A Revision of *Erato* (Compositae: Liabeae)

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Communicating Editor: Thomas G. Lammers

**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 las relaciones dentro de *Erato* solo tienen soportes débiles. Creén que el genero es una radiación reciente a causa de la semejanzas morfológicas entre de las especies y porque ocurren en unos de los áreas mas jóvenes de los Andes.

**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.

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

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 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. Figure 2 is the bootstrap consensus tree. *Erato* is monophyletic and sister to *Philoglossa*; *E. polymnioides*...
Table 2. Data matrix for Erato.

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<th>Taxa</th>
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<td>Erato polymnioides</td>
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<td>Erato stenolepis</td>
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<td>Erato costaricensis</td>
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<td>Erato vulcanica</td>
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<td>Erato sodiroi</td>
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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 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 yellow, 7.0–9.0 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 stamates 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. **Achene** 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 columella 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*
3. Heads small, < 40 disc florets; involucral bracts rarely or never with 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*
4. Heads very small, 11–16 disc florets; ray corollas 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 principales; tomento aracnoide en el ápice de las brácteas involucrales .......................... 2
2. Aqueños 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 brácteas involucrales; Ecuador .......... 2. *E. sodiroi*
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 largas, largo/anchura >7; tubo de flores radiadas glabros; Perú .......................... 3. *E. stenolepis*
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; arbusito de 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, *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 involucrales apice pserapea 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; peduncle 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* 50–75 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
Erato costaricensis. Habit, head, disc corolla, stamens and style, ray corolla and style, disc style, achene and pappus. Illustration by Alice Tangerini (US).

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-
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.

Representative Specimens Examined. **COSTA RICA.** Alajuela: Vera Blanca - San Miguel rd, 17 Aug 1994, Kress 4810 (US); Vera-blanca intersection on the rd to Puerto Viejo, 28 Feb 1986, Almeda 5172 (US); Cartago: Tapantí Hydroelectric Project, 25 Jun 1976, Utley 5173 (US); S of Tapantí, 12 Dec 1969 Burger 6790 (MO); 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 (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).


Coarse herbs, occasionally scrambling or shrub-like, usually 1–3(–5) m tall, sap milky. **Stems** terete, sometimes hexagonal when dry, brownish, pubescent 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 hisrate, hairs long; lamina 15.5–22.5 × 1.0–1.5 mm, apical teeth 3, 0.5 mm long; styles 10 mm, style branches 0.7 mm, apices acute. **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 hisrate 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 siodroi* 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.


**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).


**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).

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


ECUADOR. Bolivar: Balsapampa, 19 May 1968, Harling 9645 (US). Cañar: 78 km W of Canar, 23 Jan 1979, King 7779 (US); Rd El Triunfo-Canar, 5 Feb 1976, King 7002 (NY, US); 40 km E of bridge at Guayquil, 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, Caron, E-3152 (MO, NY, US); Pallatanga, Jul 1903, Sodiro s.n. (NY); 20 Jul 1935, Madsen 350 (MO); 13 kms N of Nono, 21 Jul 1977, Swensen 4861 (MO); 11 km W of Tandapi, 26 Oct 1974, Lawesson 43957 (US); 30 Jul 1980, Arroyo 7780 (US); 20 Jul 1985, Asplund 2439 (MO, US); 27 Jan 1985, Samples 7091 (US).

Erato polymonioides DC.

Fig. 8. Map showing the distribution of Erato polymonioides (Klatt) H. Rob.

Erato vulcanica (AGP) (Klatt) H. Rob.

Fig. 9. Map showing the distribution of Erato vulcanica.


Liabium insignis Badillo, Bol. Soc. Venez. Cienc. Nat. 10: 313, 1946.—TYPE: VENEZUELA. Merida: Bosques húmedos, Los quebraditos, arriba de Japi, 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; inter- nodes 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. 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, triangular to oblong with tufts of arachnoid tomentum at the apices; outer bracts 7.0–11.0 × 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.

**ACKNOWLEDGEMENTS.** We thank the following herbaria for the use of specimens and for information and digital images of types (AAU, BAF, BP, F, G, GH, K, MO, NY, P, PMA, QAP, QPLS, US, VEN). Without such inter-institutional cooperation, revisions would be impossible. We also thank Tom HOLLOWELL, for assistance with graphics, and Pedro Acevedo for his help with the Spanish translations. The Latin diagnosis was written with the help of Elizabeth Wolfram and Harold Robinson and the illustrations were prepared by Alice Tangerini. We thank Drs. Carol E. Ceron M., Director ad honorem del Herbario “Alfredo Paredes” (QAP) for taking the time to make a special trip to visit QPLS and find the botanic material; John Clark (US) helped facilitate that search. We thank a number of individuals who spent time searching their herbaria for types: Zoltán Barina (BP), Mireya Correa (PMA), B. C. Giberti (BAC), Nicholas Hind (K), Fernand Jacq uemoud (G), Christine Niezgodzka (F), John Pruski (MO), Leyda Rodriguez (VEN), Amber Swanson (GH), Anne-Elizabeth Wolf (P), and Emily Wood (GH). This study was undertaken as part of the Research Training Program at the National Museum of Natural History, funded by the National Science Foundation; unfortunately this program has now been discontinued at NMNH.

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