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A Revision of *Erato* (Compositae: Liabeae)

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ABSTRACT. *Erato* DC. contains five species, distributed from Costa Rica to Bolivia, with its main center of diversity in Ecuador. The revision includes a new species endemic to Costa Rica and Panama, ***Erato costaricensis*** E. Moran & V. A. Funk. Morphological and molecular data support *Erato* as a monophyletic group, sister to *Philoglossa*. The phylogenetic analysis based on morphology used *Munnozia* Ruiz & Pavon, *Chrysactinium* (H.B.K.) Wedd., and *Philoglossa* DC. as outgroups. The phylogeny supports the monophyly of *Erato*, but the relationships among the species within *Erato* have only weak support. The genus is believed to be a recent radiation because of the morphological similarity among the taxa and their location in some of the youngest areas of the Andes.

RESUMEN. El genero *Erato* contiene 5 especies, distribuidas desde Costa Rica hasta Bolivia, con su centro de distribución en Ecuador. Este revista incluye una nueva especie que es endémica de Costa Rica y Panamá, *Erato costaricensis* E. Moran & V. A. Funk. Datos morfológicos y genéticos confirman la hipótesis que *Erato* es un grupo monofilético hermano a *Philoglossa*. El análisis filogenético utilizó *Munnozia* Ruiz & Pavón, *Chrysactinium* (HBK) Wedd. y *Philoglossa* DC. como grupos externos. La filogenia confirma *Erato* como un grupo monofilético, pero los relaciones dentro de *Erato* solo tienen soportes débiles. Créen que el genero es una radiación reciente a causa de la semejanzas morfológicas entre de las especies y porque occurien en unos de los áreas mas jóvenes de los Ándes.

KEYWORDS: Asteraceae, biogeography, Compositae, endemic, phylogeny, taxonomy.

Erato DC. (Compositae), which has not previously been revised, contains five species. It is a member of the tribe Liabeae, which has approximately 180 species in 15 genera, all confined to the Neotropics. Most of the Liabeae are perennial herbs or shrubs; some are annuals, small trees, or climbers. Characteristics of the tribe include milky sap, opposite leaves, and arachnoid tomentum, but not all genera possess all three of these characteristics. The complex history of the classification of the Liabeae reflects the difficulty of both determining the genera to be included in this tribe and inferring the relationships among them (Kim et al. 2003).

Erato is distributed from Costa Rica to Bolivia; three of the five species are native to Ecuador. *Erato* was originally described by Candolle (1836) and was placed in a position remote from other Liabeae. It was later placed within *Liabum* by Bentham in Bentham and Hooker (1873). In the generic revision of the Liabeae, Robinson and Brettell (1974) placed it within a broad concept of *Munnozia*. It was restored to separate generic status during a study of the members of the tribe in Ecuador (Robinson 1976, 1978) and since then has remained as such.

Currently, *Erato* is recognized as part of the subtribe Munnoziinae, which also includes the genera *Munnozia* Ruiz & Pavon, *Chrysactinium* (Kunth in H.B.K.) Wedd., and *Philoglossa* DC. This subtribe is distinguished by the presence of black or dark anther thecae. *Philoglossa* is usually identified as the sister group of *Erato*, with which it shares stiff, thick-based hairs on the stems and leaves, irregularly dispersed pollen spines, and a reduced number of achene ribs, two in *Philoglossa* and four in *Erato*.

Characteristics that distinguish *Erato* from other members of the Liabeae include ovate leaves that are bright green above and paler below, blades that are palmately veined with 5–9 main veins and dentate margins, and petioles that are often reddish. Arachnoid tomentum, characteristic of most of the Liabeae, is almost totally lacking in *Erato* except for tufts on the apices of the involucral bracts in two species. In *Erato* the indument usually consists of stiff, thick-based hairs and the achenes are usually four sided. Members of *Erato* are coarse, upright herbs to shrubs; *Munnozia* species are lax shrubs with many-sided achenes, found in open often sloped areas, *Philoglossa* species are small herbs found in wet areas, with single heads arising from the leaf axils, and the species of *Chrysactinium* are small acaulus herbs covered in tomentum and having solitary heads.

Our goals in this study were to use morphological characters, combined with some genetic data, to determine the phylogenetic relationships among the species of *Erato* and to identify the closest relative of *Erato* within the Munnoziinae. Close examination of herbarium collections revealed that populations of *Erato* in Costa Rica and northern Panama, previously identified as *E. vulcanica*, were a distinct species.

TABLE 1. Character List for *Erato* and outgroups.

1. Habit. Small herb (0), large herb to shrub (1)
2. Milky sap. Absent (0), present (1)
3. Petioles. Present (0), absent (0)
4. Number of main veins in leaves. 3 (0), 1 (1), 5–7 (2)
5. Pattern of leaf venation. Tri-nervate (0), pinnate (1), palmate (2)
6. Leaf dentation-1. Entire (0), irregular small teeth (1)
7. Leaf dentation-2. Entire (0), large regular teeth (1)
8. Base of hairs on leaves. Gradually tapering (0), bulbose (1)
9. Inflorescence form. Branched (0), single solitary (1), multiple solitary (2)
10. Inflorescence location. Terminal (0), axils of leaves (1), solitary (2)
11. Peduncle pubescens. Arachnoid and purplish hairs (0), stiff, erect, white hairs (1), appressed white hairs (2), long bulbose based hairs (3), tomentose and glandular (4)
12. Tufts of arachnoid tomentum on bracts. Absent (0), few, scattered (1), many, dense (2)
13. Outer involucral bracts (both surfaces): without stiff hairs (0), with stiff hairs (1)
14. Number of main veins in involucral bracts. 3 (0), 5 (1), 7 (2)
15. Inner involucral bract l/w ratio. 5 or less (0), 7 or more (1)
16. Pales. Present (0), absent (1)
17. Number of ray florets. Less than 70 (0), 75–120 (1), 120–225 (2)
18. Ray floret length. 12.5–26.5 mm (0), 7–11 mm (1)
19. Number of disc florets. 30–100 (0), 25–33 (1), < 16 (2), > 100 (3)
20. Style length. 4.5–7 mm (0), 8–13 mm (1)
21. Pappus type. Long bristles (0), small squamell or awns in one series (1), absent (2), short, multiseriate awns (3)
22. Pappus persistence. Persistant (0), deciduous or possibly absent (1)
23. Achene indument. Pubulent (0), glabrous (1)
24. Achene keels. Absent (0), present (1)
25. Achene shape. Prismatic; 6–10 ribs (0), compressed; two ribbed (1), 4-sided (2)
26. Pollen spines. Regularly dispersed (0), irregularly dispersed (1)
27. Molecular data-1. Absent (0), several site mutations supporting the *Munnozia-Chrysactinium* clade as monophyletic (1)
28. Molecular data-2. Absent (0), several site mutations supporting the *Erato-Philoglossa* clade (1)

MATERIALS AND METHODS

Characters. The morphological study was based on specimens in AAU, MO, NY, and US, all of which have extensive plant collections from Ecuador and Peru. The data derived from the specimens were supplemented by information from the literature. For microscopic examination, floral parts were rehydrated and mounted on microscope slides using Hoyer's mounting solution. A total of 26 morphological characters were assessed, as well as two genetic characters from a previous study by Kim et al. (2003; Tables 1, 2). The Kim et al. study used ITS sequence data to evaluate the monophyly of the subtribe Munnoziinae and to separate the four genera and some of the species of the subtribe; two species of *Erato* were included in the study. Each genetic "character" in this study is derived from a well supported node on the molecular cladogram of Kim et al. (2003): "character 27" represents 19 base pair changes (the node had a bootstrap value of 99%) and "character 28" represents 16 base pair changes (the node had a bootstrap value of 98%).

Most characters are self-explanatory (Table 1), but there are several that may seem similar and therefore need some discussion. Characters 4 and 5 may appear to be the same, but they are distinct in that one is the overall pattern of venation and the other is the number of main veins. The removal of either of these characters from the analysis does not change the results. In characters 6 and 7, the small teeth are independent of the larger regular teeth, and in characters 24 and 25, the compression and number of ribs are believed to be independent from the keels. Although there were 28 characters in total, only five were informative within the genus *Erato*.

Not all specimens studied are listed in this paper; however, the label information from all specimens used in this project has been sent to MO to be deposited in their online database, TROPICOS.

Outgroups. The monophyly of the four genera of the subtribe Munnoziinae was demonstrated using ITS sequence data (Kim et al. 2002); 13 base pair changes defined the node supporting the monophyly of the subtribe (98% bootstrap value). Therefore, *Munnozia*, *Chrysactinium*, and *Philoglossa* were included as outgroups. It should be noted that, according this same molecular analysis, *Chrysactinium* is nested within *Munnozia*. However, since not all species of *Munnozia* were sampled and because of the disparity in morphology between the two, they are maintained here as separate genera.

Data Analysis. Maximum parsimony analysis and parsimony bootstrap analysis (with 1000 replicate runs, each with 10 random taxon additions, TBR branch swapping, and MULPARS in effect) of the data matrix were preformed using full heuristic searches with PAUP* (Swofford 2002). No weighting was used. Maximum parsimony analysis (with ACTRAN) using a branch-and-bound search was also performed. The bootstrap runs employed 1000 replicates with branch-and-bound searches.

