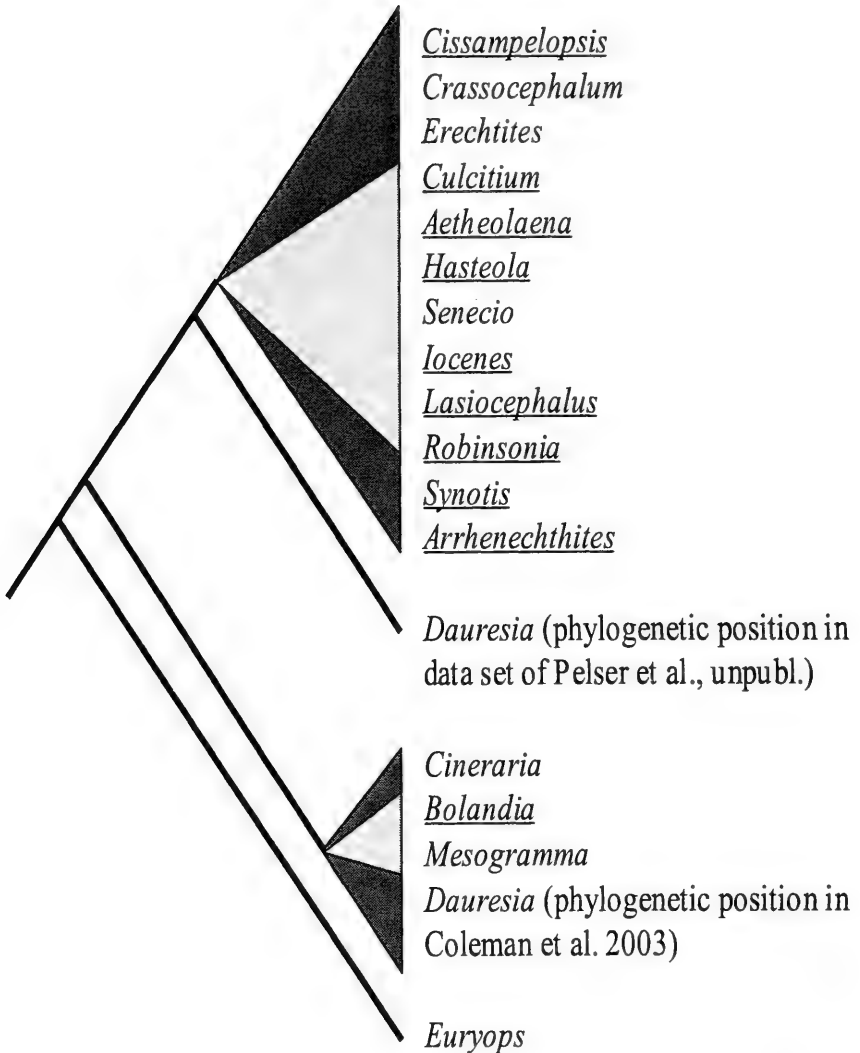


Fig. 5. Schematic representation of the phylogenetic position of *Dauresia* and *Mesogramma* in Senecioneae, redrawn from COLEMAN et al. 2003 and supplemented with select taxa from the ITS data set of PELSER et al. (unpubl.). Genera that are underlined were not included in COLEMAN et al. 2003. Triangles represent clades within which no further relationships are shown. The light-grey clades fall within the dark-grey clades.

Ecology of Cuban Asteraceae

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Abstract

An ecological assessment of Cuban Asteraceae (two subfamilies, 13 tribes, 117 genera, 400 species) is made. Alien synanthropic species and man-made ecotopes were not taken into account except anthropic savannas which are readily colonized by native species. Native ecotopes and their climatic and vegetation characteristics were determined and an inventory of native species (in %) in those habitats was carried out. Evolution led to dominance of edaphic specialists, species from dry ecotopes that seldom exhibit strong xerophytic traits, aquatic and subaquatic taxa having no particular adaptations to their habitats and in general lowland and premontane taxa (altitude \leq 1000 m) thriving mostly below 800-1200 m a.s.l.

Keywords: Asteraceae, ecology, Cuba

Introduction

Ecology plays a leading role in Cuban Asteraceae. Two trends are noticeable: alien taxa prefer man-made ecotopes where some native species can also be found, whereas native species are almost always restricted to primary and open, edaphically or geographically specialized ecotopes where alien species can not establish themselves. Due to this behaviour, which is also common in many other families of Cuban angiosperms, Asteraceae is divided in two groups: 1) native and 2) alien but naturalized in synanthropic ecotopes. Their taxonomy has already been published (ALAIN 1962, 1969) but little is known about their ecology, however with scattered observations in current bibliography.

Assuming that many genera of Asteraceae prefer open spaces, avoid closed canopy forests (CRONQUIST 1994, BREMER 1994) and are usually not found in wet, humid or aquatic habitats, and also assuming that the current ecology of a genus reflects at least in part its original ecology, the main objective of this paper is to assess the ecology of the Cuban genera of Asteraceae in order to elucidate their relations with Cuban open spaces, closed canopy forests and wet and/or humid ecotopes.

Materials and Methods

The Cuban species of Asteraceae were studied in the field and laboratory for 25 years. Native and alien species and their ecotopes (vegetation units) were determined. After this initial stage, several specialized habitats related to native Asteraceae became evident and were placed in 7 groups (Table 1). Percentage of species, genera and tribes in those ecotopes were recorded.

Data concerning vegetation units included in these 7 groups and their rainfall, temperature, soil and current geology were taken from CAPOTE & BERAZAÍN (1984) and Instituto de Geodesia y Cartografía (1978) and are presented in Table 2. The most difficult forests to define from an altitudinal standpoint were the gallery forests which run through all vegetation units from sea level to 1800 m and the pine forest which has a similar behaviour.

Anthropic and seminatural savannas are accepted in the system of classification of Cuban vegetation units (CAPOTE & BERAZAÍN 1984) but natural savannas were not considered. However, white sand (quartz) savannas in western and central Cuba seem to be natural depending on the quotient quartz sand/clay. Being a subject of controversy among Cuban scientists, white sand savannas should be placed in the "seminatural savannas" for the time being, though they are referred to as "white sand savannas" in the graphics.

The general scope was adapted from YOUNG (1995). Corrections and adjustments in taxonomy were taken from ALAIN (1962), and LIOGIER (1996, 1997) for genera and species, BREMER (1994) for genera, tribes and subfamilies, and KING & ROBINSON (1987) for the tribe Eupatorieae. Data on distribution are from ALAIN (1958, 1962, 1969), LIOGIER (1996, 1997), ADAMS (1972), ACEVEDO-RODRÍGUEZ (1996) and CORRELL & CORRELL (1982). Morphological terms are based on FONT QUER (1973).

Four vegetation units are defined as the orophilous series: humid evergreen forest + mountain rainforest + cloud forest + mountain scrub. These four units are always found in that order from an altitude of 400–600 m (lower limit) to 1974 m (upper limit). Though there is a switch at 800–1000 m from tropical lowland climate to "cool" or "air-conditioned" climate (19–21° C and even cooler in the cloud forest and montane scrub) involving also a change in floristic composition all these vegetation units have a closed canopy, and since they are avoided by most Cuban Asteraceae, they can be grouped in a single but not homogeneous unit. However, a few genera or small groups of species within a genus are restricted to these ecotopes.

Altitude, temperature and rainfall are also approximated. Many factors not always well understood have a definite influence on these variables, e. g., there is a cool climate in the Escambray mountains (central Cuba) at 600–800 m even in July. However, altitude corresponds to humid evergreen forests or the lower limit of mountain rainforest and

humid evergreen forest and mountain rainforest are not cool, at least in Cuba. Ecotones, exposition and slope add confusion to the scheme.

Low altitude is here taken as 0-600 m, medium altitude as 600-1200m and high altitude (true montane ecotopes) as 1200-2000 m. This agrees with BURGER (1995) and WEBSTER (1995).

Results and Discussion

Ecology and distribution of alien taxa

The Cuban taxa of Asteraceae comprise 2 subfamilies, 13 tribes, 117 genera and 400 species. Three tribes were introduced: Anthemideae (*Achillea*, *Leucanthemum*, *Matricaria*), Cardueae (*Cirsium*), and Lactuceae (*Launaea*, *Sonchus*, *Taraxacum*, *Youngia*). In addition, 36 genera and 76 species were introduced (30 % and 19 % of all extant genera and species respectively) (Table 3).

Alien species are now scattered all over the Cuban archipelago. These exotic taxa have become naturalized and are found in the following anthropic vegetation units covering 3/4 of the Cuban territory:

- 1) Ruderal ecotopes.
- 2) Cultivated fields.
- 3) Open secondary forests, secondary scrubs, anthropic savannas and grasslands.
- 4) Highways, roadsides, forest gaps and paths traversing across primary vegetation units, but the synanthropic species are always near access routes, never inside the primary vegetation units.

Ecology and distribution of native taxa

Subfamily 1. Cichorioideae

Tribe 1. Mutisieae

4 genera (*Chaptalia*, *Gochnatia*, *Proustia*, *Trixis*).

