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 género *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 monofiletico hermano a *Philoglossa*. El análisis filogenético utilizó *Munnozia* Ruiz & Pavon, *Chrysactinium* (H.B.K.) Wedd. y *Philoglossa* DC. como grupos externos. La filogenia confirma *Erato* como un grupo monofiletico, pero los relaciones dentro de *Erato* solo tienen soportes débiles. Creen que el género es una radiación reciente a causa de la semejanzas morfológicas entre de las especies y porque ocurren en unos de las áreas mas jóvenes de los Andes.

**KEYWORDS:** Asteraeae, biogeography, Compositae, endemic, phytogeny, 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 *Liabium* 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 (1)
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), bulbous (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 pubescent. Arachnoid and purplish hairs (0), stiff, erect, white hairs (1), appressed white hairs (2), long bulbous 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 squarrel or awns in one series (1), absent (2), short, multiseriate awns (3)
22. Pappus persistence. Persistent (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 performed using full heuristic searches with PAUP* (Swofford 2002). No weighting was used. Maximum parsimony analysis (with ACTTRAN) 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, c.i. = 0.804, r.i. = 0.655). Figure 2 is the bootstrap consensus tree. Erato is monophyletic and sister to Philoglossa; E. polymnioides...
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**


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 lackingomentum; 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 Chrysactinium are shown as sister taxa because of information from a previous publication (Kim et al. 2003; see text for details).

Munnozia

Chrysactinium

Philoglossa

E-polymnioides

E-stenolepis

E-costaricensis

E-vulcanica

E-sodiroi

5 changes

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

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. Involutural bracts with 7 main veins; arachnoid tomentum at apices of involutural 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
3. Achenes puberulous, with tufts of arachnoid tomentum; surfaces of involutural bracts with hairs; inner involutural bracts long, length/width ratio > 7; ray floret tubes glabrous; Perú ............................................... 3. E. stenolepis
4. Heads 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. Bracteas involucrales con 7 nervios principales; tomento aracnoide en el ápice de las bracteas 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 disco 110–150; tomento principalmente en el reverso de las bracteas involucrales; Ecuador .......................................................... 2. E. sodiroi
3. 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
4. Heads involucrales con 5 nervios principales; tomento aracnoide ausente o raro ................................................ 3
3. Capítulos largos, con ca. 120 flores del disco; bracteas involucrales sin tomento aracnoide; bracteas involucrales pubescentes en ambas superficies, y bracteas interiores largas, largo/ancho > 7; tubo de las flores radiadas glabros; Perú .... 3. E. stenolepis
4. Capítulos pequeños, con < 40 flores del disco; bracteas involucrales raramente o nunca con tomento aracnoide; bracteas involucrales glabras o con pocos pelos; y bracteas interiores cortas, largo/ancho < 7; tubo de las flores radiadas pubescente .............. 4
5. E. polymnioides
5. Cappitulos muy pequeños, con 11–16 flores del disco; flores radiadas 13.0–16.0 mm de largo; bracteas involucrales a veces con un poco de tomento aracnoide; arbusito 0.5–3.0 m de altura; pedúnculos cano-sericeos; 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, E. Almada 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 latum, flores disici 11–16, bracteae involucrae apice persaepe cum caespibus tomenti aracnoidei, bracteae externae 5 ad 6 mm X 1.5 ad 2.0 mm latae, flores radii corolla longiora, 13 ad 16 mm, flores disici 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 X 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 X 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 X 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 X 1.2–2.0 mm, apices rounded to acute. Ray florets 80–113; corollas yellow, 13–16 mm long, tubes 4.0–5.5 X 0.25 mm, sparsely puberulous distally; lamina 9.0–10.5 X 0.3–0.5 mm, apical teeth 3, 0.5 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 X 0.5 mm, throats 4.5–5.5 X 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
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-
er in December, February, March, May, June, and August.

Notes. *Erato costaricensis* can be distinguished from other species in the genus by its relatively 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.


COSTA RICA. Panamá: 15 km NE of Santa Domingo, 31 Dec 1974, Taylor 17868 (US); 18 Aug 1967, Taylor 4539 (MO, NY, US); San Jose: La Hondura, 2-4 Mar 1924, Maxon 8030 (US); 17 Aug 1994, Kress 4810 (US); Varablanca intersection on the rd to Puerto Viejo, 28 Feb 1986, Utley 5173 (MO, US); S of Tapanti, 10 Jan 1980, Funk 3063 (US); Monteverde, Mirador La Ventana, 9 Feb 1994, Le Péz 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 Río Culebra, 11 Feb 1979, Himmel 6146 (MO, PMA).


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 1.0–1.3 × 1.2–2.5 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 hissute 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 keeled 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 road-sides, 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.


3. **ERATO STENOLEPSIS** (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 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 acumenate; 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 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 branch-es 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.

**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).


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; inter-nodes 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...
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 ca 7.0 × 1.5 mm, lanceolate to oblanceolate, 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
yellow, 6.5–7.0 mm long, tubes 3.0–3.5 × 0.5 mm, hairy, throat 3.5 × 2.5–3.5 mm, glabrous except at base, lobes ca. 2.5 mm long; stamens 6.0 mm long, theca 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.

**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.


**Fig. 8.** Map showing the distribution of *Erato polymnioides* DC.

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


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 axially, 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 slight- ly to strongly dentate; apices acute to shortly and sharply acuminate; both surfaces sparsely to densely strigose or pubescent, hairs short, appressed. Inflores- cence 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, trian- gular to oblong with tufts of arachnoid tomentum at the apices; outer bracts 7.0–11.0 × 2.5–3.5 mm, trian- gular 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. Disc 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.


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