RESULTS

Because of morphological differences, specimens from Costa Rica previously identified as *Erato vulcanica* were described as a new species, *E. costaricensis*.

Maximum parsimony analysis yielded one most parsimonious tree for relationships within *Erato*; Fig. 1 is a phylogram of that tree with the branch lengths representing the number of characters (L=51, ci=.804, ri=.655). Figure 2 is the bootstrap consensus tree. *Erato* is monophyletic and sister to *Philoglossa*; *E. polymnioides*

TABLE 2. Data matrix for *Erato*.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Munnozia	1	1	0	0&1	0&1	1	0	0	0	0	4	0	0	0	0	0	0	1	0	?	0&1	0	0	0	0	0	1	0
Chrysactinium	0	0	1	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0&1	0	0	0	0	0	0	1	0
Philoglossa	0	0	0	0	0	1	0	1	2	1	3	0	1	0	0	1	0	1	0	0	1&2	1	1	0	1	1	0	1
Erato polymnioides	1	1	0	2	2	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0	0	1	0	2	1	0	1
Erato stenolepis	1	1	0	2	2	1	1	1	0	0	1	0	1	1	1	1	1	0	3	0	0	0	1	0	2	1	0	1
Erato costaricensis	1	1	0	2	2	1	1	1	0	0	2	1	0	1	0	1	1	0	2	1	0	0	1	0	2	1	0	1
Erato vulcanica	1	1	0	2	2	1	1	1	0	0	1	2	0	2	0	1	2	0	0&1	1	0	0	1	0	2	1	0	1
Erato sodiroi	1	1	0	2	2	1	1	1	0	0	1	2	1	2	0	1	1	0	3	1	3	1	0	1	2	1	0	1

is always the sister species to the rest of the genus. *Erato costaricensis*, *E. vulcanica*, and *E. sodiroi* form a monophyletic group and *E. stenolepis*, the Peruvian species with the wide involucral bracts, is sister to that clade. Bootstrap support for the monophyly of *Erato* was 95% and 92% for the *Erato*/*Philoglossa* clade. The relationships within *Erato* have short branches and weaker bootstrap support with four of the taxa collapsing into a polytomy and only 68% support for the clade including all species except *E. polymnioides*. The fact that the species of *Erato* are not sorting out in a morphological analysis is not surprising, for although the genus is unique in the family, and each species within the genus has several apomorphies, there are few synapomorphies among the taxa.

DISCUSSION

The species of *Erato* have a narrow range of morphological and ecological diversity and this similarity could be interpreted as the result of a recent radiation. This scenario fits with the geologic history of the area. The Andean Cordillera is thought to be of recent origin; it was (and continues to be) formed by the Nazca plate colliding with the South American plate along the Peru-Chile trench (James 1973; Jordan et al. 1983). About three million years ago the Isthmus of Panama first connected North and South America and there is evidence of faunal movement across the isthmus at 2.8 MYA (Knowlton et al. 1991; Bermingham pers. comm.). Sea level fluctuated several times; as little as 12,000 years ago it was lowered, exposing the isthmus. At the same time the climatic zones in the Andes were lowered (B. S. Vuilleumier 1975; Gentry 1982). It may have been at this later date that *Erato*, along with some other members of the tribe, *Liabum*, *Munnozia*, and *Oligactis*, managed to colonize Central America and southern Mexico. Molecular and morphological studies (Funk et al. 1996; Kim et al. 2003) indicate that an ancestor of the extant members of the Munnoziinae was most likely a beautiful herb from Ecuador and northern Peru.

TAXONOMIC TREATMENT

ERATO Candolle, Prodr. 5:318, 1836.—*Munnozia* subg. *Erato* (Candolle) H. Robinson & Brettell, Phytologia 28:56, 1974.—TYPE: *Erato polymnioides* Candolle.

Perennial herbs to large shrubs, occasionally climbers, 1–5 m tall, sap milky. *Stems* sparsely to densely pubescent, hairs stiff, white; lengths of internodes variable, usually 3–16 cm. *Leaves* opposite, lighter green abaxially and lacking tomentum; stipules 0.5–5.0 cm long, broadly oblong, usually emarginate; petioles 1–25 cm long, unwinged, often reddish in color; blades ovate to broadly ovate; 3–27 × 3–27 cm, pal-

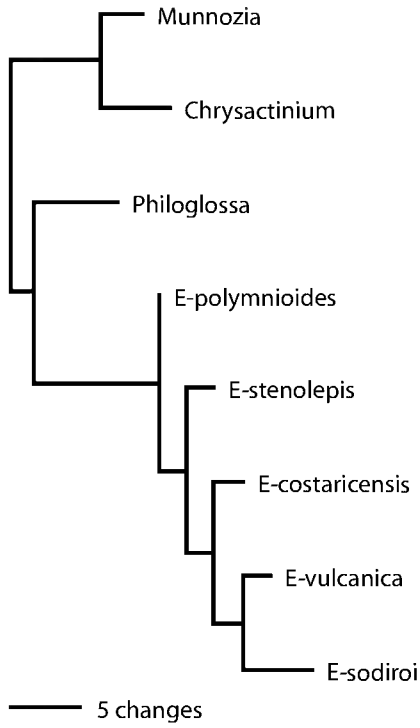

FIG. 1. The most parsimonious tree for the five species of *Erato* and its three outgroups. Munnozia and Chrysactinia are shown as sister taxa because of information from a previous publication (Kim et al. 2003; see text for details).

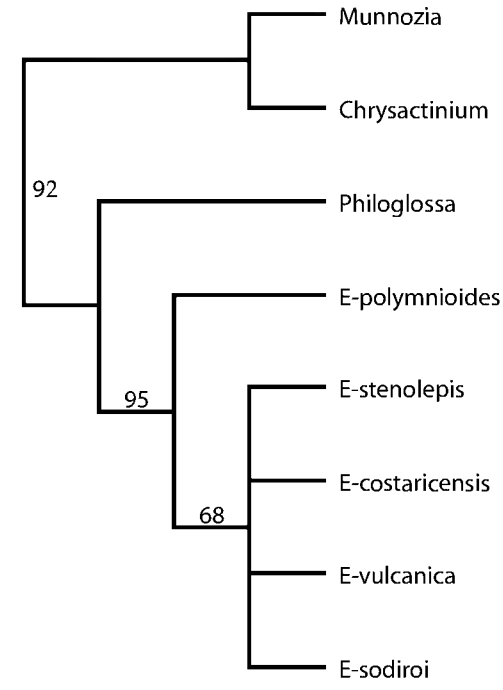

FIG. 2. Bootstrap tree for the five species of *Erato* plus outgroups; branches show bootstrap values.

mately veined, main veins 5–7 (–9), bases truncate, cordate, rounded, attenuate, or slightly indented, sometimes asymmetrical; margins usually irregularly dentate; apices acute to shortly and sharply acuminate; both surfaces strigose or pubescent, hairs short, appressed. *Inflorescence* terminal, loosely cymiform to densely subumbelliform; peduncles 1–13 cm long, lightly to densely hispid, hairs stiff, white. *Heads* broadly campanulate, usually 0.6–1.8 × 0.6–2.7 cm. *Involucral bracts* (phyllaries) 40–100 in 4–6 series, triangular to lanceolate, sometimes with tufts of arachnoid tomentum at apices, inner and outer series distinct; outer bracts 3.0–10.5 × 1.7–3.0 mm, triangular to lanceolate, main veins 5 or 7 main, margins ciliate, apices acute with herbaceous tips; inner bracts 7–12 × 1.5–2.5 mm, lanceolate to oblong, usually lighter in color, sometimes with ciliate margins, apices acute to rounded. *Ray florets* 75–225, fertile; corollas yellow, 7.0–26.5 mm long, tubes 2.5–5.5 × 0.25–0.50 mm; laminae 5.0–22.5 × 0.5–1.0 mm, 2–3 apical teeth 0.3–0.5 mm long; styles 5.9–10.0 mm long, style branches 1–3 mm long. *Disc florets* 11–150, bisexual; corollas 6.5–9.0 mm long, tubes 2.5–5.0 × 0.5 mm, throats 3.2–5.5 × 2.0–3.5 mm, lobes 2.5–3.0 mm long with stomates near margin and apices strongly spiculiferous; stamens 6–8 mm long, cells of anther collars not or weakly annulated on walls, thecae 2.5–3.0 mm long, black, not digitate at bases, apices 0.2–0.5 mm, acute; nectaries elongate, slightly lobed; style branches short. *Achenes* four-sided, one species with keel-like ridges on two sides, glabrous or puberulous, 1.2–2.0 × 0.5–1.0 mm, light to dark brown. *Pappus* of either 20–48 persistent pale bristles, 4–8 mm long, or ca. 20, short, broad, fragile, pale, straw-colored scales (awns) 0.5–1.5 mm long. *Pollen* grains 30–40 μm in diameter, spines unevenly dispersed, distinct internal columellae grouped under spines.