58 % of the species of *Gochnatia* (Fig. 1) thrive on serpentine barrens and 42 % on karstic limestone. Therefore, extreme ecotopes play a very important role. Mesophytic and humid ecotopes are absent. The genus is restricted to the left side of the graphic (Fig. 1). Pioneer species are almost absent and there are no weedy species.

The Cuban species of *Gochnatia* are found all along the main island (Cuba), but never in the keys and smaller islands such as Isla de la Juventud, and always in scattered and isolated "ecological islands". They thrive on karstic limestone rocks, either bare or covered by open and low vegetation, or on serpentine barrens or soils derived from

serpentine. They are edaphic specialists having xerophytic and heliophilous traits and avoid closed canopy forests. They prefer low to medium altitudes (from 0-1225 m) though most species are found below 1000 m. It could be assumed that low altitudes in high latitudes (Cuba) are a compensation to high altitudes in low latitudes (Andes).

Chaptalia, *Proustia*, *Trixis* (Fig. 2). 50 % in the orophilous series, 27 % on serpentine, 22 % on karstic limestone. Mesophytic ecotopes as important as dry and arid habitats. An increasing trend from the left side to the center of the graphic. There are no pioneer species and a single weedy species (*Chaptalia dentata*).

Concerning altitude, the rest of Mutisieae behaves in a similar way to *Gochmatia* except *Chaptalia* which is a successful colonizer of bare limestone crevices and rocks in the orophilous series (up to 1976 m, the highest altitude in the tribe). Pine forest soils (quartz, serpentine) are also preferred by *Chaptalia*. As a rule, edaphic specialization prevails in the Cuban species of this tribe. *Proustia* and *Trixis* thrive in open shrubby forests on karstic limestone but avoid serpentine rocks and soils. Unlike the shrubs (*Gochmatia*) and climbing shrubs (*Proustia*, *Trixis*), the rosulate herb type (*Chaptalia*) has colonized mesophytic and even humid ecotopes. There are no endemic genera in the tribe and speciation has taken place in 29 endemic species of *Gochmatia* (20) and *Chaptalia* (9).

Tribe 2. Vernonieae

7 genera (*Ekmania*, *Elephantopus*, *Lachnorhiza*, *Pacourina*, *Struchium*, *Trichospira*, *Vernonia*) (Fig. 3). 36 % in the orophilous series, 35 % on serpentine, 17 % on limestone and 6 % on white sand savannas and swampy ecotopes respectively. A trend towards the center and left side of the graphic, but wet ecotopes begin to appear (though in a small percentage). Some pioneer species and a single weedy species (*Elephantopus scaber*).

Vernonia is a large, widely distributed paraphyletic genus, quite diversified in Cuba (44 species) and divided by ALAIN (1962) in three groups with regard to synflorescence: 1) scorpioid cymes, 2) glomerules and 3) panicles. There are three aquatic or subaquatic herb species from South America: *Pacourina* and *Trichospira*, both perennials, and *Struchium* (annual). Two endemic and monotypic genera thriving in opposite ecotopes: *Ekmania*, a shrub that occurs on the summit and cliffs of a large limestone hillock (Yunque de Baracoa, in northeastern Cuba, an "ecological island" surrounded by serpentines) and *Lachnorhiza*, a scapose herb from periodically flooded white sand savannas and also from serpentine barrens in western and central Cuba; the two genera are quite unrelated. *Elephantopus* is somewhat contradictory since it has two groups, also quite unrelated: pappus of scales, white sand savannas, endemic species, versus pappus of bristles (a little if at all enlarged at the base), forests at medium to montane altitudes, species widely distributed in the tropics and subtropics.

The tribe is composed of edaphic specialists, xerophytes (*Ekmania*, *Elephantopus*) and premontane species, rarely montane. Aquatic and subaquatic taxa in *Vernonieae* do not exhibit extreme adaptations to their ecotopes, and in addition they brought their own pattern of evolution from South America.

48 species are endemic: *Vernonia* (44), *Ekmania* (1), *Elephantopus* (2), *Lachnorhiza* (1).

Tribe 3. Liabeae

A single genus (*Liabum*) (Fig. 4). All species are in the orophilous series (100 %). Pioneer or weedy species absent.

Four montane species from 500 m in lowland rainforest on serpentine under heavy rainfall to 1976 m in mountain rainforest, cloud forest and montane scrub. The species are strongly related to those of Hispaniola and there is a single endemic species. A revision of the genus is needed.

Subfamily 2. Asteroideae

Tribe 4. Plucheeae

6 genera (*Epaltes*, *Pluchea*, *Pseudoconyza*, *Pterocaulon*, *Rhodogeron*, *Sachsia*). (Fig. 5). 27 % in swampy ecotopes, 27 % in anthropic savannas (a secondary ecotope!), 18 % on serpentine, 18 % on white sand savannas and 9 % on limestone. Oriented towards the centre and right part of the graphic. Some relatively abundant, weedy species (e. g., *Pluchea carolinensis*, *Pseudoconyza lyrata*).

The species of this tribe are partial to periodically or permanently flooded lowlands, e. g., the genus *Pluchea* includes two semi-aquatic species; *Sachsia* thrives under grasses and sedges in wet grasslands; *Rhodogeron* occurs in river banks on serpentine, whereas *Pluchea carolinensis*, *Pseudoconyza lyrata* and *Pterocaulon* (2 species) prefer sandy and rocky coasts, anthropic savannas, ruderal ecotopes and swampy areas under man's impact.

As a rule, they are edaphic specialists (*Epaltes*, *Pluchea*, *Pterocaulon*, *Rhodogeron*, *Sachsia*) and aquatic or subaquatic species (*Pluchea*, *Pseudoconyza*): wet white sand savannas (*Epaltes*, *Pluchea*), anthropic savannas (a secondary ecotope!), periodically flooded areas near rivers and brooks on serpentine (*Rhodogeron*, *Sachsia*) and swamps on muddy, chalky soils (*Pseudoconyza*). However, there is no specialization in the aquatic taxa. *Rhodogeron* is the only endemic genus but there are three endemic species in *Epaltes* (1), *Sachsia* (1) and *Rhodogeron* (1).

Tribe 5. Gnaphalieae

A single genus (*Gnaphalium*) (Fig. 6). Oriented towards the mesophytic and humid part of the graphic. 50 % in the orophilous series, 33 % in swampy ecotopes and 17 %

in anthropic savannas (a secondary ecotope!). Apparently, wet soils seem to be a compensation for lack of high altitudes.

They occur in the orophilous series, swamps, river and brook bank grasslands and anthropic savannas, and the strong colonization of montane ecotopes is a sharp contrast with Plucheeae, but the species are as hard to find as *Pterocaulon* (Plucheeae) and therefore difficult to observe and define. Apparently, no edaphic specialization exists though there is a trend towards montane and wet habitats. Endemic species are lacking.

Tribe 6. Astereae

6 genera (*Aster*, *Baccharis*, *Egletes*, *Erigeron*, *Gundlachia*, *Solidago*) (Fig. 7). 40 % in swamps, 21 % in the orophilous series, 21 % on serpentine, 9 % on limestone, 7 % on wet white sand savannas and 2 % in mangrove forest. One pioneer species in the genus *Baccharis* and some unimportant weedy species in humid or wet ecotopes having their origin in North America (*Aster*).

Colonization of swamps and wet grasslands has been strong (*Aster*, *Baccharis*, *Solidago*). Serpentine soils and the orophilous series display similar values indicating that adaptation has been equally successful in both ecotopes. *Baccharis* and *Gundlachia* have even invaded the mangrove forest as edaphic specialists, but as a rule mangrove taxa are scarce. Endemic genera are lacking though there are 20 endemic species: *Aster* (3), *Baccharis* (6), *Erigeron* (7), *Gundlachia* (4).

Tribe 7. Senecioneae

3 genera (*Olfeldtia*, *Pentacalia* s. l., *Shafera*). (Fig. 8). A strong switch towards the dry part of the graphic. 68 % on serpentine, 26 % in the orophilous series and only 6 % on limestone. Pioneer and weedy species are lacking though *Shafera* colonizes road banks.

Edaphic specialists in pine forest and scrub barrens on serpentine (most species of *Pentacalia* s. l. and *Shafera*), in montane rainforest on serpentine (a few species of *Pentacalia* s. l. and *Oldfeltia polyphlebia*), and few species on rocky (karstic) limestone (e. g., *Pentacalia almironcillo*, *Pentacalia trineura*). Xerophytic traits, e. g., a dense tomentum, are found in *Shafera* and the tomentose species of *Pentacalia* s. l.

The taxonomy of the Cuban species of *Senecio* is being revised in Sweden (B. NORDENSTAM), and current views claim that the only Cuban species of *Senecio* s. s. is *S. vulgaris*, a European weed that does not persist under Cuban climatic conditions. So far, the quite large number (20 species) of the Cuban taxa of *Senecio* s. l. have been segregated in 3 genera (*Oldfeltia*, *Pentacalia*, *Senecio*) but splitting is sure to continue in the near future. *Shafera* (1 species) and *Oldfeltia* (1) are monotypic and

endemic whereas 18 endemic species provisionally belong to *Pentacalia* s. l.

