

**TWO NEW GENERA OF
Vernonieae (Asteraceae)
FROM THE NORTHERN ANDES
WITH DISSECTED COROLLA LIMBS**
Cuatrecasanthus and Joseanthus

by

Harold Robinson*

Resumen

Robinson, H.: Two new genera of Vernonieae (Asteraceae) from the northern Andes with dissected corolla limbs. *Cuatrecasanthus* and *Joseanthus*. Rev. Acad. Colomb. Cienc. 17 (65): 207-213, 1989, ISSN 0370-3908.

Se proponen dos taxones para los cuales se discuten ampliamente los caracteres diagnósticos y se proporcionan claves para diferenciar las especies incluidas en los nuevos géneros y se describe una nueva especie de *Joseanthus*, dedicada al Dr. J. Cuatrecasas.

During studies of *Critoniopsis* Sch. Bip. (Robinson 1980) and various other vernonieae (Robinson 1985) a small number of species was noted from the northern Andes that had corolla limbs dissected to the base. The species involved were omitted from the resurrected genus *Critoniopsis*, and were left in the broad concept of *Vernonia* Schreb. awaiting more accurate generic placement. Two new genera are now provided for these species with deeply lobed corollas as part of a continuing effort to correct the excessively paraphyletic concept of *Vernonia*. The occasion is taken to also provide various comments on some of the characters found in either of the two new genera, dissected corolla limbs, opposite leaves, and few-flowered heads with deciduous inner involucre bracts. Also, one new species is described.

The effort to restrict the generic concept of *Vernonia* has been a progressive one. The fact that governs the entire process is the recognition that *Vernonia novaboracensis* (L.) Michx. of eastern North America is the type species of *Vernonia*, and that any proper generic concept must center on the

North American group. A secondary consideration to be taken into account is the basic difference noted by Jones (1977) between the New World and Old World members of the tribe recognized at that time as the core genus *Vernonia*. The differences cut across the generic concepts persisting from the time of Bentham and Hooker (1873). It has remained the present author with various coauthors to begin the process of purifying *Vernonia*. Previous segregates have included some like *Lepidonia* Blake and *Stramentopappus* Robins. & Funk (Robinson and Funk 1987) that should never have been placed in *Vernonia* because their pappus form; *Distephanus* Cassini (Robinson and Kahn 1986), a genus in the atypical paleotropical part of the tribe that also violated the generic concept of *Vernonia* in flower color and tailed anther thecae; *Critoniopsis* (Robinson 1980) which is more closely related to *Piptocarpha* R. Br. than to *Vernonia*; and a series of genera of the *Lepidaploa* Cassini relationship (Robinson 1987a, b, c, 1988a, b, c) that have lophate pollen forms not found in typical *Vernonia*. The process remains far from complete even with the present contribution. The ultimate aim of the process is to attain a totally refined generic concept of *Vernonia* based on that the genus "is" rather than on what it "is not".

* Department of Botany, National Museum of Natural History Smithsonian Institution, Washington, DC. 20560.

The two genera segregated from *Vernonia* in the present paper have the spinose pollen type seen in typical *Vernonia*. The pollen type is considered derived in the tribe (Robinson and Kahn 1986), but is nevertheless widespread in both hemispheres and cannot be considered a recent apomorphy that binds together the groups in which it occurs. Robinson and Kahn (1986) and Robinson (1988a) show evidence that the reversion has occurred many times. The co-occurrence of such spinose pollen in *Vernonia*, *Critoniopsis* and the two new genera is not particularly meaningful. Of greater interest are the characters of the corolla, opposite leaves, and heads with few flowers and deciduous inner involucre bracts.