Distribution and Habitat. *Erato* is native to Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, and Bolivia at 360–3800 meters. Its members often grow in open forest, pastureland, and forest edges, or along roadsides and streams, in part shade to full sun.

Chromosomes. *Erato* generally has numbers of $n = 7$ or 9, in contrast to $n = 18$ in *Philoglossa* and $n = 10, 11, 12$, c. 13, c. 24 in *Munnozia*/*Chrysactinium* (Robinson et al. 1985).

Notes. *Erato* is easily recognizable because of its unusual leaves, which are opposite, shiny green, and palmately veined, with reddish petioles and margins that are irregularly dentate or with two levels of dentation. Production of latex varies over time; sometimes plants might seem to lack latex.

Key to Species of *Erato* (English)

1. Involucral bracts with 7 main veins; arachnoid tomentum at apices of involucral bracts in prominent or sparse tufts 2
   2. Achenes puberulous with 2 prominent keel-shaped ridges; pappus of ca 20 short, broad, deciduous scales, 0.5–1.5 mm; ray florets 90–120; disc florets 110–150; tufts of arachnoid tomentum mainly on the inside of involucral bracts; Ecuador . . . . . 2. *E. sodiroi*
   2. Achenes glabrous, without keels; pappus of 27–48 persistent bristles 4–7 mm long; 120–225 ray florets; 25–100 disc florets; arachnoid tomentum sparse on outside of involucral bracts; Venezuela, Colombia, and Ecuador . . . . . 5. *E. vulcanica*
1. Involucral bracts with 5 main veins; arachnoid tomentum at apices of involucral bracts either absent or, rarely, in small tufts 3
   3. Heads large, ca 120 disc florets; involucral bracts without tufts of arachnoid tomentum; surfaces of involucral bracts with hairs; inner involucral bracts long, length/width ratio > 7; ray floret tubes glabrous; Peru . . . . . 3. *E. stenolepis*
   3. Heads small, < 40 disc florets; involucral bracts rarely or never with tufts of arachnoid tomentum; surfaces of involucral bracts with few to no hairs; inner involucral bracts short, length/width ratio < 5; ray floret tubes hairy 4
      4. Heads small, 23–33 disc florets; ray corollas 7.0–11.5 mm long; involucral bracts never with tufts of arachnoid tomentum; plants 1–5 m tall; peduncles with white, stiff, erect hairs; elevation 360–3050 m; Colombia, Ecuador, Peru, and Bolivia . . . . . 4. *E. polymnioides*
      4. Heads very small, 11–16 disc florets; ray corolla 13.0–16.0 mm long; involucral bracts occasionally with small tufts of arachnoid tomentum; plant 0.5–3.0 m tall; peduncles covered with white, appressed hairs; elevation 1200–1700 m; Costa Rica and Panama . . . . . 1. *E. costaricensis*

Key To Species of *Erato* (Spanish)

1. Brácteas involucrales con 7 nervios principale; tomento aracnoide en el ápice de las brácteas involucrales 2
   2. Aquenios puberulentos, con dos quillas prominentes; pappus de ca. 20 escamas cortas, anchas, y deciduas, 0.5–1.5 mm; flores radiadas 90–120; flores del disco110–150; tomento principalmente en el reverso de las brácteas involucrales; Ecuador . . . . . 2. *E. sodiroi*
   2. Aquenios glabros, sin quillas; pappus de 27–48 cerdas persistentes, 4–7 mm de largo; flores radiadas 120–225; flores del disco 25–100; presente en Venezuela, Colombia y Ecuador . . . . . 5. *E. vulcanica*
1. Brácteas involucrales con 5 nervios principales; tomento aracnoide ausente o raro 3
   3. Capítulos largos, con ca. 120 flores del disco; brácteas involucrales sin tomento aracnoide; brácteas involucrales pubescentes en ambas superficies, y brácteas interiores largas, largo/anchura >7; tubo de flores radiadas glabros; Perú . . . . . 3. *E. stenolepis*
   3. Capítulos pequeños, con < 40 flores del disco; brácteas involucrales raramente o nunca con tomento aracnoide; brácteas involucrales glabras o con pocos pelos, y brácteas interiores cortas, largo/anchura <5; tubo de las flores radiadas pubescente 4
      4. Capítulos pequeños, con 23–33 flores del disco; flores radiatas 7.0–11.5 mm; brácteas involucrales sin tomento aracnoide; arbusto de 1–5 m de altura; pedunculos 1.0–7.5 con pelos blancos cano-hirsutos; rango altitudinal 360–3050 m; presente en Colombia, Ecuador, Perú y Bolivia . . . . . 4. *E. polymnioides*
      4. Capítulos muy pequeños, con 11–16 flores del disco; flores radiadas 13.0–16.0 mm de largo; brácteas involucrales a veces con un poco de tomento aracnoide; arbusto 0.5–3.0 m de altura; pedunculos cano seríceos; rango altitudinal 1200–1700; Costa Rica y Panamá . . . . . 1. *E. costaricensis*

1. **Erato costaricensis** E. Moran & V. A. Funk, sp. nov.,—TYPE: COSTA RICA. Cartago: Refugio Nacional de Vida Silvestre Tapantí, 14 Feb 1992, *F. Almeda 7001* (Holotype: US!; isotypes NY! CA). Fig. 3.

Similis Erato polymnioides sed: Frutex vel herba grossa 0.5 ad 3.0 m altus, aliquando scandens, pedunculi cum pilis albis appressis, capitulum 0.8 ad 1.3 cm altum, 0.8 ad 1.9 cm latum, flores disci 11–16, bracteae involucralae apice persaepe cum caespibus tomenti arachnoidei, bracteae externae 5 ad 6 mm × 1.5 ad 2.0 mm latae, flores radii corolla longiora, 13 ad 16 mm, flores disci pauci 11 ad 16.

Perennial herbs to shrubs, 0.5–3.0 m tall, sometimes vine-like, sap milky. *Stems* terete, hairs scattered, stiff, white; internodes variable in length, usually 3.5–13.0 cm; stipules 1.1–1.8 cm long, hairs sparse. *Leaves* darker green adaxially, lighter abaxially; petioles 2–15 cm long, reddish; blades ovate to broadly ovate, 10.5–22.5 × 4–20 cm, main veins 5–7, base usually rounded, sometimes truncate or slightly indented, margins irregularly dentate; apices shortly to sharply acuminate; both surfaces with scattered, slender, short, appressed hairs. *Inflorescence* terminal, cymiform; peduncles 1.5–8.2 cm long, densely pubescent, hairs appressed. *Heads* broadly campanulate, usually 0.8–1.3 × 0.8–1.9 cm. *Involucral bracts* 50–70 in 5–6 series, oblong to lanceolate, usually without tufts of arachnoid tomentum; outer bracts 5–6 × 1.5–2.0 mm, triangular to oblong, main veins 5, margins lightly ciliate, apices acute; inner bracts lighter in color, oblong with hyaline margins, 5.5–8.5 × 1.2–2.0 mm, apices rounded to acute. *Ray florets* 80–113; corollas yellow, 13–16 mm long, tubes 4.0–5.5 × 0.25 mm, sparsely puberulous distally; lamina 9.0–10.5 × 0.3–0.5 mm, apical teeth 3, 0.3 mm long; styles ca 8.0 mm, style branches 1.5–2.5 mm. *Disk florets* 11–16; corollas yellow, 7–9 mm long, tubes 2.5–3.5 × 0.5 mm, throats 4.5–5.5 × 2.5 mm, sparsely puberulous distally, lobes 2–3 mm long; stamens 6–8 mm long, thecae 2.2–2.5 mm long, black, apical appendages 0.2 mm, acute; styles 7–10 mm, style branches 0.6

FIG. 3. *Erato coastaricensis* E. Moran & V. A. Funk. A. habit, B. head, C. disc corolla, stamens and style, D. ray corolla and style, E. disc style, F. achene and pappus. Illustration by Alice Tangerini (US).

mm, apices acute. *Achenes* 1.5 × 0.4–0.6 mm, brown, glabrous. *Pappus* of ca 30 setae, 4.0–6.5 mm long, white to straw-colored.

Distribution and Habit. *Erato costaricensis* is known mostly from Costa Rica with one collection from Panama (Fig. 4). It is usually found in wet forest, on forested hillsides, or in cut-over areas and along roadsides. It grows in part shade to full sun at 1,200–1,700 meters.

Phenology. This species has been collected in flow-

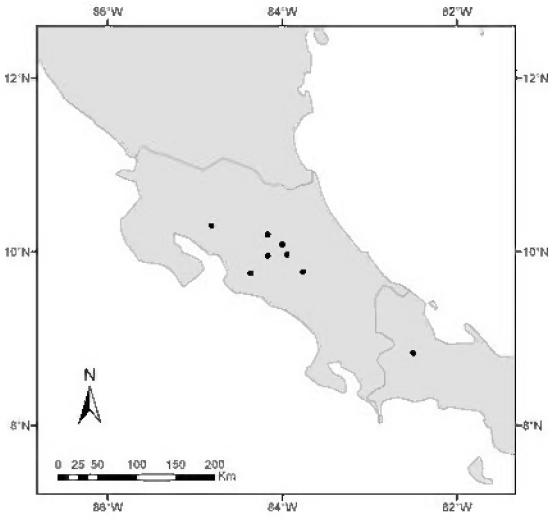

FIG. 4. Map showing the distribution of *Erato costaricensis* E. Moran & V. A. Funk.