Tribe 8. Helenieae

7 genera (*Flaveria*, *Harnackia*, *Helenium*, *Lebetina*, *Lescaillea*, *Pectis*, *Thymopsis*) (Fig. 9). Strongly oriented towards the dry part of the graphic. 37 % on limestone, 37 % on serpentine, 21 % on white sand savannas and 5 % in swampy ecotopes. The Cuban species of *Pectis* tend to be weedy.

This tribe is partial to dry ecotopes and therefore, rich in xerophytic species though xerophytic traits are never very strong, a typical feature of Cuban Asteraceae. Evolution of endemic and monotypic genera (*Harnackia*, *Lescaillea*) took place in pine forest on serpentine at an altitude from 300 to 1000 m. There is a strong trend towards rocky limestone or gravelly sand ecotopes in *Flaveria*, *Lebetina* and *Pectis*. The genus *Pectis* has undergone a strong speciation (6 endemic species out of 15) in Cuba. The remaining endemic species are found in *Lebetina* (1), *Helenium* (1), and *Harnackia* (1).

Tribe 9. Heliantheae

21 genera (*Acmella*, *Ambrosia*, *Ancistrophora*, *Bidens*, *Borrchia*, *Clibadium*, *Enydra*, *Heptanthus*, *Iva*, *Koehneola*, *Lantanopsis*, *Melanthera*, *Neurolaena*, *Pinillosia*, *Salmea*, *Sphagneticola*, *Spilanthus*, *Tetraperone*, *Verbesina*, *Viguiera*, *Wedelia*) (Fig. 10). A slight switch towards the dry part of the graphic. 28 % on limestone, 19 % on serpentine and 10 % on white sand savannas. Mesophytic and wet ecotopes have 24 % in the orophilous series, 15 % on swampy soils and only 1 % and 3 % in anthropic savannas and mangrove forest respectively. Many species are pioneers and weedy and in general there is a strong trend towards weedy behavior.

The Cuban species of Heliantheae occur in all ecotopes, though dry habitats (57 %) at low and medium altitudes are better represented, connecting Heliantheae and Helenieae, which from a phylogeny standpoint are quite related. *Bidens reptans*, a climber, reaches an altitude of 1976 m, something that few Cuban Asteraceae have been able to do. Evolution towards endemic genera took place in pine forest on serpentine and to a lesser extent in white sand savannas, e. g., *Ancistrophora*, *Heptanthus* and *Koehneola* thrive on serpentine whereas *Tetraperone* is the only endemic genus on white sand savannas. Endemic species are 19: *Acmella* (4), *Ancistrophora* (1), *Heptanthus* (6), *Koehneola* (1), *Salmea* (3), *Tetraperone* (1), *Verbesina* (1), *Wedelia* (2).

Tribe 10. Eupatorieae

19 genera (*Adenostemma*, *Ageratina*, *Ageratum*, *Antillia*, *Brickellia*, *Chromolaena*, *Ciceronia*, *Conoclinium*, *Critonia*, *Eupatorium*, *Grisebachianthus*, *Hebeclinium*, *Isocarpha*, *Koanophyllon*, *Lepidesmia*, *Mikania*, *Phania*, *Spaniopappus*,

Urbananthus) (Fig. 11). The orophilous series prevails (51 %) followed by serpentine (25 %), limestone (18 %), swampy ecotopes (5 %) and white sand savannas (1 %), a sharp contrast with Helenieae and Heliantheae. The genera segregated from *Eupatorium* s. l. (*Ageratina*, *Chromolaena*, *Hebeclinium*, *Koanophyllon*) tend to invade anthropic savannas and secondary vegetation units. *Conoclinium* is a swamp dweller.

Speciation took place in the orophilous series and also on inland cliffs, sierras, karstic hillocks, rocky limestone coasts and serpentine soils (mainly in pine forest and scrub barrens). Edaphic specialists (with xeric adaptations in *Lepidesmia*) and premontane or montane species abound. *Koanophyllon* and *Mikania* reach an altitude of 1976 m though most species thrive at low or medium altitudes. *Mikania* and *Adenostemma* are two of the few shade-loving genera found in Cuban Asteraceae.

Antillia (1 sp.), *Ciceronia* (1), *Grisebachianthus* (8) and *Spaniopappus* (5) are endemic genera whereas *Urbananthus* (1) has a related species in Hispaniola. Endemic species are 47.

Conclusions

Thirteen tribes of Asteraceae have been recorded in Cuba but three of these are alien (Anthemideae, Cardueae and Lactuceae). Therefore, there are ten native tribes although they have several alien taxa, in all 36 genera and 76 species. These are mostly weeds introduced by man with or without intention.

Alien taxa are found in four anthropic vegetation units: 1) Ruderal ecotopes, 2) Cultivated fields, 3) Open secondary forests, secondary scrubs, anthropic savannas and grasslands, and 4) Highways, roadsides, forest gaps and paths traversing across primary vegetation units, but the synanthropic species are always near access routes, never inside the primary vegetation units.

The native taxa of Asteraceae are 'fragmentary' with ecological, geographical or even phylogenetic gaps, being restricted to ecological islands that usually date back to the Late Paleogene or Early Neogene (karstic limestone, serpentine barrens), though Quaternary white sand savannas seem to be an exception. High altitude mountains (1500-2000 m) do not seem to suit most Cuban Asteraceae nor closed canopy forests. They are edaphic specialists and prefer low to medium altitudes. Alien and native species can be found in anthropic savannas but both avoid mangrove forests. Aquatic and subaquatic species are scarce. Insularity, isolation, scarcity of native open spaces, and diversity of soils have influenced their Holocene trends.

Some native species display xerophytic traits (tomentose stems and leaves, small and leathery leaves, small capitula) though these are not strong since succulence, thick

layers of wax, spiny leaves and thorny stems are usually absent or very rare. This is a characteristic of Cuban Asteraceae.

Isolated relicts, either paleoendemics or neoendemics, are frequent. Speciation and evolution leading to endemic genera and species sometimes follow unpredictable trends which do not always agree with or match their continental counterparts, e. g., most Cuban species of *Gochnatia* have spine-toothed leaves; involucre are multiseriate in *Shafera* although it is a member of Senecioneae; synantherologists are not in agreement with the position of *Feddea* in current systems of classification.

Only two somewhat weedy tribes have invaded anthropic savannas either in lowlands or highlands: Plucheeae (27%) and Gnaphalieae (17%). In general, Heliantheae (1%) have kept themselves away from these secondary vegetation units.

The tropical climate, prevalence of lowlands and soil melange are characteristic of the Cuban archipelago, but these three variables are not found together in any other Caribbean country. Therefore, results and conclusions of this paper can not be applied to the continental Caribbean or the rest of the West Indies.

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Table 1. Specialized ecotopes of Cuban (native) Asteraceae**Dry ecotopes**

- 1) Coastal and premontane limestone karst (cliffs, sierras and hillocks, 0-1100 m a. s. l.) (19 % of Cuban Asteraceae occur in these two shrubby forest or scrub ecotopes).
- 2) Skeletic serpentine and red or brown soils derived from serpentine (pine forest and dry barren scrubs) (0-1200 m) (30 %).
- 3) White sand savannas (0-100 m) (pine forest, scrub barrens and seminatural savannas) (5 %).

Mesophytic and humid ecotopes

- 4) Orophilous series from the humid evergreen forest (400-800 m a. s. l.) to the mountain rainforest (800-1400 m), cloud forest (1400-1972 m) and mountain scrub (prealpine) (1700-1972 m) (33 %).
- 5) Anthropic savannas (mostly lowland) (1,8 %).

Aquatic and semi-aquatic ecotopes

- 6) Swamps and riverbank grasslands (10,5 %).
- 7) Mangrove forest (a few specialists) (0,7 %).

Table 2. Cuban vegetation units (CAPOTE & BERAZAIN 1984). Numbers in brackets correspond to Table 1. Abbreviations: ALT (altitude, meters), MAT (mean annual temperature, degrees centigrade), MAR (mean annual rainfall, millimeters)

1. Lowland rainforest. ALT: 0-500. MAT: 23-25,2. MAR: 2000-2400 or more. Avoided by most Cuban Asteraceae though there are a few specialists.
2. Mountain rainforest. ALT: 500-1400. MAT: 17-22. MAR: 2400-3000. (4). Avoided by most Cuban Asteraceae though there are a few specialists.
3. Cloud forest. ALT: 1400-1972. MAT: 13-20. MAR: more than 3000. (4). Avoided by most Cuban Asteraceae though there are a few specialists.
4. Humid evergreen forest. ALT: 300-800. MAT: 20-24. MAR: 1800-2000. (4). Avoided by most Cuban Asteraceae though there are a few specialists.
5. Dry evergreen forest. ALT: 0-300. MAT: 24-26. MAR: 600-1200. (1). Avoided by most Cuban Asteraceae though there are a few specialists.
6. Semideciduous forest. ALT: 0-600. MAT: 23-25,2. MAR: 1200-1400. Avoided by most Cuban Asteraceae though there are a few specialists.
7. Dry semideciduous forest. Species of Asteraceae do not occur.
8. Swamp forest. ALT: 0-100. MAT: 25-26. MAR: 1200-1400. (6). Some rheophytes are abundant.
9. Gallery forest. Found in all vegetation units except the montane scrub. Rich in scapose Asteraceae.
10. Mangrove forest. ALT: 0. MAT: 25-26. MAR: 1200-1400. (7). Avoided by most Cuban Asteraceae though there are a few specialists.
11. Pine forest. ALT: 0-1800. MAT: 14-25,2. MAR: 1200-3000. (2). Rich in Asteraceae.
12. Coastal and subcoastal scrub. ALT: 0-200. MAT: 24-26. MAR: 600-1200. Rich in Asteraceae, mostly in the south coast of Granma, Santiago de Cuba and Guantánamo, eastern Cuba.
13. Dry thorny scrub on serpentine. ALT: 0-500. MAT: 23-25,2. MAR: 1200-1400.(2). Rich in Asteraceae.
14. Dry scrub on serpentine. No thorns present except for *Agave* in Nipe. ALT: 500-1200. MAT: 20-23. MAR: 1400-2000. (2). Rich in Asteraceae.
15. Mountain scrub. ALT: 1700-1972. MAT: 13-18. MAR: 2000-2400. (4). Avoided by most Cuban Asteraceae though there are a few specialists.