Corolla form. Elongate and linear lobes are found in almost all discoid radially symmetrical corollas of the subfamily Cichorioideae and occur in various small groups in the subfamily Asteroideae. In most of the corollas with such elongate lobes the depth of the dissection of the limb has some capacity of variation. In some species, especially in *Lepidaploa* (Cassini) Cassini of the Vernonieae, the throat may be very short, but it is always present. In contrast, corollas with the limb dissected completely to the base, at essentially the level of the filament insertion, are comparatively restricted in distribution, and they tend to have some stability in such genera as *Psacalium* Cassini, *Paragynoxys* Cuatr. and parts of *Gynoxys* Cassini of the tribe Senecioneae. In the neotropical Vernonieae the occurrence of such corollas seems to be restricted to two small groups in the northern Andes. These groups were briefly mentioned in a review of the genus *Critoniopsis* (Robinson 1980). The existence of three to five species in each group with consistent corolla form indicates some stability of the character in these groups similar to that in the above mentioned Senecioneae. It is considered likely that the corolla form in the two Andean groups in the Vernonieae has a single origin, and the distribution of the character is possibly aided by intergeneric hybridization. The dissected limbs effectively distinguish the two groups from other members of the tribe placed in the genera *Vernonia* and *Critoniopsis*. Nevertheless, the character is not considered an adequate basis for placing the two groups together in a single genus because other distinctions are too important.

Opposite leaves. The seemingly simple character of leaf insertion has a rather taxonomically interesting distribution in the Asteraceae. The members of the family with opposite leaves are concentrated in the Eupatorieae and Heliantheae of the subfamily Asteroideae. The only tribe of the Cichorioideae with basically opposite leaves is the Liabeae, but isolated examples occur in Mutisieae like *Dinoseris* Griseb. and *Chuquiraga* Juss. and in various Vernonieae such as *Erlangea* Sch. Bip. of Africa. In the Vernonieae the opposite-leaved condition obviously arose separately in the African *Bo-*

thriocline, and it seems to have arisen more than once in the neotropical forms. The Brazilian *Vernonia stellata* (Spreng.) Blake (*V. oppositifolia* Less.) seems to have no close relation to various Andean species. *Critoniopsis pichinchensis* (Cuatr.) H. Robins. is one member of its genus with consistently opposite leaves (Robinson 1980). The latter species and *Vernonia harlingii* H. Robinson (1979), also from Ecuador, show a number of differences from the group of opposite-leaved species in the present study. They are obviously not more closely related to the five opposite-leaved species named here as *Joseanthus* than any of them are to strictly alternate-leaved species such as those named here as *Cuatrecasanthus*. In particular, the Ecuadorian *Vernonia harlingii* with its large, sessile, opposite leaves has an aspect superficially similar to *Joseanthus*. The corymbose inflorescence and the heads with numerous flowers approach the condition in *Joseanthus*, but details of the long corolla throat and the five-ribbed achenes with distinct raphids indicate considerable phyletic separation.

In spite of the various species with opposite leaves long known in *Vernonia*, the study by Robinson (1976) was apparently the first to find a closest relationship between two such species. At present, *Joseanthus* with five species is the largest group known in the Vernonieae with consistently opposite leaves.

Few-flowered heads with deciduous inner bracts. One of the elements in the present study, *Cuatrecasanthus*, has singleflowered heads and deciduous inner involucre bracts of a type usually placed in Vernonian genera which have distinct corolla throats, *Critoniopsis*, *Pollalesta* H.B.K. and *Eremosis* (DC) Gleason. The relationship seems to lead ultimately to *Piptocarpha* R. Br. with its 3-20-flowered heads and highly deciduous involucre. The genus that is closest to *Cuatrecasanthus* in corolla form, *Joseanthus*, has heads with numerous flowers and more persistent involucre bracts and on this basis would seem less closely related. This difference, more than the difference in leaf insertion, causes the present separation of *Cuatrecasanthus* and *Joseanthus* into two separate genera.

The possible relationship of *Cuatrecasanthus* to other genera with few flowers and deciduous inner bracts is complicated by still further facts. The almost entirely South American *Critoniopsis*, *Pollalesta* and *Piptocarpha* all share habits and nearly smooth achenes that have been regarded as evidence of a related subtribe Piptocarphinae. In contrast, the Central American *Eremosis* has a different kind of weaker-walled multiribbed achene, and it has variations toward other Central American Vernonieae that are not as yet distinguishable from *Vernonia*. Except for the few flowers and deciduous bracts in the heads, *Eremosis* would not be considered a relative of the Piptocarphinae. The final confusing fact is that *Cuatrecasanthus* has densely corymbose

inflorescence and achene structure that is more like *Eremosis* than like the *Piptocarphinae* with which it shares geography. The pattern strongly suggests to the author that there is reticulating evolution in the group. It seems probable that the recognition of a subtribe *Piptocarphinae* as delimited by Robinson et al. (1980) will prove untenable if such intergeneric hybridization is proven. At this time it seems best to simply recognize the various elements of the puzzle at the generic level and defer conclusions on detailed relationships.