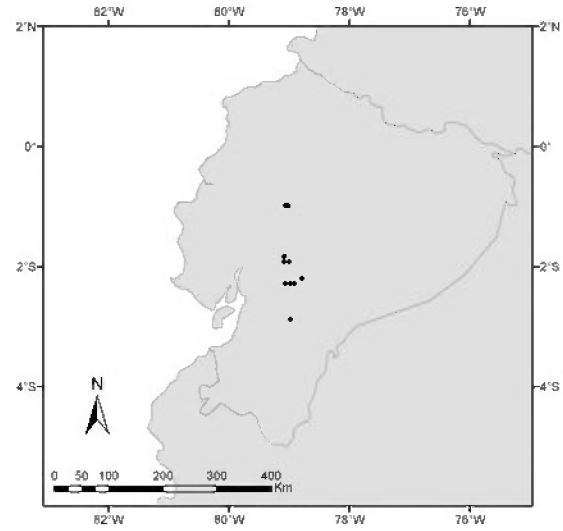

FIG. 5. Map showing the distribution of *Erato sodiroi* (Hieron.) H. Rob.

er in December, February, March, May, June, and August.

Notes. *Erato costaricensis* can be distinguished from other species in the genus by its relataively small heads (disc florets 11–16), long ray florets (13–16 mm), appressed, rather than bristly, hairs on the peduncles, and a pappus of ca. 30 setae.

Representative Specimens Examined. COSTA RICA. **Alajuela:** Vera Blanca - San Miguel rd, 17 Aug 1994, *Kress 4810* (US); Varablanca intersection on the rd to Puerto Viejo, 28 Feb 1986, *Almeda 5172* (US). **Cartago:** Tapantí Hydroelectric Project, 25 Jun 1976, *Utley 5173* (US); 25 Feb 1990, *King 10001* (MO, US); S of Tapantí, 12 Dec 1969 *Burger 6790* (MO); 9 km NW of Tapantí Dam, 10 Aug 1980 *Wilbur 30775* (MO). **Heredia:** 15 km NE of Santa Domingo, 31 Dec 1974, *Taylor 17868* (US); 35km. NE of Alajuela, 18 Aug 1967, *Taylor 4539* (MO, NY, US). **San Jose:** La Hondura, 2–4 Mar 1924, *Standley 36589* (US); La Palma, 17–18 Jul 1923, *Maxon 8030* (US); Nubes, 13 Jun 1974, *King 6782* (US); ca. 5 km N of Tunel Zarqui, 5 Dec 1995 *Hammel 20005* (INB, MO). **Puntarenas:** Monteverde Reserve, 10 Jan 1980, *Funk 3063* (US); Monteverde, Mirador La Ventana, 9 Feb 1994, *Lépiz 144* (CR, NY); Guanacaste, rd at Continental Divide, 1 Nov 1977, *Dryer 1111* (MO).

PANAMA. Bocas del Toro: 5 km ENE of Cerro Pate Macho, headwaters of Rio Culebra, 11 Feb 1979, *Hammel 6146* (MO, PMA).

2. ERATO SODIROI (Hieronymus) H. Robinson, Phytologia 34:379, 1976.—*Liabum sodiroi* Hieron., Bot. Jahrb. 29:61, 1900. *Munnozia sodiroi* (Hieron.) H. Robinson & Brettell, Phytologia 28:57, 1974.—TYPE: ECUADOR. Near San Florencio, Pallatanga etc., growing in subtropical regions, *s.d., Rev. P.(A.) Sodiro S.J., s.n. (55/11)* (B [destroyed]; Lectotype here designated: QPLS, photos of lectotype have been examined).

Coarse herbs, occasionally scrambling or shrub-like, usually 1–3(–5) m tall, sap milky. *Stems* terete, sometimes hexagonal when dry, brownish, pubescence dense, hairs stiff, white; internodes variable in length, usually 3.5–8.0 cm; stipules 0.5–1.2 cm long, puberulous. *Leaves* darker green adaxially, lighter abaxially; petioles 1–10 cm long; blades ovate to very broadly ovate, 4–16 × 2–14 cm, main veins 5–7, base truncate, in older leaves slightly indented, in younger leaves often attenuate, margins irregularly dentate, teeth coarse; apices shortly and sharply acuminate; adaxial surface sparsely to densely strigose, abaxial surface with dense, short, slender, appressed hairs. *Inflorescence* terminal, loosely cymiform with few branches; peduncles 3.0–12.0 cm long, densely hispid, hairs stiff, white. *Heads* broadly campanulate, usually 1.0–1.7 × 1.3–2.5 cm. *Involucral bracts* 60–100 in 4–5 series, apices with tufts of arachnoid tomentum; outer bracts triangular to lanceolate, ca 7.0 × 3.0 mm, main veins 7, both surfaces with stiff hairs, margins ciliate, apices acute with herbaceous tip, 3–7 mm long; inner bracts lanceolate to oblong, ca 9.0 × 2.5 mm, lighter in color with hyaline margins, apices rounded to acute. *Ray florets* 90–120; corollas yellow, 18.5–26.5 mm long, tubes 3.0–4.0 × 0.25 mm, distally densely hirsute, hairs long; lamina 15.5–22.5 ×1.0–1.5 mm, apical teeth 3, 0.5 mm long; styles 10 mm, style branches 3 mm. *Disk florets* 110–150; corollas yellow, 8 mm long, tubes ca. 4.0 × 0.5 mm, throat 4.0 × 2.5 mm sparsely puberulous to hirsute distally, lobes 2.5 mm long; stamens 6 mm long, thecae 3 mm long, dark brown to black, apices 0.25 mm, acute; styles 10.5 mm, style branches 0.7 mm, apices acute. *Achenes* with prominent keel-shaped ridges on two edges, ca 2 × 1 mm, brown, puberulous. *Pappus* of ca. 20 scales, 0.5–1.5 mm long, broad, fragile, pale, straw colored.

Distribution and Habitat. *Erato sodiroi* is known from Ecuador, in disturbed cloud forest, on steep roadsides, and along creeks in wet forests (Fig. 5). It is

sometimes described as climbing over shrubs. It grows at 1780–2769 meters.

Phenology. This species blooms between late May and early September, most commonly in July.

Notes. *Erato sodiroi* can be distinguished from other species in the genus by its short, easily deciduous pappus scales and its puberulous, double-keeled achenes.

Conservation Status. Vulnerable.

Specimens Examined. ECUADOR. **Azuay:** Cuenca, 3 Aug 1996, *Palacios 13812* (MO). **Bolivar:** Chillanes-Bucay rd, 1 Sep 1987, *Zak 2680* (AAU, MO, NY, US); E of Chillanes on rd to Pallatanga, 23 May 1990, *King 10202* (MO, US); Chillanes-Yaquibusu Rd, 20 Jul 1991, *Van der Werff 12528* (NY, US); Chillanes-Tambillo-Trigoloma rd, 5 Sep 1987, *Zak 2756* (AAU, MO, NY, US); Guaranda-San Pablo rd, 28 Aug 1987, *Zak 2548* (AAU, MO, NY, US). **Cañar-Chimborazo border:** Between Sta. Rosa and Joyagshi, 6–9 Jul 1945, *Camp, E-4034* (NY, US). **Chimborazo:** Chunchí, 27 Jul 1959, *Barclay 8314* (MO, US); Huigra 28 Aug 1918, *Rose 22413* (NY, US); Cañon of the Rio Chanchan, ca. 5 km N of Huigra 19–28 May 1945, *Camp E-3263* (MO, NY); N of the intersection of the southernmost entrance to Huigra and the Pan American Hwy on rd to Riobamba, 5 Jul 1992, *Panero 2930* (US); Valle de Pallatanga, *s.d., Spruce s.n.* (NY); Valle Pallatango and M. Chimborazo, s.d., *Sodiro s.n.* (BAF, presence confirmed but specimen not seen). **Cotopaxi:** E of Macuchi, 1–24 Jul 1982, *Dodson 13440* (MO, US); Pilaloa-Macuchi rd, 17 Nov 1939, *Haught 2959* (NY, US).

3. ERATO STENOLEPIS (S. F. Blake) H. Robinson, Phytologia 28:43–63, 1974.—*Liabum stenolepis* S. F. Blake, J. Wash. Acad. Sci. 17:302, 1927.—TYPE: PERU. Huanuco: Muña, trail to Tambo De Vaca, 2440 m, 27 Jun 1923, *J.F. Macbride 4338* (Holotype: US!; Isotype: F, presence of isotype at F was confirmed, specimen was not seen).