16. Aquatic communities in fresh water. ALT: 0-1000. MAT: 20-25,2. MAR: 1200-2000. (6). Some rheophytes occur.
17. Halophytic communities. ALT: 0-100. MAT: 25-26. MAR: 600-1200. Avoided by most Cuban Asteraceae though there are a few specialists.
18. Swamp grassland. ALT: 0-100. MAT: 24-25,2. MAR: 1200-1400. (6). Some specialists occur.
19. Riverbank grassland. Similar to gallery forest. (6).
20. Karstic hillock vegetation complex. ALT: 0-700. MAT: 22-25,2. MAR: 1200-1400. (1). Summit and cliffs rich in Asteraceae.
21. Rocky coast vegetation complex. ALT: 0-100. MAT: 25-26. MAR: 600-1200. (1). Rich in Asteraceae.
22. Sandy coast vegetation complex. ALT: 0-50. MAT: 25-26. MAR: 600-1200. Moderately rich in Asteraceae.
23. Secondary forest. Invaded by alien Asteraceae though some native species occasionally occur.
24. Secondary scrub. Invaded by alien Asteraceae though some native species occasionally occur.
25. Seminatural savannas. ALT: 0-300. MAT: 24-25,2. MAR: 1200-1400. (3). Rich in Asteraceae, mostly endemics.
26. Anthropogenic savannas. They have taken the place of the semideciduous forest after heavy anthropic impact. ALT: 0-300. MAT: 24-25,2. MAR: 1200-1400. (5). Rich in alien Asteraceae when impact is steady. Some native species occur when the impact ceases.
27. Ruderal vegetation. It depends on human communities but is usually found below 1000 m altitude. Rich in alien Asteraceae.
28. Crop fields. Always located at low altitude except in the case of coffee plantations. Rich in alien Asteraceae.

Table 3. Alien taxa of Cuban Asteraceae

<i>Acanthospermum hispidum</i>	<i>Erechtites hieracifolia</i>
<i>Acanthospermum humile</i>	<i>Flaveria trinervia</i>
<i>Achillea millefolium</i>	<i>Fleischmannia microstemon</i>
<i>Ageratina riparia</i>	<i>Helenium amarum</i>
<i>Ageratum conyzoides</i>	<i>Helenium quadridentatum</i>
<i>Ageratum conyzoides</i> subsp. <i>latifolium</i>	<i>Lagascea mollis</i>
<i>Ageratum houstonianum</i>	<i>Launaea intybacea</i>
<i>Ambrosia elatior</i>	<i>Leucanthemum vulgare</i>
<i>Ambrosia peruviana</i>	<i>Lourteigia ballotifolia</i>
<i>Baltimora recta</i>	<i>Matricaria maritima</i>
<i>Bidens alba</i> var. <i>radiata</i>	<i>Melampodium divaricatum</i>
<i>Bidens laevis</i>	<i>Melampodium perfoliatum</i>
<i>Bidens mitis</i>	<i>Milleria quinqueflora</i>
<i>Bidens subalternans</i>	<i>Parthenium hysterophorus</i>
<i>Bidens tenera</i>	<i>Pectis floribunda</i>
<i>Brickellia diffusa</i>	<i>Pectis prostrata</i>
<i>Calyptocarpus vialis</i>	<i>Pluchea carolinensis</i>
<i>Chromolaena corymbosa</i>	<i>Porophyllum ruderale</i>
<i>Chromolaena odorata</i>	<i>Pseudelephantopus spicatus</i>
<i>Chromolaena ossaena</i>	<i>Pseudoconyza lyrata</i>
<i>Chrysanthellum americanum</i>	<i>Rudbeckia hirta</i>
<i>Cirsium mexicanum</i>	<i>Senecio vulgaris</i>
<i>Clibadium sylvestre</i>	<i>Sonchus oleraceus</i>
<i>Condylidium iresinoides</i>	<i>Spilanthes oleracea</i>
<i>Conyza apurensis</i>	<i>Synedrella nodiflora</i>
<i>Conyza bonariensis</i>	<i>Tagetes erecta</i>
<i>Conyza canadensis</i>	<i>Tagetes patula</i>
<i>Cosmos bipinnatus</i>	<i>Taraxacum officinale</i>
<i>Cosmos caudatus</i>	<i>Tithonia diversifolia</i>
<i>Cosmos sulphureus</i>	<i>Tithonia rotundifolia</i>
<i>Cyanthillium cinereum</i>	<i>Tridax procumbens</i>
<i>Delilia biflora</i>	<i>Verbesina encelioides</i>
<i>Eclipta prostrata</i>	<i>Wedelia caracasana</i>
<i>Elephantopus scaber</i>	<i>Wulffia havanensis</i>
<i>Eleutheranthera ruderalis</i>	<i>Xanthium strumarium</i>
<i>Emilia fosbergii</i>	<i>Youngia japonica</i>
<i>Emilia sonchifolia</i>	<i>Zinnia elegans</i>
<i>Epaltes brasiliensis</i>	<i>Zinnia multiflora</i>

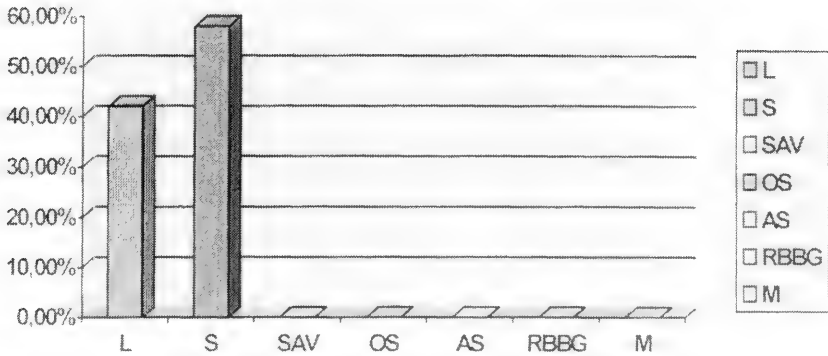


Fig 1. Ecological patterns of species of *Gochnatia*.

It is characterized by the distribution in ecological islands but with tendencies to very sun shine environment.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

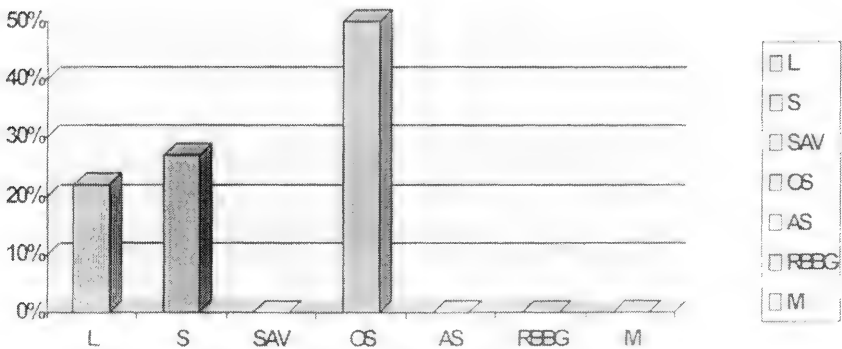


Fig. 2. Ecological patterns of Mutisieae tribe except *Gochnatia*.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

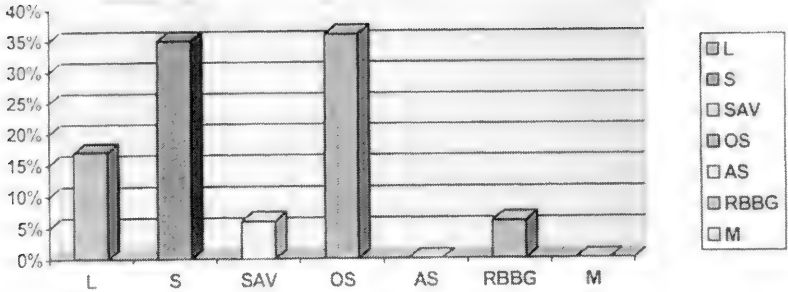


Fig. 3. Ecological patterns of Vernoniae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

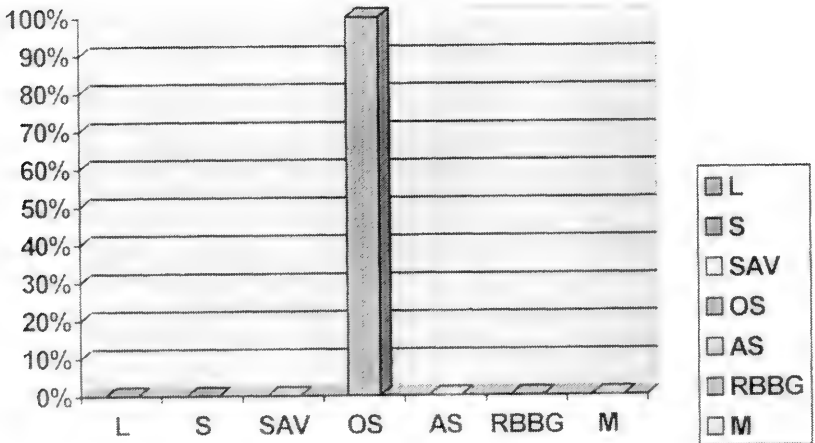


Fig. 4. Ecological patterns of Liabeae.