Other characters. *Cuatrecasanthus* and *Joseanthus* are alike in a number of other characters of restricted occurrence. Both genera have short sterile appendages on the base of the anther thecae with a prominent fringe of teeth. These bases are essentially like those of *Critoniopsis* but much shorter than the tails that characterize *Piptocarpha*. Both genera have at least a few slender hairs on the outer surface of the corolla and have few to many glands. The walls of the achene are mostly glanduliferous and neither genus has numerous long setulae. Raphids of the type seen in *Vernonia harlingii* are not present.

In addition to the differences between the genera in leaf insertion and head construction, there are some notable differences in the achenes. The walls of the *Joseanthus* achenes are somewhat firmer, and the mature achenes seen show differentiated non-glandular idioblasts on the surface of the type sometimes called resin cells. The weaker walls of *Cuatrecasanthus* are more like those of *Eremosis* in texture, and the mature examples seen show no resin cells. The achenes seem shorter at maturity with many shorter cells on the surface in *Cuatrecasanthus*, while the long mature achenes seen in *Joseanthus* have longer surface cells. The pappus of *Joseanthus* has a distinct shorter outer series while that of *Cuatrecasanthus* has comparatively undifferentiated outer bristles.

The distinctions of the two new genera from North American and Neotropical *Vernoniae* with spinulose pollen can be summarized in the following key.

1. Corollas with distinct throat, lobes not divided to level of anther filament insertion
Vernonia and most other *Vernonieae*
1. Corollas without distinct throat, with lobes divided to level of filament insertion at the top of the basal corolla tube 2
2. Leaves alternate; heads with one flower, with easily deciduous inner involucre bracts; achenes without distinct shorter outer pappus series *Cuatrecasanthus*
2. Leaves opposite; heads with 9-12 flowers, with rather persistent inner involucre bracts; achenes

with distinct shorter outer pappus series *Joseanthus*

The two new genera are both named for Dr. José Cuatrecasas who is known among many other things for his study of the *Critoniopsis* group in the northern Andes (Cuatrecasas 1956).

Cuatrecasanthus H. Robinson, gen. nov.

Plantae erectae leniter fruticosae ad 3.5 m altae. Folia alterna petiolata; laminae ellipticae apice argute acuminatae subtus dense appresse albo-tomentosae et dense pilosae, nervis secundariis pinna-tis utringue 4-6 ascendentibus. Inflorescentiae in ramis terminales late alterne ramosae, ramis distaliter dense corymbosis. Capitula in glomerulis sessilia cylindrica, bractae involucri ca. 15 in seriebus 5-6 inaequilongae graduatae imbricatae interiores facile deciduae extus subglabrae vel leniter pilosae. Flores in capitulo 1; corollae lavandulae extus minute et sparse glanduliferae superme interdum longe pilosulae, tubis anguste cylindricis ca. 3.5-4.0 mm longis, faucibus nullis, lobis fere ad tubo basilare divisus linearibus ca. 4.0-4.5 mm longis et 0.7 mm latis, nervis marginibus apice non latioribus; thecae antherarum base truncate et breviter papilloso-fimbriate appendiculatae, appendicibus apicalibus ovate-oblongis glabris; basi stylorum breviter nodiferi, nodis obturaculiformis in parietibus cellularum incrassatis; pili abaxiales ramorum non septati apice obtusi vel breviter acuti. Achaenia prismatica base sensin angustiora in parietibus subtenuia 10-costata, costis prominentibus plerumque in cellulis superficialibus linearibus, superficiis intercostalibus minute sparse glanduliferis et persparse minute spiculiferis cellulis subquadratis non resiniferis omnino obsitis; setae pappi persistentes plerumque longe capillares ca. 65 et ca. 7 mm longae apice plerumque distincte lateriores et extus sublaeves, setae exterioribus brevibus saepe paucae et indistinctae. Grana pollinis in diametro ca. 45 μ m spinulifera sublophata (typus A.).

Type: *Vernonia sandemanii* H. Robinson.

The genus contains the following three species that were not recognized as close relatives until the study by Robinson (1985).