Large perennial herbs, occasional climber, sap milky. *Stems* terete, hairs scattered to moderately dense, stiff, white; stipules 0.6–1.5 cm long, sparsely hairy. *Leaves* darker green adaxially, lighter abaxially; petioles 1.5–7.0 cm long; blades ovate, 6.5–13.0 × 3.5–11.0 cm, main veins 5–9, base acute, margins dentate; apices acuminate; leaf surfaces densely strigose or pubescent, hairs short, appressed. *Inflorescence* terminal, loosely cymiform with few branches; peduncles 1.0–11.5 cm long, densely hispid, hairs stiff, white. *Heads* broadly campanulate, usually 1.2–1.8 × 1.1–2.7 cm. *Involucral bracts* 72–88 in 4–5 series, margins ciliate; outer bracts ca 10.5 × 2.0 mm, oblong to lanceolate, main veins 5, both surfaces with stiff hairs, apices acute; inner bracts ca 12.0 × 1.0–1.5 mm, lighter in color, elongate, margins sometimes darker in color, apices acute. *Ray florets* ca 100; corollas lemon yellow to greenish yellow, 16–20 mm long, tubes 6–8 × 0.25 mm, glabrous; lamina 10–12 × 1 mm, apical teeth 3, 0.5 mm long; styles 9 mm, style branches 2.5 mm. *Disk florets* ca 120; corollas yellow, 8.0 mm long, tubes ca 4.0 × 0.5 mm, throat 4.0 × 2.5 mm, hirsute at base, lobes 3 mm long; stamens 8.0 mm long, thecae 2.7 mm long, black, apices 0.5 mm, acute; styles 6 mm, style branches 1.5 mm, apices acute. *Achenes* four-sided, 1.25–1.5 × 0.5–0.7 mm, brown, glabrous. *Pappus* of 24–45 setae, 5–8 mm long, straw colored.

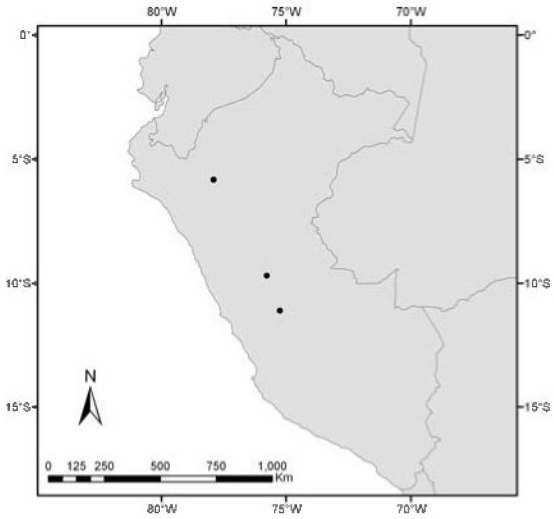

FIG. 6. Map showing the distribution of *Erato stenolepis* (S. F. Blake) H. Rob.

Distribution. *Erato stenolepis* is endemic to Peru, found at elevations of around 2000 meters (Fig. 6).

Notes. This species can be distinguished from other species in the genus by its large heads and extremely long and narrow inner involucral bracts. In his original description Blake quoted from the label that the plant was a "Liana, flowers lemon-yellow." (Blake 1927).

Specimens Examined. PERU. **Amazonas:** Florida, 18 Jan 1983, *King 9237* (US). **Junin:** La Merced, 15 Aug 1957, *Hutchison 1190* (NY, US).

4. ERATO POLYMNIOIDES deCandolle, Prodr. 5:318, 1836.—TYPE: PERU. "Peruvian mountains", 1791, *T. Haenke, 8161* (G-DC! Image of holotype seen). *Munnozia polymnioides* (DC.) H. Robinson & Brettell, Phytologia 28:56, 1974.

Liabum pallatangense Hieron. Bot. Jahrb. 29:60, 1900. TYPE: ECUADOR. Pallatanga valley and Piloton, s.d., *Rev. P. Sodiro s.n.* 55/12 (Holotype: B [destroyed]). Fig. 7.

Shrubs to coarse herbs, 1–5 m tall, sap milky. *Stems* hexagonal when dry, older stems terete, brownish to reddish, usually pubescent, hairs stiff, white; internodes variable in length, usually 4.0–16.0 cm; stipules 0.9–5.0 cm long, emarginate, hairs few. *Leaves* deep to bright green adaxially, lighter abaxially; petioles 2.0–25.0 cm long; blades ovate to very broadly ovate; 9–26 × 3–27 cm, main veins 5–7(–9), base usually cordate, rounded, or attenuate, sometimes truncate or slightly indented, margins singly or doubly dentate, teeth coarse; apices shortly and sharply acuminate; both

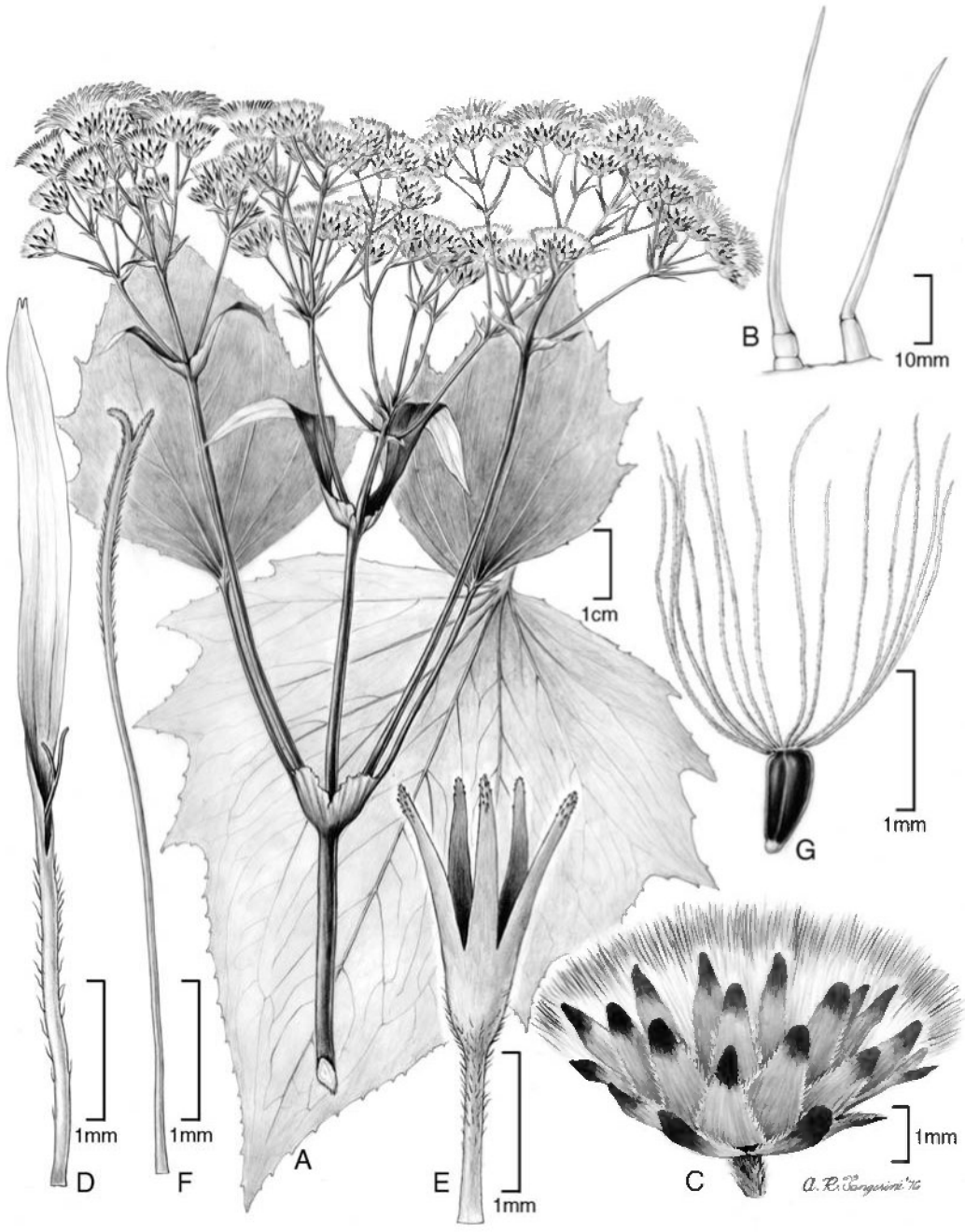

FIG. 7. *Erato polymnioides* DC. A. habit, B. hairs from disc corolla, C. head, D. ray corolla and style, E. disc corolla, F. disc style, G. achene with pappus. Illustration by Alice Tangerini (US).

surfaces sparsely to moderately densely strigose or pubescent, hairs short, appressed. *Inflorescence* terminal, usually strongly cymose to densely subumbellate; peduncles 1.0–7.5 cm long, lightly to densely hispid, hairs stiff, white. *Heads* broadly campanulate, often densely clustered, usually 0.6–1.8 × 0.6–2.4 cm. *Involucral bracts* 40–70 in 4–5 series, triangular to oblong, no arachnoid tomentum; outer bracts 3.0–5.5 × 1.7–2.0 mm, triangular to lanceolate, main veins 5, hairs absent or few, margins ciliate, apices acute with short herbaceous tip; inner bracts ca 7.0 × 1.5 mm, lanceolate to oblong, apices acute to slightly rounded. *Ray florets* 75–100; corollas yellow, 7.0–11.5 mm long, tubes 2.5–4.5 × 0.25 mm, puberulous, lamina 5.0–7.5 × 0.5 mm, 2–3 apical teeth 0.5 mm long; styles 5.9–7.0 mm, style branches 1.0–1.4 mm. *Disk florets* 23–33; corollas