The only genus *Liabum* occurs in the montane rainforest and cloud forest.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

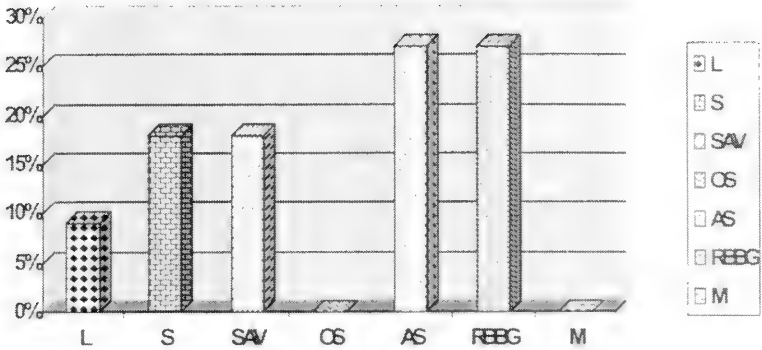


Fig.5. Ecological patterns of Plucheeae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

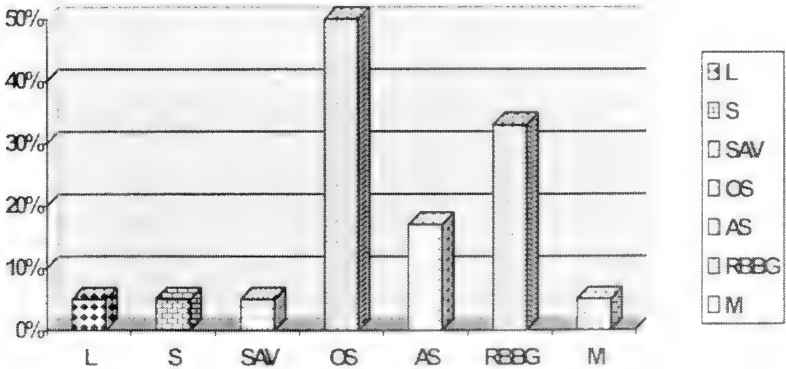


Fig. 6. Ecological patterns of Gnaphalieae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

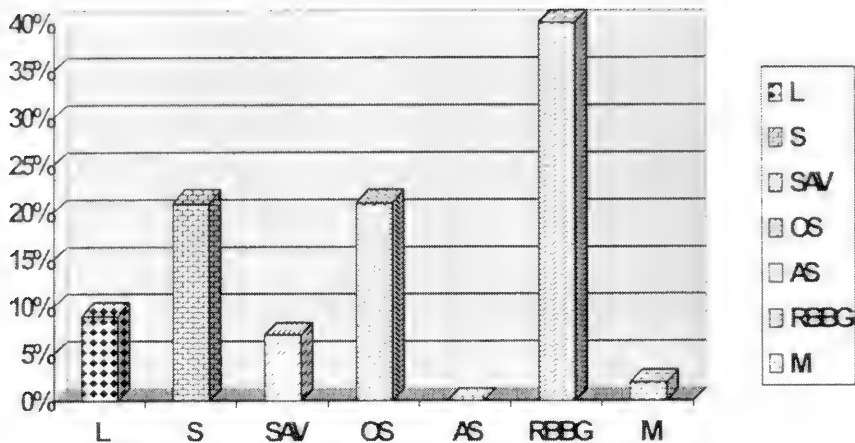


Fig. 7. Ecological patterns of Astereae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

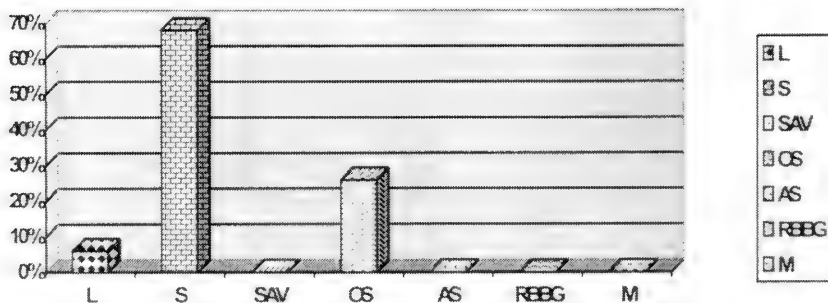


Fig. 8. Ecological patterns of Senecioneae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

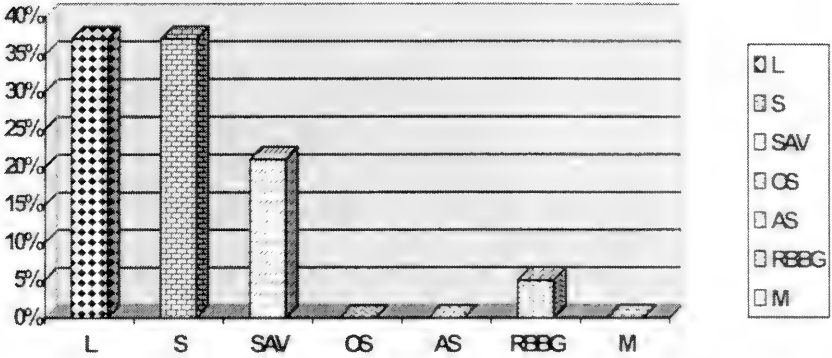


Fig. 9. Ecological patterns of Helenieae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

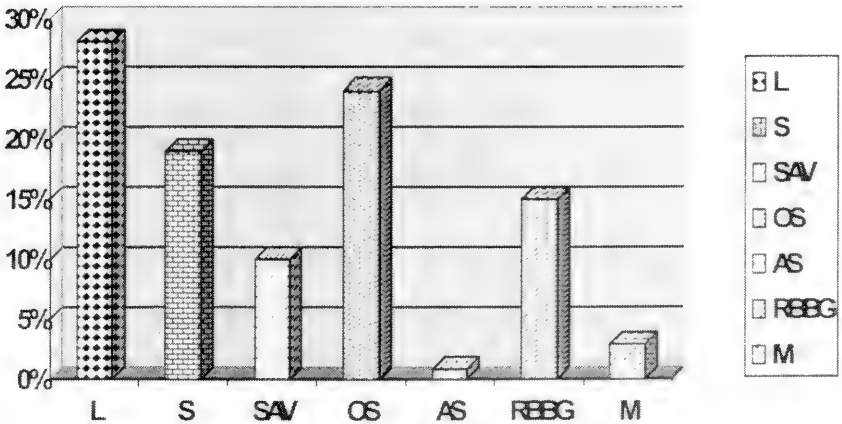


Fig. 10. Ecological patterns of Heliantheae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

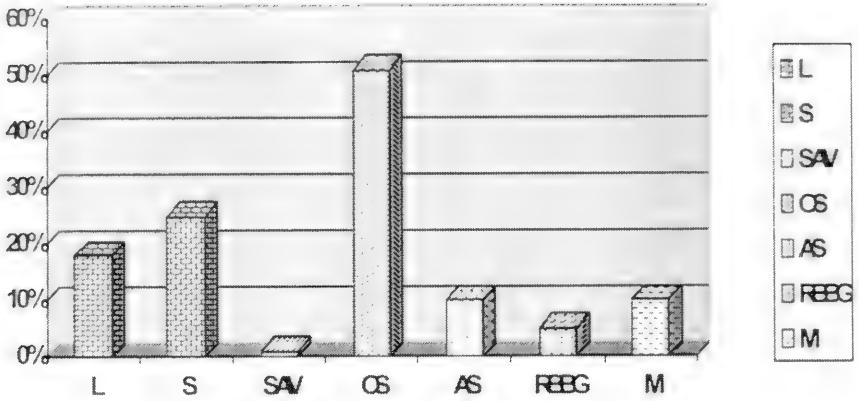


Fig. 11. Ecological patterns of Eupatorieae.