Key to the species

1. Midrib of leaf densely covered with erect hairs; petioles ca. 3 mm long, broadened by erect hairs; inflorescence with short branches; involucre bracts mostly short-acute
C. jelskii
1. Midrib of leaf densely covered with antrorsely appressed hairs; petioles mostly 4 or more mm long, slender with appressed hairs; inflorescence widely branched; involucre bracts mostly obtuse or rounded 2

2. Leaf undersurface with prominent reticulate venation; involucre bracts pale-brown

C. flexipappus

2. Leaf undersurface with scarcely prominent crossveins; involucre bracts reddish

C. sandemanii

Cuatrecasanthus flexipappus (Gleason). H. Robinson, comb. nov.

Vernonia flexipappa Gleason, Bull. Torrey Bot. Club 52: 186. 1925.

Vernonia giannasii Stutts, Brittonia 32: 162. 1980. Ecuador (Loja, Morona-Santiago, Zamora-Chinchipec).

The species has been collected numerous times in southern Ecuador in recent years. Collections other than the types include, from Loja: King 7920; Thien 781; and from Zamora-Chinchipec: Camp E-1619 (US); King 7928 (US). The specimens are all from ca. 2.800 m elevation in the mountains along the border between the two southernmost Provinces. The type of *V. giannasii* is from slightly farther north in southern Morona-Santiago.

Cuatrecasanthus jelskii (Hieron). H. Robinson, comb. nov.

Eremanthus jelskii Hieron., Bot. Jahrb. Syst. 36: 462. 1905, non *Vernonia jelskii* Hieron., Bot. Jahrb. Syst. 36: 459. 1905.

Vernonia sharynensis MacLeish, Syst. Bot. 9: 135. 1984. Peru (Cajamarca?).

The species is known only from the type series. The limited material available shows a short median vein in the apical part of the corolla lobes in addition to the marginal veins. The corollas examined of the other species lack the median vein.

Cuatrecasanthus sandemanii (H. Robinson) H. Robinson, comb. nov.

Vernonia sandemanii H. Robinson, Phytologia 58: 253. 1985. Peru (Huanuco).

Two additional collections have been seen since the description of the species, all from Carpish, on the road to Tingo Maria, Ferreyra 1214, 2347 (US).

Joseanthus H. Robinson, gen. nov.

Plantae erectae arborescentes vel frutescentes 2-6 m altae, pilis interdum T-formibus (*J. sparrei*). Folia opposita breviter petiolata, petiolis 2-15 mm longis; laminae ellipticae vel anguste oblongae base et apice obtusae vel breviter acutae margine integrae supra laeves vel prominule reticulatae glabrae vel evanescentiter puberulae subtus tomentosae et glanduliferae, nervis secundariis pinnatis utrinque ca. 7-9 late patentibus. Inflorescentiae in ramis ter-

minales supra basem plerumque alterne remosae dense corymbosae, ramis dense velutinis. Capitula breviter pedunculata campanulata; bractae involucri ca. 20-30 ca. 4-5-seriatae inaequilongae graduatae subimbricatae saepe in apicem reflexae persistentes extus saepe villosae. Flores in capitulo ca. 9-12; corollae violaceae extus minute glanduliferae in lobis saepe dense pilosulae, tubis anguste cylindricis 3-5 mm longis, faucibus nullis, lobis fere ad tubo basilare divisus linearibus ca. 2-5 mm longis et 0.6-0.7 mm latis, nervis marginalibus apice non latioribus; thecae antherarum base truncatae et breviter papilloso-fimbriate appendiculatae, appendicibus apicalibus ovato-oblongis glabris; basi stylorum breviter noduliferi, nodis obturaculiformibus in parietibus cellularum incrassatis; pili abaxiales ramorum non septati apice obtusi vel breviter acuti. Achaenia prismatica base angustiora in parietibus aliquantum firma 3-8-costata; cellulis superficialibus plerumque linearibus in partibus resiniferis, superficiis intercostalibus distincte glanduliferis in costis superne minute spiculiferis; setae pappi persistentes interiores capillares ca. 40-50 ca. 5-7 mm longae apice plerumque distincte latiores margine et extus scabriduae, squamae in seriebus exterioribus distinctae. Grana pollinis in diametro ca. 40-45 μ m spinulifera sublophata (typus A).

Type: *Joseanthus cuatrecasatii* H. Robinson

The genus contains the following five species.