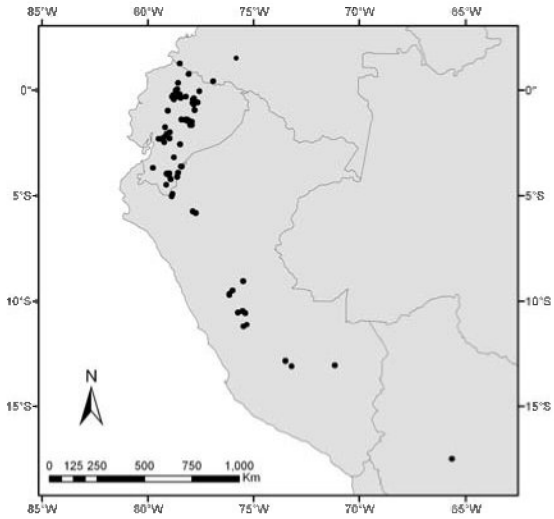

FIG. 8. Map showing the distribution of *Erato polymoniodes* DC.

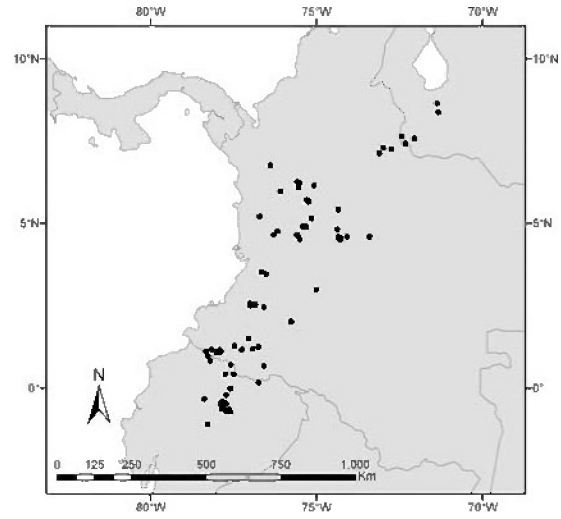

FIG. 9. Map showing the distribution of *Erato vulcanica* (Klatt) H. Rob.

yellow, 6.5–7.0 mm long, tubes 3.0–3.5 × 0.5 mm, hirsute, throat 3.5 × 2.5–3.5 mm, glabrous except at base, lobes ca. 2.5 mm long; stamens 6.0 mm long, thecae ca. 2.5 mm long, black, apices 0.25 mm, acute; styles 4.0–5.5 mm, style branches 1mm, apices acute. *Achenes* four-sided, 1.2–1.5 × 0.5 mm, light to dark brown, glabrous. *Pappus* of 20–40 setae, 4–6 mm long, persistent, pale.

Distribution and Habitat. *Erato polymnioides* is native to Ecuador, Peru, Colombia, and Bolivia. It is found in primary, secondary, or disturbed moist forests, pastureland, scrub chaparral, steep rocky slopes and is often along roads or riverbanks or in pastureland, usually in bright to partial sun. It is often locally abundant at elevations from 360–3050 meters. Fig. 8.

Phenology. This species apparently blooms throughout the year.

Notes. *Erato polymnioides* can be distinguished from other species in the genus by its small heads with involucral bracts that are completely lacking tufts of arachnoid tomentum and by the bristly pubescence on the peduncle.

Representative Specimens Examined. BOLIVIA. **Cochabamba:** Colomi- Tunari rd, 8 Feb 1978, *King 7702* (MO, US).

COLOMBIA. **Caqueta:** Florencia-Suaza rd, km 47, 20 Nov 1993 *Ramirez 5329* (JAUM, MO). **Valle:** Buga-El Placer rd, 12 Sep 1991, *Silverstone-Sopkin* 6369 (US).

ECUADOR. **Bolivar:** Balsapampa, 19 May 1968, *Harling 9645* (US). **Cañar:** 78 km W of Canar, 23 Jan 1979, *King 7797* (US); Rd El Triunfo-Cañar, 5 Feb 1976, *King 7002* (NY, US); 40km E of bridge at Guayaquil, 21 Jan 1979, *King 7734* (US). **Carchi:** near Maldonado, 31 May 1978, *Madison 4823* (AAU). **Chimborazo:** Rd to Chillanes, 22 May 1990, *King 10190* (US); Near Huigra, 7 Sep 1918, *Rose 22583* (NY, US); 7–14 May 1945, *Camp, E-3152* (MO, NY, US); Pallatanga, Jul 1903, *Sodiro s.n.* (US); s.d., *Sodiro s.n.* (BAF, location confirmed but specimen not seen, MO); Jul 1903, *Mille s.n.* (NY). **Cotopaxi:** Macuchi, 1 May 1968, *Harling 8872* (NY, US). **El Oro:** Trail from Sambotambo along hwy to Portovelo, 29 Aug 1943, *Steyermark 54229* (NY); W of Piñas, 4 Feb 1979, *King 7971* (US). **Guayas:** 21 km E of El Triunfo, 25 Jan 1979, *King 7799* (US). **Imbabura:** Cotacachi, Hda. La Florida, 28 Aug 1992, *Alvarez 630* (MO, US); Cotachi-Nangulbí and Apuela rd, 11–14 Aug 1990, *Rubio 536* (AAU, MO, US). **Loja:** Loja-Zamora rd, km 15, 23–24 Apr 1988, *Madsen 74012 (AAU).* **Morona-Santiago:** Sigsig-Chiquinda rd, 26 Oct 1995, *Funk 11455* (US); Guarumales (Cola de San Pablo), 19–20 Sep 1983, *Larsen 45309* (AAU); 9–10 km SE of San Juan Bosco, 27 Jan 1981, *Gentry 30845* (MO). **Napo:** Baeza, 28 Jul 1974, *Plowman 3902* (US); Cerro Huacamayos, 9–10 Aug 1980, *Øllgaard 35901* (AAU, US); Cordillera del Guacamayo, 3 Aug 1984, *Dodson 14850* (US); Cosanga, 21 Feb 1978, *Kirkbride 4271* (US); E of Papallacta, 26 Mar 1972, *MacBryde 1265* (US); Salcedo-Napo rd, 4 Feb 1977, *Boeke 900* (AAU, NY, US); San Ramón, 8–12 Jun 1929, *Killip 24529* (US); Yanayacu Biological Station, 28 Dec 2000, *Clark 5784* (US); Parque Nacional Llanganates, Salcedo-Tena rd, km 74–75, 14 Sep 1998, *Vargas 2349* (MO, QCNE); Cotundo-Coca, new rd km 2, 5 Aug 1984, *Dodson 15025* (MO). **Napo-Pastaza:** Mera, in rastrojo, 4 Apr 1956, *Asplund 20135* (NY). **Pastaza:** Mera, 27 Mar 1968, *Harling 7880* (US); 30 Jul 1980, *Øllgaard 35575* (AAU, US); 5 km NE of Mera Carretera al Rio Ansu, 3 Mar 1985, *Neill 5941* (AAU, MO, NY); Puyo 18–20 Feb 1935, *Mexia 6957* (US); Veracruz, 24 Jun 1968, *Lugo 36* (NY, US); 2 km N of Shell-Mera, 6 Jun 1968, *Holm-Nielsen 350* (AAU, NY). **Pichincha:** Bosque Protector Maquipucuna 1 Sep 1993, *Webster 30106* (US); Old rd to Chiriboga km 39, 23 Jul 1984, *Dodson 14348* (AAU, US); Cornejo Astorga (Tandapi), 7–10 May 1968, *Harling 9390* (US); Quito Cantón, 3 Dec 1996, *Clark 3536* (MO, US); Reserva Florística-Ecológica "Rio Guajalito", 18 Aug 1985, *Zak 566* (AAU, MO, NY, PMA, US); Saloya, 28 Jun 1939, *Asplund 7300* (US); San Juan to Chiriboga, 23 Feb 1993, *Funk 11044* (US); Lloa-Mindo rd, btw km 30–34, 4 Jul 1987, *Zak 2114* (AAU, MO, NY); 13 kms N of Nono, 21 Jul 1977, *Stuessy 4861* (MO); 11 km W of Tandapi, 26 Oct 1974, *Gentry 12086* (AAU, MO); Chillogallo-Santo Domingo rd below Chiriboga, 13 Aug 1980, *Holm-Nielsen 24850* (AAU); Parroquia Nanegal, Reserva Maquipucuna, 12 Jul 1990, *Webster 28177* (MO). **Sucumbios:** Reserva Ecológica Cayambe-Coca, 12 Aug 1999, *Vargas 3958* (MO, US). **Tungurahua:** Baños, 25 Sep 1923, *Hitchcock 21793* (NY, US); Btw Ambato & Baños, 10 Jan 1981, D'Arcy 13998 (MO); NW of Puyo, 23 Jan 1974, *King 6575* (NY, US); Baños-Mera rd ca. 30 from Mera, 27 Mar 1983, *Lawesson 43287* (AAU). **Zamora-Chinchipe:** Cordillera del Cóndor, 15 Dec 2000, *Montenegro 163* (MO, US); Loja-Zamora rd, 30 Dec 1980, *Balslev 1264* (AAU, NY, US); Loja-Zamora rd, Km 24.5, 9 Aug 1997, *Lewis*

3423 (US); Nangaritza Canton Pachicutza, 18 Oct 1991, *Palacios 8278* (MO, US); Tapichalaca Reserve, 29 May 2003, *Clark 8084* (US); Río Tundayme, 12 Dec 2000, *Cerna 405* (MO, US); 4 km E of Paquishsa, *6* Feb 89, *Øllgaard 90432* (AAU, NY); Trail at Romerillo towards Parque Nacional Podocarpus, *6* Dec 1988, *Madsen 75860* (AAU).