(L) Limestone soil; (S) Serpentine soils; (SAV) Savannas of white sands; (OS) Orophilous series; (AS) Anthropic savannas; (RBBG) Swamps and HOAR; (M) Mangrove

Checklist of roadside Compositae weeds in southwestern Nigeria

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Abstract

The occurrence of Compositae weed species along roadsides, in five major routes in southwestern Nigeria, which cut across three major vegetation subtypes, was investigated. Results obtained revealed that Compositae weeds found along the roadsides were mostly annuals reproducing from seeds. The seed dispersal and dormancy, and the species association with arbuscular mycorrhizae fungi might have contributed immensely to the establishment of the species.

Introduction

Recent studies on floristic composition in Nigeria are skewed towards members of the family Compositae which invariably constitute a major proportion of the plant species in southwestern Nigeria (KAYODE 1999).

Southwestern Nigeria comprises a diversity of ecosystems, which are vulnerable habitats subject to change by farming, especially by the prevailing shifting cultivation type, and by road construction. These factors have resulted in habitat fragmentation, loss of biodiversity and ecological succession.

Although information on various colonization strategies that enhance growth and developments of many plant species now abounds in literature, yet the need for phytosociological knowledge of the species composition and diversity and their variation in space and time has been stressed (CANTERO et al. 2000). KAYODE (1999, 2003) examined the phytosociological effects of farming with respect to Compositae weed species in a study area. The study reported here focuses on the phytosociological effects of road construction on the distribution of Compositae weed species.

Materials and methods

The study area

Southwestern Nigeria (6°20'–8°50'N, 2°50'–5°40'E) comprises six out of the present thirty-six states of the federation of Nigeria. The existing vegetation subtypes in the region include mangrove swamp, freshwater swamp, rainforest, and derived Guinea savanna. Two climatic seasons prevail in all the vegetation subtypes, viz., a rainy season between March and October, and a dry season between November and February.

Methods

Field studies were conducted between October 2000 and September 2003 along the following roads:

Route A: Ado-Ekiti – Ore – Shagamu – Lagos Road

Route B: Ado-Ekiti – Ibadan – Ogbomoso Road

Route C: Ore – Okitipupa – Igbokoda Road

Route D: Ado-Ekiti – Otun-Ekiti Road

Route E: Ado-Ekiti – Ikole-Ekiti – Omuo-Ekiti Road.

In each route, inventories (enumerations) of roadside Compositae species were carried out at every 15 km interval. In each inventory, phytosociological relevés were performed in a 5m² sampling area. Species were documented with vouchers in the Herbarium of the Department of Plant Science, University of Ado-Ekiti, Ado-Ekiti, Nigeria.

Results and discussion

Compositae weed species were found in all the vegetation subtypes present in the study area. The descriptive features of the routes sampled are shown in Table 1. A total of 53 enumerations were carried out and 23 Compositae weed species were observed. Most of the weeds were found in the rainforest vegetation (Table 2).

Table 3 reveals that most of these weeds are annual plants and all of them reproduce by seeds. They are mostly dispersed by wind thus producing a rain of seeds to the disturbed environment. The seed rain often results in seed banks, especially during unfavourable conditions inducing dormancy in the seeds. Seed dormancy in weeds is now known to be a survival strategy (HARPER 1977). Previous studies have asserted that seeds remain dormant in the soil until they are exposed to suitable conditions (AUGUSPURGER 1994a & b, OBERBANER & STRAIN 1985). For example, the breaking of dormancy in *Tridax* (LONGMAN 1969) and *Chromolaena* (AULD & MARTINS 1975) was

attributed to light. Also KAYODE (2000) suggested that seed dormancy in most tropical weeds is broken by light.

Compositae association with arbuscular mycorrhizae fungi (AMF) could also enhance the rapid establishment in degraded soils that often accompanies road construction sites. WARCUP & MCGEE (1983), WARCUP (1990) and RAI & ACHARYA (1999) have provided evidence of the occurrence of AMF in some naturally occurring Compositae. AMF enables the plants to be more efficient in acquiring phosphorus (DURGA & GUPTA 1995, VARMA & JAMALUDDIN 1995). Phosphorus and nitrogen are the limiting nutrients in roadside soils.

Acknowledgements

I wish to thank Mrs. G. M. KAYODE for her assistance in conducting the fieldwork.

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Table 1. Descriptive features of routes sampled in southwestern Nigeria

Route	Vegetation Type(s)	Distance sampled (km)	No. of enumerations
A	Rainforest	362	24
B	Rainforest, Derived Guinea Savanna	260	17
C	Freshwater Swamp, Rainforest	60	4
D	Rainforest, Derived Guinea Savanna	60	4
E	Rainforest, Derived Guinea Savanna	60	4

Table 2. Vegetational distribution of roadside Compositae weed species in southwestern Nigeria

Vegetational zone	No. of Compositae weed species
Freshwater Swamp	5
Rainforest	16
Derived Guinea Savanna	13

Table 3. Occurrence of roadside Compositae weed species in southwestern Nigeria

Compositae weed species	Frequency of Occurrence/Route					Growth Habit	Ecological Attributes
	A (n=24)	B (n=17)	C (n=4)	D (n=4)	E (n=4)		
<i>Acanthospermum hispidum</i>	11	6	0	1	0	Annual herb	Reproduces from seeds
<i>Ageratum conyzoides</i>	13	3	0	0	0	Annual herb	Reproduces from seeds
<i>Aspilia africana</i>	12	8	2	2	1	Perennial herb	Reproduces from seeds, Flowers almost throughout the year
<i>Aspilia bussei</i>	0	2	0	1	0	Annual herb	Reproduces from seeds
<i>Bidens pilosa</i>	19	12	2	3	4	Annual herb	Reproduces from seeds
<i>Chromolaena odorata</i>	21	15	2	3	4	Annual herb	Reproduces effectively from seeds
<i>Chrysanthellum indicum</i>	0	2	0	0	1	Annual herb	Reproduces from seeds
<i>Coryza sumatrensis</i>	0	1	0	1	1	Annual herb	Reproduces from seeds
<i>Emilia coccinea</i>	2	0	1	0	1	Annual herb	Reproduces from seeds
<i>Laggera aurita</i>	0	0	0	0	1	Annual herb	Reproduces from seeds
<i>Lactuca taraxacifolia</i>	9	6	2	0	1	Rhizomatous annual or perennial herb	Reproduces from seeds and proliferating rhizome
<i>Melanthera scandens</i>	9	12	2	1	1	Perennial herb	Reproduces from seeds
<i>Sclerocarpus africanus</i>	0	2	0	0	1	Annual herb	Reproduces from seeds
<i>Spilanthes filicaulis</i>	11	7	2	1	1	Annual herb	Reproduces from seeds
<i>Synedrella nodiflora</i>	10	14	3	2	1	Annual herb	Reproduces from seeds
<i>Tithonia diversifolia</i>	8	6	1	1	0	Perennial herb	Reproduces from seeds
<i>Tridax procumbens</i>	19	16	4	3	2	Annual herb	Reproduces from seeds
<i>Vernonia ambigua</i>	6	7	1	0	1	Annual herb	Reproduces from seeds
<i>Vernonia amygdalina</i>	5	5	0	0	1	Woody shrub	Reproduces from seeds
<i>Vernonia colorata</i>	0	1	0	0	1	Tree	Reproduces from seeds
<i>Vernonia cinerea</i>	4	2	1	1	1	Annual herb	Reproduces from seeds
<i>Vernonia galamensis</i>	1	1	0	2	2	Annual herb	Reproduces from seeds
<i>Vernonia tenoreana</i>	0	2	0	1	1	Annual herb	Reproduces from seeds

*n= the number of enumerations carried out in each route

Studies on the reproductive biology of *Emilia* (Asteraceae – Senecioneae)

1. Flowering and post-pollination developments in the capitulum

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Abstract

A study of the flowering and post-pollination developments in the capitulum of the genus *Emilia* (CASS.) CASS. (Asteraceae – Senecioneae) was conducted in order to correlate and document various observations made on the stages of development of floral parts. The protectional role of floral parts is highlighted, both while flower is in bud and at fruit development phase. The co-operative features of floral parts (phyllaries, florets and receptacle) in the display of flowers for pollination and fruits for dispersal are elaborated. The probable reasons for the usual occurrence of *E. sonchifolia* and *E. coccinea* as isolated populations are discussed.

Introduction

The genus *Emilia* is represented in Nigeria and West Africa by three species (ADAMS 1963). These are *E. coccinea* (SIMS) G. DON, *E. sonchifolia* (L.) DC. and *E. praetermissa* MILNE-REDH. They are economically important. They can be eaten as vegetables and can also be used for medicinal purposes (BURKILL 1985, ABBIW 1990).

OLORODE & OLORUNFEMI (1973) reported a chromosome number of $2n = 10$ for *E. coccinea* and *E. sonchifolia*, and $2n = 20$ for *E. praetermissa*. They concluded that *E. praetermissa* is an allotetraploid hybrid between *E. sonchifolia* and *E. coccinea*.

In all plants, the demands of flowering and fruiting phases interact. According to BURTT (1975), the structure and organization of the capitulum of the Compositae (or Asteraceae) must meet the demands of both phases. He was also of the opinion that the study of the co-evolution of the flowering and fruiting phases of the life history of plants has been neglected. He therefore called for more studies of these two phases. The condition and exposure of a plant during the flowering and fruiting phase determines much the quality of fruits produced and the seeds set.