Key to the species of *Joseanthus*

1. Leaf blades herbaceous, margins not recurved, secondary veins spreading at near 45°; petioles often over 10 mm long 2
2. Leaves acute at apex; heads ca. 15 mm high; involucre densely villous; corolla lobes ca. 3.5 mm long, with numerous hairs outside; without T-shaped hairs
J. trichotomus
2. Leaves with rounded apices; heads ca. 9 mm high; involucre mostly glabrous; corolla lobes 2.0-2.3 mm long, with few hairs outside; with T-shaped hairs
J. sparrei
1. Leaf blades coriaceous, margins recurved, secondary veins spreading at 75-90° or obscured; petioles usually less than 10 mm long 3
3. Leaves linear to narrowly oblong, with tomentum completely obscuring lamina below between midrib and recurved margin; involucre bracts ovate with short-acute tips
J. cuatrecasatii
3. Leaves elliptical to elliptical-oblong, with tomentum not obscuring veins on lower surface between midrib and recurved margin; in-

volucral bracts oblong with obtuse or apiculate tips4

4. Leaves up to 4-7 cm long and 1.8-2.6 cm wide; heads rather abruptly differentiated from the peduncle, peduncle without obvious scattered bracteoles; corolla lobes with few or no hairs on outer surface

J. chimborazensis

4. Leaves mostly 2-4 cm long and 1 cm or less wide; bases of heads partially obscured by minute peduncular bracteoles; corolla lobes with numerous hairs on outer surface

J. crassilanatus

Joseanthus crassilanatus (Cuatr.) H. Robinson, comb. nov.

Vernonia crassilanata Cuatr., Bot., Jahrb. Syst. 77: 67. 1956.

Colombia (Putumayo), Ecuador (Azuay, Loja).

The species seems most common in southern Ecuador, but the type and one Mutis specimen without precise locality are from Colombia.

Joseanthus cuatrecasii H. Robinson, sp. nov. Fig. 1

Plantae arborescentes 2.0-2.5 m altae dense ramosae. Caules subteretes dense erecte fulvo-velutini, internodiis plerumque 1-2 cm longis. Folia opposita, petiolis 2-4 mm longis dense tomentellis; laminae oblongae vel anguste oblongae 1.2-3.5 cm longae et 3-4 mm latae base et apice rotundatae margine integrae et valde recurvatae supra evanescentiter pilosulae glabrescentes laeves vel minute alveolatae subtus inter constam et marginem dense tomentosae, nervis secundariis obrutis. Inflorescentiae diffusae generaliter elongate thyrsoidae in terminis ramorum dense cymosae vel subcorymbosae plerumque opposita ramosae; ramis ultimis 3-5 mm longae dense pallide tomentosae raro minute bracteoliferae. Capitula ca. 10 mm alta et 5-6 mm lata; bracteae involucri ca. 23 subimbricatae ca. 5-seriatae valde inaequilongae 1.5-6.0 mm longae et 0.6-1.2 mm latae apice breviter acutae et saepe reflexae extus dense villosae. Flores ca. 10 in capitulo; corollae lavandulae ca. 6 mm longae extus superiore sensim densius pilosulae et glanduliferae, tubis cylindricis 3 mm longis, lobis ca. 3 mm longis et 0.7 mm latis; thecae antherarum ca. 2.3 mm longae; appendices antherarum oblongae ca. 0.55 mm longae et 0.27 mm latae. Achaenia ca. 3.5 mm longa ca. 10-costata et distincte glandulifera, costis irregulariter disposita; setae pappi interiores 50-60 ca. 5 mm longae, setae exteriores ca. 1 mm longae in partibus squamiformes lineares anguste acutae. Grana pollinis in diametro ca. 45 μ m.

Type: ECUADOR: Azuay: Cuenca, Parroquia Baños. Hacienda Yanasacha. Second growth cloud forest, dominant trees including *Weinmannia*, *Embothrium*, *Rapanea*, *Escallonia* and *Vallea*. 3,000-3,200 m. Shrub to 2.5 m. Inflorescence white to pink. Very common. 14 July 1978. J. D. Boeke & J. Jaramillo 2410 (holotype US; isotype NY). Paratypes: ECUADOR: Azuay: About 3 km SE of Jima on road towards San Miguel de Cuyes, 3,000 m secondary scrub. Shrub, to c. 2 m tall. Flowers white to purplish-pink. 27 April 1985. G. Harling & L. Anderson 24697 (US, GB); Cruz Pambo region above Baños (ca. 15 km. southeast of Cuenca); 9,000-10,000 ft. elev. Shrub 2 m. Lvs dark green, subnitid above. Pubescence on under surface of lvs., stems and bracts pale ochraceous. Pappus white. Corolla pale lavender. Anthers at first reddish purple, later brown. Stigmas deep lavender. June 29-30, 1945. Collectors M. Giler & F. Prieto, W.H. Camp E-3953 (US, NY); Without precise locality. W. Jameson s.n. (two specimens US).