PERU. **Amazonas:** 17 kms N of Pedro Ruiz, 14 Jul 1995, *Sanchez Vega 8015* (MO, US); Trail from La Peca to Serrania de Bagua, 13 Jun 78, *Gentry 22847* (MO); Btw El Soro and Playa Granda, 4 Nov 1991, *Sanchez Vega 6027* (MO). **Ayacucho:** San Miguel, 7 Jun 1915, *Cook 1111* (US). **Cajamarca:** Paraguay, 7 Aug 1994, *Leiva 1372* (MO, US); San Ignacio-El Chaupe rd, 4 Jan 1995, *Leiva 1567* (MO, NY, US); San José de Lourdes, 28 Oct 1995, *Rodríguez 670* (MO, US); 4 Apr 1997, *Campos 3750* (US); San Martín, 4 Aug 1994, *Leiva 1337* (US). **Cuzco:** Ceja de Selva, Kosñipata, San Pedro, 28 Mar 1991, *Nuñez 13364* (MO, US); Llactahuaman, N of Río Apuramic, 14 Jul 1998, *Baldeon 3058* (US); Cord. Verónica, 30 Apr 1957, *Raupt-Hirsch P1063* (NY); Machu Pichu, 21 Apr 1957, *Raupt-Hirsch P8321* (NY). **Huánuco:** Carpish, 3 Oct 1950, *Ferreyra 8168* (MO, US); 16 Nov 1979, *Jones 9234* (US); 15 Jun 1958, *Humbert 30946* (NY); Rd along summit of Cerro Carpish, 28 Feb 1978, *Luteyn 5481* (NY); Carpish - Tingo María rd, 10 Jan 1986, *Diaz 1989* (MO, US); Muña, 23 May-4 Jun 1923, *Macbride 4054* (US). **Junin:** Huacapistana, 6 Jun 1929, *Killip 24282* (NY, US); Oxapampa, Aug 1944, *Soukup 2421* (US); Between Tarma and La Merced, 9 Sept 1972, *Canne 268* (US); 51 km NE of Tarma, rd to San Ramon, 19 Dec 1978, *Dillon 1426* (MO). **Loreto:** 20 km NNE of Tingo Maria, rd to Pucallpa, 16 Jul 1981, *Dillon 2643* (MO). **Pasco:** Mallampampa, 22 Jan 1984, *Smith 5842* (MO, US); Oxapampa, 27 Aug 1968, *Riccio 5701* (US); 30 May 1979, *Teppner 18* (US). **San Martin:** La Divisoria, 14 Aug 1946, *Ferreyra 1647* (MO, US); Pedro Ruiz-Moyobamba rd, 29 Jul 1983, *Smith 4497* (MO, US); Tingo María-Pucallpa rd, 17 Nov 1949 to15 Jan 1950, *Allard 21316* (US); 1 Nov 1949–5 Jan 1950, *Allard 22063* (US); Plantación Margarita, 14 Aug 1946, *Ferreyra 1056* (MO, NY, US).

5. ERATO VULCANICA (Klatt) H. Robinson, Phytologia 34:379, 1976.—*Liabum vulcanicum* Klatt, Bot. Jahrb. 8:47, 1887.—TYPE: COLOMBIA. Cauca: Near Puracé, western slopes of mountains, 2600–3200 m, 2 Jan 1884, *F.C. Lehmann 3504* (Holotype: B [destroyed]; lectotype here designated: US!; isolectotype: GH!, digital image seen). *Munnozia vulcanica* (Klatt) H. Robinson & Brettell, Phytologia 28:57, 1974.

Liabum anatinum Benoist, Bull. Soc. Bot., France 84:633, 1938.—TYPE: ECUADOR. Pichincha: San José de Minas, flowers yellow, 3 Mar 1931, *R. Benoist 3962* (Holotype: P; isotypes: PC). *Munnozia anatina* (Benoist) H. Robinson & Brettell, Phytologia 28:56, 1974.

Liabum insigne Badillo, Bol. Soc. Venez. Cienc. Nat. 10: 313, 1946.—TYPE: VENEZUELA. Merida: Bosques húmedos, Los quebraditos, arriba de Jají, 2590 m, 21 Apr 1944, *J. Steyermark 55981* (Holotype: VEN; isotypes: NY(2)!) [type from VEN was seen as digital image].

Coarse herbs to shrubs, 1–4(—5)m tall, sap milky. *Stems* terete, sometimes hexagonal when dry, brownish to reddish, hairs scattered to dense, stiff, white; internodes variable in length usually 3.0–15.0 cm; stipules 0.6–2.0 cm long, scarcely emarginate, hairs scattered, particularly along margins. *Leaves* dark to light green adaxially, paler abaxially; petioles 1.0–17.0 cm long, often reddish to purplish; blades ovate to very broadly ovate, mostly 7–27 × 3–26 cm, main veins 5–7(–10), base rounded, truncate, attenuate, or cordate, occasionally indented or asymmetrical, margins usually slightly to strongly dentate; apices acute to shortly and sharply acuminate; both surfaces sparsely to densely strigose or pubescent, hairs short, appressed. *Inflorescence* terminal, cymose to subumbellate; peduncles 1–13 cm long, densely hispid, hairs stiff, white to light brown. *Heads* broadly campanulate, usually 0.8–1.7 × 1.3–2.5 cm. *Involucral bracts* 50–80 in 4–6 series, triangular to oblong with tufts of arachnoid tomentum at the apices; outer bracts 7.0–11.× 2.5–3.5 mm, triangular to lanceolate, main veins 7, margins ciliate, apices acute, herbaceous to 4.0 mm; inner bracts 9.0–10.0 × 1.5–2.5 mm, oblong to lanceolate with hyaline margins, apices rounded. *Ray florets* 120–225; corollas yellow, 12.5–14.0 mm long, tubes 4.0–5.0 × 0.25 mm, sparsely puberulous above; lamina 7.5–10.0 × 0.5 mm, apical teeth 3, ca 0.3 mm long; styles 7.0–7.5 mm, style branches 1.5–2.5 mm. *Disk florets* 25–100; corollas yellow, 7.0–8.0 mm long, tubes 3.0–4.8 × 0.5 mm, sparsely puberulous distally, throat 3.2–4.0 × 2.0–3.0 mm, lobes 2.0 mm long; stamens 7.0–8.5 mm long, thecae 2.5 mm long, black, apices 0.4 mm, acute; styles 8.5 mm, style branches 1 mm, apices acute. *Achenes* four-sided, 1.2–1.8 × 0.5 mm, dark brown, glabrous. *Pappus* of 27–48 setae, 4–7 mm long, slender, persistent.

Distribution and Habitat. *Erato vulcanica* is native to Colombia, Ecuador, and Venezuela where it is found in open, disturbed, or secondary forest, along forest edges and slopes, near streams, or along the roadside, often in wet environments in open sun to part shade. This species is often locally abundant and is found at elevations from 1100–3800 meters, rarely as low as 255 meters. Fig. 9.

Phenology. This species has been collected in flower during every month of the year, but in Colombia and Venezuela it is most commonly collected in June and July.

Notes. *Erato vulcanica* can be distinguished from other species in the genus by its largish heads bearing involucral bracts with prominent tufts of arachnoid tomentum, but without stiff hairs on both surfaces of the bracts. Like *E. sodiroi* it has seven main veins in the involucral bracts but it has a glabrous achene while *E. sodiroi* has a puberulous one.

This species is variable in the length of its peduncle. In Ecuador in parts of Napo, Sucumbios, and Carchi the peduncles are much longer than the usual 3–7 cm, regularly reaching 8–10 and sometimes up to 13 cm long. Some might chose to recognize these populations as a separate species, but it seems more like a local variant. Also, two or three specimens in this same area have involucral bracts that are glabrous.