The objective of this study is to correlate and document the various observations made on the stages of development of floral parts (that is, the capitulum and its contents) via pre-pollination and post-pollination studies in the West African species of *Emilia*.

Materials and Methods

Observations were made regularly on the field, garden and screen-house plants. 5–10 plants of each species in the garden and screen-house carried labels on which regular entries were recorded. Data gathered on capitulum development included: flower bud at anthesis; fertilization of florets; appearance of pappus on ripe fruits (achenes) in the capitulum and the mode of achene dispersal. Special observations on the post-fertilization events were made with respect to changes in the phyllaries and the receptacle of the capitulum. Photographs of important occurrences were recorded during the flowering and post-pollination stages of the capitulum.

Bar diagrams illustrating the incidence of receptacle reflexing and the incidence of withered florets adherent to pappus and seeds among the species were prepared.

Results

A wall of phyllaries encapsulates the *Emilia* capitulum in bud (Fig. 1A). In all the species studied, the peripheral florets opened and were pollinated before the central florets (Fig. 1A & B). The post-pollination sign in all the species was the withering of the corolla of pollinated florets within 18 hours after pollination (Fig. 2A & B). This was followed by the gradual reclosure of the involucre, the diameter of the capitulum becoming smaller (Fig. 2A & B). The phyllaries remained green as the fruits from pollinated florets matured.

The capitulum thereafter reopens gradually with the diameter increasing, showing first the pappus of the peripheral matured achenes (Fig. 2C). The phyllaries become dried up, turning brown. With receptacle reflexing, all pappus subsequently radiates from matured achenes and the withered florets dropped off (Figs. 2D – E & 3A).

Capitulum receptacle may be completely reflexed in some cases, becoming turned inside-out when dry, like a closed umbrella (Fig. 4D). They may be partially reflexed (Fig. 4A – C) or not reflexed at all (Fig. 4A). However, the incidence of capitulum receptacle reflexing varied among and within the species (Fig. 5).

Dispersal of achenes is largely with the aid of wind. As the wind blows, the achenes are dispersed with the aid of the pappus on them (Fig. 3B). It was observed that efficient seed dispersal occurred only when the receptacle was completely reflexed

exhibiting all the seeds and pappus with the withered florets dropped off (Figs. 2E & 3A). However, a special event was observed where the receptacle was completely reflexed but the withered florets did not drop off from the top of the pappus separately (adherent to it) but pulled and eventually dropped off with the pappus and seeds, all together (Fig. 3C). The pappus was not fully exhibited for seed dispersal because the withered florets did not drop off. This was encountered more in *E. coccinea* followed by *E. sonchifolia*. It was a rare occurrence in *E. praetermissa*. The incidence of withered florets adherent to pappus and eventually dropping off with the pappus and seeds varied among the species (Fig. 6).

Discussion

BURTT (1977) itemized four major factors necessary to meet demands of both the flowering and fruiting phases. Two of these factors are related to the flowering phase, namely the efficiency of pollination and the balance of the breeding system (i.e. the ratio of inbreeding to outbreeding). The other two factors have to do with the fruiting phase, namely the protection of the maturing achenes and their adequate dispersal.

The structure of the capitulum in *Emilia* and the organization of the constituent parts, namely the phyllaries, florets and receptacle, show meaningful adaptive values which meet the demands of both the flowering and fruiting phases. For instance, the phyllaries which encapsulate the capitulum buds, serve as protection for the internal structures. This protectional role recurs after pollination, as the involucre recluses (Fig. 2A & B), ensuring the safety of the developing achenes (fruits).

The phyllaries remain green while the fruits are maturing, becoming dry only in matured flower heads. A participatory role of the phyllaries in the net provision of photosynthetic products in the fruits is a possibility. Just as the phyllaries open initially at anthesis to expose the florets, so they are reopened when the fruits are matured for dispersal (Figs. 1A & 2C).

Receptacle reflexing was observed as an essential phenomenon aiding efficient fruit dispersal (AYODELE 1992). This can be compared with the explosive mechanism in some Euphorbiaceae. A combination of light-weight fruits and fully reflexed receptacle resulted in a longer distance of fruit dispersal, even in the absence of wind (AYODELE 1992). However, in this study two factors are observed to be hindering adequate seed dispersal largely in *E. coccinea* and *E. sonchifolia*, rarely in *E. praetermissa*. Firstly, partial reflexing and no reflexing of the receptacle is encountered in them (Fig. 4A – C). Secondly, even when receptacle reflexing is complete, occasionally, the withered florets do not drop off from the pappus preventing the pappus from radiating adequately for seed dispersal and eventually drop off with the pappus and seeds, all together (Fig. 3C). These may probably be some of the reasons why *E. coccinea* and

E. sonchifolia are not as widely and evenly distributed as *E. praetermissa*. They usually occur in scattered isolated populations.

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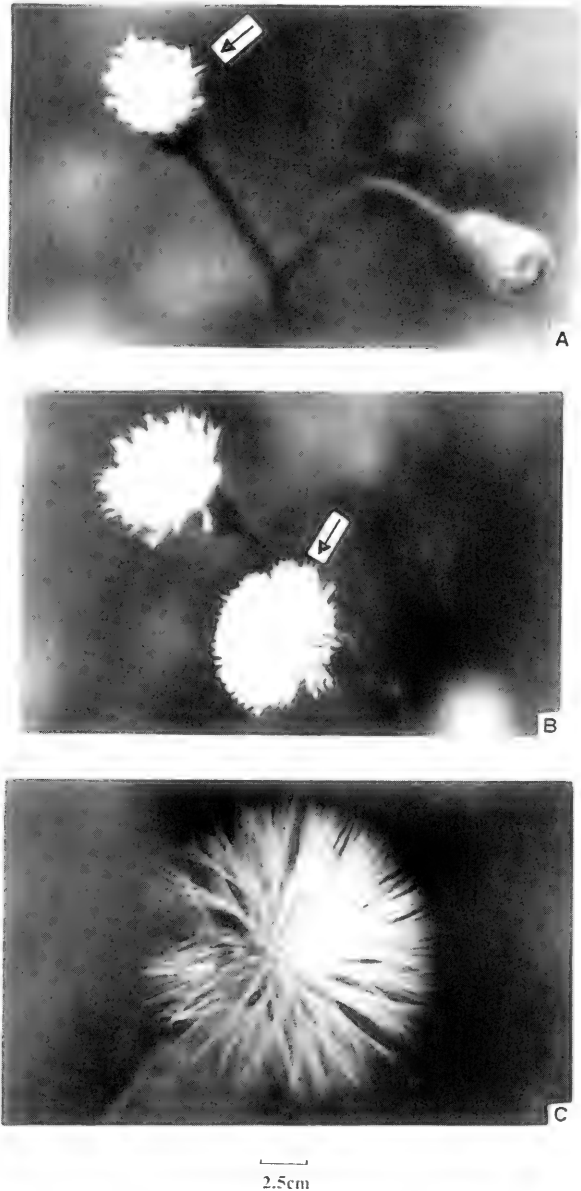


Fig. 1. Capitulum development in *Emilia*.

- A: Peripheral florets opening first (with arrow)
Capitulum in bud (without arrow)
- B: Florets fully opened (with arrow)
- C: Capitulum with pappus