Material of the species has been previously been identified as *J. crassilanata* which occurs in the same area. The species has a superficial resemblance to some members of *Diplostegium* of the Astereae, and the Jameson specimens were at one time annotated as possible members of that genus.

Joseanthus chimborazensis (Hieron.) H. Robinson, comb. nov.

Vernonia chimborazensis Hieron., Bot. Jahrb. Syst. 28: 559. 1901.

Vernonia neogleasoniana Cuatr., Phytologia 23: 357. 1972. Ecuador (Chimborazo, Imbabura).

The species is known only from the two specimens cited by Cuatrecasas (1972) and from the Hieronymus type.

Joseanthus sparrei (H. Robinson) H. Robinson, comb. nov.

Phytologia 34: 302. 1976.

Ecuador (Loja).

The species is known only from the type.

Joseanthus trichotomus (Gleason) H. Robinson, comb. nov.

Bull. Torrey Bot. Club 52: 190. 1925.

Colombia (Cauca).

The species is known only from the type.

Acknowledgement. — The illustration of *Joseanthus* has been prepared by Alice Tangerini, Staff Illustrator, Dept. of Botany, Smithsonian Institution.

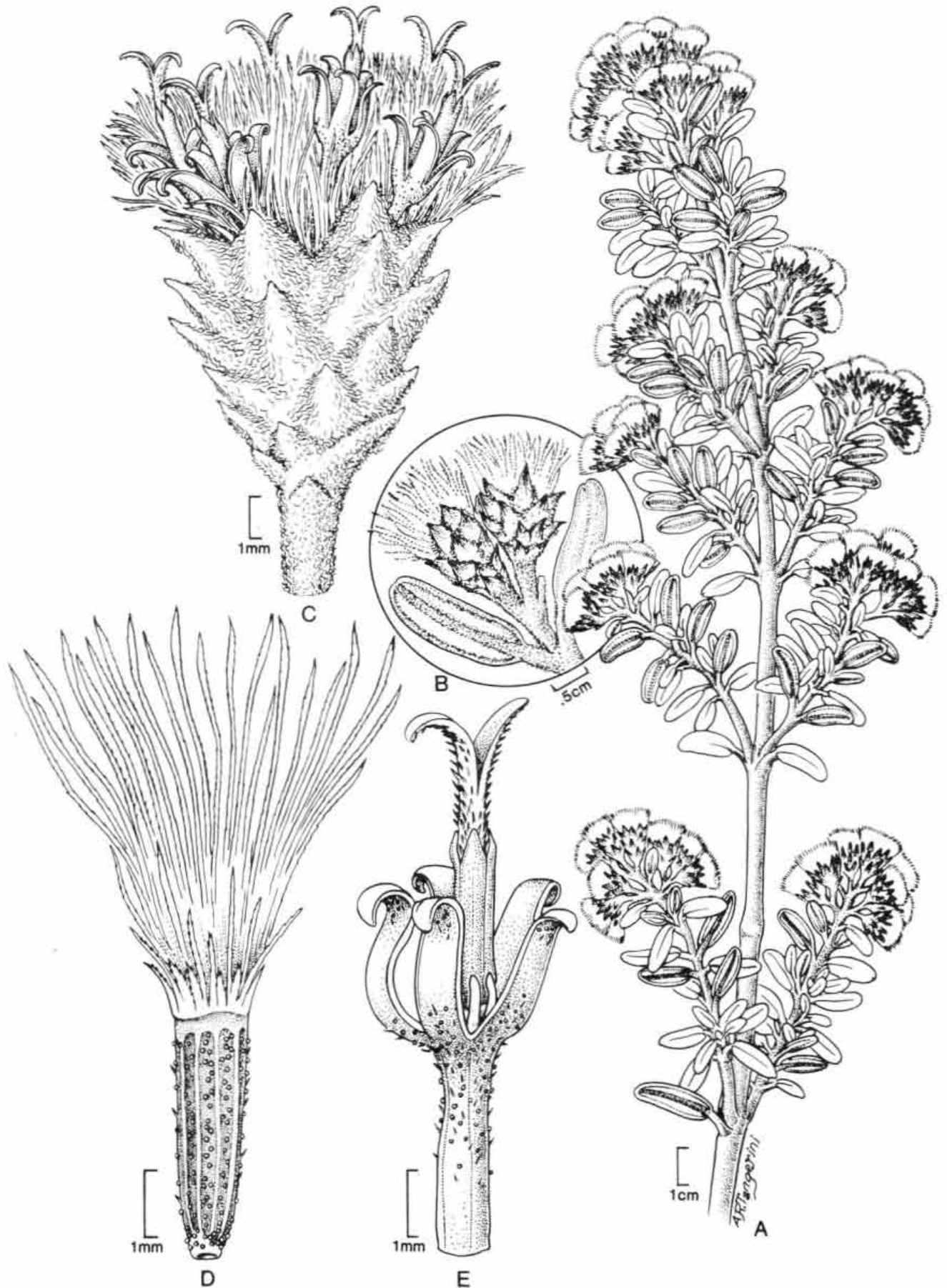


FIGURA No. 1

A-D. *Joseanthus cuatrecasii* H. Robinson. A. Branch of postanthesis plant (Camp E-3953). B. Enlargement of branch tip. C. Enlargement of head (Boeke 2410, Type). D. Achene. E. Corolla showing deeply cut lobes, stamens, and style branches.

LITERATURE CITED

- CUATRECASAS, J. 1956. Neue *Vernonia*-Arten und Synopsis der andinen Arten der Sektion *Critoniopsis*. Bot. Jahrb. Syst. 77: 52-84.
- . 1972. Miscellaneous notes on neotropical flora II. Phytologia 23: 350-365.