Representative Specimens Examined. COLOMBIA. **Antioquia:** Páramo de Sonsón, 8 Jan 1956, *Garganta Fabrega 2116* (US); de La Ceja a Sonsón, 12 Apr 1951, *Romero-Castañeda 2380* (AAU); Sonsón-Nariño rd km 11, 1 Apr 1987, *Zarucchi 5210* (MO, NY, US); Granada-San Carlos rd, 21 Feb 1989, *MacDougal 4121* (MO, US); Las Palmas, 27 May 1948, *Gutierrez 171* (US); La Planada Reserve, 25 Jul 1986, *Gentry 55129* (MO, US); Rio Medellín, 27 Jan 1984, *Juncosa 1966* (MO, US); 10 km NE Sonsón, 27 Mar 1979, *Luteyn 7148* (NY, US); Nutibara-Murri rd km 15.5, 22 Sep 1987, *Zarucchi 5605* (NY, US); paraje Paramitos, Jul 1951, *Uribe 2140* (US); San Jose de San Andreas, 1 May 1948, *Correa 30* (US); Vereda La Corrala, 27 Apr 1987, *Escobar 7590* (US); between Yarumal and the Llanos de Cuiba, 20 Feb 1942, *Metcalf 30139* (MO, US). **Caldas:** Las Brisas to La Carbonera, 16 Oct 1946, *Cuatrecasas 22182* (US); La Selva, 13 Jan 1946, *Von Sneidern 5480* (US); 21 km ESE of Manizales, 16 Jul 1965, *King 5976* (NY, US); Salento, 27 Jul 1922, *Killip 8825* (NY, US); Pinares above Salento, 2–10 Aug 1922, *Pennell 9402* (NY, US); Nevado del Ruiz, 15–16 Jul 1965, *King 5966* (NY). **Cali:** Jugar, near La Habana, 27 Feb 1969, Ramos 3674 (MO). **Caqueta:** 29 km SE of Guadalupe on rd to Florencia, 9 Jan 1974, *Davidse 5607* (MO, NY); 30 km SE of Guadelupe, 9 Jan 1974, *Gentry* (AAU). **Carpinterias:** Forest between the cerros de Muchique y Altamira, 15 Jul 1939, *Arbelaez 6132* (US). **Cauca:** Coconuco – Popayan rd, 19 Jun 1922, *Pennell 6899* (US); "La Gallera" Micay valley, 1 Jul 1922, *Killip 7965* (NY, US); Cerro Munchique, 5 Nov 1968, *Espinal 3194* (CUVC, MO, US); "San Jose" San Antonio, 30 Jun 1922, *Pennell 7563* (NY, US); Tambo, 13 Nov 1946, *Haught 5246* (US); 22 Km NW of El Tambo, 3 Jun 1977, *Olsen 516* (NY); Parque Nacional Munchique, 25 Apr 1979, *Luteyn 7437* (NY); Rio Palo, 15 Dec 1944, *Cuatrecasas 19324* (MO). **Choco:** Cerro del Torra, 8 Aug 1988, *Silverstone-Sopkin 4190* (MO, NY, US); un lugar denomina do La Mansa, 21 Jan 1949, *Molina 19Ch-31* (US); Rd Ansermanuevo-San José del Palmer, 18 Feb 1977, *Forero 2891* (MO, NY). **Choco-Antioquia:** headwaters of Rio Duro, 4 Mar 1944, *Fosberg 21534* (US). **Cundinamarca:** El Colegio, 13 Jul 1979, *Stuessy 5529* (US); 21 km NW of Facatativa, 14 Jul 1965, *Kinget al. 5934* (NY, US); 24 km NE of Fusagasuga, 19 Jun 1965, *King 5673* (NY, US); Salto de Tequendama, 1–3 Oct 1938, *Cuatrecasas 256* (type of fma. macrolepis Cuatre., holotype: US, photo of holotype: NY); 20 Aug 1942, *Schultes 4032* (US); Apr 1972, *Barclay 3309* (US); Tequendama Falls, near Bogota, 27 Feb 1945, *Schiefer 469* (NY); Sibate, 23 Jun 1944, *St. John 20527* (US); San Francisco, 7 Mar 1985, *Sanabria 75* (US); 15 km NW of Medina, Gazaunta Valley, 24 Sep 1944, *Grant 10275* (NY, US). **Huila:** Guadalupe en Resina, 20 Mar 1940, *Arbelaez 8377* (US); E of San Antonio, 26 May 1944, *Little 7950* (US); E of Neiva, 1–8 Aug 1917, *Rugby 557* (NY); Around Mehrenberg rd from Popoyan, 6 Jul 1984, *D'Arcy 15615* (MO). **Medellin:** Santa Elena, 20 Nov 1946, *O'Donoghue 50* (US). **Meta:** Rio Grande (?) S of Cordillera de las Cruces, 21 Aug 1943, *Fosberg 20880* (US). **Nariño:** Ipiales, 5 Aug 1939, *Barriga 7781* (US); Pasto-Sandona Rd, 31 May, *Vogelmann 2018* (US); Rd Tuquerres-Tumaco, 3 Apr 1989, *Smith 1535* (US); Victoria, 23 Sep 1944, *Ewan 16185* (US); La Planada Biological Reserve, 7 Km S of Chucunez, 10 Aug 1990, *Luteyn 13990* (NY). **Putumayo:** between Sachamate and [pueblito] San Antonia, 7 Jan 1945, *Ewan 16685* (US); San Pedro, 3 Aug 1963, *Chindoy 171* (US); Sibundoy-Moccoa rd, 15 Mar 1953, *Schultes 18821* (NY, US). **Quindo:** Salento, 25–31 Jul 1922, *Pennell 8908* (US); 29 Jul 1922, *Killip 8963* (US). **Santander:** Charta, 1–11 Feb 1927, *Killip 19130* (NY, US); Pamplona-Bucaramanga rd, 15 Jul 1968, *Barkley 380249* (US); Bucaramanga, 5 May 1983, *Croat 56528* (MO, US); near Las Vegas, 21–23 Dec 1926, *Killip 16080* (NY, US); Between Piedecuesta and Las Vegas, 19–23 Dec 1926, *Killip 15529 (NY, US).* **Tolima:** btw Cajamarca and summit of Divide, 27–28 Mar 1939, *Killip 34658* (US); Fresno, 16–17 Jul 1965, *King 5996* (NY, US); Nevado del Ruiz, 15–16 Jul 1965, *King 5966* (US). **Valle:** Alban, 17 Aug 1941, *Dugand 3032* (US); Rd El Cairo-Rio Blanco, 31 Mar 1988, *P. Silverstone-Sopkin 3853* (US); Rio Cali, 2 Nov 1944, *Cuatrecasas 18464* (US); Cuesta de Tocota, Dec 1905, *H. Pittier 733* (US); Rio Guadalajara, 27 Feb 1969, *Cuatrecasas 27594* (US); Rd to Cerro del Inglés, 22 Jul 2004, *Pedraza* 1115 (NY).

ECUADOR. **Carchi:** El Carmen to Chical rd, Agua Amarilla, 8 Jul 2003, *Clark 8538* (US); NW side of Río Gualpi Chico, 25 Jan 1988, *Hoover 3059* (MO, US); Páramo del Angel, Tulcán to Chicai Rd, 26 Feb 1995, *Ortiz 430* (NY); Julio Andrade-El Carmelo rd, turn off towards El Ajún, 10 Aug 1990, *92372 Jørgensen* (AAU, US); Above San Marcos de los Coaiqueres, 7 Feb 1985, *Øllgaard 57457* (AAU); 19 Jan 1983, *Barfod 41505* (AAU). **Imbabura:** Pimampiro, 17 Sept 1988, *Zak 3816* (AAU, MO, US). **Napo:** Baeza-Lago Agrio Rd, 7 Aug 1980, *Øllgaard 35625* (AAU, US); Hollín-Loreto rd, km 40–50, 10–22 Oct 1988, *Hurtado 658* (AAU, MO, US); Reserva Ecológica Antisana, 2 Jul 1995, *Tirado 1583* (MO, QCNE, US); Btw Tena and Papallacta, 12 Jan 1981, *D'Arcy 14111* (MO, US); Slopes of Guagua Urdu above Río Borja, 25 Sep 1980, *Holm-Nielsen 27025* (AAU, US); Río Panteor SW of Borja, 22 Sep 1980, *Holm-Nielsen 26688* (AAU). **Pichincha:** Near Quito, Valle Chillos, 1906, *Mille 591* (NY, US). **Sucumbios:** Julio Andrada-La Bonita rd, 6 Mar 1992, *Funk 11085* (US); El Salado, Río Quijos, 27 May 1990, *Cerón 10010* (MO, US); San Rafael, NE of cascada, 11 Oct 1990, *Jaramillo 13201* (NY); Playón de San Francisco, rd to Santa Bárbara, 30 Dec 1980, *Jaramillo 3960* (AAU).

VENEZUELA. **Mérida:** La Carbonera, Jul 1957, *Aristeguieta 2830* (NY, US); Btw Merida and La Azulita, 15 km SE of La Azulita, 7 Aug 1982, *Croat 54824* (MO, US). **Táchira:** Btw Alcitran and San Vincente de la Revancha on rd to Las Copas, 3 Jan 1989, *Hahn 4951* (NY, US); Btw Bramón y Las Delicias, 15–16 May 1967, *Steyermark 98292* (NY); Mata Mula, N of Delicias, 26 Jul 1979, *Steyermark 118738* (MO, US); 20–25 KM.

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