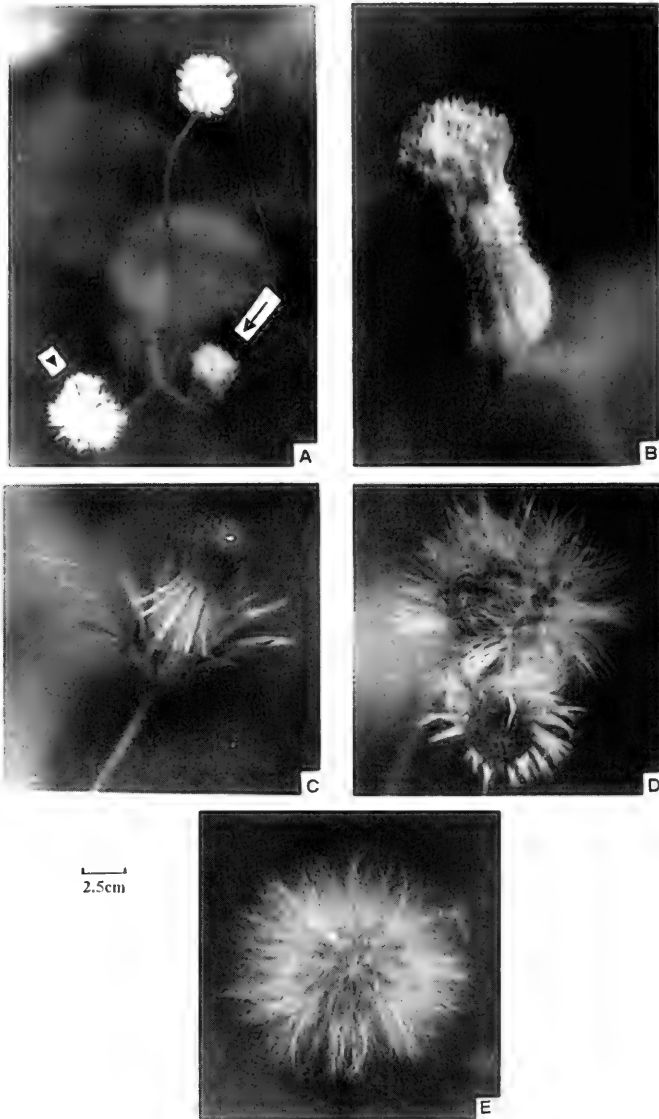
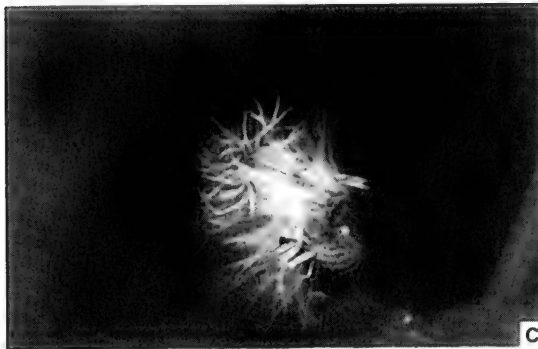
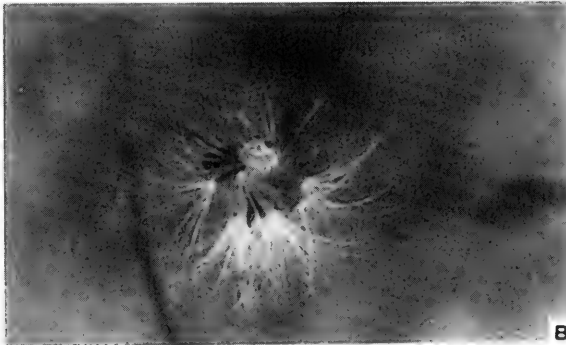
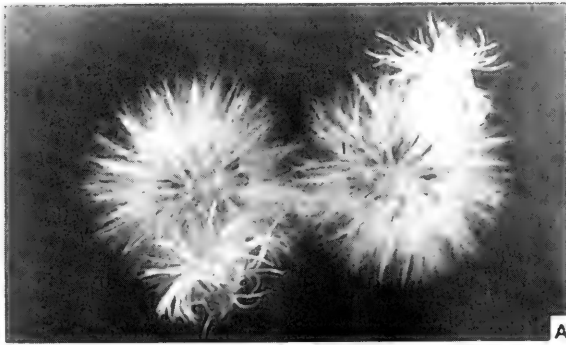


Fig.2. Capitulum development in *Emilia* (contd.).

- A: Capitulum with withered florets (with arrow)
- B: Capitulum reclosure
- C: Capitulum re-opening
- D: Withered floret dropping off (after capitulum re-opening)
- E: Capitulum with pappus



2.5cm

Fig. 3. Capitulum development in *Emilia* (contd.).

- A: Capitulum with pappus and seeds (showing withered florets dropping off)
- B: Capitulum with few seeds
- C: Withered florets adherent to pappus and seeds, dropping off together

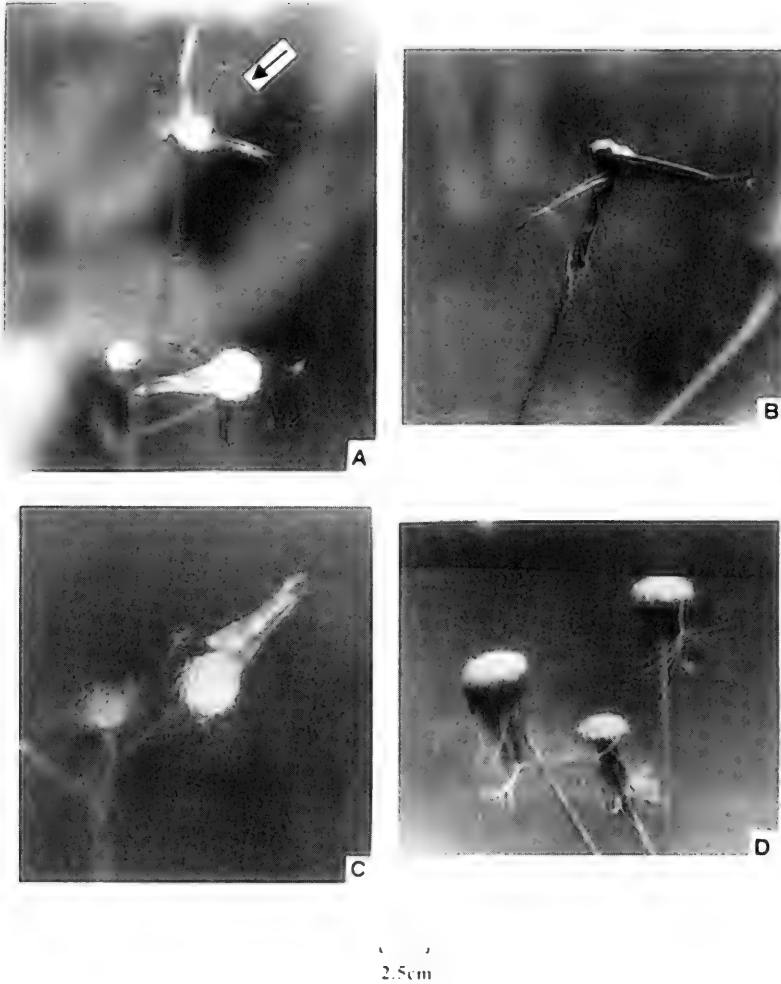


Fig. 4. Capitulum development in *Emilia* (contd.).

- A: No receptacle reflexing (with arrow)
- Partial receptacle reflexing (without arrow)
- B: Partial receptacle reflexing
- C: Partial receptacle reflexing
- D: Total receptacle reflexing



Fig. 5. Incidence of receptacle reflexing in ripe capitula on plants of the *Emilia* species.

Key to species numerals:

1. *E. coccinea*
2. *E. sonchifolia*
3. *E. praetermissa*

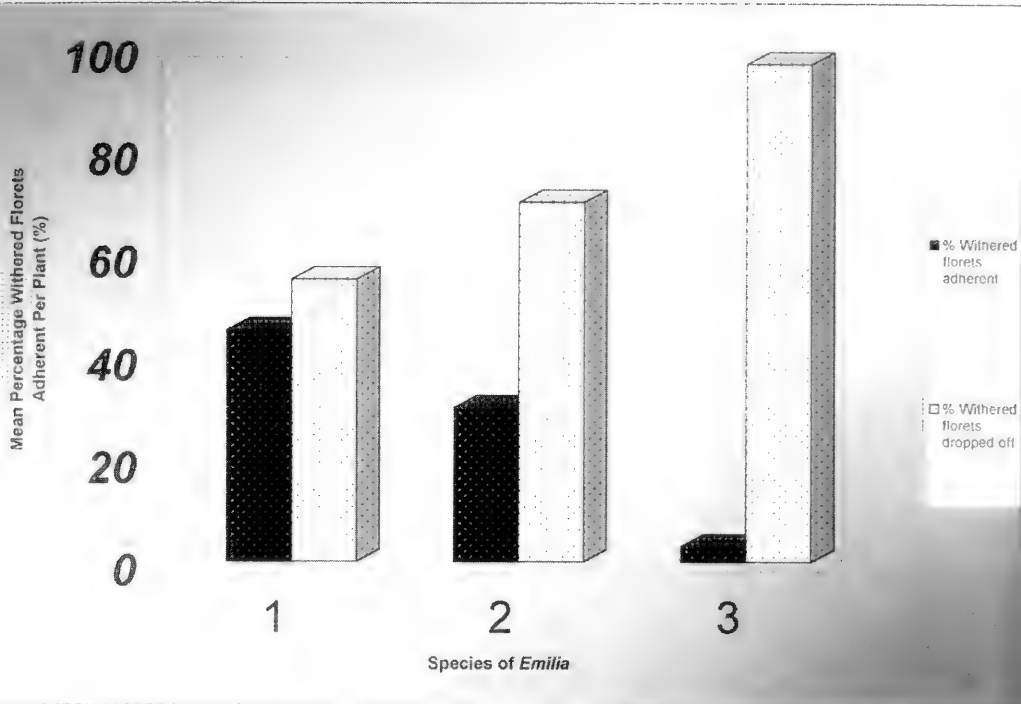


Fig. 6. Incidence of withered florets adherent to pappus and seeds on some plants of the *Emilia* species.

Key to species numerals:

1. *E. coccinea*
2. *E. sonchifolia*
3. *E. praetermissa*

New taxa and combinations published in this issue

Aequatorium pascoense H. BELTRÁN & H. ROB., sp. nov.: p. 5

Amblyperma minor G. J. KEIGHERY, sp. nov.: p. 27

Dauresia B. NORD. & PELSER, gen. nov.: p. 76

Dauresia alliariifolia (O. HOFFM.) B. NORD. & PELSER, comb. nov.: p. 76

Hypochaeris albiflora (OK.) C. F. AZEVÊDO-GONÇALVES & N. I. MATZENBACHER,
comb. nov.: p. 3

Hypochaeris pinnatifida (SPEG.) C. F. AZEVÊDO-GONÇALVES & N. I. MATZENBACHER,
comb. nov.: p. 2



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