- ROBINSON, H. 1976. A new species of *Vernonia* from Ecuador. Phytologia 34: 301-304.
- . 1979. New species of Vernonieae (Asteraceae). I. *Vernonia harlingii* from Ecuador. Phytologia 44: 65-69.
- . 1980. Re-establishment of the genus *Critoniopsis* (Vernonieae: Asteraceae). Phytologia 46: 437-442.
- . 1987a. Studies of the *Lepidaploa* Complex (Vernonieae: Asteraceae). I. The genus *Stenocephalum* Sch. Bip. Proc. Biol. Soc. Wash. 100: 578-583.
- . 1987b. Studies of the *Lepidaploa* Complex (Vernonieae: Asteraceae). II. A new genus, *Echinocoryne*. Proc. Biol. Soc. Wash. 100: 584-589.
- . 1987c. Studies of the *Lepidaploa* Complex (Vernonieae: Asteraceae). III. Two new genera, *Cyrtocymura* and *Eirmocephala*. Proc. Biol. Soc. Wash. 100: 844-855.
- . 1988a. Studies of the *Lepidaploa* Complex (Vernonieae: Asteraceae). IV. The new genus, *Lessingianthus*. Proc. Biol. Soc. Wash. 101: 929-951.
- . 1988b. Studies of the *Lepidaploa* Complex (Vernonieae: Asteraceae). V. The new genus, *Chrysolaela*. Proc. Biol. Soc. Wash. 101: 952-958.
- . 1988c. Studies of the *Lepidaploa* Complex (Vernonieae: Asteraceae). VI. A new genus, *Aynia*. Proc. Biol. Soc. Wash. 101: 959-965.
- and V.A. Funk. 1987. A phylogenetic analysis of *Leiboldia*, *Lepidonia*, and a new genus, *Stramentopappus* (Vernonieae: Asteraceae). Bot. Jahrb. Syst. 108: 213-228. 1987.
- and B. Kahn. 1985. New species of *Vernonia* from Bolivia and Peru (Vernonieae: Asteraceae). Phytologia 58: 252-257.
- and ———. 1986. Trinervate leaves, yellow flowers, tailed anthers, and pollen variation in *Distephanus* Cassini (Vernonieae: Asteraceae). Proc. Biol. Soc. Wash. 99: 493